

On the evolution of smut fungi on their hosts

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The modern phylogenetic system for the Ustilaginomycetes, which integrates morphological, ecological, ultrastructural, and molecular data has revealed many previously unknown monophyletic groups. Additional studies have made the smut fungi one of the best-known groups of Basidiomycota in terms of phylogeny. Molecular data support a high degree of host specificity in most smut species, which was postulated by earlier workers based on microscopical and experimental data. The hosts of species of major smut lineages like the Ustilaginales s. str. or the Tilletiales are mainly grasses and grass-like plants, hence an early smut radiation on progenitors of monocots seems likely. After establishment on these hosts different combinations of sorting, duplication, and cospeciation events, as well as jumps, are likely to have caused the present distribution of smut fungi on their hosts. Host jumps were probably the predominant event, but apparently were often restricted to closely related hosts. In this article we discuss the present state of knowledge about the evolution of smut fungi on their hosts using examples from the genera *Entyloma*, *Exobasidium*, *Ustilago/Sporisorium*, and *Microbotryum*. Patterns where smut groups are restricted to certain host clades are common, but are not necessarily the result of cospeciation as the major speciation mode of the parasites. The available data are interpreted with respect to the theory of host-parasite coevolution and alternative approaches.

Smut fungi are one of the most important groups of plant parasites, responsible for quite dramatic yield losses in barley and other cereals (THOMAS & MENZIES 1997). They comprise more than 1500 species, their hosts being distributed over the whole system of angiosperms (BAUER, OBERWINKLER & VÁNKY 1997, BAUER et al. 2001). Typically, smuts are identified by black or brownish powdery teliospores, which served as their most important character in the past (BAUER et al. 2001). Traditionally, they were grouped in the Heterobasidiomycetes, as their basidiospores may germinate via hyphae, secondary spores, or budding cells, and most smut fungi are characterised by a saprophytic yeast stage in their life cycle (BEGEROW, BAUER & BOEKHOUT 2000).

Most species concepts for smut fungi assume that smut species infect only a few susceptible hosts or that they even are restricted to a single plant species. The results of a quantitative evaluation of the host index in VÁNKY'S (1994) monograph on European smut fungi are presented in Fig. 1. Accordingly, more than 55 % of the approx. 600 recorded smut species are specific to a single host species, more than 86 % occur on one to five hosts and more than 93 % occur on one to ten hosts, respectively. Only eleven smut species were reported to occur on more than 20 hosts (not included in Fig. 1). The resulting distribution of the number of host species per parasite species is thus strongly right-skewed

