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The stem smuts of Stipa and Oryzopsis in North America

George W. Fischer

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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[1]*

By GEORGE W. FISCHER[2]
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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[1] 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.

[2] 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[3]

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

1. USTILAGO MINIMA Arth. Bull. Iowa Agr. Coll. Dept. Bot. 1884: 172. 1884.

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

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

Stipa comata Trin. and Rupr. Neb.
Stipa neomexicana (Thurb.) Scribn. Ariz.
Stipa spartea Trin. Iowa, S. Dak.
Stipa sp. Calif., Colo.

This species has been much confused in the various herbaria with the next species, *U. nummularia* (*U. hypodytes* Auct.). There appears to have been a tendency to consider the membrane as evanescent, and therefore of little taxonomic value. Hence many herbarium speci-

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

[4] See also *U. spegazzinii* var. *agrestis*. Some collections of this variety have inconspicuous bipolar areas and might be keyed out as *U. nummularia*.

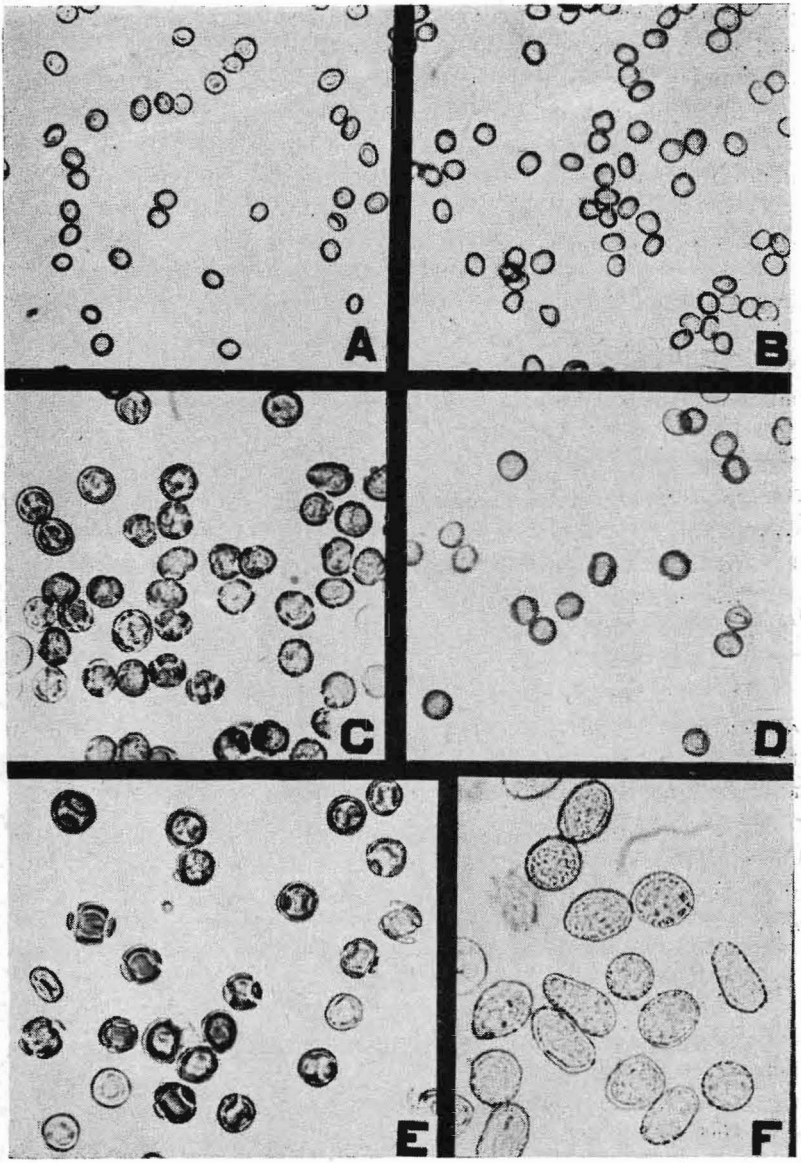

Figure 1. Photomicrographs of the chlamydospores of the species of *Ustilago* causing stem smut on *Stipa* and *Oryzopsis* in North America. A. *Ustilago minima;* B. *U. nummularia;* C. *U. williamsii,* form with cracked exospore but few appendages; D. *U. spegazzinii;* E. *U. williamsii,* form with appendages open; F. *U. jacksonii.* x approx. 600.

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.

2. USTILAGO NUMMULARIA Speg. An. Mus. Nac. de Buenos Aires, (ser. 3) 1: 59. 1902.

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.

On: *Oryzopsis hymenoides* Colo. Idaho, Mont., Utah, Wash., Wyo., Sask.

Stipa comata Calif., Idaho, Mont., Ore., 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.

3. USTILAGO SPEGAZZINII Hirsch. Notas del Museo de La Plata, Botanica 4: 415-419. 1939.

Caeoma hypodytes Schlecht. Fl. Berol. 2: 129. 1824. (in part).

Ustilago hypodytes Auct.

Sori chiefly surrounding the internodes, but sometimes also involving more or less the inflorescence, although usually the latter is entirely aborted, olive-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 echinulate, clear yellowish-brown to olivaceous-brown, mostly 4-6μ in diameter, or 3.5-4 x 4-7μ. Fig. 1, D; fig. 4, A; fig. 6, C.

On: *Stipa mucronata* HBK. (*S. setigera*) Mexico
Stipa spartea Ill., Iowa, Wisc.

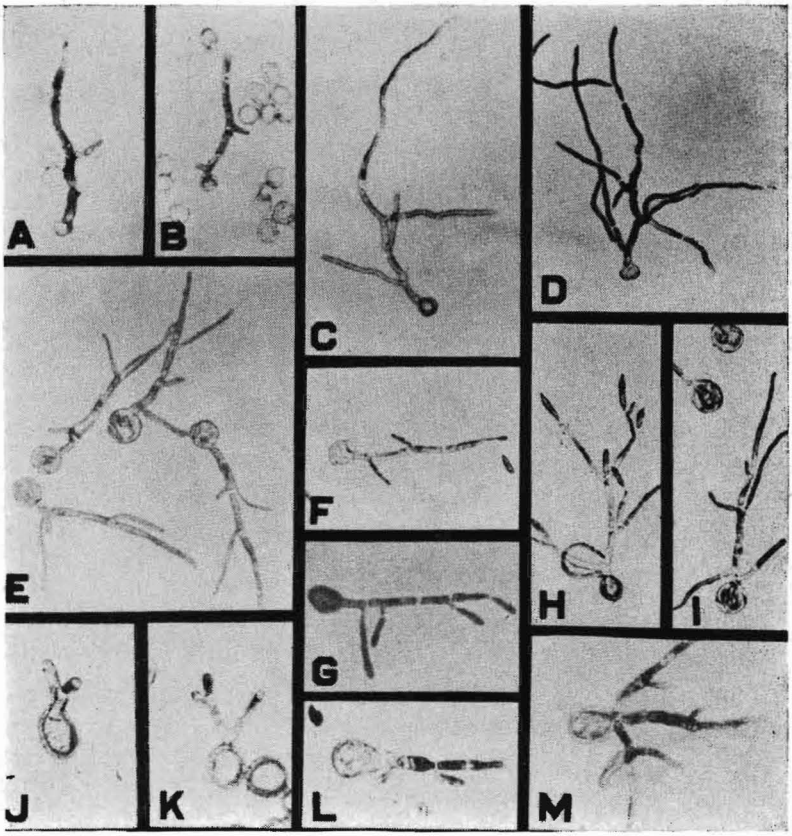

Figure 2. Photomicrographs of germinating spores of stem smut fungi: A, B, *Ustilago spegazzinii*, from *Stipa viridula;* C, *U. nummularia*, from *Stipa comata;* D, *Ibid.*, from *Oryzopsis hymenoides;* E-I, *U. wiliamsii*: E and I, from *Stipa speciosa*, F, from *Stipa cernua;* G & H, from *Oryzopsis hymenoides;* J-M, *U. jacksonii*, from *Stipa lettermani*. X approx. 500.

Stipa robusta Scribn. (*S.* vaseyii) N. Mex.
Stipa viridula Trin. N. Dak., S. Dak., Mont.

3a. USTILAGO SPEGAZZINII var. AGRESTIS (Syd.) G. W. Fisch. and Hirsch.. Mycologia 37: 1945.
Ustilago hypodytes 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 spartea Ill.
Stipa pulchra Hitchc. Calif.
Stipa viridula N. Dak.

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

Spore germination has been described by Fischer and Hirschhorn (l.c.). After 24 hrs. or more a single germ tube emerges, elongates, and usually soon becames 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 sproidia. Fig. 2, A & B.

4. USTILAGO WILLIAMSII (Griff.) Lavrov Trav. Inst. Sci. Biol. Univ. Tomsk 2: 22. 1936.

Ustilago hypodytes Auct.

Sorosporium williamsii Griff. Bull. Torr. Bot. Club 29: 290-301. 1902.

Ustilago appendiculata Speg. Myc. Arg. en Ann. Mus. Nat. de Buenos Aires. Ser. 3, 12: 288. 1909.

Tranzchiella othophora Lavrov. Trav. Inst. Sci. Biol. Univ. Tomsk 2: 29. 1936.

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 hymenoidcs Mont., Wyo.
Stipa californica Calif.

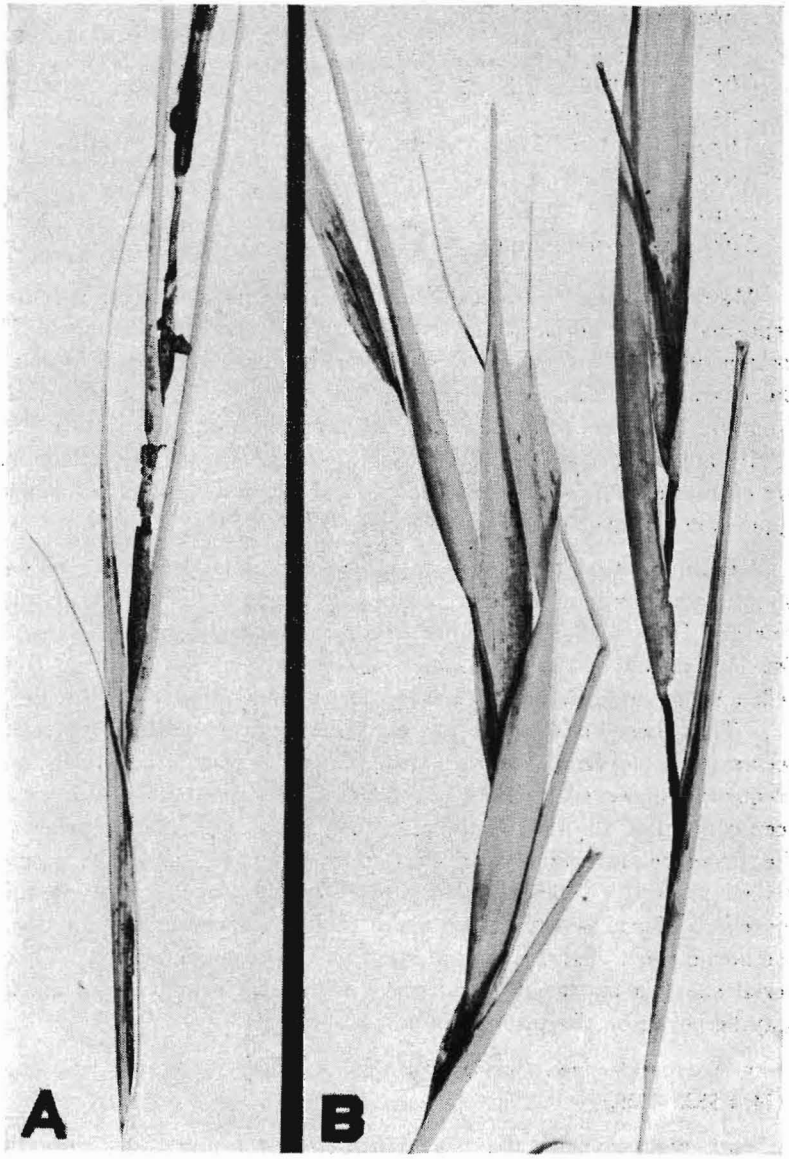

Figure 3. A, *Ustilago minima*, on *Stipa neomexicana*. Note persistent membrane around sori; B. *U. nummularia*, on *Oryzopsis hymenoides;* Approx. nat. size.

Stipa comata Ore., Mont.
Stipa cernua Stebbins and Love Calif.
Stipa coronata Thurb. Calif.
Stipa lettermani Wyo.
Stipa occidentalis Calif., Ore.
Stipa richardsoni Link Mont., Wyo.
Stipa speciosa Trin. and Rupr. Calif.
Stipa viridula Mont.
Stipa thurberiana Piper Wash.

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. spegazzinii* var. *agrestis.* 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 appendaged 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, I). 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.

5. USTILAGO JACKSONII Zundel and Dunlap. North American Flora 7(14): 982. 1939.

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, verruculose, mostly 10-12μ in diameter, but often 14μ in length. Fig. 1, F; fig. 5, B; fig. 6, E.

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[3] 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 there 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 williamsii*. 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 smut fungus.

6. UROCYSTIS FRASERII Clint. & Zundel. N. Amer. Flora 7(14): 1018. 1939.

Sorosporium granulosum Ell. & Tracy Jour. Myc. 6:77. 1890.

Sori more or less surrounding the upper internodes, giving the appearance of a stem smut, but actually composed of numerous more or less confluent linear sori running up into and involving the rachis, surrounded when young by a membrane composed of the host epidermis, the whole elongating from 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 5-10μ 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.

On: *Stipa clandestina* Hackel Coahuila, Mexico
Stipa comata Colo., Mont., Sask., Wyo.
Stipa spartea Nebr.
Stipa viridula Colo.

[3] On *Stipa lettermani*. Monte Cristo Mt., Rich Co., Utah. 8-17-41 leg. W. R. Rader, fid. G. W. Fischer, No. 209, Bur. Plant Ind. Myc. Coll. No. 85065.

Figure 4. A, *Ustilago spegazzinii*, on *Stipa viridula;* B, *U. williamsii*, on *Stipa speciosa*. Approx. nat. size.

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 *Tillitiaceae*. 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 fraserii*, 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. fraserii* 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-

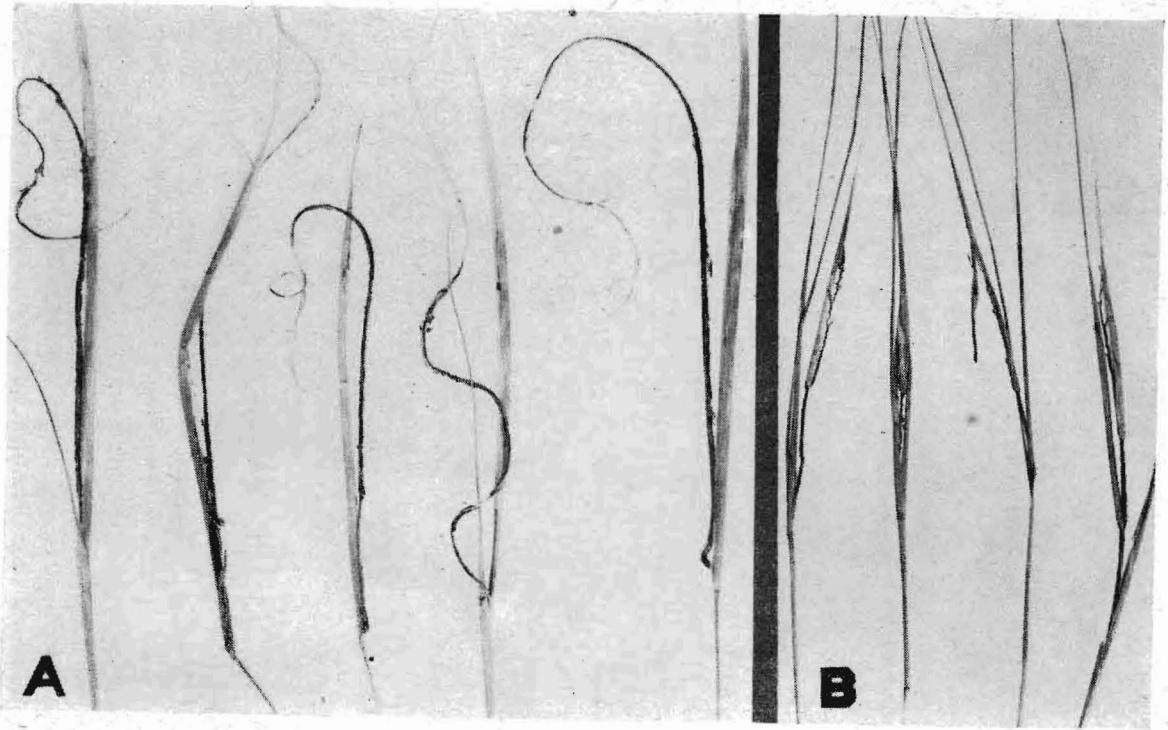

Figure 5. A, *Urocystis fraserii*, on *Stipa comata*; B, *Ustilago jacksonii*, on *Stipa lettermani*. Slightly reduced.

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 microtome. 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 fraserii* and *Ustilago minima*, 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. minima* indicate destruction of the epidermis. Finally, it is seen that the parasitism of *Urocystis fraserii* 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.

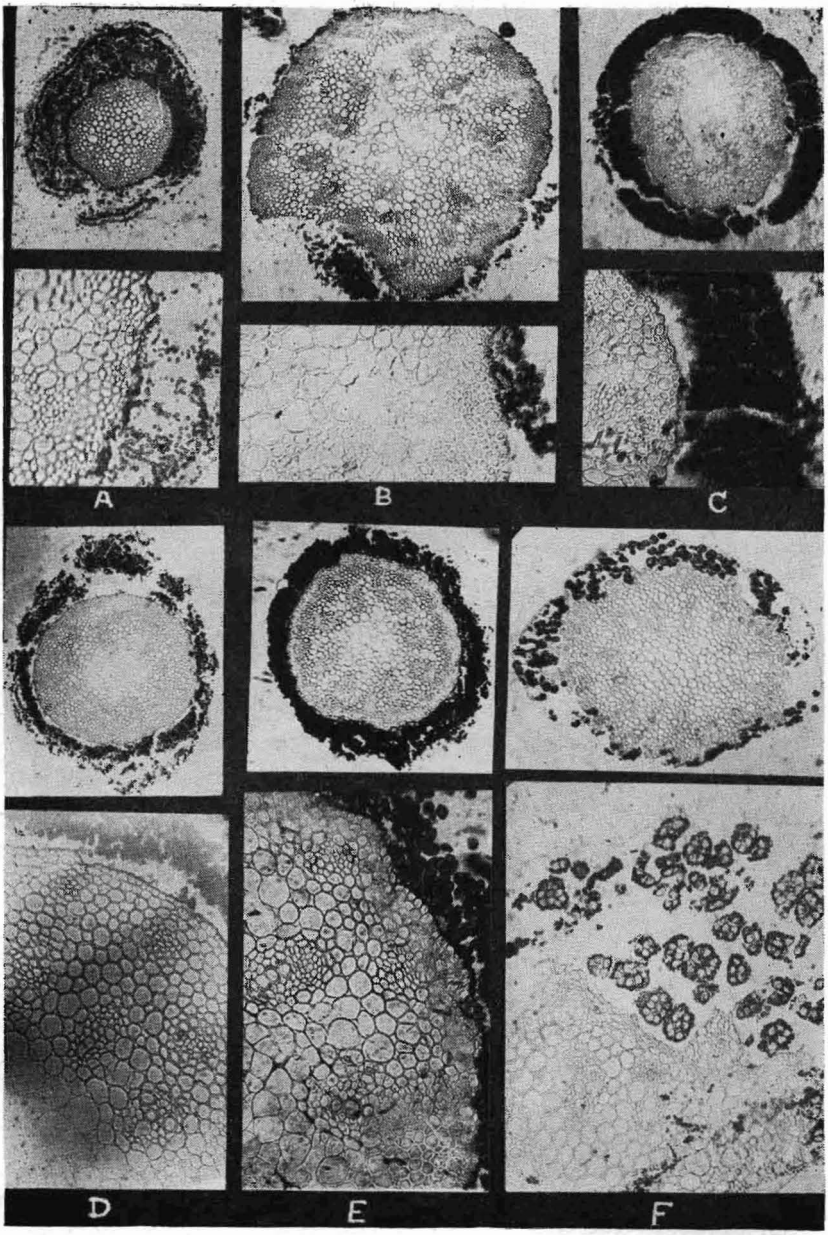

Figure 6. Comparative pathological histology of stems of *Stipa* and *Oryzopsis* affected with stem smuts. Cross sections of the sori and stems (upper row),

LITERATURE CITED

1. CLAPP, EARLE H. The major range problems and their solution. A resume in, The Western Range. United States Senate Document No. 199 (74th Congress, 2nd Session) xvi + 620 pp. 1936.
2. CLINTON, G. P. North American Ustilagineae. Jour. Myc. 8: 128-156. 1902.
3. ———— ————. North American Ustilagineae. Proc. Boston Soc. Nat. Hist. 31: 329-529. 1904.
4. FISCHER, GEORGE W., AND HIRSCHHORN, ELISA. A critical study of some species of *Ustilago* causing stem smut on various grasses. Mycologia 37: 1945. (In press.)
5. HIRSCHHORN, ELISA. Las especies del genero "Ustilago," en la Argentina. Darwiniana 3: 347-418. 1939.
6. ZUNDEL, GEORGE L. Ustilaginales. Additions and corrections. N. Amer. Flora 7(14): 971-1045. 1939.

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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. nannularia* on *Stipa comata;* C, *U. spegazzinii* on *Stipa viridula;* D, *U. williamsii,* on *Stipa richardsoni;* E, *U. jacksonii,* on *Stipa lettermani;* F, *Urocystis fraserii,* on *Stipa comata.* Stem sections x approx. 50; enlarged portions x approx. 200.