Phylogeny and taxonomic revision of *Thelonectria discophora* (Ascomycota, Hypocreales, Nectriaceae) species complex.

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Abstract

Thelonectria discophora (*Thelonectria*, Nectriaceae, Hypocreales) is a conspicuous group of saprobic fungi on decaying plant material, characterized by red perithecia each with a broad mammiform (nipple-like) apex. The anamorphic state is characterized by a cylindrocarpon-like morphology, with 3–5 septate macroconidia, unicellular microconidia and chlamydospores are rarely produced in culture. In the past, *T. discophora* was regarded as one species with a wide geographic distribution. However, a recent study rejected the monophyly and cosmopolitanism of this species, and showed the existence of at least sixteen cryptic species based solely on molecular data. In the present paper, we revise the taxonomy of *T. discophora* species complex by describing twelve

new species and four new combinations based on historic names. Individual diagnostic morphological characters for each species could not be identified; however, discrete morphological traits corresponding to each one of the three main groups of species were discovered. Lineages could be differentiated by average values of morphological traits as well as presence/absence of characteristic asexual propagules and colony growth at 30 C. Description, illustrations and keys for identification are provided for the recognized species.

Key words

Canker, new species, species concept, taxonomy, *Thelonectria*

Introduction

Thelonectria discophora (Mont.) P. Chaverri & C. Salgado 2011 is a complex of morphologically similar species in the Nectriaceae (Hypocreales, Ascomycota). First described in 1835 from material collected in Chile, it is the type species of the genus *Thelonectria*. This species was previously considered to have a cosmopolitan distribution because it had been encountered on every continent, excluding Antarctica and the Arctic regions (Brayford et al. 2004), and has been found in fungal diversity surveys throughout the world (e.g., Samuels et al. 1990; Brayford et al. 2004; Guu et al. 2007; Hirooka and Kobayashi 2007). However, recent studies have discovered that even though truly cosmopolitan fungal species exist (James et al. 1999; Finlay 2002; Pringle et al. 2005; Fierer and Jackson 2006; Rydholm et al. 2006; Queloz et al. 2011), cosmopolitanism could not be found in *T. discophora* species complex, as it is an assemblage of morphologically similar but genetically divergent species (Salgado-Salazar et al. in press).

Species in the *T. discophora* complex occur on a diverse set of habitats and plant substrates, such as bark of twigs, branches or trunks of recently dead or dying trees (Samuels et al. 1990; Brayford et al. 2004; Guu et al. 2007). These cryptic species show little intraspecific morphological variability. Perithecia occur singly or in groups and are smooth, shiny, red to dark-red colored, often with a broad mammiform (nipple-like) apex. The ascospores are bicellular and colorless or pale yellow with a spinulose surface. The anamorphic state produces long, curved, 3–5 septate macroconidia with round ends (Booth 1966; Brayford et al. 2004; Chaverri et al. 2011). Microconidia and chlamydospores are rarely reported. These morphological characters equally describe other species in *Thelonectria*, such as *T. lucida*, making the accurate identification of these species difficult when based solely on morphological characters (Brayford et al. 2004).

Thelonectria discophora is among the first colonizers on newly dead organic plant material (Samuels et al. 1990; Brayford et al. 2004). It is common in disturbed areas with recently fallen or cut plant material and is rarely found fruiting in old growth forests (Chaverri and Vilchez 2006). Rarely collected on living plant material, one variety of this species, "*Neonectria" discophora* var. *rubi* (Osterw.) Brayford & Samuels 2004, has been associated with a distinctive basal canker of cultivated *Rubus idaeus* and *R. fruticosus* (Brayford 1991, Cedeño et al. 2004). Even though this variety causes a disease, it has been regarded as a secondary or weak pathogen because the disease outbreaks have been mostly correlated with stressed plants following wind damage or waterlogging (Brayford 1991; Brayford et al. 2004). "*Neo." discophora* var. *rubi* belongs to *Thelonectria*; however, it has not been formally transferred to this genus and has not been

included in molecular studies. Because *T. discophora* was assumed to be common and cosmopolitan, many names of morphologically similar species were considered taxonomic synonyms (see Brayford et al. 2004; Chaverri et al. 2011). Based on the modification of the code of nomenclature, the generic name "*Cylindrocarpon"*, previously applied to the anamorphic name of *T. discophora*, should not be used. In spite of that, *C. ianthothele* and *C. ianthothele* var. *majus* have not been formally regarded as synonyms of *T. discophora.* The name *Cylindrocarpon* sensu stricto is regarded as the asexual state name for *Neonectria* sensu stricto (Chaverri et al. 2011).

Because *Thelonectria discophora* was determined to be a species complex (Salgado-Salazar et al., in press), the main goal of this paper is to provide a phylogenetic overview of the species in this complex. In addition each species is defined using molecular and informative morphological characters with descriptions, illustrations and a key to identify the species. Many recently collected and herbarium specimens with their anamorphic states were obtained, and analyses were conducted using sequences from six nuclear loci. These analyses combined with the morphological observations allowed us to asses the genetic diversity of the group and assign species limits.

MATERIALS AND METHODS

Fungal isolates

A total of 77 isolates from different localities and hosts were included in this study (Online Resource 1). From those, 56 correspond to *Thelonectria* cf. *discophora*, five to "*Neonectria" discophora* var. *rubi*, two to "*Cylindrocarpon" ianthothele* var. *majus*, and one to *C. ianthothele. "Cylindrocarpon" ianthothele* var. *majus* and *C. ianthothele* are included as they belong to the *T. discophora* species complex (Salgado-Salazar et al. in

press). Eight isolates representing *T. lucida* (Höhn.) P. Chaverri & Salgado 2011, two representing *T. trachosa* P. Chaverri, C. Salgado & Samuels 2011, and four representing *T. westlandica* P. Chaverri & C. Salgado 2011 were used as outgroups in the phylogenetic analyses. Specimens and cultures were obtained from CABI Bioscience (IMI); Centraalbureau voor Schimmelcultures (CBS); Japanese Ministry of Agriculture, Fisheries and Food Collection (MAFF); New York Botanical Garden (NY); and U.S. National Fungus Collection (BPI, G.J.S, A.R., now deposited in CBS).

DNA extraction, PCR, sequencing and alignments

Strains listed in Table 1 were grown in Petri dishes (6 cm diam.) containing Difco™ potato-dextrose broth. Plates were incubated at 25 ºC for *ca*. 1 wk. DNA was extracted from the mycelial mat harvested from the surface of the broth using the PowerPlant™ DNAIsolation Kit (MO BIO Laboratories, Inc., Carlsbad, California, USA). Six nuclear loci were sequenced for this study: partial large nuclear ribosomal subunit (LSU, ca. 900 bp), complete internal transcribed spacers 1 and 2 (ITS, including 5.8S of the nuclear ribosomal DNA, ca. 600 bp), partial β-tubulin (*tub*, ca. 500 bp), α-actin (*act*, ca. 600 bp), RNA polymerase II subunit 1 (*rpb1*, ca. 700 bp), and translation elongation factor 1α (*tef1*, ca. 700 bp) (Table 1). These nuclear loci are commonly used for phylogenetic studies of nectriaceous fungi proving useful for species level studies (Chaverri et al. 2011; Hirooka et al. 2012, Salgado-Salazar et al. in press). Protocols for PCR were carried out as described by Chaverri et al. (2011). Clean PCR products were sequenced in both directions at the University of Maryland DNA Sequencing Facility (Center for Agricultural Biotechnology, University of Maryland, College Park, Maryland, USA). Sequences were assembled and edited using the program Sequencher 4.9 (Gene Codes,

Madison, Wisconsin, USA). Alignments were performed using PRANK (Loytynoja and Goldman 2005) implemented by The GUIDANCE Server (http://guidance.tau.ac.il/index.html, Penn *et al.* 2010) using default settings.

Concatenated phylogenetic analyses

Posterior distributions of trees were reconstructed from the combined nuclear genes using Bayesian Inference analysis (BI) in MrBayes v. 3.1 (Huelsenbeck et al. 2001; Ronquist and Huelsenbeck 2003). A combined data set was created to obtain the total evidence phylogeny from which to infer the relationship between cryptic species. JModeltest v 0.1.1 (Posada 2008) was used to determine the best nucleotide substitution model using AIC criteria (Table 2). For the concatenated analyses, we used a partitioned approach with model parameters estimated previously. The analyses were initiated from random starting trees, run for 15 million generations with four chains (Metropolis-coupled Markov Chain Monte Carlo, Huelsenbeck and Rannala 2004) and sampled at intervals of 1000 generations. Default priors were used in all analyses. Two independent BI analyses were run. To evaluate stationarity and convergence between runs, log-likelihood scores were plotted using TRACER v. 1.5 (Rambaut and Drummond 2007). In addition, we examined the distribution of split frequencies using the online program AWTY (Are We There Yet, Nylander et al. 2008) in order to assess whether an MCMC analysis has run long enough such that tree topologies were sampled in proportion to their true posterior probability distribution, independent of the apparent stationarity detected in TRACER. Trees generated prior to stationarity were discarded and the rest of the trees were summarized in a majority-rule consensus tree from the four independent runs (Huelsenbeck et al. 2001). Bayesian posterior probabilities (PP) were assessed at all

nodes, and clades with PP ≥ 0.95 were considered well supported (Huelsenbeck and Rannala 2004). Maximum likelihood (ML) analyses were performed in RAxML (Stamatakis 2006), using the RAxML GUI vs. 1.1.1 (Silvestro and Michalak 2011). Branch support was assessed with 1000 nonparametric bootstrapping replicates using the same model parameters settings than BI analyses. Final trees were visualized with FigTree v1.3.1 (Rambaut 2005).

In order to better visualize differences among clades, we calculated nucleotide divergence (Dxy, pairwise average number of nucleotide substitutions per site between groups; Nei 1987) using the program DnaSP v.5 (Librado and Rozas 2009). For these calculations, groups to be compared were defined based on clade assignment of each individual in the concatenated ML and Bayesian phylogeny. The randomization test to assess the significance of Dxy values between groups of clades was calculated using 1000 permutations in DnaSP v.5 (Hudson et al. 1992, Librado and Rozas 2009). Singletons or orphan isolates were not included in these calculations since these methods compare clades of multiple isolates.

Morphological studies

The morphology of species in the *T. discophora* complex including specimens and associated cultures was studied according to Salgado-Salazar et al. (2012). For the teleomorph, only the length and width of ascospores were recorded, as these are the most informative characters (Samuels et al. 1990, Brayford and Samuels 1993, Samuels and Brayford 1994). The anamorph structures studied on SNA (Synthetic Nutrient Deficient Agar), SNA + soil extract, and ¼ PDA (Difco potato-dextrose-agar) media were incubated under a day/night light treatment for the required time to observe conidiation.

Growth rates and colony characteristics were determined on plates containing 20 mL of PDA inoculated with 4-mm-diam. mycelium plugs. Four different temperatures were evaluated, namely 15, 20, 25, 30; cultures growing at 20 C were selected to describe colony characteristics and standard growth. Color terminology is based on Rayner (1970).

Statistical analysis of morphological characters

Measurements of continuous characters for both anamorph and teleomorph structures (length, width) were made using Scion Image software v. 4.0.2 (Scion Corporation, Frederick, Maryland, USA) and are based on 30 units per structure. Descriptive statistics for the morphological characters, such as mean, minimum and maximum values, standard deviation and 95% confidence intervals were obtained using MYSTAT Software v. 12.02.00 (Systat Software Inc. Chicago, Illinois, USA). Ranges are reported as the extremes (maximum and minimum) in brackets separated by the mean ± one standard deviation, followed by average values.

RESULTS

Phylogenetic analyses

The nucleotide sequences generated in this study were deposited in GenBank (Online Resource 1). The concatenated data set including the six loci contained 4306 characters of which 3317 were constant, 173 parsimony-uninformative, and 816 parsimony informative (Table 1). The data from the concatenated data set have been deposited under doi:XXX at the DRYAD data repository (http://datadryad.org/).

Based on the concatenated phylogenetic analyses, a total of sixteen cryptic species in the *Thelonectria discophora* species complex were recovered, having significant ML bootstrap (>70%) and BI posterior probability (>0.95) support (Figure 1). The ML best

tree topology shown in Figure 1 was the same as the majority rule consensus tree from MrBayes analysis, consequently only ML best tree topology is shown in Figure 1. Although in previous studies significant incongruence was found between the ITS data set and the rest of the loci (*act*, LSU, *rpb1*, *tub*, *tef*) (Salgado-Salazar et al. in press), in the concatenated alignment this does not affect the recovery of the true relationships among the species in the complex. The majority of the internal nodes in the phylogeny are resolved and well supported.

The 16 cryptic species group into three large clusters: the first containing clades I to VI, the second containing clades VII to X, the third containing the clades XIII to XV. Clades XI and XII appear basal to clades I to X and are surrounded by singletons (single-isolate lineages) (Figure 1). Isolates of *Cylindrocarpon ianthothele* var. *ianthothele (=Neonectria discophora* var. *rubi)*, known to be pathogenic to *Rubus* spp. (clade XVI), were recovered as the most basal clade of the group being distantly related to the rest of *T. discophora*-like species and even to the outgroup species *T. lucida*. Since the type specimen of *T. discophora* was originally described from Chile, clade XIV (Figure 1) is here recognized as the type clade thus as true *T. discophora*. Three other cryptic species and three singletons are closely related to the type clade (XV), which include isolates from China and Japan (Clade XVI), and New Zealand, Scotland and Switzerland (clade XIII).

In total, nine isolates were found to be singletons. These singletons or orphan isolates either do not cluster with the closest related putative species having significant branch support, *i.e.*, the branch support decreases if they are included, or they are separated from them by a long branch (Figure 1). Single gene tree analyses recovered the

16 putative species and singletons as observed in the concatenated analyses (see Salgado-Salazar et al. in press). In the single gene phylogenies, the Bayesian and ML analyses recovered the same clades. However, the species positions in the trees and those of some singleton isolates differ from the positions seen in the combined analyses (data not shown). Although some of the clades were not significantly supported, they were also not contradicting the general clustering, consequently fitting the criteria for species delimitation using genealogical concordance (Dettman et al. 2003).

Zeng and Zhuang (2013) reported two new species with affinities to the *T. discophora* species complex, *T. beijingensis* and *T. yunnanica*, based on a phylogenetic analysis of ITS and partial b-tubulin regions. To investigate the relationship of these species to *T. discophora* species complex, we constructed a two-loci (ITS+*tub*) dataset of the isolates used in this study and those by Zeng and Zhuang (2013) and analyzed it using ML analysis following the settings included in Materials and Methods. As depicted by Online Resource 2, *T. beijingensis* cluster with isolate MAFF241569, here identified as a singleton lineage, and *T. yunnanica* cluster with isolates in the *T. purpurescens* species.

Genetic distances, as measured by Dxy values obtained between all pairs of species, ranged from 0.002 to 0.064 (Table 2). The highest average genetic distances were observed between clusters 1 (I–XII) and 2 (XIII–XV) with values ranging from 0.031 to 0.064. The species containing the pathogenic isolates (clade XVI) is the most distantly related to clusters 1 and 2, with genetic distances ranging from 0.039 to 0.048 (Table 2). The species *T. brayfordii* and *T. pinea* showed the lowest genetic divergence in the group of species (0.002). The degree of genetic distance between pairs of species was not related to geographic distance. For example, *T. brayfordii* and *T. mammoidea* contain

isolates from New Zealand, with no geographic restrictions however genetically divergent (Table 2)

Ecology and geographic distribution of species

Even though geographical segregation at various levels was observed, it is not a strong character for defining species in this complex (Online Resource 1, Figure 1). From the combined phylogenetic analyses we could observe species formed by isolates from the same geographic region (*T. brayfordii, T. japonica, T. pinea, T. porphyria, T. tyrus*); isolates from close-by regions (*T. blattea, T. conchyliata, T. phoenicea, T. purpurea*); and isolates from distant regions (*T. ianthina, T. mammoidea, T. purpurescens, T. violaria,* among others) (Online Resource 1, Figure 1). Interestingly, a correlation with ecology was observed for all species. With the exception of *T. blattea,* the isolates of most species were collected in their sexual state, *i.e.,* as fruiting bodies (perithecia) on decaying plant material. Isolates in *T. blattea* were collected as saprobes in soil in their asexual state. One isolate of *T. mammoidea* (CBS 32881) was also collected in its asexual state (Online Resource 1; Brayford 1991). *T. rubi* a plant pathogen on several species of *Rubus,* was also collected in its sexual state. None of the remaining species has been found on *Rubus* and causing disease. Isolates in the outgroup and sister species *T. lucida, T. trachosa* and *T. westlandica* were collected as sexual fruiting bodies on decaying plant material. Based on our observations, no host specificity was shown by the putative species, except for *T. pinea,* which here is redefined to include *T. discophora*-like isolates collected on *Pinus radiata* in New Zealand. Since one more isolate belonging to *T. mammoidea* was collected on *P. radiata* (ICMP 5287), their segregation can be based on growth rate at 25 C, morphology and genetic divergence estimates. The lack of information about the host

on which some of the species were collected makes it almost impossible to reach a definite conclusion about host specificity or preference (Online Resource 1).

Morphological analyses

Teleomorph

We could not detect significant differences in the morphology of the teleomorph. The variation in perithecial morphology, such as size, formation of flattened ostiolar disk or appearance of the external layer of cells in the wall of perithecia, and the size of asci and ascospores do not present discontinuities. A high intraspecific variation of these characters could be seen in each one of the species, including those by Zeng and Zhuang (2013). Ascospore size ranges from 10–15 × 4–6 μm in all species. *Thelonectria phoenicea* has on average the smallest ascospores (10.6 × 4.7 μm), and *T. mammoidea* and *T. pinea* have on average the largest ascospores (16.5 × 7.4 μm and 18 × 7.5 μm, respectively).

Anamorph

As the original descriptions of *T. discophora* stated, the anamorph produces characteristic purple to cinnamon colonies and pigments to the media, with the intensity of the color varying from species to species and dependent on growth temperature (See Taxonomy section). Higher quantities of pigments are produced when colonies are grown at low temperatures (15 C) and none of the species, except *T. tyrus*, produced pigment at high temperatures such as 30 C. Zeng and Zhaung (2013) did not report if *T. beijingensis* and *T. yunnanica* produced pigments in the media. In all species in the *T. discophora* complex optimum temperatures for colony growth range between 20 and 25 C; however, reduced colony growth can be observed at 15 C. Only six species (*T. conchyliata, T. ianthina, T.*

phoenicea, T. porphyria, T. purpurescens, T. tyrus) showed the ability to grown at 30 C (Online Resource 3). There are no significant differences among the species growing at 15 C, 20 C and 30 C; however, significant differences at 25 C between *T. asiatica, T. discophora, T. mammoidea* and *T. rubi* and the rest of the species could be observed (Online Resource 3). These species mentioned above have low growth rates at 25 C when compared with the rest of the species in the complex.

The morphological characters of the anamorph are more informative than those of the teleomorph. As opposed to the original description of members in the genus *Thelonectria* (Booth 1966, Brayford et al. 2004, Chaverri et al. 2011), we observed that, although rare, some species produce microconidia and chlamydospores in culture. Two species (*T. asiatica* and *T. rubi*) in the *T. discophora* complex produce microconidia and *T. blattea* produces chlamydospores in culture. None of the remaining species in the complex produce microconidia or chlamydospores in culture.

Macroconidia in the *T. discophora* complex present the typical 'cylindrocarpon' shape, with long conidia that can be cylindrical or curved with round ends. We observed variation in the presence of macroconidia with differing septation patterns, which vary from 1 to 6-septate (average 3–5 septate), depending on the species. Macroconidial septation varies as follows: *Thelonectria asiatica* and *T. violaria* 1–3 septate; *T. pinea* 1–4 septate; *T. tyrus* 2–5 septate; *T. brayfordii*, *T. mammoidea*, *T. phoenicea* and *T. purpurea* 1–5 septate; *T. conchyliata*, *T. discophora*, *T. ianthina* and *T. porphyria* 3–5 septate; and *T. blattea*, *T. japonica* and *T. purpurescens* 3–6 septate. The differences in septation among species are not correlated to biogeography or genetic divergence. Among these species the ability to produce a certain number of septa has been gained and

lost multiple times over the course of their evolutionary history (Figure 1, Online Resource 3). *Thelonectria asiatica* and *T. violaria* are the only species to produce 1–3 septate macroconidia, however, *T. asiatica* produces microconidia in culture. Among the species that produce 1-septate macroconidia, *T. phoenicea* and *T. rubi* showed length sizes significantly smaller than the other species with this character. *Thelonectria rubi* has the smallest 1-septate macroconidia, significantly different from *T. phoenicea* (Online Resource 2). Among the species that produce 6-septate macroconidia, *T. japonica* and *T. purpurescens* are significantly longer compared to *T. asiatica* and *T. blattea*. In species having 2–5 septate macroconidia the size is overlapping with values that are not significantly different, even though average values are slightly different. There are no differences in width of micro- and macroconidia whose values range from 4–7 μm, as well as in phialides length and width.

Thelonectria beijingensis and *T. yunnanica* have clear genetic affinities with species in *T. discophora* complex; however, discrepancies were observed in the morphology presented by Zeng and Zhuang (2013) and the one provided here. In the phylogenetic analyses, *T. beijingensis* clusters with *T. purpurescens*; however, the description of the morphological characters does not agree with that of *T. purpurescens.* *Thelonectria beijingensis* produces microconidia and macroconidia 1–3 septate in culture. On the other hand, *T. purpurescens* described here does not produce microconidia and macroconidia are 3–6 septate. *Thelonectria yunnanica* is also reported to produce microconidia in culture; however, the isolate MAFF241569 does not produce them in culture.

TAXONOMY

We use a combination of phylogenetic analyses, DNA sequence divergence tests and morphological observations to define species in the *Thelonectria discophora* complex. Sixteen lineages that correspond to species are described here as new. For the newly described species only a brief description is provided, mainly including those characters that are different or diagnostic from the narrowly defined species of *T. discophora*. Based on the modification of the code of nomenclature, the generic name "*Cylindrocarpon"*, which was previously applied to the anamorph of *T. discophora*, should not be used. *Cylindrocarpon* names related to *T. discophora* are here regarded as synonyms of the *T. discophora* species described below.

Thelonectria discophora (Mont.) P. Chaverri & C. Salgado

Mycobank MB518569

Figure 2 A–F.

Basionym: *Sphaeria discophora* Mont., Ann. Sci. Nat. Bot. II 3: 353. 1835.

≡ *Neonectria discophora* (Mont.) Mantiri & Samuels var. *discophora*, Canad. J. Bot. 79: 339. 2001

= *Nectria tasmanica* Berk. in Hooker, Flora Tasmaniae 2: 279. 1860.

= *Nectria umbilicata* Henn., Hedwigia 41: 3. 1902.

= *Creonectria discostiolata* Chardón, Bol. Soc. Venez. Ci. Nat. 5: 341. 1939.

Holotype of Sphaeria discophora*:* Chile. Juan Fernandez, sur cortice arborum, date unknown, Bertero 1700 (PC!; ISOTYPE, PC!)

Mycelium not visible on host. Perithecia globose to subglobose with smooth and shiny or slightly roughened surface, (250–)300–550(–650) μm high, (100–)240–300(–400) μm

wide, solitary or gregarious in groups of 20 or less, superficial or with the base immersed in substratum on a minute stroma, not collapsed when dry, red to rust with the ostiolar area often having a darker color (chestnut), red to rose in 3% KOH, yellow in lactic acid, nonpapillate or with a broad mammiform apex 150–200 μm wide. Cells at surface of perithecial wall lacking a definite outline appearing to be intertwined hyphae with lumina irregular in shape 2–2.5 μm, 2–4 μm thick. Perithecial wall 30–50 μm wide of two intergrading regions: outer region 20–30 μm wide, continuous over perithecium to form a uniform palisade of hyphal cells perpendicular to surface of perithecium, lumina <1 μm wide and tips rounded; inner region of perithecial wall 10–20 μm wide, cells lacking a definite outline but with long axes parallel to surface of perithecial wall, cells increasingly more compacted, thin-walled towards perithecial locule; perithecial apex of vertically elongated cells, continuous with lateral perithecial wall forming a disk around perithecial opening. Asci cylindrical to clavate, (66–)72–95(–119) × 7–10(–15) μm, 8-spored, apex with a refractive ring. Ascospores ellipsoid to fusiform, (10.4–)11.5–15.6(–16.7) × (4.5–)4.9–6.3(–7.0) μm (mean 13.6 × 5.6 μm), symmetrically two-celled, sometimes with one side curved and one side flattened, not constricted at septum, spinulose, hyaline becoming yellowish. Colonies on PDA 17–28 mm diam. (mean 23 mm) after 12 d at 20 C, aerial mycelium floccose, mauve to pale vinaceous, producing purple pigment into media at 15–20 C, no pigment produced at > 20 C, colony reverse mauve to dark vinaceous. Conidia on SNA forming in hyaline, slimy droplets in aerial mycelium or on agar surface; pionnotes sometimes formed close to filter paper on SNA. Phialides borne apically on irregularly branching clusters of cells or directly from hyphae, cylindrical or slightly swollen (13.2–)16.0–20.6(–23.4) × (–2.5)3.5–4.4(–5.1) μm (mean

18 × 4), with periclinal thickening and collarette. Macroconidia slightly fusiform, curved with round tips, 3–5(–6)-septate: 3-septate (40.5–)46.9–58.9(–71.4) × (4.4–)4.9–5.8(–7) μm (mean 53.3 × 5.4 μm), 4-septate (44.6–)55–67.5(–74.4) × (4.4–)5–6(–6.5) μm (mean 61.2 × 5.5 μm), 5-septate (60–)65.4–77(–82.5) × (4.4–)5.2–6.3(–6.6) μm (mean 71.2 × 5.8 μm). Microconidia and chlamydospores not produced on SNA.

Habitat and distribution. Saprobic on decaying bark of shrubs and trees. Known from Chile (type locality) and Scotland; possibly distributed in temperate regions of Europe and America.

Additional specimens examined: CHILE. Llanquihue Province: Los Lagos Region, Vicente Perez Rosales National Park, on wood of a recently killed *Tepualia stipularis* tree, April 2011, Andrés de Errasti (BPI 892687, culture A.R. 4742 = CBS 134034). SCOTLAND. Cowal Peninsula, Argyll Forest Park, ca. 10 km north of Dunoon, Yourger Botanic Garden 50–100 m, on *Aesculus* sp. dead branchlets, 11-13 April 1992, G.J. Samuels, D. Brayford (BPI 802901, culture G.J.S. 92-48 = CBS 134031).

Notes. As a result of the phylogenetic analysis, the following names are no longer synonyms of *T. discophora* because of their distinctive genetic divergence: *Nectria mammoidea* (≡ *Creonectria mammoidea*), *Nectria nelumbicola*, *Nectria mammoidea* var. *rugulosa*, *Nectria mammoidea* var. *minor*, and *Nectria pinea*.

Thelonectria asiatica C. Salgado & Hirooka sp. nov.

Mycobank XXX

Figure 2 G–M.

Similar to *T. discophora*, microconidia present, macroconidia 1–3 septate.

Holotype. JAPAN. Nagano Prefecture, Sugadaira, Ueda City, on twigs, 02 Sept 2006, Y. Hirooka (TPP-h548, BPI 881963, ex-type culture MAFF 241576).

Etymology. Refers to the geographic range where this species is found.

Mycelium not visible on host. Perithecia globose to subglobose with smooth and shiny or slightly roughened surface, 300–600 μm high, 200–300 μm wide, solitary or gregarious in groups of 20 or less, superficial or with the base immersed in substratum on a minute stroma, not collapsed when dry, peach to orange with ostiolar area often having a darker color (rust), red to rose in 3% KOH, yellow in lactic acid, nonpapillate or with a small mammiform apex 50–100 μm wide. Cells at surface of perithecial wall lacking a definite outline appearing to be intertwined hyphae with lumina, irregular in shape 2–2.5 μm, 2–4 μm thick. Perithecial wall 30–50 μm wide. Asci cylindrical, (68–)75–98(–119) × 7–10 μm, 8-spored, apex with a refractive ring. Ascospores ellipsoid to fusiform, (13–)14–15.4(–15.8) × (4.6–)5.2–5.9(–6.2) μm (mean 14.7 × 5.5 μm), symmetrically two-celled, sometimes with one side curved and one side flattened, not constricted at septum, spinulose, hyaline. Colonies on PDA 16–17 mm diam. after 12 d at 20 C, aerial mycelium floccose, pale vinaceous to lilac, producing purple to cinnamon pigment into media at temperatures ≤ 25 C, no pigment produced at > 25C, colony reverse sienna to livid purple. Conidia on SNA forming in hyaline, slimy droplets in aerial mycelium or on agar surface; pionnotes sometimes formed close to filter paper on SNA. Phialides borne apically on irregularly branching clusters of cells or directly from hyphae, cylindrical or slightly swollen (13.3–)18.3–26.4(–30.7) × (–2.6)3.1–4(–4.5) μm (mean 22.3 × 3.5), with periclinal thickening and collarette. Macroconidia cylindrical or slightly fusiform, curved with round tips, 1–3- septate: 1-septate (20.1–)28.5–40.3(–49.8) × (3.7–)4.2–5.4(–6.6)

μm (mean 34.4 × 4.8 μm), 2-septate (32.1–)37.5–48.3(–53.9) × (3.6–)4.4–5.5(–6.1) μm (mean 42.7 × 5 μm), 3-septate (34.1–)42.7–51.8(–57.4) × (3.9–)4.6–5.9(–6.8) μm (mean 47.2 × 5.2 μm). Microconidia produced in culture, cylindrical with round ends, (6.4–)7.2–8.8(–9.6) μm (mean 8 × 4.1 μm). No chlamydospores formed in culture.

Habitat and distribution. Saprobic on decaying bark of shrubs and trees. Known from Japan (type locality) and China. Possibly distributed throughout Asia.

Additional specimens examined. CHINA. Yunnan Province, Lijiang region, on bark submerged in stream, 4 Nov 1988, R.P. Korf (only culture examined G.J.S. 88-84 = IMI 348190).

Notes. This species is sister to the type clade. It produces microconidia in culture and macroconidia 1–3-septate, which are lacking in true *T. discophora*. Two additional newly described species from Taiwan, *T. beijingensis* and *T. yunnanica*, are reported to be related to *T. discophora* and produce microconidia in culture (Zeng and Zhuang 2013). As explained in the results and discussion section, there is disagreement about the species reported in this study and those by Zeng and Zhuang (2013).

Thelonectria blattea C. Salgado & P. Chaverri sp. nov.

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Figure 3 A–F.

Only known from the asexual state. Anamorph similar to *T. discophora*. Occurs on soil.

Holotype. GERMANY. Kiel-Kitzeberg, in wheat field soil, Dec 1968, W. Gams (Ex-type culture CBS 95268).

Etymology. Refers to the purple color the colony that this fungus produces.

Colonies on PDA 32–35 mm diam. (mean 33 mm) after 12 d at 20 C, aerial mycelium

floccose, white to livid vinaceous, no pigment produced into media, colony reverse also white to livid vinaceous. Conidia on SNA forming in hyaline, slimy droplets in aerial mycelium or on agar surface; pionnotes sometimes formed close to filter paper on SNA. Phialides borne apically on irregularly branching clusters of cells or directly from hyphae, cylindrical or slightly swollen (13.2–)16–20.6(–23.4) × (–2.5)3.5–4.4(–5.1) μm (mean 18 × 4 μm), with periclinal thickening and collarette. Macroconidia cylindrical or slightly fusiform, curved with round tips, 3–5(–6)-septate: 3-septate (40.5–)46.9–58.9(–71.4) × (5.1–)6.2–7(–7.9) μm (mean 54.4 × 6.4 μm), 4-septate (42–)55–67.5(–74.2) × (6.2–)6.4–6.8(–7) μm (mean 60.3 × 6.6 μm), 5-septate (45.3–)60–70(–84) × (6–)6.4–6.8(–7) μm (mean 63 × 6.6 μm), 6-septate (55–)58.5–63.5(–76) × (3.5–)53.8–4.2(–5) μm (mean 60 × 6.4 μm). Microconidia not produced in culture. Chlamydospores formed in culture (mean 8.7 × 7.4 μm),

Habitat and distribution. Isolated from soil in agricultural settings. Known from Germany and The Netherlands; possibly distributed across Europe.

Additional culture/specimens examined. THE NETHERLANDS. Wageningen, on roots in clay soil, Jan 1977, J.W. Veenbaas-Rijks (culture CBS 14277).

Thelonectria brayfordii C. Salgado & Samuels sp. nov.

Mycobank XXX

Figure 3 G–L.

Similar to *T. discophora*. Macroconidia 1–5-septate, found only in New Zealand on hosts other than *Pinus radiata*.

Holotype. NEW ZEALAND. Auckland, on *Quercus rubur*, March 2005, C.F. Hill (Ex-

type culture CBS 118612).

Etymology. In honor of David Brayford, a British mycologist who contributed greatly to the taxonomy of hypocrealean fungi.

Colonies on PDA 31–34 mm diam. (mean 32 mm) after 12 d at 20 C, aerial mycelium floccose, white to mauve, producing purple to cinnamon pigment into media at temperatures ≤ 25 C, no pigment produced at > 25 C, colony reverse rosy vinaceous to rust. Conidia on SNA forming in hyaline, slimy droplets in aerial mycelium or on agar surface; pionnotes sometimes formed close to filter paper on SNA. Phialides borne apically on irregularly branching clusters of cells or directly from hyphae, cylindrical or slightly swollen (13.6–)14.5–22.7(–29.5) × (–3.5)3.7–4.6(–4.9) μm (mean 18.5 × 4.2 μm), with periclinal thickening and collarette. Macroconidia cylindrical or slightly fusiform, curved with round tips, 1–5-septate: 1-septate (22.8–)27.9–38.4(–44.1) × (3–)3.3–4.4(–4.9) μm (mean 33.1 × 3.8 μm), 2-septate (30.2–)36.7–56.6(–58.2) × (4–)4.6–6.1(–6.3) μm (mean 51.5 × 5.3 μm), 3-septate (65.7–)50.5–59.4(–65.7) × (4.7–)5.2–6.1(–6.8) μm (mean 54.9 × 5.6 μm), 4-septate (49.3–)56.3–65.8(–72.5) × (4.7–)5.3–6.3(–6.8) μm (mean 61 × 5.8 μm), 5-septate (55.3–)63.3–71.5(–77.7) × (5.1–)5.7–6.7(–7.5) μm (mean 67.4 × 6.2 μm). Chlamydospores and microconidia not produced in culture.

Habitat and distribution. On decaying bark of *Quercus rubur* and roots of various plants. Only known from New Zealand.

Additional specimens examined. NEW ZEALAND. Bay of Plenty, Tauranga locality, on rotting root of unknown proteaceus plant, April 1 2000, C.F. Hill (culture only ICMP 14105). Ibid. on root of unknown dead plant, Apr 2000, H.M. Dance, LYN10 (culture only IMI 384045).

Notes. The description of this species is based only on characters obtained from the anamorph. Two species in the *T. discophora* complex occur in New Zealand, *T. brayfordii* and *T. pinea; T. pinea* occurs only on *P. radiata* and has macroconidia 1–4-septate.

Thelonectria conchyliata C. Salgado & P. Chaverri sp. nov.

Mycobank MB XXX

Figure 4 A–G.

Similar to *T. discophora*. Macroconidia 3–5 septate, average colony growth on SNA at 30 C > 13 mm.

Holotype. GUYANA. Cuyuni-Marazuni: Mazaruni Subregion, VII-2, along Koatse river, ca. 2 km east of Pong River, ca. hr walk west of Chinoweing, 05°28'N 60°04'W, 600-650 m, Feb-March 1987, on wood, G.J. Samuels, J. Pipoly, G. Gharbarran, J. Chin, R. Edwards (BPI 747133, ex-type culture G.J.S. 87-45 = IMI325855).

Etymology. Refers to the purple color of the colony and pigment that this species produces in culture.

Mycelium not visible on host of some specimens. Perithecia globose to subglobose with smooth, shiny or slightly roughened surface, 400–500 μm high, 340–400 μm wide, solitary or gregarious in groups of 20 or less, superficial or with base immersed in substratum on a minute stroma, not collapsed when dry, peach to bay with ostiolar area often having a darker color (rust), red to rose in 3% KOH, yellow in lactic acid, nonpapillate or with a broad mammiform apex 150–200 μm wide. Perithecial wall 30–50 μm wide of two intergrading regions: outer region 20–30 μm wide. Asci cylindrical, (75–

)85–100(–120) × 8–10 μm, 8-spored, apex with a refractive ring. Ascospores ellipsoid to fusiform, (8.4–)9.4–15.7(–20) × (3.1–)4.3–6.5(–8.2) μm (mean 12.5 × 5.4 μm), symmetrically two-celled, sometimes with one side curved and one side flattened, not constricted at septum, spinulose, hyaline becoming yellowish in mature ascospores. Colonies on PDA 27–44 mm diam. (mean 33 mm) after 12 d at 20 C, aerial mycelium floccose, white to lilac, producing purple to cinnamon pigment to media in some isolates at temperatures < 30 C, colony reverse mauve to bay. Conidia on SNA forming in hyaline, slimy droplets in aerial mycelium or on agar surface; pionnotes sometimes formed close to filter paper on SNA. Phialides borne apically on irregularly branching clusters of cells or directly from hyphae, cylindrical or slightly swollen (9.5–)12.5–17.6(–23.2) × (–2.6)3.6–4.7(–5.8) μm (mean 15 × 4.2 μm), with periclinal thickening and collarette. Macroconidia slightly fusiform, curved with round tips, 3–5-septate: 3-septate (39.1–)45.4–55.3(–63.8) × (4.5–)5.8–6.9(–7.8) μm (mean 50.3 × 6.4 μm), 4-septate (47.7–)51.7–60.5(–66.2) × (5.4–)5.9–7(–8.1) μm (mean 56.1 × 6.5 μm), 5-septate (52.3–)57.2–66.4(–74.1) × (5.2–)6.1–7.2(–8.7) μm (mean 61.8 × 6.7 μm). Microconidia and chlamydospores not produced on SNA.

Habitat and distribution. Saprobic on decaying bark of *Ocotea* sp., palms and possibly other hardwood species. Distributed in tropical South America and Central America.

Additional specimens examined. GUYANA. Cuyuni-Marazuni: Mazaruni Subregion, VII-2, along Koatse river, ca. 2 km east of Pong River, ca. hr walk west of Chinoweing, 05°28’N 60°04’W, 600-650 m, 28 Feb 1987, on branchlets of recently dead tree, G.J. Samuels, J. Pipoly, G. Gharbarran, J. Chin, R. Edwards (BPI 744725, culture G.J.S. 87-49 = CBS 112461); Potaro-Sinupari Region, base of Mt. Wokomung, ca. 5.5 hr walk NE

of Kopinang Village in legume-dominated forest, 05°05'N 59°49'W, 27 Jun 1989, on bark of recently fallen tree, G.J. Samuels 6269A, B.M. Boom, G. Bacchus (NY, culture G.J.S. 89-57 = CBS 112459); 720 m, G.J. Samuels 6281, B.M. Boom, G. Bacchus (NY, culture G.J.S. 89-60); Mt. Wokomung, Wokomung Base Camp, ca. 8 hr walk NE of Kopinang Village in wet forest dominated by Euphorbiaceae, 05°05'N 59°50'W, 1070 m, Jun-Jul 1989, G.J. Samuels 6318, B.M. Boom, G. Bacchus (NY, culture G.J.S. 89-65 = CBS 123970). PUERTO RICO. 350-400 m, on *Ocotea* sp. twigs, 20 Feb 1996, G.J. Samuels, H.J. Schroers, D.J. Lodge (BPI 744683, culture G.J.S. 96-22 = IMI 370946). VENEZUELA. Sucre State, NW of Irapa, trail between Los Pocitos and peak of Cerro Humo, on stem of unidentified palm, 12 Jul 1972, K.P. Dumont VE 4769, R.F. Cain, G.J. Samuels, G. Morillo, J. Farian (NY, culture C.T.R. 72-90); Aragua State, Henri Pittier National Park, Rancho Grande Biological Station, trail to Guacamayo, 1250-1400m, 10°21'N, 67°41'W, on bark of unidentified tree, 04 Dec 1990, G.J. Samuels, B. Hein, S.M. Huhndorf (BPI 842123, culture G.J.S. 90-212 = CBS 134028).

Notes. This species is similar to *T. ianthina*, which also produces 3–5 septate macroconidia. On average, *T. conchyliata* has a faster growth rate of the colony on PDA at 30 C than *T. ianthina*.

Thelonectria ianthina C. Salgado & Guu J.-R sp. nov.

Mycobank XXX

Figure 4 H–N.

Similar to *T. discophora*. Macroconidia 3–5-septate, average colony growth on SNA at 30 C < 13 mm.

Holotype. COSTA RICA. Heredia Province, Braulio Carrillo National Park, Zurquí Street entrance, 10°02’N 84°01’W, 1562 m, on bark, 13 March 2010, C. Salgado-Salazar, C. Herrera, Y. Hirooka, A. Rossman, G.J. Samuels, P. Chaverri PC1001 (BPI 892691, ex-type culture G.J.S. 10–118 = CBS 134023).

Etymology. Refers to the purple color of the colony and pigment produced by this species.

Mycelium not visible on host. Perithecia globose to subglobose with smooth and shiny or slightly roughened surface, 300–600 μm high, 200–350 μm wide, solitary or gregarious in groups of 15 or less, superficial or with base immersed in substratum on a minute stroma, not collapsed when dry, red to bay with ostiolar area often having a darker color (bay to umber), red to rose in 3% KOH, yellow in lactic acid, papillate or with a small mammiform apex 50–100 μm wide. Cells at surface of perithecial wall lacking a definite outline appearing to be intertwined hyphae with lumina irregular in shape 2–2.5 μm, 2–4 μm thick. Perithecial wall 35–50 μm wide. Asci cylindrical or slightly clavate, (60–)70–90(–111) × 7–10 μm, 8-spored, apex with a refractive ring. Ascospores ellipsoid to fusiform, (11.7–)12.2–13.99(–15) × (5.3–)5.6–6.1(–6.4) μm (mean 13.1 × 5.8 μm), symmetrically two-celled, sometimes with one side curved and one side flattened, not constricted at septum, spinulose, hyaline. Colonies on PDA 31–35 mm diam. (mean 33 mm) after 12 d at 20 C, aerial mycelium floccose, white to purple, producing purple pigment in media at temperatures ≤ 25 C, colony reverse white to bay. Conidia on SNA forming in hyaline, slimy droplets in aerial mycelium or on agar surface; pionnotes sometimes formed close to filter paper on SNA agar. Phialides borne apically on irregularly branching clusters of cells or directly from hyphae, cylindrical or slightly

swollen (12.2–)13.7–20.4(–25.9) × (–2.7)3.2–4.2(–4.9) μm (mean 17 × 3.7 μm), with periclinal thickening and collarette. Macroconidia cylindrical or slightly fusiform, curved with round tips, 3–5-septate: 3-septate (37.9–)45.9–57.1(–64.7) × (4.7–)5.4–7(–8.7) μm (mean 51.5 × 6.2 μm), 4-septate (49.6–)55.1–63(–68.2) × (5.8–)6.2–7.5(–8.3) μm (mean 59.1 × 6.8 μm), 5-septate (52–)59.4–62.3(–69.7) × (3.5–)6.2–8(–8.7) μm (mean 60.9 × 7.1 μm). No microconidia or chlamydospores produced in culture.

Habitat and distribution. Saprobic on decaying bark of trees and shrubs. Known from Costa Rica (type locality) and Taiwan.

Additional specimens examined. TAIWAN. Taipei County, Jingtung, Jungtung historical trail, on bark, 21 Dec 2003, J.-R. Guu 92122107 (BPI 892688, culture Guu 92122107 = CBS 134038).

Notes. This species is similar to *T. conchyliata*, which also produces macroconidia 3–5-septate. They can be distinguished on the slower average colony growth rate on PDA at 30 C of *T. ianthina*.

Thelonectria japonica C. Salgado & Hirooka sp. nov.

Mycobank MBXXX

Figure 5 A–F.

Similar to *T. discophora*. Macroconidia 3–6-septate. Only known from Japan.

Holotype. JAPAN. Okutama-gun, on twigs of undetermined plant, 20 Nov 2003, Y. Hirooka TPP-h-229-2 (BPI 882092, ex-type culture MAFF 241524).

Etymology. Refers to the geographic location where this species was found.

Mycelium not visible on host. Perithecia globose to subglobose with smooth and shiny or

slightly roughened surface, 300–610 μm high, 200–350 μm wide, solitary or gregarious in groups of 15 or less, superficial or with base immersed in substratum on a minute stroma, not collapsed when dry, peach to sienna with ostiolar area often having a darker color (rust), red to rose in 3% KOH, yellow in lactic acid, papillated. Cells at surface of perithecial wall lacking a definite outline, appearing to be intertwined hyphae with lumina irregular in shape 2–2.5 μm, 2–4 μm thick. Perithecial wall 25–40 μm wide. Asci cylindrical, (50–)68–90(–100) × 7–11 μm, 8-spored, apex with a refractive ring. Ascospores ellipsoid to fusiform, (10.6–)11.6–13.7(–15.4) × (4.7–)5.2–6.1(–6.7) μm (mean 12.7 × 5.6 μm), symmetrically two-celled, sometimes with one side curved and one side flattened, not constricted at septum, spinulose, hyaline. Colonies on PDA 33–44 mm diam. (mean 38 mm) after 12 d at 20 C, aerial mycelium floccose, white to purple, no pigment produced in media, colony reverse also white to purple. Conidia on SNA forming in hyaline, slimy droplets in aerial mycelium or on agar surface; pionnotes sometimes formed close to filter paper on SNA. Phialides borne apically on irregularly branching clusters of cells or directly from hyphae, cylindrical or slightly swollen (9.3–)11.5–18.2(–22.5) × (–3)3.5–4.8(–5.2) μm (mean 14.8 × 4.1 μm), with periclinal thickening and collarette. Macroconidia cylindrical or slightly fusiform, curved with round tips, 3–6-septate: 3-septate (45.2–)54–67.3(–79.8) × (4.6–)5.3–6.3(–7.2) μm (mean 60.6 × 5.8 μm), 4-septate (57–)64.3–75.6(–88.8) × (4.2–)5.4–6.7(–7.5) μm (mean 69.9 × 6.1 μm), 5-septate (64.3–)72.2–82.5(–90.7) × (5.2–)5.6–6.6(–7.4) μm (mean 77.3 × 6.1 μm), 6-septate (86.9–)86.5–90.2(–90.4) × (5.7–)5.8–6.7(–6.7) μm (mean 88.3 × 6.2 μm). No microconidia or chlamydospores are formed in culture.

Habitat and distribution. Saprobic on decaying bark of *Fagus crenata,* and possibly on

bark of other shrubs and trees. Known only from Japan.

Additional specimens examined. JAPAN. Miyagi Prefecture, Kenminnomori, Rifu-cho, Miyagi-gun, on twigs of unknown plant, 5 Aug 2004, Y. Hirooka TPP-305-2 (BPI 882109, culture MAFF 241543). Kanagawa Prefecture, Yamakitagawayosa, Ashigarakami-gun, on bark of undetermined dead tree, 30 Oct 2004, Y. Hirooka TPP-h374-2 (BPI 881926, culture MAFF 241554); on bark of dead *Fagus crenata*, 17 Apr 2005, Y. Hirooka TPP-h-433-2 (BPI 881944, culture MAFF 241563).

Notes. There is one other species that can also be found in Japan, *T. porphyria*. However *T. japonica* produces macroconidia 3-6-septate, while *T. porphyria* produces macroconidia 3-5-septate.

Thelonectria mammoidea (W. Phillips & Plowr.) C. Salgado & R.M. Sánchez comb. nov.

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Figure 5 G–L.

Basionym: *Nectria mammoidea* W. Phillips & Plowr., Grevillea 3: 126. 1875

≡ *Creonectria mammoidea* (W. Phillips & Plowr.) Seaver. Mycologia 1: 188. 1909.

≡ *Cucurbitaria mammoidea* (W. Plowr. & Plowr.) Kuntze, [as 'mammodea'] Revis. gen. pl. (Leipzig) 3: 461. 1898.

= *Nectria mammoidea* var. *rugulosa* Weese, Sber. Akad. Wiss. Wien, Math.-naturw. Kl., Abt. 1 125(7 & 8): 552. 1916.

= *Nectria nelumbicola* Henn., Verh. Bot. Vereins. Prov. Brandenburg 40: 151. 1898.

= *Cylindrocarpon ianthothele* var. *majus* Wollenw., Z. Parasitenk. (Berlin) 1: 161. 1928.

= *Cylindrocarpon ianthothele* var. *rugulosum* C. Booth, Mycol. Pap. 104: 25. 1966.

Type specimen/culture. ENGLAND. Norfolk County: North Wootton, on bark of unknown plant, Jan 1897, C.B. Plowright (Holotype E 00456070); Surlingham City, on *Smyrnium olusatrum* seeds, 1957, E.A. Ellis (ex-epitype culture IMI 69361). *Mycelium* sometimes visible on host. Stroma arising from cortex of host, cells angular to circular in outline, continuous with cells of outer region of perithecial wall. Perithecia globose to subglobose with smooth and shiny or slightly roughened surface, 400–700 μm high, 240–340 μm wide, solitary or gregarious in groups of 20 or less, superficial or with base immersed in substratum on a minute stroma, not collapsed when dry, peach to sienna with the ostiolar area often having a darker color (rust), red to rose in 3% KOH, yellow in lactic acid, nonpapillate or with a broad mammiform apex 150–190 μm wide. Perithecial wall 30–50 μm wide of two intergrading regions; outer region 20–30 μm wide, continuous over perithecium to form a uniform palisade of hyphal cells perpendicular to surface of perithecium, lumina <1 μm wide and tips rounded; inner region of perithecial wall 10–25 μm wide, cells lacking a definite outline but with long axis parallel to surface of perithecial wall, cells increasingly more compacted, thin-walled towards perithecial locule; perithecial apex of vertically elongated cells, continuous with lateral perithecial wall, forming disk around perithecial opening. Asci cylindrical, (70–)80–100(–130) × 8–10 μm, 8-spored, apex with a refractive ring. Ascospores ellipsoid to fusiform, (12.6–)15.3–17.7(–18.8) × (6–)6.7–8.0(–9.7) μm (mean 16.5 × 7.4 μm), symmetrically two-celled, sometimes with one side curved and one side flattened, not constricted at septum, spinulose, hyaline becoming yellowish. Colonies on PDA 25–27 mm diam. (mean 26 mm) after 12 d at 20 C, aerial mycelium floccose, white to lilac or rosy buff, with cinnamon pigment produced in media, colony reverse white to

mauve or cinnamon. Conidia on SNA forming in hyaline, slimy droplets in aerial mycelium or on agar surface; pionnotes sometimes formed close to filter paper on SNA. Phialides borne apically on irregularly branching clusters of cells or directly from hyphae, cylindrical or slightly swollen, (13–)16.5–20.9(–23.7) × (–2.9)3.5–4.4(–5.1) μm (mean 17.5 × 4 μm), with periclinal thickening and collarette. Macroconidia slightly fusiform, curved with round tips, 1–5-septate: 1-septate (28.7–)29.5–36.9(–39.3) × (5.5–)5.6–6.2(–6.3) μm (mean 33.2 × 5.9 μm), 2-septate (35.9–)39.7–48.1(–50.5) × (5.8–)6–7(–7.5) μm (mean 43.9 × 6.5 μm), 3-septate (41.1–)45.8–57.9(–64) × (5–)5.7–7.0(–7.9) μm (mean 51.9 × 6.4 μm), 4-septate (52–)57–67.2(–73.7) × (5–)5.9–6.9(–7.6) μm (mean 62.1 × 6.4 μm), 5-septate (70.3–)69.6–74.2(–75) × (6.3–)6.3–6.4(–6.5) μm (mean 71.9 × 6.4 μm). No microconidia or chlamydospores produced on SNA.

Habitat and distribution. Saprobic on *Fuchsia excorticata*, *Pinus radiata* and possibly on diverse hardwood trees. Also on herbaceous plants (e.g., *Smyrnium olusatrum*) and decaying plant organic matter. Known from Europe and New Zealand, probably distributed throughout temperate regions.

Additional specimens examined. NEW ZEALAND. Southland, Catlin's State Forest Park, Lake Wilkie, on bark of unidentified tree, 18 Apr 1985, G.J. Samuels, P.K. Buchanan, L.M. Kohn (PDD 50050, BPI 802469, culture G.J.S. 85-27 = CBS 112457); South Island, Westland, Franz Joseph, track to Lake Wombat, on bark of *Fuchsia excorticata*, 10 Apr 1983, G.J. Samuels, R.H. Petersen (PDD 46365, BPI 1109329, culture G.J.S. 83-188 = IMI 326256); Waitomo, on bark of indetermined tree, 26 Apr 1983, G.J. Samuels, P.R. Johnston, R.H. Petersen (PDD 46410, culture G.J.S. 83-206 = IMI 326258); on *Pinus radiata*, 01 Nov 1965, J. M. Dingley (culture ICMP 5287). SCOTLAND. Cowal

Peninsula, Argyll Forest Park, ca 5 km south of Strachur along river Cur, vic Glenbranter Village, Lauder Broadleaf Walk ca. 50 m, on bark of unidentified dead hardwood tree, 12 Apr 1992, G.J. Samuels, D. Brayford (BPI 802649, culture G.J.S. 92-34 = CBS 134030). SWITZERLAND. May 1981, O. Petrini (culture CBS 32881).

Notes. The isolate ICMP 5287 was collected in New Zealand on *Pinus radiata*; however, it is genetically divergent from isolates in *T. pinea* (5.9 % Dxy) and produces macroconidia 1–5-septate. *Thelonectria pinea* produces macroconidia 1–4-septate.

Thelonectria phoenicea C. Salgado & P. Chaverri sp. nov.

Mycobank MBXXX

Figure 6 A–F.

Similar to *T. discophora*. Macroconidia 1–5-septate. Found in Australia, Indonesia and Taiwan.

Holotype. INDONESIA. North Sulawesi, Eastern Dumoga-Bone National Park, at confluence of Toraut and Tumpha Rivers, Project Wallace Base Camp, 0°34'N 123°57'E, 211 m, on twig of unidentified tree, Sep-Nov 1985, G.J. Samuels (NYBG 2222A, ex-type culture G.J.S. 85-179 = IMI 329113).

Etymology. Refers to the purple coloration of the anamorph and pigment produced in culture.

Mycelium not visible on host. Perithecia globose to subglobose with smooth and shiny or slightly roughened surface, 300–600 μm high, 200–350 μm wide, solitary or gregarious in groups of 15 or less, superficial or with base immersed in substratum on a minute stroma, not collapsed when dry, peach to sienna with ostiolar area often having a darker

color (bay), red to rose in 3% KOH, yellow in lactic acid, papillated. Cells at surface of perithecial wall lacking a definite outline appearing to be intertwined hyphae with lumina irregular in shape 2–2.5 μm, 2–4 μm thick. Perithecial wall 25–40 μm wide. Asci cylindrical, (50–)66–89(–105) × 7–11 μm, 8-spored, apex with a refractive ring. Ascospores ellipsoid to fusiform, (9.2–)9.7–11.6(–13.2) × (3.9–)4.3–5(–5.7) μm (mean 10.6 × 4.7 μm), symmetrically two-celled, sometimes with one side curved and one side flattened, not constricted at septum, spinulose, hyaline. Colonies on PDA 29–30 mm diam. after 12 d at 20 C, aerial mycelium floccose, white to purple, producing purple pigment at ≤ 25 C, colony reverse white to bay. Conidia on SNA forming in hyaline, slimy droplets in aerial mycelium or on agar surface; pionnotes sometimes formed close to filter paper on SNA. Phialides borne apically on irregularly branching clusters of cells or directly from hyphae, cylindrical or slightly swollen (10.7–)11–21.8(–59.2) × (–2.8)3.6–4.7(–6.4) μm (mean 16.4 × 4.1 μm), with periclinal thickening and collarette. Macroconidia cylindrical or slightly fusiform, curved of round tips, 1–5-septate: 1-septate (17.8–)22.6–30.6(–31.6) × (3.8–)4.2–5(–5.4) μm (mean 26.6 × 4.6 μm), 2-septate (28.6–)28.3–37.1(–37.3) × (5–)5.1–5.5 μm (mean 32.7 × 5.3 μm), 3-septate (31.5–)44.9–58.5(–64.8) × (4.2–)5.4–6.5(–7.2) μm (mean 51.7 × 5.9 μm), 4-septate (49.8–)59.1–67.4(–72.7) × (4.9–)5.9–6.9(–7.6) μm (mean 63.3 × 6.4 μm), 5-septate (58.1–)62.7–70.4(–76.6) × (5–)6.1–7.2(–7.9) μm (mean 66.5 × 6.6 μm). No microconidia or chlamydospores formed in culture.

Habitat and distribution. Saprobic on decaying *Acacia celsa* and other plants. Distributed in the type locality (Indonesia), Australia and Taiwan.

Additional specimens examined. AUSTRALIA. Queensland: Atherton City, Davis Creek,

on *Acacia celsa*, 2 Feb 2009, A.Y. Rossman, P. Chaverri PC 883 (BPI 879019, culture G.J.S. 09-509). INDONESIA. Sulawesi, Demoga-Bone National Park, 0o28'N, 1230N, 47'E, ca. 810m, 18 Oct. 1985, G.J. Samuels GJS 2278 (BPI XXX, culture GJS 85-187 = ATCC 76748). TAIWAN. Kaohsiung County, Liou-guei, Shan-ping, on bark of unidentified tree, 10 Mar 2005, J. –R. Guu (BPI 892688, culture Guu 94031007 = CBS 134039).

Notes. Species other than *T. phoenicea* produce 1–5-septate macroconidia that can be distinguished based on their geographic locations: *T. phoenicea* in Australia, Indonesia and Taiwan; *T. purpurea* in Central and northern South America.

Thelonectria pinea C. Salgado & P. Chaverri comb. nov.

Mycobank MBXXX

Figure 6 G–L.

≡ *Nectria pinea* Dingley, Trans. Roy. Soc. New Zealand 79: 198. 1951.

= *Cylindrocarpon pineum* C. Booth, Mycol. Pap. 104: 26. 1966.

Type specimens. NEW ZEALAND. Bay of Plenty: Rotorua, Whakarewarewa, on bark of *Pinus radiata*, Sept 1949, G.B. Rawlings (Holotype PDD 7510, ex-type culture); Bay of Plenty, Rotorua, on *Pinus radiata*, coll. Margaret Dick; Epitype designated here BPI XXX = NZFS 1793, ex epitype culture A.R. 4324 = CBS 125153))

Mycelium visible on host. Perithecia globose to subglobose with smooth and shiny or slightly roughened surface, 400–800 μm high, 200–350 μm wide, solitary or gregarious in groups of 3–25, superficial or with base immersed in substratum on a minute stroma, not collapsed when dry, orange to sienna with ostiolar area often having a darker color

(bay) mainly in young perithecia, red to rose in 3% KOH, yellow in lactic acid, papillated. Cells at surface of perithecial wall lacking a definite outline appearing to be intertwined hyphae with lumina irregular in shape 2–2.5 μm, 2–4 μm thick. Perithecial wall 40–50 μm wide. Asci cylindrical, 100–130 × 8–9 μm, 8-spored, apex with a refractive ring. Ascospores ellipsoid to fusiform, 17–19 × 7–8 μm (mean 18 × 7.5 μm), symmetrically two-celled, sometimes with one side curved and one side flattened, not constricted at septum, spinulose, hyaline. Colonies on PDA 31 mm diam. after 12 d at 20 C, aerial mycelium floccose, white to lilac, producing purple pigment in media at temperatures ≤ 20 C, colony reverse also white to lilac. Conidia on SNA forming in hyaline, slimy droplets in aerial mycelium or on agar surface; pionnotes sometimes formed close to filter paper on SNA. Phialides borne apically on irregularly branching clusters of cells or directly from hyphae, cylindrical or slightly swollen (13.3–)15.1–22.3(–27.5) × (–3.1)3.4–4.3(–4.8) μm (mean 18.7 × 3.8 μm), with periclinal thickening and collarette. Macroconidia cylindrical or slightly fusiform, curved with round tips, 1–4-septate: 1-septate (22.8–)27.9–38.4(–44.1) × (3–)3.3–4.4(–4.9) μm (mean 33.1 × 3.8 μm), 2-septate (30.2–)36.7–45.4(–56.4) × (3.8–)4–5.2(–5.8) μm (mean 41 × 4.7 μm), 3-septate (34.6–)41.4–48.2(–60.6) × (3.5–)4.3–5.4(–6.2) μm (mean 46.3 × 4.9 μm), 4-septate (44–)47.9–61.7(–71.2) × (4.8–)5.2–6.4(–6.9) μm (mean 54.8 × 5.8 μm). No microconidia or chlamydospores formed in culture.

Habitat and distribution. Saprobic on decaying bark of *Pinus radiata*. This species has only been reported from New Zealand.

Additional specimens examined. NEW ZEALAND. Northland: on *Pinus radiata*, 10 Sep 2003, Margaret Dick NZFS 1069 (culture only, A.R. 4321 = CBS 134033)

Notes. This species is only known from New Zealand, however, the original author, Dingley (1951) described this species as occurring in New Zealand as well as Europe and North America. Here the name *T. pinea* is circumscribed to include species only found on *Pinus radiata* in New Zealand. Isolates of *Nectria*-like fungi on *Pinus* in other parts of the world probably constitute different species.

Thelonectria porphyria C. Salgado & Hirooka sp. nov.

Mycobank MB XXX

Figure 7 A–F.

Similar to *T. discophora*. Macroconidia 3–5-septate, known only from Japan.

Holotype. JAPAN. Kochi Prefecture, Tosa-cho, on bark of dead tree, 04 Aug 2004, Y. Hirooka TPP-h171-1 (BPI 882162, ex-type culture MAFF 241515).

Etymology. Refers to the purple coloration of the anamorph and pigment produced in culture conditions.

Mycelium not visible on host. Perithecia globose to subglobose with smooth and shiny or slightly roughened surface, 300–600 μm high, 200–350 μm wide, solitary or gregarious in groups of 20 or less, superficial or with base immersed in substratum on a minute stroma, not collapsed when dry, orange to sienna with ostiolar area of same color than rest of perithecium, red to rose in 3% KOH, yellow in lactic acid, papillated. Cells at surface of perithecial wall lacking a definite outline appearing to be intertwined hyphae with lumina irregular in shape 2–2.5 μm, 2–4 μm thick. Perithecial wall 25–40 μm wide. Asci cylindrical, (55–)69–89(–100) × 7–11 μm, 8-spored, apex with a refractive ring.

Ascospores ellipsoid to fusiform, (12.0–)12.8–14.7(–16.1) × (5–)5.7–6.9(–7.9) μm (mean 13.7 × 6.3 μm), symmetrically two-celled, sometimes with one side curved and one side flattened, not constricted at septum, spinulose, hyaline. Colonies on PDA 30–35 mm diam. (mean 33 mm) after 12 d at 20 C, aerial mycelium floccose, white to purple, producing purple to cinnamon pigment to media at temperatures ≤ 25 C, colony reverse also white to bay. Conidia on SNA forming in hyaline, slimy droplets in aerial mycelium or on agar surface; pionnotes sometimes formed close to filter paper on SNA. Phialides borne apically on irregularly branching clusters of cells or directly from hyphae, cylindrical or slightly swollen (11.4–)15.1–20.4(–25.1) × (–3.1)3.7–4.6(–5.2) μm (mean 17.7 × 4.1 μm), with periclinal thickening and collarette. Macroconidia cylindrical or slightly fusiform, curved with round tips, 3–5-septate: 3-septate (42.7–)47.9–59.2(–68.8) × (4.5–)5.4–6.6(–7.5) μm (mean 53.6 × 6 μm), 4-septate (44.3–)51.2–66.3(–79.3) × (4.5–)5.5–6.7(–7.5) μm (mean 58.7 × 6.1 μm), 5-septate (50.9–)61.8–77.6(–88.4) × (5–)5.7–6.9(–7.4) μm (mean 69.7 × 6.3 μm). No microconidia or chlamydospores are formed in culture.

Habitat and distribution. Saprobic on decaying bark of *Cryptomeria japonica* and other woody substrates. Found only in Japan.

Additional specimens examined. JAPAN. Kochi Prefecture, Tosakitakaido, Tosa-cho, on twigs of *Cryptomeria japonica*, 04 Aug 2003, Y. Hirooka TPP-h178-2 (BPI 882164, culture MAFF 241517); Miyagu Prefecture, Akiuootaki, Aki-cho, Taihaku-ku, on twigs of undetermined dead tree, 04 Aug 2004, Y. Hirooka TPP-h292-2 (BPI 882106, culture MAFF 241539).

Notes. See notes for *T. japonica*.

Thelonectria purpurea C. Salgado & P. Chaverri sp. nov.

Mycobank MB XXX

Figure 7 G–L.

Similar to *T. discophora*. Macroconidia 1–5-septate, known only from Central America (Costa Rica) and northern South America (Venezuela).

Holotype. COSTA RICA. Heredia Province, Braulio Carrillo National Park, Zurquí Street entrance, 10°03'N 84°01'W, 1734 m, on bark of undetermined twigs, 14 March 2010, C. Salgado-Salazar, C. Herrera, Y. Hirooka, A. Rossman, G.J. Samuels, P. Chaverri PC1060 (BPI 892689, ex-type culture G.J.S. 10-131 = CBS 134024).

Etymology. Refers to the purple coloration of the anamorph and pigment produced in culture conditions.

Mycelium visible on host. Perithecia globose to subglobose with smooth and shiny or slightly roughened surface, 350–7400 μm high, 210–350 μm wide, solitary or gregarious in groups of up to 20, superficial or with base immersed in substratum on a minute stroma, not collapsed when dry, sienna with ostiolar area often having a darker color (umber) mainly in mature perithecia, red to rose in 3% KOH, yellow in lactic acid, papillated. Cells at surface of perithecial wall lacking a definite outline appearing to be intertwined hyphae with lumina irregular in shape 2–2.5 μm, 2–4 μm thick. Perithecial wall 43–52 μm wide. Asci cylindrical, (55–)68–82(–98) × 7–10 μm, 8-spored, apex with a refractive ring. Ascospores ellipsoid to fusiform, (10.8–)12–14.1(–15.4) × (3.8–)4.8–6.1(–6.6) μm (mean 13.0 × 5.5 μm), symmetrically two-celled, sometimes with one side curved and one side flattened, not constricted at septum, spinulose, hyaline. Colonies on

PDA 33–38 mm diam. (mean 35 mm) after 12 d at 20 C, aerial mycelium floccose, white to purple or saffron, producing purple pigment in media at temperatures ≤ 25 C, colony reverse white to purple or saffron. Conidia on SNA forming in hyaline, slimy droplets in aerial mycelium or on agar surface; pionnotes sometimes formed close to filter paper on SNA. Phialides borne apically on irregularly branching clusters of cells or directly from hyphae, cylindrical or slightly swollen (11.4–)15.9–22.8(–30.6) × (–3.8)3.8–4.7(–5.4) μm (mean 19.4 × 4.3 μm), with periclinal thickening and collarette. Macroconidia cylindrical or slightly fusiform, curved of round tips, 1–5-septate: 1-septate (21.1–)22–44.6(–67) × (4.3–)4.6–6.2(–7.1) μm (mean 32.6 × 5.4 μm), 2-septate (31.9–)32.8–46.2(–47.9) × (5.2–)5.3–5.7(–5.8) μm (mean 39.5 × 5.5 μm), 3-septate (4.2–)47.3–60.7(–69) × (4.7–)5.4–6.4(–7.3) μm (mean 54.5 × 5.9 μm), 4-septate (49.9–)57.6–67.4(–76.4) × (4.5–)5.4–6.7(–7.6) μm (mean 62.5. × 6.1 μm), 5-septate (57.7–)62.1–71.9(–81.2) × (5–)5.7–7.0(–7.7) μm (mean 67 × 6.4 μm). No microconidia or chlamydospores formed in culture.

Habitat and distribution. Saprobic on decaying bark of woody substrates. Known from Venezuela and Costa Rica, possibly widely distributed in the Neotropics.

Additional specimens examined. COSTA RICA. Heredia Province, Braulio Carrillo National Park, Zurquí Street entrance, 10°03’N 84°01’W, 1734 m, on bark of undetermined dead tree, 14 March 2010, C. Salgado-Salazar, C. Herrera, Y. Hirooka, A. Rossman, G.J. Samuels, P. Chaverri PC1081 (BPI 882335, culture G.J.S. 10-145 = CBS 134025). VENEZUELA. Aragua State, Henry Pittier National Park, ca. 20 km above Maracay, on Maracay-Choroni road, on wood of unidentified dead tree, 13 Jul 1971, K.P. Dumont, J.H. Haines, G.J. Samuels (NY Dumont-VE 2173, culture C.T.R. 71-281 = CBS 112458); Merida State: Sierra Nevada National Park, above Tabay, Qda. Coromoto, La

Mucuy, 08°36’N 71°02’W, ca. 2000 m, on palm fruit, G.J. Samuels et. al. G.J.S. 7244A (BPI 1109900, culture G.J.S. 90-155 = CBS 123966)

Notes. See notes for *T. phoenicea*.

Thelonectria purpurescens C. Salgado & P. Chaverri sp. nov.

Mycobank MBXXX

Figure 8 A–F.

Similar to *T. discophora*. Macroconidia 3–6-septate, collected in the sexual state, saprobic, from Puerto Rico, Venezuela and Japan.

Holotype. PUERTO RICO. Caribbean National Forest, Luquillo Mountains, Río Grande, trail to El Toro from rt 186, 650–750 m, on bark of unidentified recently dead tree, 24 Feb 1996, G.J. Samuels, H.-J Schroers, D.J. Lodge (BPI 745542, culture G.J.S. 96-23 = IMI 370947).

Etymology. Refers to the purple coloration of the anamorph in culture conditions.

Mycelium not visible on host. Perithecia globose to subglobose with smooth and shiny or slightly roughened surface, 300–600 μm high, 200–350 μm wide, solitary or gregarious in groups of 20 or less, superficial or with base immersed in substratum on a minute stroma, not collapsed when dry, peach to sienna with ostiolar area darker than rest of perithecium (bay), red to rose in 3% KOH, yellow in lactic acid, papillated. Cells at surface of perithecial wall lacking a definite outline appearing to be intertwined hyphae with lumina irregular in shape 2–2.5 μm, 2–4 μm thick. Perithecial wall 25–40 μm wide. Asci cylindrical, (56–)67–86(–98) × 7–12 μm, 8-spored, apex with a refractive ring. Ascospores ellipsoid to fusiform, (10.3–)11.1–12.4(–13.6) × (4.0–)4.7–5.6(–13.6) μm

(mean 11.8 × 5.2 μm), symmetrically two-celled, sometimes with one side curved and one side flattened, not constricted at septum, spinulose, hyaline. Colonies on PDA 31–34 mm diam. (mean 32 mm) after 12 d at 20 C, aerial mycelium floccose, white to purple, not producing pigment in media, colony reverse white to purple. Conidia on SNA forming in hyaline, slimy droplets in aerial mycelium or on agar surface; pionnotes sometimes formed close to filter paper on SNA agar. Phialides borne apically on irregularly branching clusters of cells or directly from hyphae, cylindrical or slightly swollen (11.8–)14.9–19.5(–22.8) × (–3.4)4–4.9(–5.8) μm (mean 17.2 × 4.4 μm), with periclinal thickening and collarette. Macroconidia cylindrical or slightly fusiform, curved with round tips, 3–5- septate: 3-septate (40–)45.5–66.4(–69.1) × (4.8–)5.5–7.6(–9) μm (mean 55.9 × 6.5 μm), 4-septate (53.7–)62.6–76(–82.2) × (5.2–)5.9–7.8(–9.2) μm (mean 69.3 × 6.8 μm), 5-septate (66.2–)68.1–88.4(–107.8) × (5.2–)6.2–7.9(–9.2) μm (mean 78.2 × 7 μm). No microconidia or chlamydospores formed in culture.

Habitat and distribution. Saprobic on several woody substrates. Found at the type locality in Puerto Rico, Venezuela and Japan; possibly widely distributed in the tropics and subtropics around the world.

Additional specimens examined. JAPAN. Tokyo, Sakaigatake, Hahajima, Ogasawara-mura, on bark of unidentified dead tree, 22 Jun 2005, Y. Hirooka TPP-h488-2 (BPI 881951, culture MAFF 241564). VENEZUELA. Bolivar State, The Gran Sabana National Park, 1139 m, on wood of unidentified dead tree, 29 Jun 2009, C. Salgado-Salazar, Y. Hirooka, YH09-124 (BPI 882679, culture G.J.S. 09-1327 = CBS 134022).

Notes. This species is similar to *T. blattea*. *Thelonectria blattea* has been collected only in the anamorphic state on soil while *T. purpurescens* has been collected in the teleomorphic

state as a saprobe of decaying plant material.

Thelonectria rubi (Osterw.) C. Salgado & P. Chaverri stat. nov. et comb. nov.

Mycobank MBXXX

Figure 8 G–L.

≡ *Nectria rubi* Osterw., Ber. Deutsch. Bot. Ges. 29: 620. 1911.

≡ *Hypomyces rubi* (Ostew.) Wollenw., Phytopathology 3: 224. 1913.

= *Neonectria discophora* var. *rubi* (Osterw.) Brayford & Samuels, Mycologia 96: 572. 2004.

= Cyl*indrocarpon ianthothele* var. *ianthothele* Wollenw., Ann. Mycol. 15: 56. 1917.

= *Cylindrocarpon ianthothele* Wollenw., Annls mycol. 15: 56. 1917.

Holotype. SWITZERLAND. Horgen District: Wadenswill Locality, on *Rubus idaeus* roots, 1911, A. Osterwalder (only ex-type culture CBS 113.12 = IMI 113918).

Mycelium not visible on host. Perithecia globose to subglobose, smooth, 300–500 μm, solitary or gregarious in groups up to 5 growing on poorly developed stroma, not collapsed when dry, bright red to umber with ostiolar area the same color than rest of perithecium, red to rose in 3% KOH, yellow in lactic acid, papillated. Perithecial wall 80–100 μm. Asci cylindrical to clavate 80–120 x 5-6 μm, 8-spored, ascospores ellipsoid, 1-septate (11.5–)12–16(–23) × (4.5–)5.5–6.5(–8) μm (mean 14 × 6 μm), not constricted at septum, becoming pale yellow when mature, spinulose. Colonies on PDA 23–29 mm diam. (mean 24 mm) after 12 d at 20 C, aerial mycelium floccose, white to purple, no pigment produced in media, colony reverse white to purple. Conidia on SNA forming in hyaline, slimy droplets in aerial mycelium or on agar surface; pionnotes sometimes

formed close to filter paper on SNA. Phialides borne apically on irregularly branching clusters of cells or directly from hyphae, cylindrical or slightly swollen (15.1–)16.8–23.3(–28.8) × (–3.2)3.8–4.8(–5.5) μm (mean 20 × 4.3 μm), with periclinal thickening and collarette. Macroconidia cylindrical or curved with round tips, with one end thicker than other, 1–6-septate (except 2-septate): 1-septate (10–)10.1–12.9(–14.2) × (4.2–)4.4–5.6(–5.7) μm (mean 11.5 × 5 μm), 3-septate (37.9–)47.1–61.8(–68.6) × (5.1–)5.8–(–7) μm (mean 54.4 × 6.4 μm), 4-septate (42–)56.5–67.2(–74.2) × (5.5–)6–7.2(–7.7) μm (mean 63 × 6.6 μm), 5-septate (45.3–)56.2–69.7(–84) × (5.1–)6–7.2(–7.7) μm (mean 60.3 × 6.3 μm), 6-septate (45.9–)46–77.3(–79.1) × (4.9–)5.8–6.9(–8) μm (mean 60.3 × 6.3 μm). Microconidia produced in culture, cylindrical with round ends, (7.3–)7.9–10(–11.5) × (4.2–)4.6–5.5(–6.3) μm (mean 9 × 5 μm). Chlamydospores formed in culture, 4 × 5 μm.

Habitat and distribution. On roots of diseased *Rubus* species. Found in the type locality (Wadenswill, Switerland); also Europe and one report from Venezuela (Cedeño et al. 2004).

Additional cultures examined. SCOTLAND. Locality unknown, 1929, H.M. Wollenweber (CBS 241.29 = IMI 113919). UNITED KINGDOM. England, location unknown, R.M. Nattrass (culture CBS 177.27 = IMI 113917).

Notes. Brayford et al. (2004) observed that perithecia of *T. rubi* were morphologically and anatomically indistinguishable from those of *T. discophora*. However, data suggest that true *T. rubi* only grows associated with roots and crowns of *Rubus* species. Although the type locality is Wadenswill, Switzerland, it is possible to find this species wherever *Rubus* species are known.

Thelonectria tyrus C. Salgado & P. Chaverri sp. nov.

Mycobank MBXXX

Figure 9 G–L.

Similar to *T. discophora*. Macroconidia 3–5-septate, only found in the eastern United States.

Holotype. UNITED STATES. North Carolina: Macon County, Ellicott Rock Trail, off of Bull Pen Road, 35°02'N 83°08'W, 915 m, on bark of living *Quercus* sp., G.J. Samuels, A.Y. Rossman, Y. Doi (BPI 1107126, ex-type culture G.J.S. 90-46 = CBS 134029).

Etymology. Refers to the purple coloration of the anamorph and pigment produced in culture conditions.

Mycelium not visible on host. Perithecia globose to subglobose with smooth and shiny or slightly roughened surface, 300–600 μm high, 200–400 μm wide, solitary or gregarious in groups of 20 or less, superficial or with base immersed in substratum, not collapsed when dry, peach to sienna with ostiolar area same color as rest of perithecium, red to rose in 3% KOH, yellow in lactic acid, papillated. Cells at surface of perithecial wall lacking a definite outline, appearing to be intertwined hyphae with lumina irregular in shape 2–2.5 μm, 2–4 μm thick. Perithecial wall 35–42 μm wide. Asci cylindrical, (57–)60–81(–100) × 7–12 μm, 8-spored, apex with a refractive ring. Ascospores ellipsoid to fusiform, (12–)13–14(–15) × (5.5–)6–6.5(–7) μm (mean 13.8 × 6.2 μm), symmetrically two-celled, sometimes with one side curved and one side flattened, not constricted at septum, spinulose, hyaline. Colonies on PDA 21–27 mm diam. (mean 24 mm) after 12 d at 20 C, aerial mycelium floccose, white to purple, producing purple pigment in media at temperatures ≤ 30 C, colony reverse white to bay. Conidia on SNA forming in hyaline,

slimy droplets in aerial mycelium or on agar surface; pionnotes sometimes formed close to filter paper on SNA. Phialides borne apically on irregularly branching clusters of cells or directly from hyphae, cylindrical or slightly swollen (13.3–)15.8–21.2(–24.2) × (–3.2)3.6–4.5(–4.9) μm (mean 18.5 × 4 μm), with periclinal thickening and collarette. Macroconidia cylindrical or slightly fusiform, curved with round tips, 2–5-septate: 2-septate (35–)34.7–36.4(–36.7) × (5.6–)5.6–5.8(–5.9) μm (mean 35.7 × 5.7 μm), 3-septate (41.9–)47.6–56.2(–60.9) × (4.9–)5.6–6.5(–7) μm (mean 51.9 × 6.1 μm), 4-septate (50.9–)53.9–60.7(–65) × (5.6–)6.1–6.9(–7.1) μm (mean 57.3 × 6.5 μm), 5-septate (57–)59.8–65.5(–67.4) × (6.5–)6.6–7.5(–8) μm (mean 62.7 × 7.1 μm). No microconidia or chlamydospores formed in culture.

Habitat and distribution. Saprobic on decaying bark of woody substrates including *Quercus* sp. and *Fagus grandifolia*. Found in Connecticut and North Carolina, possibly in other states in eastern United States.

Additional specimens examined. UNITED STATES. Connecticut: New Haven, West Rock Ridge State Park, on bark of dead *Fagus grandifolia*, Oct 2007, R. Marra (BPI 878945, culture A.R. 4499 = CBS 125172).

Notes. This species is similar to *T. conchyliata*, *T. ianthina* and *T. porphyria* in that they produce macroconidia 3–5-septate. However, only *T. tyrus* is found in the eastern United States.

Thelonectria violaria C. Salgado & R.M. Sánchez sp. nov.

Mycobank MBXXX

Figure 9 A–F.

Similar to *T. discophora*. Macroconidia 1–3septate only, no microconidia produced in culture.

Holotype. ARGENTINA. Tucumán Province: road to Catamarca, Camino Las Lenguas, near to Río Cochuna, 400 m, on bark of a rotting fallen tree, C. Salgado-Salazar, A.Y. Rossman, A. Romero (BPI 892690, ex-type culture A.R. 4766 = CBS 134035).

Etymology. Refers to the purple coloration of the anamorph in culture conditions.

Mycelium not visible on host. Perithecia globose to subglobose with smooth and shiny or slightly roughened surface, 300–600 μm high, 200–350 μm wide, solitary or gregarious in groups of 20 or less, superficial or with base immersed in substratum, not collapsed when dry, sienna to chestnut with the ostiolar area darker than the rest of perithecium (blood color), red to rose in 3% KOH, yellow in lactic acid, papillated. Cells at surface of perithecial wall lacking a definite outline appearing to be intertwined hyphae with lumina irregular in shape 2–2.5 μm, 2–4 μm thick. Perithecial wall 35–45 μm wide. Asci cylindrical, (57–)68–86(–98) × 7–11 μm, 8-spored, apex with a refractive ring. Ascospores ellipsoid to fusiform, (9.9–)10.5–12.8(–14.0) × (4.1–)4.6–6.0(–7.0) μm (mean 11.7 × 5.3 μm), symmetrically two-celled, sometimes with one side curved and one side flattened, not constricted at septum, spinulose, hyaline. Colonies on PDA 30–35 mm diam. (mean 33 mm) after 12 d at 20 C, aerial mycelium floccose, white to mauve, producing purple to cinnamon pigment in media at temperatures < 20 C colony, reverse white to bay. Conidia on SNA forming in hyaline, slimy droplets in aerial mycelium or on agar surface; pionnotes sometimes formed close to filter paper on SNA. Phialides borne apically on irregularly branching clusters of cells or directly from hyphae, cylindrical or slightly swollen (13.2–)14.3–20.1(–24.5) × (–3.2)3.8–4.8(–5.3) μm (mean

17.2 × 4.3 μm), with periclinal thickening and collarette. Macroconidia cylindrical or slightly fusiform, curved with round tips, 1–3-septate: 1-septate (31.4–)38.9–47.7(–49) × (3.4–)4.4–5.6(–6) μm (mean 43.3 × 5 μm), 2-septate (48.1–)48–54.3(–56.9) × (5–)5.1–5.5(–5.7) μm (mean 51.1 × 5.3 μm), 3-septate (36.7–)47.6–57.8(–68.4) × (4.6–)4.9–5.9(–7) μm (mean 52.7 × 5.4 μm). No microconidia or chlamydospores formed in culture.

Habitat and distribution. Saprobic on decaying bark of several woody substrates. Found in the type locality (Tucumán, Argentina) and Venezuela; possibly distributed widely in tropical and subtropical regions of South America.

Additional specimens examined. VENEZUELA. 13 km NE of Colonia Tovar on road between Colonia Tovar and El Tigre, Dto. Fed., on bark of unidentified tree, 19 Jul 1972, K.P Dumont, R.F. Cain, G.J. Samuels, B. Manara (NY Dumont-VE 6503, culture C.T.R. 72-188 = CBS 134040).

Notes. This species is similar to *T. asiatica* and *T. rubi* in that 1–3-septate macroconidia are produced in culture. However, *T. violaria* can be distinguished, as it does not produce microconidia, and macroconidia with septations >4 are not observed.

Possible additional species

Thelonectria beijingensis Z.Q. Zeng, J. Luo & W.Y. Zhuang

Mycobank MB564936

See Zeng and Zhuang (2013) for description and illustrations.

Thelonectria yunnanica Z.Q. Zeng & W.Y. Zhuang

Mycobank MB564937.

See Zeng and Zhuang (2013) for description and illustrations.

DISCUSSION

Historically, specimens with similar teleomorphic and anamorphic morphology to that of the type species were labeled *Thelonectria discophora* sensu lato. Because this species was found in many regions around the world, it was assumed to have a cosmopolitan distribution. Our phylogenetic and morphological analyses of a significant number of specimens and cultures of *T. discophora* revealed at least sixteen previously unrecognized cryptic species. Using the genealogical concordance phylogenetic species concept principles (Dettman et al. 2003), we have formally described those sixteen cryptic species as separate and independent entities. The genetic distances between putative species mostly exceeded standard values of genetic distance (0.01–0.03) used to delimit operational taxonomic units (OTU), revealing them as independent entities (Salgado-Salazar et al. in press). This indicates a > 16-fold increase in the species diversity in the genus *Thelonectria,* a genus recently established for nectriaceous fungi typically with a broad mammiform (nipple-like) perithecial apex.

Our phylogenetic analyses also detected nine single isolate lineages or singletons. These lineages, together with those found by Zeng and Zhuang (2013), *T. beijingensis* and *T. yunnanica* (Online Resource 2), constitute additional distinctive evolutionary entities that make up a considerable portion of the diversity of species in this complex. In systematics, no consensus exists on how singleton lineages should be treated (Seifert and Rossman, 2011). In phylogenetic analyses, singleton lineages are located in branches with unknown support (i.e. bootstrap, posterior probability), as a branch should have at least two tips to obtain statistic support. Even thought *T. beijingensis* and *T. yunnanica* were found to have affinities to the species here described, their lack of agreement in the

morphological characters of the anamorphic states prevents us from reaching a definite conclusion. Further increase in taxon and molecular data sampling would determine if the singleton lineages here described and those by Zeng and Zhuang (2013) represent different species and if they should be formally described. In spite of this, many of these singletons likely constitute rare taxa, which highlight even more the importance of preserving the habitat where they can be found (Dahlberg and Mueller 2011).

Species in the *T. discophora* complex appear not only to be consistent with allopatric but also sympatric speciation (Giraud et al. 2008). The *T. discophora* complex contains species that correlate with geographic origin, that is, the putative species group isolates from the same or close-by regions. However, this complex also includes species with isolates from distant geographic locations. Since no definite explanation can be given for this phenomenon, it probably means that members of these species have not been sampled thoroughly and by adding more samples, a better geographic structure might be observed. According to our data, ten species were found only in temperate regions such as the United States, Europe, Asia and New Zealand. Fewer species were found in tropical regions. However, this could be a result of the lower taxon sampling as for example, collections from Venezuela represent at least four species. Thus, one may assume that *T. discophora*-like species can be found in tropical and temperate regions equally. Due to their small size and ecological preferences, these fungi have only been collected serendipitously translating into limited taxon sampling. As is the case with poorly studied organisms, increasing their collection can further support assumptions about the geographic range of the putative species or about their center of origin. The role of human-mediated movement of species of *T. discophora*, contributing to the actual

geographic distribution of species, cannot be discarded. However, because these species do not include invasive or pathogens of commercial or forest plants, their presence can be overlooked and movement difficult to track.

The results from our research support previous studies with other microorganisms, including fungi, suggesting that there are very few truly cosmopolitan species (Pringle et al. 2005; Taylor et al. 2006; Carriconde et al. 2008; Salgado-Salazar et al. 2013 in press). Because *T. discophora* is a species complex that includes various species with limited geographic distribution and ecology, we hypothesize that the lack of mechanisms for long-distance spore dispersal could be affecting their distribution. Only two species in this group have been found to produce microconidia, which could be easily carried by wind currents. However, they are also found to be geographically restricted. The majority of *T. discophora* species have asexual spores (macroconidia) that are colorless and longer than 30 μm, sometimes reaching 100 μm; their sexual spores (ascospores) are also colorless or non-melanized. More importantly, both sexual and asexual spores do not have shapes that could improve dispersal, possibly landing after traveling short distances (Roper et al. 2008; Roper et al. 2010). These characteristics together may limit considerably the range of dispersal of these fungi, and consequently populations undergo independent evolutionary trajectories and ultimately, species divergence. The marked genetic structure observed among the species in *T. discophora* likely reflects the interplay between their poor dispersal capabilities and the restrictions to gene flow, either imposed by geographical or reproductive barriers.

With the exception of T. *rubi*, all the species in the *T. discophora* complex are saprobic on decaying plant material or soil. Species occurring in unconnected, but similar

habitats and under similar selection pressures often display strikingly comparable morphology, behavior and life history and, without a phylogeny, it is often difficult to separate whether similar traits are a result of *in situ* diversification or independent colonization. Based on the results obtained in this study we determined that shared morphological and ecological characters of these species represent a case of convergence, and are the result of their similar habitat and selection pressures. As other species in the genus *Thelonectria*, such as *T. coronata*, *T. jungneri*, *T. lucida* and *T. veuillotiana*, can also be found in the same habitat as *T. discophora* species, it is possible that the ability of these species to produce extracellular secondary metabolites, such as the characteristic purple pigment, could represent an adaptive advantage for the species. Studies on the nature of pigments produced by these species are lacking, and further investigations will help elucidate their role in adaptation.

Since many historical species shared morphological characters with *T. discophora*, several monographic accounts regarded these species as synonyms. With this study, we revised the taxonomic synonyms and updated the current status of the names, using them when appropriate. For example, *Nectria mammoidea*, *N. pinea* and *Neonectria discophora* var. *rubi*, were redefined and epytypified. Anamorphic names in the case of *Thelonectria* are no longer used, consequently the names *Cylindrocarpon ianthothele* and *C. ianthothele* var. *ianthothele* are synonyms of *Thelonectria rubi*, *C. ianthothele* var. *majus* is synonym of *T. mammoidea*, and *C. pineum* is synonym of *T. pinea*. According to several taxonomic revisions (Booth 1966; Samuels et al. 1990; Brayford et al. 2004; Chaverri et al. 2011) no *Cylindrocarpon* name was ever correctly assigned to *T. discophora*, as all *Cylindrocarpon ianthothele* names were based on the

conidial state of *T. mammoidea* (=*Nectria mammoidea*). One isolate of *Nectria tasmanica* was checked during this study (ICMP 5290). However, it was found to produce an anamorph with morphology similar to *Fusarium* and consequently it needs further revision to determine if it is related to the *T. discophora* species complex.

In conclusion, we demonstrate that a combination of both morphological and phylogenetic analyses is effective for the clarification of taxonomic status of species, especially those that have been difficult to resolve using morphological characters alone. The unlinked nuclear markers and phylogenetic analyses enabled us to resolve the species level relationships in this group, despite the presence of recently diverged clades. Our results confirm high lineage diversity in this group of fungi, and highlight the importance of a comprehensive delimitation of species within highly diverse groups to better understand the factors that drive the diversification of biota, and for correctly identifying targets for conservation.

KEY TO THE SPECIES

1a. Micro- and macroconidia produced on SNA……. 2a

1b. Only macroconidia produced on SNA……... 3a

2a. Found causing a distinctive basal canker in *Rubus* sp. in Europe, including Switzerland (type locality) and United Kingdom.…… *T. rubi*

2b. Not found causing canker in *Rubus* sp., saprobe distributed in China and Japan (type locality), macroconidia 1–3-septate…….. *T. asiatica*

3a. Macroconidia 1–3-septate, found in Argentina (type locality) and Venezuela……. *T. violaria*

3b. Macroconidia 1–4- or 1–5- septate, known from temperate and tropical

regions……..… 4a

4a. Macroconidia 1–4- septate, known from New Zealand (type locality), saprobe, restricted to plant material of *Pinus radiata*……...……. *T. pinea*

4b. Macroconidia 1–5-septate, including isolates from New Zealand, not on *P. radiata*…….…… 5a

5a. Macroconidia 1–5-septate, including isolates from New Zealand (type locality) on decaying plant material different than *P. radiata*, including *Quercus* sp. …...*T. brayfordii*

5b. Macroconidia 1–5-septate, with isolates known from New Zealand and elsewhere..6a

6a. Microconidia 1–5-septate, with isolates from New Zealand, United Kingdom and Switzerland (type locality)…….. *T. mammoidea*

6b. Macroconidia 1–5-septate, with isolates from Central and South America and Australasia……... 7a

7a. Macroconidia 1–5-septate, with isolates from Central America (Costa Rica, type locality) and north of South America (Venezuela) only…….*T. purpurea*

7b. Macroconidia 1–5-septate, with isolates not from Central and South America…… 8a

8a. Macroconidia 1–5-septate, with isolates from Australia, Indonesia and Taiwan …… *T. phoenicea*

8b. Macroconidia 3–6-septate……. ….. 9a

9a. Macroconidia 3–6-septate, known from Japan (type locality)……...*T. japonica*

9b. Macroconidia 3–6-septate, found other than Japan……... 10a

10a. Macroconidia 3–6-septate, collected as the asexual state in soil in Germany (type locality) and The Netherlands……. *T. blattea*

10b. Macroconidia 3–6-septate, collected as the sexual state on bark of decaying plant

material…….. 11a

11a. Macroconidia 3–6-septate, collected as the sexual state, known from Japan, Puerto Rico (type locality) and Venezuela……. *T. purpurescens*

11b. Macroconidia 3–5 septate, from temperate regions ……12a

12a. Macroconidia 3–5-septate, including isolates from Chile (type locality) and Scotland…… *T. discophora*

12b. Macroconidia 3–5 septate, not including isolates from Chile nor Scotland…..13a

13a. Macroconidia 3–5 septate, only known from Japan (type locality)…….. *T. porphyria*

13b. Macroconidia 3–5 septate, known from regions other than Japan……..... 14a

14a. Macroconidia 3–5-septate, known from eastern United States…….. *T. tyrus*

14b. Macroconidia 3–5-septate, known from other than eastern United States…… 15a

15a. Macroconidia 3–5-septate, average colony growth on PDA at 30 C > 13 mm……..*T. conchyliata*

15b. Macroconidia 3–5-septate, average colony growth on PDA at 30C < 13 mm…….. *T. ianthina*

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FIGURE LEGENDS

Figure 1. Majority rule Bayesian phylogram showing relationships among isolates of

Thelonectria discophora-like species based on the concatenated analysis of six loci. Thick branches indicate Bayesian posterior probabilities >0.95 and ML bootstrap >70%. No thick branches indicate branch was not recovered/supported. "*" indicates where the *T. discophora* species complex starts. Underlined isolates indicate type specimen. *Thelonectria lucida*, *T. trachosa* and *T. westlandica* were used as outgroups.

Figure 2. A–F. *Thelonectria discophora* s. str. G–M. *Thelonectria asiatica*. A. T. discophora s. str. perithecia (A.R. 4742 = BPI 892687). B, C. Asci and ascospores in KOH and cotton blue (G.J.S. 92–48 = BPI 802901). D. Macroconidia on SNA (G.J.S. 92–48 = CBS 134031). E. Colony on PDA (A.R. 4742 = CBS 134034). F. Colony reverse on PDA (A.R. 4742 = CBS 134034). G. *T. asiatica* perithecia (MAFF 241576 = BPI 881963). H, I. Asci and ascospores in KOH and cotton blue (MAFF 241576 = BPI 881963). J, K. Conidiophores, macroconidia and microconidia on SNA (G.J.S. 88–84 = IMI 348190). L. Colony on PDA (MAFF 241576). M. Colony reverse on PDA (MAFF241576). Bars: A, G = 500 μm; B–D, H–K = 50 μm.

Figure 3. A–F. *Thelonectria blattea*. G–L. *Thelonectria brayfordii*. A–B. *T. blattea* conidiophores and macroconidia on SNA (CBS 14277). C. Colony on PDA (CBS 14277). D. Colony reverse on PDA (CBS 14277). E. Colony on PDA (CBS 95268) F. Colony reverse on PDA (CBS 95268). G–H. *T. brayfordii* macroconidia on SNA (ICMP 14105). I. Colony on PDA (ICMP 14015). J. Colony reverse on PDA (ICMP 14105). K. Colony on PDA (IMI 384045) L. Colony reverse on PDA (IMI 384045). Bars: A–B, G–H = 50 μm.

Figure 4. A–G. *Thelonectria conchyliata*. H–N. *Thelonectria ianthina*. A. *T. conchyliata* perithecia (G.J.S. 89–57 = NY Samuels 6269A). B, C. Asci and ascospores in KOH and cotton blue (G.J.S. 87–49 = BPI 744725). D–E. Conidiophores and macroconidia on SNA (G.J.S. 89–57 = CBS 112459). F. Colony on PDA (G.J.S. 87–49 = CBS 112461). G. Colony reverse on PDA (G.J.S. 87–49 = CBS 112461). H. *T. ianthina* perithecia (G.J.S. 10-118 = BPI 892691). I–J. Asci and ascospores in KOH and cotton blue (Guu 92122107 = BPI 892688). K–L. Conidiophores and macroconidia on SNA (G.J.S. 10–118 = CBS 134023). M. Colony on PDA (G.J.S. 10–118 = CBS 134023). N. Colony reverse on PDA (G.J.S. 10–118 = CBS 134023). Bars: A, H = 500 μm; B–E, I–L = 50 μm.

Figure 5. A–F. *Thelonectria japonica*. G–L. *Thelonectria mammoidea*. A. *T. japonica* perithecia (MAFF 241524 = BPI 882092). B, C. Asci and ascospores in KOH and cotton blue (MAFF 241524 = BPI 882092). D. Conidiophores and macroconidia on SNA (MAFF 241554). E. Colony on PDA (MAFF 241543). F. Colony reverse on PDA (MAFF 241543). G. *T. mammoidea* perithecia (G.J.S. 83–206 = PDD 46410). H, I. Asci and ascospores in KOH and cotton blue (G.J.S. 83–206 = PDD 46410). J. Conidiophores and macroconidia on SNA (G.J.S. 86–206 = IMI 326258). K. Colony on PDA (IMI 69361). L. Colony reverse on PDA (IMI 69361). Bars: A, G = 500 μm; B–D, H–J = 50 μm.

Figure 6. A–F. *Thelonectria phoenicea*. G–L. *Thelonectria pinea*. A. *T. phoenicea* perithecia (Guu 94031007 = BPI 892685). B, C. Asci and ascospores in KOH and cotton

blue (Guu 94031007 = BPI 892685). D. Conidiophores and macroconidia on SNA (Guu 94031007 = CBS 134039). E. Colony on PDA (Guu 94031007 = CBS 134039). F. Colony reverse on PDA (Guu 94031007 = CBS 134039). G–H. *T. pinea* conidiophores and macroconidia perithecia (A.R. 4321 = CBS 134033). I. Colony on PDA (A.R. 4321 = CBS 134033). J. Colony reverse on PDA (A.R. 4321 = CBS 134033). K. Colony on PDA (A.R. 4324 = CBS 125153). L. Colony on PDA (A.R. 4324 = CBS 125153). Bars: A = 500 μm; B–D, G–H = 50 μm.

Figure 7. A–F. *Thelonectria porphyria*. G–L. *Thelonectria purpurea*. A. *T. porphyria* perithecia (MAFF 241515 = BPI 882162). B, C. Asci and ascospores in KOH and cotton blue (MAFF 241515 = BPI 882162). D. Macroconidia on SNA (MAFF 241539). E. Colony on PDA (MAFF 241517). F. Colony reverse on PDA (MAFF 241517). G. *T. purpurea* perithecia (G.J.S. 10–131 = BPI 892689). H. Asci and ascospores in KOH (G.J.S. 10–131 = BPI 892689). I, J. Conidiophores and macroconidia on SNA (G.J.S. 90–155 = CBS 123966). K. Colony on PDA (G.J.S. 10–145 = CBS 134025). L. Colony reverse on PDA (G.J.S. 10–145 = CBS 134025). Bars: A, G = 500 μm; B–D, H–J = 50 μm.

Figure 8. A–F. *Thelonectria purpurescens*. G–L. *Thelonectria rubi*. A. *T. purpurescens* perithecia (G.J.S. 96–23 = BPI 745542). B. Ascospores in KOH (G.J.S. 96–23 = BPI 745542). C–D. Conidiophores and macroconidia on SNA (MAFF 241564). E. Colony on PDA (MAFF 241564). F. Colony reverse on PDA (MAFF 241564). G. *T. rubi* chlamydospores on SNA (CBS 11312). H–I. Conidiophores and macroconidia on SNA

(CBS 11312). J. Chlamydospores forming on macroconidia on SNA (CBS 17727). K. Colony on PDA (CBS 11312). L. Colony reverse on PDA (CBS 11312). Bars: A = 500 μm; B–D, G–J = 50 μm.

Figure 9. A–F. *Thelonectria tyrus*. G–L. *Thelonectria violaria*. A. *T. tyrus* pionnotes on SNA (G.J.S. 90–46 = CBS 134029). B–D. Conidiophores and macroconidia (G.J.S. 90–46 = CBS 134029). E. Colony on PDA (G.J.S. 90–46 = CBS 134029). F. Colony reverse on PDA (G.J.S. 90–46 = CBS 134029). G. *T. violaria* perithecia (A.R. 4766 = BPI 892690). H–I. Asci and ascospores in KOH (A.R. 4766 = BPI 892690). J. Conidiophores and macroconidia on SNA (A.R. 4766 = CBS 134035). K. Colony on PDA (C.T.R. 72–188 = CBS 134040). L. Colony reverse on PDA (C.T.R. 72–188 = CBS 134040). Bars: A = 250 μm; B–D, H–J = 50 μm; G = 500 μm.

Online Resource 2. Majority rule Bayesian phylogram showing relationships among isolates of *T. discophora*-like and *T. beijingensis* and *T. yunnanica* species based on the concatenated analysis of ITS and *tub* loci. Thick branches indicate Bayesian posterior probabilities >0.95 and ML bootstrap >70%. No thick branches indicate branch was not recovered/supported.

Online Resource 3. Average colony growth of *T. discophora* species complex under different temperatures. Bar indicates 95% confidence interval.

Table 1. List of molecular markers and descriptive statistics for the six loci used in this study.

Locus	Substitution model	Aligned length	Variable sites (%)	Parsimony informative sites (%)	%GC	Primers	Reference
act	GTR + I + G	550	20 (3.6)	60 (10.9)	56.6	F 5'TGGCACCACACCTTCTACAATGA3' R 5'TCCTCCGCTTATTGATATGC3'	Samuels *et al*. 2006
ITS	TPM2uf + I + G	723	24 (3.3)	107 (14.8)	55.4	F 5'GGAAGTAAAAGTCGTAACAAGG3' R 5'TCCTCCGCTTATTGATATGC3'	White *et al*. 1990
LSU	TrN + I + G	808	7 (0.8)	53 (6.5)	53.7	F 5'ACCCGCTGAACTTAAGC3' R 5'TCCTGAGGGAAACTTCG3'	Vilgalys n.d.
tef	TPM3uf + I + G	955	49 (5.1)	194 (20.3)	55.7	F 5'CATCGAGAAGTTCGAGAAGG3' R 5'ACHGTRCCRATACCACCRAT3'	Carbone & Kohn, 1999
tub	TrN + G	588	44 (7.4)	172 (29.2)	56.5	F 5'AACATGCGTGAGATTGTAAGT3' R 5'TAGTGACCCTTGGCCCAGTTG3'	O'Donnell & Cigelnik, 1997
rpb1	TrN + I + G	642	29 (4.5)	230 (35.8)	53.3	F 5'CAYCCWGGYTTYATCAAGAA3' R 5'CCNGCDATNTCRTTRTCCATRTA3'	Castlebury *et al*. 2004

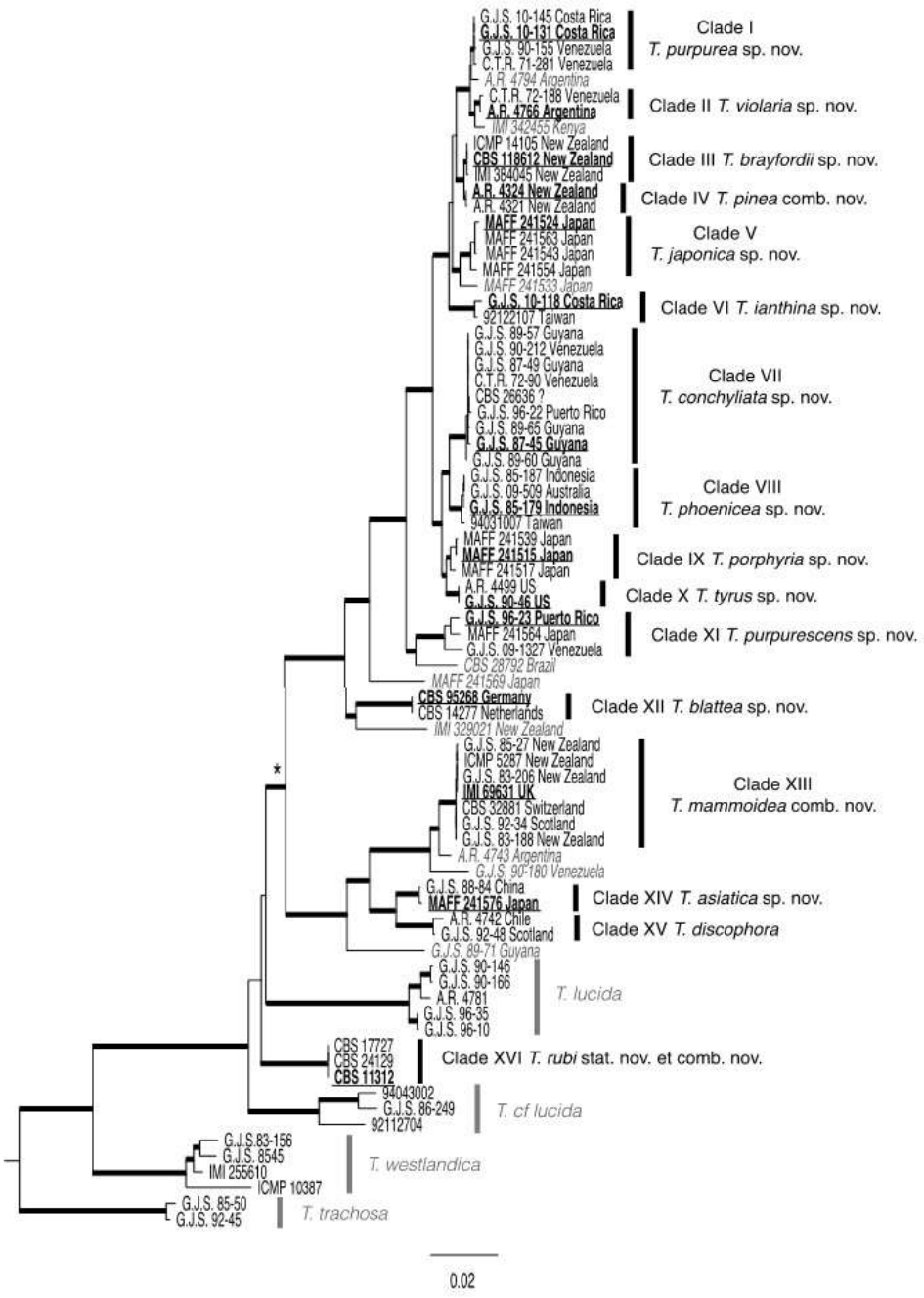
Table 2. Nucleotide divergence (Dxy*) for all pairwise comparisons of putative species identified within *T. discophora* species-complex. All positions containing gaps were eliminated for a total of 3559 positions. Numbers across the top row correspond to putative species numbers in the first column.

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
1. *T. purpurea*																
2. *T. violaria*	0.004															
3. *T. brayfordii*	0.006	0.008														
4. *T. pinea*	0.006	0.008	0.002													
5. *T. japonica*	0.008	0.010	0.007	0.007												
6. *T. ianthina*	0.013	0.015	0.009	0.009	0.013											
7. *T. conchyliata*	0.014	0.013	0.012	0.012	0.013	0.015										
8. *T. phoenicea*	0.016	0.015	0.014	0.013	0.013	0.017	0.008									
9. *T. porphyria*	0.012	0.012	0.011	0.010	0.011	0.014	0.009	0.008								
10. *T. tyrius*	0.013	0.012	0.012	0.011	0.012	0.016	0.009	0.009	0.005							
11. *T. purpurescens*	0.026	0.026	0.025	0.025	0.026	0.028	0.023	0.024	0.022	0.023						
12. *T. blattea*	0.035	0.036	0.034	0.033	0.033	0.037	0.034	0.034	0.031	0.033	0.034					
13. *T. mammoidea*	0.061	0.062	0.060	0.059	0.059	0.063	0.061	0.060	0.058	0.058	0.064	0.057				
14. *T. discophora*	0.057	0.058	0.056	0.055	0.055	0.058	0.057	0.055	0.054	0.056	0.059	0.052	0.031			
15. *T. asiatica*	0.054	0.055	0.053	0.052	0.052	0.054	0.053	0.052	0.051	0.052	0.056	0.048	0.028	0.015		
16. *T. rubi*	0.044	0.045	0.043	0.042	0.044	0.046	0.043	0.044	0.042	0.043	0.048	0.039	0.046	0.044	0.040	

* $p < 0.001$

17 Online Resource 1. Taxa used in this study, including information about the origin of the fungal material, collection codes and
18 GenBank accession numbers.
19

Strain	Code	Host	Origin	GenBank accession numbers					
				act	ITS	LSU	*rpb1*	*tef1*	*tub*
Cyl. ianthothele var. ianthothele	CBS 11312	*Rubus idaeus*	Switzerland	KC121380	KC153718	KC121444	KC153911	KC153847	KC153783
Cyl. ianthothele	CBS 118612	*Quercus rubur*	New Zealand	KC121381	KC153719	KC121445	KC153912	KC153848	KC153784
Cyl. ianthothele var. ianthothele	CBS 14277	On soil	Netherlands	KC121382	KC153720	KC121446	KC153913	KC153849	KC153785
Cyl. ianthothele var. ianthothele	CBS 17727	*Rubus idaeus*	England	KC121383	KC153721	KC121447	KC153914	KC153850	KC153786
Cyl. ianthothele var. ianthothele	CBS 24129	*Rubus idaeus*	Scotland	KC121384	KC153722	KC121448	KC153915	KC153851	KC153787
Cyl. ianthothele var. minus	CBS 26636	unknown	Germany	KC121385	KC153723	KC121449	KC153916	KC153852	KC153788
Cyl. ianthothele var. majus	CBS 28792	On soil	Brazil	KC121386	KC153724	KC121450	KC153917	KC153853	KC153789
Cyl. ianthothele var. majus	CBS 32881	Unknown	Switzerland	KF569826	KF569836	KF569845	KF569873	KF569854	KF569863
Cyl. ianthothele var. majus	CBS 95268	On soil	Germany	KC121387	KC153725	KC121451	KC153918	KC153854	KC153790
Neonectria mammoidea	C.T.R. 72-188 (= CBS 134040)	Unknown	Venezuela	KC121389	KC153727	KC121453	KC153920	KC153856	KC153792
Neonectria mammoidea	IMI 69361	*Smyrnium olusatrum*	UK	KC121425	KC153763	KC121489	KC153956	KC153892	KC153828
Nectria rubi	ICMP 14105	Unknown	New Zealand	KC121420	KC153758	KC121484	KC153951	KC153887	KC153823
Nectria pinea	ICMP 5287	Unknown	New Zealand	KC121421	KC153759	KC121485	KC153952	KC153888	KC153824
T. discophora	92122107 (=CBS 134038)	unknown	Taiwan	KC121373	KC153711	KC121437	KC153904	KC153840	KC153775
T. discophora	94031007 (=CBS 134039)	unknown	Taiwan	KC121374	KC153712	KC121438	KC153905	KC153841	KC153776
T. discophora	A.R. 4321 (=CBS 134033)	*Pinus radiata*	New Zealand	KC121375	KC153713	KC121439	KC153906	KC153842	KC153777
T. discophora	A.R. 4324 (=CBS 125153)	*Pinus radiata*	New Zealand	HM352875	HM364294	HM364307	HM364326	HM364345	HM352860
T. discophora	A.R. 4499 (=CBS 125172)	*Fagus grandifolia*	U.S	HM352877	HM364296	HM364309	HM364327	HM364347	HM364327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G.J.S. 90-155 Venezuela
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A.R. 4794 Argentina
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T. purpurea sp. nov.
C.T.R. 72-188 Venezuela
A.R. 4766 Argentina
IMI 342455 Kenya
Clade II T. violaria sp. nov.
ICMP 14105 New Zealand
CBS 118612 New Zealand
IMI 384045 New Zealand
Clade III T. brayfordii sp. nov.
A.R. 4324 New Zealand
A.R. 4321 New Zealand
Clade IV T. pinea comb. nov.
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MAFF 241563 Japan
MAFF 241543 Japan
MAFF 241554 Japan
MAFF 241533 Japan
Clade V
T. japonica sp. nov.
G.J.S. 10-118 Costa Rica
92122107 Taiwan
Clade VI T. ianthina sp. nov.
G.J.S. 89-57 Guyana
G.J.S. 90-212 Venezuela
G.J.S. 87-49 Guyana
C.T.R. 72-90 Venezuela
CBS 26636 ?
G.J.S. 96-22 Puerto Rico
G.J.S. 89-65 Guyana
G.J.S. 87-45 Guyana
G.J.S. 89-60 Guyana
Clade VII
T. conchyliata sp. nov.
G.J.S. 85-187 Indonesia
G.J.S. 09-509 Australia
G.J.S. 85-179 Indonesia
94091007 Taiwan
Clade VIII
T. phoenicea sp. nov.
MAFF 241539 Japan
MAFF 241515 Japan
MAFF 241517 Japan
Clade IX T. porphyria sp. nov.
A.R. 4499 US
G.J.S. 90-46 US
Clade X T. tyrus sp. nov.
G.J.S. 96-23 Puerto Rico
MAFF 241564 Japan
G.J.S. 09-1327 Venezuela
CBS 28792 Brazil
Clade XI T. purpurescens sp. nov.
MAFF 241569 Japan
CBS 95268 Germany
CBS 14277 Netherlands
Clade XII T. blattea sp. nov.
IMI 329021 New Zealand
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G.J.S. 85-27 New Zealand
ICMP 5287 New Zealand
G.J.S. 83-206 New Zealand
IMI 69631 UK
CBS 32881 Switzerland
G.J.S. 92-34 Scotland
G.J.S. 83-188 New Zealand
Clade XIII
T. mammoidea comb. nov.
A.R. 4743 Argentina
G.J.S. 90-180 Venezuela
G.J.S. 88-84 China
MAFF 241576 Japan
Clade XIV T. asiatica sp. nov.
A.R. 4742 Chile
G.J.S. 92-48 Scotland
Clade XV T. discophora
G.J.S. 89-71 Guyana
G.J.S. 90-146
G.J.S. 90-166
A.R. 4781
G.J.S. 96-35
G.J.S. 96-10
T. lucida
CBS 17727
CBS 24129
CBS 11312
Clade XVI T. rubi stat. nov. et comb. nov.
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G.J.S. 86-249
92112704
T. cf lucida
G.J.S.83-156
G.J.S. 8545
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T. westlandica
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G.J.S. 92-45
T. trachosa
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C.T.R. 72-188
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CBS 118612
ICMP 14105
IMI 384045
A.R. 4321
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HMAS 183564 T. beijingensis
G.J.S. 09-1327
MAFF 241564
G.J.S. 96-23
Clade XI T. purpurescens sp. nov.
HMAS 188498 T. yunnanica
MAFF 241569
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CBS 95268
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CBS 17727
CBS 11312
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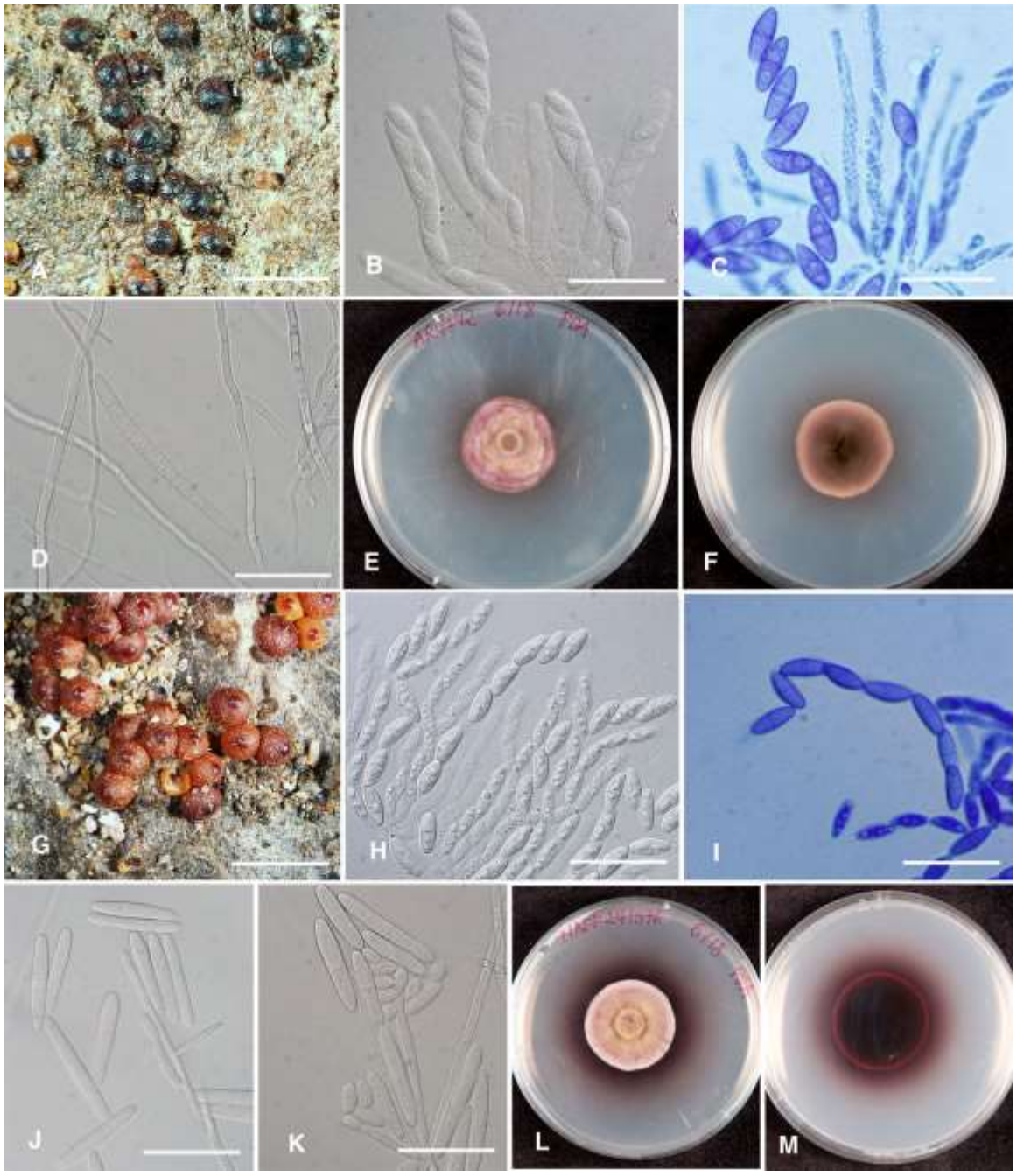
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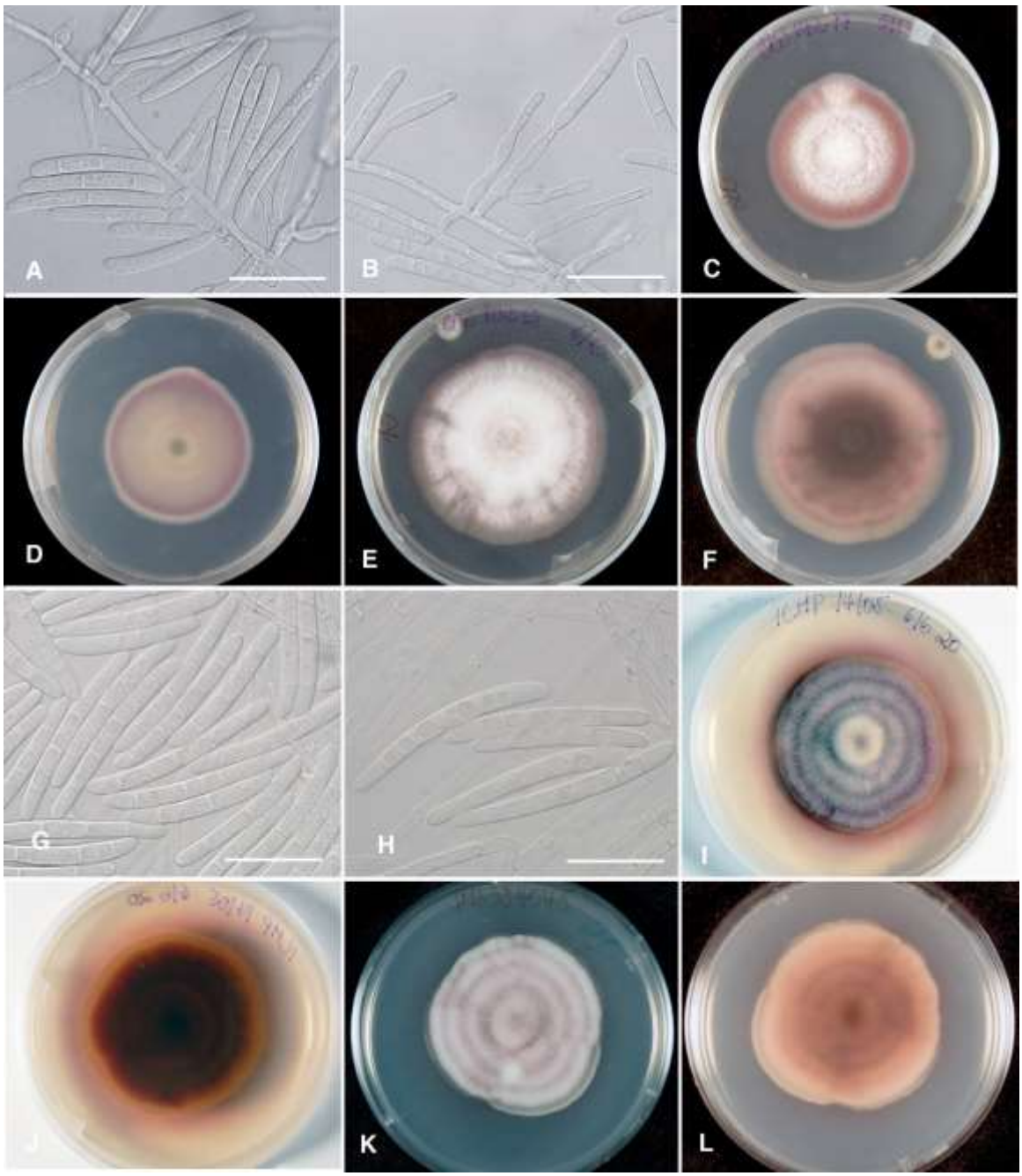
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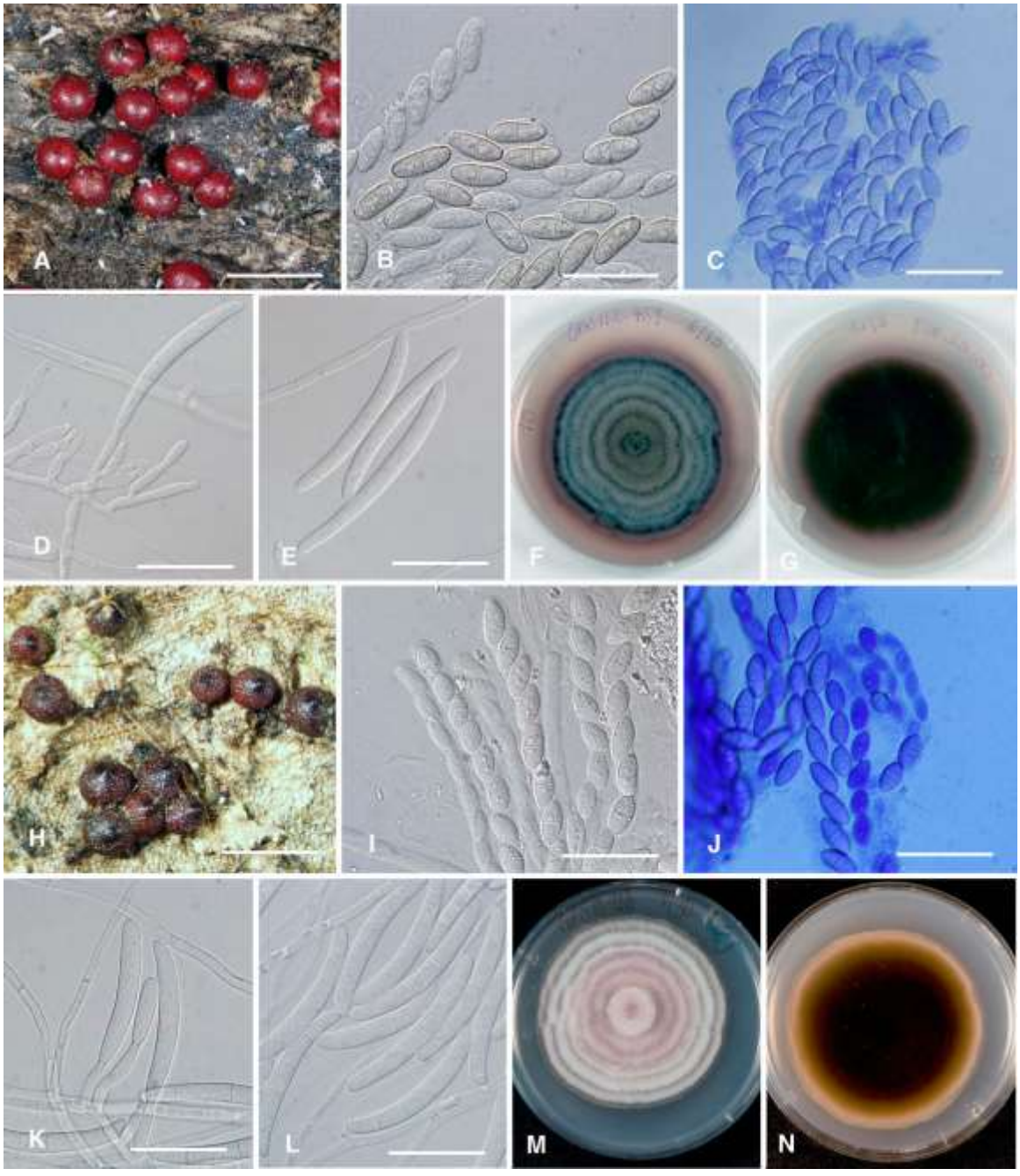
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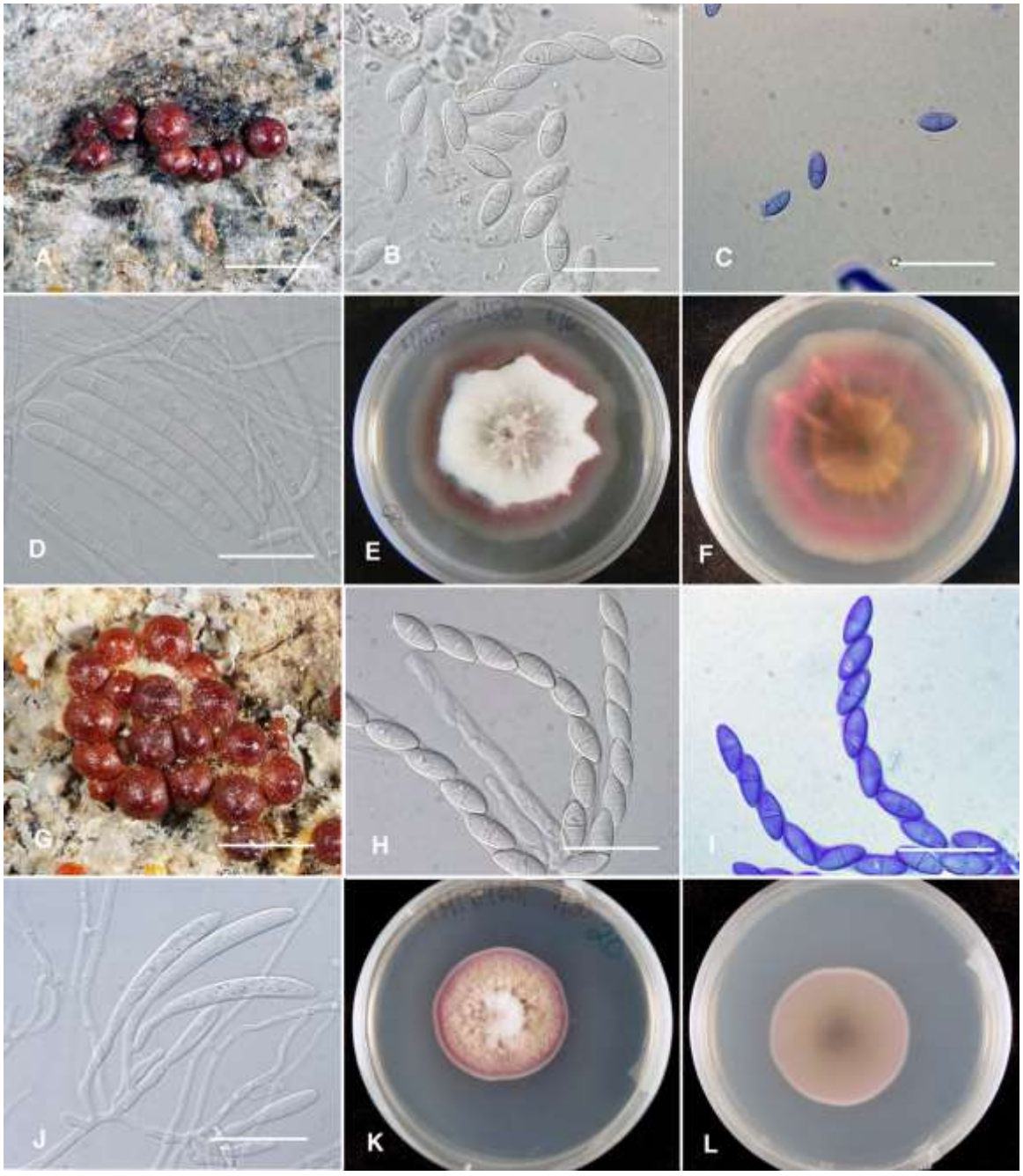
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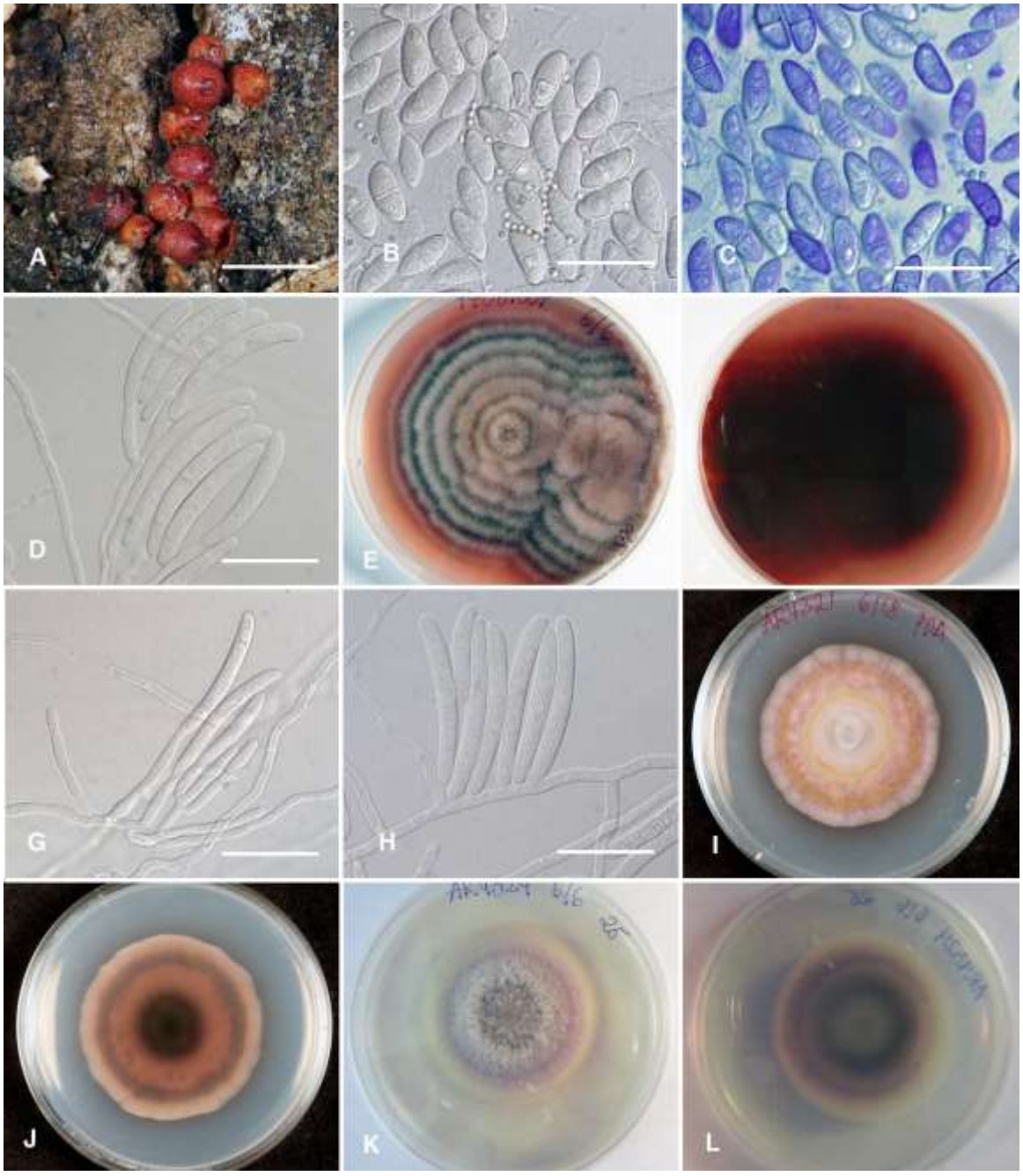
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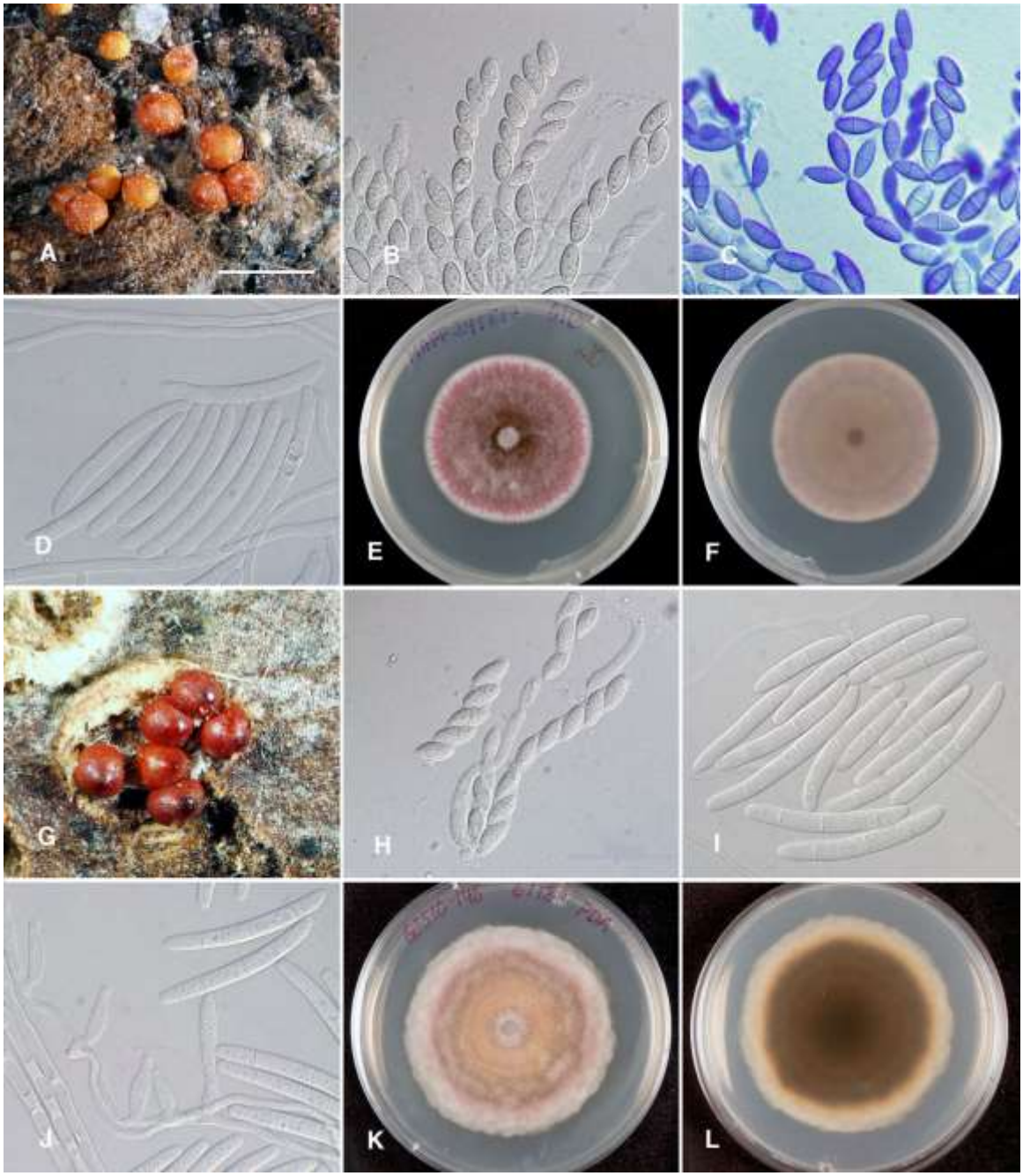
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