

INTRODUCTION TO THE TAXONOMY  
OF THE GENUS *ENTOLOMA* SENSU LATO (AGARICALES)

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(With 9 Text-figures)

A survey is given of the infrageneric classification of the genus *Entoloma* sensu lato (Basidiomycetes, Agaricales), underlying the author's recent revisions of *Entoloma* in the Netherlands and adjacent regions (Noordeloos, 1979, 1980, 1981). The taxonomic value of the characters currently used in this genus is discussed. Three new subgenera are described, viz. *Allocybe*, *Inocephalus*, and *Omphaliopsis*, and subgenus *Paraleptonia* Romagn. is validated; several new combinations are made.

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INTRODUCTION

The genus *Entoloma* is one of the larger genera of the Agaricales. In the last 40 years many important treatises have appeared. The more notable of these publications are — Europe: Kühner & Romagnesi, 1953. — Africa: Romagnesi, 1941, 1957; Romagnesi & Gilles, 1979. — North America: Hesler, 1967; Largent, 1977; Mazzer, 1976. — South America: Dennis, 1953; Horak, 1978. — Australasia: Horak, 1973, 1980. Altogether some 1500 species have been described so far, but our knowledge is still far from complete (Horak, 1980: 14). It is clear that

in such a large genus in which the number of species is still increasing, problems concerning the infrageneric classification will arise.

In the following pages the characters are discussed which are used for classification in my revisions of *Entoloma* in the Netherlands and adjacent regions (Noordeloos, 1979, 1980, 1981). This discussion is followed by a synopsis of the classification accepted in these publications.

#### THE DELINEATION OF ENTOLOMA

*Entoloma* is the type-genus of the family Entolomataceae Kotlaba & Pouzar (syn. Rhodophyllaceae Sing.). This family is characterised by the following combination of characters: Spore-print pinkish-brownish, spores thin- to relatively thick-walled, hyaline or stramineous as seen under the lightmicroscope, angular in apical view or in all views or rough to verruculose in all views on account of the presence of ridges and warts caused by a special formation of the endospore (the epicorium of Clemençon, 1970: 117).

At present three agaricoid genera and one gasteroid genus are known, which can be distinguished as follows:

- |  |                                       |
|--|---------------------------------------|
| 1a. Spores more or less rough or verruculose, not angular . . . . .  | <i>Rhodocybe</i> R. Maire             |
| b. Spores angular, at least when seen in apical view . . . . .   | 2                                     |
| 2a. Spores smooth except for longitudinal ridges or ribs or facets, thus appearing angular when seen in apical view only . . . . . | <i>Clitopilus</i> (Fr.) Kumm.         |
| b. Spores angular in all views, entirely covered with facets delineated by ridges . . . . .  | 3                                     |
| 3a. Fruitbodies agaricoid . . . . .  | <i>Entoloma</i> (Fr.) Kumm.           |
| b. Fruitbodies gasteroid . . . . .   | <i>Richoniella</i> Costantin & Dufour |

Recently Horak (1978) demonstrated the resemblance of the spores of some species of *Rhodocybe* with weakly nodulose-warty spores with those of some species of *Entoloma* with weakly angular-nodulose spores. As a matter of fact with only the aid of the light microscope, it is not always easy to distinguish a species of *Rhodocybe* from a species of *Entoloma*. A very close observation of the spores, preferably with the aid of scanning electron microscopy, may well be necessary then.

Kühner (1979: 357) brought the families of Entolomataceae, Pluteaceae and Macrocystidiaceae together in a new order, the Pluteales. Although the last two families have entirely smooth, usually thin-walled spores, they show fundamentally the same ultrastructure of the spore wall as is found in the Entolomataceae, viz. a strongly developed endospore, made up in the same way as the epicorium, and a strongly reduced mixosporium, a structure which is unique among the Agaricales.

#### THE INFRAGENERIC CLASSIFICATION OF ENTOLOMA

Fries (1821, 1838) distinguished five tribes in the genus *Agaricus* to accommodate the species with a pink spore print and a pileus continuous with the stipe, viz.,

1. *Entoloma*: stipe fleshy and fibrous; lamellae sinuate; habit similar to that of species of *Tricholoma*.
2. *Clitopilus*: stipe fleshy and fibrous; lamellae decurrent; habit similar to that of species of *Clitocybe*.
3. *Leptonia*: stipe with cartilaginous cortex; pileal margin involute at first; lamellae secedent; habit similar to that of species of *Collybia*.
4. *Nolanea*: stipe cartilaginous; pileal margin straight; lamellae narrowly adnate to almost free; habit similar to that of species of *Mycena*.
5. *Eccilia*: stipe cartilaginous; lamellae decurrent; habit similar to that of species of *Omphalia*.

Later many authors accepted this classification, but often treated the Friesian taxa on other taxonomic levels, viz. as *subgenera* (Loudon, 1829; Rabenhorst, 1844) or as *genera* (Kummer, 1871; Quélet, 1872).

Quélet (1886) united again Kummer's entolomatoid genera into one large genus, which he called *Rhodophyllus*. This name was and is used by many European authors (Kühner & Romagnesi, 1953; Romagnesi, 1941, 1974a & b, 1978; Moser, 1967). Many others, however, preferred several small genera to distribute the same group of species. They maintained the Friesian taxa, raised to generic level by Kummer (1871), and added new ones, such as *Claudopus* Gill. for species with a crepidotoid habit, *Pouzaromyces*, originally monotypic, based upon the aberrant species *Nolanea fumosella* Wint. with strigose hairs on pileus and stipe, and *Alboleptonia* Largent & Benedict for a small group of white or pale coloured species with a collybioid habit, formerly placed in the genus *Leptonia* or *Entoloma*.

Romagnesi (1937) completely abandoned the Friesian classification and proposed a new one, mainly based on the structure of the base of the spores. He proposed a number of sections arranged into two groups: one with so-called symmetrical spores and one with so-called asymmetrical spores. This classification-scheme was extended by Romagnesi in 1941 to accommodate also tropical species. Romagnesi's system was also adopted by Singer (1943, 1951).

Later Romagnesi changed and emended the circumscription of many of his taxa on account of the evidence supplied by the many new, mainly tropical species with which he was confronted. This culminated in his most recent classification (Romagnesi, 1974b, 1978) in which many of the Friesian names were retained for restricted or emended taxa on subgeneric level.

Largent (1974) largely emended the Friesian classification using macro- and microscopical characters besides chemical ones., such as the urea-content of the fruitbodies. He distinguished six genera, viz. *Entoloma*, *Leptonia* (incl. *Eccilia*), *Nolanea*, *Claudopus*, *Alboleptonia* and *Pouzaromyces*.

In the present paper *Entoloma* is treated following the concept of Donk (1949: 158), which means including all agaricoid fungi with pink spores that are angular in all views (in other words: with a spore-wall consisting of angular facets) thus covering the same group of species as *Rhodophyllus* Quél. The latter name is rejected here for nomenclatural reasons. It is a superfluous later synonym of *Entoloma*, and was published illegitimately according to the rules of the International Code of Botanical Nomenclature.

Largent's classification of the entolomatoid fungi in several genera is not accepted here. In the author's experience there are no clear-cut taxa in *Entoloma* sensu lato that deserve generic rank.

It was difficult enough to delimitate such taxa when only the temperate species were relatively well-known. The new information supplied by the numerous recently found species from the tropics (Romagnesi, 1941, 1957; Romagnesi & Gilles, 1979; Horak, 1973, 1978, 1980) made this still harder.

It is not difficult to distinguish certain groups of taxa from each other, for example *Entoloma* versus *Nolanea* in my restricted sense, on a lower taxonomic level, but raising these units to the rank of genus would have as consequence that for a number of intermediate species a series of aberrant, often monotypical 'genera' would have to be added to those already known. I prefer to place such taxa in separate sections in a more or less isolated position in, or in new subgenera in between, the subgenera already accepted and not to create new genera for them.

It is obvious that in many cases there are links between the subgenera I have used. For example section *Fernandae* forms a distinct link between subgenus *Nolanea* and *Pouzaromyces* with respect to pigmentation, type of pileipellis, and lack of clamp-connections. A similar case is found in section *Griseorubida*, which is intermediate between subgenus *Nolanea* and *Leptonia*. Several other examples can be found.

In the present work the infrageneric classification of Romagnesi (1978) is largely adopted with only slight alterations; some taxa are emended, some new ones are added. Unfortunately quite a few nomenclatorial changes are necessary as a consequence of the use of the name *Entoloma* instead of *Rhodophyllus*.

Of course the classification of *Entoloma* s.l. as proposed here is not a final one. First because of my knowledge of the genus is restricted to a small geographical area, second because so far I have studied only a part of the genus on monographic level (*Pouzaromyces*, 1979; *Nolanea*, 1980; *Entoloma*, *Allochybe* and *Trichopilus*, 1981) Moreover it is to be expected that many new species will be discovered in the future, especially in alpine, arctic and tropical regions, which undoubtedly will necessitate the alteration of the concepts of some of the infrageneric taxa and the addition of new ones to the system.

## NOTES ON THE CHARACTERS USED IN THE TAXONOMY OF ENTOLOMA

### 1. Macroscopical characters

#### 1.1. *Habit of the carpophore.*

In general the habit of the carpophore is a useful character with which to recognize groups. In *Entoloma* the habit is very variable from fairly robust and tricholomatoid to very small and omphalioid or crepidotoid. However, in most cases in this genus, habit characters are subordinate to characters such as the structure of the pileipellis, the type of pigmentation and the presence or absence and topography of clamp-connections.

#### 1.2. *Pileus.*

1.2.1. SIZE AND SHAPE.—In *Entoloma* size and shape of the pileus vary considerably and in addition change in the course of the development of the carpophore. In general two lines can be distinguished, viz. (1) conical when young, expanding via conico-campanulate to plano-convex, usually with umbo or papilla, as found in subgenera *Entoloma*, *Nolanea*, *Pouzaromyces*, and *Inocephalus*, and (2), pileus semiglobose to convex when young, with slight central depression or

(deep) umbilicus, hardly expanding with age, as is found in subgenera *Leptonia*, *Omphaliopsis*, *Alboleptonia* and *Claudopus*.

1.2.2. COLOUR.—The colour of the pileus is usually some shade of brown or grey with or without reddish and/or yellowish tinges; rarely the pileus is pigmentless, brilliantly white or brightly coloured.

1.2.3. HYGROPHANITY.—Hygrophanity plays an important role in the classification of *Entoloma*. Generally speaking most hygrophanous species are found in the subgenera *Entoloma* and *Nolanea*. There the pileus distinctly fades on drying, usually along radial streaks. In some cases the hygrophanity is weak, then the pileus usually is translucently striate when moist, becoming opaque but not changing colour very much on drying. This is found in some species of subgenera *Leptonia*, *Omphaliopsis* and others.

1.2.4. SURFACE.—The surface of the pileus varies from entirely smooth, sometimes with a slightly tomentose-fluffy centre, to strongly radially fibrillose-costate or squamulose. The aspect of the pileal surface is closely connected with the structure of the pileipellis and plays an important role in the delineation of infrageneric taxa.

### 1.3. Lamellae.

1.3.1. INSERTION.—The insertion of the lamellae is very variable and ranges from adnate decurrent to adnate emarginate or almost free, sometimes even within one species or section. Therefore it is of minor importance for the infrageneric taxonomy and was somewhat overestimated in the classical Friesian delimitation of subgenera.

1.3.2. COLOUR.—In most species of *Entoloma* the lamellae turn pink when mature, owing to the accumulation of ripe spores. Many species have in addition pigmented hyphae in the mediostratum which give the lamellae a brownish or greyish, rarely green or yellow tinge. This character plays a role in the specific delimitation more than in infrageneric classification.

Some species, particularly in the subgenus *Leptonia* have a coloured lamellar edge, which is caused by the presence of intracellular pigment in the cheilocystidia. This is considered a character of minor importance (see also under cheilocystidia below).

### 1.4. Stipe.

1.4.1. SHAPE AND SIZE.—In most species the stipe is central and more or less cylindrical, sometimes with a slightly broadened or attenuated base, sometimes flattened or twisted. Considering the variability within most species, this is a character of minor importance. Also the width of the stipe cannot be used to distinguish subgenera, as was done by Largent & Benedict (1971: 35) in the case of subgenus *Entoloma* versus subgenus *Nolanea*.

1.4.1. STRUCTURE AND SURFACE.—On account of the structure and surface of the stipe two types can be distinguished in the genus *Entoloma*. (1) Species with a fibrous stipe, easily splitting lengthwise. The surface of this type of stipe is fibrillose striate lengthwise and usually slightly aeriferous with silvery fibrils alternating with white or colored ones. This type is found in many species of subgenera *Entoloma* and *Nolanea*. (2) Species with a more or less cartilaginous stipe, easily snapping across and with a smooth surface, as if polished. This type of stipe is found in many species of subgenera *Leptonia*, *Omphaliopsis* and *Nolanea*. Intermediate stipe structures occur, however, in all subgenera mentioned.

### 1.5. *Smell and taste.*

Many species of *Entoloma* have a farinaceous smell and taste. In others a distinct smell and/or taste is completely lacking. A few individual species scattered throughout the genus can be recognized by their very typical smell. Smell and taste, however, must not be overestimated as a character, as it is shown to be rather variable in many species and also because the possibility of perception by observers varies considerably.

## 2. Microscopical characters

### 2.1. *Spores.*

The french mycologist Fayod (1889: 381) was the first to draw attention to the complex morphology of the spores in *Entoloma*: being angular from all sides, as the sporewall consists of many rectangular or polygonal facets. Kühner & Boursier (1929: 264–278) developed a series of geometric models of spores of *Entoloma*, divided into two main groups, based on the morphology of the base of the spore. The first type, called 'symmetrical', has a base in which the hilar appendix is attached to the edge of two facets (a dihedral base or 'diedre basal'). In the second type, called 'asymmetrical', the hilar appendix is attached to a basal facet ('face basal'). Romagnesi (1937), being much convinced of the importance of this character for the infrageneric classification of *Rhodophyllus*, based an entirely new system on the characters of the base of the spores. Probably because of the difficulty in many cases of interpreting the structure of the base of the spores with the light microscope, this system did not find much recognition.

Pegler & Young (1978) provided a thorough study of the geometric configuration of the spores of *Entoloma* based upon observations with the scanning electron microscope. They recognized altogether twelve types of spores arranged in two series which are largely the same as those of Kühner & Boursier, viz. one group, comprising eight types, with the basal region of the spore formed by a single facet and another group, comprising of four types with the basal region of the spores made up of two facets, a dihedral base. One of the most important results from the work of Pegler & Young is that, contrary to Romagnesi, they did not find a strong correlation between their classification of spore-types and systematic groups based on other characters. It seems to early, however, to draw definite conclusions from their observations with regard to infrageneric taxonomy of *Entoloma*, as they studied only a fraction of all species of the genus known so far.

It is my experience that in many cases the structure of the base of the spore can be determined with the light microscope, but a great deal of practice is needed. Only after careful examination and comparison of thousands of spores does one get a good understanding of the structure of the base of the spores. Quite a few species however remain in which it is difficult to determine the structure of the base of the spores. In my revisions I have indicated the characteristics of the base of the spores in all cases in which they were visible by ordinary means, but I have avoided the use of this character in the keys as much as possible.

Another characteristic of the spores which I have consistently indicated is the length-width ratio (Q). Sometimes this character makes it possible to distinguish taxa of which the spores have approximately the same extreme values of length and width.

## 2.2. *Basidia*.

Most species of *Entoloma* have clavate, 4-spored basidia which measure about  $25-50 \times 7.5-15 \mu\text{m}$ . In subgenera *Pouzaromyces* and *Entoloma*, however, they are usually slightly to distinctly larger. It should be noted that in subgenus *Pouzaromyces* also the largest spores of the genus have been found. Two-spored basidia occur scattered throughout the genus.

In some sections, viz. *Pouzaromyces*, *Versatilia* and *Allocybe* basidia are found filled with a dark brown pigment. As I failed to find this in other sections, this character seems to be of taxonomic value.

Basidia with thickened, hyaline walls ('sklerobasidia') are sometimes found, but do not seem to be constant in any species.

## 2.3. *Cystidia*.

2.3.1. CHEILOCYSTIDIA.—Many species of *Entoloma* have cheilocystidia. The presence and shape of cheilocystidia are important characters for distinguishing species, in some cases even for the delineation of sections or subgenera. The following types can be distinguished.

1. Cylindrico-clavate cystidia.—This is the most common type of cheilocystidia. They usually have about the same size and shape of the basidia, and are recognised by their entirely vacuolised contents.
2. Vesiculose cystidia.—These vary from broadly clavate to subglobose or obpyriform. Sometimes they bear an apical projection and are intermixed with this and the lageniform type. In subgenus *Pouzaromyces* the vesiculose cheilocystidia have encrusted walls.
3. Fusoid to lageniform cystidia.—This type of cystidia usually protrudes from the hymenium and is easy to localize. The apex can be acute or rounded, sometimes capitate.
4. Tibiiform cystidia.—This type of cystidia is characteristic for some groups, such as section *Trichopilus*, but occurs also scattered in other subgenera.

In some species the cheilocystidia, usually of the first type, are filled with a brightly coloured pigment (usually blue or brown). This character is often used in distinguishing species but in my experience at least in some species, it is a character of minor importance, as the pigmentation of the cystidia appears to be very variable and may be present, or only partly present or lacking in one collection of the species.

2.3.2. PLEUROCYSTIDIA.—Pleurocystidia occur rarely and then always together with cheilocystidia, usually of about the same size and shape as the latter.

2.3.3. CAULOCYSTIDIA.—Caulocystidia are rare in the genus *Entoloma*. If present, then they are more or less cylindrical or clavate, rarely capitate.

## 2.4. *Subhymenium*.

The subhymenium is usually poorly developed and filamentous, made up of thin-walled, narrow hyphae. Sometimes, particularly in subgenus *Entoloma*, the hyphal walls are slightly gelatinized. A subcellular subhymenium is found in subgenus *Pouzaromyces*.

## 2.5. *Hymenophoral trama*.

In *Entoloma* the hymenophoral trama is regular. Kühner (1977: 450) suggested that the size and shape of the elements of the trama in lamellae and pileus form a useful character for the

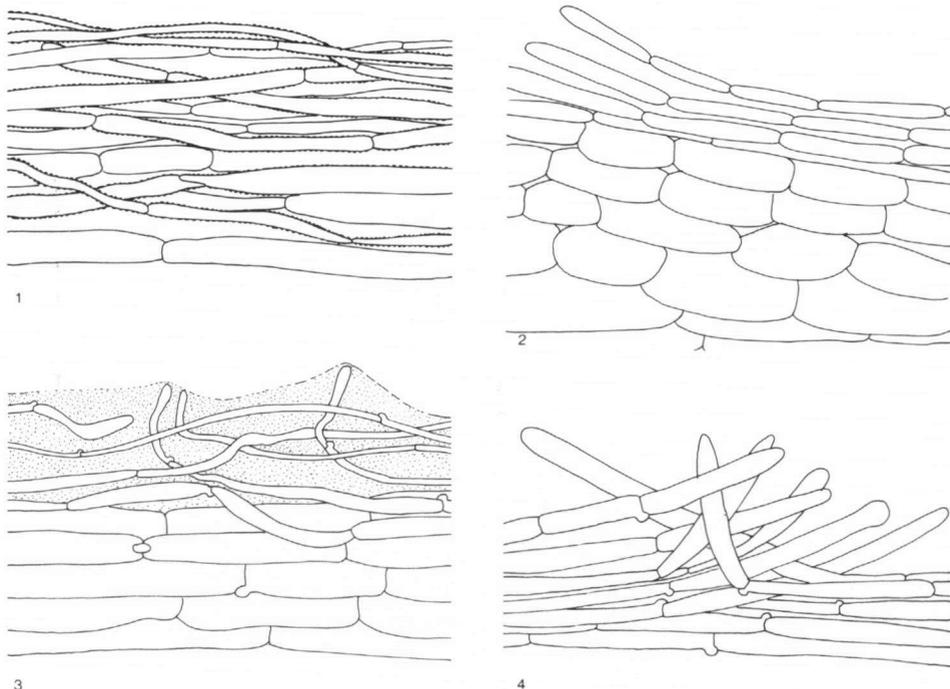
delineation of infrageneric taxa in *Entoloma*. I checked this for subgenera *Nolanea*, *Entoloma*, *Pouzaromyces*, *Allocybe* and *Trichopilus*, and the results indicate that this character has a great taxonomic value indeed.

In subgenus *Nolanea* the hymenophoral trama is made up of relatively long, cylindrical or fusoid cells (on the average 150–450  $\mu\text{m}$ ), whereas in subgenus *Entoloma* these cells are relatively short (mostly 50–150  $\mu\text{m}$ ) and usually slightly to distinctly inflated (like chains of sausages'. In subgenus *Pouzaromyces* the elements of the hymenophoral trama are generally narrowly cylindrical, not fusoid or inflated and general 100–300  $\mu\text{m}$  long. In subgenera *Trichopilus* and *Allocybe* I found the elements of hymenophoral trama more or less 'nolaneoid', viz. relatively long and cylindrical to fusoid. Particularly with regard to the delimitation of subgenus *Entoloma* against subgenera *Nolanea* and *Trichopilus* is this character a useful criterion.

### 2.6. *Pileipellis*.

The structure of the pileipellis is one of the major characters in *Entoloma* for the delimitation of infrageneric taxa. Together with the nature and topography of the pigments it forms the base of the classification of Romagnesi (1974b, 1978) and the present one.

Watling and Largent (1977) published a thorough analysis of the cortical layers of some families of the Agaricales, including the Entolomataceae, which is a very important contribution



Figs. 1–4. Types of pileipellis in *Entoloma*. — 1. Cutis, *E. papillatum*. — 2. Cutis with well-developed subpellis, *E. conferendum*. — 3. Ixocutis, *E. aprile*. — 4. Trichoderm, *E. fuscomarginatum* (all figs. 670  $\times$ ).

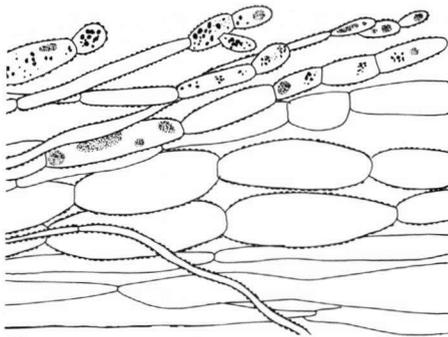
to the insight into the value of the structure of the pileipellis for taxonomy on infrageneric and generic level.

The most simple structure found in *Entoloma* is a dry cutis of radially arranged, narrowly cylindrical hyphae with a poorly developed subpellis, gradually passing into the pileitrama (Fig. 1). This simple type is found particularly in subgenus *Nolanea*. Differentiation occurs in several ways. First a distinct subpellis of inflated cells is developed (Fig. 2). In other species the situation at centre of the pileus is slightly different from that on the limb. There the terminal ends of the cuticular hyphae are ascending and form tufts. In section *Fernandae* the most complicated type of cutis is found within the subgenus *Nolanea*. There the suprapellis is made up of loosely arranged hyphae, which sometime form small semi-erect tufts with dark brown, coarsely encrusted walls and additional intracellular pigment clots (Fig. 5).

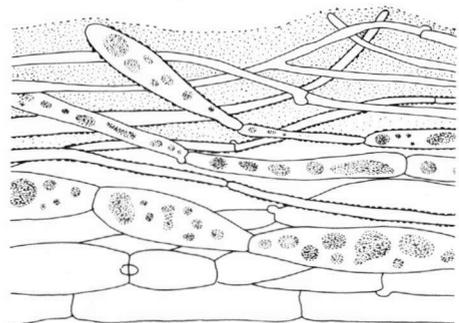
In subgenus *Entoloma*, particularly in section *Nolanidea*, the hyphal walls of the suprapellis desintegrate and form a gelatinuous layer (an ixocutis, Figs. 3 and 6).

A second type of pileipellis commonly found in the genus *Entoloma* is the trichodermium. This type of pileipellis probably originated from a cutis-like pileipellis of which the terminal elements have taken an ascending or erected position. This is the most common type of pileipellis found in subgenera *Trichopilus*, *Inocephalus* and section *Leptonia* (Fig. 4).

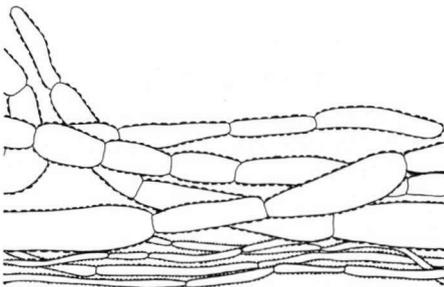
In *Pouzaromyces* the pileipellis is a cutis/trichoderm, made up of coarsely encrusted, thick-



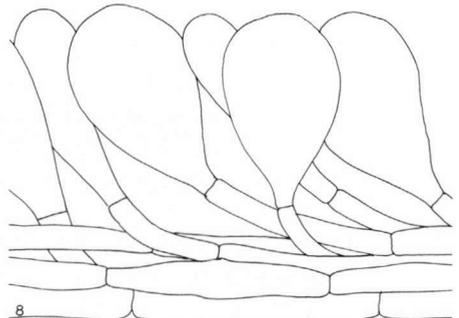
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8

Figs. 5-8. Types of pileipellis in *Entoloma*. — 5. Cutis with transitions to trichoderm, *E. fernandae*. — 6. Ixocutis, *E. myrmecophilum* var. *atrogaleatum*. — 7. Trichoderm, *E. dysthaloides*. — 8. Hymeniderm, *E. incanum* (all figs. 670  $\times$ ).

walled, multiseptate hairs (Fig. 7). In *E. strigosissimum* we find setiform hairs (Noordeloos, 1979: 213, fig. 6).

In subgenus *Leptonia* section *Paludocybe* and in some tropical species of subgenus *Entoloma* a hymeniform pileipellis is found, which is made up of (semi-)erect clavate or subglobose cells (Fig. 8). This type of pileipellis can be simple to fairly complicated (compare Watling & Largent, l.c.). Some tropical species of these subgenera have an epithelium of globose cells.

### 2.7. Pigmentation.

As I have pointed out above, the type and topography of the pigments is a very important character for the infrageneric classification of *Entoloma*.

Three basic types can be found:

1. Intracellular pigment.—Pigment present in plasma and/or vacuoles inside the hyphal elements. This pigment can be diffuse or present itself as smaller or larger granulae or clots, which sometimes agglutinate.
2. Membranal pigment.—Pigment present in the hyphal wall.
3. Encrusting.—Pigments present on the outer wall of the hyphal elements in the form of minute to rather large crust-like patches, which sometimes form distinct patterns (e.g. a 'zebra' pattern). This type of pigment is usually easy to recognise, even in dried specimens. In some cases the encrustations are very minute and inconspicuous and should be looked for carefully, particularly on the narrowest hyphae of pileipellis and pileitrama, and near the septa.

Combinations of different types of pigment frequently occur, particularly (1) and (2), or (1) and (3).

### 2.8. Pileitrama.

The pileitrama in *Entoloma* is regular, at least in the limb of the pileus, and in general made up of the same type of elements as found in the hymenophoral trama. At centre of the pileus the tissue can be more irregular or even pseudoparenchymatical, particularly in thick-fleshed specimens.

### 2.9. Stipitepellis.

In most species of *Entoloma* the stipitepellis is a simple cutis of narrow cylindrical hyphae; in species with a cartilagenous stipe the hyphae are tightly packed together; in species with an aeriferous, fibrillosely striate stipe surface the hyphae are loosely arranged. A trichoderm-like stipitepellis is found in subgenus *Pouzaromyces* (Noordeloos, 1979). Some species of *Entoloma* have a pruinose stipe which is caused by the more or less recurving ends of the surface hyphae. These terminal cells can be simply cylindrical (e.g. in *E. lanuginosipes* or *E. cuneatum*) or have a capitate tip (e.g. in *E. cuspidiferum*). Real caulocystidia are rare in the whole genus.

### 2.10. Clamp-connections.

The presence or absence of clamp-connections is a very important character in *Entoloma*, particularly when their distribution in the fruit-body is also taken into account. Many sections are characterised by the absence of clamp-connections in all tissues, whereas for example many species of subgenus *Nolanea* have clamp-connections only in the hymenium, and many species of *Entoloma* are rich in clamp-connections in all tissues. To establish the presence or absence of

clamp-connections in a species it is often necessary to stain thoroughly (a 10% ammoniac 1% Congo-red solution is recommended) because clamp-connections are often scarce and small and easily overlooked. When searching for clamp-connections in the hymenium one should be aware of the possibility of proliferation of the clamp-connections as is described by Bas (1965: 355 and 1969: 319) for *Amanita* and Maas Geesteranus (1978: 130) for *Mycena*. Clamp-connections have to be looked for preferably at the base of young basidia, as in many species of *Entoloma* (particularly in subgenus *Nolanea*) mature basidia have lost almost every trace of clamp-connections at their base, except for a slight nick in the basal septum.

#### GEOGRAPHICAL DISTRIBUTION

*Entoloma* has a world-wide distribution, but our knowledge on the geographical distribution of subgenera and sections is still far from complete. However, some conclusions can already be drawn. Subgenus *Entoloma*, although it is found to occur in tropical areas (Romagnesi & Gilles, 1979; Horak 1980), seems to have its main distribution in the temperate and cold regions. On the other hand, subgenus *Inocephalus* is restricted to (sub-)tropical areas. The subgenera *Nolanea*, *Pouzaromyces*, *Leptonia*, *Omphaliopsis*, and *Claudopus* are widely distributed in tropical as well as temperate and cold areas. Less distributional information is available on the smaller subgenera *Allocybe*, *Alboleptonia* and *Paraleptonia*, but at least some temperate as well as tropical species are known of each of them.

On the sectional level the picture is obscured by the fact that the information on many of the species described is so incomplete that it is impossible to determine to which section they belong. However, large sections, such as sections *Entoloma*, *Rhodopolia*, *Cosmeoexonema*, *Endochromonema*, *Pouzaromyces*, *Versatilia*, and *Trichopilus* have a (world-)wide distribution. Romagnesi (1978) described three sections in subgenus *Omphaliopsis* and one in subgenus *Alboleptonia* that seem to be restricted to tropical Africa.

#### RELATIONSHIPS

A schematic view on the relationships between the subgenera and sections of *Entoloma* is given in Fig. 9. The assumed affinities of the taxa is based on degrees of similarity in certain characters, in particular the habit of the carpophores, degree of hygrophanity of the pileus, pigmentation, structure of the hymenophoral trama and the pileitrama, and occurrence and distribution of clamp-connections in the carpophore. The following hypothetical lines of development have also played their part in making the scheme:

1. Habit collybioid or mycenoid → tricholomatoid, omphalioid or pleurotoid.
2. Pileus hygrophanous → not hygrophanous.
3. Pileipellis a cutis or ixocutis → trichoderm → hymeniderm.
4. Clamp-connections abundant in all tissues → clamp-connections only locally present (hymenium) → clamp-connections absent.

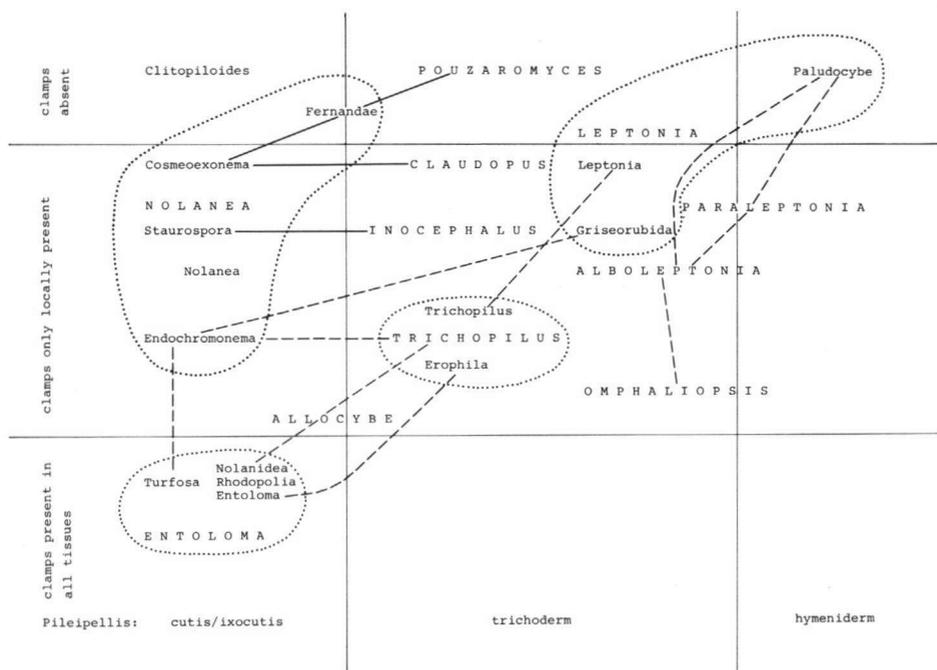


Fig. 9. Relationships between the subgenera and sections in *Entoloma*; continuous lines symbolize great affinities, broken lines indicate fairly great affinities. (Subgeneric names in capitals; sections of each of the larger subgenera surrounded by dotted lines).

Clear affinities are found between subgenus *Nolanea* and subgenus *Pouzaromyces* in the rather intermediate section *Fernandae* of subgenus *Nolanea* and between subgenus *Nolanea* and subgenus *Inocephalus* in section *Staurospora* of subgenus *Nolanea*.

*Claudopus* is considered a reduced series originating from nolaneoid species. *Omphaliopsis* and *Paraleptonia* seem to be sidelines of the *Leptonia*-complex which itself has similarities with subgenus *Nolanea*. The position of the subgenera *Allochybe* and *Trichopilus* is somewhat isolated; they bear some resemblances to subgenera *Entoloma* and *Nolanea* at one hand and to subgenus *Leptonia* at the other hand.

## TAXONOMIC PART

ENTOLOMA (Fr.) Kumm. *emend.* Donk<sup>1</sup>

*Agaricus* trib. *Entoloma* Fr., *Epicr.*: 143. 1838. — *Agaricus* subgen. *Entoloma* (Fr.) Rabenh., *Deutschl. KryptogFl.* 1: 508. 1844.—*Entoloma* (Fr.) Kumm, *Führ. Pilzk.*: 23. 1871.—Lectotype (Donk, 1962: 95): *Agaricus prunuloides* Fr.

*Nolanea* (Fr.) Kumm., *Führ. Pilzk.*: 24. 1871.—Lectotype (Largent, 1974: 1001): *Agaricus hirtipes* Schum. ex Fr.

*Leptonia* (Fr.) Kumm., *Führ. Pilzk.*: 24. 1871.—Lectotype (Clements & Shear, 1931: 349): *Agaricus euchrous* Pers. ex Fr.

*Eccilia* (Fr.) Kumm., *Führ. Pilzk.*: 23. 1871.—Lectotype (Donk, 1949: 158): *Agaricus politus* Pers. ex Fr.  
*Claudopus* Gill., *Hymen. Fr.*: 426. 1876.—Lectotype (Konrad, 1934: 177): *Agaricus byssisedus* Pers. ex Fr.  
*Rhodophyllus* Quél., *Enchir.*: 56. 1886.—Lectotype (Romagnesi, 1954: 36–37): *Agaricus prunuloides* Fr.  
*Latzinaea* O. Kuntze, *Rev. Gen. Pl.* 2: 857. 1891.—Lectotype (Donk, 1962: 157): *Agaricus pascuus* Pers. ex Fr.

*Leptoniella* Earle in *Bull. N. Y. bot. Gdn.* 5: 424. 1909.—Lectotype (Donk, 1962: 171): *Agaricus euchrous* Pers. ex Fr.

*Lanolea* Nieuwl. in *Amer. Midl. Nat.* 4: 381. 1916.—Lectotype (Donk, 1962: 157): *Agaricus pascuus* Pers. ex Fr.

*Pouzaromyces* Pilát in *Acta Mus. Nat. Prag. (B)* 9 (2): 60. 1953.—Holotype: *Nolanea fumosella* (Wint.) Lange sensu Pilát (= *Nolanea strigosissima* Rea).

*Alboleptonia* Largent & Benedict in *Mycologia* 62: 439. 1970.—Holotype: *A. sericella* (Fr.) Largent & Benedict.

*Pouzarella* Mazzer in *Biblta mycol.* 46: 69. 1978.—Holotype: *Pouzarella nodospora* (Atk.) Mazzer.

Habit variable: tricholomatoid, mycenoid, collybioid, clitocyboid, omphalioid or pleurotoid; lamellae almost free, adnexed to adnate, adnate-emarginate or adnate-decurrent; veil none or rarely present in the shape of traces of cortina at margin of pileus; spores with angular outline when seen from all sides, thin- to relatively thick-walled; spore print pink or pinkish brown; basidia 4-, rarely 2-spored; cheilocystidia present or absent; pleurocystidia rare and only occurring in combination with cheilocystidia; hymenophoral trama regular; subhymenium usually thin, filamentous, in some cases (subgen. *Pouzaromyces*) well differentiated and subcellular, rarely somewhat gelatinized (subgenus *Entoloma*); pileipellis varying from a simple cutis and then sometimes with a well-differentiated, subcellular subpellis, to a trichoderm of cylindrical or inflated hyphal tips or a trichoderm of well differentiated, attenuate, encrusted

<sup>1</sup> Singer & Smith (1948: 628–629) and Singer (1951: 25–26) added *Acurtis* Fr. to the synonyms of *Entoloma* because Singer said he had been able to prove the correctness of Burt's suggestion (1922: 68) that the genus *Acurtis* was based upon *Clavaria gigantea* which was considered identical with *Entoloma abortivum* (Berk. & Curt.) Donk.

Donk rejected this synonymy on the basis of Art. 59 of the Code of Botanical Nomenclature (1956-edition) and considered the name *Acurtis* as a nomen anamorphosum. Watling (1974: 449–469) studied the carpophoroid stages of *E. abortivum*, and discovered that these bodies are characterized by the presence of mycelium of *Armillaria mellea* and must therefore be considered a monstrosity. Furthermore he disputed the theory of Burt and Singer saying that *Clavaria gigantea* is a carpophoroid stage of *E. abortivum*, because *C. gigantea* is originally described as a large fungus of about the size of a man's head. This size is never reached by the carpophoroids of *E. abortivum*, but may easily be reached by parasitized fruit-bodies of *Tylopilus rubrobrunneus* Mazzer & Smith, a bolete described from the same geographical area as *C. gigantea*. Considering all this I agree in rejecting *Acurtis* as a valid generic name, and also as an older synonym of *Entoloma*.

hairs or hymeniform or epithelial; pigment encrusting and/or membranous and/or intracellular; pileitrama regular; vascular hyphae sometimes present; clamp-connections present or not; hyphae always inamyloid.

Development: usually gymnocarpous.

HABITAT & DISTRIBUTION.—Usually terrestrial, growing saprophytically in humus etc., rarely wood-inhabiting; some species mycorrhizal. Cosmopolitan as to the genus, but some groups seem to have definite geographic areas, e.g. subgenus *Inocephalus* occurs almost exclusively in tropical and subtropical areas, whereas subgenus *Entoloma* prefers temperate and cold areas.

#### KEY TO THE SUBGENERA AND SECTIONS IN EUROPE

- 1a. Pigment encrusting at least narrowest hyphae of pileipellis and/or underlying pileitrama, often in addition intracellular pigment present . . . . . 2
- b. Pigment never encrusting, predominantly intracellular, sometimes membranous or simultaneously intracellular and membranous . . . . . 9
- 2a. Clamp-connections absent from all tissues . . . . . 3
- b. Clamp-connections present, at least in hymenium . . . . . 5
- 3a. Pigment exclusively encrusting; pileus not hygrophanous; pileipellis a trichoderm made up of multiseptate-attenuate, thick-walled and/or coarsely encrusted hairs.
  - Subgen. *Pouzaromyces* sect. *Pouzaromyces*. . . . . 4
- b. Pigment of two types: encrusting and intracellular . . . . . 4
- 4a. Cheilocystidia present, usually large and lageniform; pileus slightly hygrophanous or not; pileipellis a trichoderm of large, fusiform hyphal ends. . . . . Subgen. *Pouzaromyces* sect. *Versatilia*.
- b. Cheilocystidia absent; pileus often distinctly hygrophanous; pileipellis a cutis of narrow, cylindrical hyphae or trichodermal, made up of chains of short, cylindrical or slightly inflated cells.
  - Subgen. *Nolanea* sect. *Fernandae*.
- 5a. Habit pleurotoid or omphalioid; pigment exclusively encrusting.
  - Subgen. *Claudopus* sect. *Claudopus*.
- b. Habit mycenoid or tricholomatoid, if omphalioid then pigment encrusting in pileitrama only and, in addition intracellular in pileipellis . . . . . 6
- 6a. Habit omphalioid; pigment predominantly intracellular; encrustations only found in upper pileitrama
  - Subgen. *Omphaliopsis* sect. *Omphaliopsis*.
- b. Habit mycenoid or tricholomatoid, encrusting pigments always distinct and predominant, sometimes in addition intracellular . . . . . 7
- 7a. Habit mycenoid or rarely tricholomatoid; hymenophoral trama and pileitrama made up of long, cylindrical or inflated-fusiform cells, on the average 150–450  $\mu\text{m}$  long; clamp-connections, if present, frequent in hymenium only, rare or lacking in trama and covering layers. . . . . Subgen. *Nolanea* p.p.
- b. Habit tricholomatoid, rarely dwarfish and more collybioid; hymenophoral trama and pileitrama made up of chains of short, inflated or cylindrical hyphae (like rows of sausages); clamp-connections numerous in all tissues. . . . . Subgen. *Entoloma* sect. *Rhodopolia*, p.p.
- 8a. Cylindrical-subcapitate cheilocystidia present; pigment of two types, encrusting and, particularly in subpellis of pileus, intracellular; spores always heterodiametrical. . . . . Subgen. *Nolanea* sect. *Nolanea*.
- b. Cheilocystidia absent, or if present, then pigment exclusively encrusting.
  - Subgen. *Nolanea* sect. *Cosmeoxonema*.
- 9a. Pileus smooth or slightly rugulose-fluffy at centre only and distinctly hygrophanous: on drying pallescent along radial streaks. . . . . 10
- b. Pileus fibrillose-rugulose or subsquamulose, more rarely smooth, but then never hygrophanous. 16
- 10a. Habit mycenoid or collybioid, hymenophoral trama made up of long, cylindrical or inflated-fusoid cells, 150–450  $\mu\text{m}$  long; clamp-connections, if present, frequent in hymenium but rare or absent in trama and covering layers . . . . . 11

- b. Habit tricholomatoid, collybioid or clitocyboid; hymenophoral trama and pileitrama made up of shortish, cylindrical or inflated cells, on the average 40–120  $\mu\text{m}$  long; clamp-connections, if present abundant in all tissues . . . . . 12
- 11a. Spores cuboid or cruciform-stellate . . . . . Subgen. *Nolanea* sect. *Staurospora*.
- b. Spores different, usually heterodiametrical. . . . . Subgen. *Nolanea* sect. *Endochromonema*.
- 12a. Vernal species often associated with Rosaceae; pileipellis an ixocutis.  
Subgen. *Entoloma* sect. *Nolanidea*, p.p.
- b. Occurring in summer or autumn; pileipellis usually a cutis, but sometimes more like an ixocutis. 13
- 13a. Spores small, 6–8  $\times$  5–7  $\mu\text{m}$ , rather thin-walled, subglobose and multi-angled in outline.  
Subgen. *Entoloma* sect. *Turfosa*.
- b. Spores usually distinctly larger and relatively thick-walled . . . . . 14
- 14a. Clamp-connections absent; carpophores clitocyboid, pileus convex with depressed to subumbilicate centre, coarsely radially fibrillose; stipe short, striate . . . Subgen. *Entoloma* sect. *Clitopiloides*.
- b. Clamp-connections present. . . . . 15
- 15a. Carpophores collybioid or even omphalioid; pileus often with depressed centre; stipe smooth, as if polished, never striate. . . . . Subgen. *Entoloma* sect. *Polita*.
- b. Carpophores tricholomatoid, rarely collybioid; pileus usually distinctly convex-umbonate when mature, rarely with depressed centre; stipe always fibrillose-striate lengthwise.  
Subgen. *Entoloma* sect. *Rhodopolia*, p.p.
- 16a. Habit tricholomatoid; pileus smooth, opaque, sometimes with micaceous patches. . . . . 17
- b. With other characters; if habit tricholomatoid, then pileal surface always strongly radially fibrillose to subsquamulose and large capitate cheilocystidia present. . . . . 19
- 17a. Vernal species, often associated with Rosaceae or *Ulmus*; pileipellis always an ixocutis with distinctly gelatinized layer; cheilocystidia always absent. . . . . Subgen. *Entoloma* sect. *Nolanidea* p.p.
- b. Fruiting in late summer or autumn; pileipellis a dry cutis or an ixocutis. . . . . 18
- 18a. Pileus white or pale leather brown, with membranous, rarely minutely encrusting pigment; intracellular pigment always absent; large lageniform cheilocystidia present. . . . . Subgen. *Allocybe*.
- b. Pileus white or coloured and then always with intracellular pigment; cheilocystidia always absent  
Subgen. *Entoloma* sect. *Entoloma*.
- 19a. Habit strongly reminiscent of that of a species of *Inocybe*; pileus conical, only slightly expanding, radially fibrillose to squamulose; pileipellis a trichoderm of long hyphal ends; clamp-connections usually present; spores often cuboid. . . . . Subgen. *Inocephalus*.
- b. With another combination of characters . . . . . 20
- 20a. Habit pleurotoid or omphalioid; clamp-connections present. . . . . 21
- b. Habit tricholomatoid, mycenoid or collybioid, if omphalioid, then clamp-connections lacking 22
- 21a. Pileus white or yellowish, pale pink, or brown, and spores with basal facet. . Subgen. *Paraleptonia*.
- b. Pileus brown or grey-brown; spores with dihedral base. . . . . Subgen. *Omphaliopsis*, p.p.
- 22a. Habit tricholomatoid, rarely mycenoid; cheilocystidia present, lageniform, often (sub-)capitate; clamp-connections present, rarely absent. . . . . Subgen. *Trichopilus* sect. *Trichopilus*.
- b. Differently characterized . . . . . 23
- 23a. Clamp-connections absent from all tissues; habit collybioid or omphalioid; pileus with flattened, depressed or umbilicate centre, exceptionally with small papilla. Subgen. *Leptonia* sect. *Paludocybe*.
- b. Clamp-connections present; habit tricholomatoid or collybioid, more rarely mycenoid. . . . . 24
- 24a. Carpophores collybioid, pale, usually white, pinkish or with slight brown or grey tinge at centre of pileus, . . . . . Subgen. *Alboleptonia*.
- b. Carpophores always distinctly coloured, usually brownish-greyish or purplish-bluish . . . . . 25
- 25a. Habit tricholomatoid; pileus minutely radially fibrillose, grey or grey-brown, never with blue tinges  
Subgen. *Trichopilus* sect. *Erophila*.
- b. Habit different or parts of carpophores with bluish-purplish tinge . . . . . 26
- 26a. Pileus usually truncate-campanulate or conico-convex with depressed to umbilicate centre, brownish or greyish; cheilocystidia long, fusiform or subcylindrical, protruding from the hymenium.  
Subgen. *Leptonia* sect. *Griseorubida*.

- b. Pileus usually conico-convex to convex with weak to pronounced umbo, rarely subdepressed at centre, but then entire carpophores violaceous blue; cheilocystidia, if present more or less clavate and their length not much exceeding that of basidia. . . . . Subgen. *Leptonia* sect. *Leptonia*.

## SYNOPSIS OF THE SUBGENERA AND SECTIONS OF ENTOLOMA IN EUROPE

### 1. ENTOLOMA subgenus ENTOLOMA

*Agaricus* trib. *Entoloma* Fr., Epicr.: 143. 1838. — *Agaricus* subgen. *Entoloma* (Fr.) Rabenh., Deutschl. KryptogFl. 1: 508. 1844. — *Entoloma* (Fr.) Kumm., Führ. Pilzk.: 23. 1871. — *Rhodophyllus* subgen. *Entoloma* (Fr.) Quél., Enchir.: 57. 1886. — *Hyporrhodius* subgen. *Entoloma* (Fr.) Schroet. in Cohn, KryptogFl. Schles. 3 (1): 616. 1889. — Lectotype (Donk, 1962: 95): *Agaricus prunuloides* Fr.

*Agaricus* trib. *Eccilia* Fr., Syst. mycol. 1: 10. 1821. — *Agaricus* subgen. *Eccilia* (Fr.) Loud., Encycl. Pl.: 998. 1829. — *Eccilia* (Fr.) Kumm., Führ. Pilzk.: 23. 1871. — *Rhodophyllus* subgen. *Eccilia* (Fr.) Quél., Enchir.: 62. 1886. — *Hyporrhodius* subgen. *Eccilia* (Fr.) Schroet. in Cohn, KryptogFl. Schles. 3 (1): 613. 1889. — Lectotype (Donk, 1949: 158): *Agaricus politus* Pers. ex Fr.

*Rhodophyllus* subgen. *Romagnesia* Singer in Anns mycol. 41: 13. 1943. — Holotype: *R. clypeatus* (L. ex Fr.) Quél.

Carpophores usually tricholomatoid, rarely collybioid or clitocyboid, mycenoid or omphalioid; pileus usually conico-convex then flattened with or without broad umbo, rarely entirely flattened, cup-shaped or with central depression, hygrophanous or not, smooth or radially fibrillose, never fibrillose-squamulose; lamellae usually deeply emarginate or adnate, rarely adnate-subdecurrent; stipe usually aeriferously-fibrillosely striate lengthwise, rarely smooth as if polished; spores often more or less isodiametrical, with basal facet or blunt dihedral base; pileipellis a cutis or ixocutis made up of cylindrical hyphae, sometimes with ascending, clavate terminal cells. Pigment usually intracellular, rarely membranous or encrusting. Hymenophoral trama and pileitr trama regular, made up of chains of relatively short (on the average 40–150  $\mu\text{m}$  long) cylindrical or inflated cells; clamp-connections usually abundant in all parts of the carpophore.

#### 1.1. Section ENTOLOMA

*Agaricus* sect. *Genuini* Fr., Epicr.: 143. 1838. — *Entoloma* sect. *Genuini* (Fr.) Quél. in Mém. Soc. Emul. Montbéliard ser. II, 5: 116. 1872. — *Rhodophyllus* sect. *Genuini* (Fr.) Quél., Enchir.: 57. 1886. — Lectotype (Donk, 1962: 95): *Agaricus prunuloides* Fr.

*Rhodophyllus* sect. *Nitidi* Romagn. in Bull. Soc. mycol. Fr. 53: 326. 1937 (nom. nud., no Latin diagn.). — Lectotype (Singer, 1951: 623): *R. nitidus* (Quél.) Quél.

*Rhodophyllus* sect. *Viscosi* Romagn. in Bull. Soc. mycol. Fr. 53: 325. 1937 (nom. nud., no Latin diagn.). — Lectotype (design. mihi): *R. lividus* (Bull. ex St.-Am.) Quél.

*Rhodophyllus* sect. *Madidi* Romagn. in Bull. mens. Soc. linn. Lyon 43: 332. 1974. — Holotype: *R. madidus* (Fr.) Quél.

Carpophores tricholomatoid, usually fairly robust; pileus not hygrophanous, not striate, whitish, greyish, brownish, blue or greenish; pileipellis a cutis passing into an ixocutis with or without intracellular pigment; fruiting in late summer and autumn.

**SPECIES.**—*Entoloma prunuloides* (Fr.) Quél.; *E. lividum* (Bull. ex St.-Am.) Quél.; *E. sinatum* (Bull. ex Fr.) Kumm.; *E. madidum* (Fr.) Quél.; *E. nitidum* (Quél.) Quél.; *E. viridans* (Fr.) P. Karst.; *E. inocybiforme* Bon

### 1.2. Section **NOLANIDEA** (Fr.) Quél.

*Agaricus* subtribus *Nolanidei* Fr., Epicr.: 146. 1838. — *Entoloma* sect. *Nolanides* (Fr.) Quél. in Mém. Soc. Emul. Montbéliard, sér. II, 5: 118. 1872. — *Rhodophyllus* sect. *Nolanidei* (Fr.) Quél., Enchir.: 59. 1886. — Lectotype (Singer 1951: 622): *Agaricus clypeatus* L. ex Fr.

*Rhodophyllus* sect. *Clypeati* Romagn. in Bull. Soc. mycol. Fr. 53: 326. 1937. — Lectotype (Singer, 1951: 622): *R. clypeatus* (L. ex Fr.) Quél.

*Rhodophyllus* sect. *Apriles* Kühn. & Romagn., Fl. anal.: 196. 1953 (nom. nud.). — *Rhodophyllus* sect. *Apriles* Kühn. & Romagn. ex Romagn. in Bull. mens. Soc. linn. Lyon 43: 332. 1974. — Holotype: *R. clypeatus* (L. ex Fr.) Quél.

*Rhodophyllus* subgen. *Romagnesia* Sing. in Annlis mycol. 41: 13. 1943. — Holotype: *R. clypeatus* (L. ex Fr.) Quél.

**EXCLUDED NAMES.**—*Rhodophyllus* sect. *Nolanidei* sensu Romagn. in Bull. mens. Soc. linn. Lyon 43: 332. 1974. — Lectotype (Romagn., 1974b: 332): *R. nidorosus* (Fr.) Quél. (= *Entoloma* sect. *Rhodopolia* sensu mihi).

*Entoloma* sect. *Nolanidei* sensu Largent in Mycologia 66: 999. 1974. — Lectotype (Largent, 1974: 999): *E. rhodopolium* (Fr.) Kumm. (= *Entoloma* sect. *Rhodopolia* sensu mihi).

Habit tricholomatoid, fleshy; pileus white, pale greyish, yellowish or brownish to dark brown or sepiceous with grey or olivaceous tinge, hygrophanous or not; lamellae adnate-emarginate, rarely with decurrent tooth; stipe usually firm and fleshy, white to grey or grey-brown; smell and taste farinaceous; pileipellis an ixocutis of narrow cylindrical hyphae with gelatinized walls and pigment intracellular when present; strictly vernal, often associated with Rosaceae or *Ulmus*.

**SPECIES.**—*Entoloma clypeatum* (L. ex Fr.) Kumm. and varieties; *E. aprile* (Britz.) Sacc.; *E. niphoides* (Romagn.) P. D. Orton; *E. saundersii* (Fr.) Sacc.; *E. sepium* (Noul. & Dass.) Richon & Roze.

In the present revision *E. clypeatum* is considered the lectotype of sect. *Nolanidea* following Singer (1951: 622). From Fries' publications it is obvious that he considered this species as very typical for the section. In 1849 (: 287) Fries called the concerning group 'stirps *A. clypeati*'. Therefore the choice of *Agaricus nidorosus* by Romagnesi (1974b: 332) and *A. rhodopolium*, chosen by Largent (1974: 999) are rejected as lectotypes. As a consequence of this 'section *Nolanidei*' sensu Romagnesi, Largent is to be now called section *Rhodopolia* (see below).

### 1.3. **Entoloma** section **Rhodopolia** (Fr.) Noordeloos, *comb. nov.*

*Agaricus* subtribus *Rhodopolii* Fr., Syst. mycol. 1: 195. 1821 (basionym). — *Rhodophyllus* sect. *Rhodopolii* (Fr.) Romagn. in Bull. Soc. mycol. Fr. 63: 120. 1947. — Lectotype (design. mihi): *Agaricus rhodopolium* Fr.

*Rhodophyllus* subsect. *Nidorosi* Romagn. in Bull. Soc. mycol. Fr. 53: 327. 1937. — Lectotype (design. mihi): *R. nidorosus* (Fr.) Quél.

*Rhodophyllus* sect. *Specularii* Romagn., Rhodoph. Madag.: 42. 1941. — Lectotype (Singer, 1951: 622): *R. speculum* (Fr.) Quél.

*Entoloma* sect. *Typodochroa* Largent in *Mycologia* **66**: 999. 1974. — Holotype: *E. platyphylloides* (Romagn.) Largent.

MISAPPLIED NAMES.—*Rhodophyllus* sect. *Nolanidei* sensu Romagn. in *Bull. mens. Soc. linn. Lyon* **43**: 332. 1974. — Lectotype (Romagn. 1974b: 322): *R. nidorosus* (Fr.) Quél.

*Entoloma* sect. *Nolanidea* sensu Largent in *Mycologia* **66**: 999. 1974. — Lectotype (Largent, 1974: 999): *E. rhodopolium* (Fr.) Quél.

Habit tricholomatoid, sometimes slender and almost mycenoid; pileus white, yellow, brown or grey, usually strongly hygrophanous; stipe always fibrillose-striate lengthwise; pigment intracellular or encrusting or both; summer-autumn.

SPECIES.—*Entoloma rhodopolium* (Fr.) Kumm., *E. nidorosum* (Fr.) Quél.; *E. lividoalbum* (Kühn. & Romagn.) Kubička; *E. speculum* (Fr.) Quél.; *E. leucocarpum* Noordeloos; *E. subradiatum* (Kühn. & Romagn.) Moser; *E. sphagneti* Naveau; *E. alpicolum* (Favre) Noordeloos; *E. brassicolens* (Reid) Noordeloos; *E. gerriæ* Noordeloos; *E. atrosericeum* (Kühn.) Noordeloos; *E. venosum* Gill.; *E. myrmecophilum* (Romagn.) Moser with var. *atrogaleatum* Noordeloos; *E. majaloides* P. D. Orton; *E. sericatum* (Britz.) Sacc. with f. *salicophilum* Noordeloos; *E. sordidulum* (Kühn. & Romagn.) P. D. Orton.

#### 1.4. *Entoloma* section *Polita* (Romagn.) ex Noordeloos, *sect. nov.*

*Rhodophyllus* subsect. *Politi* Romagn. in *Bull. Soc. mycol. Fr.* **53**: 327. 1937 (nom. nud., no Latin diagnosis). — *Rhodophyllus* sect. *Politi* (Romagn.) Sing. in *Annls mycol.* **41**: 13. 1943. — Lectotype (Singer, 1951: 617). — *R. politus* (Pers. ex Fr.) Quél.

*Agaricus* subtribus *Eccilia* Fr., *Syst. mycol.* **1**, 10. 1821 — *Agaricus* subgen. *Eccilia* (Fr.) Loud., *Encyl. Pl.* **998**. 1829. — *Rhodophyllus* subgen. *Eccilia* (Fr.) Quél. *Enchir.*: 62. 1886. — *Eccilia* (Fr.) Kumm., *Führ. Pilzk.* **23**: 1871. — Lectotype (Donk 1949: 158): *Agaricus politus* Pers. ex Fr.

Statura omphaloidea vel collybioidea; pileus depressus vel umbilicatus, raro papillatus; lamellae adnatae vel uncinatae vel decurrentes; stipes glaber, politus; pileus pigmentis intracellulosis praeditus, fibulae abundantes.—Typus: *Agaricus politus* Pers. ex Fr.

Habit omphalioid or collybioid; pileus with depressed or umbilicate rarely papillate centre; lamellae adnate or uncinatae or decurrent; stipe smooth as if polished, pigments intracellular; clamp-connections abundant in all tissues.—Type: *Agaricus politus* Pers. ex Fr.

SPECIES.—*Entoloma politum* (Pers. ex Fr.) Donk with f. *pernitrosus* P. D. Orton; *E. caccabus* (Kühn.) Noordeloos; *E. bisporigerum* (P. D. Orton) Noordeloos; *E. anthracinum* (Favre) Noordeloos; *E. subflexipes* (Kühn.) Noordeloos.

Donk (1949: 158 and 1962: 92–93) argued the choice of *E. politum* as lectotype for *Agaricus* subtr. *Eccilia* so convincingly that his advice is followed here. As a consequence of this, *Eccilia* becomes a synonym of *Entoloma* sect. *Polita*, as the type species, *E. politum*, belongs to subgenus *Entoloma* according to Kühner & Romagnesi and myself. I could have given a new status, viz. that of section, to *Eccilia*, but I prefer the sectional name *Polita* for the following reason: *Eccilia* has been applied in the past for all species of *Entoloma* with a more or less omphalioid appearance viz. with a depressed to umbilicate pileus and decurrent lamellae, thus uniting species that, according to modern mycologists belong to several subgenera. Actually *Eccilia* served as a form genus. Therefore the use of the name *Eccilia* for the present section would create confusion.

### 1.5. *Entoloma* section *Clitopiloides* (Romagn.) Noordeloos, *comb. nov.*

*Rhodophyllus* sect. *Clitopiloides* Romagn. in Beih. Nova Hedwigia 59: 55. 1978 (basionym). — Holotype: *R. cyathus* Romagn. & Gilles.

Habit clitocyboid; pileus depressed, dark brown; lamellae broadly adnate to subdecurrent; stipe fibrillose striate lengthwise; spores subspherical (or cuboid in extralimital taxa); pigment intracellular; clamp-connections absent.

SPECIES.—*Entoloma costatum* (Fr.) Kumm.

### 1.6. Section *Turfosa* (Romagn.) Noordeloos

*Rhodophyllus* sect. *Turfosi* Romagn. in Bull. mens. Soc. linn. Lyon 43: 332. 1974. — *Entoloma* sect. *Turfosa* (Romagn.) Noordeloos in Persoonia 10: 529. 1979. — Holotype: *Entoloma turbidum* (Fr.) Quél.

Habit tricholomatoid or collybioid; pileus distinctly hygrophanous, smooth, grey-brown or yellowish brown; lamellae often with grey or brown tinge; spores small, 6–8(–9)  $\mu\text{m}$  long, rounded- and multi-angled in side-view, subspherical to slightly oblong in outline, very thin-walled, slightly cyanophilous; pileipellis a cutis or ixocutis made up of narrow cylindrical hyphae with intracellular pigment; clamp-connections numerous in all tissues.

SPECIES.—*Entoloma turbidum* (Fr.) Quél. with var. *pachylamellatum* Noordeloos; *E. vinaceum* (Scop. ex Fr.) Arnolds & Noordeloos with var. *violeipes* Arnolds & Noordeloos and var. *fumosipes* Arnolds & Noordeloos; *E. pseudoturbidum* (Romagn.) Moser.

The small, multi-angled and thin-walled spores are unique in the genus *Entoloma*. The section is placed in subgenus *Entoloma* on account of the size and shape of the tramal hyphae, the structure of the pileipellis, the pigmentation, and the abundant clamp-connections in all tissues which are quite typical for the subgenus. *Entoloma vinaceum* was formerly placed in subgenus *Nolanea* by several authors, on account of its slender habit, which however is more collybioid than mycenoid, but the characters mentioned above render *E. vinaceum* a typical member of subgenus *Entoloma*.

## 2. ENTOLOMA subgenus NOLANEA (Fr.) Noordeloos

*Agaricus* tribus *Nolanea* Fr., Syst. mycol. 1: 10. 1821. — *Agaricus* subgen. *Nolanea* (Fr.) Loud., Encycl. Pl.: 998. 1829. — *Nolanea* (Fr.) Kumm., Führ. Pilzk.: 24. 1871. — *Rhodophyllus* subgen. *Nolanea* (Fr.) Quél., Enchir.: 62. 1886. — *Hyporrhodius* subgen. *Nolanea* (Fr.) Schroet. in Cohn. KryptogFl. Schles. 3 (1): 612. 1889. — *Entoloma* subgen. *Nolanea* (Fr.) Noordeloos in Persoonia 10: 431. 1979. — Lectope (Largent, 1974: 1001): *Agaricus hirtipes* Schum. ex Fr.

Habit mycenoid, rarely slenderly tricholomatoid or omphalioid; pileus conical to conico-campanulate, then expanding, usually with papilla, rarely depressed at centre; hygrophanous;

mostly translucently striate when moist, smooth or slightly fluffy-rugulose at centre; lamellae almost free or narrowly adnate or emarginate, rarely with decurrent tooth; stipe slender, often more or less cartilaginous; spores variable in shape, (sub-)isodiametrical to heterodiametrical or cuboid or cruciform; cystidia present or not; pileipellis a cutis, often with a tendency to become a trichoderm at centre of pileus because of ascending hyphal endcells; pigment intracellular or membranous or encrusting or in combinations of two of these types; hymenophoral trama and pileitrama made up of relatively long, cylindrical to fusoid cells, mostly between 150–450  $\mu\text{m}$  long; clamp-connections, if present, abundant in hymenium, but elsewhere rare or entirely lacking.

*Agaricus pascuus* Pers. ex Fr. has long been considered the type-species of *Nolanea* (see Donk, 1962: 201–202). I reject this lectotype, as the name *Agaricus pascuus* has been variously interpreted, and must be considered a collective name, comprising at least three different grass-inhabiting species of *Nolanea*, including *E. conferendum* (= *E. staurosporum*), *E. vernum* and *E. sericeum* which belong in my opinion to different sections of *Nolanea*. *Agaricus pascuus* has therefore been dealt with as a nomen dubium in a previous paper (Noordeloos, 1979: 527). As a consequence the lectotypification of *Nolanea* by Largent (1974, l.c.) with *Agaricus hirtipes* Schum. ex Fr. has been followed. This is a well-known, wide-spread species, which has been included by Fries in tribus *Nolanea* (Fries, 1821: 206).

## 2.1. Section N O L A N E A

*Rhodophyllus* subsect. *Mammosi* Romagn. in Bull. Soc. mycol. Fr. 53: 331. 1937. — *Rhodophyllus* sect. *Mammosi* (Romagn. ex) Romagn. in Bull. mens. Soc. linn. Lyon 43: 331. 1974. — Holotype: *R. mammosus* (L. ex Fr.) Quél.

Pigment encrusting hyphae of pileipellis and pileitrama, in addition intracellular in subpellis; cheilocystidia present, subcylindrical, often subcapitate; spores heterodiametrical with basal facet; clamp-connections present in hymenium.

SPECIES.—*Entoloma hirtipes* (Schum. ex Fr.) Moser with var. *sericoides* (Kühn.) Noordeloos; *E. leptopus* Noordeloos.

## 2.2. Section S T A U R O S P O R A (Largent & Thiers) Noordeloos

*Nolanea* sect. *Staurospori* Largent & Thiers in Northwest Sci. 46: 37. 1972. — *Rhodophyllus* sect. *Staurospori* (Largent & Thiers) Romagn. in Bull. mens. Soc. linn. Lyon 43: 330. 1974. — *Entoloma* sect. *Staurospora* (Largent & Thiers) Noordeloos in Persoonia 10: 445. 1979. — Holotype: *Nolanea staurospora* Bres. (= *E. conferendum* (Britz.) Noordeloos).

*Rhodophyllus* subsect. *Staurospori* Romagn. in Bull. Soc. mycol. Fr. 53: 331. 1948 (nom. nud., no latin diagnosis). — Lectotype (design. mihi): *R. staurosporus* (Bres.) J. Lange.

*Rhodophyllus* subsect. *Solstitiales* Romagn. in Bull. Soc. mycol. Fr. 53: 333. 1937 (nom. nud., no latin diagnosis). — Lectotype (Singer 1951: 619): *R. solstitialis* sensu Ricken, Romagn. 1937 (= *E. rhombisporum* (Kühn. & Bours.) Horak).

Spores cuboid or prismatical (cruciform-stellate); pigment membranous, encrusting and/or intracellular.

**SPECIES.**—*Entoloma conferendum* (Britz.) Noordeloos (= *Nolanea staurospora* Bres.) and var. *pusillum* (Velen.) Noordeloos; *E. rhombisporum* (Kühn. & Bours.) Horak; *E. prismatospermum* (Romagn.) Noordeloos; *E. inodorum* (Velen.) Noordeloos.

### 2.3. *Entoloma* section *Cosmeoexonema* (Largent & Thiers) Noordeloos, *comb. nov.*<sup>2</sup>

*Nolanea* sect. *Cosmeoexonema* Largent & Thiers in Northwest Sci 46: 35. 1972. — *Rhodophyllus* sect. *Cosmeoexonema* (Largent & Thiers) Romagnesi in Bull. mens. Soc. linn. Lyon 43: 331. 1974. — Holotype: *E. sericeum* (Bull. ex Mérat) Quéf.

*Rhodophyllus* sect. *Papillati* Romagn. in Bull. mens. Soc. linn. Lyon 43: 330. 1974. — *Entoloma* sect. *Papillata* (Romagn.) Noordeloos in Persoonia 10: 246. 1979. — Holotype: *E. papillatum* (Bres.) Dennis.

*Rhodophyllus* sect. *Minuti* Romagn. in Bull. mens. Soc. linn. Lyon 43: 330. 1974. — Holotype: *E. minutum* (P. A. Karst.) Noordeloos.

*Nolanea* subsect. *Fibulatae* Largent in Mycologia 66: 1008. 1974. — Holotype: *Nolanea juncea* (Fr.) Quéf.

*Rhodophyllus* sect. *Sphaerospori* Romagn. in Bull. Soc. mycol. Fr. 53: 331. 1937 (nom. nud., no Latin diagnosis). — Lectotype: (Singer, 1951: 621): *E. sericeum* (Bull. ex Mérat) Quéf.

Pigment encrusting at least the narrowest hyphae of pileipellis and pileitrama, sometimes with intracellular pigment in addition, but this never dominant; clamp-connections present; spores iso- to heterodiametrical, never cuboid or prismatical; cystidia usually absent.

**SPECIES.**—*Entoloma papillatum* (Bres.) Dennis; *E. clandestinum* (Fr.) Noordeloos; *E. lucidum* (P. D. Orton) Moser; *E. sericeonitens* (P. D. Orton) Noordeloos; *E. ortonii* Arnolds & Noordeloos; *E. cuspidiferum* (Kühn. & Romagn.) Noordeloos; *E. juncinum* (Kühn. & Romagn.) Noordeloos; *E. nitens* (Velen.) Noordeloos; *E. minutum* (P. A. Karst.) Noordeloos with var. *polymorphum* (Romagn.) Noordeloos; *E. tenellum* (Favre) Noordeloos; *E. tibiiocystidium* Arnolds & Noordeloos; *E. ameides* (Berk. & Br.) Sacc.; *E. sacchariolens* (Romagn.) Noordeloos; *E. vernum* Lundell; *E. sericeum* (Bull. ex Mérat) Quéf. with var. *cinereo-opacum* Noordeloos and f. *nolaniforme* (Kühn. & Romagn.) Noordeloos; *E. sericeoides* (J. Lange) Noordeloos; *E. sphaerocystis* Noordeloos.

### 2.4. Section *Fernandae* Noordeloos

*Entoloma* sect. *Fernandae* Noordeloos in Persoonia 10: 486. 1979. — Holotype: *E. fernandae* (Romagn.) Noordeloos.

Two types of pigment present: one encrusting the walls of most hyphae in pileipellis and upper pileitrama, another intracellular and forming, sometimes agglutinated, granules or clots; spores 5–6–7-angled, with distinct dihedral base; clamp-connections absent.

**SPECIES.**—*Entoloma fernandae* with f. *eccilioides*; *E. acidophilum* Arnolds & Noordeloos; *E. argenteostriatum* Arnolds & Noordeloos; *E. defibulatum* Arnolds & Noordeloos; *E.*

<sup>2</sup> The sectional name *Cosmeoexonema* is older than the sectional name *Papillata*, used by me earlier (1979: 246), and has therefore priority, see Noordeloos, 1981b: 257.

*xanthocaulon* Arnolds & Noordeloos; *E. cuniculorum* Arnolds & Noordeloos; *E. fractum* (Velen.) Noordeloos; *E. psilopus* Arnolds & Noordeloos; *E. pseudotelamonina* Noordeloos.

### 2.5. Section ENDOCHROMONEMA (Largent & Thiers) Noordeloos

*Nolanea* sect. *Endochromonema* Largent & Thiers in Northwest Sci 46: 36. 1972. — *Rhodophyllus* sect. *Endochromonema* (Largent & Thiers) Romagn. in Bull. mens. Soc. linn. Lyon 43: 331. 1974. — *Entoloma* sect. *Endochromonema* (Largent & Thiers) Noordeloos in Persoonia 10: 246. 1979. — Holotype: *E. cetratum* (Fr.) Moser.

Pigment intracellular, sometimes membranous or both; spores heterodiametrical with dihedral base; cheilocystidia present or not; clamp-connections usually present.

SPECIES.—*Entoloma cetratum* (Fr.) Moser; *E. farinogustus* Arnolds & Noordeloos; *E. cuneatum* (Bres.) Moser; *E. lanuginosipes* Noordeloos; *E. occultopigmentatum* Arnolds & Noordeloos; *E. calthionis* Arnolds & Noordeloos; *E. ventricosum* Arnolds & Noordeloos; *E. infula* (Fr.) Noordeloos; *E. solstitiale* (Fr.) Noordeloos; *E. chlorinosum* Arnolds & Noordeloos; *E. verecundum* (Fr.) Noordeloos; *E. triste* (Velen.) Noordeloos; *E. undulatosporum* Arnolds & Noordeloos; *E. velenovskyi* Noordeloos with var. *longicystidium* Arnolds & Noordeloos; *E. cryptocystidium* Arnolds & Noordeloos; *E. inutile* (Britz.) Noordeloos; *E. globuliferum* Noordeloos; *E. icterinum* (Fr.) Moser; *E. chlorophyllum* Noordeloos; *E. ambrosium* (Quél.) Noordeloos; *E. pallescens* (P. A. Karst.) Noordeloos; *E. foetulentum* Noordeloos; *E. robiniae* (Velen.) Noordeloos.

### 3. ENTOLOMA subgenus POUZAROMYCES (Pilát) Moser ex Noordeloos<sup>3</sup>

*Rhodophyllus* 'subgenus' *Inopilus* Romagn. in Bull. mens. Soc. linn. Lyon 43: 329. 1974 (illegitimate name, no rank indicated, see also under subgen. *Inocephalus*, below). — Holotype: *R. versatilis* (Fr.) Quél.

*Pouzaromyces* Pilát in Acta Mus. nat. Prag. (B) 9 (2): 60. 1953. — *Entoloma* subgen. *Pouzaromyces* (Pilát) Moser in Gams, Kl. KryptogFl., 4. Aufl., 2 (b/2): 191. 1978. (not valid, no basionym cited); ex Noordeloos in Persoonia 10: 209. 1979. — Holotype: *Nolanea fumosella* (Wint.) Lange sensu Pilát = *Entoloma strigosissimum* (Rea) Noordeloos.

*Pouzarella* Mazzer in Bibliotheca mycol. 46: 69. 1976. — Holotype: *P. nodospora* (Atk.) Mazzer.

Habit mycenoid, or reminiscent of that of a species of *Inocybe*; pileus conical or campanulate, only slowly expanding, not hygrophanous, translucently striate at margin or not, with metallic sheen, strongly radially fibrillose, fibrillose-hairy or fibrillose-squamulose; lamellae adnate, emarginate or almost free, but then often with distinct decurrent tooth, usually very dark grey-brown; stipe filiform to cylindrical, concolorous with pileus or slightly paler, with fibrillose or arachnoid covering; spores angular or gibbose, often large, 9–20  $\mu\text{m}$  long, ellipsoid to elongate in

<sup>3</sup> In my paper on *Pouzaromyces* (1979: 209) I overlooked that this combination, introduced by Moser, had not been validly published and I unintentionally validated it by citing its basionym and references.

outline, fairly thick-walled; basidia 4-spored, large, when dry frequently with dark brown intracellular pigment; cheilocystidia usually present<sup>4</sup>; hymenophoral trama regular with well-developed subcellular hymenopodium; pileipellis more or less trichodermal; pigment abundant, encrusting in trama and covering layers, sometimes intracellular in addition.

### 3.1. Section POUZAROMYCES

*Rhodophyllus* section *Luctuarii* Romagn. in Bull. mens. Soc. linn. Lyon 43: 330. 1974. Holotype: *R. babingtonii* sensu Kühn. & Romagn. = *E. strigosissimum* (Rea) Noordeloos.

*Pouzarella* section *Pouzarella*.

*Pouzarella* section *Dysthales* Mazzer in Bibltca mycol. 46: 92. 1976. — Holotype: *P. dysthales* (Pk.) Mazzer.

Pileus fibrillose-hairy to fibrillose-squamulose. Pileipellis a cutis with transitions to a trichoderm with long, septate, attenuate hairs; pigment encrusting; cheilocystidia if present subcylindrical, subglobular to clavate, usually brown-encrusted.

SPECIES.—*Entoloma strigosissimum* (Rea) Noordeloos, *E. dysthales* (Peck) Sacc. with *f. acystidiosum* Noordeloos; *E. dysthaloides* Noordeloos; *E. hirtum* (Velen.) Noordeloos; *E. romagnesii* Noordeloos; *E. pulvereum* Rea.

### 3.2. Section VERSATILIA (Romagn. ex Romagn.) Noordeloos

*Rhodophyllus* sect. *Versatiles* Romagn., Rhodoph. Madag.: 44. 1941 (nom. nud., no latin diagnosis). — *Rhodophyllus* section *Versatiles* Romagn. ex Romagn. in Bull. mens. Soc. linn. Lyon 43: 329. 1974. — *Entoloma* sect. *Versatilia* (Romagn. ex Romagn.) Noordeloos in Persoonia 10: 229. 1979.—Holotype: *R. versatilis* (Fr.) Quél.

*Rhodophyllus* 'subgen.' *Inopilus* Romagn. in Bull. mens. Soc. linn. Lyon 43: 329. 1974. — Holotype: *R. versatilis* (Fr.) Quél.

Pileus micaceous-fibrillose to fibrillose-hairy; cheilocystidia lageniform; pigment intracellular in pileipellis, encrusting in pileitrama.

SPECIES.—*Entoloma versatilis* (Fr.) Quél.; *E. areneosum* (Quél.) Moser with *f. fulvostrigosum* (Berk. & Br.) Noordeloos; *E. indutum* Boud.

## 4. ENTOLOMA subgenus ALLOCYBE Noordeloos, *subgen. nov.*

*Rhodophyllus* section *Excentrici* Romagn. in Bull. mens. Soc. linn. Lyon 43: 332. 1974. — Holotype: *R. excentricus* (Bres.) Romagn.

Statura tricholomatoidea; pileus conicus vel planus, haud hygrophanus, albus vel alutaceus; pileipellis cutis, hyphae 8–20 µm latae, cylindraceae vel inflatae; pigmentum in hypharum tunica vel incrustans; spora heterodiametricae structura nominatur 'basal facet'; trama elementis hypharum longis, cylindraceis vel fusoides; fibulae basidiorum ad basin presentes. — Typus: *Entoloma excentricum* Bres.

<sup>4</sup> At least in the temperate species; in many tropical taxa cheilocystidia are lacking (Romagnesi, 1941; Horak, 1980).

Habit tricholomatoid; pileus conical or flattened, not hygrophanous, white or leather brown; pileipellis a cutis made up of 8–20  $\mu\text{m}$  wide cylindrical or inflated hyphae; pigment membranal or encrusting; spores heterodiametrical with basal facet; elements of trama 90–320  $\mu\text{m}$  long, cylindrical to fusoid; clamp-connections present at base of basidia. — Type: *Entoloma excentricum* Bres.

SPECIES.—*Entoloma excentricum* Bres.; *E. eximium* (Romagn.) Noordeloos; *E. chionoderma* (Pilát) Noordeloos.

Romagnesi (1978: 37) considered *E. excentricum* one of the most enigmatic species of *Entoloma* in Europe on account of its large spores with basal facet, large cheilocystidia and relatively simple pileipellis made up of radially arranged, narrow, cylindrical hyphae. He pointed at the resemblance to subgenus *Trichopilus*, but considered the structure of the pileipellis and the pigmentation of *E. excentricum* too different to allow inclusion of his section *Excentrici* in subgen. *Trichopilus*. Therefore he retained this section in subgen. *Entoloma* in an isolated position.

Additional characters studied by me (see Noordeloos, 1981: 251) such as size and shape of the tramal cells, structure of the pileipellis, and topography of the clamp-connections emphasized the differences between section *Excentrici* and the rest of subgen. *Entoloma* to such an extent, that I decided to create a new subgenus to accommodate the species of section *Excentrici*. The new subgenus is placed in between subgen. *Entoloma*, from which it differs mainly in size and shape of tramal elements, topography of clamp-connections and in the presence of large cheilocystidia, and subgen. *Trichopilus*, from which it differs mainly in the structure and pigmentation of the pileipellis. Further information is found in Noordeloos, l.c.

##### 5. ENTOLOMA subgenus TRICHOPILUS (Romagn.) Noordeloos, *emend.*

*Rhodophyllus* subgenus *Trichopilus* Romagn. in Beih. Nova Hedwigia 59: 50. 1978. — *Entoloma* subgen *Trichopilus* (Romagn.) Noordeloos in Persoonia 11: 86. 1980. — Holotype: *E. jubatum* (Fr.) Quél.

*Agaricus* sect. *Leptonidei* Fr., Epicr.: 145. 1838. — *Rhodophyllus* sect. *Leptonidei* (Fr.) Quél., Enchir.: 58. 1886. — *Entoloma* sect. *Leptonidei* (Fr.) Quél. in Mém. Soc. Emul. Montbéliard, sér., II, 5: 118. 1872. — Lectotype (design. mihi): *Agaricus resutus* Fr.

*Rhodophyllus* subgenus *Leptonidium* Kühn. in Bull. Soc. mycol. Fr. 93: 446. 1977 (nom. nud., no Latin description, no type indicated).

Habit tricholomatoid; pileus often umbonate, rarely flattened, not hygrophanous, silky shining, densely radially fibrillose to fibrillose-squamulose; pileipellis a trichoderm made up of ascending bundles of cylindrical or fusoid terminal cells of the underlying subpellis, up to 25  $\mu\text{m}$  wide with intracellular pigment; hymenophoral trama regular, made up of long, fusoid, up to 450  $\mu\text{m}$  long cells; clamp-connections usually abundant.

Subgenus *Trichopilus* is emended here by including sect. *Erophila*. The species of this section seem to be better on its place here than in subgen. *Inocephalus* because of their tricholomatoid habit and the structure of their pileipellis.

## 5.1. Section TRICHOPILUS

Characters as those of subgenus but (sub-)capitate lageniform cheilocystidia present.

SPECIES.—*Entoloma jubatum* (Fr.) P. A. Karst.; *E. porphyrophaeum* (Fr.) P. A. Karst.; *E. helodes* (Fr.) Kumm.; *E. fuscotomentosum* Moell.; *E. fuscomarginatum* P. D. Orton; *E. scabiosum* (Fr.) Quél.

## 5.2. Section EROPHILA (Romagn.) Noordeloos

*Rhodophyllus* sect. *Erophila* Romagn. in Bull. mens. Soc. linn. Lyon 43: 332. 1974. — *Entoloma* sect. *Erophila* (Romagn.) Noordeloos in Persoonia 11: 86. 1980. — Holotype: *E. erophilum* (Fr.) P. A. Karst.

Cheilocystidia absent; pileus often flattened or with slightly depressed centre, fibrillose-rugulose to subsquamulose; often fruiting in spring.

SPECIES.—*E. erophilum* (Fr.) P. A. Karst.; *E. plebejum* Kalchbr.

6. ENTOLOMA subgenus INOCEPHALUS Noordeloos, *subgen. nov.*

*Rhodophyllus* subgenus *Inopilus* Romagn. sensu Romagn. in Beih. Nova Hedwigia 59: 48. 1978. — Holotype: *R. inocephalus* Romagn.

Pileus plerumque conico-campanulate deinde expansus, obtusus vel mammosus, haud depressus neque hygrophanus, sed saepe translucido-striatus; cutis fibrillosa, adpresse squamulosa vel sericata, interdum velutina ac tenuiter rimulosa propter structuram hymeniformam; pigmentum intracellulosum; lamellae liberae vel adnexae, haud decurrentae; spora structura nominatur 'dihedral base', saepe cuboidea. — Holotypus: *Entoloma inocephalum* (Romagn.) Dennis.

Habit mycenoid; pileus conico-campanulate then expanding, never depressed, usually papillate, with radially fibrillose or adpressedly squamulose, velutinous or slightly rimose surface; lamellae free or narrowly adnexed, never decurrent; spores with dihedral base; pileipellis a trichoderm or hymeniderm; pigment intracellular. — Holotype: *Entoloma inocephalum* (Romagn.) Dennis.

In discordance with the Rules of Botanical Nomenclature Romagnesi (1978, l.c.) changed the type of *Inopilus* from *E. versatilis* into *E. inocephalum*, because he thought the latter species to be more representative for the subgenus he had in mind. Noordeloos (1979: 209) transferred sect. *Inopilus*, with *E. versatilis* as type, to subgen. *Pouzaromyces*. Therefore a new subgenus had to be created for the remaining taxa of the former taxon *Inopilus*. I selected *E. inocephalum* as holotype for this new subgenus, following the suggestion of Romagnesi cited above. Subgen. *Inocephalus* has, as far as we know, no European representatives, but is widespread and rich in species in subtropical and tropical areas (Romagnesi & Gilles, 1979; Horak, 1973, 1978).

## 7. ENTOLOMA subgenus ALBOLEPTONIA (Largent &amp; Benedict) Noordeloos

*Alboleptonia* Largent & Benedict in *Mycologia* 62: 439. 1970. — *Entoloma* subgen. *Alboleptonia* (Largent & Benedict) Noordeloos in *Persoonia* 10: 246. 1979. — Holotype: *E. sericellum* (Bull. ex Fr.) Kumm.

Habit collybioid or omphalioid, rarely with excentric stipe; pileus always pale, white, pinkish or with slight grey or brown tinges; pileipellis a trichoderm of interwoven hyphal tips, with pigment intracellular if present, clamp-connections usually present.

## 7.1. Section ALBOLEPTONIA

*Rhodophyllus* sect. *Candidi* Romagn. in *Bull. Soc. mycol. Fr.* 53: 333. 1937 (nom. nud., no Latin diagnosis). — Lectotype (Singer 1951: 617): *R. sericellus* (Bull. ex Fr.) Quél.

Characters as those of the subgenus, but clamp-connections always present.

SPECIES.—*Entoloma sericellum* (Bull. ex Fr.) Kumm.; *E. cephalotrichum* (P. D. Orton) Noordeloos, *E. olorum* (Favre & Romagn.) Noordeloos. *E. roseum* (Longyear) Moser.

8. ENTOLOMA subgenus LEPTONIA (Fr.) Noordeloos, *comb. nov.*

*Agaricus* tribus *Leptonia* Fr., *Syst. mycol.* 1: 10. 1821. — *Agaricus* subgen. *Leptonia* (Fr.) Loud., *Encyl. Pl.*: 998. 1827. — *Rhodophyllus* subgen. *Leptonia* (Fr.) Quél., *Enchir.*: 59. 1886. — *Leptonia* (Fr.) Kumm., *Führ. Pilzk.*: 24. 1871. — Lectotype (Clements & Shear, 1931: 349): *Agaricus euchrous* Pers. ex Fr.

*Leptoniella* Earle in *Bull. N.Y. bot. Gdn.* 5: 424. 1909. — Lectotype (Donk, 1962: 171): *Agaricus euchrous* Pers. ex Fr.

*Leptonia* subgen. *Paludocybe* Largent in *Mycologia* 66: 1011. 1974. — Holotype: *L. lampropus* (Fr.) Quél. sensu P. D. Orton.

Habit collybioid, rarely omphalioid; pileus convex with depressed or umbilicate centre, rarely papillate, opaque or translucently striate when moist, not or only very slightly hygrophanous, with fibrillose to squamulose surface; pileipellis a trichoderm, hymeniform or a pallissadoderm; pigment intracellular.

## 8.1. Section LEPTONIA

*Rhodophyllus* sect. *Leptoniarii* Romagn. in *Bull. Soc. mycol. Fr.* 53: 332. 1937 (nom. nud., no latin diagnosis). — Lectotype (design. mihi): *R. euchrous* (Pers. ex Fr.) Quél.

*Rhodophyllus* 'groupe' *Lampropodes* Kühn. & Romagn., *Fl. anal.*: 208. 1953. — *Rhodophyllus* sect. *Lampropodes* (Kühn. & Romagn.) ex Romagn. in *Bull. mens. Soc. linn. Lyon* 43: 328. 1974. — Holotype: *R. lampropus* sensu Kühn. & Romagn.

Habit collybioid, rarely more or less mycenoid or tricholomatoid; pileus rarely depressed, never umbilicate, frequently with bluish tinges; pileipellis a cutis or a trichoderm made up of bundles of repent or slightly ascending, cylindrical, multiseptate hyphae; clamp-connections present; cheilocystidia, if present, more or less clavate.

Species.—*Entoloma euchroum* (Pers. ex Fr.) Kumm.; *E. dichroum* (Pers. ex Fr.) Kumm.; *E. placidum* (Fr. ex Fr.) Noordeloos; *Rhodophyllus lampropus* sensu Kühn. & Romagn.

### 8.2. *Entoloma* section *Griseorubida* (Romagn.) Noordeloos, *comb. nov.*

*Rhodophyllus* sect. *Griseorubidi* Romagn. in Bull. mens. Soc. linn. Lyon 43: 328. 1974 (basionym).  
Holotype: *R. griseorubidus* Kühn.

Pileus truncate-campanulate with depressed centre and radially fibrillose surface, sometimes minutely squamulose at centre; with large fusiform or cylindrical cheilocystidia; clamp-connections present.

SPECIES.—*Rhodophyllus griseorubidus* Kühn.; *Entoloma cocles* (Fr.) Noordeloos.

### 8.3. *Entoloma* section *Paludocybe* (Largent) Noordeloos, *comb. & stat. nov.*

*Leptonia* subgen. *Paludocybe* Largent in Mycologia 66: 1011. 1974 (basionym). — Holotype: *L. lampropus* sensu P. D. Orton.

Habitat typically collybioid, rarely omphalioid; pileus convex to broadly convex with depressed to umbilicate, usually tomentose or squamulose centre, towards margin adpressed fibrillose or almost smooth; pileipellis usually a well-developed trichoderm, hymenoderm or pallissadoderm; clamp-connections absent; cheilocystidia, if present, never very much different from the basiodioles, sometimes with intracellular pigment.

SPECIES.—The European taxa of this section are badly in need of a critical revision. Many species have been described in the past, and many have been misinterpreted afterwards. The species of sect. *Paludocybe* are often very difficult to distinguish, as there are not many microscopical characters to support the often slight macromorphological differences. The attempted subdivisions of *Paludocybe* into groups by Largent (1974, 1977) and Romagnesi (1974, 1978) are mainly based on the colour or pileus and stipe, sometimes also on other characters, such as a lamellar edge with coloured cheilocystidia (section *Rhamphocystotae* Largent), but the resulting subdivisions do not give the impression of being 'natural'. At present I am not able to give an account of the European taxa in this section.

## 9. *ENTOLOMA* subgenus *CLAUDOPUS* (Gill.) Noordeloos, *comb. nov.*

*Claudopus* Gill., Hymen. Fr.: 426. 1876 (basionym). — *Rhodophyllus* subgenus *Claudopus* (Gill.) Romagn in Beih. Nova Hedwigia 59: 41. 1978. — Lectotype (Konrad, 1934: 177): *Agaricus byssisedus* Pers. ex Fr.

*Rhodophyllus* section *Undati* Romagn. in Bull. Soc. mycol. Fr. 53: 329. 1937 (nom. nud., no Latin diagnosis). — *Rhodophyllus* sect. *Undati* Romagn. ex Romagn. in Bull. mens. Soc. linn. Lyon 43: 327. 1974. — Holotype: *Rhodophyllus undatus* (Fr.) Quél.

Habit pleurotoid, omphalioid or clitocyboid; stipe central or excentric, sometimes lacking; lamellae often decurrent; pigment exclusively encrusting.

SPECIES.—*Entoloma byssisedum* (Pers. ex Fr.) Donk; *E. depluens* (Batsch ex Fr.) Hesler; *E. apiculatum* (Pers. ex Fr.) Noordeloos; *E. undatum* (Fr.) Moser (= *Eccilia sericeonitida* P. D. Orton); *E. rhodocylix* (Lasch) Moser; *E. rusticoides* (Gill.) Noordeloos; *E. nigrellum* (Quél.) Noordeloos; *E. lanicum* (Romagn.) Noordeloos.

Subgen. *Claudopus* is accepted here in the emended sense of Romagnesi (1974, l.c.). In this concept it covers not only the pleurotoid relatives of *E. byssisedum* but also the omphalioid species with encrusting pigments, formerly placed in the form(sub)gen. *Eccilia*, such as *E. undatum* and related species. *Claudopus* sensu Horak (1973, 1980) is a form-genus, uniting all pleurotoid species in *Entoloma*, and covering an heterogenous group of species, some with encrusting pigment, others with intracellular pigment, here placed in subgen. *Paraleptonia*.

#### 10. ENTOLOMA subgenus OMPHALIOPSIS Noordeloos, *subgen. nov.*

MISAPPLIED NAME.—*Rhodophyllus* subgen. *Eccilia* (Fr.) Quél. sensu Romagn. in Bull. mens. Soc. linn. Lyon 43: 337. 1974. — Lectotype: (Clemens & Shear, 1931: 349): *R. parkensis* Fr. sensu Kühn.

Statura omphalioida vel collybioidea, raro mycenoidea; pileus leviter hygrophanus, cutis tramaeque pigmento intracellularis, rarius leviter incrustante munitus; sporae structura nominatur 'dihedral base'; fibulae presentes vel absentes. — Typus: *Entoloma leptonipes* (Kühn. & Romagn.) Moser.

Habit omphalioid, collybioid or mycenoid; pileus sometimes slightly hygrophanous, usually not; pileipellis a cutis or trichoderm made up of wide, often inflated hyphae; pigment intracellular, sometimes in addition slightly encrusting pigment on the narrow hyphae of upper pileitrama; clamp-connections present (in extra-European taxa sometimes absent); spores with dihedral base. — Holotype: *Entoloma leptonipes* (Kühn. & Romagn.) Moser.

As I have pointed out above (see p. 138), *E. politum* must be considered the lectotype of 'Eccilia' Fr., in accordance with the typification by Donk (1949: 158). In my concept of subgen. *Entoloma* the name *Eccilia* is then a synonym of subgen. *Entoloma*.

The consequence of this is that a new subgenus is needed to accommodate the taxa of *Rhodophyllus* subgen. *Eccilia* emend. Romagn. 1974. I have chosen *E. leptonipes* as the type of this new subgen. *Omphaliopsis* because that is a fairly well-known and widespread species, whereas the identity of *Rhodophyllus parkensis* sensu Kühn. seems rather doubtful.

Subgen. *Omphaliopsis* has its main distribution in the tropics (Romagn. & Gilles, 1979); only a few species, some of which are undescribed, occur in Europa.

## 10.1 Section O M P H A L I O P S I S

*Rhodophyllus* sect. *Trichonophylli* Romagn. in Bull. mens. Soc. linn. Lyon 43: 327. 1974.—Holotype: *R. parkensis* sensu Kühn.

Pileus brown or grey-brown; stipe often with blue tinges; cheilocystidia, if present, simple, basidioliform; clamp-connections present.

SPECIES.—*Entoloma leptonipes* (Kühn. & Romagn.) Moser; *R. parkensis* sensu Kühn.

11. ENTOLOMA subgenus PARALEPTONIA Romagn. ex Noordeloos, *subgen. nov.*

*Rhodophyllus* subgen. *Paraleptonia* Romagn., Rhodoph. Madag.: 43. 1941 (nom. nud, no Latin diagn).—Holotype: *R. cancrinus* (Fr.) Quél.

Statura pleurotoidea vel collyboidea; pileus pallidus vel brunneus; sporae structura nominatur 'basal facet'; fibulae presentes vel absentes.

Habit pleurotoid or collybioid; pileus pale or brown; spores with basal facet; clamp-connections present or absent.

## 11.1 Section P A R A L E P T O N I A

Pileus white, yellowish or pale pinkish brown; stipe white or very pale.

SPECIES.—*Entoloma cancrinum* (Fr.) Noordeloos.

11.2 *Entoloma* section *Sarcita* (Romagn.) Noordeloos, *comb. nov.*

*Rhodophyllus* section *Sarciti* Romagn., Rhodoph. Madag.: 43. 1941 (nom. nud., no Latin diagn).—*Rhodophyllus* section *Sarciti* Romagn. ex Romagn. in Bull. mens. Soc. linn. Lyon 43: 327. 1974 (basionym).—Holotype: *E. sarcitum* (Fr.) Noordeloos.

Pileus and stipe dark brown.

SPECIES.—*Entoloma sarcitum* (Fr.) Noordeloos.

## NEW COMBINATIONS USED IN THE TEXT OF THIS PAPER

*Entoloma apiculatum* (Fr.) Noordeloos, *comb. nov.*—*Agaricus apiculatus* Fr., Epicr.: 159. 1838 (basionym).

*Entoloma cancrinum* (Fr.) Noordeloos, *comb. nov.*—*Agaricus cancrinus* Fr., Epicr.: 150. 1838 (basionym).

*Entoloma cocles* (Fr.) Noordeloos, *comb. nov.*—*Agaricus cocles* Fr., Epicr.: 158. 1838 (basionym).

*Entoloma lanicum* (Romagn.) Noordeloos, *comb. nov.*—*Rhodophyllus lanicus* Romagn. in Rev. Mycol. 1: 159. 1936 (basionym).

- Entoloma nigrellum** (Quél.) Noordeloos, *comb. nov.*—*Rhodophyllus nigrellus* Quél. in C. R. Ass. franc. Av Sci. (Rouen, 1883) 12: 499. 1884 (basionym).
- Entoloma placidum** (Fr.) Noordeloos, *comb. nov.*—*Agaricus placidus* Fr., Syst mycol. 1: 202. 1821 (basionym).
- Entoloma rusticoides** (Gill.) Noordeloos, *comb. nov.*—*Eccilia rusticoides* Gill., Hymenom. Fr.: 425. 1876 (basionym).
- Entoloma sarcitum** (Fr.) Noordeloos, *comb. nov.*—*Agaricus sarcitus* Fr., Epicr.: 155. 1838 (basionym).

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