Colacogloea: a new genus in the auricularioid Heterobasidiomycetes[1]

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A new genus, ***Colacogloea***, is described in the auricularioid Heterobasidiomycetes having simple septal pores. The genus is based on *Platygloea peniophorae*, a mycoparasite of some Aphyllophorales species. It is a segregate from the heterogeneous *Platygloea* s.l. The most important distinguishing features of *Colacogloea* are (*i*) the frequently simultaneous presence of basidial and conidial stages, (*ii*) a dimorphic life cycle including a yeast phase, (*iii*) mycoparasitism by colacosomes, (*iv*) simple septal pores with rounded margins, but without associated electron-opaque bandings and globules, and (*v*) aseptate basidiospores.

Key words: Heterobasidiomycetes, *Platygloea, Colacogloea peniophorae*, mycoparasitism, colacosomes.

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Un nouveau genre, ***Colacogloea***, chez les Hétérobasidiomycètes auricularioïdes pourvus de septations à pore simple, est décrit. Le genre est basé sur le *Platygloea peniophorae*, un mycoparasite chez certaines espèces d'Aphyllophorales. C'est une séparation du genre *Platygloea* s.l. hétérogène. Les caractères distinctifs les plus importants du *Colacogloea* sont (*i*) la présence souvent simultanée des stades basidien et conidien, (*ii*) un cycle vital dimorphique incluant une phase levure, (*iii*) le mycoparasitisme par colacosomes, (*iv*) des pores des septations simples avec marges arrondies, mais sans anneaux et globules opaques aux électrons associés, et (*v*) des basidiospores non septées.

Mots clés : Hétérobasidiomycètes, *Platygloea, Colacogloea peniophorae*, mycoparasitisme, colacosomes.

[Traduit par la revue]

Introduction

When excluding auricularioid taxa with simple septal pores from the Auriculariales Schroeter, Bandoni (1984) remarked that "Auricularioid taxa with simple septal pores present somewhat of a dilemma." One of these taxa is the genus *Platygloea*. The genus was introduced by Schroeter (1887) for three auricularioid species, which differed considerably from *Auricularia* by basidiocarp characteristics. In a preliminary survey of the genus, Bandoni (1956) considered the 23 taxa treated by him as a heterogeneous assortment of species. He suggested that the genus would be divided into several more uniform genera when better known.

Therefore, comparative studies are needed to clarify relationships among *Platygloea* species. In this first part, we compare systematically important characteristics of *Platygloea peniophorae* Bourd. & Galz. with those of *Platygloea disciformis* (Fr.) Neuhoff. Similarities and differences between the two species are described and illustrated.

Materials and methods

Specimens used

Platygloea peniophorae, growing on *Hyphoderma praetermissum* (Karst.) Erikss. & Strid. Strain FO 4432 collected in West Germany, Bayern, Isartal between Grünwald and Georgenstein near München, 530 m, leg. J. Poelt & F. Oberwinkler, May 1963. Strain Agerer 1066 collected in West Germany, Bayern, Landshut, Israuen, leg. R. Agerer, 1972. Strain RJB 5.1978 collected in Canada, British Columbia, Squamish, north of Vancouver, O m, leg. R. J. Bandoni, May 1978. Strain FO 36346 collected in West Germany, Baden-Württemberg, Schönbuch near Tübingen, leg. F. Oberwinkler, November 1984.

Platygloea disciformis, growing on dead twigs of *Tilia platyphyllos* Scop., collected in West Germany, Baden-Württemberg, Hagelloch, near Tübingen, 400 m, leg. F. Oberwinkler 29198, August 1979.

Microscopy

Living and dried materials were studied with a Zeiss photoscope III, using phase optics and Nomarski interference contrast optics. For transmission electron microscopy, samples were fixed in 2% glutaraldehyde in 0.1 M cacodylate buffer at pH 7.2 overnight or during several days. Following six transfers in 0.1 M cacodylate buffer, the material was postfixed in 1% O_sO_4 in the same buffer for 2 h in the dark, washed in distilled water, and stained in 1% uranyl acetate for 1 h in the dark. After five washes in distilled water, the material was dehydrated in acetone, using single 10-min changes at 25, 50, 70, 95, and (thrice) 100% acetone. The material was embedded in Spurr's plastic (Spurr 1969). Series of sections were cut on a Reichert ultramicrotome using a diamond knife and, after mounting on Formvar-coated single-slot copper grids, stained with lead citrate (Reynolds 1963) at room temperature for 5 min and washed again with water. The thin sections were examined with a Zeiss EM 109 transmission electron microscope at 80 kV.

Results and discussion

Basidiocarps of *P. disciformis*, the generic type, are composed of efibulate, strongly thick-walled hyphae (Figs. 9, 11) with porous, spongy hyphal walls (Figs. 10, 17). The con-

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spicuous, erumpent, discoid basidiocarps (Figs. 1, 2) grow on dead, but still attached, twigs of *Tilia* spp., often in association with other fungi. The hymenium contains prominent, thick-walled cystidia and large, often disarticulating basidia (Figs. 5, 7, 8). Aseptate basidiospores are produced on long sterigmata, positioned asymmetrically (Fig. 6), and released forcibly at maturity. Discharged aseptate basidiospores may develop secondary ballistospores (Fig. 3). On agar, they usually become septate and the compartments germinate with hyphae (Fig. 4) or conidia (Aoki *et al.* 1986). In contrast to *P. peniophorae*, the basidiospores and secondary spores do not bud in a yeastlike manner. Conidiophores are unknown. *Platygloea disciformis* sometimes appears to be associated with other fungi growing on *Tilia* twigs, but colacosomes (Bauer and Oberwinkler 1990) are absent. In contrast to *P. peniophorae*, the septal pores of *P. disciformis* are associated with electron-opaque bandings and globules (Fig. 18), as in some species of the genus *Septobasidium* Pat. (F. Oberwinkler, unpublished results). Furthermore, as in *Septobasidium* species (Dykstra 1974) and *Atractogloea stillata* Oberw. & Bandoni (Oberwinkler and Bandoni 1982; Oberwinkler and Bauer 1989), the slightly swollen outer margins of the septal pores in *P. disciformis* taper abruptly toward the centers of the pores. *Platygloea disciformis* shows some features in common with *Septobasidium* species. The common features are (*i*) identically structured septal pores with associated bandings and globules, (*ii*) large phragmobasidia, (*iii*) clampless hyphae, (*iv*) thick-walled hyphae, and (*v*) septate basidiospores. However, the basidiospore compartments of *P. disciformis* do not germinate by budding and the fungus is obviously not associated with scale insects, as are typical species of *Septobasidium* (Oberwinkler 1987).

Platygloea peniophorae, a mycoparasite of Aphyllophorales hosts, is well characterized morphologically by thin-walled, clamped hyphae growing internally in host fructifications, and by pulvinate to effused basidiocarps on the surface of host hymenia (Figs. 12, 13, 15, 16). Attention was drawn to the occurrence of two distinct types of hymenial conidia (Bandoni 1973). Perhaps two taxa exist or maybe there are two forms of a single species. Conidia in collections from North America are commonly of the paired, blastic type (Fig. 14); those in European collections are of the solitary, chlamydospore type (Figs. 13, 15). Basidiocarps of European collections appear to be distinctly gelatinous, whereas those from North American are predominantly mucoid, the visible mass being composed mainly of slime and conidia.

On 1.5% malt yeast peptone agar (Bandoni 1972), the basidiospores usually germinate by budding, but occasionally secondary spores or germ tubes are produced, as described in detail by Bauer and Oberwinler (1986). Secondary spore formation and budding basidiospores are also often observed in the basidiocarps (Figs. 14, 16). If individual basidia are placed on agar, the germination of the basidial cells changes dramatically. Like the basidiospores, the basidial cells bud in a yeastlike manner (Bauer and Oberwinkler, 1986). Yeast basidia of such type are typical for phragmobasidial smut fungi. In contrast to *P. disciformis*, the basidiospores of *P. peniophorae* remain aseptate during germination (Figs. 15, 16) and the septal pores lack associated electron-opaque structures (Fig. 19). Furthermore, the septal pores possess rounded, nonswollen margins (Fig. 19). Similar septal pores are known for *Stilbum vulgare* Tode, *Pachnocybe ferruginea* (Sow.:Fr.) Berk., and *Chionosphaera apobasidialis* Cox (Oberwinkler and Bauer 1989).

Platygloea peniophorae grows parasitically. Martin (1940) mentioned and illustrated "curious vesicular cells, borne upon hyphae with clamp connections and sometimes interrupted with the basidia." He interpreted them "as galls caused by a parasitic fungus." Bandoni (1956) also illustrated "hyphae with peculiar gall cells." The ultrastructure of the cellular interactions between *P. peniophorae* and *Hyphoderma praetermissum* was investigated by Bauer and Oberwinkler (1990). The cellular connection between the parasite and the host represents a special type of cell organelle for which the name colacosome was introduced. Cells of the parasite that attach to host cells form distinct vesicular bodies with electron-dense cores and electron-transparent marginal regions (Figs. 20). The vesicular content projects through the cell wall of the parasite itself and then interacts with the cell wall of the host (Fig. 21).

Mycoparasitic species of auricularioid heterobasidiomycetes occur either intrahymenially, as in *Platygloea abdita* (Bandoni 1959), *P. subabdita* (Hauerslev, 1987), and *Phragmoxenidium mycophilum* (Oberwinkler *et al.* 1990), or develop gelatinous, pustular basidiocarps externally on the host fructifications, as in species of *Cystobasidium* and *Platygloea*. Olive (1954) described *P. peniophorae* var. *interna*, a taxon occurring in dacrymycetaceous hosts.

Platygloea peniophorae differs from *P. disciformis*, the type species of the genus *Platygloea*, in (*i*) the presence of basidial and conidial stages, (*ii*) a dimorphic life cycle including a yeast phase, (*iii*) a specialized mycoparasitism by colacosomes, (*iv*) the lack of associated electron-opaque structures of the septal pores, (*v*) the absence of septate basidiospores, and (*vi*) a variety of morphological features, including thin-walled and clamped hyphae. Therefore, the genus *Colacogloea* is proposed to accommodate *P. peniophorae*.

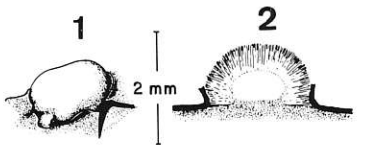
Colacogloea Oberwinkler & Bandoni, gen.nov.

Genus mycoparasiticus Heterobasidiomycetum. Carposoma gelatinosum, pustulatum. Hyphae tenuitunicatae, fibulatae, hyalinae, inter cellulas hospitalium crescunt, cellulis conidia gerentibus vel basidiis terminant. Ultrastructura septorum hypharum poris simplicibus sine parenthesomatis. Cystidia desunt et hyphidia hyphas apparant. Basidia cylindracea, mature transverse tri-septata. Basidiosporae eiectae, hyalinae, tenuitunicatae, tunicis levibus, cellulis singulis, plerumque per repetitionem germinant. Conidia terminaliter ab hyphis fibulatis abscenditur.

In fructificationibus Corticiacearum crescunt, carposomatis super hymenia hostium oreundis.

ETYMOLOGIA: *colax*, sycophant, parasite; *gloios*, slime.

FIGS. 1–11. Line drawings of *Platygloea disciformis*, FO 29198. Fig. 1. Habit sketch of basidiocarp. Fig. 2. Sectional view of basidiocarp erumpent through bark. Fig. 3. Basidiospores, two germinating by repetition. Fig. 4. One transversely septate basidiospore germinating with hyphae on 1.5% malt yeast peptone agar (Bandoni 1972). Fig. 5. Upper parts of disarticulating basidia. Fig. 6. Basidiospores asymmetrically attached to sterigmata; sterigmata with adventitious septa. Fig. 7. Portion of hymenium with basidia of different stages and partly thick-walled cystidia with secondary septation. Fig. 8. Portion of hymenium with basidia and thick-walled cystidia. Fig. 9. Hyphal branching of subhymenium. Fig. 10. Part of hypha showing porous nature of cell wall. Fig. 11. Hyphal arrangement of trama.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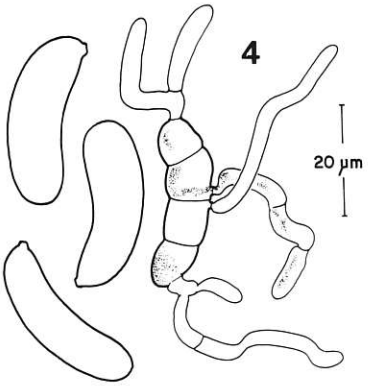
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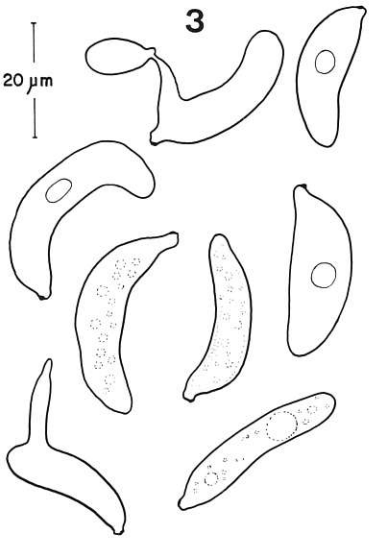
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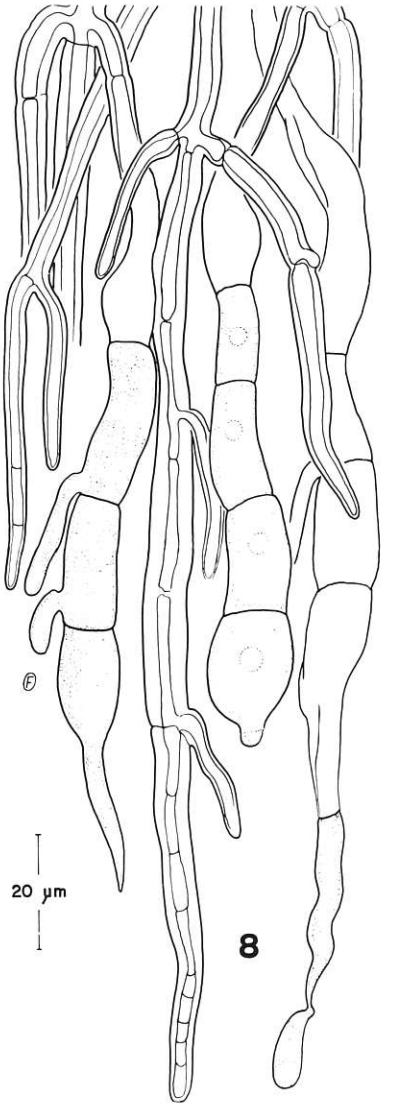
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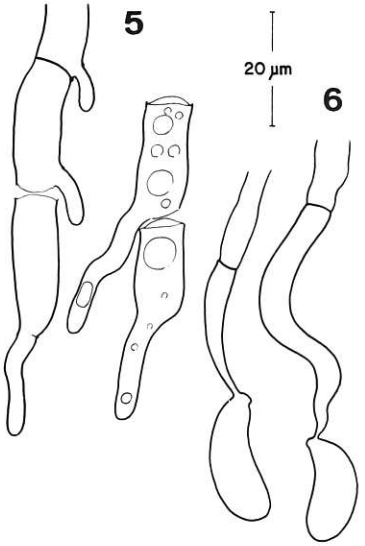
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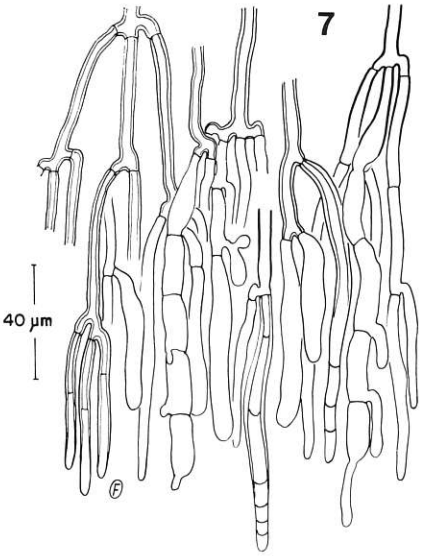
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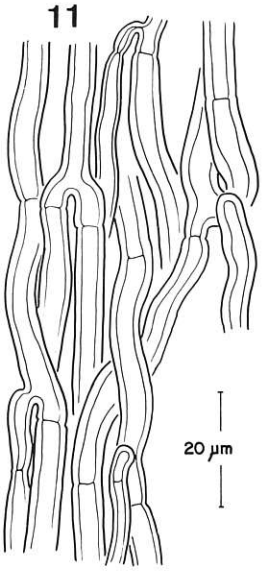
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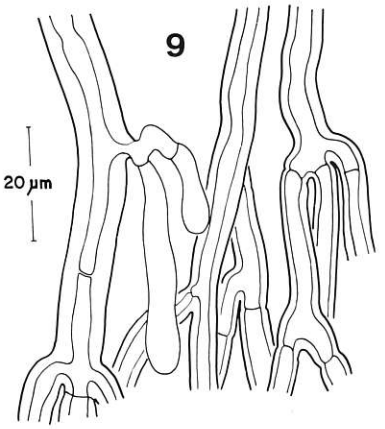
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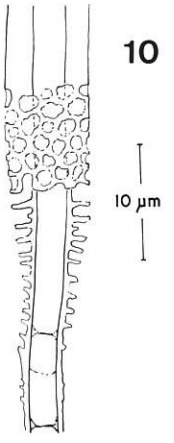
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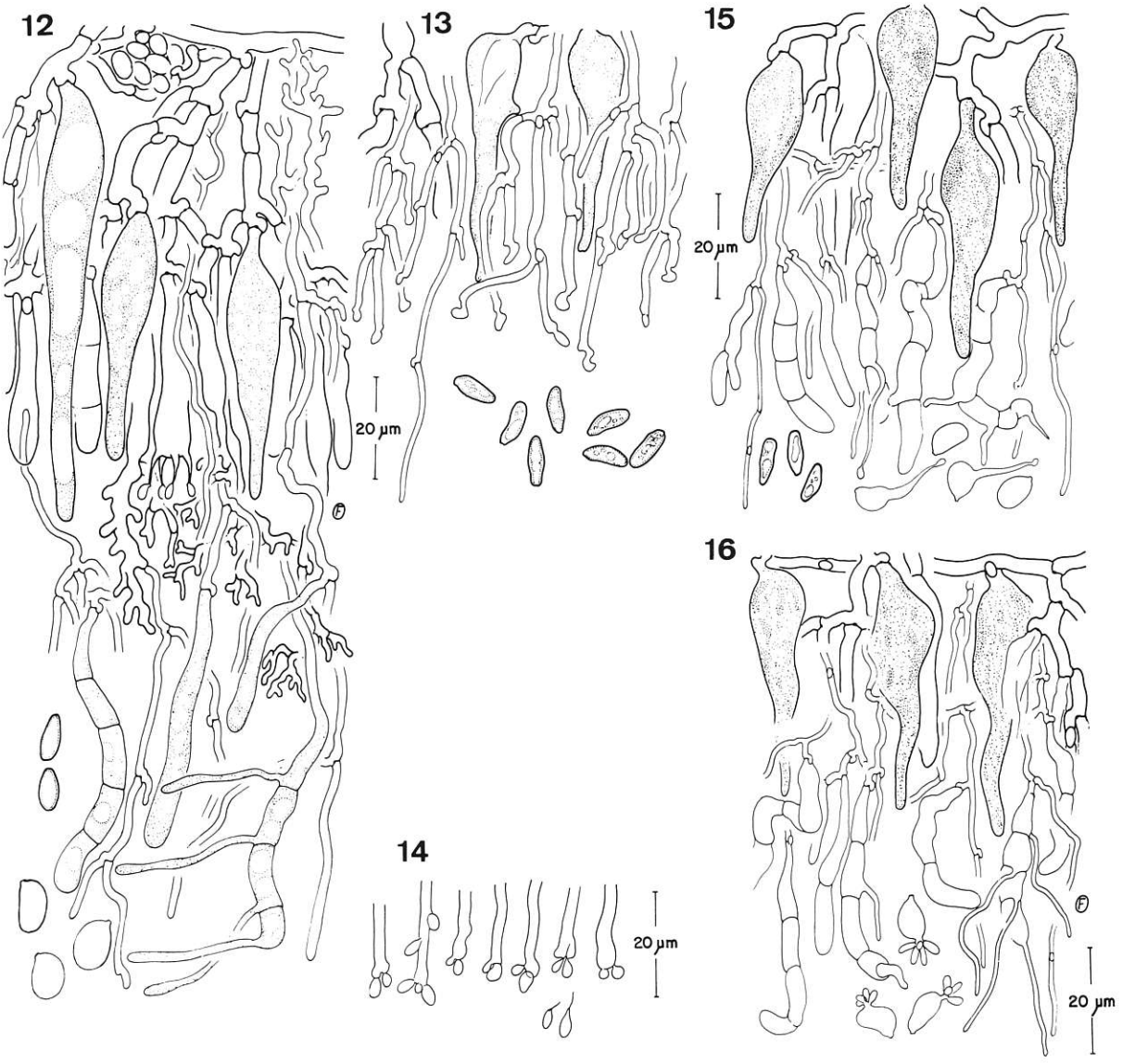

FIGS. 12–16. Line drawings of *Colacogloea peniophorae*, Agerer 1066 (Figs. 12–13), FO 4332 (Figs. 15, 16), and RJB 5.1978 (Fig. 14). Fig. 12. Section of basidiocarps of the host fungus *Hyphoderma praetermissum* and parasite *C. peniophorae* showing hyphal systems, basidia, basidiospores, and conidia. Note strongly branched hyphae of the host and the parasite. Fig. 13. Conidiophores arising from strongly decayed hymenium of host. Note loops of clamps from which conidia were released. Seven conidia. Fig. 14. Second type of conidiophores in different stages of development, and conidia with filamentous conidiophore remnants. Figs. 15 and 16. Two sections through basidiocarps of the host fungus *H. praetermissum* and the parasite *C. peniophorae* showing hyphal systems basidia, basidiospores, some germinating by repetition, others budding, and conidia.

TYPUS GENERIS: *Colacogloea peniophorae* (Bourd. & Galz.) Oberw. & Bandoni, comb. nov.; BASIONYM: *Platygloea peniophorae* Bourd. & Galz., Bull. Soc. Mycol. Fr. 25: 17 (1909).

Mycoparasitic, with pulvinate to effused, mucoid–gelatinous basidiocarps, developing in and on the surface of host hymenia. Hyphae thin-walled, hyaline, clamped, growing intrahymenially in host fructifications, and developing ana-

FIGS. 17–21. Transmission electron micrographs of *Platygloea disciformis*, FO 29198 (Figs. 17, 18), and *Colacogloea peniophorae*, FO 36346 (Figs. 19–21). Fig. 17. *Platygloea disciformis*. Oblique section through hyphae. Note porous cell wall structure. Scale bar = 1 µm. Fig. 18. *Platygloea disciformis*. Median section through a septal pore showing electron dense bandings and globules (arrows) surrounding pore orifice. Scale bar = 0.1 µm. Fig. 19. *Colacogloea peniophorae*. Septal pore without neighbouring electron-opaque structures. Scale bar = 0.1 µm. Fig. 20. Interaction stage between the parasite *C. peniophorae* (P) and the host fungus *Hyphoderma praetermissum* (T). Colacosomes (arrows) are located at the contact zone between the parasite and the host. Scale bar = 1 µm. Fig. 21. Longitudinal section through a colacosome. The electron-opaque material of the central part (C) penetrating the host cell wall. Note the invagination of the host plasmalemma opposite the colacosome. The colacosome is ensheathed by a thin cell wall layer and the cytoplasmic membrane of the parasite. T, host cell; P, parasitic cell. Scale bar = 0.1 µm.


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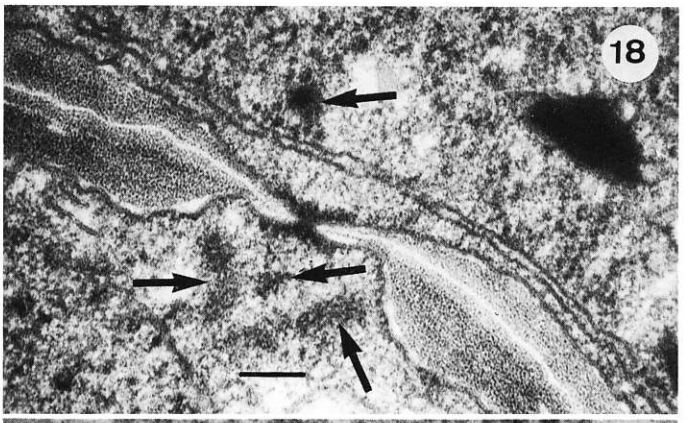
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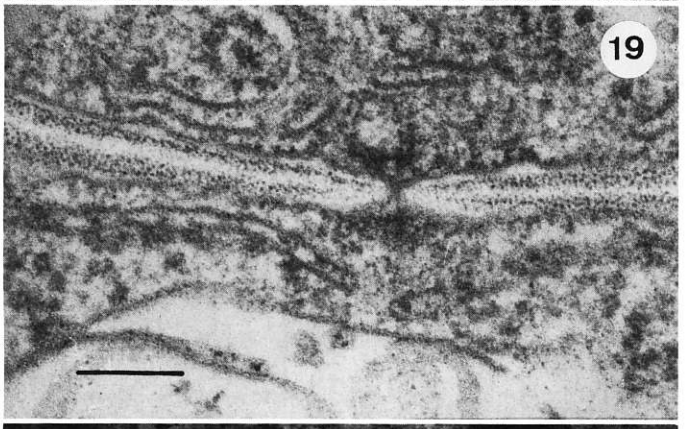
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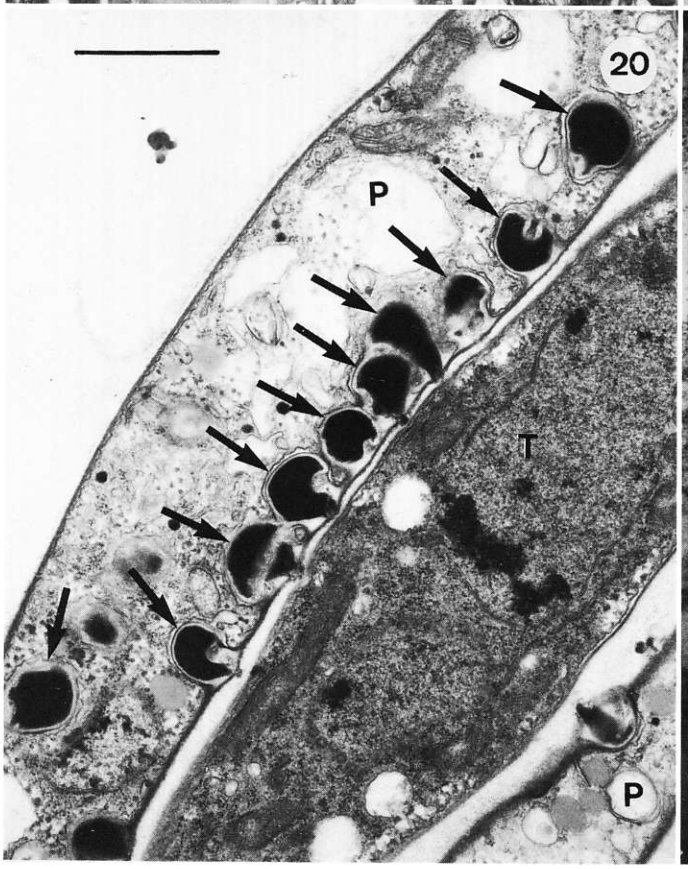
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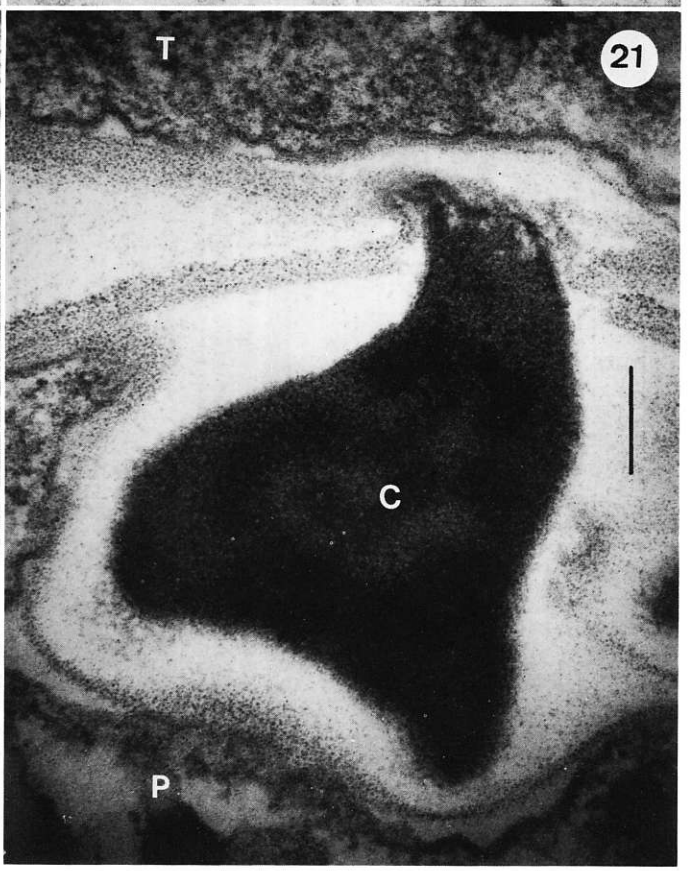
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morph and teleomorph stages on the same generative hyphae. Hyphidia slender, inconspicuous, hypha-like. Basidia without conspicuous probasidia, transversely three-septate at maturity, each basidial cell developing one long, tubular, hypha-like sterigma and an asymmetrically attached spore. Basidiospores thin-walled, smooth, hyaline, inamyloid, germinating by repetition or budding.

Conidia produced terminally on conidiophores. Conidial development and morphology varied.

Growing parasitically on fructifications of Aphyllophorales, predominantly on *Hyphoderma praetermissum* (Karst.) Erikss. & Strid, but additionally reported also from species of *Odontia*, *Peniophora*, and *Poria*. it is unclear whether all of these reports correctly refer to *C. peniophorae*.

Colacogloea is obviously not closely related to *Platygloea disciformis*, the type species of the genus *Platygloea*.

Acknowledgements

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