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THE SMUT FUNGI OF THE WORLD. A SURVEY

K. VÁNKY

Herbarium Ustilaginales Vánky (HUV), Gabriel-Biel-Str. 5, D-72076, Tübingen, Germany

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After a short historical review, our current knowledge about the smut fungi of the world, their number, classification, occurrence on host plant groups and their relationship to other groups of fungi are presented. Surprising results of the new classification of smut fungi are shown. The estimated number of existing species, expected results and trends in smut fungus taxonomy, the necessity and modalities of the conservation of smut fungi and the preparation of an illustrated world monograph of smut fungi are discussed.

Keywords: smut fungi, Ustilaginomycetes, history, classification, host plants, database, conservation, world monograph

Introduction

Smut fungi, Ustilaginomycetes, are plant parasitic microfungi, which in some years and in some regions may produce considerable losses of cultivated plants. Their delimitation and classification have changed radically during the last decade.

1. According to the classical definition, smut fungi are plant parasitic microfungi belonging to the Basidiomycetes. They produce teliospores (ustilospores), organs of dispersal and resistance.

2. The complex definition, besides classical morphological characters, takes into account also ultrastructural, chemical and molecular information in the characterization of the smut fungi. Accordingly, the smut fungi, besides plant parasitic fungi, which may or may not produce teliospores, comprise also saprophytic fungi and even human pathogens.

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3. Pure molecular characterization and classification of the smut fungi are still not elaborated. This is certainly only a question of time and money.

Short historical review

1. Tillet-Tulasne (1755–1847).
2. Tulasne-Zundel (1847–1953).
3. Zundel-New classificatory system (1953–1997).
4. Present, molecular biological period (1997).

Scientific work on smut fungi started in 1755 with the inspired experiments of Tillet on wheat bunt, followed half a century later by Prevosts (1807) study of germination of spores of *Tilletia*, outstanding for that time. Much later, in the second half of the 19th century, smut fungi attracted the attention of those giants of Mycology, the Tulasne brothers (1847, 1854), de Bary (1853, 1874, 1884) and especially Brefeld (1883, 1895a, b, 1905, 1912). They laid the foundations for work on Ustilaginales. In the late eighteen-eighties and well into the twentieth century research on smut fungi centred on sex and nuclear behaviour, and taxonomy became rather unfashionable. Nevertheless Plowright (1889), Rostrup (1890), Clinton (1902, 1904, 1906), McAlpine (1910), Liro (1924, 1938), Cunningham (1924, 1945a, b), Zundel (1938, 1939) and others made very valuable contributions in form of regional smut floras. It was George Lorenzo Zundel (1885–1950) who brought together all known smut fungi in his monumental work, *The Ustilaginales of the World* (1953). This monograph contains names, place of publication, description, synonymy, types, host plant range and family, as well as geographic distribution of all smut fungi published until 1945. A host fungus index was also compiled. Like all works of synthesis, Zundels book stimulated further taxonomic work on Ustilaginales. However, the smuts presented in Zundels book need a critical revision; many of them represent synonyms. Descriptions of species, often taken literally from the original publications, need also to be complemented by a study of the type specimens.

In the 2nd half of the last century numerous smut fungus floras have been published in various countries of the world, which reflect a great variability of species concept, originality, accuracy and level of detail. The number of the known smut fungi increased rapidly, and new genera and higher taxa have been proposed. At the end of the last century enough evidence accumulated that smut fungi are not homogenous (Gottschalk & Blanz, 1985; Swann et al., 1999; Taylor, 1995) and their classification into two families, Ustilaginaceae and Tilletiaceae, proposed by the Tulasne brothers in 1847, based on the basidial type, couldn't be maintained any longer. Based on

ultrastructural characters of the septal pore and that of host-parasite interactions, taking into consideration also classical morphological characters, a new classificatory system of the smut fungi and taxa allied with them has been elaborated by Bauer, Oberwinkler & Vánky (1997). This has been improved, complemented and extended with help of molecular data of nuclear LSU rDNA sequences (Begerow, Bauer & Oberwinkler, 1997/1998; Swann, Frieders & McLaughlin, 1999; Piepenbring, Begerow & Oberwinkler, 1999; Begerow, Bauer & Boeckhout, 2000; Bauer, Begerow, Nagler & Oberwinkler, 2001), and also based on classical morphological characters and host plant taxonomy (Denchev, 1997; Ershad, 2000; Vánky 1999a, b, 2000, 2001a, b).

The present situation and classification of the smut fungi

Currently, the 1450 known "classical" smut fungi (those possessing teliospores) are classified into 2 classes, 3 subclasses, 8 orders, 26 families and 77 genera (for detailed descriptions and illustrations see Vánky, Illustrated Genera of Smut Fungi, 2nd ed., 2002).

I. Class **U S T I L A G I N O M Y C E T E S**

1. Subclass ENTORRHIZOMYCETIDAE
    1. Order ENTORRHIZALES
        1. Family Entorrhizaceae
            Entorrhiza
2. Subclass USTILAGINOMYCETIDAE
    1. Order UROCYSTALES
        1. Family Melanotaeniaceae
            Exoteliospora, Melanotaenium, Yelsemia
        2. Family Doassansiopsaceae
            Doassansiopsis
        3. Family Urocystaceae
            Mundkurella, Urocystis, Ustacystis, Vankya
    2. Order USTILAGINALES
        1. Family Mycosyringaceae
            Mycosyrinx
        2. Family Glomosporiaceae
            Glomosporium, Thecaphora, Tothiella
        3. Family Ustilaginaceae

Farysporium, Franzpetrakia, Lundquistia, Macalpinomyces, Moesziomyces,
Moreaua, Orphanomyces, Pericladium, Restiosporium, Schizonella,
Sporisorium, Stegocintractia, Tranzscheliella, Ustilago

4. Family Anthracoideaceae Denchev
   Anthracoidea, Planetella
5. Family Cintractiaceae
   Cintractia, Heterotolyposporium, Kuntzeomyces, Leucocintractia,
   Testicularia, Tolyposporium, Trichocintractia, Ustanciosporium
6. Family Clintamraceae
   Clintamra
7. Family Dermatosoraceae
   Dermatosorus
8. Family Farysiaceae
   Farysia
9. Family Geminaginaceae
   Geminago
10. Family Melanopsichiaceae
    Melanopsichium
11. Family Uleiellaceae
    Uleiella
12. Family Websdaneaceae
    Websdanea

3. Subclass EXOBASIDIOMYCETIDAE
   1. [Order MALASSEZIALES]
      Malassezia
   2. Order GEORGEFISCHERIALES
      1. Family Georgefischeriaceae
         Georgefischeria, Jamesdicksonia
      2. Family Eballistraceae
         Eballistra
      3. Family Tilletiariaceae
         Phragmotaenium, Tilletiaria, Tolyposporella
   3. Order TILLETIALES
      1. Family Tilletiaceae

Conidiosporomyces, Erratomyces, Ingoldiomyces, Neovossia, Oberwinkleria, Tilletia

4. [Order MICROSTROMATALES]
    1. Family Microstromataceae
        Microstroma
    2. Family Volvocisporiaceae
        Volvocisporium

Superorder EXOBASIDIANAE

5. Order ENTYLOMATALES
    1. Family Entylomataceae
        Entyloma
6. Order DOASSANSIALES
    1. Family Doassansiaceae
        Burrillia, Doassansia, Doassinga, Heterodoassansia, Nannfeldtiomyces, Narasimhania, Pseudodermatosorus, Pseudodoassansia, Pseudotracya, Tracya
    2. Family Melaniellaceae
        Melaniella
    3. Family Rhamphosporaceae
        Rhamphospora
7. [Order EXOBASIDIALES]
    1. Family Brachybasidiaceae
        Brachybasidium, Dicellomyces, Exobasidiellum, Kordyana, Proliferobasidium
    2. Family Exobasidiaceae
        Exobasidium, Muribasidiospora
    3. Family Cryptobasidiaceae
        Botryoconis, Clinoconidium, Coniodictyum, Drepanoconis, Laurobasidium,
    4. Family Graphiolaceae
        Graphiola, Stylina

II. Class **U R E D I N I O M Y C E T E S**

1. Order MICROBOTRYALES
    1. Family Microbotryaceae
        Liroa, Microbotryum, Sphacelotheca, Zundeliomyces
    2. Family Ustilentylomataceae
        Aurantiosporium, Bauerago, Fulvisporium, Ustilentyloma

2. [Order UREDINALES]

The most surprising results of the new classification are:

1. The Microbotryales, comprising about 100 species, are more closely related to the rust fungi than to the classical smut fungi.

2. There are plant parasitic microfungi, human parasites and saprobic fungi that do not produce teliospores but are closely related to the smut fungi (Microstromatales, Exobasidiales, Malasseziales).

3. Similar spore ball structures evolved from different, unrelated ancestors, as an adaptation to parasitism of water plants (Doassansiopsaceae, Doassansiaceae).

4. The presence (or absence) of spore balls does not always reflect a close relationship as was thought earlier. The genera in the Doassansiaceae are characterized by spore balls excepting *Doassinga*, which has single spores. *Schizonella* and *Orphanomyces* are genera containing species with single spores and also with spore balls.

Smut fungi and their hosts

The overwhelming majority of the smut fungi are parasitising angiosperms, especially monocots but also numerous dicots. It is remarkable that no smut fungus is known on the large family of Orchidaceae, with about 18.000 species. Three smut fungi are known that parasites Pteridophyta: a species of *Exoteliospora* on Osmundaceae (*Osmunda*) and two species of *Melaniella* on Selaginellaceae (*Selaginella* spp.). Furthermore, two species of *Uleiella* are known occurring on gymnosperms (*Araucaria* spp.). The zoophilic *Malassezia* (Malasseziales, Exobasidiomycetidae), whose sexual phase is unknown, produces the superficial skin lesions of humans, known as Pityriasis versicolor. A saprobic smut, *Tilletiaria*, is known only from culture.

Selected host plant families, the number of their smut fungi, the ratio to the total number of known smut fungi, and the ratio of host plant smut fungus species.

Host plant family and number of species	Number of smut fungi	Ratio to the total number	Ratio host plant: smut fungus species
Gramineae (9000)	800	55.2%	11:1
Cyperaceae (4000)	220	15.2%	18:1
Compositae (25000)	108	7.4%	231:1

Host plant family and number of species	Number of smut fungi	Ratio to the total number	Ratio host plant: smut fungus species
Polygonaceae (800)	50	3.4%	16:1
Ranunculaceae (2000)	50	3.4%	40:1
Liliaceae (3500)	32	2.2%	109:1
Leguminoseae (17000)	21	1.4%	809:1
Juncaceae (400)	18	1.2%	22:1
Umbelliferae (3000)	18	1.2%	166:1
Caryophyllaceae (2000)	17	1.17%	117:1
Alismataceae (100)	16	1.1%	6:1
Scrophulariaceae (3000 s)	15	1.0%	200:1

Interesting is, that the teliospore-forming ("true") smut fungi, with few exceptions, are parasites of herbaceous, non-woody plants, those lacking teliospores (Microstromatales, Exobasidiales) occur mostly on woody plants. Of the 1450 "true" smut fungi only 11 occur on woody plants: one species of *Geminago* on *Triplochiton* (Sterculiaceae), four species of *Mundkurella* on four genera in the Araliaceae (*Aralia*, *Heptapleurum*, *Kalopanax* and *Schefflera*), three species of *Pericladium* on *Grewia* (Tiliaceae) and one on *Piper* (Piperaceae), and two species of *Uleiella* on *Araucaria* (Araucariaceae).

The 1450 smut fungi represent about 2% of all the 73.000 known species of fungi. On the other hand, the known smut fungi represent only a part, maybe 1/3 of the existing smut fungi, which I estimate to be not more than 4.000–4.500. The proportion of 1:3 of the known to the estimated number of smut fungi is much higher than that of 1:20 for all fungi of the world (73.000:1,500.000). The given number of the host plant species is a strongly delimiting factor for the species number of plant parasitic fungi.

Expected results and trends within taxonomic research of smut fungi

It is expected that in the future numerous smut fungi will be discovered and published. Unfortunately, still it will be difficult to obtain financial support for pure taxonomic or systematic collecting work. Therefore, mostly sporadic collections will be carried out. The number of genera will also increase, at least twice the present number of 77 genera. Small, often unspecific genera will be discovered on peculiar host plants, or large, heterogeneous genera such as *Ustilago* or *Sporisorium* will be split into smaller, more natural genera, especially with help of molecular biology. The tendency that papers dealing with molecular taxonomy dominate over papers dealing

with classical, morphological taxonomy, will remain for a while. Our knowledge of relationships between different groups of smut fungi and also to other fungi will be improved and better phylogenetic trees will be constructed. It is also expected that pure molecular taxonomy will take over the classical, morphological taxonomy, or maybe the two will exist parallel and complement each other.

Conservation and preservation of smut fungi

Unfortunately, the population explosion, with all its consequences has lead to destruction of natural habitats and floras. Increasingly, host plants and their parasites are eradicated, often before they have even been discovered. Therefore, smut fungus taxonomy is closely connected with the complex problem of conservation and preservation of the nature of our planet, reduction of pollution and of the use of pesticides and fungicides, and many, many other measures, including the moderation of the population explosion, the main cause of the increasing destruction of natural habitats. A once extinct species is lost forever. Therefore, the efforts must be increased to declare as many and as large protected areas and National Parks as possible. Inventory and collecting work of smut fungi must also be intensified and combined with the preservation of existing gene pools. In this, part from nature, collections (herbaria) and culture collections have a decisive role.

Need of and the preparatory work for a world monograph of smut fungi

The estimated number of 3.000 undescribed smut fungi means that collections of many new species are expected which have to be identified and differentiated from the already known and continuously increasing number of species. I know mycologists who found new smut fungi but hesitated to publish them not to create synonyms. On the other hand, I know mycologists who readily publish “new species” which in fact are already known. This often happens because of the lack of available taxonomic literature. It seems that there is a great need of a comprehensive work in which all known smut fungi, taxonomic and nomenclatural synonyms, as well as host plants are critically revised. There is a need of a world monograph of smut fungi, if possible also richly illustrated.

The work has to be started with the compilation of a database, which should contain the following data:

- Name of the smut fungus (genus, species)
- Name of the author
- Place and date of the publication
- Type specimen:
  - host plant name
  - host plant family
  - place and date of collection, name of the collector
  - herbarium in which it is preserved
- Description of the species
- Host plant spectrum
- Geographic distribution
- If the name is a synonym, the correct name and its author
- Illustrations of:
  - diseased plants showing the characters of the sori
  - LM, SEM and if it is relevant also TEM pictures of the spores
  - spore germination if it is typical
- Remarks

Compilation of the database from the literature has to be followed by the tremendous but exciting work of:

- Checking the original descriptions of all species, including exactness of literature citations.
- Revision of all available type specimen deposited in various herbaria, and preparation of accurate descriptions of the sori, spores, spore balls, sterile cells, etc., complemented with their illustrations.
- Establishing possible synonymies, both taxonomic and nomenclatural ones.
- Checking the host plant identity of the type specimen. (Not rarely, wrongly identified host plants lead to the description of “new species” for already known smuts).
- Checking as many as possible smut fungus specimens and their host plants preserved in various herbaria of the world.
- All results and new data have to be introduced into the database.

Where and how to collect smut fungi, how to preserve them?

I would like to encourage everybody to collect smut fungi, especially on indigenous and endemic plants. There are still large areas of the world from which relatively few or no smut fungi are known. Such areas are in the tropics and subtropics of both old- and new-world, in Africa, Asia, Indonesia, Central and South America, but even in North America, Australia, and on high mountains and numerous islands of the world.

To collect randomly may result in the discovery of rare or new smut fungi. However, efficient collecting needs much more than walking and now and then looking at plants if they are smutted or not. It must be purposeful and persistent.

For efficient collecting one needs to have knowledge of smut fungi, and knowledge of the symptoms produced on the host plants. For example, of the about 140 known species of *Tilletia* nearly all produce their sori in the seeds of Poaceae, filling them with a brown, powdery mass of spores. Species of *Entyloma* produce leaf spots on dicotyledonous host plants, the spores are colourless, embedded in the host tissue.

For efficient collecting, knowledge of at least the host plant family and smut genera occurring on that family is necessary. For example, the pale coloured not powdery spores of *Entorrhiza* are produced in galls on the roots of Cyperaceae and Juncaceae. Species of *Ustilago* and *Sporisorium* are parasitising exclusively Gramineae, producing sori in the seeds, flowers, spikelets or inflorescence, more rarely in the leaves or stems, producing brown, powdery spore masses. Species of *Mundkurella* produce brown, powdery sori in the flowers of Araliaceae, while species of *Restiosporium* replace the seeds of Restionaceae, filling the capsules with a powdery mass of spore balls, often invisible, being enclosed within the capsules.

Furthermore, efficient collecting needs the knowledge of the season in which a certain smut fungus appears. There are smuts appearing spring, summer or autumn, or even all year round. Typical spring smuts are *Urocystis galanthi* or *Urocystis. eranthidis* on *Galanthus nivalis* and *Eranthis hyemalis*, respectively. Under our climate most smut fungi appear during the end of spring and the first half of the summer while in the tropics they are mainly found towards the end of the rainy period. The sori of the mentioned *Entorrhiza* species appear late summer. Autumn is the time to collect the 1–2 mm long sori of the rare *Neovossia moliniae* in some of the seeds of reed (*Phragmites australis*), with the typical ovoid or elongated spores each possessing a long, hyaline appendage. The sori of *Ustilago grandis* on the stems of reed appear also in autumn.

Last but not least, efficient collecting needs a passion for smut fungi, needs offering of time, efforts and even money. One has to be ready to endure extreme

climatic conditions, insects and parasites, and sometimes it also needs courage to even go to dangerous places. In exchange, for instance, a three-weeks-long collecting trip to Zambia and Malawi, last year, resulted in 90 different smut fungi of which 13 were new species!

The collected material has to be dried as soon as possible to avoid moulding, followed by killing of the often present insects by chemical or physical methods. I am deep freezing the material to kill the insects. After that follows the identification of the host plant and its smut. The identified material I am placing first in a cellophane envelope, which partly retains the spores, but more importantly excludes contamination by insects which destroy the spores. The cellophane envelope is placed in a standard paper envelope on which the label is fixed. In my collection, which numbers nearly 20.000 specimens, the smut fungi are preserved in metal boxes like a card system, arranged alphabetically and chronologically, respectively. Advantages of this system are that it needs relatively little space, it is easy to find a certain collection and also to change its place if it is necessary.

Finally, I would like to encourage everybody to publish all new data regarding smut fungi, from new localities of unusual smuts to new host plant records and rare or new species. Especially useful are local floras. These are welcome contributions to the database and monograph of the smut fungi of the world. As a feedback, a more complete database will be a better help in identifying smut fungi, in writing smut fungus floras or in describing new species.

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