

### 3 Ustilaginomycetes<sup>1</sup>

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#### I. Introduction

The Ustilaginomycetes comprises more than 1300 species in ca. 80 genera of basidiomycetous plant parasites. They occur throughout the world, although many species are restricted to tropical, temperate, or arctic regions. Some species of *Ustilago* and *Tilletia*, e.g., the barley, wheat or maize smut fungi, are well known because they are of economic importance (Trione 1982; Thomas 1989; Valverde et al. 1995). For example, from 1983 to 1988, the barley smut fungi reduced annual yields by 0.7% to 1.6% in the prairie provinces in central Canada, causing annual losses of about US\$8000000 (Thomas 1989). *Tilletia contraversa* Kühn is important in the international wheat trade (Trione 1982) and, 2–5% in a corn field are generally infected by *Ustilago maydis* (DC.) Corda, while up to 80% of a field can be infected if conditions are good for the smut fungus. On the other hand, the galls of *U. maydis* are estimated as a delicacy in the Mesoamerican tradition. They are known in Mexico as huitlacoche and in parts of the USA as maize mushroom, Mexican truffles, or caviar azteca (Valverde et al. 1995).

This chapter focuses on the evolution and suprageneric classification of the Ustilaginomycetes that represents one of the three classes of the Basidiomycota (Fig. 1; Begerow et al. 1997; Swann and Taylor 1993).

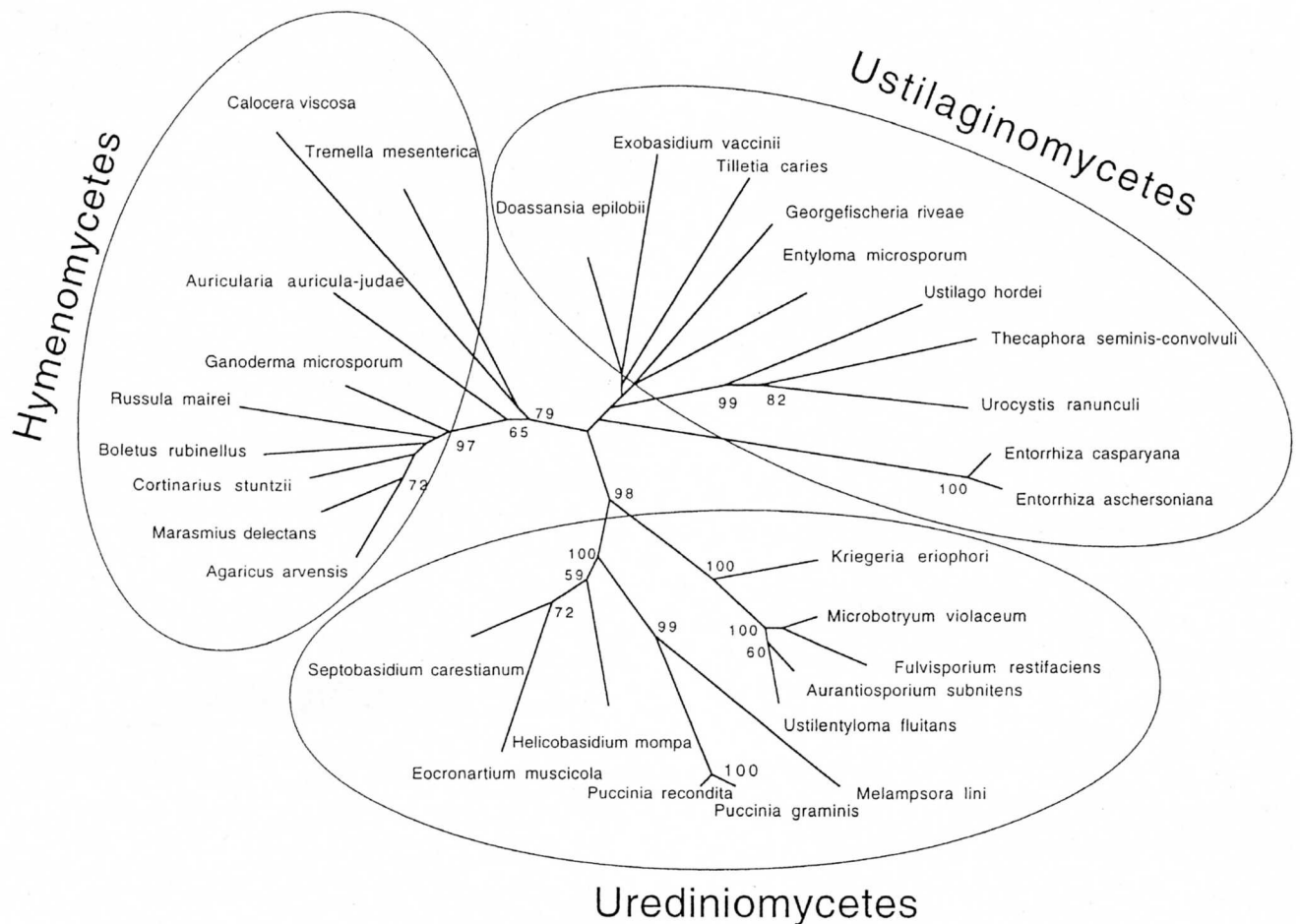
#### II. Diagnosis and Evidence for Monophyletic Origin

The Ustilaginomycetes have a distinctive cell wall carbohydrate composition with a dominance of glucose and absence of xylose that separates them from the Urediniomycetes and Hymenomycetes (Prillinger et al. 1990, 1993). They share the type B secondary structure of the 5S rRNA with the Hymenomycetes (Gottschalk and Blanz 1985) and

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**Fig. 1.** Topology obtained by neighbor-joining analysis of 518 bp from the 5'-end of the LSU rDNA sequences of 30 basidiomycetes, from Begerow et al. 1997. Percentage boot-

strap values of 1000 replicates are given at each furcation. Values smaller than 50% are not shown

the lack of multilayered endoplasmic reticulum elements (parenthesomes) at the pores with the Urediniomycetes (Bauer et al. 1997). An important apomorphy for the Ustilaginomycetes is the presence of zones of host-parasite interaction with fungal deposits, resulting from exocytosis of primary interactive vesicles (Bauer et al. 1997). This feature of the parasitic process is unique among the basidiomycetes.

In using the apomorphic characters discussed above, the Ustilaginomycetes includes all simple-septate (i.e., without multilayered, modified endoplasmic reticulum elements at the pores), holo-basidiate phytoparasites of the Basidiomycota, and all simple-septate, phragmobasidiate, teliosporic phytoparasites of the Basidiomycota, producing intracellular organs without penetration necks (Bauer et al. 1997). Sequence analysis supports the monophyly of the Ustilaginomycetes as defined above but with different statistical support in different analyses. Thus, the union of *Tilletia caries*

(DC.) L. & C. Tul., *Ustilago hordei* (Pers.) Lagerh. and *Ustilago maydis* is well supported by high bootstrap values in small-subunit (SSU) rDNA sequence analyses (Swann and Taylor 1993, 1995), whereas the bootstrap values for the Ustilaginomycetes are low in large-subunit (LSU) rDNA sequence analyses with an enlarged set of species (Fig. 1; Begerow et al. 1997). In particular, bootstrap support from our LSU data set for the Ustilaginomycetes sank when *Entorrhiza* sequences were included, possibly because *Entorrhiza* is basal in the Ustilaginomycetes and intermediate between the Ustilaginomycetes and the other basidiomycetes.

### III. Nonustilaginomycetous Smut Fungi

Like the terms agaric, polypore, lichen, etc., the term smut fungus circumscribes the organization and life strategy of a fungus, but it is not a taxo-

nomic term. Smut fungi evolved in different fungal groups. Most smut fungi are in the Ustilaginomycetes. Other smut fungi, in the Microbotryales, are members of the Urediniomycetes (Fig. 1; Bauer et al. 1997; Begerow et al. 1997). In contrast with the Ustilaginomycetes, available data indicate that the microbotryaceous taxa *Aurantiosporium*, *Bauerago*, *Fulvisporium*, *Liroa*, *Microbotryum*, *Sphacelotheca*, *Ustilentyloma*, and *Zundeliomyces* have a type A 5S rRNA secondary structure (Gottschalk and Blanz 1985; Müller 1989), mannose as the major cell wall carbohydrate (Prillinger et al. 1991, 1993), and cellular interactions without primary interactive vesicles (Bauer et al. 1997). Morphologically, they are distinguishable from the phragmobasidiate members of the Ustilaginomycetes by the lack of intracellular hyphae or haustoria (Bauer et al. 1997). Clustering of the Microbotryales with the Urediniomycetes rather than the Ustilaginomycetes is also supported by sequence analyses (Fig. 1; Begerow et al. 1997; Swann and Taylor 1995). However, there are significant convergences between the microbotryaceous and the ustilaginomycetous phragmobasidiate smut fungi. Certain taxa of both groups are similar with respect to soral morphology, teliosporogenesis, life cycle, basidial morphology, and host range.

The ultrastructural characters reveal the existence of two groups within the Microbotryales. The Ustilentylomataceae possess septa with simple pores, whereas the septa of the Microbotryaceae are poreless. The classification of the Microbotryales is as follows (Bauer et al. 1997); host families are indicated if the host range of the respective genus does not comprise more than two host families; species requiring transfer to other genera are indicated by quotation marks.

- Microbotryales R. Bauer & Oberw.
- i. Ustilentylomataceae R. Bauer & Oberw.
  - Aurantiosporium* M. Piepenbr., K. Vánky & Oberw. on Cyperaceae
  - Fulvisporium* K. Vánky on Poaceae
  - Ustilentyloma* Savile on Poaceae
- ii. Microbotryaceae R. T. Moore
  - Bauerago* K. Vánky on Cyperaceae and Juncaceae
  - Liroa* Ciferri on Polygonaceae
  - Microbotryum* Léveillé emend. K. Vánky on dicots

[There is some confusion concerning the systematic position of the “*Ustilago*” species

on dicots. The “*Ustilago*” species occurring on Asteraceae Caryophyllaceae, Dipsacaceae, Gentianaceae, Lamiaceae, Lentibulariaceae, Onagraceae, Polygonaceae, and Portulacaceae are species of *Microbotryum* (Bauer et al. 1997; Deml and Oberwinkler 1982, Prillinger et al. 1991; Vánky 1998), whereas those occurring on Brassicaceae, Campanulaceae, Haloragaceae, and Oxalidaceae are members of the Ustilaginomycetes (see below)].

*Sphacelotheca* de Bary emend. Langdon & Fullerton on Polygonaceae  
*Zundeliomyces* K. Vánky on Polygonaceae  
 Some “*Ustilago*” spp. on Commelinaceae

Even nonbasidiomycetous fungi can cause diseases with the formation of thick-walled propagules similar to those of the smut fungi. Species of *Schroeteria* Winter, for example, look superficially similar to smut fungi (Vánky 1981), but they belong to the ascomycetes (Nagler et al. 1989). Leaf spots similar to sori of *Entyloma* can be formed by representatives of the Protomyceales (Reddy and Kramer 1975).

#### IV. Life Cycle

The species of the Ustilaginomycetes share an essentially similar life cycle with a saprobic haploid phase and a parasitic dikaryophase (e.g., Sampson 1939; Fig. 2). The haploid phase usually

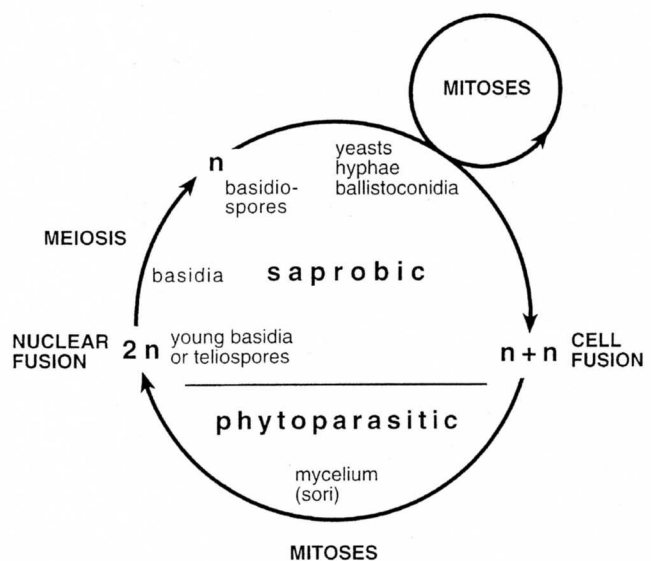


Fig. 2. Generalized life cycle of the Ustilaginomycetes

