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

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ABSTRACT

Species in *Neofabraea*, *Pezicula*, and related genera have been reported as saprobes, plant pathogens or endophytes from a wide range of hosts. The asexual morphs of *Neofabraea* and *Pezicula* had been placed in *Cryptosporiopsis*, now a synonym of *Pezicula*, 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 *Pezicula* 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. carpineae*, the type species of *Pezicula*, and for *N. malicorticis*, the type species of *Neofabraea*.

Keywords: *Dermateaceae*, *Helotiales*, multi-gene phylogeny, systematics.

Introduction

The genus *Pezicula* (*Dermateaceae*, *Helotiales*) was established in 1865, with the type species *Pe. carpineae*. The asexual morphs have been placed in *Cryptosporiopsis*, which was introduced in 1912 based on *C. scutellata*, the sexual morph of which is *Pe. ocellata*. Verkley (1999) monographed *Pezicula* and related genera based on a comprehensive 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 *N. 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 *N. 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 *N. 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 *N. 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, canker 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; Gariépy et al. 2005; Henriquez 2005; Johnston et al. 2005; Spotts 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 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 (12h light: 12h 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 (Rěblová 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 235000 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 *Pe. carpinea*, and 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 5 808 trees remaining after discarding 1 934 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, $9\text{--}13 \times 1.2\text{--}1.6\ \mu\text{m}$. 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, $16\text{--}31 \times 4.5\text{--}6\text{ }\mu\text{m}$ (av. $21.1\text{--}27.2 \times 4.7\text{--}5.4\text{ }\mu\text{m}$, $n = 46$). *Microconidia* only appear within for a short time span, cylindrical, straight, rounded at apex, truncate at base, hyaline, $6.5\text{--}10.0 \times 2\text{--}2.5\text{ }\mu\text{m}$.

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 to submerged mycelium, darkening with age, outer zone white; reverse concolorous. 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 ($17\text{--}28 \times 4\text{--}6\text{ }\mu\text{m}$, on inoculated apple) correspond well with Cordley's original description ($16\text{--}28 \times 5\text{--}7\text{ }\mu\text{m}$). 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. I* **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 carpineae (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 pretreatment 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 carpineae (Pers.) Tul. & C. Tul. ex Fuckel, *Jahrb. Nassauischen 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).
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-epitype 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) 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 $33\text{--}75 \times 4\text{--}6 \mu\text{m}$; determinate, phialidic, with indistinct periclinal thickening, or indeterminate, percurrently proliferating 1–4 times, scars close but distinct, cylindrical, hyaline, $(12\text{--})14\text{--}22.5 \times 5\text{--}6.5(7.5) \mu\text{m}$. *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, $27\text{--}36 \times 10\text{--}12.5 \mu\text{m}$, (av. $30\text{--}34.8 \times 10.1\text{--}11.7 \mu\text{m}$, $n = 32$) 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, $14\text{--}33 \times 2\text{--}5 \mu\text{m}$; determinate, phialidic, with periclinal thickening, or indeterminate, with several percurrent proliferations, hyaline, terminal cells subcylindrical to narrowly ampulliform, straight to curved, tapering towards apex, $6\text{--}12 \times 2\text{--}4 \mu\text{m}$. *Microconidia* cylindrical, straight, slightly or strongly bent, rounded at apex, truncate at base, hyaline, $5\text{--}9.5 \times 1\text{--}2 \mu\text{m}$ (av. $6.2\text{--}8.4 \times 1.4\text{--}1.8 \mu\text{m}$, $n = 38$).

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 concolorous; 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, $38\text{--}87 \times 2\text{--}3.5 \mu\text{m}$; determinate, phialidic, with distinct periclinal thickening, hyaline, terminal cells cylindrical to narrowly ampulliform, straight or slightly curved, $9\text{--}15 \times 1.5\text{--}3 \mu\text{m}$. *Microconidia*

cylindrical, straight to slightly bent, rounded at apex, truncate at base, hyaline, $8\text{--}12\text{--}(14) \times 1\text{--}2 \mu\text{m}$ (av. $8.8\text{--}11.3 \times 1.5\text{--}1.7 \mu\text{m}$, $n = 34$).

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 concolorous. 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.

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, 2).

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

MycoBank MB812371

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

In vivo: *Apothecia* erumpent, mostly solitary, rarely 2–3 on a basal stroma, sessile, or on a short, stout stalk. *Disc* circular, plane or convex, pale luteous when dry, 0.15–0.6 mm diam. *Receptacle* concolorous, 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 $2 \mu\text{m}$ 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, $91\text{--}148 \times 16\text{--}24 \mu\text{m}$, 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, $16\text{--}28 \times 6\text{--}12.5 \mu\text{m}$, (av. $17.2\text{--}21.9 \times 7.9\text{--}10.3 \mu\text{m}$, $n = 54$). *Paraphyses* filiform, septate, simple or branched at upper part, hyaline, $1.0\text{--}2.0 \mu\text{m}$ wide; apical cell swollen up to $6.5 \mu\text{m}$, 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 $40\text{--}65 \times 3.5\text{--}5 \mu\text{m}$; 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, $12\text{--}31 \times 4\text{--}6\ \mu\text{m}$. *Macroconidia* oblong to clavate, straight, rounded at apex, tapering to a protruding scar at base, granular to guttulate, hyaline, aseptate, $26\text{--}42 \times 10\text{--}15\ \mu\text{m}$, (av. $38.4\text{--}32.1 \times 11.8\text{--}14.1\ \mu\text{m}$, $n = 47$) 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, $30\text{--}61 \times 2.5\text{--}4\ \mu\text{m}$; determinate, phialidic, with minute periclinal thickening, hyaline, terminal cells subcylindrical to narrowly ampulliform, straight to slightly curved, tapering towards apex, $7\text{--}17.5 \times 2\text{--}3.5\ \mu\text{m}$. *Microconidia* cylindrical, straight to slightly bent, rounded at apex, truncate at base, hyaline, $6.5\text{--}10.0 \times 1\text{--}2\ \mu\text{m}$ ($n = 41$).

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, Marebåk 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, 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, sessile, 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 $2\ \mu\text{m}$ thick. *Medullary excipulum* hyaline to pale cinnamon, consisting of vertical rows of prismatic or isodiametric cells with hyaline walls up to $2\ \mu\text{m}$ thick, locally with brown intercellular deposits. *Ectal excipulum* olivaceous black to olivaceous brown, composed of isodiametric cells, 6–15 μm diam, with up to $2\ \mu\text{m}$ 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, $86\text{--}133(\text{--}169) \times 11\text{--}17(\text{--}24)\ \mu\text{m}$, 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, $16.5\text{--}24.5 \times 6\text{--}8.5\text{ }\mu\text{m}$, (av. $18.1\text{--}22.2 \times 6.4\text{--}7.7\text{ }\mu\text{m}$, $n = 49$). *Paraphyses* filiform, septate, simple or branched, $1\text{--}2\text{ }\mu\text{m}$ wide, hyaline; apical cell swollen up to $6\text{ }\mu\text{m}$, 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, Niederosterreich, 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 ($18\text{--}34.5 \times 7.5\text{--}14\text{ }\mu\text{m}$, 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, $25\text{--}124\text{ }\mu\text{m}$ 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, $2\text{--}3\text{ }\mu\text{m}$ 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, $21\text{--}60 \times 2\text{--}3\text{ }\mu\text{m}$; determinate, phialidic, with distinct periclinal thickening, hyaline, terminal cells subcylindrical to narrowly ampulliform, mostly straight or slightly curved, tapering towards apex, $7\text{--}14 \times 2\text{--}3\text{ }\mu\text{m}$. *Microconidia* cylindrical, straight to slightly bent, rounded at apex, truncate at base, hyaline, $7\text{--}13(\text{--}15) \times 1\text{--}2\text{ }\mu\text{m}$, (av. $7.8\text{--}12.0 \times 1.4\text{--}1.6\text{ }\mu\text{m}$, $n = 38$).

Culture characteristics: Colonies on OA reaching 53 mm diam after 14 d, covering the full plate after 21 d; flat with an even to slightly undulate margin; aerial mycelium diffuse, but in the centre well developed, tufty to woolly, white; submerged mycelium buff; reverse concolorous. 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 ($4.5\text{--}10 \times 1\text{--}2\text{ }\mu\text{m}$; 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. carpineae*. However, they cluster apart from CBS 923.96, the ex-epitype culture of *Pe. carpineae*. 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., *Annls. 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. *Macroconidiogenous 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). *Microconidiogenous 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 concolorous. 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 sessile, 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.

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 *Pezicula*.

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).

DISCUSSION

In this study we resolve the phylogenetic relationships among *Cryptosporiopsis*, *Neofabraea*, *Pezicula* and related genera by merging morphological and multi-gene phylogenetic DNA data. Based on these results, we are able to separate *Pezicula* from *Neofabraea*, *Phlyctema*, *Rhizodermea*, and introduce two previously undescribed genera, *Parafabraea* and *Pseudofabraea*.

In the multi-gene phylogenetic tree (Fig 1) the *Pezicula* clade consists of two well-supported subclades, with an additional species on a basal long branch. The type species of *Pezicula*, *Pe. carpinea*, and the type species of *Cryptosporiopsis*, *C. nigra*, considered the asexual morph of *Pe. 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 *Pezicula* (Groves 1940; Verkley 1999; Abeln et al. 2000). In the present study we compared the species in these two *Pezicula* 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, *Pezicula*, which is also in agreement with the approach taken by Johnston et al. (2014). The long branch at the bottom of the *Pezicula* 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 multigene analyses generated, this isolate always clustered within *Pezicula*, albeit on a long branch. It could be that this isolate will eventually be shown to represent a distinct genus, but the *Pezicula* 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 *Pezicula* 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 *R. veluwensis*, isolated from roots of *Erica tetralix* in the Netherlands; Verkley et al., 2010) clusters in a well-supported clade basal to *Pezicula*. Unfortunately all cultures of *R. veluwensis* known to date are sterile endophytes that only produce abundant chlamydospore-like structures in culture (absent in *Pezicula s. str.*), and thus it is not possible to make a sensible comparison with the morphology of *Pezicula* until more species of *Rhizodermea* have been collected.

Species of *Cryptosporiopsis* have in the past been linked as asexual morphs to both *Neofabraea* and *Pezicula*. The fact that *Cryptosporiopsis s. str.* is now treated as synonym of *Pezicula* (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 *Pezicula*. *Cryptosporiopsis edgertonii* was described by Gadgil & Dick (2001), who only provided a morphological description. The ITS sequence available in GenBank (JN595853) labelled as *C. edgertonii* is identical to that of the ex-type strain of *Pe. neosporulosa*. Morphologically, these two species are different, macroconidia in *C. edgertonii* are larger ($32\text{--}48 \times 10\text{--}15\ \mu\text{m}$) than in *P. neosporulosa* ($24\text{--}36.5 \times 9\text{--}12\ \mu\text{m}$), while the microconidia of *C. edgertonii* are of comparable length but narrower ($12\text{--}14 \times 1\text{--}1.5\ \mu\text{m}$) than in *P. neosporulosa* ($8\text{--}14 \times 1.5\text{--}2.5\ \mu\text{m}$). 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 *N. malicorticis*, currently includes six species: *N. actinidiae*, *N. inaequalis*, *N. kienholzii*, *N. krawtzwii*, *N. malicorticis* and *N. perennans*, all of which appear to be phytopathogenic. In the present study an epitype is designated for *Gloeosporium malicorticis* (= *Neofabraea malicorticis*), which causes anthracnose canker and Bull’s eye rot on apple and pear.

The resurrected genus *Phlyctema* is typified by *Ph. 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; Soto-Alvear et al. 2013; Quaedvlieg 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.

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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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Legends to figures

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).

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).

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. (F) Conidiogenous cells giving rise to macroconidia. (G) Microconidia. (H) Macroconidia from OA. (I) Macroconidia from inoculated apple. (J, K) Intermediate conidia between macro- and micro-conidia. All bars = 10 µm, I = H.

Fig 4 – *Pezicula carpineae* (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.

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 μ m; other bars = 10 μ m.

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 μ m.

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 μ m; C = 25 μ m; D–K = 10 μ m.

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 μ m; F, G = 25 μ m; H = 10 μ m.

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 μ m.

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 μ m.

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.

Table(s)

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

	Strain number ¹ and Status	Original name	Host/Substrate	Locality	Collector	GenBank Accession Number ²	
						28S nrDNA ITS	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	HQ094979	KR859078
	CBS 121.043, ICMP 7826a, ex-type	<i>Cryptosporiopsis actinidiae</i>	<i>Actinidia deliciosa</i>	New Zealand	G.J. Samuels, 1 Sep 1982	KR858870	KR859079
<i>Neofabraea actinidiae</i>	CBS 194.69	<i>Cryptosporiopsis</i> sp.	<i>Ilex verticillata</i>	Netherlands	–	KR858871	KR859080
<i>Neofabraea inaequalis</i>	CBS 126.75, ex-type	<i>Cryptosporiopsis inaequalis</i>	–	France	M. Morelet, 1973	KR858872	KR859081
	CBS 126.461, DAOM 240213, ex-type	<i>Cryptosporiopsis kienholzii</i>	<i>Malus domestica</i> cv. Fuji	USA	R. Spotts, 29 May 2005	KR858873	KR859082
<i>Neofabraea kienholzii</i>	CBS 318.77	<i>Cryptosporiopsis</i> sp.	<i>Acacia japonica</i>	Netherlands	H.A. van der Aa, 7 May 1977	KR858874	KR859083
<i>Neofabraea kravtzevii</i>	CBS 102.867	<i>Neofabraea kravtzevii</i>	<i>Populus x berolinensis</i>	Norway	H. Solheim, NISK	KR858875	KR859084
<i>Neofabraea malicorticis</i>	CBS 102.863, DAOM 227083	<i>Neofabraea malicorticis</i>	Apple tree canker	Canada, British Columbia	J.E. Rahe	KR858876	KR859085
	CBS 1220.30, ISC 100036, ex-neotype	<i>Neofabraea malicorticis</i>	<i>Malus</i> sp.	USA, Oregon	–	KR858877	KR859086
<i>Neofabraea perennans</i>	CBS 102.869, DAOM 227089	<i>Neofabraea perennans</i>	Apple tree canker	Canada, British Columbia	J.E. Rahe	KR858878	KR859087
	CBS 275.29, ATCC 13905, ATCC 1730	<i>Neofabraea perennans</i>	<i>Malus sylvestris</i>	–	J.S. Cooley	KR858879	KR859088
	CBS 453.64	<i>Neofabraea perennans</i>	–	UK	–	KR858880	KR859089
<i>Parafabraea caliginosa</i>	CBS 124.806, CPC 14048, ex-type	<i>Cryptosporiopsis caliginosa</i>	<i>Eucalyptus caliginosa</i>	Australia, New South Wales	B.A. Summerell, 1 Feb 2007	KR858881	KR859090
<i>Parafabraea eucalypti</i>	CBS 124.810, CPC 13755, ex-type	<i>Neofabraea eucalypti</i>	<i>Eucalyptus globulus</i>	Australia	I. Smith, 15 Feb 2007	KR858882	KR859091
<i>Pezicula acercola</i>	CBS 239.38	<i>Pezicula acercola</i>	<i>Acer spicatum</i>	Canada, Ontario	J.W. Groves, Aug 1932	KR858883	KR859092
	CBS 239.97	<i>Pezicula acercola</i>	<i>Acer spicatum</i>	Canada, Ontario	G. Verkley, 20 Sep 1996	KR858884	KR859093
<i>Pezicula acercola</i>	CBS 240.38	<i>Pezicula acercola</i>	<i>Acer spicatum</i>	Canada, Ontario	J.W. Groves, Aug 1934	KR858885	KR859094
	CBS 240.97	<i>Pezicula acercola</i>	<i>Acer spicatum</i>	Canada, Ontario	G. Verkley, 20 Sep 1996	KR858886	KR859095
<i>Pezicula acercola</i>	CBS 241.97	<i>Pezicula acercola</i>	<i>Acer spicatum</i>	Canada, Ontario	G. Verkley, 21 Sep 1996	KR858887	KR859096
	CBS 242.97	<i>Pezicula acercola</i>	<i>Acer spicatum</i>	Canada, Ontario	G. Verkley, 21 Sep 1996	KR858888	KR859097
<i>Pezicula acercola</i>	CBS 245.97	<i>Pezicula acercola</i>	<i>Acer spicatum</i>	Canada, Ontario	G. Verkley, 20 Sep 1996	KR858889	KR859098
	CBS 246.97	<i>Pezicula acercola</i>	<i>Acer spicatum</i>	Canada, Ontario	G. Verkley, 20 Sep 1996	KR858890	KR859099
<i>Pezicula acercola</i>	CBS 247.97	<i>Pezicula acercola</i>	<i>Acer spicatum</i>	Canada, Ontario	G. Verkley, 21 Sep 1996	KR858891	KR859100
	CBS 248.97	<i>Pezicula acercola</i>	<i>Acer spicatum</i>	Canada, Ontario	G. Verkley, 21 Sep 1996	KR858892	KR859101
<i>Pezicula aurantica</i>	CBS 201.46	<i>Pezicula aurantica</i>	<i>Alnus crispa</i> var. <i>molisii</i>	Canada	isol. J.W. Groves, No. 816-1	KR858893	KR859102
<i>Pezicula brunnea</i>	CBS 120.291, ex-type	<i>Cryptosporiopsis brunnea</i>	<i>Gaultheria shallon</i>	Canada	T.R. Allen, May 1998	KR858894	KR859103
<i>Pezicula californiae</i>	CBS 124.805, ex-type	<i>Pezicula californiae</i>	<i>Eucalyptus</i> sp.	USA, California	S. Denman, Mar 2009	KR858895	KR859104
<i>Pezicula carpiniae</i>	CBS 324.97	<i>Pezicula carpiniae</i>	<i>Carpinus betulus</i>	Netherlands	F.J. Stokman & G.C.N. van Zanen, 31 Jul 1996	KR858896	KR859105
	CBS 325.97	<i>Pezicula carpiniae</i>	<i>Carpinus betulus</i>	Netherlands	F.J. Stokman & G.C.N. van Zanen, 31 Jul 1996	KR858897	KR859106
<i>Pezicula carpiniae</i>	CBS 921.96	<i>Pezicula carpiniae</i>	<i>Carpinus betulus</i>	Germany	G. Verkley, 9 Jul 1996	KR858898	KR859107
	CBS 923.96, ex-epitype	<i>Pezicula carpiniae</i>	<i>Carpinus betulus</i>	Germany	G. Verkley, 9 Jul 1996	KR858899	KR859108
<i>Pezicula cinnamomea</i>	CBS 100.240	<i>Pezicula cinnamomea</i>	<i>Larix decidua</i>	Denmark	G. Verkley, 16 Sep 1997	KR858900	KR859109
	CBS 100.241	<i>Pezicula cinnamomea</i>	<i>Larix decidua</i>	Denmark	G. Verkley, 16 Sep 1997	KR858901	KR859110
<i>Pezicula cinnamomea</i>	CBS 100.247	<i>Pezicula cinnamomea</i>	<i>Abies alba</i>	Denmark	G. Verkley, 15 Sep 1997	KR858902	KR859111
	CBS 101.001	<i>Pezicula</i> sp.	<i>Taxus baccata</i>	Germany	Ullrich, Pflanzenschutzamt Frankfurt, Germany, Nov 19	KR858903	KR859112
<i>Pezicula acercola</i>	CBS 112.390	<i>Pezicula acercola</i>	<i>Fagus sylvatica</i>	Italy	R. Danti	KR858904	KR859113
	CBS 112.391	<i>Pezicula acercola</i>	<i>Fagus sylvatica</i>	Italy	R. Danti	KR858905	KR859114
<i>Pezicula cinnamomea</i>	CBS 184.50, ex-syntype of <i>Cryptosporiopsis balsamea</i>	<i>Pezicula cinnamomea</i>	<i>Abies balsamea</i>	Norway	H. Rohak	KR858906	KR859115
	CBS 203.82, PD 81.666	<i>Pezicula cinnamomea</i>	<i>Chaemoscypha</i> sp.	Netherlands	–	KR858907	KR859116
<i>Pezicula cinnamomea</i>	CBS 224.78	<i>Pezicula cinnamomea</i>	<i>Picea</i> sp.	France	isol. H. Butin	KR858908	KR859117
	CBS 226.96	<i>Pezicula cinnamomea</i>	<i>Fagus sylvatica</i>	France	G. Verkley, 7 Oct 1995	KR858909	KR859118
<i>Pezicula cinnamomea</i>	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
<i>Pezicula cinnamomea</i>	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
<i>Pezicula cinnamomea</i>	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	KR858915	KR859124
<i>Pezicula cinnamomea</i>	CBS 240.96	<i>Pezicula cinnamomea</i>	<i>Fagus sylvatica</i>	France	G. Verkley, 17 Oct 1995	KR858916	KR859125
	CBS 241.96	<i>Pezicula cinnamomea</i>	<i>Picea abies</i>	France	G. Verkley, 19 Oct 1995	KR858917	KR859126
<i>Pezicula cinnamomea</i>	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 bezelii</i>	USA	G. Verkley, 25 Sep 1996	KR858919	KR859128
<i>Pezicula</i> sp.	CBS 244.97	<i>Pezicula</i> sp.	<i>Lindera bezelii</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
<i>Pezicula cinnamomea</i>	CBS 256.32	<i>Quercus</i> sp.	–	Denmark	isol. C.A. Jørgensen, No. 732	KR858922	KR859131
	CBS 289.39	<i>Pezicula sporulosa</i>	<i>Picea sitchensis</i>	Germany	–	KR858923	KR859132
<i>Pezicula cinnamomea</i>	CBS 290.39, ex-type of <i>Pezicula plantarum</i>	<i>Pezicula cinnamomea</i>	<i>Prunus americana</i>	Germany	H.W. Wollenweber	KR858924	KR859133
	CBS 315.96	<i>Pezicula cinnamomea</i>	<i>Abies procera</i>	Germany	R.D. Kehr	KR858925	KR859134
<i>Pezicula cinnamomea</i>	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
<i>Pezicula cinnamomea</i>	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
<i>Pezicula cinnamomea</i>	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
<i>Pezicula cinnamomea</i>	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
<i>Pezicula cinnamomea</i>	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
<i>Pezicula cinnamomea</i>	CBS 329.96	<i>Pezicula cinnamomea</i>	<i>Tilia cordata</i>	Germany	G. Verkley, Schulz, Schrader & Kehr, 1 Nov 1995	KR858936	KR859145
	CBS 330.96	<i>Pezicula cinnamomea</i>	<i>Tilia cordata</i>	Germany	G. Verkley, Schulz, Schrader & Kehr, 1 Nov 1995	KR858937	KR859146
<i>Pezicula cinnamomea</i>	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. Perini	KR858939	KR859148
<i>Pezicula cinnamomea</i>	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	KR859150
<i>Pezicula acercola</i>	CBS 516.69	<i>Pezicula acercola</i>	<i>Acer pseudoplatanus</i>	Netherlands	isol. J. Blok, 1969	KR858942	KR859151
	CBS 625.96	<i>Pezicula cinnamomea</i>	<i>Quercus robur</i>	Germany	G. Verkley, Schulz, Schrader & Kehr, 1 Nov 1995	KR858943	KR859152
<i>Pezicula cinnamomea</i>	CBS 626.96	<i>Pezicula cinnamomea</i>	<i>Quercus robur</i>	Germany	G. Verkley, Schulz, Schrader & Kehr, 1 Nov 1995	KR858944	KR859153
	CBS 628.96	<i>Pezicula cinnamomea</i>	<i>Alnus glutinosa</i>	Germany	G. Verkley & Kehr, 2 Nov 1995	KR858945	KR859154
<i>Pezicula cinnamomea</i>	CBS 629.96	<i>Pezicula cinnamomea</i>	<i>Alnus glutinosa</i>	Germany	G. Verkley & Kehr, 2 Nov 1995	KR858946	KR859155
	CBS 630.96	<i>Pezicula cinnamomea</i>	<i>Acer pseudoplatanus</i>	Germany	G. Verkley & Kehr, 2 Nov 1995	KR858947	KR859156
<i>Pezicula cinnamomea</i>	CBS 631.96	<i>Pezicula cinnamomea</i>	<i>Acer pseudoplatanus</i>	Germany	G. Verkley & Kehr, 2 Nov 1995	KR858948	KR859157
	CBS 632.96	<i>Pezicula cinnamomea</i>	<i>Picea abies</i>	Netherlands	G. Verkley, 21 Nov 1995	KR858949	KR859158
<i>Pezicula cinnamomea</i>	CBS 633.96	<i>Pezicula cinnamomea</i>	<i>Picea abies</i>	Netherlands	G. Verkley, 21 Nov 1995	KR858950	KR859159
	CBS 778.95	<i>Pezicula cinnamomea</i>	<i>Larix decidua</i>	Germany	L. Pehl, Sep 1994	KR858951	KR859159
<i>Pezicula sporulosa</i>	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	–	KR858953	KR859161
<i>Pezicula cinnamomea</i>	CBS 939.70	<i>Pezicula cinnamomea</i>	<i>Abies alba</i>	Germany	–	KR858954	KR859162
	CBS 285.39	<i>Pezicula corni</i>	<i>Cornus circinnata</i>	Canada, Ontario	J.W. Groves, 22 Aug 1934	KR858955	KR859163
<i>Pezicula corticola</i>	CBS 259.31	<i>Pezicula corticola</i>	–	Denmark	isol. C.A. Jørgensen	KR858956	KR859164
<i>Pezicula corylina</i>	CBS 260.31	<i>Pezicula corticola</i>	<i>Malus sylvestris</i>	Denmark	–	KR858957	KR859165
	CBS 140.22	<i>Pezicula corticola</i>	<i>Malus sylvestris</i>	UK	isol. G.G. Gilchrist	KR858958	KR859166
<i>Pezicula corylina</i>	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
<i>Pezicula diversispora</i>	CBS 250.97	<i>Pezicula corylina</i>	<i>Corylus cornuta</i> var. <i>cornuta</i>	Canada, Ontario	G. Verkley, 20 Sep 1996	KR858961	KR859169
	CBS 185.50, ex-syntype of <i>Cryptosporiopsis diversispora</i>	<i>Cryptosporiopsis diversispora</i>	<i>Picea abies</i>	Norway	isol. H. Rohak	KR858962	KR859170
<i>Pezicula ericae</i>	CBS 282.47	<i>Alnus glutinosa</i>	–	Germany	–	KR858963	KR859171
	CBS 158.93	<i>Cryptosporiopsis ericae</i>	<i>Tilia platyphyllos</i>	Germany	R. Schröter	KR858964	KR859172
<i>Pezicula eucurtia</i>	CBS 120.290, UAMH 9445, ex-type	<i>Cryptosporiopsis ericae</i>	Roots of <i>Vaccinium membranaceum</i>	USA, Idaho	B. McCracken	KR858965	KR859173
	CBS 120.292, UAMH 10419	<i>Cryptosporiopsis ericae</i>	Roots of <i>Gaultheria shallon</i>	Canada	T.R. Allen, 6 May 1998	KR858966	KR859174
<i>Pezicula eucurtia</i>	CBS 100.249	<i>Pezicula eucurtia</i>	<i>Larix decidua</i>	Denmark	G. Verkley, 15 Sep 1997	KR858967	KR859175
	CBS 256.97	<i>Pezicula eucurtia</i>	<i>Pinus sylvestris</i>	USA, New York	G. Verkley, 26 Sep 1996	KR858968	KR859176
<i>Pezicula eucurtia</i>	CBS 257.97						

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