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Septonema lohmanii G. Delgado & O. Koukol,
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Gregorio DELGADO, Ondřej KOUKOL
Andrew N. MILLER & Meike PIEPENBRING



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Center of Excellence in Fungal Research, Mae Fah Luang University 333 M. 1 T.Tasud Muang District, Chiangrai 57100, Thailand.

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Laboratoire de Botanique, Phytochimie et Mycologie / UMR -CNRS 5175 CEFE, Faculté de Pharmacie, 15, avenue Charles-Flahault, Université Montpellier I, BP 14491, 34093 Montpellier Cedex 5, France.

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Université de Montpellier II, CEFE/CNRS Campus du CNRS, 1919, route de Mende, 34293 Montpellier Cedex 5.

Naritsada THONGKLANG

Center of Excellence in Fungal Research, Mae Fah Luang University, 333 M. 1 T.Tasud Muang District, Chiangrai 57100, Thailand.

Xiang-hua WANG

Key Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Sciences, Lanhei Road 132, Kunming 650201, P. R. China.

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***Septonema lohmanii* G. Delgado & O. Koukol, sp. nov., a new species in Mytilinidiales (Dothideomycetes) and the phylogenetic position of *S. fasciculare* (Corda) S. Hughes**

Gregorio DELGADO

EMLab P&K Houston,
10900 Brittmoore Park Drive Suite G, Houston, TX 77041 (United States)
and Department of Mycology, Institute of Ecology, Evolution and Diversity,
Goethe Universität Frankfurt, Max-von-Laue-Str. 13,
60438 Frankfurt am Main (Germany)
gdelgado@emlabpk.com (corresponding author)

Ondřej KOUKOL

Department of Botany, Faculty of Science, Charles University,
Benátská 2, CZ–128 01 Praha 2 (Czech Republic)

Andrew N. MILLER

Illinois Natural History Survey, University of Illinois,
1816 South Oak Street, Champaign, IL 61820 (United States)

Meike PIEPENBRING

Department of Mycology, Institute of Ecology, Evolution and Diversity,
Goethe Universität Frankfurt, Max-von-Laue-Str. 13,
60438 Frankfurt am Main (Germany)

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ABSTRACT

During independent surveys of microfungi associated with *Pinus* spp. in the United States and the Czech Republic, a distinct fungus matching the generic concept of *Septonema* Corda was collected. It is characterized by distinctly ornamented conidiophores, branches, conidia and hyphae, ranging from verruculose to strongly verrucose with prominent rounded warts, yellowish brown to brown or reddish brown in color and forming densely floccose, dark brown or dark reddish brown colonies on pine wood and bark. Conidia are cylindrical or subcylindrical and produced in short, simple or branched acropetal chains. Multigene phylogenetic analyses including nuclear ribosomal (LSU) and protein coding gene (EF1- α) sequence data suggest that both collections are conspecific and belong to the order Mytilinidiales (Dothideomycetes, Ascomycota) where they group distant from other mytiliniaceous fungi with known septonema-like anamorphs. To provide a proper name based on phylogenetic placement and to possibly circumscribe *Septonema sensu stricto*, a non-sporulating, putative strain belonging to *S. secedens* Corda, the generic type, was included in the analyses. DNA sequence data placed this strain within the family Venturiaceae (Venturiales, Dothideomycetes) but morphological examination of the corresponding herbarium specimen revealed that it belongs instead to *S. fasciculare* (Corda) S. Hughes. Because of the polyphyletic nature of the genus and the unknown phylogenetic position of its type species, our fungus is accommodated in *Septonema* as a new species named *S. lohmanii* G. Delgado & Koukol, sp. nov.

KEY WORDS

Anamorphic,
phylogeny,
saprobic,
new species.

RÉSUMÉ

Septonema lohmanii G. Delgado & O. Koukol, *sp. nov.*, une nouvelle espèce chez les Mytilinidiales (*Dothideomycetes*) et la position phylogénétique de *S. fasciculare* (Corda) S. Hughes.

Lors d'inventaires indépendants de micromycètes associés aux pins des États-Unis et de la République Tchèque, un champignon correspondant au concept générique de *Septonema* Corda a été récolté. L'espèce forme des colonies densément floconneuses, d'un brun à brun rougeâtre foncé. Elle est caractérisée par la présence de verrues rondes d'un brun jaunâtre à brun ou brun rougeâtre sur l'ensemble des conidiophores, branches, conidies et hyphes. Les conidies sont cylindriques à subcylindriques et produites en chaînes courtes, simples ou ramifiées de façon acropète. Des analyses phylogénétiques multigènes basées sur des séquences LSU et EF1alpha suggèrent que les deux récoltes appartiennent à une même espèce qui se situe dans l'ordre des Mytilinidiales (*Dothideomycetes*, *Ascomycota*) mais sans apparenté aux autres espèces possédant des anamorphes du type *Septonema*. Afin de pouvoir placer cette espèce plus précisément dans une phylogénie, et peut-être aussi de pouvoir délimiter *Septonema* au sens strict, une souche stérile appartenant possiblement à *S. secedens* Corda, l'espèce type du genre, a été incluse dans les analyses. Cette dernière a été placée dans la famille des Venturiaceae (*Venturiales*, *Dothideomycetes*) par notre analyse phylogénétique, alors que l'étude morphologique de la souche correspondante a montré qu'il s'agissait de *Septonema fasciculare* (Corda) S. Hughes. Suite au caractère polyphylétique du genre *Septonema* et l'incertitude de la position phylogénétique de son espèce type, notre moisissure est décrite ici comme une nouvelle espèce, *S. lohmanii* G. Delgado & Koukol, *sp. nov.*

MOTS CLÉS

Anamorphe,
phylogénie,
saprophyte,
nouvelle espèce.

INTRODUCTION

Septonema Corda is a large and heterogeneous genus of anamorphic fungi (Cannon 2009). *Septonema secedens* Corda, the type species, was first collected on rotten bark of *Betula alba* L. in Bohemia, Czech Republic (Corda 1837). The genus is characterized by macronematous conidiophores, simple or with short lateral branches, monoblastic or polyblastic, integrated, determinate conidiogenous cells, terminal or intercalary on the main conidiophore axis or branches, and cylindrical, ellipsoidal or fusiform, pale to dark olive, brown or reddish brown conidia with one or several transverse septa and formed in long, often branched acropetal chains (Hughes 1951; Ellis 1971; Holubová-Jechová 1978). Similar to other morphological descriptions at that time, Corda's original diagnosis was very brief and the illustration somewhat vague leading to the subsequent application of a rather broad generic concept for several fungal taxa producing conidia in acropetal chains. Hughes (1951) redescribed and illustrated the type species based on collections from the United Kingdom. He also examined the type specimen deposited in PRM to find out that the material was not well preserved and had almost disappeared from the substrate. Hughes (1952a, 1958) recognized the heterogeneity of the genus, accepted six species, and excluded 18 names from *Septonema* Corda considering them synonyms of other taxa mostly belonging to *Taeniolella* Hughes, a morphologically similar genus characterized by semimacronematous, mostly unbranched conidiophores, monoblastic conidiogenous cells and conidia in simple or branched acropetal chains that secede with difficulty. Ellis (1971, 1976) accepted only two species, *S. secedens* and *S. fasciculare* (Corda) S. Hughes, and transferred three species accepted by Hughes to *Heteroconium* Petr., a genus characterized by unbranched conidiophores, percurrent or

determinate conidiogenous cells and multiseptate conidia in unbranched acropetal chains. Holubová-Jechová (1978) also studied the type specimen of *S. secedens* Corda confirming that conidiophores and conidia are lacking in this material and the type material of *Helminthosporium confervoides* Corda, a heterotypic synonym of *S. secedens*. She accepted seven taxa in *Septonema* and accommodated *S. tetracoilum* (Corda) S. Hughes within *Lylea* Morgan-Jones, another genus characterized by micronematous, inconspicuous conidiophores and distoseptate, thick-walled conidia in short, frequently branched acropetal chains (Morgan-Jones 1975). Lunghini & Toscano (1997) expanded the generic concept of *Septonema* to accommodate *S. crispulum* Lunghini & F. Toscano having branched, sterile setae, but this fungus, however, seems morphologically close to *Hormiactella* Sacc. More recently, Crous *et al.* (2007a) separated *Septonema* from morphologically similar cladosporium-like genera by the presence of simple or branched conidiophores, monoblastic or occasionally polyblastic conidiogenous cells with subdentuplicate, neither thickened nor darkened, inconspicuous conidiogenous loci forming simple or branched chains of conidia, uniform in shape, size and septation. Schubert & Braun (2007) introduced and lectotypified *S. acicola* U. Braun & K. Schub. based on *Cladosporium radians* Sacc. & D. Sacc. on the account of morphological features in common with *S. secedens* Seifert *et al.* (2011) estimated that there may be ten taxa known in *Septonema* but recognized that many more are described. Ecologically, *Septonema* spp. are mainly saprobic and commonly found on rotten bark and wood of deciduous or coniferous trees, frequently on other fungi or rarely recorded from soil (Barron 1968; Holubová-Jechová 1978). A septonema-like fungus was also described from a microbial mat on sandstone building material in an unusual lichenized association with coccoid cyanobacteria and green algae (Grondona *et al.* 1997).

A comprehensive revision of the genus including morphological and DNA sequence data has not yet been undertaken and phylogenetic relationships are still obscure for many species currently accepted or previously assigned to *Septonema*, including *S. secedens*, the generic type. However, based on available taxonomic and cultural evidence, the modern generic circumscription emphasizing conidia in single or branched acropetal chains (Hughes 1951; Ellis 1971; Holubová-Jechová 1978) suggest polyphyly and the septonema-like morphology is shared among distant ascomycetous lineages. Lohman (1933a, b), using detailed cultural studies of single ascospores and conidia, linked *S. spilomeum* Berk. and *S. toruloideum* Cooke & Ellis with *Oedohysterium insidens* (Schwein.) E. Boehm & C.L. Schoch (Hysteriales, Dothideomycetes) and *Mytilinidion scolecosporum* M.L. Lohman (Mytilinidiales, Dothideomycetes), respectively. Lohman (1934) found that *S. multiplex* Berk. & M.A. Curtis is the asexual state of *Lophiosphaera velata* (Ellis & Everh.) M.L. Lohman. Barr (1992) transferred this teleomorph to the genus *Lophiotrema* Sacc. and placed it within Lophiostomataceae (Pleosporales, Dothideomycetes) in her broad concept of this family, but the genus is currently classified in its own pleosporalean family named Lophiotremataceae (Hirayama & Tanaka 2011; Hyde *et al.* 2013). Lohman (1939) reported a septonema-like anamorph associated with *Mytilinidion rhenanum* Fuckel in specimens from Finland and New England. This connection was later confirmed by Bisby (1941) and Bisby & Hughes (1952) based on specimens collected in the United Kingdom. Sivanesan (1984), on the basis of the cultural evidence cited above, described and keyed out *Mytilinidion* Duby species with *Septonema* anamorphs.

Recently, molecular phylogenetic studies of a small number of septonema-like taxa confirmed polyphyly. Nuclear ribosomal DNA sequence data placed the root endophytic, saprobic and soil inhabiting fungus *S. chaetospira* (Grove) S. Hughes within the family Herpotrichiellaceae (Chaetothyriales, Eurotiomycetes) where it clustered with several *Cladophialophora* species and therefore it was transferred to this genus (Crous *et al.* 2007c; Narisawa *et al.* 2007). Koukol (2010) revised the taxonomic and phylogenetic status of seven strains putatively identified as *S. ochraceum* Matsush. This study revealed two new species of *Fusicladium* Bonord. within the family Venturiaceae (Venturiales, Dothideomycetes), a new species of *Cladophialophora* Borelli that clustered distantly in Herpotrichiellaceae, and a cryptic species morphologically identical but phylogenetically distinct to *Devriesia americana* Crous & Dugan within the family Teratosphaeriaceae (Capnodiales, Dothideomycetes) that was later described as *D. pseudoamericana* Jana Frank, B. Oertel, Schroers & Crous (Frank *et al.* 2010). However, the phylogenetic position of *S. ochraceum sensu stricto* remained unsettled due to the absence of a corresponding type material. *Septonema verrucosum* Zachariah, Sankaran & Leelav., originally described from soil in India and characterized by verrucose conidia in acropetal, unbranched or branched chains (Zachariah *et al.* 1981), was found to be a member of the family Sympoventuriaceae (Venturiales, Dothideomycetes) together with several species of *Ochroconis*

de Hoog & Arx and therefore it is currently accepted within this genus (Machouart *et al.* 2014; Samerpitak *et al.* 2014). As currently circumscribed *Septonema* is affiliated with the family Hysteriaceae (Hysteriales) as anamorphic *Oedohysterium* E. Boehm & C.L. Schoch or Mytilinidiaceae (Mytilinidiales) as anamorphic *Mytilinidion* (Wijayawardene *et al.* 2012, 2017) together with the morphologically similar *Taeniolella* which is known to be highly polyphyletic (Ertz *et al.* 2016).

During independent surveys of saprobic microfungi associated with *Pinus* spp. in southwestern United States and the Czech Republic, specimens of a conspicuous septonema-like fungus with strongly ornamented conidiophores, hyphae and conidia in branched, acropetal chains were collected and isolated on agar media. DNA sequence data were obtained for both isolates and their phylogenetic affinities were investigated. A strain putatively assigned to *S. secedens* was also sequenced and included in the analyses in order to elucidate the systematic position of the generic type and to investigate possible relationships with our fungus. The goals of this study are to characterize this septonema-like taxon using morphological, cultural and molecular data, and to test the hypothesis whether it belongs within the generic boundaries of *Septonema*.

MATERIAL AND METHODS

ISOLATES AND MORPHOLOGICAL STUDIES

Pieces of dead wood and bark of *Pinus* spp. showing fungal colonies were collected during field trips to forested areas of Arizona, the United States, and the Czech Republic in 2014 and 2015, respectively. Specimens were mounted in lactophenol cotton blue or Melzer's reagent for microscopic study and preparations were sealed with nail polish to obtain semi-permanent slides. Isolates were obtained by removing conidia with a sterile needle and transferring them aseptically to 2 % Malt Extract Agar (MEA) for incubation at 25 °C. Original colonies were further subcultured on MEA and Potato Dextrose Agar (PDA). A strain named *Septonema secedens* was purchased from MUCL for sequencing and comparison with our septonema-like fungus. Isolates were grown on 2% MEA or water agar with sterile wooden toothpicks to induce sporulation and incubated at room temperature (22–25 °C). Colony features were observed and recorded at 21 days or 1 month due to slow growth. The corresponding dried specimen of the MUCL strain and other herbarium specimens deposited in IMI were borrowed for morphological examination. They were first rehydrated in distilled water and mounted similar to fresh specimens. Measurements are based on a total of 100 randomly selected fungal structures at 1000× magnification, and minimum, maximum, 5th and 95th percentile values were calculated with outliers given in parentheses. Line drawings were made using a drawing tube (Carl Zeiss, Oberkochen, Germany). Holotype and isotype specimens are deposited in the Herbarium of the U.S. National Fungus Collections (BPI) and the Illinois Natural History Survey Fungarium (ILLS), respectively. A paratype specimen is deposited in the Herbarium of the Charles University, Prague (PRC). Living

cultures are deposited in the Westerdijk Fungal Biodiversity Institute (CBS) and the Culture Collection of Fungi, Charles University, Prague (CCF). Fungal names follow Index Fungorum (www.indexfungorum.org) and host plant names follow International Plant Names Index (www.ipni.org). Herbaria or culture collection acronyms are cited according to Index Herbariorum (<http://sweetgum.nybg.org/science/ih/>).

DNA EXTRACTION, PCR AMPLIFICATION, AND SEQUENCING
Genomic DNA extraction from three weeks old cultures grown on MEA at 25°C together with PCR reactions to amplify the complete internal transcribed spacer (ITS) and partial nuclear ribosomal large subunit (LSU) regions along with a fragment of the translation elongation factor 1-alpha (EF1- α) gene were carried out separately for the Arizona and Czech isolates following the protocols outlined in Kirschner *et al.* (2013) and Koukol *et al.* (2018), respectively. In the case of strain MUCL 8886, DNA extraction and PCR amplification protocols were also performed separately for both the ITS-LSU and EF1- α regions based on Mardones *et al.* (2017) and Promputtha & Miller (2010), respectively. The primer pairs ITS1/ITS4 in combination with LR0R/LR5 (Vilgalys & Hester 1990; White *et al.* 1990) were used for PCR amplification and sequencing of the ITS-LSU regions of the Arizona isolate. The primer pair ITS1F/NL4 (O'Donnell 1993) was used for the same loci in the Czech fungus and the strain MUCL 8886. The EF1- α gene of the three strains used in this study was PCR amplified and sequenced with the primer pair 983F/2218R (Rehner & Buckley 2005). Consensus sequences were generated in Geneious v.6.1.5 (Biomatters, Auckland, New Zealand) and deposited in GenBank.

TAXON SAMPLING AND PHYLOGENETIC ANALYSES

The newly obtained ITS, LSU and EF1- α sequences of the Arizona and Czech septonema-like isolates were first aligned and compared for pairwise similarities. Megablast searches in the NCBI GenBank database revealed significant similarities with members of the order Mytilinidiales (Dothideomycetes) and top blast hits were used to build datasets. Allied taxa from previous phylogenetic studies (Boehm *et al.* 2009a, b; Jayasiri *et al.* 2017) were also included with emphasis on anamorphic fungi with known mytilinidiaceous affinities or hysteriaceous and mytilinidiaceous taxa with known septonema-like anamorphic states e.g. *Oedohysterium insidens*, *Mytilinidion rhenanum* and *M. scolecosporum*. Most members of Mytilinidiales in GenBank lack ITS sequence data and therefore this marker was not used for analyses. In the case of strain MUCL 8886 megablast searches of newly generated sequences revealed highest similarities with members of the order Venturiales (Dothideomycetes) and datasets were assembled with closest hits and additional sequences from recent phylogenies (Crous *et al.* 2007c; Koukol 2010; Zhang *et al.* 2011). Details of strains and sequences used in this study are listed in Table 1. The five single gene datasets (LSU, EF1- α for the septonema-like isolates and ITS, LSU, EF1- α for the MUCL strain) were aligned separately using the MUSCLE algorithm implemented in Geneious and manually edited

and concatenated in the same software. The best-fit substitution model for each gene was determined in jModeltest v.2.1.5 (Darrriba *et al.* 2012). The selected models using the Bayesian information criterion were TrN+I+G for both the LSU and EF1- α datasets of the septonema-like isolates, and TIM2ef+I+G, TrN+I+G and TrN+G for the ITS, LSU and EF1- α datasets of the MUCL strain, respectively. Phylogenetic relationships were reconstructed by Bayesian inference and Maximum likelihood (ML) approaches using MrBayes v.3.2 (Ronquist *et al.* 2012) and RAxML v.8.2.10 (Stamatakis 2014) on the CIPRES Science Gateway server (Miller *et al.* 2010), respectively. Two independent runs of 4-6 M generations were run for Bayesian analyses employing the GTRGAMMA model and sampling every 100th generation. The first 25% of samples were discarded as burn-in and the remaining trees were used to compute a 50% majority rule consensus trees with Bayesian posterior probabilities (PP) as branch support. The average standard deviation of split frequencies estimating convergence reached the level of 0.003-0.007 at the end of particular analysis. Nonparametric bootstrapping (BS) with 1000 replicates was used for ML branch support.

RESULTS

PHYLOGENETIC ANALYSES

A comparison of the newly generated sequences belonging to strains CBS 141174 and CCF 6124 revealed that they were very similar with only minor differences between them. The ITS sequences differ only by one transversion (A-T), one transition (A-G) and three gaps, the LSU by one transversion (T-A) and one transition (T-C) and the EF1- α by four transitions (A-G and T-C) and one deletion that were all located in one intron. The final concatenated LSU-EF1- α dataset consists of 1 405 characters and 69 sequences representing 49 taxa including the outgroup. The 50 % majority rule consensus tree resulting from the Bayesian analysis is shown in Figure 1. The two strains of the septonema-like fungus grouped together with high support (1.0 PP, 98% BS). They were sister to a poorly supported clade consisting of seven *Mytilinidion* species including *M. mytilinellum* (Fr.) H. Zogg, the generic neotype, and strains of other mytilinidiaceous fungi such as *Lophium elegans* H. Zogg, *Halokirschsteiniothelia maritima* (Linder) Boonmee & K.D. Hyde and *Quasiconcha reticulata* M.E. Barr & M. Blackw. *Mytilinidion* species with known septonema-like anamorphs such as *M. rhenanum* and *M. scolecosporum* grouped in a separate clade distant from our septonema-like fungus. They were placed within a monophyletic clade corresponding to the order Mytilinidiales strongly supported only in the Bayesian analysis (1.0 PP). Sequences of species of Gloniaceae grouped outside the order Mytilinidiales and sister to Hysteriales with high Bayesian support only (0.97 PP).

The final concatenated ITS-LSU dataset including the strain MUCL 8886 and venturiaceous fungi consists of 1780 characters and 60 sequences representing 48 taxa including the outgroup. The 50% majority rule consensus tree generated by

TABLE 1. — Taxa included in this study, strain information and their GenBank accession numbers. Newly generated sequences are written in bold. Abbreviations: **ANM**, Andrew N. Miller; **ATCC**, American Type Culture Collection, Manassas, United States; **BCC**, BIOTEC Culture Collection, Bangkok, Thailand; **BJFU**, Beijing Forestry University, Beijing, P.R. China; **CBS**, Westerdijk Fungal Biodiversity Institute, Utrecht, The Netherlands; **CCF**, Culture Collection of Fungi, Charles University, Prague, Czech Republic; **CPC**, Culture collection of Pedro Crous; **DAOM**, National Mycological Herbarium, Department of Agriculture, Ottawa, Canada; **EB**, Eric W.A. Boehm; **GKM**, George K. Mugambi; **FMR**, Culture Collection at the Faculty of Medicine, Rovira i Virgili University, Reus, Spain; **ICMP**, International Collection of Micro-organisms from Plants, Manaaki Whenua Landcare Research, Auckland, New Zealand; **IFM**, Culture Collection of the Medical Mycology Research Center, Chiba University, Chiba, Japan; **MFLUCC**, Mae Fah Luang University Culture Collection, Chiang Rai, Thailand; **MUCL**, Agro-food & Environmental Fungal Collection, Université catholique de Louvain, Louvain-la-Neuve, Belgium; **NBRC**, NITE Biological Resource Center, Kisarazu, Japan; **SMH**, Sabine M. Huhndorf; **UAMH**, University of Alberta Microfungus Collection and Herbarium, University of Toronto, Toronto, Canada.

Taxa	Strain	Country of origin	GenBank accession numbers			References
			ITS	LSU	EF1- α	
<i>Acrogenospora carmichaeliana</i>	CBS 206.36	Unknown	–	AY541492	DQ677931	Schoch <i>et al.</i> (2006)
<i>Acrogenospora sphaerocephala</i>	CBS 164.76	Belgium	–	GU301791	GU349059	Schoch <i>et al.</i> (2009)
<i>Apiosporina collinsii</i>	CBS 118973	Canada	–	GU301798	GU349057	Schoch <i>et al.</i> (2009)
<i>Apiosporina collinsii</i>	CPC 12229	Canada	EU035443	EU035443	–	Crous <i>et al.</i> (2007c)
<i>Byssothecium circinans</i>	CBS 675.92	United States	–	GU205217	GU349061	Schoch <i>et al.</i> (2009)
<i>Cenococcum geophilum</i>	1-17-2	United States	–	JN860135	JN860114	Spatafora <i>et al.</i> (2012)
<i>Cenococcum geophilum</i>	2-2-1	United States	–	JN860138	JN860115	Spatafora <i>et al.</i> (2012)
<i>Cenococcum geophilum</i>	3-10-1	United States	–	JN860139	JN860116	Spatafora <i>et al.</i> (2012)
<i>Cochliobolus heterostrophus</i>	CBS 134.39	Unknown	–	AY544645	DQ497603	Unpublished
<i>Cylindrosympodium lauri</i>	CBS 240.95	Spain	EU035414	EU035414	–	Crous <i>et al.</i> (2007c)
<i>Dothidea sambuci</i>	DAOM 231303	Austria	–	AY544681	DQ497606	Shoemaker & Hambleton (2005)
<i>Fusicladium africanum</i>	CPC 12829	South Africa	EU035424	EU035424	–	Crous <i>et al.</i> (2007c)
<i>Fusicladium africanum</i>	CPC 12828	South Africa	EU035423	EU035423	–	Crous <i>et al.</i> (2007c)
<i>Fusicladium amoenum</i>	CBS 254.95	Cuba	EU035425	EU035425	–	Crous <i>et al.</i> (2007c)
<i>Fusicladium cordae</i>	CBS 675.82	The Netherlands	FN549913	FN398149	–	Koukol (2010)
<i>Fusicladium cordae</i>	CCF 3843	Czech Republic	FN549910	FN377748	–	Koukol (2010)
<i>Fusicladium intermedium</i>	CBS 110746	Madagascar	EU035432	EU035432	–	Crous <i>et al.</i> (2007c)
<i>Fusicladium pini</i>	CBS 463.82	The Netherlands	EU035436	EU035436	–	Crous <i>et al.</i> (2007c)
<i>Fusicladium ramoconidii</i>	CBS 462.82	The Netherlands	–	EU035439	–	Crous <i>et al.</i> (2007c)
<i>Fusicladium rhodense</i>	CPC 13156	Greece	EU035440	EU035440	–	Crous <i>et al.</i> (2007c)
<i>Fusicladium sicilianum</i>	CBS 105.85	Italy	FN549914	–	–	Koukol (2010)
<i>Gibbera conferta</i>	CBS 191.53	Switzerland	–	GU301814	GU349041	Schoch <i>et al.</i> (2009)
<i>Glioniopsis praelonga</i>	CBS 112415	South Africa	–	FJ161173	FJ161090	Boehm <i>et al.</i> (2009a)
<i>Glioniopsis praelonga</i>	CBS 123337	United States	–	FJ161195	FJ161103	Boehm <i>et al.</i> (2009a)
<i>Glioniopsis subrugosa</i>	GKM 1214	Kenya	–	GQ221895	GU397336	Mugambi & Huhndorf (2009)
<i>Glioniopsis subrugosa</i>	SMH 557	Cuba	–	GQ221896	GU397337	Mugambi & Huhndorf (2009)
<i>Glonium circumserpens</i>	CBS 123343	Tasmania	–	FJ161200	FJ161108	Boehm <i>et al.</i> (2009b)
<i>Glonium stellatum</i>	ANM 32	United States	–	GQ221887	GQ221926	Mugambi & Huhndorf (2009)
<i>Halokirschsteiniethelia maritima</i>	CBS 221.60	United States	–	GU323203	GU349001	Schoch <i>et al.</i> (2009)
<i>Herpotrichia diffusa</i>	CBS 250.62	India	–	DQ678071	DQ677915	Schoch <i>et al.</i> (2006)
<i>Hysterium angustatum</i>	ANM 85	United States	–	GQ221898	–	Mugambi & Huhndorf (2009)
<i>Hysterium angustatum</i>	CBS 123334	United States	–	FJ161207	FJ161111	Boehm <i>et al.</i> (2009a)
<i>Hysterium angustatum</i>	CBS 236.34	United States	–	FJ161180	FJ161096	Boehm <i>et al.</i> (2009a)
<i>Hysterium barrianum</i>	ANM 1442	United States	–	GQ221884	–	Boehm <i>et al.</i> (2009a)
<i>Hysterium barrianum</i>	ANM 1495	United States	–	GQ221885	–	Boehm <i>et al.</i> (2009a)
<i>Hysterium pulicare</i>	CBS 123377	United States	–	FJ161201	FJ161109	Boehm <i>et al.</i> (2009a)
<i>Hysterium vermiforme</i>	GKM 1234	Kenya	–	GQ221897	GQ221929	Mugambi & Huhndorf (2009)
<i>Hysterobrevium constrictum</i>	SMH 5211.1	New Zealand	–	GQ221905	–	Mugambi & Huhndorf (2009)
<i>Hysterobrevium mori</i>	CBS 123563	United States	–	FJ161196	FJ161104	Boehm <i>et al.</i> (2009b)
<i>Hysterobrevium mori</i>	SMH 5273	United States	–	GQ221910	GQ221936	Mugambi & Huhndorf (2009)
<i>Hysterobrevium smilacis</i>	CBS 200.34	United States	–	FJ161177	–	Boehm <i>et al.</i> (2009a)
<i>Hysterobrevium smilacis</i>	SMH 5280	United States	–	GQ221912	GQ221914	Mugambi & Huhndorf (2009)
<i>Hysterographium fraxini</i>	CBS 109.43	Switzerland	–	FJ161171	FJ161088	Boehm <i>et al.</i> (2009b)
<i>Hysterographium fraxini</i>	CBS 242.34	Canada	–	FJ161189	–	Boehm <i>et al.</i> (2009b)
<i>Kirschsteiniethelia atra</i>	DAOM 231155	Unknown	–	DQ678046	DQ677884	Schoch <i>et al.</i> (2006)
<i>Kirschsteiniethelia atra</i>	MFLUCC15-0424	P.R. China	–	KU500578	–	Su <i>et al.</i> (2016)
<i>Kirschsteiniethelia lignicola</i>	MFLU10-0036	Thailand	–	HQ441568	–	Boonmee <i>et al.</i> (2012)
<i>Lophium arboricola</i>	CBS 758.71	United Kingdom	–	KU705843	–	Hernández <i>et al.</i> (2016)
<i>Lophium elegans</i>	EB 0366	France	–	GU323210	–	Schoch <i>et al.</i> (2009)
<i>Lophium mytilinum</i>	CBS 123344	United States	–	FJ161203	FJ161110	Boehm <i>et al.</i> (2009b)
<i>Lophium mytilinum</i>	CBS 269.34	United States	–	EF596817	DQ677926	Schoch <i>et al.</i> (2006)
<i>Lophium zalerioides</i>	MFLUCC14-0417	Italy	–	MF621587	–	Hyde <i>et al.</i> (2017)
<i>Magnohelicospora fuscospora</i>	UAMH 8757	Spain	–	AY856901	–	Tsui & Berbee (2006)
<i>Magnohelicospora fuscospora</i>	ICMP 14915	New Zealand	EF029203	–	–	Unpublished
<i>Mycosphaerella punctiformis</i>	CBS 113265	The Netherlands	–	DQ470968	DQ471092	Spatafora <i>et al.</i> (2006)
<i>Myriangium duriaei</i>	CBS 260.36	Argentina	–	DQ678059	DQ677900	Schoch <i>et al.</i> (2006)
<i>Mytilinidion acicola</i>	EB 0349	France	–	GU323209	–	Schoch <i>et al.</i> (2009)
<i>Mytilinidion acicola</i>	EB 0379	France	–	GU397346	–	Boehm <i>et al.</i> (2009a)
<i>Mytilinidion andinense</i>	CBS 123562	Argentina	–	FJ161199	FJ161107	Boehm <i>et al.</i> (2009b)
<i>Mytilinidion australe</i>	CBS 301.34	United States	–	FJ161183	–	Boehm <i>et al.</i> (2009b)
<i>Mytilinidion californicum</i>	EB 0385	France	–	GU323208	–	Schoch <i>et al.</i> (2009)

TABLE 1. — Continuation.

Taxa	Strain	Country of origin	GenBank accession numbers			References
			ITS	LSU	EF1- α	
<i>Mytilinidion mytilinellum</i>	CBS 303.34	United States	–	FJ161184	FJ161100	Boehm <i>et al.</i> (2009b)
<i>Mytilinidion mytilinellum</i>	EB 0386	France	–	GU397347	–	Boehm <i>et al.</i> (2009a)
<i>Mytilinidion resinicola</i>	CBS 304.34	United States	–	FJ161185	FJ161101	Boehm <i>et al.</i> (2009b)
<i>Mytilinidion rhenanum</i>	CBS 135.45	Unknown	–	FJ161175	FJ161092	Boehm <i>et al.</i> (2009b)
<i>Mytilinidion rhenanum</i>	EB 0341	France	–	GU323207	–	Schoch <i>et al.</i> (2009)
<i>Mytilinidion scolecosporum</i>	CBS 305.34	United States	–	FJ161186	FJ161102	Boehm <i>et al.</i> (2009b)
<i>Mytilinidion thujarum</i>	EB 0268	United States	–	GU323206	–	Schoch <i>et al.</i> (2009)
<i>Mytilinidion tortile</i>	EB 0377	France	–	GU323205	–	Schoch <i>et al.</i> (2009)
<i>Ochroconis constricta</i>	NBRC 9375	Unknown	DQ307327	AB564619	AB564641	Abe & Hamada (2011)
<i>Ochroconis humicola</i>	NBRC 32054	Israel	–	AB564618	–	Abe & Hamada (2011)
<i>Ochroconis tshawytschae</i>	CBS 100438	United States	FR832476	KF282665	–	Machouart <i>et al.</i> (2014)
<i>Oedohysterium insidens</i>	ANM 1443	United States	–	GQ221882	–	Mugambi & Huhndorf (2009)
<i>Oedohysterium insidens</i>	CBS 238.34	United States	–	FJ161182	FJ161097	Boehm <i>et al.</i> (2009b)
<i>Oedohysterium sinense</i>	CBS 123345	United States	–	FJ161209	–	Boehm <i>et al.</i> (2009b)
<i>Oedohysterium sinense</i>	EB 0339	United States	–	GU397348	GU397339	Boehm <i>et al.</i> (2009a)
<i>Phoma herbarum</i>	CBS 276.37	Sweden	–	DQ678066	DQ677909	Schoch <i>et al.</i> (2006)
<i>Phoma herbarum</i>	UAMH 10909	United States	KT389539	KT389757	DQ677909	Chen <i>et al.</i> (2015)
<i>Pleospora herbarum</i>	CBS 191.86	India	–	GU238160	–	Aveskamp <i>et al.</i> (2010)
<i>Protoventuria barriae</i>	CBS 300.93	United States	–	JQ036232	–	Zhang <i>et al.</i> (2011)
<i>Pseudocamaropycnis pini</i>	CBS 115589	P.R. China	–	KU728557	KU728594	Crous & Groenewald (2016)
<i>Psiloglonium clavisorum</i>	CBS 123339	United States	–	FJ167526	FJ161105	Boehm <i>et al.</i> (2009b)
<i>Psiloglonium clavisorum</i>	CBS 123340	United States	–	FJ161205	–	Boehm <i>et al.</i> (2009b)
<i>Purpurepithecium murisporum</i>	MFLUCC16-0611	Thailand	–	KY799173	KY887666	Jayasiri <i>et al.</i> (2017)
<i>Purpurepithecium murisporum</i>	MFLUCC17-0319	Thailand	–	KY799174	KY799177	Jayasiri <i>et al.</i> (2017)
<i>Quasiconcha reticulata</i>	EB QR	United States	–	GU397349	–	Boehm <i>et al.</i> (2009a)
<i>Scolecobasidium terreum</i>	CBS 203.27	United States	HQ667544	–	–	Samerpitak <i>et al.</i> (2014)
<i>Scolecobasidium terreum</i>	CBS 175.65	South Africa	HQ667545	–	DQ307349	Samerpitak <i>et al.</i> (2014)
<i>Scolecobasidium variabile</i>	NBRC 32268	P.R. China	–	EU107310	DQ307350	Unpublished
<i>Septonema fasciculare</i>	MUCL 8886	Belgium	LS998795	LS998795	LS998798	This study
<i>Septonema lohmanii</i> sp. nov.	CBS 141174	United States	LS998797	LS998797	LS998800	This study
<i>Septonema lohmanii</i> sp. nov.	CCF 6124	Czech Republic	LS998796	LS998796	LS998799	This study
<i>Slimacomycetes isiolus</i>	FP1465	Japan	–	AB597217	–	Unpublished
<i>Slimacomycetes isiolus</i>	P10436	Japan	–	AB597220	–	Unpublished
<i>Sympodiella acicola</i>	CBS 425.76	Canada	KY853467	KY853529	–	Hernández <i>et al.</i> (2016)
<i>Sympodiella acicola</i>	CCF 3736	Czech Republic	EU449953	–	–	Unpublished
<i>Sympoventuria capensis</i>	CPC 12839	South Africa	DQ885905	DQ885905	–	Crous <i>et al.</i> (2007b)
<i>Sympoventuria capensis</i>	CPC 12840	South Africa	DQ885904	DQ885904	–	Crous <i>et al.</i> (2007b)
<i>Tothia fuscella</i>	CBS 130266	Austria	JF927786	JF927786	–	Wu <i>et al.</i> (2011)
<i>Troposporella fumosa</i>	FMR 12437	Spain	HF678534	HF678544	–	Hernández <i>et al.</i> (2016)
<i>Troposporella fumosa</i>	MUCL 15695	United States	DQ351724	AY856914	–	Tsui & Berbee (2006)
<i>Venturia atriseda</i>	CBS 378.49	Switzerland	EU035449	EU035449	–	Crous <i>et al.</i> (2007c)
<i>Venturia barriae</i>	CBS 621.84	The Netherlands	EU035431	EU035431	–	Crous <i>et al.</i> (2007c)
<i>Venturia barriae</i>	NK145	Czech Republic	LS998793	LS998793	–	Unpublished
<i>Venturia carpophila</i>	CBS 497.62	Switzerland	–	EU035426	–	Crous <i>et al.</i> (2007c)
<i>Venturia chinensis</i>	BJFU 140826-17	P.R. China	KP689596	KP689595	–	Zhang <i>et al.</i> (2016)
<i>Venturia chlorospora</i>	CBS 470.61	France	EU035454	EU035454	–	Crous <i>et al.</i> (2007c)
<i>Venturia ditricha</i>	CBS 118894	Finland	EU035456	EU035456	–	Crous <i>et al.</i> (2007c)
<i>Venturia helvetica</i>	CBS 474.61	Switzerland	EU035458	EU035458	–	Crous <i>et al.</i> (2007c)
<i>Venturia hystrioides</i>	ATCC 96019	United States	–	AF050290	–	Untereiner & Naveau (1999)
<i>Venturia hystrioides</i>	CBS 117727	United States	EU035459	EU035459	–	Crous <i>et al.</i> (2007b)
<i>Venturia inaequalis</i>	CBS 180.47	Portugal	EU282481	–	GU349089	Schoch <i>et al.</i> (2009)
<i>Venturia inaequalis</i>	CBS 594.70	The Netherlands	KF156040	GU301879	GU349022	Schoch <i>et al.</i> (2009)
<i>Venturia inaequalis</i>	CBS 476.61	Unknown	–	–	GU456288	Zhang <i>et al.</i> (2011)
<i>Venturia inaequalis</i>	CBS 815.69	The Netherlands	–	–	GU349023	Schoch <i>et al.</i> (2009)
<i>Venturia lonicerae</i>	CBS 445.54	Switzerland	EU035461	EU035461	–	Crous <i>et al.</i> (2007c)
<i>Venturia macularis</i>	CBS 477.61	France	EU035462	EU035462	–	Crous <i>et al.</i> (2007c)
<i>Venturia maculiformis</i>	CBS 377.53	France	EU035463	EU035463	–	Crous <i>et al.</i> (2007c)
<i>Venturia minuta</i>	CBS 478.61	Switzerland	–	EU035464	–	Crous <i>et al.</i> (2007c)
<i>Venturia oleaginea</i>	CBS 113427	New Zealand	EU035434	EU035434	–	Crous <i>et al.</i> (2007c)
<i>Venturia oleaginea</i>	So-91	Italy	AF338403	AF338397	–	González <i>et al.</i> (2002)
<i>Venturia phillyreae</i>	CBS 113539	Portugal	EU035435	EU035435	–	Crous <i>et al.</i> (2007c)
<i>Venturia polygoni-vivipari</i>	CBS 114207	Norway	EU035466	EU035466	–	Crous <i>et al.</i> (2007c)
<i>Venturia populina</i>	CBS 256.38	Italy	EU035467	EU035467	–	Crous <i>et al.</i> (2007c)
<i>Venturia saliciperda</i>	CBS 480.61	Switzerland	EU035471	EU035471	–	Crous <i>et al.</i> (2007c)
<i>Venturia tremulae</i> var. <i>tremulae</i>	CBS 257.38	Italy	EU035475	EU035475	–	Crous <i>et al.</i> (2007c)
<i>Venturia viennotii</i>	CBS 690.85	France	EU035476	EU035476	–	Crous <i>et al.</i> (2007c)
<i>Veroneopsis simplex</i>	CBS 588.66	South Africa	EU041820	EU041877	–	Arzanlou <i>et al.</i> (2007)
<i>Verruconis calidifluminalis</i>	IFM 54738	Japan	AB385698	AB385698	–	Yarita <i>et al.</i> (2010)

TABLE 1. — Continuation.

Taxa	Strain	Country of origin	GenBank accession numbers			References
			ITS	LSU	EF1- α	
<i>Verruconis gallopava</i>	IFM 54737	Japan	–	AB272164	–	Yarita <i>et al.</i> (2007)
<i>Verruconis gallopava</i>	CBS 119641	Australia	–	–	JF440538	Samerpitak <i>et al.</i> (2014)
<i>Verruconis gallopava</i>	CBS 437.64	United States	–	–	AB569128	Abe & Hamada (2011)
<i>Verruconis verruculosa</i>	CBS 119775	Malaysia	KF156014	KF282668	DQ307351	Samerpitak <i>et al.</i> (2014)

the Bayesian analysis is shown in Figure 4. The backbone of the tree representing the order Venturiales lacked significant support but it was topologically congruent with previous studies in the group (Zhang *et al.* 2011; Boonmee *et al.* 2014; Machouart *et al.* 2014) and split into two clades corresponding to the families Venturiaceae and Sympoventuriaceae. The strain MUCL 8886 was placed with high support (1.0 PP, 99% BS) sister to a monophyletic group supported only in the Bayesian analysis (0.98 PP) including *Venturia inaequalis* (Cooke) G. Winter, the generic type, as well as several species of *Venturia* Sacc., *Apiosporina* Höhn., *Protoventuria* Berl. & Sacc. and *Gibbera* Fr. They clustered with a moderately supported clade (0.94 PP, 90 BS) consisting of *Sympodiella acicola* W.B. Kendr., *Tothia fuscella* (Sacc.) Bat. and *Cylindrosyodium lauri* Crous & R.F. Castañeda. and they all nested within a poorly supported group representing the family Venturiaceae. Due to poor taxon sampling the EF1- α dataset was analyzed separately. It consisted of 864 characters and 14 sequences representing only 11 taxa including the outgroup. The strain MUCL 8886 grouped without support sister to a highly supported clade (1.0 PP, 100 BS) including *Venturia*, *Gibbera* and *Apiosporina* species (tree not shown).

SYSTEMATICS

Septonema lohmanii G. Delgado & Koukol, sp. nov.
(Figs 2, 3)

ETYMOLOGY. — Named in honor of Dr Marion Lee Lohman (1903–), American mycologist who pioneered the study of hysteriaceous and mytiliniidiaceous fungi in culture and whose strains remain today a reference source of molecular data.

MATERIAL EXAMINED. — **United States.** Arizona, Coconino County, Forest Lakes Estates, Apache-Sitgreaves National Forest, around Willow Springs Lake, 34°18'45.7"N, 110°52'46.1"W, on rotting stump of *Pinus ponderosa* P. Lawson & C. Lawson, 21.IX.2014, coll. G. Delgado (holo-, BPI[BPI 910175]; iso-, ILLS[ILLS 82053]; ex-holotype culture, CBS[CBS 141174]; ex-holotype sequences, CBS[ITS-LSU LS998797, EF1- α LS998800]).

Czech Republic. Northern Bohemia, Doubice, Tokaň, 50°53'14"N, 14°25'11.4"E, on rotten bark of *P. strobus* L., 15.X.2015, coll. O. Koukol (para-, PRC[PRC 4117]; ex-paratype culture, CCF[CCF 6124]; ex-paratype sequences, CCF[ITS-LSU LS998796, EF1- α LS998799]).

MYCOBANK MB 829281

Colonies on natural substrate more or less orbicular, densely floccose, dark brown or dark reddish brown, often confluent

and forming irregular patches, sometimes effuse and hairy, with powdery spores easily dispersed when touched. *Mycelium* mostly superficial consisting of branched, septate, strongly verruculose, echinulate, verrucose or strongly verrucose, subhyaline to pale brown ascending hyphae, sometimes anastomosing, 2–4 μ m wide, and septate, smooth or sparingly verrucose, thick-walled, brown to dark brown, interwoven creeping hyphae, often constricted at the septa and forming angular or irregularly swollen cells, 5–9 μ m wide, warts when prominent more or less rounded, 2–3.5 μ m wide. *Conidiophores* macronematous or semimacronematous, mononematous, arising terminally or laterally from the hyphae, solitary, erect or somewhat repent, flexuous or sinuous, rarely straight, cylindrical or subcylindrical, mostly branched, septate, sometimes constricted at some septa and readily breaking along the constrictions, verruculose, verrucose to strongly verrucose, sometimes locally smooth or thick-walled, yellowish brown to brown or reddish brown to dark brown, up to 515 μ m long, 3–7(–9) μ m wide, width and ornamentation may vary along the length of the conidiophore, warts when prominent similar to those on hyphae, occasionally with brown blobs of mucilage 6–11 μ m diam.; branches cylindrical or subcylindrical, straight or flexuous, verruculose or verrucose, similarly ornamented as the near conidiophore, up to 205 μ m long, 4–6 μ m wide, basal cells often attenuated at the junction with the conidiophore to a truncate end and easily breaking off, 2–4 μ m wide; young hyphae, conidiophores and branches extend by forming subhyaline to pale yellow or pale brown, finely verruculose or sparingly verruculose elongations tapering to an acute, smooth apex 1.5–2 μ m wide. *Conidiogenous cells* monoblastic or polyblastic, integrated, terminal or intercalary on conidiophores and branches, determinate, cylindrical or subcylindrical, rounded at the apex or slightly attenuated to a truncate end, 5–15(–18) \times 4.5–7 μ m, with 1–2 inconspicuous conidiogenous loci. *Conidia* acrogenous or acroleptrogenous, cylindrical, subcylindrical or narrowly ellipsoidal, straight or somewhat flexuous, (1–) 2–11(–13)-septate, slightly constricted at some septa, smooth, verruculose, verrucose or strongly verrucose, sometimes ornamentation not uniform, yellowish brown or brown to reddish brown, formed in simple or branched, short acropetal chains of 2–3(–4) conidia at conidiophores or branches, each conidium with 0–3 apical or lateral inconspicuous or subdenticulate hila or 0–2 per individual conidial cell, sometimes small isthmi seen between conidia, 12–57(–63) \times 4–6(–8) μ m, apex rounded or somewhat truncate, base truncate. *Teleomorph* unknown.

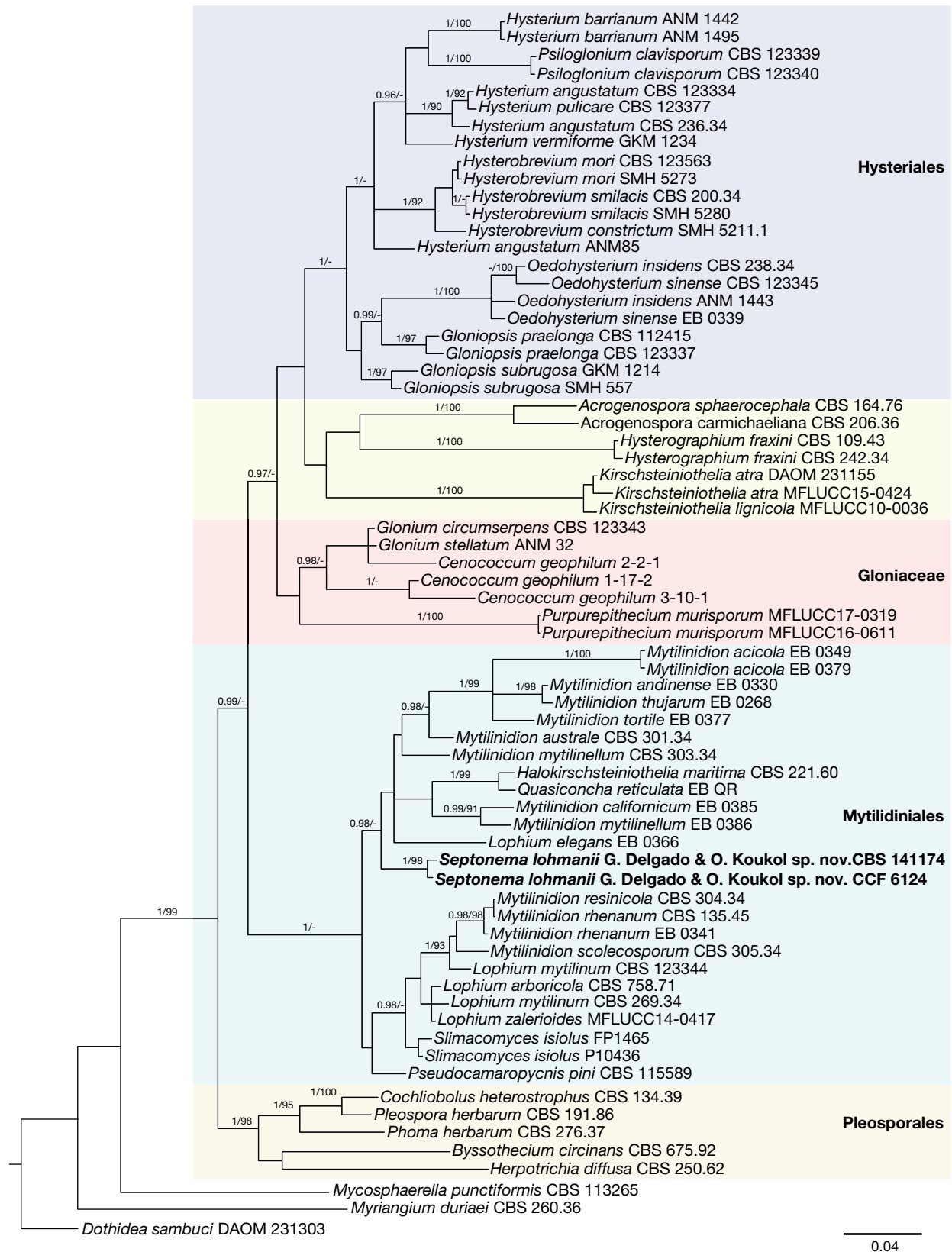


FIG. 1. — Phylogenetic tree inferred from Bayesian and ML analyses of concatenated LSU-EF1- α sequence data showing the placement of *Septonema lohmanii* G. Delgado & O. Koukol, sp. nov. within Mytilidiales and related orders in Dothideomycetes. Numbers above branches represent Bayesian posterior probabilities PP>0.95 followed by ML bootstrap support values BS \geq 90%. Strains belonging to the new taxon are highlighted in bold.

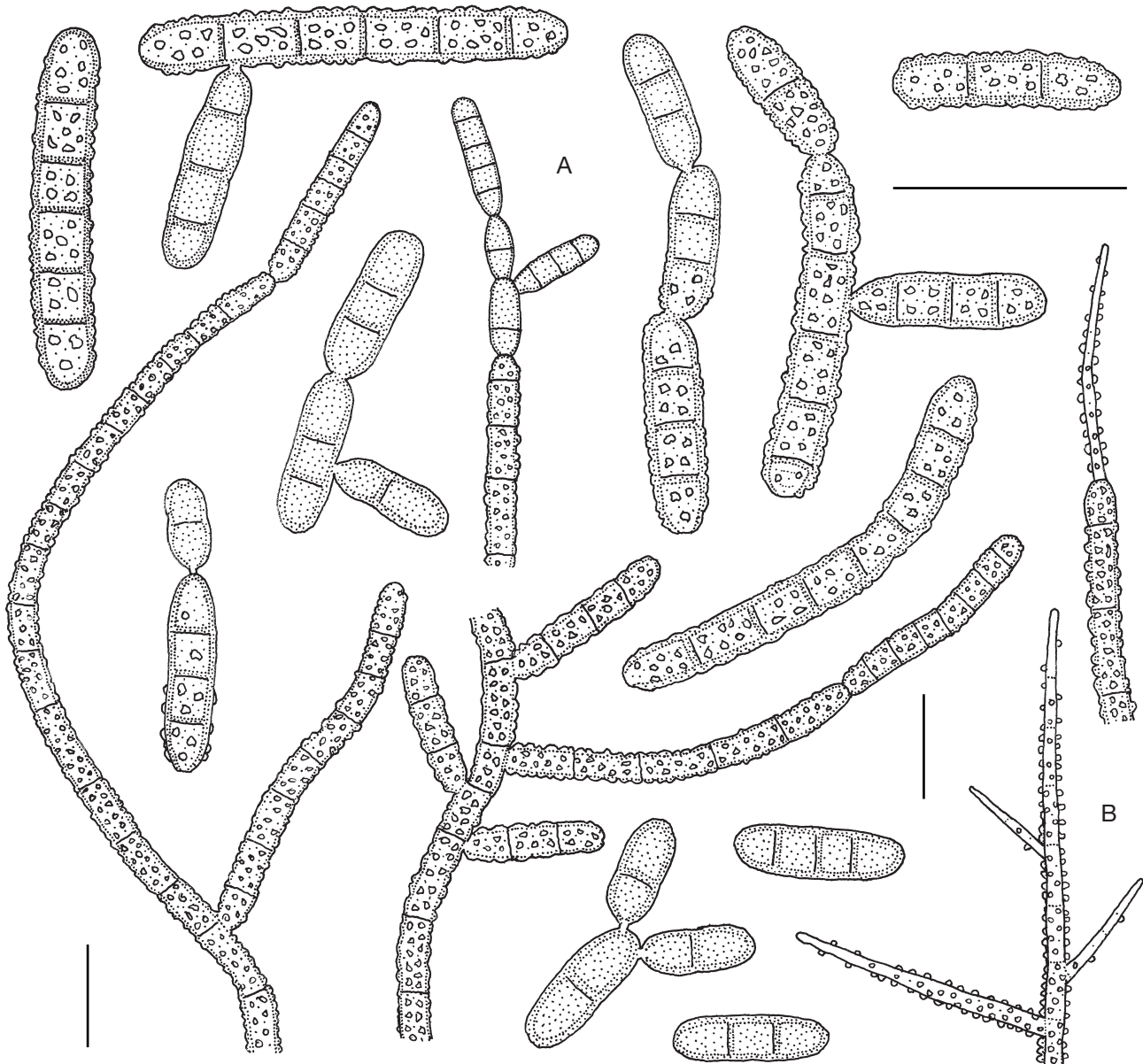


FIG. 2. — *Septonema lohmanii* G. Delgado & O. Koukol, sp. nov. (BPI 910175, holotype): **A**, conidiophores, branches and conidia; **B**, acute apices of young conidiophores and branches. Scale bars: 20 µm.

Colonies on MEA moderately slow growing, reaching 16–21 mm diam. after 21 days at 25°C, velvety, dark brown, umbonate, raised 1–3 mm at the center, sulcate, sometimes zonate with 1–2 concentric rings of growth, margin slightly undulate, whitish to pale brown, reverse blackish brown, sporulation late and abundant after 2 months. *Colonies* on PDA similar to MEA, moderately slow growing, reaching 16–17 mm diam. after 21 days at 25°C, velvety, more umbonate than on MEA, raised up to 4 mm and dark brown at the center, outer zone brown, less sulcate, margin slightly undulate, whitish to paler brown, reverse black, sporulation lacking. *Mycelium* immersed and superficial, aerial hyphae similar to those on natural substrate but width and ornamentation often not uniform and may gradually vary along the length of the hyphae, anastomosing, often with prominent,

brown to dark brown warts, 2–5 µm wide and pale brown or with brown blobs of mucilage, 3–4 µm thick, some cells inflated, thick-walled, brown, functioning as conidiogenous cells, 5–9 µm wide. *Conidiophores* similar to those on natural substrate, often strongly verrucose and distinctly warted, width and ornamentation may also vary along the length of the conidiophores, basal cell sometimes slightly narrower and then conidiophores gradually widening distally, up to 268 µm long, (3–) 4–8 µm wide; branches up to 142 µm long, 3–7.5 µm wide. *Conidia* similar to those on natural substrate, cylindrical, subcylindrical or narrowly clavate, with 2–13 transverse septa, 0–1 longitudinal septa and very rarely with 1 oblique septum, slightly constricted at some septa or around the central portion, in short, simple or branched acropetal chains of 2–4 (–5) conidia, each one with 0–4 api-

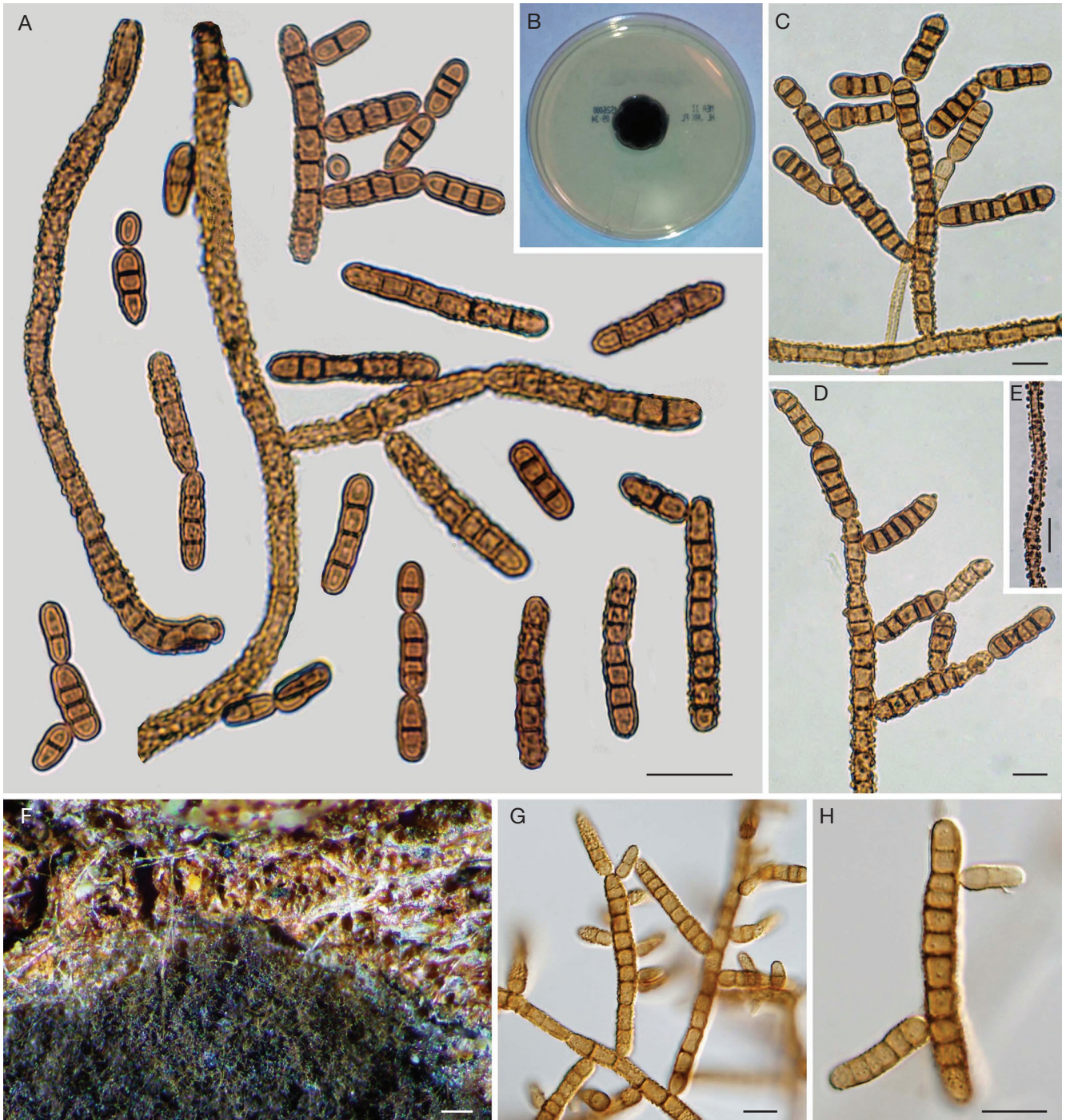


FIG. 3. — *Septonema lohmanii* G. Delgado & O. Koukol, sp. nov. (BPI 910175, holotype = CBS 141174). On natural substrate: **A**, conidiophores, branches and conidia. In culture (MEA): **B**, colony after 21 days; **C**, **D**, conidiophores, branches and conidia; **E**, hyphal segment showing warts. *Ibid.* (PRC 4117, paratype); **F**, colony on natural substrate; **G**, conidiophores, branches and conidia; **H**, conidia. Scale bars: A, 20 μ m; C-E, G-H, 10 μ m; F, 200 μ m.

cal or lateral hila or 0-2 per single conidial cell, 14-58(-63) \times (5-) 6-10(-11) μ m.

NOTES

Among species of *Mytilinidion* forming septonema-like anamorphs, *S. lohmanii* G. Delgado & O. Koukol, sp. nov. is morphologically close to anamorphic *M. rhenanum* in having coarsely ornamented semi-macronematous conidiophores,

conidia and hyphae, and producing short, simple or branched acropetal chains of 2-3 conidia on natural substrate or 2-4 conidia on PDA or MEA (Lohman 1939; Bisby & Hughes 1952). Conidia of both species are also similar in width being 6-8 μ m wide in the lectotype specimen of *M. rhenanum* from Finland where the anamorph is also present mixed with hysterothecia, and they both occur on bark and wood of *Pinus* spp. However, colonies of anamorphic *M. rhenanum* on natural



FIG. 4. — Phylogenetic tree inferred from Bayesian and ML analyses of concatenated ITS-LSU sequence data showing the placement of *Septonema fasciculare* (Corda) S. Hughes within the family Venturiaceae (Venturiales, Dothideomycetes). Numbers above branches represent Bayesian posterior probabilities PP>0.95 followed by ML bootstrap support values BS≥90 %. The studied strain MUCL 8886 is highlighted in bold.

substrate are dull black and conidiophores are shorter being up to 60 µm long. Conidia are different in shape and shorter, fusiform to oblong and 15-35 µm long, with less number of septa and 2-7 per conidium. Our fungus is also comparable to anamorphic *Oedohysterium insidens* in its strongly verrucose conidiophores and conidial walls (Hughes 1952b; Ellis 1976). However, conidial chains in *O. insidens* mature basipetally instead of acropetally with the older conidia located at the distal end of longer, simple chains of up to 15 conidia. Conidia of *O. insidens* are oblong or ellipsoidal in shape, wider being 8-18 µm wide with less 3-5(-9) transverse septa and may develop later 1-3 longitudinal septa. Conidiophores are shorter than those of *S. lohmanii* G. Delgado & O. Koukol, sp. nov., up to 50 µm long, and they arise in a palisade from a conspicuous, pulvinate and erumpent stroma.

Both specimens of *S. lohmanii* G. Delgado & O. Koukol, sp. nov. studied here were morphologically similar on natural substrate but minor variations in color, conidiophore length, branching and ornamentation were detected between them. Conidiophores and conidia of the Arizona specimen BPI 910175 were more reddish brown in color whereas the Czech material PRC 4117 was more yellowish brown. The Arizona fungus had shorter conidiophores, up to 268 µm long, than the Czech specimen with up to 515 µm long. Conidiophores were more uniformly ornamented, more consistent in width and less branched in the Arizona specimen. Segments of conidiophores and branches of the Czech fungus, on the other hand, were unevenly wide, some cells thick-walled, darker in color, smooth or sparingly verrucose, 8-9 µm wide, and abruptly constricted a few times along the length of the same conidiophore reaching 3-3.5 µm in width.

Septonema fasciculare (Corda) S. Hughes
(Figs 5, 6)

In Canadian Journal of Botany 36: 803 (1958).

MATERIAL EXAMINED. — **Belgium.** Haasrode, Meerdaalwoud, on the outer side of bark of *Pinus sylvestris* L., 16.V.1966, coll. G.L. Hennebert, isol. G.L. Hennebert (MUCL[MUCL 8886], deposited as *Septonema secedens*).

Canada. Quebec province, Gatineau Parkway, near Pink Lake, on bark of Coniferae, X.1959, coll. W.B. Kendrick, det. W.B. Kendrick (IMI[IMI 84944a]). — *Septonema secedens* Corda, Great Britain, Surrey County, Ashted Common, on bark of *Betula* sp., 12.I.1947, coll. S.J. Hughes, det. S.J. Hughes (IMI[IMI 9939]); *ibid.*, Oxshott, on periderm of *Betula* sp., 7.III.1948 (IMI[IMI 25538a]).

DESCRIPTION

Colonies on natural substrate effuse, hairy or cottony, black. *Mycelium* partly superficial, partly immersed composed of branched, septate, smooth, brown hyphae, 1.5-2 µm wide. *Conidiophores* macronematous, monomenatous, erect, simple, straight or flexuous, sometimes bent at a 90° angle or rarely bifurcating, cylindrical, septate, smooth, brown, sometimes paler distally and constricted at the septa delimiting terminal or subterminal cells, up to 480 µm long, 3-4 µm wide, 5-9 µm wide at the base. *Conidiogenous cells* monoblastic or

polyblastic, integrated, terminal or intercalary, occasionally intercalary-pleurogenous, determinate, cylindrical, subcylindrical or somewhat clavate at the tip, pale brown, brown or grayish brown, 0-1(-4) septate, sometimes constricted at the basal delimiting septa, 17-28 × 3-5(-6) µm, with 1-2 truncate or subdentate, neither thickened nor darkened apical conidiogenous loci giving rise to ramoconidia. *Ramoconidia* cylindrical to narrowly clavate, sometimes fusoid-ellipsoid, 0-1(-3)-septate, thick-walled, smooth, pale brown to brown or dark grayish brown, in chains of up to 3, 15-21(-25) × 3-5 µm, with 1-2 truncate or subdentate apical conidiogenous loci; *conidia* cylindrical, sometimes slightly attenuated in their central part, pale grayish brown to grayish brown, 1-4-septate, mostly 3, rarely up to 7 septa, thin-walled, smooth, with rounded ends, (11-)13-22(-30) × 4-5 µm, in simple or rarely branched acropetal chains of up to 9 conidia.

Colonies on MEA restricted, very slow growing, reaching 4-5 mm diam. after 1 month at room temperature (22-25° C), circular, black, velvety, convex, raised 1-2 mm, sometimes with a slight amount of dark gray aerial mycelium in the center, margin entire, reverse black, sporulation not observed after four months.

NOTES

The strain MUCL 8886 did not sporulate on any of the culture media used including nutrient poor water agar with sterile wooden toothpicks. Morphological examination of the herbarium specimen source of this strain showed that it is conspecific with *S. fasciculare* and not with *S. secedens*. The specimen closely matches previous descriptions of *S. fasciculare* (Ellis 1976; Holubová-Jechová 1978) in forming black, hairy to cottony colonies on bark of *Pinus* species, particularly *P. sylvestris*, and having simple conidiophores up to 880 µm long, cylindrical, grayish brown to brown, mostly 3- but also 1-, 2- or 4-septate conidia with rounded ends, 14-20 µm long, consistently 4-5 µm wide and produced in branched, acropetal chains (Fig. 6B-J). Further evidence of conspecificity was found by comparing MUCL 8886 with specimen IMI 84944a belonging to *S. fasciculare*. *Septonema secedens*, on the other hand, differs from *S. fasciculare* by forming olivaceous brown to dark brown, velvety colonies on natural substrate, shorter, branched conidiophores up to 200 µm long and pale brown to brown, wider conidia 5-7 µm wide, with truncate ends (Fig. 6K-N). A comparison between MUCL 8886 and two specimens of *S. secedens* deposited in IMI (9939 and 25538a) confirmed that they belong to different taxa. Dried cultures found inside the herbarium packet of MUCL 8886 and grown on MA (Malt Agar) or MEA according to their labels were sterile as well.

DISCUSSION

The novel fungus described in this study agrees well with the morphological concept of *Septonema* in having multi-septate, cylindrical conidia produced in simple or branched

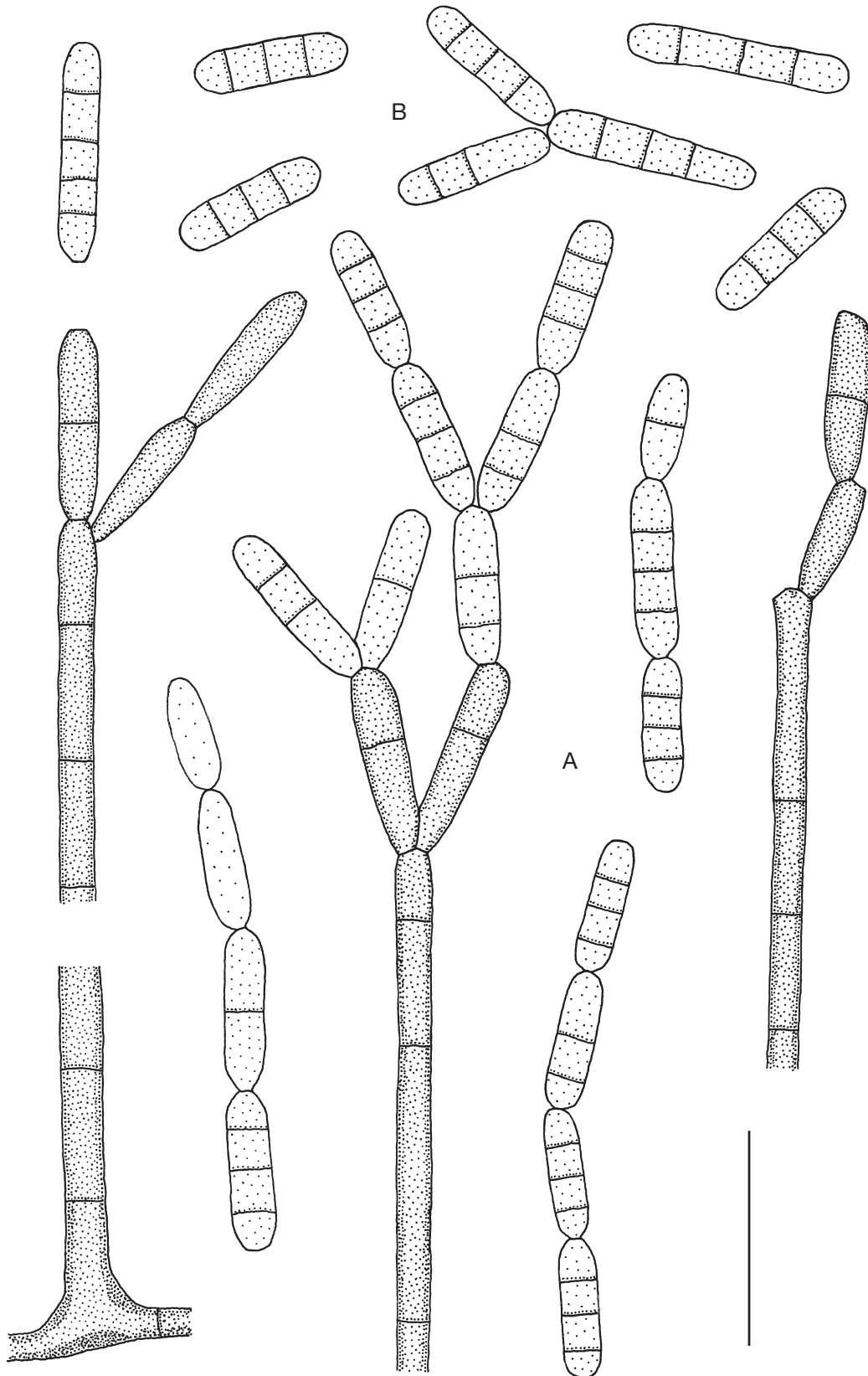


FIG. 5. — *Septonema fasciculare* (Corda) S. Hughes (MUCL 8886, herbarium specimen): **A**, conidiophores, ramoconidia and conidia in chains; **B**, conidia. Scale bar: 20 μ m.

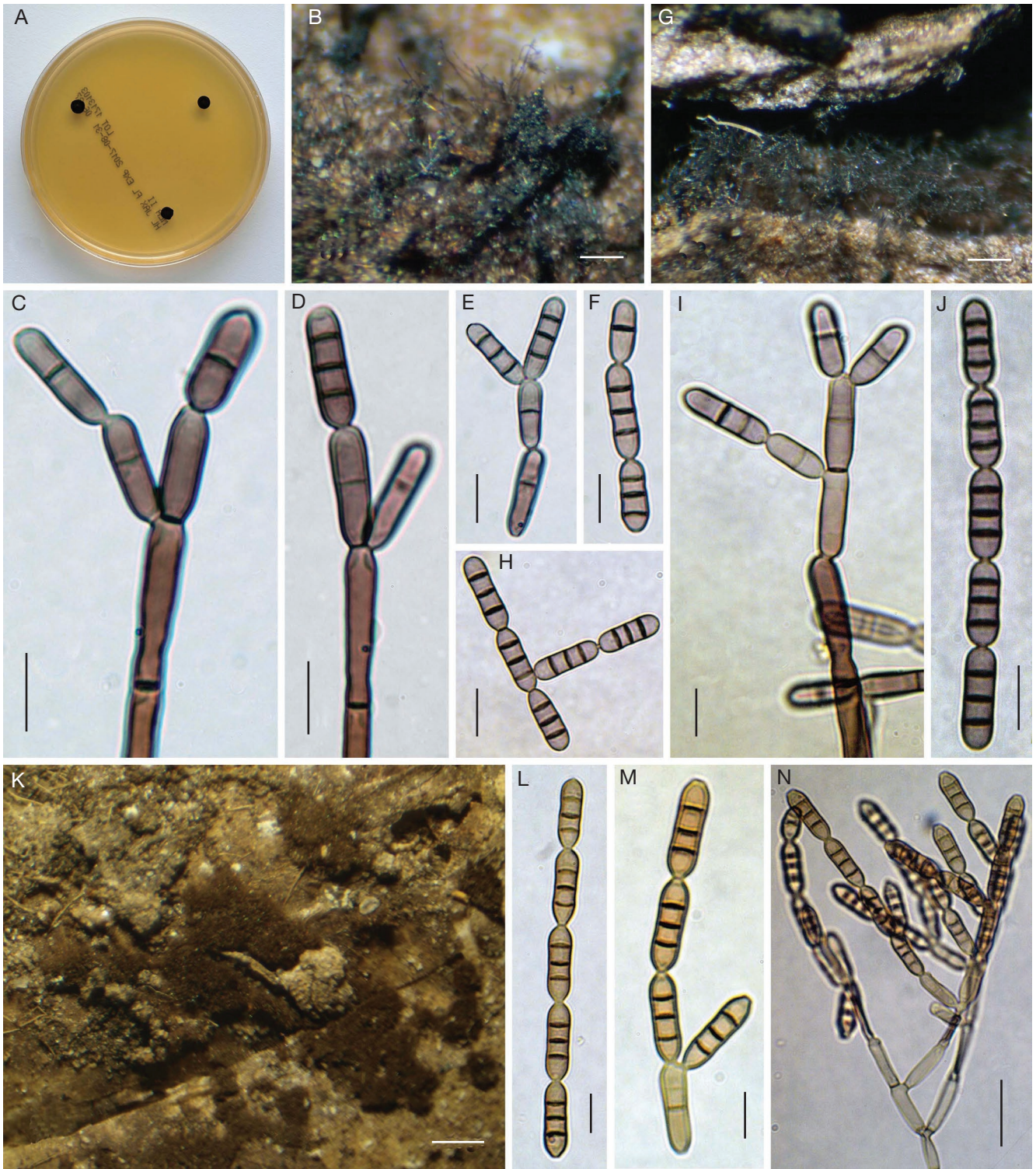


FIG. 6. — *Septonema fasciculare* (Corda) S. Hughes (MUCL 8886) in culture (MEA): **A**, colonies after 1 month. Herbarium specimen; **B**, colonies on natural substrate; **C**, **D**, conidiophores, conidiogenous cells and conidia; **E**, **F**, conidia. *Ibid.* (IMI 84944a); **G**, colonies on natural substrate; **H**, **J**, conidia; **I**, conidiophores, conidiogenous cells and conidia. *Septonema secedens* (IMI 9939); **K**, colonies on natural substrate. **L**, **M**, conidia. *Ibid.* (IMI 25538a); **N**, conidiophore, branches and conidia. Scale bars: **B**, **G**, 200 µm; **K**, 500 µm; **C**-**F**, **H**-**J**, **L**-**M**, 10 µm; **N**, 20 µm.

acropetal chains born on monoblastic or polyblastic, terminal or intercalary conidiogenous cells arising from branched, macronematous conidiophores (Hughes 1951; Ellis 1971; Holubová-Jechová 1978). The establishment of *S. lohmanii*

G. Delgado & O. Koukol, sp. nov. as a new taxon among previously described *Septonema* species, however, is supported by a distinct morphology and molecular data. The two collections on which this fungus is based, one from southwestern

United States and the other from central Europe, were morphologically close despite their disjunct geographical distribution. Minor differences observed between them are attributed to intraspecific variation and the age of each specimen, the North American one apparently older and more fragmented, or the influence of environmental conditions affecting each particular location. Arizona is a semiarid region characterized by low annual rainfall and mild to hot temperatures while the Czech Republic has a temperate continental climate, with warm summers and cold, snowy winters. Their conspecificity is also supported by highly similar ITS and LSU rDNA sequence data and the fact that they grouped together with strong support in all phylogenetic analyses. The differences in the EF1- α intron are considered intraspecific variation.

The affinity of *S. lohmanii* G. Delgado & O. Koukol, sp. nov. with members of the order Mytilinidiales based on DNA sequence data is in congruence with previous cultural or circumstantial evidence of relatedness between mytilinidiaceous ascomycetes and septonema-like anamorphs (Lohman 1933b, 1939; Bisby 1941; Bisby & Hughes 1952). Moreover, this is the first time a septonema-like anamorph is linked to the order Mytilinidiales in a phylogenetic framework using molecular data. On the basis of previously known affinities between these fungi and the end of dual nomenclature, a placement of the new species in *Mytilinidion sensu lato* was considered. However, *S. lohmanii* G. Delgado & O. Koukol, sp. nov. strains did not show a close relationship with any particular *Mytilinidion* species including *M. mytilinellum*, the proposed generic neotype (Zogg 1962; Hyde *et al.* 2013), represented by two strains which grouped separate in this and previous studies (Boehm *et al.* 2009a). The two strains of *S. lohmanii* G. Delgado & O. Koukol, sp. nov. were also distant from *M. rhenanum* and *M. scolecosporum*, with known septonema-like anamorphs and which grouped together in our phylogeny although without support. *Mytilinidion* as a whole was revealed to be paraphyletic within the order as seen in previous phylogenies. The genus is in need of further revision and taxonomic rearrangement, particularly regarding the status of the type species which still needs clarification (Vasilyeva 2001). A possible relationship between *S. lohmanii* G. Delgado & O. Koukol, sp. nov. and anamorphic *Oedohysterium insidens* based on their similar, verrucose ornamentation of conidiophores and conidia was not supported by molecular data. In addition to morphological and developmental differences, sequences of *O. insidens* clustered within the order Hysteriales. If the position of *Septonema sensu stricto* outside Mytilinidiales is confirmed, *S. lohmanii* G. Delgado & O. Koukol, sp. nov. may be accommodated in a novel genus.

Mytilinidiaceous ascomycetes and septonema-like anamorphs have often been found associated with conifers, particularly pine trees, similar to *S. lohmanii* G. Delgado & O. Koukol, sp. nov. (Lohman 1933b, 1939; Holubová-Jechová 1978; Minter 1981; Minter & Holubová-Jechová 1981; Schubert & Braun 2007). Marmolejo & Minter (2006) recorded six species of *Septonema* and several mytilinidiaceous taxa belonging to the genera *Lophium* Fr., *Mytilinidion*, *Ostreichmion* Duby, *Ostreola* Darker and *Quasiconcha* M.E. Barr & M. Blackw. on *Pinus*

spp. worldwide. An online search in the Mycology Collections data Portal showed a total of 117 records of these fungi on fourteen *Pinus* spp. across Europe, Canada and twenty-one U.S. states and territories (MyCoPortal 2018). Boehm *et al.* (2009b) consider them an ancient and ecologically successful group confined almost exclusively to conifers. In general, anamorphic fungi with mytilinidiaceous affinities are known to be morphologically diverse, primarily coelomycetous and less frequently hyphomycetous (Boehm *et al.* 2009a; Hyde *et al.* 2013; Wijayawardene *et al.* 2012, 2017). In addition to the septonema-like morphology, mytilinidiaceous hyphomycetes also include chalara-like states such as anamorphic *Quasiconcha reticulata* (Blackwell & Gilbertson 1985) or helicosporous anamorphs such as *Lophium arboricola* (Buczacki) Madrid & Gené (Buczacki 1972; Hernández *et al.* 2016), *L. zalerioides* Jin F. Li, Phook., Camporesi & K.D. Hyde (Hyde *et al.* 2017) and *Slimacomycetes isiolus* (R.T. Moore) G.Z. Zhao (Moore 1957). The latter was found to be a member of Mytilinidiales in this study based on unpublished sequences under that name available in GenBank. Likewise, all of them have been reported growing on different conifers based on literature and information available together with sequence data. Hyde *et al.* (2013) provided a key to the anamorphic genera in Mytilinidiaceae including only three hyphomycetous states: *Peyronelia* Cif. & Gonz. Frag., *Taeniolella* and *Septonema*. The type species of *Peyronelia*, *P. sirodesmioides* Cif. & Gonz. Frag., is of uncertain placement but a couple of peyronelia-like anamorphs have been linked to species of *Glyphium* Nitschke ex F. Lehm., now within the distant Patellariales (Boehm *et al.* 2015; Sutton 1970). *Taeniolella*, on the other hand, is a highly polyphyletic taxon (Ertz *et al.* 2016) with a taeniolella-like anamorph linked to *Mytilinidion gemmigenum* Fuckel (Minter & Holubová-Jechová 1981) but relatedness of this genus to Mytilinidiales is not phylogenetically verified (Heuchert *et al.* 2018). *Septonema* is the only genus whose relationships with mytilinidiaceous fungi were documented by cultural as well as circumstantial evidence (Lohman 1933a, b, 1939; Bisby 1941; Bisby & Hughes 1952) and now also by molecular sequence data.

The present attempt to clarify the phylogenetic affinities of *S. secedens*, the type species of the genus, and possibly define *Septonema sensu stricto* using molecular sequence data was unsuccessful and therefore its position within Ascomycota remains unclear. Nevertheless, the phylogenetic placement of *S. fasciculare*, represented by the strain MUCL 8886, was resolved for the first time within the family Venturiaceae (Venturiales, Dothideomycetes) distant from *S. lohmanii* G. Delgado & O. Koukol, sp. nov. in Mytilinidiales and confirming once again the polyphyletic nature of the genus. The strongly supported sister-group relationship in the ITS-LSU phylogeny (Fig. 4) between this strain and a large group of *Venturia* species including the generic type *V. inaequalis* was not supported in the EF1- α tree (not shown). This relationship deserves further study to clarify whether *S. fasciculare* is actually distinct within the family considering that members of the anamorphic genus *Fusicladium*, traditionally linked to venturiaceous teleomorphs, are now interspersed between

both Venturiaceae and its sister family Symptoventuriaceae (Machouart *et al.* 2014). Morphologically, *S. fasciculare* fits well within a broad concept of *Fusicladium* in having solitary, simple, smooth conidiophores, monoblastic or polyblastic, integrated, terminal or intercalary, determinate conidiogenous cells, with terminal or lateral, more or less denticle-like conidiogenous loci with truncate apices and 3-septate, smooth, phragmosporous, catenate conidia with rounded to truncate ends in simple or branched acropetal chains and forming blackish colonies (Schubert *et al.* 2003). The conidia at the base of chains, here referred to as ramoconidia, were found to be morphologically distinct from the terminal ones. They agree well with a broad definition of this term (Cole & Samson 1979; Seifert *et al.* 2011): dydimo- or phragmosporous, larger and darker than the apical conidia, truncate at base with one basal scar and two distal scars at the apex, marking the start of the acropetal chain and easily detached carrying the rest of the branching chain (Fig. 6E). Several *Fusicladium* species also produce ramoconidia at the base of simple or branched, sometimes long acropetal chains including fusicladium-like, anamorphic *Venturia hystrioides* (Dugan, R.G. Roberts & Hanlin) Crous & U. Braun, closely related to *S. fasciculare* in our phylogeny, or *Fusicladium rhodense* Crous & M.J. Wingf., *F. sicilianum* Koukol, Crous & de Hoog, *F. convolvularum* Ondřej or *F. africanum* Crous, more distantly related and nested within Symptoventuriaceae. Holubová-Jechová (1978) considered *S. fasciculare* to be very common in Bohemia, the type locality, on the outer or inner surface of bark of stumps or fallen trunks of pine trees, particularly *P. sylvestris*, but its current distribution and status are unknown.

Similarly, the examination of herbarium specimens of *S. secedens* revealed the presence of ramoconidia at the base of the acropetal chains that detach carrying the rest of the conidia (Fig. 6M). Hughes (1951), based on several specimens including those examined in the present study, also noticed and illustrated morphological differences between the lower, first formed conidium of a chain, often narrower and the only being 1-septate, and those produced later. Seifert *et al.* (2011), in their diagnosis of *Septonema*, first introduced the presence of ramoconidia to the genus while Heuchert *et al.* (2018) recently used this feature to separate *Taeniolella* from morphologically similar genera such as *Septonema* or *Heteroconium*. Speculatively, *S. secedens* as well as other related species such as *S. pinicola* Hol.-Jech. or *S. pseudobinum* Hol.-Jech. (Holubová-Jechová 1978), currently of uncertain phylogenetic placement, might belong to Venturiaceae considering the close morphological similarities with *S. fasciculare*. However, this hypothesis needs to be tested upon recollection of these fungi and availability of new molecular data. Holubová-Jechová (1978) considered *S. secedens* restricted to a single host genus *Betula* L. but the fungus has also been occasionally recorded on conifers such as *P. sylvestris*, *Pseudotsuga menziesii* (Mirb.) Franco or *Picea* sp. among other substrates (Hughes 1951; Ellis 1971; Cannon 2009). In the absence of sufficient information regarding the taxonomic and phylogenetic status of the type species we refrain from proposing any generic redistributions at the moment and prefer to use the current broad concept

of *Septonema* to accommodate *S. lobmanii* G. Delgado & O. Koukol, sp. nov. as well as *S. fasciculare* until fresh collections and further molecular data become available for study.

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