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Cortinarius sanguineus and equally red species in Europe with an emphasis on northern European material

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Abstract: The red species of *Cortinarius* subgenus *Dermocybe* in Europe were studied based on morphological and molecular data. Three completely red species were recognized: *C. sanguineus* (syn. C. *sanguineus* var. *aurantiovaginatus*), *C. puniceus* (syn. *C. cruentus*, *C. rubrosanguineus*) and *C. vitiosus* comb. nov. *Cortinarius sanguineus* has dusky red to red pileus, reddish yellow mycelium and lacking or with only slightly encrusted hyphae in pileipellis. It occurs in mesic to damp forests with *Picea*, often on rich soil in the boreal and montane areas of Europe, presumably also in eastern Canada. *Cortinarius puniceus* differs from *C. sanguineus* by its stronger purplish red, narrower spores and spot-like encrusted hyphae in pileipellis. It grows with deciduous trees in the temperate zone of Europe. *Cortinarius vitiosus* is known only from Fennoscandia and occurs in dry to mesic coniferous forests. It has fairly thin, often zonate, dark red to dark reddish brown pileus, pale red mycelium, small spores and encrusted lamellar trama and pileipellis hyphae. In addition to these three species *C. fervidus* and *C. phoeniceus* occasionally have red basidiomes. The relationships of the species were inferred by analysis of ITS sequences. Our study suggests that the section *Sanguinei*, as earlier defined, is polyphyletic. Here the section is limited to include *C. sanguineus*, *C. puniceus* and North American *D. sierraensis*. The relationships with other red species were not determined. Section *Dermocybe*, including *C. cinnamomeus*, *C. croceus* and *C. uliginosus*, formed a monophyletic group, and the section *Malicoriae* had some support. A total of 34 new sequences are published including nine from type specimens.

Key words: ITS, molecular systematics, phylogeny, taxonomy

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Introduction

Dermocybe was described originally by Elias Fries (1821) as a tribe in the genus *Agaricus*. It later was regarded a separate genus (e.g. Ammirati 1989; Liu et al. 1997; Moser 1972, 1974, 1976, 1978) as a subgenus (e.g. Høiland 1983, Bidaud et al. 1994, Høiland and Holst-Jensen 1998), or a section (e.g. Brandrud et al. 1989) of subgenus *Cortinarius*. Unlike other subgenera and sections of *Cortinarius*, several phylogenetic studies based on molecular data indicate that *Dermocybe* is a largely monophyletic group and currently included in the genus *Cortinarius* (e.g. Liu et al. 1997, Høiland and Holst-Jensen 2000, Peintner et al. 2004, Garnica et al. 2005).

Species in *Dermocybe* typically display bright colors, especially on the lamellae of young basidiomes. These colors are caused by anthraquinonic pigments, contained in all *Dermocybe* species (Brandrud et al. 1989). Anthraquinonic pigments have been important in systematics of *Dermocybe* (Gill and Steglich 1987), and Liu et al. (1997) showed that the rDNA sequence data was partly consistent with the chemical results.

Red *Dermocybe* species usually are classified into the group *Sanguinei*, first introduced by Kühner and Romagnesi (1953) in *Cortinarius* subgenus *Dermocybe*. It was validly described as a section of *Dermocybe* subgenus *Dermocybe* by Moser (Moser and Horak 1975). He divided the section into five stirps: *Sanguinea*, *Semisanguinea*, *Cinnabarina*, *Anthracina* and *Atropurpurea*. The *Sanguinea* stirp was characterized by the presence of emodin. Høiland (1983) recognized section *Sanguinei* at subsection rank under section *Dermocybe* and treated *Dermocybe* as a subgenus of *Cortinarius*. He also transferred *C. anthracinus* and *C. cinnabarinus* to the subgenus *Telamonia*, a hypothesis later supported by the molecular phylogenetic analyses of Garnica et al. (2005) and Niskanen et al. (2011). Bidaud et al. (1994) considered *Sanguinei* again a section in the subgenus *Dermocybe* but divided it into two stirps, *Sanguineus* and *Phoeniceus*. Brandrud et al. (1989) did not recognize supraspecific taxa within *Dermocybe* and treated *Dermocybe* as a section of subgenus *Cortinarius*. The latest addition to the group *Sanguinei* was made in 1997 by Moreno et al. when they described the new European species *D. cistoadelpha*.

Classifications mentioned above are based on morphology and pigment chemistry. Liu et al.

(1997) is the only study also based on molecular data. Their results suggest that the group *Sanguinei* is polyphyletic and should be divided into two entities, clades/D. sanguinea and /D. semisanguinea. The members of the clade/D. sanguinea are closely related and could represent one or a few species, according to Liu et al. (1997). The clade includes three validly described taxa, *C. sanguineus*, *D. sanguinea* var. *vitiosa* and North American *D. sierraensis*. The clade/D. semisanguinea consists of species with red, yellowish and brown characteristics; they are *C. semisanguineus*, *C. phoeniceus*, *C. fervidus* and *C. malicorius*. Details are provided concerning the historical classification systems of the section *Sanguinei* by European authors, compared to those proposed by Liu et al. (1997) (SUPPLEMENTARY TABLE I).

The type species of the section *Sanguinei* is *Cortinarius sanguineus* (Wulfen : Fr.) Fr. and the neotype of *C. sanguineus* was designated by Høiland in 1983. European authors have introduced several varieties and species resembling *C. sanguineus*. The taxonomic status and characteristics of *Dermocybe sanguinea* var. *vitiosa* M.M. Moser (1976) and *C. puniceus* P.D. Orton (1958) were discussed by Bidaud et al. (1994), Høiland (1983, 2008), Høiland and Holst-Jensen (1998), Moser (1972, 1974, 1976) and Orton (1958), whereas *C. sanguineus* var. *aurantiovaginatus* Fillion & Moënne-Locc., *C. sanguineus* var. *santalinus* (Scop.) Bidaud, Moënne-Locc. & Reumaux, *C. cruentus* Bidaud & Reumaux, and *C. rubrosanguineus* Bidaud, Moënne-Locc. & Reumaux were presented in Bidaud et al. (1994).

The number of taxa in the *C. sanguineus* group and their taxonomic status varies greatly among authors (SUPPLEMENTARY TABLE I). This is a common phenomenon when a morphological species concept is used. For example the number of accepted taxa in section *Calochroi* in Europe is 60–170, according to different taxonomists (Frøslev et al. 2007), and in the section *Armillati* the number is 2–14 (Niskanen et al. 2011).

The introduction of DNA sequence characteristics in fungal taxonomy has been a significant improvement. The most widely used regions for studies at species rank are rDNA ITS1 and ITS2, which have proven useful for species delimitation in *Cortinarius* by for example Frøslev et al. (2007), Garnica et al. (2009), Kytövuori et al. (2005), Lindström et al. (2008), Niskanen et al. (2009, 2011), Ortega et al. (2008) and Suárez-Santiago et al. (2009). These regions also have been proposed as species-identifier sequences (barcodes) in *Cortinarius* (Frøslev et al. 2007, Ortega et al. 2008). It is already known however that ITS sequences are not sufficiently variable for differentiation of all *Cortinarius* species (Frøslev et al. 2007, Garnica et al. 2005, Niskanen et al. 2011, Peintner 2008). Because no comparative study based on morphology and molecular data including *C. sanguineus* and other completely red species exists we wanted to determine how many species resembling *C. sanguineus* exist in Europe and what their relationships are.

MATERIALS AND METHODS

Material.—We studied the herbarium specimens of *Cortinarius sanguineus* and *Dermocybe sanguinea* var. *vitiosa* from Finland (H, TUR, OULU) as well as specimens gathered by the authors from Fennoscandia and central Europe, a total of about 360 specimens. We also examined the type specimens and some reference specimens of other *Dermocybe* species, mentioned in *Molecular analyses* below.

Herbarium acronyms follow Thiers (continuously updated) and the vegetation zones follow Ahti et al. (1968) and Knudsen and Vesterholt (2008). For biogeographical provinces in Nordic countries see Knudsen and Vesterholt (2008); for the other countries political provinces are used. Collectors are abbreviated by the acronyms; initials TN, IK, KL and PK refer to the authors and Pirjo Kytövuori.

Molecular analyses.—Several collections of the studied species (n = 15, listed under each species) from different geographical areas and type material of the following, red, European *Sanguinei* taxa were sequenced: *Dermocybe sanguinea* var. *vitiosa*, *C. cruentus*, *C. puniceus*, *C. rubrosanguineus*, *C. sanguineus* and *C. sanguineus* var. *aurantiovaginatus*. Also the following Cortinarius Flora Photographica plate collections representing the European species of subsect. *Sanguinei* s.s. Høiland (1983) were included in the molecular studies: *Cortinarius fervidus*, *C. phoeniceus* (epitype), *C. sanguineus*, *C. semisanguineus* and *C. sommerfeltii* The other *Dermocybe* groups the plate collections of *C. croceus*, *C. cinnamomeus*, *C. malicorius* and *C. uliginosus* also were studied. In addition the type material of *D. cistoadelpha* ascribed to the group *Sanguinei* by Moreno et al. (1997) and type material of *C. mirandus* described in the serie *Sanguineus* by Bidaud et al. (1994) were included in the studies. The type material of *C. croceolimbatus*, a species also included in the serie *Sanguineus* by Bidaud et al. (1994), was not available. Among the *C. sanguineus* material studied, we found two red exsiccata with smaller spores than typical for *C. sanguineus*, M. & P. Heinonen 881-2004 (TUR) and M. Ohenoja 31 Aug 1972 (H), and the collections were included in the molecular studies. We also sequenced one red exsiccatum of *C. phoeniceus* (I.K 7 Oct 2004 [H]), and one typical (P. Kallio 13 Sep 1960 (TUR), although identified as *D. sanguinea* var. *vitiosa* by Høiland, also were sequenced. Altogether 34 sequences including ITS1, 5.8S and ITS2 regions were generated (SUPPLEMENTARY TABLE II), but from *C. mirandus* only ITS1 was succesfully amplified.

Total DNA was extracted from a few milligrams of dried material (a piece of lamella) with the NucleoSpin Plant kit (Macherey-Nagel). Primers ITS 1F and ITS 4 (Gardes and Bruns 1993, White et al. 1990) were used to amplify the ITS regions. The primer combinations ITS1F/ITS2 and ITS3/

ITS4 were used on problematic material (White et al. 1990). The same primer pairs were used in direct sequencing. PCR amplification and sequencing followed Niskanen et al. (2009). Sequences were assembled and edited with Sequencher 4.1 (Gene Codes Corp., Ann Arbor, Michigan).

Intragenomic polymorphisms were observed as mixed peaks in chromatographic data.

Base polymorphisms are marked with ambiguous IUB codes and length polymorphisms with N (further information provided upon request). The sequences were compared with the material in the public databases (GenBank: http://www.ncbi.nlm.nih.gov/ and UNITE: http://unite.ut.ee/) with BLAST queries.

A sequence of every species was compared with all other sequences using BLAST to estimate their genetic distances. These sequences and the sequences of the closest ones were aligned with the Muscle program (Edgar 2004) on the European Bioinformatics Institute server (http://www.ebi.ac.uk/Tools/muscle/index.html). The following differences were visibly counted from the alignments: (i) the observed number of variable sites showing how many sites contain infraspecific and/or infragenomic polymorphisms and (ii) the differences between the closest species as minimum evolutionary events including indels (multiple base indels treated as one change), transitions and transversions. Only differences shared by all specimens of the same species were counted. The results are presented under *ITS regions* under every species.

We chose to analyze all our generated sequences and those retrieved from the public databases. We also included published sequences of North American *C. sierraensis* and *C. idahoensis*. We chose *Dermocybe olivaceopicta* as outgroup based on Liu et al. (1997). We produced an alignment of 43 sequences for the phylogenetic analysis with Muscle under default settings and followed by manual adjustments in BioEdit (www.mbio.ncsu.edu/BioEdit/bioedit.html). The alignment is 638 nucleotides long (including gaps) and available in the TreeBASE under S11635 (http://www.treebase.org/treebase-web/home.html).

Bayesian inference (BI) was performed with the program Mr.Bayes 3.1.1 (Huelsenbeck and Ronquist 2003). We analyzed the entire dataset with the GTR model including a gamma shape parameter and estimating the proportion of invariable sites. Two independent runs with four chains in each were performed for 1 000 000 generations with sampling every 100th generation. All trees sampled before stationarity were discarded with a 25% safety margin (burn-in of 2500 trees, 250 000 generations). The trees were combined in a 50% majority rule consensus phylogram with posterior probabilities (PP). The analysis was run on computer clusters of the CSC, IT Centre for Science, Espoo, Finland.

Morphological studies.—Morphological descriptions are based on material collected by the authors and published descriptions of which we have seen the original material. Macroscopic characteristics were observed from fresh basidiomes. Some of the collections also were photographed in fresh condition. Names follow the Munsell (2009) soil color charts. For *C. puniceus* the macroscopic characteristics are based only on the original descriptions, but microscopic characteristics have been observed from the type collections.

We observed microscopic characteristics from dried material mounted in Melzer's reagent (MLZ) and compared them with observations made on dried material mounted in 5% KOH. Measurements were made with an ocular micrometer using 100× oil immersion lens. We measured 20 spores from one basidiocarp in each collection (specimens marked with an s in SUPPLEMENTARY TABLES III and IV and in specimens sequenced under *C. puniceus*), from the veil or top of the stipe. The length and width were measured for each spore, and their length/width ratios (Q value) were calculated. We excluded 5% of the extreme measurements from the final values. The pileipellis structure was studied from both radial freehand sections, and scalps from the pileus center or midway between the center and margin and the pileipellis elements were measured in the radial sections.

RESULTS

Molecular analyses.—The 50% majority rule phylogram resulting from the BI analysis is provided (FIG. 1) with posterior probabilities indicated above the branches. Only two infrasubgeneric clades were well supported (1.00 PP): (i) *C. sanguineus*, *C. puniceus* and *D. sierraensis* and (ii) *C. cinnamomeus*, *C. croceus* and *C. uliginosus*. The first includes the type species of sect. *Sanguinei*, *C. sanguineus*, and the second the type species of sect. *Dermocybe*, *C. cinnamomeus*. The placement of *C. malicorius* as a separate clade was somewhat supported (0.78 PP). Other relationships were not resolved.

The red European *Dermocybe* taxa belong to three species, *C. sanguineus* (incl. *C. sanguineus* var. *aurantiovaginatus*), *C. puniceus* (incl. *C. cruentus* and *C. rubrosanguineus*) and *C. vitiosus*, and the clades were well supported (0.98–1.00 PP). The species are presented in TAXONOMY below. *Cortinarius sanguineus* and *C. puniceus* have intragenomic polymorphisms, but the sequences of *C. vitiosus* all were the same. All the species also differ by at least eight evolutionary events from the closest species. Thus the intraspecific variation is much less than the interspecific variation. (For information see *ITS regions* for each species below.)

Cortinarius fervidus and *C. phoeniceus* also can have red basidiomes. The small spored specimens under the name *C. sanguineus* (M. & P. Heinonen 881-2004 [TUR] and M. Ohenoja 31 Aug 1972 [H]) had identical sequences with the Cortinarius Flora Photographica plate collection of *C. fervidus*. The red collection of *C. phoeniceus* (I.K 7 Oct 2004 [H]) was identical to one of the non-red specimens of the species, P. Kallio 13 Sep 1960 (TUR) but differed

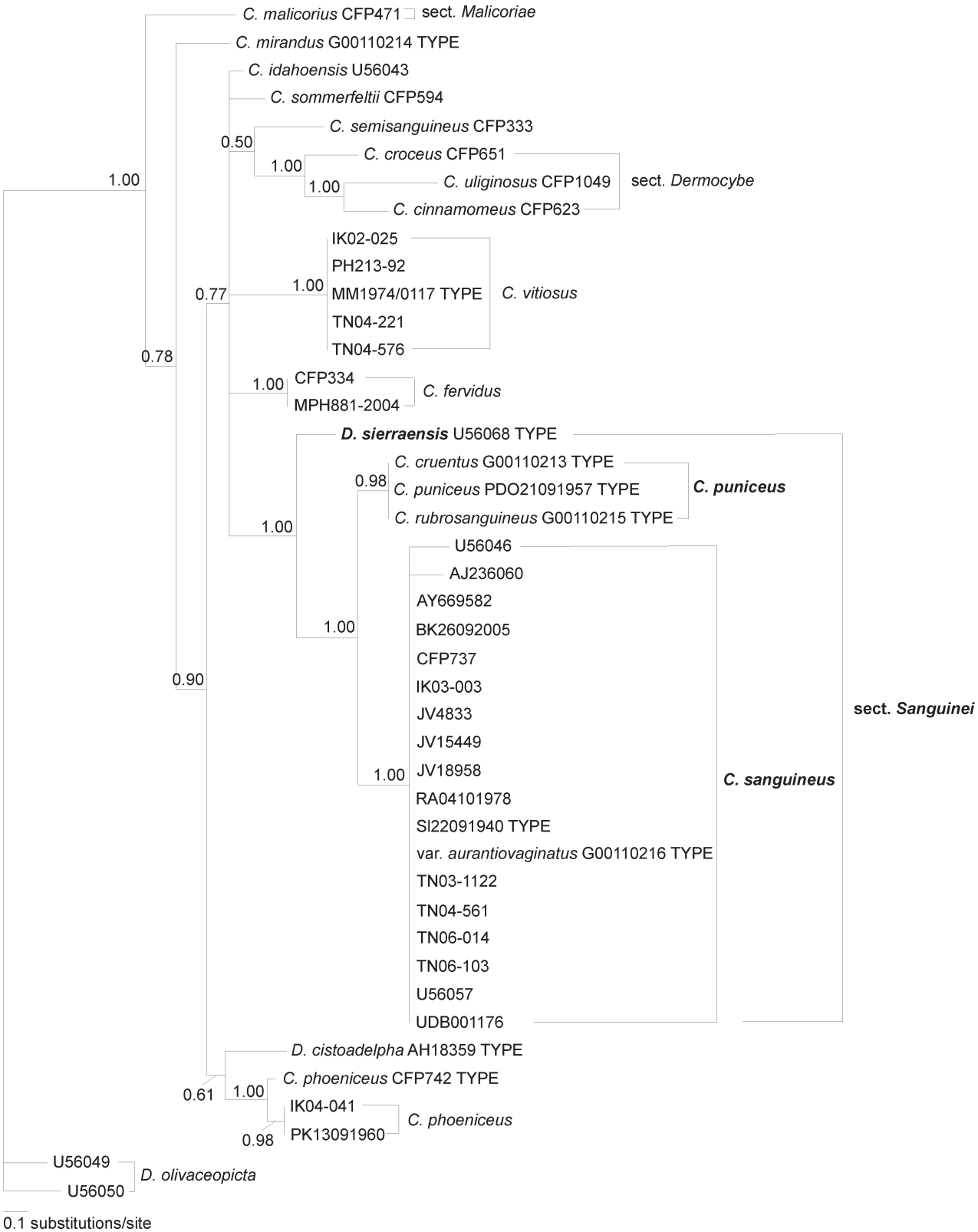

FIG. 1. The Bayesian 50% majority rule consensus tree inferred from ITS regions. PP > 0.50 are indicated above branches.

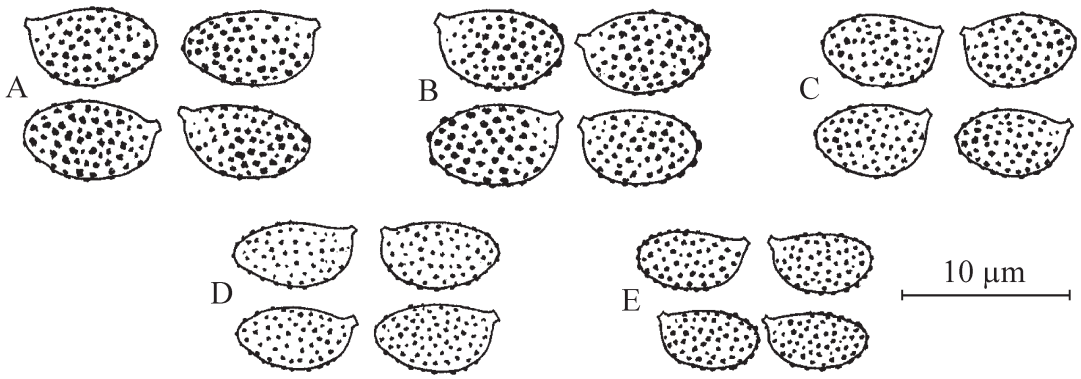

FIG. 2. Spores of (A) *Cortinarius puniceus*, (B) C. *sanguineus*, (C) *C. fervidus*, (D) *C. phoeniceus*, and (E) *C. vitiosus*, in Melzer's reagent. Drawings by T. Niskanen.

from the other, CFP742 (S), by two evolutionary changes.

A comparison of all GenBank and UNITE sequences with sequences generated in this study revealed only six belonging to the species studied here. One of them is the type sequence of *Dermocybe sanguinea* var. *vitiosa*, which includes only the ITS1 region and differs by five evolutionary changes from our material of the same taxon. The other five cluster with our *C. sanguineus* sequences. Three of them undoubtedly represented *C. sanguineus* (AY669582 Germany, U56057 Austria, UDB001176 Sweden). The other two deviate somewhat. Of these AJ236060 (Norway) had four unique bases compared to the neotype of *C. sanguineus*, but all the differences occurred in the beginning of the ITS1 region and so are presumably errors in the sequence. The other, U56046 (Canada, Ontario), differed by six evolutionary changes from the type and was deposited in GenBank under the name *Dermocybe mallochii*.

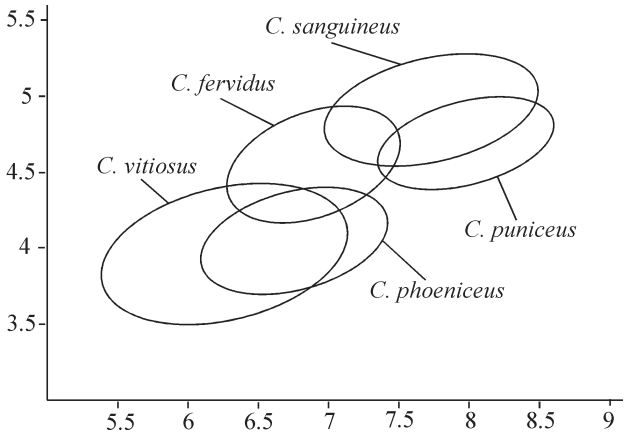

FIG. 3. Spore size of *Cortinarius fervidus*, *C. phoeniceus*, *C. puniceus*, *C. sanguineus* and *C. vitiosus*. The lines are drawn on the basis of scatter diagrams and contain 95% of the spore measurements of each species. X axis: length of spores. Y axis: width of spores.

TAXONOMY

Cortinarius sanguineus (Wulfen : Fr.) Fr., Epicr. Syst. mycol.:288 (1838). FIGS. 2B, 3, 4A, 5

Basionym: *Agaricus sanguineus* Wulfen in Jacquin, Miscell. austriac. 2:107 (1781): sanctioned in Fr., Syst. mycol. 1:229 (1821).

Type. SWEDEN. SMÅLAND: Femsjö, 22 Sep 1940, *S. Lundell* (UPS, NEOTYPE, designated by Høiland 1983). GenBank JN114099.

Cortinarius sanguineus var. *aurantiovaginatus* Fillion & Moënne-Locc. in Bidaud et al., Atlas des Cortinaires 6:192 (1994).

Type. FRANCE. HTE-SAVOIE: Plateau des Glières, on an old stump of *Picea abies*, 1500 m., 3 Aug 1993, *P. Moënne-Loccoz* 3475, G00110216 (G, HOLOTYPE). GenBank JN114100.

Illustrations. Bidaud et al. (1994: pl. 129), Brandrud et al. (1989: pl. A57).

FIG. 4. Photo of (A) *Cortinarius sanguineus* 04-561 (H) and (B) *C. vitiosus* 04-576 (H). Photograph by K. Liimatainen.

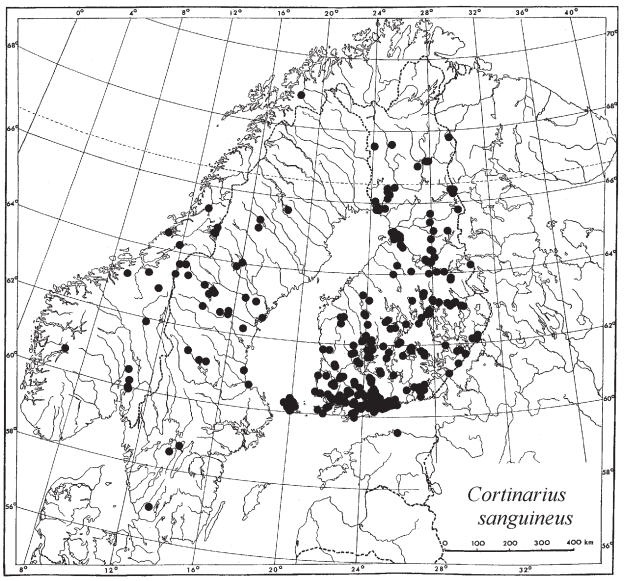

FIG. 5. Distribution of *Cortinarius sanguineus* in northern Europe according to the material examined.

Pileus 2–5 cm, hemispherical, later low convex to almost plane, sometimes slightly umbonate; surface fibrillose-tomentose, often with fibrillose scales; dusky red (7.5R 3/3, 10R 3/3) to red (7.5R 4/6, 10R 4/6), darker at the center; not to slightly hygrophanous. Lamellae medium spaced, emarginate, moderately thick, moderately broad or broad, dusky red (10R 3/4). Stipe 4–10 × 0.3–0.8 cm, cylindrical or slightly clavate, red (7.5R 4/6, 10R 4/6) with some orange tints, somewhat paler than the pileus. Cortina dark red, ochraceous or golden brown. Universal veil dark red, fibrillose. Basal mycelium reddish yellow (5YR 6/6–6/8), sometimes with a pale red tint. Context dark red (7.5 3/6) to red (7.5 4/6) in whole basidiome with orange tints toward the base of the stem. Odor in lamellae cedar -like, especially when slightly dried. Exsiccata pileus dusky red (7.5R 3/4, 10R 3/3) to dark reddish brown (2.5YR 3/3–3/4), stipe weak red (10R 4/3–4/4) to dusky red (10R 3/3–3/4) with reddish yellow (5YR 6/6–6/8, 7.5YR 6/8) mycelium.

Spores in KOH 7.0–8.3(–8.5) × 4.5–5.2 μm, av. = 7.4–7.9 × 4.7–5.1 μm, Q = 1.45–1.7, Qav. = 1.53–1.58 (140 spores, seven collections), in MLZ (6.6–)7.0–8.2(–8.8) × 4.5–5.2(–5.4) μm, av. = 7.3–7.9 × 4.7–5.0 μm, Q = 1.41–1.67, Qav. = 1.47–1.61 (400 spores, 20 collections; FIGS. 2B, 3), amygdaloid to ellipsoid, moderately verrucose, weakly dextrinoid. Lamellar trama hyphae not encrusted, with aniline red pigment and granules in KOH. Basidia four-spored, 22.5–29.5 × 6.0–8.0 μm, with granulose content, in KOH hyaline to aniline red, in MLZ hyaline to pale yellow. Pileipellis a cutis with some ascending terminal elements. Scalp preparation aniline red in KOH. Uppermost hyphae (about 4–6 layers of hyphae) 5–15(–20) μm wide, hyaline to pinkish red or grayish pink, not or finely encrusted. Lower hyphae 5–15 μm wide, often aniline red with aniline red granules, not encrusted. Hypoderm not differentiated. Clamp connections present.

ITS regions (including 5.8S region). 603 bases long (a total of 13 sequences, including sequences from two type specimens). The neotype differs from *C. sanguineus* var. *aurantiovaginatus* sequence by two intragenomic base polymorphisms. Together the other 11 sequences have four intragenomic base polymorphisms. The difference with *C. puniceus* is at least eight evolutionary changes.

Ecology and distribution. In mesic to damp mossy coniferous forests with *Picea abies*. Prefers nutrient-rich ground but also is found commonly in swampy depressions among *Sphagnum girgensohnii* and blueberry spruce forests; common in the hemiboreal and boreal zone. The northern distribution of the species follows that of *Picea abies*, however it is rarer farther north, and in Lapland, where it prefers herb-rich forests, it is rare. Basidiocarps occur from mid-July to late October, but the peak of the fruiting season is often from mid-August to late September; known in northern Europe (FIG. 5) and montane areas of central and southern Europe.

Differential diagnosis. Typical for *C. sanguineus* are dusky red to red, fibrillose-tomentose to scaly pileus, reddish yellow mycelium, completely dark red to red context, cedar-like odor, not or only slightly encrusted hyphae in lamellae and pileipellis, and mesic to damp, often somewhat nutrient-rich habitat shared with *Picea*. The sister species, *C. puniceus*, is stronger purplish red especially in the stipe context, narrower spores (FIG. 3), spot-like encrusted pileipellis hyphae and shared habitat with deciduous trees. *Cortinarius vitiosus* has fairly thin, often zonate, dark red to dark reddish brown pileus, pale red mycelium, paler context in the core, iodine-like odor, smaller spores (5.6–6.8 × 3.5–4.2 μm) and encrusted lamellar trama and pileipellis hyphae. The pileipellis is orange-red to somewhat aniline red in KOH compared to the distinctly aniline red in *C. sanguineus*. *Cortinarius vitiosus* often grows in somewhat drier and more acidic soils than *C. sanguineus*, although in mesic coniferous forests they can grow side by side.

The basidiomes of *C. fervidus* are sometimes red (e.g. M. & P. Heinonen 881-2004 and M. Ohenoja 31 Aug 1972), and the species can be confused with *C. sanguineus*, although the exsiccata is slightly more brownish (pileus dark reddish brown [2.5YR 3/4, 5YR 3/3–3/4] to reddish brown [5YR 4/4]) and especially the stipe is more yellowish brown (dark brown [7.5YR 3/4], brown [7.5YR 4/4] to yellowish red [5YR 4/6])

compared to the weak red to dusky red stipe in *C. sanguineus*. The spores of *C. fervidus* are also somewhat smaller, 6.5–7.5 × 4.0–4.7(–5.0) µm (FIG. 2C) and less dextrinoid, and the lamellar trama hyphae are orange-red in KOH. The pileipellis is orange-red with bluish purple granules in KOH and the uppermost hyphae are zebra-striped encrusted.

Cortinarius sanguineus var. *aurantiovaginatus* Fillion & Moënne-Locc. differs from *C. sanguineus* var. *sanguineus* by its orange mycelium and distinctly hygrophanous pileus, which becomes brownish when dry. We studied the type, and morphologically it did not differ from our *C. sanguineus* material. Because the ITS sequences also were similar to those of *C. sanguineus* we concluded that *C. sanguineus* var. *aurantiovaginatus* should be considered a synonym of *C. sanguineus*.

Bidaud et al. (1994) treated *Agaricus santalinus* Scop. as a variety, *C. sanguineus* var. *santalinus* (Scop.) Bidaud, Moënne-Locc. & Reumaux. Because no type specimen exists and the original description is vague the true identity of *A. santalinus* remains unclear. However it reportedly occurs in coniferous forests and Fries (1838) treated it as a synonym of *C. sanguineus* so it is possibly conspecific with the latter.

Specimens sequenced: (for the complete list of specimens examined see SUPPLEMENTARY TABLE III, a total of 323 collections): NORWAY. TROMS: Bardu, Setermoen, 5 Aug 2006, *K.L. & T.N. 06-014* (H). GenB. JN114106. SWEDEN. SMÅLAND: F emsjö, 22 Sep 1940, *S. Lundell* (UPS, NEOTYPE), GenBank. JN114099. VÄSTERGÖTLAND: Säter, Ryd-Ronna reservatet, 5 Sep 2003, leg. *H. Croneborg* (*T.N. 03-1122*, H), GenBank JN114107. ÅNGERMANLAND: Häggdånger, Sjö, 9 Sep 1988, *TE Brandrud* et al. *CFP737* (S), GenBank JN114101. FINLAND. VARSINAIS-SUOMI: Kustavi, Kaurissalo, 4 Oct 1978, *Alava* et al. (TUR), GenBank JN114109. Suomusjärvi, Lahnajärvi, 26 Sep 2005, *B. Kuhlberg* (H), GenBank JN114111. SATAKUNTA: Yläne, Vaskijärvi Strict Nature Reserve, 27 Jul 2002, *J. Vauras 18958* (TUR), GenBank JN114103. ETELÄ-HÄME: Keuruu, Haikka, 12 Sep 1999, *J. Vauras 15449* (TURA), GenBank JN114104. POHJOIS-KARJALA: Kitee, Potoskavaara, 12 Sep 2006, *S. Laine* (*T.N. 06-103*, H), GenBank JN114105. PERÄ-POHJANMAA: Rovaniemi, Pisa, 18 Aug 1990, *J. Vauras 4833* (TURA), GenBank JN114110. Tornio, Korkeamaa, Runteli, 30 Aug 2004, *K.L. & T.N. 04-561* (H), GenBank JN114102. FRANCE. HTE-SAVOIE: Plateau des Glières, 3 Aug 1993, *P. Moënne-Loccoz 3475*, G00110216 (G, HOLOTYPE of *C. sanguineus* var. *aurantiovaginatus*), GenBank JN114100. SLOVAKIA. TATRY MOUNTAINS: Vysoké and Západné, Podbanské, 2 Oct 2003, *I.K. 03-003* (H), GenBank JN114108.

Cortinarius puniceus P.D. Orton, Naturalist, Leeds (Suppl.):148 (1958). FIGS. 2A, 3

Type: GREAT BRITAIN. YORKSHIRE: Clapham, Clapham Woods, 21 Sep 1957, P.D. Orton (K, HOLOTYPE). GenBank JN114093.

Cortinarius cruentus Bidaud & Reumaux in Bidaud et al., Atlas des Cortinaires 6:189 (1994).

Type. FRANCE. ILE-DE-FRANCE: Fôret de Marly, under deciduous trees, 200 m, 10 Nov 1993, *Garbirian*, P. Moënne-Loccoz 3615, G00110213 (G, HOLOTYPE). GenBank JN114092

Cortinarius rubrosanguineus Bidaud, Moënne-Locc. & Reumaux, Atlas des Cortinaires 6:192 (1994).

Type. FRANCE. SAÔNE-ET-LOIRE: near Charolles, under *Picea abies* and deciduous trees in the middle of a pasture, on acidic clay soil, 11 Nov 1993, *Deny*, P. Moënne-Loccoz 3618, G00110215 (G, HOLOTYPE). GenBank JN114091

Illustrations. Bidaud et al. (1994: pl. 128)

Pileus 1.5–5 cm, convex, soon low convex to almost plane, sometimes slightly umbonate; surface fibrillose-tomentose or radially innately fibrillose, somewhat scaly toward the margin; purplish blood red to chestnut brown, initially carmine rose near the margin. Lamellae medium spaced, adnate or adnexed, first intensively purplish blood red or purplish chestnut brown, later brown; edge concolorous to bright blood red. Stipe 3.8–7.0 × 0.2–0.9 cm, cylindrical or slightly clavate, concolorous with pileus or somewhat paler, purplish blood red fibrillose; apex with an ochraceous tint. Cortina ochraceous. Basal mycelium rose ochraceous to pale purplish. Context purplish blood red, purplish rose when dry. Odor indistinct or of cedar. Exsiccata pileus dusky red (7.5R 3/3–3/4, 10R 3/3) to dark reddish brown (2.5YR 3/4), in some basidiomes grading dark reddish brown (2.5YR 3/4) toward the margin, stipe dusky red (7.5R 3/3) with weak red (7.5R 5/4) to pale red (10R 6/4) to reddish yellow (5YR 6/8) mycelium.

Spores in KOH 7.6–8.6 × 4.6–5.1 µm, av. = 7.9–8.1 × 4.7–4.8 µm, Q = 1.6–1.8, Qav. = 1.66–1.71 (60 spores, three collections), in MLZ 7.4–8.3(–8.5) × 4.4–4.7(–4.9) µm, av. = 7.7–8.0 × 4.6 µm, Q = 1.57–1.82, Qav. = 1.67–1.74 (60 spores, three collections; FIGS. 2A, 3), amygdaloid to somewhat ellipsoid, moderately verrucose, weakly dextrinoid. Lamellar trama hyphae smooth, with aniline red pigment and granules in KOH. Basidia four-spored, 21–30.5 × 5.5–7.5 µm, with granulose content, in KOH hyaline to aniline red, in MLZ hyaline to pale yellow. Pileipellis a cutis with some ascending to perpendicular hyphae. Scalp preparation aniline red in KOH. Uppermost hyphae (about 2–5 layers of hyphae) 3–15 µm wide, hyaline, not or finely encrusted. Lower hyphae 5–15 µm wide, aniline red with aniline red granules, spot-like encrusted, encrustations in KOH purplish brown, in MLZ yellowish brown. Hypoderm not differentiated. Clamp connections present.

ITS regions (including 5.8S region). 602–603 bases long (a total of three sequences, all from type

specimens). *Cortinarius puniceus* has five intragenomic base polymorphisms sites and one intragenomic length polymorphism site. The type material sequence of *C. puniceus* differs from the other two in four sites. Public databases do not contain sequences of this species. The difference with *C. sanguineus* is at least eight evolutionary changes.

Ecology and distribution. In deciduous and mixed forests, with *Fagus* and *Quercus* and possibly other tree species. Basidiocarps occur Sep–Nov. Known from the United Kingdom and France but also likely occurring in suitable habitats in other parts of Europe.

Differential diagnosis. *Cortinarius puniceus* resembles *C. sanguineus* but is stronger purplish red especially in the context of the stipe, rose ochraceous to pale purplish basal mycelium, narrower spores, spot-like encrusted pileipellis hyphae and shared habitat with deciduous trees. Sometimes the pileus can have brownish tints (Orton 1958, Moser 1972) unlike in *C. sanguineus*. The color of the cortina is also different, ochraceous or golden brown in *C. puniceus* and dark red in *C. sanguineus*, according to Orton (1958), but based on our and Høiland's (1983) observations the cortina of *C. sanguineus* is also often ochraceous.

Two species described in Bidaud et al. (1994), *C. cruentus* Bidaud & Reumaux and *C. rubrosanguineus* Bidaud, Moënne-Locc. & Reumaux, formed a monophyletic group with *C. puniceus* and had similar ITS sequences. Typical for the former is that it is large, has rose stipe base and a cespitose habit, and for the latter is that it has conspicuously narrow spores and rose base of the stipe, according to Bidaud et al. (1994). Our spore measurements from the type material of *C. cruentus* and *C. rubrosanguineus* were similar to the ones from the type material of *C. puniceus* (7.6–8.6 × 4.6–5.1 µm) but differed from those reported in the original descriptions of the former two; from *C. cruentus* our measurements were 7.6–8.5 × 4.7–5.1 µm, in the Latin description (6.5–)7.0–10.5 (–11.0) × 4.5–5.5 µm and from *C. rubrosanguineus* 7.6–8.6 × 4.6–4.9 µm compared to the reported (6.5–)7.0–10.0(–10.5) × 4.0–4.5 µm. *C. cruentus* and *C. rubrosanguineus* do not differ from *C. puniceus* and should be considered synonyms, according to our studies. The holotype collection of *C. cruentus* is from a deciduous forest and one of *C. rubrosanguineus* from a mixed forest of *Picea abies* and deciduous trees. The original descriptions of both species also include references to specimens collected solely under coniferous trees. Because *C. puniceus* is known to grow with deciduous trees the original descriptions also may include characteristics of *C. sanguineus*.

Specimens sequenced: GREAT BRITAIN. YORKSHIRE: Clapham, Clapham Woods, 21 Sep 1957, P.D. Orton (s) (K, HOLOTYPE). FRANCE. ILE-DE-FRANCE: Fôret de Marly, under deciduous trees, 200 m, 10 Nov 1993, *Garbirian*, Herbier P. Moënne-Loccoz 3615, G00110213 (s) (G, HOLOTYPE of *C. cruentus*). SAÔNE-ET-LOIRE: near Charolles, under *Picea abies* and deciduous trees in the middle of a pasture, on acidic clay soil, 11 Nov 1993, *Deny*, P. Moënne-Loccoz 3618, G00110215 (s) (G, HOLOTYPE of *C. rubrosanguineus*).

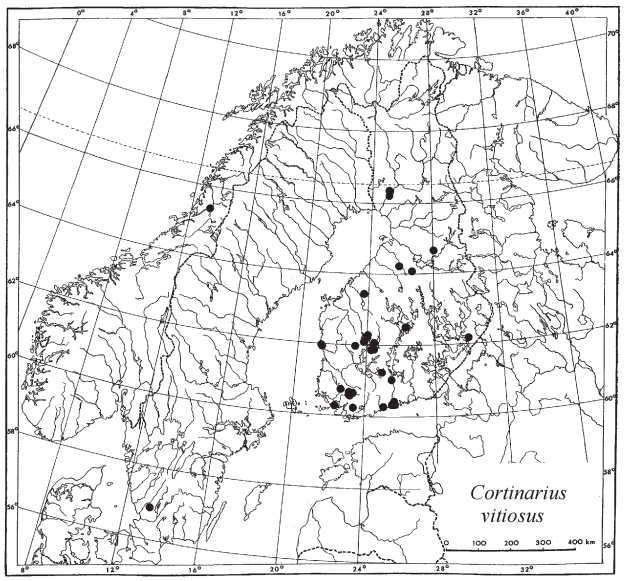

FIG. 6. Distribution of *Cortinarius vitiosus* in northern Europe according to the material examined.

Cortinarius vitiosus (M.M. Moser) Niskanen, Kytöv., Liimat. & S. Laine, comb. nov. FIGS. 2E, 3, 4B, 6 MycoBank MB560217

Basionym: Dermocybe sanguinea var. *vitiosa* M.M. Moser, Schweiz. Z. Pilzk. 54:149 (1976).

Type. SWEDEN. SMÅLAND: Femsjö, 16 Aug 1974, *M. Moser 1974/0117* (IB, HOLOTYPE). GenBank JN114098.

Pileus 2–5 cm, hemispherical, soon low convex to almost plane, often slightly umbonate; surface finely fibrillose-tomentose, often with fine fibrillose scales; dark reddish brown (2.5YR 3/4), dark red (10R 3/6, 2.5YR 3/6) to red (2.5YR4/6); somewhat hygrophanous, sometimes with hygrophanous zones. Lamellae medium spaced, emarginated, moderately thick, moderately broad or broad, dark red (10R 3/6). Stipe 4–10 cm × 0.3–0.8 cm, cylindrical or slightly clavate, red (2.5YR 4/6–5/6), often paler and silky at the apex. Universal veil dark red, fibrillose. Basal mycelium pale red (10R 6/4) to light red (2.5YR 7/6), sometimes reddish yellow (5 YR 7/6). Context surface red (2.5YR 4/6), core pinkish white (2.5YR 8/2) to almost white. Odor in lamellae weakly iodine-like, especially when slightly dried. Exsiccata pileus dark reddish brown (5YR 3/3–2.5/2) to dark brown

(7.5YR 3/2–3/3), in some basidiomes paler (7.5YR 3/4) toward the margin, sometimes the entire pileus nearly black (5YR 2.5/1), stipe weak red (10R 4/3–4/4) to reddish brown (2.5YR 4/3) with weak red (10R 5/4), red (2.5YR 5/6) to reddish yellow (5YR 6/6) mycelium.

Spores in KOH 5.6–6.8 × 3.5–4.2 µm, av. = 6.2–6.6 × 3.8–4.0 µm, Q = 1.45–1.8, Qav. = 1.54–1.73 (120 spores, six collections), in MLZ (5.4–)5.6–6.8(–7.1) × 3.5–4.2(–4.4) µm, av. = 5.9–6.5 × 3.7–4.2 µm, Q = 1.43–1.78, Qav. = 1.45–1.69 (400 spores, 20 collections; FIGS. 2E, 3), amygdaloid to ellipsoid, moderately verrucose, not dextrinoid to weakly dextrinoid. Lamellar trama hyphae spot-like and finely encrusted, in KOH with aniline red pigment and granules. Basidia four-spored, 19.5–26.5 × 4.5–6.0 µm, with granulose content, in KOH hyaline to aniline red, in MLZ hyaline to pale yellow. Pileipellis a cutis, with some ascending elements. Scalp preparation orange-red to brownish red with aniline red tint in KOH, rarely with bluish granules. Uppermost hyphae (about 4–6 layers) 5–15 µm wide, pale pinkish red to grayish pink with a faint aniline red tint, sometimes with aniline red granules, not or finely to zebra-striped encrusted. Lower hyphae 5–15 µm wide, pale yellowish brown to pale orange red, but sometimes aniline red, spot-like, zebra-striped and finely encrusted, spot-like encrustations in KOH purplish brown, in MLZ yellowish brown. Hypoderm not differentiated. Clamp connections present.

ITS regions (including 5.8S region). 604 bases long (a total of five sequences, including the sequence from the type specimen). All sequences are identical without any polymorphisms. Liu et al. 1997 sequenced the type material of *Dermocybe sanguinea* var. *vitiosa* (U56061, only ITS1 region). The sequence differs by five bases from the one we obtained from the type material. No other sequences of *C. vitiosus* exist in the public databases. The difference compared to *D. idahoensis* is at least 12 evolutionary changes, to *C. fervidus*, *C. phoeniceus*, *C. semisanguineus* and *C. sommerfeltii* 15 to 20 evolutionary changes, and to *C. sanguineus* more than 20.

Ecology and distribution. In mesic to dryish, mossy coniferous forests with *Picea abies*; occasional in the hemiboreal and boreal zone. The northern distribution of the species closely follows that of *Picea abies*; fruits from mid-July to late October peaking in mid-August to late September; known from Norway, Sweden and Finland (FIG. 6).

Differential diagnosis. In the field *C. vitiosus* can be identified by the fairly thin, often zonate, dark red to dark reddish brown pileus, pale red to light red mycelium, pinkish white to almost white context in the core, iodine-like odor, and habitat with coniferous trees. Good microscopic characteristics are the small spores, encrusted lamellar trama and pileipellis hyphae and in KOH orange-red to somewhat aniline red pileipellis. *Cortinarius sanguineus* differs macroscopically from *C. vitiosus* by dusky red to red pileus, reddish yellow mycelium, dusky red to red flesh and ceda -like odor. Microscopically it differs by having larger spores (7.0–8.3 × 4.5–5.2 µm), lacking or with only slightly encrusted lamellar trama and pileipellis hyphae, and the pileipellis distinctly aniline red in KOH. *Cortinarius sanguineus* also often occurs in damper and richer soils than *C. vitiosus*.

Cortinarius phoeniceus microscopically resembles *C. vitiosus*, but the spores are slightly larger (6.3–7.3 × 3.7–4.3 µm, FIG. 2D), amygdaloid and less verrucose, the lamellar trama hyphae are not or finely encrusted, and the pileipellis in KOH is orange-red, in places bluish purple, and with bluish purple granules. In the field *C. phoeniceus* is easily distinguished from *C. vitiosus*; it is more robust, the pileus is red-brown and the stipe is pale yellowish with blood red veil girdles. According to Høiland (1983) however a form with dark red and smaller basidiomes also occurs. One of the specimens we studied (Finland, Varsinais-Suomi, I.K. 7 Oct 2004) was almost completely red with only some yellowish brown tints on stipe (pileus dark reddish brown 2.5YR 3/4) to reddish brown (2.5YR 4/4), stipe reddish brown (2.5YR 4/4) but similar in size to normal *C. phoeniceus*. It was otherwise microscopically similar to the Cortinarius Flora Photographica collection (CFP742), except that it had fewer bluish purple granules in the pileipellis. The latter can be treated as intraspecific variation, and we included the red specimen in *C. phoeniceus*.

According to Høiland (1983), *C. sanguineus* and *D. sanguinea* var. *vitiosa* are different species, but he suggested that *D. sanguinea* var. *vitiosa* is a synonym of *C. phoeniceus* because their microscopical and chemical characteristics are almost identical. This may be due at least partly to misidentification because for example *C. phoeniceus* P. Kallio 13 Sep 1960 (TUR) was identified as *D. sanguinea* var. *vitiosa* by Høiland. Høiland (2008) presents *D. sanguinea* var. *vitiosa* again as a variety of *C. sanguineus* (invalid combination). *Dermocybe sanguinea* var. *vitiosa* is a species in its own right, separate from *C. sanguineus* and *C. phoeniceus*, based on our study.

Specimens sequenced (for the complete list of specimens examined see SUPPLEMENTARY TABLE IV, a total of 41 collections): SWEDEN. SMÅLAND: Femsjö, 16 Aug 1974, *M. Moser 1974/0117* (IB, HOLOTYPE), GenBank JN114098. FINLAND. VARSINAIS-SUOMI: Koski, Kattelus, 10 Sep 1992, *P. Heinonen 213-92* (TUR), GenBank JN114094. ETELÄ-HÄME: Ruovesi, Susimäki, 24 Aug 2004, *Ohenoja* (*T.N. 04-221*, H), GenBank JN114095. KAINUU: Puolanka, Paljakka, 15 Aug 2002, *I.K. 02-025* (H), GenBank

JN114097. PERÄ-POHJANMAA: Rovaniemi, Pisavaara, 31 Aug 2004, *K.L. & T.N. 04-576* (H), GenB. JN114096.

KEY TO RED SPECIES OF SUBGENUS *DERMOCYBE* IN EUROPE

The exsiccata of *C. bolaris* (sect. *Anomali*) can be confused with those of red species of subgenus *Dermocybe*, but the former has subglobose spores.

1. Spores > 4.5 µm wide 2
1′. Spores < 4.5 µm wide 4
    2. Lamellar trama hyphae and pileipellis orange-red in KOH . . . . . *C. fervidus*
    2′. Lamellar trama hyphae and pileipellis aniline red in KOH 3
3. With conifers in the hemiboreal and boreal zones and in montane areas; spores relatively broad, Q on average < 1.63; pileipellis hyphae not encrusted . . . . . 1. *C. sanguineus*
3′. With deciduous trees in the temperate zone; spores relatively narrow, Q on average > 1.63; pileipellis hyphae with spot-like encrustations (best seen with 40× magnification) . . . . . 2. *C. puniceus*
    4. Lamellar trama hyphae orange-red in KOH; spores on average > 4.3 µm wide . *C. fervidus*
    4′. Lamellar trama hyphae ± aniline red in KOH; spores on average < 4.3 µm wide 5
5. Lamellar trama hyphae with spot-like encrustations; spores amygdaloid to ellipsoid, moderately verrucose . . . . . 3. *C. vitiosus*
5′. Lamellar trama hyphae not or only finely encrusted; spores amygdaloid, finely verrucose . . . . . *C. phoeniceus*

DISCUSSION

Subgenus Dermocybe.—Recent molecular phylogenetic studies indicate that *Dermocybe* is a monophyletic group included in the genus *Cortinarius* (Liu et al. 1997, Høiland and Holst-Jensen 2000, Peintner et al. 2004, Garnica et al. 2005). Therefore we recognize *Dermocybe* as a subgenus.

Liu et al. (1997) suggested that the historical groups within *Dermocybe* are polyphyletic. They proposed dividing *Dermocybe* into three entities: (i) sect. *Dermocybe*, (ii) clade/D. sanguinea and (iii) clade/D. semisanguinea including sect. *Malicoriae*, although their analysis did not support the third group. The first two groups, the /D. sanguinea clade, here named section *Sanguinei*, and sect. *Dermocybe*, also were supported in our analysis (both with 1.00 PP). The species included in the clade/D. semisanguinea however did not form a uniform group. In addition *C. malicorius* formed a separate clade, although with low support (0.78 PP). The classification of the subgenus *Dermocybe* was only partly solved by us and Liu et al. (1997). Further studies including more species and other DNA regions such as RPB1 and RPB2, shown to be useful in *Cortinarius* taxonomy by Frøslev et al. (2005), are needed.

Section Sanguinei.—Section *Sanguinei* is here limited to three species, *C. sanguineus*, *C. puniceus* and *D. sierraensis*, but studies from other geographical areas most likely will reveal additional representatives. Red basidiomes and pigmentation with the emodin series in addition to the dermorubin and dermocybin series are typical (Høiland 1983, Keller and Ammirati 1983).

Cortinarius sanguineus and *C. puniceus* differ by basidiome color and ecology, as suggested by Orton (1958) and Moser (1972, 1974). Some differences in microscopical characteristics also exist. The pigment composition of the two species is similar (Høiland 1983).

Cortinarius puniceus has been treated as a separate species, for example by Bidaud et al. (1994), Moser (1974, 1978) and Orton (1958), but Brandrud et al. (1989) and Høiland (1983) considered it a synonym of *C. sanguineus*. Our study shows that *C. sanguineus* and *C. puniceus* are distinct based on molecular and morphological data and should be regarded as separate species.

Other red Dermocybe *species*.—The neighbor joining tree constructed by Liu et al. (1997) suggested the inclusion of *D. sanguinea* var. *vitiosa* in the section *Sanguinei*, but their analysis included only the ITS1 region. The sequence also differed by five bases from ours, and because all five of our sequences are identical we think that the sequence differences reported by Liu et al. (1997) are errors presumably resulting from higher error rates in earlier polymerases. Our molecular phylogenetic analysis, based on ITS1 and ITS2 regions, showed that *D. sanguinea* var. *vitiosa* is not a sister taxon of *C. sanguineus*, might not even belong to sect. *Sanguinei* and should be regarded as a species in its own right, *C. vitiosus*.

Compared to the species of section *Sanguinei*, *C. vitiosus* differs both in macroscopic and microscopic characteristics. It lacks yellow pigments, emodin and emodinglycosids (Moser 1976, Høiland 1983). The ecology of *C. vitiosus* is reportedly similar to *C. sanguineus* (Høiland 2008), but according to our study it is slightly different. *Cortinarius vitiosus* is known only from Fennoscandia and considered occasional.

Cortinarius fervidus and *C. phoeniceus* typically have reddish brown pilei and yellowish stipes, but the exsiccata sometimes can be completely red and difficult to distuinguish from *C. sanguineus* or *C. vitiosus*. We found two red collections among the studied *C. sanguineus* material, M. & P. Heinonen

881-2004 (TUR) and M. Ohenoja 31 Aug 1972 (H), which based on ITS sequences are *C. fervidus*. The micromorphology was *C. fervidus*-like, except the pileipellis hyphae were less encrusted and the spores were somewhat narrower (4.2–4.6 µm wide, Q = 1.55) than in typical *C. fervidus* (4.4–5.1 µm wide, Q = 1.50).

Høiland (1983) discovered that based on pigment chemistry, *C. fervidus* can be divided in two groups. One group had flavomannin-6,6′-dimetylether and the other did not. The pigment composition of the latter is similar to that of *C. sanguineus*, although the amounts of pigments differ. The chemical variants do not have significant morphological or ecological differences, according to Høiland (1983). The collection M. Ohenoja 31 Aug 1972 (H) however was identified as *C. sanguineus* by Høiland based on pigment chemistry. The small morphological and pigment chemistry differences between the typical and red specimens of *C. fervidus* raise the question of whether these should be regarded as two different taxa. The ITS sequences were identical, but the studies by Frøslev et al. (2007), Garnica et al. (2005), Niskanen et al. (2011) and Peintner (2008) suggest that ITS is not sufficiently variable for differentiation of all *Cortinarius* species.

Microscopic characteristics.—We observed the microscopic characteristics in both KOH and Melzer's. KOH is the most commonly used reagent in *Cortinarius* taxonomy (e.g. Høiland 1983, Lindström et al. 2008, Ortega et al. 2008), whereas we used mostly Melzer's (e.g. Niskanen et al. 2008, 2009, 2011).

KOH has one significant advantage over Melzer's with regard to the species of the subgenus *Dermocybe*. The bright pigments of the pileipellis and lamellar trama hyphae, important in species identification, are visible in KOH but are not seen or are seen only as faint orange-red in Melzer's. Although the anthraquinonic pigments dissolve in KOH and colors are best observed from fresh preparations. The contents of the hyphae and spores are also easier to observe in KOH. Melzer's reagent however also has some advantages. The spore characteristics are best seen in Melzer's. The ornamentation stands out better than in KOH and one additional characteristic, dextrinoidity of the spores, is available. The fine encrustations of the lamellar trama and pileipellis hyphae also are best observed in Melzer's. In KOH they are barely visible or not visible at all. The stronger, spot-like and zebra-striped encrustations are visible in both reagents.

We also measured spores of *C. puniceus*, *C. sanguineus* and *C. vitiosus* in Melzer's reagent and KOH but found no significant differences. We noticed however that the length variation in the spores seems fairly large in these species and deformed, oblonged spores often are observed. Therefore spore size alone might not always be sufficient for species recognition and other characteristics also should be used.

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