The stem smuts of Stipa and Oryzopsis in North America

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During the years of the journal’s publication, the Butler University Botany Department had an active program of research and student training. 201 bachelor’s degrees and 75 master’s degrees in Botany were conferred during this period. Thirty-five of these graduates went on to earn doctorates at other institutions.

The Botany Department attracted many notable faculty members and students. Distinguished faculty, in addition to Cain and Friesner, included John E. Potzger, a forest ecologist and palynologist, Willard Nelson Clute, co-founder of the American Fern Society, Marion T. Hall, former director of the Morton Arboretum, C. Mervin Palmer, Rex Webster, and John Pelton. Some of the former undergraduate and master’s students who made active contributions to the fields of botany and ecology include Dwight. W. Billings, Fay Kenoyer Daily, William A. Daily, Rexford Daudenmire, Francis Hueber, Frank McCormick, Scott McCoy, Robert Petty, Potzger, Helene Starcs, and Theodore Sperry. Cain, Daubenmire, Potzger, and Billings served as Presidents of the Ecological Society of America.

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THE STEM SMUTS OF STIPA AND ORYZOPSIS IN NORTH AMERICA*

By GEORGE W. FISCHER

Bureau of Plant Industry, Soils, and Agricultural Engineering

Over much of that great natural resource called the "Western Range," comprising some 728 million acres (1), species of Stipa and Oryzopsis are prominent and important members of the grass cover. These are commonly found affected with stem smut; often as much as 15-20 per cent of the plants are affected, and occasionally as much as 90 per cent infection is encountered. In view of the value of these grasses as components of the western range, and the general interest manifest in the nature of the stem smuts so common on them, it seemed desirable to make a study of the identity of these smuts. It soon became apparent that more smut species are responsible for stem smut on Stipa and Oryzopsis than had hitherto been recognized as occurring in North America. Also it became evident that for more than 80 years stem smuts of Stipa and Oryzopsis have been collected and curated in this country under the name Ustilago hypodytes (Schlecht.) Fr., while as a matter of fact six distinct species and one variety, in two genera were really represented. The various mor­phologic aspects of the complex of stem smut fungi masking under the name U. hypodytes on a wide variety of grasses all over the world already have been presented (4). The present paper is a taxonomic treatise on the known fungi causing stem smut in Stipa and Oryzopsis in North America. The following key will serve to differentiate them.

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*Cooperative investigations of the smuts of forage grasses, by the Division of Forage Crops and Diseases, Bureau of Plant Industry, Soils, and Agricultural Engineering, Agricultural Research Administration, United States Department of Agriculture, in cooperation with the Washington State Agricultural Experiment Station, Pullman, Washington. Published with the approval of the director as Scientific Paper No. 624.

+ A contribution in recognition of the 25th Anniversary of the Botany Department of Butler University.

+ Pathologist, Division of Forage Crops and Diseases, Bureau of Plant Industry, Soils, and Agricultural Engineering.
KEY TO THE STEM SMUT FUNGI ON STIPA AND ORYZOPSIS SPP. IN NORTH AMERICA

1. Spores in definite, persistent, large balls..............................................U. iugnoria
2. Spores free .............................................. 2
3. Spores small (3.5-7 μ), smooth and unadorned................................. 3
4. Spores larger (6-14 μ), exospore rough, cracked, verruculose, or lobed or echinulate at opposite poles......................... 4
5. Spores covered by persistent membrane of fungus tissue............. 4
6. Sori naked after emerging from leaf sheath..............................................U. williamsii
7. Spores with a cracked exospore often resulting in an ear-like appendage at opposite poles.............................U. williamsii
8. Spores with a crest of echinulations or merely with apically thickened wall at opposite poles..............................................U. spagazzini
9. Spores yellowish to olivaceous-brown, finely papillose to minutely echinulate; bipolar areas minutely echinulate to echinulate..............................U. spagazzini
10. Spores dark-brown, smooth or very finely papillose; bipolar areas consisting of smooth apical thickenings.............................................................................................................................................. U. spagazzini var. agrestis


Sori surrounding the internodes, aborting the inflorescence, covered by a persistent whitish membrane of fungus tissue; spores escaping from ruptured or detached ends of membrane, spherical, light brown, smooth, 3.5-5 μ. Fig. 1, A; fig. 3, A; fig. 6, A.

On: Oryzopsis hymenoides (Roem. and Schult.) Ricker Ariz., Colo., New Mex.

Stipa neomexicana (Thurb.) Scribn. Ariz.
Stipa spartica Trin. Iowa, S. Dak.
Stipa sp. Calif., Colo.

This species has been much confused in the various herbaria with the next species, U. numularia (U. hypodyes Auct.). There appears to have been a tendency to consider the membrane as evanescent, and therefore of little taxonomic value. Hence many herbarium specimens have not been accurately identified.

Examination under oil immersion lens is recommended in connection with microscopic characters mentioned in this key.

See also U. spagazzini var. agrestis. Some collections of this variety have inconspicuous bipolar areas and might be keyed out as U. numularia.
INGI ON STIPA AND 8TH AMERICA

Urocystis fraserii

Ustilago minima

Ustilago jacksonii

Ustilago williamsii

Ustilago spargassii

Ustilago s/>eigazzillii

U. s/>eigazzillii var. agristis

U. l//umiiaria

U. l//umiiaria

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mens have been encountered which had been entered as *U. minima* and which clearly belong in *U. nummularia*. The membrane which surrounds the sorus in *U. minima* is not evanescent; on the contrary it is a tough, persistent membrane of fungous tissue in the specimens I have examined. As pointed out by Clinton (3), Arthur did not mention this membrane, although it is present in his specimens.

Germination of the spores has not been observed. Fresh material or recent collections were not available.


*Ustilago hypodytes* Auct.

Sori surrounding the internodes and sometimes extending into the aborted inflorescence, naked except for enveloping leaf sheaths, dusty, dark brown to almost black; spores globose to sub-globose, yellowish to olivaceous-brown, smooth, chiefly 4-5μ in diameter, or 3-4 x 4-5μ. Fig. 1, B; fig. 3, B; fig. 6, B.


*Stipa comata* Calif., Idaho, Mont., Orq., Wash., Wyo.

*Stipa neomexicana* N. Mex.

*Stipa sp.* Calif.

This stem smut is most common on Indian Rice Grass, *Oryzopsis hymenoides*, and needle grass, *Stipa comata*. High percentages of infection have been observed in Washington, Oregon, southern Idaho, and northern Utah, occasionally running as high as 90 per cent.

*Ustilago nummularia* has only recently been recognized as occurring in North America. Fischer and Hirschhorn (4) showed that this species is one of several often erroneously referred to *U. hypodytes*.

Spore germination in *Ustilago nummularia* has been described by Fischer and Hirschhorn (l.c.), and is illustrated in fig. 2, C & D.


*Ustilago hypodytes* Auct.

Sori chiefly surrounding the internodes, but sometimes also involving more or less the inflorescence, although usually the latter is entirely aborted, olivaceous-brown to dark brown, entirely naked except for the enveloping leaf sheaths; spores globose to sub-globose or slightly ovoid, provided with bipolar sub-hyaline crests consisting of a prolongation of the epispore into a group of echinulations, finely papillose to minutely echinate, brown, mostly 4-6μ in diameter, or 3-5μ.

On: *Stipa maura* HBK.

*Stipa spartea* Ill. Iowa, Wis.
ed as *U. minima* membrane which
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Arthur did not
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Fresh material
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Utah, Wash., Wyo.
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finely papillose to minutely echinate, clear yellowish-brown to olivaceous-
brown, mostly 4-6 µ in diameter, or 3.5-4 x 4.7 µ. Fig. 1, D; f. 4, A; f. 6, C.

On: *Stipa mucronata* HBK. (S. setigera) Mexico

*Stipa sportea* Ill., Iowa, Wis.

**Figure 2.** Photomicrographs of germinating spores of stem smut fungi:


*Stipa robusta* Scribn. (S. vaseyi) N. Mex.

*Stipa viridula* Trin. N. Dak., S. Dak., Mont.


*Ustilago hypodiges* Auct.
Differing from the species as follows: Spores dark brown, usually smooth but under oil immersion sometimes appearing very finely papillose; erests rather inconspicuous, sometimes appearing as lacerated apical thickenings, sub-hyaline to concolorous with the spore.

On: *Stipa californica* Merr. and Davy Calif.  
*Stipa occidentalis* Thurb. Calif.  
*Stipa mucronata* (*S. setigera*) Mexico  
*Stipa purpurea* III.  
*Stipa pulchra* Hitchc. Calif.  
*Stipa viridula* N. Dak.

Fischer and Hirschhorn (4) have recently demonstrated the confused relationship of *Ustilago spagazzinii* and the var. *agrestis* to *U. hypodytes*, *U. stipae*, *U. bromi-erecti*, and *U. agrestis*.

Spore germination has been described by Fischer and Hirschhorn (1c.). After 24 hrs. or more a single germ tube emerges, elongates, and usually soon becomes differentiated more or less into a 3-4 celled promycelium. These cells, however, have not been observed to produce primary sporidia, but, instead, long slender branches. These elongate and re-branch to initiate a mycelium, which soon begins to bear chains of aerial spordia. Fig. 2, A & B.

*Ustilago hypodytes* Auct.  

Sori surrounding the upper internodes, often involving also remnants of the aborted inflorescence, dark-brown to black, naked except for enveloping leaf sheaths; spores globose to sub-globose, provided with an epispore that is smooth, but deeply cracked into large pieces, often appearing as bipolar ears or appendages, dark olivaceous-brown, 7-10µ in diameter. Fig. 1, C & E; fig. 4, B; fig. 6, D.

On: *Oryzopsis bloomeri* (Boland.) Ricker. Wash.  
*Oryzopsis hymenoides* Mont., Wyo.  
*Stipa californica* Calif.
Spores dark brown, usually smooth very finely papillose; crests rather 2-ted apical thickenings, sub-hyaline

Ricker. Wash.

Figure 3. A, Ustilago missina, on Stipa neomexicana. Note persistent membrane around sori; B, U. mammularis, on Oryzae sp. Kynoea. Approx. nat. size.
Many collections of stem smut on *Oryzopsis* and *Stipa* spp. are deposited in the herbaria as "*Ustilago hypodytes, *" but belong to *U. williamsii*. The larger spores, the cracked exospore, and especially the characteristic appendages make this stem smut species distinct from *U. spegazzini* var. *aprise*. Some collections have more distinctly appendaged spores than others. In fact occasional collections are encountered in which only the cracked exospore and an occasional appendaged spore identify the species (fig. 1, C).

Germination of the spores takes place rapidly, beginning in 4-6 hours. On dextrose-malt extract-peptone agar a slender germ tube emerges from one or the other of the appended areas and soon develops usually three cross-walls. From each of the resulting four cells a sporidium or a branch arises, more often the latter (fig. 2, E-G, 1). That these cells of the pro-mycelium represent different sexes seems probable from the fact that fusions between these cells are frequently observed, usually by means of a fusion tube, such as is seen connecting the two proximal cells in fig. 2, H. The branches of the promycelium rapidly develop more branches, and a vigorous mycelium is thus started. Very early in the development of this mycelium short, erect hyphae make their appearance and on these are borne short chains of aerial sporidia in great abundance. These aerial sporidia appear to be identical with such primary sporidia as may be borne on the promycelium.


Sori surrounding the upper internodes and more or less consuming the aborted inflorescence, covered only by the enveloping leaf sheaths; spores olivaceous-brown to dark-brown, often quite irregular in shape, globose to ovate, verrucose, mostly 10-12μ in diameter, but often 14μ in length. Fig. 1, F; fig. 5, B; fig. 6, E.

On: *Stipa lettermanii* Utah, 1939.

This is the rarest of the stem smuts in North America. According to descriptions the species was first observed in 1939. Only one viable collection of U. williamsii was observed in various stages of germinating spores. The extent of bearing sporidia (fig. 5, B) compared with the rapidity of germination of *Ustilago williamsii*. App. to reach the extent of development of the time required for germination and the development of sporidia due to invasions by contaminating slowly developing germ tubes and

6. UROCYSTIS FRASERII W. 

Sori more or less surrounding the upper internodes and more or less consuming the aborted inflorescence, covered only by the enveloping leaf sheaths; spores olivaceous-brown to dark-brown, 35-70μ smooth, with walls quite thick in place, chiefly 5-10μ in diameter or 4-6 x 5-8μ thin-walled, light brown, 8-20 or more sporidia per sporidium.

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6. UROCYSTIS FRASERII W.
and Stipa spp. are somewhat similar in appearance and belong to the same genus, but they belong to different sections. In some rare cases, occasional collections of spores from these two genera have been described (1, C).

sidly, beginning in April, in a slender germ tube is produced in a dark area and soon after this emergence, a short thick germ tube begins to protrude, and from this tube, a short thick germ tube emerges. The branches of these cells are numerous, and as a result, the process is slow compared with the rapidity of germination and subsequent development of the fungus. Approximately three days are required to reach the extent of development seen in fig. 2, M, in addition to the time required for germination to begin. Advanced states of germination and the development of mycelium have not been observed, due to invasions by contaminating molds which soon over-grow the slowly developing germ tubes and mycelia of the plant fungus.

Sorites granulosus Ell. & Tracy Jour. Myc. 6:77. 1890.
Sori more or less surrounding the upper internodes, giving the appearance of aerial stems, but actually composed of numerous more or less confluent linear sori running up into and involving the rachis, surrounded when young by a membranous composed of the host epidermis, the whole clumping of the enveloping leaf sheath as a more or less contorted mass; spore balls very firm, opaque, brown to dark brown, 35-70μ in diameter, sterile cells very irregular, smooth, with walls quite thick in places, as dark as or darker than the spores, chiefly 2-10μ in diameter or 4-6 x 5-14μ; spores globose to subglobose, rather thin-walled, light brown, 8-20 or more per ball, smooth, 14-17 x 17-22μ. Fig. 5, A: fig. 6, F.

Stipa leuconata Col. & Blatt, Sask., Wyo.
Stipa spartea Nebr.
Stipa viridula Col.

On: Stipa lettermani Utah, Colo.

This is the rarest of the stem smuts attacking Stipa and Oryzopsis in North America. According to Zundel (6), who only recently described the species, it was first collected in 1921, in Colorado. Only one viable collection of Ustilago jacksonii was available and the following observations of spore germination in this species is based on this one collection. At room temperature, spores sown on dextrose-malt extract peptone agar showed no signs of germination for three days, after which approximately 5% of the spores were observed in various stages of germination. One end of the spore begins to protrude, and from this emerges a short thick germ tube which soon begins to branch and re-branch (fig. 2, J & K). On some germinating spores the germ tube resembles a promycelium, even to the extent of bearing sporidia (fig. 2, L). The process is a slow one compared with the rapidity of germination and subsequent development of Ustilago williamsonii. Approximately three days are required to reach the extent of development seen in fig. 2, M, in addition to the time required for germination to begin. Advanced states of germination and the development of mycelium have not been observed, due to invasions by contaminating molds which soon over-grow the slowly developing germ tubes and mycelia of the plant fungus.

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Stipa leuconata Col. & Blatt, Sask., Wyo.
Stipa spartea Nebr.
Stipa viridula Col.

On: Stipa lettermani Utah, Colo.
The presence of two distinctly balls excludes this smut from the originally placed. Repeated attespores have been unsuccessful among thousands of spore balls, plate. This one germinating spores have failed to substantiate the observe that spores of this smut (species in the *Ustilaginaceae* then species of a new genus, one of *Urocystis* in the *Tilletiacae*. In that of existing genera the fungu transferring this smut to the ge binomial *U. granulosa* but this to a distinctly different and rare species described by Clinton (2).

Zundel (6) has recently described from Saskatchewan. All of this species I am convinced that under discussion and as long as *Urocystis*, then by priority Zundel's bently Zundel did not recognize the sporeum granulosum, for each is publication (6).

**COMPARATIVE PATHOLOGY**

**STEM SMUTS OF STIPA**

The apparent superficial natue the subject of interesting conje of the host plants. A casual exa *Oryzopsis* affected with these smtissues of the host were entirely n One wonders, therefore, about th in these smut diseases. A thorough tribute some valuable data of a fwork the parasitism of the fungi in hosts have been included in only.
The presence of two distinctly different kinds of cells in the spore balls excludes this smut from the genus Sorosporium, where it was originally placed. Repeated attempts to observe germination of the spores have been unsuccessful except for one germinating spore among thousands of spore balls, spores and sterile cells on an agar plate. This one germinating spore appeared similar to the large cells here considered as the spores and germination was definitely of the Ustilago type. However, no other such germinating spores were found on the same agar plate, and previous and subsequent attempts have failed to substantiate the observation. If future studies should prove that spores of this smut fungus germinate such as to place the species in the Ustilaginaceae then it probably would become the type species of a new genus, one which would be the counterpart of Urocystis in the Tilletiaceae. In the meantime, it must be admitted that of existing genera the fungus most closely resembles Urocystis. Transferring this smut to the genus Urocystis should result in the binomial U. granulosa but this name is already occupied, belonging to a distinctly different and rare smut in the spikelets of Stipa comata, described by Clinton (2). Zundel (6) has recently described Urocystis frascrii, on Stipa comata, from Saskatchewan. After a careful study of type material of this species I am convinced that it is identical with the stem smut under discussion and as long as this smut is considered to be a Urocystis, then by priority Zundel’s binomial should apply to it. Apparently Zundel did not recognize the identity of U. frascrii with Sorosporium granulosum, for each is treated independently in the same publication (6).

COMPARATIVE PATHOLOGICAL HISTOLOGY OF THE STEM SMUTS OF STIPA AND ORYZOPSIS

The apparent superficial nature of the stem smuts has long been the subject of interesting conjecture as to the pathological histology of the host plants. A casual examination of the stems of Stipa and Oryzopsis affected with these smuts would suggest that the underlying tissues of the host were entirely normal, even including the epidermis. One wonders, therefore, about the nature and extent of the parasitism in these smut diseases. A thorough study of this problem should contribute some valuable data of a fundamental nature. In the present work the parasitism of the fungi and the pathological histology of the hosts have been included in only a very preliminary fashion. Por-
tions of culms of "Stipa and Oryzopsis" by the six species treated above, infiltration and embedding processes. The sections were stained

The comparative microscopic analysis of "Stipa and Oryzopsis" is shown in figure 1. stems and "Ustilago minima," the same. In the case of "Ustilago nummularia," the stem tissues seem to be parasitized by "U. jacksonii" the stem tissues seem to be parasitized by "U. kymenoides." Finally, it is seen that such fungi develop well in the chlorophyll parenchyma, mechanical tissue.

Hirschhorn (5) describes the chlamydomospore mass and the host tissues of these stem smuts on "Stipa in Arg," where it is quite variable according to him. Some significance that in the stroma was found in any of the reports of a stroma by other inv. young sori, in which the spores converted into a spore mass. Thus the underlying mycelium or bearing stromatic layer. It can be seen that specialized tissue, however, if part of the spore mass. Obviously needed on the ontogeny of the stem tissues.
tions of culms of *Stipa* and *Oryzopsis* affected with stem smuts caused by the six species treated above were carried through the paraffin infiltration and embedding process, and sectioned with a rotary microscope. The sections were stained with Thionin and Orange G.

The comparative microscopic appearance of six stem smuts of *Stipa* and *Oryzopsis* is shown in Fig. 6. In all except *Urocystis fraseri* and *Ustilago minus*, the smut appears to be entirely superficial. In the case of *Ustilago nummularia*, *U. spegazzinii*, *U. williamsii*, and *U. jacksonii* the stem tissues seem to be quite intact. The sections of *O. hymenoides* parasitized by *U. minus* indicate destruction of the epidermis. Finally, it is seen that the parasitism of *Urocystis fraseri* is such that the fungus develops beneath the epidermis, apparently destroying the chlorophyll parenchyma cells, and even some of the mechanical tissue.

Hirschhorn (5) describes the presence of a stroma between the chlamydospore mass and the host epidermis in the case of some of these stem smuts on *Stipa* in Argentina, and states that this character is quite variable according to host species and locality. It may be of some significance that in the present studies no trace of such a stroma was found in any of the six smut species. It is possible that reports of a stroma by other investigators were based on studies of younger sori, in which the superficial mycelium had not entirely converted into a spore mass. It has long been known that spore formation in at least some of the stem smut fungi is centrifugal, and thus the underlying mycelium could easily be interpreted as a spore-bearing stromatic layer. It can scarcely be considered as such a specialized tissue, however, if the layer itself ultimately becomes part of the spore mass. Obviously some careful investigations are needed on the ontogeny of the stem smuts, to clarify such fundamental issues.
Figure 6. Comparative pathological histology of stems of *Stipa* and *Oryzaopsis* affected with stem smuts. Cross sections of the sori and stems (upper row), and enlarged portions.
LITERATURE CITED


and enlarged portions (lower rows), as follows: A, Ustilago minima on Oryzopsis hymenoides, note thickness of spore mass and the fungous membrane around same; B, U. nummularia on Stipa comata; C, U. apegazzinii on Stipa viridula; D, U. williamsonii on Stipa richardsonii; E, U. Jacksonii, on Stipa lewisteinii; F, Urocylis fraseri, on Stipa comata. Stem sections x approx. 50; enlarged portions x approx. 200.

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