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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.

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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. Sutara 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.

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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.

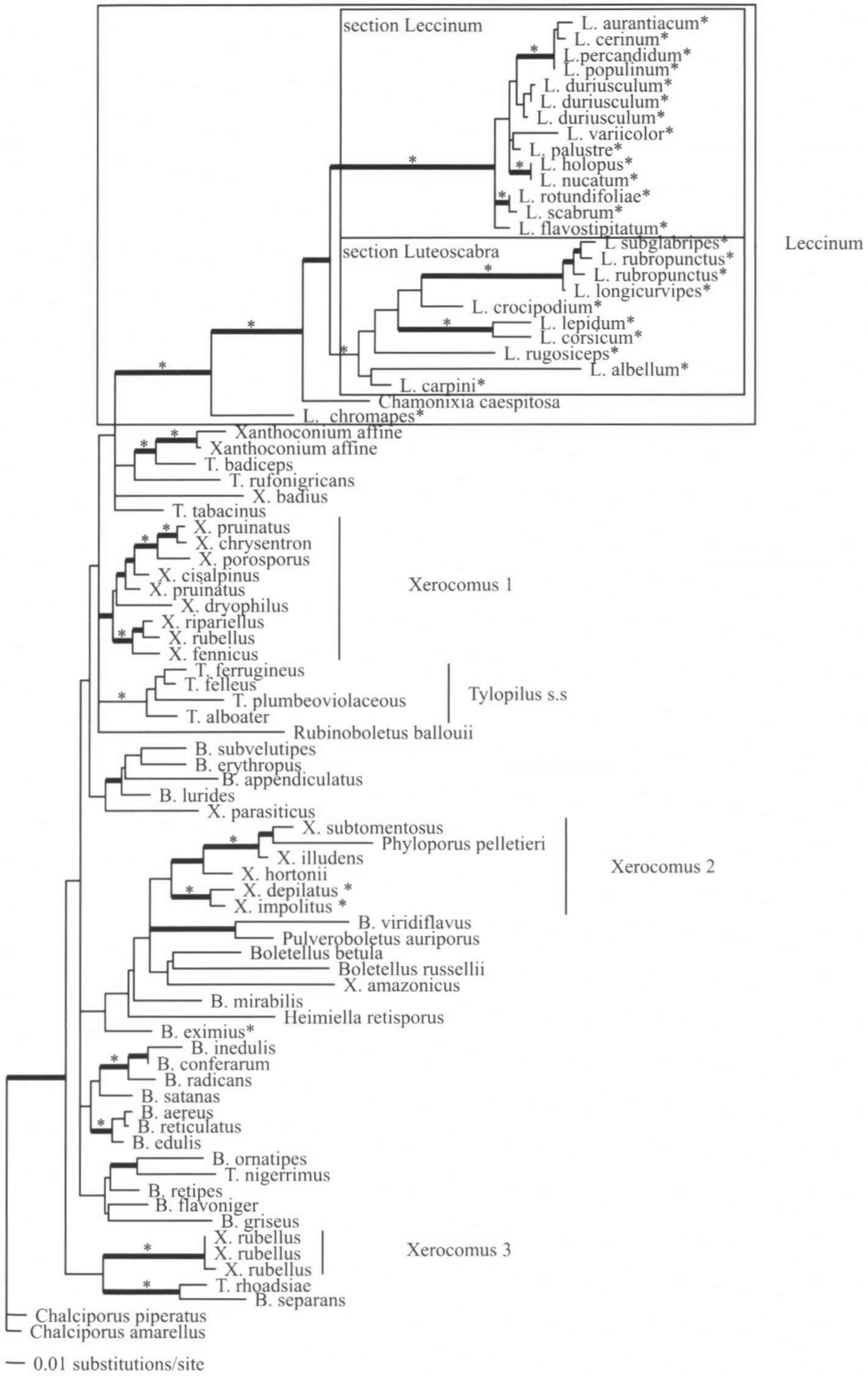
section Leccinum
L. aurantiacum*
L. cerinum*
L.percandidum*
L. populinum*
L. duriusculum*
L. duriusculum*
L. duriusculum*
L. variicolor*
L. palustre*
L. holopus*
L. nucatum*
L. rotundifoliae*
L. scabrum*
L. flavostipitatum*
section Luteoscabra
L subglabripes*
L. rubropunctus*
L. rubropunctus*
L. longicurvipes*
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
Phyloporus 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*.

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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

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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

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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

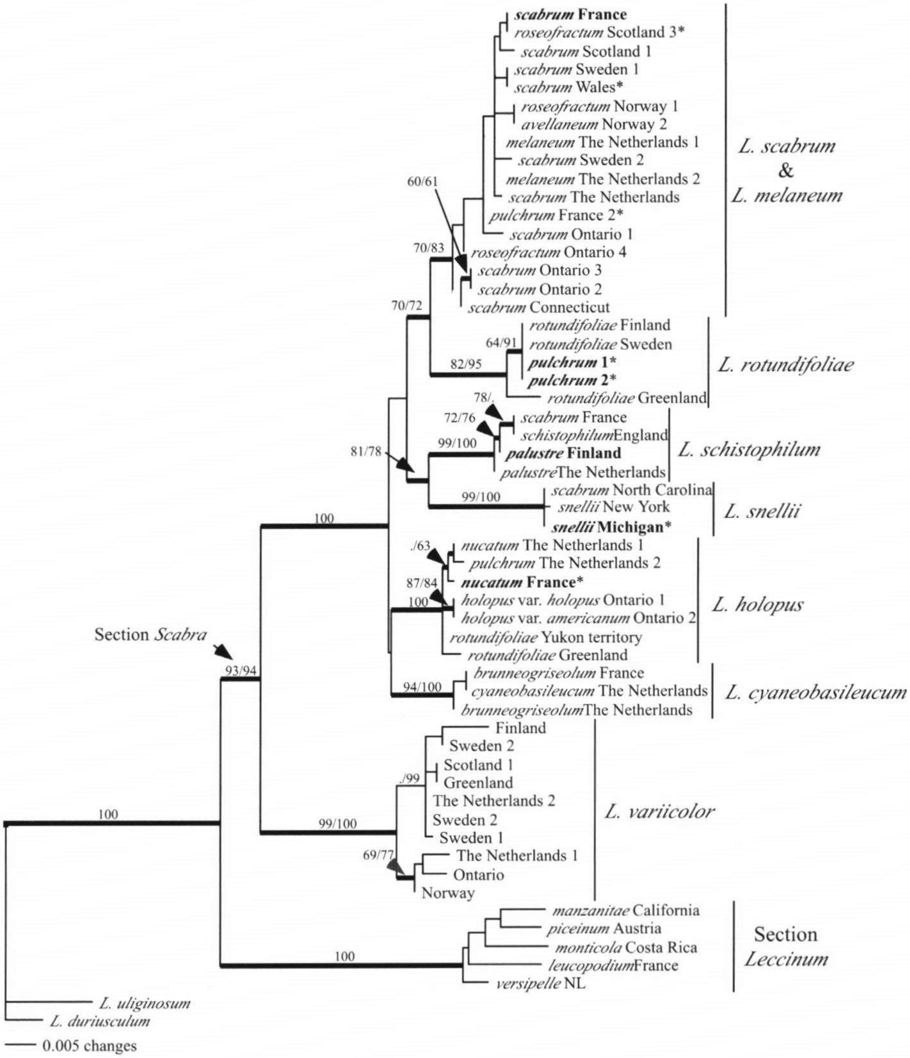

Fig. 2. One of 84 ML trees based on *Gapdh* data. Individual accessions are named with the traditional morphological criteria (Lannoy & Estades, 1995, Smith & Thiers, 1971) to the left, and to the right the accepted names are given as a result of the current species concept. Thickened branches receive 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.

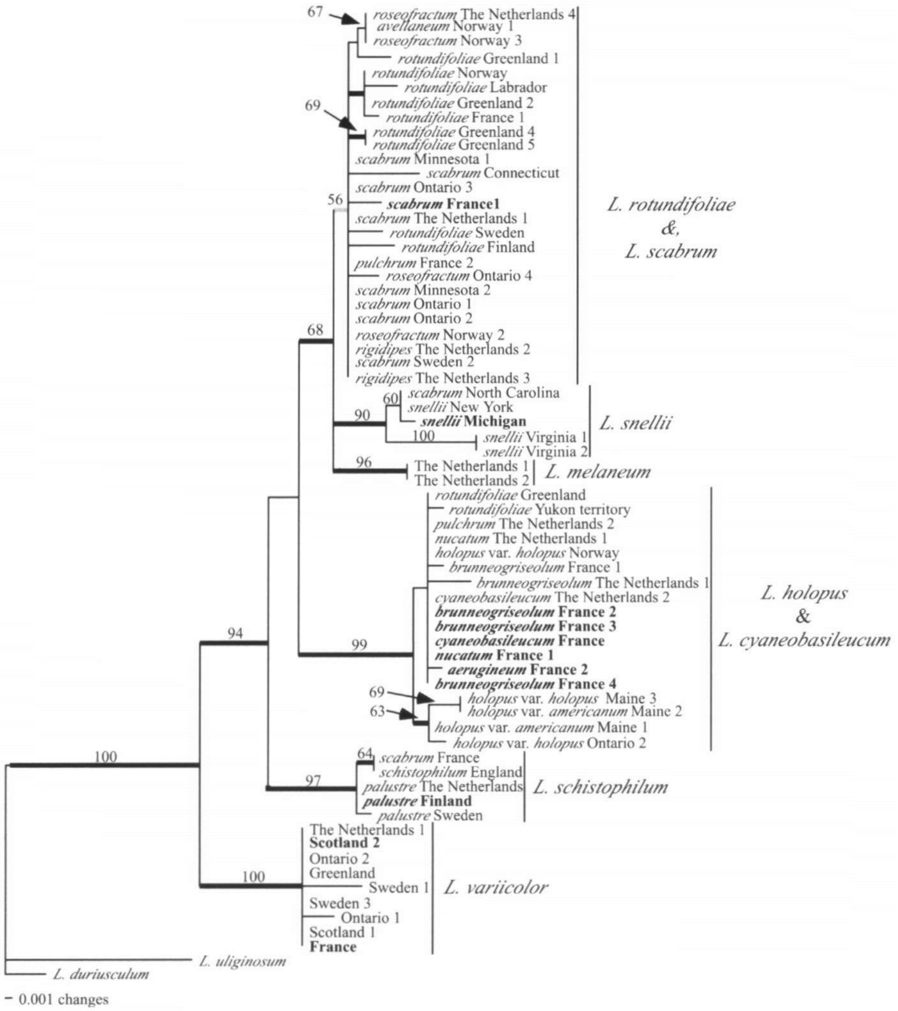

Fig. 3. ML tree based on ITS2 sequences. Individual accessions are named with the traditional morphological criteria (Lannoy & Estades, 1995, Smith & Thiers, 1971) to the left, and at the right the accepted names are given as a result of the current species concept. Thickened branches receive posterior 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

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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.

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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 S*cabra* 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.*

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[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.

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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.

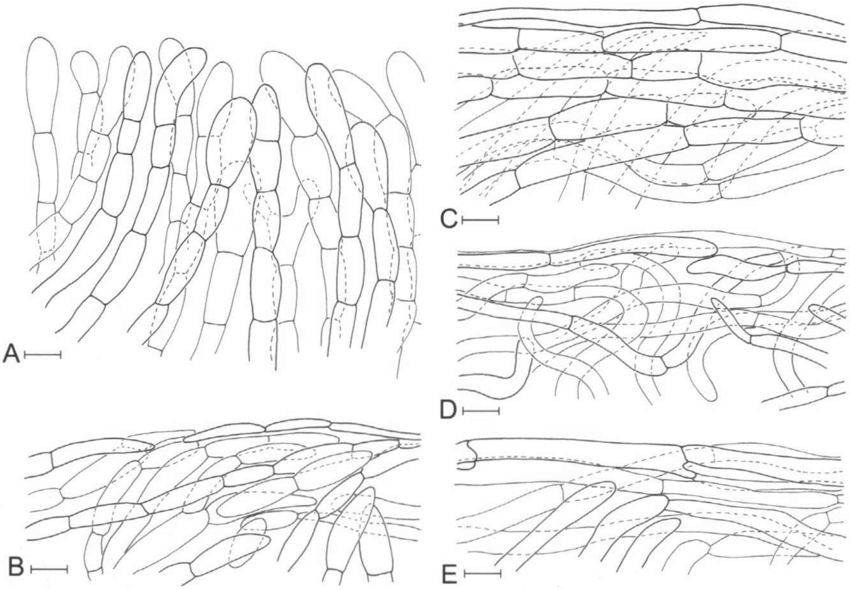

Fig. 4. Overview of pileipellis types encountered in *Leccinum* (radial sections, scale bars = 10 μm). A. A trichoderm, as found in *L. crocipodium*; B to E. cutis-like structures, named cutis in the species descriptions (B. *L. variicolor*, C. *L. versipelle*, D. *L. holopus* and E. *L. scabrum*). The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

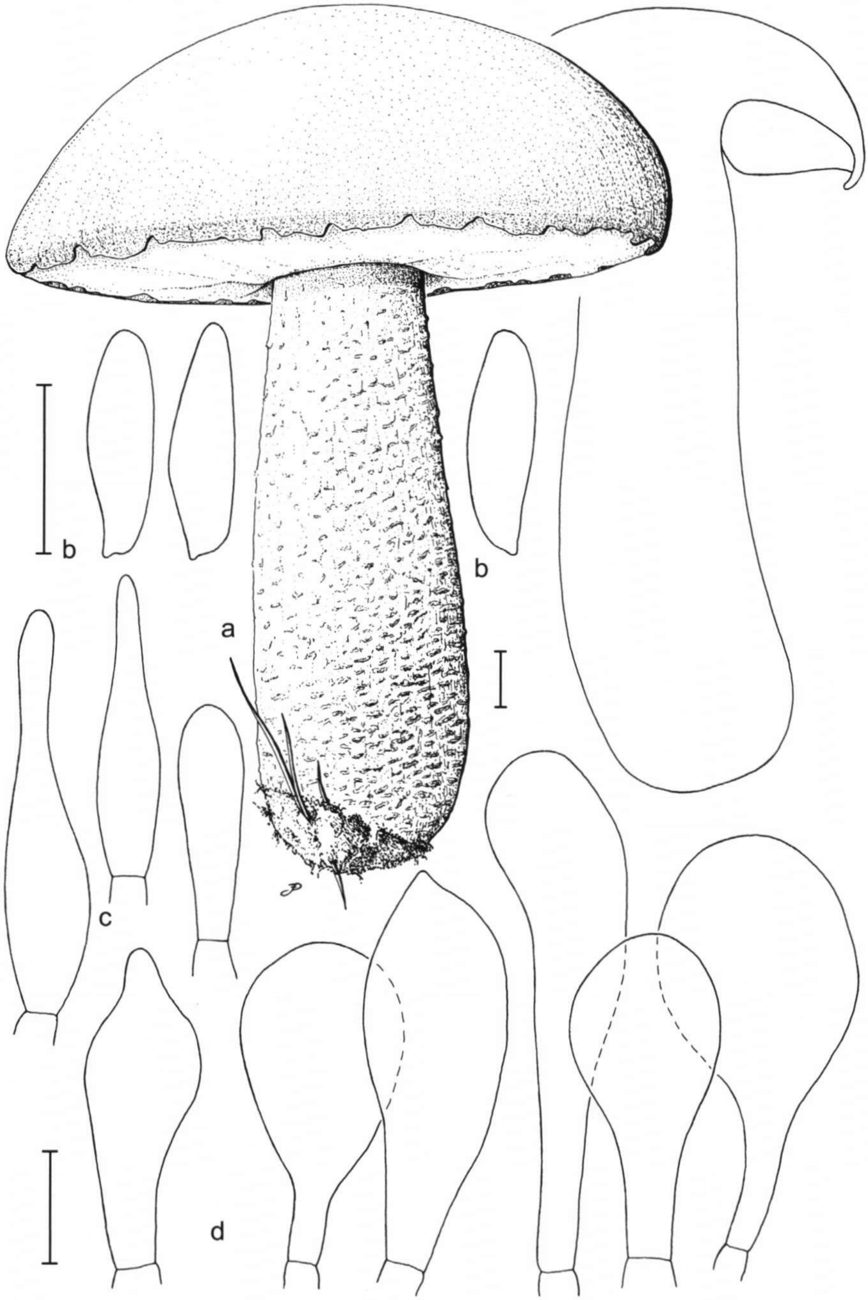

Fig. 5. *Leccinum aurantiacum*. a. Habitus; b. spores; c. hymenocystidia; d. caulocystidia. Scale bars = 10 μm resp. 1 cm.

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 x 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) x 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 x 6.5–10.5 µm, clavate, 2- or 4-spored. Hymenocystidia 20–45 x 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 x 3.0–15.5 µm, elements in suprapellis 50–70 x 5.5–12.5 µm, pigment in water vacuolar or in globules, larger elements often intracellularly granular incrusted, red-brown. Caulocystidia 30–60(–90) x (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

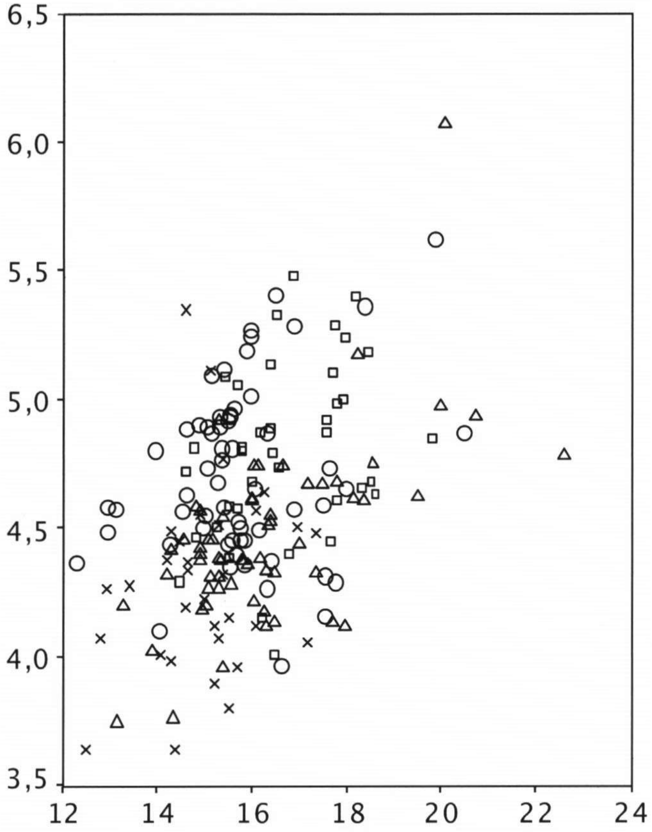

Fig. 6. Spore size in basidiocarps of of *L. aurantiacum* associated with *Populus* (Δ), *Quercus* (O), *Salix* (×) and *Betula* (□).

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; Sutara, 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.

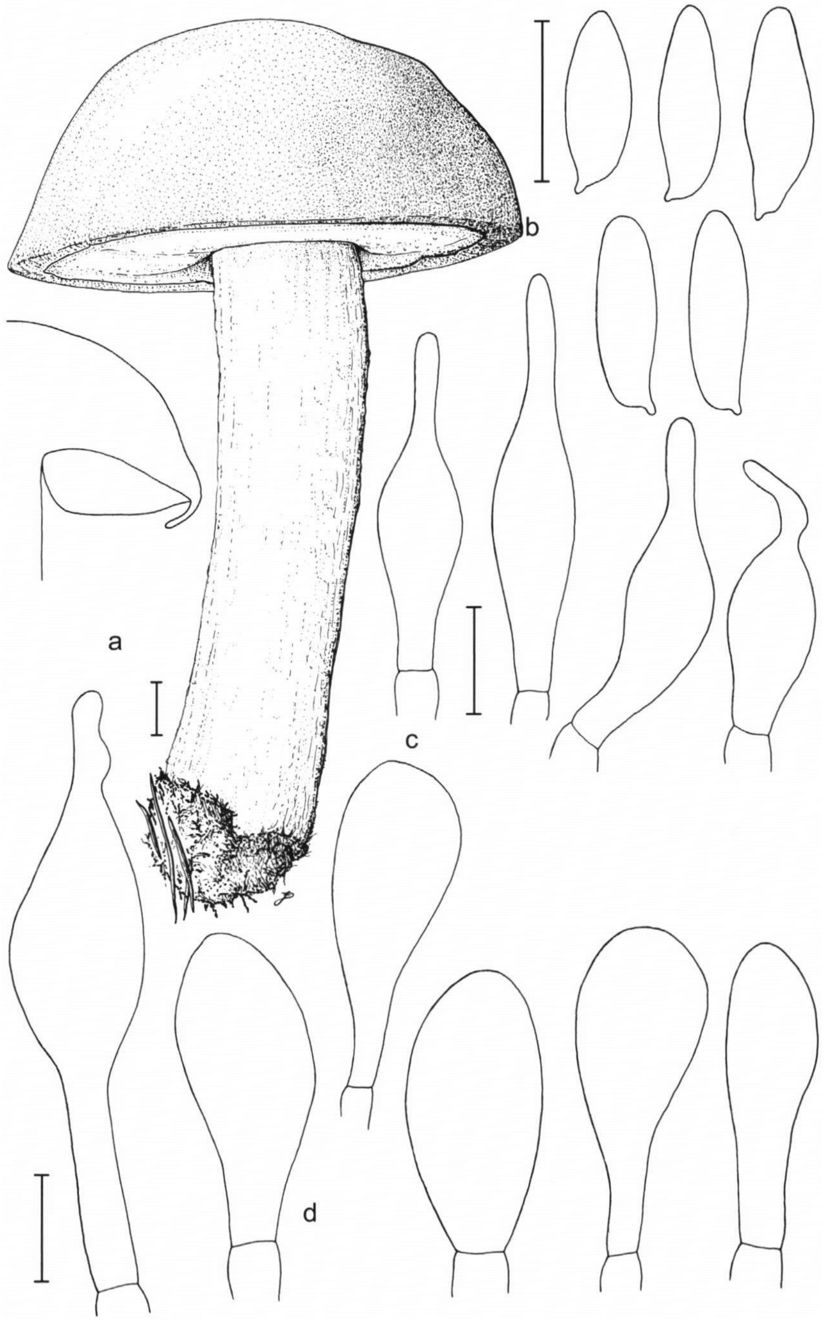

Fig. 7. *Leccinum albostipitatum*. a. Habitus; b. spores; c. hymenocystidia; d. caulocystidia. Scale bars = 10 µm resp. 1 cm.

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.

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[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

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

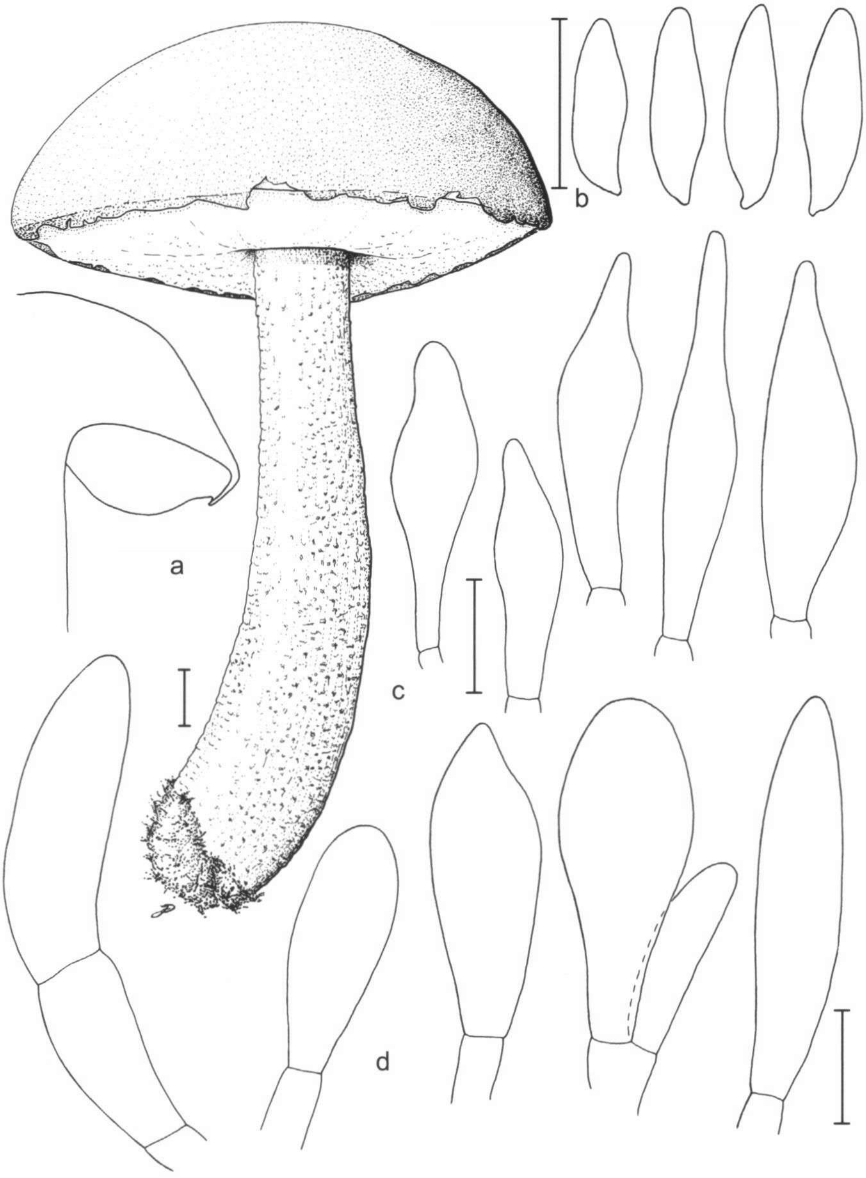

Fig. 8. *Leccinum vulpinum*. a. Habitus; b. spores; c. hymenocystidia; d. caulo cystidia. Scale bars = 10 μm resp. 1 cm.

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

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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

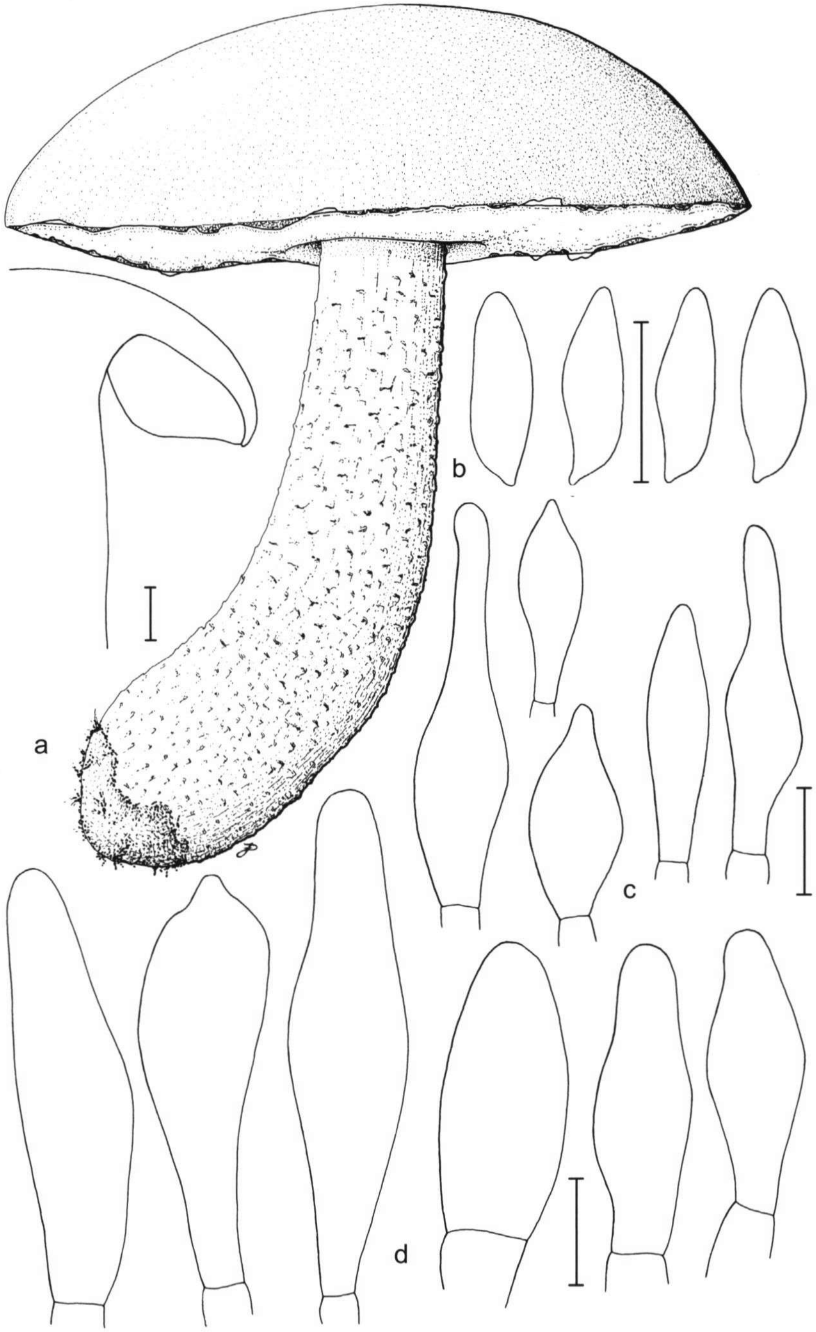

Fig. 9. *Leccinum versipelle*. a. Habitus; b. spores; c. hymenocystidia; d. caulocystidia. Scale bars = 10 μm resp. 1 cm.

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 x 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 x 4.5–6.0 μm, on average 13.0–14.0 x 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 x 6.0–9.0 μm, clavate, 4-spored. Hymenial cystidia abundant on edge and sides of the pores, 20–75 x 5.5–17 x 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) x 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 x 5.0–12 x 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*.

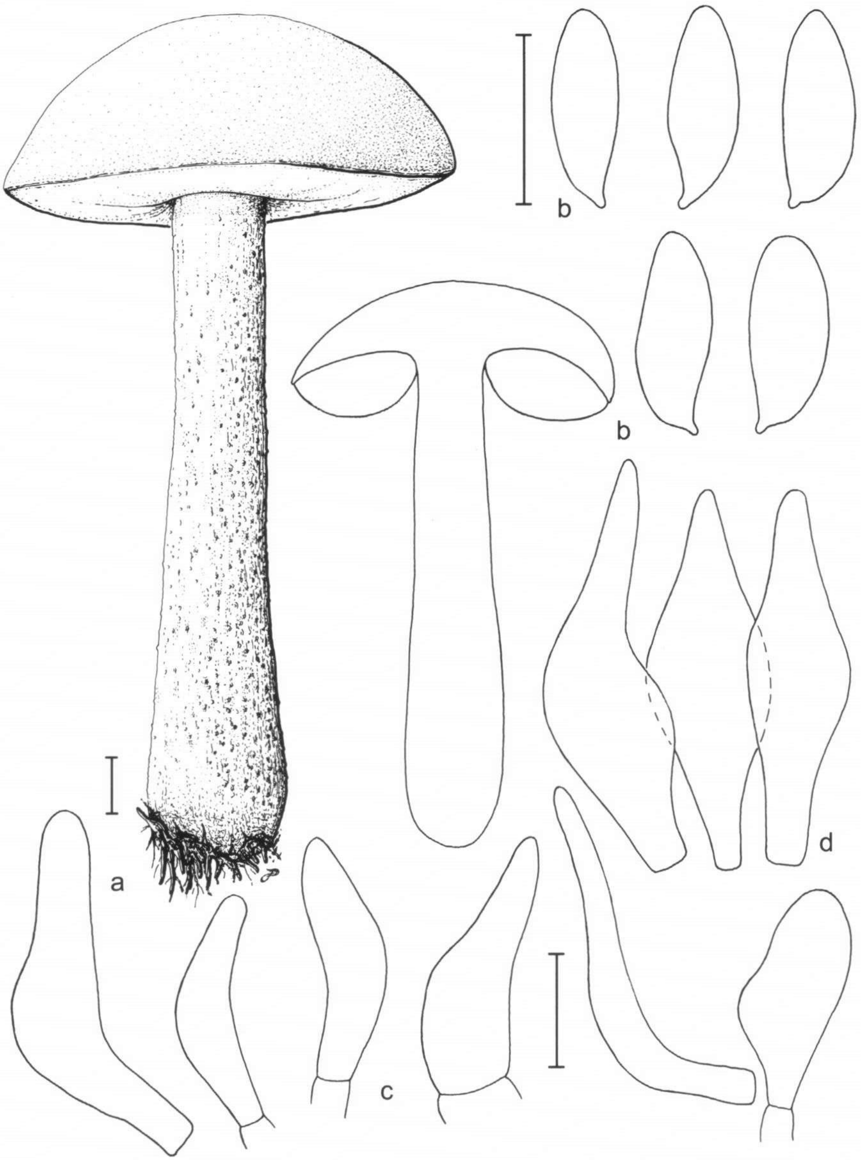

Fig. 10. *Leccinum duriusculum*. a. Habitus; b. spores; c. hymenocystidia; d. caulocystidia. Scale bars = 10 μm resp. 1 cm.

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 x 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)x (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 x 10.5–12.5 μm, 4-spored (sometimes 3-spored). Hymenocystidia 30–50 x 5.5–7.5 μm, fusiform to

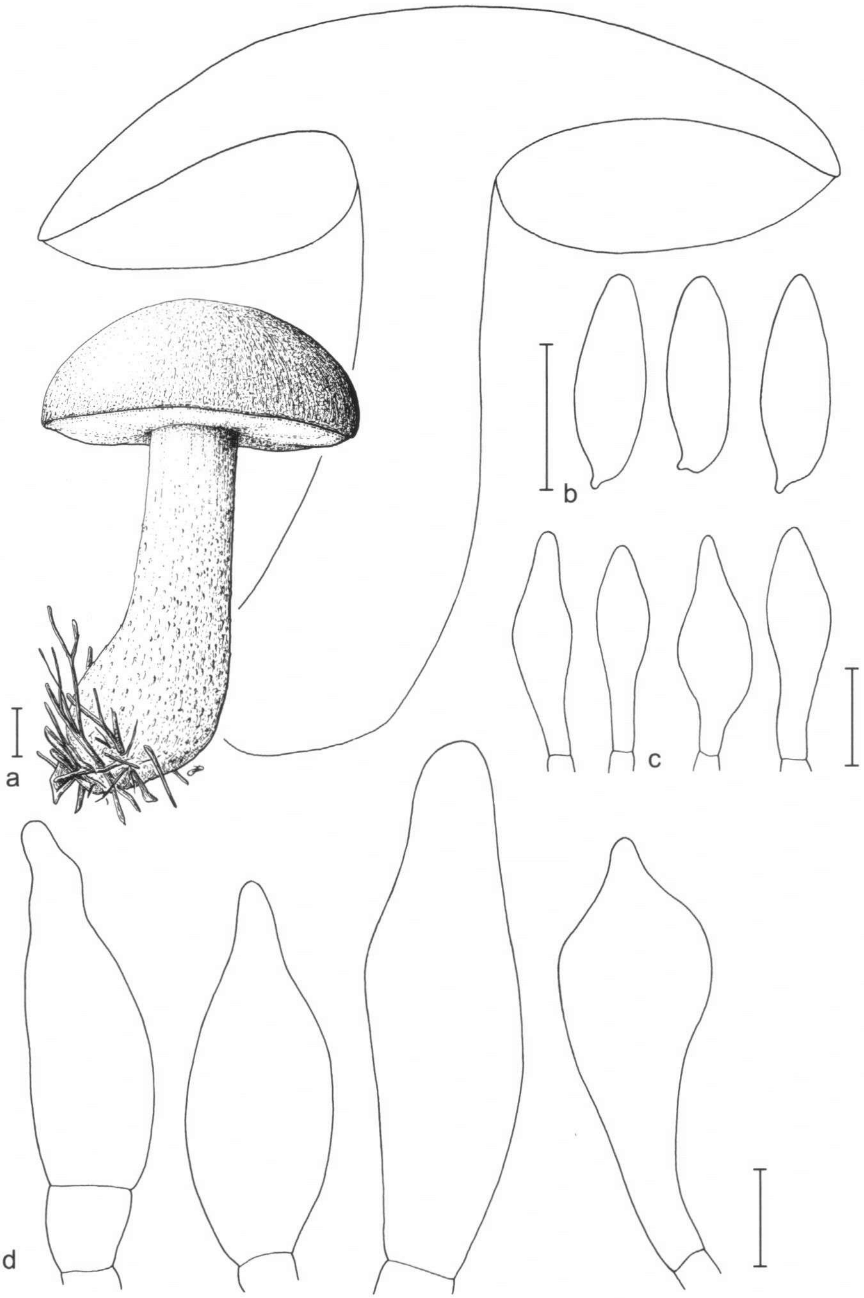

Fig. 11. *Leccinum scabrum*. a. Habitus; b. spores; c. hymenocystidia; d. caulocystidia. Scale bars = 10 μm resp. 1 cm.

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, Hřibovité 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

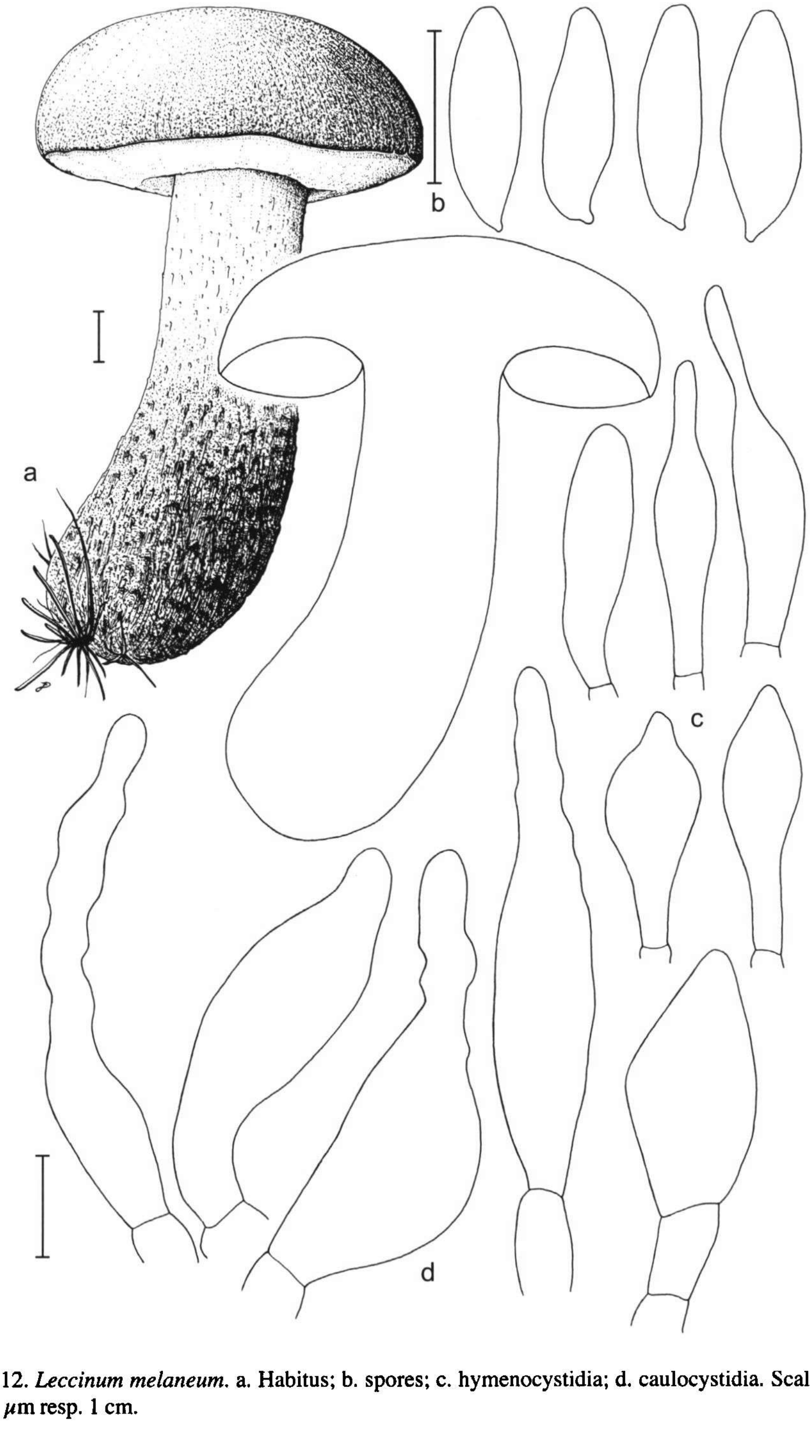

Fig. 12. *Leccinum melaneum*. a. Habitus; b. spores; c. hymenocystidia; d. caulocystidia. Scale bars = 10 μm resp. 1 cm.

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*).

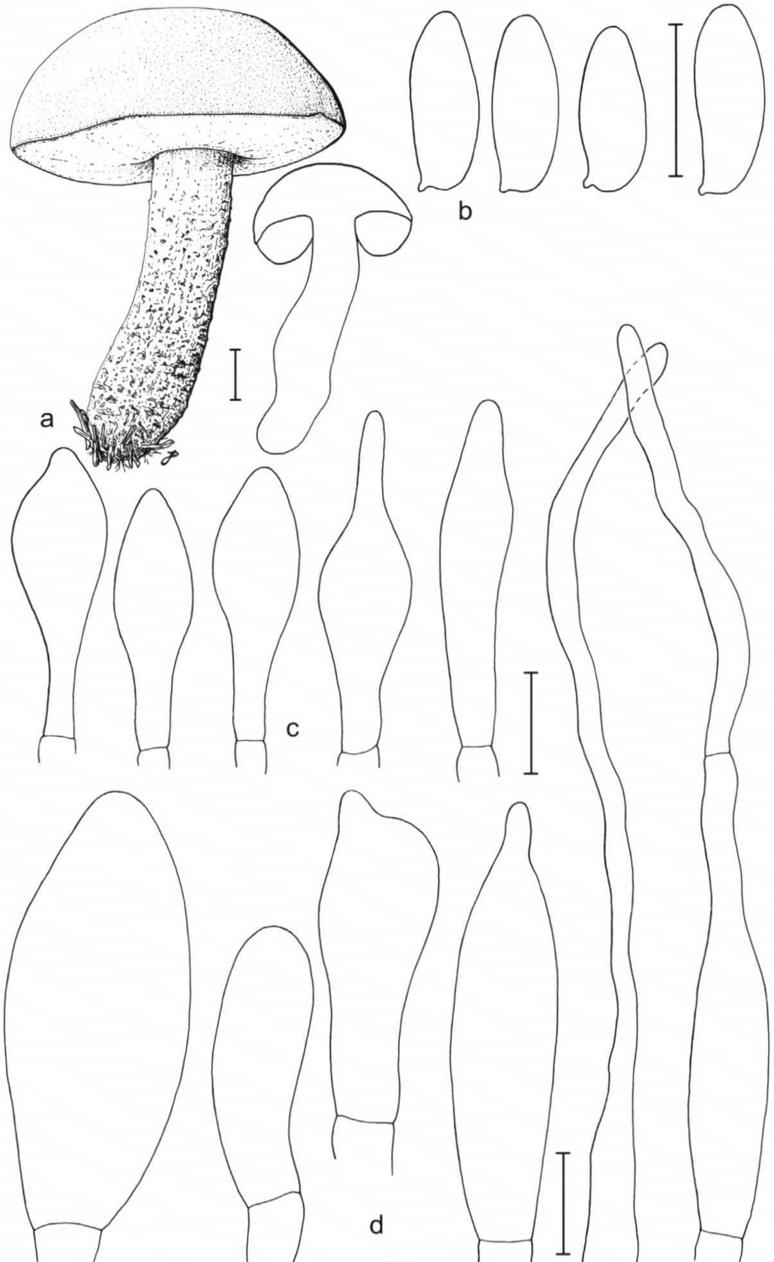

Fig. 13. *Leccinum rotundifoliae*. a. Habitus; b. spores; c. hymenocystidia; d. caulocystidia. Scale bars = 10 μm resp. 1 cm.

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 x 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) x 4.5–7.0 µm, Q=2.2–3.2, Q_{av}= 2.5–2.7(–2.9). Basidia 23.5–33.0 x 11.0–12.5 µm, clavate. Pileipellis a rather regular intricate, cutis; elements 30–95 x 3.0–8.5 µm, narrowly cylindrical, hyaline and granular incrusted or brownish and then often also granular incrusted. Caulocystidia 35–60 x 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

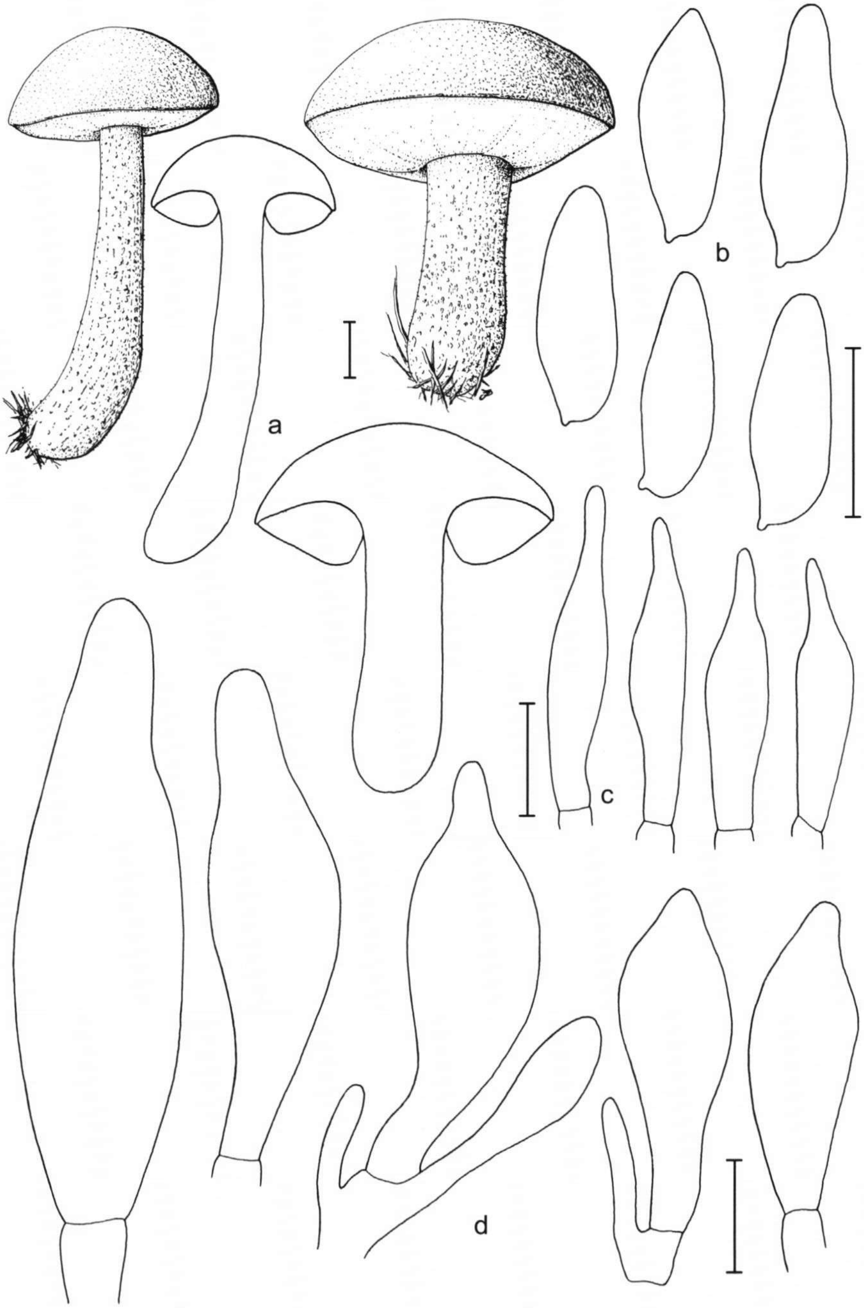

Fig. 14. *Leccinum schistophilum*. a. Habitus; b. spores; c. hymenocystidia; d. caulocystidia. Scale bars = 10 μm resp. 1 cm.

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.

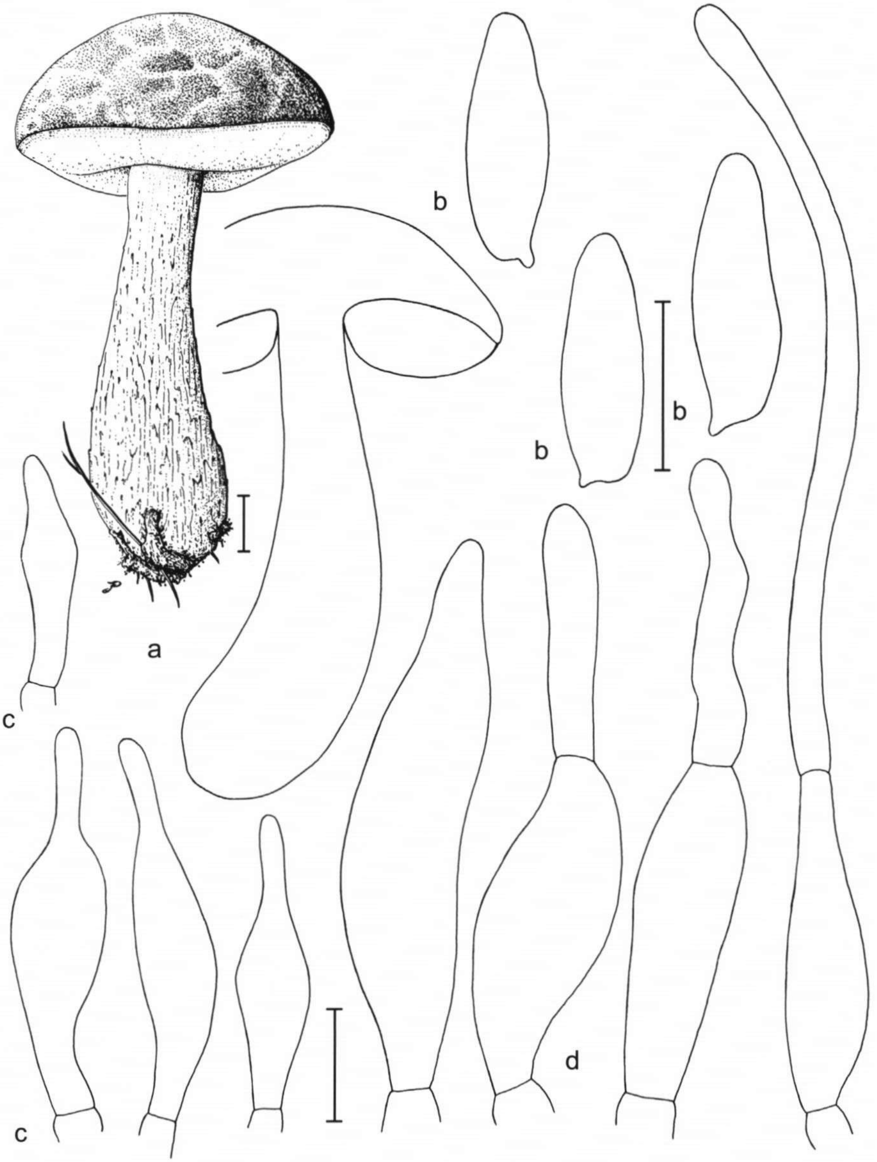

Fig. 15. *Leccinum variicolor*. a. Habitus; b. spores; c. hymenocystidia; d. caulocystidia. Scale bars = 10 μm resp. 1 cm.

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 89102414* (holotype *L. brunneogriseolum* f. *chlorinum*, LIP) ; Isère, Roybon près du Col de toutes Aures, 16 X 1988, *Estades 88101611* (holotype *L. cyaneobasileucum*, LIP).

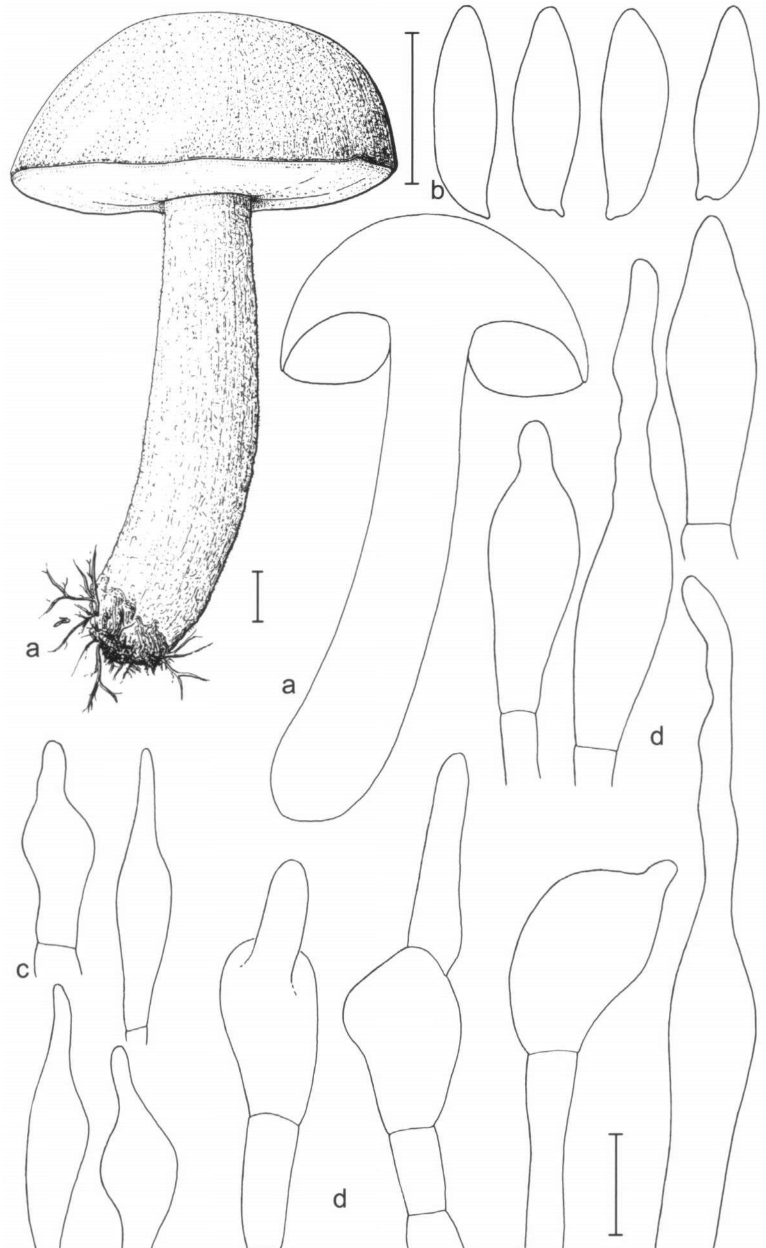

Fig. 16. *Leccinum cyaneobasileucum*. a. Habitus; b. spores; c. hymenocystidia; d. caulocystidia. Scale bars = 10 μm resp. 1 cm.

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, cylindrical 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.

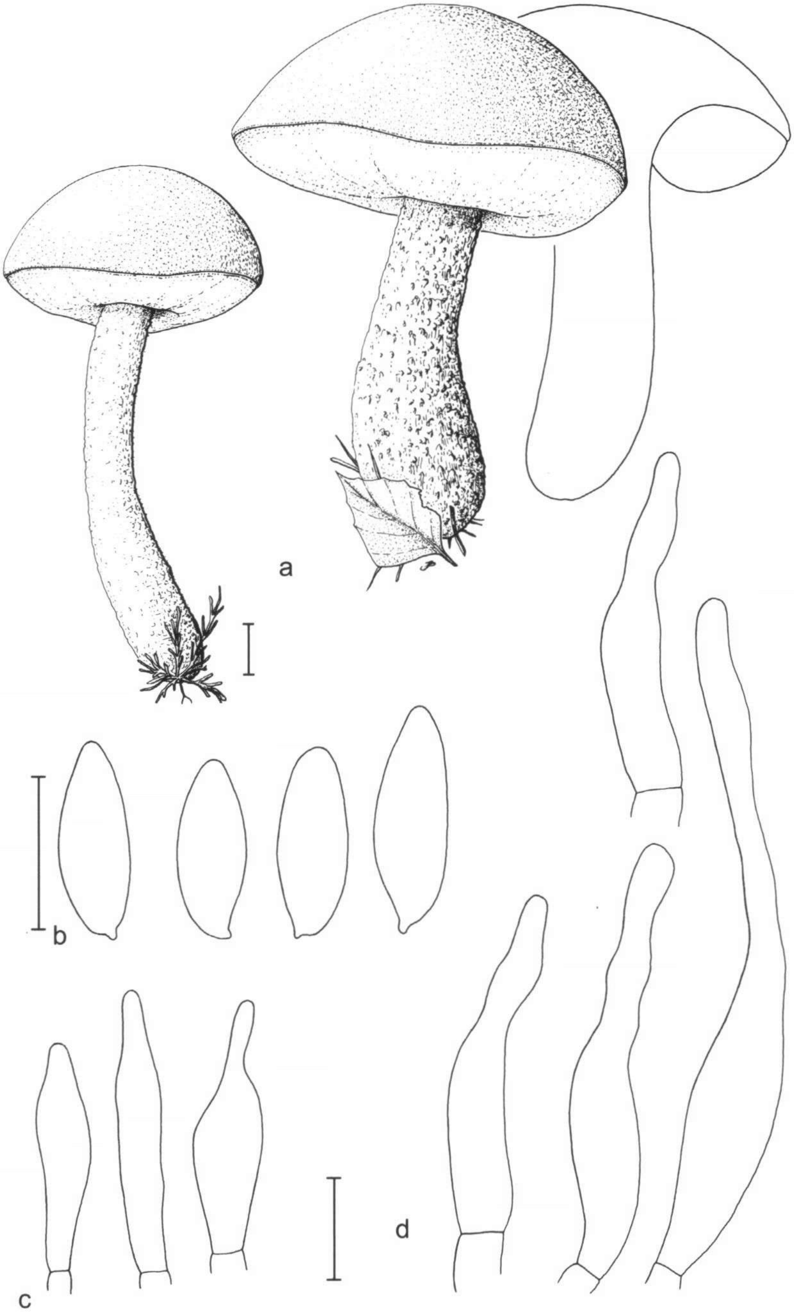

Fig. 17. *Leccinum holopus*. a. Habitus; b. spores; c. hymenocystidia; d. caulocystidia. Scale bars = 10 μm resp. 1 cm.

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

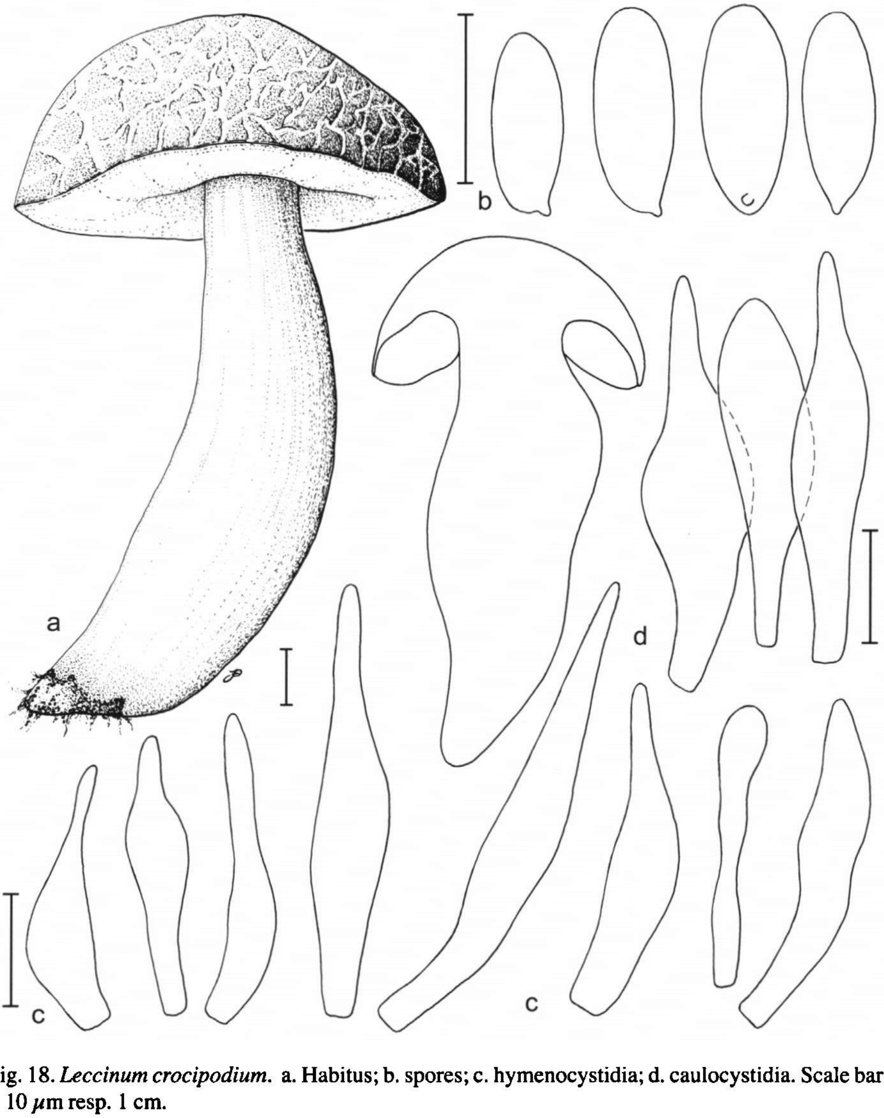

Fig. 18. *Leccinum crocipodium*. a. Habitus; b. spores; c. hymenocystidia; d. caulocystidia. Scale bars = 10 μm resp. 1 cm.

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 x 6–14 mm, cylindrical, slightly widened towards base to subclavate, sometimes flexuous, whitish to pale grey ochre, entirely covered with

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

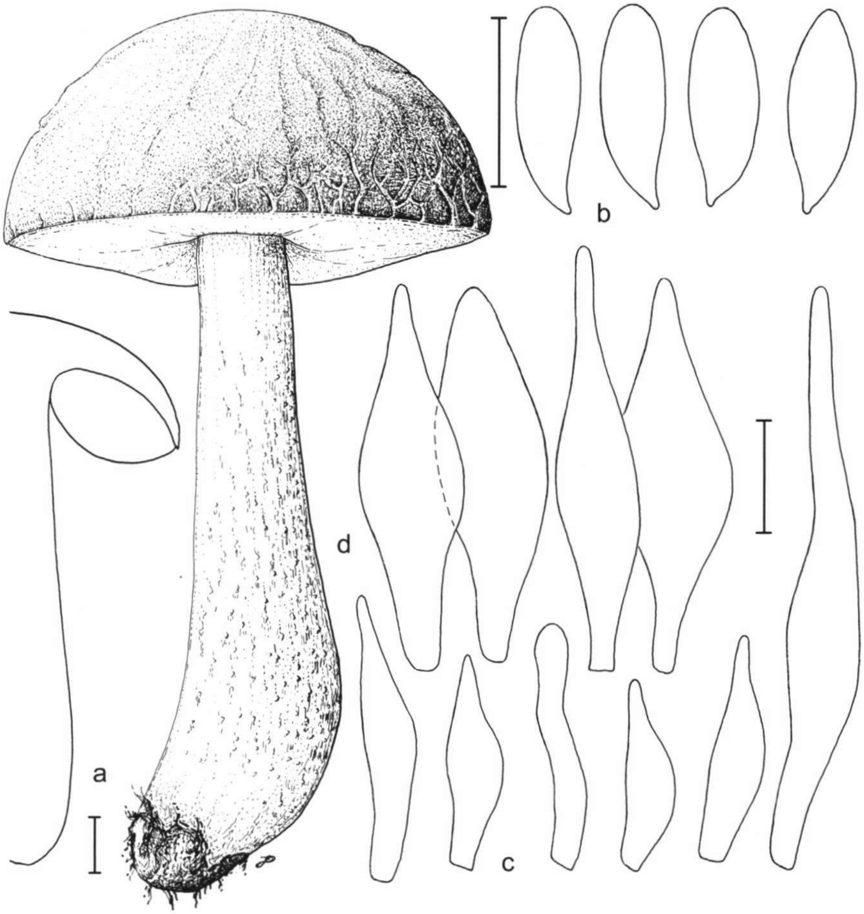

Fig. 19. *Leccinum pseudoscabrum*. a. Habitus; b. spores; c. hymenocystidia; d. caulocystidia. Scale bars = 10 µm resp. 1 cm.

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 β [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.

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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. (*L. populinum*)	AF139703	*Xerocomus dryophilus*	AF514823
		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 (*L. nucatum*)	AF139700	*Xerocomus rubellus*	AF514829
		Xerocomus rubellus	AF514830
Leccinum lepidum	AF139698	*Xerocomus subtomentosus*	AF139716
Leccinum albostipitatum (*L. aurantiacum*)	AF139689		
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).

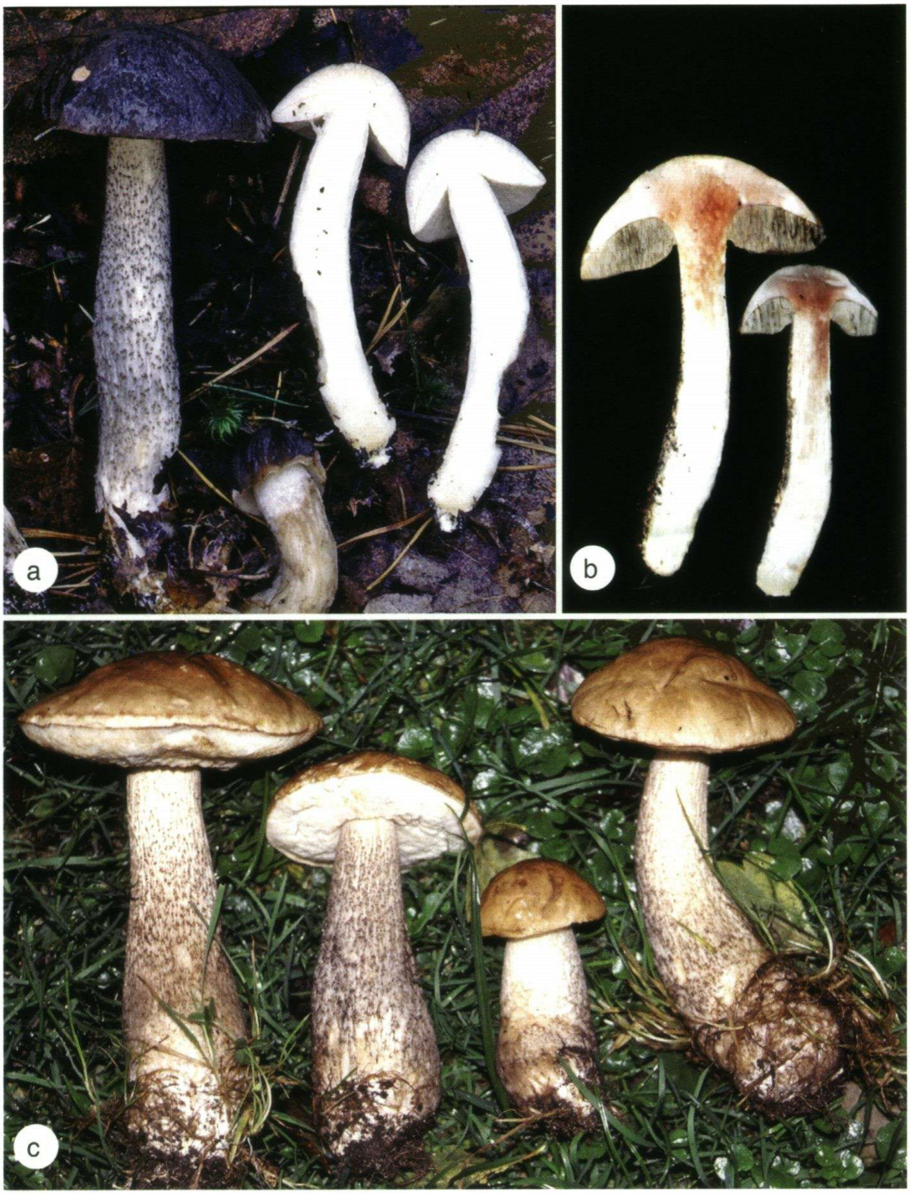

Plate 5. *Leccinum scabrum*. a. Habitus (Ontario, Canada, H.C. den Bakker); b. extreme discoloration of the context (Finland, M.E. Noordeloos); c. habitus (The Netherlands, C. Bas).

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).

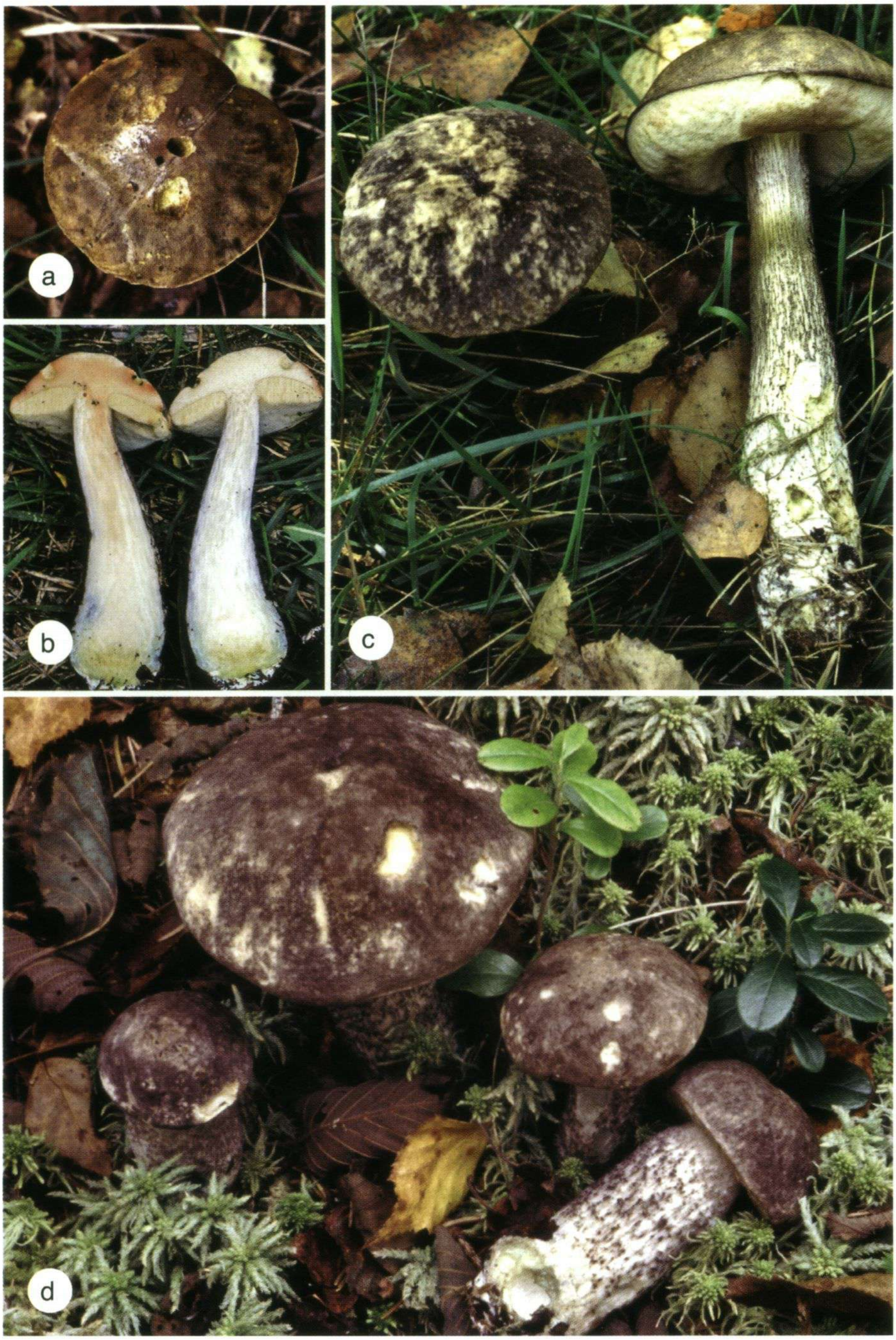

Plate 9. *Leccinum variicolor*. a. Pileus (The Netherlands, M.E. Noordeloos); b. typical discoloration of context (Ontario, Canada, H.C. den Bakker); c. (The Netherlands, M.E. Noordeloos); d. (Slovakia, M.E. Noordeloos).

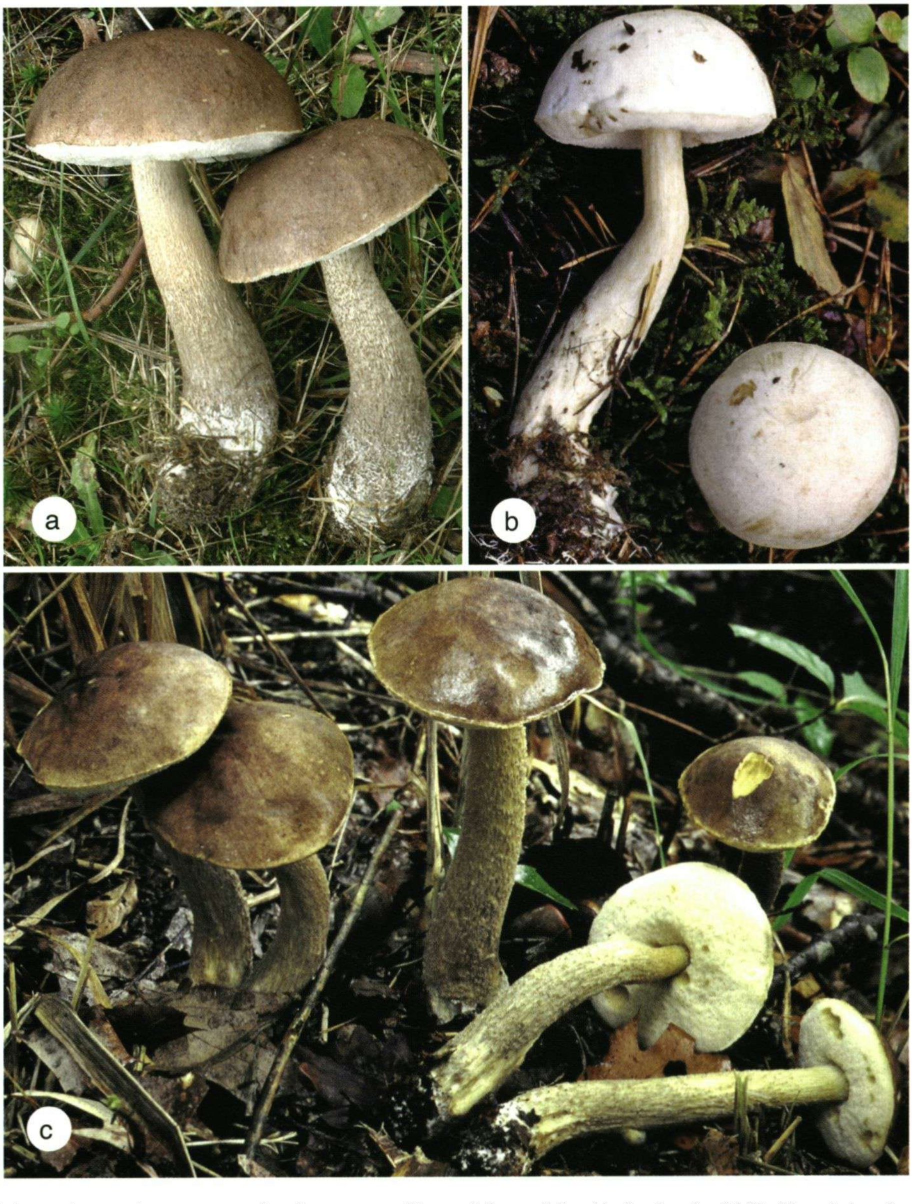

Plate 10. *Leccinum cyaneobasileucum*. a. Normal form (The Netherlands, M.E. Noordeloos); b. rare white (albinistic) form (The Netherlands, M.E. Noordeloos); c. normal form (Belgium, R. Walleyn).

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).