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Redefining common endophytes and plant pathogens in *Neofabraea*, *Pezizula*, and related genera

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ABSTRACT

Species in *Neofabraea*, *Pezizula*, and related genera have been reported as saprobes, plant pathogens or endophytes from a wide range of hosts. The asexual morphs of *Neofabraea* and *Pezizula* had been placed in *Cryptosporiopsis*, now a synonym of *Pezizula*, while *Neofabraea* was also linked to *Phlyctema*. Based on morphology and molecular data of the partial large subunit nrDNA (LSU), the internal transcribed spacer region with intervening 5.8S nrDNA (ITS), partial β -tubulin region (*tub2*), and the partial RNA polymerase II second largest subunit region (*rpb2*), the taxonomy and phylogenetic relationships of these fungi were investigated. Five new species were described in *Pezizula* based on morphology, while a further eight unnamed phylogenetic lineages revealed further diversity in the genus. Based on these results, the generic concept of *Neofabraea* was also emended. *Phlyctema*, which was previously associated with *Neofabraea*, formed a distinct clade, separate from *Neofabraea* s. str. Two new neofabraea-like genera, *Parafabraea* and *Pseudofabraea* were proposed, along with one new combination in *Neofabraea* s. str. To stabilise the application of these names, an epitype was designated for *Pe. carpinea*, the type species of *Pezizula*, and for *N. malicorticis*, the type species of *Neofabraea*.

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Introduction

The genus *Pezizula* (Dermateaceae, Helotiales) was established in 1865, with the type species *Pezizula carpinea*. The asexual

morphs have been placed in *Cryptosporiopsis*, which was introduced in 1912 based on *Cryptosporiopsis scutellata*, the sexual morph of which is *Pezizula ocellata*. Verkley (1999) monographed *Pezizula* and related genera based on a comprehensive

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morphological study of fresh materials and old type specimens, as well as RFLP analyses. In a subsequent study [Abeln et al. \(2000\)](#) studied the phylogeny of these genera based on ITS rDNA sequence data. These works provided the foundation for later studies on this generic complex. Since then, many species have been described under *Cryptosporiopsis* and *Pezicula* ([Verkley et al. 2003](#); [Johnston et al. 2004](#); [Sigler et al. 2005](#); [Cheewangkoon et al. 2009, 2010](#); [Zhu et al. 2012](#); [Lynch et al. 2013](#); [Yuan & Verkley 2014](#)). Although *Neofabraea* and *Pezicula* are morphologically and phylogenetically distinct, both genera have traditionally been linked to cryptosporiopsis-like asexual morphs, resulting in some confusion. In the light of previous studies ([Verkley 1999](#); [Abeln et al. 2000](#); [Lynch et al. 2013](#)) and the end of dual nomenclature ([Hawksworth et al. 2011](#); [McNeill et al. 2012](#); [Wingfield et al. 2012](#)), [Johnston et al. \(2014\)](#) recommended the use of *Pezicula* over *Cryptosporiopsis*, and introduced several new combinations.

Species of *Pezicula* are predominantly reported from temperate regions of the world, where they occur as saprobes on recently dead branches and twigs, or as endophytes frequently isolated from living branches and roots displaying no disease symptoms. Several antibiotics, such as (R-)mellein, mycorrhizin, cryptosporiopsin, cryptocandin, and cryptocin have been isolated from endophytic *Pezicula* and *Cryptosporiopsis* species ([Schulz et al. 1995](#); [Strobel et al. 1999](#); [Li et al. 2000](#); [Talontsi et al. 2012](#); [Zilla et al. 2013](#)). Some *Pezicula* species are weak plant pathogens, causing diseases when their hosts are under stress ([Kehr 1991](#); [Verkley 1999](#); [Lynch et al. 2013](#)).

Neofabraea was introduced based on *Neofabraea malicorticis* ([Jackson 1913](#)) to accommodate the newly discovered sexual morph of the apple anthracnose fungus. [Nannfeldt \(1932\)](#) effectively synonymised *Neofabraea* with *Pezicula*, by combining the type species *N. malicorticis* into *Pezicula*. Some researchers followed him and transferred some *Neofabraea* species into *Pezicula* ([Seaver 1951](#); [Dugan et al. 1993](#)). Based on new morphological and phylogenetic analyses, *Neofabraea* and *Pezicula* were again regarded as separate genera ([Verkley 1999](#); [Abeln et al. 2000](#)). *Pezicula alba*, which resembles species of *Neofabraea*, was placed in this genus as *Neofabraea alba* ([Verkley 1999](#)). The asexual morph of this species, *Phlyctema vagabunda*, the type species of *Phlyctema*, is characterised by aseptate, fusiform conidia, that differ markedly from the ellipsoid (and later often septate) cryptosporiopsis-like asexual morphs of the other *Neofabraea* species. In response to previous studies ([Verkley 1999](#); [Johnston et al. 2004](#); [Zhu et al. 2012](#)) and the end of dual nomenclature, [Johnston et al. \(2014\)](#) transferred related *Cryptosporiopsis* species to *Neofabraea*, and protected *Neofabraea* over *Phlyctema*, introducing the combination *Neofabraea vagabunda* to accommodate *N. alba*. Given the name changes discussed above, the generic concept of *Neofabraea* is still in flux, and several taxa in this complex have subsequently been placed in other genera ([Cheewangkoon et al. 2009, 2010](#); [Zhu et al. 2012](#)).

For a long time the type species of *Neofabraea*, *N. malicorticis*, was confused with the closely related species *Neofabraea perennans*. There were different views: in North America, they were regarded as two different species, while they were again considered as conspecific in Europe. Based on multi-gene phylogenetic analyses, [de Jong et al. \(2001\)](#) finally provided data to prove that these two taxa were distinct,

supplemented by differences in vegetative compatibility, cancer symptoms, and response to chemical treatments.

Neofabraea and its related genera are important plant pathogens. Species of *Neofabraea* are commonly known as the causal agents of bull's eye rot of apple and pear fruit, which is an important postharvest disease in the Pacific Northwest of the USA, and also occurs in Australia, Canada, Chile, Europe, and New Zealand ([de Jong et al. 2001](#); [Cunnington 2004](#); [Henriquez et al. 2004](#); [Garipey et al. 2005](#); [Henriquez 2005](#); [Johnston et al. 2005](#); [Spotts et al. 2009](#); [Soto-Alvear et al. 2013](#)). *Neofabraea* complexes also cause anthracnose canker and perennial canker on pome trees ([Verkley 1999](#); [de Jong et al. 2001](#); [Henriquez et al. 2006](#)), canker on *Populus* spp. ([Thompson 1939](#); [Roll-Hansen & Roll-Hansen 1969](#); [Kasanen et al. 2002](#)), coin canker of Ash ([Rossman et al. 2002](#)), fruit rot on kiwifruit ([Johnston et al. 2004](#)), fruit spot on olive ([Rooney-Latham et al. 2013](#)), and leaf spot on citrus ([Zhu et al. 2012](#)).

The aim of the present study was to employ morphology and multi-gene phylogenetic data to clarify relationships among *Neofabraea*, *Pezicula* and related genera, and to reassess the delimitation of these genera and the correct application of names to be used for these entities in accordance with the end of dual nomenclature ([Johnston et al. 2014](#)).

Materials and methods

Isolates

All isolates used in this study, including the outgroup *Infundichalara microchona*, were obtained from the CBS-KNAW Fungal Biodiversity Centre (CBS), Utrecht, The Netherlands ([Table 1](#)). Colonies were sub-cultured onto oatmeal agar (OA) and 2% malt extract agar (MEA) ([Crous et al. 2009b](#)).

DNA isolation, amplification, sequencing and phylogenetic analysis

Genomic DNA was isolated from fungal mycelium growing on MEA or OA, using the UltraClean™ Microbial DNA Kit (MO Bio, Carlsbad, CA, USA), or using the modified CTAB extraction method ([Damm et al. 2008](#)). The PCR reaction mixtures (12.5 µl) contained 1 × PCR buffer, 2–2.8 mM MgCl₂, 0.63 µl DMSO, 40 µM dNTPs, 0.2 µM of each primer, 0.5 U of Taq DNA polymerase (Bioline GmbH, Luckenwalde, Germany), and approximately 10 ng of template DNA. The internal transcribed spacer region (ITS) was amplified with the primers ITS5 and ITS4 ([White et al. 1990](#)), or V9G ([de Hoog & Gerrits van den Ende 1998](#)) and LS266 ([Masclaux et al. 1995](#)), the large subunit of nrDNA (LSU) with LR0R ([Vilgalys & Hester 1990](#)) or LSU1Fd ([Crous et al. 2009a](#)) and LR5 ([Vilgalys & Hester 1990](#)), β-tubulin region (*tub2*) with Bt-T2m-Up and Bt-LEV-Lo1 ([de Jong et al. 2001](#)) or with TUB4Fd ([Groenewald et al. 2013](#)) and T22 ([O'Donnell & Cigelnik 1997](#)), and RNA polymerase II second largest subunit region (*rpb2*) with RPB2-5F2 ([Sung et al. 2007](#)) or RPB2-F5 (S.I.R. Videira, unpublished data), and RPB2-7cr ([Liu et al. 1999](#)). PCR conditions for LSU, ITS and *tub2* were as follows: initial denaturation at 94 °C for 5 min, followed by 35 cycles of denaturation at 94 °C for 45 s, annealing

Table 1 – Collection details and GenBank accession numbers of isolates included in this study.

Species	Strain number ^a and status	Original name	Host/Substrate	Locality	Collector	GenBank Accession Number ^b			
						28S nrDNA	ITS	tub2	rpb2
<i>Infundichalara microchona</i>	CBS 175.74, UAMH 4933, ex-type	<i>Chalara microchona</i>	Decaying wood of <i>Pinus sylvestris</i>	Netherlands	W. Gams, Feb 1974	HQ609479	KR859078	KR859284	KR859318
<i>Neofabraea actinidiae</i>	CBS 121403, ICMP 7826a, ex-type	<i>Cryptosporiopsis actinidiae</i>	<i>Actinidia deliciosa</i>	New Zealand	G.J. Samuels, 1 Sep 1982	KR858870	KR859079	KR859285	KR859319
<i>Neofabraea inaequalis</i>	CBS 194.69	<i>Cryptosporiopsis</i> sp.	<i>Ilex verticellata</i>	Netherlands	–	KR858871	KR859080	KR859286	KR859320
	CBS 326.75, ex-type	<i>Cryptosporiopsis inaequalis</i>	<i>Chamaecyparis</i> sp.	France	M. Morelet, 1973	KR858872	KR859081	KR859287	KR859321
<i>Neofabraea kienholzii</i>	CBS 126461, DAOM 240213, ex-type	<i>Cryptosporiopsis kienholzii</i>	<i>Malus domestica</i> cv. Fuji	USA	R. Spotts, 29 May 2005	KR858873	KR859082	KR859288	KR859322
	CBS 318.77	<i>Cryptosporiopsis</i> sp.	<i>Aucuba japonica</i>	Netherlands	H.A. van der Aa, 7 May 1977	KR858874	KR859083	KR859289	KR859323
<i>Neofabraea krawtzevii</i>	CBS 102867	<i>Neofabraea krawtzevii</i>	<i>Populus × berolinensis</i>	Norway	H. Solheim, NISK	KR858875	KR859084	AF281459	KR859324
<i>Neofabraea malicorticis</i>	CBS 102863, DAOM 227083	<i>Neofabraea malicorticis</i>	Apple tree canker	Canada, British Columbia	J.E. Rahe	KR858876	KR859085	KR859290	KR859325
	CBS 122030, OSC 100036, ex-neotype	<i>Neofabraea malicorticis</i>	<i>Malus</i> sp.	USA, Oregon	–	KR858877	KR859086	KR859291	KR859326
<i>Neofabraea perennans</i>	CBS 102869, DAOM 227089	<i>Neofabraea perennans</i>	Apple tree canker	Canada, British Columbia	J.E. Rahe	KR858878	KR859087	AF281473	KR859327
	CBS 275.29, ATCC 13905, ATCC 1730	<i>Neofabraea perennans</i>	<i>Malus sylvestris</i>	–	J.S. Cooley	KR858879	KR859088	KR859292	KR859328
<i>Parafabraea caliginosa</i>	CBS 453.64	<i>Neofabraea perennans</i>	–	UK	–	KR858880	KR859089	AF281474	KR859329
	CBS 124806, CPC 14048, ex-type	<i>Cryptosporiopsis caliginosa</i>	<i>Eucalyptus caliginosa</i>	Australia, New South Wales	B.A. Summerell, 1 Feb 2007	KR858881	KR859090	KR859293	KR859330
<i>Parafabraea eucalypti</i>	CBS 124810, CPC 13755, ex-type	<i>Neofabraea eucalypti</i>	<i>Eucalyptus globulus</i>	Australia	I. Smith, 15 Feb 2007	KR858882	KR859091	KR859294	KR859331
<i>Pezicula acericola</i>	CBS 239.38	<i>Pezicula acericola</i>	<i>Acer spicatum</i>	Canada, Ontario	J.W. Groves, Aug 1932	KR858883	KR859092	–	–
	CBS 239.97	<i>Pezicula acericola</i>	<i>Acer spicatum</i>	Canada, Ontario	G. Verkley, 20 Sep 1996	KR858884	KR859093	KF376283	KF376214
	CBS 240.38	<i>Pezicula acericola</i>	<i>Acer spicatum</i>	Canada, Ontario	J.W. Groves, Aug 1934	KR858885	KR859094	–	–
	CBS 240.97	<i>Pezicula acericola</i>	<i>Acer spicatum</i>	Canada, Ontario	G. Verkley, 20 Sep 1996	KR858886	KR859095	–	–
	CBS 241.97	<i>Pezicula acericola</i>	<i>Acer spicatum</i>	Canada, Ontario	G. Verkley, 21 Sep 1996	KR858887	KR859096	–	–
	CBS 242.97	<i>Pezicula acericola</i>	<i>Acer spicatum</i>	Canada, Ontario	G. Verkley, 21 Sep 1996	KR858888	KR859097	–	–
	CBS 245.97	<i>Pezicula acericola</i>	<i>Acer spicatum</i>	Canada, Ontario	G. Verkley, 20 Sep 1996	KR858889	KR859098	KF376282	KF376213
	CBS 246.97	<i>Pezicula acericola</i>	<i>Acer spicatum</i>	Canada, Ontario	G. Verkley, 20 Sep 1996	KR858890	KR859099	–	–
	CBS 247.97	<i>Pezicula acericola</i>	<i>Acer spicatum</i>	Canada, Ontario	G. Verkley, 21 Sep 1996	KR858891	KR859100	–	–

(continued on next page)

Table 1 – (continued)

Species	Strain number ^a and status	Original name	Host/Substrate	Locality	Collector	GenBank Accession Number ^b			
						28S nrDNA	ITS	tub2	rpb2
	CBS 248.97	<i>Pezicula acericola</i>	<i>Acer spicatum</i>	Canada, Ontario	G. Verkley, 21 Sep 1996	KR858892	KR859101	–	–
<i>Pezicula aurantiaca</i>	CBS 201.46	<i>Pezicula aurantiaca</i>	<i>Alnus crispa</i> var. <i>mollis</i>	Canada	isol. J.W. Groves, No. 816-1	KR858893	KR859102	KF376335	KF376210
<i>Pezicula brunnea</i>	CBS 120291, ex-type	<i>Cryptosporiopsis brunnea</i>	<i>Gaultheria shallon</i>	Canada	T.R. Allen, May 1998	KR858894	KR859103	–	–
<i>Pezicula californiae</i>	CBS 124805, ex-type	<i>Pezicula californiae</i>	<i>Eucalyptus</i> sp.	USA, California	S. Denman, Mar 2009	KR858895	KR859104	KR859295	KR859332
<i>Pezicula carpinea</i>	CBS 324.97	<i>Pezicula carpinea</i>	<i>Carpinus betulus</i>	Netherlands	F.J. Stokman & G.C.N. van Zanen, 31 Jul 1996	KR858896	KR859105	KF376280	KF376160
	CBS 325.97	<i>Pezicula carpinea</i>	<i>Carpinus betulus</i>	Netherlands	F.J. Stokman & G.C.N. van Zanen, 31 Jul 1996	KR858897	KR859106	–	–
	CBS 921.96	<i>Pezicula carpinea</i>	<i>Carpinus betulus</i>	Germany	G. Verkley, 9 Jul 1996	KR858898	KR859107	KF376278	KF376159
	CBS 923.96, ex-epitype	<i>Pezicula carpinea</i>	<i>Carpinus betulus</i>	Germany	G. Verkley, 9 Jul 1996	KR858899	KR859108	KF376279	KF376158
<i>Pezicula cinnamomea</i>	CBS 100240	<i>Pezicula cinnamomea</i>	<i>Larix decidua</i>	Denmark	G. Verkley, 16 Sep 1997	KR858900	KR859109	–	–
	CBS 100241	<i>Pezicula cinnamomea</i>	<i>Larix decidua</i>	Denmark	G. Verkley, 16 Sep 1997	KR858901	KR859110	–	–
	CBS 100247	<i>Pezicula cinnamomea</i>	<i>Abies alba</i>	Denmark	G. Verkley, 15 Sep 1997	KR858902	KR859111	–	–
	CBS 101001	<i>Pezicula</i> sp.	<i>Taxus baccata</i>	Germany	Ullrich, Pflanzenschutzamt Frankfurt, Germany, Nov 1996	KR858903	KR859112	–	–
	CBS 112390	<i>Pezicula acericola</i>	<i>Fagus sylvatica</i>	Italy	R. Danti	KR858904	KR859113	–	–
	CBS 112391	<i>Pezicula acericola</i>	<i>Fagus sylvatica</i>	Italy	R. Danti	KR858905	KR859114	–	–
	CBS 184.50, ex-syntype of <i>Cryptosporiopsis balsameae</i>	<i>Pezicula cinnamomea</i>	<i>Abies balsamea</i>	Norway	H. Robak	KR858906	KR859115	–	–
	CBS 203.82, PD 81/666	<i>Pezicula cinnamomea</i>	<i>Chamaecyparis</i> sp.	Netherlands	–	KR858907	KR859116	–	–
	CBS 224.78	<i>Pezicula cinnamomea</i>	<i>Picea</i> sp.	Germany	isol. H. Butin	KR858908	KR859117	–	–
	CBS 226.96	<i>Pezicula cinnamomea</i>	<i>Fagus sylvatica</i>	France	G. Verkley, 7 Oct 1995	KR858909	KR859118	–	–
	CBS 227.96	<i>Pezicula cinnamomea</i>	<i>Fagus sylvatica</i>	France	G. Verkley, 17 Oct 1995	KR858910	KR859119	–	–
	CBS 236.97	<i>Pezicula cinnamomea</i>	<i>Acer saccharum</i>	USA, New York	G. Verkley, 29 Sep 1996	KR858911	KR859120	–	–
	CBS 237.97	<i>Pezicula cinnamomea</i>	<i>Acer saccharum</i>	USA, New York	G. Verkley, 29 Sep 1996	KR858912	KR859121	–	–
	CBS 238.96	<i>Pezicula cinnamomea</i>	<i>Betula pendula</i>	France	G. Verkley, 17 Oct 1995	KR858913	KR859122	–	–
	CBS 238.97	<i>Pezicula cinnamomea</i>	<i>Carpinus caroliniana</i>	USA, New York	G. Bills, 28 Sep 1996	KR858914	KR859123	–	–

CBS 239.96	<i>Pezicula cinnamomea</i>	<i>Fagus sylvatica</i>	France	G. Verkley, 17 Oct 1995	KR858916	KR859125	KF376323	KF376163
CBS 241.96	<i>Pezicula cinnamomea</i>	<i>Picea abies</i>	France	G. Verkley, 19 Oct 1995	KR858917	KR859126	—	—
CBS 242.96	<i>Pezicula cinnamomea</i>	<i>Picea abies</i>	France	G. Verkley, 19 Oct 1995	KR858918	KR859127	—	—
CBS 243.97	<i>Pezicula cinnamomea</i>	<i>Lindera bezoin</i>	USA	G. Verkley, 25 Sep 1996	KR858919	KR859128	—	—
CBS 244.97	<i>Pezicula</i> sp.	<i>Lindera bezoin</i>	USA	G. Verkley, 25 Sep 1996	KR858920	KR859129	—	—
CBS 255.97	<i>Pezicula cinnamomea</i>	<i>Carpinus caroliniana</i>	USA, New York	G. Bills, 28 Sep 1996	KR858921	KR859130	—	—
CBS 256.32	<i>Pezicula cinnamomea</i>	<i>Quercus</i> sp.	Denmark	isol. C.A. Jørgensen, No. 732	KR858922	KR859131	—	—
CBS 289.39	<i>Pezicula sporulosa</i>	<i>Picea sitchensis</i>	—	—	KR858923	KR859132	—	—
CBS 290.39, ex-type of <i>Pezicula plantarium</i>	<i>Pezicula cinnamomea</i>	<i>Prunus avium</i>	Germany	H.W. Wollenweber	KR858924	KR859133	—	—
CBS 315.96	<i>Pezicula cinnamomea</i>	<i>Abies procera</i>	Germany	R.D. Kehr	KR858925	KR859134	—	—
CBS 316.96	<i>Pezicula cinnamomea</i>	<i>Pseudotsuga menziesii</i>	France	G. Verkley, 19 Oct 1995	KR858926	KR859135	—	—
CBS 317.96	<i>Pezicula cinnamomea</i>	<i>Pseudotsuga menziesii</i>	France	G. Verkley, 19 Oct 1995	KR858927	KR859136	—	—
CBS 318.96	<i>Pezicula cinnamomea</i>	<i>Pseudotsuga menziesii</i>	France	G. Verkley, 19 Oct 1996	KR858928	KR859137	—	—
CBS 319.96	<i>Pezicula cinnamomea</i>	<i>Betula pendula</i>	Germany	G. Verkley, Schulz, Schrader & Kehr, 1 Nov 1995	KR858929	KR859138	—	—
CBS 320.96	<i>Pezicula cinnamomea</i>	<i>Betula pendula</i>	Germany	G. Verkley, Schulz, Schrader & Kehr, 1 Nov 1995	KR858930	KR859139	—	—
CBS 322.96	<i>Pezicula cinnamomea</i>	<i>Fagus sylvatica</i>	Germany	G. Verkley, Schulz, Schrader & Kehr, 1 Nov 1995	KR858931	KR859140	—	—
CBS 323.96	<i>Pezicula cinnamomea</i>	<i>Picea abies</i>	Germany	G. Verkley, Schulz, Schrader & Kehr, 1 Nov 1995	KR858932	KR859141	—	—
CBS 324.96	<i>Pezicula cinnamomea</i>	<i>Picea abies</i>	Germany	G. Verkley, Schulz, Schrader & Kehr, 1 Nov 1995	KR858933	KR859142	—	—
CBS 327.96	<i>Pezicula cinnamomea</i>	<i>Tilia cordata</i>	Germany	G. Verkley, Schulz, Schrader & Kehr, 1 Nov 1995	KR858934	KR859143	—	—
CBS 328.96	<i>Pezicula cinnamomea</i>	<i>Tilia cordata</i>	Germany	G. Verkley, Schulz, Schrader & Kehr, 1 Nov 1995	KR858935	KR859144	—	—
CBS 329.96	<i>Pezicula cinnamomea</i>	<i>Tilia cordata</i>	Germany	G. Verkley, Schulz, Schrader & Kehr, 1 Nov 1995	KR858936	KR859145	—	—

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Table 1 – (continued)

Species	Strain number ^a and status	Original name	Host/Substrate	Locality	Collector	GenBank Accession Number ^b			
						28S nrDNA	ITS	tub2	rpb2
	CBS 330.96	<i>Pezicula cinnamomea</i>	<i>Tilia cordata</i>	Germany	G. Verkley, Schulz, Schrader & Kehr, 1 Nov 1995	KR858937	KR859146	–	–
	CBS 355.51	<i>Pezicula cinnamomea</i>	<i>Betula verrucosa</i>	Portugal	isol. N. Ferreira dos Santos	KR858938	KR859147	–	–
	CBS 362.81	<i>Pezicula cinnamomea</i>	<i>Juniperus communis</i>	Switzerland	isol. O. Petrini	KR858939	KR859148	–	–
	CBS 481.97	<i>Pezicula cinnamomea</i>	<i>Betula pendula</i>	Canada, Ontario	G. Verkley, 4 Oct 1996	KR858940	KR859149	–	–
	CBS 482.97	<i>Pezicula cinnamomea</i>	<i>Betula pendula</i>	Canada, Ontario	G. Verkley, 4 Oct 1996	KR858941	AF281399	–	–
	CBS 516.69	<i>Pezicula acericola</i>	<i>Acer pseudoplatanus</i>	Netherlands	isol. J. Blok, 1969	KR858942	KR859150	–	–
	CBS 625.96	<i>Pezicula cinnamomea</i>	<i>Quercus robur</i>	Germany	G. Verkley, Schulz, Schrader & Kehr, 1 Nov 1995	KR858943	KR859151	KF376322	KF376164
	CBS 626.96	<i>Pezicula cinnamomea</i>	<i>Quercus robur</i>	Germany	G. Verkley, Schulz, Schrader & Kehr, 1 Nov 1995	KR858944	KR859152	KF376324	KF376162
	CBS 628.96	<i>Pezicula cinnamomea</i>	<i>Alnus glutinosa</i>	Germany	G. Verkley & Kehr, 2 Nov 1995	KR858945	KR859153	–	–
	CBS 629.96	<i>Pezicula cinnamomea</i>	<i>Alnus glutinosa</i>	Germany	G. Verkley & Kehr, 2 Nov 1995	KR858946	KR859154	–	–
	CBS 630.96	<i>Pezicula cinnamomea</i>	<i>Acer pseudoplatanus</i>	Germany	G. Verkley & Kehr, 2 Nov 1995	KR858947	KR859155	–	–
	CBS 631.96	<i>Pezicula cinnamomea</i>	<i>Acer pseudoplatanus</i>	Germany	G. Verkley & Kehr, 2 Nov 1995	KR858948	KR859156	–	–
	CBS 632.96	<i>Pezicula cinnamomea</i>	<i>Picea abies</i>	Netherlands	G. Verkley, 21 Nov 1995	KR858949	KR859157	–	–
	CBS 633.96	<i>Pezicula cinnamomea</i>	<i>Picea abies</i>	Netherlands	G. Verkley, 21 Nov 1995	KR858950	KR859158	–	–
	CBS 778.95	<i>Pezicula cinnamomea</i>	<i>Larix decidua</i>	Germany	L. Pehl, Sep 1994	KR858951	KR859159	–	–
	CBS 779.95	<i>Pezicula sporulosa</i>	<i>Cryptomeria japonica</i>	Netherlands	G. Verkley, 4 Apr 1995	KR858952	KR859160	–	–
	CBS 780.95	<i>Pezicula</i> sp.	<i>Larix decidua</i>	Netherlands	G. Verkley, 4 Apr 1995	KR858953	KR859161	–	–
	CBS 939.70	<i>Pezicula cinnamomea</i>	<i>Abies alba</i>	Germany	–	KR858954	KR859162	–	–
<i>Pezicula cornina</i>	CBS 285.39	<i>Pezicula corni</i>	<i>Cornus circinata</i>	Canada, Ontario	J.W. Groves, 22 Aug 1934	KR858955	KR859163	KR859296	KR859333
<i>Pezicula corticola</i>	CBS 259.31	<i>Pezicula corticola</i>	–	Denmark	isol. C.A. Jörgensen	KR858956	KR859164	–	–
	CBS 260.31	<i>Pezicula corticola</i>	–	Denmark	–	KR858957	KR859165	–	–
<i>Pezicula corylina</i>	CBS 140.22	<i>Pezicula corticola</i>	<i>Malus sylvestris</i>	UK	isol. G.G. Gilchrist	KR858958	KR859166	KR859297	KR859334
	CBS 243.38	<i>Pezicula corylina</i>	<i>Corylus rostrata</i>	Canada	J.W. Groves, Jul 1936	KR858959	KR859167	–	–
	CBS 249.97	<i>Pezicula corylina</i>	<i>Corylus cornuta</i> var. <i>cornuta</i>	Canada, Ontario	G. Verkley	KR858960	KR859168	KF376281	KF376161
	CBS 250.97	<i>Pezicula corylina</i>	<i>Corylus cornuta</i> var. <i>cornuta</i>	Canada, Ontario	G. Verkley, 20 Sep 1996	KR858961	KR859169	–	–

<i>Pezicula diversispora</i>	CBS 185.50, ex-syntype of <i>Cryptosporiopsis diversispora</i>	<i>Cryptosporiopsis diversispora</i>	<i>Picea abies</i>	Norway	isol. H. Robak	KR858962	KR859170	—	—
	CBS 282.47	<i>Pezicula</i> sp.	<i>Alnus glutinosa</i>	—	—	KR858963	KR859171	—	—
<i>Pezicula ericae</i>	CBS 158.93	<i>Cryptosporiopsis ericae</i>	<i>Tilia platyphyllos</i>	Germany	R. Schröer	KR858964	KR859172	—	—
	CBS 120290, UAMH 9445, ex-type	<i>Cryptosporiopsis ericae</i>	Roots of <i>Vaccinium membranaceum</i>	USA, Idaho	B. McCracken	KR858965	KR859173	—	—
	CBS 120292, UAMH 10419	<i>Cryptosporiopsis ericae</i>	Roots of <i>Gaultheria shallon</i>	Canada	T.R. Allen, 6 May 1998	KR858966	KR859174	—	—
<i>Pezicula eucrita</i>	CBS 100249	<i>Pezicula eucrita</i>	<i>Larix decidua</i>	Denmark	G. Verkley, 15 Sep 1997	KR858967	KR859175	—	—
	CBS 256.97	<i>Pezicula eucrita</i>	<i>Pinus sylvestris</i>	USA, New York	G. Verkley, 26 Sep 1996	KR858968	KR859176	—	—
	CBS 257.97	<i>Pezicula eucrita</i>	<i>Pinus sylvestris</i>	USA, New York	G. Verkley, 26 Sep 1996	KR858969	KR859177	—	—
	CBS 258.97	<i>Pezicula eucrita</i>	<i>Pinus sylvestris</i>	USA, New York	G. Verkley & R.P. Korf, 28 Sep 1996	KR858970	KR859178	—	—
	CBS 259.97	<i>Pezicula eucrita</i>	<i>Pinus sylvestris</i>	USA, New York	G. Verkley & R.P. Korf, 28 Sep 1996	KR858971	KR859179	KF376333	KF376205
	CBS 260.97	<i>Pezicula eucrita</i>	<i>Pinus sylvestris</i>	USA, New York	G. Verkey, H. Mashburn & R.P. Korf, 28 Sep 1996	KR858972	KR859180	—	—
	CBS 261.97	<i>Pezicula eucrita</i>	<i>Pinus sylvestris</i>	USA, New York	G. Verkey, H. Mashburn & R.P. Korf, 28 Sep 1996	KR858973	KR859181	—	—
	CBS 323.97	<i>Pezicula eucrita</i>	<i>Picea abies</i>	Germany	G. Verkley & Kehr, 2 Nov 1995	KR858974	KR859182	—	—
	CBS 326.96	<i>Pezicula eucrita</i>	<i>Larix decidua</i>	Germany	G. Verkley, Schulz, Schrader & Kehr, 1 Nov 1995	KR858975	KR859183	—	—
	CBS 627.96	<i>Pezicula eucrita</i>	<i>Pinus sylvestris</i>	Germany	R.D. Kehr & G. Verkley, 1 Nov 1995	KR858976	KR859184	—	—
	CBS 656.96	<i>Pezicula eucrita</i>	<i>Picea abies</i>	Germany	G. Verkley & Kehr, 2 Nov 1995	KR858977	KR859185	KF376332	KF376208
	CBS 657.96	<i>Pezicula eucrita</i>	<i>Picea abies</i>	Germany	G. Verkley & Kehr, 2 Nov 1995	KR858978	KR859186	—	—
	CBS 658.96	<i>Pezicula eucrita</i>	<i>Pinus sylvestris</i>	Netherlands	G. Verkley, 21 Nov 1995	KR858979	KR859187	—	—
	CBS 659.96	<i>Pezicula eucrita</i>	<i>Pinus sylvestris</i>	Netherlands	G. Verkley, 21 Nov 1995	KR858980	KR859188	—	—
	CBS 660.96	<i>Pezicula eucrita</i>	<i>Pinus sylvestris</i>	Netherlands	G. Verkley, 21 Nov 1995	KR858981	KR859189	—	—
	CBS 661.96	<i>Pezicula eucrita</i>	<i>Pinus sylvestris</i>	Netherlands	G. Verkley, 21 Nov 1995	KR858982	KR859190	—	—
	CBS 662.96	<i>Pezicula eucrita</i>	<i>Pseudotsuga menziesii</i>	Netherlands	G. Verkley, 21 Nov 1995	KR858983	KR859191	—	—
	CBS 663.96	<i>Pezicula eucrita</i>	<i>Pseudotsuga menziesii</i>	Netherlands	G. Verkley, 21 Nov 1995	KR858984	KR859192	—	—

(continued on next page)

Table 1 – (continued)

Species	Strain number ^a and status	Original name	Host/Substrate	Locality	Collector	GenBank Accession Number ^b			
						28S nrDNA	ITS	tub2	rpb2
	CBS 664.96	<i>Pezicula eucrita</i>	<i>Pinus sylvestris</i>	Netherlands	G. Verkley, 21 Nov 1995	KR858985	KR859193	–	–
	CBS 665.96	<i>Pezicula eucrita</i>	<i>Pinus sylvestris</i>	Netherlands	G. Verkley, 21 Nov 1995	KR858986	KR859194	–	–
	CBS 666.96	<i>Pezicula eucrita</i>	<i>Pinus sylvestris</i>	Netherlands	G. Verkley, 21 Nov 1995	KR858987	KR859195	–	–
	CBS 667.96	<i>Pezicula eucrita</i>	<i>Pinus sylvestris</i>	Netherlands	G. Verkley, 21 Nov 1995	KR858988	KR859196	–	–
	CBS 668.96	<i>Pezicula eucrita</i>	<i>Pinus sylvestris</i>	Netherlands	G. Verkley, 21 Nov 1995	KR858989	KR859197	–	–
	CBS 669.96	<i>Pezicula eucrita</i>	<i>Pinus sylvestris</i>	Netherlands	G. Verkley, 21 Nov 1995	KR858990	KR859198	–	–
	CBS 670.96	<i>Pezicula eucrita</i>	<i>Pinus nigra</i>	Netherlands	G. Verkley, 21 Nov 1995	KR858991	KR859199	–	–
	CBS 671.96	<i>Pezicula eucrita</i>	<i>Pinus nigra</i>	Netherlands	G. Verkley, 21 Nov 1995	KR858992	KR859200	–	–
<i>Pezicula fagacearum</i>	CBS 112400, ex-type	<i>Cryptosporiopsis</i> sp.	<i>Fagus sylvatica</i>	Italy	R. Danti	KR858993	KR859201	KR859298	KR859335
	CBS 112401	<i>Cryptosporiopsis</i> sp.	<i>Fagus sylvatica</i>	Italy	R. Danti	KR858994	KR859202	–	–
	CBS 112402	<i>Cryptosporiopsis</i> sp.	<i>Fagus sylvatica</i>	Italy	R. Danti	KR858995	KR859203	KR859299	KR859336
<i>Pezicula frangulae</i> subsp. <i>frangulae</i>	CBS 100244	<i>Pezicula frangulae</i> subsp. <i>frangulae</i>	<i>Rhamnus frangula</i>	Denmark	G. Verkley, 14 Sep 1997	KR858996	KR859204	KF376285	KF376211
	CBS 100275	<i>Pezicula frangulae</i> subsp. <i>frangulae</i>	<i>Rhamnus frangula</i>	Denmark	G. Verkley, 17 Sep 1997	KR858997	KR859205	–	–
	CBS 100276	<i>Pezicula frangulae</i> subsp. <i>frangulae</i>	<i>Rhamnus frangula</i>	Denmark	G. Verkley, 17 Sep 1997	KR858998	KR859206	–	–
	CBS 111538	<i>Pezicula frangulae</i> subsp. <i>frangulae</i>	<i>Rhamnus frangula</i>	Netherlands	G. Verkley, 5 Oct 2002	KR858999	KR859207	–	–
	CBS 286.39	<i>Pezicula frangulae</i> subsp. <i>frangulae</i>	<i>Rhamnus</i> sp.	Germany	isol. H.W. Wollenweber, No. 6128, 1937	KR859000	KR859208	–	–
	CBS 778.96	<i>Pezicula frangulae</i> subsp. <i>frangulae</i>	<i>Rhamnus frangula</i>	Netherlands	S. Helleman, Dec 1995	KR859001	KR859209	KF376286	KF376212
<i>Pezicula heterochroma</i>	CBS 199.46, ex-type	<i>Pezicula heterochroma</i>	<i>Alnus crispa</i> var. <i>mollis</i>	Canada, Nova Scotia	isol. J.W. Groves, No. 496-1	KR859002	KR859210	–	–
<i>Pezicula melanigena</i>	CBS 898.97, ex-type	<i>Cryptosporiopsis melanigena</i>	<i>Quercus petraea</i>	Austria	E. Halmschlager, 24 Jun 1993	KR859003	KR859211	–	–
<i>Pezicula microspora</i>	CBS 124641, ex-type	<i>Pezicula</i> sp.	Endophyte from <i>Berberis vulgaris</i>	Italy	–	KR859004	KR859212	KR859300	KR859337
<i>Pezicula neocinnamomea</i>	CBS 100248, ex-type	<i>Pezicula cinnamomea</i>	<i>Abies alba</i>	Denmark	G. Verkley, 15 Sep 1997	KR859005	KR859213	KF376328	KF376209
	CBS 112397	<i>Pezicula cinnamomea</i>	<i>Fagus sylvatica</i>	Italy	R. Danti	KR859006	KR859214	–	–
	CBS 116666	<i>Cryptosporiopsis</i>	<i>Ginkgo biloba</i>	Germany	J. Novozhilov	KR859007	KR859215	–	–
	CBS 219.78	<i>Pezicula cinnamomea</i>	<i>Malus sylvestris</i>	Switzerland	–	KR859008	KR859216	–	–
	CBS 257.32	<i>Pezicula cinnamomea</i>	<i>Tsuga canadensis</i>	–	–	KR859009	KR859217	–	–

	CBS 306.49	<i>Pezicula sporulosa</i>	<i>Picea abies</i>	Netherlands	isol. J.C. Went	KR859010	KR859218	—	—
	CBS 350.52	<i>Pezicula cinnamomea</i>	<i>Pinus nigra</i> var. <i>austriaca</i>	Italy	M. Ribaldi	KR859011	KR859219	—	—
	CBS 693.95	<i>Cryptosporiopsis diploidioides</i>	<i>Sorbus aria</i>	Germany	—	KR859012	KR859220	—	—
<i>Pezicula neoheterochroma</i>	CBS 127388, ex-type	<i>Pezicula</i> sp.	Branch of <i>Sorbus aucuparia</i>	Austria	W. Jaklitsch	KR859013	KR859221	KR859301	KR859338
<i>Pezicula neosporulosa</i>	CBS 100416	<i>Pezicula sporulosa</i>	<i>Amelanchier lamarckii</i>	Netherlands	G. Verkley, 25 Mar 1997	KR859014	KR859222	—	—
	CBS 101.96, ex-type	<i>Pezicula sporulosa</i>	<i>Abies alba</i>	Netherlands	G. Verkley, 11 Oct 1995	KR859015	KR859223	KF376305	KF376193
	CBS 102.96, ex-type	<i>Pezicula sporulosa</i>	<i>Abies alba</i>	Netherlands	G. Verkley, 11 Oct 1995	KR859016	KR859224	KF376318	KF376181
	CBS 634.96	<i>Pezicula sporulosa</i>	<i>Larix decidua</i>	Netherlands	G. Verkley, 26 Mar 1996	KR859017	KR859225	—	—
	CBS 635.96	<i>Pezicula sporulosa</i>	<i>Larix decidua</i>	Netherlands	G. Verkley, 26 Mar 1996	KR859018	KR859226	—	—
	CBS 636.96	<i>Pezicula sporulosa</i>	<i>Larix decidua</i>	Netherlands	G. Verkley, 26 Mar 1996	KR859019	KR859227	—	—
	CBS 660.95	<i>Pezicula sporulosa</i>	<i>Pseudotsuga menziesii</i>	Netherlands	G. Verkley, 21 Mar 1995	KR859020	KR859228	—	—
	CBS 661.95	<i>Pezicula sporulosa</i>	<i>Pseudotsuga menziesii</i>	Netherlands	G. Verkley, 21 Mar 1995	KR859021	KR859229	—	—
	CBS 723.95	<i>Pezicula sporulosa</i>	<i>Pseudotsuga menziesii</i>	Netherlands	G. Verkley, 21 Mar 1995	KR859022	KR859230	—	—
	CBS 724.95	<i>Pezicula</i> sp.	<i>Pseudotsuga menziesii</i>	Netherlands	G. Verkley, 21 Mar 1995	KR859023	KR859231	—	—
<i>Pezicula ocellata</i>	CBS 268.39	<i>Pezicula ocellata</i>	<i>Salix</i> sp.	Germany	isol. H.W. Wollenweber, 1937	KR859024	KR859232	KR859302	KR859339
	CBS 949.97	<i>Pezicula ocellata</i>	<i>Salix</i> sp.	Luxembourg	W. Gams, 6 May 1997	KR859025	KR859233	KF376284	KF376215
<i>Pezicula pruinosa</i>	CBS 292.39	<i>Pezicula pruinosa</i>	<i>Amelanchier</i> sp.	Canada, Ontario	J.W. Groves, 1 Aug 1934	KR859026	KR859234	—	—
<i>Pezicula pseudocinnamomea</i>	CBS 101000, ex-type	<i>Pezicula</i> sp.	<i>Castanea sativa</i>	Netherlands	G. Verkley, 25 Mar 1997	KR859027	KR859235	KR859303	KR859340
<i>Pezicula querciphila</i>	CBS 134525, UCROK766, ATCC MYA 4942, ex-type UCROK637	<i>Cryptosporiopsis querciphila</i>	<i>Quercus agrifolia</i>	USA, California	S.C. Lynch & A. Eskalen, 23 May 2010	—	JX144750	—	—
		<i>Cryptosporiopsis querciphila</i>	<i>Quercus agrifolia</i>	USA, California	S.C. Lynch & A. Eskalen, 23 May 2011	—	JX270770	—	—
<i>Pezicula radiculicola</i>	CBS 640.94, ex-type	<i>Cryptosporiopsis radiculicola</i>	<i>Quercus robur</i>	Poland	T. Kowalski, 8 Nov 1992	KR859028	KR859236	—	—
	CBS 681.83	<i>Cryptosporiopsis radiculicola</i>	<i>Quercus robur</i>	Austria	isol. J. Egger	KR859029	KR859237	—	—
<i>Pezicula rhizophila</i>	CBS 109839, ex-type	<i>Cryptosporiopsis rhizophila</i>	<i>Erica tetralix</i>	Netherlands	J. Zijlstra	KR859030	KR859238	—	—
	CBS 110602	<i>Cryptosporiopsis rhizophila</i>	<i>Calluna vulgaris</i>	Netherlands	isol. J. Zijlstra, 2002	KR859031	AY176754	—	—
	CBS 110603	<i>Cryptosporiopsis rhizophila</i>	<i>Calluna vulgaris</i>	Netherlands	isol. J. Zijlstra, 2003	—	KR859239	—	—

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Table 1 – (continued)

Species	Strain number ^a and status	Original name	Host/Substrate	Locality	Collector	GenBank Accession Number ^b			
						28S nrDNA	ITS	tub2	rpb2
	CBS 110604	<i>Cryptosporiopsis rhizophila</i>	<i>Calluna vulgaris</i>	Netherlands	isol. J. Zijlstra, 2000	KR859032	KR859240	–	–
	CBS 110606	<i>Cryptosporiopsis rhizophila</i>	<i>Erica tetralix</i>	Netherlands	isol. J. Zijlstra, 2004	KR859033	KR859241	–	–
	CBS 110607	<i>Cryptosporiopsis rhizophila</i>	<i>Erica tetralix</i>	Netherlands	isol. J. Zijlstra, 2005	KR859034	KR859242	–	–
	CBS 110609	<i>Cryptosporiopsis rhizophila</i>	<i>Erica tetralix</i>	Netherlands	isol. J. Zijlstra, 2000	KR859035	KR859243	–	–
	CBS 110612	<i>Cryptosporiopsis rhizophila</i>	<i>Vaccinium vitis-idaea</i>	Netherlands	isol. J. Zijlstra, 2001	KR859036	KR859244	–	–
	CBS 110617	<i>Cryptosporiopsis rhizophila</i>	<i>Vaccinium myrtillus</i>	Netherlands	isol. J. Zijlstra, 2006	KR859037	KR859245	–	–
<i>Pezicula rubi</i>	CBS 100246	<i>Pezicula rubi</i>	<i>Rubus</i> sp.	Denmark	G. Verkley, 14 Sep 1997	KR859038	KR859246	–	–
	CBS 111546	<i>Pezicula rubi</i>	<i>Rubus</i> sp.	Netherlands	G. Verkley, 5 Oct 2002	KR859039	KR859247	–	–
	CBS 251.97	<i>Pezicula rubi</i>	<i>Rubus</i> sp.	USA, New York	G. Verkley, 28 Sep 1996	KR859040	KR859248	–	–
	CBS 252.97	<i>Pezicula rubi</i>	<i>Rubus</i> sp.	USA, New York	G. Verkley, 28 Sep 1996	KR859041	KR859249	–	–
	CBS 253.97	<i>Pezicula rubi</i>	<i>Rubus</i> sp.	USA, New York	G. Verkley, 29 Sep 1996	KR859042	KR859250	KF376329	KF376204
	CBS 254.97	<i>Pezicula rubi</i>	<i>Rubus</i> sp.	USA, New York	G. Verkley, 29 Sep 1996	KR859043	KR859251	–	–
	CBS 293.39	<i>Pezicula rubi</i>	<i>Rubus</i> sp.	Canada, Ontario	J.W. Groves, 26 Oct 1935	KR859044	KR859252	–	–
	CBS 593.96	<i>Pezicula rubi</i>	<i>Rubus</i> sp.	Netherlands	G. Verkley, 27 Feb 1996	KR859045	KR859253	KF376330	KF376203
<i>Pezicula sporulosa</i>	CBS 109664, IMI 385753	<i>Pezicula</i> sp.	–	UK	H.C. Evans, Jan 2001	KR859046	KR859254	–	–
	CBS 114361	<i>Pezicula cinnamomea</i>	<i>Cercidiphyllum japonicum</i>	Russia	V. Mel'nik, 10 Jul 2003	KR859047	KR859255	–	–
	CBS 116667	<i>Pezicula sporulosa</i>	<i>Pterocarya rhoifolia</i>	Russia	V. Mel'nik, 22 Jul 2004	KR859048	KR859256	–	–
	CBS 157.93	<i>Pezicula sporulosa</i>	<i>Tilia platyphyllos</i>	Germany	R. Schröer	KR859049	KR859257	–	–
	CBS 191.39, ex-type of <i>Gloeosporium longisporum</i>	<i>Pezicula sporulosa</i>	<i>Pseudotsuga menziesii</i>	UK	isol. T.R. Peace	KR859050	KR859258	–	–
	CBS 197.69	<i>Pezicula hamamelidis</i>	<i>Hamamelis mollis</i>	Netherlands	H.A. van der Aa	KR859051	KR859259	–	–
	CBS 215.97	<i>Pezicula sporulosa</i>	<i>Fagus grandifolia</i>	USA	G. Verkley, 29 Sep 1996	KR859052	KR859260	–	–
	CBS 224.96, ex-type	<i>Pezicula sporulosa</i>	<i>Larix decidua</i>	Netherlands	G. Verkley, 21 Nov 1995	KR859053	KR859261	KF376326	KF376201
	CBS 225.96, ex-type	<i>Pezicula sporulosa</i>	<i>Larix decidua</i>	Netherlands	G. Verkley, 21 Nov 1995	KR859054	KR859262	KF376327	KF376202

	CBS 235.97	<i>Pezizula sporulosa</i>	<i>Fagus grandifolia</i>	USA	G. Verkley, 29 Sep 1996	KR859055	KR859263	–	–
	CBS 261.31	<i>Pezizula sporulosa</i>	<i>Larix decidua</i>	UK, Scotland	–	KR859056	KR859264	–	–
	CBS 262.31	<i>Pezizula sporulosa</i>	<i>Cupressus lawsoniana</i>	UK	M.J.F. Gregor-Wilson	KR859057	AF141180	–	–
	CBS 298.58	<i>Pezizula sporulosa</i>	<i>Quercus robur</i>	Netherlands	isol. Davids, Sep 1958	KR859058	KR859265	–	–
<i>Pezizula subcarnea</i>	CBS 203.46	<i>Pezizula subcarnea</i>	–	Canada	J.W. Groves, Oct 1946	KR859059	AF141171	–	–
<i>Pezizula</i> sp. 1	CBS 202.46	<i>Pezizula carnea</i>	Twig of <i>Acer</i> sp.	Canada	isol. J.W. Groves	KR859060	KR859266	KR859304	KR859341
<i>Pezizula</i> sp. 2	CBS 230.79	<i>Pezizula eucrita</i>	<i>Acer platanoides</i>	Germany	isol. J. Graf	KR859061	KR859267	–	–
<i>Pezizula</i> sp. 3	CBS 268.78	<i>Pezizula pruinosa</i>	<i>Prunus domestica</i>	Belgium	isol. J. Fraselle	KR859062	KR859268	KR859305	KR859342
<i>Pezizula</i> sp. 4	CBS 242.60	<i>Pezizula cinnamomea</i>	<i>Quercus</i> sp.	Netherlands	isol. A.C. Stolk	KR859063	KR859269	KR859306	KR859343
<i>Pezizula</i> sp. 5	CBS 267.39	<i>Pezizula ocellata</i>	<i>Salix</i> sp.	Germany	H.W. Wollenweber, 1938	KR859064	KR859270	KR859307	KR859344
<i>Pezizula</i> sp. 6	CBS 433.75	<i>Cryptosporiopsis</i>	<i>Eucalyptus</i> sp.	Australia, Australian Capital Territory	–	KR859065	KR859271	–	–
<i>Pezizula</i> sp. 7	CBS 282.39	<i>Pezizula carpinea</i>	<i>Carpinus caroliniana</i>	Canada, Ontario	H.S. Jackson, 6 Nov 1932	KR859066	KR859272	KR859308	DQ479934
	CBS 283.39	<i>Pezizula carpinea</i>	<i>Carpinus caroliniana</i>	Canada, Ontario	J.W. Groves, 29 May 1933	KR859067	KR859273	–	–
<i>Pezizula</i> sp. 8	CBS 450.68	<i>Pezizula corylina</i>	<i>Corylus avellana</i>	Belgium	W. Gams, Jun 1968	KR859068	KR859274	KR859309	KR859345
<i>Phlyctema vagabunda</i>	CBS 109875	<i>Neofabraea alba</i>	<i>Fraxinus americana</i>	USA, Michigan	A. Rossman, Jul 2001	KR859069	KR859275	AY064702	KR859346
	CBS 304.62	<i>Neofabraea alba</i>	<i>Malus sylvestris</i>	South Africa	isol. T.N. Matthee	KR859070	KR859276	KR859310	KR859347
<i>Phlyctema vincetoxici</i>	CBS 102469	<i>Phlyctema caulium</i>	<i>Paeonia</i> sp.	New Zealand	M. Braithwaite	KR859071	KR859277	KR859311	KR859348
	CBS 123727, ex-type	<i>Phlyctema vincetoxici</i>	<i>Vincetoxicum officinale</i>	Czech Republic	G. Verkley, 17 Sep 2008	KR859072	KR859278	KR859312	KR859349
<i>Pseudofabraea citricarpa</i>	CBS 130297, CGMCC 3.14880, ex-type	<i>Cryptosporiopsis citricarpa</i>	<i>Citrus unshiu</i>	China	L. Zhu, H.Y. Li & D.K. Ding, 27 Mar 2010	KR859073	KR859279	KR859313	KR859350
	CBS 130532	<i>Cryptosporiopsis citricarpa</i>	Shoot of <i>Citrus unshiu</i>	China	L. Zhu, 22 Feb 2011	KR859074	KR859280	KR859314	KR859351
	CBS 130533	<i>Cryptosporiopsis citricarpa</i>	Leaf of <i>Citrus unshiu</i>	China	L. Zhu, 22 Feb 2011	KR859075	KR859281	KR859315	KR859352
<i>Rhizodermea veluwensis</i>	CBS 110605, ex-type	<i>Rhizodermea veluwensis</i>	Roots of <i>Erica tetralix</i>	Netherlands	isol. J. Zijlstra	KR859076	KR859282	KR859316	KR859353
	CBS 110615	<i>Rhizodermea veluwensis</i>	Roots of <i>Vaccinium myrtillus</i>	Netherlands	isol. J. Zijlstra	KR859077	KR859283	KR859317	KR859354

a ATCC: American Type Culture Collection, Virginia, U.S.A.; CBS: CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands; CGMCC: China General Microbiological Culture Collection Center, Institute of Microbiology, Chinese Academy of Sciences, Beijing, China; CPC: Culture collection of Pedro Crous, housed at CBS; DAOM: Plant Research Institute, Department of Agriculture (Mycology), Ottawa, Canada; ICMP: International Collection of Microorganisms from Plants, Landcare Research, Auckland, New Zealand; IMI: International Mycological Institute, CBI-Bioscience, Egham, Basingstoke, UK; OSC: Oregon State University Herbarium, Department of Botany and Plant Pathology, 2082 Cordley Hall, U.S.A.; PD: Plant Protection Service, nVWA, Division Plant, Wageningen, The Netherlands; UAMH: University of Alberta Mould Herbarium and Culture Collection, Edmonton, Canada.

b 28S nrDNA: large subunit (28S) of the nrRNA gene operon; ITS: internal transcribed spacers and intervening 5.8S nrDNA; tub2: partial beta-tubulin gene; rpb2: partial RNA polymerase II second largest subunit region.

at 48 °C (LSU and ITS) or 55 °C (*tub2*) for 45 s, and extension at 72 °C for 2 min, followed by a final extension at 72 °C for 10 min. PCR conditions for *rpb2* followed Woudenberg et al. (2013). PCR products were sequenced in both directions, following the method of Gomes et al. (2013).

Phylogenetic analyses

Alignments of different gene regions, including sequences obtained from this study and sequences downloaded from GenBank, were initially performed by using the MAFFT v.7 online server (<http://mafft.cbrc.jp/alignment/server/index.html>), and then manually adjusted in BioEdit v.7.0.5.2 (Hall 1999). To check the congruence of different gene regions, a 70 % neighbour-joining (NJ) reciprocal bootstrap method with maximum likelihood distance was performed (Mason-Gamer & Kellogg 1996; Gueidan et al. 2007). Potential conflicts among different gene regions were checked by comparing the topologies of the resulting NJ trees (Lombard et al. 2010). Maximum likelihood (ML), maximum parsimony (MP), and Bayesian analyses were used to study the phylogeny of the multi-gene and single-gene datasets. ML analyses were performed in RAxML v.7.0.3 (Stamatakis 2006) using a GTRGAMMA model including 1000 bootstrap replicates. MP analyses were conducted in PAUP v.4.0b10 (Swofford 2003). The heuristic search option was 1000 random taxa addition replicates, and the tree bisection-reconnection (TBR) as the branch-swapping algorithm. All characters were weighted equally and alignment gaps were treated as missing data. Bootstrap analyses were based on 1000 replications. Tree length (TL), consistency index (CI), retention index (RI), and rescaled consistency index (RC) were also calculated. Bayesian analyses were performed in MrBayes v.3.2.1 (Ronquist et al. 2012). The best nucleotide substitution models of different gene regions were selected by using MrModelTest v.2.3 (Nylander 2004). The Markov Chain Monte Carlo (MCMC) analysis used four chains and started from a random tree topology. The heating parameter was set to 0.1. Analyses stopped once the average standard deviation of split frequencies were below 0.01. Sequences generated in this study were deposited in GenBank (Table 1). Alignments and phylogenetic trees were deposited in TreeBASE, and nomenclatural novelties in MycoBank (Crous et al. 2004).

Morphology

Morphological examination followed the method of Verkley (1999) with minor modifications. Colonised agar blocks (4–5 mm squares) were taken from the margins of actively growing subcultures and placed upside down onto fresh OA and MEA plates, which were placed in an incubator under near-ultraviolet light (12 h light: 12 h dark) at 18 °C. Colony diameters were measured after 7, 14, and 21 d. Colony colours were described according to Rayner (1970). Morphological descriptions were based on the cultures sporulating on OA. For some isolates, OA plates were supplemented with sterile nettle stems (*Anthriscus sylvestris*), or direct inoculation into apple fruit (*Malus domestica*) (Garipey et al. 2005) was used to induce sporulation. Dried specimens were rehydrated by using tap-water for 2–3 h, or in moist chambers overnight. Sections of rehydrated materials were made by hand or by using a Leica

CM1100 cryostat (Setpoint Technologies) at –20 °C. Melzer's reagent (Mlz) (3.75 g KI, 1.25 g I₂, in 50 ml H₂O and 50 ml chloralhydrate) was used to observe the reaction of ascus tips with iodine, and the materials were pretreated by KOH (3 %). Fungal structures were mounted in tap water. Measurements were made at ×1000 magnification by Nikon NIS-Elements D3.0 imaging software, with at least 30 measurements per structure. The number of spores (n) measured, the extremes of measurements, the average ± Standard Deviation (av.), and the length/width ratio of ascospores (L/W) followed the methods of Verkley (1999).

Results

Phylogenetic analyses

Overview phylogeny: LSU sequences obtained from this study were combined with those of related taxa downloaded from GenBank to construct a phylogeny of closely related genera. Unfortunately, neither Maximum Likelihood nor Bayesian analysis resulted in well-resolved phylogenetic trees (data not shown). Internal nodes were poorly supported showing basal polytomies, indicating that LSU sequences had limited taxonomic value for this group of fungi. Therefore, multi-gene phylogenetic analyses were conducted, using four gene regions (ITS, LSU, *rpb2*, and *tub2*) and 61 selected isolates, including the outgroup *Infundichalara microchona* (CBS 175.74), which is phylogenetically related to the studied fungi (Réblová et al. 2011).

The 70 % reciprocal bootstrap tree based on the *rpb2* dataset was well resolved. In contrast, the other three gene regions (ITS, LSU, and *tub2*) showed less phylogenetic information at generic level with several basal polytomies. There was only a single minor conflict (the placement of *Ph. vagabunda*) between the ITS and *rpb2* dataset. All terminal clades were well resolved in all four gene regions, showing an identical result with no significant conflict. DNA sequences of the four gene regions were therefore concatenated for the phylogenetic analyses.

The combined dataset consisted of 2695 characters (including gaps), of which 1904 were constant, 112 were variable and parsimony uninformative, and 664 were parsimony informative. Parsimony analysis of the aligned sequences yielded four equally most parsimonious trees (TL = 2574 steps, CI = 0.444, RI = 0.827, RC = 0.367). For the Bayesian inference, the GTR + I + G model was selected for ITS, LSU, *rpb2*, and *tub2*. The Bayesian analysis lasted 235 000 generations and the consensus trees and posterior probabilities were calculated from the 472 trees left after discarding 118 trees (the first 25 % of generations) for burn-in. The MP and Bayesian analyses produced phylogenetic trees with the same topology as the ML tree. Therefore, only the ML tree (Fig 1) is presented with distance (Neighbour Joining with HKY85 substitution model), ML and MP bootstrap support values (NJBS, MLBS and MPBS) greater than 70 %, and Bayesian posterior probabilities (PP) greater than 0.95 plotted against the tree.

The multi-gene phylogenetic tree (Fig 1) resulted in six genera with high support values. The *Pezicula* clade consisted of 38 isolates, including the type species *Pezicula carpinea*, and

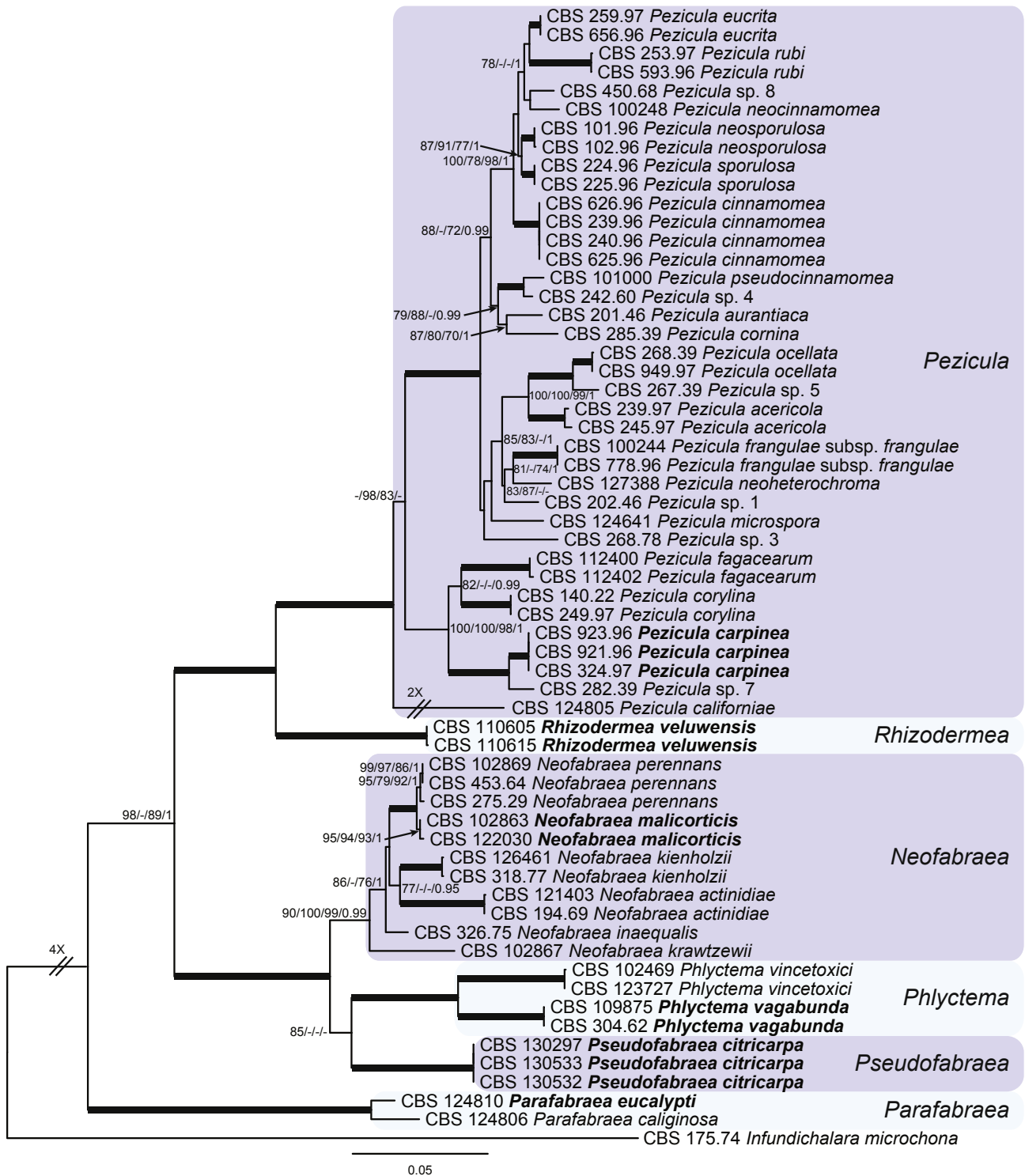


Fig 1 – The ML phylogenetic tree based on the multi-gene dataset (ITS-LSU-rpb2-tub2). Bootstrap support values greater than 70 % and Bayesian posterior probabilities greater than 0.95 are given at the nodes (MLBS/NJBS/MPBS/PP). Thickened branches are fully supported (100/100/100/1). The scale bar represents the number of nucleotide substitutions per site. The genera are indicated with blocks of different colours and the type species of each genus in bold face. The tree is rooted to *Infundichalara microchona* (CBS 175.74).

contained two well-supported subclades, with *Pezicula californiae* (CBS 124805) forming a single basal lineage with a long branch in the clade. Two isolates of *Rhizodermea veluwensis* formed a distinct clade, positioned as a sister lineage to

Pezicula. The *Neofabraea* s. str. clade, *Phlyctema* clade, and the *Pseudofabraea* gen. nov. clade clustered together with strong support. Species in these three clades were previously considered one genus, namely *Neofabraea*, but they proved to also

vary greatly in morphology. In the phylogenetic tree they formed three distinct clades, representing three different genera. Two isolates (CBS 124810 and CBS 124806) formed a basal clade, representing a new genus *Parafabraea*.

Species of Pezicula: A Bayesian analysis was conducted based on the ITS sequences of all *Pezicula* isolates. The internal nodes of the Bayesian tree were poorly supported, resulting in basal polytomies. The terminal clades were well supported, and the resulting species are consistent with results of a previous study (Yuan & Verkley 2014) based on multi-gene data. The ITS sequence data proved suitable to delimit species of *Pezicula*.

The ITS dataset consisted of 125 isolates that were selected based on ITS sequences, hosts, geographic locations, as well as two outgroups (CBS 122030 and CBS 124810). This dataset contained 532 characters (including gaps), of which 377 were constant, 46 were variable and parsimony uninformative, and 109 were parsimony informative. Parsimony analysis of the aligned sequences yielded the maximum limit of 1000 equally most parsimonious trees (TL = 401 steps, CI = 0.536, RI = 0.853, RC = 0.448). A GTR + I + G model was selected for Bayesian analysis. The Bayesian analysis lasted 3 870 000 generations and the consensus trees and posterior probabilities were calculated from the 5808 trees remaining after discarding 1934 trees (the first 25 % of generations) for burn-in. The ML and MP analyses produced phylogenetic trees with the same topology as the Bayesian tree. Therefore, only the Bayesian tree is presented (Fig 2), with ML and MP bootstrap values also plotted on the tree. The phylogenetic tree (Fig 2) delimited 35 species clades, 13 of which lack a clear identification, and might represent novel species.

Taxonomy

Neofabraea H.S. Jacks., *Rep. Oregon Exp. Sta. 1911–1912*: 187 (1913).

Type species: *Neofabraea malicorticis* (Cordley) H.S. Jacks.

Apothecia erumpent from bark, sessile to short-stalked, solitary or in clusters on a basal stroma. Disc often not well-delimited, circular, elliptical, or irregular and merged, greyish, flesh-coloured to pale reddish or brownish, drying darker, 0.5–2.0 mm diam. Asci inoperculate, cylindrical-clavate, apex rounded or truncate-rounded, attenuated into a stalk of variable length, crozier present, 8-spored; apical apparatus with a well-developed apical thickening, IKI+ or –, blue in herbarium material, Mlz+ or –. *Ascospores* inequilateral, elongated ellipsoid, ends rounded, straight or curved, aseptate, thin-walled, smooth, hyaline, with granular contents or small oil droplets; later septate, sometimes germinating or forming conidia from minute openings or phialides. *Paraphyses* numerous, filiform, septate, obtuse, simple or branched, hyaline, smooth-walled, apical cells mostly slightly swollen. *Conidiomata* erumpent from bark, stromatic, acervular, plane to pulvinate. *Conidiophores* simple or branched, smooth, hyaline, acrogenous or acropleurogenous. *Conidiogenous cells* discrete or integrated, determinate, phialidic, cylindrical to narrowly ampulliform, giving rise to macro- and/or microconidia. *Macroconidia* cylindrical-fusiform, allantoid to ellipsoid, straight or curved, rounded or somewhat pointed at apex, rounded or attenuated and with an indistinct, barely or non-

protruding scar at base, smooth, aseptate, hyaline, and thin-walled when liberated, mostly filled with numerous oil droplets; later becoming septate and brown. *Microconidia* present or absent, cylindrical, rounded at apex, narrowly truncate at base, aseptate, hyaline, thin- and smooth-walled, with minute granular contents.

Notes: The apothecia of *Neofabraea* and *Pezicula* are similar, but excipular tissues are less differentiated in *Neofabraea* (Verkley 1999). The macroconidia of *Neofabraea* are more strongly curved and the basal scar less distinct than those of *Pezicula*. *Pezicula* species have two types of conidiogenesis: conidiogenous cells are determinate and phialidic, or indeterminate and proliferating percurrently. However, only phialidic conidiogenous cells are observed in *Neofabraea* species. Most species in *Pezicula* are only known as saprobes or harmless endophytes, and occasionally as weak plant pathogens, while *Neofabraea* species are pathogenic to their hosts, and are reported as causal agents of many plant diseases.

Neofabraea inaequalis (M. Morelet) Chen, Verkley & Crous, *comb. nov.*

Mycobank MB812325.

Basionym: *Cryptosporiopsis inaequalis* M. Morelet, *Bull. Soc. Sci. Nat. Arch. Toulon & Var.* 205: 9 (1973).

Material examined: France, Charmes, Meurthe et Moselle, on twigs of *Chamaecyparis* sp., 1973, M. Morelet (CBS H-6971 holotype, ex-type culture CBS 326.75).

Notes: Sexual morph unknown. The living ex-type culture CBS 326.75 was sterile. According to Verkley (1999), this isolate only produced microconidia, 9–13 × 1.2–1.6 µm. Although the morphological data is insufficient for a generic placement, the phylogenetic analyses place this species in *Neofabraea*. According to Morelet (1973), *N. inaequalis* was associated with cankers on *Chamaecyparis* sp.

Neofabraea malicorticis (Cordley) H.S. Jacks., *Rep. Oregon Exp. Sta. 1911–1912*: 187 (1913). (Fig 3).

Basionym: *Gloeosporium malicorticis* Cordley, *Bot. Gaz.* 30: 57. 1900.

Synonyms: *Cryptosporiopsis malicorticis* (Cordley) Nannf., *Nova Acta R. Soc. Sci. Upsal.*, Ser. 4, 8: 91 (1932).

Pezicula malicorticis (Cordley) Nannf., *Nova Acta R. Soc. Sci. Upsal.*, Ser. 4, 8: 91 (1932).

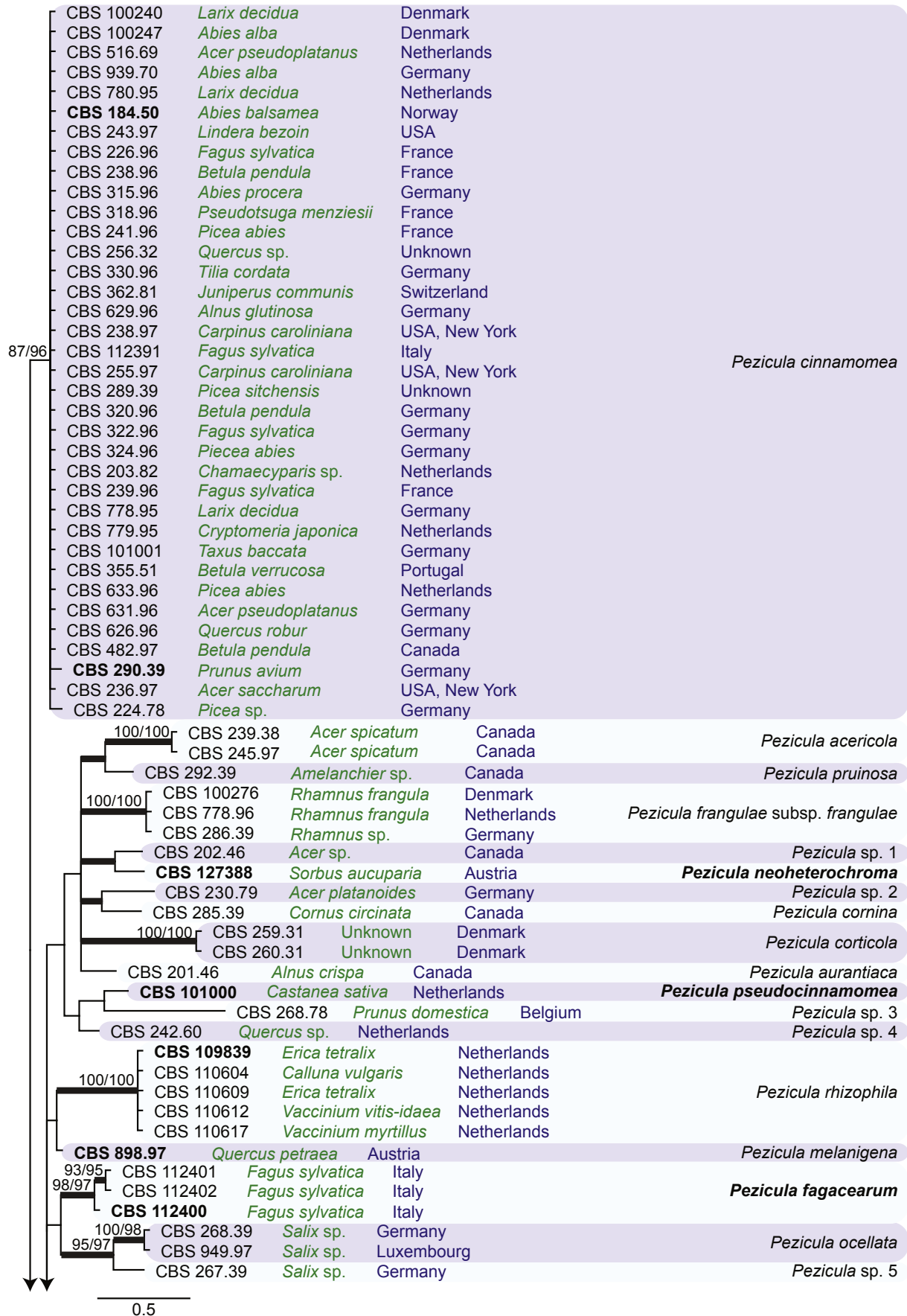
Macrophoma curvispora Peck, *Bull. Torrey Bot. Club* 27: 21 (1900).

Cryptosporiopsis curvispora (Peck) Gremmen, in Boerema & Gremmen, *Tijdschr. Plziekt.* 65: 172 (1959).

Description and illustrations: Verkley (1999).

In vitro (CBS 122030): *Conidiomata* sporodochia-like on surface of OA. *Macroconidia* long ellipsoid to fusiform, slightly curved, ends somewhat pointed, aseptate, 16–31 × 4.5–6 µm (av. 21.1–27.2 × 4.7–5.4 µm, n = 46). *Microconidia* only appear within for a short time span, cylindrical, straight, rounded at apex, truncate at base, hyaline, 6.5–10.0 × 2–2.5 µm. Intermediate conidia between macro- and micro-conidia frequent produced from conidiogenous cells, or directly from conidiogenous loci on mycelial hyphae, varying in size and shape.

Culture characteristics: Colonies on OA reaching 48 mm diam after 14 d, 71 mm after 21 d; flat with radially arranged synnema-like hyphal clusters, white, cottony, with a clear droplet on top; margin entire with a low fringe of white radiating hyphae; surface smooth, in centre hazel to olivaceous due



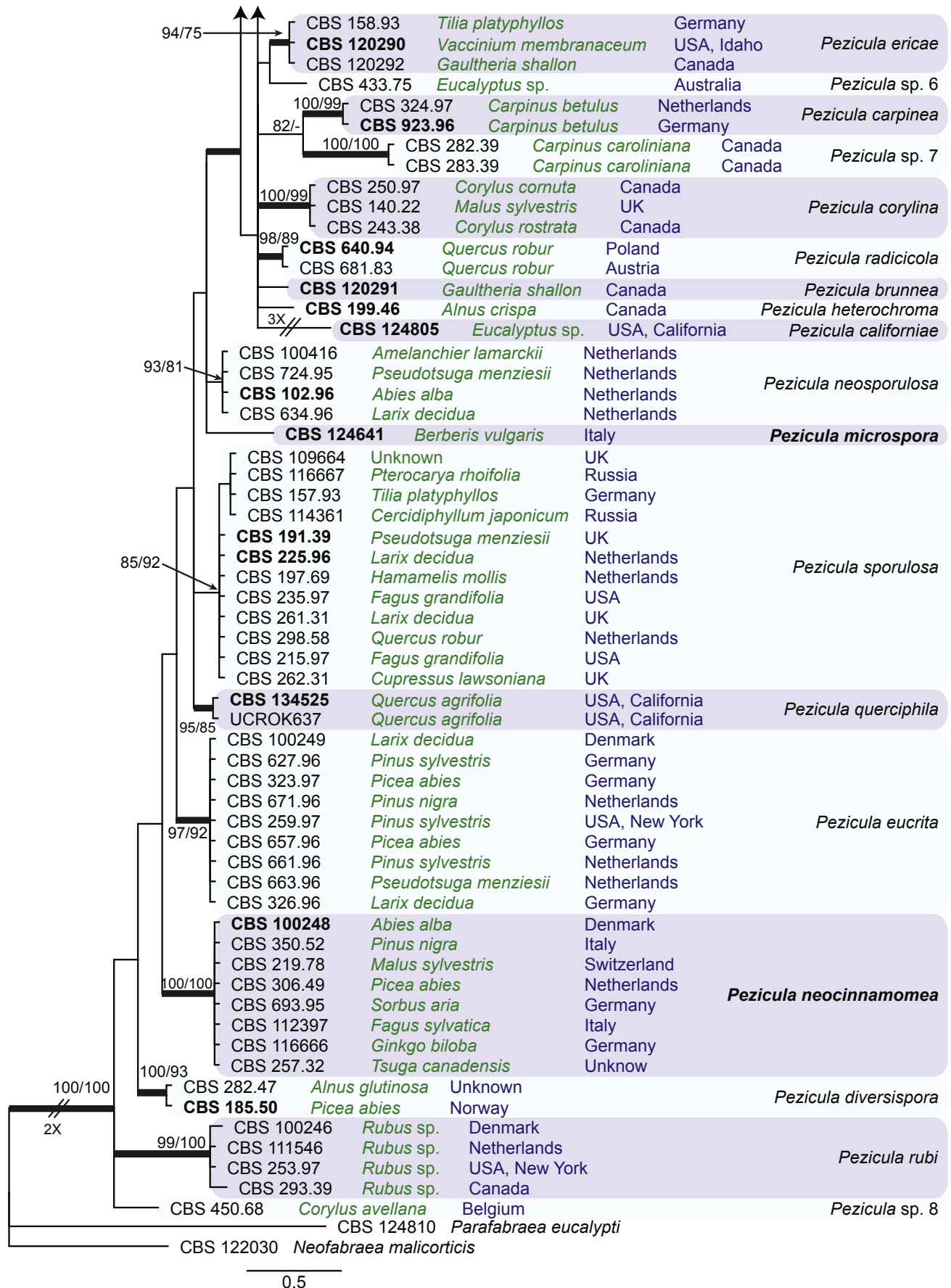


Fig 2 – (Continued)

to submerged mycelium, darkening with age, outer zone white; reverse concolourous. On MEA reaching 30–32 mm diam after 14 d, 49 mm after 21 d; flat, slightly folded in centre, edge entire; aerial mycelium sparse, white, only present at centre, dark coral, fading to flesh or white in outer zone; no diffusing pigment.

Material examined: Canada, British Columbia, Balfour, apple tree canker, May 1995, isol. J.E. Rahe, CBS 102863 = DAOM 227083 = CAL 103. USA, Oregon, Corvallis, on *Malus* sp., holotype of *Gloeosporium malicorticis* in OSC; USA, Oregon, Hood River, on apples (*Malus* sp.), date unknown, collector unknown (CBS H-22219, epitype of *Gloeosporium malicorticis* designated here, MBT201265, ex-epitype culture CBS 122030 = OSC 100036).

Notes: *Neofabraea malicorticis* causes anthracnose canker and Bull's eye rot on apple and pear. Before Jackson (1913) discovered the sexual morph of this fungus, it was known as *Gloeosporium malicorticis* or *Macrophoma curvispora*. *Macrophoma curvispora* (24 Jan. 1900) was described a few months prior to *Gloeosporium malicorticis* (19 July 1900). When Jackson (1913) proposed the new genus *Neofabraea*, he selected *N. malicorticis* as type species (Jackson 1913). Since then, the name *N. malicorticis* has been widely used (Verkley 1999; de Jong et al. 2001; Garipey et al. 2005; Spotts et al. 2009; Johnston et al. 2014), and needs to be formally proposed for conservation.

Cordley (1900) described *G. malicorticis* indicating that the examined fungus was from Corvallis in Oregon, occurring on apple branches with anthracnose canker. Since the study by Verkley (1999), the type specimen has been located at OSC. The isolate CBS 122030 forms the typical asexual morph of *N. malicorticis* on inoculated apples, and the size of its macroconidia (17–28 × 4–6 µm, on inoculated apple) correspond well with Cordley's original description (16–28 × 5–7 µm). Since it is also from the same host and geographic location, CBS H-22219 is designated here as epitype, with CBS 122030 as ex-epitype culture.

Pezicula Tul. & C. Tul., *Sel. Fung. Carpol.* 3: 182 (1865).

Synonyms: *Ocellaria* (Tul. & C. Tul.) P. Karst., *Bidr. Känn. Finl. Nat. Folk* 19: 21, 242 (1871).

Stictis subgen. *Ocellaria* Tul. & C. Tul., *Select. Fung. Carpol.* 3: 128 (1865).

Dermatella P. Karst., *Bidr. Känn. Finl. Nat. Folk* 19: 16, 209 (1871).

Dermatina (Sacc.) Höhn., *Sber. Akad. Wiss. Wien, Math.-naturw. Kl., Abt. 1* 118: 1512 (1909).

Cryptosporiopsis Bubák & Kabát, *Hedwigia* 52: 360 (1912).

Pachydiscula Höhn., *Z. Gärungsphysiol.* 5: 210 (1915).

Lagynodella Petr., in Sydow & Petrak, *Annls mycol.* 20: 207 (1922).

Additional synonyms in Verkley (1999).

Type species: *Pezicula carpinea* (Pers.) Tul. & C. Tul. ex Fuckel.

Apothecia erumpent, sessile to short-stalked, solitary or in clusters on a basal stroma. Disc circular to irregular, pruinose, pale whitish, yellow, orange, olivaceous, or orange-brown to dark brown, 0.2–3.0 mm diam. Margin first entire, often with a slightly raised rim, persistent, or irregularly torn. Asci inoperculate, cylindrical-clavate to clavate, crozier present, usually 8- or 4-spored; apical apparatus with a well-developed apical thickening, IKI+ or –, Mlz–, but often blue after pre-treatment with KOH. Ascospores inequilateral, ovoid, ellipsoid, or fusoid, straight or curved, thin-walled, smooth, hyaline, filled with numerous oil droplets, aseptate; mostly later 1–3(–7)-septate, or muriform, sometimes forming clavate to cylindrical, aseptate, hyaline, thin- and smooth-walled conidia from minute openings or phialides produced during germination. Paraphyses filiform, septate, simple or branched, hyaline, smooth-walled, apical cells often swollen. *Conidiomata* immersed or erumpent, eustromatic with a single or several fusing cavities formed on basal stroma, subglobose, irregularly pulvinate to conical or claviform; sometimes stromatic acervular, almost plane to pustulate. *Conidiophores* simple or branched, smooth, hyaline, acrogenous or acropleurogenous. *Conidiogenous cells* discrete or integrated, determinate, phialidic, or indeterminate, proliferating percurrently, cylindrical to narrowly ampulliform, giving rise to macro- and/or microconidia. *Macroconidia* present or absent, ellipsoid, pyriform, claviform or fusoid, rounded or somewhat pointed at apex, rounded or attenuated and with a barely or distinctly protruding scar at base, aseptate, thin-walled, hyaline, smooth, mostly filled with numerous oil droplets, becoming 1–3(–6)-septate, finally often muriform; sometimes forming microconidia from minute opening in wall or from phialides. *Microconidia* present or absent, cylindrical, apex rounded, base truncate, aseptate, hyaline, smooth, thin-walled, contents granular (Adapted from Verkley 1999).

Notes: The generic description of *Pezicula* was emended from Verkley (1999). Most *Pezicula* species treated in Verkley's monograph are supported in the present phylogenetic study. However, the cryptosporiopsis-like species occurring on *Eucalyptus* leaves have since been shown to represent a distinct genus, *Pseudoplagiostoma*, representing a distinct family in the *Diaporthales* (Cheewangkoon et al. 2010).

Pezicula carpinea (Pers.) Tul. & C. Tul. ex Fuckel, *Jahrb. Nas-sauischen Vereins Naturk.* 23–24: 279 (1870) (Fig 4).

Basionym: *Peziza carpinea* Pers., *Syn. meth. Fung.*: 673 (1801).

Synonyms: *Dermatea carpinea* (Pers.) Fr., *Summa Veg. Scand.*, V. 2: 362 (1849).

Peziza carpinea var. *fraxinea* Pers., *Mycol. eur.* 1: 312 (1822).

Dermatea fagi W. Phillips, *Man. Brit. Discomyc.*: 344 (1887).

Dermatella fagi (W. Phillips) Sacc., *Syll. Fung.* 8: 492 (1889).

Pezicula fagi (W. Phillips) Boud., *Hist. et Classif. des Discom. Eur.*: 159 (1907).

Fig 2 – Bayesian 50 % majority rule consensus tree based on ITS sequences of 123 strains in *Pezicula*. Thickened branches represent Bayesian posterior probabilities (PP) greater than 0.95. Bootstrap support values greater than 70 % are given at the nodes (MLBS/MPBS) and the scale bar represents the expected changes per site. Species clades are shown in coloured blocks, and the strain number is indicated for each sequence, followed by the isolation source (green text) and country of origin (blue text). New species and ex-type strains are indicated in bold face. The tree was rooted to *Neofabraea malicorticis* (CBS 122030) and *Parafabraea eucalypti* (CBS 124810). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

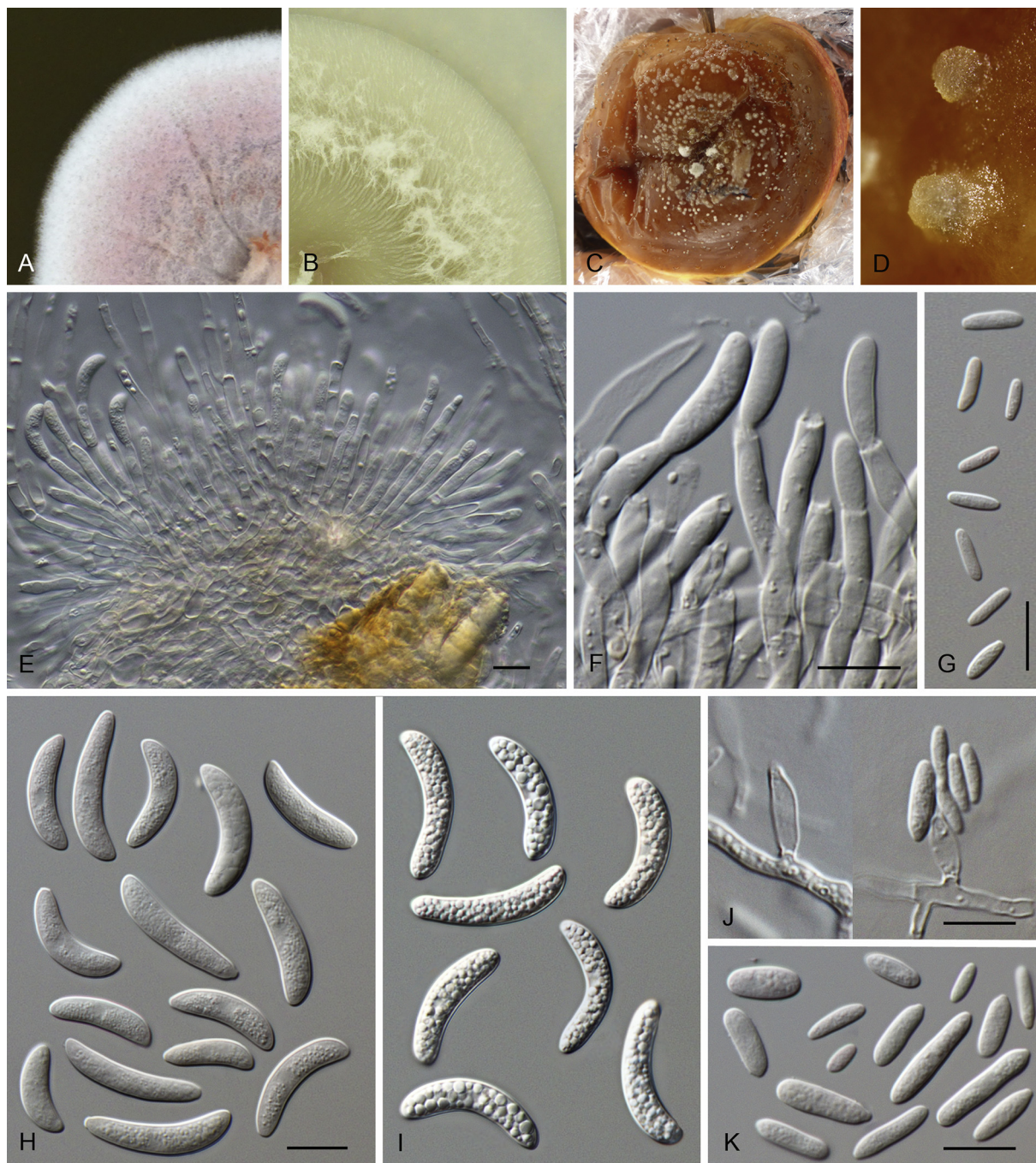


Fig 3 – *Neofabraea malicorticis* (CBS 122030). (A) Colony on MEA. (B) Colony on OA. (C) Conidiomata on inoculated apple. (D) Conidial mass on apple peel. (E) Conidiogenous cells from sporodochium on OA. (F) Conidiogenous cells giving rise to macroconidia. (G) Microconidia on OA. (H) Macroconidia from OA. (I) Macroconidia from inoculated apple. (J, K) Intermediate conidia between macro- and micro-conidia. All bars = 10 μ m, I = H.

Tubercularia fasciculata Tode, *Fung. Mecklenb. Sel.* 1: 20 (1790).
Cryptosporiopsis fasciculata (Tode) Petr., *Ann. Mycol.* 21: 187 (1923).

Pezicula fasciculata (Tode) House, *N.Y. St. Mus. Bull.* 243–244: 95 (1923).

Additional synonyms and description in [Verkley \(1999\)](#).

Materials examined: Germany, Bad Bentheim, Bentheimer Relictwald, near Kuhrort, on recently fallen

Carpinus betulus, 9 July 1996, G. Verkley (CBS H-17476, epitype of *Peziza carpinea* designated here, MBT201267, ex-type cultures CBS 923.96, CBS 921.96). Netherlands, Prov. Flevoland, Revebos, on bark of *Carpinus betulus*, 31 July 1996, F.J. Stokman & G.C.N. van Zanen (CBS H15825, culture CBS 324.97).

Notes: Following an examination of the holotype of *Pe. carpinea* and type materials of its synonyms, [Verkley \(1999\)](#)

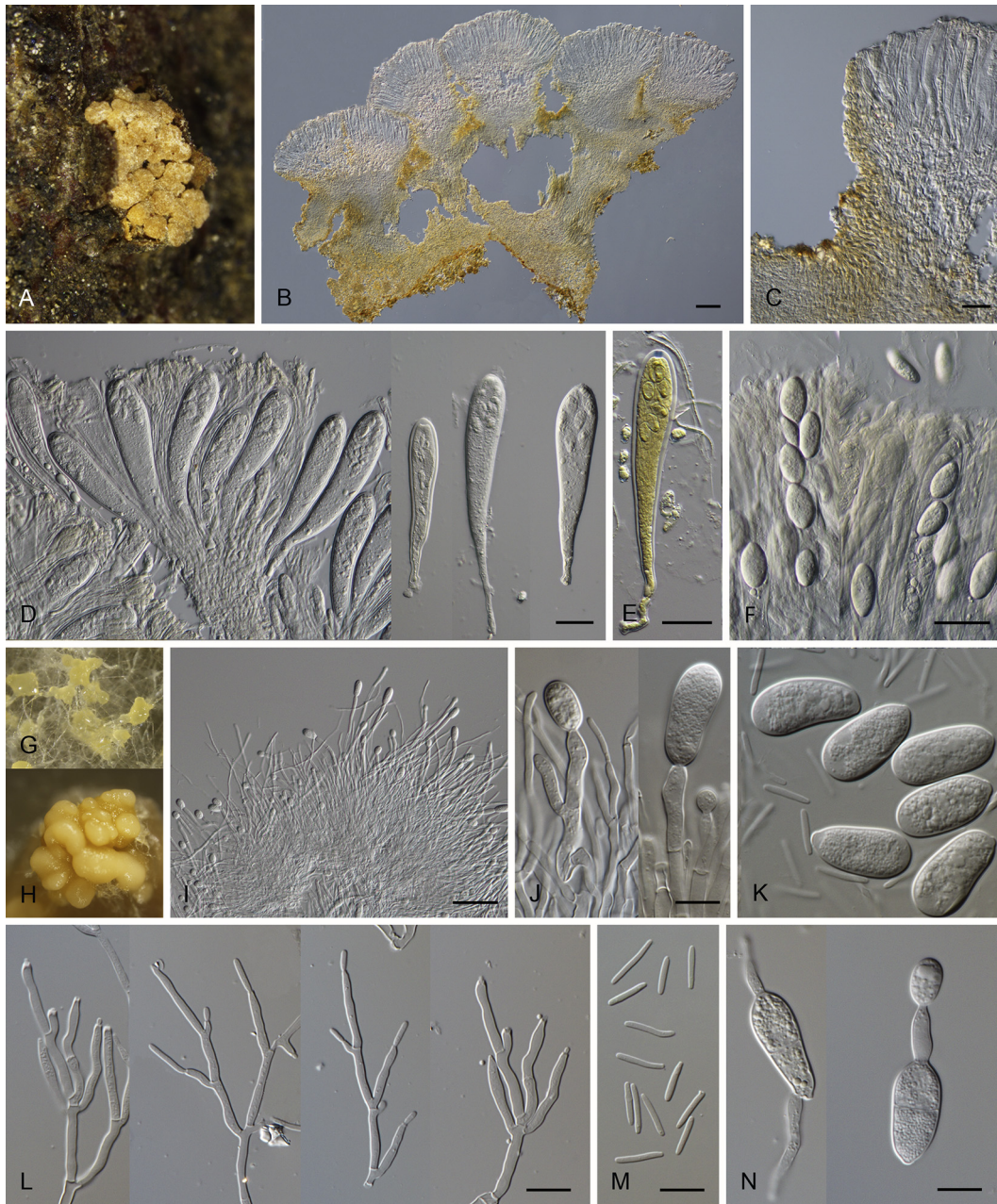


Fig 4 – *Pezicula carpinea* (CBS 923.96). (A) Dry apothecia on bark of *Carpinus betulus* (CBS H-17476). (B) Section of apothecia. (C) Ectal excipulum. (D) Asci and paraphyses. (E) Reaction with Mlz (pretreated with KOH). (F) Ascospores. (G, H) Conidiomata on OA. (I) Conidiogenous cells and sterile hyphae from sporodochium. (J) Macroconidiogenous cells giving rise to macroconidia. (K). Macroconidia. (L) Microconidiogenous cells giving rise to microconidia. (M) Microconidia. (N) Germinating macroconidia and microcyclic conidiation. Scale bars: B = 100 μ m; C, I = 50 μ m; D–F = 20 μ m; J–N = 10 μ m, K = J.

confirmed that the fungus on CBS H-17476 was *Pe. carpinea*. However, he did not propose an epitype at that time. The information of the type material is ‘S. loc., dat., coll., “Hab. ad ramos exsiccatos *Carp. betuli*” (L 910.261–293, holotype, sub *Peziza carpinea* Pers.; DAOM 84600, isotype, fragment with slide)’ (Verkley 1999). Given that the type material is very old and in rather poor condition, it is proposed here to designate CBS H-17476 as epitype of *Peziza carpinea* and the associated living cultures as ex-epitype isolates.

The oldest epithet for this species is *Pe. fasciculata* (1790), and not *Pe. carpinea* (1801). However, because the name *Pe. carpinea* has been used in numerous studies, it should be included on the list of protected species names (Wollenweber 1939; Dennis 1974; Verkley 1999; Abeln et al. 2000; Verkley et al. 2003; Lynch et al. 2013; Yuan & Verkley 2014). Moreover, *Pe. cinnamomea*, *Pe. corylina*, *Pe. frangulae* subsp. *frangulae*, and *Pe. sporulosa* are also challenged by older competing epithets, while they are also widely accepted and used in literature

(Verkley 1999; Abeln et al. 2000; Verkley et al. 2003; Lynch et al. 2013; Yuan & Verkley 2014). As in the case of *Pe. carpinea*, we suggest that these names should also be protected.

Pezicula fagacearum Chen, Verkley & Crous, sp. nov. (Fig 5). MycoBank MB812369.

Etym.: Named after the host genus from which it was collected, *Fagus*.

In vitro: Conidiomata eustromatic, superficial on agar and on nettle stems, later also submerged in agar, scattered or gregarious, 150–550 µm diam, at first spherical, closed, pale olivaceous, covered with sparse to moderate white hyphae, becoming dark olivaceous and opening by tearing or dissolution of upper wall,

releasing macroconidia in a clear droplet or white mass. In diffuse daylight, on OA, forming ochraceous, closed conidiomata, darkened with age and opening widely, releasing microconidia in creamy white droplets, later producing macroconidia. Conidiomatal wall delicate, 20–40 µm thick, composed of an outer layer of intricate, thick-walled, brown to olivaceous hyphae, and an inner layer of hyaline cells, giving rise directly to conidiophores, in large conidiomata, sometimes angular cells present. Macroconidiogenous cells discrete, or integrated in mostly simple, (1–)2–4-septate, acrogenous, rarely acropleurogenous conidiophores 33–75 × 4–6 µm; determinate, phialidic, with indistinct periclinal thickening, or indeterminate, percurrently proliferating 1–4



Fig 5 – *Pezicula fagacearum* (CBS 112400). (A) Colony on OA. (B) Colony on MEA. (C) Conidiomata on OA with white conidial mass. (D) Conidiomata on nettle stem. (E) Conidiophores, macro- and microconidiogenous cells. (F–H) Macroconidiogenous cells giving rise to macroconidia with phialides (F) or percurrent proliferation (G, H). (I) Macroconidia. (J) Microconidiogenous cells giving rise to microconidia with phialides or percurrent proliferation. (K) Microconidia. Scale bars: H, J = 5 µm; other bars = 10 µm.

times, scars close but distinct, cylindrical, hyaline, (12–) 14–22.5 × 5–6.5(–7.5) μm . *Macroconidia* aseptate, elongated ellipsoidal to clavate, curved in lower part, rounded at apex, tapering to a slightly protruding scar at base, hyaline, granular to guttulate, 27–36 × 10–12.5 μm , (av. 30–34.8 × 10.1–11.7 μm , n = 32) when liberated; later 1–3(–5)-septate, wall thickened and germinating. *Microconidiogenous* cells discrete or integrated, simple or branched, 2–4(–5)-septate, sometimes intermixed with macroconidiophores, 14–33 × 2–5 μm ; determinate, phialidic, with periclinal thickening, or indeterminate, with several percurrent proliferations, hyaline, terminal cells subcylindrical to narrowly ampulliform, straight to curved, tapering towards apex, 6–12 × 2–4 μm . *Microconidia* cylindrical, straight, slightly or strongly bent, rounded at apex, truncate at base, hyaline, 5–9.5 × 1–2 μm (av. 6.2–8.4 × 1.4–1.8 μm , n = 38).

Culture characteristics: Colonies on OA reaching 23 mm diam after 14 d, 41 mm after 21 d; flat with even margin; aerial mycelium weakly developed, white; submerged mycelium at first hyaline, then buff to rosy buff after 21 d; reverse concolourous; forming pale olivaceous conidiomata after 14 d, then darkened with age. On MEA reaching 16 mm diam after 14 d, 25 mm after 21 d; flat, margin even to undulate; aerial mycelium moderately developed, in centre mouse grey with few brown droplets, outer region white; submerged mycelium salmon to saffron after 21 d; reverse in centre umber, fading to rosy buff to saffron at margin; no diffusing pigment.

Materials examined: Italy, on bark of *Fagus sylvatica*, date unknown, R. Danti (CBS H-22216, holotype, ex-type culture CBS 112400); *ibid.* (CBS 112401, CBS 112402).

Notes: *Pezicula fagacearum* only produced its asexual morph in culture. The macroconidia of *Pe. fagacearum* are always curved in the lower part, and have attenuated bases, resembling those of *Pe. acericola* and *Pe. sporulosa*. However, *Pe. fagacearum* has shorter microconidia, and is also phylogenetically

distinct. Two isolates (CBS 112401 and CBS 112402) formed a distinct subclade, proving to be the closest phylogenetic neighbour of *Pe. fagacearum*. The two subclades have 3 and 2 nucleotide differences in ITS and LSU, respectively. However, their *rpb2* sequences were identical, and they were collected from the same location and host. Only CBS 112400 sporulated, while CBS 112401 and CBS 112402 were sterile, so they could not be compared morphologically. We prefer to retain the three isolates as one species for now.

Pezicula microspora Chen, Verkley & Crous, *sp. nov.* (Fig 6).
Mycobank MB812370.

Etym.: Named after its small microconidia.

In vitro: *Conidiomata* sporodochial, forming on hyphae, or superficial on agar, scattered, at first pale buff, later saffron, surrounded by sparse, brown hyphae. *Microconidiogenous* cells mostly integrated in branched acropleurogenous conidiophores, 38–87 × 2–3.5 μm ; determinate, phialidic, with distinct periclinal thickening, hyaline, terminal cells cylindrical to narrowly ampulliform, straight or slightly curved, 9–15 × 1.5–3 μm . *Microconidia* cylindrical, straight to slightly bent, rounded at apex, truncate at base, hyaline, 8–12(–14) × 1–2 μm (av. 8.8–11.3 × 1.5–1.7 μm , n = 34).

Culture characteristics: Colonies on OA reaching 48 mm diam after 14 d, covering full plate after 21 d; flat, margin uneven, glabrous; aerial mycelium absent, or weakly developed in centre, white, woolly to floccose after 21 d; several patches of aerial mycelium appearing on surface of agar after 30 d, on which sporodochia formed; submerged mycelium at first hyaline, later buff; reverse concolourous. On MEA reaching 31 mm after 21 d; flat, slightly raised and folded in centre, margin uneven; aerial mycelium moderately to well developed, white; submerged mycelium hyaline; reverse in centre umber, fading from saffron to hyaline at margin; no diffusing pigment.

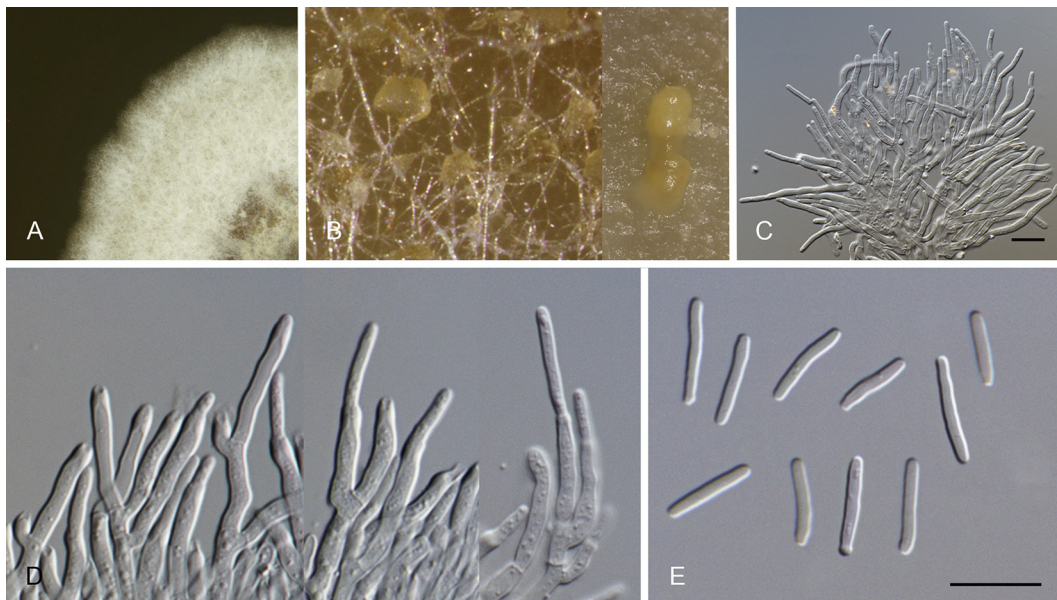


Fig 6 – *Pezicula microspora* (CBS 124641). (A) Colony on MEA. (B) Conidiomata on OA. (C) Conidiophores and microconidiogenous cells. (D) Microconidiogenous cells giving rise to microconidia. (E) Microconidia. All bars = 10 μm .

Material examined: Italy, endophyte from *Berberis vulgaris*, date unknown, collector unknown (holotype CBS H-22218, ex-type culture CBS 124641).

Notes: *Pezicula microspora* is represented by a single isolate, which forms a distinct clade in the phylogenetic tree. *Pezicula acericola*, *Pe. aurantiaca*, *Pe. neosporulosa*, *Pe. querciphila* and *Pe. sporulosa* produce microconidia in almost the same range as

those of *Pe. microspora*, but they differ phylogenetically (Figs 1 and 2).

Pezicula neocinnamomea Chen, Verkley & Crous, *sp. nov.* (Fig 7).

Mycobank MB812371.

Etym.: Named after its morphological similarity to *Pezicula cinnamomea*.



Fig 7 – *Pezicula neocinnamomea* (CBS 100248). (A) Dry apothecium on bark of *Abies alba* (CBS H-15846). (B) Section of apothecium, showing the ectal excipulum. (C) Asci and paraphyses. (D) Ascospores. (E) Conidiomata on OA, with macroconidia inside droplets. (F) Microconidiogenous cells. (G) Microconidia. (H) Macroconidiogenous cells giving rise to macroconidia. (I–K) Macroconidia. Scale bars: B = 50 µm; C = 25 µm; D–K = 10 µm.

In vivo: Apothecia erumpent, mostly solitary, rarely 2–3 on a basal stroma, subsessile, or on a short, stout stalk. Disc circular, plane or convex, pale luteous when dry, 0.15–0.6 mm diam. Receptacle concolourous, darker towards base, pruinose; margin first entire, then irregularly torn and hidden. Basal stroma immersed, pale brown, consisting of angular cells with orange-brown walls up to 2 µm thick. Medullary excipulum yellow to orange-brown, consisting of vertical rows of prismatic or hyphal cells with hyaline to yellow walls. Ectal excipulum yellow to orange-brown, in lower part, composed of angular cells with brown walls, at surface, and especially at margin, ending in club-shaped cells with hyaline to yellow walls. Subhymenium hyaline to pale orange, composed of interwoven hyphae, difficult to separate in water mounts. Asci clavate to cylindrical-clavate, apex truncate-rounded (NT), narrowed gradually or abruptly into a stalk of variable length, 91–148 × 16–24 µm, 8-spored, apical apparatus Mlz+ with KOH pretreatment. Ascospores inequilateral, ovoid to broadly ellipsoid (av. L/W 2.2–2.4), mostly straight or slightly curved, ends rounded or one slightly pointed, aseptate, thin-walled, hyaline, 16–28 × 6–12.5 µm, (av. 17.2–21.9 × 7.9–10.3 µm, n = 54). Paraphyses filiform, septate, simple or branched at upper part, hyaline, 1.0–2.0 µm wide; apical cell swollen up to 6.5 µm, wall hyaline to yellow, smooth to minutely roughened.

In vitro: Conidiomata eustromatic, superficial on agar, scattered or gregarious, (0.4–)0.6–2.0 mm diam, spherical, greenish olivaceous, covered with dense white hyphae, with single or up to 3 confluent cavities, initially closed, later opening widely by tearing or dissolution of upper wall, releasing macroconidia in clear droplet or white to buff conidial mass. Conidiomatal wall composed of an outer tissue of intricate, thick-walled hyphae, 20–34 µm thick, and an inner tissue of hyaline to pale olivaceous cells, giving rise directly to conidiophores. Macroconidiogenous cells mostly discrete, or integrated in mostly simple or branched, 2–4-septate, acrogenous conidiophores 40–65 × 3.5–5 µm; determinate, phialidic, with a minute periclinal thickening, or indeterminate and proliferating percurrently 1–3 times, scars often distant but indistinct, cylindrical or ampulliform, widest in upper half, hyaline, 12–31 × 4–6 µm. Macroconidia oblong to clavate, straight, rounded at apex, tapering to a protruding scar at base, granular to guttulate, hyaline, aseptate, 26–42 × 10–15 µm, (av. 38.4–32.1 × 11.8–14.1 µm, n = 47) when liberated; later (1–)3–4(–6)-septate, then muriform, wall thickened and germinating, occasionally turning yellowish brown before becoming septate. Microconidiogenous cells mostly integrated in simple or branched, acropleurogenous conidiophores, 30–61 × 2.5–4 µm; determinate, phialidic, with minute periclinal thickening, hyaline, terminal cells subcylindrical to narrowly ampulliform, straight to slightly curved, tapering towards apex, 7–17.5 × 2–3.5 µm. Microconidia cylindrical, straight to slightly bent, rounded at apex, truncate at base, hyaline, 6.5–10.0 × 1–2 µm (n = 41).

Culture characteristics: Colonies on OA reaching 58–60 mm diam after 14 d; covering full plate after 21 d; flat, margin even or lobed; aerial mycelium moderately to well-developed, in centre white to straw, outer zone white to olivaceous buff; submerged mycelium hazel; reverse buff in centre, outer zone olivaceous; forming pale olivaceous conidiomata. On MEA reaching 44–48 mm diam after 21 d; flat, margin even to undulate; aerial mycelium moderately developed, in

centre mouse grey with few brown droplets, outer zone white; submerged mycelium salmon to saffron after 21 d; reverse in centre umber, fading over rosy buff to saffron at margin; no diffusing pigment.

Materials examined: Denmark, Jylland, Marebåsk plantage NW of Esbjerg, on dead branches of *Abies alba*, 15 Sept. 1997, G. Verkley (holotype CBS H-15846, ex-type culture CBS 100248). Germany, endophyte from the bark of *Sorbus aria*, date unknown, collector unknown, culture CBS 693.95.

Notes: *Pezicula neocinnamomea* is widely known from Europe, where it occurs on a range of different hosts. Morphologically it is similar to *Pe. cinnamomea*, which also has a wide host range. Hosts include *Abies alba*, *Fagus sylvatica*, *Ginkgo biloba*, *Malus sylvestris*, *Picea abies*, *Pinus nigra* var. *austriaca* and *Sorbus aria* (Table 1). *Pezicula cinnamomea* is homothallic, and can develop apothecia in culture, while apothecia are not observed in cultures of *Pe. neocinnamomea*. In the phylogenetic trees (Figs 1 and 2), the two species also clustered well apart.

Pezicula neoheterochroma Chen, Verkley & Crous, sp. nov. (Fig 8).

Mycobank MB812372.

Etym.: Named after *Pezicula heterochroma*, which it resembles morphologically.

In vivo: Apothecia weakly erumpent, mostly solitary, rarely 2–8 on a basal stroma, subsessile, or on a short, stout stalk. Disc elliptical, mostly deformed due to crowding, plane, pale luteous to luteous, 0.4–1.2 mm diam when dry. Receptacle dark brown to olivaceous black; margin entire, with raised rim, persistent. Basal stroma immersed, orange-brown, consisting of a dense tissue of irregular cells with hyaline walls up to 2 µm thick. Medullary excipulum hyaline to pale cinnamon, consisting of vertical rows of prismatic or isodiametric cells with hyaline walls up to 2 µm thick, locally with brown intercellular deposits. Ectal excipulum olivaceous black to olivaceous brown, composed of isodiametric cells, 6–15 µm diam, with up to 2 µm thick walls containing fine darker deposits. Subhymenium pale orange-brown to hyaline, consisting of closely interwoven hyphae with hyaline walls and yellowish brown contents, difficult to separate in water mounts. Asci clavate to cylindrical-clavate, apex truncate-rounded, narrowed gradually into a short stalk, 86–133(–169) × 11–17(–24) µm, 8-spored, apical apparatus Mlz+ with KOH pretreatment. Ascospores inequilateral, ellipsoid to elongated ellipsoid (average L/W 2.9), straight, rarely curved, ends somewhat pointed or one slightly rounded, aseptate, thin-walled, hyaline, 16.5–24.5 × 6–8.5 µm, (av. 18.1–22.2 × 6.4–7.7 µm, n = 49). Paraphyses filiform, septate, simple or branched, 1–2 µm wide, hyaline; apical cell swollen up to 6 µm, with pale cinnamon, smooth walls, glued together by a cinnamon to pale brown extracellular matrix, forming a dark cinnamon epithecium.

Culture characteristics: Colonies on OA reaching 60 mm diam after 21 d; flat, margin uneven, glabrous; aerial mycelium absent, only in centre weakly developed, diffused, white; submerged mycelium dark ochreous; reverse sienna in centre, buff in outer zone, diffusing yellow pigment into agar. On MEA reaching 20 mm after 21 d; low convex, margin undulate to irregular lobate, white; aerial mycelium moderate, white; submerged mycelium dark amber; reverse in centre saffron, white at margin; no diffusing pigment.

Material examined: Austria, Niederösterreich, Wechsel, Mariensee, on branch of *Sorbus aucuparia*, 31 May 2010, W. Jaklitsch (holotype CBS H-20469, ex-type culture CBS 127388).

Notes: This species is only represented by a single isolate. Unfortunately, the culture proved to be sterile, and the description is based on the herbarium specimen. Morphologically, *Pe. neoheterochroma* is similar to *Pe. sepium*, which widely occurs on woody *Rosaceae*, but is distinct in having a brighter medullary excipulum, and narrower and smaller ascospores ($18\text{--}34.5 \times 7.5\text{--}14 \mu\text{m}$, av. L/W 2.0–2.2(–2.7) in *Pe. sepium*; Verkley 1999). It is difficult to distinguish *Pe. neoheterochroma* and *P. heterochroma* based solely on morphology, but the phylogenetic data prove them to be distinct.

***Pezicula pseudocinnamomea* Chen, Verkley & Crous, sp. nov.** (Fig 9).

Mycobank MB812373.

Etym.: Named after *Pezicula cinnamomea*, which also occurs on *Castanea sativa*.

In vitro: Conidiomata eustromatic, superficial or immersed in agar, solitary or in clusters, spherical, 25–124 μm diam, cinnamon, glabrous or covered by sparse white hyphae, at first closed, later opening by tearing or dissolution of upper wall, not opening widely, releasing microconidia in clear droplets. Conidiomatal wall delicate, composed of an outer layer of loosely intricate, brown to cinnamon hyphae, 2–3 μm wide, and an inner layer of angular cells, thick-walled, pale cinnamon to golden-yellow, giving rise directly to conidiophores or conidiogenous cells. Microconidiogenous cells mostly integrated in simple or branched acropleurogenous conidiophores, 21–60 \times 2–3 μm ; determinate, phialidic, with distinct periclinal thickening, hyaline, terminal cells subcylindrical to narrowly ampulliform, mostly straight or slightly curved, tapering towards apex, 7–14 \times 2–3 μm . Microconidia cylindrical, straight to slightly bent, rounded at apex, truncate at base, hyaline, 7–13(–15) \times 1–2 μm , (av. 7.8–12.0 \times 1.4–1.6 μm , n = 38).

Culture characteristics: Colonies on OA reaching 53 mm diam after 14 d, covering the full plate after 21 d; flat with



Fig 8 – *Pezicula neoheterochroma* (CBS 127388). (A) Dry apothecia on bark of *Sorbus aucuparia* (CBS H-20469). (B) Colony on OA. (C) Colony on MEA. (D, E) Section of apothecia. (F) Ectal excipulum. (G) Asci and paraphyses forming epithecium. (H) Asci and ascospores. Scale bars: D, E = 50 μm ; F, G = 25 μm ; H = 10 μm .

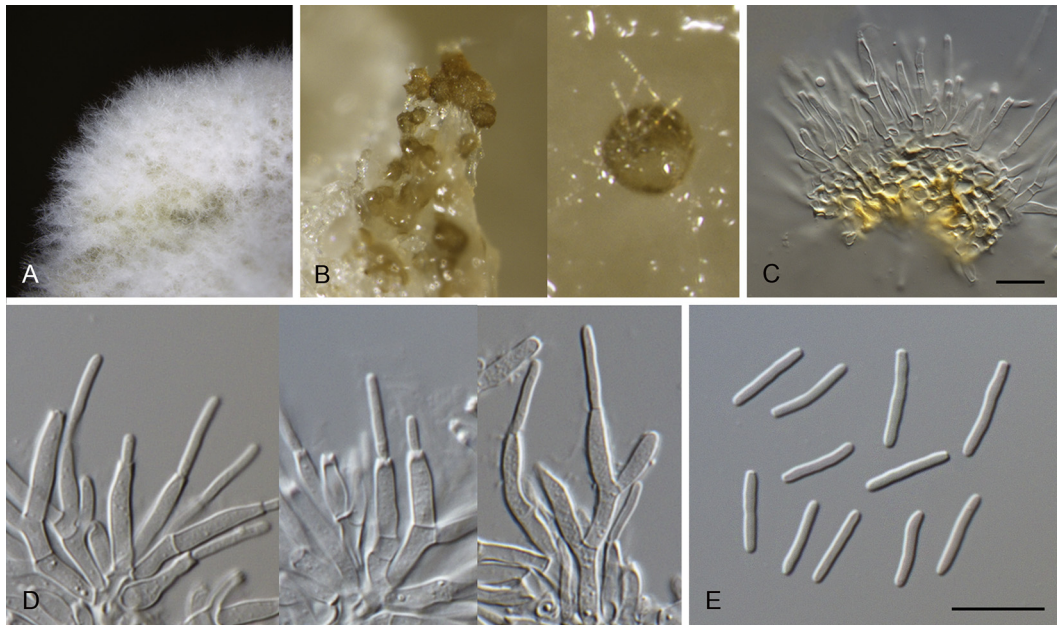


Fig 9 – *Pezicula pseudocinnamomea* (CBS 101000). (A) Colony on MEA. (B) Conidiomata on OA. (C) Microconidiogenous cells. (D) Microconidiogenous cells giving rise to microconidia. (E) Microconidia. All bars = 10 µm.

an even to slightly undulate margin; aerial mycelium diffuse, but in the centre well developed, tufty to woolly, white; submerged mycelium buff; reverse concolourous. On MEA reaching 23 mm after 21 d; low convex, margin undulate to irregularly lobate; aerial mycelium dense, woolly-floccose, white; reverse in centre saffron, white at margin; no diffusing pigment.

Material examined: Netherlands, Prov. Utrecht, Lage Vuursche, on dead branches of *Castanea sativa*, 25 Mar. 1997, G.J.M. Verkley (CBS H-22217, holotype, ex-type culture CBS 101000).

Notes: *Pezicula pseudocinnamomea* is represented by a single isolate, which forms a distinct clade in the phylogenetic tree. In spite of various incubation conditions on a range of media, *Pe. pseudocinnamomea* only produced microconidia in culture. *Pezicula cinnamomea* is also reported from *Castanea* spp., but the latter has much smaller microconidia (4.5–10 × 1–2 µm; Verkley 1999).

Eight species clades in the phylogenetic tree (Fig 2) are distinct from the other species treated here, and may represent novel taxa. Most of those species are represented by only a single isolate, and some of them were wrongly identified or without full collection details when they were submitted to the CBS. Unfortunately, all of them are represented by very old and sterile isolates. Because their identity cannot be confirmed, we will not treat them further here.

Pezicula sp. 1.

Material examined: Canada, on twig of *Acer* sp., date unknown, isol. J.W. Groves, CBS 202.46.

Note: This isolate was deposited as *Pe. carnea*, and although that name was considered a synonym of *Pe. cinnamomea*, the isolate is phylogenetically different from typical *Pe. cinnamomea* strains and all other strains investigated here.

Pezicula sp. 2.

Material examined: Germany, on branch of *Acer platanoides*, date unknown, isol. J. Graf, CBS 230.79.

Note: CBS 230.79 was previously identified as *Pe. eucrita*, but this proved to be incorrect as phylogenetically it is relatively distant from typical isolates of *Pe. eucrita*.

Pezicula sp. 3.

Material examined: Belgium, Gembloux, on twig of *Prunus domestica*, data unknown, isol. J. Fraselle, CBS 268.78.

Notes: The sterile isolate CBS 268.78 was deposited as *Pe. pruinosa*. However, it does not group with *Pe. pruinosa* (CBS 292.39) in the phylogenetic tree (Fig 2). Moreover, *Pe. pruinosa* is thus far only reported on *Amelanchier* in North America, whereas CBS 268.78 was isolated from *Prunus domestica* in Belgium.

Pezicula sp. 4.

Material examined: Netherlands, on dying twig of *Quercus* sp., date unknown, isol. A.C. Stolk, culture CBS 242.60.

Notes: This isolate was previously identified as *Pe. cinnamomea*. However, based on the ITS sequence, it is distinct from *Pe. cinnamomea* and all other *Pezicula* species investigated here.

Pezicula sp. 5.

Material examined: Germany, Berkenbrück, on *Salix* sp., 1938, H.W. Wollenweber, CBS 267.39.

Notes: Isolates CBS 267.39 and CBS 268.39 were both submitted as *Ocellaria ocellata*, the synonym of *Pe. ocellata*. CBS 268.39 and another isolate CBS 949.97 formed the *Pe. ocellata* clade, while CBS 267.39 represented a single branch closely allied to *Pe. ocellata*.

Pezicula sp. 6.

Material examined: Australia, Australian Capital Territory, from the rhizoplane of *Eucalyptus* sp., date unknown, collector unknown, CBS 433.75.

Notes: The sterile strain CBS 433.75 was isolated from the root surface of *Eucalyptus* sp. Interestingly, it is closely related to the root-inhabiting species *Pe. ericae*, which is reported from the roots of *Gaultheria*, *Tilia*, and *Vaccinium* from Europe and North America (Table 1). CBS 433.75 represents a distinct species.

Pezicula sp. 7.

Materials examined: Canada, Ontario, on *Carpinus caroliniana*, 6 Nov. 1932, H.S. Jackson, CBS 282.39; Ontario, on *C. caroliniana*, 29 May 1933, J.W. Groves, CBS 283.39.

Notes: Isolates CBS 282.39 and CBS 283.39 were formerly identified as *Pe. carpinea*. However, they cluster apart from CBS 923.96, the ex-epitype culture of *Pe. carpinea*. CBS 282.39 and CBS 283.39 appear to represent a different species, but because these isolates are now sterile the species cannot be adequately described here.

Pezicula sp. 8.

Material examined: Belgium, Eupen, on dead twig of *Corylus avellana*, June 1968, W. Gams, CBS 450.68.

Note: CBS 450.68 was originally identified as *Pe. corylina*, but it is phylogenetically distant from that species.

Phlyctema Desm., *Ann. Sci. Nat., Sér. 3, 8: 16* (1847).

Synonym: *Allantozythia* Höhn., *Annl. mycol. 22: 203* (1924).

Type species: *Phlyctema vagabunda* Desm.

Apothecia developing from acervuloid stromata, sessile. Disc circular or irregular and often merged, slightly convex. Asci cylindrical-clavate, inoperculate, 8-spored; apical apparatus turning blue in 'iodine'. Ascospores elongated ellipsoid to straight, or slightly curved, ends rounded or somewhat pointed, hyaline, firstly aseptate, later septate. Paraphyses numerous, filiform, branched, septate, obtuse, hyaline, apical cell slightly swollen (from Verkley 1999; based on Guthrie 1959). Conidiomata eustromatic, immersed, erumpent, acervuloid to sporodochial, separate, yellowish brown, pulvinate, circular, unilocular but convoluted, thick-walled; wall of *textura angularis*, darker brown and thicker-walled at base than at sides. Ostiole absent, dehiscence by irregular rupture. Conidiophores hyaline, septate, branched irregularly, cylindrical to filiform, formed from wall lining conidiomata. Conidiogenous cells enteroblastic, phialidic, integrated or discrete, determinate, hyaline, with minute collarette and periclinal thickening. Macroconidia hyaline, aseptate, fusiform, guttulate, straight to slightly curved or irregular. Microconidia present or absent, hyaline, aseptate, filiform, straight or curved, aseptate, rounded at ends.

Notes: Thus far only the type species is reported to have a known sexual morph, which is similar to *N. perennans* (Guthrie 1959). We can readily distinguish *Neofabraea* from *Phlyctema* based on their asexual morphs. *Phlyctema* species have eustromatic conidiomata, fusiform macroconidia, and filiform microconidia, while all the known *Neofabraea* species form acervular conidiomata, macroconidia that vary in shape (cylindrical-fusiform, allantoid to ellipsoid), and shorter microconidia.

Neofabraea was protected over *Phlyctema* (Johnston et al. 2014), because the type species, *Ph. vagabunda*, was considered a member of *Neofabraea*, making *Phlyctema* a synonym of *Neofabraea*. However, the present study proved that these two genera are not taxonomically congruent (see below); therefore, *Phlyctema* and *Neofabraea* are accepted as distinct genera.

Phlyctema vagabunda Desm., *Ann. Sci. Nat., Bot., Sér. 3, 8: 16* (1847). (Fig 10).

Synonyms: *Neofabraea vagabunda* (Desm.) P.R. Johnst., *IMA Fungus 5: 103* (2014).

Gloeosporium album Osterw., *Zentbl. Bakt. ParasitKde, Abt. II 18: 826* (1907).

Pezicula alba E.J. Guthrie, *Trans. Br. mycol. Soc. 42: 504* (1959).

Neofabraea alba (E.J. Guthrie) Verkley, *Stud. Mycol. 44: 125* (1999).

Additional synonyms listed in MycoBank.

Descriptions: Guthrie (1959) and Verkley (1999).

In vitro (CBS 109875): Conidiomata eustromatic, superficial or immersed in agar, mostly scattered, 150–550 µm diam, at first spherical, closed, white to buff, then becoming cinnamon. Macroconidigenous cells determinate, phialidic, terminal cells cylindrical or slightly tapered towards apex, 11–26 × 2.6–4 µm. Macroconidia subcylindrical to fusiform, curved, ends rounded or somewhat pointed, aseptate, 20–34 × 2.6–4 µm (av. 24–32 × 2.9–3.5 µm, n = 34). Microconidigenous cells determinate, phialidic, sometimes with minute collarette, cylindrical to narrowly ampulliform, 8–16 × 1.8–3 µm. Microconidia hyaline, aseptate, filiform, straight or curved, rounded at ends, 10–21 × 1–1.4 µm, (av. 12.7–18.7 × 1.1–1.3 µm, n = 32).

Culture characteristics: Colonies on OA reaching 66 mm diam after 21 d; flat with a radially arranged synnema-like hyphal cluster, white, cottony, with a clear droplet on top; margin entire with a low fringe of white radiating hyphae; surface smooth, in centre hazel to olivaceous due to submerged mycelium, darker with age, outer zone white; reverse concolourous. On MEA reaching 21–24 mm diam after 21 d; flat, slightly folded in centre, edge entire; aerial mycelium sparse, white, only present in centre, dark coral in centre, fading outwards from flesh to white in outer zone; no diffusing pigment.

Material examined: South Africa, on stored fruit of *Malus sylvestris*, date unknown, isol. T.N. Matthee, CBS 304.62. USA, Michigan, Oregon, on *Fraxinus americana*, July 2001, A. Rossman (specimen BPI 841384, culture CBS 109875).

Notes: The sexual morph of *Ph. vagabunda* appears to have been collected only once (Guthrie 1959), and the type material with the sexual morph is in rather poor condition (Verkley 1999). In contrast, the asexual morph is frequently observed in natural substrates and also forms readily in fresh isolates. The macroconidia in culture are larger than those in nature. The microconidia are only observed in culture. *Phlyctema vagabunda* is well-known as one of the causal agents of bull's eye rot on apples and pears, and reported as prevalent in the Pacific Northwestern USA, Australia, and Chile (Garipey et al. 2005; Spotts et al. 2009). It can also cause coin canker of ash trees (Rossman et al. 2002; Putnam & Adams 2005) and fruit spot on olive (Rooney-Latham et al. 2013). *Phlyctema vagabunda* is also reported as a saprobe on several woody and herbaceous plants (Verkley 1999).

In the revision of *Gloeosporium*, von Arx (1957) reduced many species into synonymy under *Ph. vagabunda*, including *G. album*. Later, this species was reported to have a sexual morph, which was described in the genus *Pezicula* as *Pe. alba*, because of its similarity with the sexual morph of *G. perennans*, known at that time as *Pe. malicorticis* (Guthrie 1959). When Verkley (1999) monographed the genus *Pezicula*, he separated *Pezicula* and *Neofabraea* as two distinct genera, and transferred *Pe. alba* to *N. alba*,

which has been widely used since then. Although it was classified in *Neofabraea* for some time, its atypical asexual morph was notably distinct from other *Neofabraea* species. Given the results of our phylogenetic analyses, the genus *Phlyctema* is resurrected to accommodate *Ph. vagabunda* and *Ph. vincetoxici*.

Parafabraea Chen, Verkley & Crous, **gen. nov.**

Mycobank MB812375.

Etym.: Named after its morphological similarity to the genus *Neofabraea*, but with relatively small asci.

Type species: *Parafabraea eucalypti* (Cheew. & Crous) Chen, Verkley & Crous.

Ascomata apothecial, sessile to subsessile, short-stalked, gregarious or confluent, clustering on a basal stroma, partly immersed, medium to dark brown. Disc turbinate, pale brown. Setae-like structures surrounding apothecia, rigid, pale brown, septate, cylindrical, straight or slightly curved, slightly

enlarged at truncate apex. Basal stroma subimmersed, composed of irregular, pale to medium brown cells. Asci inoperculate, clavate to cylindrical-clavate, apex rounded, short-pedicellate, base truncate, hyaline to pale brown, 8-spored. Ascospores inequilateral, fusoid to ellipsoid, ends rounded, straight or slightly curved, aseptate, thin-walled, hyaline, guttulate. Paraphyses numerous, cylindrical, slender, wider at base, septate, apex round, hyaline to pale brown. Conidiomata acervular, subcuticular to epidermal, separate, pale brown, dehiscence irregular, by rupture of overlying host tissues; conidiomatal wall consisting of 2–3 layers of *textura angularis*. Conidiogenous cells arising from inner cells of cavity, discrete, phialidic, cylindrical, straight to slightly curved, smooth, hyaline. Conidia elongate ellipsoidal, mostly straight, broadly obtuse at apex, tapering abruptly to a slightly protruding basal scar, aseptate, hyaline, thick-walled, minutely guttulate.

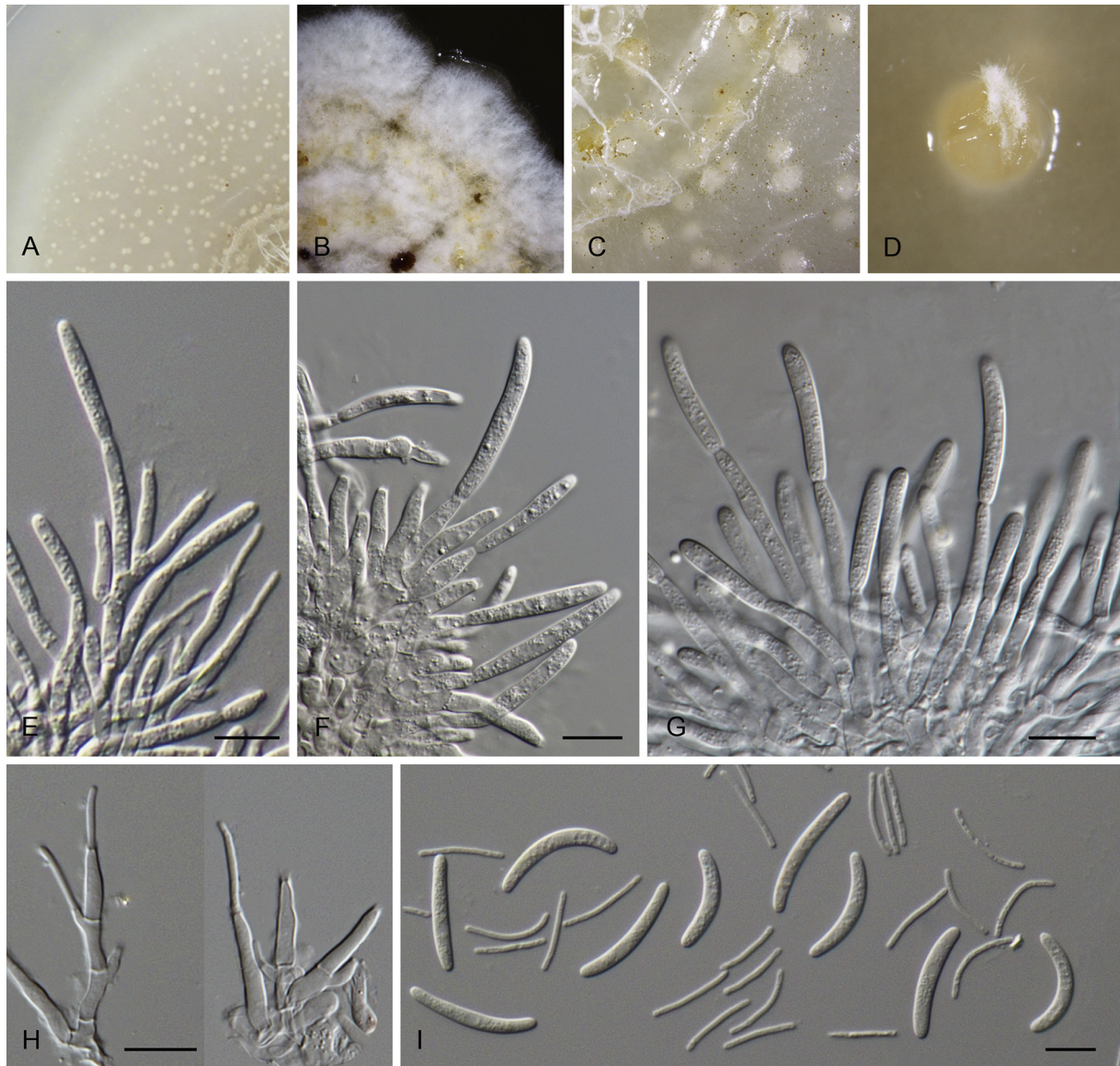


Fig 10 – *Phlyctema vagabunda* (CBS 109875). (A) Colony on OA. (B) Colony on MEA. (C, D) Conidiomata. (E–G.) Macroconidiogenous cells giving rise to macroconidia. (H) Microconidiogenous cells giving rise to microconidia. (I) Macroconidia and microconidia. All bars = 10 µm.

Notes: *Parafabraea* has a similar sexual morph to that of *Neofabraea*, but the genus is distinct in that it forms setae-like structures around the apothecia. The conidia of *Parafabraea* are thick-walled, with slightly protruding basal scars, while those of *Neofabraea* species are thin-walled, with indistinct, barely or non-protruding basal scars. Previous studies (Cheewangkoon et al. 2009 2010) and the present multi-gene phylogenetic analyses showed that *Parafabraea* formed a distinct lineage from *Neofabraea* and *Pezizula*.

Parafabraea caliginosa (Cheew. et al.) Chen, Verkley & Crous, **comb. nov.**

Mycobank MB812377.

Basionym: *Cryptosporiopsis caliginosa* Cheew. et al., *Fungal Divers.* **44**: 93 (2010).

Description and illustrations: Cheewangkoon et al. (2010).

Parafabraea eucalypti (Cheew. & Crous) Chen, Verkley & Crous, **comb. nov.**

Mycobank MB812376.

Basionym: *Neofabraea eucalypti* Cheew. & Crous, *Persoonia* **23**: 67 (2009).

Description and Illustrations: Cheewangkoon et al. (2009).

Pseudofabraea Chen, Verkley & Crous, **gen. nov.**

Mycobank MB812378.

Etym.: Named after its morphological similarity to the genus *Neofabraea*.

Type species: *Pseudofabraea citricarpa* (L. Zhu et al.) Chen, Verkley & Crous.

Plant pathogenic. *Conidiomata* stromatic, acervular, raised, subcuticular to epidermal, with a single or several confluent cavities. *Conidiophores* unbranched, hyaline. *Macroconidiogenous cells* determinate, phialidic, cylindrical to narrowly ampulliform, hyaline. *Macroconidia* cylindrical-fusiform, weakly to strongly curved, apex rounded to slightly pointed, base more or less conical then truncate, 0–1-septate, hyaline, with granular contents (emended from Zhu et al. 2012).

Pseudofabraea citricarpa (L. Zhu et al.) Chen, Verkley & Crous, **comb. nov.**

Mycobank MB812379.

Basionym: *Cryptosporiopsis citricarpa* L. Zhu et al., *Pl. Dis.* **96**: 809 (2012).

Synonym: *Neofabraea citricarpa* (L. Zhu et al.) P.R. Johnst., *IMA Fungus* **5**: 103 (2014).

Illustrations and description: See Zhu et al. (2012).

Notes: According to the description of Zhu et al. (2012), *Pseudofabraea* is similar to *Neofabraea* in the general morphology of the asexual morphs, but the macroconidia of *Ps. citricarpa* (5–9 µm) are wider than in species of *Neofabraea* (3–8 µm). *Neofabraea* species usually cause tree cankers or fruit rots, but *Ps. citricarpa* causes a leaf spot disease. Johnston et al. (2014) transferred this species to *Neofabraea* based on ITS sequence data published by Zhu et al. (2012). However, our multigene-sequence data show that the species now placed in the monotypic genus *Pseudofabraea* is clearly distinct from *Neofabraea* (Fig 1).

merging morphological and multi-gene phylogenetic DNA data. Based on these results, we are able to separate *Pezizula* from *Neofabraea*, *Phlyctema*, *Rhizodermea*, and introduce two previously undescribed genera, *Parafabraea* and *Pseudofabraea*.

In the multi-gene phylogenetic tree (Fig 1) the *Pezizula* clade consists of two well-supported subclades, with an additional species on a basal long branch. The type species of *Pezizula*, *Pezizula carpinea*, and the type species of *Cryptosporiopsis*, *Cryptosporiopsis nigra*, considered the asexual morph of *Pezizula ocellata* (Fig 11), fall into the two respective subclades. Detailed studies of the asexual morph of this fungus as well as molecular evidence resulted in its wide acceptance as a member of the genus *Pezizula* (Groves 1940; Verkley 1999; Abeln et al. 2000). In the present study we compared the species in these two *Pezizula* subclades on aspects related to morphology and ecology, but could not find any differences that were consistent with the phylogeny. According to the multi-gene dataset, the fixed differences in nucleotides between these two subclades were relatively small: LSU (8/784 bp), *rpb2* (15/874 bp). Therefore, we concluded that it is best to retain these subclades as a single genus, *Pezizula*, which is also in agreement with the approach taken by Johnston et al. (2014). The long branch at the bottom of the *Pezizula* clade is represented by a single isolate (CBS 124805). Although we contemplated introducing a new genus for this isolate, there were no obvious morphological differences, and based on the various multi-gene analyses generated, this isolate always clustered within *Pezizula*, albeit on a long branch. It could be that this isolate will eventually be shown to represent a distinct genus, but the *Pezizula* clade presently suffers from undersampling, and more taxa need to be added to generate a more robust phylogeny for the genus. We thus concluded that separating *Pezizula* into different entities was premature and unwanted, as it did not serve the user community, which value stability of names in this group of important plant pathogens and endophytes.

The monotypic genus *Rhizodermea* (based on *Rhizodermea veluwensis*, isolated from roots of *Erica tetralix* in the Netherlands; Verkley et al. 2010) clusters in a well-supported clade basal to *Pezizula*. Unfortunately all cultures of *R. veluwensis* known to date are sterile endophytes that only produce abundant chlamydospore-like structures in culture (absent in *Pezizula* s. str.), and thus it is not possible to make a sensible comparison with the morphology of *Pezizula* until more species of *Rhizodermea* have been collected.

Species of *Cryptosporiopsis* have in the past been linked as asexual morphs to both *Neofabraea* and *Pezizula*. The fact that *Cryptosporiopsis* s. str. is now treated as synonym of *Pezizula* (Johnston et al. 2014), means that the status of many *Cryptosporiopsis* spp. need to be resolved. For many of these, neither cultures nor molecular data are available or are inadequate to determine their generic placement. For example, *Cryptosporiopsis tarraconensis* has three ITS sequences in GenBank, two of which (GenBank EU707430 and EU707431) are from the same author and host as the described species, and a third sequence from other authors in Iran (GenBank KF225578). The sequences show high similarity with *Gnomonia virginianae* (*Sordariomycetes*). This species does not belong in *Pezizula*. *Cryptosporiopsis edgertonii* was described by Gadgil & Dick (2001), who only provided a morphological description. The ITS sequence available in GenBank

Discussion

In this study we resolve the phylogenetic relationships among *Cryptosporiopsis*, *Neofabraea*, *Pezizula* and related genera by



Fig 11 – *Pezicula ocellata* (CBS 949.97). (A) Dry apothecium on branch of *Salix* sp. (CBS H-15200). (B) Section of apothecium. (C) Ectal excipulum. (D) Asci and paraphyses. (E) Reaction with Mlz (pretreated with KOH). (F) Ascospores. (G) Conidiomata on OA. (H) Macroconidiogenous cells giving rise to macroconidia, with phialides or percurrent proliferation. (I, J) Macroconidia. Scale bars: B = 100 μ m; C = 50 μ m; D, E = 25 μ m; F–J = 10 μ m, I = J.

(JN595853) labelled as *C. edgertonii* is identical to that of the ex-type strain of *Pezicula neosporulosa*. Morphologically, these two species are different, macroconidia in *C. edgertonii* are larger (32–48 \times 10–15 μ m) than in *P. neosporulosa* (24–36.5 \times 9–12 μ m), while the microconidia of *C. edgertonii* are of comparable length but narrower (12–14 \times 1–1.5 μ m) than in *P. neosporulosa* (8–14 \times 1.5–2.5 μ m). Because the ITS sequence of *C. edgertonii* is not based on an ex-type strain, the identification of the strain on which this sequence was based remains uncertain. These are but two examples that underline the point that these species need to be recollected and sequenced before dealing with these old names.

Species of *Pezicula* mostly occur in temperate regions and vary in their host specificity. Some species have wide host ranges, while others are only reported from a single host species or genus (Verkley 1999). Most studies have been focused on isolates from Europe or Northern America, while few reports were based on material from Asia or the Southern

Hemisphere. Recently many endophytes were deposited in GenBank as members of ‘*Cryptosporiopsis*’ (= *Pezicula*) from Asia and Australia, most of which lack morphological descriptions and clear identifications. According to the available ITS sequences of these endophytes, some of them are probably members of *Pezicula* and distinct from known species.

Neofabraea s. str., typified by *Neofabraea malicorticis*, currently includes six species: *Neofabraea actinidiae*, *Neofabraea inaequalis*, *Neofabraea kienholzii*, *Neofabraea krawtzevii*, *N. malicorticis* and *Neofabraea perennans*, all of which appear to be phytopathogenic. In the present study an epitype is designated for *Gloeosporium malicorticis* (= *N. malicorticis*), which causes anthracnose canker and Bull’s eye rot on apple and pear.

The resurrected genus *Phlyctema* is typified by *Phlyctema vagabunda*, which previously was placed in *Neofabraea* because of a similar sexual morph to that observed in species of *Neofabraea*. With more species described and robust multigene phylogenetic data of these two genera, the distinction between *Ph.*

vagabunda and other *Neofabraea* species is recognized (de Jong et al. 2001; Cheewangkoon et al. 2009, 2010; Quaedvlieg et al. 2013; Soto-Alvear et al. 2013). Phylogenetic data generated in the present study resolved them as distinct genera (Fig 1), with species in *Phlyctema* forming eustromatic conidiomata and narrower macroconidia. Of the more than 60 taxa that have been placed in this genus, some have subsequently been transferred to other genera (Sutton 1980; Verkley 1999).

The present study also led to the introduction of two new genera, *Parafabraea* and *Pseudofabraea*. *Parafabraea* was established to accommodate two species that were previously described in *Cryptosporiopsis* and *Neofabraea* (Cheewangkoon et al. 2009, 2010), both taxa occurring on *Eucalyptus* spp. in Australia. *Parafabraea eucalypti* is only known from a sexual morph, while *Pa. caliginosa* only has an asexual morph, providing limited morphological data. These two species form a separate clade in the phylogenetic tree (Fig 1), and are distinct from *Neofabraea* and *Pezicula*. *Pseudofabraea*, typified by *Ps. citricarpa*, was introduced to accommodate the citrus pathogen originally described as *Cryptosporiopsis citricarpa* (Zhu et al. 2012), and subsequently transferred to *Neofabraea* (Johnston et al. 2014). Phylogenetically *Pseudofabraea* is distinct from *Neofabraea* (Fig 1). Although morphologically similar, *Pseudofabraea* tends to have more eustromatic acervuli than observed in species of *Neofabraea*.

Most published studies treating *Neofabraea*, *Pezicula*, and related genera have to date chiefly been based on morphology and host range, which caused ample confusion. Moreover, we observed that species in these genera tend to quickly become sterile in culture, or to display a high level of morphological variation after subculturing, which renders molecular data essential for correct identification. Unfortunately the majority of the species in these genera were described before the molecular era, and only a few are known from culture and DNA, which renders comparison and identification difficult. Therefore, the epitypification of the type species of the genera concerned is of great importance, as it provides a stable taxonomical framework to facilitate metagenomic studies working with environmental DNA and endophytic species occurring in a multitude of cosmopolitan plant hosts.

Conflicts of interest

The authors report no conflicts of interest. The authors alone are responsible for the content and writing of the paper.

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