3 Ustilaginomycetes

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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 controversa* 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 Uredinomycetes 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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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), holobasidiate 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-
onomic 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 Uredinomycetes (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, Sphaelotheca, Ustilenta, and Zundeliozymes have a type A SS rRNA secondary structure (Gottschalk and Blanz 1985; Müller 1989), mannose as the major cell wall carbohydrate (Prillinger et al. 1991, 1993), and cellular interactions with 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 Uredinomycetes 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 Ustilenta possesses septa with simple pores, whereas the septa of the Microbotryales 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. Ustilenta M. Piepenbr., K. Vánky & Oberw.
   *Aurantiosporium* M. Piepenbr., K. Vánky & Oberw. on Cyperaceae
   *Fulvisporium* K. Vánky on Poaceae
   *Ustilenta* 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, Dipsaceae, Gentianaceae, Lamiaeae, 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)].

*Sphaelotheca* de Bary emend. Langdon & Fullerton on Polygonaceae
*Zundeliozymes* 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 Protomycetales (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
commences with the formation of basidiospores after meiosis of the diploid nucleus in the basidiun and ends with the conjugation of compatible haploid cells to produce dikaryotic, parasitic mycelia. The dikaryotic phase ends with the production of basidia.

Almost all Ustilaginomycetes sporulate on or in parenchymatic tissues of the hosts. In the majority of the Ustilaginomycetes the young basidium becomes thick-walled and at maturity separates from the sorus, thus functioning as a dispersal agent, the teliospore. Dusty teliospores are efficiently dispersed by wind. Sometimes, however, teliospores are also dispersed by water or entire sori or vegetative cells are used as diasporas (Piepenbring et al. 1998a). The sori with the masses of teliospores are usually the most conspicuous stage in the smut’s life cycle. Most of the Ustilaginomycetes are dimorphic, producing a yeast or yeastlike phase in the haploid state. However, there are several variations from this generalized life cycle, e.g., homothallism in Anthracocidae (Kukkonen and Raudaskoski 1964) or Exobasidium (Sundström 1964).

A. Saprobic Phase

Multiplication in the saprobic phase with yeasts or ballistocinidia (i.e., forcibly discharged conidia) may play an essential role in the dispersal of the species and in the infection of host individuals during the vegetation period. Compatible yeast cells are able to conjugate and to infect the respective hosts, e.g., in Ustilago maydis (Snetselaar and Mims 1992, 1993) or Graphiola phoenicis (Moug.) Poiteau (Cole 1983). Ustilaginomycetous anamorphs appear to be common in nature. Thus, we have isolated numerous ustilaginomycetous anamorphs from different substrata. In addition, the species of Malassezia, Tilletiopsis, Sympodiomyces, and Pseudozyma sensu Boekhout (1995) represent ustilaginomycetous anamorphs (Figs. 33, 34, Begerow et al. 2000; Boekhout 1987, 1991, 1995; Sugiyama et al. 1991; see also Chap. 7, this Vol.) The species of the Ustilaginomycetes investigated by us produced either a yeast or yeastlike phase, with or without ballistoconidia, or a hyphal anamorph with ballistoconidia from the basidiospores.

The yeast or yeastlike cells of the Ustilaginomycetes are usually elongated and cylindrical in form and tend to produce pseudomycelia with retraction septa (i.e., septa that separate living cells from empty cells) in older cultures. In contrast to this, the yeast cells of the Microbotryales are ellipsoidal and show only yeast growth.

The ballistosporic basidiospores/conidia occurring in the Ustilaginomycetes differ from those of other basidiomycetes in form and ultrastructure. They have the form of a relatively long and narrow curved cylinder with a rounded apex and a slightly constricted base constituting the hilar appendix (e.g., Kollmorgen et al. 1980; Ingold 1987b, 1997). During germination they usually become septate. Ultrastructurally, the hilar septum of the ustilaginomycetous ballistosporic propagules is very characteristic. The median layer of the hilar septum contains electron-opaque, spheroid particles. Fine fibrils extend from the particles towards the ballistosporic basidiospores/conidia. After ejection, the electron-opaque particles remain attached to the ballistosporic basidiospores/conidia (Bauer et al. 1997; Goates and Hoffmann 1986). Thus, morphological and ultrastructural characters can be used to identify a ballistosporic propagule belonging to the Ustilaginomycetes. For example, the form of ballistoconidia indicates that Tilletiaria anomala Bandoni & Johri (Bandoni and Johri 1972) is a member of the Ustilaginomycetes.

B. Parasitic Phase

Depending upon the various ustilaginomycetous groups, parasitic hyphae grow either only intercellularly or both intercellularly and intracellularly (Figs. 3–5, 7; Bauer et al. 1997; Luttrell 1987). Haustoria or intracellular hyphae are usually not constricted where they enter or exit the host cells (Figs. 25, 26; Nagler and Oberwinkler 1989; Snetselaar and Tiffany 1990; Mims et al. 1992; Snetselaar and Mims 1994; Bauer et al. 1995b, 1997). Unlike haustoria, intracellular hyphae do not have a consistent characteristic morphology. Except for their intracellular growth and the distinctive matrix, intracellular hyphae are morphologically indistinguishable from intercellular hyphae. As intercellular hyphae, they are branched and septate. Instead of ending within the host cell as haustoria do, they pass completely through host cells, often growing from one host cell into another (Bauer et al. 1997; Luttrell 1987; Mims et al. 1992; Nagler et al. 1990; Snetselaar and Mims 1994; Snetselaar and Tiffany 1990).
In many species of the Ustilaginomycetes, hyphal branches arise from structures that look superficially like clamps (Sampson 1939; Nagler 1986; Snetselaar and Mims 1994). Nagler (1986) studied these pseudoclamps in detail and found that they do not function as clamps normally do. They seem to correspond to fusion bridges (Fischer and Holton 1957) for the transport of nuclei and are not involved in conjugate nuclear divisions. However, we found regular clamps in the members of the Doassansiales (Fig. 6), Graphiola and in some species of Exobasidium.

The teliospores are clustered in sori. Depending on the fungal species, the sori appear in or on different organs of the hosts, e.g., in roots, stems, leaves, inflorescences, flowers, anthers, ovaries, seeds, etc. In contrast with numerous rusts, the teliospores of the Ustilaginomycetes are usually not pediculate (Figs. 4–7). Although the mycelium can be either intercellular or intracellular, teliosporogenesis usually occurs intercellularly either in preformed intercellular spaces or in cavities created by disintegration of host cells (Figs. 3–5, 7; Luttrell 1987). Less commonly, teliospores are produced in host cells. Entorrhiza species, for example, sporulate inside living root cells (Deml and Oberwinkler 1981; Fineran 1980) and the species of Schizonella use more or less disinte-
grated epidermal cells for sporulation. Sporulation in disintegrating host cells also occurs in species of *Ustilago* (Langdon and Fullerton 1975; Mims et al. 1992). The species of *Clintamra*, *Exoteliopsis* and *Orphanomyces* develop their teliospores externally on the host tissue (Vánky 1987; Bauer et al. 1999a).

Teliosporogenesis varies among the Ustilaginomycetes (Figs. 3–7). One extreme is *Ustilago*, where nearly all hyphae in the sori disarticulate, lose their cell walls, and form teliospores in a matrix resulting from gelatinization of the hyphal walls (Fig. 3; Mims et al. 1992; Snetselaar and Mims 1994). *Rhamphospora* represents another extreme in that the teliospores are formed only terminally on clamped sporogenous hyphae without recognizable gelatinization (Fig. 6; Piepenbring et al. 1998b).

C. Basidia

Historically, basidiomycete classification relied on basidial morphology. However, new phylogenies based on molecular or ultrastructural characters show that basidia are not always the stable markers they were once assumed to be (e.g., Bandoni 1984; Bauer et al. 1997; Begerow et al. 1997; Swann and Taylor 1995). Within each basidiomycete class, basidial types (e.g., Oberwinkler 1977, 1978, 1982, 1985) radiated and converged. Various species of the Ustilaginomycetes, rather than sharing a single, diagnostic basidial type, exhibit a wide range of different types (Figs. 8–21; Ingold 1983, 1987a, 1988, 1989a,b,c; Oberwinkler 1978, 1982, 1985). Ustilaginomycetous basidia may be phragmobasidial, divided into compartments by internal septa (Figs. 8–11, 17), or holobasidial, lacking internal septa (Figs. 13–16, 18–21). The basidiospores of ca. 80 species in the Ustilaginomycetes are ballistosporic (i.e., forcibly discharged from the ends of sterigmata; Figs. 15–17, 21). In the other species, basidiospores are passively released (Figs. 8–14, 18–20). Multiple basidiospore production in yeastlike manner occur in many species having phragmobasidia (Fig. 9).

Some of the combinations of basidial characters common in the Ustilaginomycetes are rare in the other classes. Taxa with ballistosporic holobasidia (Figs. 16, 21) are lacking in the Urediniomycetes, whereas taxa with gastroid phragmobasidia (Figs. 8–11) are extremely rare in the Hymenomycetes. Some specific basidial characters occur only in the Ustilaginomycetes. Fusion of basidial segments, e.g., in species of *Ustilago* or *Cinctria*, or fusion of basidiospores on the basidia, e.g., in species of *Entyloma*, *Urocystis*, or *Tilletia* (Figs. 10, 18; Ingold 1983, 1987a, 1989a, 1989b; Piepenbring 1996) are unknown from basidiomycetes outside the Ustilaginomycetes. In addition, ballistosporic holobasidia with abaxially oriented hilar appendices of the basidiospores (sterigmata turned outwards, basidiospores inwards; Figs. 16, 21; Oberwinkler 1977, 1978, 1982; Ingold 1995; Bauer et al. 1999b; Vánky and Bauer 1996), occur only in the Ustilaginomycetes.

V. Hosts, and Their Role in Species Definition

In contrast with the Urediniomycetes and Hymenomycetes, the Ustilaginomycetes are ecologically well characterized by their plant parasitism. The two species of *Melaniella* occur on spikemosses, *Exoteliopsis osmundae* R. Bauer et al. on ferns, the two species of *Uleilella* on conifers, whereas all other parasitic Ustilaginomycetes parasitize angiosperms with a high proportion of species on monocots, especially on Poaceae and Cyperaceae. Thus, of the ca. 1300 species, ca. 42% occurs on Poaceae and ca. 15% on Cyperaceae. In addition, of the 78 ustilaginomycetous genera occurring on angiosperms, 48 genera have species exclusively on monocots, 25 exclusively on dicots and 5 have species on both monocots and dicots. Of the 48 monocotyledonous genera 14 occur exclusively on Poaceae and 15 exclusively on Cyperaceae (see below). Concerning the hosts, two points are noteworthy: (1) With a few exceptions, the teliospore-forming species of the Ustilaginomycetes parasitize nonwoody herbs, whereas those without teliospores prefer woody trees or bushes. However, almost all species sporulate on parenchymatic tissues of the hosts. (2) Two of the largest angiosperm families the Orchidaceae with about 20000 species and the Poaceae with about 9000 species, play a quite different role for the Ustilaginomycetes. There are no known species on Orchidaceae while the Poaceae are the most important host family of the Ustilaginomycetes. This can be tentatively explained by the completely different ecological strategies of the two families. Orchid species subsist with a few isolated individuals and are highly specialized for
insect pollination. The Poaceae, however, disperse their dusty pollen by the wind and cover about a third of the land surface with numerous individuals. The ecology of the Ustilaginomycetes, with dusty teliospores or basidiospores dispersed by wind and with the requirement of extensive host populations for successful infection, corresponds well to the ecology of the Poaceae.

Host ranges play an important role in species definition. Many species, e.g., the species of *Entyloma*, *Melanotaenium*, or *Urocystis* (see Vánky 1994), have few defining morphological characters. As a result, species based only on morphology would often be broad and would sometimes include distantly related organisms. For example, Savile (1947) lumped many species of *Entyloma* in
two collective species, whereas Vánky (1994) distinguished many different species based on morphology and hosts. To delimit narrower groups closer to "biological species" host ranges are usually considered in species definitions. Fischer and Shaw (1953) argued that morphologically similar smut fungi producing similar symptoms should be considered different species if they parasitize hosts in different families. Vánky (1994) followed a similar approach.

When similar smut fungi parasitize similar hosts, the situation is less clear. Indications can be obtained in the field when a potential host without infection stands close to a systematically related host with heavy infections. Particularly perplexing are the closely related smut species that hybridize under laboratory conditions (Carris and Gray 1994; Fischer and Holton 1957; Huang and Nielsen 1984). For example, Tillettia traversa and Tillettia caries (associated mainly with wheat but capable of infecting Bromus spp. and other grasses) require different conditions for germination and they differ in spore ornamentation and spore fluorescence. Russell and Mills (1993, 1994) demonstrated overlap in phenotypic characters including karyotype, spore ornamentation, and fluorescence for the two taxa, and Trail and Mills (1990) showed that Tillettia traversa and Tillettia caries hybridize when inoculated onto the same plant. Both species can be hybridized with Tillettia bromi Brockm. (infecting Bromus spp. and other grasses) under laboratory conditions (Carries and Gray 1994). Do these species exchange genes in nature, or do differences in their biology keep them segregated? Determining whether such smut populations belong to the same species will require detailed analysis of population genetic structures to establish the limits of gene exchange (McDermott and McDonald 1993). Only in few cases have fungal species delimitations been subjected to this kind of detailed analysis (McDermott and McDonald 1993; Bucheli and Leuchtmann 1996).

VI. The System

Beginning with Tulasne and Tulasne (1847), the smut fungi have traditionally been divided into the phragmobasidiate Ustilaginaceae or Ustilaginales and the holobasidiate Tilletiaceae or Tilletiales (e.g., Kreisel 1969; Oberwinkler 1987). Durán (1973) and Vánky (1987) discussed difficulties in smut classification in detail but did not list higher taxa in the group. Thus, Vánky (1987) treated all smut fungi in a single order, Ustilaginales, with one family, Ustilaginaceae. The basidiozymecous nature of Graphiola was revealed by Oberwinkler et al. (1982). Microstroma has traditionally been placed in the Exobasidiales (Hennings 1900).

The classification discussed below is based predominantly on characteristics of host-parasite interactions and septal pore apparatus (Fig. 32; Bauer et al. 1997) and is supported by LSU rDNA sequence analyses (Figs. 33, 34; Begerow et al. 1997), mode of teleosporogenesis and the ultrastructure of teleospore walls (Piepenbring et al. 1998b,c,d). Groups of the Ustilaginomycetes recognized by Bauer et al. (1997) are also evident in both maximum-parsimony and neighbor-joining analyses of LSU rDNA sequence data and are well supported by bootstrap values (Figs. 33, 34; Begerow et al. 1997). In fact, differences between the ultrastructural and the LSU rDNA sequence analyses concern only Thecaphora (Glomosporiaceae). Thecaphora was interpreted by Bauer et al. (1997) together with Glomosporium as basal taxon of the Ustilaginaeae (Fig. 32), whereas in the LSU rDNA analyses Thecaphora appears in a position at the base of the Urocystales (Figs. 33–34; Begerow et al. 1997). However, sequence analyses of additional species, such as more species of Thecaphora and members of Glomosporium, and Mycosyrinx (see Fig. 32), are required before any conclusion concerning this discrepancy may be drawn. Melanotaenia endogenum (Unger) de Bary was interpreted by Bauer et al. (1997) as a basal taxon of the Urocystales (Fig. 32) and appears in the maximum-parsimony analyses of Begerow et al. (1997) in that position, but not in the analyses of this chapter (Figs. 33, 34). In contrast with the LSU rDNA sequence studies (Figs. 33, 34; Begerow et al. 1997), the ultrastructural analyses at least resolve the relationships among three orders of the Exobasidiomycetidae (Fig. 32, see Exobasidiales; Bauer et al. 1997). Two possible explanations for the lack of resolution in the molecular studies exist: (1) the available sequences of ca. 540 bp are too short to resolve the phylogeny within the Exobasidiomycetidae or (2) the relationships among the orders of the Exobasidiomycetidae cannot be resolved by this kind of sequence analyses because the ancestor of the Exobasidiomycetidae diverged into several groups within a very short time.
The fundamental characters used in classifying the Ustilaginomycetes were discussed in detail by Bauer et al. (1995a, 1995b, 1997) and are therefore only briefly summarized here.

**A. Fundamental Characters**

1. **Cellular Interactions**

Hyphae of the Ustilaginomycetes in contact with host plant cells possess zones of host-parasite interaction with fungal deposits resulting from exocytosis of primary interactive vesicles. These zones provide ultrastructural characters diagnostic for higher groups in the Ustilaginomycetes (Fig. 32; Bauer et al. 1997). Initially, primary interactive vesicles with electron-opaque contents accumulate in the fungal cell. Depending on the fungal species, the primary interactive vesicles may fuse with one another before being exocytosed from the fungal cytoplasm. Electron-opaque deposits also appear at the host side, opposite the point of contact with the fungus (Figs. 22–26). Detailed studies indicate that these deposits at the host side originate from the exocytosed fungal material by transfer towards the host plasma membrane (Bauer et al. 1995b, 1997).

The following major types, minor types, and variations were recognized by Bauer et al. (1995b, 1997).

**a) Local Interaction Zones** (Figs. 22–25)

Short-term production of primary interactive vesicles per interaction site results in local interaction zones.

1. **Local interaction zones without interaction apparatus** (Fig. 22). Primary interactive vesicles fuse individually with the fungal plasma membrane. Depending upon the species, local interaction zones without interaction apparatus are present in intercellular hyphae or haustoria.

2. **Local interaction zones with interaction apparatus** (Figs. 23–25). Fusion of the primary interactive vesicles precedes exocytosis.

**b) Local interaction zones with complex interaction apparatus** (Figs. 24–25). Numerous primary interactive vesicles fuse to form several secondary interactive vesicles per interaction site. Fusion of the secondary interactive vesicles then results in the formation of a complex cisternal net.

i. **Local interaction zones with complex interaction apparatus containing cytoplasmic compartments** (Fig. 24). The intercisternal space of the cisternal net finally becomes integrated in the interaction apparatus. Depending upon the species, interaction zones of this type are formed by intercellular hyphae or haustoria.

ii. **Local interaction zones with complex interaction apparatus producing interaction rings** (Fig. 25). The intercisternal space does not become integrated in the interaction apparatus. Transfer of fungal material towards the host plasma membrane occurs in two or three steps. The first transfer results in the deposition of a ring at the host plasma membrane. Depending upon the species, interaction zones of this type are located in intercellular hyphae or haustoria.

**b) Enlarged Interaction Zones** (Fig. 26)

Continuous production and exocytosis of primary interactive vesicles results in the continuous deposition of fungal material at the whole contact area with the host cell. Depending upon the species, this type of interaction zones is located in intercellular hyphae, intracellular hyphae or haustoria.

2. **Septation**

Septal pore architecture plays an important role in the arrangement of basidiomycetes (Oberwinkler 1985; Wells 1994). In general, the pores of the Ustilaginomycetes are not associated with differentiated, multilayered caps or sacs derived from the endoplasmic reticulum. The septa produced in the saprobic phase of the dimorphic species of the Ustilaginomycetes are devoid of distinct septal pores. Five types of septation of soral hyphae were recognized by Bauer et al. (1997): (1) Presence of simple pores with two tripartite membrane caps (Fig. 27), (2) presence of simple pores with two outer tripartite membrane caps and two inner non-
membranous bands (Fig. 28; see also Bauer et al. 1995a), (3) presence of dolipores without membrane caps or bands (Figs. 29; see also Deml and Oberwinkler 1981), (4) presence of dolipores with tripartite membrane bands (Fig. 30; see also Roberson and Luttrell 1989), and (5) septa without distinct pores (Fig. 31), designated poreless septa.

B. Overview

In the following, an overview of the taxa included in the Ustilaginomycetes is given. Host families are indicated if the host range of the respective genus does not comprise more than two families. On the basis of morphology and LSU rDNA sequence analyses (Figs. 33, 34), the anamorphic species are ascribed to teleomorphic taxa. The data indicate that several species require transfer to new genera or families. Species requiring transfer to new genera are indicated by quotation marks.

1. Ustilaginomycetes
   R. Bauer, Oberw. & K. Vánky
I. Entorrhizomycetidae R. Bauer & Oberw.
   1. Entorrhizales R. Bauer & Oberw.
      i. Entorrhizaceae R. Bauer & Oberw. 
       Entorrhiza Weber on Cyperaceae and Juncaceae
II. Ustilaginomycetidae Jülich emend. R. Bauer & Oberw.
   1. Urocystales R. Bauer & Oberw.
      i. Melanotaeniaceae Begerow, R. Bauer & Oberw.
       Exoteliospora R. Bauer, Oberw. & K. Vánky on Osmundaceae 
       Melanotaenium de Bary on dicots

Figs. 22–26. Cellular interactions in the Ustilaginomycetes. Material illustrated in Fig. 26 was prepared using freeze substitution. Bars 0.5 μm. Fig. 22. Local interaction zone without interaction apparatus, representative for the Entorrhizomycetidae, Georgieschieriales, Tilletiales, and Microstromatales. Intercellular hypha (i) of Conidiosporomycetes ayresii (Berk.) K. Vánky with the secretion profile of one primary interactive vesicle (arrow) in contact with host cell wall (HW). Note the electron-opaque deposit at the host side (arrowhead). Host response to infection is visible at R. Fig. 23. Local interaction zone with simple interaction apparatus, representative for the Entylomatales. Intercellular hypha (i) of Entyloma hieraci H. & P. Sydow in contact with host cell wall showing the exocytosis profile of the simple interaction apparatus (arrow). Note the electron-opaque deposit at the host side (arrowhead). Host response to infection is visible at R. Fig. 24. Local interaction zone with complex interaction apparatus containing cytoplasmic compartments, representative for the Doassansiellales. Intercellular hypha (i) of Doassinga callitrichis (Liro) K. Vánky et al., in contact with host cell wall (HW) showing the exocytosis profile of one complex interaction apparatus (arrow). The interaction apparatus and its intercisternal space is excluded from the cytoplasm. Note the electron-opaque deposit at the host side (arrowhead). Host response to infection is visible at R. Fig. 25. Local interaction zone with complex interaction apparatus producing interaction ring, representative for the Exobasidiomatales. Haustorium (h) of Exobasidium sp. with interaction apparatus (arrow). Note the sectioned interaction ring (arrowheads) at the top of the haustorium. Fig. 26. Enlarged interaction zone, representative for the Ustilaginomycetidae. Haustorium (h) of Ustacystis waldsteiniae (Peck) Zundel is surrounded by an electron-opaque matrix.
Figs. 27–31. Septation of soral hyphae in the Ustilaginomycetes. Material illustrated in Figs. 28, 30, 31 was prepared using freeze substitution. Bars 0.1 μm. Fig. 27. Simple pore with two membrane caps (arrows) of Doassinsa callitrichis (Liro) K. Vánky et al. representative for the Melanotaeniaceae, Microstromatales and the Exobasidiales. Fig. 28. Simple pore with two outer membrane caps (arrows) and two inner nonmembranous bands (arrowheads) of Ustacystis waldsteiniae (Peck) Zundel, representative for the Urocystaceae and Doassansiopsaceae. Fig. 29. Dolipore without membrane bands of Entorrhiza casparyana (Magnus) Lagerh., representative for the Entorrhizales. Fig. 30. Dolipore with membrane bands (arrows) of Tillettia barclayana (Bref.) Sacc. & P. Sydow, representative for the Tilletiales. Fig. 31. Poroid structure in a septum of Mycosyrinx cissi (DC.) G. Beck, representative for the Ustilaginales and Georgefisscheriales.
Franzpetratia Thirum. & Pavgi emend. Guo, K. Vánky & Mordue on Poaceae
Geminaigo K. Vánky & R. Bauer on Sterculiaceae
Heterotolyposporium K. Vánky on Cyperaceae
Kunzeomyces P. Henn. ex Sacc. & P. Sydow on Cyperaceae
Leucoecintractia M. Piepenbr., Begerow & Oberw. on Cyperaceae
Macalpinomyces Langdon & Full. emend. K. Vánky on Poaceae
Melanopsischium G. Beck on Polygonaceae
Moesiomyces K. Vánky on Poaceae and Eriocaulaceae
Moreaua T.N. Liou & H.C. Cheng on Cyperaceae
Orphanomyces Savile on Cyperaceae
Pericladium Pass. on Tiliaceae
Planetella Savile on Cyperaceae
Schizonella Schröter on Cyperaceae
Sporisorium Ehrenb. on Poaceae
Stegocintractia M. Piepenbr., Begerow & Oberw. on Juncaceae
Tolyposporium Woronin ex Schröter on Juncaceae
Trichocintractia M. Piepenbr. on Cyperaceae
Ustanciosporium K. Vánky emend. M. Piepenbr. on Cyperaceae
Ustilago (Pers.) Roussel on Poaceae
(There is some confusion concerning the systematic position of the species of Ustilago. The host range of Ustilago is restricted to Poaceae. Non-graminicolous “Ustilago” species belong to other genera, mostly to Microbotryum).
Websdanea K. Vánky on Restionaceae Anamorphs:
Pseudozyma Bandoni emend. Boekhout Probably in this family:
Testicularia Klotzsch on Cyperaceae
Tranzscheliella Lavrov on Poaceae
Uleiella Schröter on Araucariaceae

1. Malasseziales Moore emend. Begerow, R. Bauer & Boekhout
Malassezia Baillon
2. Georgerhscheriales R. Bauer, Begerow & Oberw.
   i. Georgerhscheriaceae R. Bauer, Begerow & Oberw.
Georgerhscheria Thirum. & Narash. emend. Gandhe on Convolvulaceae
Jamesdicksonia Thirum., Pavgi & Payak emend. R. Bauer Begerow, A. Naglér & Oberw. on Cyperaceae and Poaceae
   ii. Tillettariaceae Moore
Phragmotaenium R. Bauer, Begerow, on Poaceae
Tillettia Bandoni & Johri
Tolyposporella Atkinson on Poaceae
Anamorphs:
Tillettiosps flavs (Tubaki) Beokhout
Tillettiosps fulvescens Gokhale
   iii. Eballistraceae (in prep.)
Eballistra A. Nagler & Oberw. on Poaceae
3. Tillettiales Kreisel ex R. Bauer & Oberw.
Conidiosporomyces K. Vánky on Poaceae
Erratomyces Piepenb. & R. Bauer on Fabaceae
Ingoldiomyces K. Vánky on Poaceae
Neovossia Körn. on Poaceae
Oberwickleria K. Vánky & R. Bauer on Poaceae
Tilletia L. & C. Tul. on Poaceae
   i. Microstromataceae Jülich
Microstoma Niessl on Juglandaceae and Fagaceae
   ii. Volvocisporiaceae Begerow, R. Bauer & Oberw.
Volvocisporium Begerow, R. Bauer & Oberw. on Tiliaceae
5. Entylomatales R. Bauer & Oberw.
   i. Entylomataceae R. Bauer & Oberw.
Entyloma de Bary on dicots
   i. Melaniellaceae R. Bauer, K. Vánky, Begerow & Oberw.
Melaniella R. Bauer, K. Vánky, Begerow & Oberw. on Selvidginel-laceae
   ii. Doassansiaceae (Azb. & Karat.)
Moore emend. R. Bauer & Oberw.
Burrillia Setchell on monocots and dicots
Doassania Cornu on monocots and dicots
Doassinga K. Vánky, R. Bauer & Begerow on Callitrichicaceae
Heterodoassania K. Vánky on monocots and dicots
Nannfeldtiomyces K. Vánky on Sparnganiaceae
Narasimhanthia Thirum. & Pavgi emend. K. Vánky on Alismataceae
Pseudodoassania (Setchell) K. Vánky on Alismataceae
Pseudodermatosorus K. Vánky on Alismataceae
Pseudotracya K. Vánky on Hydrocharitaceae
Tracya H. & P. Sydow on Hydrocharitaceae and Lemnaceae
iii. Rhamphosporaceae R. Bauer & Oberw.
Rhamphospora Cunn. on Nymphaeaceae
   i. Brachybasiaceae Gáum.
   Brachybasidium Gäumann on Araceae
   Dicellomyces L.S. Olive on monocots
   Exobasidiellum Donk on Poaceae
   Kordyana Racib. on Commelinaceae
   Proliferobasidium Cunningh. on Heliconiaceae
   ii. Exobasidiaceae P. Henn.
   Exobasidium Woronin on dicots
   Muribasidiospora Kamat & Rajendren on Anacardiaceae and Ulmaceae
   iii. Cryptobasidiaceae Malencon ex Donk
   Botryoconis H. & P. Sydow on Lauraceae
   Clinoconidium Pat. on Lauraceae
   Coniodictyum Har. & Pat. on Rhamnaceae
   Drepanoconis Schröter & P. Henn. on Lauraceae
   Laurobasidium Jülich on Lauraceae
   "Sphacelotheca" cinnamomi Hirata on Lauraceae
   "Ustilago" onumae (Shirai) S. Ito on Lauraceae
   iv. Graphiaceae E. Fischer
   Graphiola Poiteau on Araceae
   Stylina H. Sydow on Araceae

2. Taxa Not Ascribed to Any Family
   i. Ceraceosorus bombacis (Bakshi) Bakshi on Bombacaceae
      This species is a member of the Exobasidiomyetidae, but of uncertain systematic position within this group.
   ii. Sympodiomyopsis paphiodedillii Sugiyama, Tokuoka & Komagata
      This anamorphic species is a member of the Microstromatales but of uncertain systematic position within this group.
   iii. Tilletiopsis albescens Gokhale
      This anamorphic species is a member of the Exobasidiomyetidae, but of uncertain systematic position within this group (Figs. 33, 34).
   iv. Tilletiopsis creema Tubaki, Tilletiopsis lilacina Tubaki, Tilletiopsis washingtonensis Nyland
      These three anamorphic species are members of the Entylomatales and appear to be anamorphic representatives of a currently unknown family of the Entylomatales (Figs. 33, 34).
   v. Tilletiopsis minor Nyland
      This anamorphic species is a member of the Georgefoliferiales, but of uncertain systematic position within this group (Figs. 33, 34).
   vi. Tilletiopsis pallescens Gokhale
      This anamorphic species is a member of the Exobasidiomyetidae, but of uncertain systematic position within this group (Figs. 33, 34).

C. Description

Within the Ustilaginomycetes three major groups are evident in the dendrograms resulting from ultrastructural and LSU rDNA sequence analyses (Figs. 32–34; Bauer et al. 1997; Begerow et al. 1997).

1. Entorrhizomycetidae

The Entorrhizomycetidae is the basal group of the Ustilaginomycetes (Figs. 1, 32; Bauer et al. 1997; Begerow et al. 1997). Lack of membrane bands or caps at the pores (Fig. 29) and the presence of local interaction zones without interaction apparatus characterize this group (Bauer et al. 1997). The species of Entorrhiza, the single genus currently identified in this group, have dolipores (Fig. 29; Bauer et al. 1997; Deiml and Oberwinkler 1981),
Fig. 32. Phylogenetic tree of the Ustilaginomycetes based predominantly on ultrastructural apomorphies, after Bauer et al. (1997). Apomorphies are illustrated. Their pleiomorphic states occur in the respective sister groups. Clusters on interrupted lines must be regarded as potentially paraphyletic. The apomorphies and their respective pleiomorphic states used in the tree are as follows: 1 interaction with primary interactive vesicles/without primary interactive vesicles; 2 membranous pore caps or bands/without membranous pore caps or bands; 3 dolipores/simple pores; 4 haustoria/intercellular hyphae; 5 enlarged interaction zones/local interaction zones; 6 haustoria/intercellular hyphae; 7 loss of septal pores/simple pores; 8 septal pores with nonmembranous bands/without nonmembranous bands; 9 basidia reduced to telosporia/telosporia only function as probasidia; 10 intracellular hyphae/intercellular hyphae; 11 Exobasidium basidia/ballistoconidia (repeated loss of ballistosporic basidiospores not labeled); 12 loss of septal pores/simple pores; 13 dolipores/simple pores; 14 loss of telosporia/telosporia; 15 interaction apparatus/primary interactive vesicles; 16 complex interaction apparatus/simple interaction apparatus; 17 interaction apparatus with cytoplasmic compartments/without cytoplasmic compartments; 18 haustoria/intercellular hyphae; 19 interaction ring/without interaction ring; 20 basidia in chains/not in chains; 21 clamped haustoria/intercellular hyphae; 22 unclamped haustoria/intercellular hyphae (this feature is only illustrated to show the taxa of the Exobasidiales having haustoria; it is not considered as apomorphic).
Fig. 33. Strict consensus tree of 71 most parsimonious trees (1516 steps) of 540 bp from the 5'-end of the LSU rDNA sequences of teleomorphic or anamorphic (indicated by asterisks) species of the Ustilaginomycetes, after Begerow et al. (2000). Topology was rooted with Entorrhiza. Percentage bootstrap values of 100 replications are given at each furcation. Percentages under 50% are not shown.
Fig. 34. Topology obtained by neighbor joining analysis of 540bp from the 5’-end of the LSU rDNA sequences of teleomorphic or anamorphic (indicated by asterisks) species of the Ustilaginomycetes, after Begerow et al. (2000). Topology was rooted with Entorrhiza. Percentage bootstrap values of 1000 replicates are given at each furcation. Percentages under 50% are not shown.
they form teliospores in living host cells (Fineran 1980; Dmêl and Oberwinkler 1981) in which the exosporium of the teliospores is probably formed by the host (Piepenbring et al. 1998b), and they cause galls on roots of members of the Juncaceae and Cyperaceae. The teliospores germinate internally by becoming four-celled phragmobasidium with cruciform septation (Fig. 8; Weber 1884; Fineran 1982). Although meiosis has not been studied in *Entorrhiza*, the changes in nuclear numbers from binucleate to mononucleate to four-nucleate (Bauer et al. 1997; Fineran 1982) support interpreting the teliospore germings as basidia. The basidiospores (Fig. 8) resemble conidia of aquatic hynohymcyetes (Ingold 1979). Thus, the basidia of *Entorrhiza* show some adaptations to water dispersal in the soil. The haploid phase of *Entorrhiza* is unknown.

2. Ustilaginomycetidae

Presence of enlarged interaction zones (Fig. 26) characterizes this group (Bauer et al. 1997). The members of the Ustilaginomycetidae are teliosporic, gastroid, and dimorphic. Morphologically and ecologically, they are diverse (Figs. 9–12, 18; see Vánky 1987, 1994), but both ultrastructural and LSU rDNA sequence analyses unite them (Figs. 32–34; Bauer et al. 1997; Begerow et al. 1997). Two groups are recognized.

a) Urocystales

Among the Ustilaginomycetidae, the Urocystales are characterized by the presence of haustoria and of pores in the septa of soral hyphae (Figs. 26, 28; Bauer et al. 1997). Most of the Urocystales sporulate in vegetative parts of the hosts. Three groups are evident by the interpretation of the ultrastructural and LSU rDNA sequence analyses and correlated characters (Figs. 32–34; Bauer et al. 1997; Begerow et al. 1997).

The Melanotaeniaeae represent the basal group of the Urocystales. Lack of the nonmembranous bands in the pores characterizes this group. This family comprises at least *Melanotaenium endogenum* and *Melanotaenium euphorbiae* (Lenz) M.D. Whitehead & Thirum., *Exotieliospora osmundae*, “Ustilago” speculaires and probably all described *Melanotaenium* species occurring on dicots. *Melanotaenium endogenum* and *M. euphorbiae* form gastroid holobasidia and a Tilletiopsis-like pseudohyphal anamorph with ballistoconidia (e.g., Ingold 1988). Basidia of *Exotieliospora osmundae* have not been observed. Among the Ustilaginomycetidae, formation of ballistoconidia is currently restricted to the Melanotaeniaeae. The ultrastructural as well as the LSU rDNA sequence analyses revealed that smut fungi morphologically similar to *Melanotaenium endogenum*, the type of the genus, evolved in different ustilaginomycetous groups (Figs. 32–34; Bauer et al. 1997; Begerow et al. 1997). Thus, the species of “*Melanotaenium*” occurring on monocots are not closely related with *Melanotaenium endogenum*, belonging to the Urocystaceae (see below) or Georgeffächerinales (designated in Figs. 32–34 as members of *Eballistra*, *Jamesdicksonia* or *Phragnotaeum*).

The Doassansiopsaceae represents the sister group of the Urocystaceae. The Doassansiopsaceae share with the Urocystaceae, but not with the Melanotaeniaeae, an essentially identical septal pore apparatus (Bauer et al. 1997). It is composed of a simple pore with two outer tripartite membrane caps and two inner nonmembranous bands (Fig. 28; Bauer et al. 1995a). The species of *Doassansiopsis*, the single genus currently placed in the Doassansiopsaceae, possess complex teliospore balls with a central mass of pseudoparenychymateous cells surrounded by a layer of firmly adhering, lightly colored, teliospores and an external cortex of sterile cells (Fig. 7; Vánky 1987). *Doassansiopsis* species form gastroid holobasidia and a yeast anamorph without ballistoconidia. The position of *Doassansiopsis* in the Urocystales is surprising. Based on teliospore ball morphology and the parasitism of aquatic plants, *Doassansiopsis* was grouped with *Burillia*, *Doassania*, *Heterodoxassania*, *Nannfeldtioymyes*, *Narasimhania*, *Pseudodoxassania*, and *Tracya* (Vánky 1987, 1994). However, both the ultrastructural as well the LSU rDNA sequence analyses show that *Doassansiopsis* is not closely related to the other complex teliospore ball-forming taxa (Figs. 32–34; Bauer et al. 1997; Begerow et al. 1997).

The Urocystaceae comprises morphologically diverse species with colored teliospores. “*Melanotaenium*” *ari* produces single teliospores, *Mundkurella* is characterized by one- to four-celled teliospores, *Urocystis* (Fig. 18) and *Ustacystis* by teliospores united in balls (Vánky 1987, 1994). In addition, *Mundkurella* and *Ustacystis* (Zundel 1945) are phragmobasidiate, whereas *Urocystis* is holobasidiate (Fig. 18). Basidia of “*Melanotaenium*”
niun" are have not been observed. The species in *Urocystis* living on monocots and dicots appear to form a monophyletic group (Figs. 33, 34). The Urocystaceae form a yeastlike anamorph without ballistoconidia.

The evolutionary separation of the Doassansiopsiaceae from the Urocystaceae and their respective evolutionary radiations may have an ecological basis. Host species belong to a variety of monocots and dicots in both families, but the hosts of *Doassansiopsis* are exclusively paludal or aquatic plants, whereas those of the Urocystaceae are terrestrial.

**b) Ustilaginales**

Poreless septa (Fig. 31) characterize the Ustilaginales. Most of the species of this group sporulate in the reproductive parts of their hosts and possess the disarticulating type of teliosporogenesis. A prominent gelatinization of hyphal walls usually precedes teliospore formation (Fig. 3; Luttrell 1987; Snetselaar and Tiffany 1990; Mims and Snetselaar 1991; Mims et al. 1992; Snetselaar and Mims 1994; Piepenbring et al. 1998b). The anamorphs fit the concept of *Pseudozyma* sensu Boekhout (1995). Based on ultrastructural and LSU rDNA sequence analyses the Ustilaginales are divided into three families (Figs. 32–34; Bauer et al. 1997; Begerow et al. 1997; for the discrepancy concerning the systematic position of *Thecaphora* see above).

The Mycosyringaceae may represent the basal group of the Ustilaginales distinguished from the other ustilaginaceous groups by the lack of intracellular hyphae (Fig. 32; Bauer et al. 1997). *Mycosyrinx* is the only genus in the Mycosyringaceae. *Mycosyrinx* species produce teliospores in pairs and their host range is restricted to members of the Vitaceae (Vánky 1996). Basidia, known only from *M. cissi* (DC.) G. Beck, have a unique morphology, being reduced to the teliospores. The basidiospores are sigmoid in shape (Fig. 12; Piepenbring and Bauer 1995), indicating that they may be dispersed by water. The haploid phase is unknown.

The Glomosporiaceae share with the Ustilaginaceae the formation of intracellular hyphae (Bauer et al. 1997). The species of the three genera currently classified in the Glomosporiaceae possess light brown teliospore balls (Vánky 1987) and differ from those of the Ustilaginaceae by the formation of holobasidia. *Glomosporium leptideum* (H. & P. Sydow) Kochmann has true holobasidia (Kochmann 1939), whereas the teliospores of *Tothiella thlaspeos* (Beck) K. Vánky usually germinate with long hyphae in which the cytoplasm is located at the apex (Vánky 1999). Teliospore germination among the species of *Thecaphora* is variable, ranging from true holobasidia to asetolate or septate hyphae that sometimes bear basidiospores (Nagler 1986; Ingold 1987c; Piepenbring and Bauer 1995). We interpret these hyphal germinations as atypical germinations resulting possibly from nonoptimal environmental conditions. For example, for *Thecaphora haumanni* Speg. both germination types have been reported (Piepenbring and Bauer 1995). The hosts of the Glomosporiaceae are dicots.

In contrast with the Glomosporiaceae, the numerous species of the Ustilaginaceae form phragmobasidia (Figs. 9–11) and darkly colored teliospores. Depending upon the species and sometimes also on the environmental conditions, the phragmobasidia vary in morphology (Figs. 9–11; Ingold 1983, 1987a, 1989a, 1989c). The basidia in *Anthracoidea* species are generally two-celled (Fig. 11), whereas those in the other species are usually four-celled (Figs. 9, 10). This family contains many genera (Figs. 32–34; Bauer et al. 1997; Begerow et al. 1997) and comprises, except for 17 species, all phragmobasidiate members of the Ustilaginomycetes. Some of the *Ustilago* species, e.g., *Ustilago hordei*, *U. maydis* or *Ustilago tritici* (Pers.) Rostrup, cause economically important plant diseases on cultivated Poaceae (Thomas 1989; Valverde et al. 1995). The genera are based mainly on characteristics of teliospores and sori, e.g., teliospores free or united in balls, presence or absence of peridia, columellae, sterile cells or sterile hyphae, etc. (see Vánky 1987, 1994). *Anthracoidea* species, for example, form sori with free, black teliospores around ovaries of Cyperaceae. The sori are initially covered by peridia of fungal hyphae. The sori of *Sporisorium* species are also covered by peridia but these can be composed of host tissue as well as of fungal hyphae. The teliospores are free or arranged in balls. Teliospore balls and special soral structures are lacking in *Ustilago* species whose simple teliospores develop by destroying host tissue. We agree with Bandoni (1995) that in many cases (e.g., *Ustilago*) features, upon which ustilaginaceous genera are based, are in need of reevaluation (e.g., see Figs. 33, 34).

Thus, based on morphological and sequence data the *Cintractia* complex was divided in several
genera (Piepenbring et al. 1999). With a few exceptions, the Ustilaginaceae occur on monocots, especially on Poaceae (ca. 65%) and Cyperaceae (ca. 30%).

3. Exobasidiomycetidae

The Exobasidiomycetidae represents the sister group of the Ustilaginomycetidae (Figs. 32–34; Bauer et al. 1997; Begerow et al. 1997). The teleomorphic members of the Exobasidiomycetidae share with those of the Ustilaginomycetidae the presence of membrane caps or bands at the septal pores (Figs. 27, 28, 30). However, in both groups, taxa with poreless septa evolved. The Exobasidiomycetidae differ from the Ustilaginomycetidae by forming local interaction zones. Except for the Tilletiariales (Fig. 17), the Exobasidiomycetidae are holobasidiate (Figs. 13–16, 18–21). Among the basidiospores, formation of ballistosporic holobasidia, in which the hilar appendices of the basidiospores are oriented abaxially (sterigmata turned outwards, basidiospores inwards; Figs. 16, 21), is restricted to the Exobasidiomycetidae. In addition, basidia of this type are common in the Exobasidiales, but occur also in species of the Doassansiales, Georgischeheriales and Tilletiales (Figs. 16, 21; Oberwinkler 1977, 1978, 1982; Ingold 1995; Bauer et al. 1999b; Vánky and Bauer 1996). Therefore, the Exobasidium basidium with the specific orientation of the ballistosporic basidiospores may represent an apomorphy for the Exobasidiomycetidae (see Fig. 32).

Teliospores are absent or present within the Exobasidiomycetidae. Formation of teliospore balls occurs only in the Doassansiales and in Tolyposporella. The smut fungi among the Exobasidiomycetidae show terminal or intercalary teliospore formation (Figs. 4–6; Piepenbring et al. 1998b,d; Roberson and Luttrell 1987; Trione et al. 1989). A gelatinization of hyphal walls preceding teliospore formation is either lacking or not clearly recognizable.

Six groups are recognized on the basis of the ultrastructural characters within the Exobasidiomycetidae (Fig. 32; Bauer et al. 1997). These groups are also evident in the phylogeny resulting from LSU rDNA sequence analyses (Figs. 33, 34; Begerow et al. 1997). In addition, LSU rDNA sequence analyses indicate that the species of the anamorphic genus Malassezia represent a group of its own within the Exobasidiomycetidae (Figs. 33, 34; Begerow et al. 2000).

a) Malasseziales

The anamorphic genus Malassezia comprises medically important, lipophytic yeasts that constitute part of the fungal microflora of the skin of warm-blooded animals. They have been found associated with a variety of pathological conditions in humans including pityriasis versicolor, seborrhiec dermatitis, folliculitis and systemic infections (see Boekhout and Bosboom 1994; Howard and Kwon-Chung 1995; Guého et al. 1998; Begerow et al. 2000; and the references therein). The cell wall of the Malassezia yeasts is thick, multilamellate and reveals a unique substructure with an electron-opaque, helicoidal band that corresponds to a helicoidal evagination of the plasma membrane (Takeo and Nakai 1986; Guillot et al. 1995). The sexual phase of Malassezia is unknown.

The position of Malassezia in the Exobasidiomycetidae is surprising and suggests that either the Malassezia species are phytotrophic in the dikaryophase, or that they originated at least from plant parasites.

b) Georgischeheriales

Among the Exobasidiomycetidae, presence of poreless septa in the soral hyphae characterizes this group. The Georgischeheriales are teliosporic and dimorphic. They interact with their respective hosts by forming local interaction zones without interaction apparatus (Bauer et al. 1997). Haustoria or intracellular hyphae are lacking. The Georgischeheriales sporulate in vegetative parts of the hosts, predominantly in leaves (for Tilletiariales see below). Teliospores are yellow to brown in the species of Georgefischeria and darkly colored in the other taxa.

Except for Georgischeheria with its two species on Convolvulaceae and a few species on Cyperaceae, the Georgischeheriales occur on Poaceae. Because Tilletiaria anomala appeared in a plate over which a polypore growing on decaying wood had been suspended (Bandoni and Johri 1972), nothing is known of its life strategy. Like Tilletiaria anomala, smut fungi occasionally form teliospores and basidia in culture (Bauer et al. 1997). It is, therefore, conceivable that Tilletiaria anomala is a phytotrophic, probably on grasses.

The data resulting from neighbor-joining LSU rDNA analyses (Figs. 33, 34; Begerow et al. 1997) correlate well with the family conception proposed by Bauer et al. (1997). The species of the
Georgefischeriaceae are characterized by holobasidia (Figs. 15, 16) and a Tilletiopsis-like pseudohyphal anamorph that produces ballistoconidia. The Tilletiariaceae also form a Tilletiopsis-like pseudohyphal anamorph that produces ballistoconidia, but they are phragmobasidiate (Fig. 17; Bandoni and Johri 1972). The members of the Eballistraceae are holobasidiate and characterized by forming a budding yeast phase without ballistoconidia from the basidiospores (Singh and Pavgi 1973). The yeasts produced by the members of the Eballistraceae are spherical to ellipsoidal in form, do not form pseudomycelia, and grow very slowly on agar media. These features are unusual among the Ustilaginomycetes.

c) Tilletiales

Presence of dolipores in the septa (Fig. 30) characterizes the Tilletiales among the Exobasidiomycetidae (Fig. 32; Bauer et al. 1997). In contrast with all other groups of the Exobasidiomycetidae, the Tilletiales are not dimorphic. They form local interaction zones without interaction apparatus (Fig. 22) and hyphal anamorphs with ballistoconidia (e.g., Ingold 1987b, 1997). Among all the smut fungi we have studied from cultures, only the Tilletiales presented distinct pores in the septa of the saprobic hyphae. The septa in cultured hyphae of the other taxa were poreless even when distinct pores occurred in septa from sori, e.g., in species of Entyloma, Rhamphospora, Urocystis, and Ustacystis. This might explain why Moore (1972) and Boekhout et al. (1992) did not find distinct pores in some of these taxa.

The members of the Tilletiales are homogeneous, morphologically and ecologically (Figs. 4, 14). Haustoria and intracellular hyphae are lacking. The teliospores of this group are usually much larger than those of other groups of the Ustilaginomycetes and they are not arranged in balls. Except for Erratomyces on Leguminosae, they parasitize grasses and the sori, with the exception of Erratomyces, and a few species of Tilletia with teliospores in vegetative host organs, appear in ovaries (Piepenbring and Bauer 1997; Vánky 1994; Vánky and Bauer 1992, 1995, 1996). Some telitian species are economically important. Tilletia caries and T. controversa, for example, can cause heavy losses in production of wheat grains (Trione 1982; Mathre 1996). In India and the American tropics the angular black spot disease on leaves of beans is caused by Erratomyces patellii (Pavgi & Thirum.) M. Piepenbr. & R. Bauer (Piepenbring and Bauer 1997).

d) Microstromatales

Among the Exobasidiomycetidae, the Microstromatales are characterized by the presence of simple pores and local interaction zones without interaction apparatus (Fig. 32; Bauer et al. 1997). Currently, only four teleomorphic species are known in this group: Microstroma with its three species on hamamelids and Volvocisporium triumfetticola (M.S. Patil) Begerow et al. on Tiliaceae (Hennings 1900; Patil 1977). They are not teliosporic. The young basidium protrudes through the stomata and sporulates on the leaf surface (Oberwinkler 1978; Patil 1977). Volvocisporium differs mainly from Microstroma by the formation of highly septate basidiospores. The Microstromatales form a budding yeast phase without ballistoconidia and pseudomycelia. In contrast with most of the Ustilaginomycetes, the yeast cells are more or less spherical in form.

The identified species of the Microstromatales may represent only the "tip of the iceberg" of this group. Except for Microstroma juglandis (Bereng.) Sacc., the known species of the Microstromatales are difficult to detect in nature. In addition, we have isolated some yeasts belonging to this group.

The following orders of the Exobasidiomycetidae are grouped by Bauer et al. (1997) into the superorder Exobasidiales. The members of the Exobasidiales possess local interaction zones with interaction apparatus.

e) Entylomatales

The Entylomatales are characterized by the presence of simple interaction apparatus at the interaction sites (Figs. 23, 32; Bauer et al. 1997). Currently, this group comprises only species of Entyloma occurring on dicots with the type of Entyloma, Entyloma microsporum (Unger) Schröter (Fig. 5). The ultrastructural as well as the LSU rDNA sequence analyses revealed that the genus Entyloma is polyphyletic and that the "Entyloma" species occurring on monocots belong to the Georgefischeriaceae (designated in Figs. 32–34 as members of Eballista or Jamesicksonia; Bauer et al. 1997; Begerow et al. 1997). The teliospores of Entyloma species assigned to the Entylomatales are lightly colored, whereas those
of "Entyloma" species belonging to the George-fischeriales are darkly colored.

The members of the Entylomatales are morphologically very similar (Figs. 5, 13). In fact, the species are not easy to distinguish from each other (Vánky 1994). They form a Tilletiopsis-like pseudohyphal anamorph that usually produces ballistoconidia (Boekhout 1991).

**f) Doassansiales**

A complex interaction apparatus including cytoplasmic compartments (Fig. 24) characterizes this order (Fig. 32; Bauer et al. 1997). The known species of this group have parasitic hyphae with clamps, they are teliosporic and dimorphic and they do not form ballistoconidia in the haploid phase. Although they differ morphologically, they are ecologically uniform. The members of Burriilia, Doassansa, Heterodoassansa, Nannfeldiomyces, Narasimhania, Pseudodoassansa, Pseudodermatosorus, Pseudotracaya, and Tracaya have complex spore balls (Vánky 1987), whereas Doassinga, Melaniella and Rhamphosphora produce single spores (Bauer et al. 1999b; Vánky et al. 1998). In addition, teliospores are darkly colored in Melaniella, and lightly colored in Doassinga, Rhamphosphora, and the genera with complex teliospore balls. The hosts of the Doassansiales are systematically diverse, comprising spikemosses and various angiosperms.

However, the Doassansiales are ecologically well characterized by their occurrence on paludal or aquatic plants. They apparently evolved in the ecological niche of aquatic plants and developed complex spore balls and more or less sigmoid basidiospores in adaptation to water dispersal (Bauer et al. 1997). Interestingly, the species of Doassansiopsis in the Urocystales likewise parasitize aquatic plants and possess similar complex spore balls (see above). Thus, Doassansiopsis and the Doassansiales are an excellent example for the independent evolution of similar structures under the same environmental pressure.

The morphological and the LSU rDNA sequence analyses reveal a basal dichotomy between Melaniella and the other taxa of the Doassansiales (Bauer et al. 1999b). The next dichotomy is between Rhamphosphora and the Doassansiaceae (Figs. 32–34; Bauer et al. 1977, 1999b; Begerow et al. 1997). In contrast with the members of the Doassansiaceae, Rhamphosphora nymphaeae D. Cunn., the single species currently placed in the Rhamphosphoraceae, forms highly branched haustoria (Bauer et al. 1997).

**g) Exobasidiales**

The Exobasidiales are characterized by the presence of interaction rings produced by complex interaction apparatus (Figs. 25, 32; Bauer et al. 1997). The union between the species of this group is well supported by LSU rDNA sequences (Figs. 33, 34; Begerow et al. 1997). The members of the Exobasidiales are holobasidiate and dimorphic. They do not form teliospores in the parasitic phase and ballistoconidia in the saprobic phase. In most of the species, the basidiospores become septate during germination. Hosts are monocots and dicots. The sori predominantly appear on leaves. We currently recognize four families in this order.

The Brachybasidiales sporulate on the surface of the host organs. The basidia protrude through stomata or emerge from the disintegrated epidermis. The basidia are elongate, basistomporic, and two-sterigmate. The basidiospores are thin-walled. Available data indicate that the hilar appendices of the basidiospores are oriented adaxially at the apex of the basidia (see Figs. 2 and 6 in Cunningham et al. 1976; Figs. 1, 10–2, 1, 10–3 in Oberwinkler 1982; Fig. 4 in Oberwinkler 1993, Fig. 1–G in Ingold 1985). *Brachybasidium pinangae* Gäumann, *Dicellomyces gloeosporus* Olive, and *Proliferobasidium heliconiae* Cunningham form persistent probasidia which are arranged in delimited fructifications. In contrast with the other taxa, the basidiospores of the *Kordyana* species usually remain asperate during germination. The species of the Brachybasidiales live on monocots (Cunningham et al. 1976; Gäumann 1922; Oberwinkler 1978, 1982, 1993; Olive 1945).

The Exobasidiales are morphologically similar to the Brachybasidiales. Like the Brachybasidiales, the Exobasidiales sporulate through stomata (Fig. 21) or from the disintegrated epidermis, the basidia are elongate and basistomporic, and the basidiospores are thin-walled. In contrast with the Brachybasidiales, however, the hilar appendices of the basidiospores are oriented abaxially at the apex of the basidium (Fig. 21; Oberwinkler 1977, 1978, 1982). In most Exobasidiales species, the number of sterigmata per basidium is not fixed, varying from two to eight, with four as the most frequent number. Only a few
species form generally two-sterigmate basidia. This family comprises Exobasidium and Muribasidiospora. However, our analysis revealed that the genus Muribasidiospora is polyphyletic (see above). The Exobasidiaceae occur on dicots, predominantly on Ericaceae (Rajendren 1968; Hennings 1900; Mims et al. 1987; Nannfeldt 1981; Oberwinkler 1977, 1978, 1982, 1993).

In contrast with the Brachybasiidaceae and Exobasidiaceae, except for Laurobasidium the Cryptobasiidaceae sporulate internally by producing holobasidia in peripheral lacunae of the host galls. During maturation, the galls rupture and liberate the basidiospore mass. The basidia are gastroid and lack stigmata. The basidiospores are usually thick-walled, resembling the ureidospores of rust fungi or the teliospores of smut fungi. In addition, old fructifications often resemble smut sori. These characters may explain why some members of this group were described as smut fungi (see above), while others were originally described as rusts (e.g., Clinoconidium farinosum (P. Henn.) Pat. as Uredo farinosa P. Henn.).

In contrast to the other members of the Cryptobasiidaceae, however, Laurobasidium lauri (Geyler) Jülich sporulates on the surface of the host organ. In addition, the basidia of this species resemble those of Exobasidium, but they are gastroid as in the other members of the Cryptobasiidaceae. Thus, Laurobasidium, may occupy a systematic position at the base of the Cryptobasiidaceae and intermediate between the Cryptobasiidaceae and the other Exobasidiaceae.

Except for Coniodictyum, the host range of the Cryptobasiidaceae is restricted to laurels. Cryptobasiidaceae species are mainly known from Japan, Africa, South and Middle America (Donk 1956; Lendner 1920; Malençon 1953; Maublanc 1914; Oberwinkler 1977, 1978, 1982, 1993; Sydow 1926).

The Graphioliaceae are parasites of palms. Fructification of the Graphioliaceae starts between the chlorenchyma and hypodermal tissue (Cole 1983). During differentiation of the cylindrical basidiocarp, the epidermis ruptures and globose basidia are produced in chains by disarticulation of sporogenous hyphae within the basidiocarpars. The passively released basidiospores arise laterally on the basidia. (Fig. 20; Fischer 1921, 1922; Oberwinkler et al. 1982). The haustoria are constricted at the point of penetration and consist of a clamped basal body (Bauer et al. 1997).

VII. Conclusions

A. Evolution of the Basidium

The sequence of events occurring in the evolution of the basidium of the Ustilaginomycetes is unknown. Nevertheless, a tentative sequence can be outlined from the distribution of the basidial types among the different groups. The presence of simple pores in many members of the Ustilaginomycetes suggests that the first members of this line diverged from simple-septate ancestors. Among the simple-septate basidiomycetes, phragmobasidia are the rule and holobasidia are known only from Pachnocybe Berk. and Chionosphaera Cox (Oberwinkler and Bauer 1989), two taxa that are phylogenetically distant from the Ustilaginomycetes. Entorrhiza, the basal taxon of the Ustilaginomycetes, is phragmobasidiate. From this situation it can be postulated that the common ancestor of the Ustilaginomycetes probably was phragmobasidiate. In the Ustilaginomycetidae and Exobasidiomycetidae, however, phragmobasidia occur only in the Ustilaginaceae, Tilletiaceae, Mundkurella, and Ustacystis waldsteiniae (C.H. Beck) Zundel. In other words, except for eight species, the phragmobasidial taxa of the Ustilaginomycetidae and Exobasidiomycetidae are concentrated in a single family, whereas the holobasidial taxa are distributed throughout all orders of the Ustilaginomycetidae and Exobasidiomycetidae. In addition, the basal groups of the Ustilaginomycetidae and Exobasidiomycetidae are holobasidiate. This distribution of basidial types suggests that the common ancestor of the Ustilaginomycetidae and Exobasidiomycetidae was holobasidiate. Consequently, the sepation of the basidia of the Ustilaginaceae, Tilletiaceae Mundkurella, and Ustacystis must be interpreted as the result of convergent evolution.

B. Coevolution

Except for five species, the host range of the Ustilaginomycetes is restricted to angiosperms. As discussed by Bauer et al. (1997, 1999b), the occurrence of these five species on nonangiosperms may be the result of jumps. Most of the Ustilaginomycetes are parasites of monocots, especially the members of the Poaceae and Cyperaceae. This host distribution suggests that the Usti-
laginomycetes may have evolved as pathogens on either early angiosperms or on early monocots with subsequent jumps to the dicots. Thus, the Ustilaginomycetes may have appeared later in the phylogeny of the basidiomycetes than the rusts. Rusts apparently arose as parasites of early vascular plants (Savile 1955). As partly discussed above, within the Ustilaginomycetes there are evident examples of evolution with angiosperm relationships (e.g., the Tilletiales, Georgefischeriales and the Ustilago-Sporisorium complex with Poaceae, Entorrhiza with Juncaceae and Cyperaceae, Graphiola with palms, Anthracoidea with Cyperaceae, Mycosyrinx with Vitaceae, Exobasidium with Ericaceae, etc.). On the other hand, the Doassansiiales and Doassansiopsis are two excellent examples for evolution with ecosystems. In general, the host ranges of the different groups (e.g., the Georgefischeriales on Poaceae with a few species on Convulvulaceae and Cyperaceae, the Tilletiales on Poaceae with five species on Leguminosae, the Ustilaginomycetes on monocots with a few genera on dicots, etc.) reveal that the Ustilaginomycetes ancestors have not only undergone periods of parallel evolution with their hosts; jumps to new hosts may have stimulated the evolution of a large number of taxa.

C. Evolutionary Trends

Our analyses suggest the following evolutionary trends within the Ustilaginomycetes:

- cellular interactions from simple to complex forms,
- multiple evolution of intracellular fungal elements,
- multiple evolution of spore balls,
- repeated loss of septal pores,
- repeated change from simple pores to dolipores,
- primary change from septate to as septate basidia,
- repeated secondary change from as septate to septate basidia,
- repeated loss of teliospores as propagules,
- multiple evolution of gastroid taxa,
- repeated loss of the ballistosporic mechanism,
- evolution with host groups, but also with ecosystems,
- repeated jumps to unrelated hosts.

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