

Notes on *Clitocybe s. lato* (Agaricales)

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Agaricus nebularis Batsch : Fr. is approved as the lectotype of the genus *Clitocybe* (Fr.) Staude (Agaricales: Tricholomataceae). *Lepista* (Fr.) W.G. Smith is a younger taxonomic synonym. Diagnostic characters of *Clitocybe* are discussed; among the less known ones are: (i) a proportion of the detached spores adhere in tetrads in microscopic mounts, (ii) the spore wall is cyanophilic, and (iii) the mycelium is capable of reducing nitrate. Three new nomenclatural combinations in *Clitocybe* are made. The new genus *Infundibulicybe* Harmaja, with *Agaricus gibbus* Pers. : Fr. as the type, is segregated for the core group of those species of *Clitocybe s. lato* that do not fit to the genus as defined here. *Infundibulicybe* mainly differs from *Clitocybe* in that: (i) the spores do not adhere in tetrads, (ii) all or a proportion of the spores have confluent bases, (iii) all or most of the spores are lacrymoid in shape, (iv) the spore wall is cyanophobic, and (v) the mycelium is incapable of reducing nitrate. Thirteen new nomenclatural combinations in *Infundibulicybe* are made. Two new nomenclatural combinations are made in *Ampulloclitocybe* Redhead, Lutzoni, Moncalvo & Vilgalys (syn. *Clavicybe* Harmaja), a recent segregate of *Clitocybe*.

Key words: carminophily, *Clitocybe*, cyanophily, *Lepista*, myxosporium, nitrate reduction, nomenclature, taxonomy, typification

Introduction

A monograph on the genus *Clitocybe* (Fr.) Staude in Fennoscandia (NW Europe) constituted my Ph.D. thesis (Harmaja 1969b). *Agaricus nebularis* Batsch : Fr. = *Clitocybe nebularis* (Batsch : Fr.) P. Kumm. was accepted as the lectotype of the genus. The circumscription of the genus adopted by me appeared more natural than those of other students of *Clitocybe*; for instance, I had excluded lignicolous species as well as those associated with mosses or algae. H. E. Bigelow, working in North America, in par-

ticular, had assumed an exceptionally wide and unnatural concept of the genus. In my contribution (Harmaja 1969b), I reported 43 species from the study area; I considered the genus anyway rather clearly heterogeneous as they were sorted in three subgenera and 16 sections, e.g., *C. clavipes* (Pers. : Fr.) P. Kumm. was assigned to a section of its own. In fact, two deviating species should have been excluded from my treatment: *C. harperi* Murrill (= *Rhodocybe harperi* (Murrill) Harmaja: Harmaja 1978a) and *C. schulmannii* Harmaja (= *Lyophyllum schulmannii* (Harmaja) Harmaja: Harmaja 1979b).

Later I accepted *Agaricus gibbus* Pers. : Fr. = *Clitocybe gibba* (Pers. : Fr.) P. Kumm. (with cyanophobic spore wall) as the lectotype of *Clitocybe* and consequently had to transfer the remaining species that possessed cyanophilic spore walls to *Lepista* (Fr.) W.G. Smith which I considered a valid, related genus (Harmaja 1974a, 1976a). The species that were left under *Clitocybe* had cyanophobic spore walls; of them, the *C. hydrogramma* (Bull. : Fr.) P. Kumm. species group was assigned to a genus of its own, *Singerocybe* Harmaja (*Singerella* Harmaja, *nom. illeg.*; Harmaja 1974b, 1988) while *Ampulloclitocybe* Redhead, Lutzoni, Moncalvo & Vilgalys (syn. *Clavicybe* Harmaja) was created for the *C. clavipes* group (Redhead *et al.* 2002, Harmaja 2002). Even after all these procedures, the remaining assemblage of species having cyanophobic spore walls and considered belonging to *Clitocybe*, still appeared heterogeneous.

After a long time of weighing and evaluating the different alternatives, the choice of *Agaricus nebularis* now seems to me unavoidable (*see* next chapter). This species is characterized by two features which are clearly diagnostic at the generic level: the spore wall is cyanophilic due to the presence of a myxosporium layer (Singer 1972, Harmaja 1974a) and the mycelium is able to reduce nitrate (Bresinsky & Schneider 1975). Consequently, species that are congeneric with *Clitocybe nebularis* continue being as members of *Clitocybe* but for the remaining species, i.e. the non-reducers with cyanophobic spore walls, at least one genus of their own needs to be assigned. A well-defined natural entity that consists of *C. gibba* and related species can be considered as the core group of this remainder. As there is no generic name available for this species aggregate, the new genus *Infundibulicybe* is described for it below in this paper.

***Clitocybe* (Fr.) Staude**

A holotype of this taxon was not designed. Over the years, no less than four species have been proposed for the lectotype of *Clitocybe* (of them, *Agaricus gibbus* for a conserved one), but as a consensus has not been achieved the question still remains open (Redhead *et al.* 2002 sum-

marize the lively discussion on this item and give literature references). At the beginning of my work on *Clitocybe* (Harmaja 1969b) I accepted *A. nebularis*, proposed by Earle (1909) for the first time, and supported e.g. by Donk (1949). Later on, I rejected *A. nebularis* as the lectotype and concurred with those who preferred *A. gibbus*. However, actually there is no reason to reject Earle's (1909) proposal (*A. nebularis*); this choice seems to have gained more support in recent time (by e.g., Redhead *et al.* 2002).

Molecular studies performed so far (Moncalvo *et al.* 2002) would appear to confirm that *Clitocybe nebularis* is closely related to or even congeneric with a great number of clitocyboid and a few tricholomoid species, having smooth or warted cyanophilic spores; an idea presented by me already in the 1970s. Almost all of the epithets of these species have already been combined under the generic name *Clitocybe*.

Besides many well-known characters, the important diagnostic features of *Clitocybe* also include (cf. Harmaja 1976a, 1978b): (i) the fresh spore deposit is commonly (mostly?) not pure white but somewhat coloured, (ii) a variable amount (almost all to a small minority) of the detached spores stick together to form tetrads (and dyads) in microscopic mounts (in different mountants) made of dried lamellae (Harmaja 1974a: fig. 1b), (iii) the spore wall is often collapsed or wrinkled in spores in mounts made of dried lamellae (Harmaja 1974a: fig. 1b), (iv) the spore shape varies but little: the spores can be considered to represent different degrees of the ellipsoid basic pattern, (v) the outermost layer of the spore wall is a thin cyanophilic myxosporium (the French such as Lamoure and Fichet 1962 and those cited by Kühner 1973 were the first to detect this; Singer 1972, Harmaja 1974a: fig. 1b, Cléménçon in Singer 1975, Harmaja 1976a), (vi) the organism (mycelium) does not seem have obligate association with photosynthetic green plants (algae, mosses or mycorrhiza-forming vascular plants), and (vii) the organism (mycelium) is capable of reducing nitrate (the type and several additional species examined: Bresinsky and Schneider 1975).

The spores of *Clitocybe cerussata* (Fr.) P. Kumm., *C. inversa* (Scop.) Quél. and *C. nebularis* are uninucleate (Kühner 1945), as are those

of *C. phyllophila* (Pers. : Fr.) P. Kumm. (Harmaja 1969b) and *C. diatreta* (Fr.) P. Kumm. (Harmaja 1979a: p. 22). I also wish to remind here of the responses of three microscopic structures to acetocarmine observed by me (Harmaja 1978b: p. 50, 1979a: p. 22) in dried fruit bodies of some species of *Clitocybe* in the present sense as they may have diagnostic taxonomic and phylogenetic value: (i) the spore walls are carminophobic, (ii) the basidial walls are carminophobic, and (iii) the basidia of *C. polygonarum* Laursen, O.K. Miller & Bigelow and five other described species as well as a few undescribed ones contain small and weakly staining carminophilic/siderophilic granules (it should be cleared up whether these organelles are lysosomes and whether this character is diagnostic to *Clitocybe*). Moreover, in all those species that were studied by me (Harmaja 1978b: p. 50) the basidial walls were very weakly (but undoubtedly) cyanophilic.

The revised concept of *Clitocybe* adopted by me here is thus identical with *Lepista sensu* Harmaja (1976a). *Lepista* is a younger taxonomic synonym of *Clitocybe*; the automatic type species of the former is *Agaricus lepista* Fr. : Fr. (= either *L. densifolia* (J. Favre) Singer & Clémentçon or *L. subconnexa* (Murrill) Harmaja).

The following three new nomenclatural combinations in *Clitocybe* are necessary:

***Clitocybe ovispora* (J.E. Lange) Harmaja, comb. nova**

BASIONYM: *Clitocybe aggregata* (Schaeff.) Gillet var. *ovispora* J.E. Lange, Dansk Bot. Ark. 6: 58. 1930. — *Lyophyllum aggregatum* (Schaeff.) Kühner var. *ovisporum* (J.E. Lange) Kühner & Romagn., Fl. Anal.: 164. 1953 (*nom. illeg.*: not validly published as reference to basionym defective). — *Lyophyllum ovisporum* (J.E. Lange) D.A. Reid, Nova Hedwigia 15, Suppl.: 13. 1968. — *Lepista ovispora* (J.E. Lange) Gulden, Sydowia 36: 67. 1983.

? *Lepista fasciculata* Harmaja, Karstenia 14: 129. 1974. The synonymy is uncertain as (i) a difficult species group is concerned and (ii) no type material of J. E. Lange's variety is in existence.

***Clitocybe rickenii* (Singer) Harmaja, comb. nova**

BASIONYM: *Lepista rickenii* ('*Rickenii*') Singer, Sydowia 2: 26. 1948.

? *Lepista polycephala* Harmaja, Karstenia 15: 14. 1976. The synonymy is provisional as an intricate species aggregate, also including *C. ovispora*, is concerned.

***Clitocybe singeri* (Harmaja) Harmaja, comb. nova**

BASIONYM: *Lepista singeri* Harmaja, Karstenia 14: 130. 1974.

***Infundibulicybe* Harmaja, gen. nov.**

Clitocybe subg. *Hygroclitocybe* Bon sect. *Geotropae* Bon, Doc. Mycol. 13(51): 9.1983. — Type: *Agaricus geotropus* Bull.

Agaricalium genus. Genus *Clitocybem* (typus *C. nebularis*) in mentem revocat. Ab ea inter alia differt: sporae (saltem pars earum) lacrymoideae cum basi confluenta non nec tunica sporarum haud cyanophiloidea. — Typus: *Infundibulicybe gibba* (Pers. : Fr.) Harmaja (*Agaricus gibbus* Pers. : Fr.).

Agaricales; habitus of basidiocarp as in *Clitocybe*. Veil completely absent; development of the fruit body apparently gymnocarpic. Pileus mostly not hygrophanous, white or some shade of brown, slightly depressed to deeply infundibuliform when adult; margin inrolled at first; surface dry, smooth or somewhat scaly or slightly areolate. Stipe concolorous with pileus or paler to white, mostly equal; surface dry, smooth. Lamellae decurrent, whitish, yellowish or brownish. Flesh mostly not hygrophanous. Odour when fresh indistinct, or faintly camphor-like or somewhat like that of oil of bitter almonds (benzaldehyde; this odour may result from the production of cyanic acid, HCN). Taste mild. Basidia without carminophilic/siderophilic granules (Harmaja 1976b: one species studied; reported here: type species studied); wall cyanophobic (Harmaja 1976b: one species studied; reported here: type species studied) and carminophobic (Harmaja 1976b: one species studied; reported here: type species studied). Spores very pale yellow (pure white in some species?) in fresh deposit; detached ones, in microscopic mounts made of dry gills, neither sticking together to form tetrads nor with conspicuously collapsed walls; all or

a proportion of the spores with confluent bases (Harmaja 1969b: fig. 2c, 1974a: fig. 1a); all or most of the spores lacrymoid in shape being broadest above their middle (Harmaja 1969b: fig. 2b and c); uninucleate (Harmaja 1976b: one species studied; reported here: type species studied). Spore wall perfectly smooth (also under the electron microscope, type species studied: Pegler & Young 1971), without germ-pore, hyaline, inamyloid, cyanophobic (Singer 1972: two species, Harmaja 1974a: p. 84: type and 6 other species, and Harmaja 1976b: one species studied), and carminophobic (Harmaja 1976b: one species studied; reported here: type species studied); hilar appendix/apicular region large, ca. 0.7–1.3 μm in diameter, with a nodulose hilum (type species studied: Pegler & Young 1971). Spore contents cyanophilic, homogeneous or with small, mostly indistinct oil drops. Cystidia of any kind absent. Pileus cortex weakly differentiated, being a cutis of narrow, parallel to interwoven hyphae; pigmentation inconspicuous, pigment mostly intracellular. Hymenophoral trama regular or subregular, i.e., composed of parallel to somewhat interwoven hyphae. Clamp connections abundant everywhere in the basidiocarp. Dried pileus, stipe, lamellae, basal mycelium, flesh, and spore deposit of the type species (from a herbarium specimen dried several years ago) do not display fluorescence but retain their colours under ultraviolet light (with wave lengths 254 nm and 366 nm) (reported here; see also Harmaja 1969b). Saprobies, occurring mainly in litter of leaves and needles, sometimes in remnants of herbaceous plants or on seemingly bare mineral soil. Association of the mycelium with photosynthetic green plants (algae, mosses or mycorrhiza-forming vascular plants) seemingly lacking. The organism (mycelium) is incapable of reducing nitrate (the type and another species examined: Bresinsky & Schneider 1975).

Infundibulicybe altaica (Singer) Harmaja, *comb. nova*

BASIONYM: *Clitocybe altaica* Singer, Ann. Mycol. 41: 37. 1943.

Infundibulicybe bresadolana (Singer) Harmaja, *comb. nova*

BASIONYM: *Clitocybe bresadolana* ('*bresadoliana*') Singer, Rev. Mycol., N.S., 2: 228. 1937.

Infundibulicybe catinus (Fr.) Harmaja, *comb. nova*

BASIONYM: *Agaricus catinus* Fr., Epicr. syst. mycol.: 72. 1838. — *Clitocybe catinus* (Fr.) Quél., Champ. Jura Vosges: 235. 1872. — *Omphalia catinus* (Fr.) Quél., Enchir. fung.: 24. 1886.

Infundibulicybe costata (Kühner & Romagn.) Harmaja, *comb. nova*

BASIONYM: *Clitocybe costata* Kühner & Romagn., Bull. Soc. Nat. Oyonnax 8: 73. 1954.

Infundibulicybe dryadum (Bon) Harmaja, *comb. nova*

BASIONYM: *Clitocybe bresadolana* Singer var. *dryadum* Bon, Bull. Féd. Mycol. Dauphiné-Savoie 25(97): 29. 1985.

This taxon appears to deserve the specific rank. It differs from *Infundibulicybe bresadolana* especially: the fruit bodies are smaller, the pileus apparently becomes hygrophanous in age, the centre of the pileus is areolate, and the occurrence above the forest limit associated with *Dryas octopetala*. Four specimens that were included in *Clitocybe bresadolana* by Harmaja (1969b) originated from the oroarctic (alpine) zone of Finland, Sweden and Norway. They represent *I. dryadum*.

Infundibulicybe geotropica (Bull.) Harmaja, *comb. nova*

BASIONYM: *Agaricus geotropus* Bull., Herb. France 12: 573. 1792. — *Clitocybe geotropica* (Bull.) Quél., Champ. Jura Vosges: 89. 1872. — *Omphalia geotropica* (Bull.) Quél., Enchir. fung.: 22. 1886.

***Infundibulicybe gibba* (Pers. : Fr.)**Harmaja, *comb. nova*

BASIONYM: *Agaricus gibbus* Pers., Syn. meth. fung.: 449. 1801: Fr., Syst. mycol. 1: 81. 1821. — *Clitocybe gibba* (Pers. : Fr.) P. Kumm., Führ. Pilzk.: 123. 1871.

Infundibulicybe gigas* (Harmaja) Harmaja, *comb. nova

BASIONYM: *Clitocybe gigas* Harmaja, Karstenia 18: 29. 1978.

Infundibulicybe glareosa* (Röllin & Monthoux) Harmaja, *comb. nova

BASIONYM: *Clitocybe glareosa* Röllin & Monthoux, Mycol. Helv. 1: 237. 1984.

Infundibulicybe lapponica* (Harmaja) Harmaja, *comb. nova

BASIONYM: *Clitocybe lapponica* Harmaja, Karstenia 10: 68. 1969.

Infundibulicybe montana* (Harmaja) Harmaja, *comb. nova

BASIONYM: *Clitocybe montana* Harmaja, Karstenia 15: 19. 1976.

Infundibulicybe sinopicoides* (Peck) Harmaja, *comb. nova

BASIONYM: *Clitocybe sinopicoides* Peck, Bull. New York State Mus. Nat. Hist. 157: 80. 1912.

Infundibulicybe squamulosa* (Pers. : Fr.) Harmaja, *comb. nova

BASIONYM: *Agaricus squamulosus* Pers., Syn. meth. fung. 449. 1801: Fr., Syst. mycol. 1: 82. 1821. — *Clitocybe squamulosa* (Pers. : Fr.) P. Kumm., Führ. Pilzk.: 123. 1871. — *Omphalia infundibuliformis* (Schaeff. : Fr.) Quél. var. *squamulosa* (Pers. : Fr.) Quél., Enchir. fung.: 23. 1886.

Infundibulicybe corresponds exactly to *Clitocybe* sect. *Infundibuliformes* (Fr.) in the restricted delimitation used by me (Harmaja 1969b). The above thirteen species that are transferred to it are either (the majority) known to me personally or have been described adequately in the literature as to appear acceptable.

Infundibulicybe differs from *Clitocybe* (type *C. nebularis*; *Lepista sensu* Harmaja 1976a) especially: (i) the detached spores do not adhere in tetrads but are single in microscopic mounts made of dry lamellae, (ii) all or a proportion of the spores have confluent bases, (iii) all or most of the spores are lacrymoid in shape, being broadest above the middle, (iv) the spore wall is cyanophobic, and (v) the mycelium is incapable of reducing nitrate. It is not yet known which is the phylogenetic relation of *Infundibulicybe* to *Clitocybe*; GenBank does not contain sequences from species of the first-named genus.

The new genus at least hitherto comprises a rather small number of species that are distributed mainly in the temperate, boreal and alpine (oroarctic) zones of the northern hemisphere.

Ampulloclitocybe* Redhead *et al.

The publishing process of my paper on new genera of the Agaricales (Harmaja 2002) was delayed in an unfortunate way. In 2002, a new genus with the well-known *Clitocybe clavipes* (Pers. : Fr.) P. Kumm. as the type was described twice: by me (Harmaja 2002: *Clavicybe* Harmaja) and independently by Redhead *et al.* (2002: *Ampulloclitocybe* Redhead, Lutzoni, Moncalvo & Vilgalys). The publishing date of Harmaja (2002) is 31 December while Redhead *et al.* (2002) was published on the 5th of November. Consequently, the generic name *Ampulloclitocybe* has the priority, and the name *Clavicybe* is illegitimate as a younger homotypic synonym. Unfortunately, *Ampulloclitocybe* was only beset with a short and defective description; it is to be regretted that Redhead *et al.* (2002) did not comment on the deviating pattern of hygrophanity of *C. clavipes* that appears sig-

nificant at the generic level (already published in Harmaja 1969a and 1969b, and emphasized by Harmaja 2002). *Ampulloclitocybe* was considered monotypic (Redhead *et al.* 2002) but three species were included in *Clavicybe* (Harmaja 2002). The two combinations made by me in *Clavicybe* are illegitimate as this genus to which they were assigned is illegitimate. Accordingly, the following two new nomenclatural combinations are needed.

***Ampulloclitocybe avellaneialba* (Murrill)**

Harmaja, *comb. nova*

BASIONYM: *Clitocybe avellaneialba* Murrill, *Mycologia* 5: 207. 1913. — *Clavicybe avellaneialba* (Murrill) Harmaja, *Karstenia* 42: 42. 2002 (*nom. illeg.*).

***Ampulloclitocybe squamulosoides* (P.D.**

Orton) Harmaja, *comb. nova*

BASIONYM: *Clitocybe squamulosoides* P.D. Orton, *Trans. Brit. Mycol. Soc.* 43: 187. 1960. — *Clavicybe squamulosoides* (P.D. Orton) Harmaja, *Karstenia* 42: 42. 2002 (*nom. illeg.*).

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