MYCOLOGIA
2021, VOL. 113, NO. 4, 776–790
https://doi.org/10.1080/00275514.2021.1890969

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Desarmillaria caespitosa, a North American vicariant of *D. tabescens*

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ABSTRACT

Desarmillaria caespitosa, a North American vicariant species of European *D. tabescens*, is redescribed in detail based on recent collections from the USA and Mexico. This species is characterized by morphological features and multilocus phylogenetic analyses using portions of nuc rDNA 28S (28S), translation elongation factor 1-alpha (*tef1*), the second largest subunit of RNA polymerase II (*rpb2*), actin (*act*), and glyceraldehyde-3-phosphate dehydrogenase (*gpd*). A neotype of *D. caespitosa* is designated here. Morphological and genetic differences between *D. caespitosa* and *D. tabescens* were identified. Morphologically, *D. caespitosa* differs from *D. tabescens* by having wider basidiospores, narrower cheilocystidia, which are often irregular or mixed (regular, irregular, or coralloid), and narrower caulocystidia. Phylogenetic analyses of five independent gene regions show that *D. caespitosa* and *D. tabescens* are separated by nodes with strong support. The new combination, *D. caespitosa*, is proposed.

ARTICLE HISTORY
Received 27 March 2020
Accepted 12 February 2021

KEYWORDS
28S; *act*; *Armillaria*; *gpd*; new combination; Physalacriaceae; *rpb2*; *tef1*; 1 new taxon

INTRODUCTION

Two separate genera are distinguished among former species of *Armillaria* (Fr.) Staude. The genus *Armillaria* s.str. contains the annulate taxa (39 species; He et al. 2019), whereas *Desarmillaria* (Herink) R.A. Koch & Aime includes exannulata taxa, of which only two are known. One of them, *D. ectypa* (Fr.) R.A. Koch & Aime, in contrast to other relative species, is not lignicolous and occurs in Eurasian marshes and peat bogs. Moreover, it forms single growing basidiomata with an apparently smooth pileus. The second species, *D. tabescens* (Scop.) R.A. Koch & Aime, is lignicolous and similar to the annulate taxa in many ecological aspects.

Herink (1973) was the first author who separated annulate and exannulate taxa of *Armillaria* into two distinct subgenera, *Armillaria* and *Desarmillaria* Herink. However, recognition of these subgenera was largely overlooked for decades, likely because it was published in Czech in the proceedings from a conference about *A. mellea* (Vahl) P. Kumm (Hašek 1973). Singer (1975, 1986) also divided these species (as *Armillariella* P. Karst.) into annulate and exannulate groups, but without any formal taxonomic solution. Based on previous multilocus phylogenetic analyses, armillarioid (Physalacriaceae) were determined to contain three genera: (i) *Guyanagaster* T.W. Henkel, M.E. Smith & Aime, a gasteroid genus that is the earliest diverging lineage; (ii) *Desarmillaria*, an exannulate mushroom-forming *Armillaria* subgenus that was elevated to genus level and comprises two species: *D. tabescens* and *D. ectypa*; and (iii) *Armillaria*, the sister lineage of *Desarmillaria* that comprises annulate mushroom-forming species that form melanized rhizomorphs (Koch et al. 2017). Based on morphology and ecology, Antonín et al. (2006) determined that *A. socialis* (DC) Fayod was the correct name for *D. tabescens* (as *A. tabescens* (Scop.) Emel). Subsequently, Redhead et al. (2012) proposed to conserve the name *A. tabescens*, and this proposal was approved (May 2017).

Based on the biological species concept used for *Armillaria* s.l. (e.g., Korhonen 1978; Anderson and Ullrich 1979), mating tests showed that *D. tabescens* (as *A. tabescens*) isolates from eastern Asia (i.e., Japan, China) were interfertile with European isolates (Ota et al. 1998; Qin et al. 2007), whereas *D. tabescens* (as

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Published online 29 Apr 2021

A. tabescens) isolates from eastern Asia and Europe were found intersterile with North American isolates (Guillaumin et al. 1989; Ota et al. 1998). A previous study by Darmono et al. (1992) reported interfertility of *D. tabescens* (as *A. tabescens*) isolates of southeastern, eastern, and central USA, which provided evidence for a single biological species of *D. tabescens* in the USA, whereas other mating tests provided supporting evidence that *D. tabescens* isolates from Eurasia and North America were reproductively incompatible. In reference to mating tests of *D. tabescens* (as *A. tabescens*), Guillaumin et al. (1989) stated that *A. tabescens* is probably also a complex including several species, and Kile et al. (1994) accepted the opinion by Mohammed and Guillaumin (unpublished; cited by Kile et al. 1994) that the most appropriate name for the North American fungus is "*Armillaria*" *monadelpha* (Morgan). Qin et al. (2007) concluded: "It is obvious that this species needs further investigation."

Multilocus phylogenetic analyses demonstrate a clear separation of *D. tabescens* isolates from Eurasia and those from North America (e.g., Tsykun et al. 2013; Coetzee et al. 2015; Guo et al. 2016; Koch et al. 2017), which is further supported by phylogenetic analysis of translation elongation factor 1-α (*tef1*) gene sequences (Klopfenstein et al. 2017; Coetzee et al. 2018). Based on this evidence, Klopfenstein et al. (2017) and Coetzee et al. (2018) concluded that a taxonomic study focused on North American and Eurasian *A. socialis*/*tabescens* (*D. tabescens*) is needed to determine whether multiple phylogenetic species exist within the exannulate clade and to solve the taxonomic treatment of *A. tabescens* from Europe, North America, and Asia. Park et al. (2018) demonstrated the presence of *D. tabescens* in South Korea based on both DNA sequences (internal transcribed spacer [ITS] and *tef1*) and morphology. According to their results, however, it seems that the South Korean collections of *D. tabescens* may be phylogenetically different from the European specimens.

Berkeley (1847) described *Lentinus caespitosus* Berk. based on material collected in Waynesville, Ohio. Pegler (1983), who revised the type specimen, mentioned its identity with *A. tabescens*. The latter name is older; therefore, this fungus was published under this name in the literature referring to specimens from North American (e.g., Ross 1970; Cox 2004; Cox et al. 2006; Schnabel et al. 2005, 2006; Kuo 2017). In the case that the American fungus is different from true *D. tabescens*, the name *Lentinus caespitosus* is the oldest name available for this taxon.

On the aforementioned bases, the objective of this study was to compare *D. tabescens* from North America and Europe using morphological and multilocus phylogenetic analyses to determine whether specimens from these continents are conspecific or allospecific.

MATERIALS AND METHODS

Isolates/specimens and culture.—Five specimens of *D. tabescens* from North America and six from Europe were used for morphological and phylogenetic analyses (TABLE 1). In addition, several specimens of *D. tabescens* were used for studies of morphological variability within this species. The North American material was collected in Waynesville, Ohio, USA, and in Xalapa, Veracruz, Mexico. For comparisons, European specimens originated from the Burgas region, Bulgaria; South Moravia, Czech Republic; Bourgogne, France; Bratislava, Nitra region, and southern parts of Banská Bystrica region, Slovakia; and Panovec, Slovenia.

Morphology.—The macroscopic description was based on fresh basidiomata collected in Mexico and the USA. Color abbreviations followed Kornerup and Wanscher (1983). The microscopic description was based on dry basidiomata. Sections were mounted in KOH, Melzer's reagent, and Congo red and observed using an Olympus BX-50 light microscope (Tokyo, Japan) with a magnification of 1000×. For basidiospores, the factors Q (quotient of length and width in any one spore) and mean values were used. Herbarium abbreviations followed Thiers (continuously updated) (FIGS. 1–3).

DNA extraction, sequencing, and phylogenetics.—Following the protocols of Elías-Román et al. (2018), DNA was extracted from each culture isolate, and DNA quality and quantity were estimated using a Nanodrop 2000 spectrophotometer (ThermoScientific, Waltham, Massachusetts). Sequencing of five loci was attempted for selected isolates (North America: XAL MAX21WF, OHIO_2018PB-1, OOI-210, OOI-99, AT-MU-S2; Europe: MENDELU 171, 519, 520, 521, 522, and 525), including portions of nuc 28S rDNA (28S), *tef1*, the second largest subunit of RNA polymerase II (*rpb2*), actin (*act*), and glyceraldehyde-3-phosphate dehydrogenase (*gpd*) (TABLE 1). Amplification reaction mixtures (total 25 µL) contained 20–40 ng of template DNA (or no DNA template for negative control), 2.5 µL 10× Standard *Taq* Reaction Buffer (New England BioLabs, Ipswich, Massachusetts), 0.5 µL 10 mM dNTPs (Roche Applied Science, Madison, Wisconsin), 1 µL each of 10 µM primer, and 0.125 µL (0.6 U) *Taq* DNA Polymerase (New England BioLabs). Amplifications were performed using the following polymerase chain reaction (PCR)

Table 1. List of *Desarmillaria caespitosa* and *D. tabescens* reference isolates/specimens used for morphological comparison and phylogenetic analyses.

					GenBank accession numbers[b]					
Species	Basidiome-derived culture isolate[a] (herbarium voucher specimen)	Source	Host	Origin	ITS	*tef1*	*rpb2*	*gpd*	28S	*act*
D. caespitosa	XAL MEX21WF (BRNM 825654)	Kim et al. 2010; this study	*Araucaria araucana*	Veracruz, Mexico	—	MT232066	MN990677	MN996978	MT163178	—
D. caespitosa	OHIO_2018PB-1 (DBG F-030611/culture CBS 147612)	This study	*Acer saccharinum*	Ohio, USA	MT007923	MT232065	MN990681	—	MT238204	—
D. caespitosa	OOI-210	Schnabel et al. 2005; Ross-Davis et al. 2012	*Prunus persica*	Georgia, USA	AY213590	JF313111	MN990679	MN996984	AY509191	MT225098
D. caespitosa	OOI-99	Schnabel et al. 2005; Ross-Davis et al. 2012	*P. persica*	Georgia, USA	AY213589	JF313112	MN990678	MN996985	AY509192	—
D. caespitosa	AT-MU-S2[c]	Kim et al. 2006; Ross-Davis et al. 2012		South Carolina, USA	AY213588	JF313113	MN990680	—	AY509189, AY509190	MT225099
D. tabescens	MENDELU 171	Lochman et al. 2004; this study	*Quercus robur*	Lanžhot, Cahnov, Czech Republic	AY175806	MT221654	MN990671	MN996979	MT163172	—
D. tabescens	MENDELU 519	Antonín et al. 2006; This study	*Quercus* sp.	Břeclav, Czech Republic	DQ784799	MT221655	MN990672	MN996980	MT163173	MT225095
D. tabescens	MENDELU 520 (BRNM 695685)	This study	*Quercus* sp.	Břeclav, Czech Republic	—	—	MN990673	MN996983	MT163174	MT225096
D. tabescens	MENDELU 521 (BRNM 695686)	This study	*Quercus* sp.	Břeclav, Czech Republic	—	MT221656	MN990674	MN996981	MT163175	—
D. tabescens	MENDELU 522 (BRNM 695687)	This study	*Ulmus* sp.	Břeclav, Czech Republic	—	MT221658	MN990675	MN996982	MT163176	—
D. tabescens	MENDELU 525 (BRNM 699839)	Antonín et al. 2006; this study	*Acer campestre*	Břeclav, Czech Republic	DQ784800	MT221657	MN990676	—	MT163177	MT225098

[a]More information about isolates is available on the references in parentheses.
[b]ITS = internal transcribed spacer; *tef1* = translation elongation factor 1-alpha; *rpb2* = RNA polymerase II; *gpd* = glyceraldehyde-3-phosphate dehydrogenase; 28S = nuclear ribosomal large subunit 28S; *act* = actin.
[c]Stipe-derived culture.

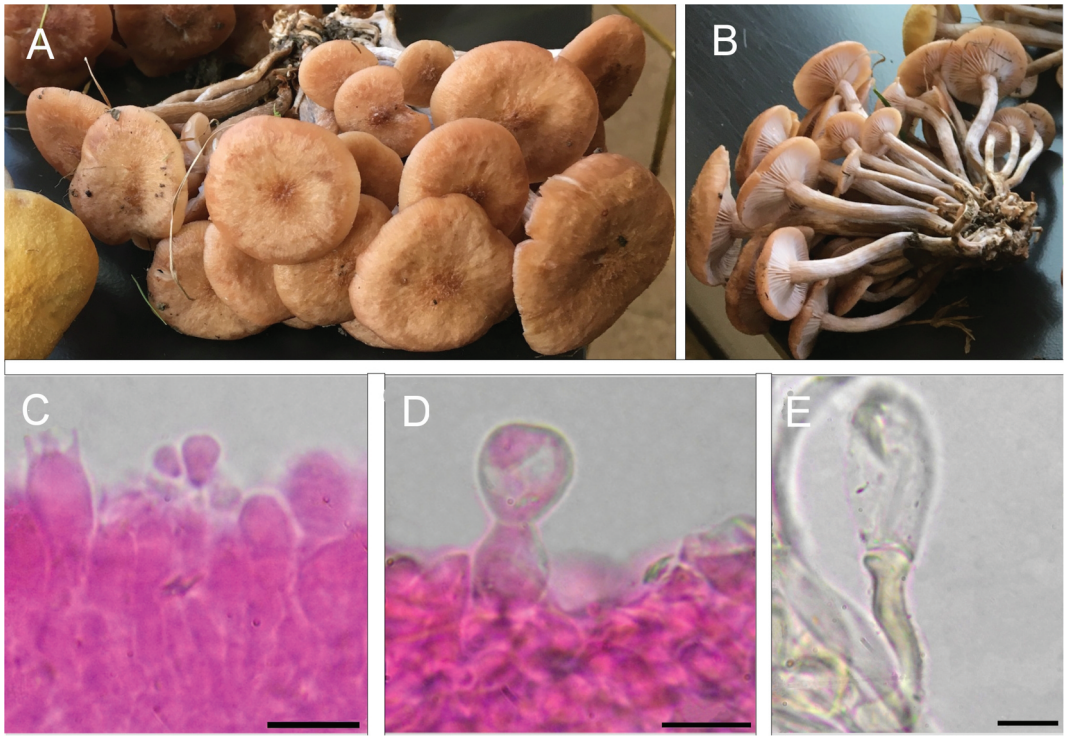

Figure 1. *Desarmillaria caespitosa*. A–B. *Desarmillaria caespitosa* basidiomata from Ohio, USA (pilei 40–55 mm broad in mature basidiomata). C. Basidium in 5% KOH. D. Cheilocystidium in 5% KOH. E. Caulocystidium in 5% KOH (microscopic structures from basidiomata from Mexico) (XAL MEX21WF). Bars: C, D = 10 µm; E = 100 µm. Photographs: E. Bonello (A–B) and R. Medel (C–E).

conditions: 94 C for 1 min, 35 cycles at 95 C for 30 s, 55–58 C (depending on the primers used: 28S: 58 C, *tef1*: 55 C, *rpb2*: 56 C, *act*: 57 C, and *gpd*: 55 C) for 30 s, and 72 C for 45 s, and finally 72 C for 10 min. Primer pairs used to amplify each locus included LROR and LR5 for 28S (Rehner and Samuels 1994; Vilgalys and Hester 1999); EF983F and EF2218R for *tef1* (Rehner and Buckley 2005); bRPB2-6F and bRPB2-7.1R for *rpb2* (Matheny 2005); ACT-181 and Act-875R for *act* (F.O.P. Stefani et al. pers. comm.); and GPD10F and GPD522R for *gpd* (F.O.P. Stefani et al. pers. comm.) (TABLE 2). PCR products were electrophoresed in 1.5% agarose gels with 0.5× TBE buffer (45 mM Tris-pH 8.3, 45 mM Boric acid, 1 mM Na_2EDTA) and stained with GelRed (Biotium, Fremont, California). Bands were visualized using ultraviolet light (UV) light. PCR products were treated with ExoSAP-IT PCR Product Cleanup (Affymetrix, Santa Clara, California) following the manufacturer's protocol and sequenced at Eurofins MWG Operon USA (Louisville, Kentucky). Phylogenies of the individual five gene regions were inferred with reference isolates of closely related species. The suite of reference isolates varied depending on the locus, and GenBank numbers are shown in FIGS. 4–8. To test the genealogical concordance phylogenetic species recognition (GCPSR; Taylor et al. 2000) criteria on *D. tabescens* collected from North American and Europe, phylogenies for each locus were estimated separately to examine well-supported separation of isolates for each locus (Taylor et al. 2000). Phylogenies were estimated using maximum likelihood (ML) in PhyML (Guindon et al. 2010) and Bayesian inference (BI) in MrBayes 3.2 (Ronquist et al. 2012) as implemented in Geneious (Kearse et al. 2012; https://www.geneious.com/). DT-ModSel (Minin et al. 2003) was used to estimate the best-fit nucleotide substitution models for each data set. Robustness and support for clades for the ML phylogeny were assessed using 1000 bootstraps (BS). BI was performed with parameter settings suggested by the best-fit nucleotide substitution models. The Markov chain Monte Carlo (MCMC) search was run with four chains for 3 million generations generating 30 001 trees; the first 6000 trees were discarded as "burn-in," and node support was indicated by posterior probability (PP). Convergence and proper mixing of Bayesian analyses were assessed by examining the trace plots that were generated for two independent runs. Analyses were run until the effective sampling size was >300 for all analyses.

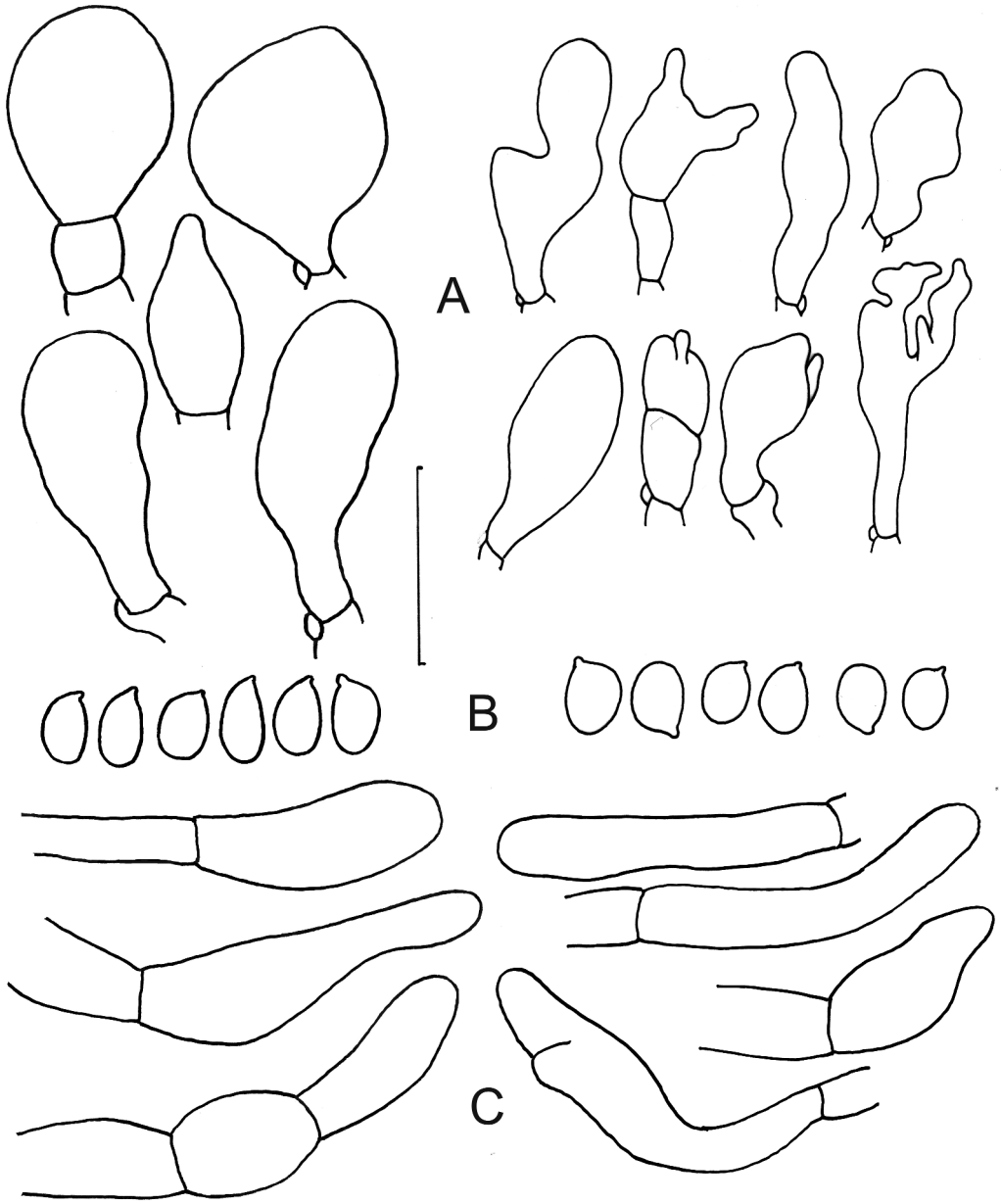

Figure 2. Comparison of microscopic characters of *Desarmillaria caespitosa* (neotype, left) and *D. tabescens* (right). A. Cheilocystidia. B. Basidiospores. C. Terminal cells of stipitipellis hyphae. Bar = 20 µm. Del. V. Antonín.

RESULTS

Phylogeny.—A total of 4154 nucleotides were sequenced at the 28S, *tef1, rpb2, act*, and *gpd* loci, with 1591, 561, 834, 681, and 487 bp, respectively. Of all the loci, the 28S showed the least resolution for all the *Desarmillaria*/*Armillaria* species, including *D. tabescens* isolates (MENDELU 171, 519, 520, 521, 522, and 525) collected from Europe and *D. caespitosa* isolates (XAL MEX21WF, OHIO_2018PB-1, AT-MU-S2, OOI-99, and OOI-210) collected from North America. *Desarmillaria tabescens* and *D. caespitosa* were separated by the following numbers of sites at each locus: 28S (0), *rpb2* (10), *gpd* (4), *act* (3), and *tef1* (25). Nucleotide variation did not separate *D. tabescens* and *D. caespitosa* isolates at the 28S region (FIG. 4). However, phylogenies of *tef1* and *gpd* each showed separation of *D. tabescens* and *D. caespitosa* with strong support (100% BS and 1.00 PP) (FIGS. 5, FIGS. 6; TABLE 3). This separation also occurred in the *act* phylogeny with 100% BS, but lower (0.70) PP support (FIG. 7; TABLE 3). However, at the *rbp2, D. caespitosa* was contained within a well-supported monophyletic subclade within a paraphyletic clade that contained both *Desarmillaria* species (FIG. 8).

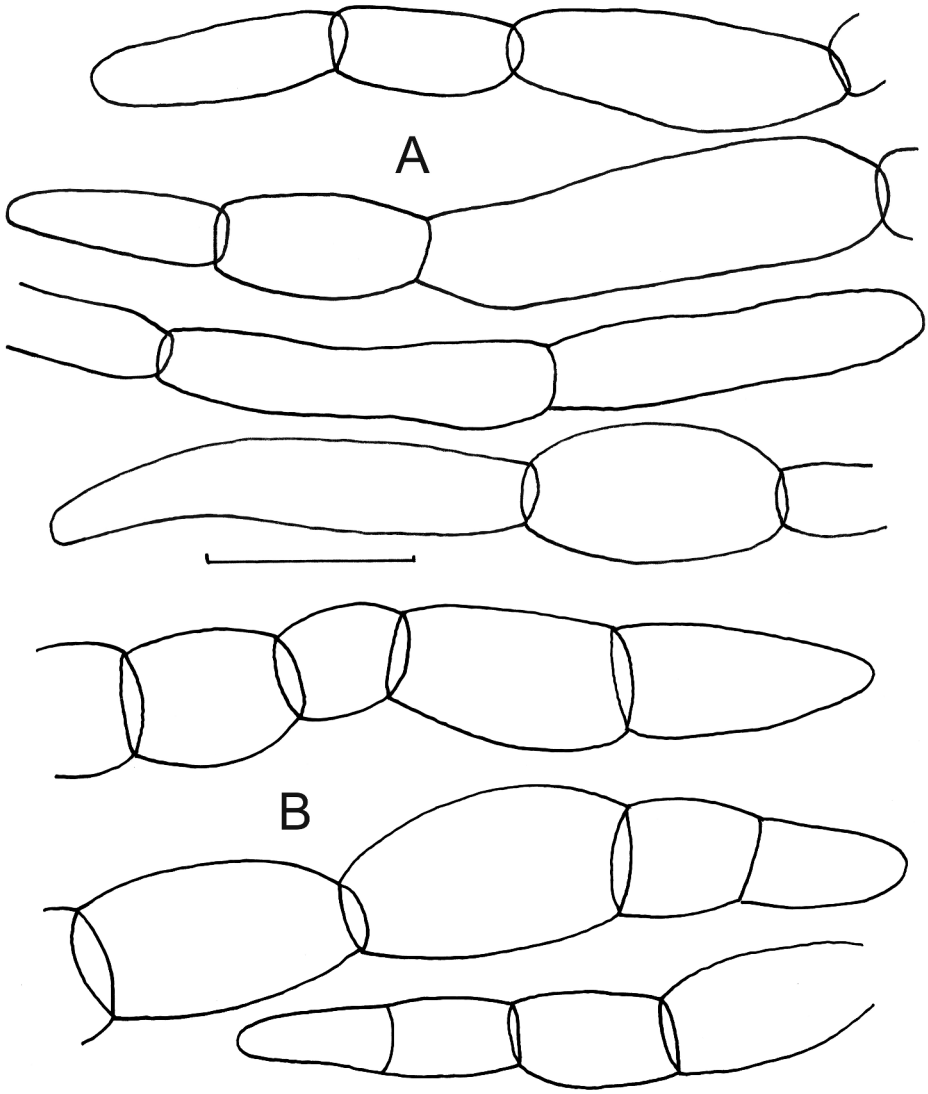

Figure 3. Pileipellis scales hyphae. A. *Desarmillaria caespitosa* (neotype). B. *D. tabescens*. Bar = 20 µm. Del. V. Antonín.

Table 2. PCR primers used for amplifications.

Region/gene	Primers	Nucleotide sequence (5′ → 3′)	Source
nuclear large subunit 28S rDNA (28S)	LROR LR5	ACC CGC TGA ACT TAA GC TCC TGA GGG AAA CTT CG	Rehner and Samuels 1994; Vilgalys and Hester 1999
translation elongation factor 1-alpha (*tef1*)	EF983F EF2218R	GCY CCY GGH CAY CGT GAY TTY AT ATG ACA CCR ACR GCR ACR GTY TG	Rehner and Buckley 2005
RNA polymerase II (*rpb2*)	bRPB2-6F bRPB2-7.1R	TGG GGY ATG GTN TGY CCY CG CC CAT RGC YGT YTT MCC CAT DGC	Matheny 2005
glyceraldehyde-3-phosphate dehydrogenase (*gpd*)	GPD10F GPD522R	GCN TCN TGC ACV ACS AAC TG YCC SRA CTC GTT GTC GTA CC	F.O.P. Stefani, J.A. Berube, and R.C. Hamelin pers. comm.
actin (*act*)	ACT-181F Act-875R	GAA CAG GGA GAA GAT GAC C TCA GCA ATA CCA GGG AAC	F.O.P. Stefani, J.A. Berube, and R.C. Hamelin pers. comm.

Sequences at the five loci were not obtained for all isolates; however, representatives of both species were present for each locus. At the *tef1* locus, comparisons with *D. tabescens* collected from widely separated locations indicate that *D. caespitosa* is indeed a North American vicariant (FIG. 5).

TAXONOMY

Desarmillaria caespitosa (Berk.) Antonín, J.E. Stewart & Medel, comb. nov. FIGS. 1–3

MycoBank MB837370, MBT393843

Basionym: Lentinus caespitosus Berk., in Hooker, London J Bot 6:317. 1847.

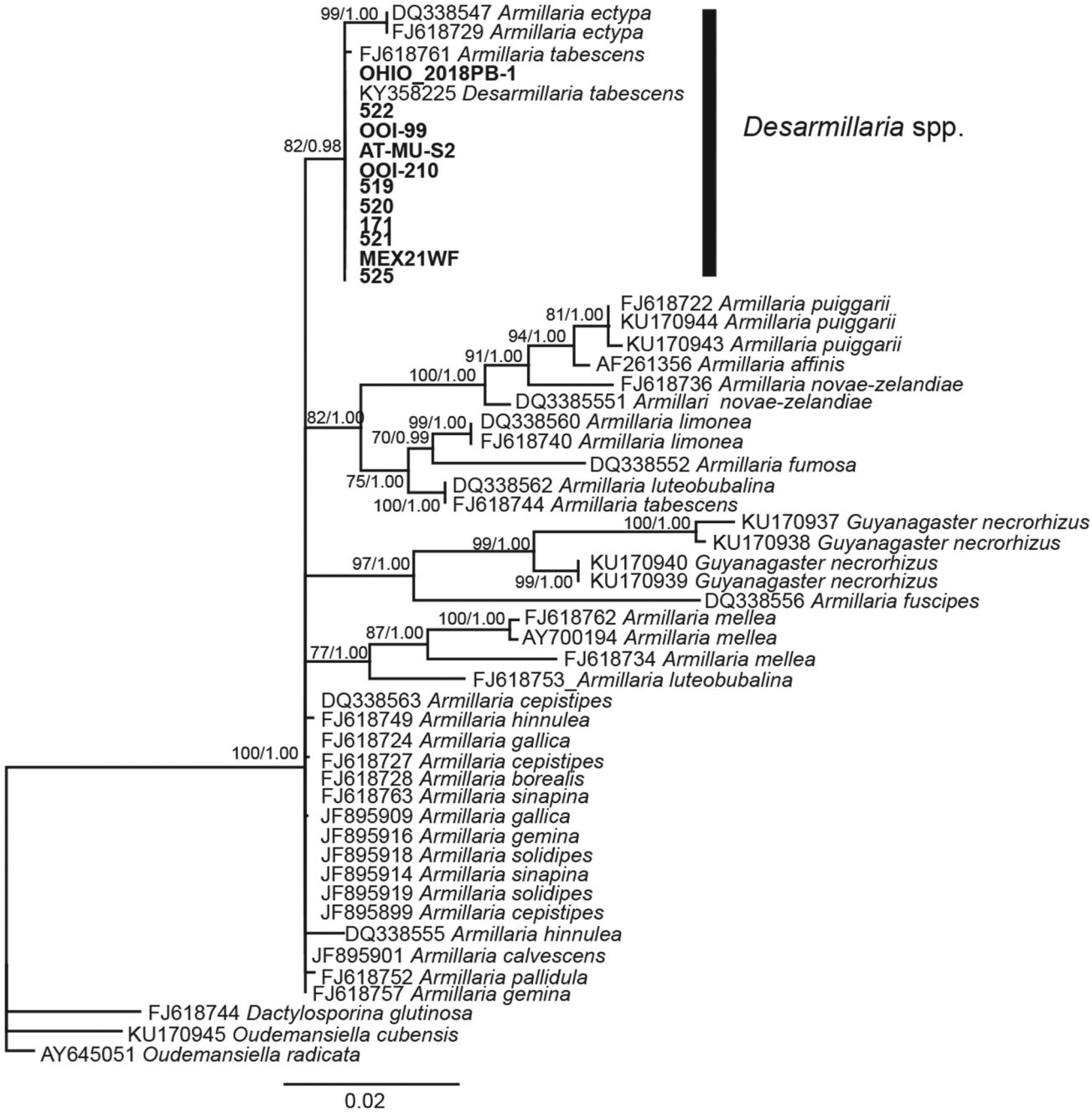

Figure 4. Maximum likelihood phylogeny of a portion of the 28S region with *Desarmillaria tabescens* and *D. caespitosa* forming a single clade with strong bootstrap and posterior probability support (BS/PP). Isolates of both *D. tabescens* and *D. caespitosa* are described in TABLE 1.

≡ *Agaricus caespitosus* (Berk.) Berk. & M.A. Curtis, J Linn Soc Bot 10:287. 1869. — *Pleurotus caespitosus* (Berk.) Sacc., Syll Fung 5:352. 1887. — *Pocillaria caespitosa* (Berk.) Kuntze, Revisio generum plantarum 2:865. 1891. — *Dendrosarcus caespitosus* (Berk.) Kuntze, Revisio generum plantarum 3:463. 1898. — *Monadelphus caespitosus* (Berk.) Murrill, Mycologia 3:192. 1911.

= *Agaricus monadelphus* Morgan, J Cincinnati Soc Nat Hist 6:69. 1883. — *Clitocybe monadelpha* (Morgan) Sacc., Syll Fung 5:164. 1887.

Typification: USA. OHIO: Waynesville, in woods on the ground, 8 Sep 1844, *T.G. Lea* (K, C, type; Pegler 1983). Material missing (lost) in both herbaria (see notes below). USA. OHIO: Franklin County, Westerville, 6524 Cherokee Rose Drive, 40°05′29.75″N, 82°54′03.77″W, alt. 262 m, on Silver maple (*Acer saccharinum*) root in the middle of a lawn, 27 Aug 2018, *M. Bellizzi* (**neotype** BRNM 825655; **isoneotype** DBG F-030611; designated here).

Selected images: Miller (1981), Lincoff (1992), both as *Armillariella tabescens*.

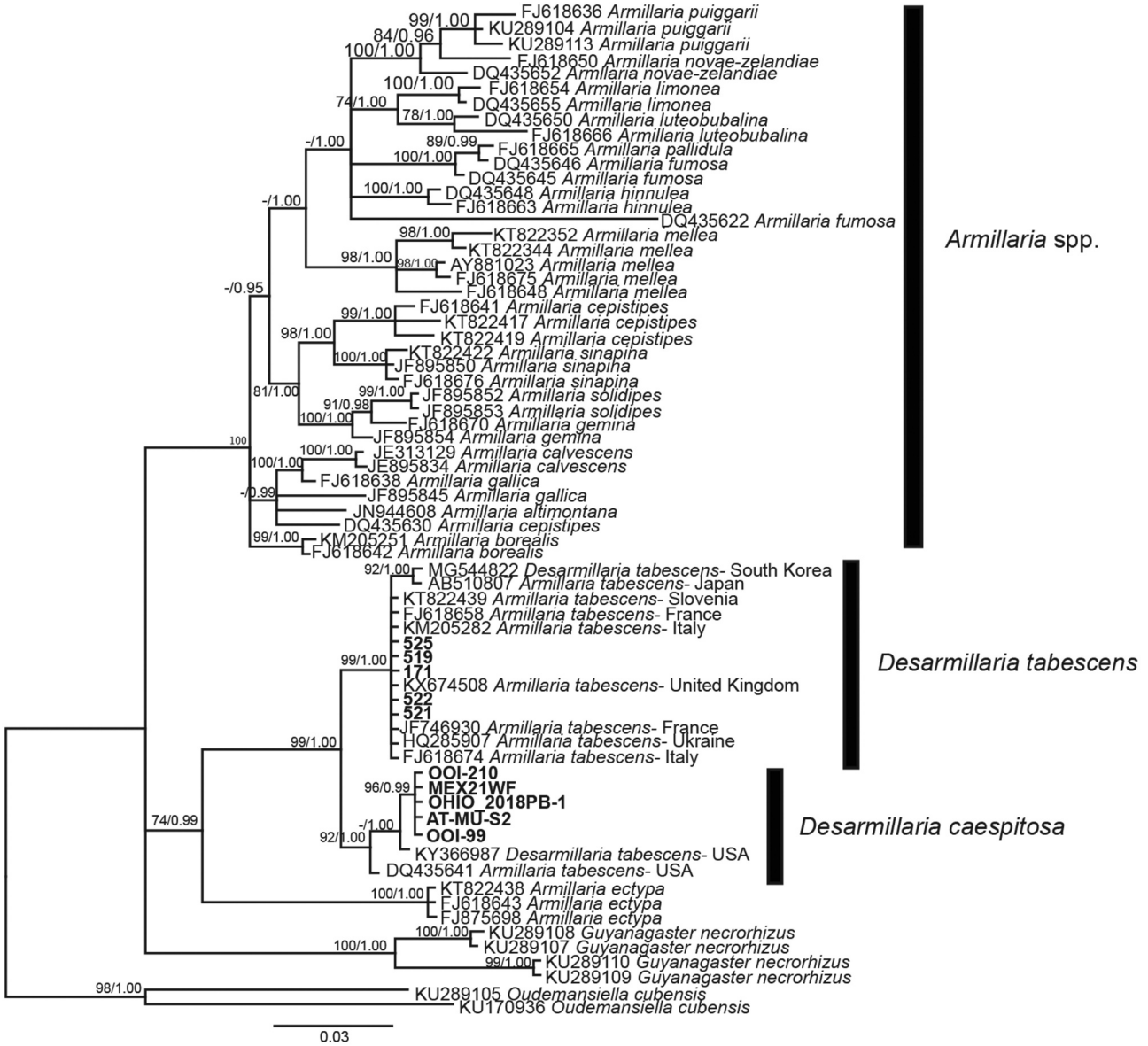

Figure 5. Maximum likelihood phylogeny of the translation elongation factor 1-alpha (*tef1*) with well-supported nodes (BS/PP) separating sequences of *Desarmillaria tabescens* and *D. caespitosa*. Isolates of both *D. tabescens* and *D. caespitosa* are described in TABLE 1.

Basidiomata caespitose, frequently gregarious, lignicolous. Pileus 40–55 mm wide, convex to plano-convex when mature, center umbonate, becoming depressed in age, orbicular in apical view; margin straight, lobed, edge entire to dentate; hygrophanous and zonate, surface of the margin smooth; yellowish brown, grayish red (7B3), reddish white (7A2) with reddish brown (9E3) when fresh to light brown (6C6; 6D5, 6D6) or brown (6D7) at the center when dry; squamules light brown (6D3–6D4), arranged mainly at the center and around it. Lamellae close, decurrent, adnate, thick, 3–5 mm broad; whitish when young, then reddish gray (8B2–8B3, 9B2) when fresh to blond to olive brown (4C4–4D4) or brown to light brown (6D6–6D7) when dry; edges smooth; lamellulae present, developed in 2–3 series. Stipe 45–75 mm length, 9–10 mm wide at the part attached to the pileus and tapering toward the stipe base up to 5 mm, central, cylindrical, hollow; annulus absent, longitudinally distinctly fibrillose to slightly grooved; white (1A1) with irregular grayish red (7B3) tones throughout the stipe when fresh, yellowish white to yellowish gray (4A2–4B2) and fibrillose when dry; rhizomorphs frequently absent. Taste and smell of fresh specimens not observed.

Basidiospores (6–)6.5–8.5(–9.5) × (4–)4.5–5.5(–6) µm, average = 7.5 × 4.9 µm, Q = (1.21–)1.27–1.72, average = 1.46, ellipsoid, broadly ellipsoid, less frequently dacryoid, ovoid, often slightly thick-walled, less frequently thin-

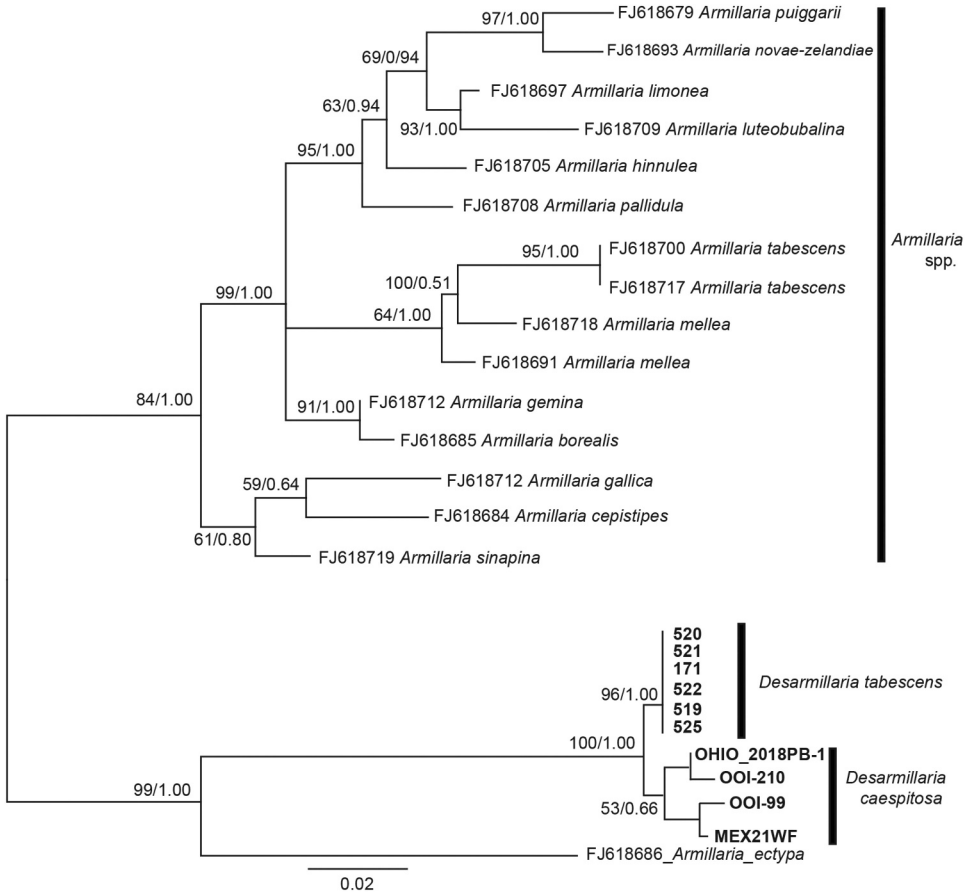

Figure 6. Maximum likelihood phylogeny of the glyceraldehyde-3-phosphate dehydrogenase (*gpd*) gene highlighting with well-supported nodes (BS/PP) separating sequences of *Desarmillaria tabescens* and *D. caespitosa*. Isolates of both *D. tabescens* and *D. caespitosa* are described in TABLE 1.

walled; white (1A1) to yellowish white (4A2) in deposit. Basidia 22–35 × (6–)7–10 µm, 4-spored, clavate, clamped. Basidioles 15–33 × 3–8 µm, clavate, (sub)cylindrical, subfusoid, clamped; with scattered, 20–30 × 5–11 µm, irregularly clavate, subutriform or (sub)capitate cells intermixed with basidia and basidioles in hymenium or on edge. Cheilocystidia (13–)20–35(–40) × (6–)8–22 µm, numerous, forming a sterile band; (broadly) clavate, (broadly) fusoid, sphaeropedunculate, pyriform, vesiculose, rarely sublageniform, rarely with apical wart, sometimes rostrate, sometimes 2-celled; often slightly thick-walled; subhymenium of cylindrical, gelatinized, branched, thin-walled hyphae 2–6 µm wide. Pileipellis a cutis composed of cylindrical or subfusoid, thin- to slightly thick-walled, clampless hyphae 3–9 µm wide; terminal cells clavate to subcylindrical, up to 12 µm wide; scales composed of chains of cylindrical, ellipsoid, barrel-shaped, (sub)fusoid, often short, clampless, mostly slightly thick-walled cells; terminal cells 15–60 × (6–)8–19(–23) µm, fusoid, conical, subutriform, subcylindrical, subulate, subellipsoid, slightly thick-walled, obtuse, rarely irregular. Stipitipellis (apex) of cylindrical, parallel, slightly thick-walled, sometimes slightly gelatinized hyphae 2–7 µm wide; terminal cells (20–)30–57(–90) × (8–)12–20(–35) µm, numerous, clavate, fusoid, subcylindrical, less frequently 2-celled or in short chains, ± slightly thick-walled.

Ecology and distribution: In hardwood and mixed woodlands, orchards, and urban areas, usually on stumps and buried wood of hardwoods (frequently *Quercus* but also *Acer, Cornus, Ilex cornuta, Pyracantha, Raphiolepis indicus, Ulmus parviflora*, and *Prunus*), less frequently on conifers (*Araucaria araucana, Juniperus squamata, Pinus, Thuja occidentalis*) and palms (*Butia capitata*). Distributed primarily in southeastern, eastern, and central USA, Mexico, and Central America (Costa Rica). Basidiomata occurring mostly occurring mostly Jun–Nov with infrequent records from Mar to May and Dec (mushroomobserver.org, mycoportal.org).

Other specimens examined: MEXICO. VERACRUZ: Xalapa, Frente al Asadero cien, stump of *Araucaria araucana*, 26 Jul 2009, *R. Medel 1899* (XAL MEX21WF, BRNM 825654).

Desarmillaria tabescens (all as *Armillaria tabescens* or *A. socialis*). BULGARIA. Banja near Nesebar, between

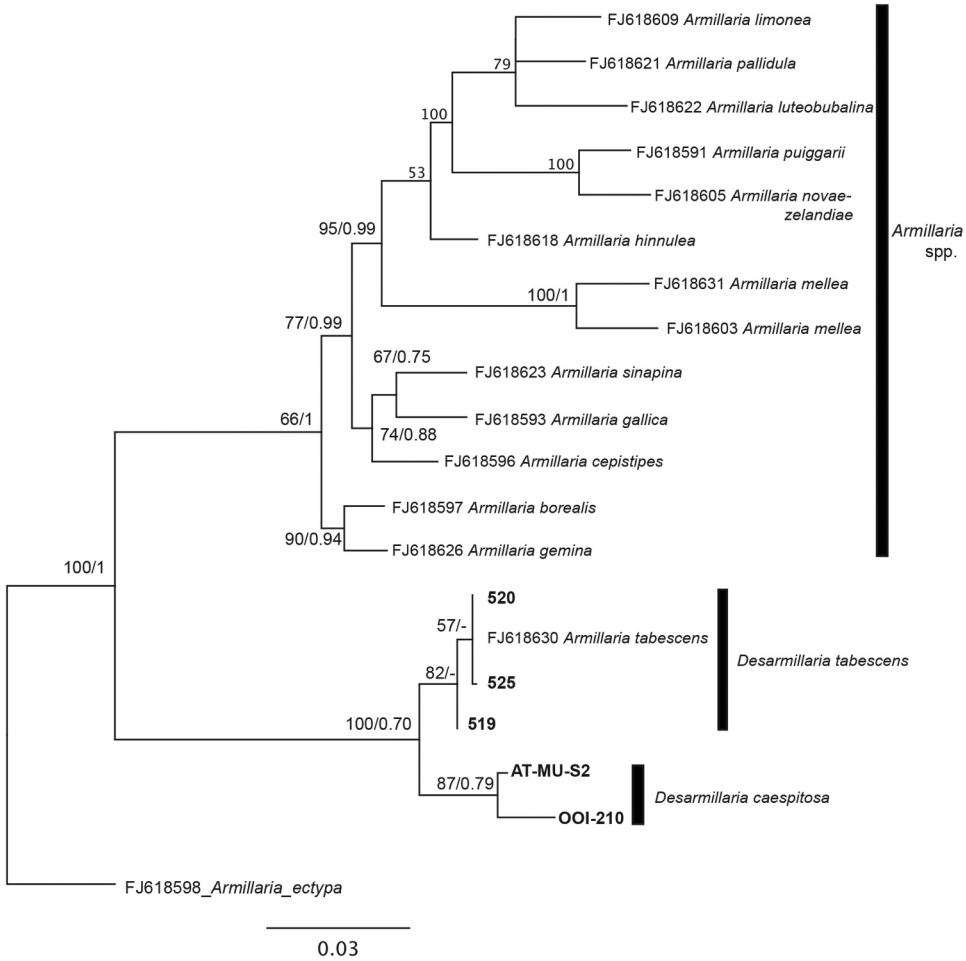

Figure 7. Maximum likelihood phylogeny of the actin (*act*) gene with well-supported nodes (BS/PP) separating sequences of *Desarmillaria tabescens* and *D. caespitosa*. Isolates of both *D. tabescens* and *D. caespitosa* are described in TABLE 1.

Obzor and Slančev Briag, 30 Aug 1983, *F. Kotlaba* (PRM 831855); Stara Planina, Lovno chanče, 2 Aug 1979, *B. Bill & F. Kotlaba* (PRM 821423); Primorsko near Burgas, in the direction of Mičurin, 21 Sep 1984, *S. Hejný* (PRM 837720). CZECH REPUBLIC. Lanžhot, Ranšpurk National Nature Reserve, on the base of a dead, ca. 300-y-old *Quercus* stem, alt. 150 m, 25 Aug 1966, *J. Lazebníček & A. Vágner* (BRNM 266006); Břeclav, Nové Mlýny, Křivé jezero National Nature Reserve, alt. 150 m, on stump of *Quercus robur*, 8 Sep 2005, *V. Antonín 05.123, 05.124,* and *05.125* (BRNM 695685, 695686, and 695687); ibid., 14 Sep 2005, *L. Jankovský* (BRNM 699839). FRANCE. Bourgogne, Aiserey, Forêt d´Izeure, alt. 200 m, in oak-hornbeam forest on calcareous clayed soil, on stump of a broadleaved tree, 12 Oct 1992, *J.-C. Verpeau* (CB M-6803). SLOVAKIA. Malé Karpaty Mts., Bratislava, Turecký vrch hill, in beech forest, 25 Sep 1994, *I. Kautmanová* (BRA 4994); Krupinská planina Mt., Čabradský Vrbovok, on dead stem of *Quercus*, alt. 320 m, 23 Sep 1987, *J. Kuthan* (BRA 4992); Strážovské vrchy Mts., Nitrianské Rudno, in the rivulet Rudnianka valley, on stump of *Quercus*, alt. 360 m, 14 Jul 1984, *J. Kuthan* (BRA 4993); Pohronský Inovec Mts., Čaradice, xerophytic, broad-leaved forest with *Quercus cerris* and *Q. petraea*, with mixed *Pinus*, on the base of *Quercus* stem, 19 Sep 1987, *V. Antonín 87.117* (BRNM 418969); Zlaté Moravce, *Quercus* forest, 19 Aug 1975, *J. Pokorný* (BRNM 266003). SLOVENIA. Panovec, 13°40′37.3″E, 45° 57′08.9″N, on declining standing tree of *Quercus petraea*, 3 Sep 2006, *G. Seljak* (LJF 2856, neotype; BRNM 737504, isoneotype; designated by Redhead et al. [2012]).

DISCUSSION

Desarmillaria caespitosa was described as *Lentinus caespitosus* from Waynesville, Ohio, by Berkeley in 1847. The type specimens were preserved at Kew (K) and the University of Copenhagen Herbarium (C) (Pegler 1983). Pegler (1983) revised these materials and synonymized the name with *Armillaria tabescens*. This opinion was supported by Volk and Burdsall (1995). However, both type specimens are missing at K and C, where it was on loan several years ago (pers. comm., C and K curators).

Figure 8. Maximum likelihood phylogeny of the RNA polymerase II (*rpb2*) with well-supported nodes (BS/PP) separating *Desarmillaria tabescens* and *D. caespitosa*. Isolates of both *D. tabescens* and *D. caespitosa* are described in TABLE 1.

Table 3. Node support (bootstrap and posterior probabilities) for the phylogenetic separation of *Desarmillaria tabescens* and *D. caespitosa*.

Locus[a]	Bootstrap	Posterior probability
28S	—	—
tef1	99	1.00
gpd	100	1.00
rbp2	100	1.00
act	100	0.70

[a]28S = nuclear large ribosomal subunit 28S rDNA; *tef1* = translation elongation factor 1-alpha; *gpd* = glyceraldehyde-3-phosphate dehydrogenase; *rpb2* = RNA polymerase II; *act* = actin.

Therefore, we decided to designate a neotype from recent material close to the type locality in Ohio.

Desarmillaria tabescens differs from *D. caespitosa* by the broader basidiospores [(6.0–)7.5–10(–11) × (4.5–)5–7 µm, Q = 1.3–1.8, average = 1.3–1.7], narrower cheilocystidia [(12–)17–41 × 5.0–10 µm], which are often irregular or mixed with regular, irregular, or coralloid ones, and narrower caulocystidia [(11–)20–50 × 7–14 µm] (Antonín et al. 2006). *Desarmillaria tabescens* mostly occurs in the southern part of Europe (Guillaumin and Lung 1985). The northern distribution limit runs through central Europe, including the Czech Republic and Slovakia (Antonín et al. 2006), latitude about 49° north. In Eurasia, *D. tabescens* (reported as *A. tabescens* or *A. socialis*) has been reported in association with diverse hosts, primarily in southern Europe and eastern Asia, where it can cause root disease or function as an orchid symbiont (Terashita and Chuman 1987; Cha and Igarashi 1995; Ota et al. 1998; Baumgartner et al. 2011; Guo et al. 2016). It has not been found in the Southern Hemisphere. Typically in Europe, *D. tabescens* has been reported in association with oaks (*Quercus*), maple (*Acer*), silver birch (*Betula pendula*), strawberry tree (*Arbutus unedo*), and introduced eucalypts (*Eucalyptus*) (Guillaumin et al. 1993; Antonín et al. 2006).

In the USA, this fungus (identified as *A. tabescens* or *Clitocybe tabescens*) is very common in southeastern states, west to Texas and Oklahoma, especially as a severe pathogen of oaks, silver maple, and peach (*Prunus persica*) (Cox 2004; Schnabel et al. 2005; Kuo 2017). In North America, it has a reported distribution in association with diverse hosts east of the Rocky Mountains and eastern Mexico, where it frequently causes root disease. As examples, *D. tabescens* was found in oak forests of the Ozark Mountains of southeastern Missouri and northwestern Arkansas (Bruhn et al.

2000; Kelley et al. 2009). In the southeastern USA, *D. tabescens* was reported to cause root disease of sand pine (*Pinus clausa*), peach, Chinese holly (*Ilex cornuta*), singleseed juniper (*Juniperus squamata*), Indian hawthorn (*Raphiolepis indicus*), northern white cedar (*Thuja occidentalis*), and pindo palm tree (*Butia capitata*) (Ross 1970; Schnabel et al. 2005, 2006). Because sequences from the isolates reported as *A. tabescens* from southeastern USA, including some sequences of isolates from Schnabel (2005), cluster within the same clade as *D. caespitosa*, it seems probable that the abovementioned hosts and root diseases are associated with *D. caespitosa* as it is presently recognized. *Desarmillaria caespitosa* was found causing root disease on an ornamental monkey puzzle tree (*Araucaria araucana*) in Veracruz, Mexico (Kim et al. 2010, as *A. tabescens*).

In Japan, *D. tabescens* (as *A. tabescens*) has been reported from Kyushu and central and southern parts of Honshu (Ota et al. 1998) on ornamental cherries (e.g., *Prunus* hybrids) in urban areas (Hasegawa 2005). It is also mentioned from China, where it is considered a pathogen on economically valuable trees, including woody ornamentals and fruit trees (Qin et al. 2007). As examples in eastern Asia, *D. tabescens* has been reported on diverse hardwood hosts, such as *Prunus, Quercus, Populus*, and *Salix* (Lee and Cho 1977; Ota et al. 1998; Qin et al. 2007), and in symbiotic association with orchids, such as *Gastrodia elata* (Cha and Igarashi 1995; Guo et al. 2016) and *Galeola septentrionalis* (Terashita and Chuman 1987; Ota et al. 1998). However, this Asian taxon may represent a separate species according to phylogenetic analysis (Park et al. 2018).

Desarmillaria ectypa is distinctly different from both *D. caespitosa* and *D. tabescens* by the single growing basidiomata with an apparently smooth pileus and, especially, by the nonlignicolous habitat in marshes and peat bogs (e.g., Zolciak et al. 1997; Ohenoja 2006). It occurs in Eurasia (e.g., Legon and Henrici 2005; Ota et al. 2005; Ohenoja 2006; Stasińska 2015; Klopfenstein et al. 2017), but not in North America or the Southern Hemisphere.

This study is not the only case of North American/European vicariance between species of similar morphology. Similar examples can be also found in other fungal groups, e.g., Hymenochaetales (*Inonotus andersonii* (Ellis & Everh.) Černý [America; A]/*I. krawtzewii* (Pilát) Pilát [Europe; E]; Zhou et al. 2014); Russulales (*Heterobasidion irregulare* Garbel. & Otrosina [A]/*H. annosum* (Fr.) Bref. [E]; Otrosina and Garbelotto 2010); Polyporales (*Resinoporia sitchensis* (D.V. Baxter) Audet [A]/*R. piceata* (K. Runnel, Spirin & Vlasák) Audet [E]; Spirin et al. 2015; *Resinoporia* is the former *Antrodia crassa* group); Polyporales (*Sparassis americana* R.H. Petersen [A]/*S. crispa* (Wulfen) Fr. [E]; Hughes et al. 2014); and Agaricales (*Hohenbuehelia angustata* (Berk.) Singer [A]/*H. wilhelmii* Consiglio & Setti [E]; Consiglio and Setti 2017). Based on the vicariance paradigm observed in the present and previous studies, *Armillaria*/*Desarmillaria*, and other members of the Basidiomycota with similar species in Europe, North America, Asia, and/or other regions warrant comparative morphological, ecological, and phylogenetic analyses to determine the appropriate taxonomic status of the vicariant species.

ACKNOWLEDGMENTS

The authors wish to thank the curators of the herbaria BRA, C, CB, K, and XAL for information about collections or their loans respectively. The authors also thank the Sam Mitchel Herbarium of Fungi at Denver Botanic Gardens. The authors also thank Luis Alberto Parra Sanchez (Aranda de Duero, Spain) for valuable nomenclatural comments; K. Otto, Dr. J. Ibarra-Caballero, and B. Lalande for excellent laboratory assistance; and M. Bellizzi for assistance in collections. The authors also wish to thank to all reviewers and editors of *Mycologia*. Mention of trade names does not constitute endorsement by the United States Department of Agriculture (USDA) Forest Service.

FUNDING

The studies of the A.V. were enabled by institutional support of long-term conceptual development of research institutions provided by the Ministry of Culture of the Czech Republic (MK000094862). Participation of M.T. was supported by the European Regional Development Fund, Project Phytophthora Research Centre CZ.02.1.01/0.0/0.0/15_003/0000453. Funding for baseline studies of *Armillaria* identification and phylogenetics was provided by the USDA Forest Service, Forest Health Protection Service, Special Technology Development Program, and Joint Venture Agreements 15-JV-11221633-160, 19-JV-11221633-093, and 20-JV-11221633-141 (to J.E.S.).

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