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THE LIFE-HISTORY OF *CHRISTIANSENIA PALLIDA*, A DIMORPHIC, MYCOPARASITIC HETEROBASIDIOMYCETE[1]

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ABSTRACT

Christiansenia pallida Hauerslev, a heterobasidiomycetous parasite of *Phanerochaete cremea* (Corticiaceae), was cultivated and studied with light and electron microscopes. Monokaryotic basidiospores bud as yeasts. Compatible cells conjugate and dikaryotic mycelia develop when yeast cells are grown together with the host on artificial media. Thread-like, monokaryotic hyphal outgrowths originate from clamps and function as haustoria, penetrating host cells. In its parasitic stage, *Christiansenia pallida* propagates chiefly by conidia. These are formed on short, terminal, monokaryotic, conidiogenous cells; conidia originate side by side, then fuse to form one dikaryotic zygoconidium. Dikaryotic conidia germinate to produce short-celled, dikaryotic hyphae which bear haustorial branches. Dikaryotic conidia are capable of dedikaryotization, thereby producing monokaryotic yeast cells. Usually, in a later stage of ontogeny, basidia develop on dikaryotic hyphae. Basidial morphology is rather variable, but suburniform basidia are typical. More than four sterigmata often are formed.

Key Words: *Christiansenia*, Heterobasidiomycetes, *Phanerochaete cremea*, basidiomycetous yeasts, zygoconidia, dimorphism, mycoparasitism.

Christiansenia pallida Hauerslev was described by Hauerslev (**1969**) as a mycoparasite on *Phanerochaete cremea* (Bres.) Parm. from Denmark. Boidin (**1970**) included *Ceratobasidium mycophagum* M. P. Christ. in *Christiansenia*. The scope of the genus was enlarged by Ginns and Sunhede (**1978**) who transferred *Tremella mycetophila* Peck, a parasite on *Collybia dryophila* (Fr.) Kummer, to *Christiansenia*. In addition, Ginns and Sunhede described two new species, *C. effibulata* Ginns & Sunhede, and *C. tumefaciens* Ginns & Sunhede, both also occurring parasitically on *Collybia dryophila*. Oberwinkler and Bandoni (**1982b**) restudied all species known at the time in *Christiansenia*, and concluded that only *C. pallida* should be recognized in that genus. They accepted *Syzygospora* Martin (**1937**) as another genus with a mycoparasitic species, *S. alba* Martin, and they proposed the genus *Carcinomyces* for *Christiansenia effibulata* and *Tremella mycetophila*.

Christiansenia pallida has until now been studied only as herbarium material, but two collections made in Tübingen enabled us to isolate pure cultures. These strains and living material of anamorph and teleomorph stages in field collections were used for detailed studies to elucidate the life history of the species.

[1] Part 29 in a series, "Studies in Heterobasidiomycetes."

MATERIALS AND METHODS

For descriptions and illustrations, the following collections were used: *Christiansenia pallida* growing on *Phanerochaete cremea,* Germany, Baden-Württemberg, Tübingen, Schönbuch bei Hagelloch, 480 m, 5-5-1981, leg. R. Bauer and F. Oberwinkler, FO 31621; Schönbuch bei Waldhausen, 470 m, 22-6-1981, leg. L. Kisimova-Horovitz, FO 31647.

The strains FO 31621 and FO 31647 are deposited in the culture collections of the Botany Departments of the University of Tübingen, W-Germany, and the University of British Columbia, Vancouver, Canada.

A malt-extract, yeast-extract, peptone medium (Bandoni, **1972**) was used for culturing the fungus. The cultural experiments were carried out either with the parasite and host together or the parasite alone.

Material was fixed for transmission electron microscopy in glutaraldehyde and osmium tetroxide, washed with distilled water, stained in aqueous uranyl acetate, dehydrated in an ethanol series, and embedded in Spurr's (**1969**) epoxy resin. Ultrathin sections were mounted on unsupported mesh copper grids, and examined with a Zeiss EM 9 S-2 transmission electron microscope.

Details of nuclear behavior were studied using HCl/Giemsa preparations. Material was dried on slides for 4 h at room temperature, followed by fixation with a 3:1 mixture of 92% ethanol and acetic acid for 12–15 h. After being rinsed several times with water, the cells were hydrolyzed in HCl (1 N, 60 C) for 6 min, rinsed in one change of water and five changes of phosphate buffer (pH 7), stained 2 h in one part Giemsa stock solution and nine parts phosphate buffer, rinsed in phosphate buffer and dipped in water, and finally dried. For light microscopy the preparations were embedded in synthetic resin.

Enzyme production was tested using the methods of Hankin and Anagnostakis (**1975**). Splitting of arbutin was studied according to van der Walt (**1970**), and hydrolysis of urea according to Seeliger (**1956**). Additionally, the color reaction with diazonium blue B for identification of heterobasidiomycetous yeasts (van der Walt and Hopsu-Havu, **1976**) was carried out on a yeast-extract, malt-extract, peptone medium. The production of siderophores was examined in a modified Sundström medium (Deml and Oberwinkler, **1980**).

RESULTS AND DISCUSSION

Basidiospores and spore germination.—Basidiospores of *Christiansenia pallida* are thin-walled, smooth, hyaline, and inamyloid. They are attached to the sterigmata asymmetrically with prominent apiculi (FIGS. 1a, 2, 3). The number of spores developed on basidia varies mainly between four and six, supernumerary spores being rather frequent. The basidiospores are uninucleate and, on artificial media, they are capable of budding (FIGS. 1b, c; 5; 6; 11–15). It is likely that such germination occurs also under natural conditions, but budding basidiospores have never been reported by previous workers. In the closely related species *Syzygospora alba* Martin, Oberwinkler and Lowy (**1981**) and Oberwinkler and Bandoni (**1982b**) found numerous budding basidiospores in dried material.

Under favorable conditions, a yeast colony with haploid cells results from one basidiospore (FIGS. 13–15). The spore itself is capable of budding repeatedly, and also the yeast cells continue to sprout (FIGS. 1c, 5, 6, 11).

Rarely, germination by formation of short, narrow tubes (FIGS. 1d, 18) was observed. Such hyphal outgrowths appear to function as conjugation tubes. Despite careful search, we could not find basidiospore germination by repetition; it has also not been reported by other workers. Germination by repetition is a

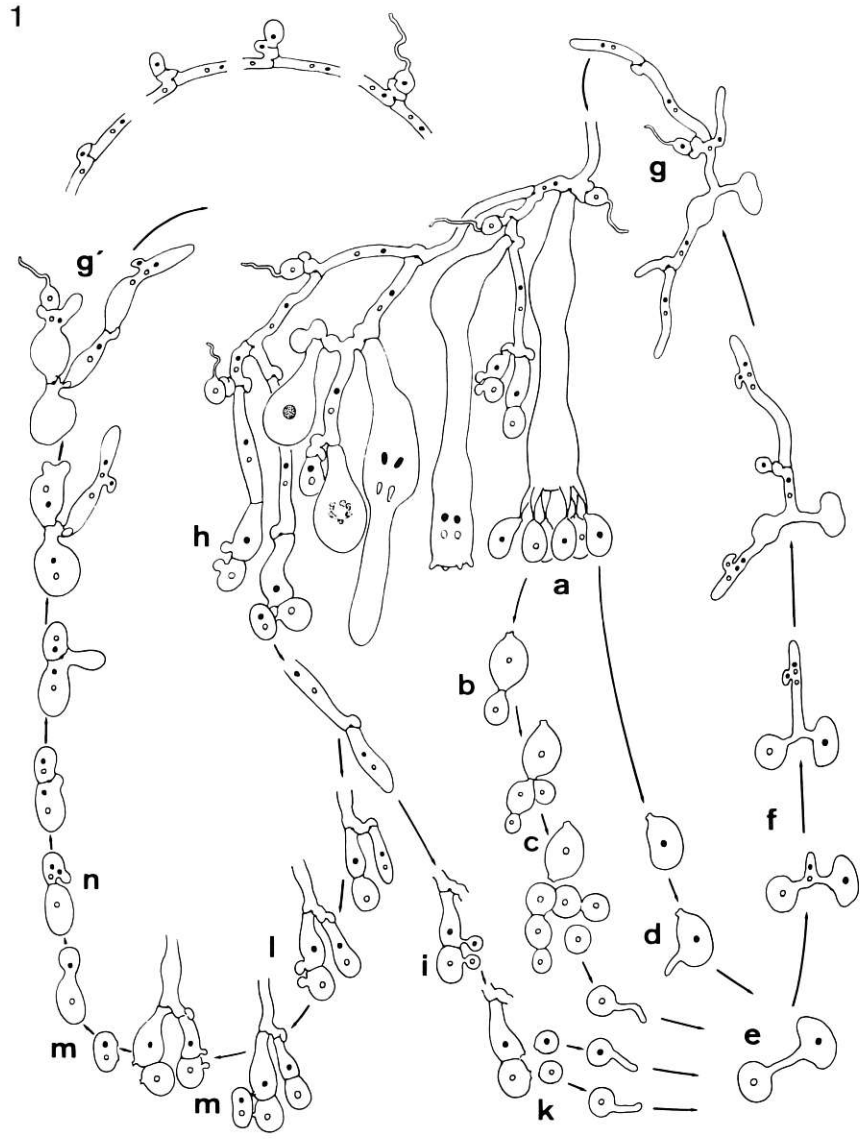

FIG. 1. Life cycle of *Christiansenia pallida*. a. Basidiospores. b. Budding basidiospore. c. Yeast colonies derived from budding basidiospores. d. Basidiospore germinating with conjugation tube. e. Conjugating monokaryotic cells. f. Hyphal formation after conjugation. g, g'. Haustoria arising from clamps. h. Conidiophores. i. Development of monokaryotic conidia. k. Monokaryotic conidia. l. Development of dikaryotic zygoconidia. m. Zygoconidia. n. Germination of zygoconidia.

common characteristic of many Heterobasidiomycetes, but there are several taxa, e.g., the Ustilaginales *s. str.*, Graphiolales (Oberwinkler *et al.*, **1982**), Atractiellales (Oberwinkler and Bandoni, **1982a**), and Dacrymycetales, in which it is not known. In all Homobasidiomycetes and a variety of Heterobasidiomycetes, basidiospore germination by germ tubes is a common feature.

Conjugation.—In yeast colonies derived from masses of basidiospores, conjugation between two yeast cells (FIGS. 1e, 19, 20) was observed repeatedly. Opposed single cells conjugate by formation of comparatively small hyphal bridges, thus initiating the dikaryotic phase and making possible further hyphal growth. It is noteworthy that conjugation took place only when the host was present.

Bandoni (**1963**) studied conjugation in *Tremella mesenterica* Fr. and found that in yeast cultures derived from single basidiospores conjugation never occurred. In contrast, by a mix of compatible isolates, conjugation readily occurred. Haploid mating strains were not isolated in this study. However, scattered occurrences of conjugation tubes and fusions of these indicate conformance with the pattern found in other dimorphic Heterobasidiomycetes, e.g., species of *Tremella* (Bandoni, **1963**; Brough, **1974**), *Rhodotorula* (Banno, **1967**), and *Sporidiobolus* (Bandoni *et al.*, **1971**). Haploid strains of such fungi, capable of both assimilation and reproduction, also function as disseminules and in the initiation of the sexual phase. Consequently, these cells play a most important part in the life histories of dimorphic fungi and the presence of dimorphism is a fundamental characteristic in their taxonomy.

We were also able to demonstrate that basidiospores can conjugate with yeast cells (FIGS. 1e, 16–18), and that mononucleate conidia (FIGS. 1k, 32, 33) also can function as conjugants. In general, it appears that any mononucleate, single cell, i.e., basidiospores, conidia, and yeasts, are all capable of serving as conjugants.

Hyphae, septa, septal pores, and haustoria.—Hyphal growth results after conjugation of two mononucleate cells (FIGS. 1f, 21–25), or by germination of originally dikaryotic conidia (zygoconidia; FIGS. 1n, 7, 34–38, 40, 41). Consequently, it appears that the dikaryon is essential for the capability of hyphal formation. Hyphal septa are regularly clamped, and branching occurs from these clamps (FIGS. 1, 2–4, 7–9, 10, 14, 15, 37–41). Hyphae in fructifications (FIGS. 1g, h, o; 2; 8; 9) of ana- and teleomorphs are long-celled and have parallel walls. Such hyphae are formed also after conjugation (FIG. 1f), or by germination of zygoconidia (FIGS. 40, 41). More often, comparatively short-celled hyphae with swollen cells develop after conjugation (FIGS. 7, 22–25) or following germination of dikaryotic conidia (FIGS. 1n, 35–38). After a time, in that case also, typical long-celled hyphae are produced.

Oberwinkler and Bandoni (**1982b**) studied the ultrastructure of the septal pore apparatus in *Christiansenia pallida* using herbarium specimens from one-year-old collections. The results obtained from the present studies of material fixed when still alive confirms the earlier findings. Dolipores lacking parenthesomes (FIGS. 48–50) are representative for the species. Electron-dense bandings occluding the pore channel orifices are rather constant. Oberwinkler and Bandoni (**1982b**) compared that dolipore type with those of *Filobasidium floriforme* Olive (Moore and Kreger-van Rij, **1972**), *Filobasidiella neoformans* Kwon-Chung (Kwon-Chung and Popkin, **1976**), *Filobasidiella arachnophila* Malloch, Kane & Lahaie (Khan *et al.*, **1981**), and *Trichosporonoides oedocephalis* Haskins & Spencer (Haskins, **1975**).

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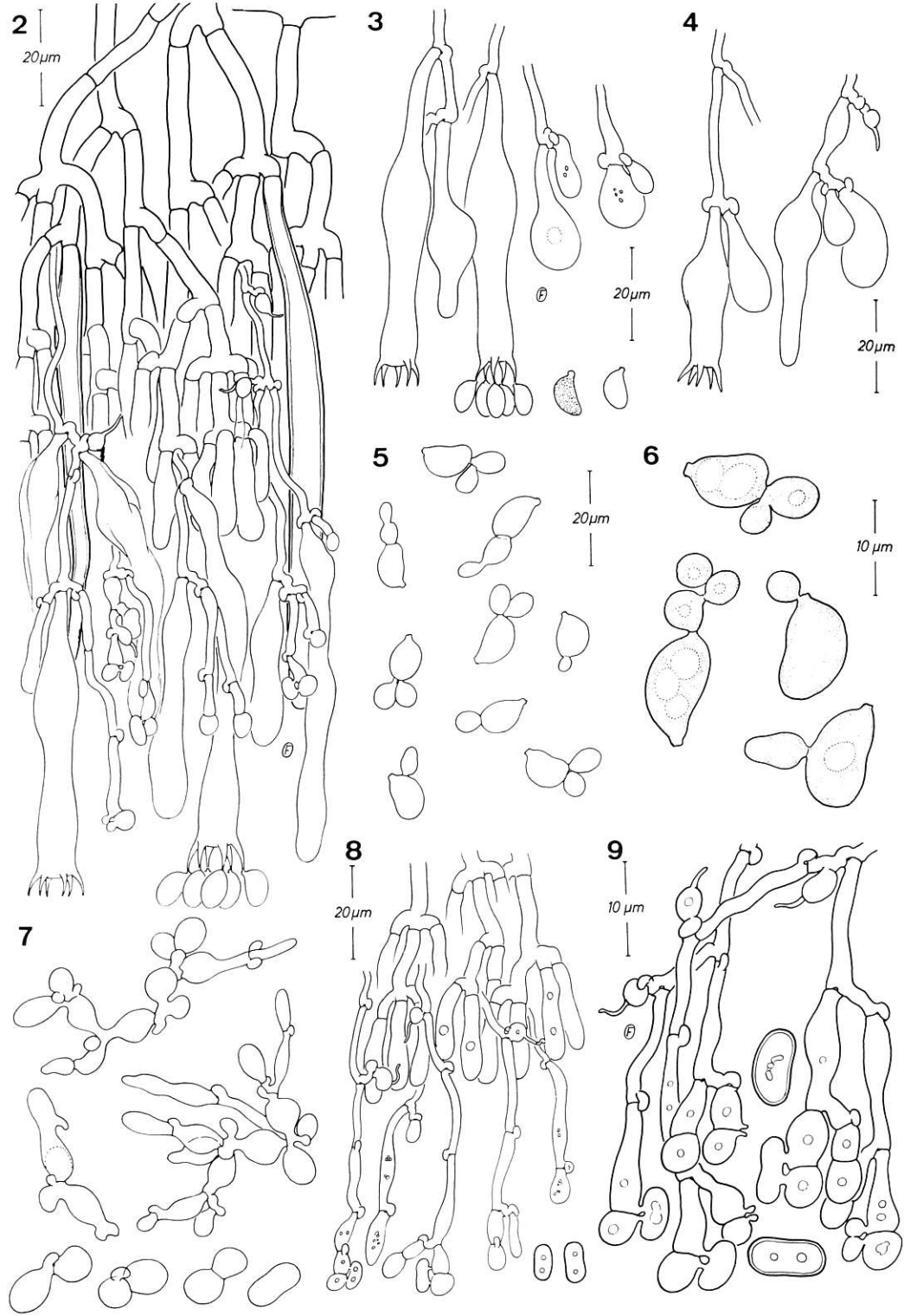
FIGS. 2–9. *Christiansenia pallida*. 2. Fully developed, ana- and teleomorph bearing parasite hyphae in host hymenium. 3, 4. Different developmental stages of basidia and basidiospores. 5, 6. Budding of basidiospores. 7. Germination of zygoconidia. 8. Zygoconidiophores associated with, and protruding from, the host hymenium. 9. Different developmental stages of conidiogenous cells and zygoconidia. 2, 8, 9 from Oberwinkler and Bandoni (**1982b**).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The haustorial type in *Christiansenia pallida* (FIGS. 1g, g'; 2; 4; 8; 9; 38; 45–57) is most characteristic. A subglobose cell develops from a clamp and is finally separated from the originating cell by another clamp. The nuclear behavior during haustorial development is remarkable: the initial outgrowth of the clamp contains one nucleus; before clamp formation, this nucleus divides and one of the daughter nuclei migrates back into the mother cell, thus leaving the haustorial cell monokaryotic. Apically, a thread-like, unbranched or rarely branched hypha develops, grows irregularly, and becomes attached to cells of *Phanerochaete cremea* (FIGS. 2, 8). The apex penetrates the host cell wall and may then function as a haustorium. Such developmental stages are difficult to study with the light microscope and rather rarely detected with the electron microscope (FIGS. 45–47). It appears to be a possible host response to surround the penetrating haustorium with a cell wall layer (FIGS. 45, 46). In these cases, no damage to the host cytoplasm can be seen. When no host cell wall is formed around the haustorium (FIG. 47), or the parasite penetrates it, degeneration of host cytoplasm occurs. These features strongly suggest that the filamentous outgrowths function as haustoria.

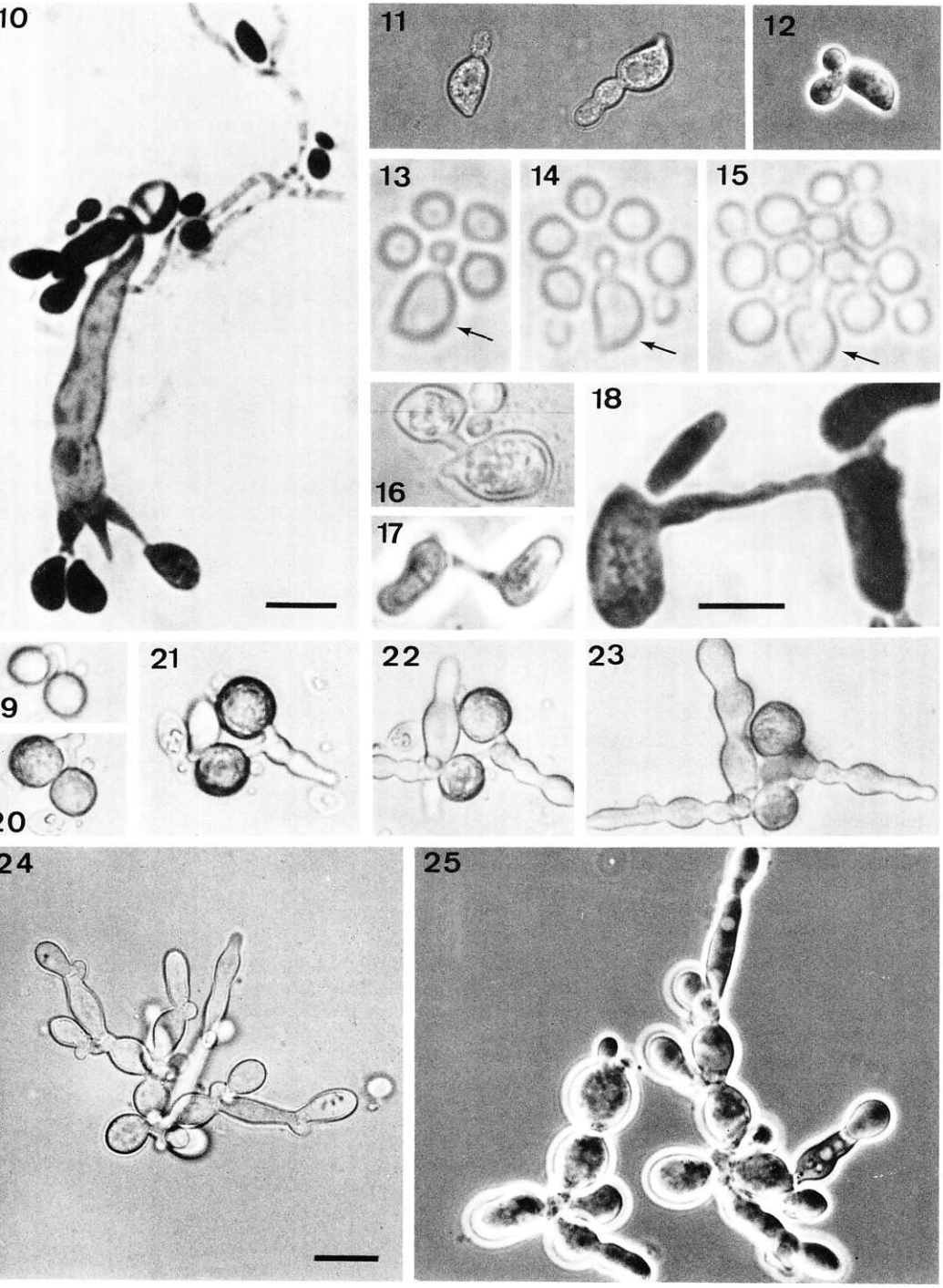
Morphologically similar haustoria have been described from a variety of *Tremella* species (Olive, **1946**; Bandoni, **1961**), and from *Tetragoniomyces uliginosus* (Karst.) Oberw. & Bandoni (Oberwinkler and Bandoni, **1981**). Bezerra and Kimbrough (**1978**) have shown the monokaryotic state of the haustorial cell in *Tremella rhytidhysterii* Bezerra & Kimbrough. *Syzygospora alba* Martin (Oberwinkler and Lowy, **1981**; Oberwinkler and Bandoni, **1982b**) has the same haustorial type. Moreover, it is also known in *Filobasidium floriforme* Olive (Olive, **1968**) and in *Filobasidiella neoformans* Kwon-Chung (Kwon-Chung, **1976**).

Conidiogenous cells and conidia.—Even in early developmental stages, terminal cells of hyphae already function as conidiogenous cells (Figs. 1i, l; 2; 8; 9; 26–33; 39). Dikaryotic apical cells are divided by an efibulate septum (FIG. 9) to produce two neighboring, mononucleate cells. Simultaneously, both cells form lateral, juxtaposed outgrowths. With the aid of TEM the mechanism of conidial development could be investigated in some detail (FIGS. 26–33). As in basidiomycetous yeast budding, outgrowth from the mother cell occurs by rupturing and splitting of the outer cell wall layers. The initial blebs expand rapidly to form subglobose cells (FIG. 26). After mitotic nuclear division, one nucleus enters the bud while the other remains in the parent cell (FIG. 27). Bud and parent cell are separated by a septum in which a central pore appears to be present (FIG. 27).

The most common type of conidiogenesis is the formation of zygoconidia (FIGS. 1k, m; 8; 9; 28–31; 39). The opposed, mononucleate conidia adhere to one another (FIG. 28) and fuse (FIG. 29) to form a dikaryotic cell (FIG. 31). At the end of its development, the propagule separates from the supporting parent cells (FIG. 31). The mature zygoconidium is thin- to slightly thick-walled, smooth and hyaline. Zygoconidia germinate to form short, swollen cells which are subtended by clamp connections (FIGS. 1n, 34–37). Haustoria arise from clamps in early hyphal development (FIGS. 1g', 38). Occasionally, germination of zygoconidia yields narrow hyphae (FIGS. 40, 41) with clamps and haustoria. The early dedikaryotization (FIGS. 42–44) of germinating zygoconidia is unexpected. In this case, single mononucleate cells bud from the germ tube.

In addition to zygoconidia, monokaryotic anamorphs may also develop (FIGS. 1k, 32, 33). Conidia formed on typical conidiogenous cells separate from mother cells without having fused, remaining mononucleate. Such conidia are potential conjugants with other monokaryotic cells, i.e., basidiospores or yeast cells.

Basidia.—In later developmental stages karyogamy and meiosis occur in terminal cells of dikaryotic hyphae. Basidial morphology undergoes considerable variation



FIGS. 10–25. *Christiansenia pallida.* 10. Mature basidium with three attached basidiospores. 11, 12. Budding basidiospores. 13–15. Different stages of yeast colony development from one basidiospore (arrows). 16–18. Conjugation of basidiospores with yeast cells. 19, 20. Conjugation of yeast cells. 21–23. Initial stages of dikaryotic hyphal growth after conjugation. 24, 25. Later dikaryotic hyphal stage with short, swollen, clamped hyphae. All bars = 10 μm, except in 18 = 5 μm.

during ontogeny. Swollen, stalked cells are commonly characteristic for the stage of nuclear fusion. During the first meiotic division, a smaller apical outgrowth develops; this is swollen above and bears the cornute sterigmata. Finally, a terminal swelling forms at the basidial apex from which cornute sterigmata develop. The number of sterigmata varies between four and six, but more than four spores commonly develop on one basidium. Basidial development and shape therefore is reminiscent of the urnigera-type basidium in *Sistotrema*. The asymmetrically-attached basidiospores are forcibly discharged from the sterigmata. Basidia can be found which originate from the same hyphae as do conidiophores (FIGS. 1a, h, o; 2).

Host specificity, enzymatic activity, and chemical tests.—In all collections which we have examined and those mentioned in the literature (Hauerslev, **1969**; Boidin, **1970**; Larsson, **1972**; Eriksson and Ryvarden, **1973**; Michelitsch, **1980**; Oberwinkler and Bandoni, **1982b**), *Christiansenia pallida* is a parasite of *Phanerochaete cremea*. Although it might be assumed that the parasite is restricted to one host species, this assumption cannot be proven at present.

We found positive reactions for amylase (weak), chitinase, DNAase, protease (weak), RNAase, and urease. The hydrolysis of urea was also positive. Lipase, polygalacturonase, pectate lyase, and phosphatase could not be detected. Splitting of arbutin was positive.

The color reaction with diazonium blue B was weakly positive after three wk. This test appears to be characteristic for heterobasidiomycetous yeasts (van der Walt and Hopsu-Havu, **1976**). Siderophores, characteristic for a variety of Heterobasidiomycetes when grown on low iron media (Deml and Oberwinkler, **1980**), were not produced.

Taxonomic considerations.—We consider the presence of a yeast stage in *Christiansenia pallida* as a taxonomically important feature and, in fact, one of major significance in defining relationships among the Basidiomycetes generally. Only Heterobasidiomycetes are known to develop yeast phases during their life cycles (Oberwinkler, **1978**, **1982**). Secondary ballistospores would be another heterobasidiomycetous feature, but such repetitive spores are unknown in *C. pallida*.

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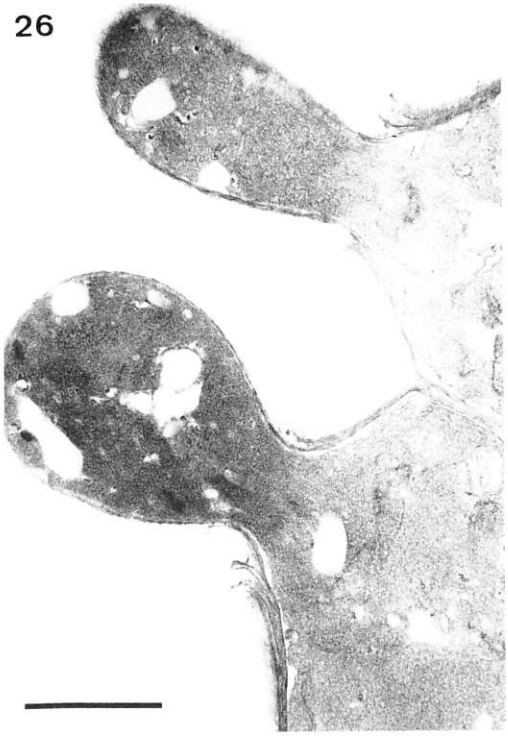
FIGS. 26–29. *Christiansenia pallida*. Conidiogenous cells and conidial development. 26. Early stage of conidial budding. Note ruptured mother cell walls at budding loci. 27. Conidiophore with young conidia. Note mononucleate conidiophorous cells, and multilamellar scars. 28. Attaching of two opposed, mononucleate conidia. 29. Fusion of two mononucleate conidia. Note separation of conidia from mother cells by cell wall formation. All bars = 1 μm.

FIGS. 30–33. *Christiansenia pallida*. Conidiophores and conidial development. 30. Zygoconidium showing the attachment points of original conidial buds. 31. Released zygoconidium. Note dikaryon of conidium and nucleus of one conidiogenous cell. 32. Conidiphore with one attached conidium. Note cell wall separating conidium and mother cell. 33. Mononucleate conidium separating from conidiophore. All bars = 1 μm.

FIGS. 34–44. *Christiansenia pallida*. 34–37. Germination of zygoconidia. 34. Early stage of germination. 35. Clamp formation at germination locus. 36, 37. Short, swollen cells of germinated zygoconidia. Note clamped septa. 38. Later developmental stage in zygoconidium germination. Note haustoria arising from clamps (arrow). 39. Giemsa staining of conidiophore and zygoconidium. Note dikaryotic hyphal cells and zygoconidium. 40, 41. Zygoconidia germinating with elongated, clamped hyphae. 42–44. Dedikaryotization of cells derived from zygoconidia. Note budding of yeast-like cells. Bar = 5 μm in FIG. 34, and same bar for FIGS. 36, 37, 39, 42; bar = 10 μm in FIG. 38 and remaining FIGS.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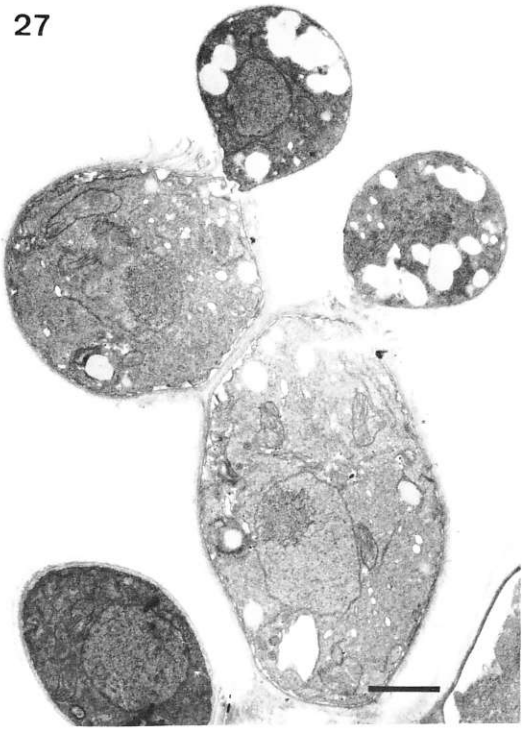
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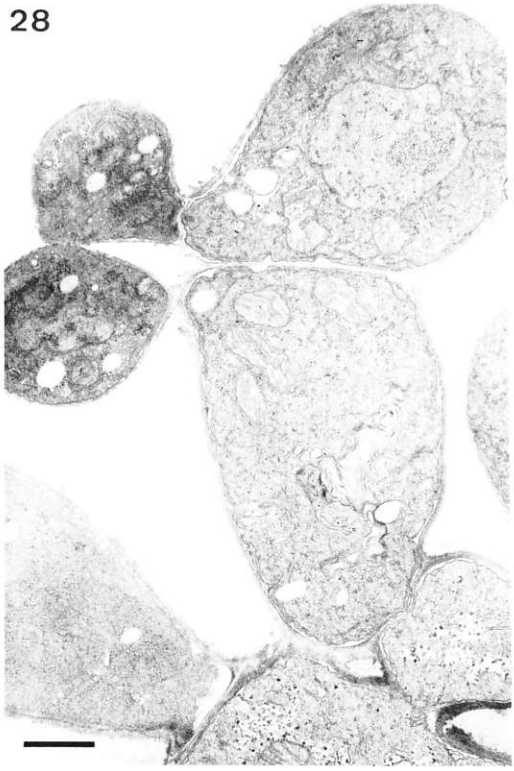
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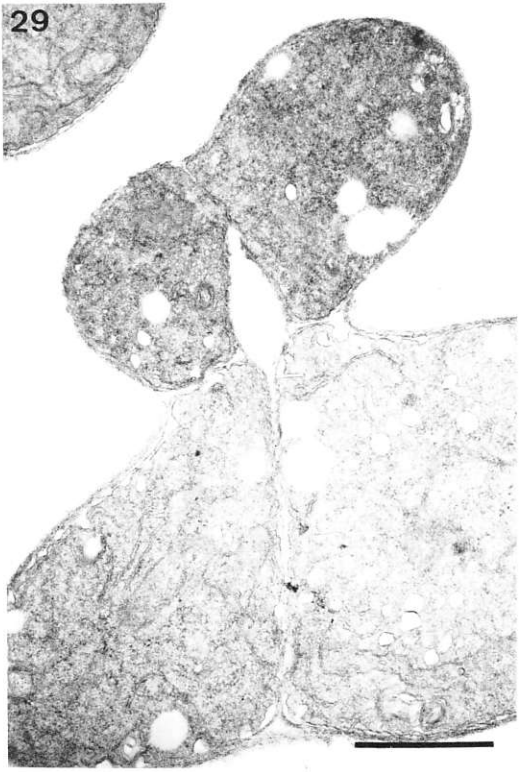
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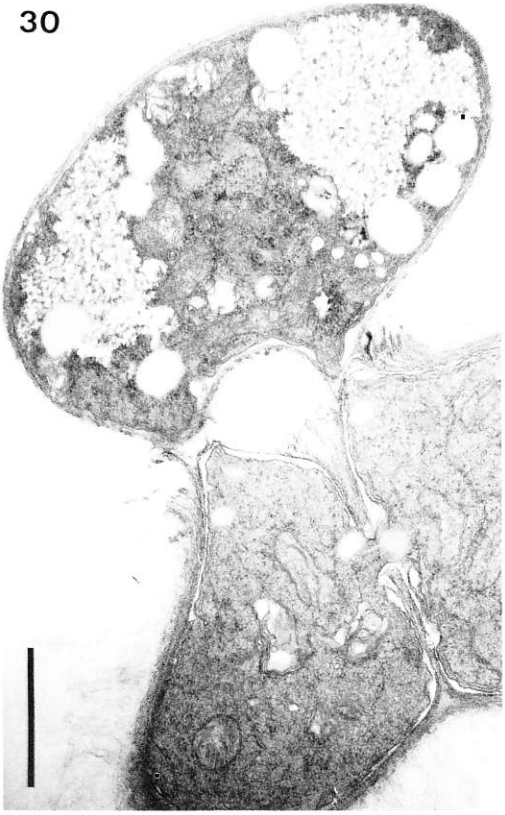
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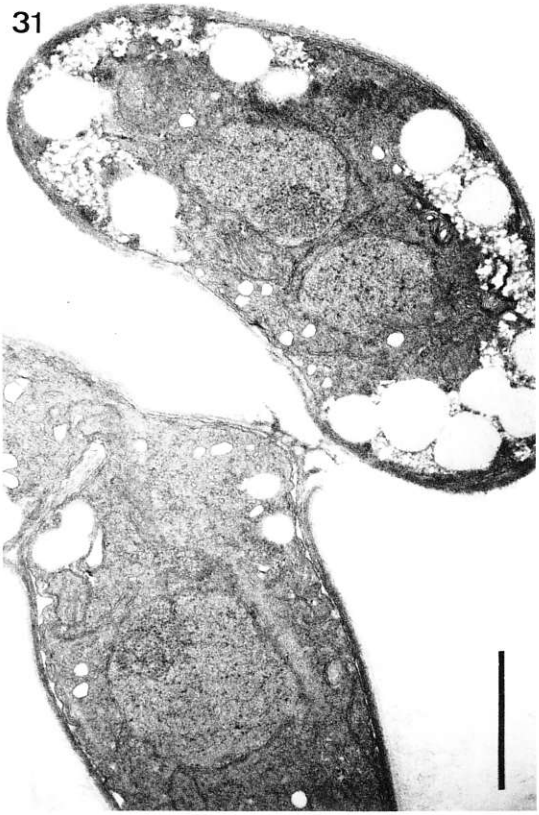
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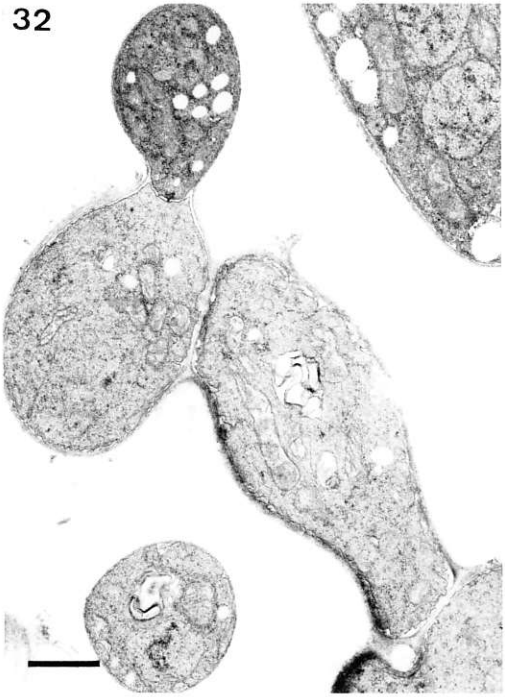
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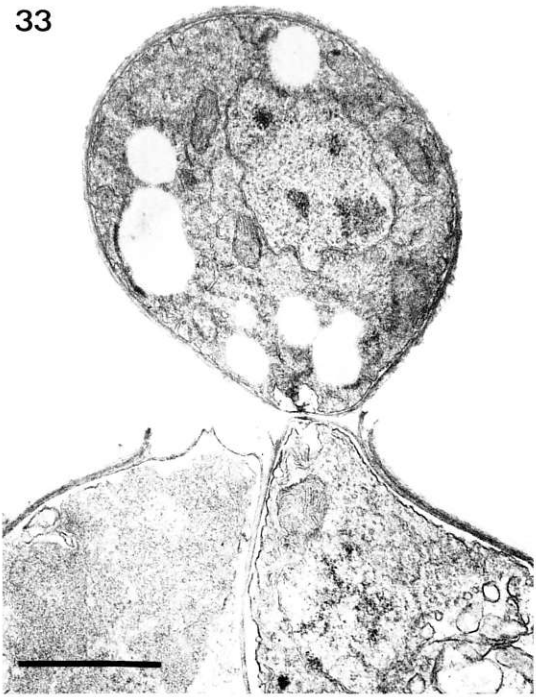
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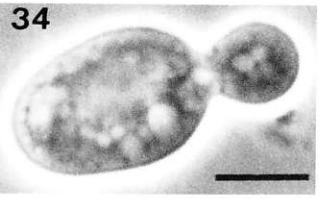
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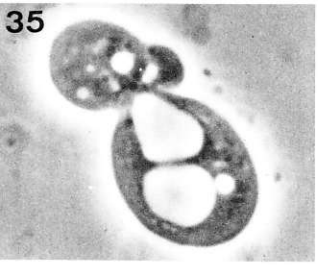
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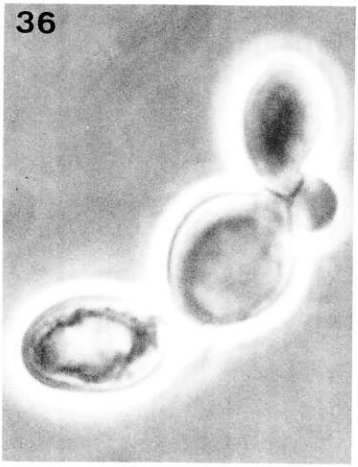
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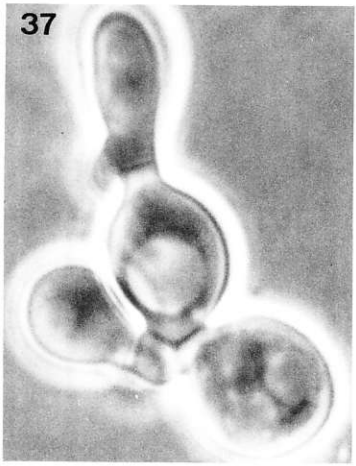
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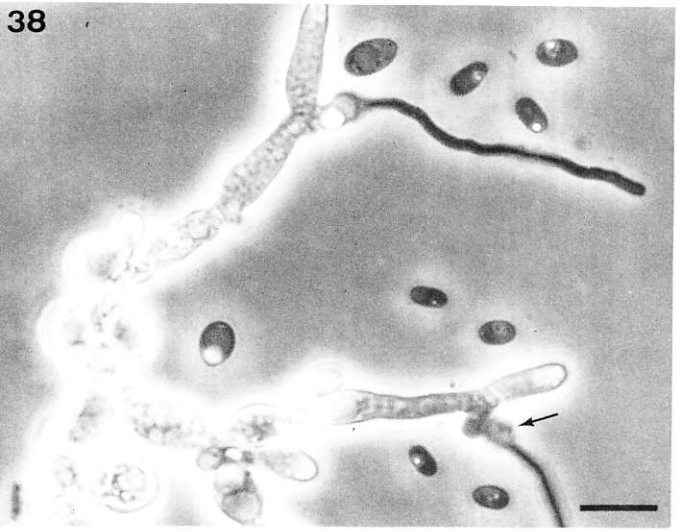
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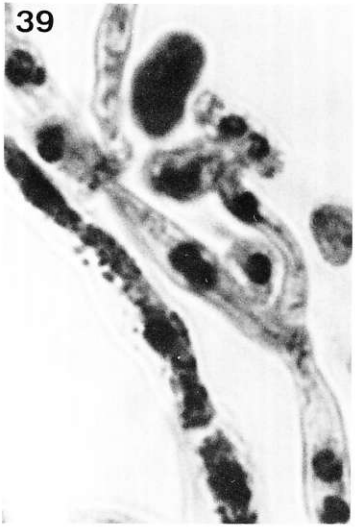
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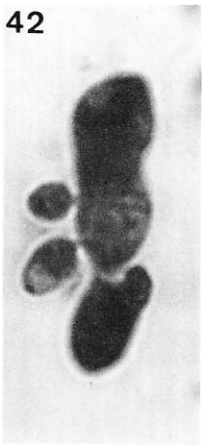
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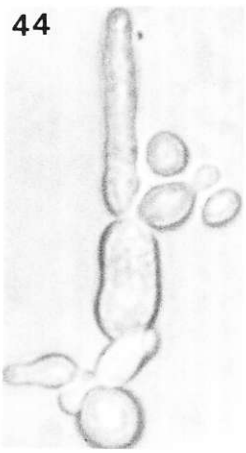
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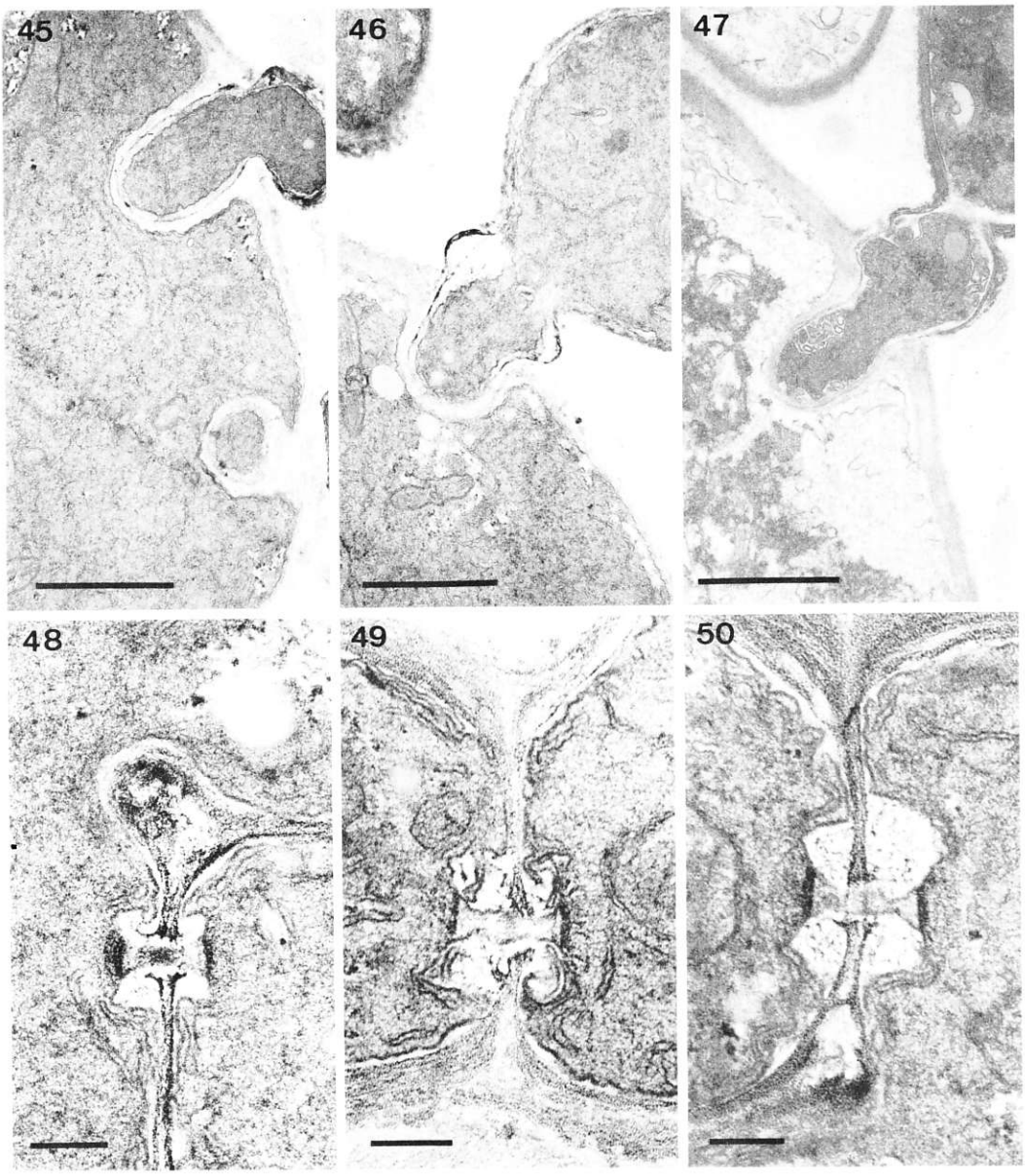

FIGS. 45–50. *Christiansenia pallida*. 45–47. Haustorial branch of *Christiansenia pallida* penetrating cells of *Phanerochaete cremea*. 45, 46. Haustoria surrounded by host cell walls. 47. Haustorial branch, the apex not covered by host cell wall. Note degenerating host cytoplasm. 48–50. Dolipores of *Christiansenia pallida*. Note lack of parenthesomes. In FIGS. 45–57 bars = 1 μm; in FIGS. 48–50 bars = 0.2 μm.

Dolipores without parenthesomes have not been found in Homobasidiomycetes, but they are known from species of the Filobasidiaceae, a heterobasidiomycetous taxon. Members of that family, like *Filobasidium floriforme* and *Filobasidiella neoformans*, are additionally characterized by the unusual tremelloid haustorial

type present in *Christiansenia pallida*. Oberwinkler and Bandoni (**1982b**) included *Christiansenia* in a new family, Carcinomycetaceae, together with the type genus *Carcinomyces*, and *Syzygospora*. They used characteristics of basidia, conidial stages, septal pore ultrastructure, and mycoparasitism for a comprehensive circumscription of the family. *Christiansenia* appears to be a genus in that taxon. *Carcinomyces*-species lack zygoconidia and, in addition, seem to be confined to the agaric host, *Collybia dryophila* (Fr.) Kummer. *Christiansenia pallida* is certainly closely related to *Syzygospora alba*, another species with zygoconidia.

Without presenting any new characteristics of the taxa under consideration, Jülich (**1982**) erected the family Syzygosporaceae, including *Syzygospora* and *Christiansenia*. His remark that the "ceraceous context and the narrowly clavate basidia point towards the Meruliales" is totally misleading. As noted above, the basidia of *C. pallida* are urnigerate; those of merulioid fungi are not. The Meruliaceae represent a typical homobasidiomycetous taxon. *Christiansenia* clearly shows characteristic heterobasidiomycetous affinities as detailed above.

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