

A revision of the generic limit between *Clitocybe* and *Lepista*

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HARMAJA, H. 1974: A revision of the generic limit between *Clitocybe* and *Lepista*. — *Karstenia* 14: 82—92. — On the basis of various spore characters, some already noted but partly neglected (e.g. cyanophilic spore wall) and some »new», it is concluded that *Lepista* (Fr.) W. G. Smith (*Agaricales*) is a valid genus, and independent of *Clitocybe* (Fr.) Staude. The current concept of *Lepista* is, however, somewhat altered, since the genus is considered to include species with smooth (under the light microscope) and deep yellow spores. The inclusion of the *Clitocybe gilva* group in *Lepista* is also considered justified. The essential characters of the amended genus *Lepista* are given, of which the strongly cyanophilic spore wall and the presence of a remarkable proportion of collapsed spores are emphasized. It seems that the type of *Lepista*, viz. *Agaricus lepista* Fr., can probably be appropriately typified, so that for the fungi concerned the generic name *Lepista* is thus indeed correct and available. Some other nomenclatural remarks are also made. Two new combinations are made in *Lepista*, the species in question having previously been referred to *Clitocybe* (the first of these even being one of the most famous species of that genus): *Lepista nebularis* (Fr.) Harmaja and *Lepista subalpina* (Big. & Smith) Harmaja.

1. Introduction

Recently BIGELOW and A. H. SMITH (1969) amalgamated the agaric genus *Lepista* (Fr.) W. G. Smith 1870 (= *Rhodopaxillus* Maire 1913) with *Clitocybe* (Fr.) Staude 1857 as a new section, *Clitocybe* sect. *Verruculosae* Big. & Smith. They unfortunately fail to give the author citation of *Clitocybe*, but this treatment must indicate that they, too, approve STAUDE instead of KUMMER as the author who elevated the Friesian tribe to the generic status, since if KUMMER with his 1871 paper were preferred, the generic name *Lepista* would have priority of one year over *Clitocybe* sensu BIGELOW & SMITH. Anyway, the name of their new section is illegitimate, being superfluous, as they include in it *Lepista nuda*, which is the type of *Rhodopaxillus* sect. *Genuinae* Konr. & Maubl. 1924—

1937, if, in agreement with SINGER (1962), that sectional name is considered to have been validly published. The classical differences, much emphasized by SINGER (e.g. 1962), between *Clitocybe* and *Lepista* lie in the spores. In the former genus they are said to be white, yellow or pale pinkish in mass, and normally smooth; if they are not smooth, then they are supposed to be always white in print. In *Lepista* the spores should be pale pinkish in deposit, and always more or less roughened. BIGELOW and SMITH (1969) considered these classical features and concluded that there is no difference of generic degree between the *Clitocybe* and *Lepista* species. Some *Clitocybe* species have spores which, though white (some of these observations on colour may be vitiated by too thin a deposit) are rough with an ornamentation similar to that found

in *Lepista*, while some have spores which, though smooth, are pale pinkish as in *Lepista*. They also pointed to the existence of *Lepista* species with extremely low warts on their spores. Their conclusion is further supported by the fact that in *Lepista* (at least in *L. irina*) the same gills may produce smooth (under the light microscope) spores besides distinctly rough ones, and these authors even claim that there exists in the *Lepista* group a species (*C. pseudoirina* Big. & Smith) with only smooth spores, in which delicate verrucae are visible only in electron micrographs.

Indeed, if the combination of pale pinkish spore colour and a roughened spore wall were in fact the only thing separating *Lepista* from *Clitocybe*, the amalgamation performed by these American authors would be understandable. Like BIGELOW and SMITH, I was dissatisfied with the common practice of separating the *Clitocybe gilva* group generically from the *Lepista* species (HARMAJA 1969), but I was unwilling to accept their solution to this problem. Instead, I suggested that this group should be included in *Lepista*, irrespective of the colour of the spores in the species of this group (which, anyway, was always pinkish in those specimens I studied).

I am now even more convinced that *Lepista*, with some amendments, is a valid genus, and thus take quite the opposite view to that of BIGELOW and SMITH, even though the classical differences do not always apply in the distinction between *Lepista* and *Clitocybe*. The reason is that during my continued studies in and around *Clitocybe* I observed two obviously diagnostic characters for separating these genera, neither of which have been mentioned by the two American authors (BIGELOW & SMITH 1969). The present contribution also includes some other taxonomical and nomenclatural notes as well as some neglected observations from the literature.

Acknowledgements. — I am indebted to Dr. Robert L. Shaffer (MICH) for placing certain specimens at my disposal. I am also grateful to Mr. Mauri Korhonen for taking the photographs.

2. The characters separating *Lepista* from *Clitocybe*

Immediately after the publication of my

paper on the Fennoscandian *Clitocybes* (HARMAJA 1969), I began to use the heated cotton blue techniques (see KOTLABA & POUZAR 1964) in *Agaricales* taxonomy, a method with which I became acquainted during studies on *Discomycetes*. Among many other interesting things, I observed that in the »classical» species of *Lepista* (*sensu* SINGER 1962) studied by me, the spore wall (or some of its outer layers), including the warts, is strongly cyanophilic. In very young spores it is still cyanophobic but it soon begins to absorb the dye, the mature and old spores staining darkest blue. The wall in the hilar appendix seems, however, to be cyanophobic (unless very weakly cyanophilic?). The species studied were: *L. irina*, *L. luscina*, *L. nuda*, *L. rickenii*, *L. sordida*, *C. subalpina* Big. & Smith (which will be formally transferred to *Lepista* later in this paper), *L. subconnexa*, and several others which were impossible to identify. Subsequently it was found that the cyanophilic spore wall of *Lepista* was by no means unknown in the literature, since LAMOURE & FICHET (1962) remark, as a mere detail, that the spore wall of a *Lepista* species they call »*Rhodopaxillus densifolius* Favre» stains intensely in »Bleu lactique» (= cotton blue). KÜHNER (1969) found the spore wall of *L. irina* to be cyanophilic, BESSON (1970), another member of the skilful French school, mentioned that the same applies to the spore wall and its ornamentation in *L. irina* and *L. luscina* (called *L. panaeola*), and finally SINGER (1972) made the same observation as regards *L. ameliae*, *L. argentina*, *L. densifolia*, *L. irina*, *L. nuda*, *L. sordida* and *L. subconnexa*.

The other character which seems to possess great diagnostic value is that a considerable proportion of *Lepista* spores (especially the immature ones still attached to the sterigmata) constantly have strikingly shrunken, or collapsed walls, being almost or completely without contents. I have so far mostly made this observation on water, Melzer, and cotton blue squash mounts, made of the lamellae of dried basidiocarps, but occasional observations on the spores of deposits also revealed the presence of collapsed spores. Strangely enough, it appears that the literature does not mention this striking phenomenon, apart from my report on *L. subconnexa* (HARMAJA 1970). The

reason for this collapse is uncertain. One explanation which suggests itself is that these shrunken spores are unripe and for some genetically determined reason have unusually soft walls, which become irreversibly collapsed in drying, especially as they are more or less devoid of contents (due to their immature stage?). Or, possibly the walls are shrunken at first in the normal fresh condition, and swell out as the spores receive their plasm (and nuclei?) and become turgid.

It subsequently appeared reasonable to check *Clitocybe* species for these two characters, to see whether they might provide a distinction between *Lepista* and *Clitocybe* at the generic level. I already considered the *C. gilva* group to belong to *Lepista*, in view of its distinctly walled and thickish-walled spores, which are pinkish-tinted in deposit (at least in the various »forms« studied by me) (HARMAJA 1969), and this group did indeed reveal a strongly cyanophilic spore wall and ornamentation as well as a conspicuous proportion of collapsed spores. The cyanophilic spore wall in this group had, however, already been reported in the literature, e.g. by KÜHNER (1969), BESSON (1970), and SINGER (1972). In addition, at high magnifications under the electron microscope, the spore ornamentation in *C. gilva* coll. is seen to be very similar to that present in *Lepista* (BIGELOW & ROWLEY 1968). These facts should be final justification of the opinion held by a small number of workers on agarics that *C. gilva* coll. is congeneric with the classical species of *Lepista*. In his paper mentioned just above, SINGER (1972) has changed his previous opinion and come to the same conclusion.

It may be mentioned here that the taxonomy of the *L. gilva* group is in urgent need of revision, and that, to my knowledge, no satisfactory solution has yet been suggested. We may have here just one very variable species, or two or three, or more. According to my observations, attention should be paid to at least the following points: the colours of the fruit body, the hygrophany of the pileus, the pileus surface when dry (whether distinctly concentrically wrinkled or not), the thickness of the context (also at the pileus margin), the exact colour of the spore deposit, the exact size and shape of the spores (whether subglobose or more or less broadly ellipsoid), the kind of spore base, the length and distribution of the verrucae of the spores, and of course the ecological and distributional features. For the present, I recommend that the name used for this group should be »*Lepista gilva* (Fr.) Roze coll.», because the

existing original material is of *Agaricus gilvus* Pers. ex Fr., consisting of one specimen in the PERSON herbarium in Leyden, studied by SINGER (1961) and by me. Sometimes PATOUILLARD is cited as the author who transferred the species to *Lepista* but ROZE's (1876: 110) combination has priority.

A great many other species ascribed to *Clitocybe* and several undescribed ones were studied. It turned out that (with one important exception to be treated below in the third section) their spore wall is either completely cyanophobic or only weakly cyanophilic, never being collapsed in notable amounts of spores (Fig. 1 a). (It should be mentioned here that a careful distinction should always be made between the spore wall and spore contents, since the latter are usually more or less cyanophilic.)

Thus it seems that we have attained a delimitation of *Lepista* which is more natural than earlier ones, and at the same time found characters which truly justify according to *Lepista* the rank of genus, and which also give a fairly convenient routine method for telling whether a single specimen belongs to *Clitocybe* or *Lepista*.

3. Relationship of *Clitocybe nebularis* to *Lepista*

The species of *Clitocybe* that forms the exception mentioned above in section 2, possessing both a strongly cyanophilic spore wall and a very striking proportion of shrunken spores (Fig. 1 b), is *C. nebularis* (Fr.) Kumm. I want to emphasize that, according to my studies, all the 21 other species included by me (HARMAJA 1969) in the type subgenus of *Clitocybe* had completely cyanophobic spore walls, including those fleshy species previously always supposed to be closely related to *C. nebularis*. (All but one of the 11 species of the sections *Latisporae*, *Ditopae* and *Strigipedes* of the subgenus *Pseudolyophyllum* also proved to have cyanophobic spore walls, while those of the subgenus *Roseospora* and the type section of the subgenus *Pseudolyophyllum* as well as *C. schulmannii* of the section *Strigipedes*, 11 altogether, possess weakly cyanophilic spore walls). SINGER (1972) also mentions that some species of *Clitocybe* have cyanophobic spore walls, while others possess cyanophilic ones. He included *C. nebularis* among the latter species, but observed that the cyanophilic



Fig. 1. Spores in heated cotton blue squash mount, prepared from dried gills. Bright field, x 1000. Photo by M. Korhonen. — a) *Clitocybe gibba* (Fr.) Kumm., the type species of *Clitocybe* (Finland, Etelä-Häme, Hattula, 25. IX. 1967, H. Harmaja; H). Note the lacrymoid shape and the thick confluent base of the spores, which drift about singly in the mountant and possess normal and very thin walls. The spores are equally dark throughout (except for some paler oil drops) as their contents are weakly to moderately cyanophilic while the very thin walls are cyanophobic and not discernible. — b) *Lepista nebularis* (Fr.) Harmaja (Finland, Varsinais-Suomi, Lohja, 2. XI. 1967, H. Harmaja; H). Note the principally ellipsoid shape of the obtuse-based spores, which, besides occurring singly, are also commonly seen in tetrads and dyads (very rarely even three adhered together), a part of them, including those immature ones still attached to the sterigmata, having collapsed walls and no contents (three of the four groups on the right representing such spores have been photographed in Melzer's reagent with a lower magnification). The spore walls are thickened and cyanophilic, the borders of the spores being seen to be darker than their contents. Some of the spore clusters are seen from above.

character in this species is weaker than in the others, in contrast to my results. (Anyway, SINGER does not use my procedure of recognizing three categories of matter on the basis of its capacity to absorb the dye: (1) weakly cyanophilic, (2) moderately cyanophilic and (3) strongly cyanophilic matter.) Even in an earlier study (HARMAJA 1969), *C. nebularis* was found to possess certain characters which were unique in *Clitocybe* (a good proportion of spores collapsed; spore deposit deep yellow; different parts of dried fruit body unusually rich in chlorine tinges under ultra-violet light), and which led me to place it in a different section from the other fleshy species! As, besides the two very important characters dealt with above, the other features of *C. nebularis* (see below) also seem to suggest a relationship with *Lepista*, or at least do not exclude this possibility, this species should be transferred to *Lepista*, although its spores are smooth (at least under the light microscope) and lack a pinkish colour.

The habit of *C. nebularis* is distinctly clitocyboid, the lamellae usually being completely decurrent, but in the classical *Lepistas* there is a well-known tendency for

the gills, mostly more or less adnate-sinuate, to be decurrent, and in *L. subconnexa* at least they are clearly decurrent (BIGELOW & SMITH 1969; HARMAJA 1970). Moreover, since the publication of my paper on the Fennoscandian *Clitocybes*, I have found fruit bodies of *C. nebularis* with many of the gills somewhat sinuate near the stipe. An even more important find was my discovery in southern Finland, in the Lohja limestone district, of a curious fungus, which was whitish and possessed a non-hygrophanous pileus and almost *Tricholoma*-like, sinuate, not even slightly decurrent lamellae. When fresh this agaric possessed an odour of *C. nebularis*, not being so fragrant as *L. irina*, and gave the impression of a *Lepista* rather than that of a *Tricholoma*. I was very eager to see what its spores looked like, and my surprise was great when they turned out to be completely smooth under the light microscope and almost identical with those of *C. nebularis* (the size of the hilar appendix is slightly different), possessing all the features treated above. Clamp connections were abundant. A spore deposit was unfortunately not obtained. According to current taxonomy, this species would have keyed out

among the clamped *Tricholomas*! This fungus should of course be included in *Lepista*, together with *C. nebularis*, being in a way a connecting link between the bulk of *Lepista* and *C. nebularis*, as it possesses a *Lepista* habitus but is microscopically extremely close to *C. nebularis*. This species, *L. singeri* HARMAJA (HARMAJA 1974), may help to solve the problem of the »smooth-spored *Lepista irina*» of some authors, which others often place in *Tricholoma*. A new subgenus of *Lepista*, based on *C. nebularis* and *L. singeri*, will be established (HARMAJA 1974). Generally, macroscopic characters, such as the attachment of the gills to the stipe and the presence versus absence of a stipe, or the position of the latter, should be used very carefully in the generic taxonomy, and only in connection with other, preferably microscopic, features.

As regards the reactions of *C. nebularis* under ultra-violet light, a typical member of *Lepista*, *L. subconnexa*, was observed by me to display a similar and even more conspicuous chlorine colour in different parts of its dried fruit body, and this feature might also be considered evidence of the relationship of *C. nebularis* to *Lepista*. BIGELOW and SMITH (1969) report that *L. subconnexa* (as *Clitocybe s.*) and *C. phyllophila* appear to be close to each other in all characters but the spore surface. However, I consider a close relationship unlikely, not only because there are several differences in their spores (e.g., the spore wall in *C. phyllophila* is smooth and only weakly cyanophilic), but because their ultra-violet responses also differ. Dried basidiocarps of these species may indeed sometimes seem very alike, but they are easily distinguished from each other without the aid of a microscope. For instance, under ultra-violet light, with a wave length of 254 nm, the pileus of *L. subconnexa* is luminously chlorine coloured, while that of *C. phyllophila* remains mat and pale, with some violet tinges.

The deep yellow spore colour present in *C. nebularis* is unknown in *Lepista* in its current concept, but I think that it can be considered to lie within the amplitude of variation in spore colour of this genus, where different shades of reddish colour are already known (see e.g. BIGELOW & SMITH 1969). The important point is that the spore print is distinctly coloured in sufficiently thick de-

posits in both the bulk of *Lepista* and in *C. nebularis*.

The smooth spores of *C. nebularis* may at first sight seem to exclude it from *Lepista*. But here I agree with BIGELOW and SMITH (1969: 165), who write about the »futility of trying to use arbitrarily a character such as spore ornamentation to separate 'natural groups'». The important point is that the *Lepista* species and *C. nebularis* evidently have a homological layer in their spore wall, viz. the strongly cyanophilic one, which generally develops projections, ranging from very small to fairly coarse ones. It should be remembered that even now the smooth-spored *C. nebularis* and *L. gilva* coll. with verruculose spores are almost uniformly considered congeneric, but both referred to *Clitocybe*! It would not be surprising if the spore wall of *C. nebularis* turned out to be uneven under the electron microscope. *L. irina* may be considered a species intermediate between the bulk of *Lepista* on the one hand and *C. nebularis* and *L. singeri* on the other, as a part of the spores of *L. irina* seem to be smooth under the light microscope, while the rest of them possess low warts. Moreover, it should be pointed out that the spores in *Lepista* and *C. nebularis* also seem to be very similar in several respects other than the most important ones already mentioned. The spore wall in *C. nebularis* is somewhat thickened, my latest studies showing it to be ca. 0.3–0.4 μm thick (in contrast to my earlier opinion), and this feature also suggests relationship with *Lepista*. In addition the spore shape, the often depressed suprahilar area of the spores, and the spore contents with a distinct oil drop or drops accord completely with the characters of *Lepista*.

Also, the odour, taste and edibility as well as the ecological and distributional characters of *C. nebularis* accord very well with the characters of *Lepista*.

In an earlier paper (HARMAJA 1969), I agreed with those who preferred to typify the genus *Clitocybe* with *C. nebularis*. Now I must change my opinion and support those considering *C. gibba* the lectotype. A most inconvenient situation would arise if my taxonomical conclusions were accepted and at the same time *C. nebularis* were regarded as the type. For instance, the name *Clitocybe* would replace *Lepista*

and a very great number of new combinations would be necessary, so that the general principle of stabilizing the nomenclature would not be followed. As *C. gibba* is also the type of the section *Infundibuliformes* (Fr.) Sing. & Dig. of *Clitocybe*, this well-known sectional name must inevitably be considered a synonym of the name of the type section, sect. *Clitocybe*.

4. The occurrence of spores adhering together in tetrads and the taxonomical significance of this character

One more interesting but neglected feature of *Lepista* spores is that in all the species studied a certain amount of the spores (including the collapsed ones) can be seen to adhere together in tetrads and dyads, e.g. in water, KOH (5 %), Melzer's reagent and heated cotton blue, when the mount was prepared from a piece of dried lamella. The proportion of adhering spores in all the detached spores drifting in the mountant may be rather small or even more than 50 per cent, varying with the species. There does not seem to be any earlier mention of this character in the literature, apart from my observation concerning *L. subconnexa* (HARMAJA 1970). In the present case this feature is not of great diagnostic value at the generic level (but evidently has significance at the infrageneric and suprageneric levels), since it is present in different groups of *Clitocybe* (HARMAJA 1969); and, conversely, the occurrence of spores adhering together in fours and twos is almost negligible in *L. gilva* coll. In this respect, too, the spores of *C. nebularis* are typical of *Lepista*, the majority of them being stuck together in this way (HARMAJA 1969) (Fig. 1b).

In my paper on the Fennoscandian *Clitocybes* cited above I perhaps did not make it sufficiently clear that the possible occurrence of spore tetrads and dyads should be studied in squash mounts made from a piece of dried lamella.

My earlier tentative explanation of this phenomenon was subsequently disproved by microscopic studies of fresh, drying lamellae of two species with single spores (*C. gibba* and *Agrocybe* cf. *dura*) and one with tetrads (*C. odora*). The lamellae were lying free on an object glass, and I found that, as the tissue dried and lost its

turgidity, the sterigmata supporting the unripe spores at their tips began to collapse and turned towards each other. Accordingly in all three species the spores, when viewed from above, were seen to come nearer and nearer to each other, until they finally touched and formed a cluster of four spores. When completely dry, these same fragments of lamellae were squashed in Melzer's reagent and the mount was observed; two different cases were seen: the spores of the *Agrocybe* species and those of *C. gibba* loosened readily from the sterigmata and also from each other, drifting about singly in the mounting liquid, while the detached spores of *C. odora* mostly occurred in fours and twos, as was of course expected (HARMAJA 1969). Thus this peculiar character observed in a major or minor part of the spores of certain species is perhaps explained in the following way. When the unripe spores on the sterigmata of these species come into contact with each other as described above, their undeveloped walls or some outer layer(s) of these are gelatinized and sticky, and thus the four spores not only touch but cling together as if glued, continuing to do so even when the gill tissue is crushed during the preparation of microscopic slides. The occurrence of spore dyads can easily be explained by the cleavage of tetrads and/or the presence of occasional two-spored basidia among the normal four-spored ones.

A different situation presumably prevails in most of the *Basidiomycetes*, where, although »spore tetrads», as viewed from above, may be seen in intact dried lamellae, the spore walls are evidently not sticky, and the spores are readily separated when the basidia are crushed or shaken during the preparation of microscopic mounts. There may also be species with rigid walls in the sterigmata, in which case the latter with their unripe spores may not approach each other when drying.

I have observed spore tetrads in the species of many other genera besides *Clitocybe* and *Lepista*, e.g. *Collybia*, *Lepiota*, *Lyophyllum*, *Pseudoclitocybe* and *Rhodocybe*, and I believe that this character, which has proved very useful in *Clitocybe* (HARMAJA 1969), may also be found to

possess diagnostic value at different taxonomic levels outside that genus.

5. *The essential characters of the amended genus Lepista*

Lepista (Fr.) W. G. Smith is thus amended to comprise species with the following characteristics (compare Fig. 1b): fruit bodies medium-sized to large, with a tricholomoid to clitocyboid habit, and very variable colours; pileus hygrophanous or not; basidia without siderophilous granulation, with inamyloid, indextrinoid and cyanophobic walls; spore print lightly coloured, either pinkish or deep yellow; spores uninucleate (KÜHNER 1945); a major to minor proportion of the spores (especially the immature ones?) stick together in tetrads and dyads, at least in water, KOH (5%), Melzer and cotton blue mounts of dried gills; a good proportion of the spores (especially the immature ones) conspicuously collapsed in water, Melzer and cotton blue mounts (at least in mounts of dried gills; also in all those cases when deposits were studied); spore base invariably obtuse (unless acute in a small proportion of the spores of *L. gilva* coll.); spore shape very ordinary, being ellipsoid or ellipsoid-oblong, rarely subglobose; suprahilar area of the spores very often depressed, if not, then applanated, being smooth under the light microscope in rough spore walls also, but often (if not always?) centrally slightly rugose under the electron microscope (BIGELOW & ROWLEY 1968; PEGLER & YOUNG 1971); spore wall somewhat thickened, inamyloid and indextrinoid, strongly cyanophilic except in very young spores, in which cyanophobic, usually verruculose with obtuse warts often increasing in number and size towards the spore apex, rarely smooth under the light microscope; hilar appendix distinct, rather small, with cyanophobic (or very weakly cyanophilic?) walls; spore contents almost always with one more or less distinct oil drop; cystidia of any kind absent; hymenophoral trama regular or nearly so; cortex of pileus rather poorly differentiated, composed of thin filamentous hyphae; all hyphae with inamyloid and indextrinoid, probably also cyanophobic walls; clamp connections abundant in all parts of the fruit body; on bare soil and in litter, often where the ground is rich in nutrients, usually not in

wet habitats or on wood, evidently not forming ectotrophic mycorrhiza; distribution cosmopolitan in very variable climatic conditions.

6. *The relationship of Lepista to certain genera*

My preliminary studies suggest that other features besides the classical differences distinguish *Tricholoma* and *Collybia* from *Lepista*. The two genera, sometimes confused with or supposed to be related to *Lepista*, evidently as a rule have a cyanophobic spore wall, and their spores are generally not conspicuously collapsed and mostly (at least in *Tricholoma*) do not occur in tetrads or dyads. SINGER (1972) also reports the spores of those species of *Collybia* and *Tricholoma* studied by him to possess cyanophobic walls (except in some very occasional spores in *T. saponaceum*; see later).

However, in certain species of *Tricholoma* (e.g. *T. caligatum*, *T. inamoenum*, *T. saponaceum*, *T. sejunctum*, *T. sulphureum*) and *Collybia* (so far only in the species of the *Rhodocollybia* group: *C. maculata*, *C. distorta* and *C. butyracea*) I have observed most curious scattered, finally sometimes secondarily septate basidia, with thick, strongly cyanophilic walls throughout, constantly occurring among normal basidia and producing spores of more or less normal size and shape (except for those of *C. butyracea* at a final stage; see below) but similarly thick-walled and strongly cyanophilic. (In addition, in *C. butyracea* narrow belts with the same colour reactions occur around the septa of some pileus hyphae.) Certain details of these basidia are different in different species. This phenomenon is, however, not connected with the cyanophily of the *Lepista* spore, since these elements occur along with the normal ones, and are also strongly dextrinoid, unlike any cell in *Lepista*. I have never seen such structures in *Clitocybe*, either.

This very peculiar situation in *Tricholoma* and *Collybia* has to my knowledge not been reported before in the literature not excepting a recent paper on *Tricholoma* (GULDEN 1969). However, SINGER (1962) does write that in *Tricholoma* a few dextrinoid spores may very infrequently be

found among the normal indextrinoid ones, and in his 1972 paper he reports that a thin cyanophilic outer layer is present in the wall of a few spores of *T. saponaceum*. However, he fails to observe the conspicuous aberrant basidia. It is very interesting to note that SINGER & CLÉMENÇON (1971) have found exactly similar basidia in *Aeruginospora hiemalis*, calling them »sclerobasidia».

Unexpectedly, spore characters have been reported as normal in the aphyllous genus *Jaapia* Bres. (see NANNFELDT & ERIKSSON 1953: Fig. 1, h—l) that are extremely similar to those present in, e.g., the aberrant spores of *C. butyracea*, viz. the apparent double structure of the wall (evidently also present in the aberrant basidia in *Tricholoma* and *Collybia*), the occurrence of septa within old detached spores and the common collapsing of the small basal cell, and the response to cotton blue (and also the dextrinoid reaction, according to my own observations on the two *Jaapia* species).

The phenomenon may be connected with a curious type of chlamyospore formation. Another possible explanation is that it is caused by some parasite (*Archimycetes?*), which has developed in the basidia and spores of the host species, inside the thin, cyanophobic, inamyloid and indextrinoid basidial and sporal walls.

The genera *Rhodocybe*, *Rhodophyllus*, *Clitopilus* and their relatives do not appear to be very closely related to *Lepista* (or *Clitocybe*). Firstly, they have binucleate spores (KÜHNER 1945), further they usually seem to have a thicker spore wall and a deeper reddish colour in their spore deposits. The two last-mentioned features accord with my observation that, when viewed under the microscope, in water, KOH, or even Melzer's reagent, even single spores of many of the species of these genera clearly have reddish-tinted walls, while in *Lepista* (and *Clitocybe*) the reddish tinge is hardly observable in single spores, even if they are pale pinkish in deposit. In addition, in these genera the walls of very young spores attached to the sterigmata are already generally more or less strongly cyanophilic, while they may in some species become less so with age, so that in certain species at least a small proportion of the completely mature spores possibly even

have cyanophobic walls (according to KÜHNER 1969 and my own studies). In *Lepista* (and certain *Clitocybes*) the opposite is true, since the spore wall is always cyanophobic in very young spores, its ability to absorb cotton blue increasing with age. Lastly, clamp connections are commonly absent from these genera with binucleate spores, while they never seem to be lacking in *Lepista* (and only very infrequently in *Clitocybe*).

The genus *Ripartites* has clamps and distinctly coloured, uninucleate (KÜHNER 1945) spores possessing verruculose, strongly cyanophilic walls (KÜHNER 1969; BESSON 1970; SINGER 1972; my own studies), and, according to my observations, a small proportion of its spores are adhered together in tetrads in preparations made of dried gills. It is thus clearly very close to *Lepista* taxonomically, as has already been pointed out, e.g. by SINGER (1962), KÜHNER (1969) and BESSON (1970), being to my mind particularly near to the *L. gilva* group. As described by SINGER (1962) however, *Ripartites* differs sufficiently from *Lepista* to deserve recognition as an independent genus. I have also found that in *Ripartites* the proportion of collapsed spores is smaller than in *Lepista*.

In the comparisons of *Lepista* with other genera, *Clitocybe* included, I have not regarded as decisive the two classical features whose combination has hitherto generally been supposed to be diagnostic of *Lepista*, i.e. the pinkish spore colour and the verruculose spore wall. This of course results from my attempts to obtain a more natural delimitation of the genus, in which the amplitude of variation of the spore characters also covers a deep yellow spore colour and a smooth spore wall as seen under the light microscope. The pinkish verruculose spores of *Lepista* of course still form an average difference from, say, *Clitocybe*. However, my most recent observations, to be published on a later occasion, show that, besides the well-known occurrence of pinkish coloured spores in *Clitocybe*, the genus also contains a few species with slightly rough spores (cf. also the spore wall of *C. atrostriata* Mét.). Moreover, PEGLER and YOUNG (1971) report the spore surface of *C. clavipes* to be rugulose under the electron microscope (this observation, by the way, confirms my 1969 opinion that this species deserves a section of its own; it would not be surprising if the

spores of the evidently closely related species *C. avellaneialba* Murr. also revealed a slightly rugose wall when studied under the electron microscope). *C. pseudoirina* Big. & Smith (type Smith 71356; MICH) is considered by BIGELOW & SMITH (1969) to occupy an intermediate position between *Lepista* and *Clitocybe* as regards its spore ornamentation (see p. 83). The authors claimed that its spores were smooth under the light microscope, even when studied with an oil immersion lens, but, on examining the type and only specimen, I can tell that in reality a large proportion are distinctly rough as in the true *L. irina*, appearing so not only when stained with cotton blue, but also in Melzer's reagent, and even at as low a magnification as x 600. Thus the classical diagnostic features of *C. pseudoirina* (pinkish spore colour; at least many of the spores verruculose) indicate that it should be placed in *Lepista*, giving no support to the idea that it is an intermediate species. This is confirmed by my further studies on the type, which showed that a part of the spores occur in tetrads, that a proportion of them are collapsed, and that the spore wall is strongly cyanophilic. Moreover, all the characters of *C. pseudoirina*, both macroscopic and microscopic, strongly suggest that it is conspecific with *L. irina*. The other species thought by BIGELOW and SMITH to have an intermediate kind of spore surface, *C. highlandensis* Hesl. & Smith, lacks clamp connections, and, as admitted by these authors, is thus not a particularly suitable example to choose in this case. The connections of this at least superficially curious species to *Rhodocybe*, *Tricholoma* and the *C. harperi* group should be checked by a careful analysis of its spore characters.

7. The basionym and typification of *Lepista*

The basionym of the generic name *Lepista* is practically invariably considered to be »*Paxillus* tribus *Lepista* Fr.» (FRIES: *Epicrisis*, 1838), subsequently elevated to the generic status by W. G. SMITH (*Clavis Agaricinarum*, 1870). The name of FRIES is, however, not validly published as he misplaced the tribe through treating it as an infrageneric taxon (*International Code of Botanical Nomenclature*, 1972, Art. 33). The only exception to this rule is the treatment of the tribes of FRIES as subdivisions of genera in »*Systema*

Mycologicum» (»Code», Art. 33). The »*Epicrisis*» is, however, a later work quite different from that starting point publication, nor is it nomenclaturally considered a part of the »*Systema Mycologicum*» according to the »Code» (unlike FRIES's »*Elenchus fungorum*», 1828). Thus the above tribe of FRIES cannot serve as the basionym for new combinations, from which it follows that the proposed new combination *Lepista* (Fr. 1838) W. G. Smith 1870 is not validly published, either. However, fortunately this problem can be solved with practically no alterations to the current taxonomy or nomenclature of *Lepista*. Somewhat later (*Summa vegetabilium Scandinaviae* 2: 306, 1849) FRIES treats the *Lepista* group immediately under the generic name *Paxillus* as an infrageneric taxon whose rank he fails to indicate: »*Paxillus* a. *Lepista*». The characters of this group »a.» are described in a few words and three species are included: »1. *P. Lepista* [in italics] / 2. *P. extenuatus* (Scop.) / 3. *P. sordarius* (Pers.)», none of them being, however, designated as the type. This taxon without a designation of rank is the first supraspecific taxon, validly published in all respects, which can be typified with *Agaricus lepista* Fr., and, although FRIES of course means by it the same group of fungi as in the »*Epicrisis*» under the same Latin epithet, *Paxillus* a. *Lepista* must be treated as a new taxon and not as a mere new combination because the name was not validly published in the »*Epicrisis*». It is this taxon »a. *Lepista*» of *Paxillus* that may validly be given a new status. To be exact, the complete citation of the name of that taxon should be »*Paxillus* a. *Lepista* Fr. ex Fr.», but the first citation »Fr.» and the word »ex» are of course not necessary in routine use. DONK (1962) interprets the taxon »a.» as section, but that procedure does not seem correct since in the work considered FRIES used this kind of letters (a, b, c, etc.) to denote stirpes in those infrequent cases when he made any mention of the rank (e.g. in the first subgenus of *Agaricus*, subg. *Amanita*). The stirps is, however, not an official rank approved by the »Code», and moreover, FRIES used the word »stirps» and those small letters rather inconsistently. The word »section» is even more rarely found in the work, denoting even less any distinctly defined taxonomical position. W. G. SMITH is thus to be considered

to have made the new combination *Lepista* (Fr. 1838 ex Fr. 1849) W. G. Smith 1870. DONK (1962) seems to have been aware of the facts mentioned above, but, apparently because he failed to present any detailed explanations and emphasize the correct form of the basionym, they escaped the attention of subsequent workers.

As the epithet of the subdivision of the genus *Paxillus*, the taxon *Paxillus* a. *Lepista*, is »identical with [or derived from] the epithet of one of its constituent species, this species [*Paxillus lepista*] is the type of the name of the subdivision of the genus unless the original author of that name designated another type» (»Code», Art. 22). Thus the »selection of a lectotype» for *Lepista*, according to DONK (1962) first made by W. G. SMITH in 1908 in favour of *P. lepista*, is superfluous.

The identity of *Agaricus lepista* Fr. (*Paxillus lepista* (Fr.) Fr.; the author citation is mostly given incorrectly as *P. lepista* Fr., though this species was originally described in the »Systema Mycologicum» under the generic name *Agaricus*) has been the subject of some discussion. To me the original description (as well as the later ones of FRIES) of this species, with notes on its macroscopic

features and the colour of its spores, strongly suggests some species in fact belonging to *Lepista*, especially *L. subconnexa* (Murr.) Harmaja (or some very closely related species). *L. subconnexa* has been shown to occur in Norway and Finland, i.e., on both sides of Sweden (HARMAJA 1970), so it is most probable that it also grows in Sweden, where it may have been collected by FRIES and been in his hands when he was preparing the original description of *Agaricus lepista*. *L. subconnexa* may be a collective species, but at least one specimen collected in southern Finland (Etelä-Häme prov., Lammi, Biological Station 1968—07—02, Pertti Uotila; H) is conspecific with the North American type as it possesses large cespitose fruit bodies and was growing on rich bare soil, or mull.

8. The formal proposals of two new combinations

Lepista nebularis (Fr.) Harmaja, n. comb. (*Agaricus nebularis* Batsch ex Fries, Systema mycologicum . . . 1: 86. 1821.)

Lepista subalpina (Big. & Smith) Harmaja, n. comb. (*Clitocybe subalpina* Bigelow & Smith, Brittonia 21: 155. 1969. — Part of holotype [MICH] studied.)

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