Systematics of *Laccaria* (Agaricales) in the Continental United States and Canada, with Discussions on Extralimital Taxa and Descriptions of Extant Types

Gregory M. Mueller
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Systematics of *Laccaria* (Agaricales) in the Continental United States and Canada, with Discussions on Extralimital Taxa and Descriptions of Extant Types

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G.M.M.
Systematics of *Laccaria* (Agaricales) in the Continental United States and Canada, with Discussions on Extralimital Taxa and Descriptions of Extant Types

Gregory M. Mueller

Abstract

The genus *Laccaria* comprises an important part of the North American mycota north of Mexico. Nineteen species are recognized from the study area. *Laccaria laccata* is further divided into two varieties. Discussions regarding the distribution, presumed ectomycorrhizal hosts, and biology of these taxa are provided along with data on select extralimital taxa. In addition to an examination of North American material, an attempt was made to examine all extant type specimens. Descriptions of these collections are offered. To facilitate further work on the genus, a tentative key to the world taxa of *Laccaria* is presented.

Extensive collecting was undertaken in much of the continental United States and southern Canada. Comparative material was collected in Costa Rica, South America, and Sweden. Data were obtained on basidioma and somatic culture mat morphology, intercollection pairing reactions, and restriction fragment length polymorphisms of mtDNA and rDNA. Cytological data and in vitro ectomycorrhizal synthesis data were also obtained and used to further characterize the genus. Taxa were delimited so that they are presumably monophyletic and are diagnosable by a unique combination of character states, either morphological or molecular. Data from intercollection pairings were used in conjunction with other data sets and did not outweigh information from the other analyses. Results of cladistic analyses were concordant with the hypothesis that *Laccaria* is a monophyletic assemblage of taxa with at least one synapomorphy (echinulate basidiospores with echinulae formed by perpendicular microtubules) supporting its monophyly. However, it was not possible to develop a fully resolved, robust hypothesis of phylogeny within the genus because of a paucity of characters, inability to polarize some of these characters, and problems in choosing appropriate outgroup(s). As expected, there was a high degree of homoplasy detected within the employed data set, and it will be necessary to utilize either extensive restriction site mapping or sequencing of selected macromolecules to develop a robust hypothesis of phylogenetic relationships within this genus. Although synapomorphies were not found to support the recognition of sections in the genus, two metasections, *Laccaria* and *Amethystina*, are recognized for logistic reasons and to provide a hypothesis to be tested during future analyses.

Introduction

*Laccaria* Berkeley & Broome is a cosmopolitan genus of mushrooms (Agaricales) collected frequently throughout North America. Its taxa make up a sizable part of the world’s mycota and have been reported from every continent except Antarctica.
Individuals of most *Laccaria* species have been reported to form ectomycorrhizal associations with numerous tree species, including many that are economically important in North America (e.g., species of *Quercus* and other Fagaceae, many species of *Pinus*, *Pseudotsuga menziesii* (Mirb.) Franco, and *Tsuga heterophylla* (Raf.) Sarg.) (Trappe, 1962).

Singer and Moser (1965) and Watling (1977) have reported that some taxa of *Laccaria* can act as pioneer species. Other studies have supported this contention by reporting that basidiomata of at least some *Laccaria* are frequently found in recently disturbed sites and young forest stands but not in mature forests (e.g., Danielson, 1984; Dighton & Mason, 1985; Dighton et al., 1986). Thus *Laccaria*, at least in some situations, may play an important role in primary and secondary succession.

Because of the relative ease with which some species of *Laccaria* can be manipulated in the laboratory, several taxa, including *L. bicolor* (Maire) Orton, *L. laccata* (Scop.: Fr.) Cooke, and *L. proxima* (Boud.) Pat., are being used actively in applied and basic research on ectomycorrhizae (see Kropp & Langlois, 1990). *Laccaria* has also proved useful in studies on the biology of fungi that form ectomycorrhizae (e.g., Fries, 1983a; Fries & Mueller, 1984; Kropp & Fortin, 1988; Armstrong et al., 1989; Barrett et al., 1989, 1990; Doudrick & Anderson, 1989; Gardes et al., 1990, 1991a,b; Mueller, 1991c; Mueller & Gardes, 1991).

Stabilization of the classification of *Laccaria*, therefore, would have applied implications because of the ecological and potential economic importance of many of its taxa, in addition to adding to our basic knowledge of fungi that form ectomycorrhizae.

Although most modern systematists consider *Laccaria* to be an autonomous genus, easily segregated from other members of the family Tricholomataceae (Singer, 1986), delimitation of infrageneric taxa is difficult in many instances. Much of this problem is due to the relative morphological simplicity of its taxa, which provides few suites of systematically informative characters, coupled with a high degree of phenoetic plasticity within certain *Laccaria* taxa, especially those that have an apparently wide geographic range. Continuing nomenclatural confusion has exacerbated this problem.

A large discrepancy exists in the number of recognized taxa in the genus for these reasons. Although nearly 100 species epithets have been used for *Laccaria* worldwide, Singer (1986) recognized only 18 clearly defined species, while McNabb (1972) indicated that there may be as many as 43 species worldwide. There also has been much confusion concerning the circumscription of several taxa, and classification in this genus remains in a state of flux (e.g., Singer, 1967, 1977, 1986; Bon, 1983; Moser, 1983; Clémenson, 1984; Ballero & Contu, 1987, 1989; Mueller, 1991a).

This study was undertaken in an attempt to resolve systematic and nomenclatural problems, to determine species composition and distribution for the genus *Laccaria* in North America north of Mexico, and to add to our knowledge of its biology. Because of the problems stated above, it was necessary to examine extralimital taxa as well as all available extant type collections, to designate lectotypes, neotypes, or representative specimens when applicable, and to examine critically characters from various stages of the life cycle. In addition to morphological characters of basidiomata and somatic culture mats, data from intra- and interstock pairing analyses, restriction fragment length polymorphisms of mitochondrial and ribosomal DNA, cytological studies, and in vitro ectomycorrhizal synthesis attempts were incorporated into this multifaceted study.

Taxa were delimited so that they are presumably monophyletic and are diagnosable by a unique combination of character states. Attempts were made to develop a classification for the genus that reflects the evolutionary history of the group.


**Taxonomic and Nomenclatural History**

**Europe and Other Extralimital Areas**

The name *Laccaria* was first proposed by Berkeley and Broome in 1883 to accommodate species of *Agaricus* subgenus *Clitocybe* that produced globose basidiospores that often formed a white pulvululence on the thick, attached lamellae. Proposed for transfer to the new genus were *Agaricus laccatus* Scopoli, *A. bellus* Persoon, and several unnamed species from Ceylon and Europe. No
new combinations were made until the following year, however, when Cooke (1884) formally transferred eight species to the genus.

Over the intervening century, the presence of clamp connections and echinulate, multinucleate basidiospores have become important characters in the modern generic concept of *Laccaria* (Kühner, 1980, 1984; Singer, 1986).

The pre-Friesian history of the genus can be summarized as follows. Scopoli (1772), describing fungi from the Tyrol of southern Austria, was the first to use the binomial *A. laccatus* for a member of the eventual genus *Laccaria*. Two more species, *A. amethystinus* and *A. farinaceus*, were described in 1778 by Hudson from the environs of London (Hudson, 1798). Hudson placed *A. laccatus* in synonymy with *A. farinaceus*, and thus *A. farinaceus* is a superfluous name. *Agaricus tortilis* was described from Halifax by Bolton (1788). Finally, Persoon (1801) named *A. bellus* and two varieties of *A. farinaceus*: var. *roseus* and var. *tortilis*.

Fries (1821) placed *A. laccatus* and *A. bellus* in tribe VIII *Clitocybe*, subtribe 4 *Oseypii*. He further divided *A. laccatus* into variety “a” (“Pileo rufo 1. carneo, siccio subochraceo”) and variety “b” (“Pileo amethystino, siccio canescente”). Additionally, he listed *A. tortilis* and *A. pachyphyllus* Fries (1815) as species that needed to be further examined.

Between 1821 and 1884, a number of workers described new species destined later to be incorporated in *Laccaria* (e.g., Fries, 1836–1838, 1874; Berkeley, 1845, 1856; Montagne, 1856; Berkeley & Curtis, 1859; Berkeley & Broome, 1871; Ellis, 1874; Karsten, 1876; Spegazzini, 1880; Boudier, 1881).

The genus *Russuliopsis* was proposed by Schroeter (1889) for all the taxa previously included in *Laccaria*. Because *Laccaria* and its included taxa were validly published, *Russuliopsis* is a later synonym and thus a superfluous name.

*Laccaria* was recognized by both Fayod (1889) and Patouillard (1900) in their attempts to develop a more natural classification system for the Hymenomycetes. Peck (1912) was the first worker in the United States to recognize the genus and one of the first in the world to publish a paper exclusively on the group.

It was not until Singer (e.g., 1943b, 1949, 1962, 1967, 1973, 1975, 1977) became interested in the genus, however, that any attempt was made to organize and formulate a coherent classification for *Laccaria* based on the world mycota. To date, Singer’s publications on the genus are the most comprehensive and influential. His classification has been the starting point for this study and for most other systematic research on the genus since the 1940s.

Several alternative classifications have been published, including those of Bon (1983), Clémençon (1984), and Ballero and Contu (1989). Additionally, numerous mycological surveys that included *Laccaria* have been published by various authors for most areas of the world. Some of these publications include Rea (1922), Kühner and Romagnesi (1953), Dennis et al. (1960), Orton (1960), Phillips (1981), Moser (1983), Dennis (1986), Ballero and Contu (1987), Watling (1987), and Mueller (1991a) for temperate Europe; Möller (1945), Lange (1955), Kobayasi et al. (1967), Miller et al. (1982), and Guldén and Jönsen (1988) for the Arctic; Vellinga (1986) for India; Malençon and Bertault (1975) for North Africa; Heinemann (1964, 1966) and Pegler (1977) for East Africa; Binyamini (1973, 1976) for Israel; Stevenson (1964) and McNabb (1972) for New Zealand; Imai (1938) and Hongo (1959, 1971) for Japan; Singer (1952, 1953), Singer and Dígilio (1952), Singer and Moser (1965), and Horak (1979) for South America; and Singer (1957), Aguirre-Acosta and Pérez-Silva (1978), and Montoya-Bello et al. (1987) for Mexico.

**North America North of Mexico**

Schweinitz (1822, 1834) was the first American mycologist to publish on the North American mycota. In his list of all the then-known fungi from America, Schweinitz (1822) included *Agaricus* (*Omphalia*) *bellus* and *A. (Omphalia) farinaceus*. In 1834 he included *A. (Clitocybe) laccatus*, *A. (Clitocybe) amethystinus*, and *A. (Clitocybe) bellus*. Several collectors working in North America, including Curtis, Lea, Sullivant, and Wright, sent specimens and notes on American fungi to various workers in Europe, especially Berkeley, and several new species (e.g., *A. ochiensis* Montagne and *A. ochropurpureus* Berkeley) were discovered and published in this manner.

Ellis (1874) described *A. (Clitocybe) trullissatus* from the sand dunes of New Jersey, and thus became the first North American to designate a new species in this group. Charles H. Peck was the first North American worker who studied and published on the group in some detail (Peck, 1890, 1893, 1895, 1897, 1903, 1907, 1912). *Laccaria amethystina* Cooke, *L. laccata*, *L. ochropurpurea*
research microscope, a Zeiss Universal photomicroscope, or a Zeiss RA standard microscope equipped with both bright field and phase contrast optics. Recent data acquisition and remeasurements were made using JAVA 1.31 (Jandel Video Analysis Software, 1989) running on an AT&T 6386 computer from images captured through an Olympus BH-2 microscope with Nomarski differential interference optics. Illustrations of micro-morphological characters were made with the aid of a drawing tube. All measurements were made on material mounted in 3% KOH. Iodine reactions were determined in Melzer’s reagent and the cyanophilic reaction was determined in cotton blue (Kotlaba & Pouzar, 1964; Singer, 1972; Largent et al., 1977). Descriptive terminology is from Snell and Dick (1971) and Largent et al. (1977).

Micromorphological data used in taxon descriptions were based on a complete, detailed examination of at least five (when possible) representative collections per taxon. The number of collections examined was dependent upon the availability of material and the amount of variability encountered within the taxon. All specimens listed in Specimens Examined (Appendix A) were examined, and any deviations from the norm were noted.

Measurements and observations were taken from several basidiomata per collection to check for uniformity. At least 10 randomly sampled cheilocystidia, pleurocystidia, and terminal cells of cuticular hyphae, and 15 randomly sampled basidium were measured per collection. Width and diameter measurements of these elements were taken at the widest point and rounded to the nearest 0.5 μm. Arrangement of hyphae comprising the pileipellis was observed in both radial and scalp sections.

All basidiospore measurements were taken from hymenial tissue and not from spor prints, in order to treat all specimens equally. The number of basidiospores measured and the number of collections examined for calculating mean size (≈ x) and length/width ratio (≈ Q) are included in brackets with basidiospore size data to give some indication of reliability of these data (Bas, 1974). When available, data on basidiospores from additional collections were included in basidiospore size range data. Ranges of collection means (x, Q) for basidiospore data, rather than overall mean values for the taxon, are provided to give a better indication of intraspecific variation. Basidiospore size data are always given without ornamentation and hilar appendix, with the hilar appendix in profile. Means and other descriptive statistics were obtained us-

Materials and Methods
Morphological Analyses of Basidiomata

Extensive collecting was undertaken throughout the United States and parts of eastern and western Canada. The following states and provinces were sampled: British Columbia, California, Colorado, Florida, Georgia, Idaho, Illinois, Kentucky, Louisiana, Massachusetts, Michigan, Minnesota, Mississippi, New York, North Carolina, Nova Scotia, Ohio, Ontario, Oregon, South Carolina, Tennessee, Texas, Virginia, West Virginia, Washington, Wisconsin, and Wyoming. Field work was also undertaken in Sweden, Mexico, Costa Rica, and much of South America as part of an ongoing project to produce a world monograph of the genus and to obtain comparative material. Dried specimens on loan from numerous herbaria (see Acknowledgments), including most extant type specimens, were also examined.

Collections were made and assembled using standard techniques (Smith, 1949; Largent, 1977). Descriptive terms were taken from Snell and Dick (1971) and Largent (1977). Unless otherwise noted, color names within parentheses and quotation marks are from Ridgway (1912), colors from Kornerup and Wanscher (1978) are listed by (page-column-row), and color names outside of parentheses are author-generated. Color names followed by M&P were taken from Maerz and Paul (1930).

Basidiomata were preserved by warm-air drying and deposited in either F, TENV, UPS, or WTU (Holmgren et al., 1981). Most examinations were made directly using either a Nikon Model S-Kt

(Berk.) Peck, L. striatula (Peck) Peck, and L. tortilis (Bolt.) Cooke were included in the North American Flora (Murrill, 1914). These same taxa were included in a study of Laccaria in North Carolina (Coker and Beardslee, 1922).


Scanning Electron Microscope Analyses

Lamellar fragments from air-dried collections were rehydrated in an acetone series, fixed in 2.5% glutaraldehyde in phosphate buffer for 3–4 hr at 4°C, dehydrated in an acetone series, and critical point dried in a Balzers CPD 030 apparatus with CO₂ as the transition fluid (Cheeseman & Grund, 1985). Samples were then attached to aluminum mounts with double-stick tape and coated with gold in a Denton Vacuum Desk II sputter coater. Basidiospores were examined and micrographs were taken at 20 kV with an Amray 1810 scanning electron microscope.

Somatic Culture Mat Analyses

The following procedure was employed to obtain heterokaryotic tissue cultures of Laccaria. Small pieces of trama tissue excised from the pileus–stipe interface were aseptically placed on modified Melin Norkrans medium (= MMN) plus benomyl (10 mg/L) in disposable test tubes (Marx, 1969; Molina & Palmer, 1982; Mueller, 1984). The benomyl was added to reduce ascomycetous contamination. Six to 10 replicates were taken for each collection utilized. Subculturing of each resulting isolate was undertaken until a pure culture was obtained. Stock isolates were then transferred to tubes containing modified MMN or N6:5 medium (Fries, 1983a) and stored in the dark at 2–4°C. Voucher herbarium material of all specimens used for tissue cultures was described and deposited in F, TENN, UPS, and WTU. All isolates are housed in the mycological culture collection at the Field Museum of Natural History.

Culture mat analyses were based on the classic work of Nobles (1948, 1965). Five-millimeter round plugs of agar containing hyphal tips taken from the advancing zone of each of 2-wk-old “stock” plates were transferred to the edge (mycelium side down) of a Petri plate containing 15–20 ml of either MMN, malt extract agar (= MEA), or potato dextrose agar (= PDA). Seven replicates of each medium for each isolate were inoculated and placed in a dark incubator at 24°C. Macro- morphological descriptions were made during the third and sixth weeks. Photographs of representative isolates were taken during the fourth week, and micromorphological characters were examined during the sixth week.

Macromorphological characters noted included (1) radius of the culture mat, (2) form and character of the advancing zone, (3) mat color and topography, and (4) the presence or absence of exudates. Terminology used was taken from Nobles (1948, 1958b, 1965).

Micromorphological characters were observed by mounting hyphae from the advancing zone, mat, and plug of each isolate in 3% KOH and examining the slide under phase contrast. Micromorphological characters examined included the presence or absence of (1) modified hyphal, (2) chlamydospores or oidia, etc., and (3) basidimata or hymenial structures such as basidia and cystidia along the mat surface. Descriptive terminology used was that of Nobles (1948, 1965).

Extracellular oxidase activity of each isolate was tested using both the Bavendamm (Davidson et al., 1938, 1942) and gum guaiac (Nobles, 1958a, 1965) tests (Mueller, 1984).

Intra- and Intercollection Pairing Analyses

Homokaryotic isolates were obtained following the techniques of Fries (1983a,b) and Fries and Mueller (1984). Homokaryotic isolates originating from one basidioma were assigned a stock number. Within a stock, each isolate received a unique extension number. All isolates are stored at 2–4°C on N6:5 medium in the mycological culture collection at the Field Museum of Natural History.

Intra- and interstock pairing analyses were carried out following the procedures outlined in Mueller and Gardes (1991). Isolates to be tested were placed ≤ 10 mm apart on N6:5 plates and allowed to grow together (2–4 wk). After an additional 1 wk or more, plugs of tissue were cut from the interface and placed on fresh N6:5 plates. Mycelia growing from these plates were checked for the presence or absence of clamp connections by examining them through the bottom of the inverted Petri plate at 200× magnification. Pairings resulting in hyphae that bore clamp connections were considered positive; those that did not yield clamped hyphae were scored as negative. Two or more testers for each stock, each containing different mating type alleles, were used when possible. As in Mueller and Gardes (1991) and Mueller (1991c), the terms incompatible and intracompatible are restricted to intrastock pairings. I used the terms intersterile for intercollection pairings.
Discussion of Systematic Characters

Many *Laccaria* taxa appear similar on superficial examination. Closer examination of the macro- and micromorphological variation, when correlated with cultural and molecular data, allows for the segregation of taxa in this phenotypically variable group. The following discussion on the delimiting characters within *Laccaria* is restricted to the 20 North American taxa, of which 18 were collected, photographed, and described during the course of this study.

Basidioma Macromorphology

COLOR—Basidioma and lamellar colors are the most diagnostic macromorphological characters. A major problem with this suite of characters is that the pigments responsible for these colors are unknown in many groups of agarics, including *Laccaria* (e.g., W. Steglich, Univ. Bonn, Germany, pers. comm., informed me that the pigments in *L. amethystina* oxidize very readily upon extraction and would take special care to analyze). Currently, it is not possible to determine homology between the pigment(s) in either the orange-brown or violet-colored *Laccaria* or to determine the primitive condition via comparison with presumably related genera (outgroup comparison). As mentioned in the section on Phylogenetic Considerations, I have made the assumption that the pigment(s) are homologous within these two groups of *Laccaria* (orange-brown vs. violet). Assumptions of homology between the pigments in *Laccaria* and pigments in potential outgroup taxa could not be made.

Because all members of the genus are hygrophanous, especially those taxa with violaceous to purple basidiomata, it is important to note the color of the pileus both when fresh and in successive stages of fading. This is most important in *L. amethysteo-occidentalis* G. M. Mueller, *L. amethystina*, and *L. vinceobrunnea* G. M. Mueller. Basidiomata of all three are bright violet to purple when young and fresh but differ markedly in their color changes associated with age (see descriptions). *Laccaria ochropurpurea* and *L. trullissata* (Ellis) Peck are light violaceous when very young but soon become buff or red-brown at maturity.

Basidiomata of specimens of most other *Laccaria* are some shade of orange-brown to flesh color. Because of the large amount of color variation found within these taxa (from light buff to a strong orange-brown or red-brown), basidioma color can rarely be used to delimit taxa in this large group.

North American species of *Laccaria* exhibit either pinkish flesh color to buff color or violaceous to purple lamellae. All of the taxa with violaceous to purple basidiomata plus *L. ochropurpurea* and *L. trullissata* have bright violet to dark purple lamellae. Basidiomata of *L. bicolor* (Maire) Orton, *L. nobilis* G. M. Mueller, and, possibly, *L. maritima* (Teodorowicz) Singer ex Huhtinen have light pinkish violet to wine-colored lamellae that occasionally fade to a pinkish color with age. All other North American taxa have flesh-colored lamellae. In some instances the lamellae of large, older specimens may develop a vinaceous appearance, but an examination of younger specimens should alleviate any confusion that this may cause. Basidiomata of *L. fraterna* (Cooke & Massee: Saccardo) Pegler, which probably is an introduced taxon, have rosy-pink lamellae when fresh.

The color of the mycelium at the base of the stipe (= basal mycelium) is also systematically important in *Laccaria*. The basal mycelium can be either violet or white. In addition to *L. trichodermophora* G. M. Mueller and *L. oblongospora* G. M. Mueller, all of the taxa with violet lamellae consistently have a violet basal mycelium. In all of these taxa, however, the basal mycelium occasionally fades to white with age.

**Basidioma Size**—Although often highly variable due to differences in age and environmental conditions, the size of the basidioma can be diagnostic in some instances. Most taxa have mature basidiomata of moderate size (pileus 20–50 mm broad, stipe up to 60 mm long), so those taxa that consistently have larger or smaller basidiomata are noteworthy. *Laccaria montana* Singer, *L. ohiensis*, *L. pumila* Fayod, and *L. tortillis* are characterized by being small (pileus rarely up to 30 mm broad); *L. amethysteo-occidentalis*, *L. nobilis*, *L. ochropurpurea*, and *L. trullissata* often have pilei greater than 60 mm broad.

The stature of the basidioma can also be systematically important. *Laccaria maritima*, *L. ochropurpurea*, and *L. trullissata* are usually robust (stipe diameter > 7 mm at apex), while all of the taxa characterized by having small basidiomata,
plus *L. striatula* (Peck) Peck, are generally gracile (stipe diameter ≤ 4 mm at apex).

Stipe and pileus ornamentation characteristics are often associated with size. Although most of the small taxa appear glabrous to finely fibrillose when fresh, taxa with large basidiomata, such as *L. nobilis*, often have pilei that become scaly to squamulose due to cuticular diffraction. Additionally, large basidiomata frequently have stipes clothed with pronounced longitudinal striations that can form reticulations or become scaly near the stipe apex (e.g., *L. amethysteo-occidentalis, L. nobilis, L. ochropurpurea, and L. trullissata*).

**Basidiospore Color in Mass**—Except for *L. amethystina* and *L. ochropurpurea*, which can have either white or light violet basidiospore deposits, all North American taxa have white spore prints. The color of the print will occasionally yellow with age.

**Additional Macromorphological Characters**—Characters such as type and degree of pileus striations, pileus shape, lamellar attachment and thickness, pileus and stipe context, or odor and taste are not systematically significant within *Laccaria*. Except for color and, in some instances, size, micromorphological and cultural characters must be used to differentiate taxa.

**Basidioma Micromorphology**

**Basidia**—The number of basidiospores borne per basidium is significant in *Laccaria*. Although many other genera of agarics have species with varying number of sterigmata in one basidioma (e.g., Hesler & Smith, 1963; Singer, 1986), the character appears to be consistent in *Laccaria*. In all of the material examined, the vast majority of the basidia observed in a mount had the same number of sterigmata. Basidia examined from material of *L. fraterna, L. pumila*, and *L. tortilis* bore 2–3 basidiospores. All of the rest of the North American taxa had 4-sterigate basidia. Bisterigmatic basidia generally had longer and stouter sterigmata. No other basidal characters appeared to have systematic significance.

**Basidiospores**—Basidiospore shape is of critical importance in designating species. Basidiospore shape terms used in this study are based on Bas (1969), with basidiospore shape described in terms of length-width ratios (*Q*): globose = 1.0–1.05, subglobose = 1.06–1.15, broadly ellipsoid = 1.16–1.23, ellipsoid or amygdaliform = 1.24–1.6, oblong = 1.65–2.0, cylindrical or sub fusiform > 2.0.

Specimens of most North American taxa have basidiospores that are subglobose to broadly ellipsoid. *Laccaria proxima* (Boudier) Patouillard and *L. oblongospora* are characterized by having ellipsoid to oblong basidiospores; basidiospores in specimens of *L. trullissata* and *L. maritima* are oblong to sub fusiform. Globose basidiospores are found in specimens of *L. amethystina, L. ochropurpurea, L. ohiensis, L. striatula, and L. tortilis*.

Basidiospore size is also an important systematic character in some instances. Individuals of most taxa have overall mean basidiospore lengths of 8–9 μm. However, *Laccaria bicolor, L. longipes* G. M. Mueller, *L. nobilis*, and *L. trichodermophora* are characterized by having relatively small basidiospores (*Q* < 8 μm long), and specimens of *L. fraterna, L. montana, L. pumila*, and *L. tortilis* have larger basidiospores (*Q* = 9.5–13 μm long). The basidiospores of *L. maritima* and *L. trullissata* are greater than 13 μm in length.

Except for *L. trullissata*, which has finely roughened basidiospores (figs. 41a, 57b–d, 72d), all species of *Laccaria* have echinulate basidiospores with a plaque near the hilar appendix. Echinulae length and width at attachment are important systematic characters within the genus.

Electron microscopic examinations of basidiospores using the carbon surface replica technique (Bigelow & Rowley, 1968; Pegler & Young, 1971), transmission electron microscopy (= TEM) (Besson & Kühner, 1971), and scanning electron microscopy (= SEM) (Pegler & Young, 1971; Muellen & Sundberg, 1981; Irving et al., 1985; Muellen, 1991c; this paper, figs. 53–58) have shown details of the surface and ornamentation characteristics. At my request, A. von Hofsten (Institute of Physiological Botany, University of Uppsala, Uppsala, Sweden) examined basidiospores from collections of several *Laccaria* species (L. bicolor, L. maritima, and L. proxima) and from a collection of *Hydnangium carneum* Wallroth *apud* Klotzsch, under the TEM (von Hofsten, unpubl.). The results of this study were concordant with the findings of Besson & Kühner (1971). The basidiospore echinulae of all *Laccaria* species examined to date, plus the gasteroid relative *Hydnangium carneum*, are composed of microtubules that run perpendicular to the epispore (Besson & Kühner, 1971; Kühner, 1980). This type of echinulae ultrastructure appears to be unique to *Laccaria, Hydnangium*, and probably *Podohydnangium*. Beaton, Pegler & Young (not examined under TEM). Echinulae ultrastructure is the primary synapomorphy that supports the recognition of these

**MUeller: Systematics of Laccaria (Agaricales)**
Fig. 1. Representative pileipellis arrangements occurring in North American taxa of *Laccaria*: a, trichodermium; b, interwoven; c, interwoven with scattered ± perpendicular fascicles of hyphae. Scale line = 10 μm.
three genera as a monophyletic group (see Phylogenetic Considerations).

The basidiospores in all taxa are nonamyloid and acyanophilic.

PILEPELLIS—Three types of hyphal arrangements were found in Laccaria (fig. 1a–c): a trichodermium, observed in most collections of L. trichodermophora; interwoven as in collections of L. ochropurpurea; or interwoven with scattered nearly perpendicular fascicles of hyphae (the most common pileipellis encountered). In L. vinaceo-brunnea and in some collections of L. amethystina, the hyphae of the pileipellis are interwoven with very numerous, long, individual hyphae that are arranged nearly perpendicular to the pileus surface. If the erect hyphae were aggregated closer together, the pileipellis could be described as a palisadoderm.

Pileipellis hyphae were often encrusted with a light to moderate yellowish brown pigment. In young specimens of L. amethystina, L. amethysteo-occidentalis, and L. vinaceobrunnea, the hyphae occasionally appeared vinaceous brown in mass.

Although data on the size of the terminal cells are presented in the species descriptions, the size and shape of these cells appeared to have little systematic significance. Additionally, the underlying tramal layer was morphologically undifferentiated and systematically uninformative.

CHEILOCYSTIDIA—The cheilocystidia of most Laccaria species, if present, are little more than elongate, filamentous hyphae that extend beyond the basidium and basidioles. Only in specimens of L. amethystina, L. amethysteo-occidentalis, and L. vinaceobrunnea were large (overall mean dimensions up to 58 × 10 μm), clavate to strangleate, abundant cheilocystidia observed. In many collections these cheilocystidia formed a nearly sterile layer. The uniqueness and consistent presence of large cheilocystidia in these three Laccaria taxa was a good diagnostic character for herbarium material that lacked micromorphological notes.

Pleurocystidia were not seen in any North American material of the genus. Morphologically undifferentiated caulocystidia are present in some taxa.

Additional Micromorphological Characteristics—The constant occurrence of clamp connections at virtually every septum and a parallel or rarely subparallel lamellar trama are important generic characteristics of Laccaria. Additionally, all hyphae were nonamyloid and, unless otherwise specified, hyaline in KOH.

The hyphae comprising the basal mycelium were tightly interwoven and either morphologically undifferentiated or barrel-shaped. The diameter of these hyphae appeared to vary as much within a taxon as between taxa.

Basidiospore and Basidium Cytology

Kühner (1980, 1984) emphasized the occurrence of multinucleate basidiospores in Laccaria in his decision to treat Laccaria in a family separate from other genera traditionally placed in the Tricholomataceae. These reports prompted us to investigate further the nuclear behavior in species of Laccaria and Hydnangiwm. To determine the significance of basidiospore and basidium cytology in the systematics of Laccaria, cytological studies on several species of Laccaria were carried out in J. F. Ammirati’s laboratory (Department of Botany, University of Washington, Seattle).

Several questions were addressed during the course of this study, including: (1) Is the occurrence of multinucleate basidiospores a characteristic of the genus, or is this feature restricted to a few taxa? (2) Where does postmeiotic mitosis occur in taxa with multinucleate basidiospores?

Basidia and basidiospores of representative specimens of each of the 11 Laccaria species and Hydnangiwm carneum listed in Table 1 were examined using fluorescent microscopy. Glutaraldehyde-fixed and nonfixed tissues were mounted in Hoescht fluorescent dye and examined using a Zeiss fluorescence microscope with 365 nm excitation and 480 nm emission filters.

Multinucleate basidiospores appear to be a constant feature within Laccaria, as they occur throughout the genus from the putatively primitive L. proxima to diverged taxa such as L. tortilis, L. amethysteo-occidentalis, and L. trullissata (table 1). These data also are concordant with the hypothesis of the close relationship of Laccaria to Hydnangiwm. According to Kühner (1980, 1984), the occurrence of multinucleate basidiospores is rare in the Tricholomataceae sensu Kühner (±Tricholomataceae sensu Singer).
The following is a summary of results obtained during studies of tetra- and bisterigate \textit{Laccaria} taxa (\textit{L. bicolor}, \textit{L. galerinoides} Singer, \textit{L. laccata} var. \textit{pallidifolia}, \textit{L. montana}, \textit{L. proxima}, \textit{L. proximella} Singer, \textit{L. pupil}, \textit{L. tortilis}, and \textit{L. vinaceousbrunnea}) using Giemsa-stained material examined under bright field microscopy. Detailed results will appear in a separate publication (G. J. Mueller, G. M. Mueller, L. Shih & J. F. Ammirati, in prep.). The dikaryotic basidium of both tetra- and bisterigate \textit{Laccaria} is more or less cylindrical in shape. The two nuclei move to the center of the basidium and fuse to form the diploid nucleus, during which time the basidium gradually enlarges and becomes clavate in shape. The diploid nucleus then moves to the apical region of the basidium, where meioses I and II occur. These divisions are chiastic, and the resulting four nuclei migrate to the center of the basidium. During these events the basidium enlarges to its mature size and shape, and sterigmata with developing basidiospores are formed. In most cases, once the basidiospores are fairly well developed, the nuclei begin to move through the sterigmata and into the basidiospores so that basidiospores from tetrasterigmate basidia each receive one nucleus, while those with bisterigate basidia each receive two nuclei. In these cases the (nucleus) nuclei in the basidiospores then undergo a mitotic division so that basidiospores from tetrasterigmate basidia are binucleate and those of bisterigate basidia are tetranucleate. Occasionally this postmeiotic mitosis occurs in the basidium before nuclear migration. In these cases, all eight nuclei migrate into the basidiospores. In both scenarios, mature basidiospores are multinucleate.

Tommerup and colleagues reported similar nuclear behavior for \textit{L. fratera} (Tommerup et al., 1991). According to them, however, nuclear behavior in \textit{Hydnangium carneum} differs in that postmeiotic mitosis occurs in the basidium prior to migration into the basidiospores. Additional information on nuclear behavior in \textit{Hydnangium} and \textit{Podopezynangium} is necessary before it will be possible to determine if multinucleate basidiospores in \textit{Laccaria} and these two genera are homologous. The \textit{Hydnangium} used by Tommerup et al. (1991) is reported to have tetrasterigmate basidia, and the illustrated basidiospores are broadly ellipsoid and finely ornamented. This is in contrast to my concept of \textit{H. carneum}. All of the collections that I have examined which are referable to this taxon have bisterigate basidia that bear strongly echinulate, globose basidiospores. Similarly, published illustrations of basidiospores and basidia for this taxon usually depict globose, strongly echinulate basidiospores and bisterigate basidia (e.g., Pegler & Young, 1979; Beaton et al., 1984; Castellano et al., 1989). Until a survey of other taxa in the genus is undertaken, and until phylogenetic relationships within the genus are resolved, it is not possible to determine the plesiomorphic condition for nuclear behavior in \textit{Hydnangium}.

### Somatic Culture Mat Morphology

Somatic culture mat studies based on the classic work of Nobles (1948, 1958b, 1965) were undertaken to obtain additional informative characters. Although becoming almost routine in studies of the wood-rotting Aphyllophorales and many groups of saprobic Agaricales, utilization of somatic culture mat data has only infrequently been used in systematic studies of fungi that form ectomycorrhizae. At least two factors are responsible for this. First, many of these fungi are recalcitrant to domestication (but see Hutchinson, 1990a,b; Hutchinson & Summerbell, 1990). Second, early work indicated that cultures of fungi that form ectomycorrhizae exhibited few morphological differences (e.g., Zak & Bryan, 1963; Zak & Marx, 1964).

Fries and Mueller (1984) reported no differences in morphology (except for the presence or absence of clamp connections) between homokaryotic and heterokaryotic isolates. Occasional differences in

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TABLE 1. Number of nuclei observed in the basidiospores of examined \textit{Laccaria} and \textit{Hydnangium} visualized with Hoechst fluorescent dye.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>No. Basidiospores per Basidium</th>
<th>No. Nuclei per Basidiospore</th>
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<tr>
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<tr>
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<tr>
<td>\textit{L. laccata var. pallidifolia}</td>
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<td>\textit{L. montana}</td>
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<tr>
<td>\textit{L. ochropurpurea}</td>
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<td>\textit{L. proxima}</td>
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<td>\textit{L. pumila}</td>
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growth rate, color intensity, and other features have since been detected between heterokaryotic isolates obtained via tissue culture, isolates originating as polysporous cultures, and homokaryotic isolates (Kropp et al., 1986; Kropp & Fortin, 1988; Mueller, unpubl.). While overall similarities are normally observed, care must be used when employing isolates of different origin for comparative studies. The following data are based primarily on isolates of tissue culture origin.

MACROMORPHOLOGY—The two primary diagnostic characters were the color of the culture mat on MMN and PDA (all isolates were white on MEA) and the rate of growth (expressed as the radius of the culture mat at week 3 and week 6) on each of the three media employed. Photographs of representative isolates are included as part of the description for a number of North American taxa (figs. 7, 10, 13, 31, 34, 37, 44).

Taxa that had white to off-white culture mats on all three media were L. fraterna, L. laccata, L. longipes, L. montana, L. ohiensis, L. proxima, L. pumila, and L. striatula. No isolates were obtained of L. maritima or L. tortilis. Isolates of all other North American taxa were violet to purple on PDA and MMN. To date there is a 100% correlation between basal mycelium color and somatic culture mat color. This supports the utility of basal mycelium color as a good delimiting field character.

Although a slight bleaching of color was often noted on the reverse side of the culture mat, no significant color changes occurred. Additionally, no exudates were apparent.

Along with color, the rate of growth could be used to delimit taxa. Isolates of most taxa grew at a moderate rate on all three media (20–50 mm on PDA, 30–70 mm on MMN, and 40–70 mm on MEA—all at week 6). Isolates of L. amethysteo-occidentalis, L. montana, and L. ohiensis grew much more slowly (often only 10–15 mm after 6 weeks’ growth). Conversely, isolates of L. bicolor, L. nobilis, L. oblongospora, and L. trichodermophora grew more rapidly.

Terminology used in discussing mat and margin texture was from Nobles (1948, 1965).

Except for an occasional pruinose, aerial layer of hyphae observed in older cultures of many taxa, the mycelium of all of the isolates grew tightly appressed to the agar surface. The transparency of the culture mat was an outcome of the thickness and intricacy of the interwoven mat. All isolates exhibited a feltly, thick culture mat on PDA. The mat texture on both MMN and MEA varied from silky to subfetly to feltly. Often the mat was thickest near the inoculation plug. In most cases, culture mats were of uniform thickness from the plug to the margin. In some taxa, however, variously distributed thicker zones were observed. These thicker zones could be scattered, small sectors (e.g., some L. trichodermophora isolates on MMN and L. bicolor on MEA), two or three concentrically arranged bands (e.g., L. amethysteo-occidentalis on MEA), or radially arranged pie-shaped or dendritic sectors radiating away from the inoculation plug (e.g., L. trichodermophora on PDA).

When describing the margin texture and color, I refer to the advancing zone of the culture mat. This zone is generally somewhat thinner than the rest of the mat and can be either a discrete, easily recognizable area or not well differentiated. On all three media, this zone was always silky to subfetly and thus presented little systematically informative data.

All of the isolates had the same musty odor on all three media.

Growth or diffusion zones were not obtained on gallic acid agar with any of the isolates. Immediate reaction to the gum guaiac drop test was observed only in some isolates of L. bicolor. I did not attempt other tests for the presence or absence of extracellular enzymes because of these basically negative results. Hutchison (1990a), however, performed drop tests of 1-naphthol and p-cresol on numerous isolates of ectomycorrhizal fungi growing on several different media and reported the presence of tyrosinase activity in all of the Laccaria that he tested (i.e., L. bicolor, L. laccata, L. ochropurpurea, and L. proxima). Only L. bicolor showed any indication of laccase activity (Hutchison, 1990a).

Hutchison (1990b) investigated enzymatic degradation of various carbon and nitrogen compounds by fungi that form ectomycorrhizae. Using the same taxa listed in the previous paragraph, he reported that Laccaria did not degrade pectin, lipid, amylose, or gelatin but showed various levels of degradation of casamino acids and urea. Hutchison and Summerbell (1990) reported that these same isolates gave red to violet reactions to Diazonium Blue B when treated with cold KOH and yellow reactions without cold KOH treatment.

MICROMORPHOLOGY—There was little hyphal differentiation observed within and between the Laccaria isolates examined during this study. No spores were formed in culture.

In all isolates, the vast majority of hyphae were morphologically undifferentiated, with clamp connections at nearly all septa (fig. 2a). Scattered among
these sparsely branched hyphae were subcoralloid to coralloid hyphae (fig. 2b,c) and/or irregularly swollen hyphae (fig. 2d). All hyphae were hyaline in KOH, except where noted. Localized, slightly thick-walled swellings were often observed in plates of all taxa (fig. 2e). These swellings could either be terminal or intercalary and could be found in chains of two to four. They are likely a response to water stress, as they become more abundant when the agar in Petri plates loses moisture. Hutchison (1989) reported similar swellings from numerous isolates of ectomycorrhizal fungi.

Pantidou et al. (1983) reported the presence of holoblastic conidia from a purported culture of *Laccaria laccata*. Hutchison (1989), however, reported that these structures were secretory cells of *Pleurotus* sp. and that the isolate used by Pantidou et al. (1983) was from a species of that genus, not *L. laccata*.

Intra- and Intercollection Pairing Reactions

Information on intra- and intercollection pairing reactions has only recently been employed for systematic and biological studies of fungi that form ectomycorrhizae (Fries, 1987). Fries (1977) first reported the successful germination of basidiospores from collections of *Laccaria*. Several years later he reported the occurrence of several intersterility groups within *L. laccata sensu lato* (Fries, 1983a). Fries and Mueller (1984) later determined that these intersterility groups were referable to separate species. They documented a good correlation between the identified intersterility groups and species based on morphological characters, using Swedish isolates of *L. amethystina*, *L. bicolor*, *L. laccata*, and *L. proxima*. Intraspecific pairings of these Swedish isolates revealed a high incidence of intercompatibility in three of these species (all but *L. laccata*). Two intersterility groups were detected within Swedish isolates from morphologically similar collections identified as *L. laccata*. The two intersterility groups within *L. laccata* were treated as sibling species because they could not be delimited on morphological characters (Fries & Mueller, 1984; Mueller & Vellinga, 1986). Studies by Kropp and Fortin (1988) and Doudrick and Anderson (1989) documented the occurrence of two or more intersterility groups within the North American population of *L. bicolor*.

When used in conjunction with data from other analyses, information on intercollection pairing reactions has proven useful for circumscribing taxa (Mueller & Gardes, 1991; Mueller, 1991c). Mueller and Gardes (1991) reported three intersterility groups within the examined material of North American *L. bicolor*. Intragroup intercompatibility was high, and most intergroup pairings were intersterile. These groups could be circumscribed on both morphological and molecular characters and consisted of isolates of *L. bicolor sensu stricto*, *L. nobilis*, and *L. trichodermophora*. Questions remain as to the relationship of Swedish material, morphologically similar to North American material of *L. bicolor sensu stricto*, to the three North American taxa. The two isolates of Swedish origin used as testers were 100, 57, and 21% intercompatible with North American isolates of *L. bicolor*, *L. nobilis*, and *L. trichodermophora*, respectively.

Interstock pairing reactions were also useful in a study of the *L. laccata* complex (Mueller, 1991c). However, because isolates of *L. laccata* var. *laccata* were not available for inclusion in these analyses, some of the systematic conclusions remain tentative. Several North American intersterility groups were detected, and all tested North American isolates were intersterile with both of the intersterility groups reported from Sweden by Fries and Mueller (1984). Most, but not all, of these groups could be delimited morphologically. Molecular divergence (detected through analyses of restriction fragment length polymorphisms of mitochondrial and nuclear ribosomal DNA) was also detected between several of these intersterility groups (Gardes et al., 1990, 1991a; see below). Intersterility groups that could be delimited from morphological characters were recognized at the species level (i.e., *L. laccata*, *L. longipes*, *L. montana*, *L. ohiensis*, and *L. striatula*).

As in the study on the *L. bicolor* complex (Mueller & Gardes, 1991), data obtained to date do not resolve questions concerning potential gene exchange between geographically distant populations of some putatively cosmopolitan species in the *L. laccata* complex (Mueller, 1991c). The most commonly collected North American taxon in the complex is *L. laccata* var. *pallidifolia*. Mueller and Vellinga (1986) and Mueller (1991a) reported this taxon as being abundant in Europe. However, North American and Swedish isolates referable to this taxon are intersterile (Mueller, 1991c). Unfortunately, representative Swedish material of this taxon was not included in the studies of Gardes et al. (1990, 1991a,b), so data are not available on molecular divergence between the two populations. It is not possible to delimit collections from...
Fig. 2. Hyphal modifications observed during micromorphological analyses of 6-week-old somatic culture mats of *Laccaria* taxa: a, typical morphologically undifferentiated hyphae—note the presence of clamp connections and the regular branching pattern; b, coralloid hyphae—note the numerous, short, intertwining branches; c, subcoralloid hyphae; d, irregularly swollen hyphae; e, hyphae with terminal and intercalary swellings. Scale line = 10 μm.
the two populations based on morphology (Mueller, 1991c). For now, therefore, I treat these two potentially intersterile populations as contaxic.

Tested isolates of *L. amethysteo-occidentalis*, *L. amethystina*, *L. proxima*, and *L. vinaceobrunnea* were intersterile in all attempted interspecific pairings. Intraspecific pairings were nearly completely intercompatible within these species. However, homokaryotic isolates were available from only two or three stocks for most of these species, so it was not possible to rigorously test the degree of intraspecific intercompatibility.

In this study I have delimited species so that they are presumably monophyletic and are diagnosable by a unique combination of character states. Data from intercollection pairings were used to help identify groups to analyze in detail for potential morphological and molecular divergence. Because data on morphology, breeding, and ecology are not always concordant, it is inadvisable to rigorously adhere to the biological species paradigm (see discussions in Mishler & Donoghue, 1982; Donoghue, 1985; de Queiroz & Donoghue, 1988, 1990; Cracraft, 1990; Vilgalys, 1991).

### Restriction Fragment Length Polymorphisms of rDNA and mtDNA

It is not yet possible to routinely obtain in vitro basidia production for any species of *Laccaria*, or most other fungi that form ectomycorrhizae. One consequence of this inability to obtain the complete life cycle for these organisms is that it is impossible to carry out genetic analyses or to determine if intercompatible isolates are fertile (would produce viable progeny). This problem, coupled with the fact that the ability to mate is a plesiomorphic character state (e.g., Donoghue, 1985), makes it necessary to have data from other analyses to substantiate hypotheses of gene exchange between populations. Gardes et al. (1990, 1991a) obtained data on restriction fragment length polymorphisms (RFLPs) for both nuclear ribosomal DNA (rDNA) and mitochondrial DNA (mtDNA) to (1) investigate possible genetic divergence between species and populations of the same putative species, (2) determine concordance of data obtained through morphological analyses and pairing analyses, and (3) evaluate molecular markers for isolate typing. The resulting data could not be used for phylogenetic reconstructions because the numerous length mutations that were detected within the segments of DNA analyzed prevented making the necessary assumptions of homology.

Comparable results were obtained with both mtDNA and rDNA for *L. amethystina* and *L. laccata sensu lato* (Gardes et al., 1990, 1991a; Mueller, 1991c), in which divergence was detected between North American and Swedish isolates of these taxa. Divergence was also detected between the tested intersterility groups of the North American *L. laccata* complex.

Conflicting results were obtained with mtDNA and rDNA within the *L. bicolor* complex (Gardes et al., 1990, 1991a; Mueller & Gardes, 1991). Divergence in rDNA was detected between the North American and Swedish populations but was not observed between North American intersterility groups. Conversely, divergence was detected between each of the North American intersterility groups but was not detected between North American and Swedish populations based on mtDNA polymorphisms. Additional European material needs to be examined to attempt to resolve this discrepancy. Only two Swedish isolates of *L. bicolor sensu lato* were utilized by Gardes et al. (1990, 1991a), so it is not possible to compare the amount of heterogeneity of either mtDNA or rDNA within North American and European populations. A possible explanation for these conflicting results is that Swedish *L. bicolor* migrated from a large North American population that contained a pool of mtDNA variation (J. W. Taylor, University of California, Berkeley, pers. comm.). The Swedish population would, therefore, contain only a subset of the mtDNA variation. Following migration, the North American population underwent divergence of morphological and pairing alleles, resulting in *L. nobilis* and *L. trichodermophora*. Some of the mtDNA variation within the original North American pool has subsequently been lost, as evidenced by the data on RFLPs, which uncovered more intraspecific than interspecific similarity in mtDNA for the three North American taxa. This hypothesis cannot be tested until a robust phylogeny for the group is obtained.

### In Vitro Ectomycorrhizal Synthesis Results

Isolates of *Laccaria* are frequently used in applied and basic studies on ectomycorrhizae (see Kropp & Langlois, 1990). In vitro mycorrhizal synthesis studies employing the growth pouch technique of Fortin et al. (1983) are ongoing as part of my studies on *Laccaria*. Experiments were
run in a Plexiglas mycorrhizal synthesis chamber, the design for which was modified from plans from Steven Miller (University of Wyoming, Laramie, pers. comm.). The primary goals of these studies have been to further characterize species of Laccaria as well as to document the ability of particular species of Laccaria to form ectomycorrhizae with select tree species in the laboratory.

To date we have synthesized ectomycorrhizae between several Laccaria species (L. amethysteo-occidentalis, L. bicolor, L. laccata var. pallidifolia, L. proxima, and L. striatula) and the following North American trees: Picea sitchensis (Bong.) Carr., Pinus ponderosa Laws., P. resinosa Ait., and Pseudotsuga menziesii (Mirb.) Franco. Ectomycorrhizae have also been synthesized between L. trullissata and Pinus resinosa and between several South American isolates of L. ohiensis and seedlings of the southern beech, Nothofagus obliqua (Mirbel) Oerst.

Although macro morphology of the ectomycorrhizae varies with the species of host tree (e.g., degree of branching), their micromorphology is similar. In all material examined to date, a well-defined, 15–60 μm thick, tightly interwoven mantle of clamped, morphologically undifferentiated hyphae was formed. No cystidia-like elements have been observed. All infected short roots had a well-developed Hartig net that extended through 70–100% of the cortex. These data coincide with published data on Laccaria ectomycorrhizae.

Ecology and Distribution

Many species of Laccaria show some degree of host specificity. Laccaria proxima and L. laccata var. pallidifolia are the only North American taxa that appear to be associated commonly with both Fagaceae and Pinaceae. Laccaria amethystina and L. ochropurpurea appear to be associated solely with temperate hardwoods, especially species of Quercus and Fagus grandifolia, while L. vinaceobrunnea has only been found under live oak, Quercus virginiana. Laccaria ohiensis has not been commonly collected in north temperate forests. In tropical and southern temperate habitats, it is found associated with Quercus and Nothofagus, respectively.

All of the members of the L. bicolor complex (L. bicolor, L. nobilis, and L. trichodermophora) appear to be associated with Pinaceae in North America. Laccaria trichodermophora can shift hosts when members of the Pinaceae are not available—it has been found under tropical Quercus in Costa Rica (Mueller & Strack, unpubl.). Similarly, although L. amethysteo-occidentalis is most commonly found with conifers, especially Pseudotsuga, it can be found under Quercus in California.

Laccaria montana and L. pumila are commonly collected in arctic and alpine habitats, where they appear to be associated with Pinaceae (especially Pinus), Salix, and Betula.

Although many species of Laccaria can be encountered growing among mosses, only L. longipes, L. bicolor, and L. proxima are found commonly in Sphagnum bogs. Laccaria trullissata and L. maritima are found only in sand dunes or other very sandy areas, where they are putatively associated with species of Pinus.

Only L. laccata var. pallidifolia, L. proxima, and L. tortilis were found throughout the study range. Laccaria bicolor occurs in all areas except southeastern North America. All other taxa showed some geographical restriction. Taxa reported only from eastern North America are L. amethystina, L. maritima, L. longipes, L. oblongospora, L. ochropurpurea, L. ohiensis, L. striatula, L. trichodermophora, L. trullissata, and L. vinaceobrunnea. Conversely, L. amethysteo-occidentalis, L. montana, L. nobilis, and L. pumila have not been reported east of the Great Lakes region.

Phylogenetic Considerations

Placement of Laccaria in Ordinal and Family Treatments

A robust hypothesis of phylogenetic relationships for the Agaricales has not been developed. Several classifications have been advanced that reflect differences in views of relationships among genera in the group (e.g., Kühner, 1980; Jülich, 1981; Singer, 1986).

Kühner (1980, 1984) proposed dividing the Agaricales into several small orders that he felt were easier to define and had sharper boundaries than those traditionally recognized (e.g., Singer, 1975). He treated Laccaria, along with its gasteroid counterpart Hydnangium, as a separate family named the Hydnangiaceae within his order Tricholomatales (Kühner, 1980, 1984) (table 2). Hydnangium is the sister taxon to Laccaria and Tricholomataceae is the sister taxon to Hydnangiaceae in this classification.

MUELLER: SYSTEMATICS OF LACCARIA (AGARICALES)
Table 2. Placement of *Laccaria* in Kühner’s (1980), Jülich’s (1981), and Singer’s (1986) classifications of agaricoid Hymenomycetes.

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Jülich (1981) also recognized the Tricholomatales as a separate order but treated *Laccaria* in his monotypic family Laccariaceae separate from, but closely related to, the Hydangiaceae (table 2). These 2 families are among the 22 families that he recognized for the order (Jülich, 1981). Unfortunately, Jülich was not explicit on intraordinal relationships except to say that he did not recognize close relationships among many of these fungi. Thus, it is not clear what he thought was the sister group to the Laccariaceae and Hydangiaceae.

Singer (1986) maintained that separation of the Agaricales into a number of smaller orders is not warranted. Within his classification, Singer (1986) placed *Laccaria* in a separate subtribe (Laccariinae) in Tribus Tricholomatae of the Tricholomataceae (table 2). Singer maintained that *Hydnangium*, as well as all other Gasteromycetes, is sufficiently distinct to prevent it from being treated in the Agaricales. Subtribe Clitocybinae is the sister taxon to *Laccaria* and Termitomycteae is the sister taxon to Tricholomataceae in this classification.

Molecular data obtained to date do not contain information with which the Agaricales sensu Singer can be divided into smaller orders. Rehner et al. (1990) reported that their sequence data of mitochondrial and nuclear ribosomal RNA genes do not resolve phylogenetic relationships within the Agaricales except to support the separation of the Boletales and the Russulales from the rest of the agarics. Lacking supportive evidence from molecular analyses, and heeding Singer’s (1986) arguments for the use of caution regarding the multiplication and upgrading of higher taxa, I treat *Laccaria*, along with *Hydnangium* and *Podohyd-| |

*Hyp* | |

*nangium* (see below), within the Tricholomataceae. It was beyond the scope of this study to try to resolve phylogenetic relationships within the Tricholomataceae. Until these relationships have been rigorously analyzed, I do not recognize inframolecular taxa in the Tricholomataceae. However, I accept Singer’s (1986) and Kühner’s (1980) view that *Laccaria* has closer affinities with genera in Singer’s Tricholomataceae and Kühner’s Tricholomataceae than with other genera in the Tricholomataceae sensu Singer (1986).
Relationship of *Laccaria* to *Hydnangium* and *Podohydnangium*

*Podohydnangium* must be considered along with *Hydnangium* in discussions of the relationship of *Laccaria* to putative gasteroid relatives. *Podohydnangium* is a monotypic genus that differs from *Hydnangium* by having a distinct stipe-columella and, therefore, appears intermediate between *Laccaria* and *Hydnangium* (Beaton et al., 1984). *Podohydnangium* was not included in Kühner’s (1980) and Jülich’s (1981) treatments because it was first described in 1984, and it was excluded from Singer’s (1986) classification for the same reason that he excluded *Hydnangium*: uncertainty of affinity.

The three classifications discussed above treat the relationship of *Laccaria* to *Hydnangium* and *Podohydnangium* differently (table 2). This is because of fundamental differences in opinion regarding the relationship of gasteroid genera to their agaric counterparts. Kühner (1980) and Jülich (1981) both treated certain gasteroid taxa within the Agaricales, incorporating them into the classification with their putative sister taxa. Singer (1986), on the other hand, maintained that the relationship of these fungi to epigeous agarics is not sufficiently resolved to justify incorporating them into the Agaricales.

Although *Laccaria*, *Podohydnangium*, and *Hydnangium* differ drastically in macromorphology, they share several presumably derived micromorphological character states, including identical basidiospore ornamentation and, at least in *Laccaria* and *Hydnangium* (*Podohydnangium* has not been examined), multinucleate basidiospores.

*Laccaria* is unique among epigeous agarics in that the conic echinulae, diagnostic features of the genus, are formed by microtubules that run perpendicular to the epispore (Besson & Kühner, 1971; Kühner, 1980; v. Hofsten & Mueller, unpubl.). SEM micrographs of basidiospores from *Podohydnangium austral* Beaton, Pegler & Young and several *Hydnangium* taxa have documented the similarity of shape of the basidiospore ornamentation between these taxa and *Laccaria* (Pegler & Young, 1979; Beaton et al., 1984; Castellano et al., 1989). Unpublished TEM data obtained by v. Hofsten (Institute of Physiological Botany, University of Uppsala, Uppsala, Sweden) documented that the basidiospore wall ultrastructure of *Hydnangium* is similar to that found in *Laccaria* (i.e., the echinulae are composed of microtubules that run perpendicular to the epispore).

All examined taxa of *Laccaria* as well as *Hydnangium carneum* have multinucleate basidiospores (table 1; Kühner, 1980; Tommerup et al., 1991).

The three genera also share several plesiomorphies such as having abundant clamp connections; having nonamyloid, acyanophilic basidiospores; and lacking a heteromeroous trama (Pegler & Young, 1979; Beaton et al., 1984). Finally, *Podohydnangium austral* and at least some species of *Hydnangium* appear similar in color to orange-brown *Laccaria*.

The genera differ in that *Hydnangium* and *Podohydnangium* have statisomsporic basidiospores that are orthotropic in development and *Laccaria* has ballistosporic basidiospores that are heterotropic in development. But, as pointed out by several authors (e.g., Pegler & Young, 1979; Beaton et al., 1984), *Hydnangium* is not closely related to any of the genera such as *Octavianina* O. Kuntze formerly treated in the polyphyletic Hymenogastrales *sensu* Singer and Smith (1960) and others.

Although *Laccaria*, *Hydnangium*, and *Podohydnangium* appear to form a monophyletic group, it is currently not possible to undertake a rigorous analysis of the relationship of these three genera to each other as no detailed systematic work has been carried out on either *Hydnangium* and *Podohydnangium* and species circumscriptions, composition, and relationships are still uncertain in these two genera. Castellano and Trappe (1990) accepted 23 names in *Hydnangium* in their bibliographic survey of Australian gasteroid fungi. Numerous systematic problems remain in the group, however, and some of these taxa probably belong in other genera. Until intra- and intergeneric relationships within this group are resolved, I choose to treat the taxa in this group as three separate genera (*Laccaria*, *Hydnangium*, *Podohydnangium*) in the Tricholomataceae *sensu* Singer (1986) amended to include *Hydnangium* and *Podohydnangium*. The inability to resolve infrafamilial relationships within the family precludes recognizing the clade composed of these genera in a formal classification (see above).

Previously Published Infrageneric Classifications Proposed for *Laccaria*

Three primary infrageneric classifications have been proposed for *Laccaria* (Bon, 1983; Singer, 1986; Ballero & Contu, 1989) (table 3). Moser (1983), Clémençon (1984), and others have published variations of these classifications that do
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Sect. Maritimae Bon</td>
<td>Stirps Trullissata</td>
<td>Sect. Maritima Bon</td>
</tr>
<tr>
<td>L. trullissata</td>
<td>L. trullissata</td>
<td>L. trullissata</td>
</tr>
<tr>
<td>L. maritima</td>
<td>L. maritima</td>
<td>L. maritima</td>
</tr>
<tr>
<td>Sect. Amethystinae Bon</td>
<td>Stirps Amethystina</td>
<td>Sect. Amethystinae Bon</td>
</tr>
<tr>
<td>L. amethystina</td>
<td>L. ochropurpurea</td>
<td>L. amethystina</td>
</tr>
<tr>
<td>L. bicolor</td>
<td>L. bicolor</td>
<td>L. calospora (= L. amethystina)</td>
</tr>
<tr>
<td>L. purpureobadia</td>
<td>L. calospora (= L. amethystina)</td>
<td>L. violaceonigra</td>
</tr>
<tr>
<td>Sect. Laccata</td>
<td>Stirps Laccata</td>
<td>L. violaceonigra</td>
</tr>
<tr>
<td>Stirps Ohiensis</td>
<td>L. laccata</td>
<td>L. masonii</td>
</tr>
<tr>
<td>L. ohiensis (= L. impolita)</td>
<td>L. proximella</td>
<td>L. bicolor</td>
</tr>
<tr>
<td>L. tortilis</td>
<td>L. proxima</td>
<td>L. bullulifera</td>
</tr>
<tr>
<td>L. altaica (= L. pumila)</td>
<td>L. tetraspora (= L. ohiensis)</td>
<td>L. farinacea (= L. trichodermophora)</td>
</tr>
<tr>
<td>L. striatula (= ?)</td>
<td>L. montana</td>
<td>Sect. Laccaria</td>
</tr>
<tr>
<td>L. lateritia (= L. fraterna)</td>
<td>L. altaica (= L. pumila)</td>
<td>Subsect. Bisporae Contu</td>
</tr>
<tr>
<td>Stirps Laccata</td>
<td>L. echinospora (= L. tortilis)</td>
<td>L. echinospora (= L. tortilis)</td>
</tr>
<tr>
<td>L. laccata</td>
<td>L. echinospora (= L. tortilis)</td>
<td>L. purpureobadia</td>
</tr>
<tr>
<td>L. affinis (= L. laccata var.</td>
<td>L. montana</td>
<td>L. lutea (= ?)</td>
</tr>
<tr>
<td>pallidifolia)</td>
<td></td>
<td>L. proxima</td>
</tr>
<tr>
<td>Stirps Tetraspora</td>
<td>L. laccata</td>
<td>L. montana</td>
</tr>
<tr>
<td>L. proxima (= ?)</td>
<td>L. laccata</td>
<td>L. laccata</td>
</tr>
<tr>
<td>L. tetraspora (= L. ohiensis)</td>
<td>L. purpureobadia</td>
<td>L. tetraspora (= L. ohiensis)</td>
</tr>
<tr>
<td>Stirps Galerinoides</td>
<td>L. purpureobadia</td>
<td>L. affinis (= L. laccata var. pallidifolia)</td>
</tr>
<tr>
<td>L. galerinoides</td>
<td></td>
<td></td>
</tr>
<tr>
<td>L. vinaceoavellanea</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stirps Purpureobadia</td>
<td></td>
<td></td>
</tr>
<tr>
<td>L. purpureobadia</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

not differ significantly from those presented in Table 3.

The primary difference between Bon’s and Ballero and Contu’s classification versus that of Singer’s is the rank at which they recognized subgeneric taxa. Singer (1986) used the term stirps (a term not recognized by the International Code of Botanical Nomenclature, Greuter et al., 1988) rather than section to reflect the small hiatus between the subgeneric groups that he accepted. Bon (1983) and Ballero and Contu (1989) recognized three sections, with section Laccaria (incorrectly named Laccata by Bon, ICBN Art. 22.1, Greuter et al., 1988) being further divided into several subgroups. All three classifications recognized a separate group composed of L. maritima and L. trullissata and a group composed of L. amethystina and other taxa with violet to purple basidiomata (table 3). Bon (1983) and Ballero and Contu (1989) each recognized the species that have bisterigate basidia as a separate subgroup. Singer (1986) included these taxa among species with teteristerigate basidia. He recognized stirps Galerinoides and Purpureobadia on differences in basidioma colors (Singer, 1986). Other differences between these three classifications (table 3) are due primarily to either varying interpretation of taxa or the inclusion of different taxa.

**Cladistic Analyses**

Cladistic analyses were undertaken to resolve infrageneric relationships within Laccaria. The infrageneric classifications of Bon (1983), Singer (1986), and Ballero and Contu (1989) discussed above were based on those authors’ interpretations of the evolutionary history of the group. These authors, however, did not provide explicit statements regarding crucial assumptions and decisions used to develop their classifications. Without explicit information on choice and weighting of characters, character state evolution, homoplasy (convergence or parallelisms), and so forth, it is impossible to make an objective comparison or rigorously choose between these conflicting classifications.
Although cladistics has been used commonly in studies of plants and animals, such analyses have infrequently been used in fungal systematics. Cladistic methods are based on the theories first expounded by Hennig (1966), which have subsequently been expanded and modified by numerous workers (see reviews in Eldredge & Cracraft, 1980; Nelson & Platnick, 1981; Wiley, 1981; Duncan & Stuessy, 1984; Stuessy, 1990). The theoretical basis for these methods includes the following: (1) phylogenetic relationships are based on the idea of common ancestry (monophyly), (2) evidence for monophyletic groups (all, and only, the descendants of a particular ancestor) can only be determined by the detection of shared derived character states (synapomorphies), and (3) shared primitive character states (symplesiomorphies) do not provide evidence for relationships. Although there are operational and theoretical difficulties involved with any technique, cladistic analyses provide a rigorous method for making hypotheses of phylogenetic relationships.

Unfortunately, Laccaria does not lend itself to cladistic analysis. Problems in determining outgroups and in using the outgroup criterion for character state polarization are treated in the next subsection. Problems in choosing characters and in determining character state homology are also treated below. Care must be used, therefore, when interpreting the following results from the cladistic analyses. They are presented only as a working hypothesis of the evolutionary history of the genus, subject to revision.

**Discussion of Choice of Outgroups—Lack of consensus regarding relationships within the Agaricales sensu Singer (1986) prevented me from making an unequivocal choice of an outgroup (see discussion at the beginning of this section and data in tables 2, 3). Uncertainty is not limited to the determination of the sister group to Laccaria, it also applies to the generic composition and circumscriptions of potential outgroups (Kühner, 1980, 1984; Singer, 1986).**

The classifications presented in Table 2 propose conflicting hypotheses regarding the sister taxon to Laccaria. I used the entire Tricholomataceae Singer, minus Laccaria, as the sister group to Laccaria. This group of taxa is roughly equivalent to the Clitocybeae plus Tricholomaeae in Kühner’s Tricholomataceae (Kühner, 1980, 1984). Cantharellus was used as the sister group to the Tricholomataceae. Although some workers do not derive the Tricholomataceae from a Cantharellus-like ancestor (e.g., Singer, 1986), I find this to be a plausible hypothesis, following the arguments of many workers (e.g., Petersen, 1971; Kühner, 1980, 1984; Bigelow, 1982).

It was well beyond the scope of this study to try to resolve relationships within the heterogeneous Tricholomataceae. Instead, I divided the group into smaller units based only on characters shared by the outgroup and ingroup. Using this criterion I used the following operational units as outgroups: Cantharellus, Clitocybe, Leptisa, Tricholomopsis 1 & 2 (differing by basidiospore shape; represented by Tricholomopsis flavissima (Smith) Singer and T. rutilians (Scheaff.: Fr.) Singer, respectively), Tricholoma 1 & 2 (differing by basidiospore shape; represented by Tricholoma aurantium (Fr.) Ricken and T. michiganense Smith, respectively), Omphalinae 1 & 2 (differing by basidiospore shape; represented by Omphalina hepatica (Fr.) Orton and Leptoglossum rickenii (Hora) Singer, respectively), and Omphalinae 3-5 (differing by the number of sterigmata per basidium and number of nuclei per basidiospore; represented by Gerroneoma chrysophyllum (Fr.) Singer, Omphalina pseudodontrosacea (Bull.) Moser, and O. griseopallida (Desm.) Quél., respectively) (table 5). For ingroups, I used all of the Laccaria taxa recognized from the continental United States and Canada. I further divided *L. lacca* into three groups, *L. lac* 1-3 (differing in basidiospore shape), because of the high degree of plasticity observed in this character in this taxon. Extralimital taxa were not included in these analyses because of a lack of information on somatic culture mat morphology and difficulties in interpreting the macromorphology, especially color, for a number of taxa that I know only from the literature and from an examination of their type specimens.

Another serious problem in determining suitable taxa to use as outgroups to Laccaria is that many of the systematically informative characters in Laccaria do not occur in prospective outgroups (e.g., length and width of basidiospore echinulae and, as coded, basidioma and culture mat pigments). It also was impossible to determine character state homology for characters such as basidoma and basidiospore size between putative outgroups and Laccaria taxa. Because of these problems, only 5 of the 14 characters employed in the final analyses could be coded for both the outgroups and ingroups (tables 4, 5). Thus, most of the ingroup characters could not be polarized directly by outgroup comparison (Watrous & Wheeler, 1981; Maddison et al., 1984).

Three separate sets of analyses were run. First,
TABLE 4. Characters and their states used in cladistic analyses.

<table>
<thead>
<tr>
<th>Character description</th>
<th>Character state</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of sterigmata per basidium</td>
<td>0 = 4; 1 = 2, 3; 2 = 5–8</td>
</tr>
<tr>
<td>Number of nuclei/basidiospore</td>
<td>0 = 1; 1 = multiple</td>
</tr>
<tr>
<td>Echinulate basidiospores with echinulae formed by perpendicularly microtubules</td>
<td>0 = absent; 1 = present</td>
</tr>
<tr>
<td>Mean echinulae length (in µm)</td>
<td>0 = rugulose; 1 = &lt; 0.5; 2 = 0.5–1; 3 = 1–2; 4 = &gt; 2</td>
</tr>
<tr>
<td>Echinulae base width (in µm)</td>
<td>0 = &lt; 1; 1 = ≥ 1.2</td>
</tr>
<tr>
<td>Mean basidiospore length</td>
<td>0 = short (&lt; 8 µm); 1 = moderate (8–10 µm); 2 = long (10–13 µm); 3 = elongate (&gt; 13.5 µm)</td>
</tr>
<tr>
<td>Basidiospore shape (Q)</td>
<td>0 = globose (Q = 1–1.05); 1 = subglobose to broadly ellipsoid (Q = 1.06–1.23); 2 = ellipsoid (Q = 1.24–1.6); 3 = oblong (Q = 1.65–2); 4 = cylindrical or fusiform (Q &gt; 2)</td>
</tr>
<tr>
<td>Cheilocystidia shape</td>
<td>0 = absent or filamentous and not strongly morphologically differentiated; 1 = subclavate to clavate; 2 = very large and inflated</td>
</tr>
<tr>
<td>Pileus color when young and fresh</td>
<td>0 = flesh color to orange-brown; 1 = violaceous; 2 = red-brown; 3 = violet-brown; 4 = ochraceous; 5 = rust</td>
</tr>
<tr>
<td>Lamellar color when young and fresh</td>
<td>0 = flesh color; 1 = vinaceous; 2 = violet to purple; 3 = rose pink</td>
</tr>
<tr>
<td>Basal mycelium color when young and fresh</td>
<td>0 = white; 1 = violet</td>
</tr>
<tr>
<td>Pileus size</td>
<td>0 = moderate; 1 = small; 2 = large</td>
</tr>
<tr>
<td>Stature</td>
<td>0 = moderate; 1 = gracile; 2 = robust</td>
</tr>
<tr>
<td>Color of somatic culture mat on PDA and MMN</td>
<td>0 = white to olive brown; 1 = violet</td>
</tr>
</tbody>
</table>

outgroup and ingroup relationships were examined using the five shared characters (fig. 3). Second, resolution of ingroup relationships was attempted using all available characters for the ingroup without the outgroups. This resulted in the unrooted network presented in Figure 4. Finally, to develop an operational classification, analyses of the combined data set were run to identify functional outgroups within Laccaria (Watrous & Wheeler, 1981), thereby constraining possible tree topologies (fig. 5).

**Discussion of Characters and Character State Assignments**—Table 4 lists the characters and their states used in these analyses. Other characters (e.g., presence or absence of striations, pileus texture, growth rate of cultures on various media, etc.) were employed in preliminary analyses but were subsequently deleted for various reasons, including a high degree of variability of such characters within and among taxa or their autapomorphic nature (i.e., they varied only in one terminal taxon and thus did not provide information on relationships among taxa). Size character (nos. 6, 17, and 18) were coded only for ingroup taxa because of the impossibility of estimating homology with states in the outgroups. Color characters (nos. 11, 12, 13, and 19) were limited to ingroup taxa for the same reason. To my knowledge, the identity and structure of the pigments in Laccaria are unknown (see Discussion of Systematic Characters). Thus, it is not possible to determine homology of pigments observed in Laccaria with those found in other genera with orange-brown and violet pigments. Lack of knowledge of the pigments in Laccaria causes problems in ingroup as well as outgroup analyses. I have made the assumption that the violet coloration observed in many Laccaria, from the lamellae and stipe basal mycelium in L. bicolor to the entire basidioma in L. amethystina, is due to the same pigment(s).

Information on number of sterigmata per basidium and number of nuclei per basidiospore (characters 1 and 2, respectively; table 4) for outgroups was obtained from a number of sources including Corner (1966), Kühner (1980, 1984), Bigelow (1982), and Singer (1986).

**Preliminary Hypothesis of Phylogenetic Relationships Based on Cladistic Analyses**—Analyses undertaken for this study were performed using PAUP Version 3.0L (Swofford, 1989) running on a MAC II ci. All multistate characters were interpreted as unordered because I could not make a priori decisions on character state transformation series. The number of taxa included in the analyses precluded the use of exact methods to find the shortest trees, so a heuristic method using branch swapping (tree bisection–reconnection) was employed to search for optimum trees. The MULPARS option was invoked to save 300 equally most parsimonious trees. A shorter tree was sometimes located even after 200 trees were saved. Ten replications using random addition sequences were employed to ensure that addition sequence did not affect tree length or topology. Characters and their states employed in the final sets of analyses are listed in Tables 4 and 5.

A strict consensus tree of the 300 most parsimonious trees saved in the analysis restricted to the characters that could be coded for both ingroups and outgroups is presented in Figure 3. This tree has a length of 28 steps with a homoplasy index (HI) of 0.643 and a rescaled consistency index (RC) of 0.211. While ingroup relationships were not resolved in this analysis, Laccaria formed a monophyletic clade apart from the outgroup taxa that was supported by one synapomorphy, basidiospore echinulae ultrastructure (character 3).

Only five characters could be used in this analysis (table 4, characters 1–3, 7, and 8) and of these
TABLE 5. Taxon by character state matrix used in cladistic analyses. Characters and character states are provided in Table 4. Outgroups employed were Cantharellus and species of Singer’s (1986) Tricholomataceae excluding Laccaria (table 2).

<table>
<thead>
<tr>
<th>Taxon</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
<th>11</th>
<th>12</th>
<th>13</th>
<th>14</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trich 1 (Tricholoma 1)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>?</td>
<td>?</td>
<td>?</td>
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<td>0</td>
<td>?</td>
<td>?</td>
<td>?</td>
<td>?</td>
<td>?</td>
<td>?</td>
</tr>
<tr>
<td>Trich 2 (Tricholoma 2)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>?</td>
<td>?</td>
<td>?</td>
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<td>?</td>
<td>?</td>
<td>?</td>
<td>?</td>
<td>?</td>
</tr>
<tr>
<td>L. a-o (amethysto-occidentalis)</td>
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<td>1</td>
<td>1</td>
<td>3</td>
<td>0</td>
<td>1</td>
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<td>1</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>L. ame (amethystina)</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1</td>
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<td>2</td>
<td>1</td>
<td>0</td>
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<td>1</td>
</tr>
<tr>
<td>L. bic (bicolor)</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>3</td>
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<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
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<tr>
<td>L. frat (fraterna)</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>0</td>
<td>2</td>
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<td>3</td>
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</tr>
<tr>
<td>L. lac 1 (laccata 1)</td>
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<td>1</td>
<td>3</td>
<td>0</td>
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<td>0</td>
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<td>L. lac 3 (laccata 3)</td>
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<td>1</td>
<td>3</td>
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<td>L. long (longipes)</td>
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<td>3</td>
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<td>1</td>
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<tr>
<td>L. mont (montana)</td>
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<td>1</td>
<td>3</td>
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<td>0</td>
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<td>0</td>
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<tr>
<td>L. nob (nobilis)</td>
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<td>1</td>
<td>1</td>
<td>3</td>
<td>0</td>
<td>0</td>
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<tr>
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<td>4</td>
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only characters 3 (presence or absence of echinulate basidiospores) and 8 (cheilocystidia shape) were not homoplastic. Character 3 is the synapomorphy supporting the Laccaria clade; character 8 occurs in 3 states. Although most taxa lack or have filamentous cheilocystidia (state 0), inflated cheilocystidia can be found in two of the outgroups. Laccaria amethysto-occidentalis, L. amethystina, and L. vinaceobrunnea have clavate cheilocystidia. The distribution of multinucleate basidiospores (character 2) along this tree is significant because Kühner (1980, 1984) emphasized the occurrence of multinucleate basidiospores in Laccaria in his rationale for recognizing the genus as a family separate from other genera typically treated in the Tricholomataceae (table 2). Although Laccaria is characterized by having multinucleate basidiospores, this character state is also present in two of the outgroup taxa (character 2, fig. 3). Until the phylogeny of the outgroup (Singer’s Tricholomataceae excluding Laccaria) is elucidated, it is impossible to determine whether the presence of multinucleate basidiospores is synapomorphic or was derived independently in two or more clades within the Tricholomataceae.

Figure 4 presents the results of the analysis of ingroup relationships utilizing all of the characters listed in Table 4 (minus characters 2 and 3 because they were uninformative for ingroup comparisons). The strict consensus tree of the 300 most parsimonious trees saved is presented as an unrooted network because no outgroup was used to root the tree. The network (fig. 4) has a length of
Fig. 3. Strict consensus tree resulting from analyses restricted to characters shared by ingroup and outgroup taxa (characters 1–3, 7, and 8 in table 4). Only characters 3 and 8 were not homoplasious. Length 28, HI = 0.643, RC = 0.211. Refer to Table 5 for abbreviations.

51 steps, a consistency index (CI) of 0.549, and an RC of 0.345. Only select characters were traced onto the network illustrated in Figure 4. All characters are mapped along the tree presented in Figure 5 (analysis of combined outgroup and ingroup data).

All characters except echinulae length (character 4), cheilocystidia (character 8), pileus color (character 9), and color of lamellae (character 10) were homoplasious. Because of this high level of homoplasy, the network is not fully resolved and not robust. The addition or deletion of a character or a change in coding of the states of one character had a profound impact on network topology.

Several subgroups within *Laccaria* were resolved during these analyses (fig. 4). *Laccaria*

Fig. 4. Unrooted network (strict consensus of 300 trees) of ingroup relationships. All characters except 2 and 3 (uninformative) listed in Table 4 were employed. Characters 4, 8, 9, and 10 were not homoplasious. Only select characters were traced onto the network. Length 51, HI = 0.549, RC = 0.345. Refer to Table 5 for abbreviations.
ochropurpurea, L. striatula, and L. tortilis formed a trichotomy separate from the other North American taxa that lack violet pigments (fig. 4). This clade was supported by the presence of strongly echinulate, globose basidiospores (characters 4, 5, and 7) and small gracile basidiomata (characters 12 and 13). Laccaria proxima and L. oblongospora formed a clade supported by the presence of finely echinulate basidiospores (state 2, character 4). These two clades, along with the other taxa that lack violet basidiomata pigments, formed an unresolved “bush” separate from taxa with violet basidiomata pigments. Resolution was higher within the North American taxa with violet pigments. This grade was supported by the presence of violet mycelium at the stipe base and violet culture mats on PDA and MMN media (characters 11 and 14). Both of these states, however, occur also in L. oblongospora, which was not placed in this grade. The L. bicolor complex (i.e., L. trichodermophora, L. nobilis, and L. bicolor) was fully resolved and formed a sister group to the taxa with violet to purple lamellae. Laccaria trullissata and L. maritima formed a trichotomy with L. ochropurpurea owing to their large basidiomata size and stature (characters 12 and 13) and similarity in coloration (characters 9–11). The clade composed of L. amethysteo-occidentalis, L. amethystina, and L. vinaceobrunnea was supported by the presence of large cheilocystidia (character 8).

The distribution of violet basal mycelium and violet somatic culture mats on PDA and MMN media (state 1 of characters 11 and 14, respectively) along this network causes difficulties in interpreting character state changes throughout Laccaria. Based on the topology of the network, violet pigments occur in two places along the tree: in L. oblongospora and in the grade that includes L. trichodermophora–L. vinaceobrunnea. It is impossible to determine which is the plesiomorphic state for these two characters. The occurrence of these states in two areas of the tree could be due either to a parallel gain of pigment(s), a reversal back to the plesiomorphic state, or the incorrect placement of L. oblongospora. This is a serious weakness in these results because, as discussed below, the major subgroups identified through these analyses are supported by pigment composition and their distribution.

Based on these analyses, bisterigmate basidia

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(state 1, character 1) arose independently three times within the North American taxa of Laccaria: in L. fraterna, L. pumila, and L. tortilis.

Laccaria laccata was divided into three operational taxa in these analyses because of plasticity of basidiospore shape within individuals referable to L. laccata on the basis of other character states. These analyses were uninformative for resolving at what rank to recognize these morphological forms of L. laccata.

The data sets (all characters for both ingroup and outgroup taxa) were combined in an effort to constrain the choice of a functional outgroup and provide an operational classification based on a tentative hypothesis of relationships among the ingroup taxa. Because only five characters were shared by the ingroup and outgroup, the results of this analysis provide only one of the possible resolutions of where to root the network presented in Figure 4. Figure 5 shows the results of this analysis. The resulting strict consensus tree of the 300 most parsimonious trees saved was 64 steps long and had a CI of 0.500 and an RC of 0.332.

The unresolved group composed of the taxa lacking violet basidioma pigments plus L. oblongospora is basal on this tree (fig. 5). The only difference in ingroup topology between this tree and the unrooted network (fig. 4) is that L. oblongospora and L. proxima are not placed together in a separate clade.

Proposed Operational Classification of Laccaria

The proposed operational classification used in this monograph is based on an attempt to rigorously analyze all available data using cladistic methods. The employed data set included data on macro- and micromorphology of basidiomata and somatic culture mats, cytology, and basidiospore wall ultrastructure.

Two major subgroups within the North American taxa of Laccaria were identified in these analyses (figs. 4, 5). One subgroup consists of all taxa lacking violet basidioma pigments plus L. oblongospora; the second subgroup consists of the remaining taxa possessing violet basidioma pigments. Although these two subgroups are clearly separated on the cladograms, they are not supported by any synapomorphies. No characters, plesiomorphic or apomorphic, support recognition of the taxa composing the basal group as a monophyletic group separate from the rest of the ingroup taxa. Additionally, although the grade consisting of L. trichodermophora through L. vinaceobrunnea appears well supported by the presence of violet mycelium at the stipe base and by violet culture mats on PDA and MMN media, these character states also occur in L. oblongospora and therefore are present in the other main subgroup. Taxa need to be based on the occurrence of unique sets of derived characters, and thus these two subgroups should not be formally recognized.

The concept of metataxa has been proposed as a means of recognizing unresolved groups (e.g., Donoghue, 1985; de Queiroz & Donoghue, 1988). Because data do not exist to refute their monophyly, the two subgroups are treated as metasections in this monograph, metasections Laccaria and Amethystina. Metasection Amethystina is supported by two character state changes: the presence of violet mycelium at the stipe base, and violet somatic mats on PDA and MMN media. Metasections were used in this treatment, even though metataxa have been criticized by a number of authors (e.g., Kluge, 1989; Nixon & Wheeler, 1990; de Queiroz & Gauthier, 1990), to provide an operational classification and a testable hypothesis of relationships within Laccaria.

Although taxa in metasection Amethystina are almost fully resolved, only the clade consisting of L. amethysteo-occidentalis, L. amethystina, and L. vinaceobrunnea is supported by a synapomorphy: the presence of large, clavate cheilocystidia (figs. 4, 5). For this reason, metasection Amethystina is not further divided. Similarly, no subgroups are recognized within metasection Laccaria.

This classification differs from previously published classifications (table 3) by the recognition of fewer subgeneric groups. The three classifications presented in Table 3 all recognized a separate group, either section or stirps, for L. trullissata and L. maritima. These two taxa formed a trichotomy with L. ochropurpurea in the cladistic analysis (figs. 4, 5) and could not be recognized as a separate monophyletic group.

The results of these analyses are in conflict with the hypothesis that the Laccaria species characterized by bisterigmate basidia compose a monophyletic group separate from tetrasterigmate taxa. Bon’s (1983) stirps Ohiensis and Ballero and Contu’s (1989) subsection Bisporae are paraphyletic according to my analyses and therefore are not recognized.

The tree topology shown in Figures 4 and 5 is concordant with the results obtained to date on relationships based on molecular data. Analyses
of RFLPs of mtDNA (Gardes et al., 1991a) indicated that *L. laccata* var. *pallidifolia* was phenetically more similar to the *L. bicolor* complex than *L. proxima* was to the *L. bicolor* complex. The employed isolates of *L. amethystina* were phenetically distant, based on mtDNA RFLPs from all of these taxa (Gardes et al., 1991a). Similarly, Gardes and colleagues (Gardes et al., 1991b) reported that sequence variation in the internal transcribed spacer (ITS) of the nuclear ribosomal repeat unit was less between the one tested isolate of *L. laccata* var. *pallidifolia* and the three tested isolates of *L. bicolor sensu lato* than between *L. proxima* and the *L. bicolor* complex. Although these data do not resolve the issue of where to root the network presented in Figure 4, they are concordant with placing *L. proxima*, *L. laccata*, and taxa in the *L. bicolor* complex in a linear series.

These conclusions are summarized below in the Conspectus of North American Taxa.

**Conspectus of North American Taxa**

**AGARICALES, TRICHOLOMATACEAE**

Metasection Laccaria

*Laccaria proxima*

*Laccaria oblongospora*

*Laccaria laccata* var. *laccata*

*Laccaria laccata* var. *pallidifolia*

*Laccaria longipes*

*Laccaria fraterna*

*Laccaria montana*

*Laccaria pumila*

*Laccaria striatula*

*Laccaria ohiensis*

*Laccaria tortilis*

Metasection Amethystina

*Laccaria trichodermophora*

*Laccaria bicolor*

*Laccaria nobilis*

**North American Taxa**


Pileus convex to plane, glabrous, finely fibrillose to fibrillose-scaly or scaly to squarrose, astriate to plicate- striate or pellucid-striate, hygrophanous, orange-brown, ochraceous, pinkish flesh color, dark violaceous, vinaceous, rusty red-brown, gray-black, or fawn; lamellae sinuate to subdecurrent, close to distant, thick, waxy appearing, narrow to broad, light flesh pink color, vinaceous, violaceous, rose pink or ash gray; stipe equal to subclavate, glabrous to coarsely fibrillose, often longitudinally striate; basal mycelium white or violet; basidiospores in mass white, rarely light violet; pileipellis morphologically undifferentiated with interwoven hyphae, or fasciculate, or a trichodermium; basidia 2- or 4-sterigmate, clavate; pleurocystidia rare; cheilocystidia absent to abundant, filamentous and morphologically undifferentiated to clavate or subcapitate; basidiospores globose to oblong and echinulate or elongate and finely roughened, multinucleate; cheilocystidae composed of microtubules that run perpendicular to epispore; clamp connections at nearly all septa; basidiospores and all elements inamylloid, not dextrinoid, acyanophilic. Terrestrial, cosmopolitan.

**Key to Laccaria Occurring in North America North of Mexico**

1. Lamellae violaceous to purple when young and fresh .................................................. 2
2. Basidiospores 13.5–22 × 5.5–9.5 μm, elongate, smooth to finely roughened or very finely echinulate (echinulae < 0.5 μm long); in sand or very sandy soil; north central and eastern North America .......................................................... 3
3. Basidiospores < 10.5 μm long, less elongate (Q ≤ 1.5), echinulae > 0.5 μm long; in sand or not in sand .......................................................... 4
3. Basidiospores subfusiform (Q = 2.4–2.5), not echinulate, appearing finely roughened on SEM; eastern and midwestern North America .................................................. *L. trullissata* (p. 64)
3. Basidiospores oblong (\(\bar{Q} = 1.7-1.8\)); finely echinulate (echinulae 0.2–0.5 \(\mu\)m long); Europe, only few Canadian collections known .................................................. L. maritima (p. 65)

4. Pileus and stipe bright violetaceous or purple when young and fresh; cheilocystidia large (up to 92 \(\times\) 12 \(\mu\)m), clavate, abundant .......................................................... 5

4. Pileus and stipe orange-brown, pinkish flesh color, wine color, avellaneous, or buff color; cheilocystidia smaller, filamentous, common to absent ........................................... 7

5. Basidiospores globose, echinulae \(> 1 \mu\)m wide at base; basidiomata fading from amethyst to grayish then buff in age; eastern North America .................................................. L. amethystina (p. 71)

5. Basidiospores subglobule to broadly ellipsoid; echinulae \(\leq 1 \mu\)m wide at base; basidiomata changing from amethyst to vinaceous or reddish brown; eastern or western North America ............ 6

6. Basidiomata large (pilei 10–90 mm diam.), amethyst, becoming vinaceous; pileipellis hyphae interwoven with scattered fascicles of perpendicular hyphae; western North America; under conifers .................................................. L. amethyste-o-occidentalis (p. 69)

6. Basidiomata smaller (pilei 7–25[–45] mm diam.); amethyst, becoming reddish brown; pileipellis hyphae interwoven with numerous, large, individual perpendicular hyphae; Gulf Coast states; under Quercus ........................................ L. vinaceobrunnea (p. 72)

7. Lamellae dark purple, thick, waxy appearing; basidiomata large (pilei up to 60–120 mm diam.), violaceous buff when young and fresh, becoming buff; basidiospores globose to subglobose, echinulae 1–1.5 \(\mu\)m wide at base; eastern North America ........................................ L. ochropurpurea (p. 67)

7. Lamellae light vinaceous, not thick or waxy appearing; basidiomata moderate to large (pilei up to 85 mm diam.), pinkish flesh color when fresh or vinaceous; basidiospores subglobose to broadly ellipsoid or ellipsoid to oblong, echinulae \(\leq 1.2 \mu\)m long and \(\leq 1 \mu\)m wide at base; eastern and western North America .................. 8

8. Basidiomata vinaceous to avellaneous; basidiospores ellipsoid to oblong (\(\bar{Q} = 1.4–1.6\)); echinulae \(\leq 0.5 \mu\)m long; southern Mississippi and Texas ........................................ L. oblongospora (p. 30)

8. Basidiomata pinkish flesh color to reddish brown; basidiospores subglobose to broadly ellipsoid, \(\bar{x} < 8.5 \mu\)m long; widely distributed ........................................ 9

9. Pileus 16–85 mm diam., often strongly scaly to squarrose; stipe large and robust (26–110[–160] \(\times\) 4–10[–16] mm), strongly stiate to reticulate; western North America and upper Great Lakes region, not commonly encountered .................................. L. nobilis (p. 61)

9. Pileus 8–50(–70) mm diam., finely fibrillose to minutely scaly; stipe smaller (23–85[–130] \(\times\) 3–6 [–10] mm) and not strongly stiate; western North America and upper Great Lakes region, commonly encountered .................................................. L. bicolor (p. 57)

10. Basidia (3-)4-sterigate ........................................ 11

10. Basidia 2(-3)-sterigate ........................................ 22

11. Basidiospore echinulae \(< 1 \mu\)m long; basidiospores broadly ellipsoid to oblong (\(\bar{Q} = 1.25–1.6\)) ............... 12

11. Basidiospore echinulae \(\geq 1 \mu\)m long; basidiospores globose to ellipsoid .................................................. 13

12. Basidiospores \(\bar{x} = 8.3–9.0 \times 5.6–6 \mu\)m, oblong (\(\bar{Q} = 1.45–1.6\)); mycelium at stipe base violet, fading white; Gulf Coast states ........................................... L. oblongospora (p. 30)

12. Basidiospores \(\bar{x} = 9–11.5 \times 6.7–8(–8.8) \mu\)m, ellipsoid (\(\bar{Q} = 1.25–1.35[–1.4]\)); mycelium at stipe base white; widely distributed .................................................. L. proxima (p. 27)

13. Mycelium at stipe base violaceous when fresh, becoming white with age; basidiospores small (\(\bar{x} = 7–8.4[–9] \times 6–8 \mu\)m) ........................................ 14

13. Mycelium at stipe base white from onset; basidiospores larger (\(\bar{x} = 8.2–13 \mu\)m long) (but see no. 20, L. longipes) .................. 16

14. Lamellae flesh-colored to pinkish flesh color; basal mycelium scant, strongly hygrophanous; basidiomata orange-brown; pileipellis a trichodermium or of interwoven hyphae with numerous large fascicles of perpendicular hyphae; southeastern North America ........................................ L. trichodermophora (p. 55)

14. Lamellae light vinaceous, occasionally fading to pinkish color; basal mycelium copious, basidiomata pinkish flesh color to reddish brown; pileipellis hyphae interwoven with scattered fascicles of perpendicular hyphae; western North America to Ontario and Michigan .................. 15

15. Pileus 16–85 mm diam., strongly scaly to squarrose; stipe large and robust (26–110[–160] \(\times\) 4–10
[17] 19. Basidiospores relatively large (ε = 9.4–12.6 × 8.5–10.5 μm); pilei up to 35 mm broad, striate to (often) strongly striate; restricted to arctic, boreal, or alpine habitats . . . L. montana (p. 42)
16. Basidiospores smaller; pilei small to large, not striate or occasionally finely striate, some translucent-striate
17. Pileus 16–85 mm diam., strongly scaly to squarrose; stipe large and robust (26–110) × 4–10
[−16] mm), strongly striate to reticulate . . . L. nobilis (p. 61)
17. Pileus smaller (5–45–60) mm diam., glabrous to finely scaly; stipe smaller, not strongly striate
18. Basidiospores globose; echinulae > 1.5 μm long, > 1.2 μm wide at base
19. Basidiospores globose to ellipsoid; echinulae 0.7–2 μm long, ≤ 1 μm wide at base
20. Stipe 20–70(–103) × 1–4 mm, darker than pileus; in moist areas, often among mosses (not Sphagnum); eastern North America, commonly encountered . . . L. striatula (p. 46)
21. Stipe 12–25(–40) × 1–2 mm, concolorous with pileus; cosmopolitan, not commonly encountered in north temperate regions . . . L. ochiensis (p. 48)
20. Basidiospores small (ε = 7.6–7.8 × 6.8–7.2 μm); pilei strongly translucent-striate; stipes long (67–138[–165] mm); growing among mosses, especially Sphagnum, usually in bogs, northeastern North America and upper Great Lakes region . . . L. longipes (p. 38)
20. Basidiospores larger (ε > 8 μm long); pileus not striate, striate or slightly translucent-striate; stipe shorter; growing among mosses or not, not normally found in bogs; widely distributed
21. Basidiospores broadly ellipsoid to ellipsoid (Q = 1.2–1.3); rarely encountered . . . L. laccata var. laccata (p. 34)
21. Basidiospores globose to broadly ellipsoid (Q = 1–1.5[–2]); commonly encountered, widely distributed . . . L. laccata var. pallidifolia (p. 35)
22. Basidiospores usually < 11 μm long; basidiomata rusty red-brown; under Eucalyptus . . . L. fraterna (p. 39)
22. Basidiospores > 11 μm long; under native North American trees
23. Basidiospores 11–17 × 10–14.5 μm, subglobose to broadly ellipsoid (Q = 1.1–1.2); echinulae < 1.5 μm long; montane, boreal, or arctic habitats . . . L. pumila (p. 44)
23. Basidiospores 10–15 × 10–15 μm, globose; echinulae > 2 μm long; temperate habitats

Laccaria Metasection Laccaria
[see p. 24 for discussion]

Basidiomata and somatic culture mats lacking violet pigment(s), or violet pigment(s) present and basidiospores ellipsoid and finely ornamented (echinulae 0.5–1 μm long).

Laccaria proxima (Boudier) Patouillard. Figures 6–8, 53a,b, 69c.

= Clitocybe laccata var. proxima (Boudier) Bresadola, Icon. Mycologica: 43. 1927.

MACROMORPHOLOGY—Pileus (7–)15–69(–83) mm broad, campanulate to convex, often becoming plane to uplifted, some depressed, not striate, occasionally translucent-striate when faded, finely fibrillose to fibrillose, some becoming fibrillo-sclare to scaly or squarrose in age, hygrophanous, reddish brown to orange-brown ("Auburn," "Sanford's Brown," "Orange Rufous," "Hazel," "Cinnamon-Rufous"), fading lighter ("Apricot Buff");

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Fig. 6. Basidiomata of *L. proxima* (GMM 2100).

Fig. 7. Somatic culture mats of *L. proxima* (GMM 1518). Top on PDA, left on MMN, and right on MEA. Photo taken during week 4.
margin incurved to decurved, sometimes becoming plane, entire to undulate, occasionally becoming eroded with age; context thin, tapering quickly to margin, pinkish flesh color ("Japan Rose" to "Shell Pink"). Lamellae sinuate to adnate, occasionally arcuate, subdistant to distant, up to 10 mm broad, pinkish flesh color ("Flesh Color," "Pale Salmon Color"). Stipe (12–)24–72(-155) × 3–11 mm, equal to subclavate, often slightly bulbous, dry, fibrillose, often longitudinally striate, striations moderate to pronounced, most of stipe concolorous with pileus; base occasionally darker ("Rood's Brown"), striations concolorous with pileus or darker red ("Hay's Russet," "Pecan Brown," or "Onion-skin Pink"). Basal mycelium white. Basidiospores white in mass.

Micromorphology—Pileipellis of interwoven hyphae with scattered to numerous large fascicles of ± perpendicular hyphae; fascicles composed of 15–30 or more hyphae; terminal cells of fascicular hyphae 27.5–92 × 4.5–16(-30) μm, filamentous, subclavate, clavate, broadly clavate, capitate or ventricose-rostrate; walls up to 0.5 μm thick, light to moderate yellowish brown; contents hyaline to light yellowish brown. Pileus trama tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. Lamellar trama parallel; hyphae mostly 3–19 μm diam., thin-walled, hyaline to light yellowish brown; cells filamentous to barrel-shaped. Subhymenium morphologically undifferentiated. Basidia (23–)33–62 × 8–15 μm, clavate, hyaline; sterigmata 4, up to 7 μm long. Cheilocystidia 19–66.5(-92) × 2–8.5 (–16.5) μm, filamentous to subclavate, occasionally subcapitate, often abundant, thin-walled hyaline. Basidiospores (excluding ornamentation) [265/20] 8–11(-12.5) × (6.5–)7–8.7(-9.2) μm (X = [8.7–]9–11.5 × 6.7–8(–8.8) μm), Q = (1.07–)1.16–1.49(-1.58) (Q = 1.24–1.34(–1.43)), broadly ellipsoid, ellipsoid or occasionally oblong, hyaline, echinulate; echinulae 0.5–1 μm long, occasionally with 1 or 2 long echinulae (up to 2 μm long) at apex, crowded; hilar appendix 1.3–2 μm long, prominent, truncate, plage present; contents occasionally uniguttulate. Basal mycelium hyphae mostly 2.5–17.5 μm diam., tightly interwoven, hyaline; cells filamentous to barrel-shaped.

Somatic Culture Mat Morphology (N = 4; Appendix B)—PDA: Radius at week 3 = 3–17 mm, week 6 = 26–43 mm; mat felt, thick, tightly interwoven, not translucent, most of uniform thickness or with slightly thicker area near plug, in one (GMM 1525) forming concentric thicker-thinner bands, white to light tan; margin 1–2 mm broad, abruptly thinner or not well differentiated, silky to subvelvety, thin, uneven, white; plug white.
or becoming olive; **hyphae** morphologically undifferentiated. MMN: **Radius** at week 3 = (6-)16–32 mm, week 6 = (18-)43–64 mm; **mat** subfertly to ferty, relatively thin to moderately thick, interwoven, translucent to not translucent, thicker near plug, uniform or thinner towards margin, white; **margin** abruptly thinner or not well differentiated, silky to subfertly, white; **plug** white; **hyphae** morphologically undifferentiated. **MEA:** **Radius** at week 3 = 11–26 mm, week 6 = 30–51 mm; **mat** subfertly to ferty, thin to relatively thick, translucent, white; **margin** not well differentiated, somewhat thinner, white; **plug** white; **hyphae** morphologically undifferentiated, occasionally irregularly swollen.

**Habitat and Distribution**—Scattered to gregarious; terrestrial, associated most commonly with Pinaceae, occasionally among mosses including *Sphagnum*; disturbed areas, early succession forests or under young planted pines in reforested areas. Cosmopolitan; common. Found throughout North America. A list of specimens examined is presented in Appendix A.

**Observations**—*Laccaria proxima* can be distinguished from *L. laccata* by its more robust, more strongly colored basidiomata, nonstriate and slightly scaly to scaly pilei, and more elongate, finely echinulate basidiospores. *Laccaria proxima* is separated from *L. montana* in having smaller, more finely echinulate basidiospores and the more robust habit of its basidiomata. Collections of *L. proxima* can be differentiated from those of *L. oblongospora* by having less elongate, larger basidiospores, white basal mycelium, and culture mats that are white on MMN, PDA, and N6:5 media. A discussion of various interpretations of the name *L. proxima* is presented in the section on type specimens.

Mueller (1982, 1984, 1985) reported that cultures of some *L. proxima* were violet to purple on PDA and MMN media. On further analysis of the collections from which these violet culture mats were derived, it was determined that these specimens were *L. bicolor* and not *L. proxima*. The basidiospores observed from these collections were much smaller and had longer echinulae than those from other collections referable to *L. proxima*. The basidiospore dimensions and cultural characteristics fit my circumscription of *L. bicolor*.

Intra- and interspecific pairing studies have supported treatment of *L. proxima* as a discrete species. No isolate of *L. proxima* has been found to mate with any other putative taxa, and no intra-specific intersterility groups have been detected (Fries & Mueller, 1984; Mueller, unpubl. data). Further support for recognizing *L. proxima* as an autonomous species was obtained during analyses of mtDNA and rDNA RFLPs of select species of *Laccaria* (Gardes et al., 1990, 1991a). A low level of intraspecific heterogeneity in mtDNA and rDNA RFLPs was detected among three isolates of *L. proxima* used in these analyses, whereas their RFLPs were distinct from RFLPs of the other tested taxa.

*Laccaria proxima* has been reported from throughout North America. It has also commonly been collected in Europe (Clémenton, 1984; Contu, 1986; Mueller, 1991a). Watling (1987) reported that *L. proximella* Singer is the alpine equivalent of *L. proxima*. As discussed previously (Mueller, 1991a), I cannot support this contention based on the large number of collections referable to *L. proxima* that I have examined from alpine and boreal habitats in Europe and North America. My interpretation of *L. proximella* is that it differs from *L. proxima* by having violet strains (or mycelium?) at the stipe base and grows in very poor, rocky soil. I have collected material referable to *L. proximella* in southern Argentina and Chile.

**Laccaria oblongospora** G. M. Mueller. Figures 9–11, 53c,d, 67d.


**Macromorphology—Pileus** (5-)12–59 mm broad, obtuse to convex, becoming plane to uplifted, often depressed, not striate, finely fibrillos, becoming fibrillose-scaly, hygrophanous, brownish orange (“Vinaceous-Rufous,” “Kaiser Brown,” “Apricot Buff,” “Burnt Sienna,” or “Sanford’s Brown”), occasionally vinaceous color (“Vinaceous-Brown,” “Vinaceous-Russet” or “Japan Rose”); disc often darker, red-brown to dark orange-brown or occasionally vinaceous (“Dark Liquid Brown,” “Deep Brownish Vinaceous,” “Hay’s Russet,” “Chocolate,” “Vinaceous-Russet,” or “Mahogany Red”); margin incurved to decurved, becoming plane to uplifted, entire to undulate, occasionally becoming eroded; context 1–2 mm thick, tapering quickly to margin, flesh color (“Pale Vinaceous-Pink”). **Lamellae** sinuate to adnate, oc-
casionally arcuate, subdistant to distant, broad, thick, pinkish flesh color (“Vinaceous-Pink,” “Buff-Pink,” “Light Congo Pink,” or “Shell Pink”), occasionally vinaceous or violaceous (“Light Brownish Vinaceous,” “Pale Brownish Vinaceous,” or “Light Pinkish Lilac”). *Stipe* (11-)20–60(–65) × 2–12 mm, equal to subclavate, often slightly bulbose, dry, fibrillosé, occasionally finely longitudinally- striate, concolorous with pileus; striations occasionally darker (“Pecan Brown”). *Basal mycelium* violet, soon fading to white. *Basidiospores* white in mass.

**MICROMORPHOLOGY—Pileipellis** of loosely interwoven hyphae with scattered large fascicles of ± perpendicular hyphae; fascicles composed of (5-)10–30 or more hyphae; terminal cells 32.5–71 × 7–24.5 μm, filamentous, subclavate, clavate, broadly clavate or capitate; walls up to 0.5 μm thick, light vinaceous; contents hyaline to light yellowish brown or light vinaceous. *Pileus trama* tightly interwoven, morphologically undifferentiated, hyaline, yellowish brown to light vinaceous toward pileipellis. *Lamellar trama* parallel; hyphae 3–10 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. *Subhymenium* morphologically undifferentiated. *Basidia* 24–35 × 6.5–10 μm, clavate, hyaline; sterigmata 4, up to 5.5 μm long. *Cheilocystidia* 31.5–53 × 3–7 μm, filamentous to subclavate, scattered, thin-walled, hyaline, found only in some collections. *Basidiospores* (excluding ornamentation) [75/5] 7.4–10 × 5–7 μm (x = 8.3–9.1 × 5.6–5.9 μm), Q = 1.3–1.76 (Q = 1.45–1.60), ellipsoid to oblong, occasionally subreniform, hyaline, echinulate; echinulae < 0.5(–1.4) μm long, those > 0.5 μm long restricted to basidiospore apex, crowded; hilar appendix 1.3–2 μm long, prominent, truncate; plagi present; contents occasionally uniguttulate. *Basal mycelium hyphae* mostly 3–11 μm diam., tightly interwoven, hyaline; cells filamentous to barrel-shaped.

**SOMATIC CULTURE MAT MORPHOLOGY** (N = 5; Appendix B)—*PDA: Radius* at week 3 = 28–39 mm, week 6 = 45–78 mm; *mat* felty, thick, tightly interwoven, with scattered smaller sectors of longer, loosely interwoven hyphae, tightly appressed to agar surface, in time forming pruinose aerial layer away from plug, not transluscent, at first dark violet, soon fading, week 3 = light to moderate violet coloration restricted either to 2–3 mm band near margin or 4–5 mm zone near plug, most of mat light orange-brown, week 6 all light orange-brown, no violet coloration present; *margin* up to 5 mm broad, silky to subfelty, thin, uneven, light violet, becoming white; *plug* concolorous with mat; *hyphae* mostly morphologically undifferentiated, occasionally irregularly swollen, subcoralloid or coralloid. *MMN: Radius* at week 3 = most 48–56 mm, one isolate 30–36 mm, week 6 = most covering agar surface, one isolate 58–78 mm, *mat* subfelty to subwoolly, thin, becoming thicker, loosely interwoven, some with subwoolly to woolly or cottony narrow strands radiating out from the plug to margin, between strands thin, tightly appressed to agar surface, transluscent, becoming somewhat transluscent, at first light violet, soon fading to light violet or white, *margin* not well differentiated, thin, uneven, concolorous; *plug* concolorous; *hyphae* most morphologically undifferentiated, occasionally irregularly swollen, subcoralloid or coralloid. *MEA: Radius* at week 3 = 26–40 mm, week 6 = 51–78 mm; *mat* subfelty, thin, loosely interwoven, some with 1–3 narrow, slightly thicker concentric bands, tightly appressed to agar surface, transluscent, white; *margin* 1–2 mm broad, not well differentiated, even to uneven, white; *plug white*; *hyphae* morphologically undifferentiated, occasionally irregularly swollen or subcoralloid.

**HABITAT AND DISTRIBUTION**—Gregarious; in very sandy soil under *Pinus palustris* Miller; Gulf Coast. A list of specimens examined is presented in Appendix A.

**OBSERVATIONS**—Laccaria oblongospora often appears similar to *L. proxima* or *L. trichoder- mophora* in the field. It differs from *L. proxima* in basidiomere shape and size, basal mycelium color, and cultural features. It can be distinguished from *L. trichodermophora* primarily on basidios- spore shape and echinulae length.

Much variation in basidioma color was observed in this taxon. Most specimens exhibited the typical orange-brown coloration of *L. laccata sensu lato*. Scattered among these were a few individual fruitbodies which were vinaceous to violaceous in color (e.g., *TENN 42524*). Initially, these vinaceous collections were thought to represent a separate taxon. However, because of the occurrence of intermediate color forms (orange-brown pilei and stipes with violaceous lamellae) and identical culture mat morphologies, they have been treated as contaxic.

Intercollection pairing studies support the treatment of *L. oblongospora* as a separate species. Isolates from two stocks obtained during this study were incompatible with each other but intersterile with all tested isolates of other species, including isolates of *L. proxima*. Material of *L. ob-
FIG. 9. Basidiomata of *L. oblongospora* (GMM 2310).

FIG. 10. Somatic culture mats of *L. oblongospora* (GMM 1105). Top on PDA, left on MMN, and right on MEA. Photo taken during week 4.
Laccaria oblongospora was not included in the analyses of mtDNA or rDNA RFLPs.

Laccaria oblongospora was consistently placed in Laccaria metasection Laccaria during cladistic analyses. Phylogenetic relationships between the taxa in this metasection, however, were not resolved during these analyses. If this is the correct placement of L. oblongospora, the pigment(s) responsible for the violet mycelium at stipe bases and culture mats would be plesiomorphic and would not be informative for resolving relationships within the genus (see Phylogenetic Considerations for further discussion).

Only a few populations of this species have been located. All of them were either in eastern Texas or southern Mississippi. Several of these populations were very large and consisted of numerous basidiomata. Specimens of L. oblongospora have only been encountered near stands of Pinus palustris.

Laccaria laccata (Scopoli: Fries) Cooke.2


2 Berkeley and Broome (1883) did not make any new combinations when proposing the genus Laccaria. Consequently, they did not validly publish L. laccata (Guerter et al., 1988, Art. 33.1).

FIG. 11. Micromorphological features of L. oblongospora (GMM 2310): a, basidiospores; b, basidia. Scale line = 10 μm.

= Agaricus laccatus Scopoli: Fries, Systema Mycologica 1: 106. 1821.
= Clitocybe laccata (Scopoli: Fries) Kummer, Führer in die Pilzkunde: 122. 1871.
= Laccaria laccata (Scopoli: Fries) Cooke, Grevillea 12: 70. 1884.
= Omphalia laccata (Scopoli: Fries) Quélet, Enchiridion Fungorum: 2C. 1886.
= Collybia laccata (Scopoli: Fries) Quélet, Flore Mycologique: 237. 1888.
= Russuliopsis laccata (Scopoli: Fries) Schroeter in Cohn, Krypt.-Fl. Schlesien 3: 622. 1889.
= Agaricus carneus Schaeffer, Fungorum Bavaria 4: 71, fig. 304. 1774. TYPE: Lacking.
= Agaricus farinaceus Hudson, Flora Anglica: 616. 1778. TYPE: Lacking.
= Agaricus subcarneus Batch, Elench. fung. Continuatio prima.: 121, fig. 100. 1786.


As discussed in Mueller and Vellinga (1986), Singer's typification of L. laccata (Singer, 1967) has perpetuated confusion in the delimitation of L. laccata. The specimen that he chose is not representative of the species because the micromorphological characters of the collection are near the extreme range for the taxon. To date, very few collections referable to L. laccata have been encountered that have basidiospores as elongated as the neotype (Mueller & Vellinga, 1986; Mueller, 1991a).

Singer (1946, 1967, 1973, 1977), Bon (1983), and others have proposed a number of species and subspecific taxa in an attempt to delimit natural taxa within this highly variable group. Descriptions of the type specimens of most of these names are presented later in this monograph (see Type Studies). Type specimens of the majority of these names have basidiospores that are globose to subglobose in shape. Only collections from the type variety and three other varieties were found to have elliptoid basidiospores (Q = 1.25–1.3) (see Type Studies and Mueller & Vellinga, 1986). For these reasons, Mueller and Vellinga (1986) and Mueller (1991a) treated most of the proposed varieties of L. laccata, L. tetraspera, and L. affinis (Singer) Bon as synonyms of one of three varieties: L. laccata var. laccata, L. laccata var. moelleri, and L. laccata var. pallidifolia.

Additional morphometric and intercollection pairing studies were undertaken, and these data were compared with information on mtDNA and rDNA RFLPs (Gardes et al., 1990, 1991a) in an attempt to resolve systematic problems surrounding L. laccata sensu lato (Mueller, 1991c). Based on a synthesis of these data, I recognize the following taxa in this complex: L. laccata var. laccata, L. laccata var. moelleri, L. laccata var. pallidifolia, L. longipes, L. ohiensis (= L. tetraspera), and L. striatula. All of these except L. laccata var. moelleri occur in North America and will be treated in detail below. Laccaria laccata var. moelleri is discussed with L. longipes below.

Laccaria laccata var. laccata. Figure 64d.

= Agaricus (Clitocybe) laccatus var. luteoviolaceus Fries, Epicr. syst. mycol.: 79. 1836–1838.

= Agaricus (Clitocybe) laccatus var. obscurus violacea Fries, Epicr. syst. mycol.: 79. 1836–1838.

= Agaricus (Clitocybe) laccatus var. rufocarnea Fries, Epicr. syst. mycol.: 79. 1836–1838.


= Russulopsis laccata var. rosellus f. psylla Schroeter in Cohn, Krypt.-Fl. Schlesien: 623. 1889.

MACROMORPHOLOGY (Teste Singer, 1967)—Pileus (6–)10–45 mm broad, convex becoming plane, often slightly depressed, occasionally umbonate, slightly striate, glabrous to finely fibrillos, occasionally becoming fibrilllose-scaly, hygrophanous, reddish brown becoming pale ochre when dry. Lamellae adnate to adnate-subdecurrent, distant, broad, rather pale and dull reddish color. Stipe 40–60–(90) × 2–7–(14) mm, equal to slightly clavate, fibrous with innate fibrils, concolorous with pileus or concolorous with lamellae at apex and brown toward base. Basal mycelium white. Basidiospores white in mass.

MICROMORPHOLOGY (Mihi)—Pilepellis of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 15–30 hyphae; terminal cells of fascicular hyphae 38–80 × 6.5–18 μm, filamentous, slightly swollen, subclavate or capitate, light yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. Pileus trama tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pilepellis. Lamellar trama parallel, hyphae 2.5–12 μm diam., thin-walled, hyaline; cells barrel-shaped. Subhymenium undifferentiated. Basidia 25.7–48 × 7–16.5 μm, clavate, hyaline; sterigmata 4, up to 12 μm long. Pleurocystidia lacking. Cheilocystidia 25–70 × 2–7.5 μm, filamentous, absent to common, hyaline. Basidiospores (excluding ornamentation) [210/7] (7–) 7.7–9.7(–11) × (5–)(6.4–8(–8.5) μm (x = 7.8–9.2 × 6.3–7.1 μm), Q = (1.08–)1.18–1.35(–1.46) (Q = 1.2–1.3), subglobose to ellipsoid, hyaline, echnulate; echinulate 1.1–1.8(–2.3) μm long, ≤ 1 μm wide at base; hilar appendix up to 1.8 μm long, prominent, truncate; plage present; contents occasionally uniguttulate.

HABITAT AND DISTRIBUTION—Solitary to gregarious; terrestrial, host unknown. Reported from only a few localities in Europe and North America; not abundant. Not commonly collected. A list of collections examined is provided in Appendix A.
Observations—The type variety is distinguished from other varieties of *L. laccata* by having broadly ellipsoid to ellipsoid, moderately ornamented basidiospores. It is sometimes difficult to differentiate *L. laccata* var. *laccata* from *L. proxima* without information on macromorphology. Major differences between them are the more robust, darker colored, scaly basidiomata of *L. proxima*, and the more coarsely ornamented basidiospores of *L. laccata* var. *laccata*.

The description presented above was based on a compilation of the protologues of the type collections for the names treated as synonyms of *L. laccata* var. *laccata* plus several collections referable to this taxon found in Swedish herbaria. I have not collected specimens referable to this taxon.

No isolates of specimens referable to *L. laccata* var. *laccata* have been included in the intra- and interspecific pairing studies (Fries & Mueller, 1984; Mueller, 1991c) or in the analyses of mtDNA and rDNA RFLPs (Gardes et al., 1990, 1991a), because I have not obtained cultures of this taxon. Data on the results of pairing studies using other recognized varieties are discussed below.

Based on available herbarium specimens, *L. laccata* var. *laccata* is not common, as few collections were encountered among the borrowed material. In Sweden this taxon appears to have a very restricted distribution. Five of the six Swedish collections examined came from Femsjö and may be from the same population or even the same individual mycelium (Mueller, 1991a). This is the same general locality from where Singer (1967) obtained the type specimen.

### Laccaria laccata var. pallidifolia (Peck) Peck.

**Pileus** 12–14, 54d–f, 68c.


#### Macromorphology—Pileus

10–45(–60) mm broad, obtuse to convex, often becoming plane to uplifted, often depressed, striate to not striate, occasionally strongly striate to plicate-striate, sometimes translucent-striate when fresh, finely fibrillose to fibrillose-scaly, infrequently slightly scaly, hygrophanous, orange-brown when fresh, becoming buff color ("Sanford's Brown," "Orange Rufous," "Hazel," "Cinnamon-Rufous," "Pinkish Cinnamon," or "Light Vinaceous-Cinnamon"), fading lighter ("Apricot Buff," "Salmon Color," "Light Pinkish Cinnamon," or "Pinkish Buff"), finally to buff ("Pale Ochraceous Buff"); disc occasionally darker orange-brown or red-brown ("Hay's Russet," "Ochraceous Tawny" or "Buckthorn Brown"); margin incurved to decurved, becoming plane to uplifted, entire to undulate, occasionally becoming eroded in age; context thin, tapering quickly to margin, concolorous. Lamellae sinuate, adnate or arcuate, rarely decurrent, close to distant, narrow to broad, relatively thin to thick, pinkish flesh color ("Flesh Color," "Salmon-Buff," "Pale Salmon Color," "Flesh-Pink," or "Light Vinaceous-Cinnamon"), some becoming slightly vinaceous with age (near "Light Grayish-Vinaceous"). *Stipe* (12–)20–65(–106) × 2–4(–8) mm, equal, subclavate or tapering toward base, occasionally slightly bulbous, dry, fibrillose, not striate to finely longitudinally striate, rarely with pronounced striations, concolorous with stipe; context stuffed, becoming hollow, concolorous with pileus context. *Basal mycelium* sparse to copious, always white. Basidiospores white in mass.

#### Micromorphology—*Pileipellis* of interwoven hyphae with widely scattered fascicles of ± perpendicularly hyphae; fascicles composed of 5–15 (~30) hyphae; terminal cells of fascicular hyphae 6–101 × 3–37.5 μm, filamentous, subclavate, cla-
Fig. 12. Basidiomata of *L. laccata* var. *pallidifolia* (GMM 1735).

Fig. 13. Somatic culture mats of *L. laccata* var. *pallidifolia* (GMM 1011). Top on PDA, left on MMN, and right on MEA. Photo taken during week 4.
vate, subcapitate or ventricose-rostrate; walls up to 0.5 μm thick, light yellowish brown; contents hyaline to light yellowish brown. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae mostly 2–17.5 μm diam., thin-walled, hyaline to light yellowish brown; cells filamentous to barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** 27.5–55 × 7.5–13.5(–16.5) μm, clavate, hyaline; sterigmata 4, up to 7 μm long. **Cheilocystidia** 23–55 × 2–7.5 μm, filamentous to subclavate, occasionally strulate, absent or scattered to abundant, thin-walled, hyaline. **Basidiospores** (excluding ornamentation) [1,000/65] (6.4–)7.4–10(–13) × (6–)7–10(–11.5) μm (ξ = [7.3–]8.2–9[–9.6] × [6.7–]7.6–8.6 μm), Q = 1–1.13(–1.3) (Q = 1–1.15[–1.2]), globose to subglobose, occasionally broadly ellipsoid, hyaline, echinulate; echinulae (0.5–)1–2 μm long, ≤ 1 μm wide at base, relatively scarce to crowded; hilar appendix 1.3–2.2 μm long, prominent, truncate; plage present; contents occasionally uniguttulate or biguttulate. **Basal mycelium hyphae** mostly 3–10.5 μm diam., tightly interwoven, hyaline; cells filamentous to barrel-shaped.

**Somatic Culture Mat Morphology** (N = 11; Appendix B)—**PDA:** Radius at week 3 = 7–23 mm or 62–73 mm, week 6 = 18–27 or 90 mm (agar surface covered); mat feltly, thick, tightly interwoven, some appearing almost crustose, tightly appressed to agar surface, occasionally forming cottony to feltly aerial layer away from plug, not translucent, white, in some becoming dark olive brown or light chocolate color away from plug; **margin** narrow to moderately broad, silky to subfelty, thin, white, entire to undulate; **plug** occasionally covered with cottony white hyphae or with long serial aggregations of hyphae growing away from top of plug, white, often becoming dark olive brown or light chocolate color; **hyphae** morphologically undifferentiated, rarely irregularly swollen. **MMN:** Radius at week 3 = 13–19 mm or (25–)29–52 mm, week 6 = 26–45 mm or 75 mm to covering agar surface; mat subfelty, felty or silky, moderately thick, interwoven, in one isolate (TENN 42964) with several radially arranged pie-shaped thicker sectors, tightly appressed to agar surface, translucent, white; **margin** narrow, silky to subfelty, not well differentiated, even to undulate, occasionally somewhat serrate, white; **plug** white; **hyphae** morphologically undifferentiated.

**Fig. 14.** Micromorphological features of *L. laccata var. pallidifolia* (GMM 1845): a, basidiospores; b, basidia. Scale line = 10 μm.
occasionally coralloid. MEA: Radius at week 3 = 12–33 mm or 53–62 mm, week 6 = 23–54 mm or covering agar surface; mat silky to subfelty, thin to moderate, appearing combed to loosely interwoven, occasionally becoming thicker near plug, tightly appressed to agar surface, translucent, white; margin not well differentiated, thin, entire to slightly serrate, white; plug white; hyphae morphologically undifferentiated.

HABITAT AND DISTRIBUTION—Solitary to gregarious, occasionally caespitose, associated with Pinaceae, Fagaceae, and Betulaceae; cosmopolitan; abundant. Collected throughout North America. A list of specimens examined is presented in Appendix A.

OBSERVATIONS—Laccaria laccata var. pallidifolia is characterized by having small- to moderate-sized, orange-brown, glabrous to finely scaly basidiomata, and basidia that bear four globose to subglobose, moderately echinulate basidiospores.

Mueller and Vellinga (1986) and Mueller (1991a) included collections now treated as L. ohiensis (= L. tetraspora) within the concept of this taxon. Reasons for this given by Mueller and Vellinga (1986) included: (1) the macro- and micromorphology of several of the proposed varieties intergraded between the two putative species; (2) basidioma and basidiospore size, as well as basidiospore ornamentation length, appeared to form a continuum for collections in this group; and (3) somatic culture mat morphology did not appear to vary between isolates referable to either of these taxa. It was not possible for Fries and Mueller (1984) to distinguish between collections of the two intersterility groups (mating groups III and IV) that they detected in the tested Swedish material of L. laccata on the basis of basidioma and basidiospore size and basidiospore ornamentation length.

Several additional intersterility groups have since been detected in North America (Mueller, 1991c). Each of these groups was found to differ markedly in RFLPs of mtDNA and rDNA (Gardes et al., 1990, 1991a). Subsequent morphometric analyses have shown that collections of some of these intersterility groups, but not others, were segregated during morphometric analyses of basidiospore data (Mueller, 1991c). Two groups were clearly delimited during morphometric analyses: one group consisted of collections with globose basidiospores with echinulae > 1.5 μm long and > 1.2 μm wide at the base; the other group consisted of specimens with globose to subglobose basidiospores with echinulae 0.7–2 μm long and ≤ 1 μm wide at the base (Mueller, 1991c). The first group consisted of collections referable to L. ohiensis and L. striatula; collections in the second group are referable to either L. laccata var. pallidifolia, L. laccata var. moelleri, or L. longipes.

Laccaria laccata var. pallidifolia is differentiated from L. ohiensis primarily by having narrow basidiospore echinulae. Collections of L. laccata var. pallidifolia with small basidiomata and globose basidiospores (characteristics of L. ohiensis) are occasionally encountered.

Laccaria laccata var. pallidifolia is differentiated from L. striatula on the basis of differences in basidiospore ornamentation and macromorphological features. Collections of L. striatula have relatively long, glabrous stipes that are usually darker than the strongly striate pileus.

Laccaria laccata var. pallidifolia is differentiated from L. longipes by having shorter stipes and larger basidiospores.

Laccaria laccata var. pallidifolia is the most commonly encountered taxon in the complex and can be found throughout the United States and Canada. No apparent habitat preference could be determined from the material collected during this study.

Laccaria longipes G. M. Mueller. Figures 15, 16, 54a, 65c.


MACROMORPHOLOGY—Pileus 11–55(–78) mm broad, convex to broadly convex, often becoming plane to uplifted, often centrally depressed, slightly to moderately translucent-striate, finely fibrillose, orange-brown (6B5–6D7) fading to buff in age; margin incurved to decurved or plane, entire to undulate, becoming slightly eroded. Lamellae adnate, distant, thick, up to 10 mm broad, light flesh color (near 6A2). Stipe 67–138(–165) × 3–9 mm, equal with slightly swollen base or narrowly clavate, dry, slightly to moderately fibrillose-striate, concolorous with pileus. Basal mycelium white. Basidiospores white in mass.

MICROMORPHOLOGY—Pileipellis of radially arranged barrel-shaped hyphae with occasional scattered small fascicles of 10–30 ± perpendicular hyphae; terminal cells 5–10 μm, morphologically...
undifferentiated to subclavate, hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline to light yellowish brown. **Lamellar trama** of parallel to subparallel hyphae, mostly 3–19 μm diam., thin-walled, hyaline; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** 28–44 × 7–10 μm, clavate, hyaline; sterigmata 4, up to 10 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) [158/7] 7–8.5(–9) × 6–7.8(–8.4) μm (μ = 7.6–7.8 × 6.8–7.2 μm), Q = (1–)1.05–1.2(–1.3) (Q = 1.08–1.13), subglobule to broadly ellipsoid, occasionally globose or ellipsoid, hyaline, echinulate; echinulae (0.7–)1–1.5(–2) μm long, less than 1 μm wide at base.

**Somatic Culture Mat Morphology** (N = 1; GMM 1929) — **PDA:** **Radius** at week 6 = 43 mm; **mat** felt, thick, tightly interwoven, tightly appressed to agar surface, not translucent, uniform texture near plug, forming dendritic thicker strands from midpoint to margin, tan to olive brown; **margin** ≤ 6 mm broad, subfely to silky, abruptly thinner than mat, tan; **hyphae** 2.5–5 μm diam., morphologically undifferentiated. **MMN:** **Radius** at week 6 = 28 mm; **mat** felt, thick, tightly interwoven, tightly appressed to agar surface, uniform texture, dull white; **margin** up to 5 mm broad, irregular, white; **hyphae** 2.5–8 μm diam., morphologically undifferentiated, occasionally irregularly swollen. **MEA:** **Radius** at week 6 = 42 mm; **mat** subfely, thin, translucent, white; **margin** 2–3 mm broad, not well differentiated, white; **hyphae** 2.5–8 μm diam., most morphologically undifferentiated, occasionally irregularly swollen.

**Habitat and Distribution**—Among mosses, especially **Sphagnum**, usually under **Picea mariana** (Mill.) B.S.P., **Larix laricina** (Du Roi) K. Koch, and **Alnus rugosa** (Du Roi) Spreng. Reported to date from the Great Lakes region (southern Ontario, Michigan, Wisconsin, Minnesota) and New York. A list of specimens examined is presented in Appendix A.

**Observations**—**Laccaria longipes** can be distinguished from other members of the **L. laccata** complex by its relatively small, subglobule basidiospores, long stipe, and restricted habitat. **Laccaria laccata** var. **moelleri** also occurs in bogs and has similar macromorphological features but differs in having larger basidiospores (μ = 8–10 × 7.3–8.3 μm). **Laccaria galericoides** Singer is another taxon that grows among **Sphagnum**. It appears to be restricted to southern Argentina and Chile and has only been reported from under **Nothofagus antarctica** (G. Forster) Derst. **Laccaria galericoides** differs from the two Northern Hemisphere taxa in having smaller, darker colored basidiomata and more elongate basidiospores (Q = 1.34; holotype).

Tested isolates of **L. longipes** were intersterile with all other tested isolates of the **L. laccata** complex, including isolates of **L. laccata** var. **moelleri** (Mueller, 1991b,c). RFLPs of mtDNA and rDNA indicate that divergence has occurred between **L. longipes** and other taxa in the **L. laccata** complex (Gardes et al., 1990, 1991a). Although isolates of **L. laccata** var. **moelleri** were intersterile with all tested North American isolates, including **L. laccata** var. **pallidifolia** (intersterility group 1), they were intercompatible with the tested Swedish isolates of **L. laccata** var. **pallidifolia**, and both taxa belong to intersterility group 3 (Mueller & Vellenga, 1986; Mueller, 1991b,c). Data on potential molecular divergence between these morphologically distinct taxa do not yet exist, however, because both isolates of intersterility group 3 tested by Gardes et al. (1990, 1991a) are referable to **L. laccata** var. **moelleri**.

Collections of **L. longipes** were cited as **L. laccata** var. **moelleri** in several recent publications (Doudrick & Anderson, 1989; Gardes et al., 1990, 1991a). The decision to treat the North American and Swedish populations as distinct taxa occurred only after a synthesis of the data on RFLPs with data on intercollection pairing reactions and morphometric similarities (Mueller, 1991b,c).

It is not yet clear whether **L. longipes** and **L. laccata** var. **moelleri** are closely related or if their similar macromorphology is due to convergence resulting from their occurrence among **Sphagnum** and other mosses.

**Laccaria fraterna** (Cooke & Massee: Saccardo) Pegler. Figures 17, 18, 54b, 62.

• **Naucoria fraterna** (Cooke & Massee) Saccardo, Syll. Fung. 9: 110. 1891.
MACROMORPHOLOGY—Pileus 9–35(–55) mm broad, strongly convex to convex, becoming plane to uplifted, often slightly depressed, not striate to slightly translucent-striate, finely fibrillose to fibrillose, rusty red-brown (8D7–9E7), eventually becoming buff; margin decurved to plane, entire to slightly undulate; contex thin, concolorous with pileus. Lamellae adnate, moderately distant to distant, thick, pinkish rose (near 8A3). Stipe (17–)25–65 × 3–5 mm, equal or slightly clavate, at times caespitose, dry, fibrillose, moderately longitudinally striate, concolorous or slightly darker than
Fig. 16. Micromorphological features of *L. longipes* (GMM 1929): a, basidiospores; b, basidia. Scale line = 10 μm.

pileus (9C5–9D6). Basal mycelium white, often copious. Basidiospores white in mass.

**Micromorphology—**Pileipellis of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 10–20 hyphae; terminal cells of fascicular hyphae 26–69 × 6.5–15 μm, filamentous to clavate; walls up to 0.5 μm thick, light yellowish brown. Pileus trama tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. Lamellar trama parallel; hyphae mostly 3–10(–15.5) μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. Subhymenium morphologically undifferentiated. Basidia 29–46 × 8–12 μm, clavate, hyaline; sterigmata 2(3), up to 11 μm long. Cheilocystidia not observed. Basidiospores (excluding ornamentation) [100/4] (7.8–) 8.5–11(–13.5) × (7.4–)8–10.5(–13.5) μm (x = 9.7–10.5 × 8.9–9.9 μm), Q = 1–1.18(–1.22) (Q = 1.01–1.11), globose to subglobose, hyaline, strongly echinulate; echinulae 1–1.8 μm long, ≤ 1 μm wide at base, crowded; hilar appendix 1.3–2.8 μm long, prominent, truncate; plage present; contents occasionally uniguttulate.

**Habitat and Distribution—**Under *Eucalyptus* and other introduced trees. *Laccaria fraterna* was probably introduced along with *Eucalyptus* throughout the world. Commonly collected under *Eucalyptus* throughout the world, including North America. A list of specimens examined is presented in Appendix A.

**Observations—** *Laccaria fraterna* can be distinguished from other small *Laccaria* taxa by its rusty red-brown basidiomata and 2-sterigate basidia that bear globose to broadly ellipsoid basidiospores that are < 11 μm long.

There has been considerable confusion in the literature concerning the correct name for this taxon. Some workers have used the name *L. ohiensis* for this taxon (e.g., Singer, 1942, 1946, 1949, 1967, 1975, 1977; McNabb, 1972), but an examination of the holotype revealed that *L. ohiensis* has 4-sterigate basidia (see Type Descriptions). Although the most commonly used name for the taxon has been *L. lateritia*, the correct name for this taxon is *L. fraterna* (Mueller & Vellinga, 1986; Vellinga & Mueller, 1987).

Tom W. May (University of Melbourne, pers. comm.) reports the finding of a potentially paratype collection at MEL that better fits the protologue but that is not contaxic with the type specimen housed at K. It has been assumed that the report of ellipsoid basidiospores in the original diagnosis of *A. fraternus* probably referred to another collection on the type sheet at K that was collected in New Zealand (Pegler, 1965; Mueller & Vellinga, 1986). If the collection housed at MEL is lectotypified, *A. fraternus* would not fit into the generic circumscription of *Laccaria* and the correct basionym for the taxon treated here would be *N. goosensiae*.

Ballero and Contu (1989) described *L. singeri* Ballero & Contu. This name, however, is a later homonym of *L. singeri* Locquin & Sarwal (Sarwal & Locquin, 1983) and Mueller and Vellinga (1990) renamed it *L. impolita* Vellinga & G. M. Mueller. *Laccaria impolita* is similar in micromorphology to *L. fraterna* but differs from it in basidioma
color, lack of pileus striations, and ectomycorrhizal hosts (north temperate trees). See the discussion under L. impolita in Type Studies.

**Laccaria montana** Singer. Figures 19, 20, 54c, 66d.

- **Laccaria montana** Singer, Sydowia 7: 89. 1973.
- **Laccaria laccata** var. montana Möller, Fungi of the Faerôes: 269. 1945.

MACROMORPHOLOGY—*Pileus* 6–35 mm broad, convex to plane, becoming uplifted, often depressed, occasionally umbonate when young, usually plicate-striate when fresh, fibrillose to finely fibrillose-scaly, hygrophanous, brownish orange (“Hazel” to “Cinnamon-Rufous”), fading to buff color; margin decurved to plane, entire to undulate, occasionally becoming eroded; context ≤ 1 mm thick at disc, flesh color “Buff-Pink”). **Lamellae** sinuate to decurrent, close to distant, pinkish flesh color to light vinaceous (“Vinaceous-Pink”). **Stipe** 13–54(–101) × 2–4(–7) mm, equal or tapering slightly toward base or apex, occasionally swollen at base, occasionally caespitose, dry, fibrillose, not striate to moderately longitudinally striate, concolorous with pileus. **Basal mycelium** white. **Basidiospores** white in mass.

MICROMORPHOLOGY—*Pileipellis* of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 10–30 hyphae; terminal cells of fascicular hyphae 39–51 × 5.5–10 μm, filamentous to subclavate, light yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown; contents hyaline to light yellowish brown. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel to subparallel, hyphae mostly 2.5–20 μm diam., thin-walled, hyaline to light yellowish brown; cells filamentous to barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** 34.5–55 × 10–15.5 μm, clavate, hyaline; sterrigmata 4, up to 11 μm long. **Cheilocystidia** 32–55.5 × 3–4.5(–7.5) μm, filamentous to subclavate,

**Fig. 17.** Basidiomata of *L. fraterna* (GMM 2126).
rarely clavate, thin-walled, hyaline, only found in one collection. **Basidiospores** (excluding ornamentation) [120/6] (7.8–8.5–14–14.7) × (7–8–12 μm (x = 9.4–12.6 × 8.5–10.5 μm), Q = 1–1.26(-1.33) (Q = 1.07–1.2), globose to broadly ellipsoid, occasionally ellipsoid, hyaline, echinulate; echinulae (0.5–)0.9–1.8 μm long, ≤ 1 μm wide at base, not crowded to crowded; hilar appendix 1.3–2 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 3–21 μm diam., tightly interwoven, hyaline; cells filamentosus to barrel-shaped.

**Habitat and Distribution**—Scattered to gregarious, occasionally caespitose; in poor soil, humus, or among mosses; under Pinaceae, Betula, or Salix; restricted to arctic, boreal, or montane habitats; common. A list of specimens examined is presented in Appendix A.

**Observations**—Laccaria montana can be distinguished from L. laccata by having larger basidiospores and an arctic to boreal distribution.

The apparent stability of basidial characters within Laccaria coupled with the potential functional differences between 2-sterigate taxa (facultative homothallism) versus 4-sterigate taxa (obligatory heterothallism?) are the justification that I use to treat L. montana and L. pumila as separate species. Although there are differences in basidiospore size between these two taxa, these are probably due to the 4-sterigate versus 2-sterigate condition and are not independent character states.

Homokaryotic isolates from only two specimens of *L. montana* have been obtained to date. Repeated attempts to obtain either intra- or intercompatible pairings with isolates of either of these stocks have failed (Mueller, 1991c). Homokaryotic isolates of *L. pumila* have not been obtained, and consequently, no test of the putative genetic isolation between these two taxa has been undertaken. Multivariate morphometric analyses only loosely grouped together the two tested collections of *L. montana* (Mueller, 1991c). Finally, data are not available on potential genetic divergence between *L. montana* and other taxa because representatives of *L. montana* are not included in the RFLP analyses carried out by Gardes et al. (1990, 1991a).

*Laccaria montana* is among the more common *Laccaria* taxa found at high elevations and northern latitudes. At least some of the reports of *L. tetraspore* from the arctic are, according to their descriptions and illustrations, *L. montana* (e.g., Kobayasi et al., 1967; Miller et al., 1982).

**Fig. 18.** Micromorphological features of *L. fraterna* (GMM 2126): a, basidiospores; b, bisterigate basidia. Scale line = 10 μm.
Laccaria pumila Fayod. Figures 21, 22, 54g, 70b.


MACROMORPHOLOGY — Pileus 3–27(–40) mm broad, convex to plane, occasionally uplifted, often depressed, usually strongly translucent-striate when fresh, glabrous to finely fibrillose, occasionally becoming fibrillose-scaly with age, hygrophanous, red-brown to orange-brown (“Hay’s Rust-set,” “Burnt Sienna,” or “Sanford’s Brown”), fading to buff (near “Xanthine Orange,” “Flesh-Ocher,” or “Salmon-Buff”); margin incurved to decurved, often becoming plane, entire to undulate, occasionally eroded; context thin, concolorous. Lamellae sinuate to arcuate, distant, thick, waxy appearing, ≤ 8 mm broad, pinkish flesh color (“Flesh Color” or “Pale Flesh Color”). Stipe 4–61(–100) x 2–5(–9) mm, equal to subclavate, often slightly bulbous, occasionally caespitose, dry, fibrillose, longitudinally striate, ± concolorous with pileus, fading to ochraceous buff (“Amber Brown,” “Flesh-Ocher,” or “Apricot Buff”). Basal mycelium white. Basidiospores white in mass.

MICROMORPHOLOGY — Pileipellis of interwoven hyphae with widely scattered fascicles of ± perpendicular hyphae; fascicles composed of 10–25 hyphae; terminal cells of fascicular hyphae 36.5–64 x 8–16 μm, filamentous, subclavate or clavate; walls up to 0.5 μm thick, light yellowish brown, often encrusted with pigment(s); contents hyaline to light yellowish brown. Pileus trama tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. Lamellar trama parallel to subparallel; hyphae mostly 3–18 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. Subhymenium
morphologically undifferentiated. Basidia 37.5–64.5 × 10.5–16 μm, clavate, hyaline; sterigmata 2(−4), up to 14 μm long. Cheilocystidia 27.5–46 × 3 μm, filamentous to subclavate, hyaline, found in one collection only. Basidiospores (excluding ornamentation) [86/6] (10−)11−16.5(−20) × (7.8–)10–14.5(−16) μm (x = 12–13[−16.3] × 10.8–13.8 μm), Q = 1–1.29 (Q = 1.1–1.19), subglobose to broadly ellipsoid, occasionally globose or ellipsoid, hyaline, echinulate; echinulae < 0.5–1.4 (−1.8) μm long, crowded; hilar appendix 1.3–2 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. Basal mycelium hyphae mostly 4–19 μm diam., tightly interwoven, hyaline; cells filamentous to barrel-shaped.

Habitat and Distribution—Scattered to gregarious, occasionally caespitose; in poor soil, humus, or among mosses; under Pinaceae, Betula, or Salix; restricted to arctic, boreal, and montane regions; common. A list of collections examined is presented in Appendix A.

Observations—Laccaria pumila appears very similar in the field to L. montana, L. tortilis, and small striate forms of L. laccata var. pallidifolia. It can easily be distinguished, however, by its 2-sterigate basidia that bear large, subglobose to broadly ellipsoid, echinulate basidiospores. Laccaria pumila has most commonly been reported under the name L. altaica Singer. As discussed by Mueller and Vellinga (1986), the name L. pumila has priority. Another name occasionally misapplied to this taxon is L. striatula sensu Singer non Peck (e.g., Singer, 1943b; Orton, 1960; Laursen & Chmielewski, 1982).

The major character distinguishing L. pumila from L. montana is that the latter has 4-sterigate basidia. Both are restricted to arctic, subarctic, alpine, and boreal habitats and can be found growing sympatrically. Singer (1977) mentioned that L. pumila may only be a two-spored form of L. montana and thus the two might be conspecific. Laahaie (1981) and data accumulated during this study, however, have supported separation of these taxa at the species rank. In all specimens examined for this study, no basidiomata were found that had both 2- and 4-sterigate basidia, and Laahaie (1981) only reported one collection in which both 2- and 4-sterigate basidia were observed.

To date it has not been possible to obtain a tissue culture or to germinate the basidiospores of L. pumila.

Laccaria pumila appears to be the dominant, if not the exclusive, 2-sterigate Laccaria found in the arctic, and the most common 2-sterigate Laccaria found in the mountains of western United States. Lange (1955) and Kobayasi et al. (1967)

Fig. 20. Micromorphological features of L. montana (GMM 1813): a, basidiospores; b, tetrasterigimate basidia. Scale line = 10 μm.
reported *L. tortilis* occurring in the arctic; however, the descriptions and illustrations of both indicate that the collections are probably *L. pumila*.

**Laccaria striatula** (Peck) Peck. Figures 23, 24, 55b, 71b.


**Macromorphology**—Pileus 6–30(–36) mm broad, convex, occasionally becoming plane, often depressed, strongly translucent-striate when fresh, occasionally plicate-striate, finely fibrillose, occasionally finely fibrillose-scaly near disc, hygrophanous, reddish brown to orange-brown ("Hazel," "Cinnamon-Rufous," or "Vinaceous-Rufous"), then lighter in color ("Salmon Color," "Seashell Pink," or "Pinkish Buff"); disc occasionally darker in color ("Hay’s Russet"); margin incurved to decurved, becoming plane, entire to undulate; context thin, concolorous. Lamellae sinuate to adnate, close to subdistant to distant, relatively narrow to broad, thin to thick, pinkish flesh color ("Flesh-Ocher" or "Pale Flesh Color"). Stipe 20–70(–103) × 1–4(–8) mm, equal, occasionally slightly bulbous, glabrous, appearing cartilaginous when fresh, reddish brown, concolorous with disc or darker ("Kaiser Brown," "Hazel," "Cinnamon-Rufous," or "Onion-skin Pink"). Basal mycelium white.

**Micromorphology**—Pileipellis of interwoven hyphae with scattered to numerous small fascicles of ± perpendicular hyphae; fascicles usually composed of 5–15 hyphae; terminal cells of fascicular hyphae 33–85 × 6–18.5 μm, filamentous, subclavate, clavate, subcapitate, or ventricose-rostrate, occasionally strangulate; walls up to 0.5 μm thick, hyaline to light yellowish brown; contents hyaline to light yellowish brown. Pileus trama tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown towardpileipellis. Lamellar trama parallel; hyphae 3–11(–27) μm diam., thin-walled, hyaline to light yellowish brown; cells filamentous to barrel-shaped. Subhymenium mor-
phologically undifferentiated. Basidia 30–59.5 × 8–14.5 μm, clavate, hyaline; sterigmata 4, up to 11 μm long. Cheilocystidia not observed. Basidiospores (excluding ornamentation) [265/13] 7–10(−12) × 7–10(−12) μm (\( \bar{x} = 8–9[-10] \times 7.7–9 [-10] \) μm), \( Q = 1(−1.12) (\bar{Q} = 1–1.04) \), globose, rarely subglobose, hyaline, echinulate; echinulae 1.4–2.8 μm long, up to 1.8 μm wide at base, crowded; hilar appendix 1.3–2 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. Basal mycelium hyphae mostly 2–12.5 μm diam., tightly interwoven, hyaline; cells filamentous to barrel-shaped.

Habitat and Distribution—Scattered to gregarious; in damp areas, often among wet mosses, usually not among Sphagnum, in mixed forests with Tsuga canadensis (L.) Carr. and/or other Pinaceae and Fagaceae, eastern North America. Material of this taxon has not been reported from Europe. In eastern North America it is common and abundant. A list of specimens examined is presented in Appendix A.

Observations—Laccaria striatula is easily recognizable by its strongly translucent-striate pileus; long, gracile, glabrous, reddish brown stipe; and globose basidiospores with long and wide echinulae. These characteristics differentiate it from L. laccata var. pallidifolia and L. ohiensis, the two taxa to which it is phenetically most similar. Because of the difficulty of interpreting dried herbarium material lacking macromorphological notes, it is sometimes difficult to differentiate between material of L. ohiensis and L. striatula.

Tissue cultures of this taxon were not obtained, but homokaryotic isolates and reconstituted dikaryons were white and grew moderately fast on all employed media. Homokaryotic isolates of L. striatula were intersterile with tested isolates of other members of the L. laccata complex (Mueller, 1991c). Material of this taxon was not included in our RFLP analyses (Gardes et al., 1990, 1991a).

Singer (1946), Orton (1960), Bon (1983), and others have treated this name as referring to a taxon with bisterigate basidia. An examination of the type specimen, however, showed it to have 4-sterigmate basidia, and that concept is used here (see Type Studies).

This taxon is abundant in wet mossy areas in the mountains of Georgia, North Carolina, New York, South Carolina, Tennessee, and Nova Scotia. It has also been collected in southern Ontario and northern Michigan and Wisconsin.

Mueller (1985) incorrectly used the name L. glabripes McNabb for this taxon. Aguirre-Acosta and Pérez-Silva (1978) reported L. glabripes from Mexico. Although I have not seen their material, it is likely that it is referable to L. striatula, not L. glabripes. All other reports of L. glabripes have...
come from Australia and New Zealand. I have not encountered material of *L. striatula* among the specimens that I have collected and examined from Costa Rica and South America.

*Laccaria ohiensis* (Montagne) Singer. Figures 25, 26, 55a, 68b.

= *Agaricus ohiensis* Montagne, Syll. Crypt: 100. 1856.
  TYPE: USA, Ohio, Columbus, before 1856, Sullivant s.n. (PC!, holotype).
= *Laccaria tetraspora* Singer, Mycologia 38: 689. 1946.


MACROMORPHOLOGY—Pileus 7–26(–50) mm broad, convex to plane, often depressed, plicate-striate and strongly translucent-striate when fresh, glabrous to finely fibrillose, hygrophanous, reddish brown (near 8D6) soon becoming orange-brown (7C5–6), finally fading to buff; margin decurved to plane, entire to undulate; context thin, concolorous. Lamellae adnexed to adnate, distant, moderately thick, pinkish flesh color (6A2–7A3). Stipe 12–25(–40) × 1–2(–6) mm, equal or slightly bulbous, dry, glabrous to finely fibrillose, striate to slightly longitudinally striate, concolorous with pileus. Basal mycelium white. Basidiospores white in mass.

MICROMORPHOLOGY—Pileipellis of interwoven hyphae with widely scattered fascicles of ± perpendicular hyphae; fascicles composed of 5–30 hyphae; terminal cells of fascicular hyphae 26–67 × 5–17.5 μm, filamentous, subclavate or clavate;
walls up to 0.5 μm thick, light yellowish brown, often encrusted with pigment(s); contents hyaline to light yellowish brown. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel to subparallel; hyphae mostly 2–10 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** 28–60 × 8–16 μm, clavate, hyaline; sterigmata 4, up to 10 μm long. **Cheilocystidia** 20–55 × 3–5.5 μm, filamentous to subcapitate, absent to relatively abundant, thin-walled, hyaline. **Basidiospores** (excluding ornamentation) [375/11] (6.4–)7.7–9.4 (–11) × (6.4–)7–9(–10.6 μm (̅x = 7.9–8.4[–9.3] × 7.8–8.4[–9.1] μm), Q = 1–1.09(–1.2) (̅Q = 1–1.05), globose to subglobose, rarely broadly ellipsoid, hyaline, echinulate; echinulae (1–)1.5–2.8 μm long, > 1.2 μm wide at base, crowded; hilar appendix 1.3–2 μm long, prominent, truncate; plage present; contents occasionally uniguttulate.

**Habitat and Distribution**—Scattered to gregarious, not commonly collected in boreal or north temperate habitats. Commonly reported from subtropical, tropical, and south temperate regions. A list of collections examined is presented in Appendix A.

**Observations**—Collections of *Laccaria ohiensis* are characterized by their small basidioma size, strongly striate pilei, short, concolorous stipes, and globose basidiospores with long and wide echinulae.

*Laccaria ohiensis* is primarily differentiated from *Laccaria laccata var. pallidifolia* by having basidiospore echinulae that are ≥ 1.2 μm wide at their base. In contrast to *L. ohiensis*, whose collections are relatively uniform in macro- and micromorphological features, collections of *L. laccata var. pallidifolia* are highly variable in most morphological characters. Collections of *L. laccata var. pallidifolia* with small basidiomata and globose basidiospores (characteristics of *L. ohiensis*) are occasionally encountered.

Tested homokaryotic isolates of these two taxa are intersterile (Fries & Mueller, 1984; Mueller, 1991c) and differ in mtDNA and rDNA RFLP patterns (Gardes et al., 1990, 1991a; Mueller, 1991c). Isolates identified as belonging to mating group III (Fries & Mueller, 1984) and intersterility group 4 (Gardes et al., 1990, 1991a; Mueller, 1991c) are referable to *L. ohiensis*.

*Laccaria ohiensis* is differentiated from *L. striatula* by differences in macromorphology. Basidiomata of *L. striatula* have relatively long, glabrous stipes that are darker in color than the strongly striate pilei. Collections of these two taxa were not segregated during morphometric analyses of basidiospore characters (Mueller, 1991c), but tested isolates of the two taxa are intersterile. The isolate of *L. ohiensis* included in the analyses of mtDNA and rDNA had unique RFLP patterns (Gardes et al., 1990, 1991a).

The holotype of *L. ohiensis* (see Type Studies) consists of basidiomata that have globose, echin-
Fig. 25. Basidiomata of *L. ohiensis* (GMM 1730).

ulate basidiospores born on 4-sterigate basidia. This agrees with Singer’s (1942) description of the type and Malençon’s (1966) and Malençon and Bertult’s (1975) concept of the taxon. In subsequent papers (e.g., Singer, 1946, 1977; Singer & Digilio, 1952; Bon, 1983), *L. ohiensis* was treated as a taxon with 2-sterigate basidia. The correct name for the 2-sterigate taxon discussed by Singer (1967, 1977), which has moderate-sized, subglobose basidiospores and normally occurs in warm and dry regions, often under *Eucalyptus*, is *L. fraterna*. *Laccaria impolita* is similar to *L. fraterna* but differs in macromorphology and association with north temperate trees (see Type Studies).

**Laccaria tortilis** (Bolton) Cooke. Figures 27–29, 55c,d, 72b.


≡ *Laccaria tortilis* (Bolton) Cooke, Grevillea 12: 70. 1884.
≡ *Clitocybe tortilis* (Bolton) Saccardo, Syll. Fung. 5: 198. 1887.
≡ *Collybia tortilis* (Bolton) Quélet, Flore Mycologique: 237. 1888.
≡ *Clitocybe laccata var. tortilis* (Bolton) Barla, Fl. mycol. ill.: 64. 1892.
≡ *Clitocybe echinospora* (Spegazzini) Saccardo, Syll. Fung. 5: 198. 1887.

**MACROMORPHOLOGY—Pileus** 5–23 mm broad, convex, becoming plane to uplifted, strongly plicate-striate, subglabrous to finely fibrillose, hygrophanous, vinaceous brown to brownish orange (“Vinaceous-Brown,” “Sorghum Brown,” or “Orange Rufous”) fading lighter in color (“Rood’s Brown” to “Vinaceous-Russet”), eventually becoming buff color; margin plane, undulate, eroded,
Micromorphological features of *L. ohiensis* (GMM 2354): a, basidiospores; b, basidia. Scale line = 10 μm.

or rimose; context thin, concolorous. Lamellae sinuate to adnate, distant, broad, thick, pinkish flesh color to slightly vinaceous ("Flesh Color" to "Light Russet-Vinaceous"). Stipe 4–15 × 1–3.5 mm, equal to subbulbous, dry, finely fibrillose, not striate, concolorous with pileus. Basal mycelium white. Basidiospores white in mass.

**Micromorphology**—Pileipellis of interwoven hyphae with widely scattered fascicles of ± perpendicular hyphae; fascicles composed of 5–15 hyphae; terminal cells of fascicular hyphae 26.5–69 × 6.5–15 μm, filamentous to clavate; walls up to 0.5 μm thick, light yellowish brown. Pileus trama tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. Lamellar trama parallel; hyphae mostly 6–14.5 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. Subhymenium morphologically undifferentiated. Basidia 33–64 × 7–16 μm, clavate, hyaline; sterigmata 2(3), up to 11.5 μm long. Cheilocystidia lacking or scarce; filamentous. Basidiospores (excluding ornamentation) [90/6] (9.2–)10–14.5(–16) × (8.3–)10–14.5(–16) μm (χ = 10.9–13 × 10.5–12.7 μm), Q = 1–1.09(–1.17) (Q = 1–1.03[–1.07]), globose, rarely subglobose, hyaline, strongly echinulate; echinulae 1.4–3.2(–4) μm long, up to 2.3 μm wide at base, crowded; hilar appendix 1.3–2.3 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. Basal mycelium hyphae 3–14 μm diam., tightly interwoven, hyaline; cells filamentous to barrel-shaped.

**Habitat and Distribution**—Scattered to gregarious, occasionally caespitose, often on bare, poorly drained soil, apparently associated with both Pinaceae and Fagaceae; cosmopolitan; not common. A list of specimens examined is presented in Appendix A.

**Observations**—*Laccaria tortilis* can be distinguished from the rest of the small, plicate-striate *Laccaria* taxa by its 2-sterigmate basidia that bear large, globose basidiospores with long and broad echinulae.

It has not been possible to obtain tissue cultures or to germinate the basidiospores of this taxon. Material of *L. tortilis* was not included in the RFLP analyses of Gardes et al. (1990, 1991a). There has been some confusion in the literature concerning the correct name for this taxon. *Agaricus tortilis* is the earliest name used for this mac-

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**Fig. 26.** Micromorphological features of *L. ohiensis* (GMM 2354): a, basidiospores; b, basidia. Scale line = 10 μm.
Fig. 27. Basidiomata of *L. tortilis* (GMM 1710).

Fig. 28. Basidiomata of *L. tortilis* (GMM 1710).
romorphological form (Bolton, 1788). Although no holotype exists, and Bolton's description did not give any morphological data, his color plate clearly illustrated the macromorphological traits of this taxon. I agree with the majority of modern workers (e.g., Dennis et al., 1960; Orton, 1960; Bon, 1983; Moser, 1983) who use the binomial *L. tortilis* for this taxon based on common usage (Korf, 1982a,b). Additionally, an examination of representative material from the environs of the type locality shows that Bolton probably had access to specimens that fit this micromorphological form. Rea (1922), Singer (1950a, 1952), Ballero and Contu (1989), and a few others consider *A. tortilis* to be a smaller-basidiospored species, and Singer (1943b, 1950a, 1952, 1967, 1977, 1986) used *L. echinospora* (Spegazzini) Singer for this taxon. Clémencón (1984) recognized both *L. tortilis* and *L. echinospora* as large-basidiospored taxa. He differentiated them on echinulae length, with *L. tortilis* having shorter echinulae than *L. echinospora*.

In an attempt to stabilize the application of the name, Mueller (1987) designated a neotype for *L. tortilis*. As discussed under *L. proxima*, the conflicting interpretations of this name have not been resolved by designating Bolton's illustration the lectotype. To stabilize the application of this epithet, the collection that was proposed as a neotype (Mueller, 1987) is now designated a "representative specimen" (see Type Studies).

In North American literature, Peck (1912) and Murrill (1914) used the name in the current sense, while Coker and Beardslee (1922) used *L. tortilis* for specimens with 4-sterigmate basidia and moderate-sized basidiospores.

Although not frequently collected, *Laccaria tortilis* occurs throughout much of the United States and Canada outside of arctic habitats. Most re-

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**Fig. 29.** Micromorphological features of *L. tortilis* (McAdoo 78#28): a, basidiospores; b, basidia. Scale line = 10 μm.
FIG. 30. Basidiomata of *L. trichodermophora* (GMM 2321).

FIG. 31. Somatic culture mats of *L. trichodermophora* (GMM 1014). Top on PDA, left on MMN, and right on MEA. Photo taken during week 4.
ports under this name from the arctic refer to collections of *L. pumila* (see Observations under *L. pumila*).

**Laccaria Metasection Amethystina**

[see p. 24 for discussion]

Basidiomata and somatic culture mats with violet pigment(s); basidia not ellipsoid to oblong with echinulations 0.5(-1.4) μm long.

**Laccaria trichodermophora** G. M. Mueller. Figures 30-32, 56c, 72c.


**MACROMORPHOLOGY—Pileus** 9–66 mm broad, convex to plane, occasionally becoming uplifted, often depressed, not striate, strongly pruinose to fibrillos, becoming fibrillos-scaly to scaly owing to cuticular diffraction, hygrophanous, brownish orange, occasionally reddish brown ("Hazel," "Vinaceous-Rufous," "Auburn," "Orange Rufous," "Cacao Brown," or "Cinnamon-Rufous"), fading light brown to buff color ("Flesh-Ocher" to "Apricot Buff"), occasionally darker reddish brown at disc ("Hay's Russet" to "Kaiser Brown"); margin incurved, decurved, or plane, entire to undulate, occasionally becoming eroded; context 1-2 mm thick, tapering quickly to margin, pinkish flesh color ("Light Congo Pink" to "Pale Vinaceous-Pink"). Lamellae sinuate to adnate, close to distant, broad, relatively thin to thick, flesh color ("Vinaceous-Pink," "Shell Pink," "Flesh Color," or "Pale Salmon Color"), at times vinaceous in age (near "Vinaceous"). Stipe 20–115 × 2–11 mm, equal, subclavate or slightly bulbous, dry, fibrillos, inconspicuously to moderately longitudinally striate, concolorous with pileus; context stuffed, becoming hollow, concolorous with pileus context. Basal mycelium violet (near "Lavender" or "Pale Violet") when fresh, strongly hygrophanous, fading to white. Basidiospores white in mass.

**MICROMORPHOLOGY—Pileipellis** of very numerous large fascicles of ± perpendicular hyphae, often forming a trichodermium in young specimens and at the disc; fascicles composed of 15–30 or more hyphae; terminal cells of fasciculate hyphae 25–73.5 × 6–32 μm, filamentous, clavate or occasionally capitulate; walls up to 0.5 μm thick, light yellowish brown; contents hyaline to light yellowish brown. Pileus trama tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. Lamellar trama parallel; hyphae mostly 3–18 μm diam., thinned, hyaline to light yellowish brown; cells fil-

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amentous to barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** 24.5–55 × 7–13(–20) μm, clavate, hyaline; sterigmata 4, up to 9 μm long. **Cheilocystidia** 17.5–60 × 2–6.5 μm, filamentous, occasionally subclavate, thin-walled, hyaline, absent, scattered or abundant. **Basidiospores** (excluding ornamentation) [415/20] (6.2–) 6.8–8.7(–10.6) × 6–8(–9.2) μm (\(\bar{x} = 7.1–8[–8.5] \times 6.3–8 \mu \text{m} \)), \(Q = 1–1.24(–1.36)(\bar{Q} = [1.01–1.08–1.17])\), subglobose to broadly ellipsoid, occasionally globose or ellipsoid, hyaline, echinulate; echinulae (0.5–0.9–1.8 μm long, irregularly spaced to crowded; hilar appendix 1.3–1.8 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 3–12 μm diam., tightly interwoven, hyaline; cells filamentous to barrel-shaped.

**Somatic Culture Mat Morphology** (N = 8; Appendix B)—**PDA:** Radius at week 3 = 15–38 mm or 42–45 mm, week 6 = (23–)29–59 mm or covering agar surface; **mat** feltly, tightly interwoven, uniformly thick or with narrow, thicker dendritic strands radiating out from plug, tightly pressed to agar surface, normally forming pruinose aerial layer away from plug with time, not translucent, bright violet fading to violet, finally to light orange-brown near plug; aerial hyphae light grayish-violet; **margin** 2–6 mm broad, subfertile, felty or silky, thin to thick, entire to uneven, light violet to white; **plug** dark violet, soon becoming light orange-brown; **hyphae** morphologically undifferentiated, occasionally subcoralloid or irregularly swollen. **MMN:** Radius at week 3 = 24–44 mm or 52–64 mm, week 6 = (43–)54–78 mm or agar surface covered; **mat** subfertile becoming felty or silky, thin to thick, with 2 or 3 narrow (2–3 mm), slightly thicker concentric zones or with slightly thicker, radially arranged, dendritic strands or uniformly thin, tightly appressed to agar surface, translucent, light violet, thicker zones somewhat darker; **margin** not well differentiated from mat, silky to subfertile, sinuate, light violet to white; **plug** concolorous with mat; **hyphae** same as in PDA. **MEA:** Radius at week 3 = 20–42 mm, week 6 = 38 mm or agar surface covered; **mat** silky to subfertile, thin or thick, occasionally thicker near plug, loosely interwoven or interwoven, tightly appressed to agar surface, translucent, white; **margin** not well differentiated from mat, silky to subfertile, entire to sulcate, white; **plug** white; **hyphae** morphologically undifferentiated, occasionally irregularly swollen.

**Habitat and Distribution**—Scattered to gregarious; commonly encountered in southeastern North America, in temperate coniferous or mixed coniferous–deciduous forests, apparently usually associated with species of *Pinus*. A list of specimens examined is presented in Appendix A.

**Observations**—**Laccaria trichodermophora** differs from *L. laccata* by having violet basal mycelium and smaller basidiospores. Its culture mat morphology differs by displaying a faster growth rate and violet coloration on PDA and MMN. Because of the ephemeral nature of the violet pigment in the basal mycelium and the slight overlap of basidiospore size and shape with those of *L. laccata var. pallidifolia*, it is occasionally difficult to differentiate between dried herbarium specimens of the two taxa.

**Laccaria trichodermophora** can be distinguished from *L. bicolor* and *L. nobilis* by its distribution, basidioma coloration, and scent basal mycelium. Additionally, the three taxa have distinct culture mat morphologies. **Laccaria bullulifera** Singer from Mexico is characterized by the occurrence of large, swollen cheilocystidia.

Mueller and Gardes (1991) summarized the results of intercollection pairing studies, phenetic analyses, and analyses of mtDNA and rDNA RFLPs for the *L. bicolor* complex. They concluded that collections of *L. trichodermophora* were well delimited from *L. bicolor* and *L. nobilis* (see Observations under *L. bicolor*). The concept of *L. trichodermophora* used here includes material termed Bi I and *L. trichodermophora* in previously published phenetic analyses (Mueller, 1985).

Singer and Moser (1965) and Singer (1973, 1977, 1986) used the name *L. farinacea* for the taxon herein referred to as *L. trichodermophora*. No type exists for *A. farinaceus*, and Hudson (1798) listed *A. laccatus* under *A. farinaceus* implying that *A. farinaceus* was only a new name for *A. laccatus*. Fries (1821) placed *A. farinaceus* in synonymy under *A. laccatus* var. “a.” In addition, neither Hudson nor Persoon (1801) mentioned the color of the basal mycelium in their description. It was necessary, therefore, to propose a new name for this taxon.

All of the collections of *L. trichodermophora* observed from the southeastern United States appeared to be associated with *Pinus*. **Laccaria trichodermophora** has not been reported from western or midwestern North America. To date, no material referable to *L. bicolor sensu stricto* or *L. nobilis* has been encountered in southeastern North America. Material from the northeastern United States or Atlantic Coast of Canada was not included in Mueller and Gardes (1991), and the oc-
currence of these three taxa in that area is not known. Collections of *L. bicolor sensu lato* are commonly collected in northeastern North America and are currently treated as *L. bicolor*. Aguirre-Acosta and Pérez-Silva (1978) and Montoya-Bello et al. (1987) reported *L. trichodermophora* (as *L. farinacea sensu Singer*) from Mexico. Mueller and Strack (unpubl.) have collected *L. trichodermophora* beneath Neotropical species of *Quercus* in Costa Rica.

**Laccaria bicolor** (Maire) Orton. Figures 33–35, 56a,b, 60c.


**MACROMORPHOLOGY—Pileus** 8–70 mm broad, convex to plane, often depressed, not striate, finely fibrillose, fibrillose-scaly or occasionally scaly, hygrophanous, pinkish flesh color (“Walnut Brown,” “Onion-skin Pink,” “Kaiser Brown,” or “Cinnamon-Rufous”) fading to buff color (“Flesh Ocher,” “Salmon Buff,” or near “Pale Salmon Color”); margin decurved to plane, entire to undulate, often eroded; context thin, tapering quickly to margin, light vinaceous (“Pale Brownish Vinaceous” or “Hydrangea Pink”). *Lamellae* adnate to arcuate, subdistant to distant, broad, thick, light vinaceous (“Pale Purplish Vinaceous,” “Pale Vinaceous,” or “Hydrangea Pink”), fading to pinkish flesh color (“Light Congo Pink” or “Shell Pink”), then light flesh color (“Pale Flesh Color” or “Pale Salmon Color”). *Stipe* 23–85(–130) × 3–6(–10) mm, equal, subclavate or slightly bulbous, dry, fibrillose, longitudinally striate, concolorous with pileus; stria- tions concolorous with ground color or slightly darker red brown. Basal mycelium copious, hygrophanous, violet when fresh (“Dull Lavender” to “Pale Vinaceous-Lilac”), becoming white.

**MICROMORPHOLOGY—Pileipellis** of interwoven hyphae with numerous large fascicles of ± perpendicular hyphae; fascicles composed of (15–)25–30 or more hyphae; terminal cells of fascicular hyphae 27.5–76 × 6–18.5 μm, subclavate, clavate, or rarely subcapitate; walls up to 0.5 μm thick, light yellowish brown; contents hyaline to light yellowish brown. Pileus trama tightly interwoven, morphologically undifferentiated, hyaline to light yellowish brown toward pileipellis. Lamellar trama parallel; hyphae mostly 2–13.5 μm diam., thin-walled, hyaline to light yellowish brown; cells filamentous to barrel-shaped. Subhymenium morphologically undifferentiated. Basidia 28.5–55 × 7.4–13 μm, clavate, hyaline; sterigmata 4, up to 9 μm long. Cheilocystidia 24.5–55 × 2.5–8 μm, filamentous to subclavate, thin-walled, hyaline, absent to abundant. Basidio- spores (excluding ornamentation) [465/28] (5.5–)7–8.7(–10) × (5.5–)6–7.8(–9.2) μm (x = 7.0–8.4[–9] × 6.2–7.8 μm), Q = 1–1.26(–1.36) (Q = 1.05–1.23), subglobose to broadly ellipsoid, occasionally globose or ellipsoid, hyaline, echinulate; echinulae 1–1.8 μm long, ≤ 1 μm wide at base; hilar appendix 1.3–2 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. Basal mycelium hyphae mostly 3–15.5 μm diam., tightly interwoven, hyaline; cells filamentous to barrel-shaped.

**SOMATIC CULTURE** MAT MORPHOLOGY (N = 10; Appendix B)—PDA: Radius at week 3 = 11–32 mm, week 6 = 18–40(–54) mm; mat feltly, thick, tightly interwoven, tightly appressed to agar surface, in time forming pruinose aerial layer away from plug, occasionally becoming furrowed owing to irregular infolding near plug, not translucent, bright violet fading to light orange-brown or remaining bright violet; aerial hyphae light grayish violet, often covering most of mat by week 6 and then masking mat color; margin 3–4 mm broad, subfertile, thin, light violet to white; plug dark violet at first, becoming light orange-brown; hyphae morphologically undifferentiated or irregularly swollen, violet in mass, pigment intracellular.

**MMN: Radius** at week 3 = 22–41 mm, week 6 = (31–)40–63 mm; mat silky, subfertile or feltly, thin or thick, loosely to tightly interwoven, occasionally with 3 or 4 narrow concentric thicker bands, tightly appressed to agar surface, translucent or not translucent, at first light violet or violet, soon buff, by week 3 violet color usually restricted to thicker bands and near margin; margin 2–4 mm broad, silky to subfertile, thin, loosely interwoven, even to serrate, light violet; plug light violet; hyphae morphologically undifferentiated or rarely irregularly swollen. **MEA:** Radius at week 3 = 19–43 mm, week 6 = 30–52 mm, TENN 42529 68–76 mm; mat subfertile to feltly, thick, interwoven, occasionally with small, scattered, thicker sectors, tightly appressed to agar surface, translucent, white;
Fig. 33. Basidiomata of *L. bicolor* (GMM 1327).

Fig. 34. Somatic culture mats of *L. bicolor* (GMM 1293). Top on PDA, left on MMN, and right on MEA. Photo taken during week 4.
margin 2–3 mm broad, subflety, not well differentiated, often very uneven, white; plug white; hyphae morphologically undifferentiated, occasionally with a few scattered irregular swollen hyphae.

HABITAT AND DISTRIBUTION—Scattered, occasionally caespitose. Very commonly encountered on soil or among conifers in western North America east to Ontario and Michigan. Specimens of *L. bicolor* sensu lato from northeastern United States and the Atlantic provinces of Canada are included under *L. bicolor* (see below). A list of specimens examined is provided in Appendix A.

OBSERVATIONS—*Laccaria bicolor* is characterized by having moderate-sized basidiomata, violaceous lamellae when fresh, and copious violet mycelium at the stipe base. *Laccaria trichodermophora* differs by having pinkish flesh-colored lamellae and sparse, strongly hygrophanous, violet basal mycelium. *Laccaria bicolor* has been reported from western and northern North America and Europe; *L. trichodermophora* has only been reported from southeastern North America, Mexico, and Costa Rica. The large, scaly basidiomata of *L. nobilis* differentiate that taxon from *L. bicolor*. *Laccaria nobilis* occurs sympatrically with *L. bicolor* in western and north central North America but has not been reported from Europe. All three of these taxa have distinct culture mat morphologies.

Mueller and Gardes (1991) summarized the results of intercollection pairing studies, phenetic analyses, and analyses of mtDNA and rDNA for the *L. bicolor* complex. Three intersterility groups were detected among 38 North American isolates tested. Matings within a group were frequent but mating between intersterility groups were rare. The three intersterility groups were delimited during phenetic analyses, indicating that these groups differed morphologically. The two Swedish isolates used were completely intercompatible with one North American group but only partially intercompatible with isolates of the other two groups. These results were more or less concordant with data obtained by RFLP analysis of mtDNA and rDNA (Gardes et al., 1990, 1991a). The North American isolates formed a relatively homogeneous group and were differentiated from the two Swedish isolates based on analyses of rDNA (Gardes et al., 1990). In contrast, analyses of mtDNA detected divergence between the North American intersterility groups but not between the Swedish isolates and North American isolates (Gardes et al., 1991a). Based on a synthesis of these data, the Swedish collections and material from western North America and areas adjacent to the Great Lakes were treated as *Laccaria bicolor* sensu stricto; *L. nobilis* was circumscribed as a taxon with large, robust, scaly basidiomata occurring sympatrically with North American material of *L. bicolor*, and material from the southeastern United States with pinkish flesh-colored lamellae was treated as *L. trichodermophora* (Mueller & Gardes, 1991).

*Laccaria bicolor* is one of the most common *Laccaria* taxa found in the coniferous forests of

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FIG. 36. Basidiomata of *L. nobilis* (GMM 2048).

FIG. 37. Somatic culture mats of *L. nobilis* (GMM 1205). Top on PDA, left on MMN, and right on MEA. Photo taken during week 4.
western North America and the Great Lakes area. Collections of L. bicolor sensu stricto were not encountered from the southeastern United States. Material of L. bicolor sensu lato from the northeastern United States or Atlantic provinces of Canada, although frequently encountered, was not available to include in the studies of Mueller and Gardes (1991). Consequently, the occurrence and distribution of these three species in that area are unknown, and collections of L. bicolor sensu lato from this region have been treated as L. bicolor in this monograph.

Isolates of L. bicolor are very frequently used in applied studies on ectomycorrhizae (Kropp & Langlois, 1990).


MACROMORPHOLOGY—Pileus 16–85 mm broad, convex to plane, occasionally becoming uplifted, depressed to deeply depressed, not striate, fibrillose-scyal Becoming scaly to squarrose, reddish brown (8C7–8D7) to brownish orange (“Sanford’s Brown” or “Cinnamon-Rufous”) 6C7, 7C6–7D7), occasionally darker at disc (“Hazel”); margin incurved, decurved or plane, occasionally upturned, entire to eroded; context thin, concolorous with lamellae. Lamellae sinuate to adnate, close to distant, thick, vinaceous (8B2–9B3) to pinkish flesh color (“Flesh Color,” “Pale Flesh Color,” or “Orange-Pink”) (7A2–7A3). Stipe (21–)26–110(–160) x 4–10(–16) mm, equal, slightly bulbous or subclavate, dry, fibrillose, with prominent longitudinal striations or reticulate ridges, often with apical recurved scales at maturity, concolorous with pileus; striations concolorous with stipe ground color or somewhat darker reddish brown. Basal mycelium violet, soon becoming white. Basidiospores white in mass.

MICROMORPHOLOGY—Pileipellis of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 15–30 or more hyphae; terminal cells of fascicular hyphae 34.5–75 x 4–19 μm, subclavate, clavate, broadly clavate or capitulate; walls up to 0.5 μm thick, light yellowish brown; contents hyaline to light yellowish brown. Pileus trama tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. Lamellar trama parallel; hyphae mostly 3–10 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. Subhymenium morphologically undifferentiated. Basidia 32–55 x 8–14 μm, clavate, hyaline; sterigmata 4, up to 9 μm long. Cheilocystidia lacking. Basidiospores (excluding ornamentation) [122/8] (6.2–)6.6–9.7(–10.6) x (5–)6.2–8.7 μm (t = [7–] 7.4–8.8 x [6–]6.3–7.8 μm), Q = 1–1.26(–1.39) (Q = [1.03–]1.16–1.22), subglobose to broadly ellipsoid, occasionally globose or ellipsoid, hyaline, echinulate; echinulae 0.5–1.4 μm long (t = 0.9 ±
FIG. 39. Basidiomata of *L. trullissata* (GMM 3048).

FIG. 40. Habitat view of *L. trullissata* (GMM 3048) illustrating typical growth in sand.
Micromorphological features of *L. trullissata* (GMM 1914): a, basidiospores; b, basidia. Scale line = 10 μm.

0.2 μm), crowded; hilar appendix 1.3–2 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. Basal mycelium hyphae mostly 2–12 μm diam., tightly interwoven, hyaline; cells filamentous to barrel-shaped.

**Somatic Culture Mat Morphology** (N = 2; Appendix B)—**PDA:** Radius at week 3 = 23–31 mm, week 6 = 35–43 mm; mat feltly, thick, tightly interwoven, almost crustose, tightly appressed to agar surface, with time forming pruinose aerial layer away from plug, not translucent, at first bright violet, by week 6 violet color restricted to a 7–9 mm band near margin, rest of mat light orange-brown; pruinose aerial hyphae light grayish purple becoming light orange-brown; margin 3–4 mm broad, subfetly, thin, uneven, light violet to white, plug concolorous with mat; hyphae morphologically undifferentiated, rarely irregularly swollen near margin. **MEA:** Radius at week 3 = 33–47 mm, week 6 = 47–77 mm; mat subfetly, thin to slightly thicker near plug, loosely interwoven, tightly appressed to agar surface, translucent, white; margin 1–2 mm broad, subfetly, thinner than mat, undulate; hyphae morphologically undifferentiated.

**Habitat and Distribution**—Solitary to scattered. Infrequently encountered under Pinaceae in western North America and areas adjacent to the Great Lakes. A list of specimens examined is presented in Appendix A.

**Observations**—*Laccaria nobilis* can be distinguished easily from other members of the *L. bicolor* complex by its large size, scaly to squarrose pileus, scaly stipe, and lack of obvious cheilocystidia. A. H. Smith proposed the name in an unpublished manuscript along with several other taxa, including *L. pisciodorus nom. prov.* (Smith no. 18812) and *L. sphagnicola nom. prov.* (Smith no. 18813).
4573). The latter two taxa were not judged sufficiently distinct, based on available material, to justify valid publication as discrete taxa.

The concept of *L. nobilis* used here has been broadened from that originally published by Mueller (1984, 1985). Interpretation of lamellae and basal mycelium colors was difficult in many of the collections included in the original description because the specimens were mature and weathered. Additional material was collected subsequently that differed from the original collections in having vinaceous lamellae and violet mycelium at the base of the stipe. Because all of these collections had large, robust basidiomata that became quite scaly in age, strongly striate to nearly reticulate stipes, and similar micromorphology and somatic culture mat morphology, they were treated as a single taxon, *L. nobilis*. Isolates of more recently collected specimens were included among the material studied by Mueller and Gardes (1991).

*Laccaria nobilis* is well delimited from *L. bicolor* and *L. trichodermophora* based on intercollection pairing studies, phenetic analyses, and analyses of mtDNA and rDNA RFLPs (Mueller & Gardes, 1991) (see Observations under *L. bicolor*).

*Laccaria nobilis* has been identified among material collected throughout much of western North America (e.g., California, Colorado, Idaho, New Mexico, Oregon, and Washington) and from Michigan and Ontario.

*Laccaria trullissata* (Ellis) Peck. Figures 39–41, 57b–d, 72d.


= *Clitocybe trullissata* (Ellis) Saccardo, Syll. Fung. 5: 195. 1887.


**Macromorphology—Pileus** 17–72 mm broad, convex to plane, occasionally depressed, not striate, fibrillose to fibrillose-scaly, grayish purple when very young (near 17B4), soon becoming red-brown, brown or buff (“Fawn Color,” “Avellaneous,” “Vinaceous-Buff,” “Pale Vinaceous-Fawn,” or “Pinkish Buff”) (6A4–5, 6B6, 7D7 or 7E5–7); margin incurved to decurved, entire to eroded; context tapering to margin, pale purple (near “Light Vinaceous-Gray”). **Lamellae** adnate to arcuate, close to subdistant, narrow to moderately broad, thick, waxy appearing, dark violaceous (“Dark Helio-
trope Gray” or “Deep Vinaceous-Gray”). **Stipe** 40–93 × 6–23 mm, subclavate to clavate, dry, fibrillose, longitudinally striate, covered with sand, occasionally with outer “cortical” layer splitting near apex, concolorous with pileus; context solid, concolorous with pileus context. **Basal mycelium** violaceous. **Basidiospores** white in mass.

**Micromorphology—Pileipellis** of interwoven hyphae with widely scattered fascicles of ± perpendicular hyphae; fascicles composed of 10–25 hyphae; terminal cells 33.5–85 × 7–16 μm, subclavate, clavate, broadly clavate or capitate, walls up to 0.5 μm thick, light yellowish brown; contents hyaline to light yellowish brown. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae mostly 3–17 μm diam., hyaline, light yellowish brown or light vinaceous color; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** 30–64.5 × 9–16 μm, clavate, hyaline; sterrig mata 4, up to 10 μm long. **Cheilocystidia** lacking or very scarce and filamentous. **Basidiospores** [75/5](13.3–)13.8–20.2(–21.6) × 5.5–8.3 μm (x = 15.3–17.3 × 6–7.3 μm), Q = 1.83–3.31 (Q = 2.37–2.51), subfusiform to fusiform-ellipsoid, hyaline, very finely roughened, not echinulate; hilar appendix 1.3–2 μm long, prominent, truncate; contents occasionally uniguttulate, rarely biguttulate. **Basal mycelium hyphae** 3–15.5 μm diam., tightly interwoven, hyaline; cells filamentous or barrel-shaped.

**Habitat and Distribution**—Solitary to scattered; sand dunes or very sandy soil; usually associated with species of *Pinus*, eastern and midwestern North America. A list of specimens examined is provided in Appendix A.

**Observations**—*Laccaria trullissata* is distinguished from other North American *Laccaria* taxa by its habitat, macromorphology, and basidiospore characteristics. Collections of *Laccaria maritima* differ from those of *L. trullissata* in having shorter, less elongate, echinulate basidiospores.

Ectomycorrhizae were synthesized between one isolate of *L. trullissata* and seedlings of *Pinus resinosa* Ait. (unpubl. data). Intrastock pairings demonstrated that *L. trullissata* has a bifactorial compatibility system as do all other tested *Laccaria*.

*Laccaria trullissata* occurs in sandy areas along the eastern coast of North America, ranging from the Maritime Provinces of Canada to North and South Carolina along the Atlantic coast and Florida to Mississippi along the Gulf of Mexico. It can be encountered also in northcentral United States.
and southcentral Canada in sand dunes along the Great lakes.

**Laccaria maritima** (Teodorowicz) Singer *ex* Huhtinen. Figures 42, 57a.

= **Hygrophorus maritimus** Teodorowicz, Grzyby wysze polskiego wybrzeza, Towarzystwo naukowe w Toruniu Badania Przyrodnicze Pomorskie 2: 31. 1936. TYPE: Fig. 5 in Teodorowicz, Grzyby wysze polskiego wybrzeza, Towarzystwo naukowe w Toruniu Badania Przyrodnicze Pomorskie 2: 31. 1936. (lectotype *fide* Mueller, 1991a).


= **Laccaria maritima** (Teodorowicz) Singer, Sydowia 15: 133. 1961. [not validly published, basionym lacking].


**MACROMORPHOLOGY**—**Pileus** up to 45 mm broad, convex to plane, becoming uplifted, often depressed, nonstriate or translucent-striate when fresh, glabrous to finely fibrillose, slightly viscid, hygrophanous, dark reddish brown to reddish-orange-brown. **Lamellae** adnate to subdecurrent, distant, thick, broad, pinkish flesh color to vinaceous. **Stipe** large and robust, equal to clavate, dry, mostly covered with sand, concolorous with pileus. **Basidiospores** white in mass.

**MICROMORPHOLOGY**—**Pileipellis** of interwoven hyphae with scattered ± perpendicular individual hyphae or fascicles of hyphae, terminal cells of hyphae 35–55 × 4–10 μm, hyaline. **Basidia** 37–60 × 9–15.5 μm, clavate, 4-sterigate. **Cheilocystidia** none seen. **Basidiospores** (excluding ornamentation) [105/4] (10–)1.5–17(–19.5) × (5.5–)7.5–9.5(–10) μm (x = 13.3–15.4 × 8–8.5 μm), Q = 1.43–2(–2.17) (Q = 1.67–1.81), oblong to subfusiform, echinulate; echinulae 0.2–0.5 μm long.

**HABITAT AND DISTRIBUTION**—Scattered to gregarious; terrestrial, in sand including dunes; with or without apparent ectomycorrhizal associate. Only reported from a few sites in eastern Canada.
Fig. 43. Basidiomata of *L. ochropurpurea* (GMM 919). Largest pileus = 8 cm diam.

Fig. 44. Somatic culture mats of *L. ochropurpurea* (GMM 1015). Top on PDA, left on MMN, and right on MEA. Photo taken during week 4.
FIG. 45. Micromorphological features of L. ochropurpurea (E. Farwell 5074): a, basidiospores; b, basidia; c, cheilocystidia. Scale line = 10 μm.

Known primarily from northern Europe. A list of specimens examined is presented in Appendix A.

Observations—Laccaria maritima is characterized by its restricted habitat, dark reddish brown pileus color, vinaceous-tinged lamellae, stipe buried in sand, and elongate, finely echinulate basidiospores. Collections of L. trullissata have larger basidiomata with deep violet lamellae and larger, more elongate (mostly 14–21.5 × 5.5–9 μm), finely roughened, not echinulate basidiospores. It has not yet been possible to obtain a tissue culture or germinate the basidiospores of this taxon. Lack of cultures has prevented attempts at in vitro ectomycorrhizal synthesis to determine the ability of this taxon to form ectomycorrhizae with putative hosts.

This species has been reported from both coastal and inland dunes of northern Europe, the Netherlands, and Greenland (e.g., Teodorowicz, 1936; Andersson, 1950; Lange, 1955; Singer, 1961; Kallio & Heikkilä, 1963; Höiland, 1976; Vellinga, 1982). Huhtinen (1987) reports it for the first time from North America, where L. trullissata is found much more commonly in sand dunes than Laccaria maritima.

Laccaria ochropurpurea (Berkeley) Peck. Figures 43–45, 58d, 68a.

= Clitocybe ochropurpurea (Berkeley) Saccardo, Syll. Fung. 5: 148. 1887.

Macromorphology—Pileus 35–100(–125) mm broad, obtuse, convex, plane or uplifted, often depressed, not striate, dry, subglabrous, finely fibrillose or occasionally fibrillose-scyal, light violaceous brown to buff color, often with violaceous tints in young, fresh specimens (“Vineaceous-Buff,” “Pale Vineaceous-Fawn,” or “Pinkish Buff”); margin inrolled, decurved, plane or uplifted, entire, slightly undulate, eroded or rimose; context ≤ 9 mm thick at disc, tapering to margin, violaceous buff. Lamellae sinuate, arcuate or subdecurrent, close to distant, narrow to broad, thick, waxy-appearing, dark purple (“Dark Heliotrope Gray”
FIG. 46. Basidiomata of L. amethysteo-occidentalis (GMM 1256).

or “Deep Vinaceous-Gray”). Stipe (15–)45–190 x (2–)6–22(–36) mm, equal, subclavate, clavate or slightly bulbous, dry, coarsely fibrillose; fibrils forming longitudinal striations, recurved scales or both, at times forming reticulations at maturity; ground color concolorous with pileus; striations brownish to reddish brown. Basal mycelium scant to copious, violet. Basidiospores light violaceous or white in mass.

MICROMORPHOLOGY—Pileipellis of tightly interwoven hyphae with occasional widely scattered ± perpendicular individual hyphae, not fasciculate; terminal cells 24–66.5 x 4–10 µm, filamentous or barrel-shaped, olive brown in mass; walls up to 0.5 µm thick, olive brown; contents hyaline, light olive brown or light yellowish brown. Pileus trama tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown to olive brown toward pileipellis. Lamellar trama parallel; hyphae mostly 3–11.5 µm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. Subhymenium morphologically undifferentiated. Basidia 33–61 x 7–11.5 µm, clavate, hyaline; stercigmata (2–)4, up to 8 µm long. Cheilocystidia 23–63.5 x 2.3–8.9 µm, filamentous, subclavate or subcapitate, abundant, thin-walled, hyaline. Basidiospores (excluding ornamentation) [60/4] (6.4–)7–9.2(–11) x (6.4–)7–8.7(–9.7) µm (f = 7.9–8.4 x 7.4–8.1 µm), Q = (0.93–)1–1.13(–1.16) (Q = 1.02–1.06), globose to subglobose, hyaline, echinulate; echinulae 0.9–1.4(–2.3) µm long, 1–1.5 µm wide at base, crowded; hilar appendix 1.3–2 µm long, prominent, truncate; plage present; contents occasionally uniguttulate. Basal mycelium hyphae mostly 3.5–10.5 µm diam., tightly interwoven, filamentous, hyaline.

SOMATIC CULTURE—MAT MORPHOLOGY (N = 3; Appendix B)—PDA: Radius at week 3 = 5–11 mm, week 6 = 7–23 mm; mat felty, thick, tightly interwoven, tightly appressed to agar surface, in time forming pruinose aerial layer away from plug, not translucent, at first bright violet, by week 6 violet coloration restricted to 2–3 mm band near margin, short aerial hyphae light grayish violet; margin 1–3 mm broad, thin, silky, becoming subfelty, even to uneven, light violet to white; plug often covered with white cottony hyphae, bright violet; hyphae morphologically undifferentiated, olivaceous brown in mass. MMN: Radius at week 3 = 11–19 mm, week 6 = 23–39 mm; mat silky,
subfelty or felty, thin to thick, interwoven, tightly appressed to agar surface, translucent, light violet, often with 1–3 concentric darker narrow bands; **margin** narrow, subfelty to silky, thin, entire to sulcate, light violet; **plug** concolorous with mat; **hyphae** morphologically undifferentiated. **MEA:** Radius at week 3 = 6–17 mm, week 6 = 10–33 mm; mat subfelty to felty, rarely silky, thin to thick, interwoven, tightly appressed to agar surface, translucent, white; **margin** not well differentiated, narrow, silky to subfelty, thin, even to undulate, white; **plug** white; **hyphae** morphologically undifferentiated.

**Habitat and Distribution**—Solitary to scattered, rarely caespitose, commonly encountered in temperate deciduous forests of eastern North America, probably in association with *Quercus* and *Fagus*. Not reported from other continents. A list of specimens examined is provided in Appendix A.

**Observations**—*Laccaria ochropurpurea* can be distinguished easily from all other *Laccaria* taxa by its large size, light violaceous brown to buff colored pileus and stipe, dark purple, thick, waxy lamellae, and globose to subglobose basidiospores. The only North American species that could be confused with it are *L. nobilis* and faded collections of *L. amethysteo-occidentalis* and *L. trullissata*. These taxa all differ in basidiospore shape and size. In addition, *L. amethysteo-occidentalis* differs in having numerous, large cheilocystidia, and *L. nobilis* has reddish brown to orange-brown, strongly scaly basidiomata. Collections of *L. trullissata* have elongate, finely roughened basidiospores and are restricted to sand or sandy soil with sand covering much of their stipe and adhering to their basidiomata.

Culture mat morphology of the five isolates utilized showed the least intraspecific variation of all the taxa examined. The slow growth rate and dark purple color on PDA were distinctive (fig. 44).

*Laccaria ochropurpurea* appears to be restricted to deciduous-coniferous forests of eastern North America. Lahaie (1981) reported that it does not occur in the coniferous boreal forests of eastern Canada. Several reports of *L. ochropurpurea* occurring in western North America have been noted (personal communications and herbarium specimens), but all of the specimens investigated during this study appeared to be either *L. amethysteo-occidentalis* or *L. nobilis*.

**Laccaria amethysteo-occidentalis** G. M. Mueller. Figures 46, 47, 58a, 59d.


**Macromorphology—Pileus** 10–65(–89) mm broad, obtuse, convex or plane, often depressed,
not striate when fresh, occasionally becoming slightly translucent-striate upon fading, finely fibrillo-lose, fibrillolose, or fibrillolose-scaly, hygrophanous, deep purple when fresh ("Taupe Brown," "Dull Indian Purple," "Dusky Dull Violet I," "Dark Hyssop Violet," or "Slate-Violet"), fading to vinaceous ("Dark Vinaceous-Drab," "Dark Vinaceous-Gray," or near "Wood Brown"), finally buff color (near "Pale Ochraceous-Salmon"); margin inrolled, decurved, or plane, entire to eroded; context thin, concolorous with pileus ("Dark Slate-Violet") with lighter gray purple to white areas intermixed ("Pale Bluish Lavender"). Lamellae sinuate to arcuate, subdistant to distant, narrow to broad, thick, occasionally waxy appearing, dark violaceous ("Deep Slate Violet" to "Slate-Violet"), fading (near "Lavender"). Stipe 18-115 × 3-12 mm, equal, subclavate or slightly bulbose, dry, strongly longitudinally striate, occasionally with recurved scales, purple ("Dark Slate Purple," "Dark Vinaceous Brown," or "Hay's Brown"), often with lighter violet or white scattered sectors ("Pale Bluish Lavender"); context solid, concolorous with pileus context. Basal mycelium violet ("Dark Slate-Purpale," "Deep Slate-Violet," or "Light Dull Bluish Violet"). Basidiospores white in mass.

MICROMORPHOLOGY—Pileipellis of tightly interwoven hyphae with scattered fascicles of ± perpendicular hyphae, fascicles composed of 15-30 hyphae; terminal cells of fascicular hyphae 28-73.5 × 7-16 µm, filamentous, clavate or broadly clavate; walls up to 0.5 µm thick, vinaceous brown; contents hyaline to light vinaceous brown. Pileus trama tightly interwoven, morphologically undifferentiated, hyaline, light vinaceous brown toward pileipellis. Lamellare trama parallel; hyphae mostly 3-11.5 µm diam., thin-walled, hyaline to light vinaceous brown; cells barrel-shaped. Subhymenium morphologically undifferentiated. Basidia 34-56 × 10-14.5 µm, clavate, hyaline, in young specimens vinaceous brown in mass; sterigmata 4, up to 9 µm long. Cheilocystidia 36.5-66.5 × 12-18.5 µm, subclavate to clavate, often abundant, thin-walled, hyaline. Basidiospores (excluding ornamentation) [81/6] 7.8-10.6 × 7-9.2 µm (S = 9-9.8 × 7.4-8.6 µm), Q = (1)-1.06-1.24(-1.36) (Q = 1.13-1.19), subglobose to broadly ellipsoid, rarely globose or ellipsoid, echinulate; echinulae 0.5-1.4 (-1.8) µm long, ≤ 1 µm wide at base, crowded, hilar appendix 1.3-2 µm long, prominent, truncate; plastid present; contents occasionally uniguttulate. Basal mycelium hyphae mostly 2.5-8 µm diam., hyaline, morphologically undifferentiated.

SOMATIC CULTURE MAT MORPHOLOGY (N = 1; GMM 1256)—Radius at week 3 < 3 mm, week 6 = 12-14 mm; mat felt, thick, tightly interwoven, tightly appressed to agar surface, not translucent, dark violet; margin up to 3 mm broad, subfelty, thick, tightly interwoven, thicker near plug, tightly appressed to agar surface, not translucent, moderate violet, darker near plug, lighter colored away from plug; margin 1-2 mm broad, subfelty to silky, not well differentiated from mat, even to serrate, light violet; plug dark violet; hyphae mostly morphologically undifferentiated, occasionally subcoralloid. MMN: Radius at week 3 = 14-22 mm, week 6 = 24-32 mm; mat felt, thick, tightly interwoven, thicker near plug, tightly appressed to agar surface, not translucent, moderate violet, darker near plug, lighter colored away from plug; margin 1-2 mm broad, subfelty to silky, not well differentiated from mat, even to serrate, light violet; plug moderate violet; hyphae same as in PDA. MEA: Radius at week 3 = 14-17 mm, week 6 = 23-27 mm; mat subfelty, thick, interwoven with a narrow (3 mm) thicker band at midpoint, tightly appressed to agar surface, translucent, white; margin 1-2 mm broad, subfelty, not well differentiated, entire to somewhat serrate, white; plug white; hyphae morphologically undifferentiated.

HABITAT AND DISTRIBUTION—Scattered to gregarious; under conifers (often Pseudotsuga menziesii [Mirb.] Franco) in western North America. A list of specimens examined is presented in Appendix A.

OBSERVATIONS—Laccaria amethysteo-occidentalis can be distinguished easily from the other two "purple" Laccaria taxa found in North America, L. amethystina and L. vinaceobrunnea, by its large size and deeper purple coloration of fresh basidiomata. Additionally, L. amethysteo-occidentalis differs from L. amethystina in having nonglobose, more finely echinulate basidiospores and from L. vinaceobrunnea in the arrangement of the hyphae composing the pileipellis. All three taxa have large cheilocystidia that form a sterile layer along the lamellar margin. This character can be used in many cases to separate barium material of L. amethysteo-occidentalis from L. nobilis.

Homokaryotic isolates of this taxon were intersterile with isolates of other tested taxa, including L. amethystina and L. vinaceobrunnea.

The above description of culture mat morphology was based on a single isolate, even though numerous attempts were made to culture from basidiomata of this species. The slow rate of growth and dark purple color of the culture mat on PDA were similar to that exhibited by cultures of L. ochropurpurea.

Laccaria amethysteo-occidentalis can be found
commonly in the coniferous forests of northwestern United States and western Canada. In contrast, *L. amethystina* appears to be restricted to the temperate deciduous or mixed coniferous–deciduous forests in eastern North America and Europe and the tropical *Quercus* forests of Central America and Colombia.

**Laccaria amethystina** Cooke. Figures 48, 49, 58b, 60a.

- *Laccaria amethystina* Cooke, Grevillea 12: 70. 1884.

**Macromorphology—Pileus** 5–32(–53) mm broad, convex to plane, often depressed, not striate or striate, occasionally translucent-striate when fresh, finely pruinose to fibulose, occasionally becoming finely fibulose-scaly, strongly hygrophanous, bright greyish purple when fresh (near "Heliotrope-Slate" or "Dark Slate-Violet 1"), fading to buff ("Vinaeous-Gray," "Pale Ochraceous-Buff," or "Light Buff"); margin inrolled to decurved, entire to undulate, occasionally eroded; context up to 3 mm thick at disc, tapering to margin, concolorous with surface. **Lamellae** sinuate to arcuate, subdistant to distant, up to 5 mm broad, thick, subconcolorous with pileus ("Heliotrope-Slate" or "Vinaeous-Drab"). **Stipe** 6–58(–70) × 1–7 mm, equal, subclavate or slightly bulbous, dry, fibulose, longitudinally striate, concolorous with pileus. **Basal mycelium** hygrophanous, violet becoming white. **Basidiospores** white or very pale violet in mass.

**Micromorphology—Pileipellis** of interwoven hyphae with scattered fascicles of ± perpendicular hyphae or with scattered individual ± perpendicular hyphae; fascicles composed of 10–20 hyphae; terminal cells of perpendicular hyphae 23–73.5 × 6.5–17 μm, filamentous, clavate, broadly clavate, capitate or ventricose-rostrate, walls up to 0.5 μm thick, vinaceous brown in young specimens, light yellowish brown in mature specimens; contents concolorous with hyphal walls. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown or vinaceous brown. **Lamellar trama** parallel to subparallel; hyphae mostly 3.5–16 μm diam., thin-walled hyaline to light yellowish brown or vinaceous brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** 30–64.5 × 8.5–14 μm, clavate, hyaline; sterigmata (2–)4, up to 10 μm long. **Cheilocystidia** 25.5–64(–92) × 4–12 μm, filamentous, clavate, broadly clavate or ventricose-rostrate, abundant, thin-walled hyaline. **Basidiospores** (excluding ornamentation) [160/11] 7–10 (–10.6) × (6.4–)7–10(–10.6) μm (x = 7.7–9 × 7.7–9 μm), Q = 1–1.07(–1.12) (Q = 1–1.02), globose, rarely subglobose, hyaline, echinulate; echinulae 1.4–2.8 μm long, > 1.2 μm wide at base; hilar appendix 1.3–2 μm, prominent, truncate; plege present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 3–12 μm diam., tightly interwoven, hyaline; cells filamentous to barrel-shaped.

**Habitat and Distribution—**Solitary to scattered, occasionally caespitose; associated with *Quercus* and *Fagus* in temperate deciduous or mixed deciduous–coniferous forests of eastern North America and Europe, under species of *Quercus* in Central America and northern South America.

**Observations—** *Laccaria amethystina* can be distinguished from the other North American "purple" *Laccaria* (*L. amethysteo-occidentalis* and *L. vinaecobrunnea*) by its small size and stature, bright greyish purple basidiomata that fade directly to buff, and globose, coarsely echinulate basidiospores.

No tissue cultures of *L. amethystina* were obtained during this study. Homokaryotic and reconstituted dikaryotic isolates were violet on MMN and PDA and grew moderately fast (radius at week 6 = ± 50 mm).

Homokaryotic isolates of *L. amethystina* were intersterile with isolates of other taxa, including
L. amethysteo-occidentalis and L. vinaceobrunnea. One North American isolate and one Swedish isolate of L. amethystina were included in RFLP analyses (Gardes et al., 1990, 1991a). These two isolates had different RFLP patterns, indicating that genetic divergence may have occurred between North American and Swedish populations of L. amethystina. However, the amount of intrapopulation variation is not known because only one isolate was examined from each population.

Mueller and Vellinga (1986, 1990) discussed the controversy that has persisted in the literature as to the correct name for this taxon. Most workers use the name L. amethystina; however, Murrill (1914), Dennis et al. (1960), and others have used L. amethystea (Bulliard) Murrill for this species. Cooke’s name is the earliest valid name for the taxon.

Laccaria gomezii Singer & G. M. Mueller (Mueller & Singer, 1988) grows sympatrically with L. amethystina in Costa Rica and Colombia. Collections of L. gomezii are characterized by having purple basidiomata that quickly turn vinaceous brown and then brown; adnate to decurrent, close to crowded, thin lamellae; and subglobose to ellipsoid basidiospores.

Laccaria amethystina appears to be restricted to temperate deciduous or mixed coniferous-deciduous forests in eastern North America and Europe and to Neotropical Quercus forests in Central America and Colombia. Lahaie (1981) did not report material of L. amethystina from boreal coniferous forests in Canada. Mueller (1991a) reported collections of this taxon from southern Sweden.

Laccaria vinaceobrunnea G. M. Mueller. Figures 50–52, 58c, 73c.


MACROMORPHOLOGY—Pileus 7–25(-42) mm broad, obtuse to convex, becoming plane to up-
lifted, often depressed, not striate or finely striate when wet, finely fibrillose, occasionally finely fibrillose-scaly, hygrophanous, when immature vinaceous (near "Purplish Lilac"), becoming vinaceous (Dark Vinaceous-Brown," "Hay's Brown," or "Vinaceous-Brown"), reddish brown ("Cameo Brown" to "Walnut Brown") then fading to orange-brown or buff ("Cinnamon-Rufous" to "Light Ochraceous-Buff"); margin decurved to plane, entire to eroded; context thin, tapering to margin, light vinaceous ("Light Brownish Vinaceous" to near "Vinaceous-Fawn"). Lamellae adnate to arcuate, subdistant to distant, broad, thick, waxy, purple ("Purplish Lilac" or "Purplish Vinaceous"). Stipe 7-56(-98) x 2-7 mm, equal, subclavate or slightly bulbous, dry, fibrillose, occasionally with recurved fibrils or finely striate, concolorous with pileus; fibrils ("Hazel" or "Vinaceous-Brown"). Basal mycelium violet. Basidiospores white in mass.

**Micromorphology**—Pileipellis of interwoven hyphae with very numerous ± perpendicular hyphae; terminal cells 32-78 x 7-14.5 μm, filamentous to clavate, hyaline to light vinaceous; walls up to 0.5 μm thick; contents hyaline. Pileus trama tightly interwoven, morphologically undifferentiated, hyaline to light olive brown in mass. Lamellar trama parallel; hyphae thin-walled, hyaline; cells barrel-shaped. Subhymenium morphologically undifferentiated. Basidia 33-60 x 8.5-9 μm, clavate, hyaline; sterigmata 4, up to 9 μm long. **Cheilocystidia** 31.5-92 x 5.5-11 μm, filamentous to clavate, abundant, hyaline. Basidiospores (excluding ornamentation) [60/4] (7-)7.4-10(-10.6) x 6.4-9.2(-9.7) (\(\bar{x} = 8.2-8.9 \times 7.3-8.3\) μm), \(Q = 1-1.26\) (\(\bar{Q} = 1.07-1.15\)), subglobule to broadly ellipsoid, occasionally globose, hyaline, echinulate; echinulae 0.5-1.8 μm long, \(\leq 1\) μm wide at base; hilar appendix 1.3-1.8 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. Basal mycelium hyphae mostly 3-8 mm diam., filamentous, tightly interwoven, hyaline.

**Habitat and Distribution**—Scattered to gregarious, often caespitose. Growing in sandy soil under Quercus virginiana Miller along the Gulf Coast. A list of specimens examined is provided in Appendix A.

**Observations**—Laccaria vinaceobrunnea can be distinguished from *L. amethystina* and *L. amethysteo-occidentalis* by habitat, coloration, unique pileipellis, and subglobule to broadly ellipsoid basidiospores. The abundant, large cheilocystidia is a reliable character to use in identifying herbarium collections that lack notes on micromorphology.

Homokaryotic isolates of *L. vinaceobrunnea* were intersterile with tested isolates of other taxa, including *L. amethystina* and *L. amethysteo-occidentalis*.

Material referable to this taxon has not been reported from outside of the Gulf Coast area. Although not yet reported, I would expect it to be found in northeastern Mexico.
Fig. 50. Basidiomata of *L. vinaceobrunnea* (GMM 1120).

Fig. 51. Basidiomata of *L. vinaceobrunnea* (GMM 2337).
Tentative Key to Laccaria for the World

The concepts for extralimital taxa included in the following key are based on an examination of type specimens and descriptions and a review of the literature. Only those taxa that I tentatively recognize are treated. The key is presented for two reasons: (1) to summarize the delimiting characters of the taxa involved and (2) to provide a framework that will facilitate further taxonomic work on the genus. It is not presented as a definitive statement on the genus for the world.

1. Lamellae gray; Japan .......................... 2
2. Basidia bisporic; basidiospores 8-11 µm diam., globose, echinulae 2-3 µm long; pileus grayish, almost black ........................................ L. nigra Hongo (p. 111)
3. Basidia tetrasporic; basidiospores 7.5-10 µm diam., globose, verruculous; pileus becoming mouse gray or subavellaneous .................................. L. murina Imai (p. 111)
4. Basidiospores large, 13.5-22 × 5.5-9.5 µm, elongate, smooth to finely roughened or finely echinulate (echinulae < 0.5 µm long); in sand or very sandy soil .................. 5
5. Basidiospores smaller (< 10.5 µm long), less elongate (Q ≤ 1.51), echinulae > 0.5 µm long; in sand or not in sand ........................................ 6
6. Basidiospores elongate (Q = 2.37-2.51), finely roughened, not echinulate; eastern North America ................................ L. trullissata (Ellis) Peck (p. 131)
7. Basidiospores less elongate (Q = 1.67-1.81); echinulae 0.2-0.5 µm long; northern Europe, rare in eastern North America .............................. L. maritima (Teod.) Singer ex Huhtinen (p. 107)
8. Lamellae bright violaceous or purple ........................................ 7
9. Lamellae pallid violaceous to vinaceous when young, fading to vinaceous flesh color ........ 13
10. Pileus bright violaceous, purple or grayish black when young and fresh .................. 8
11. Pileus fawn or buff color, often with violaceous tints .................................. 12
12. Pileus fuscosus black; lamellae purple to grayish lavender; stipe apex purple, base vinaceous brown;
cheilocystidia 30–40 × 2–6.5 μm, filamentous, numerous; New Zealand .......................................................... *L. violaceoniger* Stevenson (p. 133)

8. Basidiomata and lamellae bright violaceous or purple when young and fresh; cheilocystidia larger (up to 92 × 12 μm) clavate, numerous ......................................................... 9

9. Basidiospores globose; echinulae > 1 μm wide at base; basidiomata fading from amethyst to grayish to buff .................................................. *L. amethystina* Cooke (p. 86)

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Fig. 54. SEMs of basidiospores: a, *L. longipes* (A. Parker s.n.); b, *L. fraterna* (GMM 2126); c, *L. montana* (GMM 1813); d–f, *L. laccata* var. *pallidifolia* (GMM 1845); g, *L. pumila* (GMM 1956). Note differences in basidiospore size and shape. Scale lines = 1 μm.
9. Basidiospores subglobose to broadly ellipsoid; echinulae < 1 μm wide at base; basidiomata fading from amethyst to brown to buff ......................................................... 10
10. Basidiomata large (pileus 10–90 mm diam.), amethyst becoming vinaceous; pileipellis hyphae interwoven with scattered fascicles of perpendicular hyphae; western North America; under conifers ........................................... L. amethysteo-occidentalis G. M. Mueller (p. 86)
11. Basidiomata smaller (pileus 7–38[-65] mm diam.); amethyst to dark reddish purple, becoming reddish brown or vinaceous brown at maturity; associated with subtropical or tropical species of Quercus ................................................................. 11
11. Basidiomata violaceous, becoming vinaceous brown then reddish brown; lamellae adnate to arcuate,
FIG. 56. SEMs of basidiospores: a, L. bicolor (GMM 2027); b, L. bicolor (GMM 2038); c, L. trichodermophora (GMM 2306); d, e, L. nobilis (GMM 2048). Note relatively small basidiospore size. Scale line = 1 μm.

subdistant to distant; pileipellis hyphae interwoven with numerous large, individual, perpendicular hyphae; North America, Gulf Coast states ............... L. vinaceobrunnea G. M. Mueller (p. 133)
11. Basidiomata dark violet purple to dark reddish purple, becoming vinaceous brown; lamellae adnate to subdecurrent, crowded to close, thin; Costa Rica and Colombia .......................................................... L. gomezii Singer & G. M. Mueller (p. 99)
12. Lamellae dark purple, thick, waxy appearing; basidiomata large (pileus up to 60–120 mm diam.), violaceous buff when young and fresh, becoming buff; eastern North America ......................................................... L. ochropurpurea (Berk.) Peck (p. 114)
12. Lamellae lilac; basidiomata smaller, pileus fawn-colored with fulvous fibrils; New Zealand .......... L. lilacina Stevenson (p. 105)
13. Pileus dark purple-brown, fading to light purple-brown; stipes purplish brown at base; western Europe ......................................................... L. purpureobadia Reid (p. 123)
13. Pileus orange-brown, pinkish flesh color, reddish brown, light violaceous, or buff color; stipe ± concolorous ................................................................. 14
14. Pileus strongly radially fibrillose, buff with vinaceous tints; fibrils dark brown to black; margin often dentate to lacerate; New Zealand ......................................................... L. fibrillosa McNabb (p. 95)
14. Pileus not radially fibrillose, pinkish flesh color to reddish brown; margin entire to slightly undulate ............................................................ 15

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FIG. 57. SEMs of basidiospores: a, *L. maritima* (DAOM 159709); b–d, *L. trullissata* (GMM 1914). Note the differences in ornamentation and basidiospore shape. Scale line = 1 \( \mu m \).

15. Basidiomata violet when young, fading buff with only traces of violet remaining; basidiospores globose; New Zealand ................................................................. 16

16. Basidiomata orange-brown, pinkish flesh color or reddish brown; basidiospores subglobose to sub-ellipsoid; North America and Europe ................................................................. 17
Fig. 58. SEMs of basidiospores: a, *L. amethysteo-occidentalis* (E. Farwell 5015); b, *L. amethystina* (GMM 2237); c, *L. vinaceobrunnea* (GMM 2335); d, *L. ochropurpurea* (E. Farwell 5074). Note differences in basidiospore shape and echinulae length and width. Scale line = 1 μm.

16. Basidiospore ornamentation < 2 μm long .... *L. masonii* var. *brevispinosa* McNabb (p. 89)
16. Basidiospore ornamentation > 2 μm long .... *L. masonii* var. *masonii* Stevenson (p. 107)
17. Pileus 16–85 mm diam., often strongly scaly to squarrose; stipe large and robust (26–110[–160] × 4–10[–16] mm), strongly striate to reticulate; western North America and upper Great Lakes region ........................................... *L. nobilis* G. M. Mueller (p. 113)
17. Pileus 8–50[–70] mm, finely fibrillose to minutely scaly; stipe smaller ([23–]30–85[–130] × 3–6 [–10] mm), not strongly striate; western North America, upper Great Lakes region and Europe ....... *L. bicolor* (Maire) Orton (p. 88)
18. Basidia (3)4-sterigmate ........................................................................................................ 19
18. Basidia 2(3)-sterigmate .......................................................... 36
19. Basidiospores broadly ellipsoid to oblong ($\bar{x} = 1.24–1.6$); echinulae < 1 $\mu$m long .......... 20
19. Basidiospores globose to ellipsoid; echinulae > 1 $\mu$m long ...................................................... 22
20. Basidiospores $\bar{x} = 8.3–9 \times 5.6–6$ $\mu$m, oblong ($\bar{x} = 1.45–1.6$); mycelium at stipe base violet, fading to white; Gulf Coast states .................. *L. oblongospora* G. M. Mueller (p. 113)
20. Basidiospores $\bar{x} = 9–11.5 \times 6.7–8–(8.8)$ $\mu$m, ellipsoid ($\bar{x} = 1.24–1.34([-1.43])$; mycelium at stipe base white ............................................................................. 21
21. Stipe context flesh color, lacking purple stains at base of stipe; widely distributed ........................................... *L. proxima* (Boud.) Pat. (p. 119)
21. Stipe context purple toward base, often with purple stains at stipe base; southern Argentina and Chile .......................................................... *L. proximella* Singer (p. 120)
22. Mycelium at stipe base violaceous when fresh, becoming white with age; basidiospores small ($\bar{x} = 7–8.3[-9] \times 6–8$ $\mu$m) ........................................................................................................ 23
22. Mycelium at stipe base white from onset; basidiospores larger ($\bar{x} = 8.2–13$ $\mu$m long) (but see no. 32, *L. longipes*) .................................................................................. 26
23. Lamellae flesh color to pinkish flesh color; basal mycelium usually scant, hygrophanous; basidiomata orange-brown; pileipellis a trichodermium or of interwoven hyphae with numerous large fascicles of perpendiculal hyphae; southeastern United States, Mexico, Central America .......... 24
23. Lamellae light vinaceous, occasionally fading to pinkish color; basal mycelium copious; basidiomata pinkish flesh color to reddish brown; pileipellis hyphae interwoven with scattered fascicles of perpendiculal hyphae; western and central North America and Europe .................. 25
24. Cheilocystidia small, filamentous, present or absent; southeastern North America, Mexico, Central America .............................................................. *L. trichodermophora* G. M. Mueller (p. 130)
24. Cheilocystidia large and vesiculose (up to 9.5 $\mu$m diam.); Mexico ....................................................... *L. bullulifera* Singer (p. 90)
25. Pileus 16–85 mm diam., often strongly scaly to squarrose; stipe large and robust (26–110–[160] × 4–10[–16] mm), strongly striate to reticulate; western North America and upper Great Lakes region ............................................. *L. nobilis* G. M. Mueller (p. 113)
25. Pileus 8–50(–70) mm, finely fibrillose to minutely scaly; stipe smaller ([23]–30–85[–130] × 3–6 [–10] mm), not strongly striate; western North America, upper Great Lakes region and Europe .. *L. bicolor* (Maire) Orton (p. 88)
26. Pileus dark ochraceous brown, with light blue pruinace; USSR ................................................................. *L. chabinensis* Michal. (p. 92)
26. Pileus orange-brown, pinkish flesh color or vinaceous brown .......................................................................................................................... 27
27. Basidiospores relatively large ($\bar{x} = 9.4–12.6 \times 8.5–10.5$ $\mu$m); pileus striate; restricted to arctic, boreal, or alpine habitats ............................................................................. *L. montana* Singer (p. 110)
27. Basidiospores smaller ($\bar{x} \leq 9–[10]$ $\mu$m long); pileus not striate, finely striate or translucent-striate ........................................................................................................ 28
28. Basidiospores globose; echinulae > 1.5 $\mu$m long and $\geq 1.2$ $\mu$m wide at base ................................ 29
28. Basidiospores globose to ellipsoid; echinulae $\leq 1$ $\mu$m wide at base .................................................. 31
29. Stipe 12–25(–40) × 1–2 mm, concolorous with pileus; among mosses or not; eastern North America, Central and South America, Europe .................................................. *L. ohiensis* (Mont.) Singer (p. 115)
29. Stipe 20–70(–103) × 1–4 mm, darker than pileus; in moist areas, often among mosses (not *Sphagnum*); eastern North America or New Zealand .......... 30
30. Occurring in eastern North America ........................................................................................................ 30
30. Occurring in New Zealand ..................................................................................................................... 30
31. Pileus strongly translucent-striate; stipe 60–138(–165) mm long; growing among mosses, especially *Sphagnum*, usually in bogs ............................................................................. 32
31. Pileus not striate or striate, not strongly translucent-striate; stipe $\leq 65(–106)$ mm long; growing among mosses or not, not normally found in bogs; widely distributed ............................................................................. 34
32. Basidiospores $\bar{x} = 7.6–7.8 \times 6.8–7.2$ $\mu$m; North America ................................................................................................. *L. longipes* G. M. Mueller (p. 106)
32. Basidiospores $\bar{x} = 8–10$ $\mu$m long .............................................................................................................. 33
33. Basidiospores subglobose to broadly ellipsoid; Europe ............................................................................. *L. laccata* var. *moelleri* Singer (p. 108)
33. Basidiomers ellipsoid; south temperate forests of South America, Tierra del Fuego to Valdivian forests of Chile; under Notofagus ........................................... L. galericoides Singer (p. 97)
34. Basidiomers broadly ellipsoid to ellipsoid (Q = 1.2–1.3); rarely encountered ........................................... L. laccata (Scop.: Fr.) Cooke var. laccata (p. 103)
34. Basidiomers globose to very broadly ellipsoid (Q usually < 1.15) ........................................... 35
35. Pilei brownish vinaceous; Japan ........................................... L. vinaceovellanea Hongo (p. 131)
35. Pilei orange-brown to flesh color; common; North America and Europe ........................................... 36
36. Basidiomers < 11 μm diam. ........................................... 37
36. Basidiomers most > 11 μm diam. ........................................... 40
37. Pileus not striate, reddish tawny or rose tawny; under native European trees ........................................... L. impolita Vellinga & G. M. Mueller (p. 102)
37. Pileus striate, rusty red or light brown; under Eucalyptus and other Australasian trees ........................................... 38
38. Basidiomata light brown ........................................... L. canaliculata (Cooke & Massee) Pegler (p. 92)
38. Basidiomata rusty red; lamellae pink ........................................... 39
39. Pleurocystidia absent; widely distributed ........................................... L. fraterna (Cooke & Massee) Pegler (p. 96)
39. Pleurocystidia present; New Zealand ........................................... L. ohiensis var. paraphysata McNabb (p. 117)
40. Basidiomers 11–17 × 10–14.5 μm, subglobose to broadly ellipsoid (Q = 1.1–1.19); echinulae < 1.5 μm long; montane, boreal, or arctic habitats ........................................... L. pumila Fayod (p. 121)
40. Basidiomers 10–15 × 10–15 μm, globose, echinulae > 2 μm long ........................................... 41
41. Pileus striate, strongly undulate to distorted, orange-brown; North and South America, Europe, not commonly collected ........................................... L. tortilis (Bolt.) Cooke (p. 129)
41. Pileus not striate, reddish brown; Kew Gardens ........................................... L. nana Massee (p. 111)

Type Studies

Although this study dealt primarily with North American taxa of Laccaria, it was necessary to try to examine the type collections of all names that have been treated in the genus. When no type existed, a lectotype or neotype was designated. A representative specimen was designated when no type material or material suitable for neotypification was available or when an illustration was lectotypified.

To clarify circumscriptions and stabilize application of names in Laccaria, Mueller and Vellinga (1986, 1990) and Mueller (1987) designated neotypes in cases where names lacked type specimens but were generally accepted and whose identity could be determined by common usage (Korf, 1982a,b). This was done even in cases where an illustration was included in the protologue. The International Code of Botanical Nomenclature (Greuter et al., 1988), however, now explicitly states that an illustration is part of the original material and must be chosen as a lectotype if no specimen suitable for lectotypification is available (Art. 7.5). This rule holds even though the circumscription of a fungus name often cannot be adequately defined without information on micromorphological characters. Those proposed neotypes (Mueller, 1987) that are now superfluous because the designated lectotype (illustration) takes precedence have been redesignated as “representative specimens.” These specimens represent my interpretation of the name and are provided to fix the micromorphological characteristics of the epithet. Further clarification of the code regarding utilization of illustrations as lectotypes is needed because nomenclatural stability in the Agaricales, and other fungi, is often sacrificed by forcing workers to select illustrations as type specimens.

The importance of type studies was discussed by Ammirati and Övrebo (1979). Some of the reasons given were “... to establish species concepts and relationships, to determine synonomy, and ... for the development of a world-wide system of taxonomy for fleshy fungi” (Ammirati & Övrebo, 1979). Additionally, they mentioned the importance of making detailed macro- and micromorphological information on each type collection available for workers involved in general studies.

The following type descriptions are arranged alphabetically by the final epithet, specific or infraspecific. Unless noted under Commentary, the type collection consists of more than one basidioma and is in an adequate state of preservation.

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TYPE: Argentina, Neuquén, Parque Nacional de Nahuel Huapi, Camino a los Cántaros, 14 March 1959, Singer M1774 (BAFC!, holotype).

MACROMORPHOLOGY (Teste Singer, *ibid*.)—As in *L. tetraspora* var. scotica.

MICROMORPHOLOGY (Mihi)—*Lamellar trama* parallel; hyphae mostly 3.5–10 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. *Subhymenium* morphologically undif-
fertilized. Basidia (N = 15) 33–44 × 10–13 μm, clavate, hyaline; sterig mata 4, up to 8.5 μm long. Pleurocystidia lacking. Cheilocystidia not observed. Basidiospores (excluding ornamentation) (N = 30) 7–8.7(–9) × 7–8.7(–9.2) μm (x = 7.9 ± 0.6 × 7.8 ± 0.6 μm), Q = 1–1.05(–1.12) (Q = 1.01 ± 0.03), globose, occasionally subglobose, hyaline, echinulate; echinulae (0.9–1.4–1.8 μm long, crowded; hilar appendix 1.3–1.8 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. Basal mycelium hyphae mostly 3.5–8 μm diam., long-celled, morphologically undifferentiated, tightly interwoven, hyaline.

COMMENTARY.—The type collection is infested with an "Aspergillus-like" fungus, with numerous conidia and conidiophores present. Because of this, no observations on the arrangement of the pileipellis hyphae or morphology of cheilocystidia could be made. Singer (1967) separated this variety from L. tetraspora var. scotica on the smaller basidiospores of L. tetraspora var. aberrans, shorter basidiospore ornamentation, and difference in habitat. Laccaria tetraspora var. aberrans was found on humus while L. tetraspora var. scotica fruiting among Sphagnum.

This taxon is treated as a synonym of L. ohiensis.


MACROMORPHOLOGY (Teste Singer, ibid.)—Pileus 30–48 mm broad, convex, centrally depressed, glabrous, distinctly fibrillose-asperate under hand lens as in Hygrocybe minuta, slightly striate when moist, hygrophanous, uniform brownish rose color, fading to pale leather rose color when dehydrated; margin often crenulate-furrowed. Lamellae 5–6 mm broad, sinuate to decurrent, slightly serratate, often anastomosing and wrinkled, dull rose-colored, not as dull brownish color as in L. laccata var. anglica; lamellae wrinkled. Stipe 80–110 × 5–6.5 mm, equal or nearly so, fibrillose, longitudinally striate, brownish rose-colored ("brun fauve roussetre," Singer); striations very pale. Basal mycelium white. Basidiospores pure white in mass.

MICROMORPHOLOGY (Mihi)—Pileipellis of interwoven hyphae with widely scattered fascicles of ± perpendicular hyphae; fascicles usually composed of 5–15 hyphae; terminal cells of fascicular hyphae (N = 10) 37–55 × 6.5–13.5 μm, clavate to clavate; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. Pileus trama tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. Lamellar trama parallel; hyphae mostly 3–8 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. Subhymenium morphologically undifferentiated. Basidia (N = 15) 29–47 × 9–12.5 μm, clavate, hyaline; sterigmata 4, up to 9.5 μm long. Pleurocystidia lacking. Cheilocystidia (N = 10) 24.5–46 × (2–)3–5.5 μm, filamentous to subcapitate, occasionally strangulated, scattered, thin-walled, hyaline. Basidiospores (excluding ornamentation) (N = 30) (7–)7.8–10 × (7–)7.8–10 μm (x = 8.6 ± 0.8 × 8.6 ± 0.8 μm), Q = 1–1.05 (Q = 1 ± 0.1), globose, rarely subglobose, hyaline, echinulate; echinulae 1–1.4 μm long, crowded; hilar appendix 1.3–1.8 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. Basal mycelium hyphae mostly 3–7 μm diam., filamentous, tightly interwoven, hyaline.

COMMENTARY.—The macro- and micromorphology of this collection fit within the circumscription of L. laccata var. pallidifolia. Bon (1983) proposed L. affinis (Singer) Bon based on this holotype, but data obtained to date do not support the recognition of it as a discrete variety or species. Although homokaryotic isolates of Laccaria laccata var. pallidifolia from North America and Sweden are intersterile (Mueller, 1991c), morphological differences have not been uncovered to recognize separate taxa for these intersterile populations. Until evidence of morphological or molecular divergence is obtained, this taxon is treated as a synonym of L. laccata var. pallidifolia.

Agaricus alpestris Britzelmayr, Hymenomyc. Südbayern VIII: 4, fig. 442. 1894.

TYPE: Lacking.

MACROMORPHOLOGY (Teste Britzelmayr, ibid.)—Pileus fleshy; margin crenulate. Lamellae whitish or yellowish red-brown. Stipe bent.

MICROMORPHOLOGY (Teste Britzelmayr, ibid.)—Basidiospores 3–4 μm diam., white, yellowish. 

COMMENTARY.—The protologue stated that this taxon was similar to A. laccatus. The basidiospore dimensions, however, fall well outside the range of basidiospore size for Laccaria.
Laccaria altaica Singer, Bull. Soc. Mycol. France 83: 122. 1967. Figure 59c.


MACROMORPHOLOGY (Teste Singer, *ibid.*)—
Similar to *Laccaria echinospora* (Speg.) Singer.

MICROMORPHOLOGY (*Mihi*)—
Lamellar trama parallel; hyphae thin-walled, hyaline to light yellowish brown; cells barrel-shaped. Subhymenium morphologically undifferentiated. Basidia (*N* = 15) 38–62 × 11.5–16 µm, clavate, hyaline; sterigmata 2(–4), up to 11.5 µm long. Plectrocladia lacking. Cheloctidia not observed. Basidiospores (excluding ornamentation) (*N* = 30) (8.3–)11.5–14.5 (-15.6) × (8.3–)10–13.8 µm (*x* = 12.8 ± 1.5 × 11.5 ± 1 µm), *Q* = 1.12–(1.28) (*Q* = 1.12 ± 0.07), globose, subglobose, broadly ellipsoid or occasionally ellipsoidal, hyaline, echinulate; echinulae 0.3–1 µm long, crowded; hilar appendix 1.3–2 µm long, prominent, truncate; plage present; contents occasionally uniguttulate. Basal mycelium hyphae not present.

COMMENTARY—The name, without a description, was originally published by Singer (1949). Owing to the extremely poor condition of the type collection, with only a few gill fragments extant, no comments can be made concerning macro- and many micromorphological characters.

*Laccaria altaica* is a later homonym of *L. pumila* (Mueller & Vellinga, 1986).

Laccaria amethysteo-occidentalis G. M. Mueller, Mycotaxon 20: 103. 1984. Figure 59d.


MACROMORPHOLOGY (*Mihi*)—Pileus 10–33 mm broad (*x* = 20 mm), convex becoming plane, occasionally depressed, not striate, finely fibrillose to fibrillose, deep purple (“Taupe Brown” to “Dull Indian Purple”); margin decurved, entire; context purple (“Dark Slate-Violet”) with lighter gray-purple to white areas intermixed (“Pale Bluish Lavender”). Lamellae adnate to arcurate, distant, thick, < 5 mm broad, violaceous (“Deep Slate Violet” to “Slate-Violet”). Stipe 18–87 × 4–12 mm (*x* = 50 × 7.3 mm), equal or tapering toward apex, occasionally bulbous, dry, fibrillose, longitudinal- striate, purple (“Dark Slate-Purple,” “Dark Vi- naceous Brown,” or “Hay’s Brown”), often with lighter violet to white streaks (“Pale Bluish Lav- ender”); context solid, concolorous with pileus context. Basal mycelium violet (“Dark Slate-Purple” to “Deep Slate-Violet”). Basidiospores white in mass.

MICROMORPHOLOGY (*Mihi*)—Pileipellis of tightly interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles usually composed of 15–30 hyphae; terminal cells of fascicular hyphae (*N* = 10) 30–73.5 × 8–15 µm, filamentous to clavate, occasionally broadly clavate; walls up to 0.5 µm thick, vinaceous brown; contents hyaline to light vinaceous brown. Pileus trama tightly interwoven, morphologically undifferentiated, hyaline, light vinaceous brown toward pileipellis. Lamellar trama parallel; hyphae mostly 3–11.5 µm diam., thin-walled, hyaline to light vinaceous brown; cells barrel-shaped. Subhymenium morphologically undifferentiated. Basidia (*N* = 15) 36.5–50.5 × 9.5–15 µm, clavate, hyaline, vinaceous brown in mass; sterigmata 4, up to 8 µm long. Plectrocladia lacking. Chelocystidia lacking. Basidiospores (excluding ornamentation) (*N* = 30) 7.8–9.7 × 6–8.3 µm (*x* = 8.7 ± 0.6 × 7.3 ± 0.7 µm), *Q* = (1.05–)1.11–1.33(–1.36) (*Q* = 1.19 ± 0.08), subglobose to broadly ellipsoid, occasionally ellipsoid to amygdaliform, echinulate; echinulae 0.9–1.4 µm long, crowded; hilar appendix 1.3–2 µm long, prominent, truncate; plage present; contents occasionally uniguttulate. Basal mycelium hyphae mostly 2.5–6.5 µm diam., hyaline, morphologically undifferentiated.

SOMATIC CULTURE MAT MORPHOLOGY—See the description presented in the treatment of *L. amethysteco-occidentalis* in the section on North American taxa.

COMMENTARY—This taxon is treated in detail in the section on North American taxa.

Laccaria amethystina Cooke, Grevillea 12: 69–70. 1884. Figure 60a.


MACROMORPHOLOGY—Not provided.

MICROMORPHOLOGY (*Mihi*)—Pileipellis of interwoven hyphae with scattered ± perpendicular individual hyphae or small fascicles of 2–3 ± perpendicular individual hyphae; terminal hyphae 43–60 × 9–
16 µm, subclavate, clavate or strangulate, hyaline; walls up to 0.5 µm thick. Pileus trama tightly interwoven, morphologically undifferentiated, hyaline. Lamella trama parallel; hyphae 3–8 µm diam., thin-walled, hyaline; cells barrel-shaped. Subhymenium morphologically undifferentiated. Basidia 37–55 × 11–16 µm, clavate, hyaline; sterigmata 4, up to 11 µm long. Pleurocystidia lacking. Cheilocystidia 40–70 × 6–12 µm, filamentous, strangulate or subclavate, thin-walled, numerous, hyaline. Basidiospores (excluding ornamentation) (N = 30) (8.3–)8.7–9.7(-10) × 8.3–9.7(-10) µm (x = 9.2 ± 0.4 × 9.2 ± 0.4 µm), Q = 1–1.05 (Q = 1.01 ± 0.02), globose, echinulate; echinulae 1–1.8–(2.3) µm long, up to 1.2 µm wide at base; hilar appendix up to 1.4 µm long, prominent, truncate; plage present; contents occasionally uniguttulate.

COMMENTARY—The collection designated as neotype was selected from material requested from several herbaria. Original material or other col-
lections seen by Hudson were not located. As stated in Mueller and Vellinga (1990), the chosen collection fits Hudson’s protologue and was collected in England.

This taxon is treated in detail in the section on North American taxa.

**Laccaria lacata** var. anglica Singer, Bull. Soc. Mycol. France 83: 110-111. 1967. Figure 60b.

**TYPE:** England, Kent, Bedebury, National Pine Arboretum, 20 October 1960, Singer C3119 (BARF!, holotype).

**MACROMORPHOLOGY** (*Teste* Singer, *ibid.*)—*Pileus* 25-37 mm, convex, plane or depressed at disc, often umbonate, pellucid-striate when fresh, occasionally radially sulcate at margin, finely tomentose to tomentose-fibrillose, strongly hygrophanous, reddish brown, fading to pale beige or pale dull rose, finally to pale mouse; disc rust-red. *Lamellae* sinuate to adnate, occasionally subventricose, subcrowded, moderately broad, rose to dull rose. *Stipe* 45-100 × 2.8 mm, equal or tapering toward apex, tomentose, especially apically, hollow, subhygrophanous, brown to reddish brown. *Basal mycelium* pure white. *Basidiospores* pure white in mass.

**MICROMORPHOLOGY** (*Mihi*)—*Pileipellis* of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 10-20 hyphae; terminal cells of fascicular hyphae (N = 10) 41.5-53 × 7.5-14 μm, subclavate to clavate; walls up to 0.5 μm thick, light yellowish brown; contents hyaline to light yellowish brown. *Pileus trama* tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. *Lamellar trama* parallel to subparallel; hyphae mostly 3.5-9 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. *Subhymenium* morphologically undifferentiated. *Basidia* (N = 15) 30-44 × 8-14 μm, clavate, hyaline; sterigmata 4, up to 7 μm long. *Pleurocystidia* lacking. *Cheilocystidia* not observed. *Basidiospores* (excluding ornamentation) (N = 30) (7.4-)7.8-9.2(-9.7) × (7.4-)7.8-9.2(-9.7) μm (ξ = 8.4 ± 0.6 × 8.3 ± 0.6 μm), Q = 1-1.06 (Q = 1.01 ± 0.02), globose, occasionally subglobose, hyaline, echinulate; echinulae (l–1)1.4-1.8 μm long, crowded; hilar appendix 1.2-1.8 μm long, prominent, truncate; plaque present; contents occasionally uniguttulate. *Basal mycelium hyphae* mostly 4-10.5 μm diam., morphologically undifferentiated, tightly interwoven, hyaline; cells filamentous or barrel-shaped.

**COMMENTARY**—Although the basidiospore size and shape presented here fit the original circumscription, the length of basidiospore ornamentation observed in this study was larger than that reported by Singer (1967). Additionally, he reported numerous cheilocystidia (“cheilocystides et cystidioles nombreuses pres de l’arete, verforme, le plus souvent filamenteuses-subclavicules, simple ou fourches-ramifiees, 17-29 × 3-4, 7 μ”) that I did not observe.

This taxon is treated as a synonym of *L. lacata* var. pallidifolia.

**Agaricus bellus** Persoon, Synopsis Methodica Fungorum. p. 452. 1801.

**TYPE:** Lacking.


**COMMENTARY**—No authentic material of *A. bellus* could be found at L, LG, or GOET. Berkeley and Broome (1883) included this name in *Laccaria*, and other workers, including Rea (1922), concurred. Rea (1922) viewed this taxon as one with a dark yellow or golden pileus with darker squamules, a bright yellow stipe, and relatively small (7 × 5-7 μm), minutely warted basidiospores. Dennis et al. (1960) did not treat this taxon in their checklist. Based on the protologue, this taxon is not a *Laccaria*. Without micromorphological data, however, it is impossible to assign it to another genus.

**Laccaria lacata** var. bicolor Maire, Publ. Inst. Bot. Barcelona 3: 84. 1937. Figure 60c.

**TYPE:** Spain, Catalonia, Collado de Tosses, 7 October 1933, Maire s.n. (MPUL, holotype).


**COMMENTARY**—The single basidiocarp of the type collection is severely contaminated by an “*Aspergillus-like*” fungus. Because of distortion caused by the parasite, no micromorphological data could be obtained. My concept of the taxon is
based, therefore, on Maire's description and on the common usage of the name (Korf, 1982a,b). The following description is presented to illustrate my concept of the taxon.


**MACROMORPHOLOGY** (Mihi)—Pileus 12–43 mm broad, convex, often depressed, not striate, fibrillose-scaly, occasionally scaly, hygrophanous, pinkish flesh color ("Onion-skin Pink"), fading to ("Salmon-Buff"); margin undifferented, entire to undulate, becoming eroded. Lamellae adnate-arcuate, moderately distant, thick, light vinaceous to light pinkish flesh color ("Pale Purplish Vinaceous," "Pale Congo Pink," or "Light Congo Pink"). Stipe 48–120 × 3–10 mm, equal with bulbous base, occasionally slightly clavate, dry, fibrillose, longitudinal-striate, light pinkish flesh color ("Flesh Pink"); striations darker ("Cacao Brown" to "Pecan Brown"). Basal mycelium copious, hygrophanous, when fresh violet ("Pale Vinaceous-Lilac"), becoming white.

**MICROMORPHOLOGY** (Mihi)—Pileipellis of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 15–30 hyphae; terminal cells of fascicular hyphae (N = 10) 37–76 × (6–)10–17.5 μm, subclavate to clavate; walls up to 0.5 μm thick, light yellowish brown; contents hyaline to light yellowish brown. Pileus trama tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. Lamellar trama parallel; hyphae mostly 3.7–6 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. Subhymenium morphologically undifferentiated. Basidia (N = 15) 33–43.5 × 9.7–12 μm, clavate, hyaline; sterigmata 4, up to 6.4 μm long. Pleurocystidia lacking. Cheilocystidia (N = 10) 29–50 × 2.3–3.7 μm, filamentous to subclavate, abundant, hyaline. Basidiospores (excluding ornamentation) (N = 30) 7.8–8.3 × (6–)6.4–7.8 μm (x = 7.6 ± 0.4 × 7.1 ± 0.5 μm), Q = 1–1.16 (Q = 1.07 ± 0.05), subglobose to broadly ellipsoid, rarely globose, hyaline, echinulate; echinulae 0.9–1.8 μm long, crowded; hilar appendix 1.3–1.9 μm long, prominent, truncate; plaque present; contents occasionally uninigutulate. Basal mycelium hyphae mostly 5–9.8 μm diam., tightly interwoven, morphologically undifferentiated, hyaline.

**SOMATIC CULTURE MAT MORPHOLOGY** (representative specimen)—PDA: Radius at week 3 = 14–19 mm, week 6 = 23–30 mm; mat felty, thick, tightly interwoven, tightly appressed to agar surface, in time forming pruinose aerial layer away from plug, becoming furrowed because of irregular infolding near plug, not translucent, dark, bright violet, fading to light orange-brown, by week 6 violet only in 3–4 mm band near margin, most of mat light orange-brown; aerial hyphae light grayish violet; margin 1–2 mm broad, subfelty, thin, light violet; plug violet, becoming light orange-brown; hyphae mostly morphologically undifferentiated, occasionally irregularly swollen, purplish brown in mass. MMN: Radius at week 3 = 37–45 mm, week 6 = 58–64 mm; mat subfelty to silky, thin, loosely interwoven, tightly appressed to agar surface, translucent light violet, becoming buff-colored; margin 1–2 mm broad, subfelty to silky, thin, even to serratate, light violet; plug concolorous; hyphae morphologically undifferentiated. MEA: Radius at week 3 = 32–43 mm, week 6 = 68–76 mm; mat subfelty to felty near plug, thick, tightly interwoven, tightly appressed to agar surface, subtranslucent, white; margin subfelty, thin, loosely interwoven, uneven, white; plug white; hyphae undifferentiated.

**COMMENTARY**—This taxon is treated in detail in the section on North American taxa.

**Laccaria masonii** var. brevispinosa McNabb, New Zealand J. Bot. 10: 466–467. 1972. Figure 60d.

**TYPE**: New Zealand, Nelson, Lake Daniels track, 16 May 1969, McNabb PDD 29641 (PDD!, holotype).

**MACROMORPHOLOGY** (Teste McNabb, *ibid.*)—Pileus 5–35 mm broad, convex to plano-convex, occasionally plane at maturity, glabrous or minutely furfuraceous at disc, translucent striate at margin, hygrophanous, violaceous with buff tints when young, fading to buff at maturity. Lamellae adnexed to adnate, distant, thick, ≤ 4 mm broad, pallid violaceous when young, becoming pallid brownish pink, occasionally with faint violaceous tints, glaucous. Stipe up to 100 × 1–2.5 mm, 3–6 mm diam. at base, tough, dry, longitudinally fibrillose-sulcate, violaceous when young, becoming buff at base, finally buff except for violaceous tints at apex. Basal mycelium pallid violaceous. Basidiospores white in mass.

**MICROMORPHOLOGY** (Mihi)—Pileipellis of interwoven hyphae with scattered small fascicles of ± perpendicular hyphae; fascicles composed of 5–10 (−15) hyphae; terminal cells of fascicular hyphae

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(N = 10) 33–62 × 5.5–13 μm, filamentous, swollen, subclavate or clavate, light yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown; contents hyaline to moderate yellowish brown. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae 2.5–7 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 29–39 × 7.8–11.5 μm, clavate, hyaline; sterigmata 4, up to 6.5 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) 6–8.3(−9.2) × 6–8.3(−8.7) μm (|= 7.5 ± 0.8 × 7.2 ± 0.7 μm), Q = 1.13(−1.16) (|= 1.04 ± 0.05), globose to subglobose, occasionally broadly ellipsoid, hyaline, echinulate; echinulae 1.4–1.8(−2.3) μm long, crowded; hilar appendix 1.3–1.8 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 2.5–7.5(−15) μm diam., morphologically undifferentiated, tightly interwoven, hyaline.

**COMMENTARY**—Although the basidiospore shape and size fit the original circumscription, I measured the size of the ornamentation as slightly longer than McNabb (“spines 1.2–1.5 μm long”). Additionally, McNabb (1972) reported the presence of cystidia ("paraphyses numerous, simple or sparingly branched, filamentous, to 3 μm diam., projecting beyond basidium"). This discrepancy is probably due to the poor preservation of the collection. The specimens appear to have been overdried, and consequently the material did not rehydrate well. Because of PDD policy, only half of the type collection was sent on loan. Thus, the possibility exists that more variation is present in the complete type collection than is described above.


**TYPE:** Mexico, Popocatepetl, 21 August 1957, **Singer M1581** (Mich., holotype).

**MICROMORPHOLOGY** (Teste **Singer, ibid.**)—**Lamellar trama** parallel. **Basidia** 30–31 × 8.5–10 μm, 4-sterigmate. **Cheilocystidia** 14 × 9.3 μm, balloon-shaped to subglobose, hyaline. **Basidiospores** 7–9 × 6.3–7.7 μm (including ornamentation), globose to broadly ellipsoid, hyaline, echinulate; echinulae 0.3–0.9 μm long.

**COMMENTARY**—No material of this taxon could be located at **Mich.** Although validly published by **Singer and Moser** (1965), the full description was published earlier (**Singer, 1957**). **Aguirre-Acosta** and **Pérez-Silva** (1978) and **Montoya-Bello et al.** (1987) have included this taxon in their treatments of Mexican fungi.

This taxon appears to be most similar to **L. trichodermophora**. The large cheilocystidia and somewhat smaller basidioma size reported from collections of **L. bullulifera** delimit the two taxa. **Laccaria trichodermophora** has been reported from Mexico as **L. farinacea sensu** **Singer** (Aguirre-Acosta and Pérez-Silva, 1978; Montoya-Bello et al., 1987).

**Laccaria calospora** Singer, Sydowia 7: 7–8. 1973. Figure 61a.

**TYPE:** USA, Massachusetts, Waban, 21 June 1945, **Southwick s.n. (RHL, holotype).**

**MACROMORPHOLOGY** (**Teste** **Singer, ibid.**)—**Pileus** 15–26 mm broad, convex, becoming depressed or concave, finely fibrillose-asperate, hygrophanous, dingy purple-violet ("Vinaceous Purple") fading to dingy violaceous brown, then to buff color ("Fawn Color" to "Army Brown"); margin frequently sulate. **Lamellae** sinuate to arculate, many-ranked, distant, 2–3 mm broad, purplish ("Amaranth" or "Wild Aster"). **Stipe** 38–50 × 3–9 mm, tapering toward apex, fibrillose, striate above, concolorous with pileus. **Basidiospores** violaceous ("Pale Verbena Violet") in mass.

**MICROMORPHOLOGY** (**Mihi**)—**Pileipellis** of interwoven hyphae with numerous fascicles of ± perpendicular hyphae; fascicles composed of 10–20 hyphae; terminal cells of fascicular hyphae (N = 10) 32–69 × 8–11 μm, filamentous, clavate or capitate; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae mostly 4–11 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 32–46 × 8.5–13.5 μm, clavate, hyaline; sterigmata 4, up to 8.3 μm long. **Pleurocystidia** lacking. **Cheilocystidia** (N = 10) 36.5–64.5 × 5.5–8 μm, filamentous to subclavate, hyaline. **Basidiospores** (excluding ornamentation) (N = 30) 7.4–8.7 × 7–8.3
Representative basidiospores from type specimens: a, *L. calospora* (holotype); b, *A. canaliculata* (holotype); c, *L. chibinensis* (holotype); d, *L. laccata* var. *chilensis* (holotype). Scale line = 10 μm.

μm (x = 8 ± 0.4 x 7.7 ± 0.5 μm), Q = 1–1.12 (Q = 1.03 ± 0.04), globose to subglobose, rarely broadly ellipsoid, hyaline, echinulate; echinulae 1.4–2.3 μm long, crowded; hilar appendix 1.2–1.8 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. Basal mycelium hyphae mostly 3–12 μm diam., tightly interwoven, hyaline; cells filamentous to barrel-shaped.

COMMENTARY—Mueller and Vellinga (1986, 1990) have treated this taxon as a synonym of *L. amethystina*. Although the type collection of *L. calospora* was collected in Massachusetts, Singer (1973) also listed a collection from Colombia. There is considerable variability in size and color among the violet specimens of *Laccaria* that I have collected in Costa Rica and Colombia. Mueller
and Singer (1988) recently recognized one of these as a segregate species, L. gomezii. It is possible that additional taxa will be proposed when the Neotropical species of Laccaria are revised. Thus, although L. calospora is currently treated as a synonym, its status may change with the accumulation of additional data.

Agaricus (Laccaria) canaliculata Cooke & Massee, Grevillea 18: 2. 1889. Figure 61b.

TYPE: Australia, Brisbane, no date, Baily 710 (k!, holotype).

MACROMORPHOLOGY (Teste Cooke & Massee, ibid.)—Pileus submembranous, small, becoming umbilicate, velvety, radially sulcate, light brown; margin slightly crenulate. Lamellae adnate, subdistant, broad, flesh-colored, with a white dust. Stipe thin, equal, longitudinally fibrillose, becoming hollow, pallid.

MICROMORPHOLOGY (Mihi)—Pileipellis of interwoven hyphae; hyphae up to 10.5 μm diam.; cells undifferentiated to barrel-shaped; walls up to 0.5 μm thick, light yellowish brown; contents hyaline to light yellowish brown. Pileus trama tightly interwoven, undifferentiated, hyaline, light yellowish brown toward pileipellis. Lamellar trama parallel; hyphae 3.5–9 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. Subhymenium morphologically undifferentiated. Basidia (N = 15) 30.5–50.5 × 8–12.5 μm, clavate, hyaline; sterigmata 2–(4), up to 8 μm long. Pleurocystidia lacking. Chelioctydia not observed. Basidiospores (excluding ornamentation) (N = 30) 7.4–9.7 × (7–)7.4–9.2(–9.7) μm (± 8.6 ± 0.7 × 8.3 ± 0.7 μm), Q = 1–1.05(–1.17) (Q = 1.03 ± 0.05), globose to subglobose, rarely broadly ellipsoid, hyaline, echinulate; echinulae 0.5–1.4 (–1.8) μm long, crowded; hilar appendix 1.3–2 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. Basal mycelium hyphae mostly 8–20 μm diam., tightly interwoven, hyaline; cells barrel-shaped.

COMMENTARY—The type collection consists of a fragment from a single basidioma. Although Stevenson (1964) reported this taxon from New Zealand, McNabb (1972) stated that the material cited by Stevenson from New Zealand was referable to L. glabripes. McNabb’s description of the holotype states that the basidia were 4-sterigate. Likewise, May (1990) stated that he found the basidia in the type specimen to be 4-sterigate. Although I encountered a few 3- or 4-sterigate basidia, the majority of basidia bore two basidiospores. I agree with Pegler’s (1965) findings, therefore, and treat L. canaliculata as a bisterigate taxon.


TYPE: USA, Massachusetts, Blue Hills, 11 November 1943, Singer s.n. (FH, holotype).

MACROMORPHOLOGY (Teste Singer, ibid.)—Pileus 10–30 mm broad, convex, becoming depressed, glabrous, translucent-striate when fresh, strongly hygrophanous, reddish fawn color when fresh. Lamellae adnexed or adnate, subdistant, broad, dull rose color. Stipe 40–60 × 3–7 mm, equal or tapering toward the apex, finely fibrillose, farinaceous at apex, concolorous with pileus, apex often paler. Basal mycelium white. Basidiospores white in mass.

MICROMORPHOLOGY (Teste Singer, ibid.)—Basidia 40–47 × 9 μm, 4-sterigate. Chelioctydia not observed. Basidiospores 7.7–8.2 × 6.5–7.2 μm (including ornamentation); echinulae mostly 0.7 μm long.

COMMENTARY—The type collection could not be found at FH. The taxon is treated as a synonym of L. lacca var. lacca.

Laccaria chibinensis Michailovski, Mikologia Fitolpatologia 8: 523. 1974. Figure 61c.

TYPE: USSR, Murmansk, 5 July 1973, Michailovski s.n. (LE!, holotype).


MICROMORPHOLOGY (Mihi)—Pileipellis of interwoven hyphae with numerous scattered fascicles of ± perpendicular hyphae; fascicles composed of 10–30 hyphae; terminal cells of fascicular hyphae (N = 10) 23–53 × 5.5–10.5 μm, filamentous.
tous, swollen, subclavate, clavate or capitate, light yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae mostly 5–14 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. Basidia (N = 15) 31–42 × 7.5–11 μm, clavate, hyaline; sterigmata 4, up to 7 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. Basidiospores (excluding ornamentation) (N = 30) 6.4–7.8 × 6.4–8.3 μm (x = 7.3 ± 0.4 × 6.7 ± 0.5 μm), Q = 1–1.16 (Q = 1.08 ± 0.06), globose to subglobose, rarely broadly ellipsoid, hyaline, echinulate; echinulae (< 0.5–)1.4–1.8 μm long, crowded; hilar appendix 1.5–2.2 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 4–14 μm diam., tightly interwoven, hyaline; cells filamentous to barrel-shaped.

**COMMENTARY**—The type collection consists of a single basidioma. Singer (1967) reported infrequent cheilocystidia ("Cheilocystides et cystidioles tres esparses, filamenteuses ou versiformes").

This taxon is treated as a synonym of *L. laccata* var. *pallidifolia*.


**TYPE:** USA, New York, Warren Co., Bolton Landing, August, *Peck s.n.* (nys!, holotype).

**MACROMORPHOLOGY** (*Teste Peck, ibid.*)—**Pileus** 12–24 mm broad, convex, slightly planatelate to depressed at center, glabrous, innately fibrillose under hand lens, occasionally rivulose in age, hygrophanous, rose brown, fading to ochre when dehydrated. **Lamellae** adnate, subdistant, broad, dull rose-colored. **Stipe** at least 2.5–3 times longer than diam. of pileus, tapering slightly toward apex, slightly fibrillose with longitudinal innate fibrils, stuffed, concolorous with pileus or browner. **Basal mycelium** pure white.

**MICROMORPHOLOGY** (*Mihi*)—**Pileipellis** of interwoven hyphae with numerous fascicles of ± perpendicular loosely interwoven hyphae; fascicles composed of 5–10 hyphae; terminal cells of fascicular hyphae (N = 10) 30–55 × 4.5–9 μm, filamentous, subclavate, or rarely clavate; walls up to 0.5 μm thick, light yellowish brown; contents light yellowish brown. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae usually 3.5–10 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. Basidia (N = 15) 30–46 × 11–14.5 μm, clavate, hyaline; sterigmata 4, up to 9 μm long. **Pleurocystidia** lacking. **Cheilocystidia** (N = 10) 24–41 × 3–4.5 μm, filamentous to subcapitate, rarely branched, abundant, thin-walled, hy-
Fig. 62. Representative basidiospores from type specimens: a, C. laccata var. decurrens (holotype); b, A. (Clitocybe) echinosporus (holotype); c, L. fibrillosa (holotype); d, A. fraternus (holotype). Scale line = 10 μm.
Agaricus echinosporus Britzelmayr, Hymenomyc. Südbayern, Bot. Centralbl. 54: 5-6, figs. 512, 518. 1893.

**TYPE:** Lacking.

**MACROMORPHOLOGY** (Teste Britzelmayr, *ibid.*)—Pileus glabrous to slightly fibrillose, somewhat translucent, yellowish brown to brown. Lamellae adnate, crenate, whitish to brownish. Stipe solid, yellowish brown to brown, lighter underneath.

**MICROMORPHOLOGY** (Teste Britzelmayr, *ibid.*)—

**Basidiospores** 6-8 μm diam., angular spined.

**COMMENTARY**—The protologue stated that this taxon was similar to *A. echinosporus*. The basidiospore dimensions provided are much smaller than those of *A. echinosporus*, but without additional micromorphological data, it is impossible to tell if the dimensions provided are correct.

This taxon is treated as a synonym of *L. tortilis*.

**Agaricus (Clitocybe) echinosporus** Spegazzini, Anales Soc. Ci. Argentina 10: 123. 1880. Figure 62b.

**TYPE:** Argentina, La Baea, May 1880, *Spegazzini 2891* (UPS!, holotype).

**MACROMORPHOLOGY** (Teste Spegazzini, *ibid.*)—Pileus 5-10 mm broad, hemispheric, becoming plano-convex, centrally depressed, radially sulcate, pellucid, subhygrophanous, rose-colored; disc darker; margin straight, undulate to subcrenulate. Lamellae acute at apex, long decurrent, distant, thick, fleshy, up to 2.5 mm broad, entire, paler than pileus. Stipe 10-15 × 1.5-3.5 mm, subclavate, terete, fragile, fibrous-fleshy, rose-colored.

**MICROMORPHOLOGY** (Mihi)—Lamellar trama parallel; hyphae mostly 3-12 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 9) 39-64 x 10-14 μm, clavate, hyaline, not rehydrating well; stigermata 2, up to 11 μm long, stout. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) 11-13.8(-15.6) x 11-14.7 μm (μ = 12.5 ± 1.1 x 12.4 ± 1.0 μm), Q = 1-1.06 (Q = 1.01 ± 0.02), globose, occasionally subglobose, hyaline, echinulate; echinulae 2.3-3.2(-3.7) μm long, 1.3-1.8 μm wide at base, very crowded; hilar appendix 1.5-2.3 μm long, prominent, truncate; plage present; contents often uniguttulate.

**Laccaria fibrillosa** McNabb, New Zealand J. Bot. 10: 468-469. 1972. Figure 62c.


**MACROMORPHOLOGY** (Teste McNabb, *ibid.*)—Pileus 5-35 mm broad, strongly convex, becoming convex to plano-convex, umbonate, radially fibrillose, disc scurfy, fibers aggregated toward margin, hygrophanous, buff with faint violaceous tints, fibrils dark brown to brownish black at disc, paler toward margin; margin dentate to lacerate with age. Lamellae adnexed to adnate, distant, > 5 mm broad, pallid violaceous, becoming buff with age, glaucous. Stipe 20-70 × 1.5-3 mm, equal or slightly expanded at base, tough, dry, hollow, longitudinally fibrillose-striate, pallid, violaceous when young, fading to buff from base upward, at maturity buff with violaceous tints at extreme apex. Basal mycelium pallid violaceous. **Basidiospores** white in mass.

**MICROMORPHOLOGY** (Mihi)—Pileipellis composed of ± parallel, radially arranged hyphae cov-
ering disc, separating toward margin, yielding an appearance similar to spokes of a wheel; hyphal elements (N = 10) 33–60 × 6–10 μm; cells barrel-shaped; walls up to 0.5 μm thick, light yellowish brown; contents dark brown in mass. Pileus trama tightly interwoven, morphologically undifferentiated, hyaline to light yellowish brown. Lamellar trama parallel to subparallel; hyphae 2.5–9 μm diam., thin-walled, hyaline to yellowish brown; cells barrel-shaped. Subhymenium morphologically undifferentiated. Basidia (N = 15) 38.5–60 × 9–14 μm, clavate, hyaline; sterigmata 4, up to 7.5 μm long. Pleurocystidia lacking. Cheilocystidia not observed. Basidiospores (excluding ornamentation) (N = 30) 7–8.7 × 7–8.7 μm (x = 8.9 ± 0.6 × 8.8 ± 0.6 μm), Q = 1–1.12 (Q = 1.02 ± 0.04), globose to subglobose, hyaline, strongly echinulate; echinulae (1.4–)1.8–2.3(–2.8) μm long, not crowded; hilar appendix 1.4–2 μm long, prominent, truncate; plaque present; contents usually uniguttulate. Basal mycelium hyphae mostly 2.5–9 μm diam., morphologically undifferentiated, tightly interwoven, hyaline.

Commentary—McNabb (1972) reported that the pileipellis was "composed of unspecialized, repent, interwoven, thin-walled, clamped hyphae. . . ." This discrepancy may be due to poor rehydration in the material I examined. In longitudinal section, the arrangement of pileipellis hyphae was not discernible, so the data presented here were based on a whole mount of a scalp section. Owing to PDD policy, only half of the type collection was sent on loan. The possibility exists that more variation is present in the entire type collection than is described above.

Two taxa were included in Stevenson’s (1964) original description and illustration of L. masonii. The type collection consists entirely of basidiomata with glabrous pilei and the epithet L. masonii is restricted to that circumscription. McNabb (1972) proposed L. fibrillosa to represent the other taxon included in the protologue.


Type: lacking.

Commentary—No authentic material of this taxon was included with the material loaned from LE. In addition, I have not located a copy of the original description. At this time, therefore, I cannot make any comments regarding its affinities to other Laccaria.

Agaricus flavofuscus Britzelmayer, Hymenomyc. Südbayern VIII: 4, fig. 441. 1894.

Macromorphology (Teste Britzelmayer, ibid.)—Lamellae white or brownish.

Micromorphology (Teste Britzelmayer, ibid.)—Basidiospores smooth.

Commentary—The protologue stated that this taxon was very similar to A. alpestris and that it was difficult to tell the two apart. Based on the report that the basidiospores are smooth, A. flavofuscus cannot be a Laccaria. As stated in the Commentary under A. alpestris, I also do not treat that taxon as a Laccaria.

Agaricus fraternus Cooke & Massae, Grevillea 16: 31. 1887. Figure 62d.

Type: Australia, vic. Port Phillip, French No. 1 (k!, holotype).

Macromorphology (Teste Cooke & Massae, ibid.)—Pileus convex, depressed, umbilicate, smooth, glabrous, dark rusty-red. Lamellae broad, subdistant, adnate, rusty-red color. Stipe elongate, thin, tapering toward apex, glabrous, hollow, concolorous with pileus.

Micromorphology (Mihi)—Pileipellis of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 10–20 hyphae; individual hyphae not discernable, dark yellowish brown in mass. Pileus trama tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. Lamellar trama parallel; hyphae 3–10 μm diam., thin-walled, hyaline to light yellowish brown. Subhymenium morphologically undifferentiated. Basidia (N = 15) 29–44 × 8–12 μm, clavate, hyaline; sterigmata 2, up to 11 μm long, stout. Pleurocystidia lacking. Cheilocystidia not observed. Basidiospores (excluding ornamentation) (N = 30) (8.3–)9.2–11(–11.5) × 8.7–10.6(–11.5) μm (x = 9.9 ± 0.7 × 9.9 ± 0.7 μm), Q = (0.95–)1–1.06(–1.09) (Q = 1.01 ± 0.03), globose to subglobose, hyaline, echinulate; echinulae (0.9–)1.4–1.8 μm long, crowded; hilar appendix 1.3–2.8 μm long, prominent, truncate; plaque present; contents often uniguttulate.

Commentary—The type collection consists of a fragment from one pileus and a short segment of a stipe. Individual hyphae of the pileipellis were not discernable because of poor rehydration.
Tom W. May (University of Melbourne, pers. comm.) reports the finding of a potentially paratypic collection at MEL that better fits the protologue but that is not contaxic with the type specimen housed at k. It has been assumed that the report of ellipsoidal basidiospores in the original diagnosis of A. fraternus probably referred to another collection on the type sheet at k that was collected in New Zealand (Pegler, 1965; Mueller & Vellinga, 1986). If the collection housed at MEL is lectotypified, A. fraternus would not fit into the generic circumscription of Laccaria and the correct basionym for the taxon treated here would be N. goossensiae.

This taxon is treated in detail in the section on North American taxa.

**Laccaria galerinoides** Singer in Singer and Moser, Mycopath. Mycol. Appl. 26: 147–148. 1965. Figure 63a.

**TYPE:** Chile, Valdivia, Cordillera Pelada, 930–1000 m alt., 28 March 1963, Singer M3212 (BACF!, holotype).


**MICROMORPHOLOGY** (*Mihi*)—**Pileipellis** of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 10–20 hyphae; terminal cells of fascicular hyphae (N = 10) 37–57.5 × 6.5–12 μm, filamentous, subclavate or rarely clavate; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellae trama** parallel to subparallel; hyphae mostly 4–19 μm diam., thin-walled, hyaline to light yellowish brown. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 29–40 × 9–11 μm, clavate, hyaline; sterigmata 4, up to 6.5 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) 7.4–9.7–(10) × 5.5–7.8 μm (*= 8.5 ± 0.7 × 6.3 ± 0.6 μm), Q = 1.16–1.52 (*= 1.34 ± 0.08), ellipsoid to amygdaliform, rarely subglobose, hyaline, echinulate; echinulae 0.9–1.4(–1.8) μm long, not crowded; hilar appendix 1.5–2.3 μm long, very prominent, truncate; pleurocytic, contents occasionally uniguttulate.

**COMMENTARY**—The type collection consists of a single basidioma lacking the stipit base. The basidiospores observed were larger than those reported by Singer (Singer & Moser, 1965) ("sporis 7–8 × 6,8 μm"). In his unpublished notes on this specimen, however, Singer gives the basidiospore size as 6.8–10 × 5–7.5 μm including echinulae. Additionally, Singer (Singer & Moser, 1965) reported sparse cheilocystidia ("cheilocystis sphericus, ad nec non prope aciem visis, hyalinius, ± 2,5 μ latis").

I have collected this taxon from the type locality as well as additional locations in southern Chile and Tierra del Fuego. My findings fit those given for the taxon by Horak (1979). Although Singer (1986) placed L. galerinoides in its own stirs, this does not appear justified, based on my study of the type and the subsequent material examined. See observations under L. longipes in the section on North American taxa for additional data.

**Laccaria laccata** var. gibba Singer, Beih. Nova Hedwigia 29: 27. 1969. Figure 63b.

**TYPE:** Chile, Valdivia, Cordillera Pelada, 6 May 1967, Singer M6738 (SGO!, holotype).

**MACROMORPHOLOGY** (*Teste Singer, ibid.*)—**Pileus** 10–16 mm broad, convex, becoming plane, umbonate, glabrous, when dry with innatelyapressed fibers, radially pellucid-striate, sulcate, hygrophanous, reddish brown (between 14 A 11 and 5 C 11 M&P); margin light flesh color (11 C 7 and 12 E 8 M&P). **Lamellae** adnate, adnate-decurrent, or decurrent, distant, broad, rose-colored (between 3 A 10 and 9 A 6 M&P). **Stipe** 45–50 × 2–2.5 mm, equal or narrowed at apex, glabrous when moist, hygrophanous, dark red (6 J 12 M&P); apex lighter in color. **Basal mycelium** white.

**MICROMORPHOLOGY** (*Mihi*)—**Pileipellis** of interwoven hyphae, no fascicles of hyphae observed; terminal hyphal cells (N = 10) 38–67 × 7–18 μm, subclavate to clavate, light yellowish brown in

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mass; walls up to 0.5 \( \mu m \) thick, light yellowish brown; contents hyaline. Pileus trama tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. Lamellar trama parallel; hyphae thin-walled, hyaline to light yellowish brown. Subhymenium morphologically undifferentiated. Basidia (N = 15) 29–48 \( \times \) 7.5–11 \( \mu m \), clavate, hyaline; sterigmata (2–)4, up to 7 \( \mu m \) long. Pleurocystidia lacking. Cheilocystidia not observed. Basidiospores (excluding ornamentation) (N = 30) 7–8.7 \( \times \) (5–)6–7.4 \( \mu m \) (\( \bar{x} = 7.8 \pm 0.5 \times 6.3 \pm 0.5 \mu m \)), \( Q = 1.08–1.35 \) (–1.38) (\( \bar{Q} = 1.25 \pm 0.07 \)), occasionally subglobose, usually broadly ellipsoid to ellipsoid, hyaline, echinulate; echinulae 0.9–1.8(–2.3) \( \mu m \) long, not crowded; hilar appendix 1.3–1.8 \( \mu m \) long.
prominent, truncate; plage present; contents occasionally uniguttulate.

COMMENTARY—The type collection consists of a single pileus and a segment of the stipe without the base. Singer (1969) reported shorter basidiospore ornamentation ("spinulis 0.3–0.9 μ projicientibus") than presented here. As the specimen lacked lamellar margins, no observation of cheilocystidia was possible. Singer (1969) reported the cystidia as "inconspicuis subfilamentosis consistente."

This taxon is treated as a synonym of L. laccata var. laccata.

**Laccaria glabripes** McNabb, New Zealand J. Bot. 10: 477–478. 1972. Figure 63c.


**MACROMORPHOLOGY** (*Teste McNabb, ibid.*)—

**Pileus** 5–25(–35) mm broad, convex, becoming plano-convex, dry, distant, reflexed reddish. Spore colorous not pink, var. locystidia lacked. Terwoven iospores mostly 2–12 μm diam., tightly interwoven, hyaline; cells barrel-shaped.

**COMMENTARY**—Owing to PDD policy, only half of the type collection was sent on loan. The possibility exists that more variation is present in the complete type collection than is described above.

Collections referable to *L. striatula* were treated as *L. glabripes* in my dissertation (Mueller, 1982). Aguierre-Acosta and Perez-Silva (1978) reported *L. glabripes* from Mexico, but I believe that their material is referable to *L. striatula*. As mentioned in the Commentary under *A. canaliculata*, T. W. May (1990, pers. comm.) treats *L. glabripes* as a synonym of *L. canaliculata*. As Pegler (1965) and I found the type of *L. canaliculata* to have 2-steregimate basidia, I treat the two taxa as separate species, *L. glabripes* and *L. canaliculata*.


TYPE: USA, Connecticut, no date, Curtis 5546 (collected by C. Wright) (k!, holotype).

**MACROMORPHOLOGY** (*Teste Berkeley & Curtis, ibid.*)—

**Pileus** 25 mm broad, convex, thin, pubescent, pale rufous; margin incurved. Lamellae adnate, subdistant, white. Stipe 50 × 6 mm, solid, concolorous with pileus.

**COMMENTARY**—The type collection consists of one very moldy basidiocarp. No micromorphological observations could be obtained, and the original description does not include micromorphological data. The protologue stated that *A. glaucipes* was allied to *A. laccata*, and the epithet is treated as a synonym of *L. laccata* var. *laccata*.

**Laccaria gomezii** Singer & G. M. Mueller in Mueller and Singer, Mycotaxon 33: 224–225. 1988. Figure 63d.

TYPE: Costa Rica, Cartago Prov., along Panamerican Highway, km 55, La Chonta, 2800 m, under *Quercus* and *Magnolia*. September 1982, Gómez 18443 (f!, holotype).

**MACROMORPHOLOGY** (*Teste R. Singer, unpubl. notes*)—

**Pileus** 30 mm broad (when dried), convex with a deep umbilicus, squarrose in depression,
finely fibrillosque-squamulose or squarrose on the margin, not rimose or strongly radially fibrillosque, light violet suffused with chocolate brown, dried uniformly "blondine" to "canbaak" (M&P). Lamellae adnate-subdecurent, close, moderately broad, violet, somewhat whitish pulverulent under a lens when dry. Stipe 80 × 3–4 mm, pubescent to occasionally squamulose at apex, longitudinally sulcate when dry, coarsely woolly-strigose by the dried basal mycelium, appearing hispid in part and less distinctly violet than pileus. Context dirty white; odor and taste not annotated.

Micromorphology (Mihi)—Pileipellis of tightly interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 10–30 hyphae; terminal cells of fascicular hyphae 12–15 μm diam., filamentous to subclavate, hyaline; walls up to 0.5 μm thick. Pileus trama tightly

Fig. 64. Representative basidiospores from type specimens: a, Naucoria goossensiae (holotype); b, C. tortilis var. gracilis (holotype); c, L. laccata var. intermedia (holotype); d, A. laccatus (neotype). Scale line = 10 μm.
interwoven, morphologically undifferentiated, hyaline. Lamellar trama parallel to subparallel; hyphae mostly 4–8 μm diam., thin-walled, hyaline. Subhymenium morphologically undifferentiated. Basidia 35–43 × 9–12 μm, clavate, hyaline; sterigmata 4, up to 10 μm long. Pleurocystidia lacking. Cheilocystidia 45–80 × 6–9 μm, subclavate, abundant, forming an early sterile layer, thin-walled, hyaline. Basidiospores (excluding ornamentation) (N = 30) 7.8–9.3 × 7–7.8 μm (x = 8.7 ± 0.5 × 7.6 ± 0.4 μm), Q = 1.06–1.29 (Q = 1.14 ± 0.06), subglobose to broadly ellipsoid, rarely ellipsoid, hyaline, echinulate; echinulae 1–2.5 μm, ≤1 μm wide at base, crowded; hilar appendix 1.3–2 μm long, prominent, truncate; contents occasionally uniguttulate. Caucocybe 34–65 × 7–14 μm, subclavate, clavate or strangulate, thin-walled, hyaline to light vinaceous brown, formed from recurved surface hyphae, scattered or clustered in small groups at apex of stipe, absent or very infrequent below.

COMMENTARY—Specimens of this taxon have been collected in Costa Rica and Colombia. Laccaria gomezii occurs sympatrically with L. amethystina, with which it is morphologically similar. The two taxa are distinguished by basidioma color, lamellar thickness and attachment, and basidiospore shape. See Observations under L. amethystina in the section under North American taxa and Mueller and Singer (1988) for additional information.


TYPE: Zaïre, Ori, Noika, May 1926, Goossens 558 (brt, holotype).

MACROMORPHOLOGY (Teste Beeli, ibid.)—Pileus 25–35 mm broad, convex to umbilicate, glabrous, brownish rust color; margin incurved. Lamellae adnate or free, up to 7 mm broad, brownish red color. Stipe 45 × 4–5 mm, cylindrical, thickened at base, glabrous, hollow, concolorous with pileus.

MICROMORPHOLOGY (Mihi)—Pileipellis of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; terminal cells of fascicular hyphae (N = 5) 39–67 × 10–13 μm, filamentous to subclavate, not rehydrating well; walls up to 0.5 μm thick, light yellowish brown; contents hyaline to light yellowish brown. Pileus trama tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. Lamellar trama parallel; hyphae 2.5–10 (–16) μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. Subhymenium morphologically undifferentiated. Basidia (N = 15) 28–44 × 9–12.5 μm, clavate, hyaline; sterigmata 2(–4), up to 14 μm long. Pleurocystidia lacking. Cheilocystidia not observed. Basidiospores (excluding ornamentation) (N = 30) (7.8–)8.7–11 (11–15.5) × (7.4–7.8)–10 μm (x = 9.9 ± 0.9 × 8.9 ± 0.7 μm), Q = 1.04–1.2 (1–1.22) (Q = 1.11 ± 0.06), subglobose, broadly ellipsoid or broadly amygdaliform, echinulate; echinulae 0.3–1.5 μm long, crowded; hilar appendix 1.3–2.5 μm long, prominent, truncate; plaque present; contents occasionally uniguttulate. Basal mycelium hyphae mostly 4–13 μm diam., hyaline, light yellowish brown in mass; cells barrel-shaped.

COMMENTARY—This taxon is treated as a synonym of L. fratera but see Observations under L. fratera.

TYPE: USA, Idaho, Juliet, May 1943, W. B. Gruber 26 (MICH!, holotype).

COMMENTARY—Singer (1949) placed this taxon in Laccaria. Micromorphological analysis of this collection, however, revealed the presence of very elongate, smooth basidiospores. I agree with Bigelow and Smith (1973), therefore, that this collection does not belong in Laccaria but belongs in the monotypic genus Cantharocybe Bigelow and Smith.


TYPE: Lacking.

MACROMORPHOLOGY (Teste Scopoli, ibid.)—Pileus convex, dry, filamentous. Lamellae free, abundant. Stipe long, glabrous, hollow.

COMMENTARY—Fries (1836–1838) stated that this taxon showed affinities to A. pachyphylitus Fries, which showed affinities to A. laccatus. Both of these taxa are treated as synonyms of L. laccata.


TYPE: Cuba, Wright no. 12 (k!, holotype).

COMMENTARY—The original description stated that the basidiospores are oblong and not subglobose as in C. laccata. Micromorphological analysis of this collection revealed the presence of subfusiform, smooth basidiospores. Basidiospore shape and lack of ornamentation indicate that this collection is clearly not a Laccaria.


TYPE: (CAG, holotype).

MACROMORPHOLOGY (Teste Ballero & Contu, 1989)—Pileus 10–40 mm diam., fleshy, convex, depressed, umbilicate, dry, squamulose-areolate at disc, elsewhere tomentose, not striate, reddish tawny to rose tawny, then ochraceous; margin involute. Lamellae adnate to decurrent, distant, thick, entire to slightly denticulate, concolorous with pileus. Stipe 40–60 × 5–8 mm, cylindric to subclavate, rarely subradicate, usually thinner at apex, fibrillose striate, concolorous; basal mycelium white. Basidiospores white in mass.

MICROMORPHOLOGY (Teste Ballero & Contu, 1989)—Pileipellis a trichoderm or subpalisade; hyphae clavate, pigment(s) vacuolate or membranous. Lamellar trama regular. Basidia bisterigate. Pleurocystidia none. Cheilocystidia filamentous or subclavate. Basidiospores 8–12 μm diam., globose, hyaline, inamylloid; echinulae 1.3–1.8(–2) μm high, conic, distant. Clamp connections numerous.

COMMENTARY—Mueller and Vellinga (1990) proposed this epithet for the taxon described by Ballero and Contu (1989) as L. singeri (non L. singeri M. V. Locquin & B. M. Sarwal). According to Ballero and Contu (1989), this taxon can be differentiated from L. fraterna by the more robust stature, squamulose-areolate, astriate pilei, fibrillo-striate stipe, more coarsely echinulate basidiospores, arrangement of the pileipellis hyphae, and association with north temperate trees.

Agaricus (Clitocybe) incongruus Berkeley, J. Bot. (Hooker) 2: 48. 1850.


MACROMORPHOLOGY (Teste Berkeley, ibid.)—Pileus 31 mm broad, umbilicate, smooth, dry, cinereous-blue; margin undulate; context white. Lamellae 150 × 12 mm, subclavate, slightly fibrillose, hollow, concolorous with pileus.
COMMENTSARY — The type collection consists of a single stipe with an attached fragment of the pileus. Virtually no hymenial material was available for micromorphological analysis, and the protologue does not include micromorphological data. Only a few basidiospores were found in the examined slides mounts, and these were nodulose, not echinulate. Although Berkeley (1850) considered it "[a] very curious species, resembling somewhat the amethyst form of *A. laccatus*, and perhaps as nearly allied to that species as to any described," it is not a *Laccaria* and probably belongs in the Entolomataceae.

*Laccaria laccata* var. *intermedia* Singer, Pl. Syst. Evol. 126: 368–369. 1977. Figure 64c.


MACROMORPHOLOGY (*Teste Singer, ibid.*) — Pileus 10–24 mm broad, convex, soon becoming plane to centrally depressed, when fresh glabrous or subglabrous, fibrous to filamentous when dried, strongly hygrophanous, red-brown, flesh-colored, or pallid (e.g., 11 B 6 to 11 C 6, M&P); disc subtomentose to tomentose, darker red-brown or more sordid-rose than pileus; margin translucent-striate or sulcate. Lamellae adnate to decurrent, sub-crowded to subdistant, moderately broad, flesh-rose to dull flesh-colored. Stipe 30–62 × 1.8–5.8 mm, equal or thickened at base, glabrous, becoming coarse-fibrous and rough, hygrophanous, concolorous with pileus or darker brown along basal half. Basal mycelium white. Basidiospores white in mass.

MICROMORPHOLOGY (*Mihi*) — Pileipellis of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 15–30 hyphae; terminal cells of fascicular hyphae (*N* = 10) 33–50.5 × 6–9 μm, filamentous to subclavate, light yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. Pileus trama tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. Lamellar trama parallel, hyphae 3–12 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. Subhymenium undifferentiated. Basidia (*N* = 15) 35–48.5 × 8.5–13 μm, clavate, hyaline; sterigmata (2–4), up to 8 μm long. Pleurocystidia lacking. Cheilocystidia (*N* = 10) 31–47 × 3–7.5 μm, filamentous to stran-
gulate, hyaline. Basidiospores (excluding ornamentation) (*N* = 30) (6.4–7.4 × 10–13) × (6.4–7–10–12.4) μm (μ = 8.9 ± 1.4 × 8.6 ± 1.3 μm, Q = 0.95–1.18–(1.28) (Q = 1.04 ± 0.08), globose, subglobose, or broadly ellipsoid, hyaline, echinulate; echinulae 1.4–1.8–(2.3) μm long, not crowded; hilar appendix 1.3–2 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. Basal mycelium hyphal mostly 3–14 μm diam., tightly interwoven, hyaline; cells barrel-shaped.

COMMENTSARY — The basidiospore echinulae were longer than reported by Singer (1977) ("0.7–1.3 μm hoch ist, selten 1.5 μm erreicht").

This taxon is treated as a synonym of *L. laccata* var. *pallidifolia*.


TYPE: Goossens 859, Zaire, Binga, December 1929 (holotype).

COMMENTSARY — Micromorphological analysis of this collection revealed the presence of strongly reticulate, amyloid basidiospores. I agree with Heinemann (1964), therefore, that this collection is a *Lactarius*, not a *Laccaria*.

*Agaricus laccatus* Scopoli, Flora Carniolica 2: 444. 1772. Figure 64d.


MACROMORPHOLOGY (*Teste Singer, 1967*) — Pileus (6–)15–31 mm broad, convex becoming plane, often slightly depressed, slightly striate, finely fibrillose, hygrophanous, reddish brown becoming pale ochre when dry. Lamellae adnate to adnate-subdecurrent, moderately distant, broad, pale, dull reddish color, white from basidiospores when dry. Stipe 40–60–(80) × 3–5 mm, slightly clavate, fibrous with innate fibrils, concolorous with lamellae at apex, brown toward base. Basal mycelium white. Basidiospores white in mass. Context concolorous with surface when moist, becoming white; odor very weak; taste sweet.

MICROMORPHOLOGY (*Mihi*) — Pileipellis of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 15–30 hyphae; terminal cells of fascicular hyphae; cell wall of terminal cells of fascicular hyphae 42–80
× 8–11 μm, filamentous, subclavate or capitate, light yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel, hyphae 3–12 μm diam., thin-walled, hyaline; cells barrel-shaped. **Subhymenium** undifferentiated. **Basidia** 35–45 × 14–16 μm, clavate, hyaline; sterigmata 4, up to 12 μm long. **Pleurocystidia** lacking. **Cheilocystidia** 47–60 × 2.5–5 μm, filamentous, common, hyaline. **Basidiospores** (excluding ornamentation) (N = 30) 8.7–9.2 (–11) × 6.4–7.8 (–8.3) μm (x̄ = 9.2 ± 0.5 × 7.1 ± 0.5), Q = (1.11–1.18–1.46 (Q = 1.3 ± 0.08), subglobose to ellipsoid, hyaline, echinulate; echinulae 1–1.8 (–2.3) μm long, ≤ 1 μm wide at base; hilar appendix up to 2 μm long, prominent, truncate; plaste present; contents occasionally uniguttulate.

COMMENTARY—This taxon is treated in detail in the section on North American taxa.

**Russulopsis laricina** Velenovsky, Novitates Mycologicae. p. 77. 1939.

**TYPE:** Lacking.

**MACROMORPHOLOGY** (*Teste* Velenovsky, *ibid.*)—

**Pileus** 10 mm broad, plane, becoming depressed, glabrous, translucent-striate, dirty ochre-yellow. **Lamellae** adnate, not decurrent, crowded, narrowed at margin, white, becoming clay-colored. **Stipe** 2–3 times longer than pileus diameter, 1–1.5 mm broad, equal, straight, glabrous, translucent, fragile.

**MICROMORPHOLOGY** (*Teste* Velenovsky, *ibid.*)—

**Basidiospores** 3–5 μm diam., globose, smooth.

COMMENTARY—Type material of this taxon was not found at either PRM or PRC. Based on the protologue, this is not a **Laccaria**.

**Laccaria lateritia** Maleçon, Bull. Soc. Mycol. France 82: 189. 1966. Figure 65a.


Specimen examined as representative material: Uruguay, Montevideo, 1927, *Felippone No. 2800* (mpu).

**MACROMORPHOLOGY** (*Teste Maleçon, ibid.*)—

**Pileus** 10–25 mm broad, thin, almost hemispherical to convex, centrally truncate or slightly depressed, becoming plane, when wet pellucid-striate to disc, not striate when dry, hygrophanous, indistinctly reddish brown to dark brick red (8, 78, 82, Klincksieck), becoming pallid. **Lamellae** mostly adnate to arcuate, moderately crowded, thick, broad, pallid rose-colored to purple-ochraceous (87 or 92, Klincksieck). **Stipe** 20–25 × 2–5 mm, thickened at base, striate, often compressed-sulcate and twisted, reddish brown, base vinaeous when immature (39, 54, 58, Klincksieck; Seguy 102, 106; Saccardo radius), lacking purple color when mature, pallid when dry. **Basal mycelium** white. **Basidiospores** white in mass.

**MICROMORPHOLOGY** (*Mihi*)—Pileepellis of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 10–20 hyphae; terminal cells of fascicular hyphae filamentous, subclavate or occasionally clavate, light yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown; contents hyaline to light yellowish brown. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae mostly 3–10.5 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 29–46 × 8–11 μm, clavate, hyaline; sterigmata 2, up to 10 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) 8.3–11 (–13.3) × 8.3–10.6 (–13.3) μm (x̄ = 9.7 ± 1.04 × 9.5 ± 1.1 μm), Q = (0.95–1)–1.06 (–1.11) (Q = 1.02 ± 0.03), globose, subglobose or rarely broadly ellipsoid, echinulate; echinulae 0.8–1.4 μm long, crowded; hilar appendix 1.5–2.5 μm long, prominent, truncate; plaste present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 2.5–7 μm diam., narrow, morphologically undifferentiated, tightly interwoven, hyaline.

COMMENTARY—The micromorphological description above was based on an authentic collection on loan from Montpellier because the holotype was not available for study. Two of the four authentic collections located were not suitable. One collection was badly contaminated, and the other packet stated that it was a robust form of the taxon and, therefore, was not typical. The collection used was also somewhat contaminated, and pileipellis characters were difficult to ascertain and the presence of cheilocystidia was impossible to determine. Maleçon (1966) stated that this was the first collection that he saw of this taxon.

This taxon is treated as a synonym of *L. fraterna.*
Laccaria lilacina Stevenson, Kew Bull. 19: 3. 1964. Figure 65b.

TYPE: New Zealand, Woodside, 1 July 1955, Stevenson 924 (K!, holotype).

MACROMORPHOLOGY (Teste Stevenson, ibid.)—Pileus 40–55 mm broad, convex to plane, fibrillose, becoming finely scaly due to cuticular diffraction, fawn-colored with fulvous fibrils; margin upturned, often split. Lamellae adnate, distant, lilac, mealy. Stipe 100 × 30–40 mm, subfibrous, silky striate, dull fawn. Basal mycelium white. Basidiospores white in mass.

MICROMORPHOLOGY (Mihi)—Pilepellis of interwoven hyphae with large fascicles of ± perpen-
dicular hyphae; fascicles composed of up to 40 hyphae; terminal cells of fascicular hyphae (N = 10) 39–60 × 5–12.5 μm, filamentous to subclavate, dark yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown; contents dark yellowish brown. Pileus trama tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. Lamellar trama parallel to subparallel; hyphae 3–9 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. Subhymenium morphologically undifferentiated. Basidia (N = 15) 37–50.5 × 7–11 μm, clavate, hyaline; sterigmata 4, up to 10 μm long. Pleurocystidia lacking. Cheilocystidia not observed. Basidiospores (excluding ornamentation) (N = 30) 7–9.7 × 7–9.7 μm (x = 8.4 ± 0.7 × 8.3 ± 0.7 μm), Q = 1–1.07 (Q = 1.01 ± 0.03), globose, occasionally subglobose, hyaline, echinulate; echinulae (0.8–1.4–1.8(–2.3), up to 1 μm wide at base, crowded; hilar appendix 1.3–2.5 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. Basal mycelium hyphae 3–8 μm diam., morphologically undifferentiated, tightly interwoven, hyaline; wall up to 0.5 μm thick.

COMMENTARY—The basidiospore size and echinulae length reported here are somewhat larger than those presented in Stevenson’s original description (“Sporae 7–8 μm diam., spinis 0.5–1 μm longis”). This obviously represents a distinct taxon. An examination of additional material is necessary before comments on its relationships to other taxa can be made.


TYPE: Lacking.

COMMENTARY—No authentic material of this taxon nor a copy of the original description was located.


TYPE: Housed at PRC?

MACROMORPHOLOGY (Teste Pilát, 1948)—Pileus 10–20 mm diam., obtuse to convex, becoming plane, occasionally slightly umbonate, translucent-striate, hygrophanous, honey-colored to somber brown when fresh, almost white when dry. Lamellae broad, thin, becoming rounded-free, farinaceous, white. Stipe 2–4 times longer than pileus diameter, 2–3 mm thick, equal, base not thickened, glabrous to finely fibrilllose, longitudinally striate, covered with white basidiospores at apex, light gray color. Basidiospores white in mass.

MICROMORPHOLOGY (Teste Pilát, 1948)—Basidiospores 8–9 μm diam., globose, thick-walled, echinulate, hyaline.

COMMENTARY—A formalin-preserved specimen of this taxon sent from PRC was never received. Without additional micromorphological data, it is impossible to clarify the concept of this taxon.

Laccaria longipes G. M. Mueller, Mycotaxon 40: 145–150. 1991. Figure 65c.


MACROMORPHOLOGY (Mihi)—Pileus 11–21(–55) mm broad, convex, often centrally depressed, slightly to moderately translucent-striate, finely fibrilllose, orange-brown (6B7–6C7) fading to buff in age; margin incurved, decurved, or plane, entire to undulate, becoming slightly eroded. Lamellae adnate, distant, thick, up to 10 mm broad, light flesh color (near 6A2). Stipe 67–138 × 3–8 mm, equal with slightly swollen base, dry, slightly to moderately fibrilllose-striate, concolorous with pileus. Basal mycelium white. Basidiospores white in mass.

MICROMORPHOLOGY (Mihi)—Pileipellis of tightly interwoven hyphae with scattered fascicles of 10–20 ± perpendicular hypha; terminal cells 5–10 μm, filamentous to subclavate, hyaline. Pileus trama tightly interwoven, morphologically undifferentiated, hyaline to light yellowish brown. Lamellar trama of parallel to subparallel hyphae, mostly 3–15 μm diam., thin-walled, hyaline; cells barrel-shaped. Subhymenium morphologically undifferentiated. Basidia 28–44 × 7–12 μm, clavate, hyaline; sterigmata 4, up to 8 μm long. Pleurocystidia lacking. Cheilocystidia none seen. Basidiospores (excluding ornamentation) 7–8.5 × 5.7–8 μm (x = 7.7 ± 0.5 × 6.9 ± 0.6 μm), Q = 1–1.27(–1.34) (Q = 1.11 ± 0.08), subglobose to broadly ellipsoid, occasionally globose or ellip-
soid, hyaline, echinulate; echinulae (0.7–1.5–2) μm long, less than 1 μm wide at base.

SOMATIC CULTURE MAT MORPHOLOGY: See the description under L. longipes in the section on North American taxa.

COMMENTARY—This taxon is treated in detail in the section on North American taxa.

Agaricus (Clitocybe) laccatus var. lutea Fries, Epicyr. syst. mycol. p. 79. 1836–1838.

TYPE: Lacking.

MACROMORPHOLOGY (Teste Fries, ibid.)—As in type variety, lamellae flesh color.

COMMENTARY—This taxon is treated as a synonym of L. laccata.

Agaricus (Clitocybe) laccatus var. [pileo] luteoviolaceo Fries, Epicr. syst. mycol. p. 79. 1836–1838.

TYPE: Lacking.

MACROMORPHOLOGY (Teste Fries, ibid.)—Pileus drying ochraceous. Lamellae violaceous.

COMMENTARY—It is common for the lamellae of older specimens of Laccaria to turn violaceous as a result of drying or possible contamination. As this character by itself is not sufficient to warrant segregation, this taxon is treated as a synonym of L. laccata.

Hygrophorus maritimus Teodorowicz, Grzyby wyzsze Poleskiego wybrzeza. 1936.

TYPE: Figure 5 in Teodorowicz, Grzyby wyzsze polskiego wybrzeza, Towarzystwo naukowe w Toruniu Badania Przyrodnicze Pomorskie 2: 31. 1936. (lectotype fide Mueller, 1991a).

MACROMORPHOLOGY (Teste Teodorowicz, ibid.)—Pileus 15–45 mm broad, convex becoming depressed, glabrous, appearing moist when humid, reddish flesh color; margin always unequal, toothed. Lamellae sinate to arcuate, 0.5–1 mm thick, entire, reddish flesh color, drying dark brown. Stipe 7–35 × 6–12 mm, occasionally swollen at base, fibrillose, concolorous with pileus, apex often becoming lighter.

MICROMORPHOLOGY (Teste Teodorowicz, ibid.)—Basidia 25–38(–50) × 7.5–11 μm, 2–4 sterigmata. Cystidia lacking. Basidiospores 12.5–17.5 × 5.5–9 μm, ellipsoid to irregularly ovoid, hyaline to greenish, glabrous or granular.

COMMENTARY—Although no type specimen was found, the illustration and description presented in the protologue match the common usage of this name. This taxon is treated in detail in the section on North American taxa.

Laccaria masonii Stevenson, Kew Bull. 19: 4. 1964. Figure 65d.


MACROMORPHOLOGY (Teste Stevenson, ibid., McNabb, 1972)—Pileus 0.5–3 cm broad, convex to plano-convex when young, occasionally planate, glabrous or minutely furfuraceous at disc, pellucid-striate at margin, hygrophanous, violaceous when young, fading to buff at maturity. Lamellae adnexed to adnate, distant, up to 4 mm broad, pallid violaceous when young, becoming pallid brownish pink, occasionally with faint violaceous tints remaining. Stipe 30–100 × 1–3 mm, swollen at base, longitudinally fibrillose-sulcate, often twisted, violaceous when young, fading to buff with maturity; apex at times with violaceous tints. Basal mycelium pallid violaceous. Basidiospores white in mass.

MICROMORPHOLOGY (Mihi)—Pileipellis of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 5–10 hyphae; terminal cells (N = 10) 46–67 × 8–13 μm, filamentous to subclavate, light yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. Pileus trama tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. Lamellar trama parallel to subparallel; hyphae 2.5–6.5 diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. Subhymenium morphologically undifferentiated. Basidia (N = 15) 29.5–44 × 7.5–10.5 μm, clavate, hyaline; sterigmata 4, up to 10 μm long. Pleurocystidia lacking. Cheilocystidia not observed. Basidiospores (excluding ornamentation) (N = 30) 7.8–9.7(–10.6) × (7.4–)7.8–9.7(–10.6) μm (x = 8.9 ± 0.8 × 8.7 ± 0.8 μm), Q = 1–1.06(–1.11) (Q = 1.02 ± 0.03), globose to subglobose, hyaline, strongly echinulate; echinulae (1.4–)2.3–4.6(–6.5) μm long, up to 1.8 μm wide at base, occasionally curved, not crowded; hilar appendix 1.3–2.5 μm long, prom-
inent, truncate; plage present; contents occasionally uniguttulate. Basal mycelium hyphae mostly 3–5.5 μm diam., tightly interwoven, hyaline; cells filamentous to barrel-shaped.

COMMENTARY—Two taxa were included in the protologue that accompanied Stevenson’s original description of L. masonii. The type collection consists entirely of basidiocarps with glabrous pilei, and the epithet is restricted to that circumscription. McNabb (1972) proposed L. fibrillosa to represent the other taxon represented in the description.

Clitocybe (Lacaria) nana var. microspora Lange, Flora Agaricina Danica 1: 90. 1935.

TYPE: Not located.

MACROMORPHOLOGY (Teste Lange, *ibid.*)—Pileus 8 mm broad, convex-applanate, not striate, farinaceous, ash gray; disc somewhat darker. Lamellae attenuated behind, distant, narrow, thin, white. Stipe short, thin, pale ash gray. Basidiospores white in mass.

MICROMORPHOLOGY (Teste Lange, *ibid.*)—Pileipellis of conidiform, lanceolate, ellipsoid cells; cells 12 × 5 μm. Basidia (2–)4-sterigmate. Cystidia 6–12 μm broad, awl-shaped or conical. Basidiospores 5 μm diam., subglobose, warty spinulose.

COMMENTARY—No specimen of this taxon was acquired from C. Lange (1935) stated that this taxon is a “very strange little Agaric” and that it required further study. Based on the original description, it is not a Lacaria.


MACROMORPHOLOGY (Teste Imai, *ibid.*)—Pileus 5–10 mm broad, not striate or only slightly striate. Stipe 25–35 × 1–2 mm, subclavate. All other characters as in the type variety.

MICROMORPHOLOGY (Mihi)—Lamellar trama parallel; hyphae mostly 5–13 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. Subhymenium morphologically undifferentiated. Basidia (N = 15) 30–43 × 9–11.5 μm, clavate, hyaline; sterigmata 4, up to 7 μm long. Pleurocystidia lacking. Cheilocystidia not observed. Basidiospores (excluding ornamentation) (N = 30) 7–8.7(–9.2) × 7–8.7 μm (x = 8 ± 0.6 × 7.9 ± 0.6 μm), Q = 1–1.06 (Q = 1.01 ± 0.02), globose, rarely subglobose, hyaline, echinulate; echinulae 1–1.8 μm long, moderately crowded; hilar appendix 1.3–1.8 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. Basal mycelium hyphae mostly 4–9 μm diam., morphologically undifferentiated, tightly interwoven, hyaline.

COMMENTARY—This taxon is treated as a synonym of L. laccata var. pallidifolia.

Laccaria laccata var. moelleri Singer, Sydowia 7: 9–10. 1973. Figure 66b.


MACROMORPHOLOGY (Teste Singer, *ibid.*)—Pileus 30–69 mm broad, convex, deeply depressed, minutely fibrilloscabrous, rusty-orange-tawny (“ferrugineo-aurentiaculo-fulvo,” Singer) or tawny-reddish (“fulvido-rufo,” Singer), drying paler at disc; depression frequently minutely papillate; margin sulcate, rarely plicate or lobate. Lamellae arcuate or adnate, subcercrowded to subdistant, 6–8 mm broad, rose flesh-colored (“carneorosellis,” Singer) becoming covered with a white powder (?spores). Stipe 100–155 × 5–6(–11) mm; equal or tapering toward apex; apex finally fibrilloose, becoming glabrescent, stuffed, becoming hollow, dull yellowish brown (“fulva-brunneo,” Singer) or brownish (“brunneo,” Singer). Basal mycelium white. Basidiospores white in mass.

MICROMORPHOLOGY (Mihi)—Pileipellis of interwoven hyphae with scattered fascicles of ⊥ perpendicular hyphae; fascicles usually composed of 5–10 hyphae; terminal cells of fascicular hyphae (N = 10) 40–76 × 6.5–16 μm, filamentous to swollen, subclavate to clavate to ventricose-rostrate, light yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. Pileus trama tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. Lamellar trama parallel; thin-walled, hyaline to light yellowish brown; cells barrel-shaped. Subhymenium morphologically undifferentiated. Basidia (N = 15) 34–47 × 9.5–13 μm, clavate, hyaline; sterigmata 4, up to 6 μm long. Pleurocystidia lacking. Cheilocystidia lacking. Basidiospores (excluding ornamentation) (N = 10) 31–57.5 × 2.5–4(–8.5) μm, filamentous, abundant, hyaline.
tation) \((N = 30)\) 9.2–11 × (6.4–)7–8.3 \(\mu\)m \((\bar{x} = 10 
\pm 0.6 \times 7.3 \pm 0.4 \mu\)m), \(Q = 1.24–1.46(–1.58)\) \((Q = 1.3 \pm 0.01)\), ellipsoid to amygdaliform, hyaline, echinulate; echinulae 0.3–1.4\((-2)\) \(\mu\)m long, crowded, often with one or two long echinulae at apex; hilar appendix 1.5–1.8 \(\mu\)m long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 4–5 \(\mu\)m
diam., narrow, morphologically undifferentiated, tightly interwoven, hyaline.

**COMMENTARY**—Although basidiospore shape and echinulae length fit the original circumscription, the basidiospore dimensions measured in this study were all larger than the range presented by Singer.

For more information on this taxon, see Mueller

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Laccaria laccata var. montana Möller, Fungi of the Faeröes. pp. 269–270. 1945. Figure 66c.

TYPE: Denmark, Faeröe Ils. Oстро, Slattaratinde, 17 July 1938, Möller s.n. (cf., holotype).

MACROMORPHOLOGY (Teste Möller, ibid.)—Pileus 7–17 mm broad, convex becoming expanded, depressed in age, occasionally with a small papilla, often somewhat irregular, slightly squamulose, hygrophanous or subhygrophanous, orange-brown (6 E 12 to 4 B 10 or 7 J 12 to 7 L 12, M&P) fading to ochraceous (11 F 7, M&P); margin radially sulcate. Lamellae adnate to decurrent, occasionally anastomosing, subcrowded to distant, broad, rose flesh-colored (11 A 8, M&P), becoming cinnamon flesh-colored (5 D 10 to 5 F 11, M&P), when dry, margin purplish brown, white pulvulrent with spores. Stipe 15–20(–55) × 2–5 mm, equal, glabrous or innately fibrillose, more pallid than pileus to sub-ochraceous, frequently variegated (6 B 12 and 14 A 11, M&P). Basal mycelium white. Basidiospores white in mass.

MICROMORPHOLOGY (Mihi)—Pileipellis of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 15–30 hyphae; terminal cells of fasiccular hyphae (N = 10) 39–51 × 5.5–10 μm, filamentous to subclavate, light yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown; contents hyaline.

Pileus trama tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. Lamellar trama parallel to subparallel; hyphae 3–14 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. Subhymenium morphologically undifferentiated. Basidia (N = 15) 42–48 × 10–15.5 μm, clavate, hyaline; sterigmata 4, up to 11 μm long. Pleurocystidia lacking. Cheilocystidia not observed. Basidiospores (excluding ornamentation) (N = 30) 8.3–11.5 × (7.8–)8.3–10.6 μm (x = 10 ± 0.9 × 9.6 ± 0.9 μm), Q = 1–1.11(–1.22) (Q = 1.04 ± 0.06), globose to subglobose, rarely broadly ellipsoid, hyaline, echinulate; echinulae 0.3–1.4 μm long, crowded; hilar appendix 1.5–1.8 μm long, prominent, truncate; plage present, contents occasionally uniguttulate.

MACROMORPHOLOGY (Teste Singer, ibid.)—Pileus 7–35 mm broad, convex, occasionally papillate when young, becoming strongly umbilicate to infundibuliform; disc rimulose to finely fibrillose, becoming diffrazed to squamulose, hygrophanous or subhygrophanous, orange-brown (E 12 to 4 B 10 or 7 J 12 to 7 L 12, M&P) fading to ochraceous (11 F 7, M&P); margin radially sulcate. Lamellae adnate to decurrent, occasionally anastomosing, subcrowded to distant, broad, rose flesh-colored (11 A 8, M&P), becoming cinnamon flesh-colored (5 D 10 to 5 F 11, M&P), when dry, margin purplish brown, white pulvulrent with spores. Stipe 15–20(–55) × 2–5 mm, equal, glabrous or innately fibrillose, more pallid than pileus to sub-ochraceous, frequently variegated (6 B 12 and 14 A 11, M&P). Basal mycelium white. Basidiospores white in mass.

MICROMORPHOLOGY (Mihi)—Pileipellis of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 15–30 hyphae; terminal cells of fasicular hyphae (N = 10) 39–51 × 5.5–10 μm, filamentous to subclavate, light yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown; contents hyaline.

Pileus trama tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. Lamellar trama parallel to subparallel; hyphae 3–14 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. Subhymenium morphologically undifferentiated. Basidia (N = 15) 42–48 × 10–15.5 μm, clavate, hyaline; sterigmata 4, up to 11 μm long. Pleurocystidia lacking. Cheilocystidia not observed. Basidiospores (excluding ornamentation) (N = 30) 8.3–11.5 × (7.8–)8.3–10.6 μm (x = 10 ± 0.9 × 9.6 ± 0.9 μm), Q = 1–1.11(–1.22) (Q = 1.04 ± 0.06), globose to subglobose, rarely broadly ellipsoid, hyaline, echinulate; echinulae 0.3–1.4 μm long, crowded; hilar appendix 1.5–1.8 μm long, prominent, truncate; plage present, contents occasionally uniguttulate. Basal mycelium hyphae 3–20.5 μm diam., tightly interwoven, hyaline; cells short, barrel-shaped.

COMMENTARY—Singer (1973) reported occasional cheilocystidia ("cheilocystidii 17–47.5 × 5.5–9.5 μm, versiformibus, clavatis, ventricosis, cylindraceis vel flexuosis, frequenter pedicellatiis, hyalinis vel rubenscentibus, sat numerosis"). The discrepancy between Singer’s descriptions and this study may be due either to poor rehydration of the specimens or to the absence of cheilocystidia in the slide preparations examined.
This taxon is treated in detail in the section on North American taxa.


TYPE: Not located.

MACROMORPHOLOGY (Teste Imai, ibid.)—Pileus 10–15 mm broad, hemispherical to convex, becoming plane, subvelutinous, striate, dark, dirty brown, almost black when young and fresh, mouse gray or subavellaneous when dry; margin involuted at first. Lamellae adnate, distant, gray, becoming pruinose with white spores. Stipe 15–25 × 1.5–2.5 mm, equal or tapering slightly above, striate, subconcolorous or slightly more pallid. Basidiospores white in mass.

MICROMORPHOLOGY (Teste Imai, ibid.)—Basidiospores 7.5–10 μm, globose, verruculose.

COMMENTARY—No specimen of this taxon was included with the material loaned from SAP, and therefore I cannot comment on the appropriate disposition of this taxon.

Laccaria nana Massee, Kew Bull. 6: 2. 1913. Figure 67a.

TYPE: England, Grounds of Royal Botanic Gardens, Kew, Surrey, Massee s.n. (k!, holotype).

MACROMORPHOLOGY (Teste Massee, ibid.)—Pileus 10 mm broad, plano-convex, glabrous, smooth, dark cinnamon-colored, becoming pallid; margin at first farinaceous. Lamellae attenuate-adnate, subdistant, pallid, becoming covered with a white powder. Stipe 10 mm long, fibrillose, hollow, white.

MICROMORPHOLOGY (Mihi)—Lamellar tramə parallel; hyphae thin-walled, hyaline to light yellowish brown; cells barrel-shaped. Subhymenium morphologically undifferentiated. Basidia not rehydrating, ?clavate, hyaline; sterigmata 2. Pleurocystidia ?lacking. Cheilocystidia not observed. Basidiospores (excluding ornamentation) (N = 30) 10.6–13(–13.8) × 10.6–13(–13.8) μm (x = 11.7 ± 0.9 × 11.5 ± 0.9 μm), Q = 1–1.04(–1.09) (Q = 1.01 ± 0.03), globose, rarely subglobose, hyaline, strongly echinulate; echinulæ (2.3–)2.8–4 μm long, 1.8–2.3 μm wide at base, crowded; hilar appendix 1.3–2 μm long, prominent, truncate; plage present; contents usually uniguttulate.

COMMENTARY—The type collection consists of a few small lamellar fragments that contain numerous basidiospores.

This taxon appears to be a distinct species, apparently known only from the type collection. As it was collected on the grounds of Kew Gardens, it is not known whether it is native to England or was introduced.

Laccaria nigra Hongo, Mem. Shiga. Univ. 9: 58–59. 1959. Figure 67b.

TYPE: Japan, Omi-Jingu, Otsu, Shiga, 10 June 1958, Hongo 1779 (Herbarium Hongol!, holotype).

MACROMORPHOLOGY (Teste Hongo, ibid.)—Pileus 8–22 mm broad, obtuse, conic to convex, becoming expanded, often with large umbo, glabrous, pellucid-striate, hygrophanous, grayish-subfuscus, disc almost black; flesh thin, membranous, concolorous, with an alkaline odor. Lamellae adnexed to adnate, distant, moderately thick, 1–3 mm broad, ventricose, ash gray. Stipe 18–35 × 1.5–3 mm, equal, hollow, concolorous with pileus.

MICROMORPHOLOGY (Mihi)—Pileipellis of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 10–20 hyphae; terminal cells of fascicular hyphae filamentous, subclavate or clavate, not rehydrating well; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. Pileus tramə tightly interwoven, morphologically undifferentiated, hyaline to light yellowish brown toward pileipellis. Lamellar tramə parallel; hyphae mostly 3.5–11 μm diam., thin-walled, hyaline; cells barrel-shaped. Subhymenium morphologically undifferentiated. Basidia (N = 15) 28.5–41 × 10–15.5 μm, clavate, hyaline, not rehydrating well; sterigmata 2(–4), up to 10 μm long. Pleurocystidia lacking. Cheilocystidia not observed. Basidiospores (excluding ornamentation) (N = 30) (7.8–)8.3–10.6(–12.4) × (7.8–)8.3–10.6(–12.4) μm (x = 9.5 ± 1.04 × 9.5 ± 0.05 μm), Q = 1(–1.06) (Q = 1 ± 0.01), globose, rarely subglobose, hyaline, echinulate; echinulæ 1.8–2.8(–3.2) μm long, 1.3–1.8 μm wide at base, moderately crowded; hilar appendix 1.5–2 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. Basal mycelium hyphae...
Fig. 67. Representative basidiospores from type specimens: a, *L. nana* (holotype); b, *L. nigra* (holotype); c, *L. nobilis* (holotype); d, *L. oblongospora* (holotype). Scale line = 10 μm.
mostly 3–11 μm diam., long-celled, morphologically undifferentiated, tightly interwoven, hyaline.

**Commentary**—*Laccaria nigra* is obviously distinct as no other *Laccaria* has the coloration attributed to specimens of this taxon. Its affinities with other members of the genus are unclear.

**Russuliopsis nigricans** Velenovsky, Novitates Mycologicae. p. 77. 1939.

**Type**—Lacking.

**Macromorphology** (*Teste* Velenovsky, *ibid.*)—

**Pileus** 10–15 mm, bell-shaped, translucent-striate, hygrophanous, dark brown (almost black), becoming pale yellow. **Pileipellis** adnate becoming sinuate to free, moderately distant, broad, thick, pale, farinose. **Stipe** 3 times longer than pileus diam., 2 mm broad, equal, straight, concolorous.

**Micromorphology** (*Teste* Velenovsky, *ibid.*)—

**Basidiospores** 6–8 μm diam., globose, echinulate.

**Commentary**—Type material of this taxon was not found at either PRM or FRC. Its affinities with other *Laccaria* are unclear.

**Laccaria nobilis** Smith *apud* G. M. Mueller, Mycotaxon 20: 105–108. 1984. Figure 67c.


**Macromorphology** (*Mihi*)—

**Pileus** 30–60 mm broad (ø = 43.3 mm), convex, deeply depressed, not striate, fibrillose-scaly to scaly, brownish orange (“Sanford’s Brown” to “Cinnamon-Rufous”), occasionally darker at disc (“Hazel”); margin decurved to upturned, entire to eroded. **Pileipellis** sinuate to adnate, close, thick, broad, pinkish flesh color (“Pale Flesh Color” to “Flesh Color”). **Stipe** 37–110 × 4–10 mm (ø = 79.5 × 6.5 mm), equal or bulbous, dry, fibrillose, fibrils forming prominent longitudinal striations, scaly from apex to midstipe, concolorous with pileus. **Basal mycelium** white. **Basidiospores** white in mass.

**Micromorphology** (*Mihi*)—

**Pileipellis** of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 20–30 hyphae; terminal cells of fascicular hyphae (N = 10) 36–58 × 7–13 μm, subclavate to clavate; walls up to 0.5 μm thick, light yellowish brown; contents hyaline to light yellowish brown. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae mostly 4–10 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 37.5–55 × 8–11 μm, clavate, hyaline; sterigmata 4, up to 7 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) 7.8–9.7(–10.6) × (5–)6.4–7.8(–8.3) μm (ø = 8.6 ± 0.7 × 7.0 ± 0.6 μm), Q = (1.06–)1.13–1.26(–1.9) (Q = 1.23 ± 0.14), broadly ellipsoid, ellipsoid or amygdaliform, rarely subglobose or oblong, hyaline, echinulate; echinulae 0.5–1(–1.5) μm long, crowded; hilar appendix 1.3–2 μm long, prominent, truncate; plebe present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 2–5.5 μm diam., tightly interwoven, morphologically undifferentiated, hyaline.

**Somatic Culture** **MAT Morphology**—**PDA**:

**Radius** at week 3 = 23–31 mm, week 6 = 35–42 mm; **mat** felty, thick, tightly interwoven, tightly appressed to agar surface, in time forming pruinose aerial layer away from plug, not translucent, at first bright violet, fading by week 6 to a dark purple band (< 9 mm) near margin with rest of mat light orange-brown; pruinose aerial hyphae light grayish purple, becoming light orange-brown; **margin** 3–4 mm broad, subfelty, thin, uneven, light violet; **plug** concolorous with mat; **hyphae** mostly undifferentiated or occasionally irregularly swollen, purplish brown in mass. **MMN**:

**Radius** at week 3 = 40–44 mm, week 6 = 69–78 mm; **mat** subfelty, thin, becoming slightly thicker with age, tightly interwoven, tightly appressed to agar surface, subtranslucent, light violet; **margin** 3–4 mm broad, silky to subfelty, thin, parallel to loosely interwoven, entire, concolorous; **plug** concolorous; **hyphae** morphologically undifferentiated or rarely irregularly swollen near margin. **MEA**:

**Radius** at week 3 = 33–35 mm, week 6 = 47–55 mm; **mat** subfelty, thin, loosely interwoven, tightly appressed to agar surface, translucent, white; **margin** 1–2 mm broad, subfelty, thinner than mat, undulate, white; **plug** white; **hyphae** morphologically undifferentiated.

**Commentary**—This taxon is treated in detail in the section on North American taxa.

**Laccaria oblongospora** G. M. Mueller, Mycotaxon 20: 108–112. 1984. Figure 67d.
MACROMORPHOLOGY (Mihi)—Pileus 14–54 mm broad (ε = 29 mm), convex becoming plane, often depressed, not striate, finely fibrillose, becoming fibrillose-scaly, hygrophanous, brownish orange (“Cinnamon-Rufous,” “Hazel,” or “Sanford’s Brown”), occasionally darker at disc (“Chocolate”); margin decurved to upturned, entire to undulate, becoming eroded; context 1–2 mm thick, tapering quickly to margin, flesh-colored (“Pale Vinaceous-Pink”). Lamellae sinuate to adnate, subdistant to distant, thick, broad, pinkish flesh color (“Shell Pink,” “Vinaceous-Pink,” or near “Buff-pink”). Stipe 23–60 × 3–10 mm (ε = 41 × 5 mm), equal or bulbous, dry, fibrillose, occasionally finely longitudinally-striate, brownish orange to reddish brown (“Pinkish Cinnamon,” “Cinnamon,” or “Cacao Brown”), occasionally with darker fibrils (“Pecan Brown”). Basal mycelium white. Basidiomata white in mass.

MICROMORPHOLOGY (Mihi)—Pileipellis of loosely interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 5–15 hyphae; terminal cells of fascicular hyphae (N = 10) 28.5–69 × 13–25 μm, subclavate, clavate, or capitata; walls up to 0.5 μm thick, light yellowish brown; contents hyaline to light yellowish brown. Pileus trama tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. Lamellae trama parallel to subparallel; hyphae thin-walled, hyaline to light yellowish brown; cells barrel-shaped. Subhymenium morphologically undifferentiated. Basidia (N = 10) 29–36 × 7.5–10 μm, clavate, hyaline; sterigmata 4, up to 5 μm long. Pleurocystidia lacking. Cheilocystidia (N = 10) 31.5–53 × 2.5–7 μm, filamentous to subclavate, scattered, hyaline. Basidiomata (excluding ornamentation) (N = 30) (6.8–)7.4–9.2–(10) × (4–)5–6.4–(7) μm (ε = 8.4 ± 0.8 × 5.8 ± 0.5 μm), Q = (1.25–)1.3–1.67–(1.8) (Q = 1.46 ± 0.13), ellipsoid to oblong, occasionally subreniform, hyaline, echinulate; echinulae < 0.5 μm long, often with 1 or 2 longer spines (± 1.4 μm) at apex, crowded; hilar appendix 1.3–1.8 μm long, prominent, truncate; plebe present; contents occasionally uniguttulate. Basal mycelium hyphae mostly 4–11 μm diam., tightly interwoven, hyaline; cells barrel-shaped.

SOMATIC CULTURE MAT MORPHOLOGY—PDA: Radius at week 3 = 31–36 mm, week 6 = 70–75 mm; mat feltly, moderately thick, tightly interwoven, tightly appressed to agar surface, in time forming pruinose aerial layer away from plug, not translucent, at first dark violet, then fading; week 3 moderate violet 2–3 mm band near margin, most of mat light orange-brown, week 6 entirely light orange-brown; margin up to 5 mm broad, silky to subfelty, thin, uneven, light violet to white; plug concolorous with mat; hyphae mostly morphologically undifferentiated, occasionally irregularly swollen or subcoralloid. MMN: Radius at week 3 = 52–56 mm, week 6 = > 100 mm (plate full); mat subfelty to subwoolly, thin, loosely interwoven, tightly appressed to agar surface, translucent, initially light violet, fading to white; margin undifferentiated, uneven; plug concolorous with mat; hyphae mostly morphologically undifferentiated, occasionally irregularly swollen. MFA: Radius at week 3 = 26–31 mm, week 6 = 54–60 mm; mat subfelty, thin, loosely interwoven, tightly appressed to agar surface, translucent, white; margin 1–2 mm broad, not well differentiated, even, white; plug white.

COMMENTARY—This taxon is treated in detail in the section on North American taxa.

Agaricus (Clitocybe) ochropurpureus Berkeley, London J. Bot. 4: 299–300. 1845. Figure 68a.

TYPE: USA, Ohio, Cincinnati, no date, Lea 261 (K!, holotype).

MACROMORPHOLOGY (Teste Berkeley, ibid.)—Pileus 50 mm broad, subhemispherical becoming depressed, fleshy pliant, pale brown to light purple; cuticle easily separating; margin incurved; at first tomentose. Lamellae decurrent, thick, not anastomosing, purple. Stipe 60 mm, swollen at middle, pallid purple. Basal mycelium white. Basidiomata white in mass.

MICROMORPHOLOGY (Mihi)—Cheilocystidia parallel; hyphae 3–7 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. Subhymenium morphologically undifferentiated. Basidia (N = 3) 34–45 × 9–10.5 μm, clavate, hyaline, not rehydrating well, sterigmata 4, up to 6 μm long. Pleurocystidia not observed. Cheilocystidia not observed. Basidiomata (excluding ornamentation) (N = 30) (7–)7.4–8.7 × (6.4–)7–8.3 μm (ε = 8 ± 0.5 × 7.6 ± 0.6 μm), Q = 1–1.13–(1.16) (Q = 1.06 ± 0.05), globose to subglobose, hyaline, echinulate; echinulae (0.3–)1–1.4 μm long, crowded; hilar appendix 1.3–2 μm long, prominent, truncate; plebe present; contents occasionally uniguttulate.
**Fig. 68.** Representative basidiospores from type specimens: a, *A. ochropurpureus* (holotype); b, *A. ohiensis* (holotype); c, *C. laccata* var. *pallidifolia* (holotype); d, *L. ohiensis* var. *paraphysata* (holotype). Scale line = 10 μm.

**COMMENTARY**—Because of the poor condition of this collection, no observations could be made on the arrangement of hyphae in the pileipellis or the presence or absence of cheilocystidia. This taxon is treated in detail in the section on North American taxa.

**Agaricus ohiensis** Montagne, Syll. Crypt. p. 100. 1856. Figure 68b.

**TYPE:** USA, Ohio, Columbus, *Sullivant s.n.* (pct!, holotype).

**MACROMORPHOLOGY** (*Teste Montagne, ibid.*)—*Pileus* 30–50 mm broad, at first hemispherical, becoming convex, deeply depressed, glabrous, striate, cinnamon-colored; margin involuted to plane. *Lamellae* 3–5 mm broad, thick, subdistant, decurrent, rose-colored or more pallid than pileus; edge obtuse. *Stipe* 30–40 × 5–6 mm, thickened at base, striate, hollow, concolorous with pileus. *Basidiospores* white in mass.

**MICROMORPHOLOGY** (*Mihi*)—*Pileipellis* of interwoven hyphae, with scattered fascicles of ± perpendicular hyphae, not rehydrating well. *Pileus trama* tightly interwoven, morphologically undif-
ferentiated, hyaline, yellowish brown toward pileipellis. *Pileus trama* parallel, cells barrel-shaped.

**Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 30–46(–53) × 8.5–14.5 μm, clavate, not rehydrating well, hyaline, sterigmata (2–4), up to 8.5 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) 7.4–9.2(–10) × 7.4–9.2(–10) μm (t = 8.4 ± 0.6 × 8.4 ± 0.6 μm), Q = 0.95–1.06 (Q = 1.01 ± 0.03), globose to subglobose, hyaline, echinulate; echinulae 1.4–2.3 μm long, > 1.2 μm wide at base, hilar appendix 1.8–2.3 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 1.5–3 μm diam.; tightly interwoven, morphologically undifferentiated, hyaline.

**COMMENTARY**—The first published report of the micromorphology of the type specimen (Singer, 1942) stated that the basidia were 4-sterigmate. In subsequent papers, however, Singer (1946, 1949, 1967, 1977, 1986), Bon (1983), and others reported that the basidia were 2-sterigmate. My observations of the holotype corroborate Lahaie's description (1981) that the basidia of the holotype of *A. echinosporus* are 4-sterigmate. A small fragment of the type collection is housed also at NY.

This taxon is treated in detail in the section on North American taxa.

**Agaricus orbisporus** Britzelmayr, Revis Hymenomyc. I: 15. 1898.

**TYPE:** Lacking.

**MACROMORPHOLOGY** *(Teste Saccardo, 1912)—Pileus* 25 mm broad, conical to convex, umbonate, hygrophanous, brownish gray, becoming pale. **Lamellae** arcuate, distant, moderately thick, 4 mm broad, gray. **Stipe** 70 × 5 mm, brownish gray to white. **Basidiospores** white in mass.

**MICROMORPHOLOGY** *(Teste Saccardo, 1912)—Basidiospores* 8–10 μm diam., globose.

**COMMENTARY**—This taxon is putatively similar to *A. echinosporus* (Saccardo, 1912). *Agaricus orbisporus* is treated as a synonym of *L. tortillus*.

**Agaricus pachyphillus** Fries, Obs. Mycol. I: 76. 1815.

**TYPE:** Lacking.

**MACROMORPHOLOGY** *(Teste Fries, ibid.)—Pileus* plano-convex, becoming depressed, somewhat fleshy, grayish yellow; margin becoming rimose. **Lamellae** decurrent, light yellow. **Stipe** 1.5 unc., glabrous, solid becoming hollow, yellow.

**COMMENTARY**—Fries (1821) listed this taxon (as "A. pachyphillus") as one that needed more study. Although Fries (1836–1838) later stated that this taxon was similar to *A. laccatus*, the lamellae and stipe colors presented in the protologue make it doubtful that this taxon is a *Laccaria*.

**Clitocybe laccata** var. *pallidifolia* Peck. Annual Rep. New York State Bot. 43: 38. 1890. Figure 68c.

**TYPE:** USA, New York, Selkirk, October, C. H. Peck s.n. (NYS!, holotype).

**MACROMORPHOLOGY** *(Teste Peck, ibid.)—Lamellae* much paler than typical, with only a tinge of flesh color.

**MICROMORPHOLOGY** *(Mihi)—Pileipellis* of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 10–25 hyphae; terminal cells of fascicular hyphae (N = 10) 24–53 × 6–10 μm, filamentous to clavate, light yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae 3–9 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 39–57.5 × 10.5–15.5 μm, clavate, hyaline; sterigmata 4, up to 9 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) 7.8–11(–11.5) × 7.4–9.2(–10.6) μm (t = 9.2 ± 0.9 × 8.5 ± 0.8 μm), Q = 1–1.12(–1.2) (Q = 1.08 ± 0.06), globose to subglobose, occasionally broadly ellipsoidal, hyaline, echinulate; echinulae 0.5–1.4(–1.8) μm long, crowded; hilar appendix 1.3–2 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 5–11 μm diam., morphologically undifferentiated, tightly interwoven, hyaline.

**COMMENTARY**—The collection labeled TYPE on loan from NYS contained material from two localities, Selkirk and Lake Mohonk. Specimens from both locations were examined and found contaxic.

This taxon is treated in detail in the section on North American taxa.
Laccaria ochiensis var. paraphysata McNabb, New Zealand J. Bot. 10: 474–475. 1972. Figure 68d.


MACROMORPHOLOGY (Teste McNabb, ibid.)—
Pileus 10–35 mm broad, convex to plano-convex at maturity, occasionally depressed, inconspicuously translucent-striate at margin when wet, not so when dry, finely furfuraceous, hygrophanous, reddish brown to dark reddish brown, drying pallid fawn to buff. Lamellae adnixed to adnate, distant, thick, up to 5 mm broad, flesh pink, glaucous. Stipe 25–70 x 2–5 mm, equal or tapering slightly apically, dry, coarsely and sparingly longitudinally fibrillose, often twisted, reddish brown. Basal mycelium white. Basidiospores white in mass.

MICROMORPHOLOGY (Mihi)—
Cheilocystidia of interwoven hyphae with scattered fascicles of ± perpendicu lar hyphae; fascicles composed of 5–10 hyphae; terminal cells of fascicular hyphae (N = 10) 32–64 x 6.5–10.5 μm, filamentous, swollen, subclavate or clavate, light yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown; contents hyaline to light yellowish brown. Pileus trama tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. Lamellar trama parallel to subparallel; hyphae 3.5–11 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. Subhymenium morphologically undifferentiated. Basidia (N = 15) 33–50.5 x 8.5–12 μm, clavate, hyaline; sterigmata 2(3), up to 11 μm long. Pleurocystidia (N = 10) 27–42 x 2.5–4.5 μm, filamentous, subclavate, subcapitate or irregularly contorted, sometimes irregularly branched, thin-walled, hyaline. Cheilocystidia 20–41.5 x 1.8–3 μm, similar to pleurocystidia. Basidiospores (excluding ornamentation) (7.4–)7.8–9.7(–11.5) x 7.4–9.7(–11.5) μm (x = 9.1 ± 0.8 x 8.9 ± 0.8 μm), Q = 1–1.05(–1.12)(Q = 1.02 ± 0.03), globose to subglobose, hyaline, echinulate; echinulae 0.8–1.4 μm long, crowded; hilar appendix 1.3–2 μm long, prominent, truncate; plebe present; contents occasionally uniguttulate. Basal mycelium hyphae mostly 2.5–9 μm diam., morphologically undifferentiated, tightly interwoven, hyaline.

COMMENTARY—As discussed in the section on North American taxa, the holotype of Agarius ochiensis is tetrasporic, not bisporic as had been reported. As such, this bisporic taxon cannot be a variety of L. ochiensis but must be renamed.


TYPE: Chile, Valdivia, Cordillera Pelada, El Mirador, 5 May 1965, Singer M5515 (BAFC!, holotype).

MACROMORPHOLOGY (Teste Singer, ibid.)—As in L. tetraspora var. tetraspora.

MICROMORPHOLOGY (Mihi)—Pileipellis of interwoven hyphae with scattered fascicles of ± perpendicu lar hyphae; fascicles composed of 5–10 hyphae; terminal cells of fascicular hyphae (N = 10) 37–60 x 5–13.5 μm, subclavate to clavate; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. Pileus trama tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. Lamellar trama parallel; hyphae mostly 4.5–10 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. Subhymenium morphologically undifferentiated. Basidia (N = 15) 32–44 x 9–12.5 μm, clavate, hyaline; sterigmata 2(–4), up to 10 μm long. Pleurocystidia lacking. Cheilocystidia (N = 10) 20–34.5 x 3–4 μm, undifferentiated, thin-walled, hyaline. Basidiospores (excluding ornamentation) (N = 30) (6.4–)7–9.2 x (6.4–)7–9.2 μm (x = 7.9 ± 0.7 x 7.8 ± 0.7 μm), Q = 1–1.06(–1.01 ± 0.02), globose, occasionally subglobose, hyaline, echinulate; echinulae 0.8–1.4(–1.8) μm, crowded; hilar appendix 1.3–1.8 μm long, prominent, truncate; plebe present; contents occasionally uniguttulate. Basal mycelium hyphae mostly 6.5–18 μm diam., tightly interwoven, hyaline, walls up to 0.5 μm thick; cells filamentous to barrel-shaped.

COMMENTARY—Singer (1967) separated L. tetraspora var. peladae from L. tetraspora var. tetraspora solely on slight differences in basidiospore and basidiospore ornamentation size. Singer (1977) later transferred this taxon to L. laccata var. peladae.

This taxon is treated as a synonym of L. laccata var. pallidifolia.

Agarius (Clitocybe) laccatus var. perpusillus Rabenhorst et al., Fungi Europaei Exsiccati. Cent 5. n. 503. 1862.

TYPE: Not located.

Specimen examined as representative material: Rabenhorst No. 503, Fungi Europaei Exsiccati, Finland, Mustiala tradgard, September 1866 (NY).

MICROMORPHOLOGY (Mihi)—Basidia 2-sterigmatic. Basidiospores (excluding ornamentation)
**Fig. 69.** Representative basidiospores from type or representative specimens: a, *L. tetraspora* var. *peladae* (holotype); b, *L. tetraspora* var. *peullensis* (holotype); c, *L. proxima* (representative specimen); d, *L. proximella* (holotype). Scale line = 10 μm.

10.5–14 μm diam., globose to subglobose, hyaline, echinulate; echinulae up to 3 μm long.

**COMMENTARY**—This collection consists of fragments of two pilei. Because of the date on the collection, 1866, it is doubtful that Rabenhorst had this particular collection available to him when he first designated the variety. Other specimens in the exsiccata, therefore, may be better candidates for typification.

The micromorphology of this collection fits within the circumscription of *L. tortilis* and this taxon is treated as a synonym of *L. tortilis.*


**TYPE:** Chile, Peulla, Lago Todos los Santos, 22 March 1959, *Singer M1991* (BAFC!, holotype).

**MACROMORPHOLOGY** (*Teste Singer, ibid.)*—**Pileus** 8–10 mm broad, campanulate or conic-obtuse, glabrous, pellucid-striate, hygrophanous (13 A 8 and 14 A 9, M&P). **Lamellae** adnate, moderately broad (1 C 2 to 3 C 9, M&P). **Stipe** 50–55
× 2–3 mm, equal, slender (13 A 9 and 14 A 10, M&P). Basal mycelium pale, whitish when dry.

MICROMORPHOLOGY (Mihi)—Pileipellis of interwoven hyphae, no fascicles of hyphae observed, terminal cells (N = 10) 28–55 × 6.5–13 μm, filamentous, clavate or ventricose; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. Pileus trama tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. Pileus trama parallel; hyphae mostly 3–9 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. Subhymenium morphologically undifferentiated. Basidia (N = 15) 28.5–42 × 10–16.5 μm, clavate, hyaline; sterigmata 4, up to 8.5 μm long. Pleurocystidia lacking. Cheilocystidia (N = 10) 24–38 × 3–5.5 μm, filamentous, subcapitate or narrowly ventricose-rostrate, abundant, thin-walled, hyaline. Basidiospores (excluding ornamentation) (N = 30) 7.4–8.7(–9.7) × 7.4–8.7(–9.2) μm (x = 8.1 ± 0.6 × 8 ± 0.5 μm), Q = 1(–1.11) (Q = 1.01 ± 0.02), globose, rarely subglobose, hyaline, echinulate; echinulae 1–1.8 μm long, crowded; hilar appendix 1.3–1.8 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. Basal mycelium hyphae mostly 2–5.5 μm diam., morphologically undifferentiated, tightly interwoven, hyaline.

COMMENTARY—The collection consists of part of a single basidioma. This taxon is treated as a synonym of L. ohiensis.


TYPE: USA, Connecticut, collected by C. Wright, no date, Curtis No. 5520 (k!, holotype).

MACROMORPHOLOGY (Teste Berkeley & Curtis, ibid.)—Pileus 37 mm broad, convex, glabrous, pale dull purple. Lamellae pale purple. Stipe 25–37 × 2–3 mm, thickened upward, glabrous, purplish white.

MICROMORPHOLOGY (Teste Berkeley & Curtis, ibid.)—Basidiospores ellipsoid 1/5,750 in. long.

COMMENTARY—The original description includes little micromorphological data. Berkeley and Curtis (1859) stated that this collection “[d]iffers from A. laccatus in the numerous gills and very different spores.” The type collection consists of one very moldy basidiocarp from which no micromorphological observations could be obtained. Murrill (1916) also reported that the specimen was in poor condition, rendering interpretation difficult. He speculated that it is “Prunulus purus or one of the species of Laccaria” (Murrill, 1916). Without micromorphological data, it is impossible to clarify the concept of this taxon, and its identity remains uncertain. No material fitting this description was found during this study.

Agaricus (Clitocybe) porphyroles Berkeley & Broome, J. Linn. Soc. 11: 519. 1871.

TYPE: Ceylon, Peradeniya, November 1868, Berkeley & Broome 540 (k!, holotype).

COMMENTARY—The type collection consists of a single basidioma. Micromorphological analysis of this specimen revealed the presence of globose, smooth basidiospores. Although Cooke (1884) included this epithet when he transferred names into Laccaria (Cooke, 1884, p. 70), the lack of echinulate or roughened basidiospores excludes it from the genus.


MACROMORPHOLOGY (Teste Boudier, ibid.)—Pileus up to 30 mm broad, convex, becoming plane, depressed, covered with appressed fibrils, hygrophanous, orange-rust (“fauve orange,” Boudier), disc becoming squamulose with age; margin striate when moist. Lamellae distant, thick, pinkish flesh-colored (“rose carne,” Boudier), paler toward margin, becoming subconcolorous with pileus, often covered with a white powder (?spores). Stipe up to 40 × 4 mm long, externally fibrilllose, equal or slightly thickened at base.

MICROMORPHOLOGY (Mihi, based on representative specimen)—Pileipellis of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 10–20 hyphae; terminal cells of fascicular hyphae (N = 10) 38–64 × 4.5–9 μm, filamentous, subclavate, clavate, or occasionally subcapitate, light yellowish brown in mass; walls up to 0.5 μm thick, pale yellowish brown; contents hyaline. Pileus trama tightly interwoven, morphologically undifferentiated, hya-
line, light yellowish brown toward pileipellis. *Pileus trama* parallel; hyphae 3.5–12 µm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. *Subhymenium* morphologically undifferentiated. **Basidia** (*N* = 15) 30.5–43 × 8.5–11.5 µm, clavate, hyaline; sterigmata 4, up to 5 µm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (*N* = 30) 7.8–11 × (6.4–)7–8.3–(8.7) µm (*x* = 9.6 ± 1 × 7.6 ± 0.6 µm), *Q* = (1.05–)1.12–1.49 (*Q* = 1.3 ± 0.1), ellipsoidal or amygdaliform, rarely subglobose, hyaline, echinulate; echinulae 0.5–1–(2.3) µm long, sometimes with 1 or 2 long echinulae at apex; hilar appendix, 1.5–1.8 µm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 2.5–4 µm diam., tightly interwoven, morphologically undifferentiated, hyaline.

**COMMENTARY**—Several conflicting accounts of this name have been published as a result of different interpretations of Boudier’s (1881) illustration and brief description (see Mueller & Sundberg, 1981; Contu, 1986). While designating Boudier’s illustration as lectotype adheres to the ICBN (Greuter et al., 1988), it does not resolve the nomenclatural and taxonomic confusion that has been associated with this epithet. To stabilize the application of this epithet, the collection originally proposed as neotype (Mueller, 1987) is designated the “representative specimen.”

Although collected 23 years after the original publication date, this is the only collection of Boudier’s labeled *C. proxima* at UC. Thus, it is the only authentic material from which to designate a representative specimen. Basidiospore data of this collection closely fit those in the original description (“spores ovales, filament on echinulees”). Although difficult to discern with certainty owing to possible preservation artifacts, the basidiomata appear to fit the morphological criteria as well.

This taxon is treated in detail in the section on North American taxa.

**Laccaria proximella** Singer *in* Singer and Moser, Mycopathol. Mycol. Appl. 26: 146–147. 1965. Figure 69d.

**TYPE**: Chile, Valdivia, Cordillera Pelada, 30 March 1963, Singer M3247 (barc!, paratype).

**MACROMORPHOLOGY** (**Teste** Singer, *ibid.*)—**Pileus** 20–34 mm broad, convex, depressed, dry, radiately fibrilllose, flesh-colored-brown (“incarnato-bruno,” Singer). **Lamellae** adnate or subinuplicate, subdistant, moderately thick, broad, flesh-colored (“carneolis,” Singer). **Stipe** up to 42 × 6.5 mm, equal or tapering toward apex, ± concolorous with pileus. **Basal mycelium** white. **Stipe context** flesh-colored, sordid purple toward base of stipe. **Basidiospores** white in mass.

**MICROMORPHOLOGY** (**Mihi**)—**Pileipellis** of interwoven hyphae with scattered fascicles of ± perpendicular hyphae, fascicles composed of 10–20 hyphae; terminal cells of fascicular hyphae (*N* = 10) 42–64 × 6.5–13 µm, filamentous, subclavate, subcapitate or capitulate, light yellowish brown in mass; walls up to 0.5 µm thick, pale yellowish brown; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae mostly 5.5–10 µm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (*N* = 15) 23–40 × 8–14.5 µm, clavate, hyaline; sterigmata (2–)4, up to 7.5 µm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (*N* = 30) (8.3–)8.7–11 × 6–8.3 µm (*x* = 9.6 ± 0.7 × 7.3 ± 0.6 µm), *Q* = 1.18–1.46 (*Q* = 1.3 ± 0.1), ellipsoidal to amygdaliform, hyaline, echinulate; echinulae 0.5–1–(2.3) µm long, crowded, occasionally with one or two long echinulae at apex; hilar appendix 1.4–1.8 µm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** 5–25 µm diam., tightly interwoven, morphologically undifferentiated, hyaline.

**COMMENTARY**—Singer and Moser (1965) reported sparse cheilocystidia (“cheilocystidiis admodum sparsis, filamentosis ± 3–3.7 µ latis, hyalinis”). The discrepancy between Singer’s account and this description may be due to poor rehydration or to the absence of cheilocystidia in the slide preparations examined.

This taxon is discussed in more detail under *L. proxima* in the section on North American taxa.


**TYPE**: USA, Wyoming, Foxpark, 14 August 1909, Lovejoy 83 (rm, holotype).

**MACROMORPHOLOGY** (**Teste** Lovejoy, *ibid.*)—**Pileus** 30–50 mm broad, plano-convex, slightly depressed, dry, glabrous, shining, rich reddish
brown over salmon; margin decurved, entire, paler than pileus. Lamellae strongly decurrent, close, thin, salmon yellow, becoming powdered with white basidiospores. Stipe 50 × 10 mm, fleshy, glabrous, subconcolorous with pileus, hollow. Basidiospores white in mass.

MICROMORPHOLOGY (Teste Lovejoy, ibid.)—Basidiospores 7–10.5 μm, globose, spiny.

COMMENTARY—No authentic material of this taxon could be found at RM, and no material referable to it was found during this study.

Laccaria laccata var. pseudobicolor Bon in Bon and Haluwijin, Doc. Mycol. 12 (46): 42. 1982. Figure 70a.

TYPE: France, Carvin, Pas-de-Calais, 21 October 1970, M. Bon 70428 (Herb. M. Bon!, holotype).

MACROMORPHOLOGY (Teste Bon, ibid.)—Pileus 20–30(–35) mm broad, convex to plane, slightly depressed, slightly squamulose at disc (in the manner of L. proxima), fibrillose toward margin, orange-brown ("fauve orangé"); margin incurved, crenulate. Lamellae adnate to arcuate, relatively distant, pale rose lilac. Stipe (40–)50–70 × 3–4 (–5) mm, tough, slightly fibrillose, ± concolorous with pileus, paler or rose lilac at apex, vinaceous brown at base. Context ± concolorous or paler than pileus; odor lacking; taste bland or amarescent. Basidiospores white in mass.

MICROMORPHOLOGY (Mihi)—Pileipellis of interwoven hyphae with ascending fascicles of hyphae; terminal cells of fasciculate hyphae 8–10 (–18) μm diam., with rounded apices, brownish in mass. Pileus trama morphologically undifferentiated. Lamellar trama parallel; hyphae mostly 5–18 μm diam., filamentous or barrel-shaped. Subhymenium morphologically undifferentiated. Basidia clavate; sterigmata 4. Pleurocystidia lacking. Cheilocystidia not observed. Basidiospores (excluding ornamentation) (6.5–)7–8.5(–9) × (5.5–)6–7(–7.5) μm (X = 8.3 ± 0.5 × 6.9 ± 0.4 μm), Q = 1.15–1.35; broadly ellipsoid, occasionally ellipsoid or subglobose, echinulate; echinulae 1–1.5 μm long, ≤ 1 μm wide at base; hilar appendix truncate.

COMMENTARY—This taxon is treated as a synonym of L. bicolor.


TYPE: Brazil, Apiahy, April 1888, Spegazzini 16080 (LPS!, holotype).

COMMENTARY—The type collection consists of part of a single poorly preserved basidioma. Although pencil drawings on the packet illustrate globose, echinulate basidiospores, all the observed basidiospores were globose to oblong, reticulate, and amyloid. I agree, therefore, with Singer’s (1950b, p. 136) view that this collection is referable to Russula.


TYPE: Brazil, Apiahy, June 1882, Spegazzini 16084 (LPS!, holotype).

COMMENTARY—The type collection consists of a single, small, moldy basidioma. No basidiospores could be found, although numerous echinulate conidia were observed. Pencil sketches on the packet illustrate a typical Laccaria-shaped basidioma and globose basidiospores, some echinulate, others nodulose. Singer (1943a, p. 17) transferred this name to Laccaria but did not give the basionym. In 1950a, Singer transferred the name to Marasmiellus, stating that an examination of the type specimen revealed only echinulate conidia and no basidiospores. Singer (1950a, pp. 190–191) based this new combination on a comparison of the type specimen with another collection, presumed contaxic, that had oblong, smooth basidiospores.

Laccaria pumila Fayod, Ann. Della R. Acc. di Agric. di Torino 35: 91. 1893. Figure 70b.


MACROMORPHOLOGY (Teste Fayod, ibid.)—Pileus 5 mm broad at first, campanulate, then 10–15 mm broad, plane, centrally depressed, strongly striate, undulate, mahogany color when moist, ochraceous when dry, disc darker. Lamellae adnexed, submarginate, flesh color. Stipe 20 × 1.5 mm, slightly thickened upward, flexuous, hollow, concolorous with pileus. Basal mycelium cottony, white.

MICROMORPHOLOGY (Mihi)—Pileus trama parallel, hyphae 3–7 μm diam., thin-walled, hyaline; cells morphologically undifferentiated. Subhymenium morphologically undifferentiated. Basidia 32–55 × 10–15 μm, clavate, hyaline; sterigmata 2,
Fig. 70. Representative basidiospores from type specimens: a, *L. laccata* var. *pseudobicolor* (holotype); b, *L. pumila* (neotype); c, *L. purpureobadia* (holotype); d, *L. trullissata* f. *rugulospora* (holotype). Scale line = 10 μm.
up to 15 μm long. Pleurocystidia lacking. Cheilocystidia not observed. Basidiospores (excluding ornamentation) (N = 30) (10.5)–11–15.5 × (9–) 9.5–12.5–(15) μm (μ = 12.5 ± 1.2 × 10.4 ± 1.1 μm), Q = (1)–1.05–1.3–(1.35) (Q = 1.18), subglobose to ellipsoid, rarely globose, hyaline, echinulate; echinulae 0.7–1.2 μm long, crowded; hilar appendix up to 2 μm long, prominent, truncate; plagae present.

COMMENTARY—The type collection consists solely of lamellar fragments, so no information on pileipellis morphology could be obtained.

Although an illustration was not cited in the protologue, a watercolor housed at G reflects Fa-yod’s concept of the taxon. The illustration matches the protologue and concept of the taxon presented here and by Mueller and Vellinga (1986).

This taxon is treated in detail in the section on North American taxa.

**Laccaria purpureobadia** Reid, Nova Hedwigia 11(Suppl.): 14–16. 1966. Figure 70c.

TYPE: England, Bedfordshire, Flitwick, Folleywood, 11 October 1959, Reid s.n. (kt, holotype).

**MACROMORPHOLOGY** (Teste Reid, *ibid.*)—Pileus 20–55 mm broad, convex, occasionally umboonate, soon conspicuously depressed or umbilicate, minutely scurfy-scaly, hygrophanous, uniformly dark purple-brown when fresh (“Seal Brown”), fading to light purple-brown (“Sorghum Brown”); margin smooth, becoming distinctly sulcate, usually with a scaly effusiveness. *Lamellae* adnexed, subdistant, up to 8 mm broad, entire, pale pinkish gray (“Pale Grayish Vinaceous”) becoming pinkish purple-brown (“Livid Brown”). **Stipe** 30–60 × 3.5–8 mm, equal, slightly felt fibrillose, solid becoming hollow, purplish pink (“Light Purplish Vinaceous”) at apex, dark purple-brown (between “Dark Livid Brown” and “Warm Blackish Brown”) at base. **Flesh** purplish pink (“Light Purplish Vinaceous”).

**MICROMORPHOLOGY** (Mihi)—Pileipellis of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 10–25 hyphae; terminal cells of fascicular hyphae (N = 10) 44–64(–92) × 6.5–11.5 μm, filamentous to subclavate, light yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown, often encrusted with light yellowish brown pigments; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Pileus trama** parallel, hyphae 3–12 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 32–57.5 × 8–12.5 μm, clavate, hyaline; sterigmata 4, up to 7.5 μm long. Pleurocystidia lacking. Cheilocystidia not observed. **Basidiospores** (excluding ornamentation) (N = 30) (7.4–)8.3–10.6 × 6–7.8 μm (μ = 9.1 ± 0.8 × 7.1 ± 0.6 μm), Q = 1.12–1.41(–1.54) (Q = 1.3 ± 0.1), broadly ellipsoid, ellipsoid, or amygdaliform, hyaline, echinulate; echinulae 0.3–0.8(–1.4) μm long; crowded; hilar appendix 1.3–1.8 μm long, prominent, truncate; plagae present; contents uniguttulate. **Basal mycelium hyphae** mostly 4.5–15 μm diam., tightly interwoven, hyaline; cells filamentous to barrel-shaped.

COMMENTARY—Although this appears to be a discrete taxon, I cannot make a decision on the affinities of this taxon until I see fresh material. Few reports of this taxon have been published (e.g., Phillips, 1981). Singer (1986) placed it in a separate stirps, *Purpureobadia*.


TYPE: Not located.

**MACROMORPHOLOGY** (Teste Larsen, *ibid.*)—**Pileus** 10–20 mm broad, depressed, thin, glabrous, pale. **Lamellae** adnate-decurrent, distant, thick, concolorous. **Stipe** short, thin, concolorous. **Basidiospores** white in mass.

**MICROMORPHOLOGY** (Teste Larsen, *ibid.*)—**Basidiospores** 8–9 μm diam., globose, verrucose.

COMMENTARY—No authentic material of this taxon could be located at c. This name is a homonym of *R. laccata* var. *rosella* f. *pusilla* Schroeter, which is treated as a synonym of *L. laccata* var. *laccata*.


TYPE: Not located.

**MACROMORPHOLOGY** (Teste Rolland, *ibid.*)—**Pileus** fresh color. **Stipe** concolorous.

**MICROMORPHOLOGY** (Teste Rolland, *ibid.*)—**Basidiospores** 10 μm diam., strongly reticulate.

COMMENTARY—Based on the original description, this taxon belongs in the Russulaeaceae.

**MUELLER: SYSTEMATICS OF LACCARIA** (AGARICALES) 123
Agaricus (Clitocybe) rudis Berkeley, J. Bot. (Hooker) 8: 131. 1856.

TYPE: Brazil, Rio Negro, Panure, February 1853, Berkeley 127 (k!, holotype).

COMMENTARY—Berkeley (1856) stated that although this taxon had the same habit of *A. laccatus*, it was obviously unique. Micromorphological analysis of this collection revealed the presence of elongate, smooth basidiospores. The lack of echinulate or finely roughened basidiospores excludes it from *Laccaria*.

Agaricus (Clitocybe) laccatus var. rufocarnea Fries, Epicr. syst. mycol. p. 79. 1836–1838.

TYPE: Lacking.

MACROMORPHOLOGY (Teste Fries, *ibid.*)—As in type variety, pileus becoming subochraceous when faded.

COMMENTARY—There is considerable variation in the color of faded basidiomata within *L. laccata sensu lato*. Because such variation does not justify segregation of separate taxa, this taxon is treated as a synonym of *L. laccata* var. *laccata*.

Laccaria trullisata f. rugulospora M. Lange, Meddel. Grønland 147: 30. 1955. Figure 70d.

TYPE: Greenland, Sondre Stromfjord, Sandflugsdalen, 24 September 1946, Lange 384 (cf!, holotype).

MACROMORPHOLOGY (Teste Lange, *ibid.*)—Diffsers from the type variety in its smaller size.

MACROMORPHOLOGY (Mihi)—Pileipellis of interwoven hyphae, no distinct fascicles of hyphae seen; terminal cells (*N* = 10) 33–64 × 5.5–9 μm, filamentous, subclavate or occasionally clavate, light yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. *Pileus trama* tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. Lamellar *trama* parallel; hyphae mostly 5.5–11 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. Subhymenium morphologically undifferentiated. *Basidia* (*N* = 15) 30–40 × 8–12.5 μm, clavate, hyaline; sterigmata 4, up to 12.5 μm. *Pleurocystidia* lacking. *Cheilocystidia* not observed. Basidiospores (excluding ornamentation) (*N* = 30) 11.5–14.7(–15.6) × (6.4–)7.4–8.7(–9.2) μm (̅*x* = 13.3 ± 1.1 × 8.0 ± 0.6 μm), *Q* = 1.43–1.83 (̅*Q* = 1.67 ± 0.11), ellipsoid to oblong, hyaline, echinulate; echinulae > 0.2(–0.5) μm long, distinct, crowded; hilar appendix 1.3–1.8 μm long, prominent, truncate; contents occasionally unguttulate.


TYPE: Scotland: Lake Katrin, 1 July 1964, Singer C4002 (BAFC!, holotype).

MACROMORPHOLOGY (Teste Singer, *ibid.*)—Pileus 20–29 mm, convex, centrally depressed, umbilicate, smooth and glabrous, slightly tomentose at disc under a hand lens, hygrophanous, reddish fawn color (6 D 12, M&P), paler toward margin; margin slightly sulcate. Lamellae adnate, crowded, broad, dull rose color. *Stipe* usually 80 × 3.5–5.5 mm, equal or narrowing toward the base, glabrous or slightly fibrillose, stuffed, concolorous with pileus, paler or whitish toward the base. *Basal mycelium* white. Basidiospores white in mass.

MICROMORPHOLOGY (Mihi)—Pileipellis of intertwined hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 15–30 hyphae; terminal cells of fascicular hyphae (*N* = 10) 40–55 × 5.5–10.5 μm, subclavate to clavate; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. *Pileus trama* tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. Lamellar *trama* parallel; hyphae mostly 2.5–11 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. Subhymenium morphologically undifferentiated. *Basidia* (*N* = 15) 30–40 × 8–12.5 μm, clavate, hyaline; sterigmata 4, up to 12.5 μm. *Pleurocystidia* lacking. *Cheilocystidia* not observed. Basidiospores (excluding ornamentation) (*N* = 30) 7–9.2 × 7–9.2 μm (̅*x* = 8 ± 0.6 × 7.9 ± 0.7 μm), *Q* = 1.107(–1.13) (̅*Q* = 1.01 ± 0.03), globose to subglobose, hyaline, echinulate; echinulae 1–1.8(–2.3) μm, crowded; hilar appendix 1.3–2.3 μm long, prominent, truncate; pleate present;

COMMENTARY—Singer (1967) reported infrequent cheilocystidia ("cheilocystides et cystidioles éparses, 14–26 × 3 μ, filamenteuses") and the occurrence of rare 2-sterigmate basidia.

This taxon is treated as a synonym of L. ohiensis.


TYPE: Lacking.

MACROMORPHOLOGY (Teste Britzelmayr, ibid.)—Pileus hygrophanous, gray or brownish gray. Lamellae rather decurrent. Stipe undulating.

MUELLER: SYSTEMATICS OF LACCARIA (AGARICALES)
MICROMORPHOLOGY (*Teste* Britzelmayr, *ibid.*)—
**Basidiospores** 5–7 μm diam., echinulate.

**Commentary**—The original description stated that this taxon was similar to *A. echinosporus*. The basidiospore dimensions provided in the protologue, however, are much smaller than those found in *L. tortilis (= *A. echinosporus*) or other known *Laccaria* species. Material that matched the protologue of this name was not encountered during this study. The decurrent lamellae and gray basidioma color suggest that this taxon may be referable to *Clitocybe*, not *Laccaria*.


**Type**: Ceylon, September 1869, Berkeley 1215 (k!, holotype; illustration only).

**Macromorphology** (*Teste* Berkeley & Broome, *ibid.*)—
**Pileus** 13 mm broad, subhemispherical, slightly umbilicate, dull flesh color covered with black flocculent specks. **Lamellae** few, adnate with decurrent teeth; margin serrate, concolorous, with black specks. **Stipe** subclavate, concolorous, covered with fine black floccii, especially near apex, solid.

**Commentary**—The illustration matches the protologue. Cooke (1884) included this name when he transferred taxa into *Laccaria*. Without micromorphological data, it is impossible to clarify the concept of this taxon, and its identity remains uncertain. Material that matches the protologue was not encountered during this study.

*Clitocybe laccata* var. *striatula* Peck, Annual Rep. New York State Bot. 48: 274. 1894. Figure 71b.

**Type**: USA, New York, Catskill Mountains, September, C. H. Peck s.n. (nys!, holotype).

**Macromorphology** (*Teste* Peck, *ibid.*, 1912)—
**Pileus** 12–20 mm broad, convex to plane, translucent-striate, thin, glabrous, hygrophanous, buff red, fading to grayish or pale buff. **Lamellae** adnate, distant, broad, pale flesh color. **Stipe** 15–30 × 1–2 mm, equal, fibrous, concolorous with pileus.

**Micromorphology** (*Mihi*)—**Pileipellis** of tightly interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 5–10 hyphae; terminal cells of fascicular hyphae (N = 10) 37.5–69 × 6–12 μm, undifferentiated, yellowish brown; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae mostly 3–10 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 35–46 × 10–14 μm, clavate, hyaline; sterigmata 4, up to 10.5 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) (7–)7.8–9.7(−12) × (7–)7.8–9.7(−12) μm (̄x = 8.8 ± 0.9 × 8.7 ± 0.9 μm), Q = 1(−1.06) (̄Q = 1.0 ± 0.02), globose, occasionally subglobose, hyaline, echinulate; echinulate 1.4–2.3(−)2.8 μm long, up to 1.3 μm wide at base, crowded; hilar appendix 1.3–2 μm long, prominent, truncate; plebe present; contents occasionally uniguttulate. **Basal mycelium** hyphae mostly 2–4 μm diam., tightly interwoven, morphologically undifferentiated, hyaline.

**Commentary**—The type collection appears mixed. Two distinct sets of basidiocarps can be segregated based on basidiospore size and length of basidiospore ornamentation. Because Peck (1895, 1912) stated that the taxon had large basidiospores, the description above is based on those basidiocarps that have large basidiospores. Lahaie (1981) concurred with this segregation of the type collection.

This taxon is treated in detail in the section on North American taxa.

*Laccaria laccata* var. *subalpina* Singer, Pl. Syst. Evol. 126: 365. 1977. Figure 71c.

**Type**: CSSR, Slovakia, Hohe Tatra, Solisko, 4 September 1974, Singer C5870 (rl!, holotype).

**Macromorphology** (*Teste* Singer, *ibid.*)—**Pileus** ± 26 mm broad, convex, glabrous, radially striate, slightly pellucid, hygrophanous, flesh brown, fading to pale flesh color; margin sinuose. **Lamellae** adnate, crowded to distant, moderately broad, dirty pale lilac-pink to violet pink when young, soon becoming flesh-rose color. **Stipe** 40–45 × 3.5–4 mm, equal, striate, tortulous, coarsely fibrous, not woolly or hoary, flesh-brown to brown. **Basal mycelium** white.

**Micromorphology** (*Mihi*)—**Pileipellis** of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; terminal cells of fascicular hy-
**Laccaria tetraspora** Singer, Mycologia 38: 689–690. 1946. Figure 72a.


**MACROMORPHOLOGY** (*Teste Singer, ibid.*)—**Pileus** 10–20 mm broad, convex, becoming plane and depressed, usually umbilicate, glabrous or fibrillose, pellucid, hygrophanous, rose flesh-col-

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**Agaricus (Clitocybe) sublacatus** Berkeley & Broome, J. Linn. Soc., Bot. 11: 519. 1871.

**TYPE**: Ceylon, Peradeniya, January 1869, *Berkeley 894* (k!, holotype).

**COMMENTARY**—Micromorphological analysis of this collection revealed the presence of ellipsoid, smooth basidiospores. Although Cooke (1884) included this name when he transferred taxa into *Laccaria*, the lack of echinulate or finely roughened basidiospores excludes it from *Laccaria*.

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**Laccaria laccata** var. *tretensis* Singer, Pl. Syst. Evol. 126: 367–368. 1977. Figure 71d.

**TYPE**: CSSR, Slovakia, Hohe Tatra, Mala Studena Dolina, 13 September 1974, *Singer C6001* (k!, holotype).

**MACROMORPHOLOGY** (*Teste Singer, ibid.*)—**Pileus** 14–20 mm broad, convex, not umbilicate or umbonate, moderately depressed in age, glabrous, in age appearing submentosete, fibrous, or subsquamous under hand lens, translucent striate at margin, hygrophanous, reddish brown to dark ochre reddish brown, fading to pallid flesh color. *Lamellae* adnate to subdecurrent, substistant, flesh-colored rose when fresh. **Stipe** 24–35(–50) × 2–3.5(–7) mm, equal or rarely thickened at base; at first glabrous, becoming sulcate and rough, flesh-colored brown to almost reddish brown, drying paler. *Basal mycelium* white. Basidiospores white in mass. Odor lacking or slightly raphanoid.

**MICROMORPHOLOGY** (*Mihi*)—Pileipellis of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 15–25 hyphae; terminal cells of fascicular hyphae (N = 10) 36–55 × 4–9 µm, filamentous to subclavate, abundant, hyaline. Basidiospores (excluding ornamentation) (N = 30) (6.4–)7–7.8(–8.3) × (6–)6.4–7.4 µm (X = 7.5 ± 0.5 × 6.8 ± 0.3 µm), Q = 1–1.16(–1.22) (Q = 1.1 ± 0.06), subglobose or occasionally globose, hyaline, echinulate; echinulae (0.8–)1.4–1.8 µm long, crowded; hilar appendix 1.3–1.8 µm long, prominent, truncate; plage present; contents occasionally uniguttulate. Basal mycelium hyphae 2.5–11 µm diam.; tightly interwoven, hyaline; cells barrel-shaped.

**COMMENTARY**—Although the basidiospore shape and size fit the original circumscription, basidiospore ornamentation was longer than that reported by Singer (1973).

This taxon is treated as a synonym of *L. laccata* var. *pallidifolia*.

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phae (N = 10) 39–57.5 × 8–13 µm, filamentous to subclavate, light yellowish brown in mass; walls up to 0.5 µm thick, light yellowish brown; contents hyaline. *Pileus trama* tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. Lamellipellis parallel; hyphae thin-walled, hyaline to light yellowish brown; cells barrel-shaped. Subhymenium morphologically undifferentiated. Basidia (N = 15) 32–42 × 8–9.5(–11) µm, clavate, hyaline; sterigmata 4, up to 6.5 µm long. Pleurocystidia lacking. Cheilocystidia (N = 5) 30.5–35 × 3.5–4.5 µm, filamentous to subclavate, abundant, hyaline. Basidiospores (excluding ornamentation) (N = 30) (6.4–)7–7.8(–8.3) × (6–)6.4–7.4 µm (X = 7.5 ± 0.5 × 6.8 ± 0.3 µm), Q = 1–1.16(–1.22) (Q = 1.1 ± 0.06), subglobose or occasionally globose, hyaline, echinulate; echinulae (0.8–)1.4–1.8 µm long, crowded; hilar appendix 1.3–1.8 µm long, prominent, truncate; plage present; contents occasionally uniguttulate. Basal mycelium hyphae 2.5–11 µm diam.; tightly interwoven, hyaline; cells barrel-shaped.

**COMMENTARY**—Although the basidiospore shape and size fit the original circumscription, basidiospore ornamentation was longer than that reported by Singer (1973).

This taxon is treated as a synonym of *L. laccata* var. *pallidifolia*.
Fig. 72. Representative basidiospores from type or representative specimens: a, *L. tetraspora* (holotype); b, *A. tortilis* (representative specimen); c, *L. trichodermophora* (holotype); d, *A. trullissatus* (lectotype). Scale line = 10 μm.
ored (“incarnato-rosea,” Singer) or brownish flesh-colored (“brunneolo incarnato,” Singer) when moist, pale purple-pink (“pallid-purpuracentrosello,” Singer) when dry; margin striate when fresh, sulcate when dry. Lamellae adnate to decurrent, distant, broad, rose flesh-colored (“incarnato-roseus,” Singer), pulvulrent from basidiospores. Stipe 10–30 × 1.5–2.5 mm, equal or with expanded base, dry, subglabrous, solid, almost concolorous with pileus. Basal mycelium white, scant to copious.

**Micromorphology** (Mihi)—Pileipellis of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; terminal cells of fascicular hyphae (N = 10) 26–62 × 7.5–11.5 μm, filamentous, subclavate or subcapitate, light yellowish brown in mass; walls up to 0.5 μm thick, pale yellowish brown; contents hyaline in mass. Pileus trama tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. Lamellar trama parallel; hyphae 3–15 μm, thin-walled, hyaline to light yellowish brown; cells barrel-shaped. Subhymenium morphologically undifferentiated. Basidia (N = 15) 42–55 × 10–13 μm, clavate, hyaline; sterigmata 4, up to 8.5 μm long. Pleurocystidia lacking. Cheilocystidia not observed. Basidiospores (excluding ornamentation) (N = 30) (7.8–)8.7–11 × 8.3–10(–10.6) μm (± = 9.3 ± 0.7 × 9.1 ± 0.5 μm), Q = 0.94–1.2 (Q = 1.02 ± 0.1), globose to subglobose, hyaline, echinulate; echinulae (0.8–)1.4–2.3(–2.8) μm long, relatively sparse; hilar appendix 1.8–2.3 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. Basal mycelium hyphae mostly 2–5 μm diam., tightly interwoven, morphologically undifferentiated, hyaline.

**Commentary**—Singer (1946) reported the presence of inconspicuous cheilocystidia (“cheilocystids praesentibus sed haud conspicuis”). The discrepancy between Singer’s description and my observations may be due to poor rehydration of the specimen or to the absence of cheilocystidia in the preparations examined.

This taxon is treated as a synonym of *L. ohiensis*.

**Russuliopsis thymifila** Velenovsky, Novitates Mycologicae. p. 77. 1939.

**Type**: Lacking.

**Macromorphology** (Teste Velenovsky, *ibid.*)—Pileus 3–6 mm broad, convex, becoming plane, finely rimose, hygrophanous, cinnamon color when fresh, becoming ochraceous. Lamella adnate to arcuate, crowded, thick, broad, flesh color to cinnamon color. Stipe 3 times longer than pileus diameter, flexuous, glabrous, concolorous.

**Micromorphology** (Teste Velenovsky, *ibid.*)—Basidiospores 5–7 μm diam., globose, smooth, uniguttulate, hyaline.

**Commentary**—Type material of this taxon was not found at either PRM or PRC. Based on the original description, it is not a *Laccaria*, but there is insufficient data for an accurate determination of the disposition of this taxon.

**Agaricus tortilis** Bolton, Hist. Fung. Halifax vol. 1. p. 41, tab. XLI, fig. A. 1788. Figure 72b.


**Macromorphology** (Mihi, From representative specimen)—Pileus very small to small, convex, becoming plane to uplifted, striate, dark reddish brown; margin lobed, crumpled and distorted. Lamellae dusky color. Stipe 6 mm long, dusky flesh color.

**Macromorphology** (Mihi). From representative specimen)—Pileipellis of interwoven hyphae with scattered fascicles or ± perpendicular hyphae; terminal cells of fascicular hyphae (N = 5) 32–55 × 6.5–12.5 μm, filamentous, subclavate or occasionally clavate; walls up to 0.5 μm thick, pale yellowish brown; contents hyaline to light yellowish brown. Pileus trama tightly interwoven, morphologically undifferentiated, hyaline, pale yellowish brown toward pileipellis. Lamellar trama parallel; hyphae 3–13 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. Subhymenium morphologically undifferentiated. Basidia (N = 15) 40–60 × 9–13 μm, clavate, hyaline; sterigmata 2, up to 11 μm long. Pleurocystidia lacking. Cheilocystidia not observed. Basidiospores (excluding ornamentation) (N = 30) 11.5–14.7(–17) × 11.5–14.7(–17) μm (± = 13.4 ± 1.3 × 13.4 ± 1.3 μm), Q = 1(–1.04) (Q = 1 ± 0.01), globose, hyaline, echinulate; echinulae 2.3–4 μm long, 1.3–1.8 μm wide at base, crowded; hilar appendix 1.3–2.3 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. Basal mycelium hyphae mostly 3–5.5 μm diam., tightly interwoven, morphologically undifferentiated, hyaline.
COMMENTARY—At least two conflicting interpretations of this epithet have been used, based on the macromorphological information available in Bolton’s (1788) protologue and illustration (Mueller, 1987). As discussed in the Commentary under the type of *L. proxima*, conflicting interpretations of epithets are not always resolved by designating illustrations as lectotypes. To stabilize the application of *L. tortilis*, the collection that was proposed as a neotype by Mueller (1987) was redesignated as a representative specimen (Mueller, 1991a).

Although no specimen of *A. tortilis* is available from the vicinity of Halifax, owing to disruption of the original habitat, the representative specimen was collected in an area similar to Bolton’s original collecting sites (R. Watling, pers. comm.). Although the collection lacks morphological notes, it shows obvious resemblance to Bolton’s plate and fits well within the circumscription of the common usage of the epithet.

*Laccaria trichodermaphora* G. M. Mueller, Myco- taxon 20: 112–114. 1984. Figure 72c.

TYPE: USA, Mississippi, Harrison Co., DeSoto National Forest, Harrison Experimental Forest, Road H-6, 5 December 1980, G. M. Mueller 1062 (TENN 42523) (TENN!, holotype).

MACROMORPHOLOGY (*Mihi*)—Pileus 6–40 mm broad (x = 21 mm), convex to plane, becoming uplifted, occasionally depressed, not striate, finely fibrillose when young, becoming finely scaly due to cuticular defraction, hygrophanous, brownish orange (“Auburn,” “Sanford’s Brown,” “Burnt Sienna,” or “Cinnamon-Rufous”), occasionally darker at disc (“Kaiser Brown”); margin decurved to plane, entire to eroded; context 1–2 mm thick, tapering quickly to margin, flesh-colored (“Pale Vinaceous-Pink”). *Lamellae* sinuate to adnate, close to subdistant, thin, flesh-colored (“Pale Flesh Color” to “Salmon-Buff”). *Stipe* 25–85 x 2–7 mm (x = 53 x 4 mm), equal or occasionally tapering toward base, dry, finely fibrillose, inconspicuously striate, brownish orange to reddish brown (“Hazel,” “Pecan Brown,” “Cacao Brown,” or “Kaiser Brown”), context stuffed becoming hollow, flesh-colored (“Hydrangea-Pink” to “Pale Vinaceous-Pink”). *Basal mycelium* white. *Basidiospores* white in mass.

MICROMORPHOLOGY (*Mihi*)—Pileipellis of interwoven hyphae with numerous large fascicles of ± perpendicular hyphae, forming a trichodermium in young specimens and at the disc; fascicles composed of more than 30 hyphae; terminal cells (N = 10) 29–69 x 12–20 μm, filamentous, clavate or occasionally capitate; walls up to 0.5 μm thick, light yellowish brown; contents hyaline to light yellowish brown. *Pileus trama* tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. *Lamellar trama* parallel; hyphae mostly 5.5–11 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. *Subhymenium* morphologically undifferentiated. *Basidia* (N = 10) 31–43 x 7.5–10.5 μm, clavate, hyaline; sterigmata 4, up to 6 μm long. *Pleurocystidia* lacking. *Cheilocystidia* not observed. *Basidiospores* (excluding ornamentation) (N = 30) (6.8–)7.4–9.2 x 6.4–8.3 μm (x = 7.9 ± 0.5 x 7.2 ± 0.6 μm), Q = 1–1.22 (Q = 1.1 ± 0.06), subglobose to broadly ellipsoidal, infrequently globose, hyaline, echinulate, echinulae 0.8–1.8 μm long; hilar appendix 1.3–1.8 μm long, prominent, truncate; plaque present; contents occasionally uniguttulate. *Basal mycelium hyphae* mostly 3–5.5 μm diam., hyaline, morphologically undifferentiated.

**SOMATIC CULTURE**

**MAT MORPHOLOGY**—PDA: **Radius** at week 3 = 15–19 mm, week 6 = 32–38 mm; **mat** felty, moderately thick, tightly interwoven, tightly appressed to agar surface, in time forming pruinose aerial layer away from plug, not translucent, deep bright violet, fading to violet, finally to light orange-brown near plug; **margin** up to 4 mm broad, silky to subfleshy, thin, entire to slightly uneven, light violet to white; **plug** concolorous with mat; **hyphae** mostly morphologically undifferentiated, occasional subcoralloid or irregularly swollen. **MMN:** **Radius** at week 3 = 26–44 mm, week 6 = 54–62 mm; **mat** subfleshy, becoming felty, thin, with 2 or 3 narrow (2–3 mm) slightly thicker concentric zones, interwoven, tightly appressed to agar surface, slightly translucent, light violet, thicker zones somewhat darker; **margin** not well differentiated from mat, silky to subfleshy, sinuate, light violet; **plug** concolorous with mat; **hyphae** mostly morphologically undifferentiated, occasionally subcoralloid. **MEA:** **Radius** at week 3 = 20–22 mm, week 6 = 38–47; **mat** subfleshy, thin, loosely interwoven, tightly appressed to agar surface, translucent, white; **margin** 1–2 mm broad, thin, silky, becoming subfleshy, entire, white; **plug** white; **hyphae** mostly morphologically undifferentiated, occasionally irregularly swollen.

**COMMENTARY**—This taxon is treated in detail in the section on North American taxa.
**Agaricus (Clitocybe) trullissatus** Ellis, Bull. Torrey Bot. Club 5: 45. 1874. Figure 72d.

**TYPE:** USA, New Jersey, Newfield, no date, *Ellis s.n.* (NYS!, lectotype fide Mueller, 1987).

**MACROMORPHOLOGY (Teste Ellis, *ibid.***—Pileus plano-convex, becoming depressed, fibrose-squamose, smoother at disk, fleshy; margin thin. *Lamellae* adnate with decurrent tooth, distant, coarse, thick, unequal, purple-violet, becoming dark brick red, white pulverulent. Stipe club-shaped, radiating, fibrillose, stuffed; flesh violet-purple; stipe base tomentose, covered with sand.

**MICROMORPHOLOGY (Mihi)**—Pileipellis of interwoven hyphae with widely scattered fascicles of ± perpendicular hyphae, fascicles composed of 10–25 hyphae; terminal cells of fascicular hyphae (*N* = 10) 33–64.5 × 8.5–14(–16) μm, subclavate, clavate or broadly clavate, light yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. *Pileus trama* tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. *Lamellar trama* parallel; hyphae mostly 6.5–14.5 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. *Subhymenium* morphologically undifferentiated. Basidia (*N* = 15) 30–53 × 9–12.5 μm, clavate, hyaline; sterigmata 4, up to 8 μm long. *Pleurocystidia* lacking. *Cheilo-cystidia* not observed. Basidiospores (*N* = 30) (13.8–14.7–21.6(–36.3) × (5.5–)6–7.8(–8.3) μm (*Q* = 1.99–3.31(–6.05) (*Q* = 2.68 ± 0.7), subfusciform to fusiform-ellipsoidal, hyaline, finely roughened, not echinulate; hilar appendix 1.3–1.8 μm long, prominent, truncate; contents occasionally uniguttulate, rarely biguttulate. *Basal mycelium hyphae* mostly 3–15 μm diam., tightly interwoven, hyaline; cells filamentous to barrel-shaped.

**COMMENTARY**—Ellis (1874) did not designate a type. Two possible sources for a type exist: (1) the collection at NYS labeled COTYPE, which included a note in Ellis's handwriting giving collection data and stating that it is a new species; and (2) specimens in Ellis's exsiccata "Fungi of North America." Because the exsiccata was not distributed until 1875-1885 (Stafleu & Cowan, 1976), there is no way of knowing if the included specimens of *A. trullissatus* were in Ellis's hands at the time he designated the species. For these reasons, I have chosen to designate the NYS collection as the lectotype and consider the material in the exsiccata as authentic material.

This taxon is treated in detail in the section on North American taxa.


**MACROMORPHOLOGY (Teste Singer, *ibid.*)**—Pileus 13–21 mm broad, soon concave (13 B 9/11, M&P). *Lamellae* broad, rounded, not decurrent (10 A 6, M&P). *Stipe* 43–56 × 2.3–3.5 mm, 5–10 mm broad at widest point, more or less ventricose, near (7 H 12, M&P). *Basal mycelium* white.

**MICROMORPHOLOGY (Mihi)**—Pileipellis of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 10–20 hyphae; terminal cells of fascicular hyphae (*N* = 10) 40–60 × 7.5–17.5 μm, subclavate to clavate; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. *Pileus trama* tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. *Lamellar trama* parallel; hyphae mostly 4–12.5 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. *Subhymenium* morphologically undifferentiated. Basidia (*N* = 15) 34–48 × 10–13.5 μm, clavate, hyaline; sterigmata 4, up to 9 μm long. *Pleurocystidia* lacking. *Cheilocystidia* not observed. Basidiospores (excluding ornamentation) (*N* = 30) (7–)7.8–9.2(–10) × (7–)7.8–9.2(–10) μm (*Q* = 8.4 ± 0.6 × 8.3 ± 0.6 μm), *Q* = 1–1.06 (*Q* = 1.0 ± 0.02), globose, rarely subglobose, hyaline, echinulate; echinulae 0.8–1.8 μm long, crowded; hilar appendix 1.3–1.8 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. *Basal mycelium hyphae* mostly 2–4.5 μm diam., morphologically undifferentiated, tightly interwoven, hyaline.

**COMMENTARY**—The holotype consists of a single damaged basidioma in which many of the lamellae have been eaten by insects.

This taxon is treated as a synonym of *L. ohiensis*.

**Laccaria vinaceaovallanea** Hongo, Mem. Shiga Univ. 21: 62. 1971. Figure 73b.

MACROMORPHOLOGY (Teste Hongo, *ibid.)*—

**Pileus** 40–60 mm broad, convex, becoming expanded, occasionally umbilicate or depressed, not viscid, radially striate, subsulcate, furfuraceous, especially at disc, brownish vinaceous ("Russet-Vinaceous," "Vinaceous-Buff," etc.); flesh thin, firm, concolorous, with slight farinaceous odor. **Lamellae** adnate to subdecurrent, distant, thick, 4–6 mm broad, subconcolorous. **Stipe** 50–80 × 6–8 mm, equal, firm, fibrous, striate, concolorous with pileus, solid or hollow. **Basal mycelium** white. **Basidiospores** white in mass.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 5–10 hyphae; terminal cells of fascicular hyphae (*N* = 10) 34.5–48 × 6–10.5 μm, filamentous, subclavate or clavate, light yellowish brown in mass; walls up

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**Fig. 73.** Representative basidiospores from type specimens: a, *L. tetraspora* var. *valdiviensis* (holotype); b, *L. vinaceoavellanea* (holotype); c, *L. vinaceobrunnea* (holotype); d, *L. violaceoniger* (holotype). Scale line = 10 μm.
to 0.5 μm thick, light yellowish brown; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae mostly 3–10 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 28.5–39 × 8.5–13.5 μm, clavate, hyaline, not rehydrating well; sterigma 4, up to 8 μm long. **Pleurocystidia** lacking. **Chelioctydia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) (6.4–)7.4–9.2(–9.7) × (6.4–)7.4–9.2(–9.7) μm (\( \bar{x} = 8.2 \pm 0.7 \times 8.06 \pm 0.7 \mu m \)), \( Q = 1–1.06(–1.12) \) (\( Q = 1.02 \pm 0.03 \)), globose to subglobose, hyaline, echinulate; echinulae 1.4–2.8(–3.2) μm long, not crowded; hilar appendix 1.3–1.8 μm long, prominent, truncate; plebe present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 3.5–7 μm diam., morphologically undifferentiated, tightly interwoven, hyaline.

**COMMENTARY**—This taxon can be separated from *L. laccata* by its darker, dull color (Hongo, 1971).

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**Laccaria vinacea brunnea** G. M. Mueller, Mycota 20: 114–115. 1984. Figure 73c.

**TYPE:** USA, Louisiana, Tammany Parish, Fontainebleu State Park, under *Quercus virginiana*, 9 December 1980, G. M. Mueller, 1120 (TENN!, holotype).

**MACROMORPHOLOGY** (*Mihi*)—**Pileus** 7–26 mm broad (\( \bar{x} = 15 \) mm), convex, depressed, occasionally striate when wet, finely fibrillose, occasionally becoming finely scaly, hygrophanous, when young and fresh brownish vinaceous (“Dark Vinaceous-Brown” to “Hay’s Brown”) becoming reddish brown (“Walnut Brown” to “Cameo Brown”), fading lighter (near “Cinnamon-Rufous” to “Light Ochraceous-Buff”); margin decurved to plane, entire to eroded; context 1–2 mm thick, tapering quickly to margin, light brownish vinaceous (“Light Brownish Vinaceous” to “Vinaceous-Fawn”). **Lamellae** adnate to arcuate, subdistant, thick, broad, violaceous to vinaceous (“Purplish Lilac” to “Purplish Vinaceous”). **Stipe** 7–48 × 2–6 (\( \bar{x} = 25 \times 3.5 \) mm), equal, occasionally bulbous, dry, fibrillose, some fibrils recurved, not striate, ± concolorous with pileus, when young and at apex (“Brownish Vinaceous” to “Deep Brownish Vinaceous”), some fading to orange-brown (near “Hazel”); ground color buff (near “Light Ochraceous Buff”); fibrils darker (“Hazel” to “Vinaceous-Brown”). **Basal mycelium** violet. **Basidiospores** white in mass.

**MICROMORPHOLOGY** (*Mihi*)—**Pileipellis** of interwoven hyphae with numerous ± perpendicular hyphae, nearly forming a palisadoderm; terminal cells (N = 10) 42–50.5 × (4.5–)8.5–10 μm, filamentous to clavate, hyaline to light vinaceous; walls up to 0.5 μm thick; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline to light olive brown in mass. **Lamellar trama** parallel; hyphae thin-walled, hyaline; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 10) 42–50.5 × (4.5–)8.5–10 μm, clavate, hyaline, sterigma 4, up to 8.5 μm long. **Pleurocystidia** lacking. **Chelioctydia** (N = 10) 31.5–64.5 × 5.5–11 μm, filamentous to clavate, abundant, hyaline. **Basidiospores** (excluding ornamentation) (N = 30) (7.4–)8.3–10 × (6.4–)7.8–9.2(–9.7) μm (\( \bar{x} = 9 \pm 0.7 \times 7.8 \pm 0.6 \mu m \)), \( Q = 1.05–1.24 \) (\( Q = 1.15 \pm 0.05 \)), subglobose to ellipsoid, hyaline, echinulate; echinulae 0.8–1.8 μm long, crowded; hilar appendix 1.3–2 μm long, prominent, truncate; plebe present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 3–5.5 μm diam., tightly interwoven, hyaline.

**COMMENTARY**—This taxon is treated in detail in the section on North American taxa.

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**Agaricus (Clitocybe) laccatus var. [obscure] violacea** Fries, Epicr. syst. mycol. p. 79. 1836–1838.

**TYPE:** Lacking.

**MACROMORPHOLOGY** (*Teste Fries, ibid.*)—**Pileus** drying grayish.

**COMMENTARY**—Much variation exists in the color of dried basidiomata of *Laccaria* and this character should not be used to delimit taxa. This taxon, therefore, is treated as a synonym of *L. laccata* var. *laccata*.

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**Laccaria violaceousiger** Stevenson, Kew Bull. 19: 4. 1964. Figure 73d.

**TYPE:** New Zealand, Nelson, Dun Mt. tract, 25 April 1949, Stevenson, 506 (k!, holotype).

**MACROMORPHOLOGY** (*Teste Stevenson, ibid.*)—**Pileus** 15–35 mm broad, convex, becoming plane, appearing velvety owing to small floccose scales,
fusco-fuscos black; margin inrolled. Lamellae adnexed to decurrent, thick, purple to grayish lavender, often with white mealininess. Stipe 25–50 × 3–10 mm, swollen at base, floccose striate to subscaly; apex purple; base vinaceous brown.

MICROMORPHOLOGY (Mihi) — Pileipellis of interwoven hyphae with numerous scattered large fascicles of ± perpendicular hyphae; fascicles composed of 10–30 hyphae; terminal cells of fascicular hyphae (N = 10) 24–67 × 8–11, filamentous, subclavate, clavate or occasionally apiculate, dark yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown; contents dark yellowish brown. Pileus trama tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. Lamellar trama parallel; hyphae mostly 3–10 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. Subhymenium morphologically undifferentiated. Basidia (N = 15) 31–47 × 8.5–11.5 μm, clavate, hyaline; sterigmata 4, up to 6 μm long. Pleurocystidia lacking. Cheilocystidia (N = 10) (21–)29–39 × 2.5–6.5 μm, thin, filamentous, subclavate or strigulose, scattered, hyaline; lamellar edge nearly sterile. Basidiospores (excluding ornamentation) (N = 30) (6.4–)7–7.8 × (6.4–)7–7.8 μm (μ = 7.4 ± 0.4 × 7.3 ± 0.4 μm), Q = 1–1.07 (–1.13) (Q = 1.02 ± 0.03), gbose, occasionally subgbose, hyaline, echinulate; echinulae 0.8–1.8 (–2.3) μm long, crowded; hilar appendix 1.3–2.3 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. Basal mycelium hyphae mostly 3–7 μm diam., morphologically undifferentiated, tightly interwoven, hyaline; walls up to 0.5 μm thick.

COMMENTARY — The affinities of this taxon with other species of *Laccaria* are unknown. The coloration of the basidioma given in the protologue is unique in the genus.
color (near 6.1-10, M&P); margin bright orange-brown to flesh color or subconcolorous. Lamellae adnate to subdecurrent, crowded, becoming subdistant, up to 8 mm broad, ventricose, whitish flesh color at first, becoming pale purple or pale lilac, covered with white spores. Stipe 25-90 x 2.5-14 mm, equal or tapering toward apex, almost glabrous when young, longitudinally striate when mature, ± concolorous with pileus. Basal mycelium white.

Micro morphology (Mihi)—Pileipellis of interwoven hyphae with scattered, large fascicles of ± perpendicular hyphae; fascicles composed of 15-30 hyphae; terminal cells of fascicular hyphae (N = 10) 38-69 x 6.5-14.5 μm, filamentous, subclavate or clavate, light yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. Pileus trama tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. Lamellar trama parallel to subparallel; hyphae 2.5-9 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. Subhymenium morphologically undifferentiated. Basidia (N = 15) 33-44 x 8-11 μm, clavate, hyaline; sterigmata 4, up to 7 μm long. Pleurocystidia lacking. Cheilocystidia not observed. Basidiospores (excluding ornamentation) (N = 30) (7.4-)8.3-9.7(-11) x (6-)6.4-7.8(-8.7) μm (μ = 9 ± 0.7 x 7.1 ± 0.5 μm), Q = (1.16-)1.2-1.33(-1.45) (Q = 1.27 ± 0.06), broadly ellipsoid to ellipsoid, hyaline, echinulate; echinulae 0.5-1.4(-1.8) μm long, crowded; hilar appendix 1.3-1.8 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. Basal mycelium hyphae mostly 4-22 μm diam., tightly interwoven, hyaline to light yellowish brown in mass; cells occasionally morphologically undifferentiated, barrel-shaped.

Commentary—Singer (1977) reported sparse cheilocystidia ("cystidiis vesiculosis inconstanter et sparse prae sentibus"). The discrepancy between Singer's description and my observation may be due to poor rehydration or to the absence of cheilocystidia in the examined preparations.

This taxon is treated as a synonym of L. laccata var. laccata.


Type: Argentina, Neuquén, Bahía López, 22 November 1964, Singer M4063 (BAFC!, lectotype nov.).

Macromorphology (Teste Singer, ibid.)—Pileus 8-25 mm broad, hemispherical-convex at first, becoming planate or irregularly depressed, ± glabrous, slightly pellucid-striate, hygrophanous, dull flesh-colored rose to dull rose. Lamellae adnate, distant, broad, dull rose-colored. Stipe usually 60 x 5 mm, equal, compressed or irregular, subglabrous or slightly fibrillolose, reddish brown to rose brown. Basal mycelium white. Basidiospores white in mass.

Micro morphology (Mihi)—Pileipellis of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 5-15 hyphae; terminal cells of fascicular hyphae (N = 10) 39-64 x 5-9.5 μm, filamentous, subclavate or rarely clavate; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. Pileus trama tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. Lamellar trama parallel; hyphae mostly 3-11 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. Subhymenium morphologically undifferentiated. Basidia (N = 15) 39-53 x 10-13 μm, clavate, hyaline; sterigmata 4, up to 9.5 μm long. Pleurocystidia lacking. Cheilocystidia not observed. Basidiospores (excluding ornamentation) (N = 30) (7-)7.8-9.7 x (7-)7.8-9.7 μm (μ = 8.6 ± 0.7 x 8.6 ± 0.7 μm), Q = 1(-1.05) (Q = 1 ± 0.01), globose, rarely subglobose, hyaline, echinulate; echinulae (0.8-)1.4-2.3 μm long, crowded; hilar appendix 1.4-2.2 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. Basal mycelium hyphae mostly 2-5 μm diam., morphologically undifferentiated, tightly interwoven, hyaline.

Commentary—In the protologue, Singer (1967) cited four collections that he had studied but failed to designate a type specimen. Of the three collections sent from BAFC and all cited by Singer, M4063 had the largest number of basidiomata and was in the best condition. Collection Singer M4063 was designated the neotype for these reasons.

Singer (1967) reported the basidiospore ornamentation length as ‘1.0-1.5 μ,’ which is smaller than that presented above. The major delimiting character between var. xena and var. tetraspora is that the former has relatively shorter basidiospore ornamentation. The discrepancy between Singer's data and mine, therefore, becomes significant. He also reported the occasional presence of bisterigmate basidia, which I did not see in the collection that I examined.

This taxon is treated as a synonym of L. ohiensis.
Additions to Type Studies

Laccaria laccata var. crispa A. Thesleff, Bidrag till Kännedom af Finlands natur och folk 79: 46. 1920.

TYPE: Finland.

COMMENTARY—I have not examined the type specimen or seen the description for this taxon. The epithet is listed in Index of Fungi, vol. 5, part 18, 1989.


TYPE: Italy, Castelfusano-Roma, no. 148/87 (herbarium V. Migliozzi, holotype).

COMMENTARY—This taxon differs from the type variety by having large cheilocystidia (45–80 [-110] × 9–14[-16] μm). Although it is not listed in the synonymy section, I treat this taxon as a synonym of L. laccata var. pallidifolia.


TYPE: Sardinia, Contu 86/1109/01 (cag, holotype).

COMMENTARY—This taxon differs from the type variety by being more robust, more squamulose, and pallid ochraceous. The basidiospores are reported as being globose and 9–11.5 μm in diam. Although it is not listed in the synonymy section, I treat this taxon as a synonym of L. laccata var. pallidifolia.


TYPE: India, Punjab, Kulu-valley, Manali, 24 August 1964, Bas 4233 (l., holotype).

COMMENTARY—I have not examined the type specimen. This taxon appears to be a discrete species that is phenetically similar to L. violaceonigra.


TYPE: India, Uttar Pradesh, Mussooree, Oak-Villa, 16 September 1964, Bas 4403 (l., holotype).

COMMENTARY—I have not examined the type specimen. It primarily differs from L. laccata var. pallidifolia by having short hairs that cover the stipe.


TYPE: Sardinia, no. 84395 (herbarium M. Bon, holotype).

COMMENTARY—This taxon differs from the type variety in color (rosy) and habitat (xerophytic area under Quercus). Basidiospores are reported as globose with echinulae 1–1.5 μm long. Although it is not listed in the synonymy section, I treat this taxon as a synonym of L. laccata var. pallidifolia.


TYPE: India, Sikkim.

COMMENTARY—I have not examined the type specimen or seen the description for this taxon. The epithet is listed in Index of Fungi, vol. 5, part 15, 1988.
actions of British Mycological Society Supplement, 168 pp.


——. 1982b. Citation of authors’ names and the typification of names of fungal taxa published between 1753 and 1832 under changes in the code of nomenclature enacted in 1981. Mycologia, 74: 250–255.


SCOPOLI, J. A. 1772. Flora Cariniiola Exhibens, 2nd ed. vol. 2. Trattner, Viennae, 496 pp., index.


——. 1943a. Das system der Agaricaceae III. Annales Mycologici (Berlin), 41: 1–189.

——. 1943b. Type studies on Basidiomycetes. II. Mycologia, 35: 142–163.


SPAGAZZINI, C. 1880. Fungi Argentini. Anales de Sociedad Cientifica Argentina, 10: 123.


Appendix A. Specimens Examined

Laccaria amethysteo-occidentalis

CANADA

British Columbia: Victoria, Beaconhill Park, 17.XI.1941, 10686 (DAOM); same locality, 25.XI.1941, F10688 (DAOM); Victoria Island, Saanich, Braefoot, 1.XII.1941, F10677 (DAOM); Victoria, X.1956, 54064 (DAOM); Victoria, Thetis Park Nature Sanctuary, 7.X.1959, 67060 (DAOM); Rubble Creek, off Squamish Highway, 8.X.1966, coll. Flegel (NY); Alice Lake Provincial Park campground, 3.X.1981, 42526 (TENN, Holotype); Alice Lake Provincial Park campground, 7.X.1981, 42566 (TENN).

UNITED STATES


Laccaria amethystina

CANADA


Nova Scotia: Kings Co., Aylesford Lake, 9.VIII.1936, 110936 (DAOM); same locality, 1.IX.1972, Harrison 11880; Vesivius, 7.VII.1972, Harrison 11544 (MICH); Kentville, 25.VIII.1952, 111858 (DAOM); Paradise, 29.VIII.1953, 39102 (DAOM).

Ontario: Magnetawan, 6.IX.1921, coll. Kelly (MICH); Petawawa Forestry Experiment Station,
24.VII.1938, 8681 (DAOM); Ramsayville, 10.VIII.1962, 89296 (DAOM); Ottawa, Cromwell Drive, 18.VII.1967, coll. Groves & Dyer (srsl); St. Lawrence Island National Park, Thwartway Island, 26.VII.1976, 154695 (DAOM); same locality, 19.VIII.1976, 154694 (DAOM); same locality, 20.VIII.1976, 154693 (DAOM).

Quebec: Gatineau Park, Black Lake, 4.X.1981, 84906 (DAOM).

ENGLAND

Devon: Dartmoor, Two Bridges, Whistmans Wood, 6.IX.1971, D. N. Pegler s.n. (as L. amethystea) (k, Neotype).

Surrey: 16.IX.1951, 27779 (DAOM).

UNITED STATES


Louisiana: St. Tammany Parish, near Slidell on Military Road, 21.XI.1960, Welden 5532 (no).


Maryland: Laurel, Bells Experimental Forest, 13.IX.1969, Miller 8069 (vpl).


Minnesota: Rice Co., Wheeling Township, Nerstrand State Park area, 14.VII.1965, Weaver 1185 (MICH).


North Carolina: Chapel Hill, University of North Carolina, 19.V.1922, Grant 5119 (NCU); same locality, 6.V.1922, Grant 5178 (NCU).


Rhode Island: Beach Pond Park, 20.VII.1967, Bigelow 15118 (MICH).

Virginia: Richmond, 10.IX.1934, coll. Linder & Smart (FH).

Laccaria bicolor

CANADA


UNITED STATES

Alaska: Girdwood, Alyeska Ski Area, 27.VIII.1964, WK 1399 (TENN 42620); Girdwood Alyeska Ski Area, Winter Creek Trail, 18.IX.1969, WK 4277 (TENN 42658); same locality, 27.VIII.1980, WK 6396 (TENN 42659); Juneau, Mendenhall Glacier campground, 28.VII.1966, WK 1408 (TENN 42625); Kodiak Island, 14.IX.1966, WK 1411 (TENN 42626); Near Palmer, Finger Lake campground, 7.VIII.1967, WK 1415 (TENN 42657); Turnagain Pass, Highway, 20.IX.1965, WK 1405 (TENN 42609); same locality, 4.VIII.1966, WK 1409 (TENN 42621).


Laccaria fraterna

AUSTRALIA

Vic. Port Phillip, no date, French 1 (as Agaricus fraternus) (k, Holotype of A. fraternus).

UNITED STATES

California: Marin Co., Mt. Tamalpais watershed, near Fairfax, Bon Tempe, 5.XII.1984, G. M. Mueller 2130 (WTU, f); San Francisco Co., Park Merced Shopping Center, near San Francisco State University, 4.XII.1984, G. M. Mueller 2126 (WTU, f), San Francisco State University, 6.XII.1984, G. M. Mueller 2146 (WTU, f).

URUGUAY

Montevideo, 1927, 2800 (MPU, Representative Specimen of L. lateritia).

MUELLER: SYSTEMATICS OF LACCARIA (AGARICALES) 145
Laccaria laccata var. laccata

CHILE


CSSR

Moravia, Ostrava, Halde Lucina, 30.VIII.1968, Vesely s.n. (f, Holotype of L. laccata var. vulcanica).

SWEDEN


Laccaria laccata var. pallidifolia

[Some collections of L. ohiensis may be buried in this list because I did not note basidiospore echinulae width at the onset of this study.]

CANADA

British Columbia: Robson River, west of Jasper, 17.X.1974, 149408 (DAOM); Alice Lake Provincial Park, 3.X.1981, 43091 (TENN).


Nova Scotia: Kings Co., Kentville, Ag. Station, 27.VIII.1978, 42530, 42965 (TENN); near Scott Bay, Split Bay Trail, 28.VIII.1978, 42533 (TENN); Aylesford Lake Road, 1.IX.1978, 42539, 42971 (TENN).


CHILE


CSSR


ENGLAND


JAPAN


SWITZERLAND

Schweiz, ZH, Birmensdorf, 28.X.1965, 651338 (zt).

UNITED STATES


Alaska: Little Nelchina Campground, Glenn Highway between Eagle Summit and Lake Louise Road, 13.VII.1964, WK 1398 (TENN 43123); Chugach Mts., near Anchorage, 16.IX.1965, WK 1406 (TENN 43124); Airport Road, near Homer, 2.IX.1967, WK 1417 (TENN 43125); Talkeetna Junction, 4.VII.1966, WK 1421 (TENN 42969); Anchorage, Goose Lake, 6.X.1970, WK 4884 (TENN 42970); Girdwood, Alyeska Ski Area, 2.VII.1964, WK 1404 (TENN 42968); Potter,
Trout Trail, Cameron Rim, National Park, 39146
National Road, Copeland S. 43058 (TENN).


Ohio: Harper 9.7308a

West (WASH).

Rossbach 9.VIII.1956, 30.V.1969, 1862 (F, wru); Hailing 1936, 1872 (F, wru).


Marion Co., Ocala National Forest, Mill Dam Road, 24.VIII.1980, 43054–43057 (TENN); Ocala National Forest, fire road off 40, 24.VIII.1980, 43058 (TENN); Newman's Lake, Hatched Creek, 4.VII.1932, F16196 (FLAS).


Maryland: Laurel, Beltsville Forest Dis. Lab., Telegraph Road, 16.X.1969, Miller 8228 (VPI).


New Jersey: Mammoth Co., 18.VI, coll. Ballou (NY); Newark, 1890, coll. Ellis (NY).


16.VII.1979, 42979–42983 (TENN); same locality, 9.IX.1979, 42996–43002 (TENN); same locality, 8.VIII.1980, 42958 (TENN); same locality, 16.IX.1983, G. M. Mueller 1736 (TENN). Macon Co., Lamb Mt. Road, 13.VII.1979, 42972–42974 (TENN); near Highlands, Chiquapin Mt. Trail, 13.VII.1979, 42975 (TENN); same locality, 18.IX.1983, G. M. Mueller 1764, 1765 (TENN, F); Chattooga River Trail, 19.IX.1983, G. M. Mueller 1774 (TENN); Highlands Biological Station, near Ilges Cottage, 14.VII.1979, 42976, 42977 (TENN); Elicot Rock Trail, 17.VII.1979, 42984 (TENN); Nantahala National Forest, Wayah Bald, 18.VII.1979, 42957, 42985–42991 (TENN); same locality, 11.IX.1979, 43007–43016 (TENN); Nantahala National Forest, near Highlands, off U.S. 64, 10.IX.1979, 43003, 43004 (TENN); Nantahala National Forest, Glen Falls area, 10.IX.1979, 43005, 43006 (TENN); Highlands, Ravenel Park, 12.IX.1979, 43017–43020 (TENN); near Highlands, Horse Cove, 13.IX.1979, 43021–43025 (TENN); same locality, 14.VII.1979, 42978 (TENN); Coveeta Hydrologic Research Station, 14.IX.1979, 43026–43033 (TENN); same locality, 11.VIII.1980, 43050, 43051 (TENN); same locality, 17.IX.1983, G. M. Mueller 1751, 1755 (F). Transylvania Co., Estate of G. W. Vanderbilt, 13–24.VII.1908, coll. Murrill & House (NY).

Ohio: Carroll Co., near Leesville Lake, Old Scott Place, 28.IX.1979, 43047, 43048 (TENN).


Vermont: Starksboro, 2.IX.1880, coll. Pringle (FH); Wallingford, Elfin Lake, 6.X.1952, 38894 (CUP).


Wisconsin: Devil's Lake, VII.1911, Harper 3397 (F).


Laccaria longipes

CANADA


UNITED STATES


New York: Clinton Co., Hearn Swamp, under
**Abies, Picea, in Sphagnum bog, 23.VIII.1991, R. E. Halling 6618 (ny).**

**Wisconsin:** Ozaukee Co., UW–Milwaukee Field Station, Sapa Spruce bog, 5.X.1989, A. D. Parker s.n. (f).

**Laccaria maritima**

**CANADA**

Northwest Territories: District of Keewatin, Rankin Inlet, NE shore of the Meliadine River about 5 km from the mouth, 8.VIII.1974, E. & M. Ohenoja 8.8.1974/47a (DAOM).

**GREENLAND**


**SWEDEN**


**Laccaria montana**

**CANADA**


**DENMARK**

Faerøe Islands: Ostedø, Slottorotinde, 17.VII.1938, coll. Moller (c, Holotype of L. laccata var. montana).

**SWITZERLAND**

Valais, Borg de Fepecle, 11.VII.1971, Singer 5464 (f, Holotype of L. montana).

**UNITED STATES**

Alaska: Navy Arctic Research Lab, USIBP Tundra Biome Sites, 4.VIII.1977, Laursen 1172 (WTU); same locality, 26.VIII.1978, Laursen 1397 (WTU); same locality, 28.VII.1979, Laursen 1500 (WTU).


**Laccaria nobilis**

**CANADA**


**UNITED STATES**


New Mexico: Mountains near Santa Fe, 11.VII.1981, Potter 282 (MICH).


**Laccaria oblongospora**

**UNITED STATES**


Texas: Polk Co., Big Thicket Nature Preserve, Big Sandy Unit, 29.XI.1986, G. M. Mueller 2310 (F).

**Laccaria ochropurpurea**

**CANADA**

Nova Scotia: Kentville, 1.IX.1950, 111857 (DAOM).

Ontario: Lake Musdoda, Creighton's Point, 28.VIII.1940, 10147 (DAOM); near Ottawa, Green's Creek, 22.VIII.1927, 40933 (DAOM); same locality, 10.IX.1928, 40931 (DAOM); St. Lawrence Island National Park, McDonald Island, 154703 (DAOM); same locality, 29.IX.1976, 158826 (DAOM).

Quebec: Mt. Burnet, 5.X.1935, F5968 (DAOM); near Chelsea, Gilmour's Grove, 2.VIII.1923, 40932 (DAOM).

**UNITED STATES**


Florida: Planera Hammock, 3.I.1939, 19516 (FLAS).


Iowa: Iowa City, 12.IX.1938, 33863 (CUP).

Kentucky: Middlesboro, 1.X.1914 (NY).


Maryland: Baltimore Co., Gunpowder Region, 27.IX.1919, Kelly 207 (FH); Laurel, 6.IX.1965, Miller 3532 (VPI).


Texas: Houston, 14.I.1942, coll. Fisher (F); 8140 (CUP).


Wisconsin: Lodi, 1.X.1977, 166267 (DAOM); 8.IX.1939, coll. Olmsted (f).

Laccaria ohiensis

ARGENTINA


Rio Negro: Bahía López, 22.XI.1964, Singer M4063 (BAFC, Representative Specimen of L. tetraspora var. xena).

CHILE


SCOTLAND

Lake Katrim, 1.VIII.1964, Singer C4002 (BAFC, Holotype of L. tetraspora var. scotica).

SWEDEN


UNITED STATES


Louisiana: East Baton Rouge Parish, Burden Farm, Essen Road and I-10, 3.XII.1985, G. M. Mueller 2354 (f).


Ohio: Columbus, Sullivant s.n. (NY, Holotype of A. ohiensis).


Laccaria proxima

CANADA


FRANCE


ITALY

Trento, X.1899, Bresadola s.n. (NY).

SWEDEN


UNITED STATES

Alaska: Point Barrow, Navy Arctic Research Lab, I.B.P. site, 3.VII.1971, WK 4573 (TENN 42928); Arctic Valley, 31.VIII.1971, WK 540A (TENN 42929); NARL, USIBP Tundra Biome Site 3, 28.III.1979, Laursen 1499 (WTU).


Florida: Alachua Co., Gainesville, 29.XII.1942, F1672 (FLAS); same locality, 1.1.1949, F45770 (FLAS). Marion Co., Ocala National Forest, near

Idaho: Bonner Co., Kaniksu National Forest, Binarch Creek Road, 26.IX.1981, 42920 (TENN); same locality, 27.IX.1981, 42921, 42943 (TENN); Kaniksu National Forest, 27.IX.1981, 42944 (TENN); Kaniksu National Forest, West Side, Priest Lake Road, 28.IX.1981, 42922 (TENN).


Laccaria pumila

CANADA

Nova Scotia: Kings Co., near Scotts Bay, Split Bay Trail, 28.VIII.1978, 42531 (TENN); Alysford Lake Road, 1.XI.1982, 42541, 42550 (TENN).

FRANCE


UNITED STATES

Alaska: Barrow, between Elson Lagoon and Oil Well Road, 5.VII.1970, WK 4609 (TENN 43122); Fairbanks, Peger Road, 17.VIII.1981, WK 5323 (TENN 42551); Steese Highway (110 miles north of Fairbanks), Eagle Summit, 19.VIII.1971, WK 5355 (TENN 42549); NARL, USIBP Tundra Biome Site 1, 26.VIII.1978, Laursen 1398 (WTU); Delong Mountains, Driftwood Camp, 2.X.1978, Laursen 1424 (WTU).

Colorado: Larimer Co., Rocky Mountain National Park, Bear Lake Road, 20.VII.1940, Mains 5115 (MICH); Roosevelt National Forest, near Chambers Lake, 11.IX.1981, 42548 (TENN); Roosevelt National Forest, Blue Lake Trail, 13.IX.1981, 42547, 42552, 42554–42558 (TENN); same locality, 16.IX.1981, 42553 (TENN).


USSR


Laccaria striatula

CANADA

Nova Scotia: Kings Co., Baxter Harbor, 31.VIII.1978, 42534, 42536, 42767 (TENN); Aylesford Lake Road, 1.IX.1978, 42538, 42540, 42542, 42543, 42768, 42769, 42773 (TENN); Cape Split, Split Bay Trail, 1.IX.1978, 42776 (TENN).

UNITED STATES


Laccaria tortilis

ARGENTINA

La Baea, V.1880, Spegazzini 2891 (LPS, Holotype of A. [Clitocybe] echinosporus).

CANADA

Ontario: Grenadier Island, St. Lawrence Island National Park, 10.VII.1975, Redhead 1619 (DAOM); Leeward Island, St. Lawrence National Park, 22.VII.1976, 159029 (DAOM).

SCOTLAND

Yorkshire, Tanfield Lodge, 6.IX.1969, Orton 3642 (e, Representative Specimen); Island of Mull, near Quinish House, 7.IX.1976, Watling 12479 (e); Norfolk, Surlingham Wood, 25.VIII.1969, Orton 3641 (e); Perthshire, 17.VIII.1972, Watling 9465 (e); Perthshire, Inver, 27.X.1975, Watling 11347 (e); Yorkshire, Bishop Wood, 26.IX.1971, Watling 8947 (e).

UNITED STATES


Michigan: Cheboyan Co., Burt Lake, Colonial Point, 1.X.1960, Smith 63093 (MICH); Colonial Point, 6.IX.1969, Ammirati 3845 (MICH); Marquette, 4.IX.1933, Smith 33862 (MICH); Neebish, VIII.1909, Harper 2372 (f); Neebish, IX.1917, coll. Harper (f).


Oregon: Benton Co., Corvallis, Oregon State University, 2.XI.1981, 42955 (TENN).


Wyoming: NE Pole Mt. area, 7.VIII.1950, Smith 34564 (MICH).

THE NETHERLANDS

Noord-Brabant, Ulvenhout near Breda, 18.VIII.1959, Maas Geesteranus 12908 (MICH).

MUELLER: SYSTEMATICS OF LACARIA (AGARICALES)
Laccaria trichodermophora

UNITED STATES


Laccaria trullissata

UNITED STATES


Indiana: Deaverly Shores, Singer N1815 (f).


Maryland: Talbot Co., Choptemk River, 24.IX.1922, coll. Fisher (MICH); Hoffman Hill Road, Beltsville Exp. Forest, 6.XI.1968, Miller 7109 (VPI); Laurel, Beltsville Exp. Forest, 12.IX.1969, Miller 8071 (VPI); same locality, 14.X.1969, Miller 8225 (VPI).

Massachusetts: Franklin Co., Sunderland, 24.IX.1957, Bigelow 6314 (MASS), 82782 (DAOM); Montague Center, 4.X.1966, Bigelow 14916 (MASS); Cape Cod, near Marson’s Mill, 26.VIII.1945, coll. Linder (FH); Westport, Horseneck Beach, 27.X.1973, Bigelow 17299 (MASS).


Mississippi: Jackson Co., Horn Island, 5.XII.1985, G. M. Mueller 2360, 2361, 2363 (f).

New Jersey: Newfield, before 1874, coll. Ellis (NYS, Lectotype); Seaside Park, 29.VIII.1902, Harshberger (NYS); Browns Mills, 29.X.1945, coll. Aide; North American fungi 101 (NY, NYS, CUP).


**Laccaria vinaceobrunnea**

UNITED STATES


Appendix B. Isolates Used in Somatic Culture Mat Analyses

**Laccaria amethysteo-occidentalis**

GMM 1256 (TENN 42526)

**Laccaria bicolor**

GMM 1225 (TENN 42607); GMM 1230 (TENN 42608); GMM 1264 (TENN 42604); GMM 1293 (TENN 42606); GMM 1352 (TENN 42529); GMM 1353 (TENN 42605); GMM 1478 (TENN 42603); Hunt 018 (Oregon State University culture S-447); Trappe 4755 (OSU S-282); Trappe 4779 (OSU S-283)

**Laccaria laccata var. pallidifolia**

GMM 936 (TENN 42958); GMM 975 (TENN 43055); GMM 979 (TENN 42058); GMM 1010 (TENN 42959); GMM 1011 (TENN 42960); GMM 1030 (TENN 42961); GMM 1160 (TENN 42962); GMM 1167 (TENN 42963); GMM 1168 (TENN 42546); GMM 1470 (TENN 42964); Hunt 013 (OSU S-443)

**Laccaria longipes**

GMM 1929

**Laccaria nobilis**

GMM 1198 (TENN 42527); GMM 1205 (TENN 42893)

**Laccaria oblongospora**

GMM 1075 (TENN 42673); GMM 1080 (TENN 42674); GMM 1100 (TENN 42675); GMM 1102 (TENN 42522); GMM 1105 (TENN 42672)

**Laccaria ochropurpurea**

GMM 1004 (TENN 42907); GMM 1005 (TENN 42908); GMM 1037 (TENN 42909)

**Laccaria proxima**

GMM 1518; 1368 (TENN 42925); GMM 2100; GMM 2131

**Laccaria trichodermophora**

GMM 993 (TENN 42521); GMM 994 (TENN 42754); GMM 1014 (TENN 42752); GMM 1024 (TENN 42753); GMM 1060 (TENN 42703); GMM 1063 (TENN 42733); GMM 1067 (TENN 42705); GMM 1071 (TENN 42706)

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1 Cultures are housed in the mycological culture collection at Field Museum of Natural History under the GMM number. Voucher specimens housed at TENN are filed under the TENN number.
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