

Amylolepiota, Clavicybe and Cystodermella, new genera of the Agaricales

HARRI HARMAJA

HARMAJA, H. 2002: Amylolepiota, Clavicybe and Cystodermella, new genera of the Agaricales. – Karstenia 42: 39–48. Helsinki. ISSN 0453-3402.

Lepiota lignicola P.Karst., is referred to *Amylolepiota* Harmaja, n. gen., as *Amylolepiota lignicola* (P.Karst.) Harmaja, n. comb. *Clitocybe clavipes* (Pers. : Fr.) P.Kumm. (as the type) and two related species are separated from the externally very similar *Clitocybe* (Fr.) Staude to form a new genus, *Clavicybe* Harmaja. *Clavicybe* differs from *Clitocybe*: (i) the spore surface appears rough with a high magnification, the anatomy deviates as (ii) the hygrophanity of the fruit body is different and (iii) the gill trama is irregular. A key to the species is given. 3 new nomenclatural combinations in *Clavicybe* are made: *C. avellaneialba* (Murrill) Harmaja, *C. clavipes* (Pers. : Fr.) Harmaja, and *C. squamulosoides* (P.D.Orton) Harmaja. A third new genus, *Cystodermella* Harmaja, is described for a group of species with inamyloid spores segregated from *Cystoderma* Fayod. 12 new nomenclatural combinations in *Cystodermella* are made: *C. adnatifolia* (Peck) Harmaja, *C. ambrosii* (Bres.) Harmaja, *C. cinnabarina* (Alb. & Schwein. : Fr.) Harmaja, *C. contusifolia* (Pegler) Harmaja, *C. cristallifera* (Thoen) Harmaja, *C. elegans* (Beeli) Harmaja, *C. granulosa* (Batsch : Fr.) Harmaja (type species of *Cystodermella*), *C. japonica* (Thoen & Hongo) Harmaja, *C. luteohemisphaerica* (Dennis) Harmaja, *C. myriadocystis* (Heinem. & Thoen) Harmaja, *C. sipariana* (Dennis) Harmaja, and *C. subpurpurea* (A.H.Sm. & Singer) Harmaja. Special attention was paid to correct nomenclature and author citations.

Key words: amyloidity, arthrospores, *Clitocybe*, *Cystoderma*, Finland, *Floccularia*, gill trama, hygrophanity, *Lepiota*, nuclear DNA content, *Ripartitella*, *Squamanita*

Harri Harmaja, Botanical Museum, Finnish Museum of Natural History, P.O. Box 47, FIN-00014 University of Helsinki, Finland www.helsinki.fi/people/harri.harmaja/

AMYLOLEPIOTA

I am lucky enough to be among the very few people who have seen the unusual agaric *Lepiota lignicola* P.Karst. in the nature. This species was described in 1879 from southern Finland. According to my judgement, *L. lignicola* must be classified in a separate, new genus as described below.

Amylolepiota Harmaja, n. gen.

?*Lepiota* sect. *Amyloideae* Singer, Ann. Mycol. 41: 171. 1943. – Holotype: *Lepiota amyloidea* Singer. This synonymy is true if *L. amyloidea* is

synonymous with *L. lignicola* as claimed by Knudsen (1980).

Agaricalium generis Lepiotae affinis. Ab ea differt sporis amyloideis habitationeque ligno. Epicutis e cellulis elongatis instructa. Rarisime occurrit in silvis borealibus vetustis. – Typus: Amylolepiota lignicola (P.Karst.) Harmaja (Lepiota lignicola P.Karst.).

Basidiocarp medium-sized. Universal veil apparently present; presence of partial veil unclear. Pi-

leus convex to plane; surface dry, with appressed to squarrose brown scales. Stipe without ring; surface dry, below the ring zone with squarrose scales like those of pileus. Lamellae free, whitish. Flesh white, not changing. Odour not distinctive. Taste mild. Spores pure white in fresh deposit (pale yellow in age), binucleate, ellipsoid; wall without germ-pore, hyaline, smooth, distinctly amyloid, cyanophilic, but carminophobic. Basidia with basal clamp, without carminophilic/siderophilic granulation; wall carminophobic, with a thin cyanophilic inner layer towards apex. Cheilocystidia present, inconspicuous; pleurocystidia lacking. Epicutis, also in scales, of cells which are distinctly longer than wide; pigment essentially membranous. Hymenophoral trama regular. Clamp connections present in hyphae of fruit body. Dried pileus, stipe, lamellae, basal mycelium, flesh and spore deposit do not exhibit fluorescence but retain their colours under ultraviolet light (with wave-lengths 254 nm and 366 nm), excepting the tinges of the three first-named structures which become slightly deeper. Habitat on decaying wood (always of *Betula* ?) in forest; causes white rot.

The above description is based on my studies of fresh and dried fruit bodies of the type species. Included are the first reports of the responses of its basidiocarp to ultraviolet light and of its spores and basidia to the reagents methyl (cotton) blue and acetocarmine.

Amylolepiota is closely related to the agaric genus *Lepiota* Gray (type species *L. clypeolaria* (Bull. : Fr.) P.Kumm.); the fruit bodies remind those of the species of sect. *Echinatae* Fayod of the latter genus. The lamellae are likewise free in the new genus, but their proximal ends reach closer to the stipe apex than in *Lepiota*. The decisive differences are the amyloid spore wall and the lignicolous habit of *Amylolepiota*. In *Lepiota* the spore wall is dextrinoid and the species are saprophytes on bare humous soil or in non-woody litter. However, *L. zenkeri* Henn. has an amyloid spore wall; it has been included in a section of its own (Singer 1986). *L. zenkeri* does not appear to belong to *Amylolepiota*: it occurs in tropical Africa on non-ligneous substrate. *Cystolepiota* Singer differs from *Amylolepiota* by possessing uninucleate inamyloid spores, a pileus cortex of sphaerocysts, and non-woody habitat. *Leucopholiota* (Romagn.) O.K.Mill., T.J.Volk & Bessette (Miller & al. 1996) differs by

having rather broadly adnate lamellae: see the original illustration of the type species, *Agaricus decorosus* Peck (Peck 1873) [Romagnesi (1989) suggested that *L. lignicola* and *A. decorosus* would be identical]. In *Cystoderma* Fayod s. str., as restricted by me in this paper (see below), the universal veil is essentially composed of sphaerocysts and the lamellae are not free but adnate.

Most probably the new genus contains a single species only; the necessary new combination is made below. However, *Cystoderma carpaticum* M.M.Moser, an enigmatic fungus based on a single specimen from Poland (Moser 1979), should be compared when more material is available.

Amylolepiota lignicola (P. Karst.) Harmaja, n. comb.

Coloured illustrations: Karsten 1883: fig. 1; Korhonen 1991: Sienilehti 43(1), back cover

Basionym: *Lepiota lignicola* P.Karst., Bidrag Kännedom Finlands Natur Folk 32 [Ryssl. Hattsvamp. 1]: 547. 1879. – *Cystolepiota lignicola* (P.Karst.) Nezdobjm., Mikol. Fitopatol. 14: 389. 1980. – Holotype: Finland, Etelä-Häme, Tammela, Mustiala, in ligno mucido betulae, IX.1879 P.A. Karsten (H: Herb. P.A. Karsten no. 2034). – Other specimens examined (also when fresh): Finland, Etelä-Häme, Lammi, Evo, virgin forest 'Kotisten aarnialue', 11.IX.1973 H. Harmaja (H); exactly the same place, 11.IX.1973 U. Kurimo (H).

?*Lepiota amyloidea* Singer, Ann. Mycol. 41: 171. 1943. – Holotype: Russia, Altay Republic (as 'Oirotia, Altai'), Lake Teletskoe (LE, n.v.). Knudsen (1980) synonymizes this species with *L. lignicola*.

A detailed description of the species is given by Knudsen (1980, as *Lepiota*).

In Finland *A. lignicola* possesses a specific habitat ecology: the species is restricted to mesic old-growth forest in the southern boreal zone; the substrate is decaying wood, a fallen log or larger branch of *Betula* lying on the ground (it is unknown whether *B. pendula*, *B. pubescens* or both are concerned). The species is classified as critically endangered (CR) in Finland according to the latest Red List of Finland (Rassi & al. 2001).

During the mycology courses of the University of Helsinki, arranged at Lammi (S. Finland), the fungus was found in the same locality at Kotinen

Virgin Forest in five successive years (1972–1976), probably on the same decaying *Betula* log!

In total, specimens examined by me or literature reports that appear reliable show that *A. lignicola* has been found (i) in three localities in the inland of South Finland (in the province of Etelä-Häme, latest in 1985; according to specimens in H), (ii) in the Republic of Karelia, Russia (Kotiranta & al. 1998), and (iii) in several localities throughout the Asian part of Russia (Singer 1943 if the synonymy indicated by Knudsen [1980] is approved), Vasil'eva 1973, Nezdojminogo 1982, Petrov 1986, Kutafyeva 1989 [recorded as *L. hystrix* Möll. & J. Lange but most probably referring to the present species], Astapenko & Kutafyeva 1990, Lapitskaya 1993, Gorbunova 2001). To my judgement, the records from the U.S.A. (Knudsen 1980) and Mexico (Cifuentes & al. 1989, as *L. amyloidea*) require further study, as does the lignicolous '*Lepiota hispida* Lasch' from Italy (Bresadola 1927).

CLAVICYBE

A monograph on the genus *Clitocybe* (Fr.) Staude in Fennoscandia (northwestern Europe) constituted my Ph.D. thesis (Harmaja 1969). In that contribution, I reported 43 species from the study area; they were placed in 3 subgenera and 16 sections, and I considered the genus clearly heterogeneous. *C. clavipes* (Pers. : Fr.) P.Kumm. was assigned to a section of its own. Later I separated a part of the species and transferred them to *Lepista* (Fr.) W.G.Sm. or *Singerocybe* Harmaja (Harmaja 1974a, 1974b, 1976, 1988). Even after these procedures, *Clitocybe* still did not appear natural.

Among the Fennoscandian species, *Clitocybe clavipes* was found by me (Harmaja 1969) unique in four respects: (i) the pileus is not hygrophanous though the flesh has this character, (ii) the wet cap flesh begins to dry and fade from the periphery towards the centre, (iii) the trama of the lamellae is constructed of interwoven hyphae (vs. parallel or subparallel), and (iv) the spores contain a distinct, large, refractive oil drop. As in addition Pegler & Young (1971) found that, with a high magnification under the electron microscope (they used the carbon replica method), the spores of this species have a roughened surface, I planned to create for *C. clavipes* a genus of its own in the 1970's. Moreover, *C. clavipes* has been found "poisonous": the

antabuse-like reaction (i.e., that of the disulfiram-type) results when fruit bodies heated for food are consumed with alcohol (e.g. Cochran & Cochran 1978, Bresinsky & Besl 1985).

In a very recent phylogenetic analysis of a great number of agarics and related species (Moncalvo & al. 2002), the position of *C. clavipes* was somewhat peculiar which might support the establishment of a separate genus for the species.

Two additional species are included in *Clavicybe*: *Clitocybe avellaneialba* Murrill and *Clitocybe squamulosoides* P.D.Orton. The affinity of the former species to *Clitocybe clavipes* was earlier stated by me (Harmaja 1969); the latter was previously thought by me to represent a form of *C. clavipes* (Harmaja 1970).

***Clavicybe* Harmaja, n. gen.**

Clitocybe subg. *Clitocybe* sect. *Clavipedes* Harmaja, Karstenia 9: 58. 1969. – Type: *Clitocybe clavipes* (Pers. : Fr.) P.Kumm.

Clitocybe subg. *Infundibuliformes* sect. *Inornatae* subsect. *Albiphylloae* H.E.Bigelow, Beih. Nova Hedwigia 72: 193. 1982. – Type: *Clitocybe avellaneialba* Murrill.

Clitocybe subg. *Hygroclitocybe* Bon, Doc. Mycol. 13(51): 9. 1983. – Type: *Clitocybe clavipes* (Pers. : Fr.) P.Kumm.

Agaricalium genus. *Genus Clitocybem in mentem revocat. Ab ea inter alia differt sporis subtilissime rugulosis tramaque lamellarum e hyphis intricatis instructa.* – *Typus: Clavicybe clavipes* (Pers. : Fr.) Harmaja (*Agaricus clavipes* Pers. : Fr.).

Agaricales; habitus of basidiocarp as in *Clitocybe*. Veil completely absent. Pileus from convex to plane or somewhat depressed, not hygrophanous, brown or grey-brown; surface dry. Stipe usually clavate, concolorous with pileus; surface dry. Lamellae decurrent, whitish. Odour sweetish or indistinct. Taste mild. Flesh hygrophanous; cap flesh dries from the periphery towards the centre. Spores pure white in fresh deposit (pale yellow in age), not sticking to tetrads or with collapsed walls in mounts made of dry gills, fairly large, a proportion of them always broadly fusiform; uninucleate (Kühner 1945); wall without germ-pore, hyaline, inamyloid, cyanophobic (Singer 1972, Harmaja 1974a, 1976, 1979b), rugu-

lose under the electron microscope at least in the type species (Pegler & Young 1971, Bigelow 1981); contents with one distinct oil drop; hilar appendix large, ca. $0.9\text{--}1.1 \times 0.7\text{--}0.9\ \mu\text{m}$. Cystidia of any kind absent. Pileus cortex made of epicutis and subcutis of subparallel hyphae; pigment essentially situated within cells of epicutis. Hymenophoral trama irregular, i. e., composed of interwoven hyphae (*textura intricata*). Clamp connection abundant everywhere in the basidiocarp. Dried pileus, stipe, lamellae, basal mycelium and flesh and of the type species do not exhibit fluorescence but retain their colours under ultraviolet light (with wave-lengths 254 nm and 366 nm), excepting the tinges of the three first-named structures which become slightly deeper. Saprophytes which decay plant litter, especially needles and leaves, sometimes herbaceous litter or woody substrates.

Clavicybe avellaneialba (Murrill) Harmaja, n. comb.

Basionym: *Clitocybe avellaneialba* Murrill, Mycologia 5: 207. 1913. – Material from the U.S.A. studied (Harmaja 1969).

Clavicybe clavipes (Pers. : Fr.) Harmaja, n. comb.

Basionym: *Agaricus clavipes* Pers., Syn. meth. fung.: 353.1801: Fr., Syst. mycol. 1: 86. 1821. – *Clitocybe clavipes* (Pers. : Fr.) P.Kumm., Führ. Pilzk.: 124. 1871. – *Omphalia clavipes* (Pers. : Fr.) Quél., Enchir. fung. 20. 1886.

Clavicybe squamulosoides (P.D.Orton) Harmaja, n. comb.

Basionym: *Clitocybe squamulosoides* P.D.Orton, Trans. Brit. Mycol. Soc. 43: 187. 1960. – Isotype examined (Harmaja 1970): U.K., England, Surrey, Witley Common, 13.XII.1956 P.D. Orton (H).

Discussion

Macroscopically, the species of this new genus are very similar to the larger non-hygrophaneous species of *Clitocybe* (sensu Harmaja 1976). As mentioned above, *Clavicybe* differs from *Clitocybe* in two fundamental points: (i) the spore wall is rough when observed with the electron microscope (at least in the type species) vs. smooth and (ii) the hyphae of the gill trama are interwoven vs. running in parallel-subparallel direction as in *Clitocybe*. Also Bigelow (1982) describes the gill trama of *C. clavipes* as interwoven, likewise that of *C. avellaneialba* (as does Smith 1949). Moreover, there are two differences in the hygrophany of the fruit body as described in the introductory section above. These unusual properties of hygrophany are apparently related to each other and they may ultimately result from some anatomical peculiarity of the whole fruit body. The interwoven gill trama may also be involved.

The direction in which the hyphae are running in the trama of the lamellae is diagnostic in the Agaricales, especially at the generic level, e.g. characterizing the genus *Camarophyllus* (Fr.) P.Kumm. (Singer 1986).

Of the three species included in *Clavicybe*, *C. clavipes* is distributed over a wide area in the northern hemisphere, *C. avellaneialba* is restricted to western North America, and the poorly known *C. squamulosoides* has been found in temperate western Europe. In addition, a fungus which is sometimes called as “the pale-brown form of *Clitocybe clavipes*” occurs in the temperate deciduous woods of Central Europe. A good coloured photograph of the last-named fungus was published by Phillips (1981, p. 48, as *Clitocybe clavipes*). This taxon may be a fourth species of *Clavicybe*, or it falls within the variability of *C. squamulosoides*. Also the typical dark grey-brown *C. clavipes* decays, besides needles, leaf litter, often leaves of *Betula*; I myself have found it in the leaves of the beech (*Fagus sylvatica*) near Femsjö, Sweden.

A key to the species of *Clavicybe*

- 1 Spores ca. $6-9 \times 3.5-5.3 \mu\text{m}$, variable in shape; on litter of needles or leaves 2
 1' Spores ca. $8-10 \times 4.0-5.5 \mu\text{m}$, broadly fusiform; mostly on much decayed woody substrates (western North America) *C. avellanealba*
- 2 Cap and stipe dark in colour, grey-brown or sepia brown; stipe distinctly clavate; in litter of needles or leaves; widely distributed *C. clavipes*
 2' Cap and stipe pale brown or avellaneous; stipe hardly enlarged downwards; mostly in leaf litter; temperate woods of western Europe *C. squamulosoides*

CYSTODERMELLA

Fayod (1889) included partly unrelated species in his new genus *Cystoderma* Fayod (see Smith & Singer 1945). Heinemann & Thoen (1973) delimited the genus in a most appropriate way, and their delimitation is essentially the current one. An universal veil possessing a thick outer layer of spherocysts is the conspicuous main diagnostic character of the genus. However, since the 1930's it has been known that the species of the genus can be assorted to two groups: those with amyloid spores and those with an inamyloid spore wall. The lectotype of the genus is *C. amianthinum* (Scop.) Konrad & Maubl. with amyloid spores (selected by Smith & Singer 1945). Generally, the genus has been divided into two sections: sect. *Cystoderma* and sect. *Granulosa* (Fr.) Locq. (type *C. granulorum* (Batsch : Fr.) Kühner) (see e.g. Singer 1986).

For decades, I have personally been interested in *Cystoderma* and made research on the genus. Now I have (i) evaluated the taxonomic weight of the spore difference within *Cystoderma* mentioned above, (ii) considered some previously unused, less exact differences or tendencies present in the genus (see Table 1), (iii) applied the results of a recent contribution on the nuclear DNA content of some species (Saar & Kullman 2000) as well as (iv) taken into consideration the results of the phylogenetic analysis of Moncalvo & al. (2002). My judgement, based on the above, is that *Cystoderma*, as currently understood (Heinemann & Thoen 1973, Singer 1986), has to be split into two genera: *Cystoderma* s. str. will comprise species that possess amyloid spores while a new genus has to be established for species with inamyloid spores. *Cysto-*

dermella Harmaja (type *C. granulorum*) is described below for the latter species group.

Cystodermella Harmaja, n. gen.

Agaricus subg. *Lepiota* [sect.?] *Granulosi* Fr., Hymenomyc. eur.: 35. 1874. – *Lepiota* [sect.?] *Granulosae* (Fr.) Qué., Enchir. fung.: 7. 1886. – *Cystoderma* sect. *Granulosa* (Fr.) Locq., Bull. Soc. Linn. Lyon 14: 88. 1945. – *Cystoderma* subg. *Granulosa* (Fr.) Wasser, Fl. grib. Ukrainy: 209. 1980. – Type: *Agaricus granulorum* Batsch: Fr.

Cystoderma sect. *Cinnabarina* Heinem. & Thoen, Bull. Soc. Mycol. France 89: 23. 1973. – Type: *Agaricus cinnabarinus* Alb. & Schwein. : Fr.

Agaricalium generis Cystodermatis proxima. Ab eo inter alia differt tunica sporarum totaliter inamyloidea. – Typus: Cystodermella granulosa (Batsch : Fr.) Harmaja (*Agaricus granulorum* Batsch : Fr.).

Agaricales; habitus of basidiocarp as in *Cystoderma*. Universal veil present. Pileus convex or plane; surface finely to coarsely granulose. Stipe covered with veil remnants except at apex; ring mostly lacking, sometimes present. Lamellae narrowly to broadly adnate. Flesh of stipe and pileus of continuous elasticity. Conidia (arthrospores) absent from context of pileus. Odour indistinct. Taste mild. Spores white in deposit, binucleate (Saar & Kullman 2000: three species examined, the type included), ellipsoid; wall without germ-pore, smooth, inamyloid, cyanophilic (at least in type species: Singer 1972). Cystidia of lamellae mostly absent; when present they are 'harpoon-

like' due to encrusted crystals. Cortex of pileus and stipe (apex excluded) formed by dry velar layer essentially composed of sphaerocysts. Hymenophoral trama of more or less parallel hyphae. Clamp connections present in hyphae of fruit body. Dried pileus, stipe, lamellae, flesh and basal mycelium of the type species do not exhibit fluorescence but retain their colours under ultra-

violet light (with wave-lengths 254 nm and 366 nm; no difference to *C. amianthinum*; these are apparently the first observations on the responses of *Cystoderma* s. lato fruitbodies to ultraviolet light). Saprophytes of non-ligneous, rarely ligneous, plant litter; sometimes among mosses at the same time but probably not truly muscicolous.

Comparison of the genera *Cystoderma* and *Cystodermella*

Table 1. A comparison of *Cystoderma* Fayod and *Cystodermella* Harmaja. The exact differences are given in bold. See the text immediately below for details and references.

	<i>Cystoderma</i>	<i>Cystodermella</i>
Spore wall in Melzer's 'Harpoon' cystidia	amyloid absent	inamyloid present in some species
Arthrospores in fruit body and/or mycelium culture	Present in some species (e.g. type)	unknown
Liability to <i>Squamanita</i>	type species susceptible	resistant
Bryophily	often strong	often not apparent
Ploidy level (both type species studied)	2x	3x or 6x
Phylogeny	type species clusters near <i>Floccularia</i> Pouz.	type species clusters near <i>Ripartitella</i> Sing.

The spore wall of *C. superbum* Huijsman is commonly reported to be amyloid in a small area only, above the hilar appendix (e.g. Heinemann & Thoen 1973). However, according to the observations of Pegler & Young (1971) the spore wall is weakly amyloid throughout, but the area mentioned (the plage) is strongly amyloid.

Kühner (1969) reported the occurrence of conidia (arthrospores) in the flesh of the fruit body and/or in the mycelium culture of some *Cystoderma* taxa with amyloid spores. Heinemann & Thoen (1973) and Harmaja (1979) likewise noted the presence of the arthrospores in the basidiocarps of some amyloid-spored species, including the type.

Saar & Kullman (2000) analyzed the nuclear DNA content (genome size, ploidy level, C value) of six species of current *Cystoderma* from the spore nuclei. They found that all three species with amyloid spores (*C. carcharias* (Pers.) Konrad & Maubl., *C. jasonis* (Cooke & Masee) Harmaja and *C. amianthinum*, the type of the genus) were on 2x ploidy level while the nuclei of three other species, belonging to the group with in-

amyloid spores, contained higher amounts of DNA: *C. adnatifolium* (Peck) Harmaja and *C. granulatum* were on 3x level and *C. cinnabarinum* (Alb. & Schw. : Fr) Konrad & Maubl. (as *C. terreii* (Berk. & Broome) Harmaja) was on 6x level.

The species of *Squamanita* Imbach (Agaricales) parasitize other agarics. They develop chimeric basidiocarps which are mixtures of the structures and tissues of the fruit bodies of the host and the parasite (Harmaja 1988, Redhead & al. 1995). Observations on these chimera fruitbodies and the agaric species growing in their immediate neighbourhood suggest that always when a *Cystoderma* s. lato is contaminated with *Squamanita*, it is *C. amianthinum* (Smith & Singer 1948, Watling 1974, Reid 1983, Harmaja 1988, Lange & Læssøe 1989, Stridvall & Stridvall 1994, Redhead & al. 1995) or *C. carcharias* (Erikson 1997).

In the woods or on rock outcrops, species of *Cystoderma* s. str., in particular, very often grow in a moss carpet with their basal mycelium tightly attached to living mosses. My field experience

even suggests that two species, at least (*C. lilacipes* Harmaja and *C. saarenoksae* Harmaja) are obligately associated with species of *Polytrichum* s. str. (Harmaja 1979a, 1985).

In the comprehensive phylogenetic work of Moncalvo & al. (2002) *Cystoderma amianthinum* and *C. chocoanum* Franco-Molano (like-wise with amyloid spores) clustered with *Floccularia albolanaripes* (G.F.Atk.) Redhead (with amyloid spores) while *C. granulosum* clustered in another clade with *Ripartitella brasiliensis* (Speg.) Singer (with inamyloid spores and often harpoon cystidia).

Discussion

The presence of a partial veil in *Cystodermella* remains to be ascertained. In *C. adnatifolia*, in particular, a whorl of white hyphae remains at the 'ring zone' of the stipe. It is unclear whether this tissue represents a separate partial veil or is formed from the inner layer of the universal veil.

Besides *Cystoderma* s. str., also *Ripartitella* Singer is closely related to *Cystodermella*. *Ripartitella* differs from *Cystodermella*: (i) a perfect universal veil is lacking, (ii) the cortical layers of the pileus and stipe are composed of elongated cells instead of sphaerocysts, and (iii) the spores are verruculose (Singer 1986).

The placement of current *Cystoderma* within the Agaricales is somewhat problematic: it has been included in the families Agaricaceae, Lepiotaceae and Tricholomataceae (e.g., Heinemann & Thoen 1973, Kühner 1980, Singer 1986, Harmaja 1979a). Pegler & Young (1969, 1971) published two interesting observations: in *C. amianthinum* the structure of hilar appendix of the spore is of the nodulose type, and the spore wall appeared thin and got easily collapsed under vacuum when carbon replicas were produced. As they pointed out, both these characters of *C. amianthinum* show affinities to the fungi of Tricholomataceae with their hyaline thin-walled spores rather than to Agaricaceae/Lepiotaceae. Unfortunately they did not examine the spore ultrastructure of *C. granulosum* or any other species with inamyloid spores. In the phylogenetic study of Moncalvo & al. (2002) the proper placements of the type species of *Cystoderma* and *Cystodermella* among the euagarics remained unresolved.

For additional information of *Cystodermella*: see the descriptions of the section *Granulosa* in

Smith & Singer (1945), Heinemann & Thoen (1973; some species are treated in sect. *Cinnabarina* Heinem. & Thoen) and Singer (1986).

At least 12 species of *Cystodermella* are well defined, the area of the genus extending from the tropical to the arctic zone. *Cystoderma* s. str. comprises roughly 17 species at present; the distribution of the genus is subcosmopolitan and extends from the arctic through the tropics to subantarctic regions. In both genera, north temperate and boreal zones with a not too continental climate display the greatest diversity known at present; my observations suggest that several undescribed species exist. For treatments of world species, consult Smith & Singer (1945), Heinemann & Thoen (1973) and Singer (1986).

Those species are transferred to the genus *Cystodermella* which are familiar to me or which appear distinct enough and well described in the literature.

New combinations in *Cystodermella*

Cystodermella adnatifolia (Peck) Harmaja, n. comb.

Basionym: *Lepiota adnatifolia* Peck, Bull. New York State Mus. Nat. Hist. 54: 947. 1902. – *Armillaria adnatifolia* (Peck) Kauffman, Pap. Michigan Acad. Sci. 2: 60. 1923. – *Cystoderma granulosum* var. *adnatifolium* (Peck) A.H.Sm. & Singer, Pap. Michigan Acad. Sci. 30: 90. 1945. – *Cystoderma adnatifolium* (Peck) Harmaja, Karstenia 14: 122. 1974.

Cystodermella ambrosii (Bres.) Harmaja, n. comb.

Basionym: *Armillaria ambrosii* Bres., Fungi Tridentini 1: 27. 1881. – *Cystoderma ambrosii* (Bres.) Singer, Ann. Mycol. 41: 170. 1943.

Cystodermella cinnabarina (Alb. & Schwein. : Fr.) Harmaja, n. comb.

Basionym: *Agaricus* A. [unranked *Lepiotae*] *granulosus* var. *ee cinnabarinus* Alb. & Schwein., Consp. Fung. Lus.: 147. 1805. – *Agaricus cinnabarinus* (Alb. & Schwein. : Fr.) Fr., Syst. mycol. 3: Index: 12. 1832. – *Lepiota cinnabarina* (Alb. & Schwein. : Fr.) P.Karst., Bidrag Kännedom Finlands Natur Folk 32 (Ryssl. Hattsvamp. 1): 14. 1979. – *Armillaria cinnabarina* (Alb. & Schwein. : Fr.) Kauffman, Pap. Michigan Acad.

Sci. 2: 60. 1923. – *Cystoderma cinnabarinum* (Alb. & Schwein. : Fr.) Konrad & Maubl., Icon. sel. fungi. 3(3): pl. 238. 1927.

Agaricus terryi ('Terreii') Berk. & Broome, Ann. Mag. Nat. Hist. 4(6): 462. 1870. – *Cystoderma terryi* (Berk. & Broome) Harmaja, Karstenia 18: 30. 1978.

Bon (1999) correctly points out that, in the index of *Systema mycologicum*, published at the end of its third part, Fries used and even sanctioned the epithet *cinnabarinus* at the specific level, so that epithet shall be used for the present species rather than *terryi* as I earlier (Harmaja 1979a) suggested.

Cystodermella contusifolia (Pegler) Harmaja, n. comb.

Basionym: *Cystoderma contusifolium* Pegler, Kew Bull., Addit. Ser. 9: 410. 1983.

Cystodermella cristallifera (Thoen) Harmaja, n. comb.

Basionym: *Cystoderma cristalliferum* Thoen, Bull. Jard. Bot. Belg. 39: 185. 1969.

Cystodermella elegans (Beeli) Harmaja, n. comb.

Basionym: *Armillaria elegans* Beeli, Bull. Soc. Roy. Bot. Belgique 59: 111. 1927. – *Cystoderma elegans* (Beeli) Thoen, Bull. Jard. Bot. Belg. 39: 188. 1969.

Cystodermella granulosa (Batsch : Fr.) Harmaja, n. comb.

Basionym: *Agaricus granulatus* Batsch, Elench. fung. 1: 170. 1783: Fr., Syst. mycol. 1: 24. 1821. – *Lepiota granulosa* (Batsch : Fr.) Gray, Nat. ar. rang. Brit. pl. 1: 602. 1821. – *Mastocephalus granulatus* (Batsch : Fr.) Kuntze, Rev. gen. pl. 2: 860. 1891. – *Armillaria granulosa* (Batsch : Fr.) Kauffman, Pap. Michigan Acad. Sci. 2: 60. 1923. [non *Armillaria granulosa* Vel., Opera Bot. Čech.

4 [Nov. mycol. noviss.]: 57. 1947; = ?] – *Cystoderma granulatum* (Batsch : Fr.) Kühner, Botaniste 17: 125. 1926.

Cystodermella japonica (Thoen & Hongo) Harmaja, n. comb.

Basionym: *Cystoderma japonicum* Thoen & Hongo, Trans. Mycol. Soc. Japan 26: 23. 1985.

Cystodermella luteohemisphaerica (Dennis) Harmaja, n. comb.

Basionym: *Cystoderma luteohemisphaericum* Dennis, Kew Bull. 15: 109. 1961.

Cystodermella myriadocystis (Heinem. & Thoen.) Harmaja, n. comb.

Basionym: *Cystoderma myriadocystis* Heinem. & Thoen, Bull. Soc. Mycol. France 89: 14. 1973.

Cystodermella sipariana (Dennis) Harmaja, n. comb.

Basionym: *Lepiota sipariana* Dennis, Kew Bull. 7: 488. 1953. – *Cystoderma siparianum* (Dennis) Thoen, Bull. Jard. Bot. Belg. 39: 190. 1969. – *Ripartitella sipariana* (Dennis) Dennis, Kew Bull., Addit. Ser. 3: 58. 1970.

C. subpurpurea (A.H.Sm. & Singer) Harmaja, n. comb.

Basionym: *Cystoderma subpurpureum* A.H.Sm. & Singer, Mycologia 40: 457. 1948.

Acknowledgements: The Lammi Biological Station of the University of Helsinki has provided me excellent research facilities during many years. Thanks are due to the curators of those herbaria which have lent material for my studies during years. Professor Teuvo Ahti made useful improvements to the manuscript. Mr. Heino Vänskä, Lic. Phil., kindly checked the Latin of the generic descriptions.

References

- Astapenko, V.V. & Kutafyeva, N.P. 1990: Dopolnenie k flore makromitsetov srednego Priangar'a. – *Novosti Sist. Nizsh. Rast.* 27: 48–52.
- Bigelow, H.E. 1981: Spore ornamentation in the Tricholomataceae 1. – *Mycologia* 73: 128–140.
- Bigelow, H.E. 1982: North American species of Clitocybe. Part 1. – *Beih. Nova Hedwigia* 72: 1–280.
- Bon, M. 1999: Novitates: Tricholomatales (Marasmiaceae, Lyophyllaceae et Dermolomataceae). – *Doc. Mycol.* 29(115): 33–34.
- Bresadola, J. 1927: *Iconographia mycologica*. Vol. 1. – Pls. 1–50. Mediolani.
- Bresinsky, A. & Besl, H. 1985: *Giftpilze*. – 295 pp. Wissenschaftliche Verlagsgesellschaft mbH, Stuttgart.
- Cifuentes, J., Pérez-Ramírez, L. & Villegas, M. 1989: Descripción de macromicetos poco estudiados en México III. – *Rev. Mexic. Micol.* 5: 101–115.
- Cochran, K.W. & Cochran, M.W. 1978: Clitocybe clavipes: Antibuse-like reaction to alcohol. – *Mycologia* 70: 1124–1126.
- Eriksen, A. 1997: Andet danske fund av gulstokket knolfod (*Squamanita paradoxa*). – *Svampe* 35: 55.
- Fayod, F. 1889: *Prodrome d'une histoire naturelle des Agaricinées*. – *Ann. Sci. Nat., Bot.*, sér. 7, 9: 181–411.
- Gorbunova, A.I. 2001: *Novye svedeniya o mikrobiote Respubliki Altay*. – *Novosti Sist. Nizsh. Rast.* 35: 57–70.
- Harmaja, H. 1969: The genus *Clitocybe* (Agaricales) in Fennoscandia. – *Karstenia* 10: 5–168.
- Harmaja, H. 1970: Type studies on Agaricales described as *Clitocybe* and *Omphalina*. – *Karstenia* 11: 35–40.
- Harmaja, H. 1974a: A revision of the generic limit between *Clitocybe* and *Lepista*. – *Karstenia* 14: 82–92.
- Harmaja, H. 1974b: *Singerella* n. gen., a separate genus for *Clitocybe hydrogramma*. – *Karstenia* 14: 113–115.
- Harmaja, H. 1976: A further revision of the generic limit between *Lepista* and *Clitocybe*. – *Karstenia* 15: 13–15.
- Harmaja, H. 1979a: Studies in the genus *Cystoderma*. – *Karstenia* 19: 25–29.
- Harmaja, H. 1979b: Type studies in *Clitocybe* 4. – *Karstenia* 19: 50–51.
- Harmaja, H. 1985: Studies on white-spored agarics. – *Karstenia* 25: 41–46.
- Harmaja, H. 1988: Studies on the agaric genera *Singerocybe* n. gen. and *Squamanita*. – *Karstenia* 27: 71–75.
- Heinemann, P. & Thoen, D. 1973: Observations sur le genre *Cystoderma*. – *Bull. Soc. Mycol. France* 89: 5–34.
- Karsten, P.A. 1883: *Icones selectae Hymenomycetum Fenniae nondum delineatorum*. 1. – 15 pp. + Pls. 1–10. Helsingforsiae.
- Knudsen, H. 1980: A revision of *Lepiota* sect. *Echinatae* and *Amyloideae* (Agaricaceae) in Europe. – *Bot. Tidsskr.* 75: 121–155.
- Kotiranta, H., Uotila, P., Sulkava, S. & Peltonen, S.-L. (eds.) 1998: *Red Data Book of East Fennoscandia*. – 351 pp. Ministry of the Environment, Finnish Environment Institute & Botanical Museum, Finnish Museum of Natural History, Helsinki.
- Kühner, R. 1945: Le problème de la filiation des Agaricales à la lumière de nouvelles observations d'ordre cytologique sur les Agaricales leucosporées. – *Bull. Soc. Mycol. Linn. Lyon* 14: 160–169.
- Kühner, R. 1969: *Cystoderma amianthinum* (Scop. ex Fr.) Fayod, var. *longisporum* (Kühner) Smith et Singer et var. *sublongisporum* Singer. – *Bull. Soc. Linn. Lyon* 38: 178–188.
- Kühner, R. 1980: Les grandes lignes de la classification des Agaricales, Pluteales, Tricholomatales (suite). – *Bull. Soc. Linn. Lyon* 49: 297–344.
- Kutafyeva, N.P. 1989: K flore gribov-makromitsetov Srednego Priangar'a 4. – *Novosti Sist. Nizsh. Rast.* 26: 65–67.
- Lange, C. & Læssøe, T. 1989: *Gulstokket Knoldfod* (*Squamanita paradoxa*) – et sjældent og mærkeligt fund. – *Svampe* 19: 35–36.
- Lapitskaya, L.S. 1993: K flore gribov-makromitsetov srednego Yeniseya. 2. – *Novosti Sist. Nizsh. Rast.* 29: 45–48.
- Miller, O.K. Jr., Volk, T.J. & Bessette, A.E. 1996: A new genus, *Leucopholiota*, in the Tricholomataceae (Agaricales) to accommodate an unusual taxon. – *Mycologia* 88: 137–139.
- Moncalvo, J.-M., Vilgalys, R., Redhead, S.A., Johnson, J.E., James, T.Y., Aime, M.C., Hofstetter, V., Verduin, S.J.W., Larsson, E., Baroni, T.J., Thorn, R.G., Jacobsson, S., Cléménçon, H. & Miller, O.K. Jr. 2002: One hundred and seventeen clades of euagarics. – *Mol. Phyl. Evol.* 23: 357–400.
- Moser, M. 1979: Über einige neue or seltene Agaricales-Arten aus dem Pieniny und aus Bieszczade, Polen. – *Beih. Sydowia* 8: 268–275.
- Nezdojminogo, E.L. 1982: K flore agarikovykh gribov severnoy chasti Krasnoyarskogo kraya. 2. – *Novosti Sist. Nizsh. Rast.* 19: 73–77.
- Peck, C.H. 1873: Report of the Botanist. – *Rep. State Bot. New York State Mus.* 25: 57–123 + Pls. 1–2.
- Pegler, D.N. & Young, T.W.K. 1969: Ultrastructure of basidiospores in Agaricales in relation to taxonomy and spore discharge. – *Trans. Brit. Mycol. Soc.* 52: 491–496 + Pls. 36–37.
- Pegler, D.N. & Young, T.W.K. 1971: Basidiospore morphology in the Agaricales. – *Beih. Nova Hedwigia* 35: 1–210 + Pls. 1–53.
- Petrov, A.N. 1986: K flore agarikovykh gribov yugozapadnogo poberezh'a ozera Baykal. 2. – *Novosti Sist. Nizsh. Rast.* 23: 152–158.
- Phillips, R. 1981: *Mushrooms and other fungi of Great Britain and Europe*. – 288 pp. Pan Books Ltd, London.
- Rassi, P., Alanen, A., Kanerva, T. & Mannerkoski, I. (toim.) 2001: *Suomen lajien uhanalaisuus 2000* (English summary: The 2000 Red List of Finnish species). – 432 pp. Ympäristöministeriö & Suomen ympäristökeskus, Helsinki.
- Redhead, S.A., Ammirati, J.F., Walker, G.R., Norvell, L.L. & Puccio, M.B. 1995: *Squamanita contortipes*, the Rosetta Stone of a mycoparasitic agaric genus. – *Canad. J. Bot.* 72: 1812–1824.

- Reid, D.A. 1983: A second British collection of *Squamanita paradoxa*. – Bull. Brit. Mycol. Soc. 17: 111–113.
- Romagnesi, H. 1989: Quelques synonymies méconnues. – Bull. Soc. Mycol. France: 105: 253–257.
- Saar, I. & Kullman, B. 2000: Nuclear DNA content and spore dimension in some species of the genus *Cystoderma*. – Folia Cryptog. Estonica 36: 87–94.
- Singer, R. 1943: Das System der Agaricales. 3. – Ann. Mycol. 41: 1–189.
- Singer, R. 1972: Cyanophilous spore walls in the Agaricales and agaricoid Basidiomycetes. – Mycologia 64: 822–829.
- Singer, R. 1986: The Agaricales in modern taxonomy. Ed. 4. – 981 pp. + Pls. 1–88. Koeltz Scientific Books, Königstein.
- Smith, A.H. 1949: Mushrooms in their natural habitats. 1. Text. – 626 pp. Sawyer's Inc., Portland.
- Smith, A.H. & Singer, R. 1945: A monograph on the genus *Cystoderma*. – Pap. Michigan Acad. Sci. 30: 71–124 + Pls. I–V.
- Smith, A.H. & Singer, R. 1948: Notes on the genus *Cystoderma*. – Mycologia 40: 454–460.
- Stridvall, L. & Stridvall, A. 1994: Släktet *Squamanita* Imbach i Sverige. – Jordstjärnan 15: 24–37.
- Vasil'eva, L.N. 1973: Agarikovye shlyapochnye griby (por. Agaricales) Primorskogo kraja. – 331 pp. + pls. I–II. Nauka, Leningrad.
- Watling, R. 1974: Notes on some British agarics: 4. – Notes Roy. Bot. Gard. Edinburgh 33: 325–331.