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Lichens or endophytes? The enigmatic genus *Leptosillia* in the *Leptosilliaceae* fam. nov. (*Xylariales*), and *Furfurella* gen. nov. (*Delonicicolaceae*)

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Abstract Based on DNA sequence data, the genus *Leptosillia* is shown to belong to the *Xylariales*. Molecular phylogenetic analyses of ITS-LSU rDNA sequence data and of a combined matrix of SSU-ITS-LSU rDNA, *rpb1*, *rpb2*, *tef1* and *tub2* reveal that the genera *Cresporhaphis* and *Liberomyces* are congeneric with *Leptosillia*. *Coelosphaeria fusariospora*, *Leptorhaphis acerina*, *Leptorhaphis quercus* f. *macrospora*, *Leptorhaphis pinicola*, *Leptorhaphis wienkampii*, *Liberomyces pistaciae*, *Sphaeria muelleri* and *Zignoëlla slaptonensis* are combined in *Leptosillia*, and all of these taxa except for *C. fusariospora*, *L. pinicola* and *L. pistaciae* are epitypified. *Coelosphaeria fusariospora* and *Cresporhaphis rhoina* are lectotypified. *Liberomyces macrosporus* and *L. saliciphilus*, which were isolated as phloem and sapwood endophytes, are shown to be synonyms of *Leptosillia macrospora* and *L. wienkampii*, respectively. All species formerly placed in *Cresporhaphis* that are now transferred to *Leptosillia* are revealed to be non-lichenized. Based on morphology and ecology, *Cresporhaphis chibaensis* is synonymised with *Rhaphidicyrtis trichosporella*, and *C. rhoina* is considered to be unrelated to the genus *Leptosillia*, but its generic affinities cannot be resolved in lack of DNA sequence data. Phylogenetic analyses place *Leptosillia* as sister taxon to *Delonicicolaceae*, and based on morphological and ecological differences, the new family *Leptosilliaceae* is established. *Furfurella*, a new genus with the three new species, *F. luteostiolata*, *F. nigrescens* and *F. stromatica*, growing on dead branches of mediterranean fabaceous shrubs from tribe *Genisteae*, is revealed to be the closest relative of *Delonicicola* in the family *Delonicicolaceae*, which is emended. ITS rDNA sequence data retrieved from GenBank demonstrate that the *Leptosilliaceae* were frequently isolated or sequenced as endophytes from temperate to tropical regions, and show that the genus *Leptosillia* represents a widely distributed component of endophyte communities of woody plants.

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INTRODUCTION

The monotypic genus *Leptosillia*, based on *L. notha*, was posthumously described by Höhnel (1928) in a manuscript edited by J. Weese, with *Harpostroma notha* as its asexual morph. As the genus name suggests, *Leptosillia* was considered to be closely related to the diaporthalean genus *Sillia*. Oddly enough, it was, however, classified in *Botryosphaeriaceae* ('*Melanopsoideae*'), which was probably added by J. Weese. Since its original description, *Leptosillia notha* has apparently never been recorded again, although it is growing on bark of *Acer pseudoplatanus*, which is a common and widespread tree in many parts of Europe. Due to the vague original description and the lack of illustrations, its systematic placement could so far not be critically evaluated, and the few references in the literature made it even more mysterious. Hawksworth (in Eriksson & Hawksworth 1987) noted that the type of *Leptosillia* was based on a specimen of *Cryptospora* (= *Sillia*) *cinctula* distributed by Rehm (Ascomyceten, no. 2047; Rehm 1913), and after studying a slide of the type at FH, the fungus was tentatively referred to *Valsaceae*. However, it is unclear how Hawksworth came to that conclusion, as the original description of *L. notha* was based on a German collection made by H. Diedicke, and neither in the original description nor on the labels of the type collection, neither *Cryptospora* (= *Sillia*) *cinctula* nor Rehm's Ascomyceten are mentioned. This misapplication was perpetuated in the latest edition of the Dictionary of the Fungi (Kirk et al. 2008), and *Leptosillia* is currently placed in *Valsaceae* in Index Fungorum (http://www.indexfungorum.org/Names/Names.asp; accessed in Feb. 2019).

In the course of an ongoing research project on phylogenetics of *Diaporthales*, the first author successfully recollected *Leptosillia notha* to clarify its systematic affiliation by morphology and DNA sequence data. We also collected, cultured and sequenced a small pyrenomycete from the corky bark strips of *Ulmus minor*, which we identified as *Cresporhaphis ulmi* (Calatayud & Aguirre-Hudson 2001). To our surprise, the ITS-LSU rDNA sequences of *Leptosillia notha* and *Cresporhaphis ulmi* turned out to be highly similar, raising the question whether both are congeneric. Nucleotide BLAST searches of the ITS also revealed a high similarity to *Liberomyces*, an endophytic coelomycetous asexual morph genus of xylarialean affinities that was isolated from the inner bark and sapwood of *Salix* and *Ulmus* species (Pažoutová et al. 2012). In addition, we collected several specimens of a pyrenomycete with a yellow scurf and valsa-like ascospores on dead branches of fabaceous mediterranean shrubs, which could not be identified but later turned out to be closely related to the isolates mentioned above as well. The monotypic genus *Delonicicola*, which was recently described from seed pods of *Delonix regia* in Thailand (Perera

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et al. 2017), also showed high sequence similarities to our isolates. This prompted us to recollect several other *Cresporhaphis* species. These were isolated in pure culture; the morphology of their sexual and asexual morphs was studied and their ecology was investigated to ascertain if these are truly lichenised as previously postulated. In addition, multi-gene analyses were performed with a matrix of SSU-ITS-LSU, *rpb1*, *rpb2*, *tef1* and *tub2* sequences to reveal their phylogenetic affiliation, to clarify genus, species and family boundaries and to settle their taxonomy in a polyphasic approach.

MATERIALS AND METHODS

Sample sources

All isolates included in this study originated from ascospores of freshly collected specimens on bark of living or recently dead branches or trunks; typical habitats of *Leptosillia* species are illustrated in Fig. 1. Details of the strains including NCBI GenBank accession numbers of gene sequences used to compute the phylogenetic trees are listed in Table 1. Strain acronyms other than those of official culture collections are used here primarily as strain identifiers throughout the work. Representative isolates have been deposited at the Westerdijk Fungal Biodiversity Centre (CBS-KNAW), Utrecht, The Netherlands. Details of the specimens used for morphological investigations are listed in the Taxonomy section under the respective descriptions. Herbarium acronyms are according to Thiers (2018), and citation of exsiccatae follows Triebel & Scholz (2018). Freshly collected specimens have been deposited in the Fungarium of the Department of Botany and Biodiversity Research, University of Vienna (WU).

Morphology

Microscopic observations were made in tap water except where noted. Methods of microscopy included stereomicroscopy using a Nikon SMZ 1500 equipped with a Nikon DS-U2 digital camera or a Keyence VHX-6000 system, and Nomarski differential interference contrast (DIC) using a Zeiss Axio Imager. A1 compound microscope equipped with a Zeiss Axiocam 506 colour digital camera. Images and data were gathered using the NIS-Elements D v. 3.22.15 or Zeiss ZEN Blue Edition software. For certain images of ascomata the stacking software Zerene Stacker v. 1.04 (Zerene Systems LLC, Richland, WA, USA) was used. Measurements are reported as maxima and minima in parentheses and the range representing the mean plus and minus the standard deviation of a number of measurements given in parentheses.

Culture preparation, DNA extraction, PCR and sequencing

Ascospore isolates were prepared and grown on 2 % corn meal dextrose agar (CMD; CMA: Sigma, St Louis, Missouri; supplemented with 2 % (w/v) D(+)-glucosemonohydrate) or 2 % malt extract agar (MEA; 2 % w/v malt extract, 2 % w/v agar-agar; Merck, Darmstadt, Germany). Growth of liquid cultures and extraction of genomic DNA was performed as reported previously (Voglmayr & Jaklitsch 2011, Jaklitsch et al. 2012) using the DNeasy Plant Mini Kit (QIAgen GmbH, Hilden, Germany).

The following loci were amplified and sequenced: the complete internal transcribed spacer region (ITS1-5.8S-ITS2) and a c. 900–1200 bp fragment of the large subunit nuclear ribosomal DNA (nuLSU rDNA), amplified and sequenced as a single fragment with primers V9G (De Hoog & Gerrits van den Ende 1998) and LR5 (Vilgalys & Hester 1990); a c. 1.2 kb fragment of the RNA polymerase II subunit 1 (*rpb1*) gene with primers RPB1-Af (Stiller & Hall 1997) and RPB1-6R1asc (Hofstetter et al. 2007); a c. 1.2 kb fragment of the RNA polymerase II subunit 2 (*rpb2*) gene with primers fRPB2-5f and fRPB2-7cr (Liu et al. 1999) or dRPB2-5f and dRPB2-7r (Voglmayr et al. 2016a); a c. 1.3–1.5 kb fragment of the translation elongation factor 1-alpha (*tef1*) gene with primers EF1-728F (Carbone & Kohn 1999) and TEF1LLErev (Jaklitsch et al. 2005) or EF1-2218R (Rehner & Buckley 2005); and a c. 1.6 kb fragment of the beta tubulin (*tub2*) gene with primers T1 and T22 (O'Donnell & Cigelnik 1997) or T1D and T22D (Voglmayr et al. 2019). PCR products were purified using an enzymatic PCR cleanup (Werle et al. 1994) as described in Voglmayr & Jaklitsch (2008). DNA was cycle-sequenced using the ABI PRISM Big Dye Terminator Cycle Sequencing Ready Reaction Kit v. 3.1 (Applied Biosystems, Warrington, UK) and the PCR primers; in addition, primers ITS4 (White et al. 1990), LR2R-A (Voglmayr et al. 2012) and LR3 (Vilgalys & Hester 1990) were used for the ITS-LSU region, TEF1_INTF (Jaklitsch 2009) and TEFD_iR (Voglmayr et al. 2018) for *tef1*, and BtHVf (Voglmayr & Mehrabi 2018) and BtHV2r (Voglmayr et al. 2016b) for *tub2*. Sequencing was performed on an automated DNA sequencer (3730xl Genetic Analyzer, Applied Biosystems).

Data analysis

Following the results of nucleotide BLAST searches of ITS and LSU sequences generated during the present study, a phylogenetic analysis was performed with an ITS-LSU rDNA sequence matrix of a representative selection of *Xylariales*. Taxon and sequence selection was based on Jaklitsch et al. (2016b), with some recent additions (Perera et al. 2017, Voglmayr et al. 2018, Wendt et al. 2018). For rooting the tree, LSU sequences of four taxa of *Sordariomycetes* (*Calosphaeria pulchella*, *Chaetosphaeria innumera*, *Diaporthe eres*, *Ophiostoma piliferum*) were included as outgroups. For detailed investigations of species relationships and delimitation within and between the genera and families, a combined matrix of five loci (partial SSU-ITS-LSU rDNA, *rpb1*, *rpb2*, *tef1* and *tub2*) was produced. Four taxa of *Sordariomycetes* (*Calosphaeria pulchella*, *Caudospora taleola*, *Juglanconis juglandina*, *Lasiosphaeria ovina*) were selected as outgroup taxa; due to alignment issues, their ITS and *tef1* introns were not included in the matrix. The GenBank accession numbers of sequences used in these analyses are given in Table 1. For some strains for which whole genome data are available, sequences were retrieved from JGI-DOE (http://genome.jgi.doe.gov/).

Sequence alignments for phylogenetic analyses were produced with server versions of MAFFT (www.ebi.ac.uk/Tools/mafft or http://mafft.cbrc.jp/alignment/server/), checked and refined using BioEdit v. 7.2.6 (Hall 1999). For *tef1* and ITS-LSU rDNA, the localpair and for *tub2* the globalpair options were selected for performing fast Fourier transform (FFTS), with a gap open penalty of 1.0 for *tef1* and *tub2*; for all other markers, the default settings were used. Poorly aligned and gappy regions were removed from the ITS and the introns of *tef1* and *tub2*, and the terminal intron of the *rpb2* was entirely removed. The final ITS-LSU matrix used for phylogenetic analyses contained 1345 and the combined five loci data matrix 7052 nucleotide characters; viz. 1626 of SSU-ITS-LSU, 1210 of *rpb1*, 1104 of *rpb2*, 1516 of *tef1* and 1596 of *tub2*. Prior to phylogenetic analyses, the approach of Wiens (1998) was applied to test for significant levels of localised incongruence among the markers used for the combined analysis, using the level of bootstrap support (Sung et al. 2007) as described in Jaklitsch & Voglmayr (2014). For this, the 70 % maximum parsimony (MP) bootstrap consensus trees calculated for each individual partition, using the same parameters as given below, were compared. Except for some nodes within the same species, no topological conflicts were observed between these bootstrap trees of the various genes, indicating the absence of significant incongruence and combinability of the five loci (Wiens 1998).

Maximum likelihood (ML) analyses were performed with RAxML (Stamatakis 2006) as implemented in raxmlGUI v. 1.5 (Silvestro & Michalak 2012), using the ML + rapid bootstrap setting and the GTRGAMMA substitution model with 1 000 bootstrap replicates. The matrix was partitioned for the different gene regions included in the combined multilocus analyses.

Maximum parsimony (MP) analyses were performed with PAUP v. 4.0a163 (Swofford 2002). All molecular characters were unordered and given equal weight; analyses were performed with gaps treated as missing data; the COLLAPSE command was set to MINBRLEN. For the ITS-LSU matrix, first a parsimony ratchet approach was used. For this, nexus files were prepared using PRAP v. 2.0b3 (Müller 2004), implementing 1 000 ratchet replicates with 25 % of randomly chosen positions upweighted to 2, which were then run with PAUP. In a second step, the best trees obtained by the parsimony ratchet

Fig. 1 Typical habitats of the *Leptosillia* species sampled; arrows denoting ascomata on cork wings (b, j), bark furrows (d, h) or bark scales (f). a–b. *Leptosillia acerina* on branches of *Acer campestre*; c–d. *Leptosillia macrospora* on bark of living trunks of *Quercus robur*; e–f. *Leptosillia muelleri* on bark of living trunks of *Acer pseudoplatanus*; g–h. *Leptosillia wienkampii* on bark of living trunks of *Salix* sp.; i–j. *Leptosillia slaptonensis* on branches of *Ulmus minor*.

Table 1 Isolates and accession numbers used in the phylogenetic analyses. Isolates/sequences in **bold** were isolated/sequenced in the present study.

Taxon	Strain[1]	Host[2]	Type[3]	Substrate/ Isolation source	Country	GenBank accession no.						References[2]
						ITS	LSU	*rpb1*	*rpb2*	*tef1*	*tub2*	
Acrocordiella occulta	RS9 = CBS 140500		E			KT949893	KT949893					
Amphibambusa bambusicola	MFLUCC 11–0617		H			KP744433	KP744474					
Amphisphaeria umbrina	HKUCC 994					AF009805	AF452029					
Annulohypoxylon truncatum	CBS 140778		E			KY610419	KY610419	–	KY624277	–	KX376352	
Anthostoma decipiens	CD = CBS 133221					KC774565	KC774565					
Anthostomella rubicola	MFLUCC 16-0479					KX533455	KX533456	–	KX789493	–	KX789494	
Arthrinium arundinis	CBS 133509 = NRRL 25634					KF144886	KF144930	genome[6]	genome[6]	genome[6]	genome[6]	
Arthrinium phragmitis	CBS 135458		H			KF144909	KF144956					
Arthrinium saccharicola	CBS 831.71					KF144922	KF144969					
Barrmaelia rhamnicola	BR = CBS 142772		E			MF488990	MF488990	**MK523257**	MF488999	MF489009	MF489018	
Bartalinia robillardoides	CBS 122705		E			KJ710460	KJ710438					
Basiseptospora fallax	PSC = CBS 129020		E			JF440983	JF440983					
Beltrania rhombica	CPC 27482					KX306749	KX306778					
Beltraniopsis neolitseae	CBS 137974		H			KX306749	KJ869183					
Biscogniauxia nummularia	MUCL 51395		E			KY610382	KY610427	–	KY624236	–	KX271241	
Cainia graminis	CBS 136.62					KR092793	AF431949					
Calceomyces lacunosus	CBS 633.88		H			KY610397	KY610476	–	KY624293	–	KX271265	
Calosphaeria pulchella	CBS 115999					–	NG_058734	genome[6]	GU180661	FJ238421	KT716476	
Camillea obularia	ATCC 28093					AF201714	KY610429					
Caudospora taleola	CBS 143508		N			–	MG495961	MG495980	MG495989	MG495998	MG496005	
Chaetosphaeria innumera	MR 1175					–	AF178551					
Collodiscula japonica	CBS 124266					JF440974	JF440974					
Coniocessia maxima	CBS 593.74		H			GU553332	GU553344					
Coniocessia nodulisporioides	CBS 281.77		I			GU553333	GU553352					
Creosphaeria sassafras	ST.MA. 14087					KY610411	KY610468	–	KY624265	–	KX271258	
Cryptovalsa rabenhorstii	CreI = CBS 125574					KC774567	KC774567					
Daldinia concentrica	CBS 113277					AY616683	KY610434	–	KY624243	–	KC977274	
Delonicicola siamense	MFLUCC 15-0670	*Delonix regia*	H	dry seed pods	Thailand	NR_156345	NG_059172	–	MF158346	–	–	Perera et al. (2017)
Delonicicolaceae sp.	MYCO-ARIZ SNP360	*Phoradendron californicum*		living stem tisue	USA	KP335540	–					Massimo et al. (2015)
	MYCO-ARIZ SNP402	*Phoradendron californicum*		living stem tisue	USA	KP335578	–					Massimo et al. (2015)
Diaporthe eres	CBS 109767					–	AF408350					
Diatrype disciformis	CBS 197.49					–	DQ470964	DQ471158	DQ470915	DQ471085	–	
Entosordaria perfidiosa	CBS 142773		E			MF488993	MF488993	**MK523258**	MF489003	MF489012	MF489021	
Eutypa lata	UCR-EL1					genome[6]	genome[6]	genome[6]	genome[6]	genome[6]	genome[6]	
Funiliomyces biseptatus	CBS 100373		H			–	AY772015					
Furfurella luteostiolata	**CE3 = CBS 143620**	*Genista acanthoclada*	H	bark	Greece	**MK527842**	**MK527842**	**MK523259**	**MK523273**	**MK523302**	**MK523330**	
Furfurella nigrescens	**CE**	*Callicotome villosa*		bark	Spain	**MK527843**	**MK527843**	–	**MK523274**	**MK523303**	**MK523331**	
	CE1 = CBS 143622	*Callicotome villosa*	H	bark	Spain	**MK527844**	**MK527844**	**MK523260**	**MK523275**	**MK523304**	**MK523332**	
	CE2 = CBS 143621	*Chamaecytisus creticus*		bark	Greece	**MK527845**	**MK527845**	–	**MK523276**	**MK523305**	**MK523333**	
Furfurella stromatica	**CE4 = CBS 144409**	*Genista cinerea*	H	bark	Spain	**MK527846**	**MK527846**	**MK523261**	**MK523277**	**MK523306**	**MK523334**	
	CE5	*Genista cinerea*		bark	Spain	**MK527847**	**MK527847**	–	**MK523278**	–	**MK523335**	
Graphostroma platystomum	CBS 270.87					HG934115	AY083827		KY624296	DQ836915	HG934108	
Hymenopleella hippophaëicola	LH = CBS 140410		E			KT949901	KT949901	**MK523262**	**MK523279**	**MK523307**	**MK523336**	
Hyponectria buxi	UME 31430					–	AY083834					

Table 1 (cont.)

Taxon	Strain[1]	Host[2]	Type[3]	Substrate / Isolation source	Country	GenBank accession no.						References[2]
						ITS	LSU	*rpb1*	*rpb2*	*tef1*	*tub2*	
Hypoxylon fragiforme	MUCL 51264		E			KC477229	KM186295	–	KM186296	–	KX271282	
Idriella lunata	CBS 204.56		H			KP859044	KP858981					
Juglanconis juglandina	CBS 133343					–	KY427149	KY427181	KY427199	KY427218	KY427234	
Kretzschmaria deusta	CBS 163.93					KC477237	KY610458	–	KY624227	–	KX271251	
Lasiosphaeria ovina	CBS 958.72					–	AY587946	genome[6]	genome[6]	genome[6]	genome[6]	
Leiosphaerella praeclara	CBS 125586					JF440976	JF440976					
Lepteutypa fuckelii	LEF = CBS 140409		N			KT949902	KT949902	**MK523263**	**MK523280**	**MK523308**	**MK523337**	
Leptosillia acerina	**CRA**	*Acer campestre*		bark	Austria	**MK527848**	**MK527848**	–	**MK523281**	**MK523309**	**MK523338**	
	CRA1 = CBS 143939	*Acer campestre*	E	bark	Austria	**MK527849**	**MK527849**	**MK523264**	**MK523282**	**MK523310**	**MK523339**	
	CRA2	*Acer campestre*		bark	Austria	**MK527850**	**MK527850**	–	**MK523283**	**MK523311**	**MK523340**	
	CRA3	*Acer campestre*		bark	Austria	**MK527851**	**MK527851**	–	**MK523284**	**MK523312**	**MK523341**	
Leptosillia macrospora	CCF 4028	*Ulmus laevis*	H[4]	living bark/sapwood tissue	Czech Republic	FR715522	FR715522	–	FR715509	–	FR715498	Pažoutová et al. (2012)
	CRM1	*Quercus robur*		bark	Germany	**MK527852**	**MK527852**	–	**MK523285**	**MK523313**	**MK523342**	
	CRM2 = CBS 143627	*Quercus petraea*	E	bark	Austria	**MK527853**	**MK527853**	**MK523265**	**MK523286**	**MK523314**	**MK523343**	
	CRM4	*Quercus robur*		bark	Austria	**MK527854**	**MK527854**	–	**MK523287**	**MK523315**	**MK523344**	
	CRM7	*Quercus robur*		bark	Germany	**MK527855**	**MK527855**	–	**MK523288**	**MK523316**	**MK523345**	
Leptosillia muelleri	**CRM**	*Acer pseudoplatanus*		bark	Austria	**MK527856**	**MK527856**	–	**MK523289**	**MK523317**	**MK523346**	
	CRM3 = CBS 143628	*Acer pseudoplatanus*	E	bark	Austria	**MK527857**	**MK527857**	**MK523266**	**MK523290**	**MK523318**	**MK523347**	
	CRM6	*Acer pseudoplatanus*		bark	Austria	**MK527858**	**MK527858**	–	**MK523291**	**MK523319**	**MK523348**	
Leptosillia pistaciae	ISPaVe 1958 = CBS 128196	*Pistacia vera*	H	canker tissue (parasite)	Italy	MH798901	MH798901	**MK523267**	MH791334	**MK523320**	MH791335	Vitale et al. (2018)
	ISPaVe 2105	*Pistacia vera*		canker tissue (parasite)	Italy	FR681904	–					Vitale et al. (2018)
	ISPaVe 2106	*Pistacia vera*		canker tissue (parasite)	Italy	FR681905	–					Vitale et al. (2018)
Leptosillia slaptonensis	**CRU1 = CBS 143629**	*Ulmus minor*		bark	Austria	**MK527859**	**MK527859**	–	**MK523292**	**MK523321**	**MK523349**	
	CRU2	*Ulmus minor*		bark	Austria	**MK527860**	**MK527860**	–	**MK523293**	–	**MK523350**	
	CRU3	*Ulmus minor*		bark	Austria	**MK527861**	**MK527861**					
	NAD = CBS 145296	*Ulmus minor*	E	bark	Austria	**MK527862**	**MK527862**	**MK523268**	**MK523294**	**MK523322**	**MK523351**	
Leptosillia sp.	A23	*Annona squamosa*		endophyte	China	EF488447	–					unpublished
	AWB8	*Aquilaria malaccensis*		living wood tissue	India	JX448359	–					Premalatha & Kalra (2013)
	PPM8003	*Calocedrus macrolepis* var. *formosana*		living host tissue	Taiwan	KX227618	KX227617					unpublished
	PPM8004	*Calocedrus macrolepis* var. *formosana*		living host tissue	Taiwan	KX242164	KX242162					unpublished
	E8520C	*Casearia prunifolia*		living stem tisue	Ecuador	HQ117861	–					unpublished
	VegaE4-79	*Coffea arabica*		living petiole tissue	USA (Hawaii)	EU009996	–					Vega et al. (2010)
	OTU173	*Coffea sp.*		leaf disk tissue	Puerto Rico	KT328745	–					James et al. (2016)
	INBio 573B	*Erythroxylum macrophyllum*		living host tissue	Costa Rica	KU204602	–					unpublished
	CX	*Eugenia uruguayensis*		leaf petiole tissue	Uruguay	KU212366	–					García-Laviña et al. (2016)
	MX17	*Hevea brasiliensis*		living sapwood tissue	Mexico	JQ905737	–					unpublished
	MX194	*Hevea brasiliensis*		living sapwood tissue	Mexico	JQ905738	–					unpublished
	E9226a	*Ilex guayusa*		living host tissue	Ecuador	JN662478	–					unpublished
	HS52	living unidentified plants		living host tissue	China	KY496833	–					unpublished
	MIB07	*Madhuca indica*		living bark tissue	India	JN604095	–					Verma et al. (2014)
	clone OTU_F75_R46	*Nothofagus fusca*		living leaves	New Zealand	MF976713	–					Johnston et al. (2017)
	E15610E	*Psammisia sodiroi*		living stem tisue	Ecuador	KM266133	–					unpublished
	E11-3111	*Ulmus macrocarpa*		living bark/sapwood tissue	China	FJ025239	–					unpublished
	M36	unknown		unknown (mangrove)	unknown	KT336540	–					unpublished
	E14625A	*Virola calophylla*		living stem tisue	Ecuador	KM265634	–					unpublished
Leptosillia wienkampii	AK8/09	*Ulmus laevis*		living bark/sapwood tissue	Czech Republic	FR715513	FR715513					Pažoutová et al. (2012)
	CCF 4020	*Ulmus laevis*	H[5]	living bark/sapwood tissue	Czech Republic	FR715515	FR715515					Pažoutová et al. (2012)
	CCF 4021	*Ulmus laevis*		living bark/sapwood tissue	Czech Republic	FR715519	FR715519					Pažoutová et al. (2012)
	CCF 4022	*Ulmus laevis*		living bark/sapwood tissue	Czech Republic	FR715516	FR715516					Pažoutová et al. (2012)
	CCF 4023	*Ulmus laevis*		living bark/sapwood tissue	Czech Republic	FR715521	FR715521					Pažoutová et al. (2012)
	CCF 4024	*Ulmus laevis*		living bark/sapwood tissue	Czech Republic	FR715520	FR715520					Pažoutová et al. (2012)

Table 1 (cont.)

Taxon	Strain[1]	Host[2]	Type[3]	Substrate/ Isolation source	Country	GenBank accession no.						References[2]
						ITS	LSU	*rpb1*	*rpb2*	*tef1*	*tub2*	
Leptosillia wienkampii (cont.)	CCF 4025	*Ulmus laevis*		living bark/sapwood tissue	Czech Republic	FR715514	FR715514					Pažoutová et al. (2012)
	CCF 4026	*Ulmus laevis*		living bark/sapwood tissue	Czech Republic	FR715518	FR715518					Pažoutová et al. (2012)
	CCF 4027	*Ulmus laevis*		living bark/sapwood tissue	Czech Republic	FR715517	FR715517					Pažoutová et al. (2012)
	CRM5	*Ulmus laevis*		bark	Austria	**MK527863**	**MK527863**	–	**MK523295**	**MK523323**	–	
	CRU	*Ulmus glabra*		bark	Austria	**MK527864**	**MK527864**	–	**MK523296**	**MK523324**	**MK523352**	
	CRW = CBS 143630	*Salix fragilis* var. *russeliana*	E	bark	UK	**MK527865**	**MK527865**	**MK523269**	**MK523297**	**MK523325**	**MK523353**	
	CRW1	*Salix fragilis*		bark	Austria	**MK527866**	**MK527866**	–	**MK523298**	**MK523326**	**MK523354**	
	CRW2	*Ulmus minor*		bark	Italy	**MK527867**	**MK527867**	–	**MK523299**	**MK523327**	–	
	CRW3	*Ulmus minor*		bark	Austria	**MK527868**	**MK527868**					
	H041	*Salix alba*		living bark/sapwood tissue	Czech Republic	FR715510	FR715510	–	FR715507	–	FR715496	Pažoutová et al. (2012)
	H077	*Salix alba*		living bark/sapwood tissue	Czech Republic	FR715511	FR715511	–	FR715508	–	FR715497	Pažoutová et al. (2012)
	H133	*Salix alba*		living bark/sapwood tissue	Czech Republic	FR715512	FR715512					Pažoutová et al. (2012)
Lopadostoma gastrinum	CBS 134632		N			KC774584	KC774584					
Lopadostoma turgidum	CBS 133207		E			KC774618	KC774618	**MK523270**	KC774563	–	MF489024	
Melogramma campylosporum	MBU = CBS 141086					JF440978	JF440978					
Microdochium lycopodinum	CBS 125585		H			JF440979	JF440979	–	KP859125	–	KP859080	
Microdochium phragmitis	CBS 285.71		E			KP859013	KP858949	–	KP859122	–	KP859076	
Obolarina dryophila	MUCL 49882					GQ428316	GQ428316	–	KY624284	–	GQ428322	
Ophiostoma piliferum	CBS 158.74					–	DQ470955					
Pestalotiopsis knightiae	CBS 114138		H			KM199310	KM116227					
Phlogicylindrium eucalyptorum	CBS 111689					KF251205	KF251708					
Phlogicylindrium uniforme	CBS 131312		H			JQ044426	JQ044445					
Polyancora globosa	CBS 118182		H			DQ396469	DQ396466					
Pseudapiospora corni	PCO = CBS 140736		N			KT949907	KT949907					
Pseudoanthostomella delitescens	MFLUCC 16-0477					KX533451	KX533452	–	KX789491	–	KX789490	
Pseudomassaria chondrospora	CBS 125600					JF440981	JF440981					
Pseudomassariella vexata	LVE = CBS 129021		E			JF440977	JF440977	genome[6]	genome[6]	genome[6]	genome[6]	
Requienella seminuda	RS12 = CBS 140502		E			KT949912	KT949912	**MK523271**	**MK523300**	**MK523328**	–	
Robillarda sessilis	CBS 114312		E			KR873256	KR873284					
Rosellinia aquila	MUCL 51703					KY610392	KY610460	–	KY624285	–	KX271253	
Seiridium marginatum	BLO = CBS 140403		E			KT949914	KT949914	**MK523272**	**MK523301**	**MK523329**	LT853249	
Strickeria kochii	C143 = CBS 140411		E			KT949918	KT949918					
Truncatella angustata	ICMP 7062					AF405306	AF382383					
Vialaea insculpta	DAOM 240257					JX139726	JX139726					
Vialaea minutella	BRIP 56959					KC181926	KC181924					
Xylaria hypoxylon	CBS 122620		E			KY610407	KY610495	–	KY624231	–	KX271279	

[1] Abbreviations: ATCC: American Type Culture Collection, Manassas, VA, USA; BRIP: Queensland Plant Pathology Herbarium, Brisbane, Australia; CBS: Culture collection of the Westerdijk Fungal Biodiversity Institute, Utrecht, The Netherlands; CCF: Culture collection of the Dept. of Botany, Charles University, Prague, Czech Republic; CPC: Culture collection of Pedro Crous, housed at CBS; DAOM: Canadian National Mycological Herbarium, Ottawa, Candada; HKUCC: The University of Hong Kong Culture Collection, Hong Kong, China; ICMP: International Collection of Microorganisms from Plants, Auckland, New Zealand; INBio: Instituto Nacional de Biodiversidad, Costa Rica; ISPaVe: Culture collection of the Consiglio per la Ricerca in Agricoltura e l'Analisi dell'Economia Agraria, Roma, Italy (CREA-DC); MFLUCC: Mae Fah Luang University Culture Collection, Chiang Rai, Thailand; MR: Culture collection of Martina Réblová, Department of Taxonomy, Institute of Botany of the Czech Academy of Sciences, Průhonice, Czech Republic; MUCL: BCCM/MUCL Agro-food & Environmental Fungal Collection, Louvain-la-Neuve, Belgium; MYCO-ARIZ: Gilbertson Mycological Herbarium, University of Arizona, Tucson, USA; NRRL: Agricultural Research Service Culture Collection, Peoria, IL, USA; ST.MA.: Culture collection of Mark Stadler, Helmholtz-Zentrum für Infektionsforschung, Braunschweig, Germany; UCR: University of California, Riverside, USA; UME: Herbarium of the Department of Ecology and Environmental Science, Umeå University, Umeå, Sweden.

[2] Hosts and References only given for GenBank sequence accessions within the *Delonicicolacaeae-Leptosilliaceae* clade.

[3] E ex-epitype strain; H ex-holotype strain; I ex-isotype strain; N ex-neotype strain.

[4] Ex-holotype strain of *Liberomyces macrosporus*.

[5] Ex-holotype strain of *Liberomyces saliciphilus*.

[6] Sequence retrieved from genome deposited at JGI-DOE (http://genome.jgi.doe.gov/).

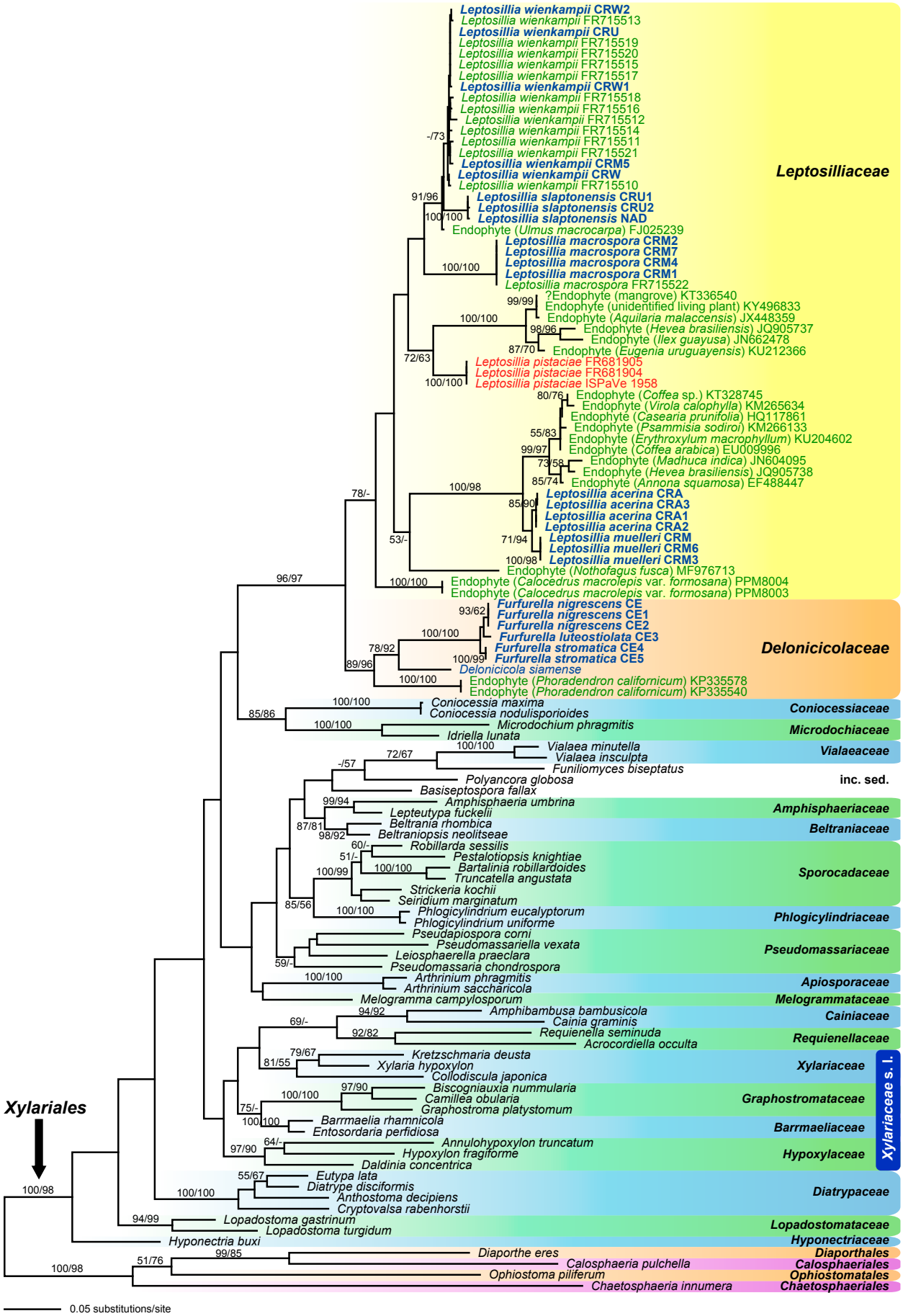

Fig. 2 Phylogram of the ML tree (lnL = -19 991.4865) revealed by RAxML from an analysis of the ITS-LSU rDNA matrix of selected *Xylariales*, showing the phylogenetic position of *Furfurella* and *Leptosillia*. Strain/culture numbers or GenBank accession numbers are given following the taxon names; for the endophyte isolates, the host is given in brackets. ML and MP bootstrap support above 50 % are given at the first and second position, respectively, above or below the branches. Accessions in **bold** were isolated and sequenced in the present study; those in green were generated in endophyte studies, those in red represent plant pathogens, and those in blue were isolated from ascomata growing on dead plant tissues (bark, wood, seed pods).

analyses were loaded in PAUP and subjected to heuristic search using TBR branch swapping (MULTREES option in effect, steepest descent option not in effect). MP analysis of the combined multilocus matrix was done using 1 000 replicates of heuristic search with random addition of sequences and subsequent TBR branch swapping (MULTREES option in effect, steepest descent option not in effect). Bootstrap analyses with 1 000 replicates were performed with the same settings, but using 5 rounds of random sequence addition and subsequent branch swapping during each bootstrap replicate; in addition, each replicate was limited to 1 million rearrangements in the ITS-LSU matrix.

RESULTS

Molecular phylogeny

Of the 1 345 characters included in the ITS-LSU analyses, 516 were parsimony informative. The best ML tree (lnL = -19 991.4865) revealed by RAxML is shown as Fig. 2. MP analyses revealed 4 598 MP trees 4 041 steps long (not shown). Most of the tree backbone was identical in all MP trees; differences were mainly present within the clade containing the *Amphisphaeriaceae*, *Apiosporaceae*, *Beltraniaceae*, *Melogrammataceae*, *Phlogicylindriaceae*, *Pseudomassariaceae*, *Sporocadaceae* and *Vialaeaceae* (AABMPPSV clade; not shown).

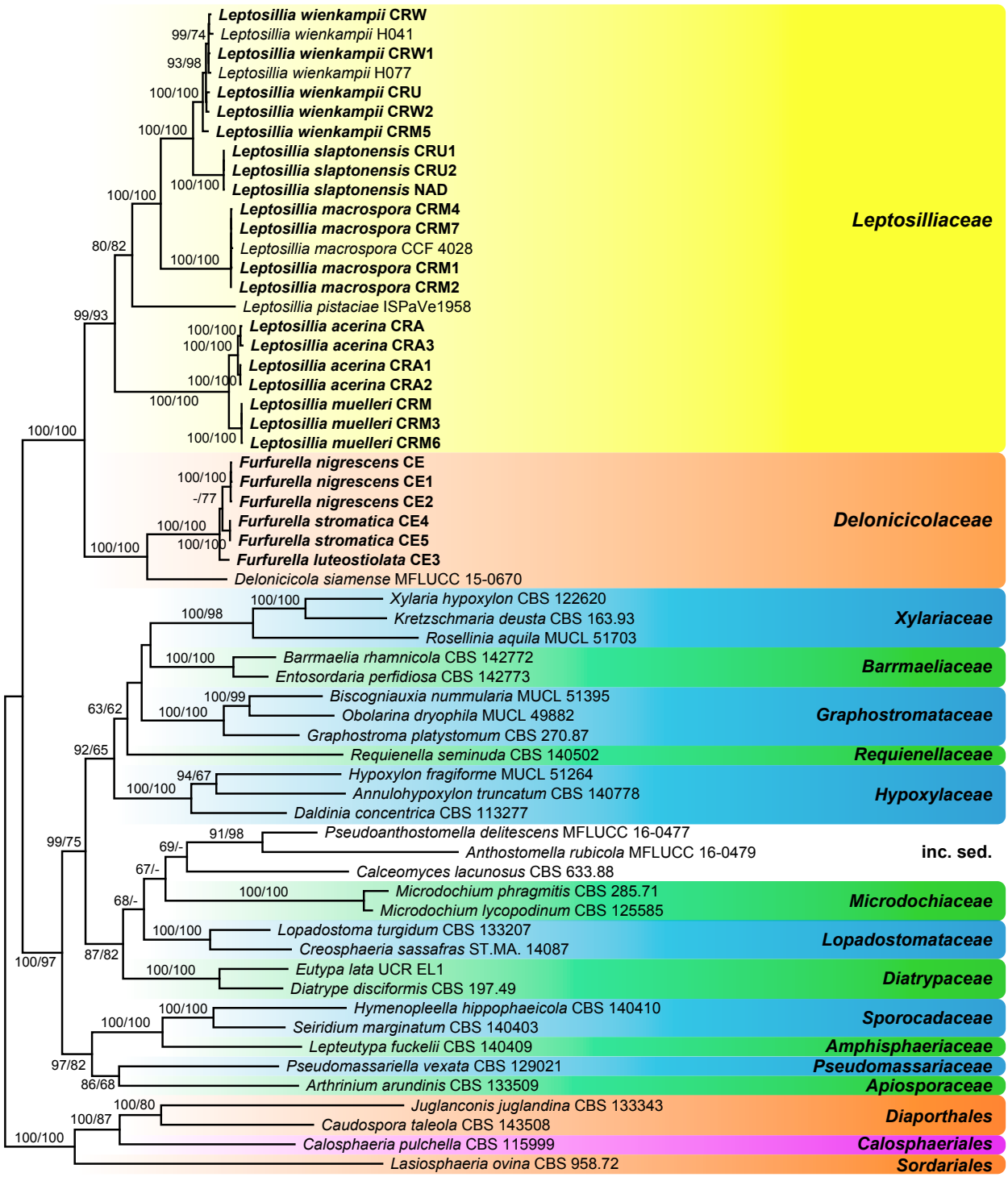

Fig. 3 Phylogram of the ML tree (lnL = -84 566.4626) revealed by RAxML from an analysis of the combined SSU-ITS-LSU-*rpb1-rpb2-tef1-tub2* matrix of selected *Xylariales*, showing the phylogenetic position of *Furfurella* and *Leptosillia*. ML and MP bootstrap support above 50 % are given at the first and second position, respectively, above or below the branches. Strain/culture numbers are given following the taxon names; accessions in **bold** were isolated and sequenced in the present study.

The MP strict consensus tree was mostly compatible with the ML tree; notable exceptions were a placement of the *Coniocessiaceae-Microdochiaceae* clade basal to the AABMPPSV clade; an interchanged position of the *Hypoxylaceae* with the *Barrmaeliaceae-Graphostromataceae* clade, and within the *Leptosillia* clade, a position of the *Calocedrus macrolepis* endophyte as sister to *Leptosillia macrospora* and of the *Nothofagus fusca* endophyte as basal to the clade containing, amongst various endophyte accessions, *Leptosillia pistaciae*, *L. macrospora*, *L. slaptonensis* and *L. wienkampii* (not shown). The clade containing *Delonicicola*, *Furfurella*, *Leptosillia* and numerous unclassified endophytes received high support in both analyses (96 % ML, 97 % MP), and the clade containing *Delonicicola*, *Furfurella* gen. nov. and the *Phoradendron* endophyte medium (89 % ML) and high (96 % MP) support. The *Leptosillia* clade, however, was resolved as monophyletic only in the ML analyses, where it received moderate support (78 %); besides the six *Leptosillia* species, this clade contained numerous ITS sequence accessions of endophytes from various geographic areas and hosts, which were scattered throughout the clade (Fig. 2). In the strict consensus of the MP trees, three subclades were placed in a polytomy:

i. the *Delonicicola* clade;
ii. a highly supported *Leptosillia acerina-L. muelleri* clade (including various endophyte isolates); and
iii. a weakly supported clade containing the residual *Leptosillia* species plus the rest of endophyte isolates (not shown).

Of the 7 052 characters included in the combined five locus analyses, 3 093 were parsimony informative (476 from SSU-ITS-LSU, 613 from *rpb1*, 579 from *rpb2*, 656 from *tef1* and 769 from *tub2*). The best ML tree (lnL = -84 566.4626) revealed by RAxML is shown as Fig. 3. The MP analysis revealed 6 MP trees 19 319 steps long (not shown); tree topologies of all MP trees were identical except for slightly different positions of *Calceomyces lacunosus*. Tree topologies of the MP trees were similar to the ML tree, except for a sister group relationship of *Diatrypaceae* and *Lopadostomataceae*, a basal position of *Requienella* to the other *Xylariaceae* s.lat., a sister group

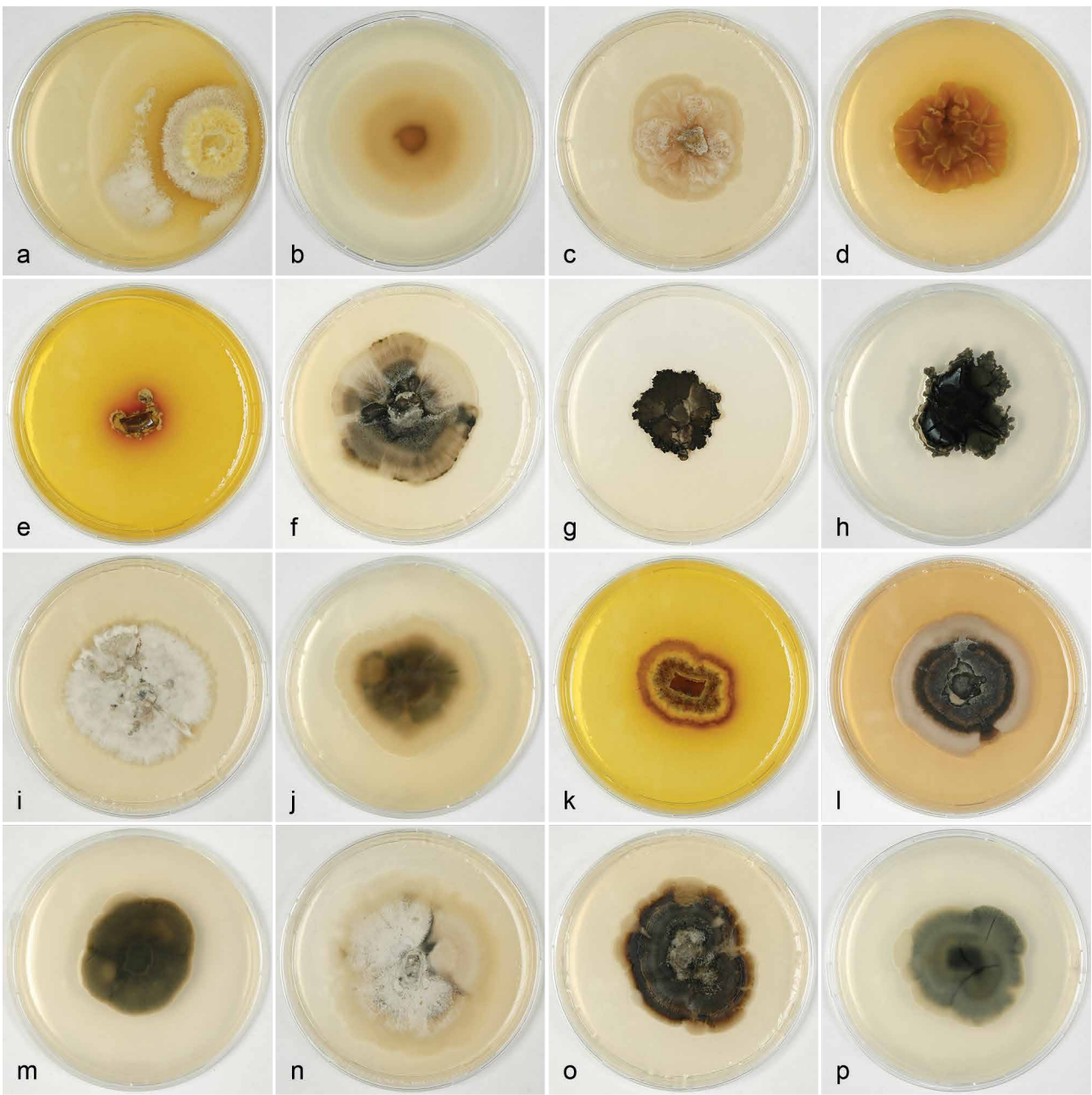

Fig. 4 Cultures on CMD at 15–17 °C. a. *Furfurella nigrescens* (CE); b. *Furfurella stromatica* (CE4); c–e. *Leptosillia acerina* (c, e: CRA1, d: CRA); f–h. *Leptosillia macrospora* (f: CRM1, g: CRM4, h: CRM2); i–k. *Leptosillia muelleri* (i, k: CRM3, j: CRM6); l–m. *Leptosillia slaptonensis* (l: CRU1, m: CRU2); n–p. *Leptosillia wienkampii* (n: CRW, o: CRW1, p: CRU). a, c, e–g, i, k–l, n–o. Surface view; b, d, h, j, m, p. Reverse. All after 58 d; except b after 27 d and e, k after 7.5 mo.

relationship of *Graphostromataceae* to *Xylariaceae* s.str., and an interchanged position of *Microdochium* and *Calceomyces* in some of the MP trees (not shown). In both analyses, the clade containing *Delonicicola*, *Furfurella* and *Leptosillia* and the *Delonicicola-Furfurella* subclade received maximum support (Fig. 3), while the *Leptosillia* subclade was highly supported (99 % ML, 93 % MP). Given the marked morphological differences (see below) and the highly supported phylogenetic subdivision in the multigene analyses, the new family *Leptosilliaceae* is established for the genus *Leptosillia*.

Culture characteristics

Culture images of two *Furfurella* and five *Leptosillia* species grown on CMD are shown in Fig. 4. Detailed culture descriptions are given under the respective species.

TAXONOMY

Delonicicolaceae R.H. Perera et al., emend. Voglmayr & Jaklitsch

Type genus. *Delonicicola* R.H. Perera et al., Cryptog. Mycol. 38: 334. 2017.

Family of *Xylariales*. *Pseudostromata* variable, from conspicuously pulvinate to virtually absent, immersed in host tissue, erumpent to rarely superficial, variously coloured, ranging from yellowish, brown to black; visible as raised, dark spots on the host surface, as black, more or less elevated patches on wood or erumpent through bark, occasionally covered by bright turquoise, yellow to yellow-green scurf. *Ascomata* perithecial, immersed in pseudostroma, aggregated, globose, subglobose to conical or irregular, subhyaline to pale brown, with an apical ostiole. *Peridium* subhyaline to medium brown, KOH-, of *textura angularis* to *prismatica*. *Ostioles* papillate. *Hamathecium* composed of hyaline, septate or aseptate, unbranched or occasionally branched paraphyses. *Asci* arising from the base or margins of the ascomata, clavate to cylindrical, straight, curved to sinuous, thin-walled, containing 8 biseriately arranged ascospores, inamyloid and without a distinct apical apparatus. *Ascospores* ellipsoid or allantoid, equilateral or inequilateral, aseptate or septate, not constricted at the septa, hyaline, thin-walled, smooth, with rounded apices, without appendages or gelatinous sheath. *Asexual morph* unknown.

Notes — We provide an emended familial description here, as the *Delonicicolaceae* in the sense of the original authors also include the taxa here segregated in a family of their own, *Leptosilliaceae* (see below), and the new genus *Furfurella* with allantoid ascospores and variously developed, immersed, erumpent or superficial pseudostromata usually covered by a bright greenish yellow scurf, is here added to *Delonicicolaceae*. The illustrations of the type species, *Delonicicola siamense*, in Perera et al. (2017), unfortunately do not allow for evaluation of stromatic configuration and ascoma morphology in detail. We also propose that other morphological features should be re-checked (e.g., the authors surprisingly reported that the paraphyses were lacking septa!).

Furfurella Voglmayr & Jaklitsch, *gen. nov.* — MycoBank MB829925

Etymology. Referring to the bright greenish to yellow scurf on its stromata.

Type species. *Furfurella stromatica* Voglmayr & Jaklitsch.

Pseudostromata variously developed, from pulvinate to virtually absent, erumpent through bark cracks or embedded in bark or wood, commonly blackening the substrate surface, usually covered by a bright yellow, yellow-green to turquoise scurf dissolving a bright yellow pigment in KOH. *Ascomata* perithecial, 120–460 µm diam, immersed in pseudostroma, usually densely aggregated in groups of 2–25, rarely scattered singly, lenticular, subglobose to pyriform, horizontally compressed when dry, with a central apical ostiole, perithecial content dull orange to brown and waxy when dry. *Peridium* light to medium brown, KOH-, becoming hyaline towards the centrum, pseudoparenchymatous to prosenchymatous, consisting of thin- or thick-walled, hyaline to brown, isodiametric to elongated cells forming a *textura angularis* or *prismatica*. *Ostioles* variously developed, from inconspicuous and not protruding to long cylindrical and protruding; ostiolar canal with c. 1 µm wide hyaline periphyses embedded in a gelatinous matrix. *Hamathecium* composed of elongate, hyaline, septate, occasionally branched, basally broad and apically tapering paraphyses. *Asci* arising from the base and the margins of the ascomata, sequentially produced; fusoid, clavate to cylindrical, straight, curved or sinuous, thin-walled, with marginal fissurate dehiscence, containing 8 biseriately or fasciculately arranged ascospores, without a stipe and an apical apparatus, inamyloid but appearing bitunicate with a distinct ocular chamber in Lugol after treatment with 3 % KOH. *Ascospores* allantoid, aseptate, hyaline, thin-walled, smooth, with rounded apices, without appendages or gelatinous sheath. *Asexual morph* unknown.

Notes — *Furfurella* can be easily discriminated from its closest relative, *Delonicicola*, by its large, allantoid, aseptate ascospores, a bright yellow, yellow-green to turquoise scurf on the stromata and ostioles, a medium brown ascoma wall, and by growth on dead branches of mediterranean fabaceous shrubs from tribe *Genisteae*.

In all species, the ascospore contours are only faintly seen in asci mounted in water, but become distinct in KOH and Lugol. Ascospores and asci shrink considerably in Lugol, therefore measurements were done in water to ensure comparability of the data.

Furfurella luteostiolata Voglmayr & Jaklitsch, *sp. nov.* — MycoBank MB829926; Fig. 5

Etymology. Referring to the yellow scurf around its ostioles.

Holotype. Greece, Crete, Chania, Omalos, 920 m a.s.l., N35.37° E23.897°, in bark of thin dead branches of *Genista acanthoclada*, soc. *Microthyrium* sp., *Diaporthe* sp., 5 June 2015, *W. Jaklitsch* & *H. Voglmayr* (WU 39989; ex-holotype culture CBS 143620 = CE3).

Pseudostromata immersed in the woody substrate and erumpent through the bark, reduced mostly to the region around the apical parts of the ascomata and covered by a bright sulphur yellow scurf, slightly blackening the bark surface around the erumpent stromata. *Ascomata* perithecial, c. 200–250 µm diam, embedded in bark or wood, solitary or in groups of up to 5, irregularly subglobose to pyriform, horizontally compressed when dry, with a central apical ostiole; perithecial contents dull brown, waxy when dry. *Peridium* 16–26 µm thick, brown, KOH-, becoming hyaline towards the centrum, pseudoparenchymatous to prosenchymatous, consisting of rather thick-walled, brown, isodiametric to elongated cells 3–16 × 2–5 µm forming a *textura angularis*, thin-walled and hyaline towards the centrum. *Ostioles* c. 110–130 µm long, 30–60 µm wide, not protruding above the stroma surface, apically black, surrounded by stromatic tissues covered by sulphur yellow scurf. *Hamathecium* composed of elongate, hyaline, septate, occasionally branched paraphyses up to 6 µm wide at the base, gradually tapering to 1.7 µm towards the distal ends. *Asci* (83–)88–107(–115) × (12.0–)12.8–14.7(–15.3) µm (n = 20), fusoid to cylindrical, straight or slightly curved, thin-walled, with fissurate dehiscence, containing 8 biseriately arranged ascospores, without a stipe and an apical apparatus, inamyloid. *Ascospores* (24–)27–32(–34) × (5.5–)6.5–7.5(–8.2) µm,

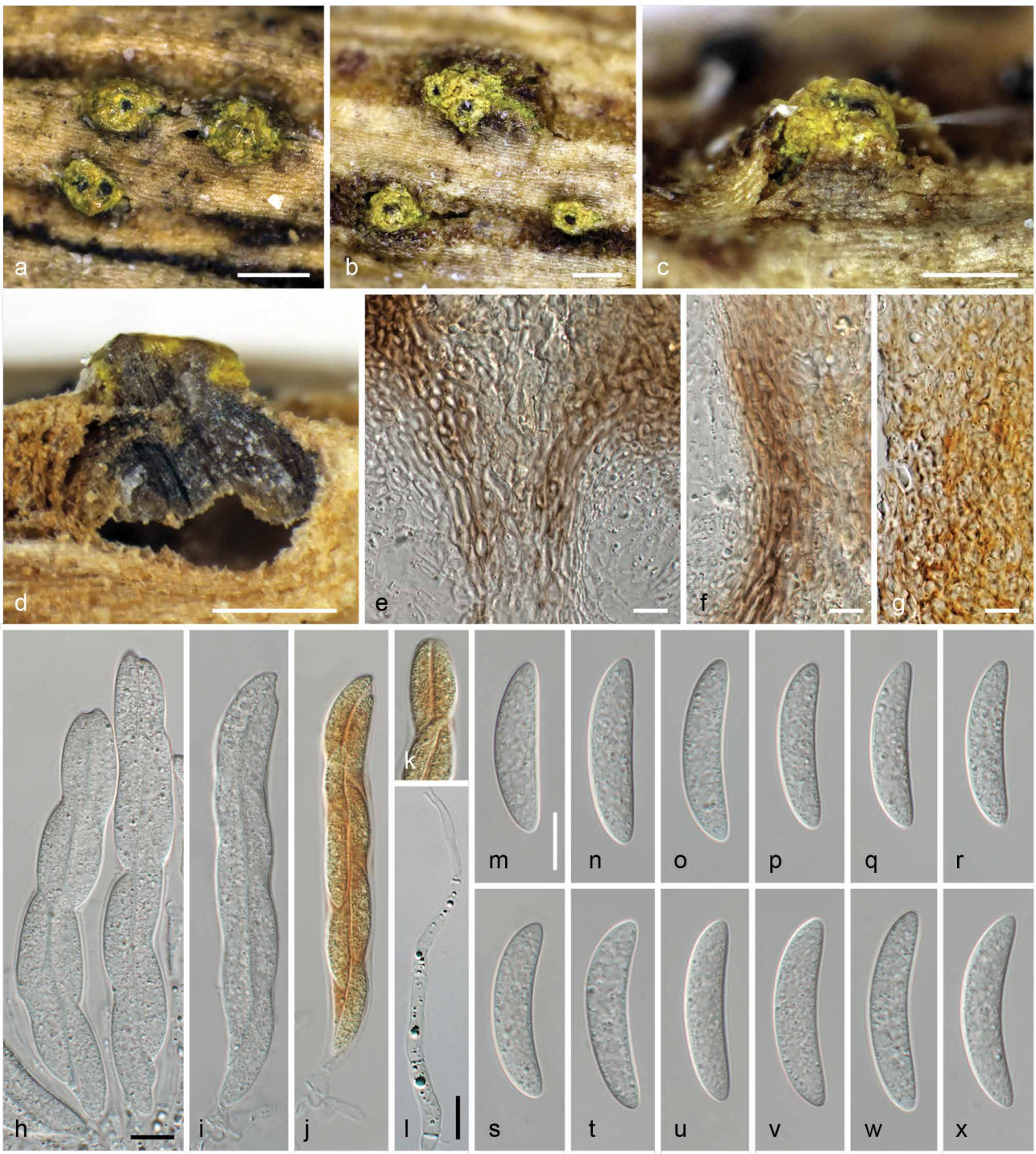

Fig. 5 *Furfurella luteostiolata* (WU 39989, holotype). a–c. Ostioles erumpent through bark with sulphur yellow scurf in surface or side view; d. pseudostroma with two perithecia in vertical section; e–f. vertical sections of perithecial walls (e. from upper part of two adjacent perithecia, f. lateral); g. vertical section of pseudostroma around ostioles, yellow brown colour originating from yellow scurf dissolved in KOH; h–j. asci; k. ascus apex; l. septate paraphysis; m–x. ascospores. All in water, except e–g in 3 % KOH, j–l in Lugol after KOH pre-treatment. — Scale bars: a–d = 200 µm; e–x = 10 µm.

l/w = (3.1–)3.8–4.8(–5.3) (n = 75), allantoid, aseptate, hyaline, thin-walled, smooth, with rounded apices, without appendages or gelatinous sheath. *Asexual morph* unknown.

Culture characteristics — On CMD colony radius 32 mm after 23 d at 22 °C. Colony whitish, very dense, turning cream with age, with abundant white aerial mycelium in the centre.

Habitat & Host range — Only known from corticated dead branches of *Genista acanthoclada*.

Distribution — Only known from the type collection in Crete (Greece).

Notes — *Furfurella luteostiolata* differs from the other two known *Furfurella* species by its broader and stouter ascospores and by the bright sulphur yellow scurf around the ostioles.

Furfurella nigrescens Voglmayr & Jaklitsch, *sp. nov.* — MycoBank MB829927; Fig. 6

Etymology. Referring to the blackening of the host surface around the pseudostromata.

Holotype. Spain, Andalucía, at km 26 between La Sauceda and Puerto Galiz, 500 m a.s.l., in bark and wood of dead branches of *Calicotome villosa*, soc. *Valsaria spartii*, 2 Apr. 2014, *W. Jaklitsch* (WU 39990; ex-holotype culture CBS 143622 = CE1).

Pseudostromata embedded in bark or wood, reduced to substrate blackening and scurf, sometimes slightly elevating the substrate, distinctly blackening the host surface and commonly covered by a bright yellow, yellowish green to turquoise scurf. *Ascomata* perithecial, 130–420 µm diam, c. 230–270 µm high,

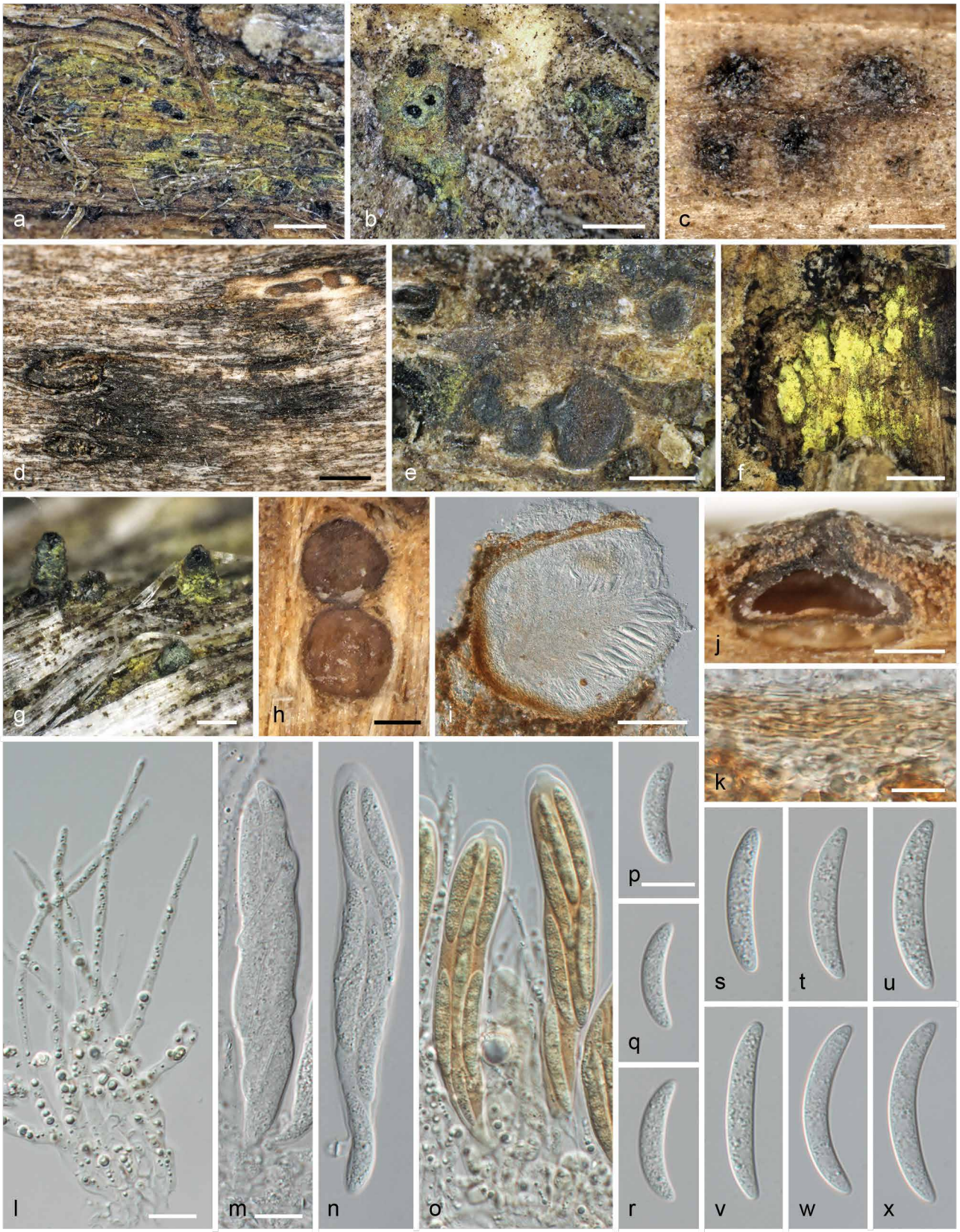

Fig. 6 *Furfurella nigrescens*. a–d. Black pseudostromata in wood or bark (a, b. with yellow-green scurf; c. clypeus-like black discoloration of bark); e, h. transverse section through pseudostromata and perithecia with dull orange, waxy perithecial contents; f. bright sulphur yellow scurf; g. black protruding ostioles laterally covered by yellow-green scurf; i. transverse section of perithecial wall and pseudostroma (bottom left); j. vertical section of pseudostroma embedded in bark with single perithecium and clypeus-like black discoloration of bark surface; k. section of peridium and pseudostroma (bottom); l. septate paraphyses; m–o. asci; p–x. ascospores. All in water, except l, o in Lugol after KOH pre-treatment, n in 3 % KOH (a–b, e–g, m–n, p–r: WU 39990 (holotype); c, h–l, o, s–v: WU 39992; d, w, x: WU 39991). — Scale bars: a–c, e = 300 µm; d, f = 500 µm; g–j = 100 µm; k–x = 10 µm.

embedded in bark or wood, solitary or aggregated in groups, lenticular, subglobose to pyriform, horizontally compressed when dry, with a central apical ostiole. *Peridium* 11–22 µm thick, light brown, KOH-, becoming hyaline towards the centrum, pseudoparenchymatous to prosenchymatous, consisting of thin-walled, light brown, isodiametric to elongated cells 5–11 × 1–3.5 µm forming a *textura angularis* to *prismatica*, becoming hyaline towards the centrum; perithecial contents dull orange, waxy when dry. *Ostioles* either flat, non-protruding, or distinctly cylindrical to conical and projecting up to 200 µm, 80–100 µm wide, black, of thick-walled, dark brown cells with narrow lumen; when protruding ostiole laterally covered by a sulphur yellow to yellowish green scurf. *Hamathecium* composed of elongate, hyaline, septate, occasionally branched paraphyses up to 5.5 µm wide at the base, gradually tapering to 1.3 µm towards the distal ends. *Asci* (64–)72–89(–99) × (10.5–)11.5–13.2(–14.5) µm (n = 35), fusoid, clavate to cylindrical, straight or slightly curved, thin-walled, with fissurate dehiscence, containing 8 ascospores biseriately arranged or in two fascicles, without a stipe and an apical apparatus, inamyloid. *Ascospores* variable in length, (18–)20–29(–35) × (4.0–)4.5–5.2(–6.0) µm, l/w = (3.7–)4.2–5.9(–7.2) (n = 157), allantoid, aseptate, hyaline, thin-walled, smooth, with rounded apices, without appendages or gelatinous sheath. *Asexual morph* unknown.

Culture characteristics — On CMD colony radius up to 34 mm after 29 d at 22 °C. Colony whitish, soon cream, very dense, with abundant bright yellow mycelium in the centre; odour fruity to yeast-like.

Habitat & Host range — On dead branches of *Calicotome villosa* and *Chamaecytisus creticus*.

Distribution — Mediterranean; known from Spain and Greece (Crete).

Additional specimens examined. Greece, Crete, Chania, SW Lakki, 580 m a.s.l., N35.392° E23.928°, in wood of thin decorticated branches of *Chamaecytisus creticus*, 5 June 2015, *W. Jaklitsch* & *H. Voglmayr* (WU 39991; culture CBS 143621 = CE2). – Spain, Andalucía, near Puerto Galiz, 450 m a.s.l., in bark of thin dead branches of *Calicotome villosa*, 2 Apr. 2014, *W. Jaklitsch* (WU 39992; culture CE).

Notes — Compared to the other two species of the genus, *Furfurella nigrescens* is more inconspicuous as its scurf is less prominent and sometimes even entirely absent. However, it is distinctly blackening the host surface, ranging from circular and clypeus-like around single ascomata in bark to extensive irregular patches around aggregated ascomata embedded in wood. In addition, its cultures develop a bright yellow aerial mycelium on CMD (Fig.4a).

Furfurella stromatica Voglmayr & Jaklitsch, *sp. nov.* — MycoBank MB829928; Fig. 7

Etymology. Referring to the well-developed pseudostromata.

Holotype. Spain, Andalucía, Jaén, Valdepeñas de Jaén, El Parrizoso, 1025 m a.s.l., N37°36'50.26" W3°43'12.34", on dead corticated branch of *Genista cinerea*, 29 Feb. 2016, *S. Tello S.T.29021601* (WU 39993; ex-holotype culture CBS 144409 = CE4).

Pseudostromata conspicuous, 0.25–2.1 mm long, 0.15–1.2 mm wide, pulvinate, superficial on wood or erumpent through bark cracks, exterior black and covered by a bright sulphur yellow, yellowish green to turquoise scurf, interior light brown. *Ascomata* perithecial, 240–460 µm diam, c. 250–280 µm high, embedded in a pseudostroma, gregarious in groups up to 25, subglobose, globose to pyriform, horizontally compressed when dry, with a central apical ostiole; perithecial content dull orange, waxy when dry. *Peridium* 21–29 µm thick, light brown, KOH-, becoming hyaline towards the centrum, pseudoparenchymatous to prosenchymatous, consisting of thin-walled, light brown, isodiametric to elongated cells 2–11.5 × 1–3.5 µm forming a *textura angularis*, becoming hyaline towards the centrum. *Ostioles* cylindrical to conical, protruding above stromata up to 250 µm, 80–160 µm wide, black, laterally covered by a sulphur yellow to yellowish green scurf. *Hamathecium* composed of elongate, hyaline, septate, occasionally branched paraphyses up to 5 µm wide at the base, gradually tapering to 1.7 µm towards the distal ends, deliquescent at maturity. *Asci* (78–)89–122(–139) × (10.7–)11.3–13.5(–14.5) µm (n = 28), clavate to cylindrical, usually slightly curved, thin-walled, with fissurate dehiscence, containing 8 biseriately arranged ascospores, without a stipe and an apical apparatus, inamyloid, easily detached at maturity. *Ascospores* variable in length, (23–)29–38(–47) × (3.7–)4.7–5.5(–6.5) µm, l/w = (5.1–)5.7–7.1(–8.1) (n = 103), allantoid, aseptate, hyaline, thin-walled, smooth, with rounded apices, without appendages or gelatinous sheath. *Asexual morph* unknown.

Culture characteristics — On CMD colony radius 40 mm after 29 d at 22 °C, covering almost the entire plate. Colony whitish, dense, thin, becoming yellowish brown to brown from the centre, with white aerial mycelium in the centre; odour sweetish.

Habitat & Host range — On dead branches of *Genista cinerea*.

Distribution — Only known from southern Spain (Andalucía).

Additional specimen examined. Spain, Andalucía, Jaén, Valdepeñas de Jaén, Cañón de Pitillos, 790 m a.s.l., N37°37'5.22" W3°41'32.14", on dead decorticated branch of *Genista cinerea*, 15 Mar. 2018, *S. Tello S.T.15031803* (WU 39994; culture CE5).

Notes — *Furfurella stromatica* is well distinct from the other known species of the genus by its conspicuous elongate pulvinate pseudostromata containing up to 25 perithecia with distinctly protruding black ostioles. This overall appearance, and in particular the fact that the asci become easily detached at maturity, the deliquescent paraphyses and the allantoid hyaline aseptate ascospores, point towards a placement of this fungus in the *Diaporthales*. Similar cases of misleading morphological evidence for taxa phylogenetically recently reclassified in *Xylariales* include e.g., *Melogramma* (previously classified in *Diaporthales*; Jaklitsch & Voglmayr 2012), *Acrocordiella* and *Requienella* (previously classified in *Pyrenulales*; Jaklitsch et al. 2016b) and *Strickeria* (previously classified in *Dothideomycetes*; Jaklitsch et al. 2016b). Of all three *Furfurella* species, *F. stromatica* has the most conspicuous bright yellow to yellowish green scurf.

Key to species of Furfurella

1. Pseudostromata conspicuous, erumpent to superficial, pulvinate, exterior black and covered by a bright sulphur yellow, yellowish green to turquoise scurf . . . . . *F. stromatica*
1. Pseudostromata inconspicuous, reduced to virtually absent, mostly in host tissue 2
2. Pseudostromata concentrated around the erumpent ostioles, at margins covered by bright sulphur yellow scurf, ascospores (5.5–)6.5–7.5(–8.2) µm wide . . . . *F. luteostiolata*
2. Pseudostromata embedded in substrate, not to slightly elevating but blackening the substrate surface, ascospores (3.7–)4.7–5.5(–6.5) µm wide . . . . . *F. nigrescens*

Leptosilliaceae Voglmayr & Jaklitsch, *fam. nov.* — MycoBank MB829929

Etymology. Referring to the name of the type genus.

Type genus. *Leptosillia* Höhn.

Family of *Xylariales*. *Ascomata* perithecial, superficial to partly immersed in bark, scattered, gregarious or confluent, black, sometimes collapsed, with a central apical ostiolar papilla. *Peridium* melanized, KOH-, of *textura angularis* or *prismatica*.

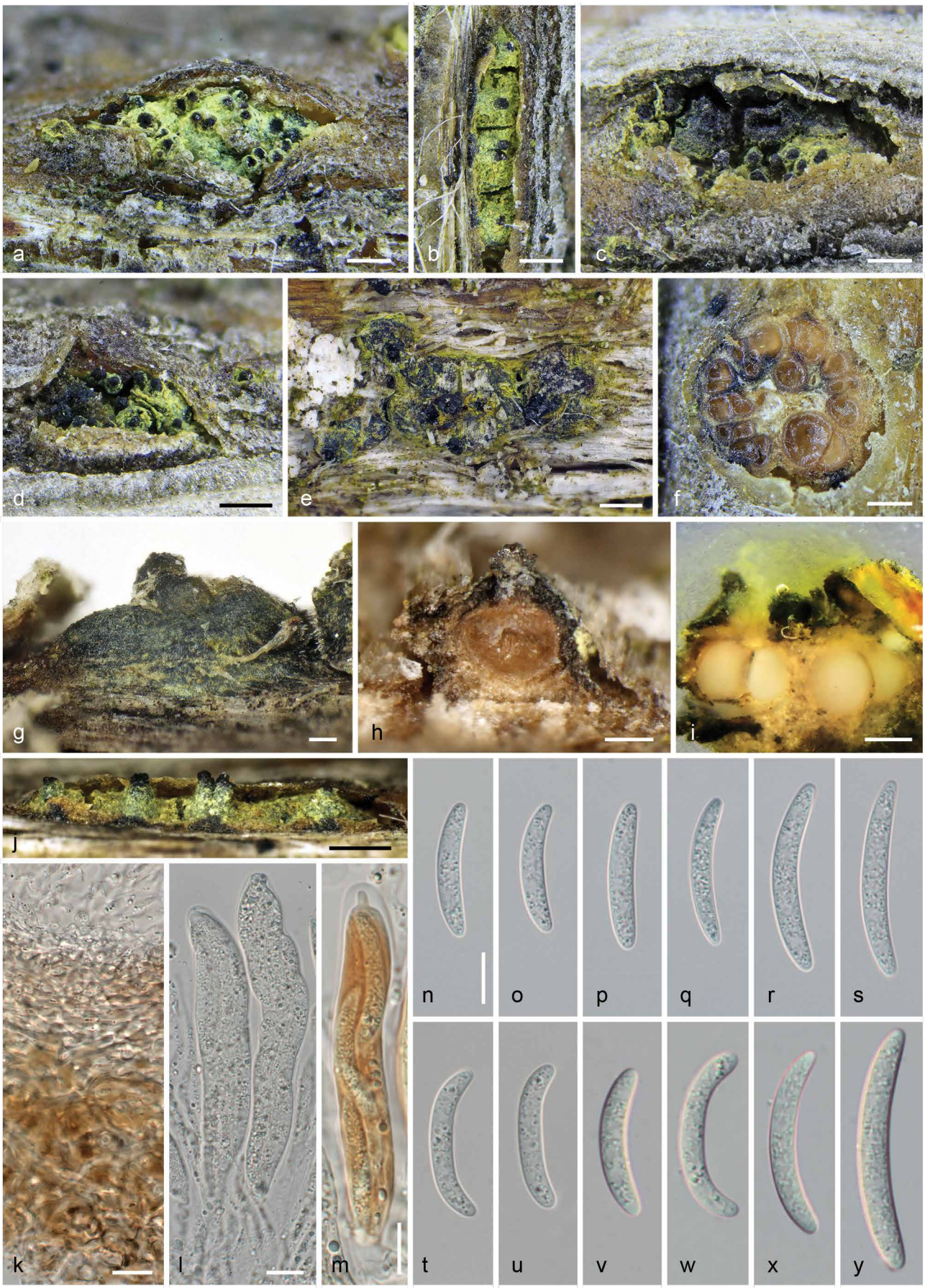

Fig. 7 *Furfurella stromatica*. a–e. Pseudostromata covered by bright yellow-green scurf and erumpent through bark (a–d) or superficial on wood (e); f. transverse section through pseudostroma and perithecia; g. side view of pulvinate stroma on wood, with protruding ostioles; h. vertical section of pseudostroma and perithecium with orange, waxy perithecial content; i. vertical section of pseudostroma and perithecia, with yellow scurf dissolving in KOH; j. black erumpent ostioles laterally covered by bright yellow-green scurf; k. section of perithecial wall and pseudostroma (lower half); l–m. asci; n–y. ascospores. All in water, except i, l in 3 % KOH, m in Lugol after KOH pre-treatment (a–d, f, i–j, l, t–y: WU 39993 (holotype); e, g–h, k, m–s: WU 39994). — Scale bars: a–f, i–j = 300 µm; g–h 100 µm; k–y = 10 µm.

Ostioles papillate, sometimes sulcate, base of the ostiolar canal sometimes with hyaline periphyses. *Hamathecium* composed of hyaline, septate, occasionally branched paraphyses embedded in a gelatinous matrix. *Asci* arising from the base of the ascomata, sequentially produced; clavate to cylindrical, curved to sinuous, thin-walled, containing 8 bi-, triseriately or fasciculately arranged ascospores, inamyloid and without a distinct apical apparatus. *Ascospores* ranging in shape from nearly straight, falcate, lunate, sinuous, sigmoid to hook-shaped, aseptate or septate, not constricted at the septa, hyaline, thin-walled, smooth, with rounded to subacute apices, without appendages or gelatinous sheath.
Conidiomata pycnidial, superficial to partly immersed in bark, globose to pyriform, black, scattered, aggregated or confluent, uni- or irregularly plurilocular. *Peridium* more or less melanized, of *textura globulosa* to *angularis*. *Conidiophores* short, hyaline, arising from the inner layer of the peridium. *Conidiogenous cells* cylindrical to lageniform. *Conidiogenesis* either enteroblastic-phialidic or holoblastic with sympodial proliferation, both types sometimes found within the same conidioma. *Conidia* commonly of two types according to their formation, allantoid, falcate or filiform, aseptate, hyaline, thin-walled.

Notes — *Leptosilliaceae* is closely related to *Delonicicolaceae*, from which it differs significantly by semi-immersed to superficial, black ascomata and, when present (*L. muelleri*), by different stroma structure.

Leptosillia Höhn., Mitt. Bot. Inst. Tech. Hochsch. Wien 5: 111. 1928

Synonyms. Cresporhaphis M.B. Aguirre, Bull. Brit. Mus. (Nat. Hist.), Bot. 21: 146. 1991.
Harpostroma Höhn., Mitt. Bot. Inst. Tech. Hochsch. Wien 5: 112. 1928.
Liberomyces Pažoutová et al., Mycologia 104: 201. 2012.

Type species. *Leptosillia notha* Höhn., a synonym of *L. muelleri* (Duby) Voglmayr & Jaklitsch.

Ascomata perithecial, 100–400 µm diam, superficial to partly immersed in bark, scattered singly, gregarious or confluent, black, smooth, sometimes collapsed, (sub)globose to pyriform, with a central apical ostiole. *Peridium* melanized, KOH-, becoming subhyaline towards the centrum, pseudoparenchymatous to prosenchymatous, consisting of thick-walled, dark brown, isodiametric to elongated cells forming a *textura angularis* or *prismatica*. *Ostioles* papillate, sometimes sulcate; base of the ostiolar canal sometimes with hyaline periphyses. *Hamathecium* composed of elongate, hyaline, filiform, septate, occasionally branched paraphyses embedded in an inamyloid gelatinous matrix; in some species with hyaline, refractive, dextrinoid granular exudates turning amber-red in Lugol. *Asci* arising from the base of the ascomata, sequentially produced; clavate to cylindrical, curved to sinuous, thin-walled, containing 8 bi-, triseriately or fasciculately arranged ascospores, with a short stipe, without a distinct apical apparatus, inamyloid but sometimes a narrow, short pore visible in Lugol. *Ascospores* from nearly straight, hooked, falcate, lunate, sinuous to sigmoid, aseptate or up to 11-septate, not constricted at the septa, hyaline, thin-walled, smooth, with rounded to subacute apices, without appendages or gelatinous sheath.
Conidiomata pycnidial, superficial to partly immersed in bark, globose to pyriform, black, smooth, scattered, aggregated or confluent, uni- or irregularly plurilocular. *Peridium* light to dark brown, continuous, composed of thin-walled, more or less isodiametric cells, forming a *textura globulosa* to *angularis*. *Conidiophores* short, hyaline, thin-walled, smooth, branched up to three times, arising from the inner layer of the peridium. *Conidiogenous cells* cylindrical to lageniform. *Conidiogenesis* either enteroblastic-phialidic and bearing usually curved, filiform, sometimes narrowly falcate conidia, or holoblastic with sympodial proliferation and bearing allantoid to falcate conidia; in some species both types of conidiogenous cells and conidia produced in the same conidioma. *Conidia* allantoid, falcate, lunate or filiform, aseptate, hyaline, thin-walled, smooth.

Notes — *Leptosillia* was posthumously described (Höhnel 1928) in a manuscript edited by J. Weese, based on a holomorphic specimen collected on bark of *Acer pseudoplatanus* in Germany. While Höhnel is given as the author of this publication, it is not clear which additions were provided by Weese.

The comment of Hawksworth (in Eriksson & Hawksworth 1987) that the type of *Leptosillia* was based on a specimen of *Sillia cinctula* distributed by Rehm in his Ascomyceten no. 2047 is erroneous. Rehm's Ascomyceten no. 2047 of *Cryptospora* (= *Sillia*) *cinctula* represents a North American collection from *Castanea dentata* (Rehm 1913), which conforms to the original description of that species and has nothing to do with *Leptosillia*.

All *Cresporhaphis* species currently accepted in Index Fungorum (accessed Feb. 2019) are here combined in *Leptosillia* except *C. chibaensis* and *C. rhoina*; for further details see below. Although no DNA data are available for *C. fusariospora* and *C. pinicola*, their morphology and habitat support inclusion in the genus.

Leptosillia acerina (Rehm) Voglmayr & Jaklitsch, *comb. nov.* — MycoBank MB829930; Fig. 8

Basionym. *Leptorhaphis acerina* Rehm, Ber. Naturhist. Vereins Augsburg 26: 51. 1881.
Synonyms. Cresporhaphis acerina (Rehm) M.B. Aguirre, Bull. Brit. Mus. (Nat. Hist.), Bot. 21 (2): 147. 1991.
Metasphaeria robergia Schulzer & Sacc., Rev. Mycol. (Toulouse) 6 (no. 22): 70. 1884.

Typification. Germany, Bayern, Franken, near Sugenheim, young deciduous forest, on cortex of living branches of *Acer campestre*, 1870, *H. Rehm*, *Ascomyc. no. 197* (S-L1668, lectotype of *Leptorhaphis acerina* selected by Aguirre-Hudson 1991; K(M) 111821, W 1923-1578, W 2009-00424: isolectotypes). – Austria, Burgenland, Breitenbrunn, Thenauriegel, on cork wings of branches of *Acer campestre*, 23 July 2016, *H. Voglmayr* (WU 39995, epitype of *Leptorhaphis acerina* here designated (MBT 385916); ex-epitype culture CRA1 = CBS 143939).

Ascomata perithecial, immersed in bark to half of their height, (105–)140–200(–240) µm diam (n = 46), black, shiny, smooth, scattered singly, subglobose to hemispherical, circular from above, often laterally or horizontally collapsed and then cupulate, with a central apical papilla. *Peridium* continuous, of a *textura angularis*, composed of an outer dark brown, 12–24 µm thick layer of thin-walled cells 2.5–7.5 µm diam with dark brown walls, and an inner, 12–16 µm thick hyaline to pale brown layer of (sub)hyaline cells slightly smaller than those of the outer layer. *Hamathecium* composed of hyaline, smooth, thin-walled, septate, occasionally branched paraphyses 2–3 µm wide, embedded in an inamyloid gelatinous matrix; periphyses not observed. *Asci* (57–)68–82(–89) × (6.0–)6.3–7.2(–7.5) µm (n = 34), unitunicate, cylindrical, slightly curved to sinuous, thin-walled, containing 8 bi- or triseriately arranged ascospores, with a short stipe, inamyloid but a narrow, short pore visible in Lugol. *Ascospores* (21–)24–30(–32) × (2.5–)2.8–3.2(–3.5) µm, l/w = (5.9–)8.2–10.1(–10.9) (n = 115), falcate, aseptate, hyaline, thin-walled, smooth, with subacute tapering ends, when vital containing numerous guttules especially towards the ends. *Pycnidia* scattered on bark, black, very similar to and practically indistinguishable from ascomata except for their slightly smaller size. *Conidiophores* short, hyaline, smooth, branched up to three times, arising from the inner wall of the pycnidium. *Conidiogenous cells* (7.0–)7.8–12.8(–17.5) × (1.9–)2.1–3.2(–3.7) µm (n = 29), enteroblastic, phialidic, lageniform to cylindrical,

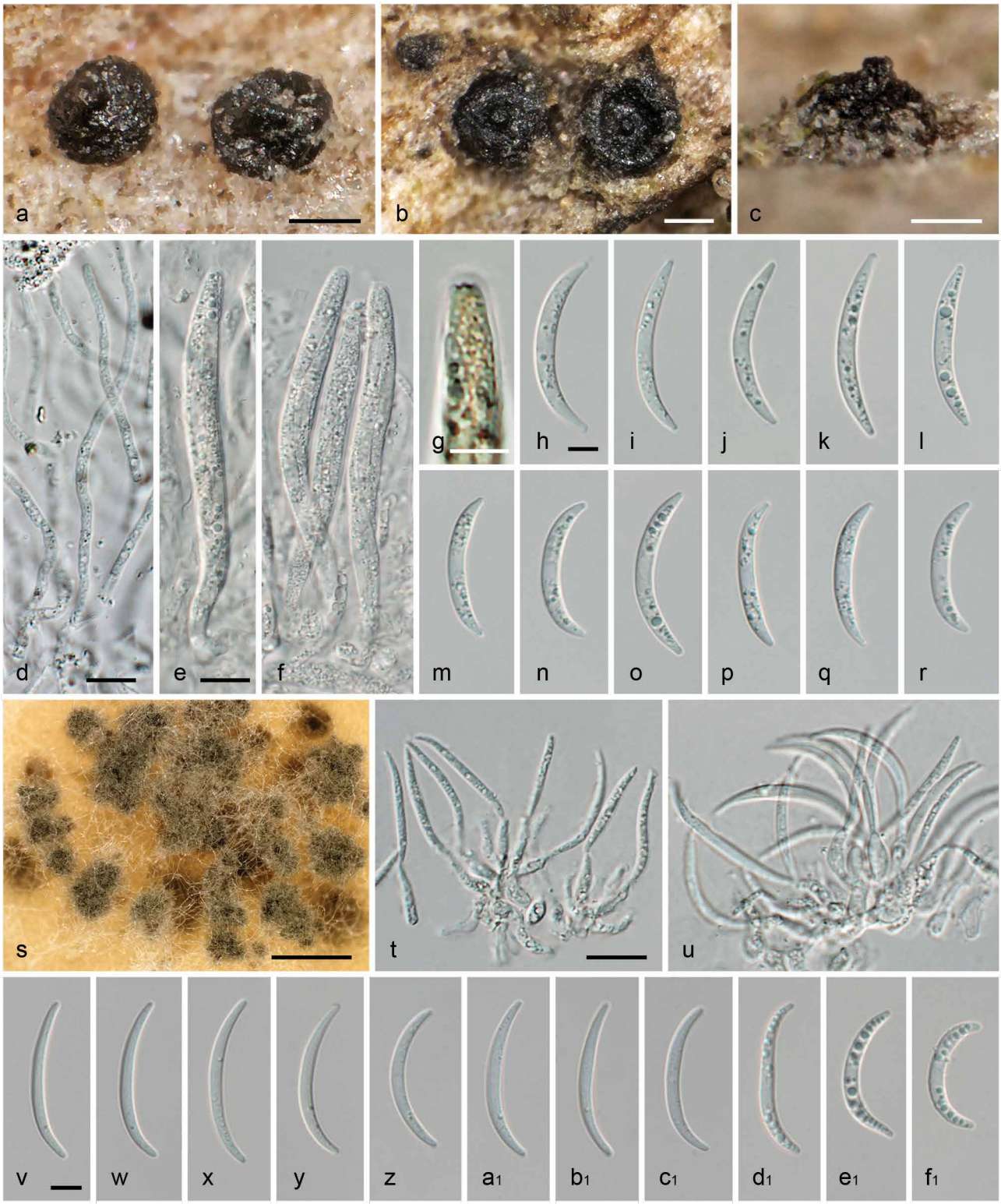

Fig. 8 *Leptosillia acerina*. a–b. Perithecia on bark (right ascoma in a. laterally collapsed, in b. horizontally collapsed and cupulate); c. side view of perithecium with apical papilla; d. paraphyses; e–f. asci; g. ascus tip in Lugol; h–r. vital ascospores; s. pycnidia in culture (CMD, isolation plate, 40 d); t–u. conidiophores, conidiogenous cells and conidia from pycnidia on natural substrate; v–c1. conidia from natural substrate; d1–f1. conidia from pycnidia in culture (CMD, isolation plate, 21 d). All in water, except where noted (a–b: WU 39995 (epitype); c, g, m–r, t–c1: WU 39998; d–f, h–l: WU 39997; s: CRA; d1–f1: CRA3). — Scale bars: a–c = 100 µm; d–f, t–u = 10 µm; g–r, v–f1 = 5 µm; s = 500 µm.

hyaline, smooth, arranged in dense terminal whorls of up to 6. *Conidia* (23–)26–29(–32) × (1.9–)2.0–2.4(–2.7) µm, l/w = (10.4–)11.4–13.5(–16.0) (n = 65), falcate, aseptate, hyaline, thin-walled, smooth, with subacute tapering ends, containing few guttules close to the wall.

Culture characteristics and asexual morph in culture — *Colony* on CMD at 16 °C reaching 37–58 mm diam after 58 d; first white, turning cream to greyish brown in the centre, with woolly aerial mycelium mostly in the colony centre, margin uneven, wavy, reverse light brown with darker brown centre, often with radial, irregularly wavy, lighter or darker lines, with age secreting a bright yellow diffusible pigment in agar. *Pycnidia* (180–)230–345(–400) µm diam (n = 20), immersed to almost superficial, black, single, aggregated to confluent, opening by an ostiole or by irregular rupture and exuding white masses of conidia. *Conidiophores* and *conidiogenous cells* similar to those from natural substrate. *Conidia* (18–)20–25(–28) × (2.0–)2.3–2.7(–3.0) µm, l/w = (7.0–)8.1–10.2(–12.5) (n = 54), falcate to lunate, asep-

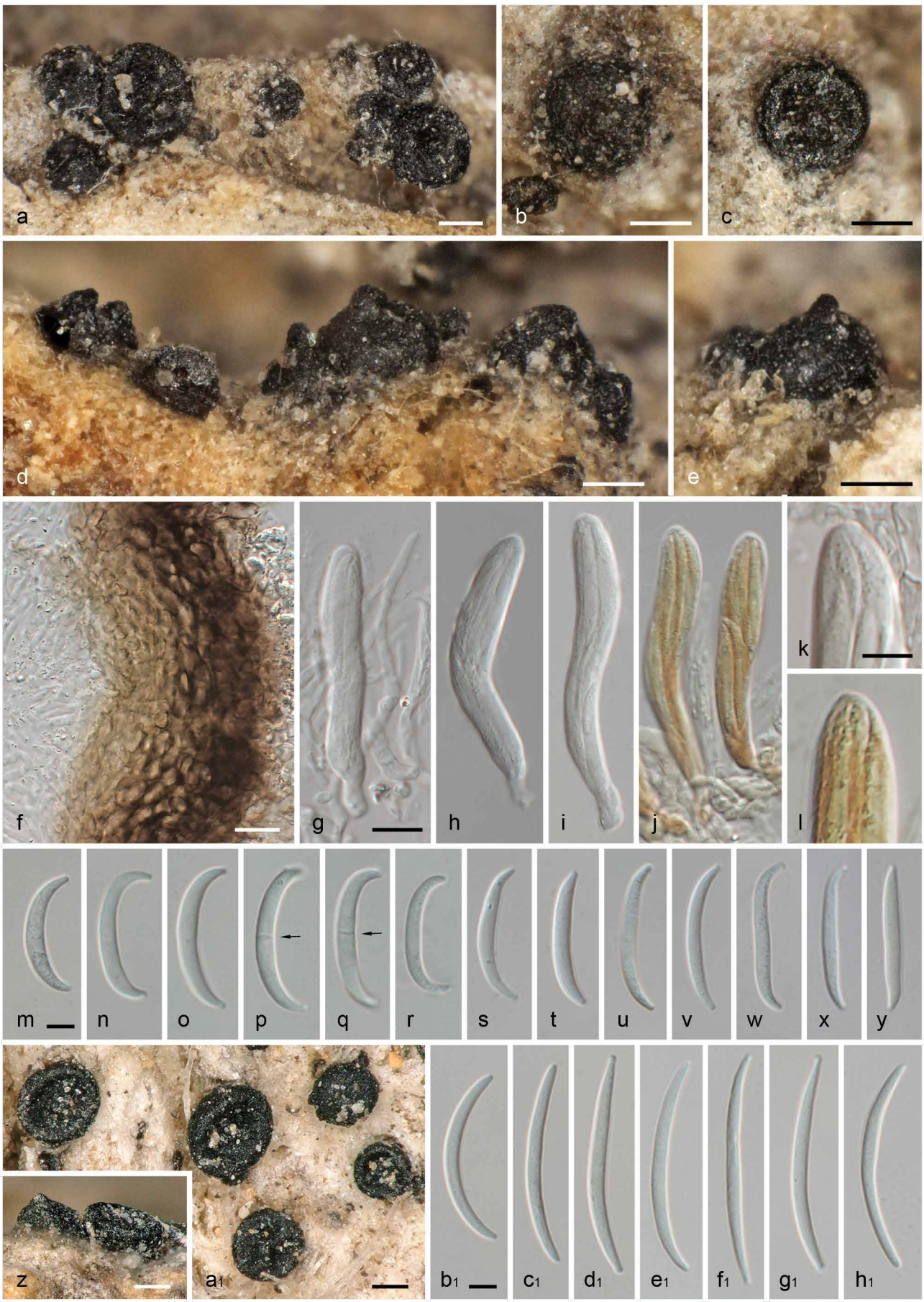

Fig. 9 a–y. *Leptosillia fusariospora* (GZU 000335714, isotype). a–c. Perithecia on bark (a, c. horizontally collapsed and cupulate); d–e. side view of perithecia with apical papilla; f. peridium in section; g–j. asci (g. with paraphysis, j. in Lugol after KOH pre-treatment); k, l. ascus tips (l. in Lugol after KOH pre-treatment); m–y. ascospores; arrows denoting septa. — z–h1. *Leptosillia* aff. *fusariospora* (NY 00270482). z, a1. Cupulate perithecia on bark in side (z) and surface (a1) view; b1–h1. ascospores. All in 3 % KOH, except where noted. — Scale bars: a–e, z–a1 = 100 µm; f–j = 10 µm; k–y, b1–h1 = 5 µm.

tate, hyaline, thin-walled, smooth, with subacute tapering ends, containing numerous guttules especially towards the ends.

Habitat & Host range — Only known from cork wings and outgrowths (the rhytidome) of living or dead branches of *Acer campestre*.

Distribution — Europe; known from Austria, Croatia and Germany (Aguirre-Hudson 1991, this study).

Additional specimens examined (all on cork wings of branches of *Acer campestre*). Austria, Niederösterreich, SE Gaaden, Am Tenneberg, 28 Jan. 2017, *H. Voglmayr* & *I. Greilhuber* (WU 39996, culture CRA3); Mödling, Richardshof, 5 Nov. 2016, *H. Voglmayr* & *I. Greilhuber* (WU 39997, culture CRA2); Pfaffstätten, near Heberlberg, 23 Apr. 2016, *H. Voglmayr* (WU 39998, culture CRA).

Notes — *Leptosillia acerina* is well characterised by its host, *Acer campestre*. It has so far been only found on cork wings of young living or recently dead branches, which are formed by young trees in open stands. Although the species has apparently not been recorded since the late 19th century and was only known from the type localities of the heterotypic synonyms (Aguirre-Hudson 1991), the current observations in eastern Austria indicate that, at least in Central Europe, it may be rather common in suitable habitats. This species has most likely been overlooked in mycological field studies.

Leptosillia fusariospora (Ellis & Everh.) Voglmayr & Jaklitsch, *comb. nov.* — MycoBank MB829931; Fig. 9

Basionym. *Coelosphaeria fusariospora* Ellis & Everh., J. Mycol. 4: 65. 1888.

Synonym. Leiosphaerella fusariospora (Ellis & Everh.) M.E. Barr, Mycotaxon 46: 62. 1993.

Typification. USA, Kansas, on bark of (living)? cottonwood trees (*Populus deltoides*), soc. *Teichospora kansensis*, without place and date, *G. Egeling*, comm. *J.W. Eckfeldt*, in Ellis & Everhart, N. Amer. Fungi Ser. 2 no. 1957 (NY 00883560, lectotype of *Coelosphaeria fusariospora* here selected, MBT 385917; GZU 000335714, K(M) 252230, K(M) 252231, NY 00883561, NY 00883562, NY 00883563 isolectotypes).

Ascomata perithecial, superficial to basally immersed in bark, (135–)160–205(–230) µm diam (n = 30), 90–190 µm high, black, shiny, smooth, scattered singly to gregarious, subglobose to hemispherical, circular from above, commonly horizontally collapsed and then cupulate, with a distinct central apical papilla c. 30–55 µm wide, 30–50 µm high. *Peridium* continuous, dark brown, becoming light brown to hyaline towards the centrum, 17–40 µm thick, of *textura angularis* composed of thick-walled, isodiametric to elongated cells 4–15 × 2–4 µm with dark brown walls, becoming thin-walled and subhyaline towards the centrum. *Hamathecium* composed of hyaline, smooth, thin-walled, septate, occasionally branched, 1.7–3.5 µm wide paraphyses embedded in an inamyloid gelatinous matrix; periphyses not observed. *Asci* (46–)51–68(–83) × (7.0–)8.0–9.5(–10.3) µm (n = 50), unitunicate, cylindrical, straight, curved to sinuous, thin-walled, containing 8 ascospores arranged biseriately or in two fascicles, with a short stipe, inamyloid and without a distinct apical apparatus. *Ascospores* (20–)24–30(–33) × (2.3–)2.7–3.3(–3.6) µm, l/w = (6.4–)7.7–10.2(–12.0) (n = 90), mostly fusiform to slightly curved with strongly curved to hooked ends, sometimes falcate to lunate, aseptate, occasionally becoming uniseptate at maturity, hyaline, thin-walled, smooth, with subacute tapering ends. *Asexual morph* not observed.

Habitat & Host range — With certainty known only from bark of living trunks of *Populus deltoides*; probably also on *Celtis occidentalis*.

Distribution — North America; with certainty only known from Kansas, the USA.

Additional specimens examined. USA, Kansas, Rockport, on bark of *Celtis orientalis*, Nov. 1893, *E. Bartholomew*, in Ellis & Everhart, N. Amer. Fungi Ser. 2 no. 3016 (K(M) 252322, NY 00270482).

Notes — *Leptosillia fusariospora* is well characterised by an ascospore shape similar to macroconidia of *Fusarium*, from which its species epithet was derived. It is similar to the European *L. acerina* in its horizontally collabent, cupulate ascomata and has aseptate ascospores of similar size; however, it differs by differently shaped ascospores occasionally becoming uniseptate at maturity, different hosts and distribution (North America vs Europe). Unfortunately, no cultures and DNA sequences are available for *L. fusariospora*, but both the morphological characteristics and the ecology of the species match with the genus *Leptosillia*, into which it is therefore combined.

Numerous copies of the type collection were distributed as Ellis & Everhart, N. Amer. Fungi Ser. 2 no. 1957, but to our knowledge no lectotype has yet been selected. In NY, where the Ellis collection is kept, there are four collections corresponding to the protologue, one (NY 00883560) labelled as holotype, two, bearing the label of Ellis & Everhart, N. Amer. Fungi Ser. 2 no. 1957 (NY 00883561, NY 00883562), as isotypes, and one (NY 00883563) without a type label but with the same data given for the other collections, but with a collection date Oct. 1887. The latter also represents an isotype as it was collected ahead of the publication of the taxon, and it includes an original note with exactly the same ascospore and ascus measurements as given in the protologue. Based on preservation, the isotype specimen NY 00883560 of the Ellis collection is here selected as lectotype. Most of the isotype specimens investigated also contain ascomata of *Teichospora kansensis*.

The collection from *Celtis occidentalis* distributed as *Coelosphaeria fusariospora* in Ellis & Everhart, N. Amer. Fungi Ser. 2 no. 3016 is here only tentatively attributed to the species. It has distinctly longer ascospores ((28–)33–41(–44) × (2.2–)2.5–2.9(–3.1) µm, l/w = (10.8–)12.1–15.3(–16.7) (n = 25)) of a different shape, being narrowly fusiform to falcate but lacking strongly curved to hooked ends (Fig. 9b1–h1), and also the ascomata are distinctly superficial (Fig. 9z, a1) and somewhat larger ((183–)206–276(–361) µm diam (n = 60)). The specimen may therefore represent a distinct *Leptosillia* species, but fresh collections and sequences are necessary for a detailed evaluation.

The treatment of *Coelosphaeria fusariospora* by Barr (1993) is confusing: first she combined it in *Leiosphaerella*, but a few pages later she considered the species to be conspecific with *Cresporhaphis rhoina*. Our detailed re-examination of type specimens of *Coelosphaeria fusariospora* and *Cresporhaphis rhoina* did not confirm this synonymy, but revealed them as two different, unrelated species. While asci, ascospores and also the corticolous ecology of *Coelosphaeria fusariospora* are in full agreement with *Leptosillia*, *Cresporhaphis rhoina* differs by an amyloid apical ascus ring, mostly fusoid to curved ascospores of irregular shapes and by growth on dead wood. The latter is therefore not considered to be congeneric with *Leptosillia* (see notes under *C. rhoina* below).

Leptosillia macrospora (Eitner) Voglmayr & Jaklitsch, *comb.* & *stat. nov.* — MycoBank MB829932; Fig. 10

Basionym. *Leptorhaphis quercus* f. *macrospora* Eitner, Jahresber. Schles. Ges. Vaterl. Cult. 78: 25. 1901 ‘1900’.

Synonyms. Cresporhaphis macrospora (Eitner) M.B. Aguirre, Bull. Brit. Mus. (Nat. Hist.), Bot. 21 (2): 149. 1991.

Liberomyces macrosporus Pažoutová et al., Mycologia 104: 201. 2012.

Typification. Poland, Silesia, Nimptsch, Klein Ellguth, on *Quercus robur*, 12 Apr. 1892, *E. Eitner* (W 19701, lectotype of *Leptorhaphis quercus* f. *macrospora* selected by Aguirre-Hudson 1991). – Austria, Niederösterreich, Schönfeld, Wacholderheide NE of the golf course, on bark of living trunks of *Quercus petraea*, 5 May 2016, *H. Voglmayr* & *I. Greilhuber* (WU 39999, epitype of *Leptorhaphis quercus* f. *macrospora* here designated (MBT 385918); ex epitype culture CRM2 = CBS 143627).

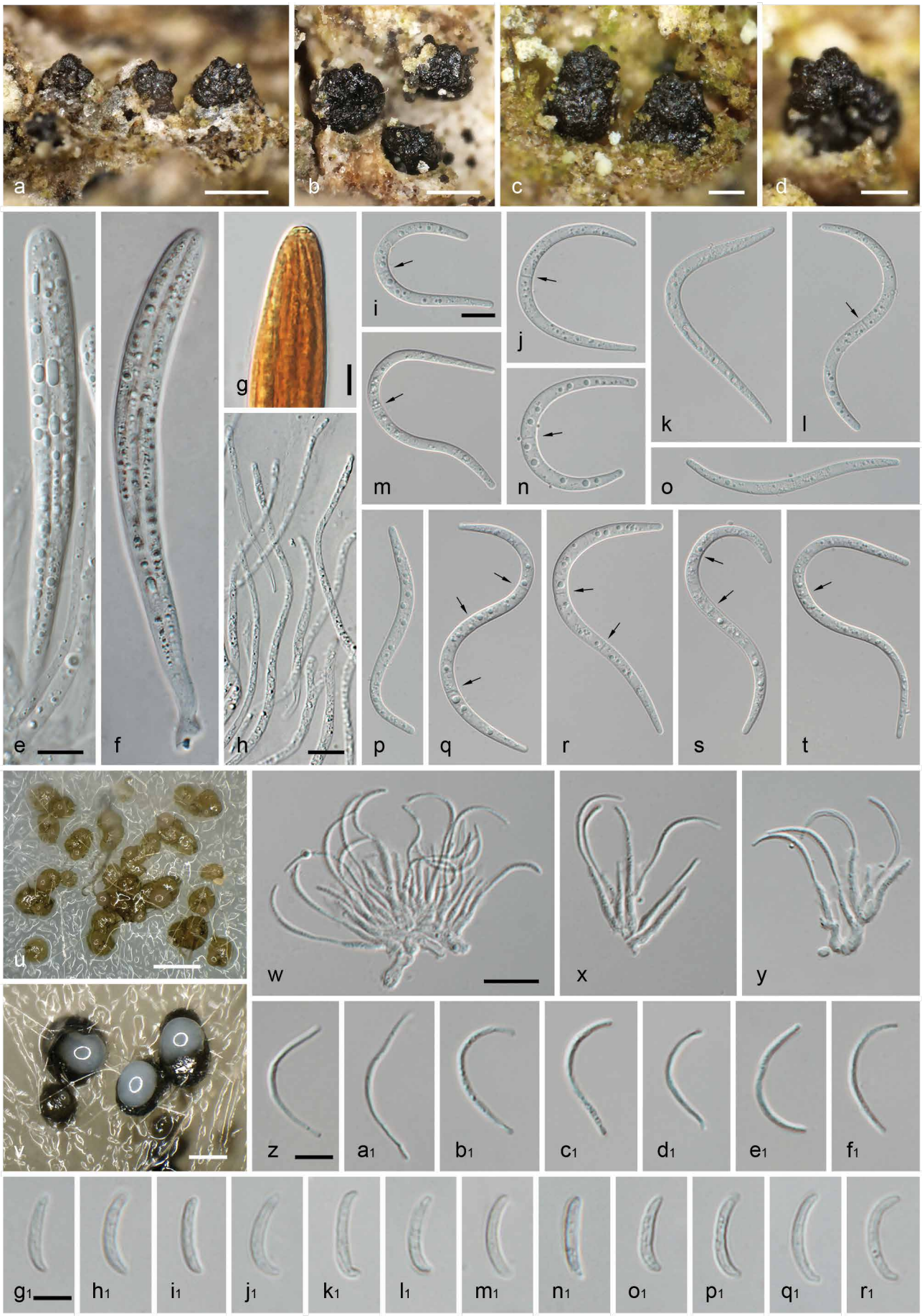

Fig. 10 *Leptosillia macrospora*. a–d. Perithecia on bark; note the stellate or sulcate structures on the apical papillae; e–f. asci in 3 % KOH; g. ascus tip in Lugol; h. paraphyses; i–t. vital ascospores; arrows denoting septa; u–v. pycnidia and conidial drops in culture (CMD, isolation plate, 7 d); w–y. conidiophores, conidiogenous cells and conidia from pycnidia on natural substrate; z–f1. conidia from natural substrate; g1–r1. conidia from pycnidia in culture (CMD, 6 mo). All in water, except where noted (a–b, i–l, n–p, w–f1: WU 39999 (epitype); c–f: WU 40004; g–h, m, q–t: WU 40000; u–v, g1–r1: CRM2). — Scale bars: a–b, u = 200 µm; c–d, v = 100 µm; e–f, h–t, w–y = 10 µm; g, z–r1 = 5 µm.

Ascomata perithecial, half-immersed in bark to superficial, (170–)200–255(–275) µm wide (n = 46), (210–)220–270(–280) µm high (n = 6), black, smooth, scattered singly, sometimes gregarious, pyriform, circular from above, sometimes laterally collapsed, with a central apical papilla laterally enlarged by stellate or sulcate structures on the surface. *Peridium* continuous, dark brown, becoming hyaline towards the centrum, 20–30 µm thick, of a *textura angularis* composed of thin-walled, isodiametric to elongated cells 4–8 µm diam with subhyaline to dark brown walls. *Hamathecium* composed of hyaline, smooth, thin-walled, septate, occasionally branched, 1.5–3.3 µm wide paraphyses embedded in an inamyloid gelatinous matrix; periphyses not observed. *Asci* (94–)104–120(–135) × (8.8–)9.5–11.5(–13.0) µm (n = 46), unitunicate, clavate to cylindrical, curved, thin-walled, containing 8 ascospores arranged in fascicles, with a short stipe, inamyloid and without a distinct apical apparatus. *Ascospores* (53–)65–93(–109) × (3.0–)3.5–4.5(–5.0) µm, l/w = (12.8–)16.1–24.2(–31.3) (n = 82), variable in shape from sinuous, sigmoid, semicircular to hook-shaped, at maturity 1–3 septate, hyaline, thin-walled, smooth, with narrowly rounded ends, multiguttulate when vital.

Pycnidia scattered on bark, black, similar to ascomata except for smaller size, c. 100–150 µm diam. *Peridium* continuous, dark brown, c. 10 µm thick, composed of few layers of thin-walled dark brown cells 3–5.5 µm diam. *Conidiophores* short, reduced, hyaline, smooth, branched up to two times, composed of short, cylindrical to almost isodiametric cells arising from the inner wall of the pycnidium. *Conidiogenous cells* (2.0–)7.3–12.0(–17.5) × (0.9–)1–1.9(–2.5) µm (n = 83), enteroblastic, phialidic, lageniform to cylindrical, hyaline, smooth, arranged in dense terminal whorls. *Conidia* (16–)18–23(–24) × (0.8–)0.9–1.1(–1.2) µm, l/w = (16.3–)17.6–23.7(–26.1) (n = 20), filiform, curved, aseptate, hyaline, thin-walled, smooth, containing few guttules when vital.

Culture characteristics and asexual morph in culture — *Colony* on CMD at 16 °C reaching 38–56 mm diam after 58 d; variable in colour and growth depending on the strain, greyish brown to black, sometimes with cream sectors, with sparse, short to woolly aerial mycelium, margin often strongly uneven, wavy, reverse light brown to black. *Pycnidia* (85–)100–160(–210) µm diam (n = 24), immersed to almost superficial, dark brown to black, single, aggregated to confluent, opening by an ostiole or irregular rupture and exuding white masses of conidia. *Ostiole* circular or oval, 20–40 µm wide; ostiolar neck 10–30 µm high. *Peridium* of an outer layer of *textura intricata* of dark brown, thick-walled cells, and an inner layer of *textura angularis* of lighter brown cells, basal parts of the peridium subhyaline, consisting of thin-walled cells. *Conidiophores* simple or irregularly branched, hyaline, smooth, arising from the inner wall of the entire conidioma. *Conidiogenous cells* of two types: a) (7–)8(–10) × 1.5–1.7 (–2) µm, holoblastic with sympodial proliferation, bearing allantoid conidia; b) similar to those observed on the natural substrate, enteroblastic, phialidic, bearing filiform conidia. *Conidia* of two types: a) holoblastic, (7.0–)9.7–12.5 (–15.2) × (1.3–)1.6–2.0(–2.2) µm, l/w = (4.5–)5.4–7.0(–8.5) (n = 150), allantoid, often typically curved on the proximal end, hyaline, smooth; b) enteroblastic similar to those observed on the natural substrate, (14–)17(–21) × 1 µm, filiform, curved.

Habitat & Host range — On bark of living trunks of various *Quercus* species (Aguirre-Hudson 1991, this study); in one occasion isolated from healthy phloem of living *Ulmus laevis* (Pažoutová et al. 2012).

Distribution — Europe; known from Austria, Croatia, Czech Republic, Germany, Hungary, Poland, Sweden, Switzerland (Aguirre-Hudson 1991, Otte et al. 2017, this study).

Additional specimens examined (all on bark of living trunks of *Quercus* spp.). Austria, Burgenland, Purbach, Purbacher Heide, on *Quercus pubescens*, 1 Apr. 2017, *H. Voglmayr* & *I. Greilhuber* (WU 40000); Niederösterreich, Stopfenreuth, Donauauen, on *Quercus robur*, 25 Mar. 2017, *H. Voglmayr* & *I. Greilhuber* (WU 40001); Oberösterreich, St. Willibald, between Oberantlang and Landersberg, on *Quercus robur*, 22 May 2016, *H. Voglmayr* (WU 40002, culture CRM4). – Germany, Bayern, Bernried am Starnberger See, park of Schloss Hohenried, on *Quercus robur*, 12 Sept. 2016, *H. Voglmayr* & *W. Jaklitsch* (WU 40003, culture CRM7); Niedersachsen, Hamburg (near), Buxtehude, by roadside, on *Quercus robur*, 30 Aug. 2015, *H.G. Wagner* (K(M) 199846); Hannover, Bückeburger Allee, on *Quercus robur*, 26 Apr. 2016, *H.G. Wagner* (WU 40004, culture CRM1); Thüringen, NE of Eisenach, W of Wolfsbehringen, on the wayside of an old oak forest, on young *Quercus robur*, 13 June 2008, *H.G. Wagner* (K(M) 158044); Zechsteingürtel, Kyffhäuser, N Bad Frankenhausen, Georg-Höhe, on *Quercus* sp., 12 Mar. 2015, *J. Eckstein 38831* (K(M) 201601).

Notes — At least in Central Europe, *Leptosillia macrospora* seems to be widely distributed and probably not uncommon on young oak trees, sometimes even found on trees planted by roadsides in towns and cities. All our recent collections were from bark crevices of oak trunks of 10–30 cm diam.

Leptosillia macrospora might be confused with several other unrelated fungi (lichenised or not) also with colourless, multiseptate, filiform ascospores; e.g., *Rhaphidicyrtis trichosporella*, also found on oaks, which differs by bitunicate asci and hamathecium gel turning deep blue in Lugol's Iodine pretreated with 10 % KOH. There are also similarities to some species of the genus *Pseudosagedia*, and in particular with *P. leptospora*, but in this the ascospores are at least 7-septate, the ascomata present an additional involucrellum over the exciple, and the thallus is clearly lichenized with *Trentepohlia*. Berger & Priemetzhofer (2000) reported the species from Austria growing on *Tilia cordata* (Donautal, Oberösterreich, Berger 9578). We requested the material for study, but instead we received another collection from the same area, also labelled as *Creporhaphis macrospora*, but growing on *Malus* sp. (Berger 12951). Examination of this voucher revealed a fungus with filiform, multiseptate ascospores (75–90 × 3.5 µm) but with distinct fissitunicate asci. This collection is probably a new species of the genus *Lophiostoma* (sensu Hirayama & Tanaka 2011), related to *Lophiostoma subcutanea* (see Huhndorf 1992: 503–504; Fig. 2), which is also found on bark of *Rosaceae* but has smaller ascospores (25–29 × 3–3.5 µm).

Based on sequence data and morphology, *Liberomyces macrosporus* represents the asexual morph of *Leptosillia macrospora*, and is therefore a synonym of the latter. The description of the asexual morph in pure culture was modified from the description of Pažoutová et al. (2012), and that of the pycnidia from natural substrate was adapted from the description in Aguirre-Hudson (1991). In the present study, pycnidia on the natural substrate could be found in only one occasion, and the pycnidium investigated only produced enteroblastically formed, filiform conidia; however, their size agrees well with those recorded from culture and given in Aguirre-Hudson (1991).

Leptosillia muelleri (Duby) Voglmayr & Jaklitsch, *comb. nov.* — MycoBank MB829933; Fig. 11, 12

Basionym. *Sphaeria muelleri* Duby, in Rabenhorst, Klotzsch. Herb. Vivum. Mycol., Edn 2: no. 642. 1858.

Synonyms. Cresporhaphis muelleri (Duby) M.B. Aguirre, Bull. Brit. Mus. (Nat. Hist.), Bot. 21: 151. 1991.

Leptosphaeria muelleri (Duby) Auersw., in Gonnermann & Rabenhorst, Mycol. Eur. Pyren. 5–6: t. 12, f. 167. 1869.

Psilosphaeria muelleri (Duby) Cooke (as '*mulleri*'), Grevillea 16 (no. 78): 50. 1887.

Zignoëlla muelleri (Duby) Sacc. & Traverso, Syll. Fung. (Abellini) 20: 1170. 1911.

Cytosporina notha (Sacc.) Died., Krypt.-Fl. Brandenburg (Leipzig) 9: 545. 1914.

Harpostroma nothum (Sacc.) Höhn. (as '*notha*'), Mitt. Bot. Inst. Tech. Hochsch. Wien 5: 112. 1928.

Leptosillia notha Höhn., Mitt. Bot. Inst. Tech. Hochsch. Wien 5: 111. 1928.

Leptorhaphis aggregata Eitner, Jahresber. Schles. Ges. Vaterl. Cult. 78 (2b Abth.): 25. 1901 [1900].

Leptorhaphis wienkampii var. *aggregata* (Eitner) Keissl., Rabenh. Krypt.-Fl. 9, 1: 246, f. 82. 1937.

Typification. France, Haute Savoie, Les Contamines, on bark of *Acer*, without date, *J. Müller Argoviensis*, in Rabenhorst, Klotzsch. Herb. Vivum. Mycol. Ed. II no. 642 (K(M) 252333, lectotype of *Sphaeria muelleri* selected by Aguirre-Hudson 1991; K(M) 252334, isolectotype). – Germany, Erfurt, on bark of *Acer pseudoplatanus*, 15 Apr. 1905, *H. Diedicke*, *Herb. A. Höhnel no. 4269* (FH 00304540, holotype of *Leptosillia notha*). – Austria, Oberösterreich, St. Willibald, Oberantlang N Siegl, on bark of *Acer pseudoplatanus*, 22 May 2016, *H. Voglmayr* (WU 40005, epitype of *Sphaeria muelleri* (MBT 385919) and *Leptosillia notha* (MBT 385920) here designated; ex epitype culture CRM3 = CBS 143628). – France, Saintes, on *Acer pseudoplatanus*, without date, *P. Brunaud no. 67*, Herb. Saccardo (PAD, holotype of *Septoria notha*).

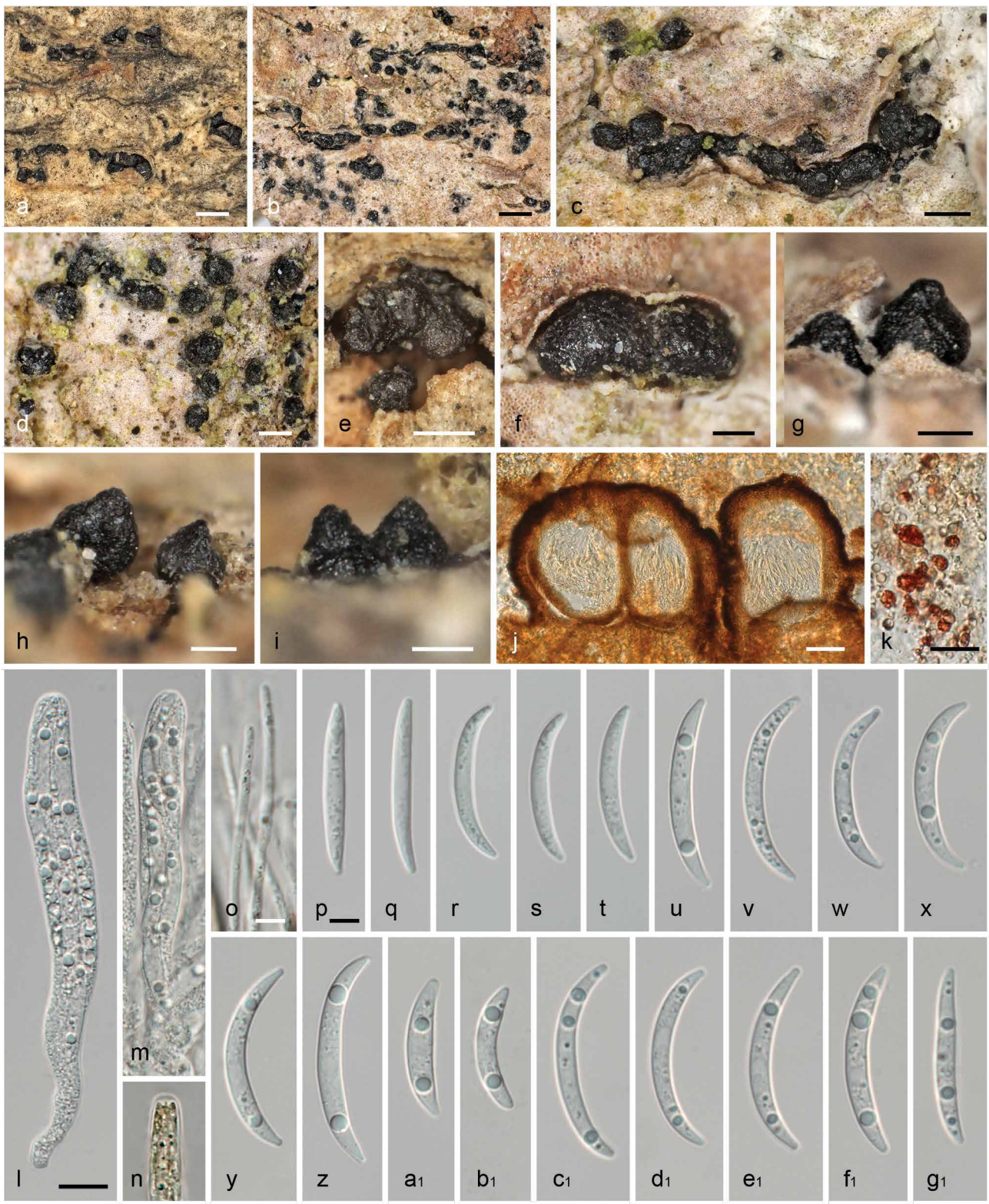

Fig. 11 *Leptosillia muelleri*, sexual morph. a–i. Single and confluent perithecia on bark in surface (a–f) and side (g–i) view; j. vertical section through pseudostroma with perithecia; k. strongly dextrinoid granular hamathecial exudates in Lugol after KOH pre-treatment; l–m. asci; n. ascus tip in Lugol; o. paraphyses; p–g1. ascospores (p–t. dead, u–g1. vital). All in water, except where noted (a, e, j, p–t: FH 00304540 (holotype of *Leptosillia notha*); b–c, f–g, l, o, u, y–z: WU 40005 (epitype); d, h, n, v–x: WU 40006; i, m, a1–b1: WU 40007; k, c1–g1: WU 40008). — Scale bars: a–b = 500 µm; c–e = 200 µm; f–i = 100 µm; j = 50 µm; k–n = 10 µm; o–g1 = 5 µm.

Ascomata perithecial, embedded in a pseudostroma, emerging from cracks on the surface of bark scales, (100–)140–210(–260) µm diam (n = 67), black, matt, smooth, rarely scattered singly and pyriform, but usually confluent and then irregular in shape and c. 1 mm long, immersed in bark to half of their height, not collapsing, with an indistinct to distinct central apical papilla. *Peridium* continuous, of a *textura angularis*, composed of an outer dark brown to black, 10–30(–45) µm thick layer of thin-walled isodiametric cells 2.5–5.5 µm diam with dark brown walls, forming a pseudostroma surrounding the inner wall, and an inner, 12–20 µm thick subhyaline to pale brown layer corresponding to the perithecium wall of (sub)hyaline to

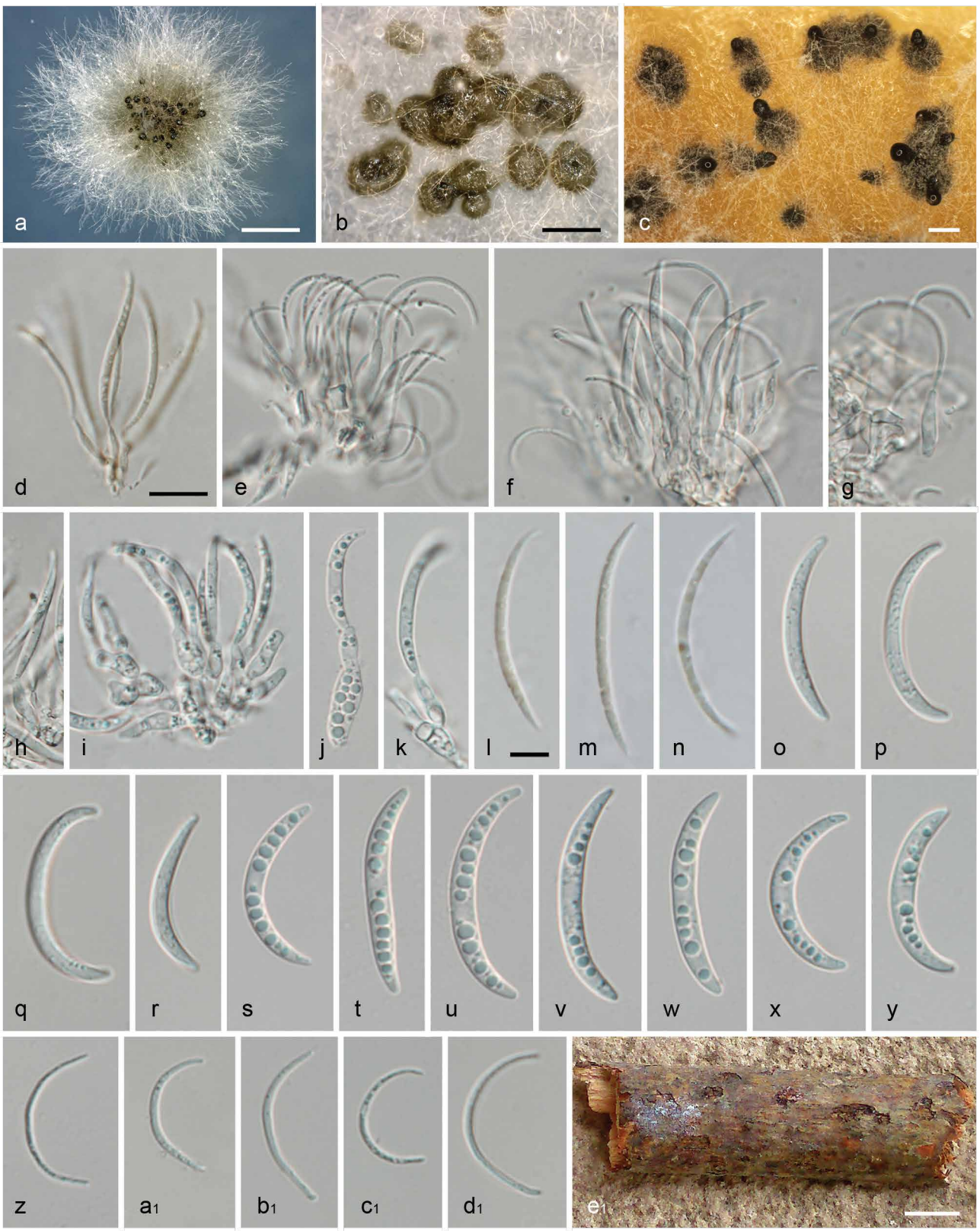

Fig. 12 a–d1. *Leptosillia muelleri*, asexual morph. a–c. Pycnidia on CMD isolation plates (a–b. 7 d; c. 37 d); d–h. conidiophores, conidiogenous cells and conidia from pycnidia on natural substrates; i–k. conidiophores, conidiogenous cells and conidia from pycnidia in pure culture (i, k. CMD 8 d; j. CMD 19 d); l–r, z–d1. conidia from natural substrate (l–n. dead; o–r, z–d1. vital); s–y. vital conidia from pycnidia in culture on CMD (s–u. 19 d; v–y. 8 d). All in water, except d, l–n from permanent slide (a–b, i, v–x: CRM3 (ex-epitype culture); c, j, s–u: CRM; d, l–n: FH 00304540 (holotype of *Leptosillia notha*); e–h, o–r, z–d1: WU 40005 (epitype); k, y: CRM6). e1. *Septoria notha* (holotype, PAD) — Scale bars: a = 1 mm; b–c = 200 µm; d–k = 10 µm; l–d1 = 5 µm; e1 = 3 mm.

light brown cells similar to those of the outer layer but slightly smaller and sometimes radially compressed changing into a *textura prismatica*. *Hamathecium* composed of hyaline, smooth, thin-walled, septate, occasionally branched, 1–3 µm wide paraphyses embedded in an inamyloid gelatinous matrix; with hyaline, refractive, strongly dextrinoid granular exudates turning amber-red in Lugol; periphyses not observed. *Asci* (65–)75–100(–107) × (7.2–)8.0–9.5(–11.3) µm (n = 25), unitunicate, cylindrical, slightly curved to sinuous, thin-walled, containing 8 bi- or triseriately arranged ascospores, with a short stipe, without a distinct apical apparatus, inamyloid but a narrow, short pore visible in Lugol. *Ascospores* (20–)25–33(–38) × (2.0–)2.8–3.7(–4.7) µm, l/w = (5.6–)7.7–10.1(–12.0) (n = 98), fusoid, lunate to falcate, aseptate, hyaline, thin-walled, smooth, with subacute to narrowly rounded tapering ends, when vital containing 2–3 large and numerous small guttules especially towards the ends.

Pycnidia on bark usually confluent, black, practically indistinguishable from ascomata. *Conidiophores* short, hyaline, smooth, simple or irregularly branched, arising from the inner wall of the pycnidium. *Conidiogenous cells* (6.8–)8.0–15.2(–27.5) × (1.2–)1.6–3.6(–5.3) µm (n = 72), lageniform to cylindrical, of two types interspersed within the same pycnidium: a) holoblastic with sympodial proliferation, bearing falcate conidia; b) enteroblastic, phialidic, bearing narrower, filiform conidia. *Conidia* of two types: a) holoblastic, 21–27(–32) × 2.0–2.5(–3.0) µm, l/w = (8.8–)9.5–11.8(–13.0) (n = 27), falcate, hyaline, smooth, with narrowly rounded ends, with few small guttules when vital; b) enteroblastic, (19–)23–28(–31) × (0.8–)0.9–1.2(–1.4) µm, l/w = (16.5–)19.9–29.0(–34.6) (n = 33), filiform, curved to semicircular.

Culture characteristics and asexual morph in culture — *Colony* on CMD at 16 °C reaching 50–55 mm diam after 58 d; first white, turning cream to greyish brown in the centre, with white woolly aerial mycelium, reverse cream, dark greyish brown in the centre, with age secreting a deep yellow diffusible pigment in agar. *Pycnidia* (115–)145–330(–500) µm diam (n = 114), immersed to almost superficial, black, single, aggregated to confluent, opening by an ostiole and exuding white masses of conidia. *Conidiophores* short, hyaline, similar to those from natural substrate. *Conidiogenous cells* holoblastic, similar to those described from natural substrate. *Conidia* (20–)24–29(–31) × (2.0–)2.5–3.3(–3.5) µm, l/w = (7.0–)8.0–10.1(–12.0) (n = 88), nearly straight, falcate, lunate to hook-shaped, aseptate, hyaline, thin-walled, smooth, with narrowly rounded tapering ends, containing numerous large guttules.

Habitat & Host range — Only known from bark scales of mature living trees of *Acer pseudoplatanus*.

Distribution — Europe; known from Austria, Czech Republic, France, Germany, Poland, Switzerland (Aguirre-Hudson 1991, this study).

Additional specimens examined (all on bark scales of mature living trunks of *Acer pseudoplatanus*). Austria, Kärnten, St. Margareten im Rosental, Oberdörfl, at Nagu, 10 Apr. 2016, *H. Voglmayr* & *W. Jaklitsch* (WU 40006; culture CRM); Niederösterreich, Lunz am See, at Mittersee, 10 May 2016, *H. Voglmayr* (WU 40007; culture CRM6); Puchberg am Schneeberg, Sonnleiten, Wasserfallweg, 5 Aug. 2017, *H. Voglmayr* & *I. Greilhuber* (WU 40008). – Czech Republic, Bohemia, Petrovice u Sušice, E Chamutice, 1 June 2018, *H. Voglmayr* & *M. Greilhuber* (WU 40009).

Notes — The holotype of *Leptosillia notha*, a holomorphic collection, from the Höhnel herbarium deposited in FH morphologically resembles our recent collections and the type of the earlier name *Sphaeria muelleri*. Remarkably, in the conidiomata observed on the natural substrate of the epitype two types of conidia are present: falcate and filiform ones, which are formed holoblastically and enteroblastically, respectively. However, in pure culture only holoblastical multiguttulate conidia were found; these were somewhat wider than those observed on the natural substrate. In a permanent mount of conidiomatal sections attached to the holotype, only phialides with filiform conidia were seen, with conidial sizes only slightly wider ((22–)26–31(–34) × (1.3–)1.4–1.7(–1.8) µm (n = 25)); this, however, may be due to the mounting medium. To preserve the holotype, we did not make new preparations of the asexual morph.

Diedicke (1915) identified the asexual morph on the holotype collection of *Leptosillia notha* as *Septoria notha* and recombined the species as *Cytosporina notha*. Subsequently, Höhnel (1928) established the monotypic genus *Harpostroma* for the latter, but challenged the conspecificity with Saccardo's *Septoria notha*. We agree that this conspecificity is doubtful. The type specimen of *Septoria notha* is extant in PAD, and although it could not be microscopically investigated, no structures resembling *Leptosillia notha* were seen on the specimen under the stereomicroscope. Also the ecology does not quite fit, as the substrate is a thin, corticated branch of c. 6 mm diam (Fig. 12e1), while *L. notha* is confined to bark scales of old living trunks. In the original description (Saccardo 1880), the host of *Septoria notha* is erroneously given as *Acer platanoides*; it is here re-identified as *Acer pseudoplatanus* based on bark and wood characters of the type specimen. This is in line with the fact that Saccardo (1880) assumed a connection with *Diaporthe hystrix*, a species commonly known from *Acer pseudoplatanus* but not from *A. platanoides* (Wehmeyer 1933).

Leptosillia pinicola (Samp.) Voglmayr & Jaklitsch, *comb. nov.* — MycoBank MB829934; Fig. 13

Basionym. Leptorhaphis pinicola Samp., Bolm Soc. Broteriana, Coimbra, sér. 2 2: 163. 1924 (1923).

Synonym. Cresporhaphis pinicola (Samp.) M.B. Aguirre, Bull. Brit. Mus. (Nat. Hist.), Bot. 21: 152. 1991.

Typification. Portugal, Estremadura, Sierra de Sintra, Castelo dos Mouros, on bark of *Pinus* sp., 11 Apr. 1943, *C. Tavares* (LISU 511, neotype designated by Aguirre-Hudson 1991; UPS L-074953!, isoneotype).

Ascomata perithecial, superficial on bark, (150–)180–230 (–280) µm wide (n = 32), black, shiny, smooth, scattered singly, sometimes gregarious, globose to pyriform, circular from above, with an indistinct central apical papilla. *Peridium* continuous, dark brown, becoming hyaline towards the centrum, c. 20 µm thick, of *textura angularis* composed of thick-walled, isodiametric to slightly elongated cells 3.5–5.5 µm diam with dark brown walls, towards the centrum becoming a *textura angularis-prismatica* of thinner-walled pale brown to subhyaline cells. *Hamathecium* composed of hyaline, smooth, thin-walled, septate, occasionally branched, 1.5–2.3 µm wide paraphyses embedded in an inamyloid gelatinous matrix; periphyses of hyaline, smooth, thin-walled, 1.5–2 µm wide hyphae. *Asci* (74–)78–89(–95) × (9.5–)9.8–11.0(–11.7) µm (n = 24), unitunicate, cylindrical to fusoid, usually slightly curved, thin-walled, containing 8 ascospores arranged in fascicles, with a short stipe, inamyloid and without a distinct apical apparatus. *Ascospores* (35–)44–58 (–65) × (1.8–)2.4–3.0(–3.5) µm, l/w = (14.1–)16.2–21.7 (–23.7) (n = 20), acicular, often slightly curved, 5–11-septate, not constricted at the septa, hyaline, thin-walled, smooth.

Notes — Only two collections from the type locality in Portugal (Sintra, near Lisbon; Aguirre-Hudson 1991), dating back to the first half of the 20th century, are confirmed here as belonging to *Leptosillia pinicola*. Unfortunately, the species could not be recollected by the first author despite extensive search on the bark of various pine species at and near the type locality. Despite the lack of fresh material for sequencing, morphologically the species fits well in the genus *Leptosillia*. The current

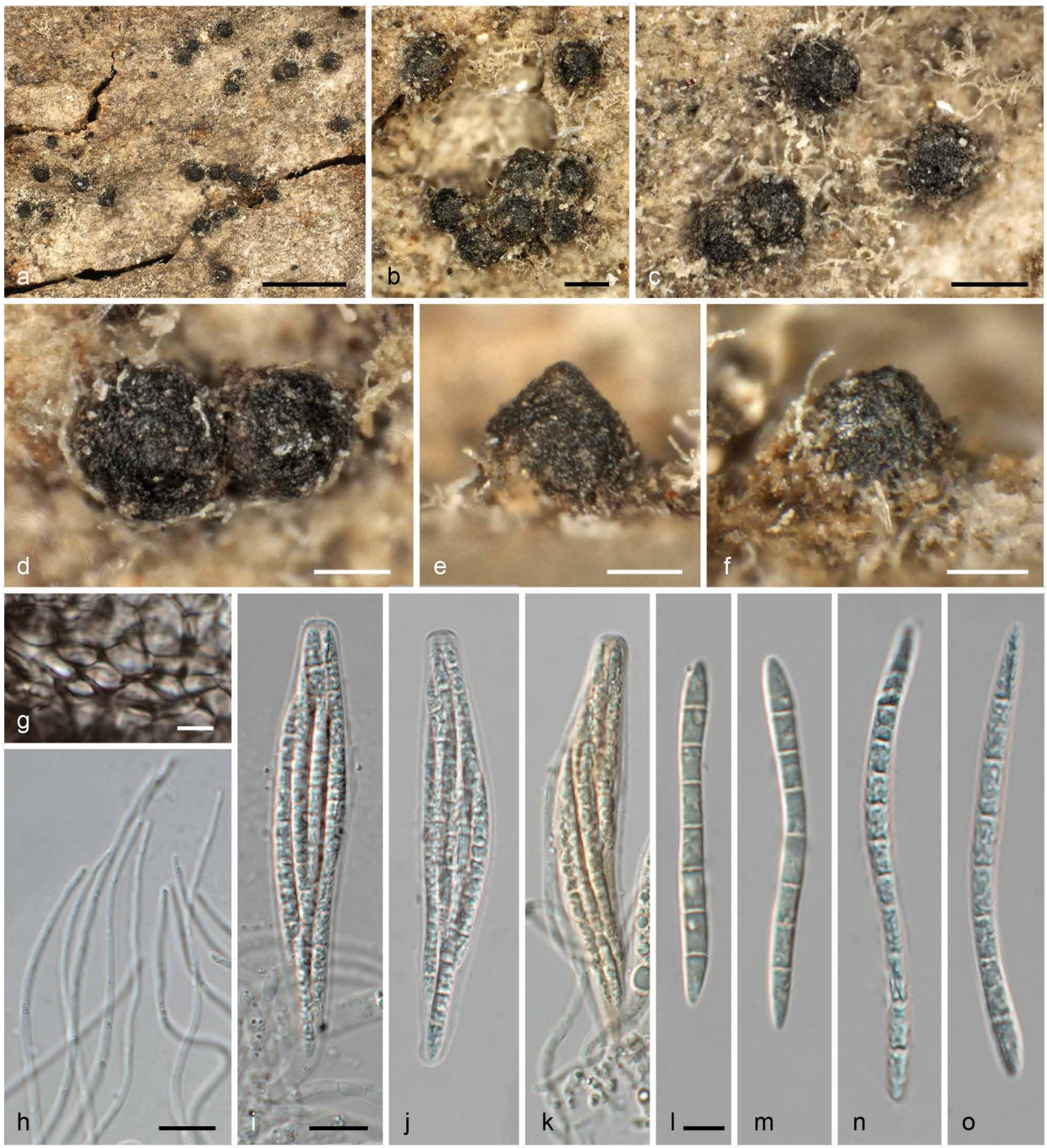

Fig. 13 *Leptosillia pinicola* (UPS L-074953, isoneotype). a–f. Single and gregarious perithecia on bark in surface (a–d) and side (e–f) view; g. peridium in section; h. paraphyses; i–k. asci (k in Lugol); l–o. ascospores. All in 3 % KOH, except where noted. — Scale bars: a = 1 mm; b–c = 200 µm; d–f = 100 µm; g, l–o = 5 µm; h–k = 10 µm.

description and illustrations are based on the isoneotype specimen from UPS, with few additions from Aguirre-Hudson (1991).

The species (as *Cresporhaphis pinicola*) has been cited from Austria by Berger et al. (1998) from bark of *Prunus avium*, and from Lithuania by Motiejūnaitė (2007) from bark of *Berberis* sp. Re-examination of the latter has confirmed that the material (K(M) 117899) is not conspecific with the type of *Leptosillia pinicola* because the ascospores are longer and more slender (62–78 × 2–3 µm), and arranged in a single fascicle in the ascus. This collection might yet represent a new species of *Leptosillia*, but DNA studies will be needed to confirm this. It is also unlikely that the material recorded from Austria is conspecific to *L. pinicola* due to the unrelatedness of the host, but we had no opportunity to study the collection.

Leptosillia pistaciae (Voglmayr et al.) Voglmayr, *comb. nov.* — MycoBank MB829935

Basionym. *Liberomyces pistaciae* Voglmayr et al., Mycokeys 40: 41. 2018.

Notes — In the current phylogenetic analyses this recently described serious canker pathogen of pistachio (*Pistacia vera*) is placed within *Leptosillia*, which necessitates a generic transfer. So far, no sexual morph is known for this species. For morphological description, illustrations and pathogenicity, see Vitale et al. (2018).

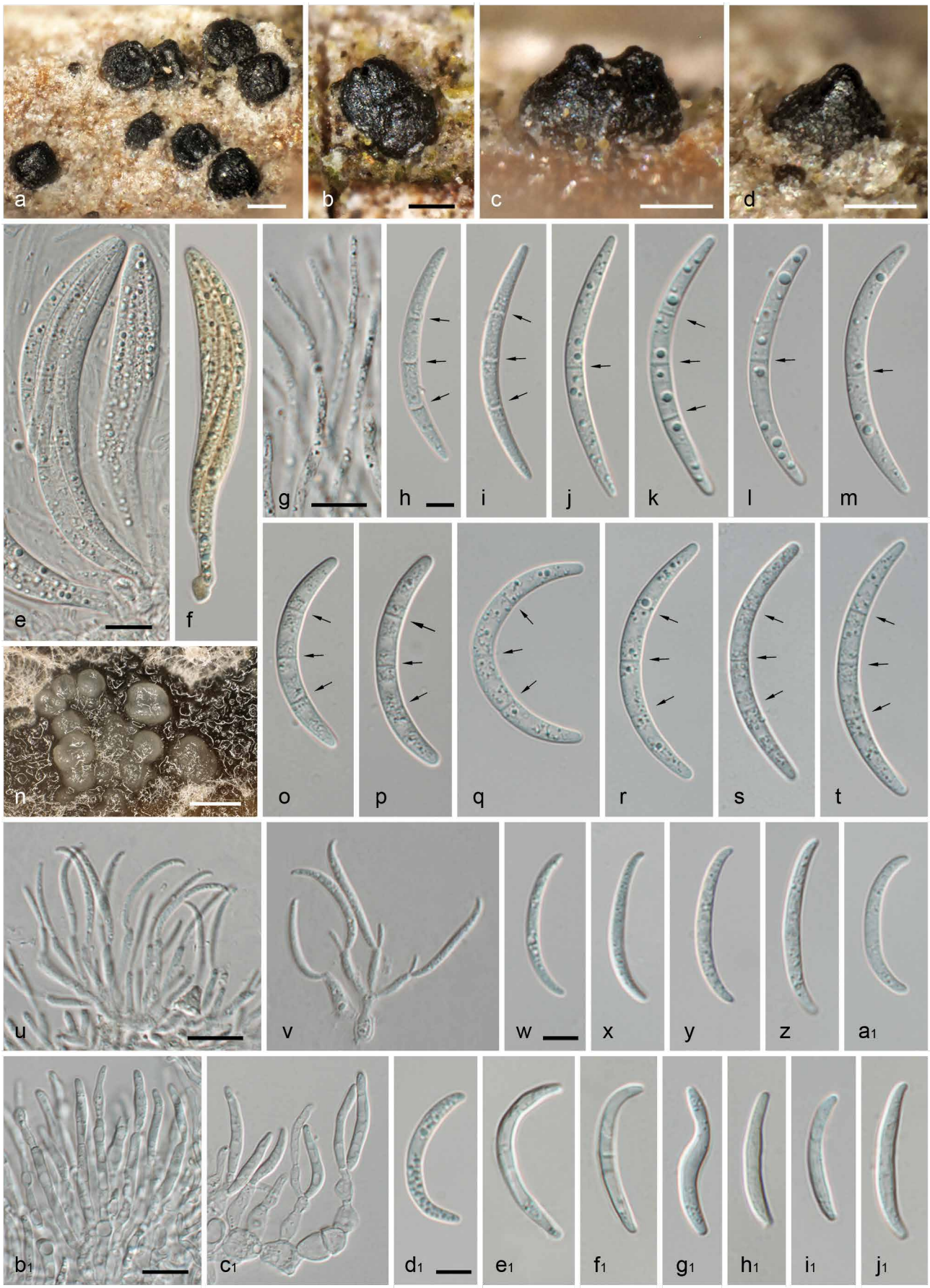

Fig. 14 *Leptosillia slaptonensis*. a–d. Perithecia on bark in surface (a–b) and side (c–d) view; e–f. asci (f. in Lugol); g. paraphyses; h–m, o–t. vital ascospores; arrows denoting septa; n. pale, translucent pycnidia in culture (CMD, isolation plate, 42 d); u–v. conidiophores, conidiogenous cells and conidia from pycnidia on natural substrate; w–a1. conidia from natural substrate; b1–c1. conidiophores and conidiogenous cells from pycnidia in culture (CMD, isolation plate, 42 d); d1–j1. conidia from pycnidia in culture (CMD, isolation plate; d1. 20 d; e1–j1. 40 d). All in water, except where noted (a–f, h–j: WU 40010 (epitype); g, o–p: WU 40012; k–m: WU 40014; q–a1: WU 40015; n, b1–c1, e1–j1: CRU3; d1: CRU2). — Scale bars: a–d = 100 µm; e–g, u–v, b1–c1 = 10 µm; h–m, o–t, w–a1, d1–j1 = 5 µm; n = 400 µm.

Leptosillia slaptonensis (P.F. Cannon) Voglmayr, M.B. Aguirre & Jaklitsch, *comb. nov.* — MycoBank MB829936; Fig. 14

Basionym. *Zignoëlla slaptonensis* P.F. Cannon, Syst. Ascomycetum 15: 129. 1997.

Synonym. *Cresporhaphis ulmi* Calat. & M.B. Aguirre, Mycol. Res. 105: 123. 2001.

Typification. Great Britain, England, South Devon, Slapton, near Kingsbridge, Slapton Ley National Nature Reserve, Marsh Lane, on dead cankered branches of *Ulmus minor*, 6 May 1994, *P.F. Cannon* (IMI 362466c, holotype of *Zignoëlla slaptonensis*). – Spain, Aragón, Teruel, between Puebla de Arenoso and Olba, close to Los Lucas, c. 2 km E of Olba, c. 700 m a.s.l., on suberose outgrowths of *Ulmus minor* twigs, 14 Mar. 1999, *V. Calatayud* (MA-Fungi 41352, holotype of *Cresporhaphis ulmi*). – Austria, Niederösterreich, Mödling, Eichkogel, on cork wings and outgrowths of branches of *Ulmus minor*, 29 Apr. 2015, *W. Jaklitsch* & *H. Voglmayr* (WU 40010, epitype of *Zignoëlla slaptonensis* (MBT 385921) and *Cresporhaphis ulmi* (MBT 385922) here designated; ex epitype culture NAD = CBS 145296).

Ascomata perithecial, superficial to partly immersed in bark, (115–)145–190(–250) µm diam (n = 77), black, shiny, smooth, scattered singly to aggregated and occasionally confluent, pyriform, circular from above, commonly laterally collapsed, with a central apical papilla. *Peridium* continuous, c. 25–30 µm thick, a *textura angularis* of thin-walled, isodiametric or somewhat elongated dark brown cells 6–10 µm diam with dark brown walls, becoming paler towards the centrum. *Hamathecium* composed of hyaline, smooth, thin-walled, septate, occasionally branched, 2–4 µm wide paraphyses embedded in an inamyloid gelatinous matrix; periphyses 2–3 µm wide, unbranched, thin-walled, smooth. *Asci* (67–)79–98(–114) × (9.5–)10.2–12.3(–14.5) µm (n = 64), unitunicate, clavate to fusiform, curved, thin-walled, containing 8 ascospores arranged in two fascicles, with a short stipe, inamyloid and without a distinct apical apparatus; with fissurate dehiscence. *Ascospores* (31–)37–46(–55) × (3.2–)3.5–4.0(–4.8) µm, l/w = (7.4–)9.4–12.6(–14.0) (n = 116), falcate, 1- or 3-septate, hyaline, thin-walled, smooth, with narrowly to broadly rounded ends, multiguttulate when vital.

Pycnidia scattered on bark, black, practically indistinguishable from ascomata except for slightly smaller size. *Conidiophores* short, hyaline, smooth, branched up to two times, arising from the inner wall of the pycnidium. *Conidiogenous cells* (5.7–)7.3–10.0(–13.5) × (1.4–)1.6–2.2(–3.1) µm (n = 75), holoblastic with sympodial proliferation, lageniform to cylindrical, hyaline, smooth, disposed in dense terminal whorls of up to 5. *Conidia* (15–)19–23(–25) × (1.5–)1.7–2.2(–2.7) µm, l/w = (7.4–)9.3–12.0(–14.0) (n = 90), falcate to lunate, aseptate, hyaline, thin-walled, smooth, with narrowly rounded ends, containing small guttules when vital.

Culture characteristics and asexual morph in culture — *Colony* on CMD at 16 °C reaching 45–51 mm diam after 58 d; first cream, turning dark grey brown to black in the centre, with sparse aerial mycelium mostly in the centre, margin even, reverse medium to dark grey brown at least in the centre. *Pycnidia* (230–)250–370(–410) µm diam (n = 10), partly immersed to almost superficial, pale whitish translucent, aggregated to confluent, opening by irregular apical ruptures. *Conidiophores* and *conidiogenous cells* similar to those from the natural substrate but less regular and more variable in shape; often producing a single conidium; sympodial conidiation rarely seen. *Conidia* (13–)15–23(–29) × (2.1–)2.3–2.7(–3.1) µm, l/w = (4.5–)6.0–9.4(–12.6) (n = 50), similar to those from the natural substrate but more irregular and variable in shape, varying from allantoid, falcate to sigmoid, aseptate, rarely becoming 1-septate, hyaline, thin-walled, smooth, with mostly broadly rounded ends, sometimes containing numerous guttules especially towards the ends.

Habitat & Host range — Only known from cork wings and outgrowths of living or dead branches of *Ulmus minor*.

Distribution — Europe; known from Austria, UK, Spain (Cannon 1997, Calatayud & Aguirre-Hudson 2001, this study).

Additional specimens examined (all on cork wings of branches of *Ulmus minor*). Austria, Niederösterreich, Marchauen E Markthof, 8 Sept. 2018, *H. Voglmayr* & *I. Greilhuber* (WU 40011, culture CRU3); Marchauen E Schloßhof, 17 June 2017, *H. Voglmayr* & *I. Greilhuber* (WU 40012); Orth an der Donau, Donauauen near Uferhaus, 10 Mar. 2018, *H. Voglmayr* & *I. Greilhuber* (WU 40013); Neunkirchen, Mollram, 24 Nov. 2018, *H. Voglmayr* & *I. Greilhuber* (WU 40022); Prellenkirchen, Spitzerberg SW Edelstal, 12 Mar. 2017, *H. Voglmayr* & *I. Greilhuber* (WU 40014, culture CRU2); Wien, 21 distr., Stammersdorf, Marchfeldkanalweg near Heeresspital, 12 June 2016, *H. Voglmayr* & *W. Jaklitsch* (WU 40015, culture CRU1).

Notes — The types of *Zignoëlla slaptonensis* and *Cresporhaphis ulmi* match in all respects, including the host, with the former name having priority. A recent Austrian collection, for which a culture and sequences are available, is here selected as epitype for both *Z. slaptonensis* and *C. ulmi* to stabilise the species concepts and the nomenclatural connection of both names. *Leptosillia slaptonensis* and *L. acerina* resemble in habitus and share a similar ecology, both growing on cork wings and outgrowths (rhytidome) of living or recently dead branches, but they differ in their hosts and by ascospore characters.

The ITS GenBank accession FJ025239, derived from an endophyte isolated by Sun et al. (2012) from twigs of *Ulmus macrocarpa* in China, represents a distinct *Leptosillia* species, apparently closely related to *L. wienkampii* and *L. slaptonensis*, which both occur on *Ulmus* species in Europe. *Leptosillia slaptonensis* is so far only known from *Ulmus minor*, a host on which also *L. wienkampii* has been found in the present study; however, the latter only occurred on bark of living trunks, while all collections of *L. slaptonensis* were found on cork wings of thin branches. *Leptosillia slaptonensis* and *L. wienkampii* are closely related (Fig. 1, 2) and have a similar ascospore shape and overlapping ascospore sizes, but can be reliably distinguished by the 1–3 septate vs aseptate ascospores, respectively.

Leptosillia wienkampii (J. Lahm ex Hazsl.) Voglmayr & Jaklitsch, *comb. nov.* — MycoBank MB829937; Fig. 15

Basionym. *Leptorhaphis wienkampii* J. Lahm ex Hazsl., Verh. Ver. Nat., Heilk. Pressb. 5: 12. 1861 (1860–1861).

Synonyms. *Cresporhaphis wienkampii* (J. Lahm ex Hazsl.) M.B. Aguirre, Bull. Brit. Mus. (Nat. Hist.), Bot. 21: 154. 1991.

Liberomyces saliciphilus Pažoutová et al., Mycologia 104: 201. 2012.

Typification. Germany, Westfalen, Münster, Handorf, on bark of *Salix fragilis*, *Nitschke*, in Rabenhorst, Lich. Eur. Exs. no. 651 (L, neotype of *Leptorhaphis wienkampii* designated by Aguirre-Hudson 1991; WU s.n., W 2009-00420 isoneotypes). – United Kingdom, England, Surrey, Richmond, Royal Botanic Gardens Kew, on bark of living trunk of *Salix fragilis* var. *russelliana*, 24 Mar. 2016, *E. Rangel* & *M.B. Aguirre-Hudson* (WU 40016, epitype of *Leptorhaphis wienkampii* (MBT 385923) here designated; ex-epitype culture CRW = CBS 143630).

Ascomata perithecial, superficial on bark, (120–)170–260(–320) µm diam (n = 65), black, matt, smooth to areolate, scattered singly, pyriform, circular from above, with a central apical papilla laterally slightly enlarged by stellate or sulcate structures on the surface. *Peridium* continuous, of a *textura angularis*, composed of an outer dark brown, 25–40 µm thick layer of thin-walled isodiametric to laterally compressed cells 4–8 × 2–4 µm with dark brown walls, and an inner hyaline to pale brown layer of (sub)hyaline to light brown cells slightly smaller than those of the outer layer. *Hamathecium* composed of hyaline, smooth, thin-walled, septate, occasionally branched, 1.3–4 µm wide paraphyses embedded in an inamyloid gelatinous matrix; with hyaline, refractive, strongly dextrinoid granular exudates turning amberred in Lugol; periphyses smooth, thin-walled, unbranched, less than 2 µm wide. *Asci* (76–)82–110(–134) × (7.8–)8.5–10.3(–11.0) µm (n = 43), unitunicate, cylindrical to clavate, strongly sinuous, thin-walled, containing 8 bi- or triseriately arranged ascospores, with a short stipe, inamyloid and without a distinct apical apparatus. *Ascospores* (22–)26–39(–48)

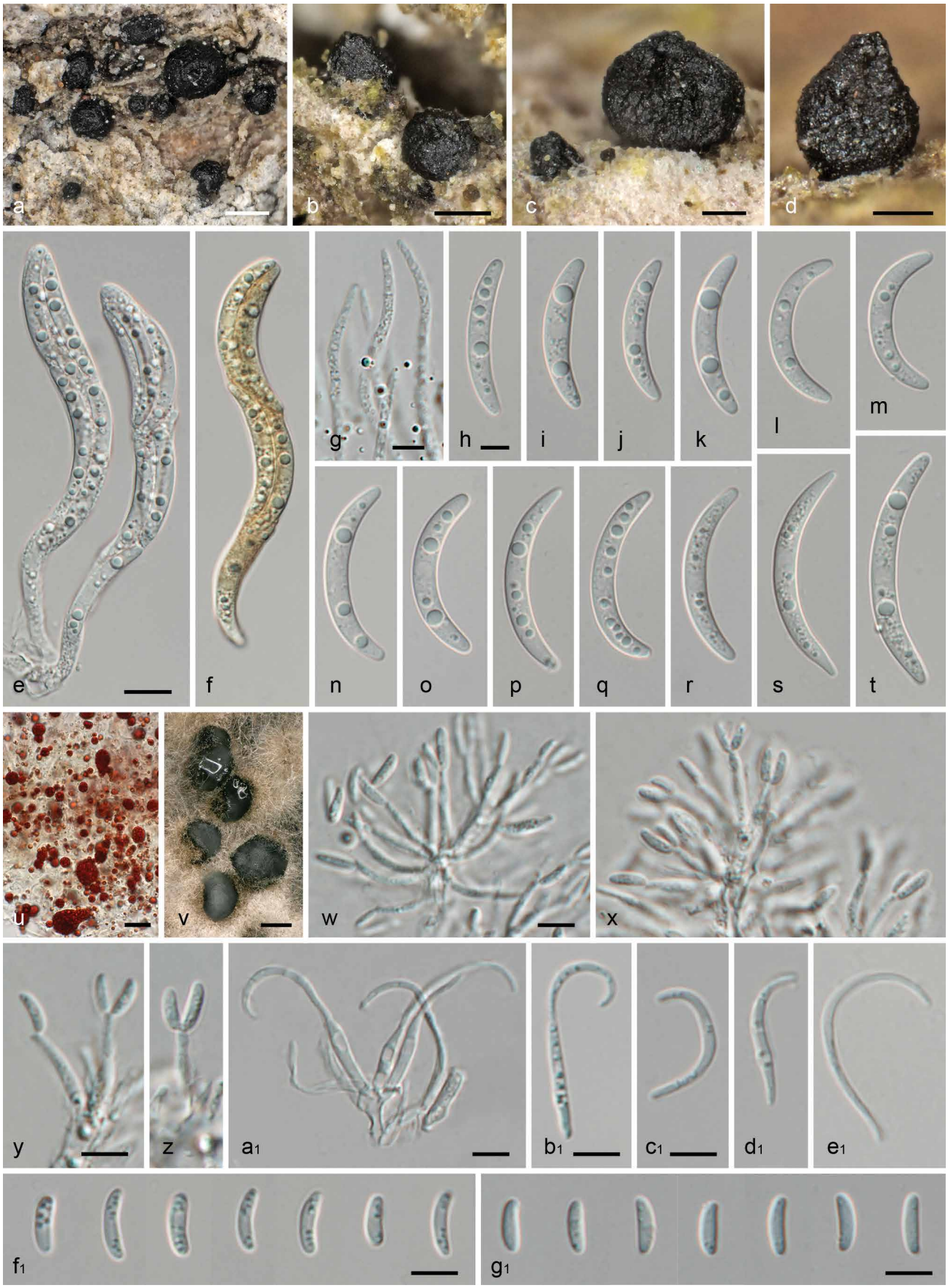

Fig. 15 *Leptosillia wienkampii*. a–d. Perithecia on bark in surface (a–b) and side (c–d) view; note the sulcate structures on the apical papillae (c–d); e–f. asci (f. in Lugol); g. paraphyses; h–t. vital ascospores; u. strongly dextrinoid granular hamathecial exudates in Lugol after KOH pre-treatment; v. pycnidia and conidial drops in culture (CMD, 16 d); w–z, g1. conidiophores, conidiogenous cells and conidia from pycnidia on natural substrate; a1–f1. conidiophores, conidiogenous cells and conidia from pycnidia in culture (CMD, isolation plate, 40 d). All in water, except where noted (a, g, r: WU 40021; b: WU 40018; c, s–t, w–z, g1: WU 40020; d–e, h–p: WU 40017; f, q: WU 40016 (epitype); u: WU 40023; v, a1, e1: CRW3; b1–d1, f1: CRW1). — Scale bars: a–b, v = 200 µm; c–d = 100 µm; e–f, u = 10 µm; g–t, w–g1 = 5 µm.

× (3.0–)3.5–4.2(–5.0) µm, l/w = (5.1–)6.3–11.1(–15.6) (n = 203), falcate to lunate, aseptate, hyaline, thin-walled, smooth, with broadly rounded ends, multiguttulate when vital, often with 2–3 large and numerous small guttules.

Pycnidia scattered on bark, black, similar to ascomata except for slightly smaller sizes. *Conidiophores* short, hyaline, smooth, densely branched up to three times, arising from the inner wall of the pycnidium. *Conidiogenous cells* (5.0–)7.5–11.5(–15.8) × (1.2–)1.5–2.0(–2.2) µm (n = 50), holoblastic with sympodial proliferation, lageniform to cylindrical, hyaline, smooth, arranged intercalarily or in dense terminal whorls on the conidiophore. *Conidia* (5.0–)5.5–6.2(–7.0) × (1.4–)1.6–1.9(–2.1) µm, l/w = (2.5–)3.1–3.7(–4.3) (n = 101), falcate, aseptate, hyaline, thin-walled, smooth, with narrowly rounded ends, containing few small guttules when vital.

Culture characteristics and asexual morph in culture — *Colony* on CMD at 16 °C reaching 50–66 mm diam after 58 d; variable in colour depending on the strain, cream, often turning dark grey brown to black with age, with sparse to abundant aerial mycelium, margin even or irregularly wavy, reverse cream with medium to dark grey brown patches in the centre or entirely dark grey brown to black. *Pycnidia* (165–)205–440(–655) µm diam (n = 66), immersed to almost superficial, black, single, aggregated to confluent, uni- or irregularly plurilocular, opening by an irregular rupture and exuding white masses of conidia. *Conidiophores* simple or irregularly branched, hyaline, smooth, arising from the inner wall of the entire conidioma. *Conidiogenous cells* of two types: a) holoblastic with sympodial proliferation similar to those from the natural substrate, (3.3–)5.5–8.7(–10.7) × (1.8–)2.0–2.7(–3.0) µm (n = 35), bearing allantoid conidia; b) enteroblastic, phialidic, (4.3–)8.5–12.5(–14.5) × (1.1–)1.4–1.9(–2.2) µm (n = 57), bearing filiform to narrowly falcate conidia. *Conidia* of two types: when holoblastically formed similar to those recorded from natural substrate, (5.0–)5.5–7.0(–7.8) × (1.2–)1.5–1.8(–2) µm, l/w = (2.9–)3.1–4.7(–6.4) (n = 34), allantoid, hyaline, smooth; when enteroblastically formed (12.7–)16.5–23.8(–29) × (0.8–)1.0–1.4(–1.7) µm, l/w = (9.4–)13.4–22.0(–25.3) (n = 57), filiform to narrowly falcate, hyaline.

Habitat & Host range — On bark of trunks of various deciduous trees; recorded from *Populus* spp., *Pyrus communis*, *Robinia pseudoacacia*, *Salix* spp. (mostly *S. alba* and *S. fragilis*), *Ulmus glabra*, *U. laevis*, *U. minor* (Aguirre-Hudson 1991, Aguirre-Hudson et al. 2005, Pažoutová et al. 2012, this study).

Distribution — Europe; known from Austria, Bulgaria, Czech Republic, Germany, Italy, Norway, Poland, Slovakia, Sweden, UK (Aguirre-Hudson 1991, Aguirre-Hudson et al. 2005, Pažoutová et al. 2012, this study).

Additional specimens examined. Austria, Niederösterreich, Baden, Helenental, on bark of living trunk of *Salix fragilis*, 23 Apr. 2016, *H. Voglmayr* & *I. Greilhuber* (WU 40017; culture CRW1); Hohenau, Marchauen near sugar refinery, on bark of living trunk of *Ulmus laevis*, 5 June 2016, *H. Voglmayr* & *I. Greilhuber* (WU 40018; culture CRM5); Neunkirchen, Mollram, on bark of living trunk of *Ulmus minor*, 1 Nov. 2018, *H. Voglmayr* & *I. Greilhuber* (WU 40019; culture CRW3); Puchberg am Schneeberg, Sonnleiten, Wasserfallweg, on bark of living trunk of *Salix* sp., 24 Nov. 2018, *H. Voglmayr* & *I. Greilhuber* (WU 40023); Steiermark, Ardning, riverine forest of the Enns adjacent to Pürgschachener Moor, on bark of living trunk of *Ulmus glabra*, 26 May 2016, *H. Voglmayr* & *I. Greilhuber* (WU 40020; culture CRU). – Italy, Sicily, Graniti, Casa delle Monache, on bark of living trunk of *Ulmus minor*, 16 June 2016, *H. Voglmayr* & *W. Jaklitsch* (WU 40021; culture CRW2). – UK, England, Surrey, Kew, Royal Botanic Gardens, Lake (NW side of), on bark crevices of *Populus lasiocarpa*, 20 Aug. 2007, *M.B. Aguirre-Hudson* & *T. Kokubun* (K(M) 154226); ibid., on bark of *Salix fragilis* var. *russelliana*, 20 Aug. 2007, *M.B. Aguirre-Hudson* & *T. Kokubun* (K(M) 154239); South Essex, VC18, Southend-on-Sea, Chalkwell Park, by pond, on bark furrows of *Salix* sp., 1 July 2014, *P.M. Earland-Bennett* (K(M) 199631); ibid., Southchurch Park, by lake in park, on bark furrows of *Salix* sp., 5 June 2014, *P.M. Earland-Bennett* (K(M) 199632).

Notes — Based on sequence data and morphology, *Liberomyces saliciphilus* represents the asexual morph of *Leptosillia wienkampii*, and is therefore a synonym of the latter. Most of the description of the asexual morph in pure culture was based on own observations, with a few additions from the description of *Liberomyces saliciphilus* by Pažoutová et al. (2012). In the present study, pycnidia on natural substrate could be found on only two specimens, and they produce holoblastically formed allantoid conidia matching those from pure culture. When describing *L. saliciphilus*, Pažoutová et al. (2012) recorded only the holoblastically formed conidia from pycnidia in pure culture; yet, in some of our pure cultures, both holoblastically and enteroblastically formed conidia were occasionally produced within the same pycnidia. Remarkably, Aguirre-Hudson (1991) recorded pycnidia on the natural substrate with enteroblastically produced, cylindrical to filiform conidia 20–25 µm × 1 µm in size, indicating that on the natural substrate the two different conidial types may be formed in different pycnidia.

Key to accepted species of Leptosillia with sexual morphs

1. Ascospores aseptate, occasionally 1-septate 2
1. Ascospores consistently 1- to multiseptate 5
2. On bark of *Acer* spp.; only known from Europe; ascospores always aseptate 3
2. On bark of other hosts; in Europe or North America; ascospores occasionally 1-septate 4
3. Ascomata commonly confluent, in a pseudostroma, not collapsed; on bark scales of mature trunks of *Acer pseudoplatanus*; on the natural substrate conidia of two types (enteroblastic-filiform, holoblastic-falcate) formed within the same pycnidium . . . . . *L. muelleri*
3. Ascomata solitary, often collapsed; on cork wings and outgrowths of branches of *Acer campestre*; only enteroblastic-falcate conidia known . . . . . *L. acerina*
4. Ascospores falcate to lunate, with broadly rounded ends; ascomata not horizontally collapsed, with an apical papilla laterally slightly enlarged by stellate or sulcate structures; asci strongly sinuous; on various broadleaf trees (mostly *Salix* and *Ulmus* spp.) in Europe . . . . . *L. wienkampii*
4. Ascospores straight to slightly curved, usually with distinctly hooked, narrowly rounded ends (similar to *Fusarium* macroconidia); ascomata commonly horizontally collapsed and cupulate, with an apical papilla without stellate or sulcate structures; asci straight, curved to slightly sinuous; on *Populus deltoides* and (probably) *Celtis occidentalis* in North America . . . . . *L. fusariospora*
5. Ascospores multiseptate; on bark of trunks of *Pinus* . . . . . *L. pinicola*
5. Ascospores 1–3-septate; on various broadleaf trees . . . 6
6. Ascospores 50–110 µm long; on trunks of *Quercus* spp. . . . . *L. macrospora*
6. Ascospores 30–55 µm long; on cork wings and outgrowths of branches of *Ulmus minor* . . . . . *L. slaptonensis*

EXCLUDED CRESPORHAPHIS SPECIES

Based on morphology and ecology, the following two species are considered not to be congeneric with *Cresporhaphis*, and they are therefore not transferred to *Leptosillia*.

Cresporhaphis rhoina M.E. Barr, Mycotaxon 46: 64. 1993; Fig. 16

Replaced synonym. *Sphaeria rhoina* Ellis & Everh., J. Mycol. 1 (7): 92. 1885, non *Sphaeria rhoina* Schwein., Trans. Amer. Philos. Soc., New Series 4 (2): 218. 1832 '1834'.

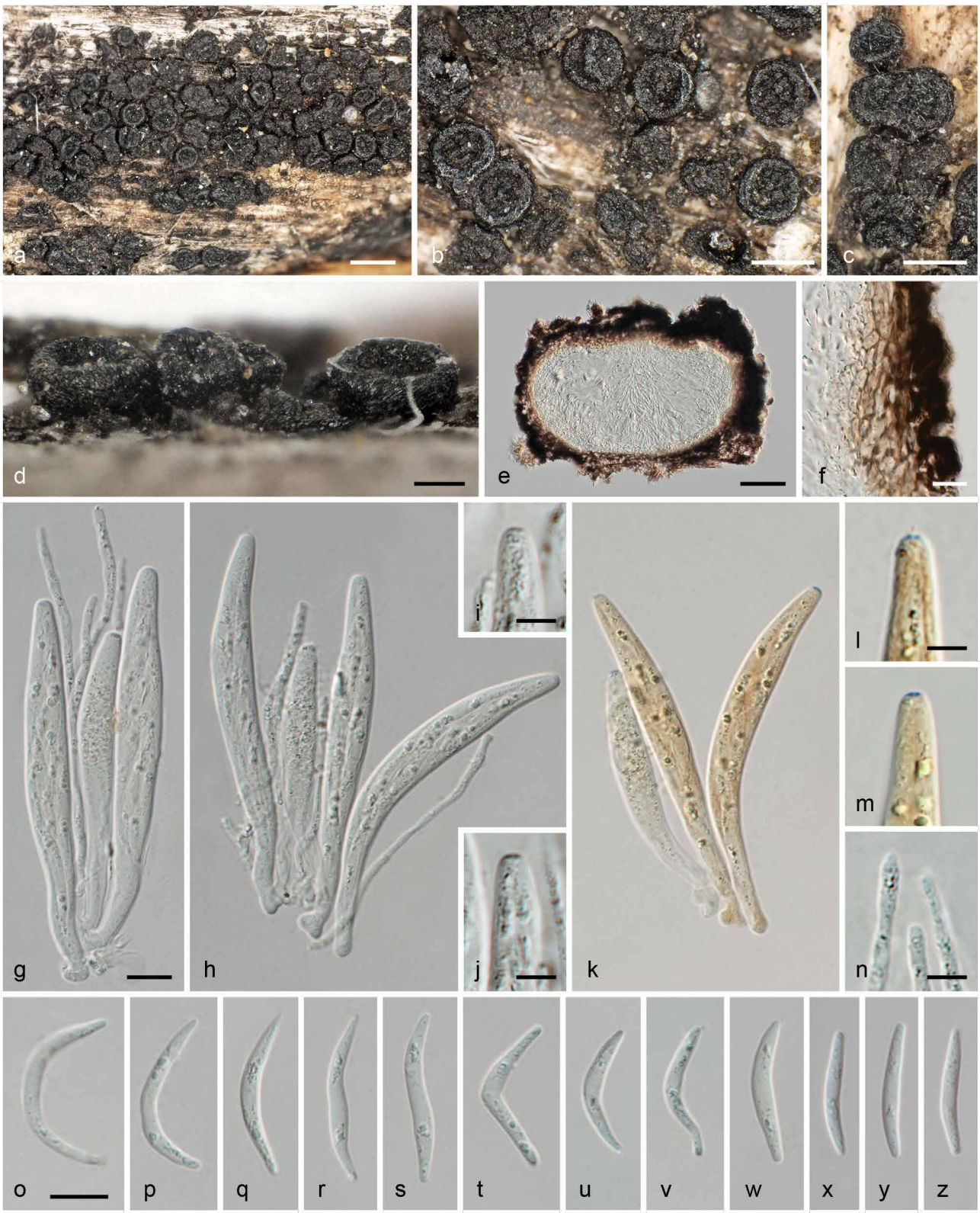

Fig. 16 *Cresporhaphis rhoina*. a–d. Horizontally collapsed, cupulate perithecia on wood in surface (a–c) and side (d) view; e. ascoma in vertical section; f. peridium in section; g–h, k. asci and paraphyses (k. in Lugol after KOH pre-treatment); i–j, l–m. ascus tips (l–m. in 3 % KOH followed by Lugol, showing the shallow amyloid apical ring); n. paraphyses tips; o–z. ascospores. All in 3 % KOH, except where noted (a–b, d–f, i–j: GZU 000335638 (isotype); c, g–h, k–w: GZU 000335637 (isotype); x–z: NY 00875175 (lectotype)). — Scale bars: a = 400 µm; b–c = 200 µm; d = 100 µm; e = 50 µm; f–h, k, o–z = 10 µm; i–j, l–n = 5 µm.

Typification. USA, New Jersey, Gloucester Co., Newfield, weather-beaten dead wood of *Rhus copallinum*, May 1885, without collector, in Ellis & Everhart, N. Amer. Fungi Ser. 2 no. 1669 (NY 00875175, lectotype of *Sphaeria rhoina* Ellis & Everh. (MBT 385924) here selected; GZU 000335637, GZU 000335638, isotypes).

Ascomata perithecial, superficial on dead wood, (140–)170–300(–460) µm diam (n = 101), 60–140 µm high (n = 20), black, matt, smooth, scattered to gregarious, lenticular, horizontally collapsed and distinctly cupulate when dry, circular from above, with or without a small central apical papilla. *Peridium* continuous, of a *textura angularis*, 23–38 µm thick, composed of an outer blackish brown, 12–28 µm thick layer of very thick-walled, more or less isodiametric cells with dark brown walls, and an inner brown, 5–20 µm thick layer of brown, elongate, thin-walled cells 5–19 × 2–5 µm. *Hamathecium* composed of hyaline, smooth, thin-walled, septate, mostly unbranched, 1.5–3 µm wide paraphyses embedded in an inamyloid gelatinous matrix; periphyses not observed. *Asci* (63–)74–87(–102) × (6.3–)7.7–9.0(–10.0) µm (n = 49), unitunicate, fusiform, straight to curved, thin-walled, containing 8 irregularly biseriately arranged ascospores, with a short stipe and a small, shallow, amyloid, c. 1.8 µm wide and 0.5 µm high apical ring. *Ascospores* (19–)23–30(–39) × (2.5–)2.8–3.2(–3.5) µm, l/w = (6.7–)7.5–10.1(–13.4) (n = 91), variously shaped from straight and fusiform, falcate, hook-shaped to sinuous, aseptate, hyaline, thin-walled, smooth, with narrowly rounded to subacute ends, containing few guttules. *Asexual morph* unknown.

Notes — Barr (1993) established *Cresporhaphis rhoina* as a new name for *Sphaeria rhoina* Ellis & Everh., a later homonym of *Sphaeria rhoina* Schwein. Based on similar ascomata, asci and ascospores, Barr (1993) considered *C. rhoina* to be closely related to the generic type, *C. wienkampii*. The asci were described as unitunicate with a shallow inamyloid apical ring. However, re-examination of the type collection showed the presence of a small but distinct amyloid apical ring in Lugol after KOH pre-treatment, which indicates xylarialean affinities but excludes the species from *Cresporhaphis*. Also the growth on dead wood differs from all confirmed species of *Cresporhaphis*, which are all corticolous. It is therefore not congeneric with *Cresporhaphis* (and accordingly *Leptosillia*), but its morphological characters are insufficient to allow a well-founded generic reclassification within *Xylariales*.

The synonymy of *C. rhoina* and *Coelosphaeria fusariospora* proposed by Barr (1993) could not be confirmed after re-examination of type material of both species; the latter lacks a distinct amyloid apical ascus ring and has ascospores and a corticolous ecology in line with *Leptosillia*, into which it is thus combined (see also notes of *L. fusariospora* above).

Numerous copies of the type collection were distributed as Ellis & Everhart, N. Amer. Fungi Ser. 2 no. 1669, but to our knowledge no lectotype has been selected. The specimen from NY bears the original notes; the ascospore size range is somewhat smaller than in the copies from GZU and exactly matches the range (20–25 µm) given in the original description in Ellis & Everhart (1885). In all other characters, the specimens from NY and GZU fully agree. Therefore, the investigated isotype specimen from NY is here selected as lectotype.

Rhaphidicyrtis trichosporella (Nyl.) Vain., Acta Soc. Fauna Fl. Fenn. 49: 217. 1921

Synonym. *Cresporhaphis chibaensis* H. Harada, Lichenology 12: 32. 2014.

Holotype of *Cresporhaphis chibaensis*. Japan, Honshu, Chiba-ken, Inzai-shi, Muzai, 15 m elev., on trunk of *Alnus japonica*, 4 Dec. 2007, *H. Harada 25172* (CBM-FL-23891).

For descriptions and illustrations of *Cresporhaphis chibaensis*, see Harada (2014).

Notes — *Cresporhaphis chibaensis* differs substantially in several respects from the generic type and the other confirmed species of *Cresporhaphis*: It is clearly lichenised with a distinct crustose lichen thallus, has perithecial ascomata with lateral, slightly sunken ostioles not situated on an apical papilla, a hamathecium composed of very thin, at least apically anastomosing threads and very long, filiform ascospores with numerous septa. It is therefore not considered to be related to the *Cresporhaphis* species here transferred to *Leptosillia*. Harada (2014) failed to note the hamathecial gel Lugol's iodine reaction in the protologue of the species. Nevertheless, and considering the other morphological features, this species is a later synonym of *Rhaphidicyrtis trichosporella*, a species known from various substrates in Northern Europe, including *Alnus* sp. (Ekman et al. 2013).

DISCUSSION

Molecular phylogeny

The molecular phylogenetic analyses confirm a close relationship of all *Cresporhaphis* species for which DNA data are available with the type species of *Leptosillia*, and further, these are closely related to *Delonicicola*. Within this clade, two highly supported lineages are evident in the multigene analyses: the *Delonicicola-Furfurella* subclade and the *Leptosillia* subclade, which we recognise as two distinct families, *Delonicicolaceae* and *Leptosilliaceae*, based also on marked morphological differences between those genera. In the ITS-LSU rDNA analyses, the *Leptosilliaceae* are resolved only in the ML analyses (Fig. 2) but not in the MP analyses. This shows that, within *Xylariales*, the ITS-LSU alone does not always resolve generic and family affiliations well, which is also known from previous studies (e.g., Voglmayr & Yule 2006, Jaklitsch & Voglmayr 2012, Jaklitsch et al. 2016b). This conflict is, e.g., also seen in the *Pseudomassariaceae*, a morphologically and ecologically well-characterised family, which is also monophyletic in the ML analyses, albeit with low support (Fig. 2), but not resolved in the MP analyses. Insufficient phylogenetic resolution may be the result of rearrangements and length differences of the ITS, causing problems in producing a reliable alignment, in combination with insufficient phylogenetically informative and/or homoplastic characters. Therefore, multigene phylogenies are necessary for an improved phylogenetic resolution within *Xylariales* (Voglmayr et al. 2018, Wendt et al. 2018).

Classification

The taxa here classified in *Leptosillia* are a case example how the historical divide of the mycological and lichenological communities led to multiple separate, independent descriptions of the same species within different classification frames, and how this also influenced the hypotheses about their ecology.

Being bark inhabitants, most of the species here classified as *Leptosillia* were first encountered and described by lichenologists, and based on ascoma and ascospore characters, most of them were originally placed in the heterogeneous genus *Leptorhaphis*. In her detailed monograph, Aguirre-Hudson (1991) confined *Leptorhaphis* to bark saprotrophs with affinities to *Arthopyreniaceae* (*Dothideomycetes*), and she transferred putatively lichenised species with thin-walled, unitunicate asci, true paraphyses and perithecial ascomata to the new genus *Cresporhaphis*, which she tentatively classified within the *Trichosphaeriales* (*Sordariomycetes*). This classification was mostly accepted up to date (e.g., Lücking et al. 2017), but challenged in Jaklitsch et al. (2016a) who considered this placement

doubtful. However, there was consensus that its phylogenetic placement required further detailed studies.

Until our present study, the then monotypic genus *Leptosillia* was classified within the *Diaporthales* (Kirk et al. 2008), with a presumed familial affiliation to the *Valsaceae* (Index Fungorum, accessed Feb. 2019). This classification was primarily based on the original description (Höhnel 1928), which hypothesised a close relationship to the diaporthalean genus *Sillia*, and was perpetuated in Eriksson & Hawksworth (1987). However, after its description the taxon was never recorded again, and the original material was never critically re-examined. Therefore, it is not surprising that no connection of the little-known *Leptosillia notha* was ever made to species classified in *Leptorhaphis*, and later *Cresporhaphis*.

As a result of our study, the comparison of the type specimens of *Cresporhaphis muelleri* and *Leptosillia notha* confirmed them to represent the same species, requiring a name change to *L. muelleri*, based on priority. As the genus *Cresporhaphis* has a different generic type species, *C. wienkampii*, the question arises whether the two genera should be kept separate or classified within the same genus, which in the latter case should be *Leptosillia* due to priority. The results of the phylogenetic analyses (Fig. 1, 2) revealed both options as tenable, as the *L. acerina-L. muelleri* and *L. macrospora-L. slaptonensis-L. wienkampii* lineages formed two distinct subclades within the *Leptosilliaceae*. However, after critical consideration we prefer a classification of all species under a single genus *Leptosillia*, as we did not find any morphological or ecological characters diagnostic for the two lineages. In addition, if *Cresporhaphis* were maintained, also *L. pistaciae* would need another generic name, as would several other lineages now only known as endophyte isolates. It would also be impossible to generically place *L. fusariospora* and *L. pinicola*, which morphologically belong to *Leptosilliaceae* but for which no DNA sequence data are available. All these arguments favour a classification within a single genus.

When describing *Delonicicola* and *Delonicicolaceae*, Perera et al. (2017) also established a new order *Delonicicolales*. However, in their phylogenetic analyses the placement of *Delonicicolaceae* as sister group to *Xylariales* did not receive statistical support. In our phylogenetic analyses of the ITS-LSU matrix the *Delonicicolaceae-Leptosilliaceae* clade was embedded within *Xylariales* (Fig. 2), while in the multi-gene analyses a sister group relationship to the other *Xylariales* was highly supported (Fig. 3). However, the latter analyses contain only a small subset of *Xylariales*, as most xylarialean lineages lack multigene sequence data. Considering these uncertainties, we do not accept a separate order *Delonicicolales* here.

Morphology of the asexual morph

Pycnidial asexual morphs were produced in culture in all *Leptosillia* species investigated so far. The asexual morph of the genus *Leptosillia* is remarkable by the common presence of two morphologically different types of conidia, which are also differently produced, i.e., enteroblastic phialidic and holoblastic with sympodial proliferation. In several species, these two types have been observed within the same conidiomata (e.g., *L. macrospora*, *L. muelleri*, *L. wienkampii*), but apparently both types are not always produced. For instance, Pažoutová et al. (2012) observed two types in *L. wienkampii*, but only a single type in *L. macrospora*, while in our investigations it was the other way round. Therefore, it cannot be excluded that both types are also formed in species for which so far only a single type has been observed (*L. acerina*, *L. slaptonensis*). Interestingly, pycnidia were commonly produced in the isolation plates, while in several species only few or no pycnidia were formed after subculturing. Apart from the species treated in our manuscript, holoblastically formed falcate conidia have been reported by Kolařík et al. (2012) for one of the endophyte isolates (VegaE4-79 from *Coffea arabica*).

In our fresh collections, pycnidia were rarely seen on the natural substrate; however, as they are very similar to ascomata except for their smaller sizes, they could have been overlooked. In these, two conidial types have only been observed in *L. muelleri*, while in the other species either the enteroblastic phialidic (*L. acerina*, *L. macrospora*) or the holoblastic type with sympodial proliferation (*L. slaptonensis*, *L. wienkampii*) was present. So far, no asexual morphs were observed for the species only known from herbarium specimens, *L. fusariospora* and *L. pinicola*.

Ecology

Based on the association with corticolous algae on bark, most of the species here classified as *Leptosillia* were commonly considered to be facultatively lichenised, which may be due to the fact that they were mainly studied by lichenologists. When establishing the genus *Cresporhaphis*, a synonym of *Leptosillia*, Aguirre-Hudson (1991) described the thallus as crustose, smooth to pulverulent, greyish white and immersed in the bark but associated with an unidentified globose chlorococcoid photobiont. In the notes to the various species included, she described them as 'probably lichenized', and later, Calatayud & Aguirre-Hudson (2001) considered *Cresporhaphis ulmi* as not lichenised. Detailed investigations of numerous fresh specimens collected during the present study as well as of herbarium specimens did not confirm the presence of a lichen thallus in the former *Cresporhaphis* species here reclassified in *Leptosillia*. Although under certain environmental conditions the ascomata may be associated with chlorococcoid algae, this association is not constantly observed and entirely missing in some collections of all species examined. In addition, all species studied in fresh condition germinate and grow easily in pure culture. Therefore, the current investigations do not support that the former *Cresporhaphis* species are lichenised, with the exception of the recently described *Cresporhaphis chibaensis*, which, however, is not considered to be congeneric with the type of *Cresporhaphis* but conspecific with the lichen *Rhaphidicyrtis trichosporella*.

The publication of Pažoutová et al. (2012) shed a new light on the ecology of *Leptosillia*. They isolated and described two asexual morph species, *Liberomyces macrosporus* and *L. saliciphilus*, as endophytes from phloem and sapwood of various, usually symptomless broadleaf trees. In our investigations, morphology and sequence data revealed the former to be synonymous with *Leptosillia macrospora* and *L. wienkampii*, respectively. This points to a primary ecology of *Leptosillia* as endophytic, which is also in line with the formation of ascomata on bark of living trees, and further supported by the numerous ITS GenBank accessions of endophytes from various hosts and geographic origins which are embedded within the *Leptosillia* clade (Fig. 2). Therefore, this indicates that the *Leptosilliaceae* comprise widespread and important components of the endophyte communities of woody hosts, and they may harbour numerous undescribed species especially in understudied tropical and subtropical areas. It is interesting that *Leptosillia pistaciae*, a recently described canker pathogen of *Pistacia vera* (Vitale et al. 2018), is also embedded within the *Leptosillia* clade, which indicates that pathogenicity may have secondarily evolved from an endophytic lifestyle. However, it also cannot be excluded that some of the strains isolated as endophytes may actually represent latent pathogens.

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