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ARTICLE

Mycosarcoma (*Ustilaginaceae*), a resurrected generic name for corn smut (*Ustilago maydis*) and its close relatives with hypertrophied, tubular sori

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Abstract: *Ustilago* is a polyphyletic genus of smut fungi found mainly on *Poaceae*. The development of a taxonomy that reflects phylogeny requires subdivision of *Ustilago* into smaller monophyletic genera. Several separate systematic analyses have determined that *Macalpinomyces mackinlayi*, *M. tubiformis*, *Tolyposporella pachycarpa*, *Ustilago bouriquetii* and *U. maydis*, occupy a unique phylogenetic position within the *Ustilaginaceae*. A previously introduced monotypic generic name typified by *U. maydis*, *Mycosarcoma*, is available to accommodate these species, which resolves one component of polyphyly for *Ustilago s. lat.* in *Ustilaginaceae*. An emended description of *Mycosarcoma* is provided to reflect the morphological synapomorphies of this monophyletic group. A specimen of *Ustilago maydis* that has had its genome sequenced is designated as a neotype for this species. Taxonomic stability will further be provided by a forthcoming proposal to conserve the name *Uredo maydis* over *Lycoperdon zeae*, which has priority by date, in order to preserve the well-known epithet *maydis*.

Key words:
model organism
name change
Pseudozyma
synapomorphy
taxonomy
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INTRODUCTION

There are 14 genera of smut fungi recognized in *Ustilaginaceae* (*Ustilaginomycetes*) on grasses: *Anomalomyces*, *Anthracocystis*, *Franzpetrakia*, *Langdonia*, *Macalpinomyces*, *Moesziomyces*, *Sporisorium*, *Stollia*, *Tranzscheliella*, *Triodiomyces*, *Tubisorus*, *Ustilago*, *Yenia,* and *Yunchangia*. These genera are distinguished by morphology of the sori and spores, as well as host range and phylogenetic relationships supported by molecular data (Begerow *et al*. 2014). Species of *Ustilago* destroy leaves and inflorescences of hosts in *Poaceae*, mostly producing sori that rupture at maturity to expose blackish spore masses. *Ustilago* became a catch-all for many unrelated species of smut fungi, and is polyphyletic (McTaggart *et al*. 2012b, Begerow *et al*. 2014, Savchenko *et al.* 2014). *Ustilago*, in the strict sense, occurs mainly on hosts in the tribe *Pooideae* and lacks soral structures, specifically, a columella, spore balls and sterile cells (McTaggart *et al*. 2012a). Additionally, members of the asexual yeast genera *Pseudozyma* and *Farysizyma* are polyphyletic in different lineages of *Ustilaginales* (Begerow *et al.* 2000, 2014, Boekhout 1995, Inacio *et al*. 2008, Wang *et al.* 2015). Some of these asexual yeasts were described without awareness of their sexual morphs, which are known to be plant pathogenic or potentially plant pathogenic (Wang *et al.* 2015). A phylogenetic species concept that places species of yeast into resolved genera has commenced for yeasts in *Anthracocystis* and other taxa (Piątek *et al.* 2015, Wang *et al.* 2015).

The known genera of smut fungi reflect synapomorphies, whether found in cellular ultrastructure or gross morphological characters of the sorus (Begerow *et al.* 2014). These synapomorphies are supported by DNA sequence data (Begerow *et al*. 2014). Recent taxonomic changes for smut fungi reflect phylogenetic classification, for example

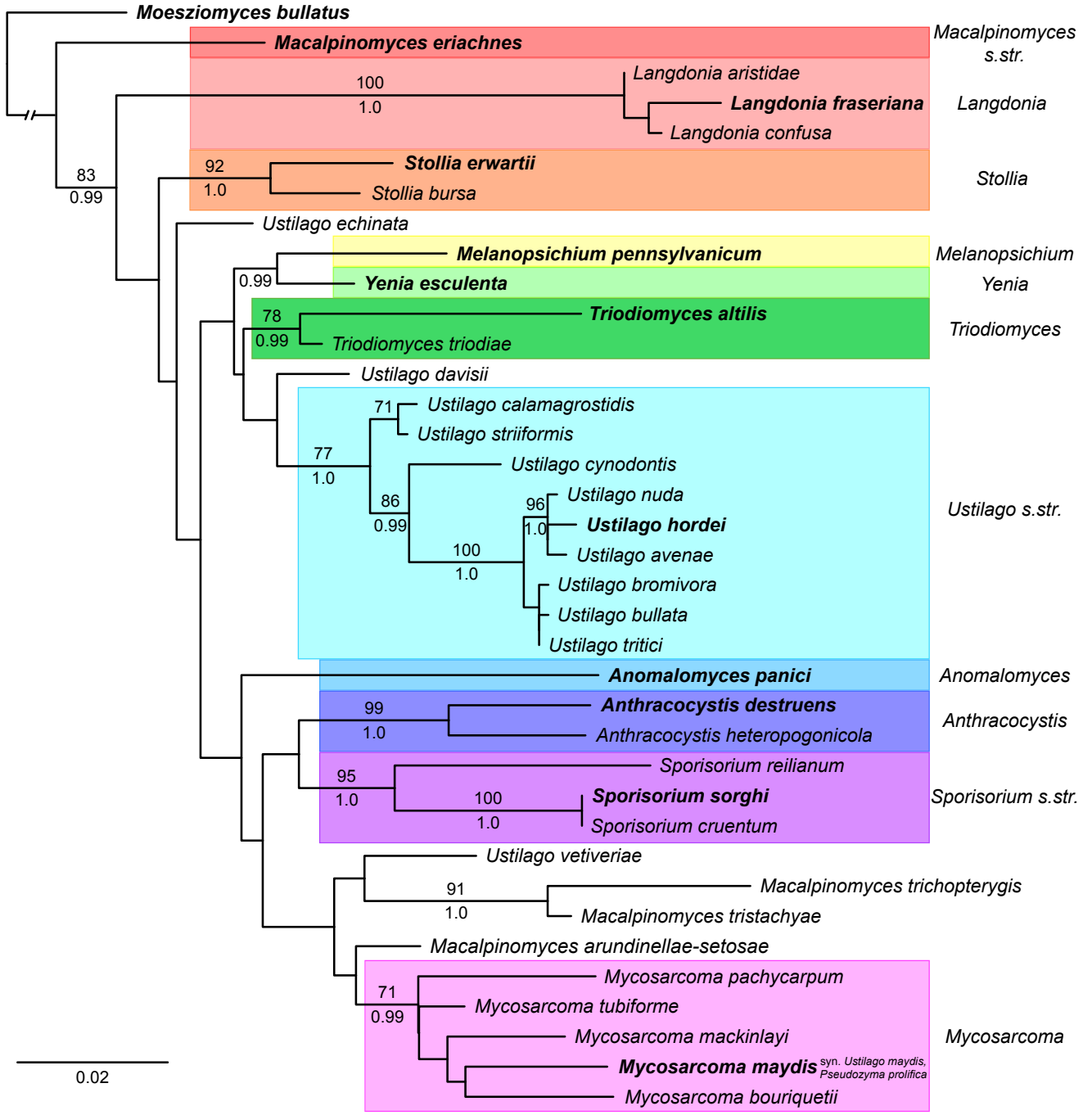

Fig. 1. Phylogram obtained from a maximum likelihood search in RAxML v8 (Stamatakis 2014) with a partitioned dataset of the internal transcribed spacer and large subunit regions of ribosomal DNA. Bootstrap values (≥70 %) from 1000 replicates in a maximum likelihood search above nodes. Posterior probabilities (≥0.95) summarized from 18 000 converged trees obtained from four runs each consisting of four chains in a Bayesian search with MrBayes (Ronquist & Huelsenbeck 2003) below nodes. GTRGAMMA was the model of evolution for both phylogenetic criteria. Taxon name, host and GenBank numbers listed in Table 1. Type species of the genera included in the *Ustilaginaceae* are in **bold** font.

the separation of *Microbotryales* from *Ustilaginomycotina* (Begerow *et al*. 1997, 2014), and division of the *Ustilago-Sporisorium-Macalpinomyces* complex into smaller, well-defined genera (McTaggart *et al.* 2012c). In the latter example, smut fungi on grasses in the *Ustilago-Sporisorium-Macalpinomyces* complex were divided into the genera *Anthracocystis*, *Langdonia*, *Stollia*, *Triodiomyces* and *Tubisorus* (Vánky & Lutz 2011, McTaggart *et al*. 2012c).

Ustilago maydis, the cause of boil or blister smut of corn (*Zea mays*), forms localized, hypertrophied sori on the stems, leaves and inflorescences. It is an important model organism for the study of reproduction (Bakkeren *et al.* 2006), infection pathways (Muller *et al.* 2008), virulence and cellular signaling in fungi (Brefort *et al.* 2009). It was the first species of *Ustilaginomycotina* to have a publicly available genome (Kämper *et al*. 2006), which has since been used for comparative genomics between corn smut and other fungi (e.g. Xu *et al.* 2007). Molecular phylogenetic studies

have shown that the mitosporic *Pseudozyma prolifica* is conspecific with *U. maydis* (Begerow *et al*. 2000, Boekhout 2011).

Comparative studies on the genomes of smut fungi have indicated that *U. maydis* is more closely related to other taxa than to species of *Ustilago*. For example, differences in the mating systems and methods of RNA silencing between *U. maydis* and *U. hordei* (the type species of *Ustilago*, notwithstanding a proposal by Thines (2016) to conserve *Ustilago* with *U. maydis* as the conserved type) indicated a relatively distant phylogenetic relationship (Bakkeren *et al.* 2006, Bakkeren *et al*. 2008, Laurie *et al.* 2008). Kellner *et al.* (2011) showed the mating type loci of *Sporisorium reilianum*, *Ustanciosporium gigantosporum* and related species had some degree of synteny to the corresponding genes of *U. maydis*. Future studies may determine whether more closely related species have higher synteny and whether genes involved in mating and self-recognition are conserved within genera.

Systematic studies showed that *U. maydis* was not closely related to species of *Ustilago s. str.*, and was instead recovered as sister to species of *Sporisorium* and *Anthracocystis* (Piepenbring *et al.* 2002, Stoll *et al.* 2005, Vánky & Lutz 2011, McTaggart *et al*. 2012a). In these studies, *U. maydis* was closely related to *U. bouriquetii*, a smut fungus that forms hypertrophied sori in the inflorescences of *Stenotaphrum* (*Poaceae*). McTaggart *et al.* (2012a) recovered *U. maydis* in a clade with *Macalpinomyces mackinlayi*, *M. tubiformis*, *Tubisorus pachycarpus* and *U. bouriquetii*, which all form hypertrophied sori in inflorescences of their hosts. McTaggart *et al*. (2012a) considered that localised, host-derived, hypertrophied sori were an apomorphy for this group (Fig. 2). Vánky & Lutz (2011) introduced a new generic name, *Tubisorus*, typified by *T. pachycarpus*, which was recovered in a clade with *U. maydis*. *Tubisorus* was characterized by tubular sori filled with spores compacted in loose spore balls.

Mycosarcoma is the earliest available generic name for the clade containing *U. maydis*, which was described as the type species (Brefeld 1912). The characters that Brefeld (1912) believed distinguished *Mycosarcoma* from *Ustilago* and *Sporisorium* were the: (1) incubation time in the host; (2) development of the sorus at the site of penetration in the host plant; (3) the development of aerial conidia; and (4) the presence of a peridium.

The current systematic understanding of the genera in *Ustilaginaceae* on *Poaceae* is shown in (Fig. 1; Table 1). In the present study the circumscription of *Mycosarcoma* is emended and the name resurrected to reflect contemporary knowledge of the synapomorphies within *Ustilaginaceae*. A taxonomic system based strictly on morphological synapomorphies is not possible for dimorphic plant pathogenic fungi like *U. maydis*, which have both asexual non-pathogenic yeast stages and sexual pathogenic teliospore stages in their life cycle.

Vánky (1990) discussed the nomenclatural history of *U. maydis*. The fungus was first described as *Lycoperdon zeae* by Beckmann, but this epithet could not be combined in *Ustilago* as it was pre-occupied by the name *U. zeae* (Link) Unger 1836 based on a different type (Vánky 1990). The next validly published binomial was *U. maydis* (DC.) Corda 1842, possibly the most well-known and intensively studied smut fungus in the world. For this reason, we seek to conserve this widely used epithet.

TAXONOMY

The following taxonomic combinations are based on the recovered phylogenetic tree (Fig. 1) and the apomorphies discussed above. Emended parts of the description are in *italic* type.

Mycosarcoma Bref., *Unters. Gesammtgeb. Mykol*. **15**: 53 (1912).

Description: Sori usually in some ovaries of an inflorescence, derived from hypertrophied host material, *often tubular, splitting longitudinally to expose the spore mass, partitioning*

Fig. 2. A. *Mycosarcoma bouriquetii* on *Stenotaphrum dimidatum* (BRIP 26403). **B.** *Mycosarcoma mackinlayi* on *Eulalia mackinlayi* (BRIP 52549). **C.** *Mycosarcoma maydis* on *Zea mays* (BRIP 52746). **D.** *Mycosarcoma tubiforme* on *Chrysopogon fallax* (BRIP 57599).

cells present or absent. *Sori* rarely in all organs: stems, leaves, inflorescences (male and female) and roots. *Columellae* absent. *Spore balls* derived from sporogenous hyphae absent. Germination of the *Ustilago*-type. Asexual; saprobic stages occur as yeasts on plant surfaces and other habitats.

Hosts: On grass hosts in subfamily *Panicoideae* (*Poaceae*).

Type species: *Mycosarcoma maydis* (DC.) Bref. 1912 (on *Zea mays*).

Mycosarcoma bouriquetii (Maubl. & Roger) McTaggart, R.G. Shivas & Begerow, **comb. nov.**
MycoBank MB811941
Basionym: *Ustilago bouriquetii* Maubl. & Roger, *Bull. Soc. Mycol. France* **50**: 327 (1934).
Synonyms: *Sphacelotheca mauritiana* Zundel, *Mycologia* **36**: 405 (1944); *fide* Vánky (1996:107).
Sorosporium stenotaphri Vienn.-Bourg., *Ann. Inst. Natl. Agron*. **47**: 43 (1963); *fide* Vánky (1996:107).

Type: on *Stenotaphrum dimidiatum*, Madagascar

Mycosarcoma mackinlayi (McTaggart & R.G. Shivas) McTaggart, R.G. Shivas & Begerow, **comb. nov.**
MycoBank MB811942
Basionym: *Macalpinomyces mackinlayi* McTaggart & R.G. Shivas, *Persoonia* **23**: 187 (2009).

Type: on *Eulalia mackinlayi*, Australia.

Mycosarcoma maydis (DC.) Bref., *Unters. Gesammtgeb. Mykol.* **15**: 53 (1912).
Basionym: *Uredo maydis* DC., *Fl. franç*., edn 3, **6**: 77 (1815).
Synonyms:*Ustilago maydis* (DC.) Corda, *Icon. Fung.* **5**: 3 (1842): type: **USA:** *Minnesota:* near St Paul, on *Zea mays* in a corn field, isolated from a germinating teliospore [collected by J.J. Christensen], *P. Schreier*, *R. Kahmann*, *S. Leong & R. Holiday* (DSM 14603 **— *neotype designated here***, MBT374099).
Lycoperdon zeae Beckm., *Hannover. Mag.* **6**: 1330 (1768).
Uredo segetum [var.] *mays-zeae* DC., *Fl. franç*., edn 3, **2**: 596 (1805).
Ustilago zeae-maydis G. Winter, *Rabenh. Krypt.-Fl*. **1**(1): 97 (1881); as „*U. Zeae Mays*".
Ustilago mays-zeae (DC.) Magnus, *Verh. Bot. Ver. Prov. Brandenburg* **37**: 72 (1896) [„1895"].
Uredo zeae Schwein., *Schr. Naturf. Ges. Leipzig* **1**: 71 (1822).
Caeoma zeae Link, *Linné's Sp. Plant.*, 4 edn, **6**(2): 2 (1825).
Ustilago zeae (Link) Unger, *Ueber Einfluß Bodens*: 211 (1836).
Ustilago euchlaenae Archang., *Erb. Crittog. Ital.*, ser. 2, no. 1152 (1882).
Pseudozyma prolifica Bandoni, *Bot. J. Linn. Soc*. **91**:38 (1985).

Notes: We are proposing elsewhere to the Nomenclature Committee for Fungi (NCF) that the name *Uredo maydis* should be conserved over *Lycoperdon zeae* in order to to preserve the well-known epithet "*maydis*", which has been used for this species for over two centuries, but does not have priority over "*zeae*" if combined into *Mycosarcoma*.

Neither Beckmann (1768) nor de Candolle (1815) designated specimens or illustrations that might serve as the nomenclatural types when *Lycoperdon zeae* and *Uredo maydis* were described. Nor were we able to locate specimens in German and French herbaria that pre-dated the descriptions by Beckmann (1768) or de Candolle (1815) that might have been studied by them. As there are no specimens or illustrations associated with the name *U. maydis* that might serve as a lectotype, we consequently designate a sequenced neotype for *Ustilago maydis* here. The neotype was chosen on the basis that it represented a typical strain of corn smut with a published genome sequenced by the Broad Institute (Kämper *et al.* 2006). Further, populations of corn smut in Europe have been found to be monophyletic (Begerow, unpubl.).

Mycosarcoma pachycarpum (Syd.) McTaggart, R.G. Shivas & Begerow, **comb. nov.**
MycoBank MB811943
Basionym: *Sorosporium pachycarpum* Syd., *Ann. Mycol*. **26**: 431 (1928).
Synonyms: *Tolyposporella pachycarpa* (Syd.) L. Ling, *Sydowia* **3**: 133 (1949).
Endosporisorium pachycarpum (Syd.) Vánky, *Mycotaxon* **56**: 213 (1995).
Tubisorus pachycarpus (Syd.) Vánky & M. Lutz, *Mycol. Balcan.* **8**: 131 (2011).

Type: on *Rottboellia ophiuroides,* Philippines.

Mycosarcoma tubiforme (R.G. Shivas & Vánky) McTaggart, R.G. Shivas & Begerow, **comb. nov.**
MycoBank MB811944
Basionym: *Macalpinomyces tubiformis* R.G. Shivas & Vánky, *Fung. Divers.* **16**: 152 (2004).

Type: on *Chrysopogon fallax*, Australia.

DISCUSSION

Mycosarcoma is resurrected here and the circumscription emended to accommodate a monophyletic group in *Ustilaginaceae*; this addresses one further component of polyphyly in *Ustilago s. lat*. This taxonomy is supported by several separate systematic analyses that have determined a unique phylogenetic position of *M. maydis* within the family (Piepenbring *et al*. 2002, Stoll *et al*. 2005, Vánky & Lutz 2011, McTaggart *et al*. 2012a). We will submit a proposal to the Nomenclature Committee for Fungi for conservation of *Uredo maydis* over the name *Lycoperdon zeae*, which has priority at species rank, to avoid a disadvantageous nomenclatural change, as '*maydis*' is an accepted and widely used epithet for corn smut in plant pathology and genetics. If this proposal is successful, the name *M. maydis* will become secure.

Future studies that include more taxa and additional phylogenetically informative molecular markers may reveal

Table 1. Taxon names and GenBank numbers of isolates used in the phylogenetic analyses.

Taxon	Host	GenBank details	
		ITS	LSU
Anomalomyces panici	*Panicum trachyrhachis*	DQ459348[1]	DQ459347[1]
Anthracocystis destruens	*Panicum miliaceum*	AY344976[2]	AY747077[2]
Anthracocystis heteropogonicola	*Heteropogon contortus*	HQ013101[3]	HQ013135[3]
Langdonia aristidae	*Aristida hygrometrica*	HQ013096[3]	NA
Langdonia confusa	*Aristida queenslandica*	HQ013095[3]	HQ013132[3]
Langdonia fraseriana	*Aristida nitidula*	HQ013100[3]	NA
Macalpinomyces arundinellae-setosae	*Arundinella nepalensis*	HQ013086[3]	NA
Macalpinomyces eriachnes	*Eriachne aristidea*	AY740037[2]	AY740090[2]
Macalpinomyces trichopterygis	*Trichopteryx dregeana*	AY740039[2]	AY740092[2]
Macalpinomyces tristachyae	*Loudetiopsis chrysothrix*	AY740164[2]	NA
Melanopsichium pennsylvanicum	*Polygonum glabrum*	AY740040[2]	AY740093[2]
Moesziomyces bullatus	*Paspalum distichum*	AY740153[2]	AY740153[2]
Mycosarcoma bouriquetii	*Stenotaphrum dimidiatum*	AY740167[2]	NA
Mycosarcoma mackinlayi	*Eulalia mackinlayi*	GU014817[4]	HQ013131[3]
Mycosarcoma maydis	*Zea mays*	AY345004[5]	AF453938[6]
Mycosarcoma pachycarpum	*Mnesithea rottboellioides*	JN871718[7]	JN871717[7]
Mycosarcoma tubiforme	*Chrysopogon fallax*	HQ013088[3]	NA
Sporisorium cruentum	*Sorghum halepense*	AY344974[2]	AF453939[6]
Sporisorium reilianum	*Zea mays*	FJ167357[8]	DQ832228[9]
Sporisorium sorghi	*Sorghum bicolor*	AF038828[10]	AF009872[11]
Stollia bursa	*Themeda quadrivalvis*	AY740154[2]	NA
Stollia ewartii	*Sarga timorensis*	HQ013087[3]	HQ013127[3]
Triodiomyces altilis	*Triodia pungens*	AY740166[2]	HQ013136[3]
Triodiomyces triodiae	*Triodia microstachya*	AY740074[2]	AY740126[2]
Ustilago avenae	*Avena barbata*	AY344997[5]	AF453933[6]
Ustilago bromivora	*Bromus catharticus*	AY740064[2]	AY740118[2]
Ustilago bullata	*Bromus diandrus*	AY344998[5]	AF453935[6]
Ustilago calamagrostidis	*Calamagrostis epigeios*	AY740065[2]	AY740119[2]
Ustilago cynodontis	*Cynodon dactylon*	AY345000[5]	AF009881[11]
Ustilago davisii	*Glyceria multiflora*	AY740169[2]	NA
Ustilago echinata	*Phalaris arundinacea*	AY345001[5]	AY740144[2]
Ustilago hordei	*Hordeum vulgare*	AY345003[5]	AF453943[6]
Ustilago nuda	*Hordeum leporinum*	AY740069[2]	JN367334[13]
Ustilago striiformis	*Alopecurus pratensis*	AY740172[2]	DQ875375[12]
Ustilago tritici	*Triticum aestivum*	AF135424[14]	NA
Ustilago vetiveriae	*Vetiveria zizanioides*	AY345011[5]	AY740149[2]
Yenia esculenta	*Zizania latifolia*	AY345002[5]	AF453937[6]

[1]Vánky *et al*. (2006); [2]Stoll *et al*. (2005); [3]McTaggart *et al*. (2012a); [4]McTaggart & Shivas (2009); [5]Stoll *et al.* (2003); [6]Piepenbring *et al.* (2002); [7]Vánky & Lutz (2011); [8]Zhang & Gao (unpubl.); [9]Matheny *et al*. (2006); [10]Roux *et al.* (1998); [11]Begerow *et al*. (1997); [12]Begerow *et al.* (2006); [13]Kellner *et al*. (2011); and [14]Bakkeren *et al*. (2000).

that other species also belong to *Mycosarcoma*. In the present study, *Macalpinomyces arundinellae-setosae* and *U. vetiveriae* fit the morphological concept of *Mycosarcoma*, but were not recovered in *Mycosarcoma* with strong support in the phylogenetic analyses. Detailed studies on the ontogeny of sori and teliospores might help to further clarify the limits of *Mycosarcoma*. For example, *Macalpinomyces trichopterygis*, *M. tristachyae,* and *M. simplex*, which were included in the phylogenetic analyses, cause systemic infections on grasses in the subfamily *Arundinoideae*. These three species also have tubular, host-derived sori, and have a phylogenetic affinity with *Mycosarcoma* as shown in previous studies (Stoll *et al*. 2005, Vánky & Lutz 2011, McTaggart *et al*. 2012a).

Thines (2016) proposed that *U. maydis* should be conserved as the type species of *Ustilago* to cement the name of this well-studied smut fungus. This was on the grounds that *U. hordei*, the current type, does not supersede *U. segetum*, which was designated as lectotype of *Ustilago*

by Clinton (1904). However, *U. segetum* was not described as a distinct taxon, but initially as a set of three varieties (Persoon 1797), and subsequently sanctioned as a set of five varieties (Persoon 1801), with *U. hordei* the alpha variety, "*Uredo segetum* α *Uredo hordei*". Most of these varieties were subsequently raised to species rank (Lagerheim 1889, Saccardo 1891), and Clinton (1906) revised the name of his typification to *U. hordei* (Clinton 1906). As the alpha or 'typical' variety, *U. hordei* represents the name of the type after the species names *Ustilago*/*Reticularia segetum* were declared *nomina utique rejicienda*. Furthermore, *Ustilago hordei* is a conserved name with a type specimen studied by Persoon.

If *Ustilago hordei* were not the type, *Ustilago maydis* would not be a suitable choice as a replacement, because it is not among the species described in the sanctioning work (Art 10.2), it is not congeneric with *Ustilago* as described by Persoon (1801), and it would require ~200 name changes for species of *Ustilago* that are not congeneric with *U. maydis*. The mycological community has previously accepted name changes for model fungi such as *Microbotryum violaceum* and *Zymoseptoria tritici*, and the adoption of *Mycosarcoma maydis* will provide stability for two genera of smut fungi.

Ustilago maydis was recombined in *Mycosarcoma* a century ago to distinguish it from other species of smut fungi, particularly species of *Ustilago*. We suggest the scientific community adopts the taxonomy proposed by Brefeld (1912) and summarized here, to ensure classification reflects evolution.

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