They seldom occur alone

Pedro W. CROUS\(^{a,b,c,*}\), Johannes Z. GROENEWALD\(^d\)

\(^a\)CBS-KNAW Fungal Biodiversity Centre, Uppsalalaan 8, 3584 CT Utrecht, The Netherlands
\(^b\)Department of Microbiology and Plant Pathology, Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, 0002 Pretoria, South Africa
\(^c\)Microbiology, Department of Biology, Utrecht University, Padualaan 8, 3584 CH Utrecht, The Netherlands

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**Abstract**

Species of Coleophoma have been reported as plant pathogenic, saprobic or endophytic on a wide host range. The genus is characterised by having pycnidial conidiomata, phialidic conidiogenous cells intermingled among paraphyses, and cylindrical conidia. Coleophoma has had a confusing taxonomic history with numerous synonyms, and its phylogeny has remained unresolved. The aim of the present study was to use a polyphasic approach incorporating morphology, ecology, and molecular data of the partial large subunit of nrDNA (LSU), the internal transcribed spacer region with intervening 5.8S nrDNA (ITS), partial \(\beta\)-tubulin (\(\beta\)-tub2), and translation elongation factor 1-alpha (\(\text{tef}1\)) gene sequences to resolve its taxonomy and phylogeny. Based on these results the genus was found to be polyphyletic, with taxa tentatively identified as *Coleophoma* clustering in Dothideomycetes and Leotiomycetes. Species corresponding to the concept of *Coleophoma* s.str. (Dermateaceae, Helotiales, Leotiomycetes) were found to form a distinct clade, with five new species. Furthermore, *Coleophoma* was found to be linked to the newly established sexual genus, *Parafabraea*, which is reduced to synonymy. Isolates occurring on *Ilex aquifolium* in the Netherlands also clustered in Dermateaceae, representing a novel genus, *Davidhawksworthia*. In the Dothideomycetes, several taxa clustered in Dothiora (Dermateaceae, Dothideales), which is shown to have Dothichiza and Hormonema-like asexual morphs, with four new species. Furthermore, *Pseudocamaropycnis* is introduced as a new genus (Mytilinidaceae, Mytilinidiales), along with *Briansuttonomyces* (Didymellaceae, Pleosporales) and *Dimorphosporicola* (Pleosporaceae, Pleosporales).

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**Introduction**

The genus *Coleophoma* (von Höhnel 1907), typified by *Coleophoma crateriformis*, was established to accommodate coelomycetous fungi that are presently known to be plant pathogenic, saprobic or endophytic, occurring on a wide range of host plants. *Coleophoma* is characterised by having pycnidial conidiomata with well developed lower, but poorly developed upper walls, hyaline conidiophores intermingled among hyaline, collapsing paraphyses, and discrete, integrated phialidic conidiogenous cells with prominent periclinal thickening, and smooth, hyaline, cylindrical, guttulate, straight conidia with obtuse ends (Nag Raj 1978; Sutton 1980).

Species of *Coleophoma* differ in their ecology, being endophytic (e.g. *Coleophoma prunicola* in living leaves of *Prunus lusitanica*; Duan et al. 2007), saprobic ( *Coleophoma empetri* on leaf litter; Wu et al. 1996), and plant pathogenic, e.g. *Coleophoma fusiformis* on leaves of *Rhododendron* (Sutton 1980; Duan et al. *\ldots* )
Calyptus (Yuan 1996; Crous et al. 2011), Coleophoma eucalypti and Coleophoma eucalyptorum on Eucalyptus (Yuan 1996; Crous et al. 2011), C. empetri on Vaccinium (Polashock et al. 2009), Coleophoma genevae on Gevuina (Bianchinotti & Rajchenberg 2004), and Coleophoma proteae on Protea caffra (Crous et al. 2012).

Based on the phylogenetic position of C. cratersiformis, De Gruyter et al. (2009) placed Coleophoma in Dothideales, while Coleophoma maculans grouped in Helotiales, showing the genus to be paraphyletic (Tanaka et al. 2015). In a subsequent study, Thambugala et al. (2014) confirmed Coleophoma s.str. to belong to Dothideales (Dothideaceae), being closely related to species of Dothiora and Cylindroseptoria. However, Dothiora is typified by Dothiora pyrenophora, which has Dothichiza sorbi as asexual morph (Sivanesan 1984). Cylindroseptoria is typified by Cylindroseptoria ceratoniae, but Cylindrosetoria pistacia was allocated to Neocylindroseptoria by Thambugala et al. (2014), as the genus was paraphyletic.

Several genera have to date been reduced to synonymy under Coleophoma based on morphology, namely Basilocula, Ceuthosira, and Xenodonomus (Nag Raj 1978), as well as Coleonaema, Bactropycnis, and Rhabdostromina (Sutton 1980). Given differences in conidial development between Coleonaema and Coleophoma, however, Duan et al. (2007) were of the opinion that Coleonaema, typified by Coleonaema oleae, should again be resurrected as distinct genus. Other than the few isolates included in phylogenetic studies dealing with other genera in Dothideales, the genus Coleophoma, which clearly includes several species associated with important plant diseases, remains insufficiently known, and in urgent need of revision (Sutton 1980). The aim of the present study was thus to employ morphology and multigene phylogenetic data to clarify relationships of Coleophoma among other genera in Dothideaceae, to resolve the paraphyletic nature of the genus, and also try to elucidate the host range of the various species known from culture.

Materials and methods

Isolates

The majority of the isolates used in this study were obtained from the culture collection of the CBS-KNAW Fungal Biodiversity Centre (CBS), Utrecht, The Netherlands. Isolates included were through the years identified as species of Coleophoma based on the fact that they had pycnidal conidiomata, and cylindrical conidia. In addition, fresh collections were made from conidiomata on symptomatic leaves of diverse hosts. Single conidial colonies were established from sporulating conidiomata on Petri dishes containing pine needle agar (PNA) (Smith et al. 1996), 2 % malt extract agar (MEA), potatodextrose agar (PDA), and oatmeal agar (OA) (Crous et al. 2009b), and incubated at 25 °C under continuous near-ultraviolet light to promote sporulation.

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). 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), the large subunit of nrDNA (LSU) with LROR (Vilgalys & Hester 1990) or LSU1F3 (Crous et al. 2009a) and LR5 (Vilgalys & Hester 1990), the β-tubulin gene (tub2) with T1 (O’Donnell & Cigelnik 1997) or Bt-2a and Bt-2b (Glass & Donaldson 1995), and translation elongation factor 1-alpha (ef1) with EF1-728F (Carbone & Kohn 1999) and EF-2 (O’Donnell et al. 1998) or EF1-96R (Carbone & Kohn 1999). PCR and reaction mixtures followed Groenewald et al. (2013) for ITS, ef1, and tub2, and Crous et al. (2009a) for LSU. PCR products were sequenced in both directions and a consensus sequence calculated, as described by Gomes et al. (2013).

Phylogenetic analyses

Novel sequences generated in this study were blasted against the NCBI’s GenBank nucleotide database to determine the closest relatives for a taxonomic framework of the studied isolates. 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) (Katoh & Standley 2013), and then manually adjusted in MEGA v. 6.06 (Tamura et al. 2007). To check the congruence of different gene regions, individual gene trees were manually compared prior to concatenation. Maximum parsimony (MP; LSU overview and species phylogenies) and Bayesian analyses (LSU overview phylogenies) were used to determine the phylogenies. The MP analyses were conducted in PAUP v. 4.0b10 (Swoford 2003) with the heuristic search option set to 100 random taxa addition, and the tree bisection-reconnection (TBR) as the branch-swapping algorithm. All characters were weighted equally and alignment gaps were treated as new state data and bootstrap analyses were based on 1000 replications. Tree length (TL), consistency index (CI), retention index (RI), and rescaled consistency index (RC) values were also calculated. Bayesian analyses were performed in MrBayes v. 3.2.5 (Ronquist et al. 2012) and the best nucleotide substitution model per gene region was selected 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 0.2 and trees were sampled every 100 generations. Analyses stopped once the average standard deviation of split frequencies was below 0.01. Sequences generated in this study were deposited in GenBank (Table 1) and alignments and phylogenetic trees in TreeBASE (www.treebase.org). Nomenclatural novelties were deposited in MycoBank (Crous et al. 2004).

Morphology

Observations were made with a Nikon SMZ25 stereo-microscope, and with a Zeiss Axios Imager 2 light microscope using differential interference contrast (DIC) illumination and a Nikon DS-Ri2 camera and software. Colony characters and pigment production were noted after 2 wk of growth on MEA, PDA, and OA incubated at 25 °C. Colony colours (surface and reverse) were rated according to the colour charts of Rayner (1970). Morphological descriptions were based on
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<th>Isolation source</th>
<th>Locality</th>
<th>Collector</th>
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<td>CBS 1155897, HKUCC 30068</td>
<td>KU728518, KU728587</td>
<td>W. Gams &amp; J.A. Stalpers</td>
<td>Netherlands: Wageningen, Germany; Hong Kong, China, Shue O</td>
<td>leaf, <em>Pinus elliotii</em>, ATCC: American Type Culture Collection, VA, USA; CPC: Culture collection of Pedro Crous, housed at CBS; DSM: Deutsche Sammlung von Mikroorganismen und Zellkulturen GmbH, Braunschweig, Germany; EHT: Swiss National Collection of Bacteria and Yeasts, Zurich, Switzerland; HKUCC: The University of Hong Kong Culture Collection, Hong Kong, China; IFO: Institute for Fermentation, Osaka, Japan; MsCL: Microbial Strain Collection of Latvia, Faculty of Biology, University of Latvia, Latvia; PD: Plant Protection Service, nVWA, Division Plant, Wageningen, The Netherlands; Shapers</td>
</tr>
</tbody>
</table>

**Table 1 (continued)**

**Phylogenetic analyses**

Based on the Blast results, the strains were divided into two groups: **Leotiomycetes** and **Dothideomycetes**, and subsequently multigene (ITS, tub2, tef1) species phylogenies were generated for species belonging to the genera *Coleophoma* and *Dothiora*, respectively.

The overview LSU/ITS phylogeny of *Leotiomycetes* consisted of 46 sequences, including the outgroup sequence *Neofusisorum umdonicola* (GenBank KF766373, EU821904). A total of 1334 characters were included in the phylogenetic analyses; 245 characters were parsimony-informative, 155 were variable and parsimony-uninformative, and 934 characters were constant. A total of 391 equally most parsimonious trees were obtained, the first of which is shown in Fig 1 (TL = 970, CI = 0.631, RI = 0.803, and RC = 0.507). In the Bayesian analysis, the LSU partition had 112 unique site patterns and the ITS partition had 219 unique site patterns, and the analysis ran for 820 000 generations, resulting in 16 402 trees of which 12 302 trees were used to calculate the posterior probabilities which are mapped onto Fig 1. Both partitions were analysed with MrBayes using dirichlet (1,1,1,1) state frequency distribution and inverse gamma-shaped rate variation across sites (GTR + I + G). The main difference between the Bayesian and MP tree was the position of the Pezicula clade; in the Bayesian tree this genus clustered sister to *Coleophoma* whereas it was sister to the lineage containing *Davidhawkinsworthia* to *Neoabaraea* in the parsimony analysis (data not shown, see TreeBASE). The LSU region alone lacked sufficient resolution to resolve the lineages in *Dermateaceae* and the *Coleophoma* clade remained without support in both the Bayesian and MP analyses, therefore the LSU sequences were combined with ITS sequences.

The overview LSU phylogeny of *Dothideomycetes* consisted of 58 sequences, including the outgroup sequence *Pseudophloeospora eucalypti* (GenBank HQ595593). A total of 819 characters were included in the phylogenetic analyses; 206 characters were parsimony-informative, 62 were variable and parsimony-uninformative, and 551 characters were constant. A maximum of 1000 equally most parsimonious trees were obtained, the first of which is shown in Fig 2 (TL = 652, CI = 0.612, RI = 0.916, and RC = 0.561). In the Bayesian analysis, this partition had 230 unique site patterns in the analysis ran for 1 750 000 generations, resulting in 35 002 trees of which 26 252 trees were used to calculate the posterior probabilities which are mapped onto Fig 2. The LSU partition was analysed with MrBayes using dirichlet (1,1,1,1) state frequency distribution and inverse gamma-shaped rate variation across sites (GTR + I + G). The Bayesian and MP tree had the same overall topology, with some rearrangements of species within families (data not shown, see TreeBASE). Coleophoma-like isolates occurred in four different families representing three different orders in this phylogeny (see the **Taxonomy** section below).
The overview LSU phylogeny of Dothideomycetes consisted of 58 sequences, including the outgroup sequence *P. eucalypti* (GenBank HQ599593). A total of 819 characters were included in the phylogenetic analyses; 206 characters were parsimony-informative, 62 were variable and parsimony-uninformative, and 551 characters were constant. A maximum of 1000 equally most parsimonious trees were obtained, the first of which is shown in Fig 2 (TL = 652, CI = 0.612, RI = 0.916, and RC = 0.561). In the Bayesian analysis, this partition had 230 unique site patterns in the analysis ran for 1 750 000 generations, resulting in 35 002 trees of which 26 252 trees were used to calculate the posterior probabilities which are mapped unto Fig 2. The LSU partition was analysed with MrBayes using dirichlet (1,1,1,1) state frequency distribution and inverse gamma-shaped rate variation across sites. The Bayesian and MP tree had the same overall topology, with some rearrangements of species within families (data not shown, see TreeBASE).

**Fig 1** – The first of 391 equally most parsimonious trees derived from the combined Leotiomycetes LSU/ITS alignment. Bootstrap support values greater than 50 % and Bayesian posterior probabilities are given at the nodes (Bayesian posterior probability/parsimony bootstrap). Thickened branches represent those branches present in the parsimony strict consensus tree and the scale bar represents the number of changes. The branch to the outgroup node was shortened three times to simplify layout of the tree. The families and orders are indicated with blocks of different colours and strains treated in the present study are printed in bold face. The tree was rooted to *Neofusicoccum umdonicola* (GenBank KF766373, EU821904).

The overview LSU phylogeny of Dothideomycetes consisted of 58 sequences, including the outgroup sequence *P. eucalypti* (GenBank HQ599593). A total of 819 characters were included in the phylogenetic analyses; 206 characters were parsimony-informative, 62 were variable and parsimony-uninformative, and 551 characters were constant. A maximum of 1000 equally most parsimonious trees were obtained, the first of which is shown in Fig 2 (TL = 652, CI = 0.612, RI = 0.916, and RC = 0.561). In the Bayesian analysis, this partition had 230 unique site patterns in the analysis ran for 1 750 000 generations, resulting in 35 002 trees of which 26 252 trees were used to calculate the posterior probabilities which are mapped unto Fig 2. The LSU partition was analysed with MrBayes using dirichlet (1,1,1,1) state frequency distribution and inverse gamma-shaped rate variation across sites. The Bayesian and MP tree had the same overall topology, with some rearrangements of species within families (data not shown, see TreeBASE). *Coleophoma*-like isolates occurred in four different families representing three different orders in this phylogeny (see the Taxonomy section below).
The multigene (ITS, tef1, tub2) phylogeny of Coleophoma s.str. consisted of 23 strains, including the two outgroup isolates of Davidhauksworthia ilicicola (CBS 734.94 and CBS 261.95). A total of 1364 characters were included in the phylogenetic analyses; 436 characters were parsimony-informative, 118 were variable and parsimony-uninformative, and 810 characters were constant. Two equally most parsimonious trees were obtained, the first of which is shown in Fig 3 (TL = 1393, CI = 0.664, RI = 0.770, and RC = 0.511). The tree resolved twelve Coleophoma species, two of which were sterile and therefore not named at the present time (see Taxonomy section below).
The multigene (ITS, tef1, tub2) phylogeny of Dothiora s.str. consisted of 21 strains, including the outgroup Pseudoseptoria obscura (GenBank KF251219, KF253175, and KF252708, respectively). A total of 1181 characters were included in the phylogenetic analyses; 211 characters were parsimony-informative, 253 were variable and parsimony-uninformative, and 717 characters were constant. Three equally most parsimonious trees were obtained, the first of which is shown in Fig 4 (TL = 816, CI = 0.812, RI = 0.804, and RC = 0.654). The tree resolved 13 Dothiora species (see the Taxonomy section below).

Taxonomy

Results obtained in this study revealed isolates tentatively identified as ‘Coleophoma spp.’ to cluster in diverse clades, which explains the confusion in present literature. Taxa are therefore treated in alphabetical order per family below.

Dermateaceae, Helotiales, Leotiomycetes


Parafabraea Chen Chen et al., Fungal Biol. 120: 1291 (2016).
Mycelium immersed, consisting of branched, septate, hyaline to pale brown hyphae. 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. Seta-like structures surrounding apothecia, rigid, pale brown, septate, cylindrical, straight or slightly curved, slightly enlarged at truncate apex. Basal stroma submersed, 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 pycnidial, separate, globose or flattened at the base, black, immersed, unilocular; wall composed of brown, thick-walled textura angularis; lower wall often thicker than upper region. Ostiole single, circular, not papillate. Paraphyses hyaline, septate at the base, intermingled among conidiophores, cylindrical or long clavate, collapsing at maturity. Conidiogenous cells phialidic, determinate, discrete and ampulliform to lageniform, or integrated and subcylindrical, hyaline,
smooth, with prominent periclinal thickening, and collarette minute. Conidia hyaline, aseptate, cylindrical, apex obtuse, base acute, thin-walled, smooth, guttulate, straight (adapted from Sutton 1980; Cheewangkoon et al. 2009).

Type species: Coleophoma crateriformis (Durieu & Mont.) Höhn.

Notes: Presently there is no culture available of C. crateriformis. The culture derived from CBS H-10464 is representative of a Dothiora sp. (see below). This means that taxonomic conclusions drawn by De Gruyter et al. (2009), and thus by default also Thambugala et al. (2014), are incorrect.

Parafabraea, the recently introduced genus for two species occurring on Eucalyptus (Chen et al. 2016), was found in the present study to represent the sexual morph of Coleophoma, a genus hitherto not known from any sexual connections. Parafabraea is therefore reduced to synonymy under the older genus, Coleophoma.

Coleophoma caliginosa (Cheew. et al.) Crous, comb. nov.


Culture characteristics: Colonies erumpent, spreading, with moderate aerial mycelium, margins lobate, reaching 30 mm diam after 2 wk on MEA, 70 mm diam on OA, and 60 mm diam on PDA. On MEA surface mouse-grey, reverse mouse-grey. On PDA surface mouse-grey, reverse olivaceous grey. On OA surface mouse-grey.

Notes: Morphologically Coleophoma camelliae is similar to C. empetri, which we regard as synonym of C. cylindrospora. Coleophoma camelliae is therefore introduced as novel species based on its distinct phylogeny.

Coleophoma coptospermatis Crous, sp. nov. (Fig 5).

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


Coleophoma camelliae Crous, sp. nov. (Fig 5).

Etymology: Named after the host genus from which the type strain was isolated, Camellia.

Conidiomata pycnidial, brown, immersed to superficial, globose, to 300 μm diam; wall of 2–6 layers of brown textura angularis. Paraphyses intermingled among conidiophores, hyaline, subcylindrical, 0–1-septate, to 70 μm long, 2–5 μm diam, with clavate apical part. Conidiophores hyaline, smooth, subcylindrical, 1–3-septate, 15–30 × 3–4 μm. Conidiogenous cells hyaline, smooth, subcylindrical to ampulliform, apical or lateral on conidiophores, 10–20 × 2.5–3 μm; tapering towards a truncate apex, 1–1.5 μm diam, with minute periclinal thickening. Conidia solitary, guttulate to granular, hyaline, smooth, subcylindrical, apex obtuse, base tapered towards flattened scar, 0.5–1 μm diam (12–16–18(–20) × 2.5–3 μm).

Type species: Coleophoma crateriformis (Durieu & Mont.) Höhn.


Notes: Coleophoma coptospermatis, isolated from leaf spots on *Coptosperma littorale* together with *C. eucalyptorum*, appears to be closely related to an isolate from *Thuja plicata* in the UK (Fig 3). However, we suspect that the latter may represent a distinct species, but this matter can only be resolved once more isolates become available. Based on the species of *Coptosperma* littorale, *C. eucalyptorum* was also cooccurred on this material (see below).

**Coleophoma coptospermatis** (Crous & Groenewald) Crous & Groenewald, **Mycotaxon** 114: 51 (2011) ex *Coptosperma littorale* (Rostr.) Petr., *Hedwigia* 62: 331 (1929).

For synonyms see Sutton (1980).

Conidiomata hypophyllous, rarely amphigenous, solitary, to 250 μm diam, rarely aggregated, subepidermal, erumpent with papillate central ostiole; mature conidiomata appear acervulus-like as the upper layers disintegrate, leaving almost a cup-like conidioma; wall of brown, thick-walled texture *angularis*, sides and bottom thick, becoming thinner towards ostiole. Conidiophores lining the inner cavity, 0–2-septate, hyaline, smooth. Conidiogenous cells integrated, short cylindrical or irregularly cuboid, giving rise to solitary conidia; terminal cells appearing as paraphyses on conidiophores, hyaline, smooth, remaining sterile, becoming gelatinised, up to 17 × 5 μm. Conidia cylindrical, hyaline, smooth, apex obtuse, base narrowly truncate, aseptate (11–14–16–17) × (2–)2.5–3(–3.5) μm, encased in a mucoid mass.

Material examined: Corsica: Bastia, on leaf litter of *Phillyrea media*, 16 Apr. 1905, von Höhnel (holotype FH 00304449).


Notes: Ascomata of a *Mycosphaerella* sp. were also observed to be present on the holotype (FH 00304449). A second specimen deposited at CBS (CBS H-10464) had conidia which were similar in size (11–15(–16) × 2.5–3(–3.5) μm. A culture (CBS 473.69) derived from this specimen, however, was of a *Dothichiza* assexual morph that belongs to *Dothiora* (Sivanesan 1984), which also cooccurred on this material (see below).

**Coleophoma cylindrospora** (Desm.) Höhn., *Ber. dt. bot. Ges.* 37: 114 (1919) (Fig 8).


Synonyms: *Phoma cylindrospora* (Desm.) Sacc., *Michelia* 1(no. 5): 527 (1879).


Conidiomata pycnidial, brown, immersed to erumpent, globose, to 250 μm diam; wall of 2–6 layers of brown texture *angularis*. Paraphyses intermingled among conidiophores, hyaline, subcylindrical, 0–1-septate, to 100 μm long, 3–6 μm diam, with swollen apical part, fusoid, tapering towards obtusely rounded apex. Conidiophores hyaline, smooth, subcylindrical, 1–6-septate, 15–45 × 3–4 μm. Conidiogenous cells hyaline, smooth, subcylindrical to ampulliform, apical or lateral on conidiophores, 5–10 × 3–4 μm; tapering towards a truncate apex, 1–2 μm diam, with minute periclinal thickening. Conidia truncate, aseptate (11–14–16–17) × (2–)2.5–3(–3.5) μm, encased in a mucoid mass.
solitary, with large guttules, hyaline, smooth, subcylindrical, apex obtuse, base tapered towards flattened scar, 0.5 μm diam (15–)18–20(–22) × (2.5–)3 μm (based on CBS 592.70).


Notes: Sutton (1980) retained C. cylindrospora (from Hedera helix, conidia cylindrical with large guttules, 16.5–24 × 2.5–3 μm) as distinct from C. empetri (from Empetrum nigrum, conidia cylindrical with small guttules, 12.5–18 × 2–3 μm). Strangely enough, conidia of our isolate from Hedera helix (CBS 592.70) fit the circumscription of C. cylindrospora, whereas conidia from Empetrum nigrum (CBS 505.71) tend to be shorter, with small guttules (12–)14–16(–19) × (2.5–)3 μm, fitting the circumscription of C. empetri. We therefore reduce C. empetri to synonymy under the older name, C. cylindrospora, as they are phylogenetically not distinguished.

Furthermore, examination of the holotype of Bactropycnis concentrica (Fig 9) found it to contain Phyllosticta concentrica, as well as material of B. concentrica (conidia cylindrical with large guttules, 20–24 × 3–3.5 μm), a small-spored Coleophoma sp. (conidia 9–11 × 2–2.5 μm), and a Colletotrichum sp. Bactropycnis concentrica is thus regarded as additional synonym of C. cylindrospora.

Coleophoma ericicola Crous, sp. nov. (Fig 10).
MycoBank No.: MB816130

Etymology: Named after the host genus from which the type strain was isolated, Erica.

Conidiomata pycnidial, brown, immersed to erumpent, globose, to 250 μm diam; wall of 2–6 layers of brown texture angularis. Paraphyses intermingled among conidiophores, hyaline, subcylindrical, 0–2–septate, to 30 μm long, 1.5–3 μm diam, with obtusely rounded apex. Conidiophores hyaline, smooth, subcylindrical, 0–1–septate, 7–15 × 2–3 μm. Conidiogenous cells hyaline, smooth, subcylindrical, apical or lateral on conidiophores, 5–10 × 1.5–2.5 μm; tapering towards a truncate apex, 1–1.5 μm diam, with minute periclinal thickening. Conidia solitary, guttulate to granular, hyaline, smooth, subcylindrical (ends becoming swollen with age), apex obtuse, base tapered towards flattened scar, 0.5 μm diam (8–)10–12(–13) × 2(–2.5) μm.

**Culture characteristics**: Colonies flat, spreading, with sparse aerial mycelium, margins feathery, reaching 30 mm diam after 2 wk on MEA, 6 mm diam on OA, and 40 mm diam on PDA. On MEA surface and reverse iron-grey. On PDA surface isabeline to cinnamon, reverse sepia. On OA surface iron-grey.

**Notes**: A single species is known to occur on *Erica*, namely *C. ericae* (von Höhn 1920), being more similar to *C. cylindrospora*. Based on its smaller conidia and distinct phylogeny, *C. ericicola* is hereewith introduced as new species.

**Coleophoma ericicola** Crous, comb. et nom. nov.


**Synonym**: *Parafabraea eucalypti* (Cheew. & Crous) Chen et al., *Fungal Biol.* 120: 1291 (2016).

**Description and illustrations**: Cheewangkoon et al. (2009).

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**Notes**: *Parafabraea* was recently described as a sexual morph similar to *Neofabraea* and *Pezicula*, but being distinct by having seta-like structures around its apothecia (Chen et al. 2016). In the present study however, *Parafabraea* was found to be the sexual morph of *Coleophoma*, which is a much older, and well-established genus. Because the epithet ‘eucalypti’ is occupied in *Coleophoma* (Yuan 1996), a new name, eucalypticola, is introduced to accommodate this fungus.

**Coleophoma eucalypticola** Crous & Summerell, *Persoonia* 27: 137 (2011) (Fig 11).

**Description and illustration**: See Crous et al. (2011).

**Materials examined**: **Australia**: New South Wales, Blue Mountains, Kurrajong Heights, on leaves of *Eucalyptus piperita*, 16 Nov. 2010, B.A. Summerell (holotype CBS H-20770, culture extype CBS 131314); Northern Territory, Darwin, on leaves of *Eucalyptus gummifera*, 9 Apr. 2011, P.W. Crous, CPC 19293.

**South Africa**: Western Cape Province, Kirstenbosch, leaf

Notes: Coleophoma eucalyptorum was found to cooccur with C. coptospermatis on the same leaf spots on Coptosperma littorale in South Africa. Contrary to what was first believed, this species appears to have a wider host range than only Eucalyptus.

Coleophoma paracylindrospora Crous, sp. nov. (Fig 12).
MycoBank No.: MB816132

Etymology: Named after its morphological similarity to C. cylindrospora.

Conidiomata pycnidial, brown, erumpent, globose, to 300 μm diam; wall of 2–6 layers of brown textura angularis. Paraphyses intermingled among conidiophores, hyaline, subcylindrical, 0–4-septate, to 100 μm long, 2–6 μm diam, branched or not, with obtusely rounded apex. Conidiophores hyaline, smooth, subcylindrical, branched, 1–3-septate, 7–25 × 3–4 μm. Conidiogenous cells hyaline, smooth, subcylindrical to allantoid, apical or lateral on conidiophores, 7–15 × 2.5–3.5 μm; tapering towards a truncate apex, 1–1.5 μm diam, with minute periclinal thickening. Conidia solitary, guttulate to granular, hyaline, smooth, cylindrical, apex obtuse, base tapered towards flattened scar, 1–1.5 μm diam (15–17–20–22) × (2.5–3) μm.


Culture characteristics: Colonies spreading, surface folded, with sparse to moderate aerial mycelium, margins lobate, reaching 40 mm diam after 2 wk on MEA, 80 mm diam on OA, and 60 mm diam on PDA. On MEA surface fuscous-black, dark mouse-grey. On PDA surface mouse-grey, reverse iron-grey. On OA surface mouse-grey.

Note: Coleophoma paracylindrospora is morphologically similar to C. cylindrospora, and can only be distinguished based on DNA phylogenetic data.

Coleophoma parafusiformis Crous, sp. nov. (Fig 13).
MycoBank No.: MB816133

Etymology: Named after the Coleophoma fusiformis, to which it has some resemblance.

Conidiomata pycnidial, brown, immersed to erumpent, globose with central ostiole, to 250 μm diam; wall of 2–6 layers of brown textura angularis. Paraphyses intermingled among conidiophores, hyaline, subcylindrical, 0–2-septate, to 120 μm long, 3–7 μm diam, with obtusely rounded apex. Conidiophores hyaline, smooth, subcylindrical, branched, 0–3-septate, 13–35 × 3–5 μm. Conidiogenous cells hyaline, smooth, subcylindrical, apical or lateral on conidiophores, 7–17 × 2.5–3.5 μm; tapering towards a truncate apex, 1.5–2 μm diam, with minute periclinal thickening. Conidia solitary, guttulate to granular, hyaline, smooth, cylindrical, apex obtuse, base tapered towards flattened scar, 1–1.5 μm diam (15–17–20–22) × (2.5–3) μm.


Culture characteristics: Colonies spreading, surface folded, with sparse to moderate aerial mycelium, margins lobate, reaching 40 mm diam after 2 wk on MEA, 80 mm diam on OA, and 60 mm diam on PDA. On MEA surface fuscous-black, dark mouse-grey. On PDA surface mouse-grey, reverse iron-grey. On OA surface mouse-grey.

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Culture characteristics: Colonies spreading, surface folded, with sparse to moderate aerial mycelium, margins lobate, reaching 40 mm diam after 2 wk on MEA, 80 mm diam on OA, and 60 mm diam on PDA. On MEA surface fuscous-black, dark mouse-grey. On PDA surface mouse-grey, reverse iron-grey. On OA surface mouse-grey.

Note: Coleophoma paracylindrospora is morphologically similar to C. cylindrospora, and can only be distinguished based on DNA phylogenetic data.

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MycoBank No.: MB816133

Etymology: Named after the Coleophoma fusiformis, to which it has some resemblance.

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Protea caffra
poort, Walter Sisulu National Botanical Gardens, on leaves of
Material examined
Description and illustration
Note
type CBS H-20962, culture extype CBS 132532).
Protea caffra
on
Davidhawksworthia
Crous,
known to occur on
2
m
straight, apex obtuse, base tapered towards flattened scar,
aline, smooth, cylindrical to fusoid, irregularly curved or
periclinal thickening. Conidia solitary, with large guttules, hy-
aline, smooth, cylindrical to fusoid, irregularly curved or
straight, apex obtuse, base tapered towards flattened scar,
2 µm diam (15--)17--20(--22) × (4--)5(--6) µm.
Materials examined: Latvia: Riga, on Rhododendron sp., I. Apine,
CBS 129169 = MSCL 1028. Sweden: Uppsala, on leaf spot of
Rhododendron sp., Nov. 2010, O. Pettersson (holotype CBS H-22478,
culture extype CBS 132692).
Culture characteristics: Colonies erumpent, folded, spreading,
with moderate aerial mycelium, margins lobate to feathery,
reaching 20–30 mm diam after 2 wk. On MEA surface dark
mouse-grey, reverse greyish sepia. On PDA surface greyish se-
pia, reverse isabelline. On OA surface honey.
Notes: Wu et al. (1996) introduced C. fusiformis as a novel spe-
cies on Rhododendron in the UK, distinguishing it from the
other Coleophoma spp. on Rhododendron on the basis that it
had fusiform conidia, and was regarded to be a pathogen of
this host. Conidia of C. fusiformis are fusiform to cylindrical,
21–25 × 4–4.5 µm, thus larger than that of C. parafusiformis,
and also much more prominently tapered, whereas conidia of
C. parafusiformis are also more irregular in shape. Further-
more, in C. fusiformis the paraphyses dissolve at maturity,
but this is not the case in C. parafusiformis. The second species
known to occur on Rhododendron, C. empetri (C. cylindrospora,
see above), differs in having conidia that are more cylindrical,
and slightly narrower (15--18--20(--22) × (2.5--)3 µm.
Description and illustration: See Crous et al. (2012).
Material examined: South Africa: Gauteng Province, Roode-
poort, Walter Sisulu National Botanical Gardens, on leaves of
Protea caffra, 5 Jul. 2011, P. Crous, M.K. Crous & M. Crous (holo-
type CBS H-20962, culture extype CBS 132532).
Note: Coleophoma proteae is associated with a leaf spot disease
on Protea caffra in South Africa, and has thus far not been re-
ported on any other host (Crous et al. 2012).
Davidhawksworthia Crous, gen. nov.
MycoBank No.: MB816134
Etymology: Named after David L. Hawksworth, in recognition
to his many significant contributions to fungal taxonomy.
Colonies giving rise to spreading, hyaline, septate hyphae that
tend to become pigmented, forming chains of chlamydospor-
like structures. Conidiophores dimorphic, thin-walled. Macroco-
idiophores erect, basal part hyaline or pale brown, smooth.
Microconidiophores penicillate, similar in morphology. Macroco-
idiogenous cells hyaline, smooth, apical, phialidic, clavate,
with apical opening and collarette, or arising from a mother
cell that gives rise to several ampulliform to doliform phi-
alides. Macroconidia aseptate, cylindrical with obtuse ends
and a flattened hilum at base, hyaline, smooth, granular, straight,
frequently aggregated in cylindrical packets.
Type species: Davidhawksworthia ilicicola Crous.
Davidhawksworthia ilicicola Crous, sp. nov. (Fig 14).
MycoBank No.: MB816135
Etymology: Named after the host genus from which it was iso-
lated, Ilex.
Colonies giving rise to spreading, hyaline, septate hyphae (on
SNA), 3–4 µm diam, but hyphae tend to become pigmented
on MEA, with chains of chlamydospore-like structures. Coni-
idiophores dimorphic. Macroconidiophores erect, basal part hya-
line or pale brown, smooth, to 200 µm tall, 3–4 µm diam.
Microconidiophores penicillate, similar in morphology, to
100 µm tall. Macroconidiogenous cells hyaline, smooth, apical,
phialidic, clavate, 20–30 × 3–4 µm, with apical opening and
collarette, or arising from a mother cell that gives rise to sev-
eral ampulliform to doliform phialides, 5–14 × 3–4 µm. Mac-
roconidia aseptate, cylindrical with obtuse ends and a flattened
hilum at base, 1 µm diam, hyaline, smooth, granular, straight,
frequently aggregated in cylindrical packets (17--)18--20(--22) × (3--)3.5 µm.
Materials examined: Netherlands: Prov. Noord-Holland, Aals-
meer, fruit of Ilex aquifolium, Jan. 1995, J.W. Veenbaas (holotype
CBS H-22479, culture extype CBS 734.94); Aalsmeer, fruit of Ilex
Culture characteristics: Colonies flat, folded, spreading, with
moderate aerial mycelium, margins smooth, even, reaching
Fig 13 – Coleophoma parafusiformis (CBS 129169). (A) Colony sporulating on OA. (B, C) Conidiogenous cells and paraphyses. (D) Conidia. Scale bars = 10 µm.
30–50 mm diam after 2 wk. On MEA surface mouse-grey, reverse olivaceous grey. On FDA surface mouse-grey, reverse pale mouse-grey. On OA surface dark mouse-grey. Notes: Davidhawksworthia is reminiscent of Cylindrodendrum (Lombard et al. 2014, 2015), but can be distinguished in that the conidia are aseptate, and formed on phialides that frequently arise from a mother cell. Furthermore, on SNA it also develops penicillate microconidiophores, which are never observed in Cylindrodendrum.

Dothideaceae, Dothideales, Dothideomycetes

Dothichiza Lib. ex Roum., Fungi Selecti Galliaei Exs.: no. 627 (1880).
Kleisslerina Petr., Annls. Mycol. 17: 74 (1920) [1919].

Synonyms from Thambugala et al. (2014), with the addition of Coleonaema, Cylindroseptoria, and Dothichiza.

Ascostromata immersed to erumpent, pulvinate to globose, black, multiloculate, wall of dark brown textura angularis. Locules globose to subglobose, broadly rounded or papillate with central ostiole. Pseudoparaphyses absent. Ascii 8- or more spored, bitunicate, fissitunicate, oblong to clavate, pedicellate, with a small ocular chamber. Ascospores biseriate to multiseriate, smooth, constricted at the primary median septum, at times with a vertical septum, hyaline, rarely pale brown, obovate to ellipsoid to fusoid, often inequilateral or slightly curved, smooth, at times with a thin mucoid sheath. Conidiomata pycnidial, separate, or aggregated in a stroma. Conidiophores reduced to conidiogenous cells lining the inner cavity, hyaline, smooth, ampulliform to doliiform, phialidic. Conidia aseptate, hyaline, smooth, subcylindrical to ovoid or oblong. Hyphae becoming brown, verruculose, and constricted at septa, giving rise to a Hormonema-like synasexual morph.

Notes: The genus Dothiora, including its type species D. pyrenophora, contains numerous species that have been linked to Dothichiza asexual morphs via cultural studies (Froidevaux 1972; Sivanesan 1984), several also producing Hormonema-like asexual morphs in culture. In the present study, several species of Dothiora with Dothichiza asexual morphs clustered with extype strains of Coleonaema and Cylindroseptoria in a well-supported clade. Although no strains of the type species Dothiora pyrenophora or Dothichiza populea are presently known from culture, Dothiora appears the oldest name presently available for this clade, and hence we allocate these taxa to it. Further collections would be required, however, to designate an epitype for Dothiora pyrenophora, and fix the application of this name. Both Dothiora and Dothichiza are in need of revision, and very little information is currently available about their phylogeny. Several species of Dothiora are described below, although only the Dothichiza or Hormonema-like morphs can be observed in culture.

Fig 14 – Davidhawksworthia ilicicola (CBS 734.94). (A) Colony sporulating on OA. (B) Microconidiophores and conidia. (C) Macro- and microconidiophores and conidia. (D–F) Macroconidiogenous cells and macroconidia. (G) Macroconidia. Scale bars = 10 µm.
**Dothiora agapanthi** Crous, sp. nov. (Fig 15).

*MycoBank No.: MB816136*

**Etymology**: Named after the host genus from which it was isolated, *Agapanthus*.

Conidiomata separate, erumpent, pycnidial, globose with long neck, brown, to 250 µm diam, with central ostiole, exuding a creamy conidial mass; wall of 3–6 layers of brown textura angularis. **Conidiophores** reduced to conidiogenous cells lining the inner cavity, hyaline, smooth, ampulliform to doliiform, 5–7 × 5–6 µm, with central phialidic locus. **Conidia** hyaline, smooth, guttulate, subcylindrical, apex obtuse, tapering to a truncate hilum (8–)10–12(–13) × 3(–3.5) µm. Hyphae becoming brown, verruculose, and constricted at septa, giving rise to a Hormonema-like synasexual morph.

**Material examined**: **South Africa**: Western Cape Province, Kirstenbosch, on leaves of *Agapanthus* sp., May 2012, P.W. Crous (holotype CBS H-22480, culture extype CPC 20600).

**Culture characteristics**: Colonies flat, spreading, with sparse aerial mycelium, margins feathery, covering dish after 2 wk. On MEA, PDA, and OA and reverse iron-grey.

**Notes**: This fungus was originally isolated as a hyphomycete (from the Hormonema-like morph), and its pycnidial conidiomata were only observed in culture. No species of *Dothiora* or *Dothichiza* have thus far been reported from *Agapanthus*.

**Dothiora bupleuricola** Crous, sp. nov. (Fig 16).

*MycoBank No.: MB816137*

**Etymology**: Named after the host genus from which it was isolated, *Bupleurum*.

Conidiomata separate, erumpent, pycnidial, globose with long neck, brown, to 250 µm diam, with central ostiole, exuding a creamy conidial mass; wall of 3–6 layers of brown textura angularis. **Conidiophores** reduced to conidiogenous cells lining the inner cavity, hyaline, smooth, globose to allantoid, 5–7 × 4–6 µm, with central phialidic locus. **Conidia** hyaline, smooth, guttulate, subcylindrical, apex obtuse, tapering to a truncate hilum (8–)9–10(–12) × 2(–2.5) µm.

**Material examined**: **France**: Avignon, Roche des Domes, on leaf spot of *Bupleurum fruticosum*, Feb. 1975, H.A. van der Aa (holotype CBS H-22481, culture extype CBS 112.75).

**Culture characteristics**: Colonies flat, spreading, with sparse aerial mycelium, margins feathery, reaching 60 mm diam after 2 wk. On MEA, PDA, and OA surface fuscous black, reverse iron-grey.

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**Fig 15** – *Dothiora agapanthi* (CPC 20600). (A, B) Colony sporulating on SNA. (C) Section through conidioma. (D) Conidia. Scale bars = 10 µm.

**Fig 16** – *Dothiora bupleuricola* (CBS 112.75). (A, B) Colonies sporulating on PNA and PDA, respectively. (C, D) Conidiogenous cells. (E) Conidia. Scale bars = 10 µm.
Notes: No species of Dothiora or Dothiciza have thus far been reported from Bupleurum. Kabatiella bupleuri occurs on dead flowers of Bupleurum gibraltarum in Spain, and has a Hormonema-like growth in culture (Bills et al. 2012), but is morphologically and phylogenetically quite distinct.

**Dothiora ceratoniae** (Quaedvl., Verkley & Crous) Crous, comb. nov.
MycoBank no.: MB816138

**Description and illustration**: See Quaedvlieg et al. (2013).

**Materials examined**:
- **Italy**: Sardegna, Cala Fuili, on dead leaves of *Nerium oleander*, 10 May 1971, W. Gams & J. Stalpers, CBS 441.72; Sardegna, Tacco di Santa Barbara, on dead leaf of *Arbutus unedo*, 10 May 1971, W. Gams & J. Stalpers, CBS 290.72.
- **Spain**: Mallorca, Can Pastilla, on leaves of *Ceratonia siliqua*, 24 May 1969, H.A. van der Aa [holotype CBS H-21300, culture ex-type CBS 477.69].

Notes: Cylindroseptoria ceratoniae is the type species of the genus Cylindroseptoria (Quaedvlieg et al. 2013), which is shown to be a synonym of Dothiora. A new combination is hereewith introduced in Dothiora to accommodate this taxon.

**Dothiora maculans** (Ellis & Everh.) Crous, comb. nov. (Fig 17).
MycoBank No.: MB816139

Conidiomata pycnidial, solitary, to 300 μm diam on OA, up to 150 μm on PNA, with central ostiole. Conidiogenous cells can have 1–2 loci, and are aggregated in pseudochains, encased in a thick, persistent mucoid layer. Conidia hyaline, smooth, subcylindrical to oblong, guttulate, apex obtuse, tapering to a truncate hilum (7–)10–12(–13) × (2.5–)3(–3.5) μm. Hormonema-like synasexual morph with ampulliform to doliiform phialidic conidiogenous cells, 5–7 × 5–6 μm (based on CBS 301.76).


Culture characteristics: Colonies flat, spreading, surface folded, with sparse aerial mycelium, margins feathery, covering dish after 2 wk. On MEA, PDA, and OA surface and reverse iron-grey.

Notes: The type specimen of ‘Phyllosticta’ maculans was described from leaves of *Populus monilifera* collected in the USA (conidia 10–14 × 3–3.5 μm), which fit well with the morphology of the present cultures studied here, and thus we believe these cultures to be representative for the name. Dothiora sphaeroides (asexual morph: Dothiciza tremulae, conidia oblong, 4–10 × 2.5–3.5 μm) is known from *Populus tremula* and *P. tremuloides* (Froidevaux 1972), but has smaller conidia.

**Dothiora oleae** (DC.) Crous, comb. nov. (Fig 18).
MycoBank No.: MB816140


**Description and illustration**: See Duan et al. (2007).


**Italy**: on leaves of *Olea europaea*, Mar. 1957, O. Verona, CBS 235.57.

**Spain**: Mallorca, Fornalutx (ca 900 m) on fallen leaves of *Olea europaea*, 26 May 1969, H.A. van der Aa, CBS 472.69.

**Turkey**: Izmir-Bornova, on rotting fruit of *Olea europaea*, 24 Nov. 1970, S. Aksu, CBS 152.71.

Culture characteristics: Colonies flat to erumpent, spreading, with sparse aerial mycelium, margins lobate, reaching 40 mm diam after 2 wk. On MEA surface iron-grey, reverse

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**Fig 17 — Dothiora maculans (CBS 301.76). (A, B) Colonies sporulating on PNA and OA, respectively. (C) Mycelium. (D, E) Conidiogenous cells. (F) Conidia. Scale bars = 10 μm.**

Notes: Duan et al. (2007) resurrected the genus Coleonaema to accommodate the fungus occurring on olive leaves, on the basis that it had a different conidiomatal development (more cupulate conidiomata) to Coleophoma s.str., and dissolving hyphal elements in its conidiomata (persistent paraphyses in Coleophoma). In the present study we found Coleonaema to cluster in the Dothiora clade, and hence a new combination is herewith proposed.

Dothiora phillyreae Crous, sp. nov. (Fig 19).
MycoBank No.: MB816141

Etymology: Named after the host genus from which it was isolated, Phillyrea.

Conidiomata solitary or aggregated in a stroma, brown, immersed in media (SNA), or superficial (OA), brown, to 300 μm diam, with central ostiole that bursts open to render the conidioma more acervular in appearance; wall of 3–6 layers of brown textura angularis. Conidiophores reduced to conidiogenous cells lining the inner cavity, hyaline, smooth, aseptate, ampulliform to broadly ellipsoid or doliform, 5–10 × 5–7 μm, holoblastic with apical locus, inconspicuously phialidic. Conidia solitary, hyaline, smooth, subcylindrical to oblong, guttulate, apex obtuse, tapering to a truncate hilum, 1 μm diam (8–)10–11(–12) × (2.5–)3(–3.5) μm. Colonies also sporulating on superficial hyphae, forming a Hormonema-like asexual morph, with hyphae becoming brown, verruculose, constricted at septa, forming chlamydospore-like cells up to 8 μm diam; older conidia become brown and verruculose, up to 15 μm long, 5 μm diam.


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Fig 19 – Dothiora phillyreae (CBS 473.69). (A) Conidiomata in vivo. (B) Colony sporulating on SNA. (C–F) Hyphae and conidiogenous cells. (G) Conidia. Scale bars = 10 μm.
Culture characteristics: Colonies flat, spreading, surface folded, with sparse aerial mycelium, margins lobate, reaching 60 mm diam after 2 wk. On MEA, PDA, and OA surface and reverse fuscous-black.

Notes: This culture of Dothiora phillyreae was derived from a specimen (CBS H-10464) of Coleophoma crateriformis, and incorrectly assumed to represent the latter fungus, with which it cooccurs. No species of Dothiora or Dothichiza are known from Phillyrea, and hence this taxon is herewith described as new.

**Dothiora prunorum** (C. Dennis & Buhagiar) Crous, **comb. nov.**


Material examined: UK, fruit of Prunus domestica, cv. ‘Belle de Louvain’, 1972, C. Dennis (extype CBS 933.72).

**Dothiora viburnicola** Crous, **sp. nov.** (Fig 20).

MycoBank No.: MB816143

Etymology: Named after the host genus from which it was isolated, Viburnum.

Conidiomata separate, erumpent, pycnidial, globose with long neck, brown, to 250 μm diam, with central ostiole, exuding a creamy conidial mass; wall of 3–6 layers of brown textura angularis. Conidiophores reduced to conidiogenous cells lining the inner cavity, hyaline, smooth, ampulliform to doliform, 5–7 × 5–6 μm, with central phialidic locus. Conidia hyaline, smooth, guttulate, subcylindrical, apex obtuse, tapering to a truncate hilum (6.5–)8–10(–13) × (2–)2.5(–3) μm.


Note: Dothiora viburnicola needs to be compared to Dothichiza viburni (conidia ellipsoid-elongate, 6–8 × 2–3 μm; Karsten 1890), although conidia of the latter species are shorter.

**Pseudocamaropycnis** Crous, **gen. nov.**

MycoBank No.: MB816144

Etymology: Named after the genus Camaropycnis, which it morphologically resembles.

Type species: Pseudocamaropycnis pini Crous.

**Pseudocamaropycnis pini** Crous, sp. nov. (Fig 21).
MycoBank No.: MB816145

Etymology: Named after the host genus from which it was isolated, *Pinus*.

Conidiomata erumpent, black, elongated, lens-shaped, to 500 μm diam, opening by irregular rupture. Paraphyses intermingled among conidiophores, hyaline, septate, branched, subcylindrical, to 70 μm long, 1.5–2 μm diam. Conidiophores hyaline, smooth, subcylindrical, 0–2-septate, branched, 10–25 × 2–3 μm. Conidiogenous cells hyaline, smooth, terminal and lateral, subcylindrical, phialidic with minute periclinal thickening, apex truncate, 1.5 μm diam, 7–17 × 2–2.5 μm. Conidia solitary, hyaline, smooth, cylindrical, straight, biguttulate (5–)6–7–(–8) × 1.5–2 μm.


Notes: Based on its conidiophores and conidia, *Pseudocamaropycnis* is morphologically similar to *Camaropycnis* (on branches of *Pinus* and *Libocedrus*), but can be distinguished by having conidiomata immersed in pine needles, and not short-stipitate as in the latter (Sutton 1980). Similarly, its conidiomata also distinguish it from *Coleophoma* s.str.

**Pleosporaceae, Pleosporales, Dothideomycetes**

**Briansuttonomyces** Crous, gen. nov.
MycoBank No.: MB816146

Etymology: Named after Dr B.C. Sutton, in acknowledgement of his valuable contributions to the taxonomy of coelomycetous fungi.

Conidiomata erumpent, euomorphic, brown, globose, with central ostiole; wall of 3–8 layers of medium brown *textura angularis*. Conidiogenous cells lining inner cavity, hyaline, smooth, thin-walled, ampulliform to globose, phialidic with periclinal thickening, and minute collarette. Conidia solitary, hyaline, smooth, guttulate to granular, cylindrical with obtuse ends, (0–)1-septate, mostly straight.

Type species: Briansuttonomyces eucalypti Crous.

**Briansuttonomyces eucalypti** Crous, sp. nov. (Fig 22).
MycoBank No.: MB816147

Etymology: Named after the host genus from which it was isolated, *Eucalyptus*.

Colonies poorly sporulating on MEA, sterile on SNA, PDA, and OA. Conidiomata erumpent, euomorphic, brown, globose, to 350 μm diam, with central ostiole; wall of 3–8 layers of medium brown *textura angularis*. Conidiogenous cells lining inner cavity, hyaline, smooth, ampulliform to globose, 4–7 × 4–11 μm, phialidic with periclinal thickening, and minute collarette. Conidia solitary, hyaline, smooth, guttulate to granular, cylindrical with obtuse ends, (0–)1-septate, mostly straight (14–)17–21 (–22) × 2.5(–3) μm.


Culture characteristics: Colonies flat, folded, spreading, with moderate aerial mycelium, margins smooth, reaching 60 mm diam after 2 wk. On MEA surface purplish grey, reverse mouse-grey. On PDA surface and reverse fuscous-black. On OA surface purpurel grey.

Notes: A specimen of *Briansuttonomyces* was sent to B.C. Sutton in IMI in 1991. At the time he commented that this fungus was best placed in *Coleophoma*, pending further study. Given the phylogenetic backbone generated for *Coleophoma* in the present study, we are now able to treat this fungus. Although *Briansuttonomyces* is morphologically *Coleophoma*-like, the conidia are 1-septate, and the conidiomata lack paraphyses. Based on these differences and its distinct phylogeny, this fungus is herewith introduced as a new genus.

**Pleosporaceae, Pleosporales, Dothideomycetes**

**Dimorphosporicola** Crous, gen. nov.
MycoBank No.: MB816148

Etymology: Named after its dimorphic conidia.

Conidiomata pycnidial, erumpent, globose, pale brown, with several dark brown ostioles per conidioma; wall of 2–3 layers
of pale brown textura angularis. Conidiophores reduced to conidiogenous cells, hyaline, smooth, lining the inner cavity, ampulliform to doliiform, phialidic with minute collarette, at times with percurrent proliferation. Paraphyses intermingled among conidiogenous cells, hyaline, smooth, subcylindrical, aseptate. Conidia dimorphic. Macroconidia cylindrical, straight or slightly curved, with obtuse ends, guttulate, hyaline, aseptate, smooth. Microconidia hyaline, smooth, ellipsoid, apex obtuse, base truncate, aseptate.

Type species: Dimorphosporicola tragani Crous.

Dimorphosporicola tragani Crous, sp. nov. (Fig 23). MycoBank No.: MB816149

Etymology: Named after the host genus from which it was isolated, Traganum.

Conidiomata pycnidial, erumpent, globose, pale brown, to 300 μm diam, with several dark brown ostioles per conidioma; wall of 2–3 layers of pale brown textura angularis. Conidiophores reduced to conidiogenous cells, hyaline, smooth, lining the inner cavity, ampulliform to doliiform, phialidic with minute collarette, at times with percurrent proliferation, 5–7 × 4–6 μm. Paraphyses intermingled among conidiogenous cells, hyaline, smooth, subcylindrical, aseptate, to 30 μm long, 3–4 μm diam. Conidia dimorphic. Macroconidia cylindrical, straight or slightly curved, with obtuse ends, guttulate, hyaline, aseptate, smooth (15–)17–21(–25) × 3.5–4(–5) μm. Microconidia hyaline, smooth, ellipsoid, apex obtuse, base truncate, aseptate, 3–7 × 3–4 μm.

Material examined: Mauritania: on leaf of Traganum nudatum var. microphyllum, unknown collection date and collector (holotype CBS H-10512, culture extype CBS 570.85).

Culture characteristics: Colonies flat, spreading, with moderate aerial mycelium, margins smooth, even, reaching 70 mm diam after 2 wk. On MEA surface isabelline, reverse cinnamon. On PDA surface vinaceous-buff, reverse rosy-buff. On OA surface rosy-buff.

Notes: Dimorphosporicola tragani was identified as a species of Coleophoma based on its pycnidial conidiomata, cylindrical conidia, and the presence of paraphyses. As member of the Pleosporaceae, D. tragani is distinct from Coleophoma by having conidiogenous cells that can also proliferate percurrently, and having dimorphic conidia.

Discussion

The aim of the present study was to resolve the phylogeny of the genus Coleophoma, listed as incertae sedis, Pezizomycotina in Index Fungorum and MycoBank. Previously, coelomycetous fungi with pycnidial conidiomata having paraphyses, and hyaline, cylindrical conidia were treated as members of Coleophoma. It is therefore not surprising that recent studies revealed Coleophoma to be polyphyletic (Quaedvlieg et al. 2013; Tanaka et al. 2015). Via convergent evolution these characters were found to have evolved in several lineages in the Dothideomycetes, namely Dothideaceae (Dothideales), Mytilinidiales (Mytilinidiales), Didymellaceae, Didymosphaeraceae, Pleosporaceae (Pleosporales), and Dermateaceae (Helotiales, Leotiomycetes).

A recent phylogenetic study on Phoma-like genera (De Gruyter et al. 2009) incorporated strain CBS 473.69, which was isolated from a specimen (CBS H-10464) corresponding to the type species of Coleophoma, Coleophoma crateriformis. The morphology of this isolate, however, was never confirmed. A subsequent revision of Dothideaceae by Thambbugala et al. (2014) assumed that this isolate was correctly identified, and based on herbarium specimens and a few cultures, revised the family, thus further perpetuating this mistake. In the latter study, two sequences of Dothiora were linked to this incorrectly identified Coleophoma species (now Dothiora phillyreae), but this matter was left unresolved.

An examination of older literature revealed that Dothiora is the sexual morph of Dothichiza (Froidevaux 1972; Sivanesan 1984). In this study we have confirmed this association, although it should be stressed that the type species of respectively D. tragani, D. phillyreae, and D. populea still want to be recollected to definitively resolve this issue. Notwithstanding this fact, however, this clade appears to be monophyletic, to which we apply the older name, Dothiora. A further point of confusion lies in the fact that D. tragani also has a Hormonema-like synasexual morph (De Hoog & Yurlova 1994; Petrini & Petrini 2010; Crous et al.)

Fig 23 – Dimorphosporicola tragani (CBS 570.85). (A) Colony sporulating on OA. (B, C) Conidiogenous cells. (D) Macro- and microconidia. (E) Macroconidia. Scale bars = 10 μm.
2015), which is commonly observed in culture, but also in nature. For instance, the newly described Dothiora agapanthi, was originally isolated as a hyphomycetous fungus from its Hormonema-like morph. Dothiora thus has a hyphomycetous and coelomycetous morph, but which clearly also play a role in its ecology. One of the more commonly known species that now belong to this genus is Dothiora oleae, a fungus with a confused taxonomy, which commonly occurs on olive leaves (Duan et al. 2007).

Although there is no available culture of the type species of Coleophoma, C. crateriformis (on leaf litter of Philyrea media, Corsica), other species exhibiting morphology typical of Coleophoma cluster together in a well-defined clade in Dermataceae (Helotiales). We therefore prefer to apply the name Coleophoma to this clade, at least tentatively, pending cultures and sequence data retrieved from C. crateriformis, the type species of this genus. Coleophoma was also for the first time linked to a sexual genus, Parafabraea (Chen et al. 2016), which is herein reduced to synonymy under the former. The genus clearly contains a mixture of saprobes, as well as foliar pathogens, such as Coleophoma eucalyptorum (Crous et al. 2011), Coleophoma proteae (Crous et al. 2012), and Coleophoma cypotispermatis (present study). Coleophoma fusiformis was described as a foliar pathogen of Rhododendron in the UK (Wu et al. 1996), and therefore it is interesting to note the presence of yet another foliar pathogen of this host in Latvia and Sweden, Coleophoma parafusiformis. The description of the genus Davidhauksworthisa from flex in the Netherlands is also interesting, in that although it is Cylindrocladium-like in morphology (Nectriaceae; Lombard et al. 2014, 2015), it also clusters in Dermataceae.

Several other Coleophoma-like genera are also described as new in this study. These include Pseudocamaropycnis (Mytiliniaceae) (on Pinus needles, Hong Kong), and two genera in the Pleosporaceae, namely Dimorphosphoricola (on Tragancum leaves, Mauritania), and Brianisuttonomyces (on Eucalyptus leaves, South Africa). Although these genera share cylindrical conidia as a synapomorphy, they are distinguishable from Coleophoma s.str. based on a set of other characters linked to their conidio mata, conidia, conidiogenesis or paraphyses. In spite of all the genera dealt with here that were previously identified as Coleophoma based on morphology, some taxa were also allied to a group of Phoma-like species related to Nothophoma gossypicola (Didymellaceae, Pleosporales, Dothideomycetes) (see Chen et al. 2015), which will be treated elsewhere.

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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