1950

Helminthosporium victoriae M. and M. and some other graminicolous species

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UMI
HELMINTHOSPORIUM VICTORIAE H. AND H.

AND SOME OTHER GRAMINICOLOUS SPECIES

by

Francos Lucille Meehan

A Dissertation Submitted to the
Graduate Faculty in Partial Fulfillment of
The Requirements for the Degree of
DOCTOR OF PHILOSOPHY

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Approved:

Signature was redacted for privacy.

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Iowa State College

1950
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INTRODUCTION

Species of *Helminthosporium* Link have been included among the more destructive cereal pathogens for nearly a century. Since Rabenhorst first described the barley stripe fungus in 1856 (36), some half dozen additional species have been characterized and associated with serious diseases of cereal grains over all parts of the world. Wherever climatic conditions have been favorable for their development, these fungi have ranked with the rusts and smuts in causing damage to graminaceous crops.

A wide range of host specificity is represented among the graminicolous species of *Helminthosporium*. Several of the cereal pathogens of this group are limited to a single host species, while others parasitize graminaceous hosts of a number of genera. The highest degree of host specificity so far attained in the genus is that shown by *H. victoriae*, the fungus causing "*Helminthosporium* blight" of oats, first described in 1946 (25). This species is apparently confined in its pathogenicity to but one variety of oats and derivatives of this variety. Because of this limitation, *H. victoriae* was unknown until great areas had been planted for several successive seasons to oat varieties all derived from this single susceptible parent. *Helminthosporium* blight developed so rapidly that it reached the proportions
of a major plant disease within 2 years after its first appearance, and now after 5 years, it has almost disappeared for lack of susceptible varieties. The short but colorful history of this disease has provided some impressive examples of the pitfalls of plant breeding, and the causal fungus itself exhibits some interesting characteristics.

The present work has been undertaken to bring together the information collected on this subject over a period of several years at the Iowa Agricultural Experiment Station in cooperation with Dr. H. C. Murphy of the United States Department of Agriculture, Bureau of Plant Industry. The purpose of this paper is to describe more fully the fungus, Helminthosporium victoriae, and to compare it morphologically, pathologically and physiologically with congeneric species commonly found on oats and with similar species on other grassyous hosts.
In the course of routine germination testing of grass seed samples in the Iowa State College Seed Laboratory, isolations of various fungi were made in order to study the fungus flora of these seeds. Among the isolates obtained in 1942 from timothy and bahia grass seed were several cultures of a greenish-spored species of Helminthosporium. This fungus became increasingly prevalent on timothy seed until 1945-46 when hardly a sample could be found free of it. In November, 1944, the first isolation of the fungus from oats was made from a seedling of the variety Tama grown in a sand-germination test. The seedling showed browning of the mesocotyl and radicle, but since the scab organism, Fusarium graminearum Schwan, was also obtained from the isolation, the necrosis was thought to have been caused by the latter fungus, since the Helminthosporium was not one of the species known to be pathogenic to oats. In January, 1945, however, the striking pathogenic action of this Helminthosporium isolate was observed when 20 tester varieties of oats, barley, and wheat were inoculated in the greenhouse with a suspension of blended mycelium and spores; the Victoria oat variety and 5 Victoria-hybrid derivatives included in the tester group were killed, while the older oat varieties, newer Bond-hybrid selections, barley and wheat were unaffected.
In April, 1945, following these first inoculation experiments, the fungus was isolated from necrotic oat seedlings in the first and second leaf stages from a number of Iowa fields. In May of that year, Dr. I. N. Atkins of Texas Experiment Station found what appeared to be a new disease of oats in Texas, affecting especially the varieties Fultex and Victorgrain. He observed that the culms of diseased plants seemed to collapse near the base, and that the crown and lower internodes of these plants were discolored. Dr. Atkins supplied infected adult plants collected from a 200-acre field of Fultex, where the disease was of considerable importance. The new Helminthosporium was isolated from the roots and basal stem parts of these plants. More than 250 oat varieties and selections (including 100 Victoria derivatives) were inoculated in the greenhouse in 1945, and numerous field observations were made of oat varieties in the first heading and later stages of maturity. Symptoms typical of those attributed to the new fungus were observed in all varieties and selections possessing the Victoria resistance to crown rust (Puccinia coronata avenae (Corda) Erikss. and E. Henn.) growing in nurseries at Ames and Kanawha, Iowa, and in a number of community trials throughout the state, as well as in the greenhouse tests. The yields in some Iowa oat fields in 1945 appeared to be reduced as much as 50 per cent by this Helminthosporium infection, and even heavier losses occurred in 1946. Without exception, all
varieties and selections lacking "Victoria-type" of crown rust resistance were resistant to the new disease.

The new oat pathogen was described and named *Helminthosporium victoriae* in 1946 (26). This name for the species was proposed in view of the apparent exclusive susceptibility of varieties possessing Victoria-type resistance to crown rust. Had it not been for *Helminthosporium* blight, a record oat crop would have been harvested in Iowa in 1946, since growing conditions were ideal, and rusts and smuts were virtually absent; instead, there were only average yields. The disease was known to be present in 19 states in that year, from Texas to New York, and from Florida to Idaho.

Although recommendations were made in 1946 for a shift to Bond derivatives and older *Helminthosporium*-resistant varieties such as Marion, not until 1948 was enough seed available for Iowa and neighboring states to make a complete change to resistant varieties. Eighty per cent of Iowa acreage was planted to Victoria-Richland crosses in 1947, but in 1948 when Clinton seed was plentiful, less than 5 per cent was devoted to Victoria derivatives. In 1949, Bond derivatives such as Clinton, Benton, Bonda, and Mohawk replaced other

---

1 The variety Victoria (C.I. 2401) was introduced from South America in 1927 for breeding purposes because of its resistance to disease, especially crown rust. The Victoria-Richland crosses played an important role in increasing oat yields from 1942-45 by virtue of their resistance to both rust and smut. In 1945, 98 per cent of the oat acreage of Iowa and over 50 per cent of the United States acreage was devoted to varieties derived from these crosses.
varieties in most of the oat-growing areas of the United States. In the southern states, however, the lack of agronomically suitable Bend derivatives and the threat of race 45 and similar races of crown rust have encouraged the continuation of planting Victoria derivatives in these areas. In the western and northwestern states where oats are grown under dry land conditions or under irrigation, the damage by Helminthosporium victoriae has proved to be less severe and some Victoria-Richland derivatives are still grown. The acreage shifts in varieties and comparative yields during the years from 1942 to 1943 are shown graphically in figs. 1 and 2, respectively.

This brief summary of the recent origin, development, and decline of a serious oat disease emphasizes the importance of evaluating all the potential factors in a disease control problem based on plant breeding. With the development of the Victoria-hybrid derivatives utilizing the source of resistance to certain races of crown rust furnished by the variety Victoria, susceptibility to Helminthosporium blight was unknowingly introduced. The Victoria resistance to most races of crown rust is of the hypersensitive type and is controlled by a single genetic factor. Susceptibility to H. victoriae is apparently either dependent upon the same factor, or the 2 factors are completely linked. Hence this valuable source of crown rust resistance is lost if this close relationship cannot be broken. Recent work by Welsh (45) in Canada has indicated that Victoria resistance to certain races of
Fig. 1. Varietal shifts in oat acreage in Iowa from 1921-1928.
Fig. 2. Comparative yields of 3 oat varieties in Iowa from 1941-1948.
crown rust including apparent bio-types of race 45 can be retrieved without carrying over *Helminthosporium* susceptibility, but there has so far been no indication of breaking the linkage as far as resistance to most races is concerned. The development of *Helminthosporium* blight has provided a convincing demonstration to plant breeders and plant pathologists of the rapidity with which a disease can spread to epidemic proportions when wide areas planted to similar germ plasm allow tremendous buildup of inoculum. Stakman, among others, has commented in reference to this specific example, that never again should broad adjoining acres be planted simultaneously to varieties of similar resistance types.

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1In an address to the Upper Mississippi Valley Section of the Phytopathological Society (1946).
LITERATURE REVIEW

The genus Helminthosporium has a very voluminous literature, but both the generic limits and the speciation are still matters of controversy. Hence a thorough review of the literature was necessary in order to preclude the possibility that *H. victoriae* had been already described. For the purposes of this paper, however, the discussion of literature has been confined to those works referring to species reported from oats. Pertinent data from those references are assembled in Table 1. Species from various graminous hosts that were found to be similar in some respects to *H. victoriae* are treated with their literature in the section on "Comparison of Species".

Of the great number of graminicolous *Helminthosporium* species that have been described, surprisingly few have been listed as either saprophytes or parasites on oats. Harvey (13), in 1895, observed yellowing and dying of oat plants in Maine which he attributed to a species identified by Ellis as *H. inconspicuum* C. and E. var. *brittanicum* Grove. As pointed out by Drechsler (9), the fungus described by Harvey neither compares closely with that species as given by Saccardo, nor is his illustration of a single spore adequate for identifying it with any certain species. The
condial dimensions according to Harvey's measurements are within
the mode found for \textit{H. victoriae}, and spores of the latter formed
under rather dry conditions frequently show no more than 5 septa
(the range reported by Harvey being 1 to 5), but the pathological
effects produced by the 2 organisms are apparently distinct. The
species \textit{H. inconspicuum} is considered by Drochslar to be synonymous
with \textit{H. tenuicium} Pass.

DaCamara (6) described a species occurring on culms of \textit{Avena
sterilis} L. in Portugal in 1936, which he named \textit{Helminthosporium
olisipponense} Pass., and connected with the ascigerous form \textit{Pyrenophora
polytricha}, to which binomial he appended "n.sp.". Drochslar (11)
showed \textit{Pyrenophora} as defined by Fuckel to be a more suitable genus
than \textit{Pleospora} Rabenh. for the ascogenous stages of the \textit{indical-
spored} species of \textit{Helminthosporium}, and cited \textit{Pleospora polytricha}
(Wallr.) Tul., as characteristic of this relationship. DaCamara's
choice of name for his fungus was unfortunate, since it causes con-
fusion with \textit{Pleospora polytricha} already named. The presence of
\textit{Helminthosporium olisipponense} on oat culms was not mentioned as
causing any damage, and the spore characteristics described are
not similar to those of \textit{H. victoriae}.

Occasional references have been made in the literature to
\textit{H. sativum} P. K. and B. as a weak, or, in a few cases, destructive
parasite of cats. The damage reported is usually in the nature of
<table>
<thead>
<tr>
<th>Species</th>
<th>Conidial Measurements</th>
<th>Color of Conidia</th>
<th>Shape</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Length</td>
<td>Diameter</td>
<td>No. of septa</td>
</tr>
<tr>
<td>H. victoriae</td>
<td>40-130</td>
<td>11-25</td>
<td>4-11</td>
</tr>
<tr>
<td>H. avenae</td>
<td>75-175</td>
<td>15-16</td>
<td>4-9</td>
</tr>
<tr>
<td>H. sativum</td>
<td>25-134</td>
<td>14-30</td>
<td>3-10</td>
</tr>
<tr>
<td></td>
<td>(60-120)</td>
<td>(15-20)</td>
<td></td>
</tr>
<tr>
<td>H. conspicum</td>
<td>40-80</td>
<td>15</td>
<td>1-5</td>
</tr>
<tr>
<td>var. Britanicum</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>H. olisipponense</td>
<td>37-65</td>
<td>8-11</td>
<td>6-9</td>
</tr>
<tr>
<td>H. sp. represented by numerous Iowa</td>
<td>55-110</td>
<td>11-16</td>
<td>6-10</td>
</tr>
<tr>
<td></td>
<td>(75)</td>
<td>(14.5)</td>
<td>(7)</td>
</tr>
<tr>
<td>H. sp. culture no. 97</td>
<td>50-92</td>
<td>11.5-15</td>
<td>5-11</td>
</tr>
<tr>
<td></td>
<td>(70)</td>
<td>(14.5)</td>
<td>(7.5)</td>
</tr>
<tr>
<td>H. sp. culture no. 194</td>
<td>30-79.6</td>
<td>13-15.9</td>
<td>6-8</td>
</tr>
<tr>
<td></td>
<td>(66.5)</td>
<td>(14.8)</td>
<td>(6.9)</td>
</tr>
<tr>
<td>H. sp. culture no. 282</td>
<td>50-250</td>
<td>11-15</td>
<td>6-10</td>
</tr>
<tr>
<td></td>
<td>(including secondary elongation)</td>
<td></td>
<td>(8)</td>
</tr>
<tr>
<td>Color of Conidia</td>
<td>Shape of Conidia</td>
<td>Mode of Germination</td>
<td></td>
</tr>
<tr>
<td>-----------------</td>
<td>-----------------</td>
<td>-------------------</td>
<td></td>
</tr>
<tr>
<td>Light green to olivaceous; typically uniform color but occasionally with darker ad cells</td>
<td>Widest at or near the middle; usually more broadly rounded at the base than at the distal end; slightly curved; hilum protruding; rather thin walls.</td>
<td>1-2 polar germ tubes, one emerging at apex, the other adjacent to hilum</td>
<td></td>
</tr>
<tr>
<td>Sub-hyaline to fuliginous</td>
<td>Cylindrical or sub-cylindrical; rounded or hemispherical ends; largest diameter often at the base; mostly straight; hilum enclosed</td>
<td>1-3 germ tubes from each end cell at oblique angles; germination also from middle segments</td>
<td></td>
</tr>
<tr>
<td>Dull olive to brown; pale area commonly at each end</td>
<td>Widest near the middle, tapering toward hemi-ellipsoidal ends; slightly curved; tend to be asymmetrical around the longitudinal axis; thick exospore</td>
<td>Bipolar</td>
<td></td>
</tr>
<tr>
<td>Brownish</td>
<td>Ellipsoid</td>
<td>Bipolar</td>
<td></td>
</tr>
<tr>
<td>Pale tawny</td>
<td>Fusoid or ellipsoid</td>
<td>Bipolar</td>
<td></td>
</tr>
<tr>
<td>Dark olivaceous, with light haloes in end cells, often heavier and septa</td>
<td>Sub-cylindrical, mostly straight; flat, slightly protruding hilum; thick walls</td>
<td>Bipolar</td>
<td></td>
</tr>
<tr>
<td>Fuliginous to medium gray</td>
<td>Widest near middle; tapering equally toward each end; rather strongly curved; thin walls</td>
<td>Bipolar</td>
<td></td>
</tr>
<tr>
<td>Olive, typically with darker end cells</td>
<td>Tapering toward both ends, but often with a distinct narrowing at the basal segment, these spores appearing bottle-shaped</td>
<td>Bipolar</td>
<td></td>
</tr>
<tr>
<td>Fuliginous or light olivaceous</td>
<td>Tapering very gradually to ends of much-elongated spores; mostly straight; hilum protruding slightly, one on each end of most spores</td>
<td>Bipolar; germ tubes develop directly into conidiophores and bear spores</td>
<td></td>
</tr>
</tbody>
</table>
root or basal stem necrosis, and no definite varietal specificity has been observed. Christensen (4,5,6), in his extensive studies on the parasitism and physiologic specialization of Helminthosporium sativum, found a number of strains, a few of which were capable of attacking oats. According to Hynes (15), prevalence of this species attained epidemic proportions on wheat and oats in New South Wales in 1929; he isolated several distinct forms which varied in virulence to wheat and oat seedlings, but in general he found that oats were very resistant.

Disregarding the spasmodic occurrence of these species of Helminthosporium on oats, H. avenae Eiden is the only member of the genus so far reported which is important as a pathogen of Avena spp. The morphological and pathological aspects of this species have been described in detail by Ravn (39), Drechsler (9), O'Brien and Dennis (32), and Ratheschlag (33). The increasing significance of this species in recent years has been noted by workers in all parts of the world.
INVESTIGATION

Symptoms and Pathogenicity Studies

The presence of *Helminthosporium victoriae* in the host was found to be manifested by well-defined characteristic symptoms, especially evident during the early and late stages in the life of the oat plant. The seedling symptoms observed on plants in the field were identical with those of plants grown from diseased seed in the greenhouse, or of seedlings grown in artificially infested soil, the only difference being that in the last case the killing was more rapid and uniform.

The initial progress of the disease was observed in oat sprouts of susceptible varieties (Tama, Boone, etc.) germinated between moist blotters in large petri dishes from infected seed. The fungus sporulated readily on the seed and on the surrounding blotter under such humid conditions, thus providing a means for its detection. Infected of the mesocotyl region was usually apparent 7 to 10 days after germination of the seed. The first internode and coleoptile became brownish in color, and the scutellum and seminal roots dark brown, so that the general appearance was not unlike that of the "foot-rot" of barley and wheat caused by *Helminthosporium*
satiwm. The most severely infected seeds produced only badly
distorted sprouts which would not emerge in soil plantings. For
comparison, seeds of Clinton oats also were planted between blotters,
and whereas after 14 days at 20° C, the basal portions of Tama sprouts
were almost 100 per cent browned and necrotic, those of Clinton remained
white and firm.

Early in the 1946 season, severe seedling blight appeared in oat
fields throughout Iowa, especially in the southern half of the state.
Such fields were characterized by having numerous plants with reddish-
tan leaves and with off-color green and striped leaves. Examination
of blighted plants disclosed in all cases severe basal necrosis,
browning and rotting of the roots and stems near the ground line.
In contrast with Pythium-injured plants, in which the roots are
usually browned and pruned from the tips upward, those affected by
Helminthosporium victoriae were necrotic from the seed downward. The
Victoria x Rainbow selection (C.I. 2192) and the varieties Overland,
Osage, and Tama were among the oats from Iowa experimental plots
carrying the greatest amount of seed-borne infection in 1945, and
when seed from these plots were planted in sterilized soil in the
greenhouse, there was often from 50 to 90 per cent of the pre- and
post-emergence dying. In 1946, the percentage of seed-borne infection
in samples of susceptible varieties was found to be largely dependent
upon the area where grown, and upon the sources of the seed planted.
Little, if any, distinction could be made as to difference in susceptibility among the numerous varieties and selections possessing the Victoria resistance to crown rust. The striking contrast, on the other hand, between the reactions to *P. victoriae* of 2 sister selections from a (Harloton x Forvie) × D69 Bend cross, one possessing Victoria resistance to crown rust and the other lacking this resistance, is shown in fig. 3.

Inoculum for most of the greenhouse experiments was prepared by scraping the aerial mycelium from 10-day-old agar plate cultures and then resuspending the fungus for 90 seconds in a Waring Blender with distilled water. For infecting sterilized soil in pots, a measured amount of this suspension was poured over the soil in each pot and covered with about 3/4 inch of additional sterile soil and plantings were made immediately. The amount of suspension used per pot was varied in different experiments; the aerial mycelium from one agar plate would usually prevent emergence completely in a 4-inch pot planted with 20 seeds of a susceptible variety. Less concentrated suspensions were used to allow emergence and to study the symptoms of plants as they became infected.

The leaf blades of seedlings growing in infested soil were slower to unroll, and were often darker green in color than those of healthy check plants. At the first, second, or third leaf stages, infected seedlings were characterized by the almost simultaneous
Fig. 3. Mature plants of two sister selections of a (Purinton x Pervic) x D69 Bond cross showing contrasting reactions to natural infection by H. victoriae; 1945 selection on the left, 1946 on the right.
appearance of several symptoms on the first leaf; a faint brown stripe extending the entire length of the blade along the midrib or along one or both edges, a bluish-grey, sometimes streaked, coloration of the area not covered by the stripe, and marginal withering. The first leaf thus affected soon wilted, and the second and third leaves followed in succession, striping and wilting, until the whole plant succumbed. This striping was probably the most easily recognizable symptom of seedling infection by *H. victoriae*. At first barely visible as a faint brown longitudinal discoloration, the stripe usually became yellowish to reddish brown within 1 to 2 days and well-defined in outline, apparently following the vascular elements. A number of leaves with over-all reddish-buff coloration were observed in the field, these being instances in which the stripes covered the entire leaf area. No seedlings which showed the first symptoms of this *Helminthosporium* disease have been observed to survive; almost without exception, the young plants died within a week after appearance of the first stripe. In greenhouse tests, a comparable situation existed in older infected plants but the decline of the host occurred more slowly.

The smooth-margined, full-length striping of leaves with subsequent loss of turgor characteristic of *H. victoriae* infection is to be contrasted to the elongated, irregularly outlined, slightly
sunken, brownish local leaf lesions caused by *H. avenae*, sometimes referred to as the stripe disease of oats. The basal-stem- and root-rot caused by *H. victoriae* is the primary source of injury, with leaf-stripping (fig. 4) being a secondary manifestation of basal infection. Resistant plants in the field at intermediate stages of maturity frequently show leaf discoloration and striping similar to that caused by *H. victoriae*, but apparently due to physiologic causes, so the leaf striping is not an infallible diagnostic character. The term "blight", designating rapid discoloration and death of the tissues over the whole plant, is considered to be the most inclusive common name.

Infection severity in susceptible varieties grown in the greenhouse ranged from killed seeds and barely sprouted distorted plants to apparently healthy month-old plants which began to show striped and wilted leaves. In many severely stunted seedlings the leaves were a bluish-gray color from the time of emergence and withered without becoming striped. Numerous brown and shriveled dead plants from 1 to 6 cm. in height were noted in the field when seedling stand counts were made, and from those *H. victoriae* was readily isolated. In addition to the foliar symptoms, the infected seedlings in the greenhouse and in the field showed the same browning and necrosis of the first internode and associated tissues as described above for sprouts between blotters. In infested soil root pruning was especially severe, and adventitious roots were commonly produced.

Decided contrasts in varietal and species reactions were obtained
Fig. 4. Leaves showing typical striping in susceptible varieties, caused by H. victoriae. Healthy leaf of resistant variety on the left.
else by a somewhat simpler method of soil inoculation: 20 seeds were
planted per pot in unsterilised soil, and 5 days later the mycelial
suspension was poured on the surface of the soil around the bases
of the young seedlings. After having been held in a moist chamber
for 24 hours, susceptible plants showed severe injury, while resis-
tant ones were comparatively unharmed. The foot-rot symptoms were
naturally more pronounced in plants inoculated by this method, and
the striping and wilting of leaves took place more rapidly than with
sub-surface inoculation. The striping and drooping leaves of the
susceptible oat variety Osage may be compared with the healthy
plants of Bond oats and Pentland barley in Fig. 5, all 3 having
been subjected to the same soil-surface inoculation. Very young
seedlings (about 5 days old) gave more uniform and marked reactions
by this method than plants even a few days older; in the latter, the
appearance of symptoms was delayed, and the plants succumbed more
closely.

Similar soil inoculations of barley and wheat plants with
mycelial suspensions of H. sativum cultures caused almost impercepti-
ble, if any, necrosis of the roots and basal stem parts, and no foliar
symptoms. These cultures were pathogenic to barley and wheat when the
spores and mycelium were sprayed on the leaves.

Another method of greenhouse inoculation used in testing for
varietal reaction to H. victoriae was that of spraying moistened
Fig. 5. Reaction of Bond oats (left), Osage oats (center), and Peatland barley (right) to H. victoriae in artificially infected soil, same quantity of inoculum for each pot.
seedlings in the first leaf stage with the blended mycelial suspension. The plants were then held in a moist chamber for 36 hours. At the time of removal from the chamber the Victoria-hybrid selections and the Victoria parent invariably showed the same response; complete water-soaking of the foliage, and a thick, white, fluffy growth of mycelium standing out from the collapsing watery leaf tissue (fig. 6). The other oat varieties, Clinton, Bond, and Marion, as well as Wisconsin 38 and Manchuria barley and Iowa wheat remained virtually unaffected by exposure to the fungus in moist atmosphere. Three days after inoculation by this method, plants of the Victoria type were for the most part completely necrotic and shriveled (fig. 7). Plants of resistant varieties at this time, if necrotic at all, were only slightly injured on the leaf tips. Readings were taken of the relative amounts of tissue necrosis and of the percentages of surviving plants on the third and tenth days, respectively, following inoculation, and these were used as indices of varietal reactions. When very dilute suspensions were used as inoculum, or when the period of exposure to high humidity was shortened, the susceptible seedlings were not immediately killed; the first leaf and half of the second were necrotic, but the plants appeared as though they might survive. As the third leaf developed, however, it showed the characteristic stripe, indicating that the organism had become established. Similar
Fig. 6. Boone seedlings (left) and Clinton (right) upon removal from greenhouse moist chamber, 36 hours after inoculation with *H. victoriae* by mycelial spray method.
Fig. 7. Plants from same inoculation test as those shown in fig. 6, 4 days later. From left to right, Boone, Tama, Vicland, Bond.
inoculations were made of the same age seedlings using only spores of the fungus in the suspension. After incubation for 36 hours in a moist chamber, numerous light yellowish-green spots with slightly depressed centers appeared on the leaves of susceptible varieties, very much like spots produced on oats by *Pseudomonas coronafaciens* (Elliott) Stapp, the halo-blight bacterium.

As indicated in an earlier paragraph, seedlings which showed symptoms of infection never lived to grow to maturity. Occasionally, however, there were oat plants in the greenhouse in later stages of maturity which showed leaf striping and basal weakness. Apparently delayed infection allowed survival of these plants for some time past the seedling stage. Infection in the seedling stage was found to be controlled to a considerable extent by seed treatment, and plants of susceptible varieties grown from treated seed showed decidedly more vigor than check plants. Apparently infection was delayed by the treatment and the progress of the disease was retarded.

In adult infected plants in the field the striping symptoms were frequently masked by or confused with discoloration due to other factors; hence the most dependable symptom for diagnosis on adult plants was basal weakening — the tendency for badly infected culms to break over at the crown or first internode (fig. 8). These plants lifted easily from the ground, as their root systems were almost destroyed (fig. 9). The lower internodes had a brownish translucent
Fig. 6. Culm portions of Boone oats showing breaking-over of weakened nodes and abundant sporulation of the fungus.
Fig. 9. Roots of Boone (left) and Marion oat plants grown in adjacent plots, the former infected with *H. victoriae*. 
appearance that often extended the entire length of the culm
but was more noticeable near the nodes. The lower nodes frequently
were covered by a dark velvety mass of conidiophores and spores as
shown in figs. 10 and 11. Infected plants ripened prematurely with
excessive lodging and showed a striking decrease in yield and test
weight of grain. Isolations of the fungus were obtained from all
parts of the plant at late stages of maturity — from the roots,
nodes, internodes, leaves, and panicle.

Infection severity showed a decided increase in many areas
in 1946 over that in 1945, the heavy build-up of soil- and air-borne
inoculum having resulted primarily from the planting of diseased
seed of 1945, much of which was untreated. Most Iowa soils were
highly infected with H. victoriae in 1946, as indicated in fig. 12,
showing Boone and Clinton seedlings growing in a flat of un-inoculated
field soil. Although seed-treatment with New Improved Cerosan afforded
partial control of seed-borne infection, it gave only temporary pro-
tection from natural soil infestation. Seed-treatment test plots of
the susceptible variety Overland are shown in fig. 13.

Combined temperature and moisture infection experiments have
indicated that H. victoriae appears to tolerate a wide range of tem-
peratures and soil-moisture levels. Field observations have shown
that, in general, the higher temperatures (25-30° C.) are more
favorable for severe infection.
FIG. 10. Healthy node of Clinton (left) and infected nodes of Boone, the latter showing heavy sporulation of *H. victorid* and characteristic translucent browning.
Fig. 11. Magnified node of Boonoe oat plant showing conidiophores of H. victoriae.
Fig. 12. Plants of Clinton (left) and Tama (right) oats growing in field soil naturally infested with *H. victorieae.*
Fig. 32. Seed treatment plots (foreground) of
Overland oats showing slight degree of
control in left plot grown from seed treated
with Rev Improved Ceresan. The check plot
(right) shows a greater percentage of lodging.
Erect plants of Clinton (from untreated seed)
in the background.
In a preliminary inheritance study (30), F₂ populations of 3 oat hybrids in the seedling stage were inoculated by spraying with a ground mycelial suspension. Each cross involved one Victoria crom rust-resistant parent, and both parents of each cross were homozygous for reaction to H. victoriae. The F₂ plants segregated in the ratio of 3 susceptible to 1 resistant in this test; seedlings of other F₂ populations of the same hybrid combinations when inoculated with race 1.5 of crom rust segregated 3 resistant to 1 susceptible. These data provided the first indications of the probability of a linkage between the gene contributing the Victoria type of resistance to crom rust and that contributing susceptibility to H. victoriae. It is interesting to note that susceptibility to Helminthosporium blight is dominant. Litsenberger (22) studied the mode of inheritance of reaction to H. victoriae in several oat crosses. He concluded that susceptibility to H. victoriae is inherited as a simple dominant and is completely linked to the hypersensitive type of resistance to crom rust possessed by Victoria.

Cultural Studies

Helminthosporium victoriae forms a dark grey, densely growing, moderately tufted colony on potato dextrose agar, and a lighter grey, fluffier growth with more abundant tufting on oat agar (fig. 14). Tendency toward formation of concentric rings is occasionally noticeable.
Fig. 1. Cat agar plate culture of the common strain of *H. victorine*. 
but not usually pronounced. Tufts are more often a very light gray than white, hence the colony color is typically composed of several shades of gray rather than of black with white tufts as is characteristic of most *H. sativum* strains.

Although definite sectoring is not frequent in isolates of *H. victoriae*, 2 types of salient strains have arisen from typical gray parent cultures, and these have retained their respective characters through more than 100 transfers. Culture no. 224 represents the only commonly appearing salient type. It originated from an isolate from timothy in 1945. This strain sporulates so profusely that on most nutrient culture media its growth consists of a greenish-black powdery mass of conidiophores and spores, with a minimum of aerial mycelium. There is a stronger tendency toward concentric somation than in the common strain. Culture nos. 491 and 729 are the only isolates obtained of the other 2 salient strains. These are alike in respect to abundance of sporulation. They resemble no. 224 in producing very little aerial mycelium, but they do not sporulate as profusely as no. 224. In fig. 15, tube slant cultures of nos. 224 and 491 are compared with no. 96, the original isolate of *H. victoriae* from oats. The growth of nos. 491 and 729 is more velvety than the

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1 Incidental comparisons with *H. sativum* are presented because this species has apparently caused more confusion among pathologists than any other in distinguishing *H. victoriae* from other species on cereals.
Fig. 15. Tube cultures of (left to right) H. victoriae typical strain, culture no. 96; H. victoriae sporulating saltant no. 224; H. victoriae sporulating saltant no. 491; H. setariae no. 529 from Holland showing pigmentation of agar (rosy); and H. avenae (non-sporulating strain).
poudery colony surface of no. 224, and the two former strains produce numerous sclerotoid bodies containing very masses of colorless cells, even in young cultures. Since these bodies become flask-shaped and have definite carbonaceous walls, they may be incipient perithecia. Nos. 491 and 729 differ in that the latter strain produces a greater number of these bodies, and a pinkish-coral pigment in the substrate in young cultures is common.

A number of methods were used to induce development of ascogenous tissue within these "perithecial primordia". Among these were the addition of vitamins, growth factors, and amino acids to the culture media in varying concentrations, flooding of cultures, ultra-violet and infra-red irradiation, and exposure to direct sunlight. Many kinds of culture media were tested, including plant tissue of several species in all stages of deterioration. A combination of biotin (5μg./1.), rotted-straw agar, and greenhouse light induced a greater number of bodies to be formed in culture no. 491 than were normally developed. Fig. 16 illustrates a culture of this kind. When no. 491 was grown on the same agar plate with a culture of H. sativum, an apparent antibiotic effect was produced; many of the flask-shaped bodies were formed at the juncture line of the two colonies. Helminthosporium victoriae, being a member of the tapered-spore section of the genus, should be expected to have its ascogenous stage in the genus Cochliobolus Dr., since all other species
Fig. 16. Perithecial initials of *H. victoriae*
culture no. 491 produced in rice culm
agar plus biotin in greenhouse.
of that group for which the perfect stage has been found have fallen in this genus. The Japanese workers, Ito and Kuribayashi (17), have been successful in obtaining the ascogenous form for a number of these tapering-spored species in culture. The media that they found most conducive to ascus formation were rice culm agar and rice polish agar. These media were tested in various concentrations, but as yet no further development of these bodies has occurred. The mutant strains are equally as pathogenic as the original strain, and no differences in spore morphology have been observed.

Toxin Production

The manner by which \textit{H. victoriae} causes necrosis has been the subject of some investigation (27). Inoculation tests with heat-killed mycelium and filtered extracts from cultures have given evidence that the fungus produces a toxin which is responsible for the characteristic longitudinal foliar striping or discoloration. Evidently the basal infection of the oat plant is the only direct manifestation of parasitic action, since the organism has not been isolated from the blighted leaves until after complete necrosis of the tissue. It may be that this fungus is too weak a parasite\textsuperscript{1} to

\textsuperscript{1}The distinction implied here between a pathogen and a parasite is based on the definition of a parasite as an organism capable of attacking living cells, whereas a pathogen may be considered a saprophyte if it can attack cells only after they have been killed by a toxic substance. Such a distinction is controversial.
establish infection in healthy tissue even of susceptible oat
varieties without the help of toxic excretion in advance. Other-
wise, a fungus that grows vigorously in culture would be expected
to progress rapidly in the plant from the basal portions to the
leaves.

Preliminary tests showed that the toxic substance was readily
formed in cultures grown on media containing either organic or
inorganic nitrogen. In a typical experiment, cultures of H.
victoriae were grown for 30 days at room temperature (24-26° C.)
in 500-ml. flasks, each containing 100 ml. of Richard's solution,
filtered through a Buchner funnel to remove the hyphal mass, and
the filtrate then passed twice through a Berkefeld filter to render
it aseptic. Boone and Clinton oat seedlings were grown for one week
in nutrient water culture, after which time the nutrient solution
was replaced by the filtrate in a series of dilutions ranging from
1:15 to 1:1000 in tap water. Observations made at 4-hour intervals
showed the following reactions in the susceptible Boone variety: at
dilutions of 1:90 or less the leaf blades became rigid and inflexible
within 40 hours, and after 48 hours these leaves showed a slight
twisting. A more critical indication of phytotoxicity (fig. 17)
was obtained at dilutions of 1:45 or less: the healthy green color
of normal leaves changed to a dull grayish-brown after 52 hours. This
color change preceded the death and drying of the leaves. The seedlings
of the resistant variety, Clinton, were unaffected by the filtrate in
these dilutions.
Fig. 17. Boone plants in jar on left, Clinton on right; roots immersed in toxic filtrate of H. victoriae cultures diluted 1 to 45 parts water for 15 hours.
Further inquiry as to the nature of the toxic substance included dialyze, extractions in boiling water, alcohol, and chloroform, thermostability and volatility tests, sugar utilization and pH determination, preparation of cell-free extracts, and development of numerous bio-assay techniques. The results of these investigations are briefly summarized below:

1) The toxin passed through a colloidal membrane, indicating that it is probably not of a colloidal nature.

2) Boiling water extracts of the mycelium were toxic to oat plants, and such extracts of *H. cetivum* and *H. avrana* were not toxic.

3) The toxin is either not soluble in, or is inactivated by, ethyl alcohol, since the extracts, after evaporation of the alcohol, were non-toxic when sprayed on plants in water suspension.

4) Extraction of dried mycelium in boiling chloroform yielded a brilliant red syrupy liquid not soluble in water.

5) The toxin in the culture extract is relatively thermostable, as it was not destroyed by autoclaving for 20 minutes at 15 pounds pressure. It was, however, destroyed in the mycelial residue by moderately low dry heat (75°C for 5 days).

6) The toxin is not volatile, since the distillate collected from evaporating the culture filtrate to dryness was non-toxic. The residue taken up in water was toxic.

7) Sugar utilization: culture no. 224 was grown 30 days in Richard's solution which at the time of inoculation contained 50 g. sucrose/liter. The mycelial growth was filtered in a Buchner funnel, the residue was saved for subsequent extractions and the filtrate used for reducing and non-reducing sugar determinations to estimate the amount of sugar used by the fungus in growth.

<table>
<thead>
<tr>
<th>Ut. sugar (sucrose)/liter Richard's solution at inoculation</th>
<th>50.0 g.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ut. total invert sugar/liter culture filtrate</td>
<td>32.25</td>
</tr>
</tbody>
</table>
It. sugar/liter used by fungus in 30 days . . . . . . 17.72 (35.45)
It. sucrose/liter of culture filtrate . 16.42
It. sugar/liter reduced by fungus in 30 days . . . . . . 53.53 (67.26)

3) pH determinations
   a. Un-inoculated Richard's solution . 4.05
   b. Full strength toxic extract from mycelium . . . 7.31
   c. Full strength toxic culture medium . . . . . . 7.35
   d. Distilled water . . . . . . 6.17

Evidently the fungus raised the pH of the culture medium from 4.1 to 7.3 in 1 month of growth.

9) Cell-free extracts were prepared by grinding washed and air-dried mycelium in a bacterial mill. The extracts were apple green in color and apparently colloidal. They were toxic to susceptible plants; thus the toxin occurs within the cells of H. victoriae as well as in the nutrient medium.

10) No bio-assay techniques were developed that yielded more reproducibility than the one already described, but less laborious methods were found. Root length measurements of 7-day-old seedlings grown in petri dishes on blotters watered with toxic dilutions yielded curves satisfactory for bio-assay. Another reliable technique is that of growing seedlings in 2-inch clay pots and watering with toxic dilutions. When it becomes possible to isolate the toxin at least in crude form, the facility of testing by any of the bio-assay methods will be increased.

Although toxin-production is common among species of phytopathogenic fungi, no member of the genus Helminthosporium has yet been shown to liberate a specific phytotoxic substance as a metabolic by-product, irrespective of the substrate on which the fungus is grown.

1Model described by Kalnitsky, Utter, and Weisman (19)
Loe's work (21) with *H. sacchari* Butler demonstrated that this fungus has a strong capacity for reducing inorganic nitrates to nitrites, and he assumed the latter compounds to be responsible for the toxic action of *H. sacchari* toward sugar cane leaves. The production of toxin by *H. victoriae* on media containing only organic sources of nitrogen is evidence that the toxicity of this species is not due to nitrite formation. Bourne (1) showed that *H. sacchari* produces ammonia in quantities that he believed to be toxic in sugar cane tissues.

Some tapering-spored species of *Helminthosporium* have been found by Raistrick et al. (37) to produce characteristic intracellular chemical compounds of the polyhydroxyxanthone series, such as ravenelion (3 methyl-1,4,6-trihydroxyxanthone) by *H. ravenelii* Curt. Further studies will be required to determine whether comparable materials are present in the toxic extracts from *H. victoriae*.

**Sporulation and Morphology**

Sporulation of the fungus on oat plants in the field was confined mainly to the lower nodes and adjacent parts of the leaf of mature, badly diseased plants. The organism was readily isolated from all nodes of these plants in later stages of infection, but fruiting structures seldom were produced in abundance above the first 2 or 3 nodes. Sparse fructifications of the fungus occurred on the basal portions of leaves adjoining the sheaths at intermediate stages of infection. Conidiophores and conidia were formed on withered leaves.
of dying plants, especially on those in contact with moist soil.

Although a description of conidiophores is of doubtful value in distinguishing *H. victoriae* from many other species of *Helminthosporium*, it is helpful to present the general characteristics of these structures, recognizing that size, color, distance between scars, etc., are extremely variable depending upon conditions of growth. Conidiophores as they appear on artificially inoculated leaves emerge singly or in clusters of 2 or 3 (occasionally up to 5), from stomata, from between epidermal cells, or from superficial hyphae on the leaf. They are light to medium brown, usually shading into dark brown at the base. Three types of basal modifications of the conidiophores are apparent, depending primarily upon their origin. When the sporophore arises from a stem or from between epidermal cells, the basal cell is a bulb-shaped enlargement as is characteristic of these structures in numerous congeneric species. Histological studies made by Paddock (33) on the formation of conidiophores by *H. victoriae* showed the presence of an enlarged sub-basal cell beneath the epidermis in addition to the bulbous basal cell on outer surface of the leaf. Conidiophores arising from hyphae growing on the surface commonly have a "foot cell" as shown in fig. 163 which is distinctly darker in color than the other cells. Young conidiophores and those borne in artificial culture usually show constrictions at the points where they are proliferated from the hyphae. Conidiophores formed in culture (2 per cent water agar) are simple, rather smoothly
Fig. 18. Spores of *H. victorina*; A, from 2 per cent water agar; B, from natural substrate.
and closely geniculate, and are olivaceous or fuliginous in color. As compared with sporophores of *H. antithrum* or of *H. avenae* growing on water aper, those of *H. victoriae* are considerably shorter, ranging mostly from 60-90 μ in length. On moist leaves, however, the conidiophore length ranges from 60-230 μ with the mode of the measurements falling between 120-160 μ. The average diameter of the conidiophores ranged fairly constantly from 5.8-10 μ, the mode being 6.5-7.8 μ.

The conidia of *H. victoriae* were found to be readily distinguishable from those of other members of the genus when the various species were studied under comparable conditions. In listing the conidial characters of size, shape, color, septation, etc., for any *Helminthosporium* species, account should be taken of the nutrient substrate on which the conidia developed. In making comparisons among the species, it has been found desirable to include in a selection of "comparable conditions" the nutrient substrate and environment which favor the most nearly normal conidial development, the concept of "normal" having been derived after observation of many spores. In the present study an effort has been made to compare as many species as possible directly from field material, and, in the absence of such specimens, to inoculate greenhouse and laboratory plants and observe the fructifications produced from these. After having arrived at certain conclusions regarding ideal substrate and environment for spore development in the genus *Helmin-
Sclerotium, semi-natural media were used to induce sporulation which was comparable with that on field plants. Such media facilitated the observation of all cultures on similar substrate in similar environment and at the same age. Corollary studies were made of spores of some species on non-nutritive media or on special substrates described in the literature for the sake of comparison with reports of previous investigators.

The most satisfactory substrate for production of typical conidia in most of the species was found to be fresh unsterilized leaf pieces from seedling oat plants laid on moist filter paper in petri dishes. For cultures recalcitrant to sporulation, the petri dishes containing such substrate were autoclaved before seeding since more time was required for sporulation and the unsterilized dishes would become too much contaminated. Other variations of this cultural technique included sterilization of the dishes in closed desiccators with propylene oxide, the use of 2 per cent water agar instead of filter paper as a supporting substrate, and 3-day-old timothy seedlings (unsterilized) instead of oat leaves. There was little variation within species as to the types of conidia produced on any of the plant material media, but it was considered desirable to adhere as closely as possible to leaf tissue in the natural condition as a substrate. The most characteristic conidia were found to be produced in comparatively young cultures (7-10 days old), and contamination by saprophytic fungi was not a limiting factor in normal sporulation within this period.
Young but fully developed conidia of *H. victoriae* are subhyaline or pale green, becoming somewhat darker green to olivaceous with age. This definite greenish spore color is probably the most evident character that distinguishes *H. victoriae* from other species. Young spores are uniformly colored throughout, but the end cells frequently become darker, especially in older spores (fig. 31A). Pale areas common in the end cells of *H. sativum* conidia, and even more noticeable in *Holminthosporium "F"* according to Henry (14), are only rarely observed in *H. victoriae*, and then they are usually associated with germination.

The conidial shape which is regarded as typical is that contour which, with modifications, appeared most consistently in sporulation on field material and on the "semi-natural" substrate described above, and which is represented by the spores illustrated in figs. 19 and 31A. The maximum diameter occurs at or near the middle, the contour tapering toward each end, more strongly toward the apex. The basal end is rounded and the distal end forms a somewhat narrower parabolic curve. This difference in end diameters, however slight in many spores, is an important character in separating this species at once from several unidentified species often isolated from oats. When the broadest part of the spore is not at the central segment, it is more often nearer the proximal end than toward the distal portion. The conidia
Fig. 19. *H. victoriae* spores (culture no. 224) from natural substrate.
are slightly curved except for those of less than average size, which are mostly straight.

Any figure set for the lower extreme in expressing dimensions of mature conidia is of uncertain validity, since maturity is a stage, the limits of which are difficult to determine. Taking allowance for this approximation, the length of normal mature spores may be said to range from 40-130 μ, the diameter from 11-25 μ, and the number of septa from 6-11. The modes of these figures for conidia under optimum conditions are 70 μ, 15 μ, and 8 septa, respectively. One of the longest spores (111 μ) observed on natural substrate is illustrated in fig. 180, d. Very few spores longer than 90 μ have been found. Sporulation of the common strain is moderate on potato dextrose agar and more abundant on oat agar, but the spores are short, and, for the most part, irregular and abnormal in shape. Conidia formed on plain agar without pieces of leaf tissue approach normality in contour (fig. 181), but are shorter and have fewer septations than those produced on plant material. A comparison of conidial measurements on natural and artificial substrates (500 spores on each) is shown graphically in fig. 20. On water agar, the mode for spore diameter is the same as for natural substrate; the spores are elongated ellipsoidal in shape, tapering more strongly toward the distal end. The exosporium is comparatively thin in contrast to the thicker walls of the darker-spored species of Helminthosporium. The septa of young spores are
Fig. 20. Length, diameter, and septation of Helminthosporium victoriae spores compared on natural substrate (A) and 2 per cent water agar (B).
sometimes associated with slight constrictions in the peripheral wall as shown in Fig. 13A,B,C. The dark, flat hilum usually protrudes perceptibly from the contour of the outer spore wall. Termination of the conidial head normally by the production of 1 or 2 polar germ tubes, the basal tube emerging adjacent to the hilum. Atypical termination occasionally occurs by means of 2 germ tubes from each end segment, and very rarely, probably only after injury to the spore, an intermediate segment gives rise to a tube.

(The mycelium of Helminthosporium victoriae as it grows in water agar culture (Fig. 18A) consists of the 2 hyphal types characteristic of most other congeneric species: the smooth, regularly septate, branching, undifferentiated, hyaline or pale fuliginous hyphae; and the terolose, fragmentary, olivaceous hyphae composed of inflated and thick-walled rounded cells. Conidiophores may arise from either type, but at least in young cultures they appear more frequently from the former.)

Comparison of Species

To describe a new species so effectively that there can be no doubt as to its identification by future workers is difficult, even with the assistance of photomicrographs and drawings. Since the erection of the species Helminthosporium victoriae has encountered some degree of skepticism as to its validity, especial effort will be made in this section to justify its species rank on the basis of its
Distinctions from other species. Some of the species mentioned in the literature review as being associated with cats (described briefly in Table 1) will not be discussed further, since their distinguishing features are self-evident. Spore illustrations of H. ovina, the most important among these, are shown in Fig. 31. Among the other species to be considered are those occasionally isolated from cats but not necessarily similar to H. victorina, and those species not found on cats but which do resemble this species morphologically. The groups will be discussed in this order.

*Helminthosporium sativum* Pammel, King, and Raksh (Figs. 22, 23, 30a)

Conidia of *H. victorina* taken from the basal portions of mature plants or weathered oat straw in the field may bear some resemblance to conidia of *H. sativum*. Such spores are often rather dark brown in color, irregular in shape, and broader in diameter than normal. These superficial similarities disappear when freshly formed spores of both species are examined from the same water agar culture plate or from natural substrate. The most obvious differences are in size and color of the conidia. When 100 spores of each species were measured at the same age (1 week), having been grown on opposite sides of the same plate of water agar, the data presented in Table 2 were obtained for the conidial characters.
Fig. 21. Spores of *H. avium*, sporulating strain grown on water agar.
Fig. 22. Spores of *P. vulgarum* from water agar.
Comparison of 1-week-old spores of *H. victoriae* and *H. sativum* grown on opposite sides of the same water agar plate.

<table>
<thead>
<tr>
<th>Species</th>
<th>Lab. In</th>
<th>Mean</th>
<th>Diam. in</th>
<th>Mean</th>
<th>No. Septa</th>
<th>Mean</th>
<th>Color</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>H. victoriae</em></td>
<td>45</td>
<td>45.8</td>
<td>12</td>
<td>11.7</td>
<td>6</td>
<td>5.7</td>
<td>Sub-ligaline or pale green to olivaceous</td>
</tr>
<tr>
<td><em>H. sativum</em></td>
<td>60</td>
<td>61.8</td>
<td>19</td>
<td>19.0</td>
<td>6.5</td>
<td>6.1</td>
<td>Med. oliv. to dark brown</td>
</tr>
</tbody>
</table>

Even greater differences are evident when both species are compared from fresh leaf pieces in a moist chamber. In *H. sativum*, both the exospore, and the space between the inner cell membranes and the outer spore wall are characteristically thick, so that even normal young spores have a plasmolyzed appearance. Spores of *H. victoriae* occasionally show the latter condition on certain media (eg. oat hulls), but to a lesser degree, and they typically exhibit very narrow interlaminal spaces. If a section were to be made across the longitudinal axis at the point of maximum diameter, a spore of *H. victoriae* would appear symmetrical around the axis; this symmetry would not be found in *H. sativum*. The cell contents of *H. sativum* conidia are coarsely granular with numerous fatty globules, while those of *H. victoriae* are nearly always finely granulated.

These 2 species may be distinguished from each other by several characteristic features visible under low power binocular magnifica-
tion (39:1). If water agar plate cultures of each species are compared, the conidia of *H. sativum* appear shiny black and large in contrast to the smaller, greenish spores of *H. victoriae*. In 3- or 4-day-old cultures, *H. sativum* conidiophores usually bear only 1 or 2 conidia, while in *H. victoriae*, clusters of 5 or 6 are developed at this stage (fig. 21). This distinction in initial rate of conidial formation is a consistent character useful in early separation of the 2 species.

*H. sativum* has been found commonly as a saprophyte on oat plants in Iowa and surrounding areas. From some of the southern states (North Carolina, South Carolina, and Mississippi), however, oat plants have been received at the Iowa station which showed severe basal stem necrosis and root rot apparently caused by this species. No varietal specificity has been observed, Bond hybrids being as badly affected as other varieties. Isolates from these specimens did not cause appreciable damage to Iowa oats in greenhouse inoculations. Apparently climatic factors are very important in promoting the pathogenicity of *H. sativum* to oats.

**Helmithosporium "H" Henry (fig. 25)**

This species, thus designated by Henry in 1924 (14) as an organism contributing to root rot of wheat, has never been undescribed and named. It is believed to be the same species that has been frequently isolated from roots, culms, and seeds of oats, barley
Fig. 24. Conidiophores and spores of *H. victoriae* on water agar.

Fig. 25. Spores of *H. sativum* grown on timothy seedlings.
and grasses in the Iowa studies. The spores of this species are typically dark olivaceous, with light halos in the end cells, thick-walled, sub-cylindrical, mostly straight, with mean spore measurements of 75 x 12.5 with 7 septa. This species is one of those most commonly occurring on oats, but it has not been found to be pathogenic.

*Helminthosporium* culture no. 97 (fig. 27)

This culture, obtained from Boone oats from Illinois, represents the only isolate of this species. The spores are somewhat similar in size, shape, and color to those of *H. leersii* Atkinson, but no inoculations of *Leersia virginiaca* Willd. (the host of the latter fungus) have been made. The culture was not pathogenic to the oat varieties tested.

*Helminthosporium* culture no. 174 (fig. 26)

Several isolates of the species represented by this culture have been obtained from oats and barley. In greenhouse tests, this isolate was harmless to oats, but moderately pathogenic to several varieties of barley, including Peatland. Spores of this species range in length from 30-79.6 μ, in diameter from 13.0-15.9 μ, and in number of septa from 6-8 (means 66.5 μ x 14.8 μ and 7.1, respectively). They are dark olivaceous and usually show a characteristic narrowing in diameter at the basal segment (somewhat bottle-shaped), with a
Fig. 25. Spores of *Helminthosporium* species common on oats and considered to be H. "11" of Henry.

Fig. 26. Spores of *Helminthosporium* culture no. 194 isolated from oats.
Fig. 27. *Helminthosporium* sp., culture no. 97 from oats. Spores grown on water agar.
slightly protruding hilum. Spores which do not become narrower resemble those of *H. victoriae* to some extent. Lighter colored halos which are common at each end of the spore are immediately adjoined by an area of condensed cytoplasm which tends to make the end cells appear darker. In this respect also, they resemble spores of *H. victoriae* formed in older leaf-tissue cultures. Growth in oat agar plate cultures is also similar to that of *H. victoriae*.

**Helminthosporium culture no. 282 (fig. 28)**

This culture was obtained from dead leaves of oats growing in the greenhouse. The species is very characteristic in that it produces fuliginous or light olivaceous tapering, bi-polar-germinating spores in catenulate fashion. Since no member of the tapering-spored, bi-polar-germinating group of the genus has yet been described which habitually produces conidiophores directly from spores, this isolate apparently represents a new species. In greenhouse tests, this organism was moderately pathogenic to several varieties of oats.

**Helminthosporium setariae** Saunders and associated species

Because plant pathologists are more familiar with the omnivorous *H. sativum* than with any other species of the genus some reluctance has arisen among them to consider *H. victoriae* a separate species. As a matter of fact, several other species are much more similar to *H. victoriae* than is *H. sativum*. Notable among these is *H. setariae*,
Fig. 26. *Helminthosporium* sp., culture no. 262 isolated from oats.
described in 1912 from Japan (40), but difficulties in procuring authentic cultures of this species in sporulating or vigorously-growing condition have made both comparison and contrast difficult. Since brief descriptions in several papers (17, 22, 31, 41) indicated similarity between \( H. \) setariae and the oat blight pathogen, considerable effort was made to obtain plant specimens, cultures, and a copy of the original description of this species previous to the naming of \( H. \) victoriae. Cultures of 4 isolates of \( H. \) setariae from as many species of \( S. \) were received from the Centraal Bureau voor Schimmelcultures in Holland. These cultures had been deposited by Hishikada in 1933, and none was in sporulating condition. Rapid sub-culturing through more than 100 transfers increased the growth vigor of 3 of the cultures, but sporulation occurred only in isolate no. 529 from \( S. \) gigantea L., and very few spores were produced even in this culture. A single spore isolate was made from these fructifications, and the resulting culture has since maintained a characteristic growth habit for over 2 years. Young cultures produce pink mycelium and a reddish pigment in the medium (fig. 15), later changing to gray. Irradiation with ultra-violet light (3650 \( \AA \)) has proved successful in stimulating early sporulation of leaf-tissue cultures of this isolate. The dishes were exposed for 3 minutes at a distance of 6 inches. It has not been possible to cause infection of \( S. \) spp. in the greenhouse with any of the Holland isolates of \( H. \) setariae.

Cultures and specimens were requested from Ito and Kuribayashi,
since these workers have described sporulation and production of
the ascogenous stage, Cochliobolus setariae Ito,\(^1\) in culture (17).
In response, Y. Asuyama sent 2 transfers of a white strain which
manifests no tendency whatever to sporulate, and dried specimens
of millet (\textit{Setaria italica} (L.) Beauv.) showing leaf spots, from
which the writer isolated only \textit{Helminthosporium victoriae} and \textit{H. actinum}.
In his accompanying letter, Asuyama commented that oat
fields there were showing blight typical of that described as being
caused by \textit{H. victoriae}. It is not unreasonable, therefore, to assume
that occurrence of the latter fungus on the \textit{Setaria} leaves was for­
tuitous, probably having spread from oats grown from infected seed
from the United States. This explanation is offered in view of
the fact that \textit{Helminthosporium victoriae} has not produced leaf
spots on any of the 4 species of \textit{Setaria} tested, nor has any necro-
sis been observed on leaves of green and yellow foxtail (\textit{S. viridis}
(L.) Beauv. and \textit{S. lutescens} (Weigel) Stunts.) in the field which
could be attributed to this fungus. These 2 grasses are the most
common weeds in mid-western oat fields.

Roderick Sprague suggested\(^2\) that spores of \textit{Helminthosporium}
victoriae resembled those identified as \textit{H. setariae} by A. G. Johnson

\(^1\)The new combination, \textit{Cochliobolus setariae} has not been proposed,
but should be adopted on the basis of Drechsler's definition of the
genus (11).

\(^2\)By personal communication.
which were obtained from leaf spots of *Setaria italica* collected in Beltsville, Maryland, and from roots and leaves of *S. viridis* and *S. italic* collected in North Dakota. Sprague was unable to furnish cultures of this species, but he provided leaf spot material of *S. italic* collected in 1935 by Haenschel in New Jersey. Spores from these leaves were not unlike the larger spores of *Helminthosporium victoriae*, but their desiccated condition made conclusive comparisons impossible.

Since all efforts to obtain authentic vigorously growing cultures of *H. setariae* failed, the writer undertook to make collections of *Setaria* leaves from various sections of the United States in the hope of isolating a culture of this fungus for comparison. From some 25 collections of *Setaria* spp. from Iowa, Nebraska, North Dakota, Colorado, Ohio, Michigan, Georgia, Kentucky, and Maryland, 10 distinct species of *Helminthosporium* were isolated, none of which could compare both morphologically and pathogenically with *H. setariae* as described by Saad, Nishikado, and Ito and Kuribayashi. Two species were found which attack the 4 *Setaria* species vigorously, but which do not closely resemble *H. setariae*, and 2 other species were obtained which are similar to *H. setariae* in spore morphology but are not pathogenic to *Setaria*. Characteristics of these isolates are presented in tables 3 and 4. Spores of some of the isolates from *Setaria* spp. including culture
### Table 3. Comparison of species of Helminthosporium from Setaria spp., similar in some ways

<table>
<thead>
<tr>
<th>Species</th>
<th>Conidial Measurements</th>
<th>Color of Conidia</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Length</td>
<td>Diameter</td>
</tr>
<tr>
<td>H. setariae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sawada's description</td>
<td>42-97</td>
<td>11-15</td>
</tr>
<tr>
<td>Combined description by Misikado and Ito and Kuribayashi</td>
<td>35-115</td>
<td>10.2-17.9</td>
</tr>
<tr>
<td>H. setariae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Culture no. 529, received from Holland collection (deposited by Misikado in 1933)</td>
<td>52.8-87.5</td>
<td>11.2-15.8</td>
</tr>
<tr>
<td>H. sp.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Culture no. 502 (author's isolate from Setaria lutescens)</td>
<td>64-132</td>
<td>12.5-14.8</td>
</tr>
<tr>
<td>H. sp.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Culture no. 575 (author's isolate from Setaria viridis)</td>
<td>47.5-78.0</td>
<td>10.6-15.0</td>
</tr>
<tr>
<td>H. sp.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Culture no. 583 (author's isolate from Setaria viridis)</td>
<td>49.5-66.7</td>
<td>11.2-15.5</td>
</tr>
</tbody>
</table>

*Other species isolated from Setaria spp. are illustrated in figs. 30, 33, 37, but are not as similar to Helminthosporium victoriae. One isolate, no. 594 from Setaria italica, is similar to one with culture no. 469 from sugarcane. (See table 4)*
barta spp., similar in some respects to Helminthosporium victoriae

<table>
<thead>
<tr>
<th>Color of Conidia</th>
<th>Shape of Conidia</th>
<th>Miscellaneous Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>(or coal (?)) to dark olive</td>
<td>Spindle-shaped; with expanded basal portions; more or less curved</td>
<td>Spores thick-walled; conidiophores comparatively short</td>
</tr>
<tr>
<td>olivaceous, lighter with darker adjoining areas (?)</td>
<td>Fusiform, obclavate ellipsoidal, mostly curved, broader at or below middle, tapering to ends</td>
<td>Nishikado's photomicrograph shows wide variety of spores; no typical shape</td>
</tr>
<tr>
<td>flesh-olivaceous, uniform</td>
<td>Elongate-ellipsoid, broader at the middle, tapering equally toward each end</td>
<td>Young cultures produce pink pigment, later changing to gray; sporulation usually only after ultra-violet irradiation</td>
</tr>
<tr>
<td>green; not greyish as in H.</td>
<td></td>
<td>Spores thick-walled; conidiophores comparatively short</td>
</tr>
<tr>
<td>prae.</td>
<td></td>
<td>Nishikado's photomicrograph shows wide variety of spores; no typical shape</td>
</tr>
<tr>
<td>tan gray, becoming olive</td>
<td>Young spores resemble H. victoriae in shape, but elongation of older spores decreases the similarity. Mature spores strongly curved</td>
<td>Severely pathogenic to Setaria spp. Cultures sporulate profusely, with a minimum of aerial mycelium</td>
</tr>
<tr>
<td>gray; heavier end septa; contents typically grey; with fatty globa.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>light gray</td>
<td>Elongate ellipsoid, broader slightly below the base; hilum mostly enclosed; more delicate-appearing than H. victoriae</td>
<td>Not as closely septate as H. sacchari (no. 469). Spores resemble Nishikado's drawings of H. setariae.</td>
</tr>
<tr>
<td>olive-gray; more than green; conidiophores light gray</td>
<td>Resemble H. victoriae spores, but not as frequently rounded at the base</td>
<td>Slightly pathogenic to Setaria spp.</td>
</tr>
<tr>
<td>olive-gray; almost green as H. victoriae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>almost as H. victoriae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>as; end cells often ar, with heavier end septa</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

In figs. 30, 33, 37, but are not included in this table since they bear little 4 from Setaria italica, is considered to be Helminthosporium sacchari and identical
Table 4. Spore data for several *Helminthosporium* isolates from *Setaria* spp., grown

<table>
<thead>
<tr>
<th>Species</th>
<th>Length</th>
<th>Conidial Measurements</th>
<th>Diameter</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>10%</td>
<td>5%</td>
<td>2.5%</td>
</tr>
<tr>
<td></td>
<td>Rice culms</td>
<td>Rice culms</td>
<td>Rice culms</td>
</tr>
<tr>
<td><em>H. victoriae</em></td>
<td>40.7-81.4</td>
<td>37.7-67.3</td>
<td>12.8-23.1l</td>
</tr>
<tr>
<td>Culture no. 588, iso-37.1-62.0</td>
<td>(53.8)</td>
<td>(55.9)</td>
<td>(16.0)</td>
</tr>
<tr>
<td>listed from <em>Setaria</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>H. victoriae</em></td>
<td>12.8-23.1l</td>
<td>12.2-22.2</td>
<td>11.5-13.1</td>
</tr>
<tr>
<td><em>H. setariae</em></td>
<td>10-18</td>
<td>63.6-99.9</td>
<td>18.5-26.1</td>
</tr>
<tr>
<td>Data of Ito and Kuri-40-120</td>
<td>-----</td>
<td>-----</td>
<td>-----</td>
</tr>
<tr>
<td><em>H. sp.</em></td>
<td>34.0-59.9</td>
<td>32.6-52.2</td>
<td>10.1-15.2</td>
</tr>
<tr>
<td>Culture no. 594, iso-31.9-53.0</td>
<td>(41.2)</td>
<td>(45.6)</td>
<td>(12.0)</td>
</tr>
<tr>
<td>listed from <em>Setaria</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>H. sp.</em></td>
<td>10.4-14.4</td>
<td>9.3-11.1</td>
<td></td>
</tr>
<tr>
<td><em>H. sacchari</em></td>
<td>63.6-99.9</td>
<td>59.2-84.0</td>
<td>18.5-26.1</td>
</tr>
<tr>
<td>Culture no. 480, iso-58.0-85.1</td>
<td>(79.5)</td>
<td>(72.7)</td>
<td>(22.2)</td>
</tr>
<tr>
<td>listed from <em>Setaria</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>H. sativum</em></td>
<td>18.5-26.1</td>
<td>18.9-25.2</td>
<td></td>
</tr>
<tr>
<td>Culture no. 480, iso-58.0-85.1</td>
<td>(72.7)</td>
<td>(22.2)</td>
<td>(21.9)</td>
</tr>
</tbody>
</table>

*These data were taken in order to compare *Helminth. victoriae* and other species isolated by Kuribayashi (17) for *Helminth. setariae*. These workers reported their measurements from 4 modes for the ranges. The data presented here show 4 distinct classes of spore length (figures), yet there is little difference among the species in septation. The considerable.
-70-

**Conidial Measurements**

<table>
<thead>
<tr>
<th>Conidial Measurements</th>
<th>Diameter</th>
<th>Number of septa</th>
</tr>
</thead>
<tbody>
<tr>
<td>Conidial Measurements</td>
<td>2.5%</td>
<td>10%</td>
</tr>
<tr>
<td>Rice culms</td>
<td>5%</td>
<td>2.5%</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Diameter</th>
<th>Number of septa</th>
</tr>
</thead>
<tbody>
<tr>
<td>37.7-67.3</td>
<td>4-8</td>
</tr>
<tr>
<td>(55.9)</td>
<td>(6.9)</td>
</tr>
<tr>
<td>12.8-23.1</td>
<td>5-8</td>
</tr>
<tr>
<td>(16.0)</td>
<td>(7.1)</td>
</tr>
<tr>
<td>12.2-22.2</td>
<td>5-8</td>
</tr>
<tr>
<td>(12.5)</td>
<td>(6.6)</td>
</tr>
<tr>
<td>11.5-17.4</td>
<td>5-8</td>
</tr>
<tr>
<td>(13.8)</td>
<td>(6.6)</td>
</tr>
<tr>
<td>4-8</td>
<td>5-8</td>
</tr>
<tr>
<td>(6.6)</td>
<td>(7.1)</td>
</tr>
<tr>
<td>5-10</td>
<td>5-10</td>
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<tr>
<td>(6.6)</td>
<td>(7.1)</td>
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<tr>
<td>6-10</td>
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<td>(7.1)</td>
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<td>6-10</td>
<td>6-10</td>
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<tr>
<td>(7.1)</td>
<td>(7.1)</td>
</tr>
<tr>
<td>9.3-14.1</td>
<td>4-8</td>
</tr>
<tr>
<td>(11.5)</td>
<td>(5.7)</td>
</tr>
<tr>
<td>6-10</td>
<td>6-10</td>
</tr>
<tr>
<td>(7.1)</td>
<td>(7.1)</td>
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<tr>
<td>6-10</td>
<td>6-10</td>
</tr>
<tr>
<td>(6.1)</td>
<td>(7.1)</td>
</tr>
<tr>
<td>10.1-15.2</td>
<td>4-8</td>
</tr>
<tr>
<td>(12.0)</td>
<td>(5.5)</td>
</tr>
<tr>
<td>10.4-14.4</td>
<td>4-8</td>
</tr>
<tr>
<td>(11.8)</td>
<td>(5.7)</td>
</tr>
<tr>
<td>9.3-14.1</td>
<td>4-8</td>
</tr>
<tr>
<td>(11.5)</td>
<td>(5.7)</td>
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<td>6-10</td>
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<td>(7.1)</td>
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<td>6-10</td>
<td>6-10</td>
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<tr>
<td>(7.1)</td>
<td>(7.1)</td>
</tr>
<tr>
<td>18.5-26.1</td>
<td>6-10</td>
</tr>
<tr>
<td>(22.2)</td>
<td>(7.8)</td>
</tr>
<tr>
<td>18.9-25.2</td>
<td>6-10</td>
</tr>
<tr>
<td>(21.9)</td>
<td>(7.8)</td>
</tr>
<tr>
<td>17.8-22.9</td>
<td>6-10</td>
</tr>
<tr>
<td>(21.1)</td>
<td>(7.8)</td>
</tr>
<tr>
<td>17.8-22.9</td>
<td>6-10</td>
</tr>
<tr>
<td>(21.1)</td>
<td>(7.8)</td>
</tr>
<tr>
<td>17.8-22.9</td>
<td>6-10</td>
</tr>
<tr>
<td>(21.1)</td>
<td>(7.8)</td>
</tr>
</tbody>
</table>

Helminth, victoriae and other species isolated from Setaria with the data of Ito and the workers reported their measurements from 10% rice culmagar, but they gave no means here show 4 distinct classes of spore length (excluding H. setarina for lack of mean the species in septation. The considerably greater diameter of Helminth, victoriae spores is
no. 529 of *H. setariae* from Holland are illustrated in figs. 29 to 37 inclusive. Culture no. 502, which is very pathogenic to *Setaria* spp., sporulates profusely on oat and potato dextrose agar, as well as on natural substrate, and the spores (fig. 29B) are somewhat similar in young cultures to those of *H. victorina* (fig. 31A). In older cultures, however, the conidia of no. 502 tend to elongate considerably and the resemblance diminishes. Spore measurements of several of the species in question were made from rice culm agar (in various concentrations) in order to simulate the conditions of growth utilized by the Japanese workers. Those data are given in table 4.

Nishikado has compiled (in Japanese) the most comprehensive work on *graminicolous* species of *Helminthosporium* yet published (31). One of the confusing factors in making comparisons of any species with his descriptions of *H. setariae* (which should be among the most authentic) is that the modes of his spore measurements of this species from 2 different species of *Setaria* deviate so greatly that it is difficult to accept them as belonging to the same species of *Helminthosporium*. His isolate from *Setaria viridis* gave a modal spore length of 65 μ, while his *S. italica* isolate yielded a mode of 90 μ. The modal diameters were 12.8 μ and 15.3 μ respectively, and a number of septa, 6 and 8 for the 2 isolates. The spores in Nishikado's photomicrograph of this species show a wide range in size and shape, and he made no statement as to the substrate from which the spores illustrated were taken.
Fig. 29. Helminthosporium species isolated from, or pathogenic to Setaria spp.

(A) *H. sativum* culture no. 480.
(B) *H. sp.* culture no. 502.
(C) *H. segeticae* culture no. 529 from Holland.
(D) *H. specchi* according to Parris. Culture no. 459. Very pathogenic to *Setaria* spp.
Fig. 30. A. *H*.* sp.* resembling *H. oryzae* isolated from sugar cane and *Setaria italica*.
B. *H.* *sp.* isolated from *Setaria sp.* by Roderick Sprague.
Fig. 31. Helminthosporium species found on Setaria spp.
(A) H. victoriae
(B) H. sacchari no. 594 from Setaria italica;
    same species as no. 469 from sugar cane
(C) H. sp. no. 575 from S. viridis
(D) H. sp. no. 583 from S. viridis
Fig. 32. II. sp. culture no. 502 from *Setaria viridis*

Fig. 33. II. sp. from *Setaria italica*
Fig. 34. H. sacchari isolated from Setaria italicca

Fig. 35. H. sp. no. 583 from Setaria viridis
Fig. 36. H. sp. no. 575 from Setaria viridis

Fig. 37. H. sp. from Setaria sp., culture received from Roderick Sprague
Ito and Kuribayashi (17) presented only the range of spore measurements, with no averages given, so these data are of little value for comparison. A copy of Saikada’s article (40) in which he originally described *Helminthosporium setariae* has been obtained from Formosa. The description of the species (translated from the Japanese)⁴ yielded no more detailed information than that quoted by Nishikado in his paper (31). The characteristics of the fungus as given by Saikada are summarized in table 3.

*Helminthosporium sacchari* Butler and associated species

A great amount of disagreement exists concerning the nomenclature of the several species of *Helminthosporium* from sugarcane. Three species are described in the literature as pathogens of sugarcane: *H. sacchari*, *H. ocellum* Paris, and *H. virescens* Dr. Some workers (1, 12, 43) consider both *H. sacchari* and *H. ocellum* to be valid species, while others, (18, 28, 29), notably Parris, (34, 35) do not recognize the latter species, but rather believe *H. sacchari* to be a widely variable species having a number of strains. In comparing *H. victoriae* with *H. sacchari*, the writer is considering the latter species as distinct from *H. ocellum*. Furthermore, the writer is in agreement with

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¹Received from Dr. C. Y. Chen, National Taiwan University, Taiwan (Formosa), China.

²The writer is indebted to Dr. Yuen Chiu, Nanking, China for this translation.
the conclusions drawn by Faris (12) to the effect that \textit{H. sacchari} is not a synonym of \textit{Cercospora sacchari} van Breda de Haan as it was so designated by Johnson and Stevenson (18). Van Breda de Haan described \textit{Cercospora sacchari} in 1892 (2) as the cause of a leaf spot disease of sugarcane which Kruger (20) subsequently named "eye-spot". When Butler and Hafiz described \textit{Helminthosporium sacchari} in 1913 (3) as the cause of a "Helminthosporiosis" of sugarcane, they commented (p.200) in regard to van Breda de Haan's fungus as follows:

From figures published in Waldner and Went's well-known textbook of sugarcane diseases (14), it appears probable that this fungus is a \textit{Helminthosporium} and not a \textit{Cercospora}. A comparison of the two fungi (\textit{C. sacchari} and \textit{Helminthosporium sacchari}) has not been possible and could alone settle the question of their identity.

Subsequent workers (7, 16, 28, 29) apparently made no attempt to obtain type material before accepting the synonymy of these 2 species. Faris, however, made considerable effort to secure authentic material for comparison and received formalin-preserved specimens of the \textit{Helminthosporiosis} fungus from India. As stated above, he concluded after careful studies that \textit{H. sacchari} is not synonymous with \textit{Cercospora sacchari}, but that his new species, \textit{Helminthosporium ocellatum} most probably is the same fungus as that described by van Breda de Haan, on the basis of spore size, conidiophore length, and symptoms on the host. Since the present paper is not primarily concerned with the species of \textit{Helminthosporium} on sugarcane, a detailed taxonomic discussion of these species
is not in order, but for the purpose of comparing *H. victoriae* with *H. sacchari* it is essential to define the writer's concept of the latter species. It is considered that there were not only 3, but 4 species of *Helminthosporium* pathogenic to sugarcane: *H. stenospilum* which is generally agreed to be a distinct species and the cause of brown stripe; *H. ocellatum* which is the cause of eyespot, and, in conjunction with associated saprophytes, the cause of ringspot as shown by Bourne (1); *H. sacchari* as described by Butler, the pathogen of "Helminthosporine" and the species identified by Lee as *H. sacchari*, but which is distinctly different in spore morphology from any of the above named species. Observations on the last species were made from spores produced in a transfer of Lee's culture obtained from the Holland collection and from a culture isolated by the author from sugarcane leaves from Louisiana. Brief descriptions of each of these species are presented in table 5, and spores of the species studied are illustrated in figs. 31, 37, 38, and 39.

Attention was at first given to *H. sacchari* as the possible identity of the oat blight fungus in view of Lee's work demonstrating a toxic action of this species in sugarcane. Since, however, morphological studies have cast doubt on Lee's fungus as being properly identified as *H. sacchari*, this similarity to *H. victoriae* cannot

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1 Received from Otto H. Coleman, Houma, Louisiana
be considered relevant. Many spores of *H. victoriae* developed under conditions not ideal for normal spore production fall within the size range designated by Butler for *H. sacchari*. The culture of *H. sacchari* used for comparative studies was one of 4 species of *Helminthosporium* isolated from sugarcane leaves from Florida.

Conidia from this culture grown on fresh sugarcane leaf-pieces on 2 per cent water agar plates were yellowish-gray or light fuliginous in color, very thin-walled, and smaller and more delicate in appearance than those of *H. victoriae* on the same substrate. Whereas the average length, diameter and number of septa for the latter species on sugarcane substrate were 69 μ, 15.1 μ, and 7.2 μ, respectively, these figures for *H. sacchari* were 52 μ, 11.3 μ, and 6.6. The hilum was inconspicuous and enclosed within the outer periphery in contrast to the protruding conspicuous hilum of *H. victoriae* spores. The widest diameter in *H. sacchari* was usually near the center of the spore, tapering somewhat more strongly toward the distal end than toward the base. On plain water agar there was little difference in the size of 1-week-old spores of the 2 species: the means for length, diameter, and number of septa of 100 spores of *H. victoriae* were 45.3 μ, 11.7 μ, and 6.3 respectively, and for *H. sacchari*, 51.6 μ, 11.1 μ, and 6.3. Under 30x magnification, spores of the latter

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1 Received from B. A. Bourne, Clewiston, Florida
Fig. 38. *H. sacchari* according to Parris; culture no. 499.
Fig. 39. *H. sacchari* according to Lee; culture no. 571.
Table 5. Comparison of species of *Helminthosporium* from sugarcane.

<table>
<thead>
<tr>
<th>Species</th>
<th>Conidial Measurements</th>
<th>Color of Conidia</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Length ( \mu m )</td>
<td>Diameter ( \mu m )</td>
</tr>
<tr>
<td><em>E. sacchari</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>According to Butler's original description</td>
<td>35-60</td>
<td>9.4-12</td>
</tr>
<tr>
<td></td>
<td>(47.5)</td>
<td>(10.7)</td>
</tr>
<tr>
<td><em>E. sp.</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Culture no. 469, <em>E. sacchari</em> isolated by the author; measured from sugarcane leaf pieces</td>
<td>41.4-62.2</td>
<td>9.6-13.0</td>
</tr>
<tr>
<td></td>
<td>(52.0)</td>
<td>(11.3)</td>
</tr>
<tr>
<td><em>E. sp.</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Culture no. 459, <em>E. sacchari</em> received from Farris</td>
<td>66.0-91.5</td>
<td>12.6-14.7</td>
</tr>
<tr>
<td></td>
<td>(76.6)</td>
<td>(13.6)</td>
</tr>
<tr>
<td><em>E. sp.</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Culture no. 571, <em>E. sacchari</em> Lee's culture from Holland</td>
<td>69-99</td>
<td>10.8-13.5</td>
</tr>
<tr>
<td></td>
<td>(85.6)</td>
<td>(12.1)</td>
</tr>
<tr>
<td><em>E. ocellatum</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>According to Farias' description</td>
<td>29-94</td>
<td>9-21</td>
</tr>
<tr>
<td><em>E. stenospilum</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>According to Drechsler's description</td>
<td>40-128</td>
<td>12-22</td>
</tr>
</tbody>
</table>
Table: Color of Conidia, Shape of Conidia, Miscellaneous observations

<table>
<thead>
<tr>
<th>Color of Conidia</th>
<th>Shape of Conidia</th>
<th>Miscellaneous observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Olive green to brown</td>
<td>Long elliptical</td>
<td>Cause of &quot;Helminthosporiose&quot; of sugarcane, not eyespot</td>
</tr>
<tr>
<td>Fuliginous to light olivaceous</td>
<td>Elongate-ellipsoid; inconspicuous hilum; thin-walled spores</td>
<td>Shorter conidiophores than in any species yet observed. Not pathogenic to <em>Setaria italica</em>.</td>
</tr>
<tr>
<td>Pale to medium olivaceous; slightly darker than no. 469.</td>
<td>Broadest diameter at middle portion, distinctly curved, older spores becoming much-elongated. More rounded at base than no. 571.</td>
<td>Lethally pathogenic to <em>Setaria italica</em>; spores thicker-walled than no. 469, and less delicate in appearance.</td>
</tr>
<tr>
<td>Pale fuliginous, subhyaline in younger spores becoming light yellowish gray; long, smoky conidiophores</td>
<td>Tapering strongly to a narrow base which is covered by a conspicuous black hilum; spores somewhat sinuous.</td>
<td>Spores very thin-walled with no visible interlaminal spaces; same species as author's isolate no. 454 from <em>Setaria italica</em> (Georgia)</td>
</tr>
<tr>
<td>Light smoky, yellow-brown</td>
<td>Slightly curved, bulge in middle third of spore</td>
<td>Conidiophores very long. Cause of eyespot of sugarcane.</td>
</tr>
<tr>
<td>Dark olivaceous</td>
<td>Broadest diameter at middle portion, tapering equally toward each end; thick walls.</td>
<td>Conidiophores intermediate in length between <em>H. sacchari</em> and <em>H. ocellum</em>. Cause of brown stripe.</td>
</tr>
</tbody>
</table>
species may be distinguished from those of the former by their smaller size, more delicate appearance, greater number of conidia per conidiophore, and absence of a greenish tinge. The conidiophores of *H. sacchari* are comparatively short, being even shorter than those of *H. victoriae*. As noted previously, precise conidiophore measurements are of little value in characterizing a species of *Helminthosporium* because of the variability of these structures according to the substrate. There is, however, a consistent tendency within a species to produce either long or short conidiophores on natural substrates. Parri noted that *H. sacchari* spores are typically borne on very short conidiophores in contrast to those of the other sugarcane species. This observation has been confirmed by the author.

*H. victoriae* produced elongated brown spots and necrosis on sugarcane leaves in the limited inoculation experiments performed with this host, but none of the sugarcane isolates was pathogenic to *Victoria* derivative oat varieties.

In addition to the Holland cultures and the Florida and Louisiana isolates, a culture of a species designated by Parris as *H. sacchari*, was obtained from this worker (see figs. 29D and 37 and table 5). One of the author's isolates from Florida sugarcane (no. 469) which corresponds to the original description of *H. sacchari* was tested for the pathogenicity to *Setaria italicca* along with the isolate from Parris (no. 459). The latter culture produces much larger spores
than no. 469 as shown in the figures, but according to Parris' recent paper (35), the spores of no. 469 would fall into the lower range of variability which he claims to be characteristic of *Helmintosporium sacchari*; hence he would consider both cultures variants of the same species. It is interesting, however, that no. 459 (Parris) caused lethal injury to the *Setaria* seedlings, while no. 469 produced no injury whatever. Further cross-inoculation studies may help to eliminate the confusion concerning these sugarcane pathogens.
HOST RANGE

During the period from 1944 to 1947 when Helminthosporium blight reached the climax of its destructiveness, *H. victoriae* could be isolated from a high percentage of seed samples of all kinds, as well as from plant tissue of numerous species. Fructifications of the fungus were found growing saprophytically even on non-gramineous hosts such as soybean (*Glycine max* Piper) and flax (*Linum usitatissimum* L.). The hosts from which at least several isolations were made, are listed below. Except from oats, the source of most of the isolates was seed.

*Agropyron cristatum* (L.) Beauv. Crested wheatgrass
*Avena sativa* L. Oats
*Chloris gayana* Kunth. Rhodes grass
*Dactylis glomerata* L. Orchard grass
*Festuca rubra* var. *commutata* Gaud. Chewing fescue
*Paspalum notatum* Flugge Bahia grass
*Phleum pratense* L. Timothy
*Setaria viridis* (L.) Beauv. Green foxtail
*Sorghum vulgare* Pers. Sorghum cane

In petri dish seed germination tests, *Helminthosporium victoriae* was frequently associated with wilted and blighted week-old seedlings of timothy and sorghum. When older plants of timothy were sprayed with a mycelial suspension of the fungus, they showed no injury. As mentioned previously, *H. victoriae* caused elongated brown spots on sugarcane leaves
in greenhouse inoculation tests. The fungus was found to be non-pathogenic to all varieties of oats other than Victoria derivatives, and to barley (Hordeum vulgare L.), wheat (Triticum aestivum L.), and Setaria spp.
DISCUSSION

In the foregoing sections *Helminthosporium victoriae* has been distinguished from congeneric *graminicolous* species primarily on the basis of morphology of the fruiting structures, host specificity, and mechanism of pathogenic action. The validity of such a separation is more acceptable if a characterization of the genus *Helminthosporium* as a whole be considered. First of all, the genus offers a great variety of morphological and pathological characteristics useful in identification of species. The large size, poly-septate condition, and color of the conidia allow for expression of many more distinctive features than is found within genera having smaller, single-celled or few-times septate hyaline or sub-hyaline conidia. These numerous potentialities for variation in conidial characters necessitate a careful examination of the sources of variation, including especially the type of substrate from which the spores studied are taken. Fortunately modern workers show an increasing tendency to include such information in the recent descriptions of these species, the most notable example being the work of Drechsler (9, 10, 11). Photomicrographs and drawings should be made from natural substrate, since spores from a nutrient agar culture are seldom characteristic or homogeneous in type. A separation of the members of the genus into more precise categories than "groups of species" is very diffi-
cult when conidia are examined from nutrient agar medium, as the distinctive spore characters are not manifest on a medium which favors vegetative development.

The primary separation of the graminicolous species of the genus into two rather well-defined groups on the basis of spore shape and other associated characters are presented in Table 6.

Table 6

Characteristics of the two main sub-divisions of the graminicolous species of *Helminthosporium*

<table>
<thead>
<tr>
<th>Characters</th>
<th>Cylindrical-spored species&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Tapering-spored species&lt;sup&gt;b&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shape of spores</td>
<td>Cylindrical or tapering only toward the distal end</td>
<td>Tapering toward each end</td>
</tr>
<tr>
<td>Curvature of spores</td>
<td>Always straight</td>
<td>Usually curved</td>
</tr>
<tr>
<td>Color of spores</td>
<td>Sub-hyaline to fuliginous, rarely darker</td>
<td>Fuliginous to dark brown, more often olivaceous</td>
</tr>
<tr>
<td>Wall thickness, interlaminal</td>
<td>Walls thin, with no interlaminal spaces</td>
<td>Thick or thin walls, more often thick. Interlaminal spaces thin or thick</td>
</tr>
</tbody>
</table>

<sup>a</sup>For these species Ito (16) has proposed the genus *Drechslera*, and Nishikado (31) has suggested the sub-genus *Cylindro-Helminthosporium*.

<sup>b</sup>Nishikado refers species of this group to *Ex-Helminthosporium*. 
<table>
<thead>
<tr>
<th>Characteristics</th>
<th>Cylindrical-spored species</th>
<th>Tapering-spored species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Germination</td>
<td>Indiscriminate, from any cell, and tubes emerging at an angle from the longitudinal axis</td>
<td>Bipolar only, and tubes emerging straight from the longitudinal axis</td>
</tr>
<tr>
<td>Sporulation in culture</td>
<td>Rare</td>
<td>Common</td>
</tr>
<tr>
<td>Conidiophores</td>
<td>Presenting an angular appearance, since points of spore attachment are rather far apart</td>
<td>Closely geniculate, spore borne in continuous succession</td>
</tr>
<tr>
<td>Host specificity</td>
<td>Highly specific; all species described are plant pathogens</td>
<td>Omnivorous, many species found saprophytic in soil and on plant debris</td>
</tr>
<tr>
<td>Chemical compounds isolated</td>
<td>Polyhydroxyanthraquinones</td>
<td>Polyhydroxyanthronones</td>
</tr>
<tr>
<td>Ascogenous stage</td>
<td>Pyrenophora</td>
<td>Cochliobolus</td>
</tr>
<tr>
<td>Occurrence of ascogenous stage</td>
<td>Usually on plant material in the field</td>
<td>Usually in agar culture</td>
</tr>
</tbody>
</table>

Most of these characteristics are so distinct that little difficulty is encountered in separating a species at once into one or the other of the two groups. Only one intermediate species which possesses basic features of both groups is known. This exception is *H. vagans* Dr., the pathogen of eyespot of bluegrass, which
has tapering, dark, thick-walled spores typical of the subgenus Eu-Helminthosporium, but which exhibit indiscriminate germination and are not produced in culture, characteristic of the Cylindro-Helminthosporium group. Raistrick and Smith (37) have consistently isolated polyhydroxyanthraquinones from the cylindrical-spored species and polyhydroxyxanthones from the tapering-spored species, but those workers have not reported any chemical studies with H. vanans. Neither has the ascogenous stage been found for this species, so it remains an interesting question, whether the perfect stage when found will be of the genus Pyrenophora or Cochliobolus or of still another group.

Morphological characteristics useful in separation of species, in addition to those enumerated in table 6, are the following: spore length, diameter, and septation, basal and apical contour of the spore, shape of the hilum, variation of color within the spore (darker or lighter end-cells or heavier end-cell walls), nature of cell contents (showing granules, globules, or homogeneity), and conidiophore length. In the present study all of these characters have been utilized in comparing the various species on natural substrate.

In defining species of this genus, the most commonly employed attributes are those of spore length, diameter, and septation. Early workers were inclined to present only a range between extremes for these data, with little attention to average measurements. With
the increase in number of described species, however, the need for
more precise characterization of species has become evident and most
recent workers have included mean or modal figures in their spore
descriptions. Referring again to the discussion on maturity and
normalcy of spores (pp. 51-52 and 55), the author wishes to call
attention to the fallacy of including indeterminate measurements
of all extremes of spore types together with the most commonly
appearing spore type in defining a species. It is considered
more valuable in offering spore data for identification purposes,
to present the modal lengths, diameters, and septations, these
providing more natural and less arbitrary lines of separation
than means of those measurements.

As a result of having studied some 25 species of Helmintho-
sporium over a period of 6 years, the writer is unable to concur
in the fairly widespread opinion that species of this genus are
not stable in characteristics of spore morphology. The greatest
variation that has been observed is in the suppression or dominance
of vegetative growth. A number of species studied have made striking
changes in culture as to tendency to sporulate, but in not a single
instance has a species changed as to basic spore characteristics when
grown on natural substrate. Decided variation in tendency to sporulate
has been observed in several species according to the section of the
United States from which they were obtained. An example of such
variation is that of *H. avonae*. All isolates of this oat pathogen from northern and middle western fields showed no tendency to sporulate in culture, even with the use of special cultural techniques. On the other hand, most isolates from southern states (Mississippi, Georgia, South Carolina, and Florida), have sporulated readily in agar culture, and profusely on natural substrate (see fig. 40).

Furthermore, even such a variable species as *H. sativum* is considered to be (5, 29, 42) has been found to vary to such an extent that the spores were not always easily recognizable as being of that species. It is true that different isolates of *H. sativum* exhibit a considerable range in nodal spore length, diameter, and septation, but these are only 3 of the numerous characters available for species distinction.

The other primary consideration of these fungi is their relationship to host plants. The several types of pathogenic action exhibited by members of the genus *Helminthosporium* have been described by Drochslcr (9) under the following categories: spotblotch, netblotch, foot-rot, white blast, and systemic invasion. The first two types, spotblotch, and netblotch, are represented by the local necrosis of barley leaves caused by *H. sativum* and *H. teres* Sacc. respectively. The former species, previously noted as being an extremely omnivorous fungus, is also the cause of foot-rot of wheat, barley, and oats as well as of numerous other gramineous hosts. Drochslcr appended the name "white blast" to the type of
Oats seed covered with conidiophores and spores of *H.avenae* (sporulating strain) from Mississippi.

**Fig. 40.**
necrosis produced by *H. turcicum* on corn, in which the fungus causes a warterscalding of the leaf tissue surrounding the locus of infection, this tissue later collapsing and becoming grayish-white in color. Systemic invasion is represented by only one species, *H. graminum* Rabh., the pathogen which follows the growing point of the host in the barley stripe disease. The type of injury caused in susceptible oat varieties by *H. victoriae* presents a new combination of foot-rot and blade blight. The possibility is suggested that this fungus may not be capable of parasitic attack of host tissue if parasitism implies the mechanical invasion of living cells. Rather, in the presence of moisture, spores or mycelium of this organism germinate and in so doing liberate toxic metabolic products which kill the host cells in advance of the growth of the fungus. Whether or not this action be considered parasitism, the results are drastic on susceptible tissues. Since oat leaf blades do not commonly show local lesions caused by this fungus in nature, and since the blades are apparently blighted only by the toxic substances produced from the basal infection, the possible explanation presents itself that chlorophyllous tissue is inhibitory to the growth of the fungus. When dilute spore suspensions were sprayed on the leaves, small halo-blight-like lesions were produced which failed to enlarge and coalesce, further supporting such an hypothesis. When heavy mycelial suspensions were sprayed on the leaves, however, a mass-action effect
was produced, causing total collapse of the plants. The observation of such severe injury led to investigation of the potentialities of dead mycelium and the subsequent discovery of toxin production by the fungus. It also may follow that the hypersensitivity of Victoria derivative oat varieties to crown rust, the basis for their resistance, is paralleled by their extreme susceptibility to the by-products of *H. victoriae*.

The example set by *Helminthosporium* blight of oats, in which a fungus previously existing as a harmless saprophyte became a serious plant pathogen, should emphasize the omnipresent danger in plant breeding that the introduction of new germ plasm may provide susceptible hosts for non-saprophytic organisms. Since cereal breeding must be continued, however, the only precaution that can be taken is that new varieties be tested during the period of their development for reaction to various species of micro-organisms present on gramineous hosts, especially from those genera of fungi known to contain cereal pathogens.

The contribution of Victoria derivatives to the economy of the country is not to be minimized. These varieties were brought to the scene just as the older varieties were being seriously damaged due to the tremendous increase in crown and stem rust inoculum. Now that most of the oat-growing areas are being sown with Bond derivatives, the threat of race 45 and similar races of crown rust is increasing. The story of *H. victoriae* is not a new one, but it represents a
striking example in cereal breeding in which a fungus not previously known as a serious pathogen became dominant on an important economic crop.
SUMMARY

A new *Helminthosporium* disease affecting mainly oats varieties and selections possessing the Victoria-type resistance to crown rust first appeared in 1944, and became widespread throughout most oat-growing regions of the United States in 1945. In the 1946 oat season infection was so severe in many areas as to cause serious reduction in yields. The causal fungus was proposed to be a new species in 1946 (26) and named *Helminthosporium victoriae* because of its specific pathogenicity to Victoria oats and derivatives of this variety. The destructiveness of *Helminthosporium* blight necessitated a shift in varieties in 1947 to Bond derivatives and older varieties resistant to this disease. At the present time Victoria derivatives (resistant to race 4.5 and other important races of crown rust) are grown only in a few areas where climatic conditions limit the severity of blight and in regions where the new Bond derivatives are not agronomically suitable.

The rapid build-up of this disease has illustrated the danger of planting large adjoining acreages to varieties of similar agronomic and disease-resistance types. Widespread planting of a single varietal type utilizing only one source of resistance to a certain disease resulted in the epiphytotic of *Helminthosporium* blight.

Plants infected in the seedling stage were characterized by necrosis of the basal portions, and striping or reddening of the leaves, progressing
upward from the lower leaves. The same symptoms were evident on plants in later stages of maturity, but the basal stem- and root-rot became the primary factors in identifying the disease, since striping and discoloration of leaves may be due to a number of causes. Mature plants in the field were blackened at the nodes with abundant sporulation of the fungus, and the lower internodes showed a characteristic brownish translucence. Culms weakened by severe infection broke over near the ground line and at the lower nodes, and excessive lodging made harvesting of many fields difficult.

Greenhouse inoculations of some 300 oat varieties and selections showed no exceptions to the rule that oat varieties possessing Victoria-type resistance to race 45 (and certain other races) of crown rust are susceptible to Helminthosporium blight. Inheritance studies showed this susceptibility to be dominant in a simple 3 to 1 ratio. Results of varietal inoculation tests in the greenhouse were in complete agreement with field observations. Seed treatment as a means of control was found to be effective only to the extent of retarding infection, older plants succumbing more slowly than those infected at the time of seed germination.

Production of a thermostable toxin to *H. victoriae* was demonstrated in experiments using heat-killed mycelium as inoculum. This toxic substance is apparently responsible for the characteristic foliar striping and reddish-tan discoloration.

Conidia of *H. victoriae* are fuliginous to dark olivaceous, slightly curved, rounded at the base, widest near the center, tapering to a
rounded tip. Normal conidia measure 40-130 (70) μ x 11-25 (15) μ with 4-11 (8) septa, have moderately thin walls, and germinate by one polar germ tube from each terminal cell. Weathered spores at bases of mature plants in the field frequently are atypical, dark brown, irregular in shape, and with thick exospore. Typical cultures form a light to medium-gray tufted colony on oat agar. Three profusely sporulating saltant strains have arisen in culture, two of these showing tendency toward perithecial production. H. victoriae resembles 3 other members of the genus in some respects: H. setariae, H. sacchari, and H. sativum. Comparisons with these species and others occurring on oats have been presented in this paper.
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The writer wishes to express her sincere appreciation to Dr. Joseph C. Gilman for his invaluable guidance throughout this study and for assistance in preparation of the manuscript; to Dr. H. C. Murphy under whose kind direction the investigation was made; to Dr. W. L. Loomis, Dr. George L. McNew, and Dr. Ian W. Tervet for their generous counsel and encouragement. Gratitude is expressed to John Staby for having made the photomicrographs and photographs and to George Morris for his excellent drawings.
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