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

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**A B S T R A C T**

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 \(\beta\)-tubulin region (\(\text{tub2}\)), and the partial RNA polymerase II second largest subunit region (\(\text{rpb2}\)), 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. carpinea, the type species of *Pezicula*, and for N. malicorticis, the type species of *Neofabraea*.

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**Introduction**

The genus *Pezicula* (Dermateaceae, Helotiales) was established in 1865, with the type species *Pezicula carpinea*. The asexual morphs have been placed in *Cryptosporiopsis*, which was introduced in 1912 based on *Cryptosporiopsis scutellata*, the sexual morph of which is *Pezicula 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 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 asceptate, fuseform 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 multigene 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 et al. 2004; Henriquez et al. 2004; Gariepy 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 Infundibululis 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 ITS1F (White et al. 1990), or V9G (de Hoog & Gerrits van den Ende 1998) and LS266 (Masciaux et al. 1995), the large subunit of nrDNA (LSU) with LROR (Vilgalys & Hester 1990) or LSU1Fd (Crous et al. 2009a) and LRS (Vilgalys & Hester 1990), β-tubulin (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 and RPB2-4Fd (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
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a ATCC: American Type Culture Collection, Virginia, U.S.A.; CBS: CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands; CMGC: 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 (Mycolgy), Ottawa, Canada; ICMP: International Collection of Microorganisms from Plants, Landcare Research, Aukland, New Zealand; IMI: International Mycological Institute, CBI-Bioscience, Egham, Bakeham Lane, 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).

**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 parameters, the number of spores (n) measured, the extremes of measurement, 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, multigene 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 (Rebolva 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 one 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...
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 Rhizoderma 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 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 phylogenetic tree (Fig 2) delimited 35 species clades, 13 of which lack a clear identification, and might represent novel species.

**Taxonomy**


**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 inequalerinal, elongated ellipsoid, ends rounded, straight or curved, asceptate, thin-walled, smooth, hyaline, with granular contents or small oil droplets; later septeate, 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 acropneumogenous. 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, asceptate, hyaline, and thinned 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, asceptate, 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 phalidic, or indeterminate and proliferating percurrently. However, only phalidic 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.


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.


**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, asceptate, 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 long fringe of white radiating hyphae; surface smooth, in centre hazel to olivaceous due
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<th>Species</th>
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Fig 2 – (Continued)
to submersed 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.


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; Gariepy 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.


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

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


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

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.)


Additional synonyms and description in Verkley (1999).


**Notes:** Following an examination of the holotype of *Peziza carpinea* and type materials of its synonyms, Verkley (1999)
confirmed that the fungus on CBS H-17476 was *Peziza 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 *Peziza fasciculata* (1790), and not *Peziza carpinea* (1801). However, because the name *Peziza carpinea* has been used in numerous studies, it should be included on the list of protected species names (Wollenweber 1939; Dennis 1974; Verkley 1999; Abein et al. 2000; Verkley et al. 2003; Lynch et al. 2013; Yuan & Verkley 2014). Moreover, *Peziza cinnamomea*, *Peziza corylina*, *Peziza frangulae* subsp. *frangulae*, and *Peziza 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. Conidial 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.
Neofabraea, Pezicula, and related genera

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

Etym.: Named after its small microconidia.

In vitro: Conidiomata sporodochial, forming on hyphae, 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 to 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.

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, 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 to 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.

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).

Etym.: Named after its small microconidia.

In vitro: Conidiomata sporodochial, forming on hyphae, 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 to 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.

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, 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 to 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.

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.
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.
**Neofabraea, Pezicula, and related genera**

1313

**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. Asc 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, asperate, 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 to conidal mass. Conidiomatal wall composed of an outer tissue of initiate, thick-walled hyphae, 20–34 μm thick, and an inner tissue of hyaline to pale olivaceous cells, giving rise directly to conidiophores. Macroconidigenous cells mostly discrete, or integrated in mostly simple or branched, 2–4-septate, acrogenous conidiophores 40–65 × 3.5–5 μm; determinant, phialidic, with a minute periclinal thickening, or indeterminate and proliferating percurrentlly 1–3 times, scars often distinct 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, asperate, 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. Macroconidigenous cells mostly integrated in simple or branched, acrogenous conidiophores, 30–61 × 2.5–4 μm; determinant, 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, Marebak plantation 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. Asc 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, asperate, 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 (18–34.5 × 7.5–14 μm, 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).

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 × 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 × 2–3 μm. Microconidia cylindrical, straight to slightly bent, rounded at apex, truncate at base, hyaline, 7–13(−15) × 1–2 μm, (av. 7.8–12.0 × 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.
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.


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.**


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. 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 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. 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 Gautheria, *Tilia*, and Vaccinium from Europe and North America (Table 1). CBS 433.75 represents a distinct species.

*Pezicula* sp. 7.


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.

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


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, aseptate, late septate. Paraphyses numerous, filiform, branched, septate, obtuse, hyaline, apical cell slightly swollen (from Verkley 1999; based on Guthrie 1959). When Verkley (1999) separated *Pezicula* as *Phlyctema* 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.


Notes: The sexual morph of *Ph. vagabunda* appears to have been collected only once (Guthrie 1959), and the type material was protected over 60 years (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*, making it a synonym of *Gloeosporium album* (Guthrie 1959). We can readily distinguish a known sexual morph, which is similar to *N. perennans* and *N. vagabunda*, which is reported from Europe and America (Table 1). CBS 433.75 represents a distinct species.


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.


Notes: The sexual morph of *Ph. vagabunda* appears to have been collected only once (Guthrie 1959), and the type material was protected over 60 years (Guthrie 1959). 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 (Gariepy 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 ellipsoid, 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 microcondia. (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 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.


**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, substicarpal to epidermal, with a single or several confluent cavities. **Conidiophores** unbranched, hyaline. **Macroconidigenous** 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.


**Synonym:** Neofabraea citricarpa (L. Zhu et al.) P.R. Johnst., IMA Fungus S: 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, *Pezicula carpinea*, and the type species of Cryptosporiopsis, *Cryptosporiopsis nigra*, considered the asexual morph of Pezicula *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; Abelín 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), rp2 (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 multi-gene 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 *Rhizodermea veluwnesis*, 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. veluwnesis* 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
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 × 10–15 μm) than in P. neosporulosa (24–36.5 × 9–12 μm), while the microconidia of C. edgertonii are of comparable length but narrower (12–14 × 1–1.5 μm) than in P. neosporulosa (8–14 × 1.5–2.5 μm). 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 krawtzewii, 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 Ps. 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 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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1322 C. Chen et al.