

# Yeasts in Pucciniomycotina

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**Abstract** Recent results in taxonomic, phylogenetic and ecological studies of basidiomycetous yeast research are remarkable. Here, Pucciniomycotina with yeast stages are reviewed. The phylogenetic origin of single-cell basidiomycetes still remains unsolved. But the massive occurrence of yeasts in basal basidiomycetous taxa indicates their early evolutionary presence. Yeasts in Cryptomycocolacomycetes, Mixiomycetes, Agaricostilbomycetes, Cystobasidiomycetes, Septobasidiales, Heterogastridiomycetes, and Microbotryomycetes will be discussed. The apparent loss of yeast stages in Tritirachiomycetes, Atractiellomycetes, Helicobasidiales, Platygloaeales, Pucciniales, Pachnocybales, and Classiculomycetes will be mentioned briefly for comparative purposes with dimorphic sister taxa. Since most phylogenetic papers suffer considerably from the lack of adequate illustrations, plates for representative species of orders have been arranged. The structural qualities are the prerequisites for specific functions that cannot be expressed by phylogenetic dendrograms.

## Introduction

There are four major historical periods in yeast research. The first one was the time of the experimentalists, culturing fungi and observing developmental stages from spore germination

to conjugation, and eventually fructification (Brefeld 1881, 1888, 1895a, b, 1912), including mating experiments (Bauch 1925; Kniep 1928). After an interval, yeast culture collections were established in various institutions and countries, and yeast manuals (Lodder and Kreger-van Rij 1952; Lodder 1970; Kreger-van Rij 1984; Kurtzman and Fell 1998; Kurtzman et al. 2011) were published, leading not only to the impression, but also to the practical consequence, that, most often, researchers studying yeasts were different from mycologists and vice versa. Though it was well-known that a yeast, derived from a fungus, represents the same species, most scientists kept to the historical tradition, and, even at the same time, the superfluous ana- and teleomorph terminology was introduced.

In contrast, biologically meaningful academic teaching required rethinking of the facts and terminology, which very simply led to a reappraisal of life-history models in which developmental stages clearly show the connexions. This process finally ended up in “one species – one name“, advertised as a new invention, and actually working only because it was nomenclatorically implemented. In connexion with big data of sequences, also for basidiomycetous yeasts, this newest trend created multi-gene-based phylogenetic hypotheses with a flood of new names that may be visualized by only very few competent mycologists. Therefore, this review has been expanded with illustrations of representative taxa, thus hopefully enlarging the readability for a broader audience.

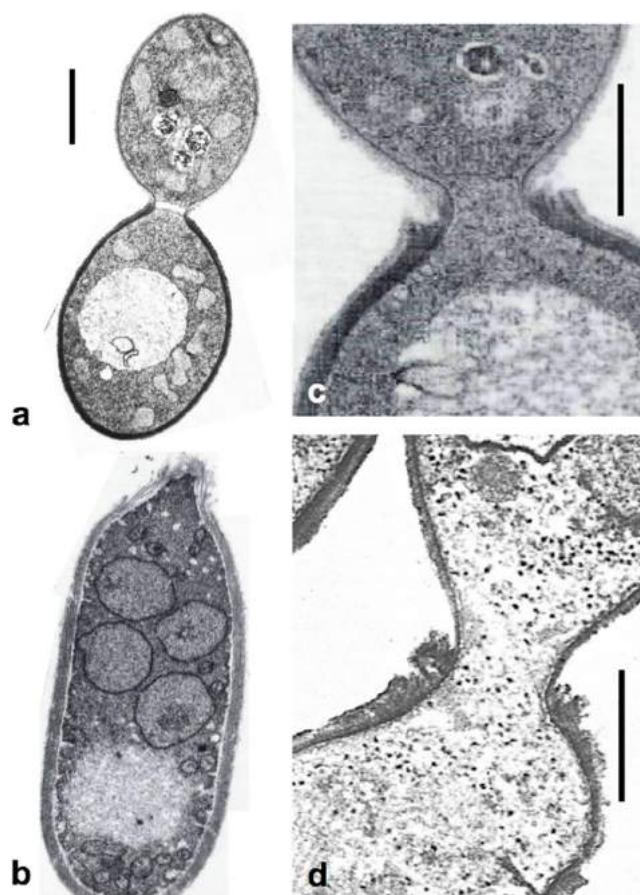
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## Basidiomycetous yeasts

In biological systems, the terminology applied for comparative purposes with a phylogenetic meaning has to follow strictly homologous criteria. Therefore, the term ‘yeast’ is used here as the budding of single cells, illustrated in Fig. 1.



**Fig. 1** Transmission electron micrographs of longitudinal sections of budding basidiomycetous yeasts. **a–c** *Agaricostilbum palmicolum*. **d** For comparison: *Graphioloa phoenicis* (Ustilaginomycotina). Note cell wall scars of mother cells at budding loci in **b–d**. Bars 2  $\mu$ m. Modified after Oberwinkler and Bandoni (1982), Oberwinkler et al. (1982), and Oberwinkler and Bauer (1989)

Consequently, in this context, fission yeast is not a yeast, and single cells formed by hyphal cell desintegration cannot be classified as yeasts. When yeasts are defined in a much broader sense (Kurtzman et al. 2011), the objective is a different one, not applicable in a comparative phylogenetic context.

Predominantly, yeasts occur in the first ontogenetic stages. Even when this may appear as an anthropocentric view, there is objectively no doubt that, after sexual reproduction of propagules, new developmental stages begin (see Figs. 6, 9, 16 in later sections). Nevertheless, single-cell reproduction as yeasts may also occur in later developmental stages, not directly following meiotically produced propagules. Such cases clearly require careful karyological determinations. Curious cases may occur, as illustrated in Fig. 1b, showing four haploid nuclei in one yeast cell without any indication of a previous meiosis, or yeast budding from apparently monokaryotic cells into empty adjacent cells (see Fig. 7d, h, i in later section).

Though various pucciniomycotinous yeasts are known exclusively in the single-cell stage, all classes and orders with yeasts contain dimorphic species. When sexual reproduction

is known, typically karyogamy and meiosis occur in the basidium, formed as a terminal cell on a hypha or emerging from a teliospore. Often, the yeast phase starts as a basidiospore, budded off directly from the meiosporangium (see Figs. 8, 9, 12, 14, 16, 17 in later sections). Frequently, basidiospore germination is yeast budding (see Figs. 3, 6, 8, 9, 11, 12, 13, 14, 15 in later sections).

### Yeasts in Pucciniomycotina

The monophyly of Pucciniomycotina was shown by single-gene (e.g. Swann and Taylor 1993, 1995a, b; Weiss et al. 2004; Bauer et al. 2006) and multi-gene analyses (Lutzoni et al. 2004; James et al. 2006; Aime et al. 2014) as well as by approaches based on genomes (Kuramae et al. 2006; Ebersberger et al. 2012; Hibbett et al. 2013; Toome et al. 2014). The subphylum was nomenclatorically established by Bauer et al. (2006) and systematically treated to ordinal level, an arrangement that corresponds to phylogenetic interpretations (Aime et al. 2006; Hibbett et al. 2007). The most recent phylogenetic approaches are those of Wang et al. (2015a, b). These authors applied seven gene analyses in 156 species, for which network results could also be achieved.

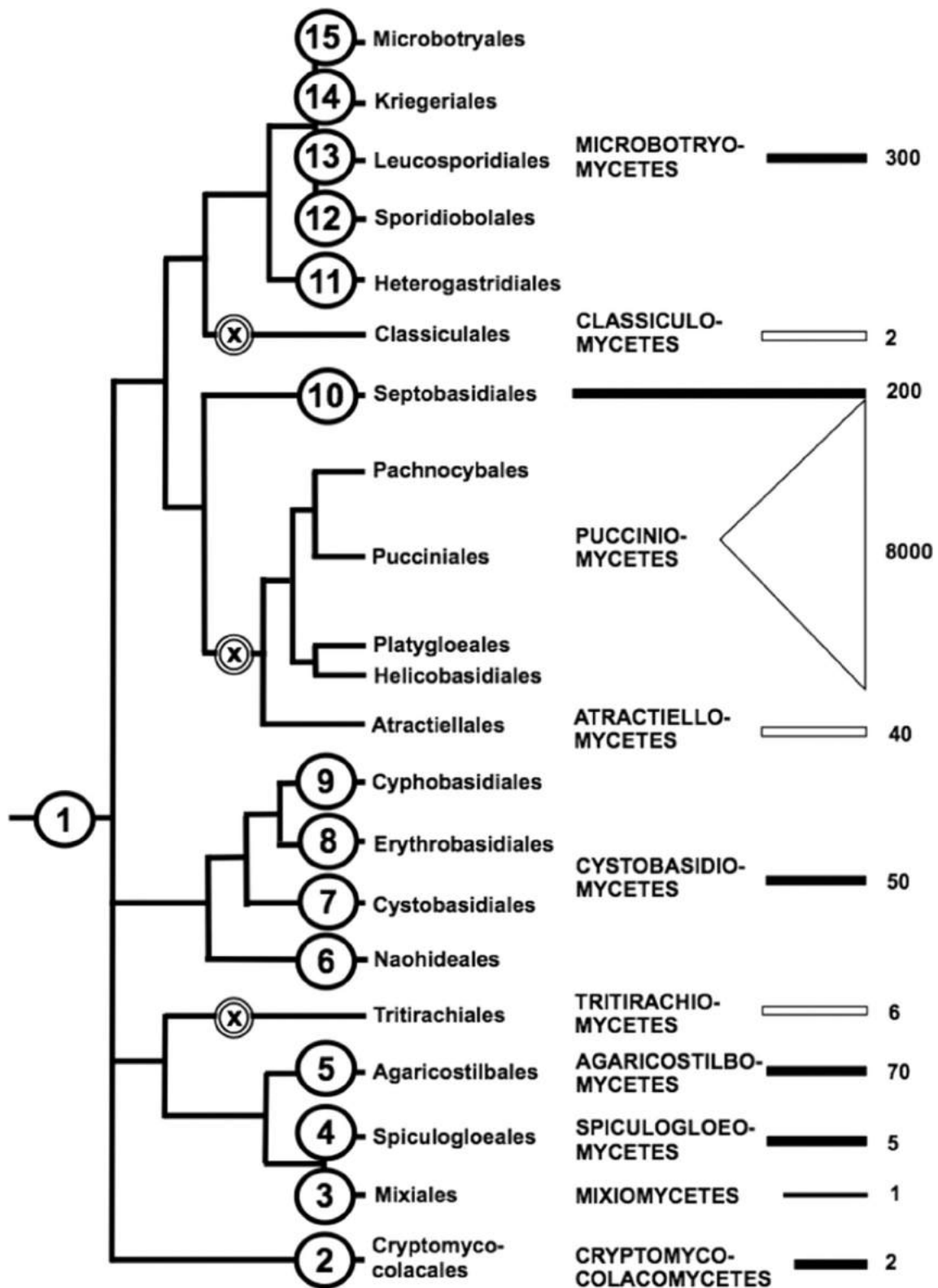
Currently, ten classes are recognized (Fig. 2). Yeasts have been reported from six classes, Cryptocolacomycetes, Mixiomycetes, Spiculogloeomycetes, Agaricostilbomycetes, Cystobasidiomycetes, and Microbotryomycetes, and 14 orders, Cryptomycocolacales, Mixiales, Agaricostilbales, Spiculogloeales, Naohideales, Cystobasidiales, Erythrobasidiales, Cyphobasidiales, Septobasidiales, Heterogastridiales, Kriegeriales, Leucosporidiales, Sporidiales, and Microbotryales.

A robust phylogeny of Pucciniomycotina is required in order to interpret the distribution pattern of yeasts in the subphylum. As discussed below, phylogenetic positions of various classes are ambiguous. Here, an attempt is made to integrate various phylogenetic hypotheses in a simplified dendrogram for the purpose of a comprehensive overview, and for critically discussing alternative possibilities (Fig. 2).

As a first priority, the most logical question arises: where is the origin of basidiomycetous yeasts (Fig. 2 (1)), and, is it monophyletic? This topic will be addressed again in the “Concluding remarks”.

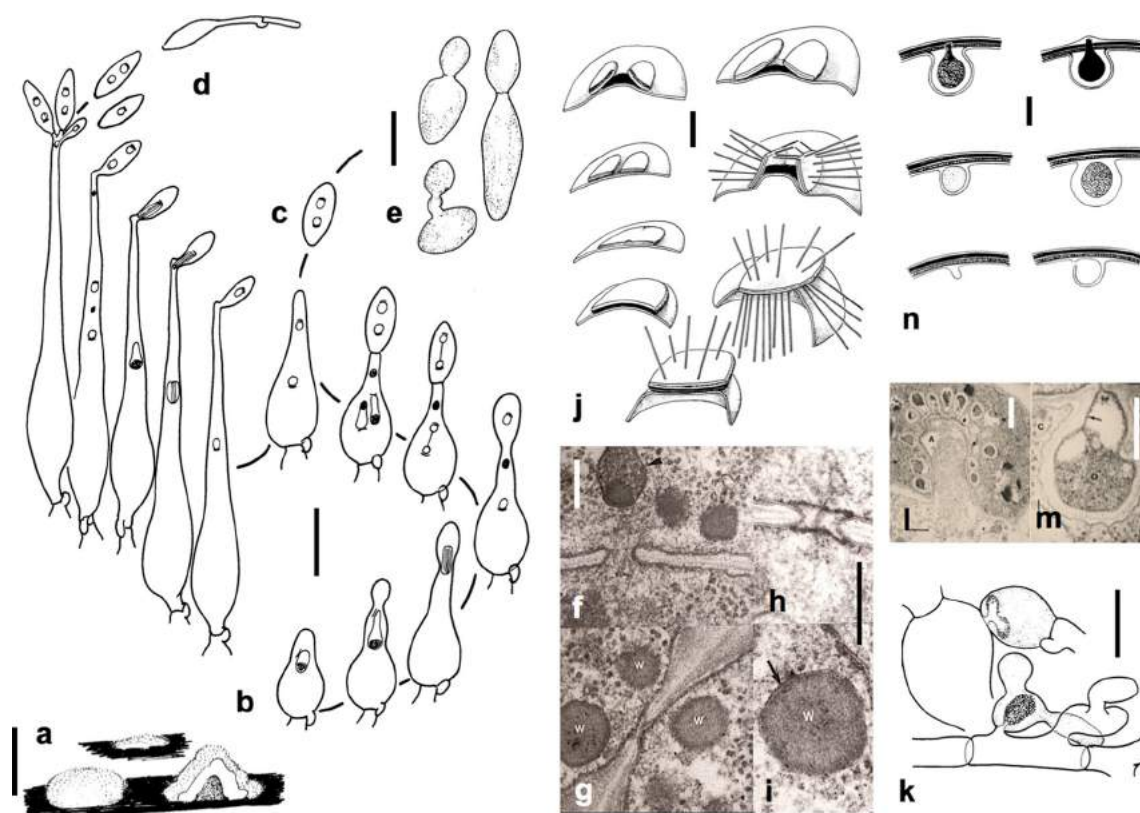
### Cryptomycocolacomycetes (Fig. 3)

Dimorphic, mycoparasitic, host–parasite interaction via colacosomes; hyphae clamped, simple pored, associated with Woronin body-like bodies; transversely 1-septate phragmobasidium disintegrating after meiosis, basal cell of meiosporangium with terminal, gasteroid basidiospores;



**Fig. 2** Schematic survey of orders and classes in Pucciniomycotina in an hypothetical phylogenetic arrangement. *Circled numbers* and *solid bars* refer to taxa with yeasts. *Double circled x*, *hollow bars* and *triangle* indicate loss of yeast stages. *Numbers in the righthand column* refer to

species of actually known or approximate numbers of the respective classes and the Septobasidiales. Adopted from Aime et al. (2014) and Wang et al. (2015a, b), modified and complemented. The following text is arranged in the sequence of the circled numbers



**Fig. 3** Cryptomycocolacomycetes, *Cryptomycocolax abnormis*. **a** Habit sketch of fructification growing in and on sclerotia of an ascomycetous host; one sclerotium longitudinally sectioned; *bar* 1 mm. **b** Basial ontogeny showing meiotic nuclear divisions; *bar* 20  $\mu$ m. **c** After meiosis II, the apical basial cell is released; basidiospore development is successive. **d** Basidiospore germinating with hyphae. **e** Yeast budding of basidiospores; *bar* 10  $\mu$ m. **f**–**i** Transmission electron micrographs of

septal pores associated with Woronin-like bodies (*w*); *bar* 0.1  $\mu$ m. **j** SPB development during meiosis; *bar* 0.1  $\mu$ m. **k** Ingrowth of the host into the cells of the parasite with the help of colacosomes. **l**, **m** Transmission electron micrographs of colacosomes; *bar* 0.5  $\mu$ m. **n** Colacosome development, based on serial sections; *bar* 0.5  $\mu$ m. Modified after Oberwinkler and Bauer (1990), and Bauer and Oberwinkler (1991)

development of upper basial cell unknown; spindlepole bodies (SPBs) disc-like (Fig. 3j). Yeast only known from *Cryptomycocolax abnormis* by lightmicroscopic observation of basidiospore germination (Fig. 3e), not available as culture. No yeast stage observed in *Colacosiphon filiformis*.

Oberwinkler and Bauer (1990) introduced *Cr. abnormis*, Cryptomycocolacaceae, and Cryptomycocolacales. Cryptomycocolacomycetes was proposed by Bauer et al. (2006). The clampless and conidia-producing *Co. filiformis* was described by Kirschner et al. (2001).

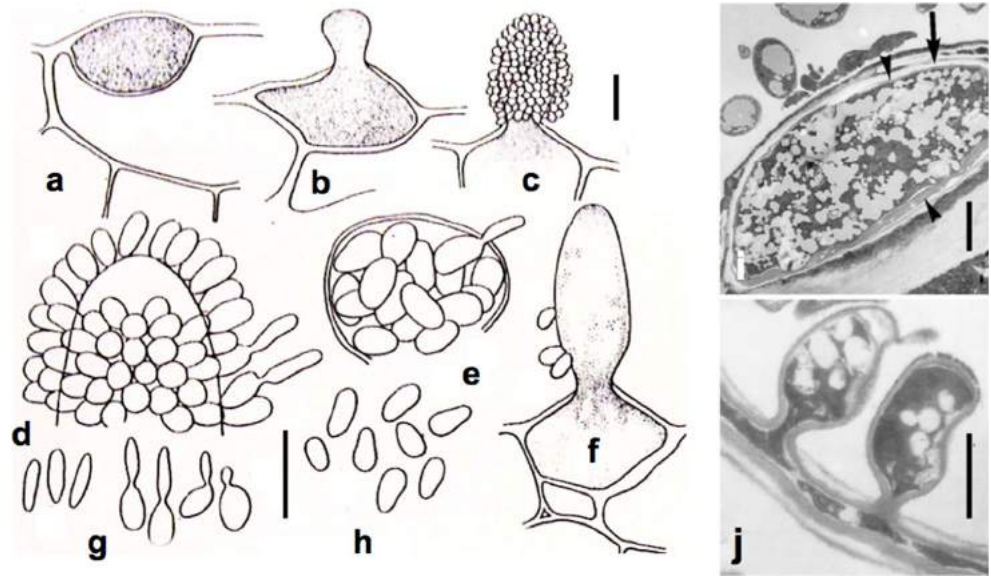
Clamped hyphae and basidiospore production of *Cr. abnormis* indicate a basidiomycetous relationship; the Woronin body-like bodies and SPB cycle show ascomycetous features. The close relationship of *Cr. abnormis* and *Co. filiformis* is supported by molecular analysis (Bauer et al. 2006); however, the phylogenetic position of Cryptomycocolacomycetes remains ambiguous. *Cryptomycocolax abnormis* is a sister clade of *Atractiella solani*, according to Weiss et al. (2004) or *Atractiellomycetes* (Aime et al. 2014), while Bauer et al. (2006) show a basal position in Pucciniomycotina.

**Comments:** Mycoparasitism is widespread in Pucciniomycotina and Tremellomycetes. However, colacosomes are only known in Cryptomycocolacomycetes, and in Heterogastridiales, Leucosporidiales and Sporidiobolales of the Microbotryomycetes. Because of two types of colacosomes in Cryptomycocolacomycetes (Oberwinkler and Bauer 1990; Kirschner et al. 2001) and the restriction to type I in Microbotryomycetes, the origin of these complex interactive organelles cannot be elucidated at present. Until the rediscovery of *Cr. abnormis*, its yeast phase is based only on a single light-microscopic observation. A unique character set, summarized above, indicates a most basal position of the Cryptomycocolacomycetes in the Basidiomycota.

#### Mixiomycetes (Fig. 4)

Multinucleate hyphae grow within the host cell walls, but are also reported to occur inter- and intracellularly (Aime et al. 2014; probably a misinterpretation of Fig. 4c, f) and sporangia

**Fig. 4** Mixiomycetes, *Mixia osmundae*. **a–h** Developmental stages (as *Phytoceratiomyxa osmundae* Sawada 1931) showing sporangial development, external sporulation, and yeast budding of spores (**g**); bars 10  $\mu\text{m}$ . **i, j** Transmission electron micrographs (modified after Bauer et al. 2006). **i** Subcuticular hypha with two cell wall layers, electron-transparent (*arrow*) and electron-opaque (*arrowheads*); bar 5  $\mu\text{m}$ . **j** Enteroblastically developing spores; bar 1  $\mu\text{m}$



with externally produced spores (Fig. 4c, d, i); unknown whether they are mitospores or meiospores (Nishida et al. 1995, 2011). Hyphal septa were not found, consequently septal pores are unknown. Inaccurate light-microscopy led to the misinterpretation of the sporangium as an ascus, i.e. with internal spore production (Mix 1947; Kramer 1958).

Spores are budding off yeasts, and yeast colonies can be obtained in pure culture. Physiological data were given by Nishida et al. (2011), and genome analyses showed that the yeast stage is haploid (Toome et al. 2014).

*Taphrina osmundae* was described by Nishida (1911) and accepted by Mix (1947), and also by Kramer (1958), proposing the new genus *Mixia* in the Protomycetaceae. Only one species is known; however, Toome et al. (2014) report on publicly available, unidentified sequences, so other plant-inhabiting relatives of *Mixia* do exist. Mixiaceae were proposed by Kramer (1958), and Mixiales and Mixiomycetes were introduced by Bauer et al. (2006). Sugiyama and Katumoto (2008a) found that *Phytoceratiomyxa osmundae* (Sawada 1929) is identical to *Mixia o.*, and has nomenclatorial priority as a correctly published name. However, they decided to propose the conservation of the name *Mixia* (Sugiyama and Katumoto 2008b).

Similar to ascomycetes, primary hyphal cell walls are electron-transparent and homogeneous, but change to the basidiomycetous opaque and fibrillar type when sporangia are developed (Bauer et al. 2006). The interphasic SPBs are double-structured and connected by middle pieces (Bauer et al. 2006). These unique ultrastructural characters indicate a basal position within the Pucciniomycotina, strongly supported by molecular hypotheses (Weiss et al. 2004; Aime et al. 2006, 2014; Bauer et al. 2006; Nishida et al. 2011; Toome et al. 2014).

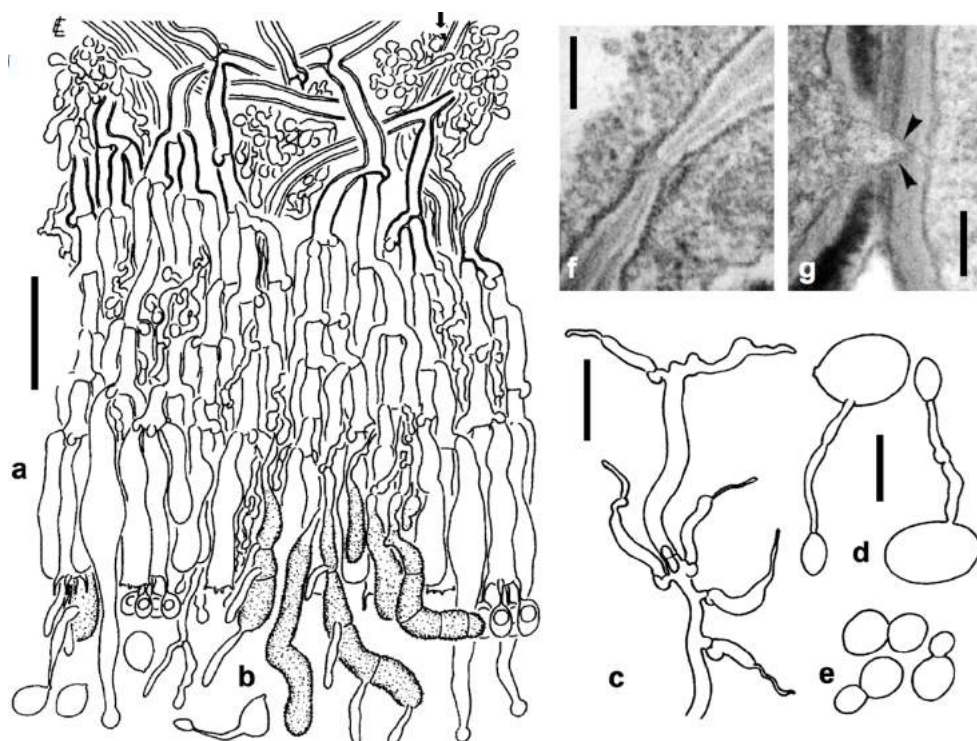
**Comments:** It is scarcely understandable why Sawada's correct microscopic drawings (1931; Fig. 4a–f) of *Phytoceratiomyxa osmundae* were overlooked until their re-discovery by Sugiyama and Katumoto (2008a). Even the generic name proposed by Sawada (1929) refers to exogenously produced spores, albeit the relationship with myxomycetes is implied. In the time in-between, Mix (1947) and Kramer (1958) misinterpreted the sporangium as an ascus due to incorrect microscopy. It required molecular restudies to elucidate the basidiomycetous nature of *Mixia* (Nishida et al. 1995; Sjamuridzal et al. 2002). Toome et al. (2014) sequenced the genome and found a complete set of mating and meiosis genes, indicating that sexual reproduction may occur. In addition, *M. osmundae* has the smallest plant pathogenic basidiomycete genome known at that time.

At least theoretically, host dependency may also shed light on the age of the parasite. Osmundaceae are considered the possible sister group of other Filicales with an approximate age of 300 Ma (Pryer et al. 1995; Sanderson and Doyle 2001). Phylogenetic analyses of ferns resolved *Osmunda* as the earliest-diverging leptosporangiate lineage (Schneider et al. 2004). Summarizing previous phylogenetic studies on ferns, Smith et al. (2006) accepted a basal position of the Osmundaceae in the Leptosporangiates. Assuming a stable host dependency for *Mixia o.*, the species would have a range of similar age.

### Spiculogloeomycetes (Fig. 5)

Perfect stage with clamped hyphae, simple septal pores, auricularioid basidia with ballisto-basidiospores, capable of germinating with secondary spores and/or budding off yeasts.

**Fig. 5** Spiculogloeomycetes, *Spiculogloea occulta*. **a–c** The mycoparasite (**b**), recognizable by granulose auricularioid basidia, producing secondary spores and conidia (arrow), growing in the basidiocarp of the host *Hyphodontia sambuci* (**a**), and attached to it by tremelloid haustoria (**c**). **d** Germinating basidiospores with terminal microconidia. **e** Yeast budding. Bars (**a, b**) 20  $\mu\text{m}$ ; (**c**) 10  $\mu\text{m}$ ; (**d, e**) 5  $\mu\text{m}$ ; (**f, g**) 0.1  $\mu\text{m}$ . Modified after Langer and Oberwinkler (1998) and Bauer et al. (2006)



Mycoparasites with tremelloid haustoria and nanometer-fusion in host-parasite interaction (Fig. 5).

Currently, two genera comprise 11 species. *Spiculogloea* with the single species *S. occulta* was introduced by Roberts (1996); a few additional species were added later (Roberts 1997; Hauerslev 1999). Spiculogloeales were proposed by Bauer et al. (2006), comprising the type genus, *Mycogloea* p.pt. and anamorphic *Sporobolomyces* spp. p.pt. Spiculogloeaceae was formally validated by Denchev (2009), and a new class, Spiculogloeomycetes, introduced by Wang et al. (2015a, b), also including *Sporobolomyces* spp. in the new genus *Phyllozyma*.

*Sporobolomyces coprosmicola* clustered with *Agaricostilbum* sp. in a molecular phylogeny of Bauer et al. (2006). In a survey of *Sporobolomyces*, Hamamoto et al. (2011) assigned several species to the *Agaricostilbum* clade. From these, *S. coprosmicola*, *S. dimennae*, *S. linderiae*, and *S. subbrunneus* were chosen, and the additional *S. corallina* and *S. novazealandicus* were added to constitute the newly erected genus *Phyllozyma*, based on the phylogenetic analysis of seven genes and the analysis of the enlarged LSU rRNA gene dataset (Wang et al. 2015a, b). According to these authors (l.c.) Spiculogloeales is the sister lineage to Mixiomycetes, rather than to the Agaricostilbales.

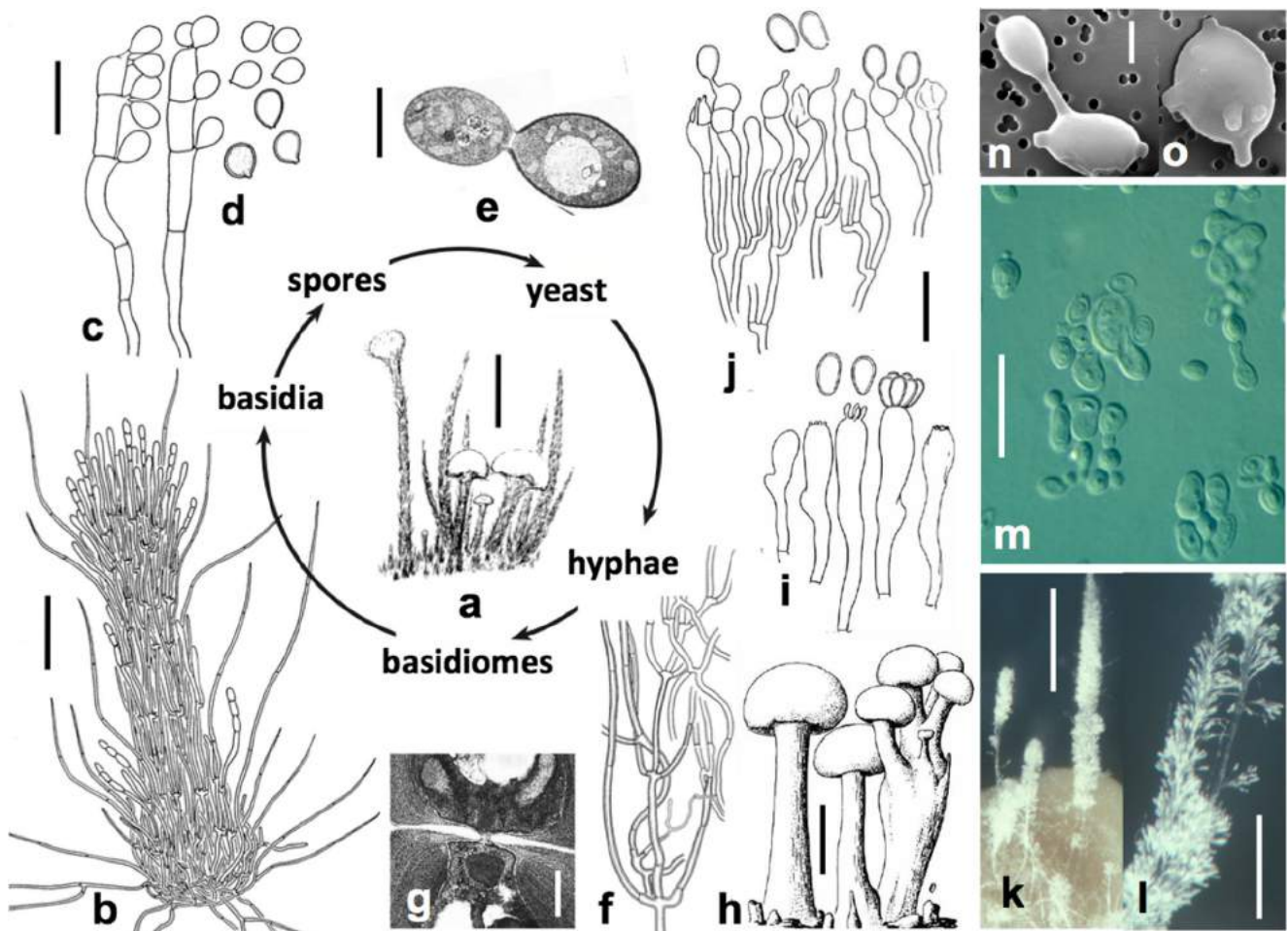
**Comments:** At present, a morphological circumscription of the *Spiculogloea* relationship with basidial stages is difficult and may have synapomorphies only as mycoparasites with tremelloid haustoria (Fig. 5c), and with scanty or lacking basidiomes. The meiosporangial type is basically the same in

*Spiculogloea* and *Mycogloea* p.pt., even when the latter ones are deciduous and not ornamented with granules. More precisely, tremelloid haustorial cells are known from species of various Pucciniomycotina genera, such as *Classicula*, *Cystobasidium*, *Jaculispora*, *Mycogloea*, *Occultifur*, *Spiculogloea* and *Zygogloea*. But it remains to be proven that these mycoparasitic organelles are truly homologous structures.

Moreover, in phylogenetic analyses, several species of *Sporobolomyces*, defined by reddish yeast colonies and ballistoconidia-producing yeasts (Kluyver and van Niel 1924), were found to be closely related with *Spiculogloea*, and in previous studies considered to belong to the *Agaricostilbum* clade. These yeast species, listed above, have been sampled from the phyllosphere of evergreen leaves and needles of shrubs and trees in a wide geographic range from Japan to New Zealand (Hamamoto et al. 2011). Though the ecology of these yeasts was not or only poorly studied, it is tempting to assume from their overall dataset that the propagules originate from meiosporangia, most likely from unknown mycoparasites of fungi on leaves or adjacent twigs. The ballistoconidia would be an excellent means for bridging the aerial spaces in between the plant and fungal habitats.

### Agaricostilbomycetes (Fig. 6)

Sexual state with pustular or stalked basidiomes, capitate when well developed, hyphae thin- to slightly thick-walled,



**Fig. 6** Agaricostilbomycetes. **a, b, e, g, k, l** *Agaricostilbum palmicolum*. **a** Life cycle and basidiomes in different developmental stages, capitate ones fully mature; *bar* 0.5 mm. **b** Young basidiome; *bar* 50  $\mu$ m. **e** Transmission electron micrograph of a longitudinally sectioned budding yeast; *bar* 5  $\mu$ m. **g** Transmission electron micrograph of a hyphal septal pore; *bar* 0.5  $\mu$ m. **k, l** Young basidiomes in culture; *bar* in (**k**) 200  $\mu$ m, in (**l**) 100  $\mu$ m. **l** Yeast culture; *bar* 20  $\mu$ m. **c, d, f, A** *hyphaenes*. **c, d** Mature and sporulating basidia, and basidiospores; *bar* 10  $\mu$ m. **f** Hyphal system

of basidiome. **h, i** *Chionosphaera apobasidialis*. **h** Mature basidiomes; *bar* 0.5 mm. **i** Holobasidia in a sequence of developmental stages in spore production from left to right, and basidiospores; *bar* 10  $\mu$ m. **j** *Stilbum vulgare*. Part of hymenium with basidia in different developmental stages, and basidiospores. **m, n** Scanning electron micrographs of *Sterigmatomyces halophilus*, *bar* 1  $\mu$ m. **m** Yeast cell with stalked blastoconidium. **n, o** Yeast cells with stalks. Modified after Oberwinkler and Bandoni (1982), Fell (2011b), and originals

septal pores without associated microbodies. Teliospores lacking. Meiosporangia transversely septate phragmobasidia in *Agaricostilbum* and *Stilbum*, or holobasidia with terminal, sessile basidiospores in *Chionosphaera* (Fig. 6). Metaphasic SPBs intranuclear, nucleoplasmic SPB separation. Dimorphic or known only in the yeast stage.

Yeast budding with short to long denticles (Fig. 6e, l–n). In *Sterigmatomyces*, the separation of the daughter cell occurs in the mid-region of the denticle. Some 70 species are distributed over 11 genera and four families. Agaricostilbaceae and Agaricostilbales were introduced by Oberwinkler and Bauer (1989), while Spiculogloceales were included in Agaricostilbomycetes, and erected by Bauer et al. (2006).

**Comments:** *Agaricostilbum* was described by Wright (1970) to accommodate a fungus on palm leaves, misinterpreted as an imperfect stage. A later study revealed its

basidiomycetous nature (Wright et al. 1981). A study of isarioid-type species by Brady et al. (1984) led to the proposal to synonymize *A. palmicolum* under *A. pulcherrimum*. *Chionosphaera* was proposed by Cox (1976), and **Chionosphaeraceae** was published by Oberwinkler and Bandoni (1982), based on a comparative morphological study of gasteroid, auricularioid heterobasidiomycetes. *Fibulostilbum phylacicola* (Seifert et al. 1992) and *Stilbum erythrinae* were included in *Chionosphaera* (Kirschner et al. 2001; Kirschner and Chen 2008). A generic survey was provided by Kwon-Chung (2011). *Ballistosporomyces* was introduced by Nakase et al. (1989), included in a polyphyletic *Sporobolomyces* (Hamamoto et al. 2011), and reintroduced by Wang et al. (2015a, b). *Cystobasidiopsis* was erected by Bauer et al. (2009) emended by Wang et al. (2015a, b). *Kurtzmanomyces*, introduced by Yamada et al. (1988) with a short diagnosis as

title of the publication “anamorphic yeast genus for the Q10-equipped organism whose conidium is freed by an end-break in the sterigma which branches or elongates to produce additional conidia and whose cells contain no xylose“, was supplemented by few additional species (Giménez-Jurado et al. 1990; Sampaio et al. 1999; Zhang et al. 2013). The **Kondoaceae** was proposed by Bauer et al. (2006) to accommodate the type genus and *Bensingtonia*. Wang et al. (2015a, b) added **Ruineniaceae** incertae sedis. These authors (l.c.) also introduced *Pseudobensingtonia* and *Jianyunia* and emended *Sterigmatomyces*, erected by Fell (1966), to include *Agaricostilbum*, based on molecular evidence.

First comparative analyses of 5S rRNA sequences (Gottschalk 1985; Gottschalk and Blanz 1985) showed that a type A secondary structure is present in *Agaricostilbum palmicolum*, *Atractiella solani*, *Phleogena faginea*, *Pachnocybe ferruginea*, *Platygløea peniophorae* (*Colacogloea p.*) and the smuts *Microbotryum violaceum*, *Sphacelotheca* sp. and *Ustilago scabiosae* (*Microbotryum s.*), and also in *Taphrina deformans*. Subsequent molecular phylogenetic studies confirmed these findings and provided more and more detailed hypotheses of natural relationships (Müller 1989; Weiss et al. 2004; Aime et al. 2006; Bauer et al. 2006, 2009; Bandoni and Boekhout 2011; Boekhout et al. 2011; Wang et al. 2015a, b).

As conceived in the presently accepted circumscription, the *Agaricostilbomycetes* comprise a wide range of dimorphic and also exclusively single-celled species. A most surprising fact is that basidiomes and meiosporangia are highly diverse (Fig. 6). However, septal pore types, SPBs, basidiospore development (Bauer and Oberwinkler 1986; Bauer et al. 1992), and sequence data support a phylogeny, as proposed by Bauer et al. (2006). Using seven genes, this phylogenetic interpretation was recently confirmed and expanded by Wang et al. (2015, b).

The synonymy of *Agaricostilbum palmicolum* and *A. pulcherrimum* was published as a simple statement without any documentation of studied characters (Brady et al. 1984). Though the wide geographical distance between Argentina and Sri Lanka might be admitted as a possible species distribution, it has to be considered that four *Agaricostilbum* spp. were described, including *A. novozelandicum* from New Zealand. Until now, there has been no comparative study of these taxa, and only *A. pulcherrimum* has been used for molecular analyses. In addition, substrate dependencies and preferences should be taken into consideration more closely. Brady et al. (1984) list several palms, and also *Pandanus fascicularis* from India and *Xanthorrhoea* sp. from Queensland as *Agaricostilbum* hosts. These facts, together with big differences of basidiome forming and exclusively single-celled species, are strong arguments against synonymizing *Agaricostilbum* under *Sterigmatomyces* as proposed by Wang et al. (2015a, b), based exclusively on sequence data.

*Sterigmatomyces* species were isolated from extremely diverse substrates, including marine habitats (Fell 2011b). *Pseudobensingtonia*, a segregate of the ballistosporic yeast genus *Bensingtonia*, comprising two species, is characterized molecularly as a sister clade of *Sterigmatomyces* (Wang et al. 2015, b). *Mycogloea nipponica* (Bandoni 1998) was unraveled as a basidial stage of the yeast genus *Kurtzmanomyces* (Kirschner et al. 2002). However, a sexual stage is not known from any other *Kurtzmanomyces* species. Also, *Ballistosporomyces* (Nakase et al. 1989) is only known in its asexual yeast stage. It was reinstated by Wang et al. (2015a, b) on molecular evidence, after being synonymized with *Sporobolomyces* by Boekhout (1991). Another, molecular-based rearrangement is an emended version of *Cystobasidiopsis* from which no yeast phase is known in its type species, *C. nirenbergiae* (Bauer et al. 2009), but which now includes yeasts of the *Sporobolomyces lactophilus* clade (Wang et al. 2015a, b). For *Stilbum vulgare*, Seifert et al. (1992) found a yeast stage derived from germinating basidiospores. Surprisingly, mitosis occurred in the parent cell and not as in *Bensingtonia yuccicola* and *A. pulcherrimum* in the bud, and typically in other basidiomycetous yeasts (McLaughlin et al. 2004). A reinvestigation of *Kondoa malvinella*, the type species of the genus (Yamada et al. 1989), revealed that auricularioid basidia develop from hyphae, and produce ballistosporiospores that germinate with yeasts (Fonseca et al. 2000).

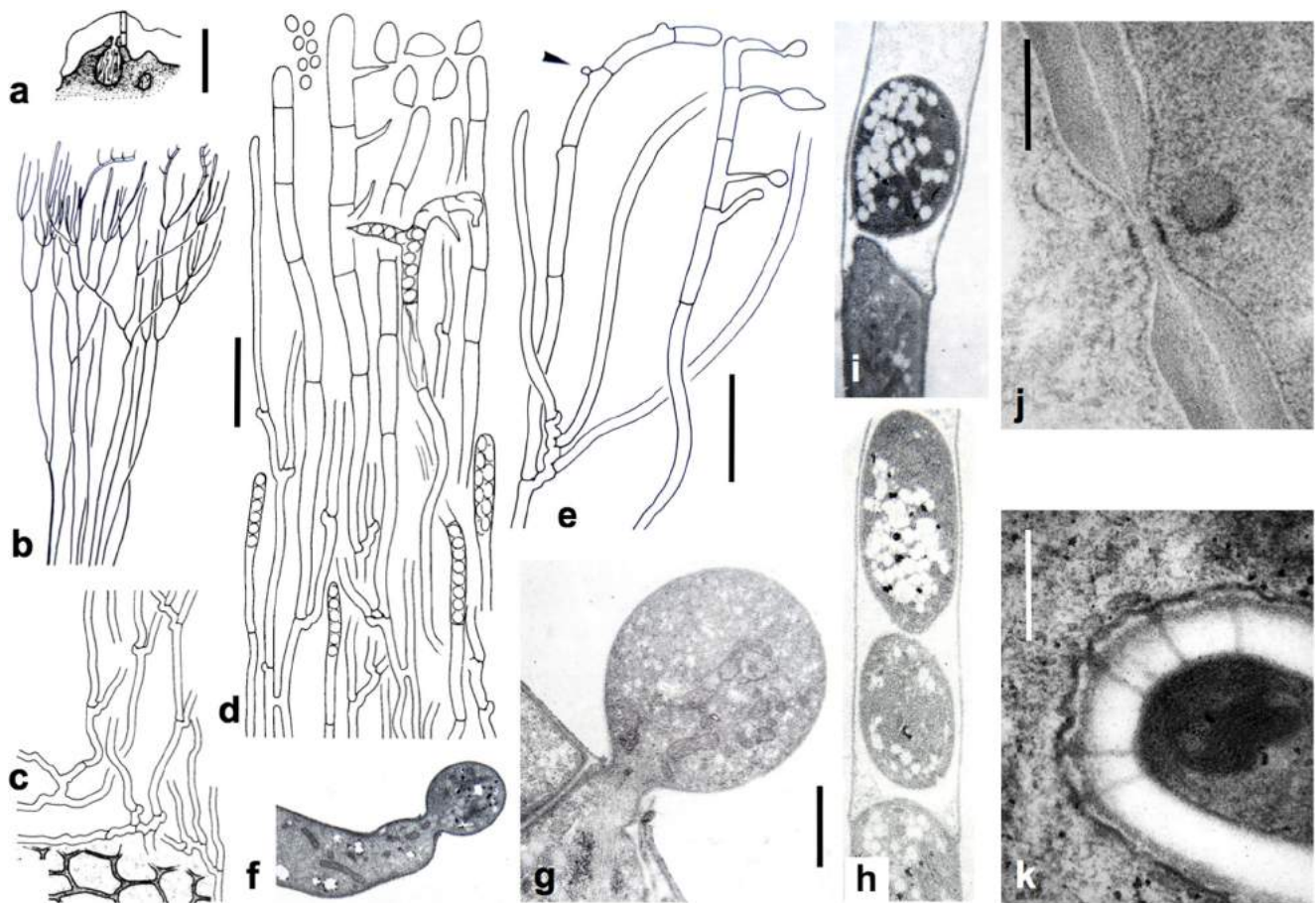
### Cystobasidiomycetes

This class was proposed and circumscribed by Bauer et al. (2006): Cell wall carbohydrate composition without fucose (Takashima et al. 2000); SPB separation in the cytoplasm and metaphysic SPBs in the nucleus. Another distinctive feature seems to be the presence of mycosporines (Boekhout et al. 2011). Three orders, Cystobasidiales, Erythrobasidiales, and Naohideales, were recognized by these authors. Meanwhile, Cyphobasidiales was also included. All species studied ontogenetically were found to have a yeast stage, and sexual stages are characterized by the presence of transversally septate or holobasidia. Approximately 50 species of 12 genera are distributed in four families.

### Naohideales (Fig. 7)

A comparison of micromorphological characters of the generic type of *Platygløea*, *P. disciformis*, with *P. sebacea*, a mycoparasite of pyrenomycetous hosts with a wide distribution in the northern hemisphere, revealed considerable differences in hyphal structure and context, and in basidial and yeast development, convincing Oberwinkler (1990) to propose a new genus, *Naohidea*, in honor of the





**Fig. 7** Naohideales, *Naohidea sebacea*. **a** Habit sketch showing parasite overgrowing pyrenomycete; bar 2 mm. **b** Part of basidiocarp showing loose hyphal arrangement and hymenium. **c** Basal hyphae growing on stroma of pyrenomycete. **d** Part of hymenium with hyphidia, basidia of different ages, basidiospores, and yeast cells in hyphae (“endospores”); bar 20  $\mu\text{m}$ . **e** Basidia of different developmental stages and spores, one

basidial cell with sessile, yeast-like spore (arrowhead); bar 30  $\mu\text{m}$ . **f, g** Yeast-like spores budding off from basidial cells. **h** Yeast cells in hypha; bar 10  $\mu\text{m}$ . **i** Yeast cell budded off in hypha. **j** Septal pore; bar 0.1  $\mu\text{m}$ . **k** Haustorial apex with nano-fusion pores; bar 0.1  $\mu\text{m}$ . Modified after Oberwinkler (1990), Bauer et al. (2006), and unpublished originals of Bauer

great Japanese Urediniologist Naohide Hiratsuka. Studying the cellular interactions of mycoparasites with its hosts, Bauer (2004) found nanometer pores in intracellular haustoria and septal pores without cystosomes in *Naohidea sebacea*. The phylogenetic position within Pucciniomycotina was shown by Weiss et al. (2004), using molecular analyses.

**Comments:** *Naohidea* is one of the monospecific genera with a curious set of characteristics, and therefore nomenclatorically treated up to ordinal rank with the intention for better taxonomic comparisons. In addition to the above-mentioned characteristics, endospore formation as yeast budding is a specialty. The phylogenetic position, as figured out by Weiss et al. (2004), was confirmed in later studies (Bauer et al. 2006; Hibbett et al. 2007; Sampaio and Chen 2011; Nguyen et al. 2014; Wang et al. 2015a, b; Yurkov et al. 2015), apparently indicating a basal lineage in the Cystobasidiomycetes.

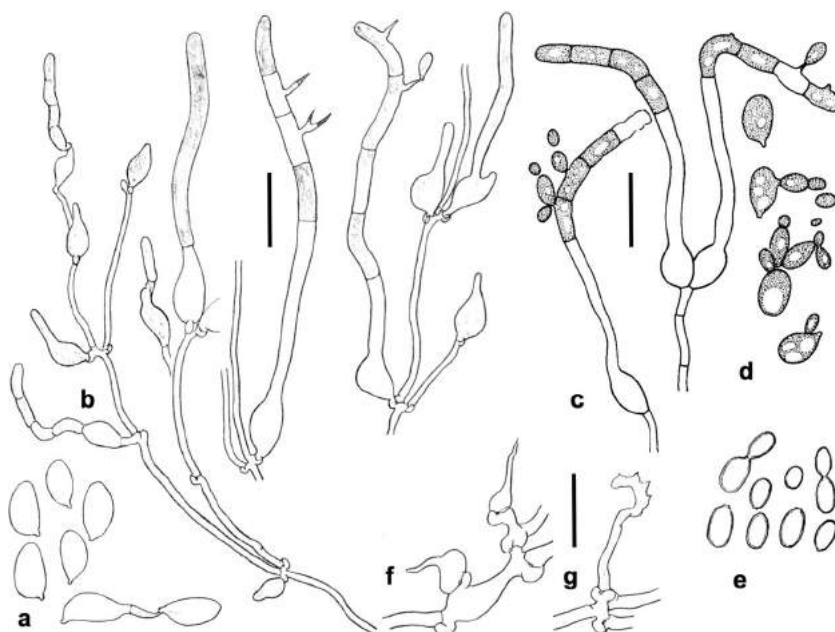
### Cystobasidiales (Fig. 8)

Dimorphic mycoparasites or only known as yeasts with pink to whitish colonies. Hyphae with clamps, tremelloid haustoria and nanometer pores in intracellular parts of the parasite in the host.

Lagerheim (1898) proposed *Cystobasidium*, Cystobasidiaceae were introduced by Gäumann (1926), and Cystobasidiales by Bauer et al. (2006).

**Comments:** The type of *Cystobasidium*, *C. fimetarium* (= *C. lasioboli*), was treated morphologically, physiologically and phylogenetically by Sampaio and Oberwinkler (2011a). According to Sampaio (2011b), *Rhodosporidium benthica*, *R. calyptogenae*, *R. lysinophilum*, *R. minuta*, *R. pallidum*, *R. pinicola*, *R. sloofiae* are only known in the yeast stage, and *R. minuta* and *R. sloofiae* are close relatives of *C. fimetarium* and nutritionally indistinguishable (Sampaio 2011c). Two lichen parasites, *C. hypogymniicola* and

**Fig. 8** *Cystobasidium fimetarium*. **a** Basidiospores, one spore germinating with a secondary spore. **b, c** Clamped hyphae with probasidia and different developmental stages of basidia. **d, e** Budding basidiospores and yeast cells; *bar* 20  $\mu\text{m}$ . **f, g** Haustorial hyphae with terminal spicules; *bar* 10  $\mu\text{m}$ . **c, d** Redrawn from Lagerheim (1898), others originals



*C. usneicola*, described by Diederich (1996), were recently transferred in the genus *Cyphobasidium* (Millanes et al. 2016, see below). Based on molecular data, these species, and also *Rhodotorula oligophaga* (Sato et al. 2013), were transferred into *Cystobasidium* by Yurkov et al. (2015), accompanied by the newly described *R. psychroaquaticum* and *R. richiei* which are also devoid of hyphal stages. For a mycoparasite with tremelloid haustoria in basidiomes of *Dacrymyces* species, Oberwinkler (1990) erected *Occultifur* with the single species *O. internus*, lacking swollen probasidia but with repetitive terminal conidia production, subtended by clamps. In interactive structures of this species, nanopores were found and septal pores were associated with cystosomes (Bauer 2004). It is uncertain whether the clampless *O. corticiorum* (Roberts 1997; Spirin et al. 2016) belongs to the genus. Sampaio et al. (1999) described *Occultifur externus*, a species developing basidia and basidiospores in culture, and it was also treated physiologically and molecularly. A congeneric relationship is most likely by the identity of morphological and ultrastructural characters. The latter ones are unknown in *O. corticiorum* (Roberts 1997), a species without clamps. A generic survey of *Occultifur* was provided by Sampaio and Oberwinkler (2011c). Meanwhile, *O. brasiliensis*, isolated from *Vriesea minarum* tanks (Gomes et al. 2015), *O. kilbournensis* from maize and associated soils in Illinois and Georgia (Kurtzman and Robnett 2015), and *O. tropicalis* (Khunnamwong et al. 2015) from sugar cane and associated soils in Thailand and Brazil, were introduced. The mixture of type and allotype strains of *O. kilbournensis* resulted in the development of clamped hyphae and “a small number of apparent basidia” (Kurtzman and Robnett 2015). The figure shown does not allow a proper

decision. Both, *O. brasiliensis* and *O. tropicalis* are only known in their yeast stages.

### Erythrobasidiales (Fig. 9)

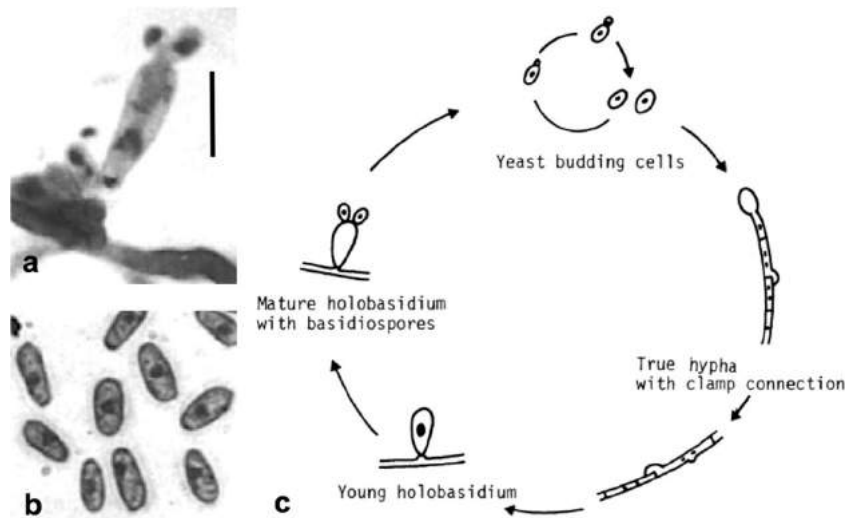
When proposing the Erythrobasidiales, Bauer et al. (2006) circumscribed it without tremelloid haustorial cells, septal pores without cystosomes, and a hydrogenated coenzyme CoQ-10H<sub>2</sub> system. The order comprises one family, Erythrobasidiaceae, which was nomenclatorically validated by Denchev (2009).

Hamamoto et al. (1988, 1991) proposed *Erythrobasidium* to accommodate the single species *Rhodotorula hasegawae* (Hamamoto 2011). The genus was emended by Wang et al. (2015a, b) and defined by features as seen in the illustrations by Hamamoto et al. (1988; Fig. 9), which appear to be the only ones available in the literature.

*Bannoa* contains species with sexual reproduction, holobasidia and clamped hyphae. The genus was erected by Hamamoto (in Hamamoto et al. 2002) and emended by Wang et al. (2015a, b).

**Comments:** A single strain of *Cyrenella* was isolated from the shore of a freshwater lake on Long Island, USA, having unique tetradiate conidia, borne apically on clamped hyphae (Gochenaur 1981; Sampaio 2011b). Teliospores have been observed and illustrated (Sampaio 2011b), but they germinated with clamped hyphae, and basidia were not detected (Gochenaur 1981). This genus and *Hasegawazyma* with ubiquinone Q-9, proposed for *Rhodotorula lactosa* from Wang et al. (2015a, b), were considered taxa incertae sedis in the Erythrobasidiales by Wang et al. (2015a, b). Yamada et al.

**Fig. 9** *Erythrobasidium hasegawianum*. **a** Basidium with two uninucleate basidiospores; bar 10  $\mu\text{m}$ . **b** Haploid yeasts. **c** Presumed life cycle. Modified after Hamamoto et al. (1988)



(1994) transferred *Rhodospodium dacryoideum* into a newly erected genus, *Sakaguchia*, dealt with by Fell (2011a) and emended by Wang et al. (2015a, b), who erected an own family for the genus, incertae sedis, in the Cystobasidiomycetes. Similar taxonomic rearrangements were proposed by these authors for *Sporobolomyces gracilis* (Derx 1930, new genus *Symmetrospora*, new family Symmetrosporaceae incertae sedis), *Torula aurantiaca* (Saito 1922, new genus *Buckleyzyma*, new family Buckleyzymaceae incertae sedis), and *Sporobolomyces magnisporus* (Nakase et al. 2003, new genus *Microsporomyces*, new family Microsporomycetaceae incertae sedis).

### Cyphobasidiales (Fig. 10)

Lichen-associated, dimorphic basidiomycetes without apparent basidiomes.

*Cyphobasidium* was erected in the Cystobasidiomycetes by Millanes et al. (2016) with two lichen-inhabiting, gall-producing species, *C. hypogymniicola* and *C. usneicola*. Originally, *C. hypogymniicola* was described as *Cystobasidium hypogymniicola* by Diederich and Ahti (in Diederich 1996).

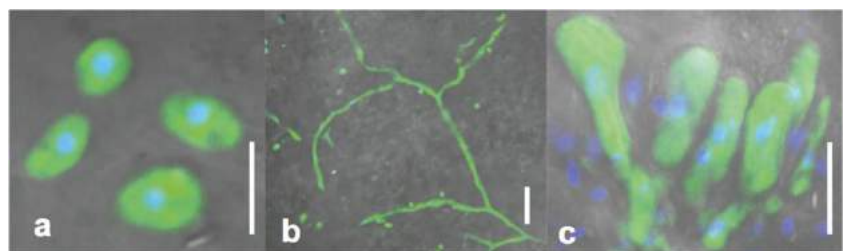
In a maximum likelihood rDNA dendrogram of the Cystobasidiomycetes, Cyphobasidiales were split into 8

clades, for which no further characteristics were given (Spribille et al. 2016).

**Comments:** The lichen-inhabiting Cystobasidiomycetes were already recorded by Park et al. (2014), but not cited in Spribille et al. (2016). *Cystobasidium hypogymniicola* and *C. usneicola* were located in conspicuous galls of their hosts (Millanes et al. 2016; Spribille et al. 2016), indicating a parasitic interaction rather than a mere endothallic inhabitancy. Though haustorial cells were not found by the authors (Diederich 1996; Millanes et al. 2016; Spribille et al. 2016), it cannot be excluded that they do exist, or that a parasitic interaction occurs without such organelles.

Curiously, Millanes et al. (2016) state “A yeast phase has not yet been observed in *Cyphobasidium*, since none of the species have yet been obtained in culture”, but Spribille et al. (2016) illustrate masses of yeast cells in the natural habitats of the lichen thalli. Already the title “Basidiomycete yeasts in the cortex of ascomycete macrolichens” (Spribille et al. 2016) suggests an unusual habitat situation with more than two symbiotic partners. The impression is strengthened in the abstract “Here we show that many common lichens are composed of the known ascomycete, the photosynthesizing partner, and, unexpectedly, specific basidiomycete yeasts.” Such statements require reexamination and reinterpretation. It is well documented that various lichens are parasitized by different fungi, inclusive of basidiomycetous mycoparasites of the Pucciniomycotina and Tremellomycetes (e.g., Diederich

**Fig. 10** Cyphobasidiales. **a** Yeasts on gall; bar 5  $\mu\text{m}$ ; **b** “Fine filaments” in lichen cortical polysaccharide matrix; bar 25  $\mu\text{m}$ . **c** Basidia and probasidia; bar 10  $\mu\text{m}$ . Nuclei stained with DAPI (blue). Modified after Spribille et al. (2016)



1996). Many of these mycoparasites are dimorphic species having a haploid yeast phase as initial stage of their ontogeny. It is a common feature of yeasts that they propagate mitotically to produce yeast colonies. The colonies inhabit and grow further on in adequate substrates. Such conditions are apparently also provided in lichen thalli. Crucial characters of the basidiomycetous yeast producing lichen inhabitants were not elaborated by Spribille et al. (2016) as shown in Fig. 10a–c. Especially, hyphal features, developmental stages of meiosporangia, and sporulation are not shown. Illustrations provided by Millanes et al. (2016) show a hyphal clamp, and a transversely septate basidium. In summary, it is obvious that basidiomycetous yeasts in lichen thalli are not a third component of symbiosis, but rather the vegetative propagules of mycoparasites.

### Pucciniomycetes

Pucciniomycetes were proposed by Bauer et al. (2006) and characterized by clampless hyphae, septal pores mainly with microbodies, metaphasic SPBs in the nuclear envelope, and predominantly metaphasic intermeiotic SPB duplication.

**Comments:** The class is dominated by the species-rich Pucciniales with mostly complex life cycles and often with host alternation. In this order and the related Helicobasidiales, Pachnocybales, and Platygloeales, yeast stages do not occur. However, a haploid yeast phase is present in Septobasidiales, which, otherwise, share pucciniomycetous characters, and cluster phylogenetically within the Pucciniomycetes.

### Septobasidiales (Fig. 11)

Species of Septobasidiales live in triple symbioses with scale insects and spermatophytes, preferably in tropical and subtropical areas (Burt 1916; Oberwinkler 1992). *Septobasidium* yeasts are the infectious agents in scale insects (Couch 1931, 1938). After conjugation of compatible yeasts inside the insects' bodies, haustoria of distinct shapes develop, and finally hyphae grow out, form hyphal mats, covering the insects, and finally consist of basidiomata with corticioid hymenia, containing transversely septate basidia that produce ballistobasidiospores, germinating repetitively and/or by yeast budding.

*Septobasidium* was erected by Patouillard (1892), Septobasidiaceae introduced by Raciborski (1909), and Septobasidiales (Couch 1938) formally validated by Donk (1964).

**Comments:** Though the life history of *Septobasidium* with the important infection stages of yeasts was elucidated by Couch (1931, 1938) and the species known were

monographed (Couch 1929, 1935, 1938), later on little attention has been paid to these fungi.

Simple septal pores, first documented by Dykstra (1974) and Sebald (1977), indicated a phylogenetic relationship with rust fungi. McLaughlin et al. (1996) studied the cytoskeleton of yeasts in *Septobasidium carestianum* and *Kriegeria eriophori* with immunofluorescence localization and found that mitosis “was typically basidiomycetous in both taxa with metaphase and part of the anaphase occurring in the bud.”

Phylogenetic analyses based on 5S rRNAs of selected basidiomycetes removed *Septobasidium* from both Auriculariales s.l. and Pucciniales (Gottschalk 1985; Blanz and Gottschalk 1986). Later molecular studies clustered *Septobasidium* in Pucciniomycetes (Maier et al. 2003; Weiss et al. 2004; Aime et al. 2006, 2014; Bauer et al. 2006; Henk and Vilgalys 2007; Hibbett et al. 2007).

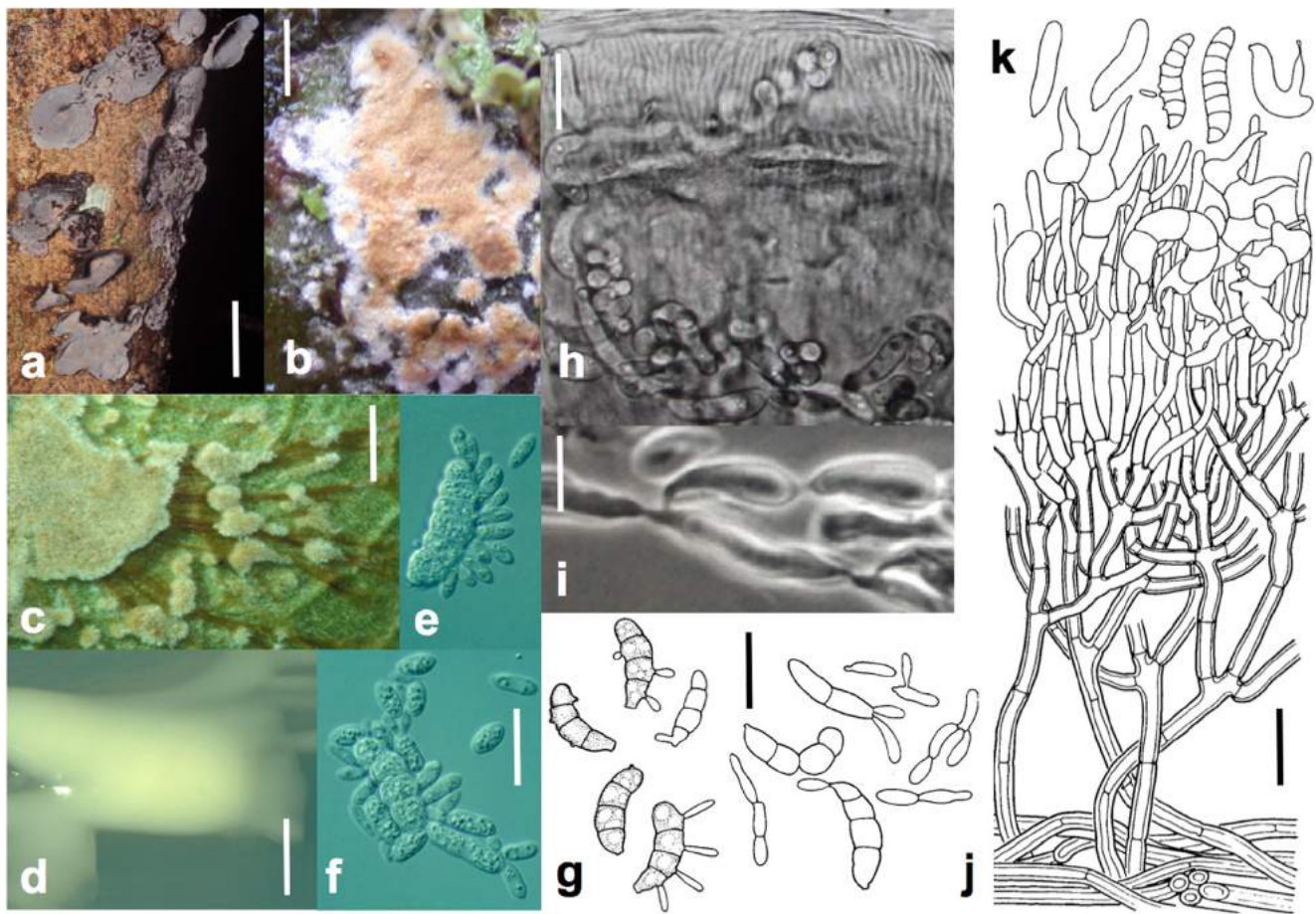
When analyzing the neutral sugar pattern of yeasts in basidiomycetes, a *Microbotryum*-type was discriminated by the absence of extracellular amyloid compounds, the dominance of mannose and the presence of fucose in the cell walls, a positive DBB-reaction and the splitting of urea, features that were also characteristic for *Septobasidium* yeasts (Prillinger et al. 1991; Prillinger and Lopandic 2015).

Henk (2005) observed that basidiospores bud and readily form yeast colonies in *S. meredithiae*, newly described from Louisiana. In a later study, Henk and Vilgalys (2007) used *Septobasidium* yeasts for DNA extraction; however, they did not mention which of the 28 species they studied. The genetic structures of *Septobasidium* species were suggested to be predominantly outcrossing (Henk and Vilgalys 2016), with colonies maintaining their genetic identity despite frequent non-self-fusions. Confusingly, these authors report either infection of scale insects by yeasts or basidiospores, the latter being functionally impossible.

Kirschner and Chen (2007) recorded an anamorphic yeast stage in *S. petchii* from Taiwan.

The diversity and coevolutionary trends in *Septobasidium* were dealt with by Oberwinkler (1993). In a series of recent publications from Chinese mycologists on *Septobasidium* (Lu and Guo 2009a, b, c, 2010a, b, c, 2011; Lu et al. 2010; Chen and Guo 2011a, b, c, d, 2012a, b, c; Li et al. 2013; Li and Guo 2013, 2014; Choi et al. 2016), host specificities were emphasized, but yeast stages were not mentioned. Only a very short note on *Septobasidium carestianum* yeast is given by Boekhout et al. (2011), however, the genus and other species are not included in “The Yeasts” (Kurtzman et al. 2011). Surprisingly, *Septobasidium* was not treated at all by Wang et al. (2015a, b) in their phylogenetic classifications of yeasts and related taxa within Pucciniomycotina.

*Auriculoscypha anacardiicola* was described as an auriculariaceous species from southwest India (Reid and Manimohan 1985), but later recognized as a member of the



**Fig. 11** Septobasidiales. **a** Basidiomes of *Septobasidium septobasidioides*; bar 2 cm. **b** Basidiome of *S. caestianum*; bar 1 cm. **c** Marginal part of developing basidiome of *S. foliicolum*; bar 0.5 mm. **d** Yeast colony of *S. caestianum*; bar 0.5 cm. **e–g** Basidiospore germination and yeast budding of *S. caestianum*; bars 10  $\mu$ m. **i, h**

Haustorial hyphae in scale insects parasitized by *Coccidioidictyon inconspicuum*; bars 10  $\mu$ m. **j, k** *Septobasidium albidum*. **j** Longitudinal section of basidiocarp. **k** Young and mature basidiospores, one spore with the beginning of secondary spore formation; bar 20  $\mu$ m. Original drawings and photographs

Septobasidiales (Kumar et al. 2007). Also, this species has typically transversely septate basidiospores and germination with budding off yeasts (Lalitha et al. 1994).

Basidiospore germination with yeast budding was not observed in *Coccidiodyton* and *Ordonia* (Oberwinkler 1989), and also not in *Uredinella* (Couch 1937, 1941).

### Microbotryomycetes

Structurally and ecologically highly diverse basidiomycetes, mostly with ontogenetic yeast stages and simple pored hyphal septa in dimorphic species. Metaphasic SPBs intranuclear (Bauer et al. 1991, 2006; McCully and Robinow 1972a, b). Predominantly myco- and plant-parasites, and saprobic yeasts. The class is monophyletic in molecularly based phylogenies (Sampaio et al. 2003; Aime et al. 2006, 2014; Bauer et al. 2006; Hibbett et al. 2007; Hamamoto et al. 2011; Turchetti et al. 2011; Toome et al. 2013; Wang et al.

2015a, b). Microbotryomycetes were proposed by Bauer et al. (2006).

**Comments:** Generally, Heterogastridiales, Sporidiobolales, Leucosporidiales, Kriegeriales, and Microbotryales are included in Microbotryomycetes. Colacosomes are found in the first three orders and are lacking in the other two. As mentioned above, such interactive organelles for mycoparasitism are also known from Cryptomycocolacomycetes. The phylogenetic relationship between both groups is not yet understood. In addition, the monophyly of colacosome fungi within the Heterogastridiales has recently been questioned (Wang et al. 2015a, b). If colacosomes represent a character of basal taxa within the class, their loss is derived, and parasitism on plants and/or saprobic nutrition modes were secondarily evolved.

Another striking fact of Microbotryomycetes is the convergent ontogeny of Microbotryales species (Fig. 16) in comparison with the bulk of the smuts of the Ustilaginomycotina.

Motivated by comparative sequence analyses, species of the yeast genera *Rhodospordium*, *Rhodotorula*, and *Sporobolomyces* were transferred into various taxa of the Microbotryomycetes (see below).

## Heterogastridiales (Fig. 12)

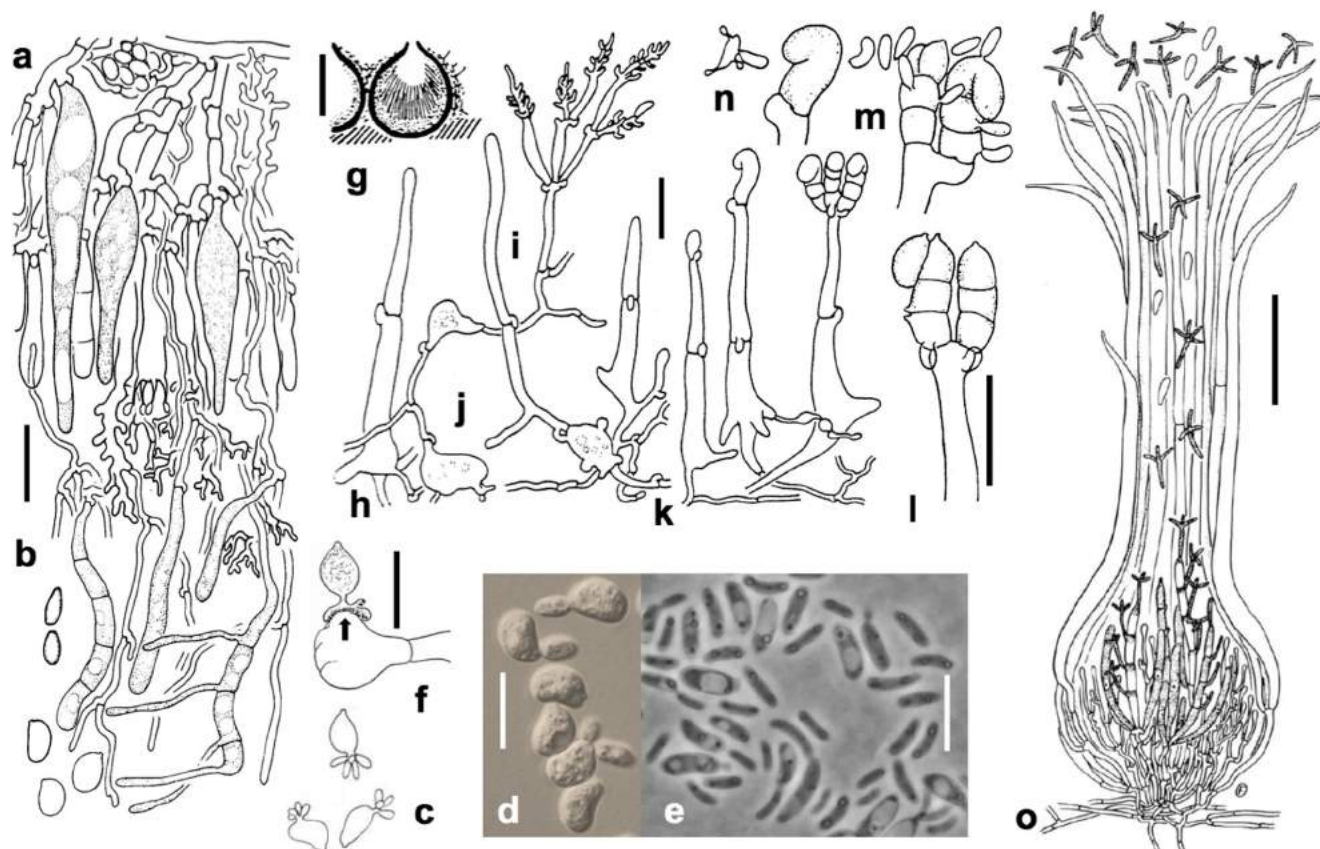
Mycoparasites with colacosomes, transversely septate basidia without teliospores (Bauer et al. 2006). Heterogastridiaceae and Heterogastridiales were introduced by Oberwinkler and Bauer in Oberwinkler et al. (1990b), Krieglsteineraceae proposed by Pouzar (1987), and Colacogloeaceae by Wang et al. (2015a, b).

**Comments:** Bandoni and Oberwinkler (1981) recognized the hyphomycete *Hyalopycnis blepharistoma* as a basidiomycete, and Oberwinkler et al. (1990b) described its basidial stage. These authors could not verify a yeast stage in the species as suggested by Seeler (1943); however, they

noticed a diazonium blue B stain reaction, typical for basidiomycetous yeasts (van der Walt and Hopsu-Havu 1976).

The circumscription of the Heterogastridiales is controversial. Originally based on the presence of colacosomes, besides *Heterogastridium* the genera *Atractocolax*, *Colacogloea*, and tentatively *Krieglsteinera* were also included (Bauer et al. 2006). Colacosomes in *Atractocolax* indicate a potential mycoparasitic nutritional mode.

When studying the mycoparasitism of *Platygløea peniophorae*, Oberwinkler et al. (1990a) and Bauer and Oberwinkler (1991) found specific mycoparasitic organelles, called colacosomes, and, consequently, the genus *Colacogloea* was proposed. Later on, colacosomes were detected in various mycoparasites, and in species of the Leucosporidiales and Sporidiobolales. Colacosomes were proven for *C. bispora* (Oberwinkler et al. 1999), *C. papilionacea* (Kirschner and Oberwinkler 2000), and *C. allantospora* (Bandoni et al. 2002) for which yeast budding was partly documented. Molecular analyses indicated that the yeast species *Rhodotorula cycloclastica*, *R. diffluens*,



**Fig. 12** Heterogastridiales. **a–e** *Colacogloea peniophorae* (**b**) in the hymenium of *Hyphoderma praetermissum* (**a**). **c** Budding basidiospores; bar 20 µm. **d** Germinating basidiospores; bar 20 µm. **e** Budding yeast; bar 20 µm. **f** First developmental stages of *Colacogloea* sp.: basidiospore germinating with an attachment by colacosomes (arrow) on a tulasnelloid host; bar 10 µm. **g–n** *Krieglsteinera lasiosphaeriae*. **g** Longitudinal section of *Lasiosphaeria ovina* covered with the

mycoparasite; bar 0.5 mm. **h** Young basidiophore. **j** Basal hyphae and initial stages of basidiophores. **i** Conidiophores. **k** Development of basidia on top of basidiophore; bar 20 µm. **l** Septate basidia. **m** Basidia with basidiospores. **n** Budding basidiospore; bar 20 µm. **o** *Heterogastridium pycnidioideum*, longitudinal section of basidiome with different stages of basidial development and tetra- and octo-radial basidiospores; bar 100 µm. Modified after Oberwinkler et al. (1990a, b) and originals

*R. eucalyptica*, *R. ferulica*, *R. foliorum*, *R. philyla*, *R. retinophila*, *R. terpenoidalis*, and *Sporobolomyces falcatus* belong to the *Colacogloea* clade (Sampaio et al. 2011), into which they were finally transferred (Wang et al. 2015a, b). For these yeasts, physiological data are available (Sampaio 2011c), and a CoQ-10 system has been reported (Yamada and Kondo 1972; Sugiyama et al. 1985; Nakase et al. 1987; Sampaio and van Uden 1991; Thanh et al. 2004).

*Kriegelsteinera* is a name change (Pouzar 1987) for *Jacobia conspicua*, published without a latin diagnosis (Arnaud 1951). The extensive description of Pouzar (1987) was supplemented by detailed comments and corrections of the original drawings of Arnaud (1951); however, his own illustrations were lacking, and yeast budding of basidiospores was not mentioned. Therefore, the cellular construction of the species is illustrated here light-microscopically, and yeast budding is shown (Fig. 12g–n).

For molecular analyses, only *Heterogastridium* and *Colacogloea* were available and appeared not monophyletic (Aime et al. 2006; Bauer et al. 2006; Sampaio et al. 2011; Turchetti et al. 2011; Toome et al. 2013; Wang et al. 2015a, b). *Atractocolax pulvinatus* has been found several times in bark beetle galleries of *Picea abies* in Germany and Switzerland (Kirschner et al. 1999), and isolated in pure cultures in which basidia developed and produced sessile basidiospores with primary blastospores but without further budding and therefore without yeast colonies.

Unfortunately, in a stilboid fungus from Ecuador, *Pycnopulvinus aurantiacus* (Toome and Aime 2014), spore production and germination are unknown. However, in a combined LSU and ITS analysis, *Pycnopulvinus* clustered

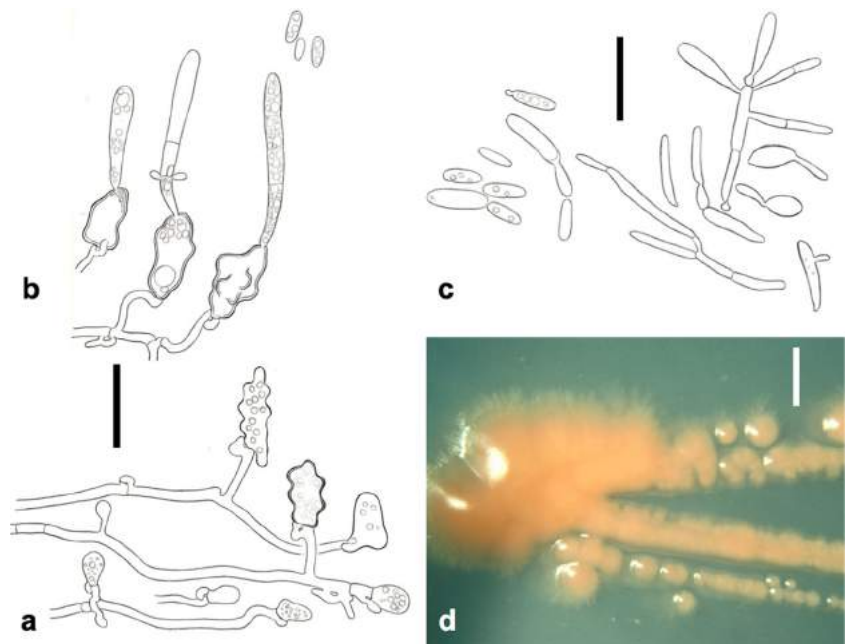
with *H. pycnidioideum* and the strain CBS 176.95, with the unpublished, provisional name *Pycnobasidium* for a fungus with a yeast stage from Costa Rica, collected during a student's excursion 1989 from Tübingen University, and isolated by Spajj and Weber. Surprisingly, the latter name is listed as a “likely fungal species (nearest neighbor)” in a table of microbial communities at Abernethy Forest Nature Reserve in the Scottish central highlands by Curlevski et al. (2011).

### Sporidiobolales (Fig. 13)

Non-phytoparasitic species with simple pored hyphae and colacosomes; teliospores, transversally septate basidia, sessile basidiospores, budding with yeasts, or only single cell stages in pink-colored colonies; physiologically negatively discriminated by the incapacity to utilize D-glucuronate and inositol, with the major CoQ systems Q-9 or Q-10 (Sampaio et al. 2003). The Sporidiobolales was erected by Sampaio et al. (2003), Sporidiobolaceae proposed by Moore (1972) and emended by Sampaio et al. (2003). Three genera were accepted by Wang et al. (2015a, b), i.e. *Rhodosporidium*, *Rhodosporidiobolus*, and *Sporobolomyces* with an approximate number of 40 species.

**Comments:** *Rhodotorula*, originally circumscribed to contain asexually propagating yeasts, has been emended by Wang et al. (2015a, b) to also include the sexual species of *Rhodosporidium*, a proposal based on sequence data. Similarly, a clade of former *Rhodosporidium* and *Sporidiobolus* species, identified by Wang et al. (2015a, b),

**Fig. 13** Sporidiobolales, *Rhodotorula toruloides* (*Rhodosporidium* t.). **a** Hyphae and different stages of probasidial development; not clamped hyphae. **b** Germination of probasidium, development of basidia and basidiospores; bar 10  $\mu$ m. **c** Various stages of yeast budding; bar 10  $\mu$ m. **d** Yeast colony; bar 5 mm. Original drawings and photograph



was considered to represent a newly defined genus, *Rhodospordiobolus*. Finally, originally conceived asexual *Sporobolomyces* is now the recipient of sexual *Sporidiobolus* taxa (Wang et al. 2015a, b). Colacosome-containing species can be assumed to represent potential mycoparasites (Bauer et al. 1997; Sampaio et al. 2003); however, no conclusive example is known.

### Leucosporidiales (Fig. 14)

Non-phytoparasitic species with simple pored hyphae and colacosomes; teliospores, transversally septate basidia, sessile basidiospores, budding with yeasts, or only single cell stages in white or cream-colored colonies. Physiologically, species of the order are discriminated against Microbotryales by assimilating D-glucosamine, D-xylose and raffinose as sole carbon sources, and growth in the absence of vitamins (Sampaio et al. 2003). The Leucosporidiales and Leucosporidiaceae were erected by Sampaio et al. (2003).

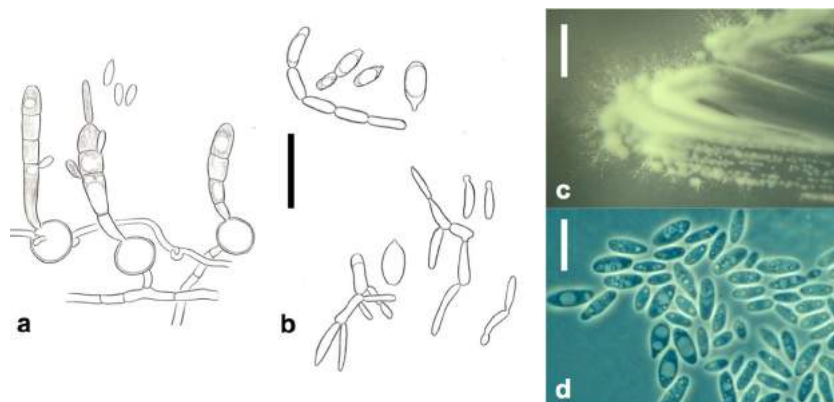
**Comments:** Leucosporidiales is defined as containing only one family, the genus *Leucosporidium*, including *Mastigobasidium* and *Leucosporidiella* (de Garcia et al. 2015; Wang et al. 2015a, b), and the recently proposed *Pseudoleucosporidium* (de Garcia et al. 2015), a genus considered incertae sedis in the Microbotryomycetes and apparently closely related to the holobasidial *Curvibasidium* (Sampaio et al. 2004; Sampaio 2011a), as revealed by multi-gene analyses (Wang et al. 2015a, b). In contrast, Santiago et al. (2017) retained *Leucosporidiella* with various species associated with antarctic *Deschampsia antarctica* and *Colobanthus quitensis*. Though colacosomes were found in Leucosporidiales species, mycoparasitism is not known in the order, even when it was assumed to be possible (Bauer et al. 1997; Sampaio et al. 2003).

### Kriegeriales (Fig. 15)

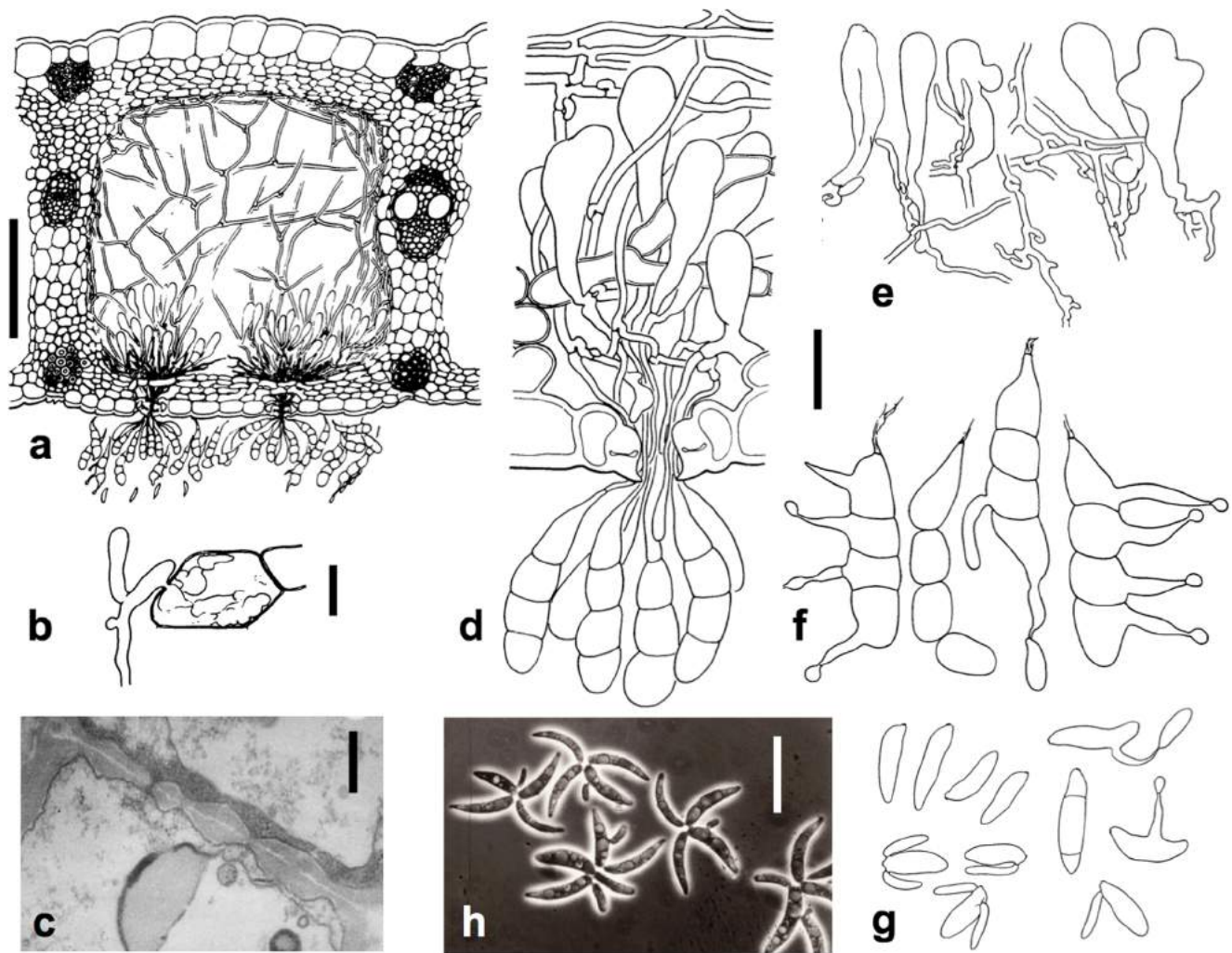
The dimorphic, plant-parasitic *Kriegeria eriophori*, the sole species of the genus, has an ontogeny with unique morphological and ecological stages. Haustoria and sack-like probasidia develop on clamped hyphae with simply multipored septa in the aerenchym cavities of *Scirpus sylvaticus*, producing very thin hyphal elongations that grow through the stomatal openings to develop deciduous basidia outside the host. Detached basidia can float on water and eject ballistobasidiospores which are capable of producing secondary ballistospores or are budding with yeasts that often form slightly attached, rosette-like, tetraradiate, apparently water-adapted stages. Another dimorphic species is *Camptobasidium hydrophilum* which is discussed below. Kriegeriales and Kriegeriaceae were proposed by Toome and Aime (Toome et al. 2013).

**Comments:** In comparing ultrastructural and molecular data of *K. eriophori* and *Microbotryum violaceum*, which were considered to have ultrastructural and molecular synapomorphies, Swann et al. (1999) concluded that these taxa belong in a monophyletic group, named Microbotryomycetidae. The isolated phylogenetic position of *K. eriophori* is supported by unique, multipored hyphal septa (Bauer et al. 2006). Sampaio and Oberwinkler (2011b) summarized the available data of the life history (Doublés and McLaughlin 1992) and added specific growth patterns. Based on molecular data, the newly described yeast *Meredithblackwellia eburnea*, forming rosettes of semi-attached cells, was included in Kriegeriaceae (Toome et al. 2013). In addition, five *Rhodotorula* species with the capability to assimilate phenol, clustering together in a phylogenetic tree of seven genes and the analysis of the enlarged LSU rRNA gene dataset, were proposed as *Phenolifera* (Wang et al. 2015a, b). Similarly circumscribed is the monotypic *Yamadamyces*, containing one species, *Y. rosulatus*, with

**Fig. 14** Leucosporidiales, *Leucosporidium scottii*. **a** Hyphae and different stages of basidial development and basidiospore production; not clamped hypha. **b** Various stages of yeast budding; bar 20  $\mu$ m. **c** Yeast colony; bar 1 cm. **d** Yeast colony; bar 20  $\mu$ m. Original drawings and photographs







**Fig. 15** *Kriegeria eriophori*. **a** Parasite in the aerenchyma of *Scirpus sylvaticus*; bar 200  $\mu\text{m}$ . **b** Haustorium with hyphal growth inside the host cell; bar 20  $\mu\text{m}$ . **c** Multiperforate hyphal septum; bar 0.2  $\mu\text{m}$ . **d** Clamped hyphae and sack-like probasidia in the host, and transversely septate, immature basidia emerging through stoma. **e** Probasidia. **f** Detached mature basidia with sterigmata and initials of basidiospores,

one basidiospore showing asymmetrical attachment, indicating the ballistospore mechanism. **g** Basidiospores germinating with secondary spores, and budding with yeasts. **h** Yeast budding of basidiospores. After Bauer et al. (2006), Sampaio and Oberwinkler (2011a, b, c), and originals

budding yeast cells remaining attached to each other and forming rosettes (Wang et al. 2015a, b).

For *Camptobasidium hydrophilum*, isolated from a stream in Alabama, Marvanová and Suberkropp (1990) reported and illustrated dikaryotic, clamped mycelia with simple septal pores, auricularioid basidia and sessile basidiospores, born in clusters on each basidial segment. Conidia were found to be typically tetradiate. In dual cultures with other fungi, coiled attachments occurred which were estimated as possible parasitic interaction stages. For this species, the family Camptobasidiaceae was introduced by Moore (1996). BLAST analyses of fungal soil clones from the forefront of the Lyman glacier in the North Cascade Mountains delivered potentially chimeric sequences of *C. hydrophilum* (Jumpponen

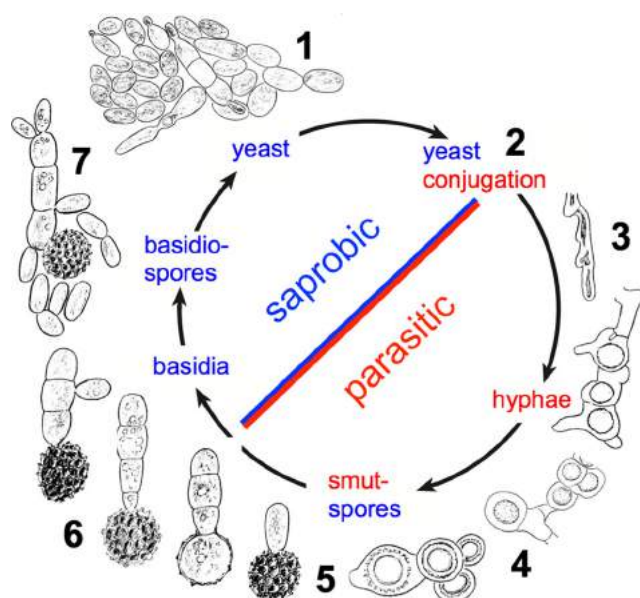
2003). Clones, isolated from maple leaf disks, exposed in a softwater stream in Nova Scotia, and analyzed molecularly, also contained closest BLAST hits for *C. hydrophilum* (Seena et al. 2008). During a study of psychrophilic yeasts from Antarctica, Greenland and Italian glaciers, Turchetti et al. (2011) found that *Leucosporidium antarcticum* and newly isolated strains formed a monophyletic clade, named *Glaciozyma*. An additional species was described from the White Sea intertidal zone by Kachalkin (2014). In an analysis of an enlarged LSU rRNA gene dataset, *Glaciozyma* species clustered in a strongly supported clade (Wang et al. 2015a, b).

Apparently, species of Kriegeriales are highly adapted to watery habitats.

## Microbotryales (Figs. 16 and 17)

Dimorphic plant parasites, lacking colacosomes, with host-specific sori of teliospores as propagules, often adapted to animal or abiotic vectors; typically transversely septate phragmobasidia with sessile basidiospores budding off yeasts. Microbotryales contains two families, Microbotryaceae (Moore 1996) and Ustilentylomataceae (Bauer and Oberwinkler in Bauer et al. 1997).

**Comments:** When Deml and Oberwinkler (1982b) became aware of the heterogeneity of former *Ustilago* species, they reintroduced *Microbotryum*, a genus erected by Lévillé (1847) and neglected since then. Most important characters of *Microbotryum* species are best summarized in a life cycle as illustrated in Fig. 16. It is strikingly evident that this ontogeny resembles that of *Ustilago* species and many of related taxa in the Ustilagomycotina. This evolutionary convergence was conclusively substantiated by rhodotorulic acid as discriminating siderophore (Deml and Oberwinkler 1981, 1982a; Deml 1985; Prillinger et al. 1991; Ruddat et al. 1991; Renshaw et al. 2002; Birch and Ruddat 2005), different cell wall components (Prillinger et al. 1991, 1993; Prillinger and Lopandic 2015) and molecular phylogenies (Gottschalk and Blanz 1985; Müller 1989; Weiss et al. 2004; Aime et al. 2006, 2014; Bauer et al. 2006; Hibbett



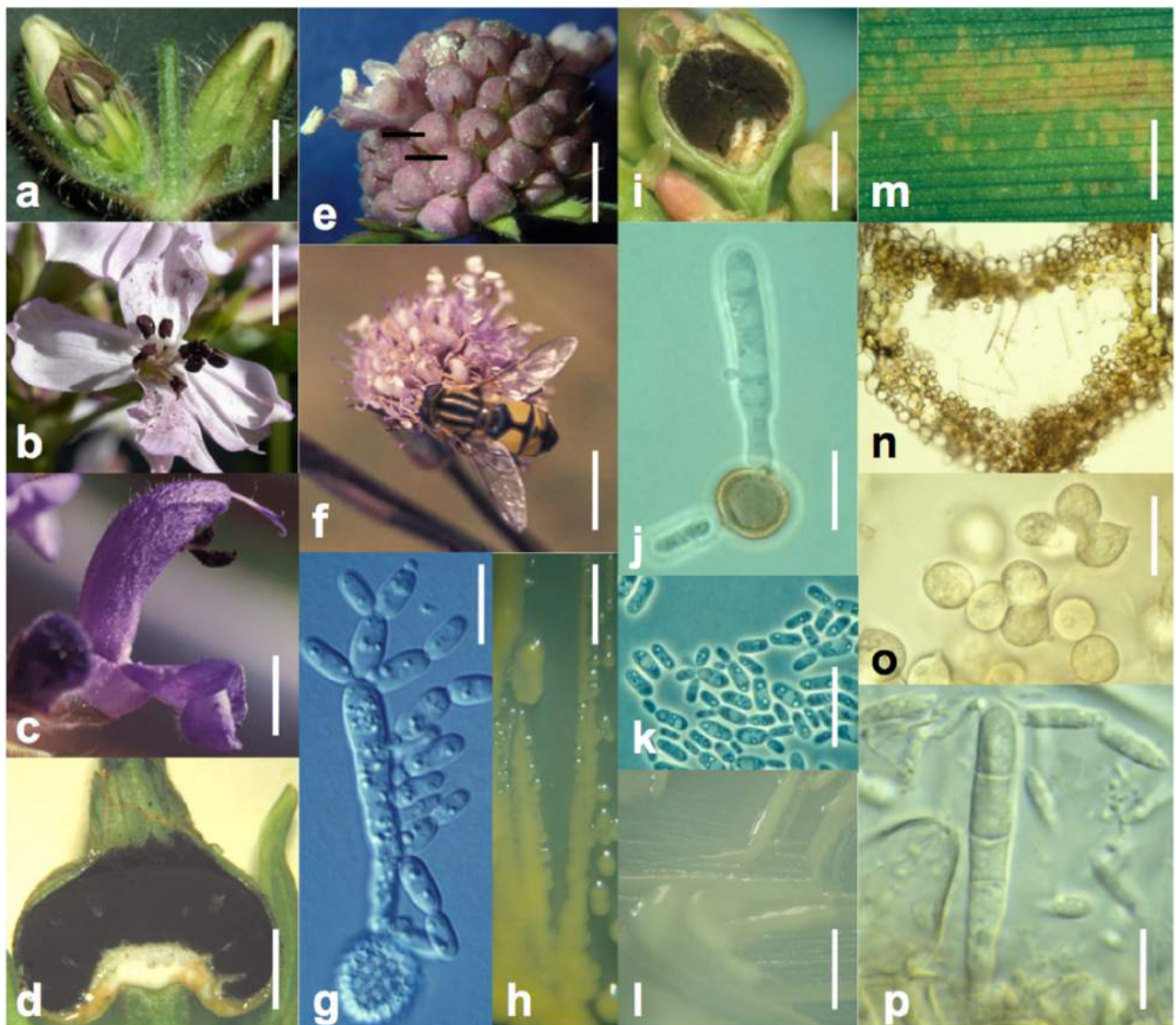
**Fig. 16** Microbotryales. Life cycle of *Microbotryum violaceum*. In most *Microbotryum* species, smut spores (6, teliospores, probasidia) are developed in the anthers of their hosts (4, 5). They germinate with basidia (6, 7) and bud off basidiospores, also called sporidia (7). Budding continues and yeast colonies develop (1), representing the saprobic stage. After conjugation of compatible yeasts, hyphae develop and infect suitable hosts (3). Smut spores originate inside hyphae (4) in specific organs of the host. Modified after Oberwinkler (2012)

et al. 2007; Boekhout et al. 2011; Ebersberger et al. 2012; Wang et al. 2015a, b).

Though members of the Pucciniomycotina, the Microbotryales were included in the “Smut fungi of the World” (Vánky 2012), thus following a traditional concept of smuts and taking into account phytoparasite collectors’ requirements. Therefore, this treatment focusses on identification and nomenclature, and, unfortunately, ontogenetic and phylogenetic data are mostly lacking.

The definition of Microbotryaceae without septal pores (Bauer et al. 1997) is at least questionable for young developmental stages, since exchange of cytoplasmic compounds between living cells of hyphae is mandatory.

The actually accepted circumscription of *Microbotryum* comprises nearly 100 species of phytoparasites on dicotyledons, producing teliospores in the anthers of their hosts. This taxonomy follows a conventional concept, nicely supported molecularly as a monophyletic taxon, however strongly contrasting the actually practised circumscription of smut genera in a much narrower sense, and neglecting easily recognizable coevolutionary groupings. Surprisingly, there is a convergent evolutionary line in the Ustilaginomycotina, named *Antherospora* (Bauer et al. 2008), with species confined to monocotyledons, and sporulating with teliospores predominantly within the anthers. Yeast stages, produced from germinating basidiospores, were found in all species that were studied more closely, more than 20 by the author, and it is obvious that the **yeast phase is an integral part of the life cycle**. Compatible yeast cells are the prerequisite for mating and therefore the start of sexual reproduction. The following hyphal stage is required for host infection and further ontogenetic development until production of teliospores. Despite the essential developmental relevance and the easy culturing methods, *Microbotryum* yeasts were not included in “The Yeasts, a taxonomic study” (Kurtzman et al. 2011) and not treated by Wang et al. (2015a, b). On the other hand, some *Microbotryum* species (Fig. 17a–h), such as *M. violaceum*, and *M. lychnidis-dioicae*, quickly progressed as **model organisms** (e.g. Antonovics et al. 2002, Martínez-Espinoza et al. 2002), especially concerning studies in **ontogeny** (Berbee et al. 1990; Hood et al. 2001; Schäfer et al. 2010), **mating systems** (Antonovics et al. 1998; Giraud et al. 2008; Petit et al. 2012; Hood et al. 2013; Badouin et al. 2015; Whittle et al. 2015; Xu et al. 2016), **infection** (Buono et al. 2014; Carlsson-Granér and Thrall 2015), **host specificities** (Kemler et al. 2006, 2009), **distribution** (Antonovics et al. 2003; Antonovics 2005; Gladieux et al. 2014), **coevolution** (Hood et al. 2010; Lutz et al. 2005, 2008; Kemler et al. 2013; Tack and Laine 2014; Feurtey et al. 2016), **population structure** (Gladieux et al. 2014; Croll and Laine 2016), and **genomics** (Antonovics 2003; Perlin et al. 2015; Fortuna et al. 2016).



**Fig. 17** Microbotryales. **a** Brownish-violaceous teliospores of *Microbotryum lychnidis-dioicae* in the anthers of *Silene dioica* (left flower bud). **b** Anthers of *Saponaria officinalis* filled with teliospores of *M. saponariae*. **c** Flower of *Salvia pratensis* showing two blackish anthers filled with *M. salviae*. **d** Longitudinal section of the inflorescence of *Tragopogon pratensis*, transformed in a big sorus of *M. tragopogonis* teliospores. **e, f** Inflorescences of *Succisa pratensis* with teliospores of *M. succisae* in the anthers. **g, h** *Sphacelotheca hydropiperis*. **g** Teliospore and basidium with basidiospores and budding yeast; bar 10  $\mu$ m. **h** Yeast

colony; bar 0.5 cm. **i-l** *Sphacelotheca polygoni-serrulati*. **i** Teliospore sorus in the floral bud of *Persicaria maculosa*. **j** Teliospore germinated with a transversely septate basidium; bar 10  $\mu$ m. **k** Budding yeast; bar 20  $\mu$ m. **l** Yeast colony; bar 0.5 cm. **m-p** *Ustilentyloma fluitans* in *Glyceria fluitans*. **m** Color changes of the host after internal development of the parasite; bar 2 mm. **n** Aerenchyma of the host, partly filled by the parasite; bar 0.3 mm. **o** Teliospores; bar 20  $\mu$ m. **p** Transversally septate basidium; bar 10  $\mu$ m. Bars (a–f, i) 1 cm. Original photographs

*Sphacelotheca* (Fig. 17i–l) was erected by de Bary (1884) for *Ustilago hydropiperis*, parasitizing *Polygonum hydropiper*, emended by Langdon and Fullerton (1978) and restricted to smuts, inhabiting species of the Polygonaceae. This taxonomy was adopted by Vánky and Oberwinkler (1994), thus excluding smuts that occur on species of other host families, e.g. the head smut of maize, *Sporisorium reilianum*, a member of the Ustilaginales. Also, *Sphacelotheca* basidia bud off basidiospores which produce a yeast stage.

For species of *Bauerago* (Vánky 1999) parasitizing Cyperaceae and Juncaceae, smutspore germination was described as “results in phragmobasidia“, but not illustrated, and basidiospore and yeast budding are unknown. Later, the genus was verified by molecular data (Bauer et al. 2006; Kemler et al. 2006). The taxonomically doubtful *Liroa emodensis* (Ciferri 1933; Vánky and Oberwinkler 1994; Vánky 2012) and *Zundeliomyces* (Vánky 1987) lack reports on yeast stages.

In contrast to Microbotryaceae, simple septal pores appear to be synapomorphic in Ustilentylomataceae (Bauer et al. 1997), a family with three teleomorphic and phytoparasitic genera, *Aurantiosporium* (Piepenbring et al. 1996), *Fulvisporium* (Vánky et al. 1997), and *Ustilentyloma* (Savile in Savile and Parmelee 1964; Vánky 1991; Fig. 17m–p). The latter genus was emended by Wang et al. (2015a, b) to include the anamorphic yeast *Rhodotorula hordeae* as *U. graminis*. In contrast to the remark of Wang et al. (2015a, b), species of the genera *Aurantiosporium* and *Fulvisporium* develop yeast stages, initiated by budding of basidiospores. In addition, the yeast genus *Microbotryozyma* has been proposed (Suh et al. 2012).

### Families and genera incertae sedis in the Microbotryomycetes

In contrast to Wang et al. (2015a, b), *Colacogloea* and Colacogloeaceae are assigned here to the Heterogastridiales (see above).

The new family Chrysozymaceae was proposed with four new genera, *Bannozyrna*, *Chrysozyrna*, *Fellozyrna*, and *Hamamotoa*, for which sexual stages are unknown (Wang et al. 2015a, b). The circumscription of these taxa is based on the phylogenetic analyses of seven genes and of an enlarged LSU rRNA gene dataset. In *Bannozyrna*, the major CoQ system is Q-9, in the remaining genera, Q-10 (Wang et al. 2015a, b).

With similar molecular analyses, the following new yeast genera were determined and described (Wang et al. 2015a, b): *Oberwinklerozyma*, *Pseudohyphozyma*, *Pseudoleucosporidium*, *Sampaiozyrna*, *Slooffia*, *Spencerozyma*, *Trigonosporomyces*, *Udeniozyrna*, *Vonarxula*, and *Yunzhangia*.

It is a challenge for further fieldwork and experimental studies to find the teleomorphic stages of these taxa and to obtain information about their ecological roles.

### Concluding remarks

The main goal of this review is to compare fungi with yeast stages in the monophyletic Pucciniomycotina. Considering their diverse life histories, it appears that budding yeasts are first ontogenetic phases in dimorphic developmental sequences. Thus, the yeast stage could reflect phylogenetically old predecessors (Oberwinkler 1978, 1985, 1987). However, the origin of the Basidiomycota is still unknown. The lack of ontogenetic yeast stages in Pucciniomycotina apparently depends on various and different substrate adaptations, as strikingly visible in Pucciniales.

Species known only in their single cell stage can be characterized molecularly and assigned to similarly defined taxa. Thus, the bulk of solely anamorphic yeasts has been taxonomically rearranged in phylogenetic hypotheses. This progress should be used for further improvements in the better

understanding of functional aspects of developmental stages and ecological adaptations. Hierarchically arranged taxa are also used in this review in an attempt to reflect possible phylogenetic distances, mainly derived from comparative character estimations, bearing a considerable load of subjectivity.

Pucciniomycotinous species discovered in the last decades indicate a huge unknown biodiversity of these fungi (Toome-Heller 2016), and could stimulate the carrying out of more fieldwork, reaching from marine environments to soil, and in various animal and plant habitats, and to pay sufficient attention to microscopic and experimental studies.

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