Amylolepiota, Clavicybe and Cystodermella, new genera of the Agaricales

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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. adnatiolofila (Peck) Harmaja, C. ambrosii (Bres.) Harmaja, C. cinnabarina (Alb. & Schwein.: Fr) Harmaja, C. contasapilofila (Pegler) Harmaja, C. cristiullifera (Thoen) Harmaja, C. elegans (Beeli) Harmaja, C. granulosa (Batsch: Fr) Harmaja (type species of Cystodermella), C. japonica (Thoen & Hongo) Harmaja, C. lateohemisphaerica (Dennis) Harmaja, C. myriacystis (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

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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.


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 to squarrose brown scales. Stipe without ring; habitat.

While possessing uninucleate inamyloid spores, a passive differences are the amyloid spore wall and pigmenmantly membranal. 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 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 sphaerocyts, and non-woody habitat. Leucopholiota (Romagn.) O.K. Mill., T.J. Volk & Bessette (Miller et 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 sphaerocyts 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: Sieneilehti 43(1), back cover


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 et 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. ligationum 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 Müll. & 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.) Stauda 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 Clitocybe: Clitocybe avellaneialba Murrill and Clitocybe squamuloides P.D. Orton. The affinity of the former species to Clitocybe clavipes was earlier noted by me (Harmaja 1969); the latter was previously thought by me to represent a form of C. clavipes (Harmaja 1970).

**Clitocybe** Harmaja, n. gen.


_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 stickling 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. 0.9–1.1 × 0.7–0.9 μm. 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.


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


Discussion

Macroscopically, the species of this new genus are very similar to the larger non-hygrophanous 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 hygrophanity of the fruit body as described in the introductory section above. These unusual properties of hygrophanity 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. squamosoides 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. squamosoides. 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 × 3.5–5.3 μm, variable in shape; on litter of needles or leaves .............................. 2

1'. Spores ca. 8–10 × 4.0–5.5 μm, broadly fusiform; mostly on much decayed woody substrates (western North America) .................................................. *C. avellaneialba*

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*

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**CYSTODERMELLA**

Fayod (1889) included partly unrelated species in his new genus *Cystoderma* Fayod (see Smith & Singer 1945). Heinemann & Thoen (1973) delimit 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. granulosum* (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. *Cystodermella* Harmaja (type *C. granulosum*) is described below for the latter species group.

*Cystodermella* Harmaja, n. gen.


*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. Hy- menophoral trama of more or less parallel hy- phae. 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 respons­ es of Cystoderma s. lato fruitbodies to ultraviolet light). Saprophytes of non-ligneous, rarely ligne­ nous, 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 Fay od and Cystodermella Harmaja. The exact differences are given in bold. See the text immediately below for details and references.

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

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 corrodes (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 & Masseve) 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-
even suggests that two species, at least \( C. \) \textit{illicipes} Harmaja and \( C. \) \textit{saarenoksa}e Harmaja) are obligately associated with species of \textit{Polytrichum} s. tr. (Harmaja 1979a, 1985).

In the comprehensive phylogenetic work of Moncalvo \\& al. (2002) \textit{Cystoderma amianthi}num and \( C. \) \textit{chocoanum} Franco-Molano (likewise with amyloid spores) clustered with \textit{Floccularia} \textit{albotanaripes} (G.F.Atk.) Redhead (with amyloid spores) while \( C. \) \textit{granulosum} clustered in another clade with \textit{Ripartitella brasiliensis} (Speg.) Singer (with inamyloid spores and often harpoon cystidia).

**Discussion**

The presence of a partial veil in \textit{Cystoderma} remains to be ascertained. In \( C. \) \textit{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 \textit{Cystoderma} s. str., also \textit{Ripartitella} Singer is closely related to \textit{Cystoderma}. \textit{Ripartitella} differs from \textit{Cystoderma}: (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 \textit{Cystoderma} within the Agaricales is somewhat problematic: it has been included in the families \textit{Agaricaceae}, \textit{Lepiotaceae} and \textit{Tricholomataceae} (e.g., Heinemann \\& Thoen 1973, Kühner 1980, Singer 1986, Harmaja 1979a). Pegler \\& Young (1969, 1971) published two interesting observations: in \( C. \) \textit{amianthi}num 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 \( C. \) \textit{amianthi}num show affinities to the fungi of \textit{Tricholomataceae} with their hyaline thin-walled spores rather than to \textit{Agaricaceae}/\textit{Lepiotaceae}. Unfortunately they did not examine the spore ultrastructure of \( C. \) \textit{granulosis} or any other species with inamyloid spores.

In the phylogenetic study of Moncalvo \\& al. (2002) the proper placements of the type species of \textit{Cystoderma} and \textit{Cystoderma} among the euagarics remained unresolved.

For additional information of \textit{Cystoderma} see the descriptions of the section \textit{Granulosa} in

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

At least 12 species of \textit{Cystoderma} are well defined, the area of the genus extending from the tropical to the arctic zone. \textit{Cystoderma} s. tr. 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 \textit{Cystoderma} which are familiar to me or which appear distinct enough and well described in the literature.

**New combinations in Cystoderma**

\textit{Cystoderma adnatifolia} (Peck) Harmaja, n. comb.


\textit{Cystoderma ambrosii} (Bres.) Harmaja, n. comb.


\textit{Cystoderma cinnabarina} (Alb. \\& Schwein. : Fr.) Harmaja, n. comb.

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


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.

Cystodermella cristallifera (Thoen) Harmaja, n. comb.

Cystodermella elegans (Beeli) Harmaja, n. comb.

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

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

Cystodermella luteohemisphaerica (Dennis) Harmaja, n. comb.

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

Cystodermella sipariana (Dennis) Harmaja, n. comb.

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

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References


