DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS
210

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IRJA SAAR

The taxonomy and phylogeny of the genera *Cystoderma* and *Cystodermella* (Agaricales, Fungi)

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LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following publications that are referred in the further text by their Roman numerals:

I. Saar I. 2003. The genera *Cystoderma* and *Cystodermella* (Tricholomataceae) in temperate Eurasia. Mycotaxon 86: 455–473.
II. Saar I, Læssøe T. 2006. Two new *Cystoderma* species from high Andean Ecuador. Mycotaxon 96: 123–127.
III. Saar I, Læssøe T. 2008. A re-evaluation of *Cystoderma luteohemisphaericum*. Mycotaxon 104: 313–319.
IV. Saar I, Põldmaa K, Kõljalg U. 2009. The phylogeny and taxonomy of genera C*ystoderma* and C*ystodermella* (Agaricales) based on nuclear ITS and LSU sequences. Mycological Progress 8 (1): 59–73.
V. Saar I. 2008. *Cystoderma* Fayod. In: Knudsen H, Vesterholt J (Eds.). Funga Nordica. Agaricoid, boletoid and cyphelloid genera. Nordsvamp, Copenhagen: 510–512.
VI. Saar I. 2008. *Cystodermella* Harmaja. In: Knudsen H, Vesterholt J (Eds.). Funga Nordica. Agaricoid, boletoid and cyphelloid genera. Nordsvamp, Copenhagen: 512–513.
VII. Saar I. A checklist of the genera *Cystoderma* and *Cystodermella*. Unpublished.

Author's contribution to each paper

	I	II	III	IV	V	VI	VII
Idea and design	+	+	+	+	+	+	+
Sampling	+	–	–	+	+	+	+
Molecular analysis	N/A	N/A	+	+	N/A	N/A	N/A
Data analysis	+	+	+	+	+	+	+
Writing	+	+	+	+	+	+	+

Abbreviations

INSD: the International Nucleotide Sequence Databases (http://www.insdc.org/), which have been developed and maintained collaboratively between DDBJ (DNA Data Bank of Japan), ENA (European Nucleotide Archive) and GenBank (NIH genetic sequence database).

ITS: internal transcribed spacer (ITS1–5.8S–ITS2).

L-INS-i: iterative refinement method incorporating local pairwise alignment information.

LSU: large subunit.

PCR: polymerase chain reaction.

rDNA: the nuclear-encoded ribosomal RNA genes (for example ITS and LSU).

TBR: tree-bisection-reconnection.

Glossary

(Compiled according to Kirk et al. 2008 and Knudsen & Vesterholt 2008)

Adnate (lamellae): broadly attached to the stipe (see Knudsen & Vesterholt 2008, fig. 23C).

Adnexed (lamellae): rounded towards the spite, narrowly attached (see Knudsen & Vesterholt 2008, fig. 23B).

Amyloid, inamyloid: staining greyish to blackish blue in Melzer's reagent or not having this reaction.

Annulus: a ring-like partial veil or part of it, round the stipe after expansion of the pileus of basidiomata (a ring).

Arthroconidium (pl. **arthroconidia**): seriate, vegetative spores resulting from fragmentation of hyphae.

Basidioma (pl. **basidiomata**): a basidium-producing organ (a fruit-body).

Basidiospore: a propagative cell containing one or two haploid nuclei, produced after meiosis on a basidium.

Basidium (pl. **basidia**): the cell diagnostic for Basidiomycetes from which, after karyogamy and meiosis, basidiospores (generally 4) are produced externally, each on an extension (sterigma) of its wall.

Caulocystidia: cystidia on the surface of the stipe.

Clamp: a hyphal outgrowth which, at cell division, makes a connection between the resulting two cells by fusion with the lower; characteristic to Basidiomycetes only.

Collybioid: resembling a *Collybia*, in the traditional sense including *Gymnopus*.

Cheilocystidia: cystidia at the edge of the lamellae.

Cystidium (pl. **cystidia**): a sterile body, frequently of distinctive shape, occurring at any surface of a basidiomata.

Decurrent tooth (lamellae): a tooth-like prolongation of the lamellae down the stipe (see Knudsen & Vesterholt 2008, fig. 23E).

Emarginate (lamellae): notched near the stipe (see Knudsen & Vesterholt 2008, fig. 23F).

Hyaline: transparent or translucent, frequently used in the sense of colourless.

Lamella (pl. **lamellae**): one of the characteristic hymenium-covered vertical plates on the underside of the pileus of an agaric (a gill).

Meiospore: a basidiospore that is the product of meiosis.

Pileus: the hymenium-supporting part of the basidioma of non-resupinate Agaricomycetes (a cap).

Pileipellis: the cellular cortical layers of a pileus, not belonging to the veils.

Pleurocystidia: cystidia at the side of the lamellae.

Sphaerocysts: globose cells in tissues of fungi.

Stipe: the pileus-bearing part of basidiomata (a stem, a stalk).

Suprahilar zone: the area above the hilar appendage – the small wart-like or cone-like projection that connects the basidiospore with the sterigma.

INTRODUCTION

Fayod (1889) established a new agaric genus *Cystoderma*, transferring several species from the tribe *Lepiota* of the genus *Agaricus* sensu Fries (1821). Six species were assigned to this new genus – *Lepiota amianthina* Scop., *L. granulosa* Batsch, *L. cinnabarina* Alb. & Schwein., *L. carcharias* Pers., *L. seminuda* Lasch, *L. fumosopurpurea*, and *L. georginae* suggested as a possible member. The first four species have been widely accepted as representatives of genus *Cystoderma*, but other species have been considered members of the other genera. Nowadays, taxon names *Cystolepiota seminuda* (Lasch) Bon, *Leucoagaricus georginae* (W.G. Sm.) Candusso and *Melanophyllum haematospermum* (Bull.) Kreisel (synonym *L. fumosopurpurea*) are accepted.

The first monograph of genus *Cystoderma* by Smith and Singer (1945) included 14 species, which were assigned into two sections: *Granulosa* (with inamyloid basidiospores) and *Amianthina* (with amyloid basidiospores); the latter was renamed *Cystoderma* by Singer (1962). Heinemann and Thoen (1973b) recognised 26 species and allocated taxa into four sections, introducing two new ones: *Superba* (basidiospores amyloid only at the suprahilar zone) and *Cinnabarina* (with inamyloid basidiospores and cheilo-, pleuro-, and caulocystidia). Harmaja (2002), having evaluated the taxonomic weight of the spore amyloidity within genus *Cystoderma*, considering the results of studies on the nuclear DNA content of selected species (Saar and Kullman 2000) and the phylogenetic analysis of nucLSU data (Moncalvo et al. 2002), divided *Cystoderma* into two genera. *Cystoderma sensu stricto* contains species possessing amyloid basidiospores and *Cystodermella*, a new genus, encompasses species with inamyloid basidiospores. Three species of both genera (*Cystoderma amianthinum* (Scop.: Fr.) Fayod, *C. carcharias* (Pers.: Fr.) Fayod, *C. jasonis* (Cooke & Massee) Harmaja and *Cystodermella adnatifolia* (Peck) Harmaja, *C. cinnabarina* (Alb. & Schwein.: Fr.) Harmaja, *C. granulosa* (Batsch: Fr.) Harmaja) feature binuclear basidiospores, but different nuclear DNA content (Saar and Kullman 2000).

Singer (1986) assigned seven genera to the tribe Cystodermateae: *Cystoderma*, *Dissoderma* (A.H. Sm. & Singer) Singer, *Horakia* Oberw., *Phaeolepiota* Maire ex Konrad & Maubl., *Pseudobaeospora* Singer, *Ripartitella* Singer and *Squamanita* Imbach. Kühner (1980) regarded three, *Cystoderma*, *Phaeolepiota*, *Squamanita*, as members of this tribe, but assigned *Pseudobaeospora* in the tribe Tricholomateae. Singer regarded the Cystodermateae as a member of the Agaricaceae, while Kühner transferred it to the Tricholomataceae. Jülich (1981) considered Cystodermateae a member of the Agaricales, raising it to the rank of family under the name Squamanitaceae (*nomen rejectum*, Greuter et al. 1994), but assigned *Phaeolepiota* in the family Cortinariaceae. Bon (1999) assigned tribes Cystodermateae and Dermolomateae Bon into the family Dermolomataceae (Bon) Bon (*nomen rejectum*, Greuter et al. 1994) under the

Tricholomatales. The latter tribe embraced the genera *Dermoloma* J.E. Lange ex Herink and *Camarophyllopsis* Herink (Bon 1999).

The exclusion of the tribe Cystodermateae from the Agaricaceae and the transfer to the Tricholomataceae based on morphological grounds (Heinemann and Thoen 1973b; Bas 1988) was supported later by phylogenetic analyses of rDNA LSU sequences (Johnson and Vilgalys 1998). In further large-scale studies of agaricoid fungi, the phylogenetic relationships of the members of the Cystodermateae remained unresolved (Moncalvo et al. 2000, 2002). The former study included two representatives from two genera (*Cystodermella granulosa* and *Ripartitella brasiliensis* (Speg.) Singer) that did not form a clade. The latter study included seven species (*Cystoderma amianthinum, C. chocoanum* Franco-Mol.*,* *Cystodermella granulosa*, *Phaeolepiota aurea* (Matt.: Fr.) Maire ex Konrad & Maubl., *Ripartitella brasiliensis*, *Squamanita odorata* (Cool) Imbach and *S. umbonata* (Sumst.) Bas) representing four genera that dispersed across various clades of the trees. Two separate lineages *Cystoderma* and *Cystodermella–Ripartitella* formed the unsupported sister groups of the clade comprising members of the Agaricaceae. Neither molecular analysis combined with conidiogenesis (Walther et al. 2005) nor basidiospore ultrastructure (Garnica et al. 2007) could resolve the phylogenetic placement of these taxa.

The recent multi-locus analysis of the Agaricales resolved the position of *Cystoderma*, together with *Cyathus* Haller and *Crucibulum* Tul. & C. Tul. as a moderately supported sister group of the Agaricaceae in the Agaricoid clade (Matheny et al. 2006). The results of the study by Garnica et al. (2007) support a close relationship between the genera *Cystoderma* and *Phaeolepiota*, which are combined with *Crucibulum* and *Cyathus* into a well-supported lineage. Unfortunately, both studies included only the type species of *Cystoderma*.

According to Kirk et al. (2008) the genus *Cystoderma* contains approximately 35 and *Cystodermella* 12 species, with *C. amianthinum* (Scop.: Fr.) Fayod and *C. granulosa* (Batsch: Fr.) Harmaja as the respective type species.

The basidiomata of genera *Cystoderma* and *Cystodermella* are collybioid and small to medium sized (figure 1). Pileus up to 10 (–20) cm wide, often umbonate, sometimes radially wrinkled, granulose to finely scaly, mat, dry, margin at first denticulate from veil remnants, with various colour. Lamellae adnexed to adnate, emarginate or with a decurrent tooth, white to pale cream or yellowish buff. Stipe silky striate at top, below minutely to coarsely granulose-floccose, concolorous with pileus. Smell unpleasantly musty-earthy or indistinct. Taste mild, indistinct to unpleasant. Spore deposit white to pale cream. Basidiospores ellipsoid, oblong or fusiform (figure 2A), smooth, without germ pore, hyaline. Pileipellis an epithelium. Outer velar layer on pileus and stipe formed by chains of inflated globose to ellipsoid sphaerocysts (figure 2C). Clamps present.

Figure 1. The basidiomata of **A.** *Cystodermella granulosa* (TU 101314); **B.** *C. cinnabarina* (TU 106009); **C.** *Cystoderma amianthinum* (TU 106010); **D.** *C. jasonis* (TU 118180); **E.** *C. carcharias* (TU 106011); **F.** *C. aureum* (TU 106197); **G.** *C. japonicum* (TU 101697); **H.** *C. simulatum* (TU 101549). Photos by Vello Liiv (A–G) and Rasmus Ejrnæs (H).

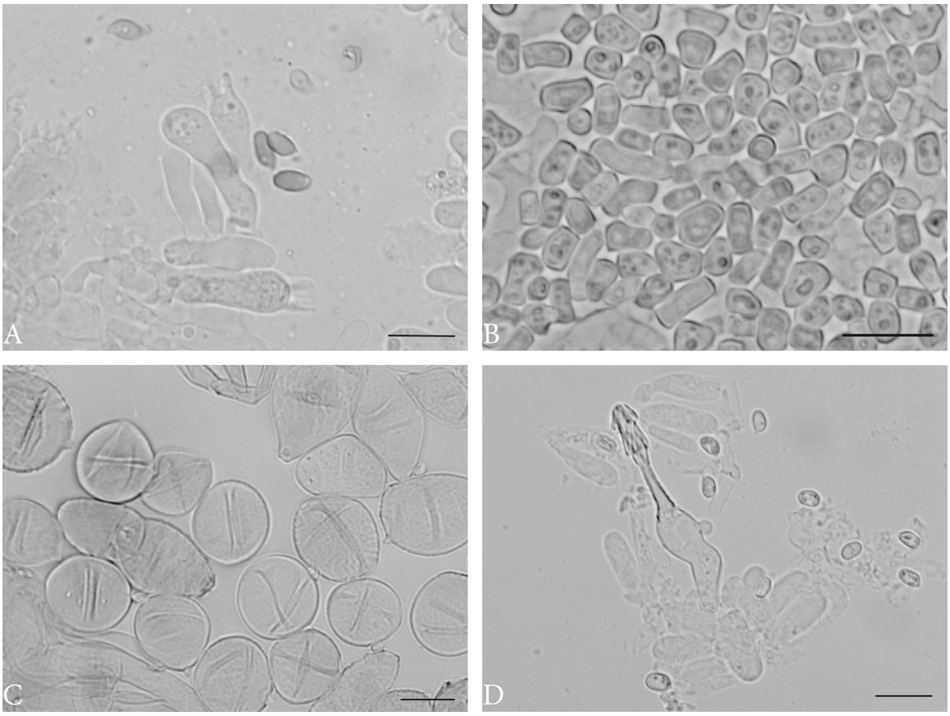

Figure 2. *Cystoderma jasonis* (TAAM 147383): **A.** Basidiospores and basidia, **B.** Arthroconidia; **C.** Sphaerocysts of *C. japonicum* (TU 101697); **D.** Pleurocystidium and basidiospores of *Cystodermella cinnabarina* (TU 106009). Bars = 10 µm.

The species of genus *Cystoderma* are characterized by weakly to strongly amyloid basidiospores, stipe with a persistent membranous annulus with granulose underside and filamentous upper surface or with an evanescent floccose-scaly ring zone, arthroconidia formed in the upper part of pileus context in a few species (figure 2B). The species of genus *Cystodermella* are characterized by inamyloid basidiospores, an evanescent floccose-scaly ring zone and presence of urticoid cheilo-, pleuro-, and caulocystidia in a few species (figure 2D).

The species of both genera can be found mostly in forest ecosystems, but also in open areas, growing on soil, among mosses and litter, some species on rotten wood remains. However, it is still unknown if *Cystoderma* and *Cystodermella* species have saprotrophic and/or biotrophic lifestyle. Their basidiospores are difficult to germinate in pure culture and probably therefore experimental studies on their lifestyle are missing. The meiospores that are hard to germinate often point to the biotrophic lifestyle, but it still needs to be proved. Pantidou et al. (1983) managed to establish pure cultures from fresh basidiomata of *Cystodermella cinnabarina* and *C. granulosa*. Walther et al. (2005) isolated the strains from basidiospore deposits of freshly collected basidiomata of species *Cystoderma amianthinum* and *C. jasonis*, but the strains of the latter did not survive. The mycelium of species *Cystoderma amianthinum* was sequenced and assigned from the soil sample in North America, but no lifestyle has been proven (Lamarche et al. 2011). The members of genus *Cystoderma* ought to be saprotrophic or according to Heinemann and Thoen (1973b) they may be symbiotic or parasitic on mosses. Harmaja (1979, 1985) suggested that at least two species (*Cystoderma lilacipes* Harmaja and *C. saarenoksae* Harmaja) are obligately associated with mosses belonging to the genus *Polytrichum*.

According to Kirk et al. (2008) the genera *Cystoderma* and *Cystodermella* are known worldwide, but the majority of species are described from temperate regions, which indicate that tropical regions are understudied.

The aims of the thesis were: (1) to present hypothesis for the species delimitation in *Cystoderma* and *Cystodermella* applying both morphological and molecular characters; (2) to verify distinction between genera *Cystoderma* and *Cystodermella* and their monophyly; (3) to recover the sister taxa of these two genera; (4) to describe new species hypothesis from Ecuador (South America); (5) to compile a global checklist of all known taxa of the genera *Cystoderma* and *Cystodermella*.

MATERIAL AND METHODS

The specimens collected by the author or other Estonian mycologists and determined by the author are deposited in TAAM or TU fungaria. The specimens' data have been uploaded into PlutoF cloud database (http://plutof.ut.ee/; Abarenkov et al. 2010b). The specimens of *Cystoderma* sensu lato from following fungaria are also studied: BR, C, FH, G, H, K, L, LE, LOU, MICH, NY, NYS, O, PDD, REG, S, SGO, TMI, TNS, TUR and WU.

The colours of the basidiomata were designated using the colour names by Kornerup & Wanscher (1974) (II, III). Microscopic investigations were carried out using a Swift M4000-D (I) or a Zeiss Axioskop 2 (II, III) light microscope at magnification x1000. Measurements were made in 3% KOH solution (II) or Melzer's reagent (I, III). The pictures were adjusted and the measurements were made with AxioVision 3.0 software (Carl Zeiss Vision GmbH) (II, III, V, VI). The spore measurements are based on ten (I) or 25 (II, III) randomly taken basidiospores from each specimen.

World geographical regions have been designated using Brummitt (2001), but locations in Fennoscandia incorporate abbreviations for biogeographic provinces in this area (Hansen & Knudsen 1992) (I). The abbreviations of fungaria are used according to the Index Herbariorum (Thiers 2011).

Molecular methods

Genomic DNA was extracted with a CTAB procedure (Gardes and Bruns 1993) with the following modifications: 1% β-mercaptoethanol in 600 μl CTAB, tissues were crushed and incubated at 65°C for 30 min, DNA eluted in 40 μl of ddH_2O or with High pure PCR template preparation kit (Roche Applied Science, Mannheim, Germany) following the protocol of the manufacturer. The CTAB extraction was followed by DNA purification with GeneClean®III kit (Qbiogene, Heidelberg, Germany) or UltraClean™15 kit (Mo Bio Lab., Carlsbad, USA), according to the manufacturers' instructions. PCR amplification was accomplished with the primer pairs ITS1F–ITS4B, ITS1F–ITS4 or ITS0Ft–ITS4 and LR0R–LR7 or CTB6–TW13 (Table 1) for ITS (ITS1–5.8S–ITS2) and partial LSU regions, respectively. PCR was performed using puReTaq Ready-To-Go™ PCR Beads (GE Healthcare, Freiburg, Germany) with 0.8 μM of each primer and 5 μl of DNA solution on a Mastercycler® EP gradient (Eppendorf AG) thermal cycler. The amplification program was as follows: an initial denaturation at 95°C for 3 min, followed by 35 cycles at 95°C for 30 sec, at 55°C for 30 sec, at 72°C for 1 min (increasing time 2 sec per cycle), and a final extension at 72°C for 10 min. PCR products were purified with QIAquick PCR purification kit (Qiagen, Hilden, Germany), UltraClean™ PCR Clean-up kit (Mo Bio Lab., Carlsbad, USA), NucleoFast® 96 PCR Clean-up kit (Macherey-Nagel, Düren, Germany) or Exo-SAP (GE Healthcare, Freiburg, Germany), according to the manufacturers' instructions. The sequences were performed on an ALFexpressII (GE Healthcare, Freiburg, Germany) automated sequencer or by MWG-Biotech AG (Ebersberg, Germany) or Macrogen Inc. (Seoul, Korea) using primers ITS1 or ITS5 and ITS4 or CTB6 and LR5 for ITS and LSU regions, respectively. In some cases, additional primers were used: ITS2, ITS3 for ITS region and LR3R, LR21, TW13, TW14 for LSU region (Table 1). For ALFexpressII sequencer cycle sequencing was performed using Thermo Sequenase Primer Cycle Sequencing kit (GE Healthcare, Freiburg, Germany), according to the manufacturer's instructions, using 0.2 µM Cy5 primers.

Sequence fragments were inspected and assembled using Sequencher 4.6–4.9 (Gene Codes, Ann Arbor, USA). DNA sequences were submitted to the European Molecular Biology Laboratory (EMBL) and PlutoF cloud databases (Abarenkov et al. 2010b). PlutoF based databases include also exhaustive specimen data, which partly are reachable through public web outputs like UNITE (http//unite.ut.ee) or Estonian National Fungarium database (http://unite.ut.ee/EestiLiigid/index.php; Abarenkov et al. 2010a).

Table 1. The sequences of primers.

Name	**Sequence 5'→3'**
CTB6	GCATATCAATAAGCGGAGG
ITS0Ft	ACTTGGTCATTTAGAGGAAGT
ITS1	TCCGTAGGTGAACCTGCGG
ITS1F	CTTGGTCATTTAGAGGAAGTAA
ITS2	GCTGCGTTCTTCATCGATGC
ITS3	GCATCGATGAAGAACGCAGC
ITS4	TCCTCCGCTTATTGATATGC
ITS4B	CAGGAGACTTGTACACGGTCCAG
ITS5	GGAAGTAAAAGTCGTAACAAGG
LR0R	ACCCGCTGAACTTAAGC
LR3R	GTCTTGAAACACGGACC
LR5	TCCTGAGGGAAACTTCG
LR7	TACTACCACCAAGATCT
LR21	ACTTCAAGCGTTTCCCTTT
TW13	GGTCCGTGTTTCAAGACG
TW14	GCTATCCTGAGGGAAACTTC

Phylogenetic analyses

Alignments were performed using L-INS-i strategy as implemented in MAFFT v 6.240 (Katoh et al 2002, 2005). Minor manual adjustments were performed with Se-Al 2.0a11 (Rambaut 1996).

Phylogenetic analyses were performed separately for the LSU and ITS datasets due to incomplete ITS data and alignment problems between distantly related genera (III, IV). The initial analyses of the LSU dataset (IV) were based on a more exhaustive data matrix that included representatives of the main groups of the euagaric clade (Moncalvo et al. 2002). For additional phylogenetic analyses of ITS data some newly acquired sequences and available sequences from INSD were incorporated (figure 4–5). *Ripartitella* for *Cystodermella* and *Crucibulum* for *Cystoderma* as outgroups were served, based on the results of previous analyses of LSU data revealed these as the closest sister groups (IV).

Maximum parsimony (MP) analyses were conducted in PAUP* 4.0b10 (Swofford 2002) using 1000 heuristic searches with random taxon addition sequences, TBR branch swapping, Maxtrees set to 10 000, the restriction to save 100 trees in each replicate applied, followed by additional swapping of the resulting trees. The confidence of branching was assessed using bootstrap resampling (bs): 1000 replicates, each with 10 random taxon addition sequences and MulTrees off. All characters were treated as unordered, equally weighted, treating gaps as missing data.

Bayesian inference of phylogeny was performed with MrBayes 3.1.2 (Huelsenbeck and Ronquist 2001, Ronquist and Huelsenbeck 2003), applying substitution model chosen by the AIK information criterion in the program MrModeltest 2.2 (Nylander 2004). The parameter of generations (*Ngen*) was modified for different datasets; otherwise default values of prior settings were used. Tracer ver. 1.4 (Rambaut & Drummond 2007) was used for summarizing the results of Bayesian phylogenetic analyses.

Additionally, two constraint analyses were performed on the LSU dataset to test the probability of two species forming a monophyletic clade together with the species of *Cystoderma*. The likelihood values of resulting constrained trees with the lowest – ln L were compared to the best unconstrained MP tree using the Shimodaira-Hasegawa test (Shimodaira and Hasegawa 1999) in PAUP* with a resampling estimated log-likelihood (RELL) bootstrap with 1000 replicates (IV). The pairwise base differences for ITS datasets were calculated with the default settings in PAUP* 4.0b10 (IV).

RESULTS

Species delimitation in genera *Cystoderma* and *Cystodermella* was evaluated based on the results of the phylogenetic relationships obtained in the analyses of ITS and LSU regions, the variation of ITS sequences based on pairwise base differences as well as morphological data (IV). Combining species was considered when the variability of ITS sequences between two taxa was less than 1% ($p = 0.01$). The study included 15 species from genus *Cystoderma* and 5 species from *Cystodermella*, the type specimens from five species were represented. The results of the analyses of ITS and LSU data supported the distinction of ten species of *Cystoderma* and four species of *Cystodermella* sensu Harmaja. Two *Cystoderma* species – *C. fallax* A.H. Sm. & Singer, *C. intermedium* Harmaja – were synonymised with *C. carcharias*, three species – *C. lilacipes*, *C. niveum* Harmaja, *C. saarenoksae* – with *C. jasonis, C. arcticum* Harmaja with *C. tuomikoskii* Harmaja, and *Cystodermella ambrosii* (Bres.) Singer with *C. granulosa*. Five new combinations were proposed: *Cystoderma carcharias* (Pers.: Fr.) Fayod var. *fallax* (A.H. Sm. & Harmaja) I. Saar, *C. jasonis* (Cooke & Massee) Harmaja var. *lilacipes* (Harmaja) I. Saar, *C. jasonis* (Cooke & Massee) Harmaja var. *niveum* (Harmaja) I. Saar, *C. jasonis* (Cooke & Massee) Harmaja var. *saarenoksae* (Harmaja) I. Saar, *Cystodermella granulosa* (Batsch: Fr.) Harmaja var. *ambrosii* (Bres.) I. Saar.

For the thesis additional phylogenetic analyses of ITS data were made incorporating some newly acquired sequences and available sequences from INSD (figure 4–5). The results of the phylogenetic analyses support the hypotheses published before by Saar et al. (2009).

The spore wall amyloidity as a main morphological character has been applied for distinguishing the genera *Cystoderma* and *Cystodermella*. The results presented in the study (IV) reveal that amyloidity of spores, considered to be consistent within the treated genera (Harmaja 2002), varies in *Cystoderma*. Harmaja transferred *Cystoderma japonicum* Thoen & Hongo to genus *Cystodermella* because possessing inamyloid basidiospores. The results of phylogenetic analyses of LSU and ITS regions, however, show that it belongs to genus *Cystoderma*. Therefore the spore wall amyloidity alone cannot be considered as a reliable feature to distinguish these two genera.

The results of phylogenetic analyses of partial LSU rDNA data have revealed *Cystoderma* and *Cystodermella* as distinct monophyletic genera, with *Ripartitella* representing a well-supported sister group of the latter. The species *Phaeolepiota aurea* represents either an unsupported sister group or a member of *Cystoderma* in the phylogenies based on LSU and ITS sequences data, respectively. The tribe Cystodermateae sensu Singer did not appear monophyletic according to analyses of LSU sequences and on the basis of these data the phylogenetic relationships of the analyzed genera could not be resolved unequivocally (IV).

Two new species, *Cystoderma andinum* I. Saar & Læssøe and *C. papallactae* I. Saar & Læssøe were described from high Andean Ecuador, the latter was transferred to genus *Cystodermella* by Vizzini (2008). The distribution data of the species from genus *Cystoderma* sensu lato in South America have been overviewed (II). *Cystoderma luteohemisphaericum* Dennis was revised based on type studies, examination and phylogenetic analysis of recent material from South America. The new combination, *Cystolepiota luteohemisphaerica* (Dennis) I. Saar & Læssøe*,* was proposed. This was the first published record of this species from Ecuador and Brazil (III, figure 3 D–F). The coloured pictures of the type specimens of *Cystoderma andinum* and *Cystodermella papallactae* are published here for the first time (figure 3 A–C).

The checklist of the genera *Cystoderma* and *Cystodermella* includes 68 taxa with information on synonymy, type specimens, original diagnoses and selected illustrations (VII). The general distribution of the species of both genera is overviewed in Tables 2–3. The morphological characters of the type specimens of following *Cystoderma* species were studied (Saar 2011): *C. simulatum* P.D. Orton (1960) collected from England, *C. clastotrichum* (G. Stev.) E. Horak (1971) from New Zealand, *C. neoamianthinum* Hongo (1974) from Japan, and *C. freirei* Justo & M.L. Castro (2003) from Spain. It revealed that all specimens belong into one species. Thus, *Cystoderma simulatum* as the earliest name should be used and other three – *C. clastotrichum*, *C. freirei, C. neoamianthinum* – are considered as synonyms. Distribution is known from Europe (Denmark, England, France, Germany, Spain), Asia-Temperate (Japan, Turkey) and Australasia (New Zealand). The first collection was found from *Nothofagus* forest in 1949 in New Zealand, where some other specimens were also collected in the 1950s and described as *Baeospora clastotricha* (Stevenson 1964). The finding of specimens in Europe started in 1957, when a specimen from the plantation of unknown trees in Surlingham was collected (East of England, United Kingdom) and described as a new species *C. simulatum* (Orton 1960). Later the findings in other countries were reported (Calonge 1986, Galliot & Sugny 2003, Glowinski & Gumbinger 1981, Kasparek 1991, Saar 2011), but this species seem to be rather rare everywhere in Europe. Thus, it is possible that this species originated from New Zealand and it has spread elsewhere. The picture of specimen found in Denmark can be seen in figure 1H.

The specimen of *Cystoderma japonicum* was collected in 2011 in Estonia (TU 101697; see figure 1G). It has probably been the first finding outside Japan, where the type specimen was found. The morphological characters and ITS sequence of this specimen are identical to the type specimen. Unlikely, it was growing on fallen rotten branches of birch, while the type specimen grew on heaps of rice-hulls (Thoen and Hongo 1985).

Figure 3. The basidiomata of **A.** *Cystoderma andinum* (C 57998, isotype); **B.–C.** *Cystodermella papallactae* (C 58002, isotype); **D.–F.** *Cystolepiota luteohemisphaerica* (TL-11724). Photos by Thomas Læssøe (A–C) and Jens H. Petersen (D–F).

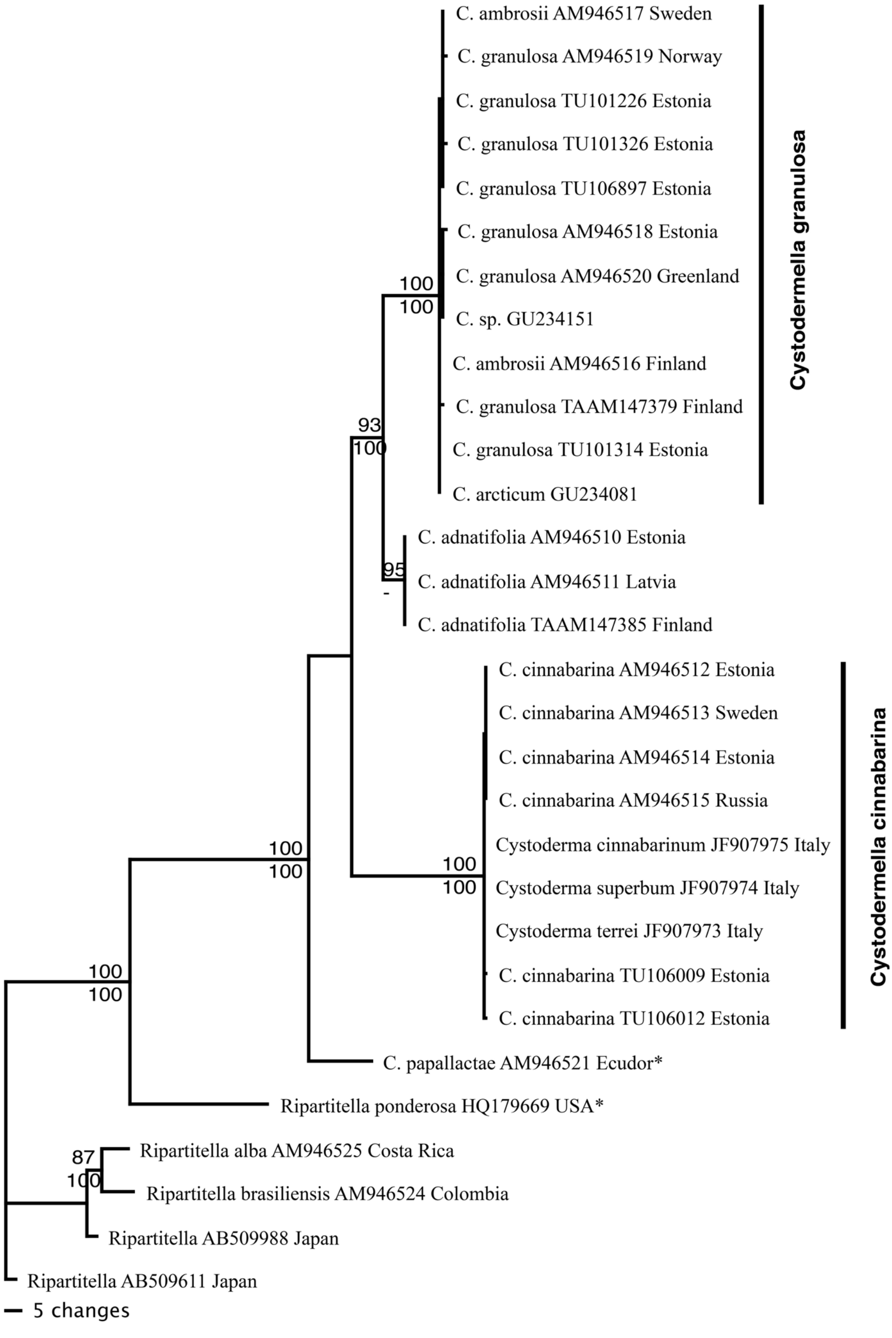

Figure 4. Phylogeny of ITS data for the *Cystodermella* inferred by MP analysis. Bootstrap support (≥70%) and posterior probabilities (≥95%) are shown above and below branches (bs/pp), respectively. The type specimens are marked with asterisks (*); the original names of INSD sequences are used; *C.* = *Cystodermella*.

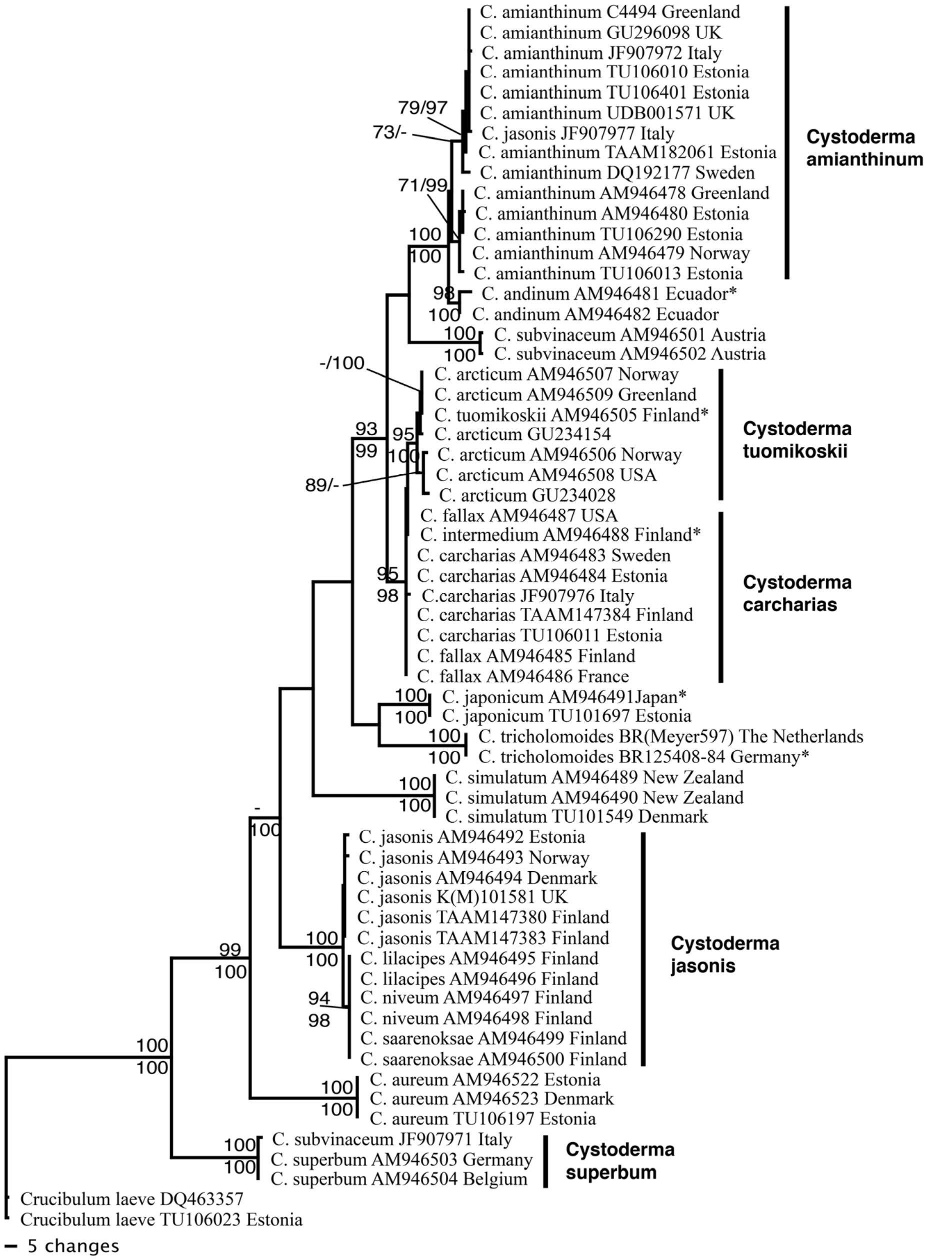

Figure 5. Phylogeny of ITS data for the *Cystoderma* inferred by MP analysis. Bootstrap support (≥70%) and posterior probabilities (≥95%) are shown above and below branches (bs/pp), respectively. The type specimens are marked with asterisks (*); the original names of INSD sequences are used; *C.* = *Cystoderma*.

Table 2. General distribution of species *Cystoderma*. The continent names are according to Brummitt (2001).

Species	**Distribution**	**References**
C. amianthinum	Europe^{T}, Africa, Asia-Temperate, Northern America, Southern America	Saar 2003
C. andinum	Southern America^{T}	Saar & Læssøe 2006
C. aureolum ^{D}	Southern America^{T}	Raithelhuber 1987
C. aureum	Europe^{T}, Asia-Temperate, Northern America	Wasser 1993
C. austrofallax	Southern America^{T}	Singer 1969, Minter et al. 2001
C. bonnardii	Europe^{T}	Thoen 2005
C. carcharias	Europe^{T}, Africa, Asia-Temperate, Northern America, Southern America	Saar 2003
C. caucasicum	Asia-Temperate^{T}	Smith & Singer 1945
C. chocoanum	Southern America^{T}	Franco-Molano 1993
C. ferruginosum	Africa^{T}, Southern America (?)	Pegler 1966, Guzmán & Guzmán-Dávalos 1984
C. granosum	Northern America^{T}	Smith & Singer 1945
C. fulvolateritium ^{D}	Southern America^{T}	Raithelhuber 1983
C. gruberianum	Northern America^{T}	Smith 1949
C. haematites	Europe^{T}	Huijsman 1956
C. japonicum	Europe, Asia-Temperate^{T}	Thoen & Hongo 1985
C. jasonis	Europe^{T}, Northern America	Saar 2003
C. jeoliense ^{D}	Asia-Tropical^{T}	Dhancholia et al. 1991
C. muscicola	Australasia^{T}	Grgurinovic 1997
C. pulveraceum	Northern America^{T}	Smith & Singer 1945
C. simulatum	Europe^{T}, Asia-Temperate, Australasia	Saar 2011
C. subornatum ^{D}	Southern America^{T}	Raithelhuber 1987
C. subvinaceum	Europe, Northern America^{T}	Smith & Singer 1945, Hausknecht 1994
C. superbum	Europe^{T}, Asia-Temperate	Huijsman 1956, Saar 2003
C. texense	Northern America^{T}	Thiers 1957
C. tricholomoides	Europe^{T}	Heinemann & Thoen 1973b
C. tuomikoskii	Europe^{T}, Asia-Temperate, Northern America	Saar 2003

^{T} = type specimen; ^{D} = doubtful species.

Table 3. General distribution of species *Cystodermella*. The continent names are according to Brummitt (2001).

Species	**Distribution**	**References**
C. adnatifolia	Europe, Asia-Temperate, Northern America^{T}	Saar 2003
C. australis	Northern America^{T}	Smith & Singer 1945
C. cinnabarina	Europe^{T}, Africa, Asia-Temperate, Northern America	Saar 2003
C. contusifolia	Southern America^{T}	Pegler 1983
C. cristallifera	Africa^{T}	Thoen 1969
C. elegans	Africa^{T}	Heinemann & Thoen 1973a, Kost 2002
C. granulosa	Europe^{T}, Africa, Asia-Temperate, Northern America, Southern America	Saar 2003
C. myriadocystis	Europe^{T}	Heinemann & Thoen 1973b
C. papallactae	Southern America^{T}	Saar & Læssøe 2006
C. subpurpurea	Europe, Northern America^{T}	Smith & Singer 1948, Cheype 1997

^{T} = type specimen

DISCUSSION

The distinction of genera *Cystoderma* and *Cystodermella* sensu Harmaja (2002) were supported in all analyses based on partial LSU and ITS rDNA sequences. In this respect, our results concur with those obtained in the analyses of LSU data in recent studies (Johnson and Vilgalys 1998, Moncalvo et al. 2002) that incorporated some members of the taxa treated here. In both studies, *Cystodermella granulosa* (as *Cystoderma*) appeared closely related with genus *Ripartitella*. *Cystoderma chocoanum* formed a sister group of the *Cystodermella-Ripartitella* clade (Johnson and Vilgalys 1998). In the analyses by Moncalvo et al. (2002) *Cystoderma chocoanum* and *C. amianthinum* formed a well-supported clade, with *Floccularia albolanaripes* (G.F. Atk.) Redhead as their sister group.

The genus *Cystoderma* sensu Harmaja (2002) appears monophyletic in the Bayesian analysis of the LSU data with the inclusion of *Phaeolepiota aurea*. While in the MP analysis, the lineage *C. superbum-Phaeolepiota* was distinguished as an unresolved sister clade with *Cystoderma*. Testing the constraint hypothesis, however, could not reject the inclusion of *C. superbum* Huijsman from the *Cystoderma* clade (IV). Heinemann and Thoen (1973b) regarded it as the single species of the section Superba, delimited by basidiospores that are amyloid only at the suprahilar zone. Singer (1986) did not accept the section Superba and treated this species as a member of the section *Cystoderma*, corresponding to genus *Cystoderma* by Harmaja (2002). Pegler and Young (1971) stated that the whole spore of *C. superbum* is weakly grey amyloid except for the suprahilar region, which is strongly amyloid. Considering the results of the phylogenetic analyses, *C. superbum* is regarded to be a member of the genus *Cystoderma*.

The study on the phylogeny of Agaricales by Garnica et al. (2007) support a close relationship between the monotypic genus *Phaeolepiota* and the type species of the *Cystoderma* (*C. amianthinum*) that form a significantly supported clade with the *Crucibulum-Cyathus* lineage. The multi-gene phylogeny presented by Matheny et al. (2006), likewise involving only the type species of *Cystoderma*, reveals the *Cystoderma-Crucibulum-Cyathus* lineage as a moderately supported sister group of the Agaricaceae in the Agaricoid clade. Walther et al. (2005) reported the similarity of the modes of conidiogenesis between *Cystoderma* and the representatives of Agaricaceae (conidiophores were not differentiated, conidia were formed by the fragmentation of branched hyphae and released rhexolytically), referring to a close relationship between these taxa. In contrast to the majority of the studied Agaricaceae, the conidia of *Cystoderma* did not usually swell. The results of the analyses of LSU data obtained in the present study, based on more extensive species sampling, do not support a close relationship between the species of *Cystoderma* and the *Cyathus-Crucibulum* lineage. The Bayesian analysis of LSU data demonstrates a well-supported sister group relationship of *Phaeolepiota aurea* and *Cystoderma* *superbum* to the *Cystoderma* clade, which does not receive considerable support in the MP analysis. Phylogenies based on ITS rDNA data, however, include *Phaeolepiota aurea* in genus *Cystoderma*. The results of the recent ITS analyses support the inclusion of *Phaeolepiota* in genus *Cystoderma* (figure 5), therefore the evaluation of the combination of *Phaeolepiota* aurea in *Cystoderma* as proposed by Kühner and Romagnesi (1953) should be preferred. Members of *Phaeolepiota* and *Cystoderma* share similar features of the epithelial covering of pileus and stipe. A chemotaxonomical study by Benedict et al. (1972) shows that the distribution patterns of urea and 10 chromatographically measured compounds supports a close relationship between these two genera.

The genetic variation of ITS region within species *Cystoderma amianthinum* exhibits paraphyletic nature of this species, which the neotropical *C. andinum* is derived from (Matheny and Griffith 2010). The results of ITS data indicate the occurrence of two infrageneric taxa, with *C. andinum* as a basal lineage (figure 5). In some other taxa, for example *C. jasonis*, *C. carcharias* and *C. tuomikoskii*, the intraspecific variation of ITS region was rather low, which brings up the issue of the species delimitation within these taxa. At least four *Squamanita* species: *S. basii* Harmaja, *S. paradoxa* (A.H. Sm. & Singer) Bas, *S. pearsonii* Bas, *S. umbilicata* Harmaja are suspected to parasitize *Cystoderma* species based on morphological evidence (Harmaja 1988, Redhead et al. 1994). Redhead et al. (1994) presume that the host of *S. phaeolepioticola* nom. prov. (*S. odorata* ss. Nagasawa et al. 1990) may be *Phaeolepiota aurea*. Matheny and Griffith (2010) succeeded in sequencing *S. paradoxa*, both parasite and host, which was determined as *Cystoderma amianthinum*. They also indicate that these *Squamanita* species may parasitize closely related species within their own clade, but this association was not supported by any analyses.

It is highly unlikely that the species *C. simulatum* occur naturally both in New Zealand and Europe. This species is presumably indigenous for New Zealand and has spread into Europe by means of imported seedlings and/ or soil. The type specimen from the UK and the only sequenced European specimen from Denmark were found in plantations. However, it is not known which tree species were cultivated in the UK plantation, whereas the Danish specimen was found in *Abies* sp. plantation. Therefore it is premature to reach the decision on the invasiveness of the species *C. simulatum* in Europe. Prior to that, more European specimens should be sequenced and the history of their habitat should be carefully recorded. It is recommended that this species should be included into nature monitoring lists in order to study if its distribution is expanding and what the rate of spreading is.

The genus *Cystodermella* appeared monophyletic in almost all analyses, receiving considerable support except for the Bayesian analysis of LSU data. MP analysis of the LSU data supported the sister group relationship between *Cystodermella* and *Ripartitella*, concordantly to the result of an earlier phylogenetic study (Moncalvo et al. 2002). Likewise, the culture studies by Pantidou et al. (1983) and Ovrebo (1988) indicated a close relationship between *Cysto-*

dermella and *Ripartitella*. The representatives of both genera shared similar conidiogenesis: conidiophores were not differentiated, arthroconidia were formed by the fragmentation of hyphae. However, the conidia of *Cystoderma* are also formed in the same way (Walther et al. 2005). *Ripartitella* differs from *Cystodermella* by echinulate spores, which are similarly inamyloid, also having trichodermium instead of epithelium in pileus and stipe (Singer 1947: 85).

In infrageneric taxonomy of the *Cystoderma* sensu Singer (1986), the spore wall amyloidity has been used extensively as a defining characteristic. The results presented in this study reveal that amyloidity of spores, considered consistent within the treated genera (Harmaja 2002), varies in *Cystoderma*. Harmaja transferred *Cystoderma japonicum* to *Cystodermella* because it produces inamyloid basidiospores. Our results, however, show that it belongs to *Cystoderma*. Based on the author's experience, determining the state of this characteristic is complicated because most basidiospores are comparatively small and the colouring reaction is often rather weak. Therefore this characteristic alone cannot be considered as a reliable feature to distinguish these genera.

Based on the studied species, the genus *Cystoderma* can be defined by the formation of amyloid basidiospores, exceptionally *C. aureum* and *C. japonicum* possessing inamyloid basidiospores, and having a persistent membranous ring on upper part of the stipe. In contrast, species of *Cystodermella* are characterised by inamyloid spores, evanescent floccose-scaly ring zone and the presence of cystidia in some species. Further studies are needed to understand the relationships between species not treated in this study. Considering only morphology can result in misleading generic relationships as recently exemplified by relocating *Cystodermella luteohemisphaerica* (Dennis) Harmaja into the genus *Cystolepiota* Singer (Saar and Læssøe 2008).

The tribe Cystodermateae sensu Singer (1986) appeared paraphyletic according to the analyses of LSU rDNA sequences. The phylogenetic relationships among the genera involved could not be unequivocally resolved based on partial LSU sequences only. The genus *Pseudobaeospora* appeared to be closely related to the genera *Tricholoma* (Fr.) Staude and *Lepista* (Fr.) W.G. Sm., concordant to Kühner (1980) who included it in the tribe Tricholomateae. Lack of support in the backbone of the trees based on LSU data indicate the need for further studies on the tribe Cystodermateae implying phylogenetic analyses of multiple genes.

CONCLUSIONS

The separation of genus *Cystodermella* from *Cystoderma* was well supported in phylogenetic analyses of LSU and ITS rDNA data. In contrast, there are no definite morphological characters distinguishing these two genera. The majority of studied species from genus *Cystoderma* are characterized by weakly to strongly amyloid basidiospores, except for *C. aureum* and *C. japonicum* having inamyloid basidiospores. Infrequently, a persistent membranous annulus or arthroconidia in the upper part of pileus context are present in a few species. The species from genus *Cystodermella* possess inamyloid basidiospores and the presence of cystidia is distinctive to few species.

The recent study on the phylogeny of Agaricales supports a close relationship between the monotypic genus *Phaeolepiota* and the type species of *Cystoderma* (Garnica et al. 2007) with *Crucibulum*-*Cyathus* lineage as significantly supported sister group (Garnica et al. 2007, Matheny et al. 2006). The results of the analyses of ITS data support the inclusion of *Phaeolepiota* in genus *Cystoderma*, therefore the following combination – *Cystoderma aureum* (Matt.) Kühner & Romagn. should be preferred. The results of previous studies and this thesis support the sister group relationship between *Cystodermella* and *Ripartitella* (Moncalvo et al. 2002, Saar et al. 2009). *Ripartitella* differs from *Cystodermella* by echinulate spores, which are similarly inamyloid, also having trichodermium instead of epithelium in pileus and stipe (Singer 1947). The representatives of genus *Ripartitella* are known from tropical America, but recently a couple of sequences from collections in Japan have been deposited in INSD.

Two new species, *Cystoderma andinum* I. Saar & Læssøe and *C. papallactae* I. Saar & Læssøe were described from high Andean Ecuador. *Cystoderma andinum*, characterised by a greyish-orange pileus and strongly amyloid, broadly ellipsoid to ellipsoid basidiospores (6.0–7.5 × 4.5–5.5 µm), is closely related to *C. amianthinum*. *Cystodermella papallactae* (I. Saar & Laessøe) Vizzini, collected in Ecuador at high elevations, is characterised by brownish-orange pileus and large inamyloid, ellipsoid to oblong basidiospores (5.0–6.0 × 3.0–4.0 µm). Evaluating the morphological and molecular characters of species *Cystoderma luteohemisphaericum*, the new combination – *Cystolepiota luteohemisphaerica* (Dennis) I. Saar & Læssøe was proposed.

The morphological study of the type specimens of some *Cystoderma* species revealed that *Cystoderma simulatum* as the earliest name should be used and the other three – *C. clastotrichum*, *C. freirei, C. neoamianthinum* – are considered as synonyms. The specimen of *Cystoderma japonicum* in Estonia was collected; it is probably the first finding outside Japan, where the type specimen was found.

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SUMMARY IN ESTONIAN

Seeneperekondade *Cystoderma* ja *Cystodermella* (*Agaricales*) taksonoomia ja fülogenees

Fayod (1889) kirjeldas perekonda *Cystoderma*, eraldades sinna seitse liiki perekonna *Agaricus* triibusest *Lepiota* (Fries 1821): *Lepiota amianthina* Scop., *L. granulosa* Batsch, *L. cinnabarina* Alb. & Schwein., *L. carcharias* Pers., *L. seminuda* Lasch, *L. fumosopurpurea* ja *L. georginae*. Esimest nelja liiki tunnistatakse siiani perekonda *Cystoderma* kuuluvat, kuid viimased kolm on hilisemate autorite poolt tõstetud teistesse perekondadesse. Nende puhul on hetkel üldkasutatavad nimed *Cystolepiota seminuda* (Lasch) Bon, *Leucoagaricus georginae* (W. G. Sm.) Candusso ja *Melanophyllum haematospermum* (Bull.) Kreisel (sünonüüm *L. fumosopurpurea*).

Esimene perekonna *Cystoderma* monograafia sisaldas 14 liiki, mis olid kandeoste amüloidsuse alusel jagatud kahte sektsiooni: inamüloidsete kandeostega *Granulosa* ja amüloidsete kandeostega *Amianthina* (Smith ja Singer 1945). Viimase asemel võttis Singer (1962) kasutusele sektsiooni nimetusega *Cystoderma*. Hilisem monograafiline uurimus (Heinemann ja Thoen 1973b) sisaldas juba 26 liiki, uuena võeti kasutusele kaks sektsiooni: *Superba*, mille kandeosed on amüloidsed ainult suprahilaarses vööndis, ning *Cinnabarina*, inamüloidsete kandeoste ja tsüstiididega.

Harmaja (2002) tõstis perekonna *Cystoderma* inamüloidsete kandeostega liigid uude perekonda *Cystodermella*, võttes arvesse Moncalvo jt (2002) rDNA LSU regiooni fülogeneetilise analüüsi tulemused ja tuuma DNA-sisalduse valitud *Cystoderma* liikides (Saar ja Kullman 2000). Singer (1986) määratles triibuse *Cystodermateae* liikmetena perekondi *Cystoderma*, *Phaeolepiota* Maire ex Konrad & Maubl., *Squamanita* Imbach., *Dissoderma* (A. H. Sm. & Singer) Singer, *Horakia* Oberw., *Pseudobaeospora* Singer ja *Ripartitella* Singer. Kühner (1980) pidas sellesse triibusesse kuuluvaks neist kolme esimest, kuid tõstis perekonna *Pseudobaeospora* triibusesse *Tricholomateae*.

Erinevad autorid on seda triibust paigutanud erinevatesse taksonitesse. Singer (1986) paigutas triibuse *Cystodermateae* sugukonda *Agaricaceae*, aga mitmed teised autorid (Heinemann ja Thoen 1973b, Kühner 1980, Bas 1988) tõstsid selle sugukonda *Tricholomataceae*. Viimaste autorite morfoloogiliste tunnuste alusel esitatud hüpoteesi kinnitas hiljem rDNA LSU geenijärjestustel põhinev töö (Johnson ja Vilgalys 1998). Hilisemates lehikseente fülogeneetilistes uuringutes jäi triibuse *Cystodermateae* paiknemine fülogeneesipuul lahendamata (Moncalvo jt 2000, 2002), seda ka juhtudel, kui molekulaarseid tunnuseid kasutati koos konidiogeneesi (Walther jt 2005) või kandeoste ultrastruktuuri andmetega (Garnica jt 2007).

Uusima seltsi *Agaricales* multigeense analüüsi põhjal lahenes perekonna *Cystoderma* asukoht fülogeneesipuul, kus see moodustas koos perekondade *Cyathus* ja *Crucibulum* esindajatega sugukonna *Agaricaceae* mõõdukalt toetatud sõsarrühma (Matheny jt 2006). Perekondade *Cystoderma* ja *Phaeolepiota* lähedane sugulus ja toetatud ühisklaadi moodustumine perekondadega *Crucibulum* ja *Cyathus* leidis kinnitust ka Garnica jt (2007) töös.

Perekonda *Cystoderma* arvatakse tänapäeval ligikaudu 35 ja perekonda *Cystodermella* 12 liiki, neist esimesel on tüüpliigiks *C. amianthinum* (Scop.: Fr.) Fayod ja teisel *C. granulosa* (Batsch: Fr.) Harmaja (Kirk jt 2008).

Perekondade *Cystoderma* ja *Cystodermella* viljakehad on väikese kuni keskmise suurusega. Kübar on kuni 10 (…20) cm laiune, sageli näsaga, mõnikord radiaalselt kurruline, teraline kuni peenelt soomuseline, matt, kuiv, erinevat värvi, serv noorelt loorijäänustega. Lamellid on kinnitunud kuni ümardunult, nõgusalt või hambaga külge kasvanud; valged kuni kahvatukreemid või kollakad. Jalg on ülaosas paljas ja õrnalt triibuline, allpool peenelt kuni jämedalt teralisvatjas, kübara tooni. Lõhn on ebameeldiv või puudub eriline lõhn üldse. Maitse poolest mahe või ebameeldiv, eriline maitse võib ka üldse puududa. Eospulber on valge kuni kahvatukreem. Kandeosed on ellipsoidsed, piklikud või käävjad, siledad, idupoorita, hüaliinsed. Kübaranahk on epiteelstruktuuriga. Üldloori jäänused kübara- ja jalapinnal koosnevad ümaratest kuni ellipsoidsetest sfärotsüstidest.

Perekonna *Cystoderma* liike iseloomustavad nõrgalt kuni tugevalt amüloidsed kandeosed; jalal esinev püsiv, teralise alaosaga nahkjas rõngas või kaduv teralisvatjasebemeline rõngas ja artrokoniidide moodustumine kübaranahaaluses seenelihas mõnedel liikidel. Perekonna *Cystodermella* liikidele on iseloomulik inamüloidsete kandeoste, kaduva teralisvatjasebemelise rõnga ja mõnel üksikul liigil ka tsüstiidide esinemine.

Mõlema perekonna liigid kasvavad enamasti metsaökosüsteemides, kuid võivad esineda ka avamaastikel, kasvades pinnasel, kõdukihil, samblas ja mõned liigid ka väga kõdunenud puidul. Siiani pole täpselt teada, kas need seened on saprotroofse ja/või biotroofse eluviisiga, kuid mitmed autorid on märganud nende kooskasvamist sammaldega ja arvanud, et tegemist võib olla sammalde biotroofidega (Heinemann ja Thoen 1973b; Harmaja 1979, 1985). Perekonnad *Cystoderma* ja *Cystodermella* on levinud ülemaailmselt, kuid enamik kirjeldatud liike on pärit parasvöötmest, mis viitab troopilise piirkonna vähesele uuritusele.

Minu töö eesmärkideks oli 1) esitada hüpoteesid perekondade *Cystoderma* ja *Cystodermella* liikide piiritlemiseks, kasutades morfoloogilisi ja molekulaarseid tunnuseid; 2) testida hüpoteesi perekondade *Cystoderma* ja *Cystodermella* monofüleetilisusest; 3) leida nende perekondade sõsarrühmad; 4) kirjeldada Ecuadorist (Lõuna-Ameerika) kogutud materjali põhjal uusi liike teaduses; 5) koostada perekondade *Cystoderma* ja *Cystodermella* kõigi teadaolevate liikide kriitiline nimestik.

Perekondade *Cystoderma* ja *Cystodermella* eristamine Harmaja (2002) poolt leidis kinnitust rDNA ITS ja LSU geenijärjestuste fülogeneetilistes analüüsides. Samas ei leitud morfoloogilisi tunnuseid, mis võimaldaks neid kahte perekonda üksteisest eristada. Suuremat osa autori poolt uuritud perekonna *Cystoderma* liikidest iseloomustavad nõrgalt kuni tugevalt amüloidsed kandeosed. Erandiks on liigid *C. aureum* ja *C. japonicum,* millel need inamüloidsed on. Harva esineb selle perekonna liikidel kas püsiv nahkjas rõngas või artrokoniidid kübaranahaaluses seenelihas. ITS geenijärjestustel põhineva analüüsi tulemused toetavad monotüüpse perekonna *Phaeolepiota* arvamist perekonda *Cystoderma*. Ka teiste autorite varasemad tööd näitasid nende kahe perekonna lähedast sugulust (Garnica jt 2007, Matheny jt 2006), mistõttu aktsepteerib selle töö autor kombinatsiooni *Cystoderma aureum* (Matt.) Kühner & Romagn. perekonna *Phaeolepiota* ainsa liigi kehtiva nimena. Varasemate tööde (Moncalvo jt 2002, Saar jt 2009) ja selle väitekirja tulemused toetavad perekondade *Cystodermella* ja *Ripartitella* sugulust lähedase sõsarrühmana. Perekonna *Ripartitella* liike iseloomustavad näsalised kandeosed, mis on sarnaselt *Cystodermella* liikidega inamüloidsed. Erinev on kübaranaha struktuur: *Ripartitella* puhul on kübaranahk trihhodermstruktuuriga, aga perekonnal *Cystodermella* on see epiteelstruktuuriga (Singer 1947).

Antud töös kirjeldati kaht uut liiki Ecuadorist: *Cystoderma andinum* I. Saar & Læssøe ja *C. papallactae* I. Saar & Læssøe. Liiki *Cystoderma andinum* iseloomustab hallikasoranž kübar ja tugevalt amüloidsed, laiellipsoidsed kuni ellipsoidsed kandeosed (6,0–7,5 × 4,5–5,5 µm). See liik on lähedane liigile *C. amianthinum*. Liigile *Cystodermella papallactae* (I. Saar & Laessøe) Vizzini on iseloomulik pruunikasoranž kübar ja suured inamüloidsed, ellipsoidsed kuni piklikud kandeosed (5,0–6,0 × 3,0–4,0 µm). Hinnates liigi *Cystoderma luteohemisphaericum* Dennis morfoloogilisi ja molekulaarseid tunnuseid, leiti, et see liik tuleb üle viia teise perekonda ja esitati uus nimekombinatsioon *Cystolepiota luteohemisphaerica* (Dennis) I. Saar & Læssøe. Mõnede *Cystoderma* liikide tüüpeksemplaride morfoloogiline uurimine viis järelduseni, et järgnevad kolm liiki – *C. clastotrichum*, *C. freirei, C. neoamianthinum* – on liigi *C. simulatum* sünonüümid.

Siiani pole teada seeneliike, mis leviksid looduslikult nii Uus-Meremaal kui ka Euroopas. Arvatavasti on liik *Cystoderma simulatum* pärit Uus-Meremaalt, kust ta on sissetoodud seemikute ja/või mullaga Euroopasse levinud. Suurbritanniast pärit tüüpeksemplar ja siiani ainuke Euroopa sekveneeritud eksemplar Taanist leiti istandustest, esimese kohta pole puuliik teada, aga teine kasvas nulupuistust (*Abies* sp.). Andmete vähesuse tõttu ei saa otsustada liigi invasiivsuse üle Euroopas, kuid soovitav oleks tulevikus molekulaarsesse analüüsi rohkem eksemplare kaasata. Ühtlasi tuleks selgitada leitud eksemplaride elupaikade muster. Riikides, kust seda liiki on juba leitud, on soovitav see lisada seiratavate liikide nimekirja, et selgitada, kas selle liigi levikuala on laienemas ja milline on levimiskiirus. Eestist leiti 2011. aastal esmakordelt liigi *Cystoderma japonicum* eksemplar, mis on ilmselt esimene leid väljaspool Jaapanit, kust selle liigi tüüpeksemplar on leitud ja kus seda on kirjeldatud.

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PUBLICATIONS

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Diversity of multitaxon assemblages associated with fruitbodies of basidiomycetes
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Publications (CC):

Saar I. 2003. The genera *Cystoderma* and *Cystodermella* (Tricholomataceae) in temperate Eurasia. Mycotaxon 86: 455–473.

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Conference presentations:

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Awards and scholarships

Molecular phylogeny of Tricholomataceae and Thelephorales (Homobasidiomycetes, Fungi), European Commission's (FP 6) Integrated Infrastructure Initiative program SYNTHESYS (DK-TAF 527), 16.01–12.02.2005.

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II. Teaduslik ja arendustegevus

Peamised uurimisvaldkonnad

Kandseente viljakehades elunevate organismide mitmekesisus

Looduskaitseliselt oluliste ning Eestis väheuuritud seenerühmade seisund ja ohustatus

Ektomükoriisat moodustavate seente ja peremeestaimede valitud taksonite koevolutsioon

Publikatsioonid (CC):

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