

Diversity of boreal small species of *Cortinarius* subgenus *Telamonia* with *Salix*

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Table 1

Sequence alignments

Abstract

This work presents the genetic and morphological diversity of small *Cortinarius* subgenus *Telamonia* species found from moist *Salix* thickets in Finland. The boreal fungi were compared with several type and other specimens from the alpine zone or similar habitats from the temperate zone. The boreal and alpine zones had many common species: nearly all boreal species grew in the alpine zone with dwarf *Salix*. The species often had wide distributions, extending to North America. The genetic analyses consisted of ITS and RPB2 sequences. Both genetic and morphological variation was high. The species formed complexes, where the boundaries among species were often obscure. Very close sibling species were delimited based on differences at the same sites. Twenty-three boreal species were recognized. Four of them are described here as new: *C. paulus* and *C. paululus* as sibling species to *C. pauperculus* J.Favre, *C. rusticelloides* as a sibling species to *C. rusticellus* J.Favre, and *C. vienoi* as a sibling species to *C. perzonatus* Reumaux. *Cortinarius sagarum*, a sibling species to *C. comatus* J.Favre and *C. vulpicolor* M.M.Moser & McKnight, is described as new from arctic-alpine zones.

Introduction

Boreal *Salix* thickets have a rich mycoflora of agarics (*Agaricales*), and the most species-rich genus there is *Cortinarius*. Nearly all these species are small and belong to subgenus *Telamonia* sections *Hydrocybe* (Fr.) Nezdobjm. and *Incrustati* Melot. Owing to the difficulties in identifying them, the purpose of this study was to clarify the number and characters of these species as well as to name them. *Cortinarius* is a very large genus that has been extensively studied in Europe, but its taxonomy is far from complete. Recently developed molecular methods have promoted the *Cortinarius* taxonomy, especially concerning boreal forest species (e.g. Niskanen et al. 2009, 2011, 2013, 2016, Liimatainen et al. 2014, 2015, 2017, Dima et al. 2016, Brandrud et al. 2018). This study focused on a specific habitat, alluvial *Salix* thickets. Surveys concerning the diversity of *Telamonia* associated with boreal *Salix* have not been published before. This study was mostly conducted in Finland, where *Salix* thickets occur commonly along lakes and rivers. The *Cortinarius* species in *Salix* thickets seemed to differ from forest species. Since most *Telamonia* species associated with *Salix* have been described from alpine habitats (Favre 1948, 1955, Lamoure 1977, 1978, Moser & McKnight 1987, Moser 1993), the comparison with alpine species was essential.

The use of the ITS (internal transcribed spacer) region has generally been sufficient for the identification of *Cortinarius* species, but the interspecific differences have been scantier when compared with many other fungal genera (e.g. Frøslev et al. 2007, Peintner 2008, Niskanen et al. 2011, 2013). Since the ITS differences among species often appeared few also in this study, another region, RPB2 (RNA polymerase II subunit), was analysed in several species complexes to help recognize species limits. The RPB2 region has sometimes been used successfully together with the ITS region to delimit *Cortinarius* species (Frøslev et al. 2005). Whether the few genetic or morphological differences are intraspecific or interspecific depends also on the interpretation. The interpretation was grounded on site-specific comparisons in this study. The observed diversity is

presented here as a whole including yet unidentified species and specimens. The results, which include several sequenced type specimens and five new species, contribute to the knowledge of boreal and arctic-alpine *Cortinarius* species.

Materials and Methods

Specimen sampling

The species descriptions are largely based on the author's own collections. The study concentrated on *Salix* habitats of eastern and northern Finland. Most specimens were collected from the municipalities of Nurmes and Valtimo in North Karelia. The district is in the transition zone between the southern and middle boreal zones. Many specimens originated also from the northern boreal and alpine zones. Alpine fungi were collected from some fjelds or mountains of Finland, Iceland, Norway, Sweden, and Switzerland. In addition to inland habitats, specimens were collected from seashores in the middle boreal zone of Finland. The North Karelian sites were visited many times during some years. All photos were taken by the author excluding a *C. comatus* photo of Emanuele Campo.

The boreal inland study sites were alluvial *Salix* thickets or shore forests with *Salix* bushes by lakes and rivers. Only few *Telamonia* were collected from other habitats, like swamps or ditches. *Salix phylicifolia* was the main tree species, mixed usually with *S. myrsinifolia*, or *S. lapponum* in Lapland, and occasional other *Salix* species. Some *Telamonia* grew with *S. repens* on seashore. The exceptional and arctic-alpine *Salix* species are mentioned with the descriptions. The soil of the boreal sites varied from muddy to sand. All North Karelian sites had a mesotrophic - eutrophic, muddy, often paludified soil. The fungi grew among hygrophilous mosses, among leaf litter, or rarely on bare soil. Tree species and other vegetation were noted at the collections sites. All specimens are deposited in TUR, unless otherwise stated.

Herbarium specimens were examined especially from TUR and TUR-A. Types or other specimens were also examined from G, described by J. Favre,

from IB, described by M. Moser and K. McKnight, from LY, described by D. Lamoure, from PC, described or collected by A. Bidaud, X. Carteret, H. Romagnesi, P.-A. Moreau and P. Reumaux, from REG, determined by N. Arnold, from private herbaria of A. Bidaud and P. Moëgne-Loccoz, and from S, the type of *Cortinarius vernus* H.Lindstr. & Melot.

The examined *Telamonia* species had pilei under ca. 50 mm in diameter and stipes under ca. 5 mm wide. Larger *Telamonia* like *C. saturninus* (Fr.: Fr.) Fr. occurred rarely in the *Salix* thickets, and were excluded from this study. The taxonomy of sect. *Saturnini* has been published by Liimatainen et al. (2017).

Morphological studies

The macroscopic descriptions were based on fresh fruitbodies, unless otherwise stated. The colour codes of fresh fungi refer to Küppers (1999). The stipe width was measured at the widest point.

Microscopic features were examined from dried material at $\times 1,000$ magnification. Spores and lamellar hyphae were examined in Melzer's reagent. Only mature spores from lamellae were considered. The number of measured spores per specimen was twenty for the types or the new species and ten for other specimens, unless otherwise stated. Spore measures excluded verrucae, and basidial lengths excluded sterigmata. The sizes of structures are given as length \times width. The interval is the range with the mean underlined. The Q value means the ratio of spore length to spore width (calculated for each spore). Pileipellis has not been regarded as useful for the identifications of closely related *Telamonia* species, since they have often had very similar cap cuticle structures (Niskanen 2008). However, pileipelles of the new species were examined in 10% NH_4OH .

Molecular methods

Molecular methods included the ITS region with 5.8S rDNA as the most important sequence. The RPB2 sequences were analysed in some of the most difficult species complexes to compare with the ITS result. All type sequences, high-quality sequences showing intraspecific divergence, and some additional sequences, especially from different countries, were submitted to GenBank and two sequences to ENA (European Nucleotide Archive). The accession

numbers are listed in Table 1 (Electronic Supplementary Material 1). All sequenced specimens have been marked with an asterisk (*) in the respective descriptions. The extraction method followed Kokkonen & Vauras (2012) except that both NucleoSpin Tissue XS and Plant II kits (Macherey-Nagel) were used. The PCR primers for the ITS region were ITS1-F, ITS4-B (Gardes & Bruns 1993), ITS2 and ITS3 (White et al. 1990) with a few exceptions. In case the primers mentioned before did not work, the primer pair ITS5 (White et al. 1990) and ITS2 was used for the ITS1 region, and one of the two new forward primers, fITS7tel or ITStel1, was used with ITS4 (White et al. 1990) for the ITS2 region. The primer fITS7tel (5'-GTGAATCATCGAATCTTTG-3') was modified from fITS7 primer (Ihrmark et al. 2012), and the sequence of ITStel1 was 5'-GAGCATGCCTGTTTGAGTG-3'. The ITS sequencing primers were ITS1 (White et al. 1990), ITS2, ITS3, fITS7tel, ITStel1, and ITS4. The RPB2 primers for PCR and sequencing were RPB2-6F and RPB2-7R (Liu et al. 2000). The PCR was run using a GeneAmp PCR system 9700 (PE Applied Biosystems), with Pure Taq Ready-To-Go PCR beads (GE Healthcare). The reaction volume 25 μl composed of 4 μl extract, 1 μl primers and 19 μl water. The PCR procedure consisted of 5 min at 94 °C, 30–40 cycles of 1 min at 94 °C, 1 min at 51–56 °C, and 1 min at 72 °C, and then a final extension step of 7 min at 72 °C. PCR products were purified with the Ezna Cycle Pure kit (Omega), or the service provided by MacroGen. All samples were sequenced by MacroGen. The sequences were edited with Seqman (DNASar), and the fasta files were aligned for comparisons using Clustalw (www.genome.jp). Positions with ambiguous bases and missing data in the conservative middle part of the ITS region were usually excluded from the comparisons.

Phylogenetic methods

For the ITS and RPB2 phylogenetic analyses, the sequences were aligned using MAFFT 7.0 (Katoh 2013) and adjusted manually in AliView (Larsson 2014). Ambiguously aligned regions were kept. The RPB2 sequences were aligned according to the codons. The alignments are in Electronic Supplementary Materials 2 and 3. The phylogenetic trees were performed by maximum likelihood (ML) analysis in raxmlGUI 2.0 (Stamatakis 2014, Edler et al. 2019)

with thorough bootstrap and GTRGAMMA model. The number of autoMRE bootstrap replicates was 500 for ITS and 950 for RPB2. The RPB2 analysis included a codon specific partition. The analyses were repeated including informative gaps coded as binary data. The gaps were coded by FastGap 1.2 (Borchsenius 2009). The resulting trees were similar, but since the influence of coded gaps was regarded as too strong among very close ITS sequences, the trees with uncoded gaps were selected. The concatenated analysis of ITS and RPB2 alignments was run for sequences of common specimens. The model was GTRCAT. The tree did not provide significant new information and is not presented. The trees were edited in MEGA X (Kumar et al. 2018) and GIMP 2.8. The Bayesian analysis was performed with MrBayes 3.2.6 (Ronquist and Huelsenbeck 2003) with GTR + I + Γ model, burninfrac 0.25, samplefreq 500, printfreq 500 and diagnfreq 1000. The number of generations was 2320000 for ITS and 680000 for RPB2. The phylogenetic analyses included sequences from public databases. *Cortinarius violaceus* sequences from GenBank (Harrower et al. 2015) were used as outgroups.

Results

CORTINARIUS CASIMIRI COMPLEX

Fungi resembling *C. casimiri* (Velen.) Huijsman occur rather commonly in boreal *Salix* thickets. They can be recognized by the large ellipsoid spores and stipe with a pale fibrillose cover. Their spore shape and size varied to some extent, but fungi from *Salix* habitats had usually somewhat smaller and more subamygdaloid spores compared with the *casimiri* collections from other habitats. These fungi were identified as *C. rufostriatus* J.Favre based on the type study. Since they deviated from the *casimiri* group only by 2 bases and 2 indels in ITS, they may be included in the variation of *C. casimiri*, but due to the observed slight morphological and possible host differences, as well as by a distinct 8 base RPB2 sequence difference, they are considered here as a sep-

arate species. Contrary to the *rufostriatus* group, the *casimiri* group was never observed with dwarf *Salix* in the alpine zone or in boreal pure *Salix* thickets, but always at least *Betula* grew nearby.

Cortinarius rufostriatus J.Favre, *Ergebn. Wiss. Unters. Schweiz. Natl. Parks* 5 (33): 204 (1955)

Synonym *Cortinarius hemitrichoides* Bidaud & Moëgne-Locc., *Atlas des Cortinaires* 19: 1506 (2010)

Figure 1

Cortinarius rufostriatus was described from the Swiss Alps growing with *Salix herbacea* (Favre 1955). Horak (1987) divided the type fruitbodies into two parts according to the spore morphology and regarded the type as a mixed specimen. By morphology and ITS analysis, both parts are regarded here to belong to the variation of *C. rufostriatus*. Their ITS sequences deviated one base and an indel from each other, but both grouped distinctly together with the Nordic *rufostriatus* specimens. A Finnish subarctic site had the same two genotypes as the type site. Considering both sites, the deviating genotype did not differ noticeably by morphology from the main group. For example, the deviating specimen had narrower and more amygdaloid spores than the main group specimen at the Finnish site, but this was other way round at the type site. Furthermore, the isotype of *C. hemitrichoides* was a genetic intermediate between the two genotypes, since it had an ambiguous base in the deviant position. *Cortinarius hemitrichoides* is reduced to a synonym of *C. rufostriatus*, considering also their similar morphology (Bidaud et al. 2010).

The morphology of *C. rufostriatus* varied much. The following description is based on Nordic collections. **PILEUS** 4–33 mm in diameter; conical when young, then campanulate, convex or applanate, usually with an obtuse or acute umbo; red brown, dark brown, or rarely orange brown, centre often blackish; delicately flocculose or fibrillose overall or only at margin, at times centre with a pale grey cover or margin with whitish veil remnants, translucently striate. **LAMELLAE** rather broad or broad, emarginate or narrowly adnate, subdistant to distant; yellow



Fig. 1. *Cortinarius rufostriatus*, Finland. **a** Valtimo, KK 79/19. **b** Valtimo, KK 619/16. **c** Posio, KK 102/19. **d** Utsjoki, KK 466/05. **e** Kalajoki, KK 258/04. **f** Kalajoki, KK 259/04.

brown, red brown, orange brown or dark brown, edge paler or concolorous. **STIPE** usually slender, 11–78 mm long, 1–4 mm wide; equal, base at times clavate; red brown, dark brown or rarely pale yellow brown, rarely with a violaceous hue; often thickly pale grey or whitish fibrillose, at times flocculose or with a white band. **CONTEXT** more or less concolorous with the surface. **CORTINA** pale grey or whitish. **SMELL** not distinctive or faintly raphanoid. **SPORES** 9.0–10.6–12.1 × 5.2–6.3–7.4 µm, range of mean values 10.3–10.9 × 6.0–6.8 µm, Q=1.47–1.69–2.05, range of mean Q values 1.62–1.79 (100 spores from 10 collections); usually narrow ellipsoid, often or occasionally with a tapering apex, rarely some spores distinctly amygdaloid or predominantly with a broad apex, some or many spores with a suprahilar depression; usually moderately to rather strongly verrucose, more rarely strongly or weakly verrucose; moderately to rather strongly dextrinoid. **CHEILOCYSTIDIA**-like structures present in some collections, hyphoid. **LAMELLAR HYPHAE** usually smooth or slightly encrusted.

The collections originate from the middle boreal zone to the alpine zone. The species seemed to be more common in *Salix* thickets along lakes and rivers in the northern boreal zone than further south. It also grew on a seashore near *S. phlyicifolia* and *Alnus incana*. The soil varied from sand to muddy.

Cortinarius rufostriatus and the divergent *C. casimiri* group were not observed to have clear morphological differences. Considering the ITS and RPB2 sequences, *C. casimiri* may include more than one species. *Cortinarius casimiri* is regarded as very common (Niskanen et al. 2012b) and only a few *C. casimiri* specimens were examined thoroughly, which is why the following comparison is preliminary. *Cortinarius rufostriatus* fungi seemed on average smaller, more slender and more reddish than usual for *C. casimiri*. A *rufostriatus* collection from seashore had galerinoid orange brown fruitbodies. The spore sizes overlapped, but the usual spore size of *C. rufostriatus* was ca. 9.5–11.5 × 5.5–6.5 µm and of *C. casimiri* ca. 10–12 × 6.5–7.5 µm. The mean spore sizes of the *C. casimiri* specimens were 11.0–11.8 × 6.5–7.1 (n=7), except one *casimiri* collection, genetically identical with the *C. casimiri* var. *hoffmannii* type sequence (Suárez-Santiago et al. 2009), had smaller spores with mean 10.7 × 6.3 µm.

Suárez-Santiago et al. (2009) also found the spores of var. *hoffmannii* exceptionally small. One *rufostriatus* specimen had exceptionally wide spores with mean width 6.8 µm. The verrucosity and dextrinoidity of spores as well as hyphal incrustations were similar for *C. rufostriatus* and *C. casimiri*. An examined *C. subsertipes* Romagn. specimen of Romagnesi had very wide spores and an ITS sequence identical with some *C. casimiri* sequences, supporting their conspecificity (e.g. Suárez-Santiago et al. 2009).

HOLOTYPE: *Cortinarius rufostriatus* J.Favre. Switzerland, Graubünden, S-charl, Val Sesvenna, Marangun, alt. 2400 m, among *Salix herbacea*, 24.VIII.1943 J. Favre 164a (GK13511). – Part 164a (Horak 1987) with 3 fruitbodies: spores 9.0–10.7–11.5 × 5.9–6.5–7.0 µm, Q=1.45–1.64–1.83 (n=20); ordinary or narrow ellipsoid, rarely cylindrical, occasionally a tapering apex; rather weakly to moderately verrucose; rather weakly to rather strongly dextrinoid. Part 164a-X with 2 fruitbodies: spores 10.1–11.2–13.1 × 5.5–6.2–6.9 µm, Q=1.59–1.82–2.03 (n=20); narrow ellipsoid, cylindrical or amygdaloid, rarely a suprahilar depression; weakly to rather weakly verrucose; rather weakly to rather strongly dextrinoid.

ISOTYPE: *Cortinarius hemitrichoides* Bidaud & Moëgne-Locc. France, Savoie, Les Arcs, lac Mar-loup, alt. 2500 m, by *Salix herbacea*, 25.VIII.1990 leg. A. Bidaud, AB 90-08-118 (Herb. A. Bidaud). – Part of type as a loan. Spores 9.0–10.7–12.2 × 5.5–6.0–6.8 µm, Q=1.53–1.77–2.03 (n=20); ellipsoid, cylindrical or subamygdaloid, rarely amygdaloid, shape very variable; rather weakly verrucose; weakly dextrinoid. Cystidia not observed. Lamellar hyphae slightly to moderately encrusted.

SPECIMEN EXAMINED: *Cortinarius subsertipes* Romagn. Locality unknown, deciduous forest, 1.IX.1951 leg. P. Ostoya, H. Romagnesi 51239 (PC, Herb. Romagnesi). – Spores 9.7–10.7–12.0 × 6.0–7.0–7.8 µm, Q=1.28–1.53–1.74 (n=20); broadly ellipsoid, rarely narrow ellipsoid or cylindrical, rarely slightly tapering at apex, suprahilar depression occasional; usually moderately verrucose, at times apex rather strongly verrucose, verrucae larger at apex; rather weakly dextrinoid. Some lamellar hyphae rather strongly encrusted.

OTHER SPECIMENS EXAMINED: *C. casimiri*: FINLAND. Varsinais-Suomi. Turku, Ruissalo, nature

reserve, mixed herb-rich forest, 6.X.2006 Kokkonen 1246/06*. Pohjois-Karjala. Kesälahti, Marjoniemi, moist *Betula* site, 21.IX.2004 S. Huhtinen 04/54*. Nurmes, Vihtasenlampi, shore forest, base of *Salix pentandra*, near *Betula*, 9.IX.2003 Kokkonen 495/03*. Inarin Lappi. Utsjoki, Tsuomasvarri, near *Salix glauca*, *S. myrsinites*, *S. myrsinifolia* ssp. *borealis* and *Betula pubescens*, 26.VIII.2005 Kokkonen 503/05*. ICELAND. Suður-Ísland. Rangárþing eystra, Básar, *Betula pubescens* forest with scattered *Salix*, near *Betula* and *S. phyllicifolia*, 14.IX.2017 Kokkonen 331/17*, Snorraríki, *Betula pubescens* forest with scattered *Salix lanata* and *S. phyllicifolia*, 13.IX.2017 Kokkonen 336/17*, 16.IX.2017 Kokkonen 329/17, 330/17*. **C. rufostriatus**: FINLAND. Keski-Pohjanmaa. Kalajoki, Hiekkasärkät, 10.IX.2004 Kokkonen 238/04, 258/04*, 259/04*, 260/04, 261/04. Pohjois-Karjala. Valtimo, Haapakylä, Heinälampi, 24.IX.2002 Kokkonen 41/02*, 20.IX.2003 Kokkonen 718/03*, 752/03, 26.IX.2009 Kokkonen 354/09, 14.IX.2019 Kokkonen 79/19*, Liuhanniemi, 30.IX.2016 Kokkonen 619/16*. Koillismaa. Kuusamo, Vuotunki, 2.9.2005 Kokkonen 394/05. Posio, Korouoma nature reserve, 14.VIII.2006 Kokkonen 161/06, 19.IX.2019 Kokkonen 102/19*. Salla, Kotala, 20.VIII.2008 Kokkonen 87/08* & J. Vauras. Sompion Lappi. Savukoski, Tulpio, 22.VIII.2008 Kokkonen 116/08*. Enontekiön Lappi. Enontekiö, Kaaresuvanto, 20.VIII.2006 Kokkonen 263/06, 273/06*, Palojoensuu, 19.VIII.2006 Kokkonen 252/06*, Peltovuoma, 22.VIII.2006 Kokkonen 301/06*. Inarin Lappi. Utsjoki, Pulmankijärvi, 28.VIII.2005 Kokkonen 465/05*, 466/05* 467/05. ICELAND. Suður-Ísland. Rangárþing eystra, Valahnúkur, among *S. herbacea*, near *S. arctica* and *Betula*, 16.IX.2017 Kokkonen 334/17*, 344/17. NORWAY. Nord-Trøndelag. Levanger, Hårskallen, near *S. herbacea*, 22.VIII.2016 Kokkonen 311/16*. SWEDEN. Lule Lappmark. Gällivare, Nieras, near *S. herbacea*, 30.VIII.2016 Kokkonen 1403/16*. SWITZERLAND. Graubünden. Scuol, Val Sesvenna, among *S. herbacea*, alt. 2525 m, 17.VIII.2017 Kokkonen 275/17*, 276/17*.

CORTINARIUS COMATUS COMPLEX

Figure 2

Cortinarius comatus J.Favre, *Ergebn. Wiss. Unters. Schweiz. Natl. Parks* 5 (33): 202 (1955)

A squamulose species occurring rarely in boreal *Salix* thickets was identified as *C. comatus* by comparing morphology and ITS sequences with the type and three alpine collections from France, Italy and Switzerland. *Cortinarius comatus* was described from the Swiss Alps (Favre 1955). The species is characterized by dark red brown fruitbodies, acute umbo, and both pileus and stipe with pale brown, cream or whitish squamules or flocculae. The veil may also be white (*C. rusticellus* in Bidaud et al. 2012). As an addition to the description in *Funga Nordica* (Niskanen et al. 2012b), the pileus diameter of boreal fungi reached 31 mm and stipe size 60 × 4 mm. Sometimes the stipe and/or pileus were only delicately fibrillose, and rarely the pileus appeared as smooth. The spores were usually moderately verrucose, rather large with mean 9.1–9.5 × 5.7–5.9 μm (n=4), ellipsoid or subamygdaloid, and usually weakly dextrinoid. The lamellar hyphae were strongly encrusted and had dark flecks. The alpine collections from Italy and Switzerland had shorter spores than the type and the boreal specimens (mean 8.5–8.6 × 5.7–6.1 μm), whereas the collection from France had larger spores (mean 10.6 × 6.7 μm).

The slightly deficient ITS1 sequence of the type was identical with the boreal, French and Swiss collections and deviated by one indel from the Italian collection. The ITS and RPB2 sequences differed slightly among all specimens, but the variation was regarded as intraspecific. The Swiss and Italian collections had one different base in the ITS region compared with the French and most Finnish collections. In addition, the RPB2 sequences deviated only by one base at most from each other, with one collection having an ambiguous base in the deviating position. Among the Finnish specimens, the ITS sequences deviated by 2 bases and an indel at most from each other, but several specimens had ambiguous bases in the deviating positions. The site with the most deviating specimen included two other sequenced specimens, which had ambiguous bases in one of the deviating positions. Furthermore, the



Fig. 2. *Cortinarius comatus* complex. **a** *C. comatus*. Finland, Nurmes, KK 624/03. **b** *C. comatus*. Finland, Nurmes, KK 425/16. **c** *C. comatus*. Italy, 14 Aug 2017 E. Campo. Photo E. Campo. **d** *C. sagarum*. Iceland, holotype. **e** *C. sagarum*. Norway, KK 307/16. **f** *C. vulpicolor*. Finland, Utsjoki, KK 464/05.

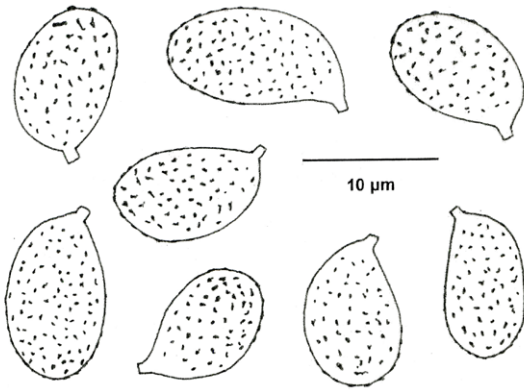


Fig. 3. *Cortinarius sagarum*. Holotype: spores.

RPB2 sequence of the most deviating specimen was identical with the other Finnish RPB2 sequences including a sequence from the same site.

In addition to shore thickets, *C. comatus* grew with boreal *Salix* bushes in a shore forest with mixed stand and among *Sphagnum* and *Mnium* mosses in a swamp with *S. phlycticifolia* and *S. lapponum*. *Cortinarius comatus* is probably connected only with *Salix*.

LECTOTYPE: *Cortinarius comatus* J.Favre. Switzerland, Graubünden, Val Plavna, National Park, among *Salix reticulata* and *S. retusa*, alt. 2100 m, 15.VIII.1941 J. Favre ZA 146a (GK 13276a). – Spores $8.4\text{--}9.6\text{--}10.6 \times 5.6\text{--}6.2\text{--}7.1 \mu\text{m}$, $Q=1.41\text{--}1.55\text{--}1.67$ ($n=20$); rather broadly ellipsoid, rarely sub-amygdaloid; weakly verrucose; weakly dextrinoid.

OTHER SPECIMENS EXAMINED: FINLAND. Pohjois-Karjala. Nurmes, Pahakala, 13.VII.2003 Kokkonen 45/03*, 8.IX.2003 Kokkonen 525/03*, 15.IX.2003 Kokkonen 624/03*, 8.IX.2016 Kokkonen 425/16*. Perä-Pohjanmaa. Kemijärvi, Vuostimo, 31.VIII.2005 Kokkonen 502/05*. Koillismaa. Kuusamo, Oivanki, 13.VIII.2006 Kokkonen 138/06*. Sompion Lappi. Savukoski, Tulppio, 22.VIII.2008 Kokkonen 117/08*. Inarin Lappi. Utsjoki, Pulman-kijärvi, 28.VIII.2005 Kokkonen 505/05*. FRANCE. Savoie. Val d'Isère, among *S. retusa* on calcareous soil, 26.VIII.2005 A. Bidaud and A. Faurite-Gendron, AB 05-08-18 (Herb. A. Bidaud, as *C. rusticellus*)*.

ITALY. Belluno. Marmolada - Rocca Pietore, among *S. retusa* on calcareous soil, 14.VIII.2017 E. Campo (TUR-A)*. SWITZERLAND. Graubünden. Scuol, Val Plavna, W of Sur il Foss, alt. ca. 2220 m, near *S. reticulata*, 12.IX.2018 Kokkonen 834/18*.

Cortinarius sagarum Kokkonen, sp. nov.

Figures 2 d, e and 3

Mycobank MB833745

ETYMOLOGY: the name refers to the sagas of Iceland and Norway. *Sagas* means also wise women in Latin.

HOLOTYPE: Iceland, Suður-Ísland, Rangárþing eystra, Útgönguhöfði, alpine zone, alt. 700 m, near *Salix herbacea*, 15.IX.2017 K. Kokkonen 350/17 (TUR; isotype ICEL), ITS MN841047, RPB2 MN807961.

PILEUS diameter 4–9 mm as dry; young obtuse conical, then convex; dark brown, with abundant white or pale brown squamules or fibrils; margin at times undulate or with scarce whitish veil remnants. **LAMELLAE** ventricose, emarginate or adnate, distant; rather dark yellowish brown, edge paler at least when young. **STIPE** 7–14 mm long and 1–2 mm wide as dry; equal or widening slightly downwards; dark brown, whitish fluffy fibrillose, at times with scarce pale brown squamules in the lower part. **SPORES** $8.9\text{--}10.3\text{--}12.3 \times 5.8\text{--}6.7\text{--}7.7 \mu\text{m}$, range of mean values $10.0\text{--}10.6 \times 6.4\text{--}6.8 \mu\text{m}$, $Q=1.31\text{--}1.55\text{--}1.78$, range of mean Q values 1.47–1.63 (60 spores from 3 collections); ellipsoid, occasionally cylindrical; moderately verrucose; weakly dextrinoid. **BASIDIA** $29\text{--}44 \times 9\text{--}13 \mu\text{m}$ ($n=16$), 4-spored. **CHEILOCYSTIDIA** absent. **LAMELLAR HYPHAE** rather strongly or strongly encrusted and with dark flecks. **PILEPELLIS** hyphae 3–25 μm wide, brownish, very coarsely encrusted, with abundant dark flecks.

HABITAT AND DISTRIBUTION: collections from two alpine zone locations near *S. herbacea* in Iceland and Norway, and from an arctic location in Svalbard; occurs also in the Austrian Alps according to three unidentified GenBank sequences.

SPECIMENS EXAMINED: ICELAND. Suður-Ísland. Rangárþing eystra, Útgönguhöfði, 15.IX.2017 Kokkonen 350/17* (holotype). NORWAY. Nord-Trøndelag. Levanger, Hårskallen, 22.VIII.2016 Kokkonen

307/16*. Svalbard. Longyearbyen, village, by the church, 31.VII.1983 S. Huhtinen 83/139 (as *C. gausapatus*)*.

COMMENTS: Three Nordic arctic-alpine collections with squamulose fruitbodies differed from most *C. comatus* specimens by 2-3 bases in ITS, and by 4-6 bases in RPB2 sequences. They were also genetically close to *C. vulpicolor*, differing from the type by 4 bases and 2 indels in ITS, but only by one base and a few indels in RPB2. Due to the morphological and genetic differences, they are described here as a new species, *C. sagarum*. The short type sequence of *C. comatus* was identical with both *C. comatus* and *C. sagarum*, but contrary to *C. comatus*, fungi of *C. sagarum* had convex pilei without umbo, stouter stipes, and larger spores excluding one *C. comatus* specimen. *Cortinarius vulpicolor* differed by smoother fruitbodies. It grew near *C. sagarum* at the Norwegian site. *Cortinarius sagarum* resembles morphologically *C. gausapatus* J.Favre and *C. hemitrichoides* Bidaud & Moëne-Loc., which were genetically distant according to the type studies. Both of my *sagarum* collections were scarce and the description outlines the features of this small distinctive species. Three GenBank sequences of uncultured environmental samples from the Austrian Alps had identical sequences (Mühlmann et al. 2008, Oberkofler & Peintner 2008, Oberkofler et al. unpubl.).

Cortinarius vulpicolor M.M.Moser & McKnight, Arctic Alpine Mycol. 2: 313 (1987)

Cortinarius vulpicolor was described from Montana, USA, growing among *Salix* sp. in the alpine zone (Moser & McKnight 1987). It was found from one northern boreal riverside, and from two alpine sites near *S. herbacea* in Finland and Norway. The ITS sequences were identical with the *vulpicolor* type, excluding 4 successive ambiguous bases in the Finnish alpine collection and one ambiguous base in the boreal collection. *Cortinarius vulpicolor* differed from *C. comatus* by 4-6 bases and 2-3 indels in ITS, and by 3-4 bases in RPB2. According to the RPB2 phylogenetic tree, *C. vulpicolor* is intermediate between *C. comatus* and *C. sagarum*, but not according to the ITS tree.

The morphology of the Nordic collections largely agreed with the description of *C. vulpicolor* (Moser

& McKnight 1987). The fruitbodies were red brown (alpine) or yellow brown (boreal), the pileus was delicately fibrillose entirely or only at margin, the lamellae were distant, and the stipe had whitish veil fibrils. The pileus margin had sometimes whitish veil remnants. The spores were rather broadly ellipsoid with mean $9.4-10.0 \times 6.1-6.3 \mu\text{m}$ ($n=3$), densely weakly or rather strongly verrucose, and rather strongly dextrinoid. The lamellar hyphae were strongly encrusted and had sometimes dark flecks.

HOLOTYPE: *Cortinarius vulpicolor* M.M.Moser & McKnight. USA, Montana, Beartooth Mts., plain north of Beartooth Pass, among *Salix* (*herbacea*-like), alt. 3550 m, 24.VIII.1983 M. Moser (IB 1983/355). – Part of type as a loan. Spores $7.9-8.6-9.9 \times 5.6-6.0-6.7 \mu\text{m}$, $Q=1.31-1.45-1-68$ ($n=20$); rather broadly ellipsoid; weakly verrucose, verrucae somewhat larger at apex; moderately dextrinoid.

OTHER SPECIMENS EXAMINED: FINLAND. Enontekiön Lappi. Enontekiö, Palojoensuu, 19.VIII.2006 Kokkonen 258/06*. Inarin Lappi. Utsjoki, Tsuomasvarri, 27.VIII.2005 Kokkonen 464/05*. NORWAY. Nord-Trøndelag. Levanger, Härskallen, 22.VIII.2016 Kokkonen 309/16*.

CORTINARIUS CUCUMISPORUS COMPLEX

Figure 4

Cortinarius cucumisporus complex is closely related to the *C. comatus* complex, and to the common *C. flexipes* (Pers.:Fr.) Fr., which also seems to be a complex. All of them include squamulose species.

Cortinarius cucumisporus M.M.Moser, Nova Hedwigia 14(2-4): 515 (1968)

Cortinarius cucumisporus was described from the alpine zone in Austria (Moser 1968). According to Funga Nordica (Niskanen et al. 2012b), it has not been recorded from Fennoscandia before. In this study, *C. cucumisporus* was identified from an alpine site in Sweden, but it was not found from the boreal zone. The ITS sequence of the Swedish collection deviated only one indel from the type and a Swiss alpine collection, excluding 2 ambiguous bases.



Fig. 4. *Cortinarius cucumisporus* complex. **a** *C. cucumisporus*. Sweden, KK 1378/16. **b** *C. cucumisporus*. Switzerland, KK 56/19. **c** *C. stenospermus*. Sweden, KK 1377/16. **d** *C. stenospermus*. Finland, Kuusamo, KK 710/18, Metsähallitus. **e** *C. diasemospermus* coll. Finland, Utsjoki, KK 511/05. **f** *C. diasemospermus* coll. Switzerland, KK 263/17. **g** *C. diasemospermus* coll. Finland, Kuusamo, KK 538/07. **h** *C. diasemospermus* coll. Finland, Kalajoki, KK 252/04.

Cortinarius cucumisporus was genetically close to the diverse *C. diasemospermus* coll. group consisting of the types of *C. diasemospermus* Lamoure and *C. stenospermus* Lamoure as well as many boreal and alpine collections. Its ITS sequence deviated only by 1-2 bases, an inversion and 4 indels from the types. However, *C. cucumisporus* seems to be a separate species, despite similar morphology. All species are characterized for example by amygdaloid spores, but the spores of *C. diasemospermus* coll. were, on average, smaller and frequently ellipsoid in many collections.

The Nordic *C. cucumisporus* specimen had rimulose fibrillose and not translucently striate pilei in contrast to a nearby specimen genetically identical with *C. stenospermus* (Fig. 4). The centre was often cracked into squamules. The veil colour was mainly white or whitish, but also brownish hue occurred. However, the fibrillosity seems to vary much both within *C. cucumisporus* and some groups of *C. diasemospermus* coll. A Swiss *cucumisporus* fruitbody had only a delicately fibrillose, slightly rugulose pileus (Fig. 4b). According to Moser (1968), at least older pilei are fibrillose or squamulose, and the veil is mainly brownish. When compared micromorphologically with the nearby *C. stenospermus*, the Nordic *C. cucumisporus* spores were more fusoid and longer. The average spore size was $10.4 \times 4.9 \mu\text{m}$ and the mean Q value 2.14. The spores were rather weakly to moderately verrucose and moderately dextrinoid. The Swiss collection had the same mean spore size. Its spores were rather weakly verrucose and weakly dextrinoid.

HOLOTYPE: *C. cucumisporus* M.M.Moser. Austria, Tirol, Ötztal, inner Obergurgler Heide, above Untergurgl, among *Salix reticulata* and *Arctostaphylos*, 4.IX.1965 M. Moser (IB Nr.1965/0048). — Part of pileus as a loan. Spores $9.1\text{—}10.0\text{—}11.6 \times 4.9\text{—}5.4\text{—}6.0 \mu\text{m}$, $Q=1.54\text{—}1.84\text{—}2.04$ ($n=20$); amygdaloid or fusoid, rarely ellipsoid or cylindrical, rarely weakly constricted, very rarely with a suprahilar depression; weakly verrucose; indextrinoid.

OTHER SPECIMENS EXAMINED: SWEDEN. Lule Lappmark. Gällivare, Nieras, among *Salix herbacea*, 30.VIII.2016 Kokkonen 1378/16*. SWITZERLAND. Graubünden. Scuol, Val S-charl, Murters da Tamangur, alt. 2375 m, among *S. herbacea*, 26.VIII.2019 Kokkonen 56/19*.

Cortinarius diasemospermus Lamoure, Trav. Sci. Parc Natl. Vanoise 9: 99 (1978), coll.

The ITS sequences of *C. diasemospermus* collections varied slightly, which raised a question, how many species are involved, and the species is treated collectively. Most specimens deviated 1 or 2 bases from each other, but the most divergent clade deviated by 3-5 bases and 2-3 indels from the types of *C. diasemospermus* and *C. stenospermus*. The before-mentioned types deviated by 1 base and 2 indels from each other. *Cortinarius stenospermus* may be a synonym of *C. diasemospermus*, but it could not be confirmed with this data set. The study of more DNA regions and collections with good morphological notes would help to delimit the species around *C. diasemospermus*.

The collections did not group genetically according to the habitats or locations, but all the larger groups occurred both in the boreal and alpine habitats, and identical ITS sequences could originate from distant locations. Also, nearby collections often varied genetically. All collections had rather similar morphologies. Dark red brown pilei, amygdaloid spores and strongly encrusted lamellar hyphae were usual common features. The fruitbodies were more distinctly fibrillose or squamulose in some groups, but a group with identical ITS sequences could include both smooth and squamulose fungi. Pelargonious smell was observed occasionally.

Both *C. diasemospermus* and *C. stenospermus* were described to grow with dwarf *Salix* in the French Alps (Lamoure 1978, 1987). *Cortinarius stenospermus* had longer spores with somewhat different shape compared with *C. diasemospermus*. Other differences were its longer stipe with a ring or a band and veil remnants in contrast to the short stipe with scarce veil of *C. diasemospermus*. The spore differences were not supported by this study. A piece of the partial type of *C. stenospermus* had about the same spore size as a piece of *C. diasemospermus* type, and the shapes were similar with frequent amygdaloid spores. The spores of the *C. diasemospermus* and *C. stenospermus* groups (Fig. 19) were also quite similar. A mixed collection of *C. stenospermus* type is possible, but more likely the spores varied within the specimen. The spore sizes and shapes of *C. diasemospermus* coll. could vary

considerably within a group. The spores of both *C. diasemospermus* and *C. stenospermus* groups varied less in the Alps or among alpine zone specimens than among boreal specimens. For the *C. diasemospermus* group, the range of mean spore size of the hemiboreal and boreal specimens was $8.3\text{--}9.6 \times 4.8\text{--}4.9 \mu\text{m}$, with mean $Q=1.69\text{--}1.96$ ($n=3$), and for the alpine specimens $9.2\text{--}9.5 \times 5.4\text{--}5.5 \mu\text{m}$ with $Q=1.69\text{--}1.73$ ($n=3$). For the *C. stenospermus* group, the range of mean spore size of the boreal specimens was $8.0\text{--}9.1 \times 4.7\text{--}5.1 \mu\text{m}$, with range of mean $Q=1.69\text{--}1.78$ ($n=2$), of the alpine specimens $8.7\text{--}8.9 \times 4.7\text{--}5.4 \mu\text{m}$ with $Q=1.64\text{--}1.88$ ($n=5$), or of the Alps specimens $8.7\text{--}8.9 \times 5.1\text{--}5.4 \mu\text{m}$ with $Q=1.64\text{--}1.76$ ($n=3$). Both groups included specimens with predominantly amygdaloid or ellipsoid spores. The spores were rather weakly to strongly verrucose and weakly to moderately dextrinoid.

Distinct macromorphological differences were neither found between the *C. diasemospermus* and *C. stenospermus* groups. Some *C. diasemospermus* fungi had a white band on stipe like *C. stenospermus*. However, *C. stenospermus* may have characteristically more abundant veil. Some *C. stenospermus* specimens had pilei with white veil patches near the margin and the pilei were squamulose in one specimen. The data for stipe size comparisons was insufficient, but especially boreal *stenospermus* exsiccata were larger than *diasemospermus* exsiccata. The boreal fungi had longer stipes than alpine fungi in both groups, likely due to the vegetation. No specimens were observed with distinctly violaceous-tinged lamellae. Lamoure (1978, 1987) reported young fruitbodies of both species to have violaceous-tinged lamellae.

Two specimens were genetically intermediate between the *C. diasemospermus* and *C. stenospermus* groups (KK511/05, KK355/17). They had an ambiguous base in the deviant position. The specimens originated from the alpine zone of Finland and from subarctic Iceland. Generally, the groups within *C. diasemospermus* coll. were separated rather well with few intermediates in ITS sequences. A group with seven specimens (Group 2 in Fig. 19) deviating from the *C. diasemospermus* group by one base and 2-3 indels included only one partial intermediate specimen. Some specimens of this group had distinctly violaceous-tinged lamellae and the stipe base could

be violaceous. The pileus varied from glabrous to squamulose. The mean spore size and spore shape varied considerably similarly to the *diasemospermus* and *stenospermus* groups, mean range $8.2\text{--}9.8 \times 4.9\text{--}5.5 \mu\text{m}$ with mean $Q=1.53\text{--}1.92$ ($n=6$), but the spores were moderately to rather strongly dextrinoid in contrast to the other two groups. All specimens of Group 2 were from the northern boreal to the alpine zone of Finland.

According to Funga Nordica (Niskanen et al. 2012b), *C. diasemospermus* grows with many tree species and is common from the temperate to the alpine zone. In this study, *C. diasemospermus* coll. occurred commonly with *Salix* bushes and dwarf *Salix* in the northern boreal and alpine zones, but rarely further south. The single *C. diasemospermus* specimen from the hemiboreal zone was from a mixed herb-rich forest with e.g. *Quercus robur* and apparently without *Salix*. *Cortinarius stenospermus* grows in the temperate zone according to a GenBank sequence from Poland (identified as *C. diasemospermus*, KX355534, Kalucka unpubl.). The only *diasemospermus* coll. specimens from the middle boreal zone grew on a seashore near *Salix phylicifolia* and *Alnus* in this study. They belonged to the most separate clade likely representing a separate species (Group 4 in Fig. 19). They had a distinctly brownish veil in contrast to the nearly always white or whitish veil of others. They may represent *C. phaeopygmaeus* J.Favre. Two collections of Group 4 originated from the Swiss Alps, where they were found among *S. herbacea*.

The two specimens of Group 1 (Fig. 19) were from the alpine zones of Finland and Switzerland. Group 1 deviated by one base and 1-2 indels from the *C. diasemospermus* group. Its spores were at the broader end with mean range $9.0\text{--}9.3 \times 5.5\text{--}5.8 \mu\text{m}$ and mean $Q=1.59\text{--}1.64$. Group 3 deviated from the *C. stenospermus* group by 2 bases and 1-2 indels. Both specimens of this group had squamulose pilei and stipes. Their spores resembled each other with mean range $8.7\text{--}9.0 \times 5.5\text{--}5.6 \mu\text{m}$. The spores were mostly ellipsoid, rather weakly verrucose and weakly dextrinoid. Both were collected from the northern boreal zone of Finland.

HOLOTYPE: *Cortinarius diasemospermus* Lamoure. France, Savoie, Vanoise, Région de Pralognan, Roc du Tambour, alt. NW 2400 m, *Salix herbacea*,

19.VIII.1969 D. Lamoure (LY). – Type scarce with a piece of pileus, a stipe and small fragments. Spores 8.3–9.5–11.0 × 5.0–5.5–6.0 μm, Q=1.44–1.73–1.94 (n=20); amygdaloid or ellipsoid, rarely constricted; moderately verrucose; weakly dextrinoid. Lamellar hyphae strongly encrusted and with dark flecks.

HOLOTYPE: *Cortinarius stenospermus* Lamoure. France, Savoie, Vanoise, Région de Pralognan, under Cirque du Dard, alt. N 2200 m, *Dryas* and *Salix reticulata*, 28.VIII.1963 D. Lamoure (LY). – Part of type as a loan. Spores 8.1–8.9–10.3 × 4.9–5.4–6.3 μm, Q=1.51–1.64–1.87 (n=20); amygdaloid, rarely ellipsoid or constricted; moderately verrucose; indextrinoid or weakly dextrinoid. Lamellar hyphae strongly encrusted.

OTHER SPECIMENS EXAMINED: FINLAND. Varsinais-Suomi. Turku, Ruissalo, 11.X.2006 Kokkonen 1314/06* and J. Vauras. Keski-Pohjanmaa. Kalajoki, Hiekkasärkät, 9.IX.2004 Kokkonen 235/04*, 252/04*. Perä-Pohjanmaa. Posio, Korouoma nature reserve, 14.VIII.2006 Kokkonen 160/06*. Koillismaa. Kuusamo, SW of Siirtola, 24.IX.2018 Kokkonen 710/18*, Vuotunki, 31.VIII.2007 Kokkonen 538/07*, 548/07* and J. Vauras. Kittilän Lappi. Kittilä, near the main village, 28.VIII.2008 Kokkonen 196/08*, Muonio, Pallastunturi, among *S. herbacea*, 18.VIII.2006 Kokkonen 235/06*. Sompion Lappi. Savukoski, Ainijärvi, 21.VIII.2008 Kokkonen 106/08* and J. Vauras. Enontekiön Lappi. Enontekiö, near Kaaresuvanto, 20.VIII.2006 Kokkonen 274/06*, 275/06*, Palojoensuu, 19.VIII.2006 Kokkonen 246/06*, 261/06*, Peltovuoma, 22.VIII.2006 Kokkonen 298/06*, Saana, 21.VIII.2006, among *S. herbacea*, Kokkonen 290/06*. Inarin Lappi. Utsjoki, near Skallovaaara, 29.VIII.2005 Kokkonen 476/05*, Tsieskuljoki, 24.VIII.2005 Kokkonen 225/05*, Tsuomasvarri, 27.VIII.2005, near *S. reticulata* and *S. myrsinites*, Kokkonen 511/05*. ICELAND. Suður-Ísland. Rangárþing eystra, Útgönguþöfði, among *S. herbacea*, 15.IX.2017 Kokkonen 351/17*, Snorraríki, *Betula pubescens* forest with scattered *Salix*, near *S. lanata*, *S. phyllicifolia*-hybrid? and *Betula*, 16.IX.2017 Kokkonen 355/17*, Valahnúkur, near *S. herbacea*, *S. arctica* and *Betula*, 16.IX.2017 Kokkonen 353/17*. ITALY. Trento. Soraga, Passo della Selle, alt. ca. 2300 m, on calcareous soil among *S. retusa* with *Euphrasia minima*, 23.VIII.2006 E. Campo (as *C. pauperculus*, TUR-A)*. NORWAY. Nord-Trøndelag. Levanger, Hårskallen,

near *S. herbacea*, 22.VIII.2016 Kokkonen 312/16*. SWEDEN. Lule Lappmark. Gällivare, Nieras, among *S. herbacea*, 30.VIII.2016 Kokkonen 1377/16*. SWITZERLAND. Graubünden. Scuol, Lai Sesvenna, alt. 2660 m, among *S. herbacea*, 17.VIII.2017 Kokkonen 286/17*, 313/17*, Piz Clünas, alt. 2640 m, near *S. herbacea*, 16.VIII.2017 Kokkonen 288/17*, Val Plavna, among *Dryas* and *S. reticulata*, 15.VIII.2017, Kokkonen 293/17*, Val S-charl, Valbella, alt. 2200 m, among *Dryas* and *S. reticulata*, 26.VIII.2019 Kokkonen 51/19*, Val Sesvenna, alt. 2525 m, near *S. herbacea*, 14.VIII.2017 Kokkonen 263/17*. Val Müstair, Piz Cotschen, alt. 2595 m, near *S. herbacea*, 13.IX.2018 Kokkonen 835/18*.

CORTINARIUS DECIPIENS COMPLEX

Figure 5

Cortinarius decipiens (Pers.:Fr.) Fr. is involved in a difficult species complex. The specimens formed genetic continuums, which is why species were difficult to delimit. No identical ITS sequence with the *decipiens* neotype (Moëne-Loccoz & Reumaux 1990b, Suárez-Santiago et al. 2009) was found from the boreal zone. The two closest clades deviated from the neotype only by 1-2 bases and 1-2 indels, and they are all treated here as *C. decipiens*. Since there appeared differences up to 3 bases within this group, and the RPB2 sequences were even more divergent, there are possibly more than one species. The *decipiens* group deviated by 3-4 bases and 0-2 indels from the somewhat morphologically different and genetically more uniform *C. pulchripes* group. *Cortinarius pulchripes* J.Favre is treated here as a separate species. It had characteristically larger spores and smaller fruitbodies than *C. decipiens*. This was remarkably clear within a site. Both species could occur at the same site without intermediates, and they were distinctly separate by the RPB2 sequences, which also support the separation. On the other hand, considering that the *C. decipiens* neotype is partially a genetic intermediate between the *decipiens* and *pulchripes* groups, *C. pulchripes* may be within the variation of *C. decipiens*.

Other species or groups belonging to the *decipiens* complex included *C. fuscoflexipes*, *C. castaneus*



Fig. 5. *Cortinarius decipiens* complex. **a** *C. decipiens*. Finland, Kuusamo, KK 661/18, Metsähallitus. **b** *C. decipiens*. Finland, Kuhmo, KK 666/18, Metsähallitus. **c** *Cortinarius* sp. Finland, Utsjoki, KK 510/05. **d** *C. fuscoflexipes*. Finland, Utsjoki, KK 417/05. **e** *C. pulchripes*. Finland, Nurmes, KK 249/03. **f** *C. pulchripes*. Switzerland, KK 22/19. **g** *C. castaneus*? Switzerland, KK 826/18. **h** *C. pulchripes*. Switzerland, KK 58/19.

neotype group, *C. pseudofusisporus*, and an unidentified group probably without *Salix* connection. Fungi belonging to this complex are widely distributed and not rare, which is why more recognized and likely also unrecognized species belonging to this complex have been described (e.g. in Atlas des Cortinaires series and Suárez-Santiago et al. 2009). To complete the taxonomy, a thorough research with abundant material would be needed. Suárez-Santiago et al. (2009) interpreted *C. decipiens sensu lato* as a highly variable species.

Cortinarius decipiens (Pers.:Fr.) Fr., Epicr.
Syst. Mycol.: 312 (1838)

Cortinarius decipiens was neotypified from France growing with *Alnus* and *Populus* (Moënné-Locoz & Reumaux 1990b). The Finnish specimens resembled macroscopically the *decipiens* neotype by dark brown pileus and stipe with a pale grey or whitish cover or flocculae. The stipe apex had rarely a violet tinge, and the colour of lamellae varied among yellow brown, red brown and dark brown. The fruitbodies were generally rather large for a small *Telamonium*, the pileus reaching 51 mm and stipe 82 × 8 mm. For the comparison to *C. pulchripes*, the largest pileus diameter varied 17–42 mm among *decipiens* exsiccata. The pileus had often pale veil patches near the margin.

The mean spore size varied 7.0–8.1 × 4.2–5.3 µm (n=12), but most specimens had spores under 8 × 5 µm. The mean Q value was 1.51–1.82. The spores were usually somewhat narrow ellipsoid, tapering at times towards apex, or rarely cylindrical, often with a suprahilar depression, moderately to strongly verrucose having often larger verrucae at apex, and usually weakly to moderately dextrinoid. Lamellar hyphae were usually without or only with slight incrustations.

Cortinarius decipiens grows both in lowland and alpine habitats. *Salix* is at least one host, since no other trees were present at two sites: *S. phylicifolia*, *S. myrsinifolia* and *S. pentandra* by a boreal lakeside, and *S. herbacea* at an alpine site. The boreal habitats were moist *Salix* thickets or shore forests by lakes, rivers, brooks or ditches, or moist mixed forests. In one case, *Salix* was not reported from the site, but

only *Alnus*, *Betula* and *Picea*. In the alpine zone, it grew among *S. reticulata* and *Dryas octopetala* or among *S. herbacea*. The collections originated from the southern boreal to the alpine zone in Finland.

A specimen having an identical ITS sequence with the *decipiens* neotype was found from the Swiss Alps (KK823/18), which confirms the occurrence of *C. decipiens* both in lowland and alpine habitats. Its spores were rather large, mean 8.8 × 5.7 µm, resembling thus more the spore size of *C. pulchripes*. Sometimes spores are larger in higher altitudes, but it was not evident among collections of this complex. Another Swiss alpine *C. decipiens* specimen deviated from the neotype by one base.

SPECIMENS EXAMINED: FINLAND. Etelä-Häme. Orivesi, Yröskulma, 17.IX.1999 J. Vauras 15582 (TUR-A)*. Pohjois-Häme. Laukaa, 12.IX.2002 Kokkonen 128/02*. Pohjois-Karjala. Nurmes, Joki-Vastimo, 18.IX.2003 Kokkonen 710/03*, Metsä-Vastimo, 24.IX.2002 Kokkonen*, Pahakala 15.IX.2003 Kokkonen 620/03*. Kainuu. Kuhmo, near Koirakangas, 8.IX.2018 Kokkonen 666/18*, Sotkamo, Tipasoja, 3.IX.2001 J. Vauras 17593, det. I. Kytövuori (TUR-A)*. Koillismaa. Kuusamo, near Petäjäkangas, 13.VIII.2006 Kokkonen 146/06*, SW of Siirtola, 24.IX.2018 Kokkonen 661/18*. Kittilän Lappi. Kittilä, near the main village, 27.VIII.2008 Kokkonen 176/08*. Inarin Lappi. Utsjoki, Tsieskuljoki, 24.VIII.2005 Kokkonen 212/05*, Tsuomasvarri, among *S. reticulata*, near *S. herbacea*, *S. glauca* and *Betula nana*, 26.VIII.2005 Kokkonen 459/05*. SWEDEN. Lule Lappmark. Gällivare, Nieras, among *S. herbacea*, 30.VIII.2016 Kokkonen 1380/16*. SWITZERLAND. Graubünden. Val Müstair, Il Jalet, alt. 2380 m, near *Dryas* and *S. reticulata*, 14.IX.2018 Kokkonen 823/18*. Scuol, Val S-charl, N slope of Mot Radond, alt. 2275 m, near *S. reticulata* and *Dryas*, 27.VIII.2019 Kokkonen 60/19*.

Cortinarius pulchripes J.Favre, Beitr. Kryptogamenfl. Schweiz 10(3): 213 (1948) Synonym *Cortinarius albonigrellus* J.Favre, Ergebn. Wiss. Unters. Schweiz. Natl. Parks 5 (33): 202 (1955)

Favre (1948) described *C. pulchripes* growing under *Salix*, and also with *Betula* and *Alnus*, on peatland in

subalpine Switzerland. The dark brown pileus was up to 30 mm, the lamellae cinnamon yellow or pale cinnamon, and the slender stipe up to 60 × 4 mm. The stipe had a violet or purple red tinge, especially above the ring and at the base. The ITS sequence of the type was identical with my boreal and alpine collections with similar morphology. The ITS sequence of the *C. albonigrellus* type, collected from an alpine site among *Salix herbacea* (Favre 1955), deviated from the *pulchripes* type by one base and is regarded here as conspecific. Two collections from the alpine zone of Switzerland had identical sequences and agreed morphologically both with *C. pulchripes* and *C. albonigrellus*: the other had both ellipsoid and cylindrical spores. Also, one boreal specimen having an identical sequence with *C. pulchripes* resembled morphologically *C. albonigrellus* by a protruding ring and predominantly cylindrical spores (KK134/02). Some subalpine collections from Switzerland had fibrillose pilei (Fig. 5). They resembled morphologically the subalpine species *C. dumetorum* J.Favre (Favre 1960), which may be a synonym.

Cortinarius pulchripes is characterised by small fruitbodies having a dark brown or red brown pileus often with blackish centre and stipe with pale grey or whitish cover, which occasionally has a violet tinge entirely or at the base. The base may also be red. The pileus diameter varied 7–35 mm, and stipe size 25–67 × 1–5.5 mm among Finnish collections. Compared with *C. decipiens*, the largest pileus among exsiccata varied 11–21 mm. The lamellae were yellow brown, red brown, or medium brown. The stipe had sometimes flocculae, a band, or a ring with a reddish rim (from spore deposit) similarly to the *C. pulchripes* painting by Favre (Favre 1948).

The mean spore size was 8.2–9.0 × 4.8–5.2 μm with mean Q value 1.59–1.87 among five boreal collections, but one specimen had exceptionally short spores with mean 7.2 × 5.0 μm and Q value 1.46, and the “*albonigrellus*” specimen had exceptionally long spores with mean 9.7 × 5.0 μm and Q value 1.94. Otherwise, the spores resembled much *C. decipiens* spores. However, the spores were more often cylindrical or ovoid, sometimes even amygdaloid, and no more than weakly dextrinoid.

The habitats were boreal inland *Salix* thickets or shore forests, subalpine brooksides, and alpine sites near *Salix herbacea*, *S. reticulata* or *S. myrsin-*

ites. *Cortinarius pulchripes* was collected from the transition between the southern and middle boreal zones to the alpine zone in Finland.

The ITS sequence of the type of *C. atrocoeruleus* M.M.Moser (Suárez-Santiago et al. 2009 and own result) deviated by 1–2 bases and an indel from the *pulchripes* sequences and is probably conspecific. Moser (1967) reported occasional pelargonoid smell, as was observed in one of my *pulchripes* collections. The type spores were more strongly dextrinoid than *pulchripes* spores. Brandrud et al. (1998) considered *C. atrocoeruleus* as a variety and Suárez-Santiago et al. (2009) as a synonym of *C. decipiens*. The types of *C. sertipes* Kühner and *C. contrarius* J.Geesink had identical sequences with *C. atrocoeruleus* (Suárez-Santiago et al. 2009).

HOLOTYPE: *Cortinarius albonigrellus* J.Favre. Switzerland, Pass of Taunter Pizza, west slope, near Pass Fuorn, alt. 2650 m, among *Salix*, sol de verrucano, 5.IX.1953 J. Favre (GK 13268). — Specimen with ca. 8 fruitbodies. Spores 8.0–8.9–9.9 × 4.4–4.8–5.8 μm, Q=1.65–1.86–2.11 (n=20); cylindrical, ellipsoid, or obtusely amygdaloid, rarely constricted; weakly or rather weakly verrucose; weakly dextrinoid.

HOLOTYPE: *Cortinarius atrocoeruleus* M.M. Moser. Austria, Tyrol, Gnadenwald, behind Gunkel, beside Moor, coniferous forest, 30.IX.1951 leg. and det. M. Moser (IB 1951/0161). — Part of type as a loan. Spores 7.5–8.2–9.4 × 4.9–5.2–5.8 μm, Q=1.34–1.54–1.80 (n=20); ellipsoid; moderately to rather strongly verrucose, verrucae larger at apex; moderately dextrinoid.

LECTOTYPE: *Cortinarius pulchripes* J.Favre. Switzerland, Hauts-Marais, Joux valley, near Pont, Sagnevagnard, “tourbière”, 19.IX.1940 J. Favre (GK 7846). — Specimen with 5 fruitbodies in good condition. Spores 7.8–8.5–9.7 × 5.2–5.6–6.1 μm, Q=1.42–1.53–1.69 (n=20); ellipsoid; usually rather weakly verrucose but apex often with few large verrucae, rarely a suprahilar depression or constricted; indextrinoid or slightly dextrinoid.

OTHER SPECIMENS EXAMINED: FINLAND. Pohjois-Karjala. Nurmes, Joki-Vastimo, 22.IX.2002 Kokkonen 134/02*, 18.IX.2003 Kokkonen 690/03*, Pahakala, 26.VIII.2002 Kokkonen 32/02*, 27.VIII.2003 Kokkonen 249/03*, 8.IX.2003 Kokkonen 520/03*, 15.IX.2003 Kokkonen 622/03*, 627/03*. Valtimo, Kalliojärvi, 9.IX.2008 Kokkonen 287/08*, 13.IX.2008

Kokkonen 315/08*. Inarin Lappi. Utsjoki, Tsuomasvarri, among *S. reticulata*, 26.VIII.2005 Kokkonen 458/05*, near *S. reticulata*, *S. herbacea* and *S. myrsinites*, 26.VIII.2005 Kokkonen 461/05*. NORWAY. Troms. Storfjord, Helligskogen, near *Salix* bushes by pond, alt. ca. 300 m, 22.VIII.2017 J. Vauras 32156F (TUR-A)*. SWITZERLAND. Graubünden. Scuol, Piz Clünas, near *S. herbacea*, alt. 2640 m, 16.VIII.2017 Kokkonen 289/17*, Tarasp, W of Lai Nair, alt. 1540 m, by a brook, beside *S. foetida?* and *S. purpurea* ssp. *gracilis*, 24.VIII.2019 Kokkonen 22/19*, Val Plavna, alt. 2320 m, near *S. herbacea*, 15.VIII.2017 Kokkonen 295/17*, Val S-Charl, by Clemgia, alt. 1950 m, under *S. foetida*, 26.VIII.2019 Kokkonen 58/19*, 59/19.

Cortinarius fuscoflexipes M.M.Moser & McKnight, Arctic Alpine Mycol. 2: 306 (1987)

Moser & McKnight (1987) described *C. fuscoflexipes* from timberline near *Salix*, Yellowstone National Park, USA. The ITS sequence of holotype was identical or deviated up to one base and an indel from some Finnish collections excluding an ambiguous base. All specimens are regarded as conspecific. The type was an intermediate having an ambiguous base in a position where the Finnish specimens had different bases. The morphologies were similar. The habitats of the Finnish specimens were a mixed forest (*Salix caprea*, *Alnus*, *Betula*, *Picea abies*, *Pinus sylvestris*) in the southern boreal zone and the alpine zone on a fjeld near *Salix reticulata*. The *fuscoflexipes* type deviated by 5 bases and 2 indels both from the *decipiens* neotype and most *C. pulchripes* specimens. The RPB2 sequences of the three Finnish specimens deviated up to three bases from each other, but grouped together. However, *C. fuscoflexipes* could fall within the variation of *C. decipiens* according to the RPB2 sequences.

Cortinarius fuscoflexipes resembles *C. decipiens* and *C. pulchripes*. Its pileus was dark brown, and the stipe had a pale grey or whitish cover, but its lamellae appeared dark brown in contrast to the yellow brown or red brown lamellae of the other *decipiens* complex specimens at the fjeld site (Fig. 5). The lamellae were described as dark brown also by Moser & McKnight (1987). The stipe had sometimes

a whitish ring or a band as with Moser & McKnight.

The Finnish collections had smaller spores than the type, and about the same size as *C. pulchripes*: mean $8.6-9.0 \times 5.3-5.7 \mu\text{m}$, mean $Q=1.60-1.68$ ($n=3$). The spores were ordinary or narrow ellipsoid, occasionally somewhat tapering towards apex, often with a suprahilar depression, and moderately to rather strongly verrucose and dextrinoid. The lamellar hyphae were smooth or variably encrusted.

HOLOTYPE: *Cortinarius fuscoflexipes* M.M. Moser & McKnight. USA, Wyoming, Yellowstone National Park, Mt. Washburn, timberline, alt. 3300 m, *Picea engelmannii* and *Salix* sp. (*herbacea*-like), 27.VIII.1983 leg. M. Moser, det. M. Moser and K. McKnight (IB 1983/0384). — Part of type as a loan. Spores $8.9-9.7-10.4 \times 5.4-6.0-6.9 \mu\text{m}$, $Q=1.37-1.61-1.79$ ($n=20$); ellipsoid, occasionally nearly amygdaloid; moderately to rather strongly verrucose; rather strongly to strongly dextrinoid.

OTHER SPECIMENS EXAMINED: FINLAND. Etelä-Savo. Savonlinna, Loikansaari, 17.IX.2004 J. Vauras 22884* and Kokkonen (TUR-A). Inarin Lappi. Utsjoki, Tsuomasvarri, 26.VIII.2005 Kokkonen 417/05*, 509/05*.

Cortinarius castaneus (Bull.:Fr.) Fr., Epicr. Syst. Mycol.: 307 (1838), ?

Cortinarius castaneus neotype (Moënné-Loccoz & Reumaux 1990a) deviated only by 2-3 bases and an indel from *C. pulchripes* specimens, and 5 bases and 2 indels from the *C. decipiens* neotype in ITS. The RPB2 sequence of a specimen having identical ITS sequence with the type was also separate. However, there exists a sequence continuum from the *castaneus* neotype via *pulchripes* to *decipiens*, which is why all may be conspecific.

It is doubtful, whether the neotype represents the original species of Fries. Fries (1821, 1838) described *C. castaneus* having lamellae with a violaceous tinge and occurring e.g. in *Fagus* and *Quercus* forests, whereas the *castaneus* neotype had rather vividly ochraceous red lamellae and occurred under *Populus nigra* (Moënné-Loccoz & Reumaux 1990a). A genetically identical collection with the neotype from the Swiss Alps also had vividly ochraceous brown lamellae (Fig. 5g). It grew among *Salix retu-*

sa. Due to the lamellar colour, at least *C. pulchripes* and *C. decipiens* do not agree with *C. castaneus*. Favre (1948) also emphasized that lamellae of *C. pulchripes* are never lilac in colour.

Cortinarius erythrinus has been interpreted variably. Moëgne-Loccoz & Reumaux (1990a) regarded it as a variety of *C. castaneus*. According to Fries (1838), *C. erythrinus* resembles *C. castaneus* strongly. However, the colour of lamellae was described as pale cinnamon, so the description implies more *C. pulchripes* or *C. decipiens* than *C. castaneus*. Some analysed herbarium specimens identified as *C. erythrinus* differed genetically distinctly from each other. Two of them from Germany matched *C. inops* coll., one German specimen along with a *C. castaneus* var. *monspeliensis* specimen from Italy matched *C. vernus*, and three had isolated sequences. *Cortinarius erythrinus* has not been typified, and its identity is left open in this publication.

NEOTYPE: *Cortinarius castaneus* (Bull.:Fr.) Fr. var. *castaneus*. France, Haute-Savoie, Sablière de Silingy, under *Populus nigra*, among leaf litter, 7.V.1986 leg. P. Moëgne-Loccoz, det. P. Reumaux (Herb. P. Moëgne-Loccoz no. 275). — Spores 7.0—7.7—8.9 × 4.6—5.0—5.3 μm, Q=1.37—1.55—1.78 (n=20); ellipsoid, occasionally somewhat elongated or with a suprahilar depression; usually rather strongly verrucose or strongly verrucose at apex; weakly dextrinoid. Some lamellar hyphae weakly to moderately encrusted.

OTHER SPECIMEN EXAMINED: SWITZERLAND. Graubünden. Val Müstair, Costainas, alt. 2553 m, 11.IX.2018 Kokkonen 826/18*.

Isolated specimens identified as *C. erythrinus*: GERMANY. Bayern. Karlstadt, below Ruine Karlburg, under *Corylus* and *Acer*, 17.IX.1995 leg. & det. L. Krieglsteiner / N. Arnold, WÜ4863, TK Nr. 6024/2 (REG 10942)*. ITALY. Parma. Borgotaro, Vighini, under *Castanea sativa*, 11.X.2006 E. Campo (TUR-A)*. Pordenone. Gaiardin-Caneva, *Picea abies* wood, calcareous soil, 2.VIII.2014 E. Campo (TUR-A)*.

Cortinarius pseudofusisporus Bidaud,
Atlas des Cortinaires 19: 1507 (2010)

Cortinarius pseudofusisporus belongs genetically to the *C. decipiens* complex, where it is a morphologically distinctive species. It has very large, often fusoid spores

and a caespitose growth habit (Bidaud et al. 2010). The ITS sequence of the holotype deviated 7 bases and 2 indels from the *decipiens* neotype sequence, 4–5 bases and 1 indel from *C. pulchripes* sequences, and 4 bases and 1 indel from the *castaneus* neotype sequence. The type was collected from a fen under *Betula pendula*. The material of this study lacked corresponding specimens. *Salix* is likely not a host.

HOLOTYPE: *Cortinarius pseudofusisporus* Bidaud. France, Haute-Savoie, Éloise, Semine forest, alt. 500 m, fen, under *Betula pendula*, 7.X.1992 A. Bidaud 92-10-262 (Herb. A. Bidaud) – Part of type as a loan. Spores 9.0—10.9—12.3 × 5.3—5.8—6.9 μm, Q=1.50—1.87—2.08 (n=20); obtusely fusoid or long ellipsoid, more rarely cylindrical, often a suprahilar depression; rather strongly to strongly verrucose and dextrinoid, verrucae larger at apex. Lamellar hyphae strongly encrusted and with dark flecks.

Additional specimens

A group of four boreal specimens collected near e.g. *Populus tremula*, *Betula* and *Alnus*, and only once near *Salix*, formed a separate clade. It deviated from the nearest species, *C. fuscoflexipes*, by 4 bases in ITS, representing likely a separate species. The RPB2 analysis supported the separation, but the group was also close to *C. decipiens*. The spore size was rather constant: mean 8.4—8.9 × 5.3—5.5 μm, mean Q value 1.58—1.67 (n=4). Like with *C. fuscoflexipes*, the spores were moderately to rather strongly dextrinoid.

SPECIMENS EXAMINED: FINLAND. Etelä-Häme. Jämsä, Paatsalo, beside *Populus tremula* in *Picea abies* dominated forest, 18.IX.2004 Kokkonen 510/04* and J. Vauras. Pohjois-Häme. Rautalampi, Hanhitaipale, *Picea abies* dominated forest with *Betula*, *Populus*, *Pinus* and *Sorbus*, 14.IX.2004 T. Rahko*. Koillismaa. Kuusamo, Oulanka National Park, E of Jäkälävaara, a fairly moist forest with *Picea*, *Betula*, and *Alnus*, brookside with ferns, 24.VIII.2005 J. Vauras 23149 (TUR-A)*, SE of Pahtamasuo, rich ditch bank, near *Salix phylicifolia*, further away *Picea* and *Betula*, 25.IX.2018 Kokkonen 658/18*.

A partial genetically intermediate specimen was collected from the fjeld, where as many as three species were identified for this complex: *C. decipiens*, *C. pulchripes* and *C. fuscoflexipes*. The identifica-



Fig. 6. *Cortinarius gossypinus*, Finland.
a Nurmes, KK 131/02: three fruitbodies on the left, KK132/02: eight fruitbodies in the middle, KK 125/02: three fruitbodies on the right.
b Valtimo, KK 762/03.
c Valtimo, KK 618/16.

tion of this specimen remains open. It did not seem to be at least a F1-hybrid, since its ITS chromatograms lacked mixed peaks. *Cortinarius pulchripes* and the above-described unidentified group were genetically closest with 3 base ITS differences, but according to RPB2, it could belong to *C. decipiens*. Its spore size resembled *C. pulchripes*, but macroscopically it resembled *C. decipiens* by pale veil patches at the pileus margin (Fig. 5c).

SPECIMEN EXAMINED: FINLAND. Inarin Lappi. Utsjoki, Tsuomasvarri, near *S. reticulata*, further away *S. glauca* and *Betula nana*, 26.VIII. 2005 Kokkonen 510/05*.

CORTINARIUS GOSSYPINUS

H.Lindstr., *Cortinarius Flora Photographica* 5: 15 (2012)

Synonym *Cortinarius mucronatus* M.M.Moser & McKnight, *Arctic Alpine Mycol.* 2: 312 (1987), nom. illegit.

Figure 6

Cortinarius gossypinus occurred commonly in boreal old *Salix* thickets in eastern and northern Finland. It was described recently from Sweden growing with *Salix* in moist deciduous forests and scrubs (Brandrud et al. 2012). *Cortinarius mucronatus* M.M.Moser & McKnight is conspecific according to the type study. The ITS sequence of the *mucronatus* type deviated only by two indels from the *C. gossypinus* sequences of this study. Since *C. mucronatus* is illegitimate (Index Fungorum, Art. 53.1), *C. gossypinus* has priority. *Cortinarius gossypinus* type was not examined, but the species is well illustrated and described in the protologue, and no other species with a similar woolly pileus occur in boreal *Salix* thickets. *Cortinarius mucronatus* was described from the alpine zone in North America (Moser & McKnight 1987). It had a smooth or fibrillose pileus in contrast to the pileus description of *C. gossypinus*, but otherwise their morphologies were similar. *Cortinarius atomatus* Bidaud ad int. (Bidaud et al. 2010) appeared also as conspecific. Its ITS sequence and morphology matched with *C. gossypinus*, except that the stipe apex was described as lilac. It was collected among *S. herbacea* from the French Alps.

The morphology of *C. gossypinus* varied rather much. Its pileus was sometimes smooth as with *C. mucronatus*, and more constant features were the white band and floccosity of the stipe. It usually had a prominent acute umbo, but the umbo could also be absent. Compared with the descriptions of *C. gossypinus* (Brandrud et al. 2012, Niskanen et al. 2012b), the fruitbodies were larger in my material, the pileus diameter commonly reaching 30 mm. The pileus size varied 7–40 mm and the stipe size 25–98 × 1.5–5.5 mm. The spore morphology varied considerably among collections and sometimes also within a collection. The mean spore size varied 8.2–9.7 × 5.2–5.8 µm and mean Q value 1.49–1.74 (n=13). The shape was usually ordinary or narrowly ellipsoid, some spores having a tapering apex, but the shape could be predominantly obtusely amygdaloid or subfusoid. Some collections had spores with frequent suprahilar depressions. The verrucosity varied commonly from weak to rather strong. The spores were usually moderately to rather strongly dextrinoid. The lamellar hyphae usually lacked incrustations or were only slightly encrusted, never strongly encrusted.

No distinct micro- or macromorphological differences were observed among collections or groups with slightly different ITS sequences. The ITS sequences deviated at most 3 bases from each other, but there always appeared intermediate sequences having ambiguous bases. *Cortinarius atomatus* had ambiguous bases in two of the deviating positions. Consequently, all specimens are regarded as conspecific. A Finnish alpine collection had an identical sequence with two arctic collections originating from Alaska and Svalbard (GenBank KC965870 Timling et al. 2014, UNITE UDB027282).

The collections of this study originated from the transition zone between the southern and middle boreal zones to the alpine zone, but the species occurs also in the hemiboreal zone (Niskanen et al. 2012b). In addition to inland shores, it was found from a swamp. It always grew with *Salix*, sometimes close to no other trees than *S. phyllicifolia* and *S. myrsinifolia*, or dwarf *Salix* at the alpine sites. In Iceland, it was found near *S. herbacea*, *S. arctica* and *Betula*. The single fruitbody resembled at least by spores *C. substriaepileus* Melot, which was described from Iceland, but had a different habitat (Melot 1995). Bidaud et al. (2010) regarded *C. gossypinus* as a possible synonym of *C. acutissimus*

(Velen.) G.Garnier. Their description of a *C. acutissimus* form from France resembles morphologically *C. gossypinus*, but deviates by a weak raphanoid smell. The description of *C. acutissimus* by Velenovsky (1921) does not quite agree with *C. gossypinus*. The lamellae have a grey brown tinge, and the habitat is deciduous forests without mention of *Salix*.

HOLOTYPE: *Cortinarius mucronatus* M.M.Moser & McKnight. USA, Wyoming, Beartooth Mts, Beartooth Pass, among *Salix* sp., 22.VIII.1983 M. Moser (IB 1983/0342). – Part of type as a loan. Spores 7.9–9.0–10.0 × 5.2–5.9–6.9 µm, Q=1.32–1.53–1.73 (n=20); ellipsoid or somewhat ovoid; weakly verrucose; moderately to rather strongly dextrinoid.

SPECIMEN EXAMINED: *Cortinarius atomatus* Bidaud ad int. France, Savoie, Bonneval-sur-Arc, cirque des Évettes, among *Salix herbacea*, alt. 2400 m, 31.VIII.1996 leg. M. Chiaffi, AB 96-08-36 (Herb. A. Bidaud). – Part of type as a loan. Spores 8.9–9.6–11.0 × 5.2–5.7–6.3 µm, Q=1.43–1.70–2.04 (n=20); ellipsoid to subamygdaloid, rarely more or less cylindrical or amygdaloid; rather weakly verrucose; weakly dextrinoid. Lamellar hyphae smooth.

OTHER SPECIMENS EXAMINED: FINLAND. Pohjois-Karjala. Nurmes, Joki-Vastimo, 2.IX.2002 Kokkonen 124/02, 18.IX.2003 Kokkonen 706/03, Metsä-Vastimo 31.VIII.2002 Kokkonen 125/02*, 131/02*, 132/02*, 24.IX.2002 Kokkonen 123/02*, 23.IX.2003 Kokkonen 783/03*, Pahakala, 26.VIII.2002 Kokkonen 138/02, 16.IX.2002 Kokkonen 126/02, 27.VIII.2003 Kokkonen 251/03. Valtimo, Haapakylä, Heinälampi, 20.IX.2003 Kokkonen 737/03*, 762/03*, Mahalanniemi, 29.VIII.2002 Kokkonen 38/02*, 5.X.2003 Kokkonen 919/03*, mouth of Matkusjoki, 22.IX.2003 Kokkonen 797/03*, Kalliojärvi, 9.IX.2008 Kokkonen 285/08*, Liuhanneemi, 30.IX.2016 Kokkonen 618/16*. Koillismaa. Kuusamo, Huotinniemi, 11.IX.2012 Kokkonen 1230/12*, Oivanki, 13.VIII.2006 Kokkonen 137/06*. Salla, Kotala, 20.VIII.2008 Kokkonen 86/08* and J. Vauras. Kittilän Lappi. Kittilä, Sirkka, 16.VIII.2006 Kokkonen 178/06*. Enontekiön Lappi. Enontekiö, Palojoensuu, 19.VIII.2006 Kokkonen 260/06, Peltovuoma, 22.VIII.2006 Kokkonen 310/06*. Inarin Lappi. Utsjoki, Tsuomasvarri, near *S. reticulata* and *S. herbacea*, 27.VIII.2005 Kokkonen 515/05*. ICELAND. Suður-Ísland. Rangárþing eystra, Valahnúkur, 16.IX.2017 Kokkonen 332/17*.

CORTINARIUS INOPS COMPLEX

Figure 7

Fungi resembling *C. inops* J.Favre were remarkably variable genetically, despite a very similar morphology. Four groups were recognized. *Cortinarius vernus* H.Lindstr. & Melot was one group. Three *C. erythrinus* collections belonged here, but they differed genetically from each other, and *C. erythrinus* also appeared to be outside this complex. The identity of *C. erythrinus* is unclear due to the lacking type. The fungi of this complex are characterized by a dark brown or black brown pileus, a pale grey or whitish fibrillose stipe, an occasional red base, and strongly verrucose ellipsoid spores. The stipe cover may have a violaceous tinge, and the lamellae are usually rather dark brown having sometimes a yellow or red tinge. No distinct morphological differences could be found among the groups. They were not found from boreal pure *Salix* thickets by lakes and rivers, but from inland mixed shore forests, among *S. repens* or *S. phylicifolia* on seashores, or with dwarf *Salix* in the alpine zone. They grow also in other mixed or deciduous forests and man-made habitats like parks in Finland. Several tree species seemed to be hosts, and the groups had some habitat differences.

Cortinarius inops J.Favre, *Ergebn. Wiss. Unters. Schweiz. Natl. Parks* 5 (33): 203 (1955), coll.

The sequence differences among the groups (Figs. 19, 20) were 2-3 bases and 1-3 indels by ITS, but as much as 8-15 bases by RPB2 suggesting separate species. Favre (1955) described *C. inops* from the Swiss Alps. Its identity remained partially open due to the low quality of the type ITS2 sequence. Its ITS1 sequence was identical with three recent collections from the Alps, which are determined here as *C. inops*. The messy ITS2 chromatograms of the type were carefully edited, but the resulting deficient ITS2 sequence is somewhat uncertain. It deviated at least by 3 bases and several indels from the other three *inops* collections. Peculiarly, the deviating bases of the type were the same in a *C. erythrinus* collection from lowland Italy (Campo 2.VIII.2014), which

collection was otherwise genetically distant. More sequenced collections will probably clear up the situation. It was a common feature within this complex that most base differences occurred in ITS2.

Favre described *C. inops* as having cheilocystidia, but cystidia did not appear as a good diagnostic character. The occurrence of cystidia varied within the groups. Also before, the occurrence of cystidia or sterile cells at the gill edge has varied intraspecifically a lot in *Telamonia* (Niskanen 2008). No cystidia were found in a small lamellar piece of the *inops* type. According to Horak (1987), cheilocystidia can not always be found from old *inops* specimens. Favre (1955) regarded the presence of cheilocystidia as a major difference between *C. inops* and *C. tenebricus* J.Favre. Two Swiss alpine collections deviating from the *inops* type at least by 5 bases and several indels (in Group 3, Fig. 19) had somewhat narrower spores, resembling thus the spore shape of *C. tenebricus*. However, their spores were as strongly ornamented as those of *C. inops* and had cheilocystidia, similarly to the recent Swiss *inops* collections. The type of *C. tenebricus* was examined morphologically (results under Additional examined types), but not sequenced.

The boreal "*C. vernus*" specimens were closer to *C. inops* than to *C. vernus* sequences judging by their ITS sequences. They were divided into two groups, which deviated by 2-3 bases in ITS, but at least by 11 bases in RPB2 from each other, and probably represent separate species. Another RPB2 group was closer to *C. vernus* than to other *C. inops* coll. specimens. The groups had different habitats. Group 2 (Figs. 19, 20) occurred in various inland habitats from the hemiboreal to the subarctic zone, and Group 3 on seashores and in the alpine zone near *Salix*, also in the Alps. Two *C. erythrinus* specimens of N. Arnold from Germany belonged to Group 2 according to the ITS sequences. They were collected from a mixed forest or near *Tilia*. Contrary to Group 3, possibly none of the Group 2 fungi were connected with *Salix*. No morphological differences were observed between the groups. For example, red stipe base was observed in both groups, similarly to *C. vernus*. Group 2 sequences were identical with *C. vernus* var. *nevadavernus* Suárez-Sant. & A.Ortega specimens of Suárez-Santiago et al. (2009). They regarded the variety conspecific with *C. vernus* due to



Fig. 7. *Cortinarius inops* complex. **a** *C. inops*. Switzerland, KK 292/17. **b** *C. inops*. Switzerland, KK 68/19. **c** *C. inops* coll. Finland, Kalajoki, KK 255/04. **d** *C. inops* coll. Finland, Pietarsaari, KK 280/04. **e** *C. inops* coll. Sweden, KK 1395/16. **f** *C. inops* coll. Switzerland, KK 38/19.

the similar morphology, but the variety lacked the aromatic smell of *vernus* and fruited only in spring. In contrast, the boreal and temperate Group 2 specimens fruited from spring to autumn.

LECTOTYPE: *Cortinarius inops* J.Favre. Switzerland, Graubünden, National Park, the upper part of Val dal Botsch, near Fuorn, alt. 2550 m, near dwarf willows, Triassic calcareous soil, 12.VIII.1953 J. Favre No ZA 155a (GK 13294a). – The specimen with 2 fruitbodies. Spores 6.5–7.3–8.1 × 4.9–5.4–5.7 μm, Q=1.20–1.35–1.56 (n=20); ellipsoid, sometimes a slight suprahilar depression; strongly to very strongly verrucose; moderately to rather strongly dextrinoid. Cheilocystidia not observed.

OTHER SPECIMENS EXAMINED: C. INOPS: ITALY. Trento. Soraga, Passo della Selle, alpine area, among *Salix retusa* with *Euphrasia minima*, calcareous soil, 23. VIII.2006 E. Campo (TUR-A)*. Belluno. Marmolada - Rocca Pietore, alpine area, among *S. retusa*, calcareous soil, 3.VIII.2017 E. Campo (TUR-A)*. SWITZERLAND. Graubünden. Scuol, Val Plavna, alt. 2320 m, among *S. herbacea*, 15.VIII.2017 Kokkonen 292/17*, Val S-charl, SW of Alp Astras, alt. 2365 m, near *S. retusa*, *S. reticulata* and *S. foetida*, 27.VIII.2019 Kokkonen 68/19*. **GROUP 2:** FINLAND. Varsinais-Suomi. Koski Tl., Myllykylä, slope by the river, wood of cultivated *Populus* (poppeli), scattered *Salix caprea* and *Betula*, riverside *Salix* bushes, mainly clay soil, 30.V.2011 M.-L. and P. Heinonen 20-2011 (as *C. vernus*)*. Turku, Ruissalo, nature reserve, herb-rich forest with *Populus tremula*, *Betula*, *Picea abies*, *Salix caprea* and *Quercus robur*, 9.VIII.2007 Kokkonen 208/07 (as *C. vernus*)*. Pohjois-Karjala. Nurmes, Pahakala, moist shore forest with *Salix* bushes, *Alnus*, *Betula* and *Picea*, 27.VIII.2003 Kokkonen 277/03 (as *C. vernus*)*. Inarin Lappi. Utsjoki, Tsieskuljoki, 20.VIII.1965 leg. P. Kallio, symposioretkikunta, det. T. Niskanen and I. Kytövuori (as *C. vernus*)*. GERMANY. Bayern. Kürn, with *Tilia*, 10.VII.1988 N. Arnold 8/88 (REG 10916, as *C. erythrinus*)*. Sauburg, mixed forest, 10.X.1990 N. Arnold 31/90 (REG 10922, as *C. erythrinus*)*. **GROUP 3:** FINLAND. Keski-Pohjanmaa. Kalajoki, Hiekasärkät, near *Salix phylicifolia* and *Alnus*, sandy soil, 10.IX.2004 Kokkonen 255/04*. Kokkola, Lohtaja, Vattajaniemi, beach, among *S. repens* and *Pinus sylvestris* seedlings, 11.IX.2004 Kokkonen 265/04*. Pietarsaari, Fäboda, beach, near *Salix phylicifolia*,

further away *Alnus*, *Pinus* and *Betula*, 12.IX.2004 Kokkonen 280/04*. SWEDEN. Lule Lappmark. Gällivare, Nieras, among *S. herbacea*, 30.VIII.2016 Kokkonen 1395/16*. SWITZERLAND. Graubünden. Scuol, Lai Sesvenna, alt. 2660 m, among *S. herbacea*, 17.VIII.2017 Kokkonen 281/17*, 25.VIII.2019 Kokkonen 38/19*.

Cortinarius vernus H.Lindstr. & Melot, *Cortinarius Flora Photographica* 3: 27 (1994)

Cortinarius vernus type sequence (UNITE UDB000742, Suárez-Santiago et al. 2009) deviated at least by 7 bases and few indels from *C. inops* sequences of this study, which is why *C. vernus* is regarded here as a separate species despite similar morphology. However, four base substitutions were very close, possibly indicating a lower number of events. Both types were examined morphologically and had similar spores.

The type of *C. vernus* was collected among cultivated *Abies sibirica* in Sweden (Brandrud et al. 1994). The species was not among my boreal and alpine material. Instead, the type sequence was nearly identical with sequences of a *C. erythrinus* collection near *Quercus* in Germany and a Mediterranean *C. castaneus* var. *monspeliensis* collection near *Cistus salviifolius* and *Pinus pinea* in Italy. Consequently, *C. vernus* seems to be absent from the alpine zone and have different hosts than the usual boreal “*C. vernus*”.

HOLOTYPE: *Cortinarius vernus* H.Lindstr. & Melot. Sweden, Ångermanland, Hemsö, Drafle, cultivated park with *Abies sibirica*, 19.VIII.1986 leg. T. E. Brandrud, H. Lindström, H. Marklund and S. Muskos, CFP443 (S). — Spores 5.8–6.9–8.1 × 4.5–5.0–6.0 μm, Q=1.13–1.40–1.68 (n=20); ellipsoid, often a slight suprahilar depression; strongly to very strongly verrucose; rather strongly to strongly dextrinoid. Cheilocystidia not observed.

OTHER SPECIMENS EXAMINED: GERMANY. Bayern. Bamberg, Hain, with *Quercus*, alt. ca. 240 m, 24.IX.1990 N. Arnold 7/90 (REG 10927, as *C. erythrinus*)*. ITALY. Grosseto. Bosco di Patanella-Orbetello, near *Cistus salviifolius* and *Pinus pinea*, 4.XI.2016 E. Campo (TUR-A, as *C. castaneus* var. *monspeliensis*)*.

CORTINARIUS PARVANNULATUS COMPLEX

Cortinarius parvannulatus Kühner, Bull. Mens. Soc. Linn. Lyon 24(2): 40 (1955)

Cortinarius cedriolens M.M.Moser, Kleine Kryptogamenflora 2b/2: 337 (1967)

Cortinarius rufoanuliferus M.M.Moser & McKnight, Arctic Alpine Mycol. 2: 314 (1987)

Cortinarius parvannulatus occurred rather commonly in boreal moist *Salix* thickets, as well as in the alpine zone with dwarf *Salix*. The identifications based on the description of Funga Nordica (Niskanen et al. 2012b). Much genetic and micromorphological variation was observed, which probably indicates the presence of multiple species, as already noted by Esteve-Raventós et al. (2014). Four small groups were formed by ITS, in addition to the clades with a single specimen (Fig. 19). A sequence of *C. cedriolens* from GenBank (AY083179, Peintner et al. 2003), along with identical sequences with it, belonged to the variation. The type of *C. rufoanuliferus* had an identical sequence with *C. cedriolens*, why *C. rufoanuliferus* may be a synonym of *C. cedriolens*. These species also have a similar morphology, except *C. rufoanuliferus* lacked a specific smell (Moser 1967, Moser & McKnight 1987). *Cortinarius cedriolens* has sometimes been treated as a synonym of *C. parvannulatus* (e.g. Suárez-Santiago et al. 2009) but not in this study, since their types were not examined. The clades deviated from each other mostly by one or two bases in the ITS sequence and possessed similar morphologies, requiring more specimens and DNA regions to be examined to resolve species limits within this complex. The tentative RPB2 results supported the separation of ITS clades, but the specimens or groups were differently related in the phylogenetic trees. A specimen was closer to *C. pseudofallax* than other *parvannulatus* specimens in the RPB2 tree. Unfortunately, several RPB2 analyses of *C. parvannulatus* specimens yielded poor chromatograms and were excluded.

As with other species complexes of this study, the presence of different genotypes having somewhat dissimilar morphologies within a site probably indicates separate species. The morphological differ-

ences between the clades were more distinct within sites than among the whole groups. For example, a collection in Group 3 had larger spores compared with a Group 1 collection from the same site concerning two sites, while the spore sizes did not much differ between all collections of these groups. The average spore widths separated groups better than the spore lengths. For example, the mean spore size was $6.8\text{--}7.8 \times 4.4\text{--}4.7 \mu\text{m}$ in Group 1 ($n=4$) and $7.4\text{--}8.2 \times 4.8\text{--}5.1 \mu\text{m}$ in Group 3 ($n=5$), and the site-specific differences were $6.8 \times 4.7 \mu\text{m}$ versus $8.2 \times 5.0 \mu\text{m}$ and $7.4 \times 4.5 \mu\text{m}$ versus $7.7 \times 4.8 \mu\text{m}$. The mean spore size in Group 2 was at the larger end: $8.0\text{--}8.7 \times 5.3\text{--}5.5 \mu\text{m}$ ($n=3$). There appeared also some other slight micromorphological differences among the clades. The spores were rather strongly or strongly verrucose in Group 2, but rather weakly to moderately verrucose in Group 3, and varied from weakly to strongly verrucose in Group 1. The spores were usually ellipsoid, but especially Group 3 specimens had also obtusely amygdaloid spores. All specimens had moderately to strongly dextrinoid spores, except the separate Icelandic specimen and the *rufoanuliferus* type had rather weakly dextrinoid spores.

Fungi belonging to the *C. parvannulatus* complex are usually easily recognized by the smell of cedar wood and red brown, orange, or yellow brown fruitbodies. In this study, the stipe had occasionally a violet tinge especially at apex and/or a white ring irrespective of the clade. However, the ring seemed to be more characteristic for Group 1, since all specimens were observed with rings. In addition, all specimens of the *cedriolens* clade lacked rings. The groups may have habitat differences as well. The two boreal collections of Group 2 grew in eutrophic fens, while others by lakes or brooks, or once in a pastured forest. One site of Group 3 had no other trees than *Salix* nearby, but other sites often included scattered *Betula*.

HOLOTYPE: *C. rufoanuliferus* M.M.Moser & McKnight. USA, Wyoming, Yellowstone National Park, Mt. Washburn, timberline, alt. 3300 m, *Picea engelmannii* and *Salix* sp. (*herbacea*-like), 27.VIII.1983 leg. M. Moser, det. M. Moser and K. McKnight (IB 1983/0342). – Part of type as a loan. Spores $6.9\text{--}7.7\text{--}8.4 \times 4.9\text{--}5.4\text{--}5.8 \mu\text{m}$, $Q=1.27\text{--}1.42\text{--}1.58$ ($n=20$); ellipsoid; weakly verrucose; rather weakly or weakly dextrinoid.

OTHER SPECIMENS EXAMINED: FINLAND. Pohjois-Häme. Laukaa, 12.IX.2002 Kokkonen 127/02*. Pohjois-Karjala. Nurmes, Metelinmäki, 23.IX.2002 Kokkonen 46/02*, Metsä-Vastimo, 15.VIII.2002 Kokkonen 130/02*, Pahakala, 27.VIII.2003 Kokkonen 239/03*, 15.IX.2003 Kokkonen 618/03*. Valtimo, Kalliojärvi, 9.IX.2008 Kokkonen 284/08*. Kainuu. Kuhmo, near Koirakangas, 8.IX.2018 Kokkonen 817/18*, 818/18*. Kittilän Lappi. Kittilä, near the main village, 28.VIII.2008 Kokkonen 438/08*. Sompion Lappi. Pelkosenniemi, E of Akanvaara, nature reserve, 20.VIII.2009 Kokkonen 99/09* and J. Vauras. Savukoski, Ainijärvi, 21.VIII.2008 Kokkonen 105/08* and J. Vauras. Inarin Lappi. Locality unknown, likely Utsjoki, VIII.1965 M. Lange (as cf. *C. pauperculus*)*. ICELAND. Suður-Ísland. Rangárþing eystra, Valahnúkur, near *S. herbacea*, *S. arctica* and *Betula*, 16.IX.2017 Kokkonen 356/17*, 358/17*. SWEDEN. Lule Lappmark. Gällivare, Nieras, near *S. herbacea*, 30.VIII.2016 Kokkonen 1404/16*. SWITZERLAND. Graubünden. Scuol, Val S-charl, Valbella, alt. 2215 m, near *S. reticulata* and *Dryas octopetala*, further away *Pinus*, 26.VIII.2019 Kokkonen 52/19*.

Cortinarius croceocingulatus N. Arnold & E. Ludw., *Libri Botanici* 7: 104 (1993)

A group of four boreal specimens deviating by 4 bases and 3 indels from most *C. parvannulatus* specimens were identified as *C. croceocingulatus* based on literal descriptions (Arnold 1993, Niskanen et al. 2012b). The specimens differed from *C. parvannulatus* by squamulose or fibrillose pilei and indextrinoid or weakly dextrinoid spores. The colour of the veil was brownish, when noted once. Young fungi had a violet tinge at stipe apex. *Cortinarius croceocingulatus* was described growing with *Salix* in Swedish Lapland (Arnold 1993). All my collections originated from the northern boreal zone of Finland. They grew by rivers near *Salix phylicifolia*, *S. lapponum* or *S. glauca*, and also near *Alnus incana* or a mixed forest at two sites. The spores were rather weakly to moderately verrucose, ellipsoid to subamygdaloid, and varied by mean size among the collections: 7.7–8.9 × 4.7–5.4 µm (n=4). An arctic collection from Svalbard was conspecific deviating only by one indel from the others. It was originally

determined as *C. phaeopygmaeus* J. Favre. According to the descriptions of Favre (1955) and Horak (1987), *C. phaeopygmaeus* lacks the smell of cedar wood and the spores are larger, why the specimen was probably misidentified. Another conspecific specimen from Svalbard has been published in BOLD database (NOBAS2354-16.ITS). It was determined as *C. parvannulatus*.

SPECIMENS EXAMINED: FINLAND. Koillismaa. Kuusamo, Oulanka National Park, near Nurmisaarenrinne, 9.IX.2012 Kokkonen 1329/12*. Kittilän Lappi. Kittilä, Köngäs, 15.VIII.2006 Kokkonen 167/06*. Sompion Lappi. Savukoski, Värriöjoki, 18.VIII.2019 Kokkonen 11/19*. Enontekiön Lappi. Enontekiö, Palojoensuu, 19.VIII.2006 Kokkonen 244/06*. NORWAY. Svalbard. Vestspitsbergen, Ny Ålesund, dry tundra heath, 11.VIII.1988 leg. E. Ohe-noja, det. D. Lamoure (as *C. phaeopygmaeus*)*.

Cortinarius neofallax Carteret & Reumaux, *Atlas des Cortinaires* 14: 907 (2004)

Cortinarius pseudofallax Carteret, *Atlas des Cortinaires* 14: 907 (2004)

Two species published as close to *C. parvannulatus*, *C. neofallax* and *C. pseudofallax*, were also found in this study. They were identified by comparing to the type sequences in GenBank (KF048129, NR131831, Esteve-Raventós et al. 2014). Both species had different habitats, and likely different hosts, than the usual *Salix* bushes of *C. parvannulatus* in this study. They deviated only by 2-3 bases in ITS from *C. parvannulatus*, and their RPB2 sequences, especially of *C. pseudofallax*, were among the variation of *parvannulatus* sequences, why they could belong to *C. parvannulatus*.

Cortinarius pseudofallax has been published from Fennoscandia growing with *Salix caprea* and some other trees (Esteve-Raventós et al. 2014, Brandrud et al. 2015). The single *pseudofallax* collection of this study also grew near *S. caprea*, together with *Betula* and *Picea*. Its habitat was a brookside in a *Picea abies*-dominated forest in the southern boreal zone. It had a violet stipe apex and small ellipsoid spores, ca. 6.5–7.5 × 4–4.5 µm, similarly to the previous reports (Bidaud et al. 2004, Esteve-Raventós et al. 2014, Brandrud et al. 2015). The spores were rath-

er strongly verrucose and dextrinoid.

Cortinarius neofallax was found from two moist sites with rich vegetation from the southern and middle boreal zones. One collection grew among e.g. *Filipendula ulmaria*, *Geranium sylvaticum* and *Rosa majalis* in a mixed shore forest by a lake and another among *Athyrium filix-femina* ferns by a brook. The lakeside forest included scattered *Salix*, while only *Picea*, *Alnus*, *Populus* and *Betula* were observed by the brook. Carteret and Reumaux described *C. neofallax* growing with hygrophilous broad-leaved trees, and *Betula pendula* was dominant at one site (Bidaud et al. 2004). Macroscopically, my collections did not differ notably from *C. parvannulatus*. The spores were rather narrowly amygdaloid to ellipsoid, rather strongly verrucose, and moderately dextrinoid. The mean spore sizes of the specimens were $7.3 \times 4.4 \mu\text{m}$ and $8.0 \times 4.9 \mu\text{m}$.

SPECIMENS EXAMINED: *C. neofallax*: FINLAND. Pohjois-Savo. Kuopio, Nilsia, Pieni-Tarpinen nature reserve, shore forest, near *Picea abies*, *Betula*, *Pinus sylvestris* and a *Salix myrsinifolia-phylicifolia* hybrid, 22.IX.2008 Kokkonen 409/08*. Kainuu. Paltamo, Kivesvaara-Keräsenvaara nature reserve, 29.IX.2018 Kokkonen 819/18*. *C. pseudofallax*: FINLAND. Pohjois-Savo. Kuopio, Puijo, 12.IX.2016 Kokkonen 531/16*.

CORTINARIUS PAUPERCULUS COMPLEX

Figure 8

Cortinarius pauperculus has not been recorded from Fennoscandia before. In this study, two boreal collections from the same locality had identical ITS sequences with the type, and several morphologically similar collections deviated genetically slightly from the type. All resembled morphologically Favre's (1955) description of *C. pauperculus* from the Swiss Alps. Most collections formed two groups. Since both groups occurred at three same sites, where they had slight morphological and genetic differences, they are described as new species.

Cortinarius pauperculus J.Favre, *Ergebn. Wiss. Unters. Schweiz. Natl. Parks* 5 (33): 203 (1955)

Cortinarius pauperculus is a small species. The two boreal collections genetically identical with the type had pileus diameters 3.5–7 mm and stipe sizes 10–17 × 0.7–1 mm. The whole fruitbodies were rather dark red brown. The pileus was conical as young and later appanate with an acute papilla. A young fruitbody had a pale fibrillose margin. The lamellae were distant and adnate. The stipe was delicately silky fibrillose having some whitish veil in the lower part. They were odourless. The specimens were collected from a sandy riverbank in a canyon near *Salix phylicifolia* and *Alnus incana* in the northern boreal zone. A single fruitbody from the Swiss Alps was genetically identical. It was also small, and the pileus had a papilla, but other notes as fresh lacked. According to Favre (1955), the pileus diameter of *C. pauperculus* extends to 16 mm and the stipe length up to 23 mm. The RPB2 sequences of the Finnish and Swiss collections were identical, but the Finnish sequence included several ambiguous bases.

The spore sizes of the boreal collections were near the type spore size: $7.0\text{--}8.4\text{--}9.8 \times 4.6\text{--}5.4\text{--}5.9 \mu\text{m}$, range of mean values $8.1\text{--}8.6 \times 5.3\text{--}5.4 \mu\text{m}$, $Q=1.40\text{--}1.57\text{--}1.73$, range of mean Q values 1.53–1.60 (20 spores from 2 collections). The spores were ellipsoid with an occasional suprahilar depression, moderately verrucose, and moderately to rather strongly dextrinoid. The lamellar hyphae had rather strong or strong incrustations and dark flecks. The spores of the Swiss collection were rather similar with mean size $8.3 \times 5.1 \mu\text{m}$ and mean Q value 1.63. They were rather strongly verrucose.

LECTOTYPE: *Cortinarius pauperculus* J.Favre. Switzerland, Graubünden, Val Sesvenna, alt. 2550 m, near S. charl, 24.VIII.1943 J. Favre 159a (GK 13303). — Specimen with ca. 20 fruitbodies in good condition. Spores $7.5\text{--}8.5\text{--}10.3 \times 5.0\text{--}5.5\text{--}6.1 \mu\text{m}$, $Q=1.36\text{--}1.56\text{--}1.75$ (n=20); ellipsoid or somewhat cylindrical; rather weakly verrucose, somewhat more strongly verrucose at apex, at times 1-2 large verrucae at apex; rather weakly to moderately dextrinoid.

OTHER SPECIMENS EXAMINED: FINLAND. Koillismaa. Posio, Korouoma nature reserve, 14.VIII.2006 Kokkonen 157/06*, 19.IX.2019 Kokko-



Fig. 8. *Cortinarius pauperculus* complex. **a** *C. pauperculus*. Finland, Posio, KK 101/19. **b** *C. paululus*. Finland, Valtimo, holotype. **c** *C. paululus*. Switzerland, KK 305/17. **d** *C. paululus*. Finland, Kuusamo, KK 99/19. **e** *C. paulus*. Finland, Valtimo, holotype. **f** *C. scotoides*. Switzerland, KK 47/19.

nen 101/19*. SWITZERLAND. Graubünden. Scuol, Lai Sesvenna, alt. 2665 m, near *Salix herbacea*, 17.VIII.2017 Kokkonen 285/17*.

Cortinarius paululus Kokkonen, sp. nov.

Figures 8 b-d and 9a

MycoBank MB833742

ETYMOLOGY: *paululus* (Latin) refers to the small size, similarly to *pauperculus*; smaller than *C. paulus*.

HOLOTYPE: Finland, Pohjois-Karjala, Valtimo, Haapakylä, Heinälampi, shore of a pond connected to river, *Salix* thicket with *S. phylicifolia* and *S. myrsinifolia*, scattered *Betula* and *Alnus incana*, 3.IX.2003 K. Kokkonen 414/03 (TUR; isotypes G, IB), ITS MN841176, RPB2 MN808008.

PILEUS diameter 4–20 mm; low convex, appanate, campanulate, or conical, often with an acute or obtuse umbo or papilla; young dark brown, then red brown, ochraceous brown, or dark brown ($S_{70}Y_{90}M_{50}$, $S_{60}Y_{40}M_{50}$), centre darker and often blackish, margin paler; smooth or delicately fibrillose especially at margin, at times margin fringy; hygrophamous, translucently striate. **LAMELLAE** up to 3 mm broad; adnate or emarginate, moderately crowded to distant; rather dark brown to dark brown ($S_{60}Y_{40}M_{50}$, $S_{60}Y_{60-70}M_{50}$) or yellowish brown ($S_{50}Y_{90}M_{50}$, $S_{50}Y_{99}M_{60}$); edge even and usually paler. **STIPE** slender, 8–56 mm long, 0.8–2.5 mm wide; equal or widening slightly downwards; somewhat paler than pileus or concolorous with it, at times darkening towards base, rarely violaceous tinge at apex; delicately silky fibrillose, especially lower part with white or whitish veil cover or slightly flocculose. **CONTEXT** concolorous with surface, or dark brown at pileus and yellow brown at stipe. **CORTINA** whitish. **SMELL** not distinctive or rarely weakly pelargonious.

SPORES 6.9–8.4–10.1 × 4.5–5.1–6.0 μm, range of mean values 7.9–9.1 × 4.7–5.4 μm, Q=1.42–1.66–2.02, range of mean Q values 1.56–1.79 (250 spores from 15 collections); ordinary or narrow ellipsoid, occasionally subamygdaloid or cylindrical in some collections, suprahilar depression rare to frequent; rather weakly to strongly verrucose, usually rather strongly verrucose, verrucae mostly larger at apex; usually moderately dextrinoid, rarely rather weakly dextrinoid. **LAMELLAR HYPHAE**

usually strongly encrusted, at times with dark narrow flecks. **PILEPELLIS** hyphae 2–32 μm wide, brownish or hyaline, mostly strongly or very strongly coarsely encrusted, often with dark red brown flecks.

HABITAT AND DISTRIBUTION: boreal *Salix* thickets or shore forests by lakes, rivers and sea, alpine zone near dwarf *Salix*; collections from the transition between the southern and middle boreal zones to the northern boreal zone in Finland and from the alpine zone in Switzerland. *Salix* is probably the only host. *Salix phylicifolia* and *S. lapponum* were the only tree species at one boreal site. Soil varies from muddy to sand. Rather common in *Salix* thickets of eastern and northern Finland.

SPECIMENS EXAMINED: FINLAND. Keski-Pohjanmaa. Kalajoki, Hiekkasärkät, seashore, near *Salix phylicifolia* and *Alnus incana*, 9.IX.2004 Kokkonen 236/04*. Pohjois-Karjala. Nurmes, Joki-Vastimo, 18.IX.2003 Kokkonen 696/03*, Pahakala 15.IX.2003 Kokkonen 626/03*, 29.VIII.2009 Kokkonen 143/09*. Valtimo, Haapakylä, Heinälampi, 24.IX.2002 Kokkonen 44/02*, 3.IX.2003 Kokkonen 414/03 (holotype)*, 415/03*, Mahalanniemi, 6.IX.2003 Kokkonen 460/03*. Perä-Pohjanmaa. Kemijärvi, Vuostimo, 23.VIII.2005 Kokkonen 487/05*. Koillismaa. Kuusamo, Oulanka National Park, Jäkälämutka, 17.IX.2019 Kokkonen 87/19*, 92/19*, 93/19*, SW of Nurmisaarenrinne, 18.IX.2019 Kokkonen 97/19*, 99/19*, Vuotunki, 31.VIII.2007 Kokkonen 539/07*, 568/07* and J. Vauras. Salla, Kotala, 20.VIII.2008 Kokkonen 95/08* and J. Vauras. Kittilän Lappi. Kittilä, Sirkka, 16.VIII.2006 Kokkonen 177/06*. Enontekiön Lappi. Enontekiö, Kaaresuivantto, 20.VIII.2006 Kokkonen 266/06*. SWITZERLAND. Graubünden. Scuol, Val Sesvenna, alt. 2525 m, near *S. herbacea*, 14.VIII.2017 Kokkonen 305/17*.

COMMENTS: *Cortinarius paululus* deviated from *C. pauperculus* type by 4 bases, and from *C. paulus* 3–4 bases and 1–2 indels in ITS. Intraspecifically, two collections including the type had an insertion of two bases compared with the others. In RPB2, it deviated from the recent Swiss *C. pauperculus* collection at least by 7 bases and from *C. paulus* at least by 5 bases. *Cortinarius paululus* resembles morphologically *C. pauperculus*. The material of *C. pauperculus* is too scarce for a detailed morphological comparison. The fruitbodies of both species from sandy river shores appeared similar, but they

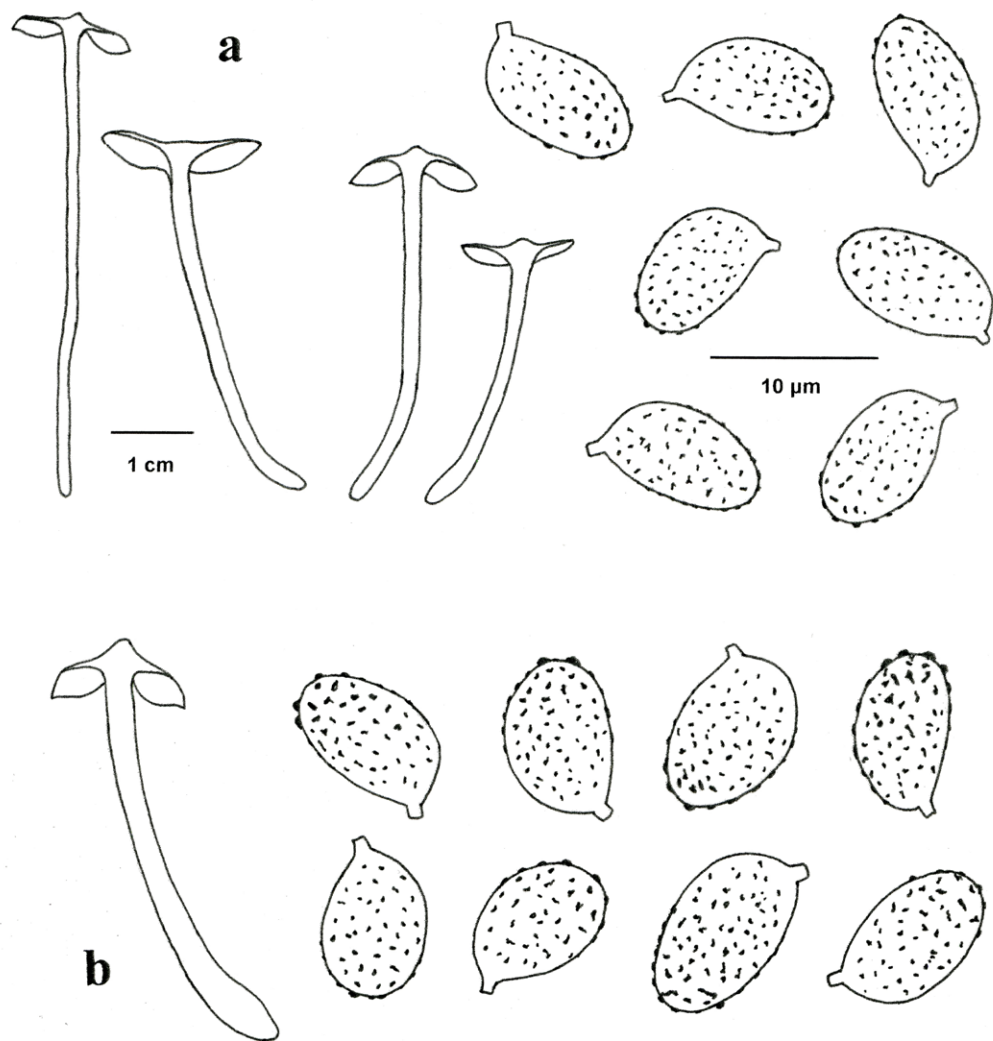


Fig. 9. a *Cortinarius paululus*. Holotype: second cross-section of fruitbody from the left, spores. KK 415/03: fruitbody on the left. KK 143/09: fruitbodies on the right. **b** *Cortinarius paulus*. Holotype: spores. KK 413/03: cross-section of fruitbody.

never grew at the same sites and probably have different requirements. *Cortinarius pauperculus* was notably rarer. The sole boreal *pauperculus* location was in a special habitat, a canyon. When compared with *C. paulus*, which occurred at the same sites as *C. paululus*, the fruitbodies of *C. paululus* were on average smaller, particularly had thinner stipes, and

had mostly smaller and especially narrower spores. The collection from the Swiss Alps grew rather near the *pauperculus* collection in the valley of the *pauperculus* type. It had an acutely conical pileus and whitish veil at stipe (Fig. 8c). Lamoure (1977) described a small alpine species, *C. galerinoides*, which differed from *C. pauperculus* by paler pileus, scarcer

veil and smaller spores. The description of *C. galerinoides* resembles *C. paululus*, but the ITS sequence of the *galerinoides* type was close to the *C. helobius* sequences.

Cortinarius paulus Kokkonen, sp. nov.

Figures 8e and 9b

Mycobank MB833743

HOLOTYPE: Finland, Pohjois-Karjala, Valtimo, Kalliojärvi, south side of Lake Kalliojärvi, *Salix* thicket with scattered *Betula* and *Alnus incana*, 14.IX.2008 K. Kokkonen 314/08 (TUR; isotype G), ITS MN841185, RPB2 MN808013.

PILEUS diameter 8–37 mm; young conical, then campanulate, low convex, or appanate, usually with an acute umbo or papilla; red brown, ochraceous brown or dark brown ($S_{40}Y_{70}M_{50}$, $S_{50}Y_{90}M_{60}$, $S_{60}Y_{50}M_{50}$, $S_{60}Y_{70}M_{60}$, $S_{70}Y_{80}M_{50}$, $S_{80}Y_{60}M_{50}$), at times centre darker; delicately fibrillose at margin or rarely overall, at times margin fringy or with scarce veil remnants; hygrophanous, translucently striate. **LAMELLAE** up to 5 mm broad; adnate or emarginate, moderately crowded to distant; concolorous with pileus, or slightly paler, or slightly more yellowish ($S_{40}Y_{70}M_{50}$, $S_{50}Y_{90}M_{60}$, $S_{70}Y_{80}M_{50}$); edge paler or concolorous. **STIPE** 23–73 mm long, 1.5–5 mm wide; equal, or narrowing or slightly widening downwards; somewhat paler than pileus or concolorous with it, at times darkening towards base, rarely violaceous tinge at base; delicately silky fibrillose, lower part usually with white or whitish veil cover or flocculose, at times a band. **CONTEXT** concolorous with surface, or dark brown at pileus and yellow brown at stipe. **CORTINA** whitish. **SMELL** not distinctive.

SPORES 8.0–9.1–11.3 × 4.9–5.7–6.5 μm, range of mean values 8.9–9.7 × 5.5–6.0 μm, Q=1.32–1.60–2.14, range of Q values 1.52–1.67 (180 spores from 9 collections); usually ordinary ellipsoid, at times frequently narrow ellipsoid, rarely subamygdaloid or cylindrical in some collections, suprahilar depression usually occasional; rather strongly to strongly verrucose, rarely moderately verrucose, verrucae mostly larger at apex; moderately to rather strongly dextrinoid. **LAMELLAR HYPHAE** usually rather strongly to strongly encrusted, at times with dark flecks. **PILEIPELLIS** hyphae

2–32 μm wide, brownish or hyaline, mostly rather strongly or strongly coarsely encrusted, at times with dark red brown flecks.

HABITAT AND DISTRIBUTION: boreal *Salix* thickets or shore forests by lakes and rivers; collections from the transition between the southern and middle boreal zones to the northern boreal zone in Finland. *Salix* is probably the only host. *Salix phylicifolia*, *S. myrsinifolia* and *S. pentandra* were the only tree species at one site.

SPECIMENS EXAMINED: FINLAND. Pohjois-Karjala. Nurmes, Metsä-Vastimo, 23.IX.2003 Kokkonen 774/03*, Pahakala, 15.IX. 2003 621/03*, 6.X.2003 Kokkonen 971/03*, Saramo, 29.IX.2003 Kokkonen 854/03*. Valtimo, Haapakylä, Heinälampi, 3.IX.2003 Kokkonen 413/03*, 20.IX.2003 Kokkonen 751/03*, Mahalanniemi, 19.IX.2002 Kokkonen 36/02*, 30.IX.2016 Kokkonen 617/16*, Kalliojärvi, 14.IX.2008 Kokkonen 314/08 (holotype)*. Perä-Pohjanmaa. Rovaniemi, Vikajärvi, 24.VIII.2007 J. Vauras and Kokkonen 453/07*.

COMMENTS: *Cortinarius paulus* had usually larger fruitbodies and spores compared with *C. pauperculus* and *C. paululus*. The most distinct difference was in the mean spore width. *Cortinarius paulus* deviated from the *pauperculus* type by 4–5 bases and one indel in ITS, and at least by 8 bases in RPB2 from the recent Swiss *pauperculus* collection. A collection (KK854/03) deviated by one base from the other *paulus* collections in ITS, but since it was morphologically similar and had a mixed peak in the deviating position in one chromatogram, it was regarded as conspecific but excluded from the description. *Cortinarius pauperculoides* Moënneloc. ad int. (Bidaud et al. 2012) is morphologically rather similar with *C. paulus* and *C. paululus*, and it was found to be genetically close, as explained below. *Cortinarius helobius* Romagn. as described by Romagnesi (1952) and Bendiksen et al. (1993) seems similar, but according to the *C. helobius* of Cortinarius Flora Photographica (Brandrud et al. 1994, Lindström et al. 2008, GenBank DQ102686) and an examined *C. helobius* collection of P. Moënnelocoz from France (Bidaud et al. 1991), it is a distant species. *C. sphagnicola* Carteret & Reumaux has also similar morphology and habitat, but it was distant according to the type study. Three species that M. Moser (1993) described from North America grow-

ing with *Salix*, *C. expallens*, *C. ferrugineifolius* and *C. paraphaeochrous*, resemble especially *C. paulus*, but they were distant according to the unpublished type sequences received from Ursula Peintner. A GenBank sequence of *C. laetissimus* Rob.Henry specimen from Canada (GQ159898, Harrower et al. 2011) deviated from *C. paulus* by 1-2 bases and an indel as well as from *C. paululus* by 2 bases. According to the protologue (Henry 1957), *C. laetissimus* differs by smaller and wider spores, a fruity smell, and the habitat in montane *Picea* forests. It was described from France.

Cortinarius scotoides J.Favre, *Ergebn. Wiss. Unters. Schweiz. Natl. Parks* 5 (33): 204 (1955)

Cortinarius scotoides was not found from the boreal zone, but only from the alpine zone in Switzerland, from where Favre (1955) described it. However, it occurs in the temperate zone, since *C. pauperculoides* Moëgne-Locc. ad int. (Bidaud et al. 2012) appeared conspecific. *Cortinarius pauperculoides* was collected under *Populus nigra* from an abandoned quarry in France. The ITS sequence of an alpine *scotoides* collection was identical with the *pauperculoides* sequence excluding two ambiguous bases, and two other *scotoides* collections differed by one base and a deletion. The difference from *C. pauperculus* was only 2 bases and 3-4 indels in ITS, but up to 17 bases in RPB2 sequences. The *scotoides* RPB2 sequences deviated as much as 8 bases and an indel from each other. From *C. paululus* and *C. paulus*, the difference was 6-7 bases and 4-5 indels in ITS.

Cortinarius scotoides and *C. pauperculoides* were described to have smaller spores than *C. pauperculus* (Favre 1955, Horak 1987, Bidaud et al. 2012), but the spore sizes were found to be about the same with range of mean values $7.9-8.2 \times 4.7-5.4 \mu\text{m}$ (50 spores from 4 collections). The spores of *C. scotoides* were often narrower with mean Q value 1.68-1.73. The spores were moderately to strongly verrucose and weakly or rather weakly dextrinoid. The Swiss fungi had a convex, applanate, or obtusely conical pileus without umbo or only with a small low umbo unlike the French *pauperculoides* and the other species of this complex. The pilei of the specimens de-

viating by one base were cracked to squamules or rugulose (Fig. 8f). *Cortinarius scotoides* was identified by comparing my collections from a *scotoides* collection site of Favre with the descriptions of Favre (1955) and Horak (1987), as well as comparing the sequences with *scotoides* sequences of Hyde et al. (2019), where a new species *C. subscotoides* Niskanen & Liimat. was described.

SPECIMEN EXAMINED: *Cortinarius pauperculoides* Moëgne-Locc. ad int. France, Haute-Savoie, Rumilly, alt. 350 m, 13.V.1991 P. Moëgne-Loccoz, PML 2176 (Herb. P. Moëgne-Loccoz). – A fruitbody as a loan. Spores $6.9-7.9-9.0 \times 4.4-4.7-5.0 \mu\text{m}$, $Q=1.47-1.68-1.89$ (n=20); mostly ellipsoid, occasionally subamygdaloid; moderately verrucose; weakly dextrinoid. Lamellar hyphae strongly encrusted.

OTHER SPECIMENS EXAMINED: SWITZERLAND. Graubünden. Scuol, Val Plavna, alt. 2255 m, near *Salix reticulata* and *Dryas*, 12.IX.2018 Kokkonen 833/18*, Val S-charl, Valbella, alt. 2180-2185 m, near *S. reticulata* and *S. retusa*, 26.VIII.2019 Kokkonen 41/19, near *S. reticulata* or *S. herbacea*, 26.VIII.2019 Kokkonen 42/19*, 43/19, 45/19, 47/19*.

Cortinarius minusculus Liimat. & Niskanen, *Fungal Diversity* 96: 182 (2019)

Cortinarius minusculus was recently described from hemiboreal and temperate mixed forests without *Salix* (Hyde et al. 2019). In this study, it was found from a riverside *Salix* thicket with scattered *Betula* and *Alnus* in the transition zone between the southern and middle boreal zones of Finland, and from subarctic Iceland. The two Icelandic collections grew in a dry *Betula pubescens* forest with scattered *Salix*. Another of them grew among *Empetrum nigrum*. The species seems to be connected at least with *Betula*. The morphology of my collections resembled the protologue description, but the fruitbodies were on average larger. The pilei of the Finnish fruitbodies reached 28 mm and the stipe width 3.5 mm. The spores of the Icelandic collections were somewhat wider, ca. $7.5-10 \times 5-6 \mu\text{m}$. The species deviated by 8-10 bases, an inversion and two indels from *C. pauperculus*.

SPECIMENS EXAMINED: FINLAND. Pohjois-

Karjala. Nurmes, Joki-Vastimo, 18.IX.2003 Kokkonen 698/03*. ICELAND. Suður-Ísland. Rangárþing eystra, Básar, near *Betula* and *Salix phylicifolia*, 14.IX.2017 Kokkonen 326/17*, Snorraríki, near *Betula* and *S. phylicifolia*, 13.IX.2017 Kokkonen 327/17*.

Additional specimens

Two collections were genetically intermediate between *C. paululus* and *C. paulus*, and they remained unidentified. They differed from *C. paulus* by 1–2 bases and an indel, and from *C. paululus* by 2 bases and 0–1 indels in ITS. Peculiarly, their RPB2 sequences deviated from each other, but were also intermediate. The spore size resembled *C. paululus*. They grew in the northernmost Finland: one in the alpine zone near *S. reticulata* and *Dryas*, and the other by a subarctic lake shore.

SPECIMENS EXAMINED: FINLAND. Inarin Lappi. Utsjoki, Pulmankijärvi, 28.VIII.2005 Kokkonen 504/05*, Tsuomasvarri, 27.VIII.2005 Kokkonen 507/05*.

A collection from the Swiss Alps differed from the *C. pauperculus* type by 5 bases and 3 indels, and from the other species of this complex by at least 4 bases. It and a nearby collection of the same species had a yellow brown veil and squamulose, dark brown pilei. The spores resembled the spores of other species in this complex. The collections resemble rather much *C. pertristis* J.Favre, which has a more or less smooth pileus (Favre 1955). They may represent a new species, but more data is needed.

SPECIMENS EXAMINED: SWITZERLAND. Graubünden. Scuol, Lai Sesvenna, alt. 2660 m, near *Salix herbacea*, 25.VIII.2019 Kokkonen 33/19, 37/19*.

CORTINARIUS RUSTICELLUS COMPLEX

Figure 10

Cortinarius rusticellus J.Favre, *Ergebn. Wiss. Unters. Schweiz. Natl. Parks* 5 (33): 204 (1955)

Cortinarius lamoureae Bon, *Doc. Mycol.* 16(63–64): 62 (1986)

Synonym *Cortinarius fallax* Lamoure, *Trav. Sci. Parc Natl. Vanoise* 9: 96 (1978), nom. illegit.

Cortinarius rusticellus grows rather commonly in *Salix* thickets of eastern and northern Finland. The identification was based on comparison with the descriptions of Favre (1955) and Horak (1987) along with collections from the Swiss Alps. Seven high-alpine collections of *C. rusticellus* were genetically identical or had at most a two indel difference by ITS compared with the boreal collections. The collections from both habitats had similar large spores with a suprahilar depression as the lectotype (Horak 1987) and characteristic red brown or dark brown fruitbodies with fibrillose stipes. The colour of the veil varied. It was whitish to yellow brown among the alpine collections, but white or whitish in boreal collections, except distinctly yellow brown in one collection of young fungi. Few boreal collections had scarce brownish fibrillae on the pileus. Favre (1955) described the cortina and ring as pale reddish brown.

The boreal fungi were larger and had smoother pilei than the alpine fungi. Their pileus diameter varied 11–38 mm. The pileus was red brown or dark red brown with a darker centre, and usually umbonate and smooth, but at times slightly fibrillose or flocculose at margin, or rarely entirely delicately fibrillose. The lamellae were red brown or rather dark, and often broad. The stipe size was 28–70 × 1.5–8 mm. It was equal or tapered downwards, had a yellowish brown or pale grey apex darkening to red brown downwards, and a ring or a band along with floccules or merely floccules.

The spore sizes varied much among both the boreal and alpine collections. The ranges of mean values were 8.5–11.1 × 5.1–6.0 μm (11 boreal collections) and 8.3–11.0 × 5.2–6.2 μm (7 alpine collections). The overall variation of boreal spores was 7.7–9.5–13.0 × 4.7–5.5–6.5 μm. The mean Q value varied 1.63–1.86 (boreal) and 1.61–1.76 (alpine). The spores were usually ellipsoid, but occasionally subamygdaloid or amygdaloid spores were about as frequent as ellipsoid spores, and occasionally also cylindrical spores occurred. The suprahilar depression was usually frequent. The spores were strongly verrucose having larger verrucae at apex, except



Fig. 10. *Cortinarius rusticellus* complex, Finland. **a** *C. rusticellus*. Nurmes, KK 136/09. **b** *C. rusticelloides*. Valtimo, holotype. **c** *C. rusticelloides*. Valtimo, KK 117/02 on the left, KK 115/02 on the right. **d** *C. rusticelloides*. Nurmes, KK 118/02.

moderately verrucose in one alpine collection, and moderately to strongly dextrinoid. The lamellar hyphae were strongly encrusted and had nearly always dark flecks.

The boreal collections originated from the transition between the southern and middle boreal zones to the northern boreal zone. Sometimes only *S. phylicifolia* and *S. myrsinifolia* were present in the *Salix* thickets. The species is probably connected only with *Salix*. The soil varied from muddy to sand. The alpine fungi grew among *S. herbacea*.

The holotype of *C. fallax* Lamoure (IF: nom. illegit., now *C. lamoureae* Bon) had an identical ITS sequence with the *rusticellus* sequences and is regarded as conspecific. It was collected from the Italian Alps. *Cortinarius lamoureae* is not reduced here to a synonym, since the type of *C. rusticellus* was not examined. The morphological description of *C. fallax* (Lamour 1978) agrees by large with *C. rusticellus*. The rather dark fruitbodies had abundant brownish veil and large spores. In contrast with *C. rusticellus* (Favre 1955), the pileus was smooth or only delicately fibril-

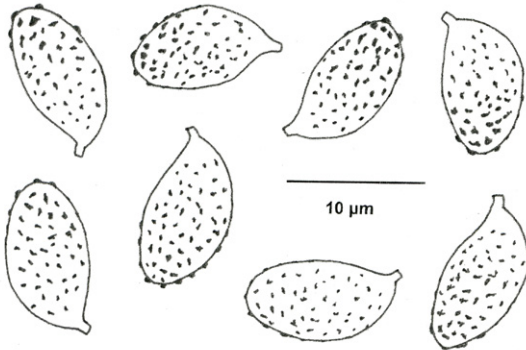


Fig. 11. *Cortinarius rusticelloides*. Holotype: spores.

lose. The spores lacked the suprahilar depression.

The ITS sequences of three boreal collections deviated by one base from the majority, but they are regarded as conspecific. No morphological differences were observed, and some specimens had ambiguous bases in two of the deviant positions. In addition, the two paratypes of *C. pseudofusisporus* Bidaud (Bidaud et al. 2010) deviated by one base from most *rusticellus* specimens. They are regarded as conspecific with some doubt. Their spores were predominantly obtusely amygdaloid or fusoid. The mean sizes of the large spores were $10.6 \times 6.1 \mu\text{m}$ and $11.6 \times 5.8 \mu\text{m}$. The macroscopical description largely agrees with *C. rusticellus*. The fungi were collected under *Betula pendula* and *Salix aurita* near a pond in France.

HOLOTYPE: *Cortinarius fallax* Lamoure. Italy, Sondrio, Bormio, under Pass of Stelvio, alt. N 2600 m, *Salix herbacea*, 20.VIII.1973 D. Lamoure (LY). – Part of type as a loan. Spores $9.1\text{--}10.0\text{--}10.8 \times 5.4\text{--}6.2\text{--}6.9 \mu\text{m}$, $Q=1.47\text{--}1.61\text{--}1.78$ ($n=20$); usually ellipsoid, occasionally obtusely amygdaloid, without a supra-hilar depression; rather strongly verrucose; weakly dextrinoid. Lamellar hyphae strongly encrusted.

OTHER SPECIMENS EXAMINED: FINLAND. Pohjois-Karjala. Nurmes, Joki-Vastimo, 18.IX.2003 Kokkonen 699/03*, 9.X.2003 Kokkonen 1004/03,

Metsä-Vastimo, 3.IX.2009 Kokkonen 163/09, 16.IX.2009 Kokkonen 285/09*, Pahakala, 16.IX.2002 Kokkonen 140/02, 15.IX.2003 Kokkonen 649/03*, 11.VIII.2009 Kokkonen 56/09*, 29.VIII.2009 Kokkonen 136/09*, 137/09*, 16.IX.2009 Kokkonen 282/09*. Valtimo, Haapakylä, Heinälampi, 20.IX.2003 Kokkonen 765/03*, Mahalanniemi, 5.X.2003 Kokkonen 921/03*, mouth of Matkusjoki, 17.IX.2003 Kokkonen 663/03*, 674/03*, 27.IX.2018 Kokkonen 33/18*. Perä-Pohjanmaa. Kemijärvi, Vuostimo, 31.VIII.2005 Kokkonen 497/05*. Koillismaa. Kuusamo, near Kuloio, 13.VIII.2006 Kokkonen 150/06*, Vuotunki, 31.VIII.2007 Kokkonen 542/07 and J. Vauras. Kittilän Lappi. Kittilä, Köngäs, 15.VIII.2006 Kokkonen 165/06*, Sirkka, 16.VIII.2006 Kokkonen 176/06*. Enontekiön Lappi. Enontekiö, Peltovuoma, 22.VIII.2006 Kokkonen 311/06*. FRANCE. Dordogne. Salagnac, Forêt de Born, alt. 200 m, 27.X.1997 leg. E. Bidaud, AB 97-10-417*, AB 97-10-418* (Herb. A. Bidaud, as *C. pseudofusisporus*). SWEDEN. Lycksele Lappmark. Sorsele, Rankbäcken W of Nissebo, 28.VIII.2016 Kokkonen 367/16*. SWITZERLAND. Graubünden. Scuol, Piz Clüinas, alt. 2640 m, 16.VIII.2017 Kokkonen 287/17*, Val Sesvenna, alt. ca. 2525 m, 14.VIII.2017 Kokkonen 268/17*, 269/17*, 303/17*, 304/17*, 17.VIII.2017 Kokkonen 282/17*, 312/17*.

Cortinarius rusticelloides Kokkonen, sp. nov.

Figures 10 b-d and 11

Mycobank MB833744

HOLOTYPE: Finland, Pohjois-Karjala, Valtimo, Haapakylä, Heinälampi, shore of a pond connected to river, *Salix* thicket with *S. phyllicifolia* and *S. myrsinifolia*, scattered *Betula* and *Alnus incana*, 3.IX.2002 K. Kokkonen 136/02 (TUR; isotypes G, IB), ITS MN841216.

PILEUS diameter 9–36 mm; applanate, campanulate or convex with papilla or low umbo, at times margin undulate; usually dark brown, or red brown, centre often blackish; smooth or delicately fibrillose, margin at times with white veil remnants; hygrophanous, translucently striate. **LAMELLAE** emarginate or adnate, moderately crowded or rather distant; dark brown or red brown, edge paler. **STIPE** 10–50 mm long, 1.5–5.5 mm wide; equal or tapering downwards; dark brown or red brown with

whitish fibrillose cover; usually a white band or ring, often white floccose below the ring, at times only few flocci or a white sheath below the ring. **CON-TEXT** yellow brown or dark brown. **CORTINA** white. **SMELL** not distinctive.

SPORES 8.9—10.5—12.9 × 5.0—5.7—6.5 μm, range of mean values 10.1—11.3 × 5.5—5.8 μm, Q=1.61—1.85—2.17, range of mean Q values 1.75—1.98 (160 spores from 8 collections); predominantly amygdaloid or fusoid, some narrow ellipsoid, rarely amygdaloid and ellipsoid spores about as frequent, occasionally some spores cylindrical, a suprahilar depression usually frequent; strongly verrucose with larger verrucae at apex; rather strongly or strongly dextrinoid, rarely rather weakly dextrinoid. **BASIDIA** 25—38 × 8—12 μm (n=26), 4-spored. **CHEILO-CYSTIDIA** absent. **LAMELLAR HYPHAE** strongly encrusted and with dark flecks, rarely flecks absent. **PILEPELLIS** hyphae 1.5—31 μm wide, brownish or hyaline, mostly strongly coarsely encrusted, with dark red brown or yellow brown flecks.

HABITAT AND DISTRIBUTION: known from five localities in eastern Finland. The habitats were moist *Salix* thickets by lakes, rivers and a spring in the transition zone between the southern and middle boreal zones. The species is connected with *Salix*, since only *S. phyllicifolia* and *S. myrsinifolia* were present in one locality.

SPECIMENS EXAMINED: FINLAND. Pohjois-Karjala. Nurmes, Kynsisaari, 30.VII.2013 Kokkonen 12/13*, Metelinmäki, 31.VIII.2002 Kokkonen 57/02*, 2.IX.2002 Kokkonen 118/02*. Valtimo, Haapakylä, Heinälampi, 3.IX.2002 Kokkonen 136/02 (holotype)*, Mahalanniemi, 18.IX.2002 Kokkonen 112/02*, 5.X.2003 Kokkonen 922/03*, mouth of Matkusjoki, 2.IX.2002 Kokkonen 116/02*, 21.IX.2002 Kokkonen 115/02*, 117/02*, 135/02*, 18.IX.2003 Kokkonen 724/03*.

COMMENTS: A species differing genetically and morphologically slightly from *C. rusticellus* is described here as a new species, *C. rusticelloides*. It shared some sites with *C. rusticellus* in eastern Finland. They differed genetically only by 2 bases in ITS, but there appeared no intermediates, and the RPB2 sequences deviated by 12–13 bases and two long indels from each other. As comparison, the variation of RPB2 sequences within *C. rusticellus* was up to three bases among four specimens, and there oc-

curred often ambiguous bases in these positions. Only one complete RPB2 sequence was obtained from *C. rusticelloides*, but an incomplete other sequence was nearly identical. The morphologies of the two species overlapped, but especially within sites, the spores had different shapes. The spores of *C. rusticelloides* were more often amygdaloid or fusoid. They were larger or about the same size compared with *rusticellus* spores within sites. Their size did not vary as much as observed with *C. rusticellus*. Macromorphologically, both had a band or floccules at stipe, but the colour of *C. rusticelloides* seemed often duller. No described species was found to match *C. rusticelloides*.

Cortinarius friesianus Carteret & Reumaux, Atlas des Cortinaires 11: 572 (2001)

Synonym Cortinarius flexibilifolius Carteret, Atlas des Cortinaires 14: 906 (2004)

Cortinarius friesianus and *C. flexibilifolius* were genetically close to *C. rusticellus* and *C. rusticelloides*. The ITS sequences of their types deviated from *C. rusticelloides* by 4 bases and 2 indels and from *C. rusticellus* by 6 bases and 2 indels. *Cortinarius flexibilifolius* is reduced to a synonym of *C. friesianus*, since they had identical sequences and similar morphology. The types were also collected by the same lake (Bidaud et al. 2001, 2004). The habitus of *C. flexibilifolius* resembles the habitus of *C. rusticellus* and *C. rusticelloides*, since its stipe had a similar band, whereas the stipe of *C. friesianus* was entirely pale. Both *C. flexibilifolius* and *C. friesianus* had ellipsoid spores, deviating thus from the spores of *C. rusticelloides*. The spores were strongly verrucose, but *C. friesianus* had on average narrower spores than *C. flexibilifolius*.

HOLOTYPE: *Cortinarius friesianus* Carteret & Reumaux. France, île-de-France, Maurepas forest, shore of Lake Courance, under *Salix* sp. and *Betula pendula*, 24.XI.1997 X. Carteret, no 97112425 (PC). – Spores 8.5—9.4—10.4 × 5.1—5.6—6.0 μm, Q=1.48—1.67—1.86, (n=20); ellipsoid, occasionally subamygdaloid, suprahilar depression occasional; strongly verrucose; strongly dextrinoid; lamellar hyphae strongly encrusted and with dark flecks.

HOLOTYPE: *Cortinarius flexibilifolius* Carteret.

France, île-de-France, Maurepas forest, shore of Lake Courance, under hygrophilous trees (incl. *Salix*, *Alnus*, *Populus* and *Betula*), 13.XI.2003 X. Carteret, no XC2003-58 (PC). – Spores $8.3\text{--}9.2\text{--}10.1 \times 5.7\text{--}6.0\text{--}6.3 \mu\text{m}$, $Q=1.41\text{--}1.55\text{--}1.71$, ($n=20$); ellipsoid, rarely subamygdaloid, suprahilar depression occasional; strongly verrucose; strongly dextrinoid. Lamellar hyphae strongly encrusted and with dark flecks.

CORTINARIUS SANIOSUS COMPLEX

Figure 12

Cortinarius saniosus (Fr.:Fr.) Fr., Epicr. Syst.

Mycol.: 313 (1838)

Synonyms *C. bavaricus* M.M.Moser,

Mycol. Helv. 1(1): 10 (1983)

C. aureomarginatus P.D.Orton,

vide Lindström et al. 2008

C. chrysomallus Lamoure,

vide Lindström et al. 2008

Cortinarius saniosus is probably the most common *Cortinarius* in boreal *Salix* thickets of Finland. Lindström et al. (2008) published an extensive morphological and genetic study of *C. saniosus* complex. Both *C. aureomarginatus* P.D.Orton from lowland England and *C. chrysomallus* Lamoure from alpine habitats were concluded to belong to the variation of *C. saniosus*. *Cortinarius saniosus* was found to grow with many hosts and in many habitats, and the small genetic variation could not be connected to morphological or ecological differences. Similarly, my collections from *Salix* habitats revealed a variation up to 2 bases and 2 indels in ITS, but they formed a coherent clade including the types of *C. aureomarginatus*, *C. chrysomallus* (from GenBank) and *C. bavaricus*. The genetic variation could not be connected to morphological variation with this limited material. Excluding the common yellow veil, the colour, size and spore morphology varied rather much. The pileus varied from dark brown to orange brown, the spore size from the usual $8\text{--}10 \times 5.5\text{--}6.5 \mu\text{m}$ to ca. $7.5\text{--}8.5 \times 5\text{--}6 \mu\text{m}$, and the spore shape from rather broad to narrowish ellipsoid among collections with identical sequences. Some collections had both ellipsoid and ovoid spores. All had rather

strongly to strongly verrucose and moderately to strongly dextrinoid spores. Unlike Lindstöm et al. (2008), violaceous colour was never observed at lamellae or stipe. The ITS sequence of the *C. bavaricus* type was identical or differed only by one or few indels from most *saniosus* specimens. The spores and other morphology of *C. bavaricus* (Moser 1983) also are similar with *C. saniosus*. Consequently, *C. bavaricus* is reduced to a synonym. The type was collected under *Alnus incana* in Germany.

HOLOTYPE: *Cortinarius bavaricus* M.M.Moser. Germany, Bayern, Bayrischen Wald, shore by Gumpenfried, under *Alnus incana*, 3.IX.1967 M. Moser (IB-Nr. 1967/0102). – Part of type as a loan. Spores $7.0\text{--}7.9\text{--}9.0 \times 4.9\text{--}5.4\text{--}5.7 \mu\text{m}$, $Q=1.31\text{--}1.47\text{--}1.64$ ($n=20$); ellipsoid or ovoid; strongly verrucose, verrucae larger at apex; moderately dextrinoid.

OTHER SPECIMENS EXAMINED: FINLAND. Pohjois-Karjala. Nurmes, Metsä-Vastimo, 20.VII.2002 Kokkonen 129/02*, 24.IX.2002 Kokkonen 21/02*, 30.VIII.2003 Kokkonen 306/03*, Pahakala, 26.VIII.2002 58/02*, 18.VIII.2003 Kokkonen 154/03*. Valtimo, Haapakylä, Heinälampi, 24.IX.2002 Kokkonen 39/02*, 137/02*, mouth of the river Matkusjoki, 29.VIII.2003 Kokkonen 1060/03*. Koillismaa. Kuusamo, Oulanka National Park, SW of Nurmisaarenrinne, 18.IX.2019 Kokkonen 100/19*, Vuotunki, 31.VIII.2007 Kokkonen 540/07* and J. Vauras. Kittilän Lappi. Kittilä, Sirkka, 16.VIII.2006 Kokkonen 174/06*. Sompion Lappi. Savukoski, Värriöjoki, 18.VIII.2019 Kokkonen 6/19*. Enontekiön Lappi. Enontekiö, Kaaresuvanto, 20.VIII.2006 Kokkonen 267/06*, Peltovuoma, 22.VIII.2006 Kokkonen 299/06*. Inarin Lappi. Utsjoki, Kevo, 29.VIII.2005 Kokkonen 513/05*, Tsuomasvarri, near *S. reticulata*, 26.VIII.2005 Kokkonen 508/05*. ICELAND. Sudur-Ísland. Rangárþing eystra, N of Valahnúkur, on moor near *S. arctica* and *Betula*, 16.IX.2017 Kokkonen 359/17*. NORWAY. Nord-Trøndelag. Fjeld between Sanddøldalen and Blåfjella-Skækerfjella Nasjonalpark, near *S. herbacea*, 26.VIII.2016 Kokkonen 347/16*. SWEDEN. Lule Lappmark. Gällivare, Nieras, near *S. herbacea*, 30.VIII.2016 Kokkonen 1384/16*



Fig. 12. *Cortinarius saniosus* complex. **a** *C. saniosus*. Finland, Nurmes, KK 154/03. **b** *C. saniosus*. Finland, Valtimo, KK 1060/03. **c** *C. saniosus*. Finland, Valtimo, KK 39/02. **d** *C. saniosus*. Iceland, KK 359/17. **e** *C. subsaniosus*. Finland, Kalajoki, KK 246/04. **f** *C. aff. saniosus*. Switzerland, KK 35/19. **g** *C. aff. saniosus*. Switzerland, KK 307/17.



Fig. 13. *Cortinarius vienoii*, Finland, Valtimo. **a** Holotype. **b** KK 679/03.

Cortinarius subsanosus Liimat. & Niskanen,
Fungal Diversity 100: 252 (2020)

One collection from a sandy seashore near *Salix phyllicifolia* and *Alnus incana* in the middle boreal zone of Finland deviated from *C. saniosus* mostly by 9–10 bases and 5 indels. Its ITS sequence was identical with a clade 2 collection of Lindström et al. (2008) from a Swedish lake shore with e.g. *S. phyllicifolia* and near their clade 2 sequences from Nordic seashores with *Salix repens*. This species was recently described as *C. subsanosus* Liimat. & Niskanen (Hyde et al. 2020). According to the protologue, it grows on sand with *Salix* and possibly other hosts. The type is from England. The species seems to be rare inland, since it was not among my many sequenced *saniosus* specimens from inland muddy or sandy shores. The morphology of my *subsanosus* collection differed from the protologue description by a stouter habitus (Fig. 12e), a red brown pileus with an indistinct or obtuse umbo, and smaller spores. The spore size was ca. $8\text{--}10 \times 5.5\text{--}6 \mu\text{m}$ with a mean $9.1 \times 5.7 \mu\text{m}$. The spores were ellipsoid or rarely sybamygdaloid. Most lamellar hyphae were slightly to moderately encrusted.

SPECIMEN EXAMINED: FINLAND. Keski-Pohjanmaa. Kalajoki, Hiekkasärkät, 10.IX.2004 Kokkonen 246/04*.

***Cortinarius* sp.**

The clade 2 of Lindström et al. (2008) included also a separate sequence from the Austrian Alps. Six collections of this study from the Swiss Alps had identical sequences with their clade 2 Austrian specimen. They deviated by 6 bases and 3 indels from *C. subsanosus* and are regarded here as a separate species. They resembled morphologically *C. saniosus* and *C. subsanosus*, but some had a scarcer and paler veil. One had a dark red stipe base. More material may establish morphological, ecological, and/or geographical differences among the three species. Lindström et al. (2008) presumed clade 2 to be a separate taxon from *C. saniosus* but refrained from conclusions owing to lack of morphological differences.

SPECIMENS EXAMINED: SWITZERLAND. Graubünden. Scuol, Lai Sesvenna, alt. 2665 m, near *S. herbacea*, 25.VIII.2019 Kokkonen 35/19*, Val Sesvenna, near *S. herbacea*, alt. 2525 m, 14.VIII.2017 Kokkonen 306/17*, 307/17*, 360/17*, 17.VIII.2017 Kokkonen 283/17*, 316/17*.

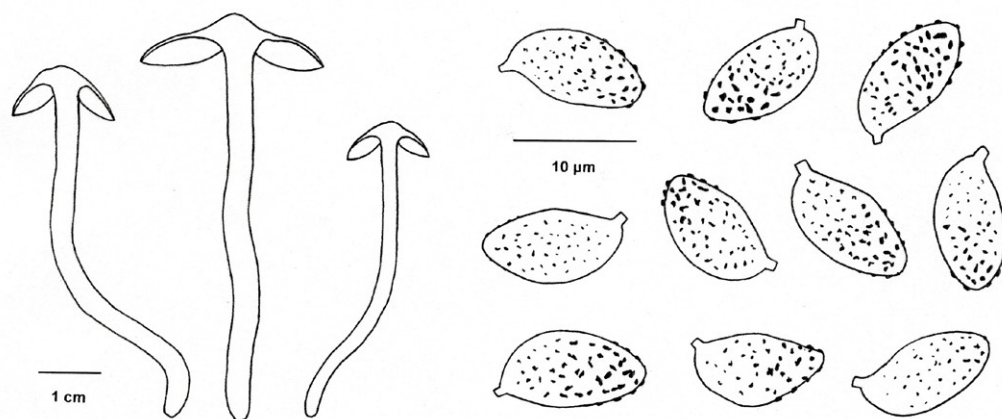


Fig. 14. *Cortinarius vienoii*. Holotype: cross-sections of fruitbodies and spores.

CORTINARIUS VIENOI

Kokkonen, sp. nov.

MycoBank MB833746

Figures 13 and 14

ETYMOLOGY: named for the memory of my father, Vieno Kokkonen. He cared for the type locality area.

HOLOTYPE: Finland, Pohjois-Karjala, Valtimo, Haapakylä, Autioniemi, lakeside *Salix* thicket with *S. phyllicifolia* and *S. myrsinifolia*, further away *Alnus incana* and *Betula*, 6.VIII.2008 K. Kokkonen 52/08 (TUR; isotype PC), ITS MN841238.

PILEUS 9–35 mm in diameter; conical when young, later broader conical or campanulate with an obtuse or rather acute umbo; red brown or ochraceous brown (ca. $S_{40}Y_{70}M_{50}$), centre darker, margin pale; delicately silky fibrillose or nearly smooth, margin pale fibrillose and at times with white veil remnants; dry, hygrophanous, translucently striate. **LAMELLAE** moderately broad, narrowly adnate, moderately crowded or rather distant; red brown or ochraceous brown ($S_{40}Y_{80}M_{50}$), when young paler ($S_{30}Y_{60}M_{40}$); edge fimbriate and paler. **STIPE** 40–65 mm long, 2.5–4.5 mm wide; equal, base roundish or somewhat tapering; when young greyish, then pale yellow brown; veil abundant, white or whitish, forming usually a distinct ring or band in the middle and floccules below, more rarely the lower part only with

few flocci or with a whitish cover; dry, fibrillose, at times base white pubescent; stuffed or fistulose when old. **CONTEXT** red brown or yellow brown. **CORTINA** pale. **SMELL** and taste not distinctive.

SPORES 9.5–10.8–13.8 × 4.7–5.5–6.3 µm, range of mean values 10.4–11.3 × 5.4–5.6 µm, $Q=1.71-1.97-2.53$, range of mean Q values 1.90–2.08 (80 spores from 4 collections); usually fusoid or amygdaloid, occasionally narrow ellipsoid, often with a suprahilar depression, rarely constricted near the apex; moderately to strongly verrucose, verrucae usually larger at apex; rather strongly to strongly dextrinoid. **BASIDIA** 27–40 × 7–10 µm ($n=11$), 4-spored, at times yellow brown (in NH_4OH). **LAMELLAR HYPHAE** variably encrusted: usually weakly, but few hyphae may be strongly encrusted. **PILEIPELLIS** hyphae 1.5–30 µm wide, pale red brown or hyaline, mostly rather strongly or strongly coarsely encrusted.

HABITAT: inland shores or swamps with *Salix* thickets. The soil is mesotrophic or eutrophic. It is connected at least with *S. phyllicifolia* and/or *S. myrsinifolia*, since no other trees grew at one site.

DISTRIBUTION: known from four sites in eastern Finland, from the middle and northern boreal zones. Two of the sites were by the same lake.

SPECIMENS EXAMINED: FINLAND. Pohjois-Karjala. Valtimo, Haapakylä, Autioniemi, 6.VIII.2008 Kokkonen 52/08* (holotype), mouth of the river Mat-



Fig. 15. *Cortinarius boreotrichus*. Finland, Kuhmo, KK 644/18, Metsähallitus.

kusjoki, thicket with *Salix phylicifolia* and *S. myrsinifolia*, 18.IX.2003 Kokkonen 679/03*. Koillismaa. Kuusamo, Oulanka National Park, Jäkälämutka, under *S. phylicifolia*, 17.IX.2019 Kokkonen 91/19*, Nurmisaarenniemi, swamp, thicket with *S. phylicifolia* and *S. lapponum*, near also *Betula* and *Picea abies*, 18.VIII.2008 Kokkonen 74/08* and J. Vauras.

COMMENTS: *Cortinarius vienoii* is characterized by red brown or yellowish brown fruitbodies with a delicately fibrillose pileus, abundantly white floccose stipe, large fusoid spores, and growth with *Salix*. It is probably a rare species, since only four localities were found, and no sequences matched in public databases. Holotype had an ambiguous base in a position, where other sequences had different bases.

Cortinarius perzonatus Reumaux is both genetically and morphologically a close species. The ITS sequence of the *perzonatus* holotype deviated from the *vienoii* sequences by 5-7 bases and 5 indels excluding ambiguous bases. Both have a similar habitus, but *C. perzonatus* has a scarcer veil (Bidaud et al. 2004), and its type spores were shorter with a lower Q value as well as of different shape: predominantly ellipsoid and only rarely distinctly fusoid. *Cortinarius perzonatus* was described growing under hygrophilous trees in France, but there exists a nearly identical sequence with the type in GenBank from a *Quercus mycorrhiza* in Romania (KM576365,

Suz et al. 2014). Thus, the two species seem to have different hosts.

Cortinarius pseudofusisporus Bidaud resembles morphologically *C. vienoii*, but its holotype differed genetically distinctly, belonging to the *C. decipiens* complex. The rather similar *C. neglectus* Carteret was distant according to the type study. *Cortinarius cucumisporus* M.M.Moser has large fusoid spores and it grows with *Salix*, as explained above, but also it was distant. Other small *Telamonia* species with fusoid spores differ for example by growing in coniferous forests or having a dissimilar morphology.

OTHER SPECIES FROM SALIX THICKETS

Cortinarius boreotrichus Kytöv., Niskanen & Liimat., Index Fungorum 339:1 (2017)

Figure 15

Cortinarius boreotrichus grew under *Salix phylicifolia* and near *Betula* by a brook in the transition zone between the middle and northern boreal zones. Formerly it has been known only from one mixed riverside forest in the northern boreal zone (Liimatainen 2017). The morphology resembled the original description, except that the pileus was dark brown and entirely squarrolous. The spores were ca. 8–9.5 × 4.5–5 μm, narrowly ellipsoid - cylindrical - subamygdaloid, rather weakly verrucose, and moderately dextrinoid. The ITS sequence was identical with the type (GenBank MF379638). The species may be connected with *Betula*, since it was not found from other *Salix* sites. The species is closely related to the *Salix* associate *C. gossypinus*. Their ITS sequences deviated by 7-10 bases and 1-2 indels from each other. Both are characterized by hairy or squamulose pilei.

SPECIMEN EXAMINED: FINLAND. Kainuu. Kuhmo, NW of Koirakangas, by Koirapuro, 8.IX.2018 Kokkonen 644/18*.

Cortinarius aff. *erubescens* M.M.Moser,
Nova Hedwigia 14(2-4): 515 (1968)

Two boreal collections growing among *Salix phylicifolia* and *S. lapponum* bushes were morphologically and genetically close to *C. erubescens*, when compared with two Nordic *erubescens* collections (BOLD NOBAS2063-16, JV25222 in TUR-A). They may represent a new species, but more data would be needed. *Cortinarius pertristis* J.Favre has a rather similar morphology (Favre 1955). A genetically identical collection with aff. *erubescens* was found near *Salix herbacea* in the Swiss Alps. The difference from *C. erubescens* was only 2 bases and 3 indels by ITS sequences. The collections were also close to *C. rusticellus* complex, but they had a dissimilar morphology. The closest species of this study, *C. rusticelloides*, differed by 5 bases and 7 indels. The fungi had a dark pileus, pale stipe, and small spores (ca. $7-8.5 \times 4.5-5 \mu\text{m}$) similarly to *C. erubescens*, but the spores were moderately verrucose in contrast with the nearly smooth spores of *C. erubescens* (Moser 1968, Niskanen et al. 2012b). One boreal fruitbody had a red stipe base. The boreal fungi grew by a sandy riverside in the northern boreal zone. The similar *C. roseobasilis* Ammirati, Beug, Niskanen, Liimat. & O.Ceska and *C. rufescentipes* Bidaud are close species. The type of *C. roseobasilis* differed by 4 bases and 5 indels (GenBank NR153059, Li et al. 2016) and the type of *C. rufescentipes* by 9 bases and 4 indels from the aff. *erubescens* collections.

SPECIMENS EXAMINED: *C.* aff. *erubescens*: FINLAND. Koillismaa. Kuusamo, Oulanka National Park, Jäkälämutka, 1.IX.2007 Kokkonen 578/07*, 580/07. SWITZERLAND. Graubünden. Scuol, Val Sesvenna, alt. 2525 m, 17.VIII.2017 Kokkonen 278/17*. *C. erubescens*: FINLAND. Salla, Morottaja, Heinäpuronkangas, dry heath forest with *Pinus sylvestris* on fine sandy soil, 2.IX.2007 J. Vauras 25222, det. T. Niskanen (TUR-A)*.

Cortinarius fulvopaludosus Kytöv., Niskanen & Liimat., Index Fungorum 344: 1 (2017)

A collection from a boreal mixed shore forest with *Salix* bushes was identified as *C. fulvopaludosus*. Its morphology differed from the protologue de-



Fig. 16. *Cortinarius fulvopaludosus* with *Lactarius tabidus*. Finland, Nurmes, KK 619/03.

scription (Liimatainen 2017) and its ITS sequence one base from the *fulvopaludosus* type (GenBank NR154868), but one of the two chromatograms had a mixed peak in the deviant position. In contrast to the protologue, the pileus was dark red brown with a blackish centre, the umbo was obtuse, and the stipe was stouter with height 40–45 mm and width 3.5–6 mm. The smell was strongly raphanoid. A *fulvopaludosus* specimen from a mixed forest in Italy also had a dark brown pileus. It was genetically identical with the type. The spores of both collections were ellipsoid to obtusely amygdaloid, moderately to rather strongly verrucose, and rather strongly to strongly dextrinoid. The mean spore size of the boreal collection was similar with the original description, but the spores of the Italian collection were smaller with mean $8.0 \times 4.8 \mu\text{m}$. The species is apparently not connected with *Salix*. In addition to moist mixed forests, it has been found mycorrhizal with *Populus* and *Fagus* (Liimatainen 2017).

SPECIMENS EXAMINED: FINLAND. Pohjois-Karjala. Nurmes, Pahakala, mixed shore forest by lake with *Salix phylicifolia*, *S. myrsinifolia*, *Alnus incana*, *Betula*, and *Picea abies*, 15.IX.2003 Kokkonen 619/03*. ITALY. Trentino. Pergine, Val dei Mochen, forest with *Larix decidua*, *Picea abies*, and scattered *Betula*, *Alnus viridis* and *Fagus sylvatica*, under *Alnus*, margin of moist and more dry soil, 5.X.2002 J. Vauras 19599 (TUR-A, as *C. decipiens*)*.

Cortinarius spp.

A *Telamonia* species collected among *Salix* in three localities from the northern boreal to the low-alpine zone could not be identified. It had a dark brown pileus and a pale fibrillous stipe. The fungi from two collections had a prominent umbo and a thin stipe. The spores were ca. $8.5\text{--}11 \times 5.5\text{--}6$ or $6\text{--}7 \mu\text{m}$, ellipsoid to subamygdaloid, strongly or rather weakly verrucose, and rather weakly dextrinoid. The ITS sequences deviated 2 indels at most from each other. Several specimens from arctic habitats had identical sequences in GenBank, and it occurred also in the Swiss Alps among *Salix retusa* and *Dryas*. The GenBank specimens were anonymous (Bjorbaekmo et al. 2010, Fujiyoshi et al. 2011, Timling et al. 2012) or identified once as *C. tenebricus* (Geml et al. 2012). They were connected with *Dryas* or arctic *Salix* species. One identical sequence was from *Kobresia myosuroides* in Austria (Mühlmann & Peintner 2008). The species is possibly restricted to northern boreal, arctic, and alpine zones.

SPECIMENS EXAMINED: FINLAND. Enontekiön Lappi. Enontekiö, Palojoensuu, riverside *Salix* thicket with *S. phylicifolia* and *S. lapponum*, *Betula* further away, 19.VIII.2006 Kokkonen 251/06*. Inarin Lappi. Utsjoki, Pulmankijärvi, lakeside *Salix* thicket with e.g. *S. phylicifolia* and *S. lapponum*, *Betula* and *Alnus incana* further away, 28.VIII.2005 Kokkonen 469/05*, Tsuomasvarri, low alpine zone, near *S. myrsinites*, *S. glauca* and *Betula nana*, 26.VIII.2005 Kokkonen 516/05*. SWITZERLAND. Graubünden. Scuol, Val S-charl, Valbella, alt. 2180 m, 26.VIII.2019 Kokkonen 46/19*.

A small group of fungi collected from *Salix* thickets in the middle boreal, northern boreal and subarctic zones was genetically between the *comatus* and *cucumisporus* complexes and near some *C. flexipes* collections (Fig. 19). The habitus resembled for example *C. vulpicolor*, but the morphology also varied much, which may be due to the habitat. The stipe was often long and slender in boreal *Salix* thickets, but short on a subarctic sandy ground. The red brown or dark fruitbodies had usually flocculose pilei and fibrillose stipes, but the pileus could also be smooth. The spores were large, mostly $9\text{--}11 \times 5.5\text{--}6 \mu\text{m}$, and ellipsoid or amygdaloid. A specimen deviating by one base from the others had weakly

verrucose spores compared with the strongly verrucose spores of others. The group deviated from the Swiss *C. comatus* specimen by 4-5 bases and 4-7 indels, from *C. vulpicolor* and *C. diasemospermus* types by 6-7 bases and 2-5 indels, from *C. flexipes* collections by 3-6 bases and 3-5 indels, and from the North American *C. fragrantissimus* Ammirati, Beug, Liimat., Niskanen & O.Ceska type by 3-4 bases and 3-6 indels (GenBank NR153058, Li et al. 2016). It lacked the violaceous lamellae and sweetish smell of *C. fragrantissimus*, indicating a separate species. The identification would require extensive research due to the poorly researched *C. flexipes* complex, and several described species, for example in the Atlas des Cortinaires series, could fit to its variation.

SPECIMENS EXAMINED: FINLAND. Pohjois-Karjala. Valtimo, Haapakylä, Heinälampi, 20.IX.2003 Kokkonen 736/03*, mouth of Matkusjoki, 18.IX.2003 Kokkonen 723/03*. Perä-Pohjanmaa. Kemijärvi, Vuostimo, 31.VIII.2005 Kokkonen 494/05*. Enontekiön Lappi. Enontekiö, Kaaresuvanto, 20.VIII.2006 Kokkonen 271/06*. Inarin Lappi. Utsjoki, Pulmankijärvi, 28.VIII.2005 Kokkonen 512/05*.



Fig. 17. *Cortinarius gausapatius*. Switzerland, KK 262/17.



Fig. 18. *Cortinarius galerinoides*. Switzerland, KK 44/19.

ADDITIONAL EXAMINED TYPES AND SPECIMENS

Cortinarius fistularis Britz., Hymenomyc. Südbayern 4: 132 (1891)

SPECIMEN EXAMINED: *Cortinarius fistularis* Britz. France, Ardennes, Sommathie forest, under hygrophilous deciduous trees, 23.IX.1986 leg. P. Reumaux (Herb. P. Moëgne-Loccoz no. 4134). – Part of specimen as a loan. Spores $7.1\text{--}8.1\text{--}9.6 \times 5.0\text{--}5.7\text{--}6.0$ μm , $Q=1.29\text{--}1.44\text{--}1.63$ ($n=20$); ordinary or broadly ellipsoid; moderately verrucose; rather weakly dextrinoid. Lamellar hyphae rather strongly encrusted.

Cortinarius gausapatus J.Favre, Ergebn. Wiss. Unters. Schweiz. Natl. Parks 5 (33): 202 (1955)

Figure 17

LECTOTYPE: *Cortinarius gausapatus* J.Favre. Switzerland, Graubünden, Murtaröl d'Aint, near Pass dal Fuorn, alt. 2500 m, among *Salix retusa*, Triassic calcareous soil, 22.VIII.1949 J. Favre ZA 147b (GK 13281). – Specimen with ca. 20 fruitbodies. Spores $9.0\text{--}10.5\text{--}12.9 \times 5.7\text{--}6.4\text{--}7.0$ μm , $Q=1.50\text{--}1.66\text{--}2.05$ ($n=20$); shape rather variable from broad to narrow ellipsoid, suprahilar depression occasional;

rather weakly verrucose; weakly dextrinoid.

SPECIMEN EXAMINED: *Cortinarius gausapatus* J.Favre. Switzerland, Graubünden, Val Stabelchod, among *Salix herbacea*, alt. 2550 m, 9.IX.1942 J. Favre ZA 147a (GK 13280). – Spores similar to the lectotype.

Cortinarius gausapatus was found only from the Swiss Alps in this study. The fruitbodies of the recent collections resembled the description of Favre (1955), having usually a distinctly squamulose or fibrillose pilei and large spores. The spores were ellipsoid to obtusely amygdaloid and rather weakly to rather strongly verrucose. All recent five *gausapatus* collections had long ITS sequences consisting of partially repetitive joint sequences, differing thus distinctly from all other sequences of this study. The five sequences were identical, except two sequences had the same gap of one base. The Favre's collections yielded only partial sequences, but they were identical with the long ones. *Cortinarius gausapatus* is closely related to the *C. inops* complex. The ITS sequences of the species differed minimum 11 bases and 5 indels from each other.

OTHER SPECIMENS EXAMINED: SWITZERLAND. Graubünden. Scuol, Val Plavna, alt. 2315 m, near *Salix herbacea* and *S. reticulata*, 15.VIII.2017 Kokkonen 262/17*, alt. 2320 m, among *S. herbacea*, Kokkonen 291/17*, 294/17*, alt. 2340 m, among *S. reticulata* and *Dryas*, Kokkonen 311/17*. Val Müstair, Costainas, alt. 2555 m, near *S. retusa*, 11.IX.2018 Kokkonen 831/18*.

Cortinarius helobius Romagn., Bull. Soc. Nat. Oyonnax 6: 62 (1952)

Cortinarius galerinoides Lamoure, Trav. Sci. Parc Natl. Vanoise 8: 133 (1977)

Figure 18

The identification of *C. helobius* Romagn. was based on a *C. helobius* collection from France (Moëgne-Locoz & Reumaux 1991) together with the information of the *C. helobius* collection of Cortinarius Flora Photographica from the boreal zone in Sweden (Brandrud et al. 1994, Lindström et al. 2008, GenBank DQ102686). They had only one different base in ITS sequences and are likely conspecific. Two collections of *C. dishonestus* (Weinm.) Moëgne-Locoz & Reumaux (Moëgne-Locoz & Reumaux 1991) had identical sequences with the French *helobius* sequence. All four specimens were from lowland habitats near *Salix*. *Cortinarius helobius* was not found from the boreal zone in this study and must be there rare. It is probably more common in the temperate zone. According to Romagnesi (1952), it occurs rather commonly in moist places with hygrophilous plants, for example in pits and by ponds.

The type of *C. galerinoides* Lamoure deviated from the French *helobius* sequences by two bases and two indels in ITS, possibly representing a separate species. However, the difference from the Swedish *helobius* collection was only one base and two indels. Two collections from the Swiss Alps growing with dwarf *Salix* had identical sequences with the type, and a Swiss alpine specimen (KK44/19) was genetically between the above-mentioned species. It deviated from *C. galerinoides* by two indels and from the *C. helobius* collections 1-2 bases. More collections including the type of *C. helobius* should be examined to clear these species. *Cortinarius galerinoides* was described from the alpine zone (Lamouré 1977), and the two species may have different habitats. In addition, *C. galerinoides* was described as paler, warm red brown. According to the limited material of this study, all collections had similar micromorphologies, but the three *galerinoides* specimens with identical sequences had somewhat narrower spores and the lamellar hyphae were more strongly encrusted. *Cortinarius helobius* and *C. galerinoides* are closely related to the *C. inops* complex. They deviated from that

complex only by 7 bases and 3 indels minimum, and four of the substitutions were adjacent to each other. Suárez-Santiago et al. (2009) had previously reported the genetic closeness of *C. helobius* to *C. vernus*.

HOLOTYPE: *Cortinarius galerinoides* Lamoure. France, Savoie, Vanoise, under Col de l'Iseran, alt. 2600 m, *Salix herbacea*, 19.VIII.1971 D. Lamoure (LY). – Piece of type as a loan. Spores 7.6–8.6–9.5 × 4.6–5.1–5.5 μm, Q=1.45–1.68–1.92 (n=20); usually ellipsoid, occasionally subamygdaloid or amygdaloid, suprahilar depression occasional, rarely constricted; rather strongly to strongly verrucose; weakly dextrinoid. Lamellar hyphae strongly encrusted.

SPECIMEN EXAMINED: *Cortinarius helobius* Romagn. France, Haute-Savoie, Rumilly, a pit, at the base of *Salix* and stunted *Populus*, or under *Salix*, 30.V.1985 and 4.V.1986 leg. P. Moëgne-Locoz, det. J. Melot (Herb. P. Moëgne-Locoz no. 052). – Part of specimen as a loan. Spores 7.8–8.6–9.5 × 5.0–5.5–5.9 μm, Q=1.40–1.55–1.70 (n=20); ellipsoid, rarely subamygdaloid or obtusely amygdaloid, suprahilar depression occasional; very strongly verrucose; weakly dextrinoid. Some lamellar hyphae slightly to moderately encrusted.

SPECIMEN EXAMINED: *Cortinarius dishonestus* (Weinm.) Moëgne-Locoz & Reumaux. France, Haute-Savoie, Alex, gravels of the river Fier, under *Salix*, 11.VI.1987 leg. P. Moëgne-Locoz, det. P. Reumaux (Herb. P. Moëgne-Locoz no. 603). – Part of specimen as a loan. Spores 7.2–8.1–9.0 × 4.9–5.3–5.9 μm, Q=1.43–1.53–1.68 (n=20); ellipsoid, rarely subamygdaloid or obtusely amygdaloid, suprahilar depression rare; very strongly verrucose; weakly or rather weakly dextrinoid. Lamellar hyphae moderately encrusted.

SPECIMEN EXAMINED: *Cortinarius dishonestus* (Weinm.) Moëgne-Locoz & Reumaux. France, Haute-Savoie, Alex, gravels of the river Fier, under *Salix*, 11.VI.1987 leg. P. Moëgne-Locoz, det. P. Reumaux (Herb. P. Moëgne-Locoz no. 606). – Part of specimen as a loan. Spores 7.5–8.3–8.9 × 5.1–5.5–6.0 μm, Q=1.44–1.50–1.56 (n=10); similar to the previous specimen. Some lamellar hyphae slightly encrusted.

OTHER SPECIMENS EXAMINED: Switzerland. Graubünden. Scuol, Val Plavna, alt. 2315 m, near *Salix reticulata*, 15.VIII.2017 Kokkonen 296/17*, 310/17*, Val S-Charl, Valbella, alt. 2185 m, near *S. reticulata*, 26.VIII.2019 Kokkonen 44/19*.

Cortinarius hinnuleus* Fr. var. *minutalis

J.Favre, *Ergebn. Wiss. Unters. Schweiz. Natl. Parks* 5 (33): 203 (1955)

LECTOTYPE: *Cortinarius hinnuleus* Fr. var. *minutalis* J.Favre. Switzerland, Graubünden, between Pass of Murter and Piz Murter, alt. 2600 m, among *Salix retusa*, Triassic calcareous soil, 1.IX.1953 J. Favre (GK 13292). – Spores 6.8–7.5–8.7 × 5.0–5.4–5.9 μm, Q=1.24–1.39–1.60 (n=20); broadly ellipsoid; strongly verrucose; weakly dextrinoid.

Cortinarius hinnuleus var. *minutalis* was found from an alpine site on a fjeld in Finland, but not from the boreal zone. It grew among *Salix reticulata*, and near *S. glauca*, *S. herbacea* and *Betula nana*. The fruitbodies were orange brown with red brown lamellae and scarce white veil on stipe. The spores were larger than in the type: 7.8–8.6–9.2 × 5.6–5.9–6.3 μm, with Q=1.38–1.46–1.58. The lamellar hyphae were smooth or slightly rough.

OTHER SPECIMEN EXAMINED: FINLAND. Inarin Lappi. Utsjoki, Tsuomasvarri, 26.VIII.2005 Kokkonen 514/05*.

***Cortinarius lacustris* f. *alboanulatus* Moënneloc. & Reumaux, Atlas des Cortinaires – Les Cortinaires Hinnuloïdes 1: 148 (1997)**

ISOTYPE: *Cortinarius lacustris* f. *alboanulatus* Moënneloc. & Reumaux. France, Île-de-France, Rambouillet forest, pond of Étang d'Or, 20.X.1987 leg. J. Poirier (Herb. P. Moënneloc. no. 1165). – Part of specimen as a loan. Spores 7.5–8.8–10.7 × 4.5–5.1–6.5 μm, Q=1.63–1.74–1.91 (n=20); dacryoid to somewhat fusoid, rarely without a suprahilar depression; usually moderately verrucose; moderately dextrinoid. Lamellar hyphae moderately encrusted.

***Cortinarius neglectus* Carteret, Atlas des Cortinaires 21: 1786 (2013)**

HOLOTYPE: *Cortinarius neglectus* Carteret. France, Île-de-France, Rambouillet forest, Étang-Neuf, under deciduous trees (*Betula*, *Quercus*), soil clay-calcareous, 15.XI.2009 X. Carteret, XC 2009-62 (PC).

– Spores 8.4–9.8–11.2 × 5.4–5.8–6.1 μm, Q=1.53–1.69–1.87 (n=20); ellipsoid, rarely subamygdaloid or amygdaloid, suprahilar depression occasional; strongly verrucose, verrucae often larger at apex; rather strongly to strongly dextrinoid. Lamellar hyphae smooth.

***Cortinarius perzonatus* Reumaux, Atlas des Cortinaires 14: 907 (2004)**

HOLOTYPE: *Cortinarius perzonatus* Reumaux. France, Ardennes, Les Alleux, under hygrophilous trees, 3.X.1998 leg. P. Reumaux, PML 5255 (PC). – Spores 7.7–9.2–11.1 × 4.9–5.7–6.6 μm, Q=1.38–1.61–1.80 (n=20); usually ellipsoid, occasionally amygdaloid, rarely fusoid, suprahilar depression frequent; rather strongly to strongly verrucose, verrucae often larger at apex; moderately to rather strongly dextrinoid. Lamellar hyphae smooth.

***Cortinarius rufescentipes* Bidaud, Atlas des Cortinaires 11: 575 (2001)**

HOLOTYPE: *Cortinarius rufescentipes* Bidaud. France, Bourgogne-Franche-Comté, environment of Belfort, alt. 350 m, under acidophilous deciduous trees, 6.X.1998 A. Bidaud (no. 5095 in PC). – Spores 6.8–7.4–8.4 × 4.6–4.9–5.2 μm, Q=1.39–1.51–1.70 (n=20); ordinary or broadly ellipsoid; rather weakly verrucose; weakly to rather strongly dextrinoid. Lamellar hyphae smooth.

***Cortinarius sphagnicola* Carteret & Reumaux, Atlas des Cortinaires 14: 908 (2004)**

HOLOTYPE: *Cortinarius sphagnicola* Carteret & Reumaux. France, Île-de-France, Rambouillet forest, pond of Étang d'Or, under hygrophilous trees, among *Sphagnum*, 18.IX.1993 leg. P.-A. Moreau, PML 3934 (PC). – Spores rather scarce; 7.0–7.7–9.0 × 4.6–5.2–5.7 μm, Q=1.25–1.50–1.73 (n=20); ordinary or broadly ellipsoid; weakly to moderately verrucose; weakly dextrinoid. Lamellar hyphae moderately encrusted.

Cortinarius subcastaneus Bidaud & Reumaux,
Atlas des Cortinaires 10: 515 (2000)

HOLOTYPE: *Cortinarius subcastaneus* Bidaud & Reumaux. France, Dordogne, Forest of Born, near a pond, under hygrophilous deciduous trees (*Betula*, *Salix*), 27.X.1997 A. Bidaud, no. 5092 (PC). — Spores 7.5–8.5–10.2 × 5.0–5.5–5.9 μm, Q=1.36–1.55–1.85 (n=20); ellipsoid or occasionally obtusely amygdaloid, suprahilar depression occasional; very strongly verrucose, verrucae large; rather strongly dextrinoid. Lamellar hyphae smooth.

Cortinarius tenebricus J.Favre, *Ergebn. Wiss. Unters. Schweiz. Natl. Parks* 5 (33): 204 (1955)

LECTOTYPE: *Cortinarius tenebricus* J.Favre. Switzerland, Graubünden, National Park, Val Plavna, between the cottage and Pass of Botsch, alt. ca. 2200 m, Triassic calcareous soil, among *Salix reticulata* and *S. retusa*, 15.VIII.1941 J. Favre ZA 168a (GK 13514). — Specimen with ca. 10 fruitbodies. Spores 6.6–7.8–9.4 × 4.8–5.2–5.7 μm, Q=1.32–1.50–1.78 (n=20); ellipsoid, sometimes a slight suprahilar depression; rather strongly to strongly verrucose; rather strongly dextrinoid. Cheilocystidia not observed.

Phylogeny

The ML phylogenetic trees are presented in Figures 19 and 20. The species complexes were similarly formed by ITS and RPB2 analyses. In the RPB2 tree, the species complexes were wider apart from each other compared with the ITS tree. Also, the distances between close species were often longer in RPB2 analyses, but there occurred also significant variation. Within some complexes, the species or specimens were differently related with each other in ITS and RPB2 trees, complicating the phylogenetic interpretation. Further, the ancestral nodes of the ITS tree had very low bootstrap values. In the concatenated tree of ITS and RPB2 sequences, the com-

plexes included the same clades as the separate trees and the new species were even more strongly supported by bootstrap values. The amount of intraspecific variation varied somewhat among the species. The intraspecific variation was more often higher among RPB2 sequences than among ITS sequences. The Bayesian trees were similar to the ML trees. Highly supported branches are shown in the ML trees. More DNA regions would be required to see the evolutionary history of all species.

Discussion

The diversity of small *Telamonia* in boreal lowland *Salix* thickets is high. Altogether 23 species were recognized in Finland. Most of them could be named and four species are described as new. The taxonomy was based on DNA analyses of the ITS region and less of the RPB2 region together with extensive morphological examinations. A large genetic and morphological variation emerged. The differences between species or clades were often small, which is why the species limits remained sometimes obscure. Nearly all species were involved in species complexes.

Ample material from some boreal sites allowed site-specific morphological and genetic comparisons to be made, which eliminated the effects of environment and geographical distance on variation. These comparisons were used to delimit species in unclear cases. Groups of specimens differing only by two or few bases in ITS sequences and having very similar morphologies were interpreted as separate species especially when they grew at the same sites without genetic intermediates, differed there morphologically at least somehow, and were separated by RPB2 sequences. The results indicate that the ITS differences of only two bases are possible between *Telamonia* species from distant locations. The ITS variation of only one base was seen as intraspecific or the interpretation was left open due to the insufficient data. Also, the occurrence of deletions and/or insertions without base changes was regarded as intraspecific. Some specimens deviating by one base, or once by two bases, from each other in ITS sequences had identical RPB2 sequences, which was regarded as a

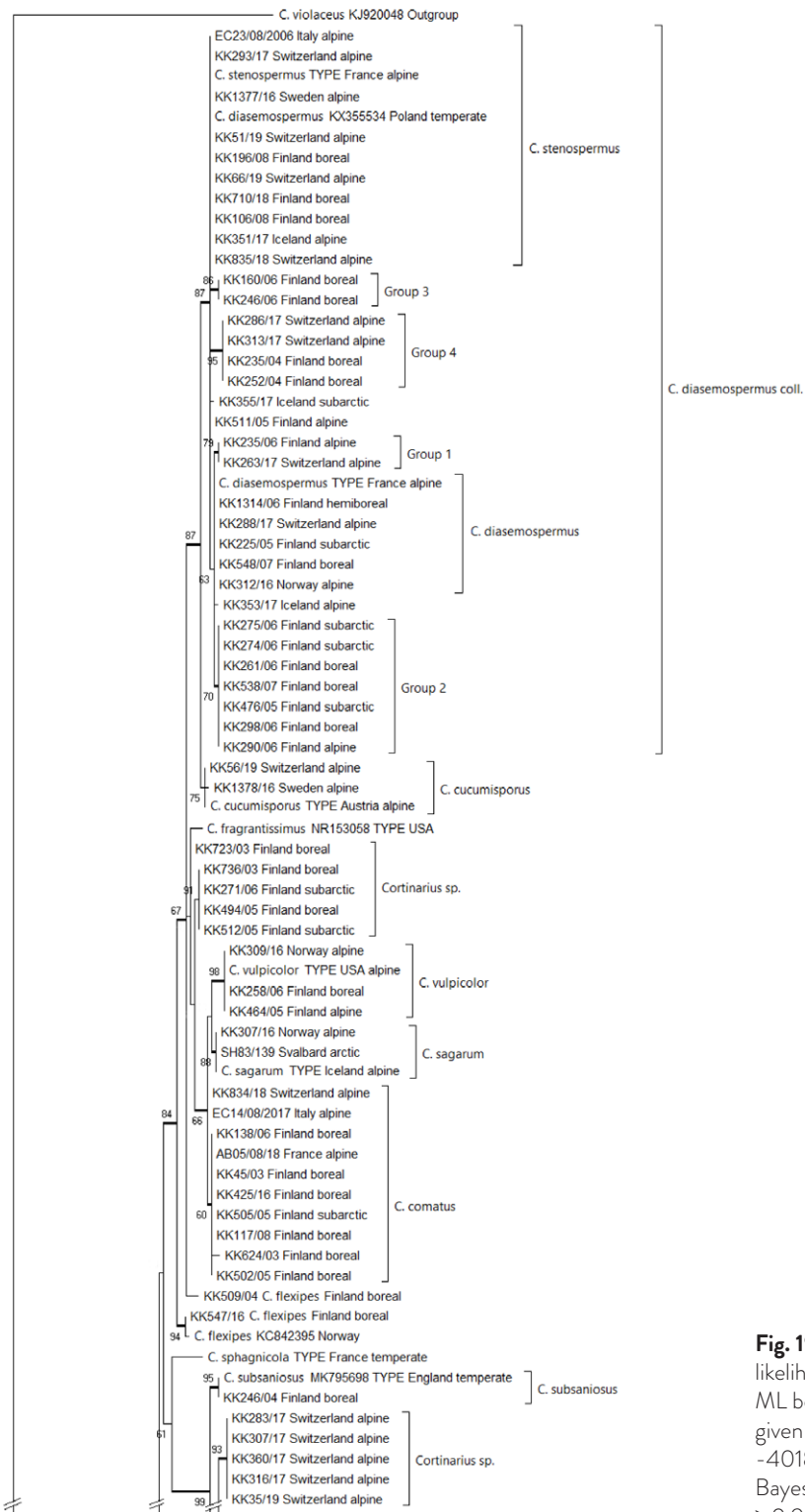


Fig. 19. (five parts) A maximum likelihood tree of ITS sequences. ML bootstrap values ≥ 50 are given at nodes. Log likelihood -4018.86. Branches with Bayesian posterior probabilities ≥ 0.95 have thick lines.

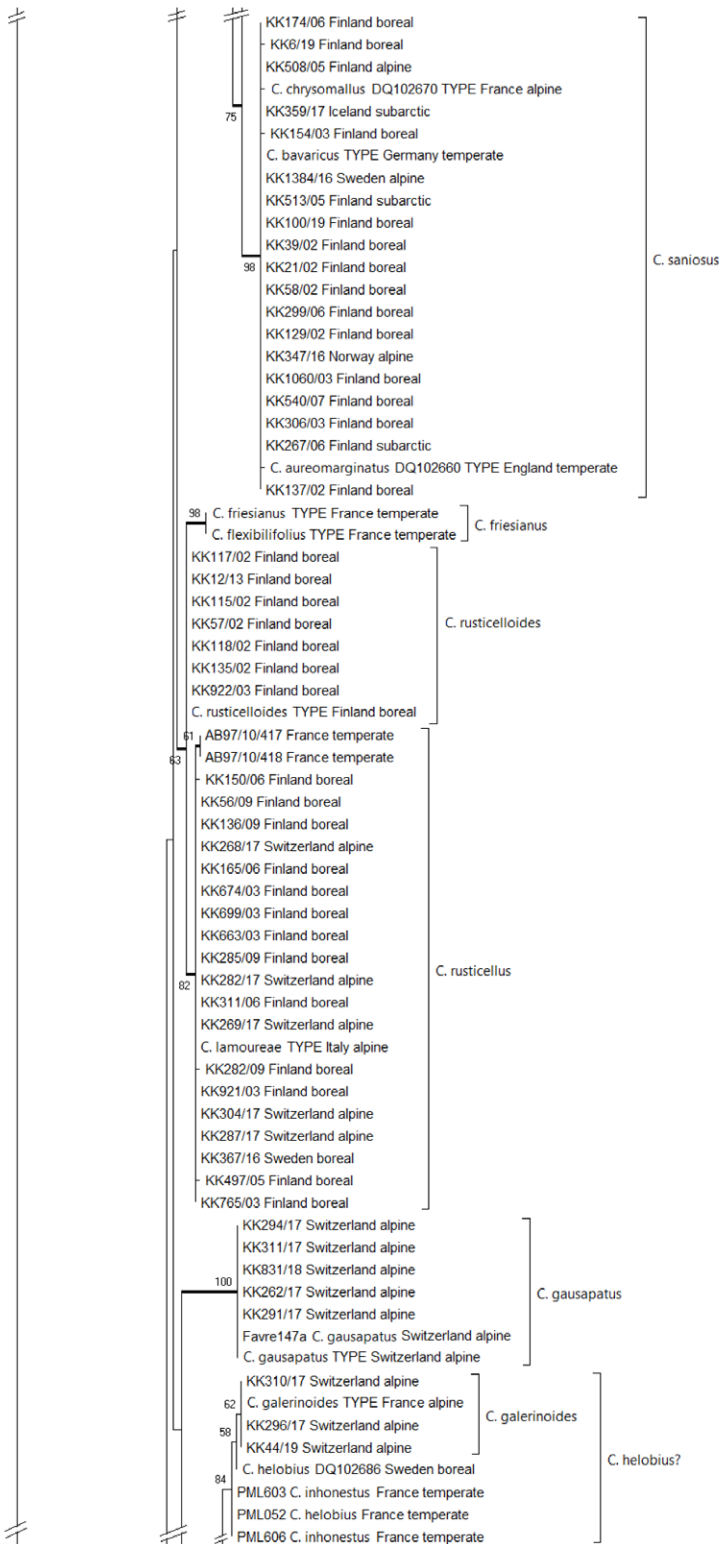


Fig. 19, part 2

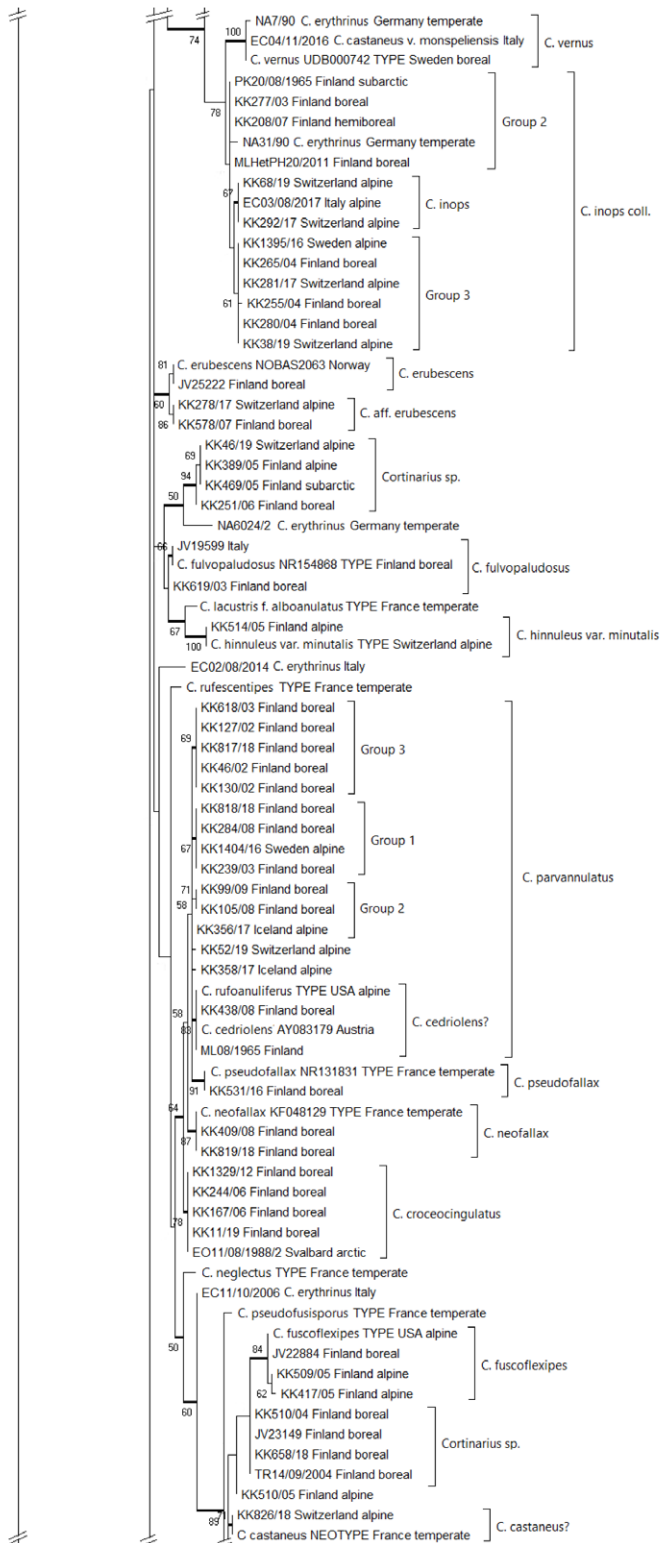


Fig. 19, part 3

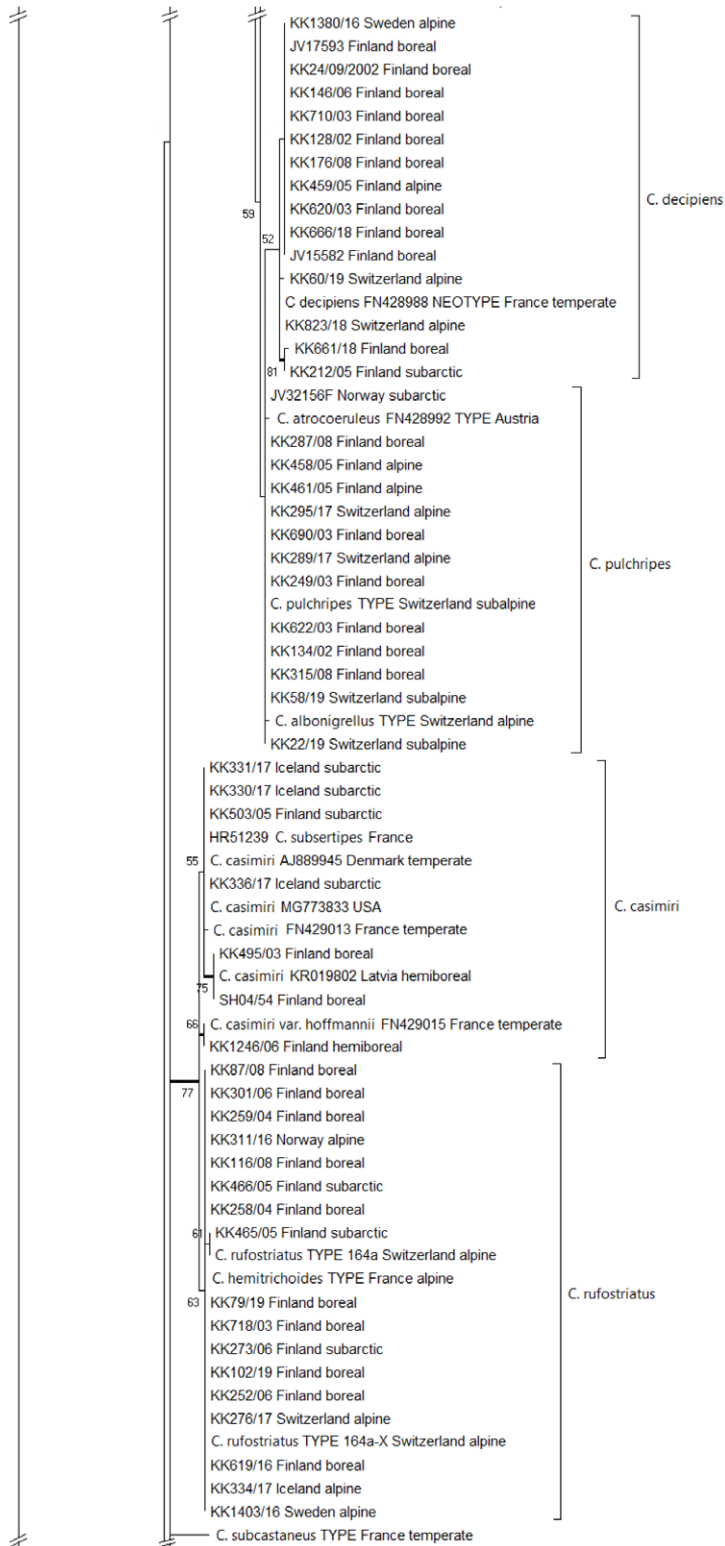


Fig. 19, part 4

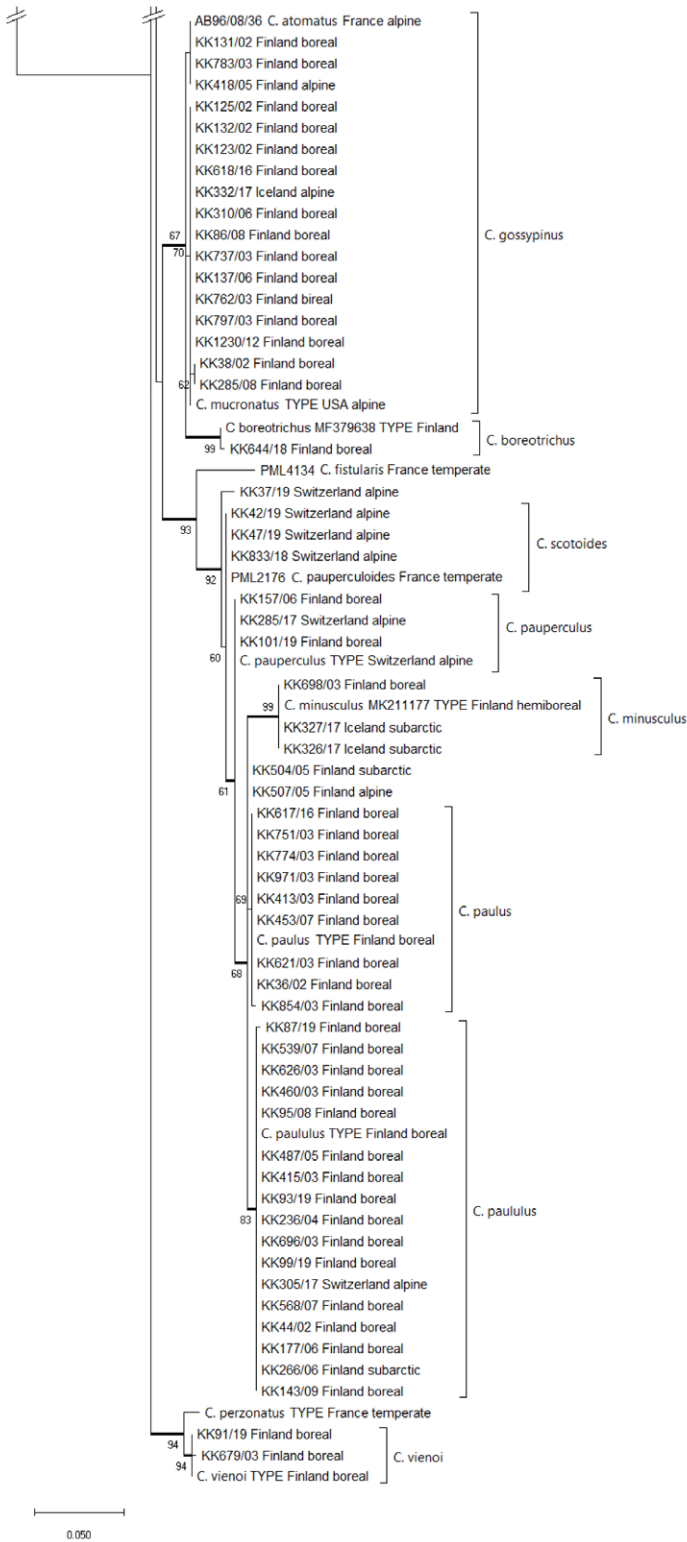


Fig. 19, part 5

clear sign of conspecificity. The results of ITS and RPB2 analyses were not fully concordant, and RPB2 analyses helped to delimit species. Inclusion of some other regions could improve the resolution still. In the study of Frøslev et al. (2005), both RPB1 and RPB2 improved the resolution of *Cortinarius* species. According to Garnica et al. (2016), the threshold values of the ITS region for species limitation vary within the *Cortinarius* genus. No fully cryptic species were identified in this study, although the possibility for cryptic species was observed especially within the *C. inops* complex. For the still obscure cases, more material should be examined. Cryptic *Cortinarius* species have been reported, but rarely (e.g. Frøslev et al. 2007, Liimatainen et al. 2015, 2017).

The mycofloras of small *Telamonia* did not differ remarkably between the boreal and alpine zones. Eighteen of the 23 species were found both with the boreal shrubby *Salix* species and with arctic-alpine dwarf *Salix*. The remaining five species are yet to be found from the arctic-alpine zone, since this study concentrated on boreal fungi. Three of these five species are described here as new, and they seem to be uncommon. One new species, *C. paululus*, was rather common and it was found also from the Alps. One species solely from the boreal zone remained undetermined. It was close to difficult species complexes including *C. flexipes*. The mycofloras of inland shores and seashores differed somewhat. Two species from the seashores were found from the alpine zone, but not from boreal inland thickets. Considering the climate gradient among high alpine, low alpine, sub-arctic and boreal environments, the occurrence of many common species is not very surprising. Furthermore, the arctic-alpine dwarf and low shrub *Salix* species are closely related to the boreal taller shrubs. Their division into separate subgenera is not supported by molecular studies (e.g. Chen et al. 2010). It may turn out that also temperate and alpine zones have many common *Cortinarius* species. Five such species were detected with the scarce temperate material of this study. On the other hand, some arctic or high-alpine species do not likely survive in lower altitudes or milder climates. Among the material of this study, at least six species were found only in the arctic - high-alpine zones, when the number of species within some complexes remained open.

The sequencing of type specimens was impor-

tant for the identifications, especially regarding several alpine types of Favre. He was the first to survey thoroughly alpine fungi growing with *Salix* (Brunner et al. 2017). Most species had wide geographical distributions in this study. A species occurring in Fennoscandia could occur in the Alps, Iceland, or North America. Only few species were found in one country. *Cortinarius* species have appeared widely distributed in the northern hemisphere in previous works (e.g. Garnica et al. 2009, Harrower et al. 2011, Niskanen et al. 2012a, 2016, Cripps et al. 2015, Liimatainen et al. 2015, 2017, Brandrud et al. 2018). The morphological features varied much within species. Especially the habitus varied among locations or environments. For example, fungi growing on sand or with dwarf *Salix* were usually smaller than fungi on boreal paludified or muddy shores. The size of fruitbodies, and the width and shape of spores were found as most useful to separate sibling species growing at the same sites. The veil colour was not always constant but varied from white to yellow brown within some species.

The sibling species within the complexes mostly occurred in the same regions. More species will likely be recognized in these complexes from different regions and hosts. Since this study focused on shrubby and dwarf *Salix*, it remained obscure to which extent the species grow with *Salix caprea* and other large tree species. At least some species were connected also with other trees: *C. fuscoflexipes* likely with *S. caprea*, *C. decipiens* likely with *Alnus* or *Betula*, *C. saniosus* with *Alnus*, and the *C. castaneus* neotype species and *C. scotooides* with temperate *Populus* (Moënné-Loccoz & Reumaux 1990a, *C. pauperculooides* ad int. in Bidaud et al. 2012). *Populus* as a close genus, as well as the often co-occurring *Alnus* and *Betula* are the most likely genera to share *Telamonia* species with *Salix*. Most *Cortinarius* species have been reported to grow only with one or few host trees or genera, or either with deciduous or coniferous trees (e.g. Frøslev et al. 2007, Garnica et al. 2009). The sibling species in this study appeared to have sometimes hosts from different genera, like *C. vienoi* and *C. perzonatus*, *C. rufostriatus* in the *C. casimiri* complex, and an anonymous species in the *C. decipiens* complex. The sibling species were probably not connected with different, closely related *Salix* species in the same habitat. In the study of Ryberg

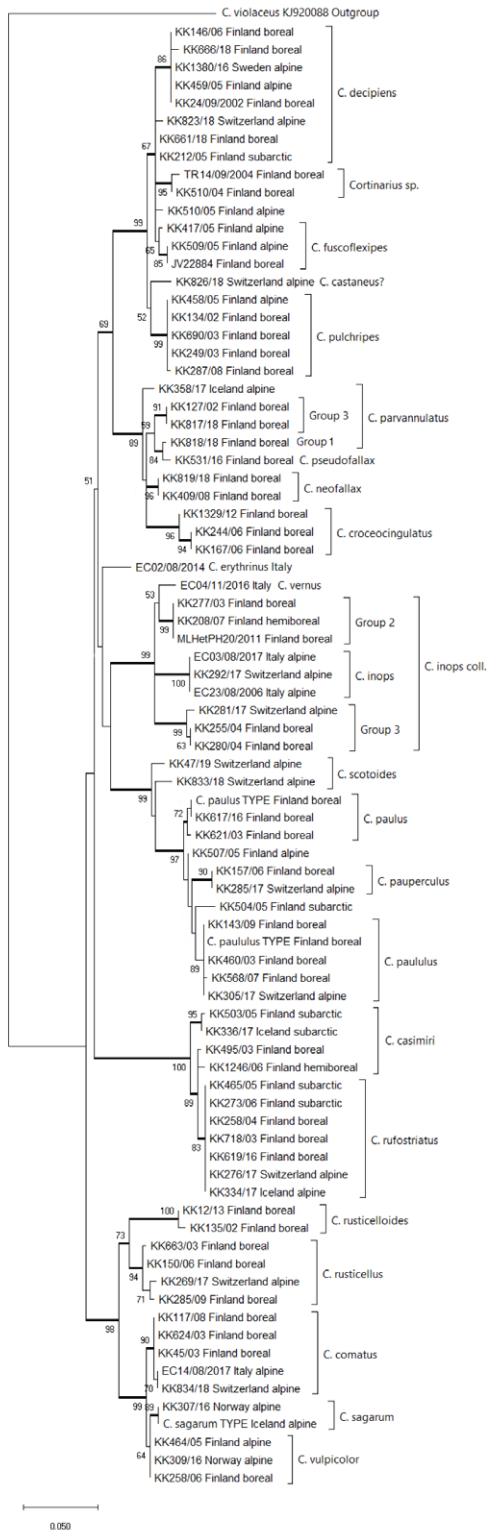


Fig. 20. A maximum likelihood tree of RPB2 sequences. ML bootstrap values ≥ 50 are given at nodes. Log likelihood -3257.56 . Branches with Bayesian posterior probabilities ≥ 0.95 have thick lines.

et al. (2011), *Salix herbacea* and *S. polaris* had similar ectomycorrhizal communities in the same alpine locality. The boreal *Salix* thickets of this study mainly consisted of *S. phylicifolia* and *S. myrsinifolia*, which commonly hybridize with each other. A site with *S. phylicifolia* and *S. myrsinifolia* as the only tree species included the sibling species *C. rusticellus* and *C. rusticelloides*. The sibling species *C. paulus* and *C. paululus* also occurred at two same sites dominated by those *Salix* species. One possible explanation for the co-occurrence of the sibling species is a previous allopatric speciation in glacial refugia, for the same or different hosts. *Salix myrsinifolia* and *S. phylicifolia* may have also been allopatric. The speciation of *Cortinarius* likely follows the speciation of hosts. The presumed rapid diversification of boreo-arctic *Salix* species during Pleistocene (Lauron-Moreau et al. 2015) is probably connected with the confusing species complexes of their *Telamonia*. The low divergence of ITS sequences within *Cortinarius* has been proposed to result from on-going speciation (Peintner 2008). Intraspecific or intragenomic polymorphism has occurred commonly within some *Cortinarius* species or sections (e.g. Frøslev et al. 2007, Niskanen et al. 2009, Suárez-Santiago et al. 2009). Intragenomic polymorphism appearing as ambiguous bases was rather common in this study, but the role of hybridization among species remained obscure.

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