# The smut fungi (*Ustilaginomycetes*) of *Boutelouinae* (*Poaceae*)

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Fourteen species of smut fungi are recognised on the grass subtribe *Boutelouinae*. Detailed descriptions and synonyms with authors and place of publication are given for all recognised species. Each species is illustrated by line drawings of the habit and in many cases also of enlarged sori, as well as by LM and SEM pictures of the spores. New species described: *Ustilago subminor* Vánky. The following three names are considered to be new synonyms of *Macalpinomyces spermophorus*: *Ustilago boutelouae* Kellerman & Swingle, *U. convertere-sexualis* Durán, and *U. pueblaensis* Durán. A further seven synonymies, established by different authors, are confirmed. Lectotypes are designated for *Ustilago boutelouae-humilis* Bref., *U. hieronymi* Schröter (= *U. buchloës* Ellis & Tracy), *U. calcara* Griffiths, and *U. hilariae* Ellis & Tracy (= *U. vilfae* G. Winter). A key to the species and a host-parasite list are provided to facilitate the identification of the smut fungi of *Boutelouinae*.

**Key words:** lectotypes, new species, synonyms, taxonomy.

## Introduction

The subtribe *Boutelouinae* Stapf, in the tribe *Cynodonteae* of the subfam. *Chloridoideae*, comprises 16 genera (Clayton and Renvoize, 1986: 245). Smut fungi have been reported on six of these genera: *Aegopogon* Willd. (a genus with 3 species, from southern USA to Peru), *Bouteloua* Lag. (24 species, from Canada to Argentina but centred on Mexico), *Buchloë* Engelm. (1 species in USA and Mexico), *Cathestecum* Presl (5 species, from USA to Guatemala), *Hilaria* Kunth (9 species, from southern USA to Guatemala), and *Opizia* Presl (one species in Mexico and the West Indies).

To pave the way towards a world monograph, the smut fungi of various grass genera have been revised (*comp*. Vánky, 2000a,b, 2001, 2002b, 2003a,b, 2004a,b,c; Shivas and Vánky, 2001; Vánky and Shivas, 2001). The revision of the smut fungi of the subtribe *Boutelouinae* is part of this project (*comp.* Vánky, 2002a). It confirmed that several smut species occur on different host species within the one host genus or even on members of several genera within

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the subtribe *Boutelouinae*. Some of the smut fungi also occur on members of the subtribes *Eleusininae* and *Sporobolinae* of the tribe *Eragrostideae*, subfam. *Chloridoideae* (*e.g. Macalpinomyces spermophorus* or *Ustilago buchloës*). This is a reason why some smut fungi have been described several times. In addition to earlier established synonymies, a further three synonyms are proposed: *Ustilago boutelouae* Kellerman & Swingle, *U. convertere-sexualis* Durán, and *U. pueblaensis* Durán, all represent *Macalpinomyces spermophorus* (Berk. & M.A. Curtis ex de Toni) Vánky, a smut for which the host plant range was further widened. Within the *Ustilago buchloës – U. minor* group, a third species, *U. subminor*, could be distinguished. *Tranzscheliella hypodytes* (Schltdl.) Vánky & McKenzie could not be confirmed on members of *Boutelouinae*.

## Materials and methods

Sorus and spore characteristics were studied using either freshly collected material or dried herbarium specimens, preserved in different herbaria or in Herbarium Ustilaginales Vánky (HUV). Herbarium names are abbreviated according to Index Herbariorum (Holmgren *et al*., 1990).

For light microscopy (LM), dried spores were rehydrated in lactophenol by gently heating to boiling point. For scanning electron microscopy (SEM), dried spores were dusted on double-sided adhesive tape, mounted on a specimen stub, sputter-coated with gold-palladium, *ca*. 20 nm, and examined in a SEM at 10 kV.

## Taxonomy

The recognised 14 smut fungi on *Boutelouinae*, including one new species, their synonyms, types, descriptions and illustrations are listed below.

***Macalpinomyces spermophorus*** (Berk. & M.A. Curtis ex de Toni) Vánky, 2003c: 210. (Figs. 1-3)

≡ *Ustilago spermophora* Berk. & M.A. Curtis ex de Toni, in Saccardo, 1888: 466.

≡ *Ustilago spermophora* Berk. & M.A. Curtis, in Curtis, 1867: 123 (as "*spermophorus*"; nomen nudum).

≡ *Sphacelotheca spermophora* (Berk. & M.A. Curtis ex de Toni) Moesz, 1921: 63. — Type on *Eragrostis poaeoides* P. Beauv. var. *megastachya* Koehler (= *E. cilianensis* (All.) Janchen), USA, Iowa, Charles City, September 1882, J.C. Arthur; isotypes in Ellis, N. Amer. fgi. no. 1098, as *Ustilago spermophorus*, HUV 10545!

= *Ustilago boutelouae* Kellerman & Swingle, 1889: 13. — Type on *Bouteloua oligostachya* Torr. (= *B. gracilis* (H.B.K.) Lag. ex Steudel), USA, Kansas, 20 December 1888, BPI 158131! (syn. nov.).

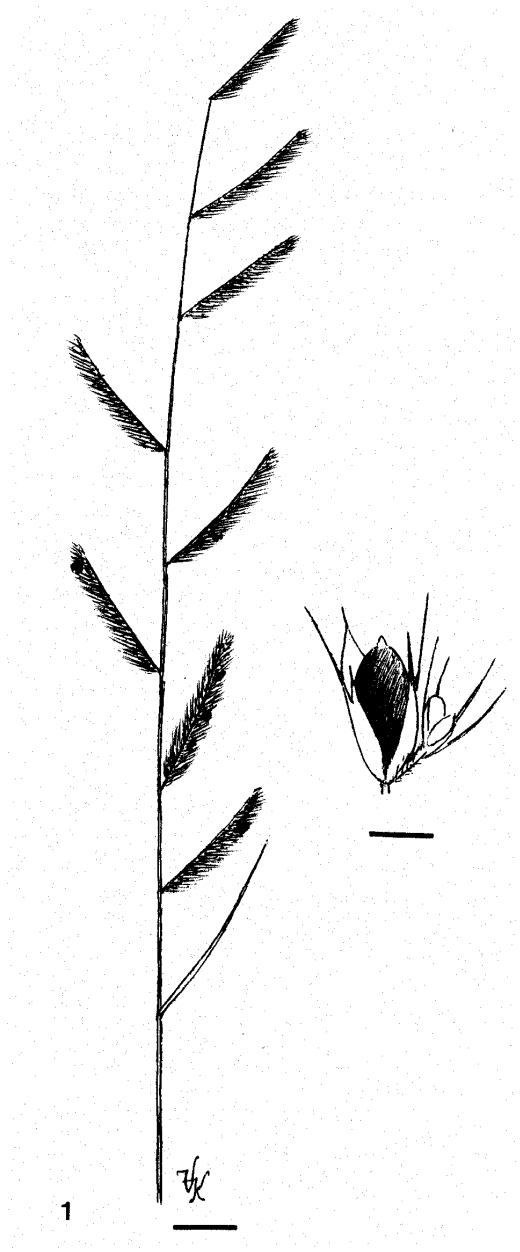



**Fig. 1.** Sori of *Macalpinomyces spermophorus* in some hypertrophied ovaries of *Bouteloua rothrockii*. Enlarged a spikelet with a sorus (glumes removed). Bars = 1 cm for habit, 1 mm for detailed drawing.

= *Ustilago kusanoana* Hennings, 1904: 140.
≡ *Sphacelotheca kusanoana* (Henn.) Hennings, 1905: 594.
≡ *Cintractia kusanoana* (Henn.) Shirai, 1905: 20. — Type on *Eragrostis ferruginea*

P. Beauv., Japan, Tokyo, September 1901, S. Kusano 350, S! (syn. by Zundel, 1953: 203, confirmed).

= *Ustilago ugandensis* Henn. var. *macrospora* Beeli, 1922: 6. — Lectotype on *Panicum* sp., Congo, Leopoldville Prov., (design. by Vánky, 2004: 115) Kisantu, July 1914, H. Vanderyst 4657, BR 1318, isolectotype BPI 194482! (syn. by Vánky, 2004: 115).

= *Ustilago orientalis* W.Y. Yen, 1935: 7 (invalid name, no Latin diagnosis).

≡ *Ustilago spermophora* Berk. & Curt. var. *orientalis* (Yen) Yen, 1937: 187 (comb. illeg.). — On *Eragrostis cilianensis* (All.) Lutati, China, Nanking, near Lingkutze, September 1930, T.N. Liou, PC. (syn. by Zundel, 1953: 204, confirmed).

= *Ustilago eragrostidis-japonicana* Zundel, 1943: 165. — Type on *Eragrostis japonica* Trin., South Africa, Cape Prov., Vryburg Distr., Welgelegen, April 1925, G.A. Pentz, PREM 20621!; isotypes BPI 160370, BPI 188933 (syn. by Vánky, 2004: 115).

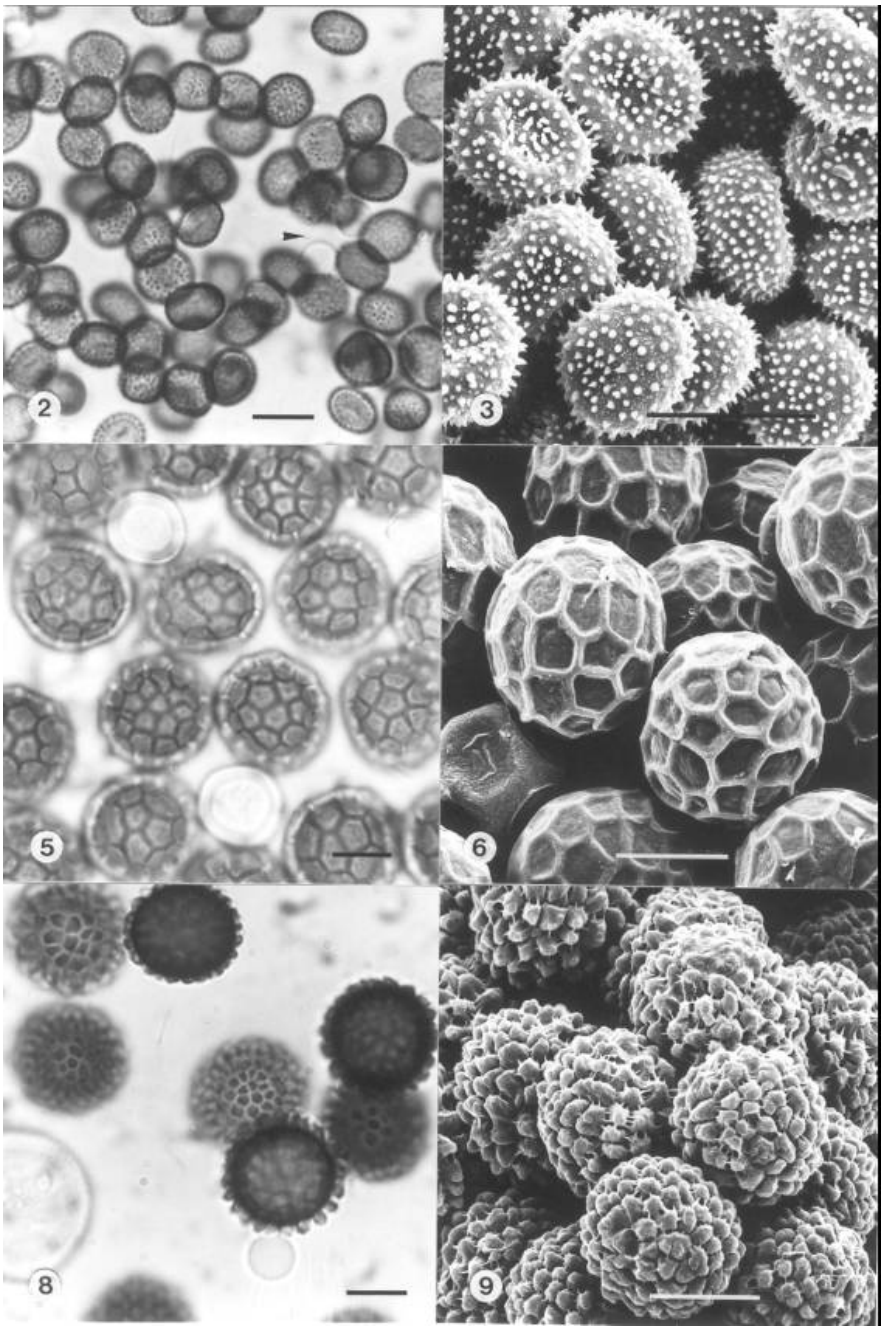
= *Sphacelotheca cheoana* Zundel, 1943: 168. — Type on *Eragrostis cilianensis* (All.) Lutati, China, Anhwei Prov., Chu Hua Shan, Ch'ing Yang Hsien, Sha Kan, 24 October 1932, S.Y. Cheo 1395, BPI 177306! (syn. by Vánky, 1990: 273).

= *Ustilago convertere-sexualis* Durán, 1987: 228. — Type on *Cathestecum prostratum* Presl, Mexico, Puebla, 3.2 km S. of Tehuitzingo, off Hwy. 190, alt. 1371 m, 16 November 1976, R. Durán & P.M. Gray, WSP 67752! (syn. nov.).

= *Ustilago pueblaensis* Durán, 1987: 243. — Type on *Cathestecum prostratum* Presl, Mexico, Puebla, 3.2 km S. of Tehuitzingo, off Hwy. 190, alt. 1371 m, 16 November 1976, R. Durán & P.M. Gray, WSP 67755! Paratype on *Cathestecum erectum* Vasey & Hack, Mexico, Puebla, 29.1 km NW. of Tehuitzingo, off Hwy. 190, on the road to Oaxaco, alt. 1432 m, 16 November 1976, R. Durán & P.M. Gray, WSP 68569; isoparatype HUV 14632! (syn. nov.).

*Sori* (Fig. 1) in some ovaries of an inflorescence as first green, later brown, spherical or pyriform bodies showing between the glumes, 1-2 × 1-3(-4) mm, covered by a peridium of fungal and host origin which ruptures irregularly to expose the dark brown, powdery spore mass intermixed with sterile cells. Often the distal part of the sorus bears a remnant of the caryopsis as a hard, yellowish-brown, acute body. Heavily infected panicles may be congested. *Spores* (Figs. 2, 3) globose, subglobose to ovoid, occasionally elongate or irregular, 6.5-9(-10) × 8-11(-13) µm, light brown; wall even, *ca*. 0.5 µm thick, finely, moderately densely verrucose-echinulate, spore profile wavy to usually finely serrulate. *Sterile cells* globose, subglobose, ellipsoidal, rarely elongate, 5.5-8 × 6-11 µm, hyaline, collapsed in old specimens; wall thin, *ca*. 0.5 µm, smooth. *Spore germination* of *Ustilago*-type (Ito, 1936: 17). That of "*U. boutelouae*" resulted in 2-5-celled basidia, 2-4 × 25-50 µm, on which elongate, cylindrical basidiospores were produced measuring 2-2.5 × 9-13 µm (Kellerman and Swingle, 1889: 13). Similar germination was obtained by Durán (1987) for "*U. convertere-sexualis*" (pg. 229, + pl. 112, fig. E) and "*U. pueblaensis*" (pg. 244 + pl. 135, fig. F)

*Hosts*: On at least 14 species of *Eragrostis* (principal host genus). Also on *Bouteloua aristidoides* (H.B.K.) Griseb., *B. chondrosioides* (H.B.K.) Benth. ex S. Wats, *B. filiformis* (Fourn.) Griff., *B. gracilis* (H.B.K.) Lag. ex Steudel, *B. hirsuta* Lag., *B. rothrockii* Vasey, *B. simplex* Lag. (*Chondrosium simplex*




**Figs. 2, 3.** Spores of *Macalpinomyces spermophorus* on *Bouteloua gracilis*, in LM and in SEM (Bartholomew, Ellis & Everharts' Fgi. Columbiani no. 2192) (as *Ustilago boutelouae*; HUV 16217). **Figs. 5, 6.** Spores and sterile cells of *Tilletia aegopogonis* on *Aegopogon tenellus*, in LM and in SEM (type). **Figs. 8, 9.** Spores and sterile cells of *Tilletia boutelouae* on *Bouteloua gracilis*, in LM and in SEM (type). Bars = 10 µm.

(Lag.) Kunth), *Cathestecum erectum* Vasey & Hack., *C. prostratum* Presl, *Hilaria belangeri* (Steudel) Nash. var. *longifolia* (Vasey) Hitchc., *Panicum* sp., and *Sporobolus australasicus* Domin.

*Known distribution*: on *Eragrostis* spp. cosmopolitan, on *Panicum* sp. Africa (Congo), on *Sporobolus* Australia, on *Bouteloua*, *Cathestecum* and *Hilaria* spp. N. America (USA, Mexico).

Presence of sterile cells between the spores, and often a remnant of the seed on the top of the sori, differentiate this smut from other, similar *Ustilago* species.

Fischer (1953: 286) and Durán (1987: 240) considered *Ustilago boutelouae* to be a synonym of *Ustilago neglecta* Niessl (= *Macalpinomyces neglectus* (Niessl) Vánky). However, the spores of *M. neglectus* are larger (8-11 × 9-14 µm) and more evidently echinulate.

The types of both *Ustilago convertere-sexualis* and *U. pueblaensis* were collected in the same place, the same day, on the same host plant species. Study of the types revealed that they are identical in every respect. Durán (1987: 229, 244) observed that when these two smuts infected staminate florets of *Cathestecum prostratum*, these developed ovaries filled with spores. According to Durán (1987: 244), *U. pueblaensis* can be distinguished from *U. convertere-sexualis* by the fungal peridia which surround the sori of *U. pueblaensis*. This difference depends certainly on the developmental stage of the sori.

***Tilletia aegopogonis*** Durán, 1970: 1100. (Figs. 4-6)

Type on *Aegopogon tenellus* (Cav.) Trin., Mexico, Chihuahua, Creel, Arroyo de Aguatos-Nacimiento del Rio Chonchos, around the Cuevas de las Pinturas, alt. 2300 m, 13 October 1969, R. Durán, WSP 58552. Topotype: 14 October 1974, R. Durán, WSP 67743; isotopotype HUV 14436!

*Sori* (Fig. 4) in all ovaries of an infected inflorescence, ovoid, 0.5-1 × 1-2 mm, showing between the floral envelopes, first covered by the thin, green to pale brown pericarp which ruptures irregularly at maturity disclosing the dark reddish-brown, powdery, foetid mass of spores and sterile cells. *Spores* (Figs. 5, 6) globose, subglobose to broadly ellipsoidal, 16.5-21 × 18.5-23 µm, yellowish- to olivaceous-brown, reticulate, 3-5 polyangular meshes per spore diameter, rarely incomplete, muri 1.5-2(-2.5) µm high, interspaces smooth to inconspicuously verruculose. *Sterile cells* (Figs. 5, 6) globose, ellipsoidal to slightly irregular, smaller than the spores, 10.5-18.5 × 11-20 µm, subhyaline; wall 1-3 µm thick, smooth, content granular, pale yellow. Intermediate forms ("immature spores") present. *Spore germination* results in multinucleate, unbranched or occasionally branched holobasidia bearing apically self-fertile, fusiform, multinucleate basidiospores which do not fuse. Basidiospores


**Fig. 4.** Sori of *Tilletia aegopogonis* in the ovaries of *Aegopogon tenellus*. Enlarged two sori. Bars = 1 cm for habit, 1 mm for detail drawings.

become septate, forming dikaryotic infection hyphae directly and/or secondary sporidia (Durán, 1980: 528-533, figs. 1-8; 1987: 147, pl. 63, fig. C).

*Host*: *Aegopogon tenellus* (Cav.) Trin.

*Known distribution*: N. America (Mexico).

***Tilletia boutelouae*** Durán, 1987: 148. (Figs. 7-9)

Type on *Bouteloua gracilis* (H.B.K.) Lag. ex Steudel, Mexico, Durango, 0.8 km on the road to San Juan de Dios, off Hwy. 45, 25 October 1978, R. Durán, WSP 67744; isotype HUV 14043! Paratypes WSP 68655, WSP 68661; isoparatypes HUV 14044, HUV 14045.

*Sori* (Fig. 7) in some ovaries of an inflorescence, fusiform, *ca*. 1 × 4-5 mm, more or less hidden by floral envelopes, first covered by the thin, greyish-brown pericarp which ruptures irregularly disclosing the dark brown, semiagglutinated to powdery mass of spores and sterile cells. *Spores* (Figs. 8, 9) globose, subglobose to broadly ellipsoidal, 17-21 × 17-24 µm, yellowish- to chestnut-brown, provided with prominent, blunt, conical or pyramidal warts, often with flattened tips, 1.5-3 µm high, in surface view appearing as darker, irregular, polygonal areas, 5-8 per spore diameter. *Sterile cells* (Fig. 8) globose, ellipsoidal or slightly irregular, 15-28 µm long, pale yellowish-brown; wall 1.5-4 µm thick, smooth to finely punctate, content granular. *Spore germination* results in multinucleate holobasidia producing apically a great number of filiform basidiospores which do not fuse. Basidiospores initially mononucleate, later multinucleate, then becoming multiseptate, each cell containing one nucleus (Durán, 1987: 149, pl. 67, fig. F).

*Host*: *Bouteloua gracilis* (H.B.K.) Lag. ex Steudel.

*Known distribution*: N. America (Mexico).

***Tilletia buchloëana*** Kellerman & Swingle, 1889: 11. (Figs. 10-12)

Syntypes on *Buchloë dactyloides* (Nutt.) Engelm., USA, Kansas, Trego Co., 1886, and Ford Co., Backlin, June 1888, FH!, BPI 172553, 172559.

= *Ustilago cathesteci* Hennings, 1897: 212.

≡ *Tilletia cathesteci* (Henn.) G.P. Clinton, 1902: 149. — Type on *Cathestecum procumbens* Parl., Mexico, without date and locality, coll. K. Schumann, BPI 172669! (synonymy supposed by Clinton, 1904: 440, confirmed by Durán and Fischer, 1961: 41).

*Sori* (Fig. 10) in all ovaries of an infected plant, ovoid or lemon-shaped, *ca*. 1 × 1.5-2 mm, more or less hidden by the floral envelopes and covered by the thin, brown pericarp which ruptures irregularly at maturity, disclosing the reddish-brown, semiagglutinated to powdery mass of spores and sterile cells. Infected plants have denser and darker inflorescences with spreading glumes. *Spores* (Figs. 11, 12) rather uniform, globose, subglobose to broadly ellipsoidal, 17.5-20(-21) × 18-22(-24) µm, including the 2-3 µm high sheath, pale yellowish-brown; wall provided with inconspicuous, pale coloured, blunt, subpyramidal tubercles about the height of the subhyaline or pale yellowish-brown sheath or somewhat shorter. In SEM spore surface slightly undulate, smooth (due to the sheath). *Sterile cells* (Figs. 11, 12) globose, ovoid to irregular, 8-20 × 10.5-21 µm, hyaline; wall 2.5-7 µm thick, multilayered, content granular, yellowish, often very much reduced. *Spore germination* results in multinucleate holobasidia, simple or branched, with an apical whorl

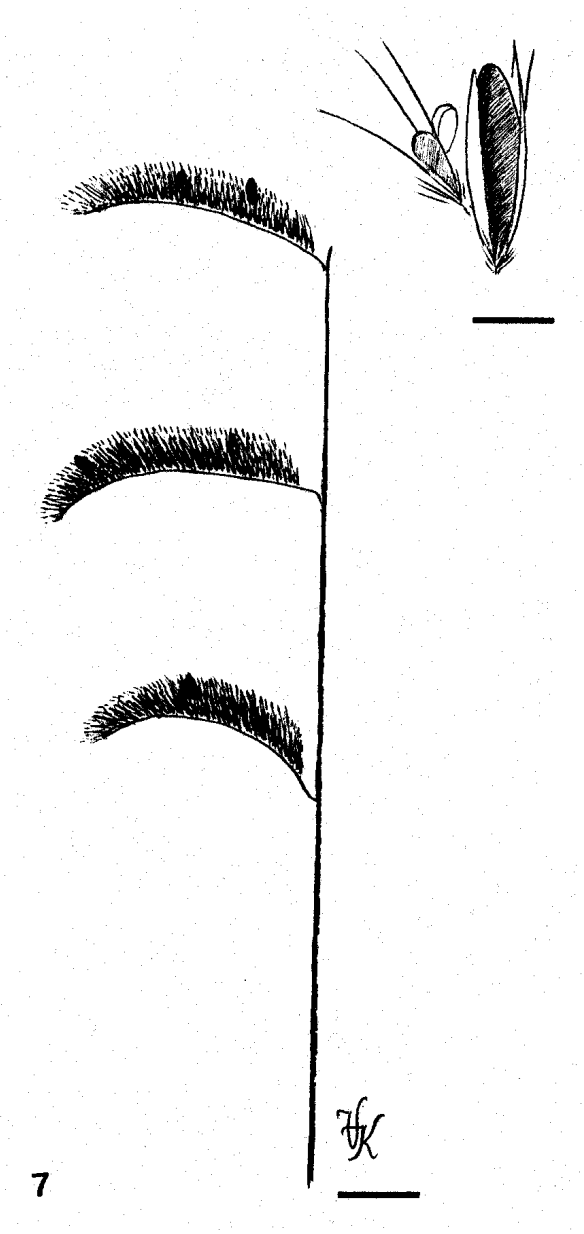



**Fig. 7.** Sori of *Tilletia boutelouae* in the ovaries of *Bouteloua gracilis*. Enlarged a young sorus in a spikelet (glumes removed). Bars = 1 cm for habit, 2 mm for detail drawings.

of mono- or binucleate basidiospores. The mononucleate basidiospores fuse in pairs at their base (Durán, 1987: 151, pl. 69, figs. C, D, pl. 70, fig. E).

*Hosts*: *Buchloë dactyloides* (Nutt.) Engelm., *Cathestecum erectum* Vasey & Hack., *C. procumbens* Parl., *C. prostratum* Presl, *Hilaria belangeri* (Steudel)

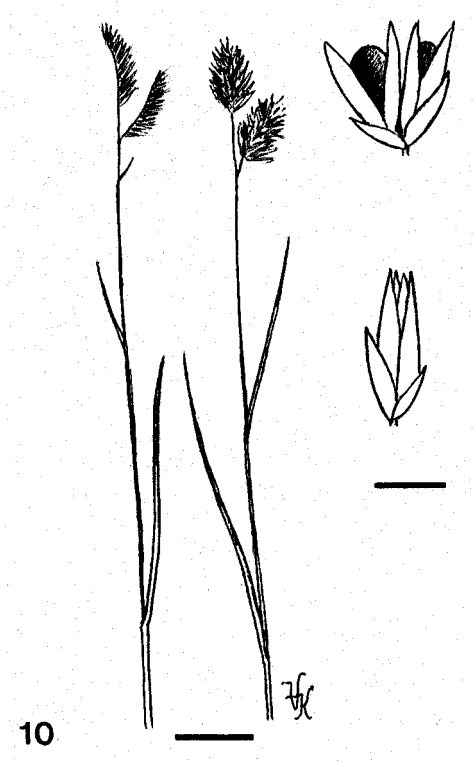



**Fig. 10.** Sori of *Tilletia buchloëana* in the ovaries of transformed staminate flowers of *Buchloë dactyloides*. To the left a healthy staminate inflorescence. Enlarged a healthy and an infected staminate spikelet with two sori. Bars = 1 cm for habit, 2 mm for detail drawings.

Nash, *Muhlenbergia distichophylla* (J. Presl) Kunth (*Podosaemum distichophyllum* J. Presl).

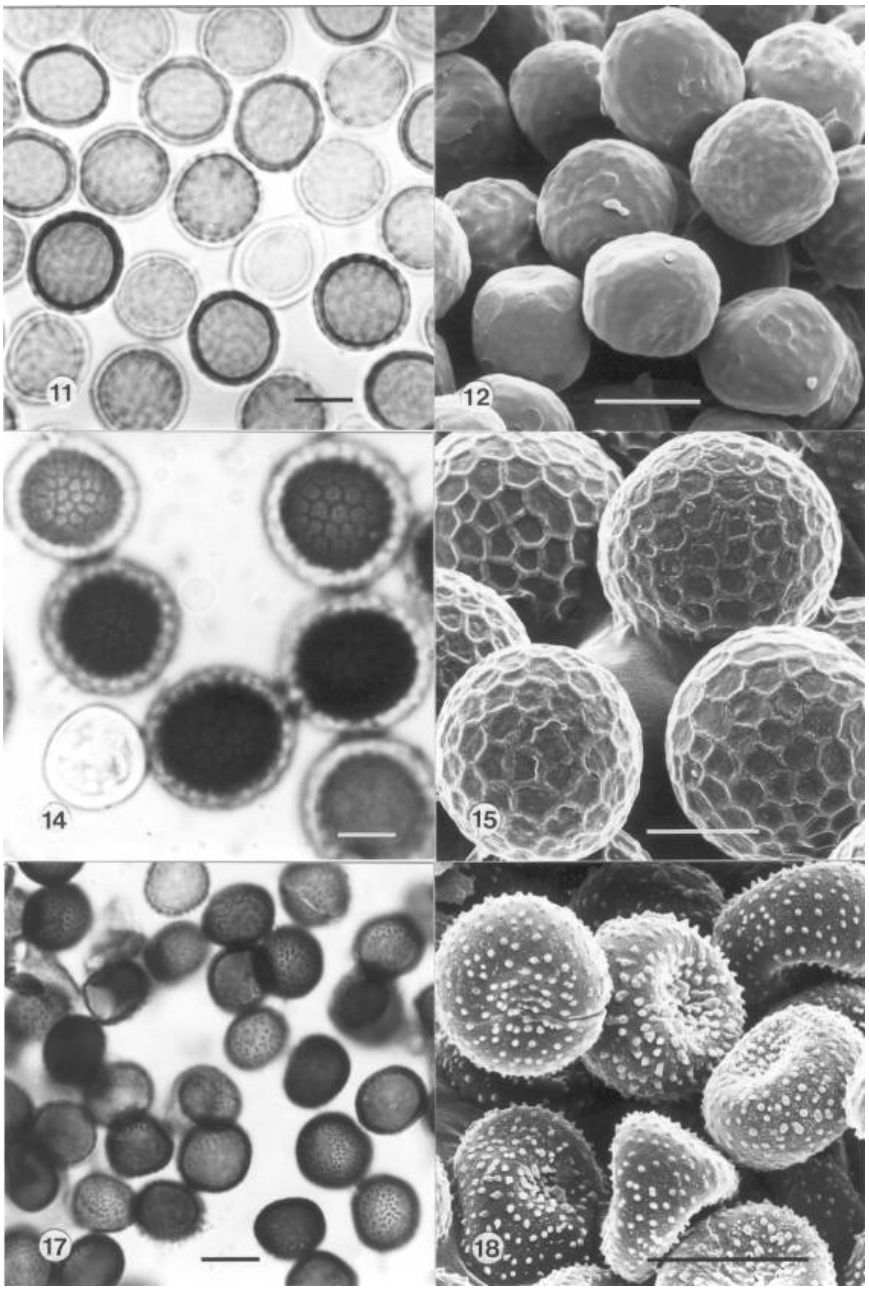
*Known distribution*: N. America (USA, Mexico).

Kellerman and Swingle (1889: 12) pointed out that infected male plants of the dioecious *Buchloë dactyloides* are transformed into female plants producing seeds filled with spores.

***Tilletia obscurareticulata*** Durán, 1987: 160 (as "*obscura-reticulata*"; ICBN, Art. 60.9). (Figs. 13-15)

Type on *Bouteloua rothrockii* Vasey, Mexico, Sonora, 44 km S. of Ciudad Obregon, off Hwy. 15, alt. 120 m, 18 October 1976, R. Durán & P.M. Gray, WSP 67747; isotype HUV 14475! Paratypes WSP 68803, WSP 68805; isoparatypes HUV 14476, HUV 14477.

*Sori* (Fig. 13) in some ovaries of an inflorescence, ovoid or lemon-shaped, 1-1.5 × 1.5-3 mm, showing between the glumes, covered by a thin, greyish-brown membrane of the pericarp which ruptures irregularly disclosing the dark brown, semiagglutinated to powdery mass of spores and sterile cells. *Spores* (Figs. 14, 15) globose, subglobose to broadly ellipsoidal, 20.5-28(-32) × 21-30(-34) µm, yellowish- to dark reddish-brown, obscurely reticulate, 5-8(-9),




**Figs. 11, 12.** Spores and sterile cells of *Tilletia buchloëana* on *Buchloë dactyloides*, in LM and in SEM (USA, Kansas, Newton, 15 June 1939; HUV 14734). **Figs. 14, 15.** Spores and sterile cells of *Tilletia obscurareticulata* on *Bouteloua rothrockii*, in LM and in SEM (type). **Figs. 17, 18.** Spores of *Ustilago aegopogonis* on *Aegopogon cenchroides*, in LM and in SEM (Mexico, 9 November 1969; HUV 14479). Bars = 10 µm.

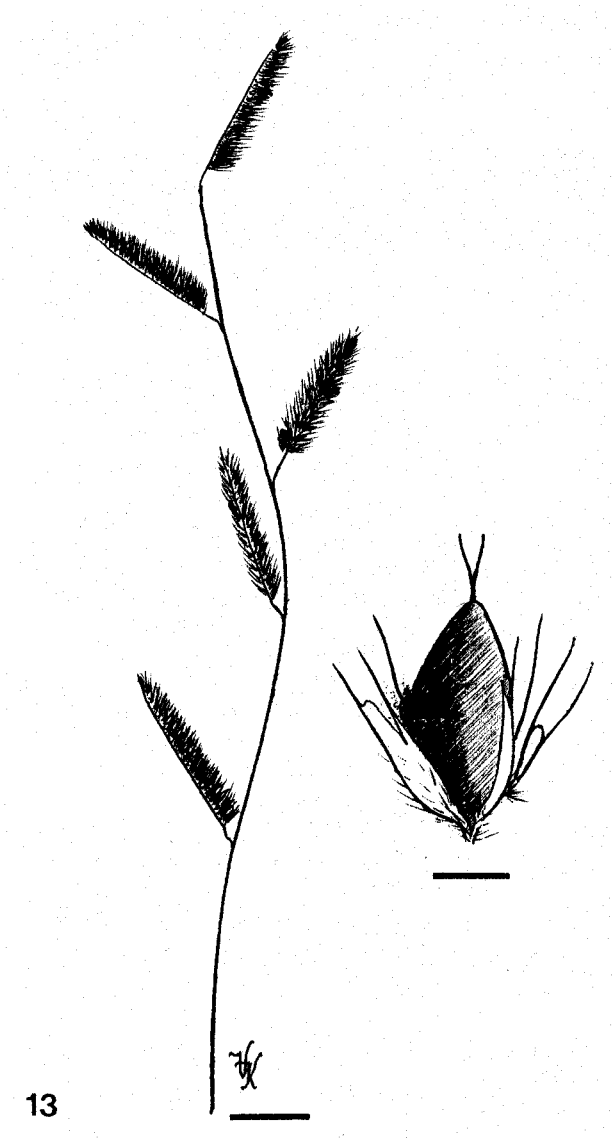



**Fig. 13.** Sori of *Tilletia obscurareticulata* in some ovaries of *Bouteloua rothrockii*. Enlarged a sorus. Bars = 1 cm for habit, 1 mm for detail drawings.

polyangular meshes per spore diameter, muri very thin, embedded in a 1-2 µm high, hyaline sheath, interspaces with 1-3 low warts. *Sterile cells* (Fig. 14) variable in shape and size, subglobose, ellipsoidal, irregular, 13-25(-30) µm long, subhyaline; wall 1.5-4 µm thick, smooth. *Spore germination* results in short, stout, usually unbranched holobasidia producing apically a large number of filiform, one-septate, binucleate basidiospores which do not fuse. (Durán, 1987: 160, pl. 85, figs. E, F, G).

*Host*: *Bouteloua rothrockii* Vasey.
*Known distribution*: N. America (Mexico).

***Ustilago aegopogonis*** Hennings, 1898: 267. (Figs. 16-18)

Lectoype (design. by Piepenbring, 2003: 152) on *Aegopogon cenchroides* H. & B. ex Willd., Mexico, near Mexico City, X.1896, E.W.D. Holway, BPI 156932!; isolectotype BPI 156934!

*Sori* (Fig. 16) on the top of shoots destroying the whole inflorescence, often comprising also the basal part or the whole uppermost leaf sheath, bearing acute leaf remnants. Sori fusiform, ovoid or cylindrical, 1-3 × 2-10(-15) mm, usually more or less hidden by leaf sheaths, covered by a first green, later brown peridium of host origin which ruptures irregularly disclosing the chocolate-brown, semiagglutinated to powdery mass of spores. *Spores* (Figs. 17, 18) often laterally slightly compressed, globoid, ellipsoidal or slightly irregular, 8-13 × 10.5-15 µm, reddish-brown; wall uneven, 0.5-1(-1.5) µm thick, thinner on the flattened sides, sparsely to moderately densely echinulate, spines short, spore profile wavy to finely serrulate. *Spore germination* results in 3-4-septate basidia producing long, ellipsoidal, mononucleate basidiospores (Durán, 1987: 221, pl. 103, fig. B).

*Hosts*: *Aegopogon cenchroides* H. & B. ex Willd., *Hilaria belangeri* (Steudel) Nash, *H. belangeri* (Steudel) Nash var. *longifolia* (Vasey) Hitchc., *H. cenchroides* Kunth.

*Known distribution*: N. America (USA, Mexico).

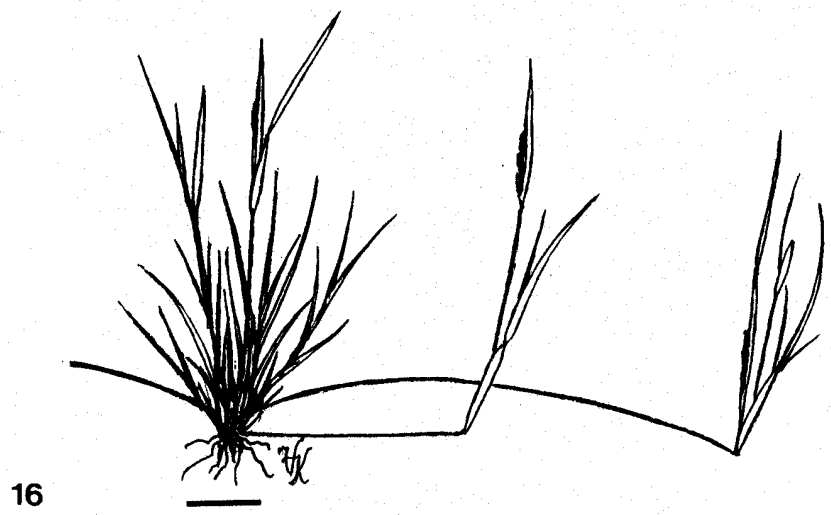



**Fig. 16.** Sori of *Ustilago aegopogonis* in the inflorescence of *Hilaria belangeri*. Bar = 1 cm.

***Ustilago boutelouae-humilis*** Brefeld, 1895: 116. (Figs. 19-21)

Neotype on *Bouteloua humilis* Hieron., Ecuador, Quito, "Exercierplatz" [drill-ground], April 1890, G. Lagerheim, (design. here) BPI 158144!

*Sori* (Fig. 19) destroying the inflorescence still enclosed by the leaves of the very small plants, long linear, 0.5-0.7 × 5-13 mm, filling the leaf sheaths with a black, powdery mass of spores surrounding the rachis of the inflorescence. No peridium, no sterile cells. *Spores* (Figs. 20, 21) globose, subglobose, ellipsoidal to slightly irregular, sometimes laterally slightly compressed, 11-17 × 14.5-18.5 µm, yellowish- to dark reddish-brown; spore wall even or slightly uneven but of variable thickness (0.5-2.5 µm), finely, densely verrucose-echinulate, spore profile smooth to very finely serrulate. *Spore germination* results in a germ tube with a short, 2-3-celled basal branch and a long, aseptate tube without forming basidiospores (Brefeld, 1895: 117, Pl. VII, fig. 13: 1-4).

*Host*: *Bouteloua humilis* Hieron.

*Known distribution*: S. America (Ecuador). Known only from the type collection.

The type specimen was lost in Berlin, during World War II, hence the designated neotype of the isotype, preserved in BPI.

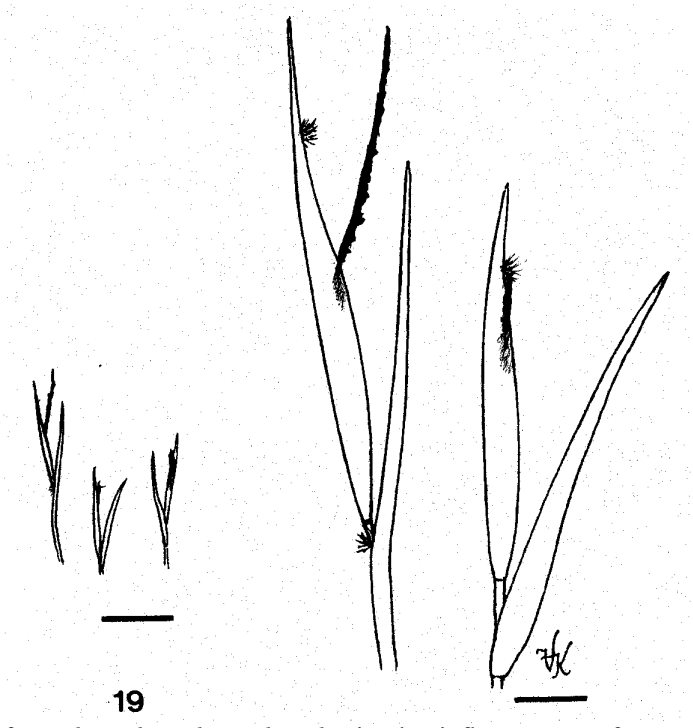
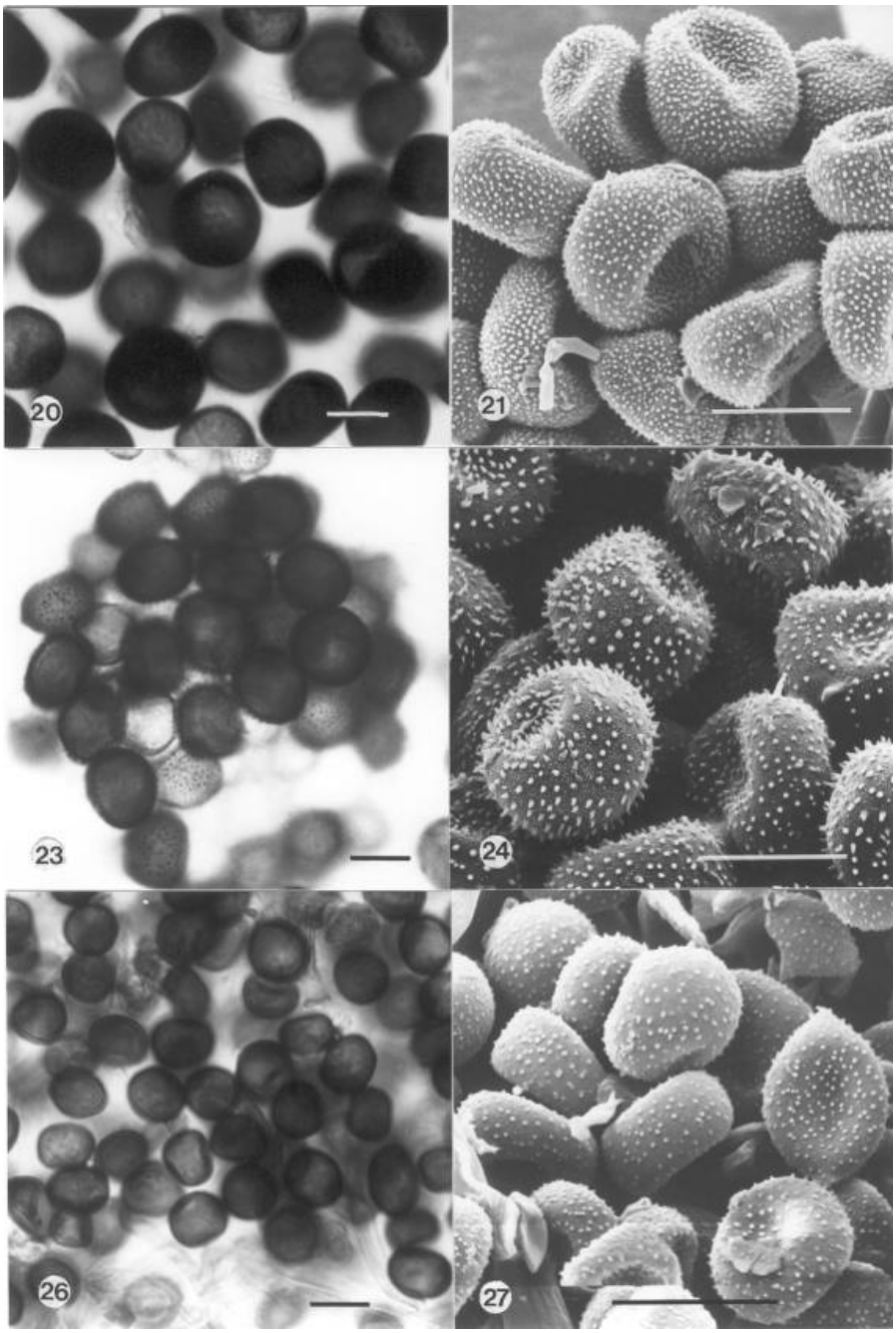



**Fig. 19.** Sori of *Ustilago boutelouae-humilis* in the inflorescence of *Bouteloua humilis*. Bars = 1 cm for habit, 2.5 mm for detail drawing.




**Figs. 20, 21.** Spores of *Ustilago boutelouae-humilis* on *Bouteloua humilis*, in LM and in SEM (type). **Figs. 23, 24.** Spores of *Ustilago buchloës* on *Bouteloua aristidoides*, in LM and in SEM (Sydow, Ust. no. 429; HUV 3401). **Figs. 26, 27.** Spores of *Ustilago calcarea* on *Bouteloua breviseta*, in LM and in SEM (type). Bars = 10 µm.

***Ustilago buchloës*** Ellis & Tracy, 1890: 77, s. lat. (Figs. 22-24)

Lectotype on *Buchloë dactyloides* (Nutt.) Engelm., USA, New Mexico, Coolidge, 20 June 1887, S.M. Tracy, (design. by Piepenbring, 2003: 158) BPI 159165!; isolectotypes BPI 159164 & 159166.

= *Ustilago filifera* Norton, 1896: 237. — Type on *Bouteloua racemosa* Lag. (= *B. curtipendula* (Michx.) Torr.) and *B. oligostachya* Torr. ex A. Gray (= *B. gracilis* (H.B.K.) Lag. ex Steudel), USA, Kansas, Riley and Wabaunsee Co., J.B.S. Norton (type ubi?). (syn. by Clinton, 1902: 129, as *U. hieronymi*).

= *Ustilago hieronymi* Schröter, in Hennings, 1896: 213. — Lectotype (design. here) on *Bouteloua ciliata* Griseb. (= *B. aristidoides* (H.B.K.) Griseb.), Argentina, Salta Prov., passage of Rio Juramento, 18-22 February 1873, G. Hieronymus & Lorentz 203, BPI 160760!; isolectotype BPI 160761! (syn. by Fischer, 1953: 246, confirmed).

= *Ustilago pseudohieronymi* Zundel, 1933: 351. — Lectotype on *Muhlenbergia squarrosa* (Trin.) Rydb., USA, Colorado, San Louis Valley, 27 June 1921, E. Bethel, (design. here) BPI 165475; isotypes BPI 165476-165478 (syn. by Fischer, 1953: 246).

= *Ustilago coloradensis* Zundel, 1933: 351. — Type on *Muhlenbergia gracillima* Torr., USA, Colorado, Manitou, 4 July 1924, E. Bethel, BPI 159658!; isotype BPI 159659! (syn. by Fischer, 1953: 246, confirmed).

= *Ustilago hieronymi* Schröter var. *insularis* Ciferri, 1933: 157. — Type on *Bouteloua heterostega* (Trin.) Griff., Dominican Republic, Cordillera Septentrional, Santiago Prov., Santiago, Cuesta de Piedra, hillside, 17 December 1930 and 15 March 1931, E.L. Ekman & R. Ciferri; isotypes in Ciferri, Mycofl. Doming. Exs. no. 134, HUV 2361! (syn. by Fischer, 1953: 246, confirmed).

*Sori* (Fig. 22) on leaves and sheaths, occasionally on stems or spikelets, forming conspicuous, bullate, globose, ovoid to linear, sausage-shaped pustules, (0.3-)0.5-1.5 × (0.3-)0.5-13 mm, first covered by the thin, greyish host epidermis which ruptures irregularly disclosing the black, semiagglutinated to powdery mass of spores. *Spores* (Figs. 23, 24) globose, ovoid, ellipsoidal or slightly irregular, some of them laterally slightly compressed, 10.5-14.5 × 11-16 µm, yellowish- to dark reddish-brown; wall more or less even, *ca*. 1 µm thick, sparsely to moderately densely echinulate, spore profile serrulate.

*Hosts*: *Bouteloua aristidoides* (H.B.K.) Griseb. (*B. ciliata* Griseb.), *B. barbata* Lag., *B. breviseta* Vasey, *B. chondrosioides* (H.B.K.) Benth. ex S. Watson, *B. curtipendula* (Michaux) Torr. (*B. racemosa* Lag.), *B. eriopoda* (Torr.) Torr., *B. filiformis* (Fourn.) Griff., *B. gracilis* (H.B.K.) Lag. ex Steudel (*B. oligostachya* Torr.), *B. heterostega* (Trin.) Griff., *B. hirsuta* Lag., *B. radicosa* (Fourn.) Griff., *B. rigidiseta* (Steudel) Hitchc., *Buchloë dactyloides* (Nutt.) Engelm., *Cathestecum erectum* Vasey & Hack., *C. stoloniferum* Griff., *Muhlenbergia richardsonis* (Trin.) Rydb. (*M. squarrosa* (Trin.) Rydb.), *M. torreyi* (Kunth) Hitchc. ex Bush (*M. gracillima* Torr.), *Tridens grandiflorus* (Vasey) Woot. & Standl., *T. pulchellus* (H.B.K.) Hitchc.

*Known distribution*: N. and S. America (USA, Mexico, Argentina), Antilles (Dominican Rep.).


**Fig. 22.** Sori of *Ustilago buchloës* on leaves and leaf sheaths of *Bouteloua aristidoides*. To the left a healthy plant. Bar = 1 cm.

There is some variation in the spore morphology between different samples from the same and from different host plants which, in my opinion, lies within the variability of this species and does not allow recognition of separate taxa.

Report of *Ustilago hieronymi* on *Triodia pungens* R. Br., and *T. mitchellii* Benth., from Australia (McAlpine, 1910: 155), refers to *U. altilis* H. Sydow.

***Ustilago calcarea*** Griffiths, 1904: 85. (Figs. 25-27)

Lectotype on *Bouteloua breviseta* Vasey, USA, New Mexico, upon the gypsum deposits 20 mi E of Roswell, 4 May 1903, D. Griffiths, (design. here) BPI 159506!; isolectotypes BPI 159502-04!, 159507-08!

*Sori* (Fig. 25) as short, superficial, not pustular striae between the veins on the modified, congested and overlapping leaf sheaths of very much shortened and repeatedly branched sterile shoots, appearing as small witches' brooms. Sori less frequently on the leaves. Spore mass blackish-brown, powdery. *Spores* (Figs. 26, 27) rather variable in shape and size, globose, subglobose, ovoid, ellipsoidal to slightly irregular, rarely pointed, 6.5-11 × 7.5-13.5(-14.5) µm, yellowish- to reddish-brown; wall even, 0.5-1.5 µm thick, apparently smooth to very finely, sparsely punctate, spore profile smooth.

*Host*: *Bouteloua breviseta* Vasey.

*Known distribution*: N. America (USA). Known only from the type locality.


**Fig. 25.** Sori of *Ustilago calcarea* forming witches' broom on *Bouteloua breviseta.* Bar = 1 cm.

***Ustilago hilariicola*** G.W. Fischer, 1952: 10. (Figs. 28-30)

Type on *Hilaria jamesii* (Torr.) Benth., USA, Nevada, Wabuska, 23 June 1947, G.W. Fischer, J.P. Meiners & R. Sprague, WSP 62098; isotypes BPI 160866, and in Fischer, Gramin. smuts N. Amer. no. 214, HUV 9939!

= *Ustilago hilariae* Hennings, 1898: 267 (later homonym, not *U. hilariae* Ellis & Tracy, 1890).

≡ *Ustilago affinis* Ellis & Everhart var. *hilariae* (Henn.) G.W. Fischer & Hirschhorn, 1945: 318.

≡ *Ustilago hilariae-henningsii* M. Piepenbring, 2003: 167 (nom. nov.). — Type on *Hilaria cenchroides* H.B.K., Mexico, near Mexico city, 2 October 1896, E.W.D. Holway, BPI 157006! (syn. by Vánky, 1996: 109).

*Sori* (Fig. 28) destroying the spikelets, isolated, 1-2 mm in diameter, or more or less merged, comprising the whole inflorescence, then 1-2 × 10-20 mm, at first protected by a thin, greyish-brown peridium which ruptures disclosing the dark brown, powdery spore mass, leaving the naked rachis behind. Sometimes only the basal part of the spikelets is destroyed. *Spores* (Figs. 29, 30) subglobose to ellipsoidal, (4-)5-7 × 5-7(-8) µm, yellowish-brown, with a tendency to be somewhat lighter coloured on one side in some of the spores; wall thin, *ca*. 0.5 µm, finely punctate-verruculose, in SEM sparsely verrucose. *Spore germination* results in 3-4 septate basidia, occasionally branching at the base, producing ellipsoidal, mononucleate basidiospores (Durán, 1987: 234, pl. 121, fig. D).

*Hosts*: *Hilaria belangeri* (Steudel) Nash, *H. belangeri* var. *longifolia* (Vasey) Hitchc., *H. cenchroides* H.B.K., *H. jamesii* (Torr.) Benth., *H. mutica* (Buckl.) Benth., *H. swallenii* Cory.

*Known distribution*: N. America (USA, Mexico).

*Ustilago hilariicola* in its appearance resembles *U. affinis* Ellis & Everh. (type on *Stenotaphrum americanum* Schrank, Jamaica) but differs from it especially in having smaller, more prominently ornamented spores. The spores in *U. affinis* are 5.5-8 × 6-10 µm, and very finely punctate. The host plants of these two smuts also belong to widely different tribes of *Gramineae*. The sori of *U. hilariicola* may resemble those of *U. aegopogonis*, in which the spores are 9-16 µm long.

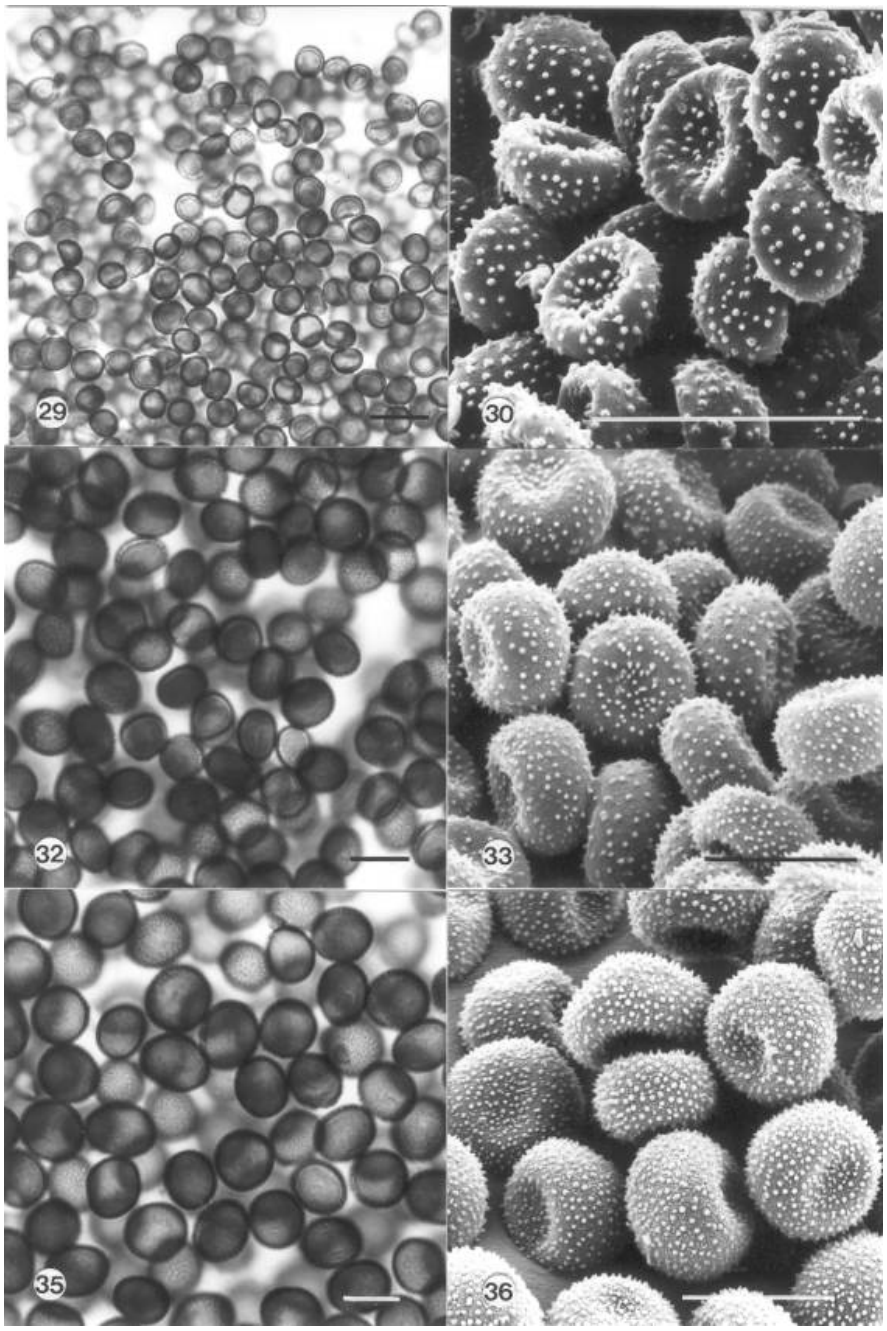
***Ustilago minor*** Norton, 1896: 238. (Figs. 31-33)

≡ *Ustilago hieronymi* Schröter var. *minor* (Norton) Ciferri, 1934: 262. — Type on *Bouteloua hirsuta* Lag., USA, Kansas, Manhattan, 22 June 1894, J.B.S. Norton; isotypes BPI 163378-163380 (scanty material).

*Sori* (Fig. 31) forming conspicuous, bullate, globose, ovoid to sausage-shaped pustules, usually in the spikelets, glumes, rachis and also on the leaves and leaf sheaths around the congested, rosette-like adventitious florets at the base of the panicles near the nodes. Sori 0.3-4 mm long, first covered by a thin,


**Fig. 28.** Sori of *Ustilago hilariicola* in the inflorescences of **A**. *Hilaria jamesii*. **B**. *Hilaria belangeri*. To the left a healthy inflorescence. Bars = 1 cm.

greyish peridium of host origin which ruptures irregularly disclosing the blackish-brown, semiagglutinated to powdery mass of spores. *Spores* (Figs. 32, 33) globose, subglobose, ovoid, ellipsoidal or slightly irregular, 7-9.5(-10.5) × 8-11 µm, yellowish-brown; wall even, *ca*. 0.5 µm thick, rather densely verruculose to echinulate, spore profile smooth to finely serrulate.




**Figs. 29, 30.** Spores of *Ustilago hilariicola* on *Hilaria jamesii*, in LM and in SEM (isotype). **Figs. 32, 33.** Spores of *Ustilago minor* on *Bouteloua aristidoides*, in LM and in SEM (Mexico, 19 October 1976; HUV 14627). **Figs. 35, 36.** Spores of *Ustilago opiziicola* on *Opizia stolonifera*, in LM and in SEM (type). Bars = 10 µm.


**Fig. 31.** Sori of *Ustilago minor* forming pustules in the spikelets and on the leaves of *Bouteloua aristidoides*. Bar = 1 cm.

*Hosts*: *Bouteloua aristidoides* (H.B.K.) Griseb. (*B. ciliata* Griseb.), *B. barbata* Lag., *B. hirsuta* Lag.

*Known distribution*: N. America (USA, Mexico).

*Ustilago minor* resembles *U. buchloës* in appearance but the sori in the latter species are commonly on the leaves and leaf sheaths, and the spores are larger (10.5-14.5 × 11-16 µm).

***Ustilago opiziicola*** Durán, 1987: 242. (Figs. 34-36)

Type on *Opizia stolonifera* Presl, Mexico, San Luis Potosi, 12.3 km W of the turnoff to El Refugio, off Hwy. 70, alt. 1158 m, 21 November 1978, R. Durán, WSP 67754; isotype HUV 14631!

*Sori* (Fig. 34) in some ovaries of an inflorescence, ovoid to cylindrical, 1-1.5 × 2-3.5 mm, often with a short acute tip, the remnant of the pistil. Sori covered by a rather thin, first green later brown peridium of host origin which ruptures irregularly at maturity, disclosing the dark brown, semiagglutinated to powdery mass of spores. *Spores* (Figs. 35, 36) globose, subglobose, ellipsoidal to slightly irregular, 8-11 × 9-13 µm, yellowish-brown; wall even, *ca*. 0.5 µm thick, finely, rather densely verruculose-echinulate, spore profile wavy to very finely serrulate. *Spore germination* results in 2-4-septate basidia with ovoid or short ellipsoidal, mononucleate basidiospores (Durán, 1987: 242, pl. 132, fig. C).

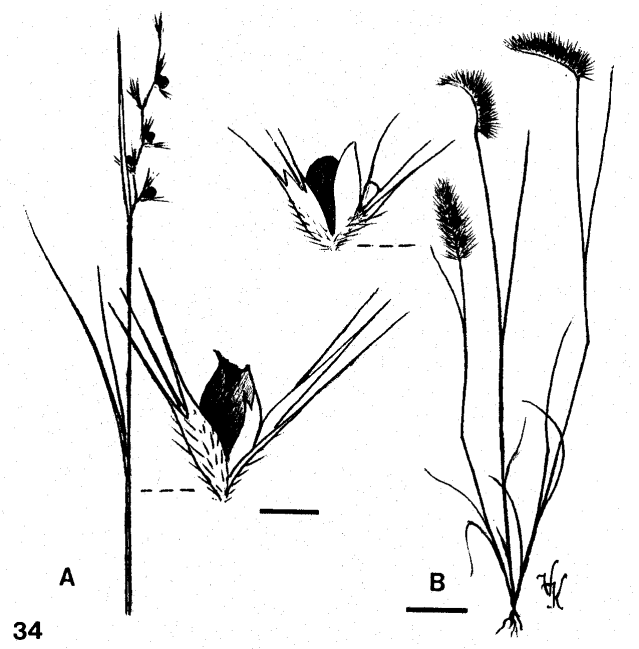



**Fig. 34.** Sori of *Ustilago opiziicola* in some ovaries of **A**. *Opizia stolonifera*. **B**. *Bouteloua simplex*. Habit and enlarged a spikelet of each with a sorus. Bars = 1 cm for habit, 2 mm for detail drawings.

*Hosts*: *Bouteloua simplex* Lag. (*Chondrosium simplex* (Lag.) Kunth), *Opizia stolonifera* Presl.

*Known distribution*: N. America (Mexico).

***Ustilago subminor*** Vánky, **sp. nov.** (Figs. 37-39)

Typus in matrice *Bouteloua rigidiseta* (Steudel) Hitchc., Mexico, Queretaro State, Tequisquiapan, 0.2 mi. NE Estacion Bernal, alt. 2042 m.s.m., sine die, leg. R. Durán et P.M. Gray. **Holotypus** in WSP 68777, isotypus in Herbario Ustil. Vánky, HUV 14682!

*Sori* sicut pustulae bullatae vel fusiformes foliorum cinereobrunneae vel striae, 0,5-1,5 × 1-10 mm, vel propter fusiones earum longiores, primo epidermide tectae, quo longitudinaliter rupto massam sporarum atrobrunneam, semiagglutinatam usque pulveream ostendentes. *Sporae* globosae, subglobosae usque late ellipsoidales, 5,5-7 × 6,5-9 µm, mediocriter atro-flavidobrunneae; pariete aequali, cca. 0,5 µm crasso, disperse punctato-verruculoso; imago obliqua sporarum levis, in SEM disperse humiliter verruculoso-echinulato.

*Sori* (Fig. 37) on the leaves as bullate or fusiform, greyish-brown pustules or streaks, 0.5-1.5 × 1-10 mm, or longer by fusion, first covered by the epidermis which ruptures longitudinally disclosing the dark-brown, semiagglutinated to powdery mass of spores. *Spores* (Figs. 38, 39) globose, subglobose to broadly ellipsoidal, 5.5-7 × 6.5-9 µm, medium dark yellowish-brown; wall even, *ca*. 0.5 µm thick, sparsely punctate-verruculose, spore profile smooth, in SEM sparsely, low verruculose-echinulate.

*Host*: *Bouteloua rigidiseta* (Steudel) Hitchc.

*Known distribution*: N. America (Mexico). Known only from the type collection.

***Ustilago vilfae*** G. Winter, 1883a: 2; 1883b: 7. (Figs. 40-42)

Type on *Vilfa vaginiflora* Torr. (= *Sporobolus vaginiflorus* (Torr.) Wood), USA, Pennsylvania, Chester Co., autumn 1881, coll. Martin Geo (Ellis no. 3729), NY; isotype BPI 169423 (devoid of sori).

= *Ustilago hilariae* Ellis & Tracy, 1890: 77 (not Hennings, 1898). — Lectotype (design. here) on *Hilaria jamesii* (Torr.) Benth., USA, New Mexico, Albuquerque, 17 June 1887, S.M. Tracy, BPI 160871!; isolectotypes BPI 160865, 160870. (syn. by Zundel, 1953: 217, confirmed).

= *Tilletia subfusca* Hume, 1902: 235. — Type on *Sporobolus neglectus* Nash, USA, Iowa, Spirit Lake, 15 November 1892, J.C. Arthur, BPI 173883! (syn. by Clinton, 1904: 331, confirmed).

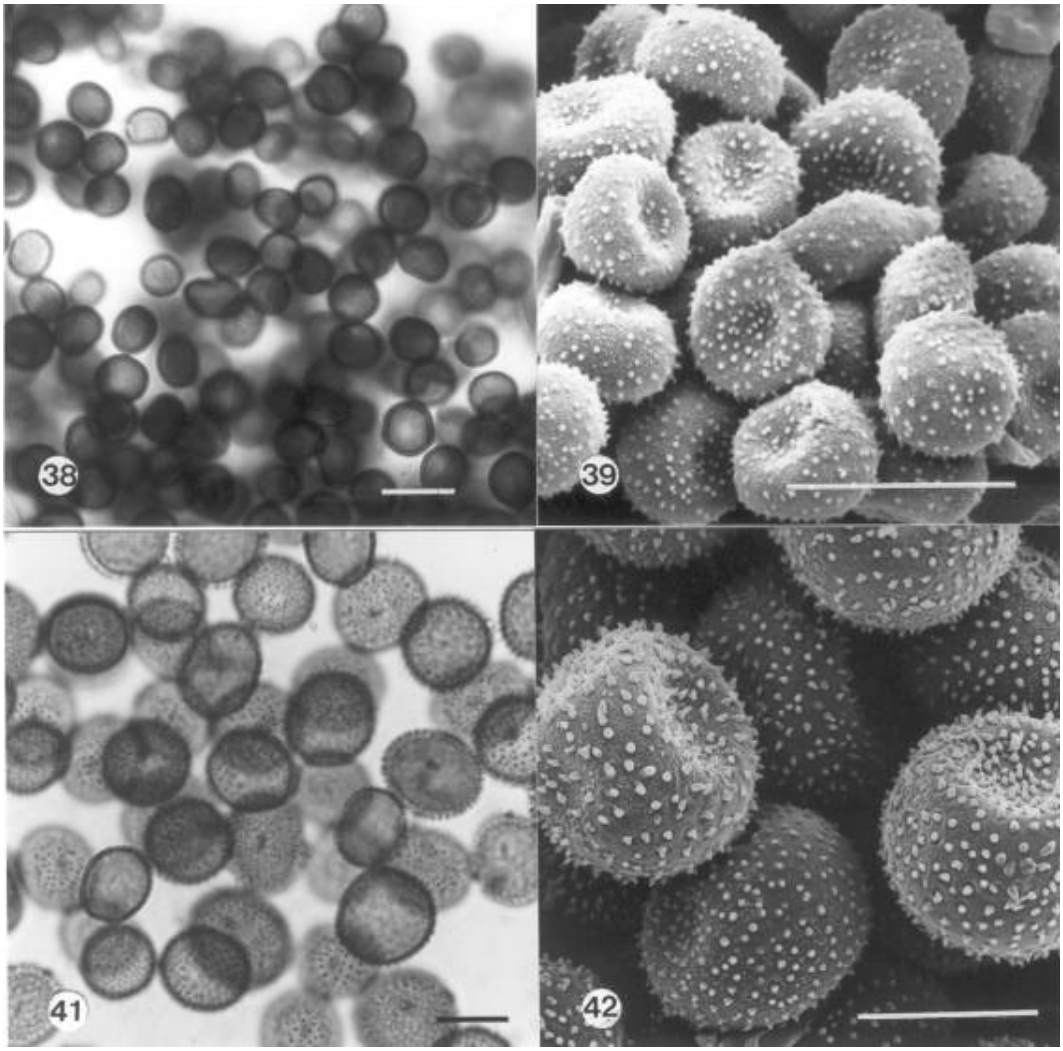
*Sori* (Fig. 40) in the inflorescence, transforming it into a dark brown, semiagglutinated to powdery spore mass, 1-3 × 4-10 mm, more or less hidden by the distal leaf sheaths, but sori may also comprise the basal part of the uppermost, congested leaf sheaths and are then larger, or they may appear on the distal part of the stems as vesicles, covered by the epidermis. *Spores* (Figs.


**Fig. 37.** Sori of *Ustilago subminor* forming bullate pustules on the leaves of *Bouteloua rigidiseta*. To the left a healthy, flowering plant. Bar = 1 cm.

41, 42) subglobose, ovoid or ellipsoidal, 12-14.5 × 12.5-16 µm, yellowish-brown; wall even, *ca*. 1 µm thick, evidently echinulate, spore profile serrulate.

*Hosts*: *Hilaria cenchroides* H.B.K., *H. jamesii* (Torr.) Benth., *H. mutica* (Buckl.) Benth., *Sporobolus neglectus* Nash, *S. vaginiflorus* (Torr.) Wood (*Vilfa vaginiflora* Torr.).

*Known distribution*: N. America (USA, Mexico).




**Figs. 38, 39.** Spores of *Ustilago subminor* on *Bouteloua rigidiseta*, in LM and in SEM (isotype). **Figs. 41, 42.** Spores of *Ustilago vilfae* on *Hilaria jamesii*, in LM and in SEM (type of *U. hilariae*; BPI 160871). Bars = 10 µm.

Zundel (1953: 165 & 217) treated *Ustilago vilfae* and *U. hilariae* as two separate species, whereas Fischer (1953: 316) considered them to be synonyms. Indeed, no differences in sorus or spore morphology could be seen between specimens on *Sporobolus* and *Hilaria*.

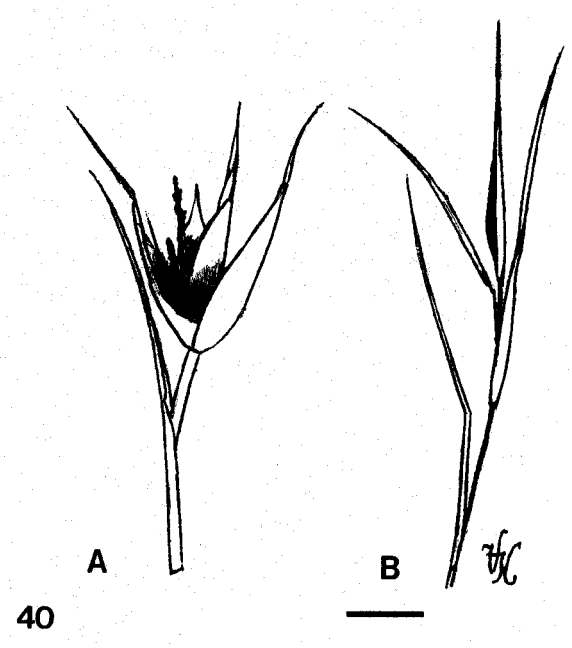



**Fig. 40.** Sori of *Ustilago vilfae* in the inflorescence of
**A**. *Hilaria mutica*,
**B**. *Sporobolus neglectus*.
Bar = 1 cm.

*Ustilago vilfae* on *Lasiurus sindicus* Henrard (= *L. hirsutus* (Forssk.) Boiss.), reported by Agarwal *et al*. (1977: 206) from India, Western Rajastan (HCIO 32094!) represents *Sporisorium desertorum* (Thümen) Vánky.

A report of *Ustilago hypodytes* (Schltdl.) Fr. (= *Tranzscheliella hypodytes* (Schltdl.) Vánky & McKenzie) on *Hilaria jamesii* (Torr.) Benth, from USA, Utah (Zundel, 1953: 169), based on a collection in BPI (no. 160959), refers to *Ustilago hilariicola* G.W. Fischer.

**Key to the smut fungi of *Boutelouinae*: *Aegopogon*, *Bouteloua*, *Buchloë*, *Cathestecum*, *Hilaria* and *Opizia* (*T.* = *Tilletia*, *U.* = *Ustilago*)**

1. Sori restricted to ovaries ..... 2
1. Sori not restricted to ovaries ..... 7

2. Sori in all ovaries of an inflorescence ..... 3
2. Sori in some ovaries of an inflorescence ..... 4

3. Spores evidently reticulate ..... ***T. aegopogonis***
3. Spores with inconspicuous, subpyramidal tubercles ..... ***T. buchloëana***

4. Spores obscurely reticulate ..... ***T. obscurareticulata***
4. Spores otherwise ornamented ..... 5

5. Spores 17-24 µm long, with blunt, pyramidal warts..... ***T. boutelouae***
5. Spores 8-13 µm long, verrucose-echinulate.....6

6. Sterile cells usually present between the spores. Sori often with seed remnant as an acute tip..... ***Macalpinomyces spermophorus***
6. Sterile cells absent. Sori without seed remnant..... ***U. opiziicola***

7(1). Sori destroying the whole inflorescence .....8
7. Sori in spikelets, on leaves or leaf sheaths.....10

8. Spores 14.5-18.5 µm long, finely verruculose-echinulate ..... ***U. boutelouae-humilis***
8. Spores shorter .....9

9. Spores 12.5-16 µm long, evidently echinulate..... ***U. vilfae***
9 Spores 5-7(-8) µm long, finely punctate-verruculose ..... ***U. hilariicola***

10(7). The fungus produces witches' brooms. Sori as not pustular striae on congested leaf sheaths ..... ***U. calcara***
10. The fungus does not produce witches' brooms. Sori otherwise .....11

11. Sori bullate, sausage-shaped on leaves, leaf sheaths or in spikelets .....12
11. Sori otherwise .....14

12. Spores 11-16 µm long..... ***U. buchloës***
12. Spores shorter .....13

13. Spores 8-11 µm long..... ***U. minor***
13. Spores 6.5-9 µm long..... ***U. subminor***

14(11). Sori destroying the inflorescence and the distal leaf sheath, fusiform, 2-10(-15) mm long. Spores 10.5-15 µm µm long ..... ***U. aegopogonis***
14. Sori in spikelets, isolated or merged. Spores 5-7(-8) µm long..... ***U. hilariicola***

**HOST – PARASITE LIST**
(*B. = Bouteloua, M. = Macalpinomyces, T. = Tilletia, U. = Ustilago*)

*Aegopogon cenchroides — U. aegopogonis*
*Aegopogon tenellus — T. aegopogonis*
*B. aristidoides — M. spermophorus*, *U. buchloës*, *U. minor*
*B. barbata — U. buchloës*, *U. minor*
*B. breviseta — U. buchloës*, *U. calcara*
*B. chondrosioides — M. spermophorus*, *U. buchloës*
*B. ciliata = B. aristidoides*
*B. curtipendula — U. buchloës*
*B. eriopoda — U. buchloës*
*B. filiformis — M. spermophorus*, *U. buchloës*
*B. gracilis — M. spermophorus, T. boutelouae*, *U. buchloës*
*B. heterostega — U. buchloës*
*B. hirsuta — M. spermophorus, U. buchloës, U. minor*

*B. humilis — U. boutelouae-humilis*
*B. oligostachya = B. gracilis*
*B. radicosa — U. buchloës*
*B. rigidiseta — U. buchloës, U. subminor*
*B. rothrockii — M. spermophorus*, *T. obscurareticulata*
*B. simplex — M. spermophorus, U. opiziicola*
*Buchloë dactyloides — T. buchloëana*, *U. buchloës*
*Cathestecum erectum — M. spermophorus*, *T. buchloëana, U. buchloës*
*Cathestecum prostratum — M. spermophorus, T. buchloëana*
*Cathestecum stoloniferum — U. buchloës*
*Chondrosium simplex = B. simplex*
*Eragrostis* spp. *— M. spermophorus*
*Hilaria belangeri — T. buchloëana*, *U. aegopogonis*, *U. hilariicola*
*Hilaria belangeri* var. *longifolia — M. spermophorus, U. aegopogonis*, *U. hilariicola*
*Hilaria cenchroides — U. aegopogonis, U. hilariicola*, *U. vilfae*
*Hilaria jamesii — Tranzscheliella hypodytes*, *U. hilariicola*, *U. vilfae*
*Hilaria mutica — U. hilariicola*, *U. vilfae*
*Hilaria swallenii — U. hilariicola*
*Muhlenbergia distichophylla — T. buchloëana*
*Muhlenbergia gracillima = Muhlenbergia torreyi*
*Muhlenbergia richardsonis — U. buchloës*
*Muhlenbergia squarrosa = Muhlenbergia richardsonis*
*Muhlenbergia torreyi — U. buchloës*
*Opizia stolonifera — U. opiziicola*
*Panicum* sp. *— M. spermophorus*
*Podosaemum distichophyllum = Muhlenbergia distichophylla*
*Sporobolus australasicus — M. spermophorus*
*Sporobolus neglectus — U. vilfae*
*Sporobolus vaginiflorus — U. vilfae*
*Tridens grandiflorus — U. buchloës*
*Tridens pulchellus — U. buchloës*
*Vilfa vaginiflora = Sporobolus vaginiflorus*

**FUNGUS NAMES**
(valid names in bold face)

***aegopogonis Tilletia***
***aegopogonis Ustilago***
*affinis Ustilago* var. *hilariae* = ***Ustilago hilariicola***
***boutelouae Tilletia***
*boutelouae Ustilago* = ***Macalpinomyces spermophorus***
***boutelouae-humilis Ustilago***
***buchloëana Tilletia***
***buchloës Ustilago***
***calcara Ustilago***
*cathesteci Tilletia* = ***Tilletia buchloëana***
*cathesteci Ustilago* = ***Tilletia buchloëana***
*cheoana Sphacelotheca* = ***Macalpinomyces spermophorus***
*convertere-sexualis Ustilago* = ***Macalpinomyces spermophorus***

*eragrostidis-japonicana Ustilago* = ***Macalpinomyces spermophorus***
*filifera Ustilago* = ***Ustilago buchloës***
*hieronymi Ustilago* = ***Ustilago buchloës***
*hieronymi Ustilago* var. *insularis* = ***Ustilago buchloës***
*hieronymi Ustilago* var. *minor* = ***Ustilago minor***
*hilariae* Ellis & Tracy, *Ustilago* = ***Ustilago vilfae***
*hilariae* Henn., *Ustilago* = ***Ustilago hilariicola***
*hilariae-henningsii Ustilago* = ***Ustilago hilariicola***
***hilariicola Ustilago***
*kusanoana Cintractia* = ***Macalpinomyces spermophorus***
*kusanoana Sphacelotheca* = ***Macalpinomyces spermophorus***
*kusanoana Ustilago* = ***Macalpinomyces spermophorus***
***minor Ustilago***
*obscura-reticulata* = ***obscurareticulata***
***obscurareticulata Tilletia***
***opiziicola Ustilago***
*orientalis Ustilago* = ***Macalpinomyces spermophorus***
*pseudohieronymi Ustilago* = ***Ustilago buchloës***
*pueblaensis Ustilago* = ***Macalpinomyces spermophorus***
*spermophora Sphacelotheca* = ***Macalpinomyces spermophorus***
*spermophora Ustilago* = ***Macalpinomyces spermophorus***
*spermophora Ustilago* var. *orientalis* = ***Macalpinomyces spermophorus***
***spermophorus Macalpinomyces***
*subfusca Tilletia* = ***Ustilago vilfae***
***subminor Ustilago***
*ugandensis Ustilago* var. *macrospora* = ***Macalpinomyces spermophorus***
***vilfae Ustilago***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