

Anatomical structure of pores in European species of genera *Boletus* s.str. and *Butyriboletus* (*Boletaceae*)

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One of the characteristic features of European species of genera *Boletus* s.str. and *Butyriboletus* is a conspicuous development of their cheilocystidia covering their pores in youth. The development of this type of cheilocystidia is partly supported by the growth of hyphae of the hymenophoral trama under the cheilocystidia. This special arrangement of cheilocystidia is an important diagnostic character distinguishing European species of the above-mentioned genera from other groups of boletes in *Boletaceae*. The microscopical structure of this type of pores is described in detail.

Key words: *Boletaceae*, anatomy, pores, cheilocystidia.

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Jedním z charakteristických znaků evropských druhů rodů *Boletus* s.str. a *Butyriboletus* je nápadný vývin jejich cheilocystid pokrývajících v mládí póry. Vývin cheilocystid tohoto typu je částečně podporován růstem hyf tramy hymenoforu pod cheilocystidami. Toto zvláštní uspořádání cheilocystid je důležitým diagnostickým znakem odlišujícím evropské druhy výše zmíněných rodů od ostatních skupin hřibů v čeledi *Boletaceae*. Mikroskopická stavba pórů tohoto typu je detailně popsána.

INTRODUCTION

Results of recent phylogenetic molecular studies have considerably changed our view of the systematics of the *Boletaceae* and shown that the genus *Boletus* L. sensu lato in the traditional broad concept is not monophyletic (see e.g. Binder & Hibbett 2006, Nuhn et al. 2013, Wu et al. 2014). The fact that section *Boletus* including *Boletus edulis* Bull.: Fr. (type species of genus *Boletus*) is distant from the other sections of *Boletus* s.l. has also become obvious from phylograms published in some other works (e.g. Desjardin et al. 2009, Halling et al. 2012, etc.). Therefore a division of *Boletus* s.l. into several new, separate genera (earlier considered sections) appears to be an adequate taxonomic solution. Examples are *Butyriboletus* D. Arora & J.L. Frank including species of sect. *Appendiculati* (see Arora & Frank 2014), *Caloboletus* Vizzini containing members of sect. *Calopodes* (see Vizzini 2014a), and *Cyanoboletus* Gelardi, Vizzini & Simonini with several boletes of sect. *Subpruinosi* (see Vizzini 2014b).

One of the morphological characters important for identification of European species of genera *Boletus* s.str. and *Butyriboletus* is a conspicuous development of cheilocystidia covering tube mouths of young fruit bodies. In the past this character was usually indicated as “stuffed”, “covered” or “closed” pores (or tubes).

The first mention of “stuffed tubes” in a bolete, as far as I know, was published by Frost in his description of the hymenophore of *Boletus speciosus* Frost (see Frost 1874).

Kallenbach mentioned this character in *Boletus regius* Krombh. [= *Butyriboletus regius* (Krombh.) D. Arora & J.L. Frank], *Boletus appendiculatus* Schaeff. [= *Butyriboletus appendiculatus* (Schaeff.) D. Arora & J.L. Frank], and *Boletus aestivalis* sensu Kallenb. [= *Butyriboletus fechtneri* (Velen.) D. Arora & J.L. Frank]. For example, pores of *B. appendiculatus* were described by Kallenbach in the following way: “... anfangs filzig-wulstig-geschlossen” (see Kallenbach 1926–1942).

Coker & Beers used the term “stuffed” in descriptions of the tube mouths of *Boletus affinis* Peck, *B. auripes* Peck, *B. edulis* Bull.: Fr., *B. speciosus*, and *B. variipes* Peck. Their description of the tube mouths of *B. edulis* was formulated as follows: “conspicuously stuffed in youth as if covered by a complete white membrane” (see Coker & Beers 1943).

The term “stuffed pores” was later used by e.g. Singer (see Singer 1947, 1986), Smith & Thiers (see Smith & Thiers 1971) and some other mycologists.

The present author first observed conspicuously developed cheilocystidia covering pores in 1986, when he studied the analogy between caulocystidia and cheilocystidia of species belonging to the *B. appendiculatus* and *B. edulis* groups. Later he (see Šutara et al. 2009, p. 44) briefly described this structure in an identification key to boletes as follows (translation into English by Šutara): “Pores of tubes in youth densely covered with a great number of conspicuously developed cheilocystidia which, in this stage, form a continuous layer on the lower surface of the hymenophore. Under a hand lens this layer looks like ‘hoarfrost’ covering the mouths of the tubes. The tube mouths become distinct only when fruit bodies and their tubes are sufficiently developed.”

Dentinger et al. described the layer on pores of boletes of section *Boletus* as follows: “... a layer of tangled white hyphae that covers the immature tubes (equivalent to a partial veil), a feature that effectively ‘plugs’ their pores and has often been referred to misleadingly as ‘stuffed pores’...” (see Dentinger et al. 2010).

As obvious from the above lines, the fact that the pores of some boletes are “stuffed” or “covered” in youth has been known for at least 140 years (cf. Frost 1874). Nevertheless, the anatomical structure of this character has not been described in detail to date (as far as I know). Therefore I have decided to present my description of this important morphological character in this article.

MATERIAL AND METHODS

Macroscopical appearance and microscopical characters of pores of species of *Boletaceae* were studied on both fresh and dried material collected in the years 1976–2013.

The anatomical structure of the pores was examined on material from a broad range of localities. During examination of this structure, attention was mainly directed to pores of young, immature fruit bodies. Microscopical sections of dried specimens were mounted both in Melzer's reagent and in a 5% solution of ammonium hydroxide (NH_4OH) with (or without) Congo Red and examined under C. Zeiss Primo Star and Meopta D816Bi microscopes with an oil immersion lens at a magnification of up to 1250 $\times$. Drawings of microscopical characters (Figs. 1, 2) were made freehand.

RESULTS AND DISCUSSION

The arrangement of cheilocystidia on pores in some taxonomic groups of *Boletaceae* is a morphological character that was earlier often overlooked or underestimated. However, the importance of this character for bolete taxonomy has considerably increased in recent years because the arrangement of cheilocystidia was found to correspond with results of some recent molecular phylogenetic studies (e.g. Nuhn et al. 2013, Wu et al. 2014), which support separate positions of genera *Boletus* s.str. and *Butyriboletus*.

European species of *Boletaceae* with a tubular hymenophore can be divided according to presence or absence of cheilocystidia covering pores into two groups: species with pores covered by cheilocystidia in youth and species with pores not covered by cheilocystidia in any phase of development.

1. Boletes with pores covered by cheilocystidia in youth. Cheilocystidia of this group of boletes undergo a conspicuous development in an early developmental stage. In this stage (before the opening of the pileus of fruit bodies) the cheilocystidia develop so intensively and in such a large number that they form a dense layer which entirely covers the pores (see Figs. 1, 3, and 5). The development of cheilocystidia is partly supported by a somewhat faster growth of hyphae of the hymenophoral trama under the cheilocystidia. This faster growth is obvious from the fact that the hypha cells under the cheilocystidia are not shortened like the elements in the normal subhymenium but are somewhat elongated already in this young stage (see Fig. 1).

The layer of cheilocystidia on the pore surface is seen not only under a microscope, but also under a magnifying glass or even with the naked eye and is visible

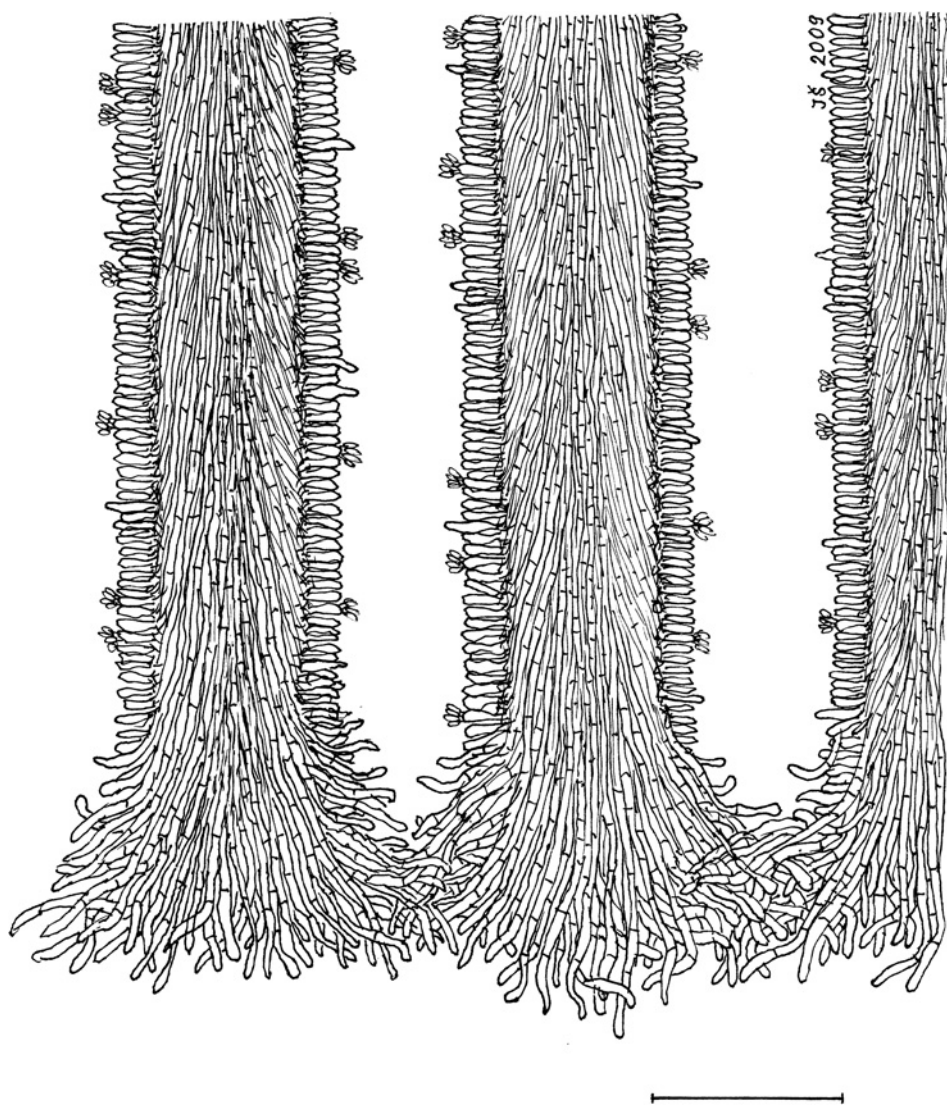


Fig. 1. Schematic drawing of structure of tube mouths in young fruit body of *Boletus edulis* (type species of *Boletus*), longitudinal section (JŠ 6161). Conspicuously developed cheilocystidia form a filamentous layer entirely covering the pores. Scale bar = 200 μ m. Del. J. Šutara.

on both fresh and dried material. Under a hand lens with a magnification of ca. 10–25 $\times$, the pore surface sometimes looks as if the tube mouths were covered with a subtomentose layer or hoarfrost (see Fig. 3).

This anatomical structure of the pores was found by the present author in the following European species of *Boletus* s.str. and *Butyriboletus*: *Boletus aereus* Bull.: Fr., *B. edulis* (including its forms and varieties) (see Figs. 1 and 3), *B. reticulatus* Schaeff., *B. pinophilus* Pilát & Dermek, *Butyriboletus appendiculatus* (see Fig. 5), *B. fechtneri*, *B. regius*, *B. roseogriseus* (Šutara, Graca, M. Kolařík, V. Janda & Kříž) Vizzini & Gelardi, *B. subappendiculatus* (Dermek, Lazebníček & Veselský) D. Arora & J.L. Frank, and *B. fuscroseus* (Smotl.) Vizzini & Gelardi (= *Boletus pseudoregius* Huber ex Estadès) (for a discussion on the correct name of *B. fuscroseus*, see Šutara et al. 2014).

As mentioned above (see Introduction), the type of pores covered with cheilocystidia is also known (mostly as “stuffed pores”) from some North American *Boletus* species (see Coker & Beers 1943, Singer 1947, Dentinger et al. 2010, etc.), but it is not clear whether this arrangement of cheilocystidia also occurs in American and Chinese species of *Butyriboletus*. For example, Arora & Frank and Li et al. do not mention this character in their descriptions of species of this genus (see Arora & Frank 2014 and Li et al. 2014).

The macroscopical appearance of pores covered with cheilocystidia is rather variable and often influenced by external conditions. Also the appearance of covered pores in *Boletus* s.str. and *Butyriboletus* is somewhat different. A difference distinct at first sight is e.g. in the colour of the pore surface, which is yellow in *Butyriboletus* but white or whitish in young fruit bodies of *Boletus* s.str. Nevertheless, despite of these predominantly macroscopical differences, the essence of the microscopical structure of pores covered with cheilocystidia in these two genera is very similar.

In my opinion, the special arrangement of cheilocystidia in *Boletus* s.str. and *Butyriboletus* is very important from the taxonomic viewpoint, because it distinctly separates European species of these two genera from other European boletes (at least from the species which I had the opportunity to study). The fact that *Boletus* s.str. and *Butyriboletus* have a very similar anatomical structure does not cause difficulties, because these two genera are sufficiently delimited from one another by several other distinctive features.

For the sake of completeness, it is also necessary to mention that the arrangement of cheilocystidia should be studied in a young developmental stage, because in this stage the cheilocystidia are best developed. In later stages they gradually collapse, become less distinct or indistinct, so that during maturing the tube mouths very slowly open up.

A characteristic feature of species with conspicuous cheilocystidia is moreover the fact that also their caulocystidia on ridges of the stipe reticulation are usually conspicuously developed (see Šutara 1989, fig. IV). It is obvious that there is a certain analogy between cheilocystidia and caulocystidia.

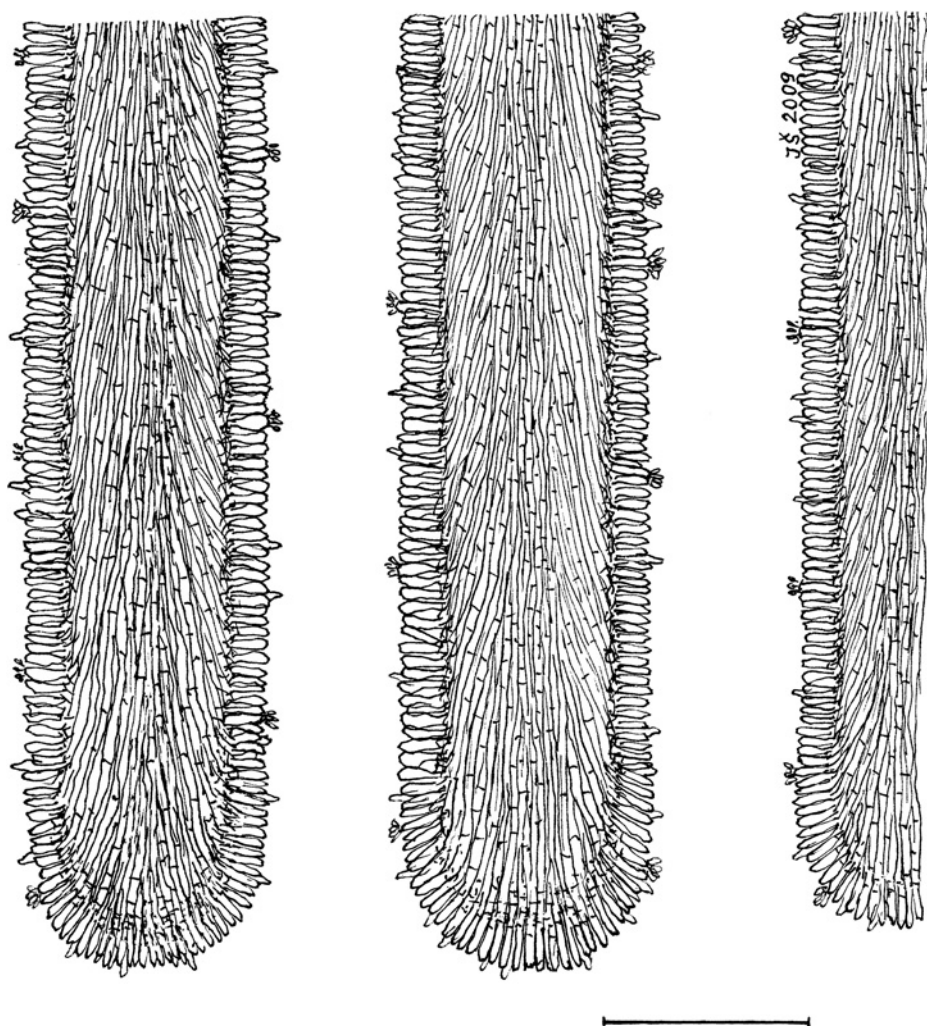


Fig. 2. Schematic drawing of structure of tube mouths in young fruit body of *Suillellus luridus* (type species of *Suillellus*), longitudinal section. Cheilocystidia are not conspicuously developed. Scale bar = 200 μ m. Del. J. Šutara.

Herbarium specimen: Vršovice (České středohoří Mts., Northwest Bohemia, Czech Republic), Velký vrch hill, under *Tilia* and *Quercus*, 20 July 2001, leg. J. Šutara & M. Vacková, det. J. Šutara (JŠ 4042).

2. Boletes with pores not covered by cheilocystidia in any phase of the development (see Figs. 2, 4, and 6). This type of pores, which is generally known, is very common and occurs in a very large number of European boletes of *Boletaceae*, e.g. *Aureoboletus gentilis* (Quél.) Pouzar, *A. moravicus*

(Vacek) Klofac, *Boletus legaliae* Pilát & Dermek, *B. luridiformis* Rostk., *B. rhodopurpureus* Smotl., *B. rhodoxanthus* (Krombh.) Kallenb., *B. rubrosanguineus* Cheype, *B. satanas* Lenz, *Caloboletus calopus* (Pers.: Fr.) Vizzini (≡ *Boletus calopus* Pers.: Fr.), *C. radicans* (Pers.: Fr.) Vizzini (≡ *B. radicans* Pers.: Fr.) (see Fig. 6), *Chalciporus piperatus* (Bull.: Fr.) Bataille, *C. rubinus* (W.G. Sm.) Singer, *Cyanoboletus pulverulentus* (Opat.) Gelardi, Vizzini & Simonini, *Hemileccinum impolitum* (Fr.) Šutara, *H. depilatum* (Redeuilh) Šutara, *Imleria badia* (Fr.) Vizzini (≡ *Boletus badius* (Fr.) Fr.), *Suillellus luridus* (Schaeff.: Fr.) Murrill (≡ *Boletus luridus* Schaeff.: Fr.) (see Figs. 2 and 4), *Suillellus queletii* (Schulzer) Vizzini, Simonini & Gelardi (≡ *B. queletii* Schulzer), *Tylopilus felleus* (Bull.: Fr.) P. Karst., species of genera *Leccinum* S.F. Gray, *Xerocomellus* Šutara, *Xerocomus* Quél., and many others.

Material examined

Abbreviations used: PRM = Mycological Department, National Museum, Prague; JŠ = private herbarium of Josef Šutara; VJ = private herbarium of Václav Janda; leg. = collected by; det. = identified by. The name of the author is shortened in the text as follows: J.Š. (J. Šutara).

Boletus aereus

Czech Republic. Bohemia. Ledce (Mladá Boleslav district, Central Bohemia), alt. ca. 270 m, under *Quercus*, 1 Aug. 2007, leg. & det. M. Kříž (JŠ 6264). – Kosmonosy, near the town of Mladá Boleslav (Central Bohemia), Baba hill, alt. 250 m, under *Quercus*, 4 June 2009, leg. & det. J.Š. & J. Malý (JŠ 6263). – Praha-Velká Chuchle (Pražská plošina plateau, Central Bohemia), Chuchelský háj, alt. 250 m, under *Quercus* and *Carpinus*, 25 Aug. 2007, leg. & det. M. Mikšík, V. Janda & J.Š. (JŠ 5153). – Kněžičky (Středolabská tabule plateau, Central Bohemia), alt. ca. 250 m, under *Quercus*, 19 Aug. 2010, leg. & det. J.Š. (JŠ 5618–31); *ibid.*, different microlocality, under *Quercus*, 3 Sept. 2010, leg. & det. J.Š. (JŠ 5700); *ibid.*, different microlocality, under *Quercus*, 20 Aug. 2011, leg. & det. J.Š. & J. Rejsek (JŠ 5814–21, 5851–52). – Radimovice u Tábora (Táborská pahorkatina hills, South Bohemia), dam of Velký lake, alt. 460 m, under *Quercus robur* and *Corylus avellana*, 13 Aug. 2005, leg. & det. P. Špinar (JŠ 3704). – Sezimovo Ústí (Táborská pahorkatina hills, South Bohemia), dam of Jezero lake, alt. ca. 420 m, under *Quercus*, 11 Sept. 1994, leg. & det. M. Beran (JŠ 6266).

Bulgaria. Primorsko, 1,5 km N of the town (SE Bulgaria, not far from the Black Sea coast), alt. 15 m, under *Quercus cerris*, *Quercus robur* and *Carpinus betulus*, 14 June 2005, leg. J.Š. & M. Vacková, det. J.Š. (JŠ 4111–12). – Primorsko, 3 km W of the town (close to the Black Sea coast), alt. 50 m, under *Quercus*, 14 June 2005, leg. M. Vacková & J.Š., det. J.Š. (JŠ 4128). – Primorsko, town park (near the Black Sea coast), alt. 20 m, under *Quercus cerris*, 21 June 2006, leg. & det. J.Š. (JŠ 4268–71).

Boletus edulis

Czech Republic. Bohemia. Střelná (Krušné hory Mts., Northwest Bohemia), alt. 420 m, under *Fagus*, 24 Aug. 2006, leg. M. Vacková & J.Š., det. J.Š. (JŠ 4336–37); *ibid.*, alt. 550 m, under *Fagus*, 6 Sept. 2006, leg. J.Š. & M. Vacková, det. J.Š. (JŠ 4379). – Mstišov (Krušné hory Mts., Northwest Bohemia), Dvojhradí, alt. 350 m, under *Carpinus*, 28 July 2005, leg. & det. J.Š. & E. Skála (JŠ 4152); *ibid.*, alt. 360 m, under *Fagus sylvatica*, 16 Aug. 2006, leg. & det. E. Skála & J.Š. (JŠ 4319–20); *ibid.*, alt. 350 m, under *Fagus*, *Carpinus* and *Betula*, 20 Aug. 2006, leg. J.Š. & M. Vacková, det. J.Š. (JŠ 4322–25); *ibid.*, alt. 370 m, under *Fagus*, *Carpinus* and *Betula*, 20 Oct. 2006, leg. M. Vacková & J.Š., det. J.Š. (JŠ 4427); *ibid.*, different microlocality, alt. 420 m, under *Fagus sylvatica*, 30 Aug. 2006, leg. J.Š. & M. Vacková, det. J.Š. (JŠ 4354); *ibid.*, alt. 400 m, under *Fagus sylvatica*, *Picea abies* and *Betula pendula*, 6 Aug. 2010, leg. J.Š. & M. Vacková, det. J.Š. (JŠ 5592–94); *ibid.*, alt. 420 m, under *Picea abies* and *Fagus sylvatica*, 31 July

2011, leg. & det. J.Š. (JŠ 5970). – Dubí (Krušné hory Mts., Northwest Bohemia), Jedlovka, alt. 700 m, under *Picea*, *Fagus* and *Betula*, 6 Sept. 2011, leg. & det. E. Skála & J.Š. (JŠ 5968). – Běhánky (Krušné hory Mts., Northwest Bohemia), alt. 450 m, under *Picea*, 23 Aug. 2011, leg. & det. J.Š. & E. Skála (JŠ 6028–33). – Braňany (České středohoří Mts., Northwest Bohemia), Kaňkov hill, alt. 390 m, under *Picea*, *Betula* and *Quercus*, 9 Sept. 1985, leg. M. Šutarová, det. J.Š. (JŠ 3146); *ibid.*, alt. 400 m, under *Picea* and *Betula*, 11 Sept. 1985, leg. J. Šutara jun. & J.Š., det. J.Š. (3149–51). – Želenice (České středohoří Mts., Northwest Bohemia), Želenický vrch hill, alt. 350 m, under *Betula* and *Quercus*, 1 Oct. 1983, leg. B. Aubrecht & E. Skála, det. J. Biber (JŠ 2675–77). – Blatno (Žihelská pahorkatina hills, West Bohemia), Blatenský svah, alt. 500 m, under *Picea abies*, 13 June 2009, leg. & det. J.Š. (JŠ 6161). – Blatno (Žihelská pahorkatina hills, West Bohemia), “V Koutech” forest between the villages of Blatno and Pastuchovice, alt. 450 m, under *Picea abies*, 12 Sept. 1992, leg. & det. J.Š. (JŠ 3598). – Žihle (Žihelská pahorkatina hills, West Bohemia), Žihelský forest, under *Picea abies*, 23 July 1992, leg. M. Šutarová & J.Š., det. J.Š. (JŠ 3535). – Lipí, near the town of Manětín (Manětínská pahorkatina hills, West Bohemia), alt. 440 m, under *Picea*, *Betula* and *Pinus*, 29 Oct. 1976, leg. & det. J.Š. (JŠ 638). – Hubenov (Manětínská pahorkatina hills, West Bohemia), alt. 510 m, under *Picea* and *Pinus*, 20 Sept. 2012, leg. & det. J.Š. (JŠ 6015). – Křečov (Plaská pahorkatina hills, West Bohemia), forest between villages of Křečov and Mladotice, alt. 420 m, under *Picea abies* and *Pinus sylvestris*, 1 Oct. 1994, leg. M. Šutarová, det. J.Š. (JŠ 3840). – Plasy (Plaská pahorkatina hills, West Bohemia), ca. 1.5 km NW of the town, alt. 360 m, under *Picea*, 19 Sept. 2010, leg. & det. J.Š. (JŠ 5745); *ibid.*, different microlocality, alt. 400 m, under *Picea*, 21 Sept. 2010, leg. & det. J.Š. (JŠ 5760); *ibid.*, different microlocality, alt. 400 m, under *Picea* and *Pinus*, 2 Oct. 2013, leg. & det. J.Š. (JŠ 6187). – Plasy (Plaská pahorkatina hills, West Bohemia), ca. 2 km SW of the town, alt. 450 m, under *Picea* and *Pinus*, 20 Sept. 2012, leg. & det. J.Š. (JŠ 6015); *ibid.*, different microlocality, alt. 430 m, under *Picea* and *Pinus*, 1 Oct. 2013, leg. M. Vacková & J.Š., det. J.Š. (JŠ 6183–84); *ibid.*, under *Picea* and *Pinus*, 3 Oct. 2013, leg. J.Š. & M. Vacková, det. J.Š. (JŠ 6185–86). – Plzeň (West Bohemia), not far from lake Bolevec, alt. 380 m, under *Picea* and *Quercus*, 21 Sept. 1983, leg. J.Š., det. J. Herink & J.Š. (JŠ 2464). – Hlinice (Táborská pahorkatina hills, South Bohemia), alt. 450 m, under *Picea*, 22 Sept. 1992, leg. P. Špinar, det. P. Špinar & J.Š. (JŠ 3704); *ibid.*, alt. 440 m, under *Picea*, 13 Sept. 1994, leg. & det. J.Š. (JŠ 3819–20). – Velmovice (Táborská pahorkatina hills, South Bohemia), alt. 540 m, under *Picea*, 22 Sept. 2009, leg. & det. J.Š. (JŠ 5451). – Turovec (Táborská pahorkatina hills, South Bohemia), alt. 430 m, under *Picea*, 21 Sept. 2012, leg. & det. V. Zita (JŠ 6167). – Kardašova Řečice (Třeboňsko Protected Landscape Area, South Bohemia), close to lake Velká Holná, alt. 480 m, under *Picea*, 23 Aug. 1983, leg. M. Šutarová & J.Š., det. J.Š. (JŠ 2294–95); *ibid.*, under *Picea*, 25 Aug. 1983, leg. R. Cuprová, det. J.Š. (JŠ 2344–45).

Slovakia. Vážec (Podtatranská kotlina basin, North Slovakia), alt. 850 m, under *Picea*, 4 Sept. 1980, leg. J. Kuthan, det. J. Kuthan & J.Š. (JŠ 320). – Čierny Balog (Veporské vrchy Mts., Central Slovakia), Dobročský prales National Nature Reserve, alt. ca. 800 m, 15 Sept. 1988, leg. L. Hruška, det. L. Hruška & J.Š. (JŠ 4033).

Boletus pinophilus

Czech Republic. **Bohemia.** Štichovice (Plaská pahorkatina hills, West Bohemia), alt. 480 m, under *Pinus*, 19 Aug. 1984, leg. J. Zecha, det. J.Š. (JŠ 2800). – Křečov (Plaská pahorkatina hills, West Bohemia), alt. 420 m, under *Pinus*, 1 Oct. 1994, leg. M. Šutarová, det. J.Š. (JŠ 3837–38). – Chlum, near Blatná (Blatenská pahorkatina hills, Southwest Bohemia), alt. ca. 510 m, under *Pinus*, 16 Aug. 1985, leg. Z. Řehoř, det. Z. Řehoř & J.Š. (JŠ 3140). – Hlinice (Táborská pahorkatina hills, South Bohemia), Velký Hutecký forest, alt. 450 m, under *Pinus*, 22 Sept. 1992, leg. P. Špinar, det. P. Špinar & J.Š. (JŠ 3705); *ibid.*, under *Pinus* and *Picea*, 5 Oct. 2007, leg. & det. J.Š. (JŠ 5233); *ibid.*, under *Pinus*, 15 Sept. 1997, leg. & det. P. Špinar (JŠ 6260). – Kardašova Řečice (Třeboňsko Protected Landscape Area, South Bohemia), near lake Velká Holná, alt. 460 m, under *Pinus*, 25 Aug. 1983, leg. Wunsch, det. J.Š. (JŠ 2387). – Malonty (Novohradské hory Mts., South Bohemia), alt. 620 m, under *Pinus*, 21 Sept. 2009, leg. & det. M. Kríž & J. Hlásek (JŠ 6261–62).

Slovakia. Vážec (Podtatranská kotlina basin, North Slovakia), alt. ca. 900 m, under *Pinus*, 14 Sept. 1988, leg. E. Skála & K. Holeček, det. E. Skála (JŠ 3418).

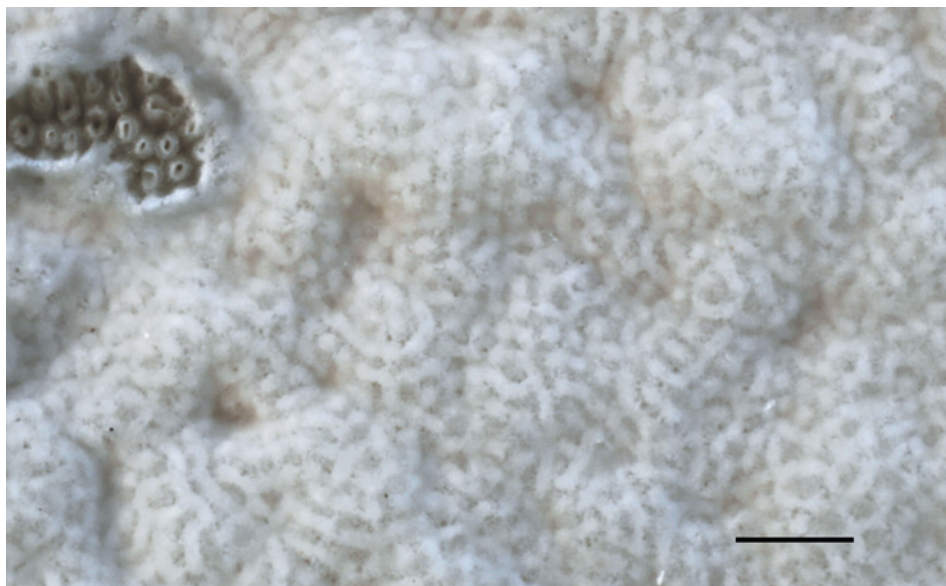


Fig. 3. Pores of young fruit body of *Boletus edulis* covered with cheilocystidia (JŠ 6187). A small place bitten by slugs (above left) shows the tube structure under the layer of cheilocystidia. Scale bar = 1 mm. Photo J. Šutara.

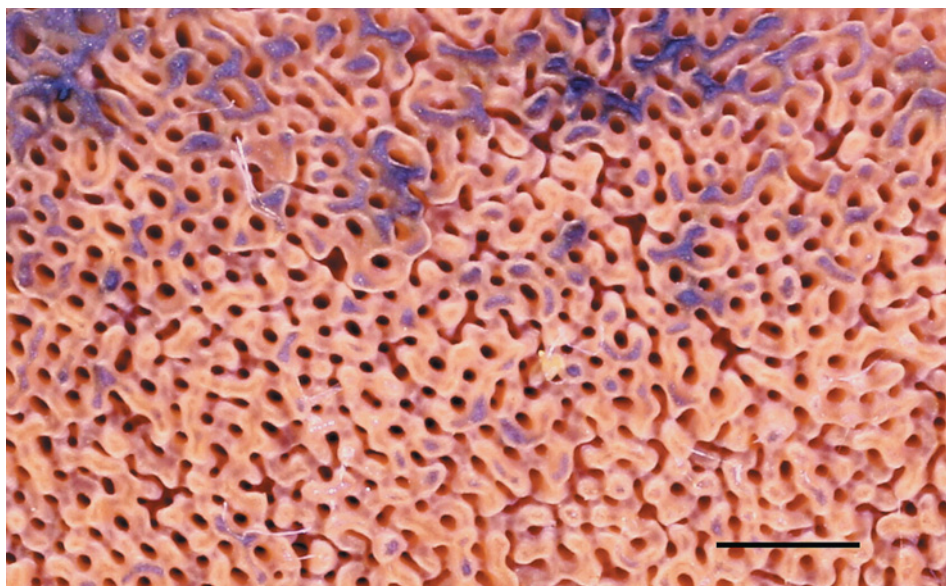


Fig. 4. Pores of young fruit body of *Suillellus luridus* not covered with cheilocystidia. Scale bar = 1 mm. Photo J. Šutara.

Herbarium specimen: Teplice (Northwest Bohemia, Czech Republic), V Lipách hill, under *Quercus*, 13 Aug. 2013, leg. & det. J. Šutara (JŠ 6194).

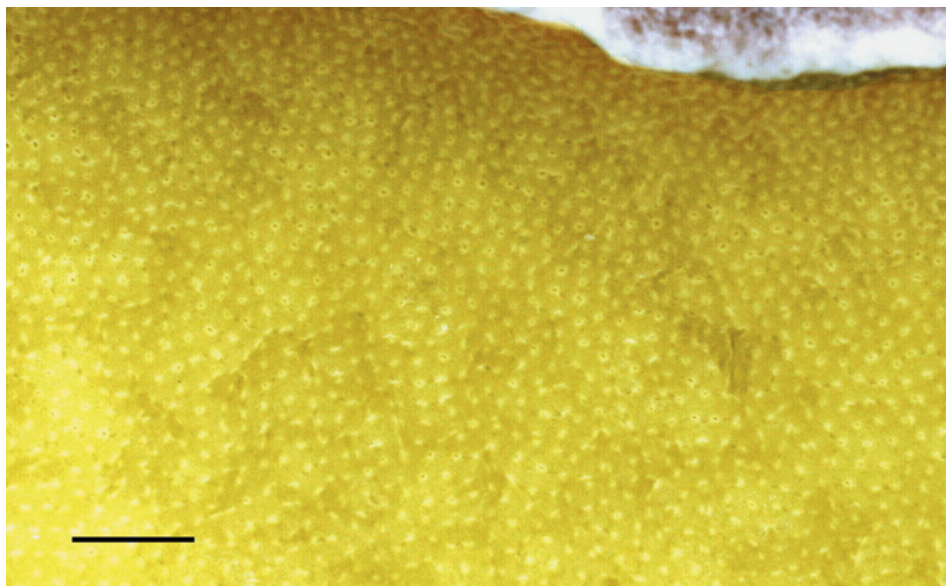


Fig. 5. Pores of young fruit body of *Butyriboletus appendiculatus* (type species of *Butyriboletus*) covered with cheilocystidia (JŠ 6163). Scale bar = 1 mm. Photo J. Šutara.

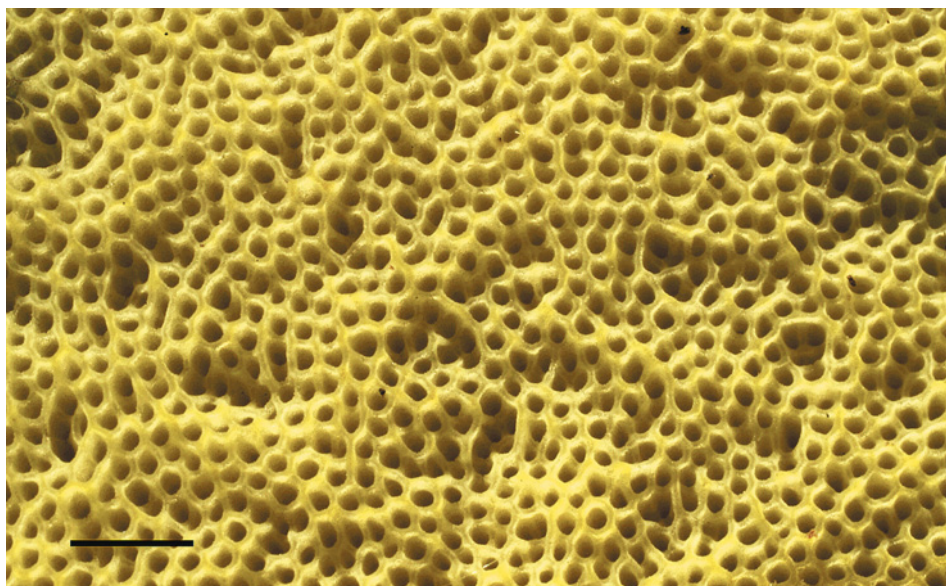


Fig. 6. Pores of young fruit body of *Caloboletus radicans* not covered with cheilocystidia. Scale bar = 1 mm. Photo J. Šutara.

Herbarium specimen: Teplice, Doubavka hill (Northwest Bohemia, České středohoří Mts., Czech Republic), alt. 270 m, under *Quercus* and *Acer*, 17 Aug. 2013, leg. & det. J. Šutara (JŠ 6267).

Boletus reticulatus

Czech Republic. Bohemia. Hrad Osek (Krušné hory Mts., Northwest Bohemia), alt. 450 m, under *Quercus*, 16 June 2007, leg. J. Křemen, det. J.Š. (JŠ 5019–22); *ibid.*, under *Quercus* and *Betula*, 2 June 2008, leg. J. Křemen, det. J.Š. (JŠ 5257). – Běhánky (Krušné hory Mts., Northwest Bohemia), alt. 430 m, under *Quercus*, 23 Aug. 2011, leg. E. Skála, det. E. Skála & J.Š. (JŠ 6042). – Teplice (České středohoří Mts., Northwest Bohemia), Doubravka hill, alt. 275 m, under *Quercus*, *Acer platanoides* and *Acer pseudoplatanus*, 11 June 2010, leg. & det. E. Skála & J.Š. (JŠ 5506–07); *ibid.*, under *Quercus*, 18 June 2010, leg. J.Š. & M. Vacková, det. J.Š. (JŠ 5210). – Teplice (České středohoří Mts., Northwest Bohemia), Písečný vrch hill, alt. 230 m, under *Quercus*, 23 July 2008, leg. & det. J.Š. (JŠ 5323–24). – Želenice (České středohoří Mts., Northwest Bohemia), Želenický vrch hill, alt. 400 m, under *Quercus*, 24 May 2002, leg. J.Š. & M. Vacková, det. J.Š. (JŠ 4474–82); *ibid.*, different microlocality, under *Quercus*, 1 June 2002, leg. J.Š. & M. Vacková, det. J.Š. (JŠ 4034); *ibid.*, different microlocality, alt. 400 m, under *Quercus cerris* and *Quercus robur*, 6 June 2008, leg. J.Š. & M. Vacková, det. J.Š. (JŠ 5263–64). – Nečichy (České středohoří Mts., Northwest Bohemia), Trhlávek hill, alt. 250 m, under *Quercus*, 17 Aug. 2005, leg. & det. E. Skála, J.Š. & P. Špinar (JŠ 4194–97). – Prodašice (near boundary of the Mladá Boleslav and Jičín districts), under *Quercus*, 19 July 2007, leg. & det. V. Janda & J.Š. (JŠ 5109–10). – Praha-Velká Chuchle, Homolka, under *Quercus*, 7 Aug. 2011, leg. & det. J.Š. (JŠ 5955). – Břístev (Středolabská tabule plateau, Central Bohemia), northern bank of Komárovský lake, alt. 210 m, under *Quercus*, 5 Aug. 2011, leg. & det. J. Rejsek & J.Š. (JŠ 5936–43). – Svídnice (Středolabská tabule plateau, Central Bohemia), southern bank of Komárovský lake, alt. 200 m, under *Quercus*, 4 Aug. 2010, leg. & det. J.Š. (JŠ 5541–47). – Kněžičky (Středolabská tabule plateau, Central Bohemia), alt. ca. 250 m, under *Quercus*, 19 Aug. 2010, leg. & det. J.Š. (JŠ 5668–78); *ibid.*, different microlocality, under *Carpinus*, 3 Sept. 2010, leg. & det. J.Š. (JŠ 5704–06); *ibid.*, different microlocality, under *Quercus*, 20 Aug. 2011, leg. & det. J.Š. (JŠ 5843). – Záhornice (Středolabská tabule plateau, Central Bohemia), northern bank of Jakubský lake, alt. 210 m, under *Quercus*, 21 Sept. 2013, leg. & det. V. Janda & L. Opat (JŠ 6211).

Bulgaria. Primorsko (SE Bulgaria, close to the Black Sea coast), under *Quercus*, 7 June 2006, leg. J.Š. & M. Vacková, det. J.Š. (JŠ 4276).

Butyriboletus appendiculatus

Czech Republic. Bohemia. Praha-Velká Chuchle (Pražská plošina plateau, Central Bohemia), Chuchelský háj, under *Quercus*, 1 Sept. 2007, leg. & det. V. Janda & J.Š. (JŠ 5261). – Břístev (Středolabská tabule plateau, Central Bohemia), northern bank of Komárovský lake, alt. 205 m, under *Quercus*, 19 Aug. 2007, leg. & det. V. Janda, J. Rejsek & J.Š. (JŠ 5099–5102); *ibid.*, under *Quercus*, 4 Aug. 2010, leg. & det. J.Š. (JŠ 5524–5525). – Dymokury (Středolabská tabule plateau, Central Bohemia), on bank of Pustý lake, under *Quercus*, 19 July 2007, leg. & det. A. Vít & J.Š. (JŠ 5095). – Záhornice (Středolabská tabule plateau, Central Bohemia), northern bank of Jakubský lake, alt. 205 m, under *Quercus*, 19 July 2007, leg. & det. V. Janda & J.Š. (JŠ 5106); *ibid.*, under *Quercus*, 26 July 2007, leg. M. Vacková, det. J.Š. (JŠ 5130). – Kněžičky (Středolabská tabule plateau, Central Bohemia), alt. 250 m, under *Quercus*, 11 Aug. 2011, leg. & det. J. Rejsek & J.Š. (JŠ 5877–5878); *ibid.*, under *Quercus*, 28 Sept. 2011, leg. & det. V. Janda, J. Rejsek & J.Š. (JŠ 5904–5912). – Turovec (Táborská pahorkatina hills, South Bohemia), on dam of Luční lake, under *Quercus*, 7 Sept. 1991, leg. & det. P. Špinar & J.Š. (JŠ 5095); *ibid.*, under *Quercus*, 19 Sept. 2012, leg. & det. P. Špinar & J.Š. (JŠ 6163–6164).

Butyriboletus fechtneri

Czech Republic. Bohemia. Nouzov near Dymokury (Středolabská tabule plateau, Central Bohemia), southern bank of Komárovský lake, under *Quercus*, 10 July 2008, leg. & det. V. Janda (JŠ 5300); *ibid.*, under *Quercus*, *Carpinus* and *Tilia*, 4 Sept. 2008, leg. Z. Kučera, det. J.Š. & Z. Kučera (JŠ 5433); *ibid.*, under *Quercus* and *Carpinus*, 4 Aug. 2010, leg. & det. J.Š. (JŠ 5434–5436). – Dymokury (Středolabská tabule plateau, Central Bohemia), on bank of Pustý lake, under *Quercus*, 25 Sept. 2013, leg. L. Opat & J.Š., det. V. Janda & J.Š. (JŠ 6206–6207). – Kněžičky (Středolabská tabule plateau, Central Bohemia), under *Quercus*, 20 Aug. 2011, leg. & det. V. Janda (JŠ 5837).

Sweden. Upland, Ljusterö parish, Siarö, Kalvholmen, under *Quercus*, 29 Aug. 1951, leg. O. Persson (PRM 518242; ex Fungi Exsiccati Suecici of S. Lundell & J.A. Nannfeldt, No. 2607).

Butyriboletus fuscoroseus

Czech Republic. Bohemia. Běrunice (Středolabská tabule plateau, Central Bohemia), Kněžičky Game Preserve, under *Quercus*, 11 Aug. 2011, leg. J. Rejsek & J.Š., det. J.Š. & J. Rejsek (JŠ 5823); *ibid.*, under *Quercus*, 20 Aug. 2011, leg. J.Š., J. Rejsek & V. Janda, det. J.Š. & V. Janda (JŠ 5844–5846, VJ 200811-01); *ibid.*, under *Quercus*, 28 Sept. 2011, leg. J. Rejsek, V. Janda & J.Š., det. J.Š. & V. Janda (JŠ 5917–5918). – Žehuň (Východolabská tabule plateau, Central Bohemia), Kozí hůra hill, under *Quercus* and *Carpinus*, 15 Aug. 2009, leg. & det. M. Mikšík (JŠ 6215). – Moravia. Kyjov (Chříby hills, South Moravia), valley of Bohuslavický stream S of Lenivá hora hill, alt. 330 m, under *Quercus* and *Carpinus*, 31 July 2008, leg. & det. J. Běfák, rev. J.Š. (JŠ 6221).

Slovakia. Ladzany (Štiavnické vrchy Mts., Central Slovakia), Studenec valley, under *Quercus*, 9 Sept. 1998, leg. & det. M. Graca (JŠ 4244). – Ladzany (Štiavnické vrchy Mts., Central Slovakia), forest plantations covering Háj and Velký Gregor hills, under *Quercus*, 12 Aug. 2010, leg. & det. M. Kříž (JŠ 5644–5645).

Butyriboletus regius

Czech Republic. Bohemia. Praha-Točná (Pražská plošina plateau, Central Bohemia), vicinity of the villages of Točná and Závist, alt. 310 m, under *Quercus*, 16 July 2012, leg. & det. L. Opat (JŠ 6204). – Jíloviště (Brdská vrchovina uplands, Central Bohemia), Strnady, under *Quercus* and *Carpinus*, 15 Sept. 1985, leg. M. Kotábová, det. Z. Pouzar (PRM 866632). – Karlík (Pražská plošina plateau, Central Bohemia), Bohemian Karst, Krásná stráň Nature Monument, alt. 300 m, under *Quercus*, 14 May 2009, leg. & det. T. Wagner & J.Š. (JŠ 6199); *ibid.*, under *Quercus*, 21 May 2009, leg. & det. T. Wagner (JŠ 6200). – Měňany (Hořovická pahorkatina hills, Central Bohemia), Bohemian Karst, under *Quercus*, 14 May 2009, leg. & det. V. Janda & J.Š. (JŠ 6196–6197); *ibid.*, under *Quercus*, 26 July 2011, leg. & det. M. Kříž (JŠ 6222). – Liteň (Hořovická pahorkatina hills, Central Bohemia), Bohemian Karst, Mramor hill, alt. 410 m, under *Quercus* and *Carpinus*, 24 July 2012, leg. & det. L. Opat (JŠ 6205). – Komárov near Hořovice (Brdská vrchovina uplands, Central Bohemia), on dam of Červený lake, alt. 410 m, under *Quercus*, 17 July 1992, leg. & det. O. Jindřich (JŠ 3525); *ibid.*, under *Quercus*, 7 Sept. 1997, leg. & det. O. Jindřich (JŠ 6213). – Moravia. Jinačovice (Bobravská vrchovina uplands, South Moravia), Sychrov hill, under *Quercus*, 25 Aug. 2006, leg. & det. L. Straka (JŠ 5227).

Croatia. Rabac (Istria), under *Quercus*, 8 Sept. 1976, leg. V. Vyčichlo, det. J. Šutara (JŠ 044).

Butyriboletus roseogriseus

Czech Republic. Moravia. Francova Lhota (Javorníky Mts., East Moravia), alt. 580–595 m, under *Abies*, *Picea* and *Corylus*, 13 Aug. 2010, leg. M. Graca, det. J.Š., M. Graca, V. Janda., M. Kříž & M. Kolařík (PRM 923483, holotype); *ibid.*, under *Abies*, *Picea* and *Corylus*, 26 Aug. 2010, leg. M. Graca & J.Š., det. J.Š., M. Graca, V. Janda., M. Kříž & M. Kolařík (JŠ 6188); *ibid.*, under *Abies*, *Picea*, *Corylus* and *Sorbus*, 1 Aug. 2012, leg. M. Graca & V. Balner, det. J.Š., M. Graca, V. Janda., M. Kříž & M. Kolařík (PRM 923480); *ibid.*, under *Abies*, *Picea* and *Corylus*, 17 Aug. 2012, leg. M. Graca, det. J.Š., M. Graca, V. Janda, M. Kříž & M. Kolařík (PRM 923482); *ibid.*, different microlocality, alt. 585 m, under *Abies*, *Picea*, *Quercus*, *Pinus*, *Populus tremula* and *Larix*, 18 Aug. 2010, leg. M. Graca & J. Polčák, det. J.Š., M. Graca, V. Janda, M. Kříž & M. Kolařík (JŠ 6191); *ibid.*, different microlocality, alt. 585 m, under *Abies*, *Picea* and *Betula*, 18 Aug. 2010, leg. M. Graca & J. Polčák, det. J.Š., M. Graca, V. Janda, M. Kříž & M. Kolařík (JŠ 6192, 6193); *ibid.*, different microlocality, alt. 610 m, under *Picea* and *Abies*, 8 Aug. 2012, leg. M. Graca & V. Balner, det. J.Š., M. Graca, V. Janda, M. Kříž & M. Kolařík (PRM 923481); *ibid.*, different microlocality, alt. 600 m, under *Abies* and *Picea*, 20 July 2012, leg. M. Graca & V. Balner, det. J.Š., M. Graca, V. Janda, M. Kříž & M. Kolařík (PRM 923479).

Butyriboletus subappendiculatus

Czech Republic. Moravia. Francova Lhota (Javorníky Mts., East Moravia), alt. ca. 600 m, under *Picea*, 8 July 2009, leg. & det. M. Graca (JŠ 6212).

Slovakia. Vážec (Podtatranská kotlina basin, North Slovakia), alt. 850 m, under *Picea*, 4 Sept. 1980, leg. J.Š., det. J.Š. & J. Kuthan (JŠ 318).

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