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Central European genera of the *Boletaceae* and *Suillaceae*, with notes on their anatomical characters

JOSEF ŠUTARA

Prosetická 239, 415 01 Teplice, Czech Republic

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A taxonomic survey of Central European genera of the families *Boletaceae* and *Suillaceae* with tubular hymenophores, including the lamellate *Phylloporus*, is presented. Questions concerning the delimitation of the bolete genera are discussed. Descriptions and keys to the families and genera are based predominantly on anatomical characters of the carpophores. Attention is also paid to peripheral layers of stipe tissue, whose anatomical structure has not been sufficiently studied. The study of these layers, above all of the caulohymenium and the lateral stipe stratum, can provide information important for a better understanding of relationships between taxonomic groups in these families. The presence (or absence) of the caulohymenium with spore-bearing caulobasidia on the stipe surface is here considered as a significant generic character of boletes. A new combination, *Pseudoboletus astraeicola* (Imazeki) Šutara, is proposed.

Key words: *Boletaceae*, *Suillaceae*, generic taxonomy, anatomical characters.

Šutara J. (2005): Středoevropské rody čeledí *Boletaceae* a *Suillaceae*, s poznámkami k jejich anatomickým znakům. – *Czech Mycol.* 57: 1–50.

Je předložen taxonomický přehled středoevropských rodů čeledí *Boletaceae* a *Suillaceae* s rourkovitým hymenoforem, včetně rodu *Phylloporus* s lupeny. Jsou diskutovány otázky týkající se vymezení hříbovitých rodů. Popisy a klíče k čeledím a rodům jsou založeny převážně na anatomických znacích plodnic. Pozornost je také věnována periferním vrstvám tkáně na třeni, jejichž anatomická stavba není dostatečně prostudována. Studium těchto vrstev, především kaulohymenia a laterálního strata třeně, může poskytnout informace důležité pro lepší poznání příbuzenských vztahů mezi taxonomickými skupinami v těchto čeledích. Přítomnost (či nepřítomnost) kaulohymenia s výtrusorodými kaulobazidiemi na povrchu třeně je zde považována za významný rodový znak hřibů. Je navržena nová kombinace: *Pseudoboletus astraeicola* (Imazeki) Šutara.

INTRODUCTION

The boletes form a conspicuous group of macrofungi which has been the centre of interest of many mycologists for more than two centuries. Currently the

most widely accepted classification of this group is that by Singer (e.g. 1951, 1962, 1965, 1967, 1975, 1986, etc.). Nevertheless, major differences in opinion on the generic and familial limits still exist. Further relevant works dealing with boletes have been those by the following authors: Karsten (1881), Quélet (1886, 1888), Bataille (1908), Gilbert (1931) as forerunners, Snell (1941), Watling (1970), Smith and Thiers (1971), Corner (1972), Arpin and Kühner (1977), Pegler and Young (1981), Alessio (1985), Engel et al. (1983, 1996), Lannoy and Estades (2001) and many others. Anatomical characters of boletes and related groups have been examined by Fayod (1889), Josserand (1932), Lohwag and Peringer (1937), Elrod and Blanchard (1939), Lohwag (1941), Disbrey and Watling (1967), Watling and Largent (1976), Reijnders and Stalpers (1992), Cléménçon (1997) etc. Authors who have studied the spore morphology in these groups are Perreau-Bertrand (1961, 1965), Pegler and Young (1971, 1981), Heinemann, Rammeloo and Rullier (1988), Oolbekkink (1991), Holec (1994), etc. Chemotaxonomic analyses by many authors, e.g. Bresinsky and Orendi (1970), Besl and Bresinsky (1977, 1997), Gill and Steglich (1987) etc., have contributed valuable data significant for bolete taxonomy. Molecular studies concerning the boletes and allied groups have been published by Bruns and Szaro (1992), Gardes and Bruns (1996), Bruns et al. (1998), Kretzer and Bruns (1999), Binder and Besl (2000), Hibbett and Thorn (2001), Binder and Bresinsky (2002), etc.

As regards the taxonomic position of the groups in question, the families *Boletaceae* and *Suillaceae* belong to the order *Boletales* Gilbert. The other families of this order [e.g. *Gyrodontaceae* (Singer) Heinem., *Gyroporaceae* (Singer) Binder et Bresinsky, *Paxillaceae* Lotsy, *Gomphidiaceae* Maire ex Jülich] and gasteroid forms recently classified as the *Boletales* (*Gastrosuillus* Thiers, *Chamonixia* Rolland, etc.) are not discussed here.

FAMILIES AND GENERA INCLUDED IN THIS PAPER

family: *Suillaceae* (Singer) Besl et Bresinsky

genera: *Boletinus* Kalchbr., *Suillus* Adans., *Mariaella* Šutara

family: *Boletaceae* Chevallier

subfamily: *Boletoideae*

genera: *Boletus* L. [including subgenus *Xerocomus* (Quél.) Maubl.], *Tyloporus* P. Karst., *Porphyrillus* Gilbert, *Chalciporus* Bataille, *Buchwaldoboletus* Pilát, *Rubinoboletus* Pilát et Dermek, *Pseudoboletus* Šutara, *Phylloporus* Quél., *Leccinum* S. F. Gray

subfamily: *Strobilomycetoideae* (Gilbert) Watling

genus: *Strobilomyces* Berk.

MATERIALS AND METHODS

This paper summarizes the results of the author's study of the anatomy of boletes in the last twenty years and supplements some of his earlier published contributions (Šutara 1987a, 1987b, 1989, 1991). A list of studied Central European species is appended to each section dealing with individual genera. The author's collections are deposited in his private herbarium (abbreviation: JŠ). Many specimens examined were loaned from National Museum, Prague (PRM), Moravian Museum, Brno (BRNM), South Bohemian Museum, České Budějovice (CB), Slovak National Museum, Bratislava (BRA), Regional Museum of Litoměřice (LIT) and Regional Museum of Hradec Králové (HK).

Anatomical and histological characters of boletes were studied predominantly on dried material. Microscopic sections were made by hand with a razor blade. Sections from dried material were revived in a 3–10 % solution of ammonium hydroxide (NH_4OH) with (or without) Congo Red or in Melzer's reagent. Microscopic structures of the studied species were mostly examined on a sufficiently large number of both young and middle-aged or mature carpophores. Material of poor quality, with various defects and abnormalities, was excluded from the examination. In several cases the carpophores were also studied in a fresh state. Microscopic examination confirmed the presumption that the results obtained from both revived dried material and fresh carpophores are very similar in every detail. Sections from fresh material were mounted in Melzer's reagent or in an aqueous solution of Congo Red.

RESULTS AND DISCUSSION

Arrangement of the hymenophoral trama

The main types (or subtypes) of arrangement of the bilateral hymenophoral trama occurring in the families *Boletaceae* and *Suillaceae* are: phylloporoid, boletoid and mariaelloid.

The boletoid and phylloporoid type. Probably the first authors who pointed out differences in arrangement of the hymenophoral trama of some poroid boletes were Lohwag and Peringer (1937). The boletoid and phylloporoid tramal structures were studied and discussed by many authors, e.g. by Singer (1951, 1962, 1975, 1986), Snell and Dick (1958), Disbrey and Watling (1967), Corner (1972), Reijnders and Stalpers (1992), etc.

In the boletoid and phylloporoid trama there is a distinctly developed mediostratum which is very similar in both types. The mediostratum is composed of a dense layer of non-gelatinous, densely septate hyphae. In a longitudinal sec-

tion the mediostratum looks like a darker, narrow stripe of tissue in the central part of the trama (see Figs. 1c, 2c, 3b).

The difference between the phylloporoid and boletoid type of the trama is based on different arrangements of lateral strata. In the phylloporoid trama the lateral strata are composed of non-gelatinous, slightly divergent, densely arranged hyphae touching each other (Figs. 2c, 2d and Šutara 1987a: Fig. 1). In the typical boletoid trama the lateral strata are more or less gelatinized, distinctly divergent, loosely arranged, with hyphae not touching each other (Figs. 1c, 1d, 3b, 3d, 4a). These differences are the main reason why the lateral strata in the phylloporoid trama are almost concolorous with the mediostratum whereas the lateral strata in the boletoid type are distinctly lighter. In microscopic preparations the contrast between the layers of the hymenophoral trama can be improved by suitable stains, e.g. Congo Red.

The phylloporoid type of the trama occurs in its typical form in the genus *Phylloporus* and a few species of the *Boletus subtomentosus* group. The true boletoid type is frequent, occurring in many boletes of *Boletus* s. str., *Leccinum*, *Buchwaldoboletus*, *Suillus*, *Boletinus*, etc. It is, however, important to note that in some boletes the hymenophoral trama is of a structure intermediate between the boletoid and phylloporoid type. This problem will be discussed in detail under *Boletus*, subgenus *Xerocomus*.

The mariaelloid type. In contrast to the boletoid and phylloporoid type, the mariaelloid hymenophoral trama is gelatinized evenly all over its width so that it is not differentiated into a mediostratum and lateral strata. The hyphae of the trama are loosely arranged (not touching each other), slightly divergent or almost parallel (Figs. 3a, 3c, 4d).

The mariaelloid trama has hitherto been found by the present author in *Mariaella bovina* (L.: Fr.) Šutara [= *Suillus bovinus* (L.: Fr.) Roussel] and in some carpophores of *Suillus flavidus* (Fr.) J. Presl and the North American *Suillus pictus* (Peck) Smith et Thiers.

Changes of the hymenophoral trama in the course of development

In his *Agaricales in Modern Taxonomy*, Singer (1986: 55) stated, 'It is essential to keep in mind that the tramal configuration may change during the individual development of a hymenophore'. This important principle should be respected during microscopic examination.

Development of the boletoid and phylloporoid hymenophoral trama. At the very beginning (i.e. at the primordial or postprimordial stage) the bilateral tramas of both the phylloporoid and boletoid type are rather densely arranged, non-gelatinous and therefore very similar to each other. During further growth, however, these two types of trama develop in a different way.

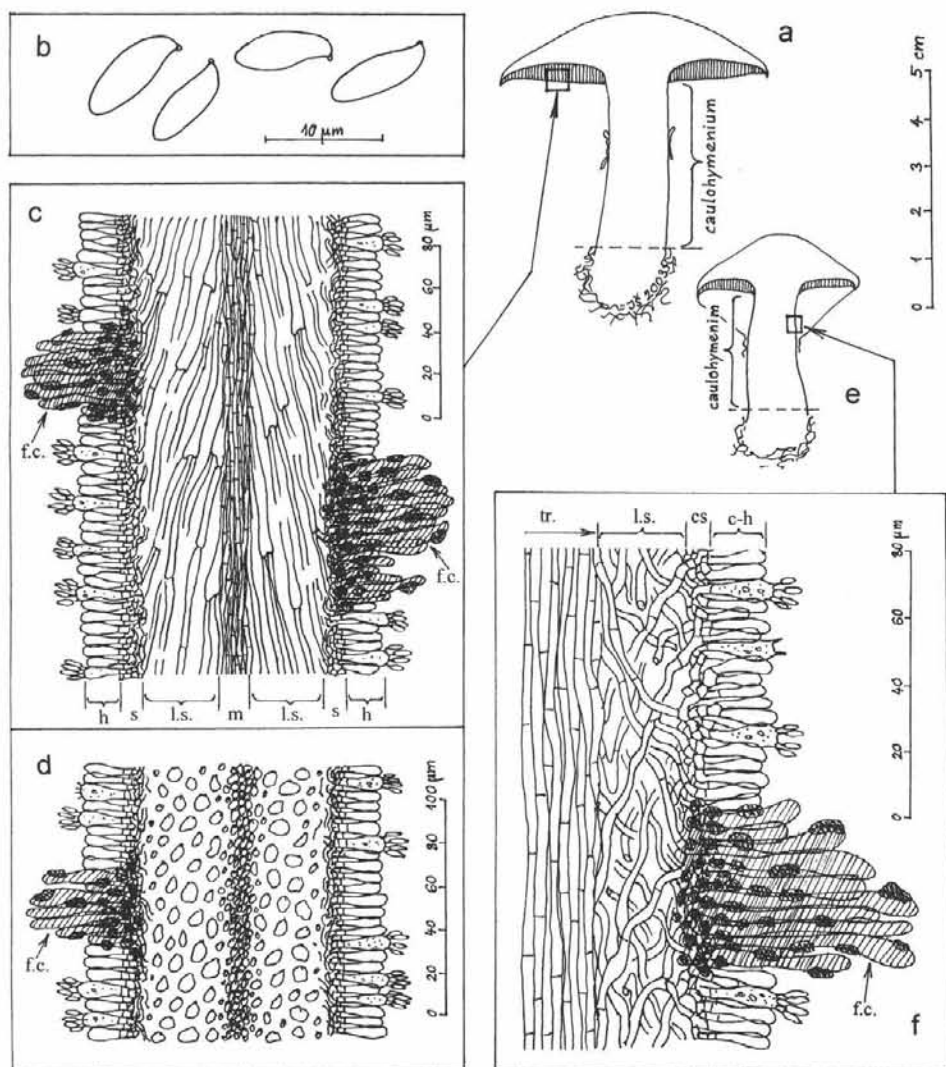


Fig. 1. *Suillus luteus* (type species of *Suillus*) – **a**: A middle-aged carpophore in a section (JŠ 4050). – **b**: Spores. – **c**: The boletoid hymenophoral trama in a longitudinal section. Both dense mediostratum and loosely arranged, gelatinous lateral strata are well distinct. Fasciculate oleocystidia of the *Suillus* type with an incrustation and dark content are present; h = hymenium, s = subhymenium, l.s. = lateral stratum, m = mediostratum, f.c. = fascicles of oleocystidia. – **d**: The boletoid trama in a transverse section. – **e**: A young carpophore in a section (JŠ 4051). – **f**: Peripheral layers of tissue in the upper half of the stipe. Beneath the caulohymenium with fertile caulobasidia there is a loosely arranged, gelatinous lateral stratum of the stipe; tr. = stipe trama proper, l.s. = lateral stipe stratum, cs = caulosubhymenium, c-h: caulohymenium, f.c. = fascicle of incrustated oleocystidia of the *Suillus* type.

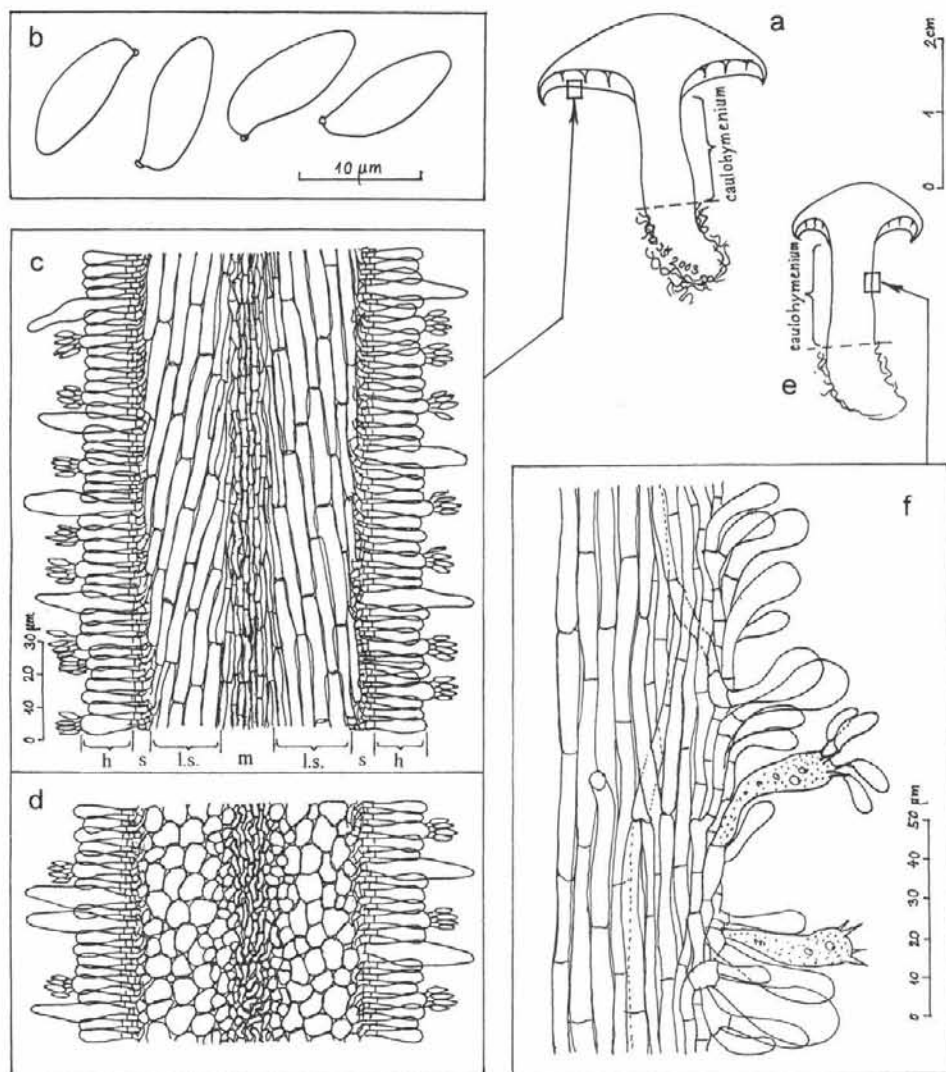


Fig. 2. *Phylloporus pelletieri* (type species of *Phylloporus*) – **a**: a middle-aged carpophore in a section (JŠ 3251). – **b**: Spores. – **c**: The phylloporoid hymenophoral trama in a longitudinal section (for abbreviations, see Fig. 1c). – **d**: The phylloporoid trama in a transverse section. Hyphae of lateral strata are non-gelatinous, densely arranged, touching each other. – **e**: A young carpophore in a section (JŠ 2722). – **f**: Surface layers of tissue in the upper half of the stipe. Beneath the caulohymenium with fertile caulobasidia there is no lateral stipe stratum.

In the phylloporoid trama both mediostratum and lateral strata remain non-gelatinous all through the development of the carpophore.

In the boletoid trama the mediostratum also remains permanently non-gelatinous but lateral strata soon gelatinize. This process of gelification, which is moreover connected with changes in density and divergence of hyphae of the lateral strata, begins already at a young age and reaches its maximum at a medium stage of development of the tubes, i.e. in younger or middle-aged carpophores. At this stage the contrast between the loosely arranged, gelatinous lateral strata and the dense, non-gelatinous mediostratum is the most conspicuous and the boletoid trama has a typical appearance, very different from the phylloporoid arrangement (Figs. 1c, 3b). During further development the gelification of the lateral strata gradually disappears. Moreover, the hymenophoral trama gradually lengthens with age so that in mature tubes the initially true boletoid arrangement changes into a structure similar to the phylloporoid or into a subregular trama.

The hymenophoral trama should thus be studied at the stage when the lateral strata are best developed and gelatinized. Examination of the trama in the other developmental stages can give skewed results because at a very young age the typical features of the boletoid structure are not yet sufficiently formed and at a more advanced age (i.e. in carpophores approaching maturity) these features gradually fade away. It is obvious that information about the age of the carpophores examined is very important. In the generic diagnoses given in this contribution the hymenophoral trama is, in all cases, described as it was ascertained by the author just in the best developed stage, i.e. in younger or middle-aged carpophores.

The arrangement of the trama may be negatively influenced by some environmental factors, particularly by dry weather. The true boletoid trama can develop well only under sufficiently favourable circumstances. Results of the microscopic study can also be dependent on the quality of the herbarium material. Specimens which were not dried carefully and whose tissues therefore revive insufficiently in microscopic preparations should be excluded from any anatomical study. The understanding of the arrangement in the hymenophoral trama of a particular species and also the understanding of all developmental changes in this structure sometimes requires repeated re-examinations of a sufficiently large number of specimens. It seems that the methodology of the study of this structure adopted by various mycologists is rather different. This is probably one of the reasons why results of some authors have been contradictory.

Development of the mariaelloid hymenophoral trama. At the very beginning (i.e. at the primordial or postprimordial stage) this hymenophoral trama is distinctly bilateral, non-gelatinous and similar to the trama in very young tubes of the other boletes. At this very early stage there exists a suggestion of a mediostratum and divergent lateral strata. However, this stage lasts only for

a short time. During further development the trama quickly changes because both mediostratum and lateral strata very soon become gelatinous. In middle-aged carpophores (which are the most suitable for the study of this type of the tramal structure) the mariaelloid trama is already fully and typically developed, viz. strongly gelatinized and loosely arranged both in the lateral layers and in the middle part (Figs. 3a, 3c, 4d). In fully mature carpophores the hyphal structure finally loses the divergent arrangement and gradually changes into a gelified, subparallel trama.

Surface of the stipe

Except for three species whose stipe surface is infertile (see the note on the stipe surfaces of *Boletinus*, *Mariaella* and *Pseudoboletus*), all the other Central European boletes of the families *Boletaceae* and *Suillaceae* have reproductive organs developed not only in the tubes but also on the stipe. These boletes have a substantial part of the stipe covered by a caulohymenium with spore-bearing caulobasidia. The caulohymenium is absent only in the lowest part of the stipe, which is hidden in the substrate and often covered with a basal tomentum. The presence of basidia on the stipe in some boletes has already been described or mentioned by many authors, e.g. Melzer (1919), Lohwag (1922), Kühner (1926), Němec (1926), Lohwag and Peringer (1937), Elrod and Snell (1940), Singer (1951, 1962, 1975, 1986), Pantidou (1961, 1962), Smith and Thiers (1964, 1968), Disbrey and Watling (1967), Watling and Largent (1976), Watling (1985), Hlaváček (1997 etc.) and others.

Anatomical study of primordial and postprimordial stages of boletes showed that the caulohymenium is in essence a continuation of the fertile hymenium from the tubes on the stipe (cf. Kühner 1926, Němec 1926, Elrod and Snell 1940, Pantidou 1961, Watling 1985, etc.). The hymenial layer on the stipe was described as e.g. 'veritable hyménium' by Kühner (1926), 'hymenial layer of the stem' by Němec (1926), 'true hymenium' by Elrod and Snell (1940), 'fertile palisade' by Pantidou (1961), 'hyménium stipitaire' by Reijnders (1963), 'caulohymenium' by Smith and Thiers (1964, 1968, 1971), Grund and Harrison (1976) and Watling (1985), 'cauline hymenium' or 'stem-hymenium' by Corner (1972), 'hyménium fertile' by Arpin and Kühner (1977), 'kaulohymenium' by Hlaváček (1997), etc. Among the terms used for the hymenial layer on the stipe, the term 'caulohymenium' has been considered the most appropriate by the present author (Šutara 1987a, 1987b, 1989). [Note: In this contribution the caulohymenium is never called 'stipe cuticle' or 'stipe cortex'. The term 'stipe cuticle' is here used only for sterile surface layers of the stipe, e.g. a trichoderm, trichodermal palisade etc.].

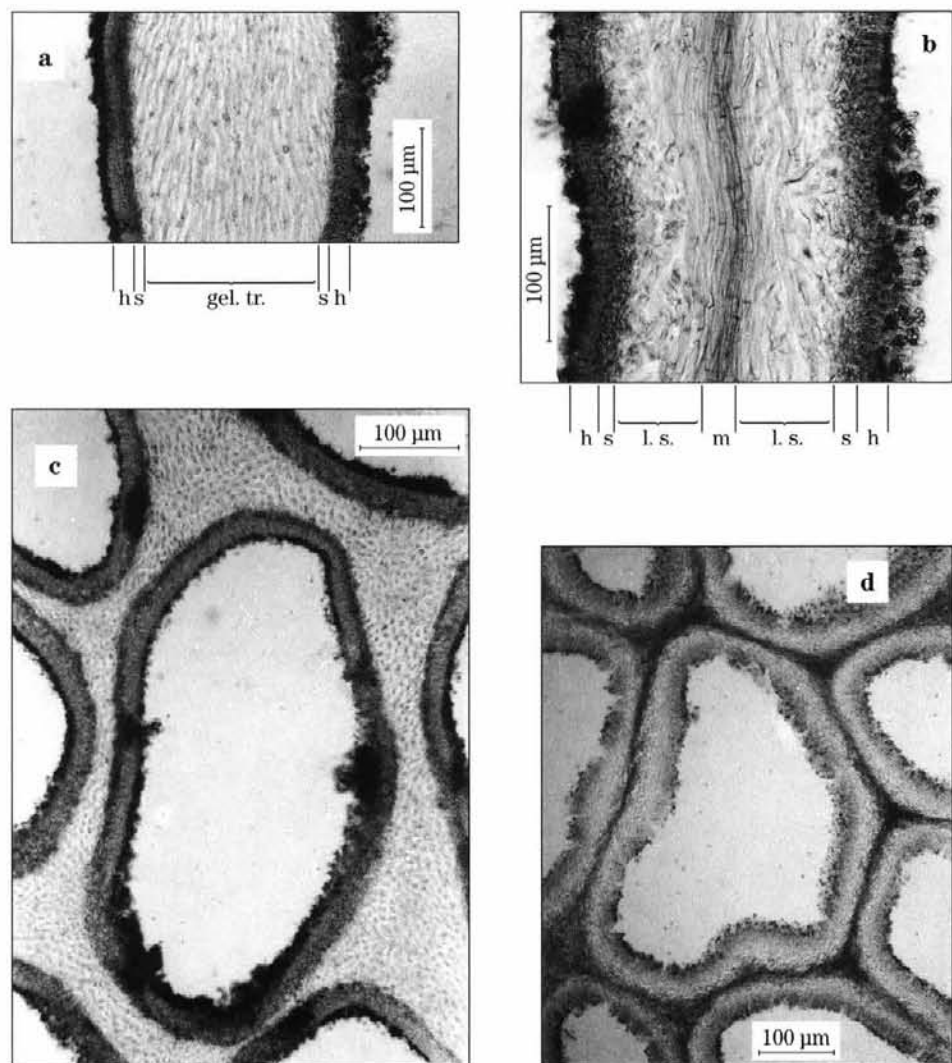


Fig. 3. – **a:** *Mariaella bovina* (type species of *Mariaella*) (JŠ 542), the mariaelloid hymenophoral trama in a longitudinal section; gel.tr. = gelatinous trama without a distinct mediostratum (for the other abbreviations, see Fig. 1c). – **b:** *Suillus variegatus* (JŠ 1566), the boletoid hymenophoral trama in a longitudinal section (for abbreviations, see Fig. 1c). – **c:** *Mariaella bovina* (JŠ 1742), the mariaelloid hymenophoral trama in a transverse section. The trama is not differentiated into a mediostratum and lateral strata. – **d:** *Gyrodontaceae* (BRNM 235941), the boletoid hymenophoral trama in a transverse section. Both dark-coloured mediostratum and light-coloured lateral strata are well distinct. (Sections 3a – 3d were stained with Congo-Red).

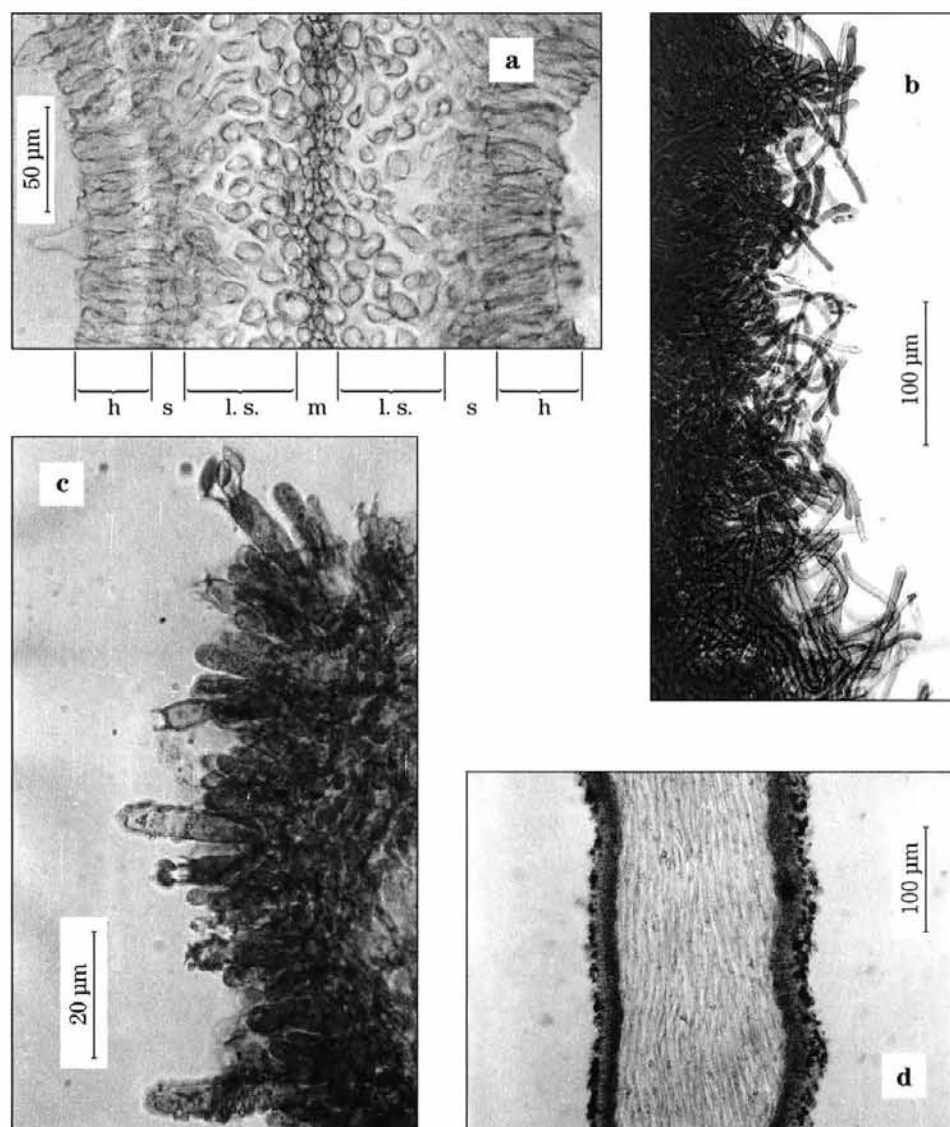


Fig. 4. – **a:** *Leccinum luteoporum* (LIT 3776/565), the boletoid hymenophoral trama in a transverse section (for abbreviations, see Fig. 1c). – **b:** *Pseudoboletus parasiticus* (type species of *Pseudoboletus*) (JŠ 2109), the infertile stipe cuticle consisting of a filamentous trichoderm (section from the upper part of the stipe). – **c:** *Suillus tridentinus* (JŠ 3073), a fragment of the caulohymenium with spore-bearing caulobasidia from the middle part of the stipe. – **d:** *Mariaella bovina* (JŠ 542), the mariaelloid hymenophoral trama in a longitudinal section. Divergence of tramal hyphae is almost indistinct. (Sections 4a – 4d were stained with Congo-Red).

Some characters of the caulohymenium

The caulohymenium is comparable with the hymenium of the hymenophore in many respects. This layer is composed of caulobasidioles, caulocystidia and sporulating caulobasidia. The term 'caulobasidia' was already used by some authors, e.g. Smith and Thiers (1968). Spores produced by the caulobasidia on the stipe are not different from those originating from the basidia in the tubes. For example, mature spores from the stipe of *Boletus porosporus* (Imler) Moreno et Bon (specimen examined: JŠ 1631) are truncate and spores from the stipe of *Strobilomyces strobilaceus* (Scop.: Fr.) Berk. (JŠ 3420) are shaped, ornamented and dark pigmented in the same way as those from the tubes. Also measurements of spores both from the hymenophore and from the stipe are in essence the same. This was tested by the present author for *Suillus luteus* (L.: Fr.) Roussel (JŠ 2285), *Suillus pictus* (PRM 715519) and some other species (see Šutara 1987b: Figs. 6b, 7c). The spore print obtained from the caulohymenium is the same colour as that from the hymenophore (material examined: *Suillus luteus*, JŠ 2285; *Strobilomyces strobilaceus*, JŠ 3420, etc.). Caulobasidia produce spores even on the places where the stipe surface with the caulohymenium is covered with a veil (or remnants of the veil). This was observed by the present author on such species as *Strobilomyces strobilaceus*, *Suillus luteus*, *Suillus pictus*, *Suillus lakei* (Murrill) Smith et Thiers, *Suillus grevillei* (Klotzsch: Fr.) Singer, *Suillus laricinus* (Berk.) O. Kuntze and *Suillus tridentinus* (Bres.) Singer.

The caulohymenium, naturally, is not as fertile as the hymenium in the tubes. Moreover, the quantity of spores produced by the stipe surface is rather different in various species. In some boletes the caulobasidia are relatively abundant, but in some others they are present only in a small number. Abundant caulobasidia occur in members of *Boletus* s. str., *Suillus*, *Leccinum*, in *Tylopilus felleus* (Bull.: Fr.) P. Karst., *Buchwaldoboletus lignicola* (Kalchbr.) Pilát, etc. A smaller number of caulobasidia is a characteristic feature of such species as *Boletus gentilis* (Quél.) Big. et Guill., *Rubinoboletus rubinus* (W. G. Smith) Pilát et Dermek, *Porphyrellus porphyrosporus* (Fr.) Gilbert, *Phylloporus pelletieri* (Lév.) Quél. and some xerocomoid boletes. The search for caulobasidia on the stipe surface can be very difficult in some cases. For example, in *Boletus pulverulentus* Opat. the caulobasidia are constantly present but are not easy to find because in this species all elements of the caulohymenium, including the caulobasidia, are covered with an amorphous incrustation.

It is also important to note that the number of caulobasidia in various parts of the stipe is very different. In the upper part of the stipe the fertile basidia are much more abundant than in the lower half where they are usually scarce or completely absent. In case of a small number of caulobasidia, the caulohymenial elements should be examined not only in longitudinal and transverse sections but also by means of scalps, in which the caulobasidia are usually best seen.

Changes of the caulohymenium in the course of development

The caulohymenium differentiates together with the hymenium of the hymenophore at a primordial stage (cf. Watling 1985: Fig. 1) and remains on the stipe surface all through the development of the carpophore. Nevertheless, it is necessary to mention that the caulohymenium (like the other surface layers of the carpophore) undergoes certain changes during development. In the primordium the caulohymenium forms a continuous layer. In further stages, however, this layer gradually breaks up into small fragments (small islands of caulohymenial elements) as the stipe grows and expands. Some of sterile caulohymenial cells, especially in the lower half of the stipe, have sometimes also a tendency to proliferate with age (Šutara 1987b: Fig. 5). Moreover, in the lower third of the stipe the caulohymenial cells are sometimes mixed with filamentous elements ascending from the tomentum on the stipe base.

Despite all the above-mentioned changes, however, the caulohymenium never loses its characteristic appearance (particularly in the upper half of the stipe) and the fertile caulobasidia are present on the stipe in all developmental stages. As showed some studies of boletes in culture, the caulobasidia are present on the stipe surface even in the cases when the stipe of a primordium never develop a pileus (cf. Pantidou 1962). Between the fertile caulohymenium and the infertile cuticle of the stipe there is always a visible difference. In boletes the presence of the caulohymenium with fertile caulobasidia on the stipe is not only an incidental deviation but a constant, genetically determined character which is the result of a long evolutionary process. Characters concerning the reproductive organs have been usually considered very important from the taxonomic point of view. Accordingly, the fertility or infertility of the stipe surface, i.e. the presence or absence of a caulohymenium with sporulating caulobasidia, is here treated as a significant generic feature of boletes (see also Šutara 1987a, 1987b, 1991, 1992a).

Lateral stipe stratum

The context of the stipe of almost all boletes is composed of a comparatively dense trama with hyphae arranged in a longitudinal way, more or less parallel to the longitudinal stipe axis. This part of the context is called 'the stipe trama proper' in this contribution.

In many boletes the hyphae beneath the caulohymenium diverge from the longitudinal trama proper and form a more or less distinct lateral layer, which is here termed the 'lateral stratum of the stipe trama' or more simply 'lateral stipe stratum' – a slightly modified English version of the original German term 'Stiellateralstratum' of

Lohwag and Peringer (1937). [Note: In an earlier paper the author (Šutara 1989) used the term 'the stipe lateral stratum'].

The lateral stipe stratum is distinguished from the longitudinal stipe trama proper mainly by its divergence, often also by its looser arrangement of the hyphae and sometimes by its gelification.

The lateral stipe stratum, if present, is best developed in the upper half, sometimes also in the middle part of the stipe. In the lower half of the stipe it is usually either very thin or absent. The lateral stipe stratum begins to differentiate beneath the caulohymenium at an early stage and its full development is reached by young or middle age. During further stages this layer usually gradually disappears so that in old age it is often not present at all. Unless otherwise stated the lateral stipe stratum is, in this paper, described as it is usually developed under sufficiently favourable conditions in the upper half (sometimes also in the middle part) of the stipe of young or middle-aged carpophores, in which this layer has usually the most characteristic appearance.

During microscopic study it is necessary to take into consideration that the development of peripheral layers of the stipe (including the lateral stipe stratum) is, to a certain extent, dependent on environmental conditions. In carpophores which grew under unfavourable circumstances (e.g. in extremely dry weather) the lateral stipe stratum is sometimes poorly developed or completely absent.

Some results of the study of the lateral stipe stratum may also be negatively influenced by poor quality of the material examined. In some herbarium specimens the surface layers on the stipe (both caulohymenium and lateral stipe stratum) may be partly or completely damaged by careless handling.

Relation between the lateral stipe stratum and the fertile caulohymenium

Almost all boletes with a fertile caulohymenium have a tendency to form a more or less distinct lateral stratum of the stipe trama under sufficiently favourable conditions. The only exception among Central European boletes is probably *Phylloporus pelletieri* (Lév.) Quél., in which no distinct lateral stipe stratum was found by the present author although the caulohymenium with fertile caulobasidia is present in this species.

On the other hand, boletes with an infertile stipe cuticle (e.g. genera *Gyrodon* Opat., *Gyroporus* Quél., *Boletinus* and *Pseudoboletus*) have no lateral stratum of the stipe trama. An exception in this regard is *Mariaella*, having sometimes a distinctly developed lateral stipe stratum despite the fact that its stipe surface is infertile.

Types of the lateral stipe stratum

Certain taxonomic groups of boletes possess their own characteristic type of the lateral stipe stratum. A very typical lateral stipe stratum (termed 'leccinoid' by the author of this contribution) is present in the genus *Leccinum*, especially in sections *Leccinum* and *Scabra* Smith, Thiers et Watling. The lateral stipe stratum in these two sections is at first a continuous, relatively thick, rather dense, non-gelatinous, almost anticlinally arranged layer of tissue, which soon disrupts into characteristic fascicles of hyphae during the growth of the stipe. This disrupted layer significantly participates in a typical scabrous stipe ornamentation of this genus (see Šutara 1989). In sect. *Luteoscabra* Singer of *Leccinum* the lateral stipe stratum is very similar but somewhat thinner and, at the initial unbroken stage, less densely arranged. A similar lateral stratum of the stipe trama is also developed in *Boletus depilatus* Redeuilh and *Boletus impolitus* Fr. The presence of this type of lateral stipe stratum, which does not occur in the other *Boletus* species, indicates that *B. impolitus* and *B. depilatus* have an isolated position in *Boletus*.

In many boletes some characters of the peripheral layers of the stipe resemble some features of the hymenophore. One of such characters is gelification of the lateral stipe stratum which rather frequently correlates with gelification of the lateral stratum in the tube trama. For example, in *Boletus* s. str. and *Suillus*, in which the hymenophoral trama has gelatinous lateral strata, the lateral stipe stratum is often also gelatinized (see Fig. 1f and Šutara 1989: Figs. 3, 4). This type of the lateral stipe stratum (termed 'boletoid' by the present author) is loosely arranged, divergent, usually well differentiated in both upper and middle part of the stipe where it is usually present from youth to maturity.

In the *Boletus chrysenteron/pruinatus* group, with a weak or almost no gelification of the hymenophoral trama, the lateral stipe stratum is usually non-gelatinous and less distinct because it is thinner and less loosely arranged than in typical representatives of *Boletus* s. str. In most species of the *Boletus chrysenteron/pruinatus* group the lateral stipe stratum is developed only under sufficiently favourable conditions and merely at a young or middle developmental stage. During later stages this layer completely disappears.

A very poorly developed lateral stratum of the stipe trama occurs in such species as *Chalciporus piperatus* (Bull.: Fr.) Singer, *Porphyrellus porphyrosporus* and *Rubinoletus rubinus*. In these species the lateral stipe stratum is developed very rarely (only under extraordinarily optimal conditions) and, if present, forms merely a very thin, almost indistinct layer, which is discernible only in the upper part of the stipe of young carpophores. This considerably reduced layer is so thin that it resembles a caulosubhymenium rather than a lateral stratum.

As was already mentioned, *Phylloporus pelletieri*, whose phylloporoid hymenophoral trama is non-gelatinous, has no distinct lateral stipe stratum (Fig. 2f).

It is, however, interesting that the *Boletus subtomentosus* group, in which the hymenophore also possesses the non-gelatinous phylloporoid trama, the lateral stipe stratum is usually well developed. The lateral stipe stratum in this group is distinctly divergent, loosely arranged, but never gelatinous (see Šutara 1991: Fig. 3).

Between the individual types of lateral stipe stratum there may, naturally, occur intermediate forms which are, to a certain extent, analogous with the intermediate forms of the structure of the hymenophoral trama. To define the distinctions between the above-mentioned types of lateral stipe stratum in a more precise way is therefore very difficult. On the other hand, however, it is obvious that more or less distinct differences in arrangement of the peripheral stipe layers (at least between certain groups of boletes) really exist. Further study of these anatomical differences could contribute to our better understanding of relationships between taxonomic groups in the *Boletaceae* and *Suillaceae*. Unfortunately, the anatomy of the stipe of boletes has been hitherto insufficiently studied. Some aspects of this matter was already discussed in the author's earlier papers (see Šutara 1987a, 1987b, 1989, 1991).

Infertile stipe surfaces of the genera *Boletinus*, *Mariaella* and *Pseudoboletus*

As suggested above, in Central Europe the *Gyrodontaceae* and *Gyroporaceae* have an infertile stipe surface whereas the *Boletaceae* and *Suillaceae* have the stipe covered by a fertile caulohymenium. Among the Central European *Boletaceae* and *Suillaceae* there are only three exceptions having the stipe surface infertile: *Boletinus cavipes* (Klotzsch) Kalchbr., *Mariaella bovina* and *Pseudoboletus parasiticus* (Bull.: Fr.) Šutara.

The genus *Boletinus* (with *B. cavipes* as the type species) has, in the author's opinion, a rather isolated position in the family *Suillaceae*. Its infertile stipe cuticle composed of a trichoderm and above all its abundant clamp connections suggest certain relations to the *Gyrodontaceae*.

It is generally accepted that *Pseudoboletus parasiticus* (\equiv *Xerocomus parasiticus*) is very close to some xerocomoid boletes. However, if *P. parasiticus* (the type species of the genus *Pseudoboletus*) and the xerocomoid boletes are closely related, they must have originated from a common ancestor. In view of the fact that the xerocomoid boletes and even all the other European *Boletaceae* have a fertile caulohymenium, it is very probable that the stipe surface of an ancestor of *Pseudoboletus* was also at first fertile. In the course of evolution it must have changed into an infertile cuticle when *Pseudoboletus* separated as an independent evolutionary branch from the group of the xerocomoid boletes. In the case of *Pseudoboletus* the loss of fertility of the stipe has been possibly a result of adaptation to the conditions of a parasitic life-strategy.

In the genus *Mariaella* (represented by the species *M. bovina*) there is a situation analogous to that in *Pseudoboletus*. *Mariaella*, with an infertile stipe cuticle, has most likely derived from the closely related genus *Suillus*, with a fertile caulohymenium. Also in this case it is very probable that the stipe of an ancestor of *Mariaella* was at first fertile and only subsequently became infertile. One of the anatomical features supporting this hypothesis is that *Mariaella* has sometimes a tendency to form a loosely arranged, gelatinous lateral stipe stratum. Such a lateral stipe stratum occurs very often in species with a fertile caulohymenium, but in boletes with infertile stipe surface (except *Mariaella*) it never appears. We can thus suppose that the lateral stipe stratum of *Mariaella* is probably a relic of the primary evolutionary stage when the stipe of the ancestor of *Mariaella* was fertile.

Pileus cuticle

The terms trichoderm, ixotrichoderm, epithelium, trichodermal palisade and undifferentiated suprapellis are here used essentially in the same sense as in the work of Largent, Johnson and Watling (1977).

The pileus cuticle (like most cortical layers) often changes its appearance in the course of development. The trichodermal elements sometimes become aggregated into tufts (macroscopically looking like a granulose-tomentose or squamulose surface) or, as the pileus grows and expands, the cuticular layer may disrupt and expose the subcuticular layer of the context in the cracks between fragments of the cuticle (an areolate-rimose surface). Very often the trichodermal hyphae on the pileus collapse with age under the influence of weather conditions so that the initially erect or suberect, anticlinal trichoderm (a tomentose or subtomentose surface) finally changes into a cuticle similar to a cutis with depressed, periclinal hyphae (a glabrous surface). It is obvious that the correct interpretation of dermal layers in older carpophores can sometimes be very difficult. Therefore the cuticle should be studied above all in younger stages whenever possible.

Key to families of Central European boletes with a tubular hymenophore (including the lamellate genus *Phylloporus*)

- 1a Clamp connections constantly present, abundant in the carpophore 2
- 1b Clamp connections absent or very rare 4
- 2a Spores of gyrodonoid shape, broadly ellipsoid or subovoid. Spore surface smooth or with a finely denticulate exosporium distinct under an electron microscope (see Perreau 1981). Partial veil absent 3

- 2b Spores of boletoid shape, narrowly subfusoid or fusoid-ellipsoid, usually with a suprahilar depression, smooth. Partial veil (annulus) present
 genus *Boletinus*, family *Suillaceae*
- 3a Peripheral zone of the stipe trama (immediately beneath the outer trichoderm) arranged in a direction more or less parallel to the longitudinal stipe axis. Spore print medium brown with an olivaceous tint. Tubes short, decurrent. Pores at first arranged somewhat irregularly (almost labyrinthiform), finally rather large, more or less radially elongated genus *Gyrodon*, family *Gyrodonaceae*
- 3b Peripheral zone of the stipe trama (beneath the outer trichoderm) of a very unusual structure, forming a hard, very compact cortex with a rather large number of hyphae arranged horizontally, around and across the longitudinal stipe axis (see Reijnders 1963, Corner 1972). Spore print light-coloured: pale yellowish or pale ochraceous. Tubes much longer than in the previous case, depressed around the stipe apex when mature. Pores small, roundish
 genus *Gyroporus*, family *Gyroporaceae*
- 4a Characteristic fascicles of oleocystidia with a conspicuous, dark incrustation present in the hymenophore. For a detailed description of these fasciculate oleocystidia which are here labelled as 'of the *Suillus* type', see the diagnosis of the genus *Suillus* family *Suillaceae*
- 4b Fascicles of conspicuously incrustated oleocystidia of the *Suillus* type absent
 family *Boletaceae*

Suillaceae (Singer) Besl et Bresinsky

Pl. Syst. Evol. 206: 239, 1997.

Type genus: *Suillus* Adans.

Characters of European genera (North American gasteroid forms, e.g. *Gastrosuillus* Thiers, are not included in this diagnosis): Carpophores pileate-stipitate, fleshy. Pileus covered by a gelatinous ixotrichoderm, filamentous trichoderm or a two-layer cuticle consisting of the upper trichodermal and lower gelatinous layer. Pileus trama composed of loosely interwoven, filamentous or somewhat broadened hyphae. Hymenophore tubular, adnate or decurrent. Pores small, medium-sized or radially elongated (boletinoid). Hymenophoral trama bilateral, mostly boletoid, rarely mariaelloid. Characteristic fascicles of oleocystidia with a dark incrustation often present in the hymenophore and sometimes also on the stipe. Basidia usually smaller than in the *Boletaceae*. Spores relatively small, smooth, of boletoid shape, i.e. elongate subfusoid or fusoid-ellipsoid. Spore print ochraceous, cinnamon-brown, medium brown, brown-olivaceous, grey-brown, ferruginous brown, chocolate-brown or purplish brown. Partial veil (annulus)

either present or absent. Stipe more or less central, mostly solid, less frequently hollow, often covered by a fertile, gradually fragmenting caulohymenium, less frequently by an infertile cuticle consisting of a trichoderm or trichodermal palisade. Basal part of the stipe infertile, usually covered with a tomentum. Lateral stipe stratum mostly present, but sometimes absent. Context of the pileus and stipe composed of a monomitic hyphal system with generative, thin-walled hyphae. Clamp connections either absent or present.

Forms mycorrhizal associations with conifers.

Delimitation: According to Besl and Bresinsky (1997: 239), the family *Suillaceae* is chemotaxonomically characterized by the presence of 'compounds of type cavipetin, suillin and/or boviquinone'. The chemotaxonomic classification has been strongly supported by modern molecular analyses (e.g. Bruns and Szaro 1992, Bruns et al. 1998, Kretzer and Bruns 1999, Binder and Bresinsky 2002, etc.). Anatomical features characterizing the Central European members of this family are obvious from the above description and key.

European genera: *Boletinus*, *Mariaella* and *Suillus*.

Key to European genera of the family *Suillaceae*

- 1a Clamp connections none or very scarce in the carpophore. Characteristic fascicles of incrustated oleocystidia of the *Suillus* type constantly present in the hymenophore, sometimes also on the stipe. Stipe solid. Under favourable conditions the carpophores have a tendency to form a lateral stipe stratum, especially in the upper half of the stipe 2
- 1b Clamp connections constantly present, abundant. Fascicles of incrustated caulocystidia of the *Suillus* type absent both in the hymenophore and in the stipe. Stipe hollow. Lateral stipe stratum never present *Boletinus*
- 2a Stipe surface infertile, composed of a trichodermal palisade of strongly incrustated filamentous elements (see Šutara 1987a, Fig. 6). Caulobasidia absent. Hymenophoral trama of the mariaelloid type, gelatinized over the whole width, not differentiated into a mediostratum and lateral strata (Figs. 3a, 3c, 4d). Atrotomentin, methyl bovinate and simple boviquinone derivatives present, but grevillins absent (cf. Høiland 1987, Gill and Steglich 1987, Besl and Bresinsky 1997). Carpophores turning vinaceous red to purple when boiled in water (F. Smotlacha 1947). Development of the carpophores gymnocarpous (Reijnders 1963) *Mariaella*

2b Stipe surface fertile, composed of a gradually fragmenting caulohymenium. Spore-bearing caulobasidia present (Figs. 1f, 4c). Hymenophoral trama usually boletoid, with a distinctly differentiated mediostratum and lateral strata (Figs. 1c, 1d, 3b), rarely mariaeloid. Atrotomentin and methyl bovinate absent. Simple boviquinone derivatives found very sporadically and, if present, occur together with grevillins (Høiland 1987, Gill and Steglich 1987, Besl and Bresinsky 1997, etc.). Carpophores not changing colour to vinaceous red or purple when boiled in water. Carpophore development (at least in all species whose ontogeny is known) pilangiocarpous or mixangiocarpous (cf. Reijnders 1963) *Suillus*

***Boletinus* Kalchbr.**

Mohls Bot. Zeitung 25: 182, 1867.

Syn.: *Euryporus* Quél., Enchir. Fung.: 163, 1886.

Typus: *Boletus cavipes* Klotzsch [= *Boletinus cavipes* (Klotzsch) Kalchbr.]

Characters: Pileus cuticle a thick trichoderm. Tubes short, decurrent. Pores large, angular, radially elongated (boletinoid). Hymenophoral trama boletoid. Cystidia scattered, not forming such conspicuous, dark incrustated fascicles as occur in *Suillus*. Spores smooth, relatively small, of boletoid shape, elongate subfusoid or fusoid-ellipsoid, with slight suprahilar depression. Spore print ochraceous olive to brown. Partial veil present, remaining as an annulus on the stipe. Stipe central, hollow. Stipe surface infertile, composed of a trichoderm (see Kühner 1927: Fig. VI and Šutara 1987b: Fig. 1). Peripheral zone of the stipe trama (immediately under the trichoderm) forming a dense, compact tissue with hyphae arranged in a longitudinal way. Lateral stipe stratum absent. Clamp connections abundant, constantly present.

Forms mycorrhizal associations with *Larix*.

Delimitation: The opinions on the taxonomic position and delimitation of this genus have been very controversial. Some authors, e.g. Smith and Thiers (1964) and Arpin and Kühner (1977), have treated *Boletinus* merely as an infrageneric taxon (as a section or subgenus) of the genus *Suillus*. On the other hand, Pegler and Young (1981) and Jülich (1982) have accepted *Boletinus* as a separate genus and have placed it even in another family, viz. in the *Gyrodontaceae*. Similarly, Høiland (1987) has placed the genera *Boletinus* and *Suillus* in two different families, the former in the *Boletaceae* and the latter in the *Gomphidiaceae*. Currently most authors, e.g. Singer (1975, 1986), Moser (1983), Engel et al. (1996), Besl and Bresinsky (1997), Lannoy and Estades (2001) and others, have accepted *Boletinus* (usually in a restricted sense) as an independent genus situated near *Suillus*.

Boletinus in the narrow concept is well distinguished from *Suillus* mainly by the following anatomical characters: (1) abundant clamp connections, (2) infertile stipe cuticle consisting of a trichoderm, and (3) absence of the fasciculate oleocystidia with dark incrustation (see Šutara 1987b). Moreover, the *Suillus* species have a more or less distinct tendency to form a divergent, loosely arranged lateral stratum of the stipe trama under favourable conditions, but in the genus *Boletinus* this layer is never developed.

Material examined: *Boletinus cavipes* (Klotzsch) Kalchbr. (JŠ 413, 661, 2578, 2580, 3061, 3102, 3105 etc.) and *Boletinus asiaticus* Singer (PRM 829078, collection from Finland).

Suillus Adans.

Fam. Pl. 2: 10, 1763.

Syn.: *Rostkovites* P. Karst., Rev. Mycol. 3: 16, 1881. – *Cricunopus* P. Karst., Rev. Mycol. 3: 16, 1881. – *Viscipelis* Quél., Enchir. Fung.: 155, 1886. – *Ixocomus* Quél., Fl. Mycol. Fr.: 411, 1888.

Typus: *Boletus luteus* L.: Fr. [= *Suillus luteus* (L.: Fr.) Roussel]

Characters: Pileus mostly covered by a strongly gelatinized ixotrichoderm, less frequently by a two-layer cuticle consisting of the upper trichoderm and the lower gelatinous layer (see Bresinsky and Schwarzer 1969: Fig. 15). Tubes short or moderately long, adnate or decurrent. Pores mostly small, roundish, less frequently enlarged or radially elongated. Hymenophoral trama usually boletoid (Figs. 1c, 1d, 3b), rarely mariaelloid. Characteristic fascicles of oleocystidia of the *Suillus* type constantly present in the hymenophore (Figs. 1c, 1d). The fasciculate oleocystidia subcylindric or narrowly clavate, conspicuously incrustated with a dark brown matter particularly in their basal part. Content of the fasciculate oleocystidia at first yellowish brown, but finally becoming dark brown or brown violet, especially in dried carpophores or by action of an alkali, e.g. ammonium hydroxide or KOH (for a more detailed description of the cystidia in *Suillus*, see Smith and Thiers 1964). Spores smooth, relatively small, elongate subfusoid or fusoid-ellipsoid, with small suprahilar depression. Spore print of various ochraceous or brownish shades, e.g. ochraceous, cinnamon-brown, olivaceous brown, medium brown, grey-brown, ferruginous brown, chocolate-brown or reddish brown etc. Partial veil (annulus) either absent or present, in a few species glutinous. Stipe central, solid, covered by a gradually fragmenting caulohymenium with fertile caulobasidia (Figs. 1f, 4c and Šutara 1987a: Fig. 7, Šutara 1987b: Figs. 2-9). So-called 'glandular dots' on the stipe (consisting of such conspicuous fascicles of dark incrustated oleocystidia as occur in the hymenophore) mostly present, but absent in several species. Under sufficiently favourable conditions young and middle-aged carpophores have a tendency to form a lateral stratum of the stipe trama, particularly in the upper half, sometimes also in

the middle part of the stipe (Fig. 1f). The lateral stipe stratum rather different in various members of this genus, in some species well developed, loosely arranged, more or less gelatinous, 40–120(–180) μm thick, but in some others inconspicuous, non-gelatinous, thinner than 40 μm . Stipe trama proper composed of densely and longitudinally arranged hyphae. Clamp connections none or very rare in the carpophore.

Mycorrhizal associations with *Pinus*, *Larix*, *Pseudotsuga* and possibly with some other conifers.

Delimitation: Some authors (e.g. Smith and Thiers 1964, 1971; Grund and Harrison 1976) have accepted a wider circumscription of the genus *Suillus*, with *Boletinus* and *Paragyrodon* as infrageneric taxa (but without several species with vinaceous or purplish brown spores which these authors transferred to a separate genus, *Fuscoboletinus* Pomerleau et A. H. Smith). A broad concept of *Suillus* has been also adopted by Kretzer et al. (1996). Currently the most widely accepted opinion on the circumscription of the genus *Suillus* is that of Singer (1967, 1975, 1986), see e.g. Moser (1983), Alessio (1985), Engel et al. (1996), Besl and Bresinsky (1997) and Lannoy and Estades (2001).

The opinion of the present author on the limits between *Suillus* and *Boletinus* was already formulated above. For the differences between *Suillus* and *Mariaella*, see the notes on the delimitation of the latter.

Material examined: *Suillus collinitus* (Fr.) O. Kuntze (PRM 654265; BRNM 346045; JŠ 2608, 3114, 4052 etc.), *Suillus flavidus* (Fr.: Fr.) J. Presl (PRM 619765; JŠ 1887, 2646, 2650, 2653), *Suillus granulatus* (L.: Fr.) Roussel (JŠ 2259, 2398, 3057, 3094 etc.), *Suillus grevillei* (Klotzsch: Fr.) Singer (JŠ 2215, 2225, 3039–40, 3101 etc.), *Suillus lakei* (Murrill) Smith et Thiers var. *landkammeri* (Pilát et Svrček) Engel et Klofac (PRM 628919, 648075; BRNM 235894), *Suillus laricinus* (Berk.) O. Kuntze [= *Suillus aeruginascens* (Opat.) Snell] (JŠ 2434, 2437, 2440, 2498 etc.), *Suillus luteus* (L.: Fr.) Roussel (JŠ 1674, 3045, 4050–51 etc.), *Suillus placidus* (Bonord.) Singer (BRNM 346081; CB 1871; JŠ 2368–69 etc.), *Suillus sibiricus* Singer (CB 143, 147), *Suillus tridentinus* (Bres.) Singer (PRM 709684; JŠ 3073, 3075–76 etc.) and *Suillus variegatus* (Swartz: Fr.) O. Kuntze (JŠ 2643–44, 3056 etc.).

Mariaella Šutara

Čes. Mykol. 41: 73, 1987.

Typus: *Boletus bovinus* L.: Fr. [= *Mariaella bovina* (L.: Fr.) Šutara]

Characters: Pileus cuticle a gelatinous ixotrichoderm. Tubes short, adnate or subdecurrent. Pores rather large, angular, somewhat radially elongated, almost boletinoid when mature. Hymenophoral trama of the mariaelloid type, strongly gelatinized, slightly divergent, not differentiated into a mediostratum and lateral strata (Figs. 3a, 3c, 4d). Fascicles of conspicuously incrusting oleocystidia of the *Suillus* type abundant in the hymenophore (see Šutara 1987a: Figs. 3, 5). Spores relatively small, smooth, elongate subfusoid or fusoid-ellipsoid, with small suprahilar depression. Spore print light olive-brown. Partial veil (annulus) absent.

Stipe central, solid. Stipe cuticle infertile, consisting of a trichodermal palisade of filamentous elements strongly incrustated with crystals and amorphous material. The initially continuous layer of the trichodermal palisade gradually fragments into small, often more or less collapsed tufts of cuticular elements as the stipe grows and expands (see Šutara 1987a: Figs. 6b, 6d). Caulobasidia not found. Lateral stipe stratum sometimes developed and, if present, forming a divergent, loosely arranged and gelatinous layer occurring especially in the upper half of the stipe of young carpophores (see Šutara 1987a: Fig. 6d). Stipe trama proper densely arranged in a longitudinal direction. Carpophores turning vinaceous red to purple when boiled in water. Flesh of carpophores more elastic than in *Suillus* species. Clamp connections in the carpophore none or very rare.

Mycorrhizal associations with *Pinus*.

Delimitation: The genus *Mariaella*, represented by the species *Mariaella bovina*, is closely related to *Suillus*, from which it differs particularly in the infertile stipe cuticle lacking caulobasidia. A further distinctive feature of *Mariaella* is the fact that the infertile stipe cuticle occurs simultaneously with the gelatinous lateral stipe stratum. Such a type of arrangement of peripheral stipe layers is exceptional, unknown in the other boletes.

A very typical anatomical character of *Mariaella* is also the mariaelloid hymenophoral trama. In the genus *Suillus* this type of the trama has been found very rarely, only in some carpophores of *Suillus flavidus* and *Suillus pictus*. The fact that the arrangement of the hymenophoral trama in *Suillus bovinus* = *Mariaella bovina* is not identical with the boletoid tramal structure in *Suillus luteus* and *Suillus granulatus* was already mentioned by Disbrey and Watling (1967).

Data published by some authors (Høiland 1987, Gill and Steglich 1987, Besl and Bresinsky 1997, etc.) show that *Mariaella bovina* (cited as *Suillus bovinus* by these authors) is also distinguished from species of *Suillus* chemotaxonomically, e.g. by the presence of atrotomentin and methyl bovinate. In the other *Suillaceae* (including the *Suillus* species) these compounds have not been found. Furthermore, *Mariaella bovina* is the only species of the *Suillaceae* which contains simple boviquinone derivatives [boviquinone-4 (bovinone), diboviquinone-4,4, methylenediboviquinone-4,4 (amitenone)], but lacks grevillins. In the 36 *Suillus* species investigated, simple boviquinone derivatives have been detected very sporadically, only in two cases: boviquinone-4 in *Suillus pictus* and diboviquinone-4,4 in *Suillus americanus* (Peck) Snell. In contrast to *Mariaella*, however, these two species, like most of the other members of *Suillus*, contain grevillins.

It is interesting that the very rare combination of the presence of boviquinones with the absence of grevillins (which is typical of *Mariaella*) occurs as well as in some *Chroogomphus* species, e.g. *Chroogomphus rutilus* (Schaeff.: Fr.) O. K. Miller, *Chroogomphus helveticus* (Singer) Moser and *Chroogomphus tomentosus*

(Murrill) O. K. Miller. The carpophores of *Chroogomphus rutilus* and *Mariaella bovina* have also some similar colour reactions, e.g. with ethanol and alkali (see Gill and Steglich 1987 and others). These facts suggest an affinity between *Mariaella* and the genus *Chroogomphus* (Singer) O. K. Miller (*Gomphidiaceae*).

Some of the characteristic macrochemical reactions of *Mariaella bovina* have been long known to mushroom pickers because the carpophores change colour to vinaceous red or purple when boiled in water and to vinaceous pink after drying (see F. Smotlacha 1947, Kluzák et al. 1985, M. Smotlacha and Malý 1986 and others). This colour change has not been observed in any species of *Suillus*.

In all the *Suillus* species whose ontogeny is known the development of carpophores is different from that in *Mariaella*. According to Reijnders (1963) the development in *Boletus bovinus* (\equiv *Mariaella bovina*) is gymnocarpous while in the species of *Suillus* pilangiocarpous (*S. americanus*, *S. granulatus*, *S. placidus*, *S. spectabilis*, *S. variegatus* and probably *S. pictus*) or mixangiocarpous (*S. luteus*, *S. aeruginascens* and probably *S. grevillei*). Also the development of *Boletinus* species, e.g. *Boletinus cavipes* and *Boletinus paluster* (Peck) Peck, is pilangiocarpous or mixangiocarpous (Reijnders 1963), i.e. pseudoangiocarpous in the terminology of some other authors (e.g. Kühner 1926, Gentile and Snell 1953). The gymnocarpous development (unknown in the other genera of this family) complements the exceptional anatomical and chemical characters of *M. bovina*, which indicate the isolated position of *Mariaella* in the *Suillaceae*.

Material examined: *Mariaella bovina* (L.: Fr.) Šutara, according to the present knowledge, the only species belonging to this genus (JŠ 277, 542, 1742, 2077, 2101, 2281–83, 2311, 3034, 3038, 3065, 3069, 4048, 4049 etc.).

***Boletaceae* Chevallier**

Flore Env., Paris 1: 248, 1826.

Syn.: *Strobilomycetaceae* Gilbert, Les Bolets: 105, 1931 (ut *Strobilomyceteae*). – *Xerocomaceae* (Singer) Pegler et Young, Trans. Brit. Myc. Soc. 76: 112, 1981.

Type genus: *Boletus* L.

Characters of European genera (gasteroid forms, e.g. *Chamonixia* Roll., are not included in this diagnosis): Carpophores pileate–stipitate, fleshy. Universal veil mostly absent, but present in one European genus (*Strobilomyces*). Pileus soft; its context composed of loosely interwoven, filamentous or somewhat swollen hyphae. Hymenophore usually tubular, exceptionally lamellate (in *Phylloporus*). Structure of the hymenophoral trama bilateral, mostly boletoid, less frequently phylloporoid or intermediate between the boletoid and phylloporoid type. Pleurocystidia scattered; cheilocystidia sometimes grouped in clusters, but never forming such conspicuous fascicles of oleocystidia with dark

incrustation as occur in *Suillus*. Spores smooth or ornamented, mostly elongate subfusoid or fusoid-ellipsoid, less frequently elongate fusoid-cylindric, rarely fusoid-truncate or shortly ellipsoid to subglobose. Stipe solid, mostly central, rarely somewhat eccentric. Except for one species with an infertile stipe cuticle (*Pseudoboletus parasiticus*), all the other European *Boletaceae* have a substantial part of the stipe covered by a fertile caulohymenium with sporulating caulobasidia. The caulohymenium gradually fragments into small islands of caulohymenial elements as the stipe expands. Basal part of the stipe infertile, often covered with a tomentum. Lateral stratum of the stipe trama mostly more or less developed, but sometimes absent. Stipe trama proper densely arranged, more or less parallel with the longitudinal stipe axis. Hyphal system both in pileus and stipe monomitic, with thin-walled generative hyphae. Thick-walled microscopic elements occur very rarely (e.g. thick-walled cystidia in the extra-European genera *Boletochaete* Singer and *Tubosaeta* Horak). Clamp connections none or extremely rare in the carpophore.

A substantial majority of members of this family are mycorrhizal, only a few species saprotrophic [e.g. *Buchwaldoboletus lignicola* (Kallenb.) Pilát]. Only one European species, *Pseudoboletus parasiticus*, is parasitic (see Kavina 1935).

European subfamilies: *Boletoideae* and *Strobilomycetoideae*.

Key to European subfamilies of the family *Boletaceae*

- 1a Carpophores covered with a true universal veil which disrupts into fragments remaining as floccose-woolly scales on pileus and stipe. The only European species of this group (*Strobilomyces strobilaceus*) has almost globose spores, with a conspicuous reticulate ornamentation distinct even under a low microscopic magnification. Spore print very dark, almost black
 subfamily *Strobilomycetoideae*, genus *Strobilomyces*
- 1b Universal veil absent. Spores usually elongated, subfusoid, fusoid-ellipsoid or fusoid-truncate, exceptionally shortly ellipsoid (in *Rubinoboletus*). Spores of European species of this subfamily have either a smooth surface or a very fine surface ornamentation discernible only under oil immersion or with an electron microscope. Spore print olivaceous, olivaceous brown, yellow-brown, pinkish brown, ferruginous, medium brown, reddish brown etc., but never almost black subfamily *Boletoideae*

Subfamily *Boletoideae*

Type genus: *Boletus* L.

Characters of European genera: Both universal and partial veil (annulus) absent. Pileus cuticle a trichoderm, trichodermal palisade or epithelium. Hymenophore usually tubular, exceptionally lamellar. Spores smooth or very finely ornamented. Spore print of various brown, olivaceous or reddish brown shades, e.g. olivaceous, olive-brown, cinnamon, ferruginous brown, pale brown, medium brown, pinkish brown, reddish brown etc. The other characters are obvious from the above diagnosis of the family *Boletaceae*.

Delimitation: The differences between the subfamilies *Boletoideae* and *Strobilomycetoideae* are apparent from the above key.

European genera: *Boletus*, *Buchwaldoboletus*, *Chalciporus*, *Leccinum*, *Phylloporus*, *Porphyrellus*, *Pseudoboletus*, *Rubinoboletus*, *Tylopilus*.

Key to European genera of the subfamily *Boletoideae*

- 1a Stipe surface infertile, composed of a filamentous trichoderm (Fig. 4b and Šutara 1991: Figs. 1, 2). Caulobasidia absent. Species growing on carpophores of gasteromycetes (*Scleroderma* or *Astraeus*). Carpophore development of the only European species of this genus (*Pseudoboletus parasiticus*) hypovelangiocarpous (paravelangiocarpous), see Reijnders (1963). Spores of *P. parasiticus* distinctly pitted under an electron microscope (see Oolbekkink 1991, Holec 1994) *Pseudoboletus*
- 1b Stipe surface more or less fertile, composed of a caulohymenium which gradually fragments into small islands of caulohymenial elements as the stipe grows and expands. Spore-bearing caulobasidia present. Species not growing on carpophores of gasteromycetes. All the European species of this group whose ontogeny is known have the carpophore development different from that in *P. parasiticus*, viz. gymnocarpous, pilangiocarpous etc. (cf. Reijnders 1963, Pantidou 1964, Watling 1985, Singer 1986 and others). Spores smooth or slightly ornamented under an electron microscope, but never pitted 2
- 2a Species saprotrophic, growing on wood *Buchwaldoboletus*
- 2b Species not lignicolous 3
- 3a Spores of boletoid shape, elongate subfusoid, fusoid-ellipsoid or fusoid-truncate, usually with small suprahilar depression 4
- 3b Spores shortly ellipsoid, some with adaxial applanation *Rubinoboletus*

- 4a Stipe surface covered by a typical scabrous ornamentation, with scabrosities dark-coloured from youth or darkening with age in a large majority of cases. The stipe scabrosities consist of characteristic fascicles of hyphae (i.e. fragments of a characteristic, disrupted, almost anticlinally arranged, non-gelatinous lateral stratum of the stipe trama) ending in elements of the caulohymenium *Leccinum*
- 4b Stipe ornamentation not as above 5
- 5a Spore print with a more or less distinct olivaceous tint, e.g. olivaceous or olive-brown 6
- 5b Spore print without olivaceous tint, e.g. pinkish brown, light brown, cinnamon-brown, ferruginous brown, chocolate- to reddish brown etc. 7
- 6a Hymenophore tubular. Carpophores having a tendency to form a lateral stipe stratum under sufficiently favourable conditions, particularly in the upper half of the stipe of young or middle-aged carpophores (see Lohwag and Peringer 1937: Figs. 6, 7; Šutara 1989: Figs. 3, 4; Šutara 1991: Fig. 3) *Boletus*
- 6b Hymenophore lamellate, with numerous anastomoses. Carpophores of the only European species of this genus (*Phylloporus pelletieri*) without a distinctly developed lateral stipe stratum (Fig. 2f) *Phylloporus*
- 7a Carpophores slender and relatively small [pileus (10-)20-60(-90) mm and stipe 20-70 x 3-10 mm in a full-grown stage]. Spore print in European species of this genus cinnamon- or ferruginous brown. Tubes adnate or subdecurrent. Pores (and often also tube-sides) ferruginous, cinnamon-brown, raspberry- to vinaceous red or vivid yellow. Flesh yellow in the stipe; basal mycelium also yellow *Chalciporus*
- 7b Carpophores usually larger [pileus (40-)50-150(-200) mm and stipe 40-160 x 10-40 mm]. Spore print pinkish brown, pale brown or chocolate- to reddish brown. Tubes long, depressed around the stipe apex when mature. Both pores and tube-sides whitish, pale pinkish or grey-cream when young, pinkish brown, grey-brown or medium brown when mature, never so vividly coloured as above. Flesh at first whitish, sometimes pale greyish, slightly brownish or dirty cream-coloured when old, but never yellow in the stipe. Basal mycelium white or dirty whitish 8
- 8a Spore print of the only European species of this genus (*Tylopilus felleus*) light-coloured: pinkish brown or pale brown. Lateral stipe stratum usually well developed under normal conditions, loosely arranged, present in both upper and middle part of the stipe *Tylopilus*

8b Spore print of the only European species of this genus (*Porphyrellus porphyrosporus*) chocolate-brown or reddish brown, darker than in the previous case. Lateral stipe stratum occurs very rarely and, if present, forms a considerably reduced, very thin, almost indistinct layer present only in the upper part of the stipe *Porphyrellus*

***Boletus* L.**

Sp. Pl.: 1176, 1753 (nom. cons.)

Syn.: *Tubiporus* Paulet ex P. Karst., Rev. Mycol. 3: 16, 1881. – *Versipellis* Quéél., Enchir. Fung.: 157, 1886. – *Dictyopus* Quéél., Enchir. Fung.: 159, 1886. – *Xerocomus* Quéél. in Mougeot et Ferry, Fl. Vosges, Champ.: 477, 1887. – *Oedipus* Bataille, Les Bolets: 13, 1908. – *Suillellus* Murrill, Mycologia 1: 16, 1909. – *Ceratomyces* Murrill, Mycologia 1: 140, 1909. – *Xerocomopsis* Reichert, Palest. Journ. Bot. Rehov. Ser. 3: 229, 1940. – *Aureoboletus* Pouzar, Čes. Mykol. 11: 48, 1957.

Typus: *Boletus edulis* Bull.: Fr. (typ. cons.)

Characters: Pileus surface mostly a trichoderm, less frequently a trichodermal palisade, rarely an epithelium consisting of hyphal chains of broad, short cells. Tubes depressed around the stipe apex, adnate or subdecurrent. Pores small or somewhat enlarged. Structure of the hymenophoral trama boletoid, phylloporoid or intermediate between the boletoid and phylloporoid type. Spores of boletoid shape, elongate subfusoid, rarely fusoid-truncate, with more or less distinct suprahilar depression. Spore surface mostly smooth, sometimes very finely ornamented, e.g. venose, rugulose or 'bacillate'. [Note: The adjective 'bacillate' was used by some authors (e.g. Heinemann, Rammeloo and Rullier 1988) for an unusual ornamentation looking as if the surface of spores was covered with rod-like bacteria (bacilli). This ornamentation is distinct only at the level of an electron microscope]. Spore print olivaceous or olive-brown when fresh. Stipe central, solid, with a reticulate or granulate ornamentation. Stipe surface composed of a gradually fragmenting caulohymenium with fertile caulobasidia. Lateral stipe stratum usually more or less developed at least in young or middle-aged carpophores. Stipe trama proper consisting of hyphae more or less parallel with the longitudinal axis of the stipe. Clamp connections none or extremely rare in the carpophore.

Mycorrhizal with both deciduous and coniferous trees.

Delimitation: *Boletus* is distinguished from related genera mainly by the following characters: (a) from *Pseudoboletus* by the fertile caulohymenium on the stipe surface and by the mycorrhizal strategy, (b) from *Rubinoboletus* by the elongate subfusoid shape of the spores, (c) from *Buchwaldoboletus* by the non-

lignicolous growth and (d) from *Tylophilus*, *Porphyrellus* and European species of *Chalciporus* by the olivaceous tint of the spore print.

European subgenera: In the European flora the genus *Boletus* is represented by the subgenera *Boletus* and *Xerocomus*.

Key to Central European subgenera of the genus *Boletus*

- 1a Structure of the hymenophoral trama more or less boletoid. Spores smooth
 subgenus *Boletus*
- 1b Structure of the hymenophoral trama phylloporoid or intermediate between the phylloporoid and boletoid type. However, the limits between the boletoid, phylloporoid and intermediate forms of the trama are not sharp (see the notes under the subgenus *Xerocomus*). Spores smooth or finely ornamented, e.g. venose, rugulose, bacillate etc. subgenus *Xerocomus*

Boletus subg. *Boletus*

Typus: *Boletus edulis* Bull.: Fr.

Characters: Pileus surface mostly a trichoderm, rarely a trichodermal palisade or epithelium. The pileus cuticle changes its appearance according to weather conditions and age of carpophores. The initially erect trichoderm often gradually collapses. In many species the surface of trichodermal hyphae may sometimes be partly covered with a thin layer of gelatinous matter. Tubes mostly long, depressed around the stipe apex when mature, rarely adnate or subdecurrent. Colour of tubes white or yellow when young, olive-yellow, yellow-brown, yellow-green or olive-brown when mature. Pores usually small, rarely medium large, mostly concolorous with tube-sides, but sometimes coloured differently, e.g. red-orange, deep red or vinaceous purple in section *Luridi*. Hymenophoral trama more or less boletoid (see e.g. Lohweg and Peringer 1937: Figs. 3, 5, 9), with a more or less distinct gelification of lateral strata. Spores smooth, of the boletoid form, elongate subfusoid or fusoid-ellipsoid, with suprahilar depression. Spore print olivaceous or olive-brown when fresh. Stipe mostly rather massive, ornamented with a reticulation or small floccose granules. Although the reticulate and non-reticulate stipe surfaces in the subgenus *Boletus* have a somewhat different macroscopic appearance, from an anatomical viewpoint they are nothing more than modified forms of one type of arrangement of peripheral stipe layers. Stipe surface fertile, composed of a gradually fragmenting caulohymenium with spore-bearing caulobasidia. Lateral stipe stratum usually well developed under normal conditions. Almost all European species of this subgenus have the lateral stipe stratum boletoid, 20-100(-150) μm thick, not disrupt-

ing, loosely arranged, rather often gelatinized, consisting of hyphae running divergently or somewhat irregularly from the longitudinal stipe trama proper towards the stipe surface (see Lohwag and Peringer 1937: Figs. 6, 7; Šutara 1989: Figs. 3, 4). Only *B. impolitus* and *B. depilatus* have the lateral stipe stratum 150–400(–640) μm thick, non-gelatinous, arranged almost anticlinally, disrupting into characteristic fascicles of hyphae, very similar to that in *Leccinum*. Flesh white, dirty yellowish or yellow.

Mycorrhizal both with deciduous trees (*Fagales*, *Betulales*, *Salicales*) and with conifers (*Pinaceae*).

Delimitation: The limits between the subgenera *Boletus* and *Xerocomus* are discussed under the latter.

Material examined: *Boletus aereus* Bull.: Fr. (BRNM 236110, 236125, 265773; CB 1348 etc.), *Boletus appendiculatus* Schaeff. (PRM 775391; JŠ 2136), *Boletus badius* (Fr.): Fr. (JŠ 373, 395, 2102, 3089, 3223–25 etc.), *Boletus calopus* Pers.: Fr. (BRA 13.9.1988; LIT 3719/171; JŠ 285, 2139 etc.), *Boletus depilatus* Redeuilh (PRM 647825, 717049; BRNM 265679, 265823, 265858, 265867; JŠ 3155 etc.), *Boletus edulis* Bull.: Fr. (JŠ 3146, 3149–51, 4032 etc.), *Boletus erythropus* Pers.: Fr. (LIT 3719/173; JŠ 058, 282, 316 etc.), *Boletus fragrans* Vitt. (herb. Drescher), *Boletus gentilis* (Quél.) Big. et Guill. (BRNM 265460; CB 1515; JŠ 2127, 4043 etc.), *Boletus impolitus* Fr. (PRM 682521; BRNM 265816; JŠ 1704, 2079–80, 2535–36 etc.), *Boletus junquilleus* (Quél.) Boud. (BRNM 236073, 265822; JŠ 3128, 4044 etc.), *Boletus legaliae* Pilát et Dermek (JŠ 3546), *Boletus luridus* Schaeff.: Fr. (JŠ 059, 317, 2769, 4041 etc.), *Boletus moravicus* Vacek (BRNM 265530–31, 265534; CB 3435–38 etc.), *Boletus pinophilus* Pilát et Dermek (JŠ 2387, 2800, 3139–40 etc.), *Boletus pulverulentus* Opat. (BRNM 265815; CB 922, 1127; JŠ 041–42, 3463 etc.), *Boletus queletii* Schulzer (PRM 836121; BRNM 236086, 265835, 266120 etc.), *Boletus radicans* Pers.: Fr. (JŠ 2785, 3144, 4035, 4037 etc.), *Boletus regius* Krombh. (JŠ 044, 3525), *Boletus reticulatus* Schaeff. (JŠ 2395, 3129–30, 4034 etc.), *Boletus rhodoxanthus* (Krombh.) Kallenb. (BRNM 265697; BRA 17.9.1988; CB 1143–44, 1781 etc.), *Boletus rhodopurpureus* Smotlacha (BRNM 265731, 265746; CB 1145, 1779 etc.), *Boletus satanas* Lenz (JŠ 3091, 3142, 4039 etc.), *Boletus subappendiculatus* Dermek, Lazebník et Veselský (JŠ 318), *Boletus torosus* Fr. (JŠ 3552).

Notes on *Boletus gentilis* and the genus *Pulveroboletus*

Boletus gentilis was transferred by Singer (1947) to the genus *Pulveroboletus* Murrill. It is, however, necessary to point out that *Boletus gentilis* and *Pulveroboletus ravenelii* (Berk. et Curtis) Murrill (the type species on which *Pulveroboletus* is based) have very different anatomical characters. *B. gentilis* has (1) a fertile caulohymenium on the stipe, (2) a typically boletoid, gelatinous lateral stratum of the stipe trama and (3) no veil. These and all the other anatomical features of *B. gentilis* are very similar to those in *Boletus* s. str. and therefore this species is here treated as a member of *Boletus*.

In contrast to *Boletus gentilis*, *Pulveroboletus ravenelii* has (1) a universal veil, (2) an infertile stipe surface consisting of an undifferentiated suprapellis, densely arranged strictly parallel with the stipe axis and (3) no lateral stratum of the stipe trama. In other words, on the stipe of *P. ravenelii* there is neither a caulohymenium

nor a trichoderm nor a palisadoderm nor any other kind of an anticlinally arranged cuticle. Such a type of the outer stipe layer is quite extraordinary from the European view, because it is not present in any European bolete. (Material examined: PRM 487647, specimen of *P. ravenelii* from North Carolina, U.S.A.).

Pulveroboletus in a narrow sense is undoubtedly a good, well separated genus with conspicuous distinctive features. However, *Pulveroboletus* in the widely extended concept adopted by Singer (1947, 1975, 1986 etc.) represents an unnatural, very heterogeneous group of considerably different species, as was already pointed out by some authors (e.g. Smith and Thiers 1971, Corner 1972, Pilát and Dermek 1974, etc.).

Note on *Boletus fragrans* and *Boletus impolitus*

On the basis of study of incorrectly identified herbarium specimens, the present author mistakenly synonymised *Boletus impolitus* with *Boletus fragrans* in one of his earlier papers (see Šutara 1989). In that paper, figure 2 with a drawing of the microstructure of the stipe surface of *Boletus impolitus* was erroneously designated as *Leccinum fragrans*. Later, after examination of a correctly identified material, the present author revised his opinion and came to the conclusion that these boletes are two distinctly separate species, differing in several characters, above all in the anatomy of peripheral stipe layers. *Boletus fragrans* has a typically boletoid lateral stratum of the stipe trama. On the other hand, in *B. impolitus* the lateral stratum of the stipe trama is much thicker and very similar to that in *Leccinum*.

Boletus* subg. *Xerocomus (Quél.) Maubl.
Champ. Comest. et Vén. 2: [CXLV], 1927.

Typus: *Boletus subtomentosus* L.: Fr.

Characters: Pileus cuticle usually non-gelatinous, consisting of a trichoderm or trichodermal palisade. Cuticular hyphae smooth or covered with an incrustation (e.g. in the *B. chrysenteron/pruinatus* group). Tubes mostly adnate, sometimes subdecurrent or slightly depressed around the stipe apex, yellow or pale yellowish, rarely whitish when young, olive-yellow, yellow-green, yellow-brown or olive-brown when mature. Pores usually medium large, concolorous with tube-sides. Structure of the hymenophoral trama phylloporoid (see Šutara 1987a: Fig. 1) or intermediate between the phylloporoid and boletoid type; gelification of lateral strata none or not very distinct. Spores of boletoid shape, elongate subfusoid, fusoid-ellipsoid or fusoid-truncate, with suprahilar depression. Spore surface smooth or very finely ornamented, e.g. venose, rugulose or

bacillate (see Heinemann, Rammeloo and Rullier 1988, Oolbekkink 1991, Klofac and Krisai-Greilhuber 1992, Holec 1994, Engel et al. 1996, etc.). Spore print olive-brown or olivaceous. Stipe mostly slender, covered with minute granules or dots, less frequently also with a more or less distinct reticulation. Stipe surface composed of a gradually fragmenting caulohymenium with sparsely scattered fertile caulobasidia. Lateral stipe stratum usually non-gelatinous and rather different in various species, sometimes well developed and loosely arranged, e.g. in the *Boletus subtomentosus* group (see Šutara 1991: Fig. 3), but sometimes developed only inconspicuously, e.g. in the *Boletus chrysenteron/pruinatus* group. Flesh yellow or whitish. Basal mycelium whitish, dirty yellowish or yellow.

Mycorrhizal with conifers (*Pinaceae*) and deciduous trees (*Fagales*, *Salicales* etc.).

Delimitation: The subgenus *Xerocomus* is distinguished from the genus *Rubinoboletus* by the elongate spores and olivaceous spore print. Defining limits between the subgenus *Xerocomus* and the genus *Chalciporus* is very difficult and is discussed under the latter.

The limit between the subgenera *Xerocomus* and *Boletus* is unclear. The taxonomic position of some species (e.g. *B. badius*, *B. moravicus* etc.) whose characters are in many regards transitional between these subgenera is still problematic and uncertain. For a detailed discussion on this problem, see below.

Material examined: *Boletus armeniacus* Quél. (JŠ 052, 2043, 2047, 2049 etc.), *Boletus chrysenteron* Bull. (JŠ 2315, 2319–20, 2401, 2674 etc.), *Boletus leguei* Boud. (= *Boletus spadiceus* ss. auct. plur., non orig. Fr.) (JŠ 1632, 1647–48, 1651, 1653 etc.), *Boletus porosporus* (Imler) Moreno et Bon (JŠ 016, 1631, 2802, 3253, 3255 etc.), *Boletus pruinatus* Fr. (JŠ 336, 1836, 1986, 4053 etc.), *Boletus rubellus* Krombh. (JŠ 2321–24, 2371, 2373, 2376–77 etc.) *Boletus subtomentosus* L.: Fr. (JŠ 039, 1548, 2042, 2144–45, 2402 etc.).

The limit between the subgenera *Xerocomus* and *Boletus*

Singer (1945, 1951, 1962, 1975, 1986) and some other authors (e.g. Snell and Dick 1958) treated the arrangement of the hymenophoral trama as the main criterion for separating the genus *Xerocomus* from *Boletus* and defining the subfamily *Xerocomoideae* Singer from *Boletoideae*. Singer (1986: 757) described the trama of the *Xerocomoideae* as 'of the *Phylloporus* type, rarely of a structure somewhat intermediate between the *Boletus*-type and *Phylloporus*-type (*Xerocomus*, sect. *Pseudoboleti*, less so in sect. *Moravici*)'. On the other hand, (according to Singer 1986: 765) the *Boletoideae* have the 'hymenophoral trama always of the *Boletus*-subtype excepting a few species of *Pulveroboletus*'. This opinion, however, was not accepted by some authors (e.g. Watling 1968, Smith and Thiers 1971, Corner 1972, Oolbekkink 1991, etc.) who pointed out that the structure of the trama in some boletes does not conform to the classification out-

lined by Singer. Also some results of the present author, especially those concerning the species whose structure of the hymenophoral trama is intermediate between the boletoid and phylloporoid type, are in disagreement with some data published by Singer. This matter is very problematic and deserves a detailed analysis.

As mentioned above, the difference between the phylloporoid and boletoid type of the tube trama is based on the different nature of their lateral strata. The lateral strata of these two types are different mainly in (1) gelification, (2) density of the hyphal structure and partly, perhaps, in (3) divergence of the hyphae. The gelification and the divergence of lateral strata are characters more or less distinct in some staining solutions (containing e.g. Congo-Red), but during microscopic observations they can be, unfortunately, assessed only approximately. As regards the density of the hyphal structure, this character can be ascertained somewhat more precisely. The distance between the hyphae of the lateral stratum is best seen in a transverse section of the hymenophore, in which this distance can even be measured. Before the measuring, however, the microscopic preparations should be prepared with particular care because a little excessive pressure on the cover slip could cause deformation of the examined microstructures. Results of the author's own study of this matter, based on examination of the tube trama in younger and middle-aged carpophores in which the hymenophoral trama is best developed, are as follows.

The boletes of the subgenera *Xerocomus* and *Boletus* including some related species can be classified according to the arrangement of the hymenophoral trama roughly into three groups.

The first group is formed by the species whose arrangement of the hymenophoral trama can be designated as phylloporoid (or of the phylloporoid type). This type of the trama occurs in *Phylloporus pelletieri* and in the *Boletus subtomentosus* group, e.g. in *Boletus subtomentosus* and *Boletus leguei* (= *Boletus spadiceus*). Lateral strata in the hymenophore of these species are non-gelatinous, with hyphae touching or almost touching each other. The distance between the hyphae, measured in transverse sections, is only 0-2(-4) μm (see Fig. 2d).

In the second group there are boletes whose structure of the tube trama is intermediate between the phylloporoid and boletoid type. This group includes e.g. species of the *Boletus chrysenteron/pruinatus* group (*Boletus armeniacus*, *Boletus chrysenteron*, *Boletus porosporus*, *Boletus pruinaeus* etc.). In these species the gelification of lateral strata is relatively weak or scarcely discernible. Hyphae of the lateral strata are slightly but distinctly distant from each other. At the best developed stage the distance between the hyphae is (1-)2-4(-6) μm .

Also in *Boletus rubellus* and *Chalciporus piperatus* the structure of the trama is intermediate between the phylloporoid and boletoid type, but in exceptional cases it may be somewhat closer to the boletoid one. In this connection it is neces-

sary to add that the difference between hymenophoral tramas of *Boletus rubellus* on the one hand and the *Boletus chrysenteron/pruinatus* group on the other hand (sometimes considered significant) is in reality very small, almost indistinct, obviously irrelevant from the viewpoint of generic taxonomy. In *Pseudoboletus parasiticus* the tube trama in the full developed stage is almost boletoid, with hyphae of the lateral strata distant 2–6(–8) μm from one another.

The arrangement of the hymenophoral trama in the third group can be designated as boletoid (or of the true boletoid type). Lateral strata in this type of the trama are more or less gelatinized, with hyphae yet more distant from each other than in the previous group. The distance between the hyphae is (2–)4–6(–10) μm (Figs. 1d, 4a). The true boletoid trama is a characteristic feature of such boletes as *Buchwaldoboletus lignicola*, *Tylopilus felleus*, most members of the subgenus *Boletus* (including *Boletus badius*, *Boletus moravicus*, *Boletus gentilis*, *Boletus pulverulentus* etc.) and many others. Paradoxically, however, it is not quite certain whether all species of the subgenus *Boletus* have really the true boletoid trama because the anatomy of tubes of some typical representatives of *Boletus* s. str. is not yet known in detail.

It is obvious that in the group of boletes from the subgenera *Xerocomus* and *Boletus* a distinct hiatus between the phylloporoid and boletoid type of the hymenophoral trama does not exist. In this group the above types of the trama and their intermediate forms overlap one another. There is no doubt that in some other cases the arrangement of the trama can significantly help to distinguish certain taxonomic groups, but in this case the difference in the tramal configuration is very unclear and therefore hardly usable for a precise definition of the generic limits. Unfortunately, neither the other characters separate *Xerocomus* from *Boletus* sufficiently clearly. In view of these facts, the author of this contribution is, after long hesitation, inclined to agree with the opinion of the mycologists who have not accepted *Xerocomus* at the generic level (e.g. Pouzar 1966, 1975, Watling 1968, 1970, 2002, Smith and Thiers 1971, Corner 1972, Grund and Harrison 1976, Arpin and Kühner 1977, Oolbekkink 1991, Hlaváček 2000, Kirk et al. 2001, etc.). Nevertheless, it seems that the taxonomic status of *Xerocomus* is a problem which is not yet fully solved. It is to be hoped that further research into the discussed taxonomic groups will bring new results which will shed new light on the matter.

Note on *Boletus badius* and *Boletus moravicus*

Boletus badius (\equiv *Xerocomus badius*) and *Boletus moravicus* (\equiv *Xerocomus moravicus*) have (1) the true boletoid hymenophoral trama and, according to some authors, (2) their spores are smooth under an electron microscope, see e.g. Pegler and Young (1981: Fig. 59) and Oolbekkink (1991: Figs. 1, 2, 32). For a photo-

graph of the microstructure of the hymenophoral trama of *B. badius*, see Ladurner and Simonini (2003: Fig. 95). The boletoid hymenophoral trama, the smooth spores and some further characters of these species (e.g. the gelatinous pileus cuticle of *B. badius* in wet weather) correspond to *Boletus* s. str. rather than to the *Xerocomus* group. Accordingly, the species *B. badius* and *B. moravicus* are placed into the subgenus *Boletus* in this contribution.

Notes on the subgenus *Xerocomus* and the genus *Boletellus*

Under a light microscope the longitudinally striate surface of spores in several species of the subgenus *Xerocomus* is sometimes seemingly similar to the spore ornamentation in the genus *Boletellus*. On the basis of this seeming similarity, some typical representatives of the *Xerocomus* group (*Boletus pruinatus*, *Boletus zelleri* Murrill and some others) were transferred to the genus *Boletellus*. This brought certain obscurities to the delimitation of these taxonomic groups. However, investigations of some authors, e.g. Pegler and Young (1981) and Heinemann, Rammeloo and Rullier (1988), showed that under an electron microscope the ultrastructure of the spore surface in these two boletaceous groups is qualitatively different.

According to Pegler and Young (1981: 112) the spores of the genus *Boletellus* are 'characterized by a prominent, longitudinally costate ornamentation... The [costate] eusporium is overlain by a persistent membranous or mucilaginous myxosporium which fragments between the costae as the spore expands'.

On the other hand, the striate spores of the *Xerocomus* group are ornamented with a very fine, venose ornamentation which is eusporial, without a myxosporium.

Tylopilus P. Karst.

Rev. Mycol. 3: 16, 1881.

Syn.: *Rhodoporus* QuéL. ex Bataille, Les Bolets: 11, 1908.

Typus: *Boletus felleus* Bull.: Fr. [= *Tylopilus felleus* (Bull.: Fr.) P. Karst.]

Characters: Pileus cuticle a trichoderm which often more or less collapses with age. Tubes depressed around the stipe apex when mature, at first white, then pale pinkish, finally pinkish brown or light brown. Pores small, concolorous with tube-sides. Hymenophoral trama boletoid (see Lohwag and Peringer 1937: Fig. 8). Spores smooth, of boletoid shape, elongate fusoid or fusoid-ellipsoid, with suprahilar depression. Spore print pinkish brown or light brown. Stipe of the only European species of this genus (*T. felleus*) ornamented with a distinct reticulation. Stipe surface composed of a gradually fragmenting caulohymenium with fertile caulobasidia. Lateral stipe stratum loosely arranged, well developed under

normal conditions. Flesh white or whitish. Basal tomentum white or dirty whitish. Clamp connections absent in the carpophore.

Forms mycorrhizal associations with both conifers and deciduous trees.

Delimitation: The anatomical structure of carpophores of *Tylopilus felleus* (the type species of *Tylopilus*) is in essence the same as in true *Boletus* species. As regards European species, the only distinction between *Tylopilus* and *Boletus* is the different colour of their spores. The spore print is pinkish brown or light brown in the former genus and olivaceous brown in the latter. However, according to some authors, this difference is not sufficiently distinct in extra-European boletes. For example, Corner (1972: 13) pointed out that Malaysian species placed by this author in the subgenus *Tylopilus* have a wide spectrum of spore-colour from pink or vinaceous brown, through cinnamon-ochraceous to olivaceous cinnamon. Corner further stated, 'In view of this spectrum, I can see no reason to single out the olive brown of *Boletus* as a generic character and I treat *Tylopilus* as a subgenus of *Boletus*, possibly a mixture of several specific alliances which cut across the formal classification. *Tylopilus* cannot be defined on spore-colour'.

The position of *Tylopilus* as an independent genus is questionable also in view of the fact that some genera, e.g. *Suillus* and *Leccinum*, comprise species both with and without olivaceous tints of spores. This can be probably stated also about *Chalciporus*. According to Baroni and Both (1991), *Boletus piperatoides* Smith et Thiers, a North American bolete with a dark smoky olive spore print, belongs to the genus *Chalciporus*, whose species (including *Chalciporus piperatus*) have their spores cinnamon-brown or ferruginous brown, without a discernible olivaceous tint. These authors have expressed the following opinion on the olivaceous and non-olivaceous colour of spores, '... we have found an interesting phenomenon concerning this feature for the species pair of *C. piperatoides* and *C. piperatus* which suggests that spore deposit color should be afforded less emphasis taxonomically at the generic level'.

In the light of the above-mentioned arguments, the position of *Tylopilus* as an independent genus seems to be very uncertain. The limits between the genera *Tylopilus* and *Porphyrellus* are discussed below, see the notes on the latter.

Material examined: *Tylopilus felleus* (Bull.: Fr.) P. Karst. and its varieties (JŠ 1809, 2423, 2569, 4030, 4046 etc.).

***Porphyrellus* Gilbert**

Les Bolets: 99, 1931.

Syn.: *Phaeoporus* Bataille, Les Bolets: 11, 1908, non J. Schröt. 1888.

Typus: *Boletus porphyrosporus* Fr. [= *Porphyrellus porphyrosporus* (Fr.) Gilbert]

Characters: Pileus cuticle dry, non-gelatinous, composed of a trichoderm which sometimes partly collapses. Tubes grey or greyish cream when young, grey-brown or brown, depressed around the stipe apex when mature. Pores medium-sized, almost concolorous with tube-sides. Structure of the hymenophoral trama mostly intermediate between the phylloporoid and boletoid type, very rarely somewhat nearer to the boletoid one, but always less gelatinized than the true boletoid trama. Spores smooth, of boletoid shape, elongate subfusoid or fusoid-ellipsoid, with suprahilar depression. Spore print reddish brown or chocolate-brown. Stipe covered by very fine granules consisting of small fragments of a caulohymenium with very sparsely scattered spore-bearing caulobasidia. In the only European species of this genus (*P. porphyrosporus*) a lateral stipe stratum occurs very rarely and, if present, forms merely a considerably reduced, very thin layer distinguishable from the stipe trama proper with difficulty. Flesh at first white or whitish, finally pale greyish, slightly brownish or dirty cream-coloured in some parts. Basal tomentum white or dirty whitish. No clamp connections found in the carpophore.

Mycorrhizal with conifers and *Fagales* (see Singer 1981).

Delimitation: The delimitation of *Porphyrellus* from *Tylopilus* (which is closely related) is very difficult. From the European view it seems that there is a certain hiatus between these two genera. *Porphyrellus porphyrosporus* is different from *Tylopilus felleus* in the darker, reddish or chocolate-brown spore print. But from a world-wide view the position of *Porphyrellus* as a separated genus is controversial. When North American, New Zealand or Malaysian species are examined, the genera *Porphyrellus* and *Tylopilus* merge into one another, as was pointed out by some authors, e.g. McNabb (1967), Smith and Thiers (1968) and Corner (1972). For this reason, *Porphyrellus* has been reduced to the level of subgenus within *Tylopilus*, e.g. by Smith and Thiers (1968, 1971) and Grund and Harrison (1976). Sometimes also both these genera have been included as infrageneric taxa in *Boletus* s. lato (see Corner 1972, Arpin and Kühner 1977, etc.).

However, in the discussion about *Tylopilus* and *Porphyrellus* it should not be overlooked that the type species of these genera are distinguished not only by the colour of their spores but also by some other characters. As regards the anatomical structure, *Tylopilus felleus* is much more different from *Porphyrellus porphyrosporus* than from most representatives of *Boletus* s. str. (including *Boletus edulis*, the type species of *Boletus*). In *Porphyrellus porphyrosporus* the lateral stipe stratum is very poorly developed and occurs very rarely, only under extraordinarily optimal conditions, whereas in *Tylopilus felleus* this layer is usually well developed under normal circumstances. The type species of *Porphyrellus* and *Tylopilus* have also somewhat different arrangements of the hymenophoral trama. In *Porphyrellus porphyrosporus* the lateral strata of the tube trama are less gelatinized than in *Tylopilus felleus*. Unfortunately, it is not known whether

these differences are also distinctly developed in the other, extra-European species of *Porphyrellus* and *Tylophilus*. Moreover, it is not quite certain whether these differences (which are not very sharp) could play a sufficiently significant role in the delimitation of these genera. This matter necessitates further study.

Material examined: *Porphyrellus porphyrosporus* (Fr.) Gilb. (= *Porphyrellus pseudoscaber* Singer nom. inval.) (JŠ 268, 3252, 3424, 4028 etc.).

***Buchwaldoboletus* Pilát**

Friesia 9: 217, 1969.

Typus: *Boletus lignicola* Kallenb. [= *Buchwaldoboletus lignicola* (Kallenb.) Pilát]

Characters: Pileus cuticle a trichoderm which gradually more or less collapses. Tubes relatively short, yellow or yellow-cinnamon, decurrent in young and maturing carpophores and subdecurrent or adnate at maturity. Pores concolorous with tube-sides, often unequal in size, both small and large on one carpophore. Hymenophoral trama boletoid, with distinctly gelatinized lateral strata. Spores smooth, elongate subfusoid or fusoid-ellipsoid, some with suprahilar depression. Spore print olivaceous or olive-brown when fresh, sometimes medium brown and without an olivaceous tint after long preservation. Stipe central or somewhat eccentric, covered by a gradually fragmenting caulohymenium with fertile caulobasidia. Lateral stipe stratum boletoid, loosely arranged, rather often gelatinized, well developed under normal conditions. Flesh more or less yellow, sometimes partly whitish. Clamp connections absent in the carpophore.

Species lignicolous, growing on decayed coniferous wood.

Delimitation: *Buchwaldoboletus* is very closely related to *Boletus*, from which it differs in the lignicolous growth. Macromorphologically, *Buchwaldoboletus* is also distinguished from *Boletus* s. str. by shorter tubes decurrent on the stipe for a relatively long time, sometimes until maturity. But the anatomical structure of *Buchwaldoboletus lignicola* (the type species of *Buchwaldoboletus*) is essentially the same as in true *Boletus* species.

Buchwaldoboletus lignicola is one of the species which have been sometimes placed in the genus *Pulveroboletus* s. lato. In the author's opinion, however, this bolete can hardly be considered congeneric with *Pulveroboletus ravenelii* (the type species of *Pulveroboletus*), which has very different anatomical features (compare the characters of *P. ravenelii* mentioned above in the note on *Boletus gentilis* and *Pulveroboletus*). In the genus *Pulveroboletus*, the species *Buchwaldoboletus lignicola* would be a heterogeneous element.

Material examined: *Buchwaldoboletus lignicola* (Kallenb.) Pilát (BRNM 235934; CB 3375-77; JŠ 3141 etc.).

Chalciporus Bataille

Les Bolets: 19, 1908.

Typus: *Boletus piperatus* Bull.: Fr. [= *Chalciporus piperatus* (Bull.: Fr.) Singer]

Characters: Carpophores small and slender. Pileus cuticle a trichoderm which rather often somewhat gelatinizes and more or less collapses with age. Tubes adnate, cinnamon, ferrugineous, reddish brown or vivid yellow. Pores medium to large, cinnamon, ferrugineous, raspberry-red, vinaceous red or vivid yellow. Structure of the hymenophoral trama usually intermediate between the boletoid and phylloporoid type, exceptionally somewhat nearer to the boletoid one, but always less gelatinized than the true boletoid trama. Spores smooth, of boletoid shape, elongate subfusoid or fusoid-ellipsoid, with suprahilar depression. Spore print of European species of this genus cinnamon-brown or ferrugineous brown. Stipe slender, covered by very fine granules consisting of small fragments of a caulohymenium with sparsely scattered fertile caulobasidia. Lateral stipe stratum occurs very rarely and, if present, forms a very thin, almost indistinct, non-gelatinous layer. Flesh pale cream-coloured, sometimes with a slight ferrugineous shade in the pileus, vivid yellow in the stipe. Basal mycelium yellow. Clamp connections none or extremely rare in the carpophore.

Mycorrhizal with conifers (*Pinaceae*) and deciduous trees (*Fagales*, *Betulales*).

Delimitation: As regards the anatomical structure of the carpophores (including the arrangement of the hymenophoral trama and peripheral stipe layers), *Chalciporus* is very similar to *Rubinoboletus* and some xerocomoid boletes. Nevertheless, *Rubinoboletus* is easily recognized by its short spores and the xerocomoid boletes are distinguished from European species of *Chalciporus* by their olivaceous spore print. However, a problem emerged when Baroni and Both (1991) proposed the transference of *Boletus piperatoides* to the genus *Chalciporus*, although the spore print of this species is olivaceous. As mentioned in the notes under *Tylopilus*, it seems that the taxonomic value of the olivaceous or non-olivaceous spore tint as a generic diagnostic character in *Boletaceae* is rather doubtful.

A character which was, until recently, considered rather important for defining the limits between *Chalciporus* and *Boletus* (incl. *Xerocomus*) was the never yellow coloration of the hymenophore in *Chalciporus* (cf. Singer 1986). This character, however, lost its diagnostic meaning for the delimitation of this taxonomic group when *Chalciporus hypochryseus* was found, because this true *Chalciporus* species (closely related to *Chalciporus piperatus*) has a yellow hymenophore similar in colour to the tubes of many members of *Boletus* (incl. *Xerocomus*); see Šutara (1992b).

In view of the difficulties with generic delimitation, the position of *Chalciporus* at the generic level appears to be questionable.

Material examined: *Chalciporus hypochryseus* (Šutara) Courtecuisse (JŠ 2016, 3451), *Chalciporus piperatus* (Bull.: Fr.) Singer (JŠ 325, 3043, 4027, 4045 etc.) and *Chalciporus pseudorubinus* (Thirring) Pilát et Dermek (PRM 672811).

***Rubinoboletus* Pilát et Dermek**

Čes. Mykol. 23: 81, 1969.

Typus: *Boletus rubinus* W. G. Smith [= *Rubinoboletus rubinus* (W. G. Smith) Pilát et Dermek]

Characters: Pileus cuticle a trichoderm which often more or less collapses. Tubes adnate or subdecurrent. Pores medium large. Structure of the hymenophoral trama probably intermediate between the boletoid and phylloporoid type. However, the arrangement of the trama needs further examination on more numerous material. Spores smooth, shortly ellipsoid, some with an adaxial applanation. Spore print light brown or (according to Skála 2003) pinkish brown. Stipe central, solid, composed of a longitudinally arranged trama. The only European species of this genus (*R. rubinus*) has a large part of the stipe covered by a fragmenting caulohymenium with very sparsely scattered fertile caulobasidia. Lateral stipe stratum occurs very rarely and, if present, forms merely a very thin layer distinguishable from the stipe trama proper with difficulty. Basal mycelium yellow. Clamp connections absent in the carpophore.

Mycorrhizal associations with *Quercus* and possibly with some other trees.

Delimitation: *Rubinoboletus rubinus* (the type species and the only European representative of *Rubinoboletus*) has essentially the same anatomical structure of the carpophores as *Chalciporus* and some xerocomoid boletes, from which it differs in the shortly ellipsoid spores. The xerocomoid boletes, moreover, differ in the olive-brown or olivaceous spore print.

Boletus rubinus was placed in *Suillus* (see e.g. Singer 1951, 1965), *Xerocomus* (Pilát 1952) and *Chalciporus* (Singer 1973, 1975, 1986, Pegler and Young 1981, Moser 1983, Alessio 1985, Lannoy and Estades 2001, etc.), but in these genera (whose common feature is the fact that all their species have a uniform, elongate boletoid shape of spores) it was in an isolated position. Therefore the separation of this species to an independent genus, *Rubinoboletus*, seems to be a fairly acceptable solution (Pilát and Dermek 1969). Nevertheless, the independent generic status of *Rubinoboletus* is still controversial. Many authors (e.g. Corner 1972, Singer 1986) have not considered the shorter spore shape as a character important at the generic level. This matter will undoubtedly require further study above all from the world-wide view.

R. rubinus (or *Rubinoboletus*) has not been generally considered closely related to *Gyrodon* or *Gyroporus*. Despite this fact, several African boletes (some of them originally described as *Gyroporus* species) have been placed by

Heinemann and Rammeloo (1983) in the genus *Rubinoboletus* and simultaneously in the family *Gyrodontaceae*. Recently Kirk et al. (2001) have included *Rubinoboletus* in the *Gyroporaceae*. It is, of course, questionable whether the placement of this genus in the *Gyroporaceae* (or *Gyrodontaceae*) is sufficiently justified. The author of this contribution had not yet an opportunity to examine the African boletes placed in *Rubinoboletus* and therefore he cannot express an opinion on the generic position of these species. It is, however, necessary to point out that *R. rubinus* (the type species on which the genus *Rubinoboletus* is based) has the only character reminiscent of the *Gyroporaceae* (or *Gyrodontaceae*), viz. the shortly ellipsoid shape of the spores. Almost all the other features of this species, e.g. the nearly xerocomoid appearance of the carpophores, the clampless hyphae, the fertile caulohymenium, the anatomical arrangement of peripheral stipe layers, the less gelatinized hymenophoral trama, the colour of spores etc., are very different from the characters of the *Gyroporaceae* (or *Gyrodontaceae*).

Material examined: *Rubinoboletus rubinus* (W. G. Smith) Pilát et Dermek (PRM 532362, 603926; LIT 15.8.2002; JŠ 4048).

***Pseudoboletus* Šutara**

Čes. Mykol. 45: 2, 1991.

Typus: *Boletus parasiticus* Bull.: Fr. [= *Pseudoboletus parasiticus* (Bull.: Fr.) Šutara]

Characters: Pileus cuticle a trichoderm which partly collapses with age. Gelification of the trichodermal hyphae not found. Tubes adnate or subdecurrent. Pores medium large. Hymenophoral trama in a well developed stage almost boletoid. Spores of boletoid shape, elongate fusoid-cylindric, with a shallow suprahilar depression. In the only European species of this genus (*P. parasiticus*) the spore surface has an unusual pitted ornamentation under an electron microscope (see Oolbekkink 1991, Holec 1994). Spore print olive-brown. Stipe solid, attached with its basal part to the carpophore of the host. Stipe surface infertile, composed of a filamentous trichoderm (see Fig. 4b and Šutara 1991: Figs. 1, 2). Caulobasidia absent. Stipe trama consisting of longitudinally arranged hyphae. Lateral stipe stratum never present. No clamp connections found in the carpophore.

Growing on carpophores of gasteromycetes (*Scleroderma* or *Astraeus*). The parasitism of *Pseudoboletus parasiticus* was thoroughly studied and described by Kavina (1935: Figs. 4, 6 and Plate 1).

Delimitation: *Pseudoboletus* (which is macroscopically most similar to xerocomoid boletes, particularly the *Boletus subtomentosus* group) is well distinguished from all European *Boletaceae* by (1) the infertile stipe surface without caulobasidia and (2) the growth on gasteromycetes.

A further character distinguishing *Pseudoboletus* from almost all the other European *Boletaceae* (including the xerocomoid boletes) is the absence of a lateral stipe stratum.

Between *Pseudoboletus parasiticus* (the type species of *Pseudoboletus*) and the *Boletus subtomentosus* group, there is also a visible difference in the arrangement of the hymenophoral trama. In *Pseudoboletus parasiticus* the trama is almost boletoid, with distinctly gelatinized lateral strata, whereas in the *Boletus subtomentosus* group the trama is phylloporoid, with lateral strata non-gelatinous. The tramal structure in *Pseudoboletus parasiticus* is even more similar to the true boletoid type than the tube trama in the *Boletus chrysenteron/pruinatus* group.

Results of ontogenetic investigations indicate that between *Pseudoboletus parasiticus* and the xerocomoid boletes there is, moreover, a significant difference in the development of the carpophores. According to Reijnders (1963), the development in *Boletus parasiticus* (\equiv *Pseudoboletus parasiticus*) is hypovelangiocarpous (paravelangiocarpous) while in *Boletus subtomentosus* (\equiv *Xerocomus subtomentosus*) and *Boletus zelleri* (\equiv *Xerocomus zelleri*) is gymnocarpous. The gymnocarpous development was observed also in other boletes which have been often treated as *Xerocomus* species, e.g. *Boletus badius*, *Boletus illudens* Peck (see Pantidou 1964), *Boletus armeniacus*, *Boletus porosporus* and other members of the *Boletus chrysenteron* group (Watling 1985). According to Singer (1981: 270), in *Xerocomus*, excepting the members of the section *Parasitici* (i.e. *Xerocomus parasiticus* and, perhaps, *Xerocomus astraeicola* Imazeki), most or all of the other species are gymnocarpous.

According to the present knowledge, we can suppose that the hypo-(para)-velangiocarpous and pileostipitocarpous development of *P. parasiticus* is a very rare phenomenon in the *Boletoideae*. In *Boletus* s. str. (see Reijnders in Singer 1986: 29) and its satellites, i.e. the genera *Tylophilus* (Singer 1986), *Buchwaldoboletus* (Pantidou 1961, 1962), *Chalciporus* (McLaughlin 1964, 1970), probably also *Porphyrellus* (Singer 1986) and *Rubinoboletus*, there occurs the same (i.e. gymnocarpous and probably stipitocarpous) type of development as in the xerocomoid boletes. In other genera of the *Boletoideae* the following types of development have been ascertained: pilangiocarpous and stipitocarpous in *Leccinum* (Watling 1985), angiocarpous in *Boletellus* (Singer 1986) and meta-velangiocarpous in some species of *Pulveroboletus* (Singer 1986).

The above data suggest that certain taxonomic groups of boletes possess a certain, genetically determined type of development. In the *Boletoideae* the carpophore development, as a rule, reflects relationships between genera (or groups of genera) and more or less corresponds with the anatomical structure of the carpophores. For example, the genera *Boletus* (including *Xerocomus*), *Tylophilus*, *Chalciporus*, *Buchwaldoboletus* and probably *Porphyrellus*, which

have a more or less similar anatomical structure, have also a similar (i.e. gymnocarpous) type of development. On the other hand, in the genera which are well distinguished from the other taxonomic groups by their anatomical characters (e.g. *Pseudoboletus*, *Boletellus* and *Pulveroboletus*) the development is different from that in the other boletaceous genera.

In the case of *Pseudoboletus parasiticus* and the xerocomoid species, the different carpophore development has obviously a connection with the different anatomy and the fertility (or infertility) of the stipe surface. In the primordium of *P. parasiticus* the infertile stipe cuticle, i.e. the trichoderm on the stipe, differentiates simultaneously with the trichoderm on the pileus (JŠ 2307, 2342) whereas in the primordium of the xerocomoid species the fertile stipe surface, i.e. the caulohymenium, is formed together with the hymenium of the hymenophore (Watling 1985: Fig. 1).

Note: Singer (1986) mentioned that the hypo-(para)-velangiocarpous carpophore development occurs probably also in *Xerocomus radicolica* Singer et Araujo, a tropical species placed by Singer in section *Brasilienses* of *Xerocomus*. It seems, however, that some characters of *X. radicolica* which could be important from a taxonomic viewpoint (e.g. the anatomical structure of the stipe surface) are still unknown or known only insufficiently. For this reason, the generic position of this species appears rather unclear.

Pseudoboletus parasiticus is, moreover, distinguished from the other European boletes (including species of *Boletus*, subg. *Xerocomus*) by the pitted ornamentation of the spores (see Oolbekkink 1991, Holec 1994). It is not known whether this spore ornamentation occurs also in the extra-European *Pseudoboletus astraeicola* (\equiv *Xerocomus astraeicola*).

European material examined: *Pseudoboletus parasiticus* (Bull.: Fr.) Šutara, (CB 2310; JŠ 2088-92, 2106, 2108-09, 2342, 3115, 3243-44 etc.).

New combination

A Japanese species of the genus *Pseudoboletus*, which has also an infertile stipe cuticle consisting of a trichoderm and grows on carpophores of *Astraeus hygrometricus* (Pers.) Morgan, is:

***Pseudoboletus astraeicola* (Imazeki) Šutara comb. nov.**

- Basionym: *Xerocomus astereicola* Imazeki, Mycol. J. Nagaoa Inst. 2: 35, 1952.
- Material examined: TFM-M-D 972, Tokyo Univ. Forest, Chiba, Japan, 20. Aug. 1992, H. Neda.

***Phylloporus* Quélet.**

Fl. Mycol. Fr.: 409, 1888.

Typus: *Agaricus pelletieri* Lév. [= *Phylloporus pelletieri* (Lév.) Quélet]

Characters: Pileus cuticle dry, subtomentose, consisting of a trichoderm. Hymenophore lamellate, with numerous anastomoses. Lamellae decurrent. Hymenophoral trama phylloporoid (Figs. 2c, 2d). Spores elongate subfusoid or fusoid-ellipsoid, with suprahilar depression. Spore surface bacillate (e.g. in *P. pelletieri*) or, in some extra-European species, slightly rugulose or smooth (see Heinemann, Rammeloo and Rullier 1988). Spore print brown-olivaceous. Stipe solid, composed of longitudinally arranged trama. The only European species of this genus (*P. pelletieri*) has a large part of the stipe covered by a fragmenting caulohymenium with very sparsely scattered fertile caulobasidia. Lateral stipe stratum not found. Clamp connections absent in the carpophore.

Mycorrhizal with various trees (Singer 1981).

Delimitation: Among the *Boletaceae*, the genus *Phylloporus* is easily recognized by its lamellate hymenophore. *Phylloporus* is moreover distinguished from almost all the other *Boletaceae* by the phylloporoid hymenophoral trama. The species which have also the phylloporoid hymenophoral trama, viz. the closely related boletes from the *B. subtomentosus* group, differ from *Phylloporus* in the tendency to form a well developed, loosely arranged lateral stratum of the stipe trama (see Šutara 1991: Fig. 3). In the type species of *Phylloporus* no distinctly developed lateral stratum of the stipe trama was ascertained by the present author (Fig. 2f). Nevertheless, this question will require further examination. It is not known whether the lateral stipe stratum is absent also in the other, extra-European species of *Phylloporus*.

Material examined: *Phylloporus pelletieri* (Lév.) Quélet [= *Phylloporus rhodoxanthus* (Schw.) Bres. subsp. *europaeus* Singer], (CB 448; HK 292/81; JŠ 281, 2722, 3251 etc.).

***Leccinum* S. F. Gray**

Nat. Arrang. Br. Pl. 1: 646, 1821.

Syn.: *Krombholzia* P. Karst., Rev. Mycol. 3: 17, 1881 (non Rupr. ex Fourn. 1876). – *Trachypus* Bataille, Les Bolets: 12, 1908 (non Reinw. et Hornsch. 1829). – *Krombholziella* R. Maire, Publ. Inst. Bot. Barcelona 3: 41, 1937.

Typus: *Boletus aurantiacus* Bull. [= *Leccinum aurantiacum* (Bull.) S. F. Gray]

Characters: Pileus cuticle mostly a trichoderm with more or less filamentous hyphae, less frequently an epithelium consisting of hyphal chains of broad and short cells. In wet weather the surface of trichodermal hyphae may be slightly gelatinized. In section *Leccinum* the cuticle of the pileus margin overlaps beyond

the tubes as an sterile, appendiculate membrane. Tubes long, depressed around the stipe apex when mature. Pores small, roundish. Hymenophoral trama boletoid (Fig. 4a). Spores smooth, of boletoid shape, elongate subfusoid or subcylindric, with suprahilar depression. Spore print of various brown shades, mostly medium brown or umber brown, less frequently olivaceous brown. Stipe central, solid, slender and more elongated than in the other European boletes. Caulohymenium with fertile caulobasidia present on a substantial part of the stipe. Lateral stipe stratum conspicuously developed, at first forming a continuous layer (Šutara 1989: Fig. 1), but soon disrupting with growth of the stipe into characteristic, almost anticlinally arranged fascicles of non-gelatinous hyphae ending in fragments of the caulohymenium. These hyphal fascicles form a typical scabrous ornamentation of the stipe. Species of sections *Leccinum* and *Scabra* have the lateral stipe stratum (200–)300–1000(–2000) μm thick, with a relatively dense and rather regular arrangement of hyphae within the fascicles. Species of section *Luteoscapra* have this layer thinner (150–320 μm) and the arrangement of hyphae within the fascicles somewhat looser and less regular. The stipe trama proper composed of hyphae densely arranged in a longitudinal way, parallel with the stipe axis. Clamp connections none or extremely rare in the carpophore.

Forming mycorrhizal associations with both deciduous and coniferous trees.

Delimitation: Singer (1975, 1986) accepted a wider concept of the genus *Leccinum*, in which he placed such species as *Leccinum chromapes* (Frost) Singer (\equiv *Boletus chromapes* Frost), *Leccinum eximium* (Peck) Singer (\equiv *Boletus eximius* Peck), *Leccinum subglabripes* (Peck) Singer (\equiv *Boletus subglabripes* Peck) and *Leccinum rubropunctum* (Peck) Singer (\equiv *Boletus rubropunctus* Peck). In the notes on the delimitation of this genus, Singer (1986: 787) stated, '...the scabrosities of the stipe, the anatomy of these scabrosities and the general habit of *Leccinum* have served as a unifying character'.

Smith and Thiers (1968, 1971) had a somewhat different opinion on the circumscription of *Leccinum*. In the taxonomic arrangement of these authors *Boletus chromapes* and *Boletus eximius* are placed in *Tylopilus* whereas *Boletus subglabripes* and *Boletus rubropunctus* are left in *Boletus*. According to Smith and Thiers (1968: 946), '...the most important character of *Leccinum* is the darkening in color of the stipe ornamentation or its being dark from the beginning'. This diagnostic character was previously mentioned by Smith, Thiers and Watling in their contributions to *Leccinum* (1966, 1967). The dark or darkening stipe ornamentation is a character which possibly helped to solve the problem with the controversial generic position of the above-mentioned species but its application in practice is not always clear. The process of darkening of the stipe scabrosities depends on many factors (not only on the mode of creation of colour pigments, but also on changes caused by oxidation, on moisture, light conditions and some other circumstances). Therefore some carpophores of *Leccinum* species which

are found in the field do not conform to the schematic classification based on the darkening or not darkening stipe ornamentation. For example, in some forms of such typical species of this genus as *Leccinum niveum* (Fr.) Rauschert [= *Leccinum holopus* (Rostk.) Watling] and *Leccinum rotundifoliae* (Singer) Smith, Thiers et Watling the stipe scabrosities are whitish when young and persistently pale coloured until maturity. On the other hand, the stipe scabrosities of some species which are mostly considered as members of *Boletus*, e.g. *Boletus impolitus*, may distinctly darken under certain conditions.

In one of his contributions, the author (Šutara 1989) attempted to analyse the differences in anatomical arrangement of the stipe surface between *Leccinum* and the other boletes in detail. A by-product of this effort was the finding that *Boletus depilatus* and *Boletus impolitus* (erroneously merged with *Boletus fragrans* by the author) have peripheral stipe layers very similar to those in *Leccinum*. On the basis of the similarity of anatomical characters, these two species were treated by the author as members of the genus *Leccinum*.

Many new important data have been published by Binder and Besl (2000) in their molecular analysis concerning *Leccinum* and allied boletes. According to the conclusions presented in this work, the recent concepts of the genus *Leccinum* are too wide and the species *Boletus chromapes*, *B. eximius*, *B. subglabripes*, *B. rubropunctus*, *B. impolitus*, *B. depilatus* and some others should be excluded from *Leccinum*.

Material examined: *Leccinum aurantiacum* (Bull.) S. F. Gray [= *Leccinum quercinum* (Pilát) Green et Watling] (CB 1616; JŠ 056, 1585, 1842-45 etc.), *Leccinum duriusculum* (Schulzer) Singer (PRM 566842, 663764; JŠ 169, 2614, 2794 etc.), *Leccinum griseum* (Quél.) Singer sensu orig. Quélet (= *Leccinum varicolor* Watling) (JŠ 460, 1851-55, 2657, 3011 etc.), *Leccinum luteoporum* (Bouchinot ap. Barbier) Šutara (PRM 648066-67; LIT 3776/565; JŠ 152 etc.), *Leccinum niveum* (Fr.) Rauschert [= *Leccinum holopus* (Rostk.) Watling] (JŠ 2317, 2564, 2661, 3007 etc.), *Leccinum piceinum* Pilát et Dermek (CB 1061, 2509; JŠ 525, 2137 etc.), *Leccinum pseudoscabrum* (Kallenb.) Šutara [= *Leccinum carpini* (R. Schulz) Moser] (PRM 520436, 520745; BRA-Fábry 95/965; JŠ 360 etc.), *Leccinum roseotinctum* Watling (JŠ 055, 171), *Leccinum rotundifoliae* (Singer) Smith, Thiers et Watling (PRM 518250, collection from Finland), *Leccinum rufum* (Schaeff.) Kreisel (= *Leccinum aurantiacum* sensu auct. plur., non orig. Bulliard) (JŠ 235, 431, 1863, 2025, 3014 etc.), *Leccinum versipelle* (Fr. sensu Smotlacha) Snell (= *Leccinum testaceoscabrum* Singer nom. inval.) (JŠ 532, 1679, 1905-07, 2160 etc.), *Leccinum scabrum* (Bull.: Fr.) S. F. Gray (JŠ 1579, 2029, 2544, 3023 etc.).

Subfamily *Strobilomycetoideae* (Gilbert) Watling

Brit. Fung. Fl. Agar. and Bol. 1: 101, 1970.

Type genus: *Strobilomyces* Berk.

Characters: Universal veil present. Hymenophore tubular. Spores subglobose, subovoid or shortly ellipsoid, conspicuously ornamented. Spore print very dark, almost black, brown-black or purplish black. Clamp connections none or very rare.

Delimitation: The differences between the *Strobilomycetoideae* and the *Boletoideae* are obvious from the delimitation of the genus *Strobilomyces*.

European genus: *Strobilomyces*.

***Strobilomyces* Berk.**

Hookers Journ. Bot. Kew Gard. Misc. 3: 78, 1851.

Syn.: *Eriocorys* Quél., Enchir. Fung.: 163, 1886.

Typus: *Boletus strobilaceus* Scop.: Fr. [= *Strobilomyces strobilaceus* (Scop.: Fr.) Berk.]

Characters: Carpophores covered with a true universal veil which disrupts into fragments remaining as floccose-woolly scales on pileus and stipe. Tubes adnate. Pores enlarged, angular. Structure of the hymenophoral trama usually intermediate between the boletoid and phylloporoid type, with a weak or scarcely distinct gelification of lateral strata. Basidia (at least in *S. strobilaceus*) relatively large and somewhat inflated. Spores subglobose, subovoid or shortly ellipsoid, conspicuously reticulate, with smooth suprahilar plage or, in some extra-European species, verrucose or echinate (see Perreau-Bertrand 1961, Corner 1972, Pegler and Young 1981, etc.). Spore print almost black when fresh, brown-black or purplish black when dried. Stipe central, solid. The only European species of this genus (*S. strobilaceus*) has a fertile caulohymenium on a large part of the stipe. Caulobasidia produce the same spores as the basidia in the hymenophore. Lateral stipe stratum occurs rather rarely, only under sufficiently favourable conditions. Stipe trama proper dense, longitudinally arranged. Clamp connections none or extremely rare in the carpophore.

Probably mycorrhizal, growing under various trees.

Delimitation: *Strobilomyces* is one of the best characterized boletaceous genera. Typical characters of this genus are above all (1) the universal veil, (2) the conspicuous shape and ornamentation of the spores and (3) the very dark, almost black spore print.

Material examined: *Strobilomyces strobilaceus* (Scop.: Fr.) Berk. [= *Strobilomyces floccopus* (Vahl.: Fr.) P. Karst.] (JŠ 035-36, 3420 etc.).

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