

# Carcinomycetaceae: a new family in the Heterobasidiomycetes

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A group of holobasidiate mycoparasites, growing on Basidiomycetes, was studied by light- and electron microscopy. The parasites develop haustoria which penetrate the host-cells. Often a hypertrophic, gall-like growth of the host is induced by this parasitic interaction. Ana- and teleomorph stages and functions are highly diverse and not yet fully understood. Two species produce unique zyoconidia. The mechanism of spore abstriction on apically sterigmate holobasidia is hymenomycetous or gasteromycetous, and the basidiospores usually germinate by budding. Dolipores without parenthesomes were found in three species. A heterobasidiomycetous relationship is proposed for the three genera, *Christiansenia*, *Szygospora*, and *Carcinomyces* gen. nov. Taxonomic considerations led to the proposal of a new family, the Carcinomycetaceae.

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## Introduction

The proposal of the genus *Christiansenia* by Hauerslev (1969) drew attention to species with highly uncommon characters for Basidiomycetes. *Christiansenia pallida* Hauerslev grows parasitically on *Phanerochaete cremea* (Bres.) Parm. and interacts with the host by special haustoria. The parasite is holobasidiate, has hymenomycetous spore abstriction, and a curious conidium development with fusion of monokaryotic conidium-initials to form a dikaryotic propagule. These zyoconidia were already known from *Szygospora alba* Martin (1937), who, however, originally interpreted the structures as special heterobasidia. Additional material which later became available enabled Kao (1956) to discover the true basidial stage and to unravel the anamorph-teleomorph connections. Boidin (1970) re-studied and reinterpreted *Christiansenia* and *Szygospora*, concluding that they are congeneric and that the name *Christiansenia* should be accepted and *Szygospora* used only for the anamorph. He also included a

third species, *Christiansenia mycophaga* (M. P. Christ.) Boidin, a taxon described in the genus *Ceratobasidium* by M. P. Christiansen (1959). When Ginns & Sunhede (1978) investigated mycotrophic fungi on *Collybia dryophila* (Fr.) Kummer they found characters reminiscent of those of *Christiansenia* and consequently decided to amend this genus for incorporation of Peck's *Tremella mycetophila* and two undescribed species. Our taxonomic investigations of mycoparasitic Heterobasidiomycetes were extended to this group several years ago and included cultural experiments and ultrastructural studies.

## Materials and methods

For descriptions and illustrations of the species, the following collections were used:

*Carcinomyces effibulatus* (Ginns & Sunhede) Oberw. & Bandoni; Canada, British Columbia, Vancouver, campus of Simon

Fraser University, 10 Jul 1980, leg. J. Hammerberg, cult. R. J. Bandoni. – Holotype: Sweden, Bohuslän, Ucklum par., Presstorp, 7 Aug 1977, Sonja Hansson (GB). – *C. mycetophilus* (Peck) Oberw. & Bandoni; as *Tremella mycetophila* Peck; USA, New York, Essex County, North Elba, Peck. Lectotype (NYS). – *Christiansenia pallida* Hauerslev; Ostalpen, Österreich, Kärnten, Karnische Alpen, ca. 6 km S von Mauthen im Gailtal, etwa 2.5 km NE vom Plöckenpass, südliche Abhänge des Polinik, Weg zur Unteren Spielboden-Alm; ca. 1400–1500 m, auf Fruchtkörpern von *Phanerochaete cremea* (Bres.) Parm. (on *Alnus viridis*), 18 Jul 1978; leg. S. Michelitsch 'GZU, Herb. Michelitsch). – *C. tumefaciens* Ginns & Sunhede. – Holotype: Denmark, Sjaelland, Vemmetofte skov. 23 Sept 1977. Karin Toft (GB). – *Szyzospora alba* Martin; Fungi of Panama, Prov. Chiriqui; Valley of the upper Rio Chiriqui Viejo, alt. 1600–1800 m, 1 Jul 1935; G.W. Martin 2167; co-type (Herb. State Univ. Iowa, now BPI). – Mexico: Entre los Guayabos y las Cabañas, 15 km al SW de Mazamitla, Carretera a Tamazula, Jalisco; bosque de *Pinus-Quercus*, muy perturbado, en transacción con vegetación subtropical; alt. 1700–1800 m, 24 Aug 1974; col. G. Guzman 11843 (Herbario de la Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional, Mexico, D.F.).

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

### Carcinomycetaceae Oberwinkler & Bandoni fam. nov.

Heterobasidiomycetes in Homobasidiomycetum carposomatia parasiticae, tumefactae, raro pustulis distinctis eruptentes. Hyphae hyalinae, tenuitunicatae, inter cellulas hospitalium crescunt saepe cum haustoriis propriis. Ultrastructura septorum hypharum doliporis sine parenthesomata notata est. Cystidia desunt. Hyphae fertiles in consuetudine ex substrato prodeuntes et conidia vel holobasidia basidiosporasque gerentes. Basidiosporae hyalinae, tenuitunicatae tunicisque levibus plerumque cellulas singulas germinant. – Typus familiae: *Carcinomyces* Oberwinkler & Bandoni gen. nov.

The new family Carcinomycetaceae includes heterobasidiomycetous mycoparasites growing on Homobasidiomycetes, often causing hypertrophic swellings of the host; rarely, the parasites develop inconspicuous pustules. All hyphae are hyaline and thin-walled, intercellular, sometimes penetrating the host cells with characteristic haustoria. Cystidia are lacking. Usually the fertile hyphae are produced on the outer surface of the host and the parasite. Sometimes, however, anamorphs are present in internal holes of host fruitbodies. The holobasidiate meiosporangia produce spores on apical sterigmata. The hyaline, thin-walled, smooth basidiospores bud in a yeast-like manner.

*Carcinomyces*, the type of the family is described in the present report.

### Key to genera

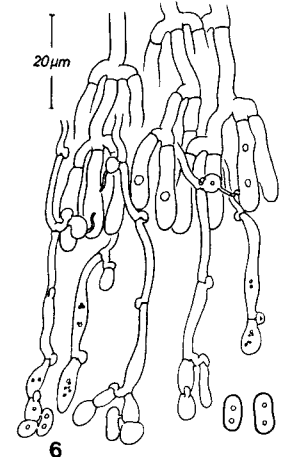
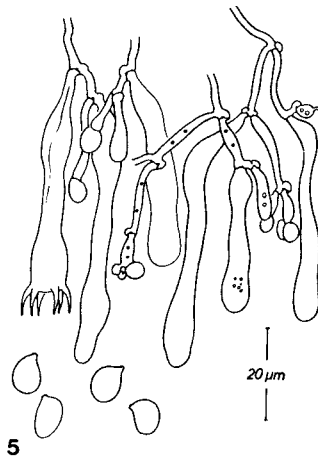
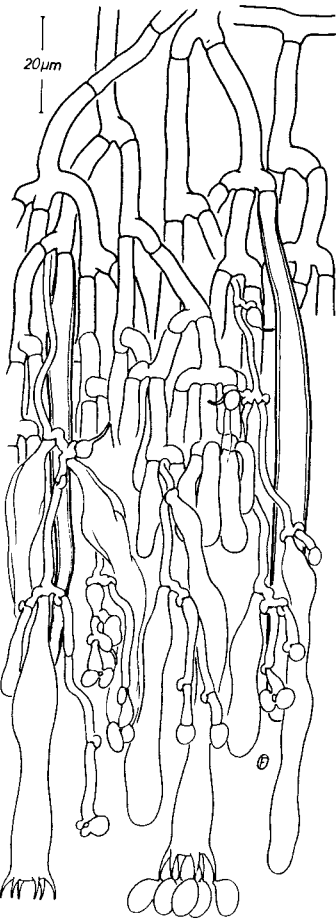
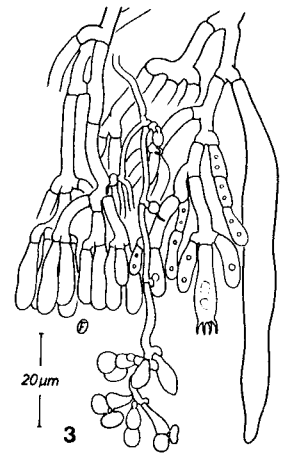
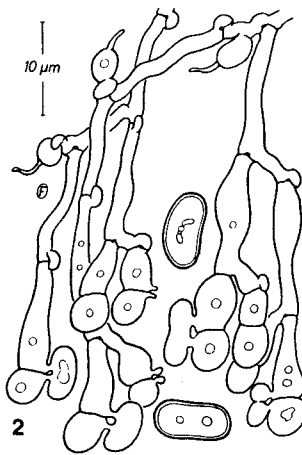
1. With zygoconidia; parasitic on corticioid Basidiomycetes ..... 2
1. Without zygoconidia; inducing galls on *Collybia dryophila* ..... *Carcinomyces*
2. Basidiocarps small, 0.1–1 mm diam, compact-gelatinous, developing in and on the hymenium of *Phanerochaete cremea* ..... *Christiansenia*
2. Basidiocarps up to 5 cm (or more) diam, tremelloid and gyrose ..... *Szyzospora*

### Christiansenia Hauerslev 1969

Basidiocarps pustulate (Fig. 1), up to 1 mm diam, rarely larger, 50–200–(300)  $\mu\text{m}$  thick, confluent with closely neighbouring pustules; soft gelatinous and watery-hyaline when fresh, ochraceous and horny when dry, shrinking to an inconspicuous film. Hyphae (Figs 2–6, 10) thin-walled, hyaline, with clamps, 1.5–3  $\mu\text{m}$  diam, gelatinizing. Hyphal branching by outgrowth of, or from the opposite side of, the clamps. Short side-branches often globose and with a filamentous and bent appendage to form a haustorium (Figs 2–8) of the *Tremella*-type (Olive 1946). Early developmental stages usually with zygoconidia (Boidin 1970): terminal, paired short-cylindrical cells simultaneously form bud-like outgrowths (Fig. 2); after further enlargement the outgrowths fuse to form one cell. This cell receives two nuclei, one passing through each of the two connections from the original mother cells. The dicaryotic zygoconidium breaks free from the mother cells (Figs 2, 6, 12); mature zygoconidia are 7–10  $\times$  3–4.5  $\mu\text{m}$ , with slightly thickened cell walls (Figs 2, 12). Apparently this spore stage is important for propagation of the parasite on appropriate hosts. Later, terminal cells elongate considerably (Figs 5, 4) with swellings close to the basal clamp and to the apex. These probasidia develop into basidia, 35–100–(140)  $\times$  6–9–(12)  $\mu\text{m}$ , with predominantly more than 4 and up to 6 horn-shaped, terminal sterigmata. The basidiospores, 7.5–11  $\times$  5–9  $\mu\text{m}$ , grow asymmetrically and mature as subglobose cells with a distinct apiculus, thin, unsculptured, hyaline, non-amyloid walls. Spore germination has not yet been observed. None of the examined fungi had budding basidiospores present, and it is thus unclear whether this characteristic is present or not.

All known collections of *Christiansenia pallida* grew on *Phanerochaete cremea* (Bres.) Parm. (Figs 3, 4, 6). The species is reported from Austria, Denmark, France and Sweden (Michelitsch 1980, Hauerslev 1969, Boidin 1970, Larsson 1972).

Hauerslev (1969) proposed the genus with one species, *Christiansenia pallida*, and described the most impor-



Figs 1–6. *Christiansenia pallida*. – Fig. 1. The parasite growing on *Phanerochaete cremea*, usually on the underside of the substratum (illustration of inverted basidiocarp). – Fig. 2. Different developmental stages of zygocidia. – Fig. 3. Young developmental stage of the parasite showing the association with the host. – Fig. 4. Fully developed, ana- and teleomorph bearing parasite in host hymenium. – Fig. 5. Ana- and teleomorphs descending from the same generative hyphae; basidiospores. – Fig. 6. Zygocnidioophores associated with, and protruding from the hymenium of the host.

tant characters, viz. cells conjugating to form conidia, basidial morphology, and the haustorial type. Judging from our own investigations and the descriptions of Christiansen (1959) and Eriksson & Ryvarden (1973), these characters seem not to be present in *Ceratobasidium mycophagum* M. P. Christ., a species

transferred to *Christiansenia* by Boidin (1970). Conidium formation is not well understood in *C. mycophagum*, probably because of the poor condition of the scanty type material. However, zygocidia are not present in the type material; the basidia are not uniform and do not produce supernumerary sterig-



Figs 7–12. TEM-micrographs of *Christiansenia pallida*. All bars equal 2  $\mu$ m. – Fig. 7. Haustorium penetrating a host-cell. – Fig. 8. Haustorial interaction with a host-cell, showing an obliquely cut dolipore. – Fig. 9. Basidiospores. – Fig. 10. Short-cylindrical part of a haustorium with basal clamp and dikaryon. – Fig. 11. Median section of a dolipore with banded pore plugs and lacking parenthesomes. – Fig. 12. Dikaryotic conidium.

mata. According to Eriksson & Ryvarden (1973) the basidiospores germinate "with globose yeastlike sprout-cells". We conclude, therefore, that *Ceratobasidium mycophagum* belongs neither in the genus *Ceratobasidium* nor in *Christiansenia*. This fungus is highly remarkable because of holobasidia and yeast-like budding by basidiospores. To our knowledge, a comparable situation (but not consequently a relationship) occurs to some extent in *Paullicorticium pearsonii* (Bourd.) J. Eriksson, basidiospores of which germinate with microconidia. Further developmental stages in both species are unknown and therefore a better interpretation is not possible at the moment. Boidin (1970) was also of the opinion that *Syzygospora alba* Martin should be transferred to *Christiansenia*. We agree that there is a close relationship between these species, as indicated by the tremelloid haustoria and zyoconidia. Different characteristics in basidiocarp construction, basidial morphology and basidiospore germination make *Syzygospora* generically different, however, as will be explained in more detail below.

*Christiansenia pallida* is a true mycoparasite that develops haustoria (Figs 7, 8). Similar haustoria are known to us only in some species of *Tremella* and related taxa, species of the *Filobasidiella* group, in *Platygløea fimetaria* (Schum. ex Pers.) v. Höhnelt (unpubl. data), as well as in *Syzygospora alba* (Oberwinkler & Lowy 1981).

Another striking character is found in the septal pore type (Fig. 11), a dolipore lacking parentheses but with electron-dense banding between the central pore-swells. Comparable septal pores are present in *Filobasidium floriforme* Olive (Moore & Kreger-van Rij 1972) and in species of *Filobasidiella* (Kwon-Chung & Popkin 1976, Khan et al. 1981). This might well be an indication of a taxonomic relationship between these taxa. Tremelloid haustoria are known in *Filobasidium floriforme* (Olive 1968) and *Filobasidiella neoformans* (Kwon-Chung 1976). However, these species strongly differ in having gasteroid basidia which produce sessile spores.

Though the type specimen of *Filobasidium floriforme* grew on dead inflorescences of *Erianthus giganteus* (Walt.) Muhl. (Poaceae), it is likely that it was associated with other fungi. There is nothing known, however, concerning a parasitic interaction. The anamorph of *Filobasidiella neoformans*, *Cryptococcus neoformans*, has been known for more than half a century as a human pathogen, but it was first isolated from peach-juice (Sanfelice 1894). It has been reported by many workers from pigeon droppings and was later isolated from soil (Emmons 1951), plants and plant debris (Staib 1971, Staib et al. 1972), and peach fruit (Staib et al. 1973). To our knowledge, mycoparasitic behavior of this fungus has not yet been reported. It must be considered that the various natural habitats from which *Cryptococcus neoformans* is known, also are the ecological niches of various other fungi. Therefore a mycoparasitic interac-

tion of *Filobasidiella neoformans* cannot be excluded.

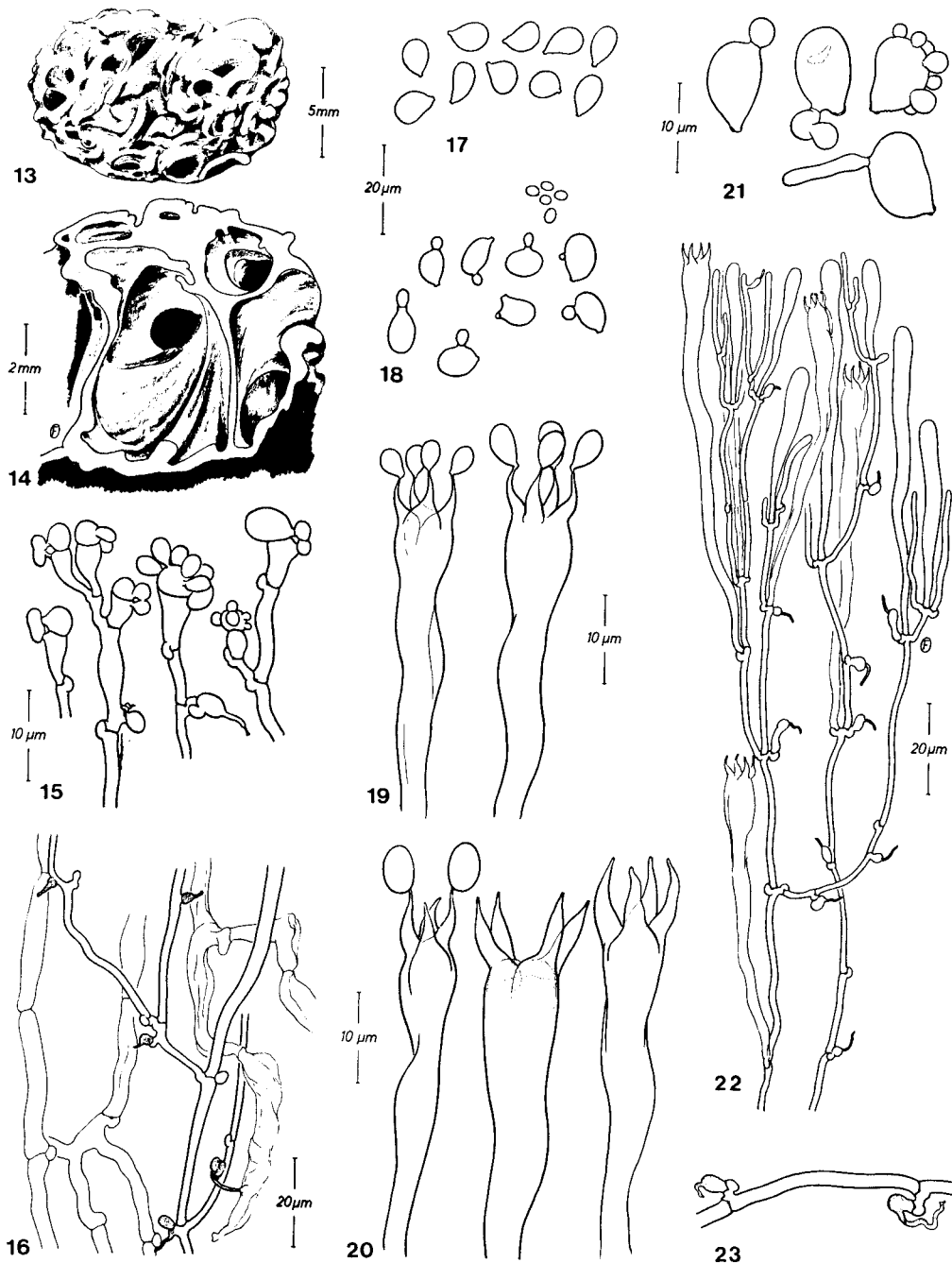
Both *Filobasidium floriforme* and *Filobasidiella neoformans* produce yeast stages during their life-cycles, but such a stage is unknown for *Christiansenia pallida*. Therefore it would be important to study the developmental stages of this species under cultural conditions.

### *Syzygospora* Martin 1937

Basidiocarps tremelloid, cerebriform with reticulate holes, up to 5 cm broad and 10 cm long or in diameter (Figs 13, 14); soft gelatinous and pure white when fresh (Martin 1937), horny and dark brown when dry. Hyphae thin-walled, hyaline, with clamps, 2–4–(5)  $\mu\text{m}$  diam, gelatinizing. Hyphal branching by outgrowth of, or from the opposite side of the clamps. Short side branches often subglobose to short cylindrical with filamentous appendages which form haustoria of the *Tremella*-type (Figs 15, 16, 22, 23) and which are attached to the host cells (Fig. 16). Zyoconidia of the *Christiansenia*-type (Fig. 15), 5–6  $\times$  2.5–4  $\mu\text{m}$ , present on outer and inner surfaces of the basidiocarps and often intermixed in the peripheral layers with basidia. Sometimes several zyoconidia are formed on the same conidiophore (Kao 1956; present contribution Fig. 15). Parts of the outer surface of the basidiocarp covered with thickening hymenia (Fig. 22) built up of basidia of different developmental stages. Very young probasidia hypha-like, then long, slender, gradually swelling, cystidia-like cells (Fig. 22), mostly with 4 terminal, horn-shaped sterigmata, the basidia appearing apically quadripartite (Figs 19, 20). Occasionally 2- and 3-sterigmate basidia can be found (Kao 1956). Basidiospores asymmetrically attached to the sterigmata (Figs 19, 20), subglobose to laterally depressed, drop-shaped, 9–11  $\times$  6–8  $\mu\text{m}$  when abstricted, (Fig. 17), thin- and smooth-walled, hyaline, non-amyloid. Germination mostly by budding (Figs 18, 21) with a scar-like rupturing of the mother cell wall, sometimes with simultaneous multiple budding (Fig. 21), rarely germinating by hyphae (Fig. 21). Repetitive secondary spores not observed.

*Syzygospora alba* Martin is a parasitic species (Fig. 16) growing on basidiomycetous hosts (Oberwinkler & Lowy 1981) which may belong to corticioid Aphyllophorales. The fungus is known only from a few collections from Panama and a single specimen from Mexico.

The species was first described as an unusual auctorioid Heterobasidiomycete by Martin (1937) who interpreted the zyoconidiophores as basidia. Well developed specimens, collected later on, were studied by Kao (1956) and enabled her to reinterpret the species: Conidial and holobasidial stages were found to originate from the very same hyphae and she concluded that



Figs 13–23. *Syzygospora alba*. Figs 13–16 and 19–23 reproduced from Oberwinkler & Lowy (1981). – Fig. 13. Fruitbody in a dry condition. – Fig. 14. Section through a fruitbody showing the internal lacunar system. – Fig. 15. Zyoconiophores with different developmental stages of zyoconidia. – Fig. 16. Parasite hyphae attached with haustoria to host hyphae. – Fig. 17. Mature basidiospores. – Fig. 18. Yeast budding of basidiospores. – Figs 19, 20. Upper parts of basidia, different stages of ontogeny. – Fig. 21. Diverse types of basidiospore germination. – Fig. 22. Thickening hymenium with basidia of different ages and hyphae with haustoria. – Fig. 23. Haustoria.

"*Syzygospora* is probably only a conidial stage of the homobasidiomycete". Boidin (1970), who investigated cotype material (Martin 2517), detected some basidiospores of the shape and measurements (taken from his illustration) reported by Kao (1956) and intermixed with innumerable zygoconidia. Finally, Oberwinkler & Lowy (1981) studied a collection made in Mexico which is in a fairly good developmental condition. This specimen was again used for the present, comparative study. In addition to the known characters, several other important features were elucidated. These include gyrose fruitbodies composed of a heteromorphic hyphal system, i.e. host and parasite hyphae intermixed, host-parasite interaction involving haustoria of the tremelloid type, thickening hymenium, partially compartmented basial apex, and dolipores with and without parentheses. The latter finding has to be interpreted very carefully because only herbarium material was available for TEM-studies. However, it appears that dolipores without parentheses belong to septa of the parasite hyphae and those with a homobasidiomycetous dolipore to the host. On the basis of all these data, Oberwinkler & Lowy (1981) concluded that there is obviously a close relationship between *Christiansenia pallida* and *Syzygospora alba*. However, they did not accept the decision of Boidin (1970) to include both species in a single genus and to use the name *Christiansenia alba* Boidin ex Martin as the nomenclatorially correct one for the teleo- and holomorph of *Syzygospora alba*.

It is obvious that uncommon morphologically and functionally identical characteristics, e.g. tremelloid haustoria, zygoconidiophores and conidia, are indicators of a close relationship. However, the other differing characteristics of *Syzygospora* cannot be neglected, e.g. a) the gyrose fruitbody composed of intermixed host and parasite hyphae, b) morphology of the mature basial apex, including the 4 sterigmata, and c) basidiospore germination by budding. The latter feature is uncertain for *Christiansenia pallida*, basidiospores of which have never been seen to produce buds by different workers (Hauerslev 1969, Boidin 1970, Eriksson & Ryvar den 1973, Michelitsch 1980) and by ourselves. It is our opinion that these differences should be accepted not only for a specific, but for generic separation of the two taxa.

Boidin (1970) gave comprehensive arguments on the nomenclatorial problem concerning the correct generic name of the teleo- and holomorph of *Syzygospora alba*. We also agree, as did Oberwinkler & Lowy (1981), with Boidin's reinterpretation of Martin's Fig. 1a (1937) as a young basidium and not a cystidium. This clearly indicates that the type material does contain the teleomorph, as well as masses of conidiophores and conidia. Despite Martin's misinterpretation of the conidiophores and failure to note the true basidia, Oberwinkler & Lowy (1981) accepted an interpretation of Art. 59 of the Nomenclatorial Code by Weresub et al. (1974)

which make the type responsible for the application of the name. We also accept this interpretation of Art. 59 and consequently use the name *Syzygospora alba* Martin for the teleomorph.

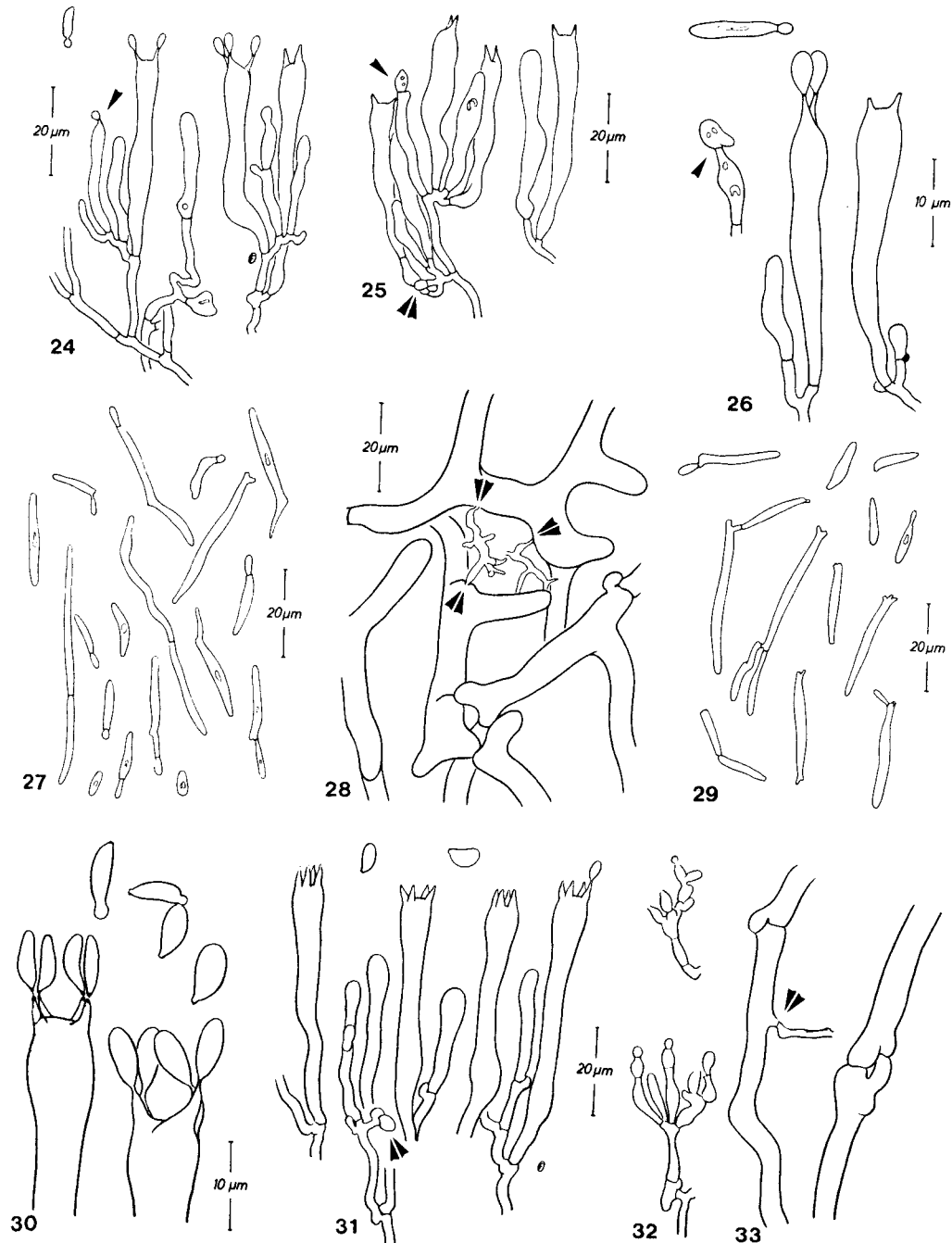
### **Carcinomyces Oberwinkler & Bandoni gen. nov.**

Fungi mycoparasitici, in carposomatis Agaricalium crescent, cellulas hospitem luxurari adducunt. Carposomata propria cystidiaque desunt. Hyphae hyalinae, tenui-tunicatae cellulis conidia gerentes vel holobasidiis terminant. Basidiosporae hyalinae, ex sterigmatibus in apice basidiorum ortae, eiectae vel delatae sunt, cellulasque singulas germinantes plerumque producunt. – Typus generis: *Christiansenia effibulata* Ginns & Sunhede, Bot. Notiser 131: 168 (1978).

Etymologia: Καρκίνος – cancer; μύκης – fungus.

*Carcinomyces* is a heterobasidiomycetous genus with species parasitic on Agaricales, presently known only on *Collybia dryophila* (Fr.) Kummer. The parasites do not produce basidiocarps by themselves but cause a hypertrophic, cancer-like growth of the hosts, i.e. galls. The hyaline and thin-walled hyphae develop terminal conidiophores (Figs 24, 25, 26, 32) and holobasidia (Figs 24, 25, 26, 30, 31) with apical sterigmata from which the basidiospores break off passively or can be forcibly discharged. The basidia of the type species (Figs 24, 25, 26) are functionally gasteroid and the basidiospores germinate by yeast-like budding (Figs 24, 26), a behavior which is assumed to be present also in the other species of the genus (Fig. 30).

Though generically different, we assume *Christiansenia pallida* and *Syzygospora alba* to be closely related because of the presence of tremelloid haustoria and zygoconidiophores. Conidia in *Carcinomyces* spp. seem to be of two types, one of which is aleuriospore-like and is here referred to as chlamyospore (Figs 25, 26: arrows), the second being blastoconidia (Fig. 24: arrow; Fig. 32). These types of conidia differ from zygoconidia, although the latter is certainly blastogenously produced. Further, tremelloid haustoria could not be found in species of *Carcinomyces* but haustorial hyphae were observed (Figs 25, 28, 31, 33: double arrows). Also, the basial morphology is quite distinct, at least in those species which lack horn-shaped sterigmata and have basidiospores which are almost symmetrically attached (Figs 24, 25, 26, 30, 31). Finally, there is a peculiar yeast type growth in the generic type, *Carcinomyces effibulatus* (Figs 27, 29), with slender cells similar to those in *Exobasidium* (Blanz 1977, 1978) and thus differing markedly from the tremelloid budding in *Syzygospora alba* (Figs 18, 21). It has yet to be determined whether or not *Carcinomyces mycetophilus* and *Christiansenia tumefaciens* possess this characteristic or not.



Figs 24–29. *Carcinomyces effibulatus*. Figs 24–26. Generative hyphae with different developmental stages of basidia. Fig. 24. Arrow: blastoconidiophore; budding basidiospore. – Fig. 25. Arrow: chlamydospore; double arrow: haustorial cell. – Fig. 26. Upper left corner: budding basidiospore; arrow: chlamydospore? – Fig. 27. Yeast stage in pure culture. – Fig. 28. Big host cells attacked by haustoria (double arrow) of the parasite. – Fig. 29. Yeast stage isolated of non hypertrophied *Collybia dryophila*. – Figs 30–33. *Carcinomyces mycetophilus*. Fig. 30. Basidiospore attachment the sterigmata; basidiospore budding. – Fig. 31. Generative hyphae with different developmental stages of basidia; basidiospores. – Fig. 32. Blastoconidiophores. Fig. 33. Host hyphae with attached haustorium (double arrow).



However, the above features clearly indicate that *Christiansenia pallida* and *Syzygospora alba* are sufficiently distinct as to be placed in separate genera.

On the other hand, some highly important similarities are evident among the three genera. All species are mycoparasites of Basidiomycetes. The host-parasite-interaction is established by haustoria penetrating into the cells (Figs 7, 8, 38). A hypertrophic growth, often macroscopically visible as galls, is the peculiar host response to species of *Syzygospora* and *Carcinomyces*. All species bear conidial stages though these are distinct in ontogeny and morphology.

Another significant element which was examined during our investigations was the septal pore apparatus. Dolipores without parenthesomes (Figs 11, 34–37) were found in *Christiansenia pallida* and *Carcinomyces effibulatus* and can be assumed for *Syzygospora alba* (Oberwinkler & Lowy 1981). All these characteristics together illustrate and justify a natural grouping of the taxa presented in this report.

According to Ginns & Sunhede (1978) 3 species can be recognized as parasites on *Collybia dryophila*. All cause identical tumors on the host. However, the authors found adequate microscopic characters which permit sufficient specific distinctions.

In 1879 Peck described *Tremella mycetophila* as a parasitic fungus growing on *Collybia dryophila*. Burt (1901) recognized some similarities of the parasite with species of the genus *Exobasidium* and consequently transferred the parasite to this genus. However, he (Burt 1915) later interpreted the galls of *Collybia dryophila* as a teratological growth of the mushroom. Ginns & Sunhede (1978) proposed the transfer of this species to the genus *Christiansenia*. In their treatment the latter authors described two more species, *Christiansenia effibulata* Ginns & Sunhede and *Christiansenia tumefaciens* Ginns & Sunhede; they were of the opinion that all 3 taxa are closely related. We agree with this interpretation based upon important identical features, e.g. mycoparasitism, lack of basidiocarps, hyphal structures and measurements, characters of basidiospores, and ontogeny and characteristics of conidiophores and conidia. *Christiansenia tumefaciens* is like *Carcinomyces mycetophilus* in being fibulate (Figs 40, 41, 43, 45). However, this is the only species in the genus which shows a definite asymmetrical attachment of the basidiospores on sterigmata (Ginns & Sunhede 1978, and Figs 40–43); therefore hymenomycetous spore abstriction is indicated.

To the best of our knowledge, no other basidiomycetous genus contains both hymenomycetous and gasteroid species, i.e., with abstricted or passively released basidiospores. It must be considered, however, that such characteristics are not commonly carefully studied. A breakdown of the abstriction mechanism in hymenomycetous species can be occasionally demonstrated in fruiting cultures, an example of which was treated in detail by Watling (1971). At present only the type col-

lection of *Christiansenia tumefaciens* is known. Though this material is well developed, further specimens should be available for determining the characteristics of this species. Therefore we are not yet prepared to transfer the taxon to another genus.

The following new combinations are proposed:

***Carcinomyces effibulatus* (Ginns & Sunhede) Oberw. & Bandoni comb. nov.**

Basionym: *Christiansenia effibulata* Ginns & Sunhede, Bot. Notiser 131: 168 (1978).

***Carcinomyces mycetophilus* (Peck) Oberw. & Bandoni comb. nov.**

Basionym: *Tremella mycetophila* Peck, Rep. New York State Museum 28: 53 (1879).

*Carcinomyces effibulatus* is easily separated from *C. mycetophilus* and *Christiansenia tumefaciens* by its lack of clamps (Figs 24–26) and the mainly two-sterigmate basidia (Figs 24–26). This species is further characterized by the morphologically and functionally gasteroid basidia with symmetrically placed basidiospores. This unusual variation was correctly interpreted by Ginns & Sunhede (1978) and confirmed in the present contribution by the study of living fungi. However, we were not able to elucidate the nuclear behavior of the basidia which we interpret as such because of their general morphology.

We had no living specimens of *Carcinomyces mycetophilus* available; therefore we can only refer to some morphological features of the basidiospores and sterigmata (Figs 30, 31). We are inclined to agree with Ginns & Sunhede (1978) that active spore liberation does not occur in this species. The spore attachment to the sterigma favors such an interpretation.

### **Mycoparasitism**

Though there are mycoparasitic species known from the Homobasidiomycetes, many more such fungi are found in the Auriculariales and Tremellales. Many species of the genus *Tremella* are parasites of other fungi and several grow on Basidiomycetes. There are conspicuous species, like *Tremella aurantia* Schw. and *Tremelloidea* (Berk.) Mass. on *Stereum hirsutum* (Willd. ex Fr.) S. F. Gray s. lat. and *T. encephala* Pers. ex Pers. on *Stereum sanguinolentum* (A. & S. ex Fr.) Fr. (Bandoni 1961). *Aleurodiscus amorphus* (Fr.) Schroet. is infected by the small, pustulate species, *Tremella mycophaga* Martin; the closely related species, *T. simplex* Jacks. & Martin (Martin 1940, Reid 1970) occurs on *Aleurodiscus tsugae* Yasuda. *T. parasitica* Fr. was reported from Clavariaceae (Saccardo 1888) and *T. versicolor* Berk. & Broome (1854) as growing on *Corticium* species. Fi-



Figs 34–38. TEM-micrographs of *Carcinomyces effibulatus*. All bars equal 1  $\mu\text{m}$ . Bar of Fig. 34 corresponds also for Fig. 35 and that of Fig. 36 to Fig. 37. Figs 34–37. Dolipores. – Fig. 38. Haustorium (arrow) attached to a host cell. – Fig. 39. TEM-micrograph of a median section of *Collybia dryophila*; bar equals 1  $\mu\text{m}$ .

nally, there are intrahymenial parasites, such as *T. obscura* (Olive) Christ. in *Dacrymyces* species (Olive 1946, Christiansen 1959, McNabb 1964) and *Sebacinia penetrans* Hauerlev (1979), with tremelloid affinities, also in *Dacrymyces* species. *Tetragoniomyces uliginosus* (Karst.) Oberw. & Bandoni (1981), the type and only species of the genus (Tetragoniomycetaceae; Tremellales) develops in sclerotia of *Rhizoctonia*.

The host-parasite-interaction of these species is realized by haustoria which may penetrate the host cells. Morphologically the haustorial type is highly characteristic: small subglobose cells subtended by basal clamps form apical, thread-like and irregularly bent outgrowths which are capable of penetrating the host cells. In *Tremella rhytidhysterii* Bezerra & Kimbrough (1978), a parasite of *Rhytidhysterium rufulum* (Spreng.) Speg., the close interaction with the host has been demonstrated by electron microscopy. In *Tetragoniomyces uliginosus*, haustorial filaments, closely attached to the host cells have been illustrated (Oberwinkler & Bandoni 1981), and the penetration of the haustorium into the host was demonstrated by TEM (unpubl. data).

Morphologically identical haustoria are present in *Christiansenia pallida* (Hauerlev 1969, Boidin 1970, Michelitsch 1980, and Figs 2–8) and in *Syzygospora alba* (Oberwinkler & Lowy 1981, and Figs 15–18). It is striking that *Filobasidium floriforme* (Olive 1968) and *Filobasidiella neoformans* (Kwon-Chung 1976) produce similar tremelloid haustoria. We know from our own studies that *Platygløea fimetaria* (Schum. ex Pers.) v. Höhnelt also possesses this haustorial type.

In Figs 7 and 8 the penetration of the haustorium into the host cell is shown by TEM-micrographs of median sections. It appears that a comparatively narrow penetration neck is formed and that inside the host cell the parasitic hypha expands again. Furthermore, in this case, the host plasmalemma surrounds the intracellular part of the haustorium.

We conclude from these findings that the specialized cells with the tremelloid haustorium morphology may function likewise in other species where they are present. It can be seen, nevertheless, that many haustoria are not attached to host cells (see Fig. 22) and, additionally, that haustoria are formed in pure cultures without the host. We believe that species with such haustoria may at least be potentially parasitic, even though a host is not known, e.g. *Tremella mesenterica* Fr.

The unique haustorial type is certainly of high taxonomic importance and may also be used for suprageneric classification.

The parasitic interactions of *Carcinomyces* species with *Collybia dryophila* are not well understood. Ginns & Sunhede (1978) found "no evidence that the parasites penetrate the host cells". In *Carcinomyces effibulatus*, we found narrow, ramified parasite hyphae with pointed ends which were attached to the host cells (Fig. 38). However, these structures did not show the

tremelloid haustorial morphology. Also, in *Carcinomyces mycetophilus* a clear morphological interaction of species could be seen in spite of the old herbarium material (Fig. 33: double arrow). With the aid of phase-contrast we were able to detect haustorial organs in *Christiansenia tumefaciens* (Figs 43–45). These structures resemble the tremelloid haustorial type to some extent.

Short terminal cells which are rich in cytoplasmic contents and which are formed as hyphal branches (Figs 25, 31: double arrows) are interpreted by Ginns & Sunhede (1978) as possible organs for obtaining nourishment by the parasite.

More detailed studies are certainly necessary to understand whether the haustorial organs of the *Christiansenia-Syzygospora*-group and those of the *Carcinomyces* species are homologous or not.

## Morphology including ultrastructure

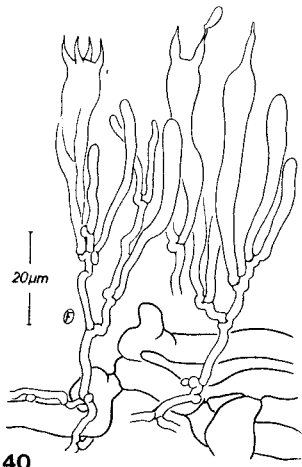
### Hyphae, septa and septal pores

In all species investigated in this study, uniform hyphal systems with thin-walled cells were found. Most cell walls are partly gelatinized, a fairly widespread character among heterobasidiomycetous taxa. This gelatinization is responsible also for the consistency of the fruitbodies which are soft gelatinous in living condition and hard, horny when dried. There is a continuous intergrading series from scattered hyphae growing in host fruitbodies and forming inconspicuous layers on host surfaces (Figs 3, 6, 24, 25, 31, 40, 42) to pustulate (Fig. 1) and even cerebriform, multilacunar, tremelloid basidiocarps (Figs 13, 14).

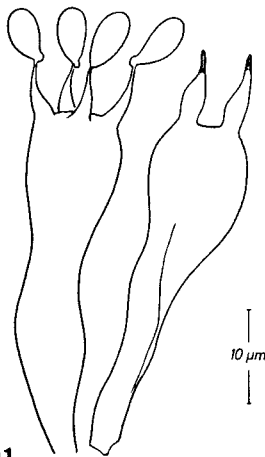
Typically, the septa are fibulate. Only one species, *Carcinomyces effibulatus* (Figs 24–26), lacks clamps and its basidia are typically two-sterigmate, the cells appearing to be dikaryotic (Figs 25, 26). Ginns & Sunhede (1978) understandably compared this with a similar situation in *Tremella mycophaga* (fibulate, basidia four-sterigmate) and *T. simplex* (efibulate, basidia two-sterigmate).

We studied the ultrastructure of the septal pore apparatus in *Christiansenia pallida*, *Syzygospora alba* and *Carcinomyces effibulatus*. Only the latter species could be fixed in a living condition; for *Christiansenia pallida*, approximately one year old herbarium material was used and the collection of *Syzygospora alba* was already 5 years old when it was fixed for TEM-studies. The latter species yielded only poor results which are not reproduced by illustrations here.

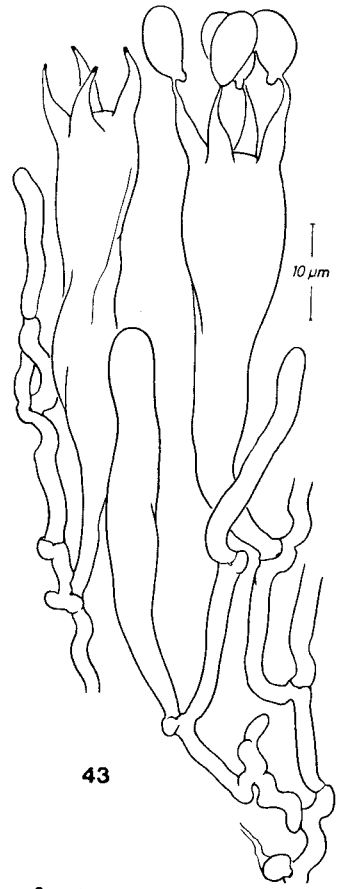
*Christiansenia pallida* and *Carcinomyces effibulatus* agree almost completely in ultrastructural differentiation of the septal pore apparatus (Figs 11, 34–37); it appears to us that *Syzygospora alba* also shares the same features. Most characteristic is the lack of parentheses in these pores. Median sections show also striated bandings which occlude the pore channel



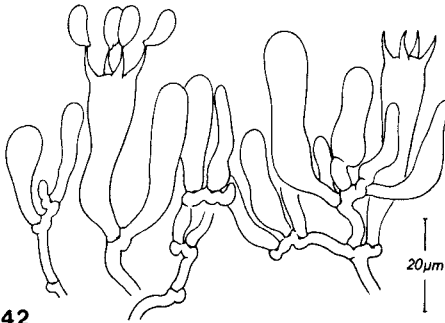
40



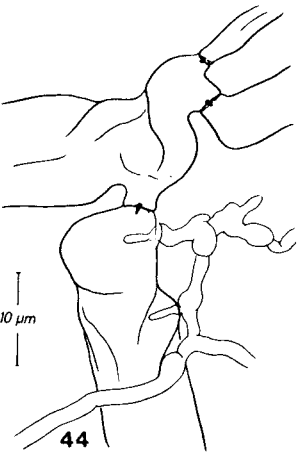
41



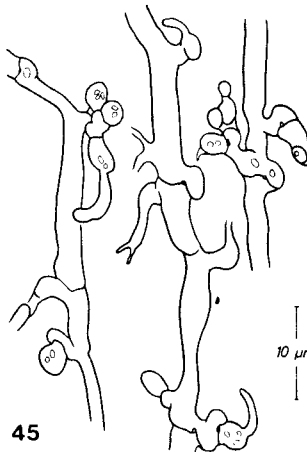
43



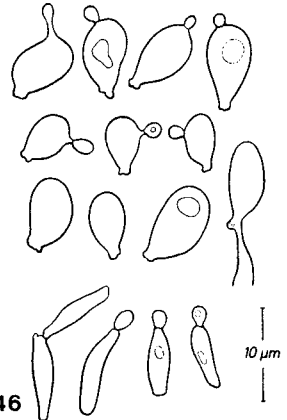
42



44



45



46

Figs 40–46. *Christiansenia tumefaciens*. Figs 40, 42, 43. Generative hyphae with different developmental stages of basidia. – Fig. 40. Big host cells surrounded by generative hyphae of the parasite. – Fig. 41. Four-sterigmate and two-sterigmate basidium. – Fig. 44. Host cells attacked by hyphae of the parasite. – Fig. 45. Haustoria. – Fig. 46. Basidiospores; budding basidiospores (above); young basidiospore attached to sterigma (to the left); budding yeasts (below).

orifices. Comparable dolipores are already known in *Filobasidium floriforme* (Moore & Kreger-van Rij 1972), *Filobasidiella neoformans* (Kwon-Chung & Popkin 1976), and in *F. arachnophila* Khan et al. 1981). Similar structures in septal pores are apparently present also in *Trichosporonoides oedocephalis* (Haskins 1975).

Arches of endoplasmatic reticula often cover the outer dolipore openings (Figs 34, 36, 37). These structures resemble to some extent those which were found by Martinez (1979) in *Moniliella acetoabutens* Stolk & Dakin and *M. suaveolens* (Lindn. ex Lindn.) v. Arx. An essentially similar dolipore construction is present in *Itersoniella perplexans* Derx, as first shown by Kreger-van Rij & Veenhuis (1971) and confirmed by our own unpublished investigations. It is likely that, in some developmental stages, the dolipores of species of some *Tremellas*, e.g. *T. mesenterica* and *T. encephala*, show similar structures. Normally, parentheses of isolated U-cups are formed in *Tremella* (Khan 1976, Moore 1978a, Bezerra & Kimbrough 1978) and in species of *Sirobasidium* (Moore 1978b), *Tetragoniomyces* (Oberwinkler & Bandoni 1981), and *Filobasidium inconspicuum* (unpubl. data).

There are other reports of dolipores without parentheses as in *Tilletiaria anomala* (Moore 1980) or irregular endoplasmatic reticulum arches as in *Entorrhiza casparyana* (Deml & Oberwinkler 1981). The latter examples demonstrate the inadequacy of our present knowledge of septal pore characteristics for making well-founded taxonomic interpretations.

## Basidia

Sexual reproduction plays a major role in the propagation of Basidiomycetes, and at least three essential steps in this process, karyogamy, meiosis, and spore production are bound to one specialized cell, the basidium. The diversity in basidial morphology of extant Basidiomycetes certainly expresses a phylogenetically meaningful variation pattern, a subject that has been discussed several times (e.g. Rogers 1934, 1971, Lindner 1940) and reinterpreted again at some length by Oberwinkler (1964, 1977, 1982).

The species studied in the present report are holobasidiate, though in *Syzygospora alba* (Figs 19, 20) the basidial apex is often partly longitudinally septate, strongly resembling the apex of the basidium in *Tremellodendropsis tuberosum* (Grev.) Craw. (Crawford 1954, Corner 1966, Oberwinkler 1972). Two other genera, *Metabourdotia* (Olive 1957) and *Pseudouluasnella* (Lowy 1964), have apically septate basidia that distinguish these genera from similar taxa that have definite phragmobasidia (*Bourdotia*) or holobasidia (*Tulasnella*).

The long clavate *Syzygospora* basidium is predominantly foursterigmate (Figs 19, 20, 22); in *Christiansenia*, supernumerary sterigmata (mostly 6) are frequent (Fig. 4) on an urniform basidium resembling that of *Sis-*

*totrema*. In both, *Syzygospora* and *Christiansenia*, an active spore discharge mechanism can be assumed because of the asymmetric spore attachment on the sterigmata.

The *Carcinomyces* basidium (Figs 24–26, 30, 31) is also long clavate, with a slight basal swelling. *Carcinomyces effibulatus* and *C. mycetophilus* appear to possess gasteroid basidia, though they are as yet only poorly understood and have to be studied in more detail in living specimens. *Christiansenia tumefaciens* has basidiospores which are obliquely attached to the sterigmata and probably abstricted (Ginns & Sunhede 1978, and Figs 40–43). This is a unique situation, at least within the Heterobasidiomycetes, in which hymenomycetous and gasteroid taxa are so closely connected.

## Dispersal

### Basidiospores and spore germination

Like basidia, basidiospores are also reliable indicators of taxonomic relationships. Hyaline, thin- and smooth-walled, non-amyloid basidiospores, as present in species of *Christiansenia*, *Syzygospora*, and *Carcinomyces*, are highly characteristic for Heterobasidiomycetes. Homobasidiomycetes, however, have a broad range of variation in spore markings, color, and iodine reactions. The typical heterobasidiomycetous repetitive or secondary spores have not been found in the group under consideration, but all species of *Carcinomyces* (Figs 24, 26) and *Syzygospora* (Figs 18, 21) have yeast-like budding of the basidiospores, a germination type not known in the Homobasidiomycetes. The only living material (*Carcinomyces effibulatus*) which we could examine and culture showed yeast-like growth comparable to that found in species of *Exobasidium* (Blanz 1977, 1978). In *Syzygospora*, germination of the spores could occasionally be observed in preserved specimens (Fig. 21), whereas in *Christiansenia pallida*, basidiospore germination has not been observed.

We are convinced that the principal types of basidiospore germination (Oberwinkler 1978), i.e. budding, repetition, conidial formation, and germ tubes, have phylogenetic significance and are therefore also taxonomically important. However, these features must be interpreted as parts of the whole life cycle of each species and cannot be expected to be absolutely invariable criteria. It is noteworthy that secondary spores and/or budding of basidiospores is widely spread in the Heterobasidiomycetes and lacking in the Homobasidiomycetes. Further, it is significant that the earliest ontogenetic stages show these fundamentally different growth patterns. Certainly, one of the major evolutionary problems of the higher fungi has been to establish hyphal growth, the basis for progressive fruit-body development as well as for substrate utilization. Therefore, it is not surprising that only among the

Heterobasidiomycetes are there numerous species with very tiny basidiocarps or with no basidiocarps at all.

### Conidia

Recently, increasing interest has been paid to anamorphs of Basidiomycetes and Kendrick & Watling's survey (1979) will certainly draw further attention to those important aspects of basidiomycetous mitotic dispersal mechanisms. It can be expected that the taxonomy of Basidiomycetes will become strongly influenced when anamorph stages can be adequately compared, i.e. ontogenetic and comparative data are more comprehensively available.

In the fungi discussed here, three systems of conidium formation are found, and these mitotic propagules often are produced simultaneously with the meiospores. Blastoc conidium ontogeny is to be expected in *Carcinomyces* because basidiospore yeast budding in *Syzygospora* and *Carcinomyces* occurs in this mode.

The unique zyoconidia in *Syzygospora alba* and *Christiansenia pallida* also develop by blastoc outgrowth from adjacent mononucleate conidiogenous cells (Figs 2, 6, 15). Fusion of these blastoc initials forms the binucleate zyoconidium (Boidin 1970), a propagule which finally is released from the supporting bridges. Kendrick & Watling (1979) used the term "isthmospore" for this unusual conidium, also described, but not illustrated, for the aricularioid fungus, *Cystobasidium sebaceum* Martin & Couch (Martin 1939).

Hyphae which disarticulate at the septa and thus perform a thallic-arthric conidial formation were reported by Ginns & Sunhede (1978) for *Carcinomyces* species, but Kendrick & Watling (1979) suspect a blastoc development by interpreting the authors' illustrations. Dikaryotic cells, still attached to the supporting hyphae (Figs 25, 26: arrows) apparently are released from the conidiophore by lysis along a layer between the two cell walls. When released, these conidia have a broad, truncate base and thus differ from the blastoc conidia.

### Taxonomic conclusions

The available data on *Christiansenia*, *Syzygospora* and *Carcinomyces* species can be used to some extent for a taxonomic interpretation of these taxa. The most important features are: a) mycoparasitism, b) haustoria, c) dolipores without parentheses, d) holobasidia, e) budding of basidiospores, f) conidial propagation.

Species of the family Filobasidiaceae have several significant characters in common with the members of the *Carcinomyces* complex. Both contain parasites which mostly have morphologically and certainly also functionally similar haustorial organs. The septal pores in taxa of the two groups are ultrastructurally identical, and thus represent, so far as known, a unique type.

Further, spore germination by budding occurs in both groups and conidial formation is also commonly present. The meiosporangia are holobasidiate; the mode of basidiospore development, however, is highly diverse, reaching from typical hymenomycetous to characteristic gasteroid patterns.

Because of the obviously different basidial morphology, basidiospore development and, in part, dissimilar spore discharge, we see no justification for including the *Carcinomyces* group in the Filobasidiaceae.

The Exobasidiaceae is another taxon with several comparable characteristics: they are parasitic, but on higher plants, often inducing gall formation by the host, develop haustoria, and have long, clavate holobasidia with a variable number of short, stout sterigmata. The basidiospores are capable of producing a yeast phase, and (micro-) conidia are frequently present. Yet, there are important differences in the morphology of the haustoria, the simple pore type, the incurved position of the basidiospores on the sterigmata, the mature transversely septate spores, and their germination by conidia. However, this group is still far from being well understood, especially in regard to the tropical relatives, e.g. the Brachybasidiaceae.

In addition to holobasidiate taxa, Phragmobasidiomycetes should also be considered for this comparison. There are significant similarities of several important characteristics in the Carcinomycetaceae and Tremellaceae. These include mycoparasitism, often of Basidiomycetes, identical haustoria and a similar range in basidiocarp complexity, i.e. no basidiocarp to conspicuous cerebriform types. The basidiocarp may have a similar gelatinous consistency, the basidiospores germinate by budding, and anamorphs are commonly present. However, the *Tremella* septal pore has several U-shaped parentheses cups and the meiosporangia usually are cruciately septate. Nevertheless, the dolipore channel with electron dense banding is present in some species of the *Tremella* group, or at least it can be found in some developmental stages. We also know that taxa closely related to *Tremella* have holobasidia, but these are commonly one-sterigmate.

It can be expected that a number of fruitbody-less, intrahymenial parasitic representatives are still to be discovered, and that they may again extend the variation of the characters discussed above.

We conclude that the Carcinomycetaceae are apparently related to the Filobasidiaceae. It might be appropriate to include both families in the Cryptococcales. On the other hand, obvious relations with the Tremellales cannot be ignored; several important characteristics also are shared with the Exobasidiaceae.

Finally, we conclude that the Carcinomycetaceae is a family of Heterobasidiomycetes, rather than of the Aphyllophorales. Likewise, we regard the Filobasidiaceae as a heterobasidiomycetous taxon.

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