

**TAXONOMIC AND NOMENCLATORIAL NOTES ON LACCARIA B. & BR.
Laccaria amethystea, L. fraterna, L. laccata, L. pumila, and their synonyms**

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Laccaria amethystea, not *L. amethystina* nor *L. calospora*, is shown to be the correct name for the amethyst colored *Laccaria*. A neotype for *L. amethystea* is proposed and a complete list of its synonyms is given. Data which support placing *L. ohiensis* and *L. tetraspora* in synonymy with *L. laccata* are discussed and three varieties within *L. laccata* are recognized. These varieties are *L. laccata* var. *laccata*, *L. laccata* var. *moelleri*, and *L. laccata* var. *pallidifolia*. Based on these data, a synonymy list and description of each variety is presented. *Laccaria laccata* var. *pallidifolia* is shown to be the most common and abundant variety. The correct name for *L. striatula* sensu Sing. non Peck is *L. pumila* and for *L. ohiensis* sensu Sing. non Montagne is *L. fraterna*.

While *Laccaria* B. & Br. (Agaricales) is well circumscribed, several taxonomic and nomenclatorial problems have persisted within the genus. This paper addresses four of these problems: (i) the correct name for the violet colored *Laccaria* species found commonly in Europe and eastern North America, (ii) the circumscription and nomenclature of *L. laccata* (Scop.: Fr.) B. & Br., (iii) the correct name for the bisporic *Laccaria* with moderate sized basidiospores and tropical to temperate distribution, and (iv) the correct name for the bisporic *Laccaria* with moderately large to large basidiospores and boreal to arctic distribution.

Laccaria amethystea (Bull.) Murrill

Agaricus amethysteus Bull., Herb. France: Pl. 198. 1784. — *Agaricus laccatus* var. *amethysteus* (Bull.) B. & Br. in J. linn. Soc. Bot. 11: 518. 1871. — *Russullopsis laccata* var. *amethystea* (Bull.) J. Schroet. in Cohn, Krypt.-Fl. Schlesien 3(1): 623. 1889 (erroneously written 'amethystina') — *Laccaria amethystea* (Bull.) Murrill in N. Amer. Fl. 10: 1. 1914.

Agaricus amethystinus Huds., Fl. angl. 2: 612. 1778; non *Agaricus amethystinus* Scop., Fl. carn. 2: 437. 1772 (= *Cortinarius* spec.); nec *Agaricus amethystinus* Schaeff., Fung. Bavariae 4: 24. 1774 (= *Cortinarius traganus*). — *Laccaria amethystina* (Huds. →¹) Cooke in Grevillea 12: 70. 1884. —

¹ The arrow (→) in an author citation indicates that the specific epithet when published by the author before the arrow was illegitimate, because of being a later homonym, and has been legalized by the author after the arrow when the latter combined it with another generic name (see Kuyper, Persoonia 12: 448. 1985).

Collybia amethystina (Huds. → Cooke) Quél., Fl. mycol. France: 237. 1888. — *Clitocybe amethystina* (Huds. → Cooke) Peck in Ann. Rep. N.Y. St. Bot. 50: 128. 1897.

Laccaria calospora Sing. in Sydowia Beih. 7: 7. 1973.

Type specimen (neotype, design. nobis): MICH — *R. L. Shaffer 4570*, 15 Aug. 1965, France, Bois de Bonnet, west of Coye-la-forêt (Oise).

Two names have been commonly used for the amethyst colored *Laccaria* in recent mycological literature. Most authors have used the epithet *amethystina* (e.g., Kühner & Romagnesi, 1953: 131; Singer, 1975: 231; Kühner, 1980: 519; Mueller & Sundberg, 1981: 584; Bon, 1983: 48; Moser, 1983: 98; Cléménçon, 1984: 5; Fries & Mueller, 1984: 633), while others have used the epithet *amethystea* (e.g., Dennis & al., 1960: 90; Phillips, 1981: 52). *Agaricus amethystinus* Huds., however, is a later homonym of *A. amethystinus* Scop. (= *Cortinarius* spec.) and of *A. amethystinus* Schaeff. (= *Cortinarius traganus* (Fr.: Fr.) Fr.) and thus is not usable. Since *A. amethysteus* Bull. was the first legitimate name published for the amethyst colored *Laccaria*, *L. amethystea* is the correct name for this taxon.

The holotype of *L. calospora* Sing. is characterized by having dingy purple-violet basidiocarps which fade buff, purple lamellae, violet spore print color, scattered cheilocystidia, and moderate sized ($7.5\text{--}8.5 \times 7.0\text{--}8.5 \mu\text{m}$, excluding ornamentation), globose to subglobose ($Q = 1.0\text{--}1.1$), echinulate basidiospores. Since these character states are included within the circumscription of *L. amethystea*, the two are considered conspecific.

The collection designated as neotype of *L. amethystea* was selected from material requested from several herbaria including BPI, FH, LG, K, MICH, and PC. Of the collections which both fit Bulliard's (1784: Pl. 198) drawing and description and had been collected near Paris (the presumed type locality), the chosen collection was the largest and best preserved. The neotype has the following micromorphological characteristics:

Basidiospores (excluding ornamentation) $8.0\text{--}9.5\text{--}(10.0) \times (7.5\text{--})8.0\text{--}9.0 \mu\text{m}$, $Q = 1.0\text{--}1.05\text{--}(1.1)$, $\bar{Q} = 1.0$, globose to occasionally subglobose, echinulate; spines up to $1.5\text{--}2.5 \mu\text{m}$ high, crowded; hilar appendage $1.5\text{--}2.5 \mu\text{m}$ long, prominent, truncate; contents occasionally uniguttulate; wall inamyloid and acyanophilous. Basidia $38\text{--}52 \times 8\text{--}12 \mu\text{m}$, clavate, elongate, hyaline, tetrasporic. Pleurocystidia absent. Cheilocystidia $40\text{--}86 \times 7\text{--}12 \mu\text{m}$, undifferentiated to subclavate or subcapitate or ventricose-rostrate, very abundant, thin-walled, hyaline. Pileipellis a cutis of radially arranged cylindrical hyphae, $8\text{--}12 \mu\text{m}$ wide with numerous more or less perpendicular individual large hyphae; terminal elements $30\text{--}85 \times 11\text{--}14 \mu\text{m}$, undifferentiated to clavate, hyaline to light vinaceous; walls up to $0.5 \mu\text{m}$ thick.

Laccaria laccata (Scop.: Fr.) B. & Br.

Agaricus laccatus Scop., Fl. carn. 2: 444. 1772. — *Agaricus laccatus* Scop.: Fr., Syst. mycol. 1: 106. 1821. — *Clitocybe laccata* (Scop.: Fr.) Kumm., Führ. Pilzk.: 122. 1871. — *Camarophyl-*

lus laccatus (Scop.: Fr.) P. Karst., Ryssl., Finl. Skand. Halföns Hattsvamp.: 231. 1879. — *Laccaria laccata* (Scop.: Fr.) B. & Br. in Ann. Mag. nat. Hist., ser. V, 12: 370. 1883. — *Omphalia laccata* (Scop.; Fr.) Quél., Enchir. Fung.: 26. 1886. — *Collybia laccata* (Scop.: Fr.) Quél., Fl. mycol. France: 237. 1888. — *Russuliopsis laccata* (Scop.: Fr.) J. Schroet. in Cohn, Krypt.-Fl. Schlesien 3(1): 622. 1889.

Agaricus carneus Schaeff., Fung. Bavariae 4: 71. 1774.

Agaricus farinaceus Huds., Fl. angl. 2: 616. 1778. — *Omphalia farinacea* (Huds.) S. F. Gray, Nat. Arr. Brit. Pl. 1: 612. 1821. — *Laccaria farinacea* (Huds.) Sing. in Sing. & Mos. in Mycopath. Mycol. appl. 26: 149. 1965 (not val. publ.; basionym lacking). — *Laccaria farinacea* (Huds.) Sing. in Sydowia Beih. 7: 8. 1973.

Agaricus rosellus Batsch, Elench. Fung. Contin. 1: 121. 1786; non *Agaricus rosellus* Fr.: Fr., Syst. mycol. 1: 151. 1821 (= *Mycena rosella*). — *Omphalia rosella* (Batsch →) S. F. Gray, Nat. Arr. Brit. Pl. 1: 613. 1821. — *Russuliopsis laccata* var. *rosella* (Batsch → S. F. Gray) J. Schroet. in Cohn, Krypt.-Fl. Schlesien 3(1): 623. 1889. — *Laccaria laccata* var. *rosella* (Batsch → S. F. Gray) Sing. in Annlis mycol. 41: 17. 1943.

Agaricus subcarneus Batsch, Elench. Fung. Contin. 1: 123. 1786.

Agaricus ohiensis Mont., Syll. Gen. Sp. Crypt.: 100. 1856. — *Clitocybe ohiensis* (Mont.) Sacc., Syll. Fung. 5: 181. 1897. — *Laccaria ohiensis* (Mont.) Sing. in Mycologia 38: 688. 1946.

Laccaria tetraspora Sing. in Mycologia 38: 689. 1946.

Excluded. — *Laccaria farinacea* sensu Sing. in Sydowia Beih. 7: 8. 1973 (= *L. bicolor* (Maire) P. D. Orton).

While Singer's (Singer, 1967: 107) typification of *L. laccata* satisfied the rules for designating neotypes established by the ICBN (Voss & al., 1983), the collection that he chose does not serve as a representative specimen for the species because the micromorphological characters of the collection are near the extreme range for the taxon. This fact, coupled with conflicting published concepts of *L. laccata* and of several segregate taxa, has perpetuated confusion in the delimitation of *L. laccata* and the taxonomy of the genus as a whole.

The following information is based on fresh material collected by us in North America north of Mexico, Sweden, the Netherlands and adjacent regions. Additionally, numerous herbarium specimens were examined including all extant *Laccaria* types. To augment these studies, somatic culture mat analysis and mating studies were undertaken (Fries & Mueller, 1984; Mueller & al., 1985).

Singer (1946, 1967, 1977) separated *L. tetraspora* from *L. laccata* primarily on basidiospore characteristics. *Laccaria tetraspora* reportedly had globose or rarely subglobose basidiospores which were normally over 10 μm in diameter (including ornamentation) with ornamentation $> 1.2 \mu\text{m}$ high, whereas *L. laccata* had subglobose to broadly ellipsoid, rarely globose or ellipsoid basidiospores which were normally $< 10.3 \mu\text{m}$ long (including ornamentation) with ornamentation rarely $> 1.3 \mu\text{m}$ high. Additionally, *L. tetraspora* basidiocarps were small- to moderate-sized while *L. laccata* basidiocarps were usually moderate-sized.

With these distinctions in mind, Singer (1967, 1977) designated 7 varieties of *L. tetraspora* (reduced to 6 in 1977) and 12 varieties of *L. laccata* based on a small number of specimens collected world-wide. These varieties were proposed to delimit phenotypically distinct and stable entities and to serve as a starting point for mating studies which are much needed in this group (Singer, 1977: 347). An examination of the type speci-

Table 1. Basidiospore characteristics for type specimens of taxa discussed under *Laccaria laccata*. Basidiospore dimensions exclude ornamentation. All measurements based on $n = 30$ and in μm . Herbarium abbreviations from Index Herbariorum.

Name	Herb.	Dimensions (L x W)	mean L x W	L/W ratio	mean L/W	Ornamentation length
<i>Agaricus ohiensis</i>	PC	7.5-9.0(-10.0) x 7.5-9.0(-10.0)	8.4 x 8.4	0.95-1.05	1.01	1.5-2.5
<i>Clitocybe torrifilis</i> var. <i>gracilis</i>	NYS	(8.0-)-8.5-10.5 x 8.0-10.0(-10.5)	9.3 x 9.1	1.0-1.05(-1.1)	1.02	1.5-2.5(-3.0)
<i>Clitocybe laccata</i> var. <i>pallidifolia</i>	NYS	8.0-11.0(-11.5) x 7.5-9.0(-10.5)	9.2 x 8.5	1.0-1.1(-1.2)	1.08	< 0.5-1.5(-2.0)
var. <i>striatula</i>	NYS	(7.0-)-8.0-9.5(-12.0) x (7.0-)-8.0-9.5(-12.0)	8.8 x 8.7	1.0(-1.05)	1.01	1.4-2.5(-3.0)
<i>Laccaria laccata</i> var. <i>laccata</i>	BAFC	8.5-9.0(-11.0) x 6.5-8.0(-8.5)	9.2 x 7.1	(1.1-)-1.2-1.35(-1.45)	1.3	1.0-2.0(-2.5)
var. <i>decurrens</i>	NYS	7.5-9.0(-11.5) x 7.0-9.0(-10.0)	8.6 x 8.0	1.0-1.15(-1.25)	1.08	(< 0.5-)-1.0(-1.5)
var. <i>chilensis</i>	BAFC	6.5-8.0 x 6.0-7.5(-8.0)	7.3 x 6.7	1.0-1.15	1.08	(< 0.5-)-1.5-2.0
var. <i>carbonicola</i> ¹	FH	7.7-8.2 x 6.5-7.2	—	—	—	0.7
var. <i>anglica</i>	BAFC	(7.5-)-8.0-9.0(-9.5) x (7.5-)-8.0-9.0(-9.5)	8.4 x 8.3	1.0-1.05	1.01	(1.0-)-1.5-2.0
var. <i>affinis</i>	BAFC	(7.0-)-8.0-10.0 x (7.0-)-8.0-10.0	8.6 x 8.6	1.0(-1.05)	1.0	1.0-1.5
var. <i>gibba</i>	SGO	7.0-8.5 x (5.0-)-16.0-7.5	7.8 x 6.3	1.1-1.4	1.25	1.0-2.0(-2.5)
var. <i>moelleri</i>	F	9.0-11.0 x (6.5-)-7.0-8.5	10.0 x 7.3	1.25-1.45(-1.6)	1.3	< 0.5-1.5(-2.0)

<i>var. vulcanica</i>	F	(7.5-)8.5-9.5(-11.0) × (6.0-)6.5-8.0(-8.5)	9.0 × 7.1	1.15-1.35(-1.45)	1.27	(0.5-)1.0-1.5(-2.0)
<i>var. subalpina</i>	F	(6.5-)7.0-8.0(-8.5) × (6.0-)6.5-7.5	7.5 × 6.8	1.0-1.15(-1.2)	1.1	(1.0-)1.5-2.0
<i>var. tatrensis</i>	F	7.5-9.0 × 7.5-9.0	8.4 × 8.2	1.0-1.1	1.03	1.0-2.0
<i>var. intermedia</i>	F	(6.5-)7.5-10.0(-13.0) × (6.5-)7.0-10.0(-12.5)	8.9 × 8.6	0.95-1.2(-1.3)	1.04	1.5-2.0(-2.5)
<i>var. pseudobicolor</i> ²		8.0-9.0(-9.5) × 6.0-7.5(-8.0)	—	—	—	<1.0
<i>f. minuta</i>	SAP	7.0-8.5(-9.0) × 7.0-8.5	8.0 × 7.9	1.0-1.05	1.01	1.0-2.0
<i>Laccaria tetraspora</i> <i>var. tetraspora</i>	FH	(8.0-)8.5-11.0 × 8.5-10.0(-10.5)	9.3 × 9.1	0.95-1.2	1.02	(1.0-)1.5-2.5(-3.0)
<i>var. peullensis</i>	BAFC	7.5-8.5(-9.5) × 7.5-8.5(-9.0)	8.1 × 8.0	1.0(-1.1)	1.01	1.0-2.0
<i>var. valdiviensis</i>	BAFC	(7.0-)8.0-9.0(-10.0) × (7.0-)8.0-9.0(-10.0)	8.4 × 8.3	1.0-1.05	1.01	1.5-2.0(-2.5)
<i>var. scotica</i>	BAFC	7.0-9.0 × 7.0-9.0	8.0 × 7.9	1.0-1.05(-1.15)	1.01	1.0-2.0(-2.5)
<i>var. xena</i> ³	BAFC	(7.0-)8.0-9.5 × (7.0-)8.0-9.5	8.6 × 8.6	1.0(-1.05)	1.0	(1.0-)1.5-2.5
<i>var. aberrans</i>	BAFC	7.0-8.5(-9.5) × 7.0-8.5(-9.0)	7.9 × 7.8	1.0-1.05(-1.1)	1.01	(1.0-)1.5-2.0
<i>var. peladae</i>	BAFC	(6.5-)7.0-9.0 × (6.5-)7.0-9.0	7.9 × 7.8	1.0-1.05	1.01	1.0-1.5(-2.0)

¹ Type not found at FH. Data from Singer (1967).

² Type not studied. Data from Bon in Bon & Haluwijn (1982).

³ No type designated. Data based on a representative specimen (Singer M4063).

mens of these varieties, however, has shown that the distinctions between the two species become blurred and, in some cases, the varieties of one species intergrade with the varieties of the other species (Table I).

Based on the following data, we consider *L. tetraspora* to be a synonym of *L. laccata*. (i) Not only does the macro- and micromorphology of several of the proposed varieties intergrade between the two putative species (Table I), but these data, along with those from numerous other specimens, do not support the presence of any distinct hiatus in either basidiospore size, shape, or ornamentation height, except for a few extreme cases. Basidiocarp size also appears to form a continuum from very small to moderate. (ii) Culture mat morphology data do not support the separation of these taxa. All examined isolates of these two putative species have similarities in growth form and color (Fries & Mueller, 1984; Mueller, 1985). (iii) Finally, mating studies using several *Laccaria* species showed that, at least in the laboratory, isolates from collections with basidiospore characteristics corresponding to either *L. laccata* or *L. tetraspora* were compatible and formed clamp connections (Fries & Mueller, 1984). Collections referable to both putative species comprised two mating groups (III and IV) in the study by Fries & Mueller (1984). These two groups, however, could not be distinguished on basidiocarp morphology, basidiospore size or shape, or basidiospore ornamentation height and were, therefore, treated as sibling species (Table II). Thus, the character states which were to separate *L. laccata* and *L. tetraspora* were found in both mating groups and were not usable in delimiting the two groups.

The holotype of *L. ohiensis* consists of basidiocarps which have moderate-sized, globose, echinulate basidiospores born on 4-sterigmate basidia and lack cheilocystidia (Table I). This agrees with Singer's (1942: 102) description of the type and Malençon's (1966: 187) and Malençon & Bertault's (1975: 194) concept of the taxon. In subsequent papers (e.g., Singer & Digilio, 1952: 24; Singer, 1977: 348), however, Singer treats *L. ohiensis* as being bisporic. Since the type collection is tetrasporic and has its macro- and micromorphological characters in common with *L. laccata*, the two are treated as synonyms. The correct name for the bisporic taxon discussed by Singer (Singer, 1967: 119; 1977: 350) which has moderate sized subglobose basidiospores and normally occurs in warm and dry regions, often under *Eucalyptus*, is *L. fraterna* (Cooke & Mass.) Pegl. (see below).

The species that we recognize from North America north of Mexico and western Europe which could be confused with *L. laccata* are *L. bicolor* (Maire) P. D. Orton, *L. striatula* (Peck) Peck, *L. montana* Sing., *L. nobilis* Mueller, *L. oblongospora* Mueller, *L. proxima* (Boud.) Pat., and *L. trichodermophora* Mueller. All but *L. montana* and *L. striatula* have recently been discussed by Mueller (1984, 1985). *Laccaria montana* is distinguished primarily from *L. laccata* by its relatively large (usually 10–14 μm long excluding ornamentation), subglobose to broadly ellipsoid, short spined basidiospores, and its habitat (arctic, subarctic, boreal, and alpine).

Laccaria striatula has only been reported in the study area from very moist and well shaded habitats, often in moss, in eastern North America (Mueller, 1985: 127 as *L. gla-*

Table II. Basidiospore characteristics of the *Laccaria laccata* collections used in mating studies by Fries & Mueller (1984) arranged by mating group. Within a mating group monokaryotic isolates formed clamp connections when paired.

Stock no.	Mating group	Mean spore size in μm (n = 30–40)	Mean spore length/width ratio (n = 30–40)	Maximum length of echinulae per spore in μm
369	III	8.3 × 8.1	1.03 (= globose)	1.5–2.5
1505	III	8.5 × 8.1	1.02 (= globose)	2.0–2.5
1604	III	8.3 × 8.2	1.01 (= globose)	1.0–2.0(–2.5)
363	IV	7.8 × 7.2	1.09 (= subglobose)	0.5–1.5
367	IV	8.7 × 8.0	1.08 (= subglobose)	0.5–2.0
368	IV	8.5 × 7.9	1.08 (= subglobose)	0.5–1.5
1495	IV	8.6 × 7.6	1.13 (= subglobose)	0.5–1.5
1512	IV	8.4 × 8.2	1.02 (= globose)	1.5–2.0
1515	IV	8.1 × 7.6	1.06 (= subglobose)	0.5–1.5
1519	IV	8.5 × 8.2	1.04 (= globose)	0.5–1.5(–2.0)
1523	IV	7.9 × 7.7	1.02 (= globose)	0.5–1.5(–2.0)
1560	IV	8.2 × 7.9	1.05 (= subglobose)	0.5–1.5
1588	IV	8.4 × 8.1	1.03 (= globose)	0.5–1.5
1599	IV	9.0 × 8.3	1.09 (= subglobose)	0.5–1.5

bripes). It is characterized by having strongly translucent striate pilei and thin, cartilaginous, glabrous stipes that are darker than or concolorous with the pilei. Its micromorphological features are similar to those found in *L. laccata*. Mating studies on this taxon have not yet been done, and consequently, the rank at which to recognize this taxon is still unclear. Although *L. striatula* has occasionally been treated as a bisporic taxon (e.g., Singer, 1943: 151; Orton, 1960: 281), an examination of its type revealed moderate sized basidiocarps, 4-sterigmated basidia, no cheilocystidia, and moderate to relatively large, globose, strongly ornamented basidiospores (Table I). The bisporic taxon with moderately large to large, broadly ellipsoid basidiospores normally restricted to arctic, boreal, and alpine habitats in the Northern Hemisphere is referable to *L. pumila* Fay. (see below).

Following the definitions for subspecific taxa outlined by Singer (1975: 151), we use the term variety to indicate morphologically distinct infraspecific taxa for which important data, including the degree of interfertility, are unknown. While we agree with Singer (1977: 347) on the need for undertaking infraspecific mating studies within *L. laccata* and of the need to describe and delimit morphologically distinct forms within this species, we recognize far fewer subspecific taxa within *L. laccata* than have been proposed. An examination of the extant types of the published infraspecific taxa revealed that the vast majority of them could not be differentiated on morphological characters.

For the most part, the variation in macro- and micromorphological characters formed a continuum (Table I) and only three discrete, morphologically distinct units were discernible. Most of the published varieties and formae were based on very small morphological differences (e.g., attachment of lamellae or shape of the pileus, very small differences in basidiospore size and/or ornamentation height) coupled with differences in ecology (e.g., growing on humus versus growing among moss). Because of the large amount of observed variation in these features, even within a single collection, these morphological differences were determined to be taxonomically insignificant based on our examination of large numbers of specimens. Thus, most of the published subspecific taxa do not fit into Singer's definition of a variety and are not recognized.

The following infraspecific taxonomy within *L. laccata* is presented not to be a final statement on the subject, but to clarify the synonymy and taxonomy of the group based on available names and concepts of taxa. Some additional subspecific taxa may need to be recognized once the variation in this species has been more fully investigated and additional mating studies undertaken.

Only those putative taxa which have been reported from the U.S.A., Canada, and Europe are treated in this paper since fresh material of the extralimital taxa has not been seen by us. The extralimital names which have been proposed are: *L. tetraspora* var. *aberrans* Sing., *L. laccata* var. *chilensis* Sing., *L. laccata* var. *gibba* Sing., *L. laccata* var. *minuta* (Imai) Hongo, *L. tetraspora* var. *peladae* Sing., *L. tetraspora* var. *peullensis* Sing., *L. tetraspora* var. *valdiviensis* Sing., and *L. tetraspora* var. *xena* Sing. A decision on which of these putative taxa to recognize should be postponed until additional material has been examined and pairing studies undertaken.

The differences between the three varieties that we recognize from North America north of Mexico and Europe are summarized in the following key and further characterized in the discussion after the synonymy lists and descriptions.

KEY TO THE NORTH AMERICAN (NORTH OF MEXICO) AND EUROPEAN
VARIETIES OF *LACCARIA LACCATA*

1. Stipe very long (most 70–120 mm long); pileus convex becoming depressed, often with papilla in depression; basidiospores subglobose to broadly ellipsoid, rarely ellipsoid. (Q = (1.0–)1.05–1.25(–1.6)); in moss including *Sphagnum* var. *moelleri* Sing.
1. Stipe short to moderately long (most 17–65 mm long); pileus convex to plane, sometimes depressed or umbonate, lacking papilla; basidiospores globose to occasionally broadly ellipsoid or broadly ellipsoid to ellipsoid; in moss or not in moss.
 2. Basidiospores globose to subglobose, occasionally broadly ellipsoid (Q = 1.0–1.1(–1.15))
var. *pallidifolia* (Peck) Peck
 2. Basidiospores broadly ellipsoid to ellipsoid (Q > 1.2) var. *laccata*

Laccaria laccata var. *laccata* — Fig. 1

Clitocybe laccata var. *rufo-carnea* Barla, Fl. mycol. ill.: 79. 1892.

Laccaria laccata var. *carbonicola* Sing. in Bull. trimest. Soc. mycol. Fr. 83: 110. 1967.

Laccaria laccata var. *vulcanica* Sing. ex Veselsky & Sing. in Sing. in Plant Syst. Evol. 126: 362. 1977.

Laccaria laccata var. *pseudobicolor* M. Bon in M. Bon & Haluwijn in Doc. mycol. 12(46): 42. 1982.

Russuliopsis laccata var. *rosella* f. *pusilla* J. Schroet. in Cohn, Krypt.-Fl. Schlesien 3(1): 623. 1889.

Type specimen (neotype): BAFC — *Singer C4083*, 17 Aug. 1964, Sweden, Femsjö.

Pileus 5–45(–60) mm, when young hemispherical with or without involute margin, later expanding to applanate or plano-convex, often with a shallow depression, hygrophanous, when moist orange-brown, pink-brown, rarely very pale buff or cream colored, or flesh colored vinaceous, with darker center and striae (Munsell 2.5 YR 4/4–6/8, 5 YR 4/4–7/6), fading to pale yellow, pale yellowish pink, very pale pinkish brown (Munsell 5 YR 5/4–10 YR 8/4), not striate or translucent-striate up to 1/3 of radius, rarely striate up to center; margin entire to undulate, occasionally becoming eroded with age; surface glabrous when moist, becoming radially adnately fibrillose, rarely squamulose at disc. **Lamellae** ($L = (12-)15-26/1 = 1-4(-5)$), close to distant, when young arcuate, becoming adnate or slightly emarginate or decurrent with tooth, relatively thin to thick, rarely very thick, pinkish flesh color (Munsell 7.5 YR 8/4), often becoming slightly vinaceous or dark pink-brown (10 R 5/3), white pruinose with age; edge entire, concolorous. **Stipe** (12–)17–65(–105) × 1.5–5(–12) mm, cylindrical to sub-clavate or tapering towards base, occasionally with subbulbous base, sometimes compressed, sometimes slightly eccentric, solid, later fistulose, concolorous with pileus, fibrillose, not striate to finely longitudinally striate, very rarely with pronounced striations. **Basal mycelium** sparse to copious, white. **Context** of pileus thin, hygrophanous and concolorous with, to slightly paler than surface. **Context** of stipe similar to pileus context. **Smell** fungoid, sometimes herbaceous fungoid or subraphanoid; taste mild fungoid. **Spore print** white.

Basidiospores (excluding ornamentation) 7.0–9.0(–11.0) × (5.0–)6.0–8.0(–8.5) μm , $Q = (1.1-)1.15-1.35(-1.45)$, $Q = 1.2-1.3$, broadly ellipsoid to ellipsoid, echinulate; spines 0.5–2.0(–2.5) μm high, crowded; hilar appendage 1.5–2.0 μm long, prominent, truncate; contents occasionally uni- or biguttulate; basidiospore wall up to 1 μm thick. **Basidia** 27.5–55 × 7.5–13.5(–16.5) μm , clavate, elongate, hyaline, tetrasporic, very rarely bi- or trisporic. **Pleurocystidia** absent. **Cheilocystidia** (15–)25–55(–70) × 2–5(–7.5) μm , filiform to narrowly clavate, occasionally strangulate, sometimes branched, absent or scattered to abundant, thin-walled, hyaline. **Pileipellis** a cutis of radially arranged cylindrical hyphae 10–15 μm wide, often with scattered fascicles of more or less perpendicular hyphae; terminal elements of fascicular hyphae up to 37.5 μm in diam., undifferentiated to broadly clavate; contents hyaline to yellowish brown due to intracellular and slightly encrusting moderately yellowish brown pigment. **Stipitipellis** a cutis of 8–10 μm wide hyphae with yellowish brown intracellular and slightly encrusting pigment.

Habitat & distribution. — Solitary to gregarious, terrestrial, on humus or volcanic or burnt soils; cosmopolitan, not abundant.

Laccaria laccata var. *laccata* is apparently uncommon. Neither of us have collected it and only few collections referable to it were found among the herbarium material that we have examined. Those names for which no type specimen and good micromorphological description exists are placed under this variety along with three of the varieties proposed by Singer (1967: 110; 1977: 362) and one by Bon (1982: 42). The holotypes

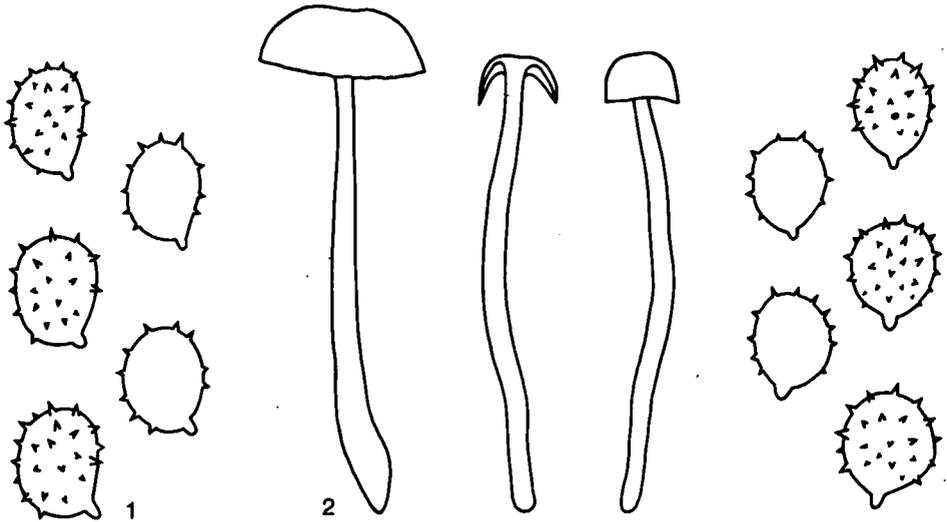


Fig. 1. *Laccaria laccata* var. *laccata*. — Spores ($\times 1500$, from neotype).

Fig. 2. *Laccaria laccata* var. *moelleri*. — Habit ($\times 0.5$), spores ($\times 1500$). (Both from Mueller 1926, 18 Sept. 1984, Canada, Ontario, Algonquin Prov. Park, Spruce Bog Trail, WTU).

of these synonyms differed from the type variety in several minor ways, but *L. laccata* var. *laccata*, *L. laccata* var. *pseudobicolor*, *L. laccata* var. *carbonicola*, and *L. laccata* var. *vulcanica* are all macromorphologically similar and all share the important character state of relatively elongate basidiospores and are thus treated as contaxic.

This variety is differentiated from the other varieties of *L. laccata* by its broadly ellipsoid to ellipsoid, moderately ornamented basidiospores. All of the varieties, however, are tied together by their macromorphology. Although members of *L. laccata* var. *laccata* have not been included in mating studies, members of the other two varieties have been shown to be at least partly compatible with each other and genetically isolated from all other species tested (Fries & Mueller, 1984; Mueller & al., 1985).

Laccaria laccata var. *laccata* can only be differentiated from *L. proxima* with some difficulty. *Laccaria proxima* differs by being more robust and having somewhat darker colored and more scaly basidiocarps and more finely ornamented basidiospores.

Laccaria laccata var. *moelleri* Sing. — Fig. 2

Laccaria laccata var. *moelleri* Sing. in *Sydowia* Beih. 7: 9. 1973.

Type specimen (holotype): F — Singer C5227, 30 Sept. 1970, CSSR, Treboň.

Macromorphology as in type variety except where noted. Pileus (11–)18–42(–78) mm, often depressed, usually with papilla. Stipe (38–)70–120(–165) \times 3–6(–11) mm.

Basidiospores (excluding ornamentation) $(7.0-8.0-10.0(-11.0) \times 7.0-8.5 \mu\text{m}$, $Q = (1.0-1.05-1.25(-1.6))$, $\bar{Q} = 1.1-1.3$, subglobose to broadly ellipsoid, occasionally globose or ellipsoid, echinulate; spines $0.5-1.5(-2.0) \mu\text{m}$ high, crowded. All else as in type variety.

All other micromorphology as in type variety.

Habitat & distribution. — Gregarious, among moss, often *Sphagnum*; Europe and North America, not abundant.

This variety is characterized by its very long stipe, papilla in the pileal depression, subglobose to broadly ellipsoid basidiospores, and restricted habitat (among moss, especially *Sphagnum*). Singer reports this variety from Eastern Europe and one of us (G.M.M.) has collected it in Sweden and Canada.

In the laboratory, members of this variety will successfully mate with at least some members of *L. laccata* var. *pallidifolia* (Peck) Peck. Since several widely separated populations of *L. laccata* var. *moelleri* have been found, the two varieties may be partially genetically isolated and thus both taxa need to be recognized.

Laccaria laccata var. *pallidifolia* (Peck) Peck — Fig. 3

Clitocybe laccata var. *pallidifolia* Peck in Ann. Rep. N.Y. St. Bot. 43: 38. 1890. — *Laccaria laccata* var. *pallidifolia* (Peck) Peck in Ann. Rep. N.Y. St. Bot. 157: 92. 1912.

Clitocybe tortilis var. *gracilis* Peck in Ann. Rep. N.Y. St. Bot. 67: 36. 1903.

Laccaria laccata var. *decurrens* Peck in Ann. Rep. N.Y. St. Bot. 157: 92. 1912.

Laccaria laccata var. *anglica* Sing. in Bull. trimest. Soc. mycol. Fr. 83: 110. 1967. — *Laccaria anglica* (Sing.) M. Bon in Doc. mycol. 11(44): 22. 1981. (not val. publ.; basionym lacking). — *Laccaria affinis* var. *anglica* (Sing.) M. Bon in Doc. mycol. 13(51): 50. 1983.

Laccaria laccata var. *affinis* Sing. in Bull. trimest. Soc. mycol. Fr. 83: 111. 1967. — *Laccaria affinis* (Sing.) M. Bon in Doc. mycol. 13(51): 49. 1983.

Laccaria tetraspora Sing. in Mycologia 38: 689. 1946. — *Laccaria tetraspora* var. *tetraspora* automatically established by var. *peullensis* Sing. in Bull. trimest. Soc. mycol. Fr. 83: 113. 1967.

Laccaria tetraspora var. *scotica* Sing. in Bull. trimest. Soc. mycol. Fr. 83: 114. 1967. — *Laccaria scotica* (Sing.) M. Bon in Doc. mycol. 11(44): 23. 1981. (not val. publ.; basionym lacking).

Agaricus ohiensis Mont., Syll. Gen. Sp. Crypt.: 100. 1856. — *Clitocybe ohiensis* (Mont.) Sacc., Syll. Fung. 5: 181. 1887. — *Laccaria ohiensis* (Mont.) Sing. in Mycologia 38: 688. 1946. — *Laccaria ohiensis* var. *ohiensis* automatically established by var. *paraphysata* McNabb in N. Z. J. Bot. 10: 474. 1972.

Laccaria laccata var. *subalpina* Sing. in Plant Syst. Evol. 126: 365. 1977.

Laccaria laccata var. *tatrensis* Sing. in Plant Syst. Evol. 126: 367. 1977.

Laccaria laccata var. *intermedia* Sing. in Plant Syst. Evol. 126: 368. 1977.

Laccaria tetraspora var. *tetraspora* f. *major* Sing. in Bull. trimest. Soc. mycol. Fr. 83: 113. 1967. (not val. publ.; type specimen not designated). — *Laccaria tetraspora* var. *major* (Sing.) M. Bon & Haluwijn in Doc. mycol. 14(53): 6. 1984.

Excluded. — *Laccaria ohiensis* sensu Sing. in Lilloa 22: 177. ('1949') 1951; sensu Sing. & Digilio in Lilloa 25: 23. 1952; sensu auct. plur. (in all cases *L. fraterna*).

Type specimen (holotype): NYS — Peck, October, USA, Selkirk.

Macromorphology as in type variety.

Basidiospores (excluding ornamentation) $(6.5-7.5-10.0(-13.0) \times (6.0-7.0-10.0(-12.5) \mu\text{m}$, $Q = (0.95-1.0-1.15(-1.3))$, $\bar{Q} = 1.0-1.1(-1.15)$, globose to subglo-

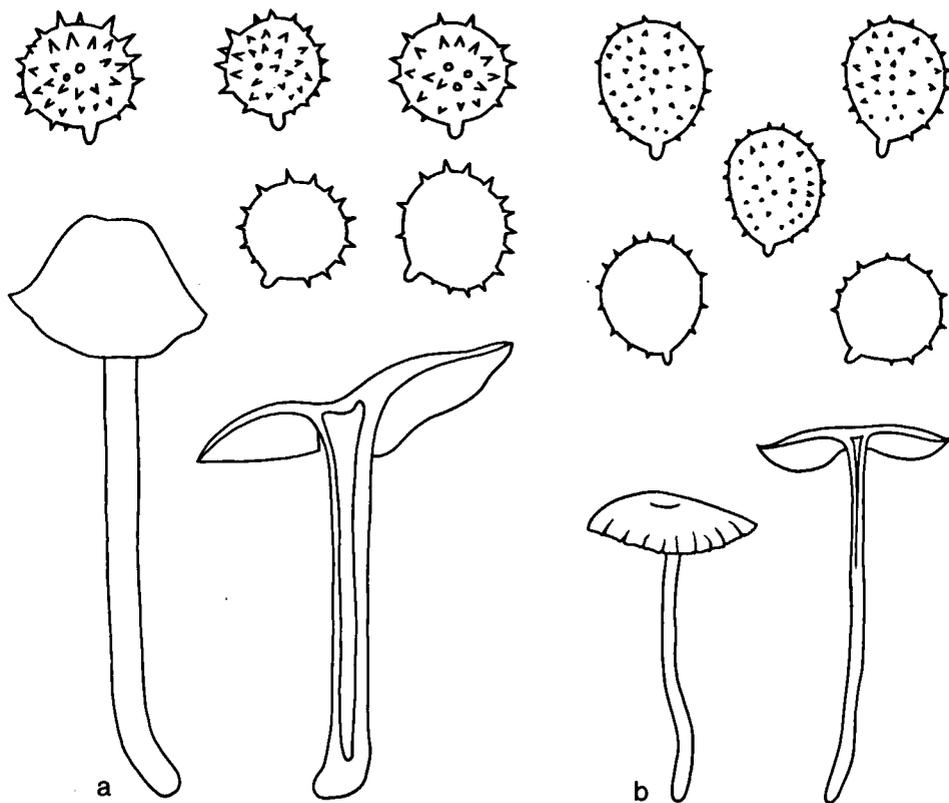


Fig. 3. *Laccaria laccata* var. *pallidifolia*. — Habit ($\times 1$), spores ($\times 1500$). (a. From *Vellinga 384*, 1 Aug. 1981, Netherlands, IJsselmeerpolders, Bremerbergbos, L; b. from *Vellinga 573*, 4 Nov. 1983, Netherlands, Noord-Holland, Zwanewater, L).

bose, rarely broadly ellipsoid, echinulate; spines $0.5\text{--}2.5\ \mu\text{m}$ high, up to $1.5\ \mu\text{m}$ wide at base. All else as in type variety.

All other micromorphology as in type variety.

Habitat & distribution. — Gregarious, more rarely solitary or caespitose, terrestrial on sand, soil or among moss including *Sphagnum*; cosmopolitan; abundant.

Laccaria laccata var. *pallidifolia* is by far the most common variety in the species and can be found in a wide variety of habitats. It differs from the type variety by having globose to subglobose or occasionally broadly ellipsoid, moderately to strongly ornamented basidiospores.

As can be seen from the lengthy list of synonyms, numerous names have been proposed for this taxon. All of these names were based on type specimens characterized by

having small to moderate sized, orange brown, glabrous to finely scaly basidiocarps, white mycelium at the base of the stipe, 4-sterigmate basidia, and globose to subglobose, moderately to strongly ornamented basidiospores (Table I).

Laccaria fraterna (Cooke & Mass.) Pegl.

Agaricus fraternus Cooke & Mass. in *Grevillea* 16: 31. 1887. — *Naucoria fraterna* (Cooke & Mass.) Sacc., *Syll. Fung.* 9: 110. 1891. — *Laccaria fraterna* (Cooke & Mass.) Pegl. in *Aust. J. Bot.* 13: 332. 1965.

Naucoria goossensiae Beeli in *Bull. Soc. Roy. Bot. Belgique* 61: 88. 1928. — *Laccaria laccata* f. *bispora* Heinemann in *Bull. Jard. Bot. État* 34: 310. 1964. (change of name).

Laccaria lateritia Malenç. in *Bull. trimest. Soc. mycol. Fr.* 82: 189. 1966.

Misapplied names. — *Laccaria ohiensis* sensu Sing. in *Lilloa* 22: 177 ('1949') 1951; sensu auct. plur.

Type specimen (holotype): K — *French No. 1*, Australia, vic. Port Phillip.

As mentioned above, neither *L. ohiensis* or *L. striatula* can be used for the bisporic *Laccaria* with moderate sized basidiospores (mostly 9–11 × 8–11 μm excluding ornamentation) because both are tetrasporic. Cooke & Masee (1887: 31) described *Agaricus fraternus* from Port Phillip, Australia as a dark rusty red mushroom growing on wood with ellipsoid, moderate sized basidiospores. Its type specimen has 2-spored basidia which bear moderate sized, globose to subglobose, echinulate basidiospores (Table III). As mentioned by Pegler (1965: 332), the report of ellipsoid spores in the original diagnosis of *A. fraternus* probably refers to another collection on the type sheet from New Zealand which Singer has annotated as a 'strophariaceous species.'

Two later names whose type specimens also have bisporic basidia which bear moderate sized basidiospores are *Naucoria goossensiae* Beeli and *L. lateritia* Malenç. (Table III). The major differences between the three type specimens is that *A. fraternus* was reportedly collected 'on logs', while the other two were growing under *Eucalyptus*. Since it is not uncommon to find other terrestrial *Laccaria* species growing on decomposed wood, the difference in their habitat does not appear significant and the three are considered contaxic.

Based primarily on ecological differences, Malençon (1966) and Pegler & Rayner (1969) recognized two bisporic species with moderate sized basidiospores: (i) *Laccaria fraterna* (as *L. lateritia*) growing in warm, dry regions (e.g., Australia, Mediterranean regions, and parts of South America) under *Acacia*, *Eucalyptus*, and *Coffea* and (ii) *L. striatula* sensu Singer growing in cool moist areas (e.g., Great Britain and the French Alps) in moss including *Sphagnum*. We consider these two forms as separate taxa, *L. fraterna* and *L. pumila* Fay., respectively.

Laccaria pumila Fay.

Laccaria pumila Fay. in *Annali Accad. Agric. Torino* 35: 91. 1893. — *Clitocybe pumila* (Fay.) Sacc., *Syll. Fung.* 17: 13. 1905. — *Laccaria laccata* var. *pumila* (Fay.) J. Favre in *Ergebn. wiss. Unters. schweiz. Natn Parks* V, 33: 51. 1955 (not val. publ.; basionym not mentioned).

Table III. Characteristics of the three names discussed under *Laccaria fraterna*. Herbarium abbreviations from Index Herbariorum. Macromorphology based on original diagnosis. Micromorphology based on examination of cited specimens.

	<i>Agaricus fraternus</i> Holotype at K <i>French No. 1</i>	<i>Naucoria goossensiae</i> Holotype at BR <i>Goossens No. 588</i>	<i>Laccaria lateritia</i> Representative specimen at MPU <i>Felippone No. 2800</i>
Pileus:	convex, glabrous, dark rusty-red	convex, glabrous, brownish rust color	convex to depressed, striate to glabrous, red brown to dark brick-red
Lamellae:	adnate, rusty-red	adnate, brownish red color	adnate to arcuate, pallid rose to purple ochraceous
Stipe:	elongate, thin, glabrous, concolorous	elongate, relatively thin, glabrous, concolorous	short, thin, striate & twisted, reddish brown
Basidia:	2-sterigmate, clavate	2(-4)-sterigmate, clavate	2-sterigmate, clavate
Spores: (n = 30)	(8.5-)9.0-11.0(-11.5) × 8.5-10.5(-11.5) μm mean L × W = 9.9 × 9.9 μm mean L/W = 1.01	(8.0-)8.5-11.0(-11.5) × (7.5-)8.0-10.0 μm mean L × W = 9.9 × 8.9 μm mean L/W = 1.11	8.5-11.0(-13.5) × 8.5-10.5(-13.5) μm mean L × W = 9.7 × 9.5 μm mean L/W = 1.02
Echinulae:	(1.0-)1.5-2.0 μm long	< 0.5-1.5 μm long	1.0-1.5 μm long
Habitat:	on logs	under <i>Eucalyptus</i>	under <i>Eucalyptus</i>

Laccaria altaica Sing. in Bull. trimest. Soc. mycol. Fr. 83: 122. 1967.

Misapplied names. — *Laccaria striatula* sensu Sing. in Mycologia 35: 151. 1943; sensu auct. plur.

Laccaria tortilis sensu M. Lange in Meddr Grønland 147: 29. 1955; sensu O. K. Miller & al. in Mycologia 74: 583. 1982.

Type specimen (neotype, design. nobis): L — *J. Trimbach 1463*, 18 July 1976, France, dept. Alpes maritimes, Col de la Cayolle, alt. 2500 m.

Fayod (1893: 91) described a small bisporic *Laccaria* from the Italian side of the French Alps (Torre Pellice) under the name *L. pumila*. While he stated that it differed from *L. tortilis* (Bolt.) Cooke, he did not designate a type specimen. The original description and Fayod's watercolor and line drawings of its micromorphology support treating *L. pumila* as a separate taxon.

A specimen collected by J. Trimbach (*J. Trimbach 1463*) in the French Maritime Alps approximately 80 km south southwest of the type locality of *L. pumila* fits the original description and drawing of *L. pumila*, represents our concept of this taxon, and is designated as the neotype. This collection has the following characteristics:

Macromorphology: See Trimbach (1978: 44–45).

Basidiospores (excluding ornamentation) $(10.5-11.0-12.0(-15.0) \times (9.0-9.5-10.5(-15.0) \mu\text{m}$, $Q = (1.0-1.05-1.3(-1.35)$, $\bar{Q} = 1.18$, subglobose to broadly ellipsoid or ellipsoid, a few globose, echinulate; spines $0.5-0.8(-1.0) \mu\text{m}$ high, very crowded; hilar appendage up to $2 \mu\text{m}$ long, prominent, truncate; basidiospore wall up to $1 \mu\text{m}$ thick. Basidia $47-55 \times 10-15 \mu\text{m}$, narrowly clavate, elongate, hyaline, bisporic.

As was already suggested by Trimbach (1978: 45), *L. pumila* and *L. altaica* Sing. are conspecific. Both have the same morphology (small, strongly striate pileus and bisporic basidia which bear large, elongate, finely ornamented basidiospores) and were first described from alpine habitats.

Laccaria pumila differs from *L. fraterna* by having larger basidiospores (most $11-16 \times 10-15 \mu\text{m}$ versus most $9-11 \times 8-11 \mu\text{m}$ in *L. fraterna*), orange-brown basidiocarp color versus rusty red-brown basidiocarp color in *L. fraterna*, and a preference for cooler, more humid, alpine, boreal, to arctic habitats.

Laccaria pumila differs from *L. tortilis* by having subglobose to ellipsoid finely ornamented basidiospores instead of the globose, strongly echinulate basidiospores of *L. tortilis*. Additionally, *L. tortilis* often displays highly contorted basidiocarps with very few and widely spaced lamellae.

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