PERSOONIA

18 / 4
2005

AN INTERNATIONAL
MYCOLOGICAL JOURNAL

PERSOONIA

An International Mycological Journal

Published by the Nationaal Herbarium Nederland, Universiteit Leiden branch, The Netherlands

Persoonia is a journal devoted to mycology, with emphasis on the taxonomy of fungi. Papers on morphology, cytology, ultrastructure, genetics, or chemistry are only accepted when the link to taxonomy is clear.

Publication in Persoonia is not restricted to members of the staff of the Nationaal Herbarium only, but limited space will also be available for other authors and invited papers. Those interested are requested to contact the Editors.

All manuscripts submitted to Persoonia are externally reviewed before acceptance or refusal.

Correspondence concerning manuscripts for Persoonia should be directed to the Editors.

Persoonia will be published once a year, with about 150 pages per part. Four parts will constitute a volume. Persoonia can be obtained by subscription or by exchange.

Exchange with mycological journals or with periodicals regularly containing mycological papers will be appreciated.

Correspondence concerning orders and subscriptions should be addressed to the Publications Department, Nationaal Herbarium Nederland, Universiteit Leiden branch, P.O. Box 9514, 2300 RA Leiden, The Netherlands. E-mail: publications@nhn.leidenuniv.nl.

PERSOONIA
Volume 18, Part 4, 449–470 (2005)

BASIDIOME DEVELOPMENT OF XEROMPHALINA CAMPANELLA (TRICHOLOMATALES, BASIDIOMYCETES)

H. CLÉMENÇON

Department of Ecology and Evolution, University of Lausanne, CH-1015 Lausanne, Switzerland.
E-mail: Heinz.Clemencon@bluewin.ch

The agaricoid Hymenomycete *Xeromphalina campanella* is exocarpic, apertopileate and amphiblemate. Metablemas develop separately on the pileus and on the stipe, but they do not form any kind of veil. The pileoblema becomes a gelatinous pileipellis, and the cauloblema forms a hairy coating on the lower part of the stipe of the mature basidiomes. The hymenophoral trama is bidirectional in the gill rudiments, but becomes more physalo-irregular at maturity and contains many narrow hyphae with smooth or incrusted walls. The context of the stipe resembles a sarcodimitic structure, but the thin-walled inflated cells are rarely fusiform, although they are frequently gradually narrowed at one end. Between the physalohyphae, narrow, incrusted hyphae and ramified connective hyphae occur in the stipe and in the pileus context. The hyphae of the pileus of a young basidiome contain granular deposits of glycogen.

The only note on the basidiome development of *Xeromphalina campanella* published so far consists of a few lines and a single photograph at the end of a taxonomic paper by Hintikka (1957). Since no trace of any kind of veil is visible in the photograph, Hintikka cautiously concluded that the development is probably gymnocarpic. Singer (1965) was more confident and stated that his *X. austroandina* is gymnocarpic, based on the "same observations as indicated by Hintikka (1957) for *X. campanella*", without giving any further details. Later, in his fundamental work on the genera of gill fungi, Singer (1986: 425) only mentioned the gymnocarpic development of *X. campanella*, giving credit to Hintikka, but he did not mention his own observations on *X. austroandina* any more. Since the reported observations are rather scanty and no other species of this genus was studied, Watling & Turnbull (1998: 147) cautiously wrote that the development is "not known".

In March 2002 a large population of *X. campanella* basidiomes with primordia in all developmental stages was found near Lausanne, Switzerland, which enabled a study of the carpogenesis of this species.

MATERIAL AND METHODS

Xeromphalina campanella (Batsch) Maire, 'Les Liaises', north of Lausanne, Switzerland, 800 m above sea level; basidiomes densely gregarious on the black remains of a stereoid fungus still attached to the fallen conifer trunk it was growing on. Leg. H. Clémençon, 18.III.2002, coll. *HC 02/009* (LAU).

Patches of the black, fibrous substrate were inspected with a dissecting microscope. Excised substrate fragments bearing primordia were fixed for 25 h at 20–22°C in a solution of 0.9% formaldehyde and 1.25% glutaraldehyde in tap water (63 mg/L Ca^{++}).

No vacuum was applied. The fixed material was transferred to cold methyl cellosolve and carried over ethanol and propanol into butanol (Feder & O'Brien, 1968). It was embedded in methacrylate, and the microtome sections were stained with aluminium-zirconium-haematoxylin (Clémençon, 2000), basic fuchsine or with the tannin-iron reaction for polysaccharides followed by haematoxylin as follows (all manipulations done at room temperature of 20–22°C): a) Immerse the sections in a 3% tannin (tannic acid) solution in distilled water for 30–40 minutes. Do not use gallic acid; it does not work. b) Rinse in 3 or 4 charges of distilled water, about 5 minutes each. c) Immerse in 5% iron(III)chloride in distilled water for 20–40 minutes. The sections stain dark gray to black, methacrylates remain unstained. d) Rinse in 2 or 3 charges of distilled water, about 5 minutes each. e) Stain in 0.1% ripened hematoxylin in distilled water for 15–20 minutes. f) Rinse in 2 or 3 charges of distilled water, about 5 minutes each. g) Stabilise the stain in calcium-rich tap water. If no hard tap water is available, use a 0.2% sodium bicarbonate solution. h) Briefly rinse in distilled water, dry the sections on a hot bench or in an oven, apply a synthetic resin (Entellan or a similar product) and a cover glass. As a result the cell walls and gelatinous substances colour dark gray to black; some cell contents, mainly protein crystals, are sometimes stained. Selected sections were photographed with an Olympus DP11 digital camera mounted on a Leitz Orthoplan microscope. The photographs were prepared for printing using Adobe Photoshop with a Macintosh G4 computer.

RESULTS

A summary of the early development of *X. campanella* is shown in Figs. 1 and 2. Already the smallest nodulus is hairy (Figs. 1a, 2a). The Figs. 1c–e and 2c–e show the first developmental stages of the pileus, the growth of the metablema, and the beginning of hyphal inflation. The smallest nodulus studied was 160 μm wide and 150 μm high and had a stalk 65 μm long and 35 μm thick, sunken in the substrate (Fig. 3). The parallel hyphae of the stalk deviate and ramify at the base of the nodulus and become subregularly arranged, still growing upward. The context in the centre of the nodulus is slightly more irregular than in the peripheral parts. The hyphae of the surface of the nodulus have a slightly thickened, light brown wall, staining deeper in the permanent

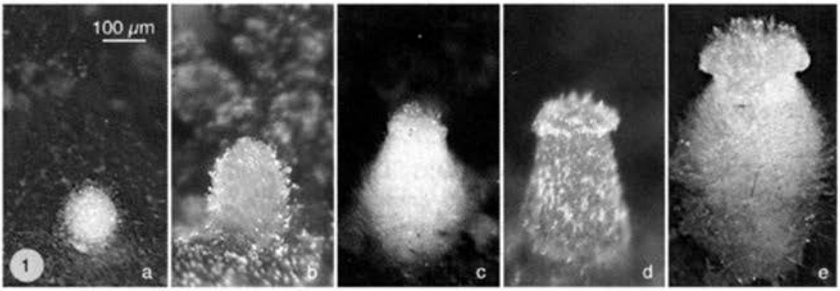


Fig. 1. Selected stages of early primordium development. Living specimens photographed on the substrate, illustrating the hirsute metablemas and the initiation of the pileus.

mounts. The nodulus is moderately hairy from free hyphal ends. The small groove on the top has no relation with the funnel-shape of the mature basidiome, as in other noduli and young primordia studied it is lacking (e.g. Fig. 2a).

In the next stage (Figs. 1b, 2b) a primordial shaft has begun its upward growth from the top of the nodulus, changing the nodulus into a cone-shaped body with a rounded base and a narrow, flat top (Fig. 4). The hyphae in the rudiment of the primordial shaft are subregularly arranged in a general vertical orientation. The bulbous nodulus bears many slightly thick-walled peripheral hyphae in an obliquely upward and outward orientation, giving this part a hirsute appearance. These hairs constitute a noduloblema. The cauloblema on the young primordial shaft is less developed, so this part is less hirsute than the nodulus. The cauloblema and the noduloblema intergrade smoothly, forming a continuous hairy coating. Most hyphal cells are binucleate (Figs. 5a, b).

The pileus initial becomes visible as a short horizontal rim on top of the primordial shaft (Figs. 1c, 2c, 6–8). It consists of more or less horizontal or obliquely downward oriented hyphae. No prehymenial palisade is present at this stage. The pileoblema is strongly developed and consists of greatly inflated hyphae. The top of the primordial shaft is usually slightly convex because of the form of the pileoblema, but in many primordia the future funnel-shaped pileus is already perceptible by the general orientation of the thin generative hyphae of the context beneath the pileoblema (Fig. 8a). Under the pileus initial the primordial shaft is composed of subregular generative hyphae with a general vertical orientation, growing upward. This part is the stipe initial. In most primordia it is covered with a cauloblema consisting of hyphal ends growing in an oblique outward-upward direction. At the base, the hyphae of the nodulus started to inflate (Figs. 6, 8b).

The pileus margin grows outward and curves downward, and the underside of the pileus initial becomes lined with a prehymenial palisade (Fig. 9). The pileoblema and the cauloblema grow considerably and become a loose layer of erect hyphae, but the prehymenial palisade remains naked. The stipe base consists of the nodulus with a characteristic secondary structure composed of irregularly arranged and irregularly inflated hyphae. Hyphal inflation is minimal in the stipe just below the pileus, and strong again in the top part of the pileus, contributing here to the expansion of the cap.

During further development the pileus margin grows outward and curves downward, but it never reaches the stipe surface (Figs. 2e, 10, 14). The pileoblema is most voluminous in the centre of the cap, where it forms a flat, inverted cone filling the funnel-shaped pileus rudiment. Laterally the pileoblema forms a thin periclinal layer on the pileus context. Although the transition from pileus context to pileoblema is gradual, the funnel-shaped, denser pileus context is perceptible in Fig. 10. The prehymenial palisade begins to produce meiotic basidia protruding considerably beyond the level of the palisade cells (Figs. 10, 11). In the stipe context many hyphae swell and elongate enormously and become multinucleate (Figs. 12, 13). Some hyphae end bluntly within the stipe context (Fig. 13), but the end cells do not become acrophysalides.

With the growth of the pileus, the prehymenial palisade becomes arched, and individual hyphae of the cauloblema may grow into the space between the pileus margin and the stipe, but no 'partial veil' is formed. The pileoblema grows down laterally on the pileus margin, its hyphae taking a periclinal orientation, but it does not join the cauloblema (Fig. 14). It is not yet gelatinous. In this developmental stage the gill initials are still lacking (Fig. 15).

When the pileus reaches a diameter of about 1 mm, gills begin to grow down from its lower surface. The first gill trama is bidirectional with the vertical hyphae slightly diverging (Fig. 16). Maturing basidia protrude considerably beyond the general level of the hymenium. When the pileus reaches a diameter of about 3 mm, more pronounced plectological differentiations take place. In the gill trama the hyphae of the mediostratum begin to inflate (Figs. 17a, b), and the pileoblema changes its architecture. Its hyphae become radially adherent to the pileus surface, and a gelatinous substance is formed, so that the result is a radial ixocutis. Some hyphae of the pileoblema remain more or less erect, and their often inflated end cells are sometimes called pileocystidia (Miller, 1968; Klán, 1984; Redhead, 1988). In the pileus context many cells now contain granular glycogen staining brown in iodine solutions and black with the tannin-iron reaction (Fig. 18). In the hymenium well-differentiated pleurocystidia and cheilocystidia are present, but the latter are by far the more numerous. The surface of the pleurocystidia seems to be sticky enough to capture spores liberated by the basidia (Fig. 19). The time of the first appearance of the hymenial cystidia is difficult to establish, since big, prominent cells protruding beyond the level of the prehymenial palisade may develop either into basidia or cystidia.

Basidiomes with a pileus 4–5 mm wide are fully differentiated. The mature gill trama consists of irregular to bidirectional physalohyphae, and thin, brown-walled, irregularly arranged hyphae with smooth or incrusted walls and almost no stainable cell content (Figs. 20 a–d). A few very thin and extremely thin-walled hyphae rich in cytoplasm occur in the gill trama and in the pileus context (Figs. 21a, b). The pileus is covered by an ixocutis of radial hyphae bearing some erect hyphae and isolated inflated cells called pileocystidia (Fig. 22). The ixocutis and the pileocystidia are the product of the pileoblema. The stipe of the mature basidiome is composed of three hyphal types (Figs. 23a–c). Most prominent are the greatly inflated, multinucleate and highly vacuolated physalohyphae. Their cells are sometimes cylindrical, sometimes elongate-conical at one septum and cylindrical-blunt at the other (Figs. 23a, b), only rarely the cells are fusiform. Because of the conical structures Redhead (1987) called this context sarcodimitic. Besides the physalohyphae many thin, approximately cylindrical hyphae with brown incrusted walls, and thin, highly ramified, colourless connecting hyphae are present in the stipe context (Fig. 23c). The context of the pileus has the same structure.

DISCUSSION

Using the traditional terminology, the development of *X. campanella* should be called gymnocarpic, as did Hintikka (1957) and Singer (1986). The primordia lack any kind of veil, universal or partial, the pileipellis does not extend over the pileus margin toward the stipe, and the pileus margin itself never touches the stipe surface. Thus no closed gill cavity ever exists. But this simple term does not take into account the massive development of metablemas on the stipe and on the pileus.

(*text continued on p. 469*)

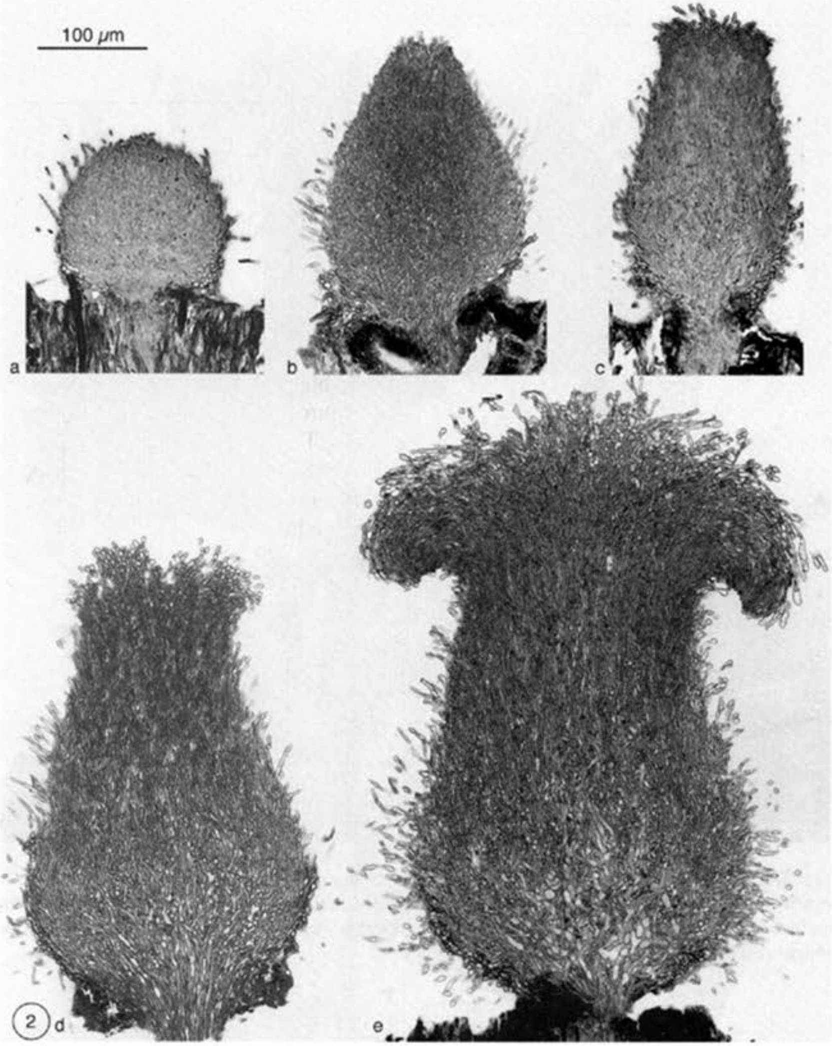


Fig. 2. Selected stages of early primordium development. Longitudinal sections showing the development of the metablemas, the stipe rudiment and the pileus initial.

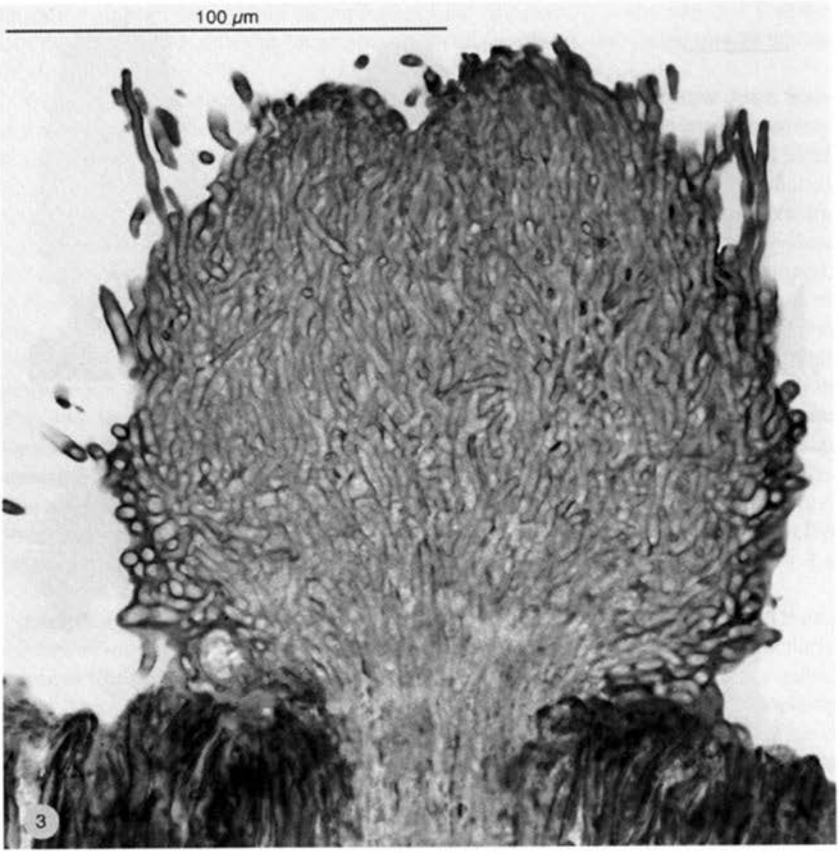


Fig. 3. A nodulus rooting in the substrate, the dead remains of a stereoid fungus. The hyphae in the centre are slightly more irregularly arranged than in the peripheral parts. The erect hyphae on the surface can be termed a noduloblema. The slight indent on top is accidental; it is not related to the funnel shape of the mature pileus.

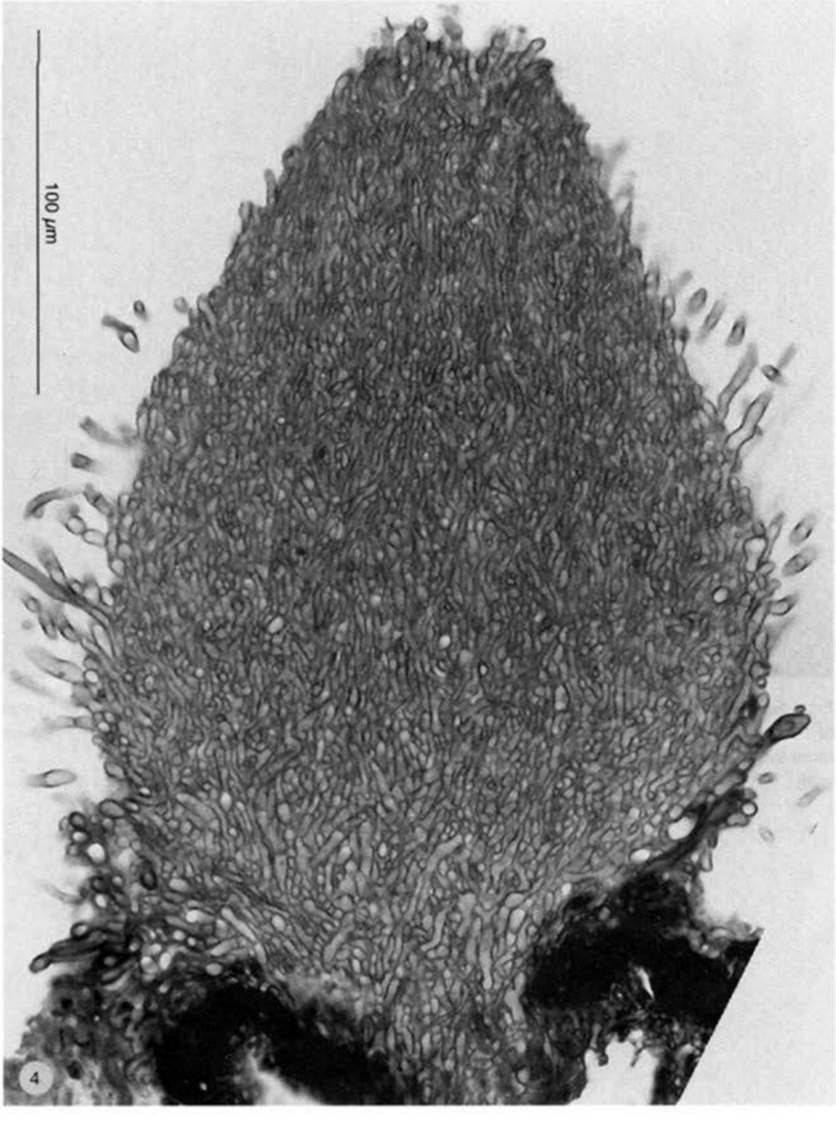
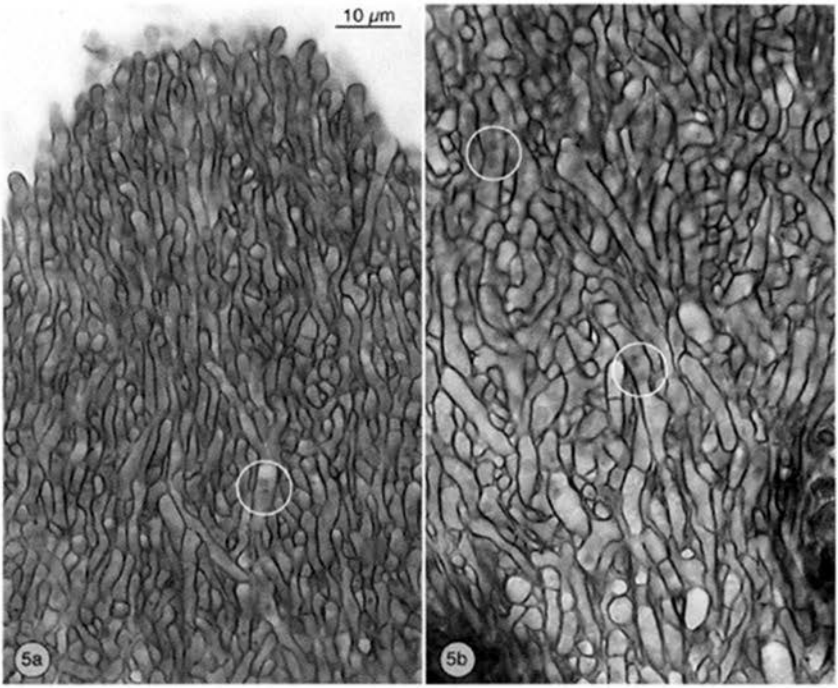
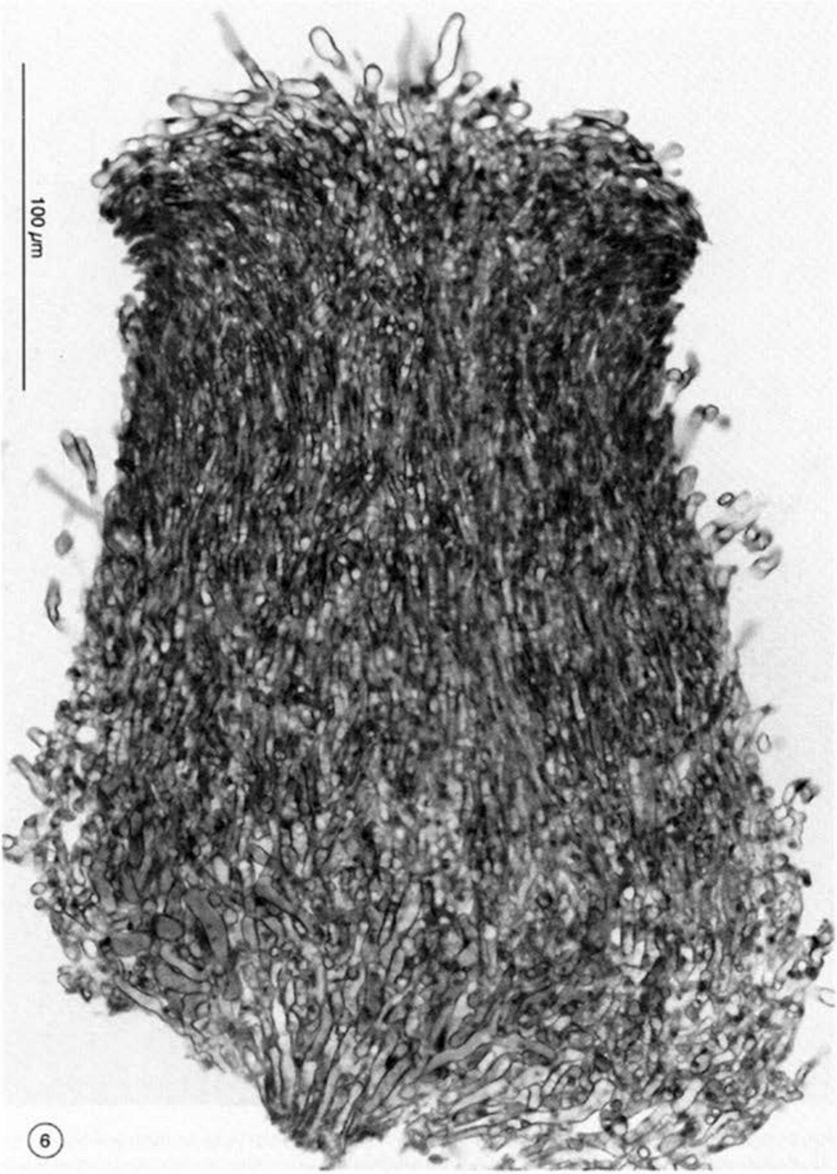


Fig. 4. A young primordium composed of a rooted nodulus and a conical primordial shaft bearing a developing cauloblema.



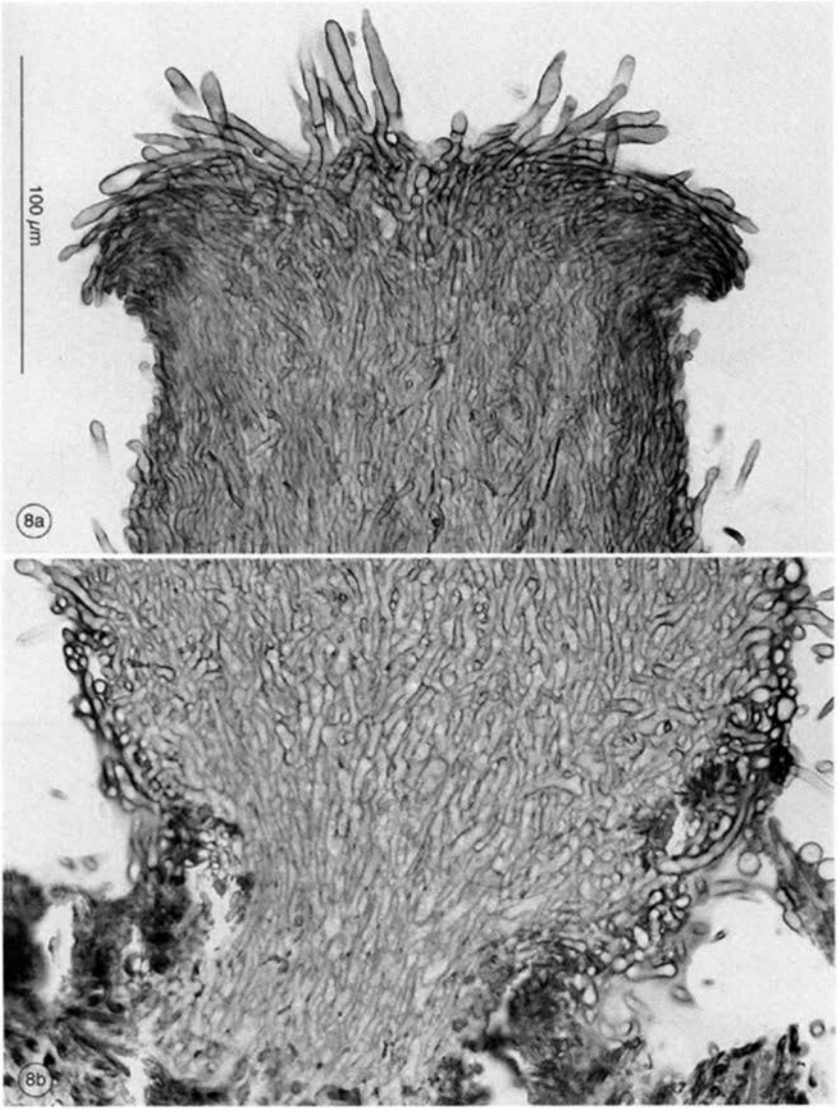
Figs. 5a, b. Top and base from the same primordium shown in Fig. 4, different sections. The hyphae of the top are subparallel and growing upward; in the base they are more irregularly arranged and more inflated. Nuclear pairs indicated by the circles.



6

Fig. 6. A young primordium detached from its substrate and its root broken off. The pileus starts to form, and the pileoblema begins to grow out. A prehymenial palisade is still lacking.

Fig. 7. Detailed view of the section shown in Fig. 6. The voluminous cells on the top belong to the pileoblema, the narrower, club-shaped, downward oriented surface cells are the precursors of the pileus margin and the very narrow, more or less horizontal surface cells are the precursors of the palisade.



Figs. 8a, b. Top and base of a slightly more developed primordium showing a more pronounced pileus margin, a more developed pileoblema and already some pigmented cells in the primordial shaft. The funnel shape of the future pileus is already perceptible. Under the left pileus margin, the very young palisade initial composed of clavate, horizontal hyphal end cells is visible. In the base, the hyphae are more inflated than in the shaft, and in the rooting base they are subparallel.

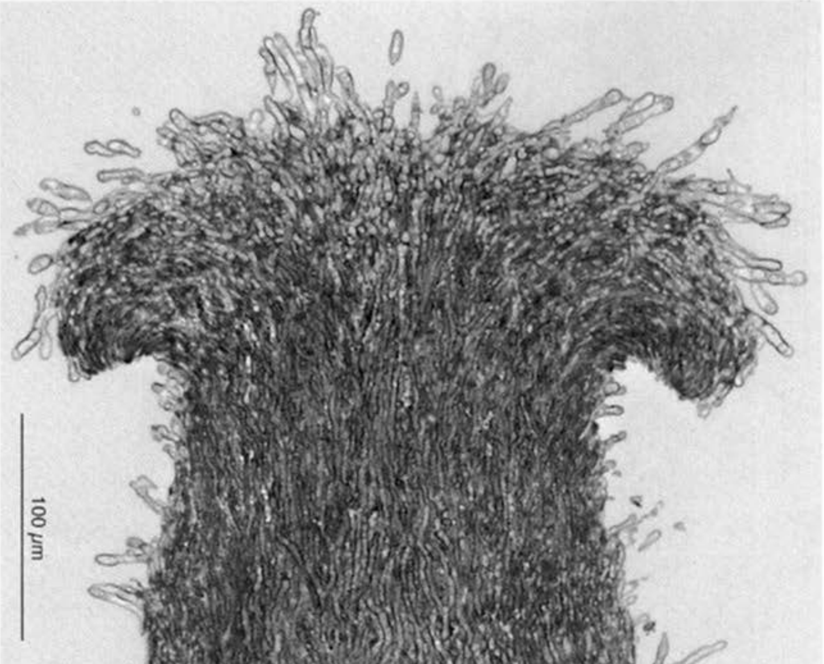


Fig. 9. Although in this primordium the cauloblema and the pileoblema are well developed, no partial veil is formed. The underside of the pileus bears a palisade of narrowly clavate cells, but no basidia are present yet. The stipe rudiment consists of densely packed, subparallel hyphae. The nodulus in the base of the stipe has developed the secondary structure characterised by inflated, irregular hyphae. The rooting base is broken off.

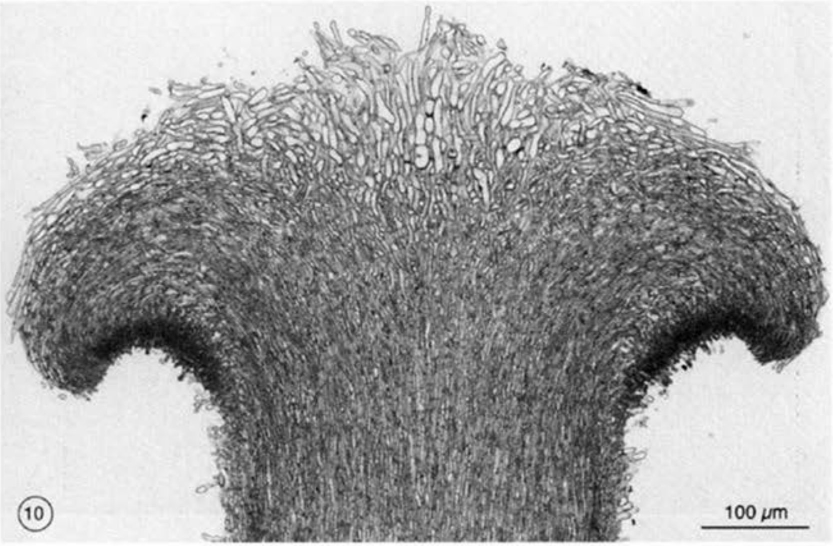


Fig. 10. Pileus of an older primordium with well-developed prehymenial palisade from which numerous young basidia are projecting. The pileus is funnel-shaped, but the funnel is filled with the large-celled pileoblema.

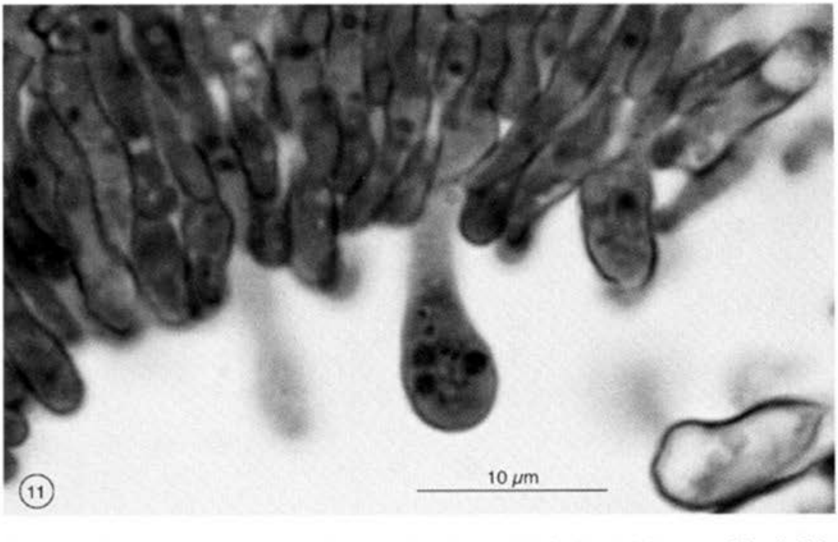


Fig. 11. Prehymenial palisade with a young basidium projecting far beyond the general level of the palisade. Even at this early primordial stage, meiosis is already completed in this basidium, and three of the four nuclei are visible.

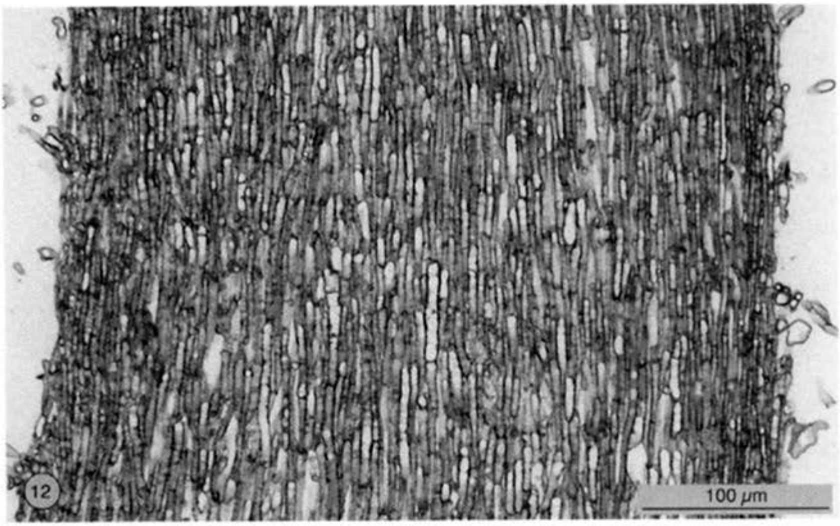


Fig. 12. The stipe of the primordium shown in Fig. 11 contains many inflated hyphae, but no sarcodimitic structure is visible yet.

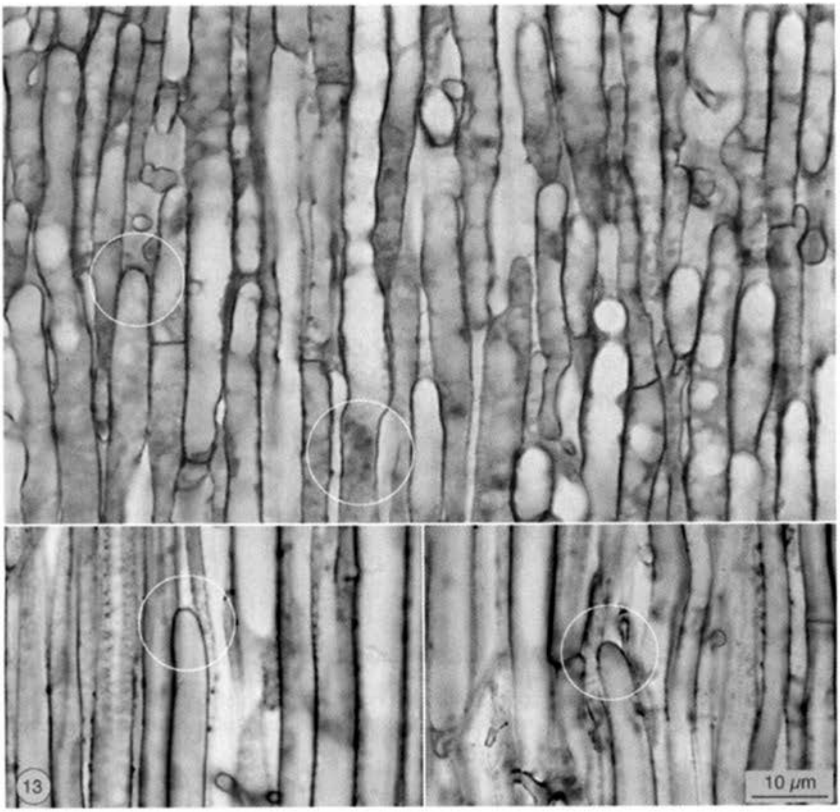
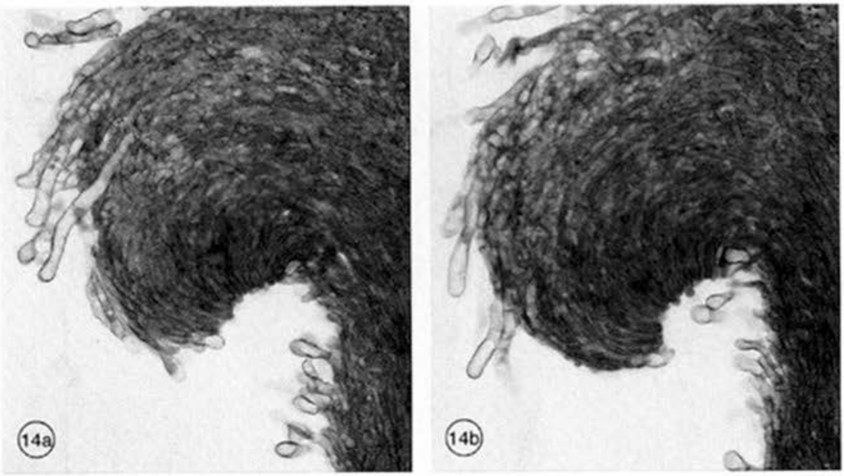


Fig. 13. An enlarged view of the stipe context of the primordium shown in Figs. 11 and 12 reveals many free hyphal end cells, but they are not swollen into acrophysalides. The physalohyphae are multinucleate.



Figs. 14a, b. Well-developed metablemas cover the pileus and the stipe, but they do not meet and do not form a 'partial veil'.

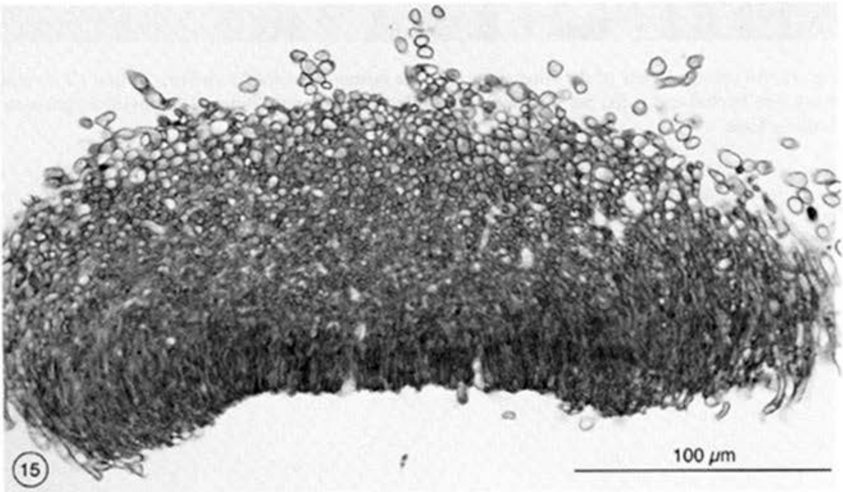


Fig. 15. The prehymenial palisade of the same primordium shown in Fig. 14 is smooth, no gill initials are present. The projecting cell is either a young basidium or a young cystidium.

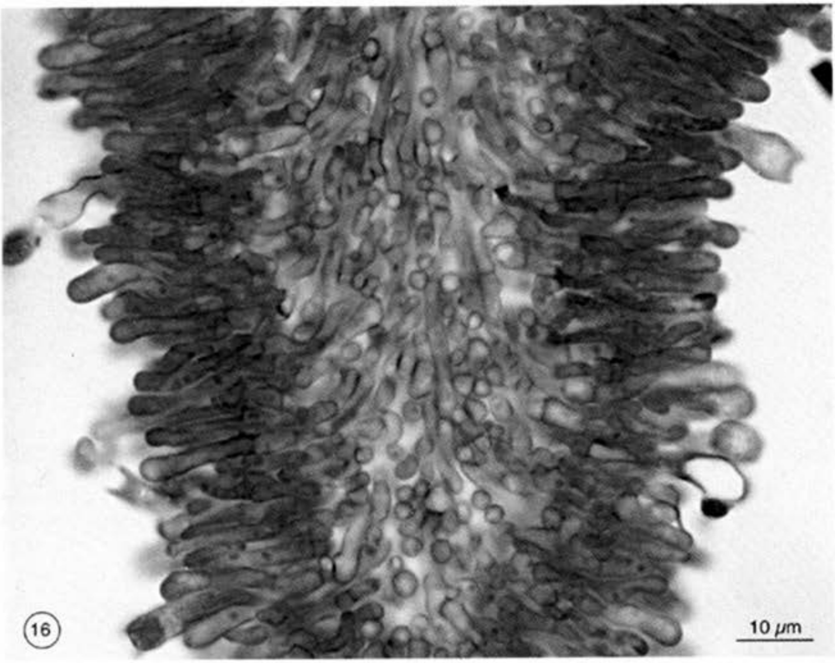
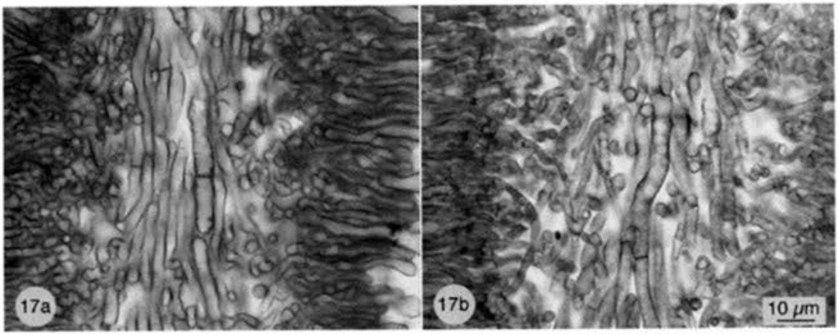


Fig. 16. A primordial gill in perradial section shows the divergent-bidirectional arrangement of the trama hyphae. Some basidia already bear sterigmata and spores.



Figs. 17a, b. Plectological differentiation in an older primordium is initiated by turgescent inflation of some hyphae in the gill trama.

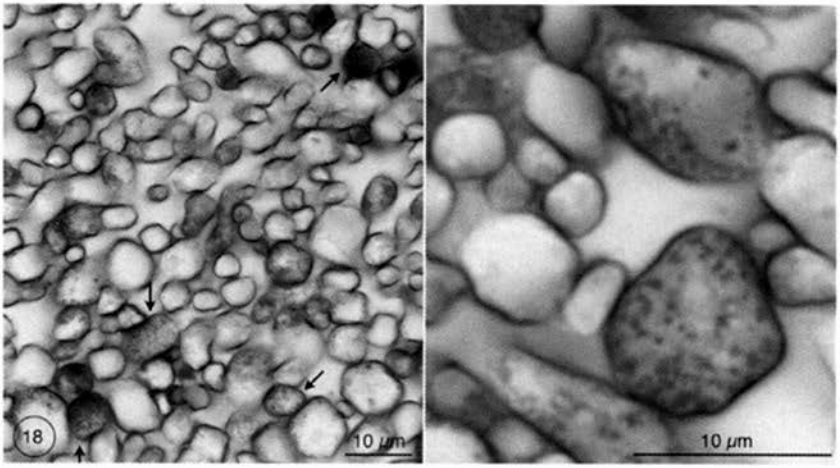


Fig. 18. At the time of gill trama differentiation glycogen granules are present in the hyphae of the pileus trama. Some cells containing glycogen are indicated by arrows. Tannin-iron reaction followed by haematoxylin.

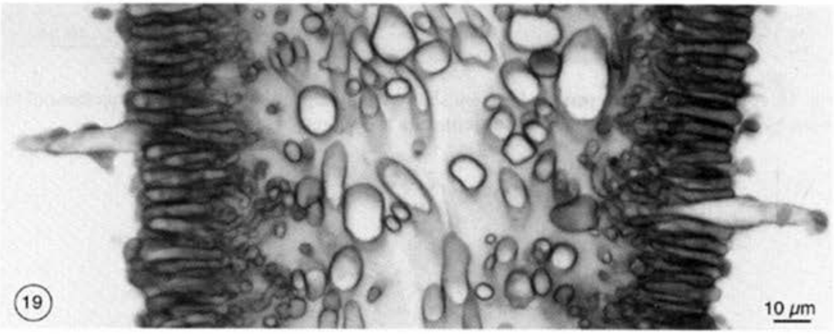
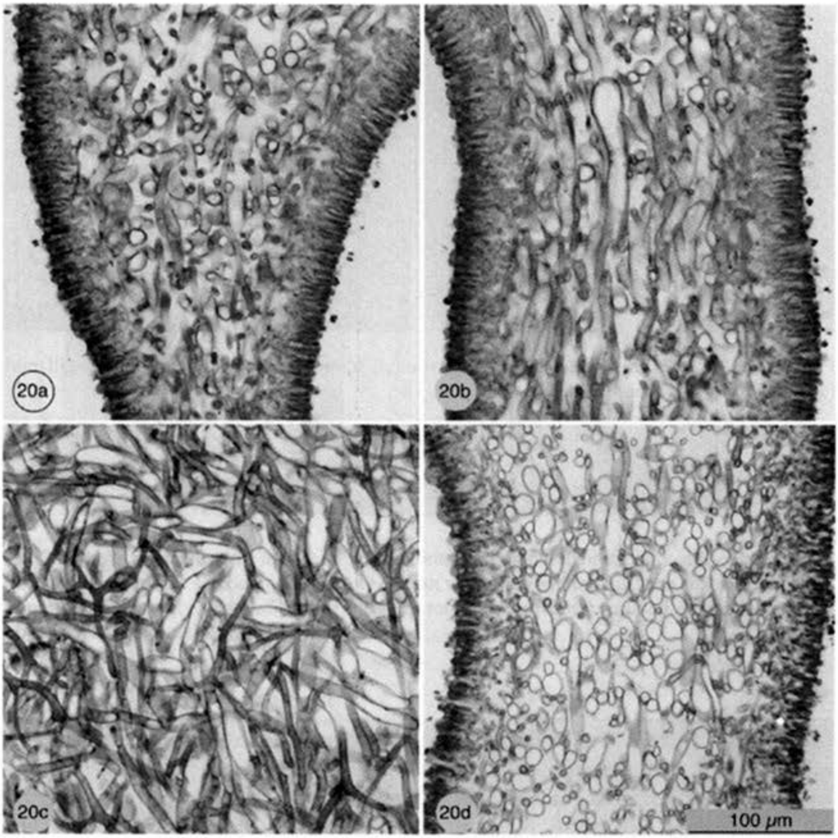
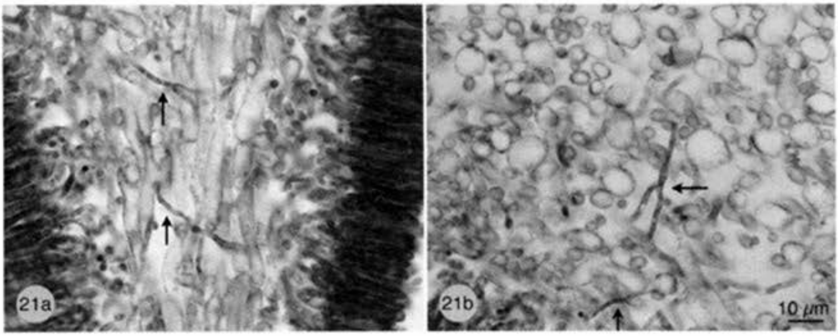


Fig. 19. A young basidiome with a cap diameter of 3.1 mm has a fully developed hymenium with sporulating basidia and pleurocystidia. The latter are sticky and trap released spores. The gill trama is physalo-irregular, and the subhymenium is slightly gelatinous. Tannin-iron reaction followed by haematoxylin.



Figs. 20a–d. Architecture of the mature gill trama in perradial (a, b), parahymenial (parallel to the hymenium, c) and paracial (parallel to the gill edge, d) sections. The wide physalohyphae are more or less bidirectionally oriented, with some hyphae running down from the gill base to the gill edge, others running more or less parallel to the gill edge. Between the physalohyphae occur many narrow, cylindrical, more irregularly arranged hyphae.



Figs. 21a, b. Very thin, thin-walled hyphae with strongly stainable content are present in the gill trama (a) and in the pileus trama (b).

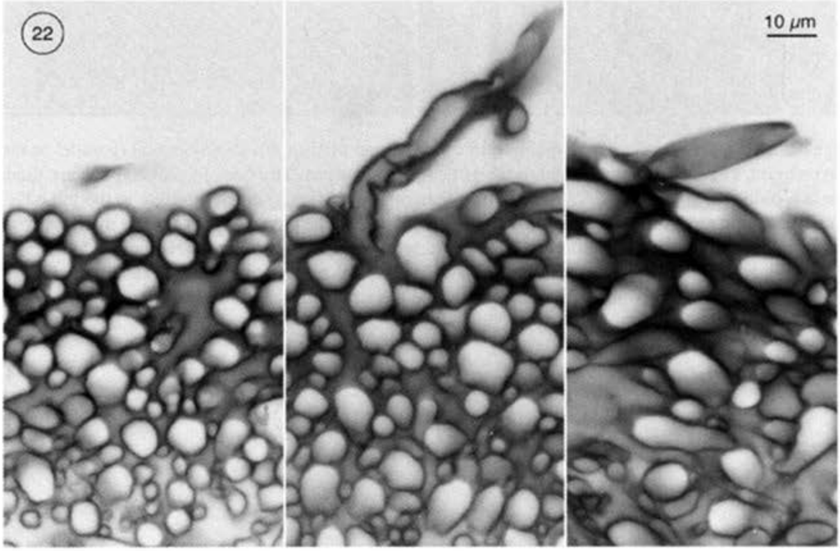
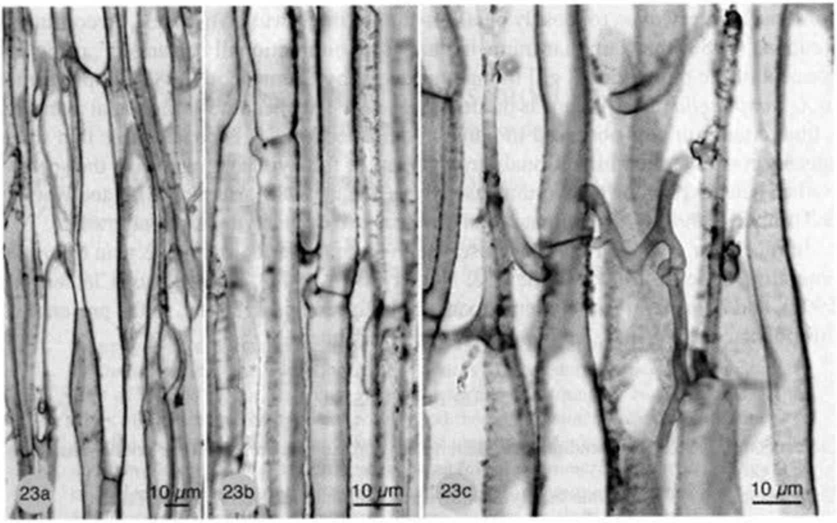


Fig. 22. The pileoblema is now a gelatinous cutis with radial, periclinal hyphae. Some erect hyphae and some erect inflated cells, called pileocystidia, can still be found on the cap of the mature basidiome.



Figs. 23a–c. Architecture of the mature stipe. The context is composed of strongly inflated physalohyphae reminiscent of the sarcodimitic structure (a), but very often without fusiform shape (b). Narrow, cylindrical and strongly incrusted hyphae and some tortuous, frequently ramified, smooth connective hyphae occur between the physalohyphae (c).

Cauloblemas and pileoblemas often produce a partial veil, e.g. in *Panus tigrinus* (Kühner, 1925) and *Boletinus cavipes* (Kühner, 1926), and the difference with *X. campanella* concerns only the degree of the growth of the metablemas: a slightly more extended growth of either metablema would produce a partial veil, and, as a consequence, the developmental type of *X. campanella* would change from gymnocarpy to secondary angiocarpy, creating the illusion of a fundamentally different carpogenesis.

In the terminology proposed by Clémençon (1997), *X. campanella* is exocarpic since the primordium does not develop within a primordial shaft, amphiblemate since a pileoblema and a cauloblema are produced independently and never form a partial veil, and apertopileate since the pileus margin never touches the stipe.

Xeromphalina campanella is a good example to illustrate the fact that 'metablema' is not synonymous with 'emanated veil', since in this fungus the pileoblema and the cauloblema independently develop into a pileipellis and into a hirsute stipe covering, respectively.

The structure of the hymenophoral trama in the genus *Xeromphalina* is controversially described in the literature. According to Singer (1986: 424) the gill trama of mature basidiomes "is regular, its hyphae close, rather voluminous, subparallel and axiallarly arranged ..."; where 'axial' means "... the hyphae run ... from the plane of attachment to the pileus down to the edges of the hymenophore ..." (Singer, 1986: 56). Klán (1984: 215) confusingly writes "Hymenophoral trama regular, composed of irregular to loosely interwoven thin-walled hyphae ...", and Miller (1968: 159) describes the gill trama "of loosely interwoven to loosely parallel, thin- to thick-walled hyphae". According to Redhead (1988) the "lamellar trama hyphae [are] bidirectionally arranged", using the concept of the bidirectional gill trama introduced by Clémençon (1982). In primordia of *X. campanella* the gill trama is bidirectional at first but becomes irregular at maturity, a final condition best observed in parahymenial sections. It is conceivable that some species conserve the bidirectional arrangement of the hyphae longer than the species studied here, explaining the wording used by Redhead (1988). Horak (1979) and Watling & Turnbull (1998) remain silent about the structure of the hymenophoral trama.

Intracellular glycogen has been observed in several agaricoid fungi, e.g. in *Coprinus cinereus* (Madelin, 1960; Matthews & Niederpruem, 1972), *C. trisporus* (Clémençon, 1997), and *Lepista flaccida* (Clémençon, unpublished observation), so the presence of this polysaccharide in *X. campanella* is not surprising.

REFERENCES

Clémençon, H. 1982. Kompendium der Blätterpilze. Europäische omphalinoide Tricholomataceae. Z. Mykol. 48: 195–237.

Clémençon, H. 1997. Anatomie der Hymenomyceten. Kommissionsverlag Flück, Teufen.

Clémençon, H. 2000. Mycelial morphology, mitospores and primordium formation of Simocybe sumptuosa in laboratory cultures. Persoonia 17: 407–433.

Feder, N. & T.P. O'Brien. 1968. Plant microtechnique: Some principles and new methods. Amer. J. Bot. 55: 123–142.

Hintikka, E.V. 1957. Über die finnischen Arten und Varietäten der Gattung Xeromphalina Kühner & Maire. Karstenia 4: 5–9.

Horak, E. 1979. Xeromphalina and Heimiomyces in Indomalaya and Australia. Sydowia 32: 131–153.

Klán, J. 1984. The genus Xeromphalina (Tricholomataceae) in Europe. Ceska Mykol. 38: 205–217.

Kühner, R. 1925. Le développement de Lentinus tigrinus. C.R. Acad. Sci. 180: 137.

Kühner, R. 1926. Le développement du Boletinus cavipes Kalchbr. Le Botaniste 17: 177–181.

Madelin, M.F. 1960. Visible changes in the vegetative mycelium of Coprinus lagopus Fr. at the time of fruiting. Trans. Brit. Mycol. Soc. 43: 105–110.

Matthews, T.R. & D.J. Niederpruem. 1972. Differentiation in Coprinus lagopus. I. Control of fruiting and cytology of initial events. Arch. Mikrobiol. 87: 257–268.

Miller jr., O.K. 1968. A revision of the genus Xeromphalina. Mycologia 60: 156–188.

Redhead, S.A. 1987. The Xerulaceae (Basidiomycetes), a family with sarcodimitic tissues. Canad. J. Bot. 65: 1551–1562.

Redhead, S.A. 1988. Notes on the genus Xeromphalina (Agaricales, Xerulaceae) in Canada: biogeography, nomenclature, taxonomy. Canad. J. Bot. 66: 479–507.

Singer, R. 1965. Monographs of South American Basidiomycetes, especially those of the East Slope of the Andes and Brazil. X. Xeromphalina. Bol. Soc. Argent. Bot. 10: 302–310.

Singer, R. 1986. Agaricales in modern taxonomy. Ed. 4. Koeltz Scientific Books, Koenigstein.

Watling, R. & E. Turnbull. 1998. British Fungus Flora. Agarics and Boleti. Vol. 8. Royal Botanic Garden Edinburgh.

PERSOONIA
Volume 18, Part 4, 471–483 (2005)

REVISION OF LACTARIUS FROM MEXICO
Additional new records

LETICIA MONTOYA & VICTOR M. BANDALA

Departamento Biodiversidad y Sistemática, Instituto de Ecología, A.C., A.P. 63,
Xalapa, Veracruz, 91000, México.
E-mail: montoya@ecologia.edu.mx, bandala@ecologia.edu.mx

Three species of *Lactarius* from Mexico were studied: *L. deceptivus*, *L. luteolus* and *L. rimosellus*. The latter two concern new records from western Mexico and from the Gulf of Mexico region, respectively, and the former was found on new localities. A study of their respective type collections and those of *L. tomentosomarginatus* and *L. echinatus* was made in order to support the identity of Mexican specimens. Based on a morphological study we propose reducing *L. tomentosomarginatus* to synonymy of *L. deceptivus* and agree with other authors that *L. echinatus* is conspecific with *L. luteolus*. Descriptions and illustrations are given of the three Mexican records.

Key words: Russulales, taxonomy, ectomycorrhizal fungi, type studies.

The study of the genus *Lactarius* in Mexico indicates that Mexican *Lactarius* mycota is more similar to that reported from the USA (Hesler & Smith, 1979), while the percentage of taxa described from other continents is lower (Montoya & Bandala, 2002). However, new undescribed *Lactarius* species, either from temperate or tropical sites, have also been found (Montoya & Bandala, 2003). Other new species are currently under study. To confirm the identity of Mexican collections of *Lactarius* it has become necessary to restudy types of several selected taxa, which include those of species poorly known since their respective descriptions from northern areas in America, and record their range of distribution as far as this latitude. Extended descriptions and illustrations based on Mexican material are given here, as well as data after comparison with the type specimens. *Lactarius luteolus* Peck, *L. rimosellus* Peck and *L. deceptivus* Peck are taxa documented from other areas, but up to now the first two are unknown in Mexico. *Lactarius deceptivus* deserved additional study on its ecological distribution and variation.

MATERIAL AND METHODS

Macroscopic descriptions are based on fresh material. Colour codes indicated in the descriptions follow Kornerup & Wanscher (1978). Microscopic structures are described from hand sections of revived tissues; their measurements and colours were observed in 3% KOH, except for basidiospores, which were studied in Melzer's reagent. The following notations are used: RM = range of means of length × width; QM = length/width ratio of spores, indicated as a range in n collections. The methods followed to make measurements and SEM analyses are those used by Montoya & Bandala (2003). Herbarium acronyms are according to Holmgren et al. (1990).

STUDIED SPECIES

Lactarius deceptivus Peck — Figs. 1–9

Lactarius deceptivus Peck, Ann. Rep. N.Y. Mus. St. Mus. 38 (1885) 125.
= *Lactarius tomentosomarginatus* Hesler & A.H. Sm., N. Amer. Sp. Lactarius (1979) 195.

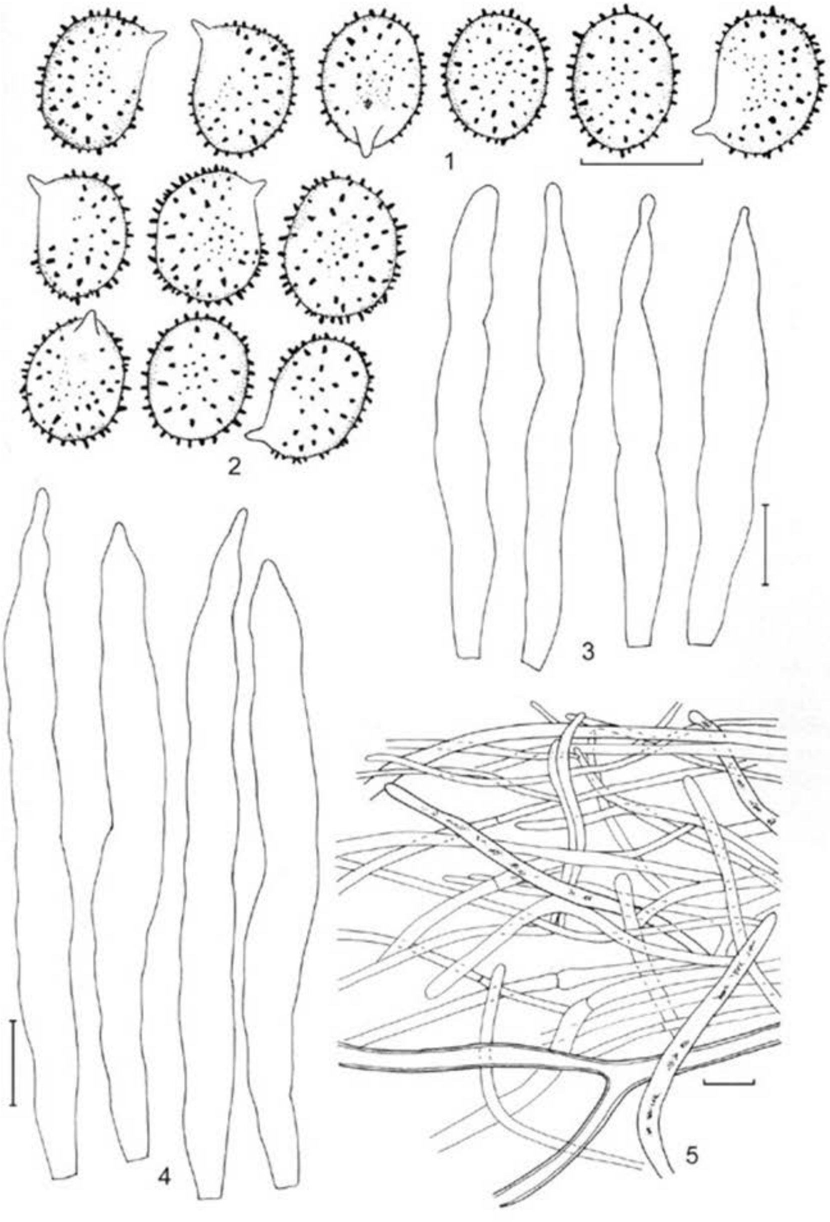
Pileus 61–160 mm in diameter, convex to plano-convex, infundibuliform with age, white to cream-coloured, smooth, with a soft texture in young stages, cracked with pileus expansion, then the surface appears somewhat squamulose and progressively fibrillose or fibrillose-squamulose, the centre of the disc with short cracks which become somewhat squamulose, staining yellowish then brown when handled; margin involute, soft, cottony, expanded, broken, and fibrillose with age. Lamellae decurrent, crowded in young stages, close to subdistant and even distant in older specimens, broad, bifurcate, white to cream-coloured, thick. Stipe 32–60 × 20–40 mm, cylindrical to attenuated towards base, velvety, at times with remains of cottony tissue near lamellae attachment, white, staining yellowish then brown, compact. Latex white, invariable, staining cut surfaces yellowish then brown, strongly acrid. Context white, compact, staining brownish. Odour somewhat like chlorine, taste acrid.

Basidiospores (8.8–)9–12(–12.8) × 7.2–9.6 μm; RM = 10.3–11.4 × 7.9–8.7 μm; QM = 1.2–1.4, broadly ellipsoid to ellipsoid, verrucose; verrucae 0.25–1.10(–1.5) μm high; under SEM the ornamentation appears as isolated, semiconic and obtuse, at times rounded or cylindrical warts. Basidia 57.6–79.6 × 10.4–12.8 μm, clavate to subfusiform, tetrasporic. Pleurocystidia 52–100 × (6.4–)7.2–10.4 μm, subcylindric, subfusiform, with an attenuated apex, thin-walled, abundant. Cheilocystidia 40–52(–60) × 4.8–8 μm, similar in shape to pleurocystidia, thin-walled, frequent. Pileipellis made of hyphae loosely arranged, intermixed irregularly, in a cutis or projected, 2.4–12 μm in diameter, curved, thin-walled, with some laticifers and occasionally with slightly thick-walled hyphae (0.8 μm thick). Hymenophoral trama hyphae 3–7 μm in diameter, laticifers 8–14 μm in diameter and sphaerocytes 12–16 μm in diameter. Context hyphae 3.2–7.2 μm in diameter, laticifers 4–10.4 μm in diameter, scarce, sphaerocytes 16–32 μm in diameter. Stipitipellis a trichodermis composed of numerous caulocystidia 80–500 × 5.2–9.6 μm, thick-walled, 1.6–2.4(–3.2) μm thick, attenuated at apex, born from hyphal elements, 2.4–8 μm in diameter, intermixed.

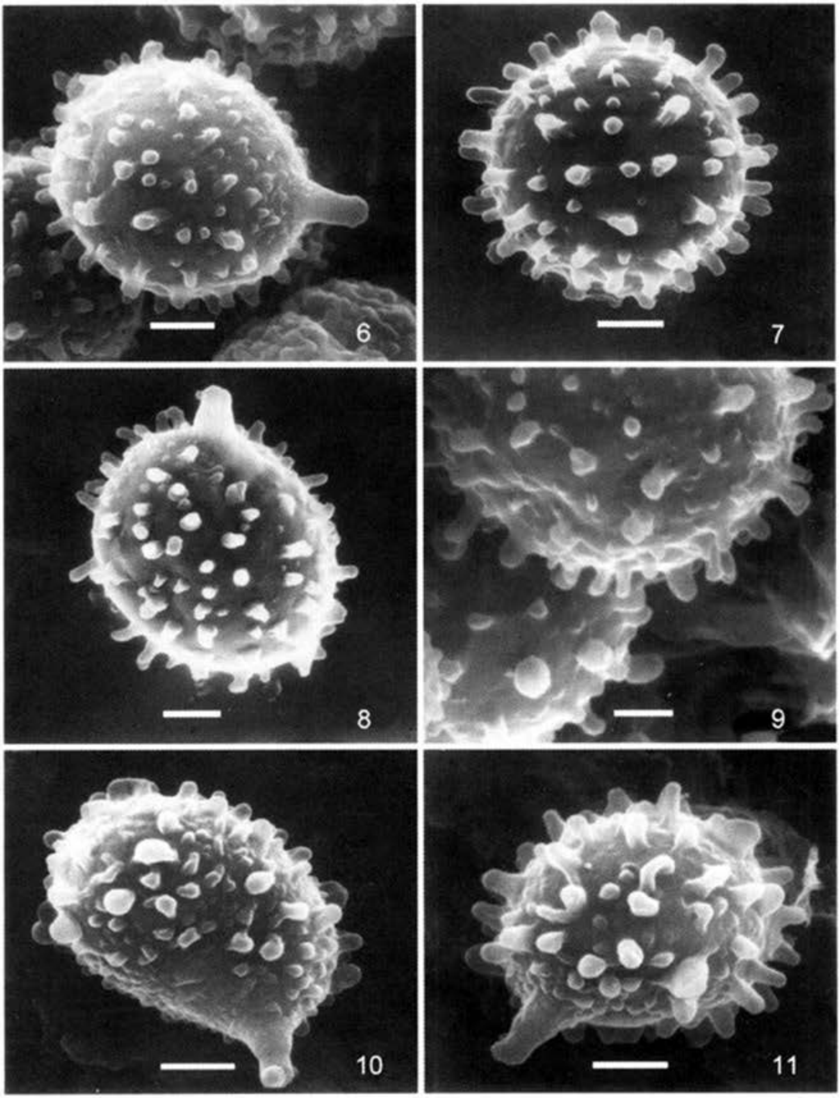
Habitat — In mesophytic forest, *Quercus* forest and in associations of *Pinus* and *Quercus*.

Material studied. MEXICO: Chihuahua, Mpio, Bocoyna, Babureachi, 6–7 km NE Bocoyna, 14.VIII.1992, *Moreno-Fuentes V-16* (FCME); Durango, Mpio, Pueblo Nuevo, El Mil Diez, 2.IX.1983, *Guevara 139* (ITCV, XAL); Guerrero, Mpio, Chilapa de Alvarez, 14 km from Atzacoaloya to Hueycaltenango, 19.VIII.1981, *Capello 159* (FCME); Oaxaca, Mpio, Ixtlán de Juárez, 3–5 km E Ixtlán de Juárez, 21.IX.1967, *Ruth Mc Vaugh 1265, 1290, 1292* (all in MICH under *L. tomentosomarginatus*); Puebla, Mpio, Huauchinango, 25.VIII.1987, *Gutierrez-Ruiz 2* (FCME), Mpio, Teziutlán, around Teziutlán, Cerro Techachapa, 9.VIII.1991, *Montoya 1968* (XAL); Veracruz, Mpio, Banderilla, SW Banderilla, Cerro La Martinica, 12.VII.1983, *López 160* (XAL).

Other material studied. USA: New York, Sandlake, *Peck s.n.* (lectotype of *L. deceptivus*, NYS); Maine, Penobscot Co., VIII.1967, *Homola 2380*; near Pushaw Lake, 22.IX.1976, *Homola 4012* (ENCB; XAL); Michigan, Oscoda Co., Perry Creek, 27.VIII.1973, *Nimke 506* (holotype of *L. tomentosomarginatus*, MICH).



Figs. 1–5. *Lactarius deceptivus*. 1, 2. Basidiospores (1. *Peck s.n.*, holotype of *L. deceptivus*; 2. *Nimke 506*, holotype of *L. tomentosomarginatus*); 3. pleurocystidia; 4. cheilocystidia; 5. pileipellis (*Peck s.n.*). Scale bars: 10 μm, except for 5 = 20 μm.



Figs. 6–11. *Lactarius* basidiospores under SEM. 6–9. *L. deceptivus* (6, 7. *Guevara 139*; 8. *Nimke 506*, holotype of *L. tomentosomarginatus*; 9. *Peck s.n.*, holotype of *L. deceptivus*). 10, 11. *L. luteolus* (*Thiers 1700*, holotype of *L. echinatus*). Scale bars: 2 μm, except for 9 = 1 μm.

Lactarius deceptivus is a well-known species from North America. It is widely spread in the eastern regions, from Canada across the east coast of USA to the Gulf of Mexico (Peck, 1885; Burlingham, 1908; Kauffman, 1918; Murrill, 1948; Hesler & Smith, 1979;

Homola & Czapowskyj, 1981; Montoya et al., 1990; Phillips, 1991; Montoya & Bandala, 1996; Bessette et al., 1997). It is a distinctive species characterized by white to cream-coloured basidiomes which stain brown, surface fibrillose-squamulose with age, distinctly involute margin of pileus which is cottony in young stages, velvety stipitipellis, white latex which is invariable in colour but stains the cut surfaces brown, acrid taste and ellipsoid basidiospores with a verrucose ornamentation pattern (Peck, 1885; Burlingham, 1908; Hesler & Smith, 1979; Montoya et al., 1990; Montoya & Bandala, 1996).

Among the examined specimens, those of Mc Vaugh from South Mexico were found at MICH labelled as *L. tomentosomarginatus* Hesler & A.H. Sm., a close relative of *L. deceptivus* (Hesler & Smith, 1979). Basidiomes of these collections, however, show the same morphologic variability (macro- and microscopic) as was observed in the examined collections of *L. deceptivus*, including the type specimen. Hesler & Smith (1979) used the following set of characters to distinguish *L. tomentosomarginatus* from *L. deceptivus*: (i) the low basidiospore ornamentation [0.2–0.7 μm in *L. tomentosomarginatus* vs 0.5–1(–1.5) μm in *L. deceptivus*]; (ii) basidiospores slightly shorter [9–11 × 7–8.5 μm vs 9–12(–13) × 7.5–9 μm]; (iii) the crowded, bifurcate and narrow lamellae; and (iv) the pileipellis without cracks.

Our analysis revealed that all specimens studied exhibit a wide variation regarding these features, which does not allow us to recognize discontinuity among the samples. Within a basidiome there may be variation in the height of the basidiospore ornamentation. Under SEM Peck's collection exhibited basidiospores with isolated verrucae, 0.3–1.1(–1.5) μm high. The verrucae are somewhat variable in shape (even within a single basidiospore), often appearing as rods, papillas or cylindrical, conical, broad or rounded verrucae, but these fit a consistent verrucose pattern. A similar variation was found in the Homola specimens from Maine and the other specimens considered (Figs. 1, 6, 7, 9). The height of the spore ornamentation in the three Mexican specimens labelled as *L. tomentosomarginatus* shows a range of 0.25–1.1 μm (measured under SEM), meanwhile the type collection (from USA, *Nimke 508*) even shows a wider range, up to 1.13(–1.5) μm (Figs. 2, 8). On the other hand, our data on the basidiospore size (Table 1) revealed only minor differences, which we consider of no taxonomic value.

Table 1. Basidiospore size of studied collections related with *L. deceptivus*.

Collections	RM	QM
Peck s.n. (Sandlake)	11 × 8 μm	1.4
Mc Vaugh's collections	10.1–11.3 × 8.3–8.9 μm	1.2–1.3
Nimke 508 (holotype of *L. tomentosomarginatus*)	10.8 × 7.8 μm	1.4
Other samples studied (*Capello 159, Moreno-Fuentes V-16, Guevara 139, Homola 2380, 4012*)	10.3–11.4 × 7.9–8.7 μm	1.2–1.4

Basidiomes in Peck's Sandlake material exhibit crowded to close lamellae, which agree with the variation of the arrangement observed in the type of *L. tomentosomarginatus*. Among the three collections of Mc Vaugh, some basidiomes even have broader and more distant lamellae than in Peck's specimen of *L. deceptivus*, similar to the wide variation observed in other Mexican collections. Furthermore, the pileus cuticle tends to crack with the expansion of the pileus and this cracking is probably also influenced by environmental conditions. At any rate, the microscopic structure of pileipellis is similar among all the samples examined (Fig. 5). The holotype of *L. tomentosomarginatus* (*Nimke 508*) is composed of young basidiomes which are of small to medium size, with the pileus margin still involute and a mostly uncracked pileipellis, except for some specimens of which the pileipellis is somewhat cracked towards the margin. The lectotype material of *L. deceptivus* exhibits a somewhat wider macroscopic variation due to the different stages of development of the basidiomes represented in this collection (but includes basidiomes similar in size to those of the type of *L. tomentosomarginatus*). The pileus cuticle in the individuals of this latter collection is scarcely cracked in younger basidiomes, and cracked into fibrillose patches in the older ones.

As a result of these morphological studies we conclude that the basidiomes of the studied material show the morphologic variation of a single taxon, and therefore we interprete the differences used by Hesler & Smith (1979) to distinguish *L. deceptivus* from *L. tomentosomarginatus* as representing part of such variation. *Lactarius tomentosomarginatus* is in our opinion a synonym of *L. deceptivus*.

Lactarius deceptivus is represented in Peck's herbarium (NYS) by the collection from Sandlake mentioned above which is recorded as the type material. This collection, labelled as 'type', was gathered by Peck in August (year not indicated), and is accompanied by drawings of fresh basidiomes, and also by a handwritten note by H.D. House (who succeeded Peck as State Botanist at NYS Museum): "… Peck did not designate a type collection or locality for *L. deceptivus*, hence the mounted material from Sandlake, accompanied by drawings and spore print may – perhaps not? (these two words not clearly legible) – serve the purpose of a type …". Also, it is accompanied by a study of the microscopic features of the basidiomes made by G. Bills in1982 with the indication of being the type specimen.

Several authors (Saccardo, 1887; Burlingham, 1908; Kauffman, 1918; Hesler & Smith, 1979; Walleyn et al., 1996), including databases (Type Specimen Database of the New York State Museum Mycological Collections, NYS; Russulales News Website) recorded the publication of Peck (1885) as the original description of *L. deceptivus*. The epithet in Peck's report, written as "*L. deceptivus* Peck", does not have an indication of the status as new species (i.e., *sp. nov.* or *n. sp.*), as clearly stated for other species described by him in the same publication (e.g. *Russula basifurcata*, *n. sp.*, *Polyporus crispellus*, *n. sp.*, *L. varius*, *n. sp.*). The information provided by Peck in that work, as stated by House in his notes, did not include a specimen nor a locality but only a date (July–September) and habitat (woods and open places, especially under hemlock trees). We have not found any previous description of *L. deceptivus* by Peck, and the material from Sandlake matches the description of 1885. This original material supports validly the lectotypification by Hesler & Smith (1979).

A description of the type specimen based on our microscopic observations is as follows.

Basidiospores (8.8–)9.6–12 × 7.2–9.6 μm (RM = 11 × 8 μm, QM = 1.4), ellipsoid, occasionally giant, verrucose; pileipellis a loosely arranged cutis also with elements in a more or less anticlinal orientation, others irregularly curved and even projected, the elements being (1.6–)2.4–6.4 μm wide, some thick-walled hyphae (wall up to 1.8 μm thick) and laticifers also present; pleurocystidia sinuous, fusiform 56–100 × 6.4–9.6 μm, thin-walled, with constricted apex, others with rounded apex; cheilocystidia 44–78.4 × 5.6–8 μm, thin-walled, similar in shape to pleurocystidia. Hymenophoral trama heteromerous. Stipitipellis a trichodermis consisting of thick-walled (1.6–2.4 μm) filamentous caulocystidia, 100–450 × 4–7.2 μm, with attenuated apex, arising from a tighten hyphal tissue.

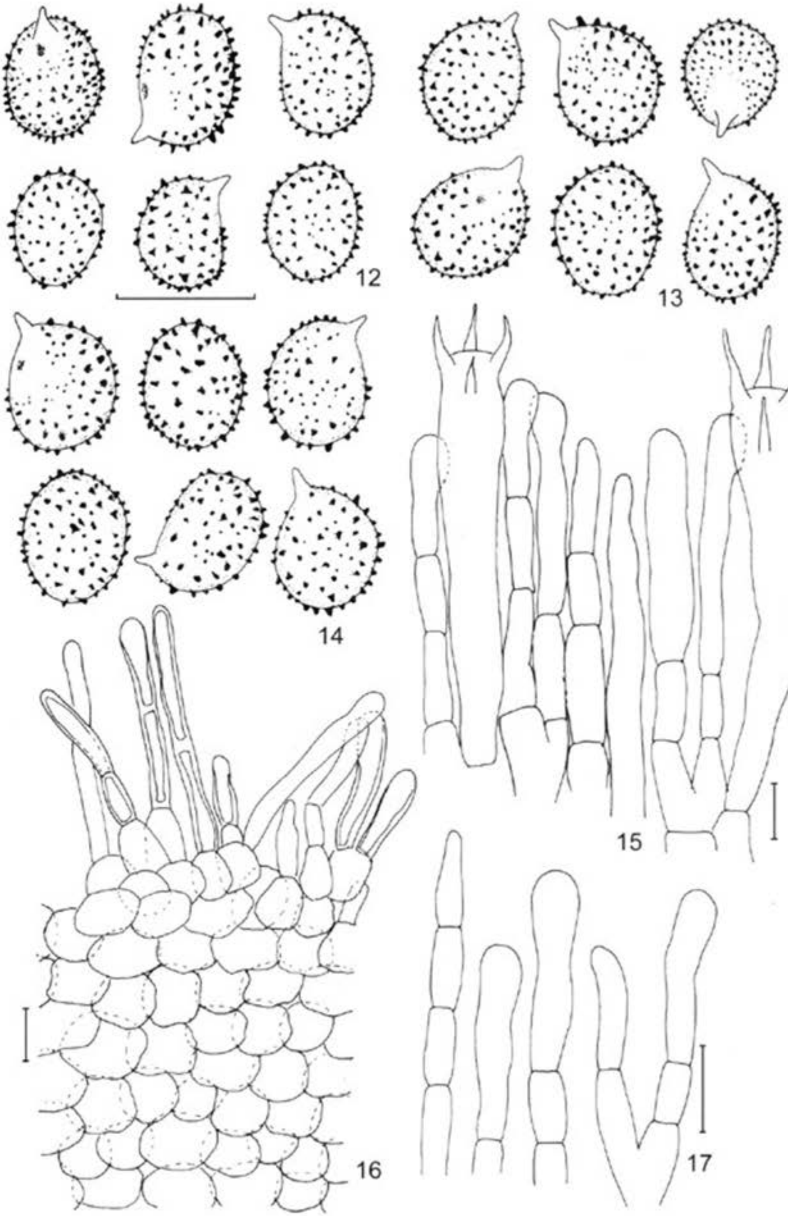
In the taxonomic arrangement followed by Hesler & Smith (1979), *L. deceptivus* was included in subgenus *Lactiflui* (Burl.) Hesler & A. H. Sm. (as *Lactifluus*, cf. Verbeken, 2001), sect. *Albati* (Bat.) Singer, the same section in which Singer (1986) treated it but without a subgeneric status. Verbeken (1998) accepted sect. *Albati* due to the absence of a pseudoparenchymatous layer in the pileipellis of its members and transferred it to subg. *Lactariopsis* (Henn.) R. Heim. Hesler & Smith (1979) and Bon (1980) argued that the pileipellis structure is a reliable character that suggests natural relationships, but in this context the stipitipellis structure, as part of the basidiome dermis should be considered as well. Taking this into account, *L. deceptivus*, which has different pileipellis, i.e. a loose cutis, but has a stipitipellis (a trichodermis composed of thick-walled elements) comparable to that observed in other *Albati*, can be included in this section and probably represents a subsection. A cladistic analysis, however, should reveal more information about this. We share the opinion of Hesler & Smith (1979), Verbeken (1998) and Basso (1999) in considering the *Albati* a distinct section, but as subg. *Lactariopsis* embraces members with more than one kind of pileipellis structure, or even with a pseudoparenchymatous subpellis (*L. velutissimus* Verbeken) (Verbeken, 1996) we provisionally consider *L. deceptivus* and sect. *Albati* in subg. *Lactiflui*, following Hesler & Smith (1979) and Basso (1999).

The documentation regarding the distribution of *L. deceptivus* in Mexico (Montoya et al., 1990, Montoya & Bandala 1996) as well as the records treated here, indicate that this species is widely spread in the country, from north to south (Guerrero, Oaxaca & Chiapas), associated with *Quercus* and also with conifers. *Quercus oleoides* Schltdl. & Cham. represents one of the most important phytobionts associated with *Lactarius* in Mexico. Trees of *Q. oleoides* have a similar distribution as *L. deceptivus* as well as that of other common *Lactarius* species in Mexico such as *L. hygrophoroides* and *L. indigo*, from the northeast to the south of the country, and also through Central America. Singer et al. (1983) also recorded the two latter species in association with *Q. oleoides* in Costa Rica, and they even cited *L. hygrophoroides* associated with *Q. oleoides* in northern South America.

Lactarius luteolus Peck — Figs. 10–17

Lactarius luteolus Peck, Bull. Torr. Bot. Club 23 (1896) 412.
= *Lactarius echinatus* Thiers, Mycologia 49 (1957) 716.

Pileus 30–55 mm in diameter, plane to planoconvex, cream-yellow to buff-coloured, staining brown to greyish-brown, pruinose to velutinous, dry, rugose. Lamellae crowded



Figs. 12–17. *Lactarius luteolus*. 12–14. Basidiospores (12. *Webster s.n.*; 13. *Thiers 1700*, holotype of *L. echinatus*; 14. *Mc Vaugh 985*); 15. hymenial elements; 16. pileipellis; 17. marginal hymenial elements (*Webster s.n.*). Scale bars: 10 μm, except for 16 = 15 μm.

at first sight but close when excluding the lamellulae, white to cream-yellow, staining brown, lamellulae in different lengths. Stipe 20–45 × 7–12 mm, cream-yellow to buff-coloured, staining brown during the development, pruinose to velutinous, solid. Latex white, staining the cut surfaces brown. Context cream-coloured, staining brown, compact.

Basidiospores 7.2–8.8(–9.6) × 5.6–7.2 μm; RM = 8.1 × 6.4 μm; QM = 1.3, broadly ellipsoid, verrucose (ornamentation 0.4–0.8 μm high), suprahilar plage frequently with amyloid dot; under SEM warts appear isolated, rounded, truncate, subcylindric, broadened towards base, at times aligned and joined at base level. Basidia 52–68 × 6.4–10.4 μm, clavate, tetrasporic. Pleurocystidia septate, versiform; terminal segments 12.8–28 × 4–6.4 μm, subcylindric, clavate, subcapitate, sublageniform; pseudocystidia 2.4–8 μm wide, with refringent contents, buried or at times conspicuous. Marginal elements versiform, septate, conspicuous, frequently projecting beyond the hymenial layer; terminal elements 15.2–20 × 3.2–6.4 μm, clavate, sublageniform, capitate. Pileipellis a trichodermis above a pseudoparenchymatous layer; suprapellis consisting of subcylindric, sinuous, erect, septate, terminal elements 26–240 × 3.2–5.6(–7.2) μm, frequently capitate, thin- or thick-walled (0.8–1.6 μm); subpellis made of subisodiametric cells, 8–36 μm wide, irregularly disposed. Context hyphae 4.8 μm wide, laticifers 4.8–7.2 μm wide, sphaerocytes 24–32 μm in diameter. Hymenophoral trama hyphae 4–8 μm in diameter; laticifers 7.2–11.2 μm wide, sphaerocytes 12–16 μm wide.

Habitat — In mesophytic forest.

Material studied. MEXICO: Jalisco, S Talpa River, La Cuesta, 24.IX.1960, *Ruth Mc Vaugh 985* (MICH).

Other material studied. USA: Massachusetts, East Milton, VIII without day and year, *H. Webster s.n.* (holotype of *L. luteolus* NYS); Texas, Walker Co., Sam Houston National Forest, near Huntsville, 10.VI.1952, *Thiers 1700* (holotype of *L. echinatus* MICH).

The occurrence of *L. luteolus* (subsect. *Luteoli* Pacioni & Lalli, subg. *Lactiflui*) in Mexico is based on the collection of *Mc Vaugh 985*, mentioned above. It was found undetermined at MICH and identified after comparison with the type specimen. The following set of characters distinguish *L. luteolus*: basidiome colour, the brownish staining by the latex, the basidiospores (size and ornamentation), the pileipellis structure, and the septate hymenial elements.

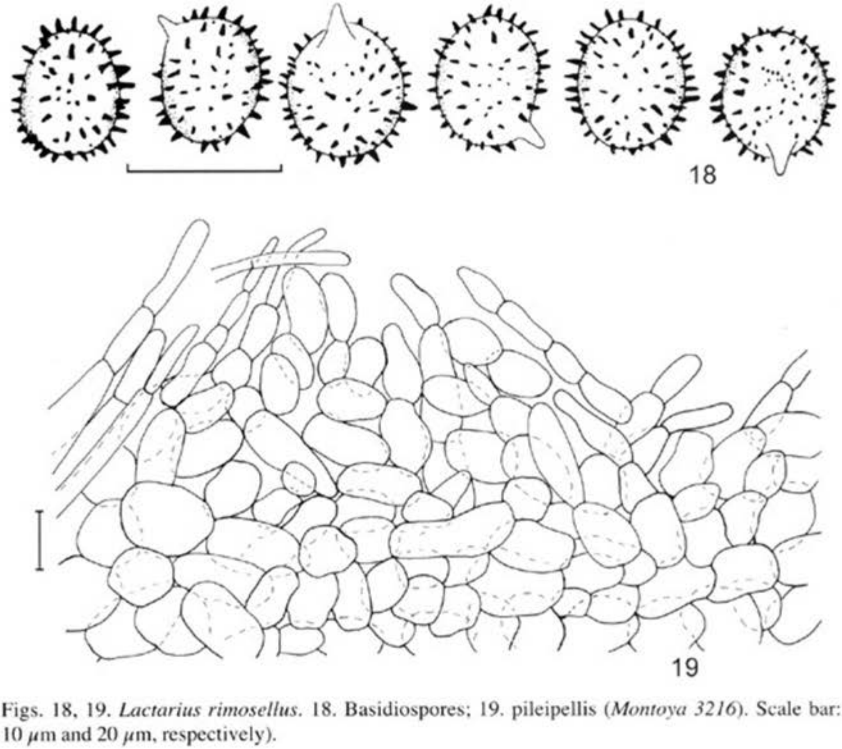
Lalli & Pacioni (1992) treated *L. echinatus* as a synonym of *L. luteolus* and we agree with this synonymy. The study of the respective holotypes indeed confirms this. They share a similar basidiospore range (RM = 8 × 6.4 μm, QM = 1.3 in *L. luteolus*; RM = 8 × 6 μm, QM = 1.4 in *L. echinatus*), pileipellis a trichodermis and septate hymenial elements. Hesler & Smith (1979) and Singer (1990), however, maintained *L. echinatus* as an autonomous species. The specimen collected in Mexico (Tamaulipas: Gómez Farias, 21.XII.1988, F1080303, leg. *J. García & G. Mueller*, F) and determined by Singer (1990) as *L. echinatus* was also examined. This material shows a different set of characters which indicates that it belongs to a different taxon in subg. *Lactarius* (Heilmann-Clausen et al., 1998; Basso, 1999). The present state of preservation of the material, however, makes study difficult. Future collections will help to complement the information on presence of other representatives of this group in Mexico. Therefore, the presence of *L. luteolus* (as *L.echinatus*) in Northeast Mexico, as suggested by Singer (1990), could not be verified.

Lactarius rimosellus Peck — Figs. 18–23

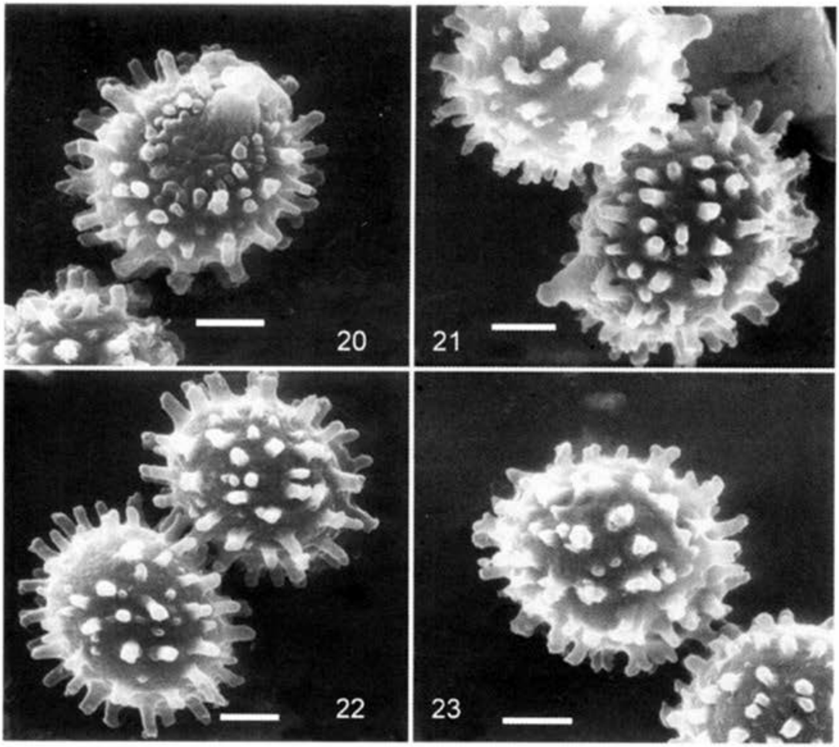
Lactarius rimosellus Peck, Bull. N.Y. St. Mus. 105 (1905) 37.

Pileus 15–40 mm in diameter, plane, planoconvex, depressed in the centre, commonly with a papilla, dry, finely areolate to rimose areolate, cracked areas dirty whitish, pileipellis brownish orange (7B5–B6, 7C6–D6), brownish with pinkish tones (7B4–B5); margin striate to crenate, undulate, decurved at maturity. Lamellae close to crowded, yellowish, pinkish beige to pinkish brown (7B4–B3), lamellulae present. Stipe 35–50 × 4–5 mm, subcylindric, straw-yellow to pinkish brown (7B3) base whitish. Latex watery to whitish, unchanging. Context beige to brownish after some minutes exposed, odour agreeable, taste mild. KOH stains the pileus and context yellow-olive.

Basidiospores (6.4–)7.2–8(–8.8) × 5.6–7.2(–8) μm; RM = 7.5–7.8 × 6.3–6.4 μm; QM = 1.19–1.23; broadly ellipsoid, verrucose and with isolate truncate spines of 0.8–1.6 μm high. Under SEM the verrucae appear isolated or rarely connected through their bases, versiform, frequently broadened towards base and cylindric upwards, with truncate apex, conic, rounded or irregular. Basidia 40–48 × 8.8–9.6 μm, clavate, tetrasporic, at times bisporic. True cystidia absent. Pseudocystidia 2.4–4 μm wide, subcylindric,



Figs. 18, 19. *Lactarius rimosellus*. 18. Basidiospores; 19. pileipellis (*Montoya 3216*). Scale bar: 10 μm and 20 μm, respectively).



Figs. 20–23. *Lactarius rimosellus* basidiospores under SEM (20 & 22. *Montoya 3216*; 21 & 23. *Peck s.n.*, holotype of *L. rimosellus*). Scale bar = 2 μm.

sinuous, refringent, projected from hymenophoral trama. Lamella edge with marginal elements of 16–28 × 5.6–8 μm, clavate, at times with basidia and some elements similar to monosporic basidia 26–32 × 5.6–7.2 μm. Pileipellis a hymeno-epithelium; elements 18.4–40(–44) × (16–)18.4–28 μm, versiform, subellipsoid to broadly inflate, vesiculose, ovoid, subglobose, at times grouped in mounds in some areas; terminal elements 16–56 × 8–17.6(–24) μm, differentiated in form, pyriform, clavate, ventricose or broadly subcylindric, some filiform (6.4–8.8 μm wide), isolate or disposed in patches. Context composed of hyphae 2.4–5.6 μm wide, laticifers 8–12 μm wide, sphaerocytes 9.6–33.6 μm wide, arranged in rosettes. Hymenophoral trama hyphae 3.2–8 μm wide, laticifers 4–9.6(–12) μm wide, sphaerocytes 8–12(–16) μm in diameter, arranged in rosettes.

Habitat — Among mosses, in a *Pinus* forest.

Material studied. MEXICO: Veracruz, Mpio. Jilotepec, around El Esquilón, 6.X.1993, *Montoya 2184*, *2191*; 13.VII.1995, *Montoya 3216* (all in XAL).

Other material studied. USA: Michigan, Winnewana Impoundment, Waterloo Rec. Area, Washtenaw Co., 23.VIII.1973, *A.H. Smith 84515* (MICH); New York, Suffolk Co., Wading River, 23.VIII.1905, *Peck s.n.*, (holotype of *L. rimosellus*, NYS).

Lactarius rimosellus (sect. *Olentes* Bat., subg. *Russularia* (Fr.) Kauffm.) is distinctive because of its basidiome colour and by the rimose-areolate pileus in combination with the verrucose ornamentation pattern of the basidiospores. The present state of the type specimen makes it difficult to revive the tissues and to study the pileipellis. The pileipellis of collection *Smith 84515* (which Hesler & Smith (1979) considered to be conspecific) was studied and fitted the description of our Mexican material: it agrees with the hymeno-epithelium type described by Heilmann-Clausen et al. (1998). Other macro- and microscopical characters of the Mexican material are in accordance with both collections from the USA.

The distribution of *L. rimosellus* appears to be related to *Pinus* and *Betula* in the USA (Burlingham, 1907; Hesler & Smith, 1979). Fieldwork conducted in the Gulf of Mexico area (State of Veracruz) suggested that *L. rimosellus* is uncommon. It has only been recorded in one location, associated with *Pinus*.

ACKNOWLEDGEMENTS

Part of this contribution was supported by CONACYT (project 139241-V). We acknowledge the help of the curators at ENCB, F, FCME, ITCV, MICH and NYS in providing specimens on loan. We are indebted to J. Rejos (AH) for the facilities at the herbarium and to J. A. Pérez and J. Priego (Universidad de Alcalá) for their help during SEM study.

REFERENCES

Basso, M.T. 1999. Fungi Europaei 7, Lactarius Pers. Mykoflora, Alassio.

Bessette, A.E., A.R. Bessette & D.W. Fischer. 1997. Mushrooms of northeastern North America. Syracuse University, Syracuse.

Bon, M. 1980. Clé monographique du genre Lactarius (Pers.: Fr.) S.F. Gray. Doc. Mycol. 10: 1–85.

Burlingham, G.S. 1907. Some Lactarii from Windham County, Vermont. Bull. Torrey Bot. Club 34: 85–95.

Burlingham, G.S. 1908. A study of the Lactariae of the United States. Mem. Torrey Bot. Club 14: 1–109.

Heilmann-Clausen, J., A. Verbeken & J. Vesterholt. 1998. The genus Lactarius. Fungi of Northern Europe vol. 2. Denmark.

Hesler, L.R. & A.H. Smith. 1979. North American species of Lactarius. Univ. Michigan, Ann Arbor.

Holmgren, P.K., N.H. Holmgren & L.C. Barnett (eds.). 1990. Index Herbariorum. Part I. The herbaria of the world, ed. 8. New York.

Homola, R.L. & M. Czapowskyj. 1981. Ectomycorrhizae of Maine 2. A listing of Lactarius with the associated hosts (with additional information on edibility). Bull. Life Sci. & Agric. Exp. St. Univ. Maine 779: 1–19.

Kauffman, C.H. 1918. The Agaricaceae of Michigan vol. 1. Michigan Geol. & Biol. Surv. Pub. 26, Biol. Ser. 5, Lansing.

Kornerup, A. & J.H. Wanscher. 1978. Methuen handbook of colour. 3rd ed. Methuen, London.

Lalli, G. & G. Pacioni 1992. Lactarius sect. Lactifluus and allied species. Mycotaxon 44: 155–195.

Montoya, L. & V.M. Bandala. 1996. Additional new records of Lactarius from Mexico. Mycotaxon 57: 425–450.

Montoya, L. & V.M. Bandala. 2002. The genus Lactarius in Mexico: Observations on its taxonomic revision and its distribution. IV Latin American Congress of Mycology. Asoc. Lat. Mic., Xalapa.

Montoya, L. & V.M. Bandala. 2003. Studies on Lactarius: a new combination and two new species from Mexico. Mycotaxon 85: 393–407.

Montoya, L., G. Guzmán & V.M. Bandala. 1990. New records of Lactarius from Mexico and discussion of the known species. Mycotaxon 38: 349–395.

Murrill, W.A. 1948. Species of Florida Lactarius Fr. Lloydia 11: 86–98.

Peck, Ch. 1885. New York species of Lactarius. Ann. Rep. New York St. Mus. Nat. Hist. 38: 111–133.

Phillips, R. 1991. Mushrooms of North America. Little, Brown & Co., Boston.

Saccardo, P.A. 1887. Sylloge Fungorum vol. 5. Reimp. E. Brothers, 1944, Ann Arbor.

Singer, R. 1986. The agaricales in modern taxonomy. 4th ed. Koeltz, Koenigstein.

Singer, R. 1990. Agaricales new for Mexico or Central America. Anales Inst. Biol. Univ. Nac. Auton. Mexico, ser. Bot. 60: 27–36.

Singer, R., Araujo I. & M.H. Ivory. 1983. The ectotrophically mycorrhizal fungi of the Neotropical Lowlands, especially Central Amazonia, Vaduz, Cramer.

Verbeken, A. 1996. New taxa of Lactarius (Russulaceae) in tropical Africa. Bull. Jard. Bot. Nat. Belg. 65: 197–213.

Verbeken, A. 1998. Studies in tropical African Lactarius species. 6. A synopsis of the subgenus Lactariopsis (Henn.) R. Heim emend. Mycotaxon 66: 387–418.

Verbeken, A. 2001. Studies in tropical African Lactarius species. 10. Infrageneric classification. Mycotaxon 77: 435–444.

Walleyn, R., A. Verbeken & M.E. Noordeloos. 1996. Published names in Lactarius Pers. Russulales News 6: 1–40.

BOOK REVIEW

G.H. Boerema, J. de Gruyter, M.E. Noordeloos & M.E.C. Hamers. *Phoma identification manual. Differentiation of specific and infra-specific taxa in culture*. (CABI publishing, Wallingford, e-mail: cabi@cabi.org; website http://www.cabi-publishing.org. 2004.) ISBN 0-85199-743-0. Pp. 470; 51 text-figs. In English. Price: £ 75.00.

This long awaited manual gives cultural descriptions of 223 specific and infra-specific taxa of *Phoma* (Coelomycetes). Fungi of this genus are common, but have always been difficult to identify. But now this book will make identification easier. It provides line drawings and keys for the identification of common pathogenic and saprotrophic species of *Phoma* in vitro, with references to additional diagnostic literature, representative cultures and documentation of the numerous synonyms (1,146 in total) formerly used in the mycological and phytopathological literature. Part of the book has been published before in the series 'Contributions towards a monograph of *Phoma*', also partly in Persoonia. Most of the *Phoma*-species in this book are widespread in western Europe, but they are often also recorded elsewhere in the world.

The book starts with an introduction of 7 pages, the nomenclator of the genus and its sections of 3 pages, an overview of the generic characters of 2 pages, an overview of the methods used for identification (5 pages). A key to the sections based on characters in vitro takes 2 pages, and notes on adjacent genera 6 pages. The rest of the book is composed of the 9 sections which are distinguished in *Phoma*. Per section a description and notes are given, followed by a key to the species, a list of hosts of the species. Per species the teleomorph and synonyms are given, together with a full description in vitro. Notes on ecology and distribution complete the description.

Thorough studies have preceded the completion of this book, and that is clear from the contents of it. A must for many laboratories dealing with the subject and for anyone else interested in the subject.

M.M. Nauta

PERSOONIA
Volume 18, Part 4, 485–497 (2005)

REVISION OF TYPE MATERIAL OF NIVICOLOUS SPECIES OF STEMONITALES

H. SINGER, G. MORENO & C. ILLANA

Dpto. Biología Vegetal, Universidad de Alcalá, 28871 Alcalá de Henares, Madrid, Spain.
E-mail: gabriel.moreno@uah.es.

The types of *Comatricha anastomosans* Kowalski, *C. filamentosa* Meyl., *C. suksdorfii* Ellis & Everh. var. *aggregata* Meyl. and *Lamproderma longifilum* H. Neubert, Nowotny & K. Baumann were studied. *Comatricha anastomosans* is synonymized with *C. filamentosa*, *C. suksdorfii* var. *aggregata* with *Symphytocarpus confluens* (Cooke & Ellis) Ing & Nann.-Bremek. A new lectotype for *C. filamentosa* is proposed. The synonymy of *L. longifilum* with *C. anastomosans* is confirmed. SEM and light microscope micrographs of spores, capillitia and sporocarps are given.

Key words: nivicolous Myxomycetes, *Comatricha*, *Lamproderma*, *Symphytocarpus*, taxonomy.

The revision of type material of nivicolous Myxomycetes (Moreno et al., 2003a, 2003b 2004; Singer et al., 2003, 2004, 2005) is continued with the application of electron microscopy in order to specify the variability of spore ornamentation. We have been able to localize and study the type of *Comatricha anastomosans* described by Kowalski, the type material of Meylan's *C. suksdorfii* var. *aggregata* Meyl., a specimen of *C. filamentosa* collected by Meylan and the type of *Lamproderma longifilum* H. Neubert, Nowotny & K. Baumann.

Several works on the revision of nivicolous species described by Kowalski have already been published (Singer et al., 2005), in which various taxa have been synonymized: *Trichia synspora* with *T. varia* (Singer et al., 2003), *Diderma nigrum* with *D. asteroides* (Moreno et al., 2003b), *Diacheopsis spinosifila* with *Lepidoderma didermoides* (Moreno et al., 2003a), *D. subcaeruleum* with *D. niveum* (Singer et al., 2004), *Lepidoderma aggregatum* with *L. chailletii* (Moreno et al., 2004) and *Lepidoderma didermoides* with *L. chailletii* (Moreno et al., 2004).

It has been necessary and important to carry out these studies in order to establish the taxonomic position of the species, which were inadequately described and thus obtain new information essential for understanding their taxonomy and applying it to previous chorological and ecological studies.

MATERIAL AND METHODS

The collected material was studied with a binocular microscope and, after mounting in Hoyer's medium, with a Nikon (Optiphot) microscope. Spore measurements were made under the oil immersion objective and include surface structures such as spines or warts.

Scanning electron microscopy (SEM) micrographs were taken in the University of Alcalá de Henares using a Zeiss DSM-950. SEM-preparation was made as sporocarps were rehydrated in concentrated ammonium hydroxide (28–30%) for 30 minutes, dehydrated in aqueous ethanol (70%) for 30 minutes, fixed for 2 hours in pure ethylene glycol dimethyl ether (= 1, 2-dimethoxymethane) and finally immersed in pure acetone for at least 2 hours followed by critical point drying and sputtering with gold-palladium.

The terminology of the spore-producing stages follows Dörfelt & Marx (1990) and Lado & Pando (1997). The spore wall ornamentation as seen in the SEM is described according to the terminology proposed by Rammeloo (1975a, b). The abbreviations for author citations follow Kirk & Ansell (1992).

TAXONOMY

Comatricha alpina — Figs. 1–5

Comatricha alpina Kowalski, Madroño 22 (1973) 152.

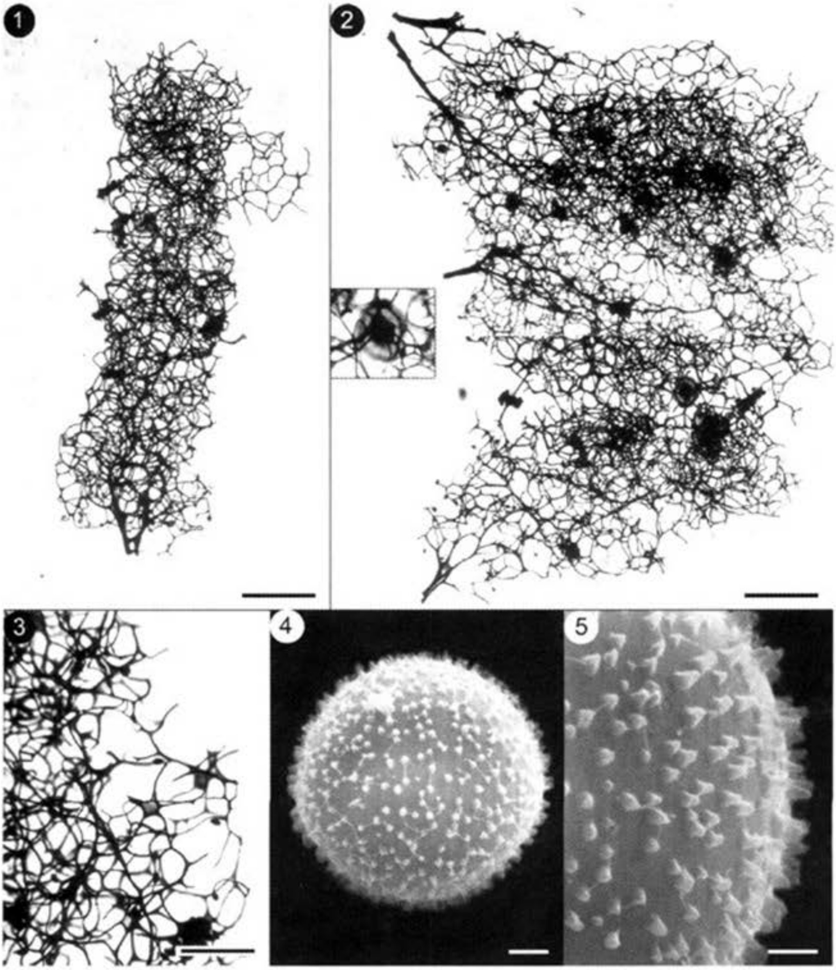
= *Comatricha suksdorfii* Ellis & Everh. var. *aggregata* Meyl., Bull. Soc. Vaud. Sci. Nat. 53 (1921) 455.

Original description (Meylan, 1921). Sporanges en touffes et confluents sur la plus grande partie de leur longueur, libres au sommet, d'un noir intense, très brièvement stipités, de 2 à 3 mm de hauteur. Columelle mal développée, s'effaçant vers la moitié de la hauteur du sporange. Capillitium très lâche, formant à la surface des sporanges libres un réseau très lâche, plus ou moins défini. Spores noires très opaques, de 10 à 13 μm de diamètre, papilleuses.

Description. Sporocarps aggregated, forming groups that are laterally fused by the capillitium, stalked, approximately 2 mm high in total; forming pseudoaethalia, black. Hypothallus iridescent silver. Stalk less than 1 mm long, blackish. Peridium evanescent, except for remains which are united at the centre with the capillitium, forming rounded plates of an irregular outline with a radial venation, up to 100 μm in diameter, with a distinct peripheral zone with abundant small perpendicular filiform veins. Columella a continuation of the stalk and concolorous, short, cylindrical, from one third to half the height of the sporotheca, or branching at the base into several branches. Capillitium formed by rigid threads, 2–5(–6) μm in diameter, dark reddish brown to blackish, branched and anastomosed, forming a wide-meshed net, united with the capillitia of the contiguous sporothecae, with abundant spiny free ends. Spores dark brown in mass, brown in transmitted light, globose, 11–14 μm in diameter, densely verrucose to spinulose. With SEM the spore ornamentation is composed of dense baculae of regular distribution (Figs. 4, 5).

Observations. The material designated as type by Kowalski is conserved in a small carton with a piece of card at the bottom to which a small piece of bark is attached (2.5 × 1.5 cm), which bears two groups of sparse sporocarps with few spores. We found abundant remains of hypothallus where sporocarps had been broken off or lost.

Meylan (1921) proposed the new variety *Comatricha suksdorfii* var. *aggregata* because of the tufted sporocarps which are contiguous for most of their length, but free at their bases and apices. Subsequently, Kowalski (1973), after comparing the type of *C. suksdorfii* with his own collections found that his specimens did not fit this species, but resembled Meylan's type of *C. suksdorfii* var. *aggregata*. He pointed



Figs. 1–5. *Comatricha alpina* (type). 1. Sporocarps; 2. sporocarps with detail of capillitium plate; 3. detail of capillitium; 4. spore; 5. detail of spore ornamentation. Scale bars: 1, 2, 3 = 0.25 mm; 4 = 2 μm; 5 = 1 μm.

out that the differences between *C. suksdorfii* var. *suksdorfii* and *C. suksdorfii* var. *aggregata* were greater than those indicated by Meylan. Kowalski distinguished the former variety by its "widely scattered sporangia 3–4 mm long and stipes about 4 mm tall" and the latter by its "densely aggregated sporangia 1.5–3 mm long and stipes about 1 mm tall". He considered these differences sufficient to treat *C. suksdorfii* var. *aggregata* as a different species which he called *C. alpina*, as the epithet *aggregata* was already in use by Farr (1957) for another *Comatricha*.

Within the scope of the revision of types of nivicolous Myxomycetes that is presently carried out, we have restudied the type of *C. alpina*. Surprisingly, apart from observing confluent sporocarps forming pseudoaethalia, we have observed that the capillitia of the individual sporocarps are partially fused and continuous. Thus, *C. alpina* is in reality a *Symphytocarpus*. Within this genus it matches *S. confluens* (Cooke & Ellis) Ing & Nann.-Bremek., due to its rigid capillitium forming a wide-meshed net with abundant spiny free ends and the presence of the typical rounded plates described above, as indicated by Lister (1911) and Neubert et al. (2000) for this species.

The genus *Symphytocarpus* was proposed by Ing & Nannenga-Bremekamp (1967) in order to group together some species that they segregated from the genera *Amaurochaete*, *Comatricha* and *Stemonitis* and which are characterized mainly by their sporocarps, whose capillitia fuse together to form pseudoaethalia. These authors already indicated that "perhaps *C. suksdorfii* var. *aggregata* should go here too, but as we have not seen specimens of this variety, we cannot decide now". Later, Neubert et al. (2000) came to the same conclusion, studying Meylan's type but not associating it with *Symhytocarpus confluens*.

Symphytocarpus confluens is a very common species that is cited in literature. It is not nivicolous and, as Schnittler & Novozhilov (1996) indicated recently, "the solid inner wood is the microhabitat of the plasmodia".

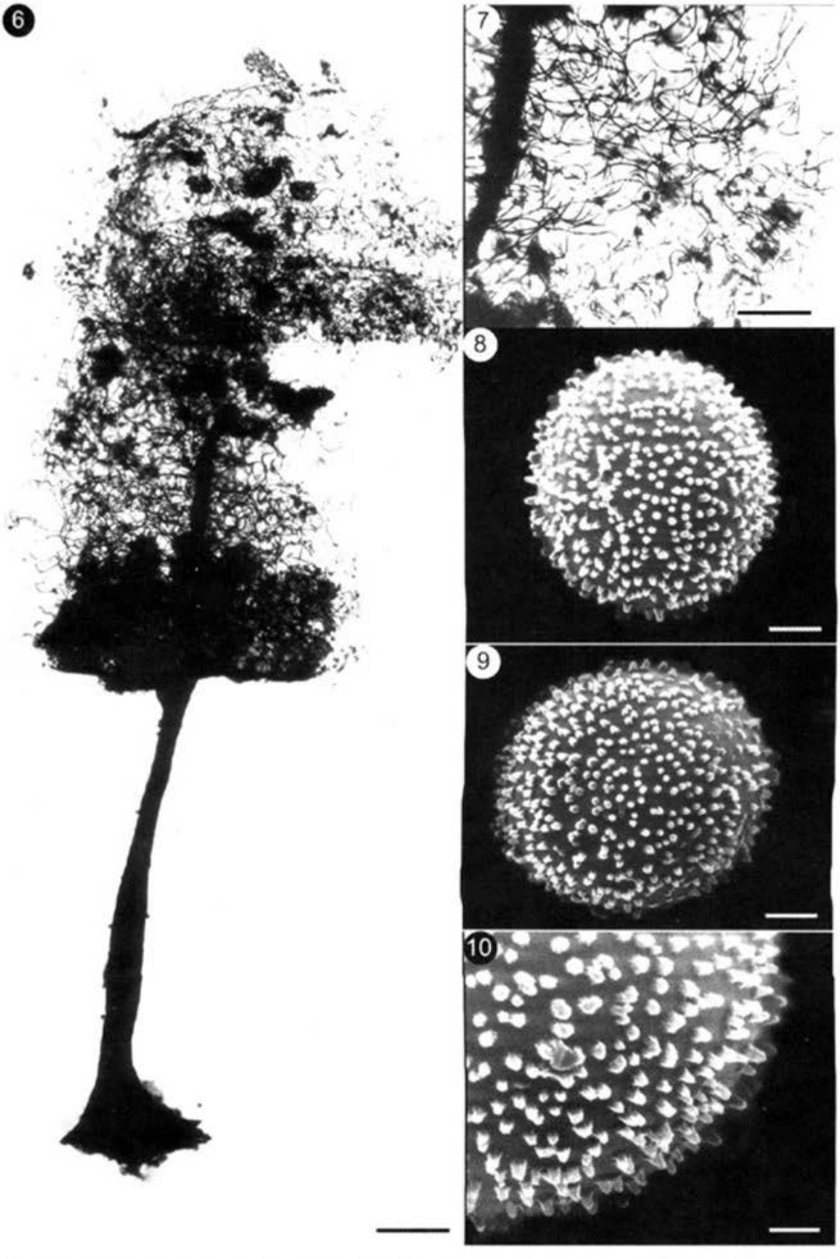
Collection examined. SWITZERLAND: Canton Vaud, Granges de Sainte Croix, 1100 m, on dead spruce branch, leg. Ch. Meylan, VIII.1920, LAU (holotype).

Comatricha anastomosans — Figs. 6–10

Comatricha anastomosans Kowalski, Mycologia 64 (1972) 362.

Original diagnosis. Sporangiis gregariis, commatis, cylindricis vel subglobosis, nigris, 1–3 mm altis; stipite nigro, in sporangium pro columella continuo, 1–2 mm in longitudinem; peridio evanescentio, sed acetabulo basilari persistenti, membranaceo, iridescenti, hypothallo nigro vel rubido-brunneo, disciformi vel continuo; columella nigra, attenuata, aliquando ad apicem sporangii attingenti; capillitio copioso, cunnato, reti flaccido formanti, terminis libris perpaucis, rubido-brunneis; sporis globosis, purpureo-brunneis, spinulosis, cum area palidiore, 11–12 μm diam; plasmodio ignoto.

Description. Sporocarps aggregated, forming large groups, united laterally by the expanding capillitium, giving the appearance of pseudoaethalia, stalked, 2–3.5 mm high in total (capillitium not expanded), black. Sporotheca 1–2.5 × 1–1.5 mm (capillitium not expanded), obovoid to subglobose. Hypothallus dark brown, shiny, confluent and forming a small blackish brown disc around the base of the stalk. Stalk 1–2 mm long, cylindrical to laterally compressed, slightly widened towards the base, longitudinally striate, with a fibrous base, blackish brown to black. Peridium membranous, generally evanescent except at the base which persists forming a basal cup, iridescent silver; sometimes small fragments attached to the capillitium can be observed. Columella continuous with the stalk and concolorous, reaching up to 3/4 to almost the total height of the sporotheca, generally tapered towards the apex, sometimes truncate. Capillitium formed by flexuous and sinuous threads of 1–2 μm in diameter, dark brown, without main branches, branched and anastomosed, forming a dense wide-meshed net, that expands and intermingles without fusing together with the threads of the capillitia of



Figs. 6–10. *Comatricha anastomosans* (type). 6. Sporocarp; 7. detail of capillitium; 8, 9. spores; 10. detail of spore ornamentation. Scale bars: 6 = 0.25 mm; 7 = 0.5 mm; 8, 9 = 2 μm; 10 = 1 μm.

adjacent sporocarps. Spores dark brown in mass, violaceous brown by transmitted light, globose, 11–12 μm in diameter, spinulose, with a clearer zone of variable size (germination pore), sometimes forming an almost complete band. With SEM the spore ornamentation is composed of dense, regularly distributed baculae (Figs. 8–10).

Observations. The type material is kept in a box at the bottom of which are glued five pieces of bark, three large and two smaller ones; one of the small pieces does not contain any material, but the others do. However, only on one of them the sporocarps are well-formed and not collapsed or parasitized by fungi.

Comatricha anastomosans is characterized by its capillitium formed by flexuous and sinuous threads that expand and intermingle with the capillitium of adjacent sporocarps which, however, do not fuse together and by its peridium that persists at the base of the sporotheca to form a basal cup.

Kowalski (1972) placed this species near the genus *Amaurochaete* on basis of its sporocarps having interconnected capillitia that resemble pseudoaethalia. *Comatricha anastomosans* can clearly be separated from *Amourochaete* by its sporocarps being visibly discrete, while species of the genus *Amaurochaete* have either true aethalia or pseudoaethalia where it is difficult or impossible to distinguish individual sporocarps.

Kowalski also considered *C. suksdorfii* to be the most closely related species in the genus. These two species, apart from sharing the mountainous habitat, have gregarious, black, cylindrical sporocarps, with a long columella that almost reaches the apex of the sporotheca and blackish spores of similar dimensions (11–12 μm diameter in *C. anastomosans* and 10–12 μm in *C. suksdorfii*). However, they can be distinguished by the peridium, capillitium and spore ornamentation. In *C. anastomosans* the peridium always persists at the base as a cup, the capillitium intermingles with that of adjacent sporocarps and the spores are spinulose with light microscope. In *C. suksdorfii* the peridium is entirely evanescent and never forms a basal cup, the capillitium of individual sporocarps is never intermingled and the spore ornamentation appears warted with light microscope.

Nannenga-Bremekamp (1974) followed by Yamamoto (1998), ascribe to *C. filamentosa* a 3–4 mm long stalk, which does not coincide with Meylan's description of this species (Meylan, 1921). Some years later, Neubert et al. (2000) concluded that these authors had confused *C. filamentosa* with *C. alta*.

Once again, Kowalski (1975), after studying the type of *C. filamentosa*, suggested that his *C. anastomosans* could be a synonym or a robust variety of *C. anastomosans*. The only differences observed by Kowalski (1975) were the height of the sporocarps (1–2 mm in *C. filamentosa* and 2–6 mm in *C. anastomosans*) and the absence of a pale zone in the spores of *C. filamentosa*. As described below, there is a difference in the height of the sporocarps, but in both species a pale zone on the spores can be observed that corresponds to a germination pore.

Lado (2001) considered the two species synonymous following Kowalski's own observations (1975), without studying their types.

Collections examined. USA: Mt. Rainier National Park, 3 miles below Sunrise Point, 5000 ft, Washington, on bark, 23.VI.1970, leg. D.T. Kowalski, *DTK 10623* in *UC 1445505* (holotype); White Pass, 4500 ft, Yakima Co., on bark, 8.VI.1968, leg. D.T. Kowalski, *DTK 8324* in *BPI 821091*.

Comatricha filamentosa — Figs. 11–15

Comatricha filamentosa Meyl., Bull. Soc. Vaud. Sci. Nat. 53 (1921) 456.

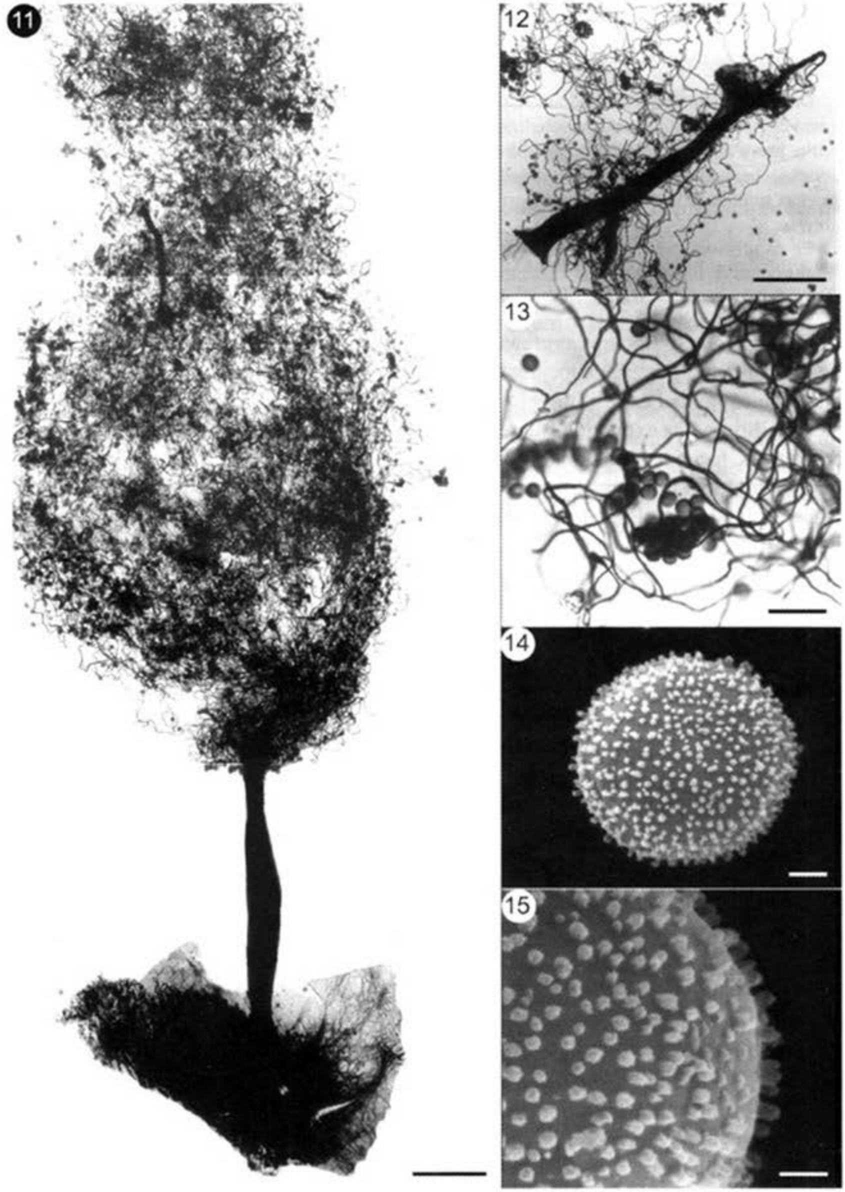
Original diagnosis. Plasmodium? Sporanges en groupes nombreux, d'un brun foncé, de 0.8 à 1 mm de hauteur, elliptiques ou subglobuleux, portés par un stipe de 0.5 à 1 mm s'élevant en columelle, jusqu'au sommet du sporange où elle s'étale parfois comme celle d'un *Enerthenema*. Capillitium lâchement adhérent à la columelle et tombant avec les spores à la maturité en formant de longues traînées à la surface du support entre les stipes, comme le capillitium des *Hemitrichia* et *Arcyria*.

Ce capillitium présente d'ailleurs les mêmes caractères extérieurs, étant formé d'un réseau ininterrompu de longs filaments anastomosés, peu ramifiés, de grosseur constante, lisses, d'un brun pourpré. Spores de 10 à 12 μm brunes spinuleuses.

Description. Sporocarps aggregated, in large groups, united laterally by the capillitia that expand and give the appearance of pseudoaethalia, stalked, 1.5–3.5 mm high in total, the expanded capillitium black. Sporotheca approximately 1–2.5 × 1 mm, after the capillitium has expanded, subglobose to obovoid. Hypothallus dark brown, shiny, continuous, forming a small blackish brown disc in the base of the stalk. Stalk 0.5–1 mm long, cylindrical to laterally compressed, tapered slightly towards the apex and somewhat widened towards the base, longitudinally striate, with a fibrous base, dark reddish. Peridium membranous, generally evanescent, persisting as a basal cup that can reach up to half the height of the sporotheca, iridescent silver. Columella a continuation of the stalk and concolorous, up to 3/4 the height of the sporotheca to almost reaching the apex, tapered towards the apex. Capillitium formed by flexuous and sinuous threads, 0.5–2 μm in diameter, frequently with widenings that are fusiform or in form of a half-moon, dark brown, without primary branches, branched and anastomosed, forming a dense wide-meshed net, that expands and intermingles without fusing together with the threads of the capillitium of adjacent sporocarps. Spores dark brown in mass, violaceous brown with transmitted light, globose, 10–12 μm in diameter, spinulose, with a clearer zone of variable size (germination pore). With SEM the spore ornamentation is composed of dense baculae of regular distribution (Figs. 14, 15).

Observations. Two specimens from Meylan with the same collection data have been studied. The first consists of five pieces of bark each of which bears a group of approximately 30–40 sporocarps, stuck on card, within a box (this specimen is considered as the new lectotype). The second specimen is conserved in a match box and consists of four pieces of wood with a group of approximately 20 sporocarps on each, also stuck on card (this specimen is considered the new isolectotype).

After studying Meylan's specimens, we characterize *C. filamentosa* by its capillitium of flexuous and sinuous threads forming a net that expands and intermingles with the capillitium-threads of adjacent sporocarps without fusing together, by its short stalk (0.5–1 mm) and by the peridium persisting as a basal cup. This species was first determined by Meylan as *C. alta*, as can be seen on the labels on the boxes and subsequently corrected to *C. filamentosa*. *Comatricha alta* is close to this species but differs principally in its longer stalk (reaching 5 mm) and entirely evanescent peridium. As already mentioned, Neubert et al. (2000) considered *C. filamentosa* synonymous with *C. alta*, but they did not study type material.



Figs. 11–15. *Comatricha filamentosa* (type). 11. Sporocarp; 12. detail of stalk and columella; 13. detail of capillitium; 14. spore; 15. detail of spore ornamentation. Scale bars: 11, 12 = 0.25 mm; 13 = 40 μm; 14 = 2 μm; 15 = 1 μm.

After revising the available material determined by Meylan in the herbarium LAU, we have created a new lectotype, since the one proposed by Kowalski (1975) can not been found and is possibly lost.

Collections examined. SWITZERLAND: La Grandsonnaz, Le Chasseron, 1450 m, Canton Vaud, on bark of decayed wood, leg. Ch. Meylan, X.1920, *LAU* (new lectotype and isolectotype).

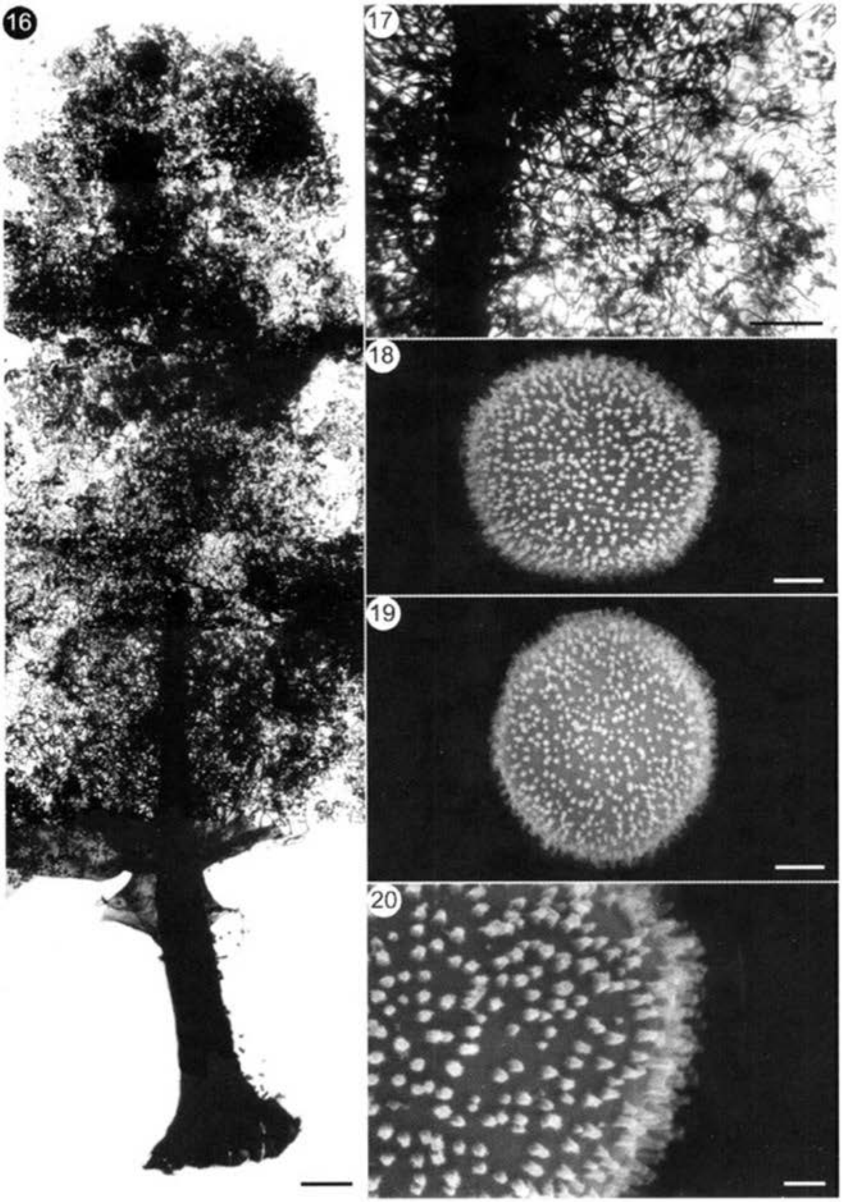
Lamproderma longifilum — Figs. 16–20

Lamproderma longifilum H. Neubert, Nowotny & K. Baumann, Carolinea 47 (1989) 35.

Original diagnosis. Sporocarpia stipitata, globosa, gregaria, dua at quattuor cohaerentia, 1.5 mm in diametro, ad 3 mm in altitudine universa. Hypothallus subfuscus, ad basim stipitis nigro-fuscus vel fuscus, splendens, contura irregulari, sporocystibus communis. Stipes ater, splendens, usque ad 1.5 mm longus, ad acumen 0.15 mm, ad basim 0.5 mm in diametro, in coni modum hypothallo adiunctus. Peridium argenteum, iridescens, tenue, cum zonis obscurioribus, crassioribus, ucidis, breviter eminentibus, ad zonas tenues incomposite aperiens, deinde zonae crassiores capillitio coniunctae, lucem orientem versus visum brunnescens, zonae obscurae reticulatae in forma nervi, contura irregulari, in forma stellae. Columella atra, duas partes sporocarpii attingens, forma cylindrica, acumine tenuiore. Capillitium elasticum, tota columella orines, ad partem inferiorem columellae rubiginosum, fasciatum, circiter 5 μm in diametro, primo reticulum formans, lacunae reticula circiter 40 μm in diametro, deinde sicut ad partem superiorem columellae filiforme, circiter 1.5 μm in diametro, sine reticulis, plus minusve ramificatum et unda simile formatum, ad peridium ex filamentis libere exeuntibus vel rarius zonis crassioribus peridii adnexum compositum, filamenta levia, nigro-brunnea, lucem orientem versus visae brunneae, dense et minute spinulosae, spinae 0.5 μm non attingentes, 11–12 μm in diametro, porus germinativus distinctus, clarior, paulum eminens. Plasmodium ignotum.

Description. The only three sporocarps that are conserved appear more or less grouped, stalked, up to 3 mm in total height, black. Sporotheca up to approximately 1.5 mm in diameter, globose. Hypothallus dark brown, shiny, continuous, common to the groups of sporocarps. Stalk up to 1.5 mm long, cylindrical to laterally compressed, tapered slightly towards the apex and somewhat widened towards the base, longitudinally striate, with a fibrous base, dark reddish. Peridium membranous, persistent, golden iridescent, with darker maculae; irregular dehiscence into large flakes. Columella a continuation of the stalk and concolorous, up to 2/3 of the height of the sporotheca, with an obtuse apex. Capillitium formed by flexuous and sinuous threads of 1.5–2 μm in diameter, dark brown, with main branches up to 5 μm in diameter originating along the whole length of the columella, branched and anastomosed, forming a dense net, with few free ends. Spores dark brown in mass, violaceous brown with transmitted light, globose, 11–12 μm in diameter, spinulose, with a clearer zone of variable size (germination pore). With SEM the spore ornamentation is composed of dense baculae of regular distribution (Figs. 19, 20).

Observations. The type of *L. longifilum* consists of a piece of wood of *Pinus mugo* of approximately 3.5 cm of length, with only three sporocarps that conserve abundant remains of peridium attached to the capillitium. At its base, remains of the hypothallus can be found. The substrate is stuck on a white card that is kept in a box of transparent plastic. A microscope slide with two sporocarps is also conserved. *Lamproderma longifilum*



Figs. 16–20. *Lamproderma longifilum* (type). 16. Sporocarp; 17. detail of capillitium; 18, 19. spores; 20. detail of spore ornamentation. Scale bars: 16 = 0.25 mm; 17 = 0.5 mm; 18, 19 = 2 μm; 20 = 1 μm.

is characterized by its aggregated sporocarps, globose sporotheca with a persistent peridium, cylindrical stalk with the same height as the sporotheca, capillitium formed by flexuous and sinuous dark reddish threads and spores 11–12 μm in diameter, which are spiny, with an ornamentation by SEM formed by dense baculae of uniform distribution.

The type material and two further specimens of *L. longifilum* were kindly sent to us by Nowotny for the preparation of SEM photos. Surprisingly, the spore ornamentation with SEM does not agree with photos of the same material published by the authors of the species in the monograph of Neubert et al. (2000). We interpret this as a mistake in the printing of the book and it remains possible that the photos of *C. anastomosans* (= *L. longifilum*) have been confused with another species of *Comatricha* (for example *C. fusiformis,* which has the type of spore ornamentation consisting of baculae with star-like apices, as shown in the book).

Collections examined. AUSTRIA: Feuerkogel, Ebensee, Oberösterreich, 1600 m, on dead twigs of *Pinus mugo*, leg. W. Nowotny, 2.VI.1984, Herb. *Nowotny 1200* (holotype); ibidem, 25.V.1989, 20.V.1993, Herb. *Nowotny 2376* and Herb. *Nowotny 5367* (as *C. anastomosans*); ibidem, on dead plant stems, 25.V.1989, Herb. *Nowotny 2376* (as *C. anastomosans*).

CONCLUSION

Following the study of the type material of *C. suksdorfii* Ellis & Everh. var. *aggregata* Meyl. (1921: 455) we consider *C. alpina* synonymous with *Symphytocarpus confluens* (Cooke & Ellis) Ing & Nann.-Bremek. (Figs. 1–5).

As Kowalski (1975) has already suggested, we agree that *C. anastomosans* "is very close, if not identical, with *C. filamentosa*". There are only minimal differences in the height of the sporocarps, 2–3.5 mm in *C. anastomosans* (with the capillitum not expanded) and 1.5–3.5 mm in *C. filamentosa* (with the capillitium expanded) and there are no significant differences in the dimensions of the sporothecae. We have observed that the sporothecae of *C. anastomosans* are 1–2.5 × 1–1.5 mm (capillitium not expanded) and of *C. filamentosa* 1–1.5 × 1 mm (capillitium expanded). We have to point out that the dimensions of the sporocarps of these species are difficult to measure as a result of the tendency of the capillitium to expand. As there are no other significant differences, synonymy of these species is proposed.

We propose the synonymy of *Lamproderma longifilum* with *C. anastomosans*. When Neubert et al. (1989) described *L. longifilum*, they noted its similarity to *C. anastomosans*. These species are separated, according to these authors, because *C. anastomosans* has cylindrical sporothecae, each with a columella that is markedly tapered and reaches almost to the apex, where it gives rise to the capillitium with few free ends. In *L. longifilum* the sporothecae are globose, the columella is shorter and is only slightly tapered or blunt, the capillitium has free ends and the peridium shows dark spots.

Neubert et al. (2000), after consulting Meyer who studied Kowalski's American material of *C. anastomosans*, observed similarities in the microscopy of the two species and proposed the synonymy of *L. longifilum* with *C. anastomosans*. We agree with this view, as the differences between these species do not justify their separation.

The distinct spots, present in all of Neubert's collections of *L. longifilum* that we have studied, are not present in *C. anastomosans* and *C. filamentosa,* as these specimens were very mature and lacked sporothecae with a complete peridium.

In conclusion we make the following taxonomic proposals:

Symphytocarpus confluens (Cooke & Ellis) Ing & Nann.-Bremek. in Nannenga-Bremekamp, Nederlandse Myxomyceten ('1974' 1975) 174.

= *Stemonitis confluens* Cooke & Ellis, Grevillea 5 (1876) 51.

= *Comatricha suksdorfii* Ellis & Everh. var. *aggregata* Meyl., Bull. Soc. Vaud. Sci. Nat. 53 (1921) 455.

= *Comatricha alpina* Kowalski, Madroño 152 (1973) 22.

Comatricha filamentosa Meyl., Bull. Soc. Vaud. Sci. Nat. 53 (1921) 456.

= *Comatricha anastomosans* Kowalski, Mycologia 362 (1972) 64.

= *Lamproderma longifilum* H. Neubert, Nowotny & K. Baumann, Carolinea 35 (1989) 47.

ACKNOWLEDGEMENTS

This study has been partly financed by the Research Project of the Ministry of Science and Technology, National Plan of Scientific Investigation, Technological Development and Innovation, REN2002-01965. We express our gratitude to Mr. D.W. Mitchell for the revision of the manuscript and wish to thank J.A. Perez and A. Priego of the Electron Microscopy Service of the University of Alcalá for their invaluable help with the SEM and the curators of the herbaria BPI, LAU and UC and especially Dr. J. Rejos, curator of the herbarium AH. We also thank Mr. W. Nowotny.

H. Singer is thankful to the National Program of the Professorship Formation, Ministry of Education and Culture of Spain, for the award of a scholarship to complete his doctoral thesis in the University of Alcalá.

REFERENCES

Dörfelt, H. & H. Marx. 1990. Zur Terminologie der sporenbildenden Stadien der Myxomyceten. Beitr. Kenntn. Pilze Mitteleurop. 6: 5–14.

Farr, M.L. 1957. A checklist of Jamaica slime-moulds (Myxomycetes). Bull. Inst. Jamaica Sci. Ser. 7: 1–67.

Ing, B. & N.E. Nannenga-Bremekamp. 1967. Notes on Myxomycetes XIII. Symphytocarpus nov. gen. Stemonitacearum. Proc. K. Ned. Akad. Wet. (Ser. C) 70: 217–231.

Kirk, P.M. & A.E. Ansell. 1992. Authors of fungal names. A list of authors of scientific names of fungi, with recommended standard forms of their names, including abbreviations index of fungi supplement. CAB International, Wallingford, UK. 95 pp.

Kowalski, D.T. 1972. Two new alpine Myxomycetes from Washington. Mycologia 64: 359–364.

Kowalski, D.T. 1973. Notes on western Myxomycetes. Madroño 22: 151–153.

Kowalski, D.T. 1975. The Myxomycete taxa described by Charles Meylan. Mycologia 67: 448–494.

Lado, C. 2001. Nomenmyx, a nomenclatural taxabase of Myxomycetes. Cuadernos de Trabajo de Flora Micológica Ibérica 16. CSIC, Real Jardín Botánico, Madrid.

Lado, C. & L. Pando. 1997. Flora Mycologica Iberica. Vol. 2. Myxomycetes, I. Ceratiomyxales, Echinosteliales, Liceales, Trichiales. Madrid. Real Jardín Botánico, Königstein. Cramer in Koeltz.

Lister, A. 1911. A monograph of the Mycetozoa. A descriptive catalogue of the species in the Herbarium of the British Museum. Second edition, revised by G. Lister. London.

Meylan, C. 1921. Contribution à la connaissance des Myxomycètes de la Suisse. Bull. Soc. Vaud. Sci. Nat. 53: 451–463.

Moreno, G., H. Singer & C. Illana. 2003a. Diacheopsis spinosifila, a synonym of Lepidoderma didermoides. Mycotaxon 88: 123–128.

Moreno, G., H. Singer, C. Illana & M. Lizárraga. 2003b. Diderma nigrum, a synonym of Diderma asteroides (Myxomycetes). Österr. Z. Pilzk.12: 101–105.

Moreno, G., H. Singer & C. Illana. 2004. A taxonomic review on the nivicolous species decribed by Kowalski. II. Order Physarales and Trichiales (Myxomycetes). Österr. Z. Pilzk. 13: 61–74.

Nannenga-Bremekamp, N.E. 1974. De Nederlandse Myxomyceten. Koninklijke Nederlandse Natuurhistorische Vereniging.

Neubert, H., W. Nowotny & K. Baumann. 1989. Myxomyceten aus der Bundesrepublik Deutschland V. (Mit Berücksichtigung von Vorkommen in Oberösterreich). Carolinea 47: 25–46.

Neubert, H., W. Nowotny, K. Baumann & H. Marx. 2000. Die Myxomyceten Deutschlands und des angrenzenden Alpenraumes unter besonderer Berücksichtigung Österreichs. Band 3. Stemonitales. Gomaringen. Karlheinz Baumann Verlag.

Rammeloo, J. 1975a. Structure of the epispore in the Stemonitales (Myxomycetes) as seen with the scanning electron microscope. Bull. Jard. Bot. Belg. 45: 301–306.

Rammeloo, J. 1975b. Structure of the epispore in the Trichiaceae (Trichiales, Myxomycetes) as seen with the scanning electron microscope. Bull. Soc. Roy. Bot. Belgique 107: 353–359.

Schnittler, M. & Y.K. Novozhilov. 1996. Myxomycetes of the winter-cold desert in Western Kazakhstan. Mycotaxon 74: 267–285.

Singer, H., G. Moreno & C. Illana. 2004. A revision of the types of Diderma subcaeruleum and Diderma globosum var. europaeum. Mycotaxon 89: 311–320.

Singer, H., G. Moreno & C. Illana. 2005. A taxonomic review on the nivicolous species described by Kowalski. I. Order Stemonitales. Mycol. Progr.: 4: 3–10.

Singer, H., G. Moreno, C. Illana & M.Lizárraga. 2003. Trichia synspora, a synonym of Trichia varia. Mycotaxon 87: 243–248.

Yamamoto, Y. 1998. The Myxomycete Biota of Japan. Toyo Shorin Publishing Co., Ltd., Tokyo.

BOOK REVIEW

P. Döbbeler & G. Rambold. *Contributions to Lichenology. Festschrift in honour of Hannes Hertel*. (J. Cramer, Stuttgart, Berlin; e-mail: mail@schweizerbart.de; website http://www.borntraeger-cramer.de. 2004.) ISBN 3-443-58067-X. Pp. 739; 181 text-figs. (partially coloured). In English. Price: EUR 148.00 (hardcover).

This Festschrift contains 44 lichenological contributions and is published on the occasion of Hertel's 65th birthday. The 79 contributing authors represent 19 different countries.

Lecidiaceae sensu lato are well represented in this book, which covers a vast array of lichens of different sytematic position, growth form, ecological characters and distribution. Various aspects of lichenology are dealt with in this book: anatomical and ontogenetic studies, chemical, physiological and molecular research, analyses of the structure and mechanisms of lichen photobionts, systematic studies, biogeographical studies. The contributions to this Festschrift show the current lichenological problems and progress, but still a lot is unknown of certain groups of lichens, especially the more inconspicuous ones. Only a limited part of the world has been inventoried more or less completely, and also numerous specimens are in the Botanische Staatssammlung München (where Hertel was curator) are still waiting for investigation.

This book is recommended for all students in lichenology and is a must for all the libraries who want to keep informed on modern lichenological research.

M.M. Nauta

PERSOONIA
Volume 18, Part 4, 499–504 (2005)

NEW OBSERVATIONS ON THE BASIDIOME ONTOGENY OF CHAMONIXIA CAESPITOSA (SEQUESTRATE BOLETACEAE)

H. CLÉMENÇON

Institut d'Ecologie, Université de Lausanne, CH-1015 Lausanne, Switzerland
E-mail: Heinz.Clemencon@bluewin.ch

The description of basidiome development of *Chamonixia caespitosa* made by Eduard Fischer during the first quarter of the last century is extended, based on a new investigation of the original permanent mounts. This puffball-like fungus is exocarpic, claustropileate and amphicleistoblemate. A hymeniform palisade on the primordial stipe becomes partly covered and obliterated by the pileus margin and an amphicleistoblema. The morphological data confirm the molecular-taxonomic position of *Chamonixia* in the Boletaceae.

Chamonixia caespitosa Rolland is a puffball-like Basidiomycete with a finely tomentose peridium turning blue when bruised. Molecular analyses showed that the genus *Chamonixia* has phylogenetic affinities with the boletes (Bruns et al., 1998; Kretzer & Bruns, 1999).

In 1925 the Swiss mycologist Eduard Fischer published a description of the fruitbody development of *C. caespitosa* based on thick sections that he made from material collected by E. Soehner (1922, as *Hymenogaster caerulescens* Soehner). He strongly emphasised the resemblance of the early stages of *Chamonixia caespitosa* with early stages of gymnocarpic agarics with a free pileus margin, such as *Gymnopus dryophilus* (*Collybia dryophila*), and he explained the puffball-like appearance of the mature basidiome with the fact that the pileus margin grows towards the primordial stipe and fuses with it, while the hymenophore, instead of being regular as in agarics, becomes sponge-like (Fig. 1). Therefore, Fischer (1925) called the development of *C. caespitosa* gymnocarpic, whereas Reijnders (1963), who based his judgement exclusively on the description made by Fischer, called it pilangiocarpic. Fischer described and made drawings of numerous hyphae growing out of the pileus surface and pileus margin, but neither he nor Reijnders (1963) took this fact into consideration when assigning this fungus to a developmental type.

In this paper, the presence of a pileoblema, a cauloblema, a hymeniform palisade on the primordial stipe, and an irregular context in the primordial stipe base are described, using the sections made by Fischer.

MATERIAL AND METHODS

Eduard Fischer left a legacy of 12 unstained permanent mounts that are conserved at the Institute of Plant Sciences (formerly Botanical Institute) of the University of Bern, Switzerland. The slides were examined with bright field microscopy and photographed with an Olympus D11 digital camera mounted on a Zeiss Orthoplan microscope.

Fig. 1. Early development of *Chamonixia caespitosa*. Drawings by Fischer (1925) and photographs by Clémençon (2004) of the permanent mounts that served to make the drawings. At first the pileus margin is free, but later it fuses with the primordial stipe. Gleba chambers develop instead of gills. The hyphae growing out from the pileus surface and margin are clearly drawn.

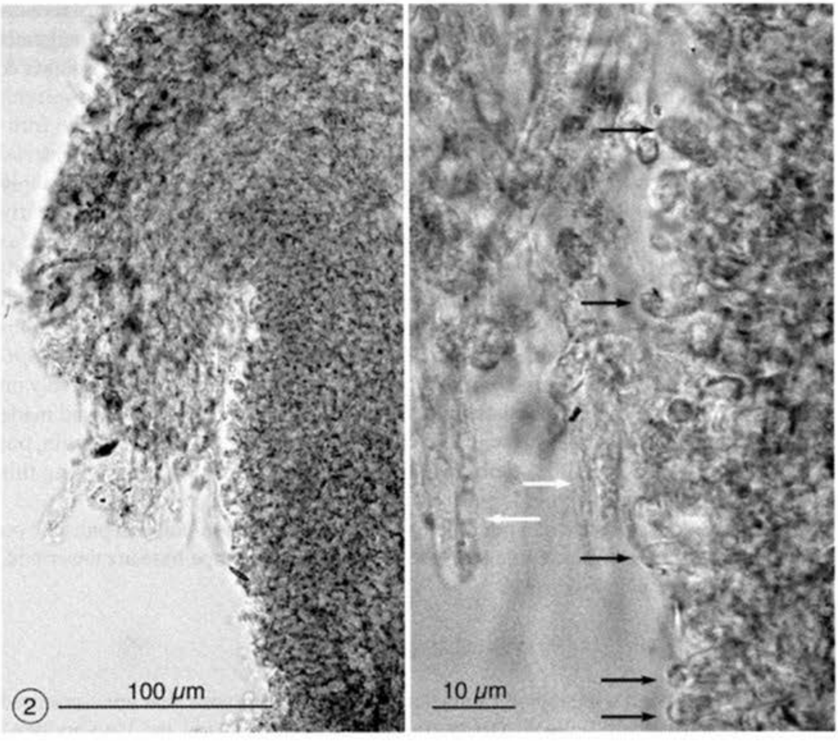


Fig. 2. Hyphae growing out from the pileus margin (white arrows) and palisade layer on the primordial stipe (black arrows) of the small primordium in Fig. 1.

The photographs were adjusted for printing with Adobe Photoshop on a Macintosh G4 computer. Since Fischer's sections are thick, it was difficult to make useful photographs, but the details necessary for a reappraisal are still visible, albeit not in optimal quality.

RESULTS

The hyphae growing out from the pileus margin and pileus surface are readily visible (Figs. 2, 4). In older primordia, hyphae are also growing out from the stipe surface, but Fischer (1925) did not mention them. The hyphae on the upper part of the stipe grow obliquely upward to meet the hyphae growing down from the pileus margin (Fig. 4), but the hyphae of the lower part of the stipe grow more or less horizontally and intertwine frequently. At maturity, a tomentose layer originating on the pileus and on the stipe covers the entire basidiome.

Inspection of Fischer's slides reveals the presence of a hymeniform layer on the stipe (Figs. 2, 3). It extends from within the narrow fold formed by the pileus margin to almost down to the base and becomes buried under the involute pileus margin and the tomentose layer of outgrowing hyphae. Fischer (1925) does not mention this hymeniform layer.

The context in the base of the stipe is composed of slightly inflated and irregularly arranged hyphae (Fig. 3). This context contrasts with the subregular, vertical hyphae of the stipe, as indicated in the drawings by Fischer (1925), but this author did not pay any attention to it.

DISCUSSION

Fischer's drawings of the hyphae growing out of the pileus and stipe strongly suggest an emanated veil (Reijnders, 1948, 1963). It is therefore surprising that Reijnders (1963) did not pay any attention to it. Moreover, Reijnders (1963) specifically affirmed that there is no marginal veil in *C. caespitosa*.

In 1997 Clémençon introduced the concept of metablemas formed by hyphae growing out of almost any part of a basidiome. Metablemas are not synonymous with emanated veils, since the final organs formed by them may become not only veils, but also surface layers such as pileipelles and stipitipelles. The hyphae growing out of the pileus and stipe of *C. caespitosa* are a pileoblema and a cauloblema, respectively. Since the hyphae of the two blemas intermingle at the level of the pileus margin and form a continuous, veil-like layer, *Chamonixia caespitosa* is covered by an amphicleistoblema.

One year after Fischer's publication, Kühner (1926a, b) published his studies on the basidiome development of two boletes, *Suillus grevillei* (as *Suillus flavus*) and *Boletinus cavipes* (Fig. 5). The pilei of both boletes curve down toward the stipe to form a secondary prehymenial cavity. In *Boletinus cavipes* the pileus margin does not quite touch the stipe, but the small distance left is bridged by an amphicleistoblema. In *Suillus grevillei* the pileus margin touches the stipe, and a pileocleistoblema grows down from the pileus onto the stipe. The secondary cavity of both species is lined with a hymeniform layer that also covers the surface of the stipe, extending down well beyond the level of the pileus margin. Part of the hymeniform layer becomes buried under the pileus margin and the cleistoblema.

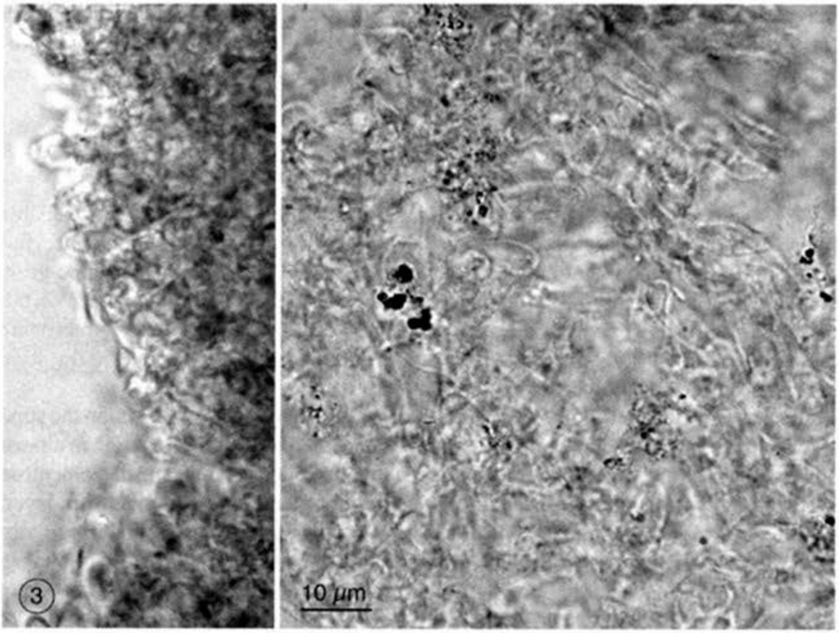


Fig. 3. Palisade layer on the lower part of the primordial stipe (left) and irregular context in the stipe base, indicating the presence of a nodulus. From the small primordium in Fig. 1.

Comparing the carpogenesis of *Chamonixia* with that of the two boletes, we find four developmental steps in *Chamonixia* identical with those described from *Suillus* and *Boletinus*: An involute pileus margin forming a secondary cavity; a cleistoblema; a hymeniform layer extending from the cavity onto the stipe; and an overgrowth of part of this layer by the pileus margin and the cleistoblema.

There is still another developmental similarity between *Chamonixia* and the two boletes. The irregularly arranged, inflated hyphae in the stipe base of *Chamonixia* indicate the presence of a nodulus from which a shaft of subregularly arranged hyphae grows up and forms the primordial stipe. Thus, in the terminology of Clémençon (1997, 2004) *Chamonixia* is epinodular and exocarpic like *Suillus grevillei* and *Boletinus cavipes*.

Conclusion: The development of *C. caespitosa* is remarkably similar to that of the two boletes, confirming the taxonomic conclusion based on the molecular studies mentioned above.

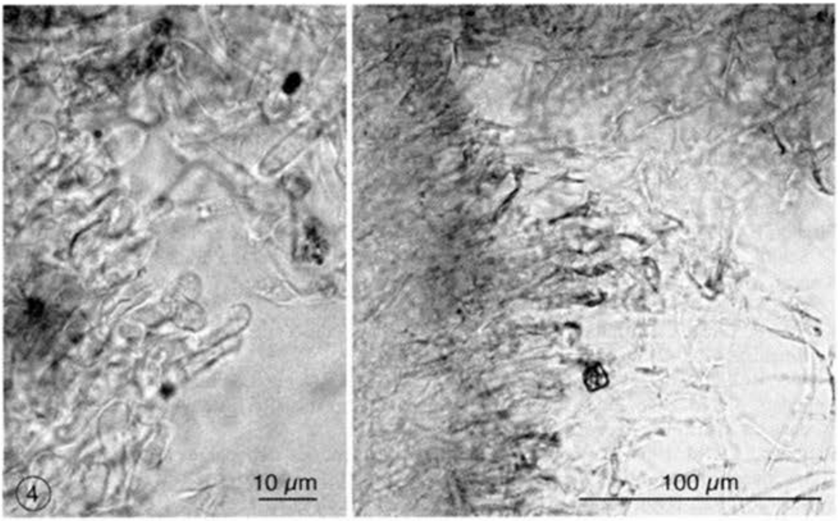


Fig. 4. Development of the cauloblema and the pileoblema. The left photograph is from the right primordium in Fig. 1, the right photograph is from an older primordium not discussed by Fischer (1925). Both blemas form a loose weft of long, thin hyphae and intermingle under the pileus margin, forming an amphicleistoblema. This is the tomentose peridium described by Fischer.

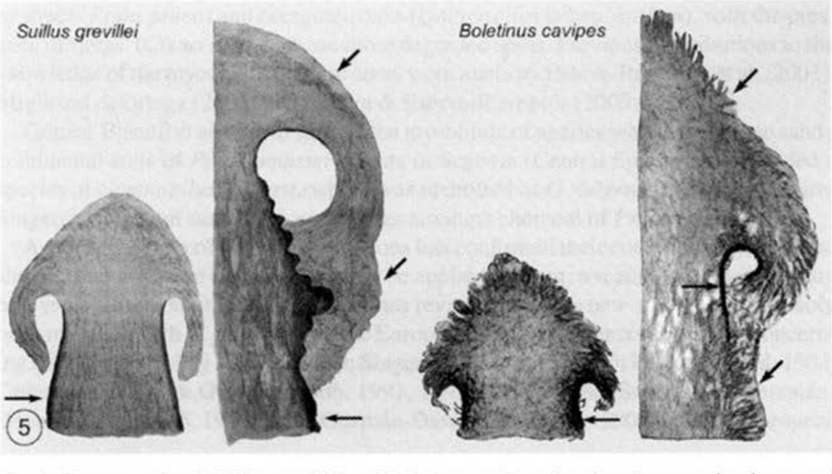


Fig. 5. Carpogenesis of *Suillus grevillei* and *Boletinus cavipes* showing the same developmental details as *Chamonixia caespitosa*: Involute margin, cleistoblemas (slanted arrows), and a partly covered hymeniform layer extending from the secondary cavity down over the stipe (horizontal arrows; from Kühner, 1926a, b).

REFERENCES

Bruns, T.D., T.M. Szaro, M. Gardes, K.W. Cullings, J.J. Pan, D.L. Taylor, T.R. Horton, A. Kretzer, M. Garbelotto & Y. Li. 1998. A sequence database for the identification of ectomycorrhizal basidiomycetes by phylogenetic analysis. Molec. Ecol. 7: 257–272.

Clémençon, H. 1997. Anatomie der Hymenomyceten. Kommissionsverlag Flück-Wirth, Teufen, Switzerland.

Clémençon, H. 2004. Cytology and Plectology of the Hymenomycetes. Bibliotheca Mycologica Volume 199. J. Cramer in der Gebrüder Borntraeger Verlagsbuchhandlung, Berlin, Stuttgart.

Fischer, E. 1925. Zur Entwicklungsgeschichte der Fruchtkörper der Secotiaceen. Festschrift Carl Schröter. Veröffentlichungen des Geobotanischen Institutes Rübel in Zürich 3: 571–582.

Kretzer, A.M. & T.D. Bruns. 1999. Use of atp6 in Fungal Phylogenetics: An Example from the Boletales. Molec. Phylogen. Evol. 13: 483–492.

Kühner, R. 1926a. Contribution à l'étude des Hyménomycètes et spécialement des Agaricacées. Le Botaniste 17: 5–218.

Kühner, R. 1926b. Le développement du Boletinus cavipes Kalchbr. Le Botaniste 17: 177–181.

Reijnders, A.F.M. 1948. Etude sur le développement et l'organisation histologique des carpophores dans les Agaricales. Rec. trav. bot. Néerl. 41: 213–396.

Reijnders, A.F.M. 1963. Les problèmes du développement des carpophores des Agaricales et de quelques groupes voisins. Junk, Den Haag.

Soehner, E. 1922. Hymenogaster caerulescens (spec. nov.). Z. Pilzk. 1: 6–8.

PERSOONIA
Volume 18, Part 4, 505–510 (2005)

A NEW SPECIES OF GYMNOPILUS (CORTINARIACEAE) FROM SANDY SOILS IN PINUS FORESTS

A. ORTEGA[1] & F. ESTEVE-RAVENTÓS[2]

The new species *Gymnopilus arenophilus* A. Ortega & Esteve-Rav. is described. It is characterized by its particular habitat in sandy, sometimes burned, soils of thermophilous *Pinus* forests. Macroscopically *G. arenophilus* resembles *G. penetrans*, from which it differs in the larger spores and the scarcely bitter taste. Microscopically *G. arenophilus* reminds of *G. fulgens*, with which it has probably been mistaken in the past. The latter species has very different macroscopical features, spore ornamentation and a paludicolous habitat. A discussion of European and some non-European related species is also given.

Gymnopilus arenophilus has been found in large amounts in the province of Sevilla (Spain) in the last years, during a research project carried out by one of us (A.O.) to compile and list the mycobiota of the macromycetes growing in an area close to the river Guadiamar basin. This territory suffered in April 1998 an important ecological damage, caused by a toxic mineral waste after the breaking of a mining pond (Cabezudo et al., 2003; Ortega, 2003). One of the most interesting areas of study in this territory has been the Mediterranean plant communities which develop on sandy soils, such as the thermo-mediterranean xero-psammophilous cork-oak forests (Myrto communis-Querceto suberis halimietoso halimifolii S. (Cabezudo et al., 2003)). These cork-oak forests, which always develop in acid soils, are often wide open forests, accompanied by pines (*Pinus pinea*) and evergreen oaks (*Quercus ilex* subsp. *ballota*), with the presence of 'jaras' (*Cistus* spp.) in those more degraded spots. Previous contributions to the knowledge of the mycobiota of these areas were made by Esteve-Raventós et al. (2001), Migliozzi & Ortega (2001) and Ortega & Esteve-Raventós (2003; in prep.).

Gómez-Busutil et al. (1996) studied the mycobiota of agarics which develop in sandy continental soils of *Pinus pinaster* forests in Segovia (Central Spain), and recorded a species of *Gymnopilus* P. Karst. which was identified as *G. fulgens* (J. Favre & Maire) Singer, growing on sandy soil, sometimes amongst charcoal of *Pinus* debris.

A thorough study of all these collections has confirmed their conspecificity, and also showed that the name *G. fulgens* cannot be applied to them; a scanning of the literature of *Gymnopilus* available to the authors has revealed that this new species has probably been mistaken with *G. fulgens* by some European authors. Other contributions concerning American taxa (e.g., Hesler, 1969; Singer, 1969; Dennis, 1970; Pegler & Fiard, 1983; Guzmán-Dávalos & Guzmán, 1986, 1991, 1995; Pegler, 1988; Seidl, 1989; Guzmán-Dávalos, 1994, 1995, 1996, 2003; Guzmán-Dávalos & Ovrebo, 2001) or extra-European

---

1) Departamento de Botánica, Facultad de Ciencias, Universidad de Granada, E-18071 Granada, Spain. E-mail: aortega@ugr.es.

2) Departamento de Biología Vegetal, Facultad de Biología, Universidad de Alcalá, E-28871 Alcalá de Henares (Madrid), Spain. E-mail: fernando.esteve@uah.es.

taxa (e.g., Pegler, 1977, 1986; Horak, 1989; Høiland, 1998; Rees & Ye, 1999; Rees et al., 1999, 2002; Rees, 2003; Thomas et al., 2003), do not treat any species with the combination of morphological and ecological characters of *G. arenophilus*, therefore it is described here as new.

Gymnopilus arenophilus A. Ortega & Esteve-Rav., *spec. nov.* — Fig. 1a–d

Pileus 10–50 mm diam., primo conico-convexus, deinde plano-convexus ad applanatus, obtuso-umbonatus, aurantiacus deinde disco brunneo-aurantiacus, margine luteo-aurantiaco; glabrosus vel minute fibrillosus. Lamellae adnatae, flavae, ad maturitas ferrugineo-aurantiae. Stipes 20–60 mm longus, 4–7 mm crassus, cylindraceus, primo pallidus, deinde flavidus vel concoloribus, sericeo-fibrillosus, rhizomorphis albidis. Velum album vel flavidum, sericeo-fibrillosum, arachnoideum, fugax. Caro sapore subamaro.

Sporae 8.5–10.8 × 5.5–6.5 μm, Qm = 1.6, ellipsoideae, oblongae vel subamygdaliformae, verrucosae, dextrinoideae. Basidia 4-sporigera. Cheilocystidia 25–45 × 5.5–9(–11) μm, lageniformia, apice capitato vel subcapitato (4.5–6.5 μm lato). Pleurocystidia nulla.

In solis arenosis in Pineto (*P. pinaster, P. pinea*), interdum in solis adustis.

Holotypus: Hispania, Sevilla, Aznalcázar, 2.XII.2000, L. Alcoba & A. Ortega (GDA 47384).

Carpophores in groups, sometimes rather numerous. Pileus 10–50 cm in diameter, conical to conical-convex when young, soon convex to plano-convex or applanate, even subdepressed at centre in old specimens, with an obtuse and conspicuous umbo, scarcely hygrophanous, not striate, orange to chestnut-orange (Mu. 7.5 YR 5/6–8, 4/6), paler towards margin, which is yellowish-orange (2.5 Y 7/8; 10 YR 6/8, 7/8), slightly pallescent on drying; surface dry, smooth or slightly fibrillose, sometimes forming radial fibrillose adpressed flecks or squamules; margin when young with short fringe of whitish veil remnants. Lamellae moderately crowded to subdistant, L = 28–40, l = 1–2, broadly adnate to emarginate, with decurrent tooth in old specimens, 2–6 mm broad, at first pale yellow, becoming orange-yellow, in some cases with ferrugineous spots in or near the edge, with whitish or paler denticulate edge. Stipe 20–60 × 4–7 mm, cylindrical or progressively enlarged towards base, often curved, hollow with age, at first beige to buff, then becoming concolorous with pileus or paler, sometimes spotted orange-brownish with age or upon handling; surface longitudinally fibrillose with whitish veil remnants, glabrescent with age, at base white tomentose, with several small white rhizomorphs. Context pale yellow. Smell indistinct. Taste hardly bitterish.

Spores 8.5–9.6–10.6(–10.8) × 5.5–6–6.5 μm, Qm = 1.42–1.6–1.77 (n = 30), ellipsoid, oblong to subamygdaliform, with obtuse apex, slightly thick-walled, clearly warty, the warts sometimes subconnected but not crested, without suprahilar plage, quickly but moderately dextrinoid, without germ pore. Basidia 25–33(–37) × 7.5–9 μm, 4-spored, cylindrical to subclavate, with long sterigmata 3–5 μm. Lamella edge mostly homogeneous, composed of cystidia and dispersed, few basidia. Cheilocystidia 25–45 × 5.5–9(–11) μm, lageniform, mostly capitulate, capitula 4.5–6.5 μm wide, sometimes filled with yellowish content. Pleurocystidia not seen. Pileipellis an entangled and hardly gelified cutis, formed by septate hyphae 5–10 μm wide, with scarce free and cylindrical terminal cells; pigment yellow-orange, both 'zebroid' encrusting and parietal; subcutis formed by less pigmented hyphae, –20 μm wide. Lamella trama formed by parallel, 4–13 μm wide hyphae, with yellowish pigment. Pileocystidia not seen. Caulocystidia not seen. Clamp-connections present at all septa.

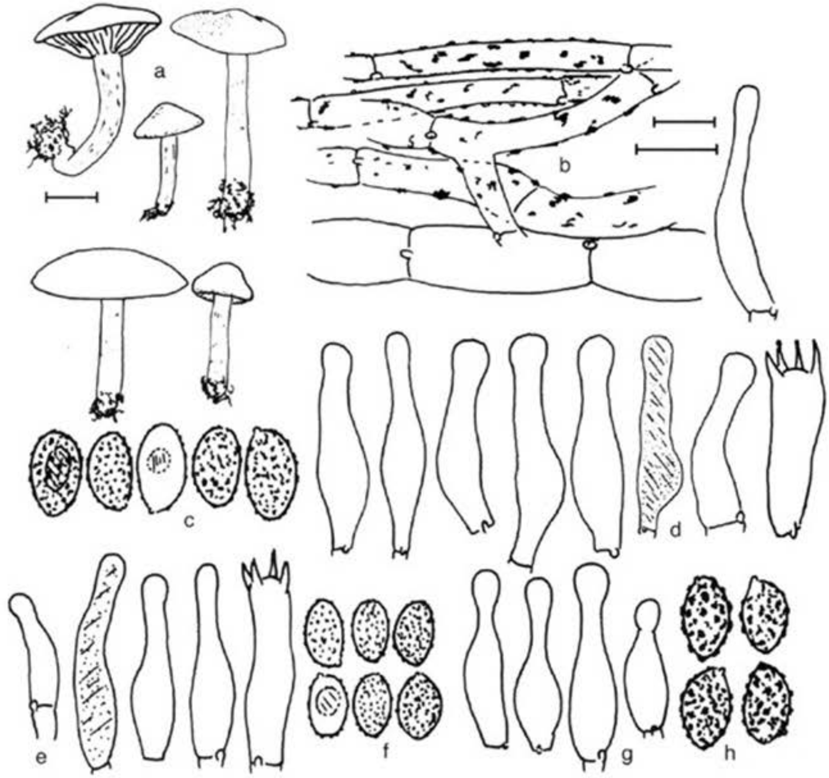


Fig. 1. *Gymnopilus arenophilus* (Holotype). a. Fruit-bodies; b. pileipellis; c. spores; d. cheilocystidia and one basidium. — *Gymnopilus penetrans* (AH 19899). e. Cheilo-, pleurocystidia and one basidium; f. spores. — *Gymnopilus fulgens* (AH 30751). g. Cheilocystidia; h. spores. Scale bars: 1 cm for fruit-bodies, 10 μm for microscopical characters (small bar), except spores (large bar).

Habitat & distribution — Gregarious, humicolous, saprotrophic, on sandy soil of thermophilous *Pinus* forests (*P. pinea*, *P. pinaster*), sometimes attached to woody chips buried in the sand, or in some cases to charcoal and burned woody debris; known from acid soils up to now.

Material studied. SPAIN: Segovia, Sebúlcor, pinar de Sebúlcor, 2.XI.1994, *M. Heykoop & S. Gómez Busutil* (AH 19157); Sevilla, Aznalcázar, pinar de Aznalcázar, 2.XII.2000, *L. Alcoba & A. Ortega* (GDA 47384; holotype, isotype in AH 30900); idem (GDA 47385, GDA 47386); ibidem, 19.I.2001 (GDA 47387); ibidem, 20.XI.2002 (GDA 47388); Sevilla, El Madroño, 29.X.2002, *L. Alcoba & A. Ortega* (AH 30901).

Comparative material examined.

Gymnopilus penetrans (Bull.) Murrill. SPAIN: Avila, Casavieja, 26.XI.1995, on woody debris of *Pinus pinaster*, *M. Villarreal* (AH 19989).

Gymnopilus fulgens (J. Favre & Maire) Singer. SPAIN: Guadalajara, Aldeanueva de Atienza, near river Pelagallinas, 6.IX.2003, among *Sphagnum* and other mosses, in peaty soil in *Pinus sylvestris* forests, *F. Esteve-Raventós* (AH 30751).

The most important diagnostic characters of this new species are its large spores and arenicolous, subcarbonicolous habitat. There are not many species of *Gymnopilus* reaching the spore measurements of *G. arenophilus* in Europe, especially in those devoid of a membranous annulus (subgenus *Gymnopilus*, according to Hesler, 1969 and Bon & Roux, 2002). In a recent classification of *Gymnopilus* proposed by Guzmán-Dávalos & Guzmán (1995), *G. arenophilus* would have to be included within section *Macrospori* Guzm.-Dáv. (species with spores 8–11(–12) μm in length).

However, according to its macroscopical characters, *G. arenophilus* resembles *G. penetrans* (Fr.) Murrill sensu lato (incl. *G. sapineus* (Fr.) Maire and *G. hybridus* (Bull.) Maire, see Høiland (1990)); in fact, both species may share the brown-ferrugineous spots on the lamellae, and show similar colours, pileus surface and habit. *Gymnopilus penetrans*, however, is strictly lignicolous, normally fructifying on conifers logs or wood chips, its taste is strongly bitter and the spores are much smaller, measuring 7–8.5(–9) × 4.5–5.5 μm (Fig. 1f). Also, pleurocystidia are commonly present in *G. penetrans* complex (Robich, 1989), whereas they seem to be absent in the new species.

Some European authors, e.g. Bon & Chevassut (1989), have probably described *G. arenophilus* previously under the name *G. fulgens*; the description given of *G. fulgens* by these authors fits perfectly *G. arenophilus*: the spores are large, no pleurocystidia have been observed, the habitat agrees and the taste is said to be slightly bitter. In the same way, Gómez-Busutil et al. (1996) misidentified *G. arenophilus* with *G. fulgens*, owing to the large spores which did not fit within the range of *G. penetrans*. According to the recent monographical study of Bon & Roux (2002), *G. fulgens* is considered a strictly hygrophilous species, bound to peat bogs (which is the original sense of Favre & Maire, 1937); however, in the past, *G. fulgens* has also been considered an arenicolous or carbonicolous taxon, found in dunes or burned soils (Orton in Watling & Gregory, 1993). In fact, a comparison of spore ornamentation of Spanish collections of *G. arenophilus* and *G. fulgens*, has revealed important differences, as *G. fulgens* shows spores with rather coarse and prominent warts, partially connected forming crests (Fig. 1h), whereas in *G. arenophilus* the warts are lower, not so coarse and hardly connected (Fig. 1c).

Romagnesi (1976, 1979) described some new species collected in southern Europe; among these, *G. pseudofulgens* was described as a carbonicolus taxon with long amygdaliform spores (9–11 × 5–5.5 μm), showing a hilar plage and a *Galerina*-like habit. *Gymnopilus spadiceus* has large spores (8–10 × 4.5–6.5 μm), stout basidiomata (2.5–8 cm in pileus diameter), a squamose, dark brown-chestnut pileus, and capitula of cystidia rather wide (5–8 μm).

Moreno (1980) described *G. fulgens* var. *luteicystis* based on the yellow contents of cystidia; this character is rather variable in many species of this genus and seems to lack any taxonomical significance; in his description the spores are said to be amygdaliform, 7–8.5 × 4–5 μm, cystidia not capitate and the carpophores are fasciculate.

Growing on sandy soils in North America, *G. arenicola* Hesler differs from *G. arenophilus* in the smaller spores (7–8 × 3.5–4.5 μm), absence of veil, presence of pleurocystidia and mild taste (Hesler, 1969). Another species with rather large spores, size 7.2–9.6(–10.4) × 5.6–7.2 μm, was described from Mexico by Guzmán-Dávalos (1995) as *G. subfulgens*; it is also characterized by the strongly verrucose, widely ellipsoid to subglobose spores, reddish orange-brown pileus, and lignicolous habitat, characters that strongly differ from those of *G. arenophilus*.

ACKNOWLEDGEMENTS

Both authors wish to thank the 'Programa de Investigación del Corredor Verde del Guadiamar (Picover)' of the Junta de Andalucía, for the support given through the agreement no. 12. Also to the curators at AH (Dr. F.J. Rejos) and GDA (Dr. E. Linares-Cuesta) for their help and collaboration in supplying vouchers.

REFERENCES

Bon, M. & G. Chevassut. 1989. Agaricomycetes de la region Languedoc-Cevennes (4ème partie). Doc. Mycol. 19 (75): 25–46.

Bon, M. & P. Roux. 2002. Le genre Gymnopilus P. Karst. in Europe. Fungi non Delineati XVII: 1–52.

Cabezudo, B., A.V. Pérez-Latorre, P. Navas, D. Navas & Y. Gil. 2003. Vegetación de la cuenca del Guadiamar: bases para su conservación y restauración. In: C. Montes, J.M. Arenas & F. Borja (eds.), Ciencia y Restauración del rio Guadiamar. PICOVER 1998–2002. Consejería de Medio Ambiente. Junta de Andalucía: 352–369.

Dennis, R.W.G. 1970. Fungus flora of Venezuela and adjacent countries. Kew Bull., Addit. Ser. 3.

Esteve-Raventós, F., M. Villarreal, J.M. Barrasa & A. Ortega. 2001. Mycena dunicola, a striking new species from the Iberian Peninsula. Mycotaxon 80: 307–313.

Favre, J. & R. Maire. 1937. Sur un Naucoria des tourbières jurassiennes. Bull. Soc. Mycol. France 53: 267–270.

Gómez-Busutil, S., F. Esteve-Raventós, P. García Escolar & M. Heykoop. 1996. Catálogo micológico preliminar del Parque Natural de las Hoces del río Duratón (Segovia, España) y alrededores. Bol. Soc. Micol. Madrid 21: 273–291.

Guzmán-Dávalos, L. 1994. New species of Gymnopilus (Agaricales, Cortinariaceae) from Mexico. Mycotaxon 50: 333–348.

Guzmán-Dávalos, L. 1995. Further investigations on Gymnopilus (Agaricales, Cortinariaceae). A new section and a new species from Mexico. Mycotaxon 54: 117–124.

Guzmán-Dávalos, L. 1996. New records of the genus Gymnopilus (Agaricales, Cortinariaceae) from Mexico. Mycotaxon 59: 61–78.

Guzmán-Dávalos, L. 2003. Type studies of Gymnopilus (Agaricales) I. Mycotaxon 86: 395–423.

Guzmán-Dávalos, L. & G. Guzmán. 1986. Hongos del estado de Jalisco, VII. El género Gymnopilus (Cortinariaceae). Rev. Mex. Micol. 2: 157–185.

Guzmán-Dávalos, L. & G. Guzmán. 1991. Additions to the genus Gymnopilus (Agaricales, Cortinariaceae) from Mexico. Mycotaxon 41: 43–56.

Guzmán-Dávalos, L. & G. Guzmán. 1995. Toward a monograph of the genus Gymnopilus (Cortinariaceae) in Mexico. Doc. Mycol. 25 (98–100): 197–212.

Guzmán-Dávalos, L. & C.L. Ovrebo. 2001. Some species of Gymnopilus from Costa Rica and Panama. Mycologia 93: 398–404.

Hesler, L.R. 1969. North American Species of Gymnopilus. Mycologia Mem. 3: 1–117.

Høiland, K. 1990. The genus Gymnopilus in Norway. Mycotaxon 39: 257–279.

Høiland, K. 1998. Gymnopilus purpureosquamulosus and G. ochraceus spp. nov. (Agaricales, Basidiomycota) – two new species from Zimbabwe. Mycotaxon 69: 81–85.

Horak, E. 1989. New and additional data concerning Pyrrhoglossum and eccentric or laterally stipitate taxa of Gymnopilus (Agaricales). Opera Bot. 100: 115–129.

Migliozzi, V. & A. Ortega. 2001. Alcune Macrolepiota della sezione Macrosporae in ambiente mediterraneo. Descrizione de Macrolepiota fuligineosquarrosa, M. fuligineosquarrosa fo. psammophila, M. excoriata e M. konradii. Boll. Gruppo Micol. G. Bresadola, Trento 44 (2): 5–30.

Moreno, G. 1980. Estudios sobre Basidiomycetes I (Agaricales). Anales Jard. Bot. Madrid 36: 23–42.

Ortega, A. 2003. Estudio de la micoflora (hongos superiores) de la cuenca del Guadiamar. In: C. Montes, J.M. Arenas & F. Borja (eds.), Ciencia y Restauración del río Guadiamar. PICOVER 1998–2002. Consejería de Medio Ambiente. Junta de Andalucía: 340–350.

Ortega, A. & F. Esteve-Raventós. 2003. New and interesting species of Coprinus (Coprinaceae, Agaricales) from Andalusia (Southern Spain). Nova Hedwigia 76 (3, 4): 465–475.

Pegler, D.N. 1977. A preliminary Agaric Flora of East Africa. London, HMSO.

Pegler, D.N. 1986. Agaric Flora of Sri Lanka. Kew Bull., Add. Ser. 12.

Pegler, D.N. 1988. Revision of Agaricales of Cuba. Kew Bull. 42, 43: 1–139.

Pegler, D.N. & J.P. Fiard. 1983. Agaric Flora of the Lesser Antilles. Kew Bull., Add. Ser. 9.

Rees, B.J. 2003. Gymnopilus perplexus, a new name for G. anomalus B.J. Rees. Mycotaxon 87: 411–412.

Rees, B.J. & J.L. Ye. 1999. Pyrrhoglossum and the small-spored species of Gymnopilus (Cortinariaceae) in Eastern Australia. Aust. Syst. Bot. 12: 255–270.

Rees, B.J., D.A. Orlovich & P.B.D. Marks. 1999. Treading the fine line between small-statured Gymnopilus and excentrically stipitate Galerina species in Australia. Mycol. Res. 103: 427–442.

Rees, B.J., G.C. Zuccarello, D.A. Orlovich. 2002. Relationships between Australian and Northern Hemisphere Gymnopilus species II. A preliminary phylogeny of species of Gymnopilus and related genera based on internal transcribed spacer (ITS) region of ribosomal DNA. Mycotaxon 84: 93–110.

Robich, G. 1989. Alcuni interessanti Gymnopilus. Boll. Assoc. Micol. Bresadola 32 (5, 6): 251–263.

Romagnesi, H. 1976. Sur deux espèces nouvelles de Gymnopilus. Kew Bull. 31 (3): 443–447.

Romagnesi, H. 1979. Un Mycena et deux Gymnopilus carbonicoles. Bull. Soc. Mycol. France 95 (2): 139–147.

Seidl, M.T. 1989. A new species of Gymnopilus from Northern California. Mycotaxon 34 (1): 217–220.

Singer, R. 1969. Mycoflora Australis. Nova Hedwigia Beih. 29.

Thomas, K.A., L. Guzmán-Dávalos & P. Manimohan. 2003. A new species and new records of Gymnopilus from India. Mycotaxon 85: 297–305.

Watling, R. & N.M. Gregory. 1993. British Fungus Flora. Agarics and Boleti, 7 Cortinariaceae p.p. Royal Botanic Garden, Edinburgh.

PERSOONIA
Volume 18, Part 4, 511–587 (2005)

A REVISION OF EUROPEAN SPECIES OF LECCINUM GRAY AND NOTES ON EXTRALIMITAL SPECIES

HENK C. DEN BAKKER & MACHIEL E. NOORDELOOS

Nationaal Herbarium Nederland, Universiteit Leiden branch,
P.O. Box 9514, 2300 RA Leiden, The Netherlands;
bakker@nhn.leidenuniv.nl

This paper deals with the generic delimitation of *Leccinum* and the taxonomic and nomenclatural implications of the phylogenetic results presented in previous papers by Den Bakker et al. (2004a, 2004b). 28S nrDNA data, used in the past to answer questions concerning genus delimitation of *Leccinum*, are reanalysed. The phylogenetic inferences based on 28S nrDNA largely coincide with *Leccinum* sensu Singer. The only species that is excluded from *Leccinum* is *L. eximium*. At least one truffle-like genus, *Chamonixia*, should be included in *Leccinum*. Morphological characters proposed in the past to delimit the genus are discussed in the light of the phylogenetic results. It is concluded that there is no single diagnostic morphological character that unites species of the genus *Leccinum* and that a better sampling, and other genes that provide a finer phylogenetic resolution, are needed to reach a final answer about the genus delimitation of *Leccinum* and other genera in the Boletaceae. The second part of this paper discusses characters used in *Leccinum*-systematics in the past and contains a revision of the European species of *Leccinum* with notes on related North American species. Sixteen species are accepted for the European continent, of which one, *Leccinum albostipitatum*, is described as new to science.

In previous studies (Den Bakker et al., 2004a, 2004b, in press) we dealt with various aspects of the evolutionary ecology of the genus *Leccinum*. The phylogenetic results presented in these studies also have important taxonomic implications on various levels, ranging from family to species level. In this chapter we will discuss these taxonomic implications and present a taxonomic treatment of the European representatives of the genus, with the exception of two mediterranean species, *Leccinum corsicum*[1] and *Leccinum lepidum*[2]. Because many species occur also in North America (subsection *Leccinum* – Den Bakker et al., 2004b) or have closely related sister species on that continent (subsection *Scabra* – Den Bakker, submitted), we will also discuss, where possible, North American species in additional notes.

---

[1] *Boletus corsicus* Roll. in Bull. Soc. Mycol. France 12 (1896) 1; *Leccinum corsicum* (Roll.) Singer, Die Röhrlinge 2 (1967) 87.

[2] *Boletus lepidus* Bouchet in Essette, Bull. Trimestriel Soc. Mycol. France 80 ('1964' 1965) Atlas, pl 147; *Leccinum lepidum* (Bouchet) Quadraccia, Acad. Naz. Lincei 264 (1990) 103.

GENERIC DELIMITATION

The original genus *Leccinum* was introduced by Gray (1821) as a generic scientific name for boletes and contained species of several currently recognized genera, such as *Gyroporus*, *Boletus*, *Suillus*, *Chalciporus* and *Xerocomus*. Later the use of the name *Leccinum* has been limited to the group of fungi we now know as *Leccinum*.

Although, especially in temperate and boreal regions, species of the genus *Leccinum* are easily recognized by their prominent, squamulose stipe ornamentation, the delimitation of the genus has been a matter of discussion for decades. Smith & Thiers (1971) considered the presence of a squamulose stipe ornamentation that darkens with age diagnostic for the genus *Leccinum*. Singer (1986) considered the coarse squamulose stipe ornamentation the most important character of the genus *Leccinum*, irrespective of colour or colour changes of the squamules. According to Singer (1986) the squamules of *Leccinum* differ from those found in other boletes by the fact that the basidia, basidioles and cystidia that make up these squamules are positioned on a distinct hyphal base, while in other boletes they emerge directly from the hyphae in the cortex of the stipe. In his discussion on the delimitation of the genus *Boletus*, Singer applied an additional character to distinguish this genus from *Leccinum*. Boletes with a yellow hymenium, a squamulose stipe and a trichodermal pileipellis are considered to belong to the genus *Boletus*, while species that share the first two characters but have either a cutis-like or epithelial pileipellis are considered to belong to *Leccinum*. Surprisingly, this last character seems to be in contradiction with Singer's placement of *Leccinum crocipodium* (*L. nigrescens* in Singer, 1986) in *Leccinum*, because a strict application of his criteria would place this species, which has a trichodermal pileipellis and yellow hymenium, in *Boletus*.

Šutara (1989), in an attempt to clarify the delimitation of the genus *Leccinum*, focused entirely on the anatomy of the stipe cortex and the stipe ornamentation. According to Šutara the stipe of *Leccinum* consists of longitudinally positioned hyphae. Beneath the fertile layer composed of caulobasidia and caulocystidia, a thick (200–1000 μm) layer is present (the stipital lateral stratum) over the entire stipe that is composed of almost anticlinally positioned, non-interwoven, parallel hyphae. Usually the stipital lateral stratum disrupts at maturity of the fruit-body, which results in the typical squamulose stipe of *Leccinum*. The *Boletus*-type of the stipital lateral stratum is thin (20–80(–100) μm), does not rupture in mature fruit-bodies, its hyphae are not conspicuously anticlinally positioned, its hyphae are often interwoven and in some cases the stipital lateral stratum is gelatinized. Basically the anatomical features of the stipe lateral stratum which Šutara described are a more detailed description of the anatomical features of the stipe that were used by Singer (1986) to distinguish *Leccinum* from other genera in the Boletaceae. Šutara proposed putting all boletes with a *Leccinum*-type stipital lateral stratum in *Leccinum*. Consequently, not only taxa classically referred to *Leccinum*, but also species like *Boletus impolitus*[3], *Boletus depilatus*[4] and *Boletus fragrans*[5] belong in *Leccinum*, if the criteria of Šutara are followed.

---

3) *Boletus impolitus* Fr., Epicrisis (1838) 421; *Leccinum impolitum* (Fr.) Bertault, Bull. Trimestriel Soc. Mycol. France 96 (1980) 287.

4) *Boletus depilatus* Redeuilh, Bull. Trimestriel Soc. Mycol. France 101 ('1985' 1986) 396; *Leccinum depilatum* (Redeuilh) Šutara, Ceská Mykol. 43 (1989) 4.

5) *Boletus fragrans* Vitt., Funghi mang. (1835) 158; *Leccinum fragrans* (Vitt.) Šutara, Ceská Mykol. 43 (1989) 54.

Recently, molecular methods have been used to elucidate relationships within the Boletaceae. Binder & Besl (2000) have used partial sequences of the nuclear ribosomal large subunit (28S nrDNA) to explore phylogenetic relationships between species of *Leccinum* and genera that have traditionally been seen as transient to or possibly part of *Leccinum*. Later Bresinsky & Besl (2003) split off the genus *Leccinellum* with *Leccinum nigrescens* (Richon & Roze) Singer as type species, based on the results of the study of Binder & Besl (2000). According to Bresinsky & Besl this genus is distinguished from the other species of *Leccinum* by the presence of yellow pigments in the hymenium, a blackish or greyish discoloration of the context of the fruit-bodies when bruised and a pileus cuticle that consists of a palisade trichoderm.

Molecular data

Introduction and methods

To assess the actual support from molecular data for the delimitation of *Leccinellum* and the generic delimitations of *Leccinum* as proposed by Smith and Thiers (1971), Singer (1986) and Šutara (1989), we downloaded a large sample of 28S sequences of Boletales available on GenBank. We increased the sample size to 84 taxa, as opposed to 34 accessions in the original data set of Binder & Besl (2000). Not only did we increase the sample size of some accessions of genera that have been considered closely related to or even part of *Leccinum* (*Tylopilus*, *Xerocomus*, *Boletus* p.p.), but we also included the gasteromycete genus *Chamonixia*, since the results of Bruns et al. (1998) suggested this gasteromycete is closely related to species of *Leccinum*. We are aware of the fact that sequences submitted to Genbank can be subject to misidentification (Bridge et al., 2003; Vilgalys, 2003) and therefore results of a study based on these data have to be used with caution before using these data for taxonomic changes. Although there is a chance that part of the tree is based on wrongly identified accessions, for which we will provide likely examples below, we emphasize that re-analyzing data that have previously been used to propose taxonomic changes can provide valuable insights in the phylogenetic robustness of these data. Recently, Binder & Hibbett (2004) published a tree, based on 457 (28S nrDNA) sequences representing 333 species, of which 293 belong to the Boletales. As several sequences are not yet publicly available, we refrain from including this analysis in this chapter. We note, however, that the conclusions with regard to *Leccinum* as proposed here, do not seem to need any substantial modification based on this larger data set.

The downloaded sequences were aligned using POA (Lee et al., 2002; http://www.bioinformatics.ucla.edu/poa/POA_Online/Align.html), and adjusted by eye. Modeltest 3.4 (Posada & Crandall, 1998) and MrModeltest (Nylander, available from http://www.ebc.uu.se/systzoo/staff/nylander.html) were used to determine the least rejected model of sequence evolution. The likelihood ratio test as implemented in Modeltest and MrModeltest ($P > 0.05$) was used to select the model that was subsequently used in the Maximum Likelihood and Bayesian analyses. PAUP*4.0b10 (Swofford, 2002) was used to perform the Maximum Parsimony (MP) and the Maximum Likelihood analyses, MrBayes 3.0b4 (Huelsenbeck & Ronquist, 2001) was used to perform the Bayesian analysis. The analyses were performed as described in Den Bakker (2004b). MP bootstrap support values were calculated based on 1000 bootstrap replicates, and 1000 trees were kept per replicate.

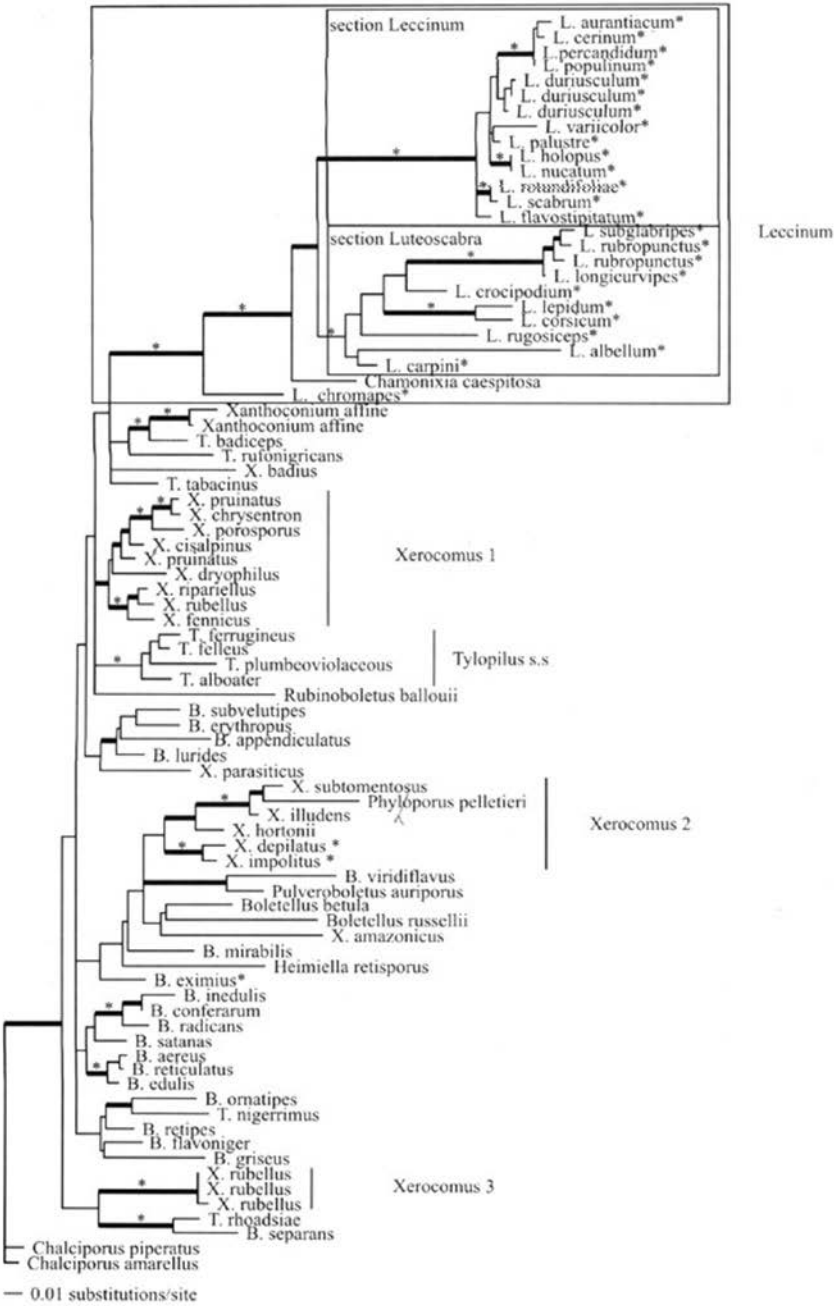

section Leccinum
L. aurantiacum*
L. cerinum*
L. percandidum*
L. populinum*
L. duriusculum*
L. duriusculum*
L. duriusculum*
L. variicolor*
L. palustre*
L. holopus*
L. nucatum*
L. rotundifoliae*
L. scabrum*
L. flavostipitatum*
section Luteoscabra
L. subglabripes*
L. rubropunctus*
L. rubropunctus*
L. longicurvipes*
L. crocipodium*
L. lepidum*
L. corsicum*
L. rugosiceps*
L. albellum*
L. carpini*
Chamonixia caespitosa
L. chromapes*
Leccinum
Xanthoconium affine
Xanthoconium affine
T. badiceps
T. rufonigricans
X. badius
T. tabacinus
X. pruinatus
X. chrysentron
X. porosporus
X. cisalpinus
X. pruinatus
X. dryophilus
X. ripariellus
X. rubellus
X. fennicus
Xerocomus 1
T. ferrugineus
T. felleus
T. plumbeoviolaceous
T. alboater
Tylopilus s.s
Rubinoboletus ballouii
B. subvelutipes
B. erythropus
B. appendiculatus
B. lurides
X. parasiticus
X. subtomentosus
Phylloporus pelletieri
X. illudens
X. hortonii
X. depilatus *
X. impolitus *
Xerocomus 2
B. viridiflavus
Pulveroboletus auriporus
Boletellus betula
Boletellus russellii
X. amazonicus
B. mirabilis
Heimiella retisporus
B. eximius*
B. inedulis
B. conferarum
B. radicans
B. satanas
B. aereus
B. reticulatus
B. edulis
B. ornatipes
T. nigerrimus
B. retipes
B. flavoniger
B. griseus
X. rubellus
X. rubellus
X. rubellus
Xerocomus 3
T. rhoadsiae
B. separans
Chalciporus piperatus
Chalciporus amarellus
0.01 substitutions/site

Fig. 1 (Opposite page). 28S nrDNA phylogram with the highest posterior probability as inferred by Bayesian analysis. Thickened branches receive posterior probabilities of ≥ 95%. Branches marked with a asterisk receive a MP bootstrap support ≥70%. Taxa marked with an asterisk have been proposed to belong to the genus *Leccinum* in the past.

Results

The alignment of the sequences contained 947 sites, of which 332 were variable and 229 were parsimony-informative. The MP analysis resulted in 1902 MP trees of 1335 steps (C.I. = 0.367, R.I. = 0.687). Based on the outcome of Modeltest the Tamura-Nei (Tamura & Nei, 1993) model with invariable sites and variable sites following a gamma distribution was chosen. For this analysis the following settings were used: base frequencies A: 0.2789, C: 0.2089, G: 0.2769, T: 0.2344; substitution rates A↔C: 1, A↔G: 2.9695, A↔T: 1, C↔G: 1, C↔T: 8.1475; G↔T: 1; assumed proportion of invariable sites = 0.4761; shape parameter $\alpha = 0.4828$. The ML analysis resulted in one tree of *-ln* L score 8021.60869. For the Bayesian analysis the general-time reversible model (Rodríguez et al., 1990) was used.

Fig. 1 shows a phylogram in which the results of the phylogenetic analyses are summarized. With respect to the position of *Leccinum* the trees obtained from the different analyses did not differ. Almost all species that were placed in *Leccinum* by Singer (1986) are found in a well-supported clade, except for *Boletus eximius*[6]. *Boletus eximius*, a species that has a strongly squamulose stipe ornamentation, differs from species of *Leccinum* by the overall dark purplish colour of its fruit-body.

Remarkably, the branches that form the *Leccinum* clade are all long in comparison to other Boletales in the phylogram, which could indicate that some of the accessions are wrongly placed in *Leccinum* because of a phenomenon called long-branch attraction (Felsenstein, 2004). Mainly phylogenies based on a MP optimalisation are susceptible to this phenomenon (Felsenstein, 2004). However, the fact that more or less the same topology is also recovered under ML and Bayesian optimalisation criteria pleas against long-branch attraction.

Although the genus *Leccinum* is represented as a well-supported clade, 28S seems to lack sufficient information to resolve the phylogeny of the Boletales. A putative sistergroup to *Leccinum* can therefore not be assigned. According to this phylogram *Leccinum* is a north-temperate genus with several species in Australasia (mainly in sect. *Roseoscabra*) and Central America. Various species in *Leccinum* have been described from tropical Africa (Heinemann, 1964), but the delimitation from tropical African species of *Tylopilus* in still unclear (Th.W. Kuyper, pers. comm.). No molecular data are available of these species and their position can therefore not be assessed. A phylogenetic analysis of tropical African species that have been described in *Leccinum* and *Tylopilus* is urgently needed.

Discussion

Morphological distinction of *Leccinum* from other boletes seems to be difficult, even if we omit the recently derived sequestrate genera *Chamonixia* and *Octavianina*.

---

[6] *Boletus eximius* Peck, J. Mycol. 3 (1887) 54; *Tylopilus eximius* (Peck) Singer, Am. Midl. Naturalist 37 (1947) 109; *Leccinum eximium* (Peck) Singer, Persoonia 7 (1973) 319.

In Europe species of the genus *Leccinum* can be recognized by the combination of the following characters: a squamulose stipe ornamentation, pores that are either brownish, whitish or yellowish (not reddish as in *Boletus erythropus*[7]), and, if the hymenium contains yellowish pigments, the context of the stipe usually discolours greyish or blackish when bruised.

According to the phylogram depicted in Fig. 1, *L. chromapes*[8] is sister to the remainder of *Leccinum* plus *Chamonixia*. Its taxonomic position is still doubtful. Halling & Mueller (2003) considered it a member of *Tylopilus*, at the same time treating another species closely resembling it as *Leccinum cartagoense*[9]. Curiously, in the cladogram produced by Binder & Hibbett (2004) *Tylopilus chromapes* (AF139709) belongs to the *Leccinum* clade, while accession AY612834 is placed in a clade with various other *Tylopilus* species. Evidently, the taxonomic identity of both accessions needs to be determined before the position of *L. chromapes* can be elucidated.

The sequestrate (truffle-like) *Chamonixia caespitosa*[10] is nested within *Leccinum*. In the MP analysis it is found in a strongly supported clade with amongst others *L. corsicum*, *L. crocipodium* and *L. pseudoscabrum*. The ML and Bayesian analyses do not support this placement and place *Chamonixia* basal to the clade containing sections *Leccinum* and *Luteoscabra*. Analyses of mtDNA (Bruns et al., 1998) and chemotaxonomic evidence (the presence of the cyclopentenones gyrocyanin and gyroporin) is consistent with such a placement (Gill & Steglich, 1987). Remarkably this is not the only sequestrate genus that is derived from a *Leccinum*-like ancestor. Binder (1999) and Binder & Hibbet (2004) showed (based on the phylogenetic analysis of 28S-sequences) that *Octavianina* is also nested within *Leccinum*. These sequences are at present not yet available on Genbank, making it impossible to reassess their phylogenetic position. The phylogenetic position of these sequestrate genera implies that the evolutionary step from a normal fruit-body to a truffle-like fruit-body is a relatively small one. Evidence for such rapid evolutionary transitions from boletoid and agaricoid ancestors to sequestrate taxa is not uncommon (Bruns et al., 1989; Peintner et al., 2001; Miller et al., 2001; Binder & Bresinsky, 2002). Interestingly, both *Chamonixia* and *Octavianina* have ornamented spores, while *Leccinum* has without exception smooth spores. A taxonomical consequence of the phylogenetic placement of *Chamonixia* (and maybe *Octavianina)* in the *Leccinum* clade could be to sink these sequestrate taxa in *Leccinum*. Other options would be to remove *L. chromapes* from *Leccinum* or to subdivide the genus *Leccinum* into smaller genera. However, lack of sufficient resolution of the cladogram and different results from the MP, ML and Bayesian analyses make it hardly recommendable to propose taxonomic changes for the time being.

Apart from *Chamonixia*, *Leccinum* consists of two clades that have been known as sect. *Luteoscabra* and sect. *Leccinum*. The MP analysis showed high bootstrap support

---

7) *Boletus erythropus* Pers., Observ. mycol. 1 (1796) 23 : Fr.; *Boletus luridus* ß [var.] *erythropus* (Pers. : Fr.) Fr., Syst. mycol. 1 (1821) 391.

8) *Boletus chromapes* Frost, Bull. Buffalo Soc. Nat. Sci. 2 (1874) 105; *Tylopilus chromapes* (Frost) A.H. Sm. & Thiers, Boletes Michigan (1971) 92; *Leccinum chromapes* (Frost) Singer, Am. Midl. Naturalist. 37 (1947) 124.

9) *Tylopilus cartagoensis* Wolfe & Bougher, Austral. Syst. Bot. 6 (1993) 191; *Leccinum cartagoense* (Wolfe & Bougher) Halling & G.M Muell. in Halling, Kew Bull. 54 (1999) 747.

10) *Chamonixia caespitosa* Rolland, Bull. Soc. Mycol. France 15 (1899) 73–78.

(77%) for the clade that largely coincides (if we do not consider the sequestrate genera) with section *Luteoscabra* Singer (1947). The posterior probability of this clade is less than 90 %, which may indicate that the strong MP bootstrap support might be caused by long-branch attraction and may falsely suggest a monophyletic (natural) group. The only difference with the original section *Luteoscabra* is that, as already indicated by Lannoy & Estades (1995), species like *L. pseudoscabrum* and *L. albellum*[11] also belong to this clade. Bresinsky & Besl's genus *Leccinellum* overlaps with the *Luteoscabra* clade found in this analysis, consisting of *L. pseudoscabrum*, *L. albellum* and *L. crocipodium* and related species, but for unclear reasons they exclude *L. subglabripes*[12], *L. rubropunctum*[13] and *'Boletus' longicurvipes*[14] from *Leccinellum*, thereby leaving the genus *Leccinellum* paraphyletic. Also from a morphological point of view we do not think there are grounds for assuming that *Leccinellum* as defined by Bresinsky & Besl forms a monophyletic group that can be discriminated from other boletes by one or more diagnostic characters. Moreover, the 28S data seem to be insufficient or even contradictory for the recognition of *Leccinellum* as a distinct genus. Taking monophyly of a genus as an essential criterion for generic recognition, our delimitation of the genus will be more or less congruent with that of Singer (1986).

The group of North American species (*B. longicurvipes*, *B. rubropunctus*, *B. subglabripes* and *B. hortonii*[15] in the analysis) that has previously been classified as *Boletus* section *Pseudoleccinum* by Smith & Thiers (1971) seems to pose a problem. Species of this section have a squamulose stipe ornamentation, a yellowish hymenium, but do not show the blackish/greyish discoloration of the context that is found in European species of *Leccinum* with a yellowish hymenium. The 28S analysis indicates that *B. longicurvipes*, *B. rubropunctus*, and *B. subglabripes* are well nested within *Leccinum* and should therefore be considered species of *Leccinum*. *Boletus hortonii* on the other hand, even though morphologically very close, is found in a clade together with species of *Xerocomus*, *B. impolitus* and *B. depilatus*. While molecular data put most of the species of section *Pseudoleccinum* in *Leccinum*, chemotaxonomic data (the presence of the pulvinic acid derivatives xerocomic acid and variegatic acid) suggest a relationship with *Boletus* and not with *Leccinum* (Gill & Steglich, 1987). To what extent these molecular and chemotaxonomic results are influenced by misidentifications and other errors in sequence databases remains to be investigated.

INFRAGENERIC DELIMITATION

Given the generic delimitation discussed above, the three main monophyletic groups correspond largely to the subdivision in sections by Singer (1986), being (1) section

---

[11] *Boletus albellus* Peck, Rept. N.Y. State Mus. 41 (1889) 149; *Leccinum albellum* (Peck) Singer, Mycologia 37 (1945) 799.

[12] *Boletus subglabripes* Peck, Bull., New York State Mus. Nat. Hist. 8 (1889) 112; *Leccinum subglabripes* (Peck) Singer, Mycologia 37 (1945) 799.

[13] *Boletus rubropunctus* Peck, Rep. New York State Mus. Nat. Hist. 50 (1898) 109; *Leccinum rubropunctus* (Peck) Singer, Amer. Midl. Naturalist. 37 (1947) 117.

[14] *Boletus longicurvipes* Snell & A.H. Sm., J. Elisha Mitchell Sci. Soc. 56 (1940) 325.

[15] *Boletus hortonii* A.H. Sm. & Thiers, Boletes Michigan (1971) 319; *Leccinum hortonii* (A.H. Sm. & Thiers) Hongo & Nagas., Rep. Tottori Mycol. Inst. 16 (1978) 50.

Roseoscabra (type species *L. chromapes*) – if indeed best classified in *Leccinum*, (2) section *Luteoscabra* (type species *L. nigrescens* = *L. crocipodium*) and (3) section *Leccinum* (type species *L. aurantiacum*). In Europe especially section *Luteoscabra* and *Leccinum* are important, species of section *Roseoscabra* are mainly found in Australasia and North and Central America (Wolfe & Bougher, 1993; Halling & Mueller, 2003). In the infrageneric classification of Smith et al. (1967) and Lannoy & Estades (1995), section *Roseoscabra* is lacking, either because it is considered a section of *Tylopilus*, as is the case in Smith et al. (1967), or simply because the subdivision is completely based on the European taxa as in Lannoy & Estades (1995).

Taking into consideration the molecular phylogenetic results of Den Bakker et al. (2004a, b), three subclades can be recognized within section *Leccinum* and these are treated here as subsections. This infrageneric subdivision will also be followed in the treatment of the genus in the Flora agaricina neerlandica:

(1) Subsection *Leccinum*. Pileus margin, especially in young fruit-bodies, consisting of irregularly disrupted flaps (see Fig. 5). Usually species in this group show a blackish or greyish discoloration of the context when bruised.
(2) Subsection *Fumosa* A.H. Sm., Thiers & Watling. Pileus margin entire (see Fig. 10), context usually discolouring greyish when bruised. Note, however, that according to our observations this reaction can be present or absent in individual fruit-bodies of the same species. Generally species of this subclade are associated with species of *Populus*.
(3) Subsection *Scabra* Pilát & Dermek. Pileus margin entire, greyish or blackish discoloration of the context is lacking. According to our data species of this section are exclusively associated with *Betula*, though some authors (Lannoy & Estades, 1995) claim that some species can also be associated with *Salix*.

SPECIFIC DELIMITATION

In the Flora agaricina neerlandica a strictly morphological species concept is used (Kuyper, 1988). In this sense Van Steenis' (1957) statement is followed: a 'good' species differs in at least two, independent morphological characters. However, from Kuyper's essay it can be deduced that we are not dealing with a typological view, but that actually the use of the morphological species concept should be seen as a hypothesis of what the boundaries of 'natural' species (biological (Mayr, 1957) or evolutionary species (Simpson, 1951; Wiley, 1978) are. Here we use the term 'natural' species for species as individuals in a philosophical sense, i.e. we assume that species exist in nature, independent of our ability to recognize them, and that species are able to evolve and speciate. This is in contrast to a strict typological species concept where species are more or less considered natural kinds, constructions of the human mind, without any necessary real existence, and evolution of the taxon is only possible when this results in a new class (species). Because we are not only interested in recognizing species, but also in their ecology and their evolutionary history, we consider species individuals. As such we see a taxonomy based on morphology as a hypothesis of what the boundaries

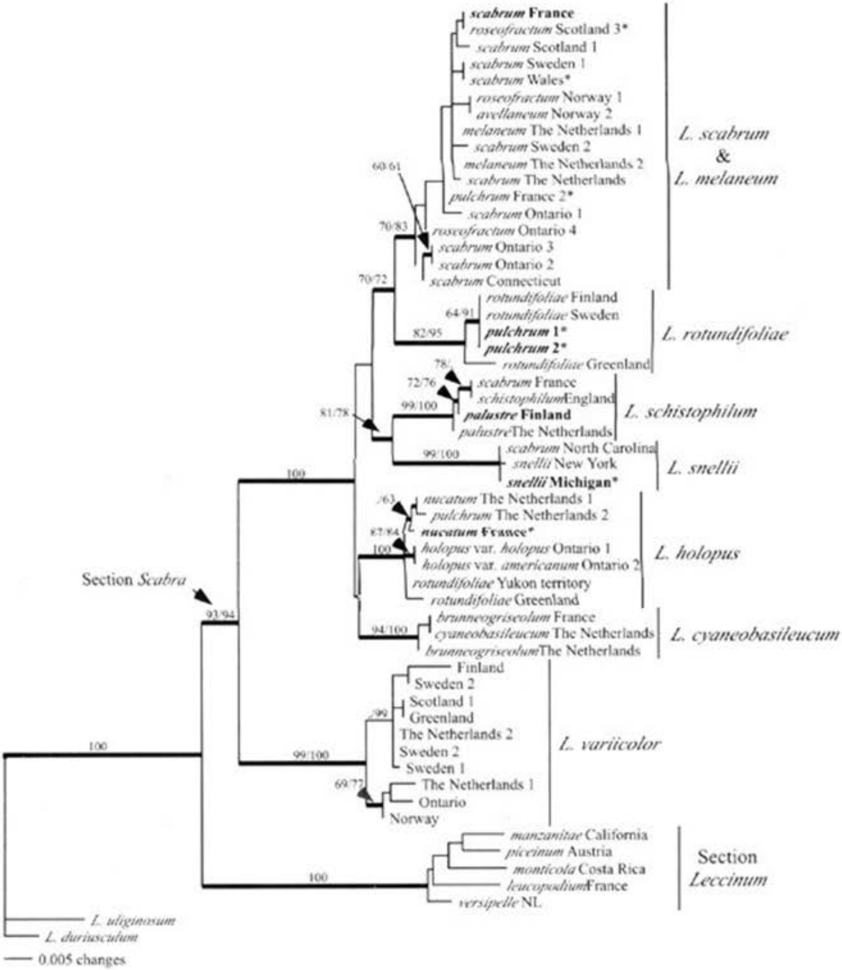


Fig. 2. One of 84 ML trees based on *Gapdh* data. Individual accessions are named with the traditional morphological criteria (Lannoy & Estades, 1995, Smith & Thiers, 1971) to the left, and to the right the accepted names are given as a result of the current species concept. Thickened branches receive posterior probabilities of ≥ 95%. Grey thickened branches receive posterior probabilities between 90-95%. Values above clades indicate MP bootstrap values, values on the left side of the slash indicate the bootstrap value calculated when partial sequences are included, on the right site bootstrap values when the partial sequences are excluded (see Den Bakker et al., 2005). Bootstrap values < 60% are not indicated. Type-accessions are printed bold.

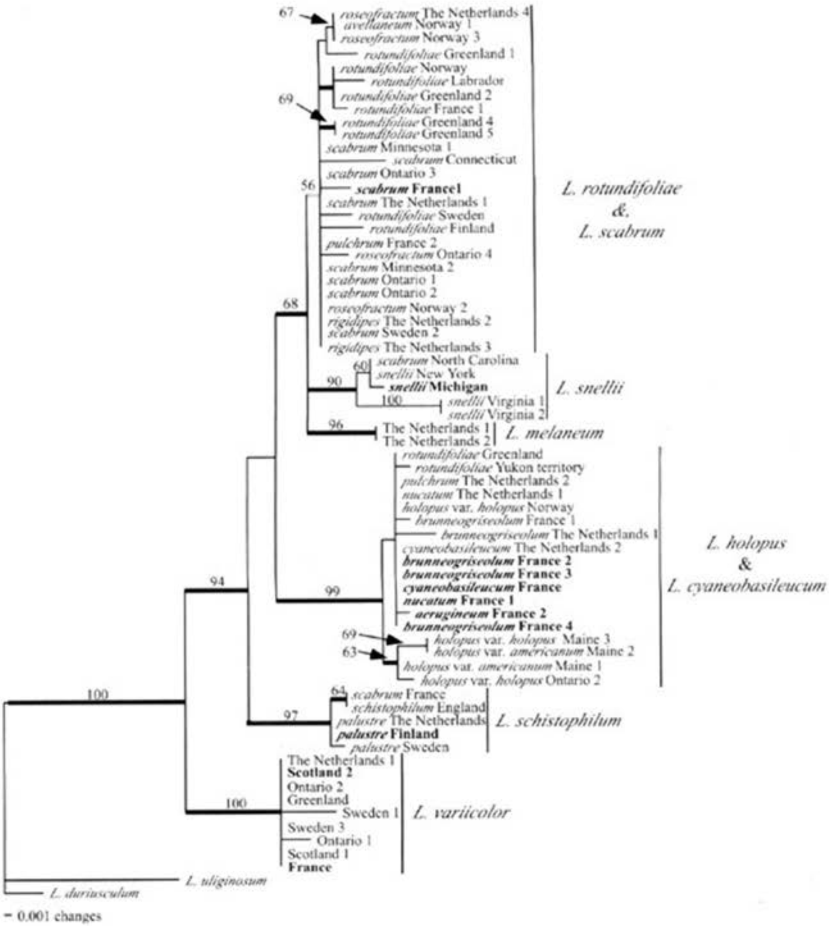


Fig. 3. ML tree based on ITS2 sequences. Individual accessions are named with the traditional morphological criteria (Lannoy & Estades, 1995, Smith & Thiers, 1971) to the left, and at the right the accepted names are given as a result of the current species concept. Thickened branches receive posterior probabilities of ≥ 95%. Grey thickened branches receive posterior probabilities between 90 and 95%. Values above clades indicate MP bootstrap values, values < 50% are not indicated. Type-accessions are printed bold.

of species as individuals are. Additional information from for instance breeding experiments and molecular phylogenies can be used to adjust the hypothesis about boundaries of species.

Combining biological (breeding experiments), evolutionary (molecular phylogenies) and phenetic (morphology) data in one species concept is by no means easy. Aanen & Kuyper (2004) described their approach in arriving at an operational species concept in the *Hebeloma crustuliniforme* complex. Their approach involved the use of a phenetic concept that is at least consistent with biological criteria (intercompatible collections should not be classified as different species) and evolutionary criteria (species that turn out to be polyphyletic should be rejected). In the case of *Leccinum*, a similar approach to arrive at consistency between phenetic and evolutionary data was used. It is important to reassess the status of morphospecies if molecular data show that the morphospecies is clearly polyphyletic.

Basically two classes of explanations for polyphyletic morphospecies can be distinguished. The first class of explanations are biological causes for polyphyly, like hybridisation. The second class of explanations is that we are actually dealing with artificial species (natural kinds) and that the morphological character states that are considered diagnostic for such a taxon fall within the phenotypic variability of more than one species. Careful reassessment of other morphological characters usually shows that other characters are indicative for the monophyletic groups that can be considered species.

Regarding the names of these groups, type specimens were used as reference points and if more than one type specimen was present in a monophyletic species, the classical nomenclatural rules with respect to priority and synonymy of names were applied.

Practical application

The practical application of the operational species concept as practised here will be illustrated with the examples of *L. scabrum*, *L. holopus* and *L. pulchrum* and two gene trees (Figs. 2, 3). In these trees the individual accessions are named on the basis of traditional morphological criteria (Lannoy & Estades, 1995) to the left, and to the right the accepted names are given as a result of the current species concept.

Leccinum scabrum

Traditionally, *L. scabrum* is considered a *Betula*-associate with a blackish stipe ornamentation and a brownish pileus. The most important diagnostic criterion, however, is the fact that the context does not change colour when bruised or becomes at most a little pinkish. The gene trees (Figs. 2, 3) show that accessions named *L. scabrum* are found in three well-supported clades in the *Gapdh* tree (the *L. snellii*[16] clade, the *L. schistophilum* and the *L. scabrum*/*L. melaneum* clade) and in one well-supported clade (*L. snellii* clade) and one weakly supported clade (*L. scabrum*/*L. rotundifoliae*) in the ITS2 tree.

As indicated above, the polyphyly of *L. scabrum* can mean two things, either *L. scabrum* is an artificial species or *L. scabrum* is a 'real' taxonomic entity and the characters that are generally considered diagnostic for the species need to be reconsidered. Of course there is a trivial third alternative explanation, viz. that the whole clade constitutes just one very variable species. However, patterns of morphological differences, correlated with molecular divergence, militate against that solution. In the case of *L. scabrum* the second option was chosen. The accessions that were named *L. scabrum* but were placed in the *L. snellii* and *L. schistophilum* clade were not microscopically different from accessions of these species that showed a typical (bluish and pinkish) discoloration of the context. Therefore it can be concluded that characters based on discoloration of the context cannot be used to discriminate *L. scabrum* from some (atypical) forms

---

[16] *Leccinum snellii* A.H. Sm., Thiers & Watling, Michigan Bot. 6 (1967) 120, Figs. 3, 4.

of other species. Morphological comparison of accessions of the *L. snellii*, *L. schistophilum* and the *L. scabrum/L. melaneum* clade in the *Gapdh* tree showed that mainly microscopical characters (pileipellis structure, spore shape and caulocystidia) can be used to distinguish accessions of these clades from each other (see key).

Leccinum holopus

Both the *Gapdh* (Fig. 2) and the ITS2 gene tree (Fig. 3) show a monophyletic clade for *L. holopus* and both trees suggest that the eastern North American accessions form a monophyletic group on their own. Morphologically, however, there is no character that can be used to tell accessions of the North American clade apart from European collections, and therefore, because basically a morphological species concept is used, this clade cannot be considered a species on its own.

Leccinum pulchrum

Specimens identified as *L. pulchrum* are found in three monophyletic clades in the *Gapdh* tree: one accession is in the *L. scabrum* clade, the accessions of the type material are found in the *L. rotundifoliae* clade and one accession designated as *L. pulchrum* is found in the *L. holopus* clade. For this reason we see *L. pulchrum* as circumscribed by Lannoy & Estades (1995) as an artificial taxon. The morphological characters (mainly the pileus colour and the discoloration of the context when bruised) on which the identification of *L. pulchrum* is based are apparently not diagnostic for a molecular monophyletic taxon. Based on the sequence data *L. pulchrum* has to be synonymized with *L. rotundifoliae*, a boreal, subalpine and arctic taxon that has been confused with *L. holopus* in the past (hence the presence of some *L. rotundifoliae* accessions in the *L. holopus* clade in the *Gapdh* and ITS2 gene trees). These results show that the morphological variability of *L. rotundifoliae* is wider than previously understood. Re-examination of the *L. pulchrum* accessions, on the basis of a set of different characters, in the *L. holopus* and the *L. scabrum* clade showed that these fit the morphological concept of these species, and must be considered as misidentifications.

INFRASPECIFIC DELIMITATION

Most species that are delimited according to the species concept that is previously discussed show a continuous variability of morphological characters like pileus colour and discoloration of the context. In *L. holopus* we observe a different pattern. In this taxon fruit-bodies that are found in *Sphagnum* bogs or other wet acidic environments have the typical slender habitus of *L. holopus*, have pale whitish stipe squamules and do not show any noticeable discoloration, except for some tiny bluish spots in the stipe base or the basal mycelium. Fruit-bodies of the same species found in drier habitats, like marshy forest, usually have a less slender habitus (comparable to *L. scabrum*), brownish to blackish stipe squamules and pinkish to reddish discoloration of the stipe context and a green bluish discoloration in the stipe base. In Europe the latter form has been described as *L. nucatum* Lannoy & Estades. Microscopically the two forms are not distinct, neither are they in the *Gapdh* and ITS2 trees. Moreover in Europe intermediates between *L. holopus* and *L. nucatum* can be found, and therefore we do not consider *L. nucatum* of any taxonomic value. The situation in North America seems to be different. Here we find apart from the normal slender, whitish form of *L. holopus*, *L. holopus* var. *americanum* [17] Smith & Thiers (see discussion under *L. holopus* for diagnostic characters of *L. holopus* var. *americanum*). Both gene trees indicate that there is a geographical distinction between accessions of *L. holopus* from eastern North America and from Europe and the arctic regions. However, there is no relation with the varieties recognized. In North America, the varieties seem to be rather constant throughout the distribution area. We therefore think it is legitimate to recognize them taxonomically.

HYBRIDISATION AND INTROGRESSION

Two taxa seem to pose a serious problem when we apply the criterion of monophyly in at least one gene tree without this monophyly being significantly contradicted by other gene trees. The first problematic taxon is *L. cyaneobasileucum* (as *L. brunneogriseolum* in Den Bakker, 2005). This taxon is morphologically distinct from *L. holopus* in most of its microscopical and macroscopical characters. The *Gapdh* tree shows that accessions of this species form a highly supported monophyletic clade and indicates that this species diverged from *L. holopus* long before a divergence of European and North American *L. holopus* took place. Moreover, the divergence between *L. holopus* and *L. cyaneobasileucum* (1.7 to 2.3 % divergence) is comparable to the divergence between *L. scabrum* and *L. rotundifoliae* (1.5 to 2.3 % divergence), which indicates that *L. holopus* and *L. cyaneobasileucum* diverged a long time ago, given the fact that *Gapdh* evolves clock-like in *Leccinum* subsect. *Scabra* (Den Bakker, 2005). The ITS2 tree, however, shows that *L. cyaneobasileucum* is placed in the European/arctic clade of *L. holopus*. Other studies (Binder, 1999; Den Bakker et al., 2004a) show that the sequence of ITS1 of this species is also identical to that of European accessions of *L. holopus*. Considering the morphological distinctness of *L. cyaneobasileucum* and the fact that *Gapdh* seems to indicate that this taxon diverged from *L. holopus* a long time ago, we consider this taxon a species with minimal phylogenetic quality. Probably recent hybridization between *L. cyaneobasileucum* and *L. holopus* and subsequent introgression has resulted in the introduction of an *L. holopus*-ITS in the *L. cyaneobasileucum* genome.

A second problem is *L. melaneum*. Collections of this species differ mainly from *L. scabrum* in the greyish colour of the stipe. In other macroscopical and microscopical characters it is identical to *L. scabrum*. The ITS2 tree shows that *L. melaneum* accessions form a well-supported clade of their own. Visual comparison of the ITS2 sequences with other sequences of species of subsection *Scabra* showed that, besides several autapomorphic character states, a deletion that is present in *L. scabrum* and *L. rotundifoliae*, but absent in other species of subsection *Scabra* is also absent in *L. melaneum*. Given the fact that *L. melaneum* shows several molecular autapomorphic characters, we think that *L. melaneum* represents an ancient hybrid between *L. scabrum* and a *L. holopus*-like ancestor. The molecular data indicate that this taxon is evolving independently from *L. scabrum*. Strictly, if we were to apply the two character rule to *L. melaneum*, we would have to consider it a variety of *L. scabrum*. However, given its putative hybridogenic origin we prefer to give it specific status, until further molecular research has resolved its taxonomic status.

---

17) *Leccinum holopus* var. *americanum* A.H.Sm. & Thiers, Boletes Michigan (1971) 183.

REVISION OF LECCINUM

MATERIAL AND METHODS

Macroscopical and ecological characters

The discussion of the macroscopical and ecological characters is mainly based on personal observations of the authors; the descriptions of the individual species are based on our own observations, sometimes supplemented with descriptions from literature or fieldnotes and descriptions of other mycologists.

Microscopical characters

The pileipellis was studied in radial section of the pileipellis and mounted in water. All observations that are discussed are made in this way unless indicated otherwise.

Spores were mounted in demineralised water and observed under oil-immersion. Only spores from the (pileal) hymenium were used and an attempt was made to measure only mature spores. Spores were considered mature when a clearly developed, slightly (brownish) coloured spore wall was present and guttules could be observed within the spore. Sometimes extremely elongate spores ($Q > 4$) were present in the hymenium of older fruit-bodies. These are considered anomalies, probably associated with unnatural aging of the fruit-bodies. These were not included in the measurements. Circa 30 spores per collection were measured. Hymenocystidia were observed in a solution of 5% KOH. To observe caulocystidia a stipital squamule was picked from halfway the stipe with a pair of fine tweezers, mounted in a 5% KOH solution and squashed.

MACROSCOPICAL CHARACTERS

Discoloration of context

In many species the context of the pileus and stipe changes colour when exposed to the air. Traditionally the discoloration of the context has been considered an important character in the classification of *Leccinum*. The most important discolorations of the usually white context are a blackish, a bluish and/or a pinkish to reddish discoloration. Especially the pinkish-reddish and blackish discolorations of the context are often easily observed when a fruit-body is cut in half and the exposed surface is bruised with a blunt object, for instance the blunt side of a knife. Usually the discoloration starts within seconds after the context is bruised, however, the bluish discoloration can sometimes appear after several hours and is sometimes only visible in parts of the fruit-body that have already been damaged by snails or arthropods.

The absence of a blackish discoloration has been used by Lannoy & Estades (1995) as a diagnostic character of subsection *Scabra*. Although our ITS results showed that subsection *Scabra*, if defined by this character, is probably polyphyletic, *Gapdh*-data show considerable support for the monophyly of subsection *Scabra* as defined by Lannoy & Estades (1995). At the species level the intensity of the blackish discoloration seems to help with species identification within subsection *Leccinum*. The context of *L. vulpinum* darkens generally less intensively than that of related species such as *L. insigne*[18], *L. aurantiacum* and *L. versipelle*.

---

[18] *Leccinum insigne* A.H. Sm., Thiers & Watling, Michigan Bot. 5 (1966) 160. Fig. 13.

A pinkish, sometimes reddish, discoloration of the context is considered to be a diagnostic character for species within subsections *Scabra* and *Leccinum*. Smith & Thiers (1971) made a distinction in their keys between species in subsection *Leccinum* that show a pinkish discoloration before turning blackish (like *L. aurantiacum* sensu Smith & Thiers) and those that do not show a pinkish discoloration, but only a blackish discoloration (like *L. insigne*). We found that this pinkish discoloration was often lacking in species that were supposed to have it according to literature and found that usually the European species can be recognized by other, more stable characters. Watling (1970) and Lannoy & Estades (1995) considered the intensity of the pinkish discoloration a distinctive character to distinguish *L. scabrum* and related species. *Leccinum scabrum* is supposed to display no or only a slightly pinkish discoloration, while species like *L. roseofractum* are supposed to show a rapid reddish discoloration. We found samples identified as *L. scabrum* and *L. roseofractum* in one clade and could not find any phylogenetic signal that these were two distinct species. Moreover, we found that the intensity of the pinkish discoloration of the context of the accessions in this clade is a gradual one and can therefore not be used as a diagnostic character of any of these species.

A bluish discoloration is present in most species of subsections *Leccinum*, *Fumosa* and *Scabra*, except in *L. scabrum* and *L. rotundifoliae*. This blue discoloration is usually found in the cortex of the stipe base and/or in the basal mycelium, though in some species like *L. variicolor*, it is found in the cortex of the lower half of the stipe. The colour is usually blue (K. & W. 23A7) or greenish blue (24A5, 25A5). In *L. variicolor* the greenish blue discoloration usually changes to yellow in dried fruit-bodies, a phenomenon rarely observed in other species of subsection *Scabra*. The absence of the bluish discoloration is diagnostic for *L. scabrum* and *L. rotundifoliae*. However, the bluish discoloration is not always clearly observable and should therefore be used with caution.

Other colour changes of the context, such as yellow and red discolorations in the stipe base and an olivaceous discoloration in the apex of the stipe are variable within species. In particular the olivaceous discoloration in the apex of the stipe seems to be associated either with a wet growing habitat or continuous wet weather. For this reason they are considered of very limited diagnostic value.

Macrochemical reactions

Lannoy & Estades (1995) considered the reaction of the context with $FeSO_4$ and Formol to be of importance for the identification of certain species groups. When $FeSO_4$ crystals are rubbed against the context of (preferably) the apex of the stipe, a greenish grey to blackish discoloration may appear. Formol, when applied to the context, sometimes induces a pinkish to reddish discoloration of the context. The usefulness of $FeSO_4$ as a reagent for the identification of species in subsection *Scabra* has been tested. It was often found to be very gradual, and difficult to assess whether the discoloration was greyish green or greyish. Moreover, there seems to be a relation between age and humidity of the fruit-body and the intensity of the reaction with either formaldehyde or $FeSO_4$. Therefore these macrochemical reactions have not been used in the present work.

Colour of pileus and overall colour of fruit-body

The colour of the pileus has always been an important diagnostic character in *Leccinum* taxonomy. In particular new species have been based on an overall pale appearance or very pale pileus colour. Often authors considered these species as pale-coloured sister species to darker coloured species. Lannoy & Estades (1995) suggested that *L. cyaneobasileucum* is a pale form of *L. brunneogriseolum*, by indicating that it resembles the latter species except for the overall colour of the fruit-bodies. The molecular data (Den Bakker et al., 2004b, 2005) suggest that most species display a whole colour range from light to dark. Based on these findings it can be concluded that for instance *L. cyaneobasileucum* is a pale variant of *L. brunneogriseolum*, and that *L. avellaneum* and *L. roseofractum* represent the lightest and darkest limits respectively of *L. scabrum*. Also *L. roseotinctum* and *L. percandidum* are just pale-coloured forms of *L. versipelle*. In addition, molecular data show that the generally white or light-coloured species *L. holopus* may form fruit-bodies with a brown pileus and dark squamules on the stipe.

Within subsection *Leccinum*, however, there is a clear distinction between species with a dark reddish pileus colour that changes to dark reddish brown in exsiccates (like *L. aurantiacum* and *L. vulpinum*) and species with a orange-brown pileus colour that changes to light brown in exsiccates (like *L. versipelle* and *L. albostipitatum*).

Stipe squamules and stipe surface colour

While the colour of the pileus is variable in most species, the colour of the stipe surface can be useful in the identification of *Leccinum* species. Care should be taken with overall pale-coloured fruit-bodies and fruit-bodies that are found in high and dense vegetation. In the first case fruit-bodies might be from a mycelium that produces a limited amount of dark pigments, in the second case shade can prevent the formation of dark pigments (personal observation of the first author).

In subsection *Leccinum* a distinction can be made between species with a basically greyish to blackish stipe ornamentation (*L. vulpinum* and *L. versipelle*) and species with a whitish to reddish brown stipe ornamentation (*L. aurantiacum* and *L. albostipitatum*). In subsection *Scabra* most species have a greyish to blackish stipe ornamentation, with the exception of *L. holopus* var. *holopus*, which has an initially white stipe ornamentation that becomes darker in mature fruit-bodies, and *L. cyaneobasileucum*, which has an initially whitish stipe ornamentation that becomes dirty greyish in older fruit-bodies.

The shape and pattern of the stipe squamules is of diagnostic value as well, especially in subsection *Scabra*. The stipe squamules are usually fine at the apex and coarser at the base of the stipe. *Leccinum scabrum* and *L. holopus* usually have overall fine squamules on the stipe, whereas *L. cyaneobasileucum* usually has a stipe covered with coarse, flocculose squamules. While in most species the squamules are more or less conical, some species (like *L. rotundifoliae*) have more warty squamules.

The colour of the stipe surface beneath the squamules is white or whitish in most European *Leccinum* species with the exception of *L. crocipodium* with yellow background colour, and *L. melaneum* in which the surface is distinctly greyish.

Pileus surface

The pileus surface in species of subsections *Leccinum*, *Fumosa* and *Scabra* is felted to fibrillose. In subsection *Leccinum* the fibrils on the pileus surface may develop into a pattern of appressed squamules. The surface may become viscid or slightly slimy in mature and wet fruit-bodies. The surface of *L. pseudoscabrum* is often distinctly rugulose, especially when young, whereas that of *L. crocipodium* is tomentose. Both in *L. pseudoscabrum* and *L. crocipodium* the surface of the pileus usually cracks with age, especially during dry periods. Other species only show a cracked surface under extremely dry circumstances.

Pileus margin

Most species of *Leccinum* have an entire margin that, especially in younger fruit-bodies, projects a few millimeters beyond the tubes. In subsection *Leccinum* the margin of the pileus is inflexed in young fruit-bodies, becoming disrupted and appendiculate when the fruit-body ages.

ECOLOGICAL CHARACTERS

Host specificity

Host specificity is often considered an important character for taxonomy (see Den Bakker et al., 2004b for further references). Species of subsection *Scabra* are associated with *Betula*, while species of subsection *Fumosa* are associated with *Populus*. *Leccinum montanum*[19] and *L. californicum*[20] are two species of the Sierra Nevada (California, USA) associated with *Populus* (Thiers, 1975). Based on the absence of a blackish discoloration of the context and their entire pileus margin Thiers referred them to subsection *Scabra*. The habitus of these species and their association with *Populus* suggests that they are actually more closely related to species of subsection *Fumosa*. In subsection *Leccinum* species are found that are exclusively associated with *Populus* (*L. albostipitatum*), with *Betula* (*L. versipelle* and *L. atrostipitatum*[21]), with Pinaceae (*L. vulpinum*, *L. piceinum*) and with Ericaceae that form arbutoid mycorrhizas (*L. manzanitae*[22] and *L. monticola*[23]). In Europe the only species that is not host specific is *L. aurantiacum*. This species is associated with *Quercus* and other Fagaceae, *Populus* and *Salix*, *Betula* and sometimes with *Tilia*. Although many species within *Leccinum* are host specific, the use of host associations in the field as a diagnostic character is often difficult, since usually more than one host is present in the vicinity of a fruit-body.

Edaphic factors

Especially in subsection *Scabra* the acidity and the humidity of the soil appear to be important factors determining the distribution of the different species. While most species of subsection *Scabra* are found in acidic habitats, *L. schistophilum* is found in basic habitats. *Leccinium holopus* var. *holopus* is found in waterlogged *Sphagnum* vegetation, *L. holopus* var. *americanum* is found in less wet, marshy *Betula* forests. Also in wet but not waterlogged habitats species like *L. schistophilum*, *L. cyaneobasileucum*, and *L. variicolor* can be found, whereas *L. scabrum* seems to be a species of drier habitats.

---

19) *Leccinum montanum* Thiers, Mycologia 63 (1971) 274.

20) *Leccinum californicum* Thiers, Mycologia 63 (1971) 273.

21) *Leccinum atrostipitatum* A.H. Sm., Thiers & Watling, Michigan Bot. 5 (1966) 555.

22) *Leccinum manzanitae* Thiers, Mycologia 63 (1971) 226.

23) *Leccinum monticola* Halling & G.M. Muell., Mycologia 95 (2003) 493.

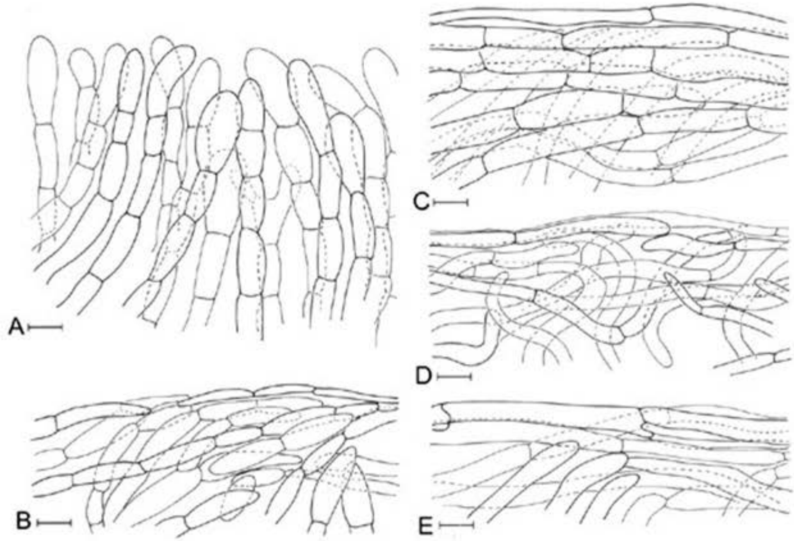


Fig. 4. Overview of pileipellis types encountered in *Leccinum* (radial sections, scale bars = 10 μm). A. A trichoderm, as found in *L. crocipodium*; B to E. cutis-like structures, named cutis in the species descriptions (B. *L. variicolor*, C. *L. versipelle*, D. *L. holopus* and E. *L. scabrum*). The pileipellis of *L. variicolor*, as depicted here, is mainly composed of so-called 'cylindrocysts'.

MICROSCOPICAL CHARACTERS

Anatomy of pileipellis

The anatomy of the pileipellis has received much attention in the taxonomy of *Leccinum* (Blum, 1970; Smith & Thiers, 1971; Lannoy & Estades, 1995). Within the genus *Leccinum*, two basic types can be recognized, viz. (1) a trichoderm of erect chains of elements, sometimes forming a palisade, typical for *L. pseudoscabrum* and *L. crocipodium* (see Fig. 4A) and (2) a complex type of intricate trichoderm, often with a cutis-like suprapellis, typical for subsections *Leccinum*, *Fumosa* and *Scabra* (Figs. 4 C, D and E). Although this cannot be considered a real cutis, and in young fruit-bodies of species of subsection *Scabra* sometimes a real trichoderm without a cutis-like suprapellis can be observed, we will for convenience call this type of pileipellis a cutis in the species descriptions. Particular in subsection *Scabra* pileipellis structures appear to be rather variable. Lannoy & Estades (1995) considered the presence or absence of so-called cylindrocysts in the pileipellis an important character for certain species in subsection *Scabra*. They defined cylindrocysts as hyphal elements that are maximal 80 μm long and minimal 10 μm wide and have length/width ratio of less than 4. According to Lannoy & Estades the presence of cylindrocysts is diagnostic for their subsection *Pseudoscabra*.

The present study revealed that the occurrence of cylindrocysts is not consistently correlated with the current species concept. Furthermore, no indication was found that subsection *Pseudoscabra* forms a natural group. Species with and without cylindrocysts have been synonymised (*L. rigidipes* and *L. scabrum*, *L. aerugineum* and *L. holopus*). However, in some species, like *L. variicolor* and *L. cyaneobasileucum* cylindrocysts are usually abundant, and may facilitate identification.

Pigmentation of pileipellis

The pigmentation of the pileipellis elements can be granularly incrusted, plaque-like incrusted or vacuolar. The pigmentation type varies within species. Certain pigmentation types occur more frequently in certain species. For instance the pileipellis elements of *L. schistophilum* and *L. aurantiacum* are often plaque-like incrusted. The colour of the pigments observed usually corresponds to the overall colour of the pileus. Smith et al. (1967) and Watling (1970) introduced another character for discriminating species in subsection *Leccinum*, viz. the capacity of the pigments to form globules when the pileipellis is mounted in Melzer's reagent. This reaction did not appear to be constant within species, and could not be used as diagnostic character.

Spore size and spore shape

Spore shape appeared to be a better diagnostic character than spore size in discriminating species. In subsection *Leccinum* the mean Q-value (length : width ratio) varies between 3.1 and 3.5, and in subsection *Scabra* between 2.7 and 2.8, with the exception of the European collections of *L. scabrum* and *L. cyaneobasileucum* in which a mean Q-value of 3.0 and 3.2 was observed. In the collections of *L. scabrum* from eastern North America the mean Q-value was 2.8. Since the mean Q-value was observed to be constant in the species of subsection *Scabra* in Europe, this could be used as an additional character.

Hymenocystidia

Hymenocystidia in the tubular hymenium (pleurocystidia) are usually lageniform. The hymenocystidia found on the pore surface (cheilocystidia) have various shapes, being either clavate, utriform or lageniform. In subsection *Leccinum* the cheilocystidia usually have a brownish content. Size and shape of hymenical cystidia were found to be of no diagnostic value.

Caulocystidia

Thus far, caulocystidia have remained relatively unstudied in *Leccinum* systematics. Smith & Thiers (1971) considered caulocystidia too variable to be of major taxonomic importance, with the exception of a certain type of caulocystidia in *L. snellii*. Smith & Thiers considered the presence of lageniform cystidia with a septum (secondary crosswall) on the transition between the swollen part of the cystidium and the neck diagnostic for this species. Examination of other species of subsection *Scabra* showed that in most species of this subsection this septate-lageniform type of caulocystidia can be found, but always in small numbers. In *L. snellii* and in *L. variicolor*, these septate-lageniform cystidia are usually common and easy to observe. This is a pattern that is seen repeatedly, as in most species in subsections *Leccinum* and *Scabra* various types of caulocystidia can be found, but in some species certain types seem to be more numerous than other types. As such caulocystidia can therefore be used as an additional character in the identification of individual species.

TAXONOMIC PART

LECCINUM GRAY

Leccinum Gray, Nat. Arr. Brit. Pl. I (1821) 646. — *Krombholzia* P. Karst., Rev. Mycol. (Paris) 3 (1881) 17, non *Krombholzia* Rupr. ex E. Fourn. 1876; *Krombholziella* Maire, Publ. Inst. Bot. 3 (4) (1935) 41. — *Trachypus* Bataille, Bolets (1908) 12, non *Trachypus* Reinw. & Hornsch. 1829. — *Leccinellum* Bresinsky & Binder, Regensb. Mykol. Schr. 11 (2003) 231.

Selected literature. Watling, Br. Fung. Fl. 1 (1970) 45–60; Lannoy & Estades, Mon. Leccinum (1995); Estades & Lannoy, Bull. Trimestriel Féd. Mycol. Daupiné-Savoie. 174 (2004) 60–73.

Basidiocarp boletoid; pileus fibrillose, tomentose or rugulose and smooth; tube layer subventricose to broadly ventricose, adnexed to narrowly adnate; pores roundish, 0.3 – 0.5 mm in diameter, whitish or yellowish. Stipe squamulose. Context whitish, in some species yellowish, discolouring greyish, bluish or pinkish when bruised, sometimes not discolouring.

Spores fusiform to broadly fusiform, smooth; cheilo- and pleurocystidia present; pileipellis an (ixo-)cutis or trichoderm; pigment in pileipellis intracellular, vacuolar, incrusting or parietal; clamp-connections absent. — Type species: *Leccinum aurantiacum* (Bull.) Gray.

Habitat & distribution — Ectomycorrhizal. Northern Hemisphere.

Note. In the nomenclator accompanying species descriptions, the combinations in *Krombholzia* and *Krombholziella* have not been listed.

KEY TO WESTERN EUROPEAN SPECIES OF LECCINUM

1a. Context almost instantly discolouring greyish to blackish when bruised 2
 b. Context not discolouring instantly greyish blackish when bruised, sometimes discolouring greyish after several hours 9
2a. Hymenium yellowish . . . . 13. *L. crocipodium*
 b. Hymenium whitish, greyish or brownish 3
3a. Margin of the pileus, especially in young fruit-bodies, overhanging with disrupted flaps, colour of pileus usually reddish brown or orange, sometimes pinkish or whitish 4
 b. Margin of the pileus entire, only slightly projecting; colour of pileus brownish . 8
4a. Stipe ornamentation whitish, brownish to reddish brown, in older specimens sometimes almost blackish; content of caulocystidia reddish brown; associated with broadleaved trees 5
 b. Stipe ornamentation brown or black, content of pigmented caulocystidia greyish, associated with Pinaceae or *Betula* 6
5a. Stipe in young fruit-bodies with reddish brown squamules, which become darker with age; pileus reddish brown, dark (reddish) brown in exsiccates
1. *L. aurantiacum*

b. Stipe in young fruit-bodies with whitish squamules, which become darker only in very mature stage; pileus orange, light brown in exsiccates
2. *L. albostipitatum*

6a. Pileus colour usually orange or brownish orange, largest caulocystidia generally utriform, fusiform, sometimes lageniform, associated with *Betula*
4. *L. versipelle*

b. Pileus brownish to reddish brown, largest caulocystidia generally clavate, associated with Pinaceae 7

7a. Pileus reddish brown, associated with *Pinus* or *Picea* . . . . 3. *L. vulpinum*

b. Pileus dull brownish, associated with *Picea*
L. piceinum (see discussion *L. vulpinum*)

8a. Surface of pileus wrinkled in young fruit-bodies; pileipellis a palisade trichoderm of broadly clavate elements, terminal elements often globose; associated with *Corylus* or *Carpinus* . . . . 4. *L. pseudoscabrum*

b. Surface of pileus never wrinkled; pileipellis a cutis with ellipsoid or filiform terminal elements; associated with *Populus* . . . . 5. *L. duriusculum*

9a. Cylindrocysts in pileipellis abundant; stipe base usually with clear greenish bluish stains 10

b. Cylindrocysts in pileipellis scarce; stipe base with or without bluish stains . . . 11

10a. Stipe squamules coarse and usually concolorous to stipe surface, forming a fibrillose dense layer; pileus evenly coloured; pileipellis elements usually easily detachable, often broad (8–15 μm); mean Q-value spores > 3.0
11. *L. cyaneobasileucum*

b. Stipe squamules fine, usually blackish, greyish and contrasting to the stipe surface; pileus often dark-coloured with lighter regions or light-coloured with darker regions; pileipellis consisting of an intricate cutis of filamentous hyphae, often with chains of cylindrocysts in the suprapellis; mean Q-value spores < 2.8
10. *L. variicolor*

11a. Stipe surface dark (greyish, blackish) almost concolorous to stipe squamules
7. *L. melaneum*

b. Stipe surface light, brownish, strongly contrasting to squamules when squamules are darkly coloured, otherwise squamules light and not contrasting to the surface
12

12a. Mean Q-value spores ≥3.0, usually large clavate caulocystidia present in caulohymenium, bluish discolorations absent in stipe base . . . . 6. *L. scabrum*

b. Mean Q-value spores < 3.0, no large clavate caulocystidia present in caulohymenium, bluish stains absent or present in stipe base 13

13a. Caulocystidia often clavate, sometimes lageniform; bluish discoloration in stipe base absent 8. *L. rotundifoliae*

b. Caulocystidia narrowly lageniform with a flexuose neck or utriform, rarely clavate; bluish discoloration in stipe base present or absent 14

14a. Stipe ornamentation composed of coarse warty or flocculose squamules; caulocystidia often narrowly lageniform with a flexuose neck; pileipellis elements with a vacuolar pigment or granualar incrustation; pileus usually whitish, light brownish, sometimes with bluish or greenish tinges . . . . 12. *L. holopus*

b. Stipe ornamentation composed of fine greyish or blackish squamules; caulocystidia often utriform, rarely lageniform with a flexuose neck; pileipellis elements often incrusted with dark plaques of pigment; pileus greyish or brownish
9. *L. schistophilum*

SECTION **LECCINUM**

SUBSECTION **LECCINUM**

Pileal margin, especially in young fruit-bodies, with appendiculate flaps. Context whitish, showing bluish, pinkish, reddish and greyish/blackish discolorations when bruised. Widely distributed throughout the Northern Hemisphere.

Type species: *Leccinum aurantiacum* (Bull.) Gray.

1. **Leccinum aurantiacum** (Bull.) Gray — Fig. 5, Plate 1

Boletus aurantiacus Bull., Herb. Fr. (1785) pl. 236; *Leccinum aurantiacum* (Bull.) Gray, Nat. Arr. Br. Pl. 1 (1821) 646. — *Boletus leucopodius* Pers., Observ. Mycol. 2 (1799) 11; *Boletus aurantiacus* ß [var.] *leucopodius* (Pers.) Pers., Syn. Meth. Fung. (1821) 504; *Leccinum aurantiacum* ß [var.] *leucopodium* (Pers.) Gray. Nat. Arr. Brit. Pl. (1821) 646; *Leccinum leucopodium* (Pers.) Dörfelt & G. Berg, Fedd. Repert. 101 (1990) 567. — *Leccinum aurantiacum* var. *quercinum* Pilát, Mushr. Other Fungi (1961) 6 (footnote) [invalid, no Latin diagnosis]; *Leccinum quercinum* (Pilát) Green & Watling, Notes Roy. Bot. Gard. Edinburgh 29 (1969) 265 [invalid, basionym not validly published]; *Leccinum quercinum* Pilát in Pilát & Dermek, Hríbovité huby (1974) 151. — *Leccinum salicola* Watling, Notes Roy. Bot. Gard. Edinburgh 31 (1971) 139. — *Leccinum populinum* M. Korhonen, Karstenia 35 (1995) 55.

Iconotype. Bulliard 1785. Herb. Fr. Pl. 236.

Epitype (designated here). France: Orne, Forêt de Bellême, 28 IX 2001, J. van Brummelen (nr. 11 + 12) (L).

Misapplication. *Leccinum rufum* sensu auct.

Excluded. *L. aurantiacum* sensu M. Korhonen, Karstenia 35 (1995) 58 (= *L. albostipitatum*); *L. leucopodium* sensu Den Bakker et al., New Phytol. 163 (2004) 201–215 (= *L. albostipitatum*).

Selected icones. Lannoy & Estades, Mon. Lecc. Europe (1995) pl. 37 (as *L. quercinum*); Korhonen, Karstenia 35 (1995) 54, fig. 1 & 2 (as *L. populinum* and *L. quercinum* respectively).

Selected descriptions. Korhonen, Karstenia 35 (1995) 55–58 (as *L. populinum* and *L. quercinum* respectively).

Characteristics — A slender to robust, medium to large *Leccinum*; pileus reddish brown, dark reddish brown in exsiccates; stipital squamules reddish in young fruit-bodies, dark reddish brown in older fruit-bodies, seldom whitish. Mycorrhizal with various kinds of broad-leaved trees (*Populus*, *Salix*, *Quercus*, *Fagus*, *Betula*, *Castanea*, *Tilia*).

Pileus 30–150 (–280) mm, truncate-conical to conico-convex or hemispherical when young, expanding to truncate conico-convex, convex or plano-convex when mature, with involute then deflexed margin, extending over tubes with distinct triangular or irregularly shaped flaps, up to 6 mm long, very evident in young specimens, and generally also in mature specimens, rarely disappearing with age; vivid red to red-brown (Mu. 2.5 YR 4/6–5/8; 10 R 3–4/3–6), towards margin sometimes more orange-yellow (7.5 YR 7/8),

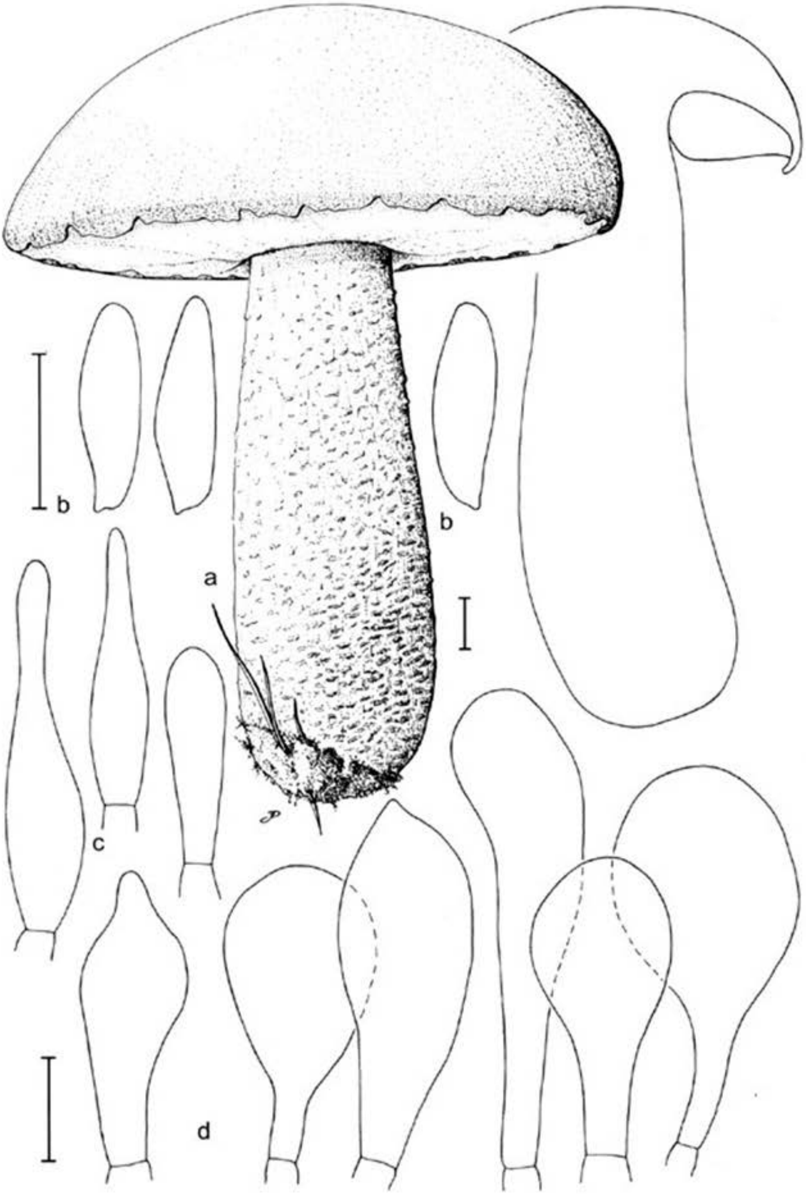


Fig. 5. *Leccinum aurantiacum*. a. Habitus; b. spores; c. hymenocystidia; d. caulocystidia. Scale bars = 10 μm resp. 1 cm.

initially finely tomentose, breaking up with age in small appressed squamules all over. Tubes adnexed to adnate, segmentiform to ventricose, 9–30 mm long, cream-white to very pale brown (10 YR 6/4). Pores c. 0.2–0.5 mm in diameter, yellowish white to very pale brown (10 YR 7/4), discolouring brownish when bruised. Stipe 50–270 × 15–50 mm, cylindrical to clavate to fusiform, whitish, often with a distinct blue discoloration at base, especially when handled, entirely covered with squamules, which are small and isolated at apex, and coarse and more dense and sometimes agglutinated towards base, initially reddish, darkening to red-brown or reddish black with age. Context white, turning violaceous grey, grey or blackish when bruised; in stipe base often turning blue-green.

Spores 12.5–18.5(–22.5) × 3.5–5.0(–6.0) μm, Q = 2.8–4.1, Q_{av}= 3.2–3.6; fusiform *with conical apex, with distinct suprahilar depression, pale, purplish brown in water.* Basidia 15 –25.0 × 6.5–10.5 μm, clavate, 2- or 4-spored. Hymenocystidia 20–45 × *5–8 μm, narrowly lageniform and hyaline in tubular hymenium, clavate or utriform* with reddish brown content on pore surface. Pileipellis an intricate trichoderm of (narrowly) cylindrical elements, terminal elements often conical or cylindrical with a mucronate apex, 30–100 × 3.0–15.5 μm, elements in suprapellis 50 – 70 × 5.5–12.5 μm, pigment in water vacuolar or in globules, larger elements often intracellularly granular incrusted, red-brown. Caulocystidia 30– 60(–90) × (6.5–)12.5–20.5 μm, clavate with acute or obtuse apex to almost spheropedunculate, rarely utriform or fusiform, often in addition small lageniform cystidia present; large cystidia usually with reddish brown content in KOH; small lageniform cystidia usually hyaline. Clamp-connections absent.

Habitat & distribution — Solitary or gregarious, ectomycorrhizal, associated with *Populus*, *Quercus* and *Betula*, rarely with *Salix*, *Fagus*, *Castanea* and *Tilia*, on mesotrophic, sandy or loamy soils; moderately common in the Netherlands, widespread in Europe.

Collections studied. THE NETHERLANDS: Drenthe, Gieten, Boekweitveen, 16 X 2000, *H.C. den Bakker 54*; Roden, 20 IX 2000, J. Wisman, *H.C. den Bakker 102*; Gelderland, Heiligenberg, 2001, J. Wisman, *H.C. den Bakker 286*; Noord-Holland, Amsterdamse Waterleiding Duinen, 14 VIII 1999, *H.C. den Bakker 3*. — BELGIUM: Namur, Oignies-en-Thiérache, 22 IX 1999, *Ruben Walleyn 1683*. — CZECH REPUBLIC: Bohemia, distr. Turnov, Masov-Sedmihorky, *H. Schmidt, PRM 521031* (holotype *L. quercinum*, PRM) – ENGLAND: Berkshire, Windsor Great Park, 2001, *A. Hills 2001219*. — FINLAND: Nylandia, Vantaa, 12 IX 1994, *M. Korhonen 11850* (holotype *L. populinum*, H). — FRANCE: Orne, Forêt de Bellême, 28 IX 2001, *J. van Brummelen (Fix. 3 + 4)*; Orne, Forêt de Bellême, 28 IX 2001, *J. van Brummelen (Fix. 11 + 12)*; Orne, Igé, 3 X 2001, *J. van Brummelen (Fix. 17 +18)*; Doubs, Forêt de Cessey, 8 X 2001, *J. van Brummelen (Fix. 19+20)*. — NORWAY: Sogn og Fjordane, Sogndal, 7 IX 2000, *H.C. den Bakker 94*. — SCOTLAND: Inverness-shire, Insh Nature Reserve, 17 IX 2001, *H.C. den Bakker 233*; Sutherland, Glaisgeo, 22 IX 1970, *Watling 7362* (holotype *L. salicola*, E).

Notwithstanding intensive molecular and morphological studies of collections (including holotypes) that were associated with *Populus*, *Quercus* and *Betula*, no clear support could be found for the recognition of *L. populinum* and *L. quercinum* as distinct species. Therefore we merge these taxa into one species, *L. aurantiacum*, with a broad host range (Den Bakker et al., 2004b). No obvious differences in spore size or in spore dimensions were found between collections that were associated with either *Populus* or *Quercus* (Fig. 6), in contrast to the observations by Korhonen (1995). Kibby (2002) indicated that the shape of the caulocystidia of *L. populinum* differs from those of *L. quercinum*. *Leccinum populinum* is supposed to have inflated, clavate caulocystidia, while the caulocystidia are usually fusiform capitate in *L. quercinum*. The present study revealed

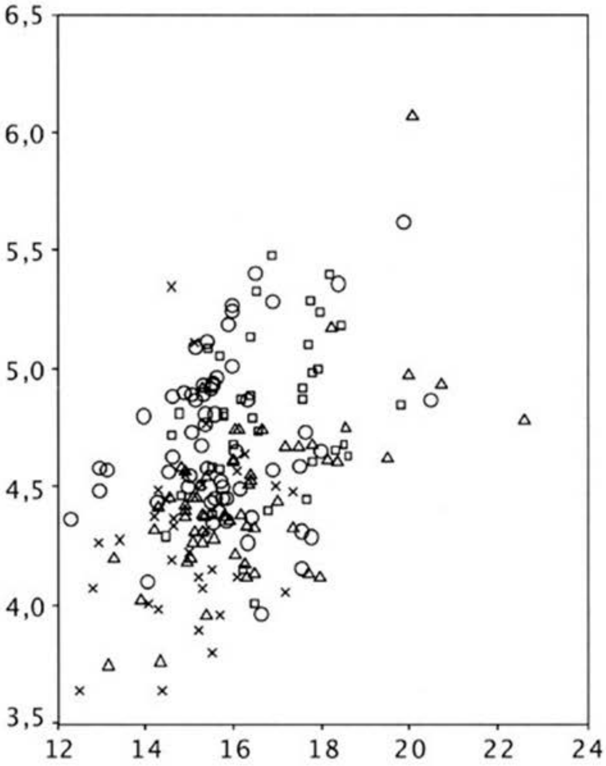


Fig. 6. Spore size in basidiocarps of of *L. aurantiacum* associated with *Populus* (Δ), *Quercus* (O), *Salix* (×) and *Betula* (□).

that caulocystidia as indicated by Kibby for *L. populinum* can be found in most collections of *L. populinum* and *L. quercinum* (including the holotype of *L. quercinum*) and that fusiform capitate caulocystidia are more rarely encountered in *Populus* or *Quercus* associated collections.

Leccinum salicola Watling was described by Watling (1971) and, according to the author, could be "… distinguished from all other members of the *L. aurantiacum* complex by the cinnamon to brick-coloured pileus, coupled with the habitat and (small and stocky) stature and the (pallid or sepia) pore colour when young…". The small stocky stature of this taxon is probably a result of the exposed nature of its habitat (*Salix repens* vegetation on cliff-tops), and both pileus and pore colour do not differ from our concept of L. *aurantiacum*. A study of the type material showed that *Leccinum salicola* fits well into our concept of *L. aurantiacum*. *Leccinum salicola* is therefore considered a synonym of *L. aurantiacum*.

Several authors (Dörfelt & Berg 1990; Redeuilh, 1990; Šutara, 1989) have discussed the identity of Bulliard's type plate of *L. aurantiacum* and came to the conclusion that it represents *L. quercinum*. Our results indicate that there is no sound morphological basis for considering *L. quercinum* a distinct species and we therefore conclude that Bulliard depicted the same taxon we currently call *L. aurantiacum*. In Den Bakker et al. (2004b) we followed the recommendations of Redeuilh (1990) and called *L. aurantiacum* sensu Korhonen *L. leucopodium* (Pers.) Dörfelt & G. Berg. Careful examination of the study of Dörfelt & Berg (1990), however, showed that their interpretation of *L. leucopodium* is the same as our concept of *L. aurantiacum*. They had introduced the name *L. leucopodium* for the taxon growing under *Populus*, as the name *L. aurantiacum* was applied for the taxon associated with *Quercus*. Therefore *L. aurantiacum* sensu Korhonen is described as a new species (*L. albostipitatum*), in order to avoid taxonomic confusion about this taxon.

2. **Leccinum albostipitatum** H.C. den Bakker & Noordel., *spec. nov.* — Fig. 7, Plate 2

Leccino aurantiaco similis, pileo aurantiaco, stipite squamulis albis demum parum rubiginosis. Populo consociatus.

Holotypus: Italy, Trento, Monte Bella, 10 IX 1996, M.E. Noordeloos 96134 (L).

Misapplication. *Leccinum aurantiacum* sensu auct p.p.; sensu Korhonen, Karstenia 35 (1995) 58. — *Leccinum leucopodium* Pers. sensu Den Bakker, New Phytol. 163 (2004) 201–215.

Selected icones. Lannoy & Estades, Mon. Leccinum (1995) pl. 34 (as *L. aurantiacum*); Korhonen, Karstenia 35 (1995) 55, fig. 3 (as *L. aurantiacum*).

Selected description. Korhonen, Karstenia 35 (1995) 58–61 (as *L. aurantiacum*).

Characteristics — Habit like *L. aurantiacum*; pileus light orange, light brown in exsiccates; stipital squamules whitish in young fruit-bodies, in older fruit-bodies light brownish. Mycorrhizal with *Populus*.

Pileus 80– 250 mm, hemispherical when young, convex to plano-convex when mature; margin especially in young fruit-bodies inflexed, with appendiculate flaps, exceeding up to 4 mm, in mature fruit-bodies margin often seemingly entire and marginal flaps absent, vivid orange (Mu. 7.5 YR 7/6–7/8); surface minutely tomentose to fibrillose squamulose. Tubes adnexed to adnate, ventricose, 9–30 mm long, pale brownish (10 YR 6/4), yellowish white. Pores c. 0.5 mm in diameter, yellowish white to very pale brownish (10 YR 7/4), discolouring brownish when bruised. Stipe 50–270 × 15–50 mm, cylindrical to subclavate, whitish, often with a clear blue discoloration in the stipe base when handled, sparsely to densely covered with fine (sometimes on the stipe base more coarse), whitish (when young) to reddish brown (in older specimens) squamules. Context white, when bruised often discolouring first vinaceous, than greyish, blackish, often discolouring bluish in the stipe base.

Spores (9.5–)11.0–17.0 × 4.0–5.0(–5.5) μm, Q = 2.3–3.6(–4.0), Q_{av} = (2.9–)3.0–3.1; fusiform with a conical apex, with a distinct suprahilar depression, pale, purplish brown in water. Basidia 25–35 × 7.5–11.0 μm, clavate, 2- or 4-spored. Hymenocystidia 20–45 μm × 7–10 μm, lageniform in tubular hymenium, form of cystidia of hymenium pore surface not clearly observed. Pileipellis an intricate cutis, composed of narrowly cylindrical and cylindrical elements, terminal elements often conical, 35–80 × 4.0–15.5 μm, pigment in water often intracellularly granular incrusted, yellowish brown. Caulocystidia 15–65 × 10.0–16.0 μm, clavate to fusiform, rarely lageniform, largest cystidia often fusiform, apex usually obtuse, content pale sepia to hyaline in KOH. Clamp-connections absent.

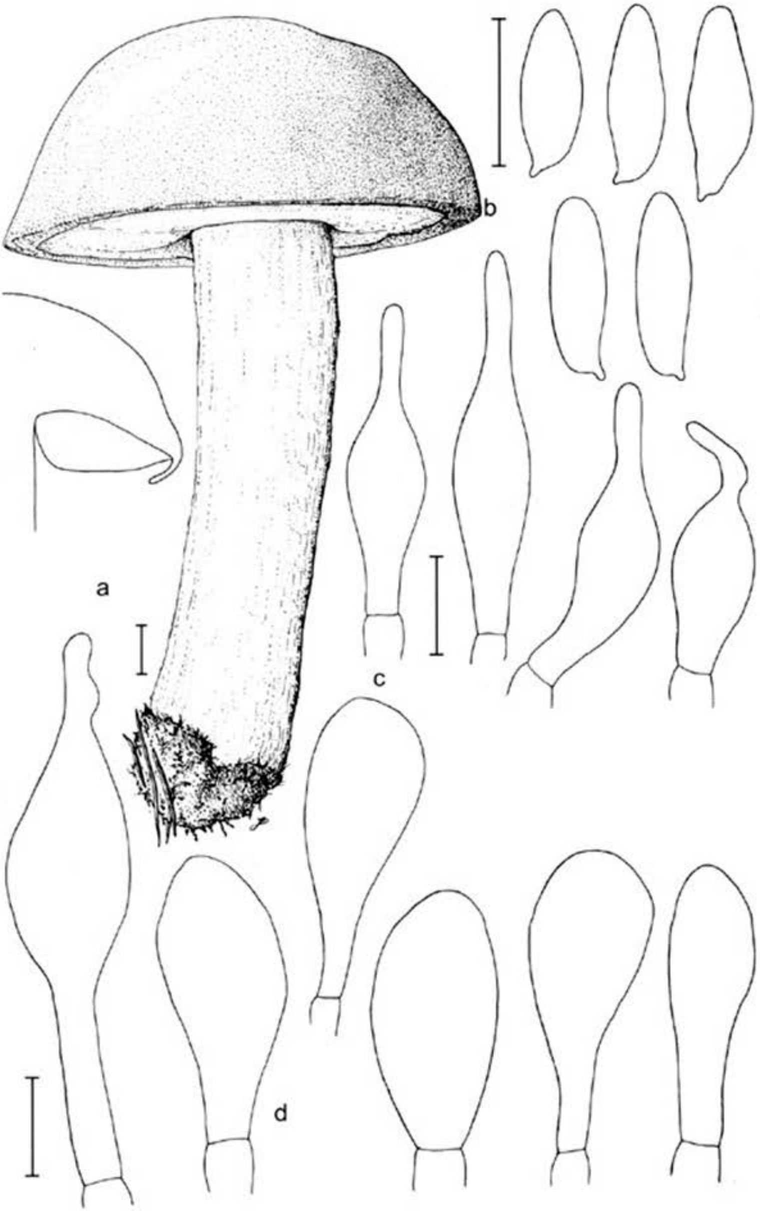


Fig. 7. *Leccinum albostipitatum*. a. Habitus; b. spores; c. hymenocystidia; d. caulocystidia. Scale bars = 10 μm resp. 1 cm.

Habitat & distribution — Solitary or gregarious, ectomycorrhizal, associated with *Populus* in mixed forest and *Populus* stands; not found in the Netherlands, probably a boreal and sub-alpine species, common in Scandinavia and the mountainous areas of central Europe, rare at lower altitudes.

Collections studied. FRANCE: Champagne-Ardenne, Sommauthe/Beaumont-en-Argonne, 20 IX 1999, *R. Walleyn 1656*. — ITALY: Trento, Monte Bella, 10 IX 1996, *M. E. Noordeloos 96134* (Holotype, L). — NORWAY: Sogn og Fjordane, Sogndal, 7 IX 2000, *H.C. den Bakker 93*.

Leccinum aurantiacum has for a long time been broadly interpreted and until recently at least two European species that are associated with *Populus* were included in the interpretation of this name. The importance of the colour of the stipital squamules has not been sufficiently appreciated. Korhonen (1995) was the first author to separate these species. However, his proposal to use the name *L. aurantiacum* for the taxon with pale squamules can not be accepted for various reasons. Consequently, the recently described species *L. populinum* has to be reduced to a synonym of *L. aurantiacum*, while *L. aurantiacum* sensu Korhonen is described here as new, viz. *L. albostipitatum*. The main difference between *L. aurantiacum* and *L. albostipitatum* is found in the colour of the stipital ornamentation and the pileus colour both in fresh and dried fruit-bodies. The first species has generally a brownish-reddish stipital ornamentation that is already reddish in young fruit-bodies, whereas *L. albostipitatum* starts with completely white stipital ornamentation that darkens slightly in older fruit-bodies. Care should be taken in using this character when the fruit-bodies are found in high vegetation. We have observed that the stipital ornamentation of *L. aurantiacum* can be almost white when the stipe is covered with grass. In these cases the pileus colour provides a better character to separate the two species. *Leccinum aurantiacum* has a vividly red to reddish brown pileus, and when dried the pileus is reddish brown. The pileus colour of *L. albostipitatum* is generally vividly orange and changes to a dull light brown in dried fruit-bodies.

Leccinum aurantiacum and *L. albostipitatum* are the only two European representatives of a group (clade) of closely related species with a (sub-)boreal distribution. While the species boundaries of the two species encountered in Europe are clearcut both morphologically and molecularly (Den Bakker et al., 2004b), the situation in North America is still taxonomically confusing and in need of a revision, which needs to be supported with additional molecular data. *Leccinum aurantiacum* is probably a European species, and no records are known from North America. The descriptions of *L. aurantiacum* in North American literature represent a mixture between a *L. vulpinum*-like, conifer associated taxon and North American species that are associated with broad-leaved trees, such as *L. insigne*, and *L. brunneum*[24]. One *L. aurantiacum*-like collection from Ontario, studied by Den Bakker et al. (2004b), belonged to the clade of *L. albostipitatum*. However, with the current literature (Smith & Thiers, 1971) it was impossible to assign a name to that collection.

3. **Leccinum vulpinum** Watling — Fig. 8

Leccinum vulpinum Watling, Trans. Bot. Soc. Edinburgh 39 (1961) 197.
Selected icones. Lannoy & Estades, Mon. Lecc. Europe (1995) pl. 36.

---

24) *Leccinum brunneum* Thiers, Mycologia 63 (1971) 269.

Selected descriptions. Watling, Br. Fung. Fl. 1 (1970) 57; Lannoy & Estades, Mon. Lecc. Europe (1995) 138–139.

Characteristics — A slender to robust, medium to large *Leccinum*; pileus reddish brown, dark reddish brown in exsiccates; stipital squamules greyish to blackish, also in young fruit-bodies. Mycorrhizal with Pinaceae.

Pileus 70–92 mm, hemispherical when young, convex to plano-convex when mature, margin especially in young fruit-bodies involute or inflexed, with appendiculate flaps, exceeding up to 6 mm, in mature fruit-bodies margin often apparently entire and marginal flaps absent; usually dark reddish brown (Mu. 2.5 YR 6–3/6, 10 R 3/6), with patches of a slightly lighter colour; tomentose to fibrillose squamulose. Tubes adnate to sinuate, ventricose, 10–16 mm long, pinkish brown (7.5 YR 7/4) pale greyish brown (10 YR 7/3–4), slightly darker when bruised. Pores c. 0.5 mm in diameter, concolorous with tubes. Stipe 70–150 × 14–31 mm, cylindrical to subclavate, sometimes fusiform, whitish, near the apex lightly covered with fine (sometimes on the stipe base more coarse) dark brown or greyish to blackish squamules, towards the base more densely covered. Context white, when bruised slowly discolouring to greyish or blackish with a violet hue in the pileus and upper half of the stipe, sometimes with bluish discolorations in the stipe base.

Spores (9.5–)11.0–15.5 × 3.5–4.5 μm, Q=2.5–3.8, Q_{av}= 3.2–3.4 (–3.7); fusiform with conical apex, with a distinct suprahilar depression, pale, purplish brown in water. Basidia 20–25 × 7.5–10.5 μm, clavate. Hymenocystidia 20–45 × 5–10 μm, lageniform, hyaline in tubular hymenium, pleurocystidia often clavate or narrowly utriform with a reddish brown content. Pileipellis cutis-like, elements 20–35 × 3.0–3.5 μm, elements in suprapellis 50–70 × 5.5–12.5 μm, pigment in water vacuolar or in globules, larger elements often intracellularly granular incrusted, red-brown. Caulocystidia 20–45 × 9.5–16.0 μm, generally clavate with an obtuse or acuminate apex, content usually brownish in KOH, larger cystidia usually hyaline. Clamp-connections absent.

Habitat & distribution — Solitary or in clusters, ectomycorrhizal, associated with *Pinus* and *Picea* in mixed and coniferous forests; not known from the Netherlands, known from Scotland, Scandinavia and Central Europe. Probably widespread in coniferous forests in subalpine and boreal regions throughout the Northern Hemisphere.

Collections studied. CANADA: Ontario, Manitoulin Island, 30 IX 2003, *H.C. den Bakker 415* — FINLAND: Vuokatti, 1 IX 2001 *M.E. Noordeloos 011243*. — NORWAY: Sogn og Fjordane, Sogndal, 7 IX 2000, *H.C. den Bakker 92*. — SCOTLAND: Inverness-shire, Rothiemurchus, *Watling 264C* (holotype *L. vulpinum*, E). — SWEDEN: Jämtland, Borgsjö, 27 VIII 1993, *M. E. Noordeloos 9396*; Borgsjö Julåsen, 3 IX 1993, *M. E. Noordeloos 93156*; Borgsjö Granbodsåsen, 31 VIII 1993; Borgsjö, 21 VIII 1999, *H.C. den Bakker 10*; Västernorrland, Ånge, 25 VIII 1999, G. Redeuilh, *H.C. den Bakker 24*.

Leccinum vulpinum can readily be recognized in the field on account of its dark reddish brown pileus and distinct black squamules on the stipe. The intensity of the blackish discoloration of the context is only a fraction of the intensity of the discoloration as seen in *L. versipelle* and *L. aurantiacum*, which, together with its association with conifers, can help to facilitate identification.

Leccinum piceinum[25] is another species that has been described from coniferous forests in Europe. This species is associated with *Picea* and was originally described

---

[25] *Leccinum piceinum* Pilát & Dermek, Hribovite huby (1974) 153.

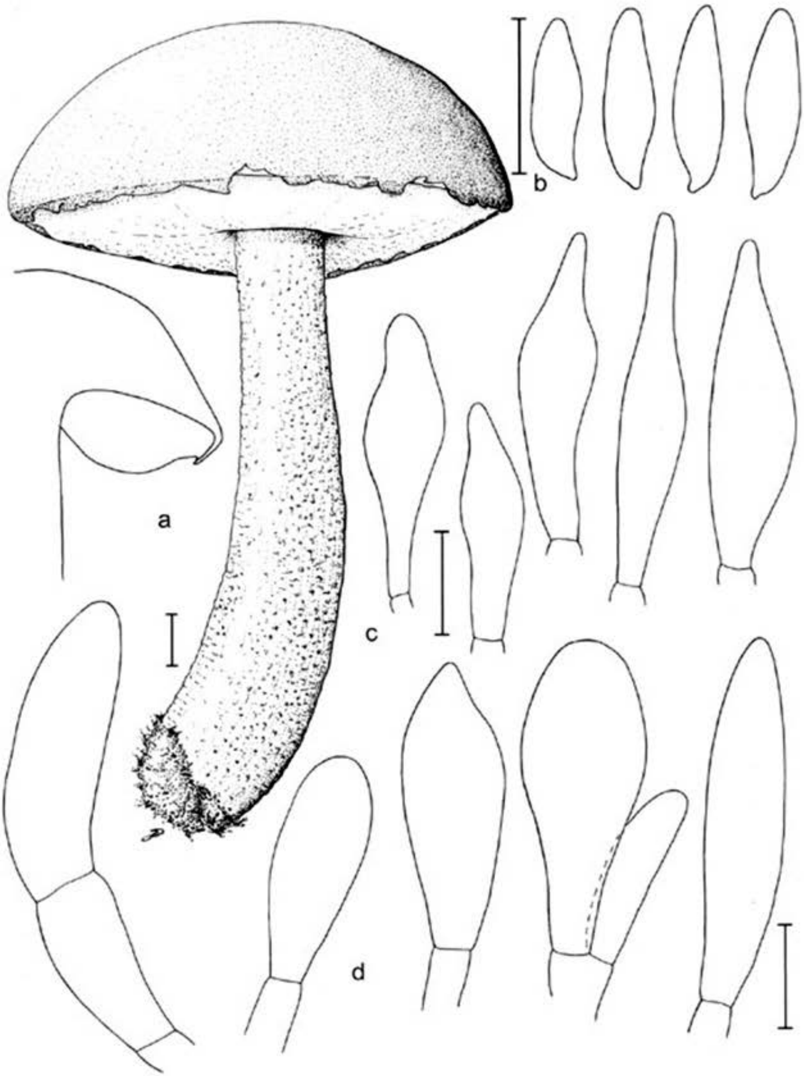


Fig. 8. *Leccinum vulpinum*. a. Habitus; b. spores; c. hymenocystidia; d. caulo cystidia. Scale bars = 10 μm resp. 1 cm.

from central Europe. Most collections from Sweden that were collected in *Picea* forest and therefore identified as *L. piceinum* did not differ in their pileus colour or other morphological characters from *L. vulpinum*. The collections from central Europe differed from *L. vulpinum* mainly by a duller pileus colour, a character that is also used by Lannoy & Estades (1995) to distinguish *L. piceinum* from *L. vulpinum*. The holotype of *L. piceinum* was not sufficiently well preserved to make a morphological study possible, however, material from the *locus typicus* did not differ from our concept of *L. vulpinum*, except for the pileus colour. In an Austrian collection of *L. piceinum* we amplified an ITS sequence type that differed from the type found in a Norwegian *L. vulpinum* (see Den Bakker et al., 2004b). Whether the central European collections associated with *Picea* with an aberrant pileus colour represent a truly genetically distinct taxon remains to be investigated.

Leccinum vulpinum is probably common in North America. A *Gapdh* sequence of a collection from Manitoulin Island (Ontario, Canada, H C den Bakker 415 (L), Genbank accession AY538793) was nearly identical to the *Gapdh* sequence of *L. vulpinum* from Norway. Apparently this species is in North America commonly confused with *L. aurantiacum*, and the descriptions of Smith & Thiers (1971) of *L. aurantiacum* and plates of *L. aurantiacum*, *L. fibrillosum* [26] and *L. subtestaceum* [27] in Bessette et al. (2000) seem to actually represent *L. vulpinum* or a closely related species. For a further discussion see under *L. aurantiacum*.

4. **Leccinum versipelle** (Fr. & Hök) Snell — Fig. 9, Plate 3

Boletus versipellis Fr. & Hök, Bol. Fung. Gen. Ill. (1835) 13; *Leccinum versipelle* (Fr. & Hök) Snell, Lloydia 7 (1944) 58. — *Boletus rufescens* Konrad, Bull. Mens. Soc. Linn. Lyon 1 (1932) 151; *Leccinum rufescens* (Konr.) Šutara, Česká Mykol. 43 (1989) 7. — *Leccinum testaceoscabrum* Singer, Am. Midl. Naturalist 37 (1947) 123 [invalid, no Latin diagnosis]. — *Boletus percandidus* Vassilkov, Sovetsk. Bot. 2 (1944) 27 [invalid, no Latin diagnosis]; *Leccinum percandidum* (Vassilkov) Watling, Trans. Brit. Mycol. Soc. 43 (1960) 691 [invalid, basionym not validly published]; *Boletus percandidus* Blum, Bull. Trimestriel Soc. Mycol. France 85 ('1969' 1970) 562; *Leccinum percandidum* (Blum) Lannoy & Estades, Monogr. Leccinum Eur. (1995) 112. — *Leccinum roseotinctum* Watling, Notes Roy. Bot. Gard. Edinburgh 29 (1969) 267. — *Leccinum cerinum* M. Korhonen, Karstenia 35 (1995) 61. — *Leccinum callitrichum* Redeuilh, Bull. Trimestriel Soc. Mycol. France 111 (1995) 169.

Neotype. Sweden, Jämtland, Kall, 1 IX 2000, H.C. den Bakker 070 (L, designated here).

Selected icones. Lannoy & Estades, Mon. Lecc. Europe (1995) pl. 24, pl. 31, pl. 32, pl. 33; Estades & Lannoy, Bull. Trimestriel Féd. Mycol. Daupiné-Savoie. 174 (3) (2004) 74 (top).

Selected description. Watling, Br. Fung. Fl. 1 (1970) 56.

Characteristics — A slender to robust, medium-sized to large *Leccinum*; pileus light brownish to orange, sometimes whitish, light brown in exsiccates. Stipital squamules greyish to blackish, also in young fruit-bodies. Mycorrhizal with *Betula*.

Pileus 80 –180 mm, hemispherical when young, convex to plano-convex when mature, with inflexed margin especially in young fruit-bodies, with appendiculate flaps, exceeding the tubes up to 4 mm, in mature fruit-bodies marginal flaps often absent and margin entire, yellowish brown (Mu. 10 YR 7/8), orange (2.5 YR 6/8) to brown (5 YR

---

[26] *Leccinum fibrillosum* A.H. Sm., Thiers & Watling, Michigan Bot. 5 (1966) 165. Fig. 14.

[27] *Leccinum subtestaceum* A.H. Sm., Thiers & Watling, Michigan Bot. 5 (1966) 145. Figs. 5, 6, 7.

5/6), sometimes whitish or whitish with pinkish or apricot tinges; minutely tomentose to fibrillose squamulose. Tubes adnexed to emarginate, segmentiform to ventricose, 8–22 mm long, yellowish white to brownish grey, violaceous to greyish when bruised. Pores c. 0.5 mm in diameter, greyish white to grey ochre (10 YR 7/3), discolouring brownish when bruised. Stipe 70–200 × 10–45 mm, cylindrical to clavate, whitish, greyish white or yellowish white, sometimes with a clear blue discoloration in the stipe base when handled, lightly to densely covered with fine (sometimes on the stipe base more coarse) greyish to blackish, sometimes whitish squamules. Context white, when bruised often discolouring greyish or blackish with a violet hue in the pileus and upper half the stipe, often discolouring bluish in the stipe base.

Spores (9.0–)11.5–16.5 × 3.5–4.0(–5.0) μm, $Q = 2.6–3.8$, $Q_{av} = 3.0–3.3$; fusiform with a conical apex, with a distinct suprahilar depression, pale, purplish brown in water. Basidia 20–35 × 6.5–11.0 μm, clavate, generally 4-spored. Hymenocystidia 20–45 μm × 7–11 μm, often lageniform and hyaline in tubular hymenium, narrowly utriform or clavate (sometimes with an obtuse or acuminate apex), hyaline or with a brownish content on the pore surface. Pileipellis an intricate cutis of cylindrical elements, terminal elements obtuse, 40 – 90 × 5.0 – 17.5 μm, pigment granular encrusted, sometimes forming small globules, pale yellowish brown. Caulocystidia (25–)40 – 70 × 8.5 – 15.0 μm, fusiform to utriform, sometimes conical or clavate, largest cystidia generally fusiform or utriform, apex usually obtuse, sometimes acute, pale brownish, with greyish content in KOH. Clamp-connections absent.

Habitat & distribution — Solitary or gregarious, ectomycorrhizal, associated with *Betula* in forests and heathland, on sandy, slightly acidic, loamy soils; rather rare and endangered in the Netherlands (Veerman, 2004), more common in Scandinavia and other parts of Europe.

Collections studied. THE NETHERLANDS: Gelderland, Leusderheide, 2001, *H.C. den Bakker 285*; Rhenen, Buurtse Berg, 8 IX 1968, *W. Wouters, s.n.*; Winterswijk, Nonnenven, IX 2000, R. Chrispijn, *H.C. den Bakker 138*. — FINLAND: Inarilapland, Utsjoki, 1995, *M.E. Noordeloos 95702*; Enontekio Lappi, Kilpisjärvi, 1993, *M. Korhonen 11452*. — FRANCE: Lozère, Aumont-Aubrac, *Redeuilh, 2270P* (holotype *L. callitrichum*). — NORWAY: Sogn og Fjordane, Lærdal, 12 IX 2000, *OF64036*. — SCOTLAND: Inverness-shire, Tomich, Badger Falls, 30 VIII 1957, *Watling 193c* (holotype *L. roseotinctum* E). — SWEDEN: Jämtland, Borgsjö, 26 VIII 1999, *H.C. den Bakker 25*; Borgsjö, IX 1999, *H.C. den Bakker 57*; Kall, 1 IX 2000, *H.C. den Bakker 70*; Kall, 1 IX 2000, *H.C. den Bakker 71*; Kall, 2 IX 2000, *H.C. den Bakker 74*; Västernorrland, delta of Indalsälven, 24 VIII 1999, *H.C. den Bakker 23*; Östavall, IX 1999, *H.C. den Bakker 4*.

The number of species around *L. versipelle* has steadily grown in the past decades. Several related or similar species have been described, such as *L. percandidum* with a white or whitish pileus that becomes pale brownish when mature, *L. roseotinctum*, with an initially white pileus that changes to pinkish when mature, *L. cerinum* with a paler orange to yellowish pileus and pale, yellowish white pores in young basidiocarps, and *L. callit-richum* with a more or less ochre pileus and dark brown elements in the pileipellis. The outcome of the molecular studies (Den Bakker et al., 2004a, 2004b) indicate, however, that a broad morphological species concept of *L. versipelle* fits better with these results. No consistent morphological and molecular characters support the recognition of species like *L. cerinum* and *L. callitrichum*. The collections of *L. roseotinctum* and *L. percandidum* showed sequences that were (almost) identical to the

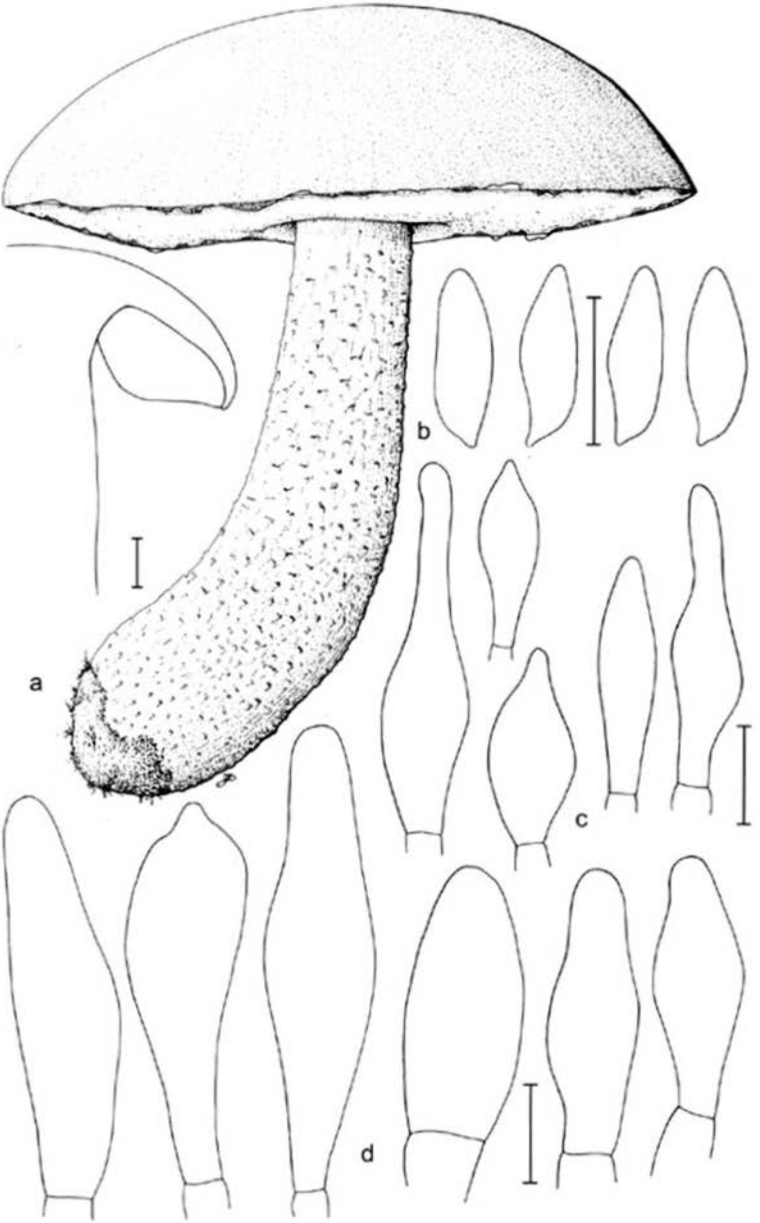


Fig. 9. *Leccinum versipelle*. a. Habitus; b. spores; c. hymenocystidia; d. caulocystidia. Scale bars = 10 μm resp. 1 cm.

sequences of collections of normally pigmented *L. versipelle*. These taxa must therefore be considered as less pigmented forms of *L. versipelle* without formal taxonomic status.

Leccinum atrostipitatum A.H. Sm., Thiers & Watling is an originally North American taxon that has been reported repeatedly from Europe (Engel, 1978) based on the observation of fruit-bodies with an extremely dark and very dense stipital ornamentation. Several European and American collections identified as *L. atrostipitatum* have been studied, but no significant morphological differences between these collections and European material of *L. versipelle* could be found. ITS2 sequences show some consistent differences between North American and European collections. We therefore think that these differences represent infraspecific, phylogeographic differences and *L. atrostipitatum* and *L. versipelle* are actually conspecific. Further North American collections should be studied and sequenced to verify this assumption. Given the fact that *L. versipelle* also occurs in the arctic we consider *L. versipelle* a *Betula*-associate with a circumboreal distribution.

SUBSECTION **FUMOSA** A.H. Sm., Thiers & Watling, Michigan Bot. 6 (1967) 138

Pileus margin entire; context white turning black when bruised, rarely unchanging. Widespread throughout the Northern Hemisphere.

Type species: *Leccinum olivaceoglutinosum* A.H. Sm., Thiers & Watling, Michigan Bot. 6 (1967) 140.

5. **Leccinum duriusculum** (S. Schulz.) Singer — Fig. 10, Plate 4

Boletus duriusculus S. Schulz. in Fr., Hymenomyc. Eur. (1874) 515; *Leccinum duriusculum* (S. Schulz.) Singer, Amer. Midl. Naturalist 37 (1947) 122. — *Leccinum duriusculum* f. *robustum* Lannoy & Estades in Doc. Mycol. 24 (94) (1994) 18. — *Leccinum nigellum* Redeuilh, Bull. Trimestriel Soc. Mycol. France 111(3) (1995) 174.

Holotype: not existent; type locality: Slavonia (Croatia).

Selected icones. Bon, Mushr. Toadst. (1987) 41; Breitenb. & Kränzl., Pilze Schweiz 3 (1991) 70, pl. 32; Engel, Rauhstielröhrlinge (1978) pl. 5a; Muñoz, Fungi non del. 13 (2000) pl. 11, 12 (as f. *robustum*); R. Phillips, Paddest. Schimm. (1981) 212; Pilát & Dermek, Hrívobité Huby (1974) pl. 75.

Selected descriptions & illustrations. Breitenb. & Kränzl., Pilze Schweiz 3 (1991) 70, pl. 32; Engel, Rauhstielröhrlinge (1978) 33, 34; Estades & Lannoy, Bull. Trimestriel Féd. Mycol. Daupiné-Savoie 174 (2004) 70 (as f. *robustum*); Muñoz, Fungi non del. 13 (2000) 30–32; Watling, Br. Fungus Fl. 1 (1970) 50.

Characteristics — Medium to large-sized and sturdy *Leccinum* with dark grey-brown to blackish pileus with an appendiculate margin without marginal flaps; pores whitish to pale ochre; stipe white with dark brown to blackish squamules, which sometimes agglutinate and form a net-like structure in upper part; context white, turning black when bruised, rarely unchanging; pileipellis cutis-like. Associated with *Populus tremula*, *P. alba* and various planted *Populus* hybrids.

Pileus 40–150(–220) mm, hemispherical, then convex, finally sometimes with slightly flattened centre, very variable in colour from rather pale grey-brown with slight violaceous tinge to rather dark greyish or reddish brown (Mu. 10 YR 4–7/4; 7.5 YR 7/4–4/2), minutely fibrillose-felted to very minutely appressedly squamulose all over, often very finely cracked with age, forming very small fibrillose-felted patches, initially concolorous with context, but later contrasting with paler context. Tubes adnexed to almost free, broadly ventricose, up to 25 mm long, creamy white then greyish buff; pores rounded, about 0.3–0.5 mm in diameter, brownish white (5 Y 7–6/3), turning brown when bruised. Stipe 80–170 × 14–20 mm, cylindrical with slightly tapering apex and rounded to subclavate base, solid, entirely minutely squamulose with fine greyish to blackish squamules, which become larger towards base, often arranged in longitudinal rows or ridges; sometimes, especially in upper part of stipe, merging into a reticulate pattern, strongly contrasting with pallid, almost white stipital surface. Context white in pileus and upper part of stipe, frequently tinged yellow-green in lower part of stipe, slowly turning violaceous pink when cut, then spot-wise turning darker greyish-violaceous black; in base of stipe locally turning yellow-green to blue-green. Spore print olivaceous-yellow brown (2.5 Y 6/6 tending to 10 YR 5/6).

Spores (11.5–)12.0–15.5 × 4.5–6.0 μm, on average 13.0–14.0 × 4.8–5.0 μm, Q=2.3–3.3, Q_{av}=2.4–2.7; fusiform with conical apex, with distinct suprahilar depression, relatively thick-walled, pale brown in water. Basidia 20–35 × 6.0–9.0 μm, clavate, 4-spored. Hymenial cystidia abundant on edge and sides of the pores, 20–75 × 5.5–17 × 2.0–4.0 μm, lageniform, often with rather long, tapering neck, colourless or with brown, intracellular-granular pigment. Pileipellis cutis-like, composed of septate hyphae, terminal elements 12–90(–120) × 2.5–7.5 μm, irregularly cylindrical with intracellular, granular pigment. Stipitipellis a cutis of narrow, cylindrical, 3.0–9.0 μm wide hyphae, with small to fairly large caulohymenial clusters of basidia and cystidia, forming the squamules on the stipital surface. Caulocystidia 25–110 × 5.0–12 × 2.0–6.5 μm, lageniform or fusiform, thin- or thick-walled, colourless or with brown granular intracellular pigment. Clamp-connections absent.

Habitat & distribution — Solitary or gregarious, ectomycorrhizal, associated with *Populus*, especially with *P. alba* and *P. tremula*, but also with various *Populus* cultivars, often along roadsides, preferably on calcareous clay, sometimes on sand or loam; in the Netherlands locally rather common, elsewhere rare, mainly in N and F, very rare in L, E, Z, D and K. Rare, but widespread in Europe.

Collections studied. THE NETHERLANDS: Utrecht, Werkhoven, IX 2004, *J. Wisman s.n.*; Gelderland, Beesd, 10 VIII 1973, *C. Bas 5865*; Neerijnen, Kasteelbos, 16 VIII 1970, *F. Tjallingii s.n.*; Lingebos, 17 VII 1993, *C. Bas 8876*; Zuid-Holland, Wassenaar, 8 VII 2004, *H.C. den Bakker s.n.* — FRANCE: Forêt de Vibraye, 11 IX 1979, *Redeuilh 4676 P* (holotype *L. nigellum*, PC).

Leccinum duriusculum f. *robustum*, which according to Lannoy & Estades (1995) differs by more robust basidiocarps, is not recognized here. A continuum in size and shape between f. *duriusculum* and f. *robustum* has been observed. The last-mentioned form, however, seems to prefer the hybrid *Populus* x *cinerea*, whereas the more slender form often grows with *Populus tremula*. Exceptions on this pattern of host association have been found, and hence the forms are not given a formal status here.

Leccinum nigellum differs from *L. duriusculum* mainly in the dark (almost) blackish colour of the pileus. Molecular data (Den Bakker et al., 2004b) show that it is closely related to or conspecific with *L. duriusculum*. Given the species concept applied in this study (a species must differ from a related species in at least two independent characters and must be monophyletic), we consider *L. nigellum* a dark form of *L. duriusculum*.

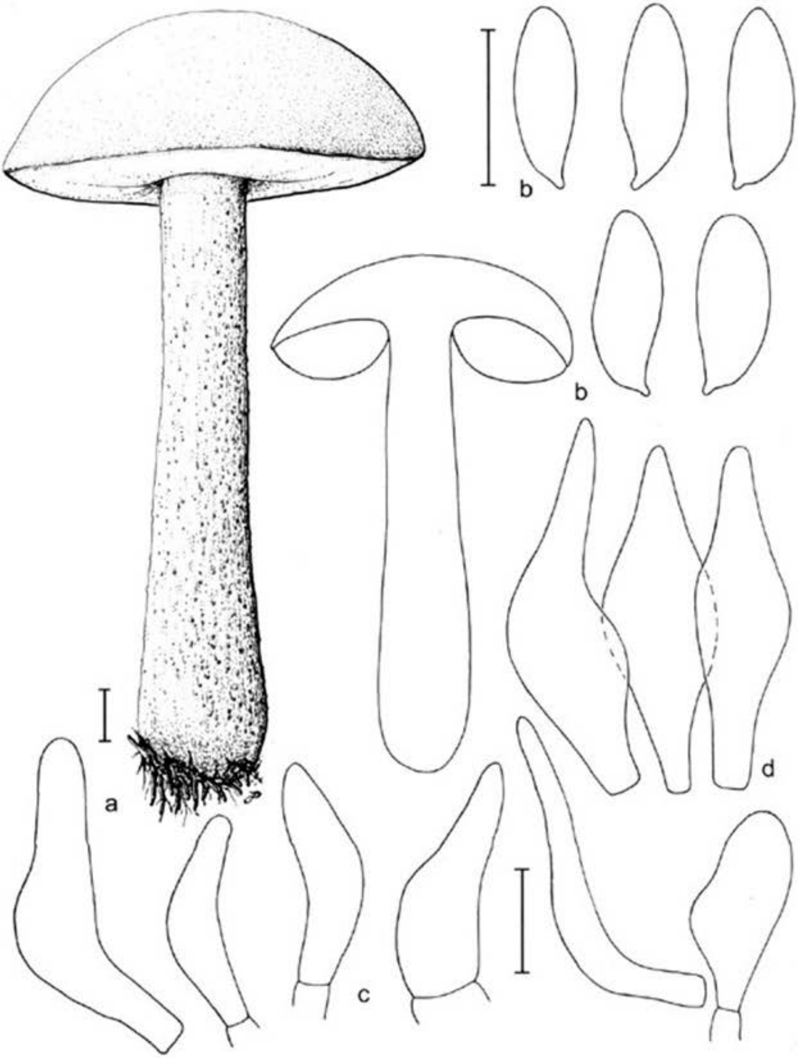


Fig. 10. *Leccinum duriusculum*. a. Habitus; b. spores; c. hymenocystidia; d. caulocystidia. Scale bars = 10 μm resp. 1 cm.

SUBSECTION **SCABRA** Pilát & Dermek, Hribovite Huby (1974) 137

Pileal margin entire. Context whitish, showing bluish, pinkish or reddish discolorations when bruised, or no discoloration at all, sometimes light greyish after several hours. Mycorrhizal with *Betula*. Throughout the Northern Hemisphere, following the distribution of *Betula*.

Type species: *Leccinum scabrum* (Bull. : Fr.) S.F. Gray

6. **Leccinum scabrum** (Bull. : Fr.) Gray — Fig. 11, Plate 5

Boletus scaber Bull., Herb. Fr. (1782) pl. 132; *Boletus scaber* Bull. : Fr., Syst. mycol. 1 (1821) 393; *Leccinum scabrum* (Bull. : Fr.) Gray, Nat. Arr. Brit. Pl. 1 (1821) 647. — *Leccinum roseofractum* Watling, Notes Roy. Bot. Gard. Edinburgh 28 (1968) 313. — *Boletus avellaneus* Blum, Bull. Trimestriel Soc. Mycol. France 85 ('1969' 1970) 560; *Leccinum avellaneum* (Blum) Bon. Doc. Mycol. 9(35) (1979) 41. — *Leccinum rigidipes* P.D. Orton, Trans. Brit. Mycol. Soc. 91 (1988) 560. — *Krombholzia scabra* f. *cinnamomea* Valsilkov, Trudy Bot. Inst. 2 (10) (1956) 370, non *Leccinum cinnamomeum* A.H. Sm., Thiers & Watling 1967; *Leccinum subcinnamomeum* Pilát & Dermek, Ziva 17 (2) (1969) 58.

Iconotype. Bull., Herb. France: pl. 132. 1782.

Epitype. J. van Brummelen 1+2, along N12, vicinity of Versailles, Guyancourt, France (L, designated here).

Selected icones. Lannoy & Estades, Monogr. Leccinum (1995) pl. 4; Marchand, Champ. Nord Midi 2 (1973) pl.169; R. Phillips, Paddest. Schimm. (1993) 213; Ryman & Holmåsen, Pilze (1992) 231; Lannoy & Estades, Monogr. Leccinum (1995) pl. 16 (as *L. rigidipes*); R. Phillips, Paddest. Schimm. (1993) 213 (als *L. oxydabile*).

Selected descriptions. Lannoy & Estades, Monogr. *Leccinum* (1995) 62–64; J. Schreiner, Beih. Z. Mykol. 9 (1999) 27–32.

Characteristics — Habit slender to robust, small to medium-sized; pileus ranging from light brownish to dark brown; stipital squamules light brownish to blackish, coarse in the lower half of the stipe and usually fine, almost glandular in the upper half of the stipe; context always without bluish discolorations. Mycorrhizal with *Betula* in (dry) acidic habitats.

Pileus 52–130 mm, convex at first, expanding to plano-convex, with entire, deflexed or inflexed margin, not or only very slightly (< 1mm) extending over tubes, yellowish brown to dark brown (Mu. 10 YR 6/6, 7.5 YR 3–6/4); minutely tomentose, breaking up into minute, appressed squamules with age, somewhat viscid when moist. Tubes broadly adnexed, 8–19 mm long, segmentiform to subventricose when mature, whitish when young, brownish grey when mature. Pores greyish white, often with brownish spots, discolouring brownish when bruised. Stipe 82–145 × 12–55 mm, cylindrical to clavate, whitish, often more brownish towards apex, entirely covered with blackish to greyish, sometimes pale brownish squamules, fine at apex, becoming gradually coarser towards base, sometimes agglutinating and almost forming a network. Context whitish, not changing colour when bruised or at most discolouring pinkish or reddish (K. & W. 9A2), finally often brownish or slightly greyish after several hours.

Spores (13.5–)14.5–19.0(–22.0)× (4.0–)5.0–6.5 μm, Q = 2.5–3.5, Q_{av} = (2.9–)3.0–3.3, fusiform with a suprahilar depression. Basidia 30–40 × 10.5–12.5 μm, 4-spored (sometimes 3-spored). Hymenocystidia 30–50 × 5.5–7.5 μm, fusiform to

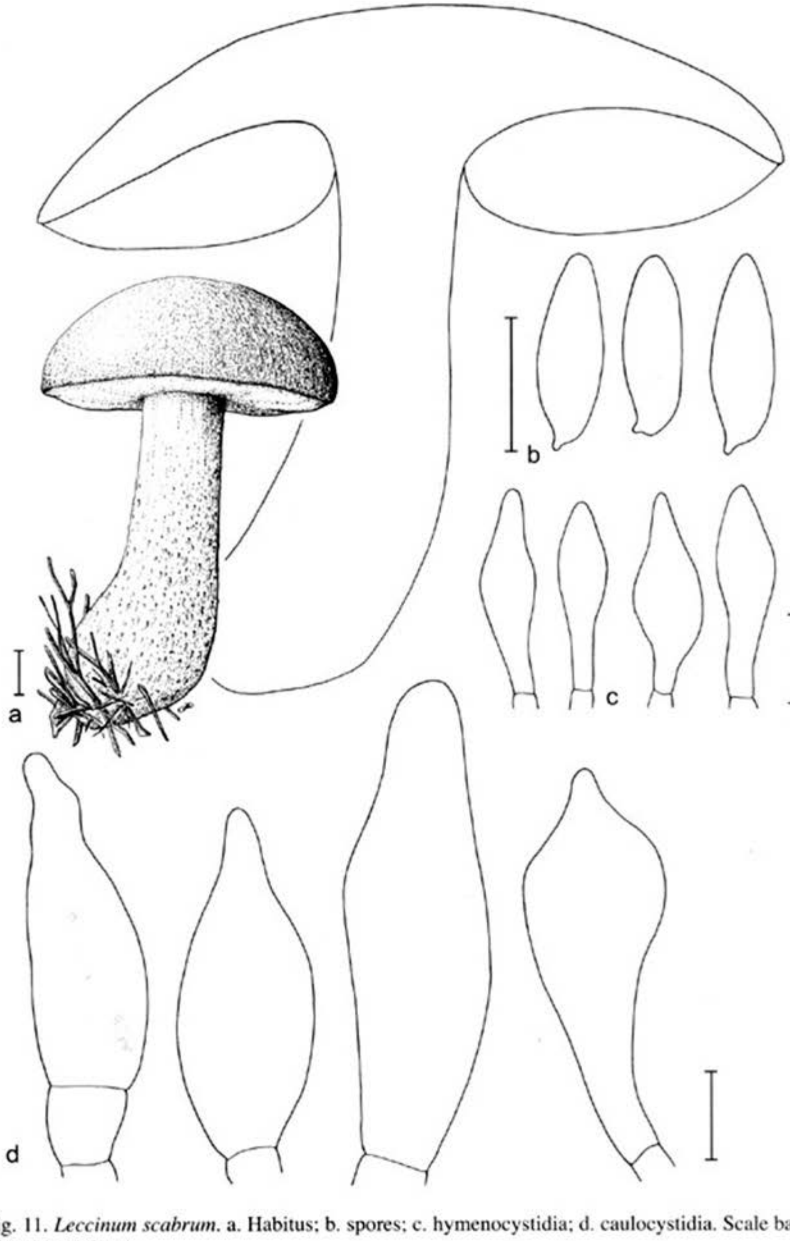


Fig. 11. *Leccinum scabrum*. a. Habitus; b. spores; c. hymenocystidia; d. caulocystidia. Scale bars = 10 μm resp. 1 cm.

lageniform, cylindrical to clavate or lageniform, apex obtuse or acuminate. Caulocystidia (35–)40–70(–90) × 9.0–18.5 μm, lageniform to clavate, hyaline or with a greyish brown content when mounted in KOH. Pileipellis a dense to loosely intricate cutis, composed of slender, hyaline to brownish intracellularly pigmented, or granular incrusted hyphal-elements, 3.5–7.0(–8.0) μm in diameter, mixed with broadly elongated hyphal elements, (7.5–)8.0–14.0(–16.0) μm in diameter, sometimes also with broad, clearly articulated, hyaline hyphal elements, (8.0–)9.0–13.5(–17.0) μm in diameter, terminal elements often conical. Clamp-connections absent.

Habitat & distribution — Solitary or gregarious, ectomycorrhizal with *Betula*, often found in lawns or oligotrophous *Festuca rubra* /*Deschampsia flexuosa* vegetations on slightly acidic, dry sandy soils; common in the Netherlands, widespread and common in Europe. Probably a species with a circumboreal distribution.

Collections studied. THE NETHERLANDS: Drenthe, Emmen, 2 X 1999, *H.C. den Bakker 44*; Nieuw Amsterdam, 4 X 1999, *H.C. den Bakker 50*; Borger, vicinity of cottage park 'Land van Bartje', 5 X 1999, *H.C. den Bakker 54*; Gieten, Boekweitveentje, 2001, *R. Enzlin 01-009*; Hoogeveen, 3 X 1999, Leg. B. de Vries, *H.C. den Bakker 48*; Noord-Holland, Amsterdamse Waterleiding Duinen, Eiland van Rolvers, 23 X 1999, *H.C. den Bakker 62*; Zuid-Holland, Wassenaar, Meijendel, 17 X 1999, *H.C. den Bakker 58*; Voorschoten, 30 IX 1999, C. Bas, *H.C. den Bakker 42*; Utrecht, Zeist, Soesterberg, 6 X 2000, *H.C. den Bakker 124*. — FRANCE: Versaille, 27 IX 2001, Van Brummelen (epitype *L. scabrum*, L); Orne, Foret de Belleme, 28 IX 2001, Van Brummelen. — NORWAY: Sogn og Fjordane, Sogndalsfjøra, 8 IX 2000, *H.C. den Bakker 95*; Sogn og Fjordane, Sogndalsfjøra, 8 IX 2000, *H.C. den Bakker 91*; Sogn og Fjordane, Sogndalsfjøra, IX 2000, *H.C. den Bakker 87*. — SCOTLAND: Inverness-shire, Aberarder Forest, 13 IX 2001, *H.C. den Bakker 239*; Insh Marshes, 12 IX 2001, *H.C. den Bakker 231*; Insh Marshes, 12 IX 2001, *H.C. den Bakker 237*; Abernethy Forest, 31 VIII 1972, *P. Orton 4399* (holotype *L. rigidipes*, E); Ross & Cromarty, Loch Maree, *R. Watling 4944* (holotype *L. roseofractum*, E). — SWEDEN: Jämtland, Borgsjö, 24 VIII 1999, *H.C. den Bakker 22*; Åre, 4 IX 2000, *H.C. den Bakker 80*. — WALES: South Glamorgan, Merthyr-mawr sand dunes, *A. Hills 2003076*.

Leccinum scabrum can usually be distinguished from other species of subsection *Scabra* by a combination of the following characters:

- the stipital ornamentation is usually coarse in the lower part of the stipe and with fine, sometimes almost 'glandular' squamules in the upper half of the stipe.
- bluish discolorations of the context are always absent.
- the presence of remarkably large (up to 92 μm long), usually clavate caulocystidia.
- the pileipellis is a loose cutis composed of a mixture of slender and broad, sometimes elliptical, elements.

Leccinum scabrum generally occurs in drier habitats than other species of subsection *Scabra*. Thanks to monographs like the one of Lannoy & Estades (1995) there is a general consensus about the identity of *L. scabrum*. The current concept, however, of *L. scabrum* is wider than that of Lannoy & Estades, and includes also *L. roseofractum*, *L. avellaneum* and *L. rigidipes*, thus including also forms with discolouring context. As such, *L. scabrum* is a fairly variable species, and *L. avellaneum* and *L. roseofractum* may be considered the extremes in a series of lighter to darker forms. Gradual differences were also found in the discoloration of the context when bruised, ranging from not reacting to discolouring pinkish to almost reddish. To consolidate the presently accepted interpretation of *L. scabrum* an epitype accompanying the iconotype, originating from the neighbourhood of Paris, is designated here.

In Europe, the slender spores ($Q_{av} \geq 3.0$) can help to separate *L. scabrum* from *L. rotundifoliae*. However, the average Q-value of collections identified as *L. scabrum* from eastern North America is lower than the average Q-value in Europe, viz. 2.8 instead of 3.0. Therefore the average Q-value can probably not be used in North America to discriminate this species from *L. rotundifoliae*. In North America the large caulocystidia and the irregular pileipellis structure can be used to distinguish *L. scabrum* from *L. rotundifoliae*.

According to Watling (1968) *L. roseofractum* differs from *L. scabrum* by the more robust habit, dark-coloured pileus, the dense black stipital ornamentation and flesh changing distinctly red. Collections were made of *L. roseofractum* in Scotland, Norway and Canada. The European collections matched all of Watling's criteria for *L. roseofractum*; the Canadian collection, however, had a slender habit, but a strong reddish discoloration, an almost blackish pileus and dark blackish stipital ornamentation. The three collections did not form a separate clade in our molecular phylogenetic analysis (Fig. 2), but were found dispersed between accessions of *L. scabrum*. Microscopically these collections and the type collection of *L. roseofractum* were not different either from collections identified as *L. scabrum*. Therefore *L. roseofractum* is considered a synonym of *L. scabrum*.

The type material and original description of Orton (1988) of *L. rigidipes* is reminiscent of *L. scabrum* in almost every morphological character, except for the presence of short hyphal elements (interpreted as cylindrocysts by Lannoy & Estades, 1995) in the pileipellis. Specimens with abundant cylindrocysts, identified as *L. rigidipes*, were molecularly identical with collections without cylindrocysts. Moreover, we noted that cylindrocysts, though in low numbers, are often present in the pileipellis of *L. scabrum*. In conclusion, *L. rigidipes* is also considered synonymous with *L. scabrum*.

The name *L. subcinnamomeum* is validly published, since Pilát and Dermek referred to *Krombholzia scabra* f. *cinnamomea* Vasilkov as being the basionym of this taxon. *Kromholzia scabra* f. *cinnamomea* Vasilkov is validly published and is not the basionym of *L. cinnamomeum* A.H. Sm., Thiers & Watling (1967). No type material of *L. subcinnamomeum* seems to be designated. Material of this species in PRM fits perfectly in our morphological concept of *L. scabrum*. Most descriptions and plates in the literature (Engel, 1978; Dähnke, 1993; Bresinsky, 1996) also refer to a taxon close to *L. scabrum* with a reddish brown pileus.

7. **Leccinum melaneum** (Smotl.) Pilát & Dermek — Fig. 12, Plate 6

Boletus scaber var. *melaneus* Smotl., Mykol. Sborn. 16 (1951) 17; *Leccinum melaneum* (Smotl.) Pilát & Dermek, Hríbovité huby (1974) 145; *Leccinum scabrum* var. *melaneum* (Smotl.) Dermek, Fung. rar. Ic. col. 16 (1987) 17.

Selected icones. Dähncke, 1200 Pilze (1993) pl. 98.

Characteristics — A dark, medium-sized to large *Leccinum*. Pileus brown to blackish brown; stipe greyish to blackish with dense blackish stipital squamules, stipe usually strongly clavate; context without any bluish discolorations. Mycorrhizal with *Betula*.

Pileus 50–130 mm, convex at first, expanding to plano-convex with age, often irregularly shaped, brown to dark brown (Mu. 7.5 YR 3/4), sometimes with lighter coloured spots; very finely tomentose, becoming subviscid with age. Tubes narrowly

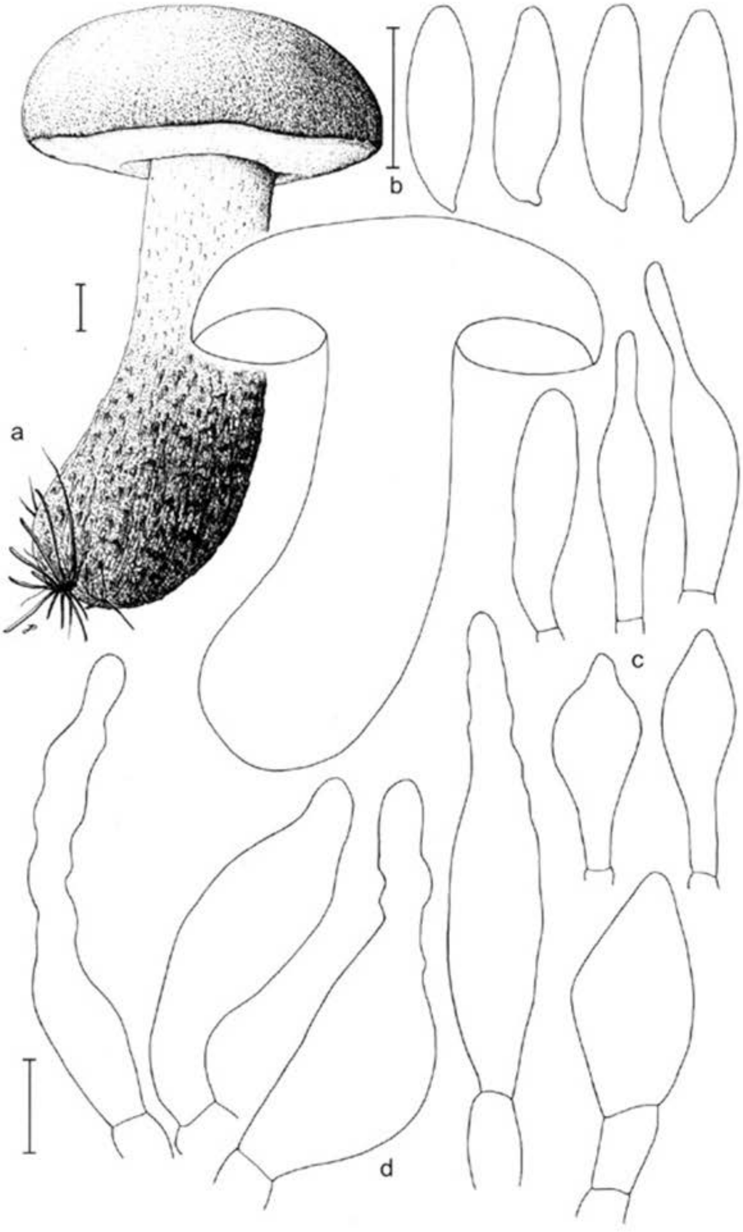


Fig. 12. *Leccinum melaneum*. a. Habitus; b. spores; c. hymenocystidia; d. caulocystidia. Scale bars = 10 μm resp. 1 cm.

to broadly adnexed, 8–19 mm long, whitish when young, greyish to brownish at maturity. Pores greyish white, often with brownish spots, brownish when bruised. Stipe 90–145 × 21–55 mm, cylindrical to (broadly) clavate, greyish to blackish, entirely covered with squamules; squamules fine near the apex of the stipe, gradually becoming coarser towards base, in basal part often agglutinated and forming a kind of reticulum. Context white, when bruised often discolouring pinkish (K. &W. 9A2), often brownish after several hours.

Spores 14.0–19.0 × 5.0–6.0 μm, $Q = 2.5–3.5$, $Q_{av} = 2.9–3.2$, fusiform with a suprahilar depression. Basidia 20–30 × 11.5–13.0 μm, 4-spored, sometimes 2-spored. Hymenocystidia 25–50 × 7.5–11.5 μm, lageniform, clavate with a mucronate apex or utriform. Pileipellis a loose intricate cutis of cylindrical, sometimes bifurcate, elements 9.0–11.5(–15.0) μm wide, with dark brown intracellular pigment. Caulocystidia 35–60 × 12.5–18.5 μm, fusiform, utriform or clavate. Clamp-connections absent.

Habitat & distribution — Solitary or gregarious, ectomycorrhizal, associated with *Betula* on sandy soils. Known from four localities in the Netherlands (Boekweitveentje, Gieten; Boswachterij Gees; Amsterdamse Waterleiding Duinen, Wisselsche Veen, Epe), susceptible (Veerman 2004). Distribution in Europe unclear, because of confusion with dark forms of *L. scabrum*.

Collections studied. THE NETHERLANDS: Drenthe, Gieten, Boekweitveentje, 3 X 1999, *H.C. den Bakker 47*; Boswachterij Gees, 5 X 1999, *H.C. den Bakker 53*; Gelderland, Epe, 25 X 2003, *Boomsluiter s.n.*; Noord-Holland, Amsterdamse Waterleiding Duinen, Eiland van Rolvers, 2 IX 1999, *H.C. den Bakker 33*.

Leccinum melaneum does not differ morphologically much from *L. scabrum*, except for the fact that the stipital surface generally is greyish or blackish in this species, as opposed to whitish to brownish in *L. scabrum*. Three of the four collections also show an unusually broad stipe base (giving the stipe a broadly clavate shape) and a slightly malformed pileus. Molecular data indicate *L. melaneum* might be a hybridogenic taxon (Den Bakker et al., in prep). In PRM several collections identified as *L. melaneum* by Pilát are present, however, as far as we know no type material for *L. melaneum* has been designated. This may mean *L. melaneum* has never been validly published. We therefore see *L. melaneum* as a 'preliminary' name, until the taxonomic and nomenclatural status of this taxon has been clarified.

8. **Leccinum rotundifoliae** (Singer) A.H. Sm., Thiers & Watling — Fig. 13, Plate 7

Krombholzia rotundifoliae Singer, Schweiz. Z. Pilzk. 16 (1938) 148; *Boletus rotundifoliae* (Singer) S. Lundell, Fungi Exs. Suec., praesert. Upsal. (1959) 2615; *Leccinum rotundifoliae* (Singer) A.H. Sm., Thiers & Watling, Michigan Bot. 6 (1967) 128. — *Leccinum pulchrum* Lannoy & Estades, Doc. Mycol. 21 (82) (1991) 3. — *L. scabrum* subsp. *tundrae* Kallio, Rep. Kevo Subarct. Res. Stat. 12 (1975) 25–27. — *Leccinum pulchrum* f. *fuscodiscum* Lannoy & Estades, Doc. Mycol. 21(82) (1991) 5.

Excluded. *L. rotundifoliae* sensu A.H. Sm., Thiers & Watling, Michigan Bot. 6 (1967) 128; sensu Kallio, Rep. Kevo Subarct. Res. Stat. 12 (1975) 25–27 (= *L. holopus*).

Neotype (selected by Lannoy & Estades, 1995). Fungi exsiccati Suecici 2615, Sweden, Norrbotten, Abisko, 27 VII 1943, *Nannfeldt* 6771(PC).

Selected icones. Lannoy & Estades, Mon. Leccinum (1995) pl. 2 (as *L. pulchrum*), pl. 3 (as *L. pulchrum* f. *fuscodiscum*), pl. 7; Estades and Lannoy, Bull. Trimestriel Féd. Mycol. Dauphiné-Savoie 174 (2004) 62 (as *L. pulchrum*).

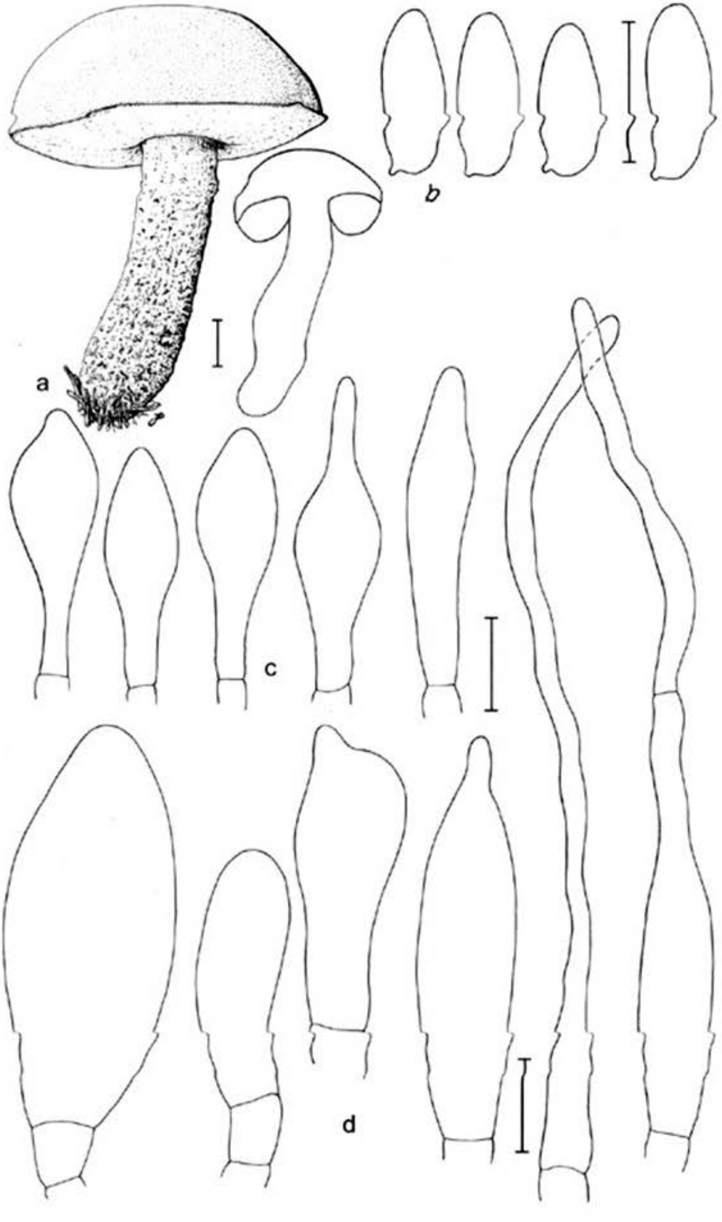


Fig. 13. *Leccinum rotundifoliae*. a. Habitus; b. spores; c. hymenocystidia; d. caulocystidia. Scale bars = 10 μm resp. 1 cm.

Selected descriptions. Kallio, Rep. Kevo Subarct. Res. Stat. 12 (1975) 25–27 (as *L. scabrum* subsp. *tundrae*).

Characteristics — A slender to robust, small *Leccinum*. Pileus pale brownish or dark brown with lighter regions; stipital squamules brownish to blackish, often warty, almost flocculose in the lower half of the stipe; context always without bluish discolorations. Mycorrhizal with *Betula* in boreal/subalpine to arctic/alpine habitats.

Pileus 25–90 mm, hemispherical to convex, expanding with age, with inflexed, entire margin, not exceeding the tubes or at most up to 1 mm, pale yellowish brown, light brown (Mu. 10 YR 5/2) to very dark brown or grey brown (10 YR 6/4), then often mottled; surface fibrillose-tomentose, sometimes appearing velutinous, frequently irregularly cracked; slightly viscid when old. Tubes adnexed to narrowly adnate, 8–21 mm long, broadly convex to ventricose, creamy white to greyish white. Pores yellowish white to brownish white, discolouring brownish when bruised. Stipe 40–100 × 7–25 mm, subclavate to clavate, whitish; entirely covered with squamules, squamules either whitish and changing to brownish with maturity or blackish, fine near the apex, gradually becoming more coarse/flocculose towards stipe base. Context whitish, when bruised unchanging or discolouring pinkish, especially in apex of stipe.

Spores (11.5–)13.5–17.5(–20.0) × 4.5–7.0 μm, Q=2.2–3.2, Q_{av}= 2.5–2.7(–2.9). Basidia 23.5–33.0 × 11.0–12.5 μm, clavate. Pileipellis a rather regular intricate, cutis; elements 30–95 × 3.0–8.5 μm, narrowly cylindrical, hyaline and granular incrusted or brownish and then often also granular incrusted. Caulocystidia 35–60 × 11.0–20.5, utriform, lageniform or fusiform, content hyaline or pale greyish brown when mounted in KOH. Clamp-connections absent.

Habitat & distribution — Solitary or gregarious, ectomycorrhizal, associated with *Betula* in wet to dry habitats (ranging from tundra to wet birch forest); not found in the Netherlands; widespread in boreal, arctic and alpine regions, probably following a circumpolar distribution. Exact distribution in subalpine regions at lower latitudes unclear because of insufficiently known morphological variability (Den Bakker et al. in prep.).

Collections studied. CANADA: Labrador, Schefferville, 4 IX 1984, *Malloch 4-9-84/1*. — FINLAND: Enontekion Lappi, Kilpisjärvi, *M. Korhonen 11429*. — FRANCE: Isère, Massif de Belledonne, Prabert, 24 X 1989, *Estades 891024/3* (holotype *L. pulchrum*, LIP); Massif de Belledonne, Les Seiglières, 28 IX 1989, *Estades 89.09.284 bisA* (holotype *L. pulchrum* f. *fuscodiscum*, LIP). — GREENLAND: Kellyville, 14 VIII 2000, *L. Jalink & M. Nauta 8263*; Sisimiut, VIII 2000, *L. Jalink & M. Nauta 8254*; Sisimiut, 19 VIII 2000, *L. Jalink & M. Nauta 8399*; Sisimiut, VIII 2000, *L. Jalink & M. Nauta 8359*. — NORWAY: Jotunheimen, 6 IX 2000, *H.C. den Bakker 86*. — SWEDEN: Jämtland, Borgsjö, 23 VIII 1999, *H.C. den Bakker 16*.

Leccinum rotundifoliae is a species of arctic, alpine, boreal and subalpine habitats. Pale-coloured fruit-bodies can be distinguished from *L. holopus* by the absence of bluish discolorations in the context of the stipe base, and the absence of greenish bluish tinges in the pileus of older fruit-bodies. In addition to differences in colour there seems to be an ecological difference in arctic regions. *Leccinum rotundifoliae* is a species of dry habitats, whereas *L. holopus* prefers wet habitats. In subalpine and boreal regions *L. rotundifoliae* can also be found in wetter habitats.

The concept of *L. rotundifoliae* of Smith et al. (1967) differs from the original description of *L. rotundifoliae*. Singer's original diagnosis states that the context does not change colour when bruised. Smith et al. (l.c.) described a pale, small species with a bluish discoloration of the context in the stipe base. Collections from arctic environments fitting the concept of Smith et al., thus with a bluish discoloration in the stipe base, appeared, however, in phylogenetic analyses in clades together with *L. holopus* (see Figs. 2, 3), and not in the *L. rotundifoliae* clade. In fact, the concept of Smith et al. actually represents an arctic phenotype of *L. holopus*.

These two different concepts of *L. rotundifoliae* have coexisted for some time in the literature and have generated abundant confusion. Kallio (1975), who was among the first to realise that two different arctic species were involved, followed the interpretation of *L. rotundifoliae* by Smith et al. when describing *L. scabrum* subsp. *tundrae*. He listed a number of morphological and ecological differences between *L. rotundifoliae* and *L. scabrum* subsp. *tundrae*, from which is apparent that his concept of *L. rotundifoliae* fits that of Smith et al., while the description of *L. scabrum* subsp. *tundrae* perfectly fits the present concept of *L. rotundifoliae*.

Leccinum rotundifoliae is generally considered a pale brown to almost whitish species. However, specimens with a dark pileus and dark stipital squamules were also sequenced. The first of these specimens to be sequenced (a collection from Borgsjö, Jämtland, Sweden) was erroneously called *L. scabrum* (Den Bakker et al., 2004a) based on the minor sequence divergence in ITS between *L. scabrum* and *L. rotundifoliae*. Analysis of an additional gene (*Gapdh*), however, supported the recognition of *L. rotundifoliae* as a separate species. When type material of *L. pulchrum* was sequenced, these accessions surprisingly appeared in the *L. rotundifoliae*-clade. Upon closer inspection of the morphology and a comparison of photographs of dark specimens of *L. rotundifoliae* from Greenland and Sweden with the picture of *L. pulchrum* in Estades & Lannoy (2004: 62) these pictures show a perfect resemblance. *Leccinum pulchrum* is therefore reduced into the synonymy of *L. rotundifoliae*. This demonstrates that *L. rotundifoliae* not only occurs in Northern Europe, but also in the Alps. One accession from the French lowlands which was identified as *L. pulchrum*, appeared, however, in the *L. scabrum* clade. Morphological data confirmed that the collection belongs to *L. scabrum*, and the name that was initially provided (*L. pulchrum*) must therefore be considered a misapplication.

In their description of *L. pulchrum*, Lannoy & Estades (1995) stated that occasionally bluish discolorations can be found in the stipe base. A collection from a marshy birch forest in the Netherlands fitted their discription well with respect to this character. But the molecular and microscopic characters placed this collection in the current concept of *L. holopus*. This normally pale-coloured species usually has bluish discolorations in the stipe base. It has been collected in the same locality as the above mentioned *L. pulchrum* and ended up in the same clade. Apparently the concept of *L. pulchrum* by Lannoy & Estades is merely based on non-diagnostic macroscopical characters, and represents a mixture of different species, including *L. scabrum*, *L. rotundifoliae* and *L. holopus*.

9. **Leccinum schistophilum** Bon — Fig. 14, Plate 8

Leccinum schistophilum Bon, Doc. Mycol. 11(44) (1981) 35, 36. — *Leccinum palustre* M. Korhonen, Karstenia 35 (1995) 63, Fig. 11.

Selected icones. Lannoy & Estades, Mon. Leccinum (1995) pl. 30; Korhonen in Karstenia 35 (1995) 63, Fig. 11 (as *L. palustre*).

Selected descriptions. Korhonen, Karstenia 35 (1995) 63 (as *L. palustre*); Bon, Doc. Mycol. 11(44) (1981) 35, 36.

Characteristics — A slender to robust, small *Leccinum*, usually with a greyish brown pileus and greyish to blackish stipital squamules; context in the lower half of the stipe with a bluish discoloration. In wet, often slightly basic habitats.

Pileus 25–110 mm, convex, expanding to plano-convex, with inflexed margin, not markedly exceeding the tubes, light yellowish brown (Mu. 10 YR 6/4), greyish brown (10 YR 5/2), to dark brown (10 YR 3-4/2), often evenly coloured, but sometimes with light spots; minutely tomentose, dull. Tubes narrowly to broadly adnate, 9–25 mm long, ventricose to broadly ventricose, yellowish white at first, in later stages greyish with a pinkish hue. Pores c. 0.5 mm in diameter, whitish to yellowish white, discolouring brownish when bruised. Stipe 46–150 mm × 9–25 mm, cylindrical to clavate, greyish white to brownish, lightly to densely covered with fine squamules, usually not markedly differing between base and apex of stipe. Squamules initially brownish, in later stages greyish to blackish, sometimes dark brown. Context (greyish) white, when bruised discolouring pinkish (9A2) in the pileus and upper half of the stipe, sometimes discolouring bluish green (25A4) in lower half of stipe; sometimes not discouloring at all, rarely discolouring greyish after several hours.

Spores (13.0–)13.5–17.0 × 5.0–6.5(–7.5) μm, $Q = 2.3–3.1(–3.4)$, $Q_{av} = 2.8–2.9$ (–3.0), subcylindrical to fusiform. Basidia 25–30 × 10.0–11.5 μm, 4-spored. Hymenocystidia 30–45 × 7.5–9.0 μm, lageniform. Pileipellis cutis-like, composed of cylindrical, brownish to dark brownish elements, (3.5–)4.5–8.0 μm wide, sometimes also with broad (7.0–11.5 μm), clearly articulated, elements. Caulocystidia 30–70 × 11.0–20.5 μm, fusiform, clavate or lageniform. Clamp-connections absent.

Habitat & distribution — Gregarious or solitary, ectomycorrhizal, associated with *Betula* on mossy, humid, alkaline, sandy soils; distribution insufficiently known, probably widespread and rather rare throughout northern and western Europe.

Collections studied. THE NETHERLANDS: Noord-Holland, Amsterdamse Waterleiding Duinen, Eiland van Rolvers, 2 IX 1999, *H.C. den Bakker 30*; ibid., 23 X 1999, *H.C. den Bakker 61*; ibid., 4 X 2000, *H.C. den Bakker 121*. — ENGLAND: Gloucestershire, 30 VIII 2000, *Alan Hills s.n.* — FINLAND: Uusimaa, Vantaa, Veromies, *M. Korhonen 11145* (holotype *L. palustre*, H). — FRANCE: Pas-de Calais, Labuissière, *Bon 741014* (holotype *L. schistophilum*, LIP); Orne, Forêt Dominial du Perche, 2 X 2001, *van Brummelen (fix 15 + 16)*. — SWEDEN: Jämtland, Borgsjö, 23 VIII 1999, *H.C. den Bakker 15*; vicinity Åre, 4 IX 2000, *H.C. den Bakker 82*.

The typical form of *L. schistophilum* can easily be identified in the field and is characterized by a small, slender habit, light greyish brown pileus, white stipe with contrasting fine, greyish to blackish squamules and a greenish-blue discolouring context in the lower half of the stipe. However, basidiocarps with a brown pileus and a non-discolouring context may occur, which accordingly can only be distinguished from *L. scabrum* by its different ecology (*L. schistophilum* usually grows in wet habitats, *L. scabrum* in drier habitats) combined with microscopic differences (caulocystidia, average Q-value of spores and differences in pileipellis structure).

Large specimens of *L. schistophilum* may be confused with *L. variicolor*. Microscopically *L. schistophilum* can easily be distinguished, however, by the structure of

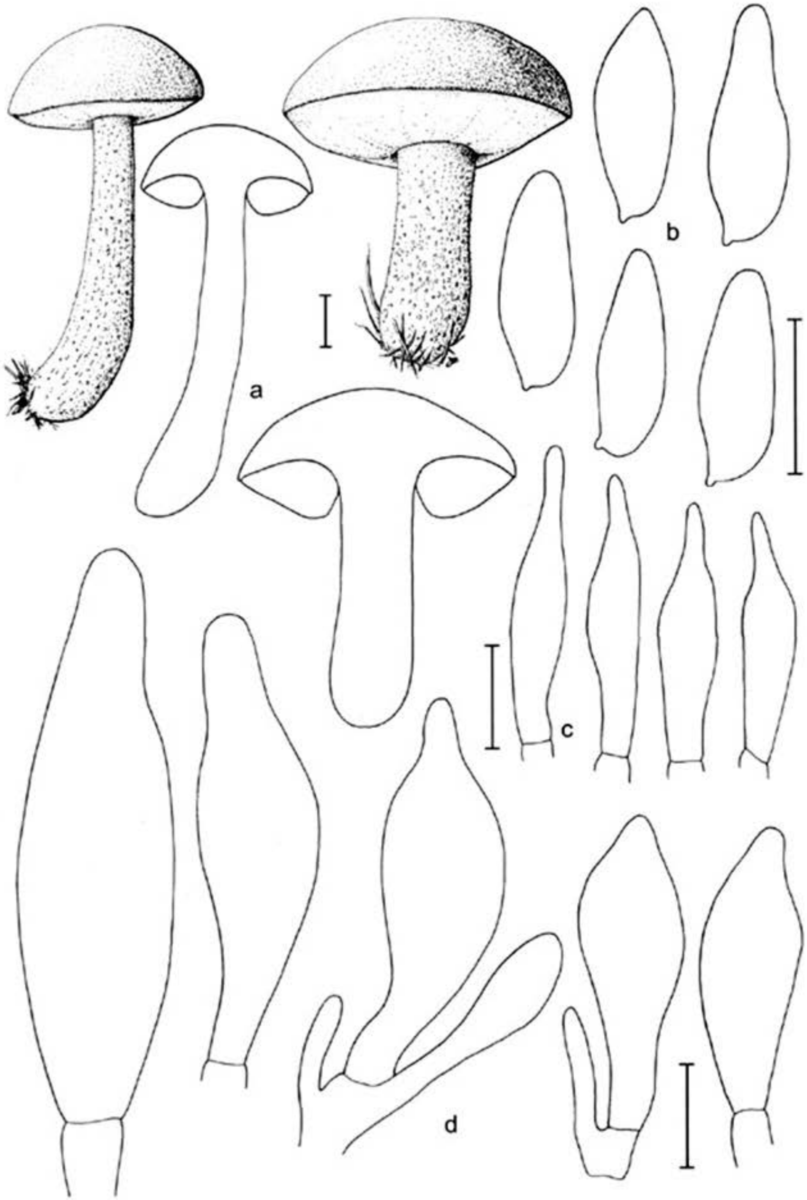


Fig. 14. *Leccinum schistophilum*. a. Habitus; b. spores; c. hymenocystidia; d. caulocystidia. Scale bars = 10 μm resp. 1 cm.

the pileipellis, which is composed of long cylindrical elements, while generally in the pileipellis of *L. variicolor* chains of short cylindrical elements (cylindrocysts) occur. Furthermore lageniform, septate caulocystidia are abundant in *L. variicolor*, while these are only occasionally observed in *L. schistophilum*.

This taxon was erroneously placed in subsection *Leccinum* by Bon (1981), because he overemphasized the importance of the grey tinges that may appear in the context several hours after it has been bruised. Den Bakker *et al.* (2004b, Chapter 3) showed that *L. schistophilum* is nested in subsection *Scabra*.

10. **Leccinum variicolor** Watling — Fig. 15, Plate 9

Leccinum variicolor Watling, Notes Roy. Bot. Gard. Edinburgh 29 (1969) 268. —*Leccinum variicolor* var. *bertauxii* Lannoy & Estades, Doc. Mycol. 21(81) (1991) 22. —*Leccinum variicolor* f. *atrostellatum* Lannoy & Estades, Doc. Mycol. 21(81) (1991) 22. —*Leccinum variicolor* f. *sphagnorum* Lannoy & Estades, Doc. Mycol. 21(81) (1991) 22.

Selected icones. Cetto, Fungi Vero 4 (1983) 1566 (als *L. thalasinum*); Dähncke, 1200 Pilze (1993) pl.97. Lannoy & Estades, Monogr. *Leccinum* (1995) pl. 13–15; R. Phillips, Paddest. Schimm. (1993) 213.

Selected descriptions. Watling, Br. Fung. Fl. 1: 55, 56. 1970.

Characteristics — A small to medium-sized, slender *Leccinum*, usually with a characteristically variegated pileus and bluish green discolorations in the cortex of the lower half of the stipe.

Pileus 35–95 mm, convex, expanding to plano-convex or sometimes broadly conical when mature, with entire margin, not markedly exceeding the tubes, at most up to 1 mm, dark brown (Mu. 5 YR 3/1–4, 10 YR 3/2–3) with a radial patttern of lighter spots, sometimes almost whitish with dark spots or entirely dark brown; very finely tomentose all over, often subviscid with age. Tubes narrowly to broadly adnate, ventricose to broadly ventricose, 7–18 mm long, greyish or cream-white, discolouring brownish when bruised. Pores c. 0.5 mm in diameter, creamy white, often with yellowish brown spots, discolouring brownish when bruised. Stipe 70–157 × 35 mm, cylindrical to clavate, whitish or greyish white, often with a distinct greenish blue discoloration in the lower half of the stipe, entirely covered with brown to black squamules: fine at apex, gradually becoming coarser towards base. Context white, when bruised often staining pinkish (K. & W. 9A3, 9A4) in pileus and upper half of the stipe, often discolouring greenish blue (24A5, 25A5) in the lower half of the stipe (in some collections limited to the cortex of the stipe only); on drying often with a yellow (3A7) discoloration in the lower half of the stipe.

Spores (10.0–)13.5–17.5(–20.0) × 5.0–6.5 μm, Q = 2.4–3.1, Q_{av} = 2.6–2.8 (–2.9), fusiform with a suprahilar depression or without a suprahilar depression. Basidia 25–35 × 8.5–11.0 μm, 2- and 4-spored. Hymenocystidia 25–45 × 8.0–10.5 μm, lageniform to clavate with a mucronate or obtuse apex. Pileipellis a loose cutis of cylindrical, hyaline or brownish intracellularly pigmented elements, 4.5–9.0(–12.5) μm wide, elements in suprapellis often arranged in chains and clearly cylindrical (cylindrocysts), terminal elements generally conical. Caulocystidia (20–)35–85 × 7.5–22.0 μm, clavate or irregular cylindrical to lageniform with a flexuose, sometimes forked neck, which is often separated from the body of the cystidium by a septum. Clamp-connections absent.

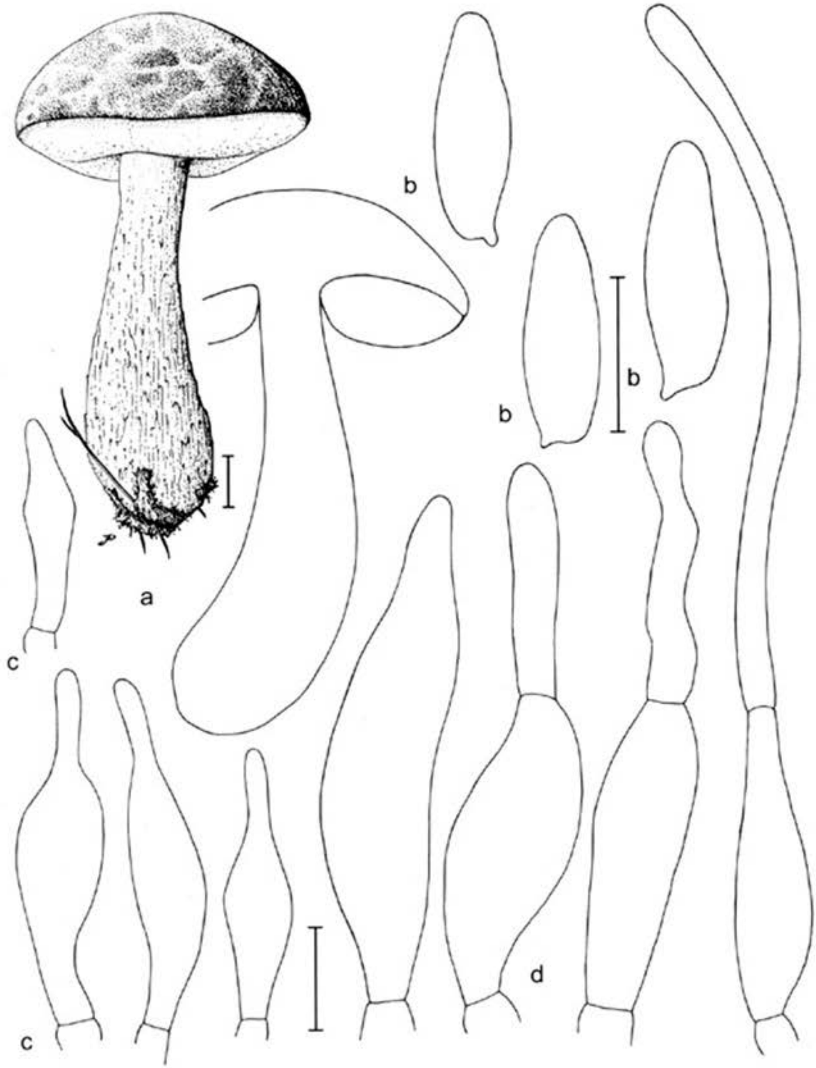


Fig. 15. *Leccinum variicolor*. a. Habitus; b. spores; c. hymenocystidia; d. caulocystidia. Scale bars = 10 μm resp. 1 cm.

Habitat & distribution — Solitary or gregarious, ectomycorrhizal, associated with *Betula* in mossy, acidic environments or in *Betula* swamps with *Sphagnum*, on peaty and sandy soil; in the Netherlands moderately common, widespread, but rather rare in Europe, probably with a circumboreal distribution. Probably unnoticed before in North America (see comments).

Collections studied. THE NETHERLANDS: Drenthe, Witteveen, Stobbeplas, 2 X 1999, *R. Chrispijn, H.C. den Bakker 45*; Erica, Oosterse Bos, 4 X 1999, *H.C. den Bakker 51*; Noord-Holland, Amsterdamse Waterleiding Duinen, Eiland van Rolvers, 2 IX 1999, *H.C. den Bakker 31*; Bergen, Buizerdvlak, 3 XI 1978, *F.A. van den Berg*; Limburg, Mariapeel, Griendtsveen, 8 X 1994, *M.E. Noordeloos 94126a*; Overijsel, Italiaanse Meertjes, 9 X 2000, *H.C. den Bakker 139*. — CANADA: Ontario, Manitoulin Island, 5 X 2002, *H.C. den Bakker 327*; Timiskaming District, 1 IX 1981, *Malloch 1-9-81/5*. — FINLAND: Perä-Pohjanmaa, Rovaniemi, *M. Korhonen10977*. — FRANCE: Isère, Massif de Belledonne, Prabert, 24 X 1989, *Estades 891024/g* (holotype *L. variicolor* var. *bertauxii*, LIP); Massif de Belledonne, Les Seiglières, 13 X 1989, *Estades 89.10.133A* (holotype *L. variicolor* f. *atrostellatum*, LIP). — GREENLAND: Sisimiut, VIII 2000, *L. Jalink & M. Nauta 8328*. — NORWAY: Sogn og Fjordane, Sogndal, 7 IX 2000, *H.C. den Bakker 90*. — SCOTLAND: Inverness-shire, Curr Wood, 11 IX 2001, *H.C. den Bakker 226*; Mull, Gruline House, 7 IX 1968, *R. Watling 6753* (holotype *L. variicolor*, E). — SWEDEN: Jämtland, Östavall, 22 VIII 1999, *H.C. den Bakker 007*; ibid., 22 VIII 1999, G. Redeuilh, *H.C. den Bakker 11*; Kall, 3 IX 2000, *H.C. den Bakker 78*.

Leccinum variicolor can be easily recognized in the field on account of its variegated pileus and distinct blue-green discoloration of the context of the stipe.

This species occurs in North America and could even be locally common, given the fact that the first author observed that this was one of the most common species of the subsection *Scabra* at the Cain Foray (Mycological Society of Toronto) near Huntsville (Ontario, Canada) and on Manitoulin Island (Ontario, Canada) in the fall of 2003. It has long been unnoticed because it has been confused with *L. snellii*. Both species have a similar discoloration of the context, and also the septate caulocystidia, that were thought to be diagnostic for *L. snellii* (Smith et al., 1967) are found in *L. variicolor*. Molecularly, however, the two species cannot even be considered closely related (Den Bakker et al., in prep.). Based on a limited number of herbarium collections and the original description of *L. snellii*, the most important differences are found in the pileipellis, in particular in the shape of the terminal elements. The pileipellis of *L. snellii* is characterized by the presence of 8 – 10 μm broad cylindrical elements and clavate to conical, terminal elements with dark brown vacuolar pigment. The pileipellis of *L. variicolor* is also characterized by the presence of short, cylindrical hyphal elements, but usually they are less broad (4.5 – 9.0 μm) and the terminal elements are conical. In particular the clavate terminal elements are distinctive for *L. snellii*, and have never been found in *L. variicolor*. There may also be an ecological difference between the two taxa. In the Great Lakes region of Canada the first author generally found *L. variicolor* in the same habitat as in Europe, viz. in humid, acidic habitats. *Leccinum snellii* was found only once, and in a completely different habitat, viz. a rich, slightly humid forest on alkaline soil. The locality of the specimens on which the original description of *L. snellii* is based can also be interpreted as a rich forest, consisting of beech, maple and yellow birch. More study is needed to understand the morphological delimitation of these two species.

Lannoy & Estades (1995) recognized three infraspecic taxa within *L. variicolor*, viz. var. *bertauxii* differing from var. *variicolor* by an evenly coloured blackish pileus and the absence of pinkish discolorations of the context in stipe and pileus, f. *atrostellatum*, differing from the typical form by a dark star-shaped pattern on the pileus, and f. *sphagnorum*, a form with uniformly coloured brownish pileus. Since all these character states fall within the normal range of variability of *L. variicolor* examined during this study, these taxa are not considered of taxonomic value.

11. **Leccinum cyaneobasileucum** Lannoy & Estades — Fig. 16, Plate 10

Leccinum cyaneobasileucum Lannoy & Estades, Doc. Mycol. 21 (81) (1991) 23.— *Leccinum brunneogriseolum* Lannoy & Estades, Doc. Mycol. 21 (82) (1991) 1. — *Leccinum brunneogriseolum* var. *pubescentium* Lannoy & Estades, Doc. Mycol. 21(82) (1991) 2.— *Leccinum brunneogriseolum* f. *chlorinum* Lannoy & Estades, Doc. Mycol. 23 (89) (1993) 65.

Selected icones. Courtec. & Duhem, Champ. France Eur. (1994) pl. 1713; Lannoy & Estades, Monogr. Leccinum (1995) pl. 18 – 21.

Selected descriptions. Lannoy & Estades, Monogr. Leccinum (1995) 96 – 101.

Characteristics — A medium-sized, slender to robust *Leccinum* with a greyish brown pileus and whitish to greyish stipital squamules. Context usually with bluish discolorations in or near the stipe base.

Pileus 48 – 80 mm, hemispherical, expanding to convex or plano-convex, with involute to deflexed margin, not markedly exceeding the tubes, greyish brown (Mu. 10 YR 5/3) to light brown (Mu. 10 YR 6/6), sometimes almost white; surface minutely squamulose tomentose, sometimes finely granulose, somewhat viscid when moist. Tubes broadly adnate, 12–16 mm long, ventricose to broadly ventricose, whitish with a brownish or greyish tinge. Pores c. 0.5 mm in diameter, whitish or light greyish, discolouring brownish when bruised. Stipe 72–110 × 11– 23 mm, cylindrical to clavate; densely covered with confluent squamules, which hardly show the background, giving the stipe an almost woolly appearance, squamules first whitish, greyish when mature. Context whitish, not staining or discolouring pinkish (K. & W. 9A3) in pileus and apex of stipe only; staining bluish (23A7) in cortex and base of stipe, especially in places where eaten by snails or arthropods.

Spores (11.0–)14.0–19.5(–21.0) × (3.5–)4.0–6.5(–7.0) µm, Q = 2.6 – 4.0(–4.1), Q_{av} = 3.1 – 3.5, fusiform to narrowly fusiform with a suprahilar depression. Basidia 20 – 30 × 11.5–13.0 µm, 4-spored, sometimes 2-spored. Hymenocystidia 30 – 45 × 5.5 – 7.5 µm, lageniform to fusiform. Pileipellis a cutis of easily detachable, wide, cylindrical, brownish (sepia) elements; terminal elements often conical, (7.0 –) 8.0 – 15.0(– 17.0) µm wide and narrowly cylindrical, dark brown elements, 4.5 – 6.0 µm wide. Caulocystidia 30 – 60 × 4.5 – 10.5 µm, narrowly lageniform, utriform or fusiform, when lageniform often with a flexuose neck. Clamp-connections absent.

Habitat & distribution — Gregarious or solitary, ectomycorrhizal, associated with *Betula* on dry to humid sandy or peaty soil, sometimes in *Sphagnum* bogs; common in the Netherlands, moderately common in large parts of Europe, although rare or probably absent in Finland, Norway and Sweden.

Collections studied. THE NETHERLANDS: Friesland, Schiermonnikoog, Berkenplas, 4 IX 1999, *H.C. den Bakker 39*; Drenthe,, Emmen, Oosterbos, 2 X 1999, *H.C. den Bakker 43*; Gelderland, Ede, Ginkelse zand 14 IX 1993, *M.E.Noordeloos 93201*; Leusden, Bos Buurtweg, 22 X 2003, *J. Wisman s.n.*; Noord-Holland, Amsterdamse Waterleiding Duinen, Eiland van Rolvers, 23 X 1999, *H.C. den Bakker 59*; Limburg, Mariapeel, Griendtsveen, Leg. N. Dam, 1994, *M.E. Noordeloos 94133*. — FRANCE: Orne, Forêt de Bellême, 28 IX 2001, *Van Brummelen*; Isère, Roybon/St Etienne de St Geoir, 1 X 1990, *Estades 9011010B* (holotype *L. brunneogriseolum*, LIP); Isère, Massif de Belledonne, Tourbière de Luitel, 20 IX 1990, *Estades 90.09.202.D.E.F.* (holotype *L. brunneogriseolum* var. *pubescentium*, LIP); Isère, Col des Mouilles, 24 X 1989, *Estades 891024/4* (holotype *L. brunneogriseolum* f. *chlorinum*, LIP) ; Isère, Roybon près du Col de toutes Aures, 16 X 1988, *Estades 881016/1* (holotype *L. cyaneobasileucum*, LIP).

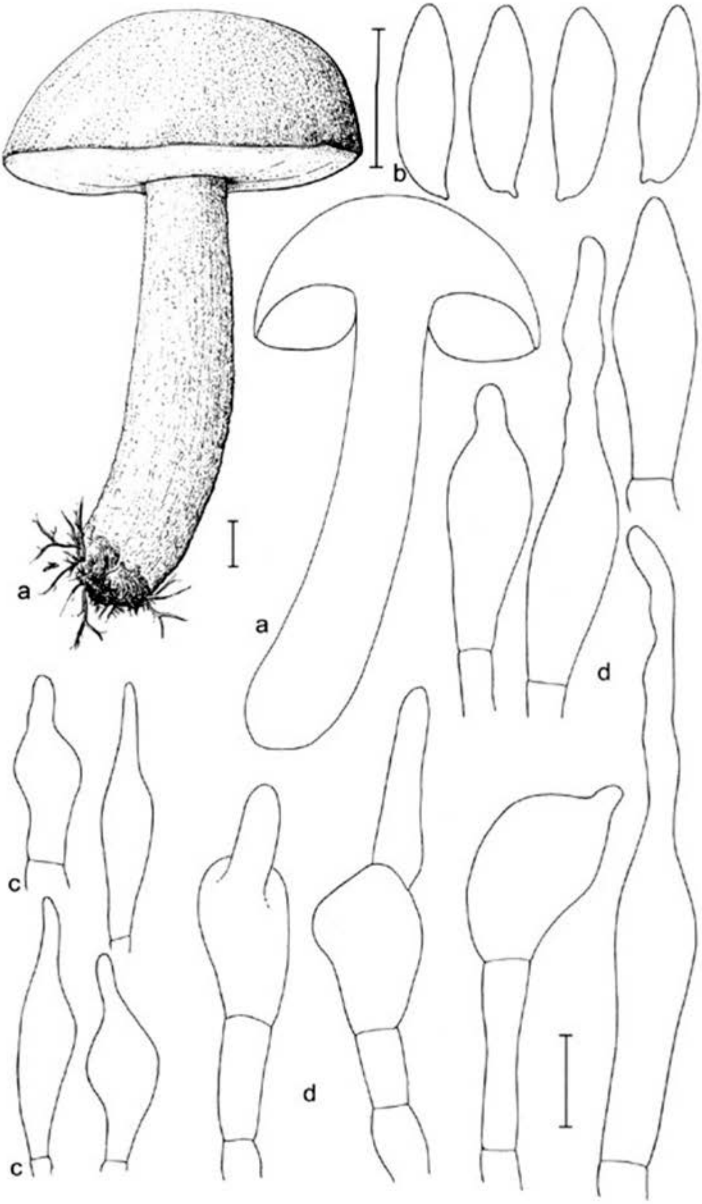


Fig. 16. *Leccinum cyaneobasileucum*. a. Habitus; b. spores; c. hymenocystidia; d. caulocystidia. Scale bars = 10 μm resp. 1 cm.

Leccinum cyaneobasileucum is easily recognized already in the field by the generally dull-coloured greyish brown pileus and woolly stipital surface. Pale and albino forms occur, which is confirmed by phylogenetic comparison of ITS and *Gapdh* sequences of material of *L. brunneogriseolum* and *L. cyaneobasileucum*. These pale and albinistic forms can be confused with *L. holopus* in the field, but differ from this taxon by their slender spores ($Q_{av} \geq 3.0$), and the abundant cylindrocysts in the pileipellis. Due to the fact that the name *L. cyaneobasileucum* was published earlier than *L. brunneogriseolum*, the first name has priority and, unfortunately, has to replace the latter.

Lannoy & Estades (1995) recognized two infraspecific taxa within *L. brunneogriseolum*, viz. var. *pubescentium*, a variety that differs from var. *brunneogriseolum* by a darker brown pileus and a robust stipe, and f. *chlorinum* a form that shows olivaceous colours in the margin in older fruit-bodies and also olivaceous, greenish tinges in the stipe. Darker brown pilei fall within the variability of the species, and greenish tinges like in f. *chlorinum* can also be observed in other taxa when they form fruit-bodies during a continuous wet period or in a wet habitat.

Though a considerable number of Scandinavian collections of species of subsection *Scabra* were examined and several field trips to Sweden, Norway and Finland were undertaken, we never observed *L. cyaneobasileucum* in Scandinavia.

12. **Leccinum holopus** (Rostk.) Watling — Fig. 17, Plate 11

Boletus holopus Rostk., Sturm's Deutschl. Flora, III (Pilze) 5 (1844) 131; *Leccinum holopus* (Rostk.) Watling, Trans. Bot. Soc. Edinburgh 43 (1960) 692. — *Leccinum nucatum* Lannoy & Estades, Doc. Mycol. 23(89) (1993) 63–65.

Iconotype. Rost., Sturm's Deutschl. Flora, III (Pilze) 5 (1844) pl. 48.

Epitype. Norway, Sogn og Fjordane, east of Haukaosen Airport, 8 IX 2000, *H.C. den Bakker* 85 (L, designated here).

Misapplication. *Leccinum niveum* sensu auct., Rauschert — *Leccinum chioneum* sensu auct., Redeuilh. — *Boletus albus* sensu auct. — *Leccinum rotundifoliae* sensu A.H. Sm., Thiers & Watling, Michigan Bot. 6 (1967) 128; sensu Kallio, Rep. Kevo subarct. Res. Stat. 12 (1975) 25–27. — *Leccinum aerugineum* sensu Lannoy & Estades, Doc. Mycol. 21(81) (1991) 23.

Selected icones. Korhonen, Karstenia 35 (1995) 64: Fig. 12; Ryman & Holmåsen, Pilze (1992) 230.

Selected descriptions. Watling, Br. Fung. Fl. 1 (1970) 50, 51.

Characteristics — A small to medium-sized, slender to robust *Leccinum*; pileus usually whitish to pale brownish, stipital squamules usually whitish to light brownish, context either without any discolorations or some bluish spots in the stipe base. Species of humid, acidic habitats.

Pileus 40–100 mm, convex, expanding to plano-convex, with entire margin, exceeding the tubes up to 1 mm, usually minutely tomentose when fresh, sometimes granular, often becoming more viscid with age, whitish to yellowish, greyish white, often with a greenish hue or bluish green in older fruit-bodies, sometimes brown (Mu. 10 YR 5/4). Tubes 7–18 mm long narrowly to broadly adnate, segmentiform to broadly ventricose, greyish white, finally brownish pinkish. Pores c. 0.5 mm in diameter, whitish with yellowish brown spots, brownish when bruised. Stipe 59–140 × 10–23 mm, cilindrical to clavate, whitish, covered with coarse whitish, in mature fruit-bodies ochre to greyish squamules, sometimes blackish squamules already present in young fruit-bodies. Context whitish, discolouring pinkish in pileus and stipe when bruised, bluish discolorations often visible in cortex of stipe base, but regularly not discolouring at all.

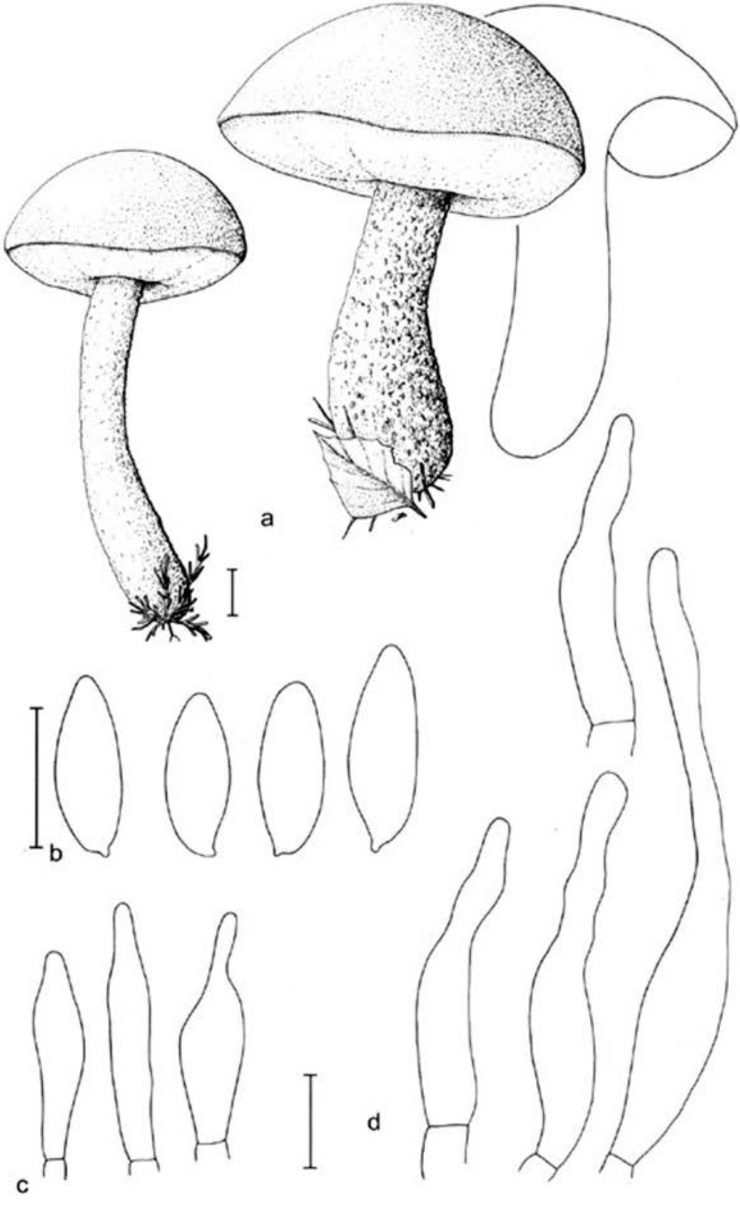


Fig. 17. *Leccinum holopus*. a. Habitus; b. spores; c. hymenocystidia; d. caulocystidia. Scale bars = 10 μm resp. 1 cm.

Spores 15.5–18.0 × 5.5–7.0 µm, Q = 2.5–3.0, Q_{av} = 2.6–2.8, broadly fusiform to fusiform with a shallow suprahilar depression. Basidia 25–35 × 11.5–12.5 µm, generally 4-spored. Hymenocystidia 40–45 × 7.5–9.0 µm, lageniform to fusiform. Caulocystidia 40–55 × 9.0–13.5 µm, fusiform, clavate to cylindrical, often with a flexuose neck. Pileipellis a cutis composed of cylindrical elements, 3.5–5.0(–7.0) µm in diameter, often hyaline, granular incrusted, sometimes with brownish vacuolar pigment; terminal elements sometimes ellipsoid, then 10.5–11.5 µm in diameter. Clamp-connections absent.

Habitat & distribution — Solitary or gregarious, ectomycorrhizal, associated with *Betula* in *Sphagnum* bogs or among grass and mosses, on humid, peaty soil; rather rare in the Netherlands, common and probably widespread throughout the (circumboreal) distribution area of its host.

Collections studied. THE NETHERLANDS: Zuid-Holland, Nieuwkoop, De Haeck, 5 IX 1999, M.E. Noordeloos, *H.C. den Bakker 37*; Nieuwkoop, De Haeck, 9 IX 1999, *H.C. den Bakker 40*. — FRANCE: Isère, Massif de l'Obiou, IX 1991, *Estades 9109251* (holotype *L. nucatum*, LIP); Isère, Massif de Belledonne, Les Seiglières, *Estades 8909221A* (neotype *L. aerugineum*, proposed by Lannoy & Estades, LIP). — GREENLAND: Sisimiut, VIII 2000, *L. Jalink & M. Nauta 8326*. — NORWAY: Sogn og Fjordane, east of Haukaosen Airport, 8 IX 2000, *H.C. den Bakker 85* (epitype *L. holopus*, L, designated here); Finnmarken, Tana Rastiggaisa, 18 VIII 1995, *M.E. Noordeloos 95095*.

The typical form of *L. holopus* is a slender, pale, almost whitish bolete, without any clear discoloration of the context when bruised, occurring in *Sphagnum*-bogs in montane, sub-boreal and boreal regions. Another, sturdier form with a darker, sometimes brownish pileus, darker stipital ornamentation and bluish discolorations in the stipe base, is found in wet, acidic birch woods. This last form has been described as a separate species by Lannoy & Estades (1993) as *L. nucatum*. No molecular evidence to support the existence of *L. nucatum* as a separate species was found. Moreover, the differences between both forms are not always clearcut and intermediates occur. For this reason the *nucatum*-type populations do not justify a formal taxonomic status and *L. nucatum* is placed into the synonymy of *L. holopus*.

Leccinum holopus can be distinguished from related taxa by a combination of the following microscopic characters: a pileipellis that is composed of slender hyphal elements of relatively even diameter (3.5–5.0 µm), abundant cylindrical caulocystidia with a flexuose neck in the lower half of the stipe and an average Q-value of spores ≤ 2.8.

Smith & Thiers (1971) recognized two varieties of *L. holopus*: var. *holopus* and var. *americanum*. According to Smith & Thiers var. *americanum* mainly differs from var. *holopus* in the pinkish reddish discoloration of the context when bruised and the blackish stipe ornamentation. Both varieties have been observed in the field by the first author in Canada, sometimes close together on the same spot. Though no molecular differences could be found that were congruent with these varieties, no intermediates were observed in the field. The absence of (morphological) intermediates seems to justify recognition of var. *americanum* as an infraspecific taxon.

SECTION **LUTEOSCABRA** Singer, Amer. Midl. Naturalist 37 (1947) 122

Pileipellis a trichoderm of septate hyphae with swollen terminal elements.
Type species: *Leccinum nigrescens* (Rich. & Roze) Singer.

13. **Leccinum crocipodium** (Letell.) Watling — Fig. 18, Plate 12

Boletus crokipodius Letell., Fig. Champ. (1836) pl. 166 (plate only, no description); *Leccinum crocipodium* (Letell.) Watling, Trans. Bot. Soc. Edinburgh 39 (1961) 200. — *Boletus tessellatus* Gillet, Hymenomycetes (1878) 636, non *B. tessellatus* Rostk. 1844. — *Boletus nigrescens* Rich. & Roze, Atl. Champ. (1888) pl. 60, fig. 5–10, non *B. nigrescens* Pallas 1771–1776; *Leccinum nigrescens* (Rich. & Roze →) Singer, Am. Midl. Naturalist 37 (1947) 112. — *Boletus luteoporus* Bouchinot in Barbier, Bull. Trimestriel Soc. Mycol. France 20 (1904) 91; *Leccinum luteoporum* (Bouchinot) Alessio, Fungi Europei vol. 2A (1991) 94. — *Boletus velenovskyi* Smotl., Sitzungsber. Königl. Böhm. Ges. Wiss. Prag. 1911 (1912) 60.

Holotype. Letell., Fig. Champ. (1836) pl. 166.

Epitype. France: Ardennes, Sommeau/Beaumont-en-Argonne, F. de Belval, 20 IX 1999, R. Walleyn 1659 (L, isotype in GENT).

Selected icones. Breitenb. & Kränzl., Pilze Schweiz 3 (1991) 72. pl. 34; Galli, Boleti (1998) 260, 261; Muñoz, Fungi non del. 13 (2000) pl. 18; Pilát & Dermek, Hrívobité Huby (1974) pl. 73 (as *L. nigrescens*).

Selected descriptions & figures. Muñoz, Fungi non del. 13: 39-40. 2000.

Characteristics — Stout species with yellow-brown, often olivaceous tinged, areolate-cracked pileus; small, yellow pores and yellowish, fusiform stipe with fine brown squamules; context staining reddish-brown to violaceous brown then black when bruised; pileipellis a trichoderm of cylindrical, clavate to fusiform elements, 7.0–15 μm wide; associated with *Quercus* and *Carpinus*.

Pileus 40–75 mm broad, hemispherical to convex with straight, appendiculate margin extending over tubes for about 1 mm, yellowish brown or reddish brown, sometimes with an olivaceous tinge, later darker olivaceous brown or blackening when strongly exposed (Mu. 2.5–5 Y 5–6/4–6), dry, appressed tomentose becoming entirely cracked with age, breaking up in small irregular patches showing pale grey context in between. Tubes adnexed to adnate, narrowly to broadly ventricose, up to 15 mm broad, pale yellow (5 Y 8/6); pores small, 0.3–0.5 mm in diameter, rounded, rather bright yellow (K. & W. 3A7–3B7), turning reddish brown, then black when bruised. Stipe 60–150 × 15–30 mm, straight, typically fusiform with broadest part below the middle, tapering at base, more rarely cylindrical, cream-white at apex, pale chrome-yellow below, minutely squamulose in longitudinal rows of small yellow to dark brown floccose squamules which become coarser towards base. Context thick, firm, pale yellow or cream-coloured, staining reddish brown to violaceous-grey when bruised, blackening in damaged parts. Smell indistinct. Taste mild.

Spores (11.5–)12.0–15.0 × 5.0–6.5.0 μm, on average 13–14 × 5.5–6.0 μm, Q = 2.0–2.9, Q_{av} = 2.3–2.4; fusiform with conical apex, often almost amygdaliform, with slight to distinct suprahilar depression, relatively thin-walled, pale brown in water. Basidia 20–35 × 5.0–9.0 μm, clavate, 4-spored. Hymenial cystidia abundant on edge and sides of the pores, 20–55 × 4.5–11 × 2.0–4.0 μm, lageniform, often with rather long, tapering neck, colourless or with brown, intracellular-granular pigment. Pileipellis a rather regular trichoderm of septate hyphae, terminal elements 12–50(–50) × 6.5–17 μm, usually rather slender, cylindrical, clavate or conical, with intracellular, incrusting and extracellular pigment. Stipitipellis a cutis of narrow, cylindrical, 4.0–7.0 μm wide hyphae, with small to fairly large caulohymenial clusters of basidia and cystidia, forming the squamules on the stipital surface. Caulocystidia 25–120 × 7.0–15 × 2.0–4.5

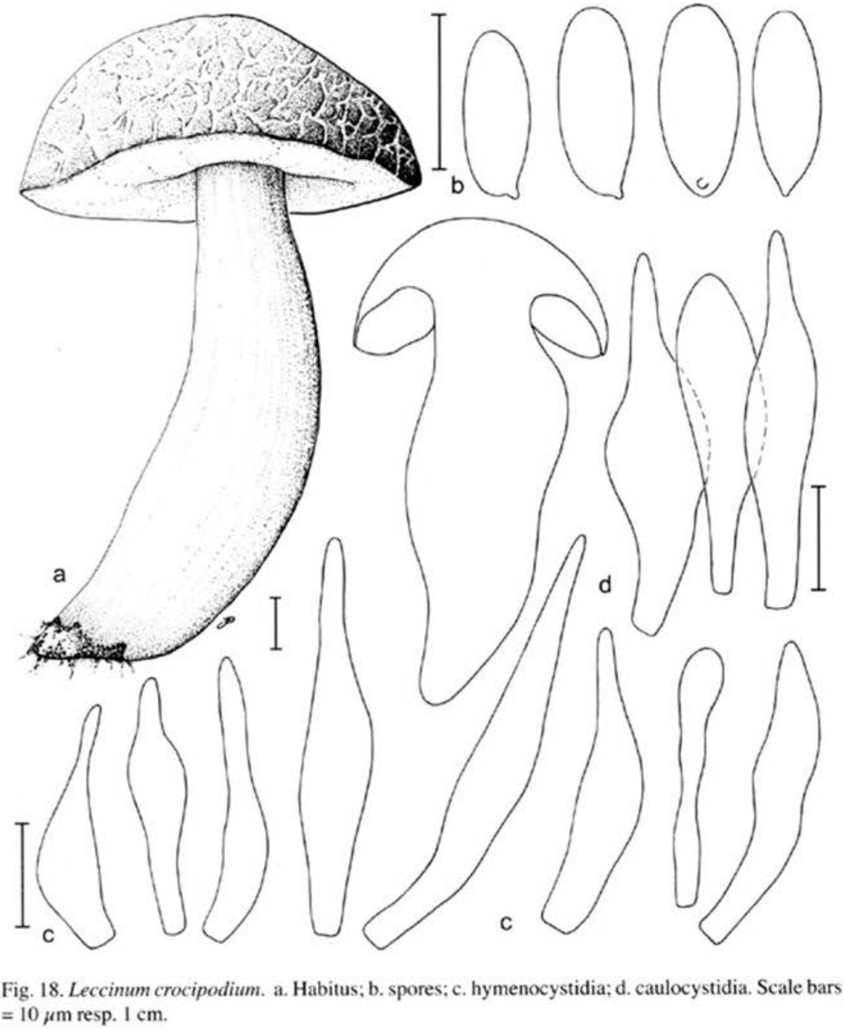


Fig. 18. *Leccinum crocipodium.* a. Habitus; b. spores; c. hymenocystidia; d. caulocystidia. Scale bars = 10 μm resp. 1 cm.

μm, lageniform or fusiform, thin- or thick-walled, colourless or with brown granular intracellular pigment. Clamp-connections absent.

Habitat & distribution — Solitary or gregarious, ectomycorrhizal, associated with *Quercus* and *Carpinus* on heavy loamy, often slightly calcareous soil; extremely rare in the Netherlands (Schaelsberg, Limburg; Sterkenburg, Utrecht), probably overlooked. Widespread, rare to locally more common in Central and Southern Europe, preferably in thermophilous deciduous forest on heavy loamy soil.

Collections studied. BELGIUM: Namur, Rochefort, Ave-et-Auffe, 14 IX 2003, *M.E. Noordeloos 200311*; ditto, Bois de Lamache, *Th.W. Kuyper s.n.*; Luxembourg, Barveaux, 13 IX. 1975, *C. Bas 6666.*

— FRANCE: Ardennes, Sommeau/Beaumont-en-Argonne, F. de Belval, 20 IX 1999, *R. Walleyn 1659*; Lorraine, Guersling, 3 IX 2000, *E.J.M. Arnolds 00-74*. — THE NETHERLANDS: Utrecht, Sterkenburg, 3 IX 1999, *G.A. de Vries s.n.*; Limburg, Valkenburg, Schaelsberg, 6 VIII 2001, *N. Dam 01021*.

The most distinctive characters of *L. crocipodium* are the rather yellow pores, combined with the blackening context. It is the only species with this combination of characters known from temperate regions in Europe, where it has a preference for thermophilous deciduous forests. The macroscopically similar *L. corsicum* and *L. lepidum* have an exclusive Mediterranean distribution, and are associated with *Cistus* spp. and *Quercus ilex* respectively. *Leccinum crocipodium* has only recently been discovered in the Netherlands in 1999, with a second observation in 2001. Whether this may be due to climate changes, or whether it has been overlooked in the past, is difficult to ascertain.

Boletus rimosus[28], often cited as a synonym, is better considered a *nomen dubium* on account of the brown-olivaceous pileus and pale pores. See also Rauschert (1987) for nomenclatural comments.

14. **Leccinum pseudoscabrum** (Kallenb.) Šutara — Fig. 19

Boletus pseudoscaber Kallenb., Die Pilze Mitteleuropas 1 (1935) 117, pl. 40; *Leccinum pseudoscabrum* (Kallenb.) Šutara, Česká Mykol. 43 (1989) 6. — *Boletus scaber* var. *carpini* R. Schulz in Michael & Schulz, Führ. Pilzfreunde 1 (1924) 95; *Boletus carpini* (R. Schulz) Pearson, Naturalist 96 (1946) 818; *Leccinum carpini* (R. Schulz) D. Reid, Trans. Bot. Soc. Edinburgh 48 (1965) 525.

Excluded. *Leccinum griseum* sensu auct.

Holotype. not existent. Type locality: unknown, Germany.

Selected icones. Bon, Mushr. Toadst. (1987) 41; Breitenb. & Kränzl., Pilze Schweiz 3 (1991) 70, pl. 31; Engel, Rauhstielröhrlinge (1978) pl. 2; Galli, Boleti (1998) 254, 255; Muñoz, Fungi non del. 13 (2000) pl. 19; R. Phillips, Paddest. Schimm. (1981) 212; Pilát & Dermek, Hrívobité Huby (1974) pl. 7.

Selected descriptions & illustrations. Engel, Rauhstielröhrlinge (1978) 14, 15; Muñoz, Fungi non del. 13 (2000) 42–44; Watling, Br. Fungus Fl. (1970) 48, 49, fig. 48, 54.

Characteristics — Slender to medium-sized species with remarkably dark, rugulose pileus and finely squamulose stipe, associated with *Carpinus betulus* or *Corylus avellana* on heavy, clayey soil.

Pileus up to 30–70 (–100) mm broad, hemispherical to conico-convex at first, expanding to truncately convex or plano-convex, with involute margin, not or only slightly exceeding the tubes for about 1 mm, pale to moderately dark grey-brown (Mu. 10 YR 3–4/3, 4–5/4–6), sometimes with slight olivaceous tinge, dry, dull, initially velvety to minutely or strongly radially rugulose or veined, usually cracked with age with concentric fissures, particularly near margin showing pale pinkish context. Tubes adnate to adnexed, subventricose to ventricose, up to 25 mm long, yellowish to pinkish brown or greyish brown (2.5 Y 8/4, 10 YR 8/4, 10 YR 3/3–4), with brownish tinge when old. Pores very small, 1–2 per mm, rounded, pale brownish, staining brown-grey when bruised. Stipe 60–130 × 6–14 mm, cylindrical, slightly widened towards base to subclavate, sometimes flexuous, whitish to pale grey ochre, entirely covered with

---

[28] *Boletus rimosus* Venturi, Stud. Micol. (1842) 31, pl. 10, fig. 93, 94.

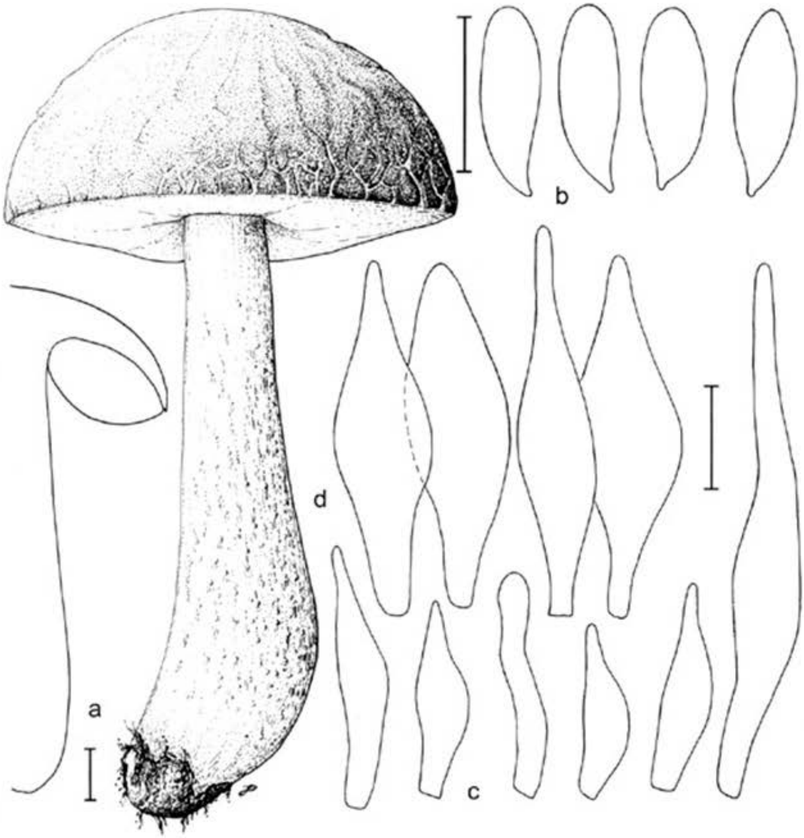


Fig. 19. *Leccinum pseudoscabrum*. a. Habitus; b. spores; c. hymenocystidia; d. caulocystidia. Scale bars = 10 μm resp. 1 cm.

brownish black (10 YR 6–5/4, 3–4/3, 3/2), very small dot-like squamules arranged in longitudinal rows, which become somewhat coarser towards the white tomentose base. Context dirty white at first with watery darker streaks, on cutting first slowly staining pink to purple then greyish to blackish with purple tinge.

Spores (12.5–)13.0–18.5 × 4.5–6.0 μm, on average 14.5–15 × 4.8–5.3 μm, Q = 2.3–3.3, Qav = 2.7–2.9; slender, fusiform with conical apex, with distinct suprahilar depression, relatively thin-walled, pale brown in water. Basidia 20–40 × 6.0–8.0 μm, clavate, 4-spored. Hymenial cystidia abundant on edge and sides of the pores, 18–70 × 5.0–14 × 2.0–4.0 μm, lageniform, often with rather long, tapering neck, usually with dark brown, intracellular-granular pigment. Pileipellis an intricate trichoderm of septate hyphae, terminal elements 15–70(–90) × 3.5–10.5 μm, irregularly cylindrical or clavate with intracellular pigment. Stipitipellis a cutis of narrow, cylindrical, 3.5–8.0 μm wide hyphae, with small to fairly large caulohymenial clusters of basidia and cystidia, forming the squamules on the stipital surface. Caulocystidia 25–90 × 5.0–12 × 2.0–8.5 µm, lageniform, clavate or fusiform, thin- or thick-walled, colourless or with brown granular intracellular pigment. Clamp-connections absent.

Habitat & distribution — Solitary or gregarious, ectomycorrhizal, associated with *Carpinus* or *Corylus* in deciduous forest and roadsides on calcareous loam and clay (Stellario-Carpinetum; Alno-Padion); rare in the Netherlands, mainly in F, very rare in D, S, K, E and Z; susceptible (Veerman 2004); widespread in Europe, not uncommon in mixed deciduous forests on clayey or loamy soil.

Collections studied. AUSTRIA: Kärnten, St. Margareten im Rosental, Gupf, 8 IX 1998, *M.E. Noordeloos 9896*. — BELGIUM: Luxembourg, Valley of Ourthe near Nandrin, 28 VII 1984, *L Jalink & M. Nauta* 1037. — GERMANY: Nordrhein-Westfalen, Eifel, Gerolstein, 12 VII 1967, *P.B. Jansen s.n.* — THE NETHERLANDS: Utrecht, Breukelen, Gunterstein, 21 IX 1994, *M.E. Noordeloos 9497*; — POLAND: Swieta Katarzyna, Wilkouska Dolina, 10 IX 1966, *C. Bas 4750*.

As on species level the epithet *pseudoscaber* is older than *carpini*, the correct name for the species is *L. pseudoscabrum*. Note that there is no connection between the name of the species and the subsection *Pseudoscabra*, an artificial assemblage of species characterized by cylindrocysts. The name *L. griseum* has also been used for this species. However, the basionym *Gyroporus griseus* Quél. is a superfluous name change for *Boletus scaber*.

EXCLUDED AND DUBIOUS NAMES

aerugineum

Boletus chioneus ß [var.] *aerugineus* Fr., Observ. Mycol. 2 (1818) 250.; *Leccinum aerugineum* (Fr.) Lannoy & Estades, Doc. Mycol. 21(81) (1991) 23.

The name was published with a very short diagnosis ("pileo stipitique verrucoso aeruginosis"). These greenish colours are not diagnostic for certain species, but can – depending on meteorological conditions – occur in several species. The name is therefore best regarded as *nomen dubium*. The neotype (from France!) belongs to *L. holopus*.

chioneum

Leccinum chioneum (Fr.) Redeuilh, Doc. Mycol. 20(78) (1990) 35; *Boletus niveus* Fr., Obs. Mycol. 1 (1815) 111, non *B. niveus* Jull. in Vill., Hist. Pl. Dauphiné 3(2) (1789) 1040; *B. chioneus* Fr., Observ. Mycol. 2 (1818) 250 [name change]; *Leccinum niveum* (Fr. →) Rauschert, Nova Hedwigia 45 (1987) 503 [illegitimate, superfluous].

This name has been considered an older name for *L. holopus*, but the greying context ["caro … tacta cinerascit"] contradicts this. Therefore it is excluded as a *nomen dubium*.

fuscoalbum

Leccinum fuscoalbum (Sow.) Lannoy & Estades, Doc. Mycol. 24(94) (1994) 18; *Boletus fuscoalbus* Sow., Col. Fig. Engl. Fungi 3 (1814) pl. 421. — *Boletus leucophaeus* Pers., Mycol. Eur. 2 (1825) 140 [illegitimate, superfluous name change]; *Leccinum leucophaeum* (Pers.) Bon in Bon & Van Haluwyn, Doc. Mycol. 11(44) (1981) 35 [illegitimate, based on illegitimate, superfluous basionym].

Ever since Fries (Syst. mycol., Ind. gen., 1832), *Boletus fuscoalbus* has been considered a synonym of *L. scabrum* or as a closely related species. The protologue by Sowerby ("inside white, sometimes changing to brown, or even black on exposure by cutting in the air, especially if in a tender state or bruised") makes clear that the name is more likely an older name for *L. pseudoscabrum* or *L. duriusculum*. Since there are apparently four different interpretations for *Boletus fuscoalbus*/*B. leucophaeus* (a synonym of *L. scabrum*; a closely related species to *L. scabrum*; *L. pseudoscabrum*; *L. duriusculum*), it seems best to consider the name as a *nomen dubium*.

molle

Leccinum molle (Bon) Bon, Doc. Mycol. 19 (75) (1989) 58; *Krombholziella mollis* Bon, Doc. Mycol. 14 (56) (1984) 22.

The description of Bon (1984) and Lannoy & Estades (1995) is applicable to a number of species since the greenish tinges and discolorations represent a character complex that is commonly encountered in several species of subsection *Scabra* when the fruit-bodies have developed during a cool, humid period. The type material is in poor condition and not sufficiently well-preserved to study its molecular and microscopical characters. The spores could be measured and have an average Q-value of 3.1, which is typical for *L. scabrum*. It is excluded as a *nomen dubium*.

murinaceum

Leccinum murinaceum (J. Blum) Bon, Doc. Mycol. 9 (35) (1979) 41; *Boletus murinaceus* Blum, Bull. Trimestriel Soc. Mycol. France 85 ('1969' 1970) 560.

The holotype of *L. murinaceum* (Blum 750, PC) is in very poor condition, and immature, and it proved to be impossible to study any molecular or morphological characters. The original diagnosis of Blum (1970) does not offer much help to clarify the identity of this taxon either. The interpretation of Lannoy & Estades (1995: 68) comes close to the current concept of *L. melaneum*. According to these authors *L. murinaceum* is not only mycorrhizal with *Betula*, but also with *Salix*, a mycorrhizal association that is exceptional in subsection *Scabra*. It is considered a *nomen dubium* for these reasons.

olivaceosum

Leccinum olivaceosum Lannoy & Estades, Doc. Mycol. 24 (94) (1994) 10.

The type material is in poor condition and could not be used for further study. The plates of Lannoy & Estades (1995) show a species that looks macro-morphologically like *L. holopus* and *L. schistophilum*. A molecular study by Binder (1999) based on material provided by the authors shows that its ribosomal sequences are reminiscent of those of *L. holopus*. Further data are needed to demonstrate if this taxon is really synonymous with *L. holopus*.

oxydabile

Leccinum oxydabile (Singer) Singer, Amer. Midl. Naturalist 37 (1947) 123; *Krombholzia oxydabilis* Singer, Schweiz. Z. Pilzk. 16 (1938) 149.

The original description *L. oxydabile* is equally applicable to *L. holopus*, *L. variicolor*, *L. cyaneobasileucum*, *L. snellii* and *L. schistophilum*. Unfortunately, no type material was designated by Singer. According to Hahn (1997) *L. oxydabile* is a taxon with a brownish pileus, a stipe base that sometimes shows traces of blue, and which has broad (up to 20 μm) pileipellis elements. This decription comes close to *L. cyaneobasileucum*. Hahn described the stipe, however, as greyish brown to blackish, which is atypical for *L. cyaneobasileucum*. Another option would be that *L. oxydabile* sensu Hahn represents *L. schistophilum*, but the broad pileipellis elements do not fit with our interpretation of that species. Given the confusion associated with the name *L. oxydabile* (Hahn, 1996), we think it is better to abandon the name and consider it a *nomen confusum*.

rufum

Boletus rufus Schaeff. Fungorum qui in Bavaria et Palatinatu circa Ratisbonam nacuntur icones nativis coloribus expressae (1774) Vol. IV; *Leccinum rufum* (Schaeff.) Kreisel, Boletus, SchrReihe 1 (1984) 30.

The name *Leccinum rufum* has often been used for *L. aurantiacum*. Dörfelt & Berg (1990) interpreted this name as the taxon we call *L. versipelle*. Schaeffer's original plate (Schaeffer, 1763) and description (Schaeffer, 1774) of *Boletus rufus* can be applied to our current concept of *L. vulpinum*, *L. versipelle* and *L. aurantiacum*. Further use of the name *Leccinum rufum* would only cause more nomenclatural confusion and as such the name should be rejected.

thalassinum

Leccinum thalassinum Pilát & Dermek, Hríbovité huby (1974) 146.

Lannoy & Estades (1995) listed this taxon as a possible synonym of *L. variicolor*. However, it cannot be excluded that it may represent *L. schistophilum*. Unfortunately the type is in poor condition, and the shape of the caulocystidia, essential to distinguish *L. schistophilum* from *L. variicolor*, could not be observed.

ACKNOWLEDGEMENTS

We would like to thank Thom Kuyper for his advice and help with the nomenclature and improvement of the text. Marijke Nauta is thanked for her editorial advice and critical, but helpful remarks on the text. We would also like to thank Jan Frits Veldkamp for his help with the Latin diagnosis. Further we are most grateful to Joanne Porck for her beautiful illustrations. Jaap Wisman, Ruben Walleyn, Alan Hills and the curators of LIP, SFSU, MICH, H, PC are thanked for providing (type)material. We are grateful to Nancy Ironside for giving the first author the opportunity to collect in Ontario, Canada.

REFERENCES

Aanen, D.K. & Th.W. Kuyper. 2004. A comparison of the application of a biological and morphological species concept in the Hebeloma crustuliniforme complex within a phylogenetic framework. Persoonia 18: 285–316.

Bessette, A.R., W.C. Roody & A.E. Bessette. 2000. North American Boletes: A Color Guide to the Fleshy Pored Mushrooms. Syracuse University Press. Syracuse.

Binder, M. 1999. Zur molekularen Systematik der Boletales: Boletineae und Sclerodermatineae subordo nov. [PhD Dissertation]. Regensburg, Germany: University of Regensburg.

Binder, M. & H. Besl. 2000. 28S rDNA sequence data and chemotaxonomical analyses on the generic concept of Leccinum (Boletales). In: Associazone Micologica Bresadola (ed.), Micologia 2000: 75–86. Grafica Sette, Brescia.

Binder, M. & A. Bresinsky. 2002. Derivation of a polymorphic lineage of gasteromycetes from boletoid ancestors. Mycologia 94: 85–98.

Binder, M. & D.S. Hibbett. 2004. Toward a global phylogeny of the Boletales. http://www.clarku.edu/faculty/dhibbett/boletales_stuff/Global_Boletales_2004_28S.gif

Blum, J. 1967a. Essai de détermination de quelques Bolets du groupe scaber. Rev. Mycol. (Paris) 32: 135–161.

Blum, J. 1967b. Essai de détermination de quelques Bolets du groupe scaber. Rev. Mycol. (Paris) 32: 336–367.

Bon, M. & C.H. van Haluwyn. 1981. Macromycètes des terrils de charbonnages du Nord de la France, 2ème Note. Doc. Mycol. 11(44): 29–59.

Bresinsky, A. 1996. Über Leccinum subcinnamomeum, Rhizopogon pumilionus und Paxillus filamentosus (Boletales). Z. Mykol. 62: 61–68.

Bresinsky, A. & H. Besl. 2003. Schlüssel zur Gattungsbestimmung der Blätter-, Leisten- und Rörhenpilze mit Literaturhinweisen zur Artbestimmung. Regensb. Mykol. Schr. 11: 5–236.

Bridge, P.D., B.M. Spooner, P.J. Roberts & G. Panchal. 2003. On the unreliability of published DNA sequences. New Phytol. 160: 43–48.

Bruns, T.D., R. Fogel, T.J. White & J.D. Palmer. 1989. Accelerated evolution of a false truffle from a mushroom ancestor. Nature 339: 140–142.

Bruns, T.D., T.M. Szaro, M. Gardes, K.W. Cullings, J.J. Pan, D.L. Taylor, T.R. Horton, A. Kretzer, M. Garbelotto & Y. Li. 1998. A sequence database for the identification of ectomycorrhizal basidiomycetes by phylogenetic analysis. Mol. Ecol. 7: 257–272.

Dähncke, R.M. 1993. 1200 Pilze in Farbfotos. AT Verlag, Aarau/Stuttgart.

Den Bakker, H.C., B. Gravendeel & Th. W. Kuyper. 2004a. An ITS phylogeny of Leccinum and an analysis of the evolution of minisatellite-like sequences within ITS1. Mycologia 96: 102–118. ✓

Den Bakker, H.C., G.C. Zuccarello, Th.W. Kuyper & M. E. Noordeloos. 2004b. Evolution and host specificity of the ectomycorrhizal genus Leccinum. New Phytol. 163: 201–215. ×

Den Bakker, H.C., G.C. Zuccarello, Th.W. Kuyper & M.E.Noordeloos. 2005. Phylogeographic patterns in Leccinum sect. Scabra an the status of the arctic/alpine species L. rotundifoliae. In: H.C. den Bakker (in press). Diversity in Leccinum, a molecular phylogenetic approach [PhD Dissertation]. Leiden, The Netherlands: Leiden University. ×

Dörfelt, H. & G. Berg. 1990. Systematische und nomenklatorische Probleme in der Gattung Leccinum (Basidiomycetes/Boletales). Feddes Repert. Spec. Nov. Regni Veg. 101: 561-570.

Engel, H. 1978. Rauhstielröhrlinge—die Gattung Leccinum in Europa. Coburg, Germany: Hilmar Schneider. 76 p.

Estades, A. & G. Lannoy. 2004. Les bolets européens. Bull. Trimestriel Féd. Mycol. Daupiné-Savoie. 174: 3–79.

Felsenstein, J. 2004. Inferring phylogenies. Sinauer Associates Inc. Sunderland.

Fries, E. M. 1832. Index Alphabeticus Generum, Specierum et Synonymorum in Eliae Fries Systemate Mycoligico. Greifswald.

Gill, M. & W. Steglich. 1987. Pigments of fungi (Macromycetes). Progr. Chem. org. nat. Prod. 51: 1–317.

Halling, R.E. & G.M. Mueller. 2003. Leccinum (Boletaceae) in Costa Rica. Mycologia 95: 488–499.

Heinemann, P. 1954. Boletineae. Fl. iconogr. Champ. Congo 3: 49-80, pl. 9–12.

Huelsenbeck, J.P. & F. Ronquist. 2001. MRBAYES: Bayesian inference of phylogenetic trees. Bioinformatics 17: 754–755.

Kallio, P. 1975. Leccinum scabrum (Fries) Gray subsp. tundrae Kallio, a new subspecies from Lapland. Rep. Kevo subarct. Res. Stat. 12: 25–27.

Kibby, G. 2002. Illustrations of rare or little-known boletes. Field Mycology 3: 78–83.

Korhonen, M. 1995. New Boletoid fungi in the genus Leccinum from Fennoscandinavia. Karstenia 35: 53–66.

Kuyper, T.W. 1988. Specific and infraspecific delimitation. In: C. Bas, T.W. Kuyper, M.E. Noordeloos & E.C. Vellinga (eds.), Flora agaricina neerlandica 1: 30–37. A. A. Balkema, Rotterdam.

Lannoy, G. & A. Estades. 1993. Contribution à l'étude du genre Leccinum 3. Doc. Mycol. 23 (89): 63–71.

Lannoy, G. & A. Estades. 1995. Monographie des Leccinum d'Europe. Fédéderation Mycologique Dauphiné-Savoie, La Roche-sur-Foron.

Lee, C., C. Grasso & M.F. Sharlow. 2002. Multiple sequence alignment using partial order graphs. Bioinformatics 18: 452-464.

Mayr, E. 1957. Species concepts and definitions. In: E. Mayr (ed.) The Species Problem: 1–22. Publication no. 50, American Association for the Advancement of Science, Washington DC.

Miller, S.L., T.M. McClean, J.F. Walker & B. Buyck. 2001. A molecular phylogeny of Russulales including agaricoid, gasteroid and pleurotoid taxa. Mycologia 93: 344–354.

Peintner, U., N.L. Bougher, M.A. Castellano, J.-M. Moncalvo, M.M. Moser, J.M. Trappe & R. Vilgalys. 2001. Multiple origins of sequestrate fungi related to Cortinarius. Amer. J. Bot. 88: 2168–2179.

Pilat, A. & A. Dermek. 1974. Hríbovité huby. Bratislava.

Posada, D. & K.A. Crandall. 1998. MODELTEST: testing the model of DNA substitution. Bioinformatics 14: 817–818.

Rauschert, S. 1987. Nomenklatorische Studien bei Höheren Pilzen III. Röhrlinge (Boletales). Nova Hedwigia 45 (3–4): 501–508.

Redeuilh, G. 1990. Etudes nomenclaturales sur les Bolets. VI corrections, additions et commentaires aux etudes I-V. Doc. Mycol. 20 (79): 25–45.

Rodriguez, F., J.L. Oliver, A. Marin & J.R. Medina. 1990. The general stochastic-model of nucleotide substitution. J. theor. Biol. 142: 485–501.

Simpson, G.G. 1951. The species concept. Evolution 5: 285–298.

Singer, R. 1947. The Boletoideae of Florida. The Boletineae of Florida with notes on extralimital species III. Am. Midl. Naturalist 37: 1–135.

Singer, R. 1986. The Agaricales in modern taxonomy. 4th ed. Koeltz Scientific Books, Koenigstein.

Smith, A.H. & H.D. Thiers. 1971. The Boletes of Michigan. The University of Michigan Press, Ann Arbor.

Smith, A.H., H.D. Thiers & R. Watling. 1966. A preliminary account of the North American species of Leccinum, section Leccinum. Michigan Bot. 5: 131–179.

Smith, A.H., H.D. Thiers & R. Watling. 1967. A preliminary account of the North American species of Leccinum sections Luteoscabra and Scabra. Michigan Bot. 6: 107–154.

Šutara, J. 1989. The delimitation of the genus Leccinum. Česká Mykol. 43: 1–12.

Swofford, D.L. 2002. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associates.

Tamura, K. & M. Nei. 1993. Estimation of the number of nucleotide substitutions in the control region of mitochondrial-DNA in humans and chimpanzees. Molec. Biol. Evol. 10: 512–526.

Thiers, H.D. 1975. California Mushrooms – A Field Guide to the Boletes. Hafner Press, New York.

Van Steenis, C.G.G.J. 1957. Specific and infraspecific delimitation. Fl. Males., Ser. 1, Spermat. 5: clxvii– ccxxxiv.

Veerman, C.P. 2004. Besluit van de Minister van Landbouw, Natuur en Voedselkwaliteit, TRCJZ/2004/5727, houdende vaststelling van rode lijsten flora en fauna. Ministerie van LNV, Den Haag.

Venturi, A. 1842. Studi Micologici: 31, pl. 10, fig. 93–94.

Vilgalys, R. 2003. Taxonomic misidentification in public databases. New Phytol. 160: 4–5.

Watling, R. 1970. Boletaceae, Gomphidiaceae: Paxillaceae. In: D.M. Henderson, P.D. Orton, R. Watling (eds.), British Fungus Flora. Agarics and Boleti 1: 45–57. Royal Botanical Gardens, Edinburgh.

Wiley, E.O. 1978. The evolutionary species concept reconsidered. Syst. Zool. 27: 17– 26.

Wolfe Jr., C.B. & N.L. Bougher. 1993. Systematics, mycogeography, and evolutionary history of Tylopilus subg. Roseoscabra in Australia elucidated by comparison with Asian and American species. Austral. Syst. Bot. 6: 187–213.

APPENDIX

28S Accessions used for phylogenetic reconstructions. When synonyms were used for the original Genbank accessions, these are put between brackets behind the epithet.

Species	GenBank Accession #	Species	GenBank Accession #
Boletellus betula	AF050642	*Leccinum schistophilum (palustre)*	AF139701
Boletellus russellii	AF050651	*Leccinum versipelle (percandidum)*	AF139702
Boletus aereus	AF456836	*Leccinum rotundifoliae*	AF139704
Boletus appendiculatus	AF456837	*Leccinum rubropunctus* 1	AF139687
Boletus coniferarum	AF456827	*Leccinum rubropunctus* 2	AY612812
Boletus edulis	AF456816	*Leccinum rugosiceps*	AY612813
Boletus erythropus	AF139683	*Leccinum variicolor*	AF139706
Boletus eximius	AF139684	*Leccinum versipelle (cerinum)*	AF139692
Boletus flavoniger	AF456829	*Leccinum scabrum*	AF139705
Boletus griseus	AF456834	*Phyloporus pelletieri*	AF456818
Boletus inedulis	AY612803	*Rubinoboletus ballouii*	AY612823
Boletus lurides	AF139686	*Tylopilus alboater*	AF139708
Boletus mirabilis	AF335451	*Tylopilus badiceps*	AY612833
Boletus ornatipes	AF456817	*Tylopilus felleus*	AF139710
Boletus radicans	AF336241	*Tylopilus ferrugineus*	AF139711
Boletus reticulatus	AF456824	*Tylopilus nigerrimus*	AF456832
Boletus retipes	AF456823	*Tylopilus plumbeoviolaceus*	AF457405
Boletus satanas	AF071528	*Tylopilus rhoadsiae*	AY612836
Boletus seperans	AF457404	*Tylopilus rufonigricans*	AY612835
Boletus subglabripes	AF139688	*Tylopilus tabacinus*	AY612837
Boletus subvelutipes	AY612804	*Xanthoconium affine* 1	AY612838
Boletus viridiflavus	AY612805	*Xanthoconium affine* 2	AF457406
Chalciporus amarellus	Af456835	*Xerocomus amazonicus*	AY612839
Chalciporus piperatus	AF336244	*Xerocomus badius*	AF050648
Chamonixia caespitosa	AF336245	*Xerocomus chrysentron*	AF514808
Heimiella retisporus	AF050650	*Xerocomus cisalpinus*	AF514812
Leccinum albellum	AY612811	*Xerocomus depilatus*	AF139712
Leccinum aurantiacum s.s.	AF139703	*Xerocomus dryophilus*	AF514823
(L. populinum)		*Xerocomus fennicus*	AF514821
Leccinum carpini	AF139691	*Xerocomus hortonii*	AF139713
Leccinum chromapes	AY612834	*Xerocomus illudens*	AF139714
Leccinum chromapes	AF139709	*Xerocomus impolitus*	AF139715
Leccinum corsicum	AF139693	*Xerocomus parasiticus*	AF050646
Leccinum crocipodium	AF139694	*Xerocomus porosporus*	AF050645
Leccinum duriusculum 1	AF139690	*Xerocomus pruinatus*	AF402140
Leccinum duriusculum 2	AF139695	*Xerocomus pruinatus*	AF514825
Leccinum duriusculum 3	AF139699	*Xerocomus ripariellus*	AF514816
Leccinum flavostipitatum	AF139696	*Xerocomus ripariellus*	AF050649
Leccinum holopus	AF139697	*Xerocomus rubellus*	AF514828
Leccinum holopus	AF139700	*Xerocomus rubellus*	AF514829
(L. nucatum)		*Xerocomus rubellus*	AF514830
Leccinum lepidum	AF139698	*Xerocomus subtomentosus*	AF139716
Leccinum albostipitatum	AF139689		
(L. aurantiacum)			
Leccinum longicurvipes	AF139685		

Plate 1. *Leccinum aurantiacum*. a. Fruit-body with aberrant light stipe (Finland, M.E. Noordeloos); b. fruit-body associated with *Populus* (The Netherlands, M.E. Noordeloos); c. fruit-body associated with *Quercus* (Austria, M.E. Noordeloos).

Plate 2. a. *Leccinum albostipitatum* (Austria, K.F. Reinwald); b. *L. vulpinum* (Finland, M.E. Noordeloos).

Plate 3. *Leccinum versipelle*. a–d. Forms with orange to brownish caps; e and f. light forms (Finland, all photos M.E. Noordeloos).

Plate 4. *Leccinum duriusculum*. a. Robust fruit-bodies (Italy, M.E. Noordeloos); b. slender fruit-bodies (The Netherlands, M.E. Noordeloos).

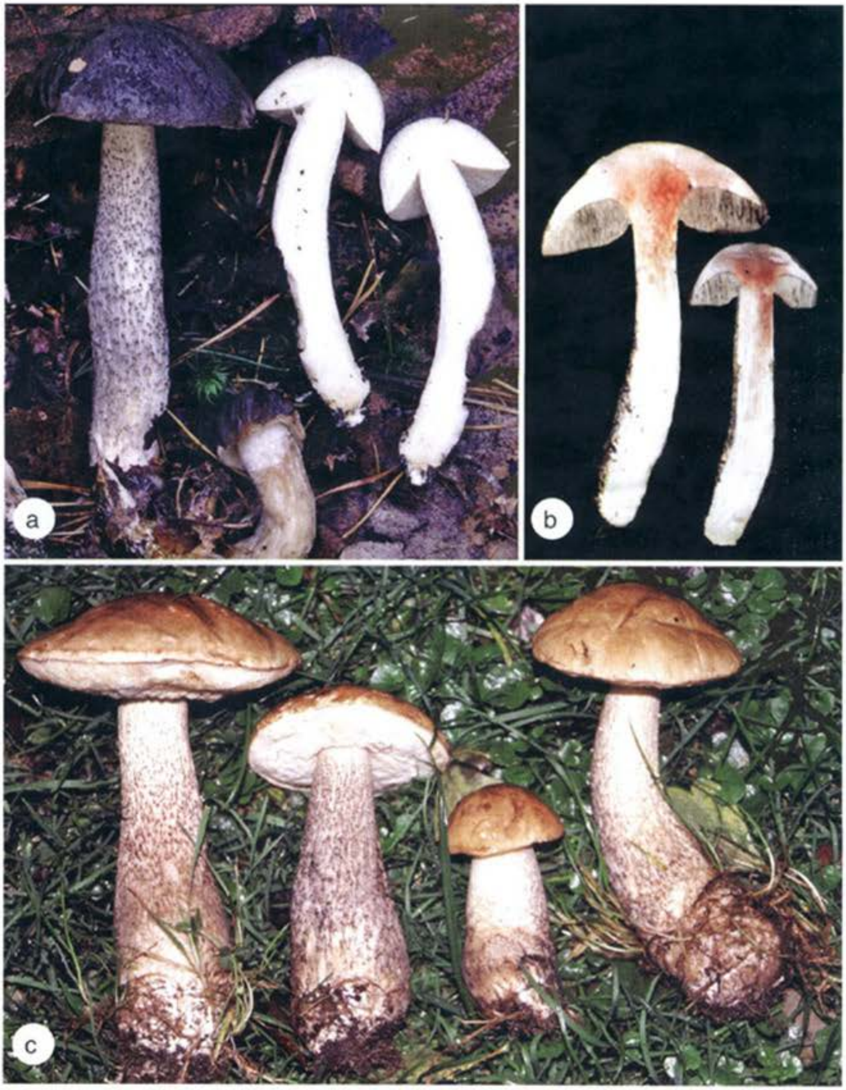


Plate 5. *Leccinum scabrum*. a. Habitus (Ontario, Canada, H.C. den Bakker); b. extreme discoloration of the context (Finland, M.E. Noordeloos); c. habitus (The Netherlands, C. Bas).

Plate 6. *Leccinum melaneum*. a. & b. Scotland, H.C. den Bakker; c. The Netherlands, M.E. Noordeloos.

Plate 7. *Leccinum rotundifoliae*. a & c. Greenland, L. Jalink & M. Nauta; b. Finland, M.E. Noordeloos.

Plate 8. *Leccinum schistophilum*. a. Typical habit (Sweden, H.C. den Bakker); b. typical habit (Finland, M.E. Noordeloos); c. atypical habit (The Netherlands, H.C. den Bakker).

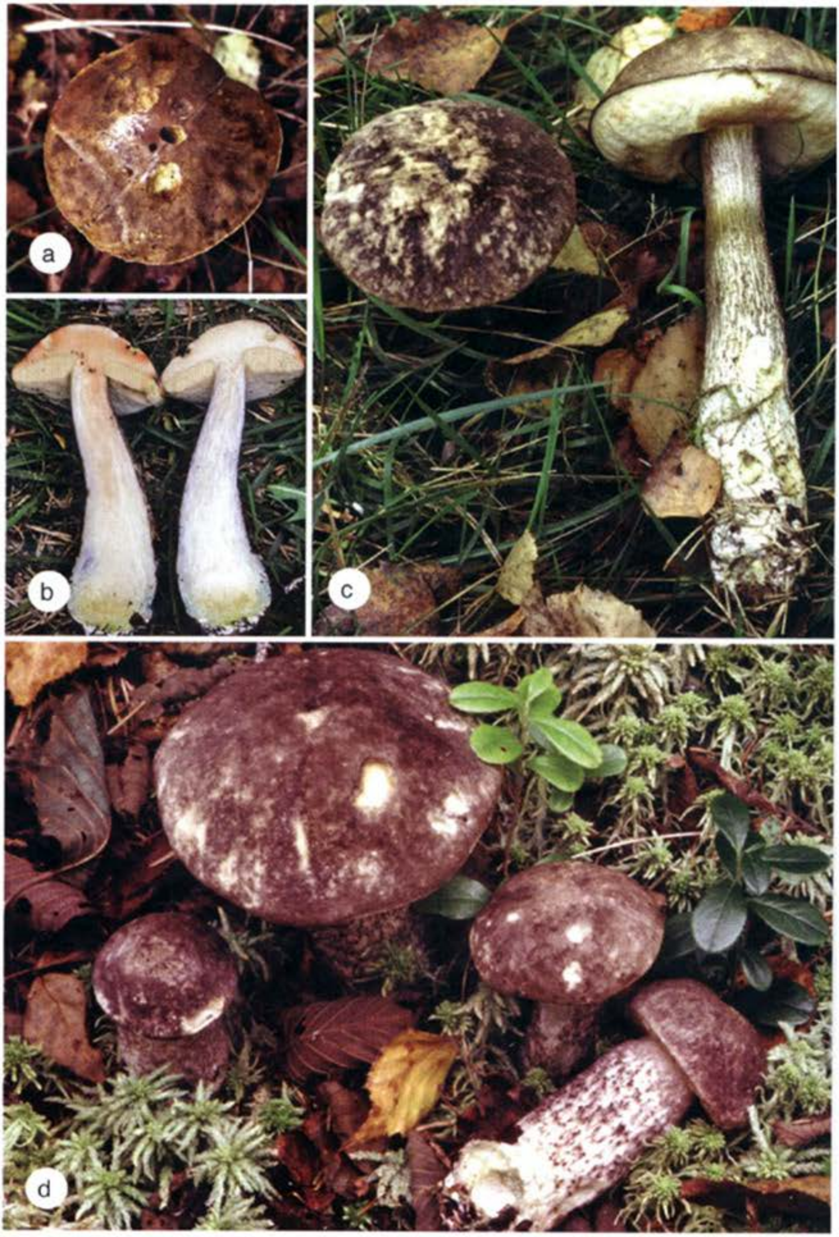


Plate 9. *Leccinum variicolor*. a. Pileus (The Netherlands, M.E. Noordeloos); b. typical discoloration of context (Ontario, Canada, H.C. den Bakker); c. (The Netherlands, M.E. Noordeloos); d. (Slovakia, M.E. Noordeloos).

Plate 10. *Leccinum cyaneobasileucum*. a. Normal form (The Netherlands, M.E. Noordeloos); b. rare white (albinistic) form (The Netherlands, M.E. Noordeloos); c. normal form (Belgium, R. Walleyn).

Plate 11. *Leccinum holopus*. a–f. Sturdy brownish forms; g. typical slender, whitish form; c & d (extreme) discoloration of the context (a & e, The Netherlands, M.E. Noordeloos, b, c, d, Scotland, H.C. den Bakker, f, Sweden, H.C. den Bakker, g, Sweden, M.E. Noordeloos).

Plate 12. a. *Leccinum crocipodium* (pileal margin of mature fruit-body is abnormally ruptured!) (The Netherlands, Peter Klok); b. *L. pseudoscabrum* (Austria, K.F. Reinwald).

BOOK REVIEWS

E.H.C. McKenzie (ed.). *Introduction to Fungi of New Zealand. The fungi of New Zealand vol. 1.* (Fungal Diversity Press, Centre for Research in Fungal Diversity, The University of Hong Kong, Hong Kong SAR, China; website http://www.hku.hk/ecology/mycology/FDP.html. 2004.) ISBN 962-86765-6-3. Pp. 498; 16 coloured plates. In English. Price: USD 80.00.

Surprisingly little is known about New Zealand's fungi, of which many are believed to be unique to New Zealand. The authors estimate that about 2/3 of the expected 22,000 species are unrecorded. This first volume seeks to provide a foundation for understanding New Zealand's fungi, including taxonomic, ecological, historical and cultural knowledge, along with inventories of recorded species. It is a cooperative initiative by several New Zealand mycologists and a Swiss mycologist (Horak). The next volumes will provide monographic treatments of selected taxonomic or ecological groups of fungi.

The book starts with an abstract in English and Maori, and 16 coloured plates which illustrate some of the more conspicuous, colourful and distinctive species found in New Zealand. The first chapter of 48 pages gives a general introduction into the diversity and ecological roles of fungi. Fungi are considered in a broad sense, i.e. including also the fungus-like members of the Protozoa and Chromista. Attention is also drawn to the endangered species of New Zealand. The following chapter gives an overview of the history of taxonomic mycology in New Zealand (31 pages), which began about mid 1800. Chapter 3 reports on the Maori knowledge of fungi (37 pages), which dates from considerably earlier. A key to the genera of agarics and boleti is given by Horak of 19 pages, followed by pages with references to descriptions, illustrations and keys. Chapter 5 counts 197 pages and contains a bibliographic checklist of agarics, boleti and related fungi. Chapter 6 gives a bibliography of New Zealand taxonomic mycology (38 pages), the last chapter gives a checklist of all New Zealand 'Fungi' (87 pages), and the book is completed with an index to Chapter 1–3.

It is to be hoped that the start of this series will soon be followed by other volumes with monographic treatments on fungi from this interesting part of the world. This first volume is already a must for every mycological library and every mycologist interested.

M.M. Nauta

F. Doveri. *Fungi fimicoli Italici. A guide to the recognition of basidiomycetes and ascomycetes on faecal material. Guida al riconoscimento dei basidiomyceti e degli ascomiceti che vivono su materia fecale.* (Associazione Micologica Bresadola, Via Volta 46, I-38100 Trento, Italy, 2004.) English and Italian, Pp. 1,104, many unnumbered line-drawings and 158 coloured photographs. Price: EUR 110.00 excl. EUR 25.00 postal charges.

This impressive and well-printed book is fully devoted to ascomycetes and basidiomycetes growing on dung. The author, Francesco Doveri, a practicing physician and endocrinologist, spent more than 15 years on the study of fimicolous fungi in

Italy. Several preliminary studies on these fungi were published in Italian and French mycological periodicals, often in co-authorship with his compatriots G. Cacialli and V. Caroti. During a period of 10 years 90 species of fimicolous basidiomycetes and 217 species of ascomycetes could be identified. A considerable amount of information concerning recent studies in Italy and from many widely distributed studies and monographs on these fungi is brought together in this book.

The introduction contains a practical guide to the study of coprophilous fungi with advice how to grow them in culture and a list of animals that have proven to provide for favourable substrate sources. An extensive glossary of terms concludes the introductory part.

The descriptive chapters form the main part of this book (p. 29–1004). All texts, keys, descriptions, and notes are presented in alternating blocks in English and Italian, which makes the book widely available, also to mycologists who read Italian less easily. Successively, coprophilous representatives of Gasteromycetes, Agaricales, Pezizomycetes, Dothideomycetes, and Sordariomycetes are treated.

As evident from the subtitle, conidial fungi, slime moulds and Zygomycetideae, often forming an important aspect of the fungi found growing on dung, are not treated. All keys, descriptions, and notes are presented as alternating blocks of English and Italian text. Although this study is primarily based on collections found all over Italy, it is of greater importance because most of the more than 300 coprophilous fungi described have a very wide distribution and many keys include all species known world-wide. Each species reported from Italy is presented with its name, an extensive alphabetic synonymy, the original diagnosis as published, a list of specimens examined, macroscopic and microscopic descriptions, and critical observations. A full page of clear microscopic line-drawings is added.

On some occasions the author followed his own experience with his previous work and deviates from results published elsewhere. So in the case of *Iodophanus carneus*, contrary to Kimbrough et al. in their treatment of *Iodophanus* with many hardly separable taxa, Doveri accepts a rather wide conception of that species. But for the completeness of information a key to 16 species of *Iodophanus* is presented. The work ends with an impressive list of references (39 pages), an index with the full names and a series of 158 coloured photographs of good quality on special paper. This book is highly recommended to those who are interested in fungi growing on dung or those who prepare mycological courses for students.

J. van Brummelen

M.E. Noordeloos. *Entoloma s.l. Supplement*. Fungi Europaei 5A. (Edizioni Candusso, Via Ottone Primo 90, I-17021, Allasio SV, Italy, e-mail: maxcandsso@libero.it. 2004.) ISBN 88-901057-4-7. Pp. 618; 3 coloured plates, 342 coloured photographs, 102 line-drawings. In Italian and English. Price: EUR 68.00.

This book is the continuation of the *Entoloma* part of the series Fungi Europaei which appeared in 1992. Since that book, which treated 246 species, many new species have been published. In the Supplement an additional 100 species are treated, and an improved key in English and Italian is published. The species are treated the same way as before, with elaborate bilingual descriptions and are mostly accompanied by drawings of the essential microscopical characters.

The Supplement starts with an introduction of 4 pages and an enumeration of the species of *Entoloma* according to section and subsection of 6 pages. The revised key occupies 61 pages, the taxonomical part 320 pages, the referencelist is 5 pages. On another 200 pages the 342 coloured photographs are found. The book is completed with an index to the Supplement and part 5 together.

The first impression is of a well-produced book with nice photographs, as we are used to from Candusso. The keys are greatly improved: more species with conspicuous characters, for example species with small thin-walled spores, are keyed out first. The lay-out of the keys is the same as in part 5: by way of a main key the user is referred to 17 other keys. The coloured plates are usually of (very) good quality, but do not depict all the newly described species. Sometimes species are depicted of which no picture was available for part 5. Although this Supplement is a must for each mycologist with a slight interest in Agaricales, some critical remarks can be made: the species in the book are renumbered, and species described in the previous part 5 are only mentioned without reference to the page where the description can be found. Of course the index can help, but it would have been of great help if the page number was given straight away. Some keys have annoying mistakes, and the line-drawings are not always of good quality.

The general advice is: buy it before it is sold out!

M.M. Nauta

R. Watling & S. Ward. *Fungi. Naturally Scottish.* (Scottish natural Heritage; pubs@snh.gov.uk; website http://www.snh.org.uk. 2003.) ISBN 1-85397-341-6. Pp. 35, several coloured plates. In English. Price: £ 4.95

In the series 'Naturally Scottish' this nice booklet about fungi has appeared. It gives an introduction to the kingdom of fungi and its main purpose is to awake interest in Britain's fungi. It introduces fungi in all their aspects and covers topics like reproduction and conservation, but also fungi and the law and conservation. All the topics are briefly treated, but it gives a good overview of what fungi are. The many coloured pictures are of good quality and as a whole this booklet is very attractive looking. Combined with easy reading this is a booklet especially for those who want a short introduction into the wonderful world of fungi. Recommended for educational purposes.

M.M. Nauta

INDEX PERSOONIA VOLUME 18

Subdivions of genera are indicated by the sign §, illustrations by an asterisk (*) added to the page number.

Instructions to authors

(A more extensive 'Checklist for preparation of manuscripts' is available)

Copy, preferably in English, to be sent to the editors, printed on one side of the paper, double-spaced, and with a left margin of about 4 cm. For fractions of numbers the decimal system should be used.

Please send one copy of the manuscript, together with a file on diskette, one set of original line drawings, and one set of original photographs to the editors of Persoonia, Nationaal Herbarium Nederland, Universiteit Leiden branch, P.O. Box 9514, NL-2300 RA Leiden.

Drawings within A4 size should be in India ink, preferably **not** on transparent or tracing-paper, and **photographs** (also within A4 size) should be mounted ready for publication on glossy paper. Magnification should preferably be indicated by a scale-bar. In other cases the author should give the magnification as in the original.

Drawings, illustrations and photographs can also be submitted as **digital files**, considering the following guide-lines: *General*: 1) submit the source-files as JPEG-, TIFF-, AI- or EPS-file, not embedded in Word, nor as an Excel or PowerPoint-file; 2) always send in the **original** hard-copy of each illustration; 3) the size of the image in the digital file should be larger than or equal to the eventual intended size in print; 4) magnification should preferably be indicated as a scale-bar. *Resolution*: 1) 300 dpi in eventual size for gray-scale or colour; 2) 1200 dpi in eventual size for monochrome images (drawings). *Format*: 1) CMYK, grayscale or line-art (Bitmap); 2) use LZW-compression for TIFF only for line-art; 3) compression for JPEG only in highest quality.

Summary. Each paper should be provided with a concise summary.

Citation of literature. Citations in the 'References' should conform to the following format:

For books, e.g.:
Fries, E.M. 1821. Systema mycologicum. Vol. 1. Lundae.
Singer, R. 1975. The Agaricales in modern taxonomy, ed. 3. Vaduz.

For chapters in a book, e.g.:
Pitt, J.I. & R.H. Cruickshank. 1990. Speciation and synonymy in Penicillium subgenus Penicillium towards a definitive taxonomy. In: R.A. Samson & J.I. Pitt (eds.). Modern concepts in Penicillium and Aspergillus classification: 103--119. New York and London.

For journals, e.g.:
Singer, R. & H. Clémençon. 1971. Neue Arten von Agaricales. Schweiz. Z. Pilzk. 49: 118--128.

Titles of journals and other publications are abbreviated mainly in accordance with the 'International Code of Abbreviations for Titles of Periodicals', and with 'A World List of Scientific Periodicals'.

Italics are ***not*** used in the references.

Write out the name(s) of author(s), i.e., do not replace author names with a long dash, when the author(s) is/are the same as in the immediate preceding citation(s).

Note: Use only a period, without a space, between the initial(s) of an author's name. Leave one space between the volume number with colon and page numbers in a journal article. Use double hyphens between page numbers, e.g., Bull. trimest. Soc. mycol. Fr. 80: 88--101.

Keys. For keys the bracketed type is strongly recommended.

Reprint orders can be submitted together with corrected proofs. Authors will, as a rule, not receive free reprints. A pdf-file will be sent to the authors on request.

ISSN 0031-5850

CONTENTS

Published by

Nationaal Herbarium Nederland

Universiteit Leiden branch
P.O. Box 9514
2300 RA Leiden
The Netherlands