Cortinarius subgenus *Telamonia* p.p. in North Europe

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This thesis is based on the following papers:

I Kytövuori, I., Niskanen, T., Liimatainen, K. ja Lindström, H. 2005: *Cortinarius sordidemaculatus* and two new related species, *C. anisatus* and *C. neofurvolaesus*, in Fennoscandia (Basidiomycota, Agaricales). – Karstenia 45(1): 33–49.

II Niskanen, T., Liimatainen, K. ja Kytövuori, I. 2006: Taxonomy, ecology and distribution of *Cortinarius rubrovioleipes* and *C. hinnuleoarmillatus* (Basidiomycota, Agaricales) in Fennoscandia. – Karstenia 46 (1): 1–12.

III Niskanen, T., Kytövuori, I. & Liimatainen, K. 2007: *Cortinarius* sect. *Brunnei* (Basidiomycota, Agaricales) in North Europe. – manuscript

IV Niskanen, T. Liimatainen, K., Kytövuori, I. & Lindström, H. 2008: Subgen. *Telamonia* (Fr.) Trog (key to sections and groups). In: Knudsen, H. & Vesterholt, J. (edit.) 2008: Funga Nordica vol 1. Agaricoid, Boletoid and Cyphelloid genera. – Nordsvamp, Copenhagen. (accepted).

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These are referred to in the text by their Roman numerals.

Contributions

The following table shows the main contributions of authors to the original papers or manuscripts.

	I	II	III	IV	V
Original idea	TN 33, IK 33, HL 33	TN 70, IK 30	TN 50, IK 50		
Morphology	TN 30, IK 50, HL 20	TN 90, IK 10	TN 50, IK 50	TN 80, IK 20	TN 55, IK 45
Molecular data	KL 100	KL 100	KL 100	KL 100	KL 100
Analyses:					
POY	TN 50, KL 50	TN 100			
TNT			KL 100		
MrBayes			KL 100		
Manuscript preparation	TN 55, IK 20, HL 20, KL 5	TN 90, KL 5, IK 5	TN 60, KL 25, IK 15	TN 75, KL 10, IK 10, HL 5	TN 85, IK 15

Initials refer to authors of the paper in question:
IK = Ilkka Kytövuori, KL = Kare Liimatainen, TN = Tuula Niskanen, HL = Håkan Lindström

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Introduction

Taxonomy of *Cortinarius*

Cortinarius is the largest genus of Agaricales with a worldwide distribution. *Cortinarius* spp. form ectomycorrhizae with different trees and shrubs mainly belonging to the order Fagales, families Pinaceae, Salicaceae, Myrtaceae, Dipterocarpaceae, Cistaceae, Rhamnaceae, and genera *Eucalyptus* and *Dryas*. Many of the species have narrow ecological preferences. Typical to all *Cortinarius* species are a cobweb-like partial veil (= cortina) and ornamented, cinnamon brown spores. Based on the latest phylogenetic studies the agaricoid genera *Cuphocybe, Rozites* and *Rapacea*, and sequestrate genera *Thaxterogaster, Protoglossum, Quadrispora* and *Hymenogaster* p.p. also belong to *Cortinarius* (Peintner et al. 2001, Peintner et al. 2002a,b).

At the genus level the name *Cortinarius* was first used by Fries (1836–1838). Since then several infrageneric classifications, based on macro-morphology, have been proposed for the northern hemisphere species. Moser (1983a) divided *Cortinarius* into six subgenera, *Cortinarius, Leprocybe, Myxacium, Phlegmacium, Sericeocybe* and *Telamonia,* and regarded *Dermocybe* as a separate genus. In Brandrud et al. (1989) the number of subgenera was reduced to four, *Cortinarius, Myxacium, Phlegmacium* and *Telamonia* and *Dermocybe* was included in the subgenus *Cortinarius*. Bidaud et al. (1994b) recognised *Cortinarius, Dermocybe, Myxacium, Phlegmacium, Telamonia* and *Hydrocybe*.

Recent phylogenetic studies, based on sequence data from rDNA internal transcribed spacer regions (ITS1 and ITS2) and/or adjacent LSU region, have shown that *Cortinarius* itself is monophyletic but many of the traditional infrageneric groups are artificial (Garnica et al. 2003a, Garnica et al. 2005, Høiland & Holst-Jensen 2000, Liu et al. 1997, Peintner et al. 2004, Seidl 2000). Still, many of the species traditionally classified in *Telamonia* form a monophyletic group, *Telamonia* sensu stricto (s. str.), which is characterised at the molecular level by one or two indels in the ITS1 region (Garnica et al. 2005, Høiland & Holst-Jensen 2000, Peintner et al. 2004). These molecular studies also suggest that *Anomali, Obtusi*, *C. cyanites, C. renidens* and *C. badiovinaceus* have their closest relatives elsewhere, while *C. raphanoides* and *C. gentilis* placed by Brandrud et al. (1989–1998) in the subgenus *Cortinarius*, should be included in *Telamonia* s. str. In this work the subgeneric division of Brandrud et al. (1989) is followed with slight modifications.

Characteristics common to all telamonioid species are a dry or fairly dry cap and stipe, and a fruitbody without bright colours. Bluish tints might be strong, however, or the stipe may have brightly coloured universal veil belts. The size of the fruitbody varies greatly from very small and slender to big and fleshy. The subgenus *Telamonia* sensu lato (s. lat.), comprising the greatest number of species, is the most poorly known of the subgenera of *Cortinarius*. The centre of diversity is in the northern hemisphere, although some species of the group are also recognised in the southern hemisphere (Garnica et al. 2005, Peintner et al. 2003b). Several internal groupings have been introduced based on macromorphology (Bidaud et al. 1994, Melot 1990, Moser 1983a), but so far no extensive molecular studies have been performed to test these classifications.

Several mycologists have studied European telamonioid species, often together with other *Cortinarius* species, and many field guides have also been published (e.g. Bidaud et al. 1992–2006, Brandrud et al. 1989–1998, Consiglio et al. 2003–2006, Fries 1821, 1836–38, 1851, Henry e.g. 1938, 1958, 1981, Melot 1989, 1992, 1995, Moser 1983a, 2001, Moënne-Loccoz et al. 1990ab, 1991, Orton 1983, 1984, Soop 2006). Few extensive studies include only telamonioid species (e.g. Arnold 1993, Bidaud et al. 1995, 1997, Henry 1955, Lamoure 1977, 1978, Lindström et al. 2007, Moser 1968). Studies of North American *Telamonia* species have been carried out for example by Kauffman (1905, 1932), Matheny & Ammirati (2006), Moser et al. (1995), Rehner et al. 1988, and Smith (1944). Hongo (e.g. 1964, 1965, 1969) has described several species from Japan.

Species level taxonomy

Species delimitation

The limitation of the species in fungi is not unambiguous, and several different species concepts have been applied. The most commonly used are the morphological species concept, the biological species concept, and the phylogenetic species concept. So far, the most commonly used has been the morphological species concept (e.g. Kuyper 1988). Its application, however, has led to very different results and numbers of species. The biological species concept is often less ambiguous, but it can not be used in *Cortinarius* because of the great difficulties of obtaining pure cultures from spores. The phylogenetic species concept is used in a growing extent in fungal taxonomy. It has been discussed in more detail by Taylor et al. (2000) and compared with the morphological and biological species recognition. The use of phylogenetic species recognition has often revealed that many species recognised by morphological or biological species concepts include several phylogenetic species (e.g. Hibbett et al. 1995, Kauserud et al. 2006).

Species recognition in *Cortinarius*, and in many other fungi too, has until recently relied almost entirely on morphology and ecology. Due to the fairly simple structure of fungi, the morphological characteristics suitable for classification are fewer than in most animal and plant groups. In addition, the fluid transitions among most of these characteristics and large number of species make the taxonomy of telamonioid species particularly difficult. This has led to a variety of different opinions on species delimitation. For example, in the sect. *Hinnulei*, which is one of the few telamonioid sections delimited by different authors in the same way, the number of species in Bidaud et al. (1997) is about 70. In Brandrud et al. (1989, 1992, 1994, 1998) 2 species and one subspecies have so far been presented. In the *Armillati* s. str., which has been studied in more detail, these numbers are 9 in Bidaud et al. (1995) and 2 plus one subspecies in Brandrud et al. (1989, 1992, 1994, 1998), (counting only species that are included in the sect. *Armillati* (Table 1, pages 16–19) in accordance with our own concept).

Sequence data in combination with the evaluation of morphological characteristics has only been used in a few *Cortinarius* studies (subgenus *Phlegmacium*: Frøslev et al. 2006, Garnica et al. 2003b, Moser & Peintner 2002a,b, subgenus *Telamonia*: Jacobsson & Soop 2000, Lindström et al. 2007, Matheny & Ammirati 2006). The most thorough study has been conducted by Frøslev et al. (2007), in which they analysed a total of 421 ITS-

sequences of 79 species of sect. *Calochroi* (subgenus *Phlegmacium*).

There are still remarkably few multi-gene species level studies of Agaricales (e.g. Den Bakker et al. 2007; Oda et al. 2004). Only one multi-gene study has so far been done in *Cortinarius* by Frøslev et al. 2005. They showed that the species level results from the RNA polymerase II genes, RPB1 and RPB2, are in concordance with the results from ITS, and in Frøslev et al. (2007) it was concluded that the ITS seems to be a suitable marker for the species level identification in *Cortinarius*. In only two cases the morphologically accepted species *C. atrovirens*/*C. ionocholorus* and *C. xanthophyllus*/*C. claroflavus* were found to have an identical ITS sequences. In *Cortinarius*, the intraspecific genetic variation of ITS-regions is usually low and specimens from different continents might have identical ITS-sequences (e.g. Moser & Peintner 2002a).

ITS regions have successfully been used for species level studies in many other fungi genera too, e.g. *Hygrophorus* (Larsson and Jacobsson 2004), and *Macrolepiota* (Vellinga et al. 2003)). However, in some groups of fungi ITS sequences have sometimes observed to be too variable, e.g. *Leccinum* (Der Bakker et al. 2004), and *Xerocomus* (Peintner et al. 2003a), or too conserved, e.g. *Hebeloma* (Aanen et al. 2000), for species level studies.

Nomenclature

When the delimitation of a species has been studied, the next challenging phase is to find out if the species has already been described. So far, over 4000 *Cortinarius* names and combinations have been published (Index fungorum, http://www.indexfungorum.org). Many names are synonyms, whereas many common species are not yet described (Brandrud et al. 1989). This is due to several reasons. Many of the earlier descriptions are difficult to interpret, because they often include only a short text without any illustrations or spore characteristics. Also, herbarium material is often lacking. A Finnish mycologist, P.A Karsten, was ahead of his time since he used microscopic characteristics and concerved herbarium specimens already in nineteenth century. The designation of type specimen did not become obligatory until 1958. Unfortunately, no restrictions exist for the quality and quantity of the type material and it can often be very scanty or in very poor condition. Because descriptions are vague and type material is not always available, or it has not been studied, many cases exist in which several different interpretations have been made from the same descriptions. Therefore, many new species have been described without realising that they are synonyms for earlier names.

Searching for relevant names can be very difficult and time consuming. Because a general consensus on the application of names does not exist and different infrageneric classifications have been used, it can sometimes be almost impossible to predict where to find relevant species descriptions.

Other problems in fungal taxonomy

The taxonomy of many macrofungi is based on the characteristics of their fruiting bodies. Most species have a certain fruiting period and not all of them produce fruiting bodies every year. In addition, many characteristics are lost when fruitbodies are dried, and fresh specimens are needed to study all the characteristics. Therefore, getting a good overall view of a species might take several years. Irregular fruiting may also lead to vague

species delimitation. In other words, the researcher learns about the species in a year when it is common, but if it does not fruit for several years, he/she starts to lump other species under that concept as well. This phenomenon can be observed from herbarium specimens collected over several years by same authors.

Fruitbodies belonging to different *Cortinarius* species can grow side by side and mixed collections are very common. This of course makes the observation of species characteristics difficult and leads to wrong conclusions.

The small amount of well documented and representative material in public herbaria can also slow down the studies. The situation is fairly good in the Nordic countries but from other areas good material is often lacking. Even if some material exists it is not easy to order, since the application of names is so ambiguous. Therefore, in order to study fresh morphological characteristics, material has to be collected. Very little is known about the distribution of the species and similarities of the mycota between different continents, which makes the selection of collection sites challenging on the larger scale. Furthermore, fruiting is also dependent on the annual weather conditions, and it can be hard to find fruiting bodies in good condition or find them at all. These problems are mainly encountered while doing the preliminary study of the species, but when the species limits have been found, poorer material can also be used for studying e.g. ecology, distribution, and variation of microscopic characteristics within a species.

Research aim

The original aim of this thesis was to study the taxonomy of selected *Telamonia* sections based on morphological and molecular data, as well as to study the ecology and distribution of the species. The study area was delimited to Fennoscandia for the practical reasons mentioned above. From Fennoscandia, I was able to get well documented material and also collect additional material fairly easily.

During the study, we found that the number of species in *Telamonia* is far more than previously thought. The taxonomical problems encountered and the difficulty in finding and studying all the relevant names and types hindered the study, and some of the groups originally intended to be included in this study were left for future investigation. Instead, we decided to publish the results in smaller parts, starting with the most unambiguous groups. In study **I**, we described two new species and presented our morpho-genetic species concept. In study **II**, we described one new section, and studied the taxonomy, ecology, and distribution of two species in Fennoscandia. Study **III** presents the known representatives of the section *Brunnei*. The aim of studies **IV** and **V** was to combine and present the current knowledge of the telamonioid species in the Nordic countries (except the sections *Anomali, Hydrocybe,* and *Incrustati* which were treated by H. Lindström). Only species with names confirmed by comparison with the type material or, if the name was Friesian, confirmed by studying the photographed collections of the Cortinarius Flora Photographica (Brandrud et al. 1989, 1992, 1994, 1998) were used whenever possible to avoid more confusion in the *Cortinarius* taxonomy. The keys are mainly based on our preliminary, new infrageneric classification of the telamonioid species (unpublished). The knowledge is biased towards *Telamonia* species occurring in boreal forests and *Telamonia* species occurring in deciduous forests are underrepresented.

Material and methods

The study is mainly based on material collected by Ilkka Kytövuori and the author (ca. 1500 specimens collected during 2002–2006), as well as herbarium material from Finland with additional specimens from Sweden, Norway, and Denmark. Many colleagues also lent their collections for study. Altogether, over 2000 specimens were studied. For clarifying the nomenclature, 55 type collections and 69 photographed collections of 66 species (photographs published in the Cortinarius Flora Photographica (Brandrud et al. 1989, 1992, 1994 and 1998), below refered as CFP collections) were studied.

Morphological characteristics

Macromorphology was studied using fresh fruitbodies (size, shape, colours, smell) and exsiccata (colour). Also, several hundred collections were photographed in fresh condition by Ilkka Kytövuori and Kare Liimatainen. Many morphological characteristics are lost when the specimens are dried and therefore it is extremely important to have a photograph and/or make detailed notes of the appearance of the fruitbody. Colour codes are used to some extent in *Cortinarius* taxonomy (e.g. Frøslev et al. 2007, Matheny & Ammirati 2006, Moser & Peintner 2002a), but were not used in this study.

Microscopic characteristics were examined using a light microscope (Leica DM/LS) and the measurements were made with a 100x oil-immersion objective. Spores were examined from the surface view of pieces of the gills of dried basidiomes, and measured (10 to 20 spores from one fruitbody) from the veil or from the top of the stipe mounted in Melzer's reagent. Length and width were measured from the same spore, and the length/width ratios (Q-value) were calculated for individual spores. Basidia, sterile cells, and the hyphae of the gill trama were examined from pieces of gills mounted in Melzer´s reagent. The pileipellis was examined from small scalps or sections of dried basidiomes (central part of the cap) made with a razor blade, and mounted in Melzer's reagent. Making sections is time consuming, because dried *Telamonia* specimens are fairly fragile. For examining and comparing a large number of exsiccata a more effective method – making scalps – is needed. This method is useful for studying the epicutis and hypoderm and the encrustations are easier to observe from the scalps than sections. However, for describing the structure of pileipellis it would be recommendable to use both methods, since the thickness of different layers is easier to observe from sections than scalps.

Melzer preparations were done using the following procedure. A drop of Melzer's reagent was placed on the microscope slide and spread evenly onto a ca. 1 cm^2 area.

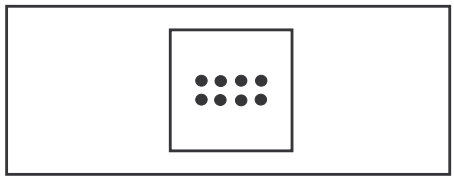

Fig. 1. Illustration of a preparation with pieces of eight specimens in two rows.

Small pieces of gill or pileipellis were properly mounted in the reagent. For making the comparison of the specimens easier, several pieces were placed in two rows under the cover slip, so that the differences or similarities could be observed with one glimpse (Fig. 1). After a few minutes, the cover slip was gently placed over the pieces without breaking the structure too much. If this is done too quickly, the typical colour reactions might not develop properly. After making the preparation it is good to wait at least 10 minutes, so that the artificial differences (e.g. in the colour reactions) between specimens disappear. For improving the visibility of the hyphal encrustation, the cover slip can be gently pressed so that the structure is slightly crushed.

DNA sequence data

For molecular work ca. 2–5 specimens per species, and in some cases over 10 specimens, were chosen for sequencing, amounting to a total of ca. 700 specimens. Collections were selected to represent as wide as an ecological and morphological variation as possible. For clarifying the nomenclature, 55 type collections and 69 photographed collections (of 66 species) published in Cortinarius Flora Photographica (Brandrud et al. 1989, 1992, 1994 and 1998) were sequenced.

The widely used rDNA internal transcribed spacer regions ITS1 and ITS2 were chosen as molecular markers (Fig. 2). In *Cortinarius*, ITS sequences vary in length from approximately 500–700 bp (GenBank: http://www.ncbi.nlm.nih.gov/). Because there are hundreds to thousand copies of these regions in fungal genome, they are more easily isolated and amplified than most low-copy nuclear loci (Burnett 2003). In addition, the small size of target DNA fragment facilitates ITS amplification by PCR, even permitting the use of very old herbarium specimens (Larsson and Jacobsson 2004).

An interesting property of rDNA genes is that the individual copies may appear to evolve more or less in unison. This uniformity arises from one or more processes of intergenic sequence homogenization that collectively are referred to as concerted evolution. However, it cannot be assumed that only one kind of ITS sequence type exists in one individual (Álvarez and Wendel 2003). Furthermore concerted evolution complicates the phylogenetic analyses, because it becomes difficult to decide which copies are really homologous, so that orthologous and paralogous copies can be mixed (Page and Holmes 1998).

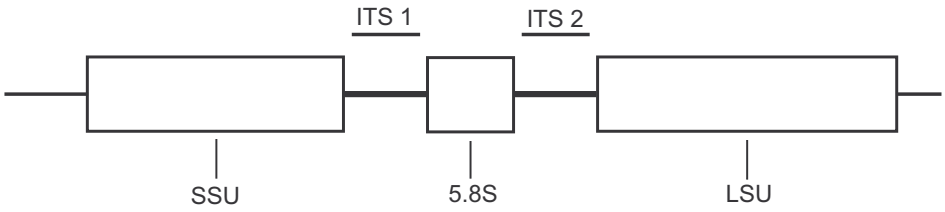

Fig. 2. Diagram to illustrate the structure of one unit of the rDNA. RNA coding regions (SSU, LSU and 5.8S) are illustrated as rectangles.

Phylogenetic analyses

Usually the alignment of DNA sequences is performed before phylogenetic analyses. The idea of alignment is to identify the homologous nucleotides in the sequences. Alignments, however, are seldom objective or repeatable when a considerable variation in the length of the sequences occurs. In addition, ambiguous parts of the alignment are normally left out of the analyses. To avoid these problems another kind of approach has been developed. This approach of direct optimisation evaluates the nucleotide homology directly in reference to topology. It is implemented in the computer program POY (Wheeler 1996, Gladstein & Wheeler 2001, Wheeler et al. 1996–2007), and it was used for phylogenetic studies in **I** and **II**.

When two computationally demanding tasks (alignment and tree search) are performed simultaneously a lot of computing time is required. In order to expedite the analyses, continuous sequences were cut into four smaller fragments: ITS1, 5.8 S, and ITS 2 into two pieces. The regions were the cuts were made were based on the preliminary alignments performed with the program ClustalW 1.8 program (Thompson et al. 1994) installed on the server of European Bioinformatics Institute (http://www.ebi.ac.uk/clustalw/index.html). In the studies **I** and **II** the datasets were so small that we were able to run analyses long enough to find the shortest trees several times. The costs 2:1:1:1 (gap open cost: extension gap cost: transversion: transition) were used in studies **I** and **II**. In study **I**, costs 1:1:1:1 were also used to see how different cost values affect the results.

In study **III** traditional approaches for phylogenetic analyses were used. Sequences were first aligned with the program Muscle (Edgar 2004), followed by manual adjustments in BioEdit (www.mbio.ncsu.edu/BioEdit/bioedit.htm). Ambiguous positions were excluded from the analyses. Parsimony analyses were performed using TNT v.1.0 (Goloboff et al. 2000) and Bayesian inference with Mr.Bayes v.3.1.1 (Huelsenbeck & Ronquist 2003).

All the analyses were made using the mainframe computers of the CSC, IT Centre for Science, Espoo, Finland.

Results and discussion

Species level taxonomy

Species concept and recognition

Genetic flow between species is usually very low. This causes discontinuous genetic variation and with time differences in morphology and ecology. Since we can not test the mating of different *Cortinarius* individuals we try to detect the characteristic differences between the species (genetic, morphological and ecological) and use them for the classification and identification of the species. The species concept used in studies **I–V** is based on this idea of discontinuous variation and correlation between the characteristics, and could be considered as a mixture of morphological and phylogenetic species recognition. We have used the name morpho-genetic species recognition for this approach (study **III**),

since a strict phylogenetic species recognition would be based on several genetic markers and does not include morphology.

Until recently species recognition was based mostly on morphology. This is especially difficult in *Cortinarius,* because so many species exist and most characteristics are strongly overlapping. The difference between intraspecific variation and overlapping characteristics is not always easy to observe, and it might be hard to decide which characteristics are relevant for species recognition. Therefore, many characteristics have been over- or underemphasised, e.g. the colour of the fruiting body, spore characteristics, etc.

The genetic level data is more unambiguous since clear character states occur, and they do not change due to age and/or environmental conditions. In addition, genetic distances might indicate the relationships of the taxa more unambiguously than morphological characteristics. The problem is, however, to find a suitable region for the study. The most commonly used species level markers in fungal taxonomy so far are the rDNAs internal transcribed spacers 1 and 2 (ITS1 and ITS2).

We tested the usefulness of the ITS regions in the species level taxonomy of *Cortinarius* preliminary by sequencing ca. three collections of about 40 morphologically well delimited *Telamonia* species from different geographical regions of Northern Europe and sometimes also from Central Europe. The species were identified by Ilkka Kytövuori who has studied the species for many years. Using the herbarium material or identifying species with little experience easily leads to misidentification and misleading results. In most cases our molecular level results correlated well with morphological species delimitation. Therefore, we concluded that ITS regions seemed suitable for species level studies, and it was also used for the classification of difficult species groups in which species limits were hard to find based on morphology alone. In most cases good morphological characteristics, supporting phylogenetic species, were later also found. For reliable phylogenetic species recognition other not related regions should also be used, but so far only a few studies including several genetic regions (ITS and RPB) have been done in *Cortinarius* by Frøslev et al. (2005, 2007). The results showed that the species delimitation based on ITS regions, however, is in concordance with the results based on RPB regions.

The observed intraspecific variation in studied *Cortinarius* species was usually less than 4 base pairs, and in most cases the sequences were identical or nearly identical (see e.g. papers **I**–**III**). The minimum pairwise difference between the ITS sequences of two species cannot be given, but in most of the species recognised in this study the pairwise interspecific difference was more than 5 base pairs. This correlates well with the results by Frøslev et al. (2007) for the subgenus *Phlegmacium*. However, in a few cases morphologically different species were found to have almost identical sequences (*C. paragaudis/C. pinigaudis*, and *C. solis-occasus/C. laniger*). Also, in the study by Frøslev et al. (2007) the morphologically accepted species *C. atrovirens*/*C. ionocholorus* and *C. xanthophyllus*/*C. claroflavus* were found to have identical ITS sequences. This raises the question as to whether the ITS is variable enough for separating all of the *Cortinarius* species, or do we need a more variable DNA region for species level studies. Identical ITS sequences might also be due to the resent hybridization of the species. The amount of hybridization in Basidiomycotina is considered to be low, since widespread mechanisms exist that regulate hyphal fusion between species (Burnett 2003). However, the existence of hybridization e.g. between *Leccinum* species has been speculated in a recent study by Den Bakker et al. (2007).

Cryptic species have already been reported from several different fungi groups (e.g. Den Bakker et al. 2007; Kauserud et al. 2006). In our studies morphologically similar but genetically distinct groups were found within some species (e.g. *C. carabus* in study **III**), a phenomenon also noticed by Frøslev et al. (2007) e.g. in *C. platypus*. Whether or not these could be considered as a cryptic species remains unclear.

The results presented above raise the question as to whether we are able to recognise taxa below the species level at all with the characteristics we use. It seems that the ITS region might be too conservative to detect taxa below the species level. Moreover, if phylogenetic, cryptic species with no distinguishing morphological characteristics are already found in many fungi, it is very probable that taxa below species level can only be recognised genetically.

Number of species

In the Nordic Macromycetes (Høiland 1992, Brandrud 1992) the number of species, corresponding to the groups of the subgenus *Telamonia* s. lat. presented in paper **V**, recognised in the Nordic countries was ca. 50. In Brandrud et al. (1989–1998), 63 Nordic species and 4 subspecies or varieties have been presented so far. In Soop (2006), ca. 80 species occurring in Sweden are presented in detail and several more in the additional notes.

Based on the species concept presented above, we recognised ca. 200 species from the Nordic countries. Only 109 of them, for which a proper name was found, were included in the studies **IV** and **V**. Six of these species have been described as new in studies **I** and **III**, and species in citation marks in study **V** will soon be described. Although our sampling is extensive, it does not equally cover all the species groups. Some sections have been sampled more than others and sampling is biased towards boreal species, leaving most of the southern deciduous forest species for future studies. For example, keys to sections *Brunnei* and *Armillati* include about 85–95 % of the known species, but most of the other keys only cover 50 % or less of the expected diversity.

Towards more unambiguous use of names in telamonioid species

When trying to find an existing name for a species, several problems arise. According to the International Code of Botanical Nomenclature (http://ibot.sav.sk/icbn/main.htm) the oldest available name for the species should be used, but those are usually also the most difficult ones to interpret, e.g. many names described by Fries have been used in several different ways over the years. Based on our current knowledge it is fairly evident, that the species delimitation of earlier authors (e.g. Fries 1836–38) in most cases differed from ours, and many of the species presumably included several related or not related species, a situation also confronted with some recent descriptions. These would be reasons for rejecting the name, but then many *Cortinarius* names would have to be rejected. An alternative approach is to retain the most suitable or commonly used names and fix it by designating an epitype, neotype, or lectotype (if original material is available). This stabilises the *Cortinarius* nomenclature and taxonomy.

The interpretation is more unambiguous when type material exists, but some problems still exist. Type material is always dried and many characteristics of the fresh fruiting

bodies are lost. Therefore, only the colour and the size of exsiccata, and the microscopic features can be used. Too often the type material is so scanty or in poor condition that even those characteristics are difficult to study. Furthermore, making a final decision based on one collection only can be difficult, especially when the species has been described from a different geographical area. There is no guarantee that it even occurs in our study area, although it may be somewhat similar to our collections morphologically. In the recent years molecular methods have provided an efficient new tool for studying poor quality type specimens, but some of them still cannot be studied. In these cases the names have to be rejected, because unambiguous interpretation can not be done. Unfortunately, not all type specimens are available for study, they can either be in private herbaria or might have been lost during the years.

For stabilising the nomenclature of *Cortinarius* species presented in studies **I–V,** type specimens or CFP collections (Brandrud et al. 1989, 1992, 1994, 1998) were studied. Only 19 species of 109 were interpreted otherwise. Of these, for *C. albovariegatus*, *C. aprinus, C. aurantiomarginatus, C. cagei, C. ionophyllus, C. minutalis, C. solis-occasus*, *C. subtorvus* and *C. trossingenensis* Cortinarius Flora Photographica plates were used as references, and *C. acetosus, C. alborufescens, C. bayeri, C. crassifolius, C. danicus, C. diosmus, C. fragrantior, C. fulvescens, C. fuscoperonatus* and *C. subbalaustinus* were interpreted based on literature or other mycologist's (H. Lindström, K. Soop, J. Vesterholt) interpretation in the Nordic countries. Most of the Friesian names are not yet typified, but the typification would be recommendable when detailed studies of the species are done, as e.g. for *C. glandicolor* in study **III**.

Study **V** is an attempt to present our current knowledge of the known Nordic species for which a proper name has been available. The species concept and limits have been confirmed by sequencing ca. 2–5 and studying microscopically several Nordic specimens per species. In addition, the nomenclature has been confirmed in most cases. All the sequences from the type material and the photo plate collections will be published in publicly accessible data repositories with clear indication as to type status. This will make the comparison of data for other researchers faster and easier, and stabilise the nomenclature used in taxonomic and ecological studies.

The main reason we almost exclusively included only studied names in study **V**, was that we wanted to avoid more confusion in the *Cortinarius* taxonomy. Even within the Nordic countries there might be a different interpretation for the same name and the comparison of species recognised by different authors is difficult. Because differences also occur in species limitation, material from the authors should always be studied before making further conclusions. The same also applies to ecological and distribution data, which cannot be unambiguously combined from different sources without first revising the material. For example of the herbarium material we have studied only about 10 % has been correctly identified.

As a conclusion for the aforementioned problems, for good taxonomy the limitation of the species has to be well studied. Furthermore, all the names used should be studied from type material, or if it does not exist a neotype should be chosen. To achieve these goals long term studies are needed, since taxonomical work can be very time consuming.

Infrageneric classification in the subgenus *Telamonia* s. lat.

The infrageneric classification of subgenus *Telamonia* s. lat. presented in studies **IV** and **V** is based on very preliminary analyses of ca. 200 ITS sequences, also including *Hydrocybe* and *Incrustati* species (tree not shown). Only clades recovered in several analyses and supported with morphological characteristics were taken into account. The preliminary classification and morphological characteristics supporting it are presented in more detail in Table 1. Compared to the subgeneric classification proposed in Melot (1990) and Brandrud et al. (1989–1998) the following changes are suggested (Fig. 3). The sections *Colymbadini* and *Brunneotincti* placed in the subgenus *Cortinarius* seem to belong to the subgenus *Telamonia* s. str., the latter is also supported by the phylogenetic results of Peintner et al. (2004). In addition, many studies show (e.g. Høiland & Jensen 2000, Peintner et al. 2004) that *C. gentilis* should be placed in the subgenus *Telamonia*, presumably in the sect. *Brunnei*. This result is also supported by our data in study **III**. Our data and studies by Matheny and Ammirati (2006) also suggest that *C. humicola* belongs to the subgenus *Telamonia*, but it has still been kept in the subgenus *Cortinarius* in Niskanen & Kytövuori (2008) for practical reasons, since it is a key and not a thorough systematic representation of the genus. The sections *Anomali, Cyanites, Fulvescentes* and *Obtusi,* and the species *C. renidens* and *C. balaustinus* placed in the subgenus *Telamonia* by Brandrud et al. (1989) do not to belong to the subgenus *Telamonia* s. str. based on our, and partly on previously published phylogenetic data (e.g. Garnica et al. 2006, Høiland & Jensen 2000, Peintner et al. 2004). In addition, our data indicates that *C. acetosus, C. camphoratus* and *C. illuminus* do not belong to the subgenus *Telamonia* s. str. Genetically the subgenus *Telamonia* s.str. is characterised by short ITS1 sequences compared to other *Cortinarius* species, but so far no distinguishing morphological characteristics of this clade from other species with a telamonioid habit has been found.

The species composition of many sections as defined based on our phylogenetic analyses (Table 1) is different from the species composition of sections as suggested e.g. in

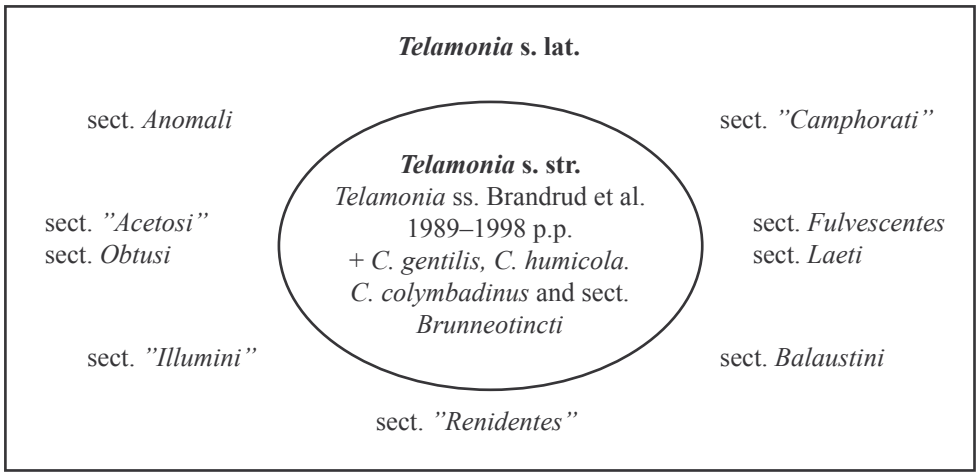

Fig. 3. Differences from the classification used in Brandrud et al. (1989-1998). Inedited names are in citation marks.

Table 1: Infrageneric classification of telamonioid species used in studies **IV** and **V** based mainly on preliminary unpublished phylogenetic analyses of ca. 200 ITS sequences. Not including the following sections of *Telamonia* s. str : *Incrustati* Melot, *Helvelloides* M.M. Moser, *Paleacei* Nespiak, *Saniosi* Moënne-Locc. & Reumaux, *Hydrocybe* (Fr.) Nezdojm, and "*Humicolae*" Liimat. & Niskanen ined. Abbreviations used: sp= spores, frb= fruitbody.

***Telamonia* s. str.**			
Section	**Species included**	**Morphological characters uniting the group**	**Basis for limitation**
Telamonia (Fr.) Gillot & Lucand	*C. torvus, C. agathosmus, C. venustus, C. ionophyllus, C. traganus, C. rusticus, C. "Virtolainen koivu"*	Frb ± with bluish tints, cap often not or slightly hygrophanous or with hygrophanous veins, universal veil whitish, ochre, greyish brown or bluish, often abundant, most species with fruity smell	Genetically and morphologically fairly uniform group
Urbici Liimat., Niskanen & Kytöv. ined.	*C. urbicus, C. diosmus*	Frb ± greyish white to brownish white, cap with hygrophanous veins, universal veil white, often fairly sparse, flesh pale greyish brown, smell slightly fruity or raphanoid, exsiccata often with silvery grey cap	Genetically and morphologically uniform group
Niveoglobosi Kytöv. Liimat. & Niskanen ined.	*C. niveoglobosus, C. "niveollkka"*	Frb ± white, cap not hygrophanous, universal veil white, fairly abundant, flesh pale greyish brown, smell possibly fruity, sp fairly small, < 9 µm long, with deciduous trees, exsiccata whitish grey to brownish	Genetically and morphologically uniform group
Lanigeri Melot	*C. laniger, C. solis-occasus, C. alborufescens*	Cap weakly hygrophanous, gills vivid red brown at least when mature, universal veil whitish, creamy or bluish, often woolly, flesh pale brownish to reddish brown.	Morphologically fairly uniform group, but *C. alborufescens* is genetically somewhat distant
Biveli Liimat., Niskanen & Kytöv. ined.	*C. bivelus*	Cap hygrophanous, innately fibrillose or not, universal veil white, flesh pale brownish to brownish, smell slightly raphanoid, sp ellipsoid.	Genetically distinct lineage
Malachii Melot	*C. malachius, C. suberi*	Frb sometimes with bluish tints, cap innately fibrillose or finely scaly, fairly weakly hygrophanous, universal veil white, flesh greyish white to brown, smell indistinct, exsiccata often with fairly dark grey brown cap but big variation within species typical	Genetically and morphologically uniform group
Fuscoperonati Liimat. & Niskanen ined.	*C. fuscoperonatus*	Cap with hygrophanous veins, universal veil greyish brown to blackish brown, sp obovoid-ellipsoid	Genetically distinct lineage
Pholidei Kühner & Romagn.	*C. pholideus*	Cap distinctly brown squarrose, universal veil dark brown, sp subglobose	Seems to belong genetically in the sect. *Brunneotincti* s. lat.

Section	Species included	Morphological characters uniting the group	Basis for limitation
Brunneotincti M.M. Moser	*C. caput-medusae, C. craticius, C. heterocyclus, C. fillioni, C. valgus, C. raphanoides*	Frb often with olivaceous tints, cap innately fibrillose and often silky shiny, with hygrophanous veins, universal veil brownish yellow to reddish, smell often raphanoid, some have olivaceous spots deep in cap cuticle, some with anthraquinoid pigments	Genetically and morphologically fairly uniform group: *C. caput-medusae* and *C. heterocyclus* form one group, *C. fillioni* and *C. valgus* other and *C. raphanoides* is somewhat closely related
Armillati M.M. Moser	*C. armillatus, C. roseoarmillatus, C. suboenochelis, C. luteo-ornatus, C. paragaudis, C. pinigaudis*	Cap with hygrohanous veins, universal veil brownish yellow to reddish, smell indistinct or raphanoid, with anthraquinoid pigments (Høiland 1980)	Genetically and morphologically uniform group
Bovini Liimat. Niskanen & Kytöv. ined.	*C. bovinus, C. "säikeislakki bovinus", C. "yöviro", C. "kallaste", C. phaeosmus C. sordidemaculatus, C. anisatus, C. neofurvolaesus,*	Cap hygrophanous or with hygrophanous veins, universal veil white, flesh ± brownish, often darker at the stem base, exsiccata brown to blackish brown, most species require or prefere calcareous soil	Genetically and morphologically fairly uniform group
Bovini others	*C. testaceofolius, C. brunneifolius, C. leiocastaneus, C melleopallens, C. ionosmus*	Cap brown to honey, flesh pale brownish, exsiccata brown to dark brown	Artificial group of unrelated brown Telamonia species, which do not clearly belong in any of the sections here
Sordescentes Melot	*C. aprinus*	Cap with hygrophanous veins, flesh brownish white to pale greyish brown, universal veil whitish to brownish, with deciduous trees, exsiccata with pale greyish brown cap and stem and dark gills	Genetically distinct lineage, not related with the sect. *Bovini*
Disjungendi Kytöv. Liimat. & Niskanen ined.	*C. disjungendus*	Flesh greyish brown to brown, often darker at the stem base, exsiccata blackish, sp > 9.5 µm long, obovoidly ellipsoid	Genetically distinct lineage
Brunnei Melot	*C. brunneus, C. glandicolor, C. caesiobrunneus, C. clarobrunneus, C. pseudorubricosus, C. albogaudis, C. ectypus, C. coleoptera, C. cicindela, C. carabus, C. gentilis*	Frb often dark brown, cap distinctly hygrophanous or with hygrophanous veins, universal veil whitish to brownish, flesh often dark brown, exsiccata blackish (except *C. gentilis*), with coniferous trees	Morphologically and genetically uniform group (study **III**)

Section	Species included	Morphological characters uniting the group	Basis for limitation
Uracei Melot	*C. uraceus, C. rigidipes, C. crassifolius*	Frb dark brown, cap distinctly hygrophanous, universal veil greyish to greenish, very sparse, sp amygdaloid or obovoid-ellispsoid, exsiccata blackish	Genetically and morphologically fairly uniform group. Closely related to *Cinnabarini* and *Colymbadini*, and somewhat also to *Brunnei*
Cinnabarini Melot	*C. cinnabarinus, C. bulliardi, C aurantiomarginatus*	Cap distinctly hygrophanous, universal veil yellow orange to red, often sparse, sp amygdaloid, exsiccata with dark brown to blackish brown or cinnabar red cap, with anthraquinoid pigments (Høiland 1980)	Genetically and morphologically uniform group
Colymbadini Melot	*C. colymbadinus*	Cap distinctly hygrophanous, universal veil greenish yellow, very sparse, sp amygdaloid, fluorescense yellow	Genetically and morphologically closely related to the sect. *Uracei* and *Cinnabarini*
Subbalaustini Liimat., Niskanen & Kytöv. ined.	*C. subbalaustinus*	Cap red brown, distinctly hygrophanous, universal veil white, flesh pale red brown, somewhat darker towards the base, smell indistinct, exsiccata with brown cap and pale greyish to brownish stem	Genetically distinct lineage
Saturnini Moënne-Locc. & Reumaux	*C. saturninus, C. subtorvus, C. lucorum*	Frb often with bluish colours, cap often with veil patches, hygrophanous, universal veil white, with deciduous trees	Genetically and morphologically uniform group
Sciophylli (Moënne-Locc. & Reumaux) Liimat. & Niskanen ined.	*C. serratissimus*	Frb with bluish tints, cap dark brown, strongly hygrophanous, flesh greyish white, distinctly bluish at the stem top, exsiccata dark greyish brown, sp fairly big, obovoidly ellipsoid	Genetically distinct lineage
Duracini Melot	*C. duracinus*	Cap distinctly hygrophanous, stem radicating and cartilaginous, universal veil white, often sparse, flesh whitish to pale brownish	Genetically and morphologically uniform group
Bicolores (M.M. Moser) Melot	*C. cagei, C. evernius, C. imbutus, C. dolabratus, C. tortuosus*	Frb often with bluish tints, cap strongly hygrophanous, stem radicating or cylindrical, universal veil white, smell indistinct, like ceder-wood, raphanoid or cellar-like, sp often somewhat fusoid.	Artificial group of species with morphological characters mentioned on the left
Firmiores (Fr.) Henn. (incl. *Sericeocybe* Nezdojm.)	*C. armeniacus, C. alboviolaceus, C. turgidus, C. quarciticus, C. carneinatus, C. biformis, C. melitosarx*	Cap often slightly viscid-sticky when moist, often strongly hygrophanous, gills pale yellowish to pale greyish brown, flesh in stem very pale, smell indistinct, sp amygdaloid to ellipsoid, exsiccata pale greyish to brownish	Genetically and morphologically uniform group
Boulderenses Niskanen, Liimat. Kytöv.	*C. rubrovioleipes* (*C. boulderensis* and *C. pseudobovinus* from North America)	Cap distinctly hygrophanous, universal veil red or brownish, flesh pale yellowish to pale greyish brown, sp ellipsoid to amygdaloid, at least some species with anthraquinoid pigments (Bendiksen & Bendiksen 1993)	Genetically and morphologically uniform group (see study **II**)

Hinnulei Melot	*C. hinnuleus, C. hinnuleoarmillatus, C. minutalis, C. roseonudipes*	Frb yellowish brown to ochre brown, cap often with blackening spots, distinctly hygrophanous, universal veil white, yellowish or orange, smell usually strong, earth-like or raphanoid, exsiccata yellow brown to reddish brown, sp often strongly verrucose, with deciduous trees	Genetically and morphologically uniform group
Safranopedes Liimat., Kytöv. & Niskanen ined.	*C. safranopes*	Otherwise much like *Hinnulei* species but exsiccata greyish brown	Genetically and morphologically fairly uniform group
Anthracini Melot	*C. anthracinus, C. danicus, C. colus*	Frb small and slender, cap hygrophanous, universal veil orange or red, with anthraquinoid pigments (Høiland 1980)	Genetically fairly uniform group
Other groups of *Telamonia* (not included in *Telamonia* s.str.)			
Section	**Species**	**Morphological characters**	**Basis for limitation**
Camphorati Liimat. & Niskanen	*C. camphoratus*	Ventriocose-fusoid cheilocystidia, strong, unpleasent smell	Genetically distinct lineage
Acetosi (Moënne-Locc. & Reumaux) Niskanen, Liimat. & Kytöv.	*C. acetosus, C. fragrantior*	Cap often somewhat rimy at the centre, distinctly hygrophanous, stem cylindrical or rooting, universal veil white, often sparse, flesh white to yellowish white, smell iodoform like or pleasent cellar-like	Genetically and morphologically fairly uniform group, closely related to the sect. *Obtusi*
Obtusi Melot	*C. obtusus, C. acutus, C. trossingenensis*	Cap distinctly hygrophanous, stem cylindrical or rooting, universal veil white, flesh yellow brown, smell of iodoform, gill trama hyphae often incrustated	Genetically and morphologically fairly uniform group
Renidentes Liimat. & Niskanen ined.	*C. renidens*	Cap distinctly hygrophanous, universal veil almost absent, sp subglobose	Genetically distinct lineage
Fulvescentes Melot	*C. fulvescens, C. bulliardioides, C. badiovinaceus, C. floccopus var. gracilis*	Cap matt, often thin fleshed, hygrophanous, stem silky shiny fibrillose, universal veil ± reddish, flesh yellowish brown	Genetically and morphologically fairly uniform group, the sect. *Laeti* could probably be included in this section
Laeti Melot	*C. detonsus, C. bayeri, C. ochrophyllus*	Universal veil yellow to ochre, otherwise like *Fulvescentes*	Genetically and morphologically fairly uniform group, could probably be included in the section *Fulvescentes*
Balaustini Moënne-Locc. & Reumaux	*C. balaustinus*	Cap with hygrophanous veins, universal veil white, smell slightly raphanoid, sp subglobose, epicutis hyphae with dark brown granules or particles in Melzer	Genetically distinct lineage
Illumini Liimat., Niskanen & Kytöv. ined.	*C. illuminus*	Cap distinctly hygrophanous, universal veil whitish, yellowish or pale pinkish, flesh pale brown to brown, sp subglobose	Genetically distinct lineage

Bidaud et al. 1994b, Brandrud et al. (1989, 1992, 1994, 1998), or Melot (1990). Many of the previously limited sections seem to be artificial, and many of the monophyletic species groups detected in our study do not seem to belong to any of them. Therefore, three new sections are proposed for *Telamonia* s. lat. species and nine for classifying the species in the subgenus *Telamonia* s. str. One new section, *Boulderenses*, was already published in study **II**. Although in Table 1 many of the sections seem to contain only one species, only *Fuscoperonati, Sciophylli,* and *Balaustini* could be considered monotypic based on our current knowledge, since for the others closely related nameless species are already known.

Based on our preliminary study, many of the characters previously used for delimiting sections are artificial or homoplasious e.g. anthraquinoid pigments or characteristics of the fruiting body (e.g. colour of the universal veil, colour of the fruiting body). After careful re-evaluation of the morphological and ecological characteristics, however, many internal groupings found in phylogenetic analyses can often be delimited based on other characteristics (Table 1 and chapter "Usefulness of morphological characteristics in identification of *Telamonia* taxa" below). In Table 1 a preliminary attempt towards a more natural classification in the subgenus *Telamonia* is proposed, but more studies are needed before further conclusion.

Ecology and distribution

In the boreal forests on nutrient poor soils *Telamonia* is the dominant subgenus of *Cortinarius*, whereas in the richer or southern habitats the proportion of *Phlegmacium* species increases. A majority of the *Cortinarius* species have narrow ecological preferences and many form ectomycorrhiza with only one or few host species. Mainly owing to that, the species composition in coniferous and deciduous forests is very different. Since our studies have concentrated on the boreal zone, especially the *Cortinarius* species occurring in southern deciduous forests are still very poorly known in the Nordic countries.

The host specificity of *Cortinarius* spp. has been found to be of little value for delimiting higher taxa in the *Phlegmacium* sect. *Calochroi* (Frøslev et al. 2007). The same applies to most *Telamonia* sections with a few exceptions: all the known species of sect. *Hinnulei* occur with deciduous trees, all *Brunnei* species with coniferous trees, and in some smaller sections (e.g. *Malachii* and *Saturnini*) the species are also limited to either coniferous or deciduous trees.

Many *Telamonia* species are common in suitable habitats. Fairly many are also rare: some of them are restricted to calcareous soil e.g. *C. albogaudis, C. crassifolius*, and *C. bovinus*, but for some species the restricting factors are not known e.g. *C. rubrovioleipes* (study **II**) and *C. ectypus* (study **III**). Several species have been included in national red lists in the Nordic countries, e.g. *C. serratissimus* (= *C. sciophyllus*), *C. cinnabarinus*, and *C. fuscoperonatus*, but many rare species are still missing from the lists because they are/have been poorly known or are not yet known at all.

Our studies **I**–**V** concentrate on North Europe, but some similarities with North European and North American taxa have been found. In the study **III** *C. carabus* and *C. pseudorubricosus* were found to have identical or nearly identical sequences to sequences from Vancouver, Canada deposited in GenBank (http://www.ncbi.nlm.nih.gov/). Through

comparison of our telamonioid data and the GeneBank sequences it can be perceived that many other European species can be found from North America too (e.g. *C. traganus* and *C. armillatus*). A lot of species not known from North Europe were also found, however, indicating that from a circumboreal or even global perspective, the species richness is even higher.

Usefulness of morphological characteristics in identification of *Telamonia* taxa

Although said to be inconspicuous and fugacious there are many good morphological characteristics that can be used in identification of telamonioid species. The most useful morphological characteristics are presented below, and they were used in the study **I–V** for identification of sections, groups, and species.

Macroscopic characteristics

At first sight most telamonioid species look more or less brownish, but with some practice it is possible to observe the whole spectrum and differences between the species. Some species have bluish tints, but variation within species can be large and make identification challenging. Typical for many telamonioid species is that their cap is weakly to strongly hygrophanous, and in dry weather most of them look similar. Therefore, it is very important to observe the colours of the cap when collections are still moist (Fig. 4). The structure of the cap surface and the type of hygrophanity seem to be good characteristics in the higher level classification (Fig. 5), also used by Brandrud et al. (1989). A weakly hygrophanous cap is often either innately fibrillose with hygrophanous veins or tomentose and evenly weakly hygrophanous, sometimes the cap can also be more or less scaly. This structure is typical e.g. for the species in the section *Armillati* and most species of the sect. *Lanigeri*. Waxy glossy cap is usually distinctly hygrophanous and this structure is typical e.g. for the many species in the section *Firmiores* and *Bicolores*. The matt and hygrophanous cap is typical for *Fulvescentes* and *Laeti*. But, as is often the case in nature, species with intermediate characteristics exist, and not all the species can be strictly classified based on this characteristic.

The colour of the flesh is also useful in the higher level taxonomy. Many species of the sect. *Bovini* have brownish flesh, often darker at the base of stem, while many species of the sections *Firmiores* and *Bicolores* have pale or bluish flesh. In telamonioid species the universal veil is often white or whitish, but when it differs from this it helps in the identification of species or groups. Sometimes the colour of the veil can change during aging (e.g. in *C. pinigaudis* from brownish yellow to vinaceous red, also observed by Soop in *C. heterocyclus*, and in *C. brunneus* from whitish to somewhat brownish), which is good to remember. The fruiting body development in the telamonioid species is stipitocarpous so the remains of the universal veil usually form incomplete or complete girdles or sometimes a sock-like sheath on the stem. The amount of universal veil and the type of girdles are somewhat typical for the species, but quite a lot of intraspecific variation exists.

Most of the species have either an indistinct or raphanoid smell, but some of them have a distinct smell helpful for identification (e.g. *C. anisatus* with aniseed smell and *C. ionosmus* with the odour of *Viola odorata*), and sometimes the smell is typical for several

Fig 4. The colour of the cap in moist (e.g. lower row centre) and dry (e.g. upper row left) condition. Photo K. Liimatainen.

Fig. 5. a) Tomentose and weakly hygrophanous cap (*C. laniger*, sect. *Lanigeri*), **b)** innately fibrillose cap with hygrophanous veins (*C. paragaudis*, sect. *Armillati*), **c)** matt and hygrophanous cap (*C. sp.*, sect. *Fulvescentes*), **d)** distinctly hygrophanous, waxy-glossy cap (*C. armeniacus*, sect. *Firmiores*). Photos K. Liimatainen.

closely related species (e.g. the earthy smell in sect. *Hinnulei*, the fruity odour in sect. *Telamonia*, the iodoform-like smell in sect. *Obtusi*). Often the smell is best observed from the gills, but the iodoform-like smell is strongest at the stem base and some species have a typical smell in flesh (e.g. *C. diosmus*). The colour of the gills can also be of taxonomical value: species of the sect. *Lanigeri* often have vivid brick red gills, *Firmiores* have fairly pale gills, and species of the sect. *Bovini* often have dark gills with age. Bluish tints are best observed in young fruitbodies.

The colour of the exsiccata is often typical for a species or species groups, and it is a useful characteristic for higher level taxonomy (Fig. 6). The blackish exsiccata, for example, is typical for many species in the sections *Brunnei*, *Uracei,* and "*Disjungendi*". Many closely related species have similar exsiccata, but this characteristic can help with identifying morphologically fairly similar, but distantly related species e.g. *C. quarciticus* (pale exsiccata) and *C. suberi* (dark exsiccata). But one should take into account that the condition of the fresh fruitbody can affect to the colour of the exsiccata, if e.g. *C. brunneus* has already dried in the field, the exsiccata can remain more intensively brownish. Also, the colour of the exsiccata can be darker than normal if the specimen is exposed to too much moisture before pressing as a herbarium specimen.

We did not test macrochemical reactions. In the subgenus *Phlegmacium* KOH is used for species and group level identification (e.g. Brandrud et al. 1989, 1992. 1994, 1998, Frøslev et al. 2007). It has been used to a lesser extent in the subgenus *Telamonia*. Traditionally e.g. *C. safranopes* is considered to have a blackish-violet alkaline reaction in the flesh of stem base, the species of the sect. *Armillati* a lilac-red reaction on the universal veil, and e.g. Soop (2006) has tested NaOH and $AgNO_3$ reactions in many species. The age and condition of the fruitbody may affect on the intensity of the reaction.

Fig. 6. Fresh fruitbodies and exsiccata: **a)** *Cortinarius disjungendus* (sect. *"Disjungendi"*, **b)** *C. quarciticus* (sect. *Firmiores*). Photos K. Liimatainen.

A peculiar characteristic in some *Cortinarius* species is the fluorescence, e.g. in *C. colymbadinus* (sect. *Colymbadini*, subgenus *Telamonia*) and in the unrelated species of sect. *Veneti* (subgenus *Cortinarius*). Therefore it seems that this characteristic has developed several times during the evolution of *Cortinarius*. In a wider extent the fluorescence has been used for taxonomy of the subgenus *Telamonia* in Arnold (1993). Anthraquinoid pigments have also been used in *Telamonia* taxonomy. Høiland (1980) limited the sect. *Armillati* to only include the species with anthraquinoid pigments, although later Høiland & Jensen (2000) showed that the species possessing this characteristic do not form a monophyletic group.

Microscopic characteristics

The most commonly used reagent in *Cortinarius* taxonomy is KOH (e.g. Garnica et al. 2003, Lindström et al. 2007, Matheny & Ammirati 2006, Moser & Peintner 2002a), but it provides very little additional characteristics in telamonioid species. The colour of the spores can be observed well, but most of the species have rusty brown spores and only in a few cases differences are found (e.g. *C. bibulus* has pale spores, and the spores of *C. armillatus* become red). KOH also loosens the structures so spores move quite freely in the reagent, making the comparison of several gill pieces under one cover slide difficult – a technique that makes the observation and comparison of small differences much easier. Also, the structure of the cap cuticle is more difficult to observe from the scalps when different layers slide apart. Melzer's reagent, however, does not loosen the structure too much and provides one new characteristic, the dextrinoidity of the spores. In addition, some encrustations of the hyphae are better seen in Melzer than in KOH, but thorough comparison of the differences has not been done. The reagent has rarely been used in *Cortinarius* taxonomy and thus dextrinoidity has almost totally been missed. Also, in other brown spored agarics, e.g. in *Hebeloma* and *Galerina*, the dextrinoidity has been noticed to be of taxonomical value (Moser 1983, Vesterholt 2005).

The spores provide many useful characteristics for identification such as size, shape, wall-thickness, verrucosity and dextrinoidity, but those are often not utilised to the full extent. Spore characteristics are most useful at the species level, but in some cases they can also be used in higher level taxonomy (the subglobose spores in the sect. *Illumini*, often strongly ornamented, ± subglobose to ellipsoid spores in many of the species in the sect. *Hinnulei*). The spore characteristics can best be presented in the side-view drawings from which the most typical spores for that species can be chosen. Although, not seen in all the spores, some characteristics can be so typical that for identification it is good to slightly highlight these characteristics in drawings. Also photographs are sometimes used to illustrate spores, but the problem is that most spores are often out of focus and/or in the wrong position and untypical spores are included too. The photos, however, can provide one additional characteristic, colour, which is lacking from the drawings.

The range of spore size of the *Cortinarius* species is about 5–15 x 3–8 µm. Accurate measurements are needed to present the differences between the species. It makes sense to report the spore size as accurately as possible (the theoretical resolution for a light microscope is 0.2 µm). The 0.5 µm scale used in studies **IV** and **V** (due to the editor's request) can obscure discernible differences, because for example the almost non-overlapping measurements of 4.8–5.3 µm and 5.2–5.7 µm will be the same 5–5.5 µm.

For the measurements only mature, normally developed spores should be used, not unripe or abnormal ones. Often the normal spores can be distinguished from the others by their well developed ornamentation. Spore measurements from spore deposits on the veil or top of stipe are normally more representative. In size, these spores can be fairly similar to the spores from the gill, but the variation on the gill is often larger. In some species the differences in the spores from the gill and the veil can be so big that they are not comparable (e.g. study **II**, *C. hinnuleoarmillatus*), or the variation in spores from the gill is so large that "typical" spores can not be detected (e.g. often in *C. clarobrunneus*).

The shape of the spores is often only described briefly, although with careful examination differences can be found. The Q-value (length/width ratio) tells something about the spore shape and is a fairly unambiguous characteristic to be used in distinguishing species. It does not tell all about the shape, however, since ellipsoid and amygdaloid spores may have the same Q-value, although they look very different. The shape of the spores in telamonioid species varies from subglobose, ovoid, amygdaloid, and ellipsoid to fusoid, but citriform spores, typical for some species in the subgenus *Phlegmacium* and the sect. *Myxacium*, are lacking. It is also important to observe where the widest point of the spore is, is the spore e.g. ovoid or obovoid. The different spore shapes are presented in more detail in Fig. 7. Most of the species have ± amygdaloid to ellipsoid spores, while subglobose or fusoid spores are found in a minority. The shape varies somewhat within the species, and more so in some species than in the others. Weather conditions can also affect the spores, e.g. specimens collected in the late autumn can have spores that are longer than usual and are somewhat deformed.

Wall thickness should also be observed in the telamonioid species. For example *C. anisatus, C. armillatus, C. laniger*, and *C. aprinus* have spores with thick walls (indicated with two lines in the drawings) and *C. luteo-ornatus* and *C. ectypus* have thin walls (difficult to indicate in the drawings), but in most species the wall thickness is moderate.

Ornamentation of the spores is a good characteristic in species identification. The strength of the verrucosity varies from almost smooth or very finely verrucose (e.g. *C.*

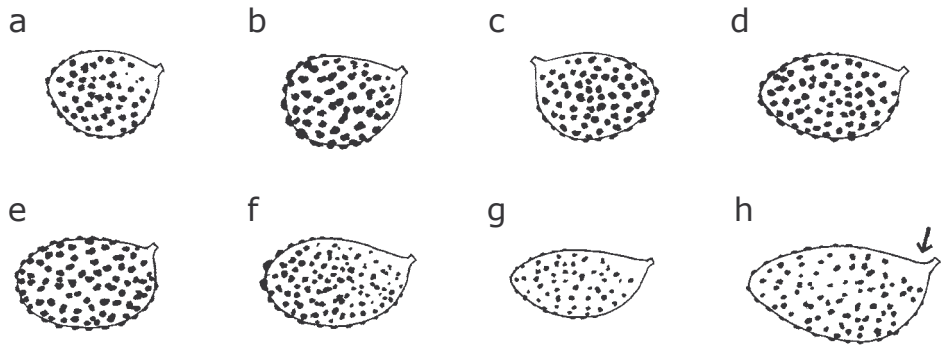

Fig. 7. Spores in telamonioid species are **a)** ovoidly subglobose (*C. "pinigaudis"*), **b)** obovoidly subglobose (*C. coleoptera*), **c)** ovoid (*C. anisatus*), **d)** amygdaloid (*C. sordidemaculatus*), **e)** ellipsoid (*C. rubrovioleipes*), **f)** obovoidly ellipsoid (*C. phaeosmus*), **g)** fusoid (*C. alborufescens*), or **h)** have a suprahilar depression (*C. bayeri*).

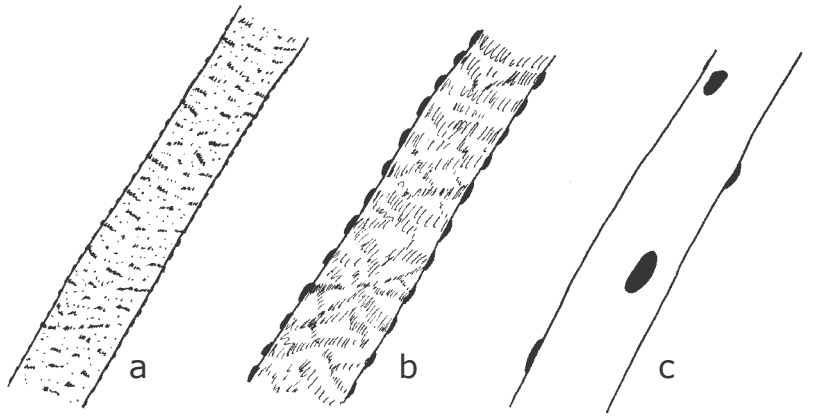

Fig. 8. Different types of encrustations observed on gill trama hyphae: **a)** finely encrusted hyphae (*C. biformis*, sect. *Firmiores*), **b)** zebra-striped encrusted hyphae (*C. cicindela*, sect. *Brunnei*), **c)** spot-like encrusted hyphae (*C. laniger*, sect. *Lanigeri*).

alborufescens, C. melleopallens) to very strongly verrucose (e.g. *C. fuscoperonatus, C. crassifolius, C. hinnuleus*). Verrucosity can be either even (e.g. *C. neofurvolaesus*) or uneven mixture of larger and smaller warts (e.g. *C. hinnuleus*). In many species the verrucosity is stronger at the apex (very clear e.g. in the spores of *C. serratissimus*). In most species the verrucae are moderately high and moderately broad, but in some species they have a spiny or sharp appearance (e.g. *C. urbicus*), they are coarse (e.g. *C. carabus*) or low and wide (e.g. *C. renidens*). In some species the verrucosity is dense (e.g. *C. turgidus*). The type of ornamentation is often typical for the species, but in some cases big intraspecific variation occurs, for example in *C. bivelus* the spores are typically moderately verrucose, but specimens with almost smooth spores are also found.

The dextrinoidity of the spores provides considerable information for species level identification. Dextrinoidity can be roughly evaluated on a four class scale: non dextrinoid, weakly dextrinoid, moderately dextrinoid, and strongly dextrinoid. Only a few species are almost non dextrinoid e.g. C. *ectypus*, weakly dextrinoid species are e.g. *C. melleopallens*, and *C. camphoratus*, most species have moderately dextrinoid spores, and *C. armeniacus* and *C. armillatus* are examples of species with strongly dextrinoid spores. Typical for some species is that the reaction is slow. In some specimens the reaction can be weak, although the species should for example have strongly dextrinoid spores. This phenomenon is probably due to the condition or age of the exsiccata.

Only few *Cortinarius* species have distinctly differentiated cystidia. Ventricose-fusoid to weakly lageniform cheilocystidia are often abundant in *C. camphoratus* and balloon-shaped cheilocystidia in *C. acutus* and related taxa (Peintner 2003), but all the species in subgenus *Telamonia* s. str. lack true cheilocystidia. Sterile cells at the gill edge may be abundant and the size varies between species, but a lot of intraspecific variation occurs, and they are not very useful for identification. The same applies to basidia, which are normally 4-spored.

The encrustations of the gill trama hyphae also provide some characters for identification. The hyphae of many telamoniod species are smooth to finely encrusted,

but some species have distinct encrustations, e.g. *C. laniger* and *C. testaceofolius* have spot-like encrusted hyphae and most species e.g. of the sect. *Brunnei* (study **III**) and *Obtusi* have strongly zebra-striped or spot-like encrusted hyphae. The encrustations are more common in small *Telamonia* species (e.g. in the sect. *Incrustati*) than in bigger species. The encrustations are best observed from dried herbarium specimens since not all the characteristics are visible on fresh material. The different types of encrustations are presented in Fig. 8.

The structure of the cap cuticle in the subgenus *Telamonia* s. lat often is a pileipellis duplex, which includes two distinct layers: a thin, filamentous epicutis often with fairly narrow hyphae, and hypoderm with often short and wide cells. Closely related species have often very similar cap cuticles, but some characteristics can be found and used for group level identification, e.g. *C. valgus*, *C. fillionii* and *C. raphanoides* have typical olivaceous spots deep in the cap cuticle, and *C. balaustinus* has epicutis hyphae with dark brown granules in Melzer's reagent. Small species of the section *Brunnei* can be distinguished from the species of *Hydrocybe* or *Incrustati* by the lack of well developed, strongly pigmented hypoderm. We did not systematically observe the cap cuticle structures. A thorough study would be needed to find out the usefulness of this characteristic for identification purposes.

Conclusions

The diversity of the subgenus *Telamonia* s. lat. in North Europe (excluding sect. *Hydrocybe, Incrustati* and *Anomali*) was found to be far greater than previously thought. Even many of the common species have not yet been described. So far, ca. 200 species have been recognised from the Nordic countries, but the sampling in most groups does not cover the whole diversity and especially the southern deciduous forest species are underrepresented in our study. In most cases phylogenetic (only based on ITS data) and morphological species recognition were in concordance, but in a few cases morphologically delimited species had almost identical ITS sequences, raising the question as to whether ITS is always variable enough for species recognition. The opposite situation, in which a morphologically uniform species included two phylogenetically distinct lineages, however, was also encountered, suggesting the possibility of cryptic species in *Cortinarius*. In our studies no taxa below species level were recognised and the aforementioned results indicate that presumably they can only be recognised genetically. Based on our preliminary results a revision of the infrageneric classification in *Cortinarius* subgenus *Telamonia* s. lat. is needed, and more sections should be established for a meaningful and functional classification. The results based on molecular data have challenged our view of traditional classification. Many groups have turned out to be artificial, and it seems evident that many characteristics have been over- or underemphasised. Many morphological characteristics, however, are useful in the identification of telamonioid species and e.g. some spore characteristics have often been overlooked. Our studies have concentrated on North Europe, but we have found some similarities with North European and North American taxa. Many species not previously known in North Europe were also found, suggesting that from a circumboreal or global perspective the species richness is even higher.

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