Evolutionary trends in Basidiomycota

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Abstract: Basidiomycota belong to the crown group of fungi. The diversity of cellular constructions in hyphal systems and basidiocarps is the expression of a long evolutionary history. As heterotrophic Eukaryotes these fungi developed substrate dependencies of enormous ecological importance, especially in forest ecosystems.

The name „fungi" does not refer to a monophyletic group within the heterotrophic eukaryotes. We will have a brief look on the Eumycota, the Chitin Fungi as a monophylum and their successful evolution together with land plants. The crown group of these fungi are dikaryota of various dimensions and of special importance in Basidiomycota. Evolutionarily, early life strategies were also dimorphic ontogenies, comprising yeast and hyphal stages as successful adaptations for newly accessible habitats. Also hyphal systems and basidiocarps have undergone considerable changes during evolution under responding environmental conditions. Most basidiomycetous fungi developed strategies for optimizing sexual reproduction by more complex basidiocarps, thus allowing new dimensions in basidiospore production. This evolution was not a single one, it occurred several times convergently. To realize and to confirm such evolutionary trends, monophyletic groups have to be analyzed. Traditionally, such work has been done with comparative morphology, however, molecular techniques took over rapidly and are dominating now this kind of research. – The obligate dependency upon various substrates is manifold in fungi and led to considerable switches in basidiomycetous fungi. It appears most likely that ancestral groups were mycoparasites, some of which still exist and display different interaction regimes. Further on, parasites on plants were following and expanding rapidly on newly available substrates in land plants. Remarkable coevolutionary trends could be reconstructed even by comparative examination of extant groups, as rust and smut fungi, and unexpected convergent evolutionary developments as „false" and „true" smuts became obvious. When forest ecosystems evolved, fungi became the most effective wood decomposers, and Basidiomycota were heavily involved in wood decay, starting with white rot and switching to brown rot several times, and continuing to decompose lignin in specific successions. – Basidiomycota play a very important role in symbiotic systems with plants. Extant examples of liverwort associations may indicate the very early establishment of basidiomycote interactions with ancestors of land plants long before vascular plants evolved. Our knowledge is very restricted for understanding the switches of basidiomycetous fungi to roots of seed plants, replacing arbuscular mycorrhizae that most likely were present in hosts like the Pinaceae, Fagales, Ericales, Orchidaceae, and others. In symbiotic systems like these, the replacement of previous mycobionts by new ones must be considered also as advantageous for the autotrophic partners. Historically, mycorrhiza research has been heavily stimulated by studies on phenomena of the „new forest decline" in Central Europe, and expanded explosively when molecular techniques became available. – In comparison with Ascolichens, Basidiolichens are rare, but diverse in fungal-algal interactions. They evolved convergently at least four times. Animal associations of Basidiomycota could not be treated in this article.

Zusammenfassung: Basidiomyceten sind die am höchsten evolvierten echten Pilze. Die Vielfalt ihrer zellulären und makroskopischen Baupläne läßt Rückschlüsse auf eine lange Evolutionsgeschichte zu. Als heterotrophe Eukaryonten haben diese Pilze Substratbindungen entwickelt, die von sehr großer ökologischer Bedeutung für die Funktionsfähigkeit von Landökosystemen, insbesondere von Wäldern, sind.

Einleitend wird die Evolution der Eukaryonten angesprochen und dabei erläutert, dass unter der Bezeichnung „Pilze" nicht verwandte, heterotrophe Eukaryonten zusammengefasst werden. Die Evolution der echten Pilze, auch Chitinpilze genannt, kann als eine sehr erfolgreiche Anpassung an das Landleben verstanden werden. Bei den am höchsten evolvierten Pilzen ist die Dikaryophase entstanden, die bei Basidiomyceten zum dominierenden Lebensprinzip wurde. Die Bedeutung von dimorphen Pilzen, die Hefen- und Hyphenphasen durchlaufen, wird im evolutiven Kontext der Eroberung von Landhabitaten gesehen. Auch die Veränderungen von Hyphensystemen in Fruchtkörpern sind zumeist als erfolgreiche Anpassungen an neu entstandene Lebensräume zu deuten. Für die meisten Basidiomyceten trifft eine evolutiv selektierte Optimierung der sexuellen Fortpflanzung zu. Diese wurde

durch zunehmend komplexere Fruchtkörper erreicht, die enorme Steigerungsraten der quantitativen Produktion von Basidiosporen ermöglichten. Diese Evolutionsstrategien sind mehrfach konvergent abgelaufen, haben aber immer wieder zu täuschend ähnlichen Bauplänen und Funktionsmustern geführt. Um dies zu verstehen, ist es unverzichtbar, gesicherte Abstammungsgemeinschaften, Monophyla, zu analysieren. Dies wurde traditionell vergleichend morphologisch versucht, ist aber durch molekulare Methoden in kürzester Zeit überholt worden. – Die obligate Bindung von Pilzen an unterschiedliche Substrate durchzieht ihre Evolution wie ein roter Faden. Es gibt hinreichend Evidenzen, dass ursprüngliche Basidiomyceten Mykoparasiten waren und als solche, wenigstens teilweise, erhalten geblieben sind. Es folgten die Pflanzenparasiten mit enormen, koevolutiv gesteuerten Radiationen, besonders bei Rost- und Brandpilzen. Dabei sind geradezu unglaubliche Konvergenzen entstanden, wie es das Beispiel der „falschen" und „echten" Brandpilze verdeutlicht. Mit der erdgeschichtlichen Entstehung von Wald-Klimaxvegetationen wurde für Basidiomyceten auch das neue Substrat Holz verfügbar. Erneut ist in konvergent evolvierten Entwicklungslinien dieser Pilze der Holzabbau von der Weiß- zur Braunfäule und zu hoch differenzierten Sukzessionsketten der Ligninverwertung erfolgt. – Schließlich haben Basidiomyceten mehrfach konvergent die Wege der Symbiosen beschritten. Wie heutige Vergesellschaftungen von Basidiomyceten mit thallosen Lebermoosen andeuten können, sind diese Pilze vielleicht schon vor der Entstehung der Gefäßpflanzen für symbiontische Interaktionen verfügbar gewesen. Die Besiedelung der Wurzeln von Samenpflanzen, das Verdrängen arbuskulärer Mykorrhizen und das Etablieren neuartiger, obligater Mykorrhizierungen bei Kieferngewächsen, den Buchen-Verwandten und weiteren Gehölzgruppen sowie die Orchideen-Mykorrhizen und diejenigen der Heidekraut-Verwandtschaft, belegen die Erfolgsstrategie der Basidiomyceten. Dies ist nicht nur vorteilhaft für die Pilzpartner, sondern offensichtlich auch eine Optimierung der Nährstoffversorgung der betroffenen Pflanzen. Wissenschaftsgeschichtlich interessant ist, wie die Suche nach den Ursachen neuartiger Waldschäden und ihrer Auswirkungen die Mykorrhizaforschung beflügelte und wie in sehr kurzer Zeit dieser Forschungzweig mit molekularen Methoden expandierte. – Erstaunlich ist, dass im Gegensatz zu den Ascomyceten, Basidiomyceten den Weg der Lichenisierung nur zögerlich beschritten haben. Die wenigen heute bekannten Basidiolichenen belegen aber immerhin die mehrfach konvergente Entstehung dieser Flechten, die nur aus abgeleiteten Basidiomyceten entstanden sind. – In diesem Artikel konnten die Tier-Assoziationen der Basidiomycota nicht berücksichtigt werden.

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INTRODUCTION

A common traditional circumscription of fungi is „eukaryotic heterotrophs with a stationary growth in most cases". In fact, in many textbooks, including those for academic uses, downy mildews, slime molds and labyrinthuloids are treated besides the main bulk of „true fungi". Already DE BARY (1884) called Myxomycetes „Mycetozoa" in his famous book „Vergleichende Morphologie und Biologie der Pilze, Mycetozoen und Bacterien", thus very clearly refering to their behaviour as amoebae. He also illustrated very precisely the different flagellates of *Phytophthora* and chytrids. When unicellular Eukaryotes were compared structurally and functionally, it turned out that the number of flagellae, their outer appearance, and the swimming direction is of utmost importance in separating the very big eukaryotic relationships. It became clear that Heterokonts with tinsel- and whip-like flagellae are related and should be separated from Opisthokonts with a single posterior flagellum, as in animals and lower fungi. These data were available in premolecular times and adequate classifiction schemes did exist. Nowadays, phylogenetic studies are based on molecular data, favourably complemented by additional features (Fig. 1).
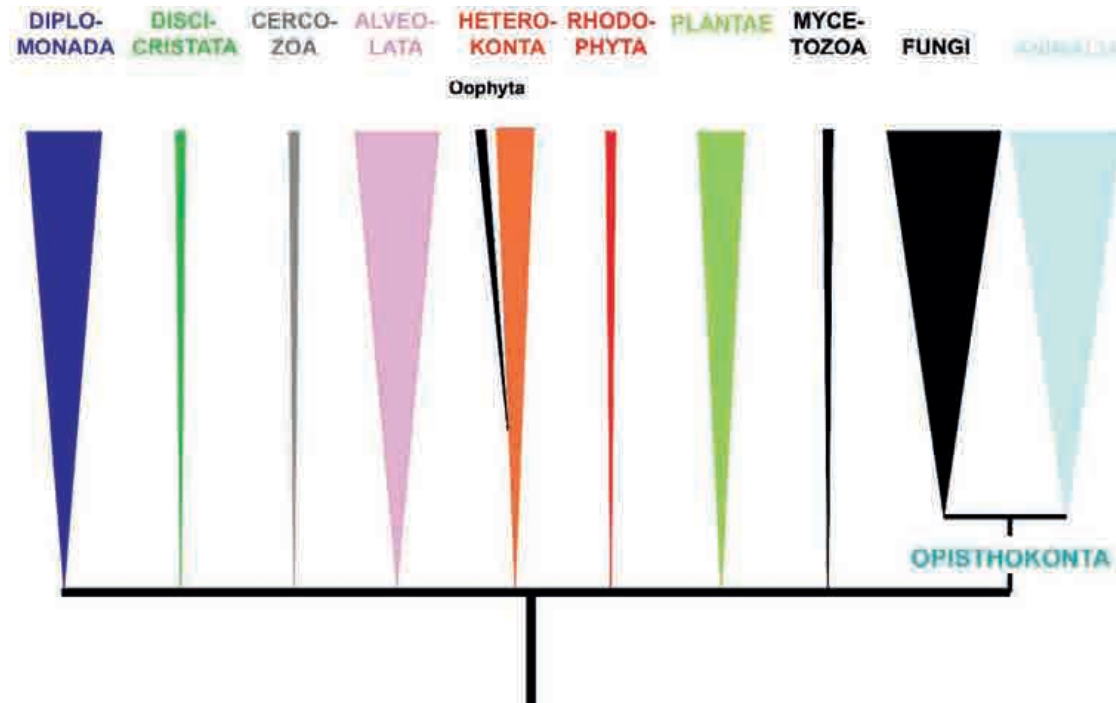
Fig. 1: A simplified scheme for the phylogeny of Eukaryotes based on recent hypotheses of various authors (see text). The main three fungal groups (black triangles) are considered here. Their independent origin is illustrated. The true fungi, also called Chitin Fungi, represent a sister group of the animals, a monophylum charaterized by opisthokontic flagellates. The slimemolds, Mycetozoa (Myxomycetes) belong into the amoebozoic relationship. False fungi, called Oomycetes by mycologists, are derived from Heterokonts, now called Stramenopiles. Compiled by F. OBERWINKLER.

The complete genomes of 21 fungi, three animals and *Arabidopsis thaliana* were used by KURAMAE et al. (2006) to construct a high confidence tree with excellent nodal support for each branch. Chitin Fungi are the sister group of animals. Other fungal-like organisms could not be included in this study because sequenced genomes were not available at that time. – In an overview of the phylogeny of Eukaryotes, BALDAUF (2008) distinguished five main groups, one of them, the Unikonts containing the Opisthokonts and Amoebozoa (= Mycetozoa), the RAS-assemblage (Rhizaria, Alveolates, and Stramenopiles) comprising the Oophyta, i.e. the „false fungi" including the downy mildews. – A phylogeny with six supergroups has been published by HAMPL et al. (2009), placing fungi and fungal-like organisms in similar phylogenetic clades. – „The six-kingdom, two-empire classification of life" was introduced by CAVALIER-SMITH (2010), essentially confirming the big evolutionary lines of previous phylogenetic hypotheses. PARFREY et al. (2011) combined multigene data of an extensive sampling together with diverse fossils to estimate the timing of divergence of major eukaryotic clades. True fungi may have diverged from the common opisthokont origin more than 1200 Ma. Amoebozoa are calculated to be 1500-1700 Ma old. The downy mildew *Phytophthora infestans* is of middle phanerozoic origin, thus adequately corresponding to the appearance of potential hostplants.

The Chitin Fungi (Fig. 2) appear monophyletic in all representative phylogenetic hypotheses based on molecular data (e.g. LUTZONI et al. 2004, JAMES et al. 2006, HIBBETT et al. 2007, STAJICH et al. 2009, WANG et al. 2009). However, the phylogenetic position of the Microsporidia is still under question, and quite recently the discovery of fungal zooflagellates as members of freshwater picoeukaryotes (LEFÈVRE et al. 2007), now called Cryptomycota (JONES et al.
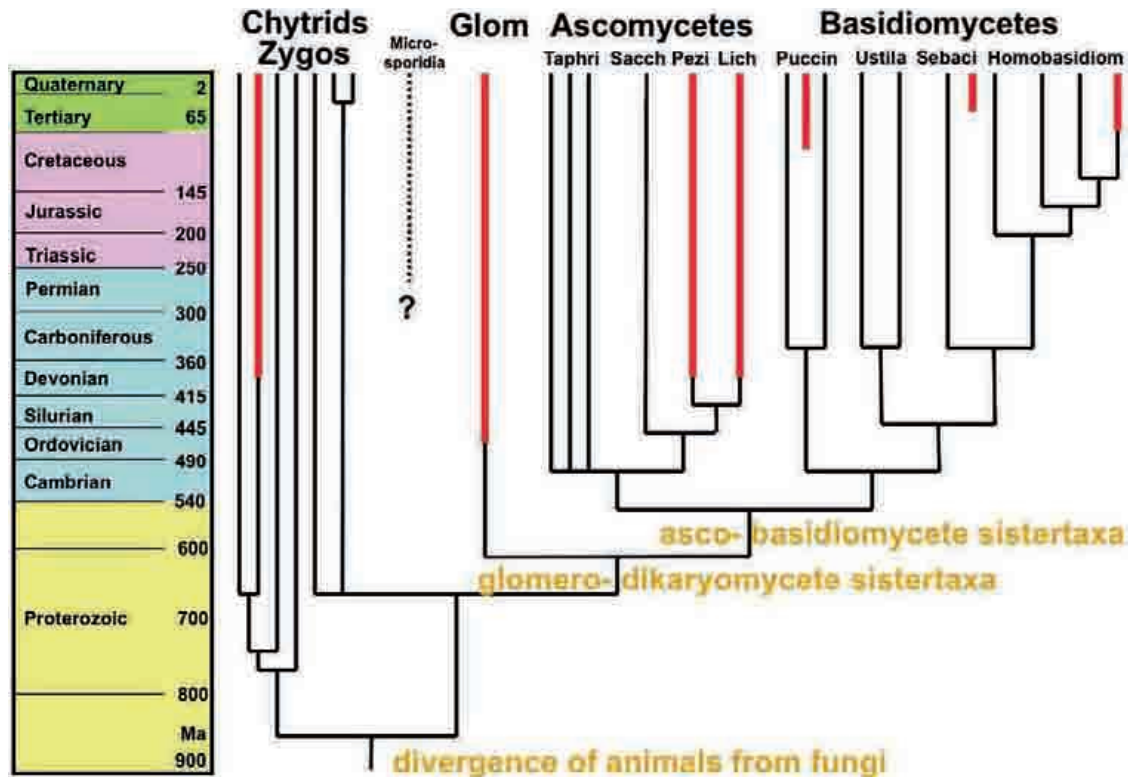
Fig. 2: A hypothesis for the phylogeny of Chitin Fungi. They may have diverged from the common opistho-kont origin more than 900-1200 Ma ago. This scheme refers also to fossil records (red columns). It is obvious that fungi with flagellate stages represent the oldest relationships. Recent representatives are grouped in the Chytridiomycota. Flagellates are lacking in all other true fungi. According to Liu et al. (2006), the loss of the flagellum happened only once in the fungal lineage. Glomeromycota are considered to be asexual fungi. They are the sister group to the dikaryomycotic fungi, comprising the Ascomycota and Basidiomy-cota. Compiled from various sources by F. Oberwinkler.

2011), compels an expanded arrangement of major fungal clades. – A fungal phylogeny was created by Fitzpatrick et al. (2006) based on a dataset of 345,829 genes that were extracted from 42 fungal genomes. The resulting supertree and concatenated phylogeny were highly congruent. All higher taxa, Zygomycota, Ascomycota with Saccharomycotina and Pezizomycotina as well as Basidiomycota were supported by 100% bootstrap scores. For Basidiomycota only *Ustilago maydis, Cryptococcus neoformans, Phanerochaete chrysosporium,* and *Coprinopsis* (as *Coprinus*) *cinereus* were included. A fungal phylogeny based on 82 complete genomes, using the composition vector method, was published by Wang et al. (2009). Again, nearly always 100% bootstrap supported clades were obtained, confirming the main fungal groups as well as lower taxa up to species, especially in extensively sampled ascomycetous yeasts. In Basidiomycota, *Puccinia graminis* and *Sporobolomyces roseus* represented the Pucciniomycotina, *Ustilago maydis* and *Malassezia globosa* the Ustilaginomycotina, *Cryptococcus neoformans* and *C. gattii* the Tremellales, *Phanerochaete chrysosporium* and *Postia placenta* the Polyporales, and *Coprinopsis* (as *Coprinus*) *cinereus* and *Laccaria bicolor* the Agaricales. The rapid development of sequencing techniques initiated more and more genome projects. „The fungal genome initiative represents an organized genome sequencing effort to promote comparative and evolutionary studies across the fungal kingdom" (Cuomo & Birren 2010). – Studying the genes of the meiotic transcriptional program of *Coprinopsis cinereus, Saccharomyces cerevisiae* and *Schizosaccharomyces pombe,* Burns et al. (2010) concluded that these fungi diverged 500–900 million years ago.
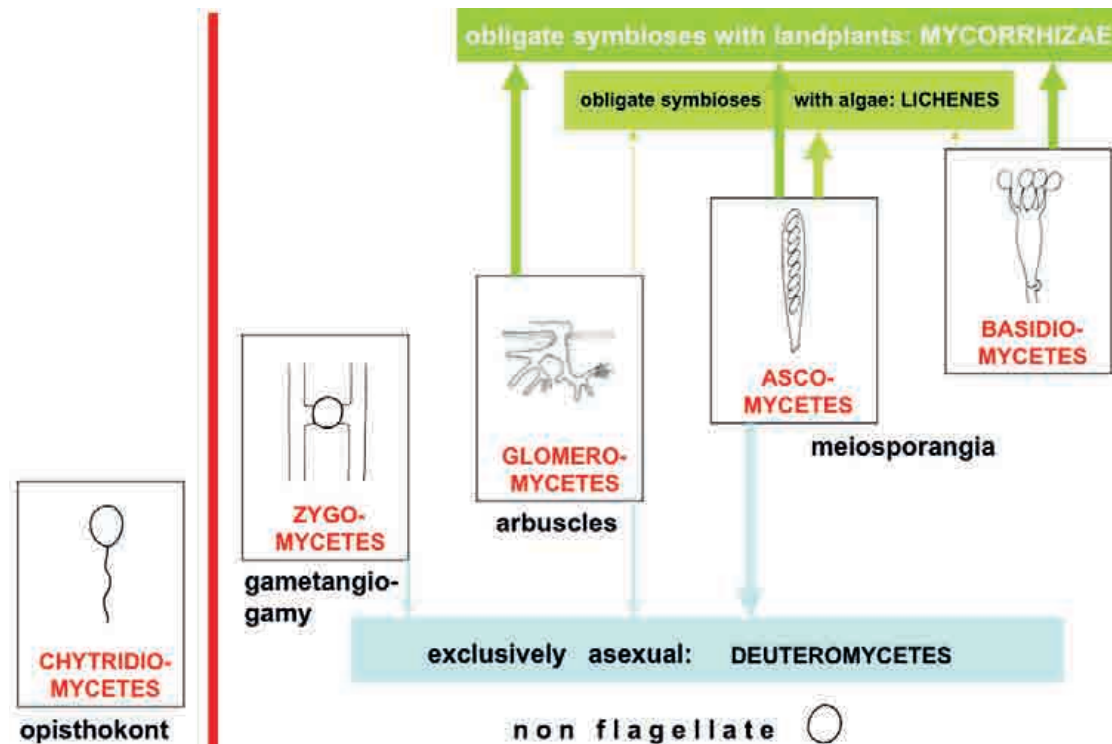
Fig. 3: Classification of Chitin Fungi. Opisthokontic zoospores and gametes are known from Chytridiomycota. All other Chitin fungi are non flagellate. Sexual reproduction of Zygomycota is by gametangiogamy. Glomeromycota are considered to live exclusively asexual. However, their multinucleate stages may eventually allow recombination (den Bakker et al. 2010). They are the mycobionts of arbuscular mycorrhizae. Only one species, *Geosiphon pyriforme*, is known to harbour *Nostoc* obligatorily. The meiosporangium of the Ascomycota is the ascus, the most important morphological and functional feature of the group. Asexual stages are common in Ascomycota. Obligate mutualistic connections with algae and cyanobacteria are probably as diverse as non-lichenized Ascomycota. There are evidences that the latter are mostly derived from lichens (Lutzoni et al. 2001). Ascomycetous fungi are also mycobionts of diverse mycorrhizae. Basidiomycota are characterized by meiosporangia developing basidiospores externally. Asexual stages and mycorrhizal associations are widespread in Basidiomycota, while basidiolichens are comparatively rare. Orig. F. Oberwinkler.

Combined approaches considering fossil records and molecular clocks yielded substantial information about the timing of eukaryotic and fungal evolution. Taylor & Berbee (2006) used fossil calibration points and a dataset of 50 genes for 25 fungi, plants and animals to investigate divergence times in fungi. To determine the Ascomycota/Basidiomycota split they considered three calibration points with the result of extremely differing divergence dates. The plant Eu-Dicotyledons/Monocotyledons divergence of approximately 200 Ma ago yields an Ascomycota/Basidiomycota split of 400 Ma, thus being in accordance with the time of an early land plant radiation. However, the 400 Ma years old fungal fossil from the Rhynie Chert, *Paleopyrenomycites devonicus* (Taylor et al. 2005), considered to be a member of the Sordariomycetes, would then be a deep branching Ascomycete. Lücking et al. (2009a) have recalibrated the fungal tree of life compared to the evolution of green plants and reassessed the systematics of *Paleopyrenomycites*. They reestimated the origin of fungi between 760 Ma and 1.06 Ba, Chytridiomycota, Zygomycota and Glomeromycota approximately 600-700 Ma, Basidiomycota and Ascomycota between 500-650 Ma ago.

Evolutionary trends:

Gametes and/or asexual single cells with flagellae > non flagellate

With sexual reproduction > asexual

Oogamy > gametangiogamy > somatogamy

The loss of flagellates may have been an adaptive response to limitations of water in land habitats. Consequently, such an evolutionary development requires either gametangiogamy or somatogamy.
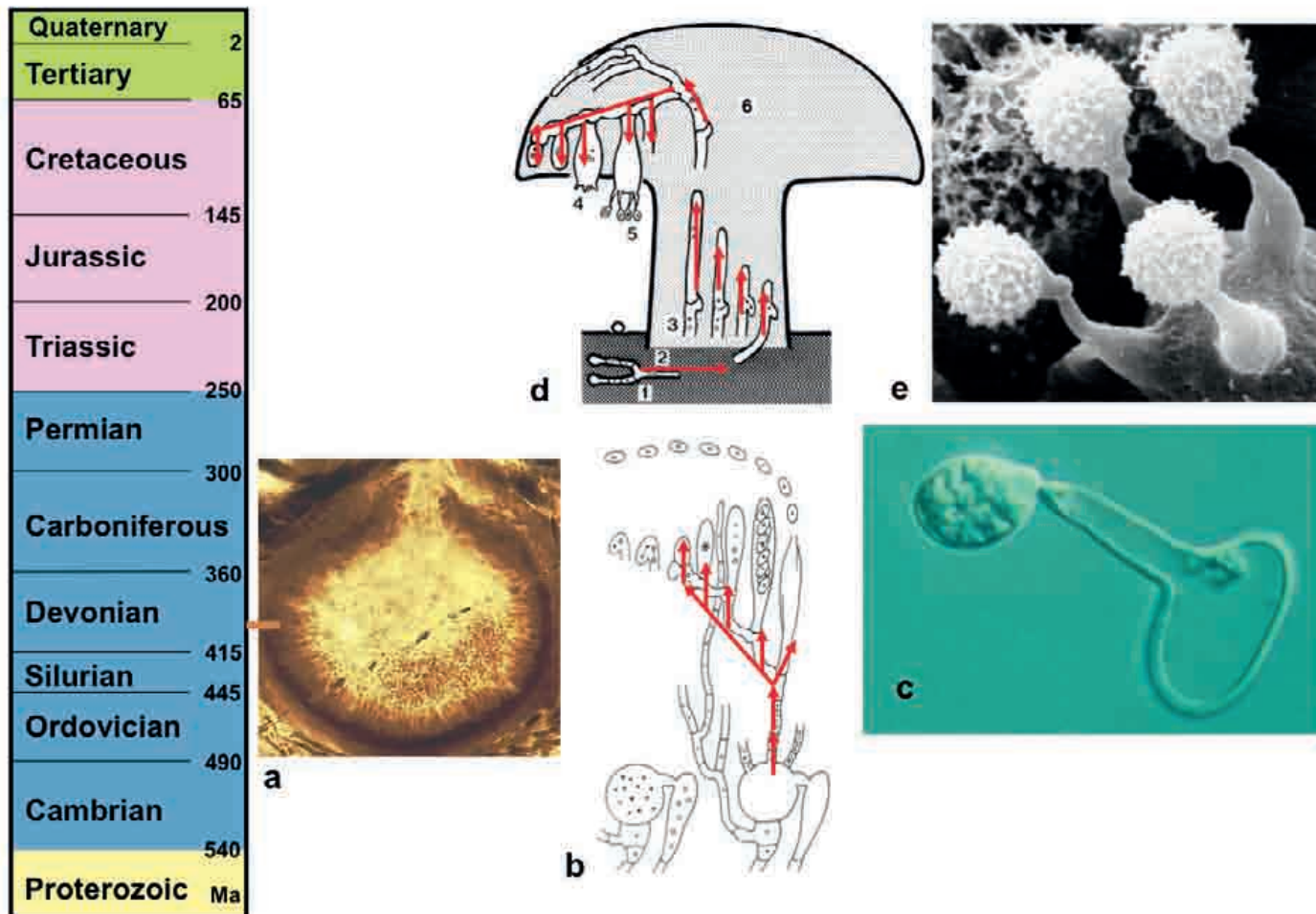
Fig. 4: The dikaryomycotic fungi, Ascomycota and Basidiomycota. **a**: Fossils of Ascomycota are known from the Devonian. The perithecium is approximately 400 µm in diameter and develops in the stomatal chamber of *Asteroxylon*. Their morphology is identical with extant representatives. The dikaryophases of typical Asco- and Basidiomycota are illustrated schematically (red arrows). **b**: In Ascomycetes the dikaryophase is restricted to short hyphae between the ascogon and the asci. **d**: In the majority of Basidiomycetes the dikaryophase extends to more or less the whole life cycle. **e**: Ballistospores ejected from sterigmata are typical for basidiomycetous meiosporangia, the basidia. **c**: A similar mechanism can occur in ballistosporous yeasts of Basidiomycetes. **a** from Taylor et al. (1999). Orig. F. Oberwinkler.

Dikarya

Dikaryotic hyphal stages are unique characteristics of Ascomycota and Basidiomycota (Fig. 3). The delay of nuclear fusion after plasmogamy varies considerably in both groups. In ascomycetous fungi the dikaryophase is restricted to ascogenous hyphae, while in most Basidiomycota dikarya are established after plasmogamy that normally occurs very early in ontogeny and karyogamy is delayed until the for-

mation of meiosporangia, the basidia (Kniep 1928). Because croziers in Ascomycota and clamps in Basidiomycota occur on dikaryotic hyphae they were considered as essential for maintaining the dikaryotic stages. However, many fungi are known with dikaryotic hyphae lacking such structures.

The evolutionary driving forces for establishing, maintaining and enlarging dikaryotic phases in higher fungi are not clear. In Basidiomycota, the nuclear behavior is even more complex

because diploid life cycles also occur. The genomic stability of two diploid individuals of *Armillaria gallica* inhabiting stable environments has been shown by Hodnett & Anderson (2000). Under such conditions, phenotypic flexibility as afforded by dikaryosis, is not needed. Anderson & Kohn (2007) suggested that nuclear spacing and associated variation in gene expression are inherent to dikaryons, but not to diploids, thus allowing them improved responses to heterogeneous environments. In

Fig. 5: *Microbotryum saponariae*, germination of smut spores. The germination hypha is a transversely septate basidium that buds off basidiospores (sporidia). A yeast colony develops by continuous budding of single cells. Orig. F. Oberwinkler.

addition, dikaryons are capable to deliver a fertilizing nucleus to a monokaryon (Buller 1930, 1931), an ability called Buller phenomenon (Quintanilha 1937, Raper 1966). In essence, all matings are a manifestation of the Buller phenomenon (Anderson & Kohn 2007).

In many rust fungi the haplophase is comparatively long, thus indicating an old evolutionary origin (e.g. Gäumann 1964).

Basidiomycota

Typical members of the Basidiomycota are well characterized by several important characters (Fig. 4 d, c, e): A normally short monokaryotic phase is followed by plasmogamy (1), allowing compatible nuclei to establish dikarya (2). These are maintained during the whole ontogeny (3) until the formation of meiosporangia (4, 5), alltogether resulting in a basidiocarp (6). The majority of basidiomycetous fungi produce basidia with characteristically curved sterigmata (Fig. 4, d 5, e), microstructures that are capable to eject basidiospores by a highly elaborate mechanism (Pringle et al. 2005). Such ballistospores are not restricted to meiosporangia, they can be produced even by single cells (Fig. 4 c) as in „jumping yeasts", e.g. the ballistoconidia of *Sporobolomyces* (Kluyver & van Niel 1924, 1927), and those of *Sporidiobolus* (Nyland 1949), a dimorphic fungus with clamp connections and teliospores. – In addition to this unique set of characteristics there exist other specific features for Basidiomycota, like septal pores, cell wall ultrastructure and metabolisms (Oberwinkler 1978). – The above mentioned phylogenetic hypotheses based on molecular data unanimously group Basidiomycota as a monophylum, comprising some 31,000 described species (Kirk et al. 2008). How molecular techniques revolutionize the knowledge of basidiomycete evolution has recently been reviewed by Yang (2011).

Evolution of morphological structures

Species of the Basidiomycota are known as yeasts, dimorphic fungi, simple hyphae, hyphal networks, and basidiocarps of different complexities.
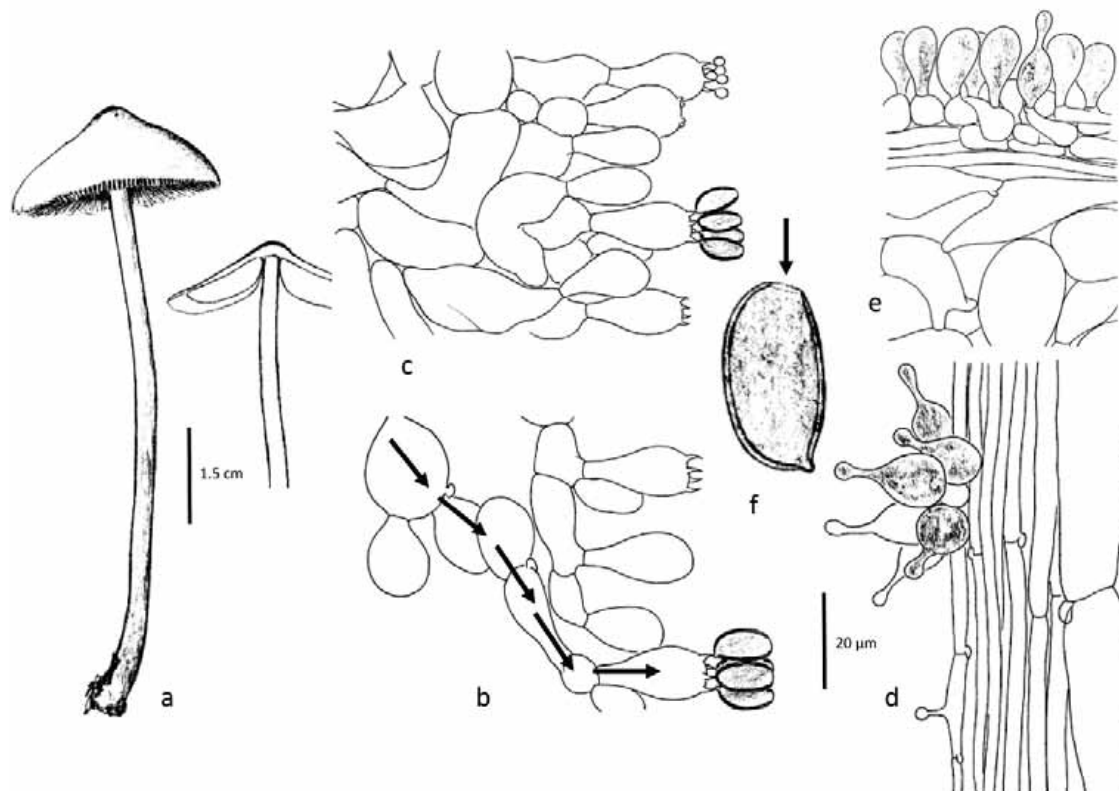
Fig. 6: *Conocybe subovata* (**a**) and *C. lactea* (**b**-**f**). **a**: Basidiocarp and longitudinal section of cap. **b**: Swollen subglobose subhymenial hyphae showing a sequence of cells in a generative hypha (arrows). **c**: Part of the hymenium with basidia of different developmental stages. **d**: Detail of stipe surface with a cluster of cystidioles. **e**: Longitudinal section of cap showing specialized hyphal structures. **f**: Thick-walled basidiospore with germ pore (arrow). Bar for microscopic figures 20 µm and 10 µm for the basidiospore. Orig. F. OBERWINKLER.

Their most characteristic feature is the basidium that evolved in various morphological types. Basidiospores have undergone considerable structural and functional changes during evolution. Septal pore ultrastructures show a remarkable evolutionary development, and other subcellular structures exist of high phylogenetic importance. An evolution of structures from budding single cells and ballistosporic yeasts to hyphal growth with convergently evolving basidiocarps marks main steps of basidiomycetous phylogeny.

Yeasts and dimorphic fungi

Fundamental properties of ascomycetous *Saccharomyces cerevisiae* yeast communities have been summarized by HONIGBERG (2011). Strain-to-strain variation appears to depend on the variability in the expression and function of adhesin proteins. Yeast colonies are embedded in a common protective matrix that also may play an important role for diffusible signals between cells to organize different community structures and functions. It can be expected that basidiomycetous yeasts behave similarly.

Budding was already intensively studied and taxonomically interpreted by BREFELD (1881, 1888), but his findings were largely neglected later. Yeast budding of basidiospores and the capability to form yeast colonies is widespread in different relationships of the Pucciniomycotina, the Ustilaginomycotina, and the Tremellomycetes.

When a filamentous basidiomycetous fungus is capable of growing with single cells, the yeast typically develops in the first ontogenetic stage by basidiospore or conidial germination. The transition from single cells to hyphal growth certainly is a major evolutionary step. Thus, the yeast stage reflects phylogenetically old Basidiomycota.

Evolutionary trends in basidiomycetous yeasts:

Life cycle in the single cell stage > dimorphic ontogeny: yeast – hyphae – yeast > loss of the yeast phase

It is most likely that the origin of Basidiomycota goes back to yeasts with specific features different from ascomycetous yeasts. None of the so far known extant taxa can be considered as such a candidate, for example species of the genera *Bensingtonia, Kurtzmanomyces, Rhodosporidium, Sporobolomyces,* and *Sterigmatomyces* of the Pucciniomycotina.

In recent dimorphic basidiomycetous species, the yeast stage is at the beginning of the life cycle. This might be a good example for considering ontogeny as a recapitulation of phylogeny. Another convincing fact for such an interpretation is that yeasts in recent Basidiomycota occur in evolutionarily old groups, like most Pucciniomycotina, the Mixiomycetes, Agaricostilbomycetes, Cystobasidiomycetes, Septobasidiales, and Microbotryomycetes. In this subdivision, however, yeasts are not kown from Cryptocolacomycetes, Classiculomycetes, Atractiellomycetes, and Pucciniomycetes except of Septobasidiales, if this is a member of the class.

In most Ustilaginomycotina and the basal Agaricomycotina, the Tremellomycetes, ontogenetic yeasts are present. In the true smut fungi, Ustilaginomycotina, remarkable anamorphic yeast genera are *Malassezia* and *Tilletiopsis* p.pte. In this relationship, yeasts are not known from the Tilletiales, the bunts.

Yeasts in Agaricomycotina are restricted to the phylogenetically basal Tremellomycetes. They are recorded from all presently accepted orders, the Tremellales, Filobasidiales, and Cystofilobasidiales. The class comprises also a considerable assemblage of anamorphic taxa of the genera *Trichosporon, Bullera* p.pte., *Cryptotrichosporon,* and *Cryptococcus* p.pte., grouped in the Trichonosporales, an order based on a molecular hypothesis.

In deep-sea environments BASS et al. (2007) recorded an unknown wide diversity of basidiomycete-like organisms with close similarities to basidiomycetous yeast groups. Curious exceptions, as a sequence taxon that clusters with the polyporaceous genus *Antrodia*, remains an unsolved riddle.

Morphology of hyphae and hyphal systems

When GIMENO et al. (1992) found that diploid *Saccharomyces cerevisiae* can undergo dimorphic transitions to grow with (pseudo)hyphae in response to starvation for nitrogen, further experimental work was initiated to elucidate this process. The yeast-to-hyphal transition in *Candida albicans*, also an ascomycetous yeast, is closely bound to virulence gene expression (THOMPSON et al. 2011). The expression of genes important for hyphal growth as well as those for virulence are simultaneously controlled by several transcriptional regulators in this case. Recently it could be shown that regulation of filamentous growth in *Saccharomyces cerevisiae* depends on evolutionarily conserved signalling pathways (CULLEN & SPRAGUE 2012). Here, evolutionary trends become obvious on the level of functional molecular processes.

Hyphae have an apical growth organized by a Spitzenkörper (GIRBARDT 1957, 1969; STEINBERG 2007; JONES & SUDBERY 2010) and the capability to produce complex networks of macroscopic dimensions. However, these structures never are tissues as in plants. This holds also for rather tight structures, as for example those of sclerotia. During evolution, hyphae and hyphal systems have undergone remarkable adaptive changes convergently, certainly as a response to environmental conditions.

## Evolutionary trends in basidiomycetous hyphae and hyphal systems:

Hyphae monokaryotic > multinucleate > dikaryotic > diploid

Hyphae with clamps > without clamps?

Hyphae cylindrical > swollen > globose

Hyphae thin-walled > thick-walled

Hyphal system monomitic > dimitic > trimitic

Hyphal system monomitic > sarcodimitic > sarcotrimitic

Cell walls hyaline > pigmented

In the majority of basidiomycetous fungi the monokaryotic state is comparatively short (Fig. 4, d 1), the dikaryon, however, extends to most of the vegetative and generative parts. Molecular communication occurs between the paired nuclei of a dikaryon (ANDERSON & KOHN 2007). Also fruiting in a monokaryotic or diploid state is occasionally possible. – Multinucleate hyphae occur in the fern parasite *Mixia osmundae* (NISHIDA et al. 1995), a species that has a basal position in phylogenetic dendrograms based on molecular data. In addition, highly multinucleate hyphal cells are known from *Heterobasidion annosum* (KORHONEN 1978, CHASE et al. 1983) and from *Agaricus bisporus* (RAPER et al. 1972).

Hyphae with and without clamps are more or less equally frequent in Basidiomycota. Clamps are not required for extending the dikaryon. There is no doubt that clamps and croziers are homologous in structure and function (ANDERSON & KOHN 2007). However, it remains unclear when and where they evolved, and it is unlikely that they have multiple convergent origins.

Generative hyphae and basidia are nearly always thin-walled, as are hyphae in short living basidiocarps or parts of them, e.g. in most Agaricales and Boletales, and many other Basidiomycota. Swelling of thin-walled hyphae during basidiocarp development is often correlated with the expansion of a pileus, as in Russulales and Agaricales (Fig. 6 b, c, e). – Gloeoplerous hyphae may well represent a synapomorphy in Russulales (Fig. 49).

Thick-walled hyphae have been evolved manifold convergently, for example in the Polyporales (Figs. 13 b, 43), the Hymenochaetales (Fig. 42) and some Russulales (Fig. 49). Also di- and trimitic hyphal systems (CORNER 1932) are the result of convergent adaptive radiations in several groups of the Agaricomycotina. Such structures lack in Pucciniomycotina and Ustilaginomycotina, and they are restricted to higher evolved taxa in the Agaricomycotina (Fig. 7). Sarcodimitic and -trimitic hyphal systems (CORNER 1966) have also to be considered as derived but may
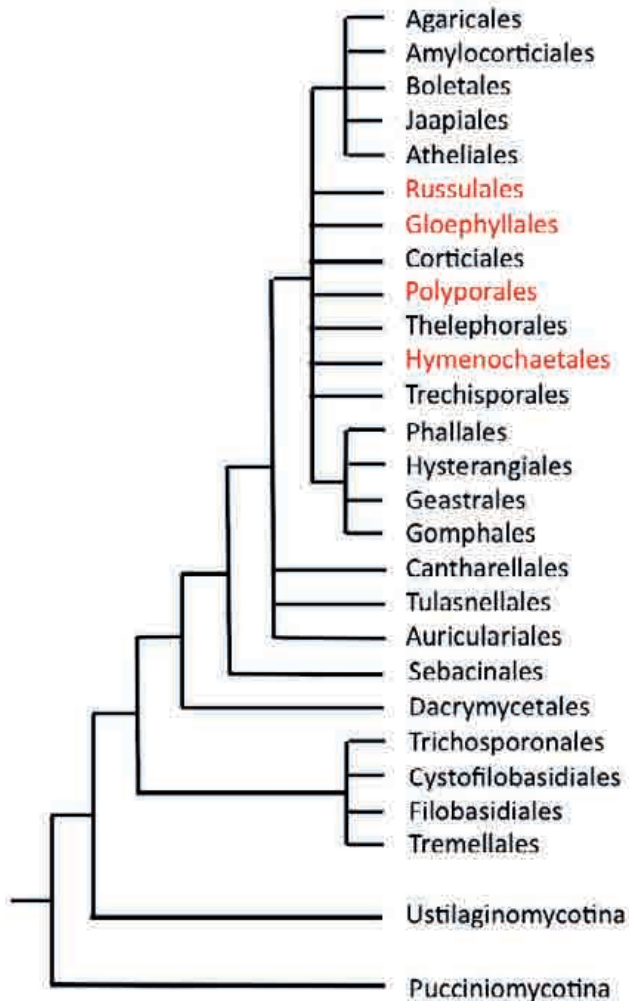
Fig. 7: Main distribution of complex hyphal systems marked in red. The phylogram is a compilation from data of various authors.

have gone lost, too (READHEAD 1987). The hyphal systems of the stipititrama of *Oudemansiella* and *Xerula*, or sections of *Oudemansiella* could not be used by YANG et al. (2009) for meaningful characterisation of these taxa.

Coprinopsis cinerea is an experimental model for studying the multicellular development in fungi (STAJICH et al. 2010). The 37-megabase genome was sequenced and assembled into 13 chromosomes. This is an essential resource in understanding the evolution of multicellularity in Basidiomycota.

Cystidia are lacking in Pucciniomycotina, rather rare in Ustilaginomycotina, and sparsely distributed in basal lineages of the Agaricomycotina. In contrast, cystidia originated in a huge diversity convergently in derived Agari-comycotina, and they are not homologous in many cases. Cystidia are very often thick-walled. Pigmentation of cell walls and also of cytoplasmatic components is another derived character in many basidiomycetous fungi, possibly often correlated with protective functions.

Meiosporangia

The basidium is a multifunctional cell for the essential steps in sexual reproduction, i.e. karyogamy and meiosis (Figs. 3, 4 d 3). Basidiospores are developed outside of the meiosporangium. Development and morphology of basidia vary considerably. This variation requires closer consideration.

When a terminal hyphal cell functions as a meiosporangium, finally four haploid nuclei are in that cell. The simplest way to use these nuclei for dispersal is a compartmentation of the hyhal-like meiosporangium by three transverse septa, thus forming four haploid cells. In fact, under experimental conditions, auricularioid basidial cells may produce yeasts, ballistospores, microconidia or hyphae (BAUER & OBERWINKLER 1986a,b) or may even disintegrate and function as propagules themselves. Such behavior is still different from ascospore formation inside the meiosporangium. Depending on the meiosporangial cell shape, basidial fragmentation may vary from transverse to longitudinal inclusive of oblique septa.
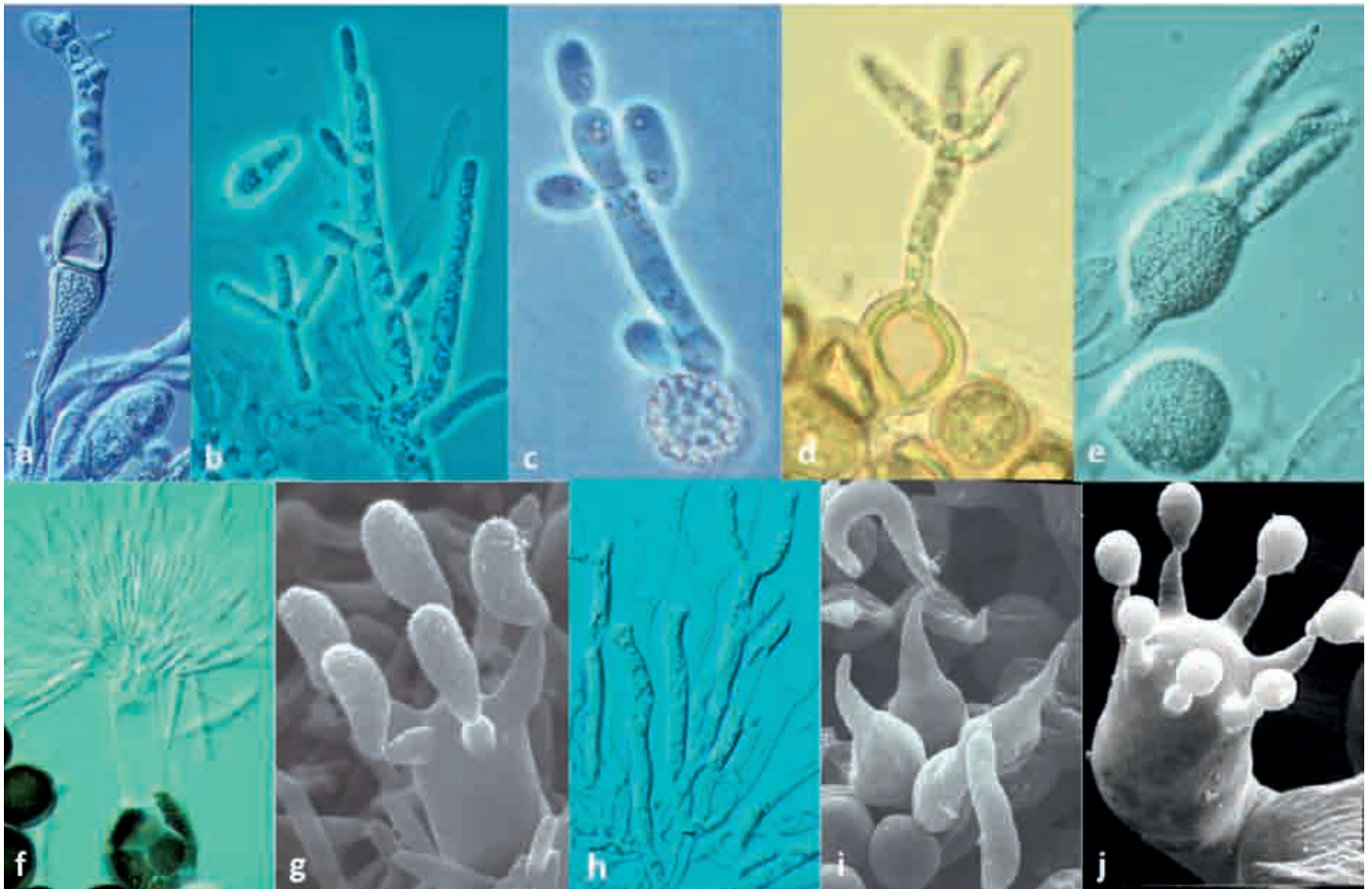
Fig. 8: Some basidial types, not to scale. Transversally septate: **a** *Puccinia*, rust fungi. **b** *Heterogastridium*, Pucciniomycotina. **c** *Microbotryum*, Microbotryomycetes. Holobasidia in the Ustilaginomycotina: **d** *Entyloma*, **f** *Neovossia*, **g** *Exobasidium*. **e** Longitudinally septate phragmobasidium of *Tremella*. Holobasidia: **h** *Dacrymyces*, **i** *Tulasnella*, **j** *Botryobasidium*. **g** SEM Orig. P. BLANZ. Orig. F. OBERWINKLER.
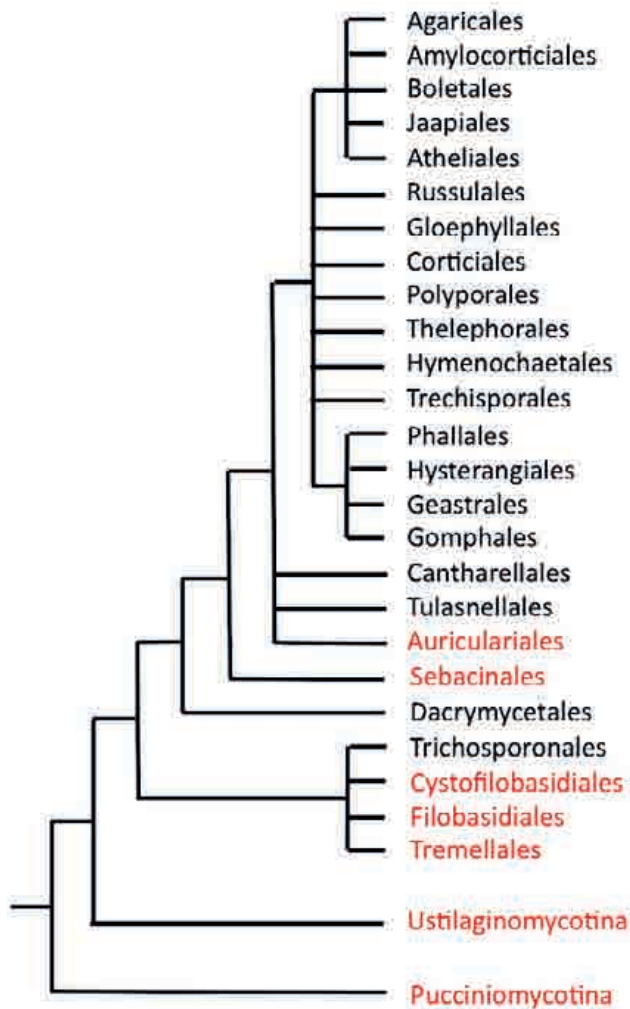
Evolutionary trends in basidial morphology:

Phragmobasidia > holobasidia

Meiosporangium transversally septate > holobasidium

Meiosporangium transversally septate > longitudinally septate > holobasidium

No probasidium > probasidium thin-walled > thick-walled (teliospore)

Phragmobasidia are restricted to Pucciniomycotina, Ustilaginomycotina, and the basal Agaricomycotina Tremellales, Sebacinales, and Auriculariales (Fig. 9). This distribution pattern certainly reflects an important evolutionary trend from phragmo- to holobasidia. However, it has to be considered that within these phragmobasidial groups frequent evolutionary transitions from phragmo- to holobasidia took place (Figs. 10, 19, 24, 36). These cases do not contradict the above interpretation, as do not the transitions from transversally to longitudinally septate meiosporangia (OBERWINKLER 1982). In the Ustilaginomycotina phragmobasidia occur only in the Ustilaginaceae and few other taxa, while holobasidiate species are present in all orders, inclusive of those that are considered as basal ones. In the Pucciniomycotina holobasidia occur in *Chionosphaera* and *Pachnocybe*.

A probasidium may be defined as a terminal cell of a hypha in which karyogamy takes place. Such cells need not to change their morphology. When meiosis also occurs in the same cell, more space is needed. Such a precondition may initiate the broadening of a premeiotic cell that is called probasidium. Often probasidia function as resting spores, structurally recognizable by considerably thickened cell walls, and often called teliospores (Figs. 10 b, 26, 32, 33, 36, 37, 39).

Fig. 9: Main distribution of phrag-mobasidial taxa marked in red. The phylogram is a compilation from data of various authors.

Evolutionary trends in basidial sterigmata and basidiospore release:

Sterigmata curved > straight > reduced > lacking

Sterigmata lateral > terminal

Sterigmata 4 > 2 > 1 sterigma

Sterigmata 4 > more than 4

Sterigmata long > sterigmata lacking

Basidiospores budding off > forcible discharge > passive release

The most important structural and functional feature in basidiomycetous fungi is the sterigma and its ballisto-sporic mechanism (Figs. 4 c, e, 8 g, i, j, 36, 47 g). Basidia that forcibly discharge basidiospores have curved ste-rigmata with very thin terminal spicula and asymmetrically growing out ba-sidiospores. This is a good example of structural prerequisites for a specific function that always should be illustrat-ed correctly. Changes in the sterigma morphology indicate the loss of ac-tive spore discharge. – The transition of auricularioid basidia to holobasidiate ones is always coordinated with a ter-minal arrangement of sterigmata. – Re-duction of sterigmata from four to two occurs in many relationships indepent-ly, the reduction to only one sterigma, however, is rare. Also, the increase of sterigmata (Fig. 8 g, j) is comparatively rare and scattered in unrelated taxa.

Basidiospores

A remarkable diversity of structural and functional features have evolved in basidiospores, most of them as a re-sult of adaptive radiation.

Evolutionary trends in basidiospores:

Spore wall thin > thick > without germ pore > with germ pore

Spore wall hyaline > pigmented

Spore wall smooth > ornamented

Spore unicellular > bicellular > mul-ticellular

Spore germination variable, with yeasts, secondary ballistospores, conidia, and/or hyphae > hy-phae

Unicellular, hyaline, thin- and smooth-walled basidiospores are pre-
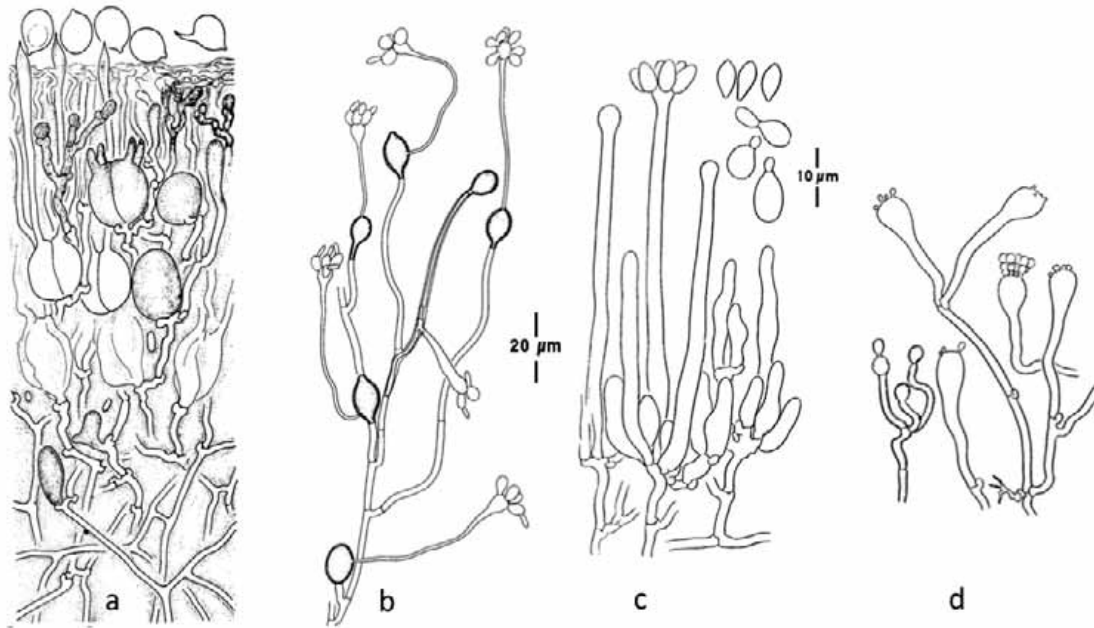
Fig. 10: Some basidial types of Tremellomycetes. **a** *Tremella mesenterica*, **b** *Cystofilobasidium capitatum*, **c** *Filobasidium floriforme*, **d** *Filobasidiella neoformans*. Orig. F. Oberwinkler.

dominant in most of the Basidiomycota. Few important exceptions are mentioned here: the russuloid basidiospore (Fig. 49) is unique in cell wall ultrastructure and the amyloid reaction of the spore ornament. In Hymenochaetales (Fig. 42) basidiospores are mostly hyaline and thin-walled, but thick-walled and pigmented ones also occur. Boletales have thick-walled and often intensively pigmented spores (Fig. 52), occasionally also strongly ornamented spore walls as in *Strobilomyces*. The evolutionary trends in basidiospore features of Agaricales were highlighted by Garnica et al. (2007).

In comparison to Ascomycota, multicellular meiospores are rare in Basidiomycota. Notable exceptions can be found in the Exobasidiales (Fig. 36), Cryptobasidiales (Fig. 36), and Dacrymycetales (Fig. 40). The convergent origin and functional aspects of these spore types can not be explained yet.

Often basidiospore germination in Pucciniomycotina and Ustilaginomycotina as well as in basal groups of the Agaricomycotina is unfixed, i.e. yeasts, secondary spores, microconidia or hyphae may primarily develop. The huge bulk of higher Agaricomycotina species has basidiospores that germinate exclusively with hyphae.

Basidiocarps

Basidiocarps evolved from simple to complex structures many times convergently, thus improving the efficiency of spore production quantitatively and of dispersal mechanisms qualitatively. The evolution of structurally increasing complexity in basidiocarps appears to be a highly intricate process. In a phylogenetic hypothesis of the Auriculariales (Fig. 41), for example the *Myxarium* and *Auricularia* clades may indicate progressive evolutionary lines (Weiss & Oberwinkler 2001) towards stalked-capitate and cyphelloid, respectively.

A high diversity of basidiocarps, hymenial types and trophic stages has been evolved in the Russulales (Fig. 49). The group, recognized already by Malençon (1931) as „La série des Astérosporées", was characterized and enlarged to cover taxa of nearly all basidiocarp types by Oberwinkler (1977). The order has been confirmed and repeatedly studied molecularly. In a detailed phylogenetic hypothesis by Miller et al. (2006) *Aleurodiscus* is included in the Stereaceae, *Boidinia* and *Gloeopeniophora* in the Russulaceae together with well-known sequestrate genera, *Heterobasidion* in the Bondarzewiaceae, *Laxitextum* and *Dentipellis* in the Hericiaceae, *Leucogaster* in the Albatrellaceae, *Gloidon* and *Lentinellus* in the Auriscalpiaceae, and inter alia *Scytinostroma* and *Vararia* in the Peniophoraceae. Species of the Albatrellaceae and Russulaceae are ectomycorrhizal, but probably not the *Boidinia* species that cluster with the Russulaceae. In total, evolutionary changes in
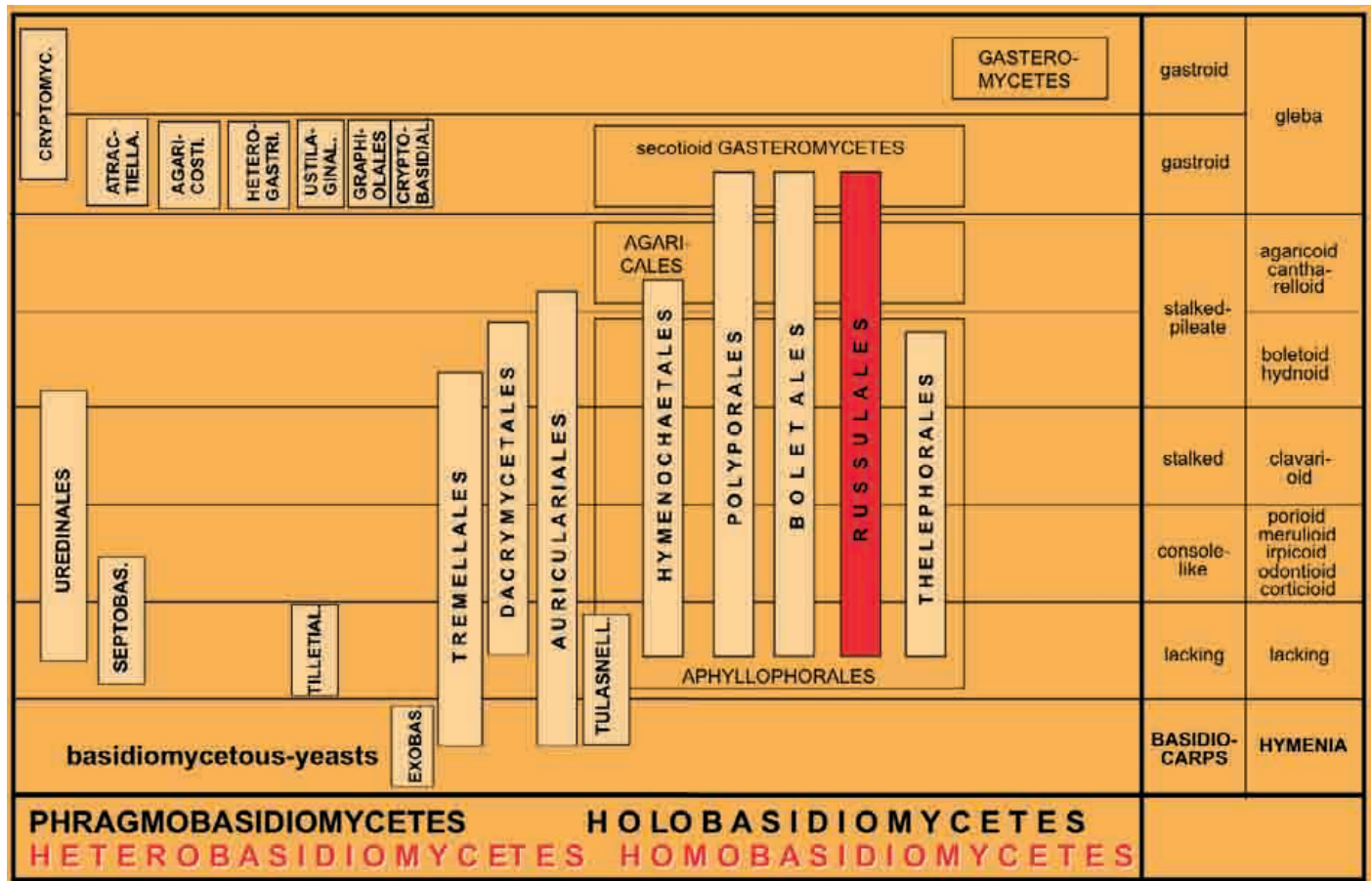
Fig. **11**: The multiple convergent evolution of basidiocarps in proposed monophyla of the former Basidiomycetes is illustrated in this scheme from premolecular times, modified after OBERWINKLER (1977). In Homobasidiomycetes the orders Hymenochaetales, Polyporales, Boletales, Russulales and Thelephorales were distinguished. Russulales, marked in red, was of specific interest to document the new systematics. The Agaricales could not be resolved, however genera of clear affinities to the other orders were transferred to them. While secotioid taxa were included in their proper relationships, the non-secotioid Gasteromycetes could not be affiliated with any hymenomycetous fungi. Also some heterobasidiomycetous orders, the Auriculariales, Dacrymycetales, and in part the Uredinales, were included in that scheme. Already at that time, several gastroid Heterobasidiomycetes had been recognized. Finally, it was obvious that basidiomycetous yeasts are restricted to heterobasidiomycetous relationships.

basidiocarp morphology led from simple to agaricoid structures and finally, many times convergently to gasteroid and hypogeous forms. The evolutionary progression of gasteromycetation in the Russulaceae has been depicted as a series by ALBEE-SCOTT (2007) from the epigeous *Russula romellii* to the hypogeous *Macowanites americanus*, and finally to the hypogeous *Gymnomyces abietis*, and also in the Albatrellaceae from „*Polyporus*" *sylvestris* over *Mycolevis siccigleba* to *Leucophlebs spinispora*.

Evolutionary trends in basidiocarps:

Basidiocarp inconspicuous > corticioid > odontioid, irpicioid, merulioid, porioid

Basidiocarp inconspicuous > cyphelloid, clavarioid, hydnoid

Basidiocarp inconspicuous > cantharelloid, boletoid

Basidiocarp inconspicuous > ...... agaricoid > cyphelloid

Various basidiocarp types > gasteroid

Molecular data of Boletales (BINDER & HIBBETT 2006) allow the interpretation of evolutionary trends in basidiocarps from resupinate or polyporoid to agaricoid and boletoid as well as frequent convergent gasteromycetation processes (Fig. 52). The authors assume that the ancestor was a brown-rot producing fungus with morphologically simple basidiocarps.

Even in trees with other focus (e.g. GARCIA-SANDOVAL et al. 2011) and therefore very selective samplings for Russulales and Boletales, the evolutionary
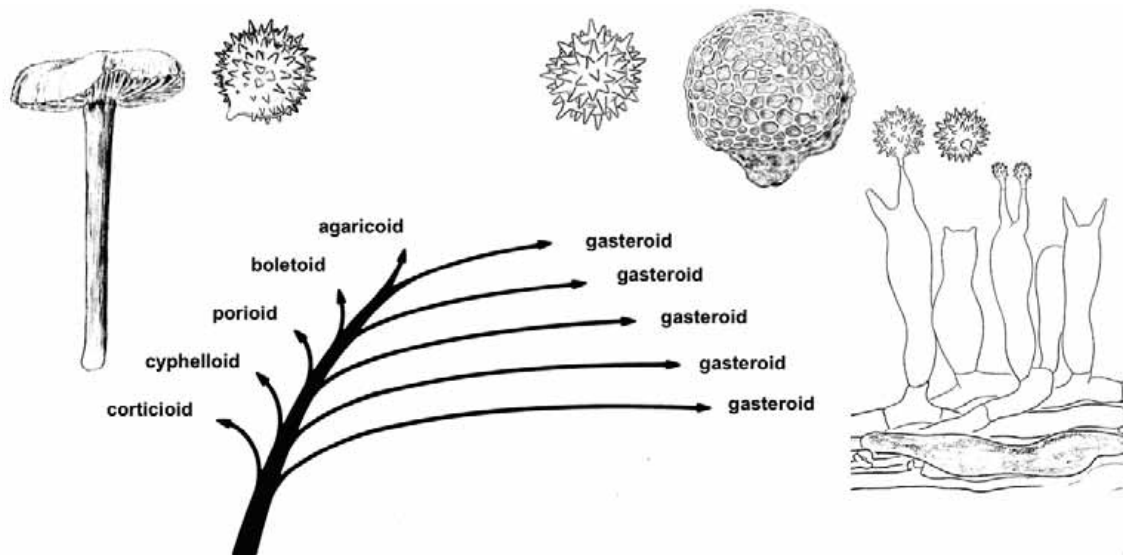
Fig. 12: Gasteromycetation in Basidiomycota happened often convergently. The diagram refers to representative examples in the Agaricomycotina. Gastroid forms also occur in the Pucciniomycotina and Ustilaginomycotina. Illustrated are basidiocarps and spores of *Laccaria laccata* to the left and *Hydnangium* sp. to the right. Orig. F. Oberwinkler.
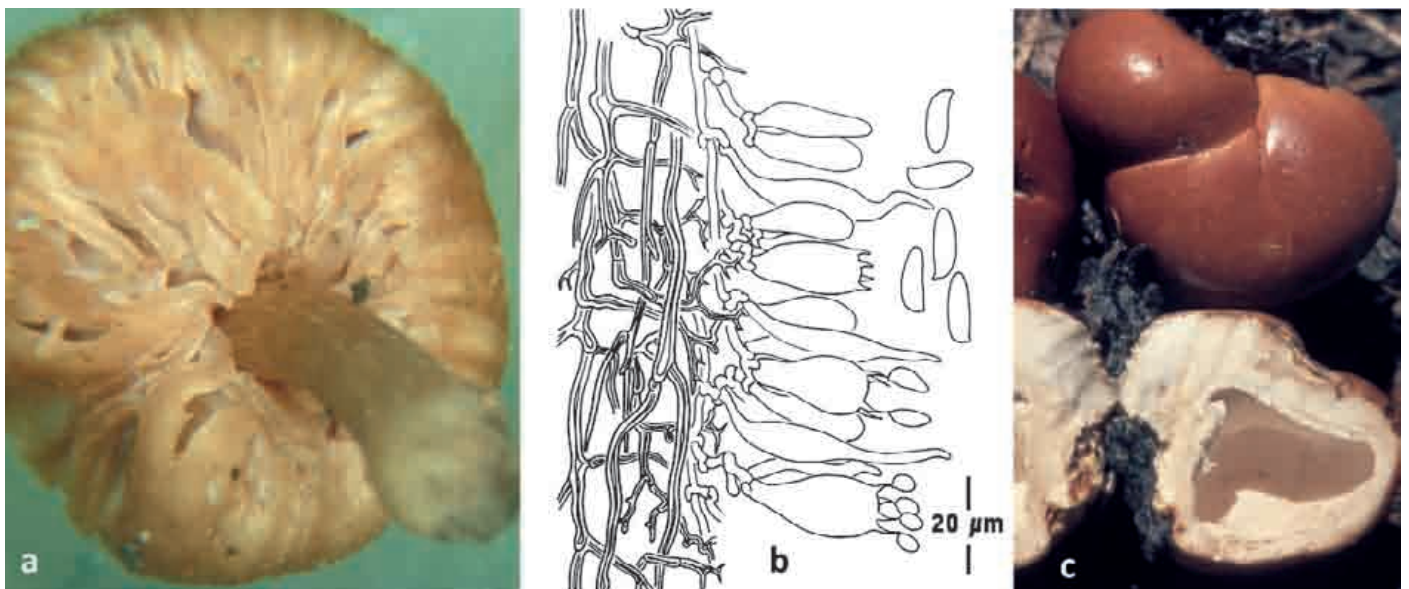
Fig. 13: Secotioid basidiocarps of *Laccaria tortuosa* (**a**) and *Cryptoporus volvatus* (**b**, **c**). Note the irregularly deformed lamellae of *L. tortuosa* and the sterigmata of *C. volvatus* indicating forcible spore discharge in a gasteroid chamber. Orig. F. Oberwinkler.
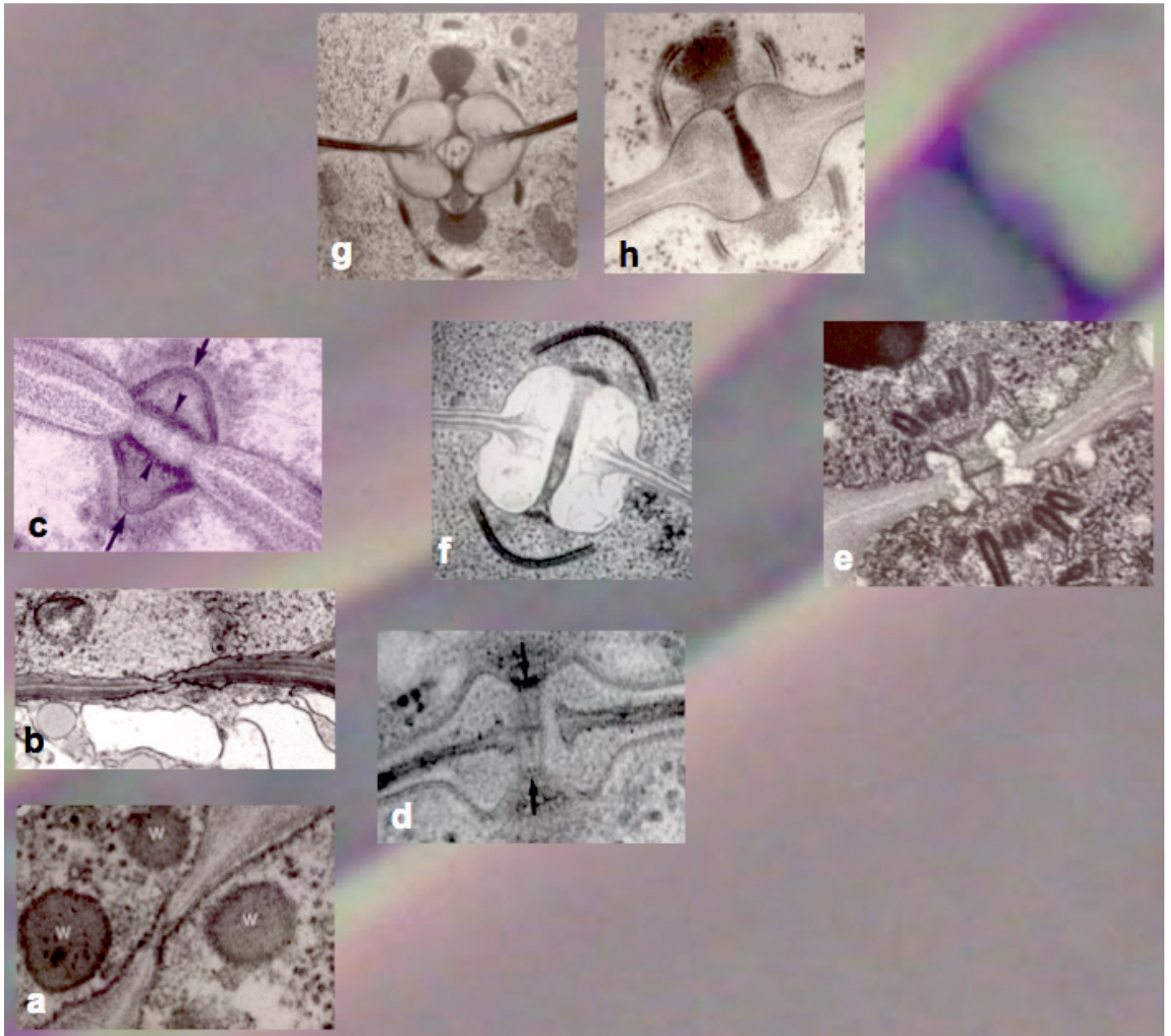
Fig. 14: Some basidiomycetous septal pores. Pucciniomycotina: **a** *Cryptomycocolax* (W = Woronin-like bodies), **b** *Gymnosporangium*. Ustilaginomycetes: **c** *Doassansia*, **d** *Tilletia*. Agaricomycotina: **e** *Tremella*, **f** *Tulasnella*, **g** *Ceratobasidium*, **h** *Schizophyllum*. In the background a lightmicroscopic photo of *Uthatobasidium* with a doliporous septum. TEM photos R. Bauer.

trends mentioned above, are confirmed.

In a comprehensive molecular study of cyphellaceous fungi, Bodensteiner et al. (2004) concluded that cyphelloid forms have about 12 or more independent origins within the Agaricales. There are many more in other relationships of the Agaricomycotina,

e.g. the Auriculariales (Fig. 41) or Dacrymycetales (Fig. 40).

The regressive, polyphyletic process of gasteromycetation (Fig. 12) occurs in many basidiomycetous relationships and is well studied and documented in several cases.

The evolutionary trends for multiple convergent evolution of sequestrate

forms are definitely unidirectional from hymenomycetoid to gasteroid types, well documented by secotioid taxa (Fig. 13), comparative micromorphology, and molecularphylogenetic hypotheses. Gasteromycetes that could not be affiliated to Hymenomycetes on morphological grounds (Oberwinkler 1977, Fig. 11) are now integrated in diverse relationships of the Agaricomycotina
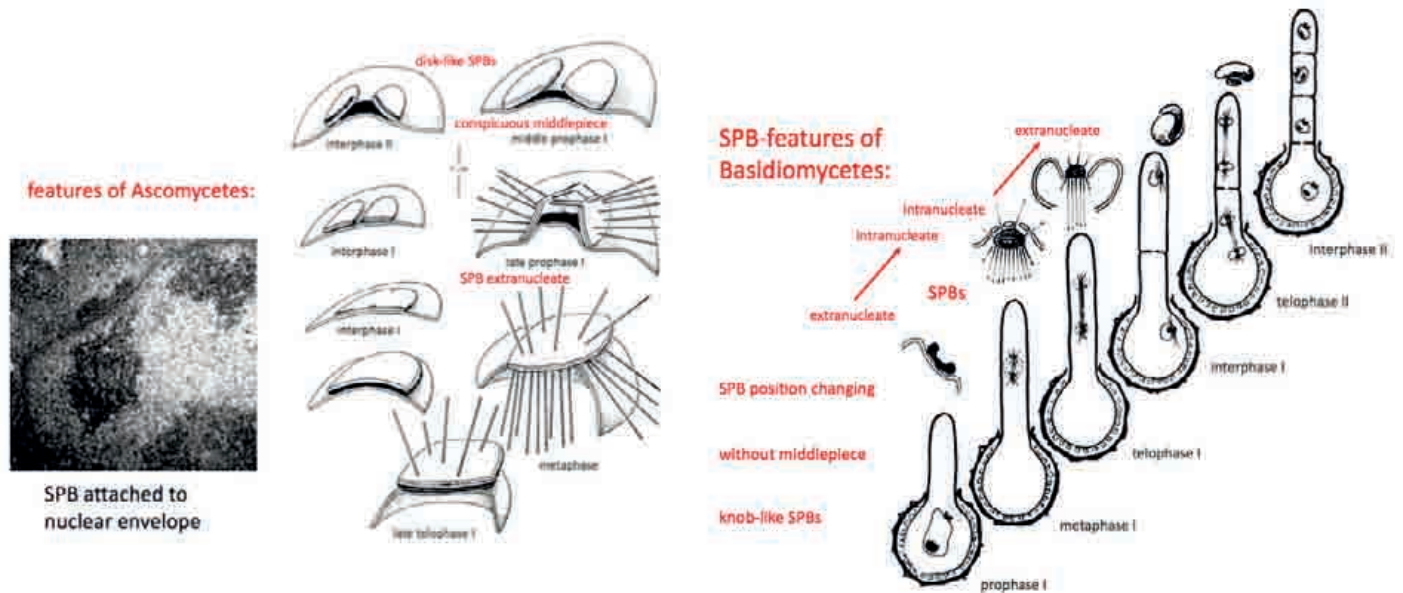
Fig. 15: **Left**: Spindle pole cycle of *Cryptomycocolax abnormis*. Modified after Oberwinkler & Bauer (1990) and Oberwinkler (1995), TEM orig. R. Bauer. **Right:** Meiosis and spindle pole cycle of *Ustilago maydis*. Redrawn and strongly modified after O'Donnell & McLaughlin (1984a,b).

through molecular data, like the gomphoid-phalloid clade (Phallomycetidae, Hosaka et al. 2006) with the Geastrales, Hysterangiales, and Phallales.

Gasteromycetation as an evolutionary trend is common in Basidiomycota and has been studied intensively, e.g. by Albee-Scott (2007) with the secotioid taxa to explain the extinction of their epigeous relatives. An interesting wood-decaying sequestrate fungal genus, *Guyanagaster*, related to *Armillaria* in the Marasmiaceae (Physalacriaceae) from Guyana, has recently been described by Henkel et al. (2010).

Ultrastructural characters

Septal pores

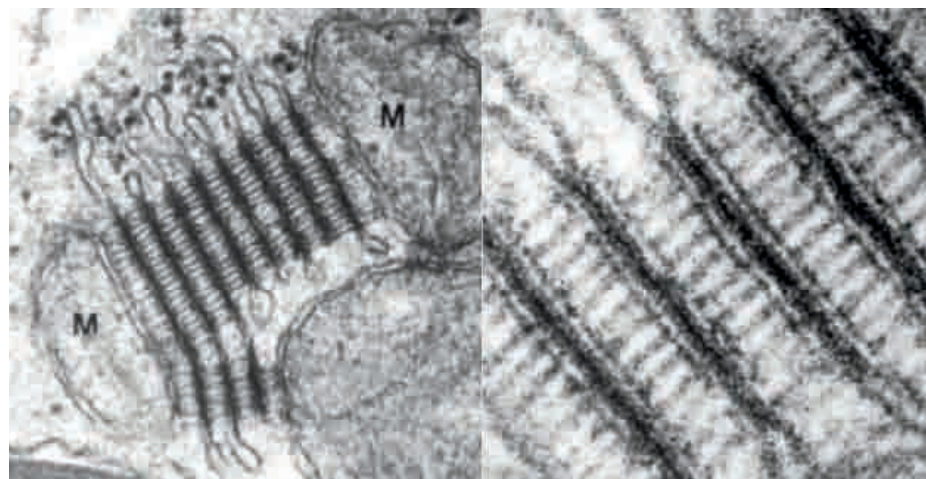The sequence from „simple" septal pores to highly elaborate dolipores in Basidiomycota reflects their main evolutionary lineages. Septal pores without rim-like swellings (dolipores) and without parenthesomes are only known from Pucciniomycotina and certain Ustilaginomycotina. Dolipores without parenthesomes have evolved several times convergently. The most complex ultrastructure of septal pores is found in dolipores with various types of parenthesomes.

Evolutionary trends in basidiomycetous septal pores:

Septal pore simple > dolipore lacking parenthesomes > dolipore with parenthesomes

Parenthesomes lacking > tubulate

Parenthesomes continuous > perforate

Several basidiomycetous monophyla are well characterized by their septal pore structures. In the simple pored Pucciniomycotina, microbodies are typical for Cryptomycocolacales, Saccoblastiaceae, and Classiculomycetes, and cystosomes for Cystobasidiales. Agaricostilbomycetes and Pucciniomycetes are devoid of such bodies. In the Ustilaginomycotina dolipores without parenthesomes occur in the Tilletiales and Entorrhizales. In the Agaricomycotina dolipores with continuous parenthesomes are characteristic for the Dacrymycetales, Sebacinales, Auriculariales, and Tulasnellales. Continuous parenthesomes are also reported for Geastrales, Gomphales, and Trechisporales (van Driel et al. 2009). The mixed occurence of dolipores with either continuous parenthesomes or perforated ones in the Cantharellales and Hymenochaetales is confusing (van Driel et al. 2009). All higher evolved Agaricomycotina have dolipores with per-

Symplechosomes

Based on transmission electron microscopic studies of *Saccoblastia farinacea*, BAUER & OBERWINKLER (1991b) reported on a unique cell organelle, the symplechosome (Fig. 16). Further investigations have shown that the symplechosome is typical for and restricted to the Atractiellomycetes (BAUER et al. 2006). Species of *Helicogloea* and *Saccoblastia* have resupinate basidiocarps, *Atractiella* and *Phleogena* contain stilboid fungi. The pycnidial members, *Basidiopycnis hyalina* and *Proceropycnis pinicola*, were introduced by OBERWINKLER et al. (2006). – Since origin and function of symplechosomes are unknown and their structural composition is uniform, evolutionary trends cannot be discussed. – The Atractiellomycetes are mentioned here because they were reported as mycobionts of orchids recently (KOTTKE et al. 2009).

Fig. 16: Symplechosomes consist of stacks of plate-like cisternae that are connected by hexagonally arranged bars. Such bars often link symplechosomes with mitochondria (M). Orig. R. BAUER.

forate parenthesomes. However, the documentation of septal pore types in Agaricomycotina is still fragmentary.

Spindlepole bodies

Spindelpole bodies (SPBs) are essential cell organelles, functionally involved in cell division. Only few studies have been carried out to clarify the ontogenetic cycles of SPBs. The data available from these investigations document considerable differences between Ascomycota and Basidiomycota (Fig. 15).

Differences of SPBs in Ascomycota and Basidiomycota and evolutionary trends

SPB disk-like > knob-like

SPB with middlepiece > without middlepiece

SPB position during nuclear division extranucleate > extranucleate – intranucleate – extranucleate

SPBs are microtubule-organizing centers, as basal bodies, nucleus-associated bodies and centrosomes. BORNENS & AZIMZADEH (2007) considered the connection of the flagellum and the nucleus as a prerequisite for the common origin of a centriole-based centrosome in the metazoa and the SPB in fungi.

Studying the ultrastructure of meiosis in the hollyhock rust fungus, *Puccinia malvacearum*, O'DONNELL & McLAUGHLIN (1981a,b,c), and in *Ustilago maydis* O'DONNELL & McLAUGHLIN (1984a,b), drew also attention to the SPB cycle (Fig. 15). Meiosis and SPB cycle have been analyzed in *Pachnocybe ferruginea* (BAUER & OBERWINKLER 1990), in *Cryptomycocolax abnormis* (OBERWINKLER & BAUER 1990), in *Microbotryum violaceum* (BERBEE et al. 1991), in *Sphacelotheca polygoni-serrulati* (BAUER et al. 1991), and in *Agaricostilbum pulcherrimum* (BAUER et al. 1992). These studies contributed to the understanding that SPBs in basal clades of the Pucciniomycotina are disk-like, as in Ascomycota. In contrast, in derived taxa of the Pucciniomycotina SPBs are subglobose, globose ones are typical for Ustilaginomycotina and Agaricomycotina.
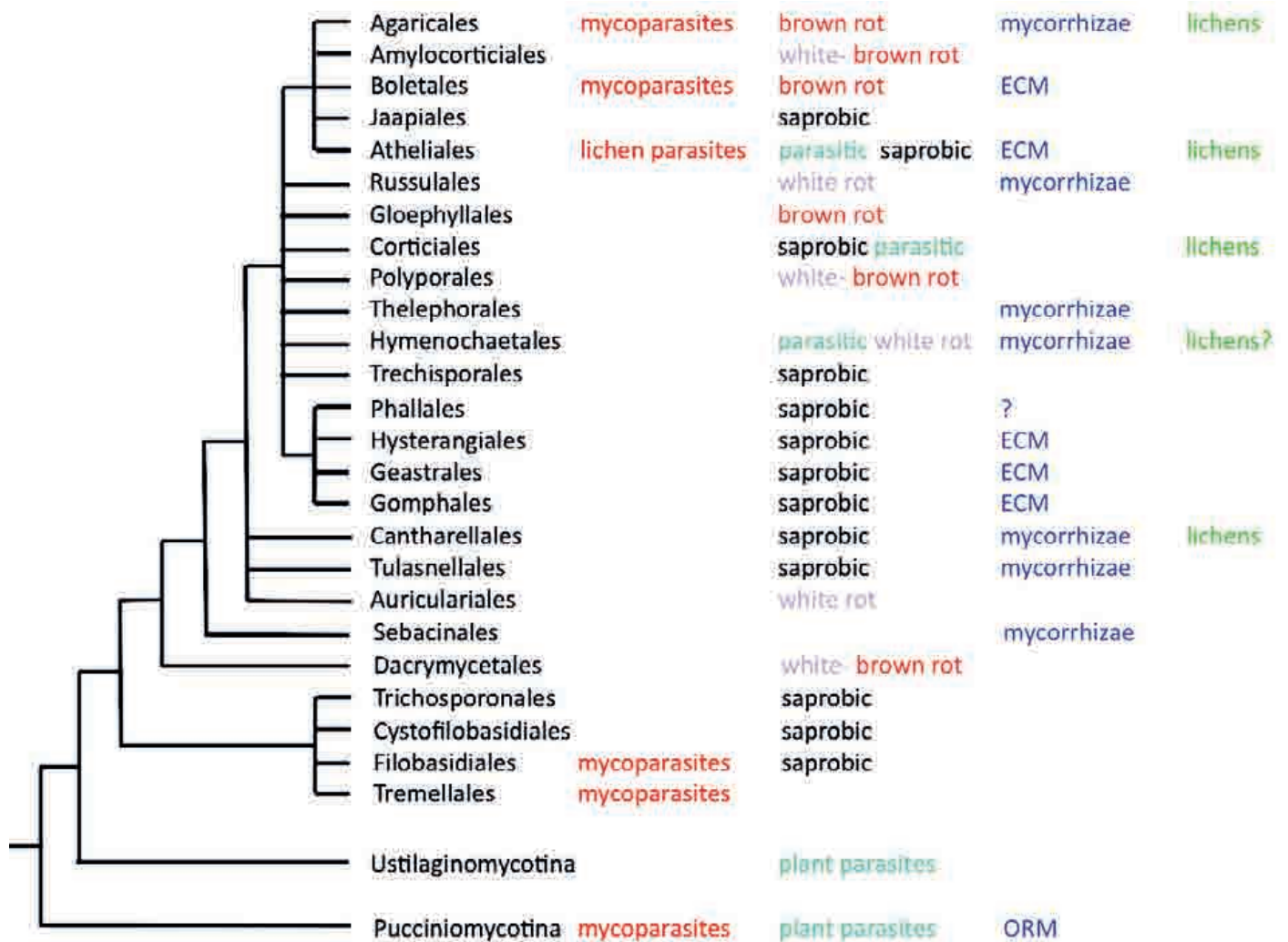
Evolution of trophic stages

As heterotrophic organisms, fungi depend on organic nutrients, the substrate dependencies of their trophic stages is of utmost importance in their evolution. In this article, we can only focus on few selected examples to trace evolutionary trends. Animal associations are excluded. A simplified overview (Fig. 17) is used as a guideline for the following chapters.

Evolutionary trends of Basidiomycota in trophic stages:

Mycoparasites > plant parasites > mycorrhizal associations

Plant parasites > saprobic stages

It can be deduced from Fig. 17 that mycoparasitism is a „fundamental initial motor in the basidiomycete evolution" (WEISS et al. 2004a). Para-

Fig. 17: Evolution of Basidiomycota and distribution patterns of main trophic stages. Though the occurrence of principal nutritional dependencies in monophyletic groups of the Basidiomycota appears as randomly distributed, meaningful evolutionary trends can be detected. Mycoparasitism is widespread in Pucciniomycotina and dominant in the Tremellales, a basal taxon of the Agaricomycotina. The huge bulk of plant parasites belongs to the Pucciniomycotina and Ustilaginomycotina. However, important plant parasites occur scattered in diverse relationships of the Agaricomycotina. ECM = ectomycorrhizae, ORM = orchid mycorrhizae; animal associations are not included in this scheme. The phylogram is a compilation from data of various authors. Orig. F. OBERWINKLER.

sites of plants are most frequent in the Pucciniomycotina and Ustilaginomycotina. Parasites on woody plants are scattered in the Agaricomycotina. The most effective mycorrhizal radiation obviously occurred in the Sebacinales (WEISS et al. 2004b). Predominantly ectomycorrhizal partners constitute the Cantharellales, Gomphales, Hysterangiales, Thelephorales, Russulales, Boletales, and Agaricales. Dacrymycetales, Auriculariales and most of the Phallales are saprobic. Widely distributed are saprobic Basidiomycota also in the Hymenochaetales, Polyporales, Russulales, Atheliales, Boletales, and Agaricales.

Mycoparasitism

The highest diversity of mycoparasitic types is known from the Pucciniomycotina, comprising the three major basidiomycetous interfungal cellular interactions (BAUER 2004), colacosomes, nanometer-fusion, and Micrometer-fusion interaction. The nanometer-fusion type is also characterized by tremelloid haustoria. Only in the *Tuberculina* mycoparasites the Micrometer-fusion pores occur. In addition, penetration of host cells by cells of the parasite is found in few agaricoid species.
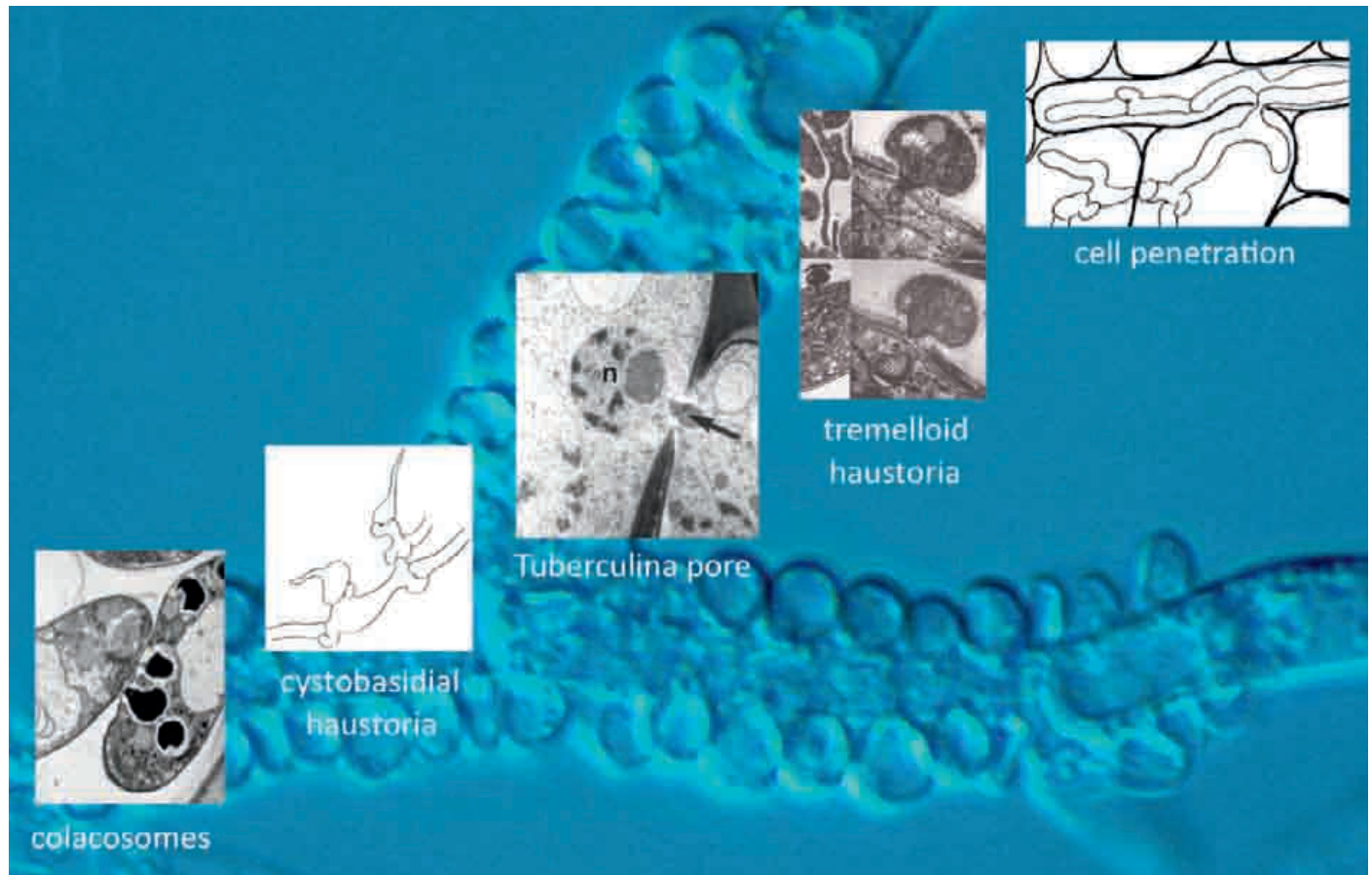
Fig. 18: Major types of cellular interactions in basidiomycetous mycoparasites. Colacosomes are exclusively known from members of the Pucciniomycotina. Cystobasidial and tremelloid haustoria are structurally very similar but occur in Pucciniomycotina and Agaricomycotina, respectively. The *Tuberculina* interaction with rust fungi is unique and only known from this genus. Cell penetration is known from the agaricoid mycoparasite *Asterophora parasitica*. The background of the figure illustrates the mycoparasitic interaction of a colacosome fungus with a *Tulasnella* host. TEM photos R. BAUER. Orig. F. OBERWINKLER.

Evolutionary trends of basidiomycetous interfungal cellular interactions:

Origin unknown > colacosomes > loss of colacosomes

Origin unknown > nanometer-fusion interaction

Origin unknown > Micrometer-fusion interaction

Colacosome fungi

So far unknown subcellular bodies, responsible for mycoparasitic interaction, the colacosomes (Fig. 20), have been detected in *Colacogloea peniophorae* (*Platygloea p.*, OBERWINKLER et al. 1990a,

BAUER & OBERWINKLER 1991a), and at the same time in *Cryptomycocolax abnormis* (Fig. 19) with two different types (OBERWINKLER & BAUER 1990). Colacosomes are exclusively known from Cryptomycocolacomycetes and Microbotryomycetes in the Pucciniomycotina. The phylogenetic distance between *Cryptomycocolax* and the colacosome fungi of the Microbotryomycetes, according to hypotheses based on molecular data, cannot be explained.

Evolutionary trends in colacosomes:

Original colacosome > two colacosome types > derived colacosome > loss of colacosome

The colacosome with a central core surrounded by a membrane that finally fuses with the host plasmalemma, thus providing direct contact of host and parasite cytoplasm, was considered the ancestral one of the two types found in *Cryptomycocolax abnormis* (OBERWINKLER & BAUER 1990). Derived colacosomes lack the pore, thus having lost the cytoplasmic fusion. They are the only ones occurring in the other colacosome fungi.

A second genus in the Cryptomycocolacomycetes, *Colacosiphon*, has been introduced by KIRSCHNER et al. (2001). Structures that show colacosomes, but not recognized as such, were already reported by KREGER-VAN RIJ & VEENHUIS (1971) from *Sporidiobolus*. Also *Atractocolax* (KIRSCHNER et al. 1999), *Leucosporidium*, *Mastigobasidium*,
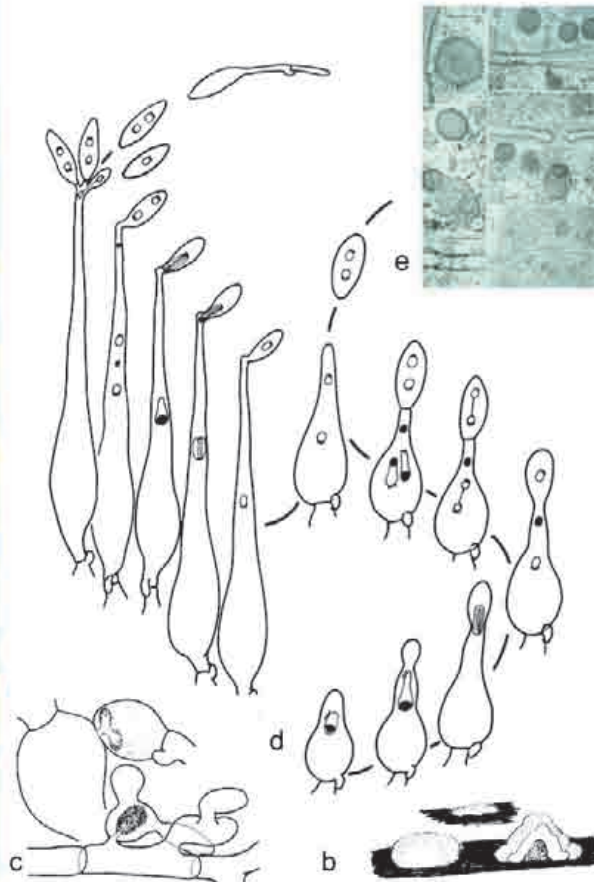
Fig. 19: *Cryptomycocolax abnormis* ecology and life cycle. **a**: *Cirsium subcoriaceum*. In old culms of this plant gelatinous pustules (**b**) were found on Mount Irazu, Costa Rica. **c**: Host-parasite-interaction through colacosomes; host hyphae without clamps, *Cryptomycocolax* hyphae with clamps. The host is forced to grow in the cells of the parasite. **d**: Basidial ontogeny: the primary phragmobasidium releases the upper cell, then the basal cell elongates and produces basidiospores apically. **e**: Simple septal pores associated with Woronin-like bodies. Orig. F. OBERWINKLER and from OBERWINKLER & BAUER (1990).
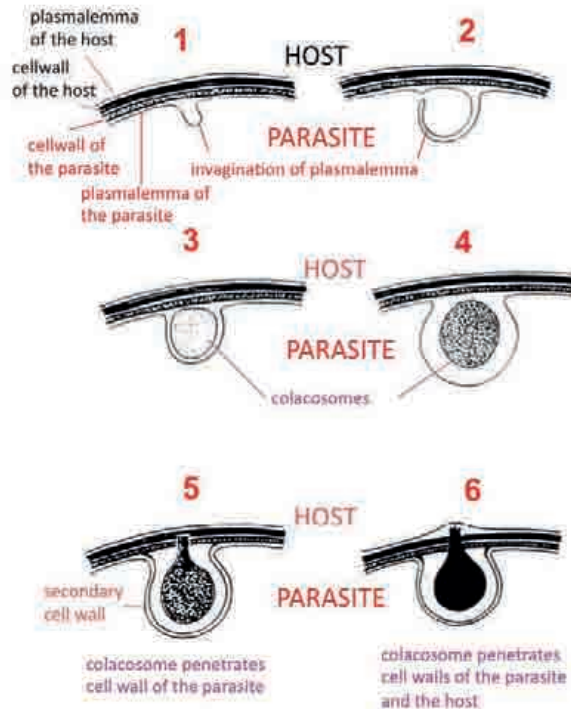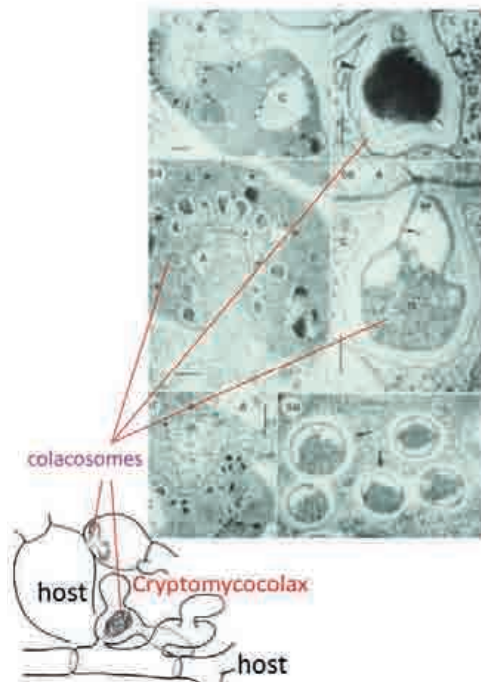
Fig. 20: Left: Colacosomes in *Cryptomycocolax abnormis* (OBERWINKLER & BAUER 1990). The host is an ascomycete that is forced to invaginate cells of the parasite. Right: Ontogeny of the derived colacosome type, deduced from *Colacogloea peniophorae* (BAUER & OBERWINKLER 1991a). The scheme illustrates a series of developmental stages, beginning with an invagination of the plasmalemma of the parasite and ending with a fully developed colacosome. The chemical compounds involved in the penetration of the cell walls of the parasite and the host are unknown.
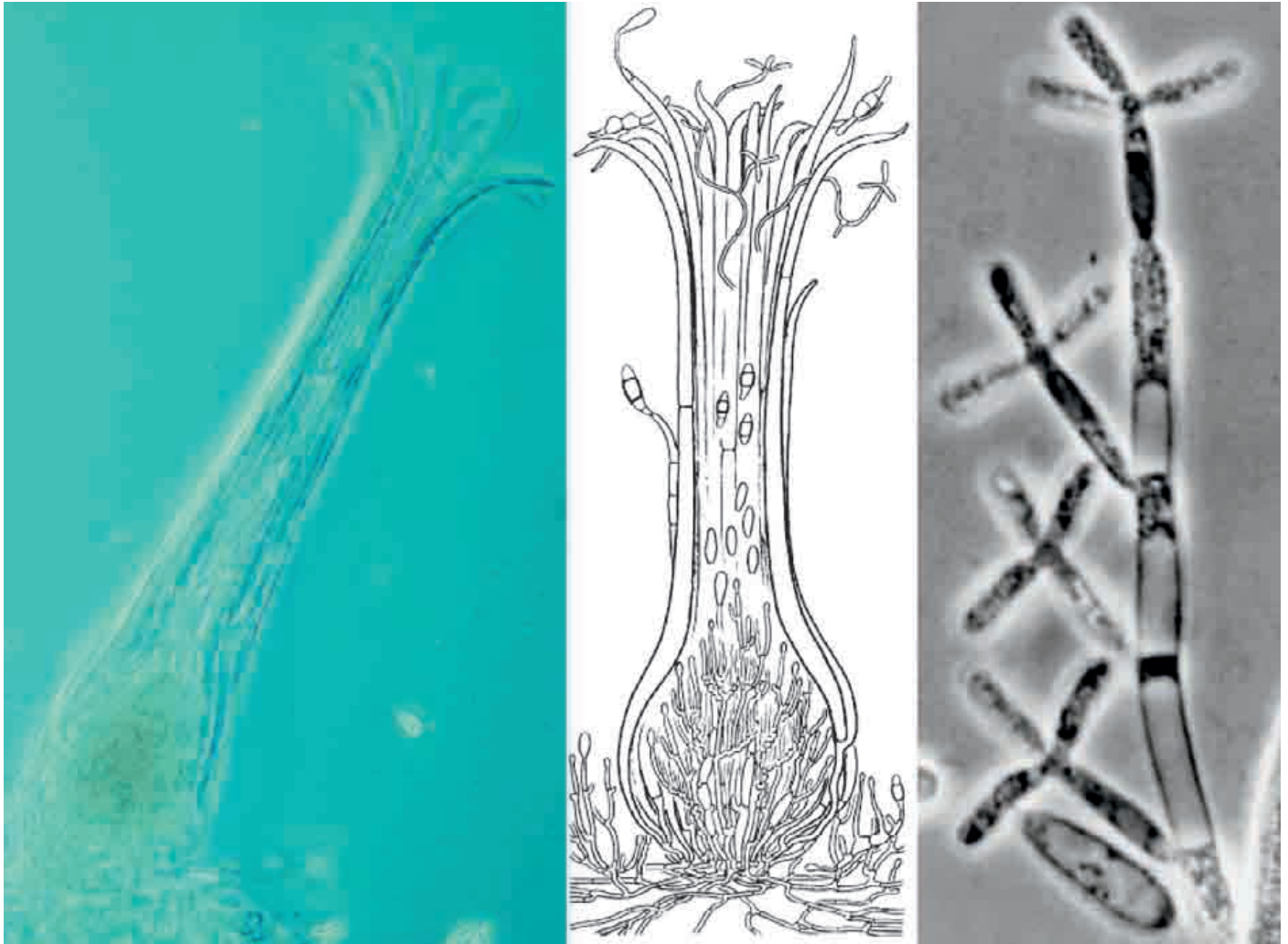
Fig. 21: Basidio- and conidiocarps of *Heterogastridium pycnidioideum*. Left: anamorph stage, *Hyalopycnis blepharistoma*, in lateral view. Drawing: longitudinal section showing conidial stages. Right: mature basidium with tetraradiate basidiospores. Orig. F. Oberwinkler and from Oberwinkler et al.(1990b).

Rhodosporidium (Sampaio et al. 2003) are colacosome fungi.

The anamorphic *Hyalopycnis blepharistoma* (Fig. 21) could be identified as a basidiomycete by Bandoni & Oberwinkler (1981), confirmed as such when the basidial stage, *Heterogastridium pycnidioideum,* was found (Oberwinkler et al. 1990b), and recognized as a mycoparasite when colacosomes were detected (Bauer 2004).

Based on molecular phylogenetic hypotheses, Heterogastridiales and Leucosporidiales cluster with the plant parasitic Microbotryales, the false smuts. In the latter no mycoparasites are known.

Tremelloid haustoria

Short hyphal branches, subtended by a clamp, basally swollen and apically tapering into a narrow filament that can protrude hyphal walls and interact with the host cytoplasm through nanometer-pores are representative for *Tremella* species (Fig. 22). Tremelloid haustoria are frequent in Tremellomycetes (Figs. 23, 24), and they are typical also for several mycoparasites in the Pucciniomycota, e. g. species of the genera *Classicula* of the Classiculales (Bauer et al. 2003), *Cystobasidium* (Sampaio & Oberwinkler 2011) and *Occultifur* (Oberwinkler 1990) of the Cystoba-

sidiales, *Spiculogloea* (Langer & Oberwinkler 1998) of the Spiculogloeales, or *Zygogloea* (Bauer 2004).

The convergent evolution of the tremelloid haustorium in Pucciniomycotina and the Tremellomycetes of the Agaricomycotina cannot be explained.

Evolutionary trends in tremelloid haustoria:

A common origin for nanometer-fusion mycoparasites of the Pucciniomycotina and the Tremellomycetes or
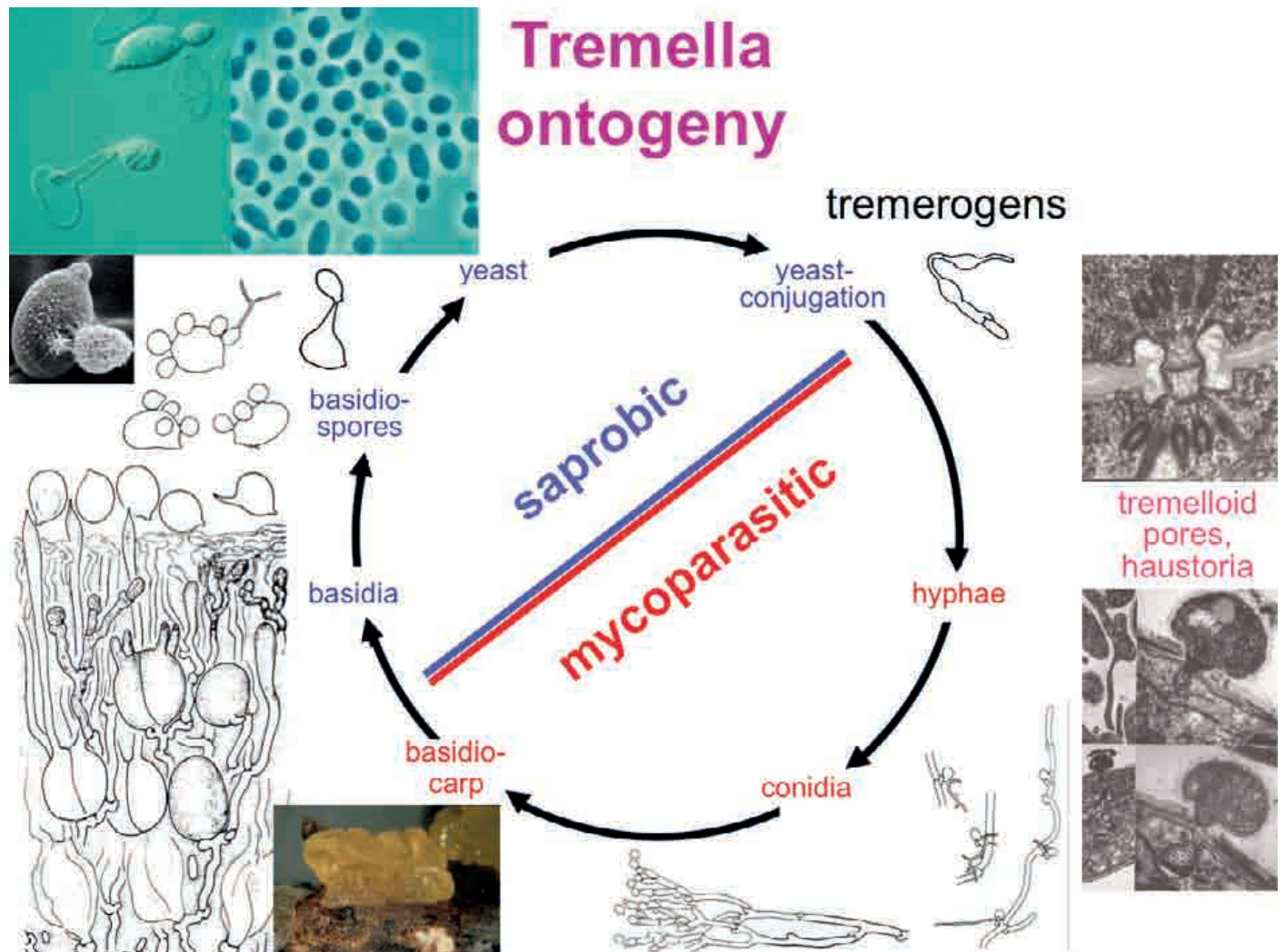
Fig. 22: Ontogeny of *Tremella*. The dimorphic and bitrophic life cycle of tremelloid fungi is compiled in this scheme. Basidiospores germinate by budding, by producing secondary spores or occasionally by hyphae. The yeast phase is saprobic. Conjugation of compatible yeast cells is initiated by tremerogens, followed by hyphal growth. Tremelloid haustoria develop early in ontogeny, sometimes already in the yeast stage. Mycoparasitic interactions occur when adequate hosts are available. Hyphal septa are characterized by tremelloid dolipores with specific tubular parenthesome cisternae. Asexual propagation with conidia occurs before or during basidiospore development. Most tremelloid species have gelatinous hyphal systems and basidiocarps. Modified from OBERWINKLER (2009).

a convergent evolution has been discussed by BAUER (2004). There is no possibility, so far, to understand evolutionary trends in tremelloid mycoparasites.

Some additional mycoparasitic interaction types

The micrometer-fusion type

LUTZ et al. (2004a,b) were able to experimentally prove that *Tuberculina*, mycoparasitic on rust fungi, is a developmental stage of the plant parasite *Helicobasidium*. Micromorphological and molecular data indicate that the Helicobasidiales are closely related with the Pucciniales. Unique micrometer-fusion channels between host and parasite cells potentially allow the transfer of cell organelles (BAUER & al. 2004). Infection experiments revealed a high diversity in host specifity (LUTZ et al. 2004c), probably indicating coevolutionary processes.

Intracellular haustoria with nanometer-fusion

Based on unique micromorphological characters, the mycoparasitic *Platygloea sebacea* has been transferred in an own genus, *Naohidea* (OBERWINKLER 1990). BAUER (2004) found intracellular haustoria with nanometer-fusion pores, typical for tremelloid haustoria. Evolutionary trends are not recognizable in the *Naohidea* mycoparasitism.
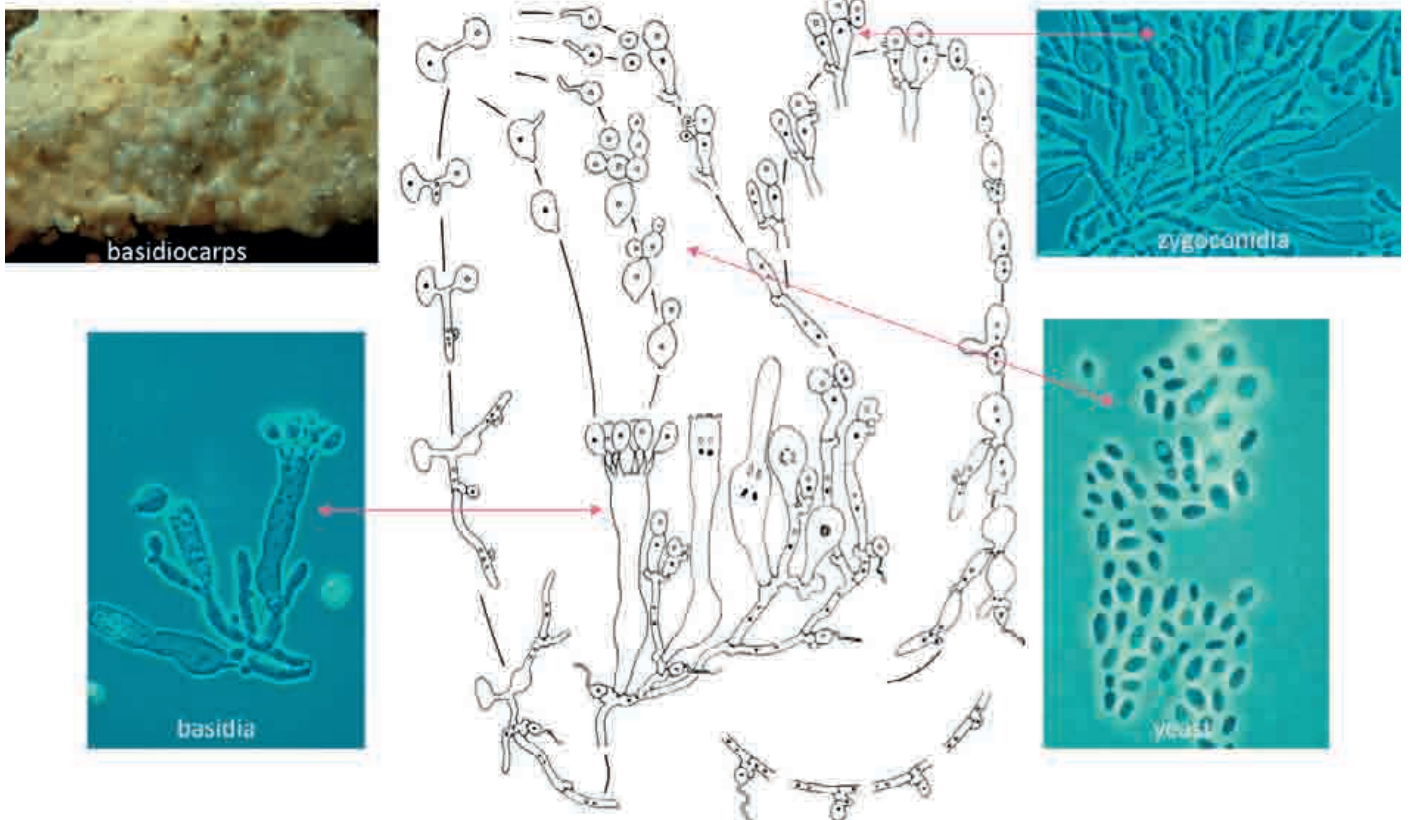
Intracellular haustoria with unknown interaction

The agaricoid *Asterophora* species grow on *Lactarius* and *Russula* hosts, often in old and decaying basidiocarps. Therefore, they are mostly considered as being saprotrophic. However, already in young developmental stages, inter- and intracellular hyphae of the mycoparasite are present in host cells. Specific haustorial structures are absent. The ultrastructure of interactive structures has not been studied.

Up to 15 species are known in the mycoparasitic genus *Squamanita* (MATHENY & GRIFFITH 2010) of the Cystodermateae in the Agaricales. The authors found that *S. paradoxa* is a specific mycoparasite of *Cystoderma amianthinum*. *Squamanita odorata* is known as a parasite of *Hebeloma mesophaeum* (MONDIET et al 2007), and *S. umbonata* occurs on *Inocybe oblectabilis* (VIZZINI & GIRLANDA 1997). MATHENY & GRIFFITH (2010) conclude that up to five species of *Squamanita* may parasitize closely related species, given that the molecularly based phylogenetic hypothesis is correct. In mycoparasitic *Squamanita* species no data are available concerning the cellular interactions of parasite and host.

The few mycoparasites known in the Boletales will be briefly mentioned later when mycorrhizae and their switches to other nutritional modes are discussed.

Evolutionary trends in parasitic Agaricales:

> Origin polyphyletic > hostrange restricted to mushrooms > hostrange restricted either to Agaricales or Russulaceae

Plant parasites

Plants are the key players in fungal evolutionary processes. Interactions between plants and fungi are manifold, but terminologically reduced to few categories, like symbiosis, mutualism, parasitism, saprophytism, or endophytism. More specific categories were chosen for this overview (Fig. 17). In all three subdivisions of Basidiomycota, plant parasites are widely distributed and ecologically of particular importance. Pucciniales, Microbotryomycetes, Ustilaginomycotina, Polyporales, Hymenochaetales and Russulales constitute the dominant plant parasites in the Basidiomycota.

Pucciniales (Uredinales), rust fungi

The most important fungal plant parasites are the rust fungi. They have a worldwide distribution and occur on ferns and seed plants with approximately 8000 species. Their whole life cycle depends on parasitic interactions and many species have obligatory host alternations.

The origin of the Pucciniales is unknown, their evolutionary trends in life cycles and host dependencies are partly well explored and experimentally proven. Molecularly based phylogenetic hypotheses can be tested for their reliability concerning coevolutionary processes in rust fungi and their host plants.

The so-called „typical rust fungus life cycle" is the one of *Puccinia graminis*, the black stem rust of grasses (Fig. 26). Because there are many other rust fungi with equivalent ontogenies, it makes sense to briefly explain this life story. There are five very important strategies involved: (1) all developmental stages are parasitic ones, (2) the haplophase depends on another host than the dikaryophase, (3) the aeciospores initiate the host alternation, (4) the urediniospores spread out the pathogen on the host for the dikaryophase, (5) the sequence of spore generations is fixed, irrespective of losses of them.

## Evolutionary trends in rust fungal host dependencies:

> Primary autoecious (hypothetical) > heteroecious > autoecious
>
> Host alternations > only one host

◄

Fig. 23: Morphology and mycoparasitism of *Tremella encephala* on *Sterum sanguinolentum*. The parasite forces the host to grow hypertrophically. Host hyphae broad and without clamps, *Tremella* hyphae narrow and with clamps, haustorial attachments marked with arrowheads. The gall-like to cerebriform growth is the result of a hyphal mixture of both fungi. The gelatinous *Tremella* hymenium is on the periphery of the galls. Orig. F. OBERWINKLER.

◄

Fig. 24: Life cycle and mycoparasitism of *Christiansenia pallida* on *Phanerochaete cremea*. Monokaryotic basidiospores bud and produce yeast colonies. Compatible yeast cells conjugate and grow with dikaryotic hyphae that produce tremelloid haustoria. Dikaryotic conidia predominantly develop in the parasitic stage, continue to grow with dikaryotic hyphae or dedikaryotize and then begin to bud. Basidia are suburniform and often more than four-spored. Strongly modified from OBERWINKLER et al. (1984).
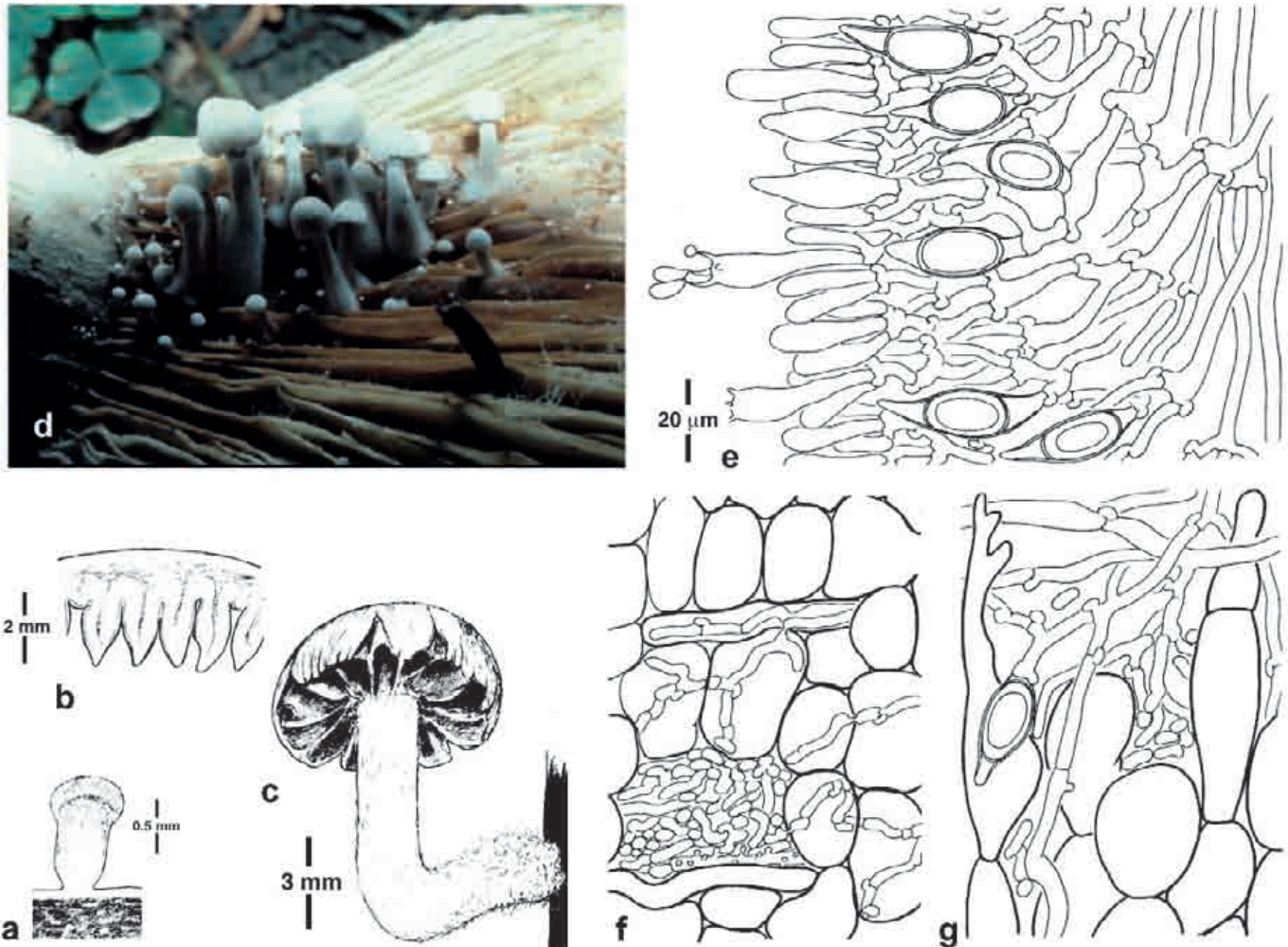
Fig. 25: Morphology and mycoparasitism of *Asterophora parasitica* on *Russula nigricans*. **a** young basidiocarp. **b** early developmental stages of lamellae. **c** mature basidiocarp. **d** colony of basidiocarps in different developmental stages, growing on the lamellae of the host. **e** hymenium and subhymenium with chlamydospores. **f** and **g** hyphae of the parasite in the host. Orig. F. OBERWINKLER.

The following discussion refers basically to Pucciniales distributed in the northern hemisphere. Data were mostly extracted from GÄUMANN (1959), POELT & ZWETKO (1997), and ZWETKO & BLANZ (2004) over a long time, and condensed to schemes for teaching purposes.

Primary autoecious rust fungi are not known but they must have existed because heteroecism requires simpler ancestors. In a molecular phylogenetic hypothesis of AIME (2006) the anamorphic rust fungus *Caeoma torreyae* is in a basal position, followed by a clade containing *Mikronegeria alba, Blastospora smilacis, Hemileia vastatrix*, and *Maravalia cryptostegiae*. – It was convincing to assume that the rust lineage begins with fern rusts, however, they have host alternations restricted to *Abies* species in the haplophase. A cladistic approach to the question „do primitive hosts harbor primitive parasites?" (HART 1988) excluded fern rusts from basal phylogenetic positions. The first molecularly based phylogenetic studies of rust fungi comprising fern rusts (SJAMSURIDZAL et al. 1999, MAIER et al. 2003) confirmed the cladistic findings.
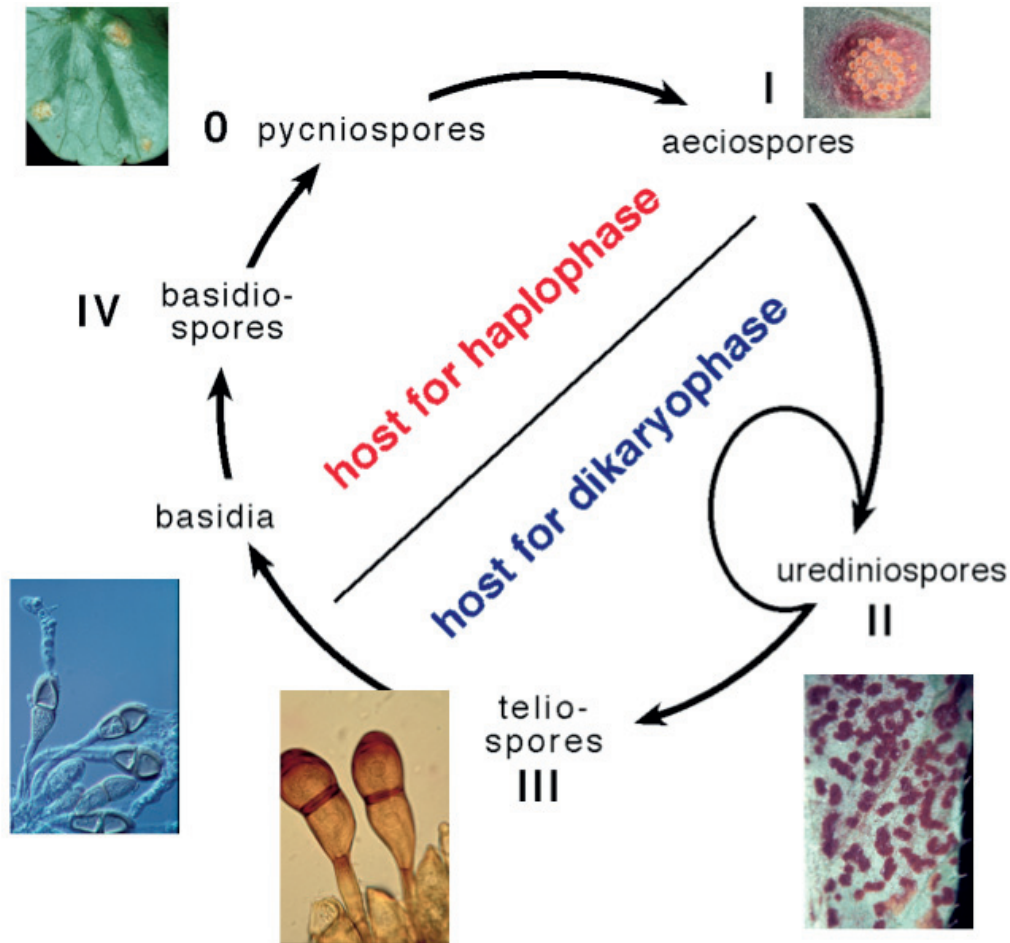
Fig. 26: The typical life cycle of rust fungi, as in *Puccinia graminis*. Basidiospores (IV) infect the specific host for the haplophase. Monokaryotic pycniospores (0) develop and can fertilize aeciospore intitial stages on the same host. This process results in dikaryotic aeciospores (I). Aeciospores are no more able to infect the host on which they were produced. In contrast, they have to be distributed randomly for finally reaching their specific second host. On that one, vegetative propagules, the urediniospores (II) are developed in quantities for the purpose of effective distributing the dikaryophase. Finally, the teliospores (III) develop on the same host. They are probasidia, i.e. karyogamy occurs in their cells. Teliospores germinate to produce meiosporangia and basidiospores that terminate the ontogenetic cycle. Orig. F. Oberwinkler.

Evolutionary trends in life cycles:

Autoecious (hypothetical) > heteroecious > autoecious

Eu-type 0, I, II, III, IV: heteroecious > autoecious

Aecidial repetition 0, I, I, I, II, III, IV: heteroecious > autoecious

Opsis-type 0, I, III, IV: heteroecious > autoecious

Brachy-type 0, II, III, IV: autoecious

Mikro-type (0), III, IV: autoecious

Endo-type (0), I, IV: autoecious

Only few examples are given for the different life cycles:

- Eu-type, heteroecious: *Puccinia graminis, Cronartium ribicola* and many others.
- Eu-type, autoecious: *Phragmidium* spp.
- Aecidial repetition, autoecious: *Phragmidium mucronatum*
- Opsis-type, heteroecious: *Gymnosporangium* spp.
- Opsis-type, autoecious: *Uromyces primulae-integrifoliae*
- Brachy-type, autoecious: *Frommea obtusa, Kuehneola uredinis, Trachyspora intrusa*
- Micro-type, autoecious: *Puccinia aegopodii, P. malvacearum*
- Endo-type, autoecious: *Endocronartium* spp., *Endophyllum* spp.

Tranzschel's rule describes a reductive coevolutionary trend: micro-type rusts live on aecial hosts of their closely related heteroecious eu-type species. The following examples can document this evolutionary process:

- *Chrysomyxa rhododendri* heteroecious: 0, I on *Picea*, II, III on *Rhododendron*
- *Chrysomyxa abietis* microcyclic: III on *Picea*
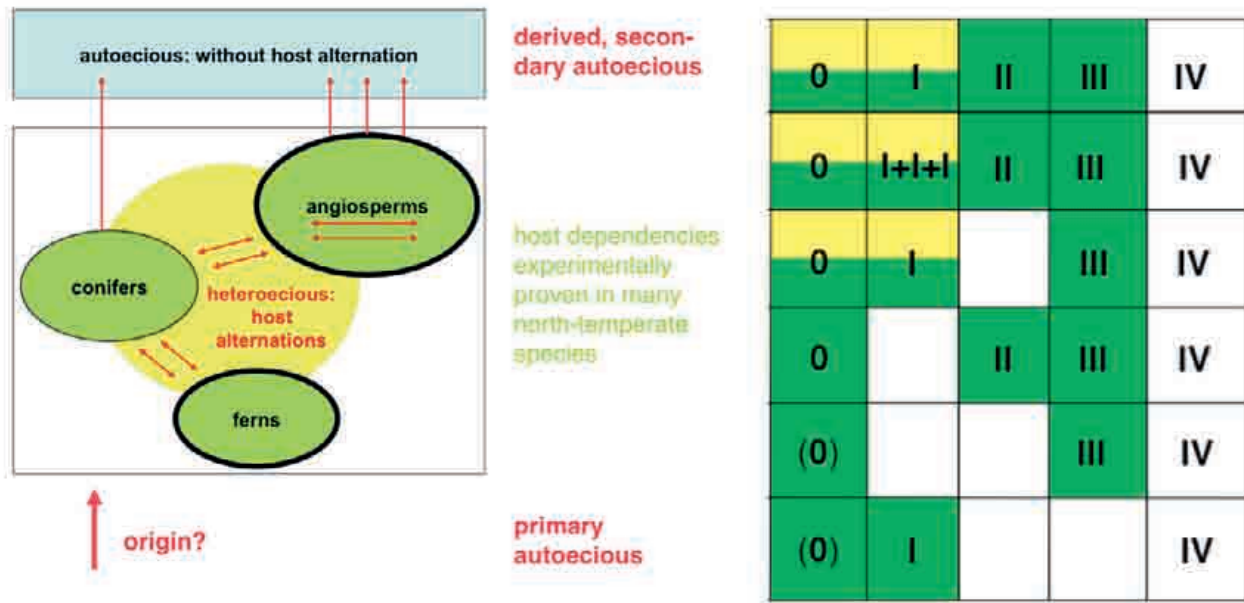
Fig. 27: Host dependencies and life cycles of rust fungi, Pucciniales. Primary autoecious rust fungi are not known. Conifers are most important hosts for haplophases of rust with alternations to ferns and angiosperms, harboring the dikaryophases. Secondary autoecious rusts evolved in many convergent lineages from orginally heteroecious ones. Strongly modified after Oberwinkler (2009). – The life cycle variations are shown in the diagram to the right and will be explained below as evolutionary trends. 0 – Pycniospores, I – Aeciospores, II – Urediniospores, III – Teliospores, IV – Basidiospores. Autoecious life cylce 0-IV: yellow – green, heteroecious life cycle 0-IV: green. White boxes without numbers: spore generation lacking.
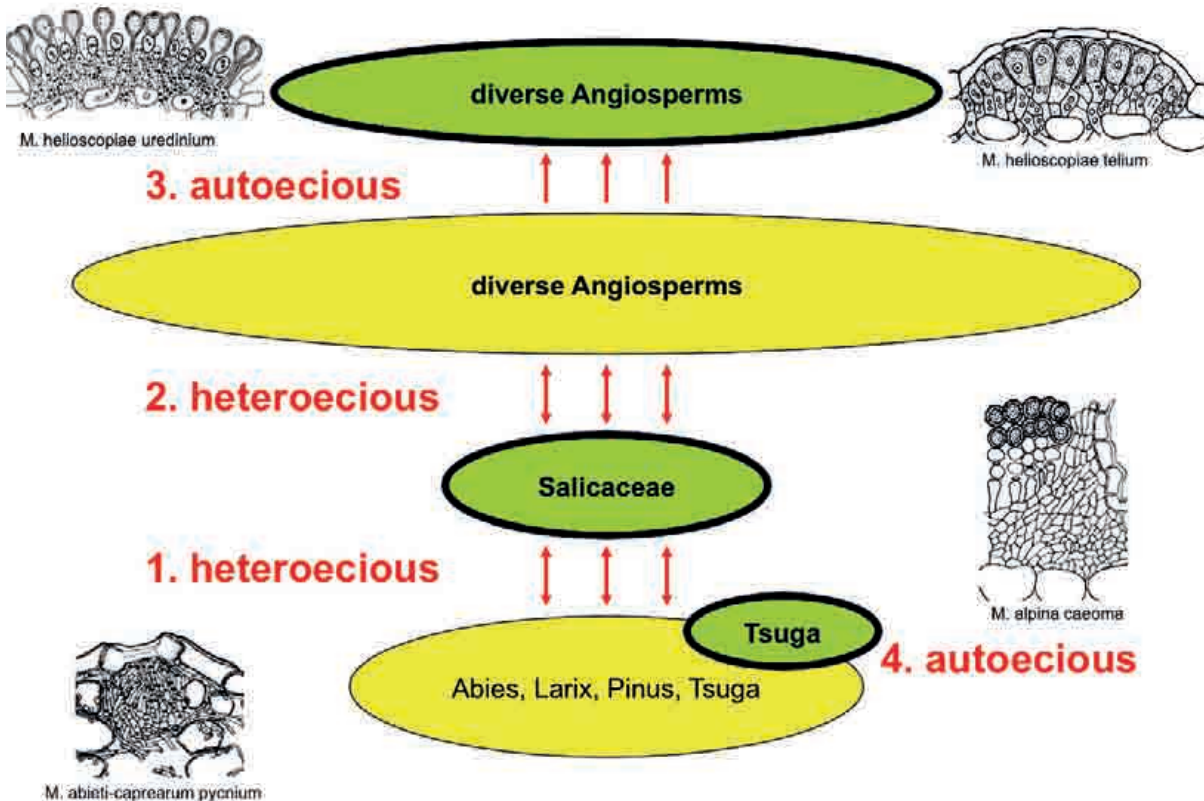
Fig. 28: Evolutionary steps in life cycles and host dependencies of *Melampsora* species. Evolutionary trends in this model genus of rust fungi are: primary heteroecious > secondary heteroecious > autoecious. The loss of a host alternation can also happen on *Tsuga,* the primary haplophase host. Illustrations from Fischer 1902, Hunter 1936, Mayor 1920, Sappin-Trouffy 1896. Orig. F. Oberwinkler.
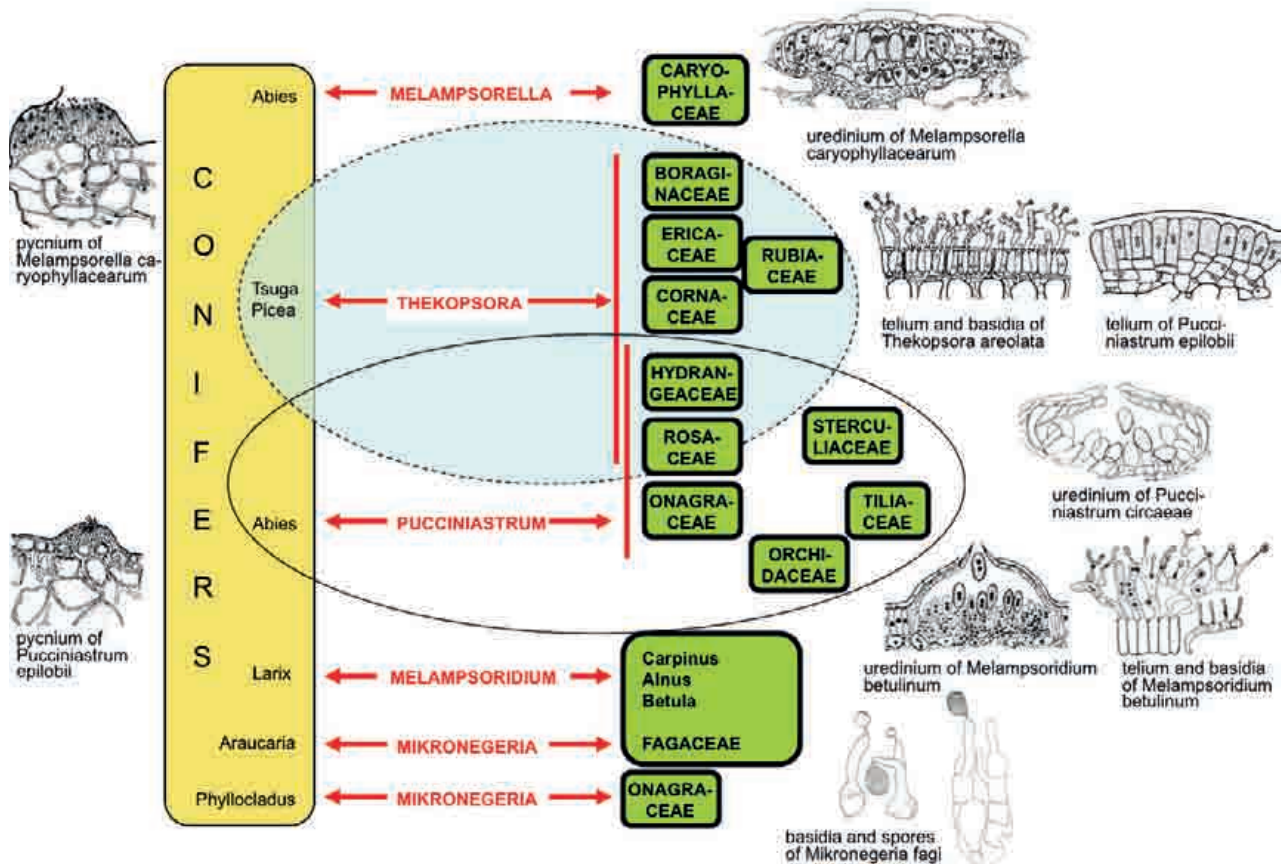
Fig. 29: Rust fungi of the Mikronegeriaceae and Pucciniastraceae with haplophases on conifers and host alternations with various Dicotyledons. The three *Mikronegeria* rust fungi are restricted to southern South America and New Zealand, Pucciniastraceae are distributed in the Northern Hemisphere within the distribution range of *Abies, Larix, Picea* and *Tsuga* species. Illustrations from Fischer 1902, Hunter 1936, Pady 1933, Sappin-Trouffy 1896, and Oberwinkler.

- *Tranzschelia pruni-spinosae* heteroecious: 0, I on *Anemone*, II, III on *Prunus*
- *Tranzschelia fusca* microcyclic: III on *Anemone*
- *Uromyces rumicis* heteroecious: 0, I on *Ficaria*, II, III on *Rumex*
- *Uromyces ficariae* microcyclic: III on *Ficaria*
- *Puccinia coronata* heteroecious: 0, I on *Rhamnus*, II, III on Poaceae
- *Puccinia mesnieriana* microcyclic: III on *Rhamnus*

The genus *Melampsora* can serve as a model taxon for documenting major evolutionary and coevolutionary trends in the Pucciniales (Fig. 28). Primary hosts for the haplophase are species of the conifer genera *Abies, Larix, Pinus,* and *Tsuga* in the Pinaceae.

The original heteroecious *Melampsora* species were heteroecious with the dikaryophase on species of *Populus* and *Salix* of the Salicaceae. Species were then evolved with host alternations to various other Angiosperms, using these as hosts for their haplophase. Finally, heteroecism broke down, and autoecious species evolved with effective radiation on closely related hosts, e.g. *Euphorbia*. Remarkable is that the transition from heteroecism to autoecism also occurred on the primary hosts for the haplophase, as documented by *Melampsora farlowii* on *Tsuga canadensis* and *T. caroliniana* in eastern North America (Hepting & Toole 1939). In phylogenetic hypotheses based on molecular data (Maier et al. 2003, Pei et al. 2005, Aime 2006), *Melampsora* is confirmed as a monophylum.

A second example of rust fungi with host alternations from conifers to angiosperms is illustrated in Fig. 29 for the Mikronegeriaceae and Pucciniastraceae. – Two *Mikronegeria* species, *M. fagi* and *M. alba*, with their dikaryophase on *Nothofagus* are known from southern South America (Butin 1969, Peterson & Oehrens 1978). The haplophase of *M. fagi* grows on *Araucaria araucana*, the one of *M. alba* on *Austrocedrus chilensis*. Crane & Peterson (2007) were able to experimentally prove the host alternation of a third species in New Zealand, *M. fuchsiae*, growing on *Phyllocladus* spp. in the haplophase and *Fuchsia excorticata, F. perscandens* and the introduced *F. magellanica* in the dikaryophase. – *Melampsoridium* rusts are restricted in the haplophase to *Larix* hosts and grow in the dikaryo-
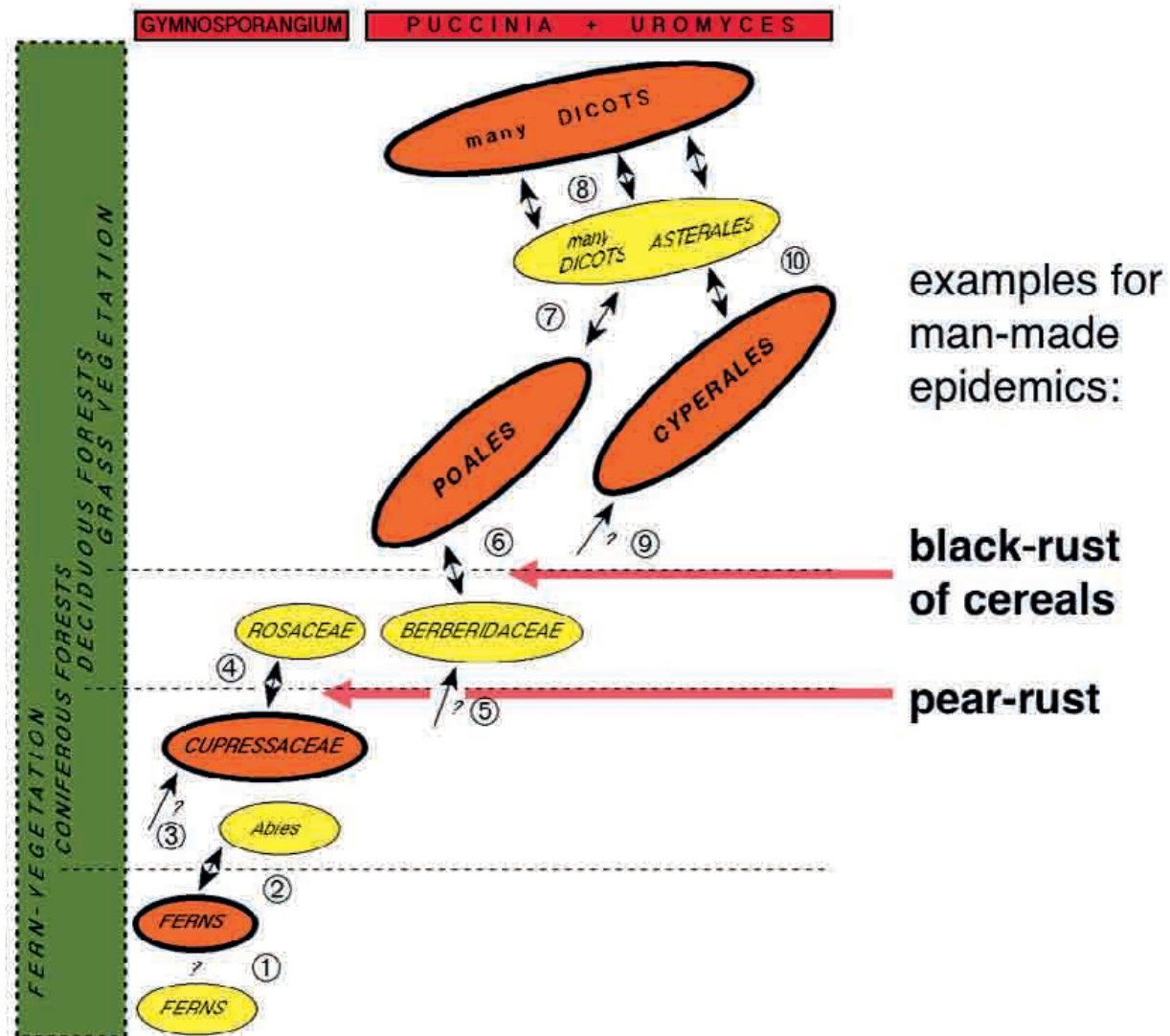
Fig. 30: A hypothesis of rust fungal coradiation with plants in evolving vegetation types of the Northern Hemisphere. Yellow ellipses show the host groups for haplophases, red ellipses those for the hosts harboring the dikaryophase stages. (1) The origin of Pucciniales as autoecious and/or as heteroecious plant parasites is not known. The extant fern rusts are not the ancestors of rust fungi according to molecular phylogenetic hypotheses. (2) Heteroecious fern rusts live in coniferous climax vegetations because they depend on *Abies* species as exclusive hosts for their haplophases. The restriction of the haplophase to one genus of the conifers cannot be explained. Autoecious fern rusts are also known outside the geographical range of *Abies*, for example in the Southern Hemisphere. (3, 4) *Gymnosporangium* rusts are exceptional because of a unique host dependency with the dikaryophase on conifers, i.e. exclusively on Cupressaceae. All hosts for the haplophase are species of the Rosaceae-Maloideae, except very few members of the Hydrangeaceae including Philadelphaceae, Juglandaceae, and Myricaceae. No explanations can be given for the origin and the host selectivity of *Gymnosporangium*. Woodlands with *Juniperus* and species of the Maloideae are a prerequisite for *Gymnosporangium* development and coevolution. (5, 6) A high diversity of *Puccinia* and *Uromyces* evolved on Poaceae as hosts of the dikaryophase. Associated woody plants of the Berberidaceae, Rhamnaceae, and Caprifoliaceae are possibly primary hosts for the haplophase. (7) Many herbaceous species of the Dicotyledons, e.g. Ranunculaceae, Crassulaceae, Oxalidaceae, Boraginaceae, Apiaceae, Asteraceae, and of the Monocotyledons served as hosts for the haplophases. (8) Numerous secondary autoecious species resulted in close coevolutionary processes, e.g. *Uromyces* on Fabaceae. (9) The origin of heteroecious rusts with their dikaryophases on Cyperaceae, mainly on *Carex*, is not known. Their hosts for the haplophases are richly diversified on Asteraceae, but occur also on Orobanchaceae, Primulaceae, Urticaceae, Celastraceae (*Parnassia*), Onagraceae, and Grossulariaceae. Microcyclic derivatives evolved frequently in the Asteraceae. The *Puccinia-Uromyces* relationship coevolved with grasslands and vegetations dominated by herbaceous plants. – The red arrows point to the positions of two economically important rust species, the black or stem rust of grasses, including cereals, *Puccinia graminis*, and the pear rust, *Gymnosporangium sabinae*. Orig. F. OBERWINKLER.
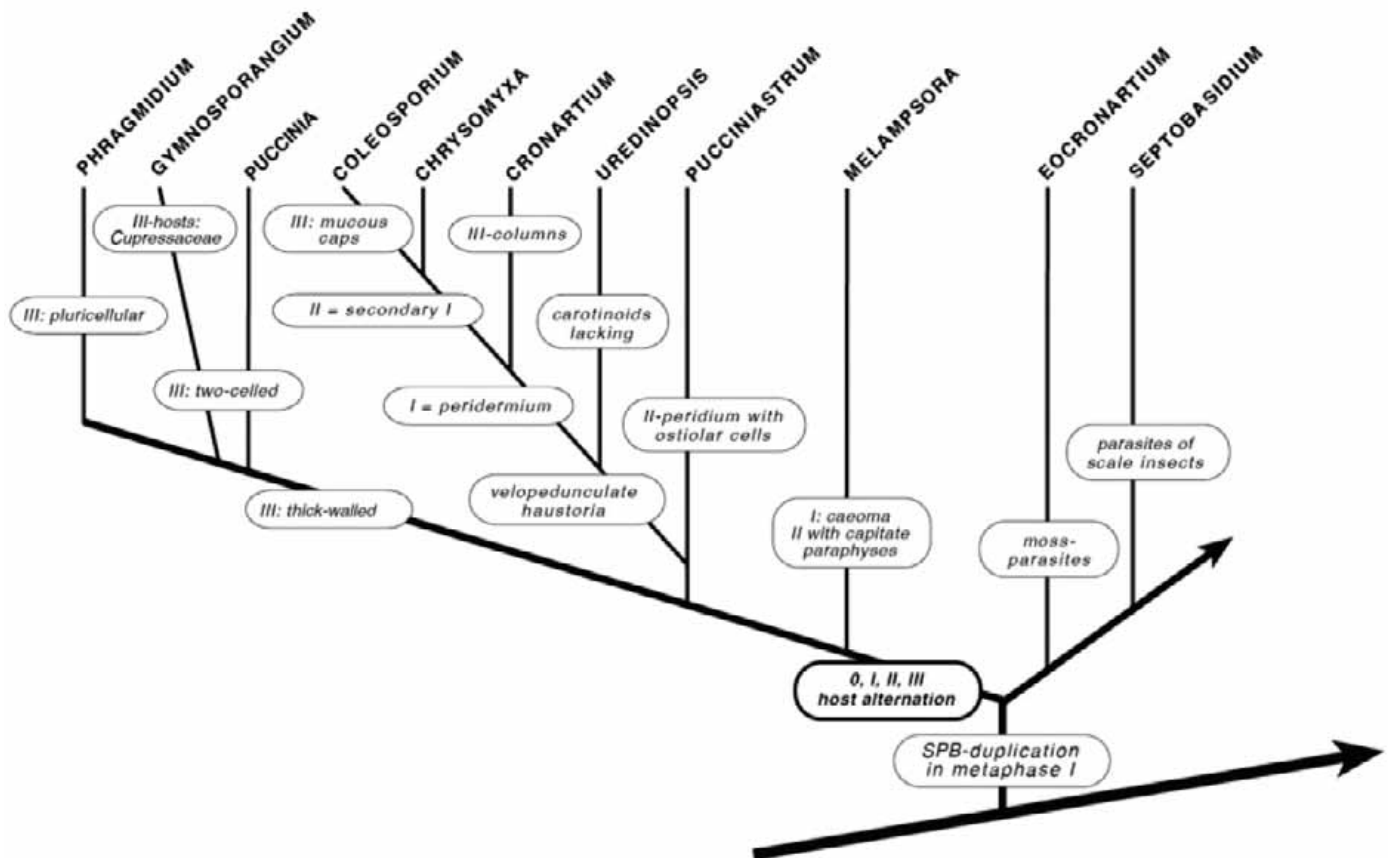
Fig. 31: Simplified phylogeny of selected genera of the Pucciniales and few related parasitic fungi of the Pucciniomycetes, based on morphological and life cycle characters. In species of the Pucciniomycetes hyphae have no clamps, septal pores are often associated with microbodies and intermeiotic SPB duplication occurs typically in metaphase (Bauer et al. 2006). Essential assumptions are primarily autoecious and subsequent heteroecious ancestors for the Pucciniales. Teliospores are thin-walled and hyaline in basal rust fungi and thick-walled and pigmented in derived ones. *Melampsora* is characterized by aecial caeomata and uredinial capitate paraphyses. *Pucciniastrum* has uredinial peridia with ostiolar cells. *Uredinopsis, Cronartium, Chrysomyxa,* and *Coleosporium* share the common feature of velopedunculate haustoria (Berndt 1996, Berndt & Oberwinkler 1997). Carotinoids are common in rust fungi, however, they are lacking in the fern rust *Uredinopsis*. An aecial peridermium is a synapomorphy for *Cronartium, Chrysomyxa,* and *Coleosporium* species. Urediniospores can be considered secondary aeciospores in *Chrysomyxa* and *Coleosporium*. *Coleosporium* basidia have mucous terminal parts and they replace teliospores (III) what has been interpreted as internal germination. *Puccinia* and *Gymnosporangium* share two-celled teliospores while *Phragmidium* has pluricellular ones. – Further mutualists within the Pucciniomycetes comprise the plant parasitic Platygloeales with *Eocronartium* in the diagram, and parasites of scale insects, the Septobasidiales. Orig. F. Oberwinkler.

phase on species of the Betulaceae. – *Abies* species harbor the haplophases of *Pucciniastrum* and *Melampsorella* rusts. Caryophyllaceae serve as the exclusive hosts for the *Melampsorella* dikaryophase, while *Pucciniastrum* species occur in their dikaryophase on host species of the Onagraceae, Rosaceae, Hydrangeaceae, and Malvaceae (Sterculiaceae and Tiliaceae), and autoecious species live on Orchidaceae. In his *Pucciniastrum* mono-

graph, Naohide Hiratsuka (1927) characterized the genus by „Uredolager von einer halbkugeligen oder kegelförmigen Pseudoperidie umschlossen, die sich mit einem scheitelständigen Porus öffnet." Teliospores are thin-walled and grouped in subepidermal layers, this in contrast to *Thecaphora* species with intracellular telia. Aecia of *Thecaphora* species are grouped, covering the inner surface of cone scales of *Picea* species.

The origin and the driving forces for the evolution of host alternations in rust fungi are unknown. Because of this unique life strategy, it seems convincing to predict one common ancestor for the Pucciniales. Their main evolutionary radiation, both as heteroecious and autoecious parasites was closely connected with the evolution of their hosts, the seed plants. A rich diversification took place on coniferous hosts (Figs. 28, 29, 30). Few addi-
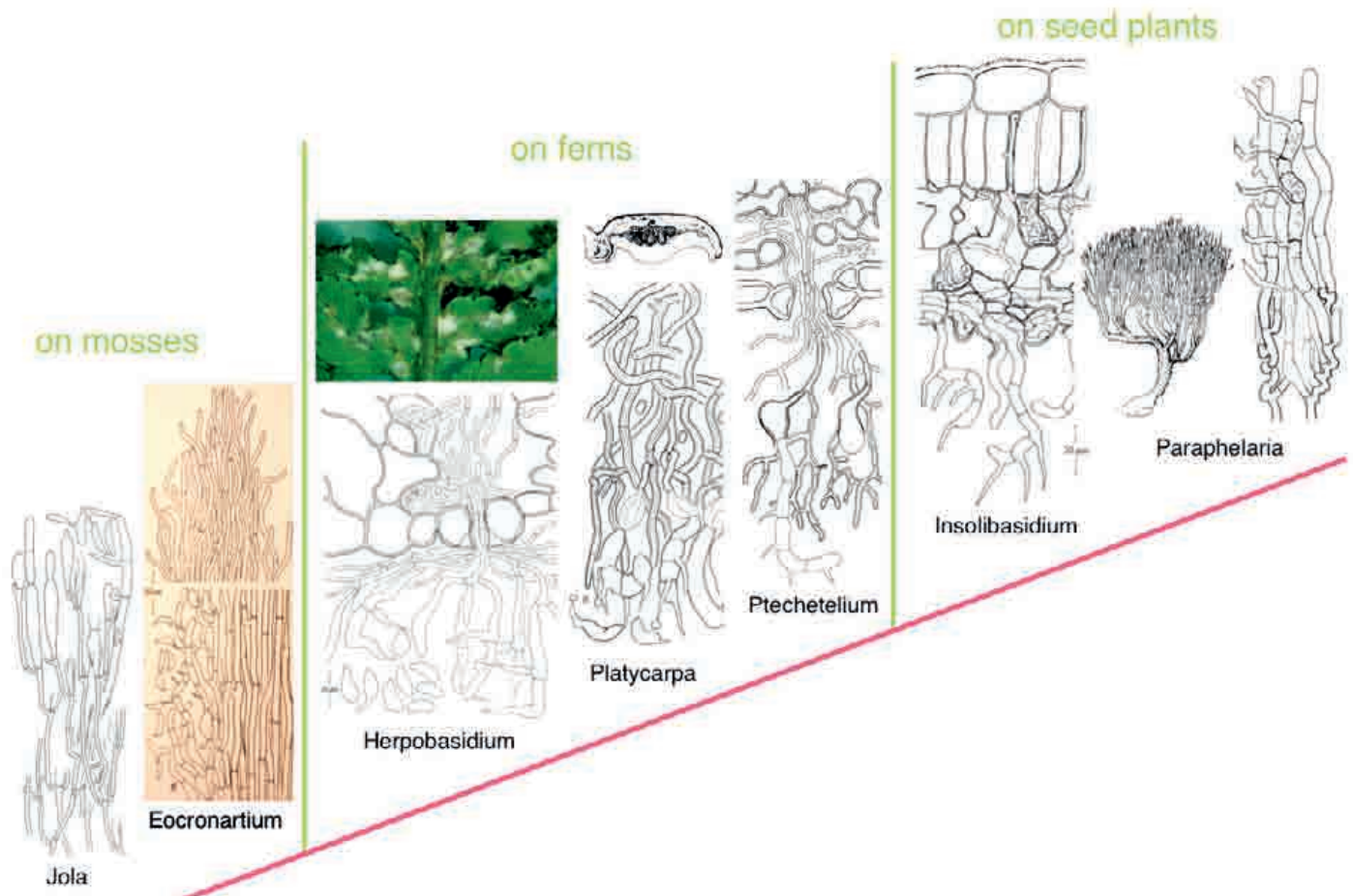
Fig. 32: Representatives of the Platygloeales arranged according to the phylogeny of their host plants. The tropic and subtropical *Jola* species produce gelatinous pustules around spore capsules of mosses (Bryopsida). *Eocronartium* is clavarioid and arises from the gametophyte or sporophyte initials of mosses. The ramarioid *Paraphelaria amboinensis* grows on roots of bamboos in Southeast Asia. The parasites on ferns, *Herpobasidium, Platycarpa,* and *Ptechetelium,* as *Insolibasidium* on Caprifoliaceae, have resupinate fructifications. Orig. F. Oᴀᴇʀᴡɪɴᴋʟᴇʀ.

tional examples will be briefly mentioned (Fig. 31).

Cronartium is characterized by long columns of teliospores. The haplophase only occurs on *Pinus* species. Most of the hosts for the dikaryophase belong to the Lamianae of the Asteridae, predominantly species of genera in the Apocynaceae, Gentianaceae and Orobanchaceae, but also in Fagaceae, Balsaminaceae, Paeoniaceae and Grossulariaceae. *Cronartium ribicola* is restricted to fife-needle pines, other species develop their haplophase on two-three-needle pines. A special reduction of the life cycle occurred in *Endocronartium* with heteroecious species and an endo-type life cycle (Fig. 27).

The haplophase of *Chrysomyxa* species is restricted to *Picea*. Ericaceae, inclusive of the former Empetraceae and Pyrolaceae are the exclusive host groups for the dikaryophase. An autoecious species is *Chrysomyxa abietis* on *Picea abies*.

Basidia with mucous caps are replacing teliospores (III) in *Coleosporium*. Heteroecious species have a host alternation between *Pinus* species for the haplophase and mainly species of the Asteridae (Apocynaceae, Rubiaceae, Orobanchaceae, Lamiaceae, Campanulaceae, Asteraceae) and

some Ranunculaceae. *Coleosporium* is also reported as autoecious from Orchidaceae.

The first representative phylogenetic hypothesis of the Pucciniales, based on molecular data (Mᴀɪᴇʀ et al. 2003), documented the common origin of *Puccinia, Uromyces, Endophyllum* and *Cumminsiella*, and the monophyly of the autoecious rusts on Rosaceae *Phragmidium, Kuehneola, Triphragmium* and *Trachyspora*. Also each of the genera *Chrysomyxa, Coleosporium, Cronartium, Gymnosporangium, Melampsora, Phragmidium* and *Tranzschelia,* as well as the Pucciniastreae sensu Dɪᴇᴛᴇʟ, are monophyletic.
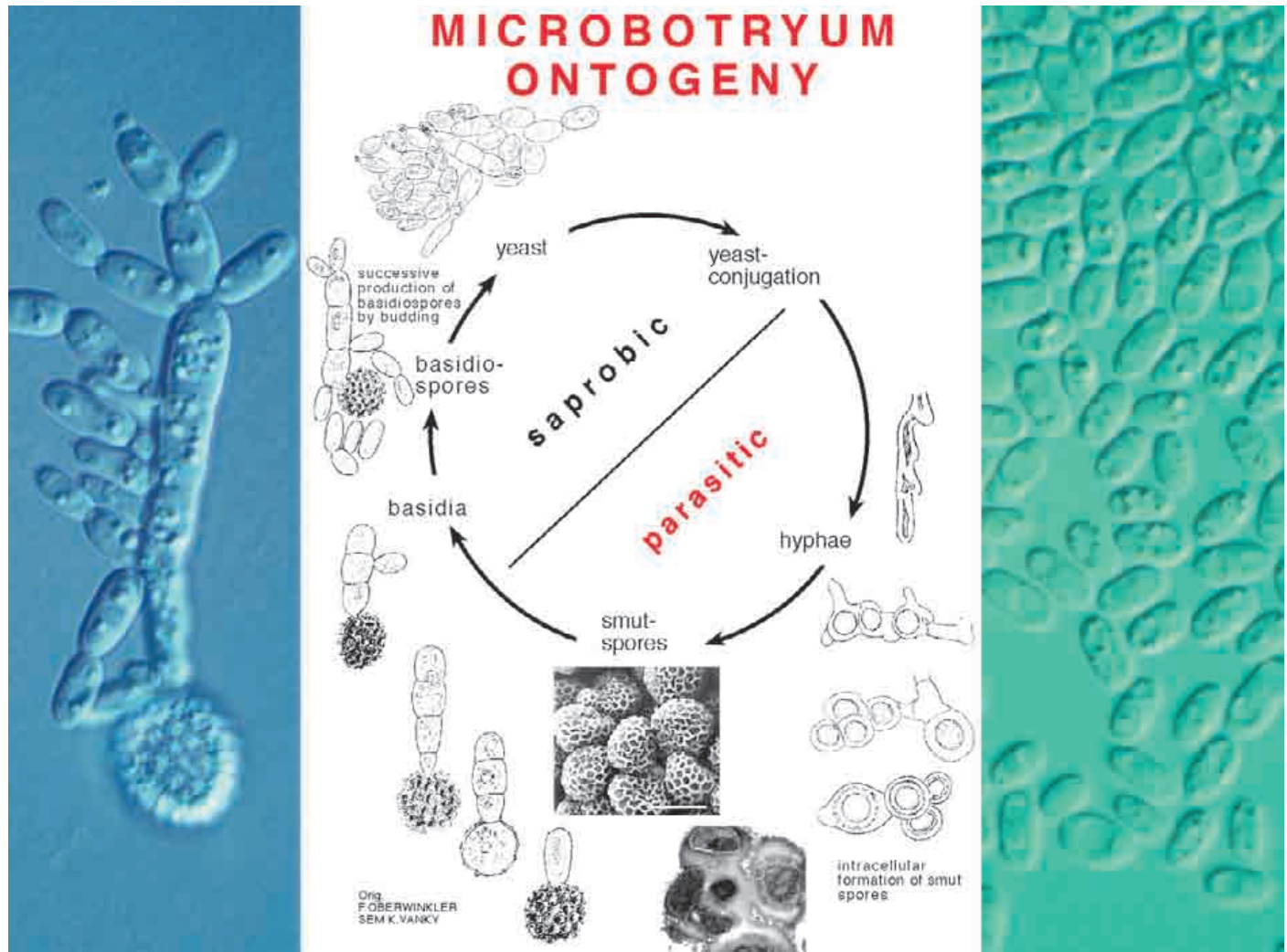
Fig. 33: Life cycle of *Microbotryum violaceum*. In most *Microbotryum* species, smut spores (teliospores, probasidia) are developed in the anthers of their hosts. They germinate with basidia and bud off basidiospores, also called sporidia (left). Budding continues and yeast colonies develop, representing the saprobic stage (right). After conjugation of compatible yeasts, hyphae develop and infect suitable hosts. Smut spores originate inside hyphae in specific organs of the host. Orig. F. Oberwinkler.

Plant parasites related to rust fungi

Besides rust fungi, Pucciniomycotina comprise additional plant parasites with particular importance for the understanding of evolutionary trends. This may be the case for the *Herpobasidium* relationship (Fig. 32), now named Platygloeales. All species in this group share unclamped hyphae, simple septal pores, and auriculariloid basidia with an active spore release. Considering host dependencies, the sequence of major steps was from mosses to ferns and seed plants. Oberwinkler & Bandoni (1984) revised the fern parasitic species of *Herpobasidium* and *Platycarpa*, introduced *Ptechetelium cyatheae*, also on ferns, and *Insolibasidium deformans* growing on species of Caprifoliaceae. In a phylogenetic hypothesis, based on molecular data (Aime et al. 2007), the Platygloeales contain *Platygloea, Insolibasidium, Eocronartium*, and *Jola. Herpobasidium, Platycarpa, Ptechetelium* and *Paraphelaria* were not included in this study.

Possible evolutionary trends in plant parasites related to rust fungi:

Coevolution with the hosts: on mosses > ferns > seed plants

Basidiocarps inconspicuous resupinate > clavarioid > ramarioid

Because of insuffient sampling, molecular phylogenetic hypotheses are fragmentary and cannot yet be used for testing the above mentioned evolutionary trends.
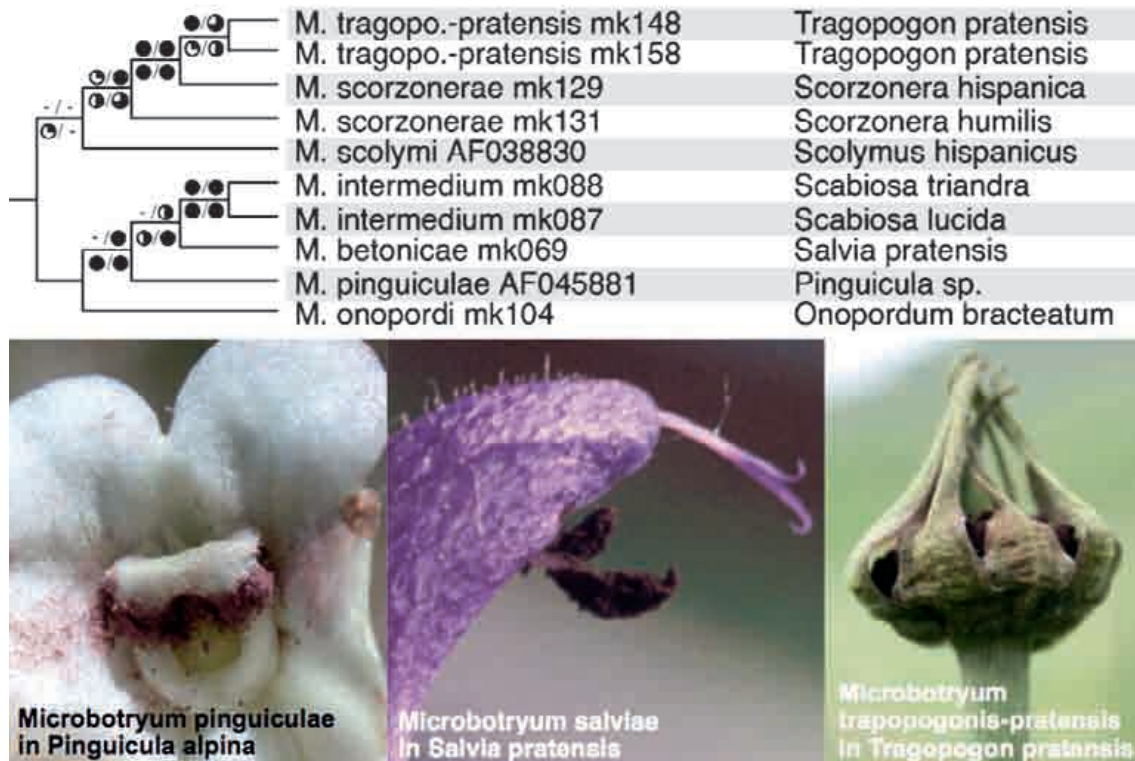
Fig. 34: Specific host dependencies in *Microbotryum* s.l. on members of the Asteridae. Both, hosts and parasites are monophyletic. However, *Microbotryum onopordi* is not congruent with the Asteraceae clade. The tree is part of a strict consensus of 1780 most parsimonious trees inferred from the dataset consisting of three concatenated, complete ITS alignments. Symbols on branches indicate the magnitude of parsimony bootstrap values from analyses of the dataset after exclusion of alignment-ambiguous sites (upper left) and of the three different, complete alignments made with MAFFT (upper right), PCMA (lower left), and POA (lower right), from Kemler et al. (2006). – *Microbotryum pinguiculae* sporulates in the anthers of *Pinguicula alpina*, *M. salviae* (*betonicae*) in the anthers of *Salvia pratensis*, and *M. tragopogonis-pratensis* in the flower head of *Tragopogon pratensis*. Photos orig. F. Oberwinkler.

Microbotryomycetes, false smuts and related fungi

Basidiomycetous fungi with basically different trophic requirements are included in Microbotryomycetes. Heterogastridiales contain mycoparasites with colacosomes (see colacosome fungi), the teleosporic Leucosporidiales and Sporidiobolales also have colacosomes, but are not considered to be mycoparasitic. The plant parasitic false smuts, Microbotryales have smut spores but no colacosomes.

The ontogeny, including trophic stages, of *Microbotryum* (Fig. 33) is for the most part a duplication of the *Ustilago* life cycle. Such comprehensive convergency is rare and may be compared in basidiomycetous fungi only with the multiple and independent evolution of agaricoid basidiomata.

When studying anther smuts of the Caryophyllaceae, Deml & Oberwinkler (1982), became aware of the heterogeneity of so-called *Ustilago* species. To accomodate *Ustilago violacea*, they reintroduced *Microbotryum*, a genus erected by Léveillé already in 1847. Since then *Microbotryum violaceum* has become a model organism for studies in coevolution of plant pathogens and their hosts as well as in population genetics.

The following discussion refers on coevolutionary aspects of *Microbotryum* s.l. and the host plants.

Evolutionary trends in Microbotryum:

The following remarks refer to the studies of Kemler et al. (2006, 2009).

Hosts Polygonaceae > Caryophyllaceae > Asteridae

Sporulation on leaves > flowers > in anthers > in inflorescences

Host specificity broad? > narrow (specific) > one host with several parasites
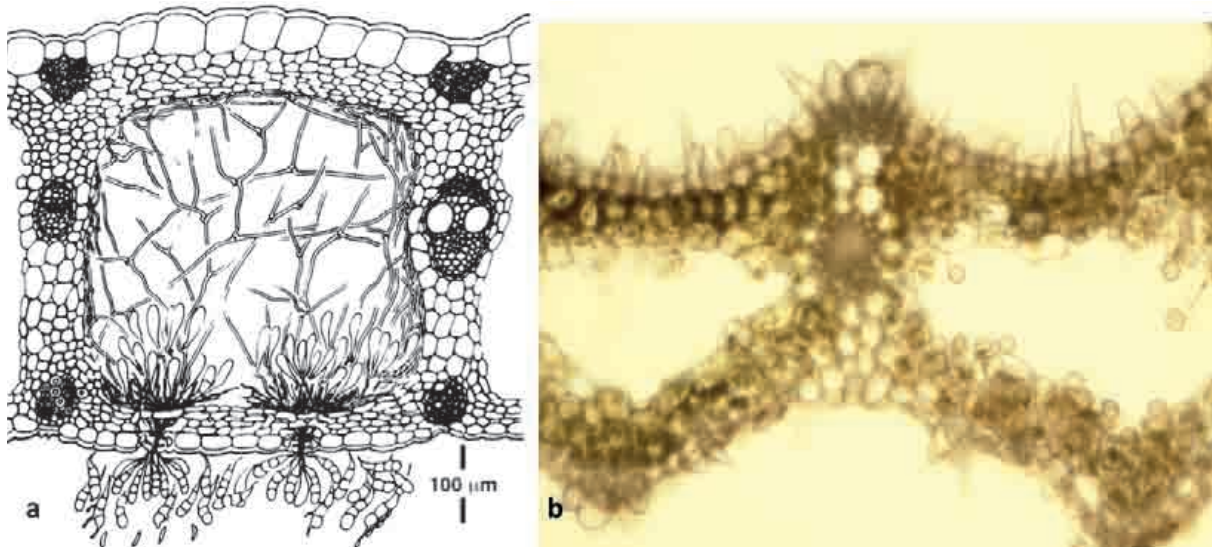
Fig. 35: **a**. *Kriegeria eriophori* in *Scirpus sylvaticus*. The parasite grows in host leaf aerenchyma. Probasidia develop inside and basidia outside of the leaf. Basidia are deciduous and can float away in the water surrounding the host plant. **b**. *Ustilentyloma fluitans* in *Glyceria fluitans*. Full development of smut spores and basidia takes place in the aerenchyma chambers. Orig. F. Oberwinkler

Molecular hypotheses are in favor for an origin of Microbotryaceae on Polygonaceae. Overlapping host ranges were found in *Fallopia*. In the Caryophyllaceae, *Microbotryum* appears monophyletic, with a strong tendency for species specificity, and sporulation in the anthers. This is also the case in members of the Portulacaceae, Lamiaceae, Lentibulariaceae, and Dipsacaceae. Kemler *et al.* (2006) assume that there may be two independent lineages of anther smuts. Cryptic species, undetectable with morphological studies remain to be discovered with molecular methods.

The term host specificity is not fully adequate to evolutionary specialization concerning host dependencies. The anther-smuts are an excellent example for organ specificity of the sporulation place including functional aspects of dispersal efficiency. In the case of *Ustilentyloma fluitans*, (Fig. 35 a), growing in *Glyceria fluitans*, and *Kriegeria eriophori* in *Scirpus sylvaticus* (Fig. 35 b), leaf aerenchyma of the hosts serve as ecological niches for the development of the parasites.

## Ustilaginomycotina, true smuts and related fungi

A highly diverse grouping of basidiomycetous fungi constitutes the Ustilaginomycotina as one of the three subdivisions in the Basidiomycota, commonly accepted at present. To verify this assemblage as a monophylum is challenging. Prillinger et al. (1990, 1993) found that the carbohydrates of these fungi are rich in glucose but lack xylose, thus distinguishing them from Pucciniomycotina and Agaricomycotina. A representative survey of septal pore types (Bauer et al. 1997, 2006) recognized membranous pore caps, and vesicle derived host-parasite interactions (Bauer et al. 1997), both most likely synapomorphies (Fig. 36). Finally, phylogenetic hypotheses, based on sequence data were taken as conclusive results. The first ones were especially remarkable because they distinguished between secondary structures of the 5S rRNA (Gottschalk & Blanz 1985). They found that the true smuts share the type B of the 5S rRNA with the Agaricomycotina. The monophyly of the Ustilaginomycotina was confirmed in later studies, but depending on sampling and sequences

used, the support values varied considerably. Actually, the Ustilaginomycotina are treated without *Entorrhiza* by phylogenists, using molecular data, (e.g. Hibbett et al 2007).

Only some evolutionary trends of true smuts and related fungi will be discussed here, following the arrangement of orders as in Fig. 36.

Evolutionary trends in Ustilaginomycotina:

Yeast phase present > lacking

Phragmobasidia > holobasidia >? Phragmobasidia

Teliospores present > lacking

Teliospores single > spore balls

Ballistospores present > lacking

Basidiospores one-celled > multicellular

Septal pores present > lacking

Septal pores simple > dolipores

Parasitic cellular interaction simple > complex

Coevolution with hostplants

Adaptation to ecological niches
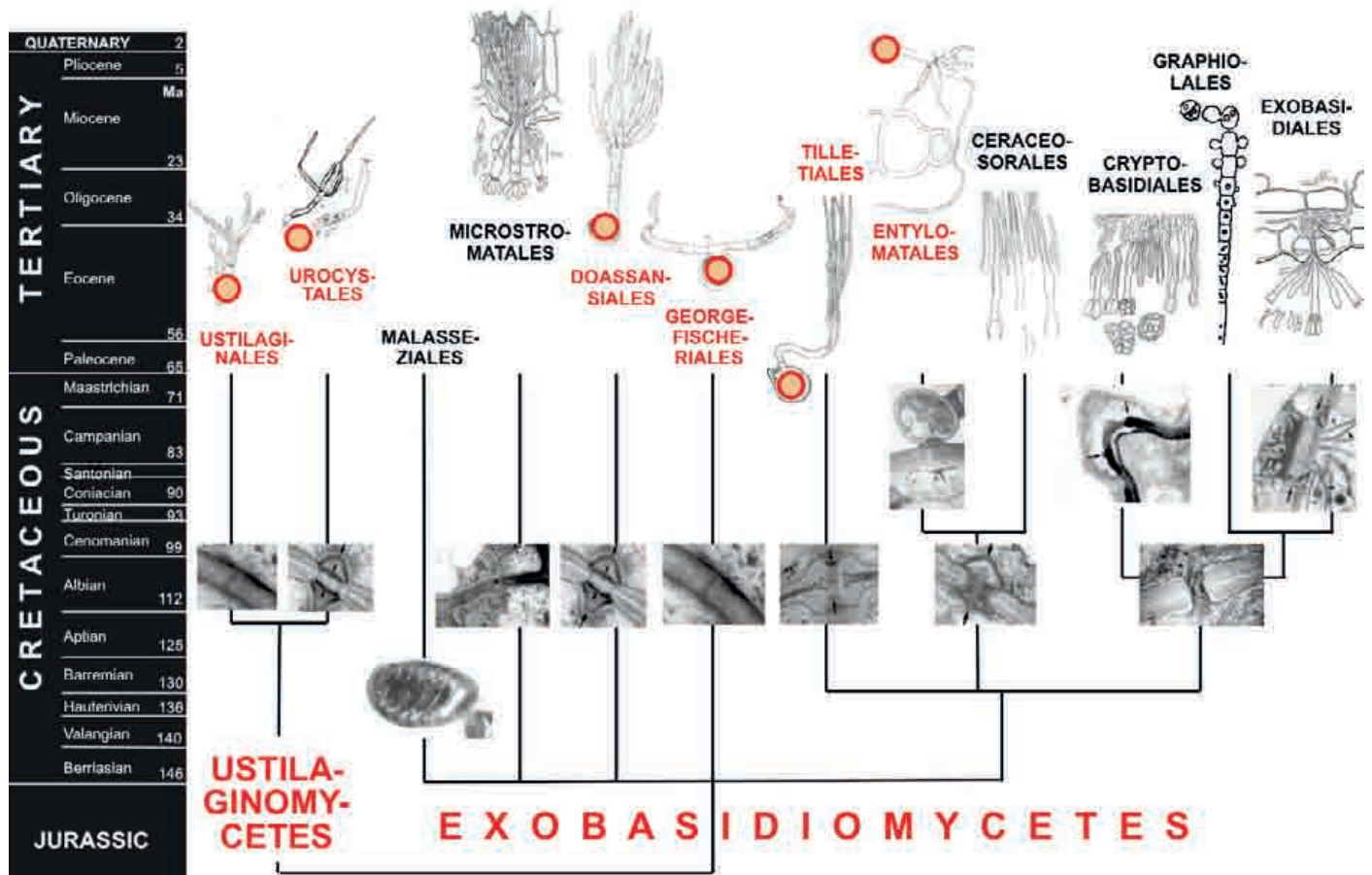
Fig. 36. Phylogenetic hypothesis for the Ustilaginomycotina, strongly modified after Bauer et al. (1997). Because nearly all smut fungi parasitize on angiosperms, a geological time table is added for the period in which the host plants evolved. Based on ultrastructural and molecular data, partly also on basidial morphology, the Ustilaginomycotina are divided in two classes, the Ustilaginomycetes and the Exobasidiomycetes. Representative septal pore types and basidia are illustrated, as well as few host-parasite interphases. In addition, the occurrence of teliospores is marked by red-yellow circles. Included are also the anamorphic Malasseziales. TEM pictures orig. R. Bauer, drawings orig. F. Oberwinkler

known from Ustilaginales, Microstromatales, Georgefischeriales, Entylomatales, and Exobasidiales. Few reports on yeasts in other smut taxa need to be confirmed. The lack of yeasts in sister taxa of these orders could be interpreted as a regressive evolutionary trend.

Phragmobasidia are common in the Ustilaginomycetes, holobasidia must be considered as derived. They are typical for the Exobasidiomycetes. The phragmobasidiate *Tilletiaria* may indicate a phragmobasidial origin of these fungi. Chains of holobasidia characterize the Graphiolales (Fig. 38).

The distribution of teliospores in members of the Ustilaginomycotina is shown in Fig. 36. Most smuts with telio-spores parasitize herbaceous plants, those without smut-spores commonly grow on woody plants. A multiple evolutionary development of teliospores is possible, as well as the loss of them as a regressive trend.

In Exobasidiomycetes teliospore balls are found in the Doassansiales and in *Tolyposporella*. Ballistospores and/or –conidia are present in the Georgefischeriales, Tilletiales (Fig. 37), Ceraceosorales, and Exobasidiales, they lack in the other orders.

Basidiospores are characteristically single-celled, rarely multicellular, as in the Volvocisporiaceae of the Microstromatales. Simple septal pores with membranous pore caps are wide-spread in the Ustilaginomycotina and represent an ancestral state. Poreless septa characterize the Ustilaginales and Georgefischeriales. Dolipores in the Tilletiales (Fig. 37) and young hyphal stages of the Gjaerumiaceae indicate an advanced septal pore type.

Parasitism is realized by different cellular interactions: intracellular hyphae, haustoria, and complex interaction structures, as in Ustilaginomycetes, Doassansiales, Entylomatales and Exobasidiales. Local interaction zones without complex structures characterize the Microstromatales.

Host selectivity and specificity are common in members of the Pucciniomycotina, and certainly reflect coevo-
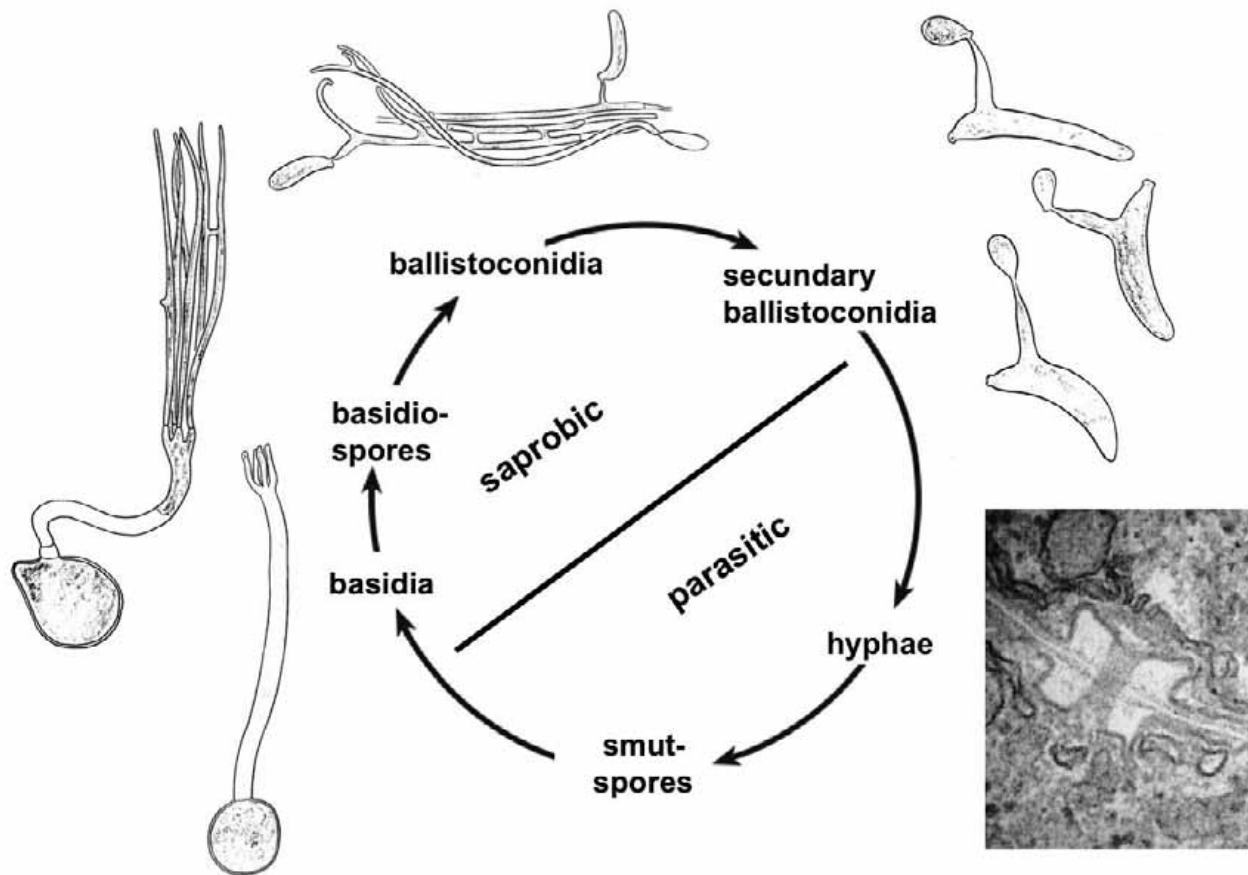
Fig. 37: Life cycle of *Tilletia*. Smut spores germinate with holobasidia, producing short, terminal sterigmata. Basidiospores (sporidia) conjugate and develop ballistoconidia that can be followed by secondary ones. Dolipores are characteristic for species of the Tilletiales. Orig. F. OBERWINKLER. TEM orig. R. Bauer.

lutionary trends. Most smut fungi parasitize on angiosperms. Rare exceptions exist with *Melaniella* on *Selaginella*, *Exoteliospora* on *Osmunda*, and *Uleiella* on *Araucaria*. More than half of the known smuts live on species of the Poaceae. Also Cyperaceae are hosts for many smuts. Surprisingly, there are no smuts known from orchids. *Ustilago* species and those of six genera of the Tilletiales exclusively grow on Poaceae, while all species of *Erratomyces* are parasitic on Fabaceae. Brachybasidiaceae live predominantly on monocotyledonous hosts, and the Graphiolaceae are exclusively parasites of palms (Fig. 38).

Most Cryptobasidiaceae are parasitic on Lauraceae, but *Coniodictyum* is confined to Rhamnaceae. Species of *Entyloma*, representing a monophyletic group, parasitize exclusively dicotyledonous hosts, the majority of them in the Asteridae, and many also in the Ranunculales. Such distribution pattern clearly document evolutionary trends in host selectivities. Another well known example is the Exobasidiaceae, restricted to dicotyledonous hosts with a high preference in Ericaceae.

Often, host specificity is connected with habitat properties as related plants may share the same or similar ecological niches. The radiation of *Anthracoidea* on *Carex*, *Ustilago* on Poaceae, or *Graphiola* on palms may illustrate such evolutionary scenarios. On the other hand, comparatively unrelated taxa can share the same biospheres, responding similarly to environmental pressures over a long time, as is documented by the convergent evolution of spore balls in *Doassansiopsis* and the Doassansiales, both living on aquatic plants in the same habitats.

Entorrhiza, an evolutionary enigma

Entorrhiza parasites live in root cells of Cyperaceae and Juncaceae (Fig. 39), initiating hypertrophic growth of the plant tissue. Together with their
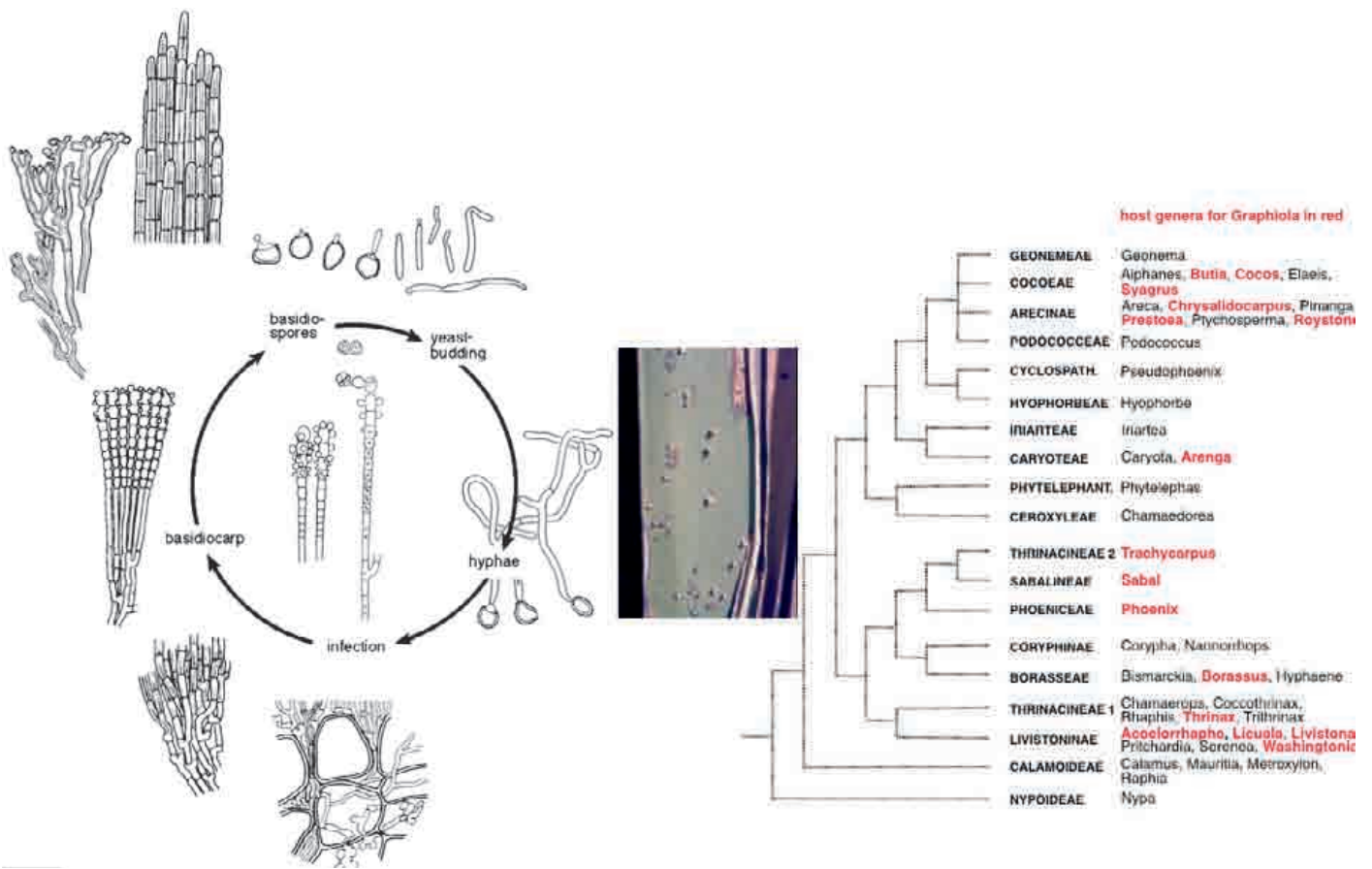
Fig. 38: Life cycle of *Graphiola* and host dependencies of palms. Haustoria provide nutrients for hyphae growing in the host. They initiate fructifications with peridia and hymenial hyphal strands. Basidia develop in chains acropetally and produce sessile basidiospores laterally arranged. Basidiospores bud off yeasts or germinate with hyphae. Graphiola species occur exclusively on palms and can often be found on cultivated *Phoenix canariensis*. Dendrogram after Hᴀʜɴ (1999), Uʜʟ & et al. (1995), Uʜʟ & Dʀᴀɴsғɪᴇʟᴅ (1999). Orig. F. Oᴮᴇʀᴡɪɴᴋʟᴇʀ.

hosts, *Entorrhiza* species have a worldwide distribution. The stem-groups of both host families have been dated to 88 million years, their crown groups 76 to 74 million years respectively, before present (Jᴀɴssᴇɴ & Bʀᴇᴍᴇʀ 2004; Bᴇsɴᴀʀᴅ et al. 2009).

Teliospores of *Entorrhiza* species are thick-walled, pigmented and ornamented and four-celled in a mature stage. Each spore cell germinates with one hypha, and hyphal septa have dolipores. These features clearly characterize *Entorrhiza* as belonging to the Basidiomycetes. However, molecular data are ambiguous so that the genus has been excluded from the Pucciniomycotina (Hɪʙʙᴇᴛᴛ et al. 2007). According to ultrastructural and molecular data Bᴀᴜᴇʀ et al. (1997) and Bᴇɢᴇʀᴏw et al. (1997) considered the Entorrhizales as a sister-group of the Pucciniomycotina. Taking into account the age of the hosts, *Entorrhiza* cannot be judged as an evolutionary old basidiomycete. However, there are no data about possible hosts available, before *Entorrhiza* evolved on their extant hosts.

Evolutionary trends in basidiomycetous wood-decay fungi

White rot > brown rot > successive degradation of lignin

Wood decay (Fig. 17) is one of the most important ecological functions in Basidiomycota that evolved in complex interrelationships with climax vegetations dominated by trees. Decomposition of wood is an intergrading process of parasitism and saprophytism. Many wood decay fungi start with parasitic phases endophytically, often causing the death of their hosts, and finally continue to break down dead wood. The distinction of white and brown rot is sometimes important, but not always clearly distinctive. In white rot, lignin and cellulose are degraded, while in brown rot lignin remains to a high percentage. White rot is considered as plesiomorphic and brown rot as several times convergently derived (Hɪʙʙᴇᴛᴛ & Dᴏɴᴏɢʜᴜᴇ 2001). Even when most wood-decay species
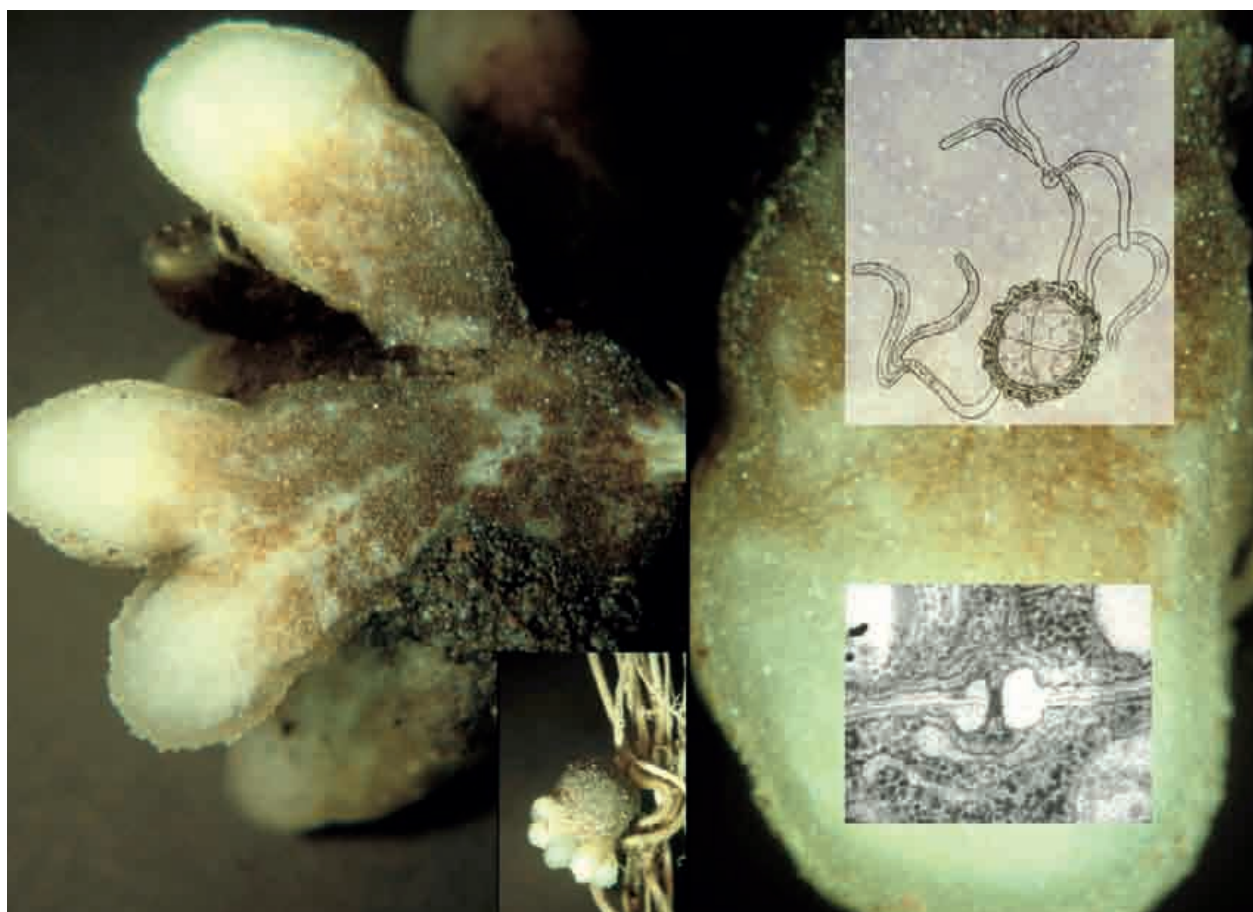
Fig. 39: *Entorrhiza casparyana*. The parasite grows in living root cells of *Juncus articulatus* and forces the host to grow hypertrophically. The brown parts inside the galls indicate mature smut spores, one of them is inserted in a mature state with germination hyphae. Dolipores are typical for the genus, indicating basidiomycetous relationships. TEM photo R. BAUER. Orig. F. OBERWINKLER.

are white rots, the brown rots associated with coniferous wood are the most important decomposers in boreal forests. The lignin residues bind nitrogen and cations, thus being essential in nutrient-poor, acidic soils of conifer forests in the Northern Hemisphere. How cellulolysis functions in absence of ligninolysis in brown rots is not known (EASTWOOD et al. 2011).

Dacrymycetales

The Dacrymycetales constitutes a monophylum in a rather basic position of the Agaricomycotina (Fig. 17). Basidiocarps are typically gelatinous, basidia two-sterigmate, and basidiospores nearly always septate and ger-minating with microconidia (Fig. 40). In a well developed stage most species synthesize carotenoids. Dacrymycetales live on wood of conifers and deciduous trees and play an important role in wood decay, predominantly in very early stages of the decomposition and in many cases on fully exposed wood. Quick changes in the water content of the substrate can interrupt the growth and wood decay, but re-soakening will initiate these activities immediately. SEIFERT (1983) studied the wood decay caused by 17 species of the Dacrymycetales. He found typical brown-rotted wood, but also the capability of removing significant amounts of lignin in many species, including *Dacrymyces stillatus, D. capitatus, D. dictyosporus, Dacryopinax spathularia, Calocera cornea, C. lutea,* and *Cerinomyces ceraceus.*

Traditionally, generic concepts in Dacrymycetales are based on basidiocarp morphology, hyphal and spore characeristics (OBERWINKLER 1993). Few and fragmentary phylogenetic hypotheses, based on molecular data available at present, do not support older systematic arrangements.

Auriculariales

Formerly, the Auriculariaceae were included in the Tremellales s.l., and circumscribed by species with auricularioid, i.e. mature transversaly septate basidia. However, considering septal
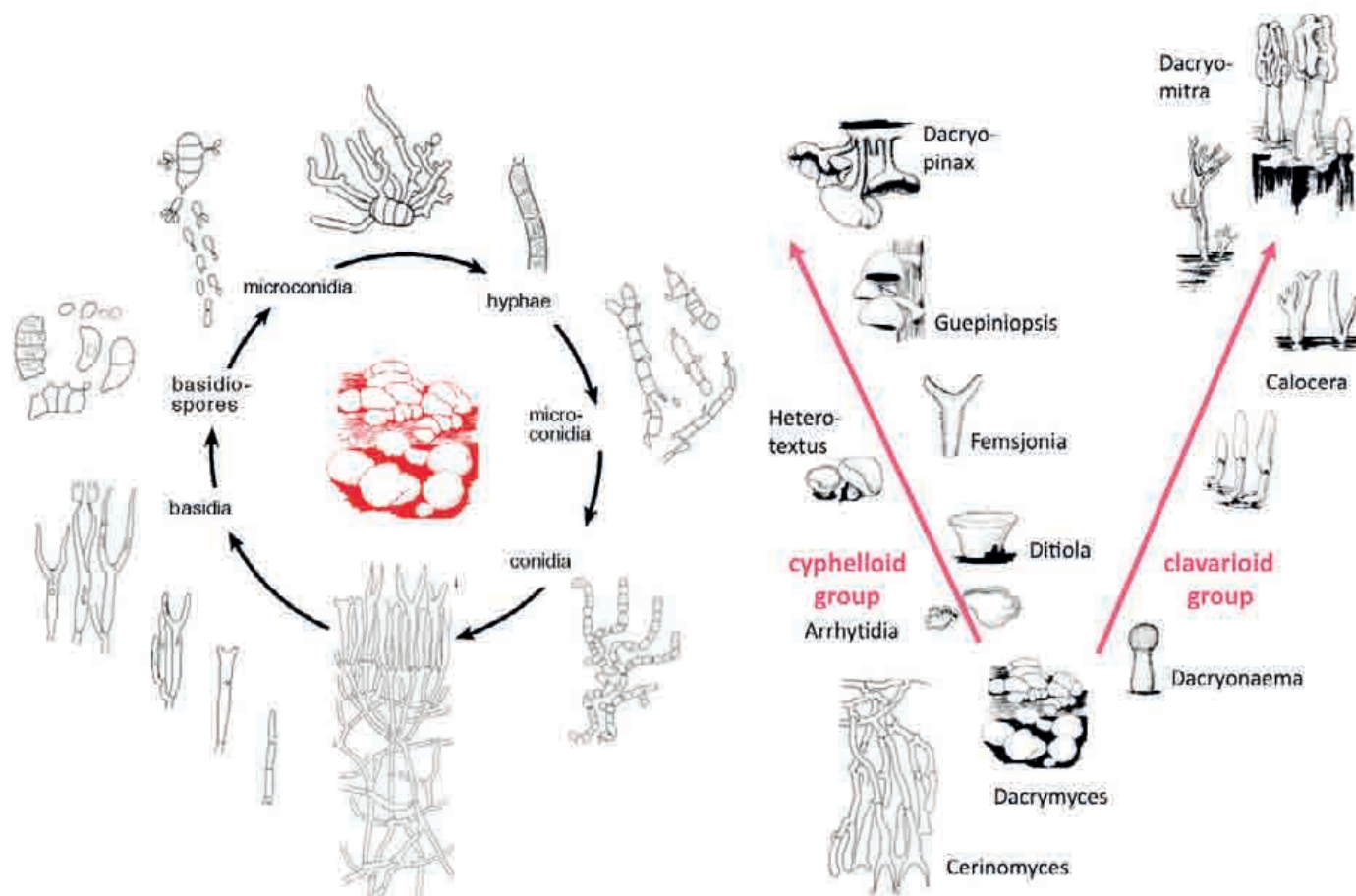
Fig. 40: Ontogeny of *Dacrymyces stillatus* and traditional genera of the Dacrymycetales, defined by basidiocarp morphology. Two-sterigmate basidia, septate basidiospores, microconidia and gelatinous basidiocarps characterize most of the Dacrymycetales species. Genera can by classified in a cyphelloid and a clavarioid group. However, these groupings appear not to reflect phylogenetic processes. Orig. F. OBERWINKLER.

pore ultrastructure, spore germination, and substrate dependencies, allowed new circumscriptions of Auriculariales and Tremellales. Poroid Tremellaceae, like *Aporpium caryae*, *Protodaedalea japonica* and *Protomerulius brasiliensis*, as studied by BANDONI et al. (1982) are Auriculariales with longitudinally septate basidia. Based on molecular data, WEISS & OBERWINKLER (2001) proposed a phylogenetic hypothesis for the Auriculariales with five groups (Fig. 41): (1) *Myxarium* and *Hyaloria* with sphaeropedunculate basidia; (2) *Basidiodendron* species with globose spores and gloeocystidia; (3) *Bourdotia* and *Ductifera* with gloeocystidia; (4) *Heterochaetella*, *Protodontia*, *Protomerulius*, and *Tremellodendropsis*; (5) *Auricularia*, *Exidia*, *Exidiopsis*, *Heterochaete* and *Eichleriella*.

Evolutionary trends in Auriculariales:

Basidiocarp resupinate > stalked

Hymenium smooth > odontioid > hydnoid

Basidia auricularioid > tremelloid

Cystidia lacking > gloeocystidia

White rot > brown rot

Most Auriculariales are white rot fungi, like species of *Aporpium*, *Auricularia*, *Ductifera*, *Eichleriella*, *Exidia*, *Exidiopsis*, *Heterochaete*, *Myxarium*, and *Protodaedalea*, but *Tremiscus helvelloides* causes a brown rot and *Pseudohydnum gelatinosum* is reported as a white and brown rot fungus (SEIFERT 1983).

Hymenochaetales

Species of *Hymenochaete*, *Hydnochaete*, *Clavariachaete*, *Inonotus*, *Phellinus*, *Cyclomyces*, and related surrogate genera often share dimitic hyphal systems (Fig. 42), thick walled, brown setae, the lack of clamps, brown hyphal pigments darkening with KOH, and exoenzymes that degrade
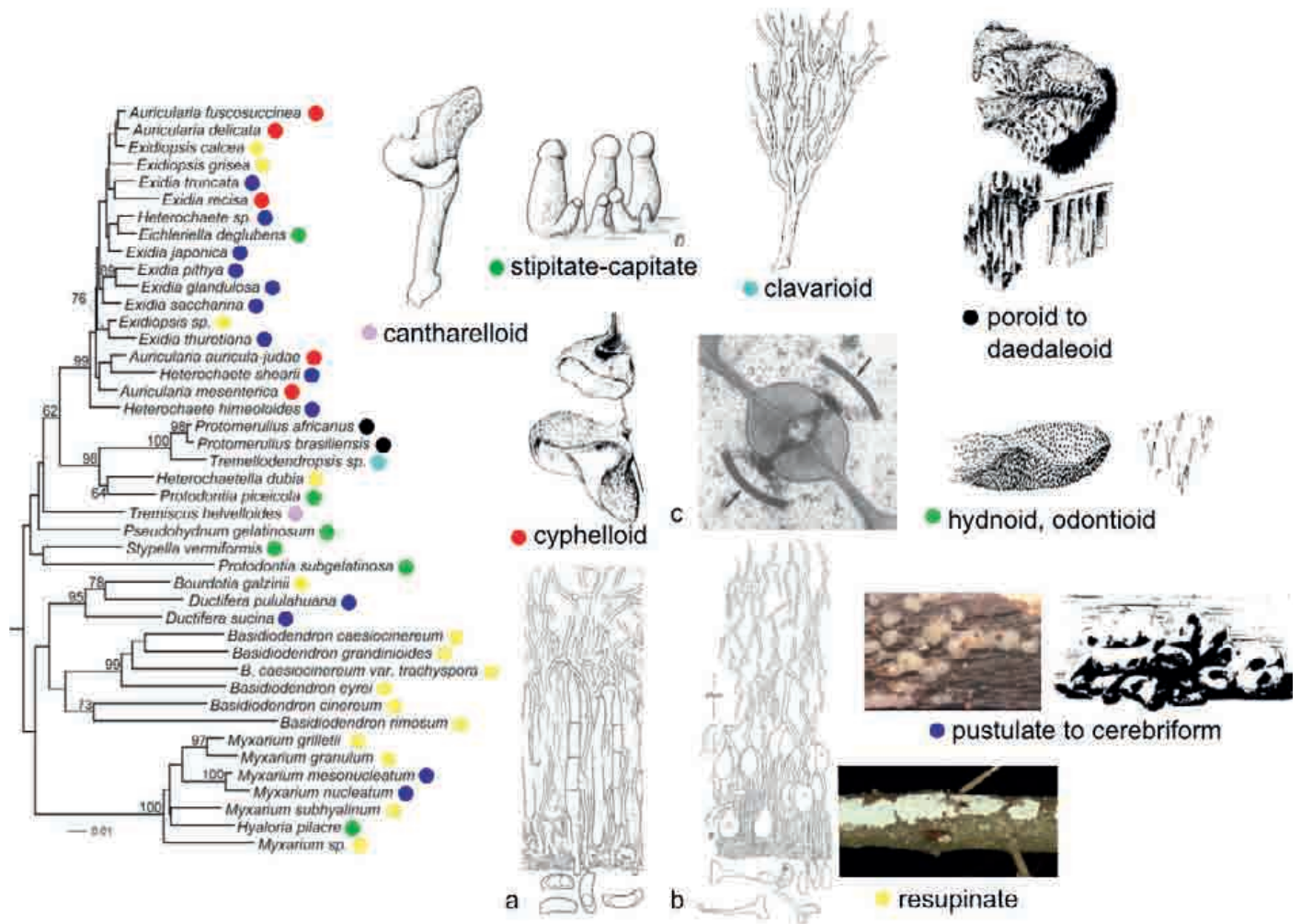
Fig. 41: Macro- and micromorphology of basidiocarps, dolipore with parenthesomes and phylogenetic hypothesis for representative species and genera of the Auriculariales. **a** *Auricularia auricula-judae*, **b** *Exidiopsis effusa*, **c** dolipore with continuous parenthesomes. The colored dots in the dendrogram refer to positions of species and genera in the phylogenetic tree. Neighbour-joining analysis of an alignment of nuclear DNA coding for the 5 terminal domain of the 28 S ribosomal large subunit. Genetic distances were computed according to the KIMURA two-parameter model. Branch lengths are scaled in terms of expected numbers of nucleotide substitutions per site. Dendrogram from WEISS & OBERWINKLER (2001). Septal pore orig. R. BAUER, illustrations orig. F. OBERWINKLER.

cellulose and lignin, thus causing white rot. Basidiocarps (Fig. 42) evolved from corticioid-stereoid to hydnoid and clavarioid, as well as to polyporoid and stalked ones with pilei and hymenia with pores or the unique concentrically arranged lamellae.

Phylogenetic hypotheses based on molecular data broadened the scope of the order to include the *Hyphodontia* clade and *Tubulicrinis* spp., and very surprisingly the *Rickenella* clade comprising also *Hyphoderma praetermissum* and *Resinicium* spp. (LARSSON et al. 2006).

Evolutionary trends in Hymenochaetales:

Basidiocarp corticioid > stereoid > odontioid > clavarioid > polyporoid > agaricoid // no gasteroid forms

Parasitic < > saprobic > specific successions of lignin degraders

Host specificity broad > narrow > conspecific

Wood decay not selective > restricted to heart-wood

Wood decay > mycorrhizae

Strong parasitism on trees is wide spread within the Hymenochaetales, as is shown by the short living *Inonotus hispidus* on *Malus* and other hosts, as well as by perennial ones, like *Phellinus cinereus* and P. *nigricans* on *Betula*, P. *hartigii* on *Abies*, P. *pini* on *Pinus*, P. *pomaceus* on *Prunus*, P. *populicola* and P. *tremulae* on *Populus*, P. *robustus* on *Quercus*, and many others. The examples document high host specificities as a common feature in these wood decayers. Also many stereoid *Hymenochaete* species are highly specialized: *H. carpatica* on *Acer pseudo-*
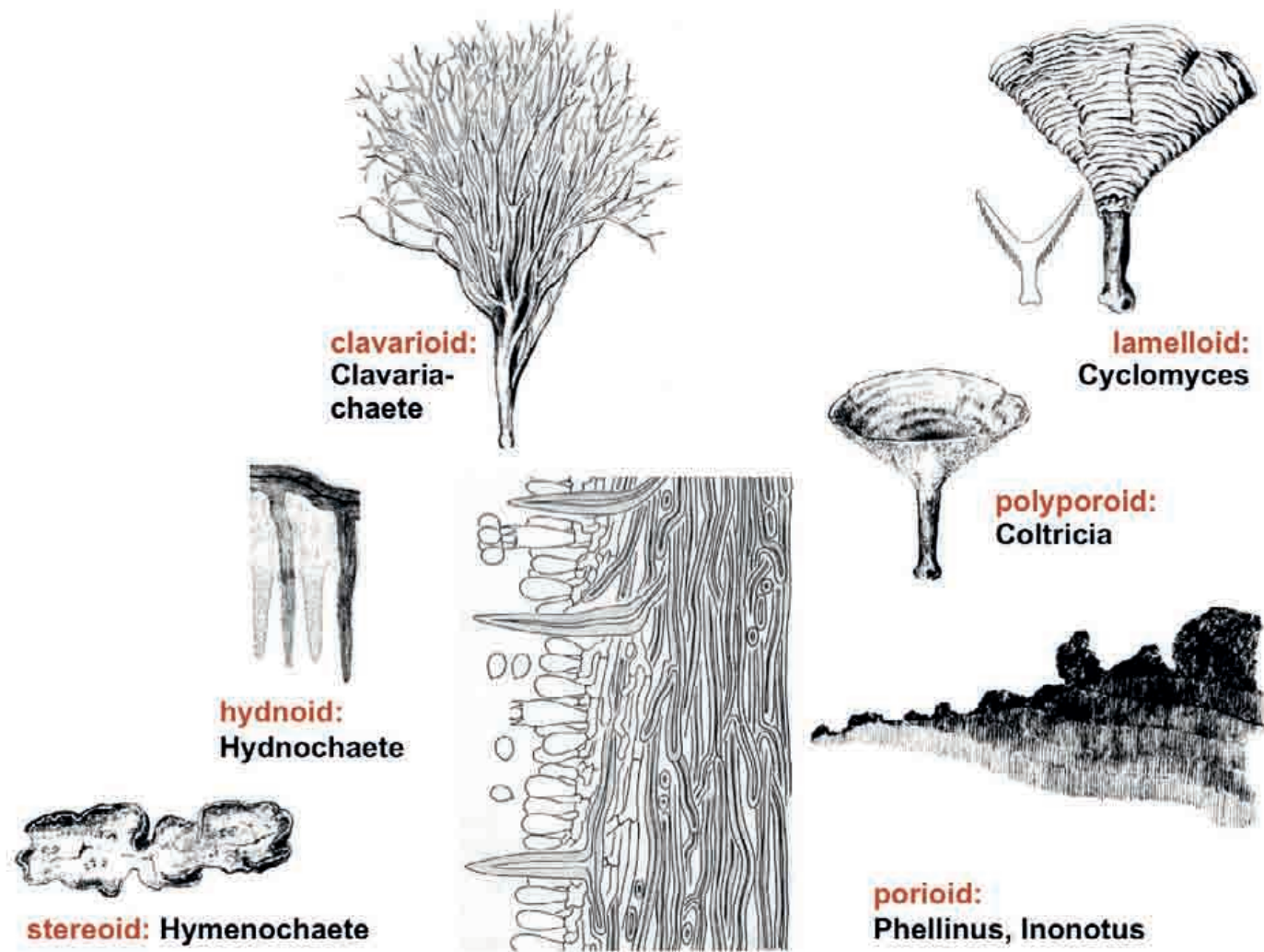
Fig. 42: Hymenochaetales s.str. The micromorphology of the Hymenochaetales has a unique set of features as illustrated in the hymenial part. Traditionally, genera were circumscribed and named according to their habit appearance and easily recognizable macroscopic characters, as *Hymenochaete, Hydnochaete, Calvariachaete,* or *Cyclomyces*. The adaptation to exposed habitats, as on trunks of trees nearly up to the crowns, required traits of structural changes to fulfill functionality, as the „woody" context of the console-like fructifications in *Phellinus* and many other species. The perennial life strategy was based on the tough dimitic hyphal system allowing thin-walled generative hyphae to survive inside the fructification and to add new hymenial layers to the polyporous underside under favorable weather conditions. Illustrations not to scale. Orig. F. Oberwinkler.

platanus, H. cinnamomea on *Corylus, H. mougeotii* on *Abies, H. rubiginosa* and *H. subfuliginea* on *Quercus, H. tabacina* on *Salix*, and others.

Molecular phylogenetic hypotheses include also very inconspicuous fungi in the Hymenochaetales, for example *Sphaerobasidium* and *Repetobasidium* species that occur exclusively on strongly brown-rotted wood, and that obviously are capable for further degrading such substrates.

In ectomycorrhizal fungal successions of *Pinus banksiana* stands following wildfire, a distinct sequence of early-stage ectomycorrhizal fungi, including the hymenochaetoid *Coltricia perennis*, was found by Visser (1995). Tedersoo et al. (2007) detected ectomycorrhizae of *Coltricia* and *Coltriciella* on Caesalpiniaceae, Dipterocarpaceae and Myrtaceae in the Seychelles. The evolutionary switches from wood decay to mycorrhizal associations remain unclear.

Polyporales and related wood-decay fungi

To trace evolutionary trends, the organisms considered must be monophyletic. Recent phylogenetic hypotheses confirmed the Polyporales as a monophylum (e.g. Hibbett et al. 2007, Larsson 2007, Garcia-Sandoval et al. 2011), however its higher level relationships varied considerably. The core Polyporales (Fig. 43) are white-rot fungi
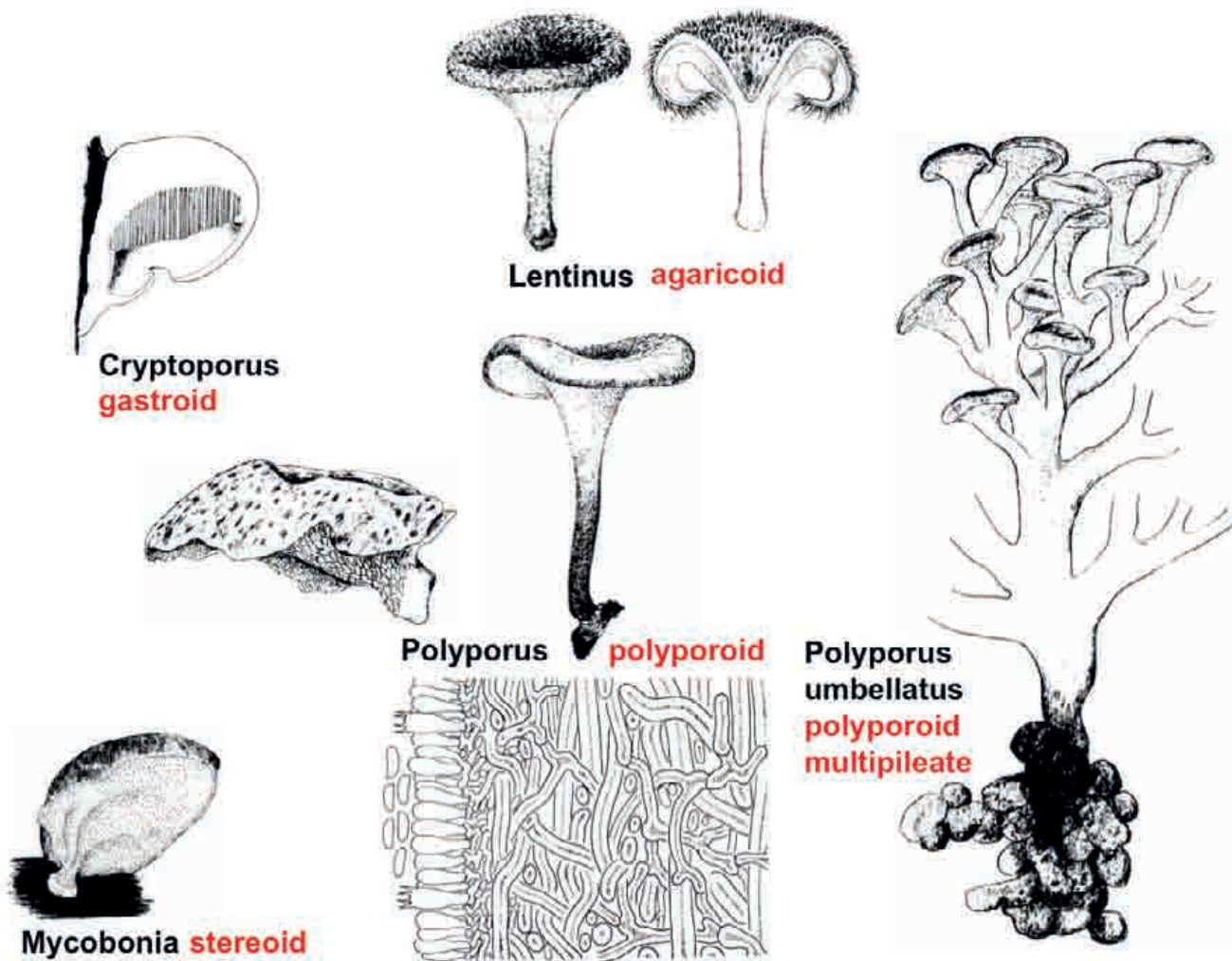
Fig. 43: Polyporales, micromorphology and basidiocarps. Di- and trimitic hyphal systems are common in Polyporales. Basidicarps are often console-like or stalked, rarely gastroid as in *Cryptoporus*, and they can originate from sclerotia, ramify and terminate with many distinct pilei. Porioid hymenia are most frequent, but stereoid and agaricoid ones occur, too. Orig. F. Oberwinkler.

comprising taxa with a broad range of basidiocarps (Fig. 11).

Also species of the phlebioid clade produce a white rot, but the *Antrodia* clade shares brown rot species with the reversal of *Grifola frondosa* to white rot (Garcia-Sandoval et al. 2011).

The **Gloeophyllales** comprise corticioid to stereoid species (*Veluticeps, Boreostereum, Chaetodermella*), polypores (*Gloeophyllum*), and agarics (*Neolentinus, Heliocybe*), most of which grow on coniferous wood and cause a brown rot. Relaxed molecular clock analyses indicate that the

Gloeophyllales arose in the Cretaceous, when the Pinaceae were already present (Garcia-Sandoval et al. 2011).

In the recently described **Amylocorticiales**, *Anomoloma* produces a white rot, some *Anomoporia* species are associated with brown rot, and wood-decay characteristics in other species are not known. (Binder et al. 2010).

Wood-decay by species of the Russulales, Boletales, and Agaricales will be discussed briefly in connection with the origin of ectomycorrhizae in these orders.

Mycorrhizae

When colonizing land habitats, the availability of sufficient water and nutrients was a challenge for plants, and mutualistic associations of thalli and roots with fungi were the most important coevolutionary processes. Arbuscular mycorrhizae (Figs. 2, 3) are known from the Ordovician (Redecker et al. 2000) and they are most common mycorrhizal partners in all groups of land plants. The evolutionary switch of certain ecologically most important plant groups to other fungi to improve symbiosis, is not yet understood. Climax

Fig. 44: *Sebacina epigaea* in a mixed forest with fructifications on soil (arrows and insert to the right). The ectomycorrhizal species are associated with pine roots in this forest, but can grow also on roots of other ectomycorrhizal host trees. Under favorable conditions fructifications appear frequently in autumn. Orig. F. OBERWINKLER.

vegetations in temperate zones of the Northern and partly the Southern Hemisphere are in fact obligate ectomycorrhizal communities with trees of the Pinaceae, Fagales and Salicaceae. In plant associations dominated by Ericales the ericoid mycorrhizae play an essential role. Early ontogenetic stages in orchid development depend on specific endotrophic fungal partners, and heterotrophic orchids require an obligate mycorrhization.

In Sebacinales all mycorrhizal types occur that are known in Basidiomycota. Tulasnellales appear to be frequent in orchid mycorrhizae and in Aneuraceae, but also occur in the main autotrophic partners, the Pinaceae and the Fagales.

Evolutionary trends in mycorrhizae:

Root associated fungi > hyphal sheaths > intercellular hyphal growth

Root parasites > endophytes > endomycorrhizae

Exclusively mycorrhizal: Sebacinales

Exclusively ectomycorrhizal: Thelephorales

Saprobic > ectomycorrhizal: Cantharellales, Gomphales

Wood decay > ectomycorrhizal: Russulales, Atheliales, Boletales, Agaricales

Sebacinales

Little attention was paid to mostly inconspicuous *Sebacina* species and related fungi until their obligatory association with plant roots was detected and molecular screenings revealed an enormous unknown and cryptic diversity (WEISS et al. 2011). It turned out that Sebacinales are mycobionts in ectomycorrhizae of Pinaceae, Fagales, Myrtaceae, and also in *Polygonum viviparum* (MÜHLMANN et al. 2008), living in subalpine and alpine grass vegetations. Sebacinales also constitute orchid mycobionts (WARCUP 1988, SELOSSE et al. 2002b, WEISS et al. 2004b, SUÁREZ et al. 2008) and they are capable to form ericoid, arbutoid, and cavendishioid mycorrhizae (BERCH et al. 2002, SELOSSE et al. 2002a, SETARO et
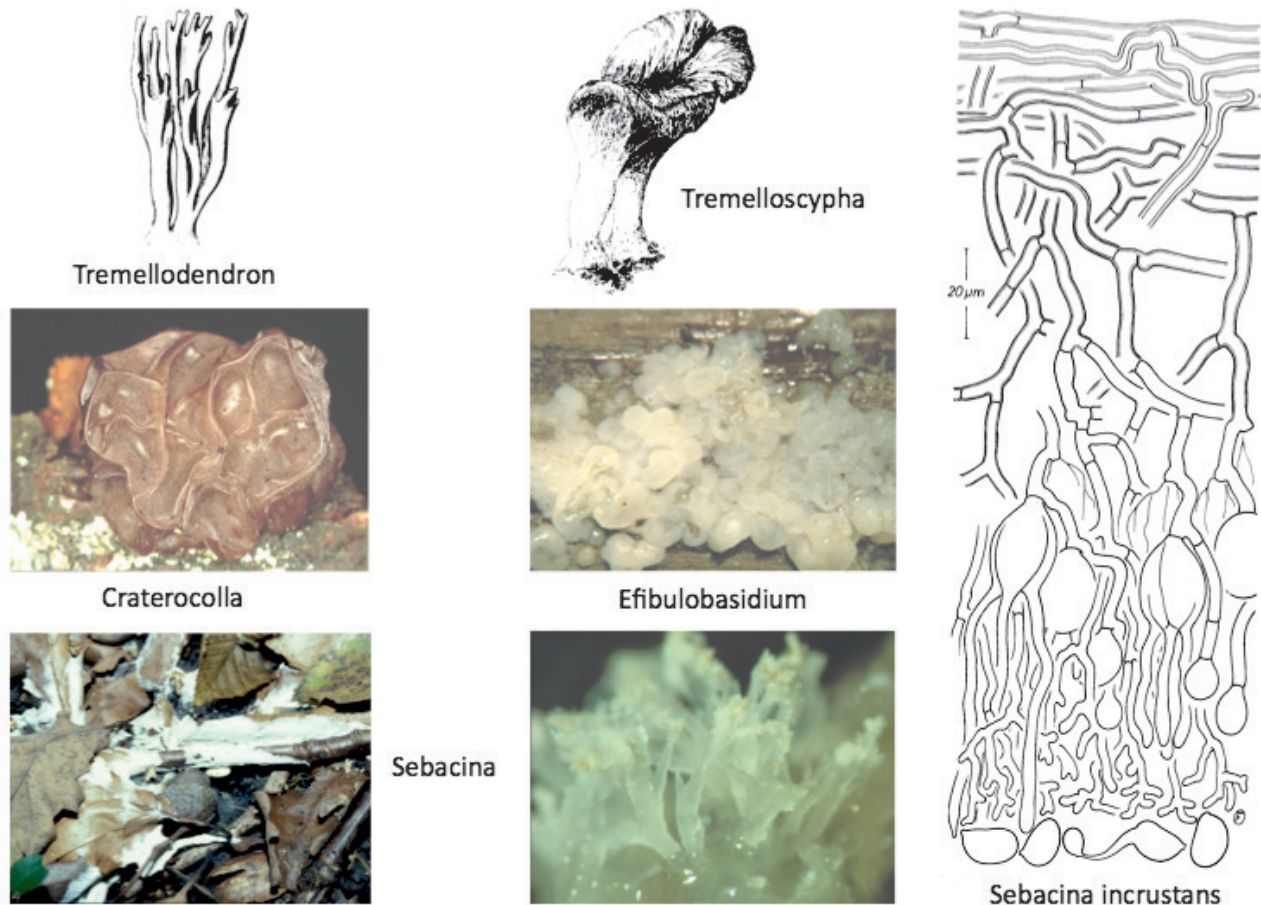
Fig. 45: Fructifications of Sebacinales and micromorphology of *Sebacina incrustans*. *Sebacina* species produce resupinate and incrusting basidiocarps on soil, litter and wood on the forest floor. *Efibulobasidium* and *Craterocolla* have gelatinous fructifications growing on dead wood. *Tremellodendron* and *Tremelloscypha* species grow on the forest floor. The micromorphology of *Sebacina incrustans* is typical also for other Sebacinales. Orig. F. Oberwinkler.

al. 2006a,b, Selosse et al. 2007, Kottke et al. 2008). In addition, Sebacinales associate with thalli of jungermannioid liverworts (Kottke et al. 2003, Nebel et al. 2004).

Evolutionary trends in Sebacinales:

Basidiocarps lacking > resupinate > pustulate > erumpent > stereoid > clavarioid

Hyphae thin-walled > thick-walled

Growth saprobic > endophytic > mycorrhizal

Liverwort associates > ectomycobionts of Pinaceae, Fagales and others

Liverwort associates > endomycorrhizae in orchids and Ericales

As in nearly all other monophyla of the Agaricomycotina, also in the Sebacinales basidiocarps evolved from inconspicuous generative hyphal networks to corticioid, pustulate, stalked-stereoid, and clavarioid structures (Fig. 45). More elaborate basidiomata and hymenia, like porioid, hydnoid, or agaricoid are not known. Hyphae are clampless at least in species with basidiocarps. Rarely, thick-walled hyphae occur, as in *Sebacina dimitica*. Basidia are longitudinally septate, and basidiospores often germinate with secondary spores.

As the Thelephorales, also Sebacinales appear to be exclusively mycorrhizal fungi. Ectomycorrhizae, arbutoid and orchid mycorrhizae have only been found in group A of a phylogenetic tree, while ericoid and cavendishioid mycorrhizae are restricted to

group B (Weiss et al. 2004b, Selosse et al. 2007, Weiss et al. 2011). It is premature to interpret evolutionary trends in these clusterings. Also, host specificities cannot be recognized so far. As in other mycorrhizal taxa, major evolutionary steps in land plants, liverworts, Pinaceae, Fagales, Ericales, orchids and others, certainly had a strong influence on adaptive radiations of Sebacinales, but these are not yet understood.

Tulasnellales

Because of the unique basidial development and morphology (Fig. 46) and their importance as liverwort and orchid mycorrhizal fungi, it seems appropriate to keep Tulasnellales as an order separate from the Cantharellales.
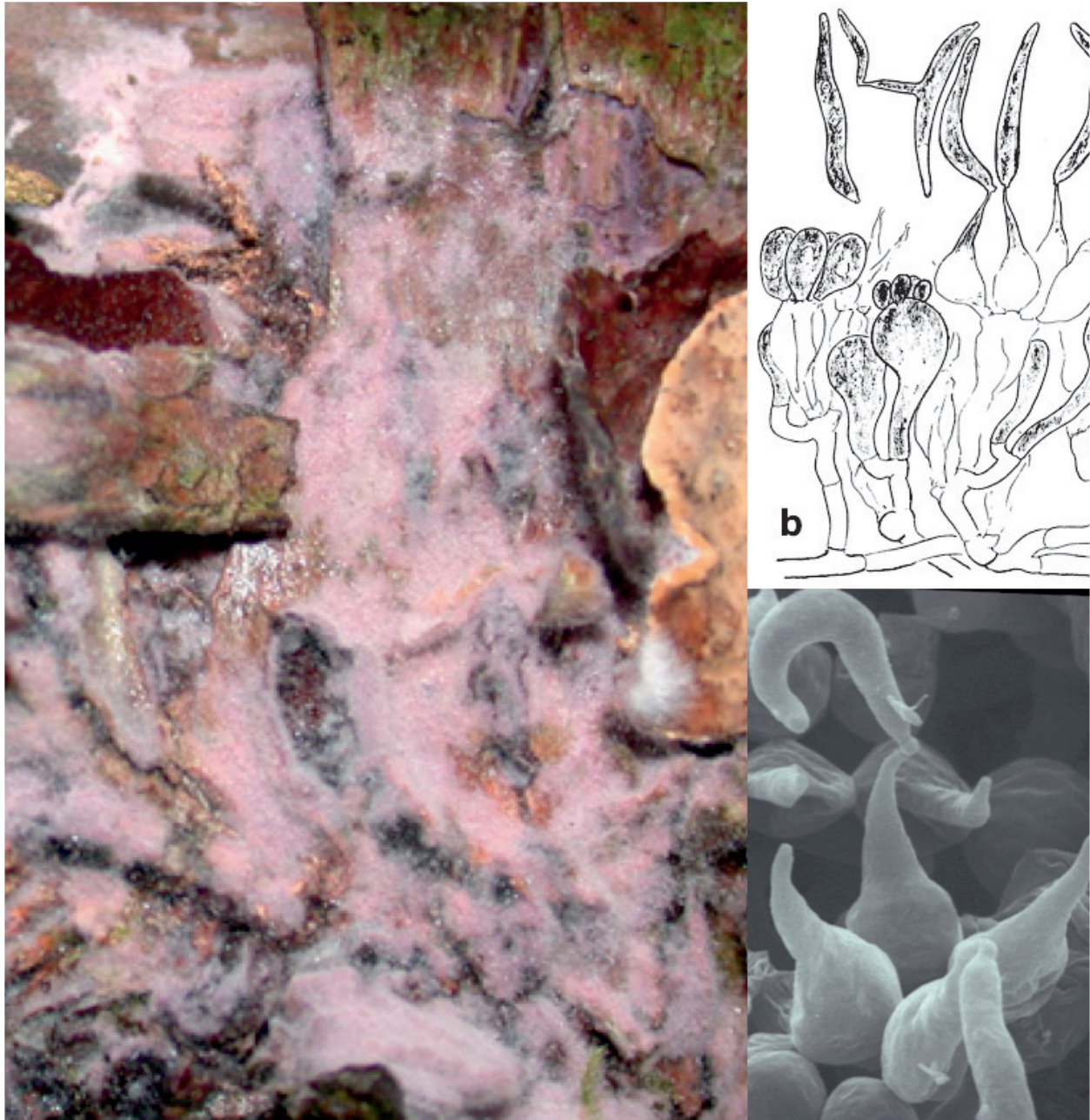
Fig. 46: *Tulasnella* spp. **a** Fully developped basidiocarp of *Tulasnella* sp. on the underside of a *Betula pubescens*-trunk. **b** Hymenium of *Tulasnella calospora* with different stages of basidial development. **c** SEM photograph of *Tulasnella vermispora*, one spore attached to the sterigma. Orig. F. OBERWINKLER.

Evolutionary trends in Tulasnellales:

- Basidiocarps lacking > resupinate
- Hyphae with clamps > unclamped
- Growth parasitic? > endophytic > mycorrhizal
- Mycothalli > endomycorrhizae in orchids > ectomycorrhizae of Pinaceae, Fagales and others

The thallose species of Aneuraceae, a family of the Metzgeriales, have *Tulasnella* mycobionts (NEBEL et al. 2004, PREUSSING et al. 2010) and were considered by KRAUSE et al. (2011) as a model of early evolved symbiotic associations. *Cryptothallus mirabilis* is a mycoheterotrophic liverwort and specialized as an epiparasite on *Tulasnella* species that form ectomycorrhizae with surrounding trees like *Betula pubescens,* *Pinus pinaster* and *P. muricata* (BIDARTONDO et al 2003). – *Tulasnella* spp. as mycobionts in orchids have been reported from various parts of the world (e.g. SHEFFERSON et al. 2005, 2007, SUÁREZ et al. 2009, CRUZ et al. 2010, YUAN et al. 2010). Even when Tulasnellales are the preferred mycobionts of orchids, Sebacinales, Thelephorales, Agaricales, and also Tuberales associate with them.
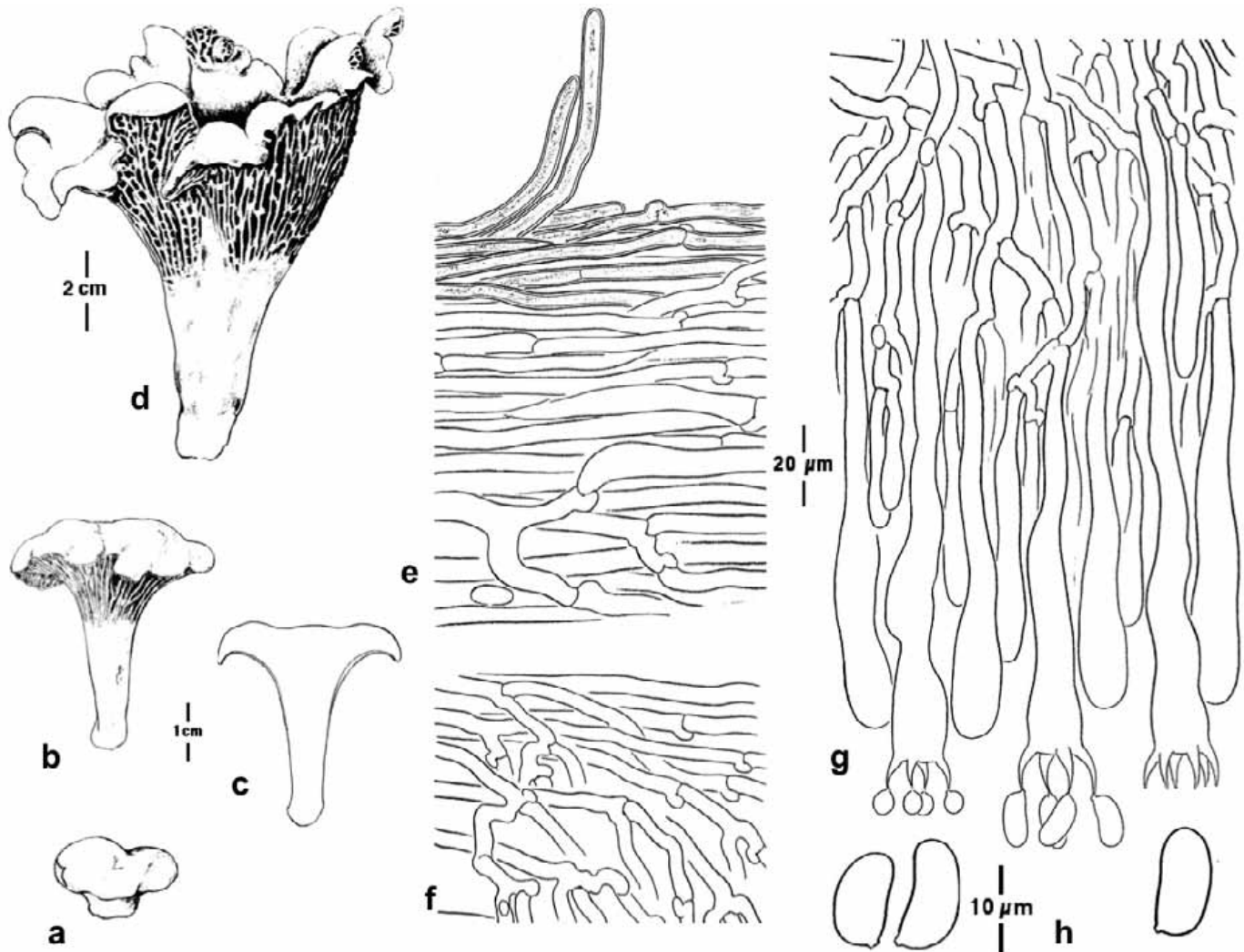
Fig. 47: Morphology of *Cantharellus cibarius*. **a-d** basidiocarps in different developmental stages, **c** longitudinal section. **e** hyphal arrangement of pileus surface, **f** subhymenial hyphae, **g** part of the hymenium with basidia of different ages, **h** basidiospores. After Oberwinkler (1977), modified with additions.

In a molecular screening of orchid mycorrhizae from Southern Ecuador (Kottke et al. 2009), sequence taxa clustered with the **Atractiellomycetes**, a relationship of the Pucciniomycotina. A specific cell organelle, the symplechosome (Fig. 16), found in intracellular hyphae, confirmed the molecular identification of these fungi. So far, this finding is unique and requires confirmation trough additional sampling. The origin of these fungi remains unclear. There are no other mycorrhizal fungi known in the Pucciniomycotina and also not in the Ustilaginomycotina.

Cantharellales

The cantharelloid clade, as circumscribed in phylogenetic hypotheses by Moncalvo et al. (2006) comprises the genera *Botryobasidium*, *Sistotrema*, *Clavulina*, *Multiclavula*, *Craterellus*, *Cantharellus*, and *Hydnum*. The authors also included the Ceratobasidiaceae and Tulasnellaceae in the Cantharellales. Species of *Botryobasidium* and *Sistotrema* are saprotrophs, *Multiclavula* species are basidiolichens, and *Clavulina*, *Craterellus*, *Cantharellus*, and *Hydnum* are ectomycorrhizal fungi. There is

no synapomorphy known for the taxa included in the Cantharellales.

Evolutionary trends in Cantharellales:

Basidiocarps resupinate > clavarioid > stalked capitate

Hymenium smooth > irregular > hydnoid > cantharelloid

Saprotrophic > lichenized

Saprotrophic > ectomycorrhizal
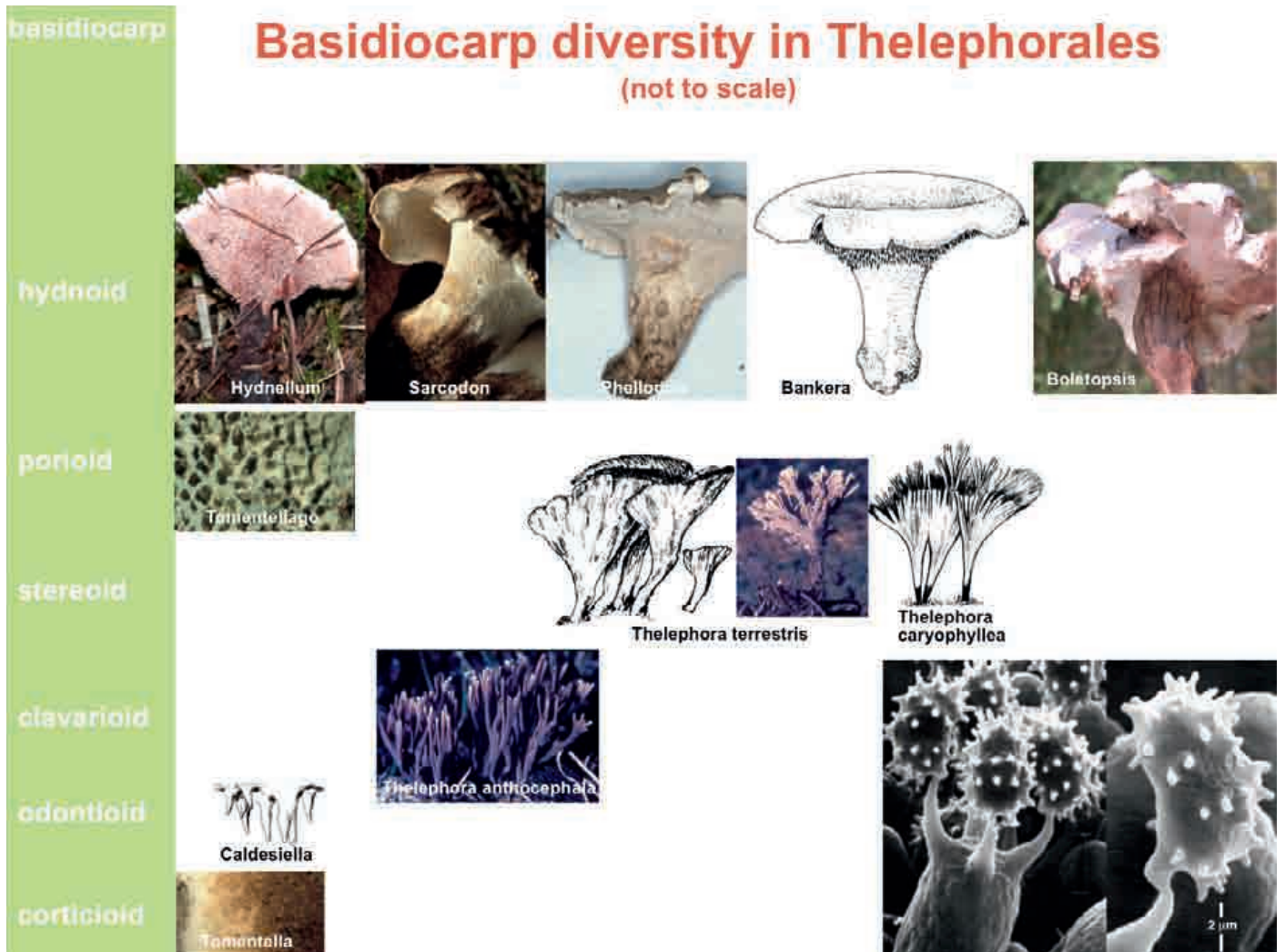
Fig. 48: Spore morphology, basidiocarps and hymenial configurations in Thelephorales. Typical basidiospores of the Thelephoraceae have pigmented and tubercular walls with spiny protuberances. Resupinate *Tomentella* species are very common in forests with acidic soils. Sometimes, basidiocarps of *Thelephora* begin to grow corticioid and continue irregularly stereoid-thelephoroid. Stalked capitate basidicarps with hydnoid hymenia are typical for the Bankeraceae. *Boletopsis* is an imitation of *Boletus*, but shares the micromorphology of the Thelephorales. Orig. F. Oberwinkler.

The evolutionary transitions from crustose to cantharelloid fructifications cannot be reconstructed. Also the origin of lichenization remains unclear, but all *Multiclavula* species are clavarioid. According to the proposed phylogenetic hypothesis of Moncalvo et al. (2006), *Cantharellus* and related genera constitute a clade separate from *Clavulina*, thus indicating that ectomycorrhizal fungi evolved at least twice in Cantharellales.

Thelephorales

Most species of the Thelephorales have brownish pigmented and characteristicly ornamented basidiospores (Fig. 48). Thelephoric acid is common and all species analyzed so far are mycobionts in mycorrhizae of seed plants. Basidiocarps and hymenia display a convergent series of corticioid, ondontioid, lenzitoid, thelephoroid-clavarioid, hydnoid and boletoid structures, but agaricoid and gasteroid basidiomata are not known (Fig. 11). All relevant phylogenetic hypotheses, based on molecular data, confirm the monophyly of the Thelephorales.

Evolutionary trends in Thelephorales:

Basidiocarps resupinate > stereoid > clavarioid > stalked capitate

Hymenium smooth > irregular > hydnoid > cantharelloid

Origin unknown > mycorrhizal
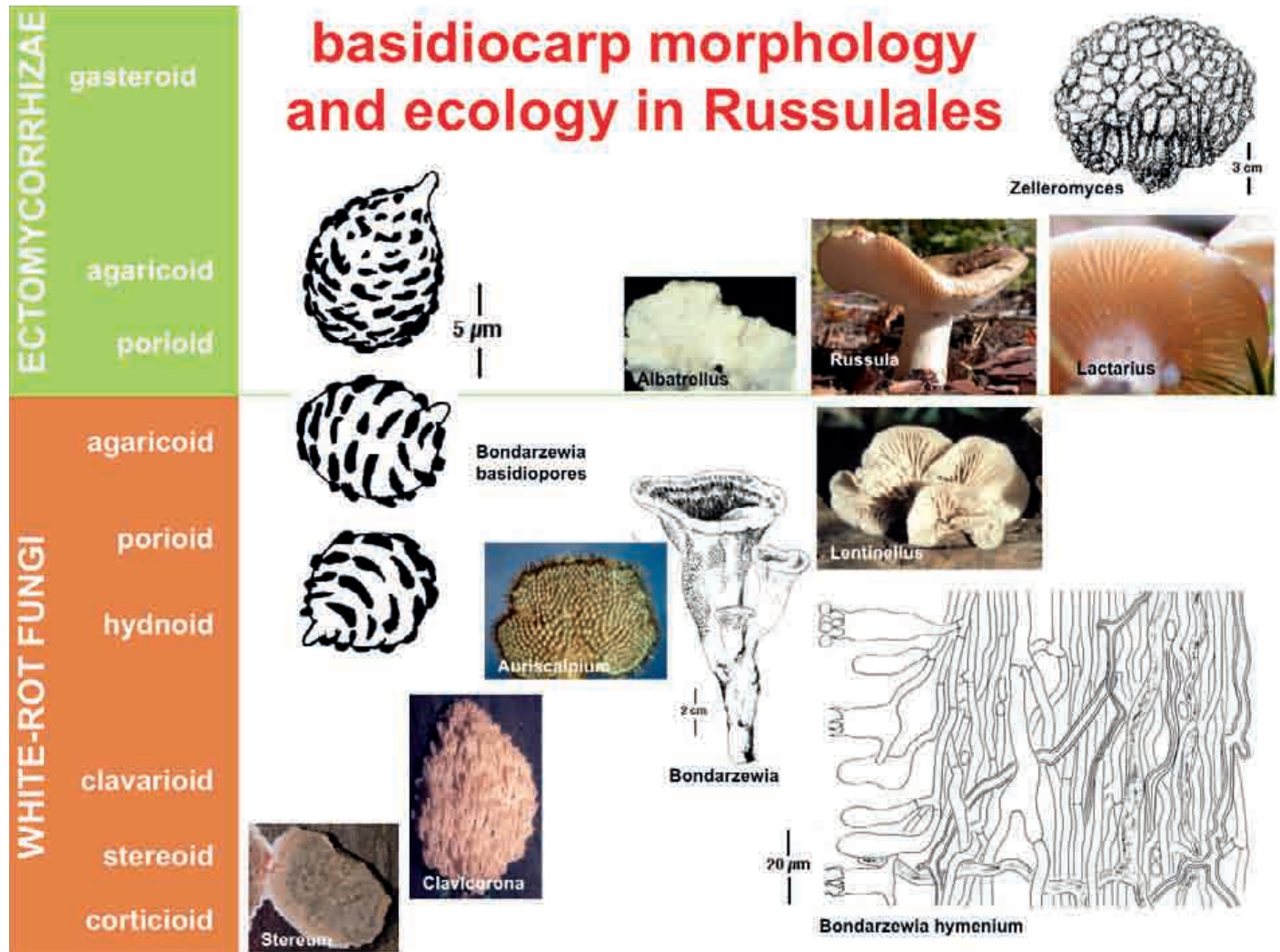
Fig. 49: Micromorphology, basidiocarps and main trophic stages in Russulales. The hymenial detail of *Bondarzewia montana* shows also the characteristic feature of gloeoplerous hyphae, the warty spore ornaments are amyloid. Some of the most characteristic basidiocarps are illustrated by representative genera. The distribution of white-rot and ectomycorrhizal fungi in the scheme applies for the Russulaceae. Orig. F. OBERWINKLER.

Many species of the *Tomentella-Thelephora* relationship and those of the Bankeraceae grow on soil in forests. In addition, many *Tomentella* species produce basidiocarps on wood and were therefore formerly considered as saprotrophs. However, all molecularly analyzed species could be identified as mycorrhizal partners (e.g. BRUNS et al. 1998, KÕLJALG et al. 2000, 2001, 2002). Thus, it is very likely that all Thelephorales are mycobionts with unknown origin. Also the distribution patterns with their hosts cannot be explained along evolutionary trends.

Russulales

Amyloid spore ornamentation together with gloeoplerous hyphae constitute a set of synapomorphies that characterize species of the Russulales (Fig. 49). It was provocative to postulate a relationship in „premolecular times" that circumscribed basidiomycetous fungi with resupinate to gasteroid basidiomata, including nearly all other fruiting body structures, and various hymenophore configurations (OBERWINKLER 1977).

Evolutionary trends in Russulales:

Basidiocarps resupinate > stereoid > discoid > clavarioid > pileate > gasteroid

Hymenium smooth > irregular > hydnoid > porioid > lamellate

Saprotrophic > parasitic

White rot > brown rot

Saprotrophic > ectomycorrhizal

Fig. 50: Host dependencies in *Lactarius* sect. *Dapetes*. *Lactarius deterrimus* is restricted to *Picea abies, L. salmonicolor* to *Abies alba*. *Lactarius deliciosus, L. sanguifluus,* and *L. semisanguifluus* are associated with *Pinus sylvestris*, but prefer different soil conditions as indicated in die diagram. Orig. F. OBERWINKLER.

Based on molecular and morphological data, MILLER et al. (2006) recognized 12 families and approximately 80 genera in the Russulales. Only Albatrellaceae and Russulaceae contain ectomycorrhizal taxa and represent separate clades. Albatrellaceae comprise predominantly pileate poroid species, however *Byssoporia terrestris* is resupinate and *Leucogaster, Leucophlebs* and *Mycolevis* are gasteroid. In Russulaceae *Lactarius* and *Russula* contain many species with a global distribution in ectomycorrhizal vegetations, in temperate regions very frequently with dominating Pinaceae and Fagales. Coevolutionary processes reached species-species dependencies in many cases (Fig. 50). Basidiocarps

in Russulaceae are exclusively agaricoid and gasteroid, the latter e.g. *Arcangeliella, Cystangium, Gymnomyces, Macowanites, Martellia,* and *Zelleromyces*. Most of these gasteroid genera appear to be paraphyletic. – The switches from white rotting ancestors to brown rot decay fungi and to ectomycorrhizal ones are unresolved.

Atheliales

The Atheliales is composed of resupinate species with loose subhymenia, smooth to slightly irregular hymenia (Fig. 51), and an unusual diversity of trophic stages (Fig. 17),

including saprotrophs, algal and lichen parasites as well as animal and plant symbionts (BINDER et al. 2005). The lichenized Lepidostromataceae (ERTZ et al. 2008) appears to be the sister clade.

Evolutionary trends in Atheliales:

Cystidia lacking > present
Basidiospores smooth > lobate > bluntly warty
Saprotrophs > parasites > symbionts
Saprotrophic > ectomycorrhizal

20 µm
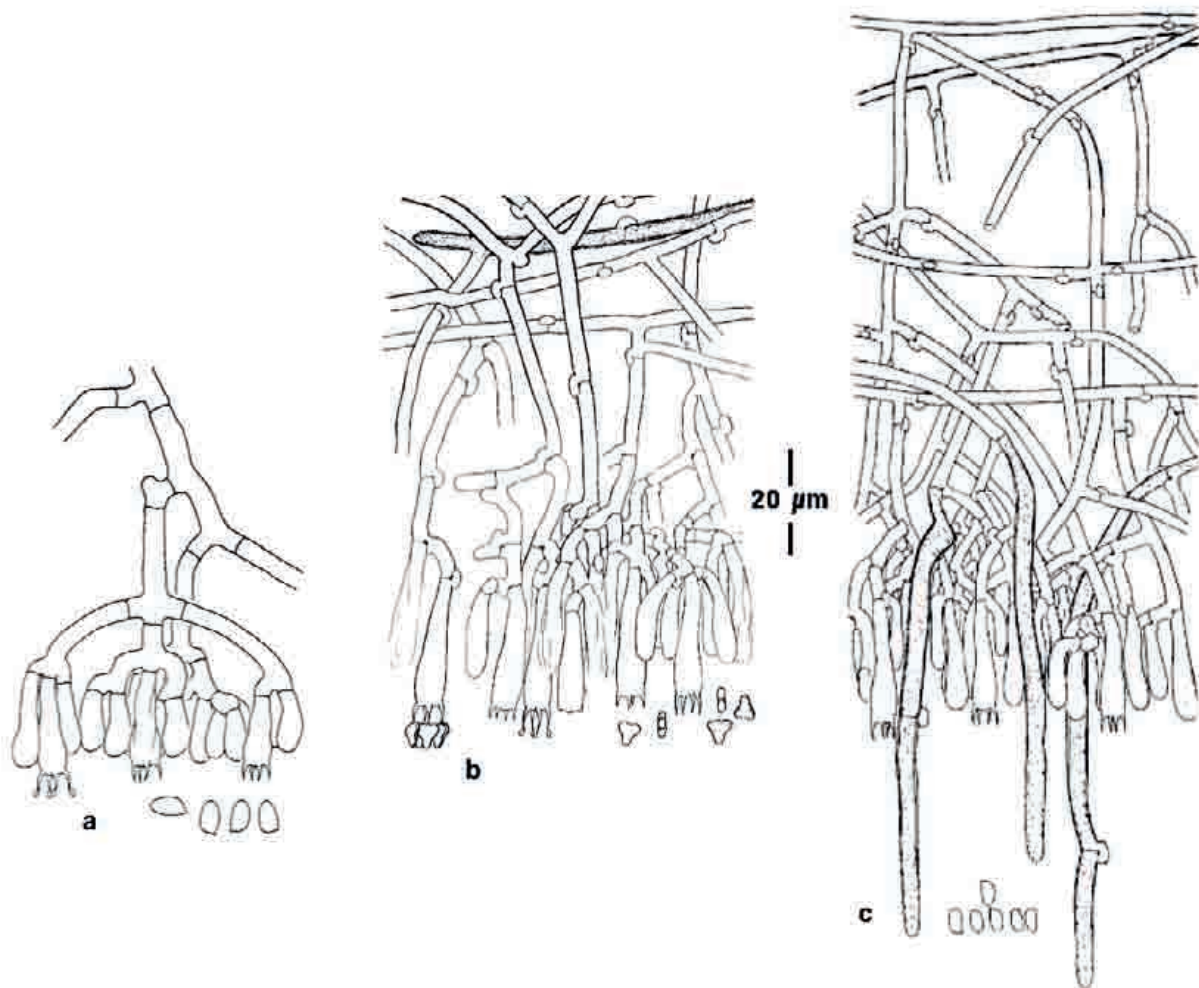
Fig. 51: Basidiocarps of representative members of the Atheliales. **a** *Athelia epiphylla,* **b** *Tylospora asterophora* and **c** *Amphinema byssoides*. Each of the figures illustrates the complete cellular construction of the species, except the hyphae in the substrate. Characteristic are the loose subhymenia and the non-thickening hymenia. **a** from Oberwinkler (1977), orig. F. Oberwinkler.

Most of the major clades in the Agaricomycotina have corticioid species in phylogenetically basal positions, thus confirming convergent evolutionary trends from simple to complex ones (Fig. 11). In the Atheliales, however, such an evolution of basidiomata is lacking. Micromorphological features, like hymenial cystidia in *Amphinema byssoides,* or oramented spores, as in species of the genus *Tylospora* (Fig. 51) cannot be interpreted in an evolutionary context. Also, the diversity of trophic stages is enigmatic, even when species of *Amphinema, Byssocorticium, Piloderma* and *Tylospora* are important and widespread ectomycorrhizal mycobionts.

Boletales

Fusiform, thick-walled and strongly pigmented basidiospores are the most common ones in Boletales. In frequent cases the hyphal system is monomitic and soft, and the large number of pigments are derivatives of pulvinic acid. These features were applied to circumscribe the Boletales in premolecular times. All phylogenetic hypotheses, based on molecular data, support the order. Basidiocarps range from resupinate to gasteroid with a major radiation in bolets (Figs. 11, 52).

Evolutionary trends in Boletales:

Basidiocarps resupinate > merulioid > porioid > pileate > gasteroid

Hymenium smooth > merulioid > hydnoid > poroid > boletoid > lamellate

Basidiospores smooth-walled > reticulate

brown rot > ectomycorrhizal > mycoparasitic

As in the Atheliales, also in Boletales resupinate basidiocarps and brown rot saprotrophism could be ancestral
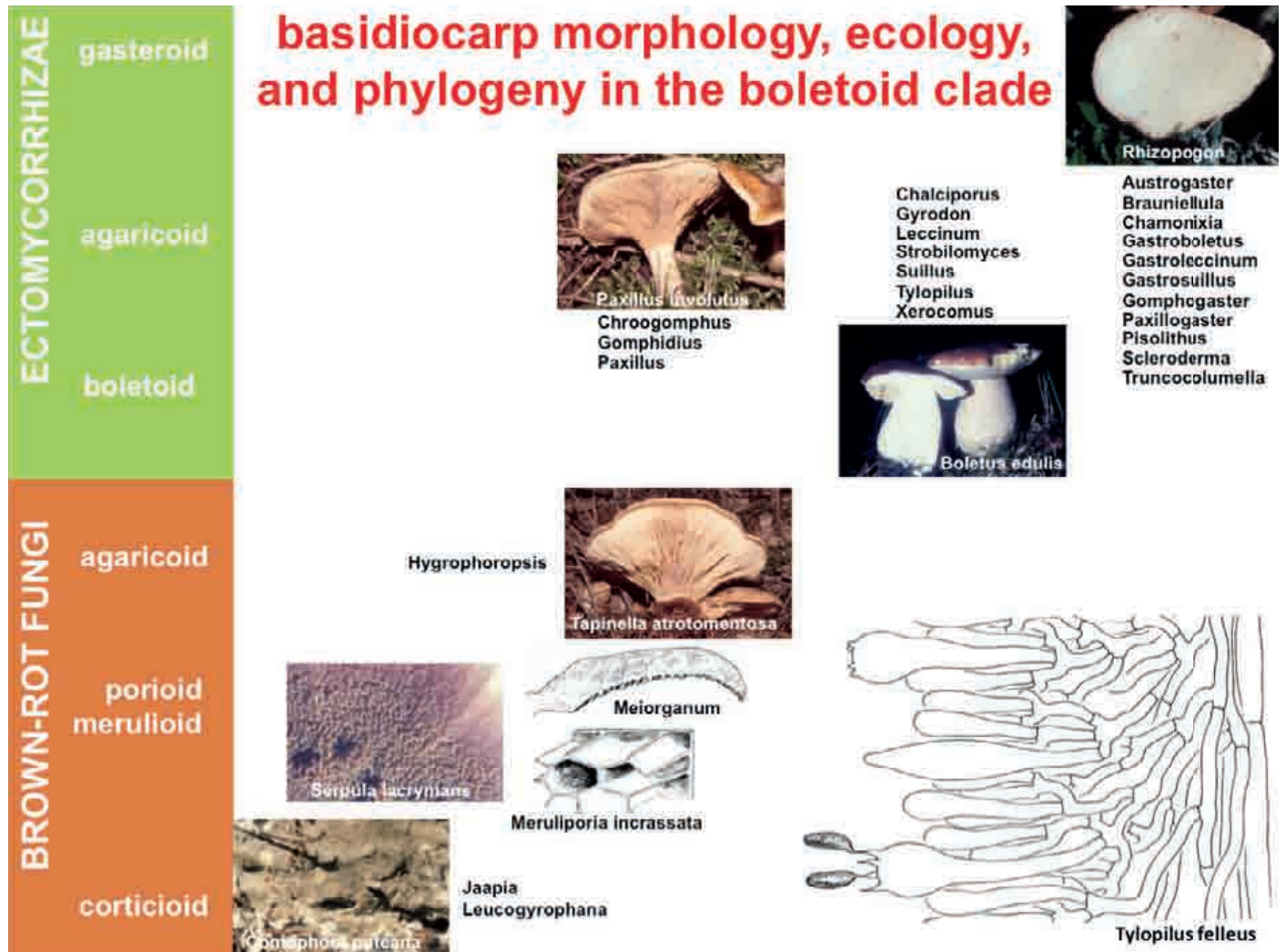
Fig. 52: Basidiocarps and hymenial micromorphology in Boletales. Part of the hymenium and subhymenium of *Tylopilus felleus* shows characteristic hyphal arrangement, basidial and spore morphology in Boletales. Basidiocarp illustrations of representative genera are arranged from resupinate to merulioid, porioid, agaricoid, boletoid, and gasteroid. Brown rot and ectomycorrhizae are the main trophic stages in Boletales. Orig. F. Oᴮᴇʀᴡɪɴᴋʟᴇʀ.

states (Bɪɴᴅᴇʀ & Hɪʙʙᴇᴛᴛ 2006). White rot is not known in these fungi, but a specific mode of brown-rot was developed by Coniophoraceae on conifers. Ectomycorrhizal associations are known from Pinaceae, Fagales, Fabales, Myrtaceae, Salicaceae and the tropical Dipterocarpaceae, and ericoid mycorrhizae with Ericales. A switch from brown rotting *Serpula* to ectomycorrhizal *Austropaxillus* and *Gymnopaxillus* species in *Nothofagus* and *Eucalyptus* forests has been reported by Cʟᴀʀɪᴅɢᴇ et al. (2001). Mycoparasitism of *Pseudoboletus parasiticus* on *Scleroderma citrinum* is known for a long time, but parasitic interactions of *Chroogomphus* and *Gomphid-*

ius spp. on ectomycorrhizae of *Suillus* and *Rhizopogon* spp. have been discovered some years ago (Aɢᴇʀᴇʀ 1987-1998). Ectomycorrhizal capabilities of *Pisolithus parasiticus* appear as not efficient enough for the required nutrient supply (Rᴀɪᴅʟ 1997). Reductions and losses in specific protein families were found in functional genomics of *Serpula lacrymans* (Eᴀsᴛᴡᴏᴏᴅ et al. 2011), and interpreted as adaptations to intercellular interactions with plant tissues. The known host specificity of *Leccinum* spp. could be confirmed and reconstructed using a molecular clock by ᴅᴇɴ Bᴀᴋᴋᴇʀ et al. (2004). However, *Leccinum aurantiacum* has a broad range of host trees.

Agaricales

Molecular phylogenies of the Agaricomycetes and Agaricales, based on comprehensive samplings (e.g. Mᴀᴛʜᴇɴʏ et al. 2006, Gᴀʀɴɪᴄᴀ et al. 2007, Bɪɴᴅᴇʀ et al. 2010) provided evidences for monophylies in these taxa and their subgroups. Homoplasies appear to be frequent in Agaricales, e.g. the multiple convergent evolution of sequestrate and non-gilled taxa. Morphological and/or ecological synapomorphies are not known in the order. However, several evolutionary trends may provide relevant information.
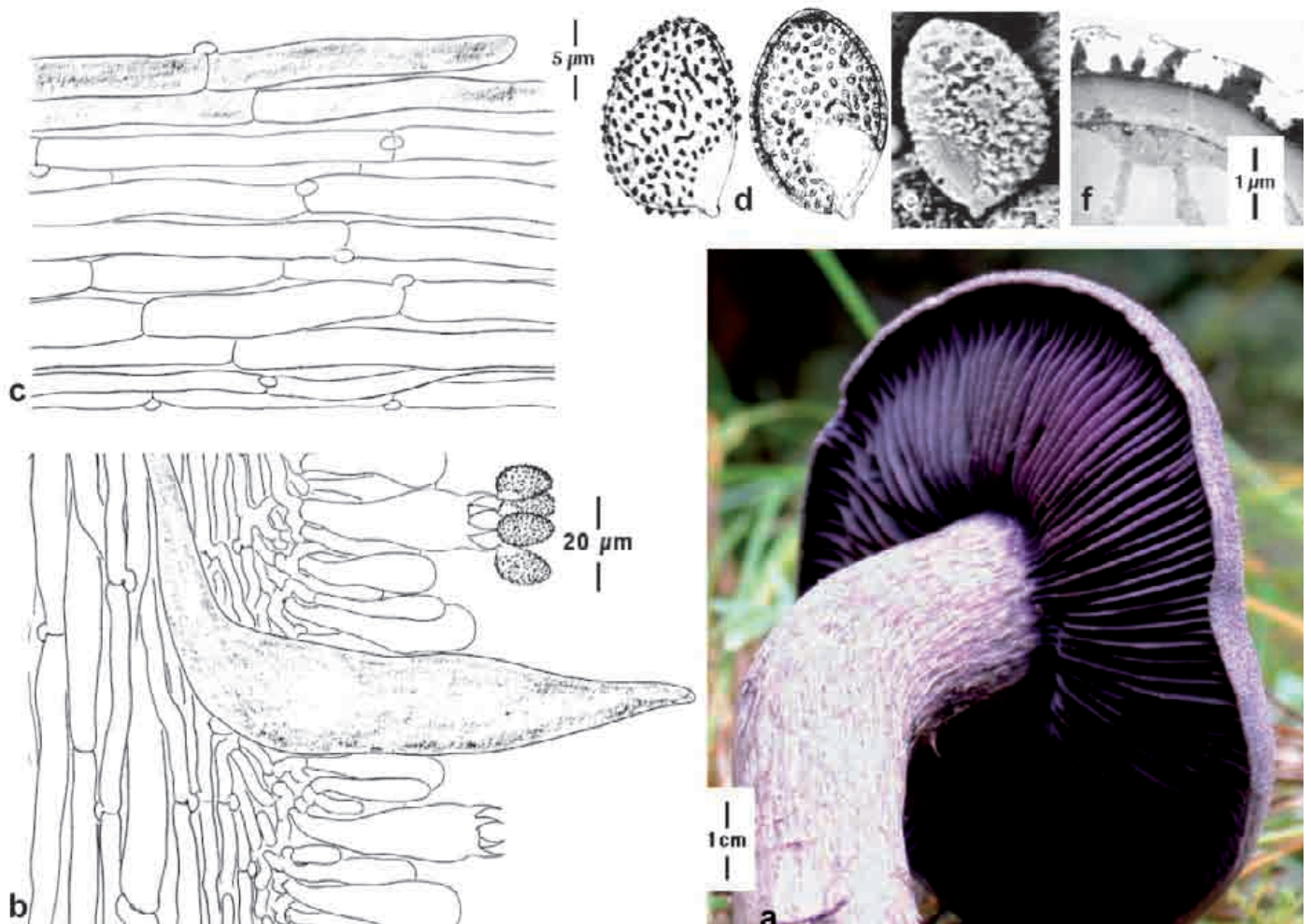
Fig. 53: *Cortinarius violaceus*, the type species of the genus. **a** basidiocarp, **b** detail of subhymenium and hymenium with basidia and cystidium, **c** hyphal context of pileus surface, **d**, **e** basidiospores, **f** TEM picture of the basidiospore wall. Orig. F. OBERWINKLER.
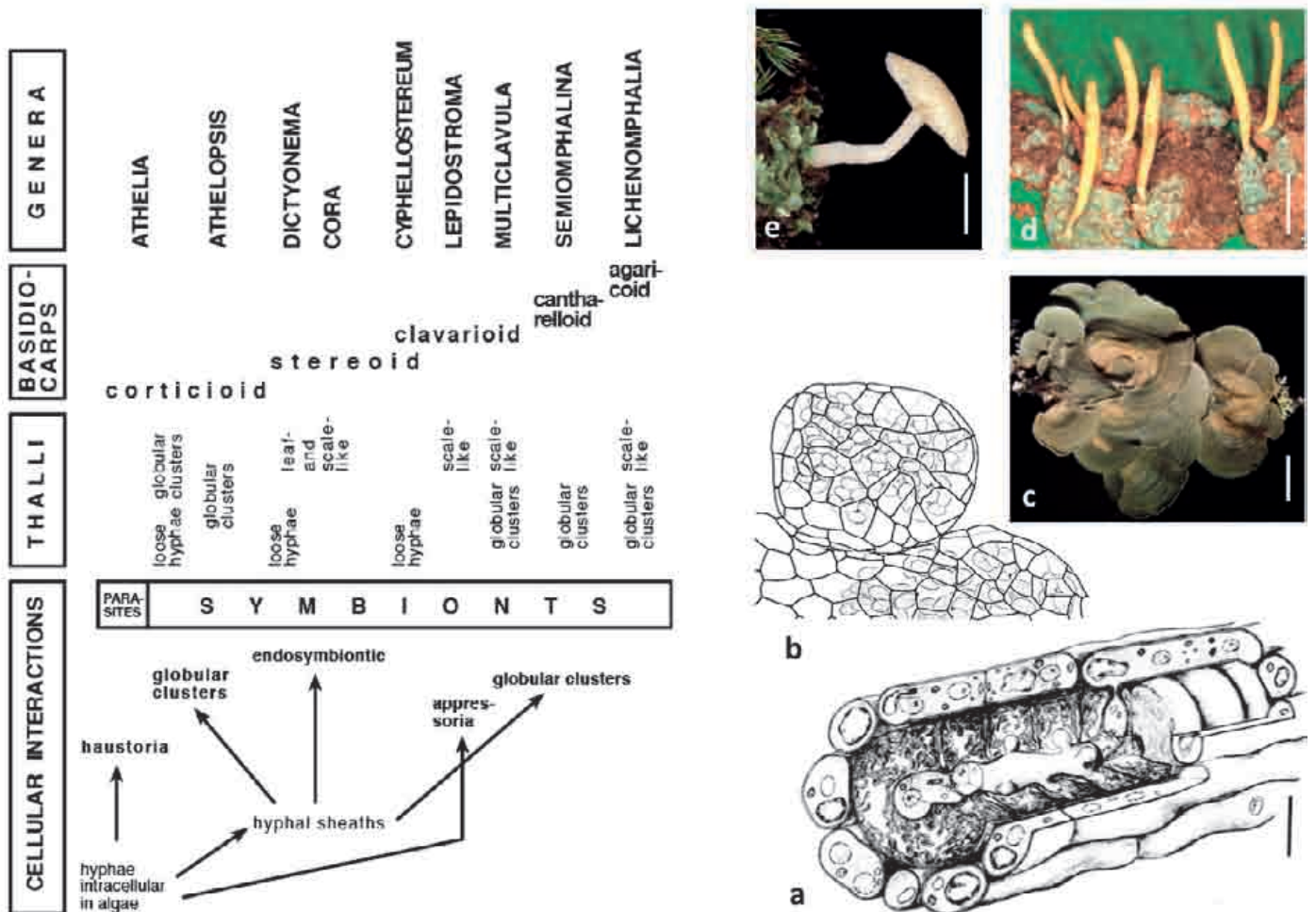
Evolutionary trends in Agaricales:

Basidiocarps clavarioid > agaricoid
Basidiocarps agaricoid > cyphelloid
Basidiocarps agaricoid > sequestrate
Basidiospores smooth-walled > ornamented
Basidiospores hyaline > pigmented
Basidiospores thin-walled > thickwalled > with germ pore
saprobic > ectomycorrhizal
saprobic > mycoparasitic
saprobic > lichenized

In several phylograms, clavarioid species, assigned to different genera, occur in basal positions of the Agaricales (MATHENY et al. 2006, GARNICA et al. 2007, BINDER et al. 2010). Considering non-agaricoid relationships, LARSSON et al. (2004) found that *Typhula* and *Macrotyphula* are closely related to some corticioid fungi, including *Coronicium*. – The reduction of agaricoid basidiocarps to non-lamellate ones happened at least 12 times in the Agaricales (BODENSTEINER et al. 2004). Major clades comprise *Schizophyllum* with *Fistulina* and *Porodisculus, Calyptella* and *Stigmatolemma, Cyphellopsis* with *Merismodes, Calathella,* Lachnella and the marine *Halocyphina* and *Nia.* Surprising is the split of *Hennigsomyces* with *Rectipilus* in two separate clades. As mentioned above, cyphellization is not restricted to Agaricales. – Convergent

gasteromycetation is a widespread evolutionary mode amongst Basidiomycota and occurred exceptionally frequent in the Agaricales. There are sequestrate relatives inter alia in *Amanita, Laccaria, Cortinarius, Coprinus,* and *Hebeloma*. Nidulariaceae are sister to *Cystoderma,* and Lycoperdaceae to Agaricaceae. The merulioid *Lindtneria trachyspora* and the hypogeous gasteromycete *Stephanospora caroticolor* share a similar micromorphology, especially in basidiospore characters. To accomodate these species, OBERWINKLER & HORAK (1979) erected the Stephanosporaceae that was confirmed in a molecular phylogeny by LARSSON (2007) who included also the corticioid *Cristinia helvetica* and *Athelidium aurantiacum*. – A general evolu-

Fig. 54: Evolutionary trends in basidiolichens (after OBERWINKLER 2012). **a** Fungus-alga-interaction of *Dictyonema sericeum*, (**b**) Complex globular thallus structures of the *Botrydina*-type, (**c**) *Cora pavonia,* upper side of thallus, (**d**) clavarioid basidiocarps of *Multiclavula sinensis* and crustous thallus, (**e**) basidiocarp of *Lichenomphalia hudsoniana* with basal *Coriscium* thalli. In the scheme, genera are arranged from simple to complex basidiocarps, i.e. corticioid-stereoid-clavarioid-agaricoid. Lichen thalli occur convergently with loose hyphae, globular clusters (**b**), and scaly structures (**e**). *Athelia* can parasitize with haustoria but also hyphae can surround algae in globular clusters. Hyphal sheaths in the *Dictyonema* group are always associated with endosymbiontic hyphae of the *Rhizonema* (formerly *Scytonema*) symbionts (**a**). Appressoria occur only in *Lepidostroma*. Comparatively simple globular clusters and scale-like thalli are formed by *Multiclavula* species (**b**). Complex globular structures of the *Botrydina*-type, and associations of globules in scale-like thalli *(Coriscium)* are present in *Lichenomphalia* (**e**). Bars: (**a**) 5 μm**,** (**c**-**e**) 1 cm. **a** from OBERWINKLER (1980), **b**-**d** from OBERWINKLER (2012).

tionary trend in basidiospore morphology is an increasing complexity of the spore wall. Thick-walled, ornamented and strongly pigmented basidiospores are typical for derived Agaricales (GARNICA et al. 2007). Such specialized propagules are well adapted to stressful environmental conditions.

Saprotrophic and symbiotic nutrition modes are the common ones in Agaricales, wood-decay, mycoparasitism and lichenization are compara-

tively rare. Main ectomycorrhizal genera include the convergently evolved *Hygrophorus, Amanita, Tricholoma, Laccaria, Cortinarius, Inocybe, Hebeloma* and their sequestrate relatives. *Cortinarius* (Fig. 53) has a worldwide distribution in ectotrophic forests and comprises at least 2000 species. MARTIN et al. (2008) suggested that the ectomycorrhizae-specific small secreted proteins of *Laccaria bicolor* have a decisive role in the establishment of the

symbiosis, and that the availability of the genome will provide further insights in the functional aspects of nutrient transfers in forest ecosystems. MATHENY et al. (2009) assumed that the Inocybaceae diversified no later than the Cretaceous in association with angiosperms in the Palaeotropics and had transitions to conifers possibly in the Paleogene. – Mycoparasites have been discussed above and basidiolichens will be considered in the following part.

Basidiolichens

Lichenized basidiomycetous fungi are known only from Agaricomycetes in which they originated in four or five different clades (Fig. 17), the Cantharellales, Corticiales, Atheliales, Agaricales, and possibly also the Hymenochaetales. Whether Lepidostromataceae should be integrated in the Atheliales or kept separate as their sister taxon is pending.

Evolutionary trends in basidiolichens:

Basidiocarps resupinate > stereoid > clavarioid > agaricoid

Lichen-thalli granules > scales > leaves

Photobiont *Rhizonema* > green algae

Fungus-alga-interaction with haustoria > appressoria > hyphal sheaths

In a first comprehensive morphological survey, basidiolichen genera were treated comparatively (OBERWINKLER 1970). Resupinate basidiocarps exist in the related *Athelia* and *Athelopsis* and convergently in *Dictyonema* and *Cora*. *Multiclavula* and *Lepidostroma* are clavarioid and evolved separately in the Cantharellales and as a sister group of the Atheliales. In the *Cora-Dictyonema* clade of the Hygrophoraceae, a basal family of the Agaricales, cluster also *Acantholichen, Cyphellostereum*, and *Lichenomphalia* (LAWREY et al. 2009). – Bulbils of algae and fungi may constitute convergent ancestral states in the evolution of basidiolichen thalli (LAWREY et al. 2007), as in the *Multiclavula* relationship, the *Marchandiomphalina* group, in lichenized *Athelia* and *Atheliopsis, Cyphellostereum pusiolum,* and *Lichenomphalia* (Fig. 54). Scales of *Lichenomphalia* and *Lepidostroma*, and finally leaf-like thalli of *Cora* are structurally complex and therefore certainly derived.

Photobionts in basidiolichens, as in ascolichens, are cyanobacteria and green algae. The lichenized scytone-

matoid cyanobacteria form a clade different from the one of free living *Scytonema* s.str. that is now called *Rhizonema* (LÜCKING et al. 2009b). Green algal photobionts, including *Coccomyxa* species, belong to the Trebouxiophyceae (BECK & PERSOH 2009). – Fungus-alga-interactions (OBERWINKLER 1980, 1984) with cyanobacteria are hyphal sheaths from which haustoria-like endosymbiontic hyphae originate (Fig. 54 a). Appressoria and globular clusters formed by densely arranged hyphae surrounding the phycobiont (Fig. 54 b) are the interaction structures with green algae. – An accelerated evolution as a consequence of transitions to mutualism has been calculated by LUTZONI & PAGEL (1997) using lichenized *Omphalina* species and related non-lichenized ones.

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