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Life-History Studie of Brazilian Ascomycetes 5 [1])

Two new species of *Ophiostoma* and their *Sporothrix* anamorphs

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Abstract: *Ophiostoma roraimense* sp. nov. and *O. grande* sp. nov. and their *Sporothrix* anamorphs are described. The relationship of *Ophiostoma* H. & P. Sydow to *Ceratocystis* Ellis & Halsted and of *Ceratocystis* to the Endomycetaceae is discussed. *Ophiostoma* and *Ceratocystis* are considered to be distinct from each other and the contention that *Ceratocystis*, sensu lat., is a member of the Endomycetaceae is rejected.

Introduction

The question of whether or not to accept *Ophiostoma* H. & P. Sydow as distinct from *Ceratocystis* Ellis & Halsted has been debated for over forty years and there is still no clear solution. The only apparent distinction between the two is in conidiogenesis with one group of species producing phialidic conidia and the other producing conidia in a holoblastic-sympodial fashion. Recent studies of the polysaccharide content of cell walls in the group (Spencer & Gorin 1971, Jewell 1974, Weijman & De Hoog 1975) indicate that there is cellulose in the walls of many of these species having holoblastic conidiogenesis. The presence of cellulose corresponds to the presence of rhamnose and specific groups of mannan-containing polysaccharides (as defined by proton magnetic resonance) that are rarely found in walls of species having a phialidic development. None of the species having phialidic conidiogenesis has cellulosic walls and rhamnose is also lacking; these species have spectrally defined groups of mannan-containing polysaccharides that, with few exceptions, differ from those found in the holoblastic group.

Cellulosic walls in the fungi are largely restricted to specific phycomycetous groups which are defined further through their manner of flagellar insertion. In the Ascomycetes, cellulose has been reported for a variety of species but proven positively only for species of *Ceratocystis* having holoblastic conidiogenesis (see review in Bartniki—

[1]) Part 1 in Sydowia 31. Supported in part by Projecto Flora Amazonica—The New York Botanical Garden (NSF INT-77-17704) and by a grant from the American Philosophical Society to the senior author. Dr. O. Petrini, ETH Zürich, prepared the Latin diagnoses.

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Garcia 1968). Because cellulose is so rare in the Ascomycetes, we accord its presence great importance in separating *Ophiostoma* from *Ceratocystis*. The method of conidiogenesis is also considered to be phylogenetically important and enteroblastic-phialidic and holoblastic-sympodial developments are two fundamentally different forms.

It is likely that *Ceratocystis* and *Ophiostoma* are derived rather than primitive genera and it is quite possible that they are unrelated. It is not surprising that they have adopted similar morphologies in response to similar habitats. There is very little variation in the outward form in the majority of lignicolous pyrenocarpous ascomycetes. Genera and higher groups differ primarily on the grounds of relationship to the surface of the substrate, ascosporal septation, ascal type and sterile, interthecial tissue. One result of reduction in ascomycetes may be the loss of a characteristic ascal type and sterile filaments. In the Xylariaceae, *Thamnomyces* Ehrenberg ex Fries and *Phylacia* Léveillé no longer have amyloid caps and their asci break down shortly after spore delimitation (personal observation). In *Pulveria* Malloch & Rogerson, apparently closely related to *Hypoxylon* Bulliard ex Fries, the asci are globose and form in chains. Similarly the hypocreaceous genus *Heliococcum* Jorgensen has globose, unordered asci in a closed ascocarp but is thought to be a derivative of *Nectria* Fries. It is therefore reasonable to suggest that the globose asci of *Ophiostoma* and *Ceratocystis* have derived from other sphaeriaceous or xylariaceous forms.

On purely morphological grounds *Ophiostoma* shows a relationship to the Xylariaceae and the Diatrypaceae. Both of these families have holoblastic-sympodial conidiogenesis. The ascospores of *Diatrype* Fries are allantoid and brown. Although the members of these two families are usually stromatic and ascomata of *Ophiostoma* are not, the two species of *Ophiostoma* described below have very thick ascomatal walls and are seated on a basal stroma thus demonstrating a potential similar to that of the Xylariaceae and Diatrypaceae.

Relationships of *Ceratocystis* sensu str. are more difficult to see. Through their *Chalara* (Corda) Rabenhorst anamorphs there is possibly a connection to sphaeriaceous genera such as *Melanochaeta* E. Müller, Harr and Sulmont and *Porosphaeria* Samuels & E. Müller. Both of these genera have *Sporoschisma* Berkeley & Broome anamorphs whose conidia are produced within a long tube as they are in *Chalara*.

Redhead and Malloch (1977) gave the Ophiostomataceae, comprised of *Ophiostoma* and *Ceratocystis*, a central position in the Endomycetaceae. Their argument was based on the production of hat-shaped, galeate, ascospores in the ascosporogenous yeasts and some species of *Ceratocystis*. Their conclusions were drawn from studies of sporogenesis in *C. fimbriata* Ellis & Halsted, a phialidic

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species (STIERS 1976), and in *Hansenula anomala* (HANSEN) H. & P. SYDOW (BANDONI et al. 1971). According to REDHEAD and MALLOCH spore formation in the two species is homologous and such peculiar ascospores are unlikely to have been evolved more than once. Reviewing the papers of STIERS (1976) and BANDONI et al. (1971) as well as that of BLACK and GORMAN (1971) for *H. wingei* WICKERHAM does show what may be significant differences in development of the hat-shaped ascospore.

The process of ascosporal delimitation is not well understood. There are, however, two features that all species studied so far have in common. Firstly, the two unit membranes surrounding the spore are derived from a double unit membrane ascus sac or vesicle of unknown origin and, secondly, the spore wall is laid down between these membranes. *Hansenula* H. & P. SYDOW and *Ceratocystis* are not exceptions. Differences occur in the final structure of the wall and in the manner of formation of the "rim" of the hat.

In *Hansenula*, soon after meiosis the delimiting, double membranes enclose each of the haploid nuclei. The early spores, in section, appear elliptic but soon assume a hat-shape. Splitting of the membranes and concommittant wall deposition then proceeds from the periphery of the "rim" and partially up the sides of the "crown" of the hat. A second wall layer of different electron density is then laid down between the membranes over the crown and between the rim and plasma membrane at the base of the spore. Only two wall layers are thus formed, that of the rim and that of the rest of the spore. A similar structure was illustrated for spores of *Pichia* HANSEN by BRESSON (1966) although the process of formation was not described.

In *Ceratocystis*, soon after meiosis the delimiting, double membranes enclose each of the haploid nuclei. The early spores, in section, appear nearly globose and remain so during wall deposition. Splitting of the membranes and wall deposition proceeds evenly around the spore. The wall then differentiates into three layers of varying electron density in an undescribed fashion. After the wall has become three-layered, the rim of the hat forms apparently through extension of the outer layer of the wall but the process was not described.

The final, galeate, form of the ascospores of *Hansenula* and *Ceratocystis* are therefore arrived at in different ways. We cannot assess the significance of the differences but they suggest that galeate ascospores may be polyphyletic. In *Hansenula* the rim is definitely formed between two unit membranes and wall formation begins at the periphery of the rim. In *C. fimbriata* the spore remains nearly globose until after all three wall layers have formed. The rim could derive from the epiplasm or could be a mixture of epiplasm and primary wall. No evidence was presented by STIERS for an extension of the membrane system in the region of the rim or for a renewal of primary wall

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deposition between two membranes after the final layering of the wall had been resolved.

In at least one respect ascospore formation in *Ceratocystis* is more like that of the yeasts than of other filamentous fungi. In the yeasts, the first formed wall layer is external to the second formed layer and this is the case for *C. fimbriata*. It is more difficult to interpret the wall layers of *Hansenula* and *Pichia* since, in *Hansenula*, the first formed wall is restricted to the rim of the ascospore while the wall of the spore body is formed later but not internal to the primary wall except at the base.

Ascospores of yeasts may be variously ornamented. Round, ovoidal, hat-, saturn-, or sickel-shaped ascospores are found in species of *Hansenula* and *Pichia*. In *Schwanniomyces* KLÖCKER they may be round or oval with an equatorial ridge and warted (PHAFF 1970, WICKERHAM 1970; KREGER—VAN RIJ 1969, 1970; VON ARX et al. 1977). In *Pichia membranaefaciens* HANSEN and *P. ohmerii* (ETCHELLS & BELL) KREGER—VAN RIJ ascospores may be round or hat-shaped and in *P. fermentans* LODDER the rim of the hat varies from being pronounced to being almost absent (KREGER—VAN RIJ 1969, 1970). The ontogeny of the ornaments has not been investigated. It would be interesting to know how they relate to each other and to ontogeny of the ornaments in the saturnate ascospores of such eurotiaceous genera as *Sartorya* VUILLEMIN and *Emericella* BERKELEY.

As striking as the morphological aspect of the hat-shaped ascospores may be, other features mitigate against a close relationship of *Ceratocystis* to the Endomycetaceae. Most obviously, there is no tendency in the yeasts to form complex fruitbodies. There is no long lasting dikaryophase in most yeasts as is found in the ascogenous hyphae of Euascomycetes [for example *Ceratocystis fagacearum* (BRETZ) HUNT, WILSON 1956]. *Cephaloascus fragrans* HANAWA produces crozier-like or clamp-like branches that fuse with the next cell of the hyphal filament or with an adjacent hypha. A single nucleus migrates through this branch into the next cell thus accomplishing dikaryotization. Immediately following nuclear pairing, there is nuclear fusion so that there is no dikaryophase (DIXON 1959, SCHIPPERS—LAMMERTSE & HEYTING 1962, WILSON 1961). In a study of cell wall composition, WEIJMAN (1976) could find no relationship of *Cephaloascus fragrans* to *Ophiostoma ulmi* (BUISMAN) NANNFELDT.

A second objection to including *Ceratocystis* in the Endomycetaceae is the apparently highly evolved type of conidial production found for *Ceratocystis*. Ascomycetes having a *Chalara*-like ontogeny are restricted to a group of genera apparently centered on *Chaetosphaeria* TULASNE. Conidiogenesis similar to that found in *Ophiostoma* is found in *Botryoascus* ARX and *Hypopichia* ARX & VAN DER WALT but conidia produced from denticles on conidiophores that elongate

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sympodially are not so specialized, being found in a variety of apparently unrelated, ascomycetous genera.

Cell wall chemistry also indicates a difference between the yeasts and the Euascomycetes (BARTNIKI—GARCIA 1968). Cellulose has not been positively identified in the walls of any of the yeasts. The mannan-glucan content of the cells of the Endomycetaceae differs from that found in both the Saccharomycetaceae and the filamentous ascomycetes, although BARTNIKI—GARCIA concluded that the Endomycetaceae is closer to the filamentous ascomycetes than to the budding yeasts in this regard.

In summary, we do not believe that *Ceratocystis* and *Ophiostoma* are necessarily closely related to each other or even belong in the same family. This conclusion is based on comparative cell wall chemistry and conidial ontogeny. However similar the final ascospore structures of *Hansenula anomala* and *Ceratocystis fimbriata* are, we do not accept the contention of REDHEAD and MALLOCH (1977) that ascosporal development in these species is homologous and not feel that *Ceratocystis* can be included in the Endomycetaceae in the sense of REDHEAD and MALLOCH. Our conclusions as well as those of REDHEAD and MALLOCH are based on detailed knowledge of a very small number of species. It would be interesting to know how hat-shaped or saturnate ascospores form in other genera of the Saccharomycetaceae, the Endomycetaceae and the Eurotiaceae.

Descriptions of the Species

1. *Ophiostoma roraimense* SAMUELS & E. MÜLLER sp. nov. — Fig. 1.

Ascomata caespitosa, parvo basali stromate insidentia, dura, nigra, globosa, 200—500 μm diametro, rostro filliformi ad 1.5 mm longo praedita; pariete ca. 70 μm crassa. Asci non visi. Ascosporae reniformes vel fere lunatae, 3—4 × 1.5—2 μm, unicellulares, hyalinae. In stromatibus *Diatrypis* cf. *stigmae*. Status conidialis: *Sporothrix* sp.

Holotypus: DUMONT-BR 329, NY. Isotypus: INPA, ZT.

ANAMORPH: *Sporothrix* sp.

TELEOMORPH: Mycelium not apparent. Ascomata perithecioid, caespitose, in groups of 6—10, seated on a small basal stroma composed of pseudoparenchymatous to prosenchymatous, ca. 5 μm wide cells having walls ca. 0.5 μm thick; black, very hard, globose, 200—500 μm diam, with a non-annulate, filiform beak ca. 1500 μm long; ascomatal wall rough and dull; not collapsing when dry, dark pigment soluble and ascomata somewhat softer in 3% KOH. Ascomatal wall ca. 70 μm thick, composed of three regions. Outer region arising from the middle region, ca. 30 μm wide, hyphal; hyphae brown, 2—3 μm diam, septate, branching. Middle region ca. 40 μm wide, composed of closely compressed hyphae with short cells (textura porrecta), cell walls very heavily pigmented, carbonized. Inner region

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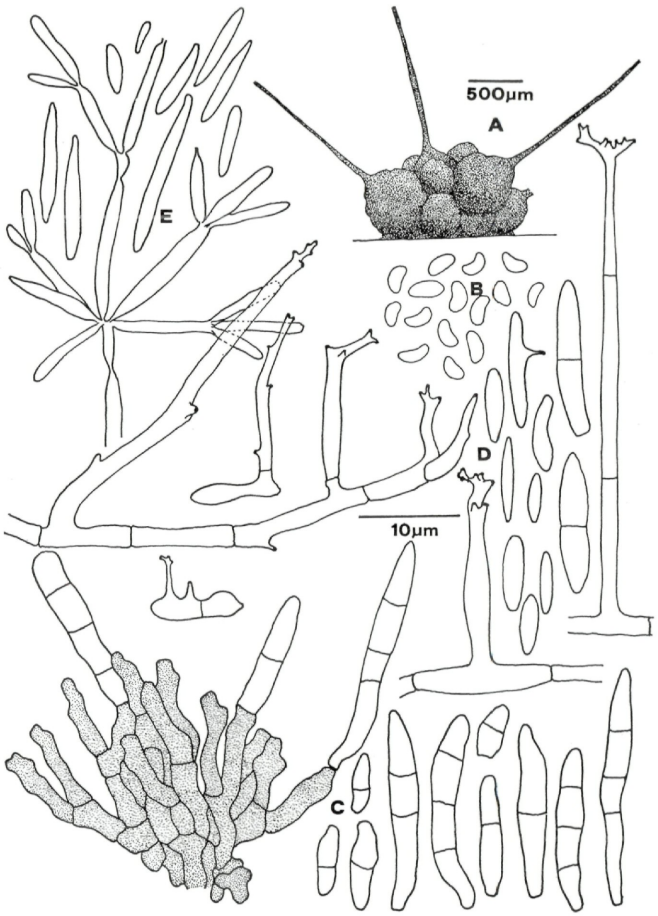

Fig. 1. *Ophiostoma roraimense* (holotype): A. Habit sketch of ascomata. B. Ascospores. C. Sporodochium and conidia from ascomatal wall. D. Conidiophores and conidia produced within 2 weeks of isolation. E. Fragmenting hypha produced after 2 months' storage

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arising from the middle region, composed of more or less loosely arranged, hyaline to light brown, septate, branching hyphae; hyphae growing into the locule. Sporodochial-like structures arising from the surface of the wall and continuous with the outer, hyphal layer; conidiogenous cells sympodially elongating, 15—22 µm long × ca. 3 µm wide; conidia holoblastic, cylindrical with a rounded to pointed tip and a flattened, non-cicatrized, basal cell, (8—) 14—22 (—28) × 2—3.5 µm, 1—3-septate, hyaline. Ascomatal beak composed of tightly bound, septate, carbonized, hyphal elements arising from the middle region of the ascomatal wall; tip of beak lacking a crown. Periphyses not seen.

Asci not seen. Ascospores reniform to nearly crescent-shaped, lacking a gelatinous sheath when stained in Trypan Blue, 3—4 × 1.5—2 µm, unicellular, hyaline, smooth.

Characteristics in culture. Colonies on Weak ME in 2 weeks at 20—23 C less than 5 mm diam, pale yellow, slimy with no aerial mycelium. Conidiophores mononematous, septate and up to 40 µm long, or micronematous. Conidiogenous cells cylindrical, 13—23 × 1.5—2 µm, producing conidia from denticles scattered along the length of the cell or from a terminal, denticulate, irregularly proliferating region.

Conidia elliptic to fusiform, straight or slightly curved, (4—) 6—12.5 × 1—2 µm, mostly 1-celled, occasionally 2-celled, hyaline, with a small, flattened base; often producing denticulate, conidiogenous elongations or producing conidiogenous denticles directly from the conidial surface.

Habitat: On stroma of *Diatrype* cfr. *stigma*.

Holotype: Brazil: Territorio de Roraima, Acampamento de 6°-BEC-Jundiá, on the Manaus-Caracaraí Rd at a point ca. 328 km from the intersection of the Manaus-Itacoatiara Rd; on stroma of *Diatrype* cfr. *stigma*; Dumont, Hosford, Samuels, Buck, Araujo, Souza, Bernardi; 16 Nov 1977 (Dumont-BR 329, NY; Isotypes: INPA, ZT).

Additional specimens examined: Brazil: Territorio de Roraima, along the Boa Vista-Manaus Rd at a point ca. 345 km from the interesection of the Manaus-Itacoatiara Rd; on stroma of *Diatrype* cfr. *stigma*; Dumont, Hosford, Samuels, Buck, Araujo, Souza, Bernardi; 17 Nov 1977 (Dumont-BR 479, INPA, NY); Amazonas, white sand Igapó N of Manaus; on stroma of *Diatrype* cfr. *stigma*; Samuels, Keel, Guitez; 14 Dec 1977 (Dumont-BR 992, INPA, NY).

Notes: Ascospores of the collection Dumont-BR 329 germinated in late January, 1978, and cultural characteristics described above were observed two weeks after the spores germinated. Two months after isolation, the colonies were inoculated onto malt extract agar (2% malt extract), cornmeal agar (Difco) and oatmeal agar. After two weeks growth, no recognizeable conidiophores were produced.

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Instead, the colonies were mucoid and light tan to brown; the mycelium was in the form of short cells which were joined to each other through denticles (fig. 1 E). Such cells were not seen in the original isolation.

According to Dr. G. S. DE HOOG (personal communication), the formation of arthroconidium-like cells in culture excludes this anamorph from *Sporothrix* HEKTOEN & PERKINS. It is, however, clear that the affinities of this anamorph are with *Sporothrix* both in conidiogenesis and in the telemorph, the known perfect states of *Sporothrix* being *Ophiostoma* (DE HOOG 1974).

The conidiomatal outgrowths of the ascomatal wall are suggestive of *Sterigmatobotrys* OUDEMANS. Conidiomata of this genus are synnematous; the biseptate conidia of *S. macrocarpa* (CORDA) HUGHES, the lectotype species (see ELLIS 1971), have a brown central cell and lighter brown end cells and are borne in slimy heads. Cells of the sporodochium of the Brazilian collections are continuous with the outer layer of the ascomatal wall thus rulling out the possibility that they are the fructifications of a hyperparasite on the *Ophiostoma*. We did not notice sporodochia on the ascomatal walls before the specimens were dried and therefore did not have the opportunity to isolate conidia in order to determine whether the *Sporothrix* phase was merely a cultural expression of the more complex conidiomata or whether *O. roraimense* has two, separate anamorphs.

2. *Ophiostoma grande* SAMUELS & E. MÜLLER sp. nov. — Fig. 2.

Ascomata caespitosa, parvo basali stromate insidentia, dura, nigra, subglobosa, 800—1000 µm alta, 600—800 µm crassa, vel globosa, ca. 800 µm diametro, rostro filiformi 2—4 mm longo praedita, pariete ca. 170 µm crassa. Asci non visi. Ascosporae reniformes vel lunatae, 3—4.5 × 1.5—2 µm, unicellulares, hyalinae. In stromatibus *Diatrypis* cf. *stigmae*. Status conidialis: *Sporothrix* sp.

Holotypus: DUMONT-BR 882, NY. Isotypus: INPA, PDD, ZT.

ANAMORPH: *Sporothrix* sp.

TELEOMORPH: Mycelium not apparent. Ascomata perithecioid, caespitose in groups of up to 6, seated on a small, basal stroma consisting of densely compacted, hyphal-like cells; black, very hard; ovoidal, 800—1000 × 600—800 µm or globose, ca. 800 µm diam, with a filiform, non-annulate beak 2—4 mm long; ascomatal wall slightly furfuraceous and tuberculate to smooth; not collapsing when dry, no soluble pigment and wall not softening in 3% KOH. Ascomatal wall ca. 170 µm wide, composed of three layers. Cells at the surface hyphal, 3 µm wide, branching, with many free ends; arising from the middle region. Middle region composed of closely compressed hyphae with short cells (textura porrecta), cells filled with black pigment, carbonized. Inner region textura epidermoidea, cells thin-walled and non-pigmented. Ascomatal beak composed of tightly bound, septate, unbranched, carbonized, 2—3 µm wide hyphae

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arising from the ascomatal wall; tip of papilla with free, light brown hyphae up to 80 μm long with acute tips. Periphyses not seen.

Asci not seen. Ascospores reniform to crescent-shaped, 3—4.5× 1.5—2 μm, unicellular, lacking a gelatinous sheath when stained in Trypan Blue, hyaline, smooth.

Characteristics in culture. Colonies on Weak ME in one week at 20—23 C, 7—8 mm diam, white with a tan center, slimy with

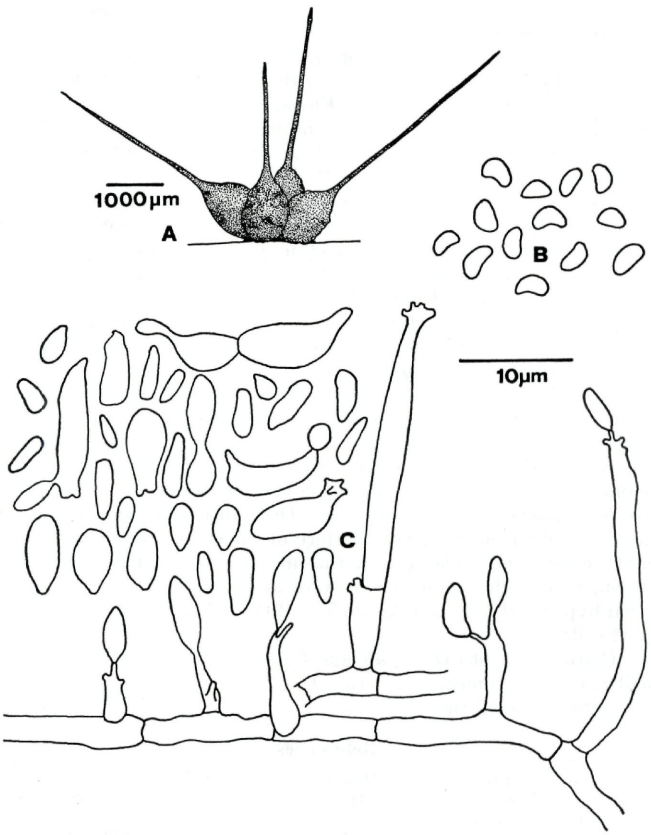

Fig. 2. *Ophiostoma grande* (holotype): A. Habit sketch of ascomata. B. Ascospores. C. Conidiophores and conidia.

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no aerial mycelium except at the margin where individual, erect hyphae are apparent.

Conidiophores micronematous, up to 30 µm long or merely denticulate hyphae. Conidiogenous cells cylindrical, 30 µm long × ca. 1.5 µm wide, producing conidia from a terminal, irregularly proliferating region, less often with intercalary, 2—6 µm long denticles. Conidia dacryoid to elliptical with a protuberant, basal abscission scar, 3.5—6 × 1.5—2.5 (—4) µm, unicellular, hyaline; often producing denticulate elongations or conidiogenous denticles arising directly from the conidial surface.

Habitat: On stroma of *Diatrype* cfr. *stigma* and on bark.

Holotype: Brazil: Territorio de Roraima, ca. 226 km N of Boa Vista on the Boa Vista-Sta. Elena, Venezuela Rd; on stroma of *Diatrype* cfr. *stigma* and on surrounding bark; DUMONT, HOSFORD, SAMUELS, BUCK, ARAUJO, SOUZA, BERNARDI; 2 Dec 1977 (DUMONT-BR 882, NY; Isotypes: INPA, PDD, ZT).

Notes: Ascomata of *O. grande* and *O. roraimense* are among the largest in the genus. *Ceratocystis megalobrunnea* DAVIDSON, HINDS & TOOLE (DAVIDSON et al. 1964), which may be a species of *Ophiostoma*, has ascomata measuring 350—450 µm in diameter and beaks that measure 1—1.5 mm in lenght. The authors did not describe the structure of the ascomatal wall nor did they elaborate on details of conidiogenesis. From their description, the conidia appear to be holoblastic and not typical of *Ceratocystis*.

According to Dr. G. S. DE HOOG (personal communication) the anamorph of *O. grande* is close to that of *O. piliferum* (FRIES) H. & P. SYDOW (see DE HOOG 1974).

As was the case with *O. roraimense*, two months after isolation, colonies reinoculated onto agar media had a different aspect than was observed immediately after isolation. On malt extract agar (2% malt extract) and oatmeal agar the surface of the colony was nearly black in the center and violaceous at the margin; the colonies were slimy although on malt extract there were areas of short and erect, tan aerial hyphae. Hyphae on the surface of the colony did not break into short cells.

Cultures of both *O. grande* and *O. roraimense* were incubated on malt extract, cornmeal and oatmeal agars at 3 C for six months but ascomata did not form.

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Zeitschrift/Journal: Sydowia

Jahr/Year: 1978/1979

Band/Volume: 31

Autor(en)/Author(s): Samuels Gary J., Müller Emil

Artikel/Article: Life-History Studies of Brazilian Ascomycestes 5. 169-179