11 Ustilaginomycotina

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CONTENTS

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I. Introduction

Ustilaginomycotina comprises **115 genera with more than 1,700 species** and represents one of the three subphyla of the Basidiomycota (Bauer et al. 2006; Begerow et al. 1997; Hibbett et al. 2007; Swann and Taylor 1993). They harbour **mostly plant parasites** (Fig. 11.1a–p) **that are restricted to the geographic distribution of their hosts, encompassing tropical, temperate, and Arctic regions** (Vánky 2012).

Well-known genera in Ustilaginomycotina are *Ustilago* and *Tilletia*, which contain economically important species such as karnal bunt of wheat, loose smut of barley, and corn smut (Thomas 1989; Trione 1982; Valverde et al. 1995). In some cases where yield loss is minimal, contamination of *Tilletia* smut spores in grain can be subjected to quarantine regulations with economic implications and restrictions to international trade (Carris et al. 2006; Pascoe et al. 2005). Corn smut *Ustilago maydis* (DC.) Corda generally infects 2–5 % of plants in a corn field, although under certain conditions it can infect up to 80 % (Christensen 1963). While considered a plant pathogen in some parts of the world, the galls of *U. maydis* are appreciated as a delicacy in Mesoamerican cooking (Juarez-Montiel et al. 2011; Zepeda 2006). Besides the well-known species on crops, a huge diversity of plant parasites exist that either induce a typical smut syndrome (Fig. 11.1i–p) or present inconspicuous infections like members of Entylomatales (Fig. 11.1b), Exobasidiales (Fig. 11.1c–e), or Microstromatales (Fig. 11.1h). In addition, Ustilaginomycotina harbours some ecologically

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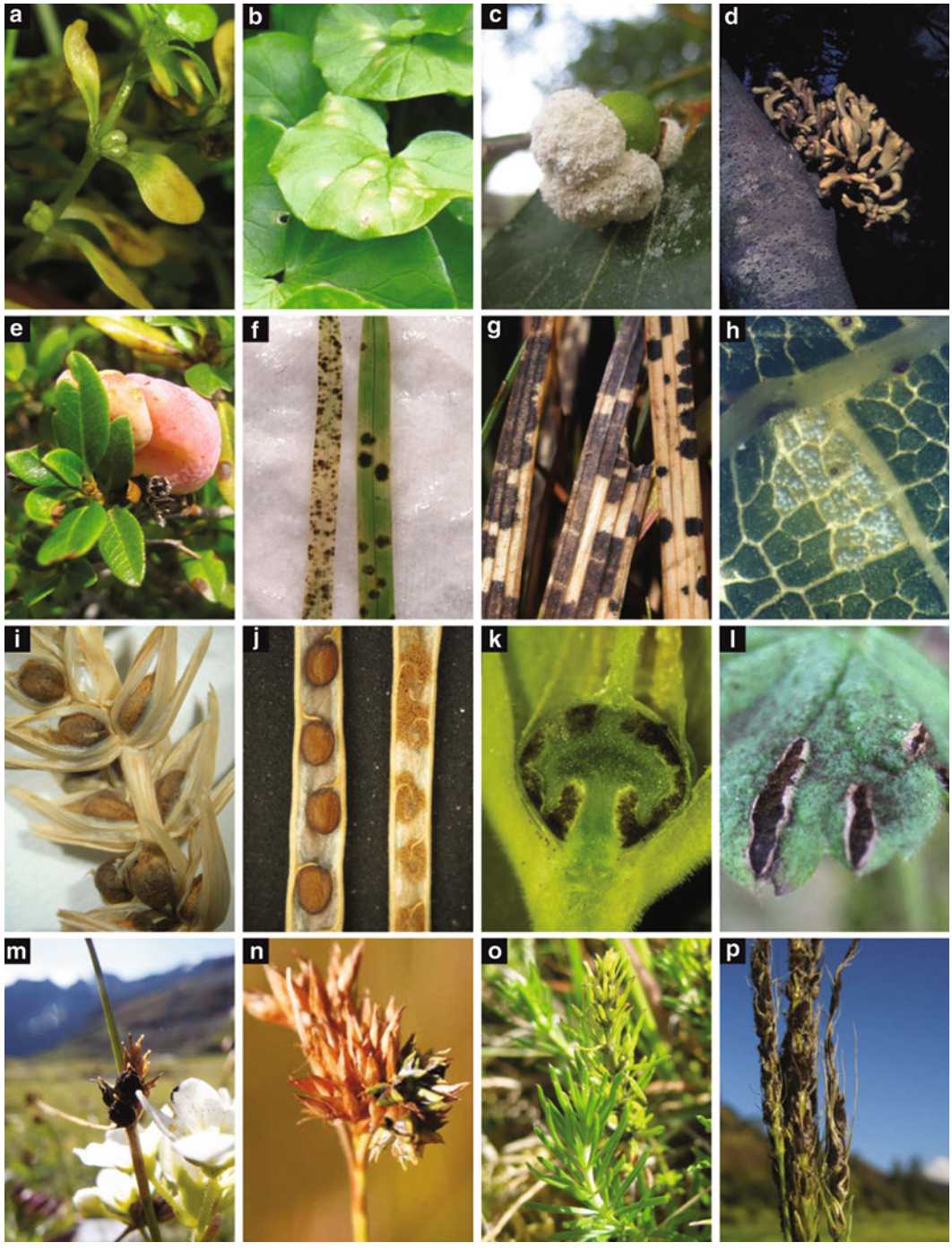

Fig. 11.1 Diversity of sori and infections of Ustilaginomycotina. (**a**) *Doassinga callitrichis* (Liro) Vánky, R. Bauer & Begerow. (**b**) *Entyloma ficariae* A.A. Fisch. Waldh. (**c**) *Coniodictyum chevalieri* Har. & Pat. (**d**) *Laurobasidium lauri* (Geyler) Jülich, (**e**) *Exobasidium rhododendri* (Fuckel) C.E. Cramer. (**f**) *Jamesdicksonia irregularis* (Johanson) R. Bauer, Begerow, A. Nagler & Oberw. (**g**) *Gjaerumia ossifragi* (Rostrup) R. Bauer, M. Lutz & Oberw. (**h**) *Microstroma juglandis* (Berenger) Sacc. (**i**) *Tilletia controversa* J.G. Kühn. (**j**) *Thecaphora thlaspeos* (Beck) Vánky. (**k**) *Urocystis primulae* (Rostr.) Vánky. (**l**) *Ustacystis waldsteiniae* (Peck) Zundel. (**m**) *Anthracoidea sempervirentis* Vánky. (**n**) *Ustanciosporium gigantosporum* (Liro) M. Piepenbr. (**o**) *Melanotaenium endogenum* (Unger) de Bary (**p**) *Ustilago hordei* (Pers.) Lagerheim.

variable anamorphic lineages such as *Malassezia*, which colonizes human and animal skin (Begerow et al. 2000, 2006).

Among the morphologically and ecologically diverse species of Ustilaginomycotina, *U. maydis* became a model organism for studying the interaction of specific plant parasites with their hosts. Using a variety of genetic tools, it has been shown that mating is an essential prerequisite to plant infection (Kahmann and Kämper 2004). ***U. maydis* was one of the first fungal genomes** sequenced, which advanced the knowledge of fungal physiology, such as the importance of secreted proteins in signaling (Brefort et al. 2009; Kämper et al. 2006). Thus, Ustilaginomycotina is a highly valuable group for comparative genomic studies in fungal pathogens and for illuminating the evolution and functionality of host–parasite interactions (Kellner et al. 2011; Schirawski et al. 2010; Xu et al. 2007).

A. Diagnosis and Evidence for Monophyletic Origin

The Ustilaginomycotina have a distinctive cell wall composition with a dominance of glucose and an absence of xylose, which separates them from the Pucciniomycotina and Agaricomycotina (Prillinger et al. 1990, 1993). They share the type B secondary structure of 5S ribosomal RNA (rRNA) with the Agaricomycotina (Gottschalk and Blanz 1985) and the lack of parenthesomes (i.e. multilayered endoplasmic reticulum elements at the septal pores) with the Pucciniomycotina (Bauer et al. 1997, 2006). Important **synapomorphies for the Ustilaginomycotina are membranous pore caps and the presence of a characteristic host–parasite interaction zone that results from fungal exocytosis of primary interactive vesicles** (Bauer et al. 1997).

Sequence analyses support the monophyly of the Ustilaginomycotina as defined earlier but with varying statistical support in different studies. Whereas the monophyly of *Tilletia caries* (DC.) L. & C. Tul., *Ustilago hordei* (Pers.) Lagerh., and *U. maydis* had high bootstrap support with small subunit (SSU) rDNA sequence analyses (Bauer et al. 2006; Swann and Taylor 1993, 1995), the bootstrap values for the Ustilaginomycotina were lower when analysed with large subunit (LSU) rDNA sequences and increased taxon sampling (Begerow et al. 1997, 2000). In particular, bootstrap support for the Ustilaginomycotina was sensitive to the inclusion or exclusion of *Entorrhiza* sequences in the LSU data set; after several analyses and varying interpretations *Entorrhiza* was excluded from the Ustilaginomycotina (Hibbett et al. 2007; Matheny et al. 2006). To date, the phylogenetic position of *Entorrhiza* remains unresolved.

B. Smut Fungi Syndrome in Other Fungal Groups

Like the terms *agaric*, *polypore*, and *lichen*, for example, **the term *smut fungus* circumscribes the organization and life strategy of a fungus** (cf. Fig. 11.1a–p) but does not represent common ancestry. Hence, **smut fungi are non-monophyletic** when based on the presence of a powdery spore mass. Most smut fungi are in the Ustilaginomycotina. Other smut fungi, in the Microbotryales, are members of the Pucciniomycotina (Bauer et al. 2006; Begerow et al. 1997; see Aime et al. 2014). In contrast to the Ustilaginomycotina, 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), all of which are synapomorphies of the Pucciniomycotina. Morphologically, they are distinguishable from the phragmobasidiate members of Ustilaginomycotina by the lack of intracellular hyphae or haustoria (Bauer et al. 1997). Grouping the Microbotryales within the Pucciniomycotina rather than the Ustilaginomycotina is also supported by sequence analyses (Bauer et al. 2006; Begerow et al. 1997; Swann and Taylor 1995). However, **there are significant convergences between the microbotryaceous and**

ustilaginomycetous phragmobasidiate smut fungi. Certain taxa of both groups are similar with respect to soral morphology, teliosporogenesis, life cycle, basidial morphology, and host range (Bauer et al. 1997, 2006).

As stated previously, *Entorrhiza* has been excluded from the Ustilaginomycotina mainly based on molecular phylogenetic analyses (Hibbett et al. 2007). Early studies using a smaller number of taxa placed *Entorrhiza* species basal to other Ustilaginomycotina with low bootstrap support (Begerow et al. 1997). Later studies questioned this position, and, depending on species sampling and outgroup selection, the position of *Entorrhiza* remains more or less unresolved (Begerow et al. 2006; Matheny et al. 2006). As long as a thorough multigene analysis is lacking, we follow the concept of Hibbett et al. (2007) and exclude *Entorrhiza* from the Ustilaginomycotina.

Interestingly, even non-basidiomycetous fungi can cause diseases with the formation of thick-walled propagules convergent to those of smut fungi. Species of *Schroeteria* Winter, for example, look superficially similar to Ustilaginomycotina (Vánky 1981) but belong to the Ascomycota (Nagler et al. 1989). Leaf spots similar to sori of *Entyloma* can be formed by representatives of the Protomycetales (Reddy and Kramer 1975), which belong to the Taphrinomycotina (Sugiyama et al. 2006; see Kurtzman and Sugiyama (2014), Chap. 1 Vol. VII, Part B) and produce ascospores in their synasci (Preece and Hicks 2001).

C. Hosts and Their Role in Species Definition

The Ustilaginomycotina, unlike the Pucciniomycotina and Agaricomycotina, generally are ecologically well characterized by parasitism. Besides some anamorphic taxa, which will be discussed in more detail later, all members of Ustilaginomycotina are plant parasites. Aside from *Exoteliospora* on ferns (Bauer et al. 1999b), two species of *Melaniella* on spike mosses (Bauer et al. 1999a), and two species of *Uleiella* on conifers (Butin and Peredo 1986; Schröter 1894), all other plant parasitic members of Ustilaginomycotina parasitize angiosperms with a high proportion of species on monocots, especially Poaceae and Cyperaceae. **The majority of the roughly 1,710 species occur on Poaceae** (45 %) **or on Cyperaceae** (13 %). The 121 ustilaginomycetous genera occurring on angiosperms include 72 genera that are exclusively found on monocots and 31 exclusively on dicots (mainly eudicots); 4 comprise species that parasitize both monocots and dicots. The genera found exlusively on monocots occur mainly on Poaceae (22) and on Cyperaceae (20, see below). Concerning the hosts, there are two remarkable points. (1) With a few exceptions, the teliospore-forming species of Ustilaginomycotina 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 angiosperm families with the highest number of species, the Orchidaceae with ca. 20,000 species and the Poaceae with ca. 10,000 species, play quite different roles for the Ustilaginomycotina. There are no known smut species on Orchidaceae, while the Poaceae are the most important host family of Ustilaginomycotina. **Grass smuts have** obviously **adapted to the ecology of their host group by wind-borne teliospores or basidiospores** and are thereby able to infect hosts that often occur in extensive, but often disconnected, host populations.

Host range used to play an important role in species definition. Many species, for instance in the genera *Entyloma*, *Melanotaenium*, and *Urocystis* (Vánky 1994), have few defining morphological characters, which, until the advent of ultrastructural techniques, were mainly limited to spore ornamentation and spore size. Therefore, host information has long been used in the delimitation of smut species as an additional defining characteristic. Different authors gave host specificity different emphases. Savile (1947), for instance, accepted only two species in *Entyloma* and lumped many already described species into these, whereas Vánky (2012) applied a narrower species definition and recognized 163 species based on spore morphology and host. Besides morphological and ecological concepts, phylogenetic species definitions have attracted much attention in recent years [for a review see Cai et al. (2011)], and phylogenetic approaches have in general confirmed the latter position (e.g. Begerow et al. 2002, 2004). These studies question the roles of host interaction and host range in maintaining species integrity of smuts. The species concept of smut fungi is especially perplexing because not only can closely related species [e.g. *Tilletia controversa* J.G. Kühn and *T. caries* (DC.) Tul. & C. Tul] hybridize under laboratory conditions (Trail and Mills 1990), but hybridization can even be observed between species that had their own evolutionary trajectory for millions of years (Kellner et al. 2011). It is unknown how gene flow is prevented in nature and how species integrity is main-

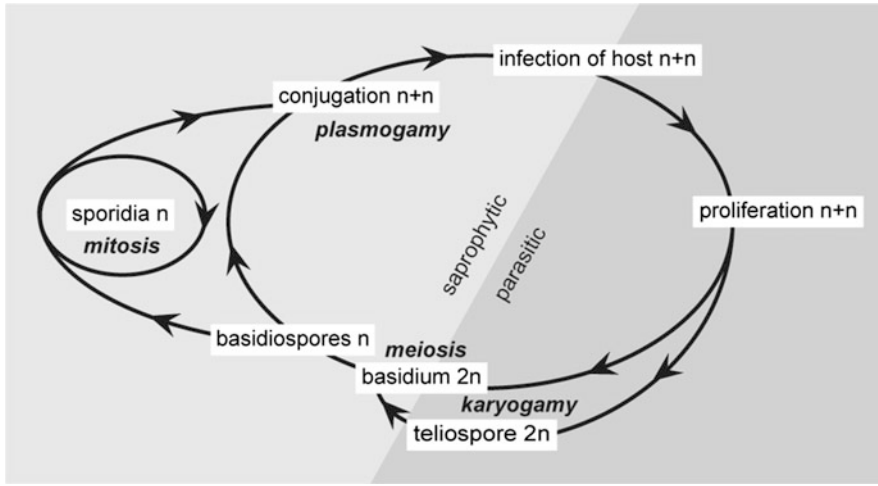

Fig. 11.2 Generalized life cycle of Ustilaginomycotina

tained for the Ustilaginomycotina, but in microbotryaceous smuts, hybrid inviability was shown to select against hybrids (De Vienne et al. 2009).

In *U. maydis*, sorus formation is initiated by a combination of parasite and host effectors. To develop teliospores, *U. maydis* specifically alters plant expression, initiating different expression profiles in different host tissues (Skibbe et al. 2010). These experiments demonstrated that the interaction between smuts and their hosts is extremely tight at the molecular level, which suggests that there are strong factors in maintaining boundaries between parasite species. Thus, species concepts incorporating host information, as applied by smut fungal taxonomists for the last century, have a biological basis, which could explain such narrow host ranges in smut fungi (Cai et al. 2011).

II. Life Cycle

Species of Ustilaginomycotina share a similar **dimorphic life cycle comprised of a saprobic haploid phase and a parasitic dikaryotic phase** (Fig. 11.2) (Brefeld 1883; de Bary 1884; Sampson 1939). The haploid phase is initiated usually by the formation of basidiospores following meiosis of the diploid nucleus in the basidium and ends with the conjugation of compatible haploid cells to produce dikaryotic, infectious hyphae. The dikaryotic phase ultimately results in the production of probasidia (i.e. often teliospores) or basidia (Fig. 11.3a–o).

Almost all Ustilaginomycotina sporulate on or in parenchymatic tissues of their hosts. In the majority of the Ustilaginomycotina, **the young basidium becomes thick-walled and at maturity separates from the sorus to function as a dispersal agent, the teliospore.** Teliospores are usually the most conspicuous stage in a smut's life cycle, representing the smut syndrome (cf. Fig. 11.1a–p). Most of the Ustilaginomycotina are dimorphic and produce a yeast or yeast-like stage in the haploid phase and form hyphae during the parasitic phase. However, there are several variations from this generalized life cycle, e.g. the occurrence of homothallism in *Anthracoidea* (Kukkonen and Raudaskoski 1964) and *Exobasidium* (Sundström 1964), the **lack of teliospores** in the Microstromatales, Exobasidiales and Ceraceosorales (Begerow et al. 2001, 2002, 2006), or even the switch to a complete anamorphic life style as assumed for *Malassezia* (Boekhout et al. 2010) and other anamorphic genera.

A. Saprobic Phase

Members of Ustilaginomycotina can survive outside their hosts during a free-living asexual state, the saprobic phase. **Many representatives are readily obtained from nature as predominantly unicellular budding states, called yeasts or sporidia**, e.g. species in *Ustilago*, *Microstroma*, and *Malassezia* (Begerow et al.

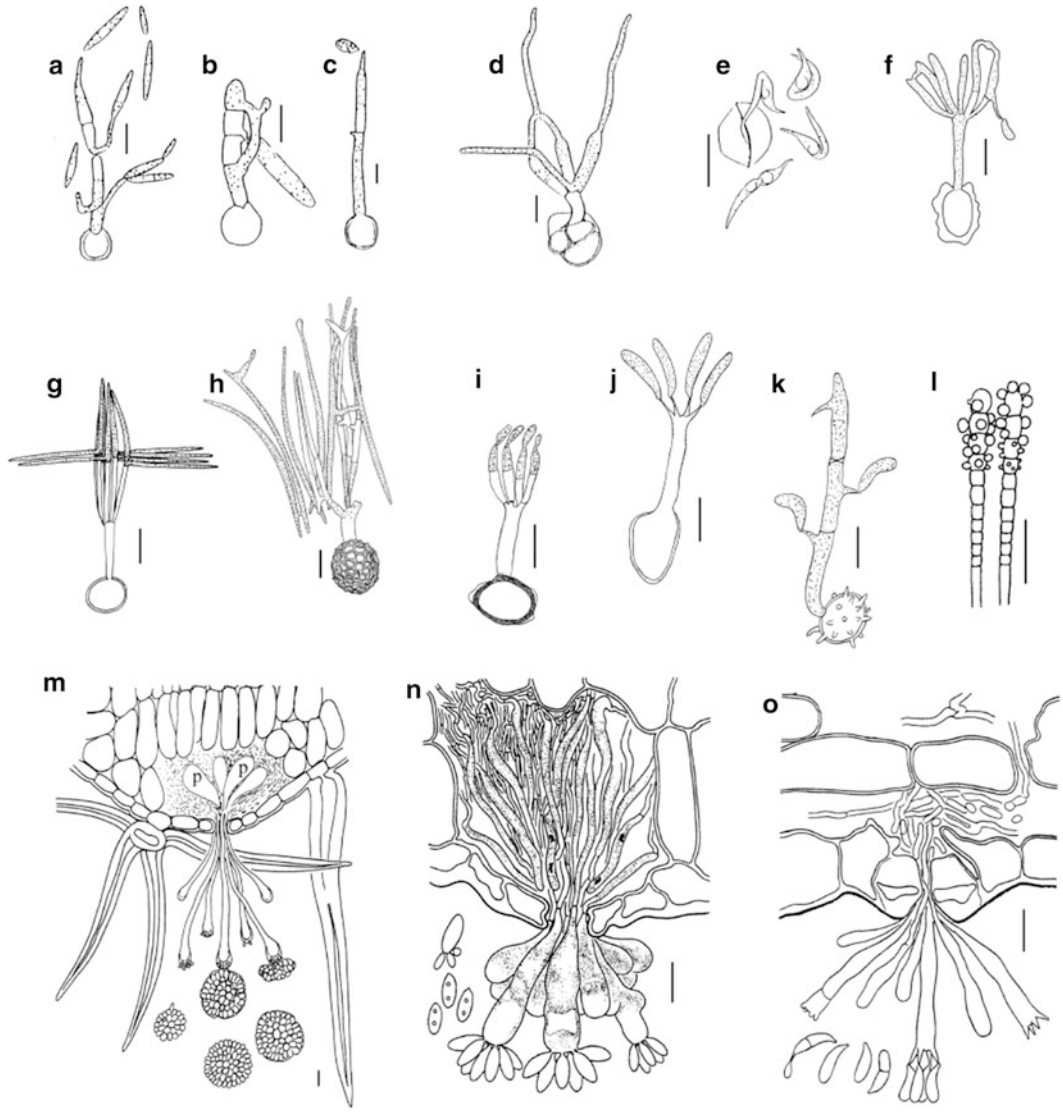

Fig. 11.3 Basidia of Ustilaginomycotina. *Bar*=10 µm. (**a**) *Ustilago maydis* (DC.) Corda. (**b**) *Cintractia axicola* (Berk.) Cornu. (**c**) *Anthracoidea altiphila* Vánky & M. Piepenb. (**d**) *Urocystis ranunculi* (Lib.) Moesz. (**e**) *Mycosyrinx cissi* (DC.) G. Beck. (**f**) *Entyloma microsporum* (Unger) Schröter. (**g**) *Rhamphospora nymphaeae* D.D. Cunn. (**h**) *Tilletia caries* (DC.) Tul. & C. Tul. (**i**) *Eballistra brachiariae* (Viégas) R. Bauer, Begerow, A. Nagler & Oberw. (**j**) *Jamesdicksonia dactylidis* (Pass.) R. Bauer, Begerow, A. Nagler & Oberw. (**k**) *Tilletiaria anomala* Bandoni & Johri. (**l**) *Graphiola phoenicis* (Moug.) Poiteau. (**m**) *Volvocisporium triumfetticola* (M.S. Patil) Begerow, R. Bauer & Oberw. (**n**) *Microstroma juglandis* (Berenger) Sacc. (**o**) *Exobasidium oxycocci* Rostr.

2000). Additionally, some smut fungi (e.g. *Exobasidium* and *Georgefischeria*) produce ballistospores to actively discharge basidiospores or secondary spores (Begerow et al. 2000). Hyphal growth is present in the saprobic phase of some members of Ustilaginomycotina; in many cases, a clear distinction between unicellular, yeast-like, pseudohyphal, and hyphal proliferation is impossible because budding cells (blastoconidia) often originate from hyphae and vice versa. This yeast–hyphal dimorphism occurs in many lineages of the Basidiomycota and might be a distinctive feature of parasitic lineages (Sampaio 2004).

In members of Ustilaginomycotina, yeast and yeast-like states are known from five orders: Ustilaginales, Entylomatales, Exobasidiales, Georgefischeriales, and Microstromatales (Begerow et al. 2000; Boekhout et al. 2011; Sampaio 2004). In the order Urocystidales, saprobic yeast-like growth of secondary sporidia was observed in some *Thecaphora* species (Vánky et al. 2008a) and in *Urocystis cepulae* Frost (Whitehead 1921). No such yeast states are known from the Doassansiales and Tilletiales.

Multiplication and propagation as yeast and yeast-like states are likely to be advantageous for survival and dispersal, and actually **some taxa are known from their asexual states only**, namely *Pseudozyma*, *Tilletiopsis*, *Sympodiomycopsis*, *Meira*, *Acaromyces*, *Jaminaea*, *Malassezia*, and probably *Quambalaria*. Members of these genera have mostly been isolated from various substrates during analyses of yeast communities in specific habitats (de Beer et al. 2006; Kurtzman et al. 2011).

Despite the economic relevance of smut infections caused by *Ustilago*, *Quambalaria*, and many others, and the rather high frequency of occurrence, little is known about the distribution of free-living yeast states. Assimilation tests, which are routinely performed for fungi historically treated as yeasts (*Pseudozyma*, *Sympodiomycopsis*, *Rhodotorula*), reveal the abilities of free-living states of Ustilaginomycotina to utilize a broad spectrum of plant-related carbohydrates, like sucrose, cellobiose, trehalose, L-arabinose, D-xylose, and some polyols (Kurtzman et al. 2011). Additionally, the capability of species of Ustilaginales (*Sporisorium*, *Ustilago*, *Farysia*, *Farysyzyma*, *Pseudozyma*), Entylomatales (*Entyloma*, *Tilletiopsis*), and Microstromatales (*Sympodiomycopsis*, *Rhodotorula*) to break down and assimilate low-weight aromatic molecules has been demonstrated (Sampaio 1999). Most of the tested cultures were able to use intermediates of lignin degradation, such as protocatechuic, *p*-coumaric acid, vanillic, and *p*-hydroxybenzoic acids (Sampaio 1999; Subba Rao et al. 1971). This adaptation seems especially interesting for dimorphic plant parasites because it might enable active degradation of cell walls, thereby allowing survival on decaying plant material. Besides the use of ligno-cellulosic derivates, the utilization of several non-conventional carbon sources of plant origin by species of Ustilaginomycotina has been reported, e.g. *Tilletiopsis washingtonensis* Nyland assimilates diverse volatile organic carbon (VOC) sources present in ripe apples (Vishniac et al. 1997). Interestingly, one component of VOC (butyl acetate), successfully utilized by *T. washingtonensis*, stimulates germination of grey mould (*Botrytis cinerea* Pers.) conidia, and the consumption of gaseous carbon products by *T. washingtonensis* decreases the development of moulds on apples (Filonow 2001). Members of Entylomatales display growth on gentisic acid (Sampaio 1999), a compound involved in regulating the defense responses of plants (Bellés et al. 2006). Members of Entylomatales and Microstromatales are able to grow on gallic acid (Sampaio 1999), a widely distributed tannin often accumulated in substantial quantities in plant material (Haslam and Cai 1994). Furthermore, the capability of some species of *Tilletiopsis*, *Pseudozyma*, and *Ustilago* to secrete enzymes, such as lipase, amylase, glucoamylase, cutinase, protease, pectinase, and xylanase, has been reported (Boekhout et al. 2006, 2011; Geiser et al. 2013; Trindade et al. 2002; Urquhart and Punja 2002).

Several interesting physiological adaptations seem to facilitate saprobic growth and survival in natural habitats. Cold tolerance is a common trait among basidiomycetous yeasts, which successfully colonize extremely cold habitats, including glaciers (Branda et al. 2010) and high-altitude regions (Connell et al. 2008; Vishniac 2006). Low temperatures also favour the development of various species of *Tilletiopsis* and anamorphs of *Entyloma* (Boekhout et al. 2006 and references therein). Extensive growth of *Tilletiopsis* spp. on apple surfaces under low oxygen concentration was reported recently (Boekhout et al. 2006). Although it is not yet clear whether this ability provides any advantage in colonizing plant substrates, several yeasts (e.g. *Meira* spp., *Pseudozyma* spp.) were reported from inside plant tissues (Abdel-Motaal et al. 2009; Gerson et al. 2008; Paz et al. 2007; Posada and Vega 2005; Takahashi et al. 2011; Tanaka et al. 2008; Yasuda et al. 2006).

The secretion of antibiotic compounds, killer toxins (proteins), and glycolipids could give yeasts a competitive advantage against other microorganisms. Glycolipids are modified long-chain fatty acids that are active against diverse groups of fungi (Golubev 2007; Mimee et al. 2005; Teichmann et al. 2007), bacteria (Kitamoto et al. 1993), and insects (Gerson et al. 2008). Antagonistic reactions towards other fungi were reported for *Acaromyces ingoldii* Boekhout, Scorzetti, Gerson & Sztejnb. and several species of the genera *Meira*, *Pseudozyma*, *Tilletiopsis*, and *Sympodiomycopsis* (Boekhout 2011; Gerson et al. 2008; Golubev 2006, 2007; Golubev et al. 2008). Consequently, some Ustilaginomycotina yeast species might even have evolved a mycoparasitic life style, as has been suggested for *T. pallescens* Gokhale, which was repeatedly isolated from basidiocarps of other fungi (Boekhout 2011). Recently, two asexual genera, *Meira* and *Acaromyces*, were found to cause the mortality of citrus mite pests (Paz et al. 2007). Although these fungi grew on mite cadavers, the capability of cell-free extracts from cultures to kill mites

suggests the toxic nature of fungal secretions rather than a parasitic life style. Interestingly, cell-free extracts effectively suppressed the growth of several plant pathogens, including moulds, mildew, and soil-borne fungi (Kushnir et al. 2011).

It is not surprising that **saprobic states of Ustilaginomycotina were found on different plant-related substrates** (Begerow et al. 2000; Fonseca and Inácio 2006; Sampaio 2004). In some cases saprobic and parasitic states co-exist in the same natural habitat; however, a considerable number of species were isolated from distinct substrates (water, nectar, and fruits) or from plants totally unrelated to the known hosts. Yeasts of the genus *Farysizyma*, probably the anamorphic stage of *Farysia*, which parasitizes Cyperaceae, have been recovered from leaves of unrelated plant species of Bromeliaceae and Cistaceae, strawberry fruits, and nectar (Inácio et al. 2008). Other substrates, i.e. water, fruit pulps and flowers, also yielded saprobic states of Ustilaginomycotina (Fell et al. 2011; Inácio et al. 2008; Liou et al. 2009; Seo et al. 2007; Trindade et al. 2002; Wang et al. 2006). Although some authors reported the isolation of *Pseudozyma* yeasts from clinical samples, **invasive disease caused by these fungi are very unusual in humans** (Lin et al. 2008; Sugita et al. 2003), and only yeasts of the genus *Malassezia* are considered to be part of the normal skin mycobiota of warm-blooded vertebrates (Findley et al. 2013). However, in many circumstances they have been reported to cause various types of skin diseases like pityriasis versicolor, seborrheic dermatitis, and folliculitis (Boekhout et al. 2010).

Finally, the dual nomenclature introduced for anamorphic strains and species remains problematic because some of them represent the anamorphic stage of a well-known teleomorph (Begerow et al. 2000; de Beer et al. 2006). The application of the new rules provided by the Melbourne Code will allow phylogenetic species recognition, and it is hoped that some of the systematic problems will be resolved in the near future (Hawksworth 2011; Hawksworth et al. 2011), but the integration of anamorphic and teleomorphic systematics and nomenclature remains a challenge.

B. Parasitic Phase

The parasitic phase in Ustilaginomycotina is initiated by the **mating process**, which induces a morphological and physiological transition from saprophytic yeast cells to biotrophic filaments (Fig. 11.2) (Kahmann and Kämper 2004; Kellner et al. 2011; Snetselaar and Mims 1992). The genetic and developmental basis of the infection process and the host–parasite interaction have been studied best in the model organism *U. maydis* and will not be reviewed in detail [for a more detailed view see Brefort et al. (2009), Kahmann and Kämper (2004) and Vollmeister et al. (2012)]. **To form an infectious dikaryotic hypha, two compatible haploid sporidia must recognize each other and fuse.** In *U. maydis* the cell cycle arrests during mating until after host penetration (Garcia-Muse et al. 2003). Penetration is achieved via non-melanized appressoria at the tip of elongated dikaryotic cells and might additionally be aided by the secretion of lytic enzymes (Schirawski et al. 2005).

The subsequent steps of infection depend on the ability of the fungus to establish an **intimate interaction with its specific host** (Fig. 11.4a–e). This is **mediated by the vesicle-based exocytosis** (Bauer et al. 1997) **of secreted effector proteins that interfere with plant defenses** (Brefort et al. 2009) and host-specific metabolic processes (Djamei et al. 2011). Depending on the respective ustilaginomycetous group, hyphae grow and proliferate either only intercellularly or both intercellularly and intracellularly (Fig. 11.4a–e) (Bauer et al. 1997). Intracellular hyphae are tightly surrounded by the plant plasma membrane and develop a characteristic vesicular matrix through the accumulation of secreted deposits (Bauer et al. 1997). **Members of Doassansiales, Entylomatales, and Exobasidiales develop a characteristic interaction apparatus** (Fig. 11.4b–d), **while other groups of Ustilaginomycotina interact with their host either via small evagination zones** (Fig. 11.4a) **or along the whole hyphae** (Fig. 11.4e). These hyphae are usually not restricted to specific entrance or exit sites of host cells and, therefore, can passage from cell to cell (Bauer et al. 1997). In the Ustilaginaceae, hyphae grow directly to plant vascular bundle cells and proliferate throughout the host in

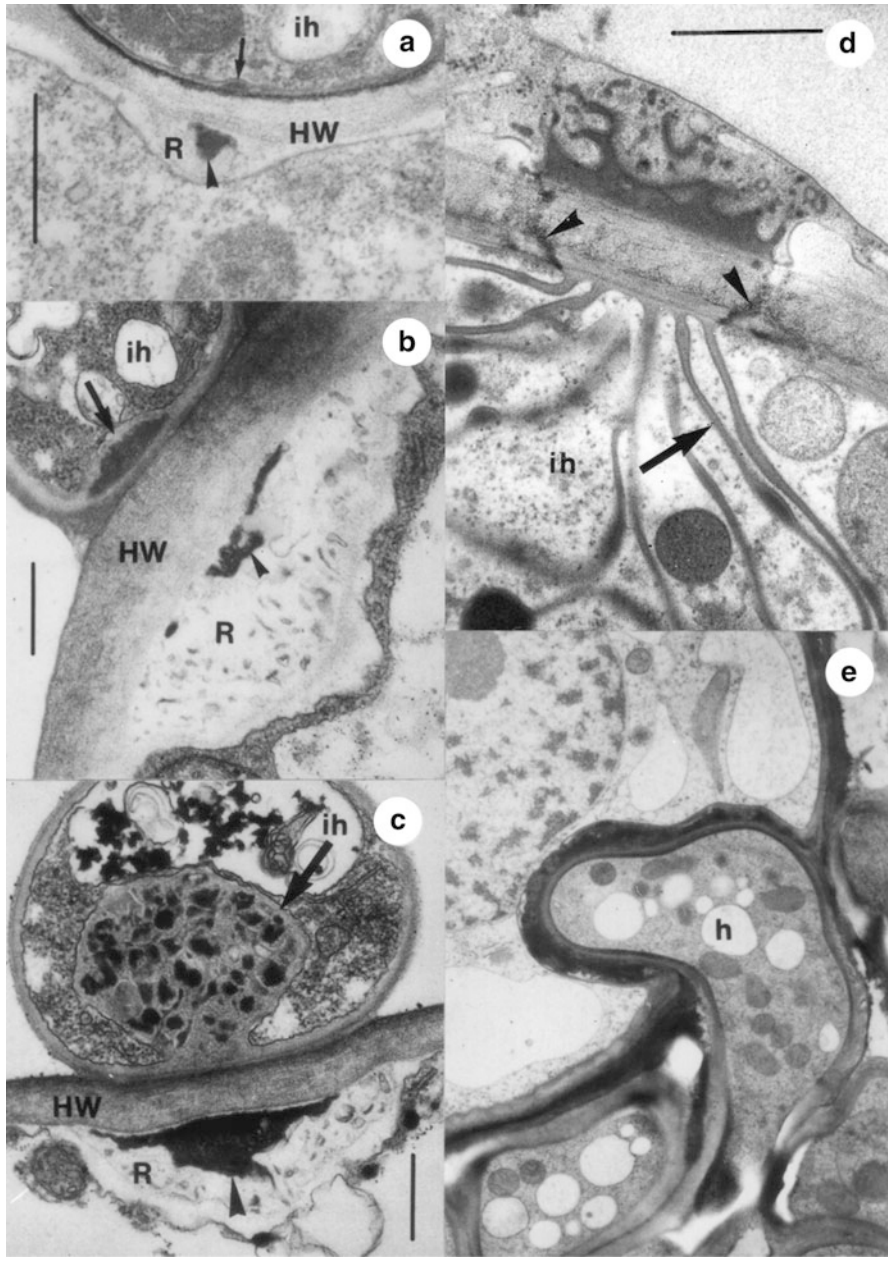

Fig. 11.4 Cellular interactions in Ustilaginomycotina. Material illustrated in (**d**) and (**e**) was prepared using freeze substitution. *Bar*=0.5 μm. (**a**)–(**d**) Local interaction zones, representative of Exobasidiomycetes. (**a**) Local interaction zone without interaction apparatus, representative of Georgefischeriales, Tilletiales, and Microstromatales. Intercellular hypha (ih) of *Conidiosporomyces ayresii* (Berk.) Vánky with secretion profile of one primary interactive vesicle (*arrow*) in contact with host cell wall (HW). Note electron-opaque deposits at host side (*arrowhead*). Host response to infection is visible at R. (**b**) Local interaction zone with simple interaction apparatus, representative of Entylomatales and Ceroceosorales. Intercellular hypha (ih) of *Entyloma hieracii* H. & P. Sydow in contact with host cell wall (HW) showing exocytosis profile of simple interaction apparatus (*arrow*). Note electron-opaque deposit at host side (*arrowhead*). Host response to infection is visible at R. (**c**) Local interaction zone with complex interaction apparatus containing cytoplasmic compartments, representative for Doassansiales. Intercellular hypha (ih) of *Doassinga callitrichis* (Liro) Vánky, R. Bauer & Begerow in contact with host cell wall (HW) showing exocytosis profile of one complex interaction apparatus (*arrow*).

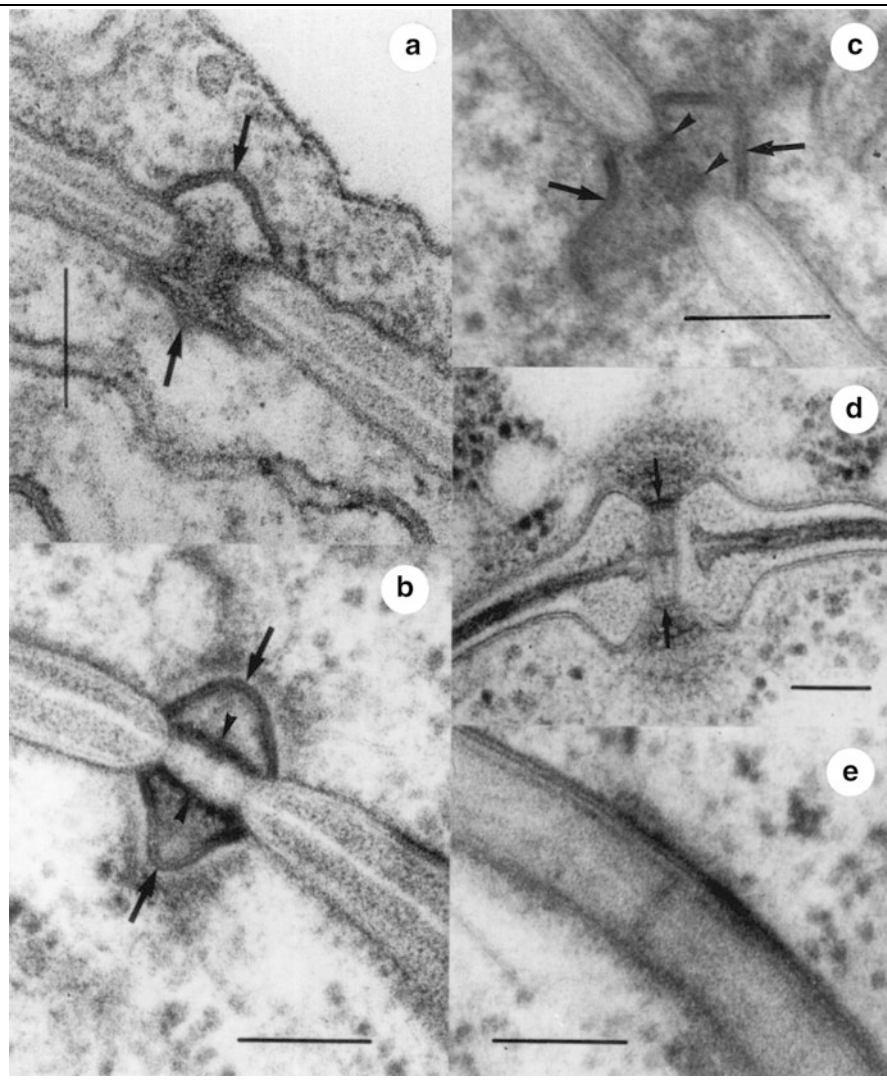

Fig. 11.5 Septation of soral hyphae in Ustilaginomycotina. Material illustrated in (**b**)–(**e**) was prepared using freeze substitution. *Scale bars*=0.1 μm. (**a**) Simple pore with two membrane caps (*arrows*) of *Doassinga callitrichis* (Liro) Vánky, R. Bauer & Begerow, representative of Melanotaeniaceae, Ceraceosorales, Doassansiales, Entylomatales, Exobasidiales, and Microstromatales. (**b**) Simple pore with two outer membrane caps (*arrows*) and two inner nonmembranous plates (*arrowheads*) of *Ustacystis waldsteiniae* (Peck) Zundel, representative of Urocystidiaceae, Floromycetaceae, and Doassansiopsidaceae. (**c**) Simple pore with two membrane caps (*arrows*) and sectioned tube in pore channel (*arrowheads*), representative of Exobasidiales. (**d**) Dolipore with membrane bands (*arrows*) of *Tilletia barclayana* (Bref.) Sacc. & P. Sydow, representative for Tilletiales. (**e**) Poroid structure in septum of *Mycosyrinx cissi* (DC.) G. Beck, representative for Georgefischeriales and core group Ustilaginales

Fig. 11.4 (continued) The interaction apparatus and its intercisternal space are excluded from the cytoplasm. Note electron-opaque deposit at host side (*arrowhead*). Host response to infection is visible at R. (**d**) Local interaction zone with complex interaction apparatus producing interaction tube, representative of Exobasidiales. Intercellular hypha (ih) of *Exobasidium pachysporum* Nannf. with interaction apparatus (*arrow*). Note sectioned interaction tube (arrowheads) at adjacent cell walls of parasitic and host cell. (**e**) Enlarged interaction zone between upper left plant cell and haustorium (h), representative of Ustilaginomycetes. The haustorium (h) of *Ustacystis waldsteiniae* (Peck) Zundel is surrounded by an electron-opaque matrix within host cell

close proximity to the vascular system until they reach their sporulation sites (Doehlemann et al. 2009). During proliferation, fungal hyphae branch and undergo mitosis and septation (cf. Fig. 11.5a–e). Members of Doassansiales, Ustilaginales, and some species of *Exobasidium* develop clamps to coordinate the synchronized division of the two nuclei. In *U. maydis* clamp primordia are formed at the tip of the growing hyphae (Scherer et al. 2006). However, clamp-like structures are observed in many species of Ustilaginomycotina. Whilst some clamps give rise to hyphal branches, others seem to correspond to fusion bridges (Fischer and Holton 1957), which ensure the migration of nuclei rather than coordinating dikaryotic mitoses.

Proliferation in the host is followed either by the direct formation of basidia, as observed in Microstomatales, Exobasidiales, and Ceraceosorales (Fig. 11.3l–o), or by the production of teliospores, which are clustered in sori (e.g. Fig. 11.1b, c, f, j–p). **Sporogenesis of teliospores often occurs in distinct organs of a plant, including roots, stems, leaves, inflorescences, anthers, ovaries, and seeds** (Fig. 11.1) (Vánky 2012). In this process biotrophic hyphae aggregate, septate, and finally differentiate into teliospores. However, teliospore formation is variable among members of Ustilaginomycotina, and propagation units range from single spores to large spore balls, which may or may not include sterile cells (Piepenbring et al. 1998). This variability can even be observed between closely related species, e.g. in *Urocystis* and *Thecaphora* (Vánky et al. 2008a). In *Ustilago* nearly all hyphae disarticulate and form teliospores in a matrix resulting from gelatinization of hyphal cell walls (Snetselaar and Mims 1994), whereas teliospores in *Rhamphospora* are formed terminally and without recognizable gelatinization (Piepenbring et al. 1998). Usually, sporogenesis occurs intercellularly either in preformed intercellular spaces or in cavities of disintegrated host cells (Luttrell 1987). The release of teliospores does not depend on living host tissue since *Schizonella* and some species of *Ustilago* sporulate within disintegrated host tissues, and species of *Clintamra*, *Exoteliospora*, and *Orphanomyces* even develop their teliospores externally to the host tissue (Piepenbring et al. 1998; Vánky 1987). Some of the varying morphological traits of soral formation or spore characteristics for ustilaginomycetous families are summarized in Fig. 11.8.

Besides the majority of Ustilaginomycota, which parasitize their host in the dikaryotic phase, there are a few examples of specific haploid yeast parasites. The most prominent ones certainly belong to the genus *Malassezia*, in which the anamorphic lipophylic yeast species specifically feed on the skin of warm-blooded animals, where they are involved in common skin diseases (Xu et al. 2007). To date, there are more species described with different specific host substrates, i.e. the mite parasitic species of *Meira* and *Acaromyces* (Gerson et al. 2008).

III. Classification System

Beginning with Tulasne and Tulasne (1847), the smut fungi have traditionally been divided into phragmobasidiate Ustilaginaceae or Ustilaginales and holobasidiate Tilletiaceae or Tilletiales (e.g. Kreisel 1969; Oberwinkler 1987). Durán (1973) and Vánky (1987) discussed the difficulties associated with smut classification in detail but did not list higher taxa in the group. Consequently, Vánky (1987) treated all smut fungi in a single order, Ustilaginales, with one family, Ustilaginaceae. Other plant parasites like *Exobasidium*, *Graphiola*, and *Microstroma* are treated in other families and orders (Hennings 1900) and are included in Ustilaginomycotina on the basis of ultrastructural characters (Bauer et al. 1997).

The **classification** proposed below **is based predominantly on characteristics of host–parasite interactions, the septal pore apparatus** (Fig. 11.6) (Bauer et al. 1997), **and LSU sequence analyses** (Fig. 11.7) (Begerow et al. 1997, 2006). However, the system is still under discussion because many groups are still poorly studied. As mentioned previously, the position of *Entorrhiza* within Basidiomycota is questionable based on molecular data, and the genus lacks some typical morphological features of Ustilaginomycotina (e.g. it does not possess membranous pore caps) (Bauer et al. 1997). The phylogenetic relationships among the different families of Ustilaginales and Urocystidales could only be clarified by molecular data and revealed the convergent evolution of several characters, e.g. the loss of septal pores or the development of intracellular hyphae (Begerow et al. 2006). Although the types of

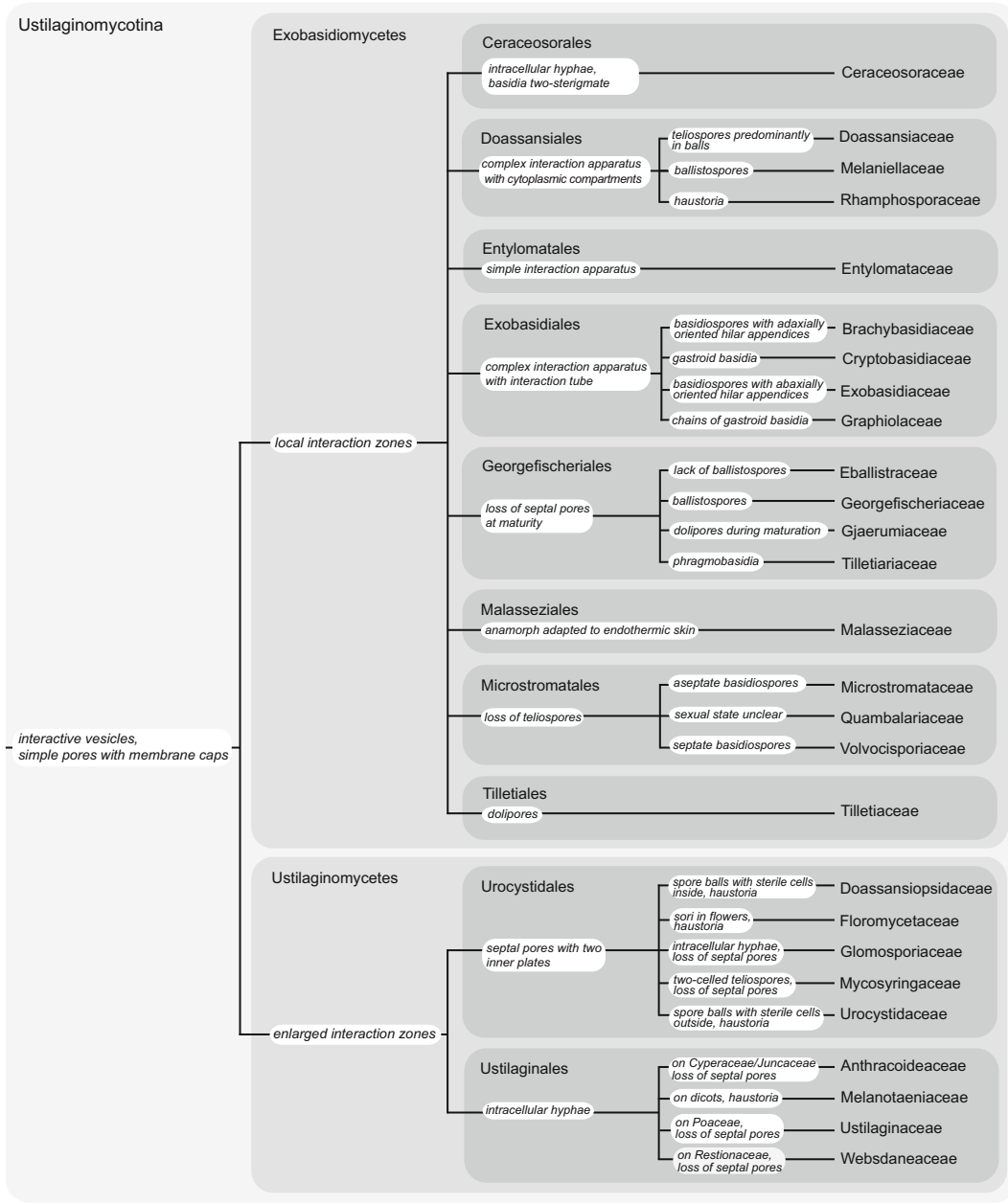

Fig. 11.6 Systematic overview of Ustilaginomycotina integrating morphological, anatomical, ecological, and molecular analyses. Characters on branches represent relevant markers reflecting apomorphies in some cases

basidial development are quite different among the various families of Exobasidiales or the families of Microstromatales, the relationships between the respective families within these orders are not always clear, and some of them are difficult to separate from each other without molecular data. Unresolved phylogenetic relationships are discussed with the respective groups in the next section. The fundamental characters used in classifying the Ustilaginomycotina were discussed in detail by Bauer et al. (1995a, b, 1997) and are therefore only briefly summarized here.

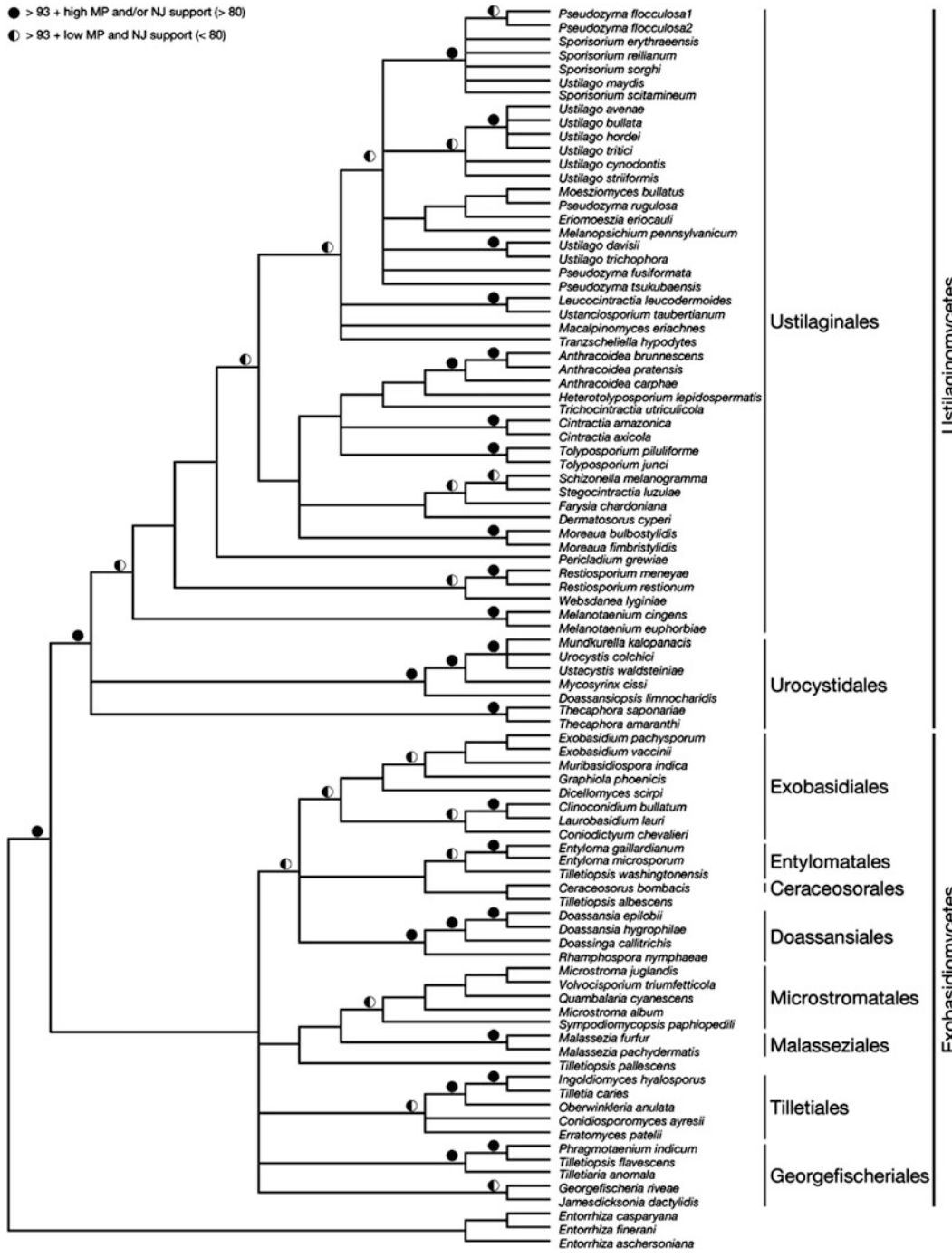

Fig. 11.7 Supertree topology from parsimony ratchet analysis (10,000 iterations) of matrix generated out of four neighbour-joining topologies (LSU, ITS, atp6, and β-tubulin genes). *Circles* next to branches summarize posterior probabilities of Bayesian analysis and bootstrap values of maximum parsimony and neighbour-joining analyses, which were based on a concatenated alignment [modified from Begerow et al. (2006)]

A. Fundamental Characters

1. Cellular Interactions

Hyphae of Ustilaginomycotina that are 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 characteristics diagnostic for higher groups in Ustilaginomycotina** (Fig. 11.6) (Bauer et al. 1997; Begerow et al. 2006). Initially, primary interactive vesicles with electron-opaque contents accumulate in the fungal cell. Depending on the fungal species, these primary interactive vesicles may fuse with one another before exocytosis from the fungal cytoplasm. Electron-opaque deposits also appear at the host side, opposite the point of contact with the fungus (Fig. 11.4a–e). 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, 2001a).

a. **Local interaction zones** (Fig. 11.4a–d). Short-term production of primary interactive vesicles at interaction site results in local inter-action zones.

1. **Local interaction zones without interaction apparatus** (Fig. 11.4a). Primary interactive vesicles fuse individually with the fungal plasma membrane. Depending on the species, local interaction zones without an interaction apparatus are present in intercellular hyphae or haustoria.
2. **Local interaction zones with interaction apparatus** (Fig. 11.4b–d). Fusion of the primary interactive vesicles precedes exocytosis.
   a) **Local interaction zones with simple interaction apparatus** (Fig. 11.4b). Primary interactive vesicles fuse to form one large secondary interactive vesicle per interaction site. Depending on the species, interaction zones of this type are located in intercellular or intracellular hyphae.
   b) **Local interaction zones with complex interaction apparatus** (Fig. 11.4c, d). 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. 11.4c). The intercisternal space of the cisternal net finally becomes integrated in the interaction apparatus. Depending on the species, interaction zones of this type are formed by intercellular hyphae or haustoria.
      ii. **Local interaction zones with complex interaction apparatus producing interaction tubes** (Fig. 11.4d). The intercisternal space does not become integrated in the interaction apparatus. Transfer of fungal material to the host plasma membrane occurs in two or three steps. The first transfer results in the deposition of a tube at the host plasma membrane. Depending on the species, interaction zones of this type are located in intercellular hyphae or haustoria.

b. **Enlarged interaction zones** (Fig. 11.4e). Continuous production and exocytosis of primary interactive vesicles results in the continuous deposition of fungal material at the entire contact area with the host cell. Depending on the species, this type of interaction zone is located in intercellular hyphae, intracellular hyphae, or haustoria.

2. Septation

Septal pore architecture plays an important role in the classification of the Basidiomycota (Oberwinkler 1985; Wells 1994). The pores of the Ustilaginomycotina 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 Ustilaginomycotina are usually devoid of distinct septal pores. **Septa in soral hyphae of the Ustilaginomycotina either have pores with membrane caps or**

are poreless. 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. 11.5a), (2) presence of simple pores with two outer tripartite membrane caps and two inner nonmembranous plates (Fig. 11.5b) (see also Bauer et al. 1995a), (3) presence of simple pores with two outer tripartite membrane caps and a tube in the pore channel (Fig. 11.5c), (4) presence of dolipores with membrane bands (Fig. 11.5d) (see also Roberson and Luttrell 1989), and (5) septa without distinct pores (Fig. 11.5e) designated as poroid or poreless septa.

B. Overview

In what follows, an overview of the taxa included in the Ustilaginomycotina is given. The system is based on a review of available studies. Discrepancies with other taxa proposed in the past are discussed subsequently. Compared to a previous overview (Bauer et al. 2001b), we have included several new genera, Malasseziales and Ceraceosorales, and excluded *Entorrhiza*, mainly based on the results of molecular analyses (Hibbett et al. 2007). Host families are indicated if the host range of the respective genera comprises one or two families. Following a unification of anamorphic and teleomorphic taxonomies (Hawksworth et al. 2011), the anamorphic species are ascribed to higher teleomorphic taxa based on molecular data (Fig 11.7) (Boekhout et al. 2011). Numbers in parentheses indicate the known species of each genus (Boekhout et al. 2011; Kirk et al. 2008; Vánky 2012; Chamnanpa et al. 2013; Denchev and Denchev 2011; Lutz et al. 2012; Savchenko et al. 2013).

Ustilaginomycotina R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw.

I. Exobasidiomycetes: Begerow, M. Stoll, R. Bauer
  a. Ceraceosorales:: Begerow, M. Stoll & R. Bauer
    i. Ceraceosoraceae Denchev & R.T. Moore
      Ceraceosorus B.K. Bakshi on Malvaceae (1)
  b. Doassansiales R. Bauer & Oberw.
    i. Melaniellaceae R. Bauer, Vánky, Begerow & Oberw.
      Melaniella R. Bauer, Vánky, Begerow & Oberw. on Selaginellaceae (2)
    ii. Doassansiaceae (Azb. & Karat.) R.T. Moore emend. R. Bauer & Oberw.
      Burrillia Setchell on monocots (4)
      Doassansia Cornu on mono- and eudicots (12)
      Doassinga Vánky, R. Bauer & Begerow on Plantaginaceae (1)
      Entylomaster Vánky & R.G. Shivas on Araceae (2)
      Heterodoassansia Vánky on mono- and eudicots (8)
      Nannfeldtiomyces Vánky on Typhaceae (2)
      Narasimhania Thirum. & Pavgi emend Vánky on Alismataceae (1)
      Pseudodermatosorus Vánky on Alismataceae (2)
      Pseudodoassania (Setchell) Vánky on Alismataceae (2)
      Pseudotracya Vánky on Hydrocharitaceae (1)
      Tracya H. & P. Sydow on Hydrocharitaceae and Araceae (2)
    iii. Rhamphosporaceae R. Bauer & Oberw.
      Rhamphospora D.D. Cunn. on Nymphaeaceae (1)
  c. Entylomatales R. Bauer & Oberw.
    i. Entylomataceae R. Bauer & Oberw.
      Entyloma de Bary on eudicots (163)
      Tilletiopsis Derx pro parte (anamorphic) (3)
  d. Exobasidiales P. Henn. emend. R. Bauer & Oberw.
    i. Brachybasidiaceae Gäum.
      Brachybasidium Gäumann on Arecaceae (1)
      Dicellomyces L. S. Olive on monocots (4)
      Exobasidiellum Donk on Poaceae (2)
      Kordyana Racib. on Commelinaceae (5)
      Meira Boekhout, Scorzetti, Gerson & Sztejnb. (anamorphic) (4)
      Proliferobasidium L.J. Cunn. on Heliconiaceae (1)
    ii. Cryptobasidiaceae Malençon ex Donk
      Acaromyces Boekhout, Scorzetti, Gerson & Sztejnb. (anamorphic) (2)
      Botryoconis H. & P. Sydow on Lauraceae (5)
      Clinoconidium Pat. on Lauraceae (2)
      Coniodictyum Har. & Pat. on Rhamnaceae (1)
      Drepanoconis Schröter & P. Henn. on Lauraceae (3)
      Laurobasidium Jülich on Lauraceae (1)
    iii. Exobasidiaceae P. Henn.
      Arcticomyces Savile on Saxifragaceae (1)
      Austrobasidium Palfner on Hydrangeaceae (1)
      Exobasidium Woronin on Ericales (50)
      Muribasidiospora Kamat & Rajendren on Anacardiaceae and Ulmaceae (3)

iv. Graphiolaceae E. Fischer
Graphiola Poiteau on Arecaceae (5)
Stylina H. Sydow on Arecaceae (1)
e. Georgefischeriales R. Bauer, Begerow & Oberw.
i. Georgefischeriaceae R. Bauer, Begerow & Oberw.
Georgefischeria Thirum. & Narash. emend. Gandhe on Convolvulaceae (4)
Jamesdicksonia Thirum., Pavgi & Payak on Cyperaceae and Poaceae (16)
ii. Gjaerumiaceae R. Bauer, M. Lutz & Oberw.
Gjaerumia R. Bauer, M. Lutz & Oberw. on Asparagaceae, Melanthiaceae and Xanthorrhoeaceae (3)
Tilletiopsis Derx pro parte (anamorphic) (2)
iii. Tilletiariaceae Moore
Phragmotaenium R. Bauer, Begerow, A. Nagler & Oberw. on Poaceae (1)
Tilletiaria Bandoni & Johri (1)
Tilletiopsis Derx pro parte (anamorphic) (4)
Tolyposporella Atkinson on Poaceae (6)
iv. Eballistraceae R. Bauer, Begerow, A. Nagler & Oberw.
Eballistra R. Bauer, Begerow, A. Nagler & Oberw. on Poaceae (3)
f. Malasseziales Moore emend. Begerow, R. Bauer & Boekhout
Malassezia Baill. (anamorphic) (14)
g. Microstromatales R. Bauer & Oberw.
i. Microstromataceae Jülich
Microstroma Niessl on Juglandaceae, Fabaceae and Fagaceae (4)
Rhodotorula F.C. Harrison pro parte (anamorphic) (3)
ii. Volvocisporiaceae Begerow, R. Bauer & Oberw.
Volvocisporium Begerow, R. Bauer & Oberw. on Malvaceae (2)
iii. Quambalariaceae Z.W. de Beer, Begerow & R. Bauer
Quambalaria J.A. Simpson on Myrtaceae (6)
Jaminaea Sipiczki & Kajdacsi (anamorphic) (2)
iv. Microstromatales *incertae sedis*
Sympodiomycopsis Sugiy., Tokuoka & Komag. (anamorphic) (2)
h. Tilletiales Kreisel ex R. Bauer & Oberw.
i. Tilletiaceae Tul. & C. Tul. emend. R. Bauer & Oberw.
Conidiosporomyces Vánky on Poaceae (3)
Erratomyces M. Piepenbr. & R. Bauer on Fabaceae (5)
Ingoldiomyces Vánky on Poaceae (1)
Neovossia Körn. on Poaceae (1)
Oberwinkleria Vánky & R. Bauer on Poaceae (1)
Salmacisia D.R. Huff & A. Chandra on Poaceae (1)
Tilletia L. & C. Tul. on Poaceae (179)
i. Exobasidiomycetes *incertae sedis*
Tilletiopsis albescens Gokhale (anamorphic)
Tilletiopsis pallescens Gokhale (anamorphic)
II. Ustilaginomycetes R. Bauer, Oberw. & Vánky
a. Urocystidales R. Bauer & Oberw.
i. Doassansiopsidaceae Begerow, R. Bauer & Oberw.
Doassansiopsis (Setchell) Dietel on mono- and dicots
ii. Floromycetaceae M. Lutz, R. Bauer & Vánky
Antherospora R. Bauer, M. Lutz, Begerow, Piątek & Vánky on Asparagaceae (8)
Floromyces Vánky, M. Lutz & R. Bauer on Asparagaceae (1)
iii. Glomosporiaceae Cifferi emend. Begerow, R. Bauer & Oberw.
Thecaphora Fingerh. (including *Glomosporium*, *Kochmania*, *Tothiella*, *Sorosporium*) on eudicots (61)
iv. Mycosyringaceae R. Bauer & Oberw.
Mycosyrinx Beck on Vitaceae (4)
v. Urocystidaceae Begerow, R. Bauer & Oberw.
Flamingomyces R. Bauer, M. Lutz, Piątek, Vánky & Oberw. on Ruppiacae (1)
Melanoxa M. Lutz, Vánky & R. Bauer on Oxalidaceae (2)
Melanustilospora Denchev on Araceae (2)
Mundkurella Thirum. on Araliaceae (5)
Urocystis Rabenh. ex Fuckel on mono- and eudicots (165)
Ustacystis Zundel on Rosaceae (1)
Vankya Ershad on Liliaceae (3)
b. Ustilaginales Clinton emend. R. Bauer & Oberw.
i. Anthracoideaceae Denchev
Anthracoidea Brefeld on Cyperaceae (101)
Cintractia Cornu on Cyperaceae (13)
Dermatosorus Sawada ex Ling on Cyperaceae (6)
Farysia Racib. on Cyperaceae (21)
Farysizyma A. Fonseca (anamorphic) (4)
Heterotolyposporium Vánky on Cyperaceae (1)
Leucocintractia M. Piepenbr., Begerow & Oberw. on Cyperaceae (4)
Moreaua T. N. Liou & H. C. Cheng on Cyperaceae (36)
Parvulago R. Bauer, M. Lutz, M. Piątek, Vánky & Oberw. on Cyperaceae (1)
Pilocintractia Vánky on Cyperaceae (2)
Planetella Savile on Cyperaceae (1)
Portalia V. Gonzáles, Vánky & G. Platas on Cyperaceae (1)
Schizonella Schröter on Cyperaceae (6)
Shivasia Vánky, M. Lutz & M. Piątek on Cyperaceae (1)
Stegocintractia M. Piepenbr., Begerow & Oberw. on Juncaceae (6)
Tolyposporium Woronin ex Schröter on Juncaceae (5)

Trichocintractia M. Piepenbr. on Cyperaceae (1)
Ustanciosporium Vánky emend. M. Piepenbr. on Cyperaceae (21)

ii. Melanotaeniaceae Begerow, R. Bauer & Oberw.
Exoteliospora R. Bauer, Oberw. & Vánky on Osmundaceae (1)
Melanotaenium de Bary on eudicots (9)
Yelsemia Walker on eudicots (4)

iii. Ustilaginaceae Tul. & C. Tul. emend. R. Bauer & Oberw.
Anomalomyces Vánky, M. Lutz & R.G. Shivas on Poaceae (1)
Anthracocystis Bref. on Poaceae (124)
Eriomoeszia Vánky on Eriocaulaceae (1)
Franzpetrakia Thirum. & Pavgi emend. Guo, Vánky & Mordue on Poaceae (3)
Langdonia McTaggart & R.G. Shivas on Poaceae (8)
Macalpinomyces Langdon & Full. emend. Vánky on Poaceae (41)
Melanopsichium G. Beck on Polygonaceae (2)
Moesziomyces Vánky on Poaceae (1)
Pericladium Pass. on Malvaceae (3)
Pseudozyma Bandoni emend. Boekhout (anamorphic) (16)
Sporisorium Ehrenb. on Poaceae (195)
Stollia McTaggart & R.G. Shivas on Poaceae (5)
Tranzscheliella Lavrov on Poaceae (17)
Triodiomyces McTaggart & R.G. Shivas on Poaceae (5)
Tubisorus Vánky & M. Lutz on Poaceae (1)
Ustilago (Pers.) Roussel on Poaceae (167)

iv. Websdaneaceae Vánky
Restiosporium Vánky on Anarthriaceae and Restionaceae (23)
Websdanea Vánky on Anarthriaceae (1)

v. Ustilaginales *incertae sedis*:
Ahmadiago Vánky on Euphorbiaceae (1)
Centrolepidosporium R.G. Shivas & Vánky on Centrolepidaceae (1)
Cintractiella K.B. Boedijn emend. M. Piepenbr. on Cyperaceae (2)
Clintamra Cordas & Durán on Asparagaceae (1)
Eriocaulago Vánky on Eriocaulaceae (2)
Eriosporium Vánky on Eriocaulaceae (2)
Farysporium Vánky on Cyperaceae (1)
Geminago Vánky & R. Bauer on Malvaceae (1)
Kuntzeomyces P. Henn. ex Sacc. & P. Sydow on Cyperaceae (2)
Orphanomyces Savile on Cyperaceae (3)
Testicularia Klotzsch on Cyperaceae (3)
Uleiella Schröter on Araucariaceae (2)

C. Description

Within Ustilaginomycotina **two major groups are evident in the dendrograms resulting from ultrastructural and LSU rDNA sequence analyses** (Figs. 11.6 and 11.7) (Bauer et al. 1997; Begerow et al. 2006). Though the monophyly of the Ustilaginomycetes is well supported, this is not always the case with the Exobasidiomycetes (Hibbett et al. 2007). However, in the absence of additional studies, we follow the earlier interpretations and retain Ceraceosorales and Malasseziales as part of the Exobasidiomycetes (Begerow et al. 2000, 2006). Although many morphological characters of sori and teliospores are not consistent at higher taxonomic levels, an overview at the family level is included in Fig. 11.8.

1. Exobasidiomycetes

Exobasidiomycetes represents the sister group of Ustilaginomycetes (Bauer et al. 1997; Begerow et al. 1997, 2006; Hibbett et al. 2007). The members of Exobasidiomycetes and Ustilaginomycetes share the **presence of membrane caps or bands at the septal pores** (Fig. 11.6). However, taxa with poreless septa evolved in both groups. **Exobasidiomycetes differs from Ustilaginomycetes in the formation of local interaction zones** (Fig. 11.5). Except for Tilletiariaceae (Fig. 11.3k), all **members of Exobasidiomycetes are holobasidiate** (Fig. 11.3f–j, l–o). Among the basidiomycetes, the formation of ballistosporic holobasidia, in which the **hilar appendices of the basidiospores are oriented abaxially** (sterigmata turned outwards; basidiospores inwards) (Fig. 11.3j, o), is restricted to Exobasidiomycetes. This type of basidium is common in Exobasidiales (Fig. 11.3o) but also occurs in species of Doassansiales, Georgefischeriales (Fig. 11.3j), and Tilletiales (Goates and Hoffmann 1986). Therefore, the *Exobasidium* basidium with the specific orientation of the ballistosporic basidiospores may represent an apomorphy for Exobasidiomycetes.

Teliospores are absent or present within the Exobasidiomycetes. **Formation of teliospore**

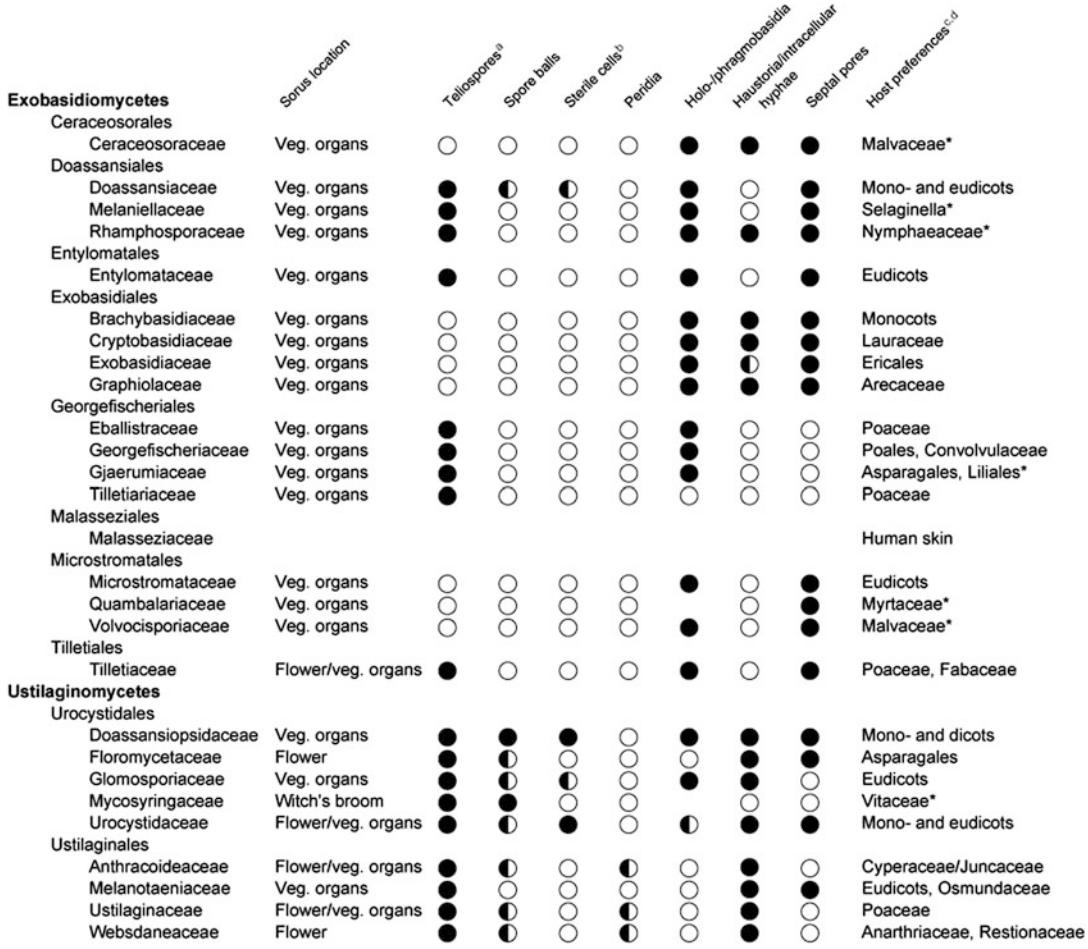

Fig. 11.8 Summary of character states of Ustilaginomycotina families. [a]*Filled circle*: presence of a character or holobasidia; *empty circle*: absence of a character or presence of phragmobasidia; *half-filled circle*: mixture of characters in respective groups. [b]Sterile cells in spore balls. [c]Host preferences are identified for families with more than 90 % of their members parasitizing the respective plant taxon. [d]*Asterisk*: families of unclear preference due to small species sampling

balls only occurs in Doassansiaceae and in *Tolyposporella*. Smut fungi among the Exobasidiomycetes show terminal or intercalary teliospore formation (Roberson and Luttrell 1987; Trione et al. 1989). A gelatinization of hyphal walls preceding teliospore formation is either lacking or not clearly recognizable.

Currently we include eight orders on the basis of ultrastructural characters and molecular phylogenetic data within Exobasidiomycetes (Fig. 11.6). A superorder, Exobasidianae, including Entylomatales, Doassansiales, and Exobasidiales, was proposed based on the apomorphy of a complex interaction apparatus (Bauer et al. 1997). This grouping is highly sensitive to sampling in molecular analyses (Fig. 11.7), and therefore we follow the system of Hibbett et al. (2007). Anamorphic species without affiliation to a teleomorph have been assigned to *Tilletiopsis*, although the genus is non-monophyletic (Begerow et al. 2000). However, some anamorphic species or lineages have been named according to a unique ecology as in *Meira* and *Jaminaea*. The **phylogenetic positions of Malasseziales and Ceraceosorales are controversial**, and some

authors have proposed a treatment as *incertae sedis* (Hibbett et al. 2007). Although apomorphic exobasidiomycetous morphological features like septal pore caps and local interaction zones are lacking, at least in Malasseziales, we follow the proposal of Begerow et al. (2006) based on molecular data (Fig. 11.7). All orders are presented alphabetically without additional hierarchy.

a) Ceraceosorales

Within Exobasidiomycetes, the **Ceraceosorales are characterized by intracellular hyphae with a simple interaction apparatus** (Fig. 11.6) (Begerow et al. 2006). The **septal pores in *Ceraceosorus bombacis*** (B.K. Bakshi) B.K. Bakshi **are simple and enclosed by membrane caps at both sides** (Fig. 11.5a), as seen in Melanotaeniaceae of the Ustilaginomycetes and in Microstromatales, Entylomatales, Doassansiales, and Exobasidiales of the Exobasidiomycetes (Bauer et al. 1997; Begerow et al. 2006). In *Ceraceosorus* and in Brachybasidiaceae, basidia protrude through stomata or emerge from the disintegrated epidermis. The basidia are elongated, basally thick-walled, and two-sterigmate and form ballistosporic basidiospores with an adaxial orientation of the hilar appendices in both groups (Begerow et al. 2002; Cunningham et al. 1976). Like Brachybasidiaceae and Exobasidiomycetes in general, *Ceraceosorus* produces local interaction zones (Begerow et al. 2006). However, molecular data do not support a closer relationship between Exobasidiales and Ceraceosorales (Fig. 11.7). The other Exobasidiomycetes lacking an interaction apparatus or establishing a simple interaction apparatus, such as Entylomatales, Georgefischeriales, Microstromatales, and Tilletiales, do not form intracellular hyphae or haustoria (Bauer et al. 1997; Begerow et al. 2006). Thus, *C. bombacis* (B.K. Bakshi) B.K. Bakshi seems to be isolated, and the monotypic order seems to be justified.

b) Doassansiales

A **complex interaction apparatus, including cytoplasmic compartments**, characterizes this order (Figs. 11.4c and 11.6) (Bauer et al. 1997). The studied **species of this group have parasitic hyphae with clamps**. They are teliosporic and dimorphic and do not form ballistoconidia in the haploid phase. The teliospore germinates with holobasidia (Fig. 11.3g) (Bauer et al. 1999a; Vánky et al. 1998). The members of *Burrillia*, *Doassansia*, *Entylomaster*, *Heterodoassansia*, *Nannfeldtiomyces*, *Narasimhania*, *Pseudodoassansia*, *Pseudodermatosporus*, *Pseudotracya*, and *Tracya* have complex spore balls (Vánky 1987, 2012), whereas *Doassinga* (Fig. 11.1a), *Melaniella*, and *Rhamphospora* produce single spores (Vánky 1994; Vánky et al. 1998). **The spore balls differ in the occurrence of sterile cells within the spore ball.** In addition, teliospores are darkly coloured in *Melaniella* and lightly coloured in *Doassinga*, *Rhamphospora*, and genera with complex teliospore balls. The hosts of the Doassansiales are systematically diverse, comprising spike mosses (Selaginellaceae) and various monocots as well as eudicots.

However, members of **Doassansiales are ecologically well characterized by their occurrence on paludal or aquatic plants, or at least on plants of moist habitats**. 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 (Fig. 11.3g) (Bauer et al. 1997). Interestingly, the species of *Doassansiopsis* in Urocystidales likewise parasitize aquatic plants and possess similar complex spore balls. Thus, *Doassansiopsis* and Doassansiales are excellent examples of the independent, convergent evolution of similar structures under the same environmental condition.

The order comprises three families. Ultrastructural and LSU sequence analyses revealed a basal dichotomy between Melaniellaceae presenting pigmented spores and Rhamphosporeaceae and Doassansiaceae showing hyaline teliospores (Bauer et al. 1999a; Begerow et al. 1997). In contrast to members of Doassansiaceae, *Rhamphospora nymphaeae* D. Cunn., the only species placed in the Rhamphosporaceae, forms highly branched haustoria (Fig. 11.8) (Bauer et al. 1997).

c) Entylomatales

Entylomatales is **characterized by the presence of a simple interaction apparatus** at the interaction sites (Fig. 11.4b) **and simple hyaline spores as well as simple septal pores** (Fig. 11.6) (Bauer et al. 1997). This group comprises only species of *Entyloma* occurring on eudicots (Fig. 11.1b), with the type species of *Entyloma*, *Entyloma microsporum* (Unger) Schröter (Fig. 11.3f), as well as anamorphic *Tilletiopsis* species. Ultrastructural and LSU sequence analyses revealed that the genus *Entyloma* was polyphyletic and that the previous "*Entyloma*" species occurring on monocots belonged to Georgefischeriales (designated as *Eballistra* or *Jamesdicksonia*) (Figs. 11.3i, j and 11.7) (Bauer et al. 1997; Begerow et al. 1997, 2002).

Although the species in the genus *Entyloma* are morphologically very similar, systematic analyses supported numerous host-specific species (Boekhout et al. 2006). The **majority of *Entyloma* species parasitize plant families in Ranunculales or Asteridae**, whereby the members of Ranunculales seem to be the older host group as its parasites are paraphyletic and show longer branch lengths (Begerow et al. 2002). Within Asteridae (including one *Entyloma* species on Saxifragaceae) an "explosive" radiation seems to have occurred, most likely caused by a rapid succession of **host jumps rather than co-cladogenesis** (Begerow et al. 2002). This is supported by the fact that *Entyloma* species on closely related host groups are not necessarily closely related to each other. Additionally, the much longer branch lengths in Asteridae hosts indicate that their interaction with *Entyloma* is younger than the radiation of the host group (Begerow et al. 2002). Finally, the inclusion of an *Entyloma* species on *Chrysosplenium* (Saxifragaceae) supports this view of host shifts as a likely explanation for the observed host range patterns (Begerow et al. 2002).

The **anamorphic *Tilletiopsis*** species, which have been assumed to be the sister group to *Entyloma* (Fig. 11.7) (Begerow et al. 2002), are now known to have evolved independently several times within the genus *Entyloma* (Boekhout et al. 2006). Research in this group has recently gained importance because so-called white haze, a post-harvest disorder of apples, has been associated with the proliferation of pseudomycelia of various *Tilletiopsis* species. This cosmetic disorder was first described as problematic under low-oxygen storage conditions but was demonstrated to additionally occur on fruits in the field. The increase in observations in the last decade is correlated mainly with an increase in humidity and new cultivation procedures in this time frame (Baric et al. 2010).

d) Exobasidiales

Members of Exobasidiales are characterized by the presence of **interaction tubes produced by a complex interaction apparatus** (Fig. 11.4d) (Bauer et al. 1997) and **septal pores with membranous caps and an additional tube inside** (Figs. 11.5c and 11.6). The monophyly of this group is also well supported by molecular data (Fig. 11.7) (Begerow et al. 2002, 2006). Members of Exobasidiales are holobasidiate and dimorphic (Fig. 11.3l–o). They do not form teliospores in the parasitic phase or ballistoconidia in the saprobic phase. In most species, the basidiospores become septate during germination. **Hosts are mono- and eudicots**. The sori appear on leaves, fruits, and stems (Figs. 11.1a–c and 8). We currently recognize four families in this order (Fig. 11.6) (Begerow et al. 2002; Hibbett et al. 2007).

The Brachybasidiaceae sporulate on the surface of host organs. The basidia protrude through stomata or emerge from the disintegrated epidermis. The basidia are elongated and ballistosporic and have two sterigmata. 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, 6, 13, 17 in Cunningham et al. 1976; Fig. 1-G in Ingold 1985; Figs. 1.10-2, 1.10-3 in Oberwinkler 1982; Fig. 4 in Oberwinkler 1993). *Brachybasidium pinangae* Gäumann, *Dicellomyces gloeosporus* Olive, and *Proliferobasidium heliconiae* Cunningham form persistent probasidia that are arranged in delimited fructifications. The species of Brachybasidiaceae live predominantly on monocots (Cunningham et al. 1976; Gäumann 1922; Oberwinkler 1978, 1982, 1993; Olive 1945). Molecular analyses placed the anamorphic genus *Meira*, isolated from pear fruits, into this family,

although teleomorphic stages are unknown (Rush and Aime 2013; Yasuda et al. 2006).

The non-smut family Cryptobasidiaceae (Fig. 11.1c, d) contrasts with Brachybasidiaceae and Exobasidiaceae because it sporulates internally by producing holobasidia in peripheral lacunae of the host galls (Fig. 11.6). During maturation, the galls rupture and liberate the basidiospore mass. The basidia are gastroid and lack sterigmata. The basidiospores are usually thick-walled, resembling the urediniospores 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), whilst others were originally described as rusts [e.g. *Clinoconidium farinosum* (P. Henn.) Pat. as *Uredo farinosa* P. Henn.]. In contrast to other members of Cryptobasidiaceae, *Laurobasidium lauri* (Geyler) Jülich (Fig. 11.1d) sporulates on the surface of host organs. Additionally, the basidia of this species resemble those of *Exobasidium* but are gastroid, as in other members of Cryptobasidiaceae [for a detailed discussion see Begerow et al. (2002)]. Thus, *Laurobasidium* may occupy a systematic position at the base of the Cryptobasidiaceae and intermediate between Cryptobasidiaceae and other Exobasidiales, although this is not supported by molecular analyses so far (Begerow et al. 2002). Except for *Coniodictyum* (Fig. 11.1c), the host range of Cryptobasidiaceae is restricted to laurels. Cryptobasidiaceae species are known only from Japan, Africa, and South America (Donk 1956; Hendrichs et al. 2003; Lendner 1920; Malençon 1953; Maublanc 1914; Oberwinkler 1978, 1982, 1993; Piepenbring et al. 2010; Sydow 1926). In molecular studies the anamorphic genus *Acaromyces* isolated from mites also clusters within Cryptobasidiacae (Boekhout et al. 2003).

Exobasidiaceae species are morphologically similar to those of Brachybasidiaceae. Like members of Brachybasidiaceae, Exobasidiaceae species sporulate through stomata or from the disintegrated epidermis (Mims and Richardson 2007), the basidia are elongated and ballistosporic, and the basidiospores are thin-walled. In contrast to the Brachybasidiaceae, the hilar appendices of the basidiospores are oriented abaxially at the apex of the basidia (Fig. 11.3o) (Oberwinkler 1977, 1978, 1982). In most Exobasidiaceae 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. Exobasidiaceae comprises *Arcticomyces*, *Austrobasidium*, *Exobasidium*, and *Muribasidiospora* (Begerow et al. 2002). The members of this family occur on eudicots predominantly on Ericaceae (Fig. 11.1e) (Hennings 1900; Mims et al. 1987; Nannfeldt 1981; Oberwinkler 1977, 1978, 1982, 1993; Piepenbring et al. 2010; Rajendren 1968).

The Graphiolaceae are parasites of palms. Fructification of the Graphiolaceae starts between chlorenchyma and hypodermal tissue (Cole 1983). During differentiation of the cupulate to cylindrical basidiocarp, the epidermis ruptures and globose basidia are produced in chains by disarticulation of sporogenous hyphae within the basidiocarps (Fig. 11.3l). The passively released basidiospores arise laterally on the basidia (Fischer 1921, 1922; Oberwinkler et al. 1982). Haustoria are constricted at the point of penetration and consist of a clamped basal body (see Fig. 11.3 in Oberwinkler et al. 1982; Bauer et al. 1997; Begerow et al. 2002).

e) Georgefischeriales

Among the Exobasidiomycetes, this group is characterized by the presence of **poreless septa in soral hyphae** (Fig. 11.6). The Georgefischeriales species have a dimorphic life cycle and form teliospores. They interact with their respective hosts via **local interaction zones without an interaction apparatus** (Bauer et al. 1997, 2001a, 2005). Haustoria or intracellular hyphae are lacking. The Georgefischeriales sporulate in vegetative parts of the hosts, predominantly in leaves (Fig. 11.1f, g). Teliospores are yellow to brown in species of *Georgefischeria* and darkly coloured in other taxa. The teliospore masses are usually not powdery, and host tissues are not fractured to expose the sori (Bauer et al. 1997, 2001a, 2005). The order is divided into four families, Georgefischeriaceae, Gjaerumiaceae, Tilletiariaceae, and Eballistraceae (Fig. 11.8).

Except for *Georgefischeria*, with its four species on Convolvulaceae and the species of *Gjaerumia* on several monocot families, the **Georgefischeriales occur on Poales**. Because *Tilletiaria anomala* Bandoni & B.N. Johri appeared in a plate over which a polypore growing on decaying wood had been suspended (Bandoni and Johri 1972), nothing is known of its ecology. Most recently, *T. anomala* was found in the intercellular spaces of rice plants, **indicating an endophytic life style** (Takahashi et al. 2011). In this study, other grass parasites, including *Ustilago* and *Tilletia*, were also found in the intercellular spaces, and, like *T. anomala*, smut fungi occasionally form teliospores and basidia in culture (Fig. 11.3k) (Bauer et al.

1997, 2005). It is conceivable that *T. anomala* is a phytoparasite, probably on grasses.

The molecular phylogenies of this group (Bauer et al. 2005) correlate well with the family concept proposed by Bauer et al. (2001a) (Figs. 11.6 and 11.8). Species of Georgefischeriaceae, Gjaerumiaceae, and Eballistraceae are characterized by holobasidia (Fig. 11.3i, j), whereas species of Tilletiariaceae are phragmobasidiate (Fig. 11.3k) (Bandoni and Johri 1972; Bauer et al. 2001a, 2005). The basidiospores of Georgefischeriaceae, Gjaerumiaceae, and Tilletiariaceae form *Tilletiopsis*-like pseudohyphal anamorphs that produce ballistoconidia (Bandoni and Johri 1972; Bauer et al. 2005). Members of Eballistraceae do not produce ballistoconidia but form budding yeasts, which are spherical to ellipsoidal in form (Singh and Pavgi 1973).

Noteworthy is the occurrence of dolipores in young septal pores of Gjaerumiaceae. So far, within the Exobasidiomycetes dolipores are only known from members of the Tilletiales. However, in contrast to members of this group, the pores of members of Gjaerumiaceae are closed during teliosporogenesis (Bauer et al. 2005).

Molecular analyses also revealed that several anamorphic species cluster within the Georgefischeriales. The current taxonomy of these species assigned to *Tilletiopsis* awaits revision (Boekhout et al. 2006).

f) Malasseziales

The **anamorphic genus *Malassezia* comprises medically important, lipophylic yeasts** that constitute part of the fungal microflora on the skin of warm-blooded animals (Guého et al. 1998; Findley et al. 2013). It has been placed within the Exobasidiomycetes based on molecular studies (Begerow et al. 2000, 2006). *Malassezia* has been found to be associated with a variety of pathological conditions in humans, including **pityriasis versicolor**, **seborrheic dermatitis**, **folliculitis**, and **systemic infections** (Gueho et al. 1998). The cell wall of *Malassezia* yeasts is thick and multilamellate and reveals a unique substructure with an electron-opaque, helicoidal band that corresponds to a helicoidal evagination of the plasma membrane (Guého-Kellermann et al. 2010). The sexual phase of *Malassezia* is unknown, although genetic analyses revealed intact mating genes (Xu et al. 2007). The position of *Malassezia* in the Exobasidiomycetes is surprising and suggests that *Malassezia* species either are phytoparasitic in the dikaryophase or originated at least from plant parasites.

g) Microstromatales

Among the Exobasidiomycetes, the **Microstromatales are characterized by the presence of simple pores and local interaction zones without an interaction apparatus** (Fig. 11.6) (Bauer et al. 1997). Teliospores are lacking. Hosts are often **woody plants**, which is similar to the ecology of Exobasidiales. Though only a few species were initially placed in this order, three families are currently recognized: Microstromataceae, Volvocisporiaceae, and Quambalariaceae (Fig. 11.8) (Begerow et al. 2001; de Beer et al. 2006).

In Microstromataceae the young basidia protrude through the stomata and sporulate on the leaf surface (Figs. 11.1h and 11.3n) (Oberwinkler 1978; Patil 1977). They are not teliosporic, and sori are mostly less than a few millimetres in diameter (Fig. 11.1h). They are characterized by single-celled, hyaline basidiospores and infect mainly trees and bushes of various eudicot families, mainly Juglandaceae, Fabaceae, and Fagaceae (Begerow et al. 2001). In culture they form budding yeasts without ballistoconidia and pseudohyphae. In contrast to most Ustilaginomycetes, the yeast cells are more or less spherical in form.

Volvocisporiaceae are characterized by large and highly septate basidiospores (Fig. 11.3m) and are known from only two species (Begerow et al. 2001; Ritschel et al. 2008). They share the ultrastructural morphology of simple septal pores and local interaction zones with all members of Microstromatales, but they are clearly separated from other families by molecular means (Ritschel et al. 2008).

In contrast to Microstromataceae and Volvocisporiaceae, members of Quambalariaceae possess septal pores with swellings resembling dolipores of other groups (Fig. 11.6) (de Beer et al. 2006). They comprise pathogens of *Eucalyptus* and *Corymbia*, and so far, almost all host taxa are native to Australia, which suggests Australia as the centre of diversity (de Beer et al. 2006; Pegg et al. 2009). Although the development of conidiophores through stomata looks very similar to basidia of *Microstroma* sporulations, meiosis has not been observed and the sexual state remains unclear (Pegg et al. 2009).

The known species of Microstromatales may only represent the so-called tip of the iceberg for this group. Most of them are difficult to detect in nature and could easily be overlooked. Additionally, several yeasts belonging to this group have been isolated, and their affiliation is not always clear. Beecause yeast anamorphs are common in *Microstroma*, addititional surveys are needed to recognize more taxa and teleomorphs. Though the included "*Rhodotorula*" species seem to be anamorphic stages of *Microstroma*, *Sympodiomycopsis* spp., and *Jaminaea angkorensis* Sipiczki and Kajdacsi, they seem to lack close relation to any studied species (Begerow et al. 2001; Mahdi et al. 2008; Sipiczki and Kajdacsi 2009).

h) Tilletiales

The presence of **dolipores in the mature septa** (Fig. 11.5d) characterizes the Tilletiales among the Exobasidiomycetes (Fig. 11.6) (Bauer et al. 1997). In contrast to all other groups of the Exobasidiomycetes, the Tilletiales are not known to be dimorphic. **They form local interaction zones without an interaction apparatus** (Fig. 11.4a), **and their hyphal anamorphs regularly produce ballistoconidia** (e. g., Carris et al. 2006; Ingold 1987b, 1997). Among all the smut fungi studied in culture, only the members of Tilletiales present distinct pores in the septa of saprobic hyphae.

Members of Tilletiales lack haustoria and intracellular hyphae (Fig. 11.8). The **teliospores** are darkly pigmented and often ornamented. Moreover, these teliospores are usually much larger than those of other groups of the Ustilaginomycotina, and they are never arranged in balls (Fig. 11.8). The teliospores of some species produce trimethylamine, which causes a foul smell in the spores. Seven genera are described in this family, six of which exclusively parasitize **Poaceae**. The genus *Erratomyces* is solely parasitic on Fabaceae. Sori are formed in ovaries of the hosts in the majority of species (Fig. 11.1i); only a few species of *Tilletia* and *Erratomyces* form teliospores in vegetative host organs (Castlebury et al. 2005; Piepenbring and Bauer 1997; Vánky 1994, 2012; Vánky and Bauer 1992, 1995, 1996). The teliospores germinate with holobasidia, producing terminal basidiospores, which often conjugate and give rise to infectious hyphae (Ingold 1989b; Vánky 2012).

Some species of *Tilletia* are economically important. *Tilletia caries* (DC) Tul. & C. Tul. and *T. controversa* J. G. Kühn on wheat and *Tilletia horrida* Takah. on rice can cause heavy losses in grain production (Carris et al. 2006; Mathre 1996; Trione 1982). In India and the American tropics the angular black spot disease on leaves of beans is caused by *Erratomyces patelii* (Pavgi & Thirum.) M. Piepenbr. & Bauer (Piepenbring and Bauer 1997).

Within Tilletiales the taxonomy is far from resolved. Molecular data especially provided controversial results for morphology-based classification (Castlebury et al. 2005). Species concepts and species delimitations are still in discussion (Cai et al. 2011). Additionally, the discovery and addition of new species might change the taxonomic concept (Bao et al. 2010; Shivas 2009).

Remarkably, *Salmacisia buchloëana* (Kellerm. & Swingle) D.R. Huff & Amb. Chandra parasitizing the buffalograss *Buchloë dactyloides* (Nutt.) Englem induces the development of ovaries in male flowers, which leads to hermaphroditism and castration of its host plant (Chandra and Huff 2008). Alteration of host reproductive structures evolved at least three times independently within smut fungi, as seen in *Salmacisia*, *Microbotryum* spp. and *Thecaphora oxalidis* (Ellis & Tracy) M. Lutz, R. Bauer & Piątek (Roets et al. 2008; Schäfer et al. 2010).

2. Ustilaginomycetes

The presence of **enlarged interaction zones** (Fig. 11.4e) **characterizes this group** (Fig. 11.6) (Bauer et al. 1997). The members of the **Ustilaginomycetes are teliosporic, gastroid, and dimorphic**. The species isolated in the anamorphic phase are usually placed in the genus *Pseudozyma*. However, for some members closely related to *Farysia* a new genus, *Farysizyma*, has been proposed (Inácio et al. 2008). Based on the new regulations of dual nomenclature, they should be included in *Farysia* (Hawksworth 2011; Hawksworth et al. 2011)

Morphologically and ecologically, members of the Ustilaginomycetes are diverse (Fig. 11.1j–p)

(Vánky 1987, 1994, 2012), but both ultrastructural and LSU sequence analyses unite them (Figs. 11.6 and 11.7) (Bauer et al. 1997; Begerow et al. 1997, 2006). Two orders are recognized.

a) Urocystidales

As part of Ustilaginomycetes the Urocystidales were originally **characterized by the presence of haustoria and pores** in the septa of soral hyphae (Bauer et al. 1997). The morphological characterization has discrepancies with molecular data, the latter supporting the inclusion of five families: Doassansiopsidaceae, Floromycetaceae, Glomosporiaceae, Mycosyringaceae, and Urocystidaceae (Fig. 11.6) (Begerow et al. 2006; Vánky et al. 2008b). Doassansiopsidaceae, Floromycetaceae, and Urocystidaceae are characterized by the presence of haustoria and pores in the septa of soral hyphae (Bauer et al. 1997), but these characters are missing in the mature infection stuctures of Mycosyringaceae and Glomosporiaceae (Begerow et al. 2006; Vánky 1996). Additionally, molecular studies do not support the monophyly of Urocystidaceae, Doassansiopsidaceae, or Melanotaeniaeae, which are characterized by the same combination of haustoria and septal pores (Fig. 11.6). Therefore, Melanotaeniaceae is no longer part of the Urocystidales but is in the Ustilaginales (Begerow et al. 2006).

Doassansiopsidaceae shares with Urocystidaceae and Floromycetaceae an essentially identical septal pore apparatus (Fig. 11.5b) (Bauer et al. 1997). It is composed of a simple pore with two outer tripartite membrane caps and two inner non-membranous plates (Fig. 11.5b) (Bauer et al. 1995a, 1997, 2008; Vánky et al. 2008b). The species of *Doassansiopsis*, the only genus of Doassansiopsidaceae, possess complex teliospore balls. A central mass of pseudoparenchymatous cells is surrounded by a layer of firmly adhering, lightly coloured teliospores and an external cortex of sterile cells (Piątek et al. 2008; Vánky 1987). *Doassansiopsis* species form gastroid holobasidia and yeast anamorphs without ballistoconidia. The position of *Doassansiopsis* in Urocystidales is surprising. Based on teliospore ball morphology and the parasitism of aquatic plants, *Doassansiopsis* was grouped with *Burillia*, *Doassansia*, *Heterodoassansia*, *Nannfeldtiomyces*, *Narasimhania*, *Pseudodoassansia*, and *Tracya* (Vánky 1987, 1994). However, both ultrastructural and molecular analyses show that *Doassansiopsis* is not closely related to the other complex teliospore-ball-forming taxa (Fig. 11.8) (Bauer et al. 1997; Begerow et al. 1997, 2006).

Floromycetaceae includes species that parasitize various members of Asparagaceae. Within this family, haustoria and septal pores in soral hyphae are present. The genus *Antherospora* forms single spores in the anthers of the host plant (Bauer et al. 2008), whereas *Floromyces* forms spore balls in flowers. The germination of the teliospores of both genera results in phragmobasidia with sterigmata (Vánky et al. 2008b).

The family Glomosporiaceae experienced a reclassification on the basis of molecular data (Begerow et al. 2006). Originally it was included in the Ustilaginales because intracellular hyphae are formed in the host interaction (Bauer et al. 1997). *Glomosporium* and *Tothiella* were identified as synonyms of *Thecaphora* (Vánky et al. 2007, 2008a). *Thecaphora* species parasitize eudicots and display light brown teliospore balls that differ in the amount of spores (Fig. 11.1j). In the majority of species, these spore balls only consist of fertile cells, in contrast to other families within Urocystidales (Fig. 11.8). The balls vary in their integrity; in some species the balls are strongly agglutinated, whilst in other species they separate easily. Moreover, there are species that have single spores, for example *T. thlaspeos* (Beck) Vánky (Vánky et al. 2007, 2008a). Teliospore germination among species of *Thecaphora* is variable, ranging from true holobasidia to aseptate or septate hyphae that sometimes bear basidiospores (Ingold 1987c; Kochman 1939; Nagler 1986; Piepenbring and Bauer 1995). We interpret these hyphal germinations as atypical germinations resulting possibly from non-optimal environmental conditions. For example, both germination types (i.e. phragmo- and holobasidia) have been reported for *Thecaphora haumanii* Speg. (Piepenbring and Bauer 1995).

Mycosyringaceae is represented by a single genus, *Mycosyrinx*. Its host range is restricted to members of Vitaceae (Vánky 1996, 2012). The teliospores come in pairs. Germination, only known from *M. cissi* (DC.) G. Beck, results directly in basidiospores with a sigmoid shape (Fig. 11.3e) (Piepenbring and Bauer 1995; Vánky 1996). The basidia seem to be small or reduced, and the meiosporangium is represented by the teliospore. The fungus does not form haustoria or intracellular hyphae in host cells (Bauer et al. 1997). At maturity, soral hyphae lack septal pores (Fig. 11.5e) (Begerow et al. 2006).

Urocystidaceae comprises morphologically diverse species with coloured teliospores in flowers or leaves and stems (Fig. 11.1k, l). The genera *Flamingomyces*, *Melanustilospora*, and *Vankya* have single teliospores. The separation of the genera is based on the results of morphological or molecular data (Bauer et al. 2007;

Denchev 2003; Ershad 2000). The genus *Melanoxa* also has single teliospores, but the wall of the teliospores is multilamellate (Lutz et al. 2011). *Mundkurella* is characterized by one- to four-celled teliospores, and *Urocystis* and *Ustacystis* by teliospores that are united in balls with fertile and sterile cells (Vánky 1987, 1994, 2012). The teliospore germination within Urocystidaceae is also diverse. *Flamingomyces* germinates with a single hypha; *Mundkurella*, *Ustacystis*, and *Vankya* (Vánky 2012; Zundel 1945) germinate with phragmobasidia, whereas *Urocystis* germinates with holobasidia (Fig. 11.3d) (Ingold 1999). The members of Urocystidaceae form a yeast-like anamorph without ballistoconidia.

With the advent of molecular systematics, the evolutionary trends in Urocystidales became less obvious. Urocystidales includes **sporeball-forming as well as single-spore-bearing taxa**, and neither sporeball formation nor basidial morphology provides a clear distinction between the different lineages as in the Georgefischeriales or Exobasidiales (Bauer et al. 2001a; Begerow et al. 2002). Given the size and diversity of the group, further studies are needed to understand the ecology and evolution that resulted in morphological variation during the radiations within Urocystidales.

b) Ustilaginales

Poreless septa characterize the Ustilaginales in general (Figs. 11.5e and 11.6). Most of the species sporulate in the reproductive parts of their hosts (Fig. 11.1m–p), and teliosporogenesis occurs by disarticulation. A prominent **gelatinization of hyphal walls** usually **precedes teliospore formation** (Luttrell 1987; Mims and Snetselaar 1991; Mims et al. 1992; Snetselaar and Mims 1994; Snetselaar and Tiffany 1990). They have darkly coloured teliospores and usually germinate with four-celled phragmobasidia (Fig. 11.3a–c). Depending on the species and sometimes on the environmental conditions, **phragmobasidia vary in morphology** (Ingold 1983, 1987a, 1989a, 1989c). Previously, a basal dichotomy in Ustilaginales was accepted at the family level, i.e. Glomosporiaceae and Ustilaginaceae. The system according to Bauer et al. (1997) was based on morphological and anatomical apomorphies and suggested a subdivision into Glomosporiaceae, Mycosyringaceae, and Ustilaginaceae (including Anthracoideaceae and Websdaneaceae) (Bauer et al. 1997). However, this grouping was incongruent with molecular phylogenies favouring a dichotomy between Melanotaeniaceae and Ustilaginaceae in the Ustilaginales and Glomosporiaceae and Mycosyringaceae as part of the Urocystidales (Begerow et al. 1997). The split of Ustilaginaceae s.l. on Poales in favour of three families on different plant families suggests a host specificity of monophyletic lineages, which is not supported by most phylogenetic analyses (Begerow et al. 1997, 2000; Stoll et al. 2005). Thus, the **systematics of Ustilaginales is far from settled**, and our grouping reflects ongoing discussion. **Based on a combination of morphology**, **host specificity**, and **LSU sequence analyses the Ustilaginales are grouped into four families** (Figs. 11.6 and 11.7) (Begerow et al. 2006). Several additional, mostly monotypic, families have been proposed based on either morphological specialities or host range (Denchev 1997; Vánky 2000, 2001, 2003). For some species like *Melanopsichium* or *Dermatosorus* it can be shown that the proposed apomorphies do not provide additional systematic information (cf. Fig. 11.8), and therefore we follow the concept proposed by Begerow et al. (2006). The families of the Ustilaginales are characterized by host specificity on the family level or higher, i.e. eudicots for the Melanotaeniaceae, Anathriaceae and Restionaceae for the Websdaneaceae, Cyperaceae and Juncaceae for the Anthracoideaceae, and Poaceae for the Ustilaginaceae, thereby ignoring the fact that host jumps to distantly related hosts occurred several times, e.g. *Melanopsichium* or *Pericladium*. Vánky (2011) argued on the basis of a germination that resembles holobasidia and the isolated molecular position of *Pericladium* to establish a new family, Pericladiaceae. However, as long as a comprehensive molecular analysis presenting clear family concepts for the whole order is still lacking, we treat several genera in a preliminary state as *incertae sedis*. At the present state of knowledge, we propose the following families (Fig. 11.6).

The first family, which was excluded from Ustilaginaceae sensu Bauer et al. 1997, was Anthracoideaceae (Denchev 1997). Species of *Anthracoidea* present a unique type of two-celled basidia (Fig. 11.3c) and almost exclusively parasitize species of *Carex*. They exhibit an expanding element in their LSU sequence, which complicates their alignment with other smut species (Hendrichs et al. 2005). In molecular analyses there is no clear separation between *Anthracoidea* species and *Cintractia*-like smuts (Figs. 11.1n and 11.3b). Therefore, one family of smuts on Juncaceae and Cyperaceae was proposed (Begerow et al. 2006). In addition to the common host group, they are morphologically and ecologically similar, often presenting a whitish peridium in immature sori, which are produced in flowers or inflorescences (Fig. 11.8). Based on molecular data, members of *Anthracoidea*, *Cintractia*, *Dermatosorus*, *Farysia*, *Farysizyma*, *Heterotolyposporium*, *Leucocintractia*, *Moreaua*, *Parvulago*, *Pilocintractia*, *Planetlla*, *Portalia*, *Schizonella*, *Stegocintractia*, *Tolyposporium*, *Trichocintractia*, and *Ustanciosporium* are included (Begerow et al. 2006). Consequently, Cintractiaceae, Dermatosoraceae, and Farysiaceae (Vánky 2001) are rejected because they are interspersed in Anthracoideaceae.

Melanotaeniaceae is represented by *Melanotaenium* on eudicots (Fig. 11.1o) and *Exoteliospora* on *Osmunda*. Previous members on Poacecae have been excluded based on morphological and molecular data and are now part of the Georgefischeriales (Begerow et al. 2001). In contrast to the other three families, members of Melanotaeniaceae are characterized by simple septal pores with membrane caps and by the development of haustoria (Fig. 11.6) (Bauer et al. 1997; Begerow et al. 2006).

Ustilaginaceae comprises the large genera *Ustilago* and *Sporisorium* and several smaller genera of species previously treated as *Ustilago* or *Sporisorium*, representing a large *Ustilago–Sporisorium–Macalpinomyces* complex with more than 550 species. Except for *Eriomoeszia*, *Melanopsichium*, and *Pericladium*, all species parasitize Poaceae. *Melanopsichium pennsylvanicum* Hirschh., which occurs on Polygonaceae, is well embedded in the supported group of the Ustilaginaceae (Fig. 11.7). This indicates that jumps to distantly related hosts occasionally occur. However, no further radiations on Polygonaceae took place, which supports the important adaptation of the Ustilaginaceae to hosts of Poaceae. Several molecular studies have shown that the separation of *Ustilago* and *Sporisorium* is very difficult on the basis of hitherto used features (Stoll et al. 2003, 2005). Some genera have been proposed to accommodate species with clear apomorphies like *Eriomoeszia*, *Anomalomyces*, *Portalia*, or *Tubisorus* (Gonzales et al. 2007; Vánky 2005; Vánky and Lutz 2011; Vánky et al. 2006), but a clear structure of the group was lacking. Most recently, a four-gene phylogeny, combined with detailed studies on sorus morphology, revealed some monophyletic groups that could be excluded from the large *Ustilago–Sporisorium–Macalpinomyces* complex (McTaggart et al. 2012a, b). Based on these data, *Anthracocystis* was reestablished and *Langdonia*, *Stollia*, and *Triodiomyces* were newly described to accommodate the well-characterized monophyletic groups, together with *Ustilago* and *Sporisorium* (McTaggart et al. 2012c). Besides the host specificity of some groups, the genera are based mainly on characteristics of teliospores and sori, e.g. teliospores free or united in balls and the presence or absence of peridia, columellae, sterile cells, or sterile hyphae (see Vánky 1987, 1994). The sori of *Sporisorium* species are also covered by peridia, but these can be composed of host tissue or 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 replacing host organs, at least partially.

Websdaneaceae includes *Websdanea* and *Restiosporium*, both of which occur on Anarthriaceae and Restionaceae. This group is well supported in several molecular phylogenetic analyses (Begerow et al. 2006). Morphologically, they are very similar to members of Anthracoideaceae, but LSU sequence data support a sister group relationship with the other members of Ustilaginales on grasses and grass-like hosts (Fig. 11.7).

Based mainly on host relationships, Vánky (2001) created the Clintamraceae for *Clintamra*, Geminaginaceae for *Geminago* and Uleiellaceae for *Uleiella*. Unfortunately, molecular data are not available for these genera, and it is unclear whether these genera represent recent or ancient host jumps. Because there is no other support for these families at the moment, we treat them as *incertae sedis*, together with other genera lacking molecular data and clear morphological characteristics to place them in one of the described groups.

IV. Conclusions

The history of smut systematics dates back to the brothers Tulasne, who separated holobasidiate and phragmobasidiate groups for the first time (Tulasne and Tulasne 1847). This grouping was consistent for more than 100 years and to our knowledge was never questioned. Differences in the sugar composition of the cell wall of *Ustilago* and *Microbotryum*

yeasts implicated a separation of smuts on monocots and dicots (Prillinger et al. 1993), but subsequent data did not support this hypothesis. The discovery of **ultrastructural markers in the host–parasite interaction and septal formation provided apomorphic characters to delimit monophyletic groups** which were supported by molecular analyses (Figs. 11.6 and 11.7) (Bauer et al. 1997; Begerow et al. 1997, 2006). Thus, the analysis of two characters remains to be discussed: basidia and host specificity. Their analyses reveal novel conclusions about the evolution of Ustilaginomycotina.

A. Basidia

The evolutionary transitions to the basidium of the Ustilaginomycotina are unknown. Nevertheless, a tentative sequence can be outlined from the distribution of the basidial types among the different groups. While the Agaricomycotina are dominated by the presence of holobasidia, and the Pucciniomycotina have almost exclusively phragmobasidia, the Ustilaginomycotina are somewhat intermediate, having both types in several groups (Fig. 11.3). The monophyly of the Agaricomycotina with the Ustilaginomycotina and the group's common ancestor with the Pucciniomycotina suggest that the **plesiomorphic state of the basidium was phragmobasidiate**. In the Ustilaginomycetes and Exobasidiomycetes, however, phragmobasidia occur only in the Anthracoideaceae, Urocystidaceae, Ustilaginaceae, Tilletiariaceae, and Websdaneaceae. Except for a few species, the phragmobasidial taxa of the Ustilaginomycetes and Exobasidiomycetes are concentrated in a single monophyletic group of the Ustilaginales, whereas the holobasidial taxa are distributed throughout all orders of the Ustilaginomycetes and Exobasidiomycetes. In addition, the early-diverged lineages of the Ustilaginomycetes and Exobasidiomycetes, i.e. Melanotaeniaceae, Glomosporiaceae, Tilletiales, and Exobasidiales, are holobasidiate. This distribution of basidial types supports a holobasidiate ancestor of the Ustilaginomycetes and Exobasidiomycetes. Consequently, the **septation of the basidia in several families must be interpreted as the result of convergent evolution.** Apart from septation, the hilar appendices responsible for the active discharge of basidiospores are unevenly distributed. Though they are present in several families of the Exobasidiomycetes showing various orientations, they seem to be absent in the Ustilaginomycetes. Hence, the **gastroid basidia** of Ustilaginomycetes might represent an apomorphy of this monophyletic group.

B. Host Specificity

Following the reorganization of the Ustilaginomycotina systematics on the basis of phylogenetic data, it became evident that **most species were highly host-specific.** Moreover, **monophyletic lineages are often restricted to monophyletic host groups** (Begerow et al. 2004). As partly discussed earlier, within the Ustilaginomycotina there are evident examples of **coevolution** with angiosperm lineages (e.g. Tilletiales, Georgefischeriales, and the *Ustilago-Sporisorium* complex with Poaceae, *Graphiola* with palms, *Anthracoidea* with Cyperaceae, *Mycosyrinx* with Vitaceae, *Exobasidium* with Ericales). On the other hand, Doassansiales and *Doassansiopsis* are two excellent examples of evolution within a given ecosystem.

As a whole, the host range of Ustilaginomycotina is restricted to angiosperms, with a few exceptions on gymnosperms and ferns, which are regarded as the result of host jumps (Bauer et al. 1997; Begerow et al. 2004). Most Ustilaginomycotina members are parasites of monocots, especially members of Poaceae and Cyperaceae. This host distribution suggests that the **Ustilaginomycotina** species **may have evolved as pathogens, either on early angiosperms or on early monocots**, with subsequent jumps to eudicots. Given the relative age of the stem group of Ustilaginomycotina of at least 300 million years (Taylor and Berbee 2006), it seems most likely that ancestral lineages date back before the radiation of angiosperms. Thus, the present specificity of some lineages could be

the result of massive extinctions during evolution. In contrast, broad host ranges of some groups, e.g. the Georgefischeriales on Poaceae with a few species on Convolvulaceae and Cyperaceae, the Tilletiales on Poaceae with five species on Leguminosae, and the Ustilaginaceae on monocots with a few genera on eudicots, indicate not only that the ancestors of Ustilaginomycotina have undergone periods of parallel evolution with their hosts, but host jumps may have stimulated the evolution of a large number of taxa.

Thus, **host specificity** seen in genera like *Ustilago* and *Tilletia* on Poaceae (Stoll et al. 2005) or *Entyloma* on asterids (Begerow et al. 2002) might be a **result of adaptive radiation**. Branch lengths of molecular analyses suggest radiations in these genera, which are younger than some 100–200 million years old.

C. Evolutionary Trends

Finally, our analyses suggest the following evolutionary trends within Ustilaginomycotina:

- Cellular interactions from simple to complex forms;
- Multiple convergent evolution of intracellular fungal elements;
- Multiple convergent evolution of spore balls;
- Repeated loss of septal pores in senescent hyphae;
- Repeated loss of teliospores as propagules;
- Multiple convergent evolution of gastroid taxa;
- Repeated loss of ballistosporic mechanism;
- Repeated change of sorus location from vegetative organs to flowers;
- Multiple convergent evolution of sporulation in anthers;
- Coevolution with host groups, but also with ecosystems;
- Repeated jumps to unrelated hosts.

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