Anomalomyces, Ustilaginaceae (Ustilaginomycetes)

There are 14 genera of smut fungi recognized in Ustilaginaceae (Ustilaginomycetes) on grasses: Anomolomyces, Anthracocystis, Franzpetrakia, Langdonia, Macalpinomyces, Moesizymyces, Sporisorium, Stollia, Tranzschelia, Triidiomyces, 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 Pooidae 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 taxra (Piątek et al. 2015, Wang et al. 2015).

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**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, Tolyposporrella pachycarpa, Ustilago bouriquetii and U. maydis, occupy a unique phylogenetic position within the Ustilaginales. 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
- Ustilaginomycotina

**INTRODUCTION**

There are 14 genera of smut fungi recognized in Ustilaginales (Ustilaginomycetes) on grasses: Anomolomyces, Anthracocystis, Franzpetrakia, Langdonia, Macalpinomyces, Moesizymyces, Sporisorium, Stollia, Tranzschelia, Triidiomyces, 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 Pooidae 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 taxra (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 sori (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

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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 (Müller 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

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.
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*

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

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

**Mycosarcoma bouriquetii** (Maubl. & R.G. Shivas & Begerow, comb. nov. MycoBank MB811941

Basionym: Ustilago bouriquetii Maubl. & Roger, Bull. Soc. Mycol. France 50: 327 (1934).

Synonyms: Sphaelotheca mauritiana Zundel, Mycologia 36: 405 (1944); *fide* Vánky (1996:107).

**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).

**Mycosarcoma maydis** (DC.) Bref., Unters. Gesamt-gb. 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); *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. Kahrmann, 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** G. Winter, Rabenh. Krypt.-Fl. 1(1): 97 (1881); as „U. Zeae Mays".

**Ustilago maydis**: 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 euthalenae** 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 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).

**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).

**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
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.

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

| Taxon | Host | ITS | GenBank details |
|-------|------|-----|----------------|
| Anomalomyces panici | Panicum trachyrhachis | DQ459348 | DQ459347 |
| Anthracostis destruens | Panicum miliaceum | AY344976 | AY740777 |
| Anthracostis heteropogonica | Heteropogon contortus | HQ013101 | HQ013135 |
| Langdonia aristae | Aristida hygrometrica | HQ013096 | NA |
| Langdonia confusa | Aristida queenslandica | HQ013095 | HQ013132 |
| Langdonia fraseriana | Aristida nitidula | HQ013100 | NA |
| Macalpinomyces arundinellae-setosae | Arundinella nepalensis | HQ013086 | NA |
| Macalpinomyces eriachnes | Eriachne aristidea | AY740037 | AY740090 |
| Macalpinomyces trichopterygis | Trichopteryx dregeana | AY740039 | AY740092 |
| Macalpinomyces tristachyae | Loudetiosis chrysotrix | AY400164 | NA |
| Melanopsischium pennsylvanicum | Polygonum glabrum | AY740040 | AY740093 |
| Moesziomyces bullatus | Paspalum distichum | AY740153 | AY740153 |
| Mycosarcoma bouriquetii | Selenatrophum dimidiatum | AY740167 | NA |
| Mycosarcoma macquiniay | Eulalia macquiniay | GU014817 | HQ013131 |
| Mycosarcoma maydis | Zea mays | AY345004 | AF453938 |
| Mycosarcoma pachycarpum | Mnesithea rotboelioides | JN871718 | JN871717 |
| Mycosarcoma tubiforme | Chrysopogon fallax | HQ013088 | NA |
| Sporisorium cruentum | Sorghum halepense | AY344974 | AF453939 |
| Sporisorium rheiiniun | Zea mays | FJ167357 | DQ832228 |
| Sporisorium sorghi | Sorghum bicolor | AF038828 | AF009872 |
| Stollia bursa | Themeda quadrivalvis | AY740154 | NA |
| Stollia ewartii | Sarga imoresin | HQ013087 | HQ013127 |
| Triodiomyces altitiss | Triodia pungens | AY740166 | HQ013136 |
| Triodiomyces triodiae | Triodia microstachya | AY740074 | AY740126 |
| Ustilago avenae | Avena barbata | AY344997 | AF453933 |
| Ustilago bromivora | Bromus catharticus | AY740064 | AY740118 |
| Ustilago bullata | Bromus diandrus | AY344998 | AF453935 |
| Ustilago calamagrostidis | Calamagrostis epeigio | AY740065 | AY740119 |
| Ustilago cynodontis | Cynodon dactylon | AY345000 | AF009881 |
| Ustilago davisi | Glycera multiflora | AY740169 | NA |
| Ustilago echinita | Phalaris arundinacea | AY345001 | AY740144 |
| Ustilago hordei | Hordeum vulgare | AY345003 | AF453943 |
| Ustilago nuda | Hordeum leporinum | AY740069 | JN367336 |
| Ustilago striiformis | Alopecurus pratensis | AY740172 | DQ875375 |
| Ustilago tritici | Triticum aestivum | AF135424 | NA |
| Ustilago vetiveriae | Vetiveria zizanioides | AY345011 | AY740149 |
| Yenia esculenta | Zizania latifolia | AY345002 | AF453937 |

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