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# *Rhynchogastrema* gen. nov. and *Rhynchogastremaceae* fam. nov. (*Tremellales*)*

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## Summary

Descriptions are provided of new heterobasidiomycetous taxa, *Rhynchogastrema coronata* gen. et sp. nov., and *Rhynchogastremaceae,* fam. nov. The taxa are characterized by hyphal septa with dolipores and parenthesomes consisting of separate cupulate elements, tremelloid haustoria, urniform, apically partly and cruciately septate basidia, with sessile basidiospores which remain attached to the meiosporangia. The taxonomic position in the *Tremellales s.str.* is discussed. The type material was obtained from an agriculatural loess soil.

Key words: *Rhynchogastrema coronata* – *Rhynchogastremaceae* – *Tremellales* – Haustoria – Mycoparasitism – Basidiomycetous yeasts – Soil microbiology

## Introduction

In recent surveys, *Bandoni* (1984, 1987) has restricted the *Tremellales* to taxa with dolipores and parenthesomes composed of several separate cupulate elements. Three families have been accepted. The *Tremellaceae* comprise the genera *Holtermannia, Sirotrema, Tremella,* and *Trimorphomyces,* with more than 200 species in total. Two genera, *Fibulobasidium,* and *Sirobasidium* are included in the *Sirobasidiaceae* which cover c. 12 species. The *Tetragoniomycetaceae* encompass the monotypic *Tetragoniomyces uliginosus.* Many species of the *Tremellales* s.str. have an ontogenic yeast stage. Tremelloid haustoria are present in most taxa of the *Tremellaceae* and *Tetragoniomycetaceae.* The delimitation of the *Tremellales* s.str. and the *Auriculariales* sensu Bandoni (*Bandoni,* 1984; *Oberwinkler,* 1985) seems clear on the basis of the septal pore apparatus. However, it is not convincing to keep the *Filobasidiales* as a separate order (*Oberwinkler,* 1987). The *Filobasidiaceae* have been surveyed taxonomically by *Kwon-Chung* (1987). Three genera, *Cystofilobasidium, Filobasidiella,* and *Filobasidium* have been accepted, a taxonomic rearrangement proposed by *Oberwinkler* et al. (1983). After identifying *Syzygospora alba* as a mycoparasitic heterobasidiomycete (*Oberwinkler* and *Lowy,* 1981), *Oberwinkler* and *Bandoni* (1982 b) have revised related taxa, recognizing 3 genera, *Carcinomyces, Christiansenia,* and *Syzygospora* which were grouped in the *Carcinomycetaceae.* Accepting only the genus *Syzygospora, Ginns* (1986) has monographed 8 species.

Here we report on the isolation of a tremellaceous fungus from a farm land loess soil, detailed studies of its life history in axenic culture, and comparative investigations. We propose a new species considered to belong to a new genus and a new family.

* Part 60 of a series, "Studies in Heterobasidiomycetes"

*List of used nonstandard abbreviations,* also explained in the text: LM: Light microscopy; MEA: Malt extract agar; SNA: Synthetic nutrient agar; TEM: Transmission electron microscopy.

## Materials and Methods

The fungus was isolated from a farm land loess soil (Fed. Rep. Germany, Niedersachsen, Ahlum near Braunschweig, 18.4.1988). It grew from a soil particle on synthetic nutrient agar

(SNA; *Nirenberg,* 1981) at room temperature. A live culture has been deposited in the microbial collection of the Biologische Bundesanstalt at Berlin-Dahlem (Nr. 65155), a dried specimen (typus) in the Botanical Museum at Berlin-Dahlem. Specimens other than the type have been deposited in the herbaria of Tübingen and Munich.

For transmission electron microscopy cultures from SNA and malt extract agar (MEA; *Pitt,* 1979) were fixed after *Karnowsky* (1965) and subsequently in 2% Osmium tetroxide buffered with 0,2 m Cacodylate, contrasted en bloc in uranylacetate (0,9%) and embedded in low viscosity epoxy resin medium (*Spurr,* 1969; Serva). Ultrathin sections were contrasted with lead citrate (*Reynolds,* 1963) and examined with a Siemens Elmiskop CT 150.

For germination tests basidiospores were detached by dipping cultures on SNA or MEA covered with a dialysis membrane to facilitate light and electron microscopy. Germination was examined after one and after a few days. Yeast colonies were streaked on nutrient agar. Single colonies were used for crossing experiments. The ability to grow in both the mono- and dikaryotic phase was also tested at 5 °C and at 37 °C.

## Results

*Rhynchogastrema* Metzler et Oberwinkler, gen. nov.

Etym.: Rhynchos (Gr.) – beak, gaster (Gr.) – body, belly, *Tremella.* Genus Heterobasidiomycetum. Hyphae hyalinae, tenuitunicatae, fibulatae, cum haustoriis propriis tremelloideis. Probasidia plusminusve subglobosa inde longicolla et apicaliter partim septis cruciatis divisa. Basidiosporae sessiles, Gasteromycetum modo non eiectae. In cultura pura cellulae gemmantes adsunt.

Typus generis: *Rhynchogastrema coronata* Metzler et Oberw., opus ipsum.

*Rhynchogastrema coronata* Metzler et Oberwinkler, sp. nov.

Etym.: coronata (Lat.) – crowned, wreathed.

In cultura pura carposomata nulla vel synnematoidea, mature rufobrunnea. Hyphae laxe vel dense aggregatae, non gelatinosae, 2.5–4 µm raro ad 5 µm in diam., irregulariter ramosae, haustoriis propriis tremeloideis, basidia dispersa vel in greges conferta gerentes. Basidium urniforme, plusminusve pendunculatum, basaliter fibulatum, 5–7 × 15–30 µm, solum in apice cruciatim et in parte septatum. Basidiosporae globosae crassitunicatae, tuberculatae, inamyloideae, 2–3 µm in diam., denique gutta subalutacea persistentique circumclusae, saepe tetradines formantes. Cellulae fermenti ovales ad fusiformes an irregulariter cylindraceae, rare globosae 4–6 × 5–12 µm.

Habitatio: Fungus ex terra agriculturae isolatus (Germania, Niedersachsen, Braunschweig, Ahlum).

Typus: Cultura exsiccata in museo botanico Berolina-Dahlemense.

Cultura viva No. 65155, "Biologische Bundesanstalt für Land- und Forstwirtschaft, Institut für Mikrobiologie" et in TUB.

In axenic culture, *R. coronata* develops a loosely interwoven hyphal mat which finally forms irregular strings of synnematous appearance. Hyphae dikaryotic, thin-walled, smooth, hyaline, not gelatinous, mostly 2.5–4 (–5) µm wide, with clamps (Figs. 1–5). Septa with dolipores and parenthesomes comprising cup-shaped vesicles of the *Tremella*-type (Figs. 11–13). Typical haustorial branches are formed consisting of a sphaeroidal basal part of c. 2 µm in diameter and a slender distal part of c. 0,5 × 5–12 µm. Usually they originate from clamp connections (Figs. 1,3), but also from intercalary positions (Fig. 10). In the presence of a potential fungal host the haustoria fuse with it (Fig. 9). Basidia often in clusters, arising from clamps; basidium with a basally swollen probasidium, distally tapering into a neck of variable length, in total 5–7 × 15–30 µm; apex of the neck partly cruciately septate; septa extending only 1–3 µm backwards into the neck (Figs. 2c, 3, 7, 8). Basidiospores sessile, mostly 4, rarely 1–6, each originating from one of the apical neck segments, exceptionally in lateral positions, maturing globose, 2–3 µm in diam., thick walled, wall yellow to brown, irregularly

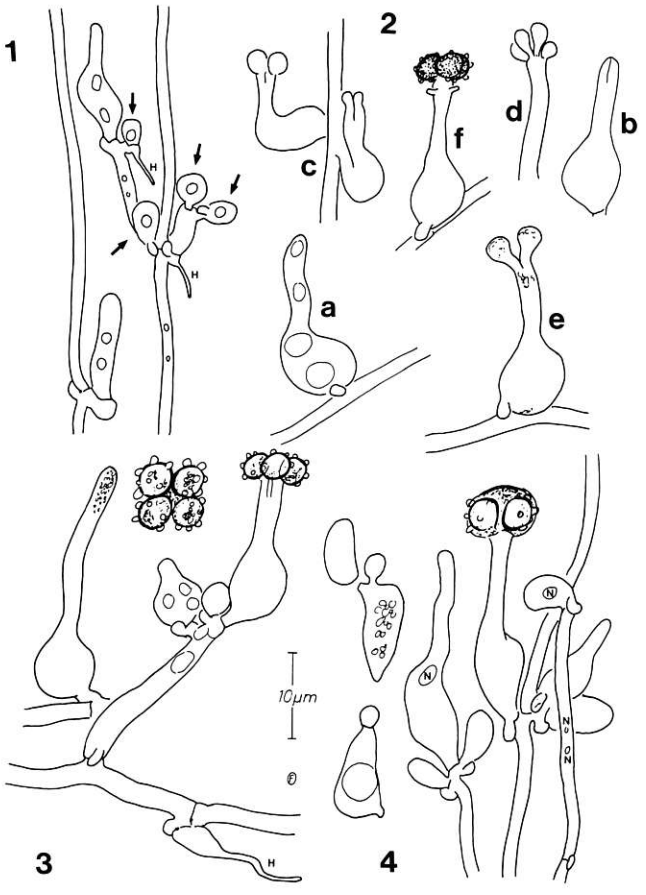



Fig. 1–4. Different stages of basidial development and hyphae; H: Haustorium, N: Nucleus. (1) Young basidial stages, Probasidia after karyogamy (arrows). (2) Basidial development. a: Young basidium before spore differentiation; b, c: Partial apical longitudinal septation; d, e: Formation of young spore initials; f: Mature basidium with ornamented spored and basidial outgrowths below. (3, 4) Different stages of basidial development, partly with mature spore tetrads. (4) (left): Yeast cells. Scale bar = 10 µm.

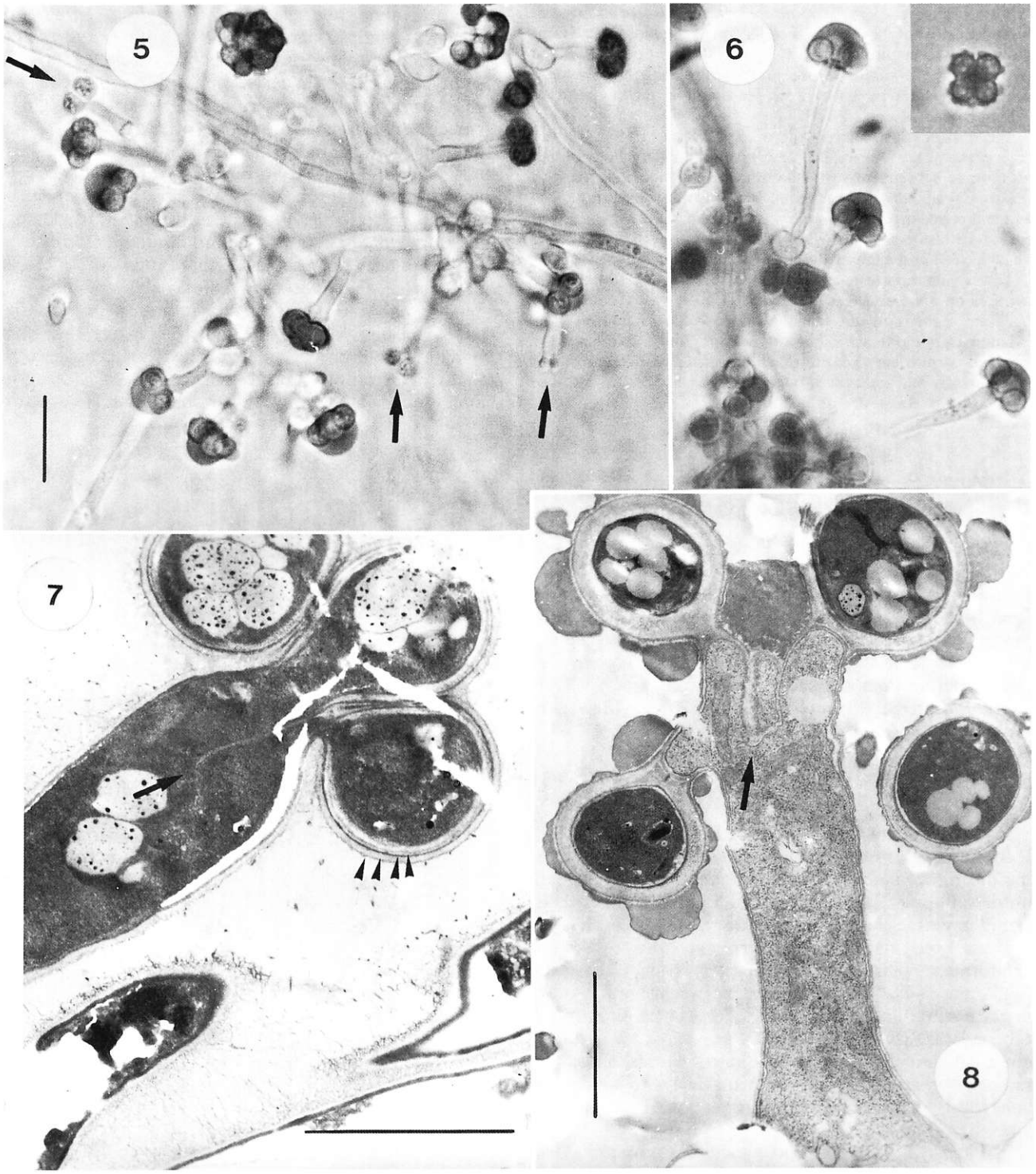



Fig. 5–8. (5, 6) Groups of basidia in different developmental stages; spore initials (arrows); mature spore tetrads are often surrounded by a solidifying droplet of sticky, pigmented material. LM. Scale bar = 10 μm. (6) Basidial ventres partly stained with cotton blue. Insert: mature spore tetrad. (7) Spore initials with multilayered walls (arrowheads); partial longitudinal septation (large arrow). TEM. Scale bar = 2 μm. (8) Mature basidium with thick-walled ornamented spores; longitudinal septation (arrow). TEM. Scale bar = 2 μm.

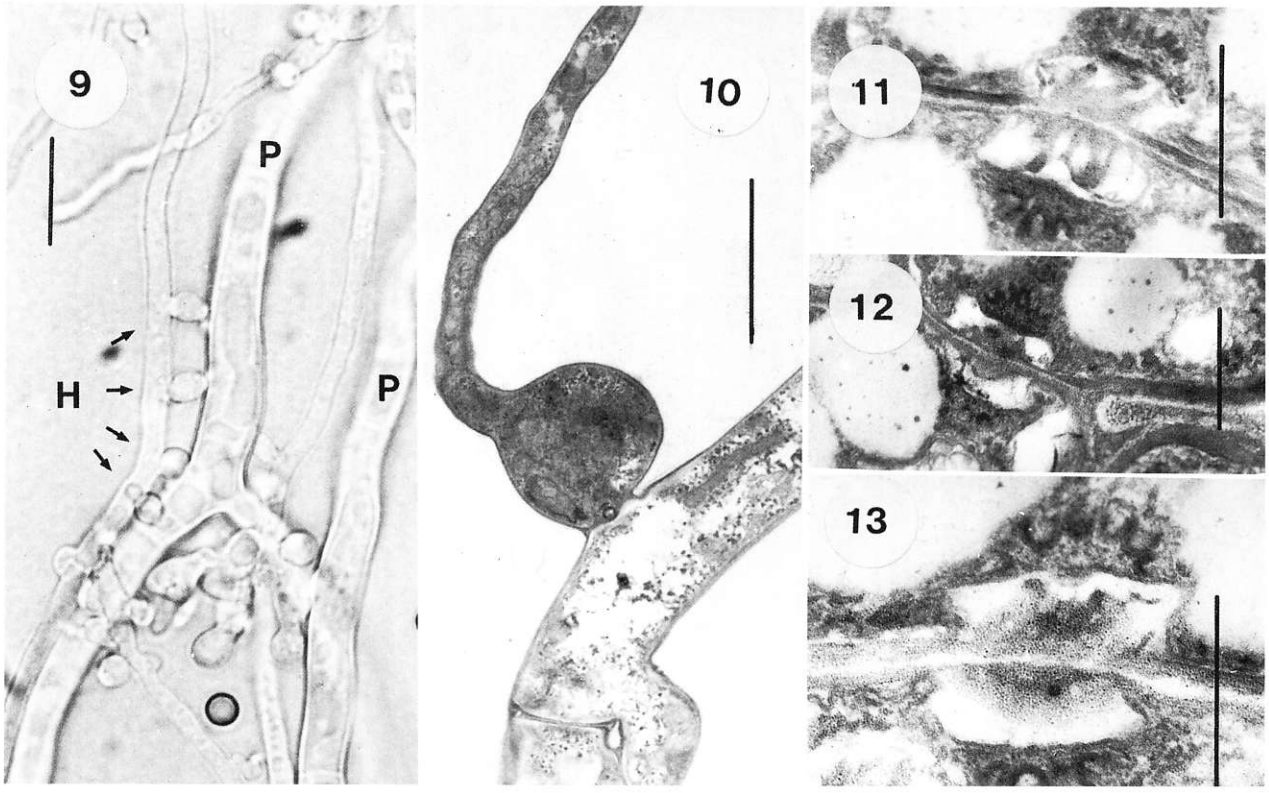



Fig. 9–13. (9) *Rhynchogastrema coronata* growing along with Penicillium hordei (P) obviously attacking it with haustoria (H). LM. (10) Haustorium inserted at a clamped hypha. TEM. Scale bar = 2 µm. (11–13) Dolipores with cup shaped parenthesomal elements. TEM. Scale bars = 0,5 µm.

warted, warts blunt. During spore maturation yellowish-brown, persistent exudate is produced which surrounds the spores, often glueing them together as tetrads of 4–7 µm in diameter. Mature spores remain attached to old basidia.

Spores germinate readily on moist substrates. The germ tube often breaks through beside the apiculus (Fig. 16). On MEA, the monokaryotic stage starts often with a primary vesicle (Figs. 14, 17 left, 23a, d, e), from which a yeast colony may originate. Yeast cells are ellipsoidal to fusiform or cylindroidal (Figs. 20, 21, 24). They often sprout along with a more or less pronounced mycelium of an irregular diameter, which easily fragments (Figs. 20, 21). The yeast cells are encapsuled with mucilage which appears filamentous in TEM (Figs. 16, 22).

If, as usual, two or more spores of a tetrad germinate simultaneously, the germ tubes fuse spontaneously and clamped hyphae of a more or less regular diameter start to grow (Figs. 15, 18, 23b, c, e). Crossing compatible yeast strains results in formation of clamped mycelium (Fig. 25). The compatibility system was not identified.

Mycelia and yeasts grow well at room temperature but scarcely at 5° and not at 37 °C during two weeks.

In contrast to the known taxa in the *Tremellales, R. coronata* has a unique basidial morphology. Also warted and pigmented basidic spores are not known in any other taxon of this order. Therefore a new family is proposed to accomodate the genus.

*Rhynchogastremaceae* Oberwinkler et Metzler, fam. nov.

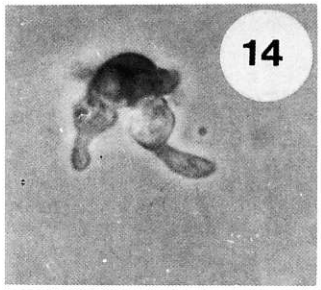
Heterobasidiomycetes; meiosporangiis in parte cruciatim septatis, Gasteromycetum modo basidiosporisque non eiectis. Septa hypharum doliporis parenthesomatibus tremelloideis perforata.

Typus familiae: *Rhynchogastrema* Metzler et Oberw., opus ipsum.

The *Rhynchogastremaceae* represent a family of the *Tremellales* as it shares the common characteristics of the tremelloid septal pore apparatus and haustorial type. Also the presence of a yeast stage is in accordance with that taxonomic interpretation.

## Discussion

The septal pore apparatus of *R. coronata* (Figs. 12, 13) is similar to the type found in a *Tremella* sp. by *Khan* (1976), and in *Tetragoniomyces uliginosus* (Karst.) Oberw. et Bandoni (*Oberwinkler* and *Bandoli,* 1981). In contrast to *Sirobasidium magnum* Boedijn (*Moore,*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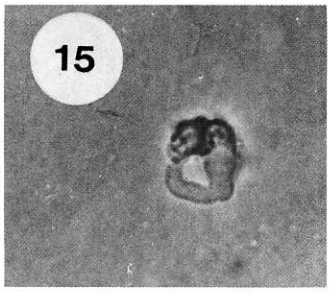
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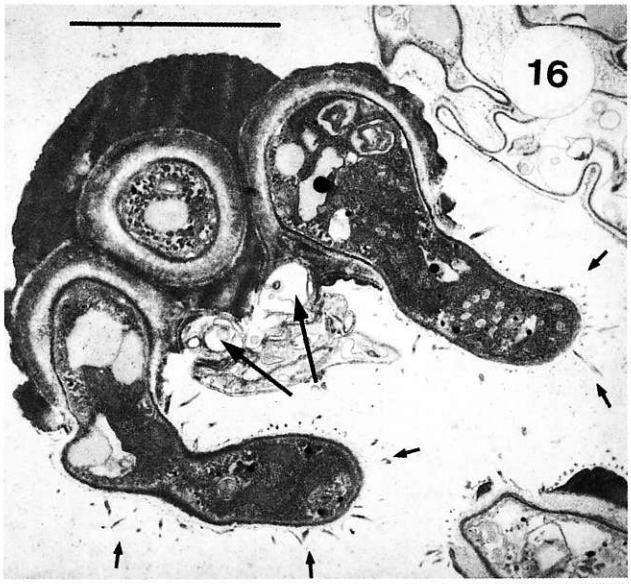
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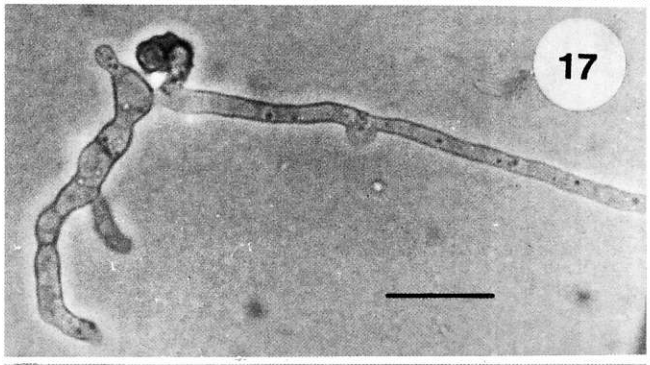
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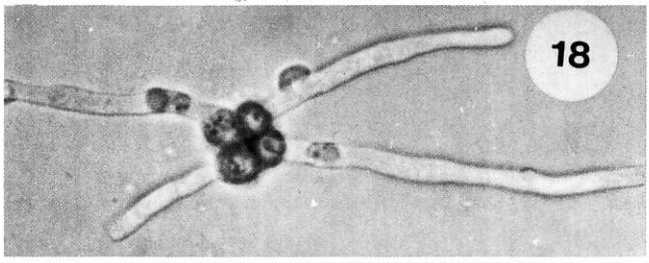
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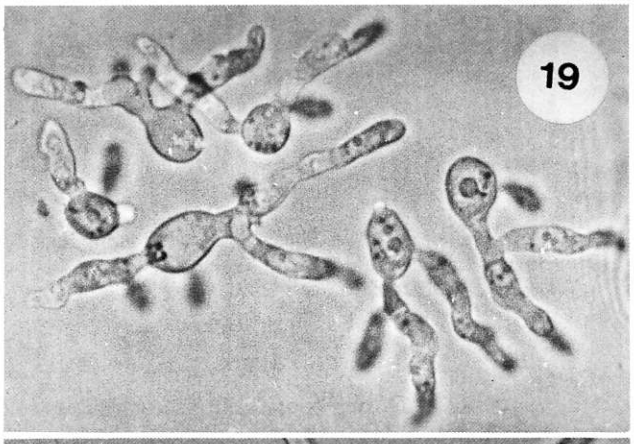
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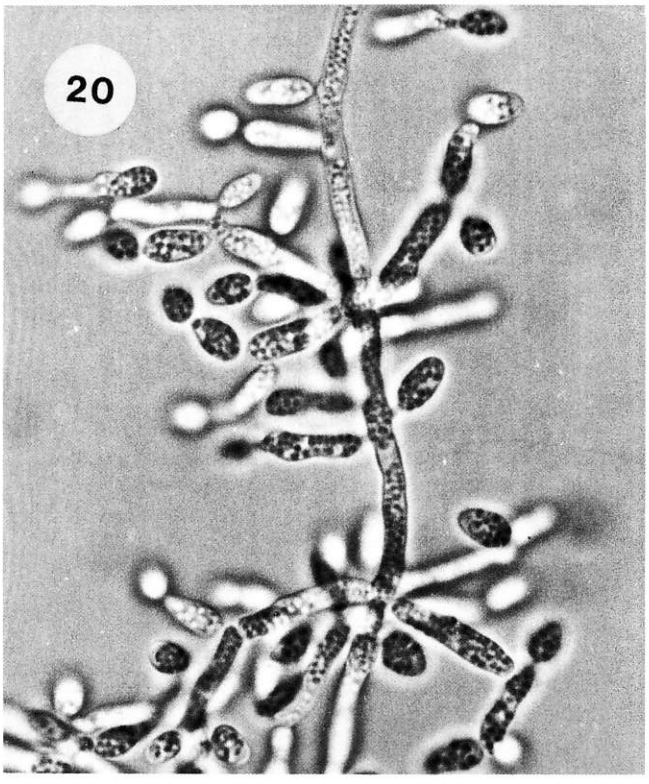
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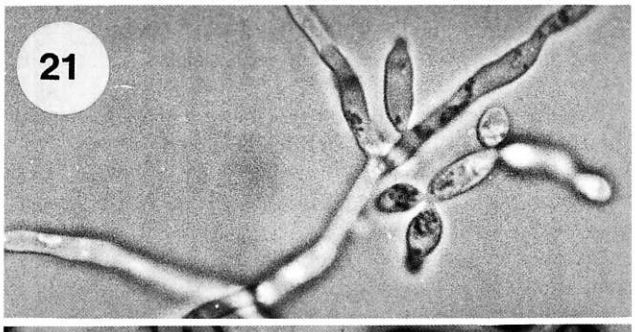
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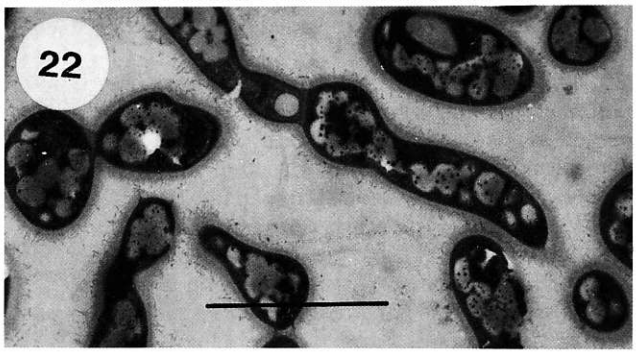
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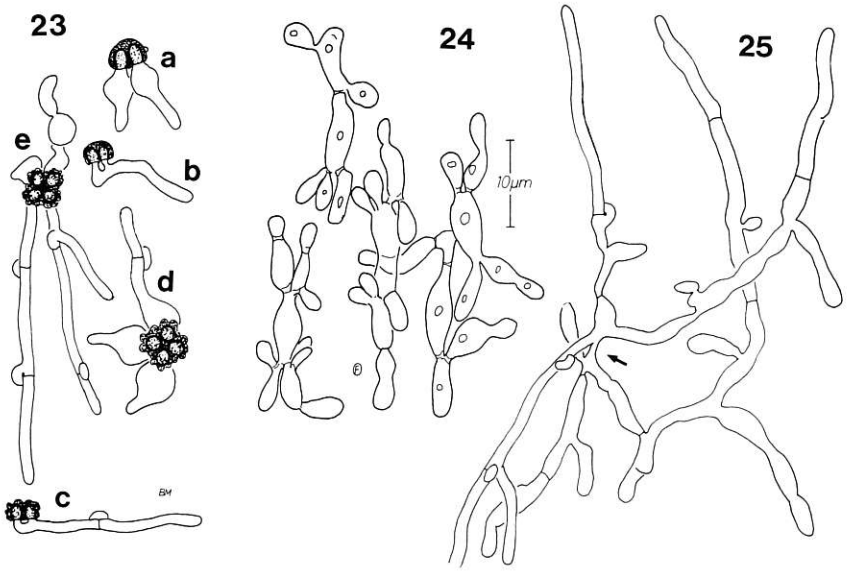


Fig. 23–25: (23) Different stages of germination of spore tetrads. a, d, and e grown on malt extract agar, b and c from synthetic nutrient agar. a: vesiculate primary germ tubes; b, c: fusion of two germ tubes and subsequent formation of a clamped hypha; e: both haploid (above) and dikaryotic phase (below) growing from one tetrad. (24) Yeast cells. (25) Artificial crossing: Fusion of two compatible haploid mycelia (arrow at the probable fusion site) and subsequent growth of clamped mycelium.

1978b), and *Tremella globospora* Reid (*Oberwinkler,* 1985; *Berbee* and *Wells,* 1988) the cupulate ampullae of the parenthesome are rather shallow. Also *Filobasidium capsuligenum* Olive has a tremelloid septal pore ultrastructure (*Moore* and *Kreger van Rij,* 1972). The tremelloid septal pore is highly indicative of a natural relationship of *Tremellales* s.str. The *Filobasidiales* are so closely related to the *Tremellales* that they should be included in this order (*Moore,* 1978a; *Oberwinkler,* 1987).

Morphologically, the tremelloid haustorial type (*Oberwinkler* and *Bandoni,* 1982b) (Figs. 1, 3, 9, 10) is highly characteristic. Small, subglobose cells, mostly subtended by basal clamps form apical, thread-like and irregularly bent outgrowths which are capable of penetrating the host cells. Such haustoria are known from species of the *Tremellales* s.str., *Tremella mycophaga* var. obscura (*Olive,* 1947), *T. encephala* (*Bandoni,* 1961), *T. rhytidhysterii* (*Bezerra* and *Kimbrough,* 1978), *Tetragoniomyces uliginosus* (*Koske,* 1972; *Oberwinkler* and *Bandoni,* 1981), *Trimorphomyces papilionaceus* (*Oberwinkler* and *Bandoni,* 1983), and most of the mycoparasitic *Tremella* spp. (*Bandoni,* 1984). In the filobasidiaceous fungi tremelloid haustoria have been reported from *Filobasidium floriforme* (*Olive,* 1968), *Filobasidiella neoformans* (*Kwon-Chung,* 1976, 1987; *Oberwinkler* et al., 1983), *Christiansenia pallida* (*Hauerslev,* 1969; *Boidin,* 1970; *Michelitsch,* 1980; *Oberwinkler* et al., 1982b), *Syzygospora alba* (*Oberwinkler* et al., 1981, *Oberwinkler* and *Bandoni,* 1982b). The unique haustorial structure has been considered to be of high taxonomic importance by *Oberwinkler* and *Bandoni* (1982b). Surprisingly, a similar haustorial type also occurs in *Platygloea peniophorae* (*Olive,* 1947), but has been suggested to be different from that in the *Tremellales* by *Bandoni* (1984). The role of *R. coronata* as a parasite of soil fungi is likely, but needs to be shown by further studies.

The most distinctive features of *R. coronata* are the gasteroid and partly longitudinally septate basidia, and the sessile, thickwalled, tuberculate, yellow to brownish pigmented basidiospores (Figs. 2–8). Partial septation is not known from any species in the *Tremellales* sensu *Bandoni* (1984). However, it occurs in the closely related *Syzygospora alba* (*Oberwinkler* and *Lowy,* 1981; *Oberwinkler* and *Bandoni,* 1982b), *S. solida, S. marasmoidea,* and *S. subsolida* (*Ginns,* 1986). In addition, the following species of several other taxa in the *Heterobasidiomycetes* are known to have partially septate basidia: *Metabourdotia tahitiensis* (*Olive,* 1957; *Oberwinkler,* 1972), *Pseudotulasnella guatemalensis* (*Lowy,* 1964; *Oberwinkler,* 1982), *Tremellodendropsis tuberosum* (resp. Aphelaria tuberosa (*Crawford,* 1954; *Corner,* 1950, 1966; *Oberwinkler,* 1972), *Sebacina* sp. (*Oberwinkler,* 1982), and *Ceratobasidium calosporum* (*Oberwinkler,* 1982). Some of these examples may be interpreted as

Fig. 14–22. (14) Simultaneously germinating tetrads of basidiospores. (15) Fusion of neighbouring germ tubes. LM. (16) Longitudinal section through a germinating spore tetrad; germ tubes covered with fibrous mucilage (arrows); apiculi (arrows) and basidial remnants below. TEM. Scale bar = 2 µm. (17) Growth of both haploid (left) and dikaryotic, clamped hyphae (right); after fusion, the left part probably slipped out of the sporal wall. LM. Scale bar = 10 µm. (18) Growth of dikaryotic, clamped hyphae evidently as a result of a previous plasmogamy immediately below the spore tetrade. LM. (19) Primary haploid colony derived from basidiospores, 24 h after germinating on malt extract agar. LM. (20, 21) Established two week old yeast colony on malt extract agar. LM. (22) Yeast cells with a coat of fibrillar mucilate. TEM. Scale bar = 5 µm.

intermediates between phragmo- and holobasidiate taxa, and thus as evidence for the convergent evolution of holobasidia (*Oberwinkler*, 1982).

Gasteroid basidia occur in many heterobasidiomycetous taxa (*Oberwinkler* and *Bandoni*, 1982a; *Bandoni*, 1984). In the *Tremellales* s.str. they are either distinct features of certain taxa such as the *Sirobasidiaceae*, and *Tremella mayorgae* (*Lowy*, 1977; *Bandoni*, 1984), or they develop occasionally as in *T. translucens*, and *T. microspora* (*Bandoni*, 1984). All species of the *Filobasidiaceae* have gasteroid basidia (*Kwon-Chung*, 1987) and species with transitional stages from hymenomycetous towards gasteroid basidia have been found in *Carcinomyces* (*Oberwinkler* and *Bandoni*, 1982b), or *Syzygospora* (*Ginns*, 1986). Sporogenous cells, morphologically similar to those in *R. coronata*, occur in *Riessia semiophora* (*Fresenius*, 1852). This species is considered to be a basidiomycetous anamorph. *Riessia naumovii* has been described by *Kamyschko* (1961) with a line drawing substituting for type material. His illustration and descriptions (Latin and Russian) do not refer to clamp connections and partially septate basidial apices. Therefore a definite conclusion about the specific identity of *R. naumovii* is impossible, and, consequently, this name has to be considered as a nomen dubium. Dolipores have been reported to have perforated parenthesomes (*Goos* and *Tubaki*, 1973) in *R. semiophora*, thus characterizing it as a member of the Homobasidiomycetes.

Ornamentation and pigmentation of the teliospores of rust and smut fungi, and of the disseminative basidia in *Tetragoniomyces uliginosus* are well known. However, basidiospores with pigmented walls are very rare in heterobasidiomycetous fungi. They are only known from species of the genus *Phleogena* and from *Pachnocybe ferruginea* (*Oberwinkler* and *Bandoni*, 1982a). In addition basidiospore wall ornamentations are exceptional in heterobasidiomycetous species. We are aware only of *Basidiodendron* species which occasionally have warty, but hyaline and thin-walled basidiospores. In contrast, pigmented, thick-walled and ornamented spores occur frequently in many species of different relationships of homobasidiomycetous fungi. However, the ornamentation on the spores of *R. coronata* is a result of solidification of the primarily amorphous exudate of high viscosity. This spore ontogeny differs markedly from that of other fungi with ornamented spore walls which are ornamented during the centripetal thickening of the sporal wall (see e.g. *Bauer*, 1980; *Keller*, 1977; *Littlefield* and *Heath*, 1979).

Morphologically distinct basidiocarps are lacking in culture. Whether they may occur under natural growth conditions is not known. Erect, fasciculate hyphae of synnematous structure develop in older cultures. Basidia are produced abundantly at the periphery of synnemata. Such growth forms resemble young fruiting structures of gastroid, auricularioid species, e.g. *Agaricostilbum* spec. (*Oberwinkler* and *Bandoni*, 1982a, Fig. 1).

*R. coronata* is a dimorphic species. Yeast budding occurs in the monokaryotic phase. As in some smut fungi (*Boekhout*, 1987) also short, easily fragmenting hyphae may develop. These monokaryotic hyphae grow irregularly, whereas the dikaryotic hyphae grow with an even diameter. The dikaryotic stage is initiated by direct fusion of neighbouring germ tubes (Figs. 15, 23b, c) or by crossing of compatible monokaryotic strains (Fig. 25).

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