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

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Sixteen species of smut fungi are recognised on the grass genus *Muhlenbergia*. 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 by LM and SEM pictures of the spores. The name *Ustilago muhlenbergiae* Henn. var. *tucumanensis* Hirschh. [*U. tucumanensis* (Hirschh.) Zundel] is considered to be synonym of *U. mexicana* Ellis & Earle. A further five synonymies, established by G.W. Fischer, are confirmed. A key to the species and a host-parasite list are provided to facilitate the identification of the smut fungi of *Muhlenbergia*.

**Key words:** synonym, taxonomy.

### Introduction

Preparing a world monograph, *i.a.*, 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 *Muhlenbergia* is part of this project (*comp.* Vánky, 2002a).

*Muhlenbergia* Schreb., in the subfam. *Chloridoideae*, tribe *Eragrostideae*, subtribe *Sporobolinae*, has *ca.* 160 species in the New World, especially southern USA and Mexico, and *ca.* 8 species in southern Asia (Clayton and Renvoize, 1986: 227). Of the eight genera belonging to the subtribe *Sporobolinae*, smut fungi are known on *Crypsis* (one smut fungus), *Lycurus* (2 smuts), *Sporobolus* (16 spp., revised by Vánky, 2003c), and on *Muhlenbergia*. The recognised 16 smut fungi of *Muhlenbergia* are:

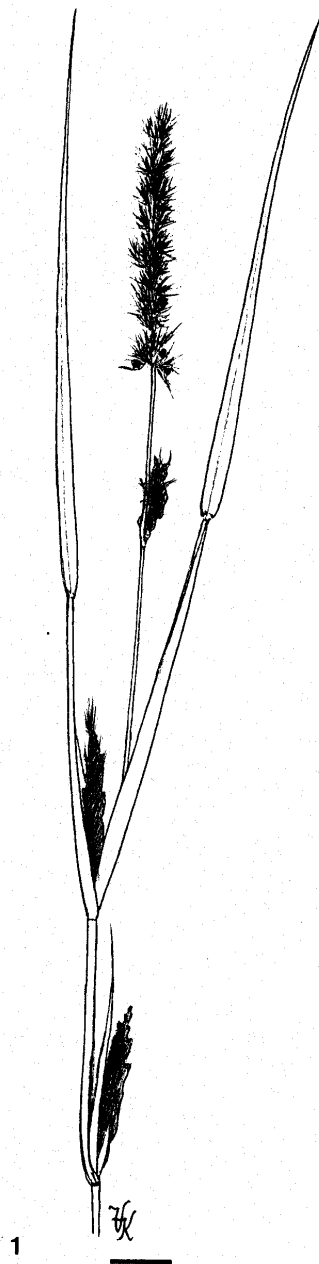
***Sporisorium montaniense*** (Ellis & Holway) Vánky, 1985: 118. (Figs. 1-3)

≡ *Ustilago montaniensis* Ellis & Holway, in Ellis and Everhart, 1890: 119.

≡ *Sphacelotheca montaniensis* (Ellis & Holway) G.P. Clinton, 1902: 141. — Type on *Muhlenbergia glomerata* (Willd.) Trin., USA, Montana, Sand Coulee, December 1887, F.W.

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**Fig. 1.** Sori of *Sporisorium montaniense* in the inflorescences of *Muhlenbergia glomerata*. Bar = 1 cm.

Anderson. Topotypes, collected in July 1888, BPI 163401!, 163402!, 195684!, and also distributed as "n. sp." in Ellis & Ev., N. Amer. fgi. no. 2263, HUV 1964!

= *Ustilago strangulans* Issatchenko, 1896: 225.

≡ *Sphacelotheca strangulans* (Iss.) G.P. Clinton, 1904: 392.

≡ *Sphacelotheca strangulans* (Iss.) Moesz, 1921: 62 (comb. superfl.). — Lectotype (design. by Vánky, 1985: 119) on *Eragrostis poaeoides* P. Beauv. (= *E. minor* Host), Russia, Cherson Prov., Nikolaiev, 2 July 1894. Topotype, collected in August 1897 by S. Fedossejew;

isotopotypes in Jacz., Kom., Tranz., Fgi. Ross. exs. no. 153, HUV 1965! (syn. by Fischer, 1953: 143, confirmed).

*Sori* (Fig. 1) on top of the shoots, usually destroying the whole inflorescence (although some healthy or aborted distal spikelets may be present), surrounding distal internodes and including also the basal part of the uppermost leaves. Sori irregularly cylindrical or ovoid, 1-4 mm wide, from a few mm to 2-3 cm long, partly protected by leaf-sheaths and covered by a whitish peridium composed of fungal elements and host tissue. At maturity, the peridium ruptures irregularly to expose the dark brown, powdery spore mass surrounding a stout, narrowing, central columella, often with short, lateral branches. Rarely, sori restricted to individual spikelets only. *Spores* (Figs. 2, 3) globose, ovoid to slightly irregular,  $10-14.5 \times 12.5-15 \mu\text{m}$ , yellowish-brown to reddish-brown; wall even,  $0.8-1 \mu\text{m}$  thick, moderately densely echinulate, spore profile finely serrulate, in SEM sparsely to moderately densely, minutely verruculose between the spines. *Sterile cells*, if present among the spores, in easily separable, irregular groups, subglobose to irregular, smaller than the spores, hyaline, thick-walled, smooth.

*Hosts*: numerous *Eragrostis* species, cosmopolitan. Also on *Muhlenbergia asperifolia* (Nees & Meyen) Parodi, *M. cuspidata* (Torr.) Rydb., *M. glomerata* (Willd.) Trin., *M. pulcherrima* Scribner, *M. racemosa* (Michaux) B.S.P.

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

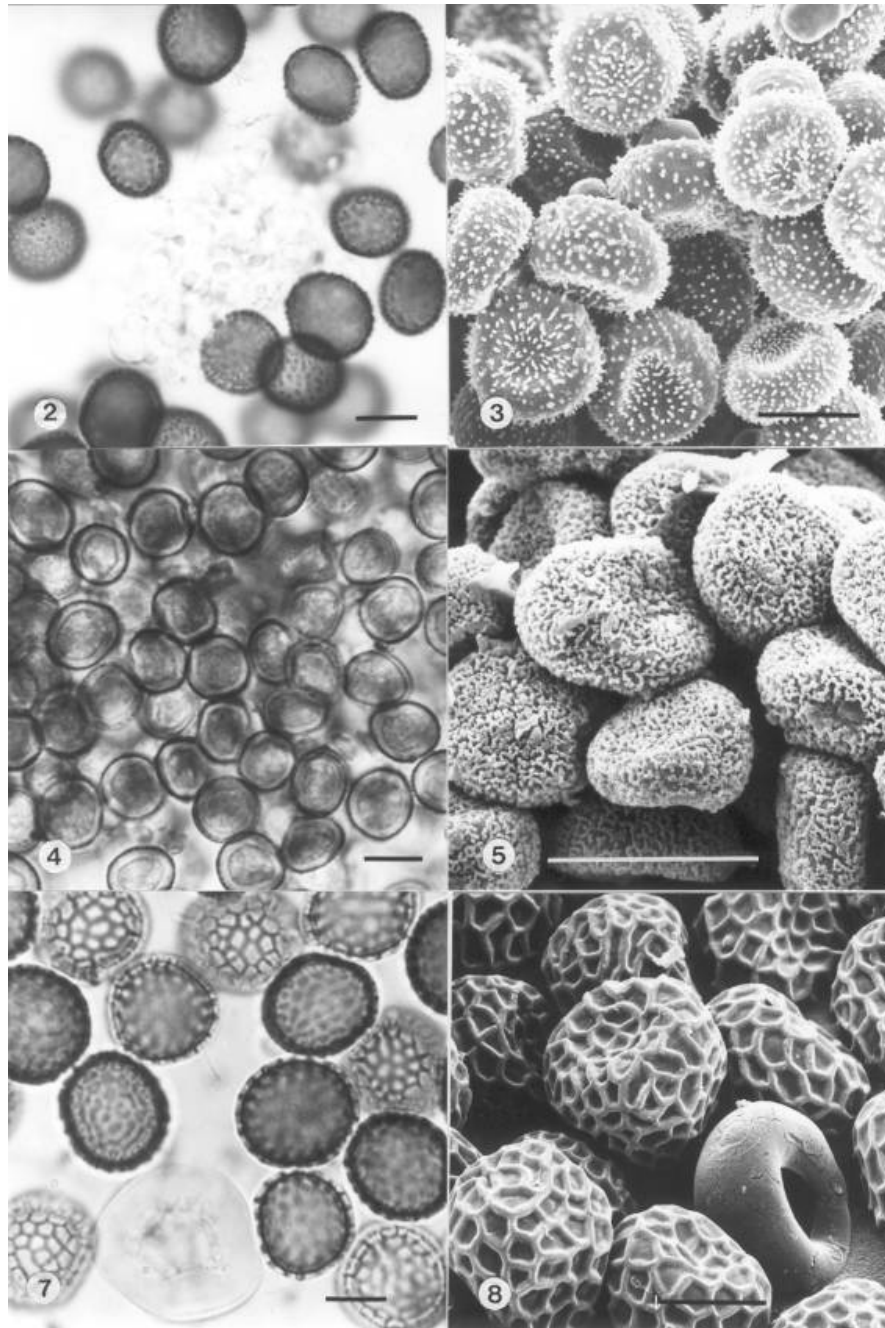
***Sporisorium parodii*** (Hirschh.) Vánky, 2003b: 59. (Figs. 4-5)

≡ *Ustilago parodii* Hirschhorn, 1939: 404. — Type on *Muhlenbergia diffusa* Willd. (= *M. schreberi* Gmel.), Argentina, near La Plata, Bosque, October 1935, L.R. Parodi, Herb. Hirschhorn 35; isotype LPS 3055! Topotype LPS 3054.

*Sori* comprising the distal part of the shoots (inflorescence? and some terminal leaves), long cylindrical,  $3-4 \times 10-12 \text{ mm}$ , first covered by a whitish-brown peridium with the tips of 1-2 leaves. The peridium ruptures longitudinally disclosing the brown, granular to powdery mass of spores surrounding 8-12 filiform columellae of the length of the sorus. *Spores* (Figs. 4, 5) single when mature, globose, subglobose, ellipsoidal to slightly irregular,  $8-12 \times 8-15 \mu\text{m}$ , globose spores  $8-12 \mu\text{m}$  in diameter, yellowish-brown; wall even,  $1-2 \mu\text{m}$  thick, finely, densely verruculose, spore profile wavy to finely serrulate, in SEM warts in irregular, small groups or short, irregular, labyrinthiform rows. *Sterile cells* not seen. *Spore germination* results in 4-celled basidia developing mycelia (Hirschhorn, 1939: 405 + fig. 4C).

*Host*: *Muhlenbergia schreberi* Gmelin (*M. diffusa* Willd.).

*Known distribution*: S. America (Argentina).



**Figs. 2, 3.** Spores and sterile cells of *Sporisorium montaniense* on *Muhlenbergia glomerata*, in LM and in SEM (topotype). **Figs. 4, 5.** Spores of *Sporisorium parodii* on *Muhlenbergia schreberi*, in LM and in SEM (type). **Figs. 7, 8.** Spores and sterile cells of *Tilletia asperifolia* on *Muhlenbergia asperifolia*, in LM and in SEM (Fischer, Gramin. smuts N. Amer. no. 2; HUV 9966). Bars = 10  $\mu$ m.



**Fig. 6.** Sori of *Tilletia asperifolia* in the ovaries of *Muhlenbergia asperifolia*. Enlarged a spikelet with two sori. Bars = 1 cm for habit, 1 mm for the detail drawing.

***Tilletia asperifolia*** Ellis & Everhart, 1887: 55. (Figs. 6-8)

Type on *Sporobolus asperifolius* Nees & Meyen (= *Muhlenbergia asperifolia* (Nees & Meyen) Parodi), USA, Rocky Mountains, comm. F.L. Scribner.

= *Tilletia eremophila* Spegazzini, 1909: 291.

≡ *Tolyposporella eremophila* (Speg.) Ciferri, 1938: 224. — Lectotype (design. by Vánky, 2003b: 36) on *Sporobolus asperifolius* Nees & Meyen, Argentina, Mendoza, 5 December 1902, C. Spegazzini, LPS 3676; syntype LPS 3675. (syn. by Durán and Fischer, 1961: 30, confirmed).

*Sori* (Fig. 6) in all ovaries of an inflorescence, ovoid or broadly ellipsoidal, 0.5-1 × 0.5-1.5 mm, evident between the spreading floral envelopes, first covered by the greyish-brown, delicate pericarp which ruptures irregularly, disclosing the light to dark reddish-brown, powdery mass of spores and sterile cells. *Spores* (Figs. 7, 8) globose, subglobose, ovoid, ellipsoidal to slightly irregular, 17-22.5 × 20-25 µm, pale to medium dark yellowish-brown; wall reticulate, meshes polyangular, of very variable diameter, rarely incomplete, 6-8 per spore diameter, muri 1.5-2.5 µm high, in optical median view acute, spiniform, rarely subacute, embedded in a hyaline or yellowish-brown tinted sheath extending just beyond the muri. *Sterile cells* (Figs. 7, 8) subglobose, ovoid, elongated, often subpolyhedrally irregular, of variable size, 11-24 × 13-35 µm, subhyaline, content pale yellowish-brown tinted, granular; wall 2-7 µm thick, smooth.

*Hosts*: *Muhlenbergia arenacea* Buckl. (*Sporobolus auriculatus* Vasey), *M. asperifolia* (Nees & Meyen) Parodi (*Sporobolus asperifolius* Nees & Meyen).

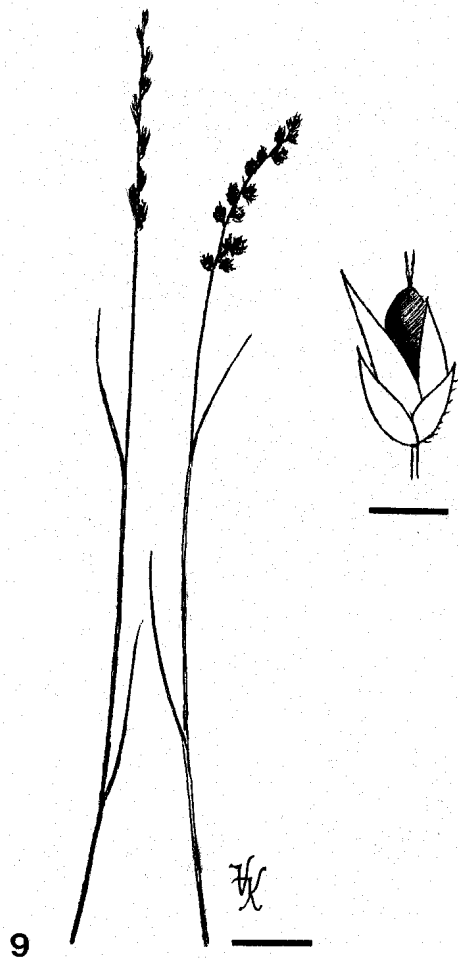
*Known distribution*: N. and S. America (Canada, USA, Mexico, Argentina), common.

Other host plants, given in the literature, such as *M. arenacea* (Buckl.) Hitchc. (*Sporobolus auriculatus* Vasey), *M. filiformis* (Thurb.) Rydb., *M. minutissima* (Steudel) Swallen, *Sporobolus confusus* Vasey, have to be checked. At least *M. minutissima* (*Sporobolus microspermus* (Lag.) Hitchc.) from USA, Colorado, 31 August 1899, coll. Bartholomew 2582 (as on *S. confusus* Vasey), BPI 172516, 172517, 172474, represents *Muhlenbergia asperifolia* (teste K. Vánky).

***Tilletia asperifolioides*** G.W. Fischer, 1952: 6. (Figs. 9-11)

Type on *Muhlenbergia cuspidata* (Torr.) Rydb., USA, Colorado, Sand Creek, 10 August 1948, G.W. Fischer, R. Sprague & J.P. Meiners; isotypes in Fischer, Gramin. smuts N. Amer. no. 237, HUV 9972! Paratype on *Muhlenbergia filiformis* (Thurb.) Rydb. (= misnamed *M. cuspidata*, teste K. Vánky), USA, Oregon, Silvies Creek, 28 July 1950, G.W. Fischer & R. Sprague; isoparatypes in Fischer, Gramin. smuts no. 253, HUV 9973!

*Sori* (Fig. 9) in all ovaries of an inflorescence, narrow ellipsoidal to ovoid, with a short acute tip and remnant of the style, 0.5-1 × 1-2 mm, more or less hidden by the floral envelopes, first covered by the greenish- to greyish-brown, delicate pericarp which ruptures irregularly, disclosing the blackish-brown, powdery mass of spores and sterile cells. *Spores* (Figs. 10, 11) globose, subglobose, broadly ellipsoidal to slightly irregular, 23-29(-32) × 24-30(-34) µm, medium to dark reddish-brown; wall reticulate, meshes polyangular, often incomplete, (4-)5-6 per spore diameter, muri 1.5-2.5 µm high, in optical median view subacute or acute, spiniform (especially in young spores). Meshes embedded in a hyaline or yellowish-brown tinted sheath, which in young, pale



**Fig. 9.** Sori of *Tilletia asperifolioides* in the ovaries of *Muhlenbergia cuspidata*. Enlarged a sorus. To the left a healthy inflorescence. Bars = 1 cm for habit, 1 mm for the detail drawing.

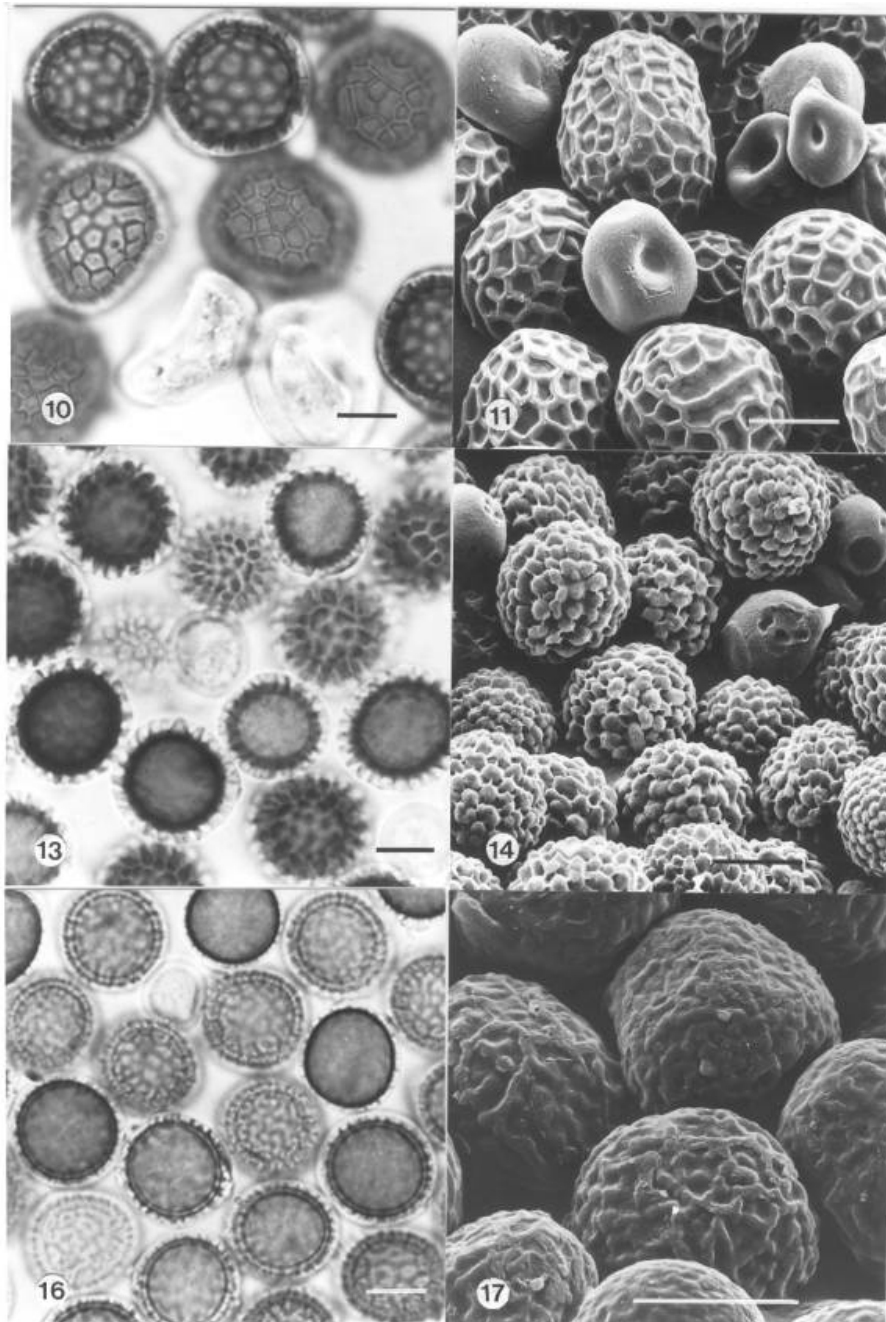
coloured spores exceed the muri by 1-2  $\mu\text{m}$ , in dark spores sheath is apparently lacking. *Sterile cells* (Figs. 10, 11) variable in shape and size, subglobose, ellipsoidal, usually subpolyhedrally irregular, 15-28  $\times$  16-38  $\mu\text{m}$ , subhyaline to pale yellowish-brown tinted; wall 2-7  $\mu\text{m}$  thick, smooth; the large, thick-walled cells are often irregularly verrucose or with trace of a reticulum ("immature spores", "intermediate forms").

*Host:* *Muhlenbergia cuspidata* (Torr.) Rydb.

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

*T. asperifolioides* differs from *T. asperifolia* especially by the larger, darker spores with fewer meshes per spore diameter and higher muri.

The host plants of the HUV sample of the paratype, and those of a further collection (HUV 6878 ex WSP 62023) are *Muhlenbergia cuspidata* (Torr.)



**Figs. 10, 11.** Spores and sterile cells of *Tilletia asperifolioides* on *Muhlenbergia cuspidata*, in LM and in SEM (Fischer, Gramin. smuts N. Amer. no. 257; HUV 9972). **Figs. 13, 14.** Spores and sterile cells of *Tilletia macrotuberculata* on *Muhlenbergia pulcherrima*, in LM and in SEM (type). **Figs. 16, 17.** Spores and sterile cells of *Tilletia montana* on *Muhlenbergia filiformis*, in LM and in SEM (type). Bars = 10  $\mu$ m.



Rydb., possessing acute glumes, not the closely related *M. filiformis* (Thurb.) Rydb., which has ovate, obtuse glumes.

***Tilletia macrotuberculata* Durán, 1987: 156. (Figs. 12-14)**

Type on *Muhlenbergia pulcherrima* Scribner, Mexico, Durango, 55.3 km W of Durango, off Hwy. 40, alt. 2621 m, 27 October 1976, R. Durán, WSP 67746; isotype HUV 14464! Paratypes on *Muhlenbergia wolfii* (Vasey) Rydb., Mexico, Durango, 2.6 km W of the turnoff to Lecheria, off Hwy 40, alt. 2682 m, 12 & 21 October 1978, R. Durán & P.M. Gray, WSP 68617 & 68675; isoparatypes HUV 14465 & 14466.

*Sori* (Fig. 12) in all ovaries of an inflorescence, spherical to ovoid, 0.5-1 × 0.5-1 mm, showing between the spreading floral envelopes, first covered by the yellowish- to dark brown, fragile pericarp which ruptures irregularly, disclosing the dark reddish-brown, powdery mass of spores and sterile cells. *Spores* (Figs. 13, 14) globose, subglobose to broadly ellipsoidal, 19-23(-25) × 21-24(-28) μm, pale to dark yellowish-brown, provided with 2.5-4 μm high, blunt, subcylindrical or subpyramidal warts or tubercles with subacute or flattened tip, embedded in a subhyaline or amber tinted sheath. In surface view, the warts appear as darker, irregular, polyangular spots, (4-)5-7(-8) per spore diameter. *Sterile cells* (Figs. 13, 14) subglobose, ovoid, ellipsoidal, to slightly irregular, smaller than the spores, 10-18.5 × 12-24 μm, subhyaline with a pale yellow, granular content; wall 1.5-3(-4) μm thick, smooth, occasionally finely laminated. *Spore germination* results in holobasidia bearing a terminal whorl of ca. 16, long, fusiform, first mononucleate, later septate and binucleate basidiospores which do not fuse (Durán, 1987: 157, pl. 79, Figs. G, H).



**Fig. 12.** Sori of *Tilletia macrotuberculata* in the ovaries of *Muhlenbergia pulcherrima*. Enlarged a sorus and a healthy spikelet. Bars = 1 cm for habit, 1 mm for the detail drawing.

*Hosts: Muhlenbergia pulcherrima* Scribner, *M. wolfii* (Vasey) Rydb.  
*Known distribution:* N. America (Mexico).

***Tilletia montana*** Ellis & Everhart, 1887: 55. (Figs. 15-17)

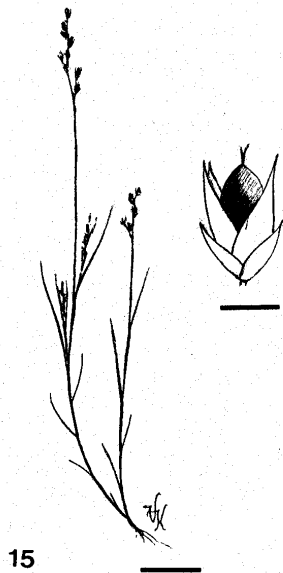
Lectotype on *Sporobolus gracillimus* Vasey (= *Muhlenbergia filiformis* (Thurb.) Rydb.), USA, Rocky Mountains, 1886, F.L. Scribner, (design. here) BPI 173611; isolectotype BPI 173610.

*Sori* (Fig. 15) in all ovaries of an inflorescence, ovoid or ellipsoidal, 0.5-1 × 0.5-1.5 mm, more or less hidden by the floral envelopes, first covered by the pale or greyish-brown, delicate pericarp which ruptures irregularly, disclosing the reddish-brown, powdery mass of spores and sterile cells. *Spores* (Figs. 16, 17) globose, subglobose, ellipsoidal to slightly irregular, 18-20 × 19-24 μm, pale to medium dark honey-yellow; wall basically reticulate but mostly incompletely and irregularly, giving the spore surface a peculiar, irregular aspect, muri 1-1.5 μm high, in optical median view acute, spiniform, embedded in a hyaline sheath, which usually exceeds the muri by 0.5-1 μm. Spores occasionally lacrymiform, with an acute tip, more often only with a hyaline papilla or a narrow appendage, the remnant of the sporogenous hypha. In SEM muri appear thick (due to the dried sheath), irregular, cerebriform. *Sterile cells* (Fig. 16) few, rounded irregular, often with flattened sides, smaller than the spores, 6.5-12 × 8-16 μm, subhyaline; wall 0.5-4 μm thick, smooth.

*Host: Muhlenbergia filiformis* (Thurb.) Rydb. (*Sporobolus gracillimus* Vasey; *S. simplex* Scribner).

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

The HUV sample (no. 14736) of "*Tilletia asperifolia*" on *Sporobolus simplex*, in Griffiths, W. Amer. fgi. no. 226, represents *T. montana*.



**Fig. 15.** Sori of *Tilletia montana* in the ovaries of *Muhlenbergia filiformis*. Enlarged a sorus. Bars = 1 cm for habit, 1 mm for the detail drawing.

***Tilletia muhlenbergiae*** G.P. Clinton, 1906: 49. (Figs. 18-20)

Type on *Muhlenbergia schaffneri* Fourn. var. *elongata* Scribner, Mexico, north-eastern Durango, October 1905, C.G. Pringle, BPI 173618; isotype BPI173617.

*Sori* (Fig. 18) in all ovaries of an inflorescence, fusiform, ellipsoidal or ovoid, often with a short, acute tip, 0.5-1 × 1-3 mm, more or less hidden by the floral envelopes, first covered by the greyish-brown pericarp which ruptures at maturity, disclosing the dark reddish- to blackish-brown, powdery mass of spores and sterile cells. *Spores* (Figs. 19, 20) globose, subglobose, ovoid, ellipsoidal to slightly irregular, 28-33 × 29-36(-38) μm, yellowish- to dark reddish- or smoke-brown; wall coarsely reticulate, meshes polyangular, regular to irregular, rarely incomplete, 4-6 per spore diameter, muri 2-4 μm high, in optical median view acute, interspaces rough to finely verruculose, sheath lacking. *Sterile cells* (Figs. 19, 20) subglobose, ovoid, ellipsoidal to slightly irregular, smaller than the spores, 12-25 × 16-30 μm, subhyaline or yellowish tinted; wall 1.5-4 μm thick, smooth. *Spore germination*: on top of holobasidia fusiform, multinucleate, aseptate basidiospores are produced which do not fuse (Durán, 1987: 158, pl. 81, fig. B).

*Hosts*: *Muhlenbergia depauperata* Scribner, *M. microsperma* (DC.) Kunth, *M. quadridentata* Kunth, *M. schaffneri* Fourn. var. *elongata* Scribner, *M. tenella* (H.B.K.) Trin.

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

***Tilletia pachyderma*** G.W. Fischer, 1952: 7. (Figs. 21-22)

Type on *Muhlenbergia utilis* (Torr.) Hitchc., Mexico, Mexico State, Temascaltepec Distr., ca. 50 km SW of Toluca, Tequexquiapan, 28 October 1932, G.B. Hinton 2319, WSP 34683 (lacking sori); isotype BPI 173661 (poor material).

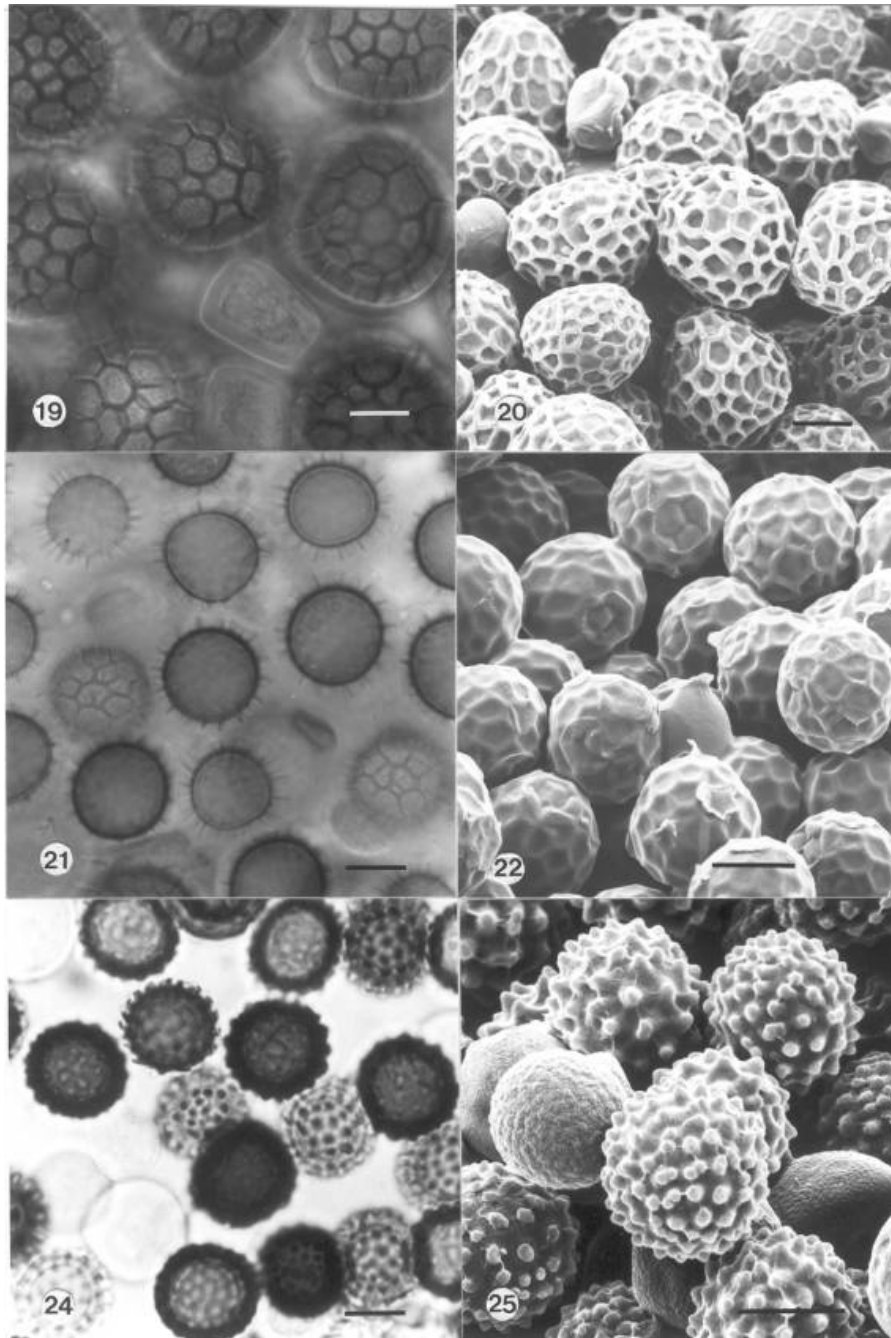
*Sori* in all ovaries of an inflorescence, 2-3 mm long, showing through the lemma and palea, first covered by the rather durable, olive-green to greyish-green pericarp which upon rupturing releases the light golden- to honey-brown, semiagglutinated to powdery mass of spores and sterile cells. *Spores* (Figs. 21, 22) globose, subglobose to broadly ellipsoidal, 18.5-22.5 × 18.5-24 μm (excluding the sheath); wall reticulate, 3-6(-7) meshes per spore diameter, muri in optical median view acute, 1.5-3(-4) μm high, embedded in a thick, hyaline sheath, usually considerably exceeding the muri. In SEM, due to the dried sheath, the spores appear only with shallow meshes. *Sterile cells* (Figs. 21, 22) few, subglobose, ovoid to irregular, 16-25 μm long, hyaline; wall two-layered, 4-7 μm thick, smooth, content yellowish-tinted, granular.

*Host*: *Muhlenbergia utilis* (Torr.) Hitchc.

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



**Fig. 18.** Sori of *Tilletia muhlenbergiae* in the ovaries of *Muhlenbergia microsperma*. Enlarged a sorus and a healthy spikelet. To the left a healthy inflorescence. Bars = 1 cm for habit, 1 mm for the detail drawing.



**Figs. 19, 20.** Spores and sterile cells of *Tilletia muhlenbergiae* on *Muhlenbergia microsperma*, in LM and in SEM (Mexico, Oaxaca State, Las Animas, 16 November, 1978, R. Durán & P.M. Gray, HUV 14470). **Figs. 21, 22.** Spores and sterile cells of *Tilletia pachyderma* on *Muhlenbergia utilis*, in LM and in SEM (type). **Figs. 24, 25.** Spores and sterile cells of *Tilletia tuberculata* on *Muhlenbergia depauperata*, in LM and in SEM (type). Bars = 10  $\mu$ m.



**Fig. 23.** Sori of *Tilletia tuberculata* in the ovaries of *Muhlenbergia depauperata*. Enlarged a spikelet with a sorus and a healthy spikelet. Bars = 1 cm for habit, 1 mm for the detail drawing.

*Tilletia tuberculata* Durán, 1987: 164.

(Figs. 23-25)

Type on *Muhlenbergia depauperata* Scribner, Mexico, Durango, 8 km W of Durango, off Hwy. 40, alt. 2072 m, 27 October 1976, R. Durán, WSP 67749; isotype HUV 14049! (For paratypes see Durán, 1987: 165).

*Sori* (Fig. 23) in some ovaries of an inflorescence, long fusiform, often with widened basal part,  $0.5-1.5 \times 1.5-4(-5)$  mm, showing between the floral envelopes, first covered by the thin, olivaceous- to dark brown pericarp, which ruptures irregularly at maturity, disclosing the dark brown, semiagglutinated to powdery mass of spores and sterile cells. *Spores* (Figs. 24, 25) globose or subglobose,  $15-20(-21.5) \times 15-21(-23)$   $\mu\text{m}$ , from pale yellowish- to dark reddish-brown, provided with subacute or blunt, conical warts (tubercles), 1-2.5  $\mu\text{m}$  high, in surface view appearing as rounded, darker spots, (3-)4-6(-8) per spore diameter. The warts are connected with each other by thin, darker lines, evident especially in LM, on dark spores. *Sterile cells* (Figs. 24, 25)

subglobose, broadly ellipsoidal to slightly irregular, extremely variable in size, subglobose cells 8-28  $\mu\text{m}$  in diameter, subhyaline to pale yellowish-brown; wall 1-3  $\mu\text{m}$  thick, smooth, sometimes concentrically slightly laminated. *Spore germination* results in multinucleate holobasidia producing a terminal whorl of ca. 16-20, long, fusiform, first mononucleate, later one-septate and binucleate basidiospores which do not fuse (Durán, 1987: 165, pl. 92, Figs. D, E).

*Hosts:* *Muhlenbergia depauperata* Scribner, *M. pectinata* C.O. Goodding.

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

***Tilletia zonata*** Brefeld, 1895: 161.

Type on *Muhlenbergia ligularis* (Hack.) Hitchc., Ecuador, Quito, G. Lagerheim.

*Sori* in the ovaries, filled by a black, powdery mass of spores. *Spores* chiefly globose, ca. 19-24  $\mu\text{m}$  in diameter, including the 2-3  $\mu\text{m}$  thick, hyaline sheath (spores without sheath 15-18  $\mu\text{m}$ ), yellowish-brown, reticulate. Judged from the illustrations, meshes polyangular, rather regular, sometimes incomplete, 3-5 per spore diameter. *Spore germination* results in a holobasidium apically bearing 4-8 basidiospores which fuse in pairs, giving rise to hyphae on which sickle shaped, secondary ballistoconidia are produced on short sterigmata (Brefeld, 1895: 161, pl. X, Figs. 3-7).

*Host:* *Muhlenbergia ligularis* (Hack.) Hitchc.

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

The type material probably no longer exists. Recollection is desired. Brefeld's original description is very poor, except for that of the spore germination. The description above is based on Brefeld's description and on his illustrations.

***Ustilago bethelii*** Zundel, 1933: 350. (Figs. 26-28)

Type on *Muhlenbergia montana* (Nutt.) Hitchc., USA, Colorado, Idaho Springs, 3 September 1923, E. Bethel, BPI 157974!; isotypes BPI 157973, 157978.

*Sori* (Fig. 26) forming slightly swollen, lead-coloured striae on the leaves between the veins, 0.2-0.5  $\times$  0.5-40 mm or longer, first covered by the epidermis which ruptures longitudinally disclosing the blackish, semiagglutinated to powdery mass of spores which is scattered, leaving behind perforated or shredded leaves. Occasionally, sori may appear on the stems, exceptionally in the spikelets. *Spores* (Figs. 27, 28) subglobose, ellipsoidal, ovoid to slightly irregular, 11-16  $\times$  12-18(-21)  $\mu\text{m}$ , yellowish- to reddish-brown, wall even or slightly uneven, 0.8-2(-2.5)  $\mu\text{m}$  thick, finely, rather densely verrucose-echinulate, spore profile wavy to finely serrulate. *Spore*



**Fig. 26.** Sori of *Ustilago bethelii* forming striae on the leaves of *Muhlenbergia montana*. To the left a healthy inflorescence. Bar = 1 cm.

*germination* results in mononucleate mycelia or in basidia with branches producing mononucleate sporidia (Durán, 1987: 225, pl. 108, fig. E).

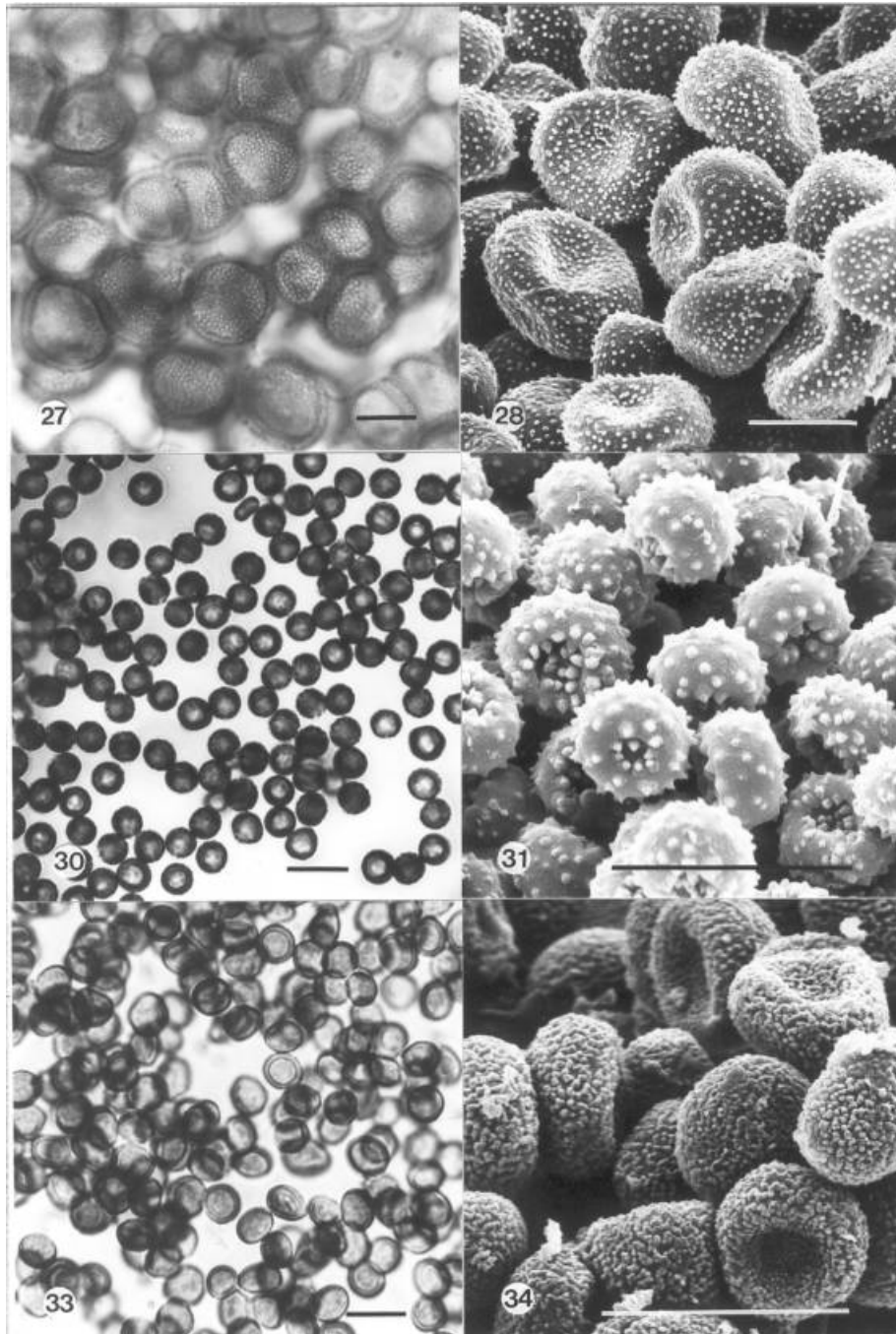
*Host:* *Muhlenbergia montana* (Nutt.) Hitchc. (*M. gracilis* auctt. Amer.).

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

***Ustilago buchloës*** Ellis & Tracy, 1890: 77, s. lat.

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!





**Figs. 27, 28.** Spores of *Ustilago bethelii* on *Muhlenbergia montana*, in LM and in SEM (Fischer, Gramin. smuts N. Amer. no. 157; HUV 10042). **Figs. 30, 31.** Spores of *Ustilago hyalinobipolaris* on *Muhlenbergia porteri*, in LM and in SEM (USA, Arizona, Silver Bell Mts., 12 February 1981, G.B. Cummins; HUV 10424). **Figs. 33, 34.** Spores of *Ustilago mexicana* on *Muhlenbergia* sp., in LM and in SEM (type). Bars = 10 µm.

= *Ustilago pseudohieronymi* Zundel, 1933: 351. — Lectotype on *Muhlenbergia squarrosa* (Trin.) Rydb., USA, Colorado, San Luis Valley, 27 June 1921, E. Bethel, (design. by Vánky, 2004c: 182) BPI 165475; isotypes BPI 165476-165478. (syn. by Fischer, 1953: 246, confirmed).

= *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).

For further synonyms, description, illustrations and host plant range see Vánky, 2004c: 182.

*Hosts:* *Bouteloua*, *Buchloë*, *Cathestecum*, *Tridens* species, but also on *Muhlenbergia richardsonis* (Trin.) Rydb. (*M. squarrosa* (Trin.) Rydb.), *M. torreyi* (Kunth) Hitchc. ex Bush (*M. gracillima* Torr.).

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

***Ustilago hyalinobipolaris* G.W. Fischer & Hirschhorn, 1945: 324. (Figs. 29-31)**

Replacing ≡ *Ustilago muhlenbergiae* G.P. Clinton, October 1902: 133 (later homonym, not Hennings, April 1902). — Type on *Muhlenbergia texana* Turb. (= *M. porteri* Scribner), USA, southern Arizona, August 1884, C.G. Pringle, FH!; isotypes BPI 163423-26, 163428.

*Sori* (Fig. 29) on the top and along sterile shoots at the base of leaves, globose to ovoid, 1-2.5 × 1-4 mm, with long, acute leaf remnants on their top, covered by a thin, greyish peridium which ruptures irregularly at maturity, disclosing the black, semiagglutinated to powdery mass of spores and some host tissue remnants, like a short, ramifying columella. *Spores* (Figs. 30, 31) globose, subglobose, laterally slightly compressed, 5-5.5 × 5-6.5 μm, dark brown; wall uneven, ca. 0.4-0.8 μm, thinner on the flattened sides, evidently, sparsely verrucose-echinulate, spore profile wavy to sparsely, finely serrulate on the flattened sides. In excessively rehydrated spores the flattened, thin-walled sides protrude as paler, bipolar areas.



**Fig. 29.** Sori of *Ustilago hyalinobipolaris* in the inflorescence of *Muhlenbergia porteri*. Enlarged two sori. Bars = 1 cm for habit, 2 mm for the detail drawing.

*Hosts: Muhlenbergia microsperma* (DC.) Kunth, *M. pauciflora* Buckl., *M. porteri* Scribner (*M. texana* Turb.).

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

*Ustilago hyalinobipolaris* is close to *U. muhlenbergiae*, both on *Muhlenbergia* species. Not only are the sori identical but also the shape, size and wall thickness of the spores. However, they differ in the colour and ornamentation of the spores. It is questionable if *U. hyalinobipolaris* merits separate specific rank or should be considered as an extreme variation within *U. muhlenbergiae*. Clinton (1904: 347) considered his *U. muhlenbergiae* to be "in all probability" a synonym of *U. muhlenbergiae* Henn., published a few months earlier. For the present, I accept *U. hyalinobipolaris* as a separate species until intermediate forms are seen.

***Ustilago mexicana* Ellis & Everhart, 1887: 56. (Figs. 32-34)**

Lectotype on *Muhlenbergia* sp., Mexico, Chihuahua, Mts. near Batopilas, alt. ca. 1859 m, 1885, E. Palmer, (design. by Piepenbring, 2003: 175) BPI 163303!; isolectotypes BPI 163300-163302, 163305, and in Ellis & Ev., N. Amer. fgi., Ser. 2, no. 1891, HUV 4116!

= *Ustilago muhlenbergiae* Henn. var. *tucumanensis* Hirschhorn, 1939: 386.

≡ *Ustilago tucumanensis* (Hirschh.) Zundel, 1953: 182.

≡ *Ustilago tucumanensis* (Hirschh.) Hirschhorn, 1986: 327 (comb. superfl.) — Type on *Muhlenbergia caerulea* (Gris.) Mez. (= *M. angustata* (Presl) Kunth), Argentina, Tucuman Prov., San José, 2200 m, 26 January 1933, L.R. Parodi 10709, BPI 163406! (syn. nov.)

= *Ustilago epicampida* Zundel, 1942: 123. — Type on *Epicampes emersleyi* (Vasey) Hitchc. (= *Muhlenbergia emersleyi* Vasey), Mexico, Michoacan State, Cerro Tancitaro, alt. 355 m, 19 August 1940, W.C. Leavenworth 718, BPI 160368!; isotype BPI 160369! (syn. by Fischer, 1953: 281, confirmed).

*Sori* (Fig. 32) in all spikelets of an inflorescence, globoid, 0.5-1.5 mm in diameter, showing between the spreading glumes, first covered by a peridium of host origin, often with 1-2 acute remnants of inner floral organs and even awns. The peridium ruptures irregularly at maturity disclosing the blackish-brown, semiagglutinated to powdery mass of spores. *Spores* (Figs. 33, 34) globose, subglobose, ellipsoidal to slightly irregular with a more or less flattened side, 5-8 × 5.5-9 μm, yellowish-brown, paler on one side; wall uneven, 0.5-0.8 μm thick, thinner on the paler, flattened side, in LM finely, densely punctate, spore profile smooth to finely wavy on the flattened side, in SEM finely, very densely verruculose.

*Hosts: Muhlenbergia angustata* (Presl) Kunth (*M. caerulea* (Gris.) Mez.), *M. distichophylla* (Presl) Kunth, *M. emersleyi* Vasey (*Epicampes emersleyi* (Vasey) Hitchc.), *Muhlenbergia* sp.

*Known distribution:* N. and S. America (Mexico, Argentina).

No material of *Ustilago tucumanensis* was seen, but according to the original description it appears identical with *U. mexicana*. Hirschhorn (1939:



**Fig. 32.** Sori of *Ustilago mexicana* in the ovaries of *Muhlenbergia* sp. Enlarged a sorus.  
Bars = 1 cm for habit, 1 mm for the detail drawing.

386) mentioned the presence of spore balls, but later (Hirschhorn, 1986: 327) she suspected that these could be artefacts.

The spores of the type of *Ustilago epicampida* are slightly larger ( $5.5\text{-}8 \times 6.5\text{-}9 \mu\text{m}$ ), paler, more evidently ornamented, and the spore wall is more evenly thick than in the spores of the type of *U. mexicana* which measure  $5\text{-}7 \times 5.5\text{-}8 \mu\text{m}$ . These differences are considered variations within the same species.

***Ustilago muhlenbergiae*** Hennings, April 1902: (61). (not Clinton, October 1902, *q.e. Ustilago hyalinobipolaris*). (Figs. 35-37)

Type on *Muhlenbergia pringlei* Scribner (= *M. pauciflora* Buckl.), USA, New Mexico, Hot Springs, 15 September 1896, E.W.D. Holway (not Mexico, as stated in the original description); isotypes BPI 163410, and in Seymour & Earle, Econ. fgi., Suppl. C, no. 142, HUV 9730!

*Sori* (Fig. 35) on top of the shoots, destroying the inflorescence, comprising also the basal part of some congested, distal leaf sheaths, subspherical, ovoid or fusiform, first hard, somewhat gall-like,  $1.5\text{-}3 \times 2.5\text{-}6$  mm, partly hidden by leaf sheaths, covered by a yellowish-grey, rather thick peridium, often with floral remnants on it and also with long, setaceous leaf remnants on its top. At maturity the peridium becomes thinner, ruptures irregularly, disclosing the blackish-brown, agglutinated, later powdery mass of spores. *Spores* (Figs. 36, 37) globose to subglobose, laterally slightly compressed,  $5\text{-}5.5 \times 5.5\text{-}6(-6.5) \mu\text{m}$ , dark yellowish-brown; wall uneven,  $0.4\text{-}0.8 \mu\text{m}$ , thinner on the flattened sides which, in excessively rehydrated spores may protrude and even rupture, reminiscent of spores of *Tranzscheliella williamsii* (see Fischer, 1953: 284, fig. 111 B). Spore surface in LM finely, moderately densely punctate, spore profile smooth, on the flattened sides finely wavy, in SEM finely, densely verruculose. *Sterile cells* absent.

*Hosts*: *Muhlenbergia pauciflora* Buckl. (*M. pringlei* Scribner), *M. porteri* Scribner (*M. texana* Turb.).

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

***Ustilago sonoriana*** Zundel, in Fischer, 1953: 295. (Figs. 38-40)

Type on *Muhlenbergia dumosa* Scribner, Mexico, Sonora, near Bavispe, Santa Rosa Canyon, 19 July 1938, S.S. White, BPI 166514!

*Sori* (Fig. 38) destroying the inner floral organs, globoid to ovoid,  $0.5\text{-}1 \times 1\text{-}1.5$  mm, with a short acute tip, partly hidden by leaf sheaths and outer floral envelopes, at first covered by a thin, greyish peridium of host origin, sometimes with the tips of destroyed inner floral envelopes. At maturity, the peridium ruptures irregularly disclosing the blackish-brown, powdery mass of spores. *Spores* (Figs. 39, 40) globose, subglobose, ellipsoidal or like a rugby ball,  $5.5\text{-}7 \times 5.5\text{-}8 \mu\text{m}$ , yellowish-brown, often with a wide, slightly darker,



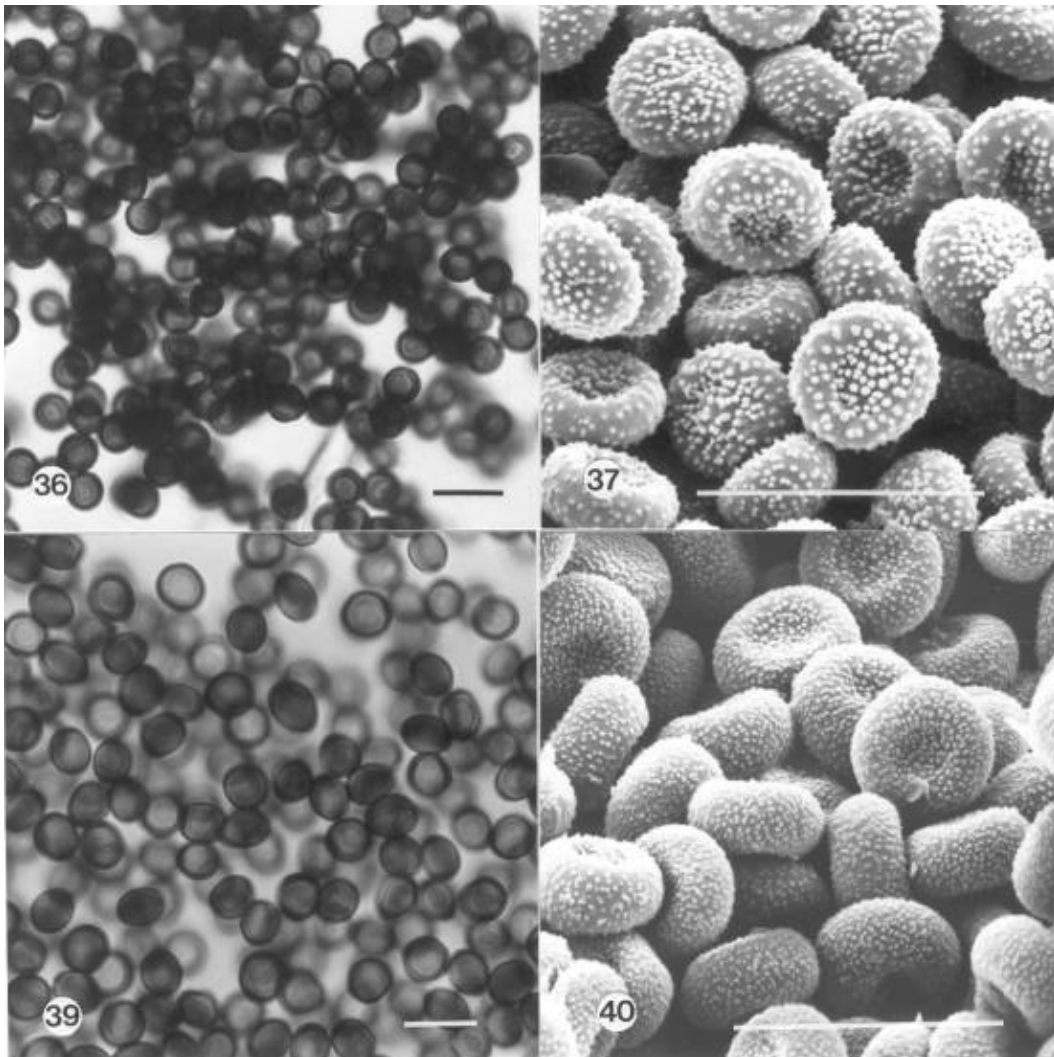
**Fig. 35.** Sori of *Ustilago muhlenbergiae* in the inflorescence of *Muhlenbergia pauciflora* Buckl. To the left a healthy inflorescence. Bar = 1 cm.

longitudinal band; wall uneven, 0.5-8  $\mu\text{m}$  thick, thicker at the longitudinal end of the spores, surface apparently smooth to indistinctly punctate.

*Host:* *Muhlenbergia dumosa* Scribner.

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

Two additional smut fungi on *Muhlenbergia* from Argentina have been published invalidly (no Latin diagnosis, ICBN 36.1, and no type indicated, ICBN 37.1), under the names of *Tilletia atacamensis* Hirschhorn (1986: 148),



**Figs. 36, 37.** Spores of *Ustilago muhlenbergiae* on *Muhlenbergia pauciflora*, in LM and in SEM (type). **Figs. 39, 40.** Spores of *Ustilago sonoriana* on *Muhlenbergia dumosa*, in LM and in SEM (type). Bars = 10  $\mu$ m.

and *T. georfischeri* Hirschhorn (1986: 177). No specimens were available for study to validate the names or to establish synonymy.

#### HOST — PARASITE LIST

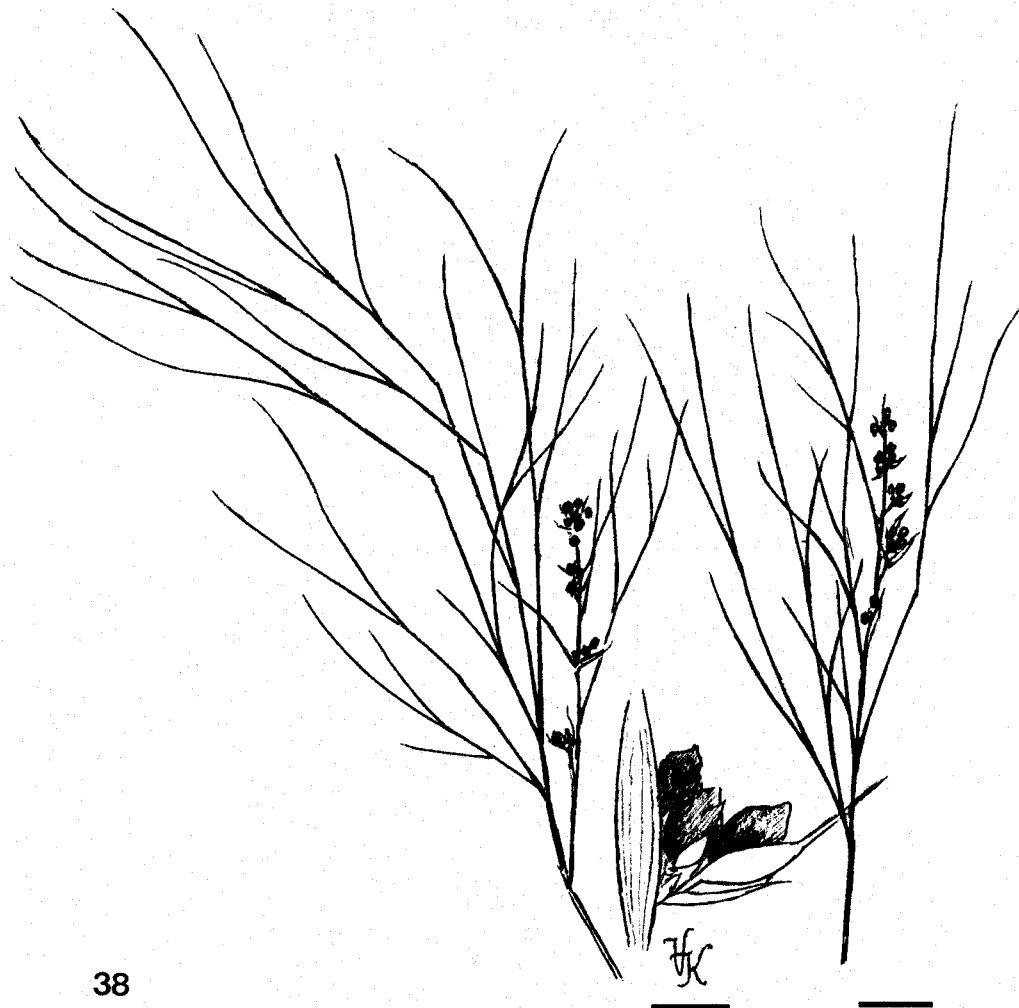
(*M.* = *Muhlenbergia*, *T.* = *Tilletia*, *U.* = *Ustilago*)

*Bouteloua* spp. — *U. buchloës*

*Buchloë* spp. — *U. buchloës*

*Cathestecum* spp. — *U. buchloës*

*Epicampes emersleyi* = *M. emersleyi*



**Fig. 38.** Sori of *Ustilago sonoriana* in the flowers of *Muhlenbergia dumosa*. Enlarged three sori. Bars = 1 cm for habit, 1 mm for the detail drawing.

- Eragrostis* spp. — *Sporisorium montaniense*  
*M. angustata* — *U. mexicana*  
*M. arenacea* — *T. asperifolia*  
*M. asperifolia* — *Sporisorium montaniense*, *T. asperifolia*  
*M. caerulea* = *M. angustata*  
*M. cuspidata* — *Sporisorium montaniense*, *T. asperifolioides*  
*M. depauperata* — *T. muhlenbergiae*, *T. tuberculata*  
*M. diffusa* = *M. schreberi*  
*M. distichophylla* — *U. mexicana*  
*M. dumosa* — *U. sonoriana*



*M. emersleyi* — *U. mexicana*  
*M. filiformis* — *T. asperifolia*, *T. montana*  
*M. glomerata* — *Sporisorium montaniense*  
*M. gracillima* = *M. torreyi*  
*M. ligularis* — *T. zonata*  
*M. microsperma* — *T. muhlenbergiae*  
*M. minutissima* — *T. asperifolia*  
*M. montana* — *U. bethelii*  
*M. pauciflora* — *U. hyalinobipolaris*, *U. muhlenbergiae* Henn.  
*M. pectinata* — *T. tuberculata*  
*M. porteri* — *U. hyalinobipolaris*, *U. muhlenbergiae* Henn.  
*M. pringlei* = *M. pauciflora*  
*M. pulcherrima* — *Sporisorium montaniense*, *T. macrotuberculata*  
*M. quadridentata* — *T. muhlenbergiae*  
*M. racemosa* — *Sporisorium montaniense*  
*M. richardsonis* — *U. buchloës*  
*M. schaffneri* var. *elongata* — *T. muhlenbergiae*  
*M. schreberi* — *Sporisorium parodii*  
*M. squarrosa* = *M. richardsonis*  
*M. tenella* — *T. muhlenbergiae*  
*M. texana* = *M. porteri*  
*M. torreyi* — *U. buchloës*  
*M. utilis* — *T. pachyderma*  
*M. wolfii* — *T. macrotuberculata*  
*M. sp.* — *U. mexicana*  
*Sporobolus asperifolius* = *M. asperifolia*  
*Sporobolus auriculatus* = *M. arenacea*  
*Sporobolus confusus* — *T. asperifolia*  
*Sporobolus gracillimus* = *M. filiformis*  
*Sporobolus simplex* = *M. filiformis*  
*Tridens* spp. — *U. buchloës*

#### FUNGUS NAMES

(valid names in bold face)

*asperifolia* *Tilletia*

*asperifolioides* *Tilletia*

*bethelii* *Ustilago*

*buchloës* *Ustilago*

*coloradensis* *Ustilago* = *Ustilago buchloës*

*epicampida* *Ustilago* = *Ustilago mexicana*

*eremophila* *Tilletia* = *Tilletia asperifolia*

*eremophila* *Tolyposporella* = *Tilletia asperifolia*

*hyalinobipolaris* *Ustilago*

*macrotuberculata* *Tilletia*

*mexicana* *Ustilago*

*montana* *Tilletia*

*montaniense* *Sporisorium*

*montaniensis* *Sphacelotheca* = *Sporisorium montaniense*

*montaniensis* *Ustilago* = ***Sporisorium montaniense***  
*muhlenbergiae* G.P. Clinton, *Ustilago* = ***Ustilago hyalinobipolaris***  
*muhlenbergiae* Henn., ***Ustilago***  
*muhlenbergiae* ***Tilletia***  
*muhlenbergiae* *Ustilago* var. *tucumanensis* = ***Ustilago mexicana***  
***pachyderma* *Tilletia***  
***parodii* *Sporisorium***  
*parodii* *Ustilago* = ***Sporisorium parodii***  
*pseudohieronymi* *Ustilago* = ***Ustilago buchloës***  
***sonoriana* *Ustilago***  
*strangulans* (Iss.) G.P. Clinton, *Sphacelotheca* = ***Sporisorium montaniense***  
*strangulans* (Iss.) Moesz, *Sphacelotheca* = ***Sporisorium montaniense***  
*strangulans* *Ustilago* = ***Sporisorium montaniense***  
***tuberculata* *Tilletia***  
*tucumanensis* (Hirschh.) Hirschh., *Ustilago* = ***Ustilago mexicana***  
*tucumanensis* (Hirschh.) Zundel, *Ustilago* = ***Ustilago mexicana***  
***zonata* *Tilletia***

**Key to the smut fungi of *Muhlenbergia* (*T.* = *Tilletia*, *U.* = *Ustilago*)**

1.	Sori in the ovaries .....	2
1.	Sori elsewhere.....	9
2.	Spores verrucose-tuberculate .....	3
2.	Spores reticulate.....	4
3.	Spores 15-21(-23) µm long. Tubercles 1-2.5 µm high .....	<b><i>T. tuberculata</i></b>
3.	Spores 21-24(-28) µm long. Tubercles 2.5-4 µm high .....	<b><i>T. macrotuberculata</i></b>
4.	Spores 28-53 µm long, including the 3-14 µm thick sheath. Meshes 3-5 per spore diam. .	
	.....	<b><i>T. pachyderma</i></b>
4.	Spores shorter. Sheath thinner or absent. Meshes more per spore diam. ....	5
5.	Spores 29-36(-38) µm long. Muri 2-4 µm high .....	<b><i>T. muhlenbergiae</i></b>
5.	Spores shorter. Muri shorter .....	6
6.	Spores 24-30(-34) µm long. Muri 1.5-2.5 µm high .....	<b><i>T. asperifolioides</i></b>
6.	Spores 19-25 µm long.....	7
7.	Spores basically reticulate but mostly incompletely and irregularly. Muri 1-1.5 µm high.	
	.....	<b><i>T. montana</i></b>
7.	Spores clearly reticulate. Muri higher.....	8
8.	Meshes 6-8 per spore diam. Sheath extending just beyond the 1.5-2.5 µm high muri .....	
	.....	<b><i>T. asperifolia</i></b>
8.	Meshes ca. 3-5 per spore diam. Sheath 2-3 µm thick .....	<b><i>T. zonata</i></b>
9(1).	Sori predominantly on leaves or also on leaf sheaths forming pustules or striae.....	10
9.	Sori not so .....	11

10. Sori on leaves forming slightly swollen striae ..... *U. bethelii*  
 10. Sori on leaves and leaf sheaths forming bullate pustules or sausage-shaped striae .....  
 ..... *U. buchloës*
11. Sori in spikelets. Spores paler and flattened on one side ..... *U. mexicana*  
 11. Sori in the whole inflorescence and distal leaf sheaths. Spores not so ..... 12
12. Columella present. Spores up to 15 µm long, without paler polar areas ..... 13  
 12. Columella absent. Spores up to 9(-10) µm long, with paler polar areas ..... 14
13. Columella one, stout. Spores echinulate ..... *Sporisorium montaniense*  
 13. Columella 8-12, filiform. Spores verruculose ..... *Sporisorium parodii*
14. Spores 6-9(-10) µm long ..... *U. sonoriana*  
 14. Spores 5.5-6.5 µm long ..... 15
15. Spores finely punctate. Spore profile smooth to wavy ..... *U. muhlenbergiae*  
 15. Spores evidently verrucose-echinulate. Spore profile wavy to finely serrulate .....  
 ..... *U. hyalinobipolaris*

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### References

- Brefeld, O. (1895). Untersuchungen aus dem Gesamtgebiete der Mykologie. XII. Hemibasidii. Brandpilze III. Münster i. W., Commissions-Verlag v. H. Schöningh. IV + 99-236p. + Pls. VI-XII.
- Ciferri, R. (1938). Ustilaginales. Flora Italica Cryptogama, Pars I. Fungi, Fascicolo 17: 1-443.
- Clayton, W.D. and Renvoize, S.A. (1986). Genera graminum. Grasses of the world. Kew Bulletin Additional Series XIII. London, UK, 389p.
- Clinton, G.P. (1902). North American Ustilagineae. Journal of Mycology 8: 128-156.
- Clinton, G.P. (1904). North American Ustilagineae. Proceedings of the Boston Society of Natural History 31: 329-529.
- Clinton, G.P. (1906). Order Ustilaginales. North American Flora 7: 1-82.
- Durán, R. (1987). Ustilaginales of Mexico. Taxonomy, symptomatology, spore germination, and basidial cytology. Washington State University, Pullman, USA, 331p.
- Durán, R. and Fischer, G.W. (1961). The genus *Tilletia*. Washington State University, 138p.
- Ellis, J.B. and Everhart, B.M. (1887). New species of Ustilagineae and Uredineae. Journal of Mycology 3: 55-57.
- Ellis, J.B. and Everhart, B.M. (1890). New species of Uredineae and Ustilagineae. Journal of Mycology 6: 118-121.
- Ellis, J.B. and Tracy, S.M. (1890). A few new fungi. Journal of Mycology 6: 76-77.
- Fischer, G.W. (1952). Some new species of Ustilaginales from North America. Research Studies of the State College of Washington 20: 3-10.

- Fischer, G.W. (1953). Manual of the North American Smut Fungi. New York, Ronald Press Co., 343p.
- Fischer, G.W. and Hirschhorn, E. (1945). Observations on certain species of *Ustilago* on *Hilaria*, *Stenotaphrum*, and *Muhlenbergia*. Mycologia 37: 318-325.
- Hennings, P. (1902). Fungi nonnulli novi ex regionibus variis. Hedwigia, Beiblatt 41: 61-66.
- Hirschhorn, E. (1939). Las especies del género *Ustilago* en la Argentina. Darwiniana 3: 347-418 + Pls. I-VI.
- Hirschhorn, E. (1986). Las Ustilaginales de la flora Argentina. La Plata, CIC, 530p.
- Issatchenko, V. (1896). (Ueber die parasitischen Pilze des Gouvernements Kherson). Botanicheskije Zapiski. 12: 219-244.
- Moesz, G. (1921). Mykologiai közlemények. IV. (Mycological notes. IV; in Hungarian). Botanikai Közlemények 19: 44-66.
- Piepenbring, M. (2003). Smut fungi (Ustilaginomycetes p.p. and Microbotryales, Basidiomycota). Flora Neotropica. Monograph 86. New York Botanical Garden Press, New York.
- Shivas, R.G. and Vánky, K. (2001). The smut fungi on *Cynodon*, including *Sporosorium normanensis* sp. nov. from Australia. Fungal Diversity 8: 149-154.
- Spezzazzini, C. (1909). Mycetes argentinenses (Series IV). Anales del Museo Nacional de Buenos Aires, Ser. 3, 12: 257-458.
- Vánky, K. (1985). Carpathian Ustilaginales. Symbolae Botanicae Upsalienses 24: 1-309.
- Vánky, K. (2000a). Taxonomical studies on Ustilaginales. XX. Mycotaxon 74: 161-215.
- Vánky, K. (2000b). The smut fungi on *Saccharum* and related grasses. Australasian Plant Pathology 29: 155-163.
- Vánky, K. (2001). Taxonomical studies on Ustilaginales. XXI. Mycotaxon 78: 265-326.
- Vánky, K. (2002a). The smut fungi of the world. A survey. Acta Microbiologica et Immunologica Hungarica 49: 163-175.
- Vánky, K. (2002b). Taxonomical studies on Ustilaginales. XXII. Mycotaxon 81: 367-430.
- Vánky, K. (2003a). The smut fungi (Ustilaginomycetes) of *Hyparrhenia* (Poaceae). Fungal Diversity 12: 179-205.
- Vánky, K. (2003b). Taxonomical studies on Ustilaginales. XXIII. Mycotaxon 85: 1-65.
- Vánky, K. (2003c). Smut fungi (Ustilaginomycetes) of *Sporobolus* (Poaceae). Fungal Diversity 14: 205-241.
- Vánky, K. (2004a). The smut fungi (Ustilaginomycetes) of *Bothriochloa*, *Capillipedium* and *Dichanthium* (Poaceae). Fungal Diversity 15: 219-244.
- Vánky, K. (2004b). Taxonomic studies on Ustilaginomycetes - 24. Mycotaxon 89: 55-118.
- Vánky, K. (2004c). The smut fungi (Ustilaginomycetes) of *Boutelouae* (Poaceae). Fungal Diversity 16: 167-198.
- Vánky, K. & Shivas, R.G. (2001). Smut fungi (Ustilaginomycetes) of *Sorghum* (Gramineae) with special regard to Australasia. Mycotaxon 80: 339-353.
- Zundel, G.L. (1933). New and rare North and South American Ustilaginales. Mycologia 25: 349-355.
- Zundel, G.L. (1942). Studies on the Ustilaginales of the world. II. Mycologia 34: 123-127.
- Zundel, G.L. (1953). The Ustilaginales of the World. Pennsylvania State College, School of Agriculture, Department of Botany. Contributions 176: XI + 1-410.

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