The genus *Dermoloma* is more diverse than expected and forms a monophyletic lineage in the Tricholomataceae

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Abstract

We present the first phylogenetic evaluation of the genus *Dermoloma*, which is resolved as monophyletic and closely related to *Pseudotricholoma*, a poorly known *Dermoloma*-like lineage within the family Tricholomataceae. The position of *Dermoloma* is confirmed by the placement of the type species, *Dermoloma cuneifolium*, represented by multiple samples including the neotype. Based on our phylogenetic analyses, we recognised 25 European operational taxonomic units (OTUs) but could only assign species names to ten of them based on ex-type sequences. Furthermore, only five additional published *Dermoloma* names of uncertain status are available for the remaining 16 potential European species, thus demonstrating an unexpected amount of taxonomic diversity. Samples from Europe and North America seem to be endemic on a continental scale. North American samples formed six unique OTUs, but only one could be reliably named, *Dermoloma hymenocephalum*. *Dermoloma* is morphologically defined by basidiomata with brown, grey and white colours with a farinaceous odour and a pluristratous hymeniderm type of pileipellis. Our phylogenetic analyses support the subdivision of the genus into two subgenera and four sections, and species with inamyloid basidiospores are placed in subg. *Dermoloma* and those with amyloid basidiospores in subg. *Amylospora*. Both subgenera are further divided into two sections. The analysis of spore morphology shows that sect. *Conica* of subg. *Dermoloma* and sect. *Nigrescentia* of subg. *Amylospora* have a very distinctive spore shape. Sect. *Atrobrunnea* of subg. *Amylospora* showed relatively high variability of spores among species, but spores of sect. *Dermoloma* were similar and not useful for species discrimination.

Keywords  Agaricales · Infrageneric classification · Systematics · Cryptic diversity · CHEGD fungi

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**Introduction**

The genus *Dermoloma* (J. Lange) Singer ex Herink is a poorly known group of agarics defined by small- to medium-sized basidiomata of collybioid to tricholomatoid habit with dull grey, brownish or white colourations; sinuate to adnate-decurrent lamellae; farinaceous smell (or taste); smooth, hyaline, amylloid or inamyloid basidiospores; and a pileipellis of a pluristratous (multi-layered) hymeniderm type (Arnolds 1992; Singer 1975, 1986). Thirty-nine unique names at species and lower rank have been published or combined in the genus ([http://www.mycobank.org](http://www.mycobank.org), [http://www.indexfungorum.org](http://www.indexfungorum.org)). Among them, 25 were published from Europe, six from the Americas and eight from other continents. Among European names, four are invalid or illegitimate and three are infraspecific taxa. This means that 18 valid species names are published from Europe (Table 1).

The number of accepted species has varied over the years in Europe. Bon (1986, 1998) accepted eight species, but only three were adopted by Arnolds (1992, 1993), who later added one more European species (Arnolds 2002). It is not clear if Contu et al. (2008) accepted all previously described European species as separate taxa, but they considered that the diversity of European *Dermoloma* was higher, and described four new species, one of which was not validly published. Only three species are included in a recent key of Nordic mycobiota (Vesterholt 2008, 2012). European species are mostly found in grassland ecosystems and are part of a group of fungi with special conservation interest that has been referred to as CHEGD (acronym of taxon names with the last letter referring to *Dermoloma*) (Griffith et al. 2013). The diversity of the genus in North America has not been explored, and only a single species, *Dermoloma hymenocephalum* (A.H. Smith) Singer, has been described from the USA (Singer 1962).

*Dermoloma* is classified in the family Tricholomataceae R. Heim ex Pouzar ([www.mycobank.org](http://www.mycobank.org)) based on morphological characters (Singer 1975, 1986). Bon (1979) proposed an alternative morphology-based placement based on the pileipellis structure in the family Dermolomataceae (Bon) Bon, but this was not generally accepted. The first phylogenetic study that included a member of the genus placed *Dermoloma* in the monophyletic genus *Tricholoma* (Fr.) Staude. In their phylogenetic tree, the monophyletic genus *Pseudotricholoma* (Singer) Sánchez-Garcia and Matheny is nested within *Tricholoma*, making the latter paraphyletic. *Dermoloma* species are traditionally grouped into two sections: D. sect. *Dermoloma* with inamyloid basidiospores and D. sect. *Atrobrunnea* with amylloid basidiospores (Contu et al. 2008).

Different opinions about classification at family rank suggest that the morphological concept of the genus *Dermoloma* might correspond to several unrelated phylogenetic lineages. Variable species concepts in the European literature focused on spore characters, in combination with additional field characters, suggest that species taxonomy needs extensive revision. Here, we produce the first phylogenetic study of the genus. Our aims are to (i) verify if morphological circumscription of the genus corresponds to a monophyletic group; (ii) define the phylogenetic placement of the genus, including morphological and phylogenetic limits; (iii) estimate if species diversity in Europe and North America correspond to current taxonomic opinions; (iv) assign species names to clades fixed by sequencing type collections; and (v) specify phylogenetic signal and taxonomic relevance of spore characters.

**Material and methods**

**Taxon sampling**

The study combined type material and other samples collected or gathered by the authors. We were able to borrow 20 of 23 existing *Dermoloma* types from Europe and North America (Table 2). Recent material consisted of additional 87 specimens collected from Estonia (1 collection), France (14), Italy (2), Romania (8), Slovakia (26), Switzerland (1), UK (33) and the USA (2), and 21 borrowed herbarium specimens from Italy (9), Sweden (4) and the USA (8). *Dermoloma* samples collected by the authors of this study were identified based on agaricoid basidiomata of grey, brown and white colours, hymeniderm pileipellis and usually conspicuous farinaceous odour (Arnolds 1992).

**DNA extractions and sequencing**

A small piece of dried material (10–30 mg) was removed and ground in a 1.5-ml tube with sterilized sand, liquid nitrogen and a micropestle. Genomic DNA was extracted using the E.Z.N.A. Fungal DNA Mini Kit (Omega Bio-Tek, Inc., Norcross, GA, USA) and the E.Z.N.A. HP Fungal DNA Kit (Omega Bio-Tek) following the manufacturer’s instructions. Genomic DNA was serially diluted into two 1:10 dilutions with sterile water. The following loci were targeted: (i) the internal transcribed spacer regions of nuclear ribosomal DNA (nrITS), (ii) nuclear ribosomal large subunit (nrLSU), (iii) the first largest subunit of RNA polymerase II (*rpb1*) and (iv) the most variable region between domains 6 and 7 of the nuclear gene encoding the second largest subunit of RNA polymerase II (*rpb2*). Amplification of DNA was performed using a PCR mix consisting of approximately 2 ng/μl of template DNA, forward and reverse primers (10 pmol/μl), 5× HOT FIREPol® Blend Master Mix (Solis BioDyne, Tartu, Estonia), and PCR conditions as described in the materials and methods section.
Table 1 List of all species and lower rank taxa published or combined in the genus *Dermoloma* sorted by continent with information of the type country of origin

| Continent       | Species Information                                                                 |
|-----------------|--------------------------------------------------------------------------------------|
| Africa: 1 name  | *Dermoloma griseocarneum* Pegler, *Kew Bulletin Additional Series* 6: 213 (1977)   |
| Holotypus:      | Uganda                                                                               |
| America: 6 names| *Dermoloma atrobrunneum* (Dennis) Singer ex Bon, *Documents Mycologiques* 17(65): 51 (1986)  |
| Holotypus:      | Trinidad and Tobago (Trinidad Isl.)                                                  |
|                | *Tricholoma atrobrunneum* Dennis, *Transactions of the British Mycological Society* 34: 476 (1951)  |
|                | ≡ *Dermoloma atrobrunneum* Singer, *Sydowia* 9(1–6): 375 (1955)                      |
|                | Holotypus: USA                                                                       |
|                | *Dermoloma aposcenum* Singer, *Fieldiana Botany* 21: 88 (1989)                       |
|                | Holotypus: Mexico                                                                    |
|                | *Dermoloma hymenocephalum* (A.H. Sm.) Singer, *Sydowia* 15(1–6): 142 (1962)         |
|                | ≡ *Collybia hymenocephala* A.H. Sm., *Papers of the Michigan Academy of Sciences* 26: 61 (1941)  |
|                | ≡ *Hydropus hymenocephalus* (A.H. Sm.) Redhead, *Sydowia* 37: 266 (1984)             |
|                | Holotypus: USA                                                                       |
|                | *Dermoloma inconspicuum* Dennis, *Kew Bulletin* 15(1): 78 (1961)                    |
|                | Holotypus: Venezuela                                                                  |
|                | *Dermoloma pataguae* Singer, *Fieldiana Botany* 21: 89 (1989)                       |
|                | Holotypus: Chile                                                                     |
|                | *Dermoloma yungense* Singer, *Beilh. zur. Sydowia* 7: 61 (1973)                     |
|                | Holotypus: Bolivia                                                                   |
| Asia: 4 names   | *Dermoloma cystidiatum* Manim. & Arnolds, *Persoonia* 17(1): 149 (1998)              |
| Holotypus:      | India                                                                                |
|                | *Dermoloma indicum* K.N.A. Raj & Manim., *Phytopaxa* 177(4): 239 (2014)              |
|                | Holotypus: India                                                                     |
|                | *Dermoloma keralense* K.N.A. Raj & Manim., *Phytopaxa* 177(4): 241 (2014)            |
|                | Holotypus: India                                                                     |
|                | *Dermoloma scotodes* (Berk. & Broome) Pegler, *Kew Bulletin Additional Series* 12: 182 (1986)  |
|                | ≡ *Agaricus scotodes* Berk. & Broome, *Botanical Journal of the Linnean Society* 11(56): 522 (1871)  |
|                | Holotypus: Sri Lanka                                                                  |
| Australia and Oceania: 3 names | *Porpoloma amyloideum* (G. Stev.) E. Horak, *New Zealand Journal of Botany* 9(3): 407 (1971)  |
| Holotypus:      | New Zealand                                                                          |
|                | *Dermoloma amyloideum* (G. Stev.) G. Stev., *Field Guide to Fungi* 73 (1982)         |
|                | ≡ *Tricholoma amyloideum* G. Stev., *Kew Bulletin* 19(1): 15 (1964)                  |
| Europe: 21 valid names and 4 invalid names | *Dermoloma alexandri* Cons., *Micolgia e Vegetazione Mediterranea* 22(2): 84 (2008)  |
| Holotypus: Italy|                                                                                      |
|                | *Dermoloma atrocinereum* (Pers.) P.D. Orton, *Transactions of the British Mycological Society* 43(2): 175 (1960)  |
|                | ≡ *Agaricus atrocinereus* Pers., *Synopsis methodica fungorum* 348 (1801)             |
|                | – *Dermoloma atrocinereum* (Pers.) Herink, *Sb. severočeského Musea* Historia Naturalis 1: 62 (1958)  |
| Neotypus designed by Contu, Consiglio & Setti (2008): Italy | *Dermoloma bellerianum* Bon, *Documents Mycologiques* 28(nos. 109–110): 6 (1998)  |
| Holotypus: France|                                                                                      |
|                | [*Dermoloma chelilocystidiatum* Contu, *Bollettino dell’Associazione Micologica ed Ecologica Romana* 15(no. 48): 4 (2000), nom. inval. published as nomen provisorium]  |
| Authentic material: Italy | *Dermoloma coryleti* Singer & Clémençon, *Schweizerische Zeitschrift für Pilzkunde* 49(9): 120 (1971)  |
Estonia) and molecular grade water added up to 20 μl, or using a mixture of 5× buffer, GoTaq and dNTPs supplied by Invitrogen Corp. (Carlsbad, CA, USA). All PCRs started with an initial denaturation step at 95 °C for 15 min.

The nrITS was amplified with the primers ITS1F-ITS4 (Gardes and Bruns 1993; White et al. 1990), Reaction conditions consisted of denaturation at 95 °C for 35 s, annealing at 55 °C for 55 s and elongation at 72 °C for 45 s, then followed...
by 13 cycles of denaturation at 95 °C for 35 s, annealing at 55 °C for 55 s and elongation at 72 °C for 2 min and the last 9 cycles with the same conditions for denaturation and annealing, with a longer elongation of 3 min. A final extension was carried out at 72 °C for 10 min. The nrLSU was amplified using the primer pairs LR0R/LR16, LR0R/LR5 or LR0R/LR7 (Vilgalys and Hester 1990, https://sites.duke.edu/vilgalyslab/rdna_primers_for_fungi/). The PCR conditions were as follows: 1 min at 95 °C, 1 min at 50 °C, 1 min at 72 °C, repeated 35 times, and a final extension step for

| Species | Collection details | Herbarium | Type status | Sequencing outputs |
|---------|--------------------|-----------|-------------|--------------------|
| D. alexandri Cons. | Italy; Mesole (FE), Boscone della Mesola, G. Consiglio, M. Panchetti, R. Bolletta & C. Orlandini, 12 Sep 2004 | Herbarium of G. Consiglio (GC04317) | HT | MW193776 |
| D. atrocinereum (Pers.) P.D. Orton | Italy; Villleta Barrea (AQ), Abruzzo, M. Contu et al., 19 Sep 2003 | AQUI (Contu 19.IX.2003) | NT | MW193803 |
| D. bellerianum Bon | France; Beller, 30 Sep 1972 | LIP (Bon 912) | HT | Not located |
| D. coryleti Singer & Cléménçon | Czechia; Kroměříž, R. Singer, 30 Sep 1970 | F (R. Singer C-5230) | HT | Not located |
| D. cuneifolium (Fr.: Fr.) Bon | Sweden; Småland, Femsjö, ‘Avaberget’, S. Lundell & G. Haglund, 19 Sep 1948 | UPS F-631065 | NT | MW193843 |
| D. cuneifolium var. punctipes Arnolds | Netherlands; prov. Limburg, Wijlre, ‘Wakelberg’, E. Arnold, 22 Oct 1984 | L 0821553 | HT | Failed |
| D. emiliae-dlouhyi Svrček | Czechia; Brdské hřebeny Mts., Vížina, M. Svrček, 20 Sep 1965 | PR 610931 | HT | Failed |
| D. fuscobrunneum P.D. Orton | UK; Somerset, Backham Wood, Crawley, P.D. Orton, 24 Oct 1975 | E 16876 | HT | Failed |
| D. hybridum (Kühner) Bon | France; bois d’Avoudrey (près Besançon), R. Kühner, 16 Oct 1946 | G 126676 | HT | Failed |
| D. hygrophorus Joss. | France; Ain, Quincieu, Lacombe & Josserand, 14 Aug 1956 | GG00127362 | HT | MW193845, partial ITS sequence |
| D. hymenoecephalum (A.H. Sm.) Singer | USA; Michigan, Dexter, Silver lake, A.H. Smith, 23 Sep 1938 | MICH 10228 | HT | MW193846, partial ITS sequence |
| D. intermedium Bon | France; Somme, Warlus, towards Airaines, M. Bon, Oct 1967 | LIP (Bon 71081) | HT | Failed |
| D. intermedium var. coniferarum Bon | France; Argol, Mornand, 28 Oct 1982 | LIP (Bon 8116) | HT | sequencing successful, not Dermoloma |
| D. josserandii Dennis & P.D. Orton | UK; South Somerset, Spaxton, Hawkridge, E. Marrigae, 15 Sep 1958 | K(M) 37580 | HT | Failed |
| D. longibasidiatum Cons., Contu & Setti | Italy; Pergine (TN), Susa, G. Consiglio, G. Marasca et B. Oss-Emer, 30 Nov 1993 | Herbarium of G. Consiglio (GC93318) | HT | Failed |
| D. magicum Arnold | Netherlands; Limburg, Epen, Cotessen, E. Arnold, 21 Oct 1995 | L (Arnolds 6701) | HT | Not located |
| D. murinellum E. Horak | Switzerland; Graubünden, N des Albupasses (Terrassas), E. Horak, 30 Aug 1982 | ZT Myc 42786 (Horak ZT1573) | HT | Failed |
| D. paeoepodium P.D. Orton | UK; Devon, Membury, P.D. Orton, 28 Oct 1977 | E 16877 | HT | MW193852 |
| D. pragense Kubička | Czechia; Praha, „Kinského sady“, E. Wichanský 22 Jun 1965 | PR 611173 | HT | Failed |
| D. pragense f. obscurum Cons. & Contu | Italy; Monte Grino, near Piobbico (PU), G. Consiglio & M. Maletti, 22 Oct 2006 | Herbarium of G. Consiglio (GC06186) | HT | MW193853 |
| D. pseudocuneifolium Herink ex Bon | France; near Saint-Valery-sur-Somme, Oct 1968 | LIP (Bon 81006) | HT | Failed |
| D. pusillum Contu | Italy; Sardinia, Olbia (OT), Pittolongu, M. Contu, 30 Dec 2006 | AQUI (Contu 30.XII.2006) | HT | MW193861 |
| D. simulatum Cons., Contu & Setti, nom. inval. | Italy; Trento-Alto Adige, Susa (TN), G. Consiglio, G. Marasca & B. Oss-Emer, 30 Oct 1993 | Herbarium of G. Consiglio (GC02284) | AM | Failed |

Codes starting with MW are GenBank numbers
HT holotype, NT neotype, AM authentic material
10 min at 72 °C. The primers bRPB2-6F and bRPB2-7.1R (Matheny 2005) were used to amplify the rpb2 region. PCR conditions were as follows: 1 min at 95 °C, 1 min at 58 °C, an increase of 1 °C per 5 s to 72 °C and 1 min at 72 °C, repeated 35 times and finalized for 10 min at 72 °C. The RPB1 region was amplified using the primers gRPB1-A for and RPB1-C rev (Matheny et al. 2002) under the following PCR conditions: 1 min at 95 °C, 1 min and 30 s at 55 °C, an increase of 1 °C every 5 s to 72 °C and 2 min at 72 °C, repeated 35 times and finalized for 10 min at 72 °C.

The targeted fragments were purified using a PCR Purification Kit (Qiagen, Hilden, Germany). Sequence reactions were performed with BigDye Terminator 3.1 (Applied Biosystems, Foster City, CA, USA) and purified using Sephadex G-50 columns (General Electric Healthcare, Piscataway, NJ, USA). Sequencing was performed at the University of Tennessee Genomics Core and at the SEQuencing company (Dobřiš, Czech Republic).

Sequence editing and phylogenetic analyses

Sequence files were edited in Geneious (version R10) (Kearse et al. 2012). Intra-individual polymorphic sites having more than one signal were marked with NC-IUPAC ambiguity codes. For phylogenetic placement of the genus Dermoloma within the family Tricholomataceae, we used Dermoloma samples represented by sequences of at least two DNA loci supplemented with sequences of the genera Albonagister Sánchez-García, Birkebak & Matheny; Cornieriella Sánchez-García; Dennisonymyces Singer; Leucopaxillus Boursier; Porpoloma Singer; Pseudobaespora Singer; Pseudotricholoma; and Tricholoma and an undetermined genus published by Sánchez-García et al. (2014) and Sánchez-García and Matheny (2016). Pseudoomphalinus kalchbrenneri LAS06/037 was used as the outgroup. We performed an independent analysis of the genus Dermoloma adding also internal transcribed spacer (ITS) sequences retrieved from material of low-quality DNA including the types. The clade that was inferred as a sister to Dermoloma in the Tricholomataceae analysis was used as the outgroup in the Dermoloma tree. This second analysis allowed us to identify species clades based on the placement of the type specimens and to estimate more accurately the diversity of the genus. The datasets were aligned in MAFFT 7 using the E-INS-i strategy (Katoh and Standley 2013) and manually improved in Geneious R10 (Kearse et al. 2012). Divergent and ambiguously aligned positions of ITS and large subunit (LSU) were removed with Gblocks (Castresana 2000) using the least stringent parameters. Intronic positions of rpb1 and rpb2 were manually removed. Final alignment files are uploaded to TreeBase (#27219 for Tricholomataceae analysis and #27216 for Dermoloma analysis).

The final multi-locus datasets were analysed using the CIPRES Science Gateway (Miller et al. 2010) with two different methods: Bayesian inference (BI) and maximum likelihood (ML). For the ML analyses, the concatenated alignments were uploaded as FASTA files and analysed using RAxML-HPC2 on XSEDE (8.2.12) (Stamatakis 2014) as a partitioned dataset under the GTR + GAMMA model with 1000 bootstrap iterations. For the BI analysis, the dataset was divided into ten partitions: ITS1, 5.8S, ITS2, LSU and the 1st, 2nd and 3rd codon positions of rpb1 and rpb2. The best substitution model for each partition was computed jointly in PartitionFinder 1.1.1 (Lanfear et al. 2012). The aligned FASTA datasets were converted to nexus format using Mesquite 3.61 (Maddison and Maddison 2019) and further analysed using MrBayes 3.2.6 (Ronquist et al. 2012) on XSEDE. Bayesian runs were computed independently twice with four MCMC chains for 10 million generations until the standard deviation of split frequencies fell below the 0.01 threshold. The convergence of runs was visually assessed using the trace function in Tracer 1.6 (Rambaut et al. 2013). The trees were visualized and annotated with TreeGraph 2 (Stöver and Müller 2010) and graphically improved in CorelDRAW X5 (Ottawa, Canada).

Morphological observations

Based on field observations and photographs, we assigned basic general basidiomata morphology to the resulting clades. Since previous works have emphasized the importance of spore characters in this genus, we measured spore dimensions and amyloid reaction of five individuals (when available) per each operational taxonomic unit (OTU) defined in our Dermoloma phylogeny. Spores were observed under an Olympus BX43 microscope by Promicra 3-3CP camera. Spores were measured 20 or 30 times per sample using QuickPHOTO MICRO 3.2 software. Spore amyloidity was assessed in Melzer’s reagent. Spore statistics were calculated with MS Excel and plotted using CorelDRAW X5 software.

Results

Phylogeny

In total, we analysed 119 Dermoloma samples. In our multi-locus analysis, they are represented each by ITS sequences (119 in total) and by 55 LSU sequences, 51 rpb2 sequences and 17 rpb1 sequences (Supplementary Table S1). The resulting alignment for the Tricholomataceae dataset resulted in 453 nrITS positions, 882 nrLSU positions, 449 rpb1 positions and 699 rpb2 positions. The Dermoloma dataset alignment
consisted of 568 nrITS positions, 805 nrLSU positions and identical rpb1 and rpb2 position numbers.

Almost all of the sequenced Dermoloma samples were placed in a large and well-supported monophyletic group within the family Tricholomataceae. This core Dermoloma clade is a sister to a clade containing the genus Pseudotricholoma, and a clade we referred to as ‘Dermoloma-like’ (Fig. 1). There is distinct clustering within the genus that corresponds to two clades classified at the subgeneric rank into the subgenus Dermoloma and the subgenus Amylospora (see below). The subgenus Dermoloma was identified by placement of the neotype sequence of the type species Dermoloma cuneifolium (Fr.) Singer ex Bon. Each subgenus consisted of one large core clade with tens of collections and a small residual clade with few samples. Both small residual clades were strongly supported on a long branch, and therefore, we propose further subdivision of subgenera into sections. Sections Dermoloma and Conica sect. nov. are placed in the subg. Dermoloma and sections Atrobrunnea Contu and Nigrescentia sect. nov. in the subgenus Amylospora. Two sequences putatively identified as Dermoloma (Dermoloma-like clade in Fig. 1) may represent an undescribed genus sister to Pseudotricholoma.

We recognised, in total, 31 OTUs within the genus Dermoloma that may represent potential species (Fig. 2). Fifteen OTUs are represented by a single collection. Section Dermoloma is represented by 11 OTUs, section Conica by two, section Atrobrunnea by 16 and section Nigrescentia by a single species Dermoloma magicum Arnold. All OTUs strictly consisted of material from a single continent, either Europe or North America. Five OTUs of the section Atrobrunnea were North American, and a single representative of the section Dermoloma is a collection from Tennessee (USA) placed as a sister to D. cuneifolium. All other OTUs in our analysis originated from Europe.

Sequencing of 19 available type specimens from Europe and North America (Table 2) and authentic material of ‘Dermoloma simulatum’ nom. inval. resulted in 12 successful attempts. Unfortunately, the remaining samples yielded either contaminant or low-quality DNA due to old or poorly preserved specimens. Nine type sequences were represented in our phylogenetic tree (Fig. 2). Based on ex-type sequence position, we identified D. cuneifolium, Dermoloma alexandri Cons., Dermoloma atrocinereum (Pers.) P.D. Orton, Dermoloma phaeopodium P.D. Orton and Dermoloma pusillum Contu. Two collections clustered in our tree with the type of D. hymenocephalum (A.H. Sm.) Singer (Fig. 2), and since they are morphologically similar, we considered them as belonging to this species; the low BI support is probably due to short- and low-quality sequences of the type. Dermoloma emilii-dlouhyi Svrček is a synonym of D. cuneifolium, and Dermoloma pragense f. obscurum Cons. & Contu is a synonym of D. atrocinereum. The ex-type sequence of Dermoloma hygrophorus also belongs to the genus Dermoloma, but it is not represented by a recent collection in our tree. Type sequencing excluded Dermoloma intermedium var. coniferarum Bon as a member of the genus; indeed, a 100% sequence similarity, based on a BLAST search, suggested this taxon corresponds to Pseudolaccaria pachyphylla (Fr.) Vizzini & Contu.

**Morphological observations**

Our field observations were based on material collected by the authors that consisted of 92 specimens of the genus Dermoloma (more than 80% of all studied samples). Our observations confirmed the previous delimitation of the genus defined by Arnold (1992): basidiomata with collybioid or tricholomatoid habit; adnate, sinuate or subdecurrent lamellae; farinaceous odour; and a white spore deposit. In addition, we observed only dull colours on basidiomata that combine grey, brown or white. Microscopic structure of all sequenced collections is always a hymeniderm or pruristratous hymeniderm, and the hyphae always bear clamp connections.

Two North American collections (TENN-F-029387, TENN-F-066899) identified putatively as Dermoloma but placed on a residual branch sister to Pseudotricholoma have similar morphology to Dermoloma. The basidiomata are fleshy and unstaining, lack a veil and resemble in stature D. magicum; the pale greyish colouration matches Dermoloma bellerianum; the pileipellis is a hymeniderm; the spores are amyloid, short-ellipsoid and white in deposit; and clamp connections are present. In addition to this unusual combination of characters, they can be distinguished from Dermoloma by an unpleasant rancid odour even when fresh, although the taste is farinaceous. Macrochemical reactions, viz. KOH and PDAB, are negative.

Infrageneric classification of the genus corresponded to two previously recognised groups: species with inamyloid spores are classified here in the subgenus Dermoloma (Fig. 3a) and species with amyloid spores in the subgenus Amylospora (Fig. 3b). These two groups are usually easily distinguishable in the field: the first has pilei usually with mainly grey colour and pale grey to almost white hymenium and stipe. The second group has either brown-grey pilei or darker grey or grey-brown hymenium and stipe.

Representatives of sect. Conica were distinguished from other inamyloid species of the core section by large basidiomata with conical pilei and very pale, almost white lamellae and stipe (Fig. 3c, d). The single species of sect. Nigrescentia, D. magicum, is distinguished from other species with amyloid spores (classified in sect. Atrobrunnea) by blackening basidiomata (Fig. 3e, f).
Morphological identification of species was traditionally based on spores. Therefore, we took special attention to spore observations and measured up to 5 collections (depending on material availability) per each OTU defined in our phylogenetic tree (Fig. 2). The majority of OTUs had spores 5–6.5 μm long with a length-and-width ratio (Q) of 1.25–1.50. Members of sect. *Dermoloma* showed little variability and fell within these ranges. Two OTUs of sect. *Conica* had narrower spores compared to members of sect. *Dermoloma* but showed no spore differences between each other. *Dermoloma magicum* of sect. *Nigrescentia* had large spores exceeding 7 μm in length. There was only a single OTU of sect. *Atrobrunnea* with such large spores (*D. sp. 10*). More distinct differences in both length and shape (Q value) were observed among members of sect. *Atrobrunnea*. Our spore measurements support the identity of two US collections clustered with the ex-type sequence of *D. hymenoecephalum* without a good BI support in our phylogenetic analysis (Fig. 2), probably due to low type sequence quality. Spores of these two collections are similar to the type, and we suggest that all three collections represent a single species.

Some taxa in this study were not identified by a sequence from a type or authentic material but by morphology. Our sequencing of the type species of sect. *Atrobrunnea*, *Dermoloma atrobrunneum* (Dennis) Bon (described from Trinidad), failed, but our morphological analyses confirmed the pileipellis structure and amyloid spores were typical for *Dermoloma pseudocuneifoliolum* and other members of this group. The conical pilei of *D. bellerianum* and blackening basidiomata of *D. magicum* defined these two species sufficiently. *Dermoloma marinellum* E. Horak was represented by a single collection from the type locality at high elevation in the Alps, and the spores matched our observations of the type specimen. We assigned the species name *D. pseudocuneifoliolum* to the largest supported clade of sect. *Atrobrunnea* that corresponded to a widely adopted concept of the species. Based on pileipellis and spore morphology, we confirmed that *Dermoloma fascobrunneum* P.D. Orton, *D. intermedium* Bon and *Dermoloma longibasidiatum* Cons., Contu & Setti belonged to sect. *Dermoloma*, and *Dermoloma josserandii* Dennis & P.D. Orton and *D. pragense* Kubička belong to sect. *Atrobrunnea*, but their phylogenetic positions were not resolved (and these names were not represented in our tree). Our morphological study excluded *Dermoloma hybridum* (Kühner) Bon as a member of the genus *Dermoloma* because the type has a pileipellis of repent cylindrical hyphae possibly corresponding to the genus *Tricholoma* Singer.

**Taxonomy**

*Dermoloma* (J. Lange) Singer ex Herink, Sborník Severočeského Musea 1: 62. 1958
≡ *Tricholoma* stirs *Dermoloma* J. Lange, Dansk. Bot. Ark. 8(3): 12. 1933
Type: *Dermoloma cuneifolium* (Fr.) Singer ex Bon
Description: Basidiomata agaricoid with well-developed central pileus and lamellate hymenophore. Pileus up to 75 mm wide, mainly convex and expanding to plain when mature, with pale or dark colours, combining white, brown and grey tints, sometimes distinctly hygrophanous, translucent- striate or not, surface usually smooth, glabrous, at times cracked when dry. Lamellae adnate to sinuate, at times weakly decurrent, concolourous or paler than pileus. Stipe usually equally long or longer than pileus diameter, up to 15 mm wide, central, cylindrical, sometimes narrowly fusiform or attenuated near the base, usually coloured like the pileus. Context fragile in pileus, white or pale, odour strongly farinaceous. Pileipellis a hymeniderm, pluristratate hymeniderm or transitional to an epithelium, composed of one or two rarely more layers of inflated, broadly clavate, spearopedunculate cells. Basidiospores broadly ellipsoid to ellipsoid, usually almost symmetrical, thin-walled, hyaline, white in deposit. Caulocystidia always present. Hyphae with clamp connections, hyphal terminations in pileipellis and stipitipellis with dark brown parietal or sometimes also incrusted pigments.

*Dermoloma* subgenus *Dermoloma*
Description: Basidiomata usually with dominating grey tints. Spores inamyloid

*Dermoloma* subgenus *Amylospora* Adamčík, subgenus novus
Type: *Dermoloma phaeopodium* P.D. Orton
MycoBank No.: MB 837547
Diagnosis: Basidiomata usually with dominating brown tints. Spores amyloid
Etymology: The name refers to amyloid spores.

*Dermoloma* section *Dermoloma*
Description: Pileus convex and soon expanding plane. Spores broadly ellipsoid to ellipsoid, Q < 1.5

*Dermoloma* section *Conica* Adamčík, sectio nova
Type: *Dermoloma bellerianum* Bon
MycoBank No.: MB 837545
Diagnosis: Pileus conical, when old expanding plane and with distinct umbo. Spores ellipsoid to oblong, Q > 1.5
Etymology: The name refers to conical pileus of the type species.

*Dermoloma* section *Atrobrunnea* Contu, Boletim da Sociedade Broteriana 65: 80. 1992

Type: *Dermoloma atrobrunneum* (Dennis) Bon

Description: Context does not change colour when bruised.

*Dermoloma* section *Nigrescentia* Adamčík, sectio nova

Type: *Dermoloma magicum* Arnolds

MycoBank No.: MB 837546.

Diagnosis: Context of basidiomata turns black when bruised.

Etymology: The name refers to colour change of basidiomata context when bruised.

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Fig. 2 Maximum likelihood (RAxML) phylogeny of the genus *Dermoloma* inferred from nrITS, nrLSU, *rpb1* and *rpb2* DNA loci. Maximum likelihood bootstrap support values greater than 70 and Bayesian posterior probabilities greater or equal to 0.95 are indicated at nodes. Bold lines represent branches supported by both ML and BI. Asterisks indicate ML = 100 or BI = 1.00. Type specimens are indicated in red. American lineages are labelled in red and European ones in black. Spore pictures at the nodes show an amyloid reaction typical for each subgenus. Pictures of basidiomata show typical members of the sections: sect. *Dermoloma* is represented by *D. cuneifolium*, sect. *Conica* by *D. bellerianum*, sect. *Atrobrunnea* by *D. pseudocuneifolium* and sect. *Nigrescentia* by *D. magicum*. Diagrams to the right represent spores, and the size is proportional to the spore average calculated from the spore measurements from all the collections of the recognised lineages. The colours inside the ellipses correspond to spore length, and the colours of the outline correspond to the spore length/width ratio (*Q*). Colour scales are shown to the right.

Fig. 3 Examples of *Dermoloma* morphology. a Inamylloid spores of subgenus *Dermoloma* (*D. cuneifolium*, SAV F-4423). b Amyloid spores of subgenus *Amylopora* (*D. pseudocuneifolium*, SAV F-4422). c Basidiomata of section *Dermoloma* (*D. cuneifolium*, SAV F-4436). d Basidiomata of section *Conica* (*D. bellerianum*, SAV F-4416). e Basidiomata of section *Atrobrunnea* (*D. pseudocuneifolium*, SAV F-4420). f Basidiomata of section *Nigrescentia* (*D. magicum*, SAV F-4242). Scale of 10 mm represents for basidiomata.
Discussion

Phylogenetic placement of the genus

Our phylogenetic study confirmed that the genus Dermoloma is a member of the Tricholomataceae as resolved by the most recent phylogenetic study that includes the family (Sánchez-García and Matheny 2016). The latter study placed the genus Pseudotricholoma nested within samples identified as Dermoloma, because of one sample recognised in our study as Dermoloma-like genus (Fig. 1). The study of Sánchez-García and Matheny (2016) was the first showing the phylogenetic placement of the genus, but our study suggested surprisingly high diversity within the genus not expected by any previous study. These results are even more surprising because this genus with at least 23 species in Europe and probably with worldwide distribution has not been included in phylogenetic studies that focused on the Tricholomataceae (Sánchez-García and Matheny 2016; Hofstetter et al. 2014). Taxonomic identity of the genus Dermoloma in our study is resolved by the placement of the type species D. cuneifolium. The phylogenetic placement of Dermoloma inconspicuum in the family Agaricaceae (Kropp 2008) indicates that this species is one of a few that has yet to be combined in other genera, together with D. hybridum and D. intermedium var. coniferarum, which were excluded from Dermoloma in this study.

Morphological delimitation of the genus and its lower rank taxa

Our study showed clear morphological and phylogenetic circumscription of the genus Dermoloma. Morphologically, it is defined by a combination of farinaceous odour and pluristratous hymeniderm pileipellis of inflated balloon-shaped elements. However, both characters are present also in multiple phylogenetic lineages of the Tricholomataceae and they should not serve as limits to define a group on above-family rank as proposed by Bon (1979), who defined the family Dermolomataceae based on a hymeniderm pileipellis structure typical for the genus Dermoloma. Genera included by Bon in this family occurred in different places of the Tricholomataceae tree (Sánchez-García and Matheny 2016), and a very similar pileipellis structure can be observed in very unrelated agarics, for example in the genus Hodomophilus (Birkebak et al. 2016).

Taxa excluded in this study either have no distinct smell or have different pileipellis structures. Dermoloma belongs to a group of small brown mushrooms (SBMs), the popular term referring to a hyperdiverse morphological fungal group of polyphyletic origin and difficult morphological identification of species. In our experience, Dermoloma can resemble, in the field, some members of Dennisiomyces, Pseudoporporellaria, Pseudotricholoma, Tricholoma and possibly also species out of Tricholomataceae. Field identification of Dermoloma should be supplemented with microscopical observations, and we recommend paying special attention to spore and pileipellis morphology.

It is worth to mention inconsistencies about spore amyloidity of some species in the literature. Even the concept of the type species D. cuneifolium was inconsistent. Some authors attributed amyloid spores to this species (Josserand 1958; Svřeček 1966), but Orton (1980) disagreed with this interpretation and he thought that the species has inamyloid or sometimes weakly amyloid spores. In response, Arnolds (1992) designated a neotype for D. cuneifolium with inamyloid spores and Bon (1986) proposed the name D. pseudocuneifolium for D. cuneifolium in sense of Josserand (1958) (with amyloid spores). The confusions about spore amyloidity have not stopped afterwards. In our study, type specimens of D. alexandri and D. pragense f. obscurum are placed in the section Dermoloma but original descriptions (Contu et al. 2008) report weakly amyloid spores. This weakly amyloid reaction is observed as a grey hue under certain focus in the light microscope, and it is usually seen in some members of the section Dermoloma. We performed a test placing lamellae fragments of D. cuneifolium and D. alexandri, reported as having non-amyloid and weakly amyloid spores respectively by Contu et al. (2008), but there was no distinguishable difference in the amyloid reaction. We therefore recognised as amyloid spores only those with strong reaction resulting to dark grey to black tints when spores are accumulated in mass or collapsed.

The species number in the subgenus Dermoloma accepted in the literature (Arnolds 1992, 1993; Contu et al. 2008; Vesterholt 2008, 2012) ranges between three to eight, whilst we recognised 12 species supported by our phylogeny (Fig. 2). Our morphological observations suggest that spore characters used in the literature to distinguish species within the subgenus Dermoloma are usually not reliable, e.g. D. cuneifolium, D. alexandri and D. atrocinereum have very similar spores (Fig. 2). Future taxonomic studies should include more observations of pileipellis, stipitpellis and lamellae edges, but also more detailed descriptions of macromorphological characters.

Species diversity, distribution and ecology

A high number of singletons in our tree and apparent geographic limits of some species suggest that species diversity in Europe might be even higher than the 23 recognised OTUs. Based on the sequenced types and morphological characters, we assigned ten species names to the clades in our tree (Fig. 2). We did not study the type of D. corilleti, but based on the original description (Singer and Clémenton 1971), it does not have a distinct farinaceous odour and the spores are inamylloid and much larger than any species of the section Dermoloma mentioned in this study. Therefore, it is likely that this species is not a member of the genus Dermoloma. Concluding from all our abovementioned observations, for
the remaining 17 unidentified OTUs in our tree, we have only available five species names that were not assigned to a phylogenetically identified OTU: *D. fuscobrunneum, D. intermedium, D. josserandii, D. longibasidiatum* and *D. pragense*. Some of them may represent synonyms. It means that a minimum of 12 species in Europe are so far undescribed. In addition, some species might have not been included in our study. To avoid nomenclatural confusions, a description of new European *Dermoloma* species will require not only type studies but detailed observations of morphological characters combining more characters than are so far used in the nomenclature.

Our study strongly suggests that North America has its authentic *Dermoloma* diversity different from Europe, because none of the OTUs studied was found in both, Europe and North America. The sampling of the genus in our tree seems to be even more insufficient for North America with only 6 recognised OTUs. Five OTUs are members of the section Atrobrunnea together with *D. hymenocephalum*. The single Tennessee (USA) sample in the tree placed in the section *Dermoloma* is probably the first published record of a species without amyloid spores in North America. There is an online record of a non-amyloid species identified as *D. cuneifolium* (http://www.mushroomexpert.com/dermoloma_cuneifolium.html), but this record seems to be misidentified because it has amygdaliform spores that are much narrower than we observed within the genus *Dermoloma*. This online record is another evidence of insufficient and very rudimental knowledge of the genus in North America.

Ecology of members of *Dermoloma* is equal to other members of the so-called CHEGD fungi, where this genus is included together with Clavariaceae, *Hygrocybe* (and other genera of Hygrophoraceae previously placed in this genus), *Entoloma* and Geoglossaceae (and some species of Leotiaceae previously placed in this family). In Europe, CHEGD fungi are typically found in grassland habitats, but in North America, they usually grow in forests associated with non-ectomycorrhizal trees (Adamčík et al. 2016; Lodge et al. 2014). It seems that more important than the presence or absence of trees is their affinity to undisturbed sites with a conservation value (Griffith et al. 2013). Their ecology may have a strong link to trophy that is so far unresolved. Analysis of C and N isotopes and $^{13}$C pulse label experiments and high natural abundance stable isotopes of $^{15}$N and low of $^{13}$C in basidiocarps suggest that they form unspecified biotrophic associations with plants (Halbwachs et al. 2018). They have a particular response to available nutrition changes linked to management practices when compared to other grassland fungi (Caboń et al., unpublished data). In our opinion, at least two other *Tricholomataceae* genera, *Pseudobaeospora* and *Pseudotricholoma*, are associated with undisturbed traditionally managed grasslands and accompany *Dermoloma* species and should be included among other CHEGD fungi.

**Conclusion**

Our results demonstrated that the real number of species in Europe and North America is higher than expected according to the literature, and the number of OTUs recognised in our phylogeny is much higher than the number of available published *Dermoloma* names. Before the description of new species, there is an urgent need to fix the morphological concept of already described species and to designate epitypes that will represent species in the phylogeny and provide reference sequences. The morphological arguments and characters used in the previous literature must be reconsidered and supplemented by new characters and more precise observations. The high number of OTUs represented by a single sample suggests that the diversity of the genus will be even higher with increasing sampling efforts from Europe, North America and elsewhere. There are 13 *Dermoloma* names from other continents, but the only available sequence from outside the USA and Europe corresponds to *D. inconspicuum* from Belize (type of the species is from Venezuela). This suggests that extra-European taxa need urgent revision and sequence data to specify their geographical distributions and morphological and genetic limits.

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1007/s11557-020-01651-y.

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**Authors’ contributions** SA and MSG designed the study, contributed to the main conceptual ideas and wrote the paper with support from PBM. KA and MSG performed the DNA extractions, and SA and MSG edited the sequences. MSG, MC and SA designed the molecular part of the study and performed the molecular and phylogenetic analyses. MK, SJ and SA performed the morphological measurements. PBM, PAM and AV contributed to the data interpretations. AV, PAM, SA and SJ and contributed with collecting of European samples and macromorphological descriptions, and MSG and PBM provided the study with the material and sequences of North American species. PBM provided critical feedback to the study design and paper. All authors revised and approved the final manuscript.

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**Data availability** The sequences generated and/or analysed during the current study are available in the GenBank repository (https://www.ncbi.nlm.nih.gov/genbank/). All analysed specimens are deposited in public herbaria indicated in the Supplementary table.
Compliance with ethical standards

Competing interests The authors declare that they have no competing interests.

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