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TABLE OF CONTENTS, VOLUME TWENTY-FIVE

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NEMATOCTONUS AND THE TRIBE RESUPINATEAE IN ONTARIO, CANADA[1]

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ABSTRACT

Eight form-species of ***Nematoctonus***, including 5 new species, were found in Ontario, and one extralimital species is described as new. Twelve of the 16 species recognised in ***Nematoctonus*** are described. In several cases, a single form-species includes the anamorphs of more than one teleomorph species. Eight species of ***Nematoctonus*** are not known to have teleomorphs. Twelve new teleomorph-anamorph connections are made. All teleomorphs occur in ***Hohenbuehelia*** (tribe Resupinateae), and all species of ***Hohenbuehelia*** treated have ***Nematoctonus*** anamorphs. The other genera of the Resupinateae were not nematophagous. Species of ***Resupinatus*** and ***Stigmatolemma*** lack ***Nematoctonus*** anamorphs, but have hyphal structures that suggest that they are parasitic. ***Asterotus*** and ***Stromatocyphella*** are unknown in culture. Twelve species of ***Hohenbuehelia***, four of ***Resupinatus***, and one in each of ***Asterotus***, ***Stigmatolemma*** and ***Stromatocyphella*** occur, or are likely to occur, in Ontario. ***Hohenbuehelia*** is characterised by possession of hymenial metuloids and a ***Nematoctonus*** anamorph. In addition, fruit bodies of ***Hohenbuehelia*** have distinctive cystidia in the hymenium or on the surface of the pileus or stipe, which terminate in one or more hour-glass-shaped cells, each surrounded by a mucoid droplet.

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[1] Portion of a thesis submitted by the senior author to the University of Guelph in partial fulfillment of the requirements for the degree of Master of Science.

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These gloeosphex cystidia are unique among the agaric genera and resemble the capture organs of *Nematoctonus*. Species of *Resupinatus* lack metuloids, gloeosphex cystidia and *Nematoctonus* anamorphs, but possess diverticulate cheilocystidia and diverticulate cuticular hyphae, which are not found in *Hohenbuehelia*. The tribe Resupinateae should be classified in the Polyporaceae (= Pleurotaceae) to reflect the affinity of the Resupinateae with the genus *Pleurotus*. Parallel study of anamorphs and teleomorphs clarified the taxonomy of the Resupinateae at the generic and species levels. New species are: ***Nematoctonus angustatus*** Thorn & Barron, ***N. brevisporus*** Thorn & Barron, ***N. cylindrosporus*** Thorn & Barron, ***N. geogenius*** Thorn & Barron, ***N. hamatus*** Thorn & Barron, and ***N. subreniformis*** Thorn & Barron. New combinations are: ***Hohenbuehelia atrocaerulea*** (Fr.) Sing. var. ***grisea*** (Peck) Thorn & Barron, and ***H. tremula*** (Schaeffer: Fr.) Thorn & Barron.

INTRODUCTION

Species of *Nematoctonus* attack nematodes in soil or rotting wood. Drechsler (1941) described the genus to accommodate two species that differed from all other nematode-destroying fungi in that their hyphae had clamp connections. These fungi produce simple, hyaline conidia on short pegs along their hyphae. Nematodes are captured by adhesive processes formed on conidia or vegetative hyphae, and are then penetrated, colonized and digested. The adhesive trapping devices on hyphae of of predatory species of *Nematoctonus* have a secretory cell with a characteristic hour-glass shape, similar to the adhesive processes on germinated conidia of some of the endoparasites.

The outstanding feature of *Nematoctonus*, the presence of clamp connections, is characteristic of many heterokaryotic Basidiomycotina. Drechsler (1941) recognized the affinities of *Nematoctonus* to the Basidiomycotina and noted the similarity to cultures of *Corticium incrustans* (Nobles 1937), and *Pleurotus pinsitus*, as described by Vandendries (1934). The illustrations of *Pleurotus pinsitus* by Vandendries (1934) probably referred to *Hohenbuehelia geogenia* (Kuehner and Romagnesi, 1954). Unfortunately, Drechsler never observed a basidiome associated with any of his isolates of *Nematoctonus*.

Thirty-five years after Drechsler described *Nematoctonus*, a small agaric formed in a pure culture of an isolate of *Nematoctonus* (Barron and Dierkes, 1977). In the presence of nematodes, each discharged basidiospore germinated to produce a terminal adhesive process, with an hour-glass secretory cell typical of **Nematoctonus**. This mushroom, a species of **Hohenbuehelia**, represented the first conclusive evidence of a sexual state in **Nematoctonus**. The apex of the cheilocystidia of their **Hohenbuehelia** was identical in appearance to the hour-glass adhesive knobs of **Nematoctonus** species, and Barron and Dierkes (1977) postulated that adhesive knobs may have evolved from such cystidia. Hour-glass secretory cells are common on the cystidia on the gills, the surface of the cap and stalk of many species of **Hohenbuehelia**. Kuehner et al. (1962) illustrated similar cystidia in **Hohenbuehelia longipes** and what appears to be the **Nematoctonus** state, complete with hour-glass adhesive trapping devices and conidia. Hoiland and Schumacher (1982) reported hour-glass secretory cells on the basal mycelium of **Hohenbuehelia panelloides** and presumed it to be nematophagous. The secretory cystidia in **Pleurotus** (Hilber 1982) differ slightly in that the apex is not as neat an hour-glass as those in **Hohenbuehelia**.

Thorn and Barron (1984) reported the nematophagous ability of some wood-inhabiting agarics. The cultures of six species of **Hohenbuehelia** (one misidentified as **Resupinatus silvanus**) and five species of **Pleurotus** attacked and consumed nematodes, and all six species of **Hohenbuehelia** that attacked nematodes had **Nematoctonus** anamorphs. Species of **Pleurotus** have a unique method of capturing nematodes (Thorn and Barron, 1984). Nematodes were immobilized following contact with toxic droplets on the hyphae. Hyphae in the vicinity of an immobilised nematode grew toward its mouth then down its oesophagus. Giuma and Cooke (1971) reported that nematodes were immobilised by contact with germinating conidia of **Nematoctonus haptocladus** and **N. concurrens** or by the extracts of the mycelia or culture filtrates. The toxin involved is thermostable and probably polysaccharide in nature (Giuma et al., 1973). This toxin differs substantially from the toxin of **Pleurotus** in that effects were noted after 24 hours (Giuma and Cooke, 1971) or 56 hours (Giuma et al., 1973), whereas the toxin of **Pleurotus** acted within one minute (Barron and Thorn, unpublished data). The **Pleurotus** toxin has not been characterized.

It is important to make the connection between species of **Hohenbuehelia** and their **Nematoctonus** asexual states. Nine species of **Nematoctonus** have been validly described (Giuma and Cooke, 1972), and occur in soils worldwide (Feder, 1962; Gazzano, 1973; Gray, 1983; Kitz and Embree, 1979; McCulloch, 1977). Barron (1978) reported five named and one unknown species of **Nematoctonus** from Ontario. **Hohenbuehelia** is classified by Singer (1975) in the tribe Resupinateae, along with the genera *Aphyllotus*, *Asterotus*, *Resupinatus*, *Stigmatolemma* and *Stromatocyphella*. No monograph indicates how many species of the Resupinateae might occur in Ontario, but Coker (1921, 1944) reported 17 species from North Carolina.

This paper reports an investigation of the Ontario species of *Nematoctonus* and the fungi belonging to the Resupinateae that might represent their teleomorphs. This study consisted of two parts. Part one is a study of *Nematoctonus*. A survey was conducted to isolate *Nematoctonus* from varied habitats across Ontario and to collect fruit bodies and make cultures of any members of the Resupinateae encountered. Part two is a taxonomic study of the Ontario species of Resupinateae.

PART I: *NEMATOCTONUS*

When Drechsler (1941) described *Nematoctonus*, he emphasised just three things: species of *Nematoctonus* develop within minute living animals, have hyaline hyphae with clamp connections, and produce simple conidia on sterigmata along their hyphae. The conidia of *N. leiosporus* and *N. tylosporus* germinate to produce an adhesive process that adheres to the cuticle of nematodes (Drechsler, 1941). Fungi that attack nematodes by adhesive or ingested spores are termed parasites (Drechsler, 1941) or endoparasites (Barron, 1977). *Nematoctonus leptosporus* and *N. pachysporus* (Drechsler, 1943) are also endoparasitic. The six other described species of *Nematoctonus*, *N. haptocladus* Drechsler, 1946), *N. concurrens* (Drechsler, 1949), *N. campylosporus* (Drechsler, 1954), *N. robustus* (Jones, 1964), *N. lignicola* (Salonen and Ruokola, 1968; not validly published), and *N. tripolitanius* (Giuma and Cooke, 1972), produce adhesive trapping devices, sometimes called capture pegs or adhesive knobs, directly on their hyphae so that a number of nematodes can be caught by a single hyphal system. Fungi that capture nematodes in this way are termed predatory, or predaceous (Drechsler, 1941; Barron, 1977).

Giuma and Cooke (1972) provided a key to the nine validly-published species that emphasised the presence or absence of chlamydospores (= resting spores, or aleuriospores in this case), the presence or absence of predatory adhesive knobs on the hyphae, and the size and shape of the conidia. Two additional new species have since been described under provisional names (Alger, 1980). Surveys of nematophagous fungi by Barron (1978), Kitz and Embree (1979) and Gray (1983) each reported an unidentified species of *Nematoctonus*. Our preliminary investigations (Thorn and Barron, 1984, and this study) revealed a number of *Nematoctonus* isolates that did not correspond with the descriptions of known species.

Barron (1978) surveyed the nematophagous fungi in 500 soil samples from Ontario, and recorded ***Nematoctonus campylosporus*, *N. concurrens*, *N. haptocladus*, *N. leiosporus*, *N. pachysporus***, and one unidentified species of ***Nematoctonus***. This survey, however, did not sample all habitats occupied by species of ***Hohenbuehelia*** and ***Resupinatus*** in Ontario, and provided no descriptions of the species reported.

MATERIALS AND METHODS[1]

A: Isolation Techniques

We attempted to isolate ***Nematoctonus*** from samples of soil, rotting wood, moss, or other substrates that were collected in a variety of habitats and locations in Ontario (Table 1). A total of 713 samples of 400-500 mL were collected and processed during the spring, summer and fall of 1983 and 1984. Most samples were processed by both the Baermann funnel technique (Giuma and Cooke, 1972) and the centrifuge technique (Barron, 1977), and a few were processed as soil sprinkle plates (Barron, 1977). All of the species of ***Nematoctonus*** found in a survey of Ontario farm soils (Barron, 1978) were recovered by the combination of the Baermann funnel and centrifuge techniques.

The Baermann funnel technique used in this study was simplified from that described by Giuma and Cooke (1972) and Barron (1977). First, the samples were mixed roughly by shaking the collecting bags, and breaking up any large clumps. A subsample of 100 to 150 mL was wrapped in two layers of Kimwipe tissue, and set on a screen tray in the Baermann funnel apparatus (illustrated in Barron, 1977). Nematodes were collected approximately 12 and 24 hours after setting up the funnels and transferred in 0.5 mL water to a petri plate containing approximately 10 mL of 2% water agar (WA). These WA plates, about a week old, were slightly dry and quickly absorbed the drop of water containing the nematodes.

The centrifuge technique (Barron, 1977) was modified slightly. A subsample of approximately 150 mL, without stones, was placed in a 500 mL mason jar. Approximately 200 mL of distilled water was added and the mixture blended at

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[1] See Appendix 1: Media and Reagents

medium speed with one blade of an Iona hand mixer. Part of the slurry was passed through a 0.7 mm mesh nylon screen to fill a sterile 50 mL round-bottomed centrifuge tube and spun in a clinical centrifuge for 8 minutes at one quarter-speed to remove the heavier soil particles and large spores. Approximately 14-15 mL of the cloudy supernatant was decanted into a 15 mL conical centrifuge tube, spun one hour at full speed, and all but 0.5 mL of the clear supernatant pipetted off with a sterile pasteur pipette and discarded. The residue was stirred with the tip of the pipette then spread in three crossing lines on a one-week-old WA plate.

Two drops of concentrated, mixed nematode suspension from stock cultures of ***Rhabditis terricola*** Dujardin (from the University of Guelph) and ***Panagrellus redivivus*** (L.) Goodey (obtained from B. Nordbring-Hertz, University of Lund, Sweden) were added to each of the WA plates containing the centrifuge residue. Stock cultures of these nematodes were maintained at room temperature in petri plates of Nigon's agar (Barron, 1977). Nematode stock cultures were transferred every two weeks by swirling 1 mL of sterile saline in a stock plate and pouring one third into each of three one-week-old plates of Nigon's agar.

Soil sprinkle plates (Barron, 1977) were prepared by sprinkling approximately one mL of sample across a WA plate which had been baited with two drops of nematode suspension as above.

The Baermann samples and baited plates were examined periodically for three weeks using a dissecting microscope at 10X, with an intense light set at a low angle to facilitate finding nematodes infected with ***Nematoctonus***. Nematodes infected by species of ***Nematoctonus*** could usually be recognized under the dissecting microscope by the fine, wispy fertile hyphae, and then confirmed quickly under the compound microscope by the presence of clamp connections on these hyphae.

B: Cultural Studies

Pure cultures of ***Nematoctonus*** were isolated in the following way. Once the presence of ***Nematoctonus*** was established, the plate was searched for a freshly-infected nematode, with clamped hyphae just emerging from the body of the host. This nematode was transferred with a fine needle to a plate of potato dextrose agar (PDA) amended with 60 ppm chlorotetracycline ("aureomycin") and 2.5 ppm benomyl (PD+AB agar). The nematode was dragged gently through the agar with the needle, then the needle flamed and cooled, and the nematode transferred to a clean area of the plate.

In most instances, hyphae of the *Nematoctonus* grew quickly out of the transferred nematode onto the PD+AB agar. The aureomycin suppressed bacterial growth, and the benomyl suppressed most contaminant fungi such as *Penicillium* and *Aspergillus* (Edgington et al., 1971). A pure culture of the *Nematoctonus* could usually be obtained by a transfer from the margin of the colony radiating from the original infected nematode.

The procedures used for the isolation of *Nematoctonus* cultures from fruit bodies of *Hohenbuehelia* are outlined in Part II.

The ability of cultures to consume nematodes was tested using the technique of Thorn and Barron (1984). After a new colony on WA had attained a diameter of about 3 cm, 10 to 20 clean, active nematodes were added to the colony surface. Observations on interactions between nematodes and the test fungus were made immediately and at 15-minute intervals for the first hour, then hourly for the next 8-12 hours, and again after 24 hours. More nematodes were added daily to the cultures and observations continued for 7 days.

Morphological features of *Nematoctonus* cultures were studied using a similar technique. Cultures on WA were seeded with a few nematodes. After one or more days, when abundant adhesive knobs or adhesive conidia had formed, more nematodes were added. Clean nematodes representing different infection stages, from first capture to total colonisation with abundant reproduction on external hyphae, were transferred on minute chips of agar to microscope slides, fixed with acetic alcohol, and mounted in PVLG (Koske and Tessier, 1983).

C: Taxonomic Characters

Species of *Nematoctonus* possess few morphological features useful in identification. These features are their hyphae, spores and adhesive processes.

A colony of *Nematoctonus* consists of assimilative hyphae within the body of the host nematode, and fertile hyphae on the exterior. The diameter of the assimilative and fertile hyphae may be relatively consistent within a species. The conidiogenous pegs that subtend and produce conidia (sometimes called sterigmata or conidiogenous denticles) vary between species as to length, branching, and breadth at the base and apex, although they vary within isolates as well. The conidiogenous pegs of most *Nematoctonus* species are simple but those of *N. tylosporus* and *N. leptosporus* were reported to be branched once or twice (Drechsler, 1941, 1943). Specialized branches bearing multiple conidia in ***N. robustus*** (Jones, 1964) and ***N. lignicola*** (Salonen and Ruokola, 1968) were observed in cultures grown on nutrient agar, on which conidiation and growth may be atypical. These reports may thus be disregarded for taxonomic purposes.

Fertile hyphae produce asexual spores of one or two types: smooth, thin-walled conidia of various shapes, and thick-walled aleuriospores (= resting spores or chlamydospores), which are elliptical or ovate and often spiny. The size and shape of the conidia are among the most important features for the identification of species of ***Nematoctonus***. The presence or absence of aleuriospores provides clear-cut distinctions between species of ***Nematoctonus***, since only ***Nematoctonus tylosporus***, ***N. pachysporus*** and ***N. tripolitanius*** have aleuriospores. The final set of morphological characters used in the taxonomy of ***Nematoctonus*** refers to the adhesive processes by which nematodes are caught and consumed. Predatory species have adhesive knobs on their hyphae (predatory adhesive knobs) and, as mentioned above, may or may not readily produce adhesive knobs on their conidia. Hyphal adhesive knobs of all species are produced by hour-glass-shaped secretory cells, but may vary in their location (terminal, intercalary, or both). The conidial adhesive processes of most species of ***Nematoctonus*** develop from hour-glass-shaped secretory cells, but those of ***N. leptosporus*** and ***N. tylosporus*** develop from the morphologically undifferentiated tips of conidial germ tubes. The hour-glass cells of both conidial and hyphal adhesive knobs are sometimes quite characteristic of different species of ***Nematoctonus***.

Cultural characters, such as those used in the identification of wood-rotting fungi (Nobles, 1965) were not employed in this study, nor were characters of physiology or biochemistry. The agar beneath different species of ***Nematoctonus*** is often discoloured red, brown or yellow, and these colours may reflect the production of antibiotics (Robbins et al., 1947) or other metabolites. This discolouration was a feature of strains as well as species, since different single-spore isolates of ***Nematoctonus robustus*** (isolate T-14) produced either no colour or deep red-brown colouration in the PDA on which they were grown.

Measurements are given in micrometres (μm), with figures in parentheses representing values occurring in less than 10% of the measurements made. Acronyms of culture collections and herbaria are those listed by Holmgren et al. (1981).

RESULTS AND DISCUSSION

A: THE ONTARIO *NEMATOCTONUS* SURVEY

A total of 713 samples from soil, rotting wood, moss, and other suitable nematode habitats yielded 49 isolates of ***Nematoctonus***, representing 5 form-species (Table 1). ***Nematoctonus leiosporus*** (25 isolates) and ***N. hamatus*** (14 isolates) were most common. The best substrates for ***Nematoctonus*** were compost, with ***Nematoctonus*** isolated from 37.5% of the samples, followed by barnyard soil and dung (19.7%), sawmill wastes (15%), and rotting hardwoods (9.3%). Coniferous forest soil and duff, and mosses, lichens, and samples from bogs yielded no isolates of ***Nematoctonus***.

The Baermann funnel technique yielded 29 isolates of ***Nematoctonus***, the centrifuge technique 21 isolates, and soil sprinkling 5 isolates (Table 2). The Baermann funnel and centrifuge techniques were highly complementary, since only four isolates were duplicated by both techniques. Four of the five isolates of ***Nematoctonus*** found by soil sprinkling were not found by the Baermann funnel or centrifuge techniques. Thus, if time had been available for the routine use of the soil sprinkling technique, considerably more isolates of ***Nematoctonus*** might have been detected.

Three of the five form-species of ***Nematoctonus***

Table 1. Substrates Sampled and ***Nematoctonus*** Species Recovered

Substrate (# Samples)	**A***	**B**	**C**	**D**	**E**	**Frequency****
Barnyard Soil & Dung (76)	1	1	12	1	0	19.7%
Other Agric. Soils (60)	0	0	4	0	0	6.7%
Turf & Meadows (58)	1	1	1	0	0	5.2%
Compost (8)	0	0	3	0	0	37.5%
Hardwood Forest Duff & Soil (137)	0	3	2	2	0	5.8%
Coniferous Forest Duff & Soil (74)	0	0	0	0	0	0%
Rotted Hardwood (140)	0	6	3	1	3	9.3%
Rotted Conifer (52)	0	1	0	0	0	1.9%
Sawmill Wastes (20)	1	2	0	0	0	15.0%
Mosses, Lichens & Bogs (67)	0	0	0	0	0	0%
Total (713)	3	14	25	4	3	7.0%

*A = ***Nematoctonus geogenius***
B = ***N. hamatus***
C = ***N. leiosporus***
D = ***N. robustus***
E = ***N. subreniformis***

**Expressed as a per cent of recoveries per samples studied

Table 2. A Comparison of Techniques for Recovery of *Nematoctonus*

Species	Baermann Funnel	Centrifuge Technique	Soil Sprinkling	Total
N. geogenius	2	1	1	3*
N. hamatus	4	10	2	14
N. leiosporus	23	4	1	25
N. robustus	0	3	1	4
N. subreniformis	0	3	0	3
Total	29	21	5	50

*Some isolates recovered by more than one sampling technique

encountered during the survey are described as new. Four species of *Nematoctonus* reported to occur in Ontario (Barron, 1978) were not encountered during this survey, and we believe that the occurrence of *N. campylosporus*, *N. concurrens*, and *N. haptocladus* in Ontario is doubtful. The occurrence of the fourth species, *N. pachysporus*, is documented in reference cultures.

Nematoctonus angustatus (teleomorph *Hohenbuehelia angustata*) and *N. brevisporus* (teleomorphs *H. pinacearum* and *H. unguicularis*) were not recovered, despite the known occurrence of their teleomorphs in Ontario. A large number of samples of substrates suitable for these teleomorphs were studied in the hope of recovering their anamorphs, without success. *Nematoctonus angustatus* and *N. brevisporus* are predatory species, and the recovery of predators is more favoured by the soil sprinkling technique than the Baermann funnel or centrifuge techniques (Barron, 1977). Both species produce small conidia that should be readily recovered by the centrifuge technique, but studies of these species indicates that the bait nematodes used in this study are not their preferred hosts. Conidia of *N. brevisporus* failed to germinate to produce adhesive knobs in the presence of bait nematodes, and the conidia of *N. angustatus* that had produced adhesive knobs failed to adhere to and infect bait nematodes. In addtion, *N. angustatus* produced conidia sporadically and in small numbers, in culture on WA with nematodes.

This survey indicated preferred habitats for *Nematoctonus* in Ontario. More intensive surveys of these habitats, coupled with more intensive sampling and processing, will undoubtedly indicate *Nematoctonus* to be more frequent and widespread, and might also uncover additional species.

B: TAXONOMIC PART

NEMATOCTONUS (Drechsler, 1941: 779)

The original description of ***Nematoctonus*** was as follows, "Mycelium filamentous, hyaline; the assimilative hyphae more or less branched, developing within living animals; the nonassimilative hyphae developing outside of animals, mostly sparse, often prostrate, provided with clamp connections, at intervals producing hyaline conidia, together sometimes with slightly coloured spores, on simple or slightly branched ascending sterigmata" (Drechsler, 1941).

The original description distinguished ***Nematoctonus*** from all other genera of Hyphomycetes. ***Antromycopsis broussonetiae*** Pat. & Trab., the anamorph of ***Pleurotus cystidiosus*** (Pollack and Miller, 1976), is nematophagous (Thorn and Barron, 1984), but the conidia are black, and produced in slimy coremia, unlike those of ***Nematoctonus***.

Ten species of ***Nematoctonus*** have been described, but one, ***N. lignicola*** Salonen and Ruokola (1968), is not validly published since no type was designated. A key to the nine validly published species was provided by Giuma and Cooke (1972). Since then, two new species were described under provisional names (Alger, 1980). Several surveys of nematophagous fungi have reported one or more unidentified species of ***Nematoctonus***, without providing descriptions (Barron, 1978; Kitz and Embree, 1979; and Gray, 1983). A key to all known species of ***Nematoctonus***, including five new species, is provided.

The importance of observing and describing the morphology of ***Nematoctonus*** isolates on the basis of nematode culture on non-nutritive agar cannot be emphasised too strongly. On nutrient agar, characters such as the method of production of conidia and conidium shape differ considerably from these characters in nematode culture (Barron and Dierkes, 1977).

KEY TO FORM-SPECIES OF *NEMATOCTONUS*

1. Conidia simple, not transversely septate **2**
1. Conidia 2-celled, allantoid, 9.0-13.6 X 2.8-4.0 µm; presence of adhesive knobs and consumption of nematodes unknown .... ***Nematoctonus lignicola* nom. invalid.** Salonen and Ruokola (1968)
    2. Adhesive knobs present on hyphae; predatory species **3**
    2. No adhesive knobs present on hyphae (check closely); endoparasitic species **13**

3. Aleuriospores present, 10-15 (17.5) X 7.5-10 µm; conidia large, 15-20 (25) X 5-7.5 µm .... *Nematoctonus tripolitanius* Giuma and Cooke (1972)
3. No aleuriospores present; conidia narrower **4**
   4. Adhesive knobs predominantly terminal; hour-glass cells 3.5-6.5 µm long **5**
   4. Adhesive knobs predominantly intercalary; hour-glass cells 6-14 µm long **7**
5. Conidia narrow; straight or strongly curved **6**
5. Conidia stout; slightly or strongly curved, 9-14 X 3-5 µm .... *Nematoctonus subreniformis*
   6. Conidia straight or slightly curved, 11-18 X 3.3-4.5 µm .... *Nematoctonus haptocladus*
   6. Conidia rarely straight, most quite curved; (9.3) 10.0-13 (14.7) X 2.5-4 µm .... *Nematoctonus campylosporus*
7. Conidia cylindric, majority distinctly curved, 7-15 (18.5) X 2.5-4 µm .... *Nematoctonus robustus*
7. Conidia cylindric, elliptical, or tapering; straight or slightly curved **8**
   8. Many conidia over 13 um long; 10-24 X 3.2-5.6 µm **9**
   8. Majority of conidia under 13 um long; 7-14 X 1.7-5.0 µm **11**
9. Conidia fusoid **10**
9. Conidia cylindric, 10-23 X 3.3-5.6 µm (if conidia are consistently broader than 5 µm, see *N. tripolitanius*, above) .... *Nematoctonus concurrens*
   10. Conidia often with a distinct hook at apex, 12-24 X 3.5-4.5 µm .... *Nematoctonus hamatus*
   10. Conidia without an apical hook, (7.5) 10-18 X 2 µm .... *Hohenbuehelia longipes* anamorph, cf. Kuehner et al. (1962)
11. Conidia cylindric, 7-11.5 X 2.1-4.0 µm; hour-glass cell of predatory adhesive knobs narrow, 8-11.5 X 2-3.2 µm .... *Nematoctonus brevisporus*
11. Conidia not cylindric, or with broader hour-glass cell in adhesive knobs **12**
   12. Conidia narrowly fusoid, 7.8-13.5 X 1.5-2.6 µm, in rotting hardwood logs .... *Nematoctonus angustatus*
   12. Conidia elliptic, broadly fusoid or cylindric, 7.5-14.5 X 3-4.5 µm; apex often slightly curved; in rich soil, woody debris or peat .... *Nematoctonus geogenius*
13. Aleuriospores present **14**
13. Aleuriospores absent **15**

14. Aleuriospores narrowly elliptic, 8-11 X (3.3) 4-4.5 µm; conidia 15.5-22 X 2.2-2.9 µm .... ***Nematoctonus tylosporus*** Drechsler (1941)

14. Aleuriospores broadly elliptic, 10-13 X 5.5-8.8 µm; conidia 12-19 X 4-5.5 µm .... ***Nematoctonus pachysporus***

15. Conidia fusoid, with prominent hook at apex, 12-24 X 2.7-5.4 µm ...... ***Nematoctonus hamatus***

15. Conidia without hooked apex **16**

16. Conidia rod-shaped, 21-28 X 1.7-2.2 µm; adhesive apex without hour-glass secretory cell .... ***Nematoctonus leptosporus***

16. Conidia broader, with distinct hour-glass cell in apical adhesive knob **17**

17. Conidia fusoid, 14-30 X 2.3-4.0 µm; hour-glass cell with subapical constriction, terminal bulge approximately spherical, 0.6-1.2 µm diam .... ***Nematoctonus leiosporus***

17. Conidia shorter or more cylindric **18**

18. Conidia cylindric, 12-23.5 X 2.2-4.2 µm; in rotting logs (deciduous or coniferous) .... ***Nematoctonus cylindrosporus***

18. Conidia elliptic, broadly fusoid or cylindric, 9-16 X 3-4.5 µm, apex often slightly curved, and germinating to form one or two bulges prior to hour-glass cell; in soil, woody debris, or peat .... ***Nematoctonus geogenius*** (if conidia are as above but 7.5-11 X 2.0-2.8 µm, see comments on N84-604 under ***N. geogenius***)

SPECIES DESCRIPTIONS

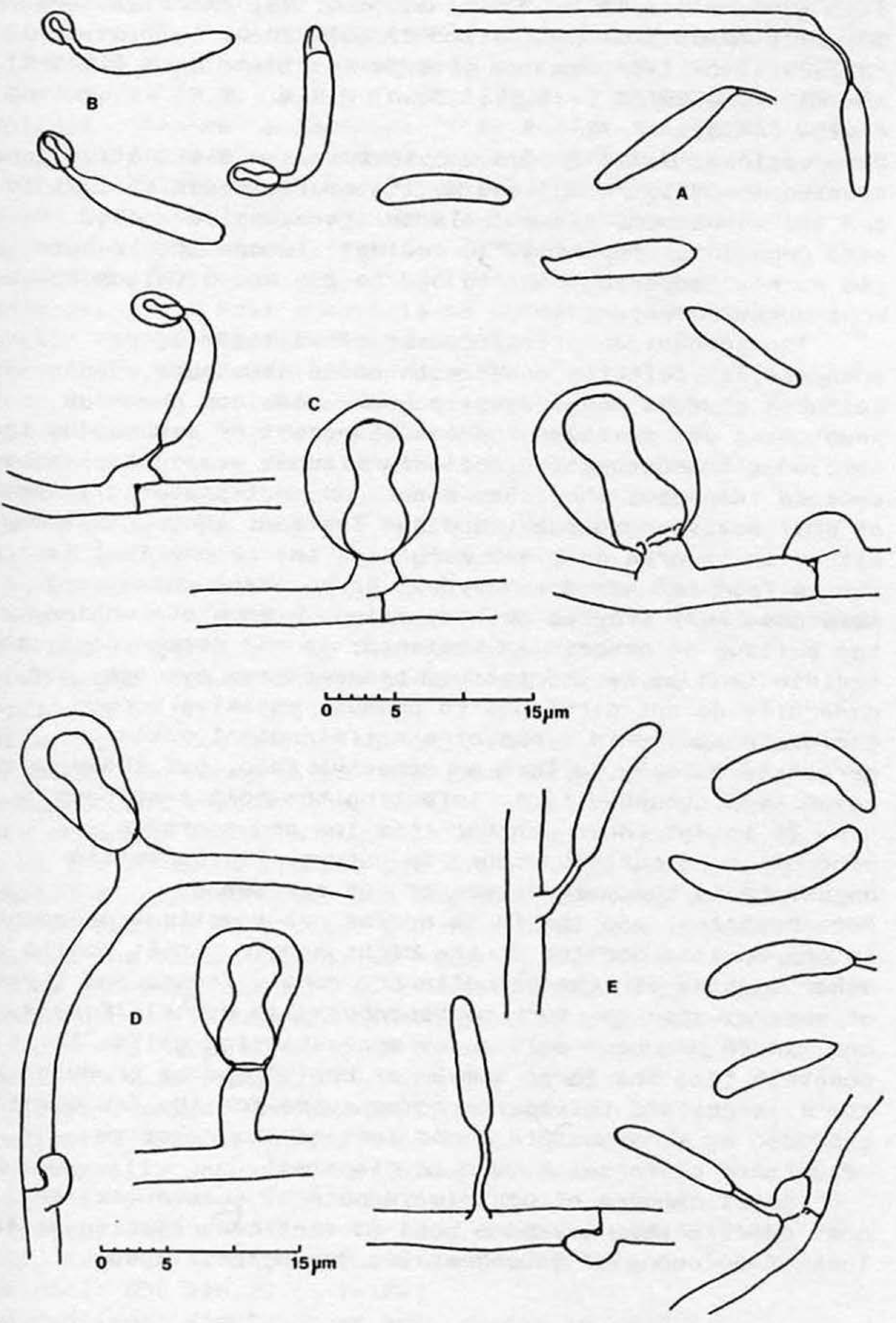
Nematoctonus angustatus Thorn et Barron, sp. nov. Fig. 1

Processus glutinosi hypharum vermiculos nematoideos adhaerentes; cellulae secretoriae 8-11 µm longae X 3-5 µm crassae, medio constrictae; mucus 9-12 X 6-8 µm. Conidia hyalina, laevia, plerumque anguste ovata, (7.8) 8.5-12 (12.5) X (1.7) 1.8-2.2 µm. Hyphae fibulatae, hyalinae; hyphae assumentes 2-3 µm crassae; hyphae extri 1.2-3.0 µm crassae. Typus DAOM #193369.

Assimilative Hyphae developing within living nematodes that are caught by adhesive knobs on external hyphae, and presumably also infecting by adhesive conidia, hyaline, with clamp connections, 1.8-3.0 µm diam., filling the body of the host and digesting its contents, then perforating the cuticle to emerge as external, fertile hyphae. **Fertile**

Hyphae hyaline, with clamp connections, 1.2-3.0 (3.5) µm diam., bearing numerous adhesive knobs and, in certain regions of the colony, conidia that are borne on thread-like stalks 0.8-6.0 µm long X 0.2-0.6 µm, sometimes inflated to 1.5 µm broad at the base, arising from the surfaces and apices of hyphae and from clamp connections. **Predatory Adhesive Knobs** predominantly intercalary on lateral branches up to 5 µm long X 3.5 µm diam., hour-glass cell at first small and naked, then growing and swelling to 8-11 X 3-5 µm, and becoming surrounded by adhesive mucus 8-14 X 5-11 µm, then capturing nematodes, which generally are first caught in the head region, and then become attached to one or more additional adhesive knobs in other body regions during thrashing attempts to escape, the hour-glass cells of the attached adhesive knobs then germinating to penetrate the cuticle of the nematode, and in addition several, often 10 or more, accessory adhesive branches home in on the head of the nematode from a distance of approximately 50 µm and can be seen entering the buccal cavity or penetrating the cuticle nearby. **Aleuriospores** none. **Conidia** hyaline, most tapering to the apex, straight or slightly curved, some narrowly cylindric, (7.8) 8.5-13 (13.5) X (1.5) 1.8-2.4 (2.6) µm, germinating to form an upturned germ tube tipped with an adhesive knob, the hour-glass cell 2.5-3.5 X 0.8-1.0 µm, usually surrounded by a mucoid droplet 3-4 X 2.5-3 µm.
Teleomorph: *Hohenbuehelia angustata* (Berk.) Singer.
Hosts: Adhesive conidia were never seen to infect nematodes in our mixture of *Rhabditis terricola* and *Panagrellus redivivus*, but the predatory adhesive knobs caught these nematodes readily and the nematodes were subsequently consumed. Although the substrate beneath fructifications of *Hohenbuehelia angustata* was sampled repeatedly, the anamorph was never isolated in Baermann, centrifuge, or sprinkle plates.
Habitat and Distribution: *Hohenbuehelia angustata* is found on soggy, brown-rotted hardwood logs in the eastern United States and Canada. It seems likely that the *Nematoctonus* state occurs in the wood as well.
Isolates Studied: *Hohenbuehelia angustata*: Blair, Ontario:

Figure 1 A-E: *Nematoctonus angustatus*, from cultures of *Hohenbuehelia angustata*. A-C: T-91 (RGT #830820/10). A) conidia; B) conidia germinated to form adhesive knobs; C) predatory adhesive knobs. D-E: T-87 (RGT #830822/10). D) predatory adhesive knobs (at a slightly reduced scale); E) conidia and fertile hyphae.


B
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R.G. Thorn #840722/02 (= T-151) and RGT #840722/03 (= T-152); Pinery Provincial Park, Ontario: RGT #830822/10 (= T-87); Rondeau Provincial Park, Ontario: RGT #830812/01 (= T-80), RGT #830812/02 (= T-81), RGT #830820/05 (= T-88), RGT #830820/10 (= T-91, source of **type** specimen, DAOM #193369), and RGT #830820/08 (= T-92); Iowa, U.S.A.: R.L. Gilbertson #14724 (ARIZ; = T-72).

Observations: ***Nematoctonus angustatus*** is a distinctive form-species, readily recognised by its small, tapering conidia and the stout hour-glass cells in its adhesive knobs. The name ***angustatus*** (meaning "narrowing") is applicable both to its narrow, tapering conidia and to its known teleomorph, ***Hohenbuehelia angustata***.

The production of conidia is often minimal, and sporadic, in cultures on WA with added nematodes. These cultures produce many adhesive knobs and trap numerous nematodes, yet sometimes become senescent or overrun by the nematodes and associated bacteria without ever producing any conidia. Conidia, when they occur, are not produced in areas of most active nematode trapping. Instead, they are formed either in an area near the margin of the colony that is remote from the added nematodes, or in areas where many nematodes were trapped but the colony became overwhelmed by the buildup of associated bacteria. In the former case, the conidia tend to be shorter and broader than average, and generally do not germinate to produce adhesive knobs. Conidia produced in areas of great microbial activity germinate quickly to form an adhesive knob, but these were never seen attached to or infecting the bait nematodes.

It is not known whether this low and sporadic production of conidia occurs in nature. ***Hohenbuehelia angustata*** is the most common of our species of ***Hohenbuehelia***, and its fruit bodies are sometimes abundant in appropriate habitat at the right season. Fruit bodies of other species of ***Hohenbuehelia*** are rarely found, and those of several species, such as ***Hohenbuehelia cyphelliformis***, are minute and have only a few spore-bearing gills. It is possible that the large number of basidiospores produced by the ***H. angustata*** teleomorph compensates for the few conidia produced by ***N. angustatus***, and lessens the relative importance of these conidia in dispersal.

Small numbers of conidia in natural substrates, and host specificity, may have been factors contributing to the lack of recovery of ***N. angustatus*** during this study.

Nematoctonus brevisporus Thorn et Barron, sp. nov. Fig. 2

Processus glutinosi hypharum vermiculos nematoideos adhaerentes; cellulae secretoriae (7) 8-11 µm longae X 2.5-3.0 µm crassae, medio constrictae, 1.2-1.5 um crassae; mucus 9-12 X 6-9 µm; conidia hyalina, cylindracea, laevia, (8.2) 8.8-11.0 X (2.8) 3.0-3.8 (4.0) µm. Hyphae fibulatae, hyalinae; hyphae assumentes (1.5) 2-3 µm crassae; hyphae extri (1.5) 2-3.5 µm crassae. Typus DAOM #193368.

Assimilative Hyphae developing within living nematodes caught by adhesive knobs on the external hyphae, hyaline, with clamp connections, 1.5-3.0 (3.5) µm diam., filling the body of the host and digesting its contents, then penetrating the host's cuticle to emerge as external, fertile hyphae. **Fertile Hyphae** hyaline, with clamp connections, both aerial and prostrate, (1.2) 1.5-3 (4) µm diam., bearing conidia on tapering pegs 1-6 um long X 0.5-1.5 um broad at the base, 0.2-0.8 µm broad at the apex.
Predatory Adhesive Knobs intercalary or occasionally terminal; the side branches on which the intercalary knobs are borne 3-12 µm long X 1.5-2.5 µm diam.; the hour-glass cells (7) 8-11.0 (11.5) X (2.0) 2.2-3.2 (3.8) µm.
Aleuriospores none. **Conidia** hyaline, more or less cylindric, smooth, (7.0) 7.2-10.5 (11.5) X (2.1) 2.2-3.3 (4.0) µm, not observed to germinate to form adhesive knobs.
Teleomorphs: ***Hohenbuehelia pinacearum*** Thorn and ***H. unguicularis*** (Fr.) Miller.
Hosts: Some nematodes in the bait mixture of ***Rhabditis terricola*** and ***Panagrellus redivivus*** were captured and consumed, but whether one, or the other, or both species were consumed is not known. The consumption of nematodes on WA by the isolates studied did not keep up with the bait nematodes' reproduction, and the colonies were usually overrun about 7 days after the nematodes were added.
Habitat and Distribution: ***Hohenbuehelia pinacearum*** fruits on trunks and twigs of dead conifers, particularly ***Abies***, in Europe and North America. ***Hohenbuehelia unguicularis*** occurs on logs and twigs of dead hardwoods, particularly ***Populus***, and is likewise found in Europe and North America.
Isolates Studied: ***Hohenbuehelia pinacearum***: Algonquin Provincial Park, Ontario: R.G. Thorn #831015/04 (= T-107). ***Hohenbuehelia unguicularis***: Black Sturgeon Lake, Thunder Bay District, Ontario: DAOM #159734 (= T-47, source of type specimen, DAOM #193368); Cantley, Quebec, DAOM #191960; Star Lake, New York : DAOM #155519 (= T-100); France (det. R. Kuehner): CBS 606.79 (= T-184).
Observations: ***Nematoctonus brevisporus*** is readily distinguished from other members of the genus by its short,

cylindric conidia. These conidia were not seen to germinate to form adhesive knobs, even after prolonged association with nematodes and bacteria. In one plate of T-184, conidia germinated feebly 4 days after the colony had been overrun by nematodes. The germ tubes were cylindric, and soon ceased growth (Figure 2 C). The ability of ***N. brevisporus*** to infect nematodes endoparasitically remains unknown, but is nonetheless likely. It may be that neither of the bait nematodes used are the preferred hosts of ***N. brevisporus***.

Hohenbuehelia pinacearum and ***H. unguicularis*** are both quite uncommon. ***Nematoctonus brevisporus*** was not recovered during this survey, despite repeated sampling of habitats suitable to its teleomorphs. This could be explained in part by the rarity of these fungi, and the possibility of host preference for species of nematodes other than those that were used as bait.

Nematoctonus campylosporus Drechsler (1954: 82) Fig. 3 A

Nematoctonus campylosporus was reported from Ontario (Barron, 1978), but not found during this study. An Ontario isolate (Barron #17, Fig. 3 B), previously identified as ***N. campylosporus***, has been redetermined as ***N. robustus***. The key features of ***N. campylosporus***, according to the original description (Drechsler, 1954), are the slender hyphae 1.7-2.5 µm wide; small, terminal adhesive knobs with hour-glass cells 3.5-5 µm long by 1.6-2.0 µm wide; and strongly curved conidia 10-13 X 2.5-4 µm. The following description is based on two isolates from Argentina examined during this study:

Assimilative Hyphae hyaline, clamped, 1.5-2.5 µm diam. **Fertile Hyphae** hyaline, clamped, 0.8-1.8 µm diam., swelling to 2.5-3.0 µm diam. in the subapical segment, supporting the adhesive knobs. **Predatory Adhesive Knobs** predominantly terminal, occasionally intercalary; hour-glass cells 3.5-6.0 X 1.5-2.8 µm, surrounded by mucoid drop 4.5-7 X 3.5-5 µm. **Aleuriospores** none. **Conidia** hyaline, smooth, cylindric,

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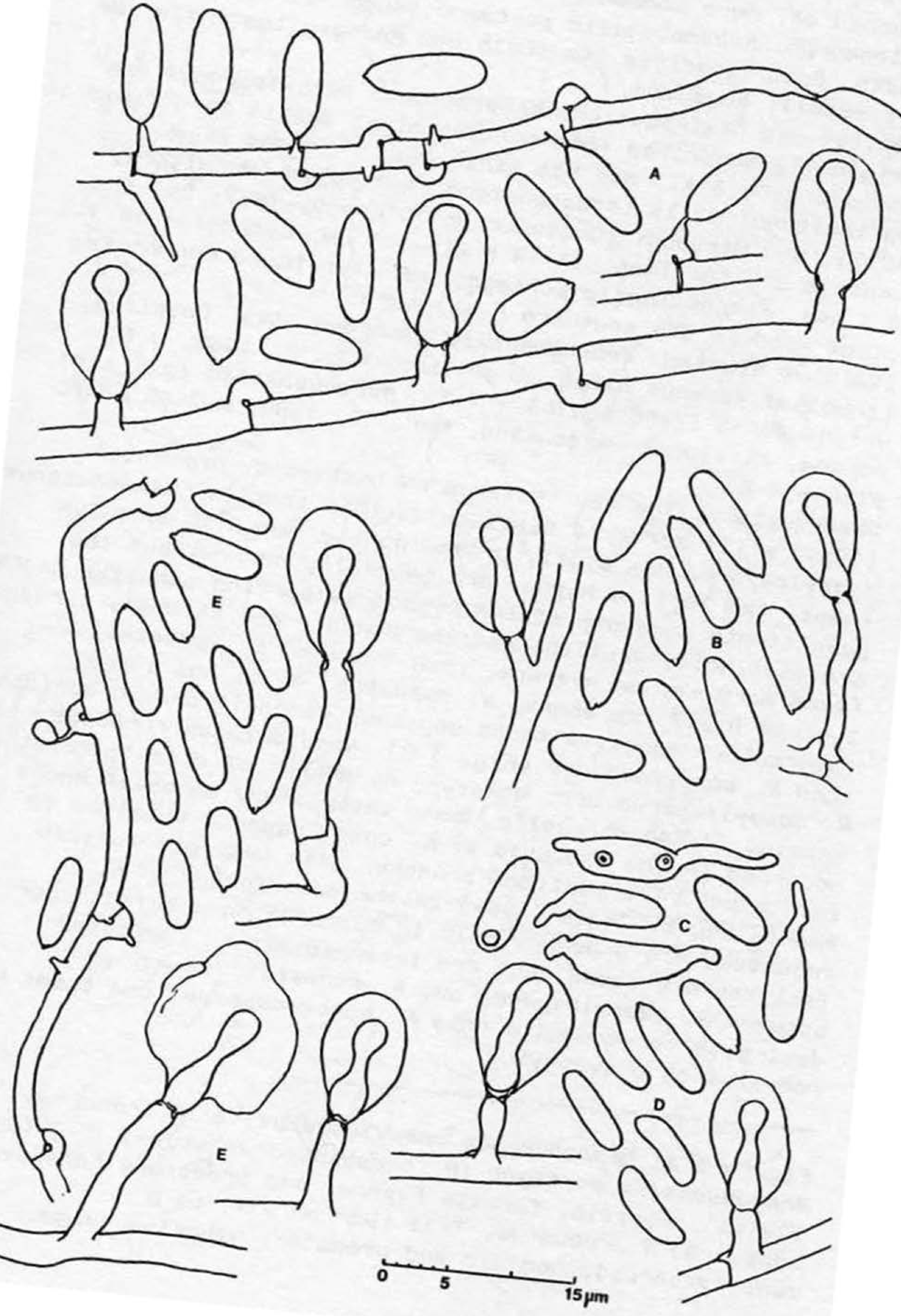
Figure 2 A-E: ***Nematoctonus brevisporus*** A) ***Hohenbuehelia unguicularis***, T-47 (DAOM #159734), conidia, fertile hyphae and predatory adhesive knobs. B) ***H. unguicularis***, T-100 (DAOM #155519), conidia and adhesive knobs. C-D) ***H. unguicularis***, T184 (CBS 606.79). C) four germinated conidia, and two showing swelling prior to germination; D) conidia and predatory adhesive knobs. E) ***Hohenbuehelia pinacearum***, T-107 (RGT #831015/04), conidia, fertile hypha and predatory adhesive knobs. Adhesive mucus of one adhesive knob spread and flattened in mounting.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strongly curved, 10-15 X 2.4-3.6 µm, with rounded apices and rounded or, more commonly, broadly conical bases.

Teleomorph: ***Hohenbuehelia portegna*** (Spegazzini) Singer.

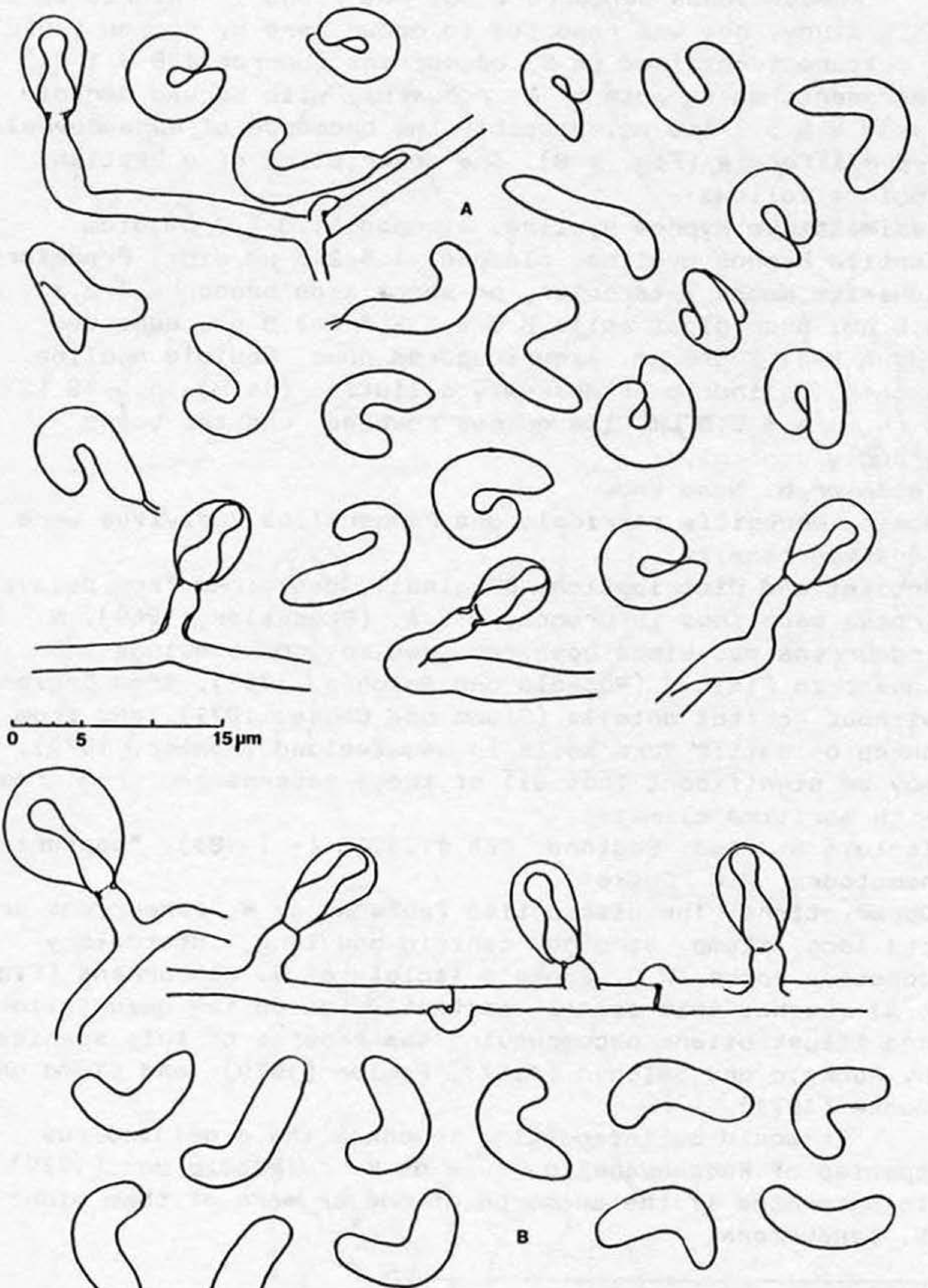
Hosts: Both ***Rhabditis terricola*** and ***Panagrellus redivivus*** are readily consumed.

Habitat and Distribution: ***Nematoctonus campylosporus*** was originally described from rotting plant debris in a field in Louisiana, U.S.A., and has since been reported from agricultural soils in Queensland, Australia (McCulloch, 1977), and Missouri (Castaner and O'Leary, 1967; but the conidia are too long, 14-19 X 2.5-3.5 µm, averaging 16.3 X 3.1 µm). ***Hohenbuehelia portegna*** has been found on rotting dicot wood in the southern hemisphere.

Isolates Studied: ***Hohenbuehelia portegna***: Sta. Catalina, Llavallol, Buenos Aires, Argentina, Nov. 3, 1968, J.E. Wright #1136 (BAFC #29143 = T-7). ***Hohenbuehelia*** sp.: Alto Parana, Missiones, Argentina, Mar. 10, 1980, M-3405 (BAFC #186 = T-8).

Observations: The key features emphasized by Drechsler (1954) still serve to distinguish this species. ***Nematoctonus campylosporus*** has small, predominantly terminal adhesive knobs; the fertile hyphae are generally narrow, but the penultimate segments of the hyphae supporting adhesive knobs are distinctly swollen; and the conidia are strongly curved (much more so, on average, than those of ***N. robustus***). Isolate B #17 represents ***N. robustus***, as it has large, intercalary adhesive knobs and less strongly curved conidia than ***N. campylosporus*** (Fig. 3 B). ***Nematoctonus robustus*** and ***N. campylosporus*** are, however, anamorphs of closely-related species of ***Hohenbuehelia***. Some intercalary adhesive knobs occurred in the isolates of ***N. campylosporus*** examined in this study. The vertical branches with multiple conidia, emphasized by Jones (1964) in the description of ***N. robustus***, are produced only in cultures on nutrient agar. If isolates are found that are intermediate in character between ***N. campylosporus*** and ***N. robustus***, it may be desirable to recognise only ***N. campylosporus***, and treat ***N. robustus*** as a synonym.

Figure 3 A: ***Nematoctonus campylosporus***; **B**: ***N. robustus***. A) ***Hohenbuehelia portegna*** (***N. campylosporus*** state), T-7 (BAFC #29143), conidia, fertile hyphae, and predatory adhesive knobs. B) ***N. robustus***, T-12 (Barron #17, as ***N. campylosporus***), conidia and predatory adhesive knobs.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Nematoctonus concurrens Drechsler (1949: 382) Fig. 4 A

Nematoctonus concurrens was not found in Ontario during this study, but was reported to occur here by Barron (1978). A culture identified as ***N. concurrens*** (Barron #98 = T-21) represents an isolate of ***N. robustus***, with curved conidia 11-14.4 X 3.2-4.0 µm, possibly the anamorph of ***Hohenbuehelia cyphelliformis*** (Fig. 4 B). The description of a British isolate follows:

Assimilative Hyphae hyaline, clamped, 1.8-3.2 µm diam. **Fertile Hyphae** hyaline, clamped, 1.5-2.5 µm diam. **Predatory Adhesive Knobs** intercalary on short side branches 3-8 X 2.2-3.0 µm, hour-glass cells 8.5-9.5 X 3.0-3.5 µm, adhesive mucus 9-11 X 5-6 µm. **Aleuriospores** none. **Conidia** hyaline, smooth, cylindric or narrowly elliptic, (14.8) 15.5-19 (21) X (4.2) 4.5-5.8 µm, the apices rounded, and the bases broadly conical.

Teleomorph: None known.

Hosts: ***Rhabditis terricola*** and ***Panagrellus redivivus*** were consumed readily.

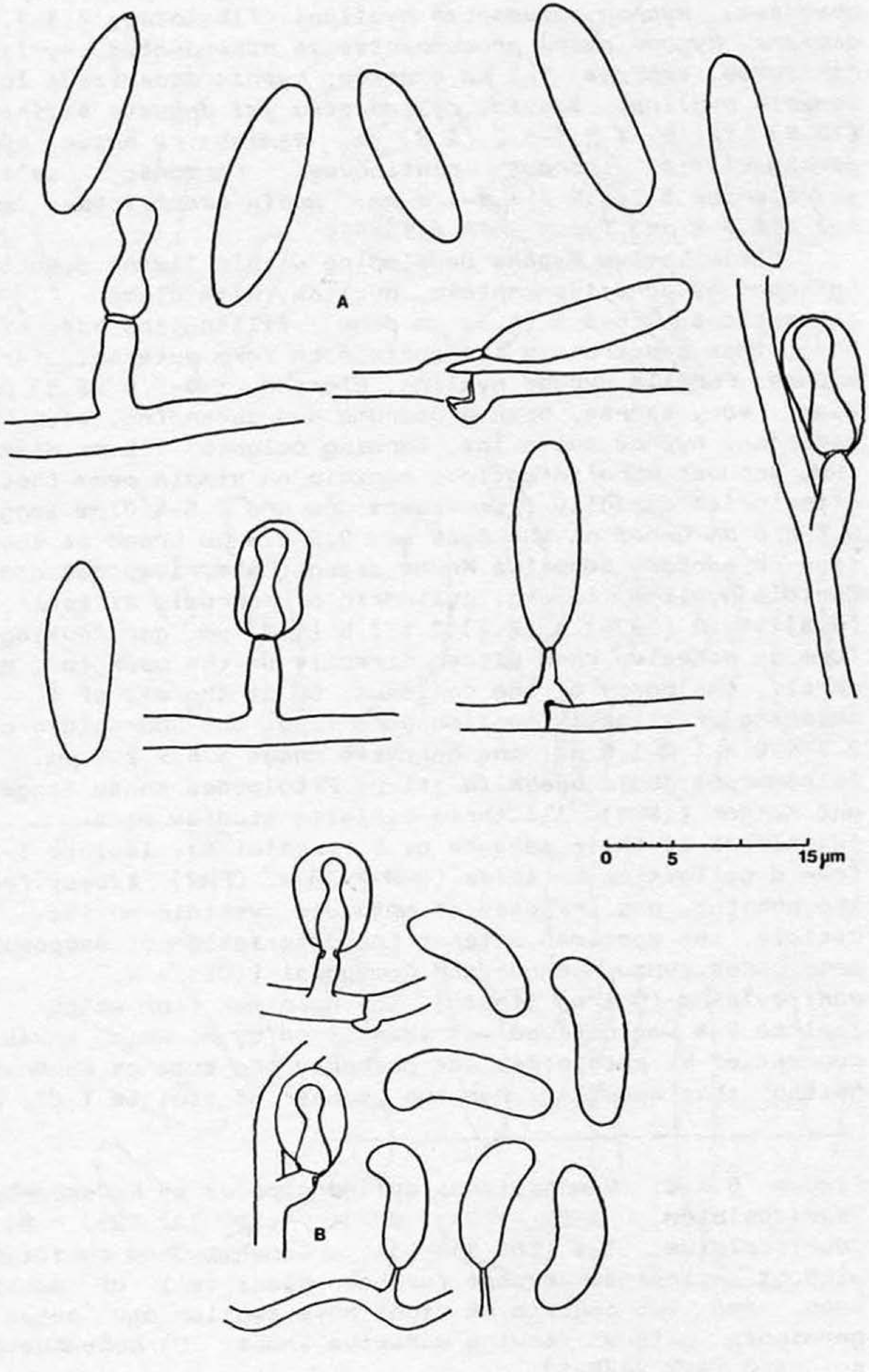
Habitat and Distribution: Originally described from decaying ***Bromus secalinus*** in Oregon, U.S.A. (Drechsler, 1949), ***N. concurrens*** has since been recorded in wood shavings from saunas in Finland (Ruokola and Salonen, 1967), from England, without habitat details (Giuma and Cooke, 1971), and from sheep or cattle-yard soils in New Zealand (Fowler, 1970). It may be significant that all of these records are from areas with maritime climates.

Isolate Studied: England: CBS #129.68 (= T-183), "capturing nematodes, R.C. Cooke".

Observations: The distinctive features of ***N. concurrens*** are its long, plump, straight conidia and long, intercalary adhesive knobs. R.C. Cooke's isolate of ***N. concurrens*** (Fig. 4 A) matched this concept perfectly, as do the descriptions and illustrations accompanying the records of this species by Ruokola and Salonen (1967), Fowler (1970), and Giuma and Cooke (1971).

It would be interesting to check the graminicolous species of ***Hohenbuehelia***, such as ***H. culmicola*** Bon (1979), to determine if the anamorph of one or more of them might be ***N. concurrens***.

Figure 4 A: ***Nematoctonus concurrens***; **B**: ***N. robustus***; A) ***N. concurrens***, T-183 (CBS 129.68), conidia, fertile hyphae, and predatory adhesive knobs. B) ***N. robustus*** T-21 (Barron #98, as ***N. concurrens***).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Nematoctonus cylindrosporus Thorn et Barron, sp. nov. Fig. 5

Species endoparasitica; processus glutinosi hypharum absentes. Hyphae assumentes hyalinae, fibulatae, 1.5-3.0 µm crassae. Hyphae extri procumbentes et ascendentes, hyalinae, fibulatae, sparsae, 1-2 µm crassae; hyphis ascentibus laxae. Conidia hyalina, laevia, cylindracea vel anguste elliptica, (10.5) 12-16 X 2.5-3.2 (3.8) µm, denique ex apice hypham germinationis corpus glutinosus formans; cellulae secretoriae 3.5-4.5 X 1.8-1.8 µm, medio constrictae; mucus 4-5 X 2.5-4 µm. Typus DAOM #193366.

Assimilative Hyphae developing within living nematodes infected by adhesive conidia, hyaline, with clamp connections, 1.5-3.5 (4.5) µm diam., filling the body of the host, then penetrating its cuticle to form external, fertile hyphae. **Fertile Hyphae** hyaline, clamped, 1.0-2.5 (3.5) µm diam., very sparse, both prostrate and ascending, with the ascendant hyphae quite lax, forming colonies 1-2 mm diam that produce more infectious conidia on simple pegs that often arise dorsally from clamps and are 0.5-4.0 um long X 0.5-2.0 µm broad at the base and 0.2-0.6 µm broad at the tips. **Predatory Adhesive Knobs** absent. **Aleuriospores** none. **Conidia** hyaline, smooth, cylindric or narrowly elliptic, (8.5) 11-18 (23.5) X (2.2) 2.5-3.5 (4.2) µm, germinating to form an adhesive knob either directly on the apex (or, more rarely, the base) of the conidium, or at the end of a tapering or slightly swollen germ tube; the hour-glass cell 2.7-4.0 X 1.2-1.8 µm; the adhesive mucus 3-5 X 2-4 µm. **Teleomorphs**: *Hohenbuehelia* stirps Petaloides sensu Singer and Kuthan (1980). All three isolates studied were identified by their senders as *H. petaloides*. Isolate T-2 is from a collection on *Abies* (OKM-2478-s, CFMR). Except for the habitat, and presence of metuloid cystidia on its cuticle, the specimen matches the description of *Geopetalum petaloides* sensu Kuehner and Romagnesi [1953 = *H. auriscalpium* (Maire) Singer]. The specimen from which isolate T-4 was derived was identified by R. Heim, whose concept of *H. petaloides* was probably the same as Kuehner's. Neither this specimen, nor the voucher of isolate T-82, were

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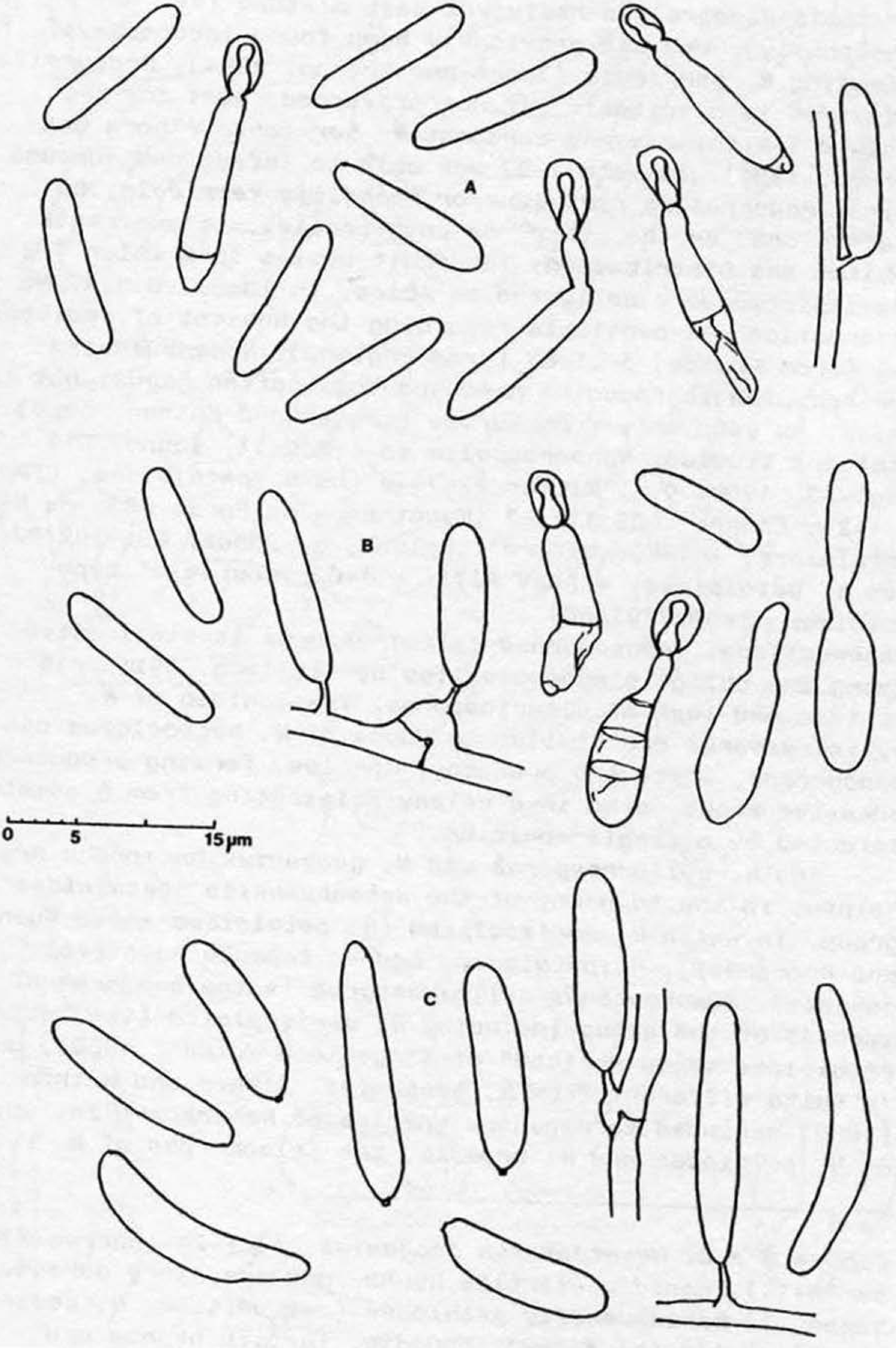
Figure 5 A-C: *Nematoctonus cylindrosporus* A) *Hohenbuehelia ?auriscalpium*, T-82 (CSAV #373; CBS 102.82). B) *H. ?auriscalpium*, T-4 (CBS 114.43), one germinated conidium is without cytoplasm except for hour-glass cell of adhesive knob, and two conidia at right have swollen and begun to germinate without forming adhesive knobs. C) *Hohenbuehelia* sp., T-2 (OKM 2478-S).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available for study.

Hosts: Isolate T-2 consumed nematodes of the *Rhabditis terricola-Panagrellus redivivus* bait mixture (but not vigourously), and had previously been found incapable of infecting *R. terricola* (Thorn and Barron, 1984). *Panagrellus redivivus* is a suitable, if not preferred, host for T-2. Isolate T-4 infects and consumes *R. terricola* (Thorn and Barron, 1984). Isolate T-82 was able to infect and consume either *Panagrellus redivivus* or *Rhabditis terricola*, but whether one, or the other, or both species, is uncertain.

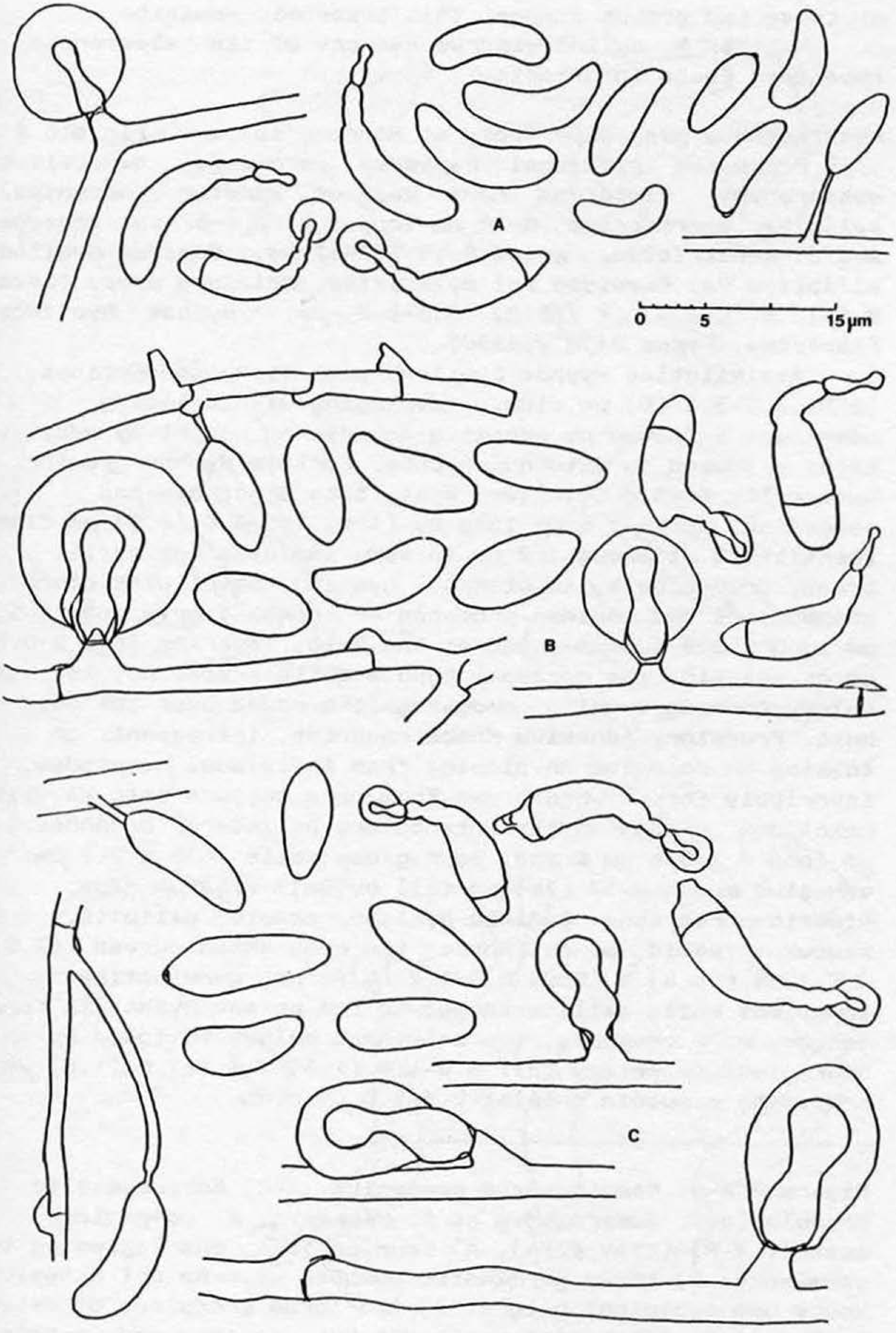
Habitat and Distribution: The fruit bodies from which T-2 was isolated were collected on *Abies*, in Idaho, U.S.A. No information was available regarding the habitat of isolates T-4 (from France) or T-82 (from England). *Hohenbuehelia auriscalpium* is found on hardwood logs, often *Fagus*, but is known, as yet, only from Europe (Singer and Kuthan, 1980).

Isolates Studied: *Hohenbuehelia* sp.: McCall, Idaho, U.S.A., Aug. 30, 1964, O.K. Miller #2478-s (as *H. petaloides*, CFMR; = T-2); France: CBS 114.43 (Mycotheque de Paris #67, as *H. petaloides*; = T-4); Oxford, England, E. Jones, CBS 102.82 (as *H. petaloides*; = CSAV #373; = T-82; source of **type** specimen, DAOM #193366).

Observations: *Nematoctonus cylindrosporus* is distinctive among the obligate endoparasites by its long, cylindric conidia and lack of aleuriospores. The conidia of *N. cylindrosporus* are similar to those of *N. haptocladus* and *N. concurrens*, which are predatory species, forming predatory adhesive knobs, even in a colony originating from a nematode infected by a single conidium.

The *N. cylindrosporus* and *N. geogenius* anamorphs are helpful in the taxonomy of the *Hohenbuehelia* "*petaloides*" group, in which *H. auriscalpium* (*H. petaloides* sensu Kuehner and Romagnesi), *H. petalodes*, and *H. tremula* have been confused. *Nematoctonus cylindrosporus* is the anamorph of species of the group including *H. auriscalpium* (the "stirps Petaloides sensu stricto" of Singer and Kuthan, 1980), and is quite different from *N. geogenius*. Singer and Kuthan (1980) excluded terrigenous species of *Hohenbuehelia*, such as *H. petalodes* and *H. tremula*, the teleomorphs of *N.*

Figure 6 A-C: *Nematoctonus geogenius*. A) T-24 (Barron #184, as "N-1"), conidia, fertile hypha, and predatory adhesive knobs. B) *Hohenbuehelia petalodes* (det. Miller; *N. geogenius* state), T-130 (VT #1342), conidia, fertile hyphae and predatory adhesive knobs. C) *H. petalodes*, T-180 (BLT #411), conidia, fertile hyphae, and predatory adhesive knobs.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geogenius, from stirps Petaloides. The different anamorphs of these two groups support this taxonomic decision.

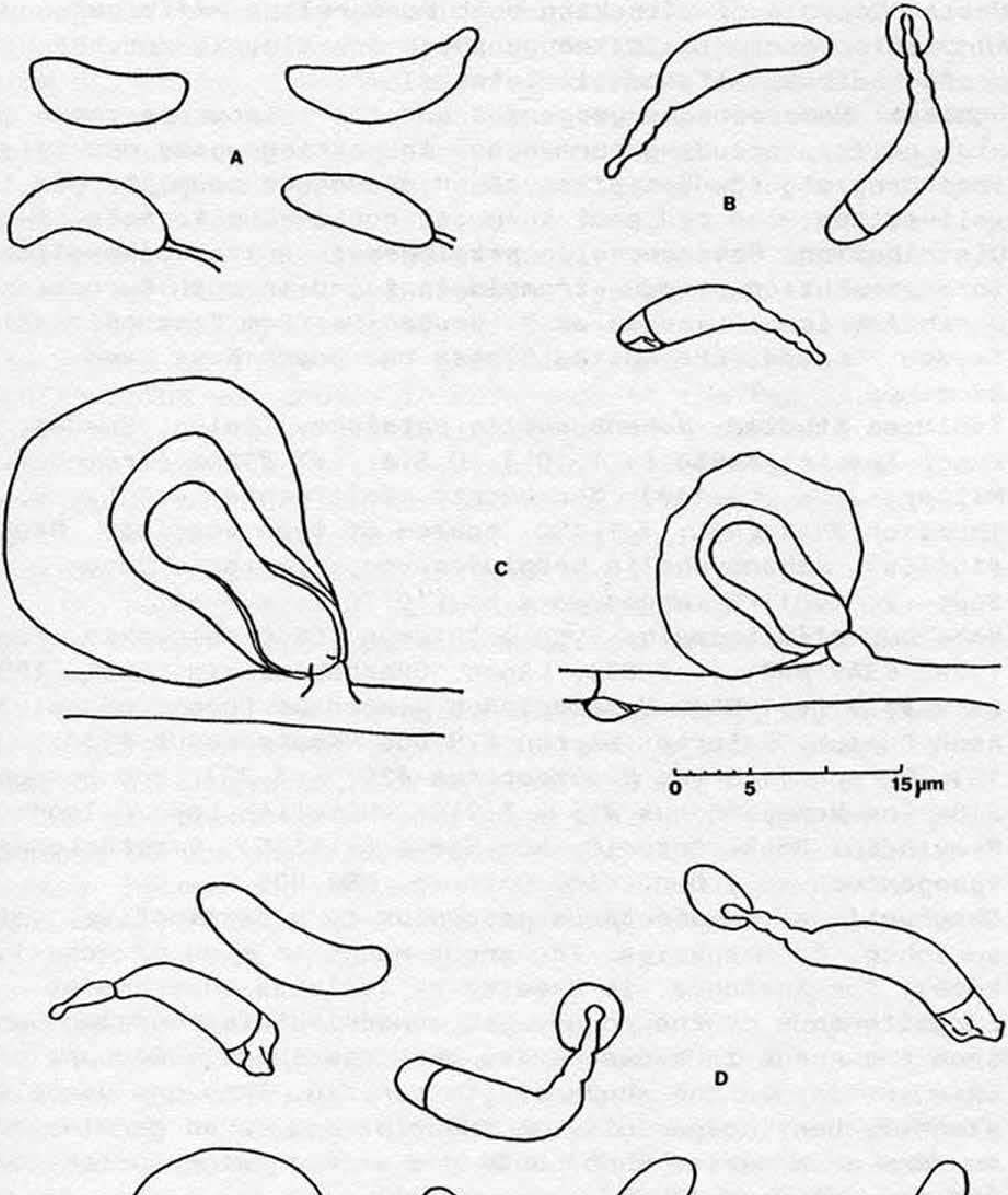
Neither ***N. cylindrosporus*** nor any of its teleomorphs have been found in Ontario.

Nematoctonus geogenius Thorn et Barron, sp. nov. Fig.s 6 & 7

Processus glutinosi hypharum vermiculos nematoideos adhaerentes (interdum rari vel ut videtur absentes); cellulae secretoriae 8-14 µm longae X 3.5-5 µm crassae, medio constrictae; mucus 9-15 X 7-12 µm. Conidia hyalina, elliptica vel fusoidea vel cylindrica, apicibus saepe flexa, 9.5-12.5 (13.0) X (3.2) 3.5-4.2 µm. Hyphae hyalinae, fibulatae. Typus DAOM #193365.

Assimilative Hyphae hyaline, with clamp connections, (1.0) 2.0-3.5 (5) µm diam., developing within living nematodes infected by adhesive conidia or caught by adhesive knobs produced on external hyphae. **Fertile Hyphae** growing externally from a colonized host, both prostrate and ascending, up to 1.5 mm long by (1.0) 1.5-3.5 (4.0) µm diam. (consistent at about 1.2 µm in some isolates but quite broad, or variable, in others), hyaline, beset with clamp connections and conidia produced on short, simple pegs 1-5 µm long X 0.5-1.5 µm broad at the base, tapering to 0.2-0.5 µm at the tip; the ascedant hyphae quite erect, not lax, the colony forming a white, hedgehog-like mound over the dead host. **Predatory Adhesive Knobs** abundant, infrequent, or lacking on colonies developing from individual nematodes, invariably formed when grown from pure culture onto WA with nematodes, predominantly intercalary on lateral branches 2-5 µm long X 2.5-4 µm broad; hour-glass cells 7-15 X 2-7 µm; adhesive mucus 7-17 (24) µm tall by 6-17 (24) µm diam. **Aleuriospores** none. **Conidia** hyaline, smooth, elliptic, somewhat fusoid, or cylindric, the apex often curved, (7.5) 8.5-12.5 (14.5) X (2.8) 3.0-4.2 (4.9) µm, germinating, sometimes while still attached to the parent hypha, to form one or, more commonly, two prominent bulges followed by an hour-glass secretory cell 3.0-4.0 (4.5) X 1.2-1.5 (1.8) µm, producing a mucoid droplet 2.5-3.5 µm diam.

Figure 7 A-D: ***Nematoctonus geogenius***. A-C) ***Hohenbuehelia tremula*** (det. Semerdzieva as ***H. rickenii***; ***N. geogenius*** state), T-83 (CSAV #374). A) Four conidia, one beginning to germinate; B) three germinated conidia with apical adhesive knobs and subapical bulges; C) two large predatory adhesive knobs. D) ***N. ?geogenius*** var., N84-604, conidia and fertile hyphae.


A
B
C
D
0
5
15 µm

Teleomorphs: ***Hohenbuehelia petalodes*** (Bull.: Fr.) Schulz. and ***H. tremula*** (Schaeff.: Fr.) Thorn & Barron.
Hosts: Capable of attacking both ***Panagrellus redivivus*** and ***Rhabditis terricola***, although these are clearly not the preferred hosts of some isolates.
Habitat: ***Nematoctonus geogenius*** and its teleomrphs occur in rich soils, including farmyards, in rotting woody debris, including old sawdust piles at an abandoned sawmill, and in well-rotted wood and peat in mossy coniferous forests.
Distribution: ***Hohenbuehelia petalodes*** is quite cosmopolitan in distribution, and ***H. tremula*** is found in both Europe and North America. Cultures of ***N. geogenius*** from Czechoslovakia, Sweden, Canada, the United States and Japan have been examined.
Isolates Studied: ***Hohenbuehelia petalodes***: Falun, Sweden, Fungi Suecici #4656 (= T-104); U.S.A., VT #1342 (from O.K. Miller, Jr.; = T-130); Sacramento, California, U.S.A., B.L. Thompson #411 (HSC; = T-180, source of **type** specimen, DAOM #193365). ***Hohenbuehelia petalodes*** var.: Tottori, Japan, Sept. 2, 1981, E. Nagasawa s.n. (TOTTORI; = T-3). ***Hohenbuehelia tremula***: Vysoký Chlumec, Czechoslovakia, Feb. 1979, CSAV #374 (= T-83); Lipon, Czechoslovakia, Sept. 1981, CSAV #375 (= T-84). ***Nematoctonus geogenius*** (anamorph only): near Guelph, Ontario: Barron #78 (as ***Nematoctonus*** #130; = T-19), Barron #145 (as ***Nematoctonus*** #20; = T-22), and Barron #184 (as ***Nematoctonus*** #1; = T-24); Whitefish Lake, Algonquin Provincial Park, Ontario: N84-589-1 (= T165). ***Nematoctonus ?geogenius*** var.: Denfield, Ontario, N84-604.
Observations: ***Nematoctonus geogenius*** is a distinctive, yet variable, form-species. The great range in size of adhesive knobs, for instance, is created by isolates that are at opposite ends of the range, yet other isolates overlap, and span the range in between. The most distinctive feature of this species is the shape of its conidia. They are usually slightly bent, especially at the tip, and, when germinated to form an adhesive knob, have one or two bulges prior to the hour-glass cell.

The two teleomorph species are similar to each other and presumed to be closely related (Kuehner and Romagnesi, 1953), and the shared anamorph form-species supports this view. The anamorph of ***H. tremula*** has slightly longer than average conidia (10-14.5 µm versus 8.5-11.5 in many), but one isolate of ***N. geogenius*** had conidia ranging from 7.5-13 µm in length. One culture of ***H. tremula*** (T-83) also had much larger predatory adhesive knobs than most cultures (hour-glass cells 12-15 X 4.5-7 µm), but another (T-84) had hour-glass cells as small as 8.5 X 4.5 µm, well within the size range of other isolates of ***N. geogenius***.

The fact that colonies of ***N. geogenius*** originating from nematodes infected by adhesive conidia often do not produce predatory adhesive knobs on their fertile hyphae can be quite misleading, especially if an isolate under study is not obtained in pure culture. Thus, two species from Nova Scotia, described as endoparasites under provisional names (Alger, 1980), are probably identical to ***N. geogenius***. Both ***Nematoctonus reniformis*** (nom. prov.) and ***N. bicatenulatus*** (nom. prov.) were collected in farmyard soils, and have conidia very similar to those of ***N. geogenius***, if somewhat longer (up to 16 µm long). Their conidia germinate in the same manner as those of ***N. geogenius***, and the name ***bicatenulatus*** was chosen in reference to the two bulges adjacent to the hour-glass, identical to those in ***N. geogenius***. Additional circumstantial evidence supporting our synonymy is the similar habitat of the three form-species, and the common occurrence (K.A. Harrison, pers. comm.) of ***H. geogenia*** (= ***H. petalodes***) in Nova Scotia.

The name *geogenius* is derived both from the habitat, and the better-known name of one of the teleomorphs of this species.

One isolate from farmyard soil (N84-604), which was not successfully cultured, had conidia of a similar shape to those of ***N. geogenius***, but narrower, (7.5) 9-11 X (2.0) 2.2-2.8 µm. It seemed to be restricted to a tiny, unidentified nematode in the Baermann sample, which may explain its narrower hyphae and smaller conidia. Predatory adhesive knobs were not seen. Its true identity remains uncertain, but it is closest to ***N. geogenius***.

Nematoctonus hamatus Thorn et Barron, sp. nov. Fig.s 8 & 9

Processus glutinosi hypharum vermiculos nematoideos cellulae secretoriae 7.5-10 µm longae, 2.5-4 µm crassae, adhaerentes (interdum rari vel ut videtur absentes); medio constrictae; mucus 8-10 X 4.5-6.5 µm. Conidia hyalina, anguste ovata vel fusoidea, laevia, (13.5) 14-22 (24) X 3.2-4.2 (4.5) µm, mox hamata, denique ex apice hypham germinationis corpus glutinosus formans; cellulae secretoriae 3-5 X 1.2-1.8 µm, medio constrictae; mucus 4-6 X 2.5-5 µm. Hyphae hyalinae, fibulatae. Typus DAOM #193364.

Assimilative Hyphae developing within living nematodes infected by adhesive conidia or caught by adhesive knobs on external hyphae, hyaline, with clamp connections, 1.5-3.0 µm diam., filling the body of the host and digesting its contents, then perforating the cuticle to form external, fertile hyphae. **Fertile Hyphae** hyaline, clamped, 1.0-2.5

(3.7) µm diam., both prostrate and ascending, moderately dense, bushy, sparingly branched, up to 1.5 mm long; the ascendant hyphae often somewhat lax; producing conidia from simple, tapering pegs 0.5-6.6 µm long X 0.6-1.5 µm broad at the base, 0.3-0.5 µm broad at the tip; and also producing scattered, inconspicuous predatory adhesive knobs (often absent from colonies originating from single infected nematodes). **Predatory Adhesive Knobs** predominantly intercalary, on lateral branches 1-4 µm long X 2-3 µm broad, the hour-glass cells 7.5-10.5 X (2.0) 2.5-3.5 µm, surrounded by an ovoid mucoid ball 8-11 X 5-7 µm. **Aleuriospores** none. **Conidia** hyaline, fusoid, broadest at the base, tapering to the apex where there is often a slight to distinct hook, (9.5) 12.5-20 (24) X (2.7) 3.0-4.5 (5.4) µm, germinating to form an adhesive knob at the end of a short germ tube, or directly above the apical hook; hour-glass cells 3-5 (5.5) X 1.2-1.8 µm; adhesive mucus 4-6 X 2.5-5 (6) µm.

Teleomorph: ***Hohenbuehelia mastrucata*** (Fr.: Fr.) Singer.

Hosts: ***Nematoctonus hamatus*** readily attacks both ***Panagrellus redivivus*** and ***Rhabditis terricola***.

Habitat: ***Nematoctonus hamatus*** was isolated from rotting wood and woody debris, primarily that of deciduous trees, but recorded once (N84-287) from heart-rot in ***Pinus strobus***; from hardwood forest duff and soil; a lawn; and farmyard soil.

Distribution: ***Nematoctonus hamatus*** was found in Ontario and Quebec, but ***Hohenbuehelia mastrucata*** is widely distributed in the northern hemisphere.

Isolates Studied: ***Hohenbuehelia mastrucata***: West Gate, Algonquin Provincial Park, Ontario, R.G. Thorn #820902/12 (= T-25); near Guelph, Ontario, Barron #167 (as ***Nematoctonus*** 289; = T-23, source of **type** specimen, DAOM #193364). ***Nematoctonus hamatus*** (anamorph only): near Guelph, Ontario, Barron #24 (as ***Nematoctonus*** #3; = T-16), and N83-27; Blair, Ontario, N82-C19 (= T-11); West Gate, Algonquin Park, N83-149 and N84-241; Whitefish Lake, Algonquin Park, N84-224 (= T-136) and N84-589-2 (= T-166); Barron Canyon Trail,

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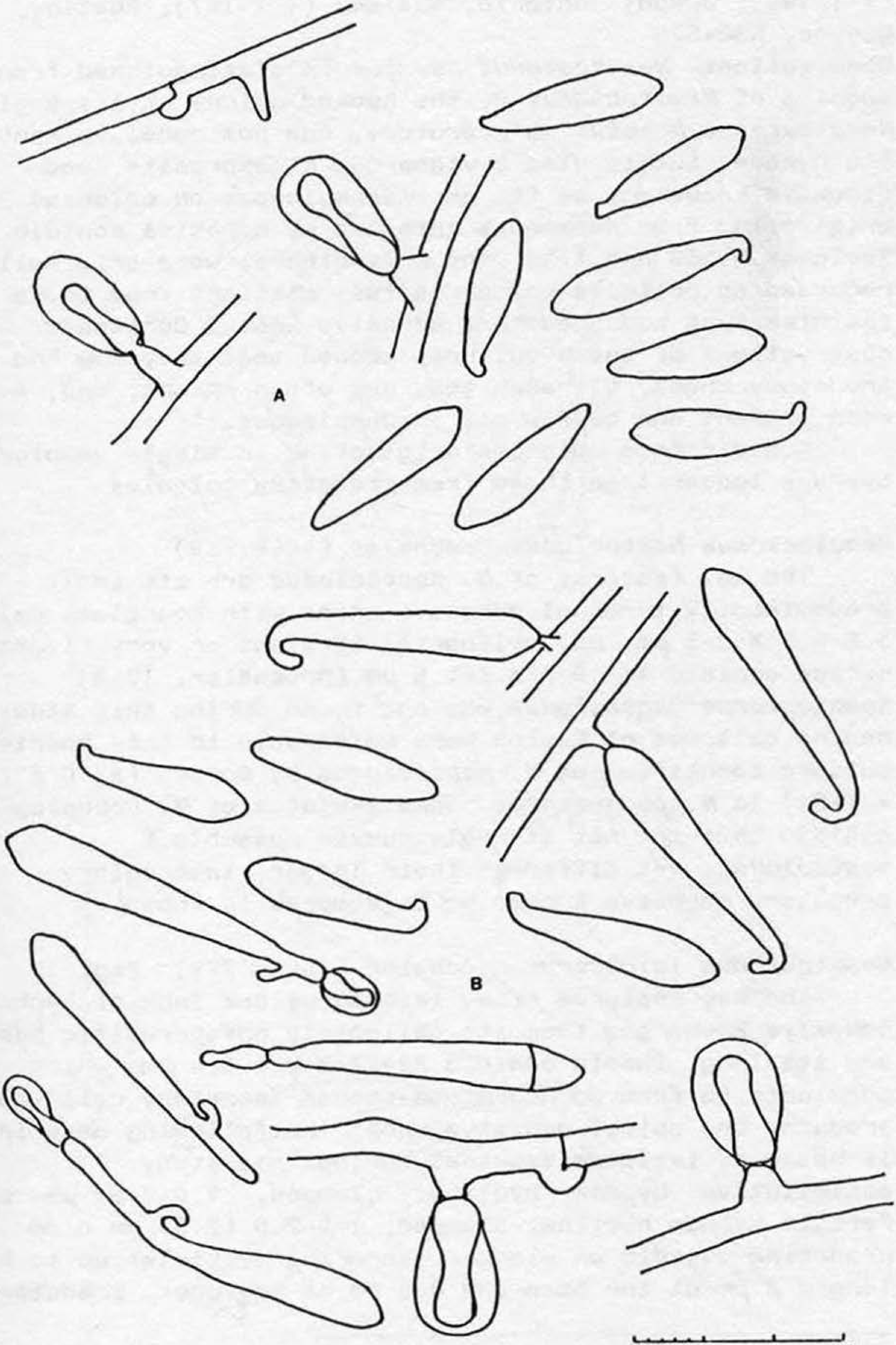
Figure 8 A-B: ***Nematoctonus hamatus*** A) T-166 (N84-589-2), conidia, hypha with conidiogenous peg, and predatory adhesive knobs. B) T-23 (Barron #167, "N-289") conidia, some germinating to form adhesive knobs, fertile hyphae, and predatory adhesive knobs. Long conidia were formed in colonies originating from single infected nematodes; short conidia from extensive colonies capturing nematodes with predatory adhesive knobs.


A
B
0
5
15 µm

Algonquin Park N84-287 (= T-143); Renfrew, Ontario, N84-409 (= T-149); Dundas, Ontario, N84-E47 (= T-167); Cantley, Quebec, N84-575.

Observations: ***Nematoctonus hamatus*** is distinguished from all species of ***Nematoctonus*** by the hooked apices of its conidia. ***Nematoctonus hamatus*** is predatory, and has adhesive knobs on its hyphae, but is also a vigourous endoparasite, and adhesive knobs may be few or inconspicuous on colonies originating from nematodes infected by adhesive conidia. Isolates N-289 and T-25, and many others, were originally regarded as obligate endoparasites, distinct from those isolates that had predatory adhesive knobs. Continued observations of these cultures showed that they too had predatory knobs, although they are often absent, and, even when present can be few and inconspicuous.

Conidia from colonies originating on single nematodes average longer than those from predatory colonies.

Nematoctonus haptocladus Drechsler (1946: 19)

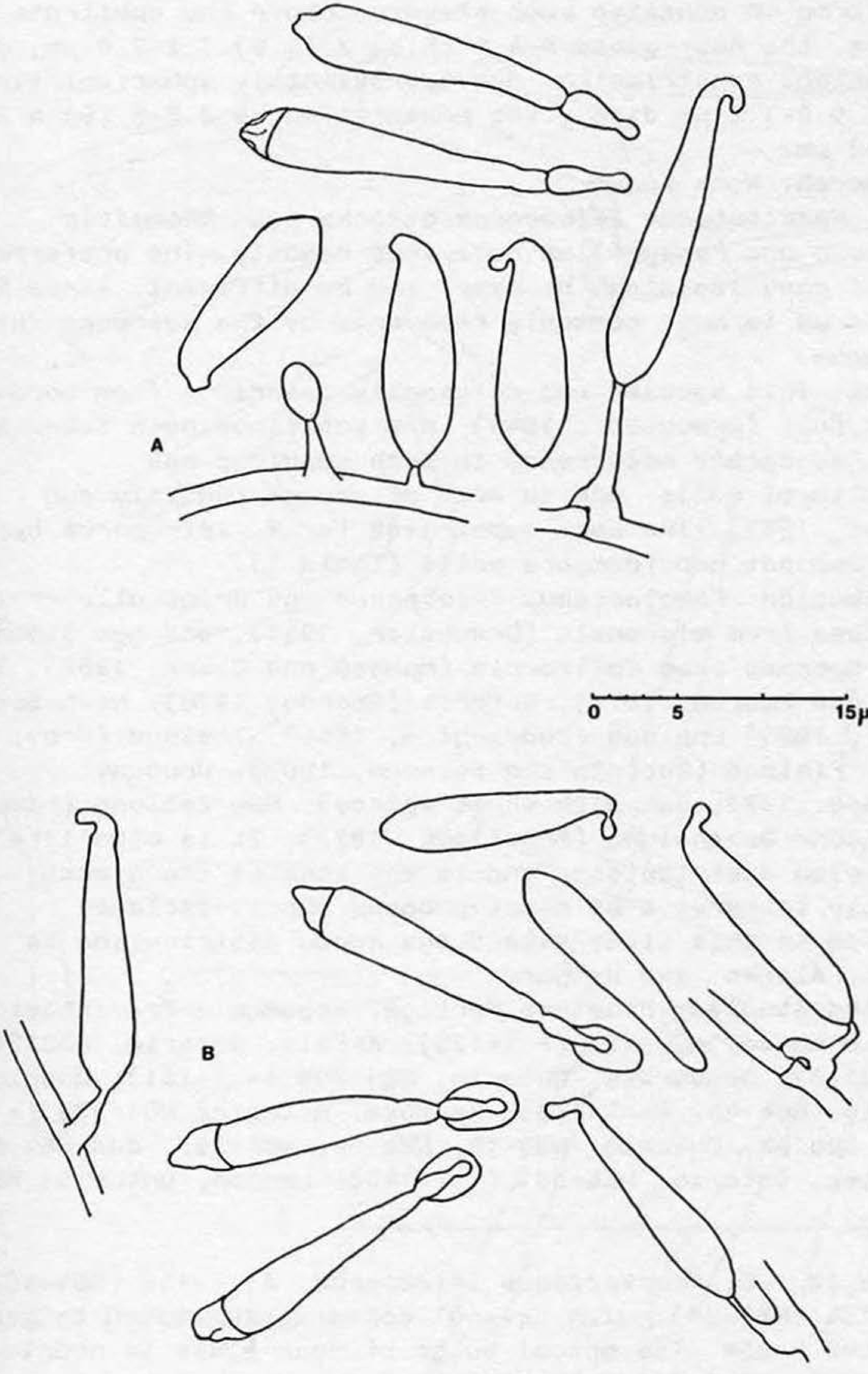
The key features of ***N. haptocladus*** are its small, predominantly terminal adhesive knobs with hourglass cells 3.5-5.5 X 2-3 µm, and cylindric, straight or very slightly curved conidia 11-18 X 3.3-4.5 µm (Drechsler, 1946). ***Nematoctonus haptocladus*** was not found during this study, and no cultures at Guelph were referrable to this species. A culture identified as ***N. haptocladus*** by Barron (ATTC #22119, = T-61) is ***N. pachysporus***. Some isolates of ***N. robustus*** with conidia that are not strongly curved resemble ***N. haptocladus***, but differ in their larger, intercalary predatory adhesive knobs. No teleomorph is known.

Nematoctonus leiosporus Drechsler (1941: 779) Fig. 10

The key features of ***N. leiosporus*** are lack of hyphal adhesive knobs and thus its obligately endoparasitic habit, and its long, fusoid conidia 20-27 X 2.6-3.4 µm, which germinate to form an hourglass-shaped secretory cell that produces and apical adhesive knob. The following description is based on isolates examined during this study:

Assimilative Hyphae hyaline, clamped, 1.0-2.5 µm diam. **Fertile Hyphae** hyaline, clamped, 1.0-2.0 (2.5) µm diam., producing conidia on slender, tapering denticles up to 5 um long X 2 µm at the base and 0.6 µm at the apex. **Predatory**

Figure 9 A-B: ***Nematoctonus hamatus*** A) T-16 (N82-C19), conidia, showing apical crook, and fertile hyphae. B) N84-575, conidia and fertile hyphae.


A
0
5
15µm
B

Adhesive Knobs none. **Aleuriospores** none. **Conidia** hyaline, narrowly fusoid, smooth, (14) 17.5-27 (30.5) X (2.1) 2.2-4.0 (4.2) µm, germinating to form a bent, tapering germ tube that forms an adhesive knob elevated above the substrate by 5-10 µm, the hour-glass 3-4.5 (5.5) X (0.9) 1.2-2.0 µm, with a subapical constriction, and approximately spherical final bulge, 0.6-1.2 µm diam.; the adhesive mucus 3.5-5 (6) X 2.5-4.0 (5) µm.

Teleomorph: None known.

Hosts: *Nematoctonus leiosporus* attacks both *Rhabditis terricola* and *Panagrellus redivivus* readily. The preferred host of many isolates, however, may be different, since ***N. leiosporus*** is most commonly recovered by the Baermann funnel technique.

Habitat: This species was originally described from hardwood forest duff (Drechsler, 1941), and has since been found to be of widespread occurrence in both woodland and agricultural soils, and in wood of saunas (Ruokola and Salonen, 1967). The best substrates for ***N. leiosporus*** appear to be compost and farmyard soils (Table 1).

Distribution: *Nematoctonus leiosporus* was originally described from Wisconsin (Drechsler, 1941), and has since been reported from California (Mankau and Clark, 1959), Iowa (Kitz and Embree, 1979), Ontario (Barron, 1978), Nova Scotia (Alger, 1980) England (Duddington, 1954), Ireland (Gray, 1983), Finland (Ruokola and Salonen, 1967), Uruguay (Gazzano, 1973; but with short spores), New Zealand (Fowler, 1970), and Queensland (McCulloch, 1977). It is clearly of world-wide distribution, and is the species found most commonly in surveys of nematophagous fungi. Isolates examined in this study extend the known distribution to Quebec, Alaska, and Hungary.

Isolates Studied: Pinetree Portage, Algonquin Provincial Park, Ontario, N84-193 (= T-135); Arkell, Ontario, N83-29 and N83-32; Desbarats, Ontario, N84-509 (= T-161); Douglas, Ontario, N84-407 (= T-150); Eramosa, Ontario, N84-373 (= T-147); Guelph, Ontario, N83-18, N84-54, N84-393, and N84-608; Hespeler, Ontario, N84-361 (= T-146); London, Ontario, N84-

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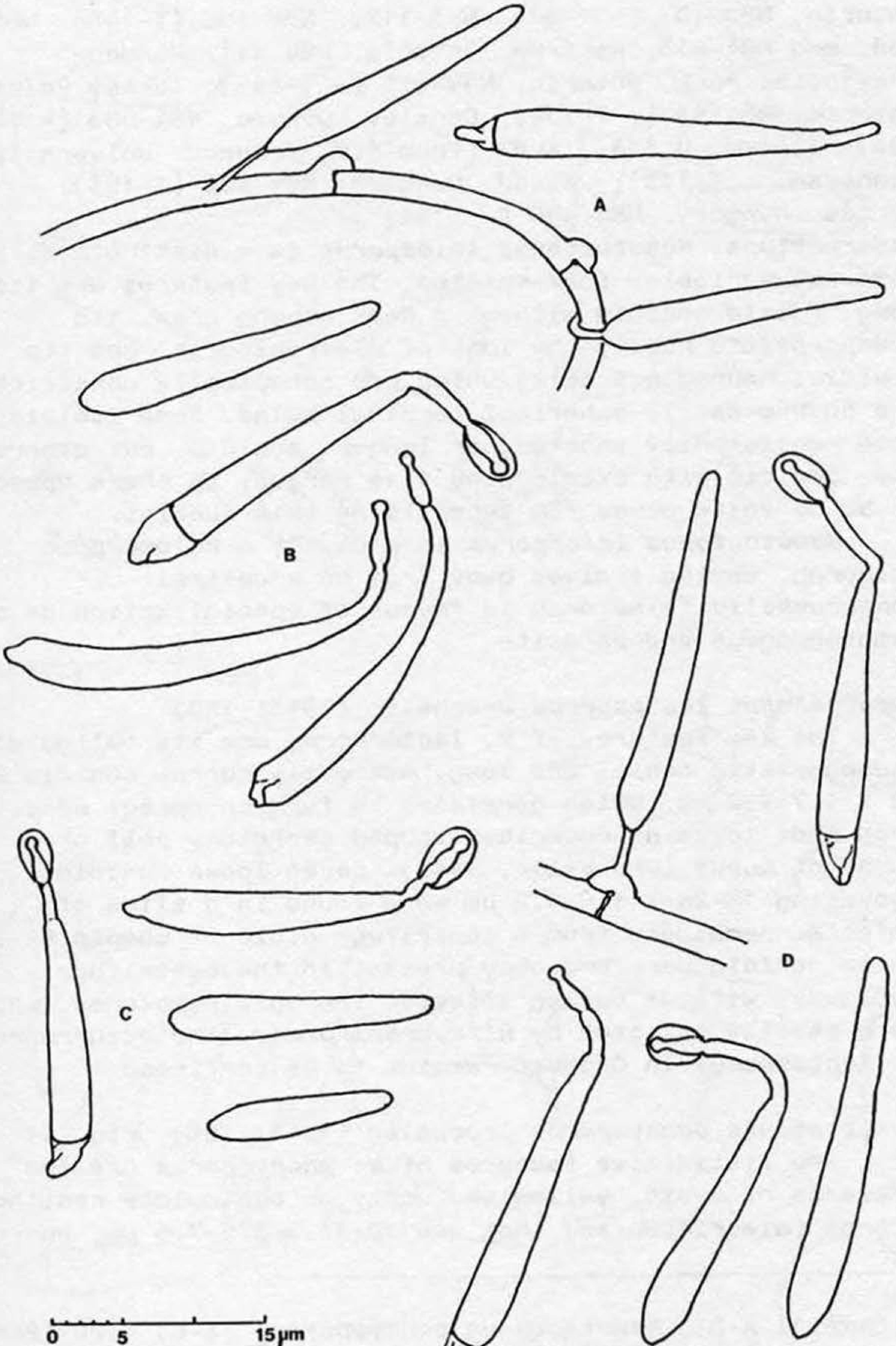
Figure 10 A-D: *Nematoctonus leiosporus*. A) T-150 (N84-407). B) T-134 (N84-93), with several conidia germinated to form adhesive knobs. The apical bulge of hour-glass is nearly spherical. C) T-111 (N83-173), one conidium with a three-lobed secretory cell. Conidia of this isolate were shorter than average. D) T-113 (AL #2), showing conidia that are slightly longer than average for ***N. leiosporus***.


A
B
C
D
0
5
15µm

376 (= T-148); Morriston, Ontario, N83-173 (T-111); Preston, Ontario, N83-107 (= T-58), N83-112,, N84-356 (T-145), N84-359, and N84-613; Renfrew, Ontario, N84-411; Rondeau Provincial Park, Ontario, N84-475 (= T-155); Turkey Point, Ontario, N84-93 (= T-134); Cantley, Quebec, N84-583 (= T-163); Alaska, U.S.A., AL#2 (from E.C. Bernard, University of Tennessee; = T-113); Acsád, Hungary, N84-492 (T-153); Vertés, Hungary, N84-498 (= T154).

Observations: ***Nematoctonus leiosporus*** is a distinctive, but somewhat variable, form-species. The key features are its long, fusoid conidia without a hook at the apex, its endoparasitic habit, the lack of aleuriospores, and its conidial hour-glass cells which are subapically constricted and have a nearly spherical terminal bulge. Some isolates have consistently shorter, or longer, conidia, but others have conidia with overlapping size ranges, so there appears to be no valid cause for subdividing this species.

Nematoctonus leiosporus is probably a holomorphic anamorph, having evolved away from an ancestral ***Hohenbuehelia*** teleomorph in favour of specialization as a nematophagous endoparasite.

Nematoctonus leptosporus Drechsler (1943: 188)

The key features of ***N. leptosporus*** are its obligately endoparasitic habit, and long, extremely narrow conidia 21-28 X 1.7-2.2 µm, which germinate to form an apical adhesive knob that lacks an hourglass-shaped secretory cell or abundant mucus (Drechsler, 1943). Seven loose conidia measuring 18-24 X 1.6-1.9 µm were found in a slide of infected nematodes from a centrifuge plate of sample 84-243. These conidia were probably present in the centrifuge sediment, without having infected the bait nematodes, which were heavily infected by ***N. subreniformis***. The occurrence of ***N. leptosporus*** in Ontario remains to be confirmed.

Nematoctonus pachysporus Drechsler (1943: 185) Fig. 11

The distinctive features of ***N. pachysporus*** are the presence of ovoid, yellowish, warty or echinulate resting spores (aleuriospores) that are 10-13 X 5.5-7.5 µm; narrowly

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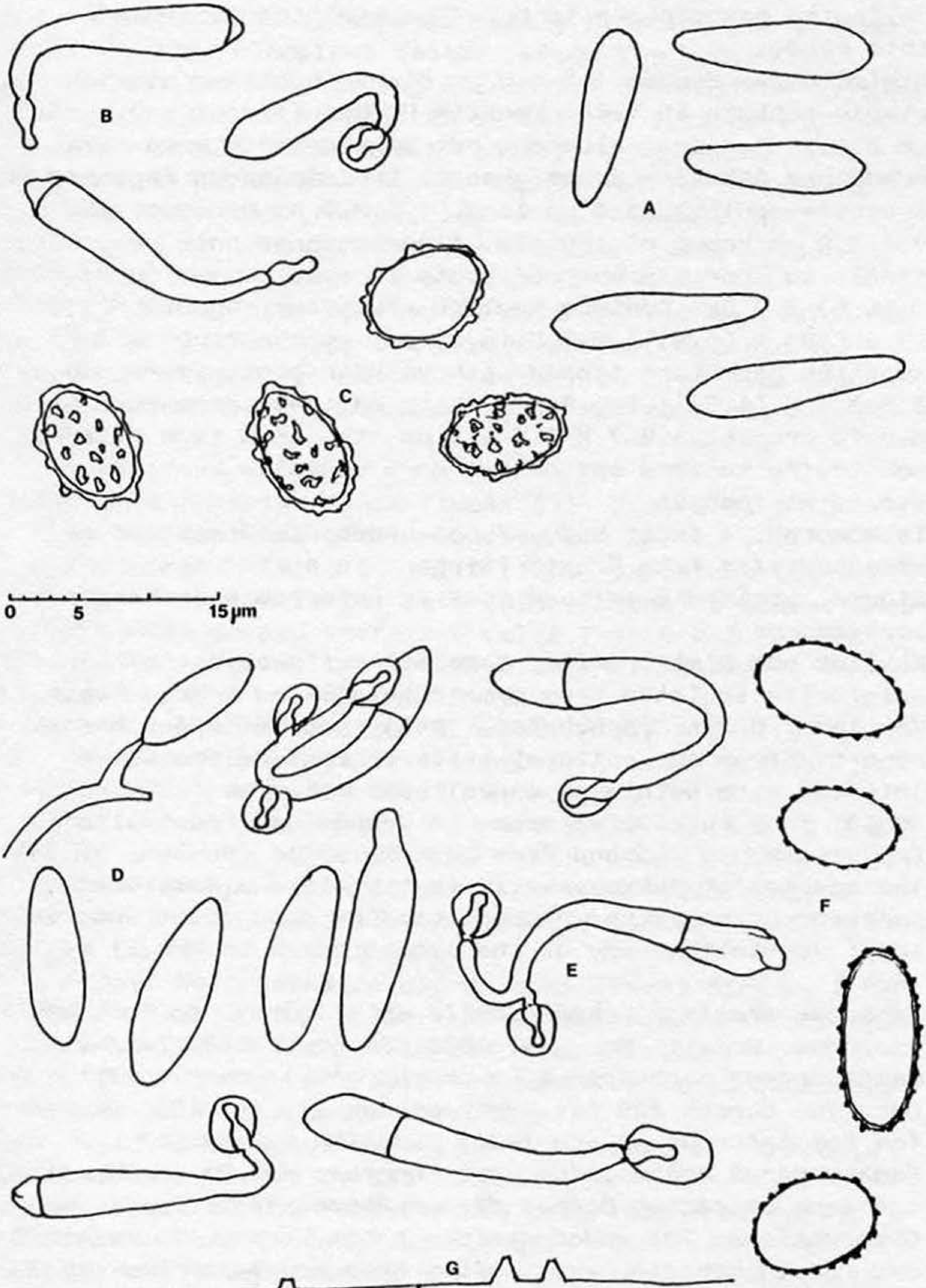
Figure 11 A-G: ***Nematoctonus pachysporus***. A-C) T-20 (Barron #93). A) conidia; B) germinated conidia with adhesive knobs; C) aleuriospores. D-G) ***Hohenbuehelia*** sp. (***N. pachysporus*** state), T-74 (Singer B12424). D) conidia; E) germinated conidia with adhesive knobs; F) aleuriospores; G) simple-septate fertile hypha with conidiogenous pegs.


B
A
C
0
5
15 µm
D
E
F
G

ovate, smooth and hyaline conidia 12-19 X 4-5.5 µm; and the lack of hyphal adshesive knobs (Drechsler, 1943). The following description is based on isolates examined during this study:

Assimilative Hyphae 1.5-3.5 µm diam., hyaline, clamped, but simple-septate in T-74. **Fertile Hyphae** (1.0) 1.5-2.5 (3.0) µm diam., hyaline, clamped, but simple-septate in T-74. **Predatory Adhesive Knobs** absent. **Conidiogenous Pegs** simple, truncate-conical, 1-3 µm long, 1.5-2.0 µm broad at the base, 0.6-1.0 µm broad at the tip. **Aleuriospores** pale yellowish, finely to coarsely warted, ovate to subglobose, (8.5) 10-13 X (5.5) 6-8 µm. **Conidia** hyaline, fusiform, smooth, (13) 14-17.5 (19) X (3.0) 3.2-4.8 (5.2) µm, germinating to form a tapering germ tube tipped with an hour-glass secretory cell 3.5-4.5 X (1.2) 1.5-1.8 µm, which becomes surrounded by a mucoid droplet 3.5-7 X 2.8-4.0 µm; the germ tube often continuing to form one or two more adhesive knobs in a sympodial fashion.

Teleomorph: A fruit body of an undescribed species of *Hohenbuehelia* from Brazil (Singer, in press) sent by R. Singer, yielded a culture that is referrable to *Nematoctonus pachysporus*.

Habitat and Distribution: *Nematoctonus pachysporus* was originally isolated from nematode-infested tomato roots from Maryland, U.S.A. (Drechsler, 1943), and has since been reported from agricultural soils in England that were infested with potato or cereal root eelworms (Duddington, 1954), from cultivated areas in Queensland, Australia (McCulloch, 1977), and from Ontario soils (Barron, 1978). The species of *Hohenbuehelia* that yielded a *Nematoctonus pachysporus* anamorph was collected on dead dicot wood in the igapó vegetation zone of the Amazon basin in Brazil (Singer, 1984).

Isolates Studied: *Hohenbuehelia* sp.: Igarape do Tarumazinho, Amazonas, Brazil, Mar. 13, 1983, Singer B12424 (= T-74). *Nematoctonus pachysporus* (anamorph only): near Guelph, Ontario, Barron #25 (as *Nematoctonus* #2; = T-18), Barron #93 (as *Nematoctonus* sp.; = T-20) and ATTC #22119 (as *Nematoctonus haptocladus*, det. Barron; = T-61; and probably the same as either Barron #25 or Barron #93).

Observations: The endoparasitic habit, broad aleuriospores, and fusoid conidia, which often have more than one adhesive knob, make *N. pachysporus* a very distinctive form-species. Reports in the literature of *N. pachysporus* can be accepted with much more confidence than those of certain other species of *Nematoctonus*, such as *N. haptocladus*.

Culture T-74 was originally isolated as a heterokaryotic culture with clamp connections from a gill fragment of a dried specimen of a new species of *Hohenbuehelia*. This culture evidently contained or produced a monokaryotic, clampless sector, which was subsequently selected accidentally during a transfer for routine culture maintenance. This monokaryotic isolate is interesting in several respects. It is still readily recognisable as ***N. pachysporus***, and is still quite capable of infecting and consuming nematodes. The ability of monokaryons of ***Nematoctonus*** to infect nematodes has been noted by Barron and Dierkes (1977) and Kitz and Embree (1979). The monokaryotic isolate reported by Kitz and Embree (1979) was regarded as most similar to ***N. pachysporus***, but did not produce aleuriospores, which isolate T-74 did. Kitz and Embree's isolate, from woodland soil, may possibly represent ***N. hamatus***.

Nematoctonus robustus Jones (1964: 57) Figure 3B & 12

The key features of ***N. robustus*** are the curved, cylindric conidia (9.1) 9.3-17.0 (18.1) µm (along the curve) x 2.5-4 µm; and the large, intercalary hyphal adhesive knobs with hourglass-shaped secretory cells 7-10.5 X 2.5-3 µm (Jones, 1964). The following description is based on isolates examined during this study:

Assimilative Hyphae hyaline, clamped, (1.0) 1.5-3 (4) µm diam. **Fertile Hyphae** hyaline, clamped, (1.0) 1.5-3 (4) µm diam. **Predatory Adhesive Knobs** intercalary or rarely terminal, hour-glass cells (4.5) 6.5-9 (10) X (2.0) 2.2-3.2 (3.8) µm, becoming surrounded by mucoid balls (5) 7-10 (11) X (3.5) 5-7 (8) µm. **Aleuriospores** none. **Conidia** hyaline, smooth, cylindric, slightly or strongly curved, (7.5) 8.5-15 (18.5) X (2.1) 2.5-4.0 (4.5) µm.

Teleomorphs: ***Hohenbuehelia approximans*** (Peck) Singer, ***H. cyphelliformis*** (Berk.) Miller, ***H. atrocaerulea*** (Fr.) Singer var. ***grisea*** (Peck) Thorn & Barron, and a culture (T-132) sent by O.K. Miller, Jr. as ***H. nigra*** all yielded anamorphs referrable to ***Nematoctonus robustus***.

Hosts: Both ***Panagrellus redivivus*** and ***Rhabditis terricola*** were readily consumed by all isolates.

Habitat: ***Nematoctonus robustus*** was described from forest leaf litter (Jones, 1964), but is also found in rotting wood, where its teleomorphs are known to occur, and soil. ***Hohenbuehelia cyphelliformis*** fruits near the ground on dead stems of woody perennials, but may make its way there from the soil, in order to gain a slight height advantage for the release of basidiospores.

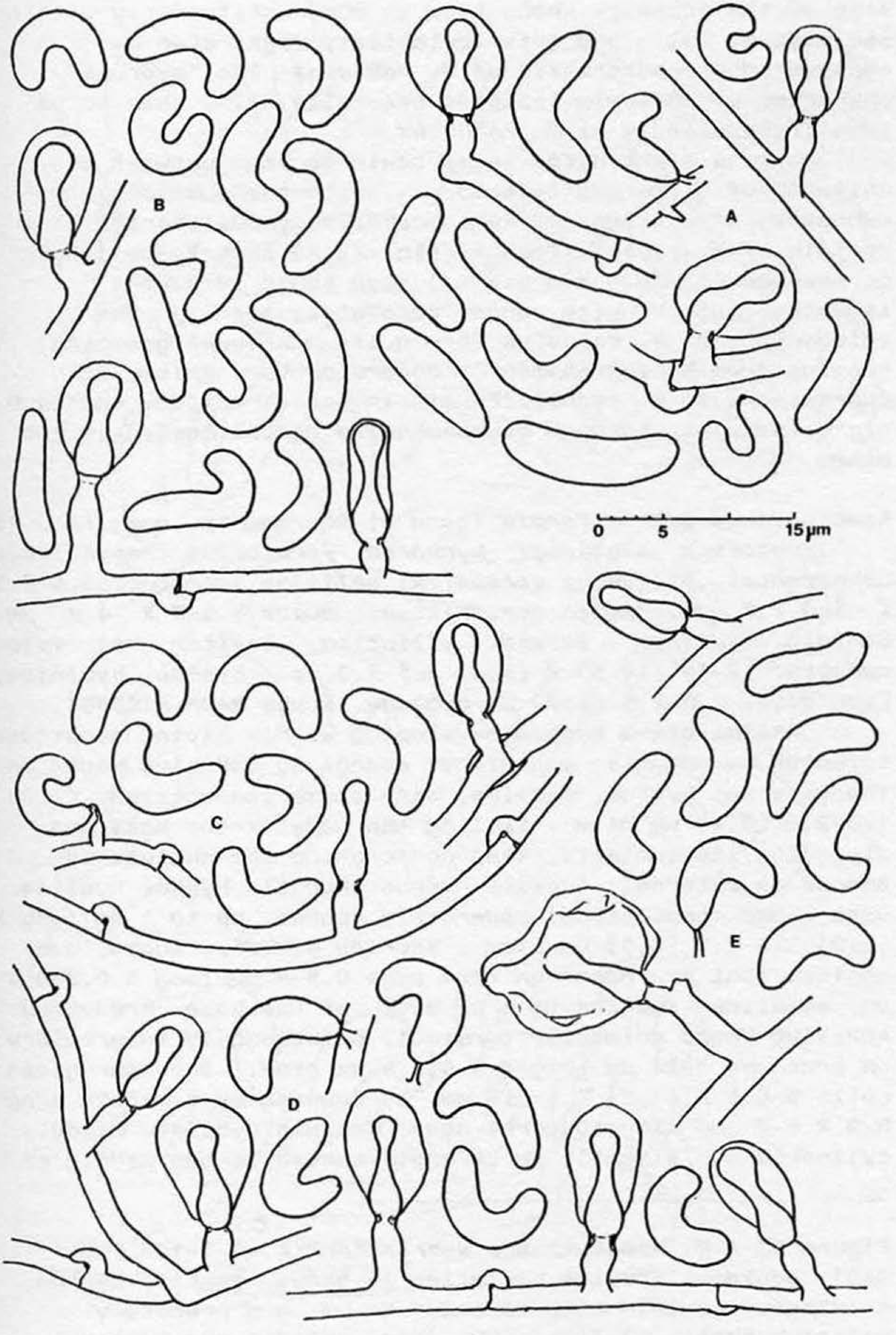
Distribution: ***Nematoctonus robustus*** was described from Ghana

(Jones, 1964), and has since been found in Iowa (Kitz and Embree, 1979), Nova Scotia (Alger, 1980), Finland (Salonen and Ruokola, 1968), New Zealand (Fowler, 1970), and Ontario (below). The report by Castaner and O'Leary (1967) of ***N. campylosporus*** from Missouri may represent this species, as the conidia were reported as 14-19 µm long. ***Hohenbuehelia atrocaerulea*** var. ***grisea*** is found world-wide. ***Hohenbuehelia approximans*** and ***H. nigra*** are, as yet, only known from the Americas.

Isolates Studied: ***Hohenbuehelia approximans***: Eramosa, Ontario, R.G. Thorn #841117/01 (= T-176); Point Pelee National Park, Ontario, DAOM #188324 (= T-116); U.S.A., VT #1365 (from O.K. Miller, Jr.; = T-131). ***Hohenbuehelia cyphelliformis***: Algonquin Provincial Park, Ontario, RGT #841013/01 (= T-171); Eramosa, Ontario RGT #841117/02 (= T-175). ***Hohenbuehelia atrocaerulea*** var. ***grisea***: U.S.A., CBS #354.34 (= Overholts #2948; = T-5); Bell's Corners, Ontario, DAOM #48912 (= T-9); Cantley, Quebec, RGT #840909/02 (= T-177). ***Hohenbuehelia nigra***: U.S.A., VT #1324 (from O.K. Miller, Jr.; = T-132). ***Nematoctonus robustus*** (anamorph only): Petawawa River, Algonquin Provincial Park, Ontario, N84-274 (= T-141) and N84-275 (= T-142); Douglas, Ontario, N84-404; near Guelph, Ontario, Barron #17 (as ***Nematoctonus campylosporus***; = T12), Barron #20 (as ***Nematoctonus*** 90; = T-14), Barron #21 (as ***Nematoctonus*** sp.; = T-15), and Barron #98 (as ***Nematoctonus concurrens***; = T-21); Cantley, Quebec, N84-579 (= T-162); U.S.A., ATTC #22525 ("J. Roxon, bark"; = T-62).

Observations: ***Nematoctonus robustus*** is an inclusive form-species that can be recognised by its slightly to strongly curved, cylindric conidia, its intercalary adhesive knobs that are longer than those of ***N. campylosporus***, and its moderately thick hyphae. Some isolates with small, intercalary adhesive knobs are somewhat intermediate between ***N. robustus*** and ***N. campylosporus***, and others, with most conidia only slightly curved, are intermediate between ***N.***

Figure 12 A-E: ***Nematoctonus robustus***. A) ***Hohenbuehelia cyphelliformis*** (***N. robustus*** state), T-171 (RGT #841013/01), conidia, fertile hyphae and predatory adhesive knobs. B) T-62 (ATCC #22525). C) ***Hohenbuehelia atrocaerulea*** var. ***grisea*** (***N. robustus*** state), T-162 (N84-579, from beneath fruiting bodies of RGT #840909/02, and identical to culture of that collection). D) ***H. approximans*** (***N. robustus*** state), T-176 (RGT #841117/01). E) ***H. nigra*** (det. Miller; ***N. robustus*** state), T-132 (VT #1324).


B
A
0 5 15µm
C
E
D

robustus and ***N. concurrens***. The shape of the conidia and the size of the adhesive knobs tend to vary considerably within isolates as well, and this variability might even be considered characteristic of ***N. robustus***. The "average" character of variable isolates generally allow them to be identified clearly as ***N. robustus***.

No consistent differences could be seen between the cultures of different teleomorphs, with the possible exception of cultures of ***Hohenbuehelia cyphelliformis***. The conidia of ***H. cyphelliformis*** (Fig. 12 A) tend to be longer on average (12-18.5 X 3-4.2 µm) than those of other isolates, but the size ranges completely overlap. The teleomorphs of ***N. robustus*** form quite a natural grouping, ranging from ***Hohenbuehelia atrocaerulea*** var. ***grisea*** to ***H. approximans*** to ***H. cyphelliformis*** in one direction, and to ***H. nigra*** (possibly through ***Hohenbuehelia mustaliensis***) in the other.

Nematoctonus subreniformis Thorn et Barron, sp. nov. Fig. 13

Processus glutinosi hypharum vermiculos nematoideos adhaerentes, plerumque termiales; cellulae secretoriae 5-6.5 X 1.5-2.5 µm, medio constrictae; mucus 5.5-8 X 4-7 µm. Conidia hyalina, laevia, elliptica, leviter vel valde curvata, 9-14 (14.5) X (3.2) 3.5-5.0 µm. Hyphae hyalniae, fibulatae, 1.5-2.5 (3.0) µm crassae. Typus DAOM #193363.

Assimilative Hyphae developing within living nematodes infected by adhesive conidia or caught by adhesive knobs on the external hyphae, hyaline, with clamp connections, (1.0) 1.5-2.5 (3.0) µm diam., filling the body of the host and digesting its contents, then perforating the cuticle to emerge as external, fertile hyphae. **Fertile Hyphae** hyaline, with clamp connections, moderately sparse, up to 1 mm long X (1.0) 1.5-2.5 (3.0) µm diam., bearing adhesive knobs, and conidia that are borne on fine pegs 0.5-4 µm long X 0.2-0.4 µm, sometimes swollen to 1 µm diam. at the base. **Predatory Adhesive Knobs** primarily terminal, occasionally intercalary on branches 3-23 µm long X 2.0-2.5 µm diam., the hour-glass cells 5-6.5 X (1.5) 1.8-2.5 µm, surrounded by a mucoid drop 5-9 X 4-7 µm. **Aleuriospores** none. **Conidia** hyaline, broadly cylindric and slightly to strongly curved in the middle or

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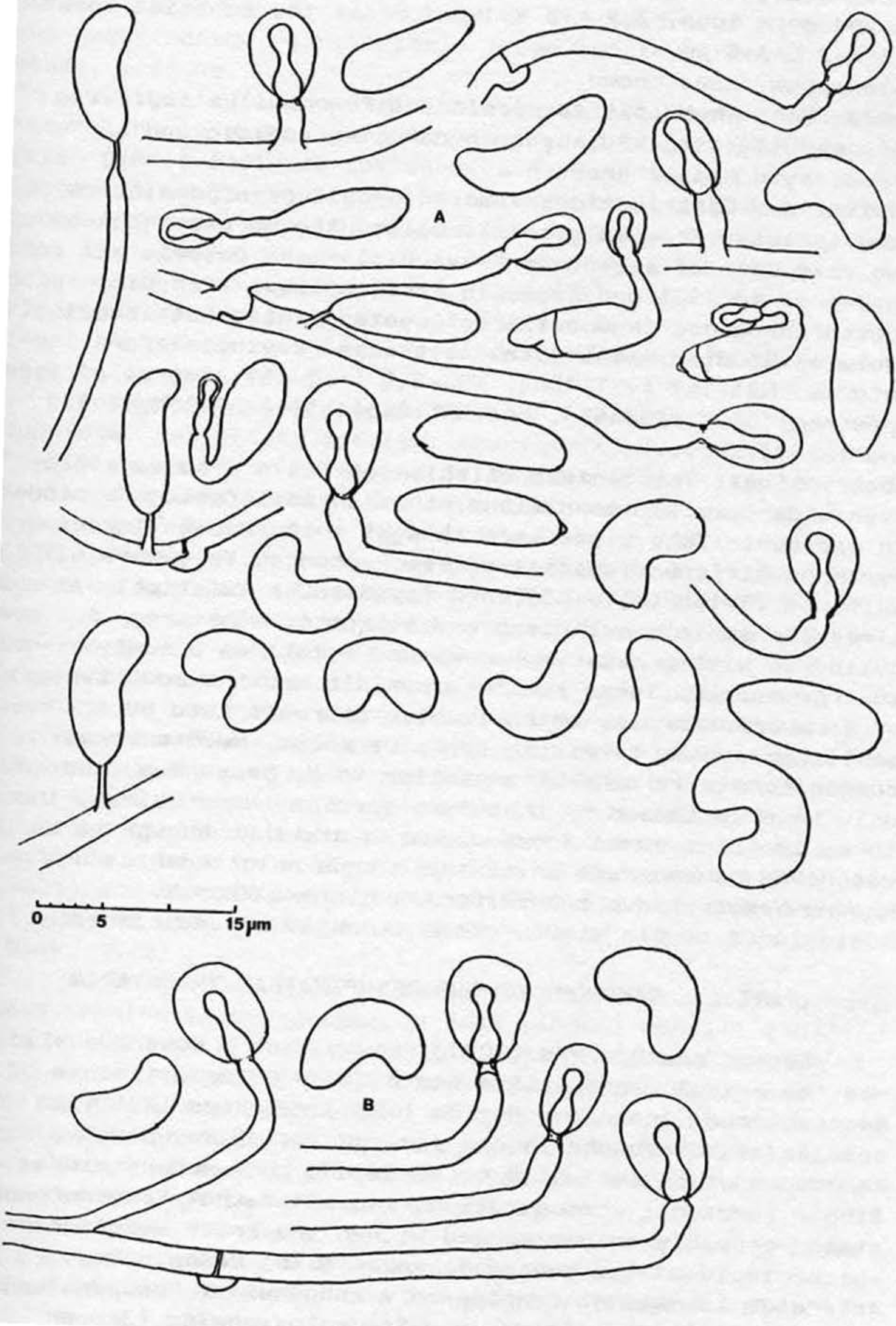
Figure 13 A-B: ***Nematoctonus subreniformis*** A) T-137 (N84-240), conidia, showing variation in shape, fertile hyphae, germinated conidia with adhesive knobs, and predatory adhesive knobs. B) T-140 (N84-243), conidia and terminal predatory adhesive knobs.


A
0
5
15 µm
B

toward the tip, 9-14 (14.5) X (3.2) 3.8-4.8 (5.0) µm, germinating to form an adhesive knob at the end of a usually curved germ tube, 3.5-4.5 X 1.5-1.8 µm, the adhesive mucus 4-5 X 2.5-3.5 µm.

Teleomorph: None known.

Hosts: Both *Rhabditis terricola* and *Panagrellus redivivus* were readily attacked, by both adhesive conidia and predatory adhesive knobs.

Habitat and Distribution: *Nematoctonus subreniformis* has been isolated from only one locality, the hardwood forest at the West Gate of Algonquin Provincial Park, Ontario. It was recovered in 1983 and 1984, in three samples of humic, rotted hardwood, from different spots within that locality.

Isolates Studied: West Gate, Algonquin Provincial Park, Ontario, N83-147 (= T-108), N84-240 (= T-137; source of type specimen, DAOM #193363), and N84-243(1-3) (= T-138, T-139 and T-140).

Observations: The conidia of this species are so variable, even under similar conditions, that three infected nematodes in one centrifuge plate were thought to have been infected by three different species of *Nematoctonus*. They were all cultured (T-138 to T-140), and found to be identical. At times the conidia are plump and elliptic, sometimes cylindric with a decurved apex, and sometimes broadly sausage-shaped. These reniform conidia are the most typical of *N. subreniformis*, which is also characterised by its small, generally terminal, adhesive knobs. *Nematoctonus subreniformis* is otherwise similar to *N. geogenius*, and may only be a variation of that form-species. Nonetheless, the three isolates named above appeared distinct enough to be described as separate until their true relationships are known. *Nematoctonus subreniformis* differs from *N. haptocladus* by its stout, often strongly curved, conidia.

PART II: TAXONOMY OF THE RESUPINATEAE IN ONTARIO

Barron and Dierkes (1977) showed that a *Hohenbuehelia* was the sexual reproductive state of an Ontario isolate of *Nematoctonus*. Thorn and Barron (1984) reported that five species of *Hohenbuehelia* and one species of *Resupinatus* had *Nematoctonus* states which attacked and consumed nematodes. Singer (personal communication) indicated that *Nematoctonus* states probably only occurred within the tribe Resupinateae, which includes the genera *Hohenbuehelia*, *Resupinatus*, *Asterotus* (sometimes considered a subgenus of *Resupinatus*), *Aphyllotus*, *Stigmatolemma*, and *Stromatocyphella* (Singer 1962, 1975). Although species of *Panellus*, *Campanella* and

Faerberia have many similarities in habitat, morphology and anatomy, those tested were non-nematophagous (Thorn and Barron, 1984). A review of some of the taxonomic history of the Resupinateae, particularly those species treated in this study, follows.

The gilled members of the Resupinateae were previously known largely under the name *Pleurotus* (Fr.) Kummer (1871). Fries (1821) included the species he knew in his "tribe" (actually subgenus) *Pleurotus* of the almost all-encompassing genus *Agaricus*. Many subsequent mycologists did not agree that the species that now make up the Resupinateae were congeneric with the large and fleshy species, such as *Pleurotus ostreatus*, the type of *Pleurotus*. Since 1821, at least 10 genera have been created to accommodate various species in this group.

Resupinatus was proposed by S.F. Gray (1821) for the cupulate, resupinate species, *Agaricus applicatus* Batsch. *Phyllotus* Karsten (1879) and *Calathinus* Quélet (1886) included *A. applicatus* when described, and are obligate typonyms of *Resupinatus* Gray (Voss et al., 1983, Article 63). *Hohenbuehelia* Schulzer (in Schulzer et al., 1866) was based on *Agaricus* (*Pleurotus*) *petaloides* Bulliard: Fries. It was not until 1871 that Kummer raised *Pleurotus* to the generic level, but it has since gained widespread acceptance. In contrast, *Resupinatus* Gray (1821) was not used again until Murrill (in Murrill et al., 1915) revived it, and *Hohenbuehelia* was lost until Donk (1949) showed that it was validly published and Singer (1951) brought it into use. Since *Pleurotus* (Fr.) Kummer (1871) included both *Agaricus applicatus* and *A. petaloides* when described, it would have been an obligate typonym of *Resupinatus* Gray (1821) and *Hohenbuehelia* Schulzer (Schulzer et al., 1866) if it had not been conserved against both of these genera (Donk, 1949).

North American gilled members of the Resupinateae have been treated in monographs by Peck (1886), Murrill (1916; and Murrill et al., 1915), Pilát (1935), Coker (1944), Miller and Manning (1976), Libonati-Barnes (1981), and Miller (in press). Confusion of species concepts has been a problem, especially in the monograph by Pilát (1935), and many names were misapplied, by Pilát and others. Peck (1886) treated six species of *Pleurotus* that belong in the Resupinateae. Of these, only *P. atrocaeruleus* var. *griseus* and *P. striatulus* are treated under the same trivial names today (in *Hohenbuehelia* and *Resupinatus*, respectively).

Singer (1951 a) placed the gelatinized, pleurotoid agarics with inamlyoid spores in the tribe Resupinateae of the Tricholomataceae. Species with metuloids went into *Hohenbuehelia*, and those without into *Resupinatus*. Kuehner and Romagnesi (1953) treated *Resupinatus* and *Hohenbuehelia* as the subgenera *Phyllotus* and *Acanthocystis* of *Geopetalum*. Kuehner (1980) placed all of these species in *Resupinatus*.

Miller (in press), in a preliminary monograph of the species of *Hohenbuehelia* of North America, follows essentially the species concepts of Coker (1944), plus he provides descriptions and illustrations of the characters of anatomy and micromorphology that are emphasized in modern classifications. *Hohenbuehelia* is characterized by the gelatinized pileus, inamyloid, elliptical spores, and capitate, fusoid cheilocystidia. Miller transferred *Resupinatus cyphelliformis*, *Pleurotus silvanus* sensu Coker and *Pleurotus unguicularis* sensu Coker to *Hohenbuehelia*. Earlier, Miller (Miller and Manning, 1976) treated these species in *Pleurotus* because they all had the elliptical spores and fusoid cheilocystidia so common in *Pleurotus* but not found in *R. applicatus*, the type of *Resupinatus*. Miller (in press) reunited these species with the other species of the Resupinateae, with which they form a more natural group.

The species of the Resupinateae without gills, termed cyphelloid, or "reduced" agarics, were treated in large and unnatural genera such as *Cyphella*, *Solenia* and *Porotheleum* and were more or less lost until their similarity to species of *Resupinatus* was recognised by Romagnesi (1953, in Donk, 1962 b), Donk (1962 b), and Singer (1962, 1975). Despite these similarities, the cyphelloid species have never been included with the gilled members of the Resupinateae in any monograph. Their biology is relatively unknown.

Our aim was to identify and describe the species of the Resupinateae that occur in Ontario, in order to provide a basis for connecting *Nematoctonus* anamorphs with their teleomorphs in the Resupinateae.

MATERIALS AND METHODS[1]

This portion of the study was based on examination of about 300 specimens of the Resupinateae at the University of Toronto Cryptogamic Herbarium (TRTC) and the National Mycological Herbarium in Ottawa (DAOM), plus fresh specimens collected in and around Ontario. Acronyms of herbaria are those used in Holmgren et al. (1981). The publication dates of taxonomic works are those accepted by Stafleu (1967) and Stafleu and Cowan (1976-1983).

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[1] See Appendix 1: Media and Reagents.

A: EXAMINATION OF SPECIMENS

Notes on fresh specimens, recorded soon after collection, included colours, texture, taste, odour, and other characters that would be lost or changed on drying. Colours were recorded in descriptive terms and in the standard code of Kornerup and Wanscher (1978). Spore prints were obtained on white paper. No chemical spot tests were made. Collections were air-dried on screen racks 30-50 cm above two 100 watt household lightbulbs.

Herbarium specimens were hand-sectioned for study of microscopic characters using burdock (*Arctium* sp.) pith to support the wedge of the specimen being sectioned. The mountants most commonly used were water, 3% KOH in water, Melzer's reagent and solutions of Brilliant Cresyl Blue and Trypan Blue. Water mounts allowed the study of natural colours and hyphal encrustations that dissolve in other mountants. Tissues of dried specimens were revived in 3% KOH without added stain since slides were examined using phase-contrast microscopy. Melzer's Reagent was used primarily to test colour reactions of spores, metuloids and hyphae, but also to highlight hyphal encrustations. Brilliant Cresyl Blue was used to highlight gelatinous zones and metuloids.

The substrate beneath the fruiting bodies was identified and searched for conidia of a possible ***Nematoctonus*** state, adhesive knobs, or other characters of the vegetative hyphae. Woody substrates were sectioned, and soil was crumbled then centrifuged (as in Part I) to separate fungal hyphae and spores from soil particles. These preparations were usually examined in trypan blue.

B: TAXONOMIC CHARACTERS

The taxonomic characters used in the Resupinateae are those in use throughout the Agaricales (see Singer, 1975). The terms used for macroscopic characters are in agreement with those used by Largent (1973) with one exception. The term used herein for narrowly obovate fruit bodies is spathulate (Largent, 1973, calls this petaloid). Petaloid is used in this paper to describe the shape of ***Hohenbuehelia petalodes***, which is actually semi-infundibuliform (see Fig. 24).

Microscopic features are essential in the classification or identification of the Resupinateae. They might be divided into features of general fruit body anatomy and construction, features of the hymenium, the cuticle, and the spores. An attempt has been made to follow the terminology of Singer (1975) and Largent et al. (1977).

The fruit body is usually made up of a number of layers, with a gelatinous zone usually directly beneath the cuticle. This gelatinous zone is a characteristic feature of the Resupinateae. In this zone thin hyphae (actually the narrow, refractive lumens) are generally widely dispersed in a gelatinous matrix (generally formed by highly gelatinized outer walls), and may be arranged more or less horizontally (radially or tangentially), vertically, or in a tangle. Singer (in Singer and Kuthan, 1980) places great taxonomic emphasis on the arrangement of the hyphae in the gelatinous zone, whereas Donoso (1981) believes that there is too much variation within fruit bodies and between collections of some species to be useful. While there is some intraspecific variation in this character, certain useful patterns emerged among many collections. The depth of the gelatinous zone was also an important character to Kuehner (in Kuehner and Romagnesi, 1953, 1954) and Singer (in Singer and Kuthan, 1980). Singer gave explicit instructions on where and how to measure the depth of the gelatinous zone, emphasising that no pressure should be applied to the cover-glass before it is measured. Measurements of anatomical zones were made with no cover-glass over the sections, as even allowing the cover-glass to settle on the section in ample mountant could double the thickness of the gelatinous zone.

Beneath the gelatinous zone is usually a less gelatinized layer of densely-woven, thicker hyphae, that is occasionally divided by a second gelatinous zone. When this zone (the trama, or trama proper) is thin or absent, the fruiting body appears transparent. The walls of the hyphae in this zone may be thin, or thickened and gelatinized. This zone usually extends into the lamellae to form the lamellar trama, in which the hyphae are arranged vertically in a parallel to slightly interwoven fashion (regular to subregular). The pigmentation of the lamellar trama, subhymenium and hymenium can be taxonomically important.

In the hymenium, the colour, shape, size, and number of sterigmata of the basidia, and the presence, colour, shape, and size of cystidia are valuable taxonomic characters. Thick-walled, lanceolate cystidia (metuloids, or lamprocystidia) are characteristic of *Hohenbuehelia* (although sometimes inconspicuous) and lacking in *Resupinatus* (Singer, 1951 a, 1975). These metuloids are usually metachromatic in cresyl blue (turning bright magenta), and inamyloid to faintly dextrinoid (turning pale brick-red in Melzer's reagent).

Most species of *Hohenbuehelia* have a second type of cystidium in addition to metuloids that are thin-walled, and often have a tapering neck that is capped with an hour-glass secretory cell and its mucoid droplet. The apex of these cystidia (Fig. 22 B, E, and G) resembles the adhesive processes found in ***Nematoctonus***. We name this distinctive capitulum a gloeosphex, so that cystidia bearing such capitula may be referred to readily. **Gloeosphex cystidia** are distinct from secretory cystidia found in other agarics, such as ***Baeospora*** and ***Gloiocephala***, and are diagnostic for ***Hohenbuehelia***. These occur most commonly as cheilocystidia, but also as pleuro-, pilo- and caulocystidia. The gill edge is often a sterile zone of cheilocystidia mixed with metuloids (Fig. 16 D).

The gill margins of ***Resupinatus*** species are commonly sterile, with a type of cystidium not found in ***Hohenbuehelia***. These are club-shaped cells with irregular, knobbed, tapering, or finger-like branches at their tips (Fig. 28 A and F). These diverticulate cheilocystidia are diagnostic for ***Resupinatus***. ***Asterotus*** and ***Stigmatolemma*** have diverticulate cheilocystidia (surrounding the cap margin in ***Stigmatolemma***), indicating their affinities with ***Resupinatus***.

Characters of the cuticle (or pileipellis), including the epicutis of tomentum or other superficial hyphae, are taxonomically valuable in the Resupinateae. In ***Hohenbuehelia***, the cuticle usually consists of repent, interwoven hyphae (a cutis) in a thin zone that is poorly distinguished from the gelatinous zone beneath. The hyphae of the cuticle, however, tend to be broader and more pigmented (often opaque) than those of the gelatinous zone. Pigmentation may be intracellular or extracellular, and in the latter case may take the form of distinct hyphal encrustations or amorphous masses between hyphae. The epicuticular hyphae are generally hyaline, and may have thin, thickened, gelatinized, or encrusted walls. Singer (1977) emphasizes the degree of hyphal encrustation, but its value as a taxonomic character in ***Hohenbuehelia*** is questioned, since it varied between sections from a single fruit body and from fruit bodies of a single collection. ***Resupinatus***, ***Asterotus***, ***Stigmatolemma*** and ***Stromatocyphella*** all have a cuticle of diverticulate hyphae. In ***Asterotus***, these diverticulate hyphae form a deep layer (an asterostromelloid layer or dichophysoid layer). The branchlets are cylindric, and the hyphae are not encrusted. In ***Resupinatus***, ***Stigmatolemma*** and ***Stromatocyphella*** the branchlets are knobbed, tapering or irregular, and certain branchlets exude a substance that forms yellowish or brownish crystalline or amorphous encrusting material. This encrusting material is often so copious as to obscure details of the hyphae.

The basidiospores of the Resupinateae show a relatively small range of variation, but what variation there is is sometimes diagnostic at the species level. The spores are white or nearly white in print, and hyaline, inamyloid, acyanophilic, and smooth under the light microscope. They range in shape from globose to elliptic, bean-shaped (phaseoliform) or sausage-shaped (allantoid). Basidiospores of the Resupinateae have thin walls, and collapse readily (Coker, 1944; Vandendries 1934), and are considered similar in this regard to those of *Pleurotus* (Pegler and Young, 1971). An attempt was made to measure 20 or more spores from each collection examined (measurements exclude the length of the hylar appendage). In reporting spore sizes (and other measurements where large populations were sampled), figures in parentheses represent those dimensions that appeared in less than 10% of all observations.

C: CULTURAL STUDIES

Single-spore, monokaryotic cultures and dikaryotic cultures were obtained when possible from fresh collections. Dikaryotic cultures were obtained by allowing minute portions of fruit body tissue to grow out onto PD+AB agar, or by allowing two to several monokaryotic cultures to anastomose.

Single-spore cultures were obtained in the following way. A small, clean portion of a cap was suspended with Vaseline from the lid of a petri plate so that it shed spores onto the agar below. When the spore deposit was visible to the naked eye, a small block of agar with spores was transferred aseptically to approximately 5 mL of sterile saline in a vial. The vial was recapped and shaken to suspend the spores. Dilutions were prepared using sterile saline, and 0.5-0.75 mL of dilute spore suspension spread evenly over the surface of a PD+AB agar plate.

Spore dispersion plates were scanned under 40X or 100X over the next few days (up to 3 weeks in *Resupinatus striatulus*) following inoculation. Once widespread germination was observed, single germinated basidiospores were transferred aseptically, each on a minute chip of agar, to a plate of PD+AB or ANT B agar. The ANT B agar was particularly useful for the slow-germinating species, since bacteria resistant to tetracycline alone seemed to build up during the long germination period, and the slow species could not outgrow them.

Single-spore cultures were checked for the absence of clamp connections after they had grown out to 5 mm diameter or more. Clampless isolates were maintained on PDA for mating studies. Mating tests were conducted by plating a small piece from the margin of one single-spore culture together with an overlapping piece from another, and so on two by two in all possible combinations. Once good growth had been achieved, the circumference of the resulting colony was checked for clamp connections under 100X of the compound microscope. In some cases, because of the fine hyphae in this group, the presence of clamp connections had to be confirmed in a slide mount under 400X interference contrast. The results were scored in a matrix, which indicated the mating groups.

Studies on the nematophagous capabilities of cultures, and description of their *Nematoctonus* states, were conducted on WA in the presence of nematodes, as described fully in Part I.

RESULTS AND DISCUSSION

Tribus **RESUPINATEAE** Singer (1948 a: 30)

Type genus, originally designated: ***Resupinatus*** (C. Nees) S.F. Gray

The following description is adapted from Singer (1975): Fruit bodies pleurotoid, omphalinoid or cyphelloid (discoid to urceolate); lamellate or not; basidia normal, ie. not with siderophilous granules; basidioles clavate; spores white or whitish in mass, hyaline, inamyloid, acyanophilic, variously shaped, smooth; cheilocystidia usually present, sometimes inconspicuous, thin-walled, hyaline, often with hour-glass secretory cells as capitellae; pleurocystidia present as metuloids or absent; context soft and usually flexible when fresh, consisting of inamyloid tissue which is usually at least partially gelatinized; the gelatinous zone, trama or cuticle, or all three, usually with intracellular or extracellular, sometimes encrusting, grey to brown or black pigments; hyphae monomitic, with clamps; cuticle a poorly-differentiated cutis, or with diverticulate, tangled tomentum hyphae forming an encrusted rameales structure or a non-encrusted asterostromelloid zone. Most frequently on decaying wood, on other decaying vegetation, on soil rich in organic matter, or on diseased tissue of living Cormophyta.
Observations: The key features of the Resupinateae are the gelatinized fruit bodies with monomitic, clamped hyphae and nonamyloid spores, and usually some brownish or blackish pigmentation. The tribe represents a natural and closely related group. The members of the Resupinateae probably all

lead a parasitic existence, which is most easily shown in ***Hohenbuehelia***, but also suggested in ***Resupinatus*** and ***Stigmatolemma***. All species of ***Hohenbuehelia*** tested possess ***Nematoctonus*** states, and consume nematodes. The fact that species of ***Resupinatus*** do not consume nematodes makes this genus more interesting, in a way, than ***Hohenbuehelia***. The peculiar, jack-shaped cells of ***Resupinatus applicatus*** were not observed to become detached and germinate, and their function remains unknown. Vegetative hyphae of ***R. striatulus*** were followed through and along the surface of the substrate. Although these hyphae were often observed in areas of high microbial activity, and found closely associated with free-living green algae on the surface of the rotted wood, conclusive evidence of the biology of this fungus was not found. ***Resupinatus striatulus*** (Fig. 32 D) and ***Stigmatolemma poriaeforme*** (Fig. 32 B, C) have microdroplets on vegetative hyphae in the substrate of fruiting bodies similar to those found in ***Pleurotus*** (Fig. 32 A). No cultures of ***Stigmatolemma*** were available for study, but the microdroplets of ***R. striatulus*** were not found in culture, either on nutrient media or on WA with nematodes.

The tribe Panelleae (Tricholomataceae) has a number of similarities with the Resupinateae. Members of the Panelleae are often pleurotoid in habit, have a gelatinous zone in their cap trama, and some have metuloids, while others have diverticulate cheilocystidia. The Panelleae can be distinguished by their amyloid spores. Two species of ***Panellus*** tested in this laboratory were non-nematophagous (Thorn and Barron, 1984; and unpublished data).

The parasitic habit in the Resupinateae raises the question of relationships to the genus ***Pleurotus***. Fruit bodies of ***Pleurotus*** species are generally large, fleshy, and non-gelatinized. Hilber (1982) has illustrated secretory cheilocystidia in certain species of ***Pleurotus*** that resemble those of species of ***Hohenbuehelia*** and of ***Resupinatus alboniger***. ***Pleurotus*** is classified by Singer (1975) in the Polyporaceae of the Agaricales (often referred to as the Pleurotaceae, a later synonym, to avoid confusion with the majority of the polypores that belong to the Aphyllophorales).

The evolutionary kinship between ***Pleurotus*** and the Resupinateae appears clear. Members of the Resupinateae and ***Pleurotus*** share the parasitic mode. The similarity of the cheilocystidia in ***Pleurotus*** to those in the Resupinateae is striking. The spores of both ***Pleurotus*** and ***Hohenbuehelia*** are hyaline, thin-walled, and readily collapsing, and are regarded as similar to each other, and to those of

Polyporus, type genus of the Polyporaceae (= Pleurotaceae) by Pegler and Young (1971). The microdroplets found in *Resupinatus* and *Stigmatolemma* resemble those in *Pleurotus*. In addition, the dolipore septa in *Nematoctonus leiosporus* were shown to be of the "polypore type" (Tzean and Estey, 1977). These facts are strong evidence of the relatedness of these groups, despite the large morphological differences in their fruit bodies, and suggest that the Resupinateae should be transferred from the Tricholomataceae to the Polyporaceae (= Pleurotaceae).

KEY TO THE TAXA OF THE RESUPINATEAE STUDIED

1. Fruit bodies with definite gills **2**
1. Fruit bodies much reduced, without gills **23**
  2. Metuloids present in gills **3**
  2. No metuloids present in gills **16**
3. Fruit bodies usually 2 cm large or larger **4**
3. Fruit bodies usually less than 1 cm broad **10**
  4. Fruit bodies centrally stipitate, or nearly so; in bogs .... ***Hohenbuehelia longipes***
  4. Fruit bodies sessile or laterally stipitate **5**
5. Fruit bodies reniform or dimidiate **6**
5. Fruit bodies spathulate or petaloid **7**
  6. Spores ovate, 7-9 X 4-5.5 µm; fruit bodies pearl grey to brownish, with thick gelatinous spines .... ***Hohenbuehelia mastrucata***
  6. Spores narrower, 6.5-8.5 X 3.2-4.2 µm; upper surface glabrous to tomentose or hirsute, colour variable .... ***Hohenbuehelia atrocaerulea*** var. ***grisea***
7. Spores short, ovate, subglobose or globose, 3.0-5.5 X 3.0-4.0 µm .... ***Hohenbuehelia angustata***
7. Spores longer and usually more elliptical **8**
  8. Spores mostly ovate or short elliptic, 5.5-7.5 (9.0) X 3.0-4.5 µm, on trunks, woody debris or soil **9**
  8. Spores elliptic to phaseoliform, 7.5-9 X 4-5 µm; usually in mossy coniferous woods .... ***Hohenbuehelia tremula***
9. On soil or woody debris; fruit body petaloid, often thick-fleshed; gelatinous zone of ascendant hyphae, 100-250 µm deep .... ***Hohenbuehelia petalodes***
9. On logs; fruit body spathulate, thin-fleshed; gelatinous zone of horizontally-arranged hyphae, 40-100 µm deep .... ***Hohenbuehelia*** stirps Petaloides (see comments under ***Hohenbuehelia petalodes*** and

Nematoctonus cylindrosporus)

10. Gills white or yellowish at maturity; metuloids with hyaline walls **11**

10. Gills dark-coloured at maturity; metuloids usually with brown walls **12**

11. Cap dimidiate, straw-coloured or pale brown; gills moderately close .... *Hohenbuehelia approximans* (see also small forms of *H. atrocaerulea* var. *grisea*)

11. Cap cupulate, grey-brown to black; gills few and distant .... *Hohenbuehelia cyphelliformis*

12. Metuloids inconspicuous, imbedded in hymenium, often clavate **13**

12. Metuloids lanceolate, projecting clearly **14**

13. Cap with silvery tomentum over blackish flesh; on hardwood branches, often *Populus* .... *Hohenbuehelia unguicularis*

13. Cap jet black, mostly glabrous, with fine wisps of white hairs; on conifers, often *Abies* and *Pinus* .... *Hohenbuehelia pinacearum*

14. On conifers (*Pinus*); cap jet black, tomentose .... *Hohenbuehelia mustaliensis*

14. On hardwoods **15**

1.5 Cap jet black, mostly glabrous, with fine white hairs .... *Hohenbuehelia nigra*

15. Cap brown or olive brown, tomentose, often with dark bristles .... *Hohenbuehlia reniformis* (see under *Hohenbuehelia approximans*)

16. Spores globose or subglobose **17**

16. Spores elliptical or allantoid **19**

17. Cap with shaggy tomentum over basal area **18**

17. Cap at most pruinose, usually cupulate, less than 8 mm broad .... *Resupinatus striatulus*

18. Basal tomentum greyish or yellowish .... *Resupinatus applicatus*

18. Basal tomentum black, often in a clearly-defined disk .... *Resupinatus trichotis*

19. Gills becoming grey, brown or black at maturity; spores elliptic-phaseoliform **20**

19. Gills white; spores allantoid .... *Hohenbuehelia cyphelliformis*

20. On conifers; cap black, mostly glabrous, with fine white fibrils ...... *Hohenbuehelia pinacearum*

20. On hardwoods; cap tomentose, white, greyish or brownish **21**

21. Fruit bodies spoon-shaped, with a well-defined stem, brown, drying snow white, tomentose .... *Asterotus dealbatus*

21. Fruit bodies cupulate, sessile or with a short lateral pseudostipe **22**
    22. Hyphae of epicutis basically smooth, without lobes or branchlets; cap usually drawn into a pseudostipe ..... ***Hohenbuehelia unguicularis***
    22. Hyphae of epicutis with lobes and finger-like branches; cap usually sessile, dorsally attached .... ***Resupinatus alboniger***
23. Spores globose or subglobose 3.5-6.0 X 3.0-5.0 µm; fruit bodies minute, in troops .... ***Stigmatolemma poriaforme***
23. Spores elliptic or cylindric **24**
    24. Spores elliptical, 6-9 X 3-4 µm; fruit bodies minute; in troops on conifers .... ***Stigmatolemma conspersum*** (see under ***S. poriaeforme***)
    24. Spores cylindric, 8-10 X 3.0-3.8 µm; fruit bodies cupulate, clustered on a gelatinous base ...... ***Stromatocyphella conglobata***

ASTEROTUS Singer (1943 b: 161)

Type species (only original species): ***A. dealbatus*** (Berkeley) Singer

≡ ***Resupinatus*** (C. Nees) S.F. Gray subgenus ***Asterotus*** (Sing.) Singer (1973: 30)

The following description is modified from Singer (1962), based on examination of specimens during this study, with significant deviations from the original description indicated in bold face: Habit pleurotoid, pileus flabelliform on a well-formed, compressed or terete but lateral stem; gills well-formed, decurrent. Surface layer of the pileus and stipe formed of an asterostromelloid zone of hyaline hyphae with innumerable short, crowded, cylindric side branches coming off at right angles in all directions; **trama proper strongly gelatinised, deep brown in mass but hyaline in section**; hyphae monomitic but sometimes with thickened, gelatinised walls, inamyloid, all with clamps; basidia normal; **cheilocystidia clavate-digitate to diverticulate, sometimes abundant and forming an asterostromelloid zone on gill edge**; spores white in print, cylindric, subfusoid or suballantoid, hyaline, inamyloid, smooth. On wood.

Observations: The pigmented, gelatinized trama, inamyloid spores, and diverticulate cheilocystidia show that ***Asterotus*** is a typical member of the Resupinateae, closely allied with ***Resupinatus*** sensu stricto. The diagnostic features that separate ***Asterotus*** from ***Resupinatus*** are the strongly stipitate, flabelliform habit, and the thick asterostromelloid zone covering the cap and stem, the branchlets of which are cylindric and do not secrete amorphous or crystalline encrusting material. Species of ***Resupinatus*** are resupinate, cupulate to broadly pseudostipitate, and the coralloid diverticulae of its cuticular hyphae are knobbed, tapering or irregular, and secrete amorphous or crystalline, hyaline to brown encrusting material.

As it is now circumscribed, ***Asterotus*** is monotypic. ***Asterotus chilensis*** (Sing.) Singer (Singer and Digilio, 1953) is better placed in ***Resupinatus*** where it was originally described (Singer, 1948 b). ***Resupinatus chilensis*** is close to ***R. striatulus***, or possibly conspecific. ***Asterotus graminus*** Singer (1969) has been placed by Singer (1973) in ***Resupinatus***, where it is close to ***R. striatulus***. ***Asterotus argentinus*** Singer (Singer and Digilio, 1953) has been synonymised with ***Resupinatus alboniger*** (Pat.) Sing. by Singer (1978). Finally, ***A. bicolor*** (Mont.) Singer (1955) is a synonym of ***A. dealbatus***.

Asterotus dealbatus (Berk.) Singer (1943 b: 161) Fig. 15
- ≡ ***Panus dealbatus*** Berkeley (1847: 317)
    - ≡ ***Panellus dealbatus*** (Berk.) Murrill, in Murrill et al. (1915: 245)
    - ≡ ***Resupinatus dealbatus*** (Berk.) Singer (1973: 30)
- = ***Panus bicolor*** Montagne (1854: no. 329)
    - ≡ ***Asterotus bicolor*** (Mont.) Singer (1955: 376)
    - ≡ ***Resupinatus bicolor*** (Mont.) Singer (1973: 30)
- = ***Panus sprucei*** Berkeley (1856: 142)

This species was not seen in the fresh state. The following description is based on two dried specimens exmained during this study:

Fruit Body flabelliform and laterally stipitate, up to 2.5 cm tall by 1.2 cm broad, entirely matted-tomentose, particularly the stipe. **Pileus** white, to clay-coloured (pale 4B2) at the base, where it fans out from stipe; the margin finely tuberculate-striate. **Stipe** terete, 4-12 mm tall X 1.5-3 mm, with a bulb formed by substrate tightly bound to mycelioid base. **Gills** decurrent by fine white lines onto the stem, narrow, close and blackish. **Cuticle** a deep asterostromelloid zone formed of hyaline diverticulate hyphae about 3 µm diam., with cylindric projections up to 6 µm long by 1.0-1.5 µm (some fragments look like "jacks"). **Gelatinous Zone** forming entire trama, brown in mass, subhyaline in section, of hyphae 2-4 µm diam. in a strongly

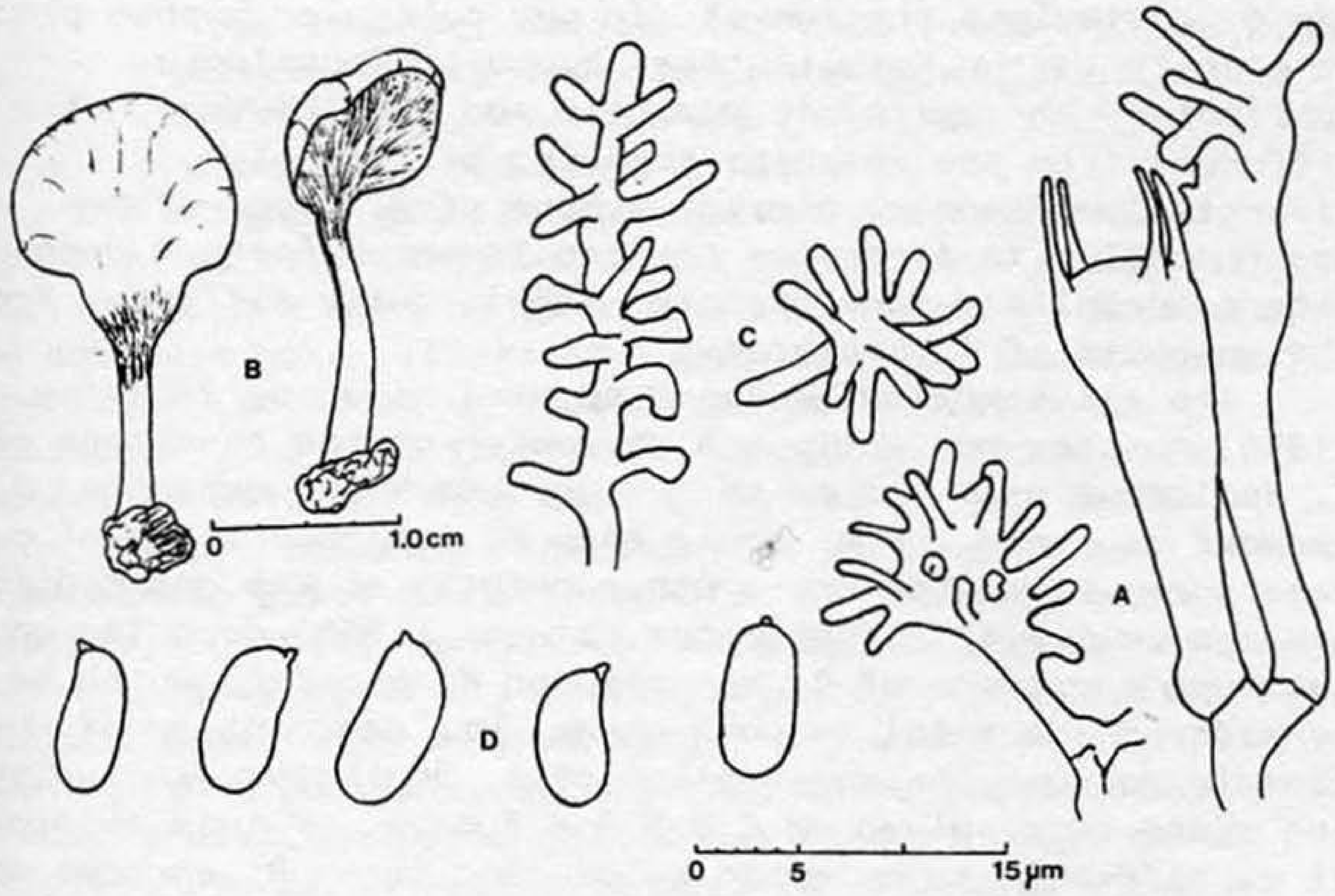

Figure 14 A-D: **Asterotus dealbatus**, Smith s.n. (Sept. 4, 1955, MICH); A) A basidium and two cheilocystidia; B) two fruit bodies; C) cuticular hyphae; D) basidiospores.

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gelatinized matrix. **Basidia** 4-pronged, clavate, 22-26 X 6-7 µm. **Cheilocystidia** clavate, or vesiculose, highly diverticulate, 12-25 X 4-10 µm. Similar pleurocystidia present **Spores** hyaline, inamyloid, smooth, narrowly elliptic-phaseoliform, (5.0) 6.0-7.0 X 2.5-3.0 µm.
Habitat: On dead wood. The 2 specimens examined were on soft, brown-rotted hardwood.
Distribution: *Asterotus dealbatus* is known from Alabama, Missouri, New York, North Carolina, Ohio (Murrill, et al. 1915) and Michigan in the United States, Quebec in Canada, and Brazil (Corner, 1981). The type of *Panus sprucei* came from southern Brazil, and that of *P. bicolor* came from French Guiana.
Specimens Examined: **Canada**: **Quebec**: Aylmer, west of Victoria Park, Sept. 11, 1893, J. Macoun, DAOM #51455. **United States**: **Michigan**: Warren's Woods, southwest Michigan, Sept. 4, 1955, A.H. Smith s.n. (MICH).

Mating System and Cultural Characters: Unknown.
Observations: ***Asterotus dealbatus*** is a striking and unmistakable fungus, particularly when dry. Its flabelliform habit and stark white upper surface, which contrasts strongly with the blackish-brown, decurrent gills, are very distinctive. The pigmented gelatinous zone in the cap, and the diverticulate cheilocystidia and cuticular hyphae place it clearly in the Resupinateae, close to ***Resupinatus applicatus***. The cylindric diverticulae are, however, very different from the knobbed, tapering or irregular diverticulae found on similar hyphae of ***R. applicatus***. Additionally, in ***Asterotus*** the cap tomentum forms a deep asterostromelloid zone (Singer, 1962), quite different from the epicutis of ***R. applicatus***.

The illustration of ***Panus sprucei*** given by Berkeley (1856) matches perfectly the character of the specimens of ***A. dealbatus*** examined in this study. Berkeley described ***P. sprucei*** as "on a larger scale than ***P. dealbatus***, and of a less pure white when dry". Other details of the description compare well with ***A. dealbatus***. Singer (1955) reported on the type specimens of ***P. sprucei*** and ***P. bicolor***, which he considered identical to each other. His description of them closely matches the description of ***A. dealbatus***, including the spore size, given as 6.5-7.3 X 3.3 µm. On this evidence it is difficult to maintain ***A. bicolor*** (with ***P. sprucei*** as a synonym) and ***A. dealbatus*** as separate species.

HOHENBUEHELIA Schulzer, in Schulzer, Kanitz and Knapp (1866: 45) [as ***Hohenbühelia***]
Type species (only original species): ***H. petalodes*** (Bull.: Fr.) Schulz.
= ***Geopetalum*** Patouillard (1887: 127)
Type species, obligatory under Article 7.11 of I.C.B.N. (Stafleu et al., 1978): ***G. petalodes*** (Bull.: Fr.) Pat. [Singer and Smith (1948) selected ***G. carbonarium***, but this is inadmissible]
= ***Pleurotus*** (Fr.) Kummer sect. ***Acanthocystis*** Fayod (1889: 338)
≡ ***Acanthocystis*** (Fayod) Kuehner (1926: 111)
Type species, selected by Donk (1949), ***A. geogenius*** (DC. ex Fr.) Kuehner [= ***H. petalodes*** (Bull.: Fr.) Schulz.]
= ***Marasmius*** Fries sect. ***Pleurotopsis*** P. Hennings, in Engler and Prantl (1898: 226)
≡ ***Pleurotopsis*** (P. Henn.) Earle 412 (1909)
Type species, designated by Earle (1909): ***P.***

spodoleucus (Berk. & Br.) Earle [= ***Hohenbuehelia cyphelliformis*** (Berk.) Miller]

= ***Agaricochaete*** Eichelbaum (1906: 58)

Type species, selected by Singer and Smith (1946): ***A. mirabilis*** Eichelbaum

= ***Urceolus*** Velenovský (1939: 44)

Type species, selected by Donk (1962 a), and only species fully described in original publication: ***U. sambucinus*** Velenovský [= ***Hohenbuehelia cyphelliformis*** (Berk.) Miller]

The original generic diagnosis of ***Hohenbuehelia*** (Schulzer et al., 1866) was based on ***Agaricus petalodes*** Bull.: Fr., and must be considerably revised to accommodate the now much wider limits of ***Hohenbuehelia***. The following description is based on that by Singer (1975), with additional data from this study: Small to medium-sized agarics (0.5-10 cm) with well developed gills; gills decurrent or radiating from point of attachment or a central or eccentric point on the underside of the cap; habit cupulate, conchate, dimidiate, petaloid or omphalinoid; stem absent or present as a lateral pseudostipe or occasionally a well-differentiated central stipe; cap usually but not always with a partially gelatinized trama (most commonly forming a distinct upper gelatinous zone directly below cuticle); hyphae monomitic, inamyloid, all with clamp connections; cuticle occasionally a hymeniform layer of inflated hyphal tips, but more commonly a cutis, often poorly differentiated, commonly with tufts of hyphae forming a sparse or dense tomentum; pigments (grey to brown or black) usually present, intercellular or extracellular as distinct ring or spiral encrustations or as amorphous-granular material; cuticular hyphae not coralloid-diverticulate nor forming a rameales structure; spores white in mass, hyaline, inamyloid, acyanophilic, varying from globose to elliptic, phaseoliform, cylindric or allantoid, thin-walled, smooth (under light microscope); pleurocystidia usually present as metuloids although occasionally rare or inconspicuous; cheilocystidia present, clavate, fusoid or lecythiform, commonly with an hour-glass secretory cell surrounded by a mucous droplet (gloeosphex) at the tip of a short or elongated neck, the neck sometimes branched and with 2-4 gloeosphex capitellae; similar gloeosphex cystidia often occurring as pleurocystidia, pilocystidia or caulocystidia; gill trama regular but hyphae often interwoven to a degree, sometimes with thickened, gelatinized walls. On the ground, on wood or living or dead herbaceous plant material. Asexual state a ***Nematoctonus***.

Observations: In Singer's (1975) system of agaric classification, ***Hohenbuehelia*** could be recognised by the presence of metuloids, inamyloid spores, and a gelatinous zone in the pileus. From this study, it can be added that species of ***Hohenbuehelia*** possess ***Nematoctonus*** anamorphs, usually indicated by the presence of gloeosphex cystidia on the gills, cap or stem of the fruit body.

Other genera with which ***Hohenbuehelia*** might be confused are ***Resupinatus*** sensu stricto, ***Campanella***, ***Panellus***, ***Faerberia*** and ***Conchomyces***. Species of ***Resupinatus*** have diverticulate cheilocystidia and cuticular hyphae, and lack hour-glass secretory cells on their cystidia, and they lack a ***Nematoctonus*** asexual state. Kuehner (1980) treats ***Resupinatus*** and ***Hohenbuehelia*** as subgenera of ***Resupinatus***, but uses some of the same characters to distinguish them. In particular, he illustrated clearly the diverticulate cheilocystidia and diverticulate cuticular hyphae of ***Resupinatus***, and the gloeosphex cystidia of ***Hohenbuehelia***. Species of ***Campanella***, which occasionally have metuloids, also lack hour-glass cells and ***Nematoctonus*** states, and have anastomosing gills that form a poroid hymenium. Species of ***Panellus*** have amyloid spores. Singer (1951 a) included ***Panellus serotinus*** in ***Hohenbuehelia*** because of its metuloids, but has since (1962, 1975) excluded it on the basis of its amyloid spores. ***Panellus patellaris*** (Fr.) Konrad and Maublanc has a well-developed gelatinous zone in the cap, and allantoid spores similar in shape to those of ***R. cyphelliformis***, but much smaller (4.5-5.5 X 0.5-1.2 µm fide Miller, 1970). Both ***Panellus serotinus*** and ***P. patellaris*** are non-nematophagous and have no ***Nematoctonus*** anamorph (Thorn and Barron, 1984; and Thorn, unpublished data). ***Faerberia*** Pouzar (1981), a monotypic genus including the species usually known as ***Geopetalum carbonarium***, differs in its dimitic hyphal system and lack of a gelatinous zone, hour-glass secretory cells, or a ***Nematoctonus*** state. ***Conchomyces*** van Overeem (1928) is also monotypic, and based on ***C. verrucisporus*** v. Overeem [= ***C. bursaeformis*** (Berk.) Horak]. Reid (1964) and Singer (1975) treat this species as ***Hohenbuehelia bursaeformis*** (Berk.) Reid, but it differs from ***Hohenbuehelia*** in its spiny spores and clavate cheilocystidia lacking gloeosphex capitellae (Horak, 1981). The decision by Horak to separate ***Conchomyces*** from ***Hohenbuehelia*** seems to be biologically well-founded.

Donk (1949) showed that ***Hohenbuehelia*** had been validly published. Singer (1951 a) adopted ***Hohenbuehelia*** for species that he had previously treated in ***Acanthocystis*** (Singer, 1943 a). Kuehner and Romagnesi (1953) preferred ***Geopetalum***, with subgenus *Acanthocystis* for the species now in *Hohenbuehelia* plus *G. carbonarium*, and subgenus *Phyllotus* for the species of *Resupinatus* sensu lato. Pouzar (1981) showed that *Geopetalum* Patouillard (1887) is an obligate typonym of *Hohenbuehelia* under Article 63 of the International Code of Botanical Nomenclature (Voss et al., 1983) because it included the type species of *Hohenbuehelia* when it was first described. Pouzar erected the genus *Faerberia* to accommodate *G. carbonarium*, a carbonicolous fungus with dimitic trama, found in Europe.

The genus *Agaricochaete* and its two original species (Eichelbaum, 1906) have remained in relative obscurity until recently. Pegler (1977) described and illustrated a third species from Kenya, which he said differed from *Hohenbuehelia* in its centrally stipitate habit. The trama is non-gelatinized, but typical metuloids, and fusoid-capitate cheilocystidia are present, and thus *Agaricochaete keniensis* Pegler is most likely a *Hohenbuehelia* allied to *H. longipes*. A fourth species, *Agaricochaete indica* Natarajan and Raman (1980), is not congeneric since the hyphae lack clamp connections, the cheilocystidia are flexuous-cylindric, and the fruit bodies are purple and mycenioid. It is perhaps a species of *Lactocollybia*.

Pleurotopsis and *Urceolus* are generally synonymised with *Resupinatus* (Donk, 1962 a; Horak, 1968; Singer, 1975). The species on which they were both based is *Hohenbuehelia cyphelliformis* (= *Pleurotopsis spodoleucus*; = *Urceolus sambucinus*), so they become synonyms of *Hohenbuehelia*.

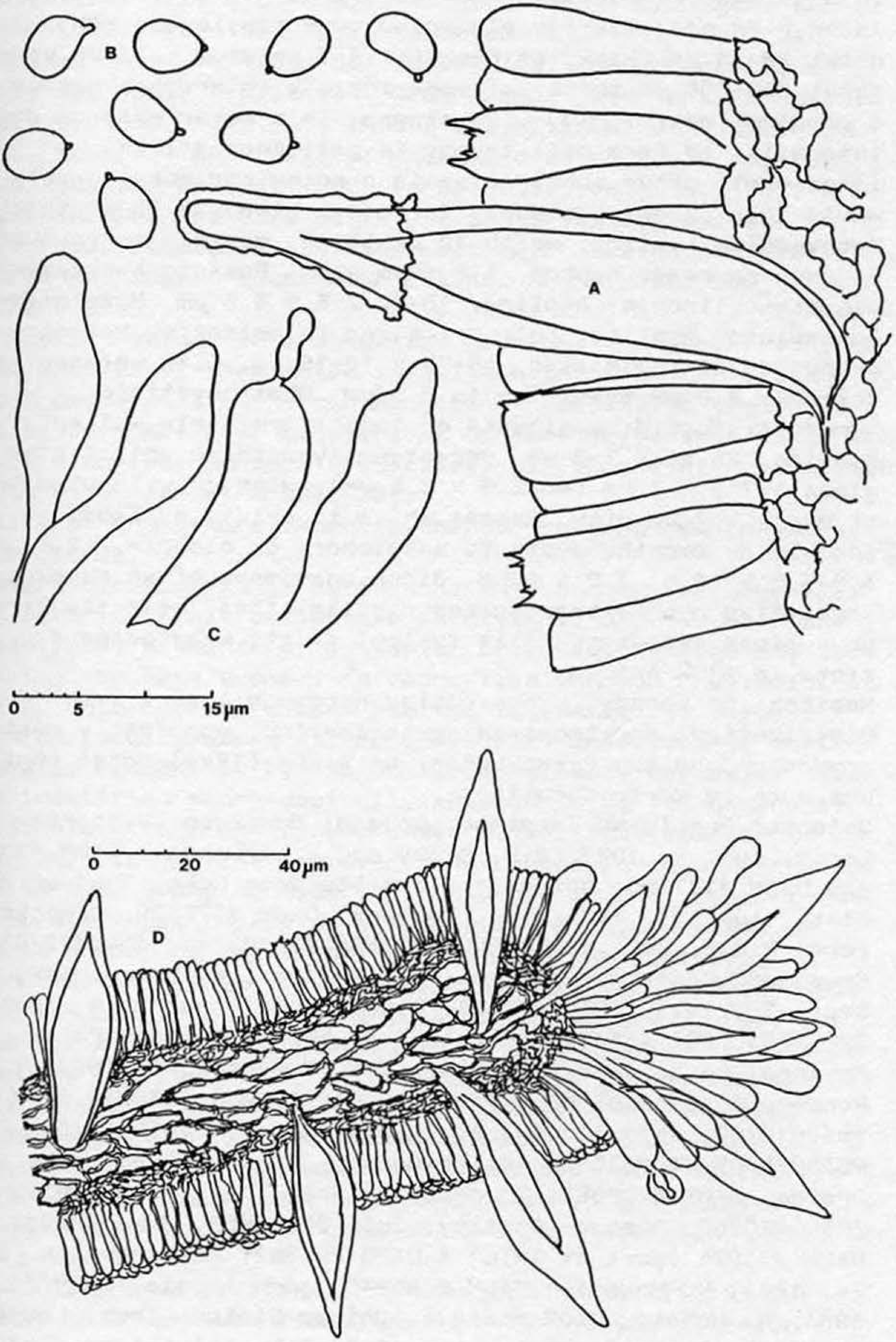
Hohenbuehelia angustata (Berk.) Singer (1951: 255) Figs. 15 & 16
≡ ***Panus angustatus*** Berkeley (1847: 318) [**non** ***Panus angustatus*** Berk., in Cooke (1892: 98); **non** ***Pleurotus angustatus*** Berkeley & Broome (1871: 528)]
    ≡ ***Geopetalum angustatum*** (Berk.) Murrill (1916: 300)
= ***Pleurotus stratosus*** Atkinson (1902: 116) (fide Murrill, 1916)
    ≡ ***Acanthocystis stratosa*** (Atk.) Singer (1943 a: 148)
= ***Pleurotus petaloides*** (Bull.: Fr.) Quélet var. ***eupetaloides*** Pilat f. ***americana*** Pilat (1935: 90) (fide Singer and Kuthan, 1980)

Pileus flabelliform to spathulate or dimidiate, 2-5 cm long X 1-4 (5)cm broad X 0.1-0.4 cm thick, margin incurved at

Figure 15: ***Hohenbuehelia angustata***, R.G. Thorn #840722/03, X 1.5

first, surface finely frosted near margin to downy tomentose near base with patches becoming glabrous in age. Ground colour off-white (A1) near margin to buff (4A2) or tan (5B3) near base, becoming darker in age to beige (4-5A3) and to warm brown (5C5) at base. **Gills** decurrent but ending in a tomentose sterile area on pseudostipe, narrow, close (6/mm), white at first, through buffy (4A2) to tan-coloured (5B4) in age or on drying, finely frosted under 10X by metuloids. **Stipe** none, though cap tapers to base (pseudostipe), which is 0.2-2 cm at point of attachment, with thick white rhizomorphs running through substrate from base. **Cuticle** a densely interwoven layer 8-15 µm thick of hyphae 1.5-5 µm diam., with clamps, with loose tufts of tomentum hyphae 50 µm or more tall, and scattered, prostrate **metuloid pilocystidia** 60-80 X 4-7.5 µm with hyaline to brownish walls about 1.0 µm thick. **Gelatinous Zone** immediately below, 180-250 µm thick, hyaline, of sparse,

Figure 16 A-D: ***Hohenbuehelia angustata***. A-C) RGT #830822/10 (T-87). A) Hymenium, showing basidia and one metuloid; B) basidiospores; C) cheilocystidia. D) RGT #830820/08 (T-92), vertical section at gill edge showing arrangement of basidia, metuloids and cheilocystidia.


B
A
C
0
5
15 µm
0
20
40 µm
D

tangled hyphae 2-5 µm diam. (most about 3 µm), with clamps, in a gelatinous matrix. **Trama** bilayered, first a densely interwoven and slightly pigmented zone (yellow in KOH), about 20-35 µm thick, of hyphae 3.5-7 µm diam.; trama proper about 250-600 µm thick, of more loosely interwoven hyphae 4-9 µm diam (most 7 µm), with clamps. This layer extends down into gills to form gill trama. In gill interstices, immediately above subhymenium is a paler and more loosely woven zone (showing clearly in cresyl blue) 15-25 µm thick. **Subhymenium** hyaline, up to 10 µm thick, densely interwoven of much narrower hyphae, 1.5-3 µm diam. **Basidia** 4-pronged, clavate-cylindric, hyaline, 18-22 X 5.5-6.5 µm. **Metuloids** lanceolate, hyaline, pale brick red in Melzer's, becoming encrusted at their tips, 45-75 X 10-16 µm, with walls commonly 2.0 µm thick, up to 3.5 µm. **Cheilocystidia** numerous, fusoid to clavate or lageniform, thin-walled, hyaline, 25-36 X 7-8 µm, occasionally with an apical hour-glass 5-7 X 2-3 µm (most 6 X 2.5 µm), with or without a ball of mucus 4-7 µm diam. **Spores** white in print, hyaline, inamyloid, smooth, ovate to subglobose or globose, (2.5) 3.0-5.5 X (2.5) 3.0-4.0 µm. Older specimens often develop vegetative hyphae between their gills; these with the large hour-glass secretory cells typical of its *Nematoctonus* state, 8-11 X 3-5 µm.

Habitat: On spongy, brown-rotted hardwood logs.

Distribution: Northeastern North America, apparently most common around the Great Lakes, as Coker (1944) noted that it was rare in North Carolina.

Selected Specimens Examined: Canada: Manitoba: Victoria Beach, Aug. 1, 1927, G.R. Bisby and W.L. Gordon, DAOM #28054 and DAOM #157659. **Ontario**: Black Sturgeon Lake, Thunder Bay Dist., Aug. 11, 1974, S.A. Redhead, DAOM #175329; Cruickston Farm, Blair, July 22, 1984, RGT #840722/02 and #840722/03; Greenwood Conservation Area, Ontario Co., W. Dobrovolsky, Sept. 26, 1971, TRTC #47171; Pinery Provincial Park, Sept. 22, 1983, RGT #830922/10 (conf. R. Singer); Point Pelee National Park, Sept. 12, 1962, J.W. Groves, DAOM #89723; Rondeau Provincial Park, Aug. 12, 1983, RGT #830812/01 & #830812/02; same locale, Aug. 20, 1983, RGT #830820/05, #830820/08, & #830820/10; Temagami, July 22, 1968, J.W. Groves, DAOM #126095; Toronto, July 26, 1942, G.S. Bell, TRTC #20700. **Quebec**: Cantley, July 22, 1952, J.W. Groves, DAOM #33824 (part at TRTC) & DAOM #28862; Melocheville, June 24, 1981, R. McNeil, DAOM #185938; same locale, July 31, 1981, R. McNeil, DAOM #185914. **United States: Iowa**: Lodges St. Park, Boone Co., June 25, 1983, R.L. Gilbertson #14724 (ARIZ). **Kansas**: Rooks Co., July 24, 1896, E. Bartholomew, Dearness #2760 (at DAOM). **Maine**: Old Town, Penobscot Co., July 12, 1970, R.L. Homola #3620 (MAINE). **Michigan**: Ann Arbor, July 26, 1921, L.E. Wehmeyer, DAOM #124163; East Lansing, Aug. 7, 1983, RGT #830807/02; Tahquamenon Falls, July 16, 1951, A.H. Smith, DAOM #26862. **New York**: Freeville, July 6, 1917, "J.H.F.", TRTC #1722; Ithaca, July 2, 1953, R.L. Shaffer, DAOM #41365; McGowan's Woods, July 16, 1903, H.S. Jackson #502 at TRTC; Varna Woods, July 13, 1903, H.S. Jackson #462 and #524 at TRTC [last 3 collections as *Pleurotus stratosus* Atkinson, det. G.F. Atkinson]. **West Virginia**: Stuart Camp, near Elkins, Aug 4, 1985, RGT #850804/03.

Mating System: Heterothallic, bipolar. Six monokaryons of RGT #840722/02 were mated in all combinations and yielded 3 A1's and 3 A2's. Nine monokaryons of #840722/03 yielded 8 A1's and 1 A2. Four monokaryons of #830812/02 that would not form dikaryons amongst themselves, all formed dikaryons with both A1 and A2 of #840722/02.

Cultural Characters: Nematophagous; anamorph ***Nematoctonus angustatus***.

Observations: This is by far the most common ***Hohenbuehelia*** in Ontario. Fruit bodies are persistent, and can be found readily by a search of suitable, brown-rotted logs any time during the late summer. In areas like Rondeau Provincial Park, Ontario, where such habitat is common, ***H. angustata*** can be locally abundant. ***Hohenbuehelia angustata*** is most readily recognised by its small, subglobose spores, but can be identified macroscopically in Ontario by its generally spathulate form and very crowded gills. This species is variable in outline, however, and ranges in colour from off-white when young through to warm brown in age, so that separate fruit bodies on a single log might be taken at first glance as representing more than one species.

Murrill (1916) recognised ***Pleurotus stratosus*** as this species, as did Coker (1944). Since Coker had a broad concept of ***Pleurotus*** that included this species, he had to use the combination ***P. stratosus*** because ***angustatus*** was occupied in ***Pleurotus***. Authentic material of ***Pleurotus stratosus*** Atk. at TRTC was examined and found to be conspecific with ***Hohenbuehelia angustata***, with spores 3-4 X 3.0-3.5 μm. The spore characters given in the original diagnosis ("oval to subglobose, 2-3 μm", Atkinson, 1902) are in error.

Pleurotus petaloides f. ***americana*** Pilat (1935) was based on a specimen from Ithaca, N.Y. (as was Atkinson's ***P. stratosus***). It is also identical to ***H. angustata***, as has been pointed out by Singer and Kuthan (1980). Its spores were described as subspherical, 3.5-4.5 µm.

This fungus was described as *Pleurotus petaloides* Fr. by Peck (1886), who noted the crowded lamellae and globose spores 3-4 µm in diameter. Kauffman (1919) followed Peck, and because of this, many early records of *P. petaloides* in the Americas (eg. Bisby et al., 1929) were based on *H. angustata*.

Hohenbuehelia approximans (Peck) Singer (1951: 255) Fig. 17
≡ *Pleurotus approximans* Peck (1911: 37)
≡ *Resupinatus approximans* (Peck) Murrill, in Murrill, et al. (1915: 241)

Pileus dimidiate, sessile, attached dorsally or broadly along the base, 4-10 mm long X 4-12 mm broad (dry), youngest example dusky brown (5D4-3 to 5C3-2 in centre, paling to buffy (4A3) on margin (dry), very finely white hispid in the centre and glabrous at both base and margin. Older examples were straw-coloured (4A-B3-4), with medium brown base (5B3-D4) (dry), margin both pellucid and sulcate, edge entire. **Stipe** none. **Gills** radiating from point of attachment with one tier of lamellulae, narrow, moderately close, creamy white to pale yellow (4A2-3) (dry), about 1 mm deep. **Flesh** very thin. Dried fruit bodies are translucent. **Cuticle** thin, 15-25 µm, pale brown in KOH, with small fascicles of hyaline, cylindric, smooth, round-tipped hyphae 25-65 µm tall X 4-6 µm diam. Cuticular hyphae prostrate, 3-6 µm diam., smooth, but in places with pale amorphous-granular coating. **Gelatinous Zone** hyaline, 150-200 µm thick, of tangled hyphae (those near cuticle nearly parallel, those near trama zig-zag and obliquely rising) 1.5-4.0 µm diam. (most 3 µm). **Trama** pale brown in KOH, 150 µm deep; hyphae horizontal and parallel in upper zone, becoming tangled below and descending to form gill trama, 3-7 µm diam., with gelatinized walls up to 2.0 µm thick. **Gill Trama** parallel-interwoven, hyaline, hyphae similar to cap trama, all with clamps. **Basidia** 4-pronged, clavate-cylindric, hyaline, 25-30 X 6-7.5 µm. **Metuloids** broadly lanceolate, hyaline, faintly dextrinoid, with encrusted apices, (35) 42-70 X (9) 10-20 (25) µm. **Cheilocystidia** fusoid-ventricose, hyaline, 20-32 X 4-6 µm, including a neck (sometimes branched once) about 5 X 2-3 µm, and an hour-glass cell about 5 X 2-2.5 µm; mucous

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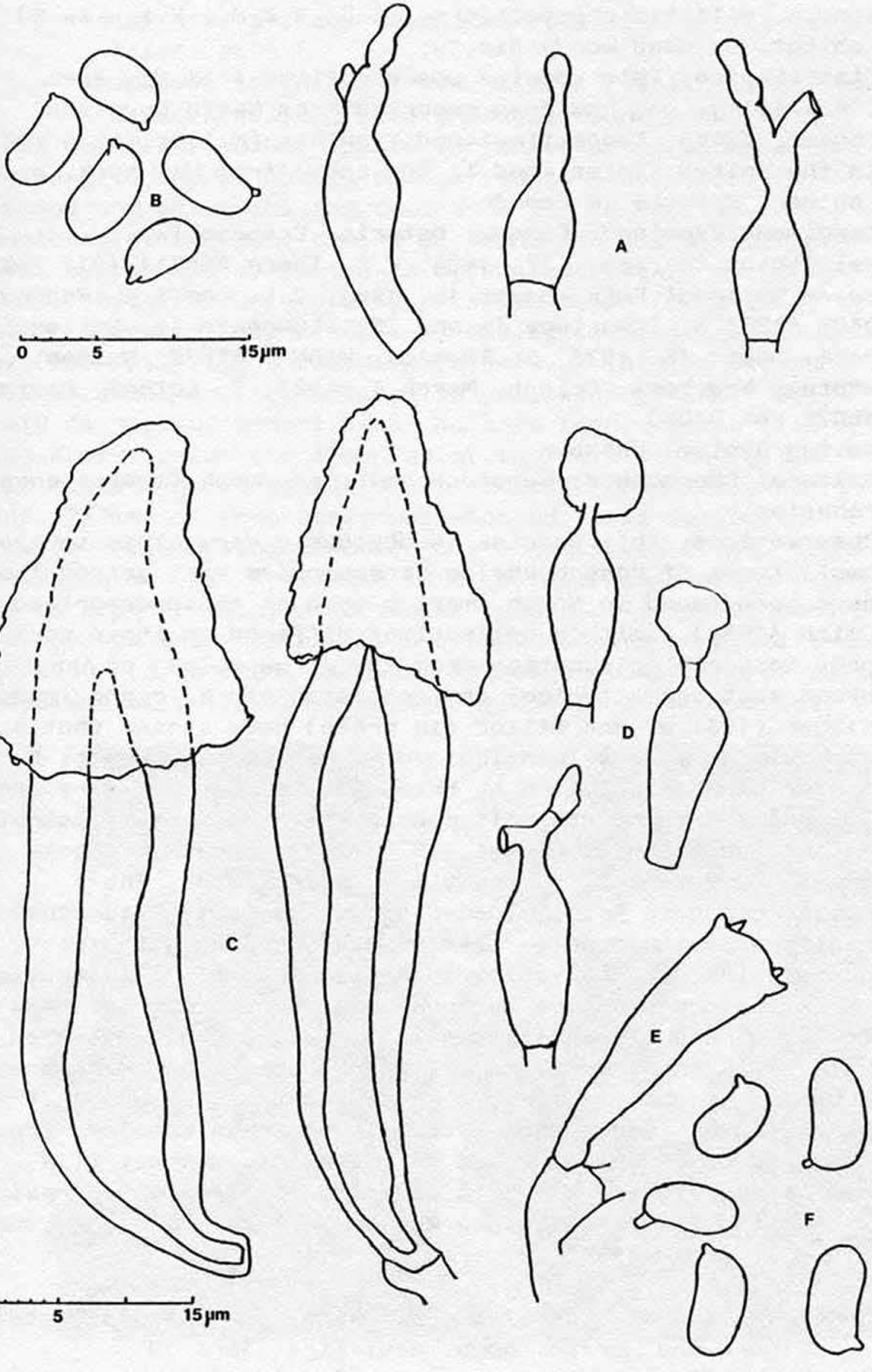
Figure 17 A-F: *Hohenbuehelia approximans*. A-B) DAOM #188324 (T-116). A) Cheilocystidia; B) basidiospores. C-F) DAOM #153672. C) Two metuloids; D) three cheilocystidia; E) a basdium; F) basidiospores.


B
A
0
5
15µm
C
D
E
F
0
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15µm

ball, when present, 4-5 µm diam. **Spores** hyaline, inamyloid, smooth, elliptic-phaseoliform, (6.5) 7.0-8.1 X 3-4 (4.5) µm.
Habitat: On dead woody dicots.
Distribution: This species was described from New York (Peck 1911), and has been reported from North Carolina (Coker, 1944), Connecticut and Virginia (Miller, in press) in the United States, and is now known from New York, and southern Ontario in Canada.
Specimens Examined: Canada: Ontario: Eramosa Twp., Wellington Co., Nov. 17, 1984, R.G. Thorn #841117/01; Point Pelee National Park, Sept. 18, 1981, J.E. and S.A. Redhead, DAOM #188324; Thwartway Island, St. Lawrence Is. National Park, Sept. 12, 1975, S. Thomson, DAOM #153672. **United States: New York**: Orient, March 1, 1923, R. Latham, Dearness #5072 (at DAOM).
Mating System: Unknown.
Cultural Characters: Nematophagous; anamorph ***Nematoctonus robustus***.
Observations: This species is obviously very close to the small forms of ***Hohenbuehelia atrocaerulea*** var. ***grisea*** that have been found in North America such as those described by Smith (1934). Smith's collections differed in their dark grey to black colouration from the straw colour or warm brown that seems typical and consistent in ***H. approximans***. Singer (1951 a) and Miller (in press) have stated that ***H. approximans*** may be identical to ***H. reniformis*** (Meyer: Fr.) Singer. The description by Fries (1821) does not give enough information to refute this possibility, but the illustration authorised by Fries (Fries, 1874) and one by M.C. Cooke (1883) do not closely resemble ***H. approximans***. The illustration in Fries' Icones shows ***Agaricus*** (***Pleurotus***) ***reniformis*** with a pale- to medium-brown cap, with spiky, black hairs, and tan-coloured gills. Cooke's illustration shows the cap as olive to khaki-brown, with coarse, dark tomentum, and olive-yellow gills. Pilát (1935) described the gills of ***P. reniformis*** as white or whitish, becoming grey, brownish or dark sooty, and mentioned that the walls of the metuloids are weakly to distinctly brown. A specimen from Japan (DAOM #187821) seemed to match this concept of ***H. reniformis*** closely, that is so different from ***H. approximans*** with its gills "nearly snow white,... becoming creamy when older" (Coker, 1944).

Hohenbuehelia atrocaerulea (Fr.) Sing. var. ***grisea*** (Peck) Thorn and Barron, **comb. nov.** Figs. 18 & 19
Basionym: ***Pleurotus atrocaeruleus*** (Fr.) Kummer var. ***griseus*** Peck (1891: 147)

≡ *Pleurotus griseus* (Peck) Peck (1909: 25)
≡ *Resupinatus griseus* (Peck) Murrill, in Murrill et al. (1915: 240)
≡ *Hohenbuehelia grisea* (Peck) Singer (1951 a: 255) [non *Hohenbuehelia grisea* (Massee) Horak (1980: 315)]

Pileus dimidiate, orbicular or conchate, up to about 3 cm long by 4 cm broad, margin downcurved to wavy; nearly glabrous and silky-shining toward margin to frosted, tomentose, or strigose toward base; margin not striate when fresh, hygrophanous, fading to off-white (4-5A2) or buffy (4A-B3, 5B3) from watery grey or olive brown (5C-D-E3-4, 6E4) or blackish brown (5-6F4-5) fading to deep brownish-grey (ca. 5D1-2), and becoming faintly striate on drying. Basal tomentum pallid, whitish to yellowish (4-5A2). **Stipe** rarely developed, amounting to no more than a small (1-3 mm long) semicircular sterile area at the base of the gills. **Gills** radiating from point of attachment, moderately narrow, close (2/ mm) or moderately well-spaced, pale yellowish white (3-4A2), drying concolourous or yellower (4A4), finely frosted under 10X. **Cuticle** a thin, pale or dark brown (KOH) zone of repent, tangled, brownish hyphae, (10) 15-25 (30) µm deep; hyphae thin-walled, with clamps, smooth or pigment-encrusted, (2) 3-6 (8) µm diam. **Epicutis** consisting of tufts of hyaline or yellowish tomentum hyphae up to 600 µm tall,

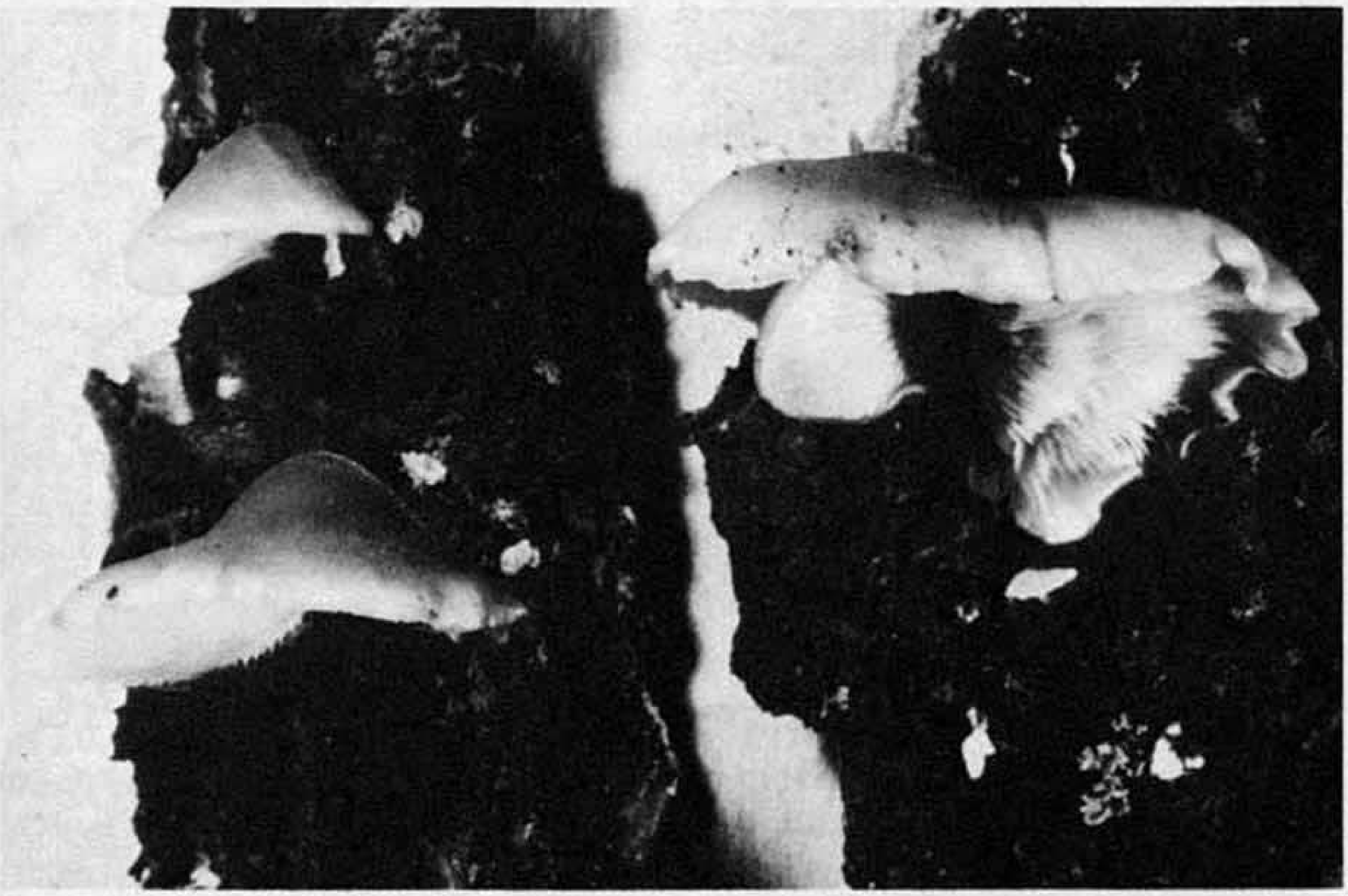


Figure 18: *Hohenbuehelia atrocaerulea* var. *grisea*, R.G. Thorn #840909/02, X 2.

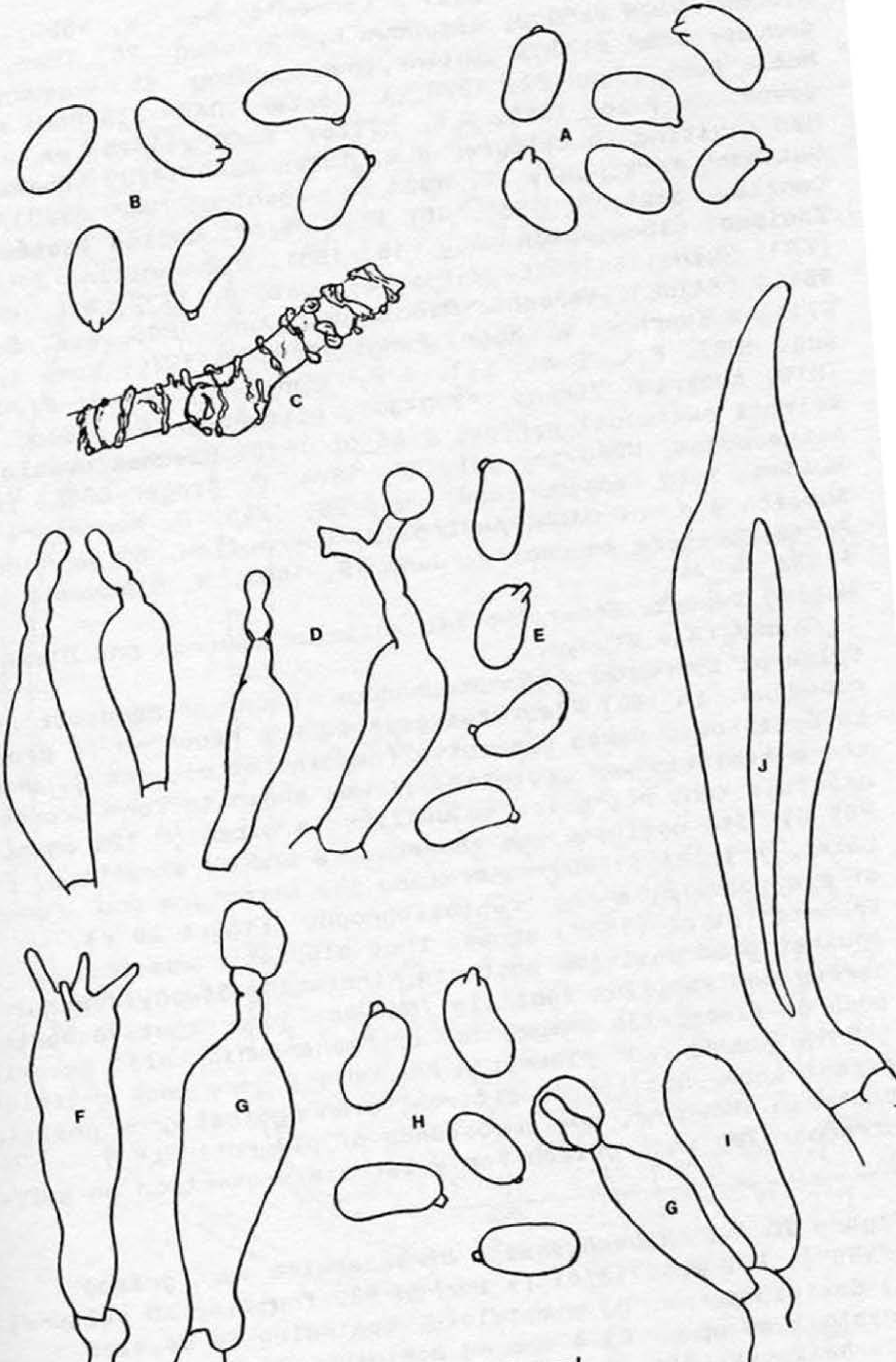
thin-walled or with walls up to 1.0 µm thick, smooth or encrusted, clamped and occasionally secondarily simple-septate, with rounded tips, 2-6 µm diam. **Gelatinous Zone** hyaline, commonly 150-250 µm deep, but up to 1000 um deep; hyphae hyaline, yellowish in Melzer's, mostly tangled-ascending, mostly smooth but often finely encrusted toward cuticle, 1.5-4.0 (6.0) µm diam., with clamps. **Trama** pale yellow-brown in KOH, deep golden yellow in Melzer's, a dense tangle of hyphae 2-5 (7) µm diam. with smooth walls gelatinized to 1.5 µm thick; descending into gills to form gill trama. **Gill Trama** hyaline or pale brownish yellow (KOH), parallel-interwoven, of hyphae 2.5-7 (12) µm diam., with walls gelatinized, commonly 0.5-2.0, up to 3.0 µm thick. **Subhymenium** hyaline, narrow, indistinct. **Hymenium** hyaline, 20-30 µm deep. **Basidia** (2-) 4- spored, hyaline, clavate, (20) 24-32 X 5-7 µm diam. **Cheilocystidia** lecythiform, clavate-rostrate, capitate, hyaline, (15) 19-30 X 5-7 (10) µm, neck usually short and tapering, 1-4 (7) X 2-3 um, hour-glass 4-5 X 1.5-2.0 µm, mucoid droplet 3-5 um diam. **Metuloids** hyaline or faintly yellow, lanceolate, encrusted in age, 27-105 X 7-26 µm, commonly 40-60 X 8-10 µm; walls up to 6.0 µm thick, pale brick red in Melzer's. **Spores** white in print, hyaline, inamyloid, smooth, elliptic-phaseoliform, typically (6.0) 6.5-8.5 (9.0) X (3.0) 3.2-4.2 (4.5) µm., but up to 11.0 X 4.4 µm in one specimen with predominantly 2-spored basidia (RGT #840713/01).

Habitat: *H. atrocaerulea* var. *grisea* occurs on both standing and fallen dead wood, almost always hardwoods, but DAOM #158848 occurred on *Juniperus*, and DAOM #58766 on *Pinus strobus*. The *Nematoctonus* state is commonly recovered from farmyard soil (Barron and Dierkes, 1977).

Distribution: Widely distributed in eastern North America and Europe, and reported (Singer and Digilio, 1953) from Argentina.

Selected Specimens Examined: **Canada**: **Nova Scotia**: Blomidon Provincial Park, Kings Co., September 1, 1985, R.G. Thorn #85009/07. **Ontario**: Almonte, Sept. 20, 1956, R. Horner, DAOM #59766; Bear Island, Lake Temagami, Sept. 4, 1934, H.S.

Figure 19 A-J: *Hohenbuehelia atrocaerulea* var. *grisea*. A) Basidiospores of Ellis and Everhart, Fungi Columbiani #1202 (TRTC). B-C) DAOM #64990. B) Basidiospores; C) an encrusted cuticular hypha. D-E) DAOM #48912. D) Four cheilocystidia; E) basidiospores. F-J) DAOM #158848. F) Basidium; G) cheilocystidia; H) basidiospores; I) basidiole; J) metuloids, with crystalline cap dissolved away.


A
B
C
D
E
J
F
G
H
G
I
0
5
15 µm

Jackson, TRTC #7602; Bell's Corner's, Nov. 2, 1955, S. Gibson, DAOM #48912; Petawawa F.E.S., Aug. 29, 1943, J.W. Groves, DAOM #17383; Mallorytown Landing, St. Lawrence Is. Natl. Park, June 22, 1976, A. Carter, DAOM #158848; North Gower, July 26, 1955, M.E. Elliot, DAOM #54625; ex Guelph, N90 fruiting in culture, R.G. Thorn #840713/01. **Quebec**: Gatineau Park, July 26, 1961, K. Aoshima, DAOM #89037; Cantley, Sept. 9, 1984, RGT #840909/02. **United States: Indiana**: Bloomington, Aug. 15, 1981, R.E. Halling #3421 (FH). **Maine**: Belfast, Waldo Co., Oct. 1, 1972, R.L. Homola #5450 (MAINE). **Vermont**: Middlebury, Aug. 1896, E.A. Burt, Ellis & Everhart N. Amer. Fungi #3505 at TRTC; same locale, Aug. 1897, E.A. Burt, Ell. & Ev. Fungi Columbiani #1202 at TRTC. **Austria**: Vienna, "7-9-31", Litschauer & Lohwag, Fungi selecti exsiccati europei #143 at TRTC. **Czechoslovakia**: Silherovice, Moravia, July 26, 1974, R. Singer C5683 (F). **Sweden**: Sala, Västmanland, June 26, 1946, R. Morander, Flora Suecica s.n. at DAOM. **Australia**: Beermullah, 80 km north of Perth, Western Australia, June 19, 1983, M. Blackwell, UWA #2833.

Mating System: Heterothallic, bipolar (Barron and Dierkes, 1977 and this study).

Cultural Characters: Nematophagous; anamorph *Nematoctonus robustus*. In 1947 *Pleurotus griseus* was reported to produce an antibiotic named pleurotin (Robbins et al, 1947). When the antibiotic was isolated, it was shown to form orange crystals that had a low solubility in water (0.125 mg/mL at 25% C). Its activity was temperature and pH sensitive. Later, Arigoni (1968) determined the structure and formula of pleurotin by x-ray crystallography (Figure 20 f). Robinson et al (1947) showed that pleurotin was active against gram positive bacteria, including *Staphylococcus aureus* and *Bacillus subtilis*, but not gram negative bacteria such as *Klebsiella pneumoniae* or *Escherichia coli*. Bauerle (1981) showed that pleurotin had only a very weak antibiotic effect under his lab conditions, even against gram positive bacteria. However, the importance of pleurotin to *H. atrocaerulea* var. *grisea* for substrate protection or self-

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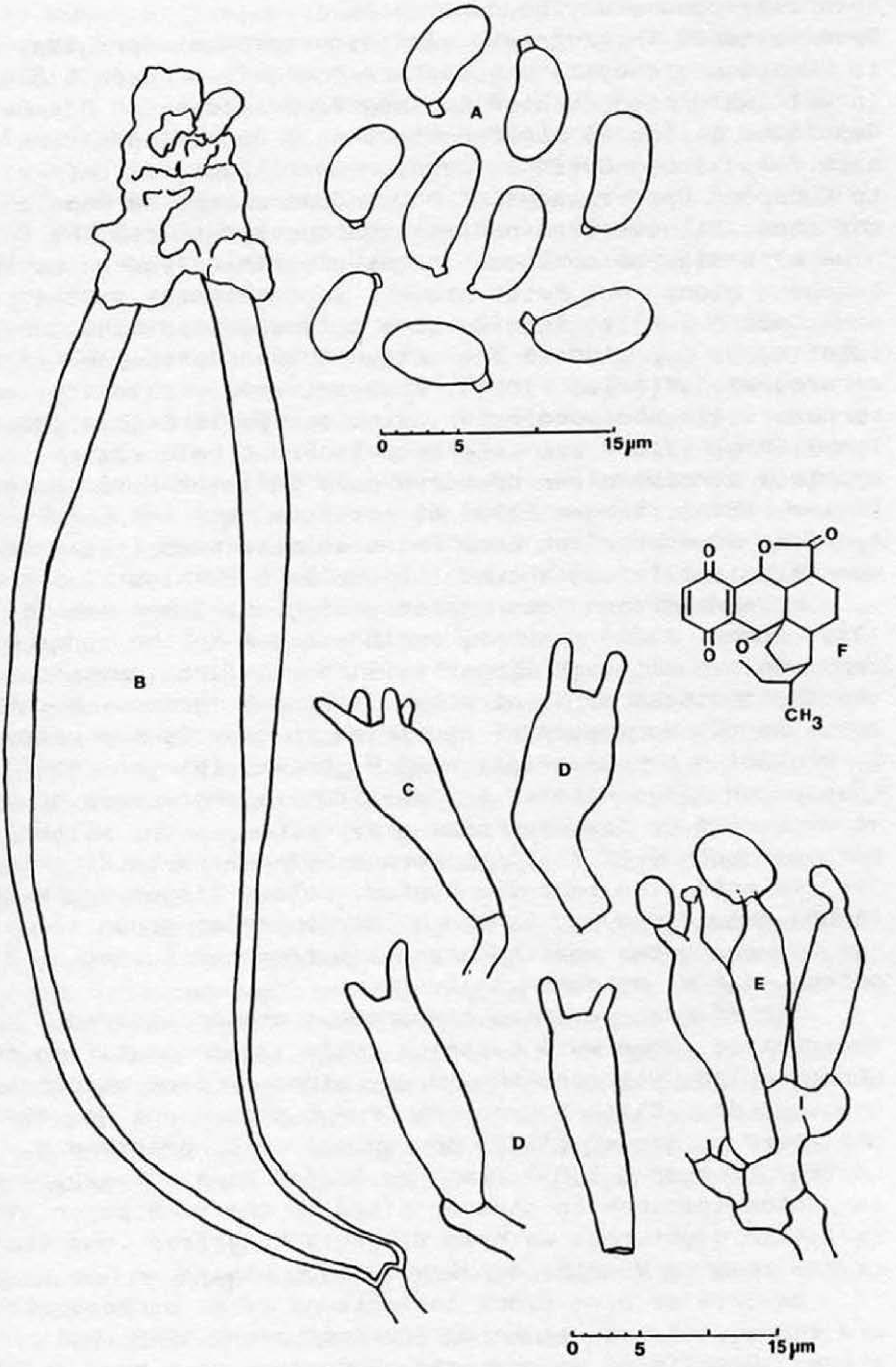
Figure 20 A-E: *Hohenbuehelia atrocaerulea* var. *grisea* ("N90"), RGT #840713/01 (= Barron #20 fruiting in culture). A) Basidiospores; B) a metuloid, beginning to develop a crystalline apex; C) 4-spored basidium; D) 2-spored basidia; E) cheilocystidia. F: Structural formula of pleurotin, $C_{21}H_{22}O_5$.


A
0
5
15µm
B
C
D
D
E
F
O
O
O
O
O
CH3
0
5
15µm

defence in the rich microbial environment where this species naturally occurs may be considerable.

Observations: This variety remains a taxonomic problem, as it has been since its description and before. Peck (1886), in writing a monograph of the New York species of *Pleurotus*, described it (as *P. atrocaeruleus* Fr.) as having a dark blue, blackish-grayish or tawny brown pileus, in deference to European descriptions of *P. atrocaeruleus*. He went on to say that, "I have seen no American specimens with the dark blue or indigo color shown in the published figures of the European plant, but Fries himself says that the pileus is sometimes brown, so that we have no doubt about the specific identity of our plant." The original description of *Agaricus atrocaeruleus* (Fries, 1821), however, simply read, "*pileo carnoso villoso atrocoeruleo, strato superiori gelatinoso, lamellis albidis*." The reference to brown colouration in *Agaricus atrocaeruleus* appeared only in later descriptions (Fries, 1838). Singer (1951 b) reported that the painting of *Agaricus atrocaeruleus* that Fries commissioned (but which was never published) showed the cap as dark blue.

Modern European descriptions of *H. atrocaerulea* (Pilat, 1935; Moser, 1983) commonly include brown in the range of cap colours. Although Singer (1951 a) at first questioned the distinctness of *H. atrocaerulea* and *H. grisea*, he has since kept them separate, and tried to clarify the situation by providing a redescription of *H. grisea* (Singer, 1977). In this paper Singer listed the distinctive characters of *H. atrocaerulea* as its dark blue-grey colour, ... , slightly narrower spores (2.7-4.3 µm versus 3.3-4.5 µm in *H. grisea*), and its encrusted tomentum hyphae. Later, Singer and Kuthan (1980) provided a key to the *H. atrocaerulea* group in which the key character was the encrusted tomentum hyphae of *H. grisea*, not *H. atrocaerulea*!

All of the specimens cited above are considered conspecific. Some were European collections identified as *H. atrocaerulea*, yet none showed any signs of blue colouration. One specimen (Ellis & Everhart, Fungi Columbiani No. 1202) was cited by Singer (1977) as typical of *H. grisea* and another (Singer C 5683), sent by Singer as *H. grisea*, was a companion specimen to another cited in the same paper. There is little doubt that we have Singer's *H. grisea*, and that it is the same as *H. atrocaerulea* to many others.

Reports of blue-black collections of *H. atrocaerulea* are infrequent but recurring (Christiansen, 1958; Miller, in press). Details of microscopic characters have been scanty, but the spores are sometimes reported as being larger than those of *H. grisea*. Those of a blue-black collection from

Denmark (Christiansen, 1958) were 8-10 X 4-5 µm, from 4-spored basidia. Singer and Kuthan (1980) have suggested that these large-spored forms possibly belong to ***H. portegna*** (Speg.) Sing., which was described from Argentina. The colours in this species range from brown (Spegazzini, 1881) to blue-black (Singer and Kuthan, 1980). According to Singer and Kuthan, the basidia are predominantly 2-spored, but also 1-, 3-, and 4-spored, with spores ranging from 8.5-11.8 (14.5) X 3.3-6.2 µm depending on the sterigmatal number. The anamorph of a specimen of ***H. portegna*** from Argentina is ***Nematoctonus campylosporus***.

A further complication is ***H. fluxilis*** (Fr.) Orton. Orton (1964) redescribed the species as having a brown cap, 2-spored basidia, and spores (8) 8.5-10 X 3.5-4.5 µm. Fruiting bodies of N90 produced in culture may shed some light on this problem. Barron and Dierkes (1977) reported the fruit bodies of N90 as greyish-brown, and to have spores 5.5-8.8 X 3.2-4.8 µm on 4-spored basidia. A fructification of the same culture that was produced on cased sawdust in a growth cabinet (RGT #840713/01) had a deep brown cap (6E-F7), predominantly 2-spored basidia, and spores 6.5-9.4 (11.0) X (2.9) 3.5-4.4 µm. Interfertility tests between single spore cultures of these "species" should be conducted to determine which are good biological species, and which are varieties of one wide-ranging, polymorphic species. The combination of ***Pleurotus griseus*** Peck as a variety of ***H. atrocaerulea*** is proposed to distinguish the common, brownish forms of ***H. atrocaerulea*** (with small spores) from the apparently rare, but typical, blue-black forms that have larger spores.

The variable cheilocystidia of ***H. atrocaerulea*** sensu lato have also led to some confusion. Most often they have only one neck and cap, and the cap has a very distinct hour-glass secretory cell. Sometimes, however, the neck is branched 2 to 4 times. In squash mounts of gills or gill sections of old herbarium material, the hour-glass cells at the ends of the neck often collapse and only the branched (or unbranched) neck remains visible. This was the basis of ***H. atrocaerulea*** var. ***dendrocystis*** (M. Lange) Bon (Lange, 1955).

Hohenbuehelia cyphelliformis (Berk.) Miller, in Thorn (1986: 32)
≡ ***Agaricus cyphelliformis*** Berkeley (1837: 511)
= ***Agaricus sylvanus*** Saccardo (1877: 1)

Additional synonymy, plus a full description and illustrations are provided by Thorn (1986).

Fruit Bodies cupulate, pendant or conchate, 2-6 mm diam., dorsally or laterally attached, greyish brown to almost black (6D-F3), appearing glabrous and translucent-striate when fresh and moist (lines one unit darker), drying black, opaque, with fine white floccose bits or whisps over surface. Margin even or slightly wavy. **Gills** radiating from a near central point on underside, stark white, becomimg faintly greyish, usually narrow, distant. **Basidia** 4-spored, clavate, (21) 26-30 X 6.2-8 µm. **Cheilocystidia** fusoid-capitate, with well-formed or poorly formed hour-glass, occasionally branched, 18-38 X 4-7 µm, hour-glass 4-6.5 X 1.2-2.0 (2.5) µm, mucoid ball 5-8 µm diam. **Metuloids** clavate or fusoid, thin-walled (up to 0.5 µm thick), not projecting (resembling basidioles), pale brown in base (KOH), 21-40 X 4.5-7.0 µm, brilliant magenta in Cresyl Blue, apices entirely obscured by conical or ovoid crystalline masses 8-12 (16) µm diam. X 12-20 µm tall. **Spores** white in print, hyaline, inamyloid, smooth, broadly allantoid, (7.5) 8-10 (11.5) X 2.8-3.8 (4.2) µm.
Habitat: On dead twigs or stems of woody dicots.
Distribution: Found in Europe, North Africa, and northeastern North America (Thorn, 1986).
Specimens Examined: **Canada: Ontario**: Dennison Farm, Opeongo Lake, Algonquin Park, R.G. Thorn #841013/01 & #841013/11; Conc. #3 Eramosa Twp., Wellington Co., RGT #841117/02.
Italy: Selva, Treviso, Mar. 1877, PAD #3644 (type of *Agaricus sylvanus* Saccardo).
Mating System: Unknown.
Cultural Characters: Nematophagous; anamorph *Nematoctonus robustus*.
Observations: *Hohenbuehelia cyphelliformis* is readily recognised by the combination of its size, cupulate habit, stark white, distant gills, strongly curved spores, and its habitat. This species seems to require rich, undisturbed habitats. The old field in Algonquin where RGT #841013/01 and #841013/10 were collected had been abandoned since 1881, when the farmer was killed by a black bear.

Hohenbuehelia longipes (Boud.) Moser, in H. Gams (1967: 108)
≡ *Pleurotus longipes* Boudier (1905: 69)

Hohenbuehelia longipes was not encountered during this study. An excellent description of the only North American collection, with illustrations and full synonymy, was provided by Redhead (1978). The following description is adapted from Boudier (1905), Favre (1948), Kuehner et al. (1962) and Redhead (1978):

Pileus infundibuliform to spathulate, 1.5-3.5 cm broad, golden brown to sooty brown, glabrous. **Stipe** lateral or nearly central, 3-8 cm long, 2-5.5 mm wide, light brown. **Flesh** off-white, with farinaceous odour and taste. **Lamellae** decurrent, white to deep cream, narrow, close. **Basidia** typically bisporic, 30-35 (45) X 6-7.5 µm, but 4-spored in S.A. Redhead #2013 (DAOM), 22-25 X 6.5-7 µm. **Cheilocystidia** lecythiform, capitate, 17-33 X 4-8 µm, with or without hourglass cell 6.5-10.5 X 2.2-4 µm, surrounded by a mucoid droplet. **Metuloids** lanceolate, thick-walled, hyaline, apices encrusted, 70-110 X 8-14 µm. **Basidiospores** white, hyaline, inamyloid, smooth, elliptic-cylindric to slightly phaseoliform, 7-13 X 4-6 µm.

Habitat: Among mosses in mountain or northern bogs or fens. Redhead (1978) suggests that it may be calciphilic. If so, *H. longipes* might be looked for in Ontario in the boggy areas of the Bruce Peninsula or Manitoulin Island.

Distribution: *H. longipes* has been recorded from France, Germany and Switzerland, and from Quebec, Canada.

Mating System: Uncertain. Kuehner et al. (1962) suggested that *H. longipes* is amphithallic (= secondarily homothallic) and tetrapolar. This conclusion was based on their observation that one monokaryon was dikaryotised through the Buller phenomenon by each of about ten dikaryons. They reasoned that because all confrontations led to dikaryotisation, tetrapolarity was more likely, whereas the opposite is true. Basidiospores were found to have one to five nuclei, with 62% having three nuclei per spore.

Cultural Characters: The illustrations of Kuehner et al. (1962) strongly indicate that *H. longipes* is nematophagous. Conidia and what look like adhesive knobs with hour-glass secretory cells were produced on Hagem's and cassein hydrolysate media. The size and shape of the conidia would undoubtedly differ in culture with nematodes, but were reported to be narrowly fusoid, 10-18 X 2 µm. Hyphae were generally 2-3 µm diam., but sometimes inflated to 10 µm, with clamps. Adhesive knobs had a mucous ball of 9-11 µm diam., and the hour-glass cells that they illustrated were 7-8 X 2.5-3 µm, with the waist about 1.5 µm. Colony characters were not described.

Observations: *H. longipes* is readily recognised within the genus by its well-developed, often central stem, and its habitat. The one collection from North America differs from those described from Europe in its 4-spored basidia and smaller spores (7-9 X 4-5 µm, Redhead, 1978). Favre (1948) reported the basidia of his collection as 2-spored, and the spores as 9.5-11 X 4.8-5.5 µm. The collection reported by

Kuehner et al. (1962) was similarly bisporic, the spores "10-11 X 4-6 µm". However, in the Kuehner collection, 20.5% of the spores were reported to be uninucleate, with a mean length of 7.9 µm. Redhead (1978) noted that 2- and 4-spored races are recognised within other species in the Agaricales, and that this one character was not sufficient to recognise the North American collection as a new species.

H. longipes is certainly worth looking for and studying further, to determine its sexuality and confirm its nematophagous habit.

Hohenbuehelia mastrucata (Fr.: Fr.) Singer (1951: 255) Figs. 21 & 22
≡ *Agaricus mastrucatus* Fries (1818: 229)
 ≡ *Agaricus mastrucatus* Fr.: Fries (1821: 190)
 ≡ *Pleurotus mastrucatus* (Fr.: Fr.) Saccardo (1887: 376)
 ≡ *Geopetalum mastrucatum* (Fr.: Fr.) Kuehner and Romagnesi **nom. invalid.** (1953: 68)

Pileus dimidiate to flabelliform, sessile, 1.5-5.5 cm long, 2-4.5 (10) cm broad, and up to 0.8 cm thick. Surface moist, colour dark, watery brownish grey (near 6E3) or blue-grey (20E2-3), becoming paler to greyish buff (5C-D3 to 4A2); covered with thick, blunt, gelatinous spines, especially near margin; white-frosted with fine white tomentum towards the base. **Stipe** none, or occasionally a small sterile zone at the base of the gills. **Gills** radiating from point of attachment, narrow, close to moderately spaced, off-white, from greyish to pale buff (4B-A2 plus white); slightly frosted on margins. **Flesh** ranging from entirely gelatinous, grey-brown (watered down 5B3) and up to 3 mm thick, to primarily white-fleshy with a fine dark line (5F5) representing the gelatinous zone, the fleshy zone up to 3 mm thick. Taste bland, odour farinaceous. **Cuticle** only slightly differentiated from gelatinous zone, visible in Melzer's reagent as 5-10 µm deep, of repent, tangled hyphae (1.5) 2-4 (6) µm diam., mostly smooth, but some finely spiral-encrusted, loose ends on surface 2-3 µm diam., almost all capped with hour-glass secretory cells, 5-7 X 1.5-2.5 µm, mucoid droplet 6-8 µm diam. X 7-10 µm tall **Gelatinous Zone** more or less hyaline, total 400-450 µm thick; of 2 subzones; lower zone 150-250 µm deep, hyaline, of smooth ascendant (60-75 % above horizontal) hyphae 1.5-3.0 µm diam.; upper zone pale brown (golden in Melzer's), 100-200 µm deep, of horizontally-arranged hyphae, some finely encrusted. **Trama** commonly 200-400 µm thick (but up to 3 mm in some specimens), clay brown in KOH, of three subzones;

Figure 21: *Hohenbuehelia mastrucata*, R.G. Thorn #820902/12, X 1.25

upper zone 40-60 µm deep, showing black inclusions under 10X objective), appearing tightly pseudoparenchymatous in tangential section, of nearly parallel, radially-arranged hyphae 2-4 (5) µm diam., dark brick-red in Melzer's; middle zone 75-150 µm thick that forms a separation layer when dry, very loosely tangled, hyphae mostly thin-walled, 2-5 (7) µm diam.; lower zone 100-150 µm thick, dense and tangled, greyish (KOH), orange-brown in Melzer's, descending to form gill trama, hyphae thin-walled, or slightly gelatinous-walled (up to 0.75 µm thick), (2) 4-7 µm diam. **Gill Trama** of hyaline, gelatinized, parallel-interwoven, hyphae, most 3-5 µm diam., some up to 10 µm diam. **Subhymenium** indistinct in KOH, deep brilliant orange in Melzer's, 20-40 µm thick. **Hymenium** about 30 µm thick, greyish brown in KOH, golden in Melzer's. **Basidia** 4-pronged, clavate-cylindric, hyaline, 24-36 (40) X 7-8.4 (9.0) µm. **Cheilocystidia** fusoid-ventricose to clavate-capitate, hyaline, 30-45 X 4.5-7.0 µm, the neck about 2.0-2.5 µm diam., sometimes branched once, the hour-glass well-formed, 6-8.5 X 3-4 µm, the waist (1.0) 1.2-1.6 (2.1) µm diam., the mucus, when present, about 6 um diam. **Metuloids** lanceolate, hyaline, becoming crystal-encrusted at their apices, (32) 44-90 (102) X 8-15 (17) µm. **Spores** white in print, hyaline, inamyloid, smooth, ovate, (6.5) 7-9

(10.5) X 4-5.5 (6.0) µm.

Habitat: On dead wood, almost always on hardwoods, but its *Nematoctonus* state was once isolated from heart rot in *Pinus strobus* (T-143). Ontario collections were on *Acer*, and one Quebec collection was on *Acer* and *Juglans*. The Algonquin collection was found in a rich, mature hardwood forest, in a soggy hollow of a large, fallen *Acer saccharum* log. The *Nematoctonus* state is far more common than the collections of fruiting bodies would suggest, and is often isolated from soil, in woods, lawns and farmyards.

Distribution: Rare, but found in northern Europe, eastern North America, and Japan (Murata, 1978).

Mating System: Unknown.

Cultural Characters: Nematophagous; anamorph *Nematoctonus hamatus*.

Specimens Examined: Canada: Ontario: Algonquin Provincial Park, West Gate, Sept. 2, 1982, R.G. Thorn #820902/12; same locale, Oct. 4, 1982, RGT #821004/03; Appin, Sept. 27, 1923, Dearness #5330 (at DAOM); Rondeau Provincial Park, Aug. 30, 1926, J. Dearness and G. Bell, Dearness #6175 (at DAOM); South March, S.C. Hoare, DAOM #40222. Also cultured fruit bodies from culture T-23 (Barron #167, ex Guelph area soil), RGT #840713/02. **Quebec**: Kingsmere, Gatineau Park, Sept. 27, 1954, DAOM #45328 (part also at TRTC). **United States: Maine**: Pushaw Lake Area, Old Town, Penobscot Co., Sept. 29, 1970, R.L. Homola #4066 (MAINE).

Observations: *Hohenbuehelia mastrucata* is readily recognised when fresh by its blue-grey to grey-brown, dimidiate pileus with squarrose gelatinous spines over its surface, particularly toward the margin. It is likely to be confused only with *H. atrocaerulea* var. *grisea*, which is glabrous to finely tomentose on the margin and finely to coarsely tomentose towards the base, and lacks gelatinous spines. Microscopically, the broadly elliptic to ovate spores distinguish *H. mastrucata* from *H. atrocaerulea* var. *grisea*, in which the spores are narrower and elliptic-phaseoliform. It is difficult to discern what fungus Pilát (1935) described under *P. valesiacus* (with *P. mastrucatus* as a questionable synonom); it may have been *H. mastrucata*, but he said that it was closest to *P. petaloides*, and had a

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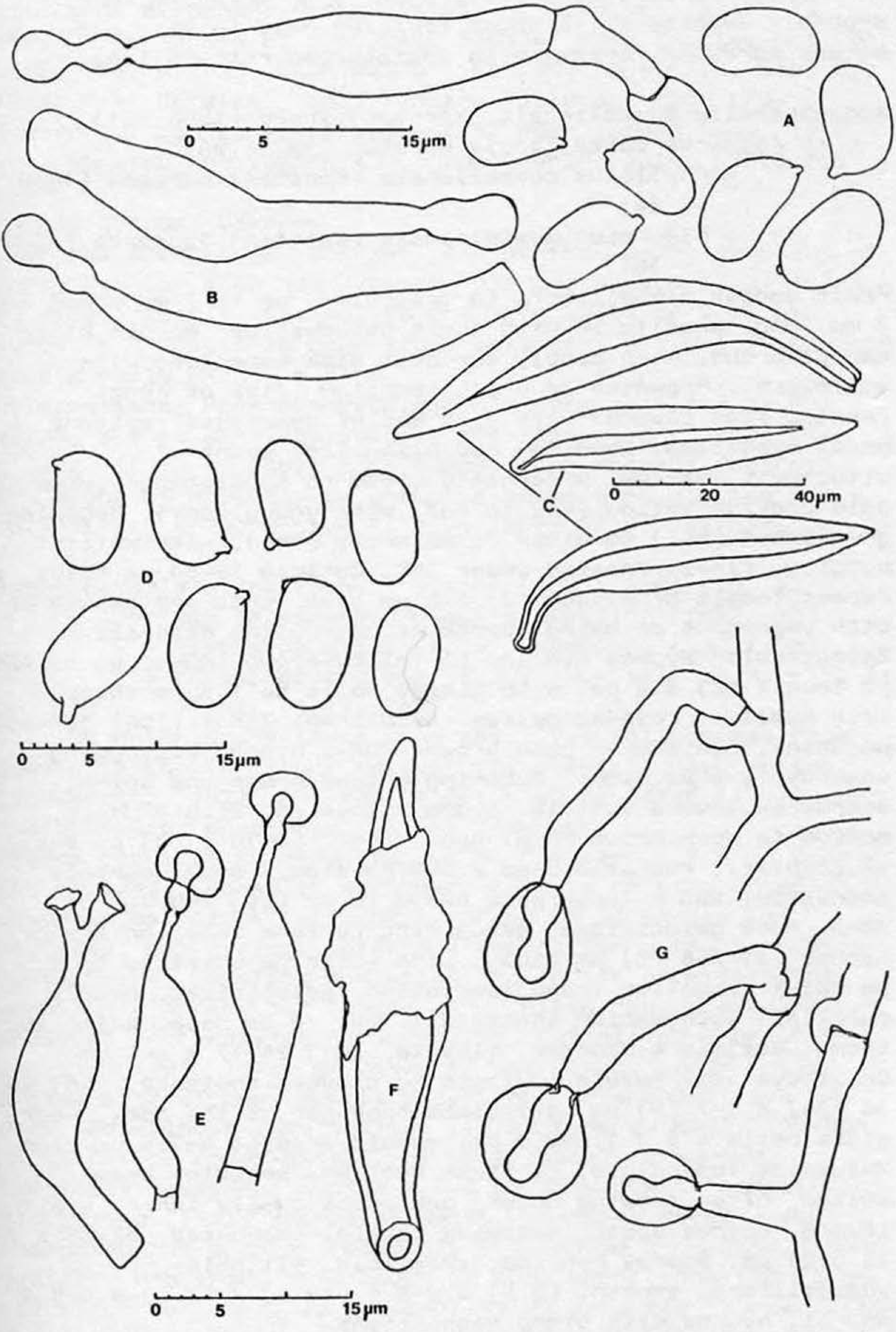
Figure 22 A-G: *Hohenbuehelia mastrucata*. A-C, and G) RGT #840713/02 (T-23 fruiting in culture). A) Basidiospores; B) cheiolocystidia; C) metuloids (at a reduced scale); G) pilocystidia. D-F) DAOM #45328. D) Basidiospores; E) cheilocystidia; F) metuloid.


0
5
15μm
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B
C
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20
40μm
D
0
5
15μm
E
F
G
0
5
15μm

whitish, hairy cap.

Hohenbuehelia mastrucata appears to be quite rare, probably because it is found fruiting only in very old, mature hardwood forests with undisturbed rotting logs.

Hohenbuehelia mustaliensis (Karsten) Thorn (1986: 61)
≡ *Agaricus mustaliensis* Karsten (1876: 99)
≡ *Phyllotus mustaliensis* (Karsten) Karsten (1879: 94)
≡ *Pleurotus mustaliensis* (Karsten) Saccardo (1887: 381)

Fruit Bodies flabelliform to orbicular, up to 7 mm broad and 7 mm long, sessile or with short pseudostipe; margin black and glabrous, with pebbly surface; disk tomentose with yellowish , brownish or black tomentum (disk of Fungi Fenniae #605 covered with deep mat of appressed, cottony basal mycelium). **Lamellae** radiating from point of attachment, narrow, moderately close to subdistant, cream to pale greyish yellow (4A2 to 4B3) when young (dry), becoming grey-brown (5D3) to black at maturity (dry), with whitish margins, finely frosted under 10X. **Cuticle** 15-30 µm thick, a repent tangle of hyphae (2) 3-8 µm diam. that are smooth or with amorphous or spiral bands of encrusting material. **Epicuticular Hyphae** hyaline to yellow-brown (KOH), up to 100 µm long X (2) 3-6 µm, with glassy walls to 1.5 µm thick, with hyaline, rounded apices. **Gelatinous Zone**: (150) 300-400 µm thick, hyaline or pale brown (KOH), hyphae zigzagging upwards, 2-4 µm diam., becoming golden brown and spiral-encrusted toward cuticle. **Trama** bilayered, with a dense, medium to dark brown (KOH) upper layer 50-70 (100) µm deep, of parallel, radial hyphae 2.5-6 µm diam., some coarsely encrusted; and a lower pale brown layer (50) 100-700 µm deep, more gelatinized, descending to form lamellar trama, hyphae (2) 3-6 (8) µm diam., with walls gelatinized to 1.5 µm thick. **Lamellar Trama** subhyaline, gelatinized, nearly parallel. **Subhymenium** indistinct, ca. 10 µm deep, paler than trama. **Basidia** 4-pronged, clavate, (21) 24-37 X 6-8 µm. **Cheilocystidia** fusoid-capitate to clavate-capitate, (18) 20-30 (34) X 5-7 (8) µm, sometimes branched at the apex, hour-glass cells 4-6 X 1.5-2.0 µm, mucoid droplet 5-7.5 µm diam. **Metuloids** lanceolate, at first hyaline, becoming brown-walled, often showing outer, and occasionally inner, hyaline layers, apices acute, becoming crystal-encrusted, 32-87 X 7-12 (15) µm. **Spores** hyaline, inamyloid, elliptic-phaseoliform, smooth, (6.8) 7.0-9.4 (10.4) X (3.5) 4.0-5.1 µm. All hyphae with clamp connections.

Habitat and Distribution: on bark of dead *Pinus sylvestris*

in Finland and *Pinus contorta* in Alberta, Canada.
Specimens Examined: Canada: Alberta: Strachan, Sept. 23, 1954, V.J. Nordin et al., DAOM #46374; same locale, Oct. 21, 1954, V.J. Nordin, DAOM #46785. **Finland**: Mustalia, Dec. 8, 1865, P.A. Karsten, Fungi Fenniae Exsiccati #605 (FH; isotype of *Agaricus mustaliensis*); same locale, Nov. 1877, P.A. Karsten, de Thümen's Mycotheca universalis #1003 (at DAOM).
Mating System: Unknown.
Cultural Characters: Unknown, except that basal mycelium of Fungi Fenniae #605 had hyaline, clamped hyphae (1.2) 1.8-5.0 µm diam., mostly thin-walled but with walls to 0.75 µm thick, and scattered hour-glass cells 4-5 X 1.5-1.8 µm, with mucoid balls 5-7.5 µm diam.
Observations: *Hohenbuehelia mustaliensis* is close to *H. nigra*, but is distinguished by its habitat and tomentose pileus. It is probably more common than records indicate, and might be expected to occur in Ontario on planted *Pinus sylvestris*, or on native *P. divaricata* or *P. resinosa*.

Hohenbuehelia nigra (Schw.) Singer (1951: 256) Fig. 23
  ≡ ***Agaricus (Pleuropus) niger*** Schweinitz (1822: 90)
    ≡ ***Pleurotus niger*** (Schw.) Saccardo (1887: 380)
    ≡ ***Resupinatus niger*** (Schw.) Murrill, in Murrill et al. (1915: 242)

No Ontario specimens were seen. Two collections from Dawson, Yukon Territory matched the original description (Schweinitz, 1822) and the description by Coker (1944), of two Scheinitz specimens, in all respects.
Pileus cupulate to conchate, up to 8 mm broad X 6 mm deep (as revived), dorsally attached, sessile or with brief pseudostipe, black, with olive brown (5E6) margin (as revived), not striate, glabrous except for a few scattered white hairs. **Lamellae** radiating from point of attachment, moderately narrow and close, dingy olive brown (5D4-5F5, as revived), markedly spiny under 10X. **Cuticle** dark brown in section (KOH), 10-15 µm thick,of encrusted, brown-walled hyphae with clamps, mostly repent and interwoven, 3-6 µm diam. **Gelatinous Zone** hyaline (in section in KOH), 300-600 µm thick (no cover-glass), of very loosely arranged, basically ascendent hyphae 1.5-3 µm diam., with conspicuous clamps and finely encrusted walls, becoming darker, more encrusted and broader (commonly 3-4, up to 5 µm diam.) near cuticle. **Cap Trama** pale brown in KOH, upper zone (50-75 µm thick) of horizontally (tangentially) arranged hyphae, below which they become tangled and descend into gill trama. Hyphae 3-5 (8) µm diam., with smooth, sometimes thickened

walls. **Gill Trama** pale brown in KOH, parallel-interwoven, hyphae (2) 4-7 (8) µm diam., some with walls up to 0.75 µm thick. **Subhymenium** indistinct 5-10 µm deep. **Hymenium** brown, darker than subhymenium or trama,, 25-37 µm deep, apices of hymenial elements often hyaline, since brown sap does not completely refill them on reviving. **Basidia** (2-) 4-pronged, clavate-cylindric, 28-38 X 6.5-8µm. **Cheilocystidia** abundant, variable, fusoid or clavate with drawn-out neck, 9-35 X 5-6 µm; neck 5-9 X 2-3 µm, hour-glass about 4 X 2.5 µm, mucous ball 5-6 um diam. **Metuloids** lanceolate, inner wall brown, extending 10-18 µm above hymenium, 33-75 X 8-12 (14) µm. **Spores** hyaline, inamyloid, elliptic-phaseoliform, smooth, (6.0) 7.5-10 (10.5) X 3.5-4.5 µm.

Habitat: on dead deciduous wood of ***Juglans*** (Schweinitz, 1822) and ***Alnus*** (Miller, in press).

Distribution: ***Hohenbuehelia nigra*** has been confused with many other species, among them ***Resupinatus applicatus***, ***R. trichotis*** and ***H. pinacearum***. Coker (1944) knew of only the Schweinitz collections. Miller (in press) reports it from Montana, Oregon, Pennsylvania and Virginia. Now known from the Yukon Territory, Canada.

Specimens Examined: Canada: Yukon Territory: Dawson, July 6, 1961, J. Holms, DAOM #89048 and DAOM #89049.

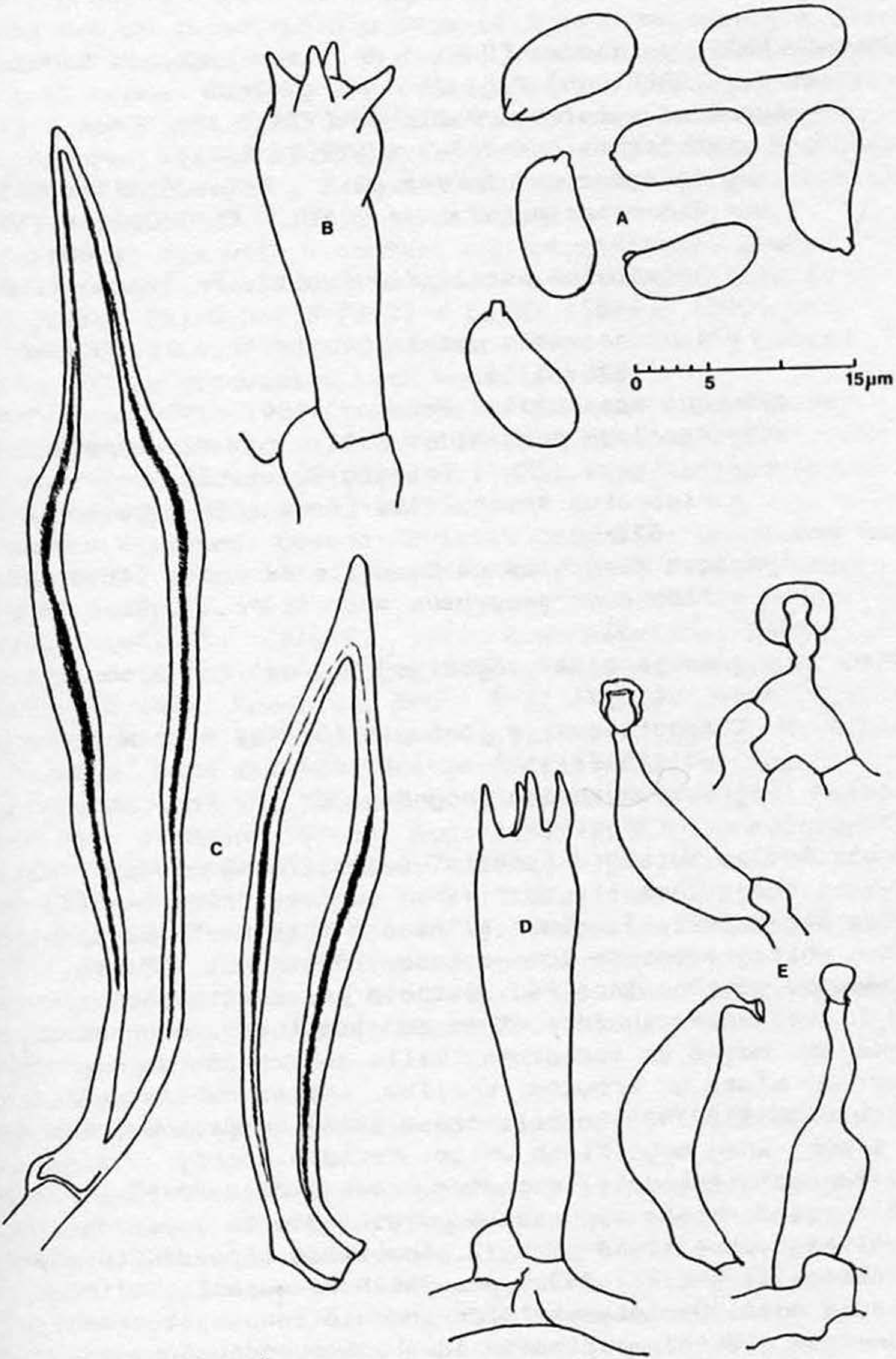
Mating System: Unknown.

Cultural Characters: A culture identified as ***H. nigra*** by O.K. Miller, Jr. (VT #1324) is nematophagous, with anamorph ***Nematoctonus robustus***. Another culture, RLG #10761, identified by Miller as ***H. niger*** and received from the Forest Products Lab, Madison, Wisconsin, is not nematophagous (Thorn and Barron, 1984).

Observations: This species seems to be quite distinctive, with its jet black, almost glabrous, cupulate cap, dark gills, brown-walled, lanceolate metuloids, elliptic spores and its occurrence on hardwoods. It is rarely collected, but since the geographic range of known specimens spans Ontario, it is possibly to be expected here.

Hohenbuehelia nigra is a member of a group of species with small, dark basidiomes, dark gills and usually brown-walled metuloids, including ***H. crustosa*** (Coker) Singer (1951; nom. invalid.), ***H. mustaliensis***, ***H. pinacearum***, ***H. subbarbata*** (Berk. & Curt.) Singer (1951), and ***H.***

Figure 23 A-E: Hohenbuehelia nigra. ***A-B) DAOM #89048. A) Basidiospores (at a slightly larger scale); B) a basidium. C-E) DAOM #89049. C) Metuloids, showing dark brown middle layer of tri-layered walls; D) basidium; E) cheilocystidia.***


B
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15µm
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unguicularis. This group appears to be closest to the genus *Resupinatus*, notably *R. alboniger*.

Hohenbuehelia petalodes (Bull.: Fr.) Schulzer, in Schulzer et al. (1866: 45) Fig. 24
≡ ***Agaricus petalodes*** Bulliard (1785: 226) [**non** ***A. petaloides*** Sommerfeldt (1826: 258)]
≡ ***Agaricus petaloides*** Bull.: Fries (1821: 183)
≡ ***Pleurotus petaloides*** (Bull.: Fr.) Quélet (1872: 226)
≡ ***Geopetalum petaloides*** (Bull.: Fr.) Patouillard (1887: 127)
≡ ***Acanthocystis petaloides*** (Bull.: Fr.) Kuehner (1926: 111)
= ***Agaricus spathulatus*** Persoon (1801: 479)
≡ ***Agaricus petaloides*** Bull.: Fr. var. ***spathulatus*** (Pers.: Fr.) Fries (1821: 183)
≡ ***Pleurotus spathulatus*** (Pers.: Fr.) Peck (1886: 63)
= ***Agaricus geogenius*** de Candolle ex Fries (1838: 134)
≡ ***Pleurotus geogenius*** (DC. ex Fr.) Quélet (1886: 149)
≡ ***Geopetalum geogenium*** (DC. ex Fr.) Patouillard (1887: 127)
≡ ***Acanthocystis geogenia*** (DC. ex Fr.) Kuehner (1926: 111)
≡ ***Hohenbuehelia geogenia*** (DC. ex Fr.) Singer (1951: 255)

Fruit Bodies petaloid (semiinfundibuliform), 3-7 cm tall X 2-5 cm broad, relatively fleshy; surface beige (4-5A3) to grey-brown (6E3-6), glabrous near margin to finely pruinose then white-tomentose toward base; margin not striate, somewhat wavy or inrolled. **Stipe** a pseudostipe, continuous with cap, upper surface often canaliculate, lower surface whitish, matte or tomentose. **Gills** decurrent, narrow or very narrow, close or crowded, shallow, whitish when fresh (notes with DAOM #180790) to pale cream (4A2) or yellow-ochre (4A5 + brown) when dry. **Flesh** white. **Cuticle** poorly differentiated, pale to medium brown (KOH), 10-15 µm deep, of tangled repent hyphae 2-5 µm diam., with loose, vertical, hyaline hyphae 10-40 µm tall, sometimes tipped with hour-glass cells 4-6 X 1.5-2.5 µm, which are usually without mucoid ball. **Dermatometuloids** inconspicuous but sometimes numerous, woven among cuticular hyphae, acicular, pale brown, 42-101 X 5-8 µm, solid or with lumen of 1-3 µm diam. **Gelatinous Zone** hyaline, 100-300 µm deep, of tangled horizontal and predominantly ascendant hyphae 2-3 (5) µm

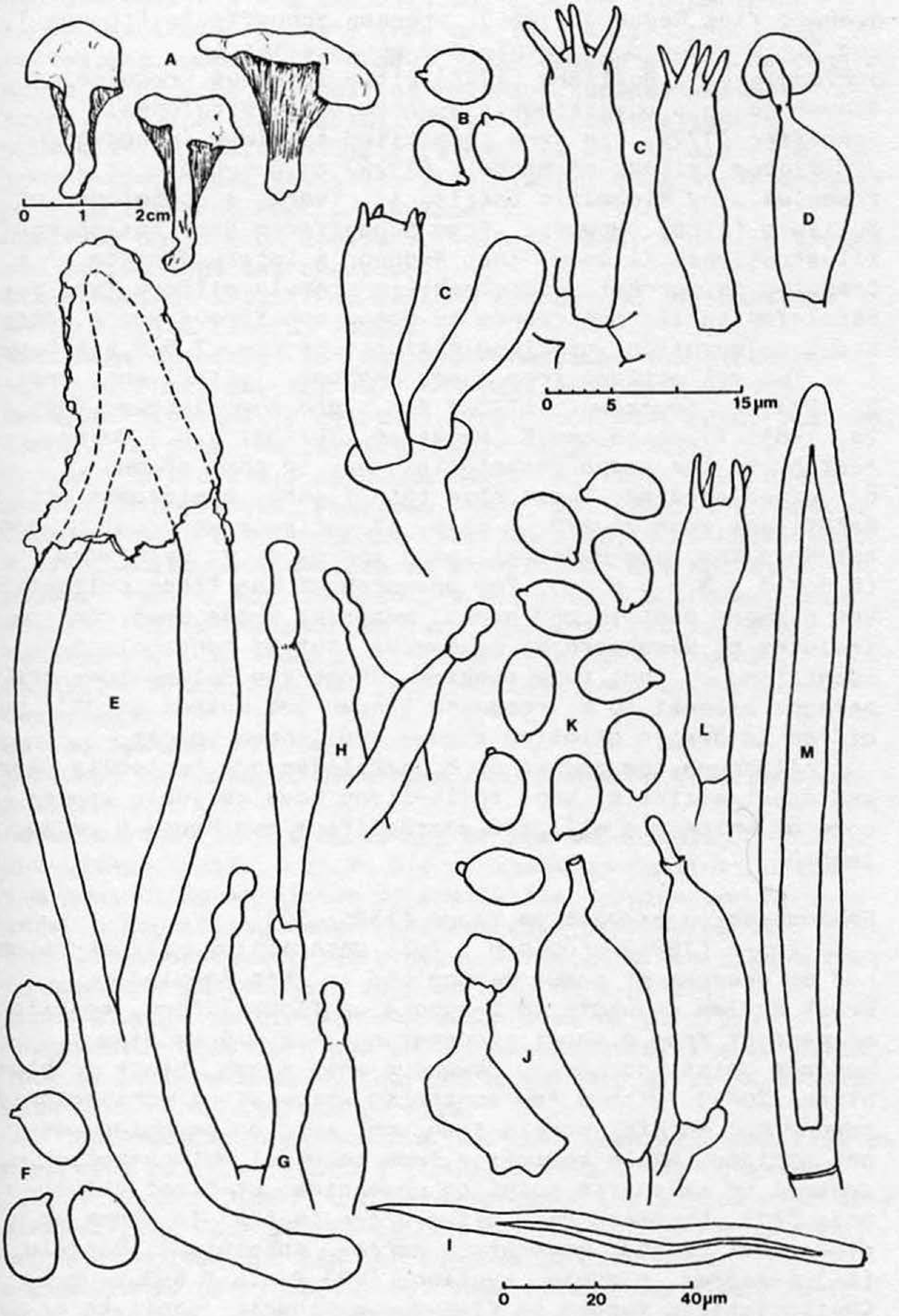
diam., with clamps. **Trama** consisting of two layers: an upper, pigmented zone 70-100 µm deep of compact, parallel hyphae 3-5 µm diam., then a deep (0.7 to 3 mm thick) hyaline context of tangled hyphae 3-6 (10) µm diam., continuous with the gill trama. **Basidia** 4-pronged, hyaline, clavate, (20) 24-36 X 5.5-8 µm. **Cheilocystidia** fusoid-ventricose or lecythiform, capitate, 16-35 X 4.5-8 µm, sometimes branched, hour-glass cells 5-7 X 2-3 µm. **Metuloids** lanceolate, hyaline or yellowish (KOH), (45) 54-92 (100) X 8-17 (20) µm, encrusted in age with a conical cap of crystals. **Spores** white in print, hyaline, inamyloid, smooth, elliptic to subglobose, (5) 5.5-7.5 (9.0) X (3.0) 3.5-4.5 (5.2) µm.
Habitat: On soil in lawns, planting beds, or with potted plants, often associated with woody debris.
Distribution: Widely distributed in Europe (Pilat, 1935), North America (Coker, 1944; Miller and Manning, 1976), and reported from Venezuela (Dennis, 1970), New Zealand (Horak, 1971) and Japan (Murata, 1979).
Specimens Examined: **Canada: British Columbia**: Brentwood Bay, Vancouver Is., Mar. 18, 1984, A. Funk, DAVP #22978; Lulu Island, Sept. 10, 1966, M.A. Waugh, DAOM #115345. **Nova Scotia**: Kentville, July 21, 1961, K.A. Harrison, DAOM #113630; **Ontario**: Ottawa, Sept. 28, 1981, A. Hamilton, DAOM #180790. **Quebec**: Knowlton, Brome Co., Aug. 22, 1974, H.W. Johnston, DAOM #148928; Quebec City, Aug. 1, 1967, M. & Mme. R. Cauchon, DAOM #127429. **United States: California**: Sacramento, Aug. 22, 1984, B.L. Thompson #411 (USC). **Maine**: University of Maine, Orono, Aug. 6, 1973, R.L. Homola #A5558 (MAINE). **Maryland**: Baltimore, July 20, 1985, W. Sullivan, R.G. Thorn #850803/01. **New York**: Ithaca cemetary, July 27, 1903, H.S. Jackson #677 (at TRTC). **Tennessee**: Anderson Co., Sept. 26, 1943, Flora of Tennessee s.n. (at TRTC); Knoxville, Oct. 8, 1936, Fl. Tenn. #9546 (at TRTC). **Sweden**: Dlr. Falun: Hemskogsvagen, Sept. 25, 1983, R. Morander, Fungi Suecici #4656.
Mating System: Unknown.
Cultural Characters: Nematophagous; anamorph ***Nematoctonus geogenius***.
Observations: ***Hohenbuehelia petalodes*** is readily recognized by its petaloid, fleshy fruit bodies that occur on soil in lawns or cultivated areas, and its short-elliptic spores. Bulliard (1792) made the following statement, which has since proven ironic: "***Rapproch. On ne peut confondre cette espece avec aucune autre***". ***Hohenbuehelia petalodes*** has, however, been confused with several other species. Fries (1821) cited Bulliard's plates in his description of ***Agaricus petaloides***, but the fungus he described is a

different species that occurs in Europe, on hardwood logs. This other species is the same one described under the names *Geopetalum petaloides* by Kuehner and Romagnesi (1953), and *Hohenbuehelia petaloides* by Singer (Singer and Kuthan, 1980). Bulliard's concept of *Agaricus petalodes* has priority, however, and is the one for which the name must be used. *Hohenbuehelia petaloides* sensu Kuehner, Romagnesi, and Singer is spathulate, thin-fleshed, and has a shallow gelatinous zone of horizontally-arranged hyphae. The most appropriate name for this species may be *Hohenbuehelia auriscalpium* (R. Maire) Singer. Fries (1838) later described *Agaricus geogenius*, based on correspondence with A.P. de Candolle. Fries noted that this species differed only slightly from *A. petaloides*, and it is clear from the description that *Agaricus geogenius* DC. ex Fries (1838) refers to *Agaricus petalodes* Bulliard (1785). Fries (1821) also added an "i" to *petalodes*, but there seems to be no reason not to accept Bulliard's original spelling.

Peck (1886) believed that the fungus now known as *Hohenbuehelia angustata* was the species that Fries (1821) had described as *A. petaloides*. This was a logical conclusion, since the macroscopic features (all that Fries described) of *H. angustata* and *H. auriscalpium* are quite similar. Peck described the true *H. petalodes* under the name *Pleurotus spathulatus*. Kauffman (1919) follwed Peck's treatment of these two species, although he also included *H. angustata* as *Panus angustatus*. The papers by Peck (1886) and Kauffman (1919) led to a number of reports of *H. "petaloides"* in North America (eg. Bisby et al., 1929) which are actually *H. angustata*.

In Europe, both *H. petalodes* (= *H. geogenia*) and *H. auriscalpium* (= *H. petaloides* sensu Singer) have been confused with *H. tremula* (= *H. rickenii* nom. invalid.). Redhead (1984) pointed out that the name *Agaricus tremulus* Schaeffer (1774) had been misapplied, and might represent the earliest available epithet for *H. rickenii*. Fries (1838) believed that part of Schaeffer's illustration of *A.*

Figure 24 A-M: *Hohenbuehelia petalodes*. A) R.L. Homola #A5558, habit of fruit bodies. B-D) DAOM #127429. B) Basidiospores; C) basidia and a basidiole; D) a cheilocystidium. E-I) DAOM #180790, E) A metuloid; F) basidiospores; G) cheilocystidia; H) pilocystidia; I) a dermatometuloid (at a reduced scale). J-M DAOM #113630. J) Cheilocystidia; K) basidiospores; L) a basidium; M) a dermatometuloid.


A
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tremulus represented ***A. tremulus*** sensu Fries (= ***Arrhenia acerosa*** fide Redhead, 1984), whereas Schaeffer's figures 1 and 2 represented ***A. petaloides*** sensu Fries (***H. auriscalpium***). Bulliard (1792) cited ***Agaricus tremulus*** Schaeffer as a questionable synonym of ***A. petalodes***. Schaeffer (1774), in turn, had cited ***Agaricum infundibulum dimidiatum imitans*** of Micheli (1729) as a synonym of ***A. tremulus***, and Micheli's species is clearly ***A. petalodes*** of Bulliard (1785). However, from Schaeffer's description and illustrations, it seems that Redhead's interpretation of ***A. tremulus*** is correct. ***Hohenbuehelia tremula*** differs from ***H. petalodes*** in its occurrence in mossy coniferous woods, dark brown colouration, and long-elliptic spores, 7.5-9 X 4-5 µm.

Two collections from Japan (Kokoge, Tottori-shi, Sept. 2, 1981, E. Nagasawa, TOTTORI s.n.; and same locale, Sept. 25, 1981, T. Hongo and E. Nagasawa, TOTTORI s.n.) do not conform to the above description, nor to that of any described species. These have thin-fleshed basidiomes with a gelatinous zone 75-170 µm deep, of entirely vertical hyphae, but have the same short-elliptic spores as ***H. petalodes*** (5.8-7.5 X 3.8-4.8 µm). The anamorph of the first collection has plumper conidia and hyphal adhesive knobs than most isolates of ***Nematoctonus geogenius***, but is nonetheless identified as that form-species. These two collections are perhaps closest to ***H. recedens*** Singer and Kuthan (1980), but differ in deeper gelatinous zone and longer spores.

Although the spores of ***H. petalodes*** are typically plump and short-elliptic, some collections have variable spores, some of which are elliptic-phaseoliform and reach 9 µm in length.

Hohenbuehelia pinacearum Thorn (1986: 37)

Thorn (1986) provided a full description, illustrations and an account of names misapplied to this species.

Fruit Bodies cupulate to conchate or flabelliform, sessile or pendant from a short pseudostipe, 0.4-0.9 cm diam., surface moist and mostly glabrous when fresh, black or blue-black (20F4), with a few scattered white wisps particularly toward the margin; margin incurved, even or becoming wavy, not striate. **Gills** radiating from point of attachment or a central or excentric point on underside; at first silver-grey (B1), becoming deep olive-brown (4-5F4) to black or blue-black (20F4); moderately narrow, subdistant. **Basidia** (2-) 4-spored, clavate, hyaline, (22) 25-32 X 6-7.5 µm. **Cheilocystidia** fusoid or flexuous-cylindric, capitate or not, 22-45 X 4-8 µm, with 1 or 2 hour-glass cells 5-8 X 2-3 µm. **Metuloids** deep-seated, lanceolate or flexuous-cylindric, hyaline, 37-50 X 6-8 µm, with walls up to 2.0 µm thick, except at the apex where they are thin-walled and collapsing, magenta in Cresyl Blue, capped with a conical mound of hyaline crystalline material. **Spores** white in print, hyaline, inamyloid, smooth, narrowly elliptic-phaseoliform, (6.0) 6.5-8.5 (9.0) X (2.5) 3.0-3.5 (3.8) µm from 4-spored collections; 7.5-10.5 (11.0) X 4.4-5.5 (5.7) µm from 2-spored Peck collection.

Habitat: On bark of conifers, both on dead, standing trunks and fallen logs and branches.

Distribution: Known from western Europe and northeastern North America (Thorn, 1986).

Specimens Examined: Canada: New Brunswick: Kouchibouguac National Park, May 16, 1977, R. Millikin, DAOM #165824. **Ontario**: Algonquin Provincial Park, Wolf Howl Pond, Oct. 15, 1983, R.G. Thorn #831015/04; Maple, May 5, 1936, J.W. Groves, TRTC #9470; Petawawa, Sept. 6, 1943, J.W. and E. Groves, DAOM #11428; Petawawa, Sept. 20, 1945, J.W. Groves, DAOM #16436; Lake Temagami, July 18, 1938, R.F. Cain, TRTC #13200, **holotype** (isotypes as DAOM #50083 and 80600). **Quebec**: Perce, Aug. 14, 1959, W.B., V.G. & S. Cooke, DAOM #84313. **United States: New York**: Bennetts [Adirondack Mountains], C.H. Peck s.n., [1884] (in NYS). **France**: Chansaye, Rhône, Jan. 3, 1933, M. Josserand XII/10, herb. Josserand.

Mating System: Unknown.

Cultural Characters: Nematophagous; anamorph ***Nematoctonus brevisporus***.

Observations: This species may be macroscopically indistinguishable from ***H. nigra*** except by habitat, unless the projecting metuloids of the latter species can be seen under a magnifying lens. ***Hohenbuehelia pinacearum*** is characterised by its jet black, nearly glabrous pileus that is cupulate to conchate in form, its dark gills, inconspicuous metuloids, and occurrence on conifers. ***Resupinatus alboniger*** can be distinguished by its complete lack of both metuloids, and cheilocystidia or pilocystidia with hour-glass secretory cells.

Hohenbuehelia pinacearum has long been misidentified as ***Pleurotus silvanus*** (Sacc.) Saccardo (1887), by Josserand (1933), Pilát (1935), and Krieglsteiner (1979); as ***Pleurotus atropellitus*** Peck (1886) by Murrill (Murrill et al., 1915) and many collectors (in herb.); and as ***Pleurotus unguicularis*** (Fr.) Quélet by Coker (1944) and Miller and Manning (1976). This species is well illustrated by Konrad and Maublanc (1937: 309 II; as ***Acanthocystis silvanus***) and Coker (1944: pl. 42, lower; as ***Pleurotus unguicularis***).

Hohenbuehelia tremula (Schaeffer: Fr.) Thorn and Barron, **comb. nov.** Figure 25

Basionym: ***Agaricus tremulus*** Schaeffer (1774: 54) [illustrated, without name, in Schaeffer (1771: pl. 224)]

≡ ***Agaricus tremulus*** Schaeffer: Fries (1821: 191) [**not** sensu Fries]

Numerous nomenclatorial synonyms of ***A. tremulus*** Schaeffer: Fries refer to the species to which Fries misapplied the name, ***Arrhenia acerosa*** (Fr.) Kuehner (1980).

= ***Geopetalum Rickenii*** Kuehner **nom. invalid**, in Kuehner and Romagnesi (1953: 70)

≡ ***Geopetalum Rickenii*** Kuehner **nom. invalid**, in Kuehner and Romagnesi (1954: 74)

≡ ***Hohenbuehelia Rickenii*** Kuehner **nom. invalid**, in Kuehner and Romagnesi (1954: 75) ["alternative name"]

≡ ***Pleurotus Rickenii*** Kuehner **nom. invalid**, in Kuehner and Romagnesi (1954: 76) ["alternative name"]

≡ ***Hohenbuehelia rickenii*** Kuehner ex Orton **nom. invalid** (1960: 176)

≡ ***Hohenbuehelia rickenii*** Kuehner ex Donoso **nom. invalid.** (1981: 157)

The following description is based on dried herbarium specimens:

Fruit Bodies spathulate to petaloid, 2-5 cm long X 1-3 cm broad, medium (oak) brown to dark (date) brown, hoary-canescent over basal area and pseudostipe. **Gills** decurrent, yellow-ochre or buffy, narrow, moderately close, frosted with metuloids. **Cuticle** thin, about 10 um thick, brownish or subhyaline, poorly differentiated from gelatinous zone, of repent, interwoven, smooth hyphae with intracellular pigment, 2-6 µm diam., often with abundant loose ends terminating in well-formed hour-glass cells 6-12 X 2-4 µm, sometimes with mucoid droplet 5-10 µm diam. **Gelatinous Zone** hyaline, or with pale brown hyphae in clear matrix, 40-75 (150) µm thick, of tangled, obliquely rising (45-60 % above horizontal), smooth hyphae 1.5-4.0 (7) µm diam. **Trama** consisting of first a dense, deeply pigmented zone 50-75 µm thick, of parallel or nearly parallel hyphae, then a paler brown zone 400-500 µm thick, of densely interwoven hyphae 2-5 µm diam. **Gill Trama** subhyaline, parallel-interwoven, hyphae similar to those of cap trama, with some inflated to 15 µm diam. **Subhymenium** hyaline, about 10 µm thick. **Hymenium** hyaline, 25-30 µm thick. **Basidia** 4-pronged, hyaline, clavate, 18-26 X 6-7.5 (8) µm. **Cheilocystidia** lecythiform, or fusoid-ventricose, capitate, (18) 24-37 X 4-7 µm, hourglass 6-9 X 2.5-4.0 µm, commonly without mucoid ball, which when present are elliptical to spherical, 6-10 µm tall X 4-7 µm diam. **Metuloids** hyaline, lanceolate, encrusted in age, (45) 50-90 (115) X 10-16 (25) µm. **Spores** white in print, hyaline, inamyloid, smooth, elliptic-phaseoliform, (7.0) 7.5-9.0 (9.5) X (3.5) 4.0-5.0 (5.5) µm.

Habitat: on peaty soil or well-rotted wood, often among mosses, in coniferous forests.

Distribution: ***Agaricus tremulus*** was described from southern Germany (Schaeffer, 1771; 1774), and ***Hohenbuehelia rickenii*** was described from the French Alps, and reported from Britain by Dennis et al. (1960). Bresadola (1928) illustrates what appears to be this species, from Italy, and cultures under this name were sent by M. Semerdzieva from Czechoslovakia.

Specimens Examined: Canada: Northwest Territories: Fort Simpson, June 2, 1955, W.J. Cody and J.M. Matte, DAOM #51088. **Ontario**: Glen Major, June 7, 1936, G.S. Bell, TRTC #9488 (parts as DAOM #50122). Quebec: La Verendrye Park, July 9, 1958, M. Pantidou, DAOM #62813; Parc Laurentides, Aug. 15, 1981, D. Lahaie et al., DAOM #180808 (**neotype**). **United States: Michigan**: Douglas Lake, June 30, 1951, S.C. Hoare, DAOM #26937.

Mating System: Unknown

Cultural Characters: Nematophagous. Cultures of ***H. rickenii*** from M. Semerdzieva (of which the voucher specimens were not seen) matched the characters of the mycelium in the substrate of a number of the specimens cited above, and are thus accepted as identical. Anamorph ***Nematoctonus geogenius***.

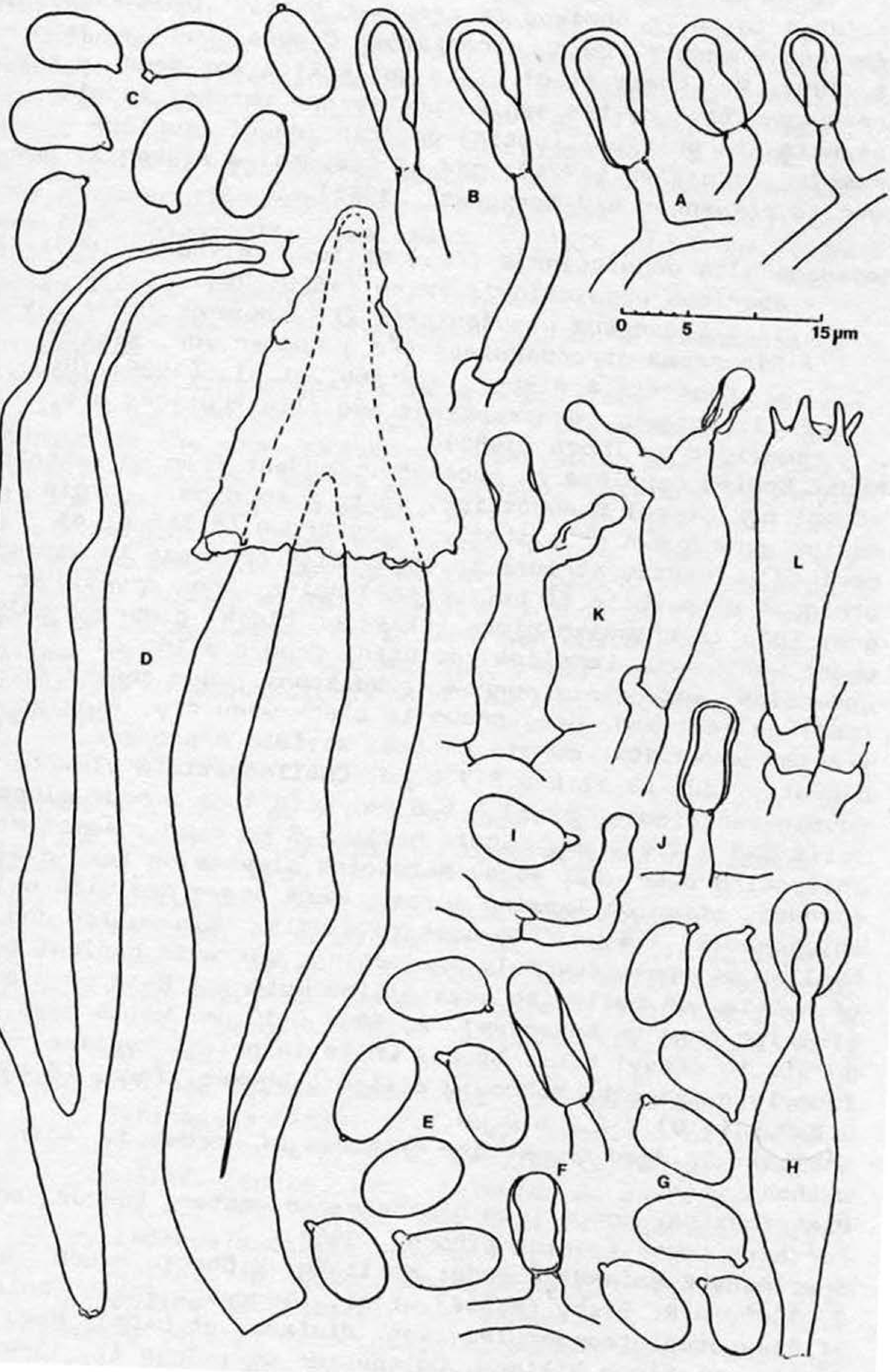
Observations: ***Hohenbuehelia tremula*** provides a classic example of nomenclatorial and taxonomic confusion. ***Agaricus tremulus*** (Schaeffer, 1774) was described as follows, "***Agaricus caulescens, solitarius, gelatinoso-coriaceus; pileo concavo, saepe deformi, dimidiati, lacero, cinereo-fusco*** ..." Schaeffer cited ***Agaricum infundibulum dimidiatum imitans*** (Micheli, 1729) as a synonym. Micheli's species has the form and description of ***Hohenbuehelia petalodes***. The illustrations of ***A. tremulus*** (Schaeffer, 1771, pl. 224, fig I-VIII) show the fungus to be blackish-brown, spathulate to petaloid, with a lateral stem, and growing among mosses. Schaeffer's plate 224, figure IX shows a white spore print on black paper; it must be in error, as it is radially symmetrical, and shows a central stipe. The globose spores shown in figure X may also be misplaced, or simply a result of the optics of the day. Somehow, Fries (1821) came to apply the name of this blackish-brown, tough-gelatinous agaric to a greyish muscigenous species with thin, fragile flesh [*Arrhenia acerosa* (Fr.) Kuehner]. Most subsequent authors (Quelet, 1872; Rea, 1922; Pilat, 1935; Coker, 1944) followed Fries (1821) in this misapplication of ***A. tremulus*** Schaeffer. Redhead (1985) studied the genera ***Arrhenia*** and ***Rimbachia*** and pointed out that the name ***A. tremulus*** Schaeffer had been misapplied, and probably referred to ***H. rickenii***, nom. invalid.

Ricken (1915) illustrated ***Pleurotus geogenius*** (= ***H. petalodes***), showing the typical petaloid habit and short, ovate spores of that species. Kuehner (in Kuehner and Romagnesi, 1953) considered Ricken's fungus too dark to be ***P. geogenius*** and so redescribed it as a new species in honour of Ricken, but based on Kuehner's specimens. ***Geopetalum rickenii*** Kuehner (1953) is not validly published because it lacked a Latin diagnosis. No type specimen was designated, but this was not a requirement of valid publication until 1958. The spore size of Kuehner's fungus does not even overlap that given by Ricken. Singer and Kuthan (1980) recognised this and so described ***H. recedens*** (from Mexico), which they suggested might be Ricken's ***P. geogenius***, but which instead is a third, different fungus.

Despite the confusion over the origin of the name, ***G. rickenii*** was well described, particularly in the "validating" publication (Kuehner, 1954) that supplied a Latin description. Unfortunately, no type specimen was designated, and the simultaneous publication of two alternative generic names made ***G. rickenii*** Kuehner (1954) invalid as well. Orton (1960) and Donoso (1981) both attempted to validate the name once again, but did not designate a type, so their combinations are also invalid.

Still, ***H. tremula*** is readily recognised by its flabelliform to petaloid habit, dark brown colours, long spores, and its occurrence in mossy coniferous forests. An excellent illustration of this species can be found in Bresadola (1928, plate 292, as ***P. geogenius***), who reports it from "sylvis coniferis", with spores 8-9 X 4-4.5 µm.

Figure 25 A-L: ***Hohenbuehelia tremula*** A-D: DAOM #180808 (neotype). A) Predatory adhesive knobs on basal mycelium; B) pilocystidia; C) basidiospores; D) metuloids, one with crystalline cap dissolved away. E-F) DAOM 51088. E) basidiospores; F) predatory adhesive knobs from basal mycelium. G-H) TRTC #9488. G) Basidiospores; H) a cheilocystidium; I-L DAOM #26937. I) Basidiospores; J) pilocystidia; K) cheilocystidia; L) a basidium.


C
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15 µm
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In order to provide a solid basis for this long-confused taxon, a neotype is proposed herein: DAOM #180808, near Lac Grandpre, Parc Laurentides, Quebec, Canada, Aug. 15, 1981, D. Lahaie et al. This collection was seen in the fresh condition by the senior author and matches in all respects the original (Latin) description of ***Agaricus tremulus*** Schaeffer (1774), and of ***Geopetalum rickenii***, nom. invalid. (Kuehner and Romagnesi, 1953).

Hohenbuehelia unguicularis (Fr.) Miller, in Thorn (1986: 43)
    $\equiv$ ***Agaricus unguicularis*** Fries (1828: 24)
        $\equiv$ ***Pleurotus unguicularis*** (Fr.) Kummer (1871: 104)
    = ***Pleurotus atrocaeruleus*** (Fr.) Kummer var. ***minimus*** Dearness & Bisby, in Bisby, et al. (1929: 104)
    Full synonymy, descriptions and illustrations are provided by Thorn (1986).

Fruit Bodies cupulate or conchate, pendent from an excentric dorsal or lateral pseudostipe, up to 6 mm diam., margin medium warm brown or slightly olive-brown (5-6E3-4; as revived), faintly striate in some, disk pruinose to densely strigose with white to buffy (4A2) hairs; when dry-silver grey (B1) to brownish-black (6E3+) or black, glabrous only where weathered. **Lamellae** radiating from a point on underside, moderately narrow, subdistant, warm grey-brown (6E3; as revived), grey-brown to black when dry, finely frosted under 10X, margin entire. **Basidia** 4-pronged, clavate, (22) 25-32 X 5.5-7.5 µm. **Cheilocystidia** clavate or fusoid-ventricose, 22-37 X 4-8 µm, with 1 or 2 hour-glass cells 5-9 X 2.5-4 µm, mucoid balls 4-6 µm diam., sometimes coalescing over gill edge. **Metuloids** clavate or fusoid with rounded, often collapsing apices, dark brown and with walls thickened to 1.5 µm from base to middle, thin-walled and hyaline at apex; scarcely projecting, but with conical cap of hyaline or yellowish crystalline material 8-12 µm diam. (looking down on hymenium), 20-60 X 6-10 µm. Walls deep purple in cresyl blue. **Spores** white in print, hyaline, inamyloid, smooth, narrowly elliptic-phaseoliform, (5.0) 6.0-8.5 (9.0) X 3.0-4.0 µm.
Habitat: On dead trunks and branches of hardwoods, with or without bark.
Distribution: Known from northern and western Europe, and northern North America (Thorn, 1986).
Specimens Examined: Canada: Manitoba: Victoria Beach, June 2, 1928, G.R. Bisby [#3906] et al., Dearness #6654 (holotype of ***Pleurotus atrocaeruleus*** var. ***minimus***, at DAOM). **Nova Scotia**: Highland Village, Colchester Co., June 17, 1954, A.G. Davidson, DAOM #46746. **Ontario**: Black Sturgeon Lake,

Thunder Bay District, June 11, 1976, S.A. Redhead, DAOM #159734; Dorset, Haliburton Co., May 28, 1963, R.F. Cain, TRTC #40707; Lobo, Nov. 8, 1931, J. Dearness #734 (at DAOM). **Quebec**: Cantley, Gatineau Co., Apr. 28, 1985, J. Ginns, DAOM #191960; Tenaga, May 1939, J. Groves and I. Mounce, DAOM #6998. **Yukon Territory**: Haines Junction, Aug. 2, 1962, J. Holms, DAOM #93025. **United States: New York**: Knowersville [now Altamont, Helderberg Mountains], Oct. [no year], C.H. Peck s.n. (NYS); Star Lake, Sept. 7, 1974, J. Ginns, DAOM #155519.

Mating System: Unknown.

Cultural Characters: Nematophagous; anamorph *Nematoctonus brevisporus*.

Observations: *Hohenbuehelia unguicularis* can be recognised by its dark, cupulate to flabelliform basidiomes with pale tomentum on the rear portion or apex, which may be drawn out into a pseudostipe, and by its lamellae that are silvery or pale tan when young and become dark in age. The peculiar, clavate metuloids, which are brown in their lower portions and hyaline and thin-walled at their apices, are diagnostic. An unusual feature of this species is that it fruits in spring or early summer, or in warm periods during winter (Gillet, 1876). Konrad and Maublanc (1937: pl. 309 III) illustrated *H. unguicularis* well, as *Acanthocystis Leightonii*.

RESUPINATUS C. Nees ex S.F. Gray (1821: 617)

Type species (only original species): *R. applicatus* (Batsch: Fr.) S.F. Gray

- = *Phyllotus* Karsten (1879: xiv) [**not** *Phyllota* Bentham, in Endlicher et al. (1837: 33)]. Type species, selected by Singer and Smith (1946) and also obligatory under Article 7.11 of the I.C.B.N. (Voss, et al., 1983): *P. applicatus* (Batsch: Fr.) Karsten
- = *Calathinus* Quélet (1886: 46) [**not** *Calathinus* Rafinesque (1838: 21)]. Type species, obligatory under Article 7.11: *C. applicatus* (Batsch: Fr.) Quélet. (Earle, 1909, selected *C. porrigens* (Pers.: Fr.) Quélet, but this is inadmissable.)
- = *Scytinotopsis* Singer **nom. nud.** (1936: 355) Type species, obligatory under Article 7.11: *S. applicatus* (Batsch: Fr.) Singer.

The following generic description is paraphrased from Singer (1975), with additional delimiting characters added on the basis of this study:

Small (0.1-2.0 cm diam.), sessile or laterally pseudostipitate, pleurotoid or cupulate fruit bodies with well-developed or reduced (but present) gills; gills radiating from point of attachment or a central or excentric point on the underside of the cap; veil none; monomitic, but a gelatinous zone usually present in the flesh, often directly beneath the cuticle; hyphae of other zones of the trama sometimes with gelatinized walls; all hyphae inamyloid and with clamp connections; epicutis consisting of a rameales structure, of coralloid-diverticulate hyphae, often with thick, brown walls, and secreting what becomes a yellowish to brownish, solid, amorphous or crystalline encrusting material from branch-tips; thus the cuticle pigmented and often heavily encrusted; spores white in mass, hyaline, inamyloid, acyanophilic, globose, elliptic or phaseoliform; basidia normal; metuloids none; pleurocystidia none; cheilocystidia clavate, clavate-rostrate or fusoid, commonly diverticulate and forming a rameales structure on the sterile and often gelatinized gill edge; hymenophoral trama regular, but hyphae often interwoven. On rotting wood or herbaceous plants, rarely on living plants; the gills facing downwards. Heterothallic, tetrapolar; without a ***Nematoctonus*** asexual state; hyphae in culture often with fine palmate-digitate terminal branchlets.

The concept of ***Resupinatus***, in Miller (in press), and with which we agree, is considerably restricted from that currently in use (Singer, 1975; Moser, 1983). Therefore the generic description has been amended to include only the type species, ***R. applicatus***, and those that are unquestionably closely related. The diagnostic features of ***Resupinatus*** sensu stricto are the pigmented, gelatinized cap and the diverticulate cheilocystidia and cuticular hyphae. ***Hohenbuehelia*** differs from ***Resupinatus*** in the possession of hymenial metuloids, gloeosphex cystidia, and ***Nematoctonus*** anamorphs. The lack of a ***Nematoctonus*** state or nematophagous habit in ***Resupinatus*** supports this distinction.

Miller (in press) has transferred ***R. cyphelliformis***, ***R. sylvanus*** sensu Coker, and ***R. unguicularis*** sensu Coker to ***Hohenbuehelia***. Miller's transfer of ***R. cyphelliformis*** and ***R. unguicularis*** sensu Coker (= ***Hohenbuehelia pinacearum***) appears well-founded: both have ***Nematoctonus*** anamorphs, as do all other species of ***Hohenbuehelia*** tested to date. ***Resupinatus silvanus*** sensu Coker has no ***Nematoctonus*** state, and does not have clearly-defined gloeosphex cystidia, either in material that I have studied or in the descriptions and illustrations of Miller (in press).

Resupinatus could be confused with several other genera with more or less gelatinized, pleurotoid fruit bodies, namely ***Marasmiellus*, *Campanella*** and ***Panellus***. Species of ***Marasmiellus*** with gelatinized cap tissues have definite, excentric stipes and are usually pale, and thus differ from the pigmented ***Resupinatus*** species, which at most develop a lateral pseudostipe that is continuous with the cap. Species of ***Campanella*** are also usually colourless, and have strongly anastomosing gills that often become poroid or honey-combed and reticulate. Species of ***Panellus*** have amyloid spores. Many features of the anatomy of ***Panellus stipticus*** (Bull.: Fr.) Karsten, the type species of ***Panellus***, are similar to those of ***Resupinatus*** sensu stricto, including gelatinized gill edges with a rameales structure formed by diverticulate cheilocystidia, partly gelatinized trama, and diverticulate cuticular hyphae. The hyphae of ***Panellus stipticus***, however, lack brown encrusting pigments, and its spores are small and elliptic to somewhat allantoid. ***Panellus ringens*** and certain allied species are brownish and have a more strongly gelatinized upper zone in the cap. ***Panellus patellarilis*** (Fr.) Konrad and Maublanc was found during this study to be tetrapolar and non-nematophagous. The relationship of these two genera requires further study, but for now ***Resupinatus*** seems more closely allied to ***Hohenbuehelia*** than to ***Panellus***.

Stigmatolemma and ***Stromatocyphella*** are cyphelloid agarics clearly derived from ***Resupinatus*** sensu stricto. The coralloid-diverticulate cuticular hyphae of the two genera are similar to those found in ***Resupinatus***, and their flesh is gelatinized. ***Resupinatus kavinii*** (Pilat) Moser (1978) of Europe seems to have evolved toward the cyphelloid habit. Its fruit bodies are cupulate and 1-3 mm diam., with up to 10 shallow lamellae. The oblong spores of ***Stromatocyphella conglobata*** are another reason for accepting the elliptic-spored ***R. alboniger*** in ***Resupinatus*** along with ***R. applicatus*** and other spherical-spored species.

Pleurotus vetlinianus Domanski (1964) has been transferred to ***Resupinatus*** by Moser (1979), but can not be accommodated in either ***Resupinatus*** sensu stricto or sensu lato, nor in ***Hohenbuehelia***. It was described as being up to 15 cm long by 9 cm broad, thick-fleshed, with gelatinized gill trama and lower cap trama, and with thick-walled, simple-septate hyphae (possibly secondarily septate) interspersed with thin-walled, clamped hyphae in the trama. Its true taxonomic affinities are unknown.

Resupinatus alboniger (Pat.) Singer (1978: 17)

≡ ***Pleurotus alboniger*** Patouillard (1893: 126)

A full description, with illustrations and synonymy, are provided by Thorn (1986).

Fruit Bodies cupulate to flabelliform, sessile, up to 6 mm broad, at first white-woolly or pruinose, becoming grey-brown to black and predominantly glabrous as this wears away. **Lamellae** radiating from point of attachment, narrow, subdistant, grey-brown to black, often with whitish margins. **Basidia** 4-pronged, clavate-cylindric, 18-25 X 5-7 µm. **Cheilocystidia** variable, fusoid, clavate, lecythiform or pyriform, with or without irregular digitate projections, 11-25 X (3.5) 5-11 µm, most thin-walled, one with walls near apex 2.0 µm thick. **Spores** hyaline, inamyloid, smooth, elliptic-phaseoliform, to cylindric and slightly curved, 5.8-7.8 X 2.7-3.6 µm.

Habitat: on dead woody dicots.

Distribution: Known from the southern and eastern United States, France, Ecuador, Venezuela and Tanzania (Thorn, 1986).

Specimens Examined: United States: Maine: Harrison, Sept. 1859, Burt #141 (FH). **Mississippi**: Ocean Springs, Feb. 1887, F.S. Earle, Ellis and Everhart's North American Fungi #2008 (at DAOM). Without source data, VT 1364 (from O.K. Miller, Jr., VPI) fruiting in culture, RGT #840810/01. **Ecuador**: Ravine near Quito, Feb. 1, 1982, Lagerheim s.n. (FH; **holotype** of *Pleurotus alboniger* Patouillard); Cotocollao, Feb. 1892, Lagerheim #87, NY (paratype). **Holland**: Veere, winter, 1830, M.A. Libert, Plantae cryptogamicae Arduennae #19-B (*ad ramos putridos Ribis grossulariae*), at DAOM. **Venezuela**: near Los Venados, El Avila, July 24, 1972, K. Dumont et al., VE 5872 (NY); near Manacal, NW of Irapa, July 9, 1972, K. Dumont et al., VE 4430 (NY).

Mating System: Heterothallic, tetrapolar. Of six single spore isolates of RGT #840810/01, three were A1B1, and one each was A1B2, A2B1, and A2B2.

Cultural Characters: Nematode negative, conidia none, neither in pure culture (PDA, MEA) nor on WA with nematodes.

Observations: *Resupinatus alboniger* can be recognized by its small, dark, sessile basidiomes that occur on woody dicots, its lack of metuloids, elliptic spores, and the presence of diverticulate cheilocystidia and diverticulate cuticular hyphae with thick, brown walls. The cheilocystidia of this species are variable and, in addition to the diverticulate ones, some collections have cheilocystidia that are fusoid, or broadly pyriform. This is the fungus described and illustrated by Coker (1944) as *Pleurotus silvanus*.

Resupinatus alboniger is similar in many ways to the small, dark species of *Hohenbuehelia*, but its diverticulate cheilocystidia and cuticular hyphae, and lack of a

Nematoctonus anamorph or metuloids show that it is correctly placed in *Resupinatus*, with the spherical-spored species such as *R. applicatus*.

Resupinatus applicatus (Batsch: Fr.) S.F. Gray (1821: 617)
Fig. 26
≡ *Agaricus applicatus* Batsch (1786: 171)
≡ *Agaricus applicatus* Batsch: Fries (1821: 192)
≡ *Pleurotus applicatus* (Batsch: Fr.) Kummer (1871: 105)
≡ *Phyllotus applicatus* (Batsch: Fr.) Karsten (1879: 94)
≡ *Calathinus applicatus* (Batsch: Fr.) Quélet (1886: 47)
≡ *Geopetalum striatulum* (Pers.: Fr.) Kuehner & Romagnesi, nom. invalid., var. *applicatum* (Batsch: Fr.) Kuehner and Romagnesi **nom. invalid.** (1953: 68)
≡ *Hohenbuehelia applicata* (Batsch: Fr.) Zerov and Peresipkin **nom. invalid.** (1979: 115)

Pileus cupulate, 3-5 mm diam., becoming spathulate or flabelliform with a lateral pseudostipe, 7-15 mm long X 5-15 mm broad, pseudostipe 2-5 mm broad, margin glabrous to pruinose, chocolate-brown (7F6) to black when wet, not striate or translucent striate, ash-grey (ca. C1) and nonstriate when dry; basal 1/3 to 2/3 covered with shaggy, stiff, coarse tomentum, especially dense over pseudostipe, pale greyish buff to brownish grey (4-5B2 but paler). **Gills** decurrent and radiating from pseudostipe, dark brown (6E3-4) when revived, moderately narrow and close, margins whitish and entire. **Flesh** gelatinous and black in mass. **Cuticle** dark brown in KOH, 20-30 μm thick, of densely woven brown, thick-walled, heavily encrusted hyphae 4-6 μm diam., with irregular or finger-like projections, apparently secreting what becomes the granular yellowish encrustation. **Epicutis** of hyaline, smooth tomentum hyphae, walls 0.5-0.75 μm thick, non-gelatinized, tips rounded and thin-walled, up to 200 μm tall, 2.0-4.0 μm diam. (most 3.0 μm), with clamps.
Gelatinous Zone 150-300 μm deep in KOH (without cover-glass) subhyaline, with pale brown, smooth, clamped hyphae 2.0-5.0 μm diam. (most 3 μm) widely dispersed in hyaline gel. **Pileus Trama** medium brown in KOH, 30-50 μm deep, of densely woven hyphae 2.5-5 μm diam. **Gill Trama** continuous with that of pileus, medium brown in KOH, very irregularly interwoven of hyphae 2-5 um diam., some with walls gelatinized to 1.0 μm thick. **Subhymenium** dark brown in KOH, 15-25 μm thick, densely woven. **Hymenium** subhyaline, pale brown in KOH, 20-25

µm thick. **Basidia** 4-pronged, clavate, hyaline or faintly brown in KOH, (18) 22-25 (30) X 5-6 µm. **Cheilocystidia** numerous, more or less clavate, with coarse and fine finger-like projections, some with fine droplets at their tips (1 µm or less diam.), 14-25 X 5-7 µm. **Spores** hyaline, inamyloid, smooth, subglobose or globose, some with prominent apiculus, (4.0) 4.4-6.0 X 4.0-4.8 µm.

Habitat: On bark and wood of fallen hardwoods. Reports in the literature of its occurrence on conifers invariably refer to *R. striatulus* (q.v.).

Distribution: Apparently worldwide, although badly confused with *R. striatulus*.

Specimens Examined: Canada: Nova Scotia: Kentville, King's Co., Apr. 26, 1953, K.A. Harrison, ACAD #7596. **Ontario**: Brant Co., New Durham, Oct. 13, 1963, TRTC #41202 (part as DAOM #115047); York Co., Nashville, Sept. 26, 1953, TRTC #24926; same locale, Oct. 11, 1953, TRTC # 24972; Toronto, Hogg's Hollow, Oct. 12, 1931, TRTC #2736. **Quebec**: Gatineau Park, Ridge Rd., Oct. 17, 1956, DAOM #54231. **United States: Indiana**: Brown County Park, Aug. 1958, W.B. Cooke, ACAD #7603 **Maine**: Harrison, Aug. 1859, G. Blake, BUF #43356. **New Jersey**: Newfield, Nov. 1901, Ellis & Everhart, Fungi Columbiani s.n., at TRTC and DAOM. **New York**: Fort Edward, n.d., E.C. Howe s.n., Peck Herbarium (NYS; **lectotype** of *Pleurotus atropellitus* Peck); Maryland, Otsego Co., [Spet. 1876], Peck s.n., Peck Herbarium (NYS; as *P. atropellitus*). **Tennessee**: Oliver Springs, Oct. 25, 1936, L.R. Hesler, Flora Tennessee #9649 (at TRTC).

Mating System: Unknown for *R. applicatus* sensu stricto.

Cultural Characters: Nematode negative. Conidia none, neither in pure cultures (PDA, MEA) nor with nematodes on WA. Kuehner et al. (1962) report conidia in *R. applicatus* sensu Josserand (= sensu stricto), but this seems questionable and may refer to *R. applicatus* in the sense of Quélet (Kuehner, 1926), which is *Hohenbuehelia pinacearum*. In culture on WA with nematodes, aerial hyphae produce remarkable knobbed cells (Fig. 26 G) that look like "jacks". These are firmly attached by a stout (1.5- 2.0 µm

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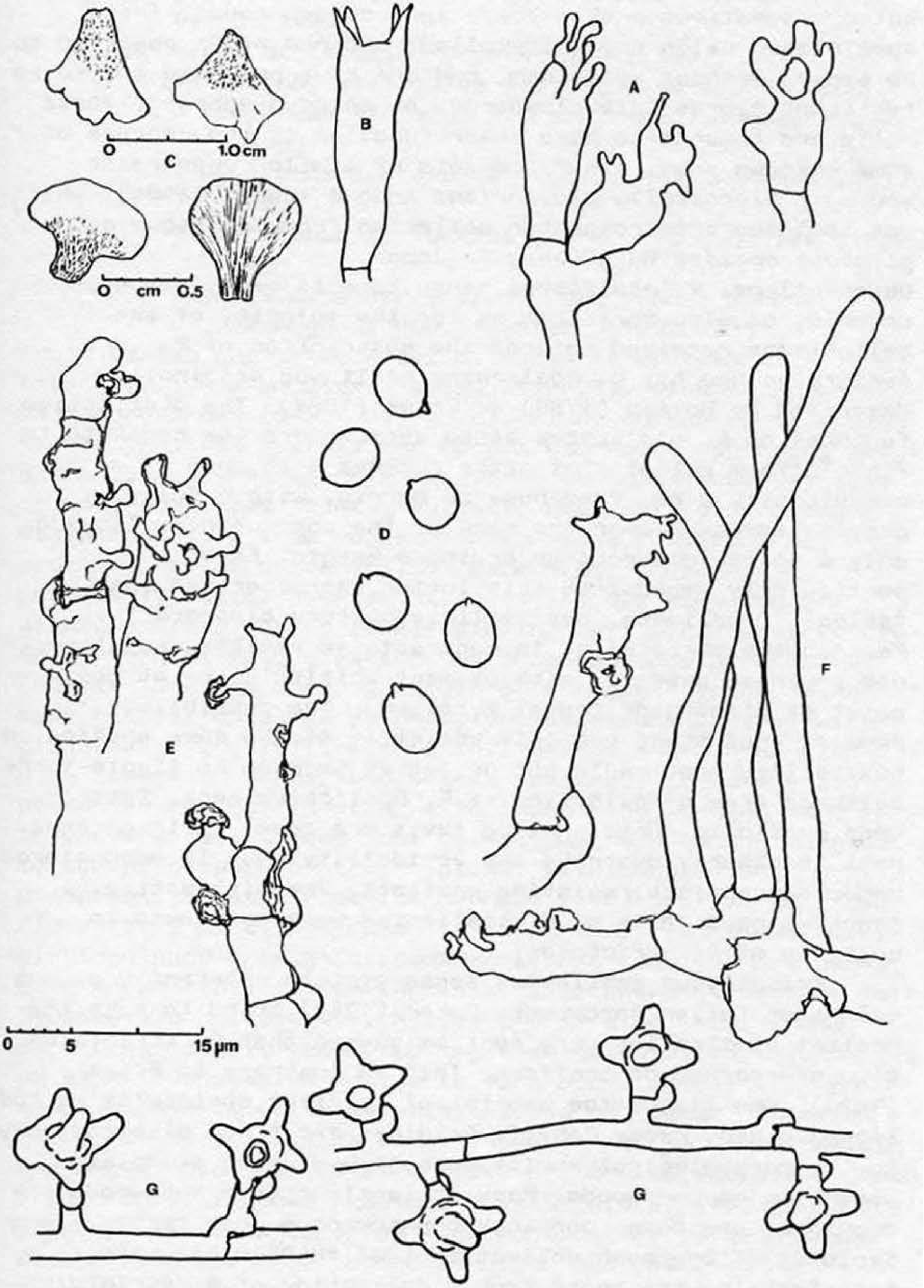
Figure 26 A-G: *Resupinatus applicatus*. A-D) DAOM #54231. A) Three diverticulate cheilocystidia; B) a basidium; C) habit of fruiting bodies; D) basidiospores. E-F) TRTC #41202. E) Diverticulate cuticular hyphae; F) tomentum hyphae. G) T-99 (DAOM #54231), jack-shaped cells on aerial hyphae in culture on WA with nematodes.


C
0
1.0 cm
0
cm
0.5
B
A
D
E
F
0
5
15 µm
G
G

diam.) peg with a clamp connection at the base of the cell, but are sometimes broken loose in a squash mount. These specialised cells are thin-walled, and are often observed to be empty, without cytoplasm, and are thus presumed not to be resistant spores (aleuriospores, or chlamydospores). These cells are thought to have their function in the capture of some unknown prey. Aleurioconidia of similar appearance occur in ***Microstella pluvioriens*** Ando & Tubaki (1984), which was isolated from rainwater collected from ***Metasequoia glyptostroboides*** Hu & Cheng in Japan.

Observations: *R. applicatus* sensu lato is very common in Ontario, as elsewhere, but by far the majority of the collections examined matched the description of ***R. striatulus*** and not ***R. applicatus*** as it was originally described by Batsch (1786) or Fries (1821). The distinctive features of ***R. applicatus*** sensu stricto are the conchate to flabelliform pileus that often reaches 1 cm, and occasionally 2 cm, from base to margin, with a felty, greyish tomentum over the back of the cap surface, leaving only a narrow glabrous or pruinose margin. Fries particularly emphasised this latter character, saying, ***"pileo ... pruinato, basi villoso obscure cinerato."*** ***Resupinatus striatulus***, in contrast, is smaller, cupulate, and pruinose overall, with at most whitish hairs at the point of attachment (basal mycelium). The possibility remains that these are only varieties of the same species, a possibility that could not be tested because no single-spore cultures from a collection of ***R. applicatus*** sensu Batsch were available. Until mating tests are done, it is perhaps best to clearly describe the variability that is encountered under appropriate, existing epithets. The distinctive "jack"-shaped cells of ***R. applicatus*** were not found in cultures of ***R. striatulus***.

Resupinatus applicatus sensu stricto apparently always occurs on fallen hardwoods. Coker (1944) tried to make the habitat distinction very neat by saying that ***R. striatulus*** always occurred on conifers. This is contrary to Fries (1821), who listed the habitat of ***Agaricus striatulus*** as ***"ad lignea pinea, ramos Coryli, Betulae, etc."*** and also contrary to the morphological variation observed among examples occurring on hardwoods. Many collections from hardwoods are cupulate, pruinose, and lack cap tomentum, and single spore isolates of one such collection (RGT #840910/03) were interfertile with those from a collection of ***R. striatulus*** from ***Pinus strobus*** (RGT #840808/09).

Resupinatus striatulus (Pers.: Fr.) Murrill, in Murrill et al., (1915: 242)
= *Agaricus striatulus* Persoon (1801: 485)
= *Agaricus striatulus* Pers.: Fries (1821: 193)
= *Pleurotus striatulus* (Pers.: Fr.) Kummer (1871: 105)
= *Phyllotus striatulus* (Pers.: Fr.) Karsten (1879: 94)
= *Calathinus striatulus* (Pers.: Fr.) Quélet (1886: 48)
= *Geopetalum striatulum* (Pers.: Fr.) Kuehner & Romagnesi **nom. invalid.** (1953: 68)

Fruit Bodies cupulate, sessile, dorsally or laterally attached, 1.5-7 mm diam., beige (4A2-B3), pinkish brown (6C-D3), grey-brown (5C2-3-D3) to blackish, darkening on drying; finely pruinose overall, or margin glabrous, appearing moist and polished when water-soaked; margin translucent-striate or not, sometimes faintly sulcate, edge entire or crisped. **Gills** radiating from point of attachment or a central or eccentric point on underside, moderately narrow to moderately thick, subdistant, concolourous with cap or slightly paler, buffy (4A2), pinkish-buff (5B2) or brown (5-6D3); margins paler, entire; surface glabrous or atomate. **Cuticle** 10-25 µm deep, a tangle of brownish hyphae, with many details obscured by heavy encrustations of yellowish granular or crystalline material. Hyphae 1.5-5.5 µm diam., with irregular knobs, branchlets, and pegs in some areas dense and repent, in other with loose ends verging on a trichoderm. **Gelatinous Zone** ca. 100 µm deep in cap margins, to 400 µm deep in centre, hyaline, with tangled and ascendent, faintly brownish hyphae, (1.0) 1.5-3.0 µm diam., clamps to 7 µm diam. **Trama** 45-150 µm deep, sometimes poorly distinguished from gelatinous zone, but usually more dense, pale brown, then descending into gills where it becomes more hyaline and gelatinised; hyphae 2-6 µm diam. **Gill Trama** extending to gill edges, making them gelatinised, hyphae 2-4 µm diam. **Subhymenium** medium to dark brown (KOH), 5-12 µm deep, hyphae becoming gelatinised and amorphous. **Hymenium** brown, often paler than subhymenium, 18-25 µm deep. **Basidia** 4-pronged, clavate, 20-27 X 5.5-7 µm. **Cheilocystidia** a dense fringe on gill edges, clavate-diverticulate, (10) 15-27 X 4-8 µm, projections tapering and needle-like, often tipped with a fine droplet 1.0-1.5 µm diam. and obscured by granular-crystalline yellowish encrusting material. **Spores** white in print, hyaline, inamyloid, globose or subglobose, (3.3) 4.0-6.0 X (3.1) 3.5-5.0 µm.

Habitat: On rotting coniferous or deciduous logs, usually having a soft white rot. Most often found on the undersides of logs.

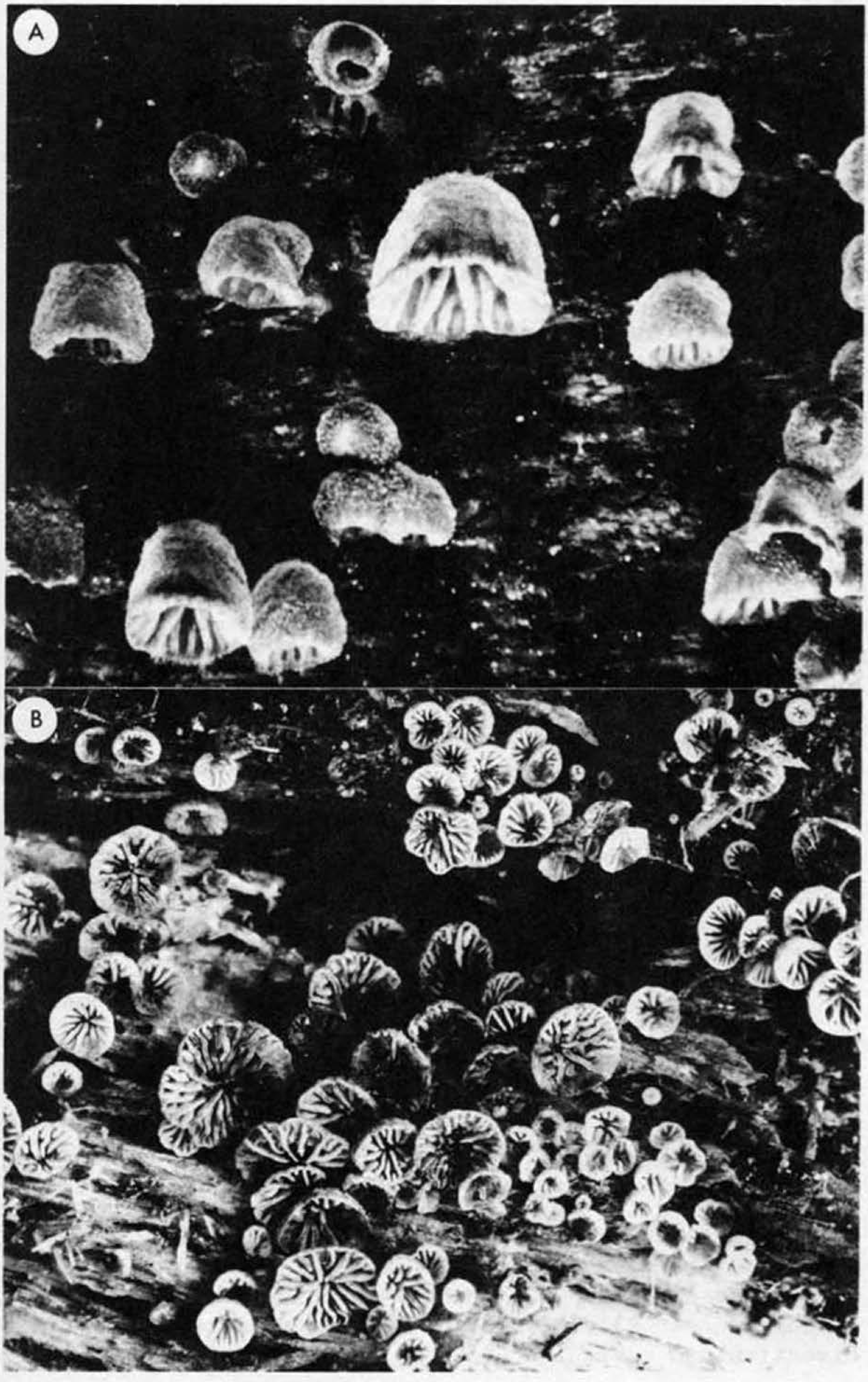
Distribution: Probably widespread in Europe and North America, confused in the literature with *R. applicatus*.

Selected Specimens Examined: Canada: British Columbia: Cowichan Lake, June 21, 1948, W.G. Ziller, DAOM #21617; Yellow Point, July 27, 1938, I. Mounce, DAOM #9172. **Manitoba**: W. Hawk Lake, near Ontario boundary, Aug. 29, 1936, G.R. Bisby, DAOM #7347. **New Brunswick**: Kouchibouguac National Park, July 28, 1978, K. Egger and R.A. Shoemaker, DAOM #170071. **Ontario**: Algonquin Provincial Park, Swan Lake, Oct. 7, 1954, S. Gibson and A. Hill, DAOM #46775; Algonquin Park, West Gate, Sept 22, 1982, R.G. Thorn #80922/06; same locale, Sept. 10, 1984, RGT #840910/03; same locale, Sept. 15, 1984, RGT #840915/03; Algonquin Park, Minkey Lake, July 28, 1984, RGT #840728/03; Hindon Twp., Haliburton Co., Sept. 16, 1966, R.F. Cain, TRTC #44650 (part as DAOM #158501); Oxbow Lake, Haliburton Co., Aug. 20, 1941, R.F. Cain, TRTC #18261 (part as DAOM #80609); Petawawa F.E.S., Sept. 1, 1941, DAOM #10533; Rondeau Provincial Park, Aug. 8, 1984, RGT #840808/09; Lake Temagami, Aug. 14, 1931, H.S. Jackson, TRTC #2665; Lake Temagami, Sept. 10, 1936, A.H. Smith, TRTC #11475 (part as DAOM #80599); Toronto, Nov. 11, 1946, H.S. Jackson, TRTC #21561; **Quebec**: Cantley, March 1, 1981, J. Ginns, DAOM #180787; Chelsea, Oct. 9, 1936, J.W. Groves, DAOM #6945; Rawdon, May 23, 1981, R. McNeil, DAOM #185912;. **United States: "New England"**:, n.d., W.G. Farlow, Rel. Farlowianae #345, at TRTC. **New York**: Alcove, Oct. 1893, C.L. Shear, New York Fungi #105 (at DAOM); Buffalo, April 1874, G.W. Clinton s.n. (BUF #43355; cited by Peck, 1886, as *Pleurotus atropellitus*). **England**: Littlehampton, Sussex, April 26, 1959, D.A. Reid, DAOM #66623. **West Germany**: Oberammergrau, Aug. 1891, Allescher & Schnabl, Fungi bavarici s.n. at TRTC.

Mating System: Heterothallic, tetrapolar. Nine monokaryons of RGT #840808/09 (collected on *Pinus strobus*) yielded 4 A1B1, 1 A2B2 and 4 A1B2. Six monokaryons of RGT #840910/03 (from *Acer saccharum*) yielded three each of two compatible mating types, and were interfertile with those of #840808/09. Nine monokaryons of RGT #840915/03 (from *Thuja occidentalis*) yielded one each of A1B1 and A2B2, 4 A1B2, and 3 A2B1.

Cultural Characters: Nematode negative, conidia none,

Figure 27: *Resupinatus striatulus*. A) R.G. Thorn #840808/09, on *Pinus*, X 6. B) RGT #820922/06, on *Acer*, X 2.2


A
B

neither in pure culture (PDA, MEA) nor on WA with nematodes. Vegetative hyphae in sections beneath fruit bodies are smooth, hyaline, clamped, (0.8) 1.5-4.0 µm diam., forming appressoria and penetration pegs 0.1-0.2 µm diam. to pierce cell walls where they do not pass through bordered pits, passing directly through most cells but present in abundance in areas of high microbial activity, including the surface of the wood where they appear associated with free-living algae, rarely producing droplets up to 4 µm diam., from fine, tapering pegs 1.5-4 µm long, 0.2-0.4 µm diam at the tip.

Observations: The distinctive features of this species are its small size, cupulate habit, and glabrous to pruinose cap that is translucent striate or slightly sulcate on the margin. Spore size and all other microscopic characters examined merge with those of ***R. applicatus*** sensu stricto. The macroscopic differences between the extremes of these two species are striking. ***R. applicatus*** has flabelliform fruit bodies that are grayish tomentose on the disk, and 5 to 10 times larger than those of ***R. striatulus***. In addition, ***R. striatulus*** occurs on old and well-rotted wood that is without bark, and is usually soft and white-rotted, whereas ***R. applicatus*** occurs most commonly on the bark of hardwood logs such as ***Quercus*** and ***Acer***, or on hard rinds formed on hardwood logs by fungi such as ***Ustulina deusta***.

Resupinatus trichotis (Pers.) Singer (1961: 48) Figs. 29 & 30
    ≡ ***Agaricus trichotis*** Persoon (1828: 18)
    = ***Agaricus racodium*** Berkeley & Curtis (1859: 288)
        ≡ ***Pleurotus rhacodium*** (Berk. & Curt.) Saccardo (1887: 380)
        ≡ ***Pleurotus applicatus*** (Batsch: Fr.) Kummer f. ***rhacodium*** Pilát (1935: 67)
        ≡ ***Resupinatus rhacodium*** (Berk. & Curt.) Singer (1951: 253)
    = ***Resupinatus subrhacodium*** Singer, in Singer & Digilio (1952: 104)

Pileus cupulate to orbicular, dimidiate, or reniform, up to 1.5 cm broad by 0.8 cm long, sessile, grey (7E-F2) to

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Figure 28 A-G: ***Resupinatus striatulus***. A-C) Libert #19-A. A) Diverticulate elements of gill edge; B) basidia; C) basidiospores. D-G) R.G. Thorn #840728/03. D) Basidia; E) basidiospores; F) diverticulate cheilocystidia; G) diverticulate cuticular hyphae.

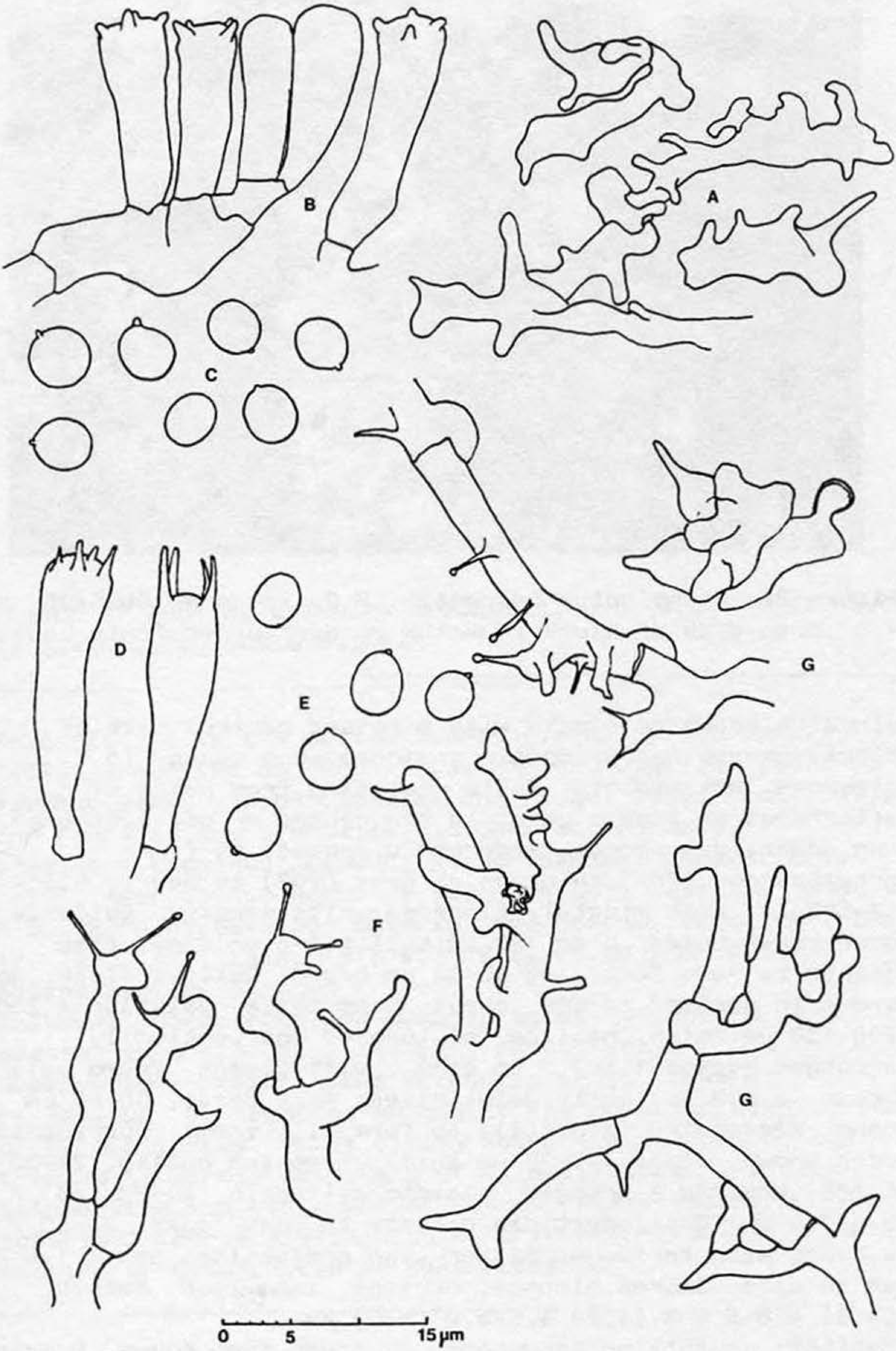

A
B
C
D
E
F
G
G
0
5
15 μm

Figure 29: *Resupinatus trichotis*, R.G. Thorn #850905/05, X 1.5. Note disk of black tomentum on overturned fruit bodies.

blackish brown or black, with a raised central disk of black, shaggy hairs; margin pruinose when young, to glabrous, not striate. **Gills** radiating from point of attachment or from a point in the centre or off-centre on the underside, narrow, moderately spaced, at first greyishbrown (7D3) to brownish grey (7D2) to nearly black (7-8F2-1), with minutely floccose white margins. **Epicutis** of dark brown hairs up to 700 µm tall X 2-3 um diam, some joined to form fascicles 25-30 µm broad. **Cuticle** black, dark brown in section in KOH, about 25 µm thick. **Gelatinous Zone** 300-400 µm thick, hyaline, of tangled and vertically arranged hyphae 1.5-2.5 µm diam., with clamps. **Trama** pale brown in KOH, slightly gelatinised, more dense, 30-50 µm deep, descending into gills to form gill trama. **Subhymenium** dark brown, dense, 10-70 µm thick. **Hymenium** pallid, 26-32 µm thick. **Basidia** 4-pronged, clavate-cylindric, 24-28 (33) X 5.5-7.0 µm. **Cheilocystidia** clavate to ventricose, 25-30 X 5-6.5 µm; with tortuous, finger-like projections about 1.5-2.0 µm in diam. **Spores** globose, hyaline, inamyloid, smooth, (4.5) 4.8-6.5 X (4.2) 4.5-5.0 (5.5) µm.

Habitat: on rotting hardwoods, recorded from *Fagus*, *Fraxinus* and *Salix*.

Distribution: Reported from Great Britain, Hungary, Italy and Yugoslavia (Babosne, 1976), Holland (Reijnders, 1977),

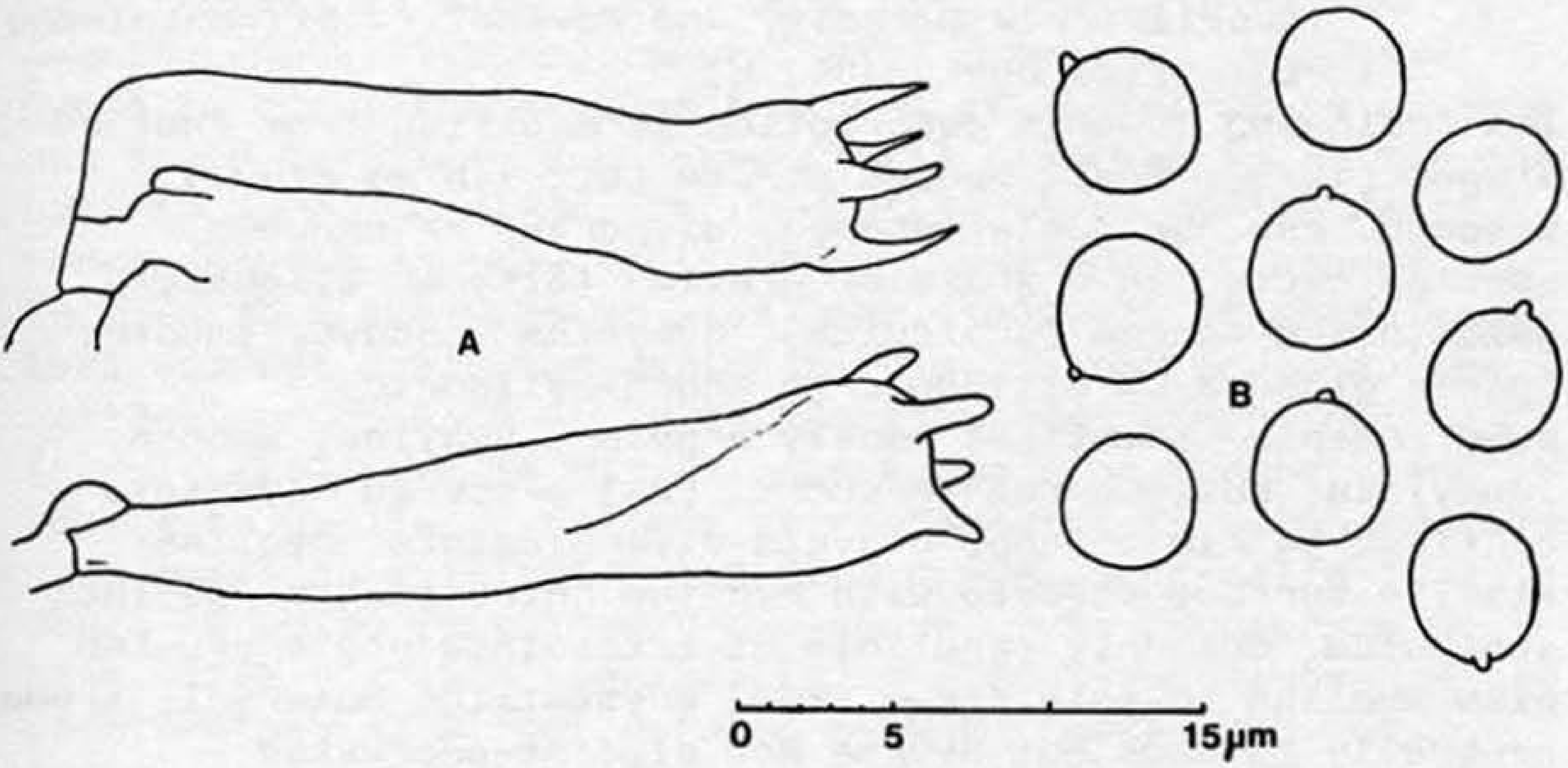


Figure 30 A-B: *Resupinatus trichotis*, R.G. Thorn #850905/05. A) Basidia; B) basidiospores.

Pennsylvania in the United States (Berkeley and Curtis, 1859), Argentina and Brazil (Singer and Digilio, 1952, as *R. subrhacodium*), Japan (Imazeki and Hongo, 1965; Hongo, 1978), and found in New Brunswick and Ontario, Canada.

Specimens Examined: Canada: New Brunswick: Lobster Cove Point, near Chance Harbour, St. John Co., Sept. 5, 1985, R.G. Thorn #850905/05. **Ontario**: New Durham, Brant Co., Sept. 12, 1958, R.F. Cain, TRTC #33929 (part as DAOM #74474).

Mating System: Unknown.

Cultural Characters: Non-nematophagous, without a *Nematoctonus* asexual state (RGT #850905/05).

Observations: *Resupinatus trichotis* could, like *R. striatulus*, be regarded as one of the more striking variants of *R. applicatus*. Pilat (1935) was of this opinion, and treated it merely as a form of *R. applicatus*. The dark pileus with its dense mat of coarse, black tomentum, and its spherical spores distinguish *R. trichotis* from all other species of *Resupinatus* or *Hohenbuehelia*.

STIGMATOLEMMA Kalchbrenner (1882: 104)

Type species (only original species): *S. incanum* Kalchbr.

= *Porotheleum* Fr.: Fr. subgenus *Stigmatolemma* (Kalchbr.) W.B. Cooke (1957: 687)

= *Rhodocyphella* W.B. Cooke (1961: 105)
Type species, originally designated: *Cyphella cupuliformis* Berkeley and Ravenel (= *Stigmatolemma taxi* fide Donk, 1962 b)

The following generic description is modified from that by Singer (1975): Fruit bodies minute (0.2-1.5 mm diam.), discoid, cup, or goblet-shaped, dispersed or crowded, usually seated in a white or greyish felty or slightly gelatinized stroma (subiculum); hymenium concave, smooth. Spores globose to ellipsoid or short-cylindric, suballantoid, sometimes weakly angular, hyaline, smooth, inamyloid; basidia rather short, (2-) 4-spored; cystidia confined to rim of cup, clavate-diverticulate, hyaline; sterile surface covered with hyaline hairs that merge into subiculum, commonly coralloid-diverticulate and encrusted with hyaline to pale brown (KOH) crystalline material; trama generally fuscous but hyphae not pigment-encrusted; subhymenium of dense, subparallel pigmented hyphae; lower trama hyaline or subhyaline and strongly gelatinized; all hyphae with clamps, inamyloid. On dead wood and stems. Presumed not to have a *Nematoctonus* state.

Observations: *Stigmatolemma* can be recognised among the genera of cyphelloid agarics by its gelatinous context, clamp connections, and greyish tomentum of diverticulate, encrusted hyphae. *Calyptella* Quelet is similar, but paler and not gelatinized.

Singer separates *Stigmatolemma* and *Stromatocyphella* in his key (1975, p. 378) on the basis of the presence of coralloid-diverticulate cuticular hyphae in *Stromatocyphella* and their absence in *Stigmatolemma*. Figure 31, plus those by Redhead (1973) of *Stigmatolemma poriaeforme* and Cunningham (1963) of *"Stromatoscypha" huia* clearly show that *Stigmatolemma* has diverticulate cuticular hyphae. Romagnesi (1953, cited in Donk, 1962 b) remarked on this character when comparing *Stigmatolemma poriaeforme* with *Resupinatus kavinii*. Figure 33, and those by Reid (1963) depict comparably diverticulate cuticular hyphae in *Stromatocyphella conglobata* and show that this character can not be used to distinguish these two genera.

Maintaining separate genera for *Stigmatolemma* and *Stromatocyphella* may be justified on the macroscopic characters of their fruit bodies, that is, the cylindric to cupulate, more or less separate fruit bodies of *Stigmatolemma* versus the cespitose cups on a common gelatinous mound in *Stromatocyphella*. It may be that more supporting characters will be added as we learn more about the biology of these genera.

In addition to the widespread *Stigmatolemma poriaeforme*, *S. taxi* (Lev.) Donk also occurs in North America (Donk, 1962 b). Burt (1915) described it (under *Cyphella cupulaeformis*) on the bark of *Juniperus* in Georgia and South Carolina, and Coker (1921) reported it on the same host in North Carolina. It is distinguished by its host range, scattered grey fruit bodies, and angular spores (4.75-5.75 X 4.5-5.25 µm vide Donk, 1962 b). *Stigmatolemma taxi* was not collected during this study nor found in the collections of DAOM or TRTC. *Stigmatolemma conspersum* (Pers.: Fr.) Donk is as yet only known from Europe where it occurs on conifers, but may be represented in North America by a specimen originally labelled *Cyphella grisella* (Quel.) Bourd. & Galz. (considered a synonym of *S. conspersum* by Donk, 1962 b). This specimen (DAOM #22841) was subsequently redetermined as *S. poriaeforme* by W.B. Cooke, who had a broad concept of that species, and was not checked during this study.

The species of *Stigmatolemma* have been treated in a variety of genera over the years. Persoon (1801) and Fries (1822) classified these species in *Peziza*. Once the basidia of these species were recognised, some species were treated in the genus *Cyphella* Fries, some in *Solenia*, and others in *Porotheleum*, depending on how crowded or dispersed the fruit bodies were, and how well-developed the subiculum was. *Stigmatolemma* is not congeneric with the types of any of these three genera (Donk, 1962 b).

Stigmatolemma poriaeforme (Pers.: Fr.) W.B. Cooke (1961: 128) (as *poriaeformis*) Figs. 31 & 32 B & C
  = *Peziza anomala* Pers. var. *poriaeformis* Persoon (1801: 656)
    = *Peziza poriaeformis* (Pers.: Fr.) Fries (1822: 106)
    = *Solenia poriaeformis* (Pers.: Fr.) Fuckel (1872: 301)
    = *Porotheleum poriaeforme* (Pers.: Fr.) W.B. Cooke (1957: 688)

Fruit Bodies 180-250 µm diam., about 300 µm tall, nearly cylindric or goblet-shaped, crowded on a felty subuculum. **Cuticle** externally clothed whith hyaline, glassy hairs, 1.5-3.0 (4.0) µm diam., some with gelatinised walls, and inflated, others thin-walled, irregularly warted and lobed, with fine secretory pegs; coated with large (5-20 µm diam.), pale brown, blocky crystals, that in fact are masses of rhombic crystals 5-12 X 1-3 µm; subiculum also covered with diverticulate hairs and cystalline material. **Trama** dark brown (KOH), densely interwoven, (10) 20-30 (50) µm deep including the poorly-defined subhymenium; hyphae (2) 3-5 µm diam., brown-walled. **Gelatinous Zone** below trama proper, subhyaline and continuous to base and forming a hyaline, gelatinous subiculum 20-50 µm thick. All hyphae, including trama and cuticle, with clamp connections. **Hymenium** subhyaline, 15-20 µm deep. **Basidia** 4-pronged, hyaline, broadly clavate or sphaeropedunculate, (12) 15-18 (22) X 6-8 µm. **Cystidia** confined to rim of cup, clavate or fusoid, diverticulate, hyaline, 12-17 X 3.5-5.0 µm. **Spores** subglobose or globose, hyaline, inamyloid, smooth, (3.0) 3.7-5.5 X (3.0) 3.3-4.5 µm.

Habitat: on rotting hardwoods and rarely conifers, often with a soft brown rot. ***Populus*** was the most frequent host noted, but specimens in TRTC and DAOM included some on ***Acer***, ***Fagus***, ***Quercus***, ***Salix***, ***Tilia***, and burnt conifer.

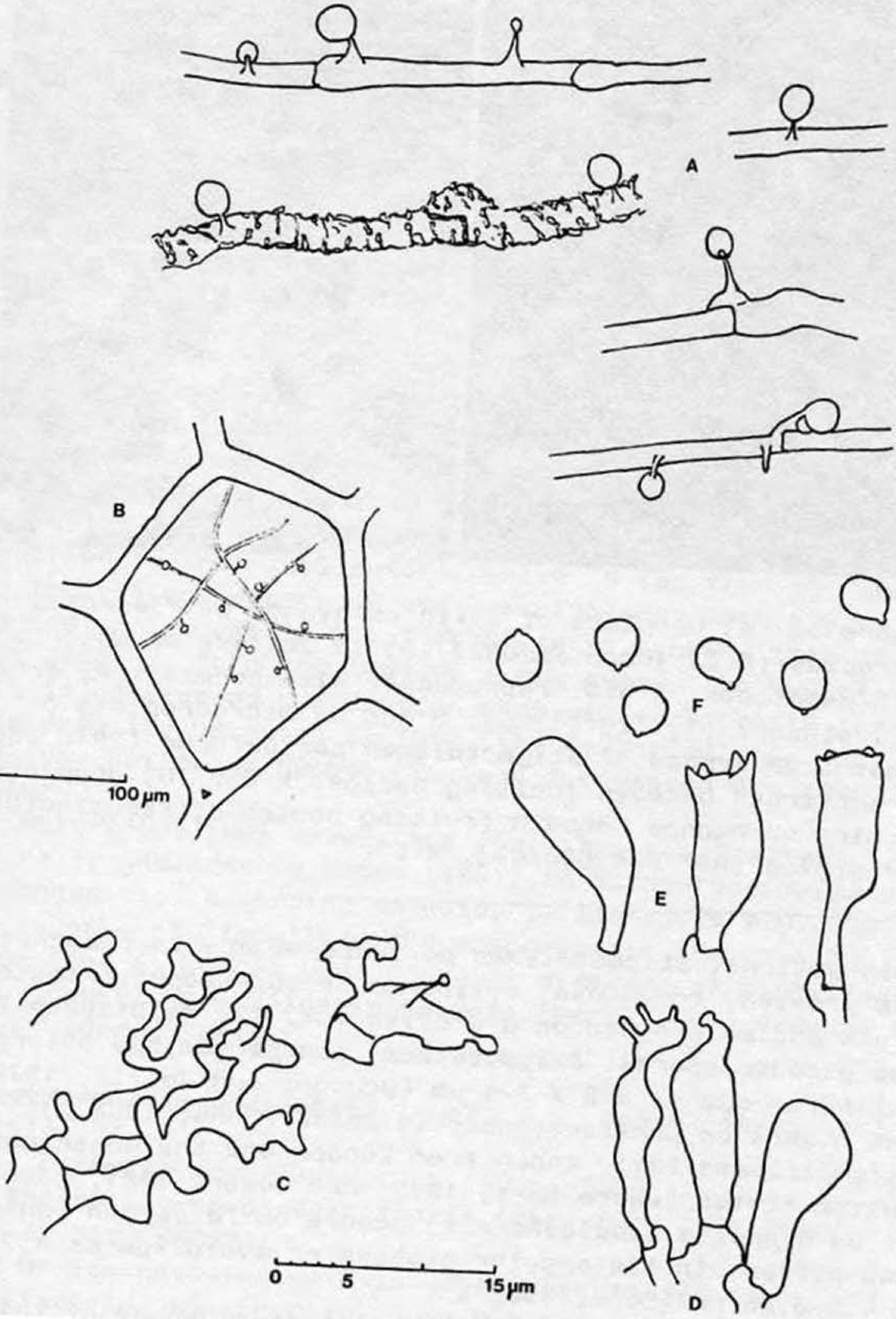
Distribution: Widespread in Europe and North America (Donk, 1962 b) and recorded in New Zealand by Cunningham (1963), who states that it is also found in South America and South Africa.

Specimen Examined: Canada: Ontario: Lot 17, Concession 3 Eramosa Twp. Wellington Co., Sept. 8, 1985, R.G. Thorn #850908/01; Lake Temagami, Kokoko Portage, Sept. 7, 1945, R.F. Cain, TRTC #50198 (part as DAOM #158465); north of Uppsala, Thunder Bay District, Sept. 13, 1944, R.F. Cain, TRTC #20075.

Mating System: Unknown.

Cultural Characters: Unknown in culture, but the following observations were made of hyphae in the substrate that were clearly connected with the basidiocarps of TRTC #50198: **Hyphae** hyaline, smooth or coarsely encrusted, with clamps, 1.5-3.0 µm diam.; with scattered fine, tapering, hyaline pegs 1.0-2.5 (3.0) µm tall by 0.3-0.6 µm at base, tapering to 0.10-0.15 µm at tip; these subtending hyaline droplets (0.8) 2-3 (4) µm diam. Where details of the droplet were visible, the tip of the secretory peg could be seen within the base of the droplet, inflated to about 0.2 µm diam. **Conidia** none seen.

Figure 31 A-F: *Stigmatolemma poriaeforme*, all TRTC #50198 (DAOM #158465). A) Vegetative hyphae with microdroplets; B) section of wood cell beneath fruit bodies, showing arrangement of hyphae and microdroplets; C)diverticulate cuticular hyphae; D) hymenial elements from cup margins (?cheilocystidia); E) basidia and a basidiole; F) basidiospores.


A
B
0
100 µm
F
E
C
0
5
15 µm
D

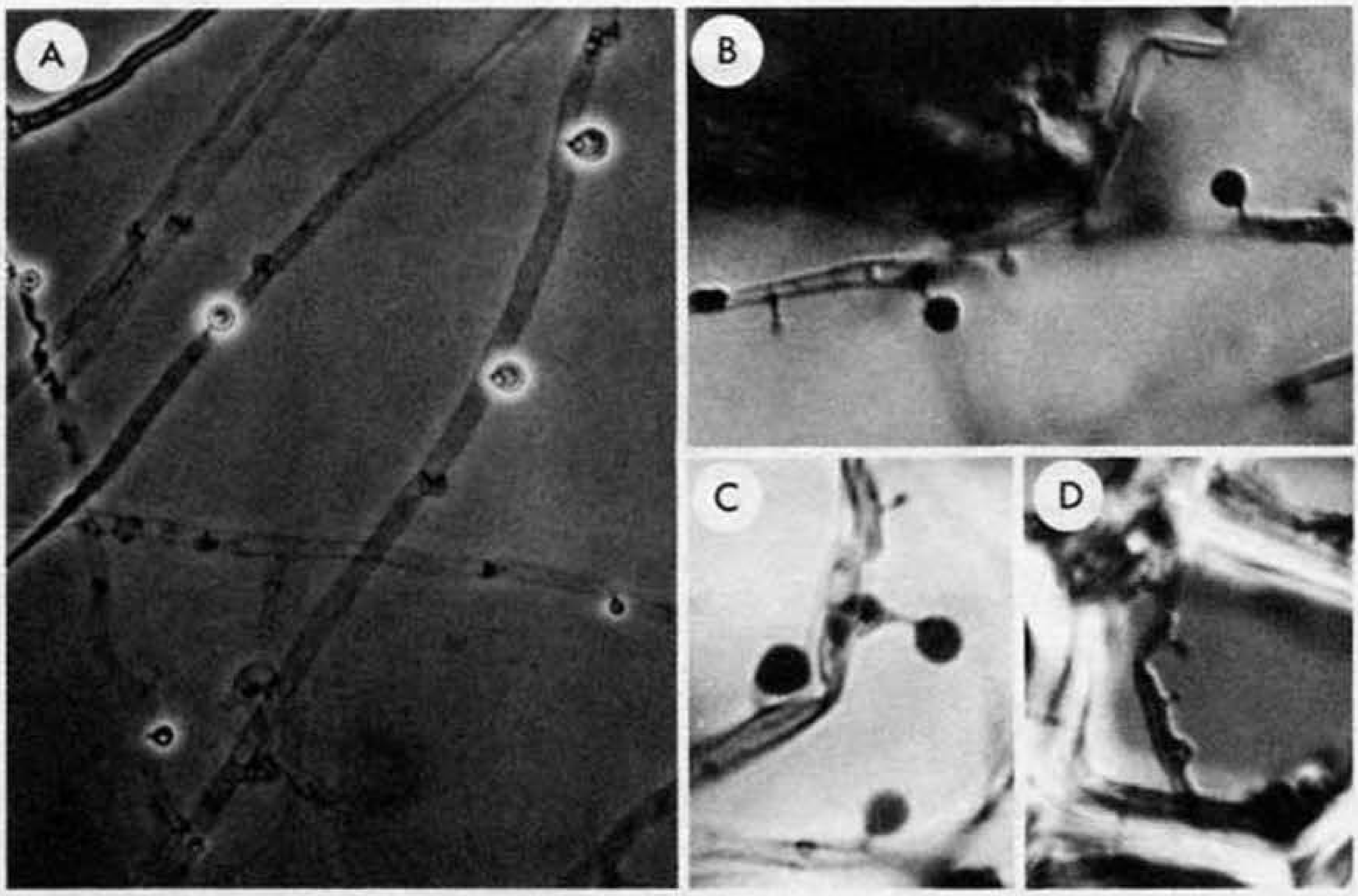


Figure 32. A) Droplets of toxin on hyphae of *Pleurotus ostreatus* (R.G. Thorn #820923/12) in culture on water agar with nematodes, X 550, reproduced, with permission, from McIlvainea 7 (1): 20 (1985); B and C) microdroplets on vegetative hyphae of *Stigmatolemma poriaeforme* (TRTC #50198) in substrate beneath fruiting bodies, X 660; D) droplets forming on hyphae beneath fruiting bodies of *Resupinatus striatulus* (RGT #840808/09), X 500.

Observations: *Stigmatolemma poriaeforme* may be recognised by its greyish, tomentose, cylindric or cup-shaped, minute fruit bodies crowded on a greyish mat, its gelatinous flesh, and globose spores. *Stigmatolemma conspersum* has oblong-cylindric spores 6-9 X 3-4 µm (Bourdot and Galzin, 1928), and occurs on conifers, notably *Abies* (Donk, 1962 b). *Stigmatolemma taxi*, known from Europe and the south-eastern United States (where Burt, 1915, and Coker, 1921, recorded it as *Cyphella cupulaeformis*) occurs on *Taxus* and *Juniperus* and differs in its angular globose or ovoid spores 4.75-5.75 X 4.5-5.25 µm (Donk, 1962 b).

The microdroplets on the vegetative hyphae of this species are of interest, but their role is unknown. These microdroplets greatly resemble those found in cultures of *Pleurotus ostreatus* that immobilise nematodes on contact (Thorn and Barron, 1984; Fig. 32 A). Droplets of similar appearance have been illustrated by Redhead (1973), occurring on the cuticular hyphae of *S. poriaeforme*, and have been found on vegetative hyphae of ***Resupinatus striatulus*** (Fig. 32 D).

STROMATOCYPHELLA W.B. Cooke (1961: 104)

Type species, originally designated: ***S. conglobata*** (Burt) W.B. Cooke.

The following description is based on those by Reid (1963) and Singer (1975): Fruit bodies consisting of small (0.4-1.5 mm diam.) cups crowded on a common, gelatinized mound, sometimes fusing with adjacent cups; hymenium smooth, concave; trama monomitic, strongly gelatinized, all hyphae with clamp connections, inamyloid. Epicutis a tangle of coralloid-diverticulate, often thick-walled hyphae, secreting what becomes crystalline encrusting material. On wood. Presumed not to have a ***Nematoctonus*** asexual state. **Observations**: This monotypic genus is remarkable and distinctive. All specimens examined were correctly identified by their collectors, which is far from the case with the gilled members of the Resupinateae. Burt (1915) remarked that ***Cyphella conglobata*** was so unusual that it might some day form the type of a new genus. The cyphelloid habit is considered a reduction from gilled forms in the genus ***Resupinatus*** sensu stricto. The diverticulate, encrusted cuticular hyphae of these two genera are very similar.

Reid (1963) has shown that the other two species originally included by Cooke (1961) in ***Stromatocyphella*** are not congeneric. According to Reid, ***S. lataensis*** W.B. Cooke is a synonym of ***Flagelloscypha erucaeformis*** (Batsch: Fr.) Singer, and ***S. aceris*** W.B. Cooke is a member of ***Cyphellopsis*** Donk, possibly ***Cyphellopsis anomala*** (Pers.: Fr.) Donk or ***C. confusa*** (Bres.) Reid.

Stromatocyphella conglobata (Burt) W.B. Cooke (1961: 104)

Fig. 33

≡ ***Cyphella conglobata*** Burt (1915: 375)

The following description is taken from TRTC #5452 (part as DAOM #8882):

Fruit Bodies reviving well in water, consisting of approximately hemispherical cups 0.4-1.2 mm diam., densely gregarious on a common stalk, erupting in groups of 5-25 from lenticels in the alder bark. When wet the margins appear glabrous or finely pruinose, a reddish caramel colour (6-7C4); the hymenium similar or paler honey-brown (5B4), smooth and satiny, concave; bases of the cups darker (6-7E5), and more coarsely pruinose to tomentose with brown

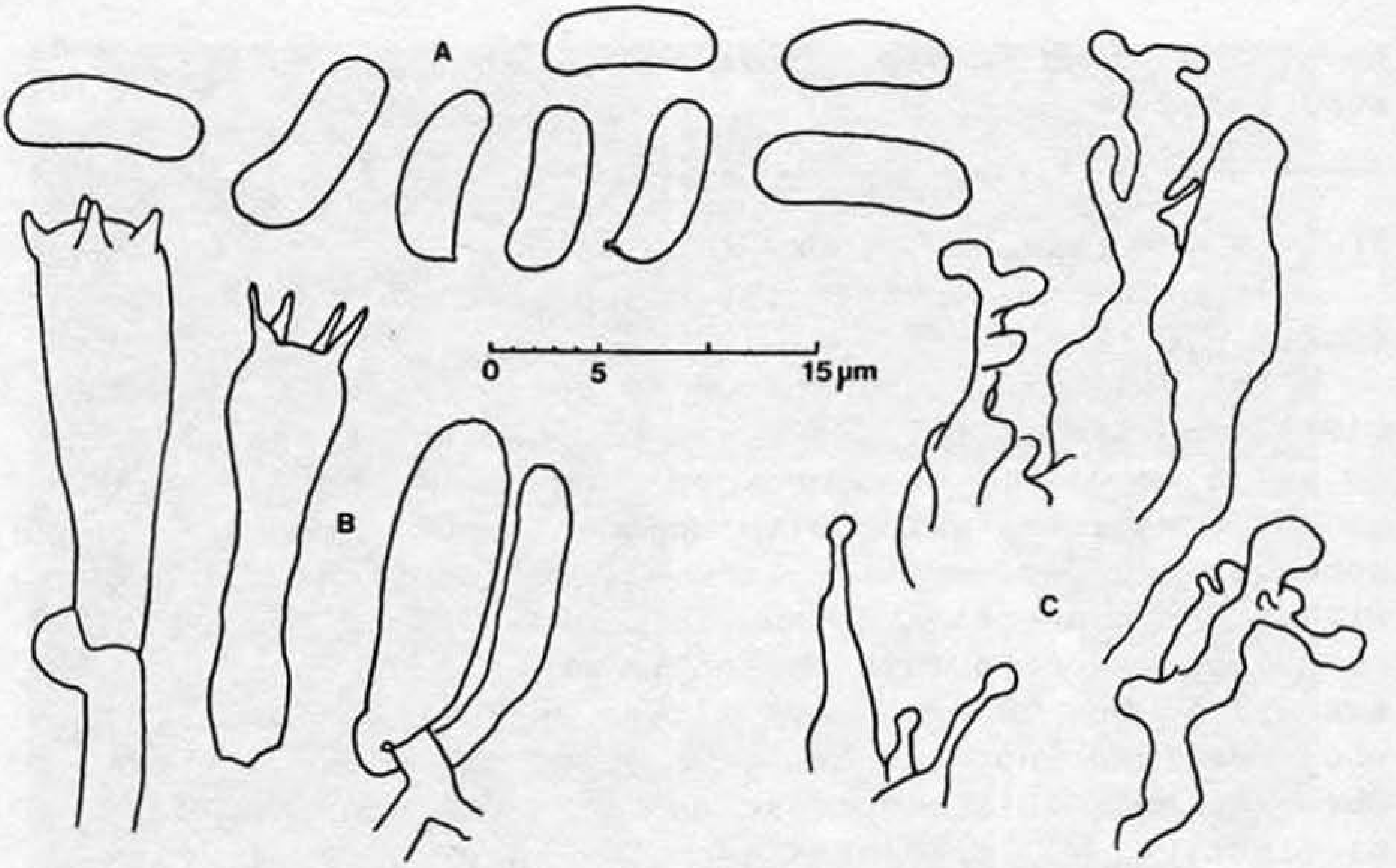


Figure 33 A-C: *Stromatocyphella conglobata*, TRTC #5452. A) Basidiospores of *S. conglobata*; B) two basidia and two basidioles; C) cuticular hyphae.

hairs. On drying the margins roll inward, and whole fruit body becomes silvery (B1), the exterior appearing pruinose to tomentose. **Stroma** subtending cups, subhyaline, more or less conical, strongly gelatinised, hyphae tangled, 1.5-3.0 µm diam. **Cuticle** of cups a pale to dark brown (KOH) zone 25-35 µm deep, of basically parallel, repent hyphae 2-5 µm diam. **Epicutis** a tangled zone of more or less vertical, branching, encrusted brown diverticulate hairs, mostly 2-3 µm diam., with branchlets 0.5-1.0 µm diam.; both hairs and cuticle obscured by dense, brown granular-crystalline encrustations that gradually dissolve in 3% KOH. **Trama** consisting of three zones: an outer, strongly gelatinised zone with hyaline hyphae (1.5) 2.0-4.0 (5) µm diam. tangled, but basically perpendicular to hymenium, 25 µm deep in cup margins to 100 µm deep at their bases, and continuous with stroma; a hyaline zone 25-40 µm deep of hyaline, slightly gelatinised hyphae 1.5-3.0 µm diam., running parallel to hymenium; a pale brown zone continuous with the last, 20-35 µm deep, of radially-arranged, parallel, smooth hyphae 1.5-4 µm diam., not or only slightly gelatinised. **Subhymenium** deep brown in KOH, 25-30 (50) µm deep, slightly to strongly gelatinised, hyphal walls not visible in some areas, those visible rising in a tangle to hymenium, 2-5 µm diam.

Hymenium hyaline, 20-27 µm deep. **Basidia** 4-spored, hyaline, clavate, 23-28 X 6.0-7.5 µm. **Cystidia** not seen. **Spores** hyaline, inamlyoid, smooth, cylindric, dented on one side, or slightly curved, only rarely with a fine, oblique apiculus, (6.0) 8.0-10.0 X 3.0-3.8 µm.
Habitat: On dead hardwood branches, usually of ***Alnus***, but also noted on ***Betula*** and ***Juglans*** (Cooke, 1961).
Distribution: Known only from North America, where it has been recorded in Michigan (Reid, 1963), New Hampshire, New York, and Pennsylvania in the United States and British Columbia, New Brunswick, Ontario and Quebec in Canada (Cooke, 1961).
Specimens Examined: Canada: Ontario: Bell's Lake, north of Parry Sound, Sept. 20-22, 1934, H.S. Jackson, TRTC #5452 (part as DAOM #8882). A total of 6 other collections were seen at TRTC and DAOM, all confirmed and cited by W.B. Cooke.
Mating System and Cultural Characters: Unknown. Neither conidia nor microdroplets were seen on vegetative hyphae in sections beneath fruit bodies.
Observations: ***Stromatocyphella conglobata*** is a distinctive fungus, but is small, inconspicuously coloured, and possibly easily missed. A search of alder thickets during this study failed to reveal this species. ***Stromatocyphella conglobata*** can be recognised by its pendant clusters of cups growing from a gelatinous trunk, protruding from the lenticels or cracks in the bark of dead branches, usually ***Alnus***. The cups are reddish brown when fresh and silvery when dry.

GENERAL CONCLUSIONS

Eight species of ***Nematoctonus***, five of them new, occur in Ontario. An additional new, extralimital species of ***Nematoctonus*** brings the total number of species in the genus to 16. Seven of these have teleomorphs in ***Hohenbuehelia*** (Table 3). Nine species have no known teleomorph, but one may be found in the future for some, such as ***N. concurrens*** and ***N. haptocladus***. It seems unlikely that some other species, such as ***N. leiosporus***, ***N. tylosporus*** and ***N. leptosporus*** will be found to have teleomorphs. These are endoparasitic species that have evolved as nematophagous fungi, even to the extent of host specialisation.

Twelve species of ***Hohenbuehelia*** occur, or are likely to occur, in Ontario. All have ***Nematoctonus*** anamorphs (Table 3). The anamorph of ***H. approximans***, ***H. cyphelliformis***, ***H. atrocaerulea*** var. ***grisea***, and ***H. nigra*** is ***N. robustus***. The anamorph of ***H. petalodes*** and ***H. tremula*** is ***N. geogenius***.

Table 3. Anamorphs and Teleomorphs of *Nematoctonus* and the Resupinateae

Teleomorph	Anamorph
Ontario Species	
Hohenbuehelia angustata	***Nematoctonus angustatus***
H. approximans	***N. robustus***
H. atrocaerulea var. ***grisea***	***N. robustus***
H. cyphelliformis	***N. robustus***
H. mastrucata	***N. hamatus***
H. petalodes	***N. geogenius***
H. pinacearum	***N. brevisporus***
H. tremula	***N. geogenius***
H. unguicularis	***N. brevisporus***
H. sp. (Singer, ined.)*	***N. pachysporus***
None Known	***N. leiosporus***
None Known	***N. leptosporus***
None Known	***N. subreniformis***
Resupinatus applicatus	None
R. striatulus	None
R. trichotis	None
Stigmatolemma poriaeforme	None Known**
Stromatocyphella conglobata	None Known**
Extralimital Species	
Asterotus dealbatus	None known**
H. longipes	***Nematoctonus*** sp.
H. nigra	***N. robustus***
H. portegna	***N. campylosporus***
Hohenbuehelia sp. (stirps Petaloides s. str.)	***Nematoctonus cylindrosporus***
None Known	***N. concurrens***
None Known	***N. haptocladus***
None Known	***N. lignicola*** nom. invalid.
None Known	***N. tripolitanius***
None Known	***N. tylosporus***
Resupinatus alboniger	None

*Teleomorph not known from Ontario

** No cultures available; no signs of ***Nematoctonus*** anamorph in substrate of fruit bodies

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Certain related species of ***Hohenbuehelia*** have anamorphs referrable to the same form-species. This is due in part to the greater number of taxonomic characters available for the classification of the teleomorphs. Connections are made for the first time between twelve species of ***Hohenbuehelia*** and their anamorphs. The anamorph of an additional species of ***Hohenbuehelia***, ***H. longipes***, was illustrated by Kuehner et al. (1962), but has not been isolated since, or identified.

Hohenbuehelia differs from ***Resupinatus*** in several major characters. The most important difference is one of biology: species of ***Hohenbuehelia*** have ***Nematoctonus*** anamorphs that are nematophagous, whereas species of ***Resupinatus*** do not.

Several morphological characters are correlated with this biological distinction. Fruit bodies of *Hohenbuehelia* have hymenial metuloids (sometimes inconspicuous) and gloeosphex cystidia, the apices of which resemble the adhesive knobs in *Nematoctonus*. The cuticle of most species of *Hohenbuehelia* is a cutis of repent, tangled, tubular hyphae. These hyphae may be smooth or pigment-encrusted, but are without conspicuous lobes or branchlets. The cuticle of *Resupinatus* species is a rameales structure composed of branched, knobbed, or spiny hyphae, which often secrete so much crystalline or amorphous encrusting material that these details are obscured. The cheilocystidia of *Resupinatus* are likewise diverticulate and encrusted, and never have the hour-glass secretory cells characteristic of *Hohenbuehelia*. Species of *Resupinatus* lack hymenial metuloids. Nonetheless, the two genera are closely related, and particularly so in *R. alboniger*. This species has elliptical spores like most species of *Hohenbuehelia* (and unlike most other *Resupinatus*), and occasional thick-walled cystidia. These cystidia, however, do not stain in cresyl blue, and are not true metuloids. In addition, *R. alboniger* does not have a *Nematoctonus* anamorph, and is thus not a *Hohenbuehelia*.

Good key characters are available to identify all Ontario species of the Resupinateae (many of which occur worldwide), once discordant elements are weeded out of the species concepts. The classifications of anamorphs and teleomorphs are mutually supporting at the species level, as well as the generic level. Certain related species of *Hohenbuehelia* share anamorphs of the same form-species, yet the distinct anamorph of *H. auriscalpium* (*N. cylindrosporus*) shows that it is distinct from *H. petalodes* (anamorph *N. geogenius*), with which it is often synonymised.

Species of *Resupinatus* may not have *Nematoctonus* anamorphs that consume nematodes, but their biology is completely unresolved. Little is known about *Asterotus*, *Stigmatolemma* and *Stromatocyphella*, except that the morphological evidence indicates that these genera are more related to *Resupinatus* than they are to *Hohenbuehelia*. The nematophagous habit indicates the relationship of the Resupinateae to the genus *Pleurotus*. This is supported by the similar cystidia in *Resupinatus* and *Pleurotus*, the microdroplets of *Resupinatus* and *Stigmatolemma* that are visually identical to those of *Pleurotus*, and the similar spore morphology of *Pleurotus* and the Resupinateae. For these reasons it is suggested that the tribe Resupinateae be classified in the family Polyporaceae (= Pleurotaceae), as has been done by Kuehner (1980), rather than in the

Tricholomataceae (Singer, 1975, and others). Julich (1981) classified ***Hohenbuehelia*** and ***Geopetalum*** (= ***Faerberia***) in the Geopetalaceae of the Polyporales, and ***Resupinatus*** in the Resupinataceae of the Tricholomatales. We believe that ***Hohenbuehelia*** and ***Resupinatus*** are members of the same tribe, and not members of different orders. In addition, ***Faerberia*** appears not to be directly related to the Resupinateae.

Thorn and Barron (1984) suggested that the consumption of nematodes provides species of ***Hohenbuehelia*** with valuable supplementary nitrogen. Species of ***Hohenbuehelia*** occur most commonly on well-rotted wood, or on woody debris in rich sites where there is intense microbial competition for available nitrogen. Since nitrogen limitation probably affects most lignicolous fungi (Thorn and Barron, 1984), it is interesting to wonder how many other such fungi capture and consume nematodes. Of 20 genera of lignicolous agarics and polypores tested (Thorn and Barron, 1984; and unpublished data), only ***Hohenbuehelia*** and ***Pleurotus*** were capable of preying on nematodes.

Although what may be the most interesting questions about the biology of the Resupinateae remain to be answered, these questions are more apparent, and the answers more easily attained, with a clearer understanding of the taxonomy of this group.

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APPENDIX 1: MEDIA AND REAGENTS

Acetic Alcohol: Three parts 95% ethanol: one part glacial acetic acid. **ANT B Agar**: 4 mL of a 0.3% sterile aqueous solution of chlorotetracyclin ("aureomycin" - gives 60 ppm), 2 mL of a 0.3% penicillin-G solution (30 ppm), 2 mL of 0.3% streptomycin solution (30 ppm), and 0.5 mL of a 0.1% solution of technical benomyl in acetone (gives 2.5 ppm), all added aseptically to 200 mL PDA just before pouring plates. **Brilliant Cresyl Blue**: a 0.05 % aqueous solution (w/v) of cresyl blue (B.D.H. Chemicals lot 2982670) **Melzer's Reagent**: 1.5 g KI dissolved in 20 mL water, then 0.5 g iodine and 22 g chloral hydrate added. **Nigon's Agar**: 0.75 g magnesium sulphate, 0.75 g dipotassium hydrogen phosphate, 2.75 g NaCl, 3.0 g potassium nitrate, 2.5 g peptone, 1.0 g lecithin, 15 g agar, all added to 1 L distilled water. **PDA** (potato dextrose agar): 200 g potatoes sliced and cooked in 500 mL distilled water for 1 h; the cooking water strained through cheesecloth and brought to 1 L with distilled water; plus 12 g dextrose and 20 g agar; autoclaved in 200 mL medicine bottles. **PD + AB Agar**: 4 mL of a 0.3 % sterile aqueous solution of chlorotetracycline ("aureomycin" - gives 60 ppm) and 0.5 mL of a 0.1% solution of technical benomyl in acetone (gives 2.5 ppm) added aseptically to 200 mL PDA just before pouring plates. **PVLG**: 50 mL of a 20% w/v aqueous solution of Sigma polyvinyl alcohol type II, with a viscosity of 20-30 centipoises at 20 degrees C, mixed with 50 mL 85% lactic acid and 5 mL glycerin (modified from Koske and Tessier, 1983). **Saline**: 0.85 % w/v solution of NaCl in distilled water. **Trypan Blue**: 0.05% w/v solution of trypan blue (Allied Chemical lot 12652) in a 14:1:1 mix of 85% lactic acid: glycerin: water. **WA** (water agar): 20 g Difco Bacto agar per litre distilled water.

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New Species Dekkera custersiana and D. lambica, Teleomorphs of Brettanomyces

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Summary

Dekkera custersiana sp. nov. and D. lambica sp. nov. are described to accommodate the perfect states (teleomorphs) of Brettanomyces custersianus van der Walt and B. lambicus Kufferath et van Laer, respectively. Ascospore formation is best observed in cultures at room temperature after one week on the vitamin-enriched Endothia complete medium (ATCC medium 686) with a pH of 4.5.

The teleomorphs or ascogenous states of Brettanomyces Kufferath et van Laer are now classified in the genus Dekkera van der Walt (3,4,5,10,11). In our authentication of the yeast strains maintained in the American Type Culture Collection (ATCC), the type cultures of Brettanomyces custersianus van der Walt ATCC 34446 and B. lambicus Kufferath et van Laer ATCC 10563 were found for the first time to produce hat-shaped ascospores on ATCC medium 686 (2), referred to as Endothia medium (6), supplemented with a vitamin solution (12). Therefore we describe the two yeasts as new species of Dekkera van der Walt (8).

Dekkera custersiana Lee et Jong, sp. nov.

Stat. Anamorphosis: Brettanomyces custersianus van der Walt, 1961.

In extracto malti post 5, 25°C, cellulae ellipsoidae, saepe ogivales, cylindricae elongataeque, 1.5-4 X 3-17μm, singulae, binae aut in catenatae. Cellulae longae pseudomycelii formatur. Sedimentum et annulus imperfectus formatur. Cultura acclivis, superficie limitata, sordida alba et nitida, verrucosa aut crispulata. Margine globro, structuris aut lobiformo. Asci e cellulis dipoidis transformatis oriuntur. Ascosporae pilleiformae ad 4 in quoque asco formantur. Ascosporae maturae ex ascis celeriter liberantur et inter se aggutinantur. Fermentatio, crescentia in variis substantiis carbonaceis et alliae naturae monstrantur in Tabula 1.

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Typus: ATCC 34446 in collectione American Type Culture Collection, Rockville, Maryland, USA.

Growth in malt extract: After 5 days at 25°C the cells are ellipsoidal, frequently ogival, cylindrical to elongate, 1.5-3 X 3-17 µm, reproducing by budding and occurring singly, in pairs or short chains. Pseudomycelium is abundantly formed. A floccose sediment is produced. Islets or a thin pellicle are usually formed. After 10 days at room temperature a thin pellicle is present. Occasionally an incomplete ring is formed. There is a slight production of a characterisitic aroma.

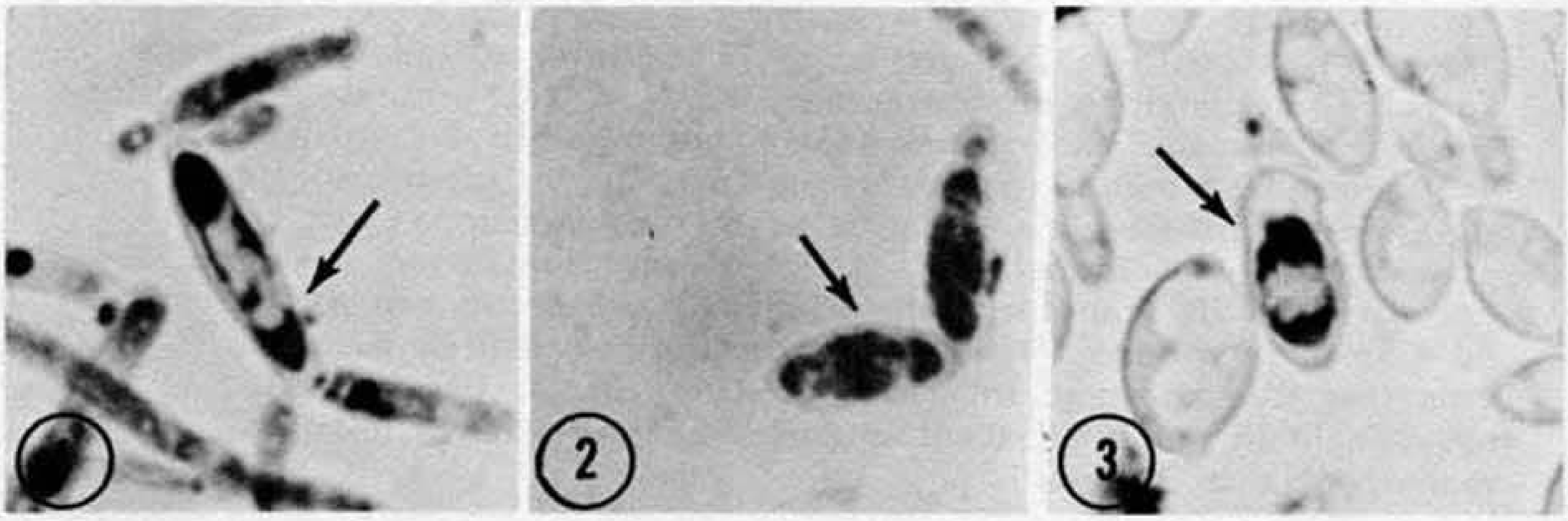
Growth on malt agar: After 6 weeks at room temperature the streak culture is raised, cream-colored to light brown, shiny to somewhat dull, smooth to verrucose. The margin is undulating to lobiform.

Growth on malt agar with 2% calcium carbonate: After 6 weeks at room temperature the streak culture is raised, cream-colored to light brown, shiny to dull, verrucose or rugose. The margin is undulating to lobiform. Acid production is slight.

Dalmau plate culture on corn meal agar: Pseudomycelium is abundantly produced. It consists of filamentous cells with few or no blastospores. Under anerobic conditions, the filamentous cells bear blastospores abundantly.

Physiological characteristics: Fermentation and growth on various carbon compounds, growth on nitrogen sources and some additional properties are summarized in Table 1.

Formation of ascospores: Vegetative cells are transformed directly into unconjugated evanescent asci, producing one to four ascospores. The ascospores are hat-shaped and can be stained with the modified Schaeffer-Fuller malachite green or Ziehl Neelsen's carbol fuchsin (Figs 1 & 2). Mature ascospores tend to agglutinate when liberated. Ascospore formation is observed in cultures at room temperature after one week on *Endothia* complete medium supplemented with vitamins.



Figs. 1-3. Asci and ascospores of *Dekkera custersiana* and *D. lambica*, stained with modified Schaeffer-Fuller malachite green. *ca.* X 2,000. 1. ATCC 34446 (Type). 2. ATCC 24195. 3. ATCC 10563 (Type).

Brettanomyces custersianus was first described from thirty strains recovered from contaminated equipment in sorghum beer breweries (7). Ascospore formation was not observed in any of the individual strains or in any matings of these strains. One of the strains, CBS 4805 (=ATCC 34446), was designated later as the type culture by van der Walt (9). In the present study, ATCC 34446 and ATCC 24195 have been found to produce ascospores on vitamin-enriched media with a pH of 4-5. Therefore, the new species *Dekkera custersiana* Lee et Jong is the perfect state (teleomorph) of *B. custersianus* and ATCC 34446 is designated as the type.

The new species differs from all the presently accepted species of *Dekkera* and *Brettanomyces* by its very limited physiological activity (10,11). Morphologically it is allied to *B. anomalus* Custers because of its marked filamentous nature. It has a coenzyme Q-9 system (13) and 38.9-39.3 mol % of guanine plus cytosine (G + C) of nuclear DNA (1).

Dekkera lambica Lee et Jong, sp. nov.

Stat. Anamorphosis: *Brettanomyces lambicus* Kufferath et van Laer,
1921.

In extracto malt post dis 5, 25°C, cellulae rotundae, ovoidae, saepe ogivales, cylindricae elongataeque, 2-7 X 4-28µm, singulare, binae aut in catenatae. Cellulae longae pseudomycelii formantur. Sedimentum et annulus formatur. Odor culturae insignitis. Asci e cellulis dipoidis transformatis oriuntur. Ascosporae maturae ex ascis celeriter liberantur et inter se agglutinantur. Fermentatio, cresentia in variis substantiis carbonaceis et alliae naturae monstrantur in Tabula 1.

Typus: ATCC 10563 in collectione American Type Culture Collection, Rockville, Maryland, USA.

Growth in malt extract: After 5 days at 25°C the cells are spheroidal, usually ellipsoidal, frequently ogival, cylindrical to elongate, 2-7 X 4-28µm, reproducing by budding and occurring singly, in pairs, short chains or small clusters. Pseudomycelium is usually present. A sediment is formed. After 10 days at room temperature a flocculent to coherent sediment is present. A slight ring may also be present. A characteristic aroma is usually produced.

Growth on malt agar: After 6 weeks at room temperature the streak culture is cream-colored, shiny, smooth to granular and raised. The margin is entire to undulating.

Growth on malt agar with 2% calcium carbonate: After 6 weeks at room temperature the streak culture is cream-colored, shiny, smooth. The margin is undulating. Acid is produced.

Dalmau plate culture on corn meal agar: Pseudomycelium is abundantly formed both aerobically and anaerobically. It consists of filamentous cells with or without blastospores. The blastospores may be arranged in chain or in somewhat branched verticils.

Physiological characteristics: Fermentation and growth on various carbon compounds, growth on nitrogen sources and some additional properties are summarized in Table 1.

Table 1. Physiological Test Results

	D. custersiana		D. lambica
	ATCC 24195	ATCC 34446	ATCC 10563
Growth in vitamin-free medium	-	-	-
Growth at 37°C	+	+	+
Splitting of arbutin	-	-	-
Urea hydrolysis	-	-	-
Diazomium blue B reaction	-	-	-
Acetic acid production	+	+	+
Starch formation	-	-	-
Fermentation of:			
Glucose	D	D	+
Galactose	-	-	-
Maltose	-	-	+
Sucrose	-	-	+
Lactose	-	-	-
Raffinose	-	-	-
Melibiose	-	-	-
Inulin	-	-	-
Cellobiose	-	-	-
Melezitose	-	-	+
Starch	-	-	-
Trehalose	D	D	+
α-Methyl-D-glucoside	-	-	+
Assimilation of:			
Glucose	+	+	+
Galactose	-	-	D
L-Sorbose	-	-	-
Maltose	-	-	+
Sucrose	-	-	+
Cellobiose	-	-	-
Trehalose	D	D	+
Lactose	-	-	-
Melibiose	-	-	-
Raffinose	-	-	-
Melezitose	-	-	+
Inulin	-	-	-
Soluble starch	-	-	-
D-Xylose	-	-	-
L-Arabinose	-	-	-
D-Arabinose	-	-	-
D-Ribose	-	-	-
L-Rhamnose	-	-	-
D-Glucosamine	-	-	-
Ethanol	+	+	D
Methanol	-	-	-
Erythritol	-	-	-

Table 1 (continued)

	D. custersiana		D. lambica
	ATCC 24195	ATCC 34446	ATCC 10563
Glycerol	D	D	D
Adonitol	-	-	-
Dulcitol	-	-	-
D-Mannitol	-	-	-
D-Sorbitol	-	-	-
α-Methyl-D-glucoside	-	-	+
Salicin	-	-	-
Inositol	-	-	-
Lactic acid	+	+	-
Citric acid	-	-	-
Succinic acid	+	+	-
Valine	-	-	-
Glycine	-	-	-
Proline	-	-	-
Arginine	-	-	-
KNO_3	-	-	-
NO_2	-	-	-
Ethylamine	-	-	-

Code in Table: (+) positive; (-) negative; (D) delayed for longer than 7 days

Formation of ascospores: Vegetative cells are transformed directly into asci, producing one to four ascospores. The spores are hat-shaped and can be stained with the modified Schaeffer-Fuller malachite green or Ziehl Neelsen's carbol fuchsin (Fig. 3). Mature ascospores tend to agglutinate when liberated. The occurrence of ascospore formation in the cultures of ATCC 10563 depends greatly on media which have been adequately enriched with vitamins. Sporulation is best observed in cultures at room temperature after one week on the Endothia complete medium (ATCC medium 686) supplemented with vitamins.

Brettanomyces lambicus Kufferath et van Laer has been recovered from Belgian lambic beer and South African grape must (11). Since the designated type culture ATCC 10563 which was originally isolated by M. Th. J. Custers in 1940 from lambic beer is the type of B. lambicus, the new species Dekkera lambica Lee et Jong is the perfect state (teleomorph) of B. lambicus. As in all the presently accepted species of Dekkera and Brettanomyces, D. lambica has a coenzyme Q-9 system (13). The G & C content of the nuclear DNA of this species is 38.7 mol % (1).

Physiologically D. lambica occupies an intermediate position between D. bruxellensis and D. intermedia. It differs from D. bruxellensis in that it assimilates galactose albeit slowly. On the other hand, D. lambica is distinguished from D. intermedia by the absence of cellobiose and salicin utilization and by not splitting arbutin (10,11).

We acknowledge with appreciation the critical review of the manuscript by Mary Jane Gantt. The work was supported in part by the National Science Foundation Grants DEB 7921031 and BSR 8413523 and by the National Institutes of Health Contract N01-OD-5-2117.

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MYCOTAXON

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STUDIES IN THE GENUS *PHOMA*. V. CONCERNING *PHOMA POMORUM*.

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ABSTRACT

Phoma pomorum Thümen [*Phoma prunicola* (Opiz) Wollenw. et Hochapf.] is described and illustrated. Its cultural characteristics and the structure of its pycnidial wall are documented.

INTRODUCTION

During a study of *Phoma americana* Morgan-Jones et White, which formed the subject of the first paper in this series (Morgan-Jones and White, 1983), we had occasion to compare it with *Phoma pomorum* Thümen, the species which it most closely resembles. Both belong to a small group of species which readily produce phaeodictyochlamydospores *in vitro*. All told, some seven species of *Phoma* bear chlamydospores but, as previously pointed out (White and Morgan-Jones, 1983), they are by no means easy to distinguish from one another with the singular exception of *Phoma epicoccina* Punithalingam, Tulloch et Leach, to whose chlamydospore state the binomial *Epicoccum purpurascens* Ehrenb. has long been applied. To facilitate confident and correct identification of *Phoma pomorum*, a comprehensive account of its characteristics is offered here. An attempt has been made to add further diagnostic criteria to those already in part documented (Boerema *et al.*, 1965; Morgan-Jones, 1967). These include colony growth rates and appearance, together with particulars of pycnidial wall organization.

Phoma pomorum is ubiquitous on many different substrates and is cosmopolitan in distribution. It appears to be more common in regions having temperate climates and is frequently present as a secondary invader on leaf spots of apple, pear and plum (Crabhill, 1913; Wollenweber and Hochapfel, 1936; Boerema and Dorenbosch, 1965). It is also known to occur with regularity on seed coats of a wide variety of plants (Leduc, 1958).

This fungus has had a rather complicated nomenclatural history, numerous names having been applied to it (Boerema *et al.*, 1977). Over the years, the binomial *Phoma prunicola* (Opiz) Wollenw. et Hochapfl. has predominated (see Morgan-Jones, 1967). However, although application of the

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specific epithet *prunicola* predates that of *pomorum* by more than twenty years, it cannot be adopted since the binomial is a later homonym of *Phoma prunicola* Schweinitz, a different fungus [a species of *Asteromella* Pass. et Thüm.]. It should also be noted that the basionym *Depazea prunicola* Opiz, the type material of which is extant, is a *nomen nudum*, having been published without a description. Another older binomial than *Phoma pomorum* also exists for this fungus, namely *Phyllosticta pyrina* Sacc. Transfer of this to *Phoma* Sacc., would, however, create yet another illegitimate homonym [of *Phoma pyrina* (Fr.) Cooke, a synonym of *Myxofusicoccum mali* (Bres.) Weindlmayr].

TAXONOMIC PART

Phoma pomorum Thümen, Fungi Pomicoli: 105, 1879 (Plate 1, figure 1)

= *Depazea prunicola* Opiz, Malá Encyclop. Nauk. Náklad. česk. Mus. 10: 120, 1852.

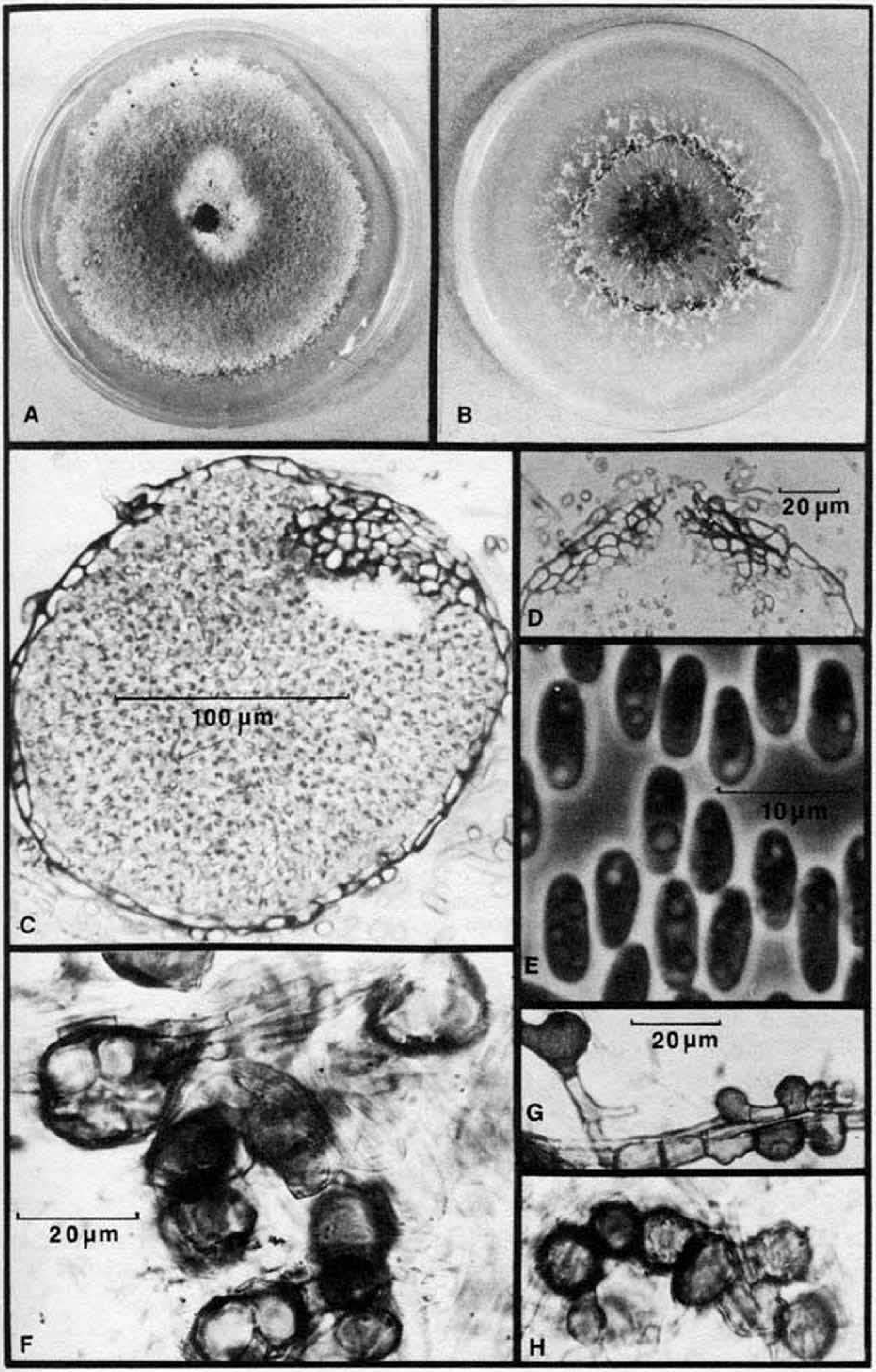
≡ *Phoma prunicola* (Opiz) Wollenw. et Hochapf., Z. Parasitkde 8: 595, 1936 [non *Phoma prunicola* Schweinitz, Trans. Am. phil. Soc. II, 4: 249, 1832].

= *Phyllosticta pyrina* Saccardo, Michelia 1: 134, 1878.

[For full synonymy see Boerema *et al.*, 1965, 1971, 1973, 1977]

Colonies on potato dextrose agar [Difco] (Plate 1, A) lanose to somewhat felty, smoky gray to olivaceous green, remaining whitish at the center and with a pale, more or less even margin, aerial mycelium abundant, attaining a diameter of 65mm at 20C after 6 days, 75mm at 25C and 25mm at 30C; reverse brownish to blackish underneath olivaceous green portions of colony, cream-colored eleswhere. Colonies on malt extract agar (Plate 1, B) densely caespitose and dark olivaceous green at the center, sparse elsewhere, salmony to whitish, with radiating, appressed, fasciculate strands of hyphae and a loose concentric ring of ascending, white hyphal tufts peripherally, attaining a diameter of 55mm at 20C after 6 days, 75mm at 25C and 25mm at 30C; reverse olivaceous green in center, colorless eleswhere. Pycnidia produced abundantly on both PDA and MEA after ten days, superficial or partly immersed in the agar. Colonies on cellulose agar with very little aerial mycelium but producing abundant pycnidia superficially after two weeks. Mycelium composed of septate, branched, subhyaline to pale brown, smooth or very slightly roughened, 2-5µm wide hyphae which are sometimes arranged in funiculose strands, especially on MEA. Pycnidia solitary or frequently confluent, subglobose, without a pronounced neck, pale to dark brown, darker in the immediate vicinity of the ostiole, pseudoparenchymatous, uni or biostiolate, glabrous, 75-175µm in diameter where solitary (Plate 1, C & D; Figure 1, A); where confluent the pycnidial group can reach up to 400µm in diameter and contain as many as ten individual units. Pycnidial wall composed of more or less isodiametric or elongated cells, in two

PLATE 1. *Phoma pomorum*. A, two-week-old colony on potato dextrose agar; B, two-week-old colony on malt extract agar; C, vertical section of pycnidium; D, vertical section through pycnidial ostiole; E, conidia; F-H, chlamydospores.


A
B
C
100 µm
D
20 µm
E
10 µm
F
20 µm
G
20 µm
H

discernible layers, up to 22µm wide, thicker around ostiole (Plate 1, D). Wall four to five cells deep except in the vicinity of the ostiole where there may be as many as seven. Cells around the ostiole mostly isodiametric and angular, 2-4µm wide, the remainder of the superficial wall cells somewhat cylindrical, 5-8 X 2-4µm. Cells of outer wall layer appreciably thicker-walled than those lining the pycnidial venter (Figure 1, C). Conidiogenous cells phialidic, hyaline, simple, smooth-walled, flask-shaped, 3-4µm in diameter, lining the entire inner wall surface up to the ostiolar region. Conidia hyaline, simple, oblong with obtuse ends or narrowly ellipsoid, continuous, guttulate (frequently having one large guttule and several slightly smaller ones), 5-8 X 2-3µm. Exuded conidial mass whitish to cream in color. Chlamydospores highly variable, produced abundantly on PDA and MEA, terminal and intercalary, single or in chains, subglobose, ellipsoid or clavate, simple, phragmosporous or dictyosporous, where simple (unicellular) mostly in chains of up to twenty elements, occasionally produced as unilateral inflations of intercalary hyphal cells (Plate 1, G), thick-walled, roughened or, more rarely, smooth, sometimes having a slightly scurfy appearance, pale brown to brown, where dictyosporous (Plate 1, F) occasionally appearing to have discrete individual cell wall layers within an outer enveloping one, 10-30µm in diameter.

Ubiquitous and cosmopolitan.

Collection examined: on *Polygonum tataricum* L., The Netherlands, 1964, G.H. Boerema, CBS 539.66, IMI 122266, ATCC 16791.

As with other *Phoma* species described thus far in this series of papers, a combination of characters serve to easily distinguish *P. pomorum*. Of particular importance are colony appearance on malt extract agar, the absence of a pycnidial neck, the configuration and shape of pycnidial wall cells and details of chlamydospore morphology. The chlamydospores bear some similarity to those of *Phoma sorghina* (Sacc.) Boerema, Dorenbosch et van Kesteren (see White and Morgan-Jones, 1983), but the two species are distinctly different in other features, notably colony color and appearance, and the presence of long pycnidial necks and inflated pycnidial wall cells in *P. sorghina*. Dictyochlamydospores of *P. americana* are different from those of *P. pomorum* in being generally thinner-walled and less pigmented. The colony characteristics of the two species on malt extract agar are widely different. Some chlamydospores produced by *P. pomorum* may somewhat resemble those of *Phoma glomerata* (Corda) Wollenw. et Hochapf. but the possession of chains of dictyochlamydospores which have a similar appearance to chains of *Alternaria* conidia by the latter serves to distinguish the two species.

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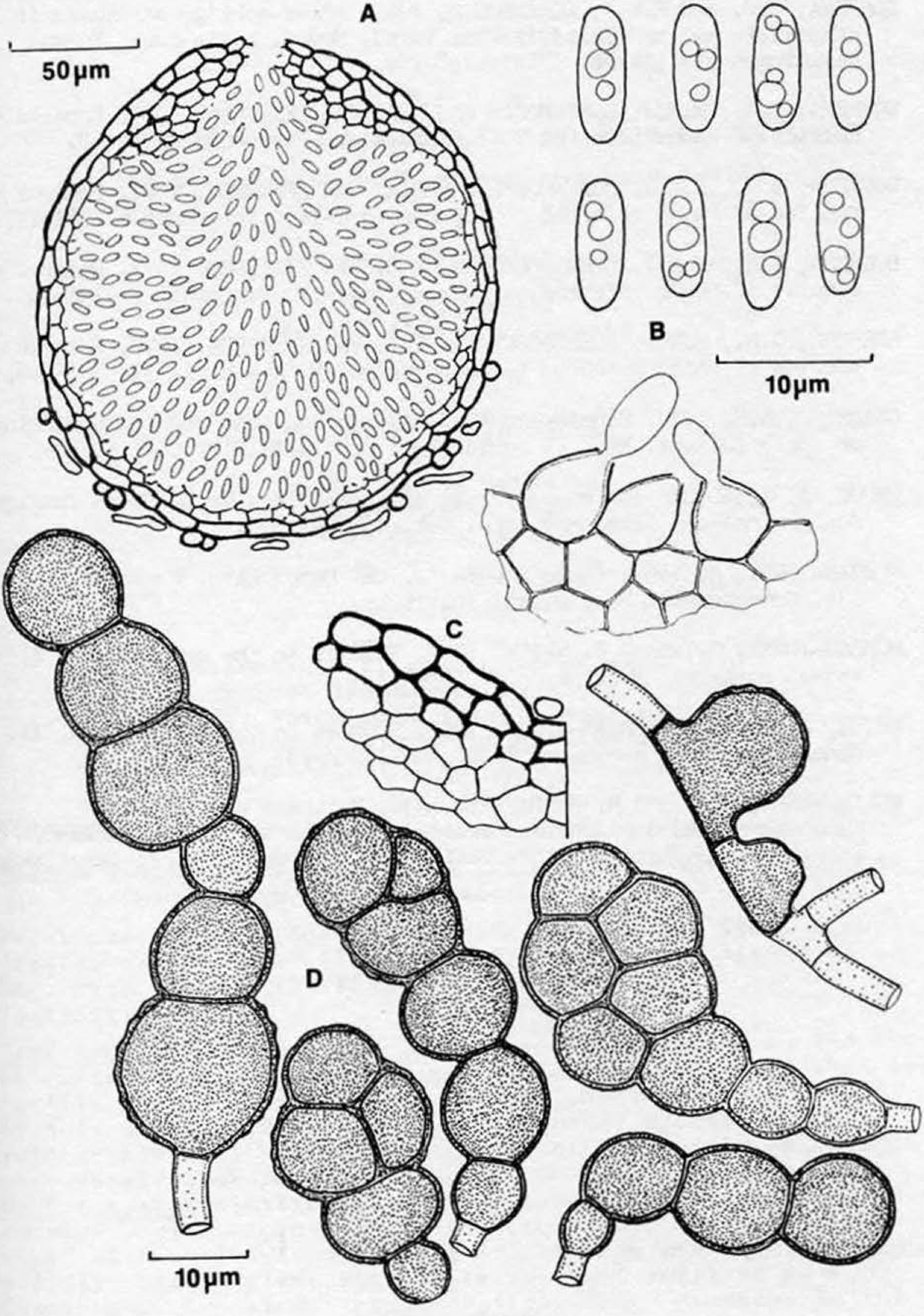
We thank Dr. Richard T. Hanlin, Department of Plant Pathology, University of Georgia, Athens, for reviewing the manuscript.

FIGURE 1. A, vertical section of pycnidium; B, conidiophores and conidia; C, section through pycnidial wall cells in the vicinity of ostiole; D chlamydospores.


A
50µm
B
10µm
C
D
10µm

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STUDIES IN
TROPICAL CORTICIACEAE (BASIDIOMYCETES) VI
A new species of Steccherinum from Brazil

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Abstract

Steccherinum subochraceum is described to replace Irpex hydneus Rick ex Rambo (1959) which is a illegitimate name because the holotype was omitted in the original description.

STECCHERINUM SUBOCHRACEUM Bononi & Hjortst. spec. nov.

Species S. ochraceo affinis et valde similis sed differt sporis globosis 3.5(-4) um in diam. vel subglobosis 3.2-3.5 x 3.8-4 um.

Holotypus: Brazil. Sao Paulo State, Sao Paulo, State Park, "Fontes do Ipiranga" (Instituto de Botánica). 1966-10-06. Leg. Hugo Requejo (SP 97591).
Isotypus: (GB).

Fruitbody effuse, adnate or with revolute margin, in the type reflexed with the margin and subiculum much paler than the fertile aculeal part, margin 2-4 mm, smooth to more commonly byssoid or fimbriate. Hymenium distinctly odontioid, pale salmon-coloured, aculei conical, smooth, subulate, simple to more rarely crowded, about 4-5 per mm and 1-2(-3) mm long. Hyphal system dimitic, generative hyphae thin-walled, 2-2.5 um wide , with clamps, in the aculeal trama interwoven and mixed with skeletals which are 4-5 um wide and lacking clamps, solidly thick-walled, with walls somewhat swelling in KOH. Cystidia of two kinds; pseudocystidia often numerous in the aculei, rare or lacking in the subiculum, strongly encrusted as much as 10-20 um in the apical part, blunt to more rarely conical, hymenial cystidia in varying numbers, but especially common in the middle part of the aculei, 30-40 um long, subconical and apically strongly encrusted, with a basal clamp. Basidia subclavate, slightly sinuous, 20-35 x 4.5-5 um, with four sterigmata and a basal clamp. Spores globose to more rarely subglobose, thin-walled, smooth, 3.5(-4) um in diam. or when subglobose about 3-3.5 x 3.5-4 um.

Remarks. Rambo (1959) described Irpex hydneus Rick but unfortunately the type specimen was not mentioned, consequently the name is illegitimate (Art.37). Geesteranus (1974) made a formal combination to Steccherinum and referred as holotype No. 22824 Brazil. Sao Salvador. 1945-04-04. J. Rick (PACA). A part of this specimen was found in SP and studied by us and shows the same characteristics as SP 97591. The latter is used as an holotype because it is much better preserved and is a relatively large specimen. A third specimen (SP 128128) from Sao Paulo, Cantareira is probably the same but no spores were found.
S. subochraceum is macroscopically similar to S. ochraceum (Pers.:Fr.) S.F. Gray. However, the spore-morphology is distinctive and together with the hymenial cystidia, which are absent in S. ochraceum, it will be sufficient to separate the two taxa. For comparison see Eriksson & al. 1984.

Acknowledgment

We thank Dr. Leif Ryvarden, University of Oslo, for his critical review of the manuscript.

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TAXONOMY OF THE **FOMITOPSIS ROSEA** COMPLEX (APHYLLOPHORALES; POLYPORACEAE)

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SUMMARY

The species of **Fomitopsis rosea** complex comprise a group of fungi distributed worldwide, with some species more adapted to temperate regions and others to tropical ones. The new combination **Fomitopsis cupreo-rosea** is proposed. Therefore, seven species are included in this complex: **F. cajanderi, F. carnea, F. cupreo-rosea, F. dochmia, F. feei, F. lilacino-gilva,** and **F. rosea.** They share the following characteristics: rose-colored context, at least when young; annual or perennial basidiocarp; trimitic hyphal system; hyaline, smooth-walled, cylindric to allantoid spores; no special structures in the hymenium (with exception of cystidioles reported for **F. cajanderi** and **F. dochmia**); and brown rot type of decay.

Members of the **Fomitopsis rosea** complex are of economic importance due to the decay losses they cause in living and dead trees and/or in wood in service. Tropical species are commonly found on hardwoods, especially dead trees or wood in service. Temperate species occur more commonly on conifers, in living or dead trees and wood in service. They all cause brown rots.

The classification of these fungi has been controversial and they have been placed in at least 4 different genera. The first classifications were based mainly on macroscopic characters of the basidiocarps and geographical distribution. Murrill (1908, 1915) recognized some of these fungi in the genus **Fomes** (Fr.) Kickx. These included **F. roseus** (Alb. & Schw.: Fr.) Cke., **F. sagraeanus** (Mont.) Murr., and **F. subferreus** Murr. **Fomes carneus** Cke. was considered by him to be a synonym of **F. roseus,** and he listed **Polyporus feei** Fr. as a questionable synonym of **Coriolus brachypus** (Lev.) Murr. Overholts (1914, 1921), making increased use of microscopic characters, pointed out the differences between **F. roseus** and **F. carneus** (**Trametes carnea** Blume & Nees), and stated that the two were so distinct that they must be regarded as separate species.

The confusion between **F. roseus** from North America and **T. carnea** described from Java remained until Weir (1923) clearly established the difference between them. To correct Berkeley's misuse of the name **Polyporus carneus** Fr. for a North American species in 1872, Weir renamed this taxon as **Trametes subrosea** (1923). **T. carnea** is considered in his paper as a synonym of **Polyporus rubidus** Berk. The similarity between basidiocarps of **T. subrosea** and **Trametes feei** (Fr.) Pat. is pointed out in his paper, but he noted that they can be distinguished based on characters of the pileus, size and shape of

University of Arizona Agricultural Exp. Sta. Journal Article 4140.

spores, the substrata and decay characteristics.

Further studies based on cultural characteristics confirmed the separation of **F. roseus** and **T. subrosea** as distinct species. Snell, Hutchinson and Newton (1928) carried out temperature studies with various isolates of the two fungi, and reported an optimum of 30 C for **T. subrosea** and 26-28 C for **F. roseus.** Included also in this study was **T. feei** with an optimum of 28 C. They also studied the moisture requirements for the two fungi, and reported that **F. roseus** is more commonly found in drier substrates than **T. subrosea.** Mounce and Macrae (1937) carried out studies on sexuality of the two species. They found that monokaryons of the two species were not interfertile, and concluded that they can be positively considered different species. Nobles (1948) noted that **F. subroseus** produced chlamydospores in culture, but **F. roseus** did not. Overholts (1933) transferred **T. subrosea** to the genus **Fomes** and in his paper on Polyporaceae of Pennsylvania (1935) stressed the differences between **F. subroseus** and **F. roseus.** Bondartsev and Singer (1941) transferred **F. subroseus** and **F. roseus** to the genus **Fomitopsis** Karst.

Complete descriptions of **Fomes subroseus** and **Fomes roseus** are given by Baxter (1951) and Overholts (1953). Included in Baxter's paper are descriptions of **T. feei, T. sagraeana** Mont, **T. cupreo-rosea** (Berk.) Lloyd, and **T. lilacino-gilva** (Berk.) Lloyd. **T. cupreo-rosea** and **T. lilacino-gilva** were originally described by Berkeley in 1856 and 1839 respectively, under the genus **Polyporus** Mich.:Fr. and redescribed by Lloyd in 1915 in his Synopsis of the genus **Fomes** under the genus **Trametes** Fr. Lowe (1955), in his descriptions of temperate and tropical species of **Fomes** with context white to rose, included **F. subferreus,** which he placed in synonymy with **F. dochmius** (Berk. & Br.) Cke., **F. feei** (previously **Polyporus feei** Fr.), **F. roseus, F. sagraeanus,** and **F. subroseus.** He considered that these fungi formed a rather homogeneous group, separated from each other by the size of the pores, shape of spores, and the macromorphology of the basidiocarp. In his type studies of polypores described by Karsten (1956) and in his monograph of the genus **Fomes** (1957, Section IV), Lowe placed **F. subroseus** in synonymy with **F. cajanderi** Karst. Three other species, **F. fraxineus** (Bull.:Fr.) Cke., **F. rubritinctus** Murr., and **F. hemileucus** (Berk. & Curt.) Cke. were also included in this section. Lowe considered these three species unrelated to the other members and to each other, but sharing the color of the context. He suggested that the other species previously placed in **Trametes** form a well-marked group with many tropical relatives, which needed to be more thoroughly studied with particular reference to microscopic characters. He also noted that interrelations within this group were difficult to determine due to specimens commonly being sterile.

Kotlaba & Pouzar (1957), based on the work of Bondartsev and Singer (1941), placed **F. cajanderi** in the genus **Fomitopsis.** Cunningham (1965) in his book on New Zealand polypores, included **T. lilacino-gilva** and **T. feei** in the genus **Trametes,** and transferred **F. dochmius** to the genus **Osmoporus** Singer. M.E.P.K. Fidalgo (1968), in her study of some fungi collected in Mato Grosso, Brazil, included **T. cupreo-rosea** and pointed out the differences between this species and **F. feei.** She considered that the species described by Montagne as **P. sagraeanus** was **T. cupreo-rosea,** and that the description of **F. sagraeanus** given by Lowe (1957) was also based on a specimen of **T. cupreo-rosea.** In 1980, Ryvarden and Johansen, in their preliminary flora of East African Polypores, included **F. carnea** (Nees) Imaz. and **F. dochmia** in the genus **Fomitopsis** Karst. due to their annual or perennial basidiocarps, the presence of a hard crust and trimitic hyphal systems. **F. feei, T. lilacino-gilva,** and **T. cupreo-rosea** were included in **Trametes** because of their annual basidiocarps and trimitic hyphal systems. They also pointed out that **F. carnea** must be a close relative of **F. rosea** and **F. cajanderi.**

Cultural descriptions of rose-colored polypores are given by Snell (**Fomes roseus**, 1922), Campbell (**F. roseus** and **F. subroseus**, 1938), Nobles (**F. roseus** and **F. cajanderi**, 1958, 1965), Stalpers (**F. roseus, F. cajanderi, T. lilacinogilva**, and **T. feei**, 1978), Van der Westhuizen (**F. cajanderi**, 1971), and Bakshi, Sen and Singh (1970) who described cultural characteristics of **F. dochmius** and **F. roseus** from India. Wright and Deschamps (1975) gave detailed macroscopic, microscopic, and cultural descriptions of **F. feei and T. lilacinogilva**, which they transferred to the genus **Fomitopsis.** Other descriptions of basidiocarps of some of these fungi have been given by Ito (1955), Bondartsev (1971), Domanski (1972), Reid (1973), Ryvarden (1976), Galvan Villanueva and Guzman (1977), Valenzuela, Guzman and Castillo (1981), Julich (1984), Gilbertson (1974), and Lindsey and Gilbertson (1978).

In this study, the inclusion of all these fungi in the genus **Fomitopsis** is proposed due to their following common characteristics: rose-colored context, at least when young; annual or perennial basidiocarp; trimitic hyphal system; hyaline, smooth-walled, cylindric to allantoid spores; no special structures in the hymenium (with exception of cystidioles reported on **F. cajanderi** and **F. dochmia**); and brown rot type of decay.

MATERIALS AND METHODS

Representative specimens of each species obtained from different Herbaria were examined. Specimens of 4 species were also observed and collected in the field by the authors (See list under each species). Free-hand sections were prepared from each specimen and mounted in 3% KOH to which a drop of aqueous phloxine was added, and in Melzer's reagent. Observations were done under a light microscope. All drawings of microscopic characters were made with the use of a camera lucida. Variations in basidiocarp morphology were encountered among specimens of the same species; consequently, the morphological description of basidiocarps of each species is based on the study of all specimens available, to include the range of characters encountered.

TAXONOMIC SECTION

Fomitopsis P. Karst., Medd. Soc. Fauna Fl. Fenn. 6:9, 1881

Basidiocarps perennial, occasionally annual, pileate, rarely resupinate, sessile or effused-reflexed, dimidiate to ungulate, often large, tough-fibrous to woody when dry; pileus surface often first slightly velvety but soon glabrous, usually sulcate, with a distinct crust; pore surface cream, brownish gray to pink, pores small, round, dissepiments often thick, entire; tubes almost concolorous with the pore surface, often stratified; context pale cream to brown or pink, fibrous to tough; hyphal system trimitic or dimitic (binding hyphae sometimes very difficult to find); generative hyphae clamped, hyaline and thin-walled, skeletal and binding hyphae hyaline to pale yellow, thick-walled, nonseptate; cystidia absent; basidiospores cylindrical to allantoid or ellipsoid, smooth, hyaline, thin-walled, negative in Melzer's reagent; causing a brown rot on conifers and hardwoods. Cosmopolitan genus.

Key to Species

1.	Pores 1-3 per mm, becoming subdaedaleoid or sinuous-daedaleoid	**3. F. cupreo-rosea**
1.	Pores 3-8 per mm, mostly circular to angular, in some cases becoming subdaedaleiod	**2**

2.	Basidiospores allantoid, 4.0-8.0 (-8.5) x 1.5-2.5 (-3) um	3
2.	Basidiospores ellipsoid to cylindrical, 4.0-11.0 x 1.5-5.0 um	4
3.	Widely distributed in the Northern Hemisphere; mainly on conifers, rarely on hardwoods	**1. F. cajanderi**
3.	Widely distributed in the Southern Hemisphere and North to Mexico and Japan; known only on hardwoods	**2. F. carnea**
4.	Basidiospores 5.0-12 x 2.5-5.0 um, on hardwoods, reported only on Myrtaceae	**6. F. lilacino-gilva**
4.	Basidiospores 4.0-8.5 x 1.5-4.0 um; on hardwoods and conifers	4
5.	Tropical species; known only on hardwoods	5
5.	Temperate species; mainly on conifers, rarely in hardwoods	**7. F. rosea**
6.	Basidiocarp with a thick black crust when old	**4. F. dochmia**
6.	Basidiocarp lacking a crust	**5. F. feei**

Description of Species

1. **FOMITOPSIS CAJANDERI** (Karst.) Kotl. & Pouz.

Ceska Mykol. 9:157, 1957.
Fomes cajanderi Karst., Fenska Vet.-Soc. Ofv. Forh. 46(11):8, 1904. **Trametes subrosea** Weir, Rhodora, 25:217, 1923. **Fomes subrosea** Overh., Penn. Agr. Exp. Sta. Tech. Bull. 316, 1935. **Fomitopsis subrosea** (Weir) Bond. & Sing., Ann. Mycol. 39:55, 1941. **Trametes carnea** Amer. aut., not **T. carnea** (Blume & Nees) Wettstein. **Trametes roseo-zonata** Lloyd, Mycol. Writ. 7:1144, f. 2182, 1922.

Basidiocarps annual, biennial or perennial, solitary or imbricate, sessile or effused-reflexed, coriaceous, corky, hard to rigid when dry; pileus applanate, conchate, pinkish brown, pinkish red or pinkish gray, darker close to the base, 1.6-17.0 x 1.1-13.5 x 0.1-4.5 cm, with a decurrent part up to 1.5 cm; upper surface finely velvety tomentose, becoming radially appressed fibrillose-rugulose to nearly glabrous when old, zonate, striate, sulcate, sometimes rough with minute tufts of short erect hairs, with protuberances or a hard brownish pink or black crust; margin light brown or pinkish, thin or thick, acute, entire, rounded or dentate; pore surface pinkish brown to reddish brown in age; pores slightly angular, round, 3.0-5.0 (-7.0) per mm, dissepiments entire; tubes concolorous with the pores, distinctly stratified, fibrillose, to corky, up to 12 mm long, 1-4 mm long each season, old tubes stuffed with white mycelium, sometimes with a dark line separating the tubes from the context; context indistinctly zonate with darker zones, concolorous, lighter or darker than the tubes, up to 1.5 cm thick, whitish pink, corky to fibrous, with a black reaction when touched with KOH.

Hyphal system trimitic; generative hyphae hyaline, with clamps, thin-walled, branching at or near the septa or unbranched, (1.5) 2.0-5.0 um in diam; skeletal hyphae thick-walled, yellowish brown, nonseptate, (1.5) 2.0-6.0 um in diam; binding hyphae thick-walled, hyaline, nonseptate, 2.0-4.0 um in diam.

Cystidioles fusoid, 12.5-14.5 x 3.0-4.0 um.

Basidia clavate or subclavate, 4-sterigmate, 12.0-20.0 (-25.0) x 4.0-6.0 um, with a basal clamp.

Basidiospores smooth-walled, hyaline, allantoid, apiculate, 4.0-8.0 x 1.5-2.5 µm, negative in Melzer's reagent.

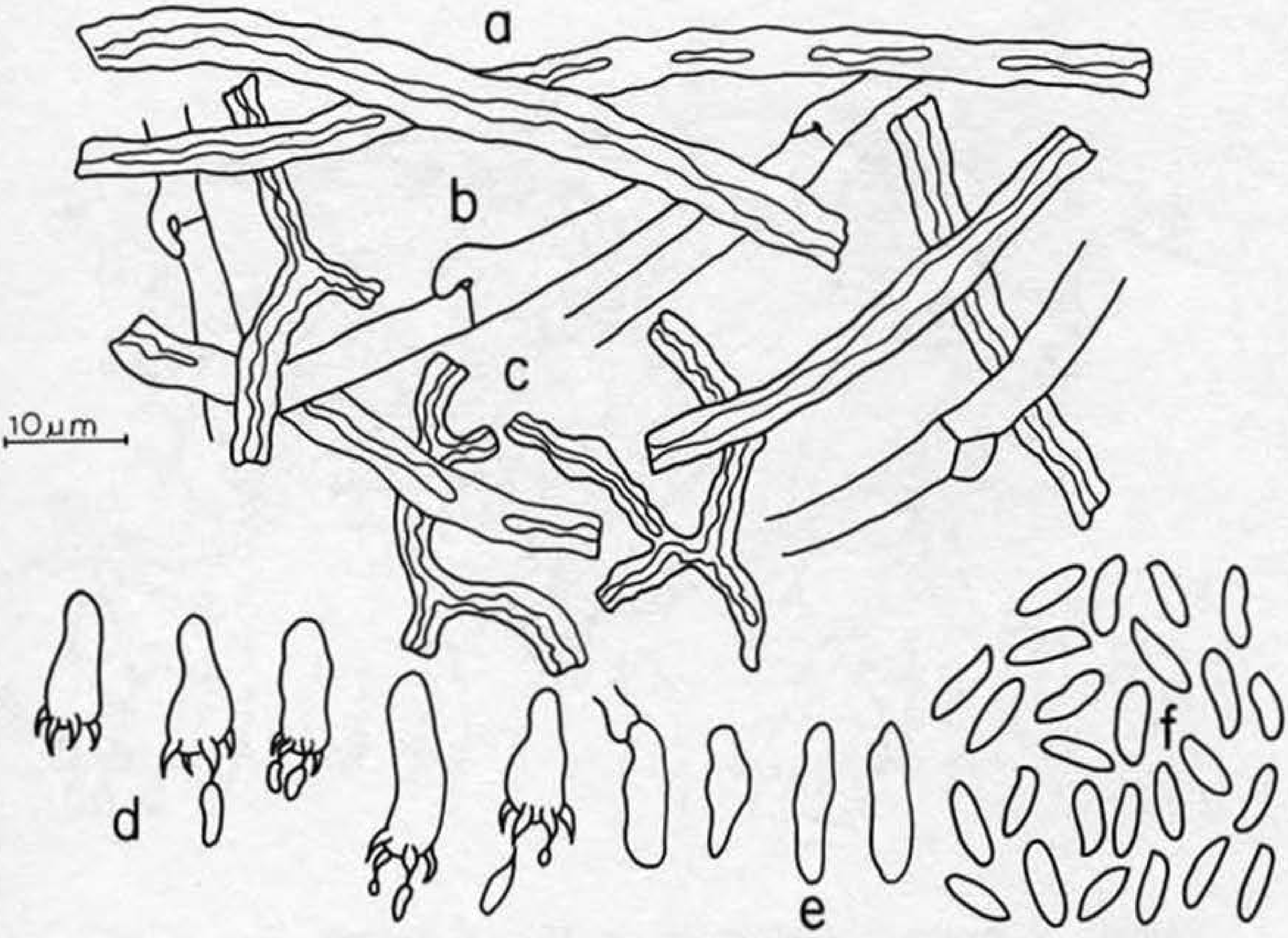

Fig. 1. **F. cajanderi** (JPL 325). a, skeletal hyphae; b, generative hypha; c, binding hyphae; d, basidia; e, cystidioles; f, basidiospores.

Type of rot: Brown cubical rot.

Substrata: On hardwood and conifer trees, mainly on conifers. Reported on Betulaceae; Salicaceae; Rosaceae; Ericaceae; Fagaceae; Pinaceae; Cupressaceae.

Distribution: Widely distributed in North America; Caribbean Islands; Asia; Europe and Russia.

Voucher specimens examined: CANADA: Alberta: Whitecourt, on **Picea mariana**, R.L. Gilbertson 6696 (ARIZ); Ontario: Petawawa Exp. Forest, B. & J. Eriksson 8822 (O); Newfoundland: Trout Brook, District of St. Georges, on **Abies balsamea**, R.L. Gilbertson 5372 (ARIZ); CHINA: Junlin Prov., Chang Bai, Shan Forest Reserve, Huang Song Pu, on **Larix olgensis**, L. Ryvarden 21571 (O); DOMINICAN REPUBLIC: On **Pinus occidentalis**, D.E. Etheridge 24 (ARIZ); MEXICO: Las Vigas a Las Lajas, Veracruz, on **Pinus sp.**, A. Lopez, L. Ryvarden 267 (ENCB); NEPAL: Khaptar, Etage Montagnard, J.F. Dohemez, L. Ryvarden (O); UNITED STATES: Arizona: Bear Wallow Santa Catalina Mts, Pima Country, on Douglas fir, J.C. Morse 8-83 (ARIZ); Mt. Graham, Pinaleno Mts, Graham County, on Douglas fir, J.C. Morse 11-83 (ARIZ); Rustler Park, Chiricahua Mts, Cochise County, on Douglas fir, J.C. Morse 159-83 (ARIZ); Minnesota: Lake Itasca State Park, Clearwater County, on **Picea sp.** R.L. Gilbertson 9453 (ARIZ); New York: Pack Forest, Warrensburg, on **Picea rubens**, R.L. Gilbertson 5801 (ARIZ).

Fig. 2. World distribution of **F. cajanderi**.

2. **FOMITOPSIS CARNEA** (Blume & Nees) Imaz.

Bull. Tokyo Sci. Mus. 6:92, 1943.
Fomes carneus Blume & Nees, Nov. Act. Acad. Caes. Leop. XIII:15, 1826.

Basidiocarps perennial, solitary or imbricate, effused-reflexed or sessile, woody when dry; pileus applanate, conchate, at first smoky pink, becoming brownish black with a definite black crust, up to 7 cm wide; resupinate portion up to 4 cm long and 1 cm deep; upper surface first tomentose and velvety, becoming glabrous, concentrically sulcate, azonate, with cracks; margin of lighter color, thin or thick, round or acute; pore surface pinkish brown or rosy with a lilac tint, margin sterile; pores round, 5.0-6.0 (-7.0) per mm, dissepiments entire and thick; tubes distinctly stratified, separated from each other by a white to pale pink thin layer, up to 3 mm thick, context brownish pink, corky to hard, slightly zonate, up to 1.7 cm thick, with a black reaction when touched with KOH.

Hyphal system trimitic; generative hyphae thin-walled, hyaline, with clamps, 2.0-4.0 (-5.0) um in diam; skeletal hyphae hyaline to yellowish brown, thick-walled, nonseptate, (3.0) 4.0-6.0 um in diam; binding hyphae light yellow, thick-walled, short-branched, 2.0-5.0 um in diam.

Cystidia or other sterile hymenial structures absent.

Basidia clavate, 4-sterigmate, 9.5-16.5 x 4.5-6.5 um; with a basal clamp.

Basidiospores cylindrical to slightly allantoid, smooth-walled, hyaline, 5.0-8.0 (-8.5) x (1.5) 2.0-2.5 (-3.0) um, negative in Melzer's reagent.

Type of rot: Brown cubical rot.

Substrata: On hardwood trees.

Distribution: Asia, Africa and Mexico.

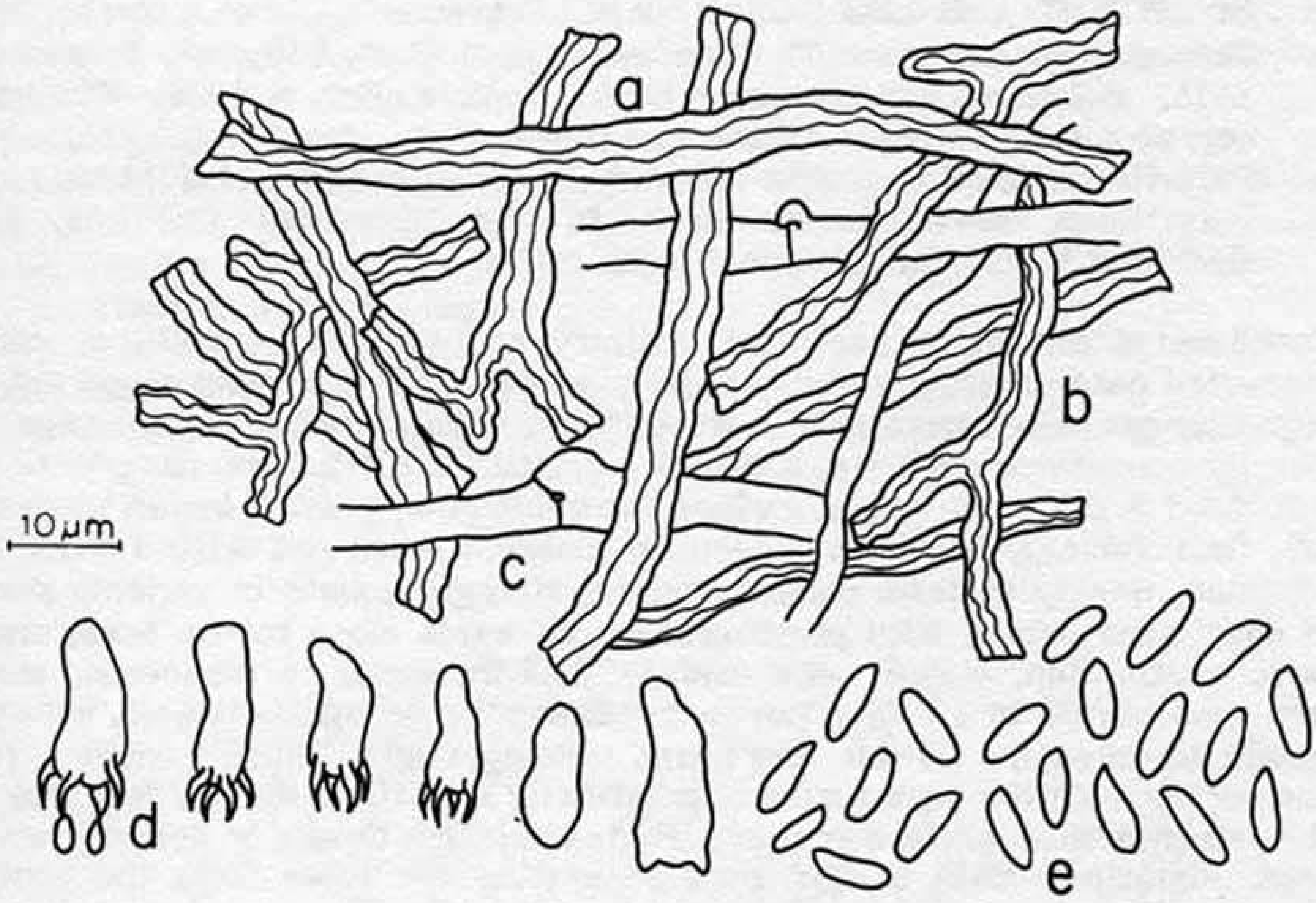

Fig. 3. **F. carnea** (O 10118). a, skeletal hyphae; b, binding hypha; c, generative hypha; d, basidia; e, basidiospores.

Fig. 4. World distribution of **F. carnea**.

Voucher specimens examined: MEXICO: El Parotal, Municipio Aguililla, Michoacan, X. Madrigal 2812 (ENCB). TANZANIA: Arusha Prov. Arusha Nat. Park, Mt. Meru, E. slope, 10118(0).

3. **FOMITOPSIS CUPREO-ROSEA** (Berk.) Carranza & Gilbn., , comb. nov. **Trametes cupreo-rosea** (Berk.) Lloyd, Mycol. Writ. 4 (Synop. **Fomes**) 226, 1915. **Polyporus cupreo-roseus** Berk., Hook. J. Bot. 8, 1856. **Microporus cupreo-roseus** (Berk.) Kuntze, Rev. Gen. Plant 3(3):495, 1898. **Polystictus cupreo-roseus** (Berk.) Cke., Grevillea 14(71):85, 1886. **Polystictus cupreo-vinosus** Berk. in Cke, Grevillea 14(71):85, 1886; Grevillea 15(73):23, 1886, nomen nudum.

Basidiocarps annual or perennial, solitary or imbricate, sessile or with a contracted base, dimidiate and broadly attached, with a resupinate poroid part frequently present, coriaceous to woody when dry; pileus applanate, conchate, laterally connate or ungulate, 5.0-16.5 x 2.6-10.3 x 0.3-2.5 cm, resupinate part up to 0.8-1.5 x 0.5 cm; upper surface brownish pink, grayish brown or grayish pink, first velvety, fibrillose, becoming glabrous when old, with a weak silky dull shine, weakly sulcate, radiate-striate, strongly zonate in variable shades, old specimens dotted with protuberances or warts close to the base; margin sharp, acute, thin, entire; pore surface pinkish brown or vinaceous, with a sterile margin up to 1.5 mm; pores round, angular or subdaedaleoid, becoming sinuous-daedaleoid, 1.0-3.0 per mm, dissepiments thick, entire; tubes concolorous with the pore surface, indistinctly stratified, up to 7 mm long, old tubes stuffed with white mycelium; context pinkish brown or darker than the pores, sometimes with a dark zone separating the tubes from the context,

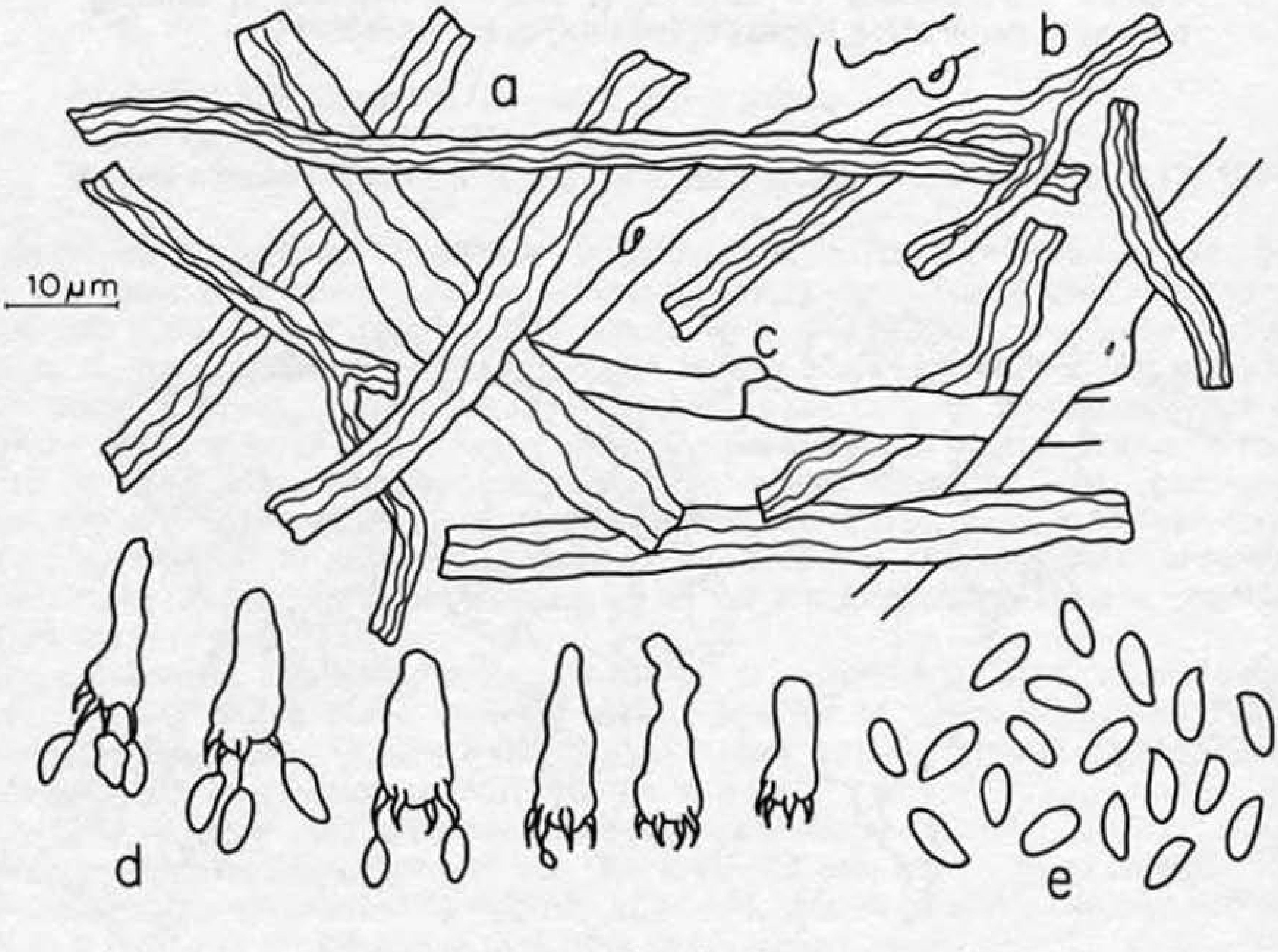

Fig. 5. **F. cupreo-rosea** (FH 66818). a, skeletal hyphae; b, binding hypha; c, generative hypha; d, basidia; e, basidiospores.

dense, fibrous, up to 1.9 cm thick, with a black or cherry red reaction when touched with KOH.

Hyphal system trimitic; generative hyphae with clamps, hyaline, thin to slightly thick-walled, occasionally branched, (1.5) 2.5-4.5 um in diam; skeletal hyphae yellowish brown or hyaline with a lilac shade, thick-walled, non-septate, (2.0) 2.5-8.0 um in diam; binding hyphae moderately branched, thick-walled (1.5) 3.0-4.0 um in diam.

Cystidia or other sterile hymenial structures absent.

Basidia clavate, 4-sterigmate, (9.0) 12.0-19.0 x 4.0-6.5 um, with a basal clamp.

Basidiospores cylindrical, hyaline, smooth-walled, 5.0-7.0 (-8.0) x (2.0) 2.5-3.5 um, negative in Melzer's reagent.

Type of rot: Brown cubical rot.

Substrata: On hardwood trees, very common on burned wood.

Distribution: Mexico, Central and South America; Caribbean Islands.

Fig. 6. World distribution of **F. cupreo-rosea.**

Voucher specimens examined: BRAZIL: St. Anna da Shapada, Humayta Madeira River, Matto Grosso, J.R. Weir and Malme 66818 (FH); BRITISH GUIANA: Bartica, R. Essequibo, D.H. Snider 599 (FH); COLOMBIA: Sierra de la Macarena, Rio Guapaza, Little 10238(0); COSTA RICA: Alto de las Palomas, Santa Ana, San Jose, on hardwood, J.C. Morse 14-81 (USJ); CUBA: (NY) No other data; MEXICO: Carretera Minatitlan, desv. Chinameca, Veracruz, San Pedro Soteapa, 203 (ENCB); PERU: Madre de Dios, Prov. Tambopata, Puerto Maldonado, Tambopata Nat. Res., P.J. Barbour 5007 (UL).

4. **FOMITOPSIS DOCHMIA** (Berk. & Br.) Ryv.
Norw. J. Bot. 19:231, 1972.
Fomes dochmius (Berk. & Br.) Cke., Grevillea 14:17, 1885. **Osmoporus dochmius** (Br.) G.H. Cunn., Polyp. New Zeal., N.Z. Dept. Scient. Ind. Res. Bull. 164, 1965. **Polyporus dochmius** Berk. & Br., Linn. Soc. Bot. J. 14:50, 1875. **Polyporus ferreus** Berk., Lond. J. Bot. 6:502, 1847. nom.

illegit. non Pers. 1825. **Fomes ferreus** Berk. : Cke., Grevillea 14:21, 1885. **Fomes subferreus** Murr., N. Amer. Fl. 9:97, 1908.

Basidiocarps annual, biennial or perennial, solitary or imbricate, sessile or effused-reflexed, dimidiate or attached by a lateral base, corky to woody when dry; pileus applanate, conchate or flabelliform, 3.0-12.0 x 2.0-15.0 x 0.6-3.0 cm; upper surface first brownish gray, becoming grayish black and with a distinct crust when old, glabrous, concentrically sulcate, radially wrinkled and cracked, creviced when old, faintly zoned, with some protuberances or warts close to the base; margin acute, thin, even, first velvety, becoming glabrous with narrow sulcate zones, ochraceous, brown or gray; pore surface pinkish gray, cream or tan when old, even, with a sterile border of 3.0-5.0 mm wide; pores round to subdaedaleoid, ochraceous pink or wood color, 5.0-8.0 per mm, dissepiments entire; tubes concolorous with the pore surface, indistinctly stratified, old tubes stuffed with white mycelium, up to 7 mm long; context ochraceous, pale pink, pinkish tan, or wood color, fibrous, up to 1.5 cm thick, sometimes darker than the pores, with a silky sheen and with a dark reaction when touched with KOH.

Hyphal system trimitic; generative hyphae with clamps, thin-walled, branched, hyaline, 2.0-4.0 um in diam; skeletal hyphae thick-walled, hyaline or yellowish brown, nonseptate, 3.0-7.0 um in diam; binding hyphae freely branched, thick-walled, branches tapering and tortuous, 2.0-5.0 um in diam.

Cystidia or other sterile hymenial structures absent, but reported by Bose (in Ryvarden and Johansen, 1980) to be clavate and finely encrusted. Lowe (1957) reported cystidioles 3.0-4.0 um in diam.

Basidia subclavate, or narrowly clavate, 4-sterigmate, 12.0-19.0 x 4.0-5.0 um, with a basal clamp.

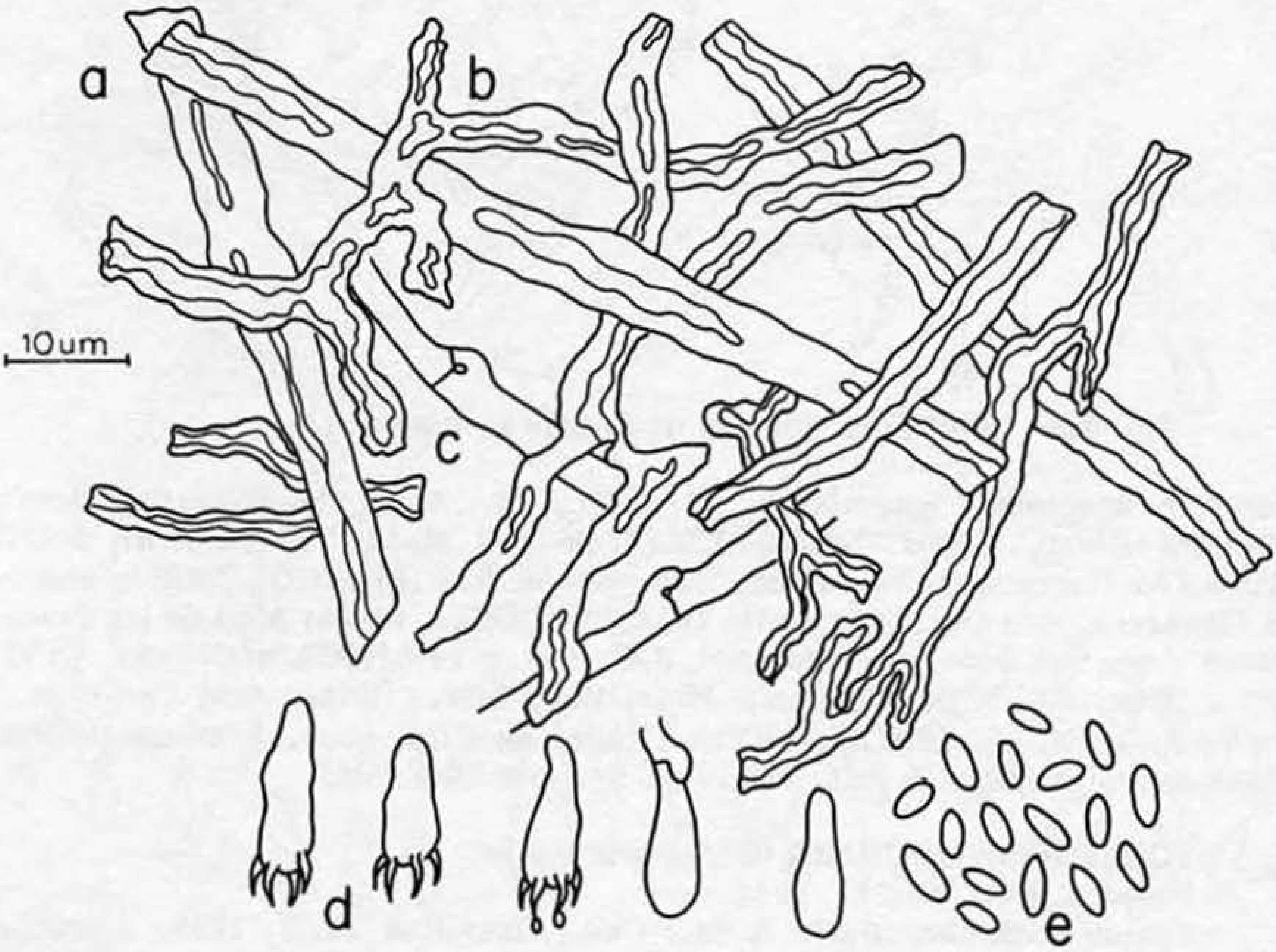

Fig. 7. **F. dochmia** (FH 4234). a, skeletal hyphae; b, binding hypha; c, generative hypha; d, basidia; e, basidiospores.

Basidiospores oblong-ellipsoid, smooth-walled, hyaline, 4.0-6.0 (-7.0) x (1.5) 2.0-2.5 um, negative in Melzer's reagent.

Type of rot: Brown cubical rot.

Substrata: On hardwood trees. Reported on Dipterocarpaceae (**Shorea robusta**) and Guttiferae (**Mesua ferrea**).

Distribution: Central and South America; Caribbean Islands, Asia and Australia.

Fig. 8. World distribution of **F. dochmia.**

Voucher specimens examined: BORNEO: Tawao, Elphinstone Prov., British North Borneo, 20618 USO 229569 (BPI). CUBA: Jaguey, Yateras Oriente W.P. Maxon 4234 (FH). ECUADOR: Canas, J.N. Rose, A. Pachans, G. Rose 23705 (FH) INDIA: Nalapani Forests, Dehra Dun on **Shorea robusta**, A. Hafizkan, USO 229242 (BPI). JAMAICA: A.E. Wright (FH). MALAYA: Johore, Danan Sadeli River, E. Corner (O). PHILIPPINES: Tawitania Island, Sulu Archipelago, H.S. Yates 36119, USO 229246 (BPI). SRI LANKA: USO229570 (BPI), No other data. THAILAND: Nakhaunsvi, Thamarat San Klang, Vee Hnoa, USO 229237 (BPI).

5. **FOMITOPSIS FEEI** (Fr.) Kreisel
Univ. Habana (Cuba), Ser. 4, Cienc. Biol. No 16:83, 1971.
Trametes feei (Fr.) Pat., Essai Taxon. p. 92, 1900. **Polyporus feei** Fr., Linnaea 5:518, 1830. **Fomes feei** (Fr.) Lowe, Mycologia 47:217, 1955. **Polyporus rubidus** Berk., Lond. J. Bot. 6:500, 1847. **Fomes sagraeanus** sensu Murrill non Mont., N. Am. Fl. 9(2):96, 1908. **Polystictus feei** (Fr.) Cke., Grevillea 14:82, 1886.

Basidiocarps annual, biennial or perennial, solitary or imbricate, sessile or effused-reflexed, with a contracted base, dimidiate, broadly attached, coriaceous-soft when fresh, corky to woody when dry; pileus applanate, conchate or flabelliform, frequently with a decurrent resupinate part, 2.8-20.0 x 2.1-10.0 x 0.4-3.0 cm; upper surface pale brown, pale brick red, grayish, pinkish brown, or dark brown, fading when drying, velutinate and soft to touch when young, becoming glabrous in age with a dull weak shine, strongly or weakly zonate, more or less sulcate, somewhat radiate-striate, old specimens frequently dotted with protuberances or warts of lighter color close to the base; margin thin, acute, sharp, entire, 2-4 mm wide; pore surface pale pinkish brown, whitish pink, or ochraceous pink, margin narrow, sterile; pores round, (3.0) 4.0-7.0 (-8.0) per mm, dissepiments entire; tubes concolorous with the pore surface, indistinctly stratified in one, two or more layers, up to 8 mm long, old tubes stuffed with whitish mycelium; context concolorous with pore surface or darker, soft to corky, fibrous, up to 1 cm thick, faintly zonate, with a cherry red or black reaction when touched with KOH.

Hyphal system trimitic; generative hyphae with clamps, thin-walled, hyaline, 2-4 µm in diam, occasionally branched; skeletal hyphae yellowish brown, hyaline or with a pale shade of lilac, thick-walled, nonseptate, 2-6.6 µm in diam; binding hyphae moderately branched, thick-walled, 2-4.5 µm in diam.

Cystidia or other sterile hymenial structures absent.

Basidia clavate, 4-sterigmate, 10.0-20.7 x 3.6-7.0 µm, with a basal clamp.

Basidiospores cylindrical, hyaline, smooth-walled, somewhat pointed at the ends (4.0) 5.0-7.0 (-8) x (1.5) 2.0-3.5 (-4) µm, negative in Melzer's reagent.

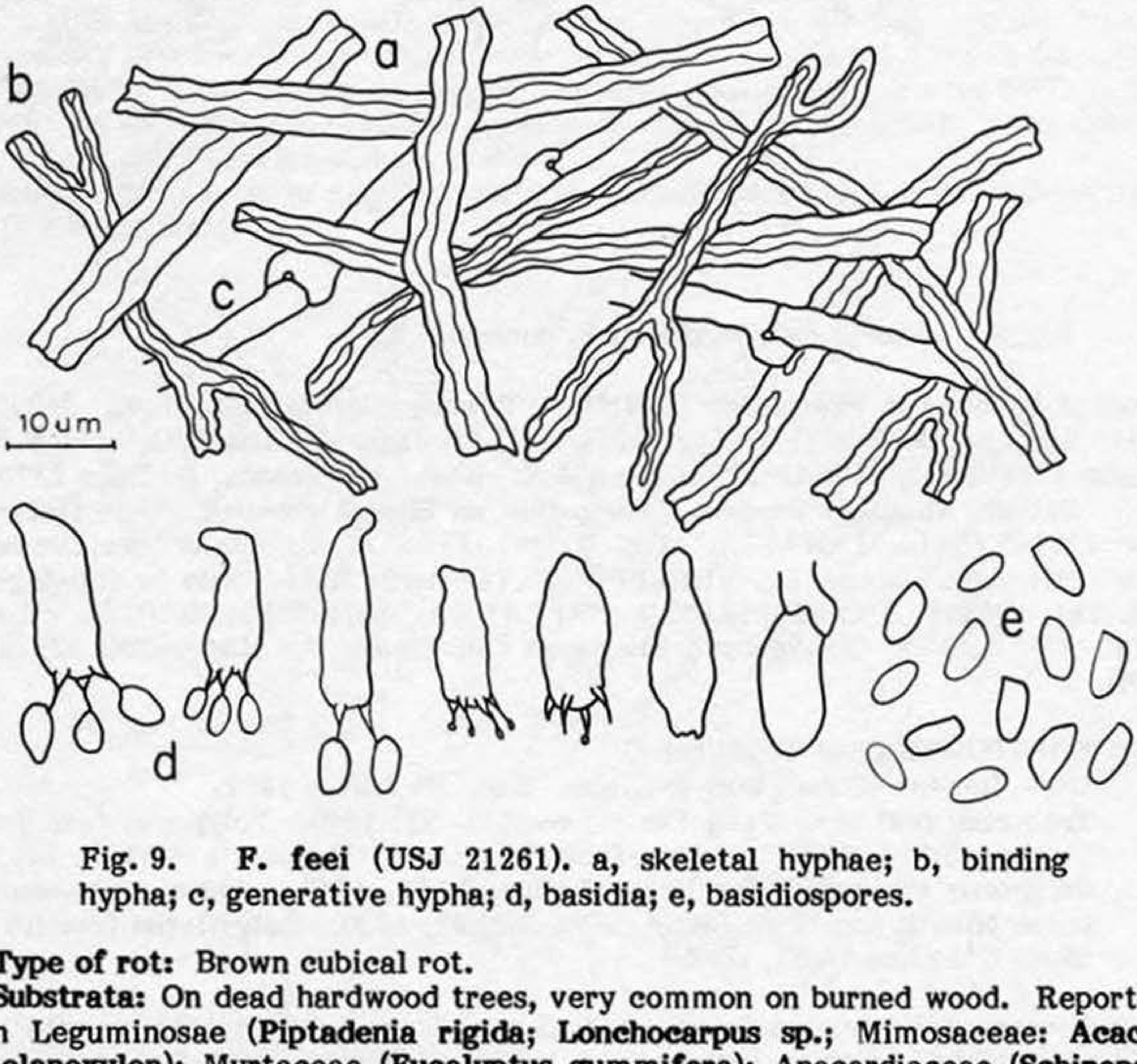

Fig. 9. **F. feei** (USJ 21261). a, skeletal hyphae; b, binding hypha; c, generative hypha; d, basidia; e, basidiospores.

Type of rot: Brown cubical rot.

Substrata: On dead hardwood trees, very common on burned wood. Reported on Leguminosae (**Piptadenia rigida; Lonchocarpus sp.**; Mimosaceae: **Acacia melanoxylon**); Myrtaceae (**Eucalyptus gummifera**); Anacardiaceae (**Schinopsis lorentzii**).

Distribution: North, Central and South America; Caribbean Islands; Asia; Australia and New Zealand.

Fig. 10. World distribution of **F. feei.**

Voucher specimens examined: ARGENTINA: Jujuy, Camino de Palma Sola a El Fuerte, on **Schinopsis lorentzii**, Cordo et al., J-175 (BAFC 23278); BOLIVIA: Bopi River Valley, O.E. White 294 (FH); BRAZIL: Km 55 Br. 317 SW of Rio Branco, on road to Xapuri, Acre, B. Lowy, S.R. Lourie and V.M. de Souza 522 Br (UL). BORNEO: (FH). No other data; COLOMBIA: Sierra Nevada de Sta. Marta, Depto Magdalena, Cerro Quemado Trail, G.W. Martin 3807 (NY); COSTA RICA: Terron Colorado, Alajuela, on hardwood, J.C. Morse 21261 (USJ); EL SALVADOR: Vicinity of La Union, Depto de La Union, USO 234591 (BPI); GUATEMALA: Depto Escuintla, along or near Rio Michatoya, Southwest of Escuintla, 89051 (BPI); MEXICO: 20 Km sur del Km 77 carretera Chetumal a Escarcega, Camino Tomas Garrido, Quintana Roo, G. Guzman 20935 (ENCB); NICARAGUA: Kellerman (BPI). No other data; PHILIPPINES: Negros, H.M. Curram 13749 (NY); THAILAND: Chanwat Chiang Doo, Doi Chiang, Doo Nat. Park, L. Ryvarden 17979 (O); VENEZUELA: Calabozo Orituce River, M. Gochfeld (NY).

6. **FOMITOPSIS LILACINO-GILVA** (Berk.) Wright & Desch.
Rev. Inv. Agrop. INTA. Buenos Aires (Arg.) serie V, Pat. Veg. Vol. XII, No. 3, p. 143, 1975.
Polyporus lilacino-gilvus Berk., Ann. Nat. Hist. 3:324, 1839; **Polystictus lilacino-gilvus** (Berk.) Cke., Grevillea 14:82, 1886; **Trametes lilacino-gilva** (Berk.) Lloyd, Synopsis **Fomes**, p. 226, 1915; **Trametes violaceus** Lloyd, Syn. Sect. Apus **Polyporus**, p. 342, 1915; **Trametes griseo-lilacina** van der Byl, S. Afr. J. Sci. 18:283, 1922; **Trametes rosea** Lloyd, Letter 59:5, 1915.

Basidiocarps annual, biennial or perennial, solitary or imbricate, dimidiate, broadly attached or with a lateral base, corky to woody when dry; pileus applanate, conchate or ungulate, 2.0-20.0 x 2.0-9.0 x 0.5-10.0 cm with a decurrent resupinate poroid part up to 3.0 x 0.2 x 0.1 cm; upper surface straw color, tan, bay, grayish or pinkish brown, darker when old, concentrically sulcate and ridged, strongly radiate-striate, strigose or setulose, becoming glabrous when old, strongly zonate, old specimens with some protuberances or warts near the base; margin velutinate, sharp to round, entire; pore surface rose pink, pinkish brown, violaceous lilac or pallid ferruginous, margin wide, sterile up to 3.0 mm; pores round, angular or some slightly labyrinthiform, (2) 3.0-5.0 (-6.0) per mm; tubes concolorous or pinkish white, faintly zonate, up to 8.0 mm long; context rose, lilac, or pinkish brown, or concolorous with the pore surface, dense, fibrous, zonate up to 0.7 cm thick, dark or reddish brown reaction when touched with KOH.

Hyphal system trimitic; generative hyphae with clamps, branched, hyaline, thin-walled, 1-4 µm in diam; skeletal hyphae yellowish brown, thick-walled, nonseptate, 2.5-7.0 µm in diam; binding hyphae nonseptate, freely branched, branches tapering and tortuous, thick-walled, 2-5 µm in diam.

Cystidia or other sterile hymenial structures absent.

Basidia subclavate, 4-sterigmate, 12.0-23.0 x 4.0-8.5 µm, with a basal clamp.

Basidiospores elliptical, hyaline, smooth-walled, apiculate, 5.0-12.0 x 2.5-5.0 µm, negative in Melzer's reagent.

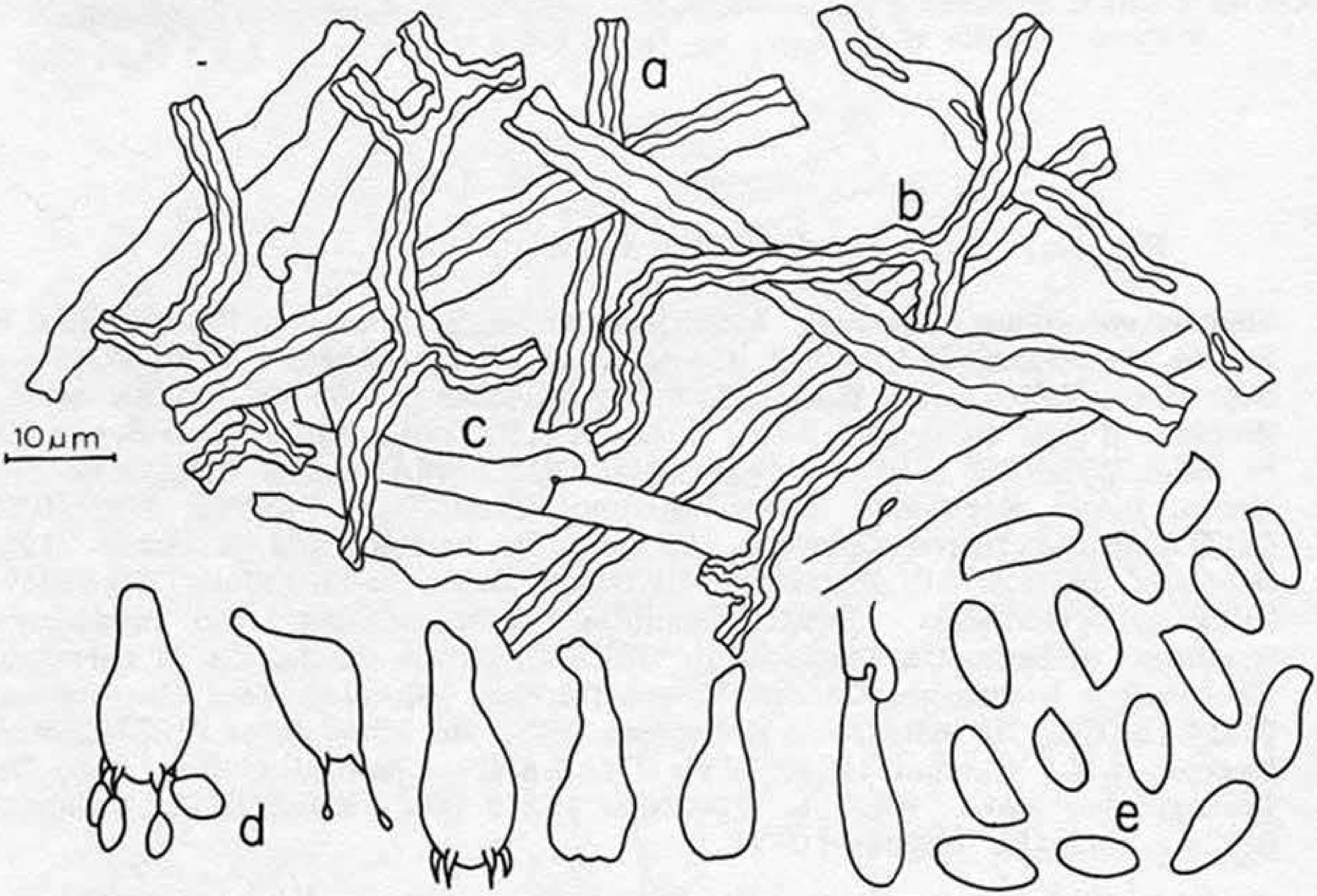

Fig. 11. **F. lilacino-gilva** (DC 9-79). a, skeletal hyphae; b, binding hypha; c, generative hypha; d, basidia; e, basidiospores.

Type of rot: Brown cubical rot.

Substrata: On decorticated hardwood trees, often on charred wood, worked timber, power poles and railway sleepers. Reported on Myrtaceae (**Eucalyptus calophylla, E. viminalis; E. globulus; Eucalyptus sp.; Tristania conferta**).

Distribution: South America; Australia; New Zealand; South Africa and Tasmania.

Voucher specimens examined: ARGENTINA: Rios Palmar de Colen, D. Cabral (O); AUSTRALIA: N.S.W. Whean Whean State Forest, J. Parker 3, DAR 35161 (O).

Fig. 12. World distribution of **F. lilacino-gilva.**

7. **FOMITOPSIS ROSEA** (Alb. & Schw.:Fr.) Karst..
Krit. Ofv. Finl. Basidsv. 306, 1889.
Boletus roseus Alb. & Schw., Consp. Fung., p. 251, 1805. **Fomes roseus** (Alb. & Schw.:Fr.) Karst., Soc. Fauna Fl. Fenn. Meddel. 5:39, 1879. **Trametes rosea** Karst., Hattsv. 2:47, 1882. **Polyporus roseus** (Alb. & Schw.) Fr., Syst. Mycol. 1:372, 1821.

Basidiocarps annual, biennial or perennial, solitary or imbricate, sessile, corky to woody when dry; pileus ungulate, conchate, applanate, with a resupinate part, 1.0-7.0 x 1.5-10.0 x 0.1-3.0 cm; upper surface pinkish brown, pinkish red, grayish brown, zonate, striate, concentrically sulcate, older parts often irregularly cracked, first very minutely tomentose, soon glabrous, sometimes slightly incrusted, with a thick rimose crust, brown to blackish in old specimens; margin undulate, acute, obtuse or rounded, thin, entire, remaining pinkish brown or lighter than the rest of the pileus; pore surface pinkish brown at first, then brown on old specimens; pores circular or subanglular, 3.0-5.0 (-6.0) per mm, dissepiments entire, thick with obtuse edges; tubes 0.5-4.0 (-5.0) mm long each season, rather distinctly to indistinctly stratified in old specimens, pinkish buff to gray, when old stuffed with white mycelium; context indistinctly zonate, white to pinkish gray or darker, compact, soft fibrillose, corky to rather hard, 0.2-1.0 cm thick, with a dark reaction when touched with KOH.

Hyphal system trimitic; generative hyphae with clamps, thin-walled, hyaline, 3.0-5.0 µm in diam; skeletal hyphae thick-walled to subsolid, pale brown to yellowish, nonseptate, 2.0-6.5 (-7.0) µm in diam; binding hyphae rather coarse, solid or nearly so, hyaline, with short branches or sometimes merely short processes, 3.0-5.5 µm in diam.

Cystidia or other sterile hymenial structures absent.

Basidia clavate, rounded, 4-sterigmate, 10.0-19.5 x 4.0-7.5 (-8.0)µm, with a basal clamp.

Basidiospores oblong, ellipsoid or almost cylindric, hyaline, smooth-walled, (5.0) 6.0-8.5 x (2.0) 2.5-3.5 (-4.0) µm, negative in Melzer's reagent.

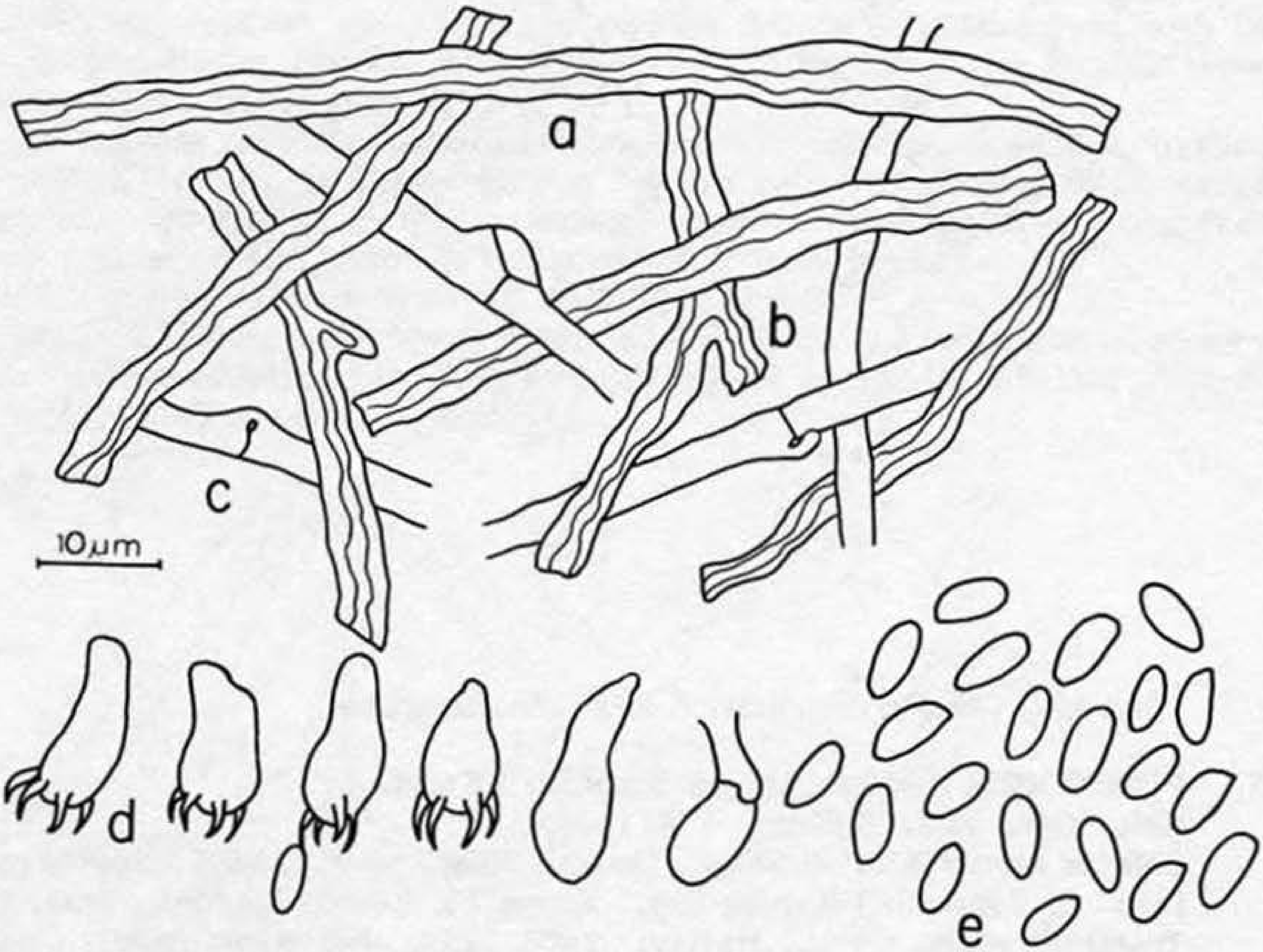

Fig. 13. **F. rosea** (RLG 6954). a, skeletal hyphae; b, binding hypha; c, generative hypha; d, basidia; e, basidiospores.

Type of rot: Brown cubical rot.

Substrata: On conifer and hardwood trees, mainly on conifers. Reported on Platanaceae; Ulmaceae, Pinaceae, and Salicaceae.

Distribution: North America; Asia; Europe and Russia. **Fomitopsis rosea** is distributed in northern latitudes or at high elevations from mixed conifer to spruce-fir forest zones.

Voucher specimens examined: CANADA: Dawson City, Yukon Territory, on **Picea glauca.** R.L. Gilbertson 8782 (ARIZ); FINLAND: Pera-Pohjanmaa, Tervola, Pisavaara Nat. Park, Liljalakie on **Picea abies**, H. Kotiranta & T. Niemela 1313 (ARIZ); MEXICO: Bosque de Chapultepec, 30 Km sur El Alto, Durango, on **Pseudotsuga menziesii.** G. Guzman, S. de la Campa 3502-A (ENCB); UNITED STATES: Arizona, Fort Apache Indian Reservation, Paradise Park, White Mts., Apache County on **Populus tremuloides.** R.L. Gilbertson 6954 (ARIZ); Soldier Creek, Pinaleno Mts. Coronado Nat. Forest, Graham County on **Populus tremuloides.** R.L. Gilbertson 10109 (ARIZ); Soldier Creek, Pinaleno Mts, Coronado Nat. Forest, Graham County on **Picea engelmannii**, R.L. Gilbertson 9083 (ARIZ); Montana: Flathead Lake, U of Montana Bio. Sta. on **Larix occidentalis.** R.L. Gilbertson 5929 (ARIZ); North Carolina: Indian Gap, Great Smoky Mountain Nat. Park, on **Picea rubens.** J.L. Lowe & R.L. Gilbertson 11071 (ARIZ); New York: Wolf Lake, on **Picea rubens.** R.L. Gilbertson 3762 (ARIZ); Washington: Olympic Peninsula, White Plains, on conifer. J.L. Lowe & R.L. Gilbertson 10493 (ARIZ).

Fig. 14. World distribution of **F. rosea.**

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Los generos **Daedalea, Fomitopsis, Heteroporus, Laetiporus, Nigroporus, Rigidoporus, Perenniporia** y **Vanderbylia.** Rev. Inv. Agrop. INTA, Argentina. Serie V. Pat. Veg. 12(3):127-204.

MYCOTAXON

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OBSERVATION D'UN *TAPHRINA* PARASITE SUR *POLYSTICHUM SETIFERUM* (Forskall) Moore ex Woynar EN FRANCE

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RESUME

Un *Taphrina* a été récolté en France, dans le Cotentin, sur *Polystichum setiferum* (Forskall) Moore ex Woynar. Il détermine sur les feuilles de petites taches décolorées, non épaissies ni cloquées. Le mycélium est uniquement sous-cuticulaire. Les asques sont pourvus d'une cellule-pied. Ce champignon paraît très proche de *Taphrina polystichi* Mix, parasite sur *Polystichum acrostichoides* (Michx.) Schott en Amérique du Nord.

SUMMARY

A *Taphrina* has been collected in France, in the Cotentin, on *Polystichum setiferum* (Forskall) Moore ex Woynar. It produces small yellowish unthickened spots, without curling, on the leaves. The mycelium grows only beneath the cuticle. The asci are provided with a stalk cell. This fungus seems very close to *Taphrina Polystichi* Mix, parasite on *Polystichum acrostichoides* (Michx.) Schott in North America.

Parmi les espèces de *Taphrina* connues s'attaquant aux Filicinées, aucune jusqu'à présent ne semble avoir été décrite sur *Polystichum setiferum* (1). Cependant, au cours de deux années différentes, nous avons eu l'occasion d'observer sur cette Fougère la présence d'un parasite appartenant à ce genre d'Ascomycètes. Les récoltes ont été effectuées au mois de juillet, dans le Cotentin, le long d'un chemin creux très ombragé, situé près de la route menant de Valognes à Périers, sur la commune de St Jores. Le champignon, bien que très abondant dans ce lieu, n'a pas été retrouvé dans diverses autres localités visitées de la même région.

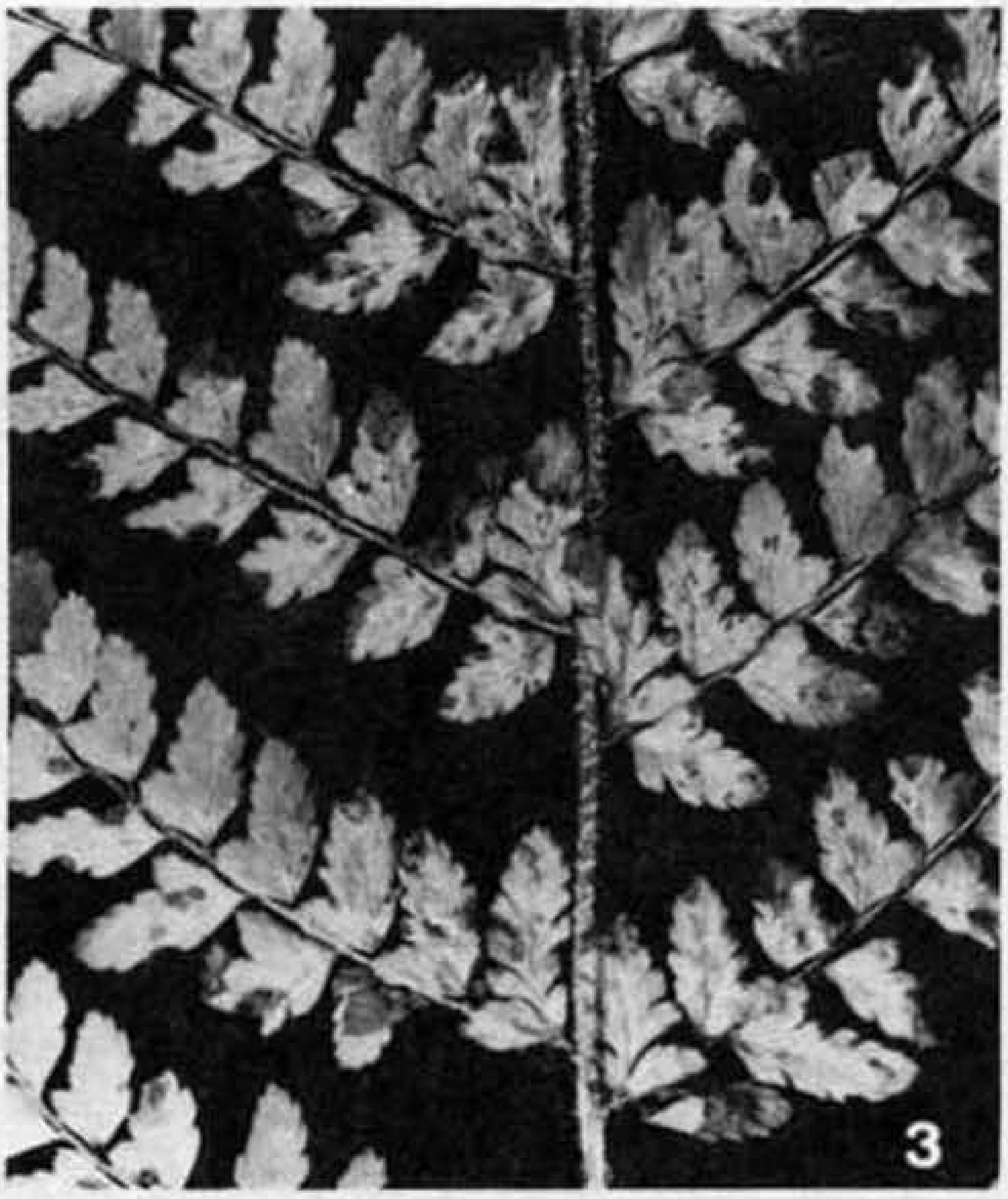
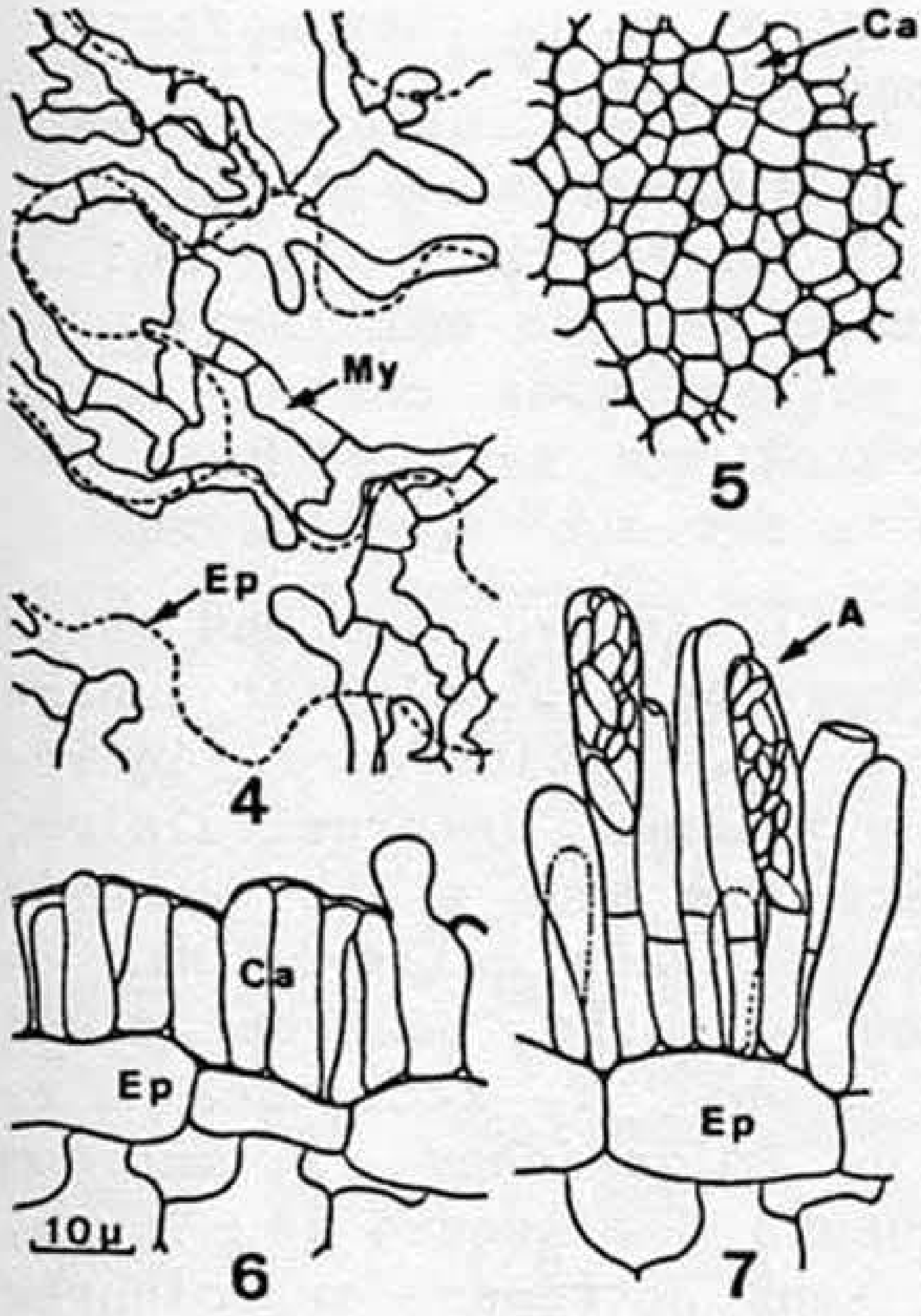
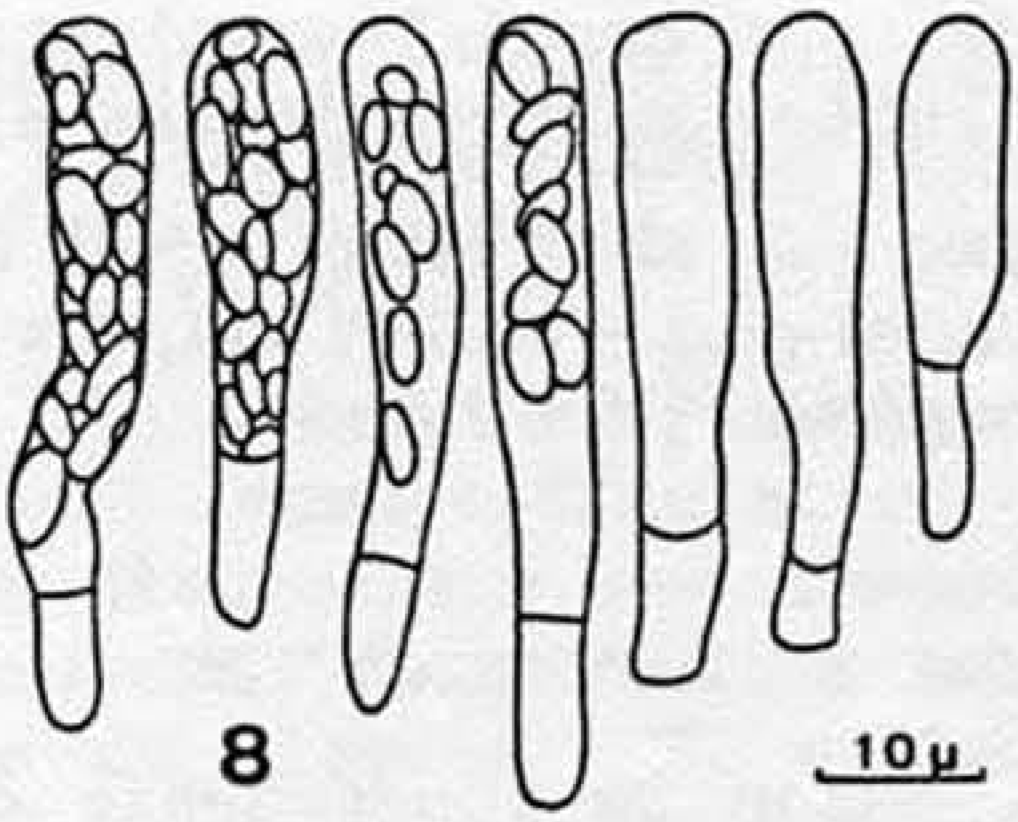


FIG. 1. Pinnules de *Polystichum setiferum*, vues par la face supérieure, portant des lésions dûes à une attaque de *Taphrina* (x 2,25). A, jeune tache décolorée. B, deux taches montrant un début de nécrose. FIG. 2. Jeunes taches (flèches) vues à la face inférieure de deux pinnules (x 2,25). FIG. 3. Portion de fronde portant de nombreuses petites taches nécrosées, résultant de l'attaque du champignon (grandeur nature).

OBSERVATIONS MACROSCOPIQUES

Les symptômes provoqués par le parasite sont au début très discrets. Ils consistent en de petites taches légèrement décolorées, dont le diamètre est le plus souvent inférieur à 2 mm, et dépasse rarement 3 mm, sauf par coalescence, de sorte qu'une même pinnule peut en porter plusieurs (Fig. 1). A leur niveau le limbe n'est ni épaissi ni boursoufflé. Les plus jeunes taches ont, sur l'une des faces (le plus souvent la face inférieure), une couleur blanchâtre, mate, caractéristique de la présence d'un mycélium sous-cuticulaire de *Taphrina* (Fig. 2). Le développement des cellules ascogènes se traduit par un soulèvement, visible à la loupe, de la surface des taches. Lorsque les asques ont rompu la cuticule, la pellicule blanchâtre fait place à un revêtement incolore, d'aspect légèrement muqueux. Ensuite les vieilles lésions deviennent brunes, et parfois se perforent. Certaines frondes peuvent être ainsi fortement altérées par suite de la présence de très nombreuses petites taches nécrosées (Fig. 3).





A, asques. Ca, cellules ascogènes. Cp, cellules-pied. Ep, cellules épidermiques; contours figurés en trait discontinu sur la FIG. 4. My, mycélium.

FIGS. 4 à 7. Différentes étapes du développement du champignon. 4, mycélium sous-cuticulaire. 5 et 6, cellules ascogènes. 7, asques à divers stades de maturité. 4 et 5, vues superficielles. 6 et 7, coupes transversales. FIG. 8. Exemples d'asques.

OBSERVATIONS MICROSCOPIQUES

Le champignon se développe uniquement sous la cuticule. Le mycélium suit d'abord plus ou moins le contour des cellules épidermiques; il est formé d'articles allongés, de diamètre régulier ou légèrement variqueux (Fig. 4). Il subit ensuite une intense ramification, tandis qu'il se recloisonne en articles courts qui deviennent les cellules ascogènes. Celles-ci s'étendent en une nappe continue à la surface des cellules épidermiques (Fig. 5 et 6).

Les septa mycéliens semblent dépourvus du disque présent chez beaucoup d'espèces de *Taphrina*. Ils ne possèdent pas de bouton central et d'autre part il n'apparaît jamais de délaminations (2).

Les asques mûrs possèdent une cellule-pied (Fig 7). Celle-ci est cylindrique ou légèrement conique, tronquée ou arrondie à la base, plus longue que large (Fig. 8). Dans chaque asque se différencient huit ascospores qui peuvent bourgeonner abondamment avant leur expulsion. Des mesures effectuées à partir des deux récoltes (notées ci-dessous A et B), sur une centaine d'asques à chaque fois, ont donné les valeurs suivantes, en µm (les moyennes calculées sont indiquées entre parenthèses):

Asques - A: 21-53 (31,6) x 5-11 (7,3). B: 21-47 (33,4) x 5-10 (7,1).
Cellules-pied - A: 5-17 (10,4) x 4-8 (5,2). B: 3-18 (10,4) x 3-7 (5,1).
Ascospores: 3-6 x 2-4.

ESSAI D'IDENTIFICATION

Selon la monographie de Mix (1), le mycélium des espèces de *Taphrina* parasites sur Fougères peut adopter quatre types de disposition: uniquement sous-cuticulaire, intercellulaire et sous-cuticulaire, uniquement intercellulaire, et enfin intrapariétale. L'espèce que nous avons observée appartient à la première catégorie. Dans celle-ci Mix en range six, dont cinq sont, comme la nôtre, pourvues d'une cellule-pied. Parmi ces cinq, l'une, *T. faulliana* Mix, parasite en Amérique du Nord un *Polystichum*, *P. munitum* (Kaulf.) Presl., mais les longueurs des asques (43-76 µm) et des cellules-pied (13-33 µm) sont nettement supérieures à celles que nous avons mesurées. Les quatre autres sont connues en Europe. Deux de celles-ci, *T. athyrii* Siem. et *T. hiratsukae* Nishida, occasionnent sur diverses Fougères de petites taches non épaissies, semblables à celles que nous décrivons, mais leurs asques et leurs cellules-pied ont des longueurs nettement plus faibles que chez notre espèce: respectivement 13-17 et 13-30 µm pour les asques, et 4,5-8 et 4-10 µm pour les cellules-pied. Les deux restantes, *T. fusca* et *vestergrenii* Giesenhag., provoquent des déformations en forme de cloques sur les frondes de plusieurs espèces de *Dryopteris* . La première a, par rapport à notre champignon, des asques plus courts (19-27 µm) et des cellules-pied plus longues (15-34 µm). La seconde présente des dimensions plus proches mais cependant encore quelque peu différentes; ci-après les valeurs, en µm, données par Mix (A) et celles que nous avons relevées nous-même à partir d'échantillons récoltés, en Ecosse, sur *Dryopteris filix mas* Schott (B):

Asques - A: 23-50 x 6-10. B: 24-49 (36) x 6-16 (10,8).
Cellules-pied - A: 10-23 x 4-10. B: 9-32 (17,4) x 4-13 (7,5)
Ascospores - A: 3,5-6 x 2,5-4. B: 5-8,5 x 3-4.

Les asques de *T. vestergrenii* ont une longueur semblable à celle des asques du parasite de *Polystichum setiferum*, mais ils sont plus larges d'après nos mensurations. Les cellules-pied sont à la fois plus larges et plus longues. Selon nous les ascospores sont aussi plus grandes.

Ces différences de dimensions, jointes à l'aspect différent des symptômes, nous conduisent à distinguer notre champignon de *T. vestergrenii*.

Parmi les espèces possédant d'autres types de disposition qu'une localisation purement sous-cuticulaire, Mix en signale deux sur *Polystichum* déterminant des symptômes comparables à ceux que nous décrivons, à savoir des taches non accompagnées de la formation de cloques : *T. wettsteiniana* Herzf. sur *P. lonchitis* (L.) Roth et *T. polystichi* Mix sur *P. acrostichoides* (Michx.) Schott. Il attribue à toutes les deux un mycélium à la fois intercellulaire et sous-cuticulaire. Chez *T. wettsteiniana* les dimensions de l'asque sont dans les limites de celles que nous avons mesurées (25-38 x 6-10 µm) ainsi que celles de la cellule-pied (6-13 x 5-8 µm), mais la présence de cette dernière n'est pas constante, alors que tous les asques que nous avons observés sur *Polystichum setiferum* en possédaient une. Par contre, chez *T. polystichi* les asques sont toujours supportés par une cellule-pied; les dimensions qu'en donne Mix sont comparables à celles des asques de notre champignon (23-53 x 4,5-8,5 µm). Nous avons eu l'occasion d'observer un échantillon de cette espèce, conservé dans l'herbier du Muséum National d'Histoire Naturelle de Paris (portant la référence: Sydow 1005). Nous n'avons pas décelé la présence d'un mycélium intercellulaire, contrairement à ce qu'indique Mix. Ce *Taphrina* semble donc très voisin de celui que nous avons récolté. D'après les mensurations de Mix il s'en différencierait toutefois par la longueur plus importante des cellules-pied (13-23 µm). Il faut aussi noter que les taches peuvent atteindre un plus grand diamètre (jusqu'à 1 cm), mais ceci pourrait être dû à la différence d'hôte, les pinnules de *Polystichum acrostichoides* étant beaucoup plus grandes que celles de *Polystichum setiferum*. Une étude comparative de souches isolées à partir des deux Fougères serait souhaitable, ainsi que des expériences d'inoculation, avant de décider si les deux parasites appartiennent ou non à la même espèce.

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THYREA POLYGLOSSA and THYREA DIVERGENS sp. nov.

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SUMMARY

Thyrea polyglossa (Nyl.) Zahlbr. is reported from Mexico. Information on the apothecia and pycnidia is given for the first time. A new species, Thyrea divergens Henssen, is described from Kenya. It is closely related to T. polyglossa, from which it differs in having erect, much-branched lobes with divergent tips. The relationship with other species of the genus is discussed.

INTRODUCTION

Thyrea polyglossa (Nyl.) Zahlbr. was described by Nylander (1876) from a sterile specimen collected by Wright in Cuba. In Mexico we found a rosette-shaped, fertile lichen which corresponded well to the original collection of T. polyglossa, and it enables us to provide a description of the fruiting structures.

An undescribed Thyrea species from Kenya, kindly sent to us by Dr. Swinscow, was found to be closely related to T. polyglossa; the new species is named here T. divergens. The two species differ in some characteristic features from the type species, T. plectospora Mass. and other species of the genus.

MATERIAL AND METHODS

The herbarium abbreviations follow Index Herbariorum. - Freezing microtome sections were embedded in lactophenol cotton-blue (LPCB). For studying the iodine reaction Lugol's solution was added without pretreatment. For habit photographs a Wild M 7 dissecting microscope was used, and for anatomical structures a Wild M 20 microscope. The measurements given refer to preparations in LPCB, or air dried material.

DESCRIPTIONS

Thyrea polyglossa (Nyl.) Zahlbr. 1924 p.808
Omphalaria polyglossa Nyl. (1876 p.558). Typus: Cuba, Wright, Lichenes Cubenses Ser. II. 47 (H: hb. Nylander 42671-lectotypus, here chosen; G, UPS-iso-lectotypi).

Further specimens examined: Mona Island near Puerto Rico, on exposed limestone, 1914, Britton et al. 1850 (MICH: no. 12420 and 13440).- Mexico, Hidalgo, Metztitlán, in seepage lines of NW exposed, vertical limestone faces along roadside at 1350 m, 1982 Henssen & Vobis 28734c (MB).

Figs 1A-D, 2A-E, 3F
Thallus blackish in flat rosettes 8-13(-17) mm wide, deeply divided into lobes, attached by a central umbilicus. Lobes flat, tongue-shaped or angular, furrowed on under side, 0.6-1.2(-1.6) mm wide, furcately branched at tip, bearing 0.05-0.2 mm long isidia or small lobules. Thallus (in section) 400-600(-1000) µm thick, heteromerous, algal zone 35-70 µm thick. Hyphae lying horizontally in thallus centre, perpendicularly towards margin; hyphal cells in thallus centre long, cylindrical, 1.5-2.5 µm thick, below and within algal zone short and enlarged to 3.5-8 µm, haustoria globose or finger-like (Figs 2B-E, 3F). Phycobiont probably a member of the Pleurocapsales, cells singly or in pairs, 4.5-8(-12) µm diam.

Apothecia marginal, submarginal or laminal on ridges, 0.25 -0.6 mm diam., constricted at base, thalline margin c. 0.1 mm thick, disc brown. Hymenium 130-140 µm high, hymenial gelatin deep blue in iodine, hypothecium 20-40 µm high, excipulum proprium 45-70 µm high, restricted to base of apothecium, composed of loosely interwoven hyphae elongated into a stipe. Asci cylindrical, 60-70 x 11-12 µm (immature), with 8 or fewer spores. Spores simple, colourless, ellipsoid, ovoid or curved, 9.5-14 x 4.5-9.5 (immature). Pycnidia c. 0.25 µm broad, wall convoluted, conidia short fusiform, 2.5-4 x 1 µm, produced terminally by elongated conidiogenous cells.

Ecology and distribution. *T. polyglossa* grows in seepage lines on calcareous rock. The lichen has been collected so far in Mexico, Cuba and Mona Island near Puerto Rico.

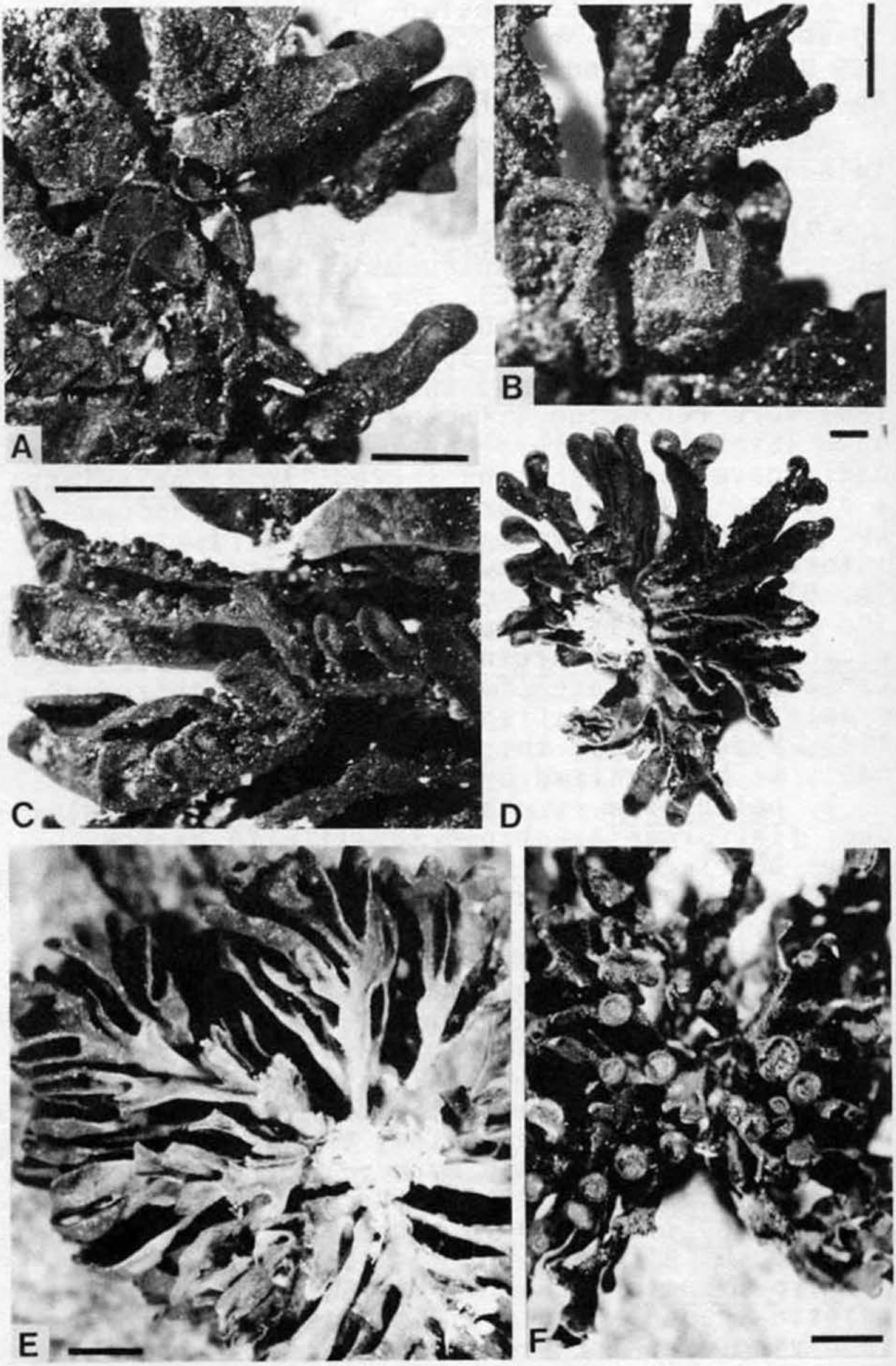
Remarks. In the material from Cuba and Mona Island the lobes are mainly flat and tongue-shaped (Fig. 1D), while in the Mexican specimen they are angular and more deeply furrowed on the under side; lobules are conspicuously developed in the type material (Fig. 1C). The isidia in the type collection may have a depressed tip, thus simulating apothecia, but no apothecia or pycnidia were found when the type and the lichen from Mona Island were reexamined. In the Mexican specimen both juvenile and large apothecia contained only badly developed asci and spores. In *T. polyglossa* a distinct excipulum proprium is not developed but replaced by a cone-shaped web of loosely interwoven hyphae below the hypothecium (Fig. 1A, D).

The phycobiont is probably a species of *Chroococcidiopsis* or *Myxosarcina*, genera of the *Pleurocapsales* which recently have been recognized as symbiotic algae in Lichinaceae (Büdel & Henssen 1983, Büdel 1985); this assumption, however, needs to be verified by culture experiments.

T. polyglossa is characterized by deeply divided, flat, rosette-shaped thalli with narrow lobes bearing large isidia, and an excipulum restricted to a basal hyphal web. A heteromerous thallus, composed of horizontally lying thin hyphae in the central part, and perpendicularly arranged large-celled hyphae in the marginal part, is a characteristic feature which *T. polyglossa* has in common with the new species *T. divergens*.

T. rotundata Büdel *et al*. is similar in habit but differs having laminal apothecia, non-isidiate lobes, and in the anatomy of the thallus. In this species the hyphae form a reticulum in the marginal part; in addition the algal cells are smaller and clustered in packets of four to eight (Henssen et al. 1985).

T. pulvinata (Schaer.) Mass., which also has a rosette-shaped, deeply divided thallus, differs in having erect, thick and wide lobes with a rather uniform net of thin hyphae, small, clustered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algal cells, and a hymenium surrounded by a cup-shaped excipulum proprium composed of parallel hyphae. T. plectospora corresponds in the anatomy of its thallus and apothecium to T. pulvinata but has an orbicular thallus which is not deeply divided into lobes and laminal, immersed apothecia (cf. Henssen 1979, Figs 4H, 6E).

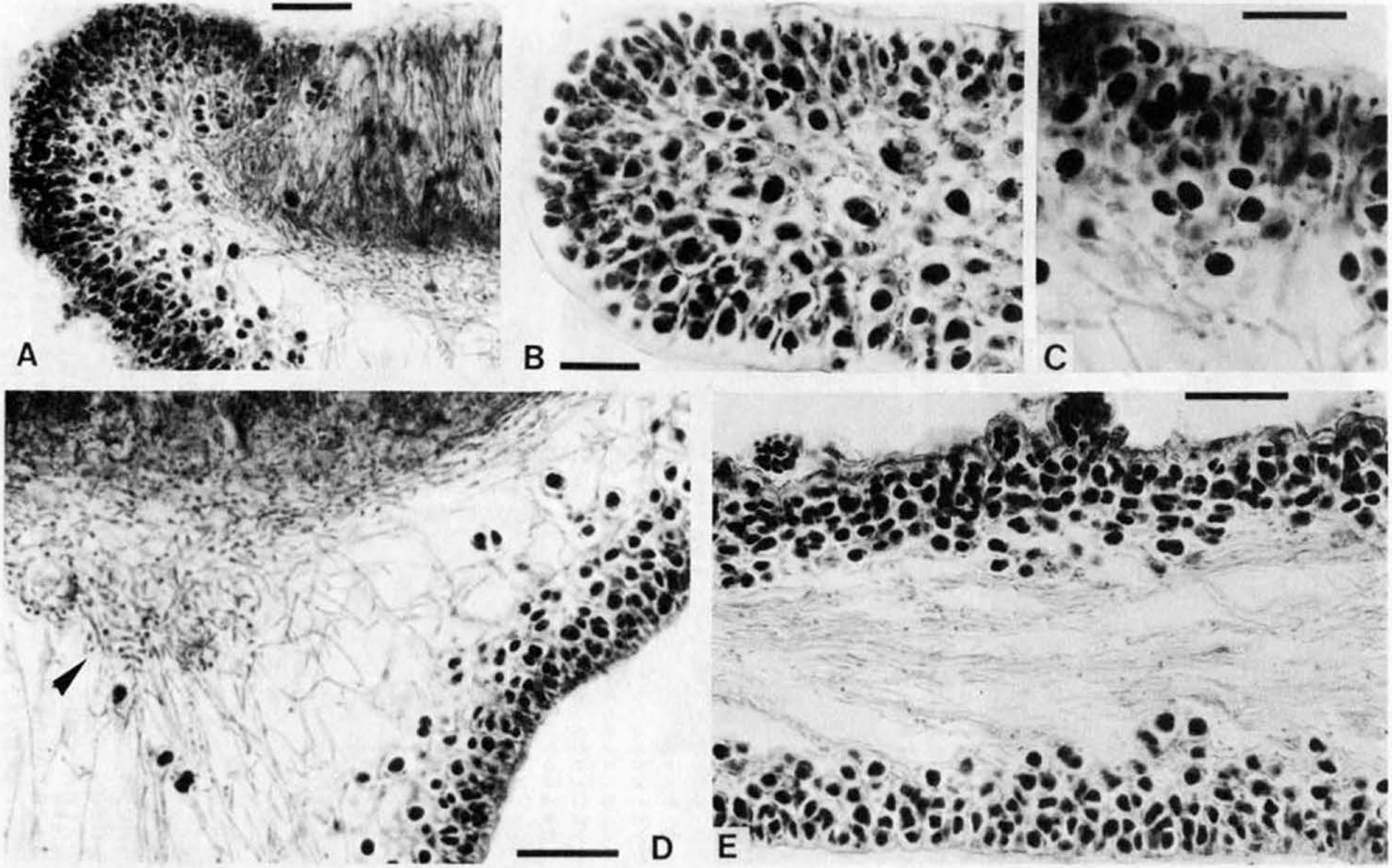
Thyrea divergens Henssen sp. nov.
Figs. 1E-F, 3A-E

DIAGNOSIS. Thallus rosulatus, fruticulosus, nigricans, isidiosus, usque ad 10 mm latus, umbilico affixus. Lobi erecti, applanati, ramosi, 3-5 mm longi et 0.5-0.8 mm lati, apice divergenti, isidia globosa, usque ad 0.3 mm lata. Hyphae ordinatae longitudinaliter in centro thalli et perpendiculariter versus marginem, cortex deest, cellulae algarum ad zonam marginale restrictae. Alga verosimiliter ad ordinem Pleurocapsales pertinens, cellulae (4.5-)6-12 µm latae. Apothecia marginalia, adnata, usque ad 1 mm lata. Hymenium 70-100 µm altum, in iodo vinosum, hypothecium 25-35 µm altum, excipulum proprium 45-50 µm crassum, ad basi restrictum et in stipite elongatum. Asci cylindracei, 6-8-spori, 60-80 x 10-12 µm. Sporae eseptatae, incolores, ellipsoideae, 12-14 x 8 µm. Pycnidia marginalia, c. 0.15 mm lata, conidia fusiformia, 2.5-4 x 1 µm.

Typus: Kenya, Eastern Province, Distr. Marsabit, Lake Turkana, Koobi Fora, 3°55'N 36°12'E, on rocks, c. 1800m, 1983, Hindmarsh 58 (MB-holotypus; BM, EA-isotypi).

Thallus blackish, to 10 mm large, rosette-shaped, fruticose, isidiate, attached by central umbilicus. Lobes more or less erect, 3-5 mm long, 0.5-0.8 mm wide and c. 0.06-0.8 mm thick, flat-

Fig. 1. Habit photographs of Thyrea species. A-D, T. polyglossa (A, isotype-UPS, B, Henssen 28734c-MB, C, isotype-G, D, lectotype-H); A, tongue-shaped lobes; B, lobe bearing submarginally a young apothecium (arrow); C, isidia in part elongated into lobuli; D, thallus under side. E-F, T. divergens (holotype); E, thallus under side; F, lobes bearing marginal apothecia. Scale = 1mm.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tened, plane or furrowed on the under side, richly branched, the side branches divergent; isidia globular, to 0.3 mm wide. Thallus heteromerous, algal zone 20-50 µm high, central hyphae 1.5-2.5 µm thick, lying horizontally, anticlinally orientated towards margin and cells enlarged to 7 µm (Fig. 3E). Phycobiont probably a member of the Pleurocapsales, algal cells singly or in pairs, cells (4.5-)6-12 µm diam.

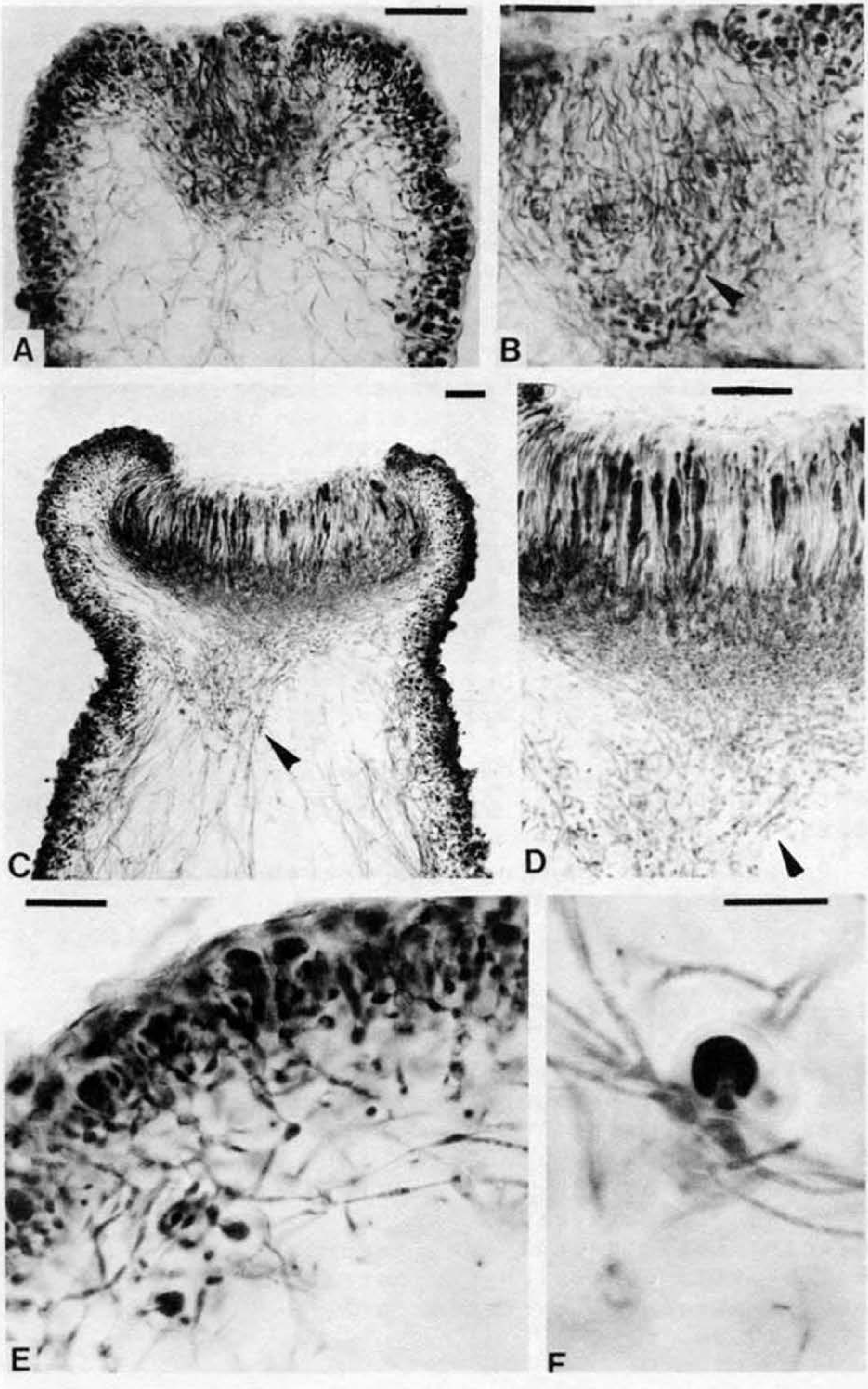
Apothecia marginal, to 1 mm diam., thalline margin c. 0.1 mm thick, disc brown. Hymenium 70-100 µm, hymenial gelatin in iodine becoming blue to wine-red, hypothecium 25-35 µm, excipulum 45-50 µm, composed of roundish cells, elongated into a stipe of loosely interwoven hyhae (Fig. 3C-D). Paraphyses 1.5-2 µm thick, the apical cells enlarged to 3.5 µm. Asci cylindrical, 60-80 x 10-12 µm, frequently containing fewer than 8 spores. Spores simple, colourless, ellipsoid, 12-14 x 7-8 µm. Pycnidia marginal, c. 0.15 mm broad, conidia short, fusiform, 2.5-4 x 1 µm, produced terminally by elongated conidiogenous cells.

Ecology and distribution. *T. divergens* grows on calcareous rock. It is known only from the type locality.

The epithet "*divergens*" refers to the divergent manner of growth of the side branches of the lobes.

Remarks. The thallus is blackish in surface view while on the under side the basal parts of the lobes adjacent to the substrate are pale from

Fig. 2. Anatomy of *Thyrea polyglossa* (microtome sections in LPCB; A-B, lectotype-H, C-D, Henssen 28374c-MB, E, isotype-UPS). A, l. s. of apothecium, branched paraphyses of varying length; B, l. s. of lobe tip in tangential section, hyphae in reticulum with vacuolated cells C, l. s. of thallus margin with anticlinaly arranged hyphae; D, l. s. of apothecium, part of hypothecium with adjacent loose hyphal web (arrow); E, l. s. of thallus with central hyphal strand and marginal zone of algal cells. Scale in A, D-E = 50 µm, in B-C = 20 µm.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decay (Fig. 1E). Only some of the thalli were fertile, bearing aggregated apothecia in the centre (Fig. 3F). The developmental morphology of the ascocarp has been followed from the initial stages. The young paraphyses and remains of ascogonia and trichogynes seen in Fig. 3A-B indicate that they develop in the manner normally found in the Lichinaceae via a hyphal web of generative tissue (cf. Henssen 1963, Henssen 1981). In mature apothecia the paraphyses are distinctly septate and only sparsely anastomotic; the tips are covered by a thick gelatinous layer (Fig. 3C-D).

In the anatomy of the thallus and apothecium *T. divergens* corresponds well to *T. polyglossa* but differs in a more distinctly developed excipulum proprium, which is a compact structure composed of roundish cells.

T. divergens is characterized by the deeply lobate, rosette-shaped thallus with erect, flat, richly branched lobes having divergent tips. From *T. polyglossa* it is easily distinguished by the branching pattern (cf. Figs. 1D and E), and fertile specimens also by the different iodine reaction. From other species of *Thyrea* it differs in the same way as *T. polyglossa* (see above).

Relationships of Thyrea polyglossa and Thyrea divergens to other species of the genus. The corresponding internal morphology of the thallus and apothecia indicates a close relationship between *T. polyglossa* and *T. divergens*. A heteromerous thallus with a distinct algal zone is found also

Fig. 3. Anatomy of *Thyrea* species (microtome sections in LPCB). A-E, *T. divergens* (holotype-MB); A-B, l. s. of apothecial primordia. Remains of trichogyne indicated by an arrow; C, l. s. of mature apothecium, stipe of loose hyphal web indicated by arrow; D, hymenium and stipe (arrow) at higher magnification. E, l. s. of thalline margin with anticlinally arranged hyphae. F, *T. polyglossa* (Henssen 28374c-MB); haustorium in algal cell. Scale in A-D = 50 µm, in E-F = 20 µm.

in *T. rotundata* and in the *T. giradii*-group. *T. girardii* (DR) Bagl. & Car. and related species differ, however, in having an orbicular thallus and laminal, immersed pycnoascocarps; the group is considered to be more closely related to *T. plectospora*, which has a similar developmental morphology of the apothecia. *T. rotundata*, on account of the characteristics mentioned above, is in our opinion intermediate between *T. polyglossa*/*T. divergens* and the *T. giradii*-group. A discussion of the delimitation of *Thyrea* from other genera of the Lichinaceae and an attempt at a subdivision of the genus into satisfactory sections will be provided in a forthcoming paper.

ACKNOWLEDGEMENTS

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ZUSAMMENFASSUNG

An Hand von fertilem Material aus Mexico können erstmals Angaben über die Apothecien und Pycnidien von *Thyrea polyglossa* (Nyl.) Zahlbr. gemacht werden. Die Flechte stimmt in Habitus und Anatomie weitgehend mit der hier neu beschriebenen *Thyrea divergens* Henssen von Ostafrika überein. Die beiden Arten zeichnen sich durch ein heteromeres Lager mit unterschiedlicher Hyphendifferenzierung im Innern und marginalem Teil des Thallus aus. Die Apothecien entwickeln sich über einen Hyphenknäuel aus generativem Gewebe, eine excipuloide, in einen Stiel sich verlängernde Struktur ist auf den basalen Teil des Fruchtkörpers beschränkt; sie besteht bei *T. polyglossa* aus einem lockeren Hphengeflecht, bei *T. divergens* aus dicht gedrängten rundlichen Zellen. Bei beiden Arten ist der umbilicate Thallus tief in Loben eingeschnitten. Er bildet bei *T. polyglossa* eine flache Rosette aus Loben mit wenig Seitenästen, bei *T. divergens* dagegen ein strauchig aufrechtes Lager aus reich verzweigten Loben, deren Enden divergieren (Name!). Beide Arten sind isidiös;

die Isidien sind bei *T. divergens* klein und kugelig, bei *T. polyglossa* größer, langestreckt und können zu Lobuli auswachsen. Asci und Sporen wurden bei beiden Arten nur in schlecht entwikkeltem Zustand beobachtet, die Hymenialgallerte färbt sich bei *T. polyglossa* blau, bei *T. divergens* über blau weinrot. Die Pycnoconidien sind bei beiden Arten kurz spindelig. Die Arten sind Kalklbewohner, *T. polyglossa* wurde bisher auf Cuba, Mona Island bei Puerto Rico und in Mexiko gefunden, *T. divergens* ist nur von der Typuslokalität in Kenya bekannt. Die beiden Arten sind nahe miteinander verwandt; die nächsten Beziehungen scheinen zu *T. rotundata* Büdel *et al.* zu bestehen, die eine Zwischenstellung zur *T. giradii*-Gruppe einnimmt.

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THE GENUS ARTHRODERMA AND ITS LATER SYNONYM NANNIZZIA

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SUMMARY

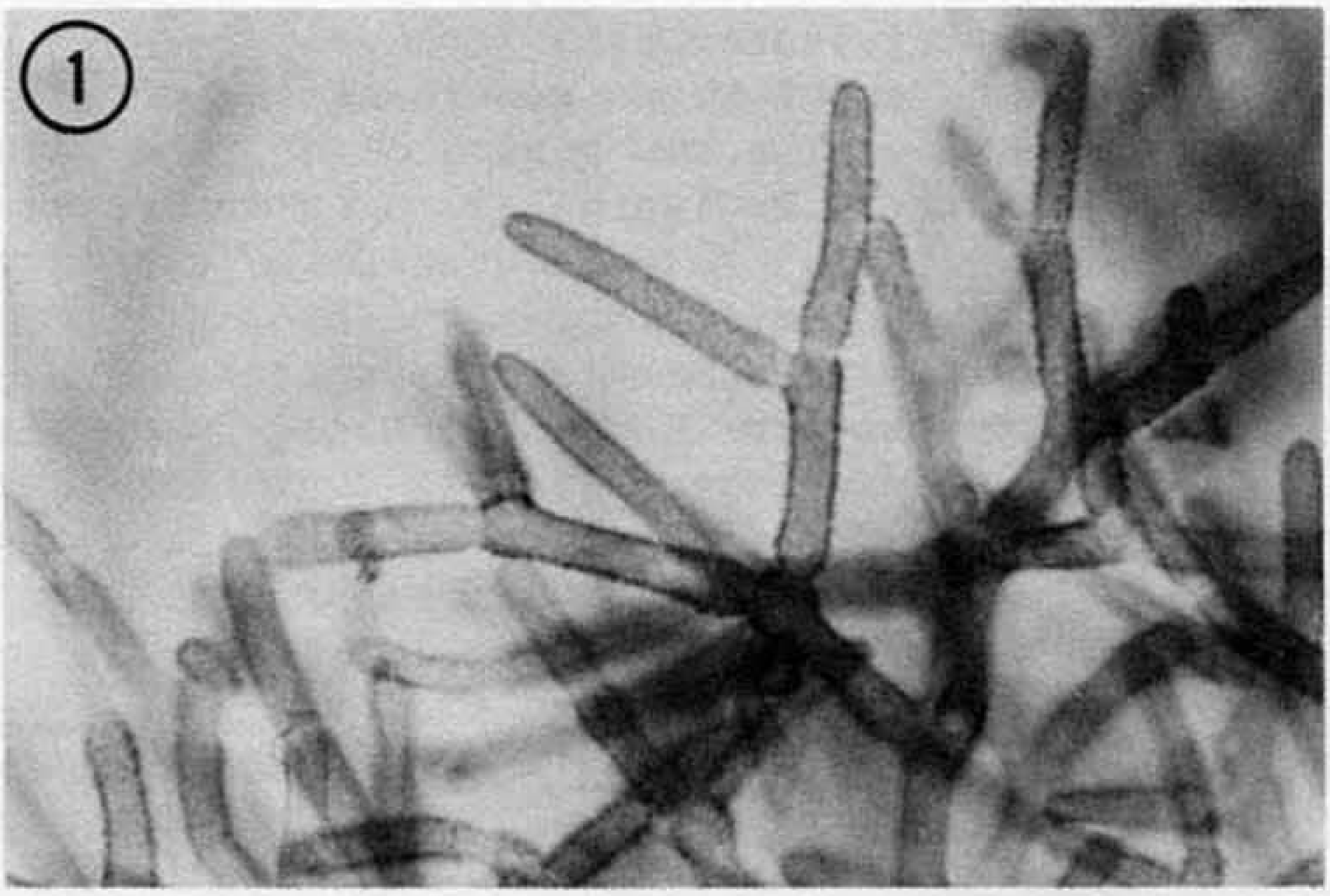
Based upon a careful evaluation of the morphological characteristics used to define the genera *Arthroderma* and *Nannizzia*, it is concluded that these two taxa are congeneric. Owing to priority, *Nannizzia* is a later synonym of *Arthroderma*. The following new combinations are proposed: *A. borellii*, *A. cajetani*, *A. cookiellum*, *A. corniculatum*, *A. fulvum*, *A. grubyi*, *A. gypseum*, *A. incurvatum*, *A. obtusum*, *A. otae*, *A. persicolor*, and *A. racemosum*. Neotypes have been designated for *A. cajetani* and *A. grubyi*.

INTRODUCTION

In 1854, Currey (10) provisionally proposed the genus *Arthroderma* for a fungus occurring on dead leaves and sticks. Berkeley (9) validated the genus *Arthroderma* in 1860 and named Currey's fungus *A. curreyi*. Saccardo misinterpreted the ascocarps of *A. curreyi* as sporodochia and incorrectly considered the genera *Illosporium* and *Arthroderma* congeneric (33). Members of the genus *Arthroderma* produce small gymnothecia having hyaline, branched, septate peridial hyphae consisting of either symmetrically or asymmetrically dumbbell-shaped densely asperulate cells. The asci are globose to subglobose, evanescent and eight-spored. The 1-celled ascospores are smooth, oblate and yellow in mass (28).

The genus *Nannizzia* was established in 1961 by Stockdale to accommodate *N. incurvata*, the teleomorph of *Microsporum gypseum* (34). Species of *Nannizzia* are characterized by producing globose gymnothecia having a peridium (Figs. 1-2) consisting of a network of hyaline, septate, verticillately branched hyphae and densely asperulate outer peridial cells that are moderately thick-walled and more or less symmetrically constricted, as well as three kinds of peridial appendages. The appendages consist of: 1) elongate, tapering, straight or loosely coiled hyphae, 2) tightly coiled hyphae (spirals), and 3) macroconidia. The hyaline, evanescent asci are globose to ovate, with eight oblate ascospores; the ascospores are yellow in mass. Even though Stockdale felt that *N. incurvata* most closely resembled *A. curreyi*, she considered the differences in the appearance of the peridium to be of sufficient significance to warrant the establishment of the new genus *Nannizzia*. The distinguishing features used to separate these two genera included: 1) the branching of the peridial hyphae in *A. curreyi* is consistently dichotomous rather than verticillate as in *N. incurvata*, 2) the cells of the outer peridium of *A. curreyi* have small protuberances which are absent in *N. incurvata*, 3) the long, straight, or loosely coiled terminal extensions of the peridial hyphae characteristic of the *Nannizzia* spp. are absent in *A. curreyi*, and 4) the spiral appendages in *A. curreyi* are predominately lateral (34).

Since the establishment of the genus *Nannizzia* (34), several new species have been described which has resulted in a broadening of the generic concept of this taxon (1,13,16,35). For example, the branching of the peridial hyphae in *N. obtusa* is mostly dichotomous and only occasionally verticillate (13). In *N. grubyi* it is dichotomous and uncinate, but never verticillate (16). As a result of these findings and unpublished observations, Stockdale expressed doubt in maintaining these fungi in two separate genera. Nevertheless, she retained them as distinct genera because of the presence of protuberances on the peridial hyphal cell walls of *Arthroderma*, structures which are absent in species of *Nannizzia* (35).



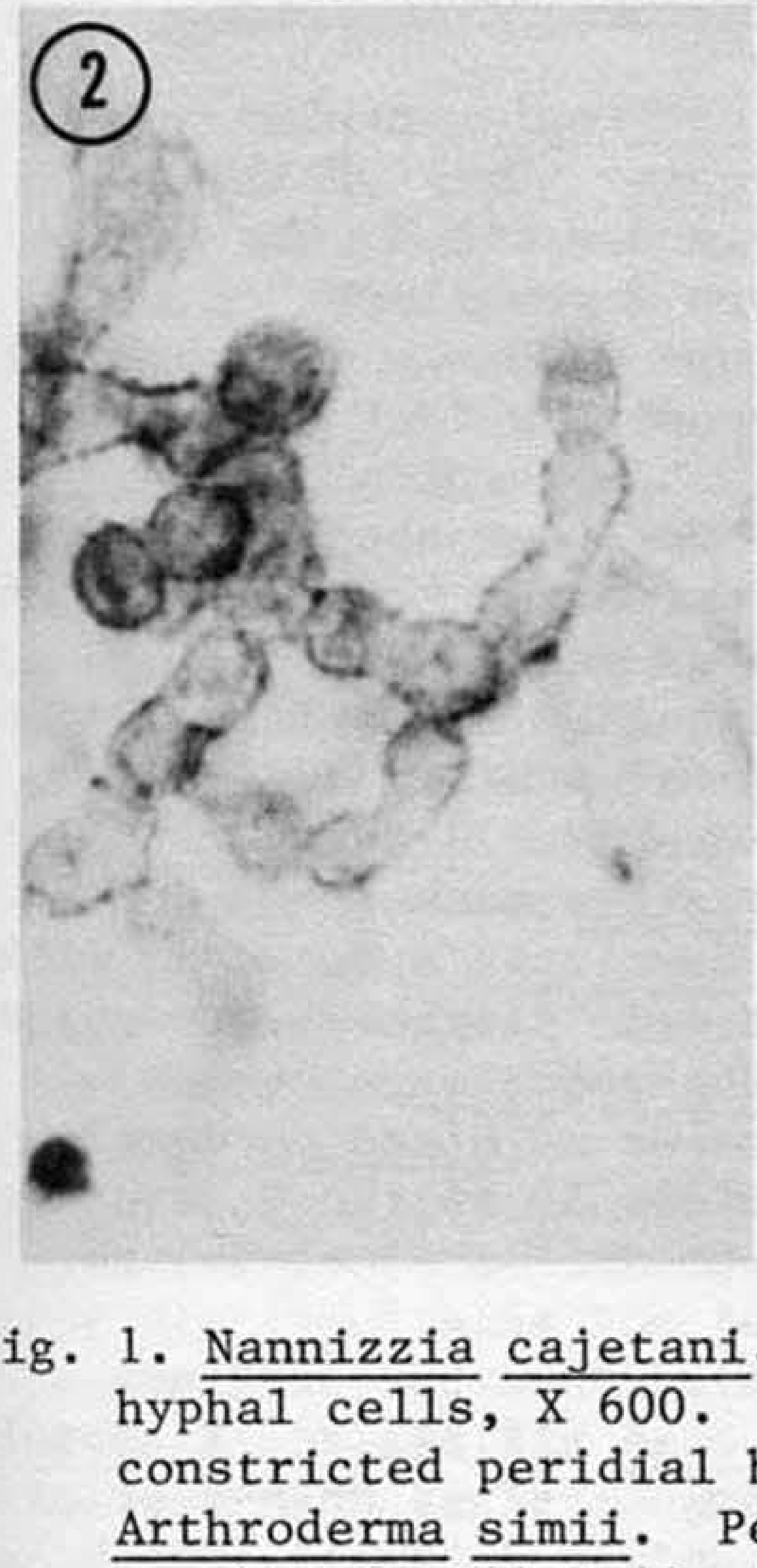


Fig. 1. *Nannizzia cajetani*. Slightly constricted peridial hyphal cells, X 600. Fig. 2. *N. otae*. Symmetrically constricted peridial hyphal cells, X 1440. Fig. 3. *Arthroderma simii*. Peridial hyphal cells showing roughened cell walls in the constricted area, X 1440. Figs. 1 and 2 reproduced with permission from Sabouraudia 1:173-177, 1961 and Trans. Br. Mycol. Soc. 81:645-650, 1983, respectively.

In 1979, Takashio (38) stated that "the only distinguishing features of these genera is the morphology of the peridial cells. The two genera might be unified in the genus Arthroderma." McGinnis (25) also suggested that Arthroderma and Nannizzia could be considered congeneric because he felt that the differences in the degree of constriction of the cells composing the peridial hyphae were not siginificant at the generic level. Because the identification of species classified in these two genera relies so heavily upon their anamorphs rather than their teleomorphs, this also tends to support the union of Arthroderma and Nannizzia. The situation involving Arthroderma and Nannizzia parallels that of Ajellomyces and its later synonym Emmonsiella (26).

CHARACTERISTICS OF ARTHRODERMA AND NANNIZZIA

In 1967, Stockdale described N. persicolor as the teleomorph of Trichophyton persicolor (36). Unlike the other Nannizzia species previously described, the peridial hyphal cells of N. persicolor were dumbbell-shaped with only one slight constriction in the middle. The peridial appendages consisted of numerous spirals that were often branched. Long, straight hyphae and macroconidia characteristic of Nannizzia spp. were not observed. Stockdale now considers the separation of these genera on the basis of the peridial hyphae as weak, but still believes that they should be maintained as separate genera because they have different conidial states, e.g. Nannizzia has a Microsporum anamorph and Arthroderma either a Trichophyton or Chrysosporium anamorph. Stockdale might have considered Nannizzia synonymous with Arthroderma, if she had not observed "slightly verruculose walls" on the macroconidia of T. persicolor, thereby, rendering it by definition a species of Microsporum (2). It is important to note that Article 59 of the Code states that an anamorph cannot be used to define a teleomorph.

Additional Nannizzia spp. deviating from the original concept of the genus include N. otae (17,24) and N. borellii (27), both of which have dichotomous rather than verticillate branching peridial hyphae, and N. cookiella which has spiral appendages (14). Nannizzia otae forms dumbbell-shaped peridial hyphal cells which are sharply constricted in the middle (Fig. 2), a key characteristic of the genus Arthroderma. In addition, it produces the three types of appendages that are characteristic of the genus Nannizzia (24).

Nannizzia-like characteristics found in species of Arthroderma include: 1) some rough rather than entirely smooth cell walls in the intervening constricted portions of the outer peridial hyphal cells as in A. simii (Fig. 3), A. benhamiae, and A. vanbreuseghemii (37), 2) symmetrically constricted dumbbell-shaped cells of the peridial hyphae lacking protuberances as in A. lenticularum (31) and A. vanbreuseghemii (37), 3) formation of elongate tapered hyphae as peridial appendages in A. benhamiae (3) and A. ciferrii (41), and 4) macroconidia occurring as peridial appendages (albeit infrequently) like those produced by A. uncinatum, A. simii, A. flavescens, and A. gertleri (28).

Current concepts for the classification of the ascomycetes emphasize the structure of the ascus and ontogeny of the centrum (8,15). However, generic descriptions of taxa within the Gymnoascaceae have been based primarily on the absence or presence of peridial hyphae and their appendages, peridial morphology, ascospore morphology and color (4,7). Von Arx (5,6) considered the peridial hyphae and their appendages of limited taxonomic significance because they may be present or absent depending upon growth media, humidity, light and age. For example, Dawson & Gentles (13) observed differences in the peridium of A. uncinatum which were dependent on the medium employed to induce the perfect state. In his discussion of the Gymnoascaceae, von Arx (5,6) considered the size and shape of the ascospores and the type of ascocarp initials as useful characters for the deliniation of the various genera. These characters, in addition to the absence or presence of the peridial hyphae and appendages, their morphology, the size and color of the ascomata, and appearance of the ascospore wall are important criteria for distinguishing the genera of the Gymnoascaceae (5). Fennell (15) considered ascocarp initials, origin of the peridial hyphae and asci, appearance of the ascospores and the anamorph to be of generic significance in her classification of the Plectomycetes.

The principal taxonomic criteria suggested by von Arx (5,6), Fennell (15), Padhye and Carmichael (28), Stockdale

(34), and others are summarized in Table 1 as a means to compare and contrast the genera *Arthroderma* and *Nannizzia*. Ascocarp initiation, the development of the ascocarp and its centrum, the ontogeny of the asci, and the appearance of the asci and ascospores are essentially the same in both genera (1,3,18,22,23,34,40,43). Ascospores, which had been described as lenticular in some *Arthroderma* and *Nannizzia* species, have been redescribed as oblate sphaeroids by Padhye & Carmichael (29).

The peridial hyphae in most species of *Arthroderma* are typically uncinately branched. The branching is sometimes dichotomous but never verticillate. The branching of the peridial hyphae in species of *Nannizzia* is commonly verticillate, sometimes dichotomous, and more rarely uncinate. Hence, there is an overlap with no sharp demarcation between these two genera. With regard to peridial appendages, lateral or terminal spirals may be found in both genera. Other appendages, such as the long straight tapered hyphae and macroconidia, are more commonly found in species of *Nannizzia*, but they may also be present in some species of *Arthroderma*. In *Arthroderma*, the outer cells of the peridial hyphae are always deeply constricted, and usually smooth in the mid-region, giving an appearance of a dumbbell. These cells may be symmetrically or asymmetrically dumbbell-shaped.

The *Nannizzia* spp. have uniformly roughened outer peridial cell walls. The degree of roughness varies with the species from minutely echinulate to densely verruculose or asperulate. The outer peridial cells are also constricted. However, depending upon the species, there may be 1-3 constrictions per cell. They may vary from minimally constricted as in *N. cajetani* (Fig. 1) to deeply constricted and dumbbell-shaped as in *N. otae* (Fig. 2), the latter thereby resembling *Arthroderma*.

CONCLUSIONS

In our opinion, the reasons for creating the genus *Nannizzia* are no longer applicable. The characteristics of the teleomorphic species, reported since the original description of this genus, are similar to those of the genus *Arthroderma* (Table 1). The only distinctions

Table 1. Summary of the principle taxonomic characteristics of Arthroderma and Nannizzia

	Arthroderma	Nannizzia
Ascocarp initiation	Club-shaped, septate antheridium surrounded by a coiled ascogonium; croziers develop from the septate ascogonial coil. Gymnothecial initial becomes surrounded by hyphae growing from the antheridium or vicinity.	Club-shaped, septate antheridium surrounded by a coiled ascogonium; croziers develop from the septate ascogonial coil. Gymnothecial initial becomes surrounded by hyphae growing from the antheridium or vicinity.
Ascocarps	Globose, whitish to pale yellow to buff, 100-970 µm excluding appendages.	Globose, pale yellow to yellow, buff to tan, 150-1250 µm excluding appendages.
Peridial hyphae	Hyaline, septate, pale yellow or pale buff, branching typically uncinate, sometimes dichotomous.	Hyaline, septate, pale yellow or pale buff, branching typically verticillate, sometimes dichotomous, rarely uncinate.
Outer cells of peridial hyphae	Dumbbell-shaped, symmetrical or asymmetrical, densely asperulate, echinulate or verruculose.	Slightly constricted to dumbbell-shaped, symmetrical, densely asperulate, echinulate or verruculose.
Peridial appendages	1. Spirals (terminal or lateral). 2. Elongate straight hyphae (usually rare). 3. Rarely, macroconidia or microconidia.	1. Spirals (terminal or lateral). 2. Elongate straight hyphae. 3. Macroconidia.
Asci	Globose to subglobose, evanescent, 8-ascospores, 3.9 - 8.3 x 3.5 - 7.5 µm.	Globose to ovate, evanescent, 8-ascospores, 4 - 7 x 5 - 7 µm.
Ascospores	Hyaline, smooth, lenticular, oval, oblate, yellow in mass, 1.5 - 3.5 x 1.4 - 3.5 µm.	Hyaline, smooth, lenticular, oval, ovate, oblate, yellow in mass, 1.5 - 6 x 1.6 - 4 µm.
Conidia	Holothallic macroconidia.	Holothallic macroconidia.
Anamorphs	Chrysosporium spp., Trichophyton spp.	Microsporum spp.

between these genera lies in their anamorphs, which are primarily differentiated from each other by the appearance of the macroconidial cell walls, i.e. roughened in the Microsporum spp. and smooth in the Trichophyton spp. However, smooth-walled mutants have been reported in M. gypseum (42,44), and M. persicolor was once considered a Trichophyton sp. because its macroconidial cell walls were originally thought to be smooth. The genera Trichophyton and Microsporum are closely related antigenically and biochemically (21). This relationship has been supported most recently by fatty acid data (20), zymogram patterns (19), DNA base ratio studies (11), and DNA hybridization analysis (12).

It is clear that the various species classified in the genera Arthroderma and Nannizzia represent a continuum. The differences observed in these fungi no longer merit maintaining them in two separate genera. We believe that Arthroderma and Nannizzia are congeneric and that the species currently classified in the genus Nannizzia must be transferred to Arthroderma.

There is some controversy regarding the relationship of these fungi to the genus Rollandina, which is based upon the type species R. capitata (30). We have excluded this genus because the ascospores of R. capitata have an equatorial band, a characteristic which is absent in all of the accepted species of Arthroderma.

TAXONOMIC PART

Arthroderma Currey ex Berkeley emend. Weitzman, McGinnis, Padhye et Ajello. Type Species: A. curreyi Berkeley. Outlines of British Fungology, p. 357, 1860.
= Nannizzia Stockdale, Sabouraudia 1:45, 1961.

Gymnothecia globose, whitish to pale yellow or buff; peridium consisting of a densely packed network of interwoven hyphae; peridial hyphae hyaline, pale yellow or buff, septate, usually uncinately, verticillately or dichotomously branched; outer peridial hyphal cell walls echinulate, densely asperulate or verruculose, with 1-3 slight to moderate constrictions, or deeply constricted in the middle, symmetrically or asymmetrically dumbbell-shaped; peridial appendages consist of tightly to loosely coiled spiral hyphae which may be terminal or lateral, some species producing additional terminal appendages consisting of elongate slender tapered hyphae, or macroconidia; gymnothecial initials composed of a clavate antheridium surrounded by a coiled ascogonium; asci globose, subglobose, or oval, evanescent, 8-spored, 3.9-8 x 3.5-7.5 µm; ascospores oval, lenticular, oblate, smooth, hyaline, yellow in mass, 1.5-6 x 1.4-4 µm; homothallic or heterothallic; *Chrysosporium*, *Microsporum*, or *Trichophyton* anamorphs.

1. *Arthroderma borellii* (Moraes, Padhye et Ajello) Padhye, Weitzman, McGinnis et Ajello, comb. nov.
   basionym: *Nannizzia borellii* Moraes, Padhye et Ajello, Mycologia 67:1112, 1975.

2. *Arthroderma cajetani* (Ajello) Ajello, Weitzman, McGinnis et Padhye, comb. nov.
   basionym: *Nannizzia cajetani* (as "*cajetana*") Ajello, Sabouraudia 1:175, 1961.

3. *Arthroderma cookiellum* (de Clercq) Weitzman, McGinnis, Padhye et Ajello, comb nov.
   basionym: *Nannizzia cookiella* de Clercq, Mycotaxon 18:24, 1983.

4. *Arthroderma corniculatum* (Takashio et de Vroey) Weitzman, McGinnis, Padhye et Ajello, comb. nov.
   basionym: *Nannizzia corniculata* Takashio et de Vroey, Mycotaxon 14:384, 1982.

5. *Arthroderma fulvum* (Stockdale) Weitzman, McGinnis, Padhye et Ajello, comb. nov.
   basionym: *Nannizzia fulva* Stockdale, Sabouraudia 3:120, 1963.
   syn: *N. gypsea* (Nannizzi) Stockdale var. *fulva* (Stockdale) Apinis, Mycol. Paper 96:33, 1964.

6. *Arthroderma grubyi* (Georg, Ajello, Friedman et Brinkman) Ajello, Weitzman, McGinnis et Padhye, comb. nov.
   basionym: *Nannizzia grubyi* (as "*grubyia*") Georg, Ajello, Friedman et Brinkman, Sabouraudia 1:194, 1962.

7. *Arthroderma gypseum* (Nannizzi) Weitzman, McGinnis, Padhye et Ajello, comb. nov.
   basionym: *Gymnoascus gypseus* Nannizzi, Atti. Accad. Fisioscr. Siena Med.-fis. 2:93, 1927.
   syn: *Nannizzia gypsea* (Nannizzi) Stockdale, Sabouraudia 3:119, 1963. *N. gypsea* (Nannizzi) Stockdale var. *gypsea*, Mycol. Paper 96:32, 1964.

8. *Arthroderma incurvatum* (Stockdale) Weitzman, McGinnis, Padhye et Ajello, comb. nov.
   basionym: *Nannizzia incurvata* Stockdale, Sabouraudia 1:46, 1961.

9. *Arthroderma obtusum* (Dawson et Gentles) Weitzman, McGinnis, Padhye et Ajello, comb. nov.
   basionym: *Nannizzia obtusa* Dawson et Gentles, Sabouraudia 1:56, 1961.

10. *Arthroderma otae* (Hasegawa et Usui) McGinnis, Weitzman, Padhye et Ajello, comb. nov.
    basionym: *Nannizzia otae* Hasegawa et Usui, Jpn. J. Med. Mycol. 16:151, 1975.

11. *Arthroderma persicolor* (Stockdale) Weitzman, McGinnis, Padhye et Ajello, comb. nov.
    basionym: *Nannizzia persicolor* Stockdale, Sabouraudia 5:357, 1967.
    syn: *Nannizzia quinckeani* Balabanov et Schick, Dermatol. Venerol. 9:35-36, 1970.

12. *Arthroderma racemosum* (Rush-Munro, Smith et Borelli) Weitzman, McGinnis, Padhye et Ajello, comb. nov.
    basionym: *Nannizzia racemosa* Rush-Munro, Smith et Borelli, Mycologia 62:858, 1970.

NEOTYPIFICATION OF *A. CAJETANI* AND *A. GRUBYI*

The holotypes for *N. cajetani* (as "*cajetana*") (1b) and *N. grubyi* (as "*grubyia*") which consisted of permanently preserved fertile gymnothecia mounted on microscope slides, have been lost. We have prepared neotypes in the form of dried colonies for *A. cajetani* (CDC B-4218) and *A. grubyi* (CDC B-4219), which have been deposited in the Division of Mycotic Diseases, Centers for Disease Control, Atlanta, Georgia.

The neotypes are identical to the original descriptions for these two taxa and were prepared from isolates derived from the cultures originally used to prepare the holotypes for *N. cajetani* (CDC B-434 and CDC B-435) and *N. grubyi* (CDC X-322 and CDC X-321).

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A NOTE ON THE TYPIFICATION OF *GUIGNARDIA*

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SUMMARY

Typification of *Guignardia* Viala et Ravaz is discussed. The prevailing concept of typification by *G. bidwellii* (Ellis) Viala & Ravaz is shown to be incorrect. *Guignardia* was introduced as a nomen novum for *Laestadia* Auersw. (non *Laestadia* Lessing) and must be based on the same type, *Laestadia alnea* (Fr.:Fr.) Auersw., which is not congeneric with *G. bidwellii*. If current taxonomic arrangements are followed, then *Guignardia* becomes a later synonym of *Plagiostoma* Fuckel. The segregation of *Guignardia* (auct.) species having *Phyllosticta* anamorphs from species (mostly referable to *Discosphaerina* v. Höhnel) with anamorphs in other genera allows *Discochora* v. Höhnel to be adopted for the teleomorphs of *Phyllosticta*.

* * *

Guignardia was introduced by Viala and Ravaz (1892) as a replacement name for *Laestadia* Auersw. 1869, a later homonym of *Laestadia* Kunth ex Lessing 1832 (Compositae). Viala and Ravaz did not provide, or refer to, a description or diagnosis for their new generic name, consequently *Guignardia* must be considered a nomen novum based on the same type as *Laestadia* Auersw., which it was proposed to replace (ICBN, Arts. 32.1.c, 72.1). Viala and Ravaz applied the name only to *Sphaeria bidwellii* Ellis, not realizing that the type species of *Laestadia* Auersw., *L. alnea* (Fr.: Fr.) Auersw., differed generically from *G. bidwellii*. The differences were noted by v. Höhnel (1918b) and he erected a new genus, *Gnomonina*, for *L. alnea*, and concluded that *Guignardia* auct. (based on *G. bidwellii*) was the same as *Phyllachorella* Sydow 1914. Sydow and Sydow (1919) saw that *Guignardia* was a replacement name for *Laestadia* and retained *L. alnea* as the type making *Gnomonina* a synonym of *Guignardia*. Müller and von Arx (1962) referred both *Laestadia* and *Gnomonina* to *Plagiostoma* Fuckel 1869. Consequently, *Guignardia* Viala et Ravaz, based on the same type as *Laestadia* and *Gnomonina*, becomes a synonym of the earlier name *Plagiostoma* in current taxonomic arrangements (Barr, 1978; Monod, 1983).

In recent years, the majority of authors have followed von Arx and Müller (1954) in maintaining the generic name *Guignardia* and citing *G. bidwellii* as the type species. According to the International Code for Botanical Nomenclature, the retention of a name in a sense that excludes the type can only be effected by conservation (ICBN, Art. 48). A proposal to conserve *Guignardia* Viala et Ravaz versus *Carlia* Bon. 1864 (non *Carlia* Rabenh. 1857) concluded with the recommendation from the nomenclatural committee that *Guignardia* be accepted as the valid name for the genus previously called *Laestadia* Auersw., and therefore in no need of conservation against *Carlia* Bon., which has no valid existence (Wakefield, 1939). This proposal erroneously cited *G. bidwellii* as the type species of *Guignardia*. There has never been a proposal to conserve *Guignardia* auct., typified by *G. bidwellii*, against *Guignardia* Viala et Ravaz, typified by *L. alnea*.

Von Höhnel (1918b) referred *G. bidwellii* to *Phyllachorella* Sydow 1914. Most recent authors consider *Phyllachorella micheliae* Sydow, the type species, to be generically distinct from *G. bidwellii*, differing in the structure of the ascomata (von Arx and Müller, 1954; Barr, 1972). *Discosphaerina* v. Höhnel 1917 was listed as the earliest synonym for *Guignardia* auct. by von Arx and Müller (1954), and this synonymy was accepted by van der Aa (1973). Petrak (1958) concluded that *G. bidwellii* and related species could be accommodated in *Botryosphaeria* Ces. & de Not. 1863, and he retained *Discosphaerina* for a group of aparaphysate species of *Guignardia* auct. Barr (1970, 1972) followed Petrak in transferring species of *Guignardia* auct. with

Phyllosticta anamorphs to *Botryosphaeria*, and referring species with depressed ascomata and numerous oblong asci to *Discosphaerina*. Van der Aa (1973) maintained the distinction between *Botryosphaeria* and *Guignardia* auct., transferring species classified as *Botryosphaeria* by von Arx and Müller with *Phyllosticta* anamorphs to *Guignardia* auct.

Punithalingam (1974) advocated that the genus *Guignardia* auct. be maintained, but only for holomorphs with *Phyllosticta* anamorphs, "as typified by *G. bidwellii*". Punithalingam's segregation of the species with *Phyllosticta* anamorphs is justified by characteristics of the teleomorphs. *Botryosphaeria* can be distinguished from this circumscription of *Guignardia* auct. by usually larger ascomata and ascospores, and an extended and frequently multilocular stroma. Van der Aa (1973) details differences between the two genera in growth characters in culture. Anamorphs for *Botryosphaeria* have been reported in the genera *Botryodiplodia*, *Lasiodiplodia*, *Dothiorella* and *Diplodia*. *Discosphaerina* differs in having depressed ascomata, a less developed stroma, more numerous asci developing almost simultaneously, and earlier disintegration of the locule tissues (Petrak, 1958, Barr, 1972). Anamorphs reported for *Discosphaerina* are in the genera *Kabatia*, *Colletotrichella*, *Placosphaeria* and *Selenophoma*. *Discochora* v. Höhnel (1918a) is the earliest available name for holomorphs with *Phyllosticta* anamorphs (Barr, 1972). Von Arx and Müller (1954) listed *Discochora* as a synonym of *Botryosphaeria*. However, the type species, *D. ilicis* v. Höhnel, was one of the species with *Phyllosticta* anamorphs classified as *Botryosphaeria* by von Arx and Müller and transferred to *Guignardia* auct. by van der Aa (1973).

In his monograph of the genus *Phyllosticta*, van der Aa cites teleomorphs for 12 species. All of these teleomorph based names, currently assigned to *Guignardia*, should be reassigned to *Discochora*, along with several names in *Guignardia* published subsequently for species with *Phyllosticta* anamorphs. The name *Discochora ilicis* (basionym: *Sphaeria ilicis* Schleich. in Ellis, N. Am. Fungi no. 196. 1879) is predated for the same fungus by *Sphaeria philoprina* Berk. & Curt. The correct name for the type species is, therefore, *Discochora philoprina* (Berk. & Curt. in Berk.) comb.

nov. (basionym: *Sphaeria philoprina* Berk. & Curt. in Berk., Grevillea 32:154. 1876).

ACKNOWLEDGEMENT

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MYCOTAXON

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VALSEUTYPELLA MULTICOLLIS SP. NOV.

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SUMMARY

Valseutypella multicollis is described as new, based on specimens collected on *Quercus ilex* ssp. *rotundifolia*. It is characterized by stromata with 10-30 perithecia and eight-spored asci.

The genus *Valseutypella* (Diaporthales) was created by v. Höhnel (1918), who designated *Diatrype tristicha* de Not. as the type species. The genus remains monotypic (Barr, 1978; Hawksworth et al., 1983). The most important characteristics of this genus are its stroma, a receptacle composed of dark pseudoparenchymatous, sclerotial cells and upright perithecia with separately erumpent beaks. The asci usually contain four ascospores.

Valseutypella tristicha is known from Europe and North America on stems of *Rosa* spp. Hubbes (1960) provided details of its morphology and determined several physiological parameters. The species appears to be host specific. Hubbes obtained only slight growth on sterilized twigs of *Salix caprea* and *Populus alba*, whereas on twigs of *Rosa* sp. pycnidia were produced in three weeks and perithecia in six weeks. The stroma of *V. tristicha* is usually about 1 cm diam and contains 10-35 perithecia. Perithecial beaks are usually erumpent for a short distance only beyond the stromatic surface, although in humid culture conditions they extend farther. The asci are normally four spored but occasional one-, two-, or three-spored asci may occur (Barr, 1978). V. Höhnel (1918) said "4-8 sporig" in his delimitation of the genus. Both asci and ascospores vary in size: asci 34-70 x 6.5-10.5 µm, ascospores (8-)11-15(-26) x (2.5-)3-4(-5) µm (Saccardo, 1882; Berlese, 1902; Hubbes, 1960; Barr, 1978). The number of ascospores per ascus would account for the extremes in size.

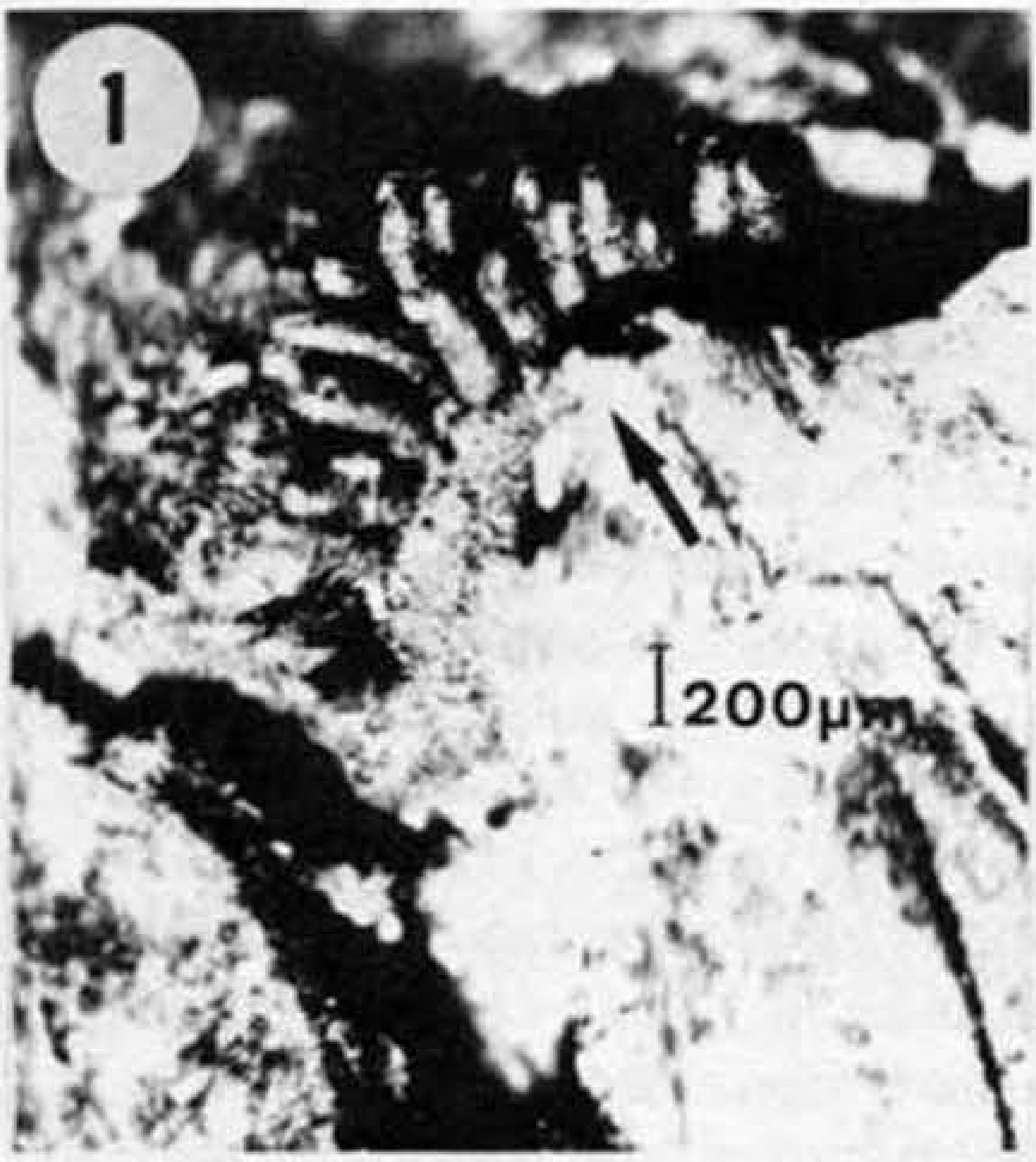
A species that forms similar but larger stromata, with long erumpent beaks and octosporous asci, was collected on *Quercus ilex* ssp. *rotundifolia* in Spain.

Valseutypella multicollis Checa, Moreno & Barr, sp. nov.

Stroma semiimmersum, circulare subglobosumve, nigrum, cuius diameter est 1.5-2.5 mm. Perithecia numero variant inter 10 et 30, colore subviridi, erecta, ostiolata; quorum venter ellipticus est et longus 430-480 µm cuius diameter est 240-340 µm; collum autem est cylindricum, angustius in apicem, emergens, rectum, 530-620 µm longum et cuius diameter est 100-150 µm, vergens super stroma. Stroma pseudoparenchymaticum, extrinsecus constitutum cellulis castaneo colore et pariete crasso, in cartilagineum tegumentum dispositis, quod est cassum 20-50 µm; intrinsecus autem fibrosum, constitutum hyphis connexis flavescente colore. Peridium ventris perithecii epidermoideae structurae, idemque colli structurae prosenchymaticae, extrinsecus tectum cellulis scleroticis castaneo colore. Asci 8 sporis praediti, cylindrico-claviformes, unitunicati, quorum apparatus apicalis est haud amyloideus, chitinoideus, 50-70 µm longus, 8-10 µm latus. Sporae biseriatele, allantoideae, glabrae, hyalinae, 14-18(-21) µm longae, 4-5 µm latae. Paraphyses absunt.

Habitat: Species lignicola fructificans in ramis mortuis *Quercus ilicis* subspeciei *rotundifoliae*, cuius corticem aufert, inter La Granja et Riofrio (Segovia, Hispania), leg. P. Yebes et J. Checa (10.VI.84), in herbarium J. Checa et G. Moreno 3854 (Holotypus). Isotypus Massachusetts Universitas (MASS).

Figs. 1-8. *Valseutypella multicollis*. 1. Macroscopic aspect of a stroma. 2. Microscopic detail of stroma and perithecium. 3. Detail of apex of beak. 4. Detail of texture of peridium. 5. Detail of texture of beak. 6. Ascus and ascospores. 7. Immature ascus. 8. Ascospores.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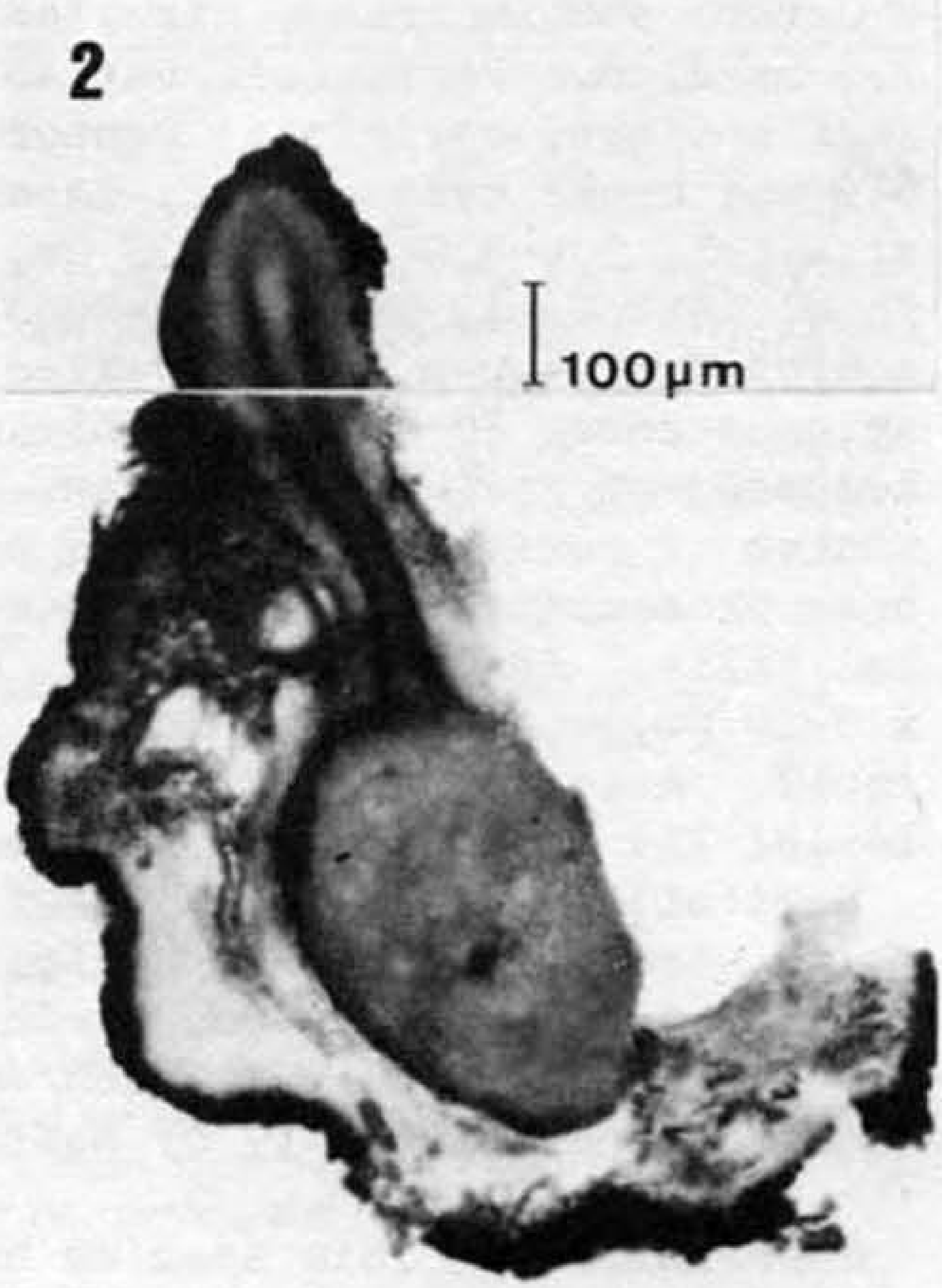
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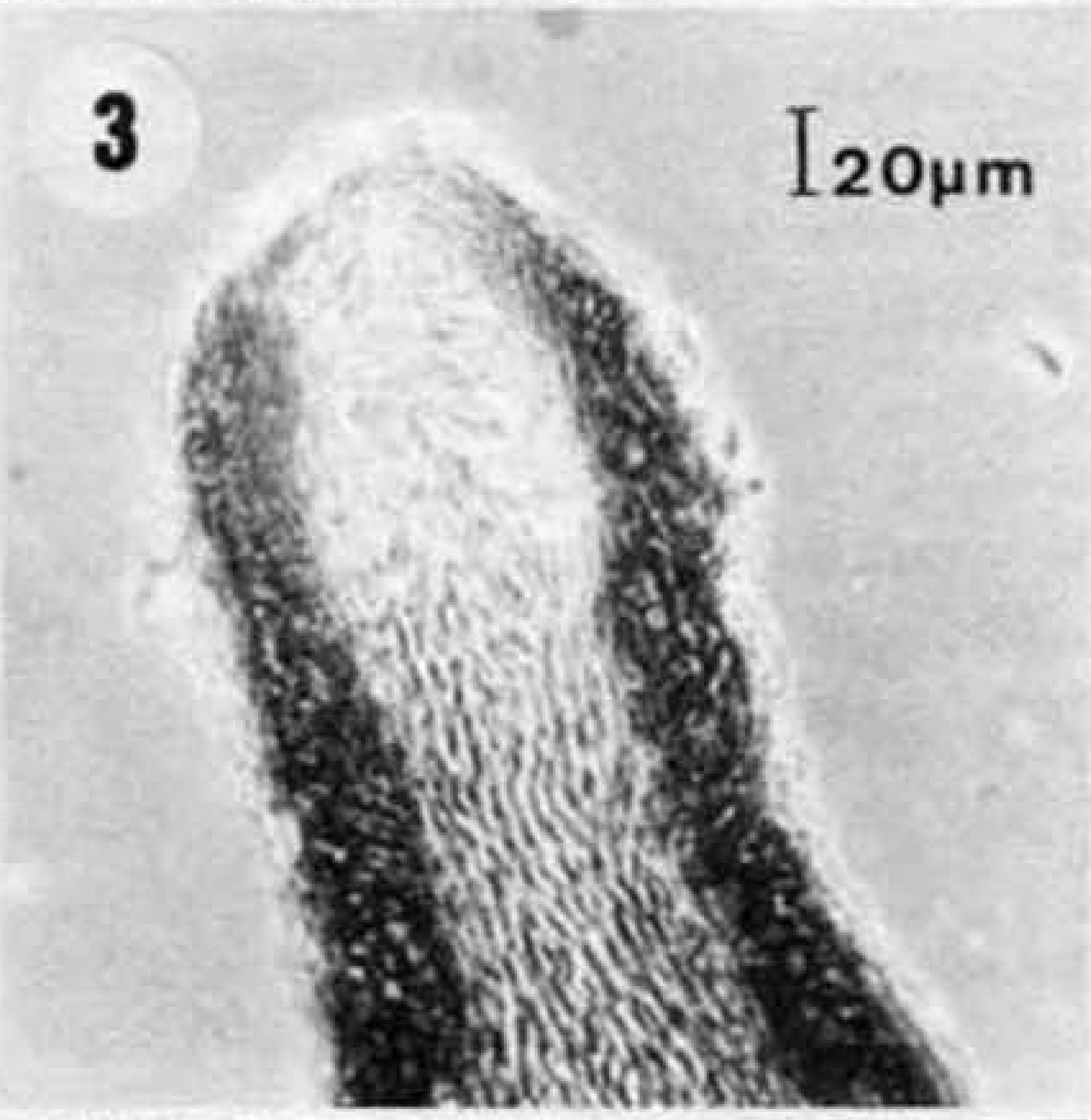
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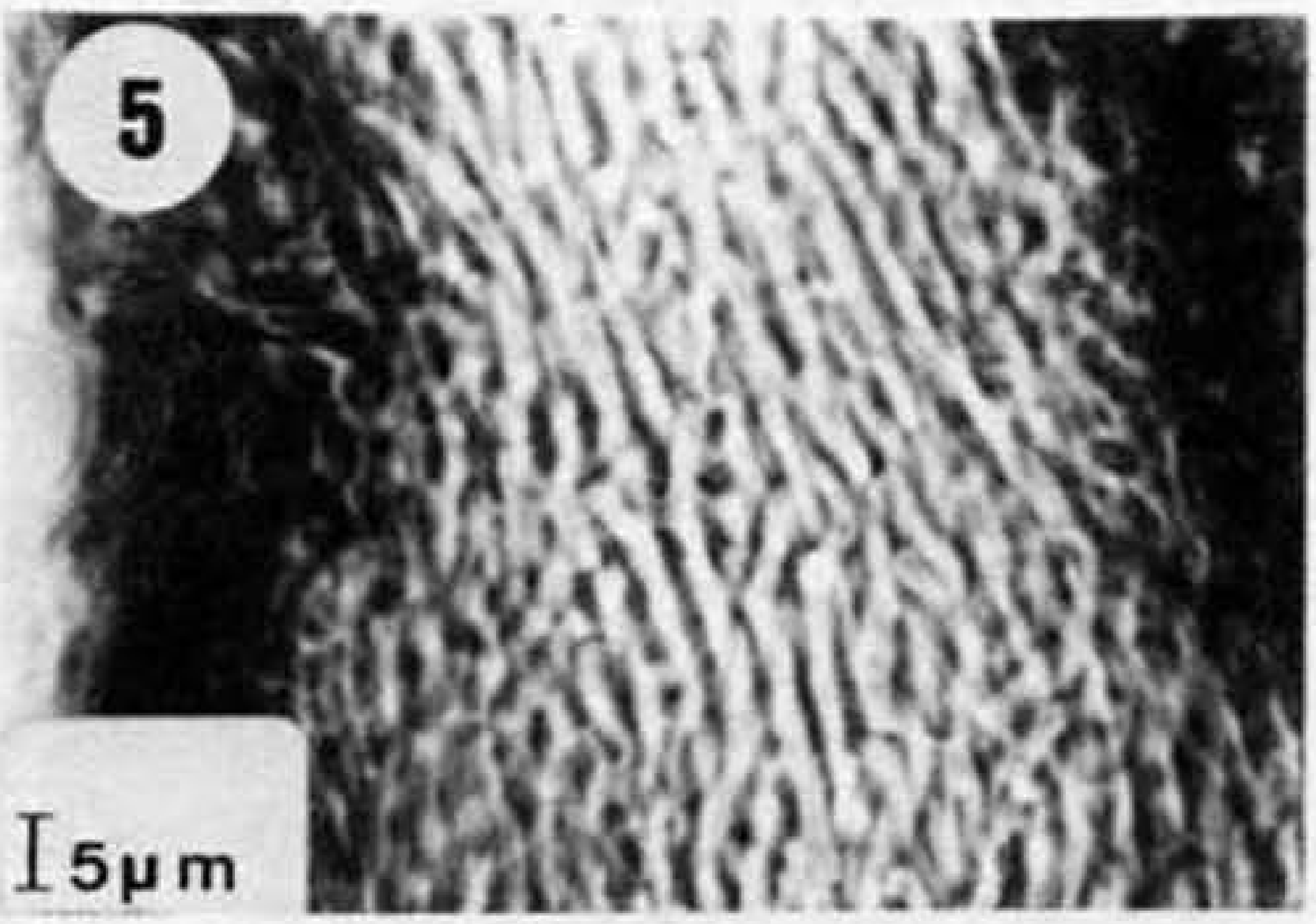
4
5µm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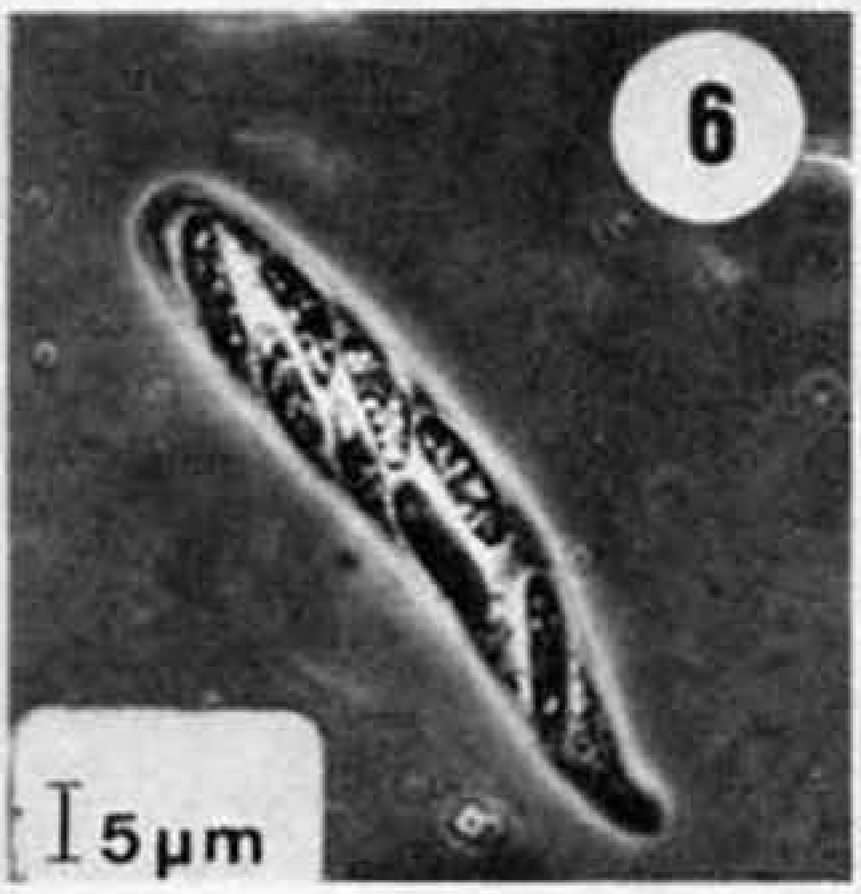
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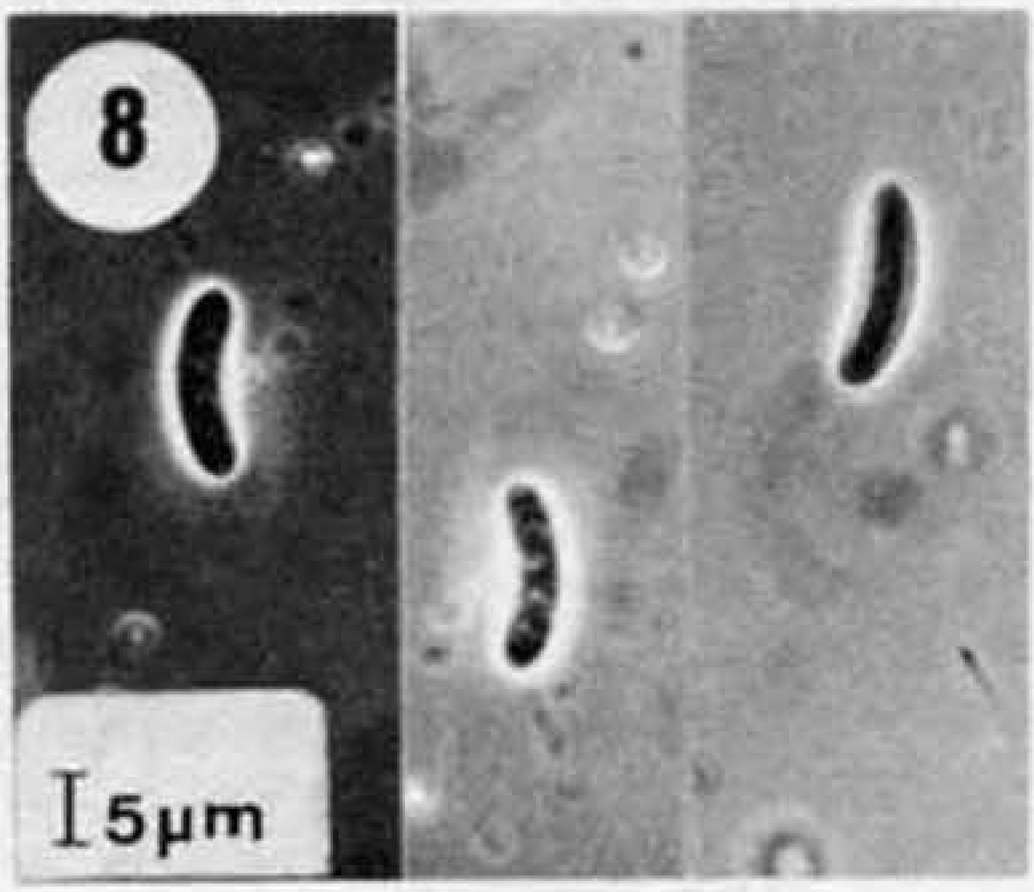
7


8
5µm

Stroma semiimmersed, circular to subglobose, black; 1.5-2.5 mm diam. Perithecia variable in number, 10-30, greenish, upright, ostiolate; venters elliptic, 430-480 x 240-340 µm; beaks cylindrical, tapering near the apex, emergent straight, 530-620 x 100-150 µm, erumpent beyond stroma surface. Stromatic tissues pseudoparenchymatous, externally composed of brown, thick-walled cells which form a cartilaginous cover 20-50 µm in thickness; internally fibrous, composed of variegated hyphae, yellowish. Peridium of venter of perithecium textura epidermoidea and peridium of beak prosenchymatous, covered externally by brown sclerotial cells. Asci eight spored, cylindric-claviform, 50-70 x 8-10 µm, unitunicate, apical apparatus nonamyloid, chitinoid. Ascospores biseriate, allantoid, smooth, hyaline, 14-18(-21) x 4-5 µm. Paraphyses not observed.

Habitat: On dead branches of *Quercus ilex* ssp. *rotundifolia*, from La Granja to Riofrio (Segovia, Spain), 30T VL0526, leg. P. Yebes and J. Checa (10.VI.84); holotype in private herbarium of J. Checa and G. Moreno 3854, isotype in Herbarium University of Massachusetts (MASS).

Observations.--This species has not yet been cultured, so that no information on anamorphic state is available. The morphological characters of *V. multicollis* that separate it from *V. tristicha* are somewhat larger stromata containing numerous perithecia, perithecial beaks elongate beyond the surface of stroma, and longer ascospores. Assuming that *V. tristicha* is indeed host specific, the occurrence of *V. multicollis* on *Quercus* provides another valid character.

We thank Dr. C. T. Rogerson, The New York Botanical Garden, for reviewing the manuscript.

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ILLINOIS FUNGI XII. FUNGI AND MYXOMYCETES FROM WOOD AND LEAVES SUBMERGED IN SOUTHERN ILLINOIS SWAMPS

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SUMMARY

One hundred and thirty-four fungal and 13 Myxomycete species were recorded on submerged, decayed plant substrates and balsa wood baits from two cypress-tupelo swamps and a hardwood swamp and its adjoining lake in southern Illinois. The mycota consists predominantly of dematiaceous and aeroaquatic Hyphomycetes and a variety of Ascomycetes. These swamps and lake contain numerous rare and indigenous fungal species and serve as the type locality for two genera and nine species.

INTRODUCTION

A number of fungi have been reported from submerged plant debris in freshwater swamps (Crane, 1971, 1972a,b; Shearer *et al.*, 1976; Shearer and Crane, 1978a,b, 1980a,b, 1985; Crane and Shoknecht, 1978, 1982; Schoknecht and Crane, 1978, 1983). There are, however, no reports of efforts made to systematically collect and identify fungi on decomposing submerged plant substrata in freshwater swamps. In this study, submerged plant substrata and balsa wood baits were collected monthly for 12 months from two cypress-tupelo swamps and a hardwood swamp and its adjoining lake. Fungi sporulating on substrata were identified and isolated when possible.

METHODS

Study Sites

Deer Pond (Elvira Cypress Swamp) and Heron Pond in Johnson County, and La Rue Swamp and adjoining Wolf Lake, in Union County, were the sites selected for study. In addition, Goose Pond (Johnson County) and Forman Swamp (Union County) were each sampled once. These sites are characterized by soil which is saturated with or covered by water for 12 or fewer months each year and by the presence of trees. Deer Pond and Heron Pond are cypress-tupelo swamps located in a bottomland region at the confluence of the Ohio and Mississippi rivers. Both swamps are flooded annually with floodwaters from the Cache River system. The dominant tree species in Deer Pond and Heron Pond are cypress (*Taxodium distichum* L.), water tupelo (*Nyssa aquatica* L.), and Drummond's red maple (*Acer rubrum* L. var. *drummondii* (Hook. & Arnott ex Nutt.) Sarge. The shrub community consists predominantly of buttonbush (*Cephalanthus occidentalis* L.), Virginia willow (*Itea virginica* L.), and swamp rose (*Rosa palustris* Marsh.). During the summer, the water surface is covered with mosquito fern (*Azolla mexicana* Presl.), duckweeds (*Spirodela polyrhiza* (L.) Schleid and *Lemna* spp.), and frogbit (*Limnobium spongia* (Bosc.) Steud). The submerged aquatic macrophyte, prickly coontail (*Ceratophyllum echinatum* Gray), occurs abundantly. Anderson and White (1970) and Dorge *et al.* (1984) have characterized the vegetation of Heron Pond in greater detail.

La Rue Swamp is located near the southwestern border of Illinois, about 15 km from the Mississippi River. This swamp is extensive and includes a variety of aquatic habitats. The swamp is fed by cool springs from the limestone cliffs which border one side of it. Extensive beaver activity is responsible, in part, for damming the swamp and reducing water flow. The flora of La Rue Swamp is quite diverse and has been treated in detail by Mohlenbrock and Voight (1965). There are only a few standing trees of cypress and water tupelo. The tree vegetation is dominated by swamp cottonwood (*Populus heterophylla* L.), pumpkin ash (*Fraxinus tomentosa* Michx.), water locust (*Gleditsia aquatica* Marsh.), and others. The shrub vegetation consists of buttonbush, Virginia willow, black willow (*Salix nigra* Marsh.), and swamp rose. A large number of aquatic macrophytes and sedges occur, and the water surface is covered with duckweeds and mosquito fern. Wolf Lake, which is adjacent to La Rue Swamp, is an old oxbow of the Mississippi River and has an extensive open water area. In this swamp and the others, organic plant material has accumulated to form a dense deposit of partially decomposed plant substrata on the swamp bottom. This deposit is anaerobic, and hydrogen sulfide and methane are released when it is disturbed.

Physical-Chemical Measurements

Temperature was measured with a thermometer, dissolved oxygen with a YSI oxygen meter, and pH with a Beckman field pH meter. Chemical water quality was analyzed by personnel at the Water Analysis Laboratory, Illinois Natural History Survey.

Collection Techniques

Strings of autoclaved balsa wood blocks (54 x 50 x 9 mm) were submerged for 1-month periods and returned to the laboratory where they were incubated at room temperature in moist chambers (petri dishes containing two pieces of filter paper moistened with distilled water and sealed with rubber dish seals). Submerged woody debris and leaves were also collected monthly and processed as above. Additional samples were collected and submerged in distilled water in glass petri dishes and incubated at 17 °C. Fungi were identified from fruiting structures found on incubated substrata. Single-spore isolates were obtained by plating spores on 1.8% distilled water agar containing 0.5 mg/l each of streptomycin sulfate and penicillin G (Sigma). Single spores were transferred to Emerson's yeast soluble starch agar (Difco) and isolates were deposited at the American Type Culture Collection (ATCC). Voucher specimens of all species found were deposited in the herbarium of the Illinois Natural History Survey (ILLS).

RESULTS

Ranges in physical-chemical water quality parameters are listed in Table 1. Temperature and dissolved oxygen fluctuated widely throughout the year (Fig. 1). High temperatures and low oxygen levels occurred in the summer and early fall, and oxygen levels remained low during leaf fall as temperatures decreased.

One hundred and thirty-four fungal and 13 Myxomycete species were found (Table 2). The greatest number of fungal species were Fungi Imperfecti and most of these were dematiaceous. The following species occurred regularly and in more than one swamp: *Didymium trachysporum*, *Oligonema flavidum*, *Cercophora* sp. I, *Chaetomium funicolum*, *Nais inornata*, *Talaromyces flavus*, *Zopfiella latipes*, *Allescheriella crocea*, *Beverwykella pulmonaria*, *Bispora betulina*, *Chloridium viride*, *Conioscypha varia*, *Dactylaria purpurella*, *Sporidesmium hyalospermum*, *Gonytrichum macrocladium*, *Neta patuxentica*, *Phaeoisaria clematidis*, *Thozetella tocklaiensis*, *Trichoderma harzianum*, and *Sporoschisma saccardoi*.

DISCUSSION

Wide ranges in all physical and chemical parameters except nitrite were encountered (Table 1). These ranges reflect the annual growth, maturation, and death of aquatic macrophytes, the autumnal input of leaf litter, alternating flooding and drying conditions, and seasonal changes in temperature. Extremes in some parameters, such as temperature, dissolved oxygen, ammonia concentrations, and water levels, could be detrimental to fungi. At certain times, inorganic nutrients such as nitrates and phosphates are absent or present only in small quantities; this condition could limit fungal growth. One might expect that these periodically fluctuating environmental conditions could have selected for a small group of distinctive fungi particularly well adapted to the swamp habitat. As far as number of species, this appears not to be the case, because 147 species were found, although only two collection and incubation techniques were used. The use of different collection and incubation techniques could yield still more species.

Evidence of the presence of a distinctive group of fungi associated solely or primarily with swamps or swamp-like portions of other aquatic habitats such as lakes and bogs is somewhat limited. The number of indigenous species that occur in the swamps studied is quite high. Of the 147 species reported, two represent new genera known only from their type locations (*Aquadiscula appendiculata* and *Lepidopterella palustris*); nine species were described as new (*Diderma diademata*, *Zopfiella lundqvistii*, *Codinaea gonytrichodes*, *Endophragmiella boeweii*, *Melanocephala triseptata*, *Phialocephala illini*, *Sporidesmium taxodii*, *Taeniolella americana*, and *Trichochladium moenitum*); and 16 species remain to be described as new. Three of the above species have been reported from other habitats and geographical areas since their original description [*E. boeweii*, Japan, Formosa (Hughes, 1979); *T. moenitum*, Canada (Hughes, 1984) as *Bactrodesmium*); *C. gonytrichodes*, Japan (Yokoyama, 1975); Alabama (Morgan-Jones, 1976) as *Codinaeopsis*]. Whether all of the other new species eventually will be found in other habitats or only in swamps remains to be seen. Cultural studies of both indigenous and frequently-occurring species are warranted to determine whether these fungi have adapted to the swamp habitat in terms of nutrition and metabolism and are therefore physiologically distinctive.

Studies of small ponds have revealed a distinctive mycota thought to be adapted to stagnant water and fluctuating water levels (Fisher, 1977). These fungi are known as "aeroaquatic" fungi and produce vegetative mycelium in submerged substrata, and conidia with morphologies modified for flotation on unsubmerged moist substrata (Webster and Descals, 1981). Given the fluctuating water levels and stagnant water characteristic of swamps, one might expect to find a number of aeroaquatic fungi. Six species with air-trapping helical spores were found: *Helicodendron conglomeratum*, *H. triglitziensis*, *H. tubulosum*, *H. westerdykiae*, *Helicoon* sp. I, and *Vanbeverwijkia spirospora*. Three species, *Candelabrum brocchiatum*, *Pseudaegerita corticalis*, and CS-717-1 have highly branched and hydrophobic propagules, and two species, *Beverwykella pulmonaria* and *Cancellidium applanatum*, produce multicellular air-filled sacs. Production of buoyant propagules is advantageous in habitats with fluctuating water levels, such as swamps. When water levels decrease, these fungi are stimulated to sporulate and as water levels rise again, their propagules float off of substrata onto the surface of the rising water and are dispersed. Michaelides and Kendrick (1982) suggest that these buoyant propagules attach to fresh-fallen tree litter as it floats on the water surface. *Neta patuxentica*, one of the most common species, and *N. lignicola* both produce conidia in baskets of highly branched, interwoven dematiaceous hyphae which trap air. The clusters of conidia inside the hyphal baskets are not easily dislodged from the substratum. The net baskets may function more to trap air so conidiogenesis can occur than as flotation devices.

A number of fungi, *Chaetomium* spp., *Cladosporium* spp., *Trichoderma harzianum*, and *Penicillium* spp., were found to sporulate on the surfaces of water films. The hairs of *Chaetomum* spp. trap air and render the ascomata water repellent and buoyant. The conidia of *Cladosporium*, *T. harzianum*, and *Penicillium* are all very hydrophobic and lie as a fine powder on the surfaces of water films in dishes.

Only *Varicosporium* sp. I, *Filosporella* sp. CS-707-1, and *Pyrimadospora* sp. CS-575-4 were typical of the so-called "Ingoldian" fungi, that is, fungi with highly branched, tetraradiate or sigmoidal conidia found commonly in streams. Absence of a variety of "Ingoldian" fungi in swamps supports the prevalent concept that these fungi occur more abundantly in clean, fast-flowing water than in stagnant water habitats (Webster and Descals, 1981). Efforts are underway to use collection and incubation techniques more favorable to the recovery of aeroaquatic and "Ingoldian" Hyphomycetes to determine

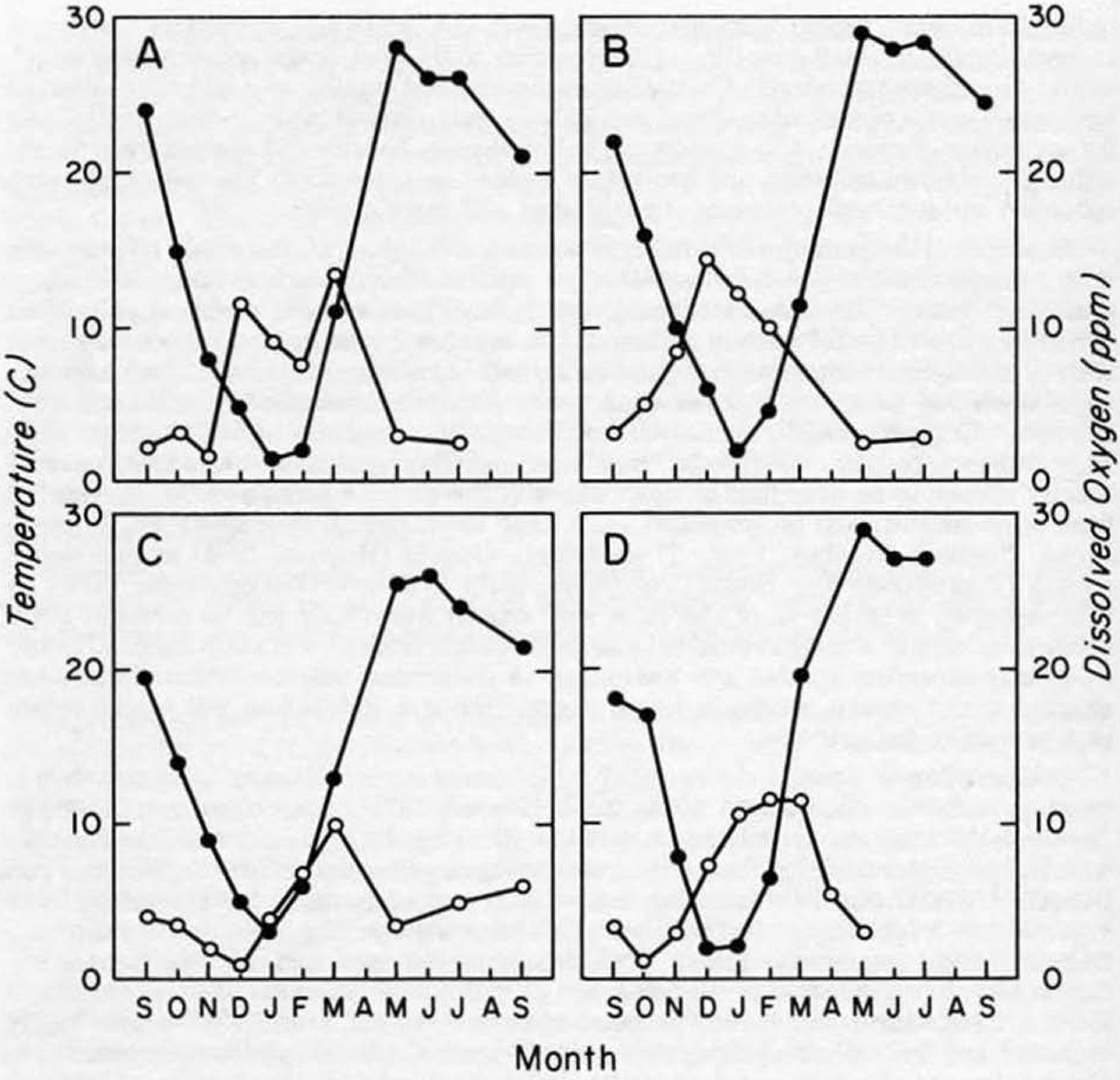

Fig. 1. Monthly temperatures and dissolved oxygen concentrations of surface waters in La Rue Swamp (A), Wolf Lake (B), Deer Pond (C), and Heron Pond (D). ●—● = Temperature. ○—○ = Dissolved oxygen.

whether additional species went undetected due to sampling procedures.

A large number of the Ascomycetes found (Table 2) have been reported from other freshwater, brackish, and marine habitats. The following species have been found in freshwater, brackish water, and marine habitats: *Aniptodera chesapeakensis* (Shearer and Miller, 1977; Minoura and Muroi, 1978; Kohlmeyer and Kohlmeyer, 1979; Shearer and von Bodman, 1983); *Halosarpheia retorquens* (Shearer and Crane, 1980b; Kohlmeyer, 1984); *Nais inornata* (Shearer and Crane, 1978b; Minoura and Muroi, 1978; Kohlmeyer and Kohlmeyer, 1979; Shearer and von Bodman, 1983; Koch and Jones, 1983; Zanial and Jones, 1984); and *Zopfiella latipes* (Shearer, 1972; Kohlmeyer and Kohlmeyer, 1979). *Luttrellia estuarina* has been reported from brackish and freshwater habitats (Shearer, 1978; Shearer and von Bodman, 1983). The following species have been reported from other freshwater habitats: *Cercophora* sp. I (Shearer and von Bodman, 1983), *Chaetomium cochlioides* (Apinis *et al.*, 1972), *C. globosum* (Eaton and Jones, 1971; Eaton, 1972), *Pseudohalonectria lignicola* (Shearer, 1972 as CS-182; Minoura and Muroi, 1978; Shearer and von Bodman, 1983), and *Trematosphaeria fallax* (Shearer, 1972). *Zalerion varium*, a Deuteromycete, has also been reported from brackish and marine habitats and inland salt lakes (see Kohlmeyer and Kohlmeyer, 1979 for summary).

A large number of the remaining species (Table 2) have been reported from decaying plant material in predominantly terrestrial habitats. This is not surprising in view of the fact that swamps dry down and become terrestrial habitats usually once a year and also because swamps receive run-off from terrestrial habitats during flooding, no doubt an annual source of propagules of terrestrial fungi. The role and extent of activity of these fungi in swamps need to be investigated.

A surprising diversity of Myxomycetes occurred regularly. These organisms, although reported frequently on dead plant substrata, have not often been reported from freshwater habitats. Olive (1975) found that one of the most productive substrates for Myxomycetes is old cattail inflorescences. Cattails occur around the edges of ponds and swamps and in drainage areas, and it is possible that emergent macrophytes in the swamp are the habitat for the Myxomycetes collected. Quantitative study of a variety of swamp substrata located at various depths in the swamp is needed to pinpoint the types of substrata colonized by Myxomycetes, and to determine their patterns of occurrence with respect to degree of submersion and location in the habitat.

In addition to regular monthly sampling, the La Rue Swamp site #1 and Deer Pond sites were sampled three additional times in later years (1979, 1983, and 1984). Because these swamps were sampled simultaneously throughout, it is possible to compare the fungi found. Similar numbers of species were found in each swamp (La Rue Swamp site #1, 59 species; Deer Pond, 66 species). Of these species, however, only 19 occurred in both swamps. The low number of species in common may simply be due to chance; the probability of finding a rare species is low when samples are collected only at monthly intervals and thus the probability of finding a rare species in both swamps is even lower. On the other hand, actual differences in species composition between swamps may indeed exist. Given the differences in vegetational composition (see Description of Study Sites) and the fact that La Rue Swamp is spring-fed and attached to a large lake while Deer Pond is not, it is possible that the two swamps are sufficiently different to support different mycotas. Further detailed comparisons of these two swamps is warranted. Because of differences in number and type of samples taken, comparisons between the other sites cannot be made now.

Although samples were collected regularly over an annual cycle, little can be said regarding seasonal changes because fungi were not sampled quantitatively and incubation conditions did not reflect seasonal changes in environmental parameters. A quantitative comparison of the fungi in La Rue Swamp and Deer Pond over an annual cycle is planned.

ACKNOWLEDGMENTS

We thank J. D. Schoknecht for the identification of the Myxomycetes.

Table 1. Ranges in physical-chemical water quality parameters.

	Location				
Parameter	La Rue site #1	La Rue site #2	Wolf Lake	Heron Pond	Deer Pond
Temperature (°C) (13 samples)	1.5–28.0	2.0–29.5	2.0–29.0	2.0–31.0	3.0–28.0
DO_2 (mg/l)	1.0–13.5	2.4–11.7	2.4–14.5	1.3–11.5	1.01–10.0
pH	3.6–7.5	5.5–7.5	3.5–6.8	6.0–7.4	5.2–7.0
EDTA hardness (mg/l)	30.0–117.0	6.0–94.0	33.0–150.0	<3.0–67.0	12.0–62.0
NH_3 (mg/l NH_3-N)	0.18–15.2	<0.05–1.56	3.8–7.3	0.08–6.3	0.05–2.55
NO_2 (mg/l NO_2-N)	0.0–0.03	<0.01–0.09	<0.01–0.28	0.0–0.01	0.0–0.01
NO_3 (mg/l NO_3-N)	0.0–5.2	0.0–<0.01	0.09–10.3	0.0–<0.05	0.0–<0.05
PO_4 (mg/l ortho-PO_4)	0.05–6.66	0.02–0.90	0.02–0.48	0.07–2.31	0.013–0.54

Table 2. Herbarium and/or collection numbers of voucher specimens and sites of occurrence for all species collected.

		Location						
Species	Herbarium or collection #	La Rue site #1	La Rue site #2	Wolf Lake	Heron Pond	Deer Pond	Goose Pond	Forman Swamp
Myxomycetes								
Acyria denudata (L.) Wettst.	36,047						+	
Comatrichia tenerrima (M. A. Curt.) G. Lister	38,643				+			
Cribaria violacea Rex	44,811	+						
Cribaria tenella Schrad.	36,583	+						
Diderma diademata Schoknecht & Crane	37,665	+				+	+	
Didymium trachysporum G. Lister	38,600	+	+	+	+		+	
Metatrichia vesparum (Batsch) Nann.-Brem.	36,581	+			+			
Oligonema flavidum (Peck) Peck	38,130				+	+	+	
Oligonema schweinitzii (Berk.) G. W. Martin	36,742					+		
Perichaena chrysosperma (Currey) A. Lister	44,812	+						
Perichaena corticalis (Batsch) Rost.	38,012	+	+					
Perichaena depressa Libert	36,099						+	
Stemonitis smithii Macbr.	36,100						+	
Ascomycetes								
Aniptodera chesapeakensis Shearer & Miller	44,779			+				
Aquadiscula appendiculata Shearer & Crane	44,301	+						
Bisporella citrina								

Table 2. (cont'd)

Species	Herbarium or collection #	La Rue site #1	La Rue site #2	Wolf Lake	Heron Pond	Deer Pond	Goose Pond	Forman Swamp
(Batsch:Fr.) Korf & Carpenter	36,046						+	
Ceratosphaeria pusilla (Fckl.) Sacc.	44,364					+		
Cercophora sp. I	39,916	+		+		+		
Chaetomium aureum Chivers	42,883	+						
Chaetomium cochliodes Palliser	44,777					+		
Chaetomium funicolum Cooke	37,059				+	+		
Chaetomium globosum Kunze:Fr.	42,908					+		
Chaetomium seminudum Ames	39,930					+		
Chaetomium trilaterale Chivers	43,768			+		+		
Chaetomium sp. I	42,907	+						
Chaetomium sp. II	42,904		+					
Coniochaeta kellermani (Ell. & Ev.) Munk	37,699				+			
Coniochaeta leucoplaca (Berk. & Rav.) Cain	43,771						+	
Coniochaeta velutina (Fckl.) Munk	37,049						+	
Emericellopsis humicola (Cain) Gilman	36,103		+					
Gnomonia sp.	44,764					+	+	+
Halosarpheia retorquens Shearer & Crane						+		
Halosarpheia sp. I	44,768	+		+				
Lepidopterella palustris Shearer & Crane	38,991					+		
Luttrellia estuarina Shearer	44,776							
Nais inornata Kohlm.	37,389	+				+		
Ophioceras sp. I	CS-408-1	+						
Passeriniella discors (Sacc. & Ellis) Apinis & Chesters	38,393					+		
Pseudohalonectria lignicola Minoura & Muroi	44,767		+			+		
Pseudohalonectria sp. I		+		+				
Rabentischia unicaudata (Berk. & Br.) Sacc.	44,775		+					
Sordaria sp. I.	44,791	+	+					
Sordaria sp. II	36,969			+				
Talaromyces flavus (Klocker) Stolk & Samson var. *flavus*	36,386	+		+	+	+		
Trematosphaeria fallax Mouton	43,804	+						
Zopfiella latipes (Lundqvist) Malloch & Cain	39,682	+	+	+	+	+		
Zopfiella lundqvistii Shearer & Crane	39,933	+			+	+		
Fungi Imperfecti								
Acremonium bacillisporum (Onions & Barron) W. Gams	43,808				+			
Acrogenospora sphaerocephala (Berk. & Br.) M. B. Ellis	37,022					+		
Allescheriella crocea (Mont.) Hughes	36,678	+		+	+	+		
Alysidium aureofulvum (Cooke & Ellis) M. B. Ellis	37,112					+		
Arthrobotrys superba Corda	36,009	+						
Berkleasmium concinnum (Berk.) Hughes	37,053				+			
Bactridiopsis sp.	44,759				+			

Table 2. (cont'd)

Species	Herbarium or collection #	Location La Rue site #1	La Rue site #2	Wolf Lake	Heron Pond	Deer Pond	Goose Pond	Forman Swamp
Beverwykella pulmonaria (Van Beverw.) Tubaki	38,473	+			+			
Bispora betulina (Corda) Hughes	37,055	+		+	+	+		
Cancellidium applanatum Tubaki	45,220						+	
Candelabrum brocchiatum Tubaki	37,178				+			
Chloridium botryoideum (Corda) Hughes	44,784	+				+		
Chloridium chlamydosporis (Van Beyma) Hughes	36,731			+				
Chloridium clavaeforme (Preuss) W. Gams & Hol. Jech.	36,901	+		+			+	
Chloridium virescens (Pers.:Fr.) W. Gams & Hol. Jech.	39,657	+			+	+		
Cladosporium sp.		+						
Cladosporium cladosporioides (Fresen.) de Vries	43,813					+		
Cladosporium oxysporum Berk. & Curt.	36,045					+		
Codinaea gonytrichodes Shearer & Crane	37,039					+		
Codinaea simplex Hughes & Kendrick	42,243				+	+		+
Codinaea anam. of *Chaetosphaeria talbotii* Hughes, Kendrick & Shoemaker	43,817				+			
Conioscypha lignicola Hoehnel	37,052	+		+	+	+		
Conioscypha varia Shearer	36,535	+		+	+	+		
Dactylaria chrysosperma (Sacc.) Bhatt & Kendrick	44,781					+		
Dactylaria purpurella (Sacc.) Sacc.	36,379	+			+	+		
Dendrophoma sp.	44,783	+						
Dendrosporium lobatum Plakidas & Edgerton ex Crane	34,949					+		
Dendryphiopsis atra (Corda) Hughes	44,225					+		
Endophragmiella boewei (Crane) Hughes	44,770					+		
Eversia subopaca (Cooke & Ellis) Crane & Schoknecht	45,219					+		
Gliocladium deliquescens Sopp	36,745					+		
Gliomastix murorum (Corda) Hughes	36,381			+	+			+
Gonytrichum macrocladium (Sacc.) Hughes	43,812		+	+	+	+		
Hainesia sp.								
Helicodendron conglomeratum Glen-Bott	38,472	+						
Helicodendron triglitziensis (Japp) Linder	36,007						+	
Helicodendron tubulosum (Reiss) Linder	44,778					+		
Helicodendron westerdykiae Beverwijk	43,789	+						
Helicoon sp.						+		
Hormiactis sp. I	43,811	+						
Melanocephala triseptata (Shearer, Crane & Miller) Hughes	40,806					+		

Table 2. (cont'd)

		Location						
Species	Herbarium or collection #	La Rue site #1	La Rue site #2	Wolf Lake	Heron Pond	Deer Pond	Goose Pond	Forman Swamp
Microsphaeropsis sp.	44,788	+						
Monacrosporium sp.	45,230							+
Neta lignicola Shearer	44,765					+	+	+
Neta patuxentica Shearer & Crane	36,050	+		+	+	+		
Penicillium sp.	44,756		+					
Phaeoisaria clematidis (Fuckl.) Hughes	39,680			+		+		
Phialocephala bactrospora Kendrick	42,224		+					
Phialocephala humicola Jong & Davis	36,585			+				
Phialocephala illini Crane	34,911					+		
Phialophora radicicola Cain	44,774	+						
Phialophora richardsiae (Nannf.) Conant	36,587	+		+		+		
Phialophora verrucosa Medlar	44,897					+		
Phoma sp.	44,771			+				
Pleurothecium recurvatum (Morgan) Hoehnel	43,810			+				
Pyrenochaeta sp.						+		
Pseudaegerita corticalis (Peck) Crane & Schoknecht	43,815		+			+		
Rhinocladiella anceps (Sacc. & Ellis) Hughes			+					
Sclerotium rolfsii Sacc.	44,790	+		+	+	+		
Scolecobasidium constrictum Abbott	36,008					+		
Selenosporella sp.						+		
Spadicoides atra (Corda) Hughes	38,122				+			
Spadicoides bina (Corda) Hughes	38,123				+			
Sporidesmium hyalospermum (Corda) Hughes	36,837			+	+	+		
Sporidesmium taxodii Crane	34,936						+	
Sporoschisma mirabile Berk. & Hughes	36,880	+						
Sporoschisma saccardoi Mason & Hughes	43,764				+			
Stachybotrys cylindrospora Jensen	38,128				+			
Staphylotrichum coccosporum Meyer & Nicot	36,006	+				+		
Stilbella erythrocephala (Ditmar:Fr.) Lindau	44,758					+		
Taeniolella americana Crane & Schoknecht	41,016						+	
Thozetella tocklaiensis (Agnih.) Pirozynski & Hodges	36,781	+	+	+	+	+		
Torula herbarum (Pers.) Link:Fr.	43,795	+		+				
Trichocladium lobatum Sutton	37,179				+			
Trichocladium moenitum Crane & Shearer	38,121				+			
Trichoderma harzianum Rifai	36,024	+		+		+		
Vanbeverwijkia spirospora Agnihotrudu	44,898					+		
Varicosporium sp. I		+						
Verticillium sp. I	44,760					+		
Virgaria nigra (Link:Fr.) Nees	43,765					+		
Wiesneriomyces laurinus (Tassi) P. M. Kirk	43,801	+	+					

Table 2. (cont'd)

		Location						
Species	Herbarium or collection #	La Rue site #1	La Rue site #2	Wolf Lake	Heron Pond	Deer Pond	Goose Pond	Forman Swamp
Xylohypha sp.	44,762							
Zalerion varium Anastasion	44,786					+		
Basidiomycetes								
Vararia pallescens (Schw.) Rogers & Jackson	44,801					+		
Undescribed Species of Fungi Imperfecti								
Filosporella sp.	CS-707-1	+						
Pyrimadospora sp.	CS-754-1	+						
Spadicoides sp.	CS-754-1	+						
CS-717-1		+						
CS-750-1		+						
Undescribed Species of Ascomycetes								
CS-429-1				+				
CS-589-1						+		
CS-603-1						+		
CS-733-1		+						
CS-734-1		+						
CS-735-1		+						
CS-746-1		+						
CS-747-1						+		
CS-749-1		+						
CS-751-1		+						
CS-753-1		+						

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SOME NEW AND NOTEWORTHY FUNGI (APHYLLOPHORALES, BASIDIOMYCETES) FROM IGUAZU, ARGENTINA

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SUMMARY

46 species of corticoid fungi are reported from Iguazu National Park, Argentina. The following new taxa are described: Coniophoropsis and Gloeocorticium nov. gen. Coniophoropsis obscura, Amethicium luteo-incrustatum, Candelabrochaete cirrata, C. dispar, Gloeocorticium cinerascens, Gloeocystidiellum triste, Hyphoderma iguazuense, Hyphodontia lutescens, H. tenui-cystidiata, H. wrightii and Odonticium helgae. The following new combinations are proposed: Cystidiodontia isabellina (Berk. & Br.) Hjortst. & Ryv., Fibricium subceraceum (Hallenb.) Bern. and Hyphodontia apacheriensis (Gilbn. & Canf.) Hjortst. & Ryv.

During a course in mycology which was arranged by the University of Buenos Aires, one of us (LR) had the opportunity to make some 580 collections, mostly polypores and corticoid species, from Iguazu National Park. It is situated in the province of Misiones in Northern Argentina and its main attraction is the enormous Iguazu waterfall on the border between Brazil and Argentina. However, there are also in the National Park extensive forests which are fairly accessible.

Several mycology courses have been given in the park, some groups of fungi such as the polypores are well known, while the corticoid species had previously not been collected and studied. Thus, the polypores are omitted, while all corticoid collections that have been determined are included in the list. Some genera like Phlebia s. lato are excluded, because more type studies are necessary before a reliable determination can be reached in this group.

The families are placed alphabetically as are the genera within each family. All collections were made in the period 1-7 March 1982. After the name, the collection number is cited. All collections are deposited in Oslo (O), while there are duplicates of the more remarkable collections in Buenos Aires.

Coniophoraceae.
Coniophoropsis Hjortst. & Ryv. gen.nov.
Coniophora aemulans, differt sporis distincte verruculosis, indextrinoidibus.
Type species: Coniophoropsis obscura Hjortst. & Ryv. spec. nov. Fig. 1.
Habitu plus minus specierum Coniophoracearum, praecipue differt sporis verruculosis.
Holotypus: Argentina. Prov. Misiones, Iguazu Nat.Park, Cataratas de Iguazu. 1-5 March 1982. L. Ryvarden No. 19677 (O). Isotypus:(GB and a portion of this in DAOM No. 188783).

Fruitbody effuse, closely adnate, smooth, effused, 0.3-0.5 mm thick, margin narrow, whitish or paler than the fertile part, hymenium brown-violet, in older parts brown with a olive tint, hyphal strands lacking in the type specimen; subiculum well separated from the hymenial layer, 0.1-0.2 mm thick, whitish, fairly loose and soft. Hyphal system monomitic; hyphae thin-walled, hyaline or some hyphae with slight yellowish tint, approximately 2.5 µm wide, without clamps, smooth or sparsely encrusted, subicular hyphae next to the substratum more or less closely packed, hyaline or more commonly yellowish, 2.5-4.5 µm wide, no clamps observed. Cystidia lacking but with protruding hyphoids (dendrohyphid-like element) above the basidia, with few, more or less perpendicular short branches. Basidia cylindrical to more or less suburniform with a median constriction, generally tapering near the base, usually 50 µm long and 10-12 µm wide in the upper part, thin-walled and normally with 4 sterigmata, young basidia with oily contents in the protoplasm. Spores subfusiform to subamygdaliform, verrucose, distinctly thick-walled with spore-walls yellowish-brown and about 0.5 (1) µm thick, without colour change in Melzer but strongly cyanophilous, 15-18(-20) x 7.5-9(-10) µm, apiculus fairly small, usually more or less hyaline and apparently with a germ-pore but difficult to discern.

Remarks. This monotypic genus differs from all other genera in Coniophoraceae by its verruculose spores. The morphology of Coniophoropsis obscura is more or less as for species in Coniophora, but some noteworthy microscopic

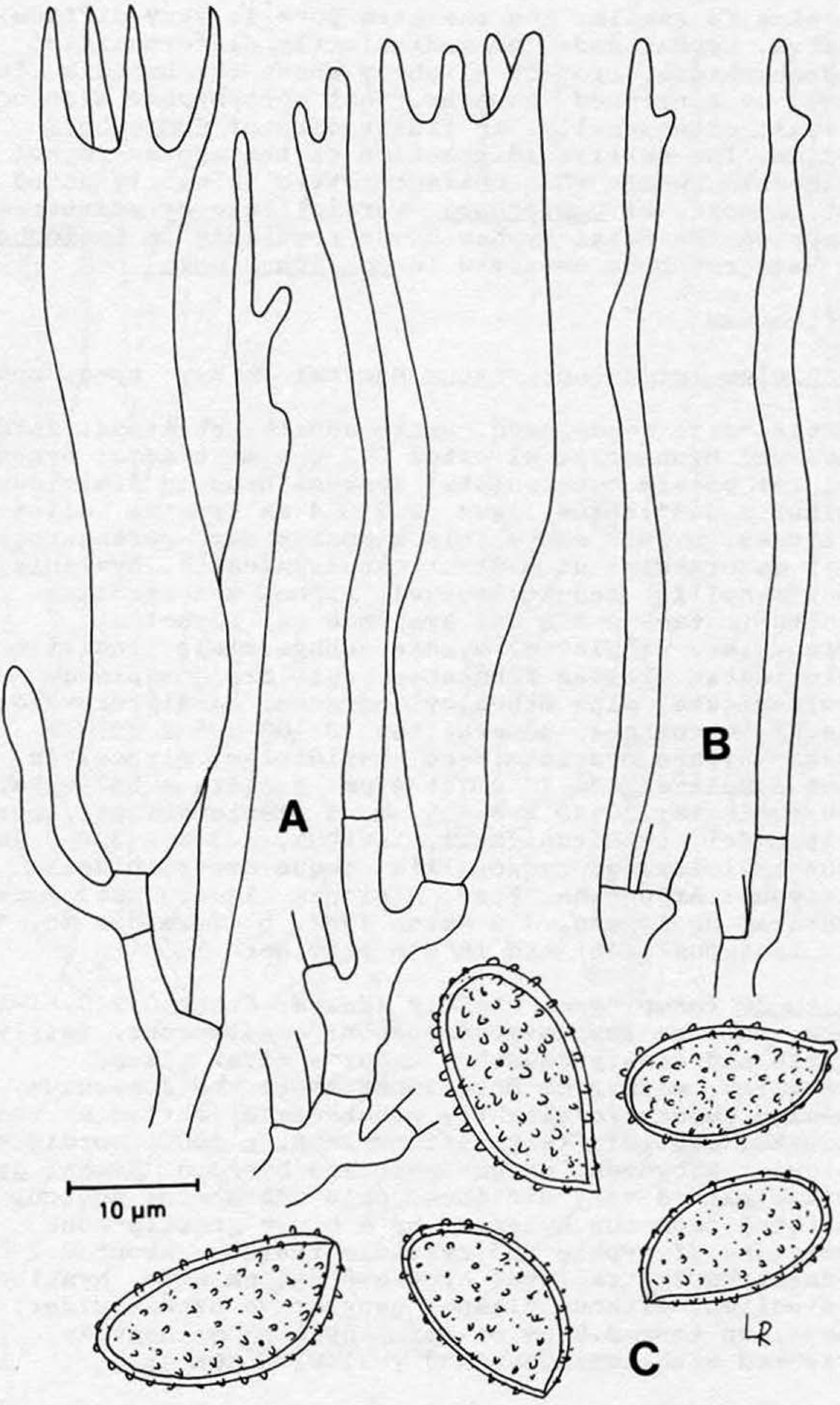

Fig. 1. **Coniophoropsis obscura** A) basidia, B) hyphoid elements, C) spores. From the holotype.

differences, except the spores, should be noted. The apiculus is smaller and the germ-pore is very difficult to observe. Hyphal ends, or indistinctly differentiated dendrohyphidia, project slightly above the basidia. It should be mentioned, however, that such hyphae also occur, at least occasionally, in fruitbodies of Coniophora species. The dextrinoid reaction of the spores is not noticeable, while this characteristic is easily noted in most species of Coniophora. Verticillate or scattered clamps on the basal hyphae occur regularly in Coniophora but have not been observed in Coniophoropsis.

Corticaceae

Amethicium luteo-incrustatum Hjortst. & Ryv. spec. nov.
Fig. 2.
Fructificatio resupinata, arcte adnata, stratosa, sordide flava vel brunneola, circiter 0.2-0-6 mm crassa; hymenio levi vel passim tuberculato; systema hyphale dimiticum; subiculum distinctum, leve, 0.2-0.4 mm crassum, dilute ochraceum, hyphis skeleticis ramosissimis, perangustis, 0.5-1 µm crassis, ut videtur tenuitunicatis, hyalinis, fibulis nullis, indextrinoidei; hyphae generatoriae tenuitunicatae, 2-2.5 µm, hyalinae vel luteolae incrustatae, fibulatae, hyphae subhymeniales indistinctae, agglutinatae, itidem fibulatae; cystidia conspicua, tenuitunicata, plus minus cylindracea, basaliter valde luteola incrustata, generaliter 70-100 x 5-8 µm; in hymenio hyphae cystidioideae (basidiolae) dispositae, plus minus subulatae, 20-30 x 3.5-4 µm; basidia subclavata, tenuitunicata, 20-40 x 4-4.5 µm, 4 sterigmatibus; sporis ellipsoidei, tenuitunicatis, levibus, 4.5-5 x 2.8-3 µm, neque amyloidei et cyanophilis, neque dextrinoidei.
Holotypus: Argentina. Prov. Misiones, Iguazu Nat. Park, Cataratas de Iguazu, 1-5 March 1982. L. Ryvarden No. 19529 (O). Isotypus: (GB, and in Hjm priv.herb.).

Fruitbody resupinate, closely adnate, about 0.2-0.6(-1) mm thick, more or less membranaceous, crustaceous, fairly brittle and easily squashed under a cover glass, stratified, with 2 or more zones above the subiculum, hymenium smooth to slightly tuberculate, dotted by reddish encrusted cystidia (very strong lens, x 100), sordidly yellow or brownish, margin soft and byssoid. Hyphal system dimitic with a very distinct, pale ochraceous subiculum separated from the hymenium by a brown sterile zone consisting of hyphae and cystidia-residua, about 0.2-0.4 mm thick, soft, skeletal hyphae 0.5-1 µm wide, hyaline, thin-walled, without clamps, generative hyphae wider, with clamps, up to 2-2.5 µm or more, hyaline or heavely encrusted with resinuous and yellowish matter.

Cystidia abundant, usually projecting 10-20 µm above the basidia, flexuose, tapering towards the obtuse tip, basally strongly encrusted with yellowish, resinuous

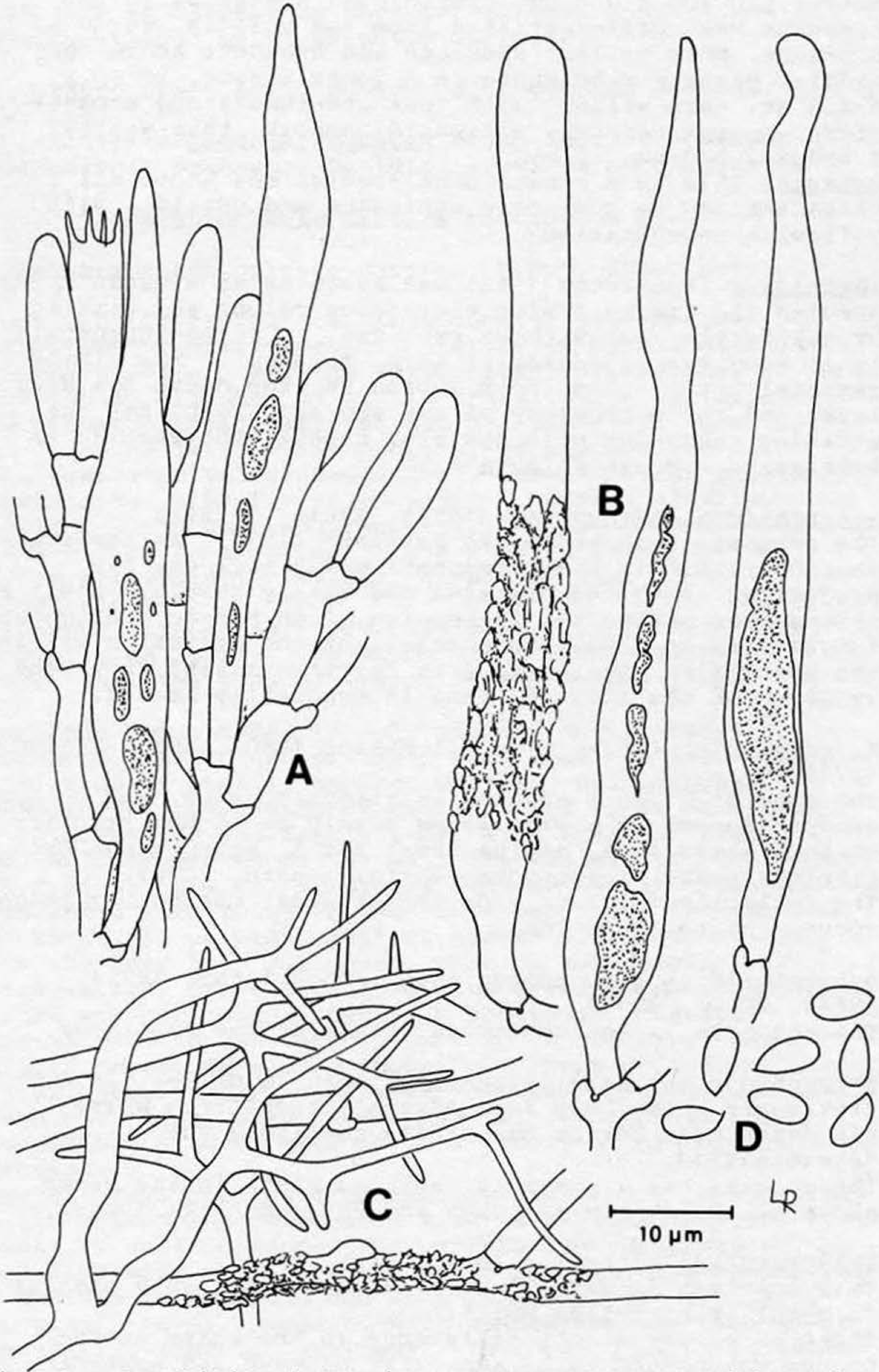

Fig. 2. **Amethicium luteo-incrustatum** A) part of hymenium with cystidia, B) cystidia, C) arboriform skeletal hyphae and generative hyphae from the subiculum, D) spores. From the holotype.

matter, 70-100 x 5-8 µm, cystidioles scattered in the hymenium well differentiated from the basidia, 20-30 x 3.5-4 µm, more or less subulate and broadest above the middle. Basidia subclavate in a dense tissue, 20-40 x 4-4.5 µm, thin-walled, with four sterigmata and a basal clamp. Spores narrowly ellipsoid, smooth, thin-walled, 4.5-5 x 2.8-3 µm.
Remarks. This is a conspicuous species and above all characterized by the loose subiculum and cystidia with yellowish encrustation.

Amethicium (Hjortstam 1983) was based on an African species (A. rimosum) with violaceous colour and dimitic hyphal system, but without cystidia. A. luteo-incrustatum is in many respects similar to A. rimosum by the similar skeletal hyphae, the loose subiculum, the dense basidial layer and the morphology of the spores. Except for the striking subiculum with skeletal hyphae, the species is similar to some in Phlebia s.l.

Asterostroma andinum Pat. 19578, 19616, 19728/B.
The concept is according to Parmasto (1979). An important characteristic is the asteroseta which have one ray projecting above the hymenium and easily observed under a strong lens giving the impression of an hymenochaetaceous fungus. The knowledge of species and the variation within the species in Asterostroma is far from satisfactory and a revision of the tropical taxa is especially needed.

A. cervicolor (Berk. & Curt.) Massee 19601, 19629, 19630, 19739.
The concept of this species is slightly vague, and we have used this name in a wide sense mainly as it has priority of such names as A. medium Bres. and A. ochroleucum Bres.
Athelopsis aff. lembospora (Bourd.) Oberw. 20069.
The collection differs from the original concept by longer spores, up to 10 µm long.

Botryobasidium lembosporum (Rog.) Donk 19659, 19721, 19849, 20045, 20104.
The anamorph is not connected in any of the specimens.

Botryohypochnus hebelomatosporus Boid. & Gilles 19854.
Previously known only from Africa (Gabon) from where it was described. Boidin has kindly confirmed the determination.
The species has a somewhat isolated place in the genus, above all by its conspicuous and Hebeloma-like spores.

Byssomerulius hirtellus (Burt) Parm. 19641.
This specimen is determined by J. Ginns as "very similar to Merulius hirtellus Burt".
There is a very slight difference in the shape of the spores which tend to be adaxially concave and somewhat narrower. Cystidia (or hyphoids) occur but are very few or

difficult to observe as they resemble of undeveloped basidia, though being slightly narrower.

Candelabrochaete Boid. subgen. Botryodontia Hjortst. & Ryv. subg. nov.
ex affinitate Candelabrochaete a qua impromis differt rhizomorphis praesens, basidiis brevibus et aliquantum obconicis.
Typus: Candelabrochaete cirrata Hjortst. & Ryv.

Candelabrochaete cirrata Hjortst. & Ryv. spec. nov.
Fig. 3.
Fructificatio resupinata, laxe adnata, plus minus caespitosa; aculeis parvis, constans ex hyphis sterilibus; systema hyphale dimiticum vel duplex; rhizomorphae conspicuae, albidae, ex hyphis crassitunicatis, dilatatis vel tenuitunicatis, alteruteris dilatatis vel angustis, tum 1.5-3 µm latis, sine fibulis; hyphae ceterae tenuitunicatae vel crassiusculae, 5-7 µm latae, passim incrustatae, sine fibulis; cystidia sparsa, clavata, circiter 40x10 µm, tenuitunicata; basidia brevia, plus minus obconica, circiter 17 x 6-7 µm, 4 sterigmatibus; sporis ellipsoidei, levibus, tenuitunicatis, indextrinoidei.
Holotypus: Argentina. Prov. Misiones, Iguazu Nat. Park, Cataratas de Iguazu, 1-5 March 1982. L. Ryvarden No. 19572, on lower side of leaves (O). Isotypus: (GB).

Fruitbody resupinate, loosely adnate, thin, almost arachnoid, tufted and provided with small aculei consisting of sterile hyphae, whitish. Rhizomorphs conspicuous, consisting of at least two types of hyphae: 1) thick-walled and fairly wide, with frequent septa 2) thin-walled or with slight wall thickening, narrow, about 1.5-2.5(-3) µm wide, seemingly septate. Other hyphae correspond with those in the fruitbody, viz. thin-walled and about 5-7 µm wide. Aculeal hyphae distinct, arising from the very thin subiculum, thin or moderately thick-walled, often encrusted with crystalline matter, all hyphae without clamps. Cystidia scattered, clavate, generally 40 µm long and 10 µm wide in the upper part. Basidia short, as a rule obconical, about 17x6-7 µm, with 4 sterigmata. Spores ellipsoid, smooth, thin-walled, 6-6.5 x 4-5 µm, often with one or several oildrops in the protoplasm, without amyloid, dextrinoid or cyanophilous reaction.
Remarks. This species differs from all others in the genus by its rhizomorphs with some kind of skeletal hyphae. Most hyphae in well developed rhizomorphs are thick-walled, up to 5-7 µm wide or narrow and 1.5-3 µm wide. The morphology of basidia is striking and as a rule they are typically obconical, never elongated with median construction as in the generic type (C. africana). In looking for a suitable genus for this new species, Candelabrochaete was chosen as the most appropriate one. The differences in basidia and

hyphae seem to justify a subgeneric treatment.

Candelabrochaete dispar Hjortst. & Ryv. spec. nov. Fig. 4. Quod habitum et fabricum internam fructificationem ad Candelabrochaeten africanam et verruculosam, a qua imprimis differt sporis globosis.
Holotypus: Argentina. Prov. Misiones, Iguazu Nat. Park, Cataratas de Iguazu. 1-5 March 1982. L. Ryvarden No. 19549 (O). Isotypus: (GB). Paratypi: 19564, 19580(O,GB).
Etymology: dispar - unlike
Fruitbody resupinate, closely adnate, when dried fragile and slightly cracked, creamish to pale ochraceous, about 0.2-0.4 mm thick, hymenium grandinioid to indistinctly odontioid with blunt aculei, cystidia somewhat projecting, hyaline and glittering, margin more or less abrupt or thinning out to a net of hyphae. Hyphal system monomitic, basal hyphae thin-walled or with thickened walls, rarely distinctly thick-walled, approximately 4-6 µm wide, branching at right angles or from an angle of 30°, long-celled and generally up to 50-80 µm between septa, subhymenial hyphae short-celled, branching in a candelabralike manner and often widest in the middle part, 4-5 µm wide, all hyphae without clamps. Cystidia tubular, thin-walled or basally with thickened walls, projecting up to 40-60 µm above the basidia, normally with 4-8 septa, about 80-120(-200) µm long and 6-9(-10) µm wide, acyanophilous.
Basidia short-clavate to almost cylindrical, (12-)15-17(-25) x 4-5(-6) µm, with four sterigmata, linear repetition not observed. Spores subglobose, smooth, thin-walled, 5-5.5 x 4-4.5 µm or about 5 µm in diam., inamyloid, indextrinoid, acyanophilous, often with a central oildrop (cotton-blue.)
Remarks. Externally this species is somewhat similar to both C. africana Boid and C. verruculosa Hjortst., but microscopically well separated by the different spores. Thin-walled conidia-like cells have been observed in all collections. In shape they are similar to the basidiospores but slightly smaller and usually born in short chains.

Cystidiodontia Hjortst., Mycotaxon 17 p.571, 1983.

This genus was described to accomodate Hydnum artocreas Berk. & Curt. ex Cooke. Unfortunately the description was based on East African specimens which later on appeared to be distinctly separated from the type of H. artocreas (Venezuela. No. 139, Kew). Thus, Cystidiodontia is a misapplied name and therefore a necessary generic emendation is given below.
The African material belongs to Kneiffia isabellina Berk. & Br. which primarily differs by its dextrinoid hyphae (skeletals). In most other characteristics such as gloeocystidia, basidia, and spores it is very similar to H. artocreas.

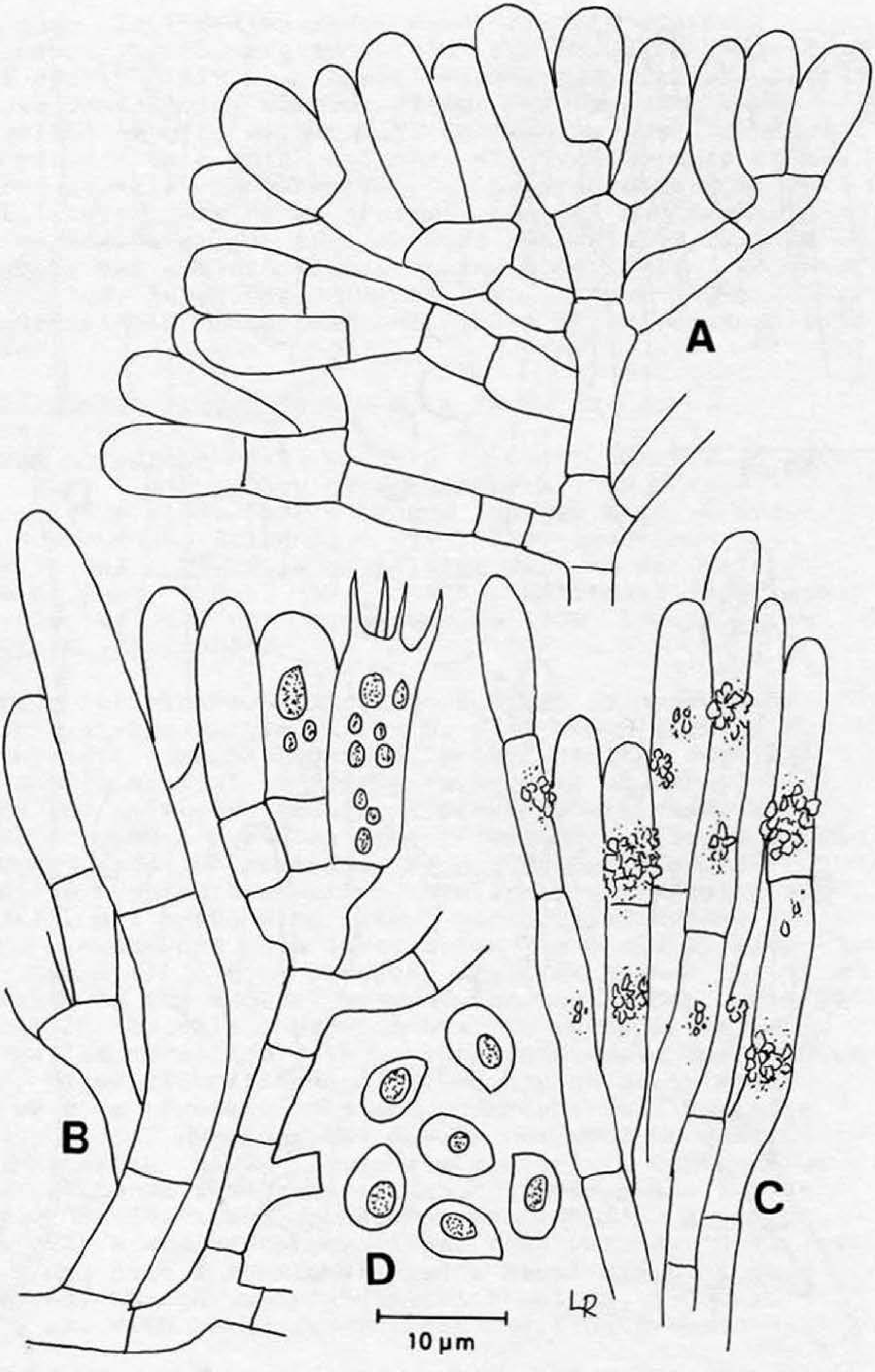

Fig. 3. **Candelabrochaete cirrata** A) cluster of unripe basidia, B) part of hymenium with cystidium, C) slightly encrusted aculeal hyphae, D) spores. From the holotype.

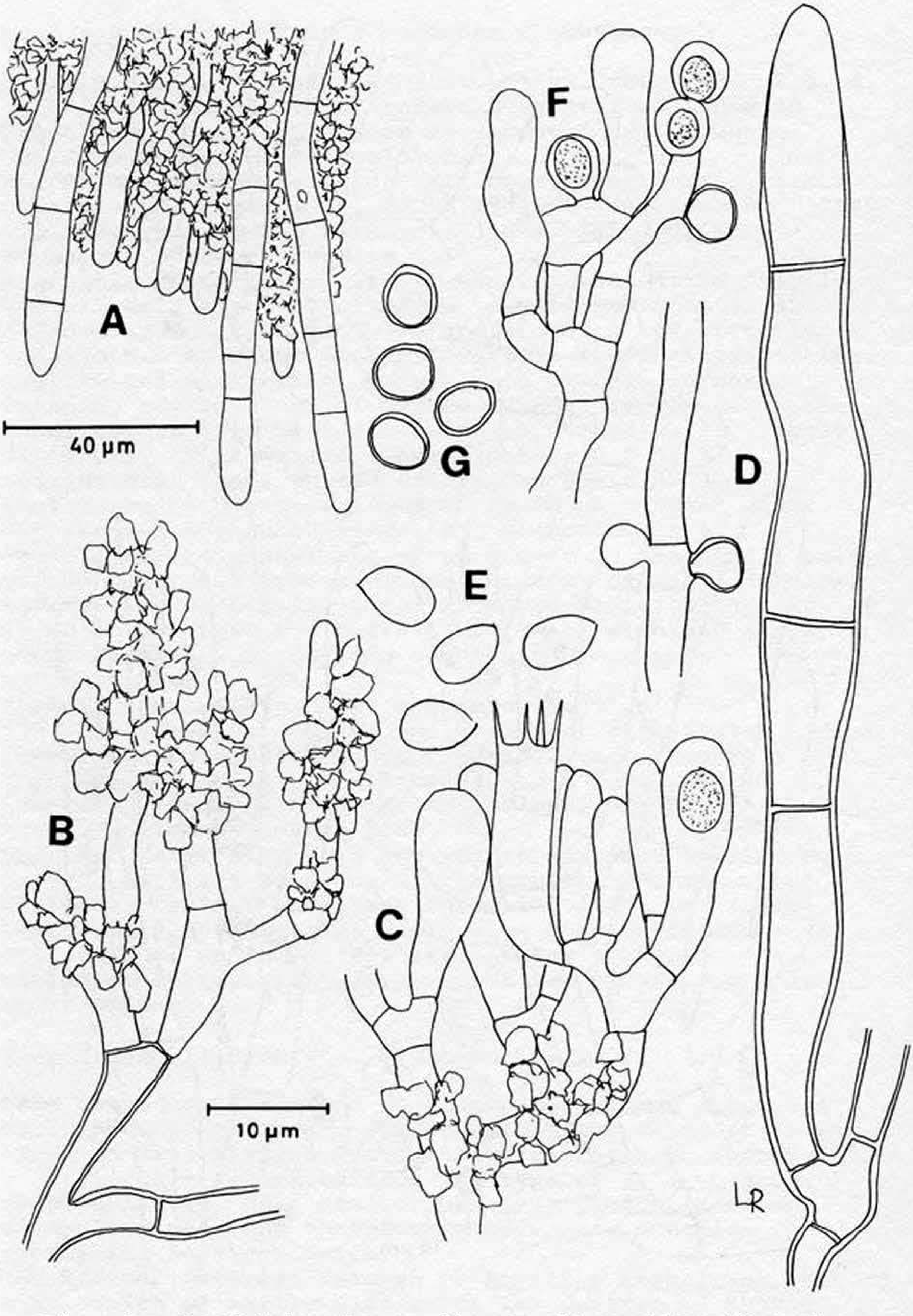

Fig. 4. **Candelabrochaete dispar** A) section through aculeus, B) encrusted hyphae from aculei, C) part of hymenium, D) cystidium, E) basidiospores, F) hyphae with condidia-like cells, G) separate conidia-like cells. From the holotype.

Emendation: Fruitbodies resupinate, closely adnate, crustaceous, hymenium grandinioid, odontioid or hydnoid; hyphal system dimitic, skeletal hyphae indextrinoid or strongly dextrinoid, without clamps, subhymenial hyphae thin-walled or with slight wall thickening, with clamps, gloeocystidia as a rule numerous, with yellowish contents, negative in sulfuric benzaldehyde, dendrohyphidia in the hymenial layer lacking or present; basidia subclavate, small to medium-sized, more or less constricted, with 4 sterigmata and a basal clamp; spores moderately thick-walled, subglobose, fairly small, about 3-4 x 2.5-3 µm, indextrinoid, inamyloid but with a slight cyanophilous reaction.

Cystidiodontia artocreas (Berk. & Curt. ex Cooke) Hjortst. Fig. 5.
- Hydnum artocreas Berk. & Curt. ex Cooke, Grevillea 20 p. 1, 1891. - nec Hydnum artocreas Berk., in Massee Journ. Bot. p. 163, 1892 = Hydnum indicum Sacc. & Syd. 1899. - necuaquam Hallenb. & Ryv. 1975, neque non Hjortst. 1983 = Kneiffia isabellina Berk. & Br. 1875.
Specimens seen: 19676, 19747, 19759. Additional specimens: Venezuela. No. 139 (K). Sao Leopoldo 1906. leg. J. Rick No. 106 (S, BPI, UPS).

Fruitbody resupinate, effused, odontioid to hydnoid or subporoid at the margin, light greyish brown, margin thinning out, somewhat byssoid, paler than the fertile part, aculei conical to flattened, simple or usually crowded and coherent, smooth or provided with small outgrowths, under a strong lens (X100) dotted by brownish excretions from the cystidia. Hyphal system dimitic; generative hyphae thin-walled, hyaline, intermingled with skeletals, all septa with clamp, subhymenial hyphae forming a dense and thin layer below the basidia, with clamps but difficult to observe. Skeletal hyphae dominating in the central part of the aculei but can also be found in the thin subiculum next to the substratum, thick-walled, hyaline, with adventitious septa but without clamps, transitions from generative hyphae often seen, 2-2.5 µm wide, indextrinoid and acyanophilous. Cystidia (Gloeocystidia) numerous and easily observed because of their yellowish content, strongly stained in cotton-blue, sinuous, thin-walled, negative in sulfuric benzaldehyde, about 20-30(-50) x 5-7 µm, with a basal clamp. Basidia small, with a median constriction, thin-walled, 10-12(-15) x 4-4.5 µm, eith 4 sterigmata and a basal clamp. Spores subglobose, smooth, moderately thick-walled, 3-3.2 x 2.5-2.8 µm, with weak cyanophilous reaction.

Cystidiodontia isabellina (Berk. & Br.) Hjortst. & Ryv. comb.nov. Basionym: Kneiffia isabellina Berk. & Br., Journ. Linn. Soc. Bot. Lond. 14 p. 62, 1875.
For detailed description see Hallenberg and Ryvarden, 1975. On the "type-sheet" of this species are three

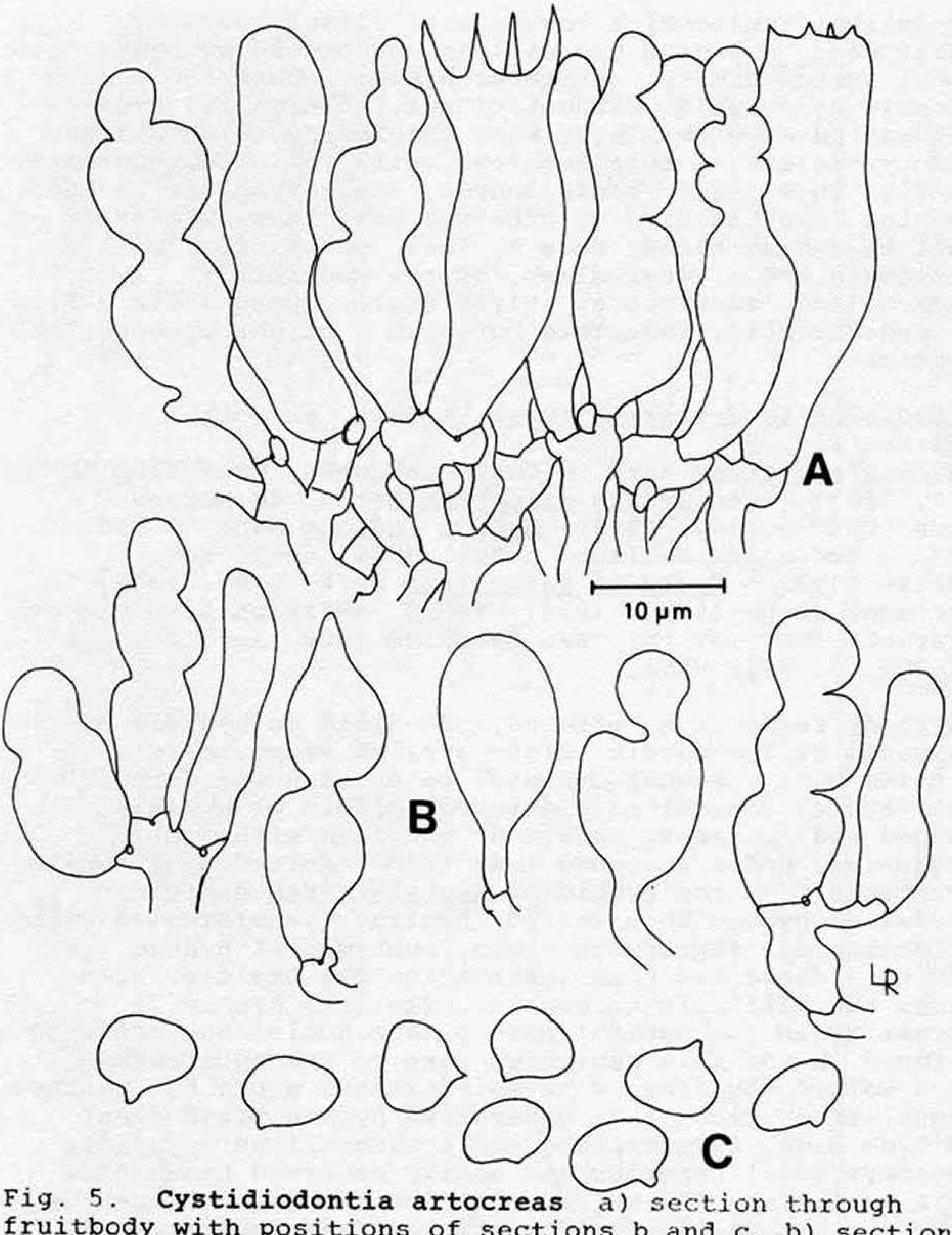

Fig. 5. **Cystidiodontia artocreas** a) section through fruitbody with positions of sections b and c, b) section through aculeus, c) cross-section through aculeus, d) skeletal hyphae, e) basidia, f) gloeocystidia. Coll. R. 19676. Drawing by J. Eriksson.

2-3(-4) µm wide, with clamps, subiculum thin to almost indistinguishable with somewhat agglutinated the hyphae. <u>Cystidia</u> conspicuous, strongly constricted to moniliform, apically often with one or several smaller protuberances, generally 20-40 µm long, distinctly amyloid, negative in sulfuric benzaldehyde. <u>Basidia</u> more or less clavate, thin-walled, slightly constricted in the middle part, about 20-25 x 6-7 µm, with 4 sterigmata and a basal clamp. <u>Spores</u> ellipsoid, thin-walled or with very slight

specimens indicated by us as A^1, A^2, and B. Specimens A^1 and A^2 are from: South of the island (Sri Lanka) July 1868, and Central province, Dec. 1868. They very likely represent what Berkeley had in hand when he described the fungus. The third specimen (B) has nothing to do with the two others and we have no name for it, but it is determined by Berkeley as <u>Kneiffia</u> <u>setigera</u> Fr. This latter species is collected in the same locality as <u>K</u>. <u>isabellina</u> and listed as no. 565.
Lectotypus: designated here, Ceylon, No. 655 A^1 (K).
It should be noted that this species is well known from eastern Africa and is hitherto not found in South-America. Its macromorphology is similar to that of <u>C. artocreas</u>, but is separated from the latter by microscopical characters.

<u>Dendrodontia</u> <u>bicolor</u> (Talbot) Hjortst. & Ryv. 19658.
Previously known only from Africa, Natal (Pietermaritzburg, type-locality), Kenya and Tanzania.
<u>Fibricium</u> <u>subceraceum</u> (Hallenb.) Bernicchia comb. nov.
Basionym: Fibrodontia subceracea Hallenb., Iran. J. Plant Path. 14:54,1978. 20068.
This species was described from Iran (Hallenberg, 1978), but in recent years also found in the Mediterranean area by Bernicchia.
As indicated in the original description, the thick-walled skeletal hyphae are morphologically different from those of <u>Fibrodontia</u> <u>gossypina</u>, and they do not occur in the aculei or in the smooth hymenium between the aculei. In most specimens they are easily distinguished as a very thin zone next to the substratum. Evidently the species does not belong in <u>Fibrodontia</u> but has similarities with <u>Fibricium</u> <u>rude</u>, especially in the nature of basidia and subhymenial hyphae. The fibre-hyphae also point to this genus.

<u>Gloeocorticium</u> <u>cinerascens</u> Hjortst. & Ryv. gen. nov. et spec. nov. Fig. 6. Fructificatio resupinata, effusa, mediocris crassa, hymenio plus minus sicco firmo ceraceo; systema hyphale monomiticum, hyphis plerumque distinctis, fibulatis; cystidia iterum atque iterum mamillata, perspicue amyloidea; basidia clavata, in typo circiter 20-25 x 6-7 µm, 4 sterigmatibus; sporis subglobosis, apiculo saepe laterale, inamyloidibus, indextrinoidibus, acyanophilis.

Type species: <u>Gloeocorticium</u> <u>cinerascens</u> Hjortst. & Ryv.
Holotypus: Argentina. Prov. Misiones, Iguazu Nat. Park., Cataratas de Iguazu. 1.-5. March 1982. L. Ryvarden No 19719 on Bamboo (O). Isotypus: (GB). Paratypi: 19600, 19612 (rather poor material), 19646, all on Bamboo.
<u>Fruitbody</u> resupinate, adnate, mostly thin, about 0.1-0.2 mm, continuous but minutely cracked, smooth, greyish-white; margin not specially differentiated. <u>Hypal system</u> monomitic, hyphae thin-walled, hyaline, smooth,

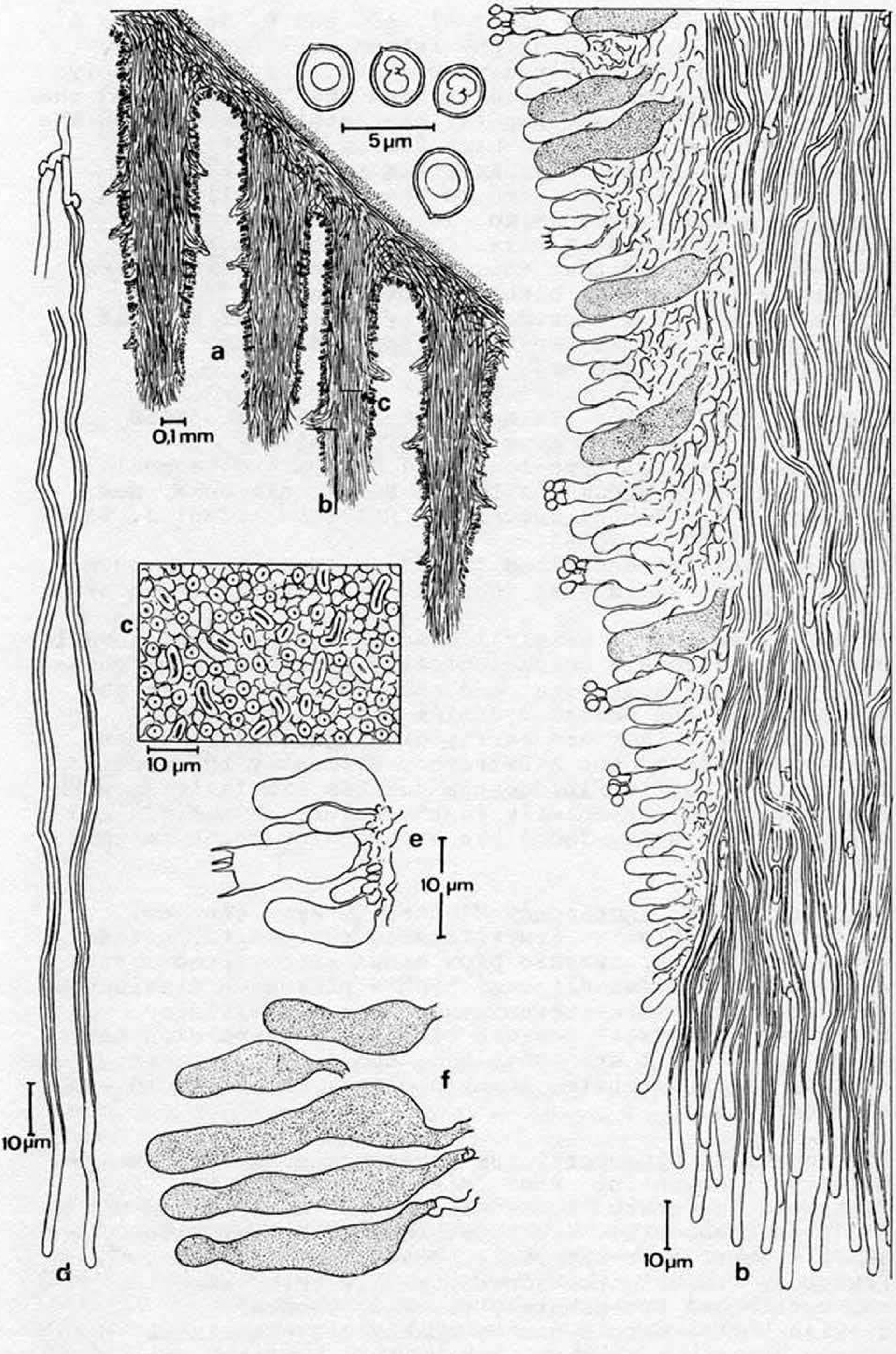

Fig. 6. **Gloeocorticium cinerascens** A) part of hymenium, B) cystidia, C) spores. From the holotype.

wall thickening, IKI- , generally 6.5-7 x 4.5-5 µm, apiculus distinct, placed laterally.
Remarks. This new genus and species has character similar to those of Radulomyces, especially the characteristic apiculus and to a certain degree also the basidia. However, the amyloid and moniliform gloeocystidia and the laterally depressed spores make the genus unique in the Corticiaceae s.l.

Gloeocystidiellum lactescens (Berk.) Boid. 19540, 19617, 19836.

Gloeocystidiellum triste Hjortst. & Ryv. spec. nov.
Fig. 7.
Fructificatio resupinata, arcte adnata, distincte stratosa, circiter 0.2-0.3 mm crassa, fere cornea; hymenio levi, pallide vel sordide brunneolo; systema hyphale monomiticum, hyphis tenuitunicatis vel crassiusculis, 2.5-3.5 µm latis, agglutinatis; hyphis subhymenialibus levibus, 2-2.5 µm latis, omnibus non-fibulatis; sulfocystidia tubularia, tenuitunicata vel basaliter crassiuscula, 100-150 (200) µm longa, 6-8(-12) µm lata; basidia clavata, 10-25(-30) x 3.5-5 µm, 4-sterigmatibus; sporis ellipsoidibus, subtiliter verrucosis, hyalinis, 5-6 x 3.5-4 µm, amyloidibus.
Holotypus: Argentina. Prov. Misiones, Iguazu Nat. Park., Cataratas de Iguazu. 1.-5. March 1982. L. Ryvarden No. 20055 (O). Isotypus: (GB).
Etymology: tristis = dull-coloured.
Fruitbody resupinate, tightly adnate, distinctly stratified and about 0.2-0.3 mm thick, consistency hard and somewhat horny, hymenium smooth, pale to sordidly brown; margin abrupt or slightly fibrillose. Hyphal system monomitic, basal hyphae thin-walled or with very slight wall thickening, hyaline, smooth, 2.5-3.5 µm wide, agglutinated in old tissues and with gelatinous interhyphal substance, subhymenial hyphae narrower, about 2 - 2.5 µm wide, hyaline, smooth, all hyphae without clamps. Gloeocystidia tubular, thin-walled or basally with thickened walls, sinuous, 100-150(-200) µm long and 6-8(-12) µm wide, often with several adventitious septa, in KOH with oily content and with a strong positive reaction in sulfuric benzaldehyde. Basidia clavate, loosely arranged, 20-25(-30) x 3.5-5 µm, with four sterigmata and without basal clamp. Spores ellipsoid, finely verrucose, hyaline, 5-6 x 3.5-4 µm, strongly amyloid.
Remarks. This species is easily recognized by its stratified fruitbody, clampless hyphae, and verrucose spores. It differs from other species with similar fructification and hyphae without clamps which are placed in Conferticium (e.g. C. karstenii (Bourd. & Galz.) Hallenb. and C. ochraceum (Fr.:Fr) Hallenb. by lacking the repetitive basidia. G. porosellum Hjortst., described from North Europe, is somewhat similar as to hyphae and

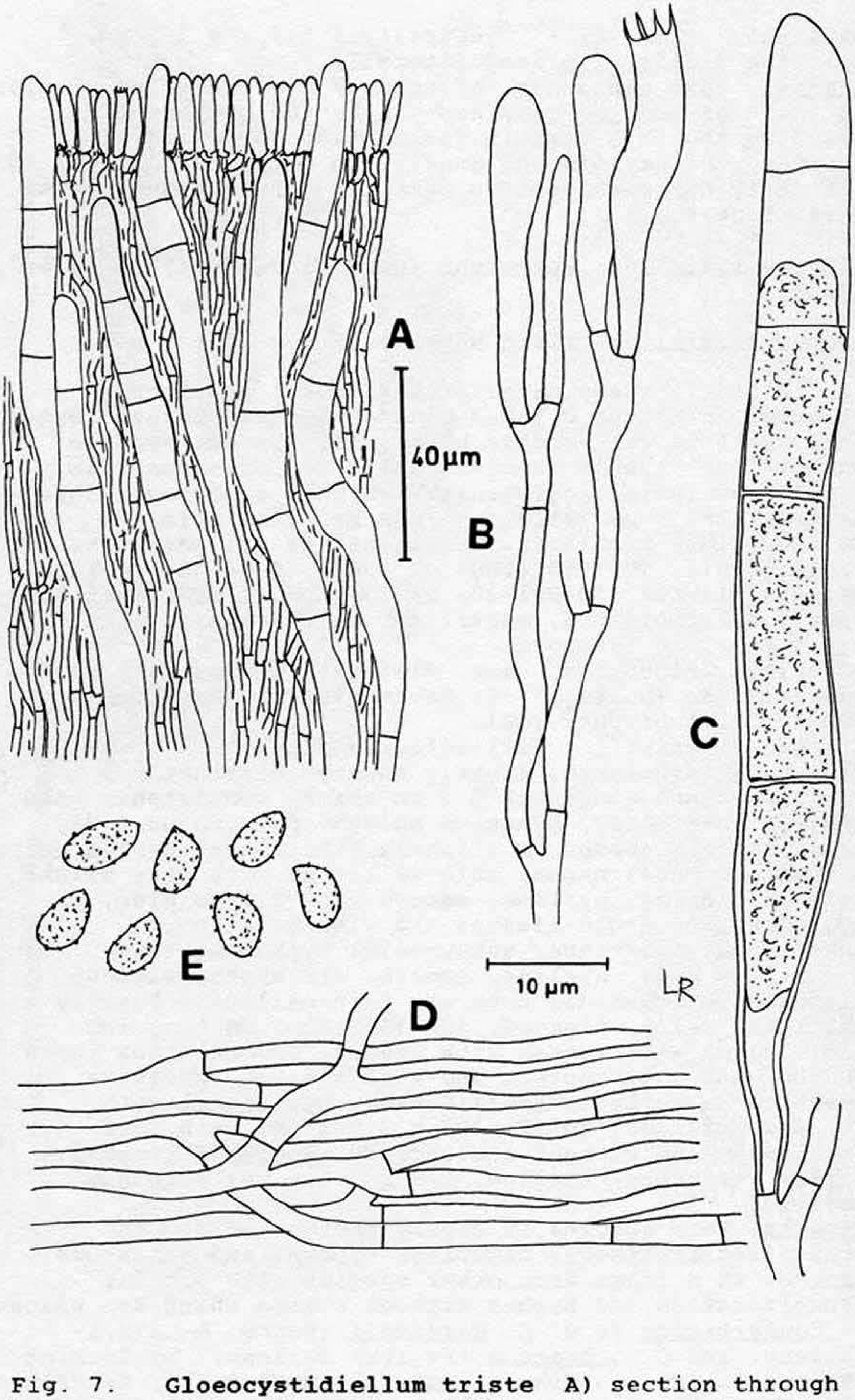

Fig. 7. **Gloeocystidiellum triste** A) section through hymenium, B) basidia, C) cystidium, D) hyphae from the subiculum, E) spores. From the holotype.

spores, but has thinner, not layered fruitbodies and is considerably softer. G. flammeum Boid. seems also to be closely related but lacks the blackish reaction in sulfuric benzaldehyde.

G. turpe Freeman 19773.
We agree with the author that this species should be placed in the vicinity of G. lactescens. However, the type of G. turpe has been examined and the Iguazu-specimen does not fully agree. The colour is more light-brown with the margin paler, and the tissue denser. The spores as well as the basidia and cystidia seem to conform to the description of G. turpe.

Hydrabasidium subviolaceum (Peck) John Erikss. & Ryv. 19741.

Hyphoderma argillaceum (Bres.) Donk 19788

Hyphoderma iguazuense Hjortst. & Ryv. spec. nov.
Fig. 8. Differt a Hyphodermate deviato cystidiis claviformibus et sporis leviter longioribus.
Holotypus: Argentina. Prov. Misiones, Iguazu Nat. park., Cataratas de Iguazu. 1.-5. March 1982. L. Ryvarden No 19576 (O). Isotypus: (GB). Paratypus: 19569 (O, GB).
Fruitbody resupinate, slightly adnate, pellicular to slightly membranaceous and more or less pliable, smooth or more commonly slightly pilose by protruding cystidia, in colour greyish white, margin indeterminable. Hyphal system monomitic; basal hyphae loosely interwoven, thin-walled to moderately thick-walled, as a rule encrusted with crystalline matter, 3.5-5.5 µm wide, sparsely ramified and in most cases branched from the clamps and forming a very thin tissue next to the substratum, subhymenial hyphae more densely united and vertically arranged, all hyphae with clamps, acyanophilous, indextrinoid. Cystidia cylindrical, subclavate or subcapitate, (30-)80-100 µm or sometimes considerably longer, thin-walled, apically widened to as much as 10-12 µm and 4-6 µm broad at the base, rarely with some adventitious septa, acyanophilous and seemingly without refractive content. Basidia more or less clavate, thin-walled, with an median constriction, (18-)20-25 x 4.5-5.5 µm, with four sterigmata and a basal clamp. Spores ellipsoid, smooth, thin-walled, (6-)6.5-8.5 x (3.2-)3.5-4 µm, with oily inclusions in the protoplasm, inamyloid, indextrinoid, acyanophilous.
Remarks. H. iguazuense is primarily separated from H. deviatum by wider and more pronounced clavate cystidia and somewhat longer spores. Further, the hymenium is whitish or cream-coloured, whereas in H. deviatum the normal colour is grey or whitish only towards the margin.

H. praetermissum (Karst.) John Erikss. & Strid 19844, 19858, 20051.

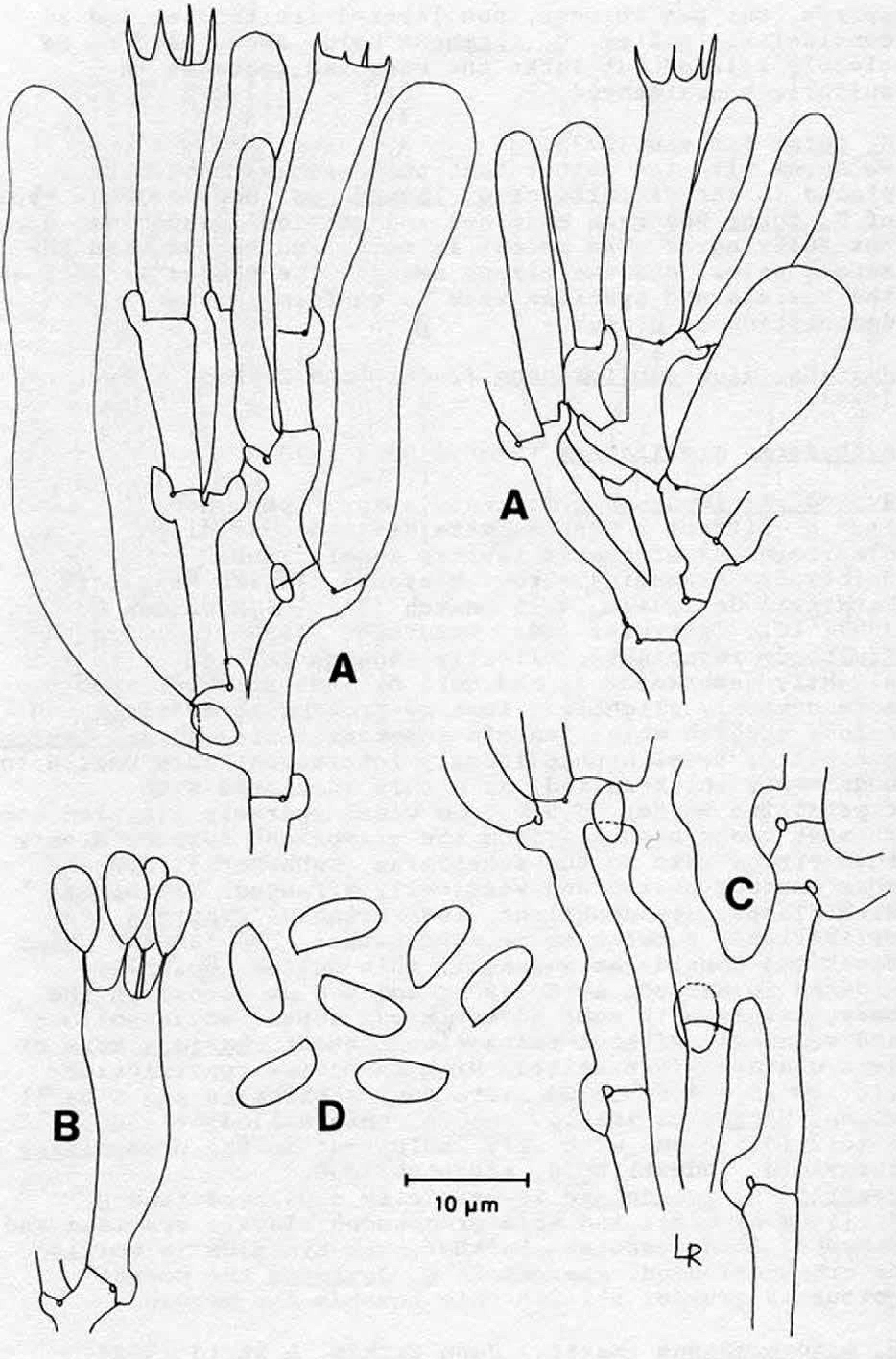

Fig. 8. **Hyphoderma iguazuense** A) part of hymenium with cystidia, B) basidium, C) hyphae from subiculum, D) spores. From the holotypes.

H. puberum (Fr.) Wallr. 19679.

H. rude (Bres.) Hjortst. & Ryv. 19771, 19773/B, 19806. The specimens conform to the type but the stephanocysts are fewer.

H. setigerum (Fr.) Donk 19632, 20092.

Hyphodermella aff. *corrugata* (Fr.) John Erikss. & Ryv. 19509, 19825.
The specimens differ in having denser fructifications, smaller basidia and spores. *H. corrugata* was found several times in Rick's collections and previously reported from Brazil by Hjortstam and Ryvarden (1982).

Hyphodontia alutaria (Burt) John Erikss. 19532, 19614, 19823.

Hyphodontia apacheriensis (Gilbn. & Canf.) Hjortst. & Ryv. comb. nov.
Basionym: *Poria apacheriensis* Gilbn. & Canf., Mycologia 65(5):1117, 1973.
This species is strictly poroid but microscopically it conforms in essential characteristics with the genus *Hyphodontia* such as hyphae (especially the ramification) and basidia. The cystidia (or cystidioles) are very similar of those of *H. aspera* and *H. breviseta*. Compare also *Poriodontia* described by Parmasto (1982).
H. aff. *brevidens* (Pat.) Tyv. 19568, 19727, 19754, 19796, 20103.
This species is in many respects very similar to *Fibrodontia gossypina* Parm., e.g. outer appearance, hyphae, basidia, and spores. After having seen the type of *Irpex brevidens* it is with some doubt we accept the Iguazu-specimens as this species or as a species of its own. The type (see Ryvarden, 1983) of *Irpex brevidens* is surprisingly well preserved and microscopically easily studied but in time the colour of the hymenium has probably changed to a more brown tint. In the centre of the aculei there are many thick-walled hyphae or skeletals with fairly dense protoplasmatic contents. These hyphae contrast conspicuously with the other hyphae by their yellow colour. We consider *I. brevidens* not to be conspecific with *F. gossypina*.
The specimens from Iguazu are all similar but in comparison with the type of *H. brevidens* they differ in having hyaline central aculeal hyphae with thinner walls. Such hyphae are often seen in many odontioid species of *Hyphodontia* though with slightly wider lumen and they are not treated as skeletals by most corticiologists. Further studies of this taxon (or taxa) in South America is needed and additional specimens will be highly appreciated.

H. sambuci (Pers.) John Erikss. 19785.

H. aff. knysnana (van der Byl) Reid 19606, 20054. Originally this species was described from South Africa and re-collected by Ryvarden in Tanzania (No. 10126, O). The Iguazu specimen corresponds well with the isotype (at Kew) as well with the Tanzanian collection but seems to have somewhat narrower spores. H. knysnana belongs in the subsection Ellipsosporae Parm. and its closest relative is H. nudiseta Warc. & Talb.

Hyphodontia lutescens Hjortst. & Ryv. spec. nov. Fig. 9. Ex affinatate Hyphodontia aspera et H. breviseta ab utroque cystidiis flexuosis, obtusis, neque capitatis, sporis ellipsoidibus, generaliter 6.5-7 x 3.5-3.8 µm. Holotypus: Argentina. Prov. Misiones, Iguazu Nat. Park., Cataratas de Iguazu. 1.-5. March 1982. L. Ryvarden No. 19758 (O). Isotypus: (GB).

Fruitbody resupinate, closely adnate, fairly tough but easily squashed under a cover-glass, creamish to pale yellowish, hymenium odontioid, with small, conical aculei, approximately 2-4 per mm, smooth or apically fimbriate by protruding hyphae or cystidial elements, hymenium between the aculei smooth, fairly firm; margin thinning out or slightly fibrillose. Hyphal system monomitic, hyphae hyaline, thin-walled or with slight wall thickening, smooth or slightly encrusted, 3-4 µm wide, straight in the centre of the aculei, irregularly interwoven in the subicular tissue, walls acyanophilous, all hyphae with clamps. Cystidial elements more or less hyphoid and little differentiated from hyphae and basidia, warying in size and appearance, usually flexuose, 30-50 µm long and 3-4 µm wide, mostly observed in the aculei but also frequently occurring in the smooth hymenium between the aculei. Basidia subclavate, after sporulation elogated, more or less urniform, thin-walled, 18-20(-30) x 4-4.5(-5) µm, with four sterigmata and a basal clamp. Spores ellipsoid, smooth, thin-walled, (6-)6.5-7(-7.5) x (3-)3.5-3.8 µm, with one or few oildrops in the protoplasm.
Remarks. Externally H. lutescens resembles of H. aspera but this species is ordinarily whitish and under a microscope immediately separated by more subglobose spores and capitate cystidial elements.

Hyphodontia tenuicystidia Hjortst. & Ryv. spec. nov. Fig. 9.
Fructificatio resupinata, adnata, circiter 0.1-0.2 mm crassa, pallide ochracea; hymenio levi vel parum tuberculato; systema hypahle monomiticum; subiculum indistinctum, hyphis paucis, parallele, tenuitunicatis, 2.5-3 µm latis, fibulatis; hyphis subhymenialibus plus minus verticalibus, densis, 2-4 µm latis, itidem fibulatis; cystidia sparsa, tubuliformia, tenuitunicata, hyalina, 90-100 x 4-6 µm, obtusa; basidia primum subclavata tum suburniformia, basaliter crassiuscula, 20-25 x 3-4 µm, 4-sterigmatibus; sporis ellipsoidibus,

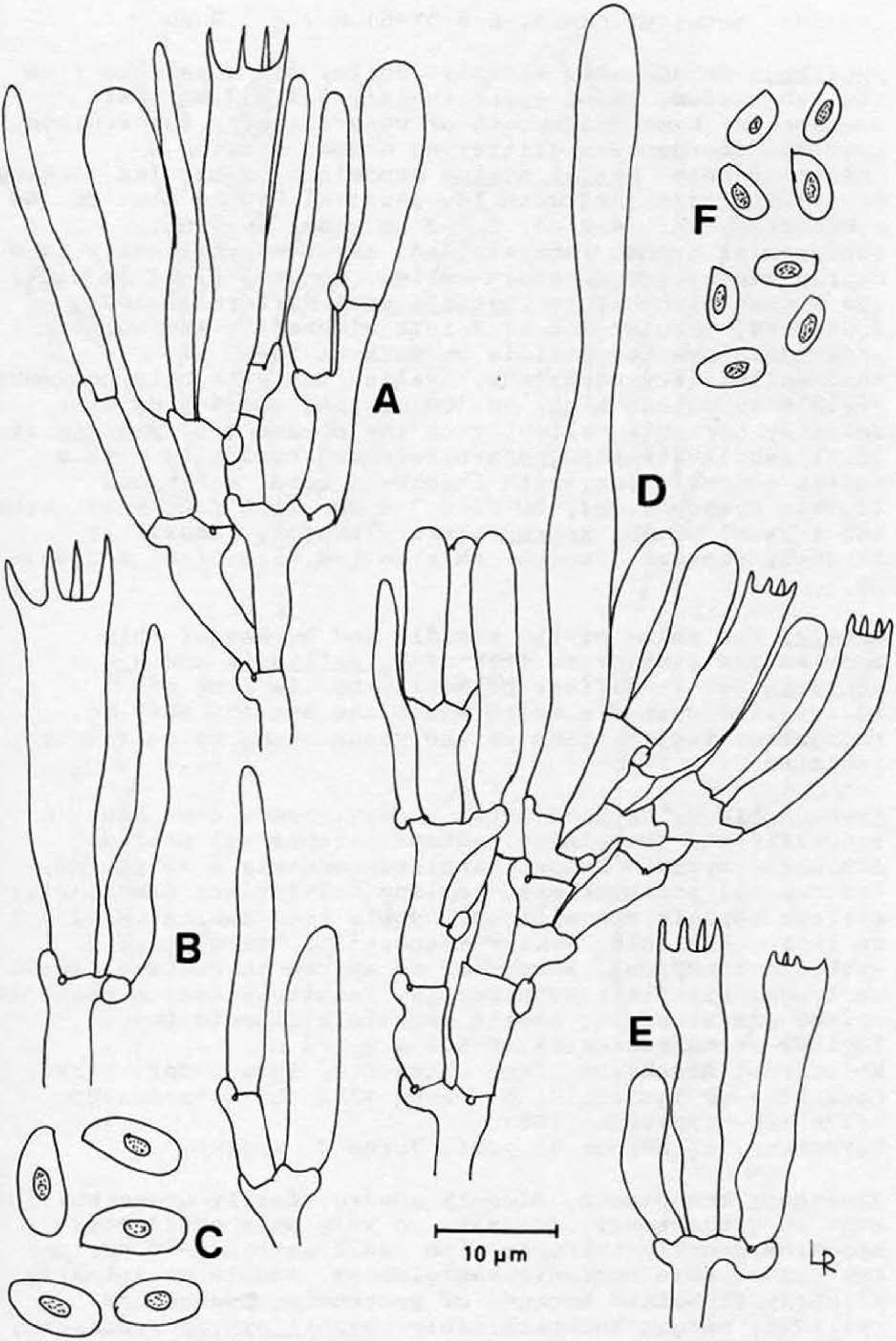

Fig. 9. **Hyphoderma lutescens** A) part of hymenium, B) basidium, C) spores. - **Hyphodontia tenuicystidia** D) hymenium with cystidium, E) basidia, F) spores. From the holotype.

levibus, tenuitunicatis, 5-5.5(-6) x 2.8-3.2 µm.

Fruitbody resupinate, closely adnate, not separable from the substratum, thin, approximately 0.1-0.2 mm, pale ochraceous; hymenium smooth or very slightly tuberculate, cystidia emergent as glittering drops; margin indeterminable. Hyphal system monomitic; subiculum lacking or mostly indistinct with few parallel hyphae next to the substratum, thin-walled, 2.5-3 µm wide, hyaline, subhymenial hyphae intermingled, arranged vertically in a fairly dense tissue, short-celled, about 2-4(-5) µm wide, all hyphae with clamps Cystidia well differentiated, scattered, tubular and as a rule widened at the base, protrude above the basidia as much as 30-50 µm, thin-walled, acyanophilous, hyaline but with oily contents visible in cotton blue, 90-100 µm long and 4-6 µm wide, apically narrowing slightly to the obtuse tip. Basidia at first subclavate then suburniform and typically with a median constriction, with thickened basal walls and lightly cyanophilous, 20-25 x 3-4 µm, with four sterigmata and a basal clamp. Spores short-ellipsoid, adaxially slightly concave, smooth, thin-walled, 5-5.5(-6) x 2.8-3.2 µm.

Remarks The shape of the basidia and hyphae of this species are similar to that of H. pallidula and H. alutaria but it differs primarily by its long and thin-walled cystidia which makes the species easy to recognize. The position in the genus seems to be fairly isolated.

Hyphodontia wrightii Hjortst. & Ryv. spec. nov. Fig. 10.
Fructificatio resupinata, adnata, cremea vel pallide ochracea; hymenio dense granulato, aculeis 6-10 per mm, conicis vel semiglobosis, levibus vel leviter fimbriatis; systema hyphale monomiticum; hyphis tenuitunicatis, 2.5-3 µm latis, hyalinis, modice cyanophilis, fibulatis; cystidia conspicua, numerosa, ad apicem incrustata, 30-50 µm longa; basidia suburniformia, tenuitunicata, a medio ad apicem crassiuscula; sporis anguste elliosoidibus, levibus, tenuitunicatis, 5-5.5 x 2.5-3 µm.
Holotypus: Argentina. Prov. Misiones, Iguazu Nat. Park., Cataratas de Iguazu. 1.-5. March 1982. L. Ryvarden No. 19636 (O). Isotypus: (GB).
Etymology: in honour of prof. Jorge E. Wright.

Fruitbody resupinate, closely adnate, fairly dense but soft in consistency, creamish to very pale ochraceous; hymenium densily granular with small warts, 6-10 per mm, conical or more commonly semiglobose, smooth or apically slightly fimbriate because of protruding hyphae and cystidia; margin indeterminable. Hyphal system monomitic; subiculum very thin to inconspicuous with few parallel hyphae, thin-walled, 2.5-3 µm wide, hyaline, subhymenial hyphae vertically arranged in a fairly dense and thin

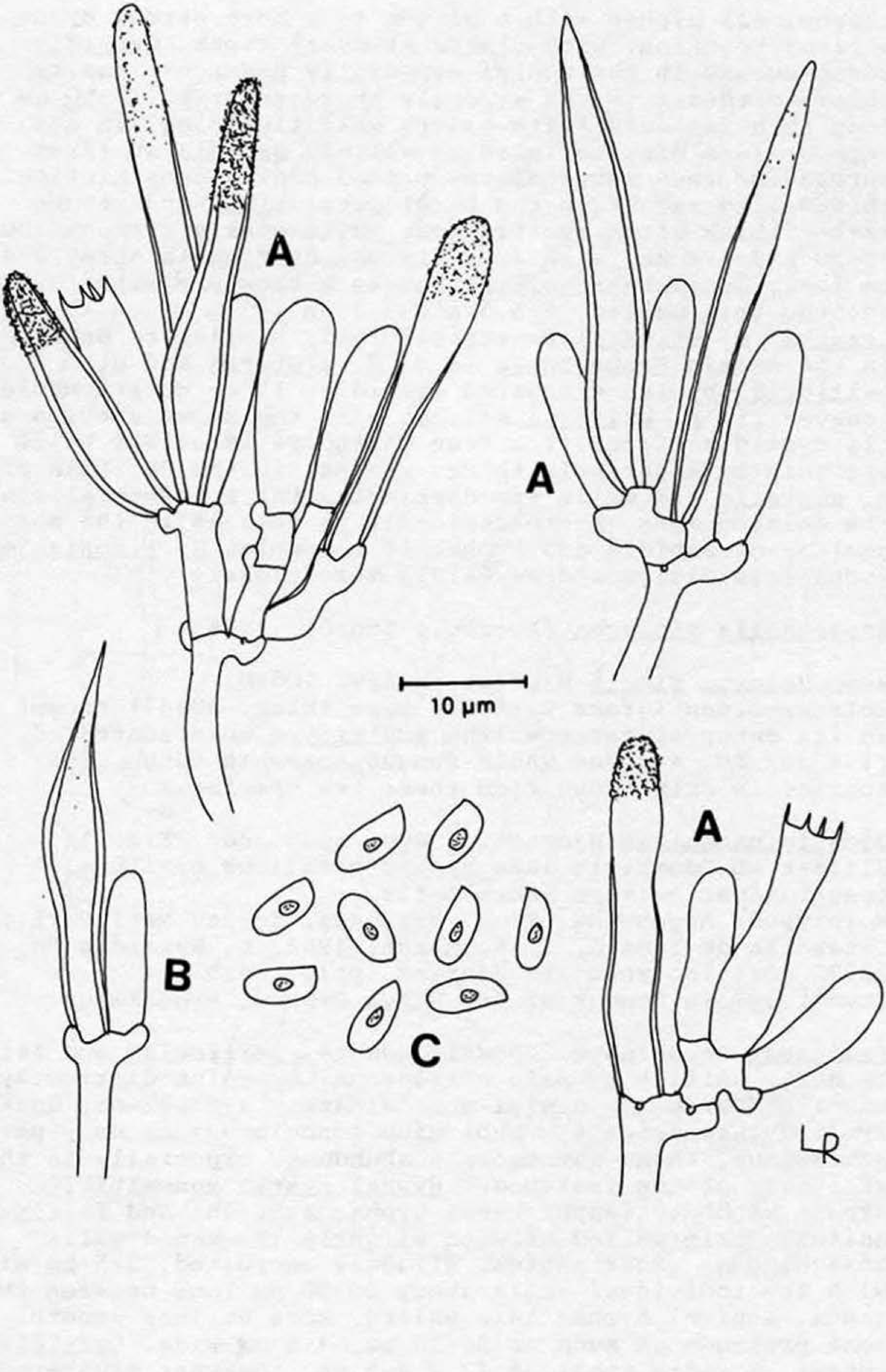

Fig. 10. **Hyphodontia wrightii** A) clusters of basidia and cystidia, B) acute cystidium, C) spores. From the holotype.

tissue, all hyphae with a slight to a more strong cyanophilous reaction, with clamps at every septa. Cystidia conspicuous, in the aculei especially numerous, easily observed thanks to the strongly encrusted tip, 30-50 µm long thin-walled or with slight wall tickening, in age more or less distinctly thick-walled. Basidia at first subclavate then suburniform, with a median constriction, thin-walled except in the basal part which tends to be rather thick after sporulation, walls weakly cyanophilous, 15-20 x 3.5-4 µm, with four slender sterigmata about 3-4 µm long, and a basal clamp. Spores narrowly ellipsoid, smooth, thin-walled, 5-5.5 x 2.5-3 µm.
Remarks. H. wrightii is superficially similar to species in the sectio Hyphodontia (e.g. H. alutaria and H. pallidula) by its encrusted cystidia. It is questionable, however, if H. wrightii belongs with the above species as its cystidia differ from true lagenocystidia. The walls are thin to moderately thick, whereas in the cystidia of H. alutaria the walls are distinctly thick, especially at the pointed apex. Macroscopically as well as in the morphology of basidia and hyphae it resembles H. rimosissima (subsectio Ellipsosporae Parm.) more closely.

Hypochnella violacea (Auersw.) Schröt. 19583.

Hypochnicium rickii Hjortst. & Ryv. 20090.
This specimen agrees with the type (Rick, 20847) except in its outer appearance. The aculei are more scattered, (3-6 per mm) and the whole fungus somewhat tough. The species is only known from these two specimens.

Odonticium helgae Hjortst. & Ryv. spec. nov. Fig. 11.
Differt ab Odonticio laxo hyphis basalibus hyalinis, tenuitunicatis. vero incrustatis.
Holotypus: Argentina. Prov. Misiones, Iguazu Nat. Park., Cataratas de Iguazu, 1.-5. March, 1982. L. Ryvarden No. 20082 (O). Isotypus: in Hjortst. priv. herb.
Etymology: in honour of Dr. Helga Grosse- Brauckmann.

Fruitbody resupinate, loosely adnate, pellicular and fairly soft, whitish to pale ochraceous; hymenium distinctly odontioid with the aculei approximately 4-6 per mm, usually fimbriate apically, subiculum concolorous or very pale ochraceous, thin, rhizomorphs abundant, especially in the periphery of the fruitbody. Hyphal system monomitic; hyphae without clamps, basal hyphae straight and fairly uniform, thin-walled or with slightly thickened walls, branching at right angles, strongly encrusted, 3-5 µm wide with the individual cells about 30-50 µm long between the septa, aculeal hyphae thin-walled, more or less smooth, some protrude as much as 20-30 µm, 4-5 µm wide. Cystidia absent. Basidia small, 8-12 x 4-5 µm, somewhat clustered, with 4 sterigmata. Spores subglobose to ellipsoid, smooth, thin-walled, 3-3.5 x 2-3.2 µm, inamyloid, indextrinoid, acyanophilous, often with a central oildrop.

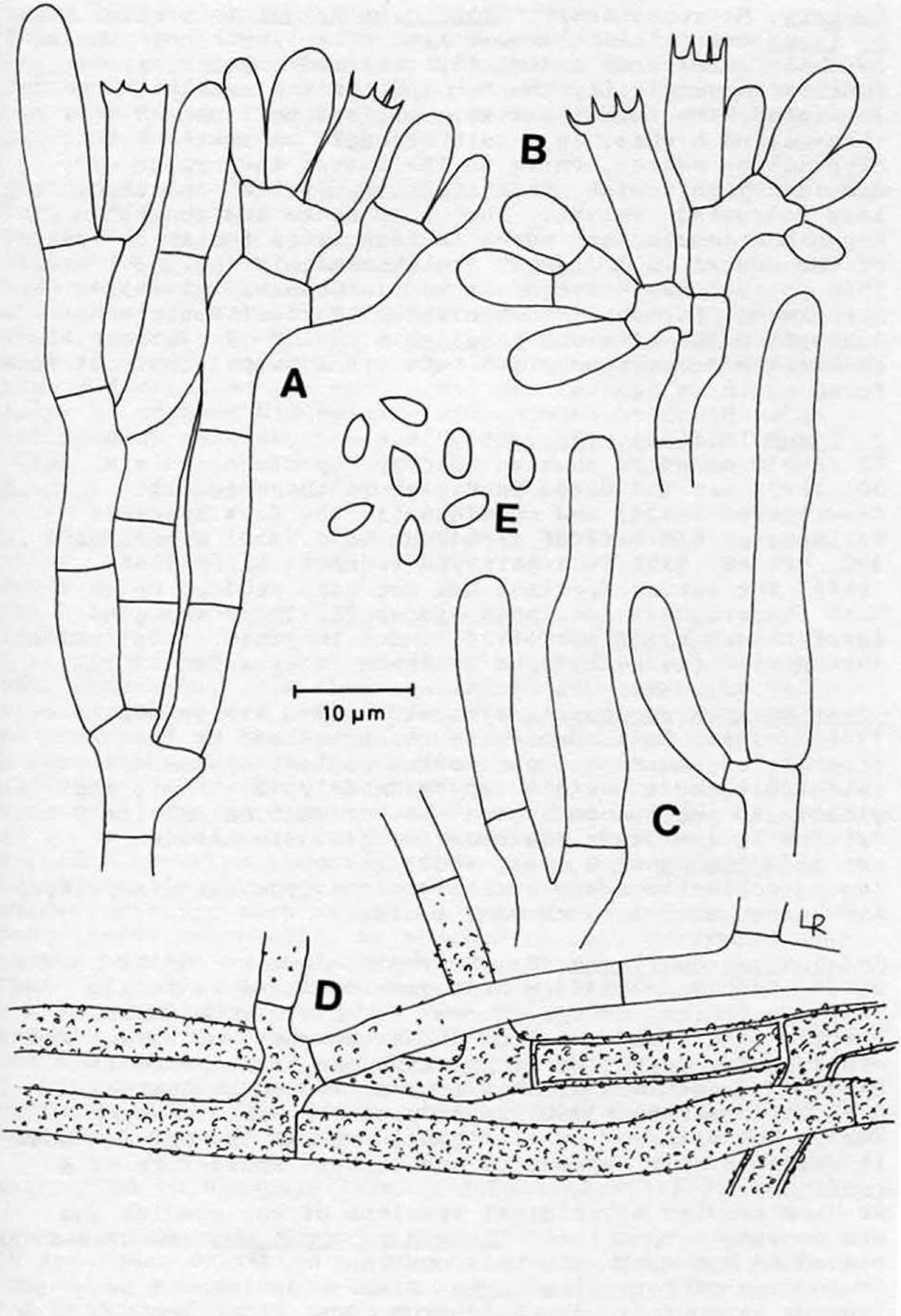

Fig. 11. **Odonticium helgae** A) part of hymenium, B) basidia, C) aculeal hyphae, D) encrusted basal hyphae, E) spores. From the holotype.

Remarks. Macroscopically Odonticium helgae is similar to O. laxum and it has the same kind of rhizomorphs, running over the substratum and easily observed under a strong lens. Microscopically the two species are easily separated. The former has more or less hyaline and thin-walled hyphae, as a rule strongly encrusted with crystalline matter, while in the latter the hyphae are distinctly yellowish, moderately thin-walled and smooth or less encrusted. Further, the conspicuous and encrusted hyphoid elements that occur abundantly in the apical part of the aculei in O. laxum, are absent in O. helgae.
This species was first collected in Germany by Grosse-Brauckmann, Larsson, and Hjortstam (Hessen, Oberrhein, Kühkopf, Dornschlag, on Fraxinus. 1983-10-17. In herb. GB and Grosse-Brauckmann priv. herb.) and surprisingly it was found again in Iguazu.

O. laxum (Miller) Ryv. 19563.
It should be noted that an holotype specimen, on elm, July 30, 1893, was indicated by Miller in the original description (1934) and consequently the Iowa specimen, Wellman, on old bark of deciduous wood, L.W. Miller No. 338. Oct. 8, 1932 is a paratype (compare Gilbertson, 1964). The latter specimen has not been studied by us. Both the original specimens are at IA. There are good descriptions by Miller (1934) and Gilbertson (1964) and an instructive figure by John Eriksson in Ryvarden (1978).

Odontiopsis hyphodontina Hjortst. & Ryv. 19559, 19847, 19859, 19864. This species is characterized by its strongly encrusted and projecting aculeal hyphae, relatively short basidia (approximately 12-15 µm), and globose to subglobose spores that are 4-5 µm in diam. Originally the genus was based on a single African specimen (Hjortst. & Ryv., 1980) and the Iguazu-collections are similar to the type but are younger and softer with less crowded aculei.

Radulomyces confluens (Fr.:Fr.) M.P. Christ. 19514, 20094. Specimen 19514 is best developed and is in all characteristics, except spores, which are subglobose, exactly like specimens from different parts of boreal and other areas. Corticium rickii Bres (in Rick, 1898) is based on a specimen of this type collected in Austria. M.P. Christiansen (1960) introduced the name in North Europe but Eriksson et al. (1981) were of the opinion that it possible only represents one extreme spore-form of R. confluens.
We have studied an original specimen of the species and are convinced that it is Thelephora confluens and herewith placed in synonymy with this species.
Lectotypus of Corticium rickii Bres.: (designated here) ad truncos Sambuci nigrae. Feldkirch. Oct. 1879, leg. J. Rick (FH).

Scopuloides rimosa (Cooke) Jülich 19531.
This specimen is in fully accordance with the type of Peniophora rimosa described from Colwyn Bay (Wales) and deposited at Kew. It should be noted that the same species has been found once in Western Germany (Hjm 14174, GB). See also Eriksson et al. (1984).

Scytinostroma aff. albo-cinctum (Berk. & Br.) Boid. & Lanq. 19740, 20049.
These collections agree well with the description and figure in Boidin and Lanquetin (1976), but we have not seen any authentic material of the species. The chatacteristic skeletohyphidia (see Parmasto, 1970), react strongly in Melzer and the ultimate branches are bent outwards. However, it should be mentioned that Boidin kindly determined the specimens, but later he changed his opinion and thought it could be an independent species. See also S. portentosum.

S. ochroleucum (Bres. & Torr.) Donk 19509/B.

S. portentosum (Berk. & Curt.) Donk 19558, 19561, 19573, 19604, 19610,19622, 19675, 19764, 19792, 19818, 19855, 20046.
The holotypes of Corticium portentosum Berk. & Curt. (Pennsylvania, Michener No. 3620) and of Stereum duriusculum Berk. & Br. (Ceylon, Kandy 1868. No. 329 & 569, apparently from same specimen) have carefully been studied and we are not convinced that the two species may be separated on the basis of macro- and micro-morphology. A separating characteristic (according to Parmasto, 1970, and others) should be the numbers of gloeocystidia. The type of S. duriusculum has some cystidia but the material is too poor for a adequate examination. Besides, a few cystidia are also present in the type of S. portentosum, which also is a rather poor material. Other characteristics such as spores and hyphae (strongly dextrinoid) can readily be studied in both specimens, but cannot be used to separate the two species.
Thus, we adopt the oldest name for the Iguazu-material. All specimens reported here have gloeocystidia in varying numbers, and some react positively in sulfuric benzaldehyde. S. albo-cinctum can be distinguished from S. portentosum by its somewhat darker hymenium and microscopically the skeletohyphidia seem to be an important separating character.

Sistotrema brinkmannii (Bres.) John Erikss. 19787.

Subulicystidium longisporum (Pat.) Parm. Very common, and 15 specimens collected in Iguazu. The species is highly variable, especially in its spore-length but also in size and encrustations of the basidia-bases and hyphae.

Trechispora farinacea (Per.:Fr.) Liberta s. lato 19537, 19631.

T. regularis (Murr.) Liberta 19570, 19575, 20108/B
Tubulicium vermiferum (Bourd.) Oberw. ex Jülich 19728.
The spores of this specimen are about 15-20 x 2.5-3 µm, less worm-shaped than normal but still with sigmoid appearance.

Vararia rugosispora Boid. et al. 19706.
The brownish fructification, hyphae without clamps, and the large spores (approximately 12-15 x 6-8 µm which are distinctly rough (properly observed in Melzer) make this species easily to recognize. Previously known only from the type-locality (Gabon, Africa). For adequate description, see Boidin & al. (1980).

V. sphaericospora Gilbn. 19528.
This specimen has been compared with the holotype (BPI) and corresponds in essential characteristics. Cystidia, however, have not been observed. A portion of Ryvarden's collection is deposited in BPI. Recently the species has also been reported from Africa and Asia (Boidin & Lanquetin, 1984).

Xenasma praeteritum (Jacks.) Donk 19522, 19695 (see below).
The first specimen is so close to Jackson's description (1950) and to the five specimens listed from the type-locality (Ontario, Frontenac) that we do not hesitate to treat our collections under this name. The other specimen is more problematic. It has larger spores and cystidia with thicker walls and it reminds of X. rimicolum (Karst.) Donk, but the material is too scarce to permit a more precise interpretation. We have, in an article from Nepal, dealt with two specimens that clearly differ from the original scope of X. praeteritum (odontioid species) and we have seen material from Africa which fits neither Jackson's species nor the Nepal collections or X. rimicolum. The genus will be treated separately in a forthcomming paper and in the Corticiaceae of North Europe (Vol. 8).

X. pruinosum (Pat.) Donk 19730.
Most basidia evidently have more than 4 sterigmata and the spores are echinulate (only visible in Melzer and Cottonblue) and measure ab. 7-8 x 4-4.5 µm.

Acknowledgments.

Dr. J. Wright of the Buenos Aires is most sincerely thanked for his generous help and assistance in arranging the excursion to the Iguazu National Park, making this paper possible. Dr. E. Parmasto of Tartu, Estonian SSR, USSR, and Dr. R.L. Gilbertson, University of Arizona, Tucson, Arizona, United States, have both suggested improvements in the text for which we are grateful.

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LASIOSPHAERIOPSIS STEREOCAULICOLA

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ABSTRACT

Sphaeria stereocaulicola Lindsay (syn. **Xenosphaeria apocalypta** Arnold) is transferred to **Lasiosphaeriopsis** D. Hawksw. & Sivanesan (Nitschkiaceae). The spores are shown to possess a few scattered pores.

INTRODUCTION

Ascomycetes characterized by perithecioid ascomata, thick-walled asci, pseudoparaphyses and coloured ascospores with two or more transsepta have usually been referred to the genus **Leptosphaeria** Ces. & De Not. Similar fungi with spores also divided by longisepta have been classified in the genus **Pleospora** Rabenh. ex Ces. & De Not. Both genera have grown very large and become heterogeneous. In current classifications some workers accept these large genera for practical purposes, others prefer to split them and recognize several more homogeneous segregate genera. With narrower generic concepts, however, there are still many foreign elements in the two genera with uncertain affinities. One of us (RS) has for a long time been aware of that the lichenicolous species **Leptosphaeria apocalypta** (Arnold) Winter has to be transferred to another genus. We have examined material of this species in detail and found that it belongs to the previously monotypic genus **Lasiosphaeriopsis** D. Hawksw. & Sivan., and that the oldest name for the species is **Sphaeria stereocaulicola** Lindsay.

MATERIALS AND METHODS

Ascomata of the species studied in this paper were embedded in Historesin, and semithin sections were made on a Historange microtome (see Yue & Eriksson 1985: 293). SEM graphs were produced with a JEOL JSM-P15.

RESULTS

Lasiosphaeriopsis stereocaulicola (Lindsay) O. Eriksson & R. Santesson comb. nov.

Basionym: (**Sphaeria sp.** Th. M. Fries, Kongl. Svenska Vet.-Akad. Handl. 7, n. 2: 36, footnote, 1867) - **Sphaeria stereocaulicola** Lindsay in Trans. R. Soc. Edinburgh 25 (2): 528 + 538 (1869). - Orig. coll.: Spitzbergen, West-Spitzbergen, Hinlopenstredet, Lovénfjellet, 1861 A.J. Malmgren. On **Stereocaulon alpinum** (thallus), (holotype, UPS).

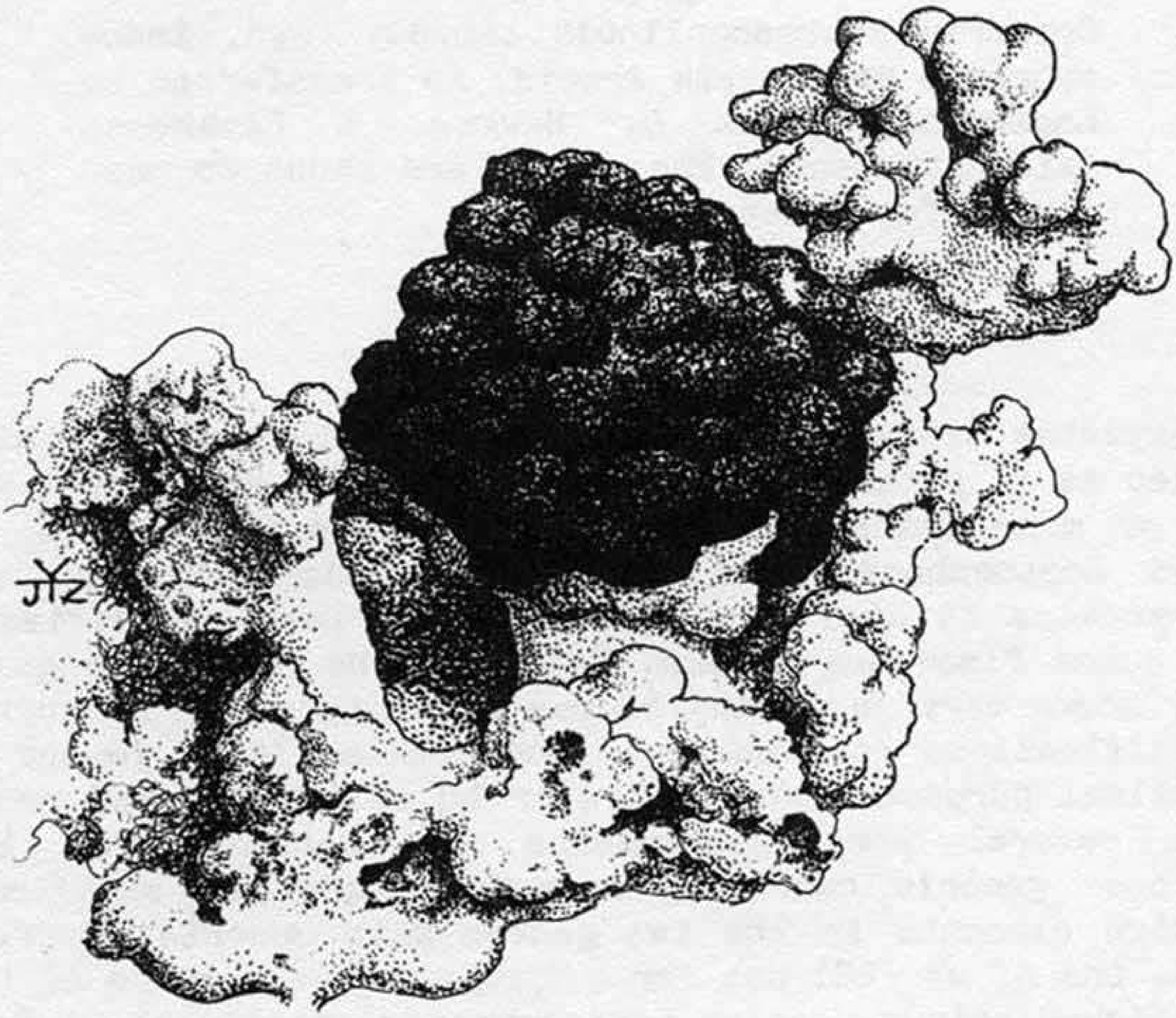

Fig. 1 **Lasiosphaeriopsis stereocaulicola**, ascomata on thallus of **Stereocaulon alpinum**. Coll.: Torne Lappmark, 1947 R. Santesson. Magn.: X25.

Synonyms: **Xenosphaeria apocalypta** Rehm (Ascom. exs. n. 346, 1876, nom. nud.) ex Arnold, Flora 60: 302 (1877). - **Leptosphaeria apocalypta** (Rehm ex Arnold) Winter, Rabenh. Krypt.-Fl., 1(2): 442 (1885). - **Arthopyrenia apocalypta** (Rehm ex Arnold) Olivier, Bull. Acad. Geogr. Bot. 16: 262 (1906). - Orig. coll.: Austria, Tirol, Ober-Inntal, Piztal, Mittagskögele bei Mittelberg, 1875 F. Arnold (Rehm, Ascom. exs. 346). On **Stereocaulon alpinum** (thallus), (isolectotypes, S, UPS.)

Figs.: 1-3, 5.

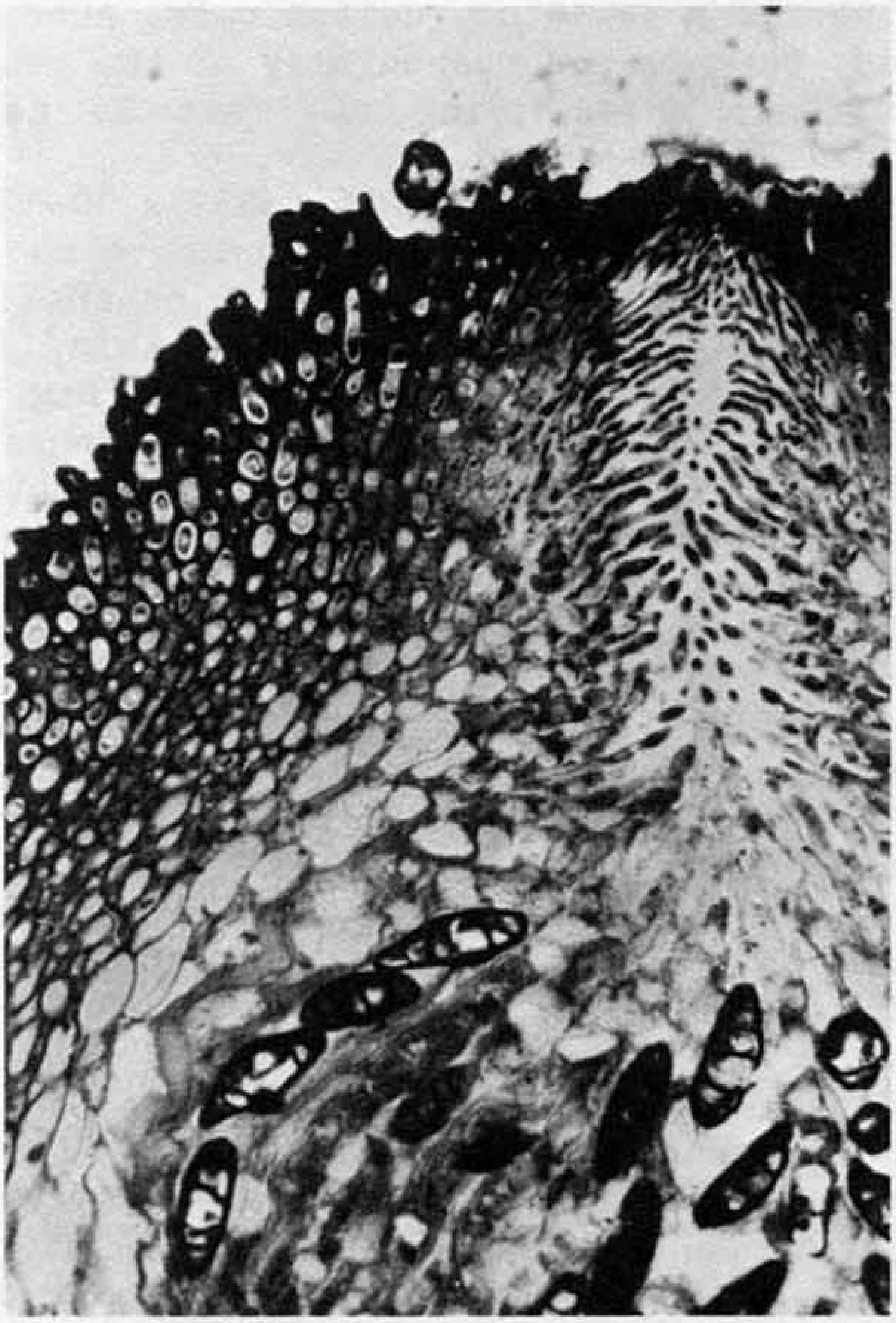

Fig. 2. **Lasiosphaeriopsis stereocaulicola**, submedian section through ostiole with periphyses. Coll.: Torne Lappmark, 1947 R. Santesson. Magn.: c. X500.

Ascomata perithecioid, rarely solitary, more often densely aggregated into moriform clusters on hypostromata, erumpent and finally ± free, subglobose, without neck, sessile, tuberculate with deep fissures, carbonaceous, black. Ascomal wall c. 50-70 µm thick, outermost part of dark-coloured, thick-walled pseudoparenchymatous cells with distinct "Munk pores", inner parts with gradually paler and thinner-walled cells. Uppermost part of locule with very large, thin-walled cells, producing periphysoids directed downwards and periphyses directed upwards; ostiolar channel c. 30-40 µm wide, lined by smaller cells producing numerous periphyses (Fig. 2), some of which at the mouth have dark-coloured, rounded tips.

Asci c. 90-100 x 12-14 µm, unitunicate, subcylindrical, short-stalked, thin-walled (especially at the rounded apex, Fig. 3A), without apical ring, I- (not I+ as given by Keissler 1930: 498), 4-spored.

Ascospores (Fig. 3B-F) c. 30-35 (-53) x 10-11 (-13) µm, broadly fusiform, with (2-)4-5(-9) transverse (or often also some oblique) septa with ± distinct central pore, dark brown, without distinct perispore, wall thin, smooth, in each segment with one very small pore (Fig. 5); each segment with one large and numerous small drops. Immature spores at first non-septate, then 2- (3-)septate, hyaline with c. 2.5-3 µm thick, non-stratified, hyaline wall (Fig. 3B, C). Each segment then divided by a transseptum and wall becoming 3-layered and pale brown (Fig. 3D).

Hosts: **Stereocaulon alpinum**, **S. glareosum**, **S. humbertii**, **S. paschale**, and **S. rivulorum**.

Material examined:

ARGENTINA, Patagonia, Prov. Chubut, Lago Menendez, on **S. paschale**, 1950 I.M. Lamb n. 5780 (UPS).

AUSTRIA. See above, the type of **Xenosphaeria apocalypta**.

SWEDEN, Härjedalen, Tännäs par., Grönvålen, alt. 1050 m., on **S. glareosum**, 1974 R. Santesson n. 25078b (M, S, UPS, US, etc.; will be distributed in R. Santesson, Fungi Lichenicoli Exs., Fasc. V), Fjällnäs, Gråstöten, on **S. sp.**, 1912 E.P. Vrang (UPS), Stora Mittåkläppen, SW. slope, alt. c. 1100 m., on **S. alpinum**, 1976 R. Santesson n. 27029b (UPS); Jämtland, Åre par., Åreskutan, Lillskutan, alt. 810 m., on **S. rivulorum**, 1948 R. Santesson n. 48579 (UPS), Åreskutan, Totthummeln, alt. 825 m., 1948 R. Santesson n. 48560 (UPS); Torne Lappmark, the Torneträsk area, Vassitjåkko, NE. slope, alt. 870 m., on **S.**

alpinum, 1947, R. Santesson (UPS), Abisko, on the railway cutting SW. of the Research Station, alt. 380 m., on **S. rivulorum**, 1959 R. Santesson n. 13404c (UPS). Karesuando par., Peldsa, the SE-top, alt. 850-1000 m., on **S. rivulorum**, 1948 T. Hasselrot (UPS).

SPITZBERGEN. See above, the type of **Sphaeria stereocaulicola** Lindsay.

UGANDA, Mt. Ruwenzori, Mijusi Valley, E. slope of Mt. Speke, alt. 4480 m., on **S. humbertii**, 1948 O. Hedberg n. 561b (UPS).

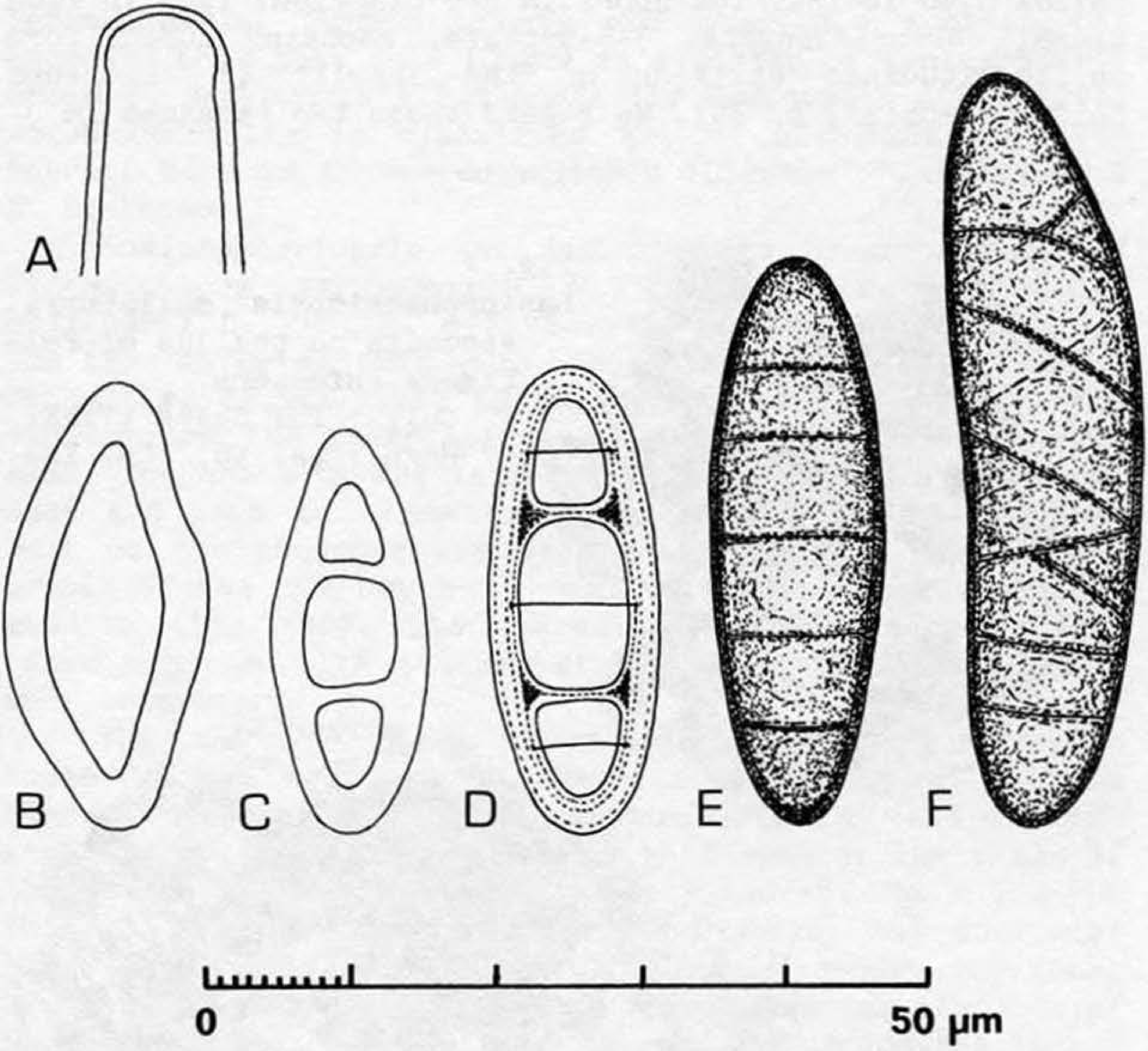

Fig. 3. **Lasiosphaeriopsis stereocaulicola.** (A) Ascus top. (B-D) Immature spores. (E) Mature, dark brown spore. (F) Abnormal spore with transsepta, oblique septa and helicoid septa. Coll.: Torne Lappmark, 1947 R. Santesson.

DISCUSSION

As mentioned above, two different epithets have been used for the characteristic fungus on **Stereocaulon spp.** treated in this paper, viz. "stereocaulicola" (Lindsay 1869: 528, 538) and "apocalypta" (Rehm 1876).

Lindsay (p. 528) referred to the fungus as "**Sphaeria (Stereocaulicola)**, Th. Fries" and (p. 538) wrote "Th. Fries* has described, without naming, a **Sphaeria** as parasitic on the thallus of **S. alpinum**, Laur., in Spitzbergen; whose sporidia, however, distinguish it from the **Microthelia.** The hymenium of the **Sphaeria** - which may appropriately bear the specific name **Stereocaulicola** - becomes yellow with iodine. The sporidia are blackish, four in each ascus, oblong-elongate, 3-5-septate, becoming submuriform by longitudinal division of the loculi" (* "Lichenes Spitsbergensis", p. 36). We regard these two passages in

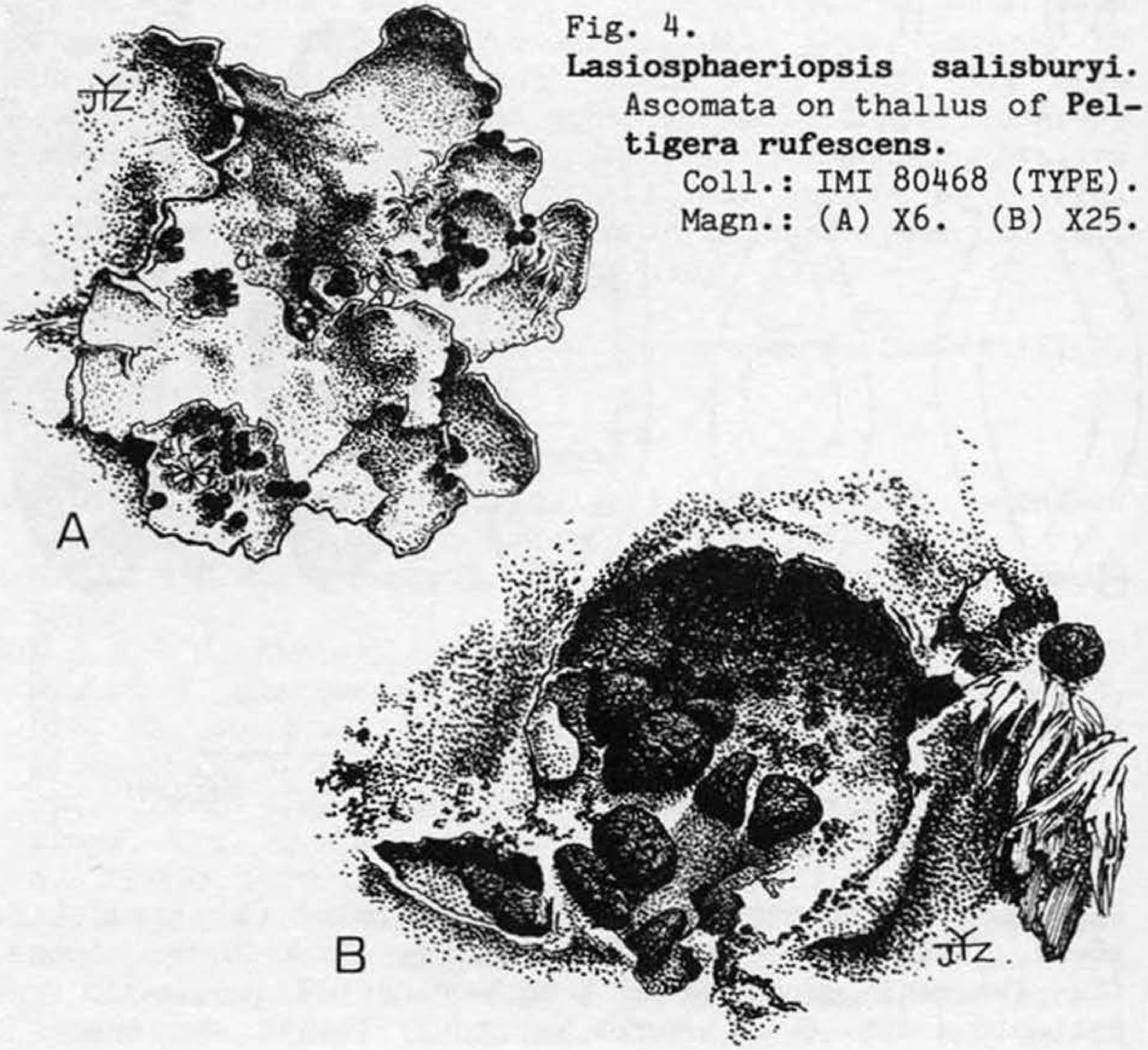

Fig. 4.
Lasiosphaeriopsis salisburyi. Ascomata on thallus of **Peltigera rufescens.**
Coll.: IMI 80468 (TYPE).
Magn.: (A) X6. (B) X25.

Lindsay (1869) as a valid description of **Sphaeria stereocaulicola** Lindsay.

Rehm distributed without any description in his exsiccatum Ascomyceten n. 346 (1876) a lichenicolous fungus named **Xenosphaeria apocalypta.** In the following year Arnold (1877a: 302, published July 1) described the species. A description was given also in Arnold 1877b: 547 ("Vorlegt in der Versammlung am 4. Juli 1877"). Arnold refers in the original description to two different collections. The one distributed in Rehm's exsiccatum is here chosen as lectotype. It was transferred to **Leptosphaeria** by Winter (1885: 442), but he pointed out that it is very doubtful whether this and some other lichenicolous species really belong to **Leptosphaeria.** Squash mounts and semi-thin sections of ascomata show that this fungus is a member of **Lasiosphaeriopsis** D. Hawksworth & Sivanesan (in Hawksworth 1980: 373), which currently is classified in the Nitschkiaceae. Its correct name is **L. stereocaulicola** (Lindsay) O. Eriksson & R. Santesson.

Lasiosphaeriopsis was described to accomodate a new lichenicolous pyrenomycete on **Peltigera rufescens, L. salisburyi** D. Hawksw. & Sivan. We have studied a part of the type material (England, Lancashire, Ainsdale, Hillside Sandhills, 23.III.1951, G. Salisbury 124, IMI 80468), and can confirm the observations made by Hawksworth & Sivanesan. The ascomata are laid down in the algal layer of the host and seem to cause local destruction of the cortex. Most of the ascomata are seen either at the margins and cracks of the thallus or in small whitish pits with naked medulla (Fig. 4B). The coarsely verrucose ascomata are often provided with a short stalk, which is usually somewhat compressed.

The ascomata of **L. stereocaulicola** are similar to those of the type species, but are more often densely aggregated into moriform structures (Fig. 1) and are not seated on a compressed stalk. In both species the walls of the ascomata are dissected by deep fissures. The walls are thick and consist of many layers of cells; the outermost are dark brown and have distinct "Munk pores", the inner are paler , with thinner walls. The hamathecium consists of short periphysoids directed downwards and periphyses in the ostiolar channel directed upwards. Asci are thin-walled and produce dark brown phragmospores. While the spores are of about the same sizes in the two species, the septation is different. The spores are 3(-4)-septate in **L. salisburyi,** (2-)5(-9)-septate in **L. stereocaulicola.**

We have examined the spores of both species with light and scanning electron microscopy. In **L. salisburyi** the spore wall is absolutely smooth, while in **L. stereocaulicola** we have observed some very small pores in the wall (Fig. 5). There appears never to be more than one pore in each segment. These pores may be very difficult to see using light microscopy. However, they are more easily seen

Fig. 5.
Lasiosphaeriopsis sterocaulicola, ascospore with pores (arrows).
Coll.: Torne Lappmark, 1947 R. Santesson.
Magn.: c X3700.

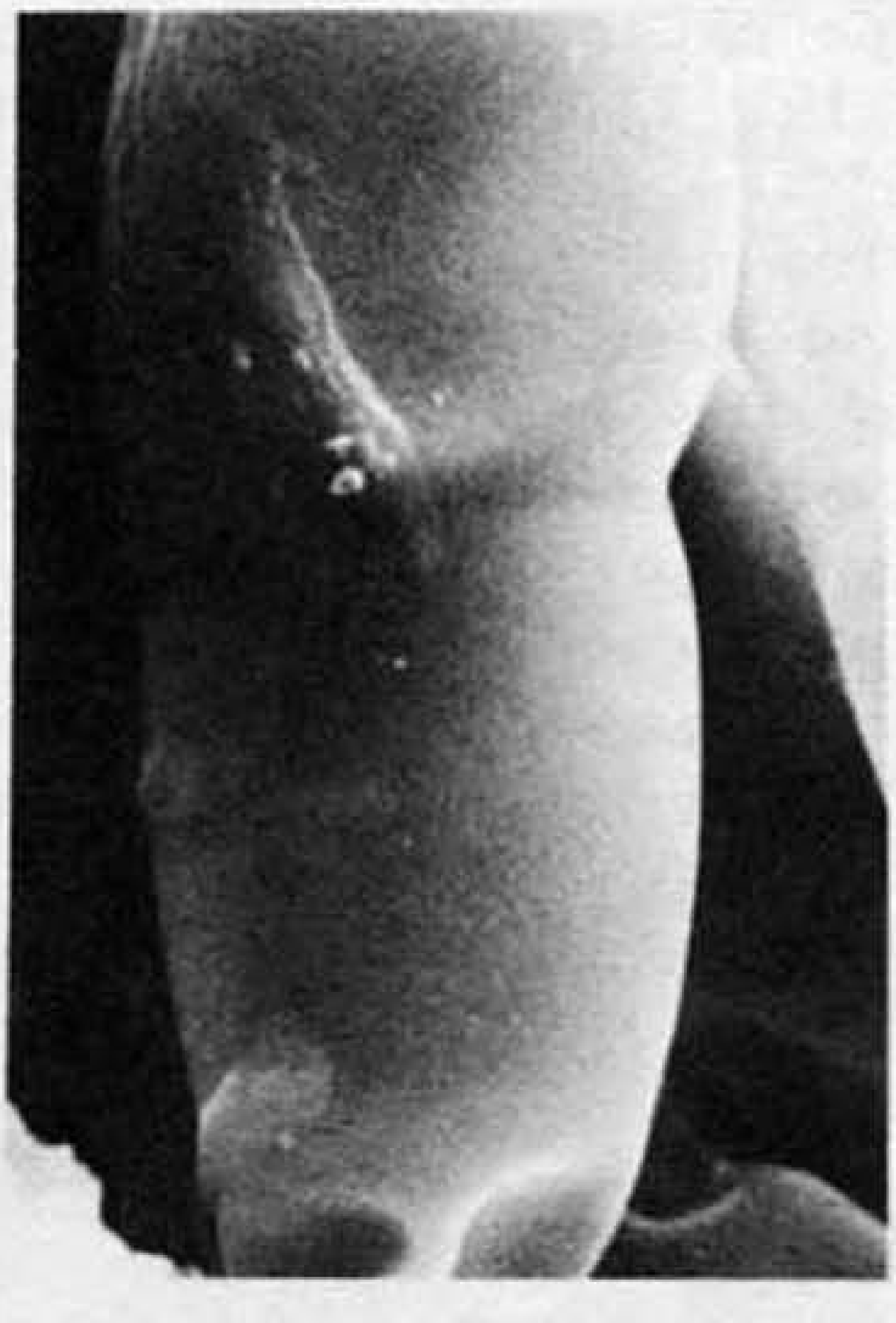

Fig. 6.
Lasiosphaeriopsis salisburyi, ascospore without pores.
Coll.: IMI 80468 (TYPE).
Magn.: c. X2600.

in fragments of spore wall not obstructed by other structures. We have not seen any germinating spores, but it is probable that the spores germinate by phialide-like germ tubes through these pores. Such phialides have been observed in the genera **Bertia** De Not. (Sivanesan 1978: 385, 387;Corlett & Krug 1984: Fig. 3D, 2566) and **Lasiosphaeriella** Sivanesan (1975: Figs. 1C and 2C).

Keissler (1930: 498) wrote about **L. stereocaulicola** (as **Leptosphaeria apocalypta**) "Auffallend erscheint die Angabe, dass die Gehäuse mit Falten und zahlreichen Spalten sich öffnen. Die Sache verdiente überprüft zu werden". The ascomata do not open in this way. They open by an ostiole lined with hyaline periphyses. Some of the periphyses at the mouth are dark-coloured in their upper halves. We found that such, almost bristle-like periphyses were also present in **Bertia moriformis** (Tode: Fr.) De Not. They seem to have been overlooked by previous authors. Nannfeldt (1975: 294) referred to the dark tissue in the opening as a plug, but is better described as densely packed, melanized periphyses tips.

Nannfeldt (1975: 289) thoroughly discussed morphological criteria and the classification of the Nitschkiaceae. He excluded some genera which had previously been included in the family, e.g. **Thaxteria** Sacc., and accepted only 5 genera. Nannfeldt assigned these genera into three groups, with regard to the morphology of the ascomata, and concluded that the differences between the groups are not so profound that separate families should be recognized. These groups are commented upon below.

Group 1 (= Nitschkiaceae s. str.).
Acanthonitschkea Speg., **Gaillardiella** Pat., and **Nitschkia** Otth ex Karsten. - This group is characterized by comparatively small ascomata (usually less than 500 µm), which are smooth or spiny, often collapsing, without an ostiole, but with a unique opening mechanism, the "Quellkörper", consisting of conglutinated hyaline, scleroplectenchymatous cells, or with this structure replaced by a low, perforated cushion. The asci are thin-walled, long-stalked and produce, in most species, a large number of small, hyaline, 1-septate spores which germinate by hyphae. A small ring is seen in the ascus top in some species (Cotton Blue!), but Nannfeldt (1975: 301) is of the opinion that it has lost its gun-function and that the ascus wall usually deliqueses rather early.

Group 2 (= Coronophoraceae).

Coronophora Fuckel. - This is the type of the family "Coronophoreen" Höhnel (an illeg. name; International Code of Botanical Nomenclature, article 18). In this genus the ascomata are usually larger than 500 µm (up to almost 2 mm), commonly non-tuberculate, have a periphysate ostiolar channel (Parguey-Leduc 1967: 27, Fig. 51) , and shrivel irregularly upon drying. The asci are thick-walled above the long and narrow stalk, except at the apex where there is a wide sub-apical chamber, capped by a thin, refringent apical dome (Parguey-Leduc, l.c.). They produce a very large number of small, allantoid, 1-septate, hyaline ascospores.

Group 3 (= Bertiaceae).

Bertia De Not. - This genus should have an isolated position in the family (Nannfeldt 1975: 299, 303). Smyk (1981: 47) erected the new family Bertiaceae. The illustrations of the type species **B. moriformis** indicate that another species was studied (Corlett & Krug 1984: 2566; Eriksson 1984: 54), however, the family name is validly published and available for **Bertia** and closely related genera if it turns out that this group should be recognized as a separate family. In fact, there may be reasons for accepting this family. Since 1975, when Nannfeldt published his paper, some genera have been found to be intermediate between the Nitschkiaceae s. str. and the Lasiosphaeriaceae. Nannfeldt (1975: 305) mentioned **Lasiosphaeria noonae-daniae** Carroll & Munk. This is the type of **Lasiosphaeriella** Sivanesan (1975). **Rhagadostoma** Körber (see D. Hawksworth and Sivanesan in Hawksworth 1980: 373) also belongs to this group, as does **Lasiosphaeriopsis**. Most species in these four genera have comparatively large ascomata (usually more than 500 µm). They are thick-walled, ±tuberculate, have a stromatic base and an ostiolar channel lined with periphyses. The asci are thin-walled, persistent and 2-8-spored. The ascospores are large, hyaline to dark brown, usually with more than one septum, and they germinate by phialides. **Spinulosphaeria** Sivanesan (1974: 35) and **Thaxteria** Sacc. may also be members of this group (cf. Nannfeldt 1975: 290).

Lasiosphaeriopsis differs from the other genera in the group by virtue of their mature dark brown spores without a perispore. **Lasiosphaerella** has similar spores, but with a perispore.

This group is certainly related to the two other groups, and we prefer not to recognize the three groups as separate families. More studies are needed of the morphology and ontogeny of the ascomata of both the Nitschkiaceae and the Lasiopsphaeriaceae. The position of, for instance, **Lasiobertia** Sivanesan (1978: 383) is uncertain. This is an aberrant monotypic genus with non-ostiolate, tuberculate, scattered or aggregated ascomata with paraphyses and asci with amyloid ring. The spores are hyaline, fusiform, 1-septate. The "Munk pores", according to Sivanesan, should not be as prominent as in "Coronophorales". The presence of paraphyses and amyloid asci are especially remarkable.

In all Nitschkiaceae s. lat. there are distinct "Munk pores" in the ascomal wall. They are not as abundant in **Lasiosphaeriopsis stereocaulicola** as in, for example, **Bertia moriformis**. In semithin sections of the latter species we have seen numerous pores, not only in the coloured, thick-walled outer cells, but also in the hyaline, thin-walled cells lining the ascomal cavity. We can confirm Nannfeldt's observation (1975: 294) that there may be more than one pore/cell.

It is probable that the Nitschkiaceae s. str. have evolved from fungi resembling species in group 3, i.e. the Bertiaceae if a separate family was recognized. The ostiole and the periphyses have dissappeared in almost all species. Thin-walled cells resembling periphyses occur in, e.g., **Nitschkia leonensis** (Sivan.) Nannf. (see Nannfeldt 1975: 298), and may be considered a primitive feature.

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BIOGEOGRAPHY OF FUNGAL ECTOPARASITES OF TERMITES

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Termites are unusual among insects in that they are hosts for at least 20 species of obligate ectoparasitic fungi, most of which are restricted to this insect group. Literature reports and recent collections indicate that Termitaria, Antennopsis, and Laboulbeniopsis are widely distributed throughout the world. Geographical ranges of species of Dimeromyces, Laboulbenia, Hormiscioideus, Coreomycetopsis, Mattirolella, and some of Termitaria are restricted. Strict host specificity was not observed; however, T. coronata was more common on termitid hosts, while T. snyderi has been found on a variety of host families, except termitids.

INTRODUCTION

At least twenty species of fungi in nine genera are obligate parasites of termites and some of their termitophiles; one additional genus, Amphoromorpha, is found on a wider range of hosts (Table 1). Only Cordycepioideus bisporus Stifler and C. octosporus M. Blackwell et Gilbertson appear to be serious pathogens. Most of the fungi are minute and cannot be seen easily except at higher dissecting microscope magnifications (x40 and above). Exceptions are species of Cordycepioideus Stifler, Termitaria Thaxter, and Mattirolella Colla which

TABLE 1
FUNGAL GENERA

TERMITE HOSTS[1]	Laboulbenia	Dimeromyces	Cordycepioideus	Laboulbeniopsis	Coreomycetopsis
KALOTERMITIDAE					
MASTOTERMITIDAE					
HODOTERMITIDAE					
HODOTERMITINAE	Libya(1)[2]				
TERMOPSINAE					
POROTERMITINAE					
CRETATERMITINAE					
STOLOTERMITINAE					
RHINOTERMITIDAE					
STYLOTERMITINAE					
TERMITOGETONINAE					
PSAMMOTERMITINAE					
HETEROTERMITINAE		Florida(1)		U.S., Italy French Guiana	U.S.
COPTOTERMITINAE					
RHINOTERMITINAE					
SERRITERMITIDAE					
TERMITIDAE					
AMITERMITINAE	Ghana(5)	Kenya(2)			
TERMITINAE					
MACROTERMITINAE	Kenya(2), Ethiopia(2,4), Mozambique(3)		Tanzania(1), Kenya(1)		
NASUTITERMITINAE			Mexico(2)	Sierra Leone, Indochina, Indonesia, Sumatra, Grenada	Grenada

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[1] Termite classification is based on Krishna (1970). Although other classifications have been proposed more recently they do not substantially reclassify termites which serve as hosts for fungi.

[2] Numbers in parentheses refer to species in figure legends.

TABLE 1, continued

TERMITE HOSTS	Amphoromorpha	Hormiscioideus	Antennopsis	Termitaria	Mattirolella
KALOTERMITIDAE			Yugoslavia(1) Madagascar(3)	Brazil(1) Samoa(1)	
MASTOTERMITIDAE				Australia(6)	
HODOTERMITIDAE					
HODOTERMITINAE				South Africa(2)	
TERMOPSINAE					
POROTERMITINAE				Chile(1), Australia(5)	
CRETATERMITINAE					
STOLOTERMITINAE					
RHINOTERMITIDAE					
STYLOTERMITINAE					
TERMITOGETONINAE					
PSAMMOTERMITINAE					
HETEROTERMITINAE	Florida		France(1), Italy(1), U.S.(1)	U.S.(1), Europe(1)	
COPTOTERMITINAE			New Guinea(2), French Guiana(2)	Sierra Leone(2) Australia(4)	
RHINOTERMITINAE			Indochina(1), Sumatra(2)	British Guiana(1)	Panama(1), British Guiana(2)
SERRITERMITIDAE					
TERMITIDAE					
AMITERMITINAE			Sierra Leone(2)	South Africa(2), Namibia(2) Sierra Leone(2), Kenya(2), Indochina(2)	
TERMITINAE				South Africa(2)	
MACROTERMITINAE	Sierra Leone			Swaziland(2)	
NASUTITERMITINAE		Brazil	Guadeloupe(2), Sumatra(2), Indonesia(2)	Australia(2), Indochina(2), Kenya(2), British Guiana(2) French Guiana(2) Philippines(2), Costa Rica(2), Brazil(3)	Panama(1)

often are visible to the unaided eye. It is probably no coincidence that the highly visible Termitaria, while relatively common, is the best known of these fungi.

Information on geographical and host ranges of the termite fungi was reviewed by Blackwell and Kimbrough (1978). Since that time additional reports on fungal taxonomy, host relations, and geographical and host ranges have been published (Rossi and Cesari Rossi, 1977; Blackwell, 1980; Blackwell and Gilbertson, 1981; Kimbrough and Thorne, 1982; Thorne and Kimbrough, 1982; Kimbrough and Lenz, 1982; Lenz and Kimbrough, 1982; Blackwell and Gilbertson, 1984; and Rossi and Blackwell, 1986). These and the records reported here make feasible a preliminary discussion of the worldwide distributions of the fungi in relation to the phylogeny and distributions of the termite hosts.

METHODS AND MATERIALS

Termites infested with fungi were acquired by one of us (W. R.) from the following sources: termites from Sierra Leone, Kenya, and Australia, were collected by W. Rossi (stored in 75% alcohol, 2% glycerine in water); from Indonesia, Central America, and South America, by J. Balazuc (stored in denatured alcohol); Indochina, Museum of Natural History of Paris, by J. Balazuc; and South Africa, Namibia, and Swaziland, J. E. Ruelle, Plant Protection Research Institute, Pretoria. Termites from U.S.A. localities were collected by M. Blackwell and preserved in 75% ethanol.

Termites infested with Termitaria spp. were oriented in 40% mucilage and frozen for cryostat sectioning. Other fungal specimens were removed with a small portion of the insect integument for direct mounting. All fungi were mounted in glycerine-containing acid fuchsin (Benjamin, 1971) on microscope slides with glass cover slips. After several days the cover slips were sealed with clear fingernail polish. Fungal species identifications were made from the original descriptions cited herein.

A great amount of literature on the biology of termites has been made available in the two volumes edited by Krishna and Weesner (1969, 1970). We have drawn heavily from this work for information on termite classification, phylogeny, biogeography, and biology; however, some additional references are also cited. Termite scientific names are those standardized by

Snyder's catalog (1949) or those from more recent species descriptions. Termites were kindly identified by S. Bacchus, British Museum (Natural History), London.

FUNGI ASSOCIATED WITH TERMITES

ASCOMYCETES

LABOULBENIALES

Laboulbenia Mont. et Robin

L. hagenii Thaxter. On *Macrotermes michaelseni* (Sjöstedt) (as *Termes bellicosus* var. *mozambica*), Africa (Thaxter, 1895).

L. felicis-caprae W. Rossi. On *Anacanthotermes ochraceus* (Burmeister), Libya (Rossi, 1974).

L. geminata Buchli ex W. Rossi et M. Blackwell. On *Odontotermes badius* (Haviland), Ethiopia (Buchli, 1966); on *Odontotermes* sp., Kenya (Buchli, 1966).

L. ghanaensis W. Rossi et M. Blackwell. On *Amitermes evuncifer* Silvestri, Ghana (Rossi and Blackwell, 1986).

L. brignolii W. Rossi et M. Blackwell. On *Macrotermes herus* (Sjöstedt), Ethiopia (Rossi and Blackwell, 1986).

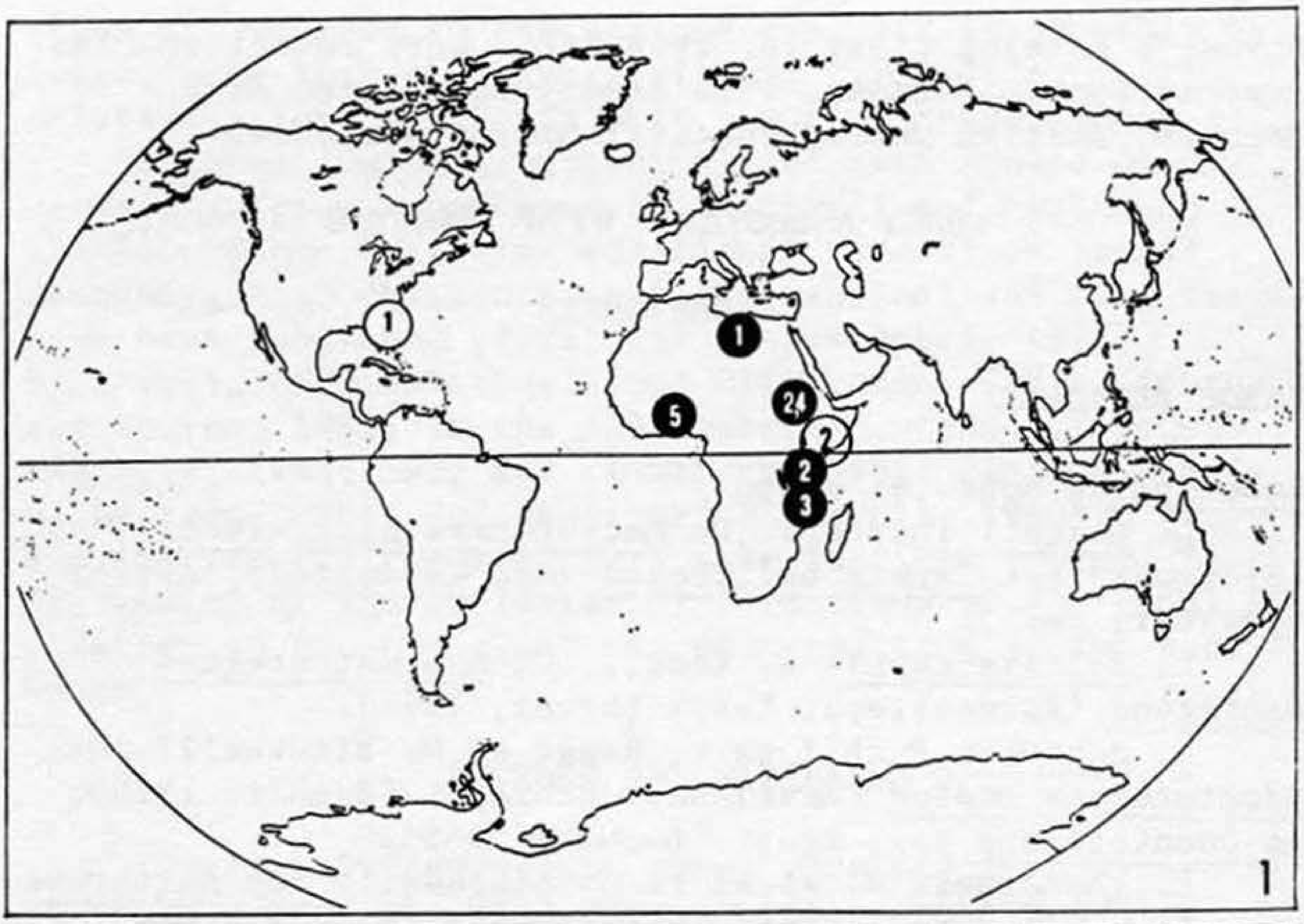
Dimeromyces Thaxter

D. isopterus Kimbrough. On *Reticulitermes flavipes* (Kollar), Florida (Kimbrough *et al.*, 1972; Kimbrough, 1986); on staphylinids, mites, Mississippi, Florida (Blackwell, Samson, and Kimbrough, 1980).

D. majewskii W. Rossi et Cesari. On *Alyscotermes kilimandjaricus* (Sjöstedt), Kenya (Rossi and Cesari Rossi, 1977).

Both laboulbeniomycete genera, *Laboulbenia* and *Dimeromyces*, occur on a wide variety of arthropod hosts. They are known from species of Coleoptera, Orthoptera, Isoptera, and mites; *Laboulbenia* is known also on hymenopteran, dipteran, and hemipteran hosts; *Dimeromyces*, from dermapterans. Species of the two genera are the only members of the Laboulbeniomycetes known from both isopterans and gryllid orthopterans (Tavares, 1980).

Laboulbenia species on termites are restricted to Africa (Fig. 1). The host species are usually inhabitants of the more arid regions of the continent (Bouillon, 1970; Noirot, 1970) and are classified in two very different termite families (Table 1). Distribution of the termite



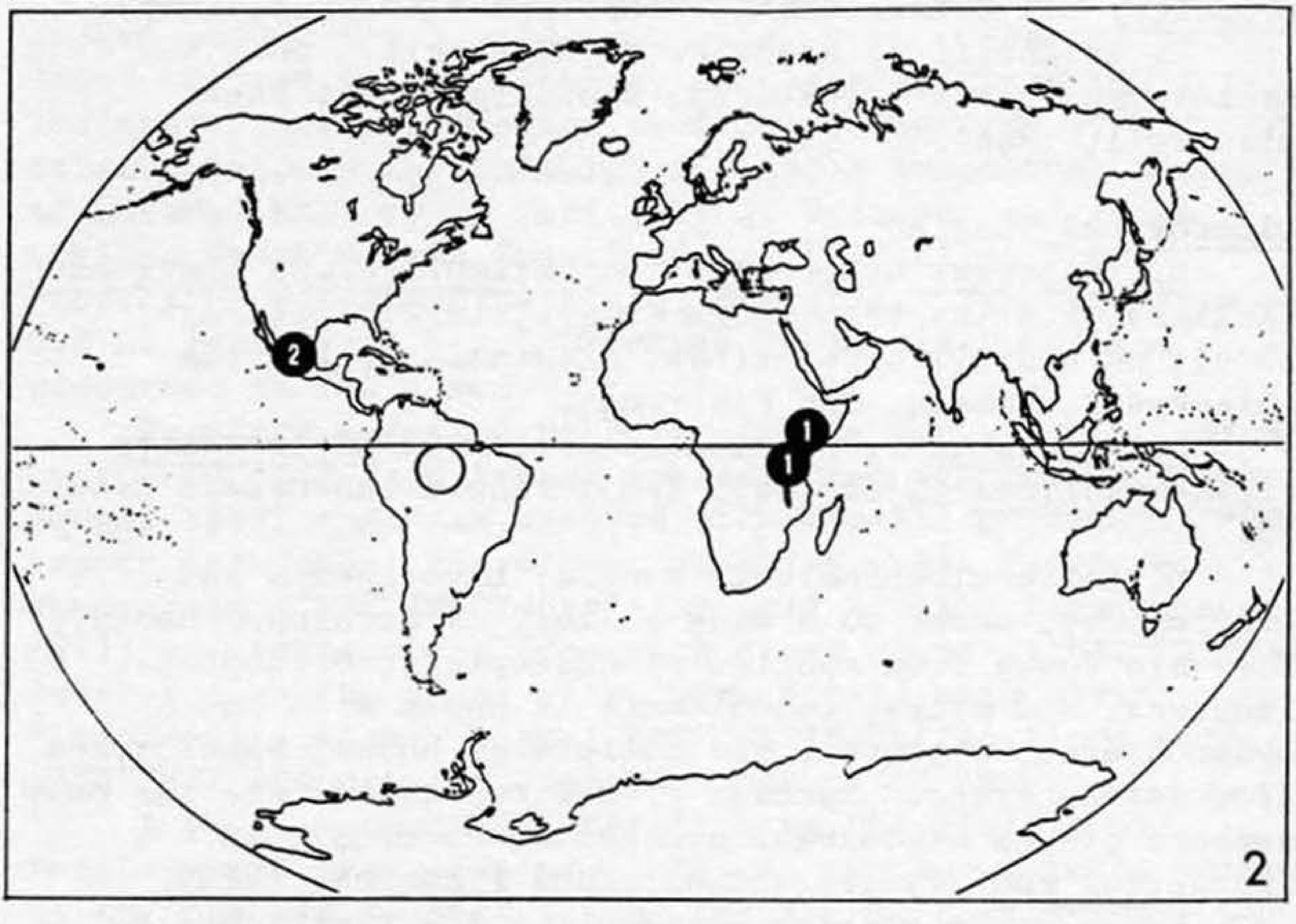


Fig. 1. Distribution of *Dimeromyces isopterus* (①), *D. majewskii* (②), *Laboulbenia felicis-caprae* (➊), *L. geminata* (➋), *L. hagenii* (➌), *L. brignolii* (➍), and *L. ghanaensis* (➎). Fig. 2. Distribution of *Hormiscioideus filamentosus* (○), *Cordycepioideus bisporus* (➊), and *C. octosporus* (➋).

genera is confined to Ethiopian and Oriental regions in the case of *Odontotermes* and *Macrotermes*, Oriental and Palearctic regions for *Anacanthotermes* (Roonwal, 1970; Harris, 1970). The restricted geographical and climatic ranges of the species of *Laboulbenia* may indicate a relatively recent association of *Laboulbenia* with termites. There is no host specificity within termite families or subfamilies.

While *Dimeromyces isopterus* is known from a single locality in Florida on *Reticulitermes flavipes* (Fig. 1, Table 1), two of its termitophiles were also infected in Florida and Mississippi (Blackwell, Samson, and Kimbrough, 1980). In fact, staphylinid beetles and mites associated with the termites are more heavily infected than termites (Kimbrough, personal communication). Although *R. flavipes* and other subterranean termites are common in the southern United States and are often collected and examined for *D. isopterus*, no additional collections of the fungus have been made.

Dimeromyces majewskii is known only from the type collection in Kenya. This species is morphologically quite different from *D. isopterus*. It is more likely that the occurrence of *D. majewskii* on Kenyan termites represents an independent evolutionary host change than evolution of the two species from a common *Dimeromyces* ancestor.

HYPOCREALES

Cordycepioideus Stifler

C. bisporus Stifler. On *Macrotermes natalensis* (Haviland), Tanzania (Stifler, 1941); on *M. michaelseni*, Kenya; on *M.* cf. *subhyalinus* (Rambur), Kenya (Blackwell and Gilbertson, 1984).

C. octosporus M. Blackwell et Gilbertson. On *Tenuirostritermes tenuirostris* (Desneax), Mexico (Blackwell and Gilbertson, 1981).

Superficially these two species resemble *Cordyceps* spp. The African species, *C. bisporus*, is certainly more common than the original report (Stifler, 1941) indicates (Blackwell and Gilbertson, 1984). *Cordycepioideus octosporus* is known only from the type collection in Mexico. The disjunct range (Fig. 2) would indicate a wider historical, if not present, range for the genus; it is probably a reflection of inadequate collection. Termite hosts are genera in two subfamilies of the higher termite family Termitidae (Table 1). *Macrotermes* is distributed in Oriental and Ethiopian regions, while *Tenuirostritermes* occurs in the New World tropics and north to Arizona and Texas (Krishna, 1970).

UNCERTAIN AFFINITY

Laboulbeniopsis Thaxter

L. termitarius Thaxter. On *Nasutitermes costalis* (Holmgren) (as *Eutermes morio*), Grenada (Thaxter, 1920); on *Reticulitermes flavipes*, Florida (Kimbrough and Gouger, 1970; Blackwell and Kimbrough, 1976b), Georgia (Blackwell, 1980), Michigan, Louisiana (reported here); on *R. virginicus* Banks, Florida (Kimbrough and Gouger, 1970); on *R. lucifugus* Rossi, Italy (Rossi and Cesari Rossi, 1977b); on *Leptomyxotermes doriae* (Silvestri), Sierra Leone (reported here, MB 55); on *Ahmaditermes* sp., Indochina (reported here, MB 35, MB 39); on *Nasutitermes* sp., Indonesia (reported here, MB 37); on *Nasutitermes* sp., Sumatra (reported here, MB 41); on *Coptotermes crassus* Snyder, French Guiana (reported here, MB 44).

Laboulbeniopsis termitarius was previously known from Grenada, Florida, Georgia, and Italy. The geographical range now has been extended to include a more northern part of the United States (Michigan), South America, Africa, and southeastern Asia (Fig. 3), (see below, *Coreomycetopsis*).

The termite host genera (Table 1) have broad ranges throughout the tropics of the world, except *Reticulitermes* which is widely distributed in Nearctic and Paelarctic regions.

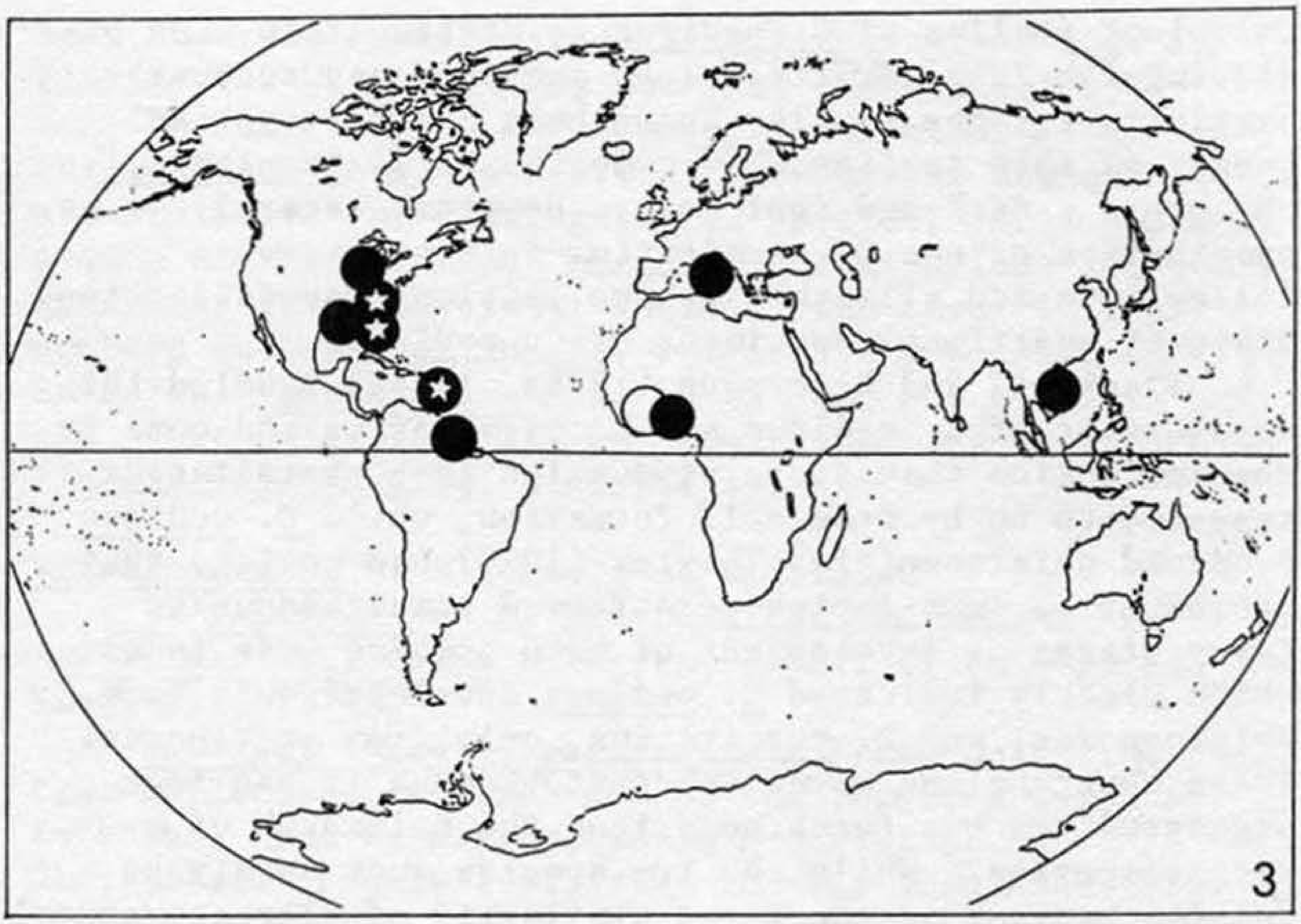
DEUTEROMYCETES

UNCERTAIN AFFINITY

Coreomycetopsis Thaxter

C. oedipus Thaxter. On *Nasutitermes costalis* (as *Eutermes morio*), Grenada (Thaxter 1920); on *Reticulitermes virginicus*, Florida (Blackwell and Kimbrough, 1976a); on *R. flavipes*, Georgia (Blackwell, 1980).

The collections of *C. oedipus* reported in the literature all have occurred in termite populations also associated with *Laboulbeniopsis termitarius*, not only sometimes on the same insect individual, but often on a single leg or antenna (Fig. 3, Table 1). The small



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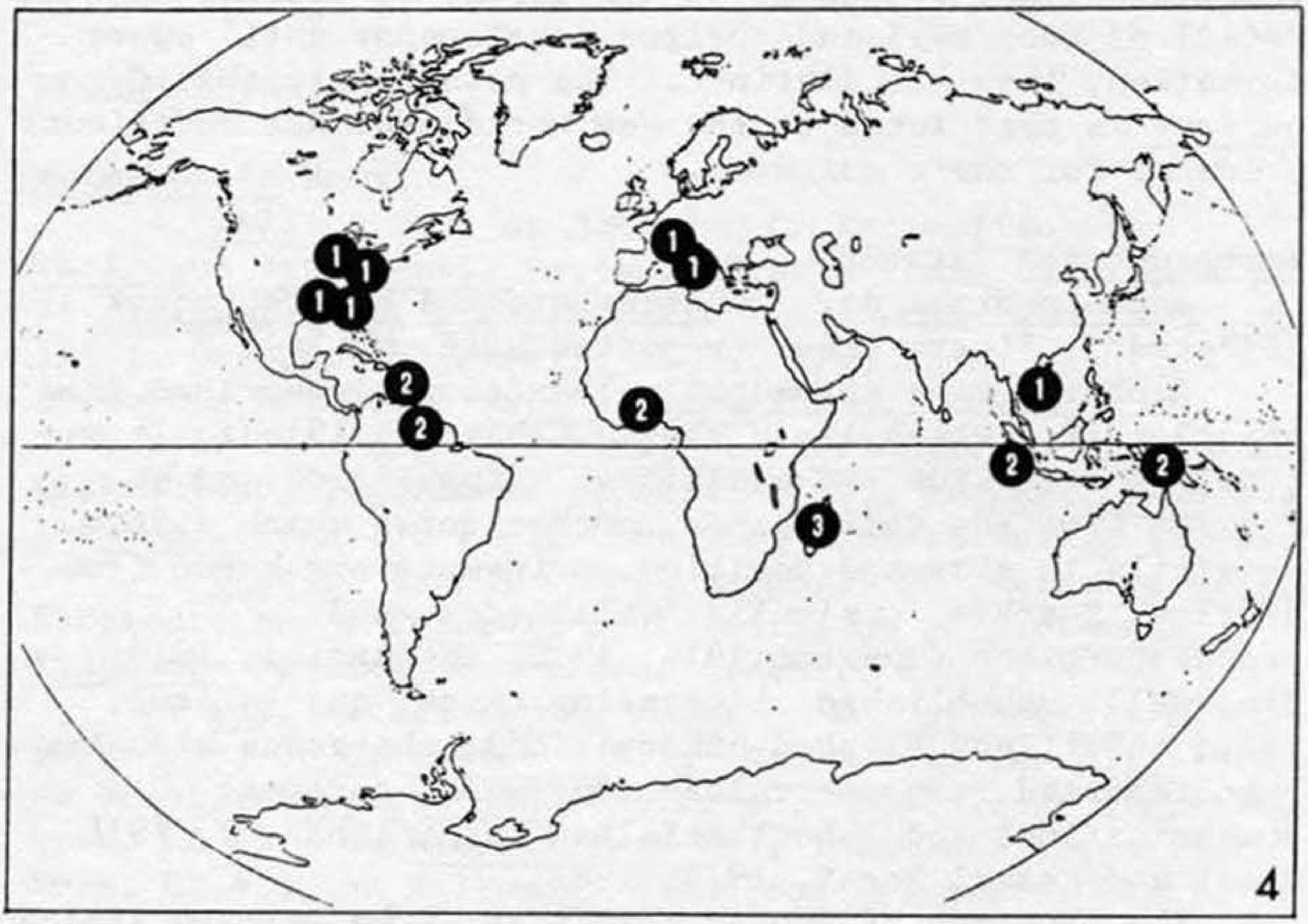

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Fig. 3. Distribution of *Amphoromorpha* spp. (○), *Laboulbeniopsis termitarius*, (●) and *Coreomycetopsis oedipus* (☆). Fig. 4. Distribution of *Antennopsis gallica* (①), *A. gayi* (②), and *A. grassei* (③).

colorless thallus of *C. oedipus* is difficult to distinguish from termite spines and this may account partially for the smaller known host and geographical ranges of this species when compared to *L. termitarius*, which has a darkened foot cell. However, careful examination of new *L. termitarius*-infected termite collections and all other new collections has failed to discover additional specimens of *C. oedipus*.

Blackwell and Kimbrough (1976a, 1976b) studied the development of *C. oedipus* and *L. termitarius* and came to the conclusion that spore production in *L. termitarius* appeared to be by free cell formation, while *C. oedipus* produced phialoconidia. Thaxter (1920) had noticed that spores of *L. termitarius* were formed simultaneously. Early stages of development of both species were found which clearly indicated *C. oedipus* developed only from phialospores, and *L. termitarius*, only from ascospores. These observations were important because it has been suggested the two forms comprised the holomorph of a single species. While the two species must surely be related because of the great similarity of ultrastructural detail of foot cell and thallus development until spore formation, they are distinct. The possibility that *C. oedipus* is restricted to the New World provides additional evidence for their autonomy.

Amphoromorpha Thaxter

Amphoromorpha sp. On *Acanthotermes acanthothorax* (Sjöstedt), Sierra Leone (reported here, MB 56).

Amphoromorpha entomophila Thaxter was described from bristles of a staphylinid beetle (Thaxter, 1914). It was also reported from two additional staphylinids and an earwing from the Philippines. Other forms which differ primarily in size and position on insects are known from beetles, roaches, a simulid, millipedes, and pseudoscorpions (Thaxter 1914, 1920; Spegazzini, 1918; Blackwell, unpublished observation; Rossi and Balazuc, 1977; Rossi, unpublished observation); the genus also has been reported from mucoralean (Benjamin, personal communication) and laboulbenialean fungi (Thaxter, 1914; Rossi and Cesari Rossi, 1979, 1982).

The specimen of *Amphoromorpha* sp. from Western Africa consists of one thallus on the right hind leg of a termite. It falls within the limits of Thaxter's (1914) description of *A. entomophila* except that the thallus is slightly longer (135 µm). A species of *Amphoromorpha* has been observed several times on *Reticulitermes* spp. in Florida (J. W. Kimbrough, personal communication).

The taxonomy of *Amphoromorpha* and other minute entomogenous forms is difficult because so few characters are available for distinguishing species. Developmental events and geographical and host distributions are poorly known for these species. Thalli often occur in small numbers on termites and few insects in a population are infested. *Amphoromorpha* is known from one tropical and one subtropical locality on termite species which are not closely related (Fig. 3, Table 1).

Hormiscioideus M. Blackwell et Kimbrough

H. filamentosus M. Blackwell et Kimbrough. On *Armitermes neotenicus* Holmgren, Brazil (Blackwell and Kimbrough, 1978).

Hormiscioideus filamentosus is known only from the type collection in which 60% of the termites were heavily infected. The termite genus is Neotropical in distribution and is restricted to damp woodlands (Fig. 2, Table 1).

GLOEOHAUSTORIALES

Antennopsis Heim

A. gallica Heim et Buchli. On *Reticulitermes lucifugus santonensis* Feytaud, France (Heim, 1951); on *R. virginicus*; on *R. flavipes*, Florida (Gouger and Kimbrough, 1969), Georgia (Blackwell, 1980), Wisconsin, Michigan (reported here); on *Reticulitermes* sp., Louisiana (reported here); on *Kalotermes* (as *Calotermes*) *flavicollis* (Fabricius), Yugoslavia (Buchli, 1960); on *Reticutitermes lucifugus* (Rossi), Italy (Rossi and Cesari Rossi, 1977b).

A. grassei Buchli (*nomen nudum*). On *Neotermes amplus* Sjöstedt; on *N. desneuxi* (Sjöstedt); on *Glyptotermes longiceps* Paulian, Madagascar (Buchli, 1960).

A. gayi Buchli (*nomen nudum*). On *Coptotermes elisae* (Desneux); on *C. obiratus* Hill, New Guinea (Buchli, 1966); on *Nasutitermes costalis* (Holmgren), Guadeloupe (reported here, MB 36); on *Nasutitermes* sp., Indonesia (reported here, MB 41); on *Amitermes evuncifer* Silvestri, Sierra Leone (reported here, MB 42).

Although the thallus of *Antennopsis* species is small, it is darkly pigmented and shows up distinctly against the nonpigmented termite. The genus is known from North America, including new reports from the northern United

States, South America, Europe, Africa, Madagascar, southeastern Asia, and New Guinea (Fig. 4).

Three species names exist in the literature. Antennopsis gallica Heim et Buchli (Heim, 1951) is validly described. Antennopsis grassei and A. gayi are nomina nuda proposed by Buchli (1960, 1966). Gouger and Kimbrough (1969) suggested that A. grassei may in fact be distinct from A. gallica, but were doubtful of the status of A. gayi. However, we have seen several new collections of Antennopsis (MB 36, MB 41) which fit the description of A. gayi. Because the three forms are recognizable on the basis of extant collections, we maintain the distinctions but do not validate the two taxa until more is known of developmental histories and distributions.

Termite hosts of Antennopsis (Table 1) are found in the Kalotermitidae, three subfamilies of the Rhinotermitidae (Heterotermitinae, Coptotermitinae, and Rhinotermitinae), and the Termitidae (Nasutitermitinae). All host genera have extremely broad ranges in tropical areas of the world. In addition Reticulitermes species are widely distributed in Paelarctic and Nearctic regions.

TERMITARIALES

Termitaria Thaxter

T. snyderi Thaxter. On Reticulitermes virginicus, Washington, DC (Thaxter, 1920), Florida (Khan and Kimbrough, 1974); on R. flavipes, Washington, DC, Massachusetts (Thaxter, 1920)), Florida (Khan and Kimbrough, 1974), Georgia (Blackwell, 1980); on Reticulitermes sp., California (Thaxter, 1920); on Rhinotermes marginalis (L.), British Guiana (Thaxter, 1920); on Porotermes quadricollis (Rambur), Chile (Colla, 1929); on Reticulitermes lucifugus, Italy (Thaxter, 1920; Rossi and Cesari Rossi, 1977b); on Neotermes (as Calotermes) samoanus Holmgren, Samoa (Tate, 1927, 1928).

T. coronata Thaxter. On Nasutitermes costalis (as Eutermes morio), Grenada (Thaxter, 1920); on Nasutitermes corniger (Motschulsky) (as Eutermes costaricensis), Costa Rica; on Nasutitermes guayanae (Holmgren); on N. surinamensis (Holmgren), British Guiana (Colla, 1929); on N. costalis, Guadeloupe (reported here, MB 36); on N. maximus (Holmgren), French Guyana (reported here, MB 46); on Amitermes evuncifer Silvestri (reported here, MB 42); on Coptotermes sjostedti Holmgren, Sierra Leone (reported here, MB 45); on Microcerotermes fuscotibialis (Sjöstedt), Sierra Leone (reported here, MB 54); on *Microcerotermes* sp., Kenya (reported here, MB 52); on *Nasutitermes* cf. *kempa* Harris, Kenya (reported here, MB 53); on *Odontotermes badius* (Haviland), Swaziland (reported here, MB 40); on *Allodontermes schultzei* (Silvestri), Namibia (reported here, MB 59), South Africa (reported here, MB 48); on *Allodontermes rhodesiensis* (Sjöstedt), South Africa (reported here, MB 47, MB 49); on *Nasutitermes fumigatus* (Brauer) (reported here, MB 36); on *N. exitiosus* (Hill); on *N. longipennis* (Hill); on *Mastotermes darwiniensis* Froggatt; on *Porotermes adamsoni* (Froggatt), on *Coptotermes lacteus* (Froggatt); on *C. acinaciformis* (Froggatt), Australia (Kimbrough and Lenz, 1982).

T. macrospora Kimbrough et Lenz. On *Mastotermes darwiniensis*, Australia (Kimbrough and Lenz, 1982).

T. rhombicarpa Kimbrough et Lenz. On *Porotermes adamsoni* Australia (Kimbrough and Lenz, 1982).

T. longiphialidis Kimbrough et Lenz. On *Coptotermes lacteus*; on *C. acinaciformis*, Australia (Kimbrough and Lenz, 1982).

T. thaxteri Reichensperger. On *Cornitermes cumulans* (Kollar); on *Nasutitermes* (as *Eutermes*) *rippertii* (Rambur); on *Nasutitermes* (as *Eutermes*) *arenarius* (Hagen), Brazil (Reichensperger, 1923).

Termitaria spp. On *Nasutitermes* (as *Eutermes*) sp.; on *Nasutitermes maculiventris* (Sjöstedt) (as *Eutermes lujae*), Belgian Congo (Reichensperger, 1923); on *Microhodotermes viator* (Latreille) (as *Hodotermes thompsoni*), South Africa (Reichensperger, 1923); on *Reticulitermes lucifugus*, France (Feytaud and Dieuzeide, 1927); on *Reticulitermes* sp., U.S. (?) (Pickens, 1952).

Species of the genus *Termitaria* are the best known of all termite ectoparasites. As mentioned in the introduction they are easily observed because of their relatively large size and dark pigmentation. Not only are the fungi wide spread geographically (Fig. 5), they also have a broad range of termite hosts which include species in five of the six extant termite families (Table 1).

The new reports included here indicate that *T. coronata* is more common on termitid hosts with only one record on a rhinotermitid species. *Termitaria snyderi* is known on rhinotermitid hosts (Rhinotermitinae, Coptotermitinae, and Heterotermitinae) and on Kalotermitidae. *Termitaria snyderi* appears to be more common in temperate regions of the Northern Hemisphere, while *T. coronata* is known from tropical and Southern

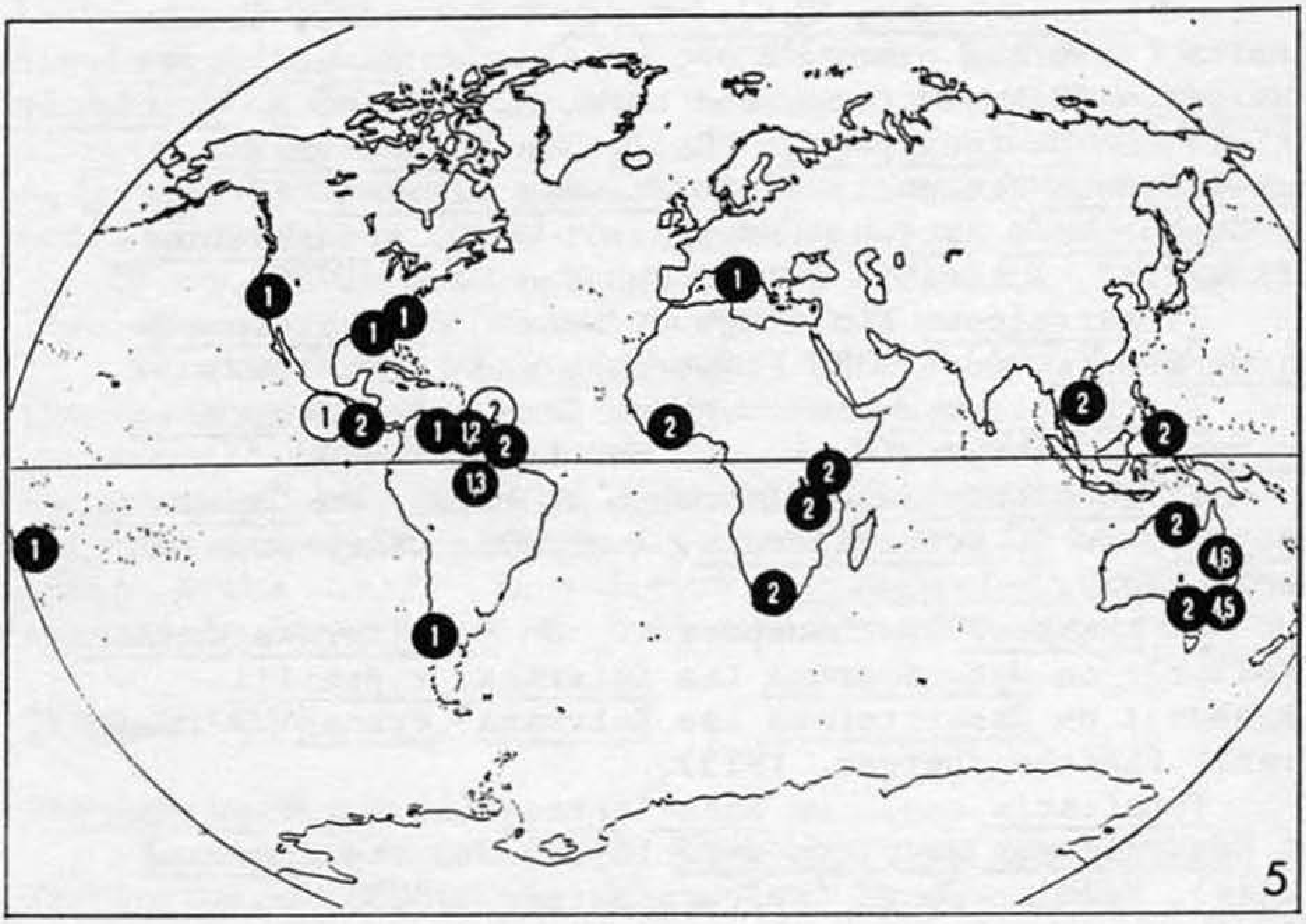

Fig. 5. Distribution of *Mattirolella crustosa* (①), *M. silvestrii* (②); and *Termitaria snyderi* (❶), *T. coronata* (❷), *T. thaxteri* (❸), *T. longiphialidis* (❹), *T. rhombicarpa* (❺), and *T. macrospora* (❻).

Hemisphere localities. The occurrence in Australia of four species (Kimbrough and Lenz, 1982), some sympatric on the same host species, is unique for the genus.

Mattirolella Colla

M. silvestrii Colla. On *Rhinotermes marginalis*, British Guiana (Colla 1929).

M. crustosa Khan et Kimbrough. On *Reticulitermes* sp., Panama (Khan and Kimbrough, 1974); on *Nasutitermes corniger*; on *N. ephratae* (Holmgren); on *N. columbicus* (Holmgren), Panama (Kimbrough and Thorne, 1982).

Khan and Kimbrough (1974) and Kimbrough and Thorne (1982) have discussed the close relationship of species of

Mattirolella and *Termitaria*. Both host range (Rhinotermitinae and Nasutitermitinae) and distribution (Central America and northern South America) of *Mattirolella* species overlap with those of *Termitaria*; however, *Termitaria* has a far wider distribution (Fig. 5, Table 1).

DISCUSSION

Termites are unusual as fungal hosts. No other insect group is known to harbor so many minute, nonmycelial fungi, most of which are restricted to termites. Isopterans are a very old group. Fossils are known from rocks at the Lower-Upper Cretaceous border in Labrador (Emerson, 1967). Emerson speculated on the basis of this find that the group may extend as far back as the Mesozoic or even Late Paleozoic. The primitive family Mastotermitidae is represented by one extant species in Australia; however, the family was worldwide in Early and Middle Tertiary (Emerson, 1965). Baltic amber (Oligocene) contains a fauna which is essentially modern and characteristic of a present day warm temperate European fauna. Miocene age amber from Chiapas contains termites similar to those of recent Neotropical faunas (Wilson, 1971).

In addition to their age which has afforded time for development of the associations, termites also maintain a temperature-stable, humid environment and provide an efficient means of local dispersal for the fungi. Dispersal of spores is probably by direct contact with termite-infested fungi or spores released into termite galleries and nests. Large populations of these social insects within a restricted area help to insure the contact necessary for spore dispersal to suitable hosts. Opportunity for interspecific infection is afforded by many instances of inquilinism involving several termite species, commensalism with other insects and mites, and use of abandoned nests and galleries of one species by other species of termites.

Dispersal over long distance does not appear to be too efficient. Although some termite individuals are winged at some stage in their life, they are unable to fly great distances. Large bodies of water serve as effective barriers to termite dispersal (Krishna, 1969); however, the insects are capable of crossing smaller water barriers, and they are known from net captures up to 1000 km from land (Gressitt, 1961). Termites are essentially a tropical group as is shown by both their fossil record and present distribution; extreme cold also serves as an effective barrier to dispersal (Krishna, 1969). The occurrence of a molt prior to alate maturation serves to remove fungal ectoparasites and, thereby, further reduces the possibility long distance dispersal.

Of the ten genera of fungi which infest termites, few appear to be closely related. Some species have a basal cell which may produce a secretion to cement the fungus to the exoskeleton (*Amphoromorpha*, *Coreomycetopsis*, and *Laboulbeniopsis*). In other cases (*Termitaria*, *Antennopsis*, *Hormiscioideus*, *Laboulbenia*, *Dimeromyces*, *Mattirolella*) a restricted haustorial system is present. Only *Cordycepioideus* is mycelial. The presence of so many nonmycelial forms may be a reflection of convergence selected by the stable, protected environment. This suggestion has been made for laboulbenialean and other fungi discussed here (Benjamin, 1971).

Amphoromorpha is known from a variety of nontermite hosts. Thaxter (1920) did not consider this genus to be related to the other nonhaustorial forms, *Coreomycetopsis* and *Laboulbeniopsis*. However, there is some evidence that *Coreomycetopsis* and *Laboulbeniopsis* may be related (Blackwell and Kimbrough, 1976a, 1976b), (see above, *Coreomycetopsis*). Relationships between these genera and other nonmycelial forms on a variety of hosts has been discussed recently (Blackwell *et al*., 1986).

The morphology of *Termitaria* and *Mattirolella* is complex enough that their high degree of similarity is certainly an indication of a close relationship (Khan and Kimbrough, 1974; Kimbrough and Thorne, 1982). A third genus, *Termitariopsis*, is part of this complex and is known on ants in Kansas and Panama (Blackwell *et al*., 1980). *Mattirolella* and *Termitariopsis* occur in isolated portions of the wide range of *Termitaria*. Some degree of speciation has occurred in Australia where four species occur on a variety of termites and are sympatric on the same host in several cases (Kimbrough and Lenz, 1982).

The two laboulbenialean genera, *Dimeromyces* and *Laboulbenia*, are not closely related to each other. Collections of *D. isopterus* have been made only in the southeastern United States and the species does not appear to be common on termites. The more common presence of *D. isopterus* on staphylinid commensals than on *Reticulitermes* and the prevalence of beetle and staphylinid hosts for

Dimeromyces may be a clue to a way in which extreme host changes come about. The occurrence of *D. majewskii* on termites probably represents a second independent host change. It will be important to determine if commensals associated with the host termites also are infected with *D. majewskii*. Such information may substantiate the idea that host shifts occur through ecological associations between unrelated hosts. The five species of *Laboulbenia* are restricted to arid regions of Africa. Indications from the present restricted geographical and host ranges of these two genera are that they have only recently become associated with termite hosts. The five species of *Laboulbenia* in Africa may have evolved from a common ancestor under the same conditions which led to development of a number of endemic termite species (Rossi and Blackwell, 1986).

Because cold climates and large bodies of water serve at least as partial barriers for termite dispersal, it seems reasonable to suggest that the fungal genera *Termitaria*, *Antennopsis*, and *Laboulbeniopsis* are very old and were established in termite populations which were the early colonizers of the continents. *Cordycepioideus* known from Africa and Mexico may also have had a similar history.

Although species of termites with broad geographical and host ranges appear morphologically similar throughout their entire range across continents and hosts (*i.e.*, *T. coronata*, *T. snyderi*, *Antennopsis gallica*, *Laboulbeniopsis termitarius*), undetectable physiological differences could exist. It is likely that the stable, protected environment of the termite acts to maintain constant morphological features in the fungi.

Only one fungal species shows some restriction to related host species. *Termitaria coronata* is much more common on termitid hosts of the subfamilies Amitermitinae and Nasutitermitinae. Although *T. snyderi* has been collected from a variety of termites it is not yet known from any termitid.

Additional, intensive collection is needed to provide information on complete host and geographical ranges for these fungi. It will be particularly interesting to determine if *Mattirolella* spp., *Cordycepioideus bisporus*, *C. octosporus*, *Hormiscioideus filamentosus*, *Termitaria rhombricarpa*, *T. longispora*, *T. macrocarpa*, *Laboulbenia* spp., *Dimeromyces isopterus*, and *Coreomycetopsis oedipus* really do have the restricted ranges indicated by the present reports. Because of the low incidence of fungal infection in many insect populations, the aid of entomologists who study the insects is imperative for obtaining specimens efficiently.

We are happy to acknowledge the contribution of S. Bacchus, J. E. Ruelle, and J. Balazuc, their help in identification and acquisition of termite specimens.

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FLAVOPARMELIA, A NEW GENUS IN THE LICHEN FAMILY PARMELIACEAE (ASCOMYCOTINA)

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Abstract.--The genus *Pseudoparmelia* Lynge is limited to a group of four tropical species, *P. cyphellata* Lynge, *P. chapadensis* (Lynge) Hale, *P. hypomilta* (Fée) Hale and *P. sphaerospora* (Nyl.) Hale. Of the other 72 species formerly assigned to *Pseudoparmelia*, 17 usnic acid-containing species (the *P. caperata* group) are segregated in a new genus, *Flavoparmelia*.

The genus *Pseudoparmelia* Lynge was based on one species, *P. cyphellata* (Lynge, 1914). This rare Brazilian lichen is in fact closely related to three other species: *P. hypomilta* (Fée) Hale, another rarely collected Brazilian lichen with an orange-red pigmented medulla; *P. chapadensis* (Lynge) Hale, a saxicolous species, also from Brazil; and *P. sphaerospora* (Nyl.) Hale, a widespread corticolous lichen in the American tropics and Africa. All four species share an unidentified pale yellow medullary pigment (?secalonic acid), rarely contain stictic or hypostictic acid in the medulla, and sporadically have traces of atranorin in the cortex. The thallus is often quite yellowish, however, apparently because of low concentrations of the medullary pigment in the cortex. The lower surface is shiny and pale brown or uniquely olivaceous brown with simple, rather sparse rhizines. The spores are small (about 6 X 9 µm) and nearly spherical, and the conidia are cylindrical to weakly bifusiform.

When I resurrected *Pseudoparmelia* in 1976 (Hale, 1976), I included in it not only these four species but another 72 from the old form genus *Parmelia* (mostly in sect. *Cyclocheila*) which lacked marginal cilia and had adnate lobes and simple rhizines with at most a narrow bare or papillate zone at the margin below. I realized at the time that my delimitation of *Pseudoparmelia* was heterogeneous in terms of chemistry, morphology and geography.

Research in the past few years by several investigators has begun to elucidate some of the discontinuities within *Pseudoparmelia* sens. lat. and pointed the way to more rational, natural generic divisions. It now appears, for example, that *Pseudoparmelia* should include only the four species mentioned above with their characteristic spore size and thalline chemistry, and that the other 72 species should be removed to other genera. I will discuss one group here, the well-known *P. caperata* group.

Parmelia caperata has always posed problems for workers in *Parmelia*. I placed it in *Pseudoparmelia* because of the lack of cilia, even though it has rather broad, apically rotund lobes. The lobes are, in fact, almost wide enough to fit the concept of *Parmotrema* Mass. (*Parmelia* subgenus *Amphigymnia*), but the bifusiform conidia exclude it from that genus. Gyelnik (1932) actually created a subsection *Eciliatae* under section *Subflavescentes* (= *Amphigymnia*) to accomodate *P. caperata*.

There are other characters which set *P. caperata* and 16 related species apart from the remainder of *Pseudoparmelia* sens. lat.: The constant presence of usnic acid in the cortex (at most with traces of atranorin), a lichenin negative reaction (Imshaug, in litt.), the black lower surface with simple rhizines and a distinct narrow bare zone below at the margins, the large spores (mature spores more than 15 µm long with an episporium about 2 µm thick), and nearly constant occurrence of the protocetraric acid group (protocetraric acid, fumarprotocetraric, malonprotocetraric acid and physodalic acid), often with fatty acids. All are temperate species, occurring frequently in dry to semi-arid forested regions.

I believe that the *P. caperata* group is not at all related to *Pseudoparmelia* sens. str. or to any of the other species groups formerly placed in the genus and constitutes a new genus, *Flavoparmelia*, as described below:

Flavoparmelia, gen. nov.

Thallus foliaceus, adnatus vel laxe adnatus, lobis subirregularibus, apice rotundatis, margine eciliatis, cortice superiori epicorticato, subtus niger, modice rhizinosus, rhizinis simplicibus, nigris. Apothecia adnata, imperforata, sporis octonis, simplicibus, conidiis bifusiformibus.

Type: *Lichen caperatus* L.

This genus contains 17 species (see Hale, 1976 for full descriptions and synonymy):

Flavoparmelia amplexa (Stirton) Hale, comb. nov.
Parmelia amplexa Stirton, Trans. Glasgow Soc. Field Nat. 5:212. 1877.
Pseudoparmelia amplexa (Stirton) Hale, Smith. Contr. Bot. 31:16. 1976.

Flavoparmelia baltimorensis (Gyel. & Fór.) Hale, comb. nov.
Parmelia baltimorensis Gyel. & Fór., Ann. Crypt. Exot. 4:167. 1931.
Pseudoparmelia baltimorensis (Gyel. & Fór.) Hale, Phytol. 28:189. 1974.

Flavoparmelia callichroa (Kurok.) Hale, comb. nov.
Pseudoparmelia callichroa Kurok. in Hale, Smith. Contr. Bot. 31:20. 1976.

Flavoparmelia caperata (L.) Hale, comb. nov.
Lichen caperatus L., Sp. Pl. 1147. 1753.
Parmelia caperata (L.) Ach., Meth. Lich. 216. 1803.
Pseudoparmelia caperata (L.) Hale, Phytol. 28:189. 1974.

Flavoparmelia euplecta (Stirton) Hale, comb. nov.
Parmelia euplecta Stirton, Scot. Nat. 4:299. 1877-78.

Flavoparmelia exornata (Zahlbr.) Hale, comb. nov.
Parmelia caperata var. *exornata* Zahlbr., Ann. Mycol. 10:379. 1912.
Pseudoparmelia exornata (Zahlbr.) Hale, Smith. Contr. Bot. 31:31. 1976.

Flavoparmelia ferax (Müll. Arg.) Hale, comb. nov.
Parmelia ferax Müll. Arg., Flora 69:257. 1886.
Pseudoparmelia ferax (Müll. Arg.) Hale, Phytol. 28:190. 1974.

Flavoparmelia gerlachei (Zahlbr.) Hale, comb. nov.
Parmelia antarctica Vain., Rés. Exp. Ant. Belgique, p. 13. 1903. Not *P. antarctica* Bitter, Hedw. 40:248. 1901 (=*Hypogymnia*).
Parmelia gerlachei Zahlbr., Cat. Lich. Univ. 6:137. 1929.
Pseudoparmelia gerlachei (Zahlbr.) Hale, Smith. Contr. Bot. 31:32. 1976.

Flavoparmelia haysomii (Dodge) Hale, comb. nov.
Parmelia haysomii Dodge, Nova Hedw. 15:295. 1968.

Flavoparmelia helmsii (Kurok. & Fils.) Hale, comb. nov.
Parmelia helmsii Kurok. & Fils., Austral. Journ. Bot. 30:539. 1982.

Flavoparmelia jelineckii (Kremplh.) Hale, comb. nov.
Parmelia jelineckii Kremplh., Verh. K.-K. Zool.-Bot. Gesell. Wien 18:321. 1868.

Flavoparmelia pachydactyla (Hale) Hale, comb. nov.
Parmelia caperata var. *isidiophora* Steiner, Sitz. Kaiser. Akad. Wissen. Wien 106:215. 1897.
Parmelia pachydactyla Hale, Bryol. 75:345. 1972.
Pseudoparmelia pachydactyla (Hale) Hale, Phytol. 28:191. 1974.

Flavoparmelia papillosa (Gyel.) Hale, comb. nov.
Parmelia papillosa Lynge ex Gyel., Ann. Mus. Nat. Hung. 29:43. 1935.
Pseudoparmelia papillosa (Gyel.) Hale, Smith. Contr. Bot. 31:40. 1976.

Flavoparmelia rutidota (Hook. & Tayl.) Hale, comb. nov.
Parmelia rutidota Hook. & Tayl., Hook. Lond. Journ. Bot. 3:645. 1844.
Pseudoparmelia rutidota (Hook. & Tayl.) Hale, Phytol. 28:191. 1974.

Flavoparmelia soredians (Nyl.) Hale, comb. nov.
Parmelia soredians Nyl., Flora 55:426. 1872.
Pseudoparmelia soredians (Nyl.) Hale, Phytol. 28:191. 1974.

Flavoparmelia springtonensis (Elix) Hale, comb. nov.
Parmelia springtonensis Elix in Elix & Stevens, Austral. Journ. Bot. 27:879. 1979.

Flavoparmelia subamplexa (Hale) Hale, comb. nov.
Pseudoparmelia subamplexa Hale, Smith. Contr. Bot. 31:50. 1976.

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RUSSULA VESICATORIA AND RUSSULA ANGUSTISPORA SP. NOV., TWO CONFUSING SPECIES OF RUSSULA SUBSECTION LACTARIOIDEAE

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KEYWORDS: *Russulaceae, Russula, mycorrhizal associations.*

SUMMARY

Russula vesicatoria, a poorly understood species previously recorded only from Florida, occurs over a wide geographic area in *Pinus* forests of the Gulf Coast and eastern seaboard of North America. An illustrated description and new information on its habitat and geographic distribution are presented. *Russula angustispora*, a taxon that has been confused with other members of the subsection *Lactarioideae*, is described as new.

INTRODUCTION

The subsection *Lactarioideae* Maire (=subsection *Plorantes* (Bat.) Singer) is one of the best known and most distinctive groups of *Russula* species. Monographs of both North American and European species of this subsection permit identification of specimens with a high degree of confidence when the collector records the necessary macroscopic and microscopic data (Shaffer, 1964; Romagnesi, 1967). A major limitation of these works has been that most of the information included was based on specimens from western Europe and northeastern or northwestern North America.

Two taxa of the *Lactarioideae* that occur commonly and predictably in specific habitats in southeastern North America have been confused often with *R. brevipes* Peck and its varieties and with other taxa of this subsection despite reference to available monographs. One of these species is *R. vesicatoria* Burlingham. The second species, *R. angustispora*, is described here as new. Descriptions, illustrations, and notes on habitat and geographic distributions are presented to facilitate their identification, to refine further their circumscriptions, and to clarify their relationships to other taxa of the subsection *Lactarioideae*.

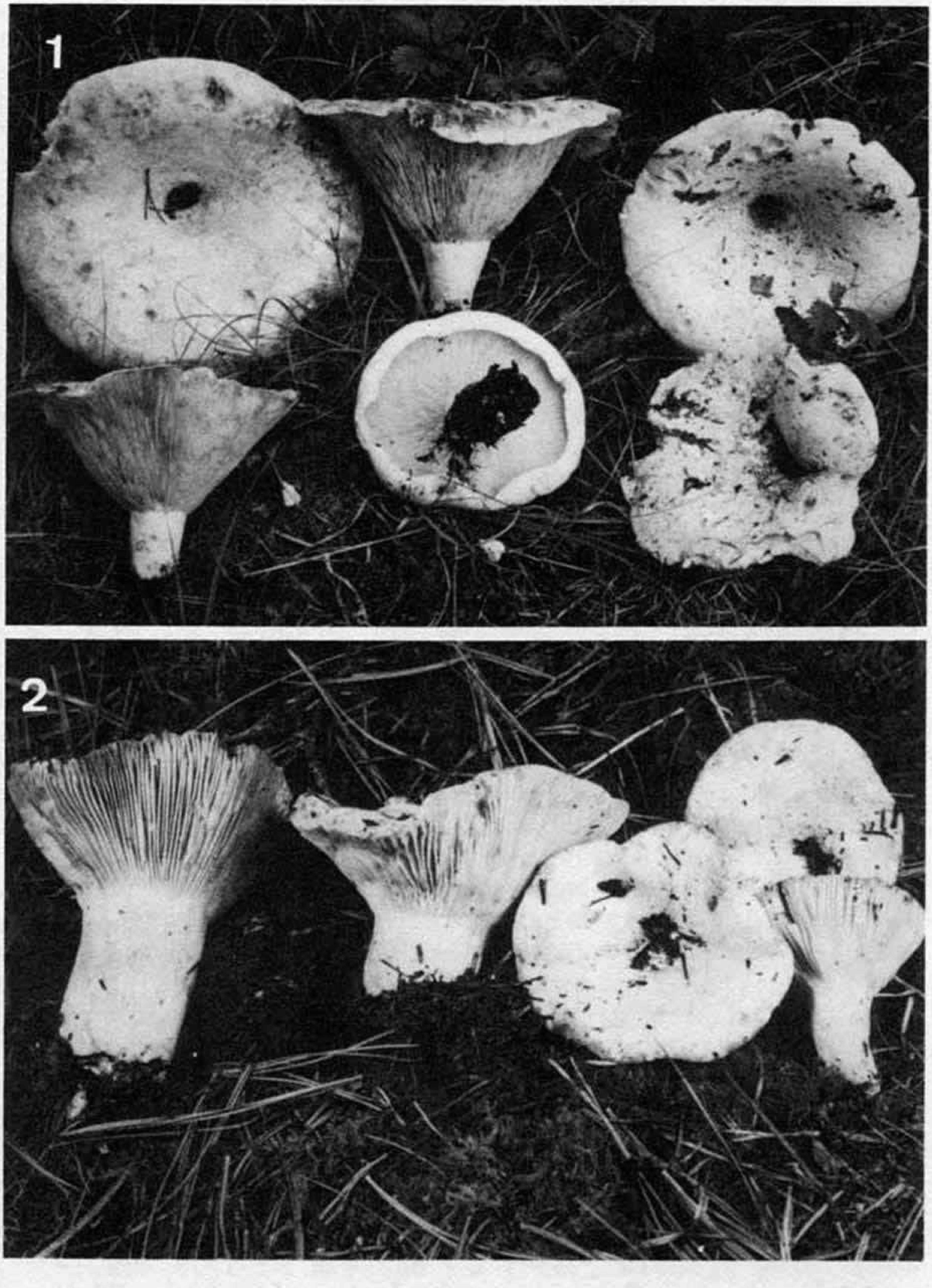
Basidiospore size and shape are from optical sections in side view and exclude the ornamentation. Capitalized color names are from Ridgway (1912). Spore-print and some lamellar colors are from Romagnesi (1967). Macro- and microchemical tests were made according to the methods of Romagnesi (1967) and Singer (1975). The letters SV stand for sulfovanillin. All specimens are deposited at BPI unless stated otherwise. For scanning electron microscopy (SEM), dried pieces of mature lamellae were rehydrated overnight and then dehydrated through an ethanol series. After critical point drying, lamellar pieces were attached to aluminum stubs, coated with gold under vacuum on a rotary stage, and examined with an AMRAY 1200B scanning electron microscope.

DESCRIPTIONS OF TAXA

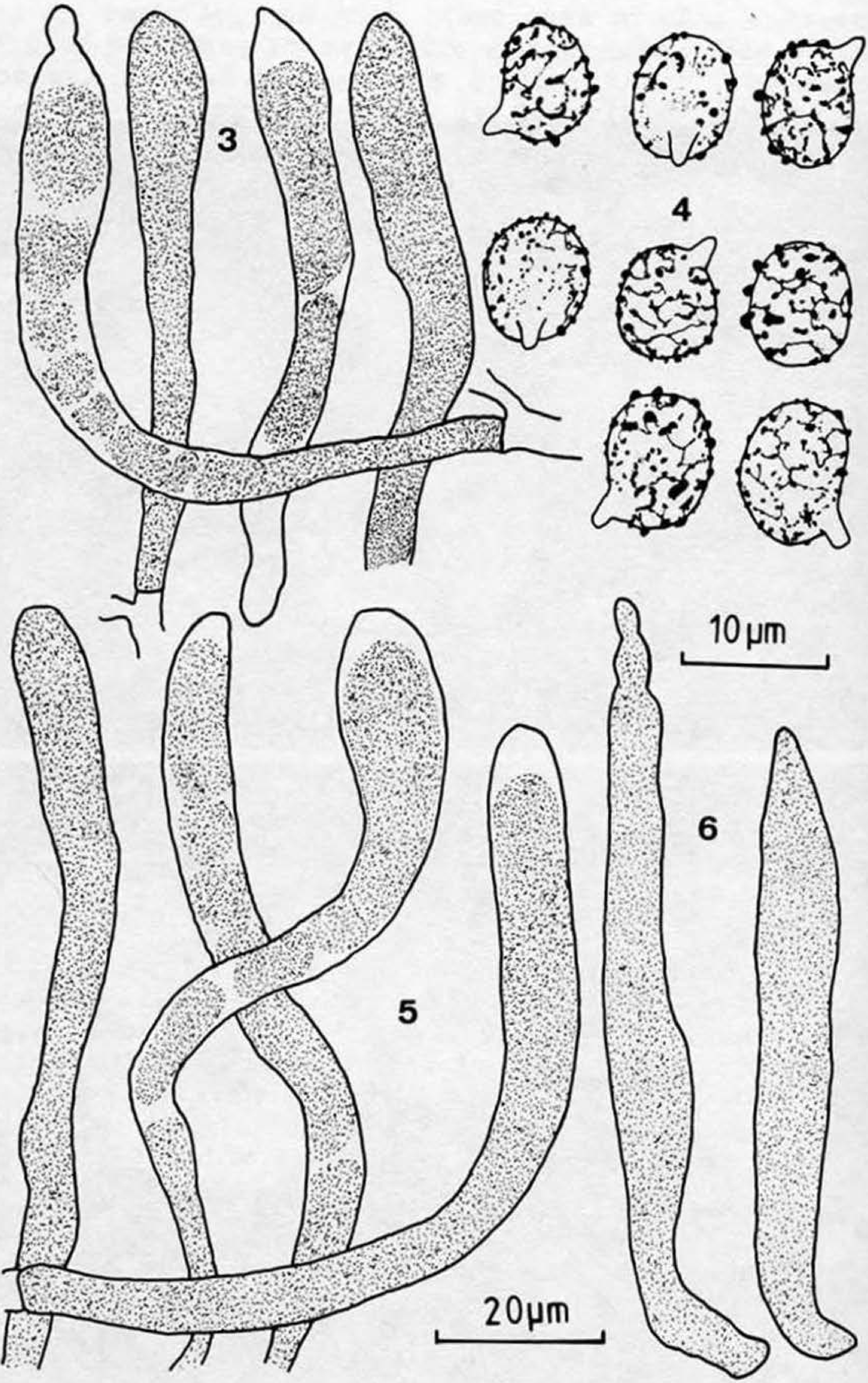
RUSSULA VESICATORIA Burlingham, *Mycologia* 36: 118. figs. 1-t, 2. 1944.

FIGS. 1, 3-6, 11, 12

PILEUS 4-20 cm broad, pulvinate to convex-depressed with involute or incurved margin when young, soon convex-depressed to shallowly or deeply infundibuliform with margin uplifted or arched in age; margin not striate, sometimes minutely felted; cuticle inseparable; surface dull, dry, subviscid when wet, chalk-like, glabrous to minutely pruinose or velvety, often developing areolate patches, sometimes becoming concentrically areolate or lacerate, especially in dry weather, white to dingy grayish white, Cream Color, pale grayish yellow, with pale yellowish brown to light brown, Pale Pinkish Cinnamon, Light Pinkish Cinnamon or, Clay Color spots or areolate areas in age; trama hard-rigid, brittle in age, up to 12 mm thick at midradius, white to cream, yellowish brown around larval channels, unchanging when cut; odor of feungreek (*Trigonella foenum-graecum* L.) or *Lactarius camphoratus* (Bull. : Fr.) Fr. when young, mild to



FIGS. 1-2. *Russula* spp. 1. *R. vesicatoria* (GB 470), X 1/3. 2. *R. angustispora* (GB 548, HOLOTYPE), X 1/2.



FIGS. 3-6. *Russula vesicatoria* (GB 916). 3. Caulocystidia. 4. Basidiospores. 5. Dermatocystidia. 6. Hymenial cystidia.

disagreeable in age; taste acrid to bitter when young, bitter to disagreeable or mild in age. LAMELLAE adnate to decurrent, extremely crowded to close, with many lamellulae of various lengths, repeatedly forked or anastomosing, especially near the stipe, acute in front, narrow, 2-5 mm broad at midradius, easily separated from pileus trama, white to pale cream or grayish yellow, Light Buff, Pale Pinkish Buff or, Pale Pinkish Cinnamon, slowly bruising dingy yellowish brown or not, reminiscent of *L. piperatus* (L. : Fr.) S. F. Gray; edges even or minutely pruinose. STIPE 1-4 cm tall, 1-3 cm wide at midpoint, robust, tapered toward the base, with white basal mycelium, often with a mass of sand adhering to basal mycelium; surface dry, dull, smooth, concolorous with pileus; trama solid or with interior hollow in age, hard but brittle, white or stained yellowish brown at base, unchanging when cut. CHEMICAL REACTIONS (stipe trama): formalin-no reaction; gum guaiac-greenish blue; $FeSO_4$ -grayish pink to pale red; phenol-grayish maroon; aniline-lemon yellow in 5 min.

BASIDIOSPORES yellow, Light Buff (Romagnesi IIIa) in mass on paper; 6.5-8.5(-10) X 5.5-7.5(-8) µm, subglobose, broadly obovate to obovate; ornamentation amyloid, up to 0.8 µm high, mostly 0.2-0.6 µm high, consisting of relatively crowded, blunt, hemispherical to cylindrical verrucae and fine particles, with verrucae often joined by a few lines, low ridges, or short chains of fine particles, usually forming a partial to nearly complete reticulum; suprahilar area depressed, unornamented or with a few fine particles. BASIDIA narrowly clavate to clavate, 42-58 X 8-10.5 µm, 4-sterigmate. HYMENIAL CYSTIDIA 51-85 X 8-10.5 µm, projecting up to 25 µm beyond basidia, narrowly clavate, cylindrical, subulate, or ventricose-rostrate, with rounded, acuminate, submoniliform, or attenuated apices, arising from trama, subhymenium, or hymenium, partially or completely filled with hyaline to pale yellow, refractive contents in KOH, grayish yellow to grayish yellow-green in SV. SUBHYMENIUM up to 35 µm thick, often poorly developed or absent, pseudoparenchymatous to interwoven. LAMELLAR TRAMA composed of sphaerocysts, interwoven connective hyphae, laticifers, and pseudoparenchyma, entirely of pseudoparenchyma and interwoven hyphae towards distal end.

PILEUS CUTICLE 225-550 µm thick, without gelatinous materials, a relatively undifferentiated cutis, composed of interwoven, horizontal to ascending hyphae, dermatocystidia, and laticifers; cuticular hyphae 3-6.5 µm in diam, septate, branched, often arranged in ascending to erect, tangled fascicles or aggregates at the pileus surface; dermatocystidia 80-300+ X 6.5-12 µm, cylindrical to clavate, curved or flexuous, usually aseptate, rarely 1-septate, arising from the laticiferous hyphal system, partially or completely filled with hyaline to pale yellow refractive contents in KOH, grayish yellow to greenish yellow-gray in SV. PILEUS TRAMA consisting of sphaerocysts, connective hyphae, and abundant laticifers; laticifers 5-10.5 µm in diam, straight to flexuous, with refractive hyaline to pale contents in KOH, grayish yellow in SV.

STIPE CUTICLE 250-500 µm thick, similar to pileus cuticle, without gelatinous materials, one-layered, composed of horizontal to ascending hyphae, laticifers, and caulocystidia; hyphae 3-6.5 µm in diam, septate, branched or not, sometimes with constricted, attenuated, or slightly inflated apices; often aggregated into ascending or erect fascicles at the surface; caulocystidia 45-300+ X 7.5-12 µm, cylindrical to clavate, with rounded, acuminate, or rarely submoniliform apices, arising from the trama or connective hyphae. STIPE TRAMA composed of connective hyphae, nests of sphaerocysts, and laticifers. CLAMP CONNECTIONS absent from all tissues.

HABIT, HABITAT, AND DISTRIBUTION. Gregarious on sand or sandy soil under 2-3 needle pines, e.g. *Pinus taeda* L., *P. australis* Michx., *P. rigida* Mill., *P. virginiana* Mill., and probably other southern *Pinus* species. Known from coastal regions of eastern North America from Mississippi to southern New Jersey.

MATERIAL EXAMINED: USA: FLORIDA: Alachua Co.: Gainesville, 18 May 1948, R. Singer F1918a, 28 Jun 1943, R. Singer F2404 (both FH), G. Bills, 10 Aug 1985; Seminole Co.: Lake Wildmere, Longwood, G. S. Burlingham, 23 Oct 1941 (HOLOTYPE, NY), 21 Oct 1941 (labeled Co-type, NY) and 6 additional collections (NY). MARYLAND: Anne Arundel Co.: Ft. Meade Golf Course, 7 Oct 1971, K. H. McKnight 12792A; Charles Co.: Cedarville State Park, 19 Jul 1973, K. H. McKnight 13696; Prince George's Co.: Greenbelt Park, 4 Sep 1981, M. Farr & C. Fritz, Greenbelt, 14-15 Aug 1977, D. Farr 2450 & 2451, Laurel, Pfister's Woods, 23 Jul 1967, J. Lindsay 50 (VPI), 6 Sep 1967, O. K. Miller 6085 (VPI), Laurel, Fox Rest Woods, 13 Aug 1967, J. Lindsay 122 (VPI), Laurel, Forest Disease Lab, 11 Aug 1965, O. K. Miller 3240 (VPI), 22 Sep 1965, O. K. Miller 3677 (VPI), Beltsville, BARC-West, Wagstaff, 15-16 Sep 1974. MISSISSIPPI: Saucier Co.: Harrison Experimental Station, 26 Jul 1983, C. Ovrebo 1544 (MICH). NEW JERSEY: Burlington Co.: Lebanon State Forest, 1 Sep 1984, GB 916. SOUTH CAROLINA: Jasper Co.: along I-95, 9 Aug 1985, G. Bills & R. Vilgalys. VIRGINIA: James City Co.: York River State Park, 14 Aug 1983, GB 470.

DISCUSSION. Prior to this report, the geographic distribution of *R. vesicatoria* has been documented accurately only in Florida by Burlingham (1944) and Singer (1957). Burlingham (1944) also mentioned H. C. Beardslee's observation of this species along the coast of North Carolina. Singer (1957) described western collections of "*R. vesicatoria*" which were later described as a new species, *R. cascadensis* Shaffer (Shaffer, 1964). Miller (1973) noted that *R. vesicatoria* occurred in Maryland and Virginia, but examination of his specimens indicated his concept was based on a mixture of *R. vesicatoria* and *R. angustispora* Bills (see next description).

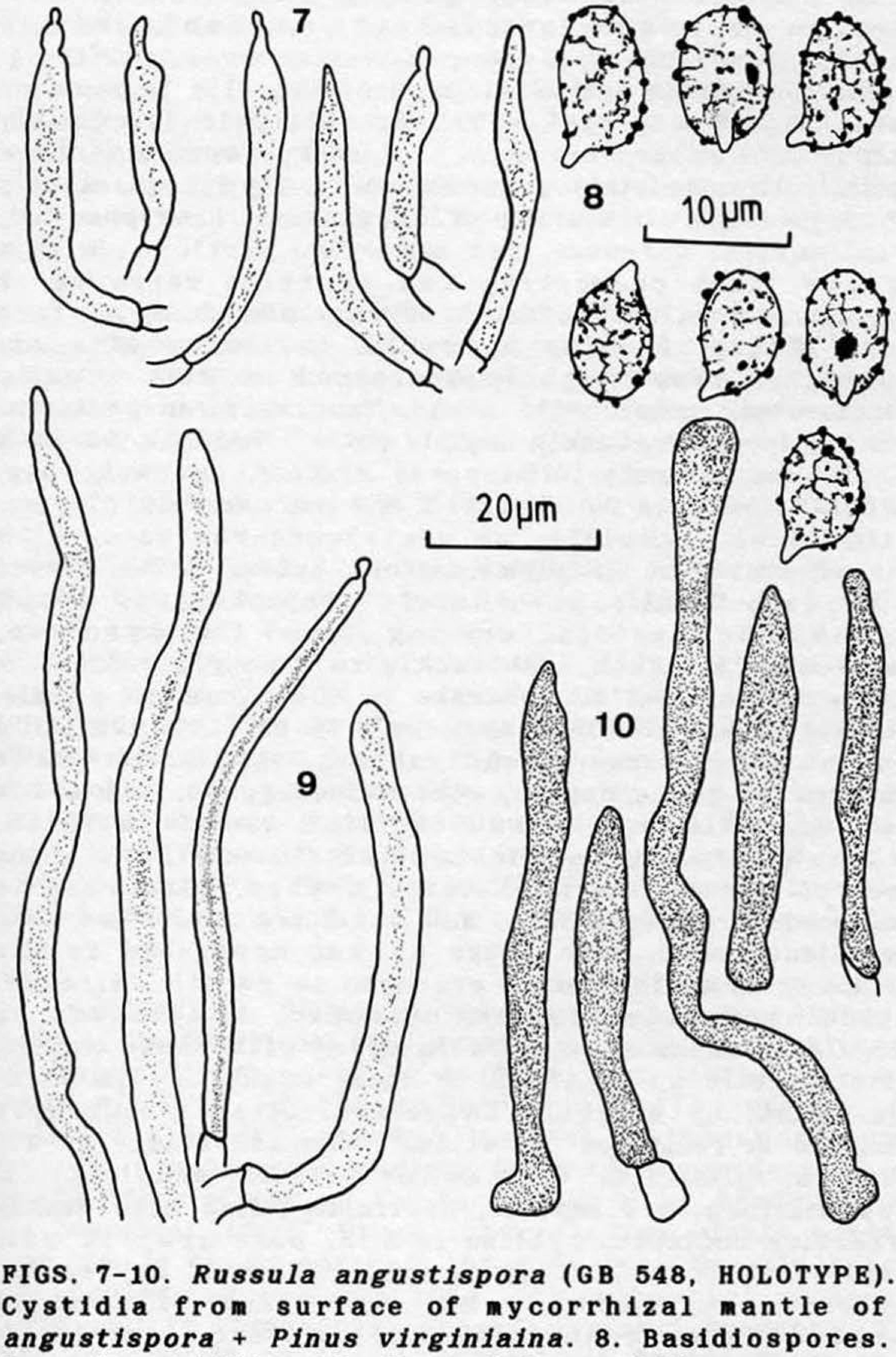
Russula vesicatoria is one of the most distinctive species of the subsection *Lactarioideae*. In the field, it can be recognized by its crowded, narrow lamellae that resemble those of *L. piperatus*, the relatively large sporocarps, and the habitat in sandy *Pinus* forests. Also the pileus surface is unusually dull and opaque and tends to crack concentrically in dry weather. Shaffer (1964) used the acrid taste and odor of *L. camphoratus* (as recorded by Burlingham) to separate *R. vesicatoria* from other taxa of subsection *Lactarioideae* with low basidiospore ornamentation. The taste and odor of *R. vesicatoria* seem to be age-dependent and therefore inconsistent characters. Old sporocarps usually lack the acrid taste and *L. camphoratus* odor but retain the bitter taste component. The abundant, weakly SV+, large dermatocystidia and laticifers of the pileus and stipe surface and the broad basidiospores with relatively low ornamentation also distinguish *R. vesicatoria* from similar taxa.

RUSSULA ANGUSTISPORA Bills, sp. nov.

FIGS. 2, 7-10, 13, 14

Sporocarpis parvis *Russulae brevipedis* similis. Pilei maturi quum plano-depressi tum infundibuliformes; superficies arida, alba primum deinde avellanea; trama juventute dura, immutata ubi scissa; odor indistinctus; sapor mitis vel parum ingratus aut acridus. Lamellae multis lamellulis instructae, quum confertae tum parum remotae, luteolae ubi maturae, nullo modo viridae. Stipes brevis, aequalis aur deorsum decrescens; superficies alba; trama armeniaca in salibus ferri. Basidiospores citrae ubi confertae, 6.5-8.5 X 4.5-6 µm, angustae, quum ellipticae tum late ellipticae, ornamentum pro parte maxima 0.2-0.6 µm altum, verrucis particulisque plerumque segregatis. Cystidia hymenialia plerumque 29-85 X 4-8 µm, gracilia, in hymenia inclusa. Cuticula pilei stratum crassitudine inconstans, hyphis horizontalibus intertextis compositum, paucis dermatocystidiis; hyphae cuticulares interdum parietibus asperis, refringentibus, aut parum incrassatis instructae. Sub *Pinum virginianum* autumno sero fructificans. Holotypus ab Estes' Farm, Blacksburg, Montgomery Co., Virginia, 20 Nov 1982, G. Bills 548 (BPI).

PILEUS 2-7.5(-9) cm broad, pulvinate to convex-depressed with involute or incurved margin when young, soon plano-depressed with incurved or arched margin, finally shallowly to deeply infundibuliform with margin arched or uplifted, sometimes slightly eccentric, occasionally perforated through the disc in age; margin not striate; cuticle separable one-half to two-thirds way to the disc; surface dull, mat, dry or rarely moist, minutely rugulose to smooth, minutely velvety, especially over the disc, initially white, soon developing cream, Cream Color, grayish yellow, grayish buff, or yellowish brown blotches or streaks, often becoming entirely grayish yellow, yellowish brown, or pale brown, Clay Color in age; trama hard when young, soon elastic to brittle, up to 9 mm thick at midradius, white to pale buff, yellowish brown around larval channels, unchanging when cut; odor not distinct; taste mild, fungoid (like *Agaricus campestris* Fr.), occasionally bitter, or with a disagreeable or slightly acrid aftertaste. LAMELLAE subdecurrent to decurrent, close to medium spaced, with many lamellulae of various lengths, often forked or anastomosing, intervenose, subacute in front, up to 5 mm broad at midradius, white when young, soon pale yellow (Romagnesi Ib-IIc), without green coloration; edges even, often developing yellowish brown to brown stains in age, white to dingy yellowish gray, unchanging when cut. STIPE 1.5-4 cm tall, 1-2 cm wide at midpoint, equal or tapered toward the base, with sparse white basal mycelium; surface dull, dry, glabrous, minutely or longitudinally rugulose,



FIGS. 7-10. *Russula angustispora* (GB 548, HOLOTYPE). 7. Cystidia from surface of mycorrhizal mantle of *R. angustispora* + *Pinus virginiaina*. 8. Basidiospores. 9. Dermatocystidia. 10. Hymenial cystidia.

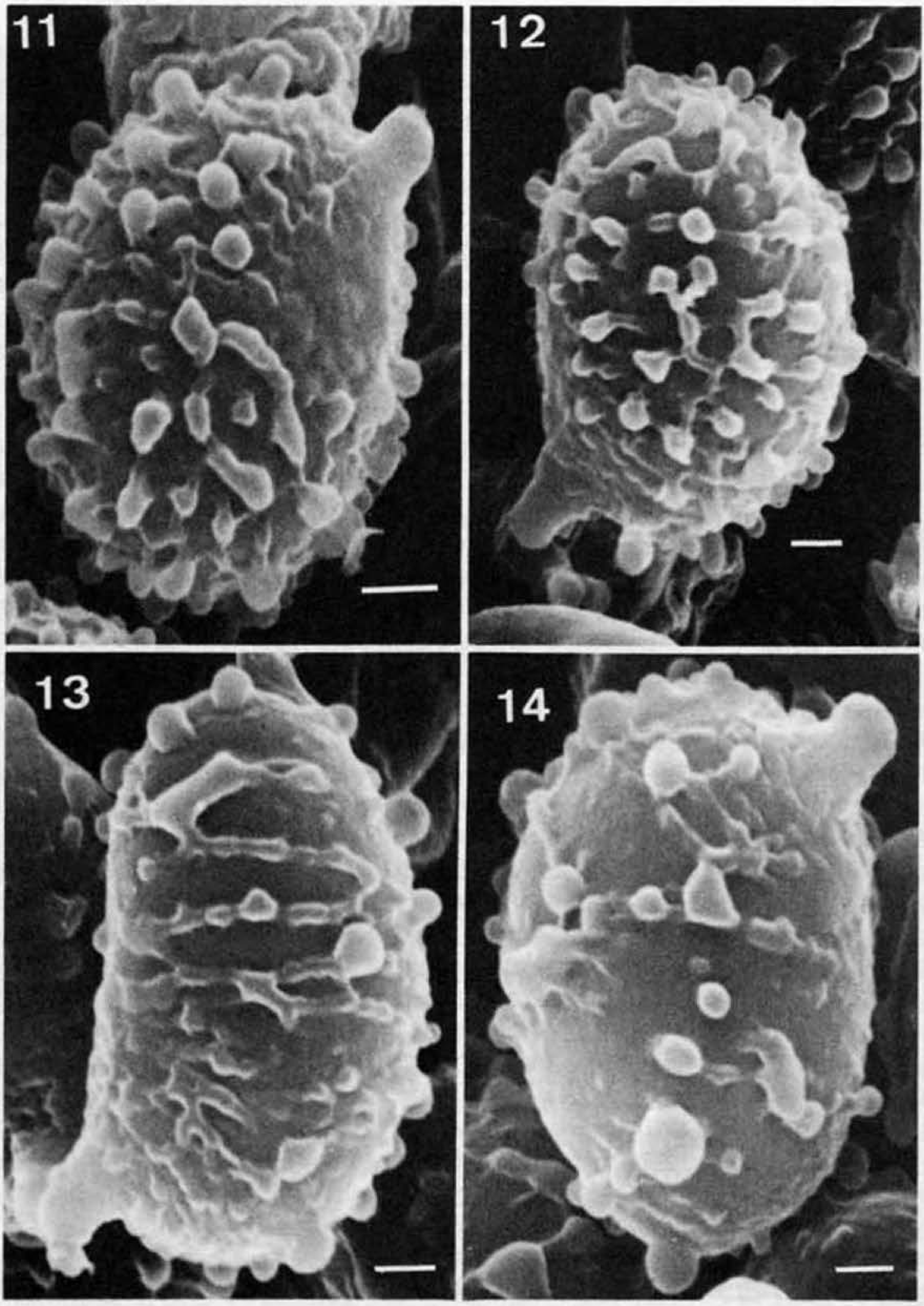
white to dingy yellow or yellowish brown in age, white to dingy yellowish gray, unchanging when cut. CHEMICAL REACTIONS (stipe trama): formalin-no reaction; gum guaiac-greenish blue; $FeSO_4$-pinkish orange; phenol-dull grayish maroon to pinkish maroon; aniline (lamellae)-yellow in 5-10 min.

BASIDIOSPORES yellow (Romagnesi IIb-IIc) in mass on glass, (6-)6.5-8.5(-9) X 4.5-5 µm, elliptical, broadly elliptical, ovate, or rarely obovate; ornamentation partially to completely amyloid, up to 1 µm high, mostly 0.2-0.6 µm high, consisting of subglobose, hemispherical, or cylindrical verrucae, and many fine particles, with a few low lines connecting two or three verrucae or particles, sometimes verrucae or particles fused to form short ridges, forming a partial reticulum at most; suprahilar area slightly depressed or not, usually unornamented, occasionally with a few scattered particles or a low irregular, weakly amyloid patch. BASIDIA 38-50 X 7.5-10.5 µm, clavate to narrowly clavate, 4-sterigmate. HYMENIAL CYSTIDIA 29-85(-120) X 4-8 µm, narrowly clavate, cylindrical, subulate, or ventricose-rostrate, with rounded, acuminate, or submoniliform apices, often curved or flexuous basally, embedded to projecting up 10 µm beyond the basidia, arising from the hymenium, subhymenium, or trama, with weakly to strongly refractive hyaline to pale yellow contents in KOH, greenish purple, grayish purple to blackish purple in SV. SUBHYMENIUM 10-25 µm thick, pseudoparenchymatous. LAMELLAR TRAMA composed of sphaerocysts, connective hyphae, and a few scattered laticifers. PILEUS CUTICLE 95-280 µm thick, without gelatinous materials, a thin to relatively thick layer of interwoven, horizontal hyphae, with rare to scattered dermatocystidia, and scattered laticifers near the pileus trama, with outer hyphae appressed to the surface or ascending, often arranged in parallel strands; cuticular hyphae septate, branched, filamentous or irregularly inflated, 2-8 µm in diam, with round apices, inflated cells up to 15 µm in diam; hyphal walls thin, refringent, or slightly thickened, often irregularly thickened or roughened in outline; dermatocystidia 25-200 X 3-8 µm, cylindrical, with apices rounded, acuminate, or submoniliform, 0-1 septate, partially filled with weakly refractive contents, hyaline in KOH, pale gray to pale purplish gray in SV, arising from cuticular hyphae and laticifers. PILEUS TRAMA consisting of nest of sphaerocysts, connective hyphae, and laticifers; laticifers flexuous, septate, 4-8 µm in diam, with refractive contents, hyaline in KOH, pale purplish gray, greenish purple, or grayish purple in SV. STIPE CUTICLE 15-90 µm thick, without gelatinous materials, consisting of a thin layer of interwoven, horizontal to ascending hyphae and laticifers; surface hyphae often aggregated in parallel strands; cuticular hyphae 2-6 µm in diam, similar to hyphae of pileus cuticle; laticifers 4-6 µm in diam, abundant, with refractive contents, hyaline in KOH, grayish yellow greenish yellow-gray in SV. STIPE TRAMA consisting of nests of sphaerocysts, connective hyphae, and scattered laticifers. CLAMP CONNECTIONS absent from all tissues.

HABIT, HABITAT, AND DISTRIBUTION. Scattered to gregarious on soil or erumpent through needle duff in pure stands of *Pinus virginiana* or mixed stands of *P. virginiana* and hardwoods from late September to December. Presently known from southeastern Maryland to southwestern Virginia, but possibly associated with *P. virginiana* throughout its geographic range.

MATERIAL EXAMINED. USA: MARYLAND: Prince George's Co.: Kettle Run, Occoquan Creek, 11 Nov 1969, K. H. McKnight 11669, Laurel, Forest Disease Lab, 4 Nov 1966, K. H. McKnight 10086, O. K. Miller 4962 & 4963 (VPI). VIRGINIA: Albemarle Co.: Ivy Creek Natural Area, near Charlottesville, 20 Oct 1984, GB 937; Highland Co.: Headwaters, along U.S. 250, 28 Oct 1984, GB 942; Montgomery Co.: near Christiansburg, Rt. 604, 1 Nov 1984, GB 946, Luster's Gate, 28 Nov 1982, GB 557 (coll. R. Vilgalys), Blacksburg, Estes' Farm, 20 Nov 1982, GB 548 (HOLOTYPE, BPI, ISOTYPE, MICH), Blacksburg airport, S. Miller 653 (pers. herb.), Price's Fork Rd., 6 Nov 1984, GB 948.

DISCUSSION. Efforts to determine this taxon using the keys of Shaffer (1964) have proven unsuccessful. Although *R. angustispora* could be confused macroscopically with several taxa of the subsection *Lactarioideae*, the relatively short, narrow, elliptical basidiospores with coarse, blunt, predominately isolated ornamentation are unlike those of any of the taxa treated by Shaffer (1964) or Romagnesi (1967). Spore ornamentation within a single specimen is highly variable, ranging from densely spaced, interconnected verrucae that form a partial reticulum (Fig. 13) to irregularly spaced, isolated verrucae (Fig. 14). In addition to the characteristic basidiospore shape



FIGS. 11–14. Basidiospores of *Russula* spp. (SEM) (standard bar=1 µm). 11. *R. vesicatoria* (GB 916). 12. *R. vesicatoria* (GB 916). 13. *R. angustispora* (GB 548, HOLOTYPE), basidiospore with predominately reticulate ornamentation. 14. *R. angustispora* (GB 548, HOLOTYPE), basidiospore with predominately isolated ornamentation.

and ornamentation, the roughened, slightly thickened or refringent walls of the pileus-cuticle hyphae, and the late-autumn, *Pinus*-associated habitat distinguish *R. angustispora* from similar taxa, e.g. the varieties of *R. brevipes*, *R. inopina* Shaffer, and *R. romagnesiana* Shaffer. Because *R. brevipes* also occurs in these habitats (usually earlier in the season), the spore deposit colors and the microscopic features of the two taxa should always be compared.

Russula angustispora is a constant component of the late-autumn agaric flora of second-growth *P. virginiana* stands and appears to be restricted to these habitats. Ectomycorrhiza formation by *R. angustispora* and *P. virginiana* has been confirmed experimentally (S. Miller and P. Dery, unpublished data). A striking feature of the ectomycorrhizal mantle formed by *R. angustispora* + *P. virginiana* is the abundant cystidia arising from a laticiferous hyphal system on the mantle surface (Fig. 7). These cystidia are similar in morphology and contents to those of the pileus and stipe surface.

ACKNOWLEDGMENTS

Portions of this study were supported by a grant from the Jeffress Mermorial Trust to Dr. O. K. Miller, Jr., V.P.I. & S.U., and a Gertrude S. Burlingham Fellowship from the New York Botanical Garden to the author. Dr. R. L. Shaffer provided critical information on taxa of *Russula* subsection *Lactarioideae*. The loan of specimens is acknowledged from the following herbaria, their curators, and their staffs: BPI, FH, MICH, NY, and VPI. Mr. J. Plaskowitz guided the preparation and photography of materials for SEM. Professor T. MacAdoo of the Foreign Languages Department, V.P.I. & S.U., kindly prepared the Latin diagnosis. Special thanks to Dr. M. E. Palm for her critical reading of the manuscript.

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ACAULOSPORA DELICATA SP. NOV. — AN ENDOMYCORRHIZAL FUNGUS FROM ARIZONA*

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SUMMARY

A newly discovered endomycorrhizal fungus, *Acaulospora delicata,* which forms typical vesicular-arbuscular mycorrhizas with Sudan grass and sorghum, is described and illustrated.

INTRODUCTION

Sand from a greenhouse bed, used for the propagation of cuttings of various ornamental plants, was wet-sieved and the resultant sievings centrifuged in sugar solution (Walker, Mize & McNabb 1982) in order to extract endogonaceous spores. After spores had been extracted, they were suspended in water and observed under a dissecting microscope. Among the spore types present was one we did not recognise. Spores of this type were separated and a representative sample studied on slide mounts under a compound microscope. All these spores proved to be morphologically similar and unlike any described species. We then selected more of these spores and added them to pots of sterilised sand sown with seeds of *Sorghum vulgare* Pers. (sorghum), *S. sudanense* (Piper) Staph. (Sudan grass) and *Lolium perenne* L. (perennial rye grass) in attempts to produce pure pot cultures. These cultures were maintained in a growth chamber with a diurnal temperature range of 15° C to 27° C and illuminated for a 16 hour photoperiod with a mixture of fluorescent and incandescent light.

The plants and their potting medium were examined after 90 days for the presence of mycorrhizas and spores. Perennial ryegrass proved to be ineffective as a host. Vesicular-arbuscular mycorrhizas were observed in the *Sorghum* spp. after clearing and staining the roots (Phillips & Hayman 1970), and abundant spores, all of similar morphology were extracted. The spores were formed laterally on the neck of a sporiferous saccule (Walker, Reed & Sanders 1984), a characteristic of the genus

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Acaulospora Gerd. & Trappe, but were different from those of any other described species in the genus (Gerdemann & Trappe 1974, Trappe 1982, Trappe & Schenck 1982, Schenck *et al* 1984).

The description of wall structures and the murographs (Fig. 1) follow the standardized terminology of Walker (1983). The species description is made from specimens mounted on microscope slides in distilled water or in polyvinyl alcohol lactophenol (PVL), to which stains and reagents had been added as required.

ACAULOSPORA DELICATA Walker, Pfeiffer & Bloss sp. nov. (Fig. 1-3)

Sporae singillatim in terra vel intra radicellas senescentes enatae, lateraliter gestae in sacculo sporifero hyalino 60-95 x 70-125 μm, hyalinae vel flavo-eburneae, ob sporae contentis scintillantes, globosae, subglobosae vel raro ovoideae vel obovoideae, 80-125(-150) x 80-110 (-140) μm. Sporarum tunicae 3-4 in turmis duabus: Turma A cum tunicae hyalinae extimae evanescenti ca. 1 μm crassae (Tunica 1), ad Tunicam 2 adhaerenti; Tunica 2, 2.5-3.5 μm crassa, laminata. Tunicae Turma B cum tunicarum una vel duabus (Tunicae 3 et 4), unaquaeque tenuis, hyalina, membranaceaque. Tunica 3 minute granulosa. Tunicae membranaceae in solutioni Melzeri cinnabarinae.

SPORES borne singly in the soil laterally on the neck of a sporiferous saccule; hyaline to pale yellowish-cream, sparkling from the nature of the spore contents; globose to subglobose (rarely ovoid to obovoid), 80-125(-150) x 80-110(-140) μm. Occasionally spores occurring in the cortical cells of senescent roots (Fig. 3C).

SPORIFEROUS SACCULE (Fig. 2A) usually broader than long, 60-95 x 70-125 μm, hyaline, consisting of the swollen tip of a thin-walled coenocytic hypha, 10-12.5 μm diam, with a single wall 1-2 μm thick. Soil particles and debris often adhering to the exterior of collapsed saccules.

SPORE WALL STRUCTURE of four walls (Walls 1-4) in two groups (Group A and Group B). (See Murograph, Fig. 1A).

WALL GROUP A consisting of a thin, hyaline, outer evanescent wall (Wall 1) approximately 1 μm thick before disintegration, closely attached to Wall 2 which is a relatively thick (2.5-3.5 μm) laminated wall with up to 6 subequal laminations that often are very difficult to observe. Soil particles and debris often adherent to the evanescent outer wall (Wall 1) (Fig. 2C).

WALL GROUP B of two thin, hyaline, membranous walls (Walls 3 & 4), ± 0.5 μm and 0.75-1 μm thick respectively. Wall 3 covered by minute granular excrescences that become increasingly crowded with age and that are difficult to see under the light microscope, but which can be observed readily with the aid of a scanning electron microscope (Fig. 3A, 3B). Membranous walls rapidly turning orange-red in Melzer's reagent. Wall 1 not reacting in this reagent; Wall 2 deepening in colour to become a slightly darker yellow.

ETYMOLOGY: Latin — *delicata,* referring to the rather fragile nature of the spores due to their thin walls.

MYCORRHIZAL ASSOCIATIONS: The species forms typical vesicular-arbuscular mycorrhizas with *Sorghum sudanense* and *S. vulgare* (Fig. 3D).

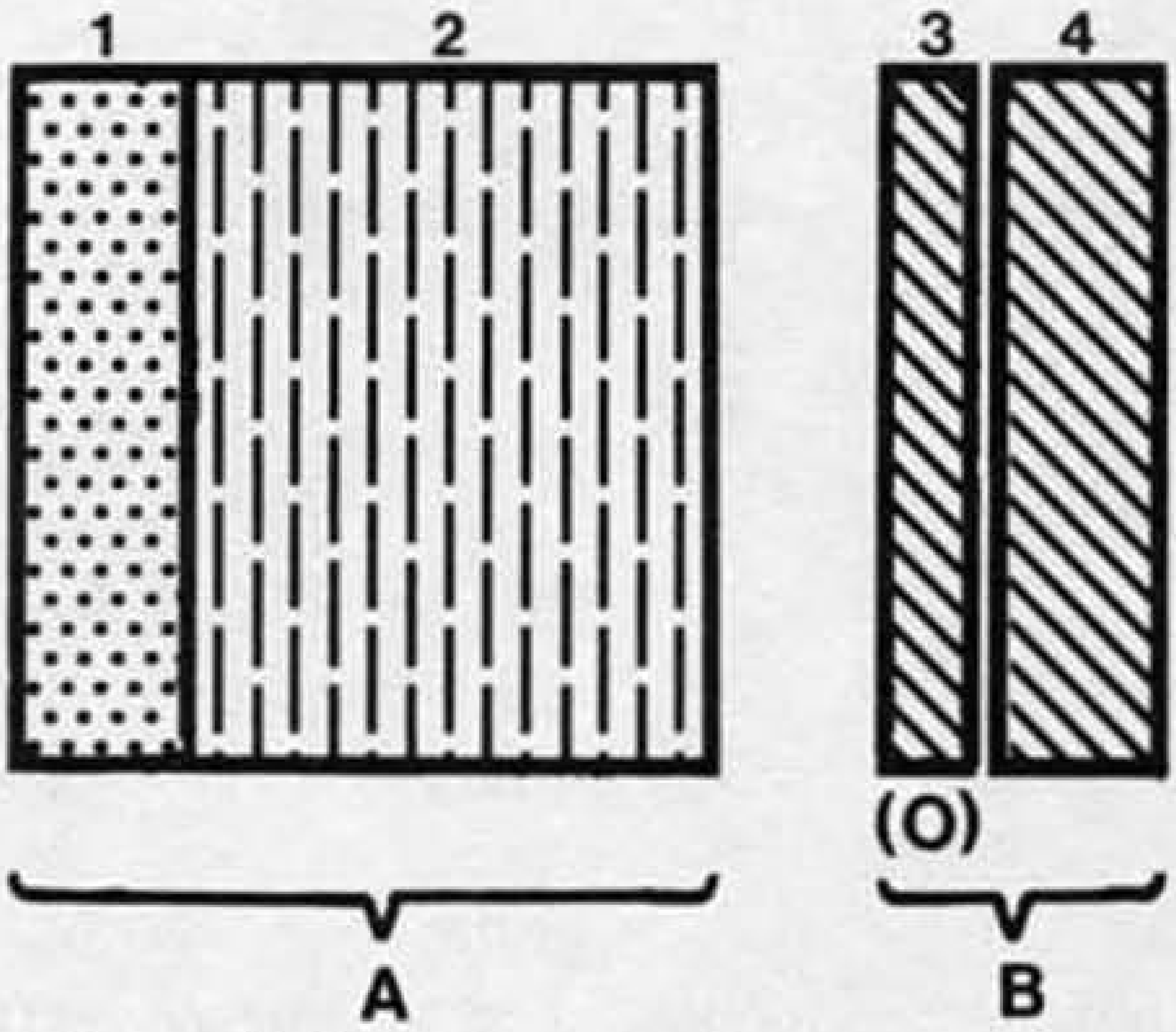

Fig. 1A: ***Acaulospora delicata***

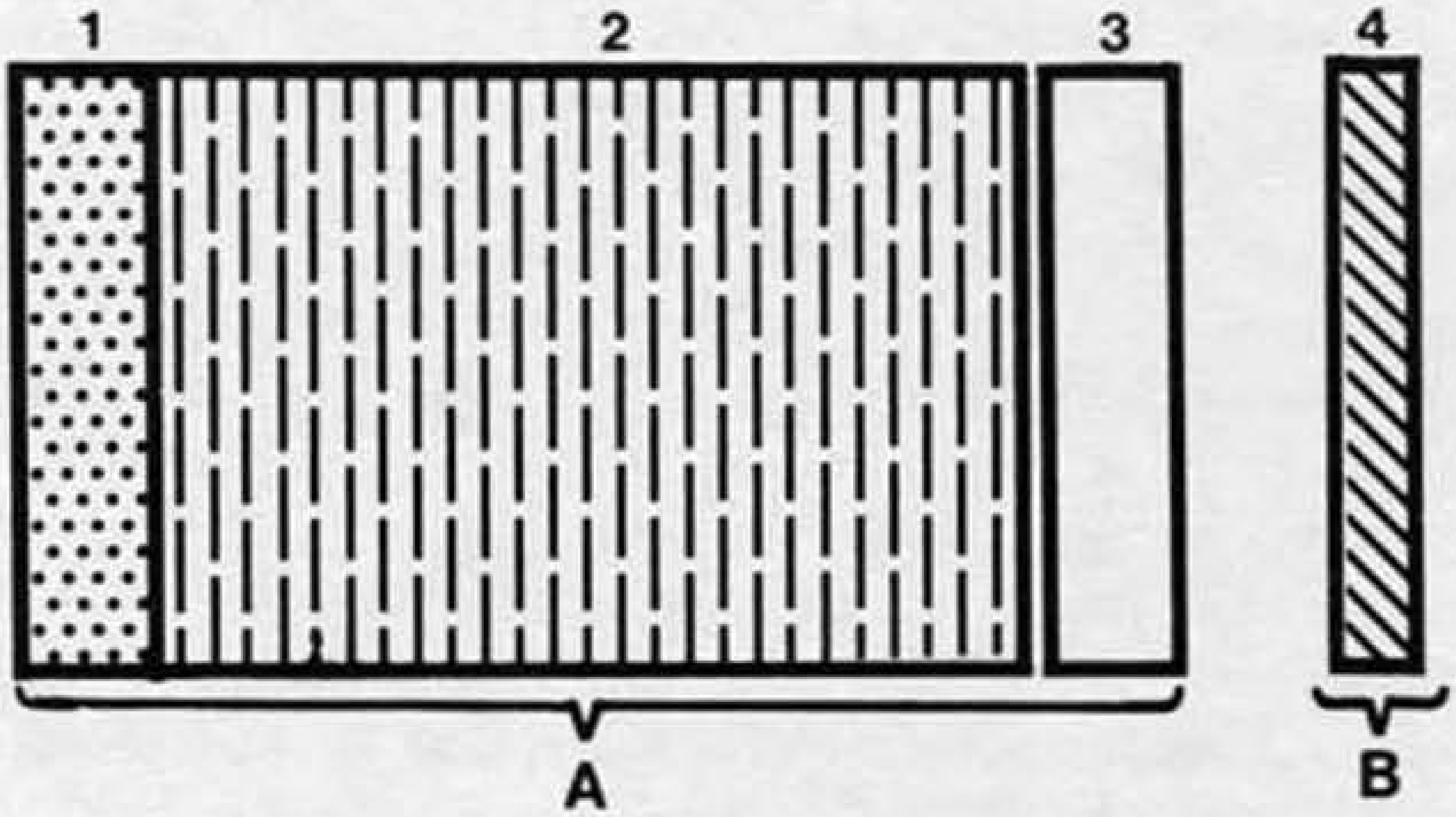

Fig. 1B: ***Acaulospora nicolsonii***

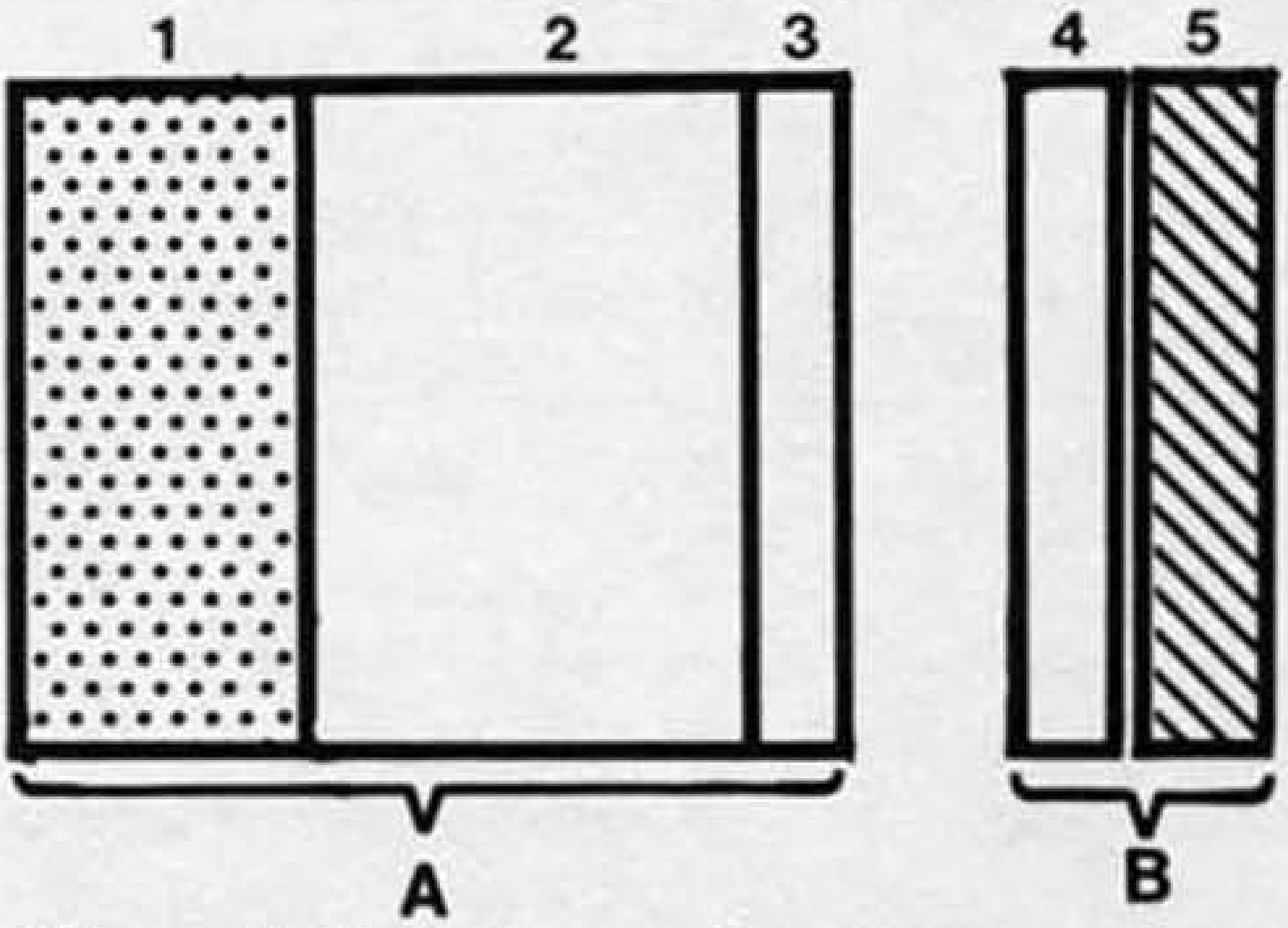

Fig. 1C: ***Acaulospora longula***

FIG. 1 Murographs (after Walker 1983) of *Acaulospora delicata* (Fig. 1A) and two superficially similar species, *A. nicolsonii* (Fig. 1B) and *A. longula* (Fig. 1C). Evanescent walls are shaded with dots, laminated walls with broken lines, membranous walls with diagonal lines, and unit walls are left unshaded. Wall 3 is ornamented, but the ornamentation is often difficult, and sometimes impossible, to observe with a light microscope.

COLLECTIONS EXAMINED

Holotype: ARIZONA - Pima County, Tucson; from a pot culture with S. *sudanense* (OSC, isotype ARIZ, K). The origin of the sand in the green house at the University of Arizona (Building 42-2R) from which the original spores were extracted is unknown.

DISCUSSION

Spores of *Acaulospora delicata* bear a superficial resemblance to those of *A. trappei* Ames & Linderman, *A. nicolsonii* Walker, Reed & Sanders, and *A. longula* Spain & Schenck, but there are differences in the size range and colour of the spores, and in the spore wall structure of the species. The size range of spores of *A. trappei* and *A. delicata* over-lap slightly 42-99 x 42-70 μm in the former compared with 80-150 x 80-140 μm in the latter) but, in general, spores of *A. trappei* are much smaller than those of *A. delicata. A. trappei* is described as having only a single wall, whereas *A. delicata* has a complex wall structure of three or four walls in two groups. There is considerable overlap in the size range of mature spores of *A. nicolsonii,* which are 99-198 X 109-218 μm, and those of *A. delicata,* though most spores of the former are larger than most of the latter. However, the differences in wall structure between these two species is clear, and is illustrated in the murographs (Fig. 1). Wall 1 of both species is evanescent, hyaline, and approximately 1 μm thick, but although Wall 2 is laminated and may be pale yellow in both species, in *A. nicolsonii* the laminae are thicker and much easier to see than in *A. delicata* and the surface of the former fractures to form fissures at maturity, whilst in the latter it remains smooth. Wall 2 is also much thicker in *A. nicolsonii* (3-10 μm) than in *A. delicata* (2.5-3.5 μm). Wall 3 in *A. delicata* is an ornamented, membranous wall in Wall Group B; whereas in *A. nicolsonii* it is a thin, brittle, unit wall in Group A. Occasionally, the inner lamina of Wall 2 in *A. delicata* becomes partially detached and could be mistaken for a separate unit wall, but examination of a number of specimens should resolve the real nature of this artefact. Wall Group B differs between the species. Mature spores of *A. delicata* have two membranous walls one of which becomes increasingly ornamented with age (Fig. 1A); whereas *A. nicolsonii* has only one membranous wall in this group which is

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FIG. 2 Light photomicrographs of spores of *Acaulospora delicata*.

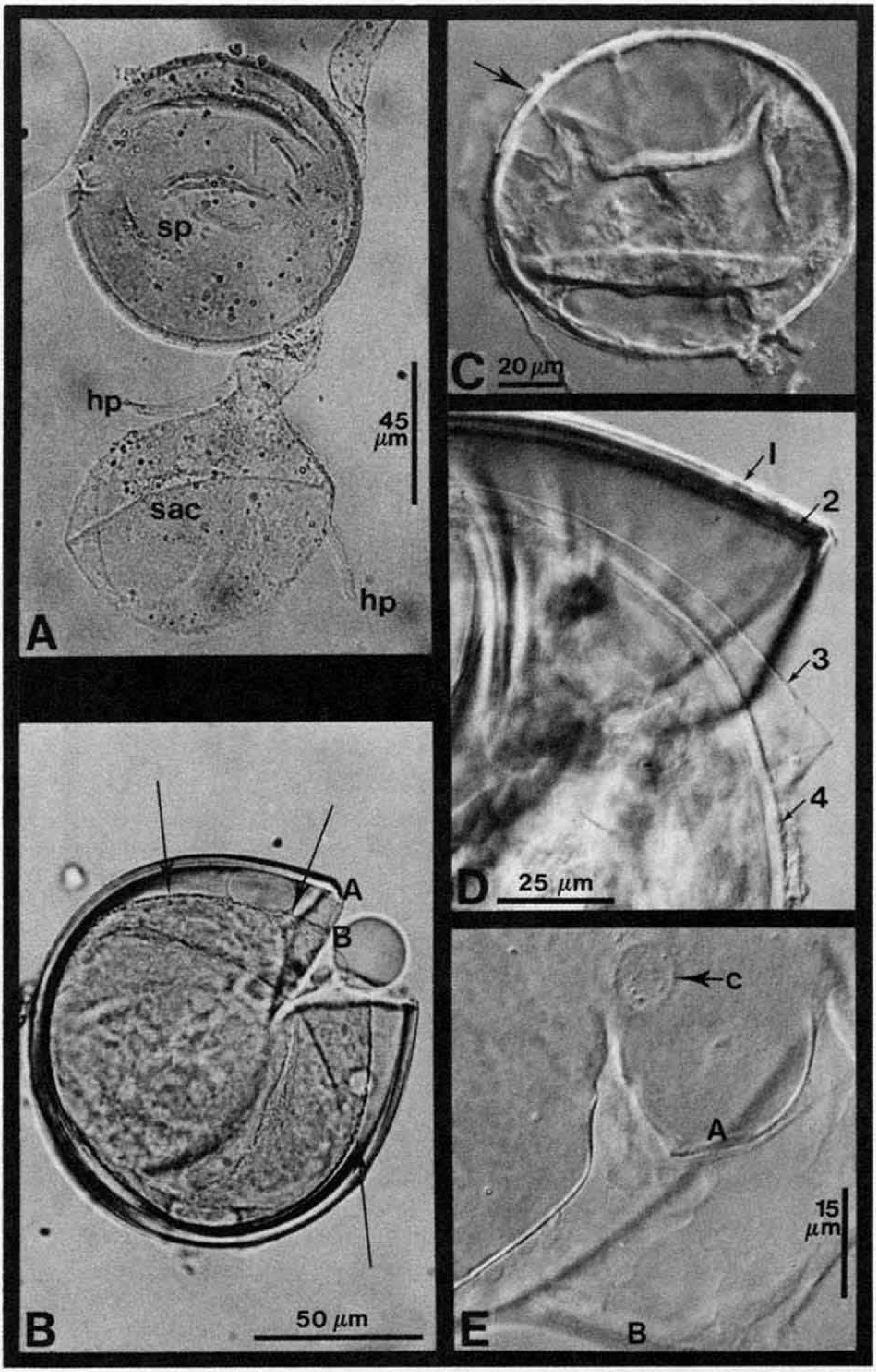
A. Sporiferous saccule (sac) with a fully-formed spore (sp) still attached. The saccule has two of the hyphal protuberances (hp) typical of the genus *Acaulospora*.

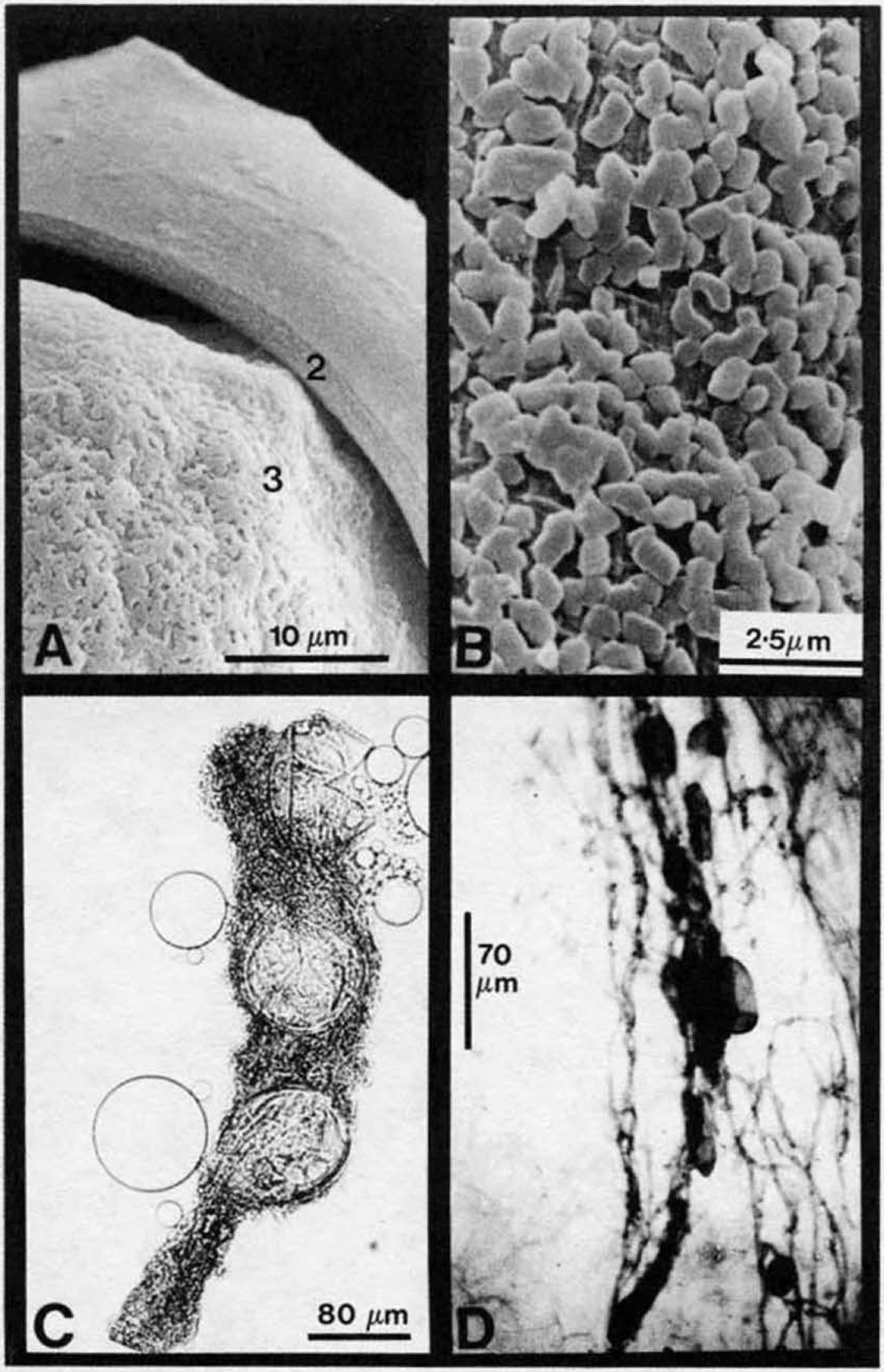
B. A fractured spore, showing the two wall groups (A and B). The ornamentation on wall 3 gives the outer surface of wall group B a finely granular appearance (arrowed).

C. A whole spore mounted in polyvinyl alcohol lactophenol to show the wrinkling of the membranous inner wall group and the debris which typically is adherent to the outer wall (arrowed).

D. In this fractured spore, all four walls (numbered as in the description and murograph) can be seen, though the ornamentation on wall 3 is not evident in this specimen.

E. Surface view of a fractured spore, showing the collar (c) formed in the outer wall group at the point of detachment from the sporiferous saccule. The two wall groups are lettered appropriately (A and B).


sp
hp
sac
hp
A
45 µm
A
B
B
50 µm
C
20 µm
1
2
3
4
D
25 µm
c
A
15 µm
E
B


2
3
A
10 μm
B
2·5μm
C
80 μm
D
70 μm

unadorned (Fig. 1B). Young spores of the former species could be confused with those of the latter, as they may seem to have only a single membranous wall with slight or no ornamentation.

Acaulospora longula spores are similar in size and colour to those of *A. delicata,* but the former has five walls and no ornamented wall in the inner wall group whereas the latter has only four walls, and has ornamentations on Wall 3 in Wall Group B (though this ornamentation may be absent in some specimens (Fig. 2D)). In addition, spores of *A. longula* are formed at distance of 100-200 μm from the sporiferous saccule, whereas spores of *A. delicata* are formed close to the base of the saccule (within 100 μm).

All other described members of the genus *Acaulospora* have either ornamented outer walls or have more deeply coloured spores (brown or yellow), and would be unlikely to be confused with *A. delicata.*

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Fig. 3 *Acaulospora delicata* spores and root-colonization.

A. Scanning electron micrograph (SEM) showing the laminated nature of wall 2 and the ornamentation on wall 3. Wall 1 has broken down and disappeared.

B. Detail of the ornamentation on wall 3 (SEM).

C. Spores formed in a senescent root from a pot culture with *Sorghum sudanense* (brightfield light microscopy).

D. Vesicles and intercellular hyphae of *A. delicata* in the roots of *S. sudanense* stained in cotton blue (brightfield light microscopy).

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BOTRYOHYPOXYLON GEN. NOV. AND ITS ANAMORPH, ILEDON GEN. NOV.

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SUMMARY

Botryohypoxylon amazonense gen. et sp. nov. (Botryosphaeriaceae) and its anamorph, *Iledon versicolor* gen. et sp. nov. are described from dead trees in amazonian Venezuela. *Botryohypoxylon* is apparently unique among loculoascomycetes in having dark unicellular ascospores with an inconspicuous elongated germination site.

INTRODUCTION

In 1984 the senior author collected an ascomycete on newly dead trees in amazonian Venezuela. Perithecia were superficially similar to those of the sordariaceous genera *Bombardia* (Fr.) Karst. and *Bombardioidea* C. Moreau ex Lundqvist (Lundqvist 1972). The asci of this fungus, however, are bitunicate. For the following reasons, we conclude that this species represents an undescribed genus of the Pleosporales, Botryosphaeriacae: 1) ascomata form on a massive, erumpent stroma and are accompanied by 'eustromatic' (*sensu* Sutton 1980) pycnidia with apparent phialides; 2) ascospores are unicellular; 3) asci are clavate and short-stipitate with a thin ectotunica and a thick endotunica (see Eriksson 1981); 4) the hamathecium (Eriksson 1981) comprises rather wide and branched pseudoparaphyses; they lack free ends; the periphyses lining the ostiolar canal are unusual in the Botryosphaeriaceae but are found in other genera of the Pleosporales (e.g. *Cucurbitaria berberidis* Persoon, see Parguey-Leduc 1966); and 5) the habit is lignicolous and possibly parasitic. *Botryohypoxylon amazonense* Samuels & Rogers, gen. et sp. nov., is proposed below.

Botryohypoxylon is unusual among the bitunicate ascomycetes in having dark unicellular ascospores with what we interpret as an inconspicuous elongated germination site. The only species known to us that have somewhat similar characters are *Semidelitschia agasmatica* Cain & Luck-Allen (Cain & Luck-Allen 1969) and *Loculohypoxylon grandineum* (Berk. & Rav.) Barr (Barr 1976). *Semidelitschia*

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agasmatica is coprophilous; its ascomata are ascostromata and its ascospores are surrounded by a gelatinous sheath and have conspicuous germ slits. Ascomata of Loculohypoxylon grandineum are also ascostromata; ascomatal anatomy of this species is very different from that of Botryohypoxylon amazonense and the ascospores have true germ slits. No anamorph has been linked to either S. agasmatica or L. grandineum. These two species are not closely related to each other; neither is closely related to B. amazonense.

The apparent germination site on the ascospore of Botryohypoxylon amazonense is enigmatic. While it appears to be an ill-defined slit resembling those of the Xylariaceae (Beckett 1976 a, b) using brightfield light microscopy, transmission electron microscopy (TEM) does not reveal a break in the inner pigmented wall layers such as seen in Daldinia concentrica (Bolt.: Fr.) Ces. & de Not. (Beckett 1976 a, b). Numerous spores were seen by TEM to have a bulge on the wall which might represent a germination site and that correlates with a lighter colored region visible by light microscopy. However, by scanning electron microscopy (SEM) one sees only obvious invaginations and bulges were not seen. The germ slit of the dormant ascospore of D. concentrica appears, by light microscopy, to be a light colored slit. By SEM this light colored line is actually seen to be a slightly raised fissure covered by the outer wall layer. As germination progresses the spore swells thus causing the rupture of the outer wall layers. At no time is invagination of the wall seen. Instead, the germ fissure continues to widen as the germ tube emerges through it. The invagination on the ascospores of Botryohypoxylon amazonense is an artifact of preparation for SEM, probably a collapsed area in a weak part of the wall--the bulge visible with TEM where germination occurs. Germination of ascospores of two collections of this species was lateral, thus supporting the notion that the light-colored stripe or slit visible by brightfield microscopy is a germination site.

Ascospores of B. amazonense germinated readily on cornmeal agar (Difco) at ca. 20° C. Pycnidia that formed in cultures were morphologically similar to those found in nature but the only pycnidia found in nature were immature or were overmature and devoid of contents. Because of the strong morphological resemblance between pycnidia formed in culture and those formed in nature we believe that the pycnidia from culture do not differ significantly from those from nature and have thus based our description of this anamorph on pycnidia formed in agar culture. The anamorph of Botryohypoxylon amazonense has not previously been described and we propose below Iledon versicolor gen. et sp. nov. Because of its eustromatic pycnidia and phialidic conidiogenesis, the closest morophological comparison is with Macrophomopsis Petrak (see Sutton 1980). Pennycook & Samuels (1985) observed phialidic conidiogenesis in the anamorph of Botryosphaeria dothidea (Moug.: Fr.) Ces. & de Not. and regarded Macrophomopsis as a synonym of Fusicoccum Corda, an anamorph genus that is linked to Botryosphaeria Ces. & de Not. Conidia of Fusicoccum are unicellular and colorless; they are much larger than those of I. versicolor.

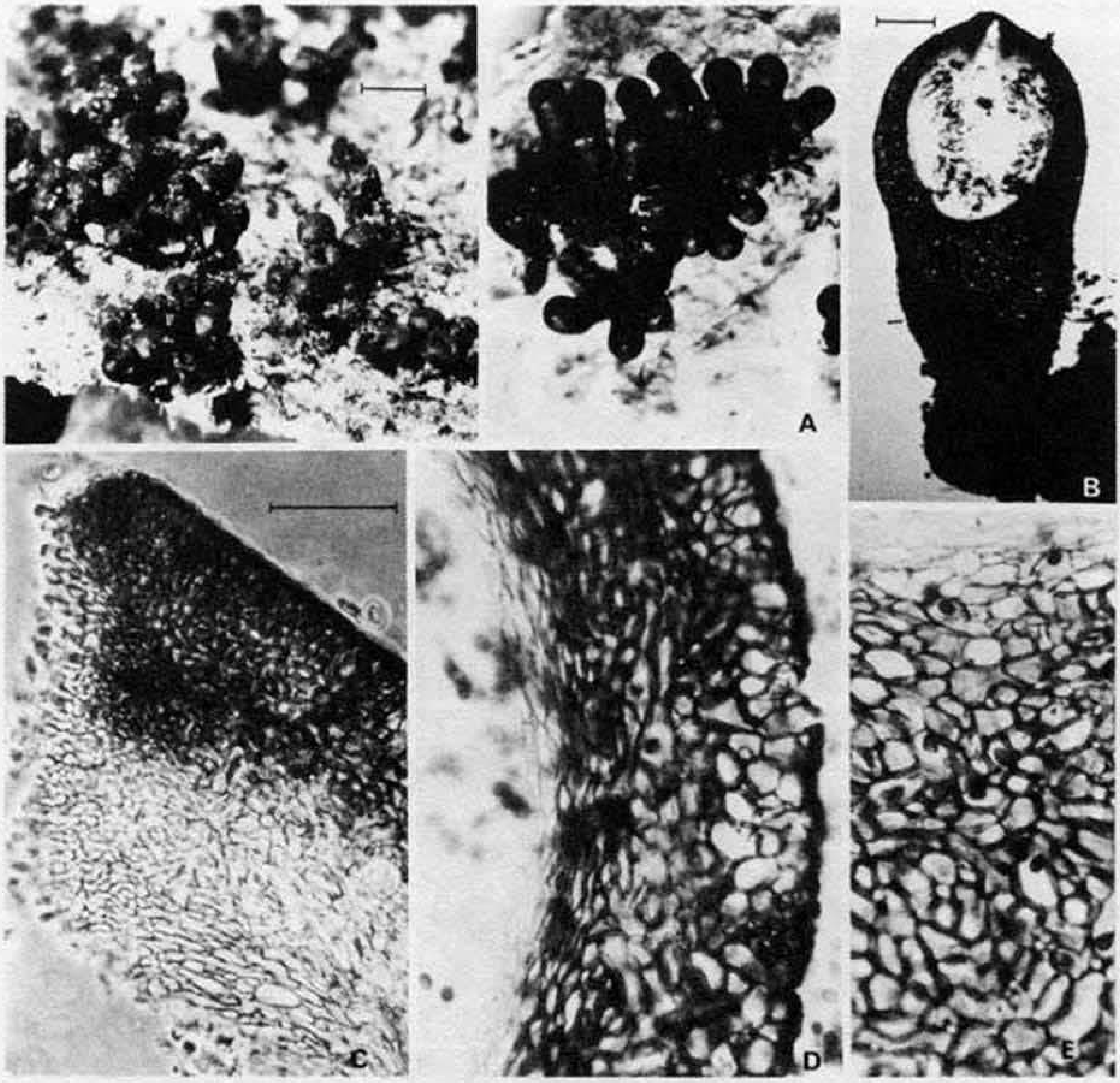

Fig. 1 *Botryohypoxylon amazonense* A: Ascomata. B: Median longitudinal section through a mature ascoma. C: Ascomatal apex with ostiolar canal and periphyses. D: Lateral wall of ascoma. E: Stroma immediately below ascomatal locule. (Lines: A = 1 mm, B = 200µm, C-E = 50 µm).

DESCRIPTION OF *Botryohypoxylon amazonense* AND *Iledon versicolor*

Botryohypoxylon Samuels & J.D. Rogers gen. nov.

Ascomata nigra, conferta, superficialia, sessilia vel stipitata, stromatica. Stroma erumpens, *Botryosphaeria dothidea* similis. Canalis apicalis periphysibus instructis. Asci bitunicati, clavati. Ascosporae unicellulares, brunneae; situs germinationis scissurae similis. Paraphyses filiformes, ramosae, basim et apicem affixae.

Ascomata clustered on a common, erumpent stroma, black, leathery. Asci bitunicate. Ascospores dark brown, unicellular, with an inconspicuous slit-like germination site. Pseudoparaphyses branched and anastomosed.

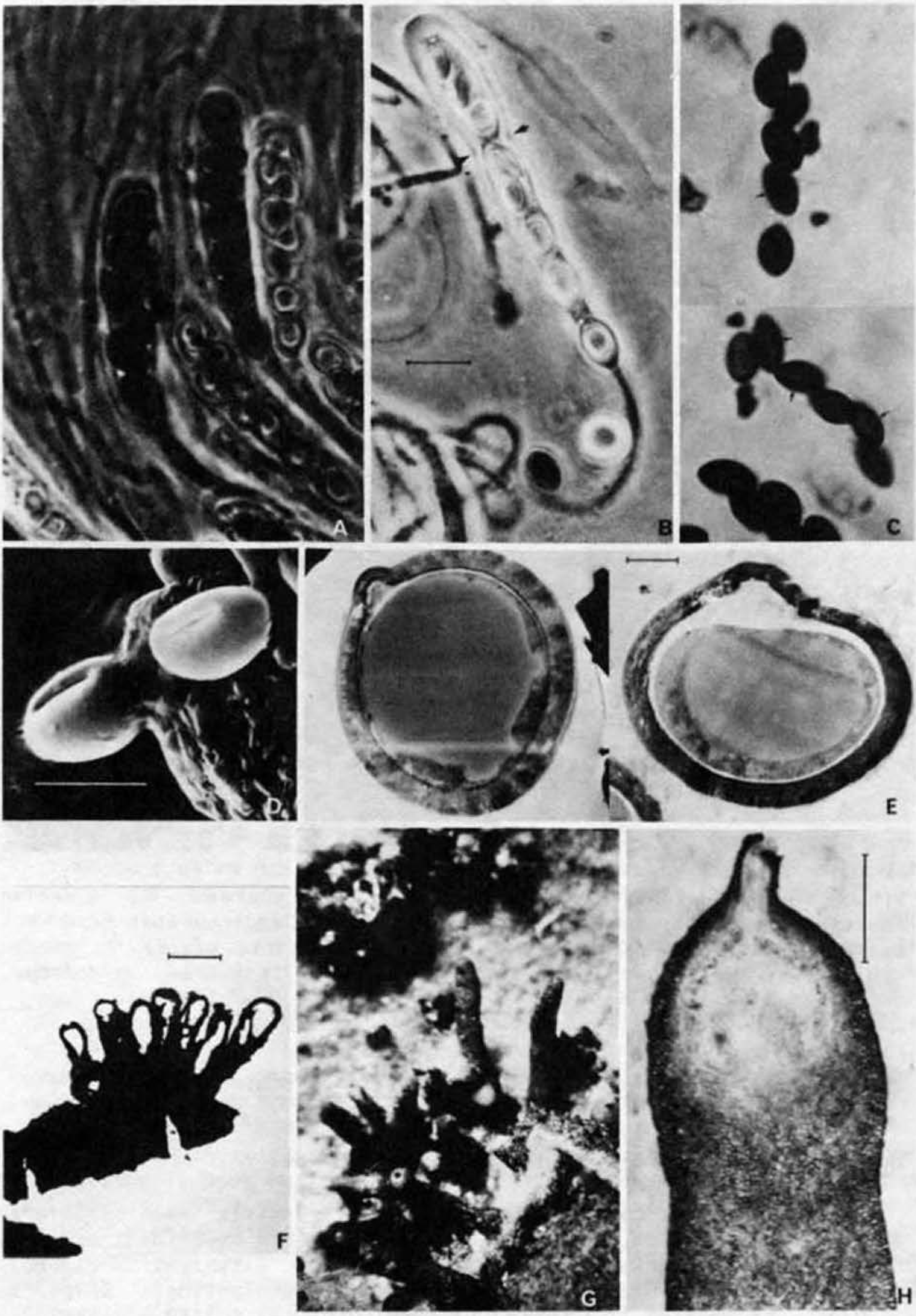

Fig. 2 Botryohypoxylon amazonense A: Asci with branching pseudoparaphyses. B: Dehisced bitunicate ascus, arrow indicates the point of dehiscence. C: Ascospores, arrows indicate spores that have visible germination sites. D: Two ascospores showing slit-like

Etymology of the generic epithet: refers to the botryose ascomata and the somewhat *Hypoxylon*-like ascospores.

Type species: *B. amazonense* Samuels & J.D. Rogers

Botryohypoxylon amazonense Samuels & J.D. Rogers, sp. nov. Figs. 1, 2 A-E, 3 A-C.

Characteribus generibus. Ascomata pyriformia, stipitata. Asci (40-)45-50(-55) x 7-9(-11) µm. Ascosporae (7-)8-9(-10) x 4-5 µm, leves.

Status anamorphosus *Iledon versicolor* Samuels & Rogers

Etymology of the specific epithet: refers to the amazonian region of Venezuela where the type specimen was found.

Iledon Samuels & Rogers, gen. nov.

Stroma erumpens. Pycnidia nigra, conferta, superficialia vel stipitata, uniloculaRia, eustromatica, pyriformia; poris apicalibus instructa. Cellulae conidiogenae phialides; a cellulis parietum pycnidiorum exorientes. Macroconidia et microconidia producta. Macroconidia septata, brunnea vel ad extremitates hyalinia. Microconidia oblongi, hyalinia.

Pycnidia eustromatic clustered on a common stroma, black, opening by a preformed pore, unilocular. Conidiogenous cells phialides, arising directly from the pycnidial wall. Macroconidia ellipsoidal, septate, intercalary cells transparent brown, terminal cells colorless. Microconidia bacillar, unicellular.

Etymology of the generic epithet: *Ile* (Greek): "clustered," refers to the clustered, botryose, nature of the pycnidia.

Iledon versicolor Samuels & J.D. Rogers sp. nov. Figs. 2 F-H, 3 D,E.

Characteribus generibus. Pycnidia pyriformia, sessilia vel stipitata. Phialides cylindricae, 10-12 x 1-2 µm. Macroconidia 9-11 x 4-5 µm, ellipsoideae, (0-)2-septata; cellula mediana brunnea, cellulae terminales hyalines. Microconidia ca. 4 x 1 µm, oblong, hyalinia.

Holotypus: ex cultura Samuels 1710 (GJS 84-532: *Botryohypoxylon amazonense*; VEN, NY).

Status teleomorphosus: *Botryohypoxylon amazonense*.

Etymology of the specific epithet: refers to the macroconidia that have a dark central cell and colorless terminal cells.

germination sites. E: Transverse sections through two ascospores showing a protruding germination site. F: Longitudinal section through several overmature pycnidia formed in nature. G: Columnar pycnidia formed in agar culture. H: Median longitudinal section through a pycnidium formed in culture. (Lines: A-C: 10 µm; D: 5 µm; E: 1 µm; F,G: 1 mm; H: 250 µm).

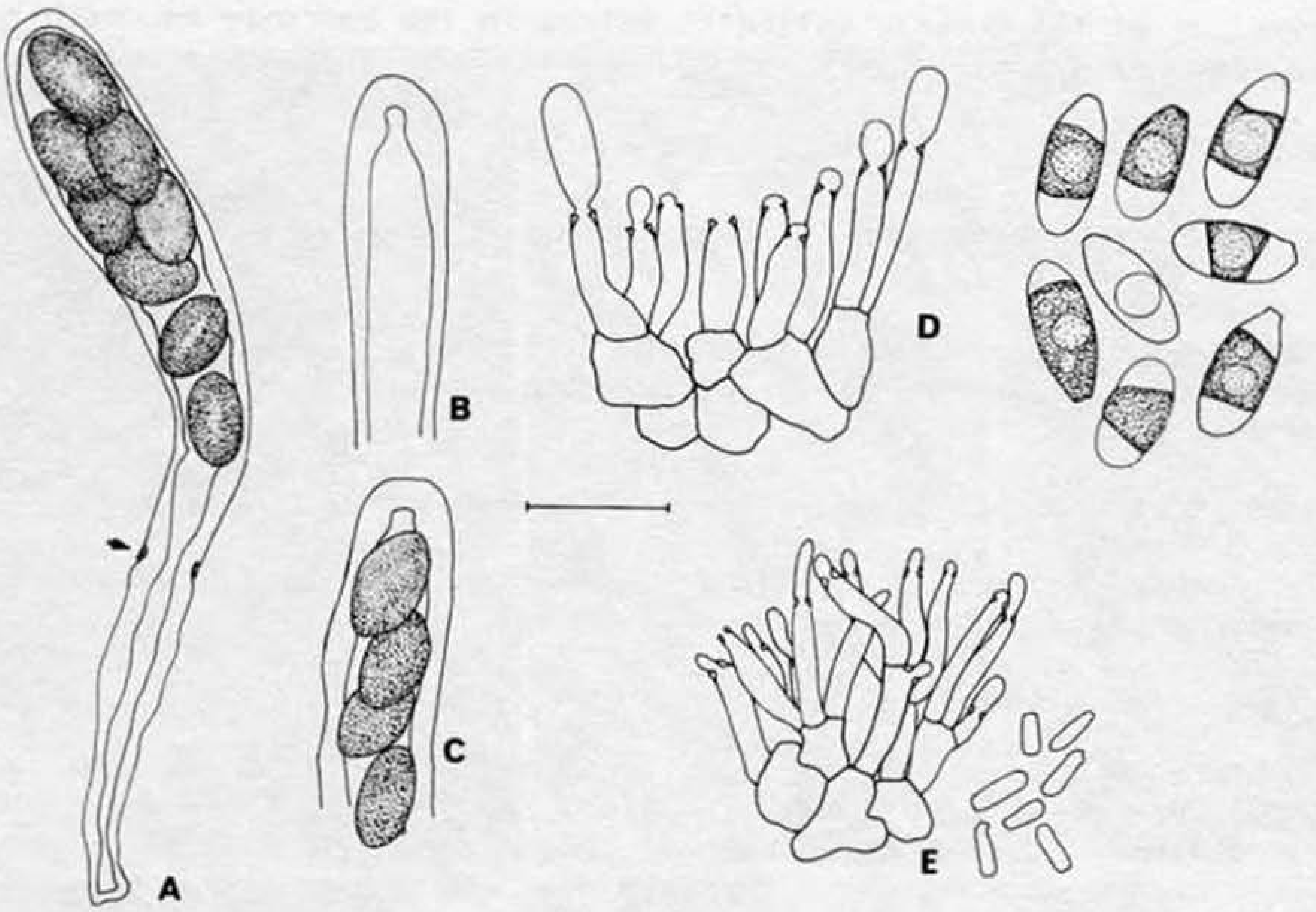

Fig. 3 Botryohypoxylon amazonense A: Dehisced ascus, arrow indicates the point of dehiscence. B: Immature ascus (Congo red). C: Mature, indehisced ascus (Congo red). D: Phialides and macroconidia. E: Phialides and microconidia. (Line = 10 µm).

Stromata subcortical, forming a distinct, thin, black, pseudoparenchymatous layer between cortex and wood with hyphae growing into the wood at scattered points; stromata breaking through the cortex at points and there up to 1 mm thick and composed of angular to circular, 10-30 x 10-15 µm cells with walls unevenly 1.5-4 µm thick, heavily pigmented; cells with long axes oriented perpendicular to the surface of the host. Pycnidia and ascomata arising from the surface of the stroma. Pycnidia with bases remaining immersed in the stroma or seated on a short pedestal, ca. 500 µm wide with locule oblong, 350-400 µm long x ca. 400 µm wide. Individual pycnidia compressed by mutual pressure, opening by a minute apical pore with wall 20-30 µm wide, consisting of angular cells and intertwined hyphae; cells short, ca. 10 x 6 µm. Pycnidia not collapsing when dry. No conidia or conidiogenous cells remain in the two known collections of this species.

Ascomata rarely solitary, more often cespitose in groups of 2-20, individually 600-700 µm diam. with locule ca. 550 µm diam. Each ascoma borne on a cylindrical 1 mm long x 0.5 mm wide pedestal, globose with a minute, acute papilla, only slightly wider than the pedestal, smooth, not collapsing when dry. Ascomatal wall ca. 120 µm thick, with three ± distinct regions. Outer region 25-30 µm wide, composed of cells textura angularis, with long axes perpendicular to the surface of the ascomatal wall, individual cells 5-10 µm in greatest dimension with pigmented walls 1-2 µm thick. Middle region 30-40 µm wide, cells ± textura epidermoidea, walls ca. 3 µm thick, adjacent cells joined by ca. 0.5 µm wide pores. Inner region 10-20 um wide, the cells ± fusoid, 10-20 µm long × ≤ 0.5 um thick, non-pigmented. Ascomatal apex composed of intertwined hyphae with lumens 1-2 µm wide and ca. 3 µm thick and pigmented, with cells at the surface ± textura angularis and continuous with cells of the surface of the wall below; within giving rise to finger-like periphyses, 10-15 × 5 µm, that line the ca. 150 µm long ostiolar canal. Asci (40-)45-50(-55) × 7-9(-11) µm, clavate, ascal cytoplasm abruptly narrowed below the ascospores at the point of dehiscence; bitunicate with thin ectoascus and endoascus rather thick throughout the entire length of the ascus; ascospores biseriate. Asci dehiscing at the midpoint, not bluing in Melzer's reagent and with no ring evident when stained in Congo Red but with conspicuous 'nasse apicale.' Asci forming a hymenium over the entire interior of the ascomatal wall. Ascospores (7-)8-9(-10) × 4-5 µm, unicellular, dark brown, nearly opaque, ellipsoidal, with what is possibly an inconspicuous germination site running the entire length of the spore and parallel to the long axis of the spore. Pseudoparaphyses ca. 2 um wide, forming a network between the asci, copious, branching, often from nodose regions, and anastomosing; free ends not seen.

CHARACTERISTICS IN CULTURE. Colonies grown one month at 20° C in diffuse daylight, on cornmeal dextrose agar (CMD), potato dextrose agar (PDA, Difco) and oatmeal agar (OA, Difco) 1-3 cm diam., faster on PDA than CMD or OA, colonies flat, surface of colony black, with or without scant, cinereous cottony aerial mycelium. Pycnidia forming sporadically on CMD and PDA, arising from a pseudoparenchymatous base, partially immersed and resembling naturally formed pycnidia or individually situated at the tip of a 4 mm long pedestal and then resembling ascomata. Pycnidial wall anatomically similar to naturally formed ascomatal wall, with entire wall of locule lined with conidiogenous cells. Ostiolar opening formed by disarticulation of small, 3-5 µm diam., thin-walled, colorless cells; conidiogenous cells not seen in the ostiolar canal. Macroconidia and microconidia forming within the same locule, the conidiogenous cells nearly identical but with macroconidial cells somewhat broader than microconidial cells. Conidiogenous cells cylindrical, 10-12 × 2-3 µm, tip with obvious periclinal thickening, not flared; arising directly from internal, non-pigmented cells of the pycnidial wall. Macroconidia 9-11 × 4-5µm, (0-)2 septate, ellipsoidal, lacking an obvious basal abscission scar, the central cell olivaceous and the end cells colorless or entire conidium colorless when unicellular. Microconidia ca. 4 × 1µm, oblong to ellipsoidal, unicellular, colorless.

HABITAT. On trunks of young, recently dead trees (? Leguminosae). Known only from type locality.

HOLOTYPE. VENEZUELA: T.F. Amazonas, Cerro de la Neblina, vic. Base Camp, on Rio Mawarinuma, ca. 140 m, 00° 50' N, 66° 10' W, on recently dead tree, Samuels (1703) & Thomas, 30 Apr 1984 (VEN. Isotype: NY).

ADDITIONAL SPECIMEN EXAMINED. Data as holotype, Samuels 1710 (VEN, NY; the dry culture from this specimen is the holotype of Iledon versicolor); second collection, same data, GJS 1669 (VEN, NY).

NOTE. Sessile pycnidia formed in culture were morphologically identical to those found in nature; we did not see stalked pycnidia in nature although they were a conspicuous feature of cultures. The type specimen of *Iledon versicolor* is a dried agar culture.

The forest in the area where the three cited collections of *B. amazonense* were made comprised approximately 60 % leguminaceous trees (A.L. Gentry, pers. comm.) and it is on this basis that we suspect the host of the species to be leguminaceous. Stromata were erumpent through the bark over long distances of the trunks of recently fallen, young trees. For this reason we suspect that *B. amazonense* either contributed to the death of the trees or was at least an early secondary invader.

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NOTES ON HYGROPHORACEAE IX

CAMAROPHYLLOPSIS HERINK, AN OLDER NAME FOR HYGROTRAMA SING.

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SUMMARY

The generic name *Camarophyllopsis* Herink, typified by *C. schulzeri* (Bres.) Herink, has priority over *Hygrotrama* Sing., typified by *H. dennisianum* Sing. Some remarks are made on the delimitation, nomenclature and infrageneric classification of the genus. New combinations are proposed for one subgenus, two sections and nine species.

1. DELIMITATION OF THE GENUS CAMAROPHYLLOPSIS.

Camarophyllopsis Herink, at present better known as *Hygrotrama* Sing., is generally assigned to the *Hygrophoraceae* Lotsy. Until c. 1920 the species belonging there were usually placed in *Hygrophorus* sensu lato. Since ± 1920 an increasing number of authors preferred to split *Hygrophorus* Fr. into 3 genera: *Hygrophorus* Fr. sensu stricto (=*Limacium* Kummer), *Hygrocybe* (Fr.) Kummer and *Cuphophyllus* (Donk) M. Bon (= *Camarophyllus* sensu auct. non Fr., see note 1). The species of *Camaro-*

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1) As Donk (1949, 1962) has pointed out, the name Camarophyllus must be based on Agaricus camarophyllus Fr. (1821) as the type. I agree with his statement that Fries (l.c.) apparently regarded that species as the most representative one of his subtribus Camarophylli. Since it was found later that Agaricus camarophyllus actually belongs to Hygrophorus sensu stricto in view of its bilateral hymenophoral trama, Camarophyllus has become a synonym of Hygrophorus. Many authors do not accept the view of Donk and wish to maintain Camarophyllus for a genus or subgenus for species with irregular hymenophoral trama, typified by Agaricus pratensis Pers.: Fr., e.g. Singer (1975).

Donk (1962) introduced the name Cuphophyllus in the rank of subgenus of Hygrocybe. In my opinion this is still the best taxonomic position (see Arnolds, 1986a). Bon (1984) raised this taxon without any new argument to the rank of genus and proposed 30 new combinations in Cuphophyllus. It should be stressed here that all these names are superfluous (but not illegitimate,ICBN art. 63.3) since Bon (l.c.) incorporated the older genus Aeruginospora Hoehn. (1908) (by Bon erroneously spelled "Aeruginosa") as a subgenus of Cuphophyllus. If Aeruginospora is a synonym of Cuphophyllus, as also suggested by Singer (1975), who made it a section of Camarophyllus,this is the correct name in the rank of genus. For namehunters a lot of new combinations are to be made!

For this moment I cannot judge whether Aeruginospora and Cuphophyllus

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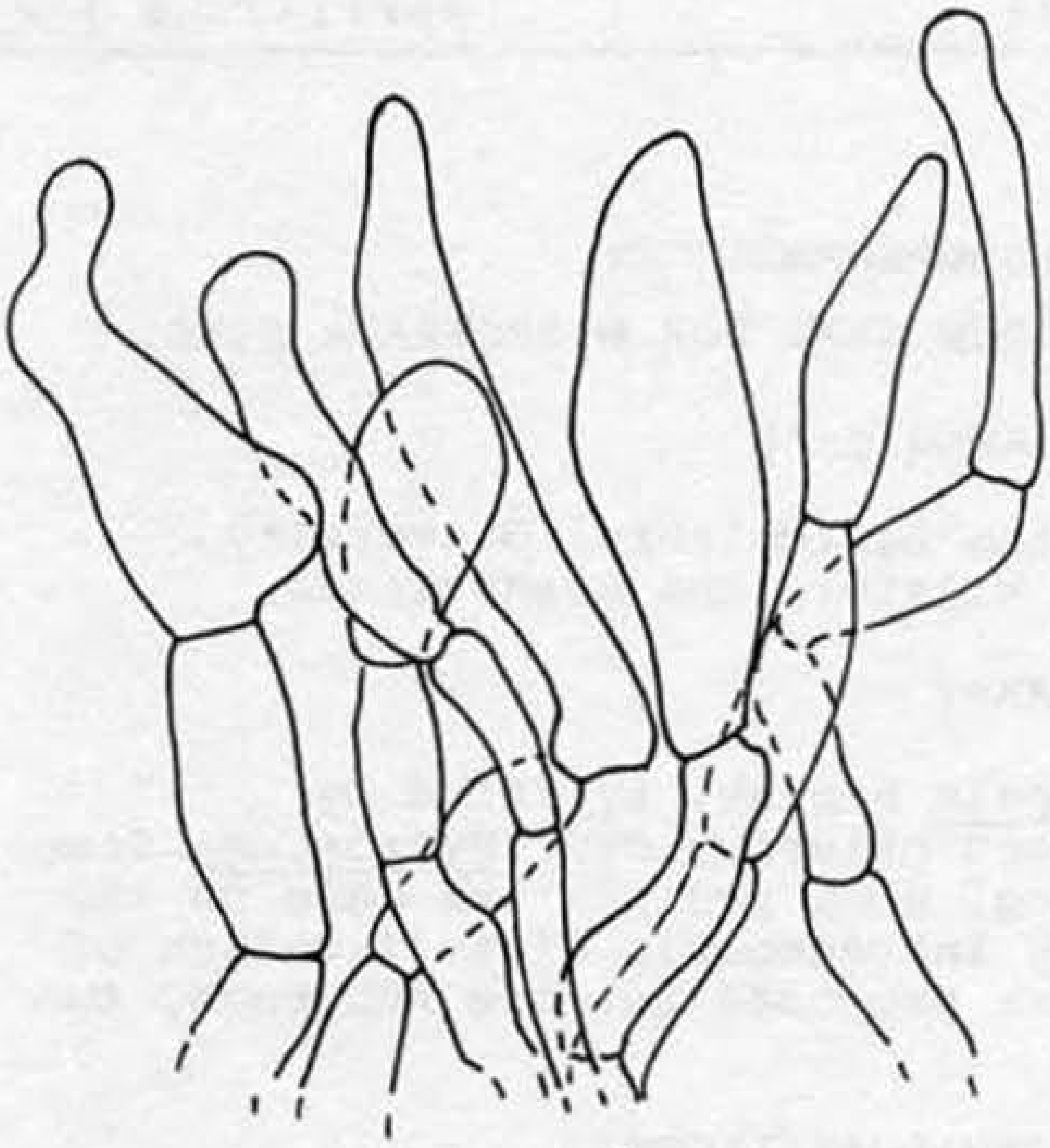
*) Communication No. 295 of the Biological Station Wijster. Communication No.100 of the Department of Plant Ecology of the Agricultural University, Wageningen.



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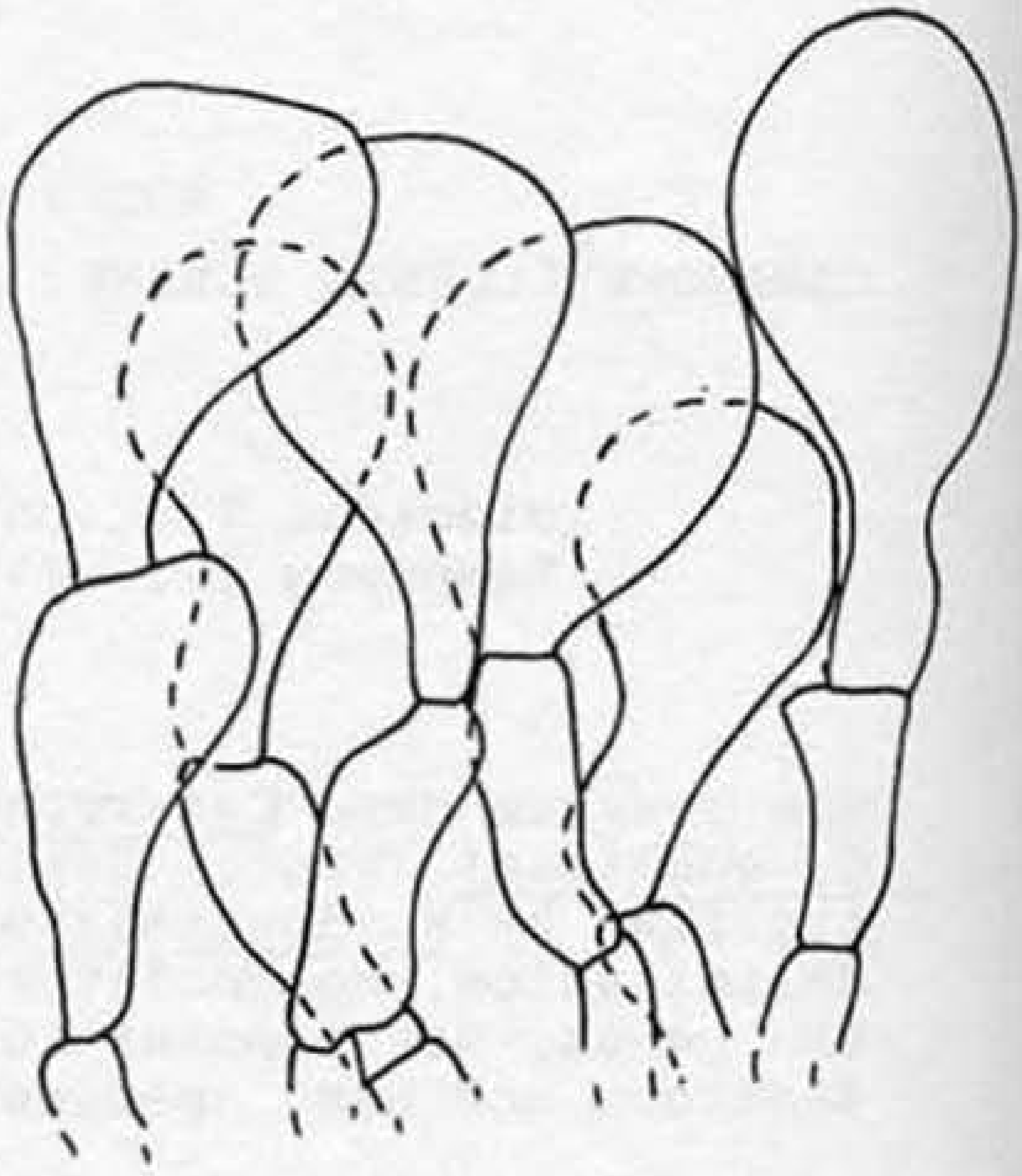

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Fig. 1. Camarophyllopsis schulzeri, radial section of pileipellis, x 850 (from H. Huyzer, 24 Oct. 1980, Herb. Biol. Station Wijster = WBS). - Fig. 2. Camarophyllopsis phaeophylla, radial section of pileipellis, x 850 (from Arnolds 4469, WBS).

phyllopsis were placed then in either Cuphophyllus or Hygrocybe. The group is characterized in macroscopic respect by small basidiocarps with broadly adnate to decurrent lamellae and dull (brown, grey, ochre) colours. The hymenophoral trama is subregular to rather irregular, often intermediate between typical Hygrocybe and Cuphophyllus. The spores are always relatively small, 3-7x2.5-5 µm. Clamps are absent in most species. The pileipellis is, at least in places, either a trichodermium made up of erect hyphae with inflated cells and often cystidiform terminal cells (Fig.1), or a hymeniderm (Fig.2), made up of several layers of strongly inflated, pyriform to globose cells (cf. Singer, 1975: 202; Arnolds, 1986b). These types of pileipellis are not sharply separated. For instance, most authors described the pileipellis of the type species C. schulzeri (Bres.) Herink as a trichodermium with clavate terminal cells (e.g. Herink, 1958: 63; Horak, 1968: 140). However, Moser (1978b: 7, Fig.3) reported that in young basidiocarps the terminal cells are subglobose, (15-25x15-20µm), but not closely packed as in a true hymeniderm.

The structure of the pileipellis is the most important diagnostic character to distinguish Camarophyllopsis from Hygrocybe and Cuphophyllus. Some dull-coloured species in Hygrocybe may have trichodermial tufts near the centre of the

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are really synonyms. Therefore I will use here the name Cuphophyllus only provisionally to indicate the group of species and without recognition as a genus in its own right.

pileus (e.g. *H. nitrata* (Pers.: Fr.) Wünsche), but they always lack subglobose cells in the pileipellis and have another habit: medium-sized to large basidiocarps with non-decurrent lamellae.

Related taxa with small, dull-coloured basidiocarps and small spores were described by Hesler & Smith (1963) in the subsection *Microspori* (A.H. Smith & Hesl.) of Hygrophorus sect. *Camarophyllopsis* Hesl. & A.H. Smith (non *Camarophyllopsis* Herink!) = *Cuphophyllus* (Fr.) M. Bon. In most of these species the pileipellis is a cutis of repent hyphae. Some species with a trichodermal pileipellis, such as *Hygrophorus microsporus* A.H. Smith & Hesl., *H. peckianus* Howe and *H. paupertinus* A.H. Smith & Hesl. have been transfered to Hygrotrama by Singer (1973). I did not study these species myself, but this solution seems to be correct.

Some modern authors treat *Hygrotrama* (= *Camarophyllopsis*) only on infrageneric level: Hesler & Smith (l.c: 96) regard it as a section of *Hygrophorus* and Orton & Watling (1969: 137) as a section of *Hygrocybe*. I agree with Singer (1975) and Kühner (1980), who argue that this group of fungi has a combination of characters sufficient to distinguish it in the rank of genus. This view is shared by e.g. Moser (1978a) and Gulden & Weholt (1984).

2. NOMENCLATURAL CONSIDERATIONS.

Heim (1957: 196) was the first author to distinguish this taxonomic group in the rank of genus. He introduced the name *Hodophilus*, but this name was invalidly published because no latin diagnosis was provided. *Hodophilus* was not validated until Heim published a latin diagnosis in 1966 (:231). Bon (1977:44) claims that *Hodophilus* was validated earlier by Herink in 1958 (: 61). Although Herink mentioned some characters of *Hodophilus* in latin (his complete publication was written in latin) I regard this name only as incidentally mentioned (ICBN art. 34). Moreover Herink (l.c) did not indicate a type species and he enumerated three species, so that his name is definitely invalid (art. 37). Since *H. foetens* was the only species listed in the validating paper by Heim (1966) it is automatically the type of *Hodophilus*.

In 1958 Herink published in a rather obscure journal, officially entitled Sborník Severočeského Muzea (or in latin Acta Musei et Horti bot. Bohemiae borealis), the valid genus name *Camarophyllopsis*, typified by *Hygrophorus schulzeri* Bres.(also only species mentioned). According to Singer (1975: 202) Herink's publication was not published in 1958 - as indicated on the journal but in July 1959. This is probably based on the date of distribution of reprints by Herink. At my request Dr. J. Klán (Prague) checked the date of publication and wrote me that the indicated issue of this journal was officially registered in the State library of Czechoslovakia on October 28, 1958 (nr. 54674734).

The exact date of publication is important since Singer published the name *Hygrotrama* only a few months later; according to his own work the month of effective publication was March 1959. The holotype of *Hygrotrama* is *H. dennisianum* Sing.

A few years later Singer (1962: 189) regarded *Aeruginospora* Hoehn. (1908) as the correct name of this genus. This idea was accepted for example by Moser (1967: 69). Horak (1968: 65) published a detailed analysis of the holotype of the type species, *Aeruginospora singularis* Hoehn. It appears that the pileipellis is made up of erect, but very slender hyphae, without diferentiated terminal cells, only 2-3.5 µm wide, so quite different from the species in *Camarophyllopsis*. Besides the spores posess a characteristic refractive pigment, according to von Höhnel blue under the microscope. On the basis of the structure of the pileipellis *Aeruginospora* was reduced by Singer (1975) to a section of the genus *Camarophyllus* Kummer (= *Cuphophyllus* (Donk) M. Bon).

The conclusion is that three validly published genus names are available, all typified by different species. If these species are considered to belong to one genus (see 3) the name *Camarophyllopsis* has priority.

3. INFRAGENERIC CLASSIFICATION.

The genus can be divided into two groups on the basis of the structure of the pileipellis: one with a trichodermium, the other with a hymeniderm. In the latter group a division can be made into species with and without clamp connections. This classification agrees with the classification proposed by Singer (1975) for *Hygrotrama*. It is remarkable that the type species of each of the genera mentioned before belong to a different section. I propose the following subdivision:

Camarophyllopsis subg. *Camarophyllopsis*
Holotype: *C. schulzeri* (Bres.) Herink

Camarophyllopsis subg. Hygrotrama (Sing.) Arnolds
nov. comb.
Basionym: *Hygrotrama* Sing. in Sydowia 12:221.1959
Holotype: *C. dennisiana* (Sing.) Arnolds

Camarophyllopsis sect. *Hygrotrama* (Sing.) Arnolds
nov. comb.
Basionym: as above
Holotype: as above

Camarophyllopsis sect. *Hodophilus* (R. Heim ex R. Heim) Arnolds
nov. comb.
Basionym: *Hodophilus* R.Heim ex.R. Heim in Revue Mycologie 30:231.1965.
Holotype: *C. foetens* (Phill. in B. & Br.) Arnolds

4. NEW COMBINATIONS FOR SOME SPECIES OF CAMAROPHYLLOPSIS.

New combinations are proposed for species studied by the author himself (marked with *, full descriptions to be published in Arnolds, 1986) and for species undoubtedly belonging here and, judging from their descriptions, deserving the rank of species.

**Camarophyllopsis atropuncta* (Pers.) Arnolds.
nov. comb.
Basionym: *Agaricus atropunctus* Pers.:Syn. Fung.: 353.1801.

Camarophyllopsis dennisiana (Sing.) Arnolds
nov. comb.
Basionym: *Hygrotrama dennisianum* Sing. in Sydowia 12: 221 1959 ("1958").

Camarophyllopsis hiemalis (Sing. & Clemençon) Arnolds *nov. comb.*
Basionym: Aeruginospora hiemalis Sing. & Clemençon in Schweiz. Z. Pilzk. 49: 118. 1971.

*Camarophyllopsis foetens (Phill. in B. & Br.) Arnolds *nov. comb.*
Basionym: Hygrophorus foetens Phill. in B. & Br. in Ann. Mag. nat. Hist., Ser. V (3): 207. 1879.

Camarophyllopsis hymenocephala (A.H. Smith & Hesl.) Arnolds *nov. comb.*
Basionym: Hygrophorus hymenocephalus A.H. Smith & Hesl. in Elisha Mitchell Sci. Soc. Jour. 56: 31. 1940.

*Camarophyllopsis phaeophylla (Romagn.) Arnolds *nov. comb.*
Basionym: Hygrophorus rugulosus var. phaeophyllus Romagn. in Bull. trimest. Soc. mycol. Fr. 86: 874. 1971 ("1970").

*Camarophyllopsis phaeoxantha (Romagn.) Arnolds *nov. comb.*
Basionym: Hygrophorus phaeoxanthus Romagn in Bull. trimest. Soc. mycol. Fr. 86: 873. 1971("1970").

Camarophyllopsis rugulosa (A.H. Smith & Hesl.) Arnolds *nov. comb.*
Basionym: Hygrophorus rugulosus in Sydowia 8: 330. 1954.

Camarophyllopsis subfuscescens (A.H. Smith & Hesl.) Arnolds *nov. comb.*
Basionym: Hygrophorus subfuscescens A.H. Smith & Hesl. in Sydowia 8: 317. 1954.

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OPHIOVALSA IN THE PACIFIC NORTHWEST

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Recently we identified four species of the genus **Ophiovalsa** Petrak (≡ **Cryptospora** Tul. **fide** Petrak, 1965) from the Pacific Northwest for the first time. This paper includes descriptions, illustrations, and a key for **O. betulae, O. femoralis, O. suffusa,** and **O. valsoides** (a new combination), the species presently known to occur there. Further collecting in this region seems likely to uncover additional species.

KEY TO SPECIES OF **OPHIOVALSA** IN THE PACIFIC NORTHWEST

1a. Four spores per ascus; ascospores with minute, hyaline appendages; asci usually indehiscent . . . . **Ophiovalsa valsoides.**

1b. Eight spores per ascus; ascospores lacking appendages; asci dehiscent . . . . 2a.

2a. Stromata with well-developed dark, pseudoparenchymatous region in center; ascospores usually 4-6 µm wide; on **Betula** . . . . **Ophiovalsa betulae.**

2b. Stromata lacking well-developed central pseudoparenchymatous zone; ascospores usually narrower; on **Alnus** . . . . 3a.

3a. Asci usually shorter than 80 µm; asci lacking refractive apical ring; ascospores usually nearly straight,

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femur-shaped . . . . **Ophiovalsa femoralis.**

3b. Asci usually longer than 80 µm; asci with refractive apical ring; ascospores usually curved, cylindrical to filiform, not femur-shaped . . . . **Ophiovalsa suffusa.**

Ophiovalsa betulae (Tul.) Petrak, Figs. 1, 5, 6, 12-18.

Stromata immersed in bark; **ca.** 1.6-2.4 mm diam.; circular to elliptical (Fig. 6); convex to subconic; exterior dark brown to black; ostioles black, circular; with brown region of pseudoparenchyma between perithecial necks (Fig. 5). Perithecia with long, convergent necks; centrum at maturity filled with paraphyses and dehisced asci (Fig. 14); peridia **textura angularis** (Fig. 1); **ca.** 0.5 mm diam. **Asci** clavate (Fig. 12), containing eight spores; dehiscent, with refractive apical rings (Fig. 13), (70-)90-108(-112) X 12-16 µm. **Ascospores** allantoid to long-cylindrical or filiform, usually curved or bent (Figs. 15-18), single-celled, multiguttulate, pale yellow, (12-)24-54(-62) X 4-6 µm.

On branches of **Betula papyrifera.**

This species differs from others in this region in the wider ascospores, and in the well-developed, central pseudoparenchymatous zone in the stroma. Ascospores in this species tend to be quite variable in size.

Specimens examined: IDAHO: D. A. Glawe No. 79-333, 13.X.1979, 2.1 km up Smith Lake Road from Highway 95, 8.1 km N Bonners Ferry, Boundary Co., on **Betula papyrifera** Marsh. D. A. Glawe No. 79-371, 14.X.1979, and D. A. Glawe No. 79-372, 14.X.1979, 3.2 km up Benton Creek Road, Priest River Experimental Forest, Bonner Co., on **Betula papyrifera** Marsh.

Ophiovalsa femoralis (Peck) Petrak, Figs. 2, 7, 8, 19-22.

Stromata immersed in bark; 0.5-1.5 mm diam.; circular to elliptical (Fig. 8); convex to subconic (Fig. 7); ostioles black, circular. Perithecia with long, convergent necks; centrum at maturity filled with dehiscent asci and deliquescent paraphyses; peridia **textura angularis** (Fig. 2); 0.3-0.6 mm diam. **Asci** fusoid to clavate (Fig. 22), containing eight spores, dehiscent, lacking identifiable apical rings (Fig. 19), 60-80(-84) X (11-)12-18 µm. **Ascospores** nearly straight, single-celled, typically femur-shaped but sometimes lacking widened ends (Figs. 20, 21), multiguttulate, pale yellow, (28-)32-48(-52) X (2-)3-4 µm, (3-)4-6 µm wide at ends.

On **Alnus rubra**.

Major distinguishing features of this species are the femur-shaped ascospores, and the asci which lack apical rings. According to Kobayashi (1970) and Barr (1978), ascospores in collections from other regions often are one-septate, but those examined in the present study were aseptate. As Kobayashi (1970) noted, ascospore septation seems to be a variable characteristic in this species.

Specimens examined: OREGON: D. A. Glawe No. 80-225, 8.V.1980, and D. A. Glawe No. 80-233, 8.V.1980, and D. A. Glawe No. 80-245, 8.V.1980, Wildwood Recreational Area, near Sandy, Clackamas Co., on **Alnus rubra** Bong. WASHINGTON: D. A. Glawe No. 79-228, 14.IX.1979, Beacon Rock State Park, Skamania Co., on **Alnus rubra** Bong. J. D. Jensen No. 4/3/82/1, 3.IV.1982, Granite Falls, near Snohomish, Snohomish Co., on dead hardwood.

Ophiovalsa valsoides (Rehm) D. A. Glawe & J. D. Jensen, **comb. nov.**, Figs. 3, 10, 11, 23-27.

≡**Cryptospora suffusa** var. **valsoides** Rehm, **Ann. Mycol.** 4: 76. 1906.

Stromata immersed in bark; 0.8-1.4 mm diam.; circular to elliptical (Fig. 10); convex to subconic (Fig. 11); ostioles black, circular; often with blackened zone beneath perithecia. Perithecia with long convergent necks, the centrum at maturity containing asci intermingled with paraphyses (Fig. 24), peridia **textura epidermoidea** to **textura angularis** (Fig. 3), 0.3-0.45 mm diam. **Asci** cylindrical to clavate (Fig. 23), containing four spores, indehiscent, with refractive apical rings (Fig. 25), (79-)88-112(-115) µm. **Ascospores** variously curved (Fig. 27); (1-)2-4 or more septate; filiform; with **ca.** 1 µm long, hyaline appendage at each end (Fig. 26); multiguttulate; pale yellow; (46-)56-85(-92) X (2-)3-4(-5) µm.

On **Alnus tenuifolia**.

Ascospore appendages are nearly impossible to see with bright-field microscopy, and are best viewed with interference contrast microscopy. Ascospore septa are difficult to see in unstained material, but are easily seen in material mounted in Melzer's solution.

Although Rehm (1906) regarded this as a variety of **C. suffusa**, critical examination of material of both species, and cultural studies, do not support this view. The following differences between the two species were found: **O. valsoides** ascospores are filiform, multiseptate, and have a minute, hyaline appendage at each end, while **O. suffusa** ascospores tend to be cylindrical, single-celled, and lack appendages; **O. valsoides** asci each contain four ascospores and remain attached to the hymenium, while **O. suffusa** asci contain eight ascospores and are dehiscent at maturity; in culture on potato dextrose agar under alternating light and darkness **O. valsoides** forms fertile perithecia while **O. suffusa** does not form the teleomorph. In our opinion these differences make it impossible to view these fungi as conspecific. In fact, one might argue, based on the ascospore appendages, centrum type (**i.e.**, indehiscent asci), and four-spored asci, that **O. valsoides** should be excluded from the genus **Ophiovalsa**, since these features differ from that genus as exemplified by the type, **O. suffusa**. However, because so little information about **Ophiovalsa** is available it seems preferable to retain this fungus in the genus until more conclusive evidence is available.

Specimens examined: AUSTRIA: HOLOTYPE (in S) F. von Hoehnel, (det. H. Rehm), 1902, Niederoesterreich: Wechsel, on **Alnus viridis**, (as **Cryptospora valsoides** Tul. var. **valsoides** Rehm). IDAHO: D. A. Glawe No. 81-16, and No. 85-209, (both coll. M. MacKenzie and D. A. Glawe), 17.X.1980, Dry Fork, Laird Park, Latah Co., on **Alnus tenuifolia** Nutt. J. D. Jensen (Glawe No. 85-214), 14.IX.1983, Laird Park, Latah Co., on **Alnus tenuifolia** Nutt.

Ophiovalsa suffusa (Fr.) Petrak, Figs. 4, 9, 28-32.

Stromata immersed in bark; 0.6-1.6 mm diam.; circular to elliptical (Fig. 9); subconic; ostioles black, circular. Perithecia with long convergent necks; centrum at maturity filled with dehiscent asci; peridia **textura angularis** to **textura epidermoidea** (Fig. 4); 0.3-0.6 mm diam. **Asci** clavate to fusiform (Fig. 28), containing eight spores, dehiscent, with refractive apical rings (Fig. 29), (40-)50-100(-128) X (12-)14-20(-24) µm. **Ascospores** nearly straight to curved (Figs. 30-32), single-celled, cylindrical to filiform, multiguttulate, pale yellow, 34-90(-96) X 3-6 µm.

On **Alnus** species.

See discussion of **O. valsoides** for further comments.

Specimens examined: IDAHO: J. D. Jensen No. 9/10/80/10X (coll. J. D. Jensen, J. D. Rogers, and D. A.

Glawe), 10.IX.1980, near Deception Creek, Kootenai Co., on **Alnus sinuata?** (Regel) Rydb. D. A. Glawe No. 85-213 (coll. J. D. Jensen), 2.IV.1980, Laird Park, Latah Co., on **Alnus tenuifolia** Nutt. J. D. Jensen No. 7/1/80, 1.VII.1980, Alder Meadow, Laird Park, Latah Co., on **Alnus** sp. J. D. Jensen No. 7/2/80/X, 2.VII.1980, Alder bottom, Laird Park, Latah Co., on **Alnus** sp.

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Kobayashi, T. 1970. Taxonomic studies of Japanese Diaporthaceae with special reference to their life-histories. **Bull. Gov. Forest Exp. Sta.** 226: 1-242.

Petrak, F. 1965. Ueber die Gattung **Cryptospora** Tul. **Sydowia** 19: 268-278.

Rehm, H. 1906. Zum Studium der Pyrenomyceten Deutschlands, Deutsch-Oesterreichs und der Schweiz. **Ann. Mycol.** 4: 471-482.

Figure Legends

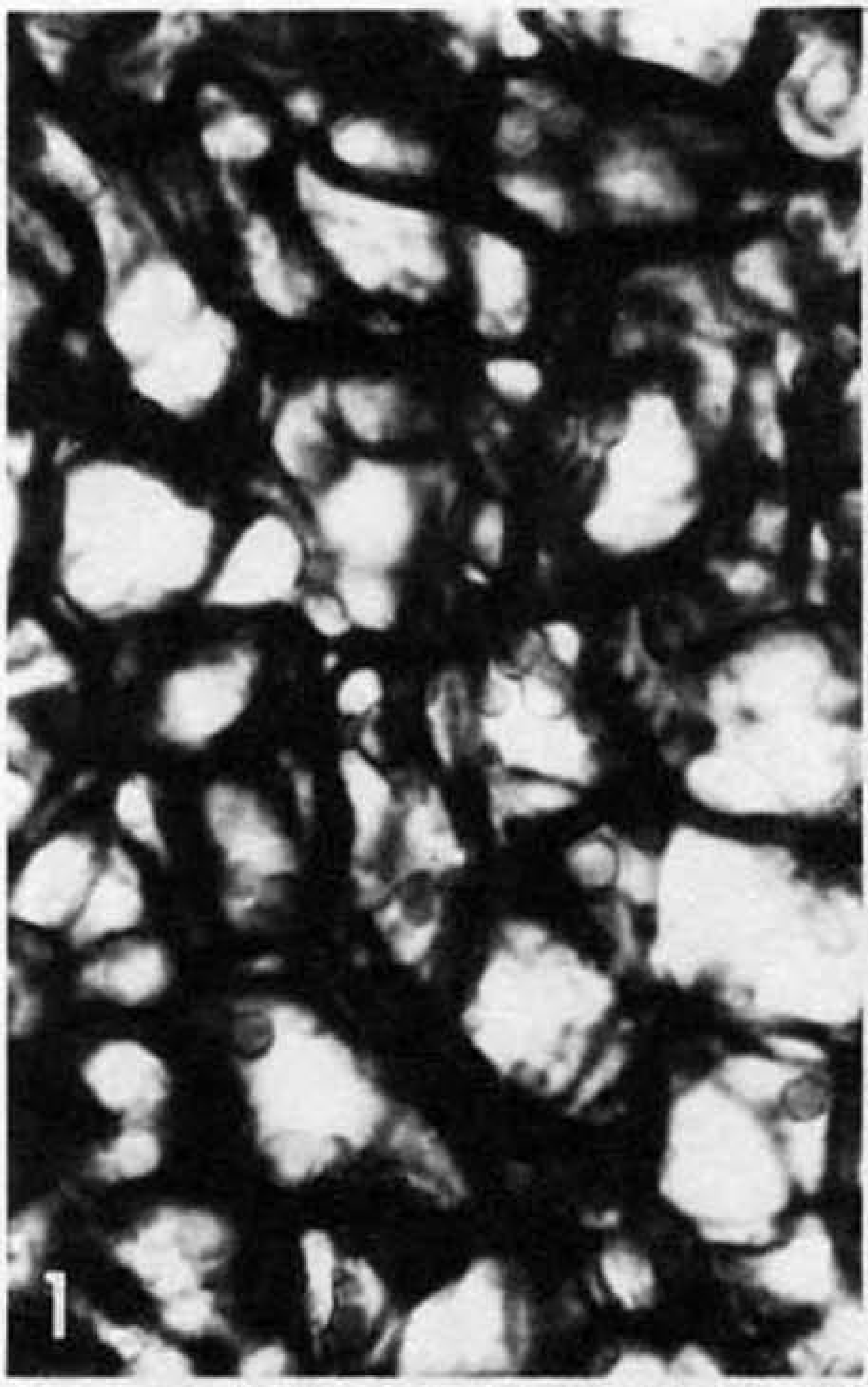
Figs. 1-4. Perithecial peridia of **Ophiovalsa** species. 1. **O. betulae**. 2. **O. femoralis**. 3. **O. valsoides**. 4. **O. suffusa**. All X1000.

Figs. 5-11. Perithecial stromata of **Ophiovalsa** species. 5, 6. **O. betulae**. 5. Longitudinal section showing perithecium (arrow) and central pseudoparenchyma (P). 6. Surface. 7, 8. **O. femoralis**. 7. Longitudinal section. 8. Cross section. 9. **O. suffusa**, cross section, arrow designates ostiolar disc of adjacent stroma. 10, 11. **O. valsoides**. 10. Cross section, surface view of adjacent stroma. 11. Longitudinal sections of stromata. Figs. 6, 8-10 X10. Fig. 5 X30. Fig. 7 X20. Fig. 11 X8.

Figs. 12-21. **Ophiovalsa betulae** and **O. femoralis.** 12-18. **O. betulae.** 12. Ascus. 13. Apical region of ascus, with refractive ring (arrow). 14. Centrum material, including paraphyses (arrow). 15-18. Ascospores. 19-21. **O. femoralis.** 19. Apical region of ascus. Note absence of apical ring. 20, 21. Ascospores. Figs. 12, 15-18, 20, 21 X1000. Figs. 13, 19 X2500. Fig. 14 X250.

Figs. 22-27. **O. femoralis** and **O. valsoides.** 22. **O. femoralis.** Ascus. 23-27. **O. valsoides.** 23. Asci. 24. Centrum material including paraphyses (arrow) and asci. 25. Apical regions of asci, each with refractive ring (arrows). 26. End of ascospore with appendage (arrow). 27. Ascospore. Figs. 22, 23, 27 X1000. Figs. 25, 26 X2500. Fig. 24 X250.

Figs. 28-32. **Ophiovalsa suffusa.** 28. Ascus. 29. Apical region of ascus with refractive ring (arrow). 30. End of ascospore. Note lack of appendage. 31, 32. Ascospores. Figs. 28, 31, 32 X1000. Figs. 29, 30 X2500.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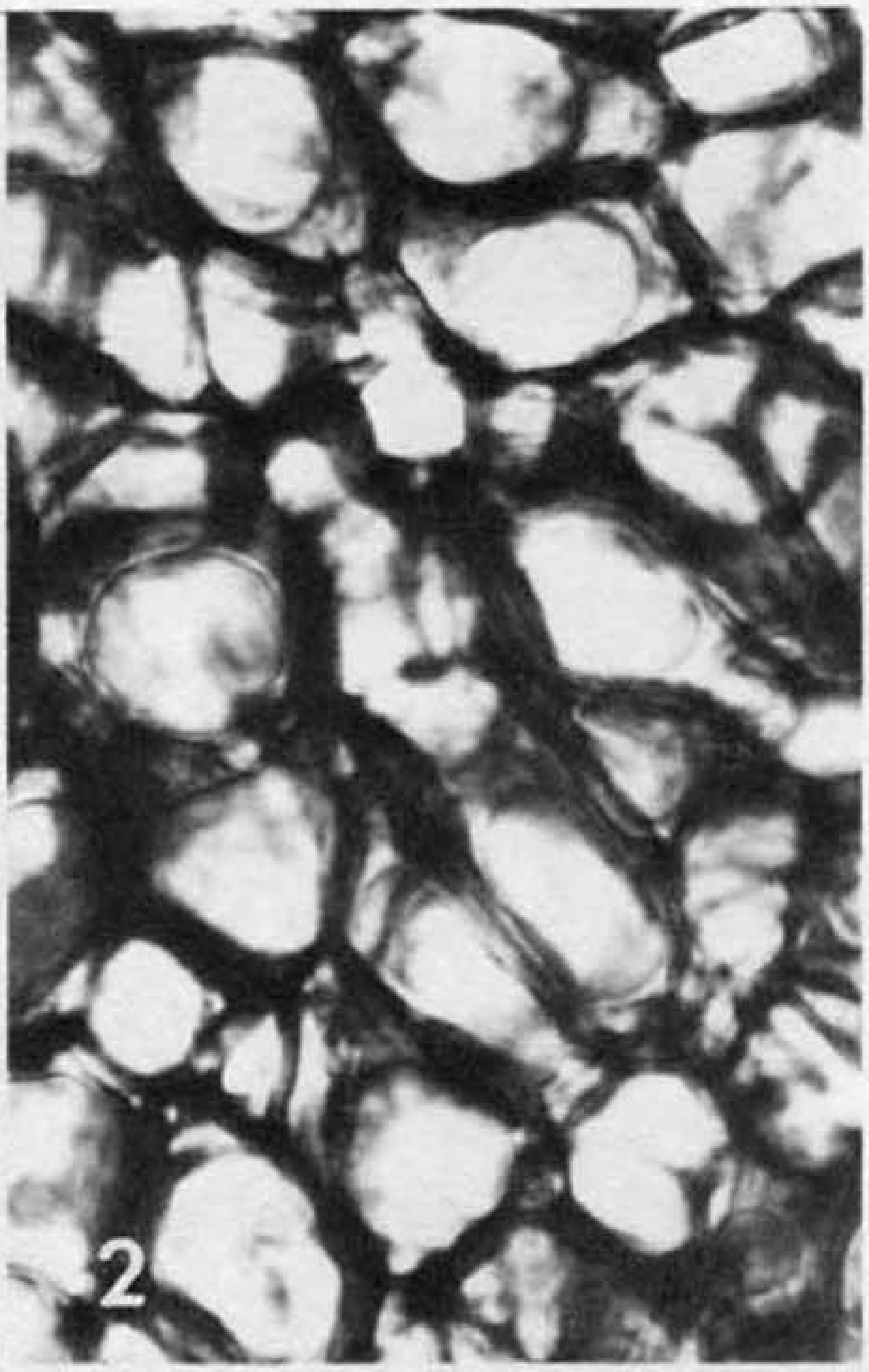
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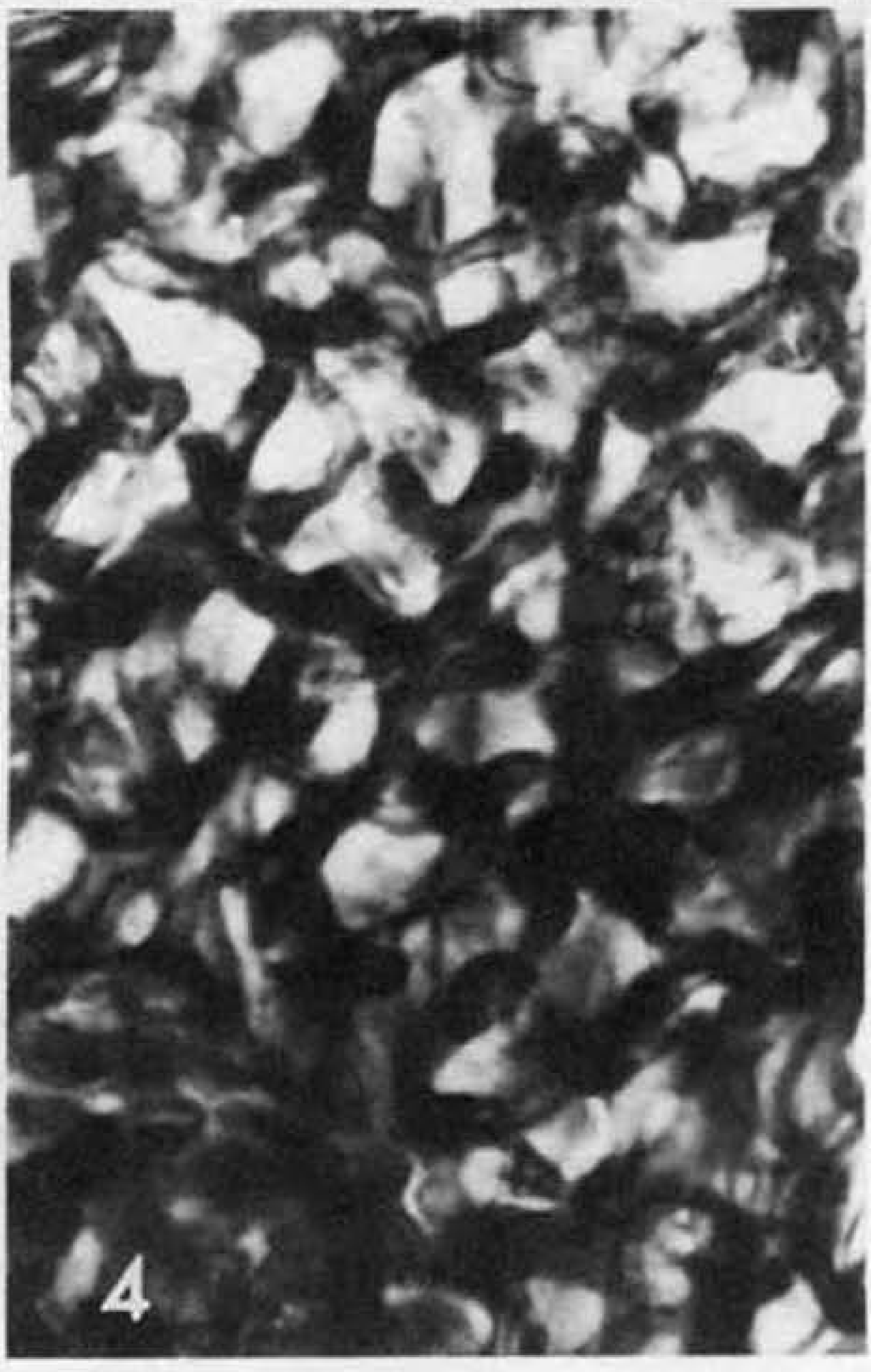
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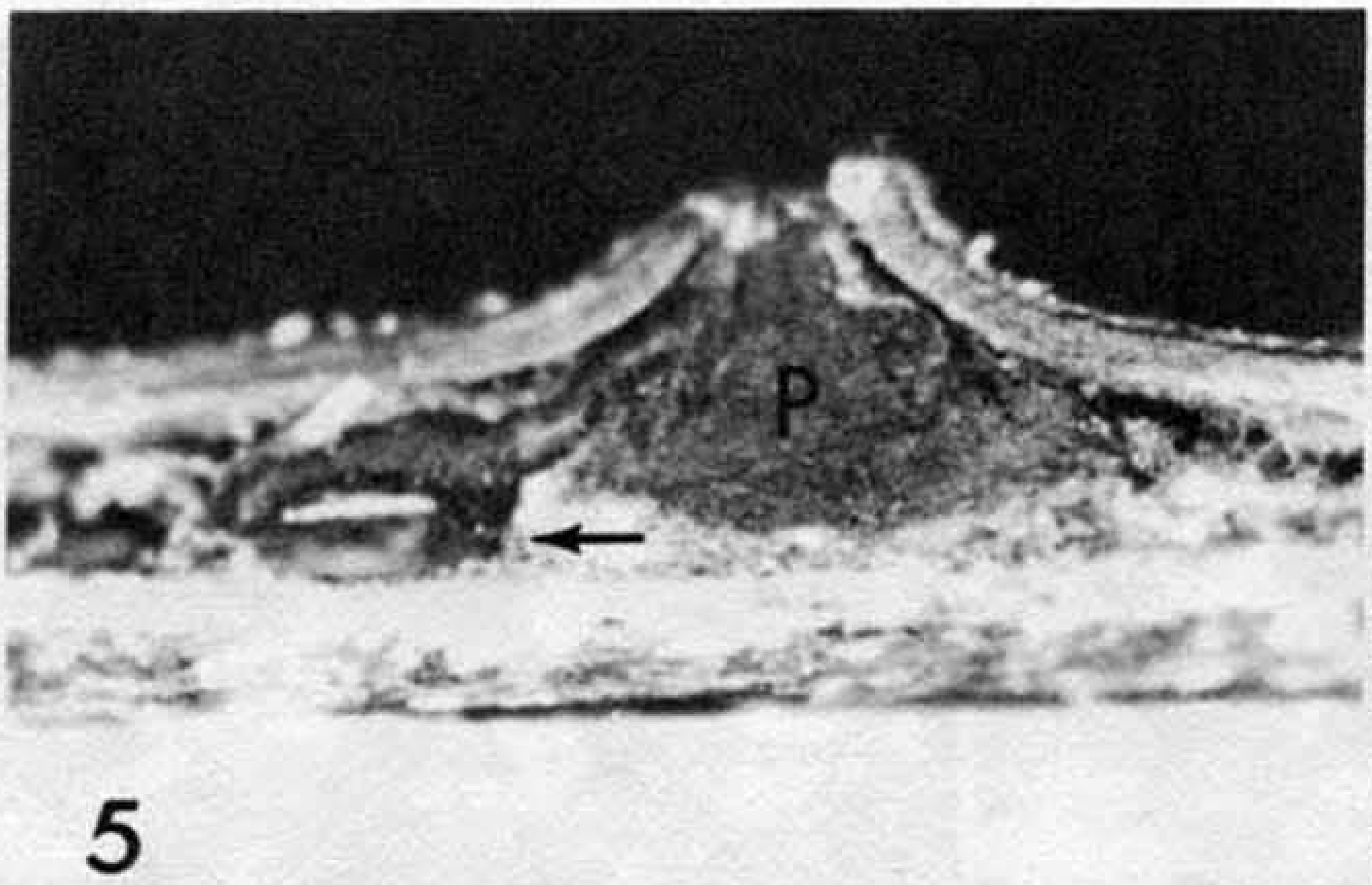

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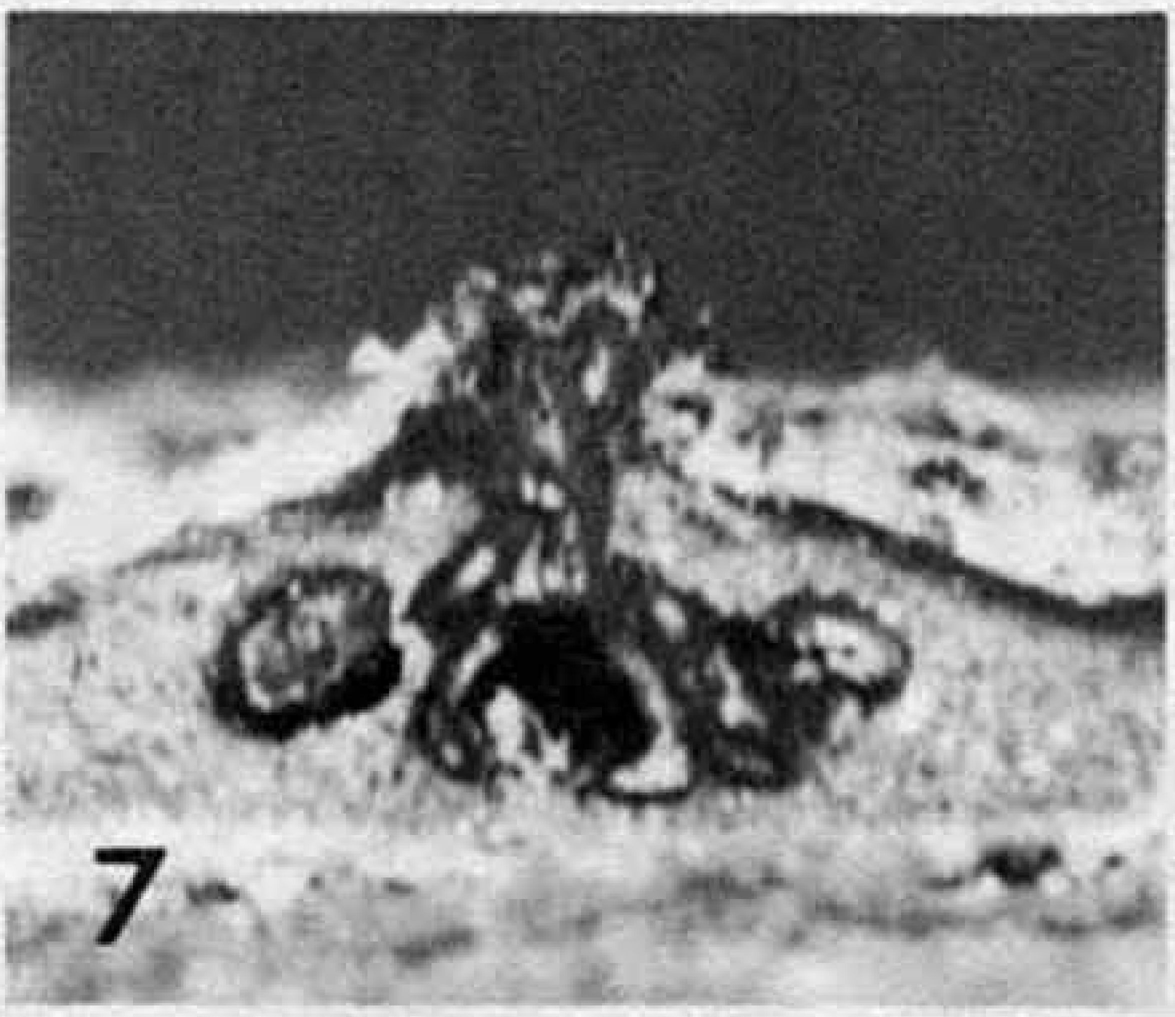

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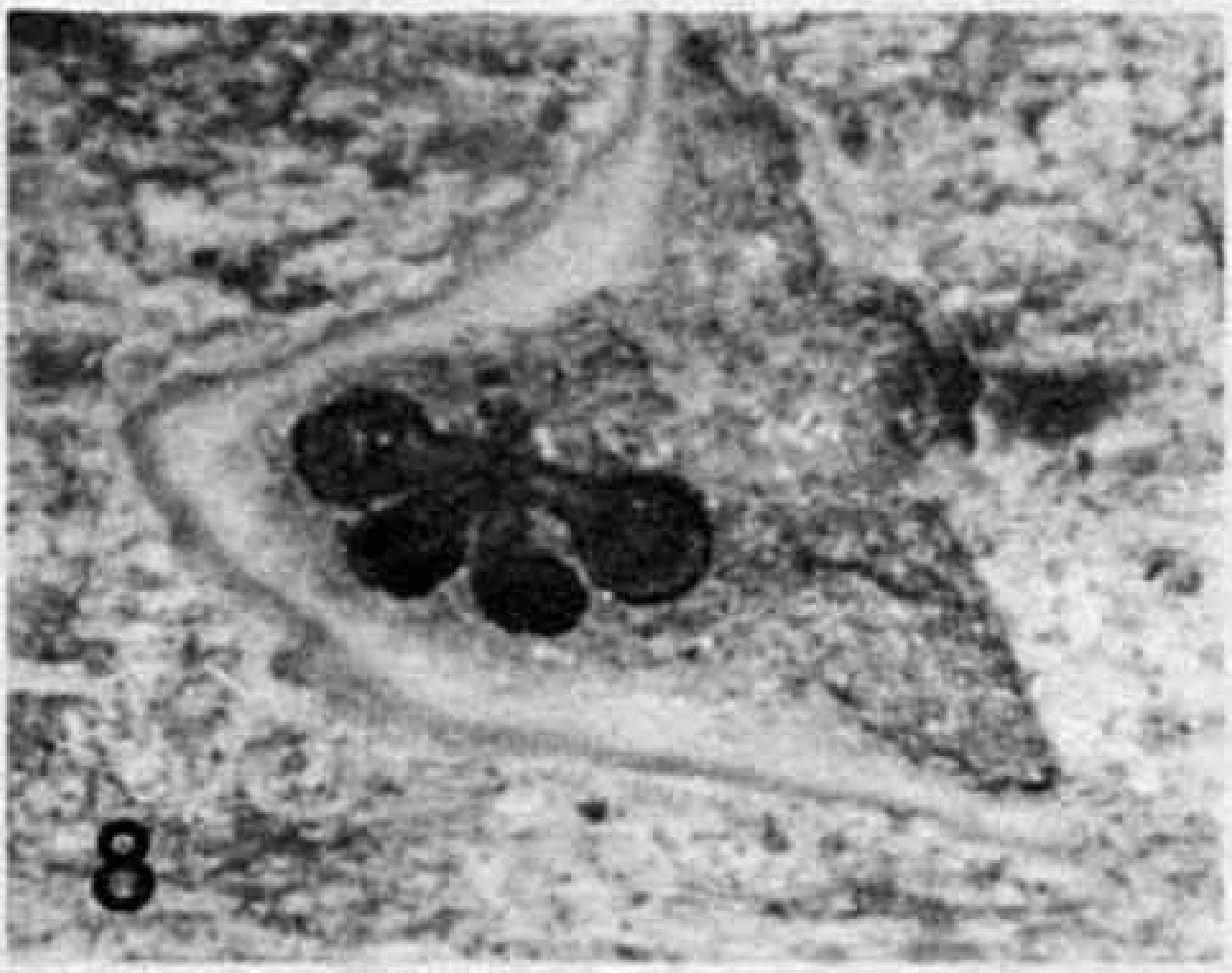

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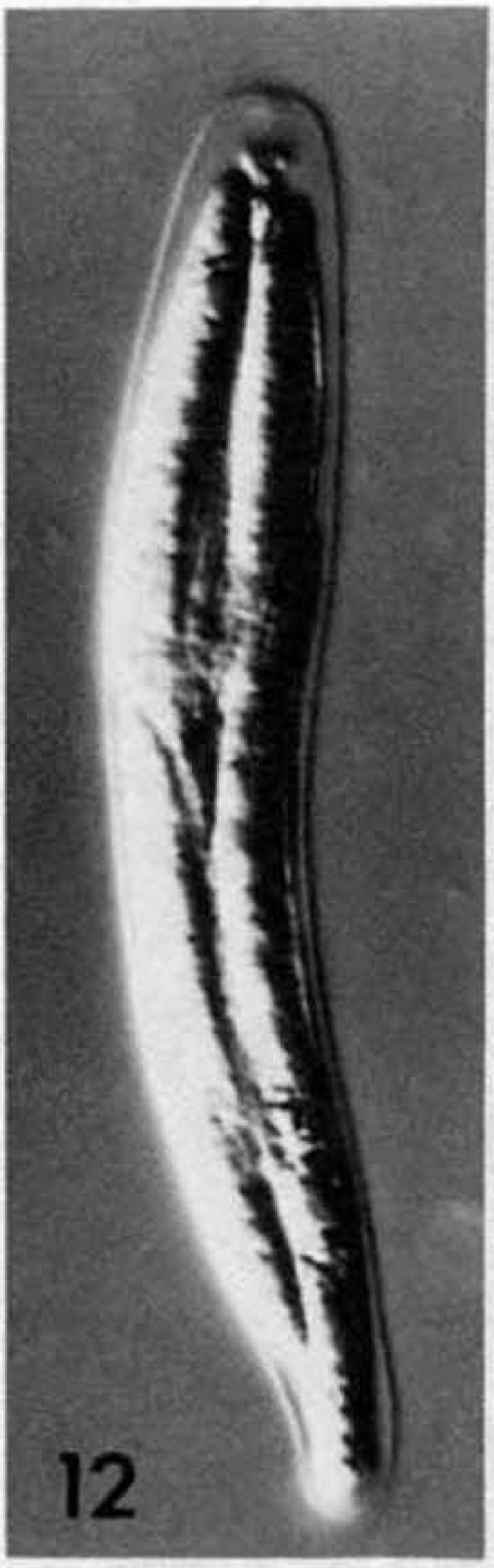
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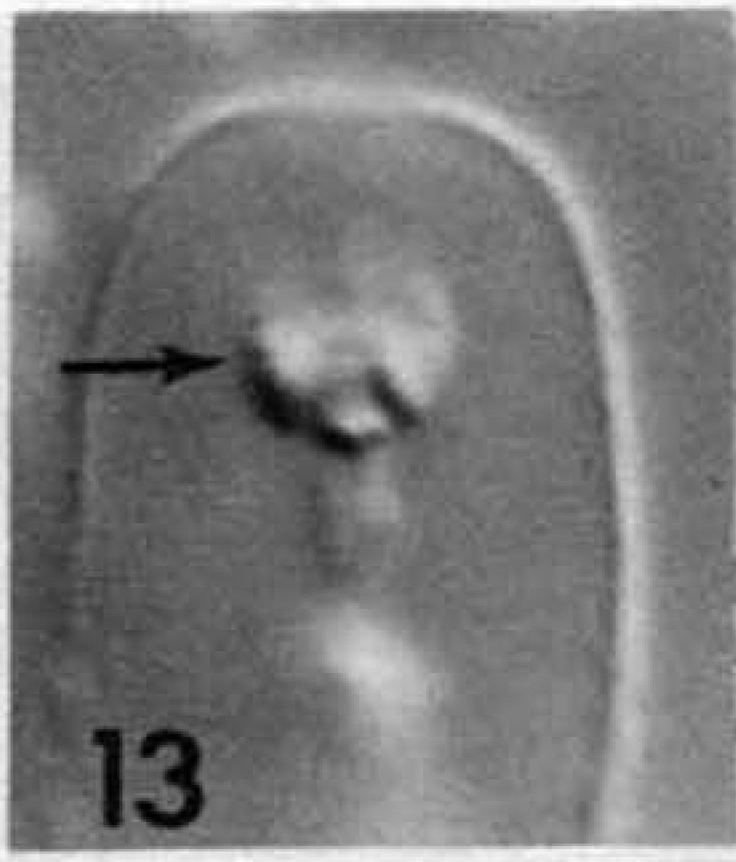
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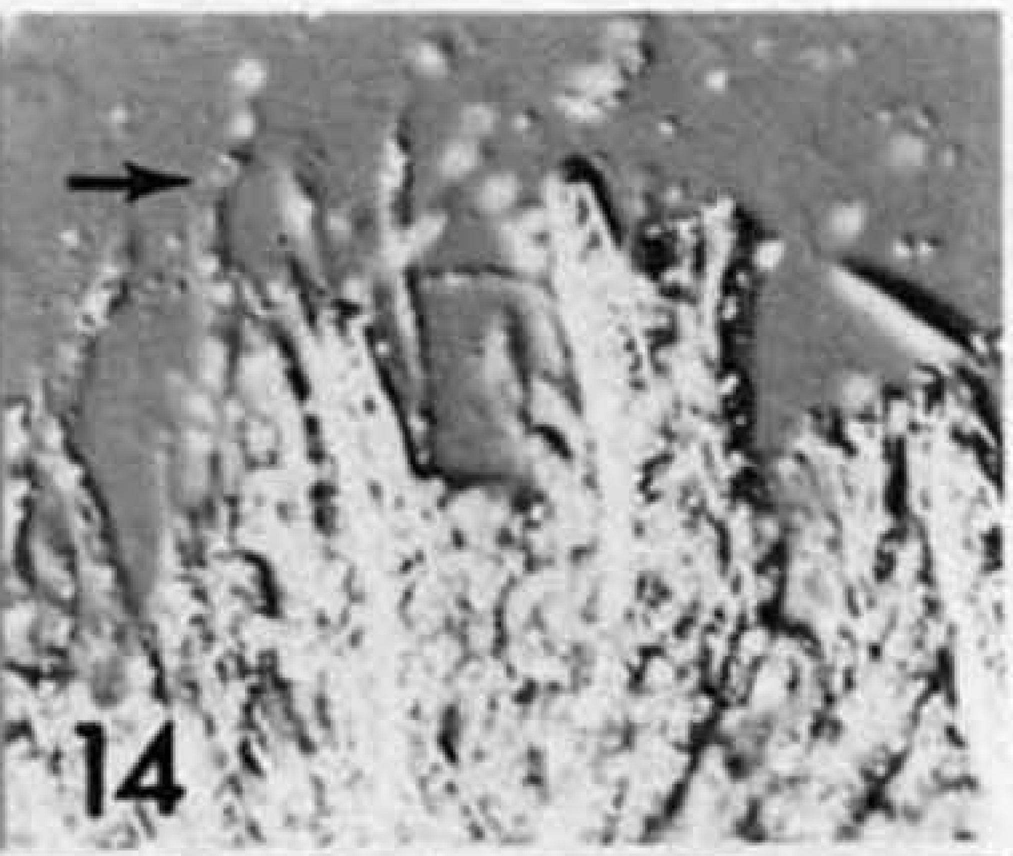
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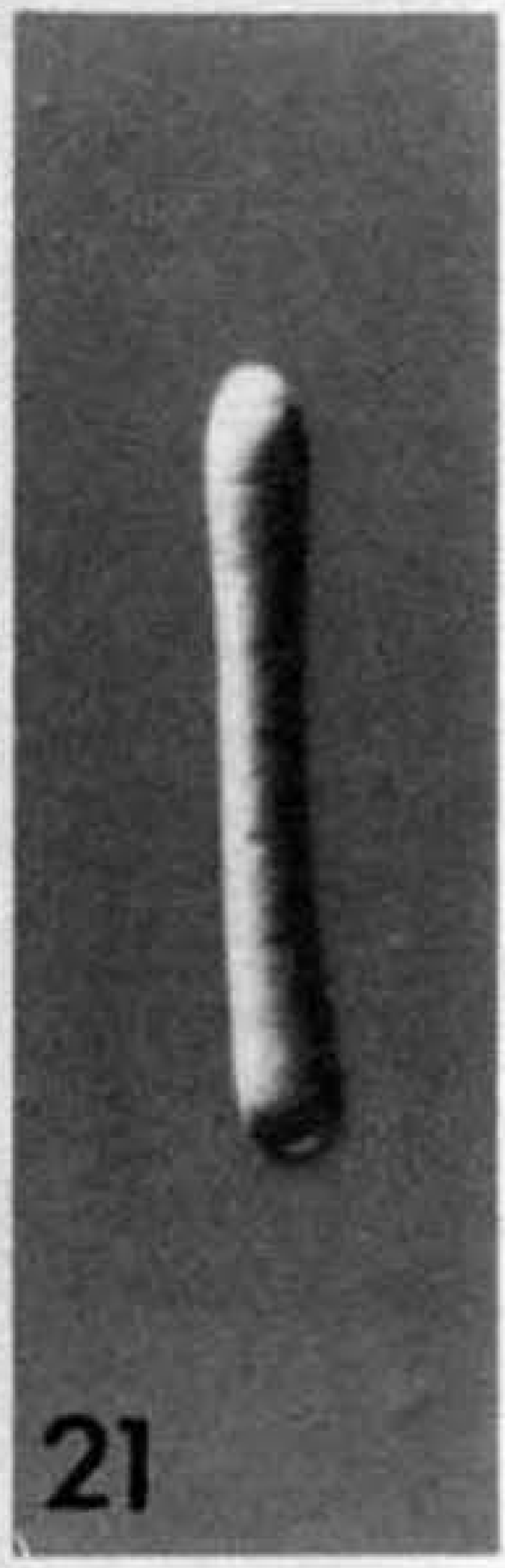
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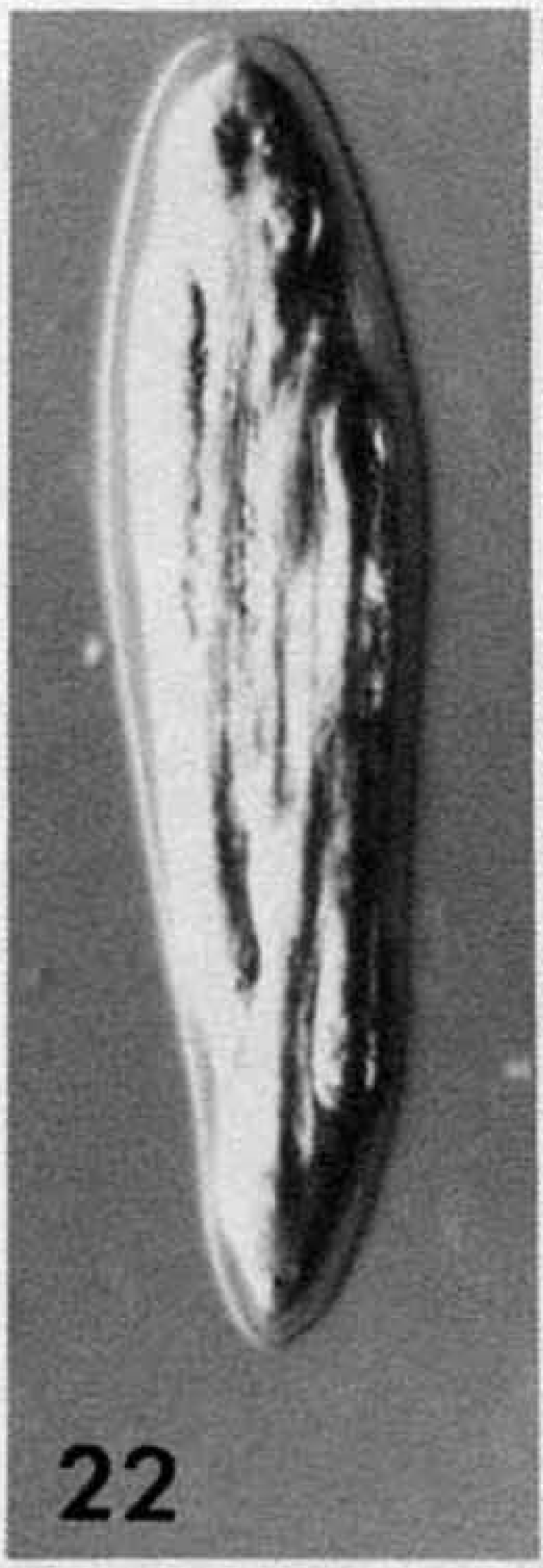
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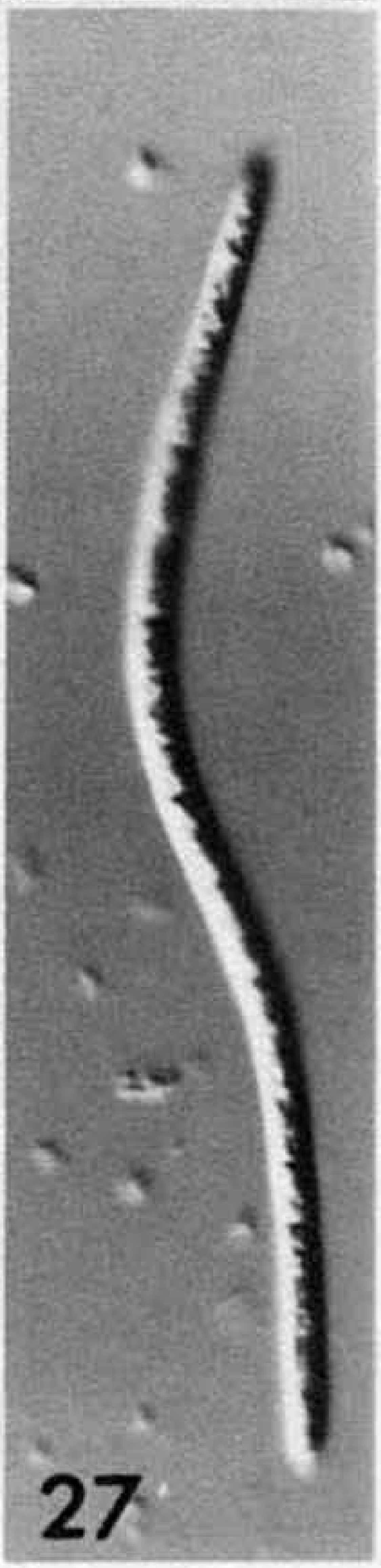
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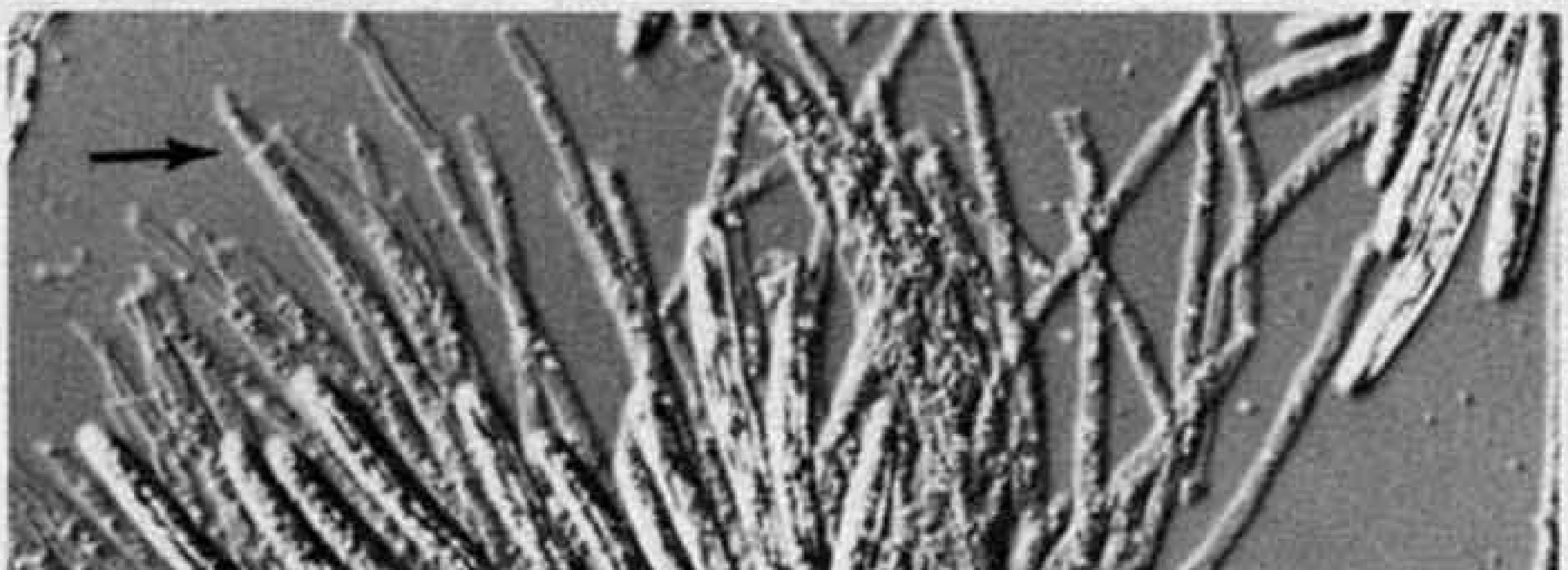
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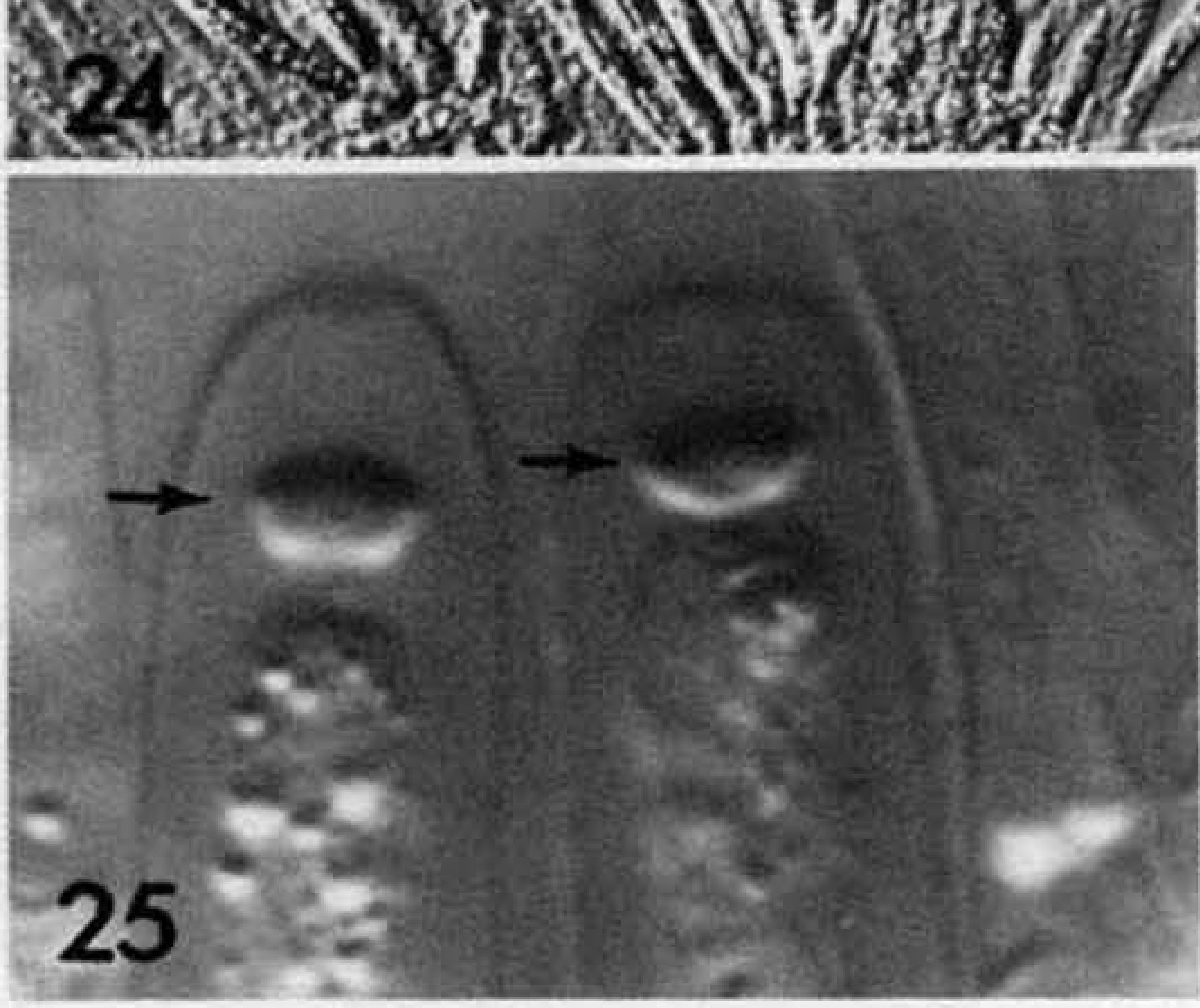
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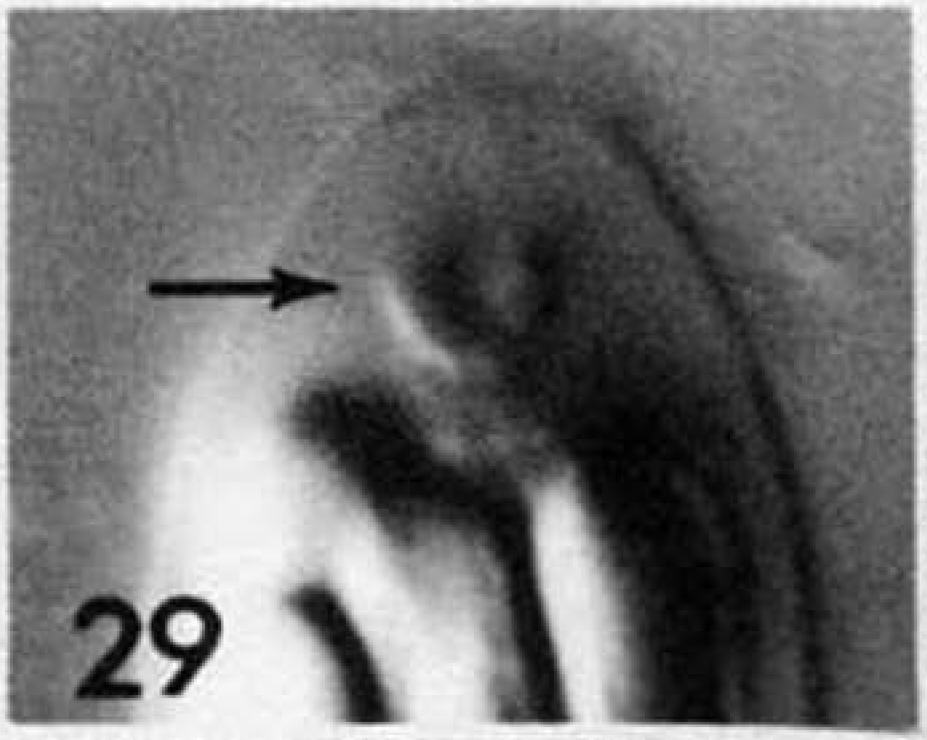
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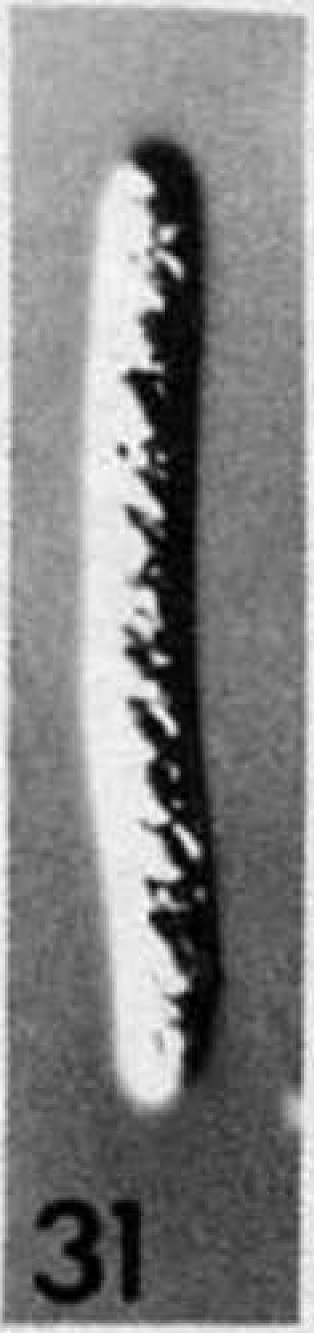
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32

MYCOTAXON

Vol. XXV, No. 2, p. 657 April-June 1986

NOTICE

A CHANGE IN EDITORIAL POLICY FOR LONG PAPERS

It is with some reluctance that we at MYCOTAXON institute, beginning with volume 26, a policy whereby full support of publication costs of longer papers shall no longer be carried by the subscription fees. Though we are still opposed to the philosophy of page charges, we have increasingly been asked to publish long, even book-length, articles.

In order to satisfy our subscribers, we must now charge partial costs for each page submitted over 64 pages for an article (or articles with the same author or the same senior author appearing in any one volume). Authers will be well advised to plan their long papers carefully - giving full thought to possible typeface reduction to achieve savings in number of pages. Advice on article preparation is always available from either of the Co-Editors.

This new policy will allow us in the future to increase the size of volumes that contain such long articles without any additional cost to subscribers.

We shall continue to offer authors the preparation cost of one free halftone for each 10 pages of the paper.

Charges for each excess halftone and for each page in excess of 64 pages are currently $15.00 (U.S.), but are subject to change as printing costs vary. These will be specified on the acceptance form sent authors, or may be ascertained beforehand by writing to the Managing Editor.

AUTHOR INDEX, VOLUME TWENTY-FIVE

INDEX TO FUNGOUS AND LICHEN TAXA, VOLUME TWENTY-FIVE

This index includes genera, infrageneric taxa, species, and infraspecific taxa. New taxa are underlined, as are the pages on which they are published.

ERRATA, VOLUME FIVE

Page	70	line 33	for Europaei 634, read Europaei 654,
	94	21	for D-7968 read D-7698
	106	4-5	for ISOTYPUS: CUP-Fairman 619 (18-56) read PARATYPUS: CUP-Fairman 827 (18-56), (same data except: 2.IX.1920).
	152	28	for D-1321 read D-6321
	170	28	for CUP-D76?9 read CUP-D-7609
	181	18	for CUP-D-6288 read CUP-D-6228
	207	39	for 2?53 read 2053
	233	12	for CUP-D-7707 read CUP-D-7709
	238	20	for 32525 read 34626
	245	38	for CUP-D-5821 read CUP-D-5281
		39	for D-142 read D-7677
		40	for D-7648 read D-7678
		42	for D-1749 read D-7749
	251	1	for Pragmopara read Pragmopora
	327	19	for 32627; 32640 read 34627; 34640

ERRATA, VOLUME TWENTY-THREE

Page	2	line 20	for difficult read different
	137-139		Add 5 to each page number of Author Index
	253	line 25	for Abdulla read Abdullah
SPINE			for i-iv. July-September 1985 read i-iv, INDICES. July-September 1985

ERRATA, VOLUME TWENTY-FOUR

Page	513	line 31	for CUP 61695 read CUP 60695
	521	45	for (G-GK 12509); read (G-GK 12590);
	540	32	FOR for clo hlorata READ for clorata read chlorata
SPINE			for 23: 1-516 + i-iv. July-September 1985 read 24: 1-540 + i-iv, INDICES. October-December 1985

ERRATA, VOLUME TWENTY-FIVE

Page	2	line 25	for E. anglica read Entomophthora anglica
	5	14	for E. sphaerosperma read Entomophthora sphaerosperma
	8	1	for E. anglica read Erynia anglica
		49	for E. carpentieri read Entomophthora carpentieri
	39	21	for silvanus read silvana
	85	30	for P. (Bulbothrix) read Parmelia (Bulbothrix)
	126	34	for DENOROTRICHOSCYPHA read DENDROTRICHOSCYPHA
	156	43	for Beauveria tundrense read Beauveria tundrensis
	188	4	for cinamomea read cinnamomea
	190	1	for Harst. read Karst.
		12	for candolieana read candolleana

ERRATA, VOLUME TWENTY-FIVE (continued)

Page	190	line	27	*for* Spingipellis *read* Spongipellis
	203	line	7	*for* 1985), *read* 1986),
	216		37	*for* [1985]. *read* 1986.
	252		51	FOR P. groenlandica READ *P. groenlandica*
	267		7	FOR Leveillula READ *Leveillula*
	330		25	*for* addtion *read* addition
	380		40	*for* *geogenius* read *geogenia*
	406		28	for *niger* read *nigra*
	412		3	for *A.* read *Agaricus*
			7	for *A.* read *Agaricus*
	413		46	for *silvanus* read *silvana*
	415		39	for *A.* read *Agaricus*
	416		4	for *A.* read *Agaricus*
			6	for *A.* read *Agaricus*
	434		3	for *cupliformis* read *cuplaeformis*
	481		22	for *violaceus* read *violacea*
	528		42	for *funicolum* rtead *funicola*
	529		15	for *Trichochladium* read *Trichocladium*
	532		25	for *Acyria* read *Arcyria*
			26	for *Comatrichia* read *Comatricha*
			28	for *Cribaria* read *Cribraria*
			29	for *Cribaria* read *Cribraria*
			33	for *vesparum* read *vesparium*
	533		10	for *funicolum* read *funicola*
			37	for *Rabentischia* read *Rebentischia*
	566		29	for *rimicolum* read *rimicola*
	577		8	for *L.* read *Lasiosphaeriopsis*
	604		1	for *P.* read *Pseudoparmelia*

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The Co-Editors express their appreciation to the following individuals who have, prior to acceptance for publication, reviewed one or more of the papers appearing in this volume.

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