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REVIEW ARTICLE

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A review of the *Ustilago-Sporisorium-Macalpinomyces* complex

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Abstract The fungal genera *Ustilago*, *Sporisorium* and *Macalpinomyces* represent an unresolved complex. Taxa within the complex often possess characters that occur in more than one genus, creating uncertainty for species placement. Previous studies have indicated that the genera cannot be separated based on morphology alone. Here we chronologically review the history of the *Ustilago-Sporisorium-Macalpinomyces* complex, argue for its resolution and suggest methods to accomplish a stable taxonomy. A combined molecular and morphological approach is required to identify synapomorphic characters that underpin a new classification. *Ustilago*, *Sporisorium* and *Macalpinomyces* require explicit re-description and new genera, based on monophyletic groups, are needed to accommodate taxa that no longer fit the emended descriptions. A resolved classification will end the taxonomic confusion that surrounds generic placement of these smut fungi.

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INTRODUCTION

Three genera of smut fungi (*Ustilaginomycotina*), *Ustilago*, *Sporisorium* and *Macalpinomyces*, contain about 540 described species (Vánky 2011b). These three genera belong to the family *Ustilaginaceae*, which mostly infect grasses (Begerow et al. 2006) and have teliospores that germinate to produce phragmobasidia (Bauer et al. 2001, Begerow et al. 2006). *Ustilago* and *Sporisorium* were shown to form a monophyletic group within the *Ustilaginaceae* after molecular phylogenetic analyses (Begerow et al. 1997, 2006, Stoll et al. 2003, 2005). The systematic position of *Macalpinomyces* is ambiguous within the *Ustilaginales* (Begerow et al. 2006).

Many taxa within *Ustilago*, *Sporisorium* and *Macalpinomyces* share two or more morphological characters indicative of the different genera. This makes taxonomic placement of species within genera problematic. The original characters used to identify genera were not sufficiently robust to encompass the full morphological diversity of novel species that have since been discovered. Taxa within *Ustilago*, *Sporisorium* and *Macalpinomyces* are part of a systematically unresolved complex (Vánky 2002a, Stoll et al. 2003, 2005, Piepenbring 2004, Vánky et al. 2006, Vánky & Shivas 2008). Three further genera, *Anomalomyces*, *Melanopsichium* and *Tubisorus*, are considered to be distinct, well-defined members of this complex.

Attempts to reconcile the taxonomy of this complex using either morphology (Vánky 1991, Piepenbring et al. 1998) or molecular phylogenetics (Stoll et al. 2003, 2005) have been unsuccessful. This paper reviews chronologically changing generic concepts in the *Ustilago-Sporisorium-Macalpinomyces* complex and presents an approach for resolving systematic anomalies.

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TAXONOMIC HISTORY

Ustilago

Ustilago, derived from the Latin *ustilare* (to burn), was named by Persoon (1801) for the blackened appearance of the inflorescence in infected plants, as seen in the type species *U. hordei*. According to Clinton (1906), Persoon adopted the name *Ustilago* from Johann Bauhin's 1651 edition of 'Historia plantarum universalis'. Persoon (1801) created *Ustilago* as a subgenus of *Uredo* in his 'Synopsis Methodica Fungorum'. He described *Uredo*, now classified within the rust subphylum *Pucciniomycotina* (Aime et al. 2006), as lacking a peridium and having spores that were powdery, loose, uniform and mostly globose. *Ustilago*, now classified in the smut subphylum *Ustilaginomycotina*, was separated from *Uredo* by possessing black to brown powdery spores that parasitize mostly plant inflorescences. *Ustilago* was promoted to the level of genus by Roussel (1806). *Ustilago* became a catch-all genus for a diversity of smut fungi. Many taxa currently regarded as belonging to *Ahmadiago*, *Antherospora*, *Anthracoidea*, *Aurantiosporium*, *Bambusiomyces*, *Bauerago*, *Cintractia*, *Eriocaulago*, *Exoteliospora*, *Farysia*, *Farysporium*, *Liroa*, *Macalpinomyces*, *Melanopsichium*, *Microbotryum*, *Parvulago*, *Pericladium*, *Schizonella*, *Sporisorium*, *Thecaphora*, *Tilletia*, *Tranzscheliella*, *Ustanciosporium*, *Vankya*, *Websdanea* and *Yelsemia* were originally described as members of *Ustilago* (e.g. Piepenbring et al. 1996, Vánky 1998a, 1999a, b, 2002a, b, 2003b, 2004b, 2011a, b, Bauer et al. 1999, 2007, 2008, Piepenbring 2000, Vánky et al. 2008).

Juliohirschhornia was proposed for its pattern of spore germination, which was considered to be intermediate to the *Ustilaginaceae* and *Tilletiaceae* (Hirschhorn 1986). Vánky (2002a) noted that *Juliohirschhornia* was an invalid genus and further considered its spore germination represented only a variant of the *Ustilago*-type. Several other genera were regarded by Vánky (2002a) as synonymous with *Ustilago*, including *Crozalsiella*, *Necrosis*, *Pericoelium* and *Ustilagidium*.

Two attempts have been made to subdivide *Ustilago*, although the proposed classifications have not been widely accepted. Firstly, Brefeld (1912) proposed the genus *Mycosarcoma* for *Ustilago maydis*. Brefeld (1912) based *Mycosarcoma* on the

structure of the peridium, incubation time in the host, localized infection and development of aerial conidia. Generic placement of *U. maydis* within the complex is contentious (Piepenbring et al. 2002, Stoll et al. 2005) and until the complex is resolved, this taxon is best left within *Ustilago* because of its importance as a model plant pathogen.

Another attempt to subdivide *Ustilago* was made in 1949 by the mycologist Tchen Ngo Liou, who considered that the basidia of *U. esculenta* differed from the type species of *Ustilago* (cited in Piepenbring et al. 2002). Liou erected the genus *Yenia*, with *Y. esculenta* as the type, and transferred seven additional *Ustilago* species into the new genus (Liou 1949). Vánky (2002a) considered that the eight taxa Liou selected were very different in biology, soral structure, spore morphology and germination patterns, and did not constitute a natural group. Piepenbring et al. (2002) in their single-locus phylogenetic analysis found that *U. esculenta* was sister to 21 species of *Ustilago* and *Sporisorium*, accepting that *U. esculenta* belonged in a separate genus to *Ustilago*. Stoll et al. (2005) did not support the separation of *U. esculenta* from *Ustilago* on the basis of a molecular phylogenetic analysis, which included this and 97 other *Ustilago*, *Sporisorium* and *Macalpinomyces* species.

Beck (1894) introduced the genus *Melanopsichium* for a taxon first described as *Ustilago austro-americanum* on *Polygonum*. The genus was characterised by compact, hard, irregularly lobed galls in the inflorescence, stems and leaves (Halisky & Barbe 1962, Vánky 2002a). Weiss et al. (2004), Begerow et al. (2004) and Stoll et al. (2005) concluded that *Melanopsichium* represented an example of a host jump from *Poaceae* to *Polygonaceae*, as *M. pennsylvanicum* belonged to the *Ustilago* clade. Begerow et al. (2006) consequently rejected the family *Melanopsichiaceae* proposed by Vánky (2001a).

Langdon & Fullerton (1975) studied the soral ontogeny of six *Ustilago* species. Their revised concept of *Ustilago* included taxa that colonised host plants with hyphae that destroyed parenchymatous tissue to then become spores, without forming fungal peridia, columellae, sterile cells or spore balls.

The gross morphology of *Ustilago* is variable (Fig. 1). Piepenbring (2004) recorded 14 different soral morphologies for *Ustilago* in her treatise of the sori found in the *Ustilaginomycotina*. Some taxa, such as *U. sparsa* and *U. trichophora*, occurred as localised galls on the host plant, inducing hypertrophied ovaries rather than destroying the entire inflorescence. *Ustilago altilis* and *U. esculenta* infected the culms of the host, and some species occurred in the leaves, for example *U. calamagrostidis* and *U. striiformis*. Vánky (2002a) considered *Ustilago* as occurring solely on hosts in the *Poaceae*, accepting 174 species (Vánky 2011b).

Sporisorium

Ehrenberg described *Sporisorium* in a letter to Link, based on a collection he had made of *S. sorghi* on the cultivated grass *Sorghum* in the *Poaceae* (Link 1825). *Sporisorium* was described as unique because it possessed columellae of equal length as the glumes, formed agglutinated spores and mutilated floral parts. *Sporisorium* also had sterile partitioning cells in groups or chains and a peridium (Link 1825, Langdon & Fullerton 1978).

Four years after the description of *Sporisorium*, Rudolphi (1829) described the confusingly named *Sorosporium* from *Saponaria officinalis* in the *Caryophyllaceae*. Many authors subsequently chose *Sorosporium* for smut taxa with peridia and spore balls including those that infected grasses (*Poaceae*). *Sporisorium* was overlooked for about 150 years until Langdon & Fullerton (1978) re-established the name. Many of the species described

Fig. 1 Diversity of soral morphology in *Ustilago*. a. *Ustilago spinificis* on *Spinifex longifolius*; b. *Ustilago xerochloae* on *Xerochloa barbata*; c. *Ustilago drakensbergiana* on *Digitaria tricholaenoides*; d. *Ustilago tritici* on *Triticum aestivum*; e. *Ustilago bouriquetii* on *Stenotaphrum dimidatum*; f. *Ustilago altilis* on *Triodia* sp.; g. *Ustilago phragmitis* on *Phragmites karka*; h. *Ustilago cynodontis* on *Cynodon dactylon*.

in *Sorosporium* and *Ustilago* have since been reclassified in *Sporisorium*. More precisely, *Sporisorium* contains at least 60 taxa originally classified as *Ustilago*, and about 170 taxa described as *Sorosporium* (Robert et al. 2005).

Sorokin described *Endothlaspis* in 1890 for two smuts, on *Sorghum* and *Melica*, of which the respective types have been lost (cited in Langdon & Fullerton 1978, Vánky 2002a). Langdon & Fullerton (1978) believed the description and illustrations of *Endothlaspis* were vague and poorly executed. Vánky (2002a) considered that *Endothlaspis* was a synonym of *Sporisorium* and that the type species was based on a host misidentification.

Lavrov (1936) and Ciferri (1938) divided *Sorosporium* into two subgenera depending on whether they infected hosts in *Poaceae* or *Caryophyllaceae* (cited in Vánky 2002a). Langdon & Fullerton (1975) noted that *Sorosporium* species on *Poaceae* differed in soral ontogeny and structure to species on *Caryophyllaceae*, essentially in that *Sorosporium* on *Caryophyllaceae* lacked a well-defined sorus. Langdon & Fullerton (1975) suggested that smuts on *Poaceae* should be grouped in a separate genus, but did not make any taxonomic revisions at that stage. Vánky (1998b) considered *Sorosporium* to be a synonym of *Thecaphora* after an examination of the types of both genera revealed no essential morphological differences. This decision was subsequently supported by molecular phylogenetic analyses (Vánky et al. 2008).

Sphacelotheca was established by de Bary (1884) for *Sph. hydropiperis* on *Polygonum*. *Sphacelotheca* was defined as having a membrane or peridium enclosing the spores and a columella (cited in Langdon & Fullerton 1978). Clinton (1902) transferred 10 taxa from *Ustilago* to *Sphacelotheca*, including *Sporisorium*

Fig. 2 Diversity of soral morphology in *Sporisorium*. a. *S. cenchri-elymoidis* on *Cenchrus elymoidis*; b. *S. cryptum* on *Yakirra* sp.; c. *S. heteropogonicola* on *Heteropogon contortus*; d. *S. bothriochloae* on *Dichanthium sericeum*; e. *S. tumefaciens* on *Chrysopogon* sp.; f. *S. iseilematis-ciliati* on *Iseilema* sp.; g. *S. themedae* on *Themeda triandra*; h. *S. aristidicola* on *Aristida* sp.; i. *S. likhitekerajae* on *Ischaemum* sp.; j. *S. doidgeae* on *Capillipedium parviflorum*; k. *S. sacchari* on *Saccharum* sp.; l. *Ustilago scitaminea* on *Saccharum officinarum*; m. *Sporisorium caledonicum* on *Heteropogon contortus*; n. *S. ischaemum* on *Ischaemum indicum*; o. *S. holwayi* on *Andropogon bicornis*.

sorghi, which he referred to as *Ustilago sorghi*. Clinton did not mention *Sporisorium*, but he attributed the authorship of *U. sorghi* to Link, indicating that he was aware of *Sporisorium* as an earlier described genus. Aside from a brief mention of the characters of *Sphacelotheca*, Clinton gave no reason why the 10 taxa would be better suited to *Sphacelotheca*. Clinton's transferral of taxa in *Sporisorium* to *Sphacelotheca* sensu Clinton was precedent for over 110 subsequent descriptions of species of *Sphacelotheca* on grasses (Robert et al. 2005).

Langdon & Fullerton (1978) ascertained that the columellae in *Sphacelotheca* species on *Polygonaceae* and *Poaceae* were not homologous. *Sphacelotheca* formed a columella from fungal cells adhering to one another on hosts in the *Polygonaceae*, whereas columellae were derived from host material in the *Poaceae*. Langdon & Fullerton (1978) also noted differences in the peridium and the development of the spore mass between *Sphacelotheca* in the *Polygonaceae* and *Poaceae*. *Sphacelotheca* occurred only on hosts in the *Polygonaceae* and has been shown by Bauer et al. (1997) to belong to the *Microbotryales* in the *Pucciniomycotina*. This systematic placement was confirmed by molecular analyses (Weiss et al. 2004, Kemler et al. 2006).

Langdon & Fullerton (1978) resurrected *Sporisorium* after showing that *Sphacelotheca* and *Sorosporium* were not suitable genera for smut fungi on grasses. They designated a new type specimen of *Sporisorium sorghi* from an Australian collection on *Sorghum leiocladum*, which Vánky (1990) believed to represent *S. cruentum*. Vánky (1990) proposed a new neotype from an Egyptian collection of *S. sorghi*. The neotype originally proposed by Langdon & Fullerton (1978) appeared to belong to a distinct species, *S. australasiaticum* (Vánky & Shivas 2001).

Langdon & Fullerton (1978) outlined the characteristics of *Sporisorium* based on their neotype of *Sporisorium sorghi*. Characters of importance included a 'hyphal peridium, columella composed of host tissues and hyphae, and spores intermixed with partitioning (sterile) cells'. These characters are variable among other *Sporisorium* species (Fig. 2).

The morphological variation of peridia, columellae, sterile cells and dimorphic spores in *Sporisorium* has led to different interpretations by mycologists. For example, Langdon & Fullerton (1975) described the presence of a columella in *Sporisorium consanguineum*, but it was later reported absent by Vánky & Shivas (2008). A columella was not described by Langdon (1962) in *Ustilago porosa*, but this species was regarded to have one by Vánky & Shivas (2001). The presence or absence of columellae, peridia, sterile cells and dimorphic spores has formed the taxonomic boundary between *Sporisorium* and *Ustilago*, and interpretations of these structures must be consistent before the complex can be resolved.

Another character used to define *Sporisorium* was that spores were often compacted in permanent (or semi-permanent) spore balls (Vánky 2002a, Vánky & Shivas 2008). Vánky (1998c) considered spore balls to be homoplasious in the *Ustilaginomycotina* and they do not occur across all taxa in *Sporisorium*. Vánky (2011b) recognised 326 species of *Sporisorium*.

Macalpinomyces

Langdon & Fullerton (1977) established *Macalpinomyces* to accommodate *M. eriachnes*, which they considered as distinct from *Sporisorium* and *Ustilago*. *Macalpinomyces* lacked columellae, produced sterile cells and the spores were uniformly ornamented and polyangular or subpolyangular (Langdon & Fullerton 1977, Vánky 1996).

Fig. 3 Diversity of soral morphology in *Macalpinomyces*. a. *M. ewartii* on *Sorghum timorense*; b. *M. arundinellae-setosae* on *Arundinella setosa*; c. *M. mackinlayi* on *Eulalia mackinlayi*; d. spores of *M. mackinlayi*; e. *M. siamensis* on *Coelorachis striata*; f. *M. eriachnes* on *Eriachne helmsii*; g. spores of *M. eriachnes*. — Scale bars: d, g = 10 µm.

The nomenclatural history of *M. eriachnes* epitomises the confusion caused by many taxa in the *Ustilago-Sporisorium-Macalpinomyces* complex. The original collection of *M. eriachnes* in Australia by the botanist Ferdinand von Mueller, was divided and sent to two mycologists, Mordecai Cooke in England and Felix von Thümen in Germany. Two new fungal taxa were described based on this single collection, *Sorosporium eriachnes* by Thümen in 1878 and *Ustilago australis* by Cooke in 1879 (Langdon & Fullerton 1977). Langdon & Fullerton (1977) later transferred this smut to a new genus, *Macalpinomyces*, nearly a century after the specimen was first described.

Vánky (1996) broadened the concept of *Macalpinomyces* to include taxa that lacked a columella but possessed sterile cells, which are morphological features shared by both *Sporisorium* and *Ustilago*. This led to numerous taxonomic combinations, for example, *M. bursus*, *M. neglectus* and *M. spinulosus*. The broadened concept of *Macalpinomyces* allowed for a variety of gross morphologies to be included, ranging from localised or systemic galls in the ovaries, to longitudinally hypertrophied sori up to 16 cm long in *M. chrysopogonicola* (Fig. 3).

Molecular phylogenetic analysis has shown that *Macalpinomyces* is polyphyletic. The type species, *M. eriachnes*, is sister to all other taxa in the complex, and forms a monotypic genus within the *Ustilaginaceae* (Stoll et al. 2005). Begerow et al. (2006), in their phylogenetic study of the *Ustilaginomycotina*, proposed that *M. eriachnes* might not belong to the *Ustilaginaceae* as it did not occur in the clade containing *Sporisorium*, *Ustilago* and *Moesziomyces*.

Species of *Macalpinomyces* have sterile cells, a peridium derived from host material, and lack true spore balls (Vánky 2011b). Vánky (2011b) accepted 46 species of *Macalpinomyces*.

Relationships within the Ustilago-Sporisorium-Macalpinomyces complex

Taxa within the *Ustilago-Sporisorium-Macalpinomyces* complex often possess morphological characters that occur in more than one genus. Overlapping characters create uncertainty for species placement, as illustrated by *Macalpinomyces eriachnes*, which was independently placed in both *Ustilago* and *Sorosporium*. In a comprehensive taxonomic study over the course of eight years, Vánky (1996, 1997, 1998d, 2001c, 2002b, 2003a, b, 2004a, b) and Vánky & Shivas (2001, 2003) combined over 30 smut species that possessed a combination of *Sporisorium* and *Ustilago* characters into *Macalpinomyces*. Taxonomic shuffling occurred later with many species described before 1978 as *Ustilago* and that were subsequently moved to either *Macalpinomyces* or *Sporisorium*. The result was that many taxa have been moved back and forth among genera without systematic evidence that they constituted natural, monophyletic groups.

New genera have been raised for some smuts that differed subtly from the type descriptions of *Ustilago*, *Sporisorium* and *Macalpinomyces*. *Endosporisorium* (Vánky 1995a), *Lundquistia* (Vánky 2001b), *Anthracocystis* (Brefeld 1912), *Yenia* (Liou 1949) and *Tubisorus* (Vánky & Lutz 2011) are examples of genera that were proposed to subdivide *Ustilago* and *Sporisorium*. The description of new genera or placement of taxa in poorly defined genera, has contributed to systematic confusion within the complex.

Vánky (1995a) described *Endosporisorium* to accommodate *Sorosporium capillipedii* (type) and *Sorosporium loudetiae* and later added two other smut taxa (Vánky 1995b). This genus differs from *Ustilago* in having sterile cells and ephemeral spore balls, and from *Sporisorium* in lacking columellae and a fungal derived peridium. The sori of *Endosporisorium* were described from the stems rather than the inflorescences. After Vánky (1996) emended *Macalpinomyces* to encompass more taxa, he subsequently synonymised *Endosporisorium* with *Macalpinomyces*, preferring a large, well-delimited genus, rather than many monotypic and closely related genera (Vánky 1997).

Vánky (2001b) originally established *Lundquistia* for *L. fascicularis* (syn. *L. panici-leucophaei*), and later added three other taxa (Vánky 2004c), which were transferred from either *Sporisorium* or *Ustilago*. The emended *Lundquistia* (Vánky 2004c) differed from *Ustilago* in having spore balls and sterile cells; from *Sporisorium* in lacking peridia and columellae; and from *Macalpinomyces* in having permanent or ephemeral spore balls. Molecular phylogenetic analyses showed that *Lundquistia* was a synonym of *Sporisorium* as it occurred in the *Sporisorium* clade (Cunnington et al. 2005, Stoll et al. 2005). Cunnington et al. (2005) included four *Lundquistia* species in their phylogenetic analysis using the ITS region and demonstrated that it was a polyphyletic group. Vánky (2001b) described *Lundquistia* as lacking true columellae, whereas, Piepenbring (1999) considered the fascicular vascular bundles mixed with fungal material as columellae in *Sporisorium panici-leucophaei* (syn. *L. panici-leucophaei*).

Brefeld (1912) described *Anthracocystis* for a smut on *Panicum miliaceum*, which is currently named *Sporisorium destruens*. He considered it different from *Ustilago* due to the peculiar formation of its soral peridium, which developed from the floral envelopes. Soral structures such as columellae and spore balls were not included in the protologue (Brefeld 1912). Vánky (2002a) erroneously considered *Anthracocystis* a nomen nudum and thereby an illegitimate name according to the then 'International Code of Botanical Nomenclature'. However, *Anthracocystis* is a validly published name, as it contained a diagnosis and was described in 1912, before Latin was required in taxonomic descriptions.

Vánky et al. (2006) described *Anomalomyces* as a monotypic genus with shared characters of *Ustilago*, *Sporisorium* and *Macalpinomyces*, but with a unique partitioning of the sorus and two types of sterile cells. They established a new genus based on the peculiar morphology and a phylogenetic analysis that placed *Anomalomyces* in a polytomy with the *Sporisorium* groups and the *Ustilago* group occurring on pooid grasses. *Anomalomyces* differed from *Ustilago* by possessing a peridium, spore balls and sterile cells, but did not fit into *Sporisorium* as it lacked columellae. It differed from *Macalpinomyces* by possessing genuine spore balls.

Some species fit unambiguously into *Sporisorium* and *Ustilago*. Molecular phylogenetic analysis has shown many morphologically similar smut species to be sister to the types of *Sporisorium* and *Ustilago* (Stoll et al. 2005). *Macalpinomyces* was resolved as a monotypic genus (Stoll et al. 2005). The difficulty with the *Ustilago-Sporisorium-Macalpinomyces* complex has been that many species do not sit strictly within the boundaries of the genera as defined by the types. To resolve this problem, the genera *Ustilago* and *Sporisorium* must be re-described and new genera, based on monophyletic groups, must be established to accommodate taxa not included in the emended genera.

DETERMINING A NATURAL CLASSIFICATION OF THE USTILAGO-SPORISORIUM-MACALPINOMYCES COMPLEX

Studies based on spore and ultrastructural morphologies were unable to resolve the *Ustilago-Sporisorium-Macalpinomyces* complex (Vánky 1991, Piepenbring et al. 1998). Langdon & Fullerton (1975) used soral ontogeny as a means to separate *Sporisorium* (as *Sorosporium*) and *Ustilago*. Molecular phylogenetic analyses showed that there were several monophyletic groups within the *Ustilago-Sporisorium-Macalpinomyces* complex, but there was no correlation between these groups and

Fig. 4 Four smuts that occur on *Themeda*. a. *Sporisorium benguetense*; b. *S. anthistiriae*; c. *S. enteromorphum*; d. *Macalpinomyces bursus*.

their morphological traits (Stoll et al. 2003, 2005). Stoll et al. (2005) noted strong evidence that smuts had co-evolved with their grass hosts, and sister taxa usually occurred on closely related grasses.

Stoll et al. (2005) considered the morphology of columellae, peridia, sterile cells, spore balls and the classification of the hosts (tribe or subtribe) in their molecular phylogenetic analysis of the *Ustilago-Sporisorium-Macalpinomyces* complex. They mapped these characters onto the hypothesised phylogeny, but none appeared consistently within the monophyletic groups. Stoll et al. (2005) concluded that soral morphology was unsuitable for delimiting genera and resolving the classification of the *Ustilago-Sporisorium-Macalpinomyces* complex.

Taxa in the Ustilago-Sporisorium-Macalpinomyces complex should not be unified under Ustilago: a case study with smuts on Themeda

Themeda belongs to the grass tribe *Andropogoneae* in the subfamily *Paniceae*. *Themeda* is parasitized by 17 species in the *Ustilago-Sporisorium-Macalpinomyces* complex, which includes four types of soral morphology (Fig. 4). Several taxa, for example, *Sporisorium themedae* (Fig. 2g), *S. exsertum* and *S. benguetense* (Fig. 4a), infect all the spikelets in an inflorescence, but leave the inflorescence architecture otherwise intact. These species also possess stout or woody columellae. *Sporisorium anthistiriae* (Fig. 4b) and *S. holstii* infect individual spikelets in an inflorescence. Species such as *Sporisorium enteromorphum* (Fig. 4c) and *S. langdonii*, destroy entire racemes with sori that have several filiform columellae. *Macalpinomyces bursus* (Fig. 4d) occurs localised in hypertrophied ovaries.

Vánky (2001a, 2002a) and Piepenbring (2004) believed one of two approaches were needed to resolve the *Ustilago-Sporisorium-Macalpinomyces* complex. The first was to synonymise all of the genera under the earliest name, *Ustilago*, and the second was to split the three genera into smaller genera and subgenera. Unification of the smuts on *Themeda* into one genus would provide a natural classification, albeit not a very useful one, and to group them based on what appear to be convergent characters would exacerbate taxonomic problems within the complex.

There has been a view that host anatomy dictates the soral morphology of smut taxa (Piepenbring 2004, Stoll et al. 2005). Holton et al. (1968) argued that gross morphology was determined by genotypic or inherently permanent factors. The gross morphology of an infection will be influenced to some extent by environmental factors (Fullerton 1975), but as in the case of the smuts on *Themeda*, the morphology of the sorus will be distinctive for different species rather than dependant on the structure of the grass.

A diverse range of soral morphologies occur in the *Ustilago-Sporisorium-Macalpinomyces* complex on other andropogonoid grasses, for example, in *Bothriochloa*, *Sorghum* and *Heteropogon*, which are host to 15, nine and eight smuts, respectively. It will be possible to distinguish genera if soral morphology is synapomorphic. We consider that this diversity necessitates the recognition of new genera or subgenera, rather than the unification of current genera in the complex into *Ustilago*.

CONCLUSION

Is there a solution to the Ustilago-Sporisorium-Macalpinomyces complex?

It has been approximately 200 years since the genera *Ustilago* and *Sporisorium* were first described. These genera contain a diversity of taxa that do not strictly conform to the original generic descriptions. In particular, the genus *Macalpinomyces* contains many species that have specific characters from both *Sporisorium* and *Ustilago*. A stable and workable taxonomy needs to be developed for these important plant pathogens.

Vánky (2002a), Stoll et al. (2005) and Vánky et al. (2006) suggested that analysing additional molecular loci could resolve the *Ustilago-Sporisorium-Macalpinomyces* complex. It is important to relate synapomorphic characters to monophyletic groups in order to create a meaningful taxonomy (Mooi & Gill 2010). Resolution of the complex will depend on a combined analysis of morphological and molecular characters.

Inclusion of morphological data will help to determine synapomorphies that can be used to define groups within the *Ustilago-Sporisorium-Macalpinomyces* complex. To accomplish this, a more detailed examination of the soral structures and their development is warranted. Langdon & Fullerton (1975) identified different soral development patterns in several species of *Sporisorium*, but lacked the advantage of molecular phylogenetic analysis on which to base a new classification. Stoll et al. (2005) considered the presence or absence of columellae and peridia in their study, but did not identify synapomorphies. It is premature to dismiss characters that were thought to be homoplasious, for example spore balls, as a means to delimit genera in the *Ustilaginaceae*. It is possible that spore balls have evolved independently within monophyletic groups in the *Ustilago-Sporisorium-Macalpinomyces* complex. Because there are limited morphological characters that can be examined it is necessary to include all the available characters to determine their systematic potential.

Generic concepts of *Ustilago*, *Sporisorium* and *Macalpinomyces* have been refined over the last 30 years, although they still remain polyphyletic genera. The diversity of taxa within the complex requires further delimitation rather than unification of all smuts under *Ustilago*. *Ustilago*, *Sporisorium* and *Macalpinomyces* need to be revised and a new classification established based on the synapomorphic characters found in monophyletic groups.

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