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Agaricolous species of *Hypomyces*

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Abstract: Thirteen species of *Hypomyces* occur on gilled fungi. Most are found on members of the Russulaceae; other hosts include *Amanita* spp., *Crepidotus* spp., *Leptonia strigosissima*, and *Pholiota* sp. Anamorphs have been proven only for the four species, *H. armeniacus* (*Cladobotryum verticillatum*), *H. odoratus* (*C. mycophilum*), *H. succineus* (*Verticillium succineum* comb. nov.), and *H. tremellicola* (*Verticillium* sp.). Anamorphs have been putatively linked to *H. lateritius* (*C. tulasnei*), *H. lithuanicus* (*C. arnoldii*), and *H. petchii* (*Verticillium* sp.).

Key Words: Agaricales, *Cladobotryum*, Hypocreaceae, *Hypomyces*, systematics, *Verticillium*

INTRODUCTION

This is the fourth in a series of publications of monographic studies of *Hypomyces* (Fr.) L.-R. Tulasne (Hypocreales). In earlier papers we have described the species that occur on discomycetes (Rogerson and Samuels, 1985), on boletes (Rogerson and Samuels, 1989), and on Aphyllphorales (Rogerson and Samuels, 1993). As in these papers, we continue to place *Peckiella* (Sacc.) Sacc. and *Apiocrea* H. Sydow in synonymy with *Hypomyces*.

Species of *Hypomyces* can be distributed along the lines of their substrata, with most found on boletes, agarics, or Aphyllphorales (including polypores and telephores) and with little overlap among the broad substratum groups. Thirteen species are recognized as occurring primarily on members of the Agaricales, including *H. lactifluorum*, the type species of the genus. Species of *Hypomyces* that parasitize boletes (Rogerson and Samuels, 1989; Helfer, 1991) and agarics (Helfer, 1991; and herewith) tend to be specific to host family or genus, whereas most species found on aphyll-

phoraceous hosts are less restricted. The Russulaceae J. P. Lott is the host family of preference for the agaricolous *Hypomyces* species, with teleomorphs of eight species found only on species of *Lactarius* or *Russula*. *Hypomyces hyalinus* is found only on *Amanita* species. Two species are on brown-spored agarics, viz. *H. succineus* on *Pholiota* sp., and *H. tremellicola* on *Crepidotus* spp.; and *H. porphyreus* is on the pink-spored *Leptonia strigosissima*. *Hypomyces odoratus* is the least specialized of the agaricolous species. Its teleomorph was previously known only in cultures of paired European isolates of its anamorph, *Cladobotryum mycophilum*, that were isolated from a variety of fungi. We have found perithecia in Puerto Rico and the United States on a polyporeaceous basidiomycete. *Hypomyces armeniacus*, better known in Europe as *H. ochraceus* (but see below), begins developing on basidiomata of *Russula* or *Lactarius*, completely destroys the host and grows away from it, then appears to be growing on the substratum of the actual host. *Hypomyces lateritius* and *H. lithuanicus* appear restricted to species of *Lactarius*. *Hypomyces lithuanicus* may be the most specialized of the parasites, occurring only on species of the *Lactarius torminosus* (Schaeff. : Fr.) S. F. Gray complex, while other species may be restricted to either *Lactarius* or *Russula* but not to any species complex. In large populations of *Hypomyces lactifluorum* where the host can be determined with some confidence, the host has proven to be *Russula brevipes*; but associated nonparasitized hosts often belong to the *Lactarius piperatus* complex. In our experience *Hypomyces luteovirens* occurs only on species of *Russula*.

Basidiomata of agaric species that have been transformed by their parasites, including *H. hyalinus*, *H. lactifluorum*, and *H. macrosporus*, are considered by some to be edible (Herrera and Guzmán, 1961; Lincoff, 1981), bearing in mind the possibility that the host itself may be poisonous. *Hypomyces lactifluorum* and *H. macrosporus* are available in Mexican markets, where they may be found mixed (Herrera and Guzmán, 1961).

TELEOMORPH CHARACTERS

All species reported here have the essential features of *Hypomyces*, the Hypocreaceae and the Hypocreales (Barr, 1990; Hanlin, 1963, 1964; Rogerson, 1970; Rogerson and Samuels, 1989; Samuels, 1973). *Hypomyces* is

most easily recognized by its basidiomycetous habitat, fusiform, apiculate ascospores, and anamorphs. Perithecia typically form in a light or brightly colored subiculum on the hymenium of agarics, boletes, or the Aphyllophorales.

The verrucose and apiculate ascospores (FIGS. 1–13) are unusual among the pyrenomycetes and are thus highly diagnostic for *Hypomyces*. Four agaricicolous species have unicellular ascospores (*H. banningiae*, *H. lateritius*, *H. luteovirens*, *H. lithuanicus*), and the ascospores of *H. hyalinus* are apiosporous with the septum in the lower third of the ascospore. Ascospores of *H. banningiae*, *H. porphyreus*, and *H. tremellicola* lack a conspicuous apiculus; rather their ends have a blunt appendage that is probably homologous with the apiculus of other species. Ascospores of *H. succineus* are merely acute although the spines may appear as apiculi when in a terminal position. Ascospores of *H. tremellicola* are also spinulose rather than warted and are neither apiculate nor acute.

While the agaricicolous species of *Hypomyces* are in general morphologically, anatomically, and biologically homogeneous, there are variations. Reaction of subiculum and perithecia with 3% (aq.) potassium hydroxide (KOH) is characteristic of a species. In some a pronounced violet to purple color forms (KOH+). The subiculum and perithecial apex of *H. lithuanicus* become reddish in KOH, but the color reaction could be overlooked easily. In others no color change is discernible (KOH–); but the natural color of their perithecia may intensify or fade.

The subiculum of most species is initially of cottony hyphae and remains cottony throughout development. Hyphae at the surface of the subiculum of *H. luteovirens*, *H. lateritius* (FIG. 50), *H. lithuanicus* (FIG. 59), and *H. banningiae* have many free ends; this feature is conspicuous in microtome sections but also is easily seen in crush mounts. Cells of these hyphae often swell and the hyphae may appear to be somewhat moniliform. Distinctive moniliform hyphae of the subiculum and from the perithecial apex are characteristics of *H. luteovirens*. In contrast, the subicular hyphae of most other species are intertwined and have few free ends. The subiculum is variously compacted and firm. The extreme in this development is *H. macrosporus* (FIG. 67) where the individual hyphae lose their in-

tegrity and the subiculum assumes a pseudoparenchymatous, stromatic aspect.

Among the agaricicolous species perithecial ontogeny has been described for *H. lactifluorum* (Hanlin, 1963) and is consistent for the genus (see references in Rogerson and Samuels, 1993). There are variations in the anatomy of the perithecial apex of the agaricicolous species. In *Hypomyces* in general the perithecial apex is formed of globose to somewhat elongated cells that are arranged in files (e.g., *H. macrosporus*, FIG. 72; *H. petchii*, FIG. 98), the terminal cells of which are more or less conspicuously clavate; the perithecial apex is not confluent with the surrounding subiculum. However, in the perithecial apex of *H. lateritius* (FIGS. 48, 49), *H. lithuanicus* (FIGS. 57, 58), and *H. luteovirens* (FIG. 63) the arrangement of papillar cells into files is not obvious, and hyphae merge the papilla with the subiculum. Cells of the papilla of *H. luteovirens* are arranged in files that separate from each other.

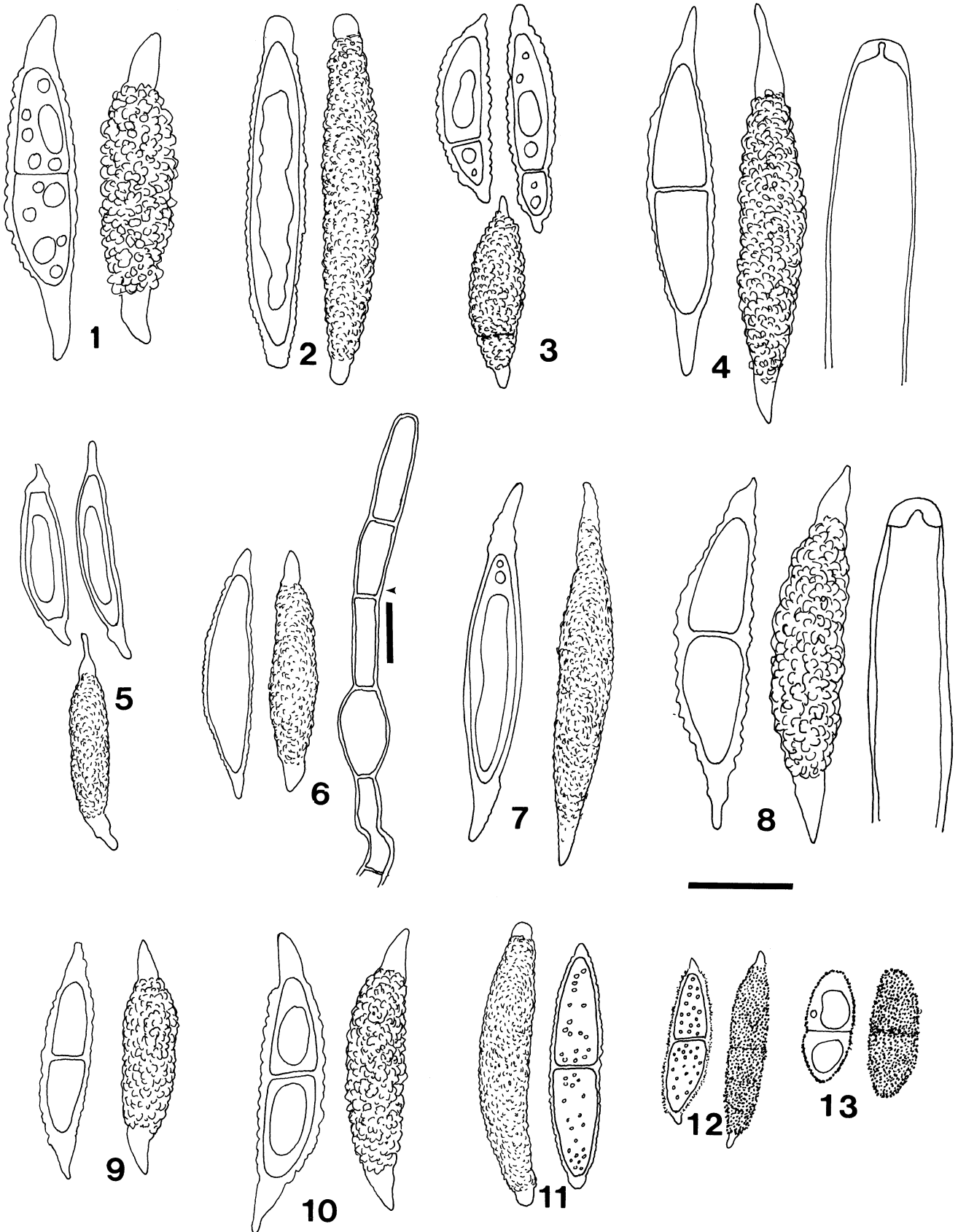
ANAMORPH CHARACTERS

Only four of the agaricicolous species of *Hypomyces* have been linked unequivocally through ascospore cultures to anamorphs, viz. *H. aremniacus* (FIGS. 20–29), *H. odoratus* (FIGS. 76–83), *H. succineus* (FIGS. 118–121), and *H. tremellicola* (FIGS. 129–131). The anamorphs of *H. armeniacus* and *H. odoratus* can be classified in *Cladobotryum sensu* Rogerson and Samuels (1993). The conidiogenous cells of the *Cladobotryum* anamorphs lack periclinal thickening at the conidiogenous locus suggesting holoblastic development; conidia are held singly or in groups of a few at the tip of the conidiogenous cell but are not aggregated in a drop of liquid. The anamorphs of *H. succineus* and *H. tremellicola* are *Verticillium* species. These *Verticillium* anamorphs produce phialides that have periclinal thickening at the tip, denoting enteroblastic conidial development, and a multiplicity of conidia held in a drop of liquid at the tip of each conidiogenous cell.

The phialidic conidiogenous cells and wet conidia of *H. succineus* and *H. tremellicola*, while typical of the Hypocreales in general (Samuels and Seifert, 1987), are equivocal in *Hypomyces* (Rogerson and Samuels, 1993). Most anamorphs of the polyporicolous species (Rogerson and Samuels, 1993) produce dry conidia

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FIGS. 1–13. *Hypomyces* species, ascospores and asci. 1. *H. armeniacus* (GJS 93-32). 2. *H. banningiae* (CTR 80-101). 3. *H. hyalinus* (Bigelow 4359). 4. *H. lactifluorum*, ascal apex on right (Schaffer, 25 Jul. 1964). 5. *H. lateritius* (CTR 84-11). 6. *H. lithuanicus*, perithecial hair on right (*Mycotheca germanica* 490, as *H. torminosus*). 7. *H. luteovirens* (Salmon River). 8. *H. macrosporus*, ascal apex on right (CTR 69-113). 9. *H. odoratus* (Poldmaa, 1967). 10. *H. petchii* (TYPE). 11. *H. porphyreus* (TYPE). 12. *H. succineus* (TYPE). 13. *H. tremellicola* (Parker, Sep. 1987). Ascospores in optical section (left) and in surface view (right). Scale bars = 10 μ m.



either singly or in chains. Many of the boleticolous species of *Hypomyces* (Rogerson and Samuels, 1989) have *Verticillium* synanamorphs with *Sepedonium*. It is interesting in this regard that none of the agaricolous species of *Hypomyces* occurs on cultivated mushrooms (*Agaricus bisporus* (Lange) Imbach). However, *Verticillium fungicola* (Preuss) Hassebrauk (Brady and Waller, 1976b; Gams and Van Zaayen, 1982) and *V. psalliotiae* Treschow (Brady and Waller, 1976a), both of which cause brown spotting on the caps of cultivated mushrooms, are at least morphologically very similar to the *Verticillium* anamorph of *H. tremellicola* (FIGS. 129–131; Gams and Van Zaayen, 1982). Cobweb disease of *Agaricus bisporus* has been attributed to *H. rosellus* (Alb. & Schw.) L.-R. & C. Tul. (anamorph = *Cladobotryum dendroides*), one of the polyporicolous species (see Pennycook, 1989 and references therein; Lane et al., 1991).

Anamorphs have been linked circumstantially to *H. patchii* (*Verticillium*; Arnold, 1971), *H. lateritius* (*Cladobotryum tulasnei*; Helfer, 1991), and *H. lithuanicus* (*C. arnoldii*; Helfer, 1991). While these may well be the anamorphs of the respective *Hypomyces* species, the connections have not been proven. Despite repeated attempts over several years, we have not observed ascospore germination in these three species, nor in *H. lactifluorum*, *H. macrosporus*, *H. hyalinus*, and *H. luteovirens*.

All of these parasites completely transform the gill surface of the host's pileus into an ascomycetous hymenium. However, in at least some cases, while making microtome sections of perithecia, we have seen basidiospores produced from basidia within infected basidiomata (e.g., *H. lithuanicus*, FIG. 56). The infected host-with-ascomycete remains firm while ascospores are discharged. We have seen *H. lactifluorum* appearing in

succeeding years in the same population of *Lactarius* or *Russula* species, indicating that infection may be effected through contaminated soil or that perhaps the *Hypomyces* is somehow integrated into the mycelium of the agaric.

MATERIALS AND METHODS

Single ascospores were isolated with the aid of a micromanipulator on cornmeal dextrose agar medium (CMD, Difco). Colony characters were taken from CMD, oatmeal agar (OA) medium (60 g oatmeal, 12 g agar, 1 L water), and potato dextrose agar (PDA, Difco).

Dry specimens were rehydrated briefly in 3% (aq.) KOH and the mounts were then flooded with water. Photographs were taken of ascospores and asci mounted in water mounts. Photographs were taken of perithecial sections mounted in 100% lactic acid.

Four types of microscopy were used in this study. These are indicated in the legends to the illustrations as bright field (BF), fluorescence (FL), interference contrast (IC), and phase contrast (PC). The optical brightener calcofluor (0.05% w/v in sodium phosphate buffer at pH 8; Sigma Chemical Co.) was used for FL.

The conventions KOH+ and KOH– are used. KOH+ indicates that the subiculum or perithecium becomes some color of red in 3% KOH and yellow in 100% lactic acid. KOH– indicates that the subiculum or perithecium did not assume a red coloration in 3% KOH and did not become yellow in 100% lactic acid.

Representative isolates have been deposited in the American Type Culture Collection and the Centraalbureau voor Schimmelcultures.

The single most frequently cited collector of the specimens cited in this work has been Clark T. Rogerson, whose name is abbreviated as CTR.

KEY TO AGARICICOLOUS SPECIES OF *HYPOMYCES*

1. Ascospores one celled 2
1. Ascospores two celled 7
 2. Ascospores averaging 20 μm or less in length 3
 2. Ascospores averaging greater than 25 μm in length 5
3. On *Pholiota* species, ascospores acute but not conspicuously apiculate 12. *H. succineus*
3. On *Lactarius* species, ascospores conspicuously apiculate 4
 4. Perithecia yellow brown, dark amber to brown, brick red, or reddish black; pale yellow or colorless in KOH ... 5. *H. lateritius*
 4. Perithecia ochraceous, pale brown to chocolate brown; pale red to purple in KOH 6. *H. lithuanicus*
5. Subiculum and perithecia dark green to black, ascospores 28–40 \times 4.5–5.5 μm , apiculate; on *Russula* spp. 7. *H. luteovirens*
5. Subiculum and perithecia in colors of yellow, brown or red; ascospores 25–40 \times 3.5–5.0 μm , without apiculi, more or less acute or rounded; on *Lactarius* or *Leptonia* 6
 6. Ascospores 36–40 \times 4–5 μm ; subiculum and perithecia in colors of yellow to pale brown; on *Lactarius* spp. ... 2. *H. banningiae*
 6. Ascospores 25–28 \times 3.5–5.0 μm ; subiculum and perithecia in colors of brown to red; on *Leptonia strigosissima* . 11. *H. porphyreus*

7. Ascospores with septum in basal part of ascospores, (13-)15-20(-25) × 4.5-6.5 μm; on *Amanita* 3. *H. hyalinus*
 7. Ascospores with septum median; on other agaric families 8
 8. Ascospores averaging greater than 20 μm in length 9
 8. Ascospores averaging less than 20 μm in length 14
 9. Ascospores not apiculate, 25-28 × 3.5-5.0 μm; subiculum brick red, KOH-; on *Leptonia strigosissima*
 11. *H. porphyreus*
 9. Ascospores apiculate 10
 10. Perithecia and subiculum turning deep red to purple to purplish black in KOH (KOH+) 11
 10. Perithecia and subiculum not changing color to red or purple in KOH (KOH-) 12
 11. Ascospores, 35-40(-50) × 4.5-7.0(-9.0) μm; subiculum bright orange to reddish purple 4. *H. lactifluorum*
 11. Ascospores 25-35 × 4-8 μm; subiculum rose, reddish to lilac 9. *H. odoratus*
 12. Host completely destroyed and no longer recognizable as an agaric; perithecia yellow orange, apricot, amber to
 reddish orange or brownish; subiculum white, flesh-colored to buff or ochraceous; ascospores 27-45 × 5-8 μm;
 anamorph *Cladobotryum verticillatum*, conidia 11-22 × 6-11 μm, 0(-1)-septate 1. *H. armeniacus*
 12. Host recognizable as an agaric; perithecia white to apricot; subiculum white to pale buff; ascospores 26-42 ×
 5-7 μm; anamorph unknown or *Verticillium*, conidia aseptate 13
 13. Perithecia white to pale buff to yellowish amber; subiculum white to buff; ascospores 34-42 × 5-7 μm
 8. *H. macrosporus*
 13. Perithecia apricot; subiculum pale buff; ascospores 26-33 × 5.0-6.5 μm 10. *H. petchii*
 14. Ascospores 12-20 × 3-5 μm, fusiform to cylindrical with ends acute or apiculate; on *Pholiota* sp. 12. *H. succineus*
 14. Ascospores 7-13 × 3.5-4.0 μm, ellipsoidal to fusiform; ends obtuse, not apiculate; on *Crepidotus* spp.
 13. *H. tremellicola*

DESCRIPTIONS OF THE SPECIES

1. *Hypomyces armeniacus* L.-R. Tulasne, Ann. Sci. Nat. Bot., Sér. IV, 13: 12. 1860. FIGS. 1, 14-29

= *Hypomyces apiculatus* (Cooke & Peck) Seaver, Mycologia 2: 73. 1910.

≡ *Hypocrea apiculata* Cooke & Peck in Peck, Ann. Rep. N.Y. State Mus. 29: 57. 1878.

≡ *Clintoniella apiculata* (Cooke & Peck) Saccardo, Syll. Fung. 16: 588. 1902.

= *Hypomyces terrestris* Plowright & Boudier in Philips & Plowright, Grevillea 8: 105. 1880.

= *Hypomyces xylophilus* Peck, Bull. Torrey Club 11: 28. 1884.

≡ *Peckiella xylophila* (Peck) Saccardo, Syll. Fung. 9: 944. 1891.

- Anamorph. *Cladobotryum verticillatum* (Link) S. J. Hughes, Canad. J. Bot. 36: 750. 1958.

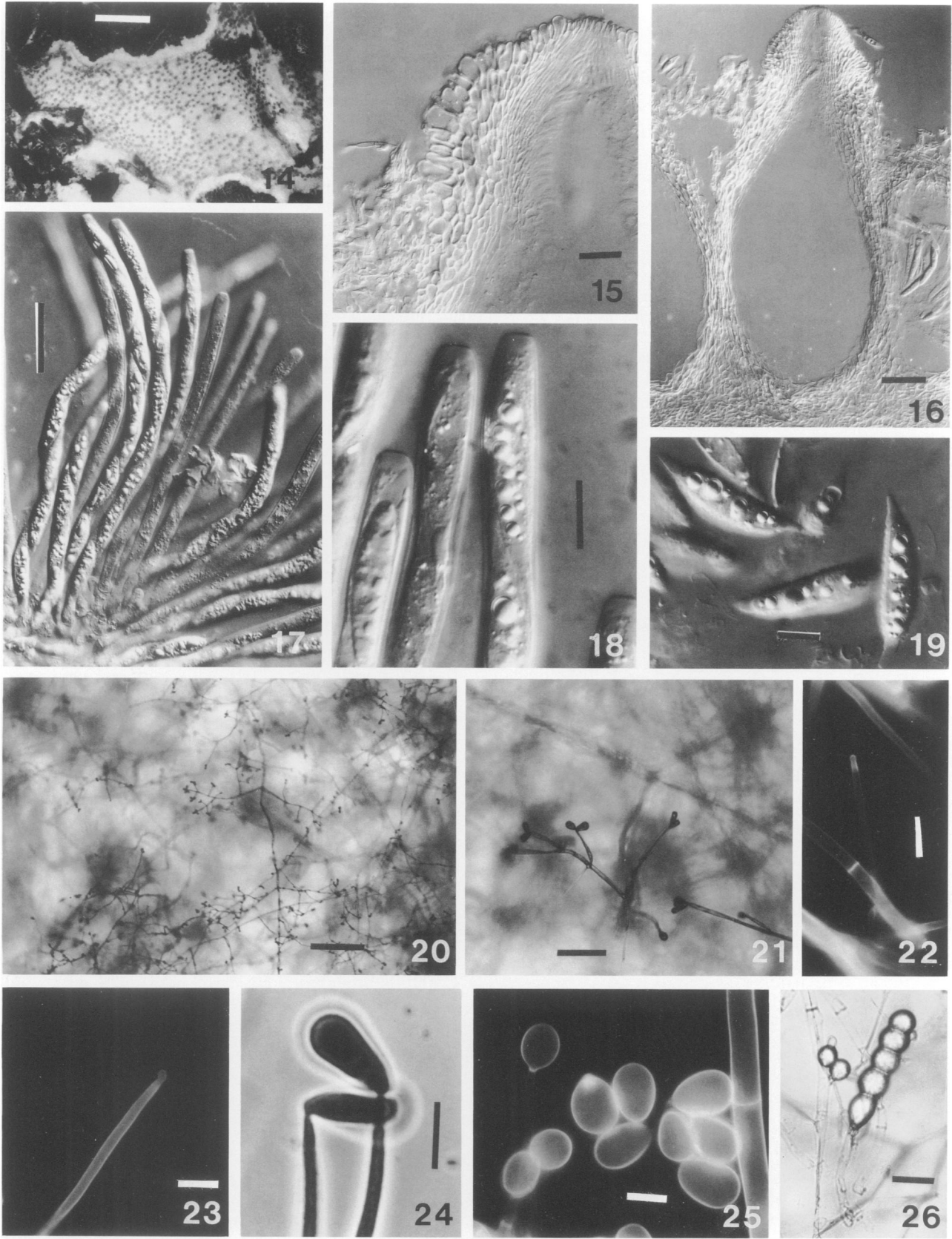
FIGS. 20-29

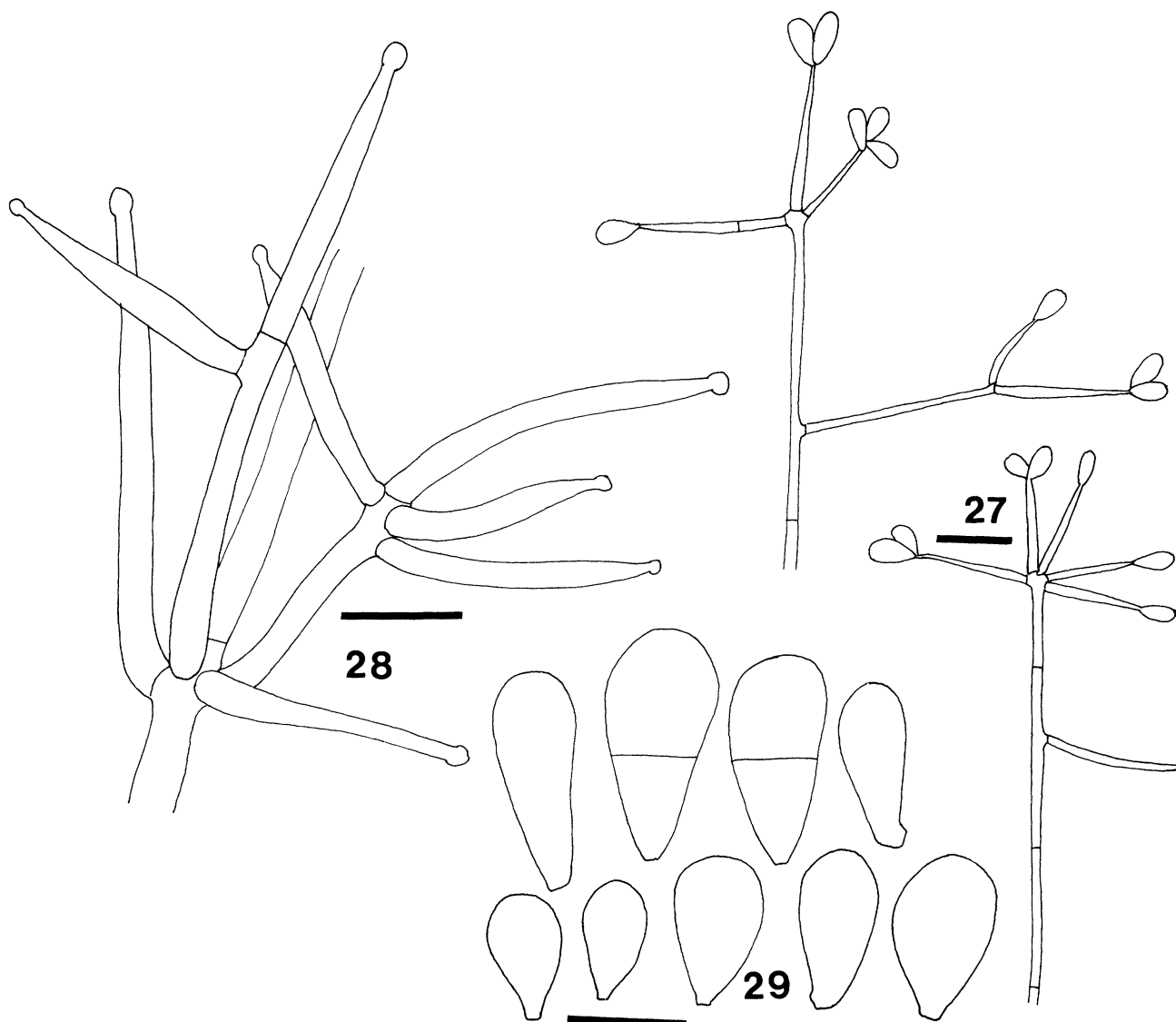
= *Acremonium verticillatum* Link, Mag. Ges. Naturf. Freunde, Berlin 3: 15. 1809.

Subiculum at first white, then flesh or buff and finally deep ochraceous to apricot, remaining white or lighter at the margin, effused, thin to fairly thick, occurring on the host substrate such as wood, mosses, and on the ground, often to 5 cm in extent, developing where the host agaric decayed; subicular hyphae 5-10 μm wide, septate, much branched, usually remaining filamentous, sometimes forming inflated cells and appearing vesicular or pseudoparenchymatous, KOH-. Perithecia subglobose, ovate to obpyriform, 260-360 × 240-250 μm, at first immersed in the

subiculum then becoming half free, on old specimens often appearing superficial, buff, yellowish orange or amber to reddish orange, KOH-; papilla prominent, 90-100 × 60-80 μm. Perithecial wall 15-20 μm wide, cells fusiform 15-20 μm long, 5-7 μm wide, walls 1 μm thick, nonpigmented. Papilla of cells 5-12 μm long, 6-10 μm wide, walls 1 μm wide and arranged in diverging files, terminal cell of each file subglobose to clavate and somewhat enlarged; cells around the ostiolar opening narrowly clavate, 6 μm wide, merging with the periphyses. Asci long cylindrical, 170-180 × 6-8 μm, apex thickened and with a pore. Ascospores fusiform, often curved, (27-)32-40(-45) × 5-8 μm, two celled, septum median, prominently verrucose and apiculate; verrucae 0.5-1.2 μm high; apiculi acute, 3-4.5 μm long.

CHARACTERISTICS IN CULTURE. Cultures derived from ascospores (*GJS 92-90*) grown 2 wk, 20-21 C, 12-h darkness and 12-h cool white fluorescent light. CMD: greater than 9 cm diam, cottony, white, conidiophores forming abundantly in the aerial mycelium. Conidiophores irregular in length, 7 μm wide, irregularly or verticillately branched and conidia joined at the base and held in pairs or dry heads of a few. Conidiogenous cells arising singly and terminating each branch or in whorls of a few, variable in length, 35-60 μm long, 1.5-2.5 μm wide at the tip, 2.5-4 μm wide at the base; tip lacking periclinal thickening and not swelled. Conidia pyriform to clavate and conspicuously broader at apex than at base, 11-22 × 6-11 μm, 0(-1)-septate, with a small, flat, slightly protuberant basal abscission scar; apparently forming holoblastically. Chlamydospores common, intercalary or





FIGS. 27–29. *Hypomyces armeniacus*, *Cladobotryum verticillatum* anamorph. 27. Two conidiophores. 28. Conidiogenous cells with developing conidia. 29. Conidia. All from GJS 92-90. Scale bars = 10 μ m.

arising as lateral branches of hyphae, appearing as chains of 2–4 cells, each cell ca 20 μ m diam with wall 2 μ m thick, hyaline, smooth.

HABITAT. On agarics. The anamorph is given by Gams and Hoozemans (1970) as occurring mostly on Russulaceae but also on boletes.

TYPE. FRANCE. Chaville, near Versailles, Herb. L. R. Tulasne (PC!).

DISTRIBUTION. Colombia. Europe (England, France, Germany). Canada (Ontario, Quebec). United States (Alabama, Connecticut, District of Columbia, Illinois, Indiana, Iowa, Kentucky, Louisiana, Maine, Maryland, Massachusetts, Michigan, Minnesota, New Hampshire, New Jersey, New

←
 FIGS. 14–26. *Hypomyces armeniacus*. 14. Perithecial habit at site of disintegrated agaric. 15, 16. Median longitudinal section through mature perithecia. Anatomy of perithecial apex shown in 15. 17, 18. Asci; ascial apex visible in 18. 19. Ascospores. 20–26. *Cladobotryum verticillatum* anamorph. 20, 21. Habit of conidiophores in agar culture. 22, 23. Conidiogenous locus with developing conidia. Note the absence of periclinal thickening. 24. Tip of conidiogenous cell with nearly mature conidium. 25. Conidia. 26. Chlamyospore. FIG. 14 from GJS 92-96, FIGS. 15–19 from GJS 90-32, 20–26 from GJS 92-90. All IC except FIGS. 14, 20, 21, 26 (BF); 22, 23, 25 (FL); 24 (PC). Scale bars: FIG. 14 = 1 mm; 15, 17, 23, 26 = 20 μ m; 16 = 50 μ m; 18, 19, 24, 25 = 10 μ m; 20 = 100 μ m; 21 = 40 μ m.

York, North Carolina, Tennessee, Ohio, Oregon, Pennsylvania, Vermont, Virginia, West Virginia, Wisconsin).

SPECIMENS EXAMINED (SELECTED). COLOMBIA. CUNDINAMARCA: road between Mosquera and La Mesa, W. of Bogotá, km 20, elev. 2400 m, on rotted wood, 5 Jun. 1978, *K. P. Dumont 8587 et al.* (CTR 78-12, NY). USA. ALABAMA: Clay County, Talladega National Forest, Cheaha State Park, Cave Creek Trail, on decorticated wood and ground, 23 Sep. 1992, CTR (GJS 92-90, BPI, NY); second collection, same locality, on ground and decorticated wood, GJS (92-96) *et al.* (BPI). CONNECTICUT: Tolland County, Hebron, Hemlocks Education Center, on rotten wood, 15 Sep. 1990, CTR (90-32) (NY). NEW YORK: Catskill Mountains, on ground and rocks, Jul. 1870, *C. H. Peck* (NYS, ISOLECTOTYPE of *Hypocrea apiculata*); Albany County, Guilderland, Pine Bush, Willow Street Exit, on mosses at base of stump along stream, 11 Sep. 1977, CTR (77-143) (NY); Rensselaer County, Sand Lake, (date unknown), *C. H. Peck* (NYS, possible SYNTYPE of *Hypocrea apiculata*); Ulster County, near Esopus Gorge, 12 mi. S of Kingston, in woods on decaying leaves, 17 Sep. 1960, CTR (60-220) and *S. J. Smith* (NY). NORTH CAROLINA: Henderson County, Cope Place, trail along Green River, near Tuxedo, on wood, 13 Sep. 1974, CTR 74-90 (NY). OHIO: on decaying wood, *Morgan* (NYS, TYPE of *Hypomyces xylophilus*).

NOTES. This species is known in Europe as *H. ochraceus* (Pers.: Fr.) Tul. However, *H. ochraceus* is a name of uncertain application. According to M. A. Donk (pers. comm., 1959) there is no material of *Sphaeria ochracea* Pers. in the Persoon herbarium (L); thus its identity remains in doubt. There is good material of *H. armeniacus* preserved in PC and thus we have adopted this unequivocal name.

Plowright (Phillips and Plowright, 1880) described *Hypomyces terrestris* Plowright & Boudier. Petch (1937) synonymized *H. terrestris* with *H. ochraceus*; Dingley (1951) placed it under *H. armeniacus*.

Barr *et al.* (1986) have discussed typification of *Hypocrea apiculata*.

Cladobotryum verticillatum is a common species most often found on members of the Russulaceae (Gams and Hoozemans, 1970; Helfer, 1991) but also occurring on boletes (Gams and Hoozemans, 1970). Redescriptions and illustrations were provided by Gams and Hoozemans (1970), Hoog (1978), and Helfer (1991). Gams and Hoozemans (1970) attributed *C. apiculatum* to *H. ochraceus* (= *H. armeniacus*), but the anamorph of this species fits *C. verticillatum* better. *Cladobotryum tulasnei* Helfer may be a synonym of *C. verticillatum*; it was described as the anamorph of *H. lateritius*, but the connection of the anamorph and teleomorph was not proven by ascospore culture. We have proven the connection between *H. armeniacus* and *C. verticillatum* by germinating ascospores of two collections.

The parasitism of *H. armeniacus* on the agaric is so complete that by the time of perithecial formation

there is usually no suggestion of an agaricaceous host. Thus, the species appears to occur on detritus and not on other fungi. On two occasions (University of Michigan Biological Station, Michigan, and Van Cortlandt Park, Bronx, New York) several basidiocarps of *Russula* and *Lactarius* species with early infection by *Cladobotryum verticillatum* were marked in the field and watched daily for over a period of 2–3 wk. The *Cladobotryum* quickly engulfed the host basidiomata which gradually disintegrated. The *Cladobotryum* persisted briefly on the ground as a white mycelium, eventually conidial sporulation ceased, the mass became densely compacted, turned apricot to orange and mature perithecia formed. In this aspect it looks like an effused species of *Hypocrea* [e.g., *H. citrina* (Fries) Fries, *H. sulphurea* (Schw.) Sacc.].

2. *Hypomyces banningsiae* Peck (as *banningii*), Bot. Gaz. (Crawfordsville) 4: 139. 1879. FIGS. 2, 30–35

= *Peckiella banningsiae* (Peck) Saccardo, Syll. Fung. 9: 945. 1891.

= *Peckiella hymenii* Peck, Bull. New York State Mus. 116: 28. 1907.

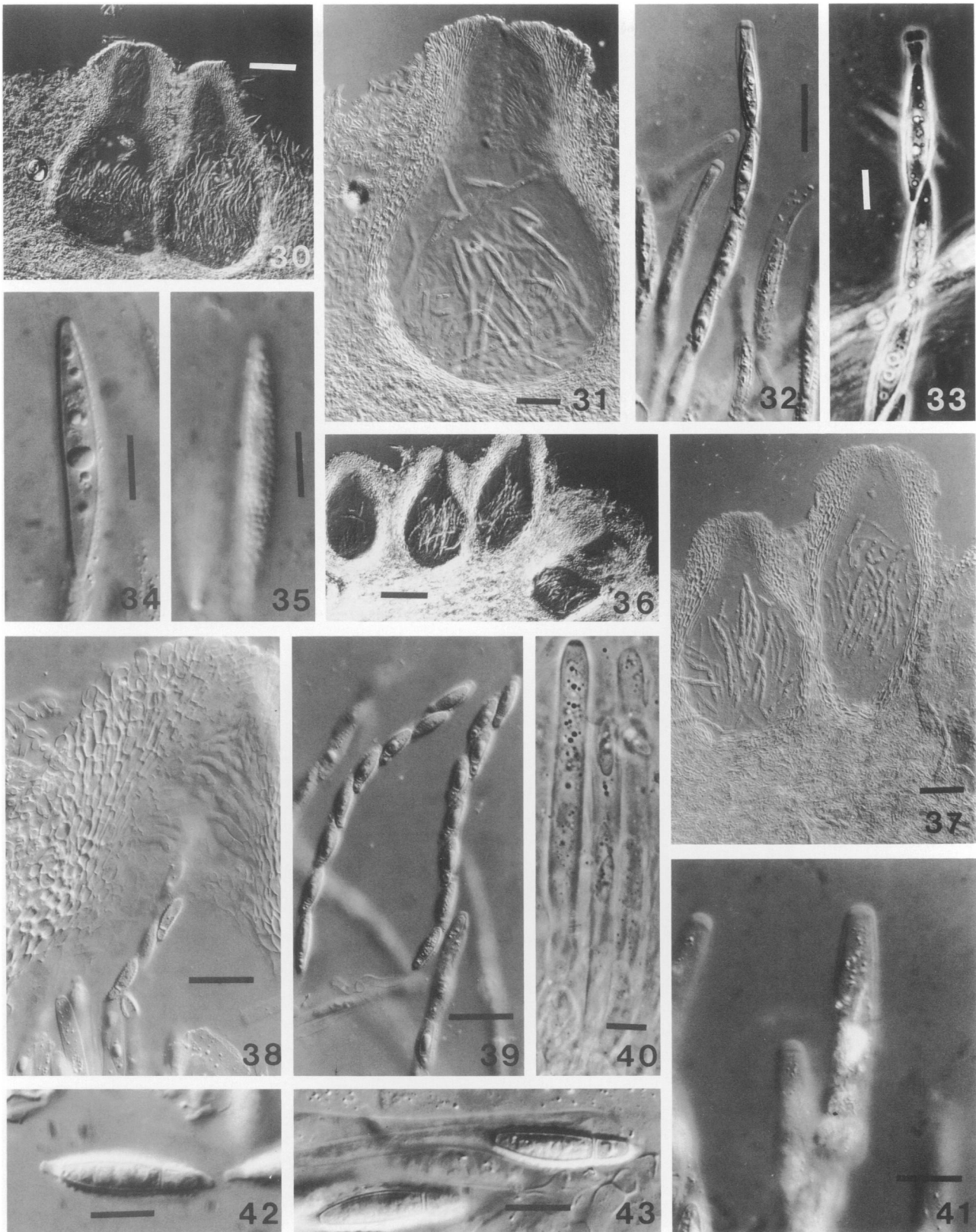
Anamorph. None known.

Subiculum at first white becoming buff, covering the gills of the host; subicular hyphae 2–3 μm wide, septate, branched, loosely interwoven, remaining filamentous, KOH–. Perithecia ovate to obpyriform, 310–325 \times 300–320 μm , at first immersed in subiculum, becoming half free, densely aggregated, pale yellow to brown, KOH–; papilla averaging 100–120 μm high, 100–120 μm wide. Perithecial wall ca 30 μm wide, cells elongated and sinuous, to 15 μm long, 3 μm wide, walls 1.5–3 μm thick, nonpigmented. Papilla of narrow hyphal elements, each ca 3 μm wide, walls 1.5 μm thick, merging with the periphyses. Asci long cylindrical, 120–130 \times 6–8 μm , apex thickened and with a pore. Ascospores fusiform or lanceolate, 28–40 \times 4.5–5.5 μm , one celled but often with two to four oil droplets within each spore, smooth to verruculose with bluntly thickened ends.

TYPE. USA. MARYLAND: Baltimore County, on decaying fungus, apparently some *Lactarius*, Aug. 1878, *M. E. Banning 23* (NYS!).

DISTRIBUTION. United States (Maryland, Massachusetts, New Jersey, New York, North Carolina, South Carolina, Pennsylvania, Virginia).

ADDITIONAL SPECIMENS EXAMINED. USA. MASSACHUSETTS: Hampshire County, Puffer's Pond, Amherst, on *Lactarius* sp., 22 Sep. 1982, *M. E. Barr 6900* (NY). NEW JERSEY: Sussex County, Stokes State Forest, S of High Point State Park, on *Lactarius* sp., 26 Sep. 1976, *C. T. Rogerson 76-157* (NY). NEW



FIGS. 30–43. *Hypomyces* species. 30–35. *H. banningiae*. 30, 31. Median longitudinal section through mature perithecia. 32, 33. Asci showing ascical apex. 34. Ascospore in optical section. 35. Ascospore in surface view. 36–43. *H. hyalinus*. 36–38. Median longitudinal section through mature perithecia. Anatomy of perithecial apex shown in FIG. 38. 39–41. Asci; ascical apex visible in FIGS. 40, 41. 42, 43. Ascospores in optical section. All IC except FIGS. 33, 40 (PC). FIGS. 30–35 from CTR 80-101; 36–43 from Bigelow 4359. Scale bars: FIGS. 30, 36 = 100 μm ; 31, 37 = 50 μm ; 32, 38, 39 = 40 μm ; 33–35, 40–43 = 10 μm .

YORK: Suffolk County, Wading River, on *Lactarius vellereus* (Fr.) Fr., Aug. 1905 (NYS, HOLOTYPE of *Peckiella hymenii*). NORTH CAROLINA: Henderson County, Green Cove Camp, S of Tuxedo, on *Lactarius* sp., 14 Sep. 1974, C. T. Rogerson 74-126 (NY), same locality and host, 20 Sep. 1980, C. T. Rogerson 80-101 (NY); Macon County, Highlands, on *Lactarius piperatus* (L.: Fr.) S. F. Gray, 30 Jul. 1973, J. Menge 511 (NY). SOUTH CAROLINA: Oconee County, Bunell's Area, Sumter National Forest, on *Lactarius* sp., 30 Jul. 1985, A. Methven 4107 (NY). VIRGINIA: Prince William County, Prince William Forest Park, on *Lactarius* sp., Sep. 1974, E. Lang s.n. (NY).

NOTES. For typification of this species and others described by C. H. Peck see Barr et al. (1986).

Hypomyces banningiae is reminiscent of *H. macrosporus* in possessing a white to buff subiculum and large ascospores. Ascospores of the latter species, however, are bicellular and clearly apiculate.

Perithecial anatomy of *Hypomyces banningiae* is unusual in that the wall and papilla are basically of intertwined hyphae. Unlike other species of *Hypomyces*, there are no circular to elliptic elements in the perithecial papilla; in this regard, *H. banningiae* resembles the polyporiculous species *H. chrysostomus* and *H. lanceolatus* Rogerson & Samuels (Rogerson and Samuels, 1993).

Attempts to germinate ascospores of *H. banningiae* were not successful and we have not observed any anamorph associated with perithecia in nature.

3. *Hypomyces hyalinus* (Schweinitz: Fries) L.-R. Tulasne, Ann. Sci. Nat. Bot., Sér. IV, 13: 11. 1860.

FIGS. 3, 36–43

- ≡ *Sphaeria hyalina* Schweinitz, Schriften der Naturforschenden Gesellschaft zu Leipzig 1: 30. 1822; Fries, Syst. Mycol. 2: 339. 1823.
- ≡ *Peckiella hyalina* (Schweinitz: Fries) Saccardo, Syll. Fung. 9: 945. 1891.
- ≡ *Apiocrea hyalina* (Schweinitz: Fries) H. Sydow, Ann. Mycol. 18: 186. 1920.
- = *Hypomyces vanbruntianus* Gerard, Bull. Torrey Club 4: 65. 1873.
- ≡ *Peckiella vanbruntiana* (Gerard) Saccardo, Syll. Fung. 9: 944. 1891.
- = *Hypomyces inaequalis* Peck, Bull. Torrey Club 25: 328. 1898.

Anamorph. None known.

Subiculum white, pallid in age or tinged with pink, yellow, or brown, effused, usually entirely covering the host, the host typically unexpanded with pileus completely deformed and fused to the stipe, the gills obliterated, KOH–; subicular hyphae loosely interwoven

between perithecia with few free ends visible, septate, branched, 2–3 μm wide. Perithecia ovate to obpyriform, 250–325 \times 180–210 μm , pallid to light orange or brownish, colorless in KOH; immersed in the subiculum except for the papilla, KOH–; papilla broadly truncate, 125 μm high, 60–100 μm diam at apex. Perithecial wall 15–20 μm wide, cells fusiform in section, 10–15 μm long, 3–5 μm wide, walls 1.0–1.5 μm thick, nonpigmented. Cells of the papilla tending to be arranged in somewhat divergent files, 7–10 μm long, 3–5 μm wide, walls 1 μm thick, the terminal cell of each file clavate to subglobose, 7–10 \times 4–6 μm , wall 0.5 μm thick; cells of the papilla progressively merging with the periphyses. Asci cylindrical to narrowly clavate, 110–130 \times 4–6 μm , apex thickened and with a pore. Ascospores fusiform, subcymbiform to oblancoolate, 15–20 \times 4.5–6.5 μm , two celled, septum near the base; apiculate and prominently verrucose, apiculi acute to obtuse, 1–2.5 μm long, verrucae 1.0–1.5 μm high.

HABITAT. On basidiocarps of *Amanita* species, including *A. frostiana* (Peck) Sacc., *A. rubescens* (Pers.: Fr.) S. F. Gray, *A. muscaria* (L.: Fr.) Hooker.

TYPE. As *Sphaeria hyalina* Schweinitz, Syn. Fung. 1191-45, Herb. Schw. Michener Set, Salem (North Carolina), Pocono (Pennsylvania) (PH!); as *Sphaeria hyalina* Schweinitz, Herb. Schw., Sal. and Pocono (FH!). Seaver (1910) indicated North Carolina as the type locality.

DISTRIBUTION. Canada (Nova Scotia, Quebec). China (Teng, 1934). Japan (Tubaki, 1975). United States (Connecticut, Delaware, District of Columbia, Georgia, Idaho, Indiana, Iowa, Louisiana, Maine, Maryland, Massachusetts, Michigan, Missouri, North Carolina, New Hampshire, New Jersey, New York, Ohio, Pennsylvania, Tennessee, Vermont, Virginia, Washington, West Virginia, Wisconsin).

SPECIMENS EXAMINED (SELECTED). USA. CONNECTICUT: West Haven, on agaric (? *Amanita*), Nov. 1888, R. Thaxter (BPI 630778); Windham County, Natchaug State Forest, on agaric, 14 Sep. 1991, V. Spock (NY). MAINE: on stout thick stemmed agaric, September, C. L. Fox (NYS, TYPE of *H. vanbruntianus*). MASSACHUSETTS: Franklin County, Mt. Toby, Sunderland, on agaric, 5 Oct. 1977, B.M.C. Foray comm. M. E. Barr Bigelow 6384 (NY); Lamoille County, Stowe, Pinnacle trail, on *Amanita muscaria*, 21 Jul. 1964, H. E. and M. E. Bigelow (MEBB 4359 pp) (NY). NEW YORK: Dutchess County, Poughkeepsie, on pileus, stipe and gills of unknown agaric, October, W. R. Gerard (NYS, TYPE of *H. inaequalis*). NORTH CAROLINA: Macon County, Highlands, Highlands Biological Station, in hemlock grove, associated with *Amanita frostiana*, 31 Jul. 1961, R. H. Petersen and CTR (NY); Macon County, same locality, two collections, on ? *Amanita* sp., 28 Jul. 1961, R. H. Petersen and CTR (NY); Transylvania County, above Rainbow Falls of Horsepasture River, Bohaynee Rd., on ? *Amanita* sp., 14 Aug. 1961, R. H. Petersen and CTR (NY).

NOTES. *Hypomyces hyalinus* is presumed only to occur on *Amanita* species because the only healthy basid-

iocarps associated with the *Hypomyces* are species of *Amanita*. The parasitism of *H. hyalinus* is so complete and the host so distorted, that in the absence of nearby healthy basidiocarps it is not possible to determine the host. Despite many attempts over many years, we have not observed ascospore germination in this species nor have we observed any consistently associated anamorph.

4. *Hypomyces lactifluorum* (Schweinitz : Fries) L.-R. Tulasne, Ann. Sci. Nat. Bot., Sér. IV, 13: 11. 1860.

FIGS. 4, 44–47

= *Sphaeria lactifluorum* Schweinitz, Schriften der Naturf. Ges. Leipzig 1: 30. 1833; Fries, Syst. Mycol. 2: 338. 1823.

= *Hypomyces insignis* Berkeley & Curtis in Berkeley, J. Linn. Soc. London 9: 424. 1867.

= *Hypomyces purpureus* Peck, Bull. Torrey Club 25: 327. 1898.

Anamorph. None known.

Subiculum pale yellowish orange to bright orange, in age becoming deep red, reddish purple to very dark purple, occasionally fading to pink, usually covering the aborted pileus, stipe and deformed gills of the host; subicular hyphae 3–5 μm wide, septate, much branched, branching very irregular, often at right angles, densely compacted but remaining filamentous, smooth, occasionally some cells swollen to 10 μm diam; KOH+ purple. Perithecia ovate to obpyriform, 400–600 \times 200–450 μm , deep orange to reddish purple, usually darker than the surrounding subiculum, immersed except for papilla, KOH+; papilla averaging 120 μm high, 120 μm wide. Perithecial wall 25–30 μm wide laterally, cells fusoid, 7–15 μm long, ca 5 μm wide, walls 1.5 μm thick, nonpigmented. Perithecial apex of circular to elliptic cells tending to be arranged in files and with long axis parallel to long axis of perithecium, 5–15 \times 3–7 μm , walls 1.5 μm thick, cells around the ostiolar opening clavate, 3–5 μm wide; ostiolar canal periphysate. Asci long cylindrical, 200–260 \times 5–10 μm , apex thickened and with a pore. Ascospores fusiform, 35–40 \times 4.5–7 μm , two celled, prominently verrucose and apiculate; verrucae 1–1.5 μm high, apiculi 4.5–7.5 μm in length, acute, straight or curved, septum median.

TYPE. NORTH CAROLINA: Salem; Pennsylvania, Bethlehem. One packet as *Sphaeria lactifluorum* Schw., Syn. Fung. 1190-44 Herb. Schweinitz, Michener Set (PH!). Seaver (1910) indicated North Carolina as the type locality.

DISTRIBUTION. Known only from North America. Canada (Manitoba, New Brunswick, Nova Scotia, Ontario, Prince Edward Island, Quebec). United States (recorded from all

states east of the Mississippi and from Arizona, Colorado, Idaho, Iowa, Kansas, Missouri, New Mexico, North Dakota, Oregon, Texas, Washington). Guatemala. Mexico (Chiapas, Chihuahua, Distrito Federal, Durango, Guerrero, Hidalgo, Jalisco, México, Morelos, Nuevo León, Puebla, Veracruz).

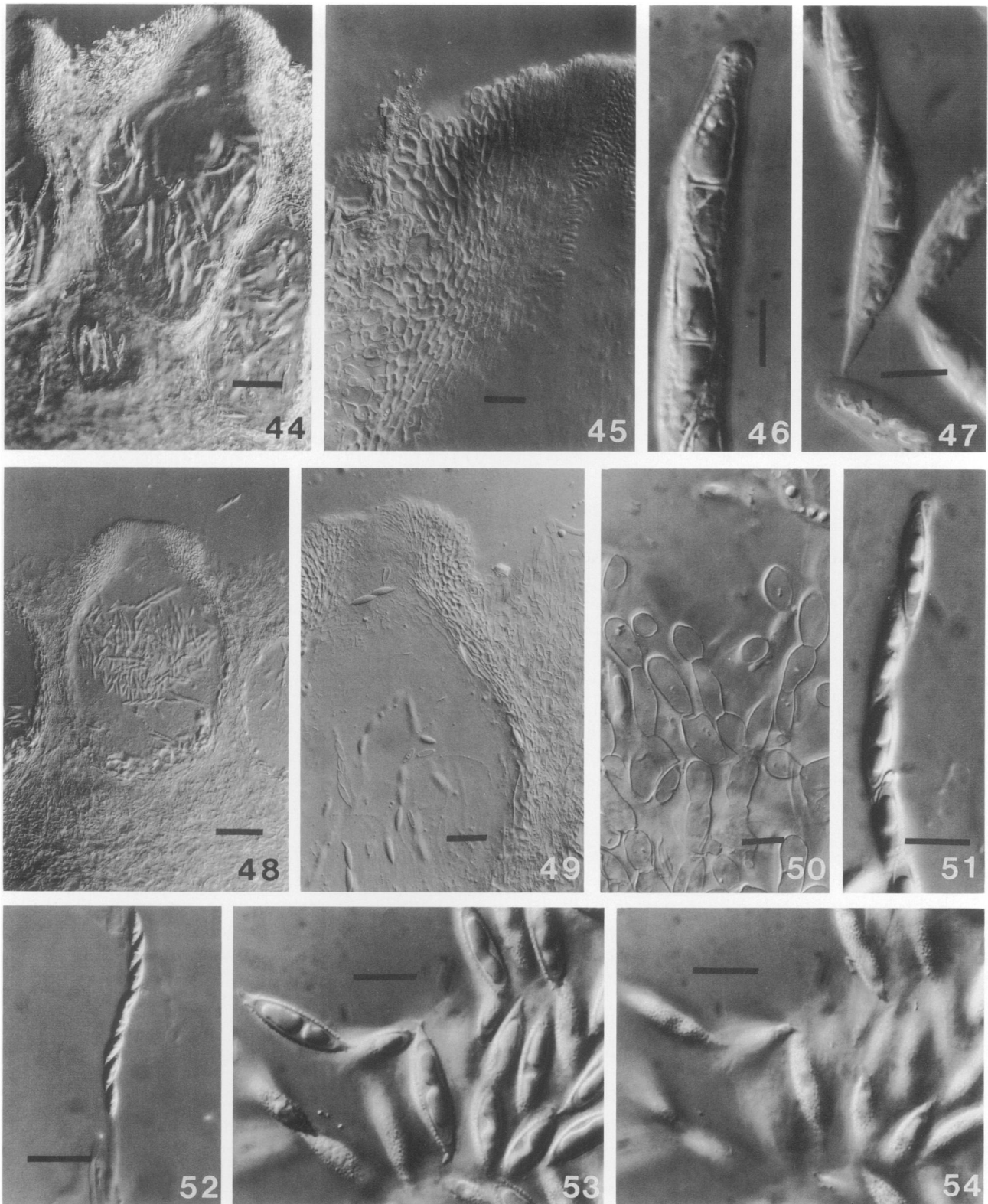
SPECIMENS EXAMINED (SELECTED). CANADA. NOVA SCOTIA: Kings County, "west" Gaspereaux Valley, (Russulaceae), 15 Sep. 1977, K. A. Harrison (ACAD 11977). USA. MICHIGAN: Cheboygan County, woods near Topinabee, on *Russula brevipes* Peck, 25 Jul. 1964, R. L. Shaffer (NY); Cheboygan County, University of Michigan Biological Station, pine woods, 31 Jul. 1964, C. T. Rogerson (NY). PENNSYLVANIA: on *Lactarius* sp., August, Charles McIlvaine (NYS, TYPE of *H. purpureus*).

NOTES. Despite many attempts using different physical conditions and pretreatments, we have never observed ascospores of this species to germinate. We have not consistently found an anamorph associated with developing or mature perithecia in nature.

Hanlin (1963) has described perithecial and ascogony ontogeny in this species. The species is common in Mexico, where it is known under several colloquial names (Herrera and Guzmán, 1961).

Hypomyces insignis is based on a Botteri collection from Orizaba, Mexico. When Seaver requested a loan of the type from Kew, he received instead drawings of a section through perithecia and subiculum, an ascus, and three ascospores plus descriptive details. Ascospores were illustrated and described as 30–35 \times 8 μm , two celled, verrucose, and apiculate. Drawings of two spores show a median septum. Despite these details, i.e., bicellular ascospores, Seaver (1910) listed *H. insignis* as a questionable synonym of *H. transformans* Peck, which has unicellular ascospores. As indicated by Rogerson and Samuels (1989), *H. transformans* occurs on boletes. The descriptions and drawings indicate to us that *H. insignis* is *H. lactifluorum*.

Hypomyces lactifluorum and *H. macrosporus* are distinguished only on perithecial color and reaction to KOH. Perithecia and the subiculum of the latter are white and do not react to KOH. We have found *H. lactifluorum* once (CTR 69-113) in Michigan with a cluster of *H. macrosporus*. Harrison and Grund (1977) found typical orange specimens of *H. lactifluorum* mixed with specimens that were variously "white," white with orange-streaks and orange-red with white streaks. They were convinced that the "white" forms were albinos of *H. lactifluorum* and need not be distinguished as a separate taxon because of what they interpreted as a minor change in genotype. We studied the specimens that they deposited in Herb. ACAD 11977. These comprised three basidiomata of the whitish form and two of the typical orange-red form. No KOH reaction was detected on the white form while only the reddish streaks of the whitish form became purple in KOH.



FIGS. 44–54. *Hypomyces* species. 44–47. *H. lactifluorum*. 44, 45. Median longitudinal section through mature perithecia. Anatomy of perithecial apex shown in FIG. 45. 46. Ascical apex. 47. Ascospore in optical section. 48–54. *H. lateritius*. 48, 49. Median longitudinal section through mature perithecia. Anatomy of perithecial apex shown in FIG. 49. 50. Moniliform hyphae from the subiculum. 51, 52. Asci; ascical apex visible in FIG. 51. 53. Ascospores in optical section. 54. Ascospores in surface view. All IC. FIG. 44. from *CTR*, 31 Jul. 1964; 45–47 from *Shaffer*, Jul. 1964; 48, 49, 52–54 from *Sheine*, Aug. 1990; 50, 51 from *Homola*, Sep. 1990. Scale bars: FIGS. 44, 48 = 50 μm ; 45, 49 = 20 μm ; 46, 47, 50, 51, 53, 54 = 10 μm ; 52 = 40 μm .

5. *Hypomyces lateritius* (Fries : Fries) L.-R. Tulasne, Ann. Sci. Nat. Bot., Sér. IV, 13: 11. 1860.

FIGS. 5, 48–54

- ≡ *Sphaeria lateritia* Fries, Syst. Mycol. 2: 338. 1823.
 ≡ *Hypocrea lateritia* (Fr.) Fries, Summa Veg. Scand. 383. 1849.
 ≡ *Peckiella lateritia* (Fr.) Maire, Ann. Mycol. 4: 331. 1906.
 ≡ *Byssonectria lateritia* (Fr.) Petch, J. Bot. Lond. 75: 220. 1937.
 = *Hypomyces volemi* Peck, Bull. Torrey Club 27: 20. 1900.
 = *Peckiella hymenioides* Peck, Bull. Torrey Club 34: 102. 1907.
 = *Hypomyces camphorati* Peck, New York State Bull. 205: 23. 1905 (1906).
 ≡ *Peckiella camphorati* (Peck) Seaver, Mycologia 2: 68. 1910.

Anamorph. None proven.

Subiculum white to lemon yellow when fresh, buff, yellowish orange, tawny, at full maturity becoming ochraceous, brick red and brown or reddish black, of loose texture, covering and apparently restricted to the deformed gill surfaces; subicular hyphae 2–5 μm wide, septate, much branched densely compacted but remaining filamentous and with many free ends at subicular surface and sometimes forming enlarged terminal or intercalary, globose to ellipsoid cells 18–25 \times 7–9 μm , KOH–. Perithecia ovate to obpyriform, 300–470 \times 170–360 μm , dark amber to reddish brown, becoming lighter and yellowish in KOH, immersed in the subiculum or half free, KOH–; papilla 120–150 μm high, 100–175 μm wide at apex. Perithecial wall 15–30 μm wide, cells fusiform to sinuous, 7–15 μm long, 3–6 μm wide, walls 1.0–1.5 μm thick, nonpigmented. Cells of the papilla with long axis parallel to long axis of perithecium and tending to be arranged in files, 7–15 μm long, 3–5 μm wide, walls 0.5–1.0 μm thick; cells around the ostiolar opening tending to be narrowly clavate, 3 μm wide, merging with the periphyses, cells of the papilla continuous with subicular hyphae at the surface, ostiolar canal periphysate. Asci long cylindrical, 90–150 \times 4–8 μm , apex thickened and with a pore. Ascospores fusiform, lanceolate or naviculate, (11.2–)15–21(–30) \times (2.6–)3.6–4.8(–6.0) μm , one celled but with inclusions giving the appearance of a median septum, verrucose and apiculate, verrucae <0.5 μm high, apiculi (0.5–)1.7–2.9(–4.2) μm long and acute.

HABITAT. On *Lactarius* species including *L. camphoratus* (Fr.) Fr., *L. chelidonium* Peck, *L. controversus* (Fr.) Fr., *L. deliciosus* (Fr.) S. F. Gray, *L. rufus* (Fr.) Fr., *L. sanguifluus* Fr., *L. thejogalus* (Fr.) S. F. Gray, *L. trivialis* (Fr.) Fr.

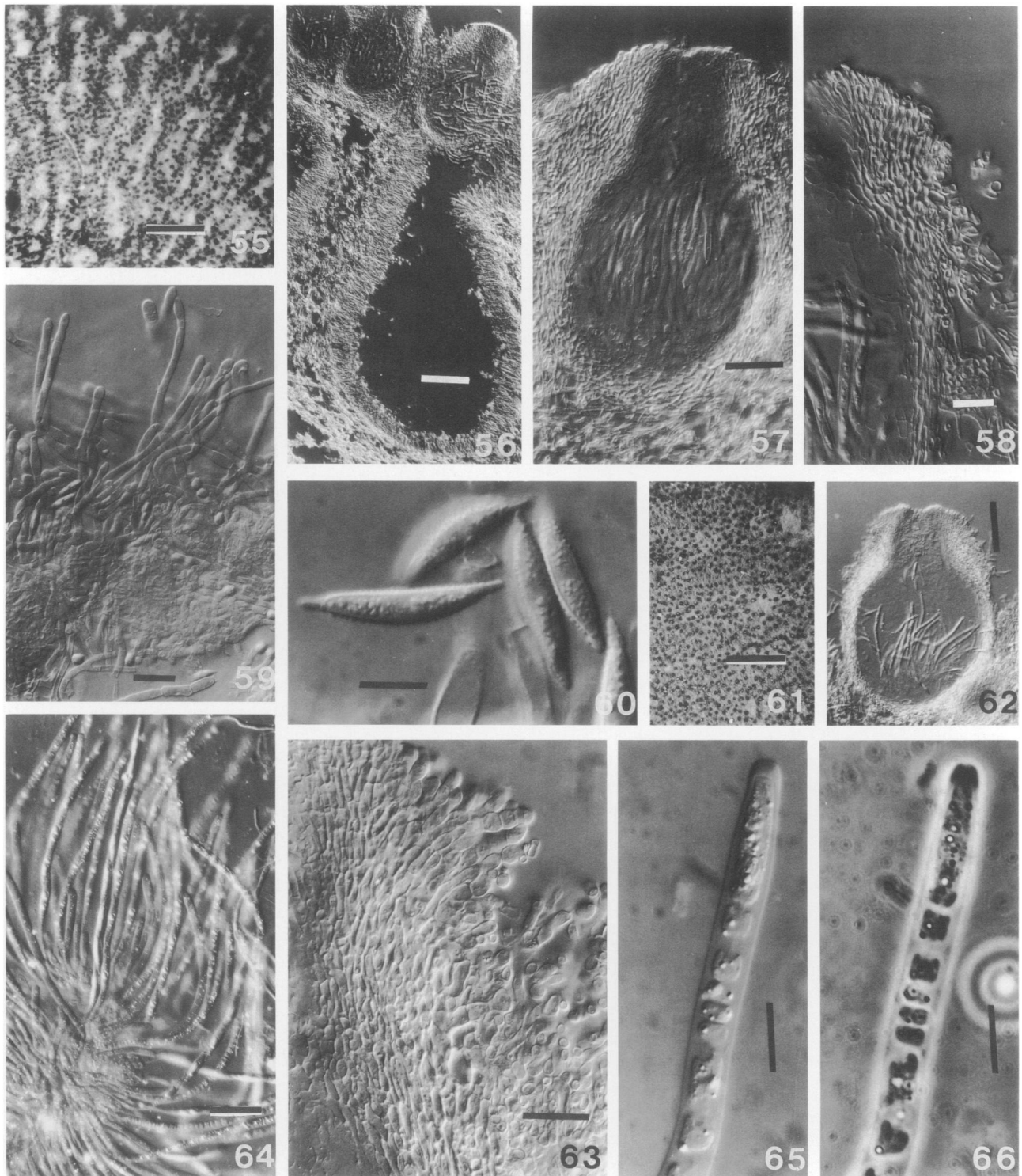
DESCRIPTION AND ILLUSTRATIONS. Schmid and Schmid (1991; Nr. 77).

TYPE. SWEDEN. Smålaand, on *Agaricus deliciosus* Fr., Jul.

DISTRIBUTION. Apparently world-wide wherever species of *Lactarius* occur. Canada (British Columbia, Nova Scotia, Ontario, Quebec). Europe (Austria, Belgium, Czechoslovakia, Denmark, England, Finland, France, Germany, Italy, Russia, Sweden). Mexico. New Zealand. United States (Alabama, Alaska, California, Colorado, Connecticut, Idaho, Iowa, Maine, Maryland, Massachusetts, Michigan, Minnesota, Montana, New Jersey, New Hampshire, New Mexico, New York, North Carolina, Ohio, Oregon, Pennsylvania, Rhode Island, South Carolina, Tennessee, Vermont, Virginia, Washington, Wisconsin, Wyoming).

SPECIMENS EXAMINED (SELECTED). FRANCE. Meaux, (on agaric, Autumn 1893, *P. Dumée* (Briosi e Cavara, I Funghi parassiti delle piante coltivate od utili 237, BPI 630776; immature). GERMANY. WESTFALIA: "zwischen Littlefeld und Welschenennst, Kreis Siegen," on *Lactarius deliciosus*, 3 Oct. 1923, A. Ludwig (Sydow, Mycotheca germanica 2140, BPI 630785); "Kr. Siegen: [?] bei Burgholdinghausen," on *Lactarius deliciosus*, 5 Aug. 1926, A. Ludwig (BPI 630773). GREAT BRITAIN. (Collecting information unknown), "Sphaeriacei Britannici Chas. B. Plowright, 1873 5. *Hypomyces lateritius*. Tul." (BPI 630775); Kings Lynn, on *Lactarius deliciosus*, Oct. 1882, C. B. Plowright (Thümen, Mycotheca uniersalis 2164, BPI 630774). ? ITALY. Moeria, on *Lactarius aurantiacus*, "Aug ? 1920," (?) *G. Bresadola* (BPI 630784). USA. ALABAMA: Talladega National Forest, on *Lactarius* sp., 23 Sep. 1992, CTR (BPI, NY). CONNECTICUT: Tolland County, Gay City State Park, on *Lactarius deliciosus*, 15 Sep. 1990, R. L. Homola (NY). MASSACHUSETTS: Hampshire County, Amherst, on *Lactarius camphoratus*, 19 Sep. 1917, P. J. Anderson (NY); Middlesex County, Lincoln, in riparian woodland on *Lactarius camphoratus-rufus* complex, Sep. 1991, B. Maleson (BPI, NY). NEW JERSEY: Malaga, on agaric (Russulaceae), Autumn 1874, J. B. Ellis (BPI 630779); Newfield, woods, on *Lactarius* sp., 29 Sep. 1901, C. L. Shear 918 (BPI 630782); Gloucester County, vic. Glassboro, on *Lactarius* sp., 17, 18 Aug. 1984, Northeastern Foray comm. S. Stein (CTR 84-11: NY). NEW YORK: Suffolk County, Port Jefferson, on hymenium of *Lactarius camphoratus*, August, C. H. Peck (NYS, HOLOTYPE of *H. camphorati*); Port Jefferson, on hymenium of *Lactarius camphoratus*, Aug. 1905, C. H. Peck (NYS); Westchester County, Pound Ridge, on *Lactarius* sp., 3 Aug. 1990, S. Sheine (NY). NORTH CAROLINA: Macon County, Blue Valley off Clear Creek Rd., along Overflow Creek, 35°00'N, 83°15'W, on *Lactarius camphoratus*, 14 Oct. 1990, R. H. Petersen (BPI 1109923, NY). PENNSYLVANIA: parasitic on hymenium of *Lactarius volemus*, Charles McIlvaine (NYS, HOLOTYPE of *H. volemus*). TENNESSEE: Great Smoky Mts. Natl Park, above Gatlinburg, on *Lactarius* sp., 21 Aug. 1939, C. L. Shear (BPI 630783). VERMONT: Newfane, on hymenium of *Lactarius uvidus*, August, G. S. Burlingham (NYS, HOLOTYPE of *Peckiella hymenioides*).

NOTES. *Hypomyces lateritius* is a variable species that may ultimately be proven to be a complex. Collections found on species of the *Lactarius camphoratus* complex tend to have a yellowish subiculum and slightly larger ascospores. We have not seen the type specimen of *H. lateritius*, assuming that it exists. Seaver (in litt., 1909, NY) requested the type from UPS and received a letter



FIGS. 55–66. *Hypomyces* species. 55–60. *H. lithuanicus*. 55. Habit of perithecia of distorted gill surface of *Lactarius torminosus*. 56. Perithecia on edge of gills of host showing fully developed hymenium of the host. 57, 58. Median longitudinal section through mature perithecia. Anatomy of perithecial apex shown in FIG. 58. 59. Hyphae from the subiculum. 60. Ascospores in optical section. 61–66. *H. luteovirens*. 61. Habit of perithecia on distorted gill surface of *Russula* sp. 62, 63. Median longitudinal section through mature perithecia. Anatomy of perithecial apex shown in FIG. 63. 64–66. Asci; ascus apex visible in FIGS. 65, 66. All IC except FIGS. 55, 61 (BF); 66 (PC). FIGS. 55, 60 from *Mycotheca germanica* 490 (BPI, as *H. torminosus*); 56, 58, 59 from CTR 82-73; 57 from Arnold, 6 Sep. 1963. Scale bars: FIGS. 55, 61 = 1 mm; 56, 62 = 100 μ m; 57 = 50 μ m; 58 = 20 μ m; 59, 63, 64 = 40 μ m; 60, 65, 66 = 10 μ m.

and specimen from the then Director at Uppsala. Dr. Juel's letter (Uppsala, Oct. 27, 1909, on file with specimen in NY) indicates "In the Bot. Mus. of Upsala there is a specimen of *Hypomyces lateritius*, collected by one of the sons of E. Fries in 1849, and as he was then only 15 years old, the determination evidently must be made by E. Fries himself." The specimen is labeled "*Hypomyces lateritius* Fr., Upsalia in *Lactario deliciosus*, 1849, E. P. Fries, Herb. E. Fries."

Hypomyces lateritius apparently has not been grown in pure culture from ascospores, and we have not succeeded in germinating ascospores of the species. Tubaki (1975) found the species on *Lactarius piperatus* in Japan but was likewise unable to germinate ascospores. Helfer (1991) has given *Cladobotryum tulasnei* (G. Arnold) Helfer as the anamorph of *H. lateritius* based upon association on the host. The illustration of this anamorph provided by Helfer, however, is strongly suggestive of *C. verticillatum*. This *Cladobotryum* is the proven anamorph of *H. armeniacus* but has a wide host range.

6. *Hypomyces lithuanicus* Heinrichson-Normet, Eesti NSV Tead. Akad. Toim., Biol. 18: 76. 1969.

FIGS. 6, 55–60

Anamorph. None proven.

Subiculum cream-ochre to cinnamon, covering and apparently restricted to the deformed gills of the host; subicular hyphae 3–7 μm wide, much branched and compact but remaining filamentous and with many free ends at the subicular surface giving the subiculum a granular or velvety aspect, cells sometimes slightly enlarged and hyphal elements tending to be moniliform, KOH+ reddish brown becoming pale yellow in lactic acid. Perithecia subglobose to ovate or obpyriform, 200–300 \times 120–200 μm , dark amber to brown becoming reddish brown in KOH and pale yellow in lactic acid, immersed in the subiculum with only papilla protruding, KOH+ reddish brown; papilla obtuse, 100–150 μm high, 120–150 μm wide at apex. Perithecial wall 15–25 μm wide, cells ellipsoidal to sinuous, 7–15 μm long \times 3 μm wide, walls 1.5 μm thick, nonpigmented. Cells of the papilla angular, small, 3–5 μm diam, walls 1–1.5 μm thick, cells surrounding the ostiolar opening tending clavate, 3 μm wide, walls 1.5 μm thick, merging with the periphyses; cells of the papilla continuous with subicular hyphae at the surface. Asci cylindrical, 100–150 \times 6 μm wide, apex thickened and with a pore. Ascospores fusiform, (13.5–) 17.1–21.7(–25.4) \times (3.4–)4.0–5.0(–5.8) μm , one celled, verrucose and apiculate, verrucae <0.5 μm high, apiculi (1.6–)2.2–3.2(–4.0) μm long and acute.

HABITAT. Gill surface of *Lactarius torminosus* and *L. pubescens* Fr.

LECTOTYPE. LITHUANIA. Krs. Varena, on *Lactarius* sp. (*L. torminosus*), 24 Aug. 1962, J. Mazelaitis (TIAA 44394b), LECTOTYPE designated herewith.

DISTRIBUTION. Canada (Ontario), Europe (Germany, Lithuania), United States (Connecticut, Michigan, Wisconsin).

ADDITIONAL SPECIMENS EXAMINED. CANADA. ONTARIO: Big Rideau Lake, Exe Island, on *Lactarius torminosus*, 29 Sep. 1974, N. Korf s.n. (NY). GERMANY. BRANDENBURG: Röntgenenthal bei Bernau, on *Lactarius torminosus*, 18 Sep. 1906, H. Sydow (Sydow, *Mycotheca germanica* 490: BPI 630933, S); Weimar, Belvedere, on *Lactarius pubescens* Fr., 6 Sep. 1963, G. R. W. Arnold (NY: ascospores all aborted). USA. CONNECTICUT: Litchfield County, Camp Jewell YMCA Camp, near North Colebrook, on *Lactarius pubescens*, 25 Sep. 1982, CTR 82-73 (NY). MICHIGAN: Presque Isle County, on *Lactarius pubescens*, 7 Oct. 1988, A. S. Methven 5365 (NY). WISCONSIN: Dane County, Blackhawk State Preserve, on *Lactarius pubescens*, 25 Sep. 1993, A. S. Methven 7638 (BPI, NY).

NOTES. Helfer (1991) described *Cladobotryum arnoldii* W. Helfer as the anamorph of *H. torminosus*, which is *H. lithuanicus* in our sense, but this was not proven through the study of cultures derived from ascospores. We have not been able to induce ascospore germination in this species, and we have not consistently found any anamorph associated with it. Thus we doubt the connection between *C. arnoldii* and *H. lithuanicus*.

Hypomyces lithuanicus replaces the older *H. torminosus* (Durieu & Montagne) L.-R. & C. Tulasne. The type collection of *H. torminosus* [*Sphaeria torminosa*: ALGERIA. On *Lactarius torminosus*, Durieu (PC, Herb. Montagne!)] includes only a *Sphaerostilbella* like (*sensu* Seifert, 1985) hypocrealean ascomycete with nearly superficial perithecia on the gill surface of an agaric. Ascospores in this collection are considerably smaller (7–8.8 \times 2.5–3 μm) than is reported for *H. torminosus*, and are bicellular and nonapiculate. Thus the type specimen of *H. torminosus* is not in accord with current usage (e.g., Plowright, 1882; Maire, 1911; Arnold, 1972; Helfer, 1991). The next oldest names for this species are *H. thiryanus* Maire and *H. vuilleminianus* Maire. We have not been able to locate type material of *H. thiryanus* (MPU, NCY, P, PC) or *H. vuilleminianus* (MPU). Maire's (1899) description and illustration of *H. vuilleminianus* on *Lactarius deliciosus* from France suggests that it is *H. lateritius* (see Seaver, 1910).

Maire (1911) reported having examined Montagne's specimen of *Sphaeria torminosa* in PC. Although he reported that ascospores in that collection are immature, he had no doubt that *H. torminosus* was an older name for *H. thiryanus*. As we have noted above, the type collection of *S. torminosa* is quite different from the current concept of *H. torminosus*. Maire may have assumed that the small, nonapiculate ascospores were immature but would eventually enlarge and be-

come apiculate. The ascospore that he (Maire, 1911, Pl. XVI, Fig. 13) illustrated for *H. torminosus* agrees well with the concept of the species that we are now calling *H. lithuanicus*, and it is highly likely that should the type of *H. thiryanus* be found it will prove to be the correct name for the species. Unfortunately, because the original description of *H. thiryanus* did not include ascospore measurements, we are not able to judge its taxonomy today.

Heinrichsen-Normet (1969) considered that *H. lateritius* and *H. torminosus* were synonymous, and he described *H. lithuanicus*, also with unicellular ascospores and also on a *Lactarius* species. According to Arnold (1972) type material of *H. lithuanicus* comprises two pieces which he has numbered respectively 44394a and b; 44394a is a basidioma of *Lactarius deliciosus* considered by Arnold to be parasitized by *H. lateritius*, while 44394b is a basidioma of *L. torminosus* considered by Arnold to be parasitized by *H. torminosus*. Arnold did not designate a lectotype. We have examined type material of *H. lithuanicus* and have found that the apical portion of perithecia in 44394b are reddish in KOH while the rest of the perithecium remains brown. Perithecia in the portion numbered by Arnold as 44394a are brown and remain unchanged in KOH. We accord the reaction of perithecia to KOH great taxonomic significance in *Hypomyces* (see Rogerson and Samuels, 1993). Arnold (1972) was not able to locate type material of *Sphaeria torminosa* (in lit. 1993) and was thus not aware of the discrepancy between the type and the current concept. We accept that *H. lateritius* and *H. torminosus* are distinct species and have designated the part of the type of *H. lithuanicus* that Arnold identified as *H. torminosus* (44394b) as the lectotype of *H. lithuanicus*. Therefore, *H. lithuanicus* is the oldest available name for the fungus currently but incorrectly known as *H. torminosus*.

Hypomyces lateritius and *H. lithuanicus* differ not only in the reaction of their perithecia to KOH but also in the sizes of their ascospores. Ascospores of specimens having KOH⁻ perithecia measure (N = 413) (11.2–)15–21(–30) × (2.6–)3.6–4.8(–6.0) μm, apiculus = 2.3 ± 0.6 μm; whereas ascospores from specimens having KOH⁺ perithecia are somewhat larger (N = 94), (13.5–)17.1–21.7(–25.4) × (3.4–)4.0–5.0(–5.8) μm, apiculus = 2.7 ± 0.5 μm. Arnold (1972) found that the average of 100 ascospores of *H. torminosus* (as *Peckiella torminosa*) measured from the basidiomata of *L. torminosus* was 18.4 × 4–5 μm, and the average of 1900 ascospores measured from 18 additional collections was 21.3 μm long. He further distinguished between the two species on the basis of their biology. For him, *H. lateritius* tended to totally deform the hymenium of the host agaric, while deformation induced by *H. torminosus* (= *H. lithuanicus*) was partial. We have not observed these biological dif-

ferences, but Arnold has examined far more collections of *H. lithuanicus* than we have.

We have not been able to germinate ascospores from either *H. lithuanicus* or *H. lateritius*, and we have not found any anamorph consistently associated with either. Helfer (1991) considered *Cladobotryum arnoldii* to be the anamorph of *H. lithuanicus* (as *H. torminosus*) apparently because it was found on *Lactarius pubescens*, a known host of *H. lithuanicus*. He did not observe ascospore germination of the *Hypomyces*.

7. *Hypomyces luteovirens* (Fries : Fries) L.-R. Tulasne, Ann. Sci. Nat., Sér. Bot. IV, 13: 13. 1860 *emend* Plowright, Grevillea 11: 46. 1882. FIGS. 7, 61–66

= *Sphaeria luteovirens* Fr., Kongl. Vetensk. Akad. Handl. 38: 251. 1817. Fr. Syst. Mycol. 2: 339. 1823.

= *Hypocrea luteovirens* (Fr. : Fr.) Fries, Summa Veg. Scand. 383. 1849.

= *Peckiella luteovirens* (Fr. : Fr.) Maire, Ann. Mycol. 9: 318. 1911.

= *Hypomyces atra* (Fries) Cooke, Grevillea 12: 80. 1883.

= *Hypocrea atra* Fr., Summa Veg. Scand. 564. 1849 (*nomen nudum*).

= *Peckiella atra* (Fries) Saccardo, Syll. Fung. 9: 944. 1891.

Anamorph. None known.

Subiculum at first yellowish to bright yellow, then yellowish green to dark green, finally blackish green, covering the deformed gills and often the stipe, sometimes spreading to the top of the pileus of the host; subicular hyphae 3–5.5 μm wide, much branched, septate, much entangled, remaining filamentous; hyphae at the surface with many 3 μm wide free ends and short cells with constrictions at the septa and mimicing the hyphae of the perithecial apex, KOH⁻. Perithecia broadly ovate to obpyriform, 380–485 × 180–290 μm, yellow when fresh, olivaceous to blackish when dry, usually darker than the surrounding subiculum, immersed except for papilla; papilla truncate or obtuse, 96–120 μm high, 180–230 μm wide at apex; KOH⁻. Perithecial wall ca 25 μm wide laterally, of sinuous 3–4 μm wide hyphae with nonpigmented walls. Perithecial apex of hyphae constricted at septa and appearing moniliform with cells 5–7 μm long, 4–5 μm wide and walls <0.5 μm thick; hyphae tending to separate from each other. Asci filiform to long cylindrical, 160–200 × 5–8 μm, apex thickened and with a pore. Ascospores fusiform to naviculate, 32–35 × 4.5–5.5 μm, one celled, nearly smooth to prominently verrucose and apiculate; verrucae to 1 μm high; apiculi 2.4–7.3 μm long, acute, straight or curved and sometimes hooked.

HABITAT. On gills, stipe and pileus of *Russula* species.

TYPE. SWEDEN. Granskogar, on underside of "Agaric. Russulae och Galorrhæi," Aug.–Sept. (UPS).

DISTRIBUTION. Widespread in north temperate regions: Europe (Czechoslovakia, Denmark, England, Estonia, France, Finland, Germany, Norway, Russia, Spain, Sweden, Switzerland). Canada (Alberta, British Columbia, Manitoba, New Brunswick, Nova Scotia, Quebec). United States (Alaska, Arizona, Colorado, Connecticut, Florida, Georgia, Idaho, Ohio, Maine, Maryland, Massachusetts, Michigan, Montana, New Hampshire, New Jersey, New Mexico, New York, North Carolina, Ohio, Oregon, Pennsylvania, Rhode Island, South Carolina, Tennessee, Texas, Utah, Vermont, Virginia, Washington, West Virginia, Wisconsin). Japan.

SPECIMENS EXAMINED (SELECTED). USA. CONNECTICUT: Litchfield County, Catlin Woods, White Memorial Foundation, S edge of Litchfield, on *Russula kromholzii* Singer, 6 Sep. 1980, CTR (NY); Tolland County, Salmon River State Forest, on *Russula* sp., 15 Sep. 1991, COMA Foray (NY). NEW YORK: Essex County, near Wadhams, Twin Valleys Camp, Plattsburg State College, on *Russula* sp., 9 Sep. 1967, S. J. Smith et al. (CTR 67-96) (NY). NORTH CAROLINA: Macon County, 4 km E of Highlands on Wilson Gap Rd. just off Bull Pen Rd., E slope of Little Fodderstack Mt., on *Russula* sp., 16 Aug. 1978, A. Y. Rossman 1282 and L. Spielman (BPI 630613).

NOTES. *Hypomyces luteovirens* is among the most distinctive of the *Hypomyces* species. It is particularly conspicuous for the yellow or green color that it imparts to the host in the course of infection, the large unicellular ascospores, and the peculiar anatomy of the perithecial apex. The perithecial apex of *H. luteovirens* is distinctive for the moniliform chains of cells that extend from the surface of the papilla.

We have never managed to germinate ascospores and have never found an anamorph associated with this species.

As indicated by Petch (1937), Berkeley and Broome (1851) used the name *Hypocrea luteovirens* for a species that grows on *Boletus*. Tulasne and Tulasne (1865), accepting and following this disposition, transferred *Hypocrea luteovirens* to *Hypomyces*. This error was pointed out by Plowright (1882), who described the fungus on *Boletus* as *Hypomyces tulasneanus* Plowright, maintaining the fungus on *Lactarius* as *Hypomyces luteovirens*. Thus we accept *Hypomyces luteovirens* (Fries) L.-R. Tulasne emend. Plowright.

Hypomyces viridis (Albertini & Schweinitz) Berkeley, based on *Sphaeria viridis* Albertini & Schweinitz (1805) is still being used by some mycologists (e.g., Helfer, 1991). The descriptions and illustrations of *S. viridis* by Albertini and Schweinitz are suggestive of *Hypomyces luteovirens* but no ascospores were described; they reported it as occurring on "*Lactifluus piperatus*" and "*Omphaliaque adusta*." According to Stafleu and Cowan (1976) the location of the herbarium of Albertini and Schweinitz is unknown, thus uncertainty about

Sphaeria viridis exists. Fries first (1817) treated it as a synonym of *S. luteovirens*, and later (Fries, 1823) as a variety of *S. luteovirens*. Nannfeldt (pers. comm., in lit. 16 Jun. 1950) reported that there is no specimen of *Sphaeria viridis* in the Fries Herbarium but an authenticated one of *Sphaeria luteovirens* Fr. does exist and this specimen represents the species that is known today as *H. luteovirens*.

Petch (1935) studied a specimen at K from Fries labelled "*Hypocrea (Hypomyces) atra* n. sp., cf. 'Summa,' p. 564, Upsaliae" and concluded that it was the same as *Hypomyces viridis* in his sense and is thus *H. luteovirens*.

8. *Hypomyces macrosporus* Seaver, *Mycologia* 2: 80. 1910. FIGS. 8, 67–70.

Anamorph. None known.

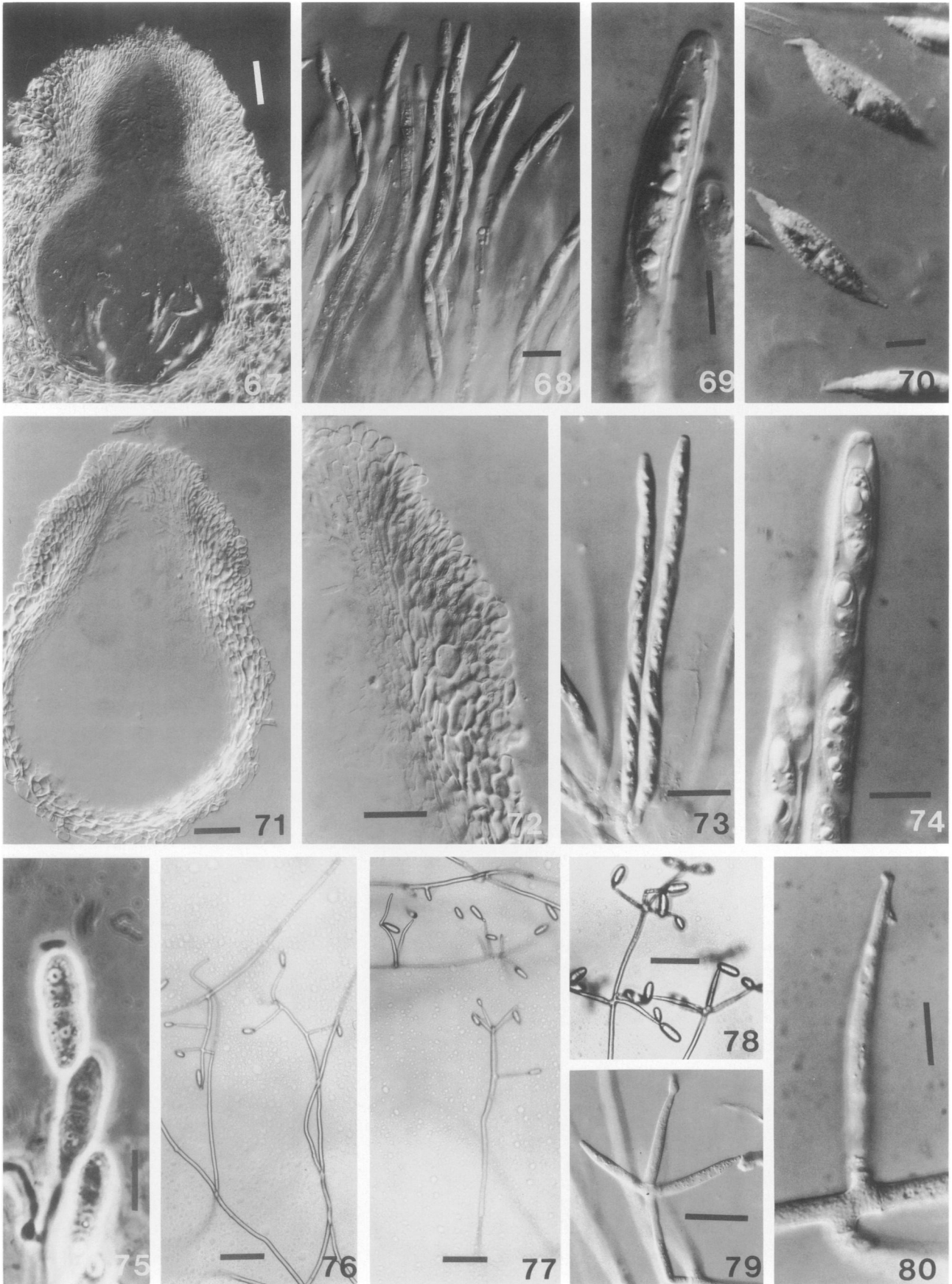
Subiculum white to buff, covering the deformed gills and stipe of the host; subicular hyphae 3–7 μm wide, becoming contorted with many cells enlarged to 15 μm or more, often globose giving a parenchymatous appearance in cross section, KOH–. Perithecia ovate to obpyriform, 325–485 \times 242–302 μm , buff to yellowish amber, immersed except for papilla, KOH–; papilla conoid, 95–100 μm high, 95–145 μm wide. Perithecial wall 25–30 μm wide laterally, cells \pm fusiform, 7–25 μm long, ca 6 μm wide, walls 1.5 μm thick, nonpigmented. Perithecial apex of circular to elliptic cells tending to be arranged in files and with long axis parallel to long axis of perithecium, 10–15 \times 5–6 μm , walls 1.5 μm thick, cells around the ostiolar opening clavate, ca 6 μm wide; ostiolar canal periphysate. Asci long cylindrical, 210–265 \times 7.5–10 μm , apex thickened and with a pore. Ascospores fusiform, 34–42 \times 5–7 μm , two celled, prominently verrucose and apiculate; verrucae 0.5–1.0 μm high, apiculi 3–7 μm in length, acute, straight or curved, septum median.

HABITAT. On Russulaceae.

TYPE. USA. ALABAMA: Lee County, Auburn (host known), fall 1898, F. S. Earle and C. F. Baker Alabama Biological Survey s.n. (NY!).

DISTRIBUTION. Mexico (Distrito Federal, México, Morelos) (Perez-Silva et al., 1983; Herrera and Guzmán, 1961). United States (Alabama, Connecticut, Maryland, New York, Ohio, South Carolina, Washington, West Virginia).

ADDITIONAL SPECIMENS EXAMINED. MEXICO. DIST. FED.: Valle de México, from the market, Jun.–Aug. 1955, T. Herrera (NY). USA. MICHIGAN: Cheboygan County, University of Michigan Biological Station, Douglas Lake, on agaric among a cluster of *H. lactifluorum*, 2 Sep. 1969, A. H. Smith (CTR 69-113) (NY). NEW YORK: Orange County, Forest near Southfields, on agaric, 1 Oct. 1961, L. Long (NY).



NOTES. The host of *H. macrosporus* is a member of the Russulaceae, but we have not been able to unequivocally identify hosts of any of the collections that we have seen.

In ascus and ascospore characters *H. macrosporus* is very close to *H. lactifluorum*; however, the different color and the lack of a reaction in KOH lead us to distinguish the two species (see notes with *H. lactifluorum*). *Hypomyces macrosporus* might be nothing more than an "albino" variant of *H. lactifluorum*. Herrera and Guzmán (1961) found it in association with *H. lactifluorum* in Mexico, and we have found it once (CTR 69-113) in Michigan mixed with a cluster of *H. lactifluorum*. *Hypomyces banningsiae*, another parasite of members of the Russulaceae, also has KOH- perithecia in a white subiculum, but ascospores of *H. banningsiae* are unicellular and nonapiculate.

We attempted to germinate ascospores from one collection (CTR 69-113) without success. We have not found any suggestion of an anamorph on any of the collections that we have seen.

Hypomyces macrosporus has been found in the market in Mexico, where it is purchased and apparently consumed.

9. *Hypomyces odoratus* G. Arnold, Ceská Mykol. 18: 144. 1964. FIGS. 9, 71-94

Anamorph. *Cladobotryum mycophilum* (Oudemans) W. Gams & Hoozemans, Persoonia 6: 102. 1970.

FIGS. 76-94

= *Dactylium mycophilum* Oudemans, Arch. Néerl. Sci. 2: 42. 1867.

Subiculum white to rosaceous lilac, effuse, cottony, subicular hyphae much branched and septate, tending to become vesiculose, 5-7 μm wide, KOH-. Perithecia globose to obpyriform, 345-610 \times 190-260 μm , reddish orange, KOH+, immersed to partially free in the subiculum, papillate; papilla 110-135 μm high, 110-150 μm diam at apex. Perithecial wall 15-20 μm wide, cells fusiform, 15 \times 4-5 μm , walls 1 μm thick, nonpigmented. Papilla of cells 7-10 μm long, 6 μm wide, disposed in divergent chains, terminal cell of

each chain subglobose to clavate, cells around the ostiolar opening narrowly clavate, 6 μm wide, merging with the periphyses. Asci cylindrical, 135-212 \times 7-8.5 μm , apex thickened and with a pore. Ascospores fusiform, oblong to lanceolate, 25-35 \times (4-)5-8 μm , two celled, septum median; verruculose and apiculate, verrucae 0.5 μm high; apiculi acute, 4-5 μm long.

Mycelium spreading rapidly on CMD and OA, aerial mycelium abundant and cottony, red pigment spreading in the agar. Conidiophores arising in aerial mycelium, indefinite in length, unbranched, irregularly branched, or often verticillately branched, each branch terminating in a single dry head of radiately or stелately disposed conidia. Conidiogenous cells 30-37 μm long, 3.5-5.3 μm wide basally and tapering slightly to the tip. Tip of conidiogenous cell lacking periclinal thickening and not flared. Conidia \pm cylindrical to narrowly ellipsoidal, (14-)15-20(-22) \times 5-6.8(-7) μm , 0- to 1-septate, septum median, with a prominent, protuberant, flat, 1 μm wide basal secession scar.

HABITAT. Anamorph reported on many agarics and members of the Aphyllophorales by Arnold (1964) and Helfer (1991) as well as on the ground and rotting wood. Perithecia found on basidiomata of members of the Aphyllophorales, but not yet found on agarics in nature.

DISTRIBUTION. Europe, but as anamorph in nature and perithecia formed in culture (Arnold, 1964); Cuba (Arnold, 1964), Puerto Rico, United States (North Carolina).

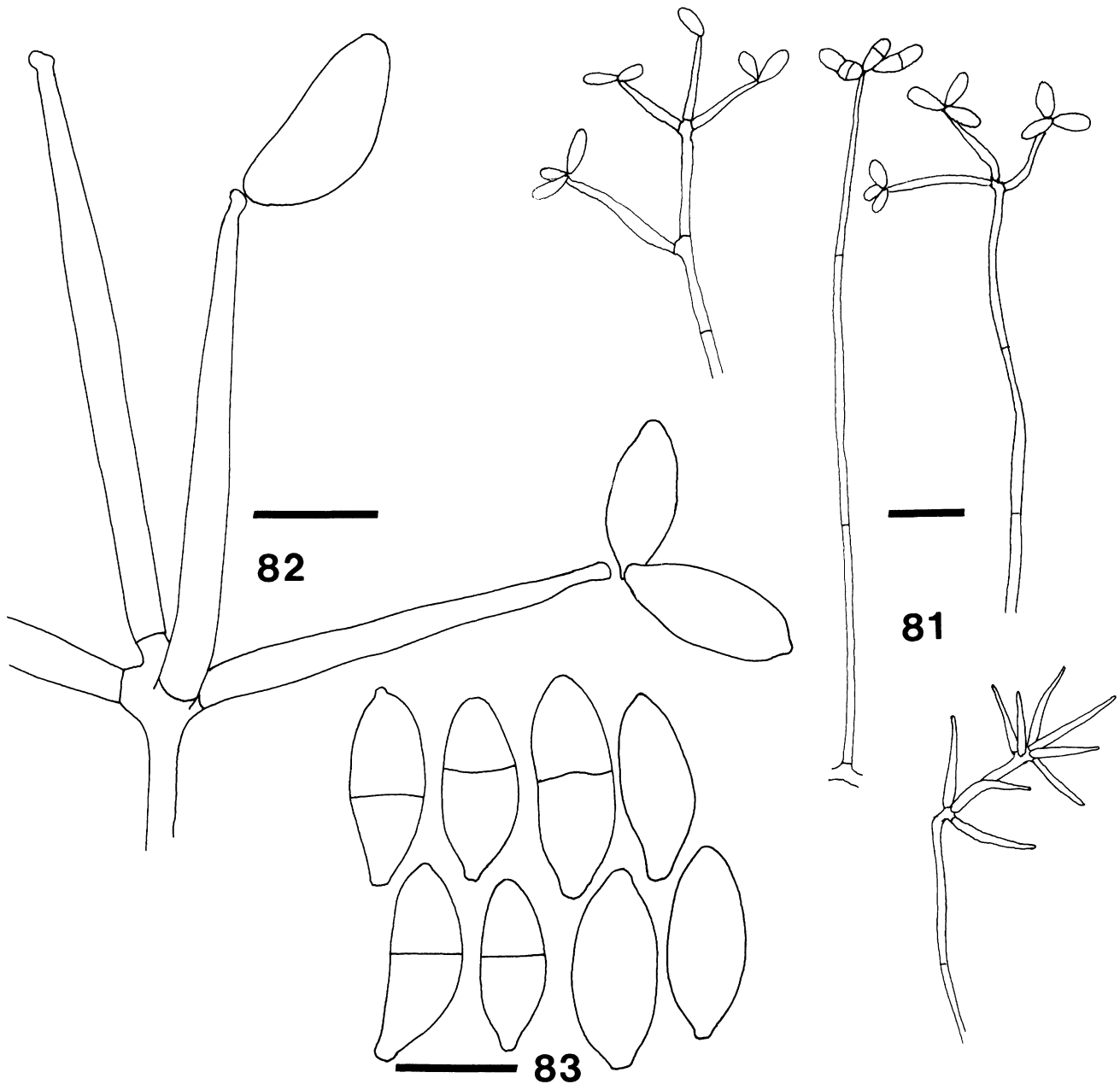
TYPE. GERMANY. Weimar, in forest Holzsdorfensi Thuringiae, on carpophore of *Tricholoma terreum* (Schaeff.: Fr.) Kummer, perithecia formed in agar culture (JE! ISOTYPE, NY).

SPECIMENS EXAMINED. ESTONIA. Hiiuma, Emmaste, isolated from *Boletus bovinus* L.: Fr., perithecia produced on *Polyporus* sp. in culture, 18 Sep. 1967, P. Poldmaa (JE, NY). GERMANY. THURINGIA: Holzsdorf near Weimar, on *Tricholoma terreum*, 29 Aug. 1961, G. R. Arnold (JE, NY). Perithecia produced in two additional cultures from Germany, near Weimar by G. R. Arnold, 29 Aug. 1965 (NY), Mar. 1965. (NY). PUERTO RICO. Bosque Estatal de Guajataca Trail, on leaf litter, 24 Nov. 1992, S. M. Huhndorf 239 (CTR culture 92-87, NY). USA. NORTH CAROLINA: Wake County, Schenck Research Forest, W of Carter Station, 1 mi. W of Raleigh, 22 Sep. 1976, L. D. Young comm. L. Grand (CTR 76-207) (NY).

NOTES. Teleomorphs of *H. odoratus* are indistin-

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FIGS. 67-80. *Hypomyces* species. 67-70. *H. macrosporus*. 67. Median longitudinal section through a mature perithecium. 68, 69. Asci; ascus apex visible in FIG. 69. 70. Ascospores in optical section. 71-80. *H. odoratus*. 71, 72. Median longitudinal section through mature perithecia. Anatomy of perithecial apex shown in FIG. 72. 73-75. Asci; ascus apex visible in FIGS. 74, 75. 76-80. *Cladobotryum mycophilum* anamorph. 76-78. Conidiophores in agar culture. 79, 80. Conidiogenous cells with developing conidia. All IC except FIG. 75 (PC), 76-78 (BF). FIGS. 67-70 from CTR 69-113; 71, 72 from Poldmaa, 18 Sep. 1967; 73-75 from CTR 76-207; 76-80 from CTR 92-87. Scale bars: FIGS. 67, 76, 77 = 50 μm ; 68 = 20 μm ; 69, 70, 74, 75, 80 = 10 μm ; 71-73, 78, 79 = 40 μm .

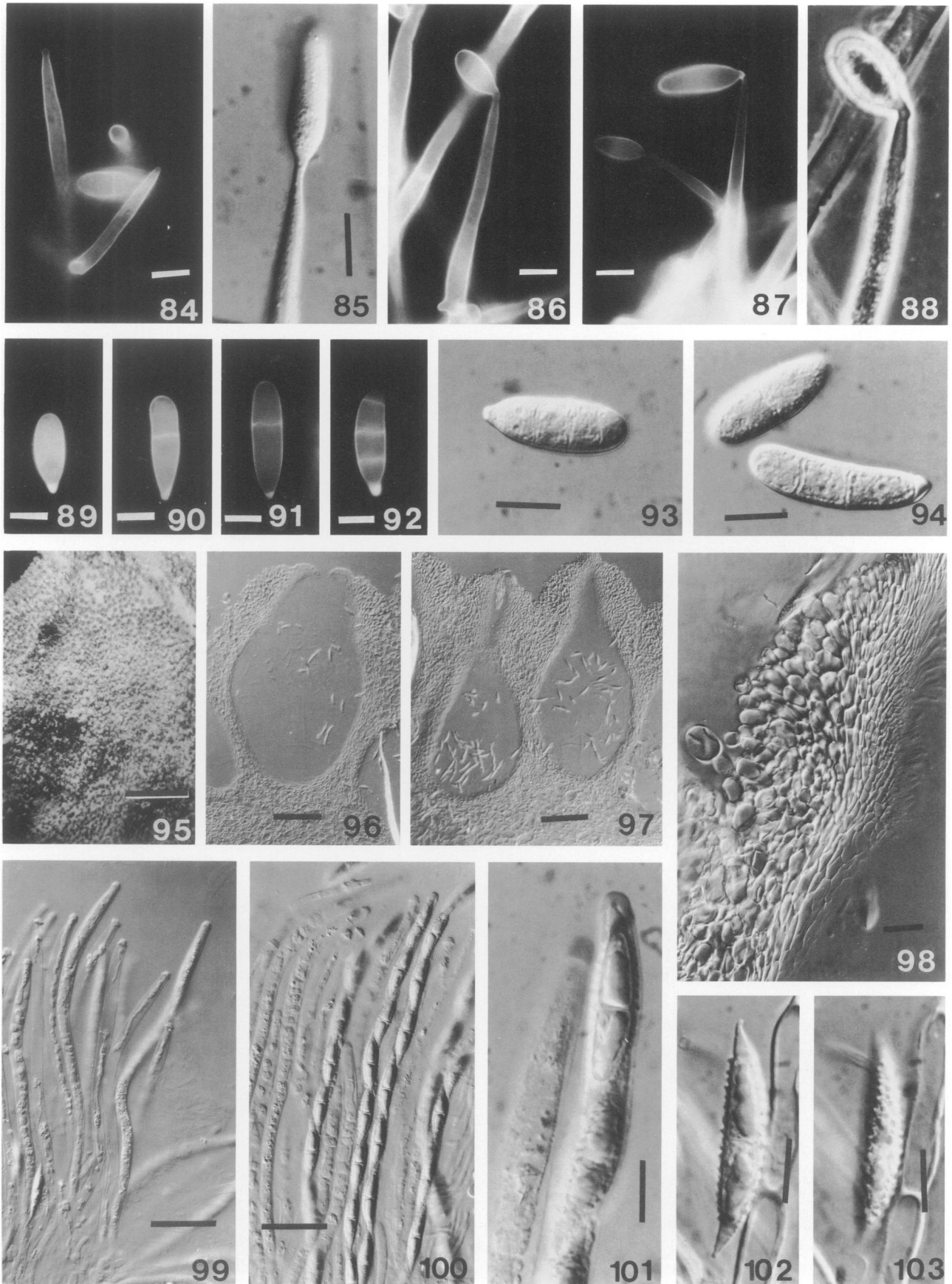


FIGS. 81–83. *Hypomyces odoratus*, *Cladobotryum mycophilum* anamorph. 81. Conidiophores. 82. Conidiogenous cells with developing conidia. 83. Conidia. All from *Huhndorf 239*. Scale bars: FIG. 81 = 25 μm ; 82, 83 = 10 μm .

guishable from those of *H. rosellus* (Albertini & Schweinitz) L.-R. & C. Tulasne, a common polyporiculous species (Rogerson and Samuels, 1993). The two species differ in their anamorphs. The conidiogenous

cells of the anamorph of *H. rosellus*, *Cladobotryum dendroides* (Bull.) W. Gams & Hoozemans, form a short rachis, while the conidiogenous cells of the anamorph of *H. odoratus* do not extend in length. Furthermore,

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 FIGS. 84–103. *Hypomyces* species. 84–94. *H. odoratus*, *Cladobotryum mycophilum* anamorph. 84–88. Conidiogenous cells with developing conidia. Note the absence of periclinal thickening at the conidiogenous locus. 89–94. Conidia. 95–103. *H. petchii*. 95. Habit of perithecia on deformed gills of *Russula* sp. 96–98. Median longitudinal section through mature perithecia. Anatomy of perithecial apex shown in FIG. 98. 99–101. Ascii; ascical apex visible in FIG. 101. 102. Ascospore in optical section. 103. Ascospore in surface view. All IC except FIGS. 84, 86–92 (FL); 95 (BF). FIGS. 84–94 from *CTR 92-87*; 95–103 from *PDD 30809*. Scale bars: FIGS. 84–94, 101–103 = 10 μm ; 95 = 1 mm; 96, 97 = 100 μm ; 98–100 = 20 μm .



conidia of *C. dendroides* tend to become more highly septate than do those of *C. mycophilum*. According to Arnold (1963) cellular masses are formed by *H. odoratus* but not by *H. rosellus*, but we have found such masses in cultures of the latter species.

Perithecia of *H. odoratus* were first discovered in cultures of *C. mycophilum* (Arnold, 1963, 1964) and have not apparently been recognized in nature until the present reports from North Carolina and Puerto Rico. Of course, the species might be much more common in nature because of its strong similarity to the better known *H. rosellus*. Species of *Hypomyces* with roseous perithecia are easily, but possibly incorrectly, identified as *H. rosellus* in the absence of information about the anamorph. We attempted crosses between single ascospore isolates of *H. rosellus* and *H. odoratus* but did not observe perithecial formation. Perithecia do form in crosses identified, respectively, as *H. odoratus* and *H. rosellus*. Both species are heterothallic.

10. *Hypomyces patchii* G. Arnold, Zeitschr. Pilzk. 37: 187. 1971(1972). FIGS. 10, 95–103

Anamorph. None proven.

Subiculum apricot, covering deformed gill surfaces and growing onto the stipe; subicular hyphae septate, branched and filamentous at first, becoming vesiculose to pseudoparenchymatous with cells 15–20 μm diam, and then no free hyphae evident among mature perithecia, KOH–. Perithecia obpyriform, 300–380 \times 410–520 μm , orange, nearly colorless in KOH, immersed in the subiculum or half free, KOH–; papilla 150 μm high, 175–200 μm wide at the apex. Perithecial wall 15–25 μm wide, cells fusiform to elliptic, 10–15 μm long, 5–7 μm wide, walls 1.5 μm thick, nonpigmented. Cells of the papilla 7–15 μm long, 8–12 μm wide, walls 1–1.5 μm thick, arranged in divergent files, the terminal cell of each file subglobose to clavate; cells around the ostiolar opening narrowly clavate, 6 μm wide, gradually merging with the periphyses. Asci long cylindrical, 125–170 \times 5–7 μm , apex thickened and with a pore. Ascospores fusiform, 26–33 \times 5.0–6.5 μm , two celled, conspicuously verrucose and apiculate; verrucae 1–1.5 μm high, apiculi 4–6 μm long and acute.

HABITAT. On Russulaceae.

DISTRIBUTION. New Zealand (Auckland).

TYPE. NEW ZEALAND. AUCKLAND: Sharp's Bush, near Henderson, on basidiome of *Russula* sp., 20 Feb. 1966, R. F. R. McNabb (JE; ISOTYPE, PDD 25041!).

ADDITIONAL SPECIMENS EXAMINED. NEW ZEALAND. AUCKLAND: Waitemata County, Waitakere Ranges, Bethells Swamps, on *Russula* sp. under *Leptospermum scoparium* J. R.

Forster & G. Forster, 5 Mar. 1965, J. M. Dingley (PDD 24490); Sharp's Bush Track, on *Russula* sp., 2 May 1973, J. M. Dingley and G. J. Samuels (73-52) (PDD 30809, NY); Manukau County, along track ca 3 mi. S of Kawakawa Bay, vic. Papakauri Hill, on ?*Lactarius* sp. under *Leptospermum* sp., 23 May 1973, J. M. Dingley and G. J. Samuels (73-82) (PDD 30876, NY).

NOTES. Arnold (1971) described a *Verticillium* anamorph for *H. patchii* on the basis of juxtaposition. There is no anamorph present with perithecia on the isotype collection (PDD 25041) and we have not found an anamorph associated with any subsequent collections. Our attempts to germinate ascospores of two collections (PDD 30809, 30876) were not successful.

Hypomyces patchii is apparently most closely related to *H. lactifluorum* and *H. macrosporus*. It is characterized by large ascospores and an apricot-colored subiculum. The species is unusual in that the hyphae of the subiculum become pseudoparenchymatous during development so that no free hyphae remain between mature perithecia. Hyphae of the subiculum of *H. lactifluorum* and *H. macrosporus* tend to become vesiculose, but still many hyphal elements remain visible among perithecia. These are in contrast with *H. lateritius*, *H. luteovirens*, and *H. lithuanicus*, the subicula of which remain hyphal and many free hyphal ends are evident at the surface of the subiculum.

11. *Hypomyces porphyreus* Rogerson & Mazzer, Michigan Bot. 10: 107. 1971. FIGS. 11, 104–111
= *Hypomyces batavus* G. Arnold, Zeitschr. Pilzk. 37: 189. 1971 (Apr. 1972).

Anamorph. None proven.

Subiculum brick-red, sparse, cottony, partly to completely covering the upper surface of the host pileus, KOH–; subicular hyphae filamentous with few free ends, smooth, septate, branched, 2–3 μm wide, cells often irregularly enlarged to 10 μm diam. Perithecia ovate to obpyriform, 300–395 μm high, 220–275 μm wide, brown with red tints or dark brick red, or chestnut, KOH–; papilla obtuse, 40–60 μm high, 150 μm diam. Perithecial wall 15–25 μm wide, cells fusiform to sinuous, 15–30 μm long, 3–5 μm wide, walls 1 μm thick, nonpigmented. Papilla of small, angular cells 7 μm diam, tending to be arranged in divergent files with the terminal cell of each file clavate, 7 μm long, 3 μm wide; cells of the papilla progressively merging with the periphyses. Asci long cylindrical, 125–190 \times 4–5 μm , apex thickened and with a pore. Ascospores fusiform to narrowly ellipsoidal, 20–30 \times 3.5–5.0 μm , one or two celled then septum median, often each end with a broad papilla or ends of spores acute to sub-

acute, verruculose; verrucae 0.5–1.0 μm high and round.

HABITAT. On *Leptonia strigosissima* (Rea) Orton (Rhodophyllaceae) (type) and undetermined agarics (Arnold, 1971).

DISTRIBUTION. Netherlands, Norway, United States (Michigan).

TYPE. USA. MICHIGAN: Cheboygan County, near junction of Brant's Rd. and Robinson Rd., on *Leptonia strigosissima*, 21 Jul. 1967, S. J. Mazzer 4969 (NY! ISOTYPE, MICH!).

ADDITIONAL COLLECTIONS EXAMINED. NETHERLANDS. NOORD-BRABANT: Dorst, on undetermined basidiome, 19 Sep. 1968, P. B. Jansen (L, Herb. Lugd. Bat. 468.235.559; HOLOTYPE of *H. batavus*). NORWAY. County of Ostfold, Borge Community, Torp, on unknown agaric, 25 Jul. 1983, Roy Kristiansen 83-129 (NY). USA (all on *Leptonia strigosissima*). MICHIGAN: Cheboygan County, near junction of Brant's Rd. and Robinson Rd., 22 Jul. 1971, S. J. Mazzer s.n. (R. L. Shaffer 6970) (CTR 71-216) (NY, TOPOTYPE); same locality, 13 Aug. 1971, CTR 71-213 (NY, TOPOTYPE); same locality, black mucky soil, small swampy area, 14 Jul. 1967, S. J. Mazzer 4930 (MICH); same locality, mucky soil, swamp margin, 13 Aug. 1967, S. J. Mazzer 5155 (MICH); same locality, black moist soil under mixed hardwoods, along edge of low swampy area, 15 Aug. 1967, S. J. Mazzer 5161 (MICH); low mucky bank along stream, across from Reese's Bog, north of Burt Lake, 27 Aug. 1967, P. A. Mazzer 156 (MICH); Emmett County, moist black mucky soil along SW side of Wycamp Lake, 5 Aug. 1967, S. J. Mazzer 5055 (MICH).

NOTES. We were not successful in germinating ascospores of *H. porphyreus*. Arnold (1971) reported a *Verticillium* associated with the type collection of *H. batavus*; it had globose conidia 2.5–3 μm diam. Arnold did not observe ascospore germination.

Rogerson and Mazzer (1971) compared *H. porphyreus* to *H. cervinigenus* Rogerson & Simms and *H. chrysotomus* Berkeley & Broome, species that have nonapiculate bicellular ascospores. Neither Rogerson and Mazzer (1971) nor Arnold (1971) observed an apiculus on ascospores of *H. porphyreus*, interference contrast microscopy does indicate the presence of a rounded papilla at the end of most ascospores.

12. *Hypomyces succineus* Rogerson & Samuels, Brittonia 44: 256. 1992. FIGS. 12, 112–121

Anamorph. *Verticillium succineum* (Rogerson et Samuels) Rogerson et Samuels, *comb. nov.*

FIGS. 118–121

= *Cladobotryum succineum* Rogerson & Samuels, Brittonia 44: 256. 1992.

Subiculum white when fresh, cream when dry, forming a dense, cottony mat over pileus, gills, and stipe of host; subicular hyphae 3–5 μm diam, intricately branched and intertwining, thin-walled, KOH–. Peri-

thecia ovate to obpyriform, 300–310(–470) μm high, (135–)188–218(–250) μm wide, immersed or semiimmersed in subiculum, scattered to aggregated in groups of 5–10, pale cream to amber or brown in age, in KOH with slight yellow tint, papillate; 60–80 μm high, 70–90 μm diam at base. Perithecial wall 20–25 μm wide laterally, cells elliptical, 6 μm long, 1.5–2 μm wide, walls ca 1 μm thick. Papilla of angular to globose cells 7–10 μm diam and tending to be arranged in files, the innermost files hyphal and merging with the periphyses. Asci cylindrical, 100–130 \times 5–6 μm , apex thickened and with a pore. Ascospores fusiform to cylindrical, (12–)16–20 \times (3–)4–5 μm , one to two celled, septum median; verruculose, verruculae \leq 1 μm high; nonapiculate or apiculate, apiculus to 2 μm long.

Colonies derived from ascospores grown on OA 5 cm diam in 1 wk at 20 C, alternating 12-h darkness and 12-h cool white fluorescent light. Mycelium dense, white, richly conidial; conidiophores arising in the aerial mycelium. Conidiophores from CMD 100–190 μm long, 3–4.5 μm wide at base, sparingly branched, each branch bearing a single terminal verticil of conidigenous cells. Conidigenous cells 30–45 μm long, 1–1.5 μm wide at tip, 2–3 μm wide at base, straight, smooth, monoblastic; tip with obscure periclinal thickening, not flared. Conidia oblong to cylindrical to ellipsoidal, (7–)8.8–13.3(–16) \times (2.4–)3.3–4.2(–5) μm , with or without a protuberant, flat, basal abscission scar, aseptate, hyaline, held in heads of a few at the tip of each conidigenous cell. Chlamydo spores not seen.

HABITAT. On basidiocarps of *Pholiota* sp.

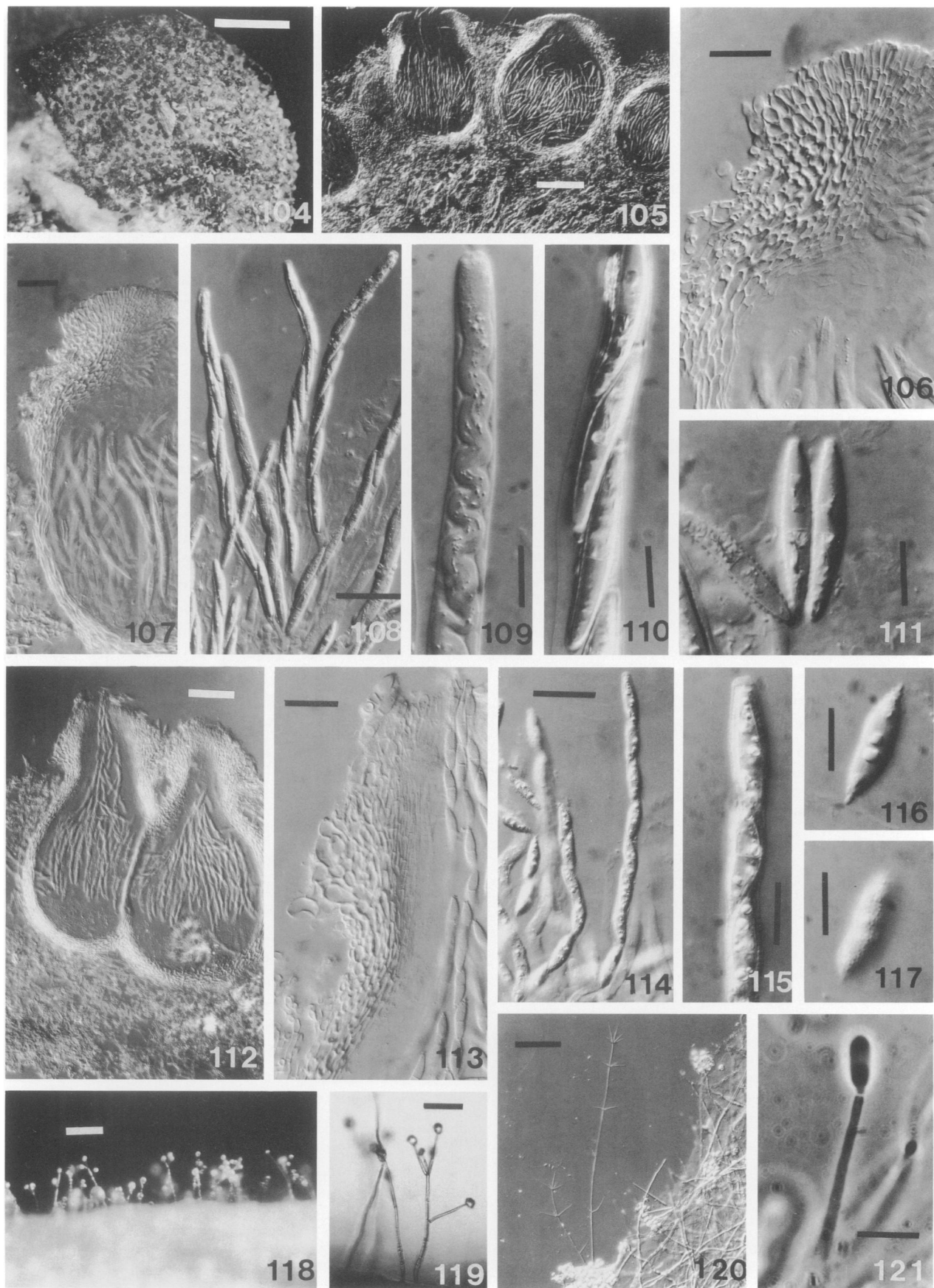
DISTRIBUTION. New York, known only from type.

TYPE. USA. NEW YORK: Hamilton County, Adirondack Mountains, near Raquette Lake, Sagamore Road, on basidiocarps of *Pholiota* sp. on log, 11 Sep. 1976, Rogerson 76-131 (NY, HOLOTYPE! ISOTYPE BPI 1109920! Culture ATCC 90494).

NOTES. Eight ascospores from each of several asci were isolated. The colonies derived from each of the ascospores were identical and produced the *Verticillium* anamorph. Perithecia formed in cultures derived from single ascospores when paired on OA and PDA. The species is thus heterothallic and the connection to *Verticillium succineum* is unequivocal.

Cultures on PDA produced a vinaceous brown pigment that was not seen on CM, OA or in the original collection. No odor was detected in any of the media. In some isolates sporadic swelling of the hyphae was seen, but chlamydo spores were not observed.

In features of subiculum, perithecia, asci and ascospores, *Hypomyces succineus* shows similarities to *H. polyporinus* Peck and to *H. semitranslucens* G. Arnold.



In all three species ascospores may be one or two celled. However, features of ascospores, anamorphs and the substrates indicate distinct differences. The anamorph of *H. polyporinus* is *Cladobotryum claviforme* (Gray & Morgan-Jones) Rogerson & Samuels with two- to three-septate conidia; the species occurs on *Trametes versicolor* (L.: Fries) Pilát. The anamorph of *H. semi-translucens* is *C. fungicola* (G. Arnold) Rogerson & Samuels with two-celled conidia; the substrate is typically a member of the Aphyllophorales. *Hypomyces succineus* is also similar to *H. tremellicola* in ascospore characters and in producing a verticillately branched conidiophore with unicellular conidia. *Hypomyces tremellicola* occurs on species of *Crepidotus*, like *Pholiota* a genus of brown-spored agarics.

We (Rogerson and Samuels, 1992) originally included the anamorph of *H. succineus* in *Cladobotryum*, but the species is better included in *Verticillium* because of the enteroblastic production of conidia in drops of liquid.

13. *Hypomyces tremellicola* (Ellis & Everhart) Rogerson in Samuels, Mem. New York Bot. Gard. 26(3): 20. 1976. FIGS. 13, 122–131

≡ *Hypocrea tremellicola* Ellis & Everhart, North American Pyrenomycetes 85. 1892.

≡ *Hypocroopsis tremellicola* (Ellis & Everhart) Seaver, Mycologia 2: 83. 1910.

≡ *Nectriopsis tremellicola* (Ellis & Everhart) W. Gams, Netherlands J. Pl. Pathol. 88: 69. 1982.

Anamorph. *Verticillium* sp. FIGS. 129–131

Subiculum white, effused, covering the somewhat deformed host or spreading over adjacent wood; hyphae irregularly branched, septate, 3–5 μm diam, with scattered warts, KOH–. Perithecia ovate to obpyriform, 450–600 μm high, 300–350 μm wide, reddish brown, KOH–, immersed in the subiculum with papilla protruding; papilla obtuse to acute, 200–225 μm high, to 300 μm wide. Perithecial wall 15–20 μm wide, cells small, 7–15 \times 3 μm , wall 0.5–1.0 μm wide, non-

pigmented; papilla of cells 6–15 μm long, 6–10 μm wide, tending to be disposed in divergent files, terminal cell of each file subglobose to clavate, 7–10 μm long, 6–8 μm wide; cells around the ostiolar opening narrowly clavate, 3 μm wide, merging with the periphyses. Asci cylindrical, 60–75 \times 4–5 μm , apex thickened and with a pore. Ascospores ellipsoidal to ovate, 7–13 \times 3–4 μm , two celled, septum median, densely verrucose, ends obtuse.

Colonies grown 1 wk, 15–18 C, diffuse daylight on PDA and OA: 5 cm diam, flat, velvety to cottony with more aerial mycelium on PDA white to sienna, sometimes with a moldy or actinomycetous odor. Conidia forming after 2 wk on PDA, conidiophores few and scattered in the aerial mycelium, macronematous, mononematous, verticillately branched, 300–400 μm long, 3–4 μm wide at base, straight, smooth, hyaline. Conidiogenous cells forming singly or in verticils of two to three along the length of the conidiophore, 20–30 μm long, 1.5–2.5 μm wide at base, 1.0–1.5 μm wide at tip; tip with slight periclinal thickening, not flared. Conidia oblong to ellipsoidal, 5–9 \times 3–4(–5) μm , one celled, with a protuberant, flat, basal abscission scar, held in a single hyaline drop of clear liquid at the tip of each conidiogenous cell.

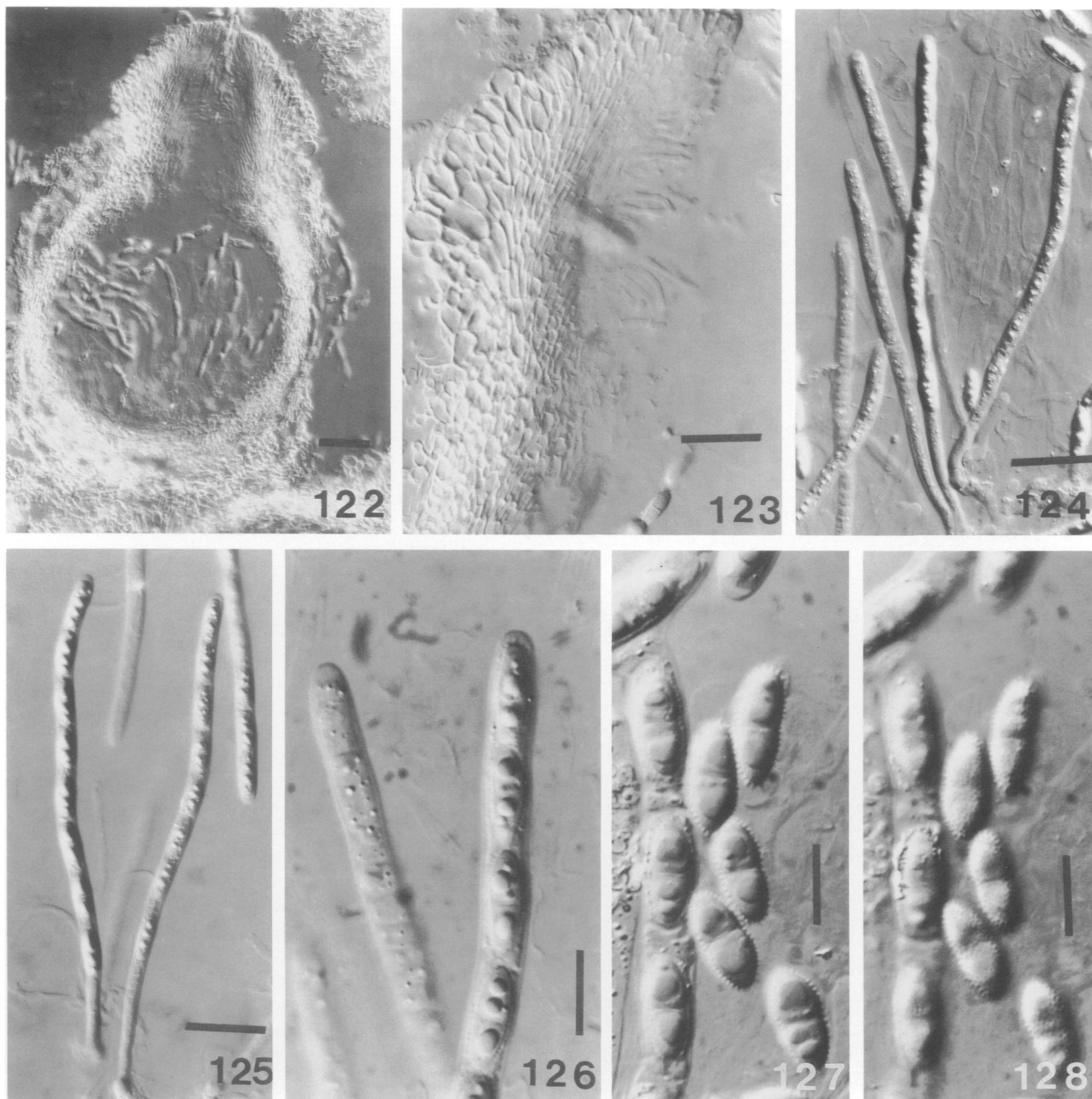
HABITAT. On *Crepidotus putrigenus* (Berk. & Curt.) Sacc., *Crepidotus* spp., less frequently on basidiocarps of *Polyporus* spp. and *Pleurotus* spp. (Samuels, 1976).

DISTRIBUTION. Canada (Ontario, Quebec). United States [Connecticut, Illinois, Indiana, Kansas, Louisiana, Maine, Maryland, Massachusetts, Michigan, Minnesota, New Jersey, New York, North Carolina, Ohio, Pennsylvania, Vermont, Wisconsin (Parker, 1990)]. New Zealand. Venezuela.

TYPE. USA. OHIO: Preston, on *Tremella albida* Huds. (incorrect determination, host is *Crepidotus* sp.), 28 Jul. 1888, *Morgan 894* (HOLOTYPE NY!).

ADDITIONAL SPECIMENS EXAMINED. NEW ZEALAND. AUCKLAND: Waitakere Ranges, Piha Rd, Cowan Track, on pleurotoid agaric, 4 Apr. 1983, *G. J. Samuels 83-112* and *A. Y. Rossman* (PDD 44199). USA. NEW YORK: Tompkins County, Danby, Michigan Hollow, on brown-spored agaric, 11 Aug. 1991, *D. Price comm. R. P. Korf* (BPI 1112820); Dutchess County, near Tompkins Pond at base of Stissing Mt., W of

FIGS. 104–121. *Hypomyces* species. 104–111. *H. porphyreus*. 104. Habit of perithecia on distorted cap of *Leptonia strigosissima*. 105–107. Median longitudinal section through mature perithecia. Anatomy of perithecial apex shown in FIGS. 106, 107. 108, 109. Asci; ascal apex visible in FIG. 109. 110, 111. Ascospores in optical section. 112–121. *H. succineus*. 112, 113. Median longitudinal section through mature perithecia. Anatomy of perithecial apex shown in FIG. 113. 114, 115. Asci; ascal apex visible in FIG. 115. 116. Ascospore in optical section. 117. Ascospore in surface view. 118–121. *Verticillium succineum* anamorph. 118–120. Conidiophores in agar culture. Note drops of liquid at the tips of conidiogenous cells in FIGS. 118 and 119, and verticillate branching in FIG. 120. 121. Conidiogenous cell with developing conidium. Note periclinal thickening at the conidiogenous locus. All IC except FIGS. 118, 119 (BF); 121 (PC). FIGS. 104–117 from the respective type collections; 118–121 from the ex type culture (*CTR 76-131*). Scale bars: FIG. 104 = 2 mm; 105 = 100 μm ; 106, 114 = 40 μm ; 107, 108 = 20 μm ; 109–111, 115–117, 121 = 10 μm ; 113, 119, 120 = 50 μm ; 118 = 125 μm .

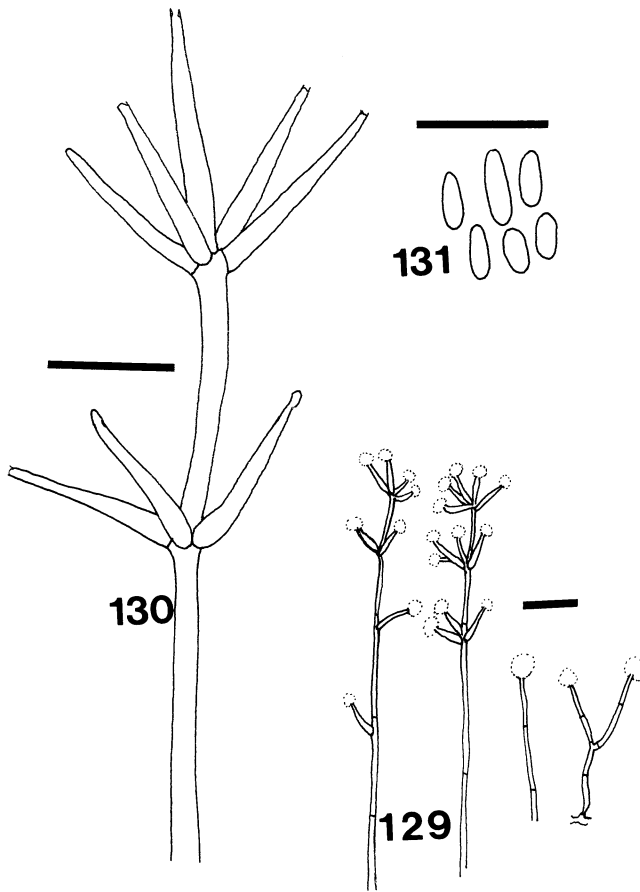


FIGS. 122–128. *Hypomyces tremellicola*. 122, 123. Median longitudinal section through a mature perithecium. Anatomy of perithecial apex shown in FIG. 123. 124–126. Ascus; ascus apex visible in FIG. 126. 127. Ascospores in optical section. 128. Ascospores in surface view. All IC. All from Parker, 5 Sep. 1987. Scale bars: FIG. 122 = 20 μm ; 123–125 = 40 μm ; 126–128 = 10 μm .

Pine Plains, on agaric (? *Crepidotus*), 9 Oct. 1965, CTR 65-106 (NY); Rockland County, Harriman State Park, woods along Stony Brook, E of Sloatsburg, on carpophores of *Crepidotus*, 10 Oct. 1965, CTR (NY). WISCONSIN: Ozaukee County, UW-Milwaukee Field Station, on unidentified agaric growing on decorticated log, 28 Aug. 1987, A. D. Parker (BPI 630937, NY); Sauk County, Aldo Leopold Memorial Reserve, on unidentified (brown-spored) agaric growing on decorticated log, 5 Sep. 1987, A. D. Parker (BPI 630936, NY).

NOTES. Samuels (1976) and Gams and Van Zaayen (1982) have redescribed this species. The latter considered that the species belonged in *Nectriopsis* and gave special emphasis to the anamorph.

Our concept of this species may be too broad because conidial measurements given above for one New Zealand collection are considerably wider than given by Gams and Van Zaayen (1982) [$3.5\text{--}6(-10.5) \times 1.4\text{--}2.2 \mu\text{m}$]. Gams and Van Zaayen suggested that collec-



FIGS. 129–131. *Hypomyces tremellicola*, *Verticillium* anamorph. 129. Conidiophores. 130. Conidiophore with conidigenous cells. 131. Conidia. All from CTR 91-41A. Scale bars: FIG. 129 = 30 μm ; 130, 131 = 10 μm .

tions of hosts other than *Crepidotus* could represent other species. They described the apparently closely related *Nectriopsis tubariicola* W. Gams (Gams and Van Zaayen, 1982), which also has a *Verticillium* anamorph. This species, which occurs on *Tubaria furfuracea* (Pers.: Fr.) Gillet (Crepidotaceae), is said to differ from *H. tremellicola* in in vitro growth rate, colony pigmentation, conidial measurements ($6\text{--}9 \times 3\text{--}3.7 \mu\text{m}$) and the absence of perithecia in vitro. We do not know this species.

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Sandy Sheine, and Sylvia Stein, have provided many records of parasitized agarics. For the loan of specimens and for requests of information, we thank the mycologists and curators of the following herbaria: ACAD, BPI, BRSL, CUP, DAOM, FH, IA, ILL, ISC, JE, K, L, MICH, NCU, NY, NYS, PAC, PC, PAD, PDD, QFB, S, TRTC, UC, UPS, WIS.

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Corrigendum

In Cisar, C. R. et al., 1994, Sequence similarity of mating type idiomorphs: A method which detects similarity among the Sordariaceae fails to detect similar sequences in other filamentous ascomycetes, *Mycologia* 86: 540–546, on p. 542 TABLE II indicates that the A- and a-probes hybridized with DNA from both stains of *Neurospora crassa* and *Sordaria brevicollis* (A and a). TABLE II should show that the A-probe hybridized with DNA from only the A strains of *N. crassa* and *S. brevicollis* and that the a-probe hybridized with DNA from only the a strains of *N. crassa* and *S. brevicollis*.