Dr. Robert Bauer (1950–2014) in memoriam: botanist, mycologist, and electron microscopist

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Unexpectedly and tragically, Robert Bauer died September 7, 2014. He was born March 20, 1950 in Großbettlingen, Baden-Württemberg. After qualification as a metal craftsman, he decided to study biology at the University of Tübingen, where he obtained a diploma for his study “Sporenbildung bei *Coleosporium tussilaginis* (Pers.) Lév.” in 1980. He continued an experimental approach to elucidate ontogenetic and karyological features in rust fungi and finished his dissertation “Experimentell-ontogenetische und karyologische Untersuchungen an Uredinales” in 1983. Expanding such studies in related groups, Bauer became more and more interested in smuts, developed special skills for transmission electron microscopy, and successfully combined culture work on fungi with newly available techniques and organisms.

This reappraisal of Bauer’s contributions to mycology is arranged systematically and partly chronologically and includes exclusively his publications as author or coauthor. A list of these scientific publications concludes this tribute to him with the intention to unroll a scientist’s life dedicated to fungi and their hosts.

Pucciniomycotina, rust fungi, and related taxa

The nomenclature for the subdivision Pucciniomycotina of Basidiomycota was introduced by Bauer et al. (2006). It included a systematic and phylogenetic rearrangement of taxa

down to ordinal level (Fig. 1). It is a comprehensive overview that since then is called “simple-septate basidiomycetes” and was adopted by later studies of Aime et al. (2006) and Hibbett et al. (2007), of which Bauer was coauthor.

Cryptomycocolax abnormis was described by Oberwinkler and Bauer (1990) from material collected on the volcano Irazú, Costa Rica, in which the species parasitizes an ascomycete through two types of colacosomes. One of these colacosomes was described by Oberwinkler et al. (1990a) and Bauer and Oberwinkler (1991) from *Platyglea peniophorae*. The simple-pored septa of *C. abnormis* are associated with Woronin body-like structures, a characteristic, found in basidiomycetes only in one additional species, *Colacosiphon filiformis* (Kirschner et al. 2001). The interphase of nuclear division shows spindle pole bodies (SPBs) whose position, structure, and duplication are similar to those of ascomycetes. In late interphase, SPB middle pieces as in basidiomycetes are developed. These subcellular organelles support the interpretation that Cryptomycocolacomycetes range in a basal position of basidiomycetous phylogeny, a view supported by molecularly based hypotheses (Bauer et al. 2006). The apparently convergent occurrence of the colacosomes, unique mycoparasitic cell organelles in **Cryptomycocolacomycetes** and **Microbotryomycetes** was discussed by Bauer et al. (2006).

Several collections of *Mixia osmundae* from Japan were kindly provided by Junta Sugiyama for electronmicroscopic studies. Unfortunately, unambiguous stages of nuclear divisions in the *Mixia* sporangium could not be detected. Thus, it remained unsolved whether *Mixia* propagules are meiospores or conidia. However, subcellular characteristics of cell walls and SPBs indicate a basal position of *M. osmundae* in Basidiomycota, an interpretation supported by molecular data (Weiß et al. 2004a, Aime et al. 2006, Bauer et al. 2006). The order Mixiales and the class **Mixiomycetes** were introduced by Bauer et al. (2006).

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Fig. 1 Simplified phylogeny of Pucciniomycotina. The ordinal phylogeny and the listed genera are intended to serve as a guideline for the accompanying text. The genus *Bauerago*, dedicated to Robert Bauer, is a member of the Microbotryales

Ontogenetic studies in phragmobasidia of *Agaricostilbum pulcherrimum*, *Gymnosporangium clavariiforme*, *Helicogloea lagerheimii*, *Phleogena faginea*, *Platyglloe peniophorae*, and *Sphacelotheca polygona-persicariae* (Bauer and Oberwinkler 1986a) under different experimental conditions led to the conclusion that external factors, such as air, water, and water agar, strongly influence germination patterns. They can induce the formation of ballistospores, microconidia, or yeast cells. Also, hyphae with terminal appressoria can be formed. The authors concluded that with the formation of basidial cells, the meiosporangial ontogeny is terminated. **Meiosis and its SPB cycle** of *A. pulcherrimum* were studied with a transmission electron microscope (Bauer et al. 1992). Together with Spiculogloaeales, the Agaricostilbales were placed in the Agaricostilbomycetes (Bauer et al. 2006). A new anamorphic yeast, *Kurtzmanomyces insolitus*, was described by Sampaio et al. (1999b). Molecular studies (Weiß et al. 2004, Aime et al. 2006, Bauer et al. 2006, Bauer et al. 2009) confirmed a basal position of Agaricostilbomycetes within the Pucciniomycotina. Members of **Spiculogloaeales** (Bauer et al. 2006) are mycoparasites with tremelloid haustoria.

In a revision of the **gasteroid, auricularioid heterobasidiomycetes**, Oberwinkler and Bauer (1989) studied basidiocarps, hyphae, cell organelles, basidia, basidiospores, yeasts, and conidia. They also considered the available data of 5S RNAs and recognized complex subcellular structures such as **symplechosomes**, apparently synapomorphic for members of the **Atractiellales**. As a taxonomical consequence for stilboid, gasteroid taxa they proposed Agaricostilbales, Agaricostilbaceae, Pachnocybaceae, and Atractogloaeaceae.

Later, two pycnidial atractielloid basidiomycetes, the teleomorph *Basidiopycnis hyalina* and the anamorph *Proceropycnis pinicola*, were described (Oberwinkler et al. 2006). Still enigmatic is the report of atractielloid fungi as mycosymbionts in epiphytic neotropical orchids (Kottke et al. 2010).

The teleomorphic genus *Classicula* and the anamorphic *Jaculispora* were included in the **Classiculales** (Bauer et al. 2003), later raised to Classiculomycetes (Bauer et al. 2006). *Classicula fluitans* is the basidial stage of *Naiadella fluitans*. They are mycoparasites with tremelloid haustoria. In *Naohidea sebacea*, Bauer (2004) detected nanometer pores in the intracellular haustoria of this mycoparasite, and Weiß et al. (2004) supported the phylogenetic position of the **Naohideales** in the Cystobasidiomycetes by molecular data.

Occultifur internus, a mycoparasite growing in the basidiocarps of Dacrymycetes species, has tremelloid haustoria with nanometer pores and septal pores with **cystosomes** (Bauer 2004). Sampaio et al. (1999a) found *Occultifur externus*, developing basidial stages under laboratory conditions, and the affiliation to **Cystobasidiales** could be proven.

Meiosis, spindle pole cycle, and septal pores of *Herpobasidium filicinum*, **Platyglloeales** were studied transmission electron microscopically by Bauer and Oberwinkler (1994).

Spectacular results were derived from intensive studies in **Tuberculina** spp., **Helicobasidiales**, turning out to be anamorphs of *Helicobasidium* (Lutz et al. 2004a), and mycoparasites of the comparatively closely related rust fungi. The identity of *Tuberculina* spp. and *Helicobasidium* spp. was

proven experimentally (Lutz et al. 2004b). Bauer et al. (2004) studied *Tuberculina persicina* parasitizing *Puccinia silvatica* and *Tranzschelia pruni-spinosae*. They found micrometer fusion channels between parasite and host cells, apparently allowing transfer of cell organelles. Experiments to elucidate host specificities revealed a high diversity of the mycoparasites (Lutz et al. 2004c). Two reports about “**The double life of a fungus**” were published by the German Research Council, DFG (Lutz et al. 2006, 2007).

The ontogeny of basidia and nuclear changes in **Pucciniales** were studied by Bauer (1983, 1986, 1987) in experimental approaches. Axenic cultures of *Coleosporium* (Deml et al. 1982a, b) later turned out to be yeast contaminations. Bauer found that **secondary spore formation** depends on the monokaryotic stage. Nuclear degeneration during **ballistospore production** was investigated in *Cronartium asclepiadeum* (Bauer and Oberwinkler 1988). The unusual case of **gasteroid basidia** in *Ochropsora ariae* was studied in vivo and in vitro (Bauer and Oberwinkler 1986b), and the ultrastructure of the host-parasite interface in the fern rusts *Milesia*, *Uredinopsis*, and *Hyalopsora* was analysed (Berndt et al. 1994). The morphology and phylogenetics of *Stomatisora*, including *Stomatisora psychotriicola* sp. nov., were investigated by Wood et al. (2014).

Comprehensive transmission electron microscopic studies resulted in data that allowed reconstructing meiosis and SPB cycle in *Pachnocybe ferruginea* (Bauer and Oberwinkler 1990c), a species that was raised in taxonomic ranks to Pachnocybaceae (Oberwinkler and Bauer 1989) and **Pachnocybales** (Bauer et al. 2006).

The detection of auricularioid basidia with sessile, tetradiate basidiospores in the pycnidoid *Hyalopycnis blepharistoma* led to the introduction of *Heterogastridium pycnidioideum* (Oberwinkler et al. 1990b). All members of the **Heterogastridiales** are mycoparasites and possess colacosomes (Bauer 2004), as described by Oberwinkler et al. (1990a) and Bauer and Oberwinkler (1991) from *Platyglaea peniophorae*, then named *Colacogloea peniophorae*. A second species, *C. bisporea*, parasitizing *Tubulicrinis* sp., with collections from Denmark and Taiwan, was described by Oberwinkler et al. (1999). A new species, vectored by bark beetles on conifers was isolated, cultivated, and described in a new genus, *Atractocolax pulvinatus* (Kirschner et al. 1999).

On the basis of nutritional, ultrastructural, and molecular data, Sampaio et al. (2003) proposed the new orders Leucosporidiales and Sporidiobolales, the new genus *Leucosporidiella* and the new species *Leucosporidium golubevii*.

A smut collected in Madeira on *Polygonum persicaria* was described as the new species *Sphacelotheca polygoni-persicariae* (Deml et al. 1985) and considered to be related to those of the genus *Microbotryum* because of their obvious

similarities. – In a comparative ultrastructural study of *Sphacelotheca polygoni-serrulati* and *Ustilago* spp., Bauer et al. (1989) realised that hyphal septa of these false and true smuts differ markedly. In *Ustilago*, the septal ingrowth stops, leaving a central pore, while in *S. polygoni-serrulati*, septal pores could not be found. Meiosis and SPB cycle of this species were studied by Bauer et al. (1991), and that of *Microbotryum violaceum* by Berbee et al. (1990), and compared with the corresponding features of *Ustilago maydis* and *Sphacelotheca polygoni-serrulati*. Analysing cell wall carbohydrates, Prillinger et al. (1993) succeeded in separating *Ustilago* s. str., *Sporisorium*, *Entyloma*, and *Melanotaenium* from *Microbotryum* and *Sphacelotheca*, later transferred to their own order, **Microbotryales** (Bauer et al. 1997). The genus **Bauerago**, introduced for *Ustilago* species parasitizing *Cyperus*, *Juncus*, and *Luzula* hosts, could be verified subsequently by molecular analyses (Bauer et al. 2006). Also, *Fulvisporium* is a genus in the Microbotryales (Vánky et al. 1997). A well illustrated life cycle of *Microbotryum lychnidis-dioicae* on *Silene latifolia* was published by Schäfer et al. (2010).

The unique basidiomycetous parasite *Kriegeria eriophori*, only found in scattered regions and occurring in aerenchymas of *Scirpus*, was studied intensively light and electron microscopically as well as molecularly (Bauer et al. 2006). Multi-pored hyphal septa were detected, unique at that time for Basidiomycota, but later also found in *Bartheletia paradoxa* (see below).

Ustilaginomycotina, true smut fungi

In the context of our research preferences, smut fungi became the main objects of Robert Bauer, to be studied with a transmission electron microscope intensively and comprehensively since the end of the 1980s. In addition, it is important to mention here that many controversial discussions were going on in our teaching and lab programmes about host dependencies of specialised parasitic fungi in general, but with a main focus on rusts and smuts. It was already well understood that Pucciniales passed through a close coevolutionary history with their host plants. In contrast, Ustilaginales were generally assumed to lack such traits, and species-rich genera with broadly spreading host ranges, like *Urocystis* and *Ustilago*, was considered convincing evidence. However, when it became clear that, for example, *Exobasidium* and *Graphiola* belong to the smut relationship, and the heterogeneity of *Ustilago* was elucidated step by step in our group, the attitude switched completely. Very quickly, smuts underwent a remarkable series of taxonomic reappraisals.

For the convenience of the reader, the phylogeny within the class (Fig. 2), as published by Bauer et al. (1997), is used here as guideline for the following text. The morphological and ultrastructural characters studied before, and interpreted

Fig. 2 Systematic arrangement and phylogeny of the Ustilaginomycetes as proposed by Bauer et al. (1997). (1) Interaction with primary interactive vesicles – without such vesicles. (2) Membranous pore caps or bands – without these structures. (3) Dolipores – simple pores. (4) Haustoria – intercellular hyphae. (5) Enlarged interaction zones – local interaction zones. (6) Haustoria – intercellular hyphae. (7) Loss of septal pores – simple pores. (8) Septal pores with membranous bands – without membranous bands. (9) Basidia reduced to teliospores – teliospores are probasidia. (10) Intracellular hyphae – intercellular hyphae. (11) Ballistospore basidiospores – repeated loss of ballisto-basidiospores.

comparatively, were applied in a cladistic approach to propose a new systematic arrangement with the intention of a phylogenetic concept. After step by step approval of this phylogeny through newly coming up molecular hypotheses (Begerow et al. 1997, Bauer et al. 1998, Begerow et al. 2006), the class was taxonomically raised to subdivisional level (Bauer et al. 2006). Because there were no justifying data to exclude smuts, such as “Ustomycota”, from Basidiomycota, Bauer and Oberwinkler (1997) rejected this proposal rigorously. The new data on smuts accumulated since then were summarised by Bauer et al. (2001a) and accepted in following generalizing treatments (Hibbett et al. 2007). Teliospore development, ultrastructure, liberation, and dispersal in Ustilaginales and Tilletiales as well as in *Microbotryum*, were studied in 120 species of 37 genera by Piepenbring et al. (1998a-c). The cellular and subcellular ustilaginomycete-host interactions were outlined by Bauer and Oberwinkler (2004). Based on

(12) Loss of septal pores – simple pores. (13) Dolipores – simple pores. (14) Loss of teliospores – teliospores. (15) Interaction apparatus – primary interactive vesicles. (16) Complex interaction apparatus – simple interaction ring. (17) Interaction apparatus with cytoplasmic compartments – without cytoplasmic compartments. (18) Haustoria – intercellular hyphae. (19) Interaction ring – without interaction ring. (20) Basidia in chains – not in chains. (21) Clamped haustoria – intercellular hyphae. (22) Unclamped haustoria – intercellular hyphae. The text follows the scheme from left to right

sequence data, yeasts of smuts could be integrated in the new phylogenetic system of Begerow et al. (2000). Bauer contributed also to assembling the fungal tree of life (Celio et al. 2006).

Traditionally, *Entorrhiza* species, parasitizing root cells of Cyperaceae and Juncaceae, were classified as smuts (Fig. 2). They were studied in our institute intensively. When maturing, the intracellular grown smut spores are internally divided into four cells, each of them producing a germination hypha (Bauer et al. 2001a). Using ultrastructural and molecular data, Bauer et al. (1997) and Begerow et al. (1997) classified the **Entorrhizales** as sister to the remaining smuts. Entorrhizaceae and Entorrhizales were described by Bauer and Oberwinkler (in Bauer et al. 1997). Vánky et al. (2007) transferred the South African *Entorrhiza calospora*, growing in roots of diverse species of Aizoaceae, Molluginaceae, and Portulacaceae, and also producing galls in the newly proposed

genus *Talbotiomyces*. Because of lacking ontogenetic, ultrastructural, and molecular data, a proper systematic treatment was impossible, but recently available sequences indicate the relationship with *Entorrhiza* (Riess et al. 2015). Simultaneously, the results of a five-gene phylogeny were taken for granted to propose the **Entorrhizomycota**, and to suggest that the teliospore tetrads of *Entorrhiza* represent the prototype of the dikaryan meiosporangium (Bauer et al. 2015).

In the new phylogenetic system of smut fungi (Bauer et al. 1997), Bauer and Oberwinkler proposed the **Urocystales** and the **Mycosyringaceae**. Bauer et al. (1995a) studied the cellular interaction of *Ustacystis waldsteiniae* and also investigated its septal pores (Bauer et al. 1995b). For *Mycosyrinx nonveilleri*, Vánky and Bauer (in Vánky 1996, not cited) introduced the new genus *Geminago*. Unusual basidial ontogenies in the Costa Rican smuts *Doassansiopsis limnochardis*, *Mycosyrinx cissi*, and *Thecaphora haumani* were found by Piepenbring and Bauer (1995). *Melanotaenium indicum*, parasitizing *Ischaemum indicum* was transferred into the new genus *Phragmotenium* by Bauer et al. (2001b). The marine *Ruppia maritima* can be infected by a smut, originally described as *Melanotaenium ruppiae*, but recognized as a separate genus, *Flamingomyces*, by Bauer et al. (2007). Another new genus, *Antherospora*, was proposed for the anther smut in *Muscari* and *Scilla* species, *Ustilago vaillantii* (Bauer et al. 2008b). The new family, **Floromycetaceae**, was introduced to accommodate this genus and *Floromyces anemarrhenae* (*Thecaphora* a.), growing in *Anemarrhena asphodeloides*, **Agavaceae**, (Vánky et al. 2008b). A revision of *Thecaphora* (**Glomosporiaceae**) showed that *Glomosporium*, *Kochmania* and *Tothiella* had to be synonymized with *Thecaphora* (Vánky et al. 2008a). For *Melanotaenium oxalidis*, known from the North American *Oxalis oregana*, a new genus, *Melanoxa*, was erected (Lutz et al. 2011).

Ustilaginales *Ustilago esculenta* causes hypertrophy in its host *Zizania latifolia* and produces edible tissues, highly esteemed in East Asia. Smut spore germination, SPBs, septal pores, and ultrastructural features of host interaction were studied by Nagler et al. (1990). They recognized the natural relationship with *Ustilago* s. str. and concluded that its own genus, *Yenia*, is justified. Bauer et al. (1999a) analysed morphological and ultrastructural characters of *Ustilago osmundae* on *Osmunda regalis* and *O. cinnamomea*. They recognized high structural conformity with the **Melanotaeniaceae**. Consequently, the smut on the royal fern was transferred into its own genus, *Exoteliospora*, and *Ustilago marina*, growing on the marine *Eleocharis parvula*, also deserved to be excluded from *Ustilago*, and was, therefore, generically renamed as *Parvulago* by Bauer et al. (2007). The female flowers of *Carex* and of other cyperaceous plants infected by *Anthracoidea* species, were long lasting objects of

intensive collecting and studies in our group (Hendrichs et al. 2005), which required also partial re-investigations of the main host itself (Hendrichs et al. 2004). Prillinger et al. (2009) reported the new *Schizonella caricis-atratae*, growing on *Carex atrata* in Austria. In a predominantly molecularly based phylogenetic approach of the **Ustilaginomycotina**, Begerow et al. (2006) confirmed the **Anthracoideaceae**, **Ustilaginaceae**, and **Websdaneaceae**, but rejected the **Cintractiaceae**, **Dermatosoraceae**, **Melanopsichiaceae**, and **Farysiaceae**.

Georgefischeriales Ultrastructural features of species in this order are local interaction zones between parasite and host and the lack of septal pores (Bauer et al. 1997). Additionally, newly available sequence data confirmed the taxon (Begerow et al. 1997). An enlarged sampling enabled Bauer et al. (2001b) to discriminate three families, **Eballistraceae**, **Georgefischeriaceae**, and **Tilletiariaceae**. *Eballistra* and *Phragmotenium* were proposed as new genera. A restudy of *Entyloma ossifragi* on *Narthecium ossifragum* (Bauer et al. 2005) provided evidence to include this smut in the **Georgefischeriales**. The new genus *Gjaerumia* and the new family **Gjaerumiaceae** were based on this species.

Tilletiales, bunts Vánky and Bauer (1992) introduced the new genus *Conidiosporomyces*, characterized by Y-shaped conidia in the smut spore layers. A smut occurring on the grass *Ortachne* (*Muhlenbergia*) *erectifolia* in the Cordillera de Mérida, Venezuela, was described by Vánky and Bauer (1995) as *Oberwinkleria anulata*. In this species, smut spores are the meiosporangia themselves, and consequently germinate with basidiospores. For *Tilletia hyalospora*, growing on *Nassella* and *Stipa* species, Vánky and Bauer (1996) proposed the genus *Ingoldiomyces*, which produces ballisto-conidia and ballisto-basidiospores. Black spots on *Phaseolus* leaves are caused by fungi known previously as *Entyloma vignae* or *Protomycopsis patelii*. Piepenbring and Bauer (1997) realised that both names cover the same parasite, which was found to be a member of the **Tilletiales**, and which was renamed as *Erratomyces*.

Microstromatales Members of this order have gasteroid holobasidia without probasidia, i.e. without smutspores. Local interaction zones between parasites and hosts were recognized as synapomorphies by Bauer et al. (1997) who also introduced the ordinal name. A revision of *Muribasidiospora* (Begerow et al. 2001, 2002b) resulted in the separation of *M. triumfetticola* from *M. indica* and the introduction of the new genus *Volvocisporium*. The latter belongs to the **Microstromatales**, but *M. indica* remains with the **Exobasidiales**. De Beer et al. (2006) described the **Quambalariaceae** for anamorphic fungal parasites of

Eucalyptus and *Corymbia* and included them in the Microstromatales according to sequence data.

Entylomatales Bauer and Oberwinkler (in Bauer et al. 1997) proposed the Entylomataceae and Entylomatales, characterized as smuts with teliospores, simple hyphal septa, and interaction apparatus with homogeneous contents.

Doassansiales The order was described by Bauer and Oberwinkler (in Bauer et al. 1997), and besides Doassansiaceae, an additional family, Rhamphosporaceae, was introduced. Host parasite interactions were found to depend on subcellular complex structures. Sequence data supported the new classification (Begerow et al. 1997). *Doassinga callitrichis* is specialised on *Callitriche* hosts (Vánky et al. 1998). Two smut species were known from *Selaginella* hosts, *Melanotaenium oreophilum* and *M. selaginellae*. A restudy (Bauer et al. 1999b) delivered facts of Doassansiales relationship, and consequently, the new genus *Melaniella* and the family Melaniellaceae were proposed.

Graphiolales, the palm smuts Until 1982 the taxonomic position of *Graphiola* was unsettled. However, our own data unambiguously showed basidiomycetous relationship. This was strongly supported by subsequently available interaction structures (Bauer et al. 1997), and sequencing results (Begerow et al. 1997, Bauer et al. 2006). The latter favoured the insertion of Graphiolales in Exobasidiales.

Exobasidiales In addition to the very distinctive meiosporangial characters of incurved basidiospore development, parasite host interaction is an important synapomorphy of the order (Bauer et al. 1997). It was mentioned already with the Microstromatales that only *Muribasidiospora indica* belongs to the Exobasidiales, but not *M. triumfeticola* (Begerow et al. 2001). Begerow et al. (2002a, 2014) preferred a broad concept of Exobasidiales, including the Exobasidiaceae, predominantly infecting Ericaceae, and the Cryptobasidiaceae preferring Lauraceae, Brachybasidiaceae on Poaceae and Graphiolaceae on palms. The Cryptobasidiaceae of tropical Central and South America with the genera *Botryoconis*, *Clinoconidium*, and *Drepanoconis* were treated by Hendrichs et al. (2003) morphologically and ultrastructurally.

Ceraceosorales Begerow et al. (2006) described the order with species having intracellular hyphae in hosts and local interaction zones. Two sterigmate basidia emerge through stomata. Based on sequence data, *Ceraceosorus* is closely related to *Entyloma*.

Agaricomycotina

To match taxonomy with phylogeny, Bauer et al. (2006) erected the subdivision Agaricomycotina whose members are said to share type B of the 5S RNA secondary structure, and to contain predominantly glucose and xylose in the cell walls.

Bartheletiaceae A most remarkable rediscovery in recent years was *Bartheletia paradoxa*, inhabiting leaves of *Ginkgo biloba* (Scheuer et al. 2008). As mentioned above, the species has multipored hyphal septa, thus reminiscent of *Kriegeria eriophori*. However, even the very careful integrative study could not solve its definite phylogenetic position.

The basal class of Agaricomycotina, **Tremellomycetes**, comprising **Tremellales**, Filobasidiales, and Cystofilobasidiales (Fig. 3), was recently reviewed by Weiß et al. (2014). A yeast, isolated from *Asterophora lycoperdoides*, developed a hyphal phase in culture. The septal pores of these hyphae were of the *Tremella* type (Laaser et al. 1988). The mycoparasitic interaction of *Tetragoniomyces uliginosus* with *Rhizoctonia* sp. was studied transmission electron microscopically by Bauer and Oberwinkler (1990a). A direct cytoplasm-cytoplasm connection through a single nanometer pore at the haustorial hyphal tip could be detected. The pore membrane appeared continuous with the plasma membrane of both cells. An intrahymenial mycoparasite, *Phragmoxenidium mycophilum*, was found in *Uthatabasidium fusisporum* (Oberwinkler et al. 1990c). Because tremelloid parenthesomes were lacking at the dolipores, the species and the family Phragmoxenidiaceae were assigned to Tremellales only tentatively. The mycoparasitic interactions of *Tremella mesenterica*, *T. encephala*, and *T. mycophaga* were analysed by Zugmaier et al. (1994) light and transmission electron microscopically. They found ultrastructural features similar to those in *Tetragoniomyces*. Also, subcellular characteristics were used by Kwon-Chung et al. (1995) to discriminate between *Filobasidiella depauperata* and *F. neoformans*. With an integrative approach, Sampaio et al. (2002) characterized two new genera, *Bulleribasidium* and *Papiliotrema*, and three new species, *Bulleribasidium oberjochense*, *Papiliotrema bandonii*, and *Fibulobasidium murrhardtense*.

Filobasidiales With the help of culture experiments, Oberwinkler et al. (1984) were successful to elucidate the life history of *Christiansenia pallida*, a mycoparasite on *Phanerochaete cremea*. The tremelloid nanometer pore interaction was found again (Bauer and Oberwinkler 1990b).

Cystofilobasidiales Crossing compatible yeast strains of *Cryptococcus ferigula* resulted in a teleomorph that was described as *Cystofilobasidium ferigula* by Sampaio et al.

Fig. 3 Systematic arrangement and part of the phylogeny of Agaricomycotina with a selection of genera discussed from below upwards in the following text. Tree compiled after Scheuer et al. (2008) and Hibbett et al. (2014), and strongly modified

(2001). The genome of the basal agaricomycete *Xanthophyllomyces dendrorhous* provided insights into the organization of its acetyl-CoA derived pathways (Sharma et al. 2015).

Dacrymycetales The uniform *Dacrymyces* dolipore with continuous parenthesomes was used for detailed ultrastructural comparison with similar pore types of the Sebaciniales, Auriculariales, and Tulasnellales (unpublished).

Sebaciniales *Sebacina* spp., sampled from European *Picea abies*, *Fagus sylvatica*, *Quercus robur*, *Carpinus betulus*, *Tilia* sp., and others, were identified molecularly and additionally characterised by dolipores with continuous parenthesomes (Selosse et al. 2002, Urban et al. 2003). Weiß et al. (2011) considered the previously overlooked sebacinean endophytes of ubiquitous distribution. The phylogenetic diversity and structure of sebacineoid fungi, associated with plant communities along an altitudinal gradient, was analysed by Garnica et al. (2012). The state of knowledge on Sebaciniales was summarized by Oberwinkler et al. (2013a). The authors concluded that “it appears to be extremely difficult with the techniques available today to gain a better understanding of this enigmatic diversity”. This topic was specifically well investigated at the regional scale in *Sebacina epigaea* and *S. incrustans* (Riess et al. 2013). Extensive collections of these species and of additional ones from genera, belonging to former “Sebaciniales group A”, then named Sebacinaceae s. str., were used to find out whether the high molecular diversity can be verified by micromorphological characteristics (Oberwinkler et al. 2014). Herbaceous plants in agricultural and grassland ecosystems were found to be

dominated by *Serendipita herbamans* sp. nov. (Riess et al. 2014).

Tulasnellales The Aneuraceae with their tulasnelloid mycobionts were considered a model for early steps in fungal symbiosis with terrestrial plants (Krause et al. 2011).

Cantharellales A taxonomic re-evaluation of the *Ceratobasidium-Rhizoctonia* complex was carried out by Oberwinkler et al. (2013b). A new species, *Rhizoctonia butinii*, attacking spruce, was described.

Occasionally, and for comparative purposes, Robert Bauer studied septal pores of mushrooms, e.g. in *Sphaerobolus* of the Geastrales, and *Schizophyllum* of the Agaricales (Hibbett et al. 2014).

Ascomycota

In the course of intensive investigations in smuts, Nagler et al. (1989) studied *Schroeteria delastrina* and *S. poeltii* and found that their septal pores have Woronin bodies, that SPBs are ascomycetes-like, and that karyogamy and meiosis are lacking in sporulating germination hyphae. These results identified *Schroeteria* as an ascomycete. – *Cymadothea trifolii* is a parasite in the leaves of *Trifolium repens*. In a transmission electron microscopic study of freeze substituted material, Simon et al. (2004) found interaction apparatus with long cisternae in the hyphae. The adjacent host cells are forced to let their plasma membranes invaginate into the parasite cells as bubbles that finally are connected with fungal interaction apparatus via tubular structures. Immunochemical tests provided

evidence that *Cymadothea* degrades pectins, but not cellulose and xyloglucan (Simon et al. 2005a). Also, the vegetative life-cycle of the clover pathogen was clarified by Simon et al. (2005b). *Mycosphaerella podagrariae*, a necrotrophic phytopathogen, produces another special cellular interaction system of electron dense appositions with its host *Aegopodium podagraria* (Simon et al. 2009). The interaction apparatus of *Asteridiella callista*, Meliolaceae, growing on *Stachytarpheta mutabilis*, was electron microscopically analysed by Rodríguez Justavino et al. (2014). They found a cisternal interaction apparatus, surrounded by a membrane in a continuum with the fungal plasma membrane, deposition of material at the host cytoplasmic membrane, an encasement of the infection area, and a final degeneration.

Bauer contributed also to broader studies dealing with the **phylogeny and systematics of fungi**, with special reference to Ascomycota and Basidiomycota, and their yeasts (Prillinger 1996, 2002).

Concluding remarks

Robert Bauer's 120 publications were concisely reviewed here to provide an insight in his scientific work. He focused decidedly on ultrastructural features of plant parasites, especially basidiomycetes, and their cellular and subcellular interactions with the hosts. The huge amount of data, accumulated over the years, were a challenge to use them for comparative analyses, with the aim to deduce phylogenetic trends for the fungi involved. The upcoming flood of molecular data did not overshadow his work. In contrast, there was a welcome chance to verify hypotheses that were exclusively based on structural characters.

During the few last years, Robert worked on several manuscripts at the same time. He concentrated on his most important, not yet published results. This task was recognized by the German Research Council, DFG, who supported this attempt that, unfortunately, could not be finished by him.

I met Robert first when he was a student of biology at our university, supervised his diploma and doctoral theses, and accompanied his academic and scientific career over 30 years. He was a vital, reliable, friendly, and at times humorous member of our former mycology group, qualities that had a very positive influence on our many students in biology for a long time.

His colleagues, worldwide, will respectfully perpetuate his memory.

Chronological list of Robert Bauer's publications

The development of research preferences, availability of new methods, and cooperative constellations can be perceived from this arrangement in a time sequence.

1980

Bauer R (1980) Sporenbildung bei *Coleosporium tussilaginis* (Pers.) Lév. Diplomarbeit, Universität Tübingen

1982

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Deml G, Bauer R, Oberwinkler F (1982b) Axenic cultures of *Coleosporium tussilaginis* (Uredinales). I. Isolation, identification and characterization of the cultures. Phytopath. Z. 104:39-45

1983

Bauer R (1983) Experimentell-ontogenetische und karyologische Untersuchungen an Uredinales. Dissertation Universität Tübingen

1984

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1985

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1986

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Bauer R, Oberwinkler F (1986b) Experimentell-ontogenetische und karyologische Untersuchungen an *Ochropsora ariae* (Fuck.) Ramsb. Z Mykol 52:271-275

1987

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1988

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1990

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Bauer R, Oberwinkler F (1990b) Haustoria of the mycoparasitic heterobasidiomycete *Christiansenia pallida*. Cytologia 55: 419-424

Bauer R, Oberwinkler F (1990c) Meiosis, spindle pole body cycle and taxonomy of the heterobasidiomycete *Pachnocybe ferruginea*. Plant Syst Evol 172:241-261

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