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, D. 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, D. 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, species with inamyloid basidiospores are placed in subg. Dermoloma and those with amyloid basidiospores in subg. Amylospora . Both subgenera are further divided in 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.

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 colorations; sinuate to adnate-decurrent lamellae; farinaceous smell (or taste); smooth, hyaline, amyloid or inamyloid basidiospores and a pileipellis of a pluristratuous (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.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, *D. 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) 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 *D. inconspicuum* Dennis close to the genus *Lepiota* (Pers.) Gray in the family Agaricaceae Chevall (Kropp 2008). Sánchez-García & Matheny (2016) recently placed five *Dermoloma* samples in the family Tricholomataceae, within a clade sister to the genus *Tricholoma* (Fr.) Staude. In their phylogenetic tree, the monophyletic genus *Pseudotricholoma* (Singer) Sánchez-García & Matheny is nested within *Dermoloma*, making the latter paraphyletic. *Dermoloma* species are traditionally grouped in two sections, *D.* sect. *Dermoloma* with inamyloid basidiospores and *D.* sect. *Atrobrunnea* with amyloid 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 90 specimens collected from Estonia (1 collection), France (14), Italy (2), Romania (8), Slovakia (26), Switzerland (1), United Kingdom (33) and the USA (2), and 13 borrowed herbarium specimens from Italy (8), 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 colour, hymeniderm pileipellis and usually conspicuous farinaceous odour (Arnolds 1992).

Table 2

List of European and North American type and authentic herbarium material and sequencing results. HT – holotype, NT – neotype, AM – authentic material, GB – will be replaced by a Genbank number.

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	GB
D. atrocinereum (Pers.) P.D. Orton	ITALY. Villeta Barrea (AQ), Abruzzo, M. Contu et al., 19. Sep 2003	AQUI (Contu 19.IX.2003)	NT	GB
D. bellerianum Bon	FRANCE. Beller, 30. Sep 1972	LIP (Bon 912)	HT	not located
D. coryleti Singer & Clémençon	CZECHIA. Kroměříš, R. Singer, 30. Sep 1970	F (R. Singer C-5230)	HT	not accessed
D. cuneifolium (Fr.: Fr.) Bon	SWEDEN. Småland, Femsjö, 'Avaberget', S. Lundell & G. Haglund, 19. Sep 1948	UPS F-631065	NT	GB
D. cuneifolium var. *punctipes* Arnolds	NETHERLANDS. prov. Limburg, Wijlre, 'Wrakelberg', E. Arnolds, 22. Oct 1984	L 0821553	HT	GB
D. emiliae-dlouhyi Svrček	CZECHIA. Brdské hřebeny Mts., Vižina, M. Svrček, 20. Sep 1965	PR 610931	HT	failed
D. fuscobrunneum P.D. Orton	UK. Somerset, Bickham 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, Quincieux, Lacombe & Josserand, 14. Aug 1956	G 260855	HT	GB, partial ITS sequence
D. hymenocephalum (A.H. Sm.) Singer	USA. Michigan, Dexter, Silver lake, A.H. Smith, 23. Sep 1938	MICH 10228	HT	GB, 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, Mornard, 28. Oct 1982	LIP (Bon 8116)	HT	GB, 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), Susà, G. Consiglio, G. Marasca et B. Oss-Emer, 30. Nov 1993,	herbarium of G. Consiglio (GC93318)	HT	failed

species	collection details	Herbarium	type status	sequencing outputs
D. magicum Arnolds	NETHERLANDS. Limburg, Epen, Cotessen, E. Arnolds, 21. Oct 1995	L (Arnolds 6701)	HT	not located
D. murinellum E. Horak	SWITZERLAND. Graubünden, N des Albulpasses (Terrassas), E. Horak, 30. Aug 1982	ZT Myc 42786 (Horak ZT1573)	HT	failed
D. phaeopodium P.D. Orton	UK. Devon, Membury, P.D. Orton, 28. Oct 1977	E 16877	HT	GB
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	GB
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	GB
D. simulatum Cons., Contu & Setti, nom. inval.	ITALY. Trento-Alto Adige, Susà (TN), G. Consiglio, G. Marasca & B. Oss-Emer, 30. Oct 1993	herbarium of G. Consiglio (GC02284)	AM	failed

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 six and seven 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 molecular grade water added up to 20 µl, or using a mixture of 5 × buffer, GoTaq, and dNTPs supplied by Invitrogen Corp. (Carslbad, 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 & 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 & 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 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 sec to 72 °C, 1 min at 72 °C, repeated 35 times, finalized by 10 min at 72 °C. The RPB1 region was amplified using the primers gRPB1-A for and fRPB1-C rev (Matheny et al. 2002) under the following PCR conditions 1 min at 95 °C, 1 min 30 s at 55 °C, an increase of 1 °C every 5 sec to 72 °C, 2 min at 72 °C, repeated 35 times, finalized by 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, California, U.S.A) and purified using Sephadex G-50 columns (General Electric Healthcare, Piscataway, New Jersey, U.S.A). Sequencing was performed at the University of Tennessee Genomics Core and at the SEQme sequencing Company (Dobříš, 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 *Albomagister*, *Corneriella*, *Dennisiomyces*, *Leucopaxillus*, *Porpoloma*, *Pseudobaeospora*, *Pseudotricholoma*, *Tricholoma* and an undetermined genus published by Sánchez-García et al. (2014) and Sánchez-Gárcia & Matheny (2016). *Pseudoomphalina kalchbrenneri* LAS06/037 was used as the outgroup. We performed independent analysis of the genus *Dermoloma* adding also ITS sequences retrieved from material of low quality DNA including the types. The clade that was inferred as 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 & Standley 2013) and manually improved in Geneious R10 (Kearse et al. 2012). Divergent and ambiguously aligned positions of ITS and 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 (# XXXXX).

The final multi-loci 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 (Madison and Madison 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 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-loci 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* positions number.

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 sister to a clade containing the genus *Pseudotricholoma* (Singer) Sánchez-García & and Matheny, and a clade we referred to as "*Dermoloma*-like" (Fig. 1). There is a distinct clustering within the genus that corresponds to two clades classified at subgeneric rank into the subgenus *Dermoloma* and the subgenus *Amylospora* subg. nov. (for formal designation of the new name see below). Subgenus *Dermoloma* was identified by placement of the neotype sequence of the type species *D. 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 *Nigrescenti* by a single species *D. magicum* Arnolds. 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 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 '*D. 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*, *D. alexandri* Cons., *D. atrocinereum* (Pers.) P.D. Orton, *D. phaeopodium* P.D. Orton and *D. 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 sequence of the type. *Dermoloma emilii-dlouhyi* Svrček is synonym of *D. cuneifolium* and *D. pragense* f. *obscurum* Cons. & Contu is synonym of *D. atrocinereum*. Ex-type sequence of *D. hygrophorus* also belongs to the genus *Dermoloma*, but is not represented by a recent collection in our tree. Type sequencing excluded *D. intermedium* var. *coniferarum* Bon as 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 Arnolds (1992): basidiomata with collybioid or tricholomatoid habit; adnate, sinuate or subdecurrent lamellae; farinaceous odor; 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 America 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, resemble in stature *D. magicum*, the pale greyish colouration matches *D. belerianum*, 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. 3D). The single species of sect. *Nigrescentia*, *D. magicum*, is distinguished from other species with amyloid spores (classified in sect. *Atrobrunnea*) by blackening basidiomata (Fig. 3F).

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 ratio of length and width Q=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 USA collections clustered with ex-type sequence of *D. hymenocephalum* 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*, *D. atrobrunneum* (Dennis) Bon (described from Trinidad), failed, but our morphological analyses confirmed the pileipellis structure and amyloid spores were typical for *D. pseudocuneifolium* and other members of this group. The conical pilei of *D. bellerianum* and blackening basidiomata of *D. magicum* defined these two species sufficiently. *Dermoloma murinellum* 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. pseudocuneifolium* 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 *D. fuscobrunneum* P.D. Orton, *D. intermedium* Bon and *D. longibasidiatum* Cons., Contu & Setti belonged to sect. *Dermoloma*; and *D. 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 *D. 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* stirps *Dermoloma* J. Lange, Dansk. Bot. Ark. 8(3): 12. 1933

Type: *Dermoloma cunneifolium* (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, pluristratous hymeniderm or transitional to an epithelium, composed of one, two rarely more layers of inflated, broadly clavate, sphearopedunculate 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 gray tints. Spores inamyloid.

Dermoloma subgenus *Amylospora* Adamčík, subgenus nova.

Type: *Dermoloma phaeopodium* P.D. Orton

Diagnosis: Basidiomata usually with dominating brown tints. Spores amyloid.

Dermoloma section *Dermoloma*

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

Dermoloma section *Conica* Adamčík, section nova.

Type: *Dermoloma bellerianum* Bon

Diagnosis: Pileus conical, when old expanding plane and with distinct umbo. Spores ellipsoid to oblong, Q>1.5.

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, section nova.

Type: *Dermoloma magicum* Arnolds

Diagnosis: Context turns black when bruised.

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 & 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 & 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 & 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 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 & Matheny 2016) and very similar pileipellis structure can be observed in very unrelated agarics, for example in the genus *Hodophilus* (Birkebak et al. 2016).

Taxa excluded in this study have either no distinct smell or have different pileipellis structure. *Dermoloma* belongs to a group of small brown mushrooms (SBM), 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*, *Pseudoporpoloma*, *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, Svrček 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 2002, 2003; Contu et al. 2008; Vesterhold 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, stipitipellis, lamellae edges, but also more detailed descriptions of macromorphological characters.

Species diversity, distribution and ecology. 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 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 studied the type of *D. coryleti*, but based on the original description (Singer & Clémençon 1971) it does not have a distinct farinaceous odour and the spores are inamyloid and much larger than any species of the section *Dermoloma* mentioned in this study. Therefore it is likely that this species is not 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, 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 with not 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*, 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 comparing to other grassland fungi (Caboň et al. in review).

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 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.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Availability of data and materials

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 Supplementary table.

Competing interests

The authors declare that they have no competing interests.

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Authors' contributions

SA, MGS and designed the study, the main conceptual ideas and wrote the paper with support from PBM. KA and MGS performed DNA extractions, SA and MGS edited sequences. MGS, MC and SA designed molecular part of the study, performed molecular and phylogenetic analyses. MK, SJ and SA performed 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, MGS and PBM provided the study with 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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Tables

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. Names in brackets are invalid.

Africa: 1 name

1. Dermoloma griseocarneum Pegler, Kew Bulletin Additional Series 6: 213 (1977)

Holotypus: Uganda

America: 6 names

2. Dermoloma atrobrunneum (Dennis) Singer ex Bon, Documents Mycologiques 17(65): 51 (1986)

≡ Tricholoma atrobrunneum Dennis, Transactions of the British Mycological Society 34: 476 (1951)

– Dermoloma atrobrunneum (Dennis) Singer, Sydowia 9(1-6): 375 (1955)

Holotypus: Trinidad and Tobago (Trinidad Isl.)

3. Dermoloma aposcenum Singer, Fieldiana Botany 21: 88 (1989)

Holotypus: Mexico

4. 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

5. Dermoloma inconspicuum Dennis, Kew Bulletin 15(1): 78 (1961)

Holotypus: Venezuela

6. Dermoloma pataguae Singer, Fieldiana Botany 21: 89 (1989)

Holotypus: Chile

7. Dermoloma yungense Singer, Beihefte zur Sydowia 7: 61 (1973)

Holotypus: Bolivia

Asia: 4 names

8. Dermoloma cystidiatum Manim. & Arnolds, Persoonia 17(1): 149 (1998)

Holotypus: India

9. Dermoloma indicum K.N.A. Raj & Manim., Phytotaxa 177 (4): 239 (2014)

Holotypus: India

10. Dermoloma keralense K.N.A. Raj & Manim., Phytotaxa 177 (4): 241 (2014)

Holotypus: India

11. 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

12. Porpoloma amyloideum (G. Stev.) E. Horak, New Zealand Journal of Botany 9(3): 407 (1971)

≡ Dermoloma amyloideum (G. Stev.) G. Stev., Field Guide to Fungi: 73 (1982)

≡ Tricholoma amyloideum G. Stev., Kew Bulletin 19(1): 15 (1964)

Holotypus: New Zealand

13. Dermoloma hemisphaericum (G. Stev.) E. Horak, New Zealand Journal of Botany 9(3): 429 (1971)

≡ Tricholoma hemisphaericum G. Stev., Kew Bull. 19(1): 14 (1964)

Holotypus: New Zealand

14. Dermoloma murinum (G.M. Taylor & G. Stev.) E. Horak, New Zealand Journal of Botany 9(3): 438 (1971)

≡ Tricholoma murinum G.M. Taylor & G. Stev., Kew Bulletin 19(1): 17 (1964)

Holotypus: New Zealand

Europe: 21 valid names, 4 invalid names

15. Dermoloma alexandri Cons., Micologia e Vegetazione Mediterranea 22(2): 84 (2008)

Holotypus: Italy

16. 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 designated by Contu, Consiglio & Segtti (2008): Italy

17. Dermoloma bellerianum Bon, Documents Mycologiques 28(nos 109-110): 6 (1998)

Holotypus: France

18. [Dermoloma cheilocystidiatum Contu, Bollettino dell'Associazione Micologica ed Ecologica Romana 15(no. 48): 4 (2000), nom. inval. published as nomen provisorium]

Authentic material: Italy.

19. Dermoloma coryleti Singer & Clémençon, Schweizerische Zeitschrift für Pilzkunde 49(9): 120 (1971)

Holotypus: Czech Republic

20. Dermoloma cuneifolium (Fr.: Fr.) Bon, Documents Mycologiques 17(65): 51. 1986.

– Agaricus cuneifolius Fr., Observationes mycologicae 2: 99 (1818)

Neotypus designated by Arnolds (1992): Sweden

21. Dermoloma cuneifolium var. punctipes Arnolds, Persoonia 14(4): 529 (1992)

Holotypus: The Netherlands

22. Dermoloma emiliae-dlouhyi Svrček, Česká Mykologie 20(3): 147 (1966)

Holotypus: Czech Republic

23. Dermoloma fuscobrunneum P.D. Orton, Notes from the Royal Botanical Garden Edinburgh 38(2): 326 (1980)

Holotypus: United Kingdom

24. [Dermoloma glauconitens (Fr.) Bon, Documents Mycologiques 17(65): 51. (1986) nom. illegit. (superfluum)]

≡ Agaricus glauconitens Fr., Syst. Mycol. 3: 22. 1832.

– Agaricus nitens Batsch, Elenchus fungorum. Continuatio secunda: 21. 1789: Fr., Syst. Mycol. 1: 116. 1821.

25. Dermoloma hybridum (Kühner) Bon, Bulletin Annual de la Fédération Centre-Est d'Histoire Naturelle et de Mycologie 1: 14 (1979)

≡ Tricholoma hybridum Kühner, Ann. Sci. Franche-Comté 2: 31 (1947)

Holotypus: France

26. Dermoloma hygrophorus Joss., Bull. Soc. Linn. Lyon 39(1): 6 (1970)

≡ Tricholoma hygrophorus Joss., Bulletin de la Société Mycologique de France 74(4): 482 (1958)

Holotypus: France

27. Dermoloma intermedium Bon, Documents Mycologiques 9(35): 42 (1979)

Holotypus: France

28. Dermoloma intermedium var. coniferarum Bon, Documents Mycologiques 17(65): 51 (1986)

Holotypus: France

29. Dermoloma josserandii Dennis & P.D. Orton, Transactions of the British Mycological Society 43(2): 226 (1960)

Holotypus: United Kingdom

30. Dermoloma longibasidiatum Cons., Contu & Setti, Micologia e Vegetazione Mediterranea 22(2): 110 (2008)

Holotypus: Italy

31. Dermoloma magicum Arnolds, Persoonia 17(4): 665 (2002)

Holotypus: The Netherlands

32. Dermoloma murinellum E. Horak, Sydowia 39: 110 (1987)

Holotypus: Switzerland

33. [Dermoloma nitens Fr. ex Raithelh., Metrodiana 8(2-3): 52 (1979), nom. inval.]
34. Dermoloma phaeopodium P.D. Orton, Notes from the Royal Botanical Garden Edinburgh 28(2): 327 (1980)

≡ Dermoloma josserandii var. phaeopodium (P.D. Orton) Arnolds, Persoonia 15(2): 195 (1993)

Holotypus: United Kingdom

35. Dermoloma pragense Kubička, Česká Mykologie 29(1): 31 (1975)

≡ Dermoloma pseudocuneifolium var. pragense (Kubička) Bon, Documents Mycologiques 17(65): 52 (1986)

Holotypus: Czech Republic

36. Dermoloma pragense f. obscurum Cons. & Contu, Micologia e Vegetazione Mediterranea 22(2): 99 (2008)

Holotypus: Italy

37. Dermoloma pseudocuneifolium Herink ex Bon, Documents Mycologiques 17(65): 52 (1986)

Holotypus: France

38. Dermoloma pusillum Contu, Micologia e Vegetazione Mediterranea 22(2): 105 (2008)

Holotypus: Italy

39. [Dermoloma simulatum Cons., Contu & Setti, in Contu, Consiglio & Setti, Micologia e Vegetazione Mediterranea 22(2): 110. 2008, nom. inval. described as ‘ad int.’]

Authentic material: Italy

Table 2. List of European and North American type and authentic herbarium material and sequencing results. HT – holotype, NT – neotype, AM – authentic material, GB – will be replaced by a Genbank number.

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	GB
D. atrocinereum (Pers.) P.D. Orton	ITALY. Villeta Barrea (AQ), Abruzzo, M. Contu et al., 19. Sep 2003	AQUI (Contu 19.IX.2003)	NT	GB
D. bellerianum Bon	FRANCE. Beller, 30. Sep 1972	LIP (Bon 912)	HT	not located
D. coryleti Singer & Clémençon	CZECHIA. Kroměříš, R. Singer, 30. Sep 1970	F (R. Singer C-5230)	HT	not accessed
D. cuneifolium (Fr.: Fr.) Bon	SWEDEN. Småland, Femsjö, 'Avaberget', S. Lundell & G. Haglund, 19. Sep 1948	UPS F-631065	NT	GB
D. cuneifolium var. *punctipes* Arnolds	NETHERLANDS. prov. Limburg, Wijlre, 'Wrakelberg', E. Arnolds, 22. Oct 1984	L 0821553	HT	GB
D. emiliae-dlouhyi Svrček	CZECHIA. Brdské hřebeny Mts., Vižina, M. Svrček, 20. Sep 1965	PR 610931	HT	failed
D. fuscobrunneum P.D. Orton	UK. Somerset, Bickham 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, Quincieux, Lacombe & Josserand, 14. Aug 1956	G 260855	HT	GB, partial ITS sequence
D. hymenocephalum (A.H. Sm.) Singer	USA. Michigan, Dexter, Silver lake, A.H. Smith, 23. Sep 1938	MICH 10228	HT	GB, 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, Mornard, 28. Oct 1982	LIP (Bon 8116)	HT	GB, 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), Susà, G. Consiglio, G. Marasca et B. Oss-Emer, 30. Nov 1993,	herbarium of G. Consiglio (GC93318)	HT	failed
D. magicum Arnolds	NETHERLANDS. Limburg, Epen, Cotessen, E. Arnolds, 21. Oct 1995	L (Arnolds 6701)	HT	not located

species	collection details	Herbarium	type status	sequencing outputs
D. murinellum E. Horak	SWITZERLAND. Graubünden, N des Albulpasses (Terrassas), E. Horak, 30. Aug 1982	ZT Myc 42786 (Horak ZT1573)	HT	failed
D. phaeopodium P.D. Orton	UK. Devon, Membury, P.D. Orton, 28. Oct 1977	E 16877	HT	GB
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	GB
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	GB
D. simulatum Cons., Contu & Setti, nom. inval.	ITALY. Trento-Alto Adige, Susà (TN), G. Consiglio, G. Marasca & B. Oss-Emer, 30. Oct 1993	herbarium of G. Consiglio (GC02284)	AM	failed

Figures

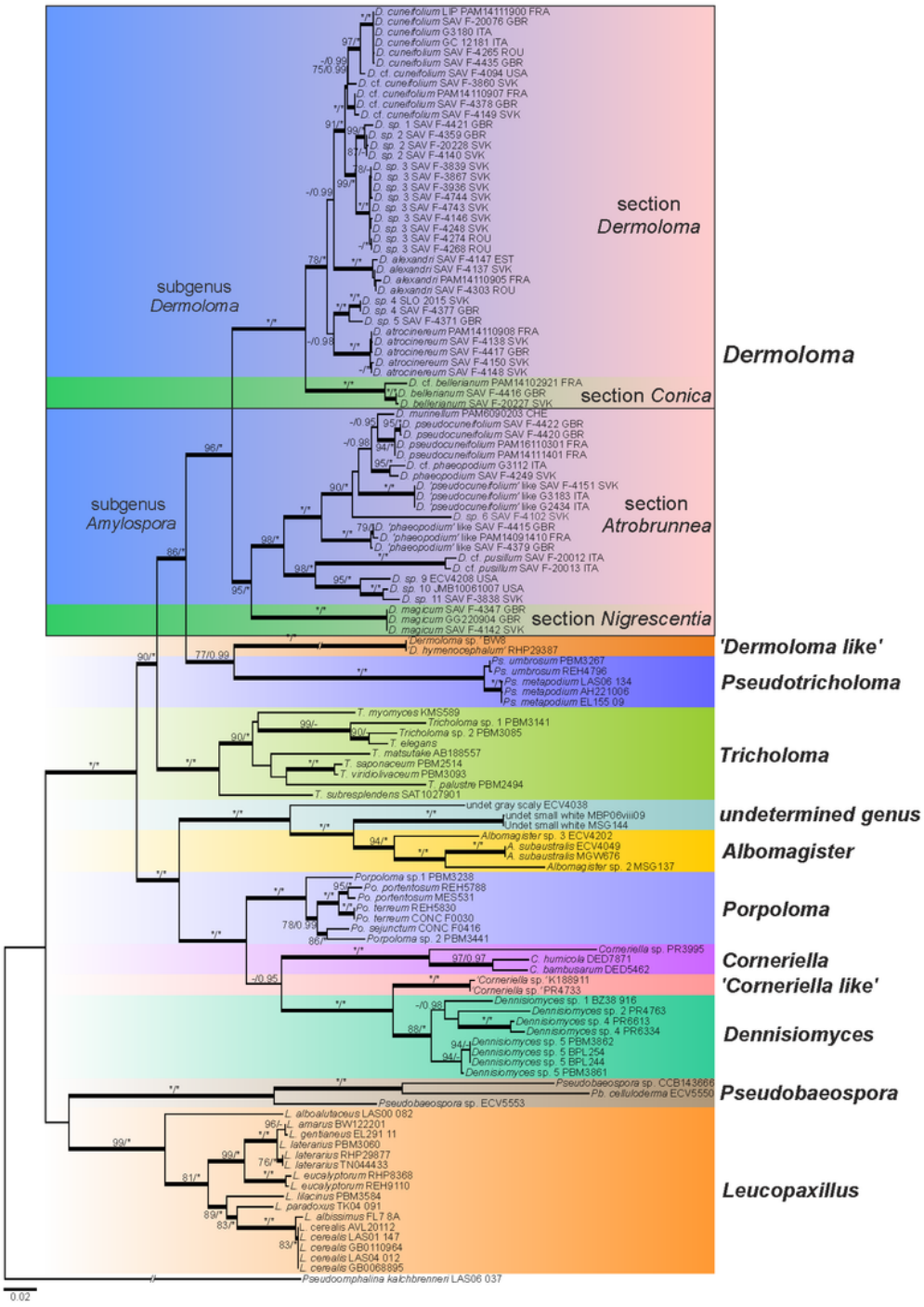

Figure 1

Maximum likelihood (RAxML) phylogeny of Tricholomataceae inferred from nrITS, nrLSU, rpb1 and rpb2 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.

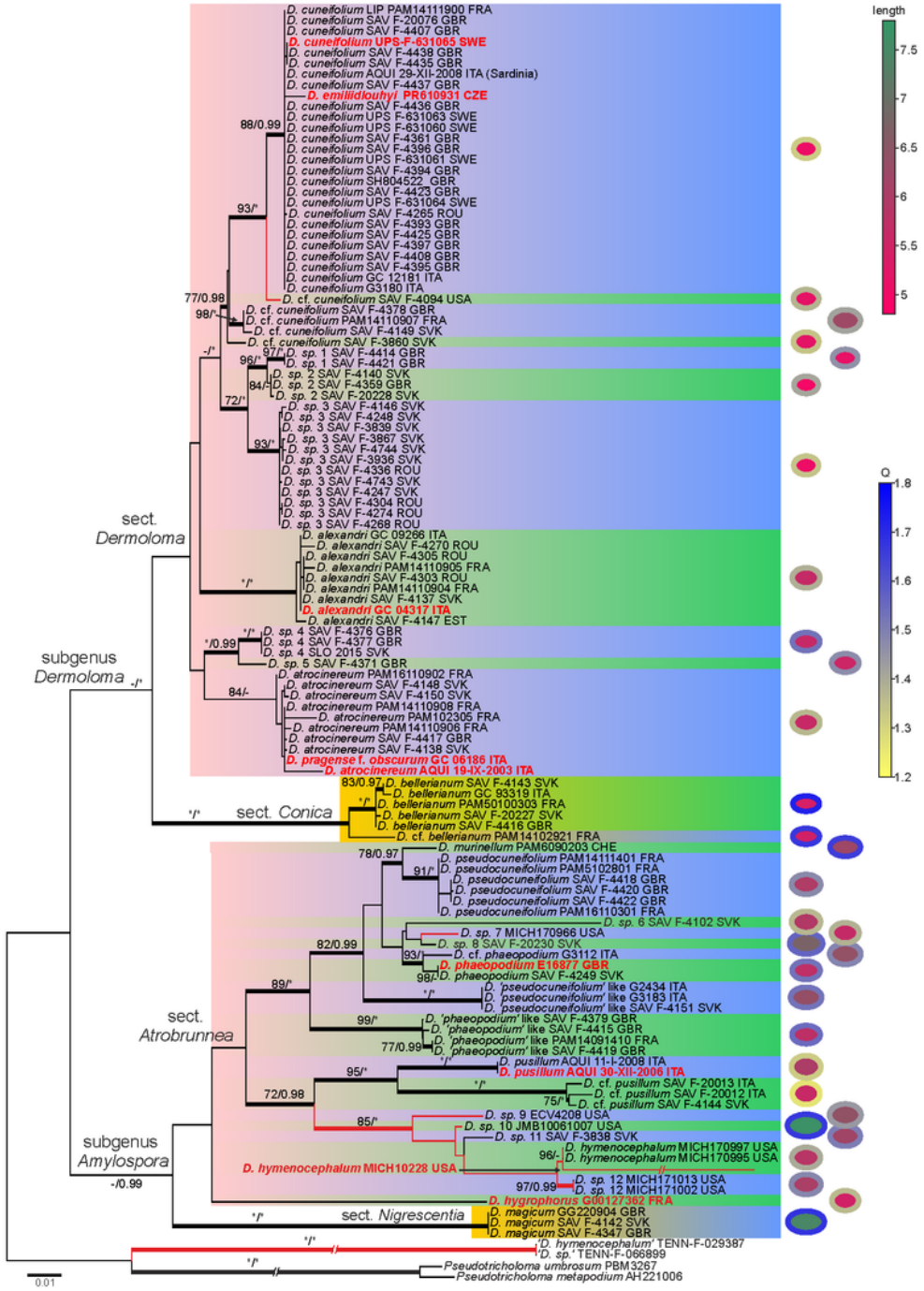

Figure 2

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 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, 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.

Figure 3

Examples of Dermoloma morphology. A. Inamyloid spores of subgenus Dermoloma (D. cuneifolium, SAV F-4423). B. Amyloid spores of subgenus Amylospora (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 represents 10 mm for basidiomata.

Supplementary Files

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