Cylindrocarpon root rot: multi-gene analysis reveals novel species within the Ilyonectria radicicola species complex

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Abstract Ilyonectria radicicola and its Cylindrocarpon-like anamorph represent a species complex that is commonly associated with root rot disease symptoms on a range of hosts. During the course of this study, several species could be distinguished from I. radicicola sensu stricto based on morphological and culture characteristics. DNA sequence analysis of the partial β-tubulin, histone H3, translation elongation factor 1-α and nuclear ribosomal RNA-Internal Transcribed Spacer (nrRNA-ITS) genes were employed to provide further support for the morphological species resolved among 68 isolates associated with root rot disease symptoms. Of the various loci screened, nrRNA-ITS sequences were the least informative, while histone H3 sequences were the most informative, resolving the same number of species as the combined dataset across the four genes. Within the Ilyonectria radicicola species complex, 12 new taxa are delineated occurring on a diverse range of hosts, the most common being Cyclamen, Lilium, Panax, Pseudotsuga, Quercus and Vitis.

Keywords Cylindrocarpon root rot · Nectria-like fungi · Phylogeny · Systematics

Introduction

The genus Cylindrocarpon was introduced in 1913 by Wollenweber, with C. cylindroides as type. Cylindrocarpon and Cylindrocarpon-like species have since been commonly associated with root and decay of woody and herbaceous plants (Domsch et al. 2007). Cylindrocarpon root rot causes losses up to 30% on ginseng (Panax quinquefolium) (Seifert et al. 2003), and plays an important role in black foot rot of grapevines (Halleen et al. 2004, 2006), apple replant disease (Tewoldemedhin et al. 2010), and beech cankers (Castlebury et al. 2006), to name but a few hosts of economic importance.

In his taxonomic revision of Cylindrocarpon, Booth (1966) divided this genus into four groups based on the presence or absence of microconidia or chlamydospores. Booth’s group 4 represents Neonectria s. str., as it accommodates the type species N. ramulariae (anamorph: C. obtusiusculum). Most of the teleomorphs of Cylindrocarpon species have since this date been classified in Neonectria (Brayford et al. 2004; Halleen et al. 2004, 2006; Mantiri et al. 2001; Rossman et al. 1999). Several phylogenetic studies have, however, revealed that Neonectria/Cylindrocarpon is paraphyletic (Castlebury et al. 2006; Halleen et al. 2004, 2006; Hirooka et al. 2005; Mantiri et al. 2001). The first step in resolving this issue was taken by Halleen et al. (2004), who proposed Campyllocarpon for species resembling Cylindrocarpon with 3–5-septate, curved macroconidia, and
lacking microconidia. A further phylogenetic study (Chaverri et al. 2011) divided the Neonectria complex into four genera based on a combination of characters linked to perithecial anatomy and conidial septation: Ilyonectria, Neonectria/Cylindrocarpon s. str., Rugonectria and Thelonectria. In this study, a single generic name was proposed for each clade in an attempt to move towards a single nomenclature for pleomorphic fungi, meaning that the Cylindrocarpon-like anamorphs of Ilyonectria, Rugonectria and Thelonectria were placed in teleomorph genera, as recently done with other groups of pleomorphic fungi (Crous et al. 2006, 2007, 2009a; Gräfenhan et al. 2011; Lombard et al. 2010; Schroers et al. 2011).

Cylindrocarpon root rot is commonly associated with “Cylindrocarpon destructans” in the literature (Hallesen et al. 2004; Samuels and Brayford 1990). This fungus was originally described as Ramularia destructans from roots of ginseng (Panax quinquefolium) collected in the USA (Zinssmeister 1918). Furthermore, it has been linked to the teleomorph Ilyonectria radicicola (Booth 1966; Chaverri et al. 2011; Samuels and Brayford 1990), which Gerlach and Nilsson (1963) described from rotting bulbs of Cyclamen persicum collected in Sweden. Samuels and Brayford (1990) commented on the morphological variation in collections of I. radicicola and its anamorph “C.” destructans. Seifert et al. (2003) showed that there was more than one “C.” destructans-like species occurring on Panax, and that none of the resolved clades correlated to the ex-type strain of I. radicicola, leading Hallesen et al. (2006) to question the purported anamorph/teleomorph link between I. radicicola (from Cyclamen, Sweden) and “C.” destructans (from Panax, USA). Based on a phylogenetic analysis of ITS nrDNA gene sequences, Schroers et al. (2008) concluded that the I. radicicola complex includes “C.” destructans, “C.” destructans var. crassum, I. coprosmae, I. liriodendri, N. austroaradiciola and N. macroconidialis.

The aim of the present study was to elucidate the morphological variation present within the I. radicicola complex, and to link fresh collections to older names introduced for species in this complex. This was addressed by combining morphological and culture characteristics with DNA sequence data derived from the Internal Transcribed Spacers (ITS) of the nrDNA gene operon, and partial β-tubulin (TUB), histone H3 (HIS), and translation elongation factor 1-α (TEF) genes.

**Materials and methods**

Isolates

This study (Table 1) included 42 “C.” destructans s. lat. isolates [including the ex-type strains of I. radicicola (CBS 264.65) and “C.” destructans f.sp. panacis (CBS 124662), “C.” destructans var. destructans and “C.” destructans var. crassum], six “C.” didymum isolates, six I. liriodendri isolates, one N. macroconidialis isolate and one I. coprosmae isolate, all deposited at the CBS-KNAW Fungal Biodiversity Centre, Utrecht, the Netherlands (CBS). Also included are two isolates that were previously identified as Ramularia mors-panacis (CBS 306.35) and R. panacica (CBS 307.35) by Hildebrand (1935).

Besides those, 10 “Cylindrocarpon” spp. isolates were obtained in Portugal from grapevine plants showing decline symptoms, either 1- to 6-year-old plants in vineyards (Cy22, Cy155, Cy158, Cy190, CBS 129078, CBS 129080, CBS 129081, CBS 129082) or from rootstock nurseries (Cy23), and from a 25-year-old grapevine plant with esca symptoms (CBS 129084). Furthermore, isolates were obtained from a young Malus domestica (Cy164) and from the stem of a young Quercus suber (Cy232) plant, both showing decline symptoms, and from Thymus sp. (Cy231) and Ficus sp. (Cy228). One isolate (Cy131) was made available by P. Lecomte (Institut National de la Recherche Agronomique, Bordeaux-Aquitaine, France) and was obtained from an internal lesion of a stem of Actinidia chinensis ‘Hayward’. Another isolate (Cy122) was made available by W.D. Gubler (University of California, Davis, USA) and was obtained from Vitis sp. All of these isolates are stored in a culture collection at the Laboratório de Patologia Vegetal “Veríssimo de Almeida” (LPVVA-ISA, Lisbon, Portugal).

An additional 25 “C.” destructans isolates used during this study were made available by K.A. Seifert (Agriculture and Agri-Food, Canada), and were isolated from commercial Panax quinquefolium gardens (CBS 120359–120369, CBS 129079, CBS 129083, CD1666, CPC 13535, CPC 13537, NSAC-SH2, NSAC-SH2.5), Picea glauca (from roots of P. glauca from Warner, NV), Poa pratensis (from roots of P. pratensis from a vineyard near Seville, Spain), and Prunus cerasus (from roots of P. cerasus from Nevern, France). Also included were 109 isolates were also included in the analysis to add phylogenetic support to this study and represent strains of the following taxa: C. cylindroides, C. obusisporum, C. pauciseptatum, species 1 to 6 (Mostert et al., in preparation; Cabral et al., in preparation), I. macrodidyma, N. ditissima, N. major, N. neomacrospora and N. ramulariae.

DNA isolation, sequencing and phylogenetic analysis

For each isolate, genomic DNA was isolated from mycelium following the protocol of Möller et al. (1992), adapted by Crous et al. (2009b). Sequencing of the ITS and part of the β-tubulin (TUB), histone H3 (HIS) and translation elongation factor 1-α (TEF) genes was performed after PCR amplification using 1× PCR buffer (Bioline, London,
| Species                        | Strain number | Collected/isolated by, year | Isolated from                                           | Location                        | GenBank accession numbers |
|-------------------------------|---------------|-----------------------------|--------------------------------------------------------|---------------------------------|---------------------------|
| Campylocarpon facsiculare,    | CBS 112613;   | F. Halkeen, 2000            | *Vitis vinifera*, trunk of young grapevine showing     | South Africa, Western Cape,     | AY677301 AY677221 JF735502 JF735691 |
| Holotype                      | STE-U 3970;   |                             | decline symptoms; scion Cabernet Sauvignon; rootstock  | Richer 99                      |                           |
| Campylocarpon pseudofacicular | CBS 112679;   | F. Halkeen, 2000            | *Vitis vinifera*, roots, asymptomatic nursery          | South Africa, Western Cape,     | AY677306 AY677214 JF735503 JF735692 |
| Holotype                      | STE-U 5472;   |                             | grapevine plant; scion Sultana; rootstock             | Capetown                        |                           |
| Neocentria macrocondialis     | CBS 119596;   | G.J. Samuels, 1985          | *Campylocarpon* sp.                                   | New Zealand, Gisborne,           | JF735259 JF735372 JF735504 JF735693 |
| Ilyonectria coprosmae         | CBS 119606;   | G.J. Samuels, 1985          | *Campylocarpon* sp.                                   | Urewera National Park, Canada,  | JF735260 JF735373 JF735505 JF735694 |
| Ilyonectria radicola, type    | CBS 264.65    | L. Nilsson, 1961            | *Campylocarpon* sp.                                   | Sweden, Westerby,               | AY677273 AY677256 JF735506 JF735695 |
| strain                        |               |                             |                                                       |                                 |                           |
| Ilyonectria liriodendri, type | CBS 110.81;   | J.D. MacDonald &             | *Liriodendron tulipifera*, root                       | USA, California, Yolo Co.,      | DQ178163 DQ178170 JF735507 JF735696 |
| strain of “C.” liriodendri    | IMI 303645    | E.E. Butler, 1978           |                                                       | Davis                           |                           |
| Ilyonectria liriodendri       | CBS 117526;   | C. Rego, 1999               | *Campylocarpon* sp.                                   | Portugal, Ribatejo e Oeste      | DQ178164 DQ178171 JF735508 JF735697 |
| Cy68                          |               |                             |                                                       |                                 |                           |
| Ilyonectria liriodendri       | CBS 117600;   | C. Rego, 1992               | *Campylocarpon* sp.                                   | Portugal, Ribatejo e Oeste      | DQ178165 DQ178172 JF735509 JF735698 |
| IMI 357400                    |               |                             |                                                       |                                 |                           |
| Ilyonectria liriodendri       | CBS 112596;   | E. Halkeen, 1999            | *Campylocarpon* sp.                                   | South Africa, Western Cape,     | AY677264 AY677239 JF735511 JF735700 |
| Cy1                           | ME              |                             |                                                       |                                 |                           |
| Ilyonectria liriodendri       | CBS 112607;   | E. Halkeen, 2000            | *Campylocarpon* sp.                                   | South Africa, Western Cape,     | AY677269 AY677241 JF735512 JF735701 |
| STE-U 3896                    | C 81           |                             |                                                       |                                 |                           |
| Ilyonectria liriodendri       | Cy164          | C. Rego, 1997               | *Malus domestica*, cultivar Lysgolden; rootstock      | Portugal, Porto de Mós, Valbon  | AM419079 AM419112 JF735513 JF735702 |
| Ilyonectria liriodendri       | Cy122          | WD. Gubler                  | *Campylocarpon* sp.                                   | USA, California                  | JF735261 JF735374 JF735514 JF735703 |
| Ilyonectria liriodendri       | Cy190          | N. Cruz, 2005               | *Campylocarpon* sp.                                   | Portugal, Monção, Cortes        | JF735262 JF735375 JF735515 JF735704 |
| Ilyonectria liriodendri       | Cy232          | L. Inácio & J. Henriques, 2007 | *Campylocarpon* sp.                                   | Portugal, Macedo de Cavaleiros  | JF735263 JF735376 JF735516 JF735705 |
| Ilyonectria robusta            | CBS 321.34     | -                           | *Loroglossum hircinum*, root                          | Tunisia, Tunis                   | AY677275 AY677253 JF735517 JF735706 |
| Ilyonectria robusta, type      | CBS 308.35     | A.A. Hildebrand             | *Panax quinquefolium*, root                           | Canada, Ontario                  | JF735264 JF735377 JF735518 JF735707 |
| strain of Ramurakia           |               |                             |                                                       |                                 |                           |
| Ilyonectria robusta            | CBS 773.83     | J. Hemerlaad, 1996          | *Campylocarpon* sp.                                   | Netherlands, Utrecht             | AY677266 AY677254 JF735519 JF735708 |
| Ilyonectria robusta            | CBS 605.92     | R. Schröder, 1992           | *Campylocarpon* sp.                                   | Germany, Hamburg                 | EF607078 EF607065 JF735520 JF735709 |
| Ilyonectria robusta            | CBS 117813;    | E. Halmichlager, 1993       | *Quercus robur*, root                                 | Austria, Niedersachsen           | JF735578 - - JF735709 |
| IFF 84                        |               |                             |                                                       |                                 |                           |
| Ilyonectria robusta            | CBS 117814;    | E. Halmichlager, 1993       | *Quercus robur*, root                                 | Austria, Niedersachsen           | JF735578 - - JF735709 |
| IFF 85                        |               |                             |                                                       |                                 |                           |
| Ilyonectria robusta            | CBS 117815;    | E. Halmichlager, 1993       | *Quercus robur*, root                                 | Austria, Niedersachsen           | JF735578 - - JF735709 |
| IFF 86                        |               |                             |                                                       |                                 |                           |
| Ilyonectria robusta            | CBS 117817;    | E. Halmichlager, 1993       | *Quercus robur*, root                                 | Austria, Niedersachsen           | JF735578 - - JF735709 |
| IFF 88                        |               |                             |                                                       |                                 |                           |
| Ilyonectria robusta            | CBS 117818;    | E. Halmichlager, 1993       | *Quercus robur*, root                                 | Austria, Niedersachsen           | JF735578 - - JF735709 |
| IFF 89                        |               |                             |                                                       |                                 |                           |
| Ilyonectria robusta            | CBS 117819;    | E. Halmichlager, 1993       | *Quercus robur*, root                                 | Austria, Niedersachsen           | JF735578 - - JF735709 |
| IFF 90                        |               |                             |                                                       |                                 |                           |
| Ilyonectria robusta            | CBS 117830;    | E. Halmichlager, 1993       | *Quercus robur*, root                                 | Austria, Niedersachsen           | JF735578 - - JF735709 |
| IFF 91                        |               |                             |                                                       |                                 |                           |
| Ilyonectria robusta            | CBS 117821;    | E. Halmichlager, 1993       | *Quercus robur*, root                                 | Austria, Niedersachsen           | JF735578 - - JF735709 |
| IFF 93                        |               |                             |                                                       |                                 |                           |
| Species          | Strain number | Collected/isolated by, year | Isolated from | Location | GenBank accession numbers |
|------------------|---------------|-----------------------------|---------------|----------|-------------------------|
| *Ilyonectria robusta* | CBS 117822; IFF 94 | E. Halmuschlager, 1993 | *Quercus robur*, root | Austria, Niederweiden | JF735270 JF735386 JF735526 JF735715 |
| *Ilyonectria robusta* | CBS 117823; IFF 95 | E. Halmuschlager, 1993 | *Quercus robur*, root | Austria, Niederweiden | JF735271 JF735387 JF735527 JF735716 |
| *Ilyonectria robusta* | CD1666 | R. D. Reeleder, 1998 | *Panax quinquefolium* | Canada, Nova Scotia | JF735331 JF735388 JF735528 JF735717 |
| *Ilyonectria robusta* | CPC 1532; DAOM 139398; K 18-3A | - | *Prunus cerasus* | Canada, Nova Scotia | JF735330 JF735389 JF735529 JF735718 |
| *Ilyonectria robusta* | Cy23 | C. Rego, 1997 | *Vitis*, root | Portugal, Ribatejo e Oeste | JF735333 AM419093 JF735719 |
| *Ilyonectria robusta* | Cy158 | C. Rego & T. Nascimento, 2004 | *Vitis vinifera*, 1-year-old, died before sprouting; scion Alicante Bouschet; rootstock 1103P | Portugal, Lamego, Cambres | JF735272 JF735390 JF735531 JF735720 |
| *Ilyonectria robusta* | CBS 129084 | R. D. Reeleder, 1998 | *Vitis vinifera*, basal end of 25-year-old plant; scion Alicante; rootstock 196-17 | Portugal, Monção | JF735273 JF735391 JF735532 JF735721 |
| *Ilyonectria robusta* | Cy231 | F. Caetano, 2005 | *Thymus* | Portugal, Lisbon | JF735274 |
| *Ilyonectria crassa* | CBS 159.30 | W. F. van Hell, 1930 | *Lilium*, bulb | Netherlands | JF735275 JF735393 JF735536 JF735725 |
| *Ilyonectria crassa* | CBS 158.31; IMI 061536; NRRL 6149 | 1930 | *Narcissus*, root | Netherlands | JF735276 JF735394 JF735537 JF735726 |
| *Ilyonectria crassa* | CBS 129083; NSAC-SH-1 | S. Hong, 1998 | *Panax quinquefolium* | Canada, Nova Scotia | JF735331 JF735395 JF735539 JF735727 |
| *Ilyonectria crassa* | NSAC-SH-2 | S. Hong, 1998 | *Panax quinquefolium* | Canada, Nova Scotia | JF735333 JF735396 JF735540 JF735728 |
| *Ilyonectria crassa* | NSAC-SH-2.5 | S. Hong, 1998 | *Panax quinquefolium* | Canada, Nova Scotia | JF735334 JF735397 JF735541 JF735729 |
| "*Cylindrocarpon*" sp. | CBS 120370; CR 20 | P. Axelrood, 1998 | *Pseudotsuga menziesii* | Canada, British Columbia | JF735335 JF735398 JF735542 JF735730 |
| *Ilyonectria rufa* | CBS 153.37 | F. Moreau, 1937 | *Dune sand* | France | JF735336 JF735399 JF735543 JF735731 |
| *Ilyonectria rufa* | CBS 155.47; IAM 14673; JCM 23100 | - | *Acaulis indica* | Belgium, Amandsberg | JF735337 JF735400 JF735544 JF735732 |
| *Ilyonectria rufa* | CBS 640.77 | F. Gourbière, 1977 | *Abies alba* | France | JF735338 JF735401 JF735545 JF735733 |
| *Ilyonectria rufa* | CBS 120371; CR 26 | P. Axelrood, 1998 | *Pseudotsuga menziesii* | Canada, British Columbia | JF735339 JF735402 JF735546 JF735734 |
| *Ilyonectria rufa* | CBS 120372; CR 29 | P. Axelrood, 1998 | *Pseudotsuga menziesii* | Canada, British Columbia | JF735340 JF735403 JF735547 JF735735 |
| *Ilyonectria rufa* | CPC 13536; DAOM 226721; CR36 | P. Axelrood, 1998 | *Pseudotsuga menziesii* | Canada, British Columbia | JF735341 JF735404 JF735548 JF735736 |
| *Ilyonectria rufa* | 94-1628 | R.C. Hamelin, 1994 | *Picea glauca* | Canada, Quebec | JF735342 JF735405 JF735549 JF735737 |
| *Ilyonectria mors-panacis* | CBS 120359; CD1561 | R. D. Reeleder, 1996 | *Panax quinquefolium* | Canada, Ontario | JF735343 JF735406 JF735550 JF735738 |
| *Ilyonectria mors-panacis* | CBS 120360; CD1567 | R. D. Reeleder, 1996 | *Panax quinquefolium* | Canada, Ontario | JF735344 JF735407 JF735551 JF735739 |
| *Ilyonectria mors-panacis* | CBS 120361; CD1596 | R. D. Reeleder, 1996 | *Panax quinquefolium* | Canada, Ontario | JF735345 JF735408 JF735552 JF735740 |
| *Ilyonectria mors-panacis* | CBS 120362; CD1598 | R. D. Reeleder, 1996 | *Panax quinquefolium* | Canada, Ontario | JF735346 JF735409 JF735553 JF735741 |
| *Ilyonectria mors-panacis* | CBS 120363; CD1635 | R. D. Reeleder, 1997 | *Panax quinquefolium* | Canada, Ontario | JF735347 JF735410 JF735554 JF735742 |
| *Ilyonectria mors-panacis* | CBS 120364; CD1636 | R. D. Reeleder, 1997 | *Panax quinquefolium* | Canada, Ontario | JF735348 JF735411 JF735555 JF735743 |
| *Ilyonectria mors-panacis* | CBS 120365; CD1637 | R. D. Reeleder, 1997 | *Panax quinquefolium* | Canada, Ontario | JF735349 JF735412 JF735556 JF735744 |
| *Ilyonectria mors-panacis* | CBS 120366; CD1639 | R. D. Reeleder, 1997 | *Panax quinquefolium* | Canada, Ontario | JF735350 JF735413 JF735557 JF735745 |
| *Ilyonectria mors-panacis* | CBS 120367; CD1640 | R. D. Reeleder, 1997 | *Panax quinquefolium* | Canada, Ontario | JF735351 JF735414 JF735558 JF735746 |
| *Ilyonectria mors-panacis* | CBS 120368; CD1641 | R. D. Reeleder, 1997 | *Panax quinquefolium* | Canada, Ontario | JF735352 JF735415 JF735559 JF735747 |
| *Ilyonectria mors-panacis* | CBS 120369; CD1642 | R. D. Reeleder, 1997 | *Panax quinquefolium* | Canada, Ontario | JF735353 JF735416 JF735560 JF735748 |
| *Ilyonectria mors-panacis* | CPC 13535; DAOM 221059; CD 0265 | R. D. Reeleder, 1989 | *Panax quinquefolium* | Canada, Ontario | JF735354 JF735417 JF735561 JF735749 |
| Species | Strain number | Collected/isolated by, year | Location | GenBank accession numbers |
|---------|---------------|----------------------------|----------|--------------------------|
| Ilyonectria mors-panacis | CPC 13537; DAOM 226727; CD 1570; A.A. Hildebrand | 1996 | Canada, Ontario | JF735413; JF735556; JF735545 |
| Ilyonectria mors-panacis | CBS 13344; DAOM 150670; CBS 558.92; Berkenkamp 1 | 1974 | Poa pratensis | JF735417; JF735541; JF735542; JF735751 |
| Ilyonectria mors-panacis | CBS 11781; CFS 58111 | 1995 | Quercus sp., root, Austria | JF735418; JF735543; JF735544; JF735554 |
| Ilyonectria mors-panacis | CBS 11824; JEF 98 | 2000 | Actinidia chinensis, stem | JF735419; JF735545; JF735546; JF735555 |
| Ilyonectria mors-panacis | CBS 12081; CFS 2200 | 2004 | Lilium regale, bulb | JF735420; JF735547; JF735548; JF735556 |
| Ilyonectria mors-panacis | CBS 12080; CFS 1977 | 2005 | Lilium sp., bulb | JF735421; JF735549; JF735550; JF735557 |
| Ilyonectria mors-panacis | CBS 12079; CFS 1976 | 2006 | Lilium sp., stem | JF735422; JF735551; JF735552; JF735558 |

**Table 1 (continued)**
| Species                      | Strain number | Collected/isolated by, year | Isolated from                  | Location                     | GenBank accession numbers |
|------------------------------|---------------|-----------------------------|--------------------------------|------------------------------|----------------------------|
| *Ilyonectria cyclaminicola*  | CBS 302.93    | M. Hoofman, 1993            | Cyclamen sp., bulb             | Netherlands, Roelofarendsveen | EF1375304 EF1375342 EF13753581 EF1375370 |
| *Cylindrocarpon pauciseptatum* | CBS 100819; LYN 16202/2 | H.M. Dance, 1998           | *Erica melanthera*, root      | New Zealand, Tauranga         | EF607090 EF607076 EF13753582 EF1375371 |
| *Cylindrocarpon pauciseptatum* | CBS 113550    | 2003                        | *H. sp., blackening areas in wood and base of trunk* | New Zealand, Keesbury Estate | EF607080 EF607079 EF13753583 EF1375372 |
| *Cylindrocarpon pauciseptatum* | CBS 120497; KIS 10763 | H.-J. Schroers, 2006     | *H. sp., brownish spots of healthy looking root of ca. 12-year-old, possibly dead, in vineyard* | Slovenia, Mrzlik | EF607085 EF607071 EF13753584 EF1375373 |
| *Cylindrocarpon pauciseptatum* | CBS 120498; KIS 10775 | M. Žerjav, 2006            | *H. sp., decayed secondary roots with black areas of 3-year-old, dead* | Slovenia, Ljutomer | EF607087 EF607072 EF13753585 EF1375374 |
| *Cylindrocarpon pauciseptatum* | CBS 120499; KIS 10780 | M. Žerjav, 2006            | *H. sp., decayed secondary roots with black areas of 3-year-old, dead* | Slovenia, Ljutomer | EF607084 EF607074 EF13753586 EF1375375 |
| *Cylindrocarpon pauciseptatum* | CBS 120171; KIS 10467 | M. Žerjav, 2005            | *H. sp., partly decayed roots of 4-year-old plant, still living but badly shooting; in vineyard* | Slovenia, Škibo | EF607089 EF607076 EF13753587 EF1375376 |
| *Cylindrocarpon pauciseptatum* | CBS 120172; KIS 10729 | M. Žerjav, 2006            | *H. sp., strongly decayed, blackish brown root of ca. 9-year-old plant, possibly dead; in vineyard* | Slovenia, Žužemberk | EF607086 EF607070 EF13753588 EF1375377 |
| *Cylindrocarpon pauciseptatum* | CBS 120173; KIS 10468 | M. Žerjav, 2005            | *H. sp., partly decayed roots of 4-year-old plant, still living but badly shooting; in vineyard* | Slovenia, Škibo | EF607088 EF607068 EF13753589 EF1375378 |
| *Cylindrocarpon pauciseptatum* | Cy 196         | N. Cruz, 2005              | *H. vinifera*, basal end of 4-year-old plant; scion Alvarinho; rootstock 196-17 | Portugal, Melgaço/Monção | EF1375305 EF1375343 EF13753590 EF1375379 |
| *Cylindrocarpon pauciseptatum* | Cy 217         | A. Cabral, 2007            | *H. vinifera*, asymptomatic; scion Gouveio | Portugal, Torres Vedras | EF1375306 EF1375343 EF13753591 EF1375380 |
| *Cylindrocarpon pauciseptatum* | Cy 238         | C. Rego, 2008              | *H. vinifera*, basal end of a 2-year-old plant; scion Petitor Verdot; rootstock 110R | Portugal, Vidigueira | EF1375307 EF1375345 EF13753592 EF1375381 |
| *Cylindrocarpon* sp 1 | CBS 162.89     | M. Barth, 1988             | Hordeum vulgare, root         | Netherlands, Noordoostpolder, Marknesse, Lovinkhoeve | AM1419060 AM1419084 EF1375360 EF1375379 |
| *Cylindrocarpon* sp 2 | Cy 108         | C. Rego, 1999              | *H. vinifera*, basal end of a 4-year-old plant showing decline symptoms; scion Aragonez; rootstock S04 | Portugal, Nelas | EF1375316 AM1419100 EF1375361 EF1375380 |
| *Cylindrocarpon* sp 2 | Cy 200         | N. Cruz, 2005              | *H. vinifera*, basal end of a 16-year-old plant; scion Alvarinho; rootstock 196-17 | Portugal, Melgaço | EF1375317 EF1375445 EF1375361 EF1375381 |
| *Cylindrocarpon* sp 2 | CBS 159.34; IMI 113891; MUCL 4084; VKM F-2656 | H.W. Wellensweber, 1934 | *Pinus laricio*, associated with dieback | Portugal, Estremoz | EF1375319 EF1375446 EF1375361 EF1375381 |
| *Cylindrocarpon* sp 2 | CBS 173.37; IMI 090176 | T.R. Peace, 1937          | *H. vinifera*, basal end of a 1.5-year-old plant showing decline symptoms; scion Aragonez; rootstock 3309 C | Portugal, Estremoz | AM1419069 AM1419105 EF1375361 EF1375384 |
| *Cylindrocarpon* sp 3 | Cy 135         | C. Rego & T. Nascimento, 2003 | *H. vinifera*, basal end of a 1.5-year-old plant showing decline symptoms; scion Aragonez; rootstock 3309 C | Portugal, Estremoz | AM1419074 AM1419107 EF1375361 EF1375385 |
| *Cylindrocarpon* sp 3 | Cy 144         | C. Rego & T. Nascimento, 2003 | *H. vinifera*, basal end of a 1.5-year-old plant showing decline symptoms; scion Aragonez; rootstock 3309 C | Portugal, Estremoz | EF1375320 EF1375448 EF1375361 EF1375386 |
| *Cylindrocarpon* sp 3 | CBS 129085; Cy 145 | C. Rego & T. Nascimento, 2003 | *H. vinifera*, basal end of a 1.5-year-old plant showing decline symptoms; scion Aragonez; rootstock 3309 C | Portugal, Estremoz | EF1375321 EF1375449 EF1375361 EF1375387 |
Table 1 (continued)

| Species | Strain number | Collected/isolated by, year | Isolated from | Location | GenBank accession numbers |
|---------|---------------|-----------------------------|---------------|----------|-------------------------|
|         |               |                             |               |          | ITS         | TUB | H3    | EF1   |
| “Cylindrocarpon” sp. 3 | Cy147 | C. Rego & T. Nascimento, 2003 | *Vitis vinifera*, grafting zone of a 1.5-year-old plant showing decline symptoms; scion Aragonez; rootstock 3309 C | Portugal, Estremoz | JF735322 | JF735450 | JF735619 | JF735808 |
| “Cylindrocarpon” sp. 3 | Cy148 | C. Rego & T. Nascimento, 2003 | *Vitis vinifera*, basal end of a 1.5-year-old plant showing decline symptoms; scion Aragonez; rootstock 3309 C | Portugal, Estremoz | JF735323 | JF735451 | JF735620 | JF735809 |
| “Cylindrocarpon” sp. 3 | Cy149 | C. Rego & T. Nascimento, 2003 | *Vitis vinifera*, basal end of a 1.5-year-old plant showing decline symptoms; scion Aragonez; rootstock 3309 C | Portugal, Estremoz | JF735324 | JF735452 | JF735621 | JF735810 |
| “Cylindrocarpon” sp. 3 | Cy150 | C. Rego & T. Nascimento, 2003 | *Vitis vinifera*, basal end of a 1.5-year-old plant showing decline symptoms; scion Aragonez; rootstock 3309 C | Portugal, Estremoz | JF735325 | JF735453 | JF735622 | JF735811 |
| “Cylindrocarpon” sp. 3 | Cy151 | C. Rego & T. Nascimento, 2003 | *Vitis vinifera*, asymptomatic 1.5-year-old plant; scion Aragonez; rootstock 3309 C | Portugal, Estremoz | JF735326 | JF735454 | JF735623 | JF735812 |
| “Cylindrocarpon” sp. 3 | Cy152 | C. Rego & T. Nascimento, 2003 | *Vitis vinifera*, asymptomatic 1.5-year-old plant; scion Aragonez; rootstock 3309 C | Portugal, Estremoz | JF735327 | JF735455 | JF735624 | JF735813 |
| “Cylindrocarpon” sp. 3 | Cy153 | C. Rego & T. Nascimento, 2003 | *Vitis vinifera*, asymptomatic 1.5-year-old plant; scion Aragonez; rootstock 3309 C | Portugal, Estremoz | JF735328 | JF735456 | JF735625 | JF735814 |
| “Cylindrocarpon” sp. 3 | Cy243 | C. Rego, 2008 | *Vitis vinifera*, basal end of a 2-year-old plant; scion Touriga Nacional; rootstock 110R | Portugal, Vidigueira | JF735329 | JF735457 | JF735626 | JF735815 |
| “Cylindrocarpon” sp. 3 | CPC 13539; 94–1685; CCFC226730 | R. C. Hamelin, 1994 | *Picea glauca* | Canada, Quebec | JF735330 | JF735458 | JF735627 | JF735816 |
| “Cylindrocarpon” sp. 5 | Cy133; IAFM Cy9-1 | J. Armengol | *Vitis vinifera* | Spain, Valencia, L’Alcudia | JF735331 | JF735459 | JF735628 | JF735817 |
| “Cylindrocarpon” sp. 5 | Cy134; IAFM Cy20-1 | J. Armengol | *Vitis vinifera* | Spain, Ciudad Real, Villamobia de los Ojos | JF735332 | AM419104 | JF735629 | JF735818 |
| “Cylindrocarpon” sp. 5 | CBS 129087; Cy159 | A. Cabral & H. Oliveira, 2004 | *Vitis vinifera*, basal end of a 3-year-old plant with root discoloration and decline symptoms; scion Sangiovese; rootstock 1103P | Portugal, Akaicer do Sal, Torrão | JF735333 | AM419111 | JF735630 | JF735819 |
| “Cylindrocarpon” sp. 6 | CBS 112593; STE-U 3990; C 107 | E. Halleen, 2000 | *Vitis vinifera*, roots of an asymptomatic nursery plant; scion Pinotage; rootstock 101–14 Mgt | South Africa, Western Cape, Wellington, Woongroenberg | AY677281 | AY677236 | JF735631 | JF735820 |
| “Cylindrocarpon” sp. 6 | CBS 112608; STE-U 3987; C 62 | E. Halleen, 2000 | *Vitis vinifera*, roots, scion Chardonnay; rootstock 101–14 Mgt | South Africa, Western Cape, Citrusdal | AY677288 | AY677235 | JF735632 | JF735821 |
| “Cylindrocarpon” sp. 6 | CBS 113552; STE-U 5713; HJS-1306; NZ C 41 | R. Bonfiglioli, 2003 | *Vitis vinifera*, sp. decline of nursery plants dead rootstocks | New Zealand, Candy P New Ground | JF735334 | JF735633 | JF735635 | JF735822 |
| “Cylindrocarpon” sp. 6 | Cy115 | WD. Gubler | *Vitis vinifera* | USA, California | JF735335 | JF735460 | JF735634 | JF735823 |
| “Cylindrocarpon” sp. 6 | Cy116 | WD. Gubler | *Vitis vinifera* | USA, California | JF735336 | JF735461 | JF735635 | JF735824 |
| “Cylindrocarpon” sp. 6 | Cy117 | WD. Gubler | *Vitis vinifera* | USA, California | JF735337 | JF735462 | JF735636 | JF735825 |
| “Cylindrocarpon” sp. 6 | Cy119 | WD. Gubler | *Vitis vinifera* | USA, California | JF735338 | JF735463 | JF735637 | JF735826 |
| “Cylindrocarpon” sp. 6 | Cy124 | WD. Gubler | *Vitis vinifera* | USA, California | JF735339 | JF735464 | JF735638 | JF735827 |
| “Cylindrocarpon” sp. 6 | Cy125 | WD. Gubler | *Vitis vinifera* | USA, California | JF735339 | JF735467 | JF735641 | JF735830 |
| “Cylindrocarpon” sp. 6 | Cy129 | WD. Gubler | *Vitis vinifera* | USA, California | JF735339 | JF735467 | JF735641 | JF735830 |
| “Cylindrocarpon” sp. 6 | Cy130 | WD. Gubler | *Vitis vinifera* | USA, California | JF735339 | JF735467 | JF735641 | JF735830 |
| “Cylindrocarpon” sp. 6 | Cy230 | E. Caetano, 2005 | *Festuca duriuscula* | Portugal, Lisbon | JF735340 | JF735468 | JF735642 | JF735831 |
| Species                     | Strain number | Collected/isolated by, year | Isolated from                                      | Location                      | GenBank accession numbers |
|-----------------------------|---------------|-----------------------------|----------------------------------------------------|-------------------------------|---------------------------|
| *Ilyonectria macrodidyma*   | CBS 112594;   | E. Halkeen, 2000            | *Vitis vinifera*, roots of an asymptomatic nursery plant; scion Pinotage; rootstock Richter 99 | South Africa, Western Cape, Malmesbury, Jakkalsfontein | AY677282 AY677231 JF735643 JF735832 |
|                            | STE-U 3991;   |                             |                                                    |                               |                          |
|                            | C 111         |                             |                                                    |                               |                          |
| *Ilyonectria macrodidyma*   | CBS 112601;   | E. Halkeen, 1999            | *Vitis vinifera*, roots with black foot symptoms; scion Pinotage; rootstock US 8-7 | South Africa, Western Cape, Tulbagh | AY677284 AY677229 JF735644 JF735833 |
|                            | STE-U 3983;   |                             |                                                    |                               |                          |
|                            | C 82          |                             |                                                    |                               |                          |
| *Ilyonectria macrodidyma*   | CBS 112603;   | E. Halkeen, 1999            | *Vitis vinifera*, trunk of a plant showing decline symptoms; scion Sauvignon blanc; rootstock Richter 110 | South Africa, Western Cape, Darling | AY677285 JF735469 JF735645 JF735834 |
|                            | STE-U 4007;   |                             |                                                    |                               |                          |
|                            | C 8           |                             |                                                    |                               |                          |
| *Ilyonectria macrodidyma*   | CBS 112605;   | E. Halkeen, 2000            | *Vitis vinifera*, basal end of an asymptomatic nursery plant; scion Sultana; rootstock 143-B Mgt | South Africa, Western Cape, Malmesbury, Jakkalsfontein | AY677287 AY677230 JF735646 JF735835 |
|                            | STE-U 3976;   |                             |                                                    |                               |                          |
|                            | C 106         |                             |                                                    |                               |                          |
| *Ilyonectria macrodidyma*   | CBS 112615;   | E. Halkeen, 2000            | *Vitis vinifera*, roots, asymptomatic nursery grapevine plant; scion Sultana; rootstock 143-B Mgt | South Africa, Western Cape, Malmesbury, Jakkalsfontein | AY677290 AY677233 JF735647 JF735836 |
|                            | STE-U 4016;   |                             |                                                    |                               |                          |
|                            | C 98          |                             |                                                    |                               |                          |
| *Ilyonectria macrodidyma*   | Cy123         | WD. Gubler                  | *Vitis vinifera*, basal end of a 1.5-year-old plant showing decline symptoms; scion Aragonez; rootstock 3309 C | Portugal, Estremoz             | JF735341 JF735470 JF735648 JF735837 |
| *holotype of C. macrodidymum* | Cy128        | WD. Gubler                  | *Vitis vinifera*, basal discolouration in rootstocks; scion Touriga Nacional; rootstock 1103 P | Portugal, Torre de Moncorvo    | JF735344 JF735473 JF735652 JF735841 |
| *Ilyonectria macrodidyma*   | Cy139         | C. Rego & T. Nascimento, 2003 | *Vitis vinifera*, basal end of a 2-year-old plant; scion Petit Verdot; rootstock 110 R | Portugal, Vidigueira           | JF735347 JF735476 JF735655 JF735844 |
| *Ilyonectria macrodidyma*   | Cy140         | C. Rego & T. Nascimento, 2003 | *Vitis vinifera*, grafting zone of a 1.5-year-old plant showing decline symptoms; scion Aragonez; rootstock 3309 C | Portugal, Extremadura          | JF735343 JF735472 JF735651 JF735840 |
| *Ilyonectria macrodidyma*   | Cy175         | C. Rego, 2004               | *Vitis vinifera*, basal discolouration in rootstocks; scion Touriga Nacional; rootstock 1103 P | Portugal, Torre de Moncorvo    | JF735344 JF735473 JF735652 JF735841 |
| *Ilyonectria macrodidyma*   | Cy181         | C. Rego, 2005               | *Vitis vinifera*, scion 140-Ru; rootstock Aragonês | Portugal, Akácer do Sal        | JF735345 JF735474 JF735653 JF735842 |
| *Ilyonectria macrodidyma*   | Cy216         | A. Cabral, 2007             | *Vitis vinifera*, asymptomatic; scion Marsanne    | Portugal, Torres Vedras        | JF735346 JF735475 JF735654 JF735843 |
| *Ilyonectria macrodidyma*   | Cy244         | C. Rego, 2008               | *Vitis vinifera*, basal discolouration in rootstocks; scion Touriga Nacional; rootstock 1103 P | Portugal, Vidigueira           | JF735347 JF735476 JF735655 JF735844 |
| *Ilyonectria macrodidyma*   | Cy258         | C. Rego, 2008               | *Vitis vinifera*, basal end of a 2-year-old plant; scion Cabernet Sauvignon; rootstock 110 R | Portugal, Vidigueira           | JF735348 JF735477 JF735656 JF735845 |
| *Cylindrocarpon* sp.4       | CBS 119.41    | H.C. Koning                 | *Fragaria sp.*, root                               | Netherlands, Baarn             | JF735349 JF735478 JF735657 JF735846 |
|                            | 188.49        | J.A. von Arx                | *Abies nordmanniana*, root                         | Netherlands, Egmond            | AM419063 AM419087 JF735658 JF735847 |
| *Cylindrocarpon* sp.4       | CBS 112604;   | E. Halkeen, 1999            | *Vitis vinifera*, roots; scion Cabernet Sauvignon; rootstock 101-14 Mgt | South Africa, Western Cape, Paarl | AY677286 AY677227 JF735659 JF735848 |
|                            | STE-U 4004;   |                             |                                                    |                               |                          |
|                            | C 10          |                             |                                                    |                               |                          |
| *Cylindrocarpon* sp.4       | CBS 112609;   | M. Swart, 1979              | *Vitis vinifera*, dark brown discoloration in trunk; scion Cabernet Sauvignon | Australia, Tasmania, Bream Creek | AY677289 AY677226 JF735660 JF735849 |
|                            | STE-U 3969;   |                             |                                                    |                               |                          |
|                            | HJS-1217      |                             |                                                    |                               |                          |
| *Cylindrocarpon* sp.4       | CBS 113555;   | R. Bonfiglioli, 2003        | *Vitis vinifera*, blackening areas in wood and roots; scion Pinot Noir; rootstock 101-14 | New Zealand, Fiddlers Green    | JF735350 JF735724 JF735661 JF735850 |
|                            | STE-U 5715;   |                             |                                                    |                               |                          |
|                            | HJS-1309;     |                             |                                                    |                               |                          |
|                            | NZ C 60       |                             |                                                    |                               |                          |
| *Cylindrocarpon* sp.4       | CBS 112598;   | E. Halkeen, 2000            | *Vitis vinifera*, roots of an asymptomatic plant; scion Sultana; rootstock Ramsey Concord Bradt grapes, roots and stems | South Africa, Western Cape, Wellington, Lelienfontein | JF735351 JF735479 JF735662 JF735851 |
|                            | STE-U 3997;   |                             |                                                    |                               |                          |
|                            | C 115         |                             |                                                    |                               |                          |
| *Cylindrocarpon* sp.4       | CPC 13333;    | H.F. Dias, 1972             | *Vitis vinifera*, asymptomatic rootstocks; rootstock SO4, clone 102 F | Portugal, Ribatejo e Oeste     | AJS75332 AM419095 JF735664 JF735853 |
|                            | CCFC 144524;  |                             |                                                    |                               |                          |
|                            | Dias 2B       |                             |                                                    |                               |                          |
| *Cylindrocarpon* sp.4       | Cy69          | C. Rego, 1999               | *Vitis vinifera*, asymptomatic rootstocks; rootstock 99R, clone 96 F | Portugal, Ribatejo e Oeste     | AJS75335 AM419096 JF73565 JF735854 |
| *Cylindrocarpon* sp.4       | Cy71          | C. Rego, 1999               | *Vitis vinifera*, asymptomatic rootstocks; rootstock 99R, clone 96 F | Portugal, Ribatejo e Oeste     | AJS75335 AM419096 JF73565 JF735854 |
| Species          | Strain number | Collected/isolated by, year | Isolated from | Location | GenBank accession numbers |
|------------------|---------------|-----------------------------|---------------|----------|--------------------------|
| “Cylindrocarpon” sp.4 | Cy72          | C. Rego, 1999               | *Vitis vinifera*, asymptomatic rootstocks; rootstock clone 113 F | Portugal, Ribatejo e Oeste | AJ875336 AM419097 JF735666 JF735855 |
| “Cylindrocarpon” sp.4 | Cy75          | C. Rego, 1999               | *Vitis vinifera*, asymptomatic rootstocks; rootstock 99R | Portugal, Ribatejo e Oeste | AJ875334 AM419098 JF735667 JF735856 |
| “Cylindrocarpon” sp.4 | Cy96          | E. Halmehlager              | *Quercus sp.*, root | Austria, Patzmannsdorf | JF735352 JF735481 JF735668 JF735857 |
| “Cylindrocarpon” sp.4 | Cy97          | E. Halmehlager              | *Quercus sp.*, root | Austria, Patzmannsdorf | JF735353 JF735482 JF735669 JF735858 |
| “Cylindrocarpon” sp.4 | Cy118         | W.D. Guhler                 | *Vitis vinifera* | USA, California | JF735354 JF735483 JF735670 JF735859 |
| “Cylindrocarpon” sp.4 | Cy120         | W.D. Guhler                 | *Vitis vinifera* | USA, California | AJ875320 AM419101 JF735671 JF735860 |
| “Cylindrocarpon” sp.4 | Cy132; IAFM Cy1-1 | J. Armengol               | *Vitis vinifera* | Spain, Alicante | JF735355 JF735484 JF735672 JF735861 |
| “Cylindrocarpon” sp.4 | Cy136         | C. Rego & T. Nascimento, 2003 | *Vitis vinifera*, basal end of a 1.5-year-old plant showing decline symptoms; scion Aragonez; rootstock 3309 C | Portugal, Estremoz | JF735356 JF735485 JF735673 JF735862 |
| “Cylindrocarpon” sp.4 | Cy137         | C. Rego & T. Nascimento, 2003 | *Vitis vinifera*, basal end of a 1.5-year-old plant showing decline symptoms; scion Aragonez; rootstock 3309 C | Portugal, Estremoz | AM419070 JF735486 JF735674 JF735863 |
| “Cylindrocarpon” sp.4 | Cy138         | C. Rego & T. Nascimento, 2003 | *Vitis vinifera*, basal end of a 1.5-year-old plant showing decline symptoms; scion Aragonez; rootstock 3309 C | Portugal, Estremoz | JF735357 JF735487 JF735675 JF735864 |
| “Cylindrocarpon” sp.4 | Cy141         | C. Rego & T. Nascimento, 2003 | *Vitis vinifera*, basal end of a 1.5-year-old plant showing decline symptoms; scion Aragonez; rootstock 3309 C | Portugal, Estremoz | JF735358 JF735488 JF735676 JF735865 |
| “Cylindrocarpon” sp.4 | Cy142         | C. Rego & T. Nascimento, 2003 | *Vitis vinifera*, grafting zone of a 1.5-year-old plant showing decline symptoms; scion Aragonez; rootstock 3309 C | Portugal, Estremoz | JF735359 JF735489 JF735677 JF735866 |
| “Cylindrocarpon” sp.4 | Cy143         | C. Rego & T. Nascimento, 2003 | *Vitis vinifera*, basal end of a 1.5-year-old plant showing decline symptoms; scion Aragonez; rootstock 3309 C | Portugal, Estremoz | JF735360 JF735490 JF735678 JF735867 |
| “Cylindrocarpon” sp.4 | Cy157         | H. Oliveira, 2004           | *Vitis vinifera*, scion Touriga Nacional; rootstock 99R | Portugal, Alequer | AM419077 AM419101 JF735679 JF735868 |
| “Cylindrocarpon” sp.4 | Cy214         | A. Cabral, 2007             | *Vitis vinifera*, asymptomatic; scion Grenache | Portugal, Torres Vedras | JF735361 JF735491 JF735680 JF735869 |
| “Cylindrocarpon” sp.4 | Cy218         | A. Cabral, 2007             | *Vitis vinifera*, asymptomatic; scion Chenin | Portugal, Torres Vedras | JF735362 JF735492 JF735681 JF735870 |
| “Cylindrocarpon” sp.4 | Cy221         | L. Leandro                  | Fragaria x ananassa | USA, North Carolina, Asheville | JF735363 JF735493 JF735682 JF735871 |
| “Cylindrocarpon” sp.4 | Cy222         | L. Leandro                  | Fragaria x ananassa | USA, North Carolina, Asheville | JF735364 JF735494 JF735683 JF735872 |
| “Cylindrocarpon” sp.4 | Cy223         | L. Leandro                  | Fragaria x ananassa | USA, North Carolina, Asheville | JF735365 JF735495 JF735684 JF735873 |
| “Cylindrocarpon” sp.4 | Cy233         | C. Rego, 2008               | *Vitis vinifera*, basal end of a 2-year-old plant; scion Cabernet Sauvignon; rootstock 110R | Portugal, Vidigueira | JF735366 JF735496 JF735685 JF735874 |
| “Cylindrocarpon” sp.4 | Cy237         | C. Rego, 2008               | *Vitis vinifera*, basal end of a 2-year-old plant; scion Chardonnay; rootstock 110R | Portugal, Vidigueira | JF735367 JF735497 JF735686 JF735875 |
| “Cylindrocarpon” sp.4 | Cy240         | C. Rego, 2008               | *Vitis vinifera*, basal end of a 2-year-old plant; scion Touriga Nacional; rootstock 140RU | Portugal, Vidigueira | JF735368 JF735498 JF735687 JF735876 |
| “Cylindrocarpon” sp.4 | Cy246         | C. Rego, 2008               | *Vitis vinifera*, basal end of a 2-year-old plant; scion Antão Vaz; rootstock 110R | Portugal, Vidigueira | JF735369 JF735499 JF735688 JF735877 |
| “Cylindrocarpon” sp.4 | Cy260         | C. Rego, 2008               | *Vitis vinifera*, basal end of a 2-year-old plant; scion Cabernet Sauvignon; rootstock 110R | Portugal, Vidigueira | JF735370 JF735500 JF735689 JF735878 |
| Species | Strain number | Collected/isolated by, year | Isolated from | Location | GenBank accession numbers |
|---------|---------------|-----------------------------|---------------|----------|--------------------------|
| **“Cylindrocarpon” sp.** | Cy262 | C. Rego, 2008 | *Vitis vinifera*, basal end of a 2-year-old plant; scion Cabernet Sauvignon; rootstock 110R | Portugal, Vidigueira | JF735371 JF735501 JF735690 JF735879 |
| **Neonectria major**, type strain | CBS 240.29; IMI 113909 | H.W. Wollenweber | *Alnus incana*, canker | Norway | JF735308 DQ789872 JF735593 JF735782 |
| **Neonectria ditissima**, authentic strain of *C. willkommii* | CBS 226.31; IMI 113922 | H.W. Wollenweber | *Fagus sylvatica*, canker Norway, Tharandt | Germany, Tharandt | JF735309 DQ789869 JF735594 JF735783 |
| **Neonectria ditissima**, representative strain of *N. gallicola* | CBS 835.97 | W. Gams, 1997 | *Salix cinerea*, dead branch of still living tree | Belgium, Marais de Sampant | JF735310 DQ789880 JF735595 JF735784 |
| **Neonectria ditissima** | Cy169 | H. Oliveira, 1997 | *Malus domestica*; scion Oregon; rootstock MM107 | Portugal, Alcobaça | AM419080 AM419113 JF735596 JF735785 |
| **Neonectria ditissima**, *N. galligena* representative strain | Cy172 | T. Nascimento, 2004 | *Neonectria ditissima*, dead branch of still living tree | Portugal, Alcobaça | AM419081 AM419114 JF735597 JF735786 |
| **Neonectria ramulare**, representative strain | CBS 118984; GJS 03-28 | L. Reitman, 2005 | *Arcjolobium tusgenes*, parasitising *Abies balsamea* | Canada, British Columbia, Vancouver Island, Spider Lake | JF735311 DQ789882 JF735598 JF735787 |
| **Cylindrocarpon cylindroides**, representative strain | CBS 324.61; DSM 62489; IMB 9628 | J.A. von Arx | *Abies concolor* | Netherlands, Zwolle | JF735312 DQ789875 JF735599 JF735788 |
| **Cylindrocarpon cylindroides** | CBS 503.67 | E. Roll-Hansen | *Abies alba*, wood | Norway, Hordaland, Fana | AV677261 JF735436 JF735600 JF735789 |
| **Cylindrocarpon sp.** | CPC 1354; DAOM 185212; CR6 | J.A. Traquair & B. Harrison, 1982 | *Pyrus* sp. | Canada, Ontario, Harrow | AV295303 JF735437 JF735601 JF735790 |
| **Neonectria ramulare**, authentic strain of *C. obtusiusculum* (=*C. magnusianum*) | CBS 151.29; IMI 113894; MUCL 28083; MUCL 28094 | H.W. Wollenweber | *Malus sylvestris*, fruit | UK, England, Cambridge | JF735313 JF735438 JF735602 JF735791 |
| **Neonectria ramulare** | CBS 182.36; IMI 113893; UPSC 1903 | H.W. Wollenweber | *Malus sylvestris*, fruit | - | JF735314 JF735439 JF735603 JF735792 |
| **Cylindrocarpon sp.** | CR21 | P. Axelrod | Pseudotoga menziesii | Canada, British Columbia | JF735315 JF735440 JF735604 JF735793 |
| **Cylindrocarpon sp.** | CPC 13530; DAOM 185722; JAT 1351 | J.A. Traquair, 1983 | *Pyrus* sp., lesions on seedlings | Canada, Ontario, Harrow | AV295302 JF735441 JF735605 JF735794 |
| **Cylindrocarpon sp.** | CPC 13531; CCFC 192672; DAOM 226722; CR6 | P. Axelrod | Pseudotoga menziesii, root | Canada, British Columbia | AV295301 JF735442 JF735606 JF735795 |
| **Cylindrocarpon obtusisporum** | CBS 183.36; IMI 113895 | H.W. Wollenweber, 1936 | *Salix tuberosum*, tuber | Germany | AM419061 AM419085 JF735607 JF735796 |
| **Cylindrocarpon obtusisporum** | CPC 13544; DAOM 182772; JAT 1386 | J.A. Traquair, 1982 | *Prunus armenica*, twigs | Canada, Ontario, Ruthven | AV295306 JF735443 JF735608 JF735797 |
| **Cylindrocarpon obtusisporum** | 94-1356 | R. C. Hamelin, 1994 | *Picea mariana* | Canada, Quebec | AV295304 JF735444 JF735609 JF735798 |

* ATCC American Type Culture Collection, USA; CBS CBS-KNAW Fungal Biodiversity Centre (Centraalbureau voor Schimmelcultures), Utrecht, The Netherlands; CCFE Canadian Collection of Fungal Cultures, Agriculture and Agri-Food Canada, Ottawa, Canada; CPC Culture collection of Pedro Crous, housed at CBS; Cy Cylindrocarpon collection housed at Laboratório de Patologia Vegetal "Verissimo de Almeida" - ISA, Lisbon, Portugal; DAOM Agriculture and Agri-Food Canada National Mycological Herbarium, Canada; DSM Deutsche Sammlung von Mikroorganismen und Zellkulturen GmbH, Braunschweig, Germany; G8 Gary J. Samuels collection; HJS Hans-Josef Schroers collection; IFAM Instituto Agroforestal Mediterráneo, Universidad Politecnica de Valencia, Spain; IMB Institute of Molecular and Cellular Biosciences, The University of Tokyo, Japan; ICMP International Collection of Microorganisms from Plants, Auckland, New Zealand; IFFL Institute of Forest Entomology, Forest Pathology and Forest Protection, Austria; IMI International Mycological Institute, CAB-Bioscience, Egham, Bakehame Lane, U.K.; JAT J. A. Traquair collection; JCM Japan Collection of Microorganisms, Japan; KIS Agricultural Institute of Slovenia, Ljubljana, Slovenia; LYN Lynchburg College, Biology Department, USA; MUCL Mycothèque de l’Université Catholique de Louvain, Belgium; NBRC NITE Biological Resource Center, Japan; NRRL Agricultural Research Service Culture Collection, USA; STE-U Stellenbosch University, South Africa; UPSC Fungal Culture Collection at the Botanical Museum, Uppsala University, Uppsala, Sweden; FKM All-Russian Collection of Microorganisms, Russia.
UK), 1.5 mM MgCl₂, 32 μM of each dNTPs, 0.24 μM of each primer, 0.5 units Taq DNA Polymerase (Bioline), and 1 μl of diluted gDNA in a final volume of 12.5 μl. The cycle conditions in a iCycler thermocycler (BioRad, Hercules, USA) were 94°C for 5 min, followed by 40 cycles at 94°C for 30 s, 52°C for 30 s and 72°C for 80 s, and a final elongation at 72°C for 10 min. Primers were V9G (de Hoog and Gerrits van den Ende 1998) and ITS4 (White et al. 1990) for ITS, T1 (O’Donnell and Cigelnik 1997) and Bt-2b (Glass and Donaldson 1995) for TUB, CYLH3F and CYLH3R (Crous et al. 2004b) for HIS, and EF1 and EF2 (O’Donnell et al. 1998) or CyIEF-1 (5’- ATG GGT AAG GA V GAVA A G A C - 3’; J.Z. Groenewald, unpublished) and CyIEF-R2 (Crous et al. 2004b) for TEF. For TEF, the following modifications were made to the amplification protocol: 2.0 mM of MgCl₂, 40 μM of each dNTPs and addition of 5% of Dimethyl sulfoxide (DMSO; Sigma-Aldrich, Zwijndrecht, Netherlands).

Amplification products of approximately 700 bases (ITS), 650 bases (TUB), 500 bases (HIS) and 600–800 bases (TEF) were obtained for the isolates listed in Table 1. The manually adjusted combined alignment contains 189 sequences (including the two outgroup sequences) and the statistical parameters for the combined and individual analyses are presented in Table 2. For the combined analysis, only a maximum of 1,000 equally parsimonious trees were saved, the first of which is presented as Fig. 1. Phylogenetic trees derived from the individual loci are available in TreeBASE. The combined analysis of the four genes enabled the identification of 37 species. However, the analysis of HIS data alone was enough to resolve these taxa. Sequences of TEF could not distinguish species 6, I. robusta, I. europaea, I. lusitanica, I. rufa and N. ditissima; whereas sequences of TUB could not separate I. robusta, species 4, and 6, while “I.” macro-

**Morphology**

Isolates were grown for up to 5 weeks at 20°C on synthetic nutrient poor agar (SNA; Nirenberg 1976) with and without two 1-cm² filter paper pieces, carnation leaf agar (CLA; Crous et al. 2009b), potato-dextrose agar (PDA; Difco, Detroit, USA) and oatmeal agar (OA; Crous et al. 2009b) under continuous n-UV light (NUV, 400–315 nm; Blacklight-Blue; Sylvania, Capelle a/d IJsssel, Netherlands).

Measurements were done on a 1-cm² agar plug removed from the colony margin, placed on a microscope slide, to which a drop of water and coverslip were added. For each isolate, 30 measurements were obtained for each structure. Measurements were done at ×1,000 magnification using a Nikon Eclipse 80i microscope, or a Leica DM2500. Images were captured using a Nikon DS-Fi1 digital camera with NIS-Elements Software, or a Leica DFC295 digital camera with the Leica Application Suite. Measurements for length and width of conidia and ascospores are given as (Minimum) Lower Limit of a 95% Confidence Interval – Upper Limit of a 95% Confidence Interval (Maximum).

**Results**

**Phylogeny**

Amplification products of approximately 700 bases (ITS), 650 bases (TUB), 500 bases (HIS) and 600–800 bases (TEF) were obtained for the isolates listed in Table 1. The manually adjusted combined alignment contains 189 sequences (including the two outgroup sequences) and the statistical parameters for the combined and individual analyses are presented in Table 2. For the combined analysis, only a maximum of 1,000 equally parsimonious trees were saved, the first of which is presented as Fig. 1. Phylogenetic trees derived from the individual loci are available in TreeBASE. The combined analysis of the four genes enabled the identification of 37 species. However, the analysis of HIS data alone was enough to resolve these taxa. Sequences of TEF could not distinguish species 6, I. robusta, I. europaea, I. lusitanica, I. rufa and N. ditissima; whereas sequences of TUB could not separate I. robusta, species 4, and 6, while “I.” macro-
**Table 2** Statistical information on the individual datasets and number of equally most parsimonious trees for each locus [Internal Transcribed Spacers (ITS) of the nuclear ribosomal RNA gene operon, and partial β-tubulin (TUB), histone H3 (HIS) and translation elongation factor 1-α (TEF) genes]

|                  | ITS  | TUB  | HIS  | TEF  | Combined |
|------------------|------|------|------|------|----------|
| Aligned characters (including gaps) | 475  | 502  | 440  | 696  | 2,113    |
| Parsimony-informative characters | 122  | 212  | 215  | 364  | 913      |
| Variable and parsimony-uninformative characters | 31   | 38   | 11   | 43   | 123      |
| Constant characters | 322  | 252  | 214  | 289  | 1,077    |
| Equally most parsimonious trees obtained | 136  | 384  | 1    | 60   | 1,000    |
| Tree length      | 294  | 603  | 1,095| 1,149| 3,259    |
| Consistency index (Cl) | 0.718| 0.660| 0.468| 0.611| 0.559    |
| Retention index (RI) | 0.978| 0.660| 0.468| 0.611| 0.559    |
| Rescaled Consistency index (RC) | 0.702| 0.642| 0.442| 0.590| 0.537    |

**didyma**, species 5, *I. liliigena* and *I. pseudodesctructans* were supported by low bootstrap values, and CBS 120370 clustered apart from the remaining isolates of *I. crassa*. Of all loci screened, ITS proved to be the least informative, being unable to resolve 22 of the species in this study. Neighbour-Joining (NJ) analyses using the three substitution models, as well as the parsimony analysis, yielded trees with similar topology and bootstrap support values for the individual and combined gene analyses. The trees obtained supported the same clades, sometimes with rearrangements in the order of these clades between the different analyses (data not shown). The results of the phylogenetic analyses are highlighted below under the taxonomic notes or in the Discussion, where applicable.

**Taxonomy**

The present study treats isolates that have been freshly collected, or previously identified and maintained in culture collections as “Cylindrocarpon destructants”, meaning cylindrical, rarely curved, 3-septate macroconidia with obtuse apices, abundant microconidia and chlamydospores (Samuels and Brayford 1990). The latter species has in the past been acknowledged as anamorph of *I. radicicola* (Booth 1966; Chaverri et al. 2011; Samuels and Brayford 1990). However, an examination of the neotype of “C.” destructans in this study [CUP-011985, conidia (18.0)23.0–30.0(35.0) × (6.0)6.5(7.0) μm], found conidia to be considerably smaller than those of *I. radicicola* (24.0)33.1–47.0 (4.9)6.4(7.8) μm (Gerlach and Nilsson 1963) (also confirmed in the present study by examination of CBS 264.65, ex-type), revealing them to represent two distinct species. Furthermore, based on the phylogenetic and morphological data obtained in the present study, several novel species could be distinguished that are phylogenetically distinct from *I. radicicola*, and morphologically distinct based on a range of characters linked to culture characteristics, conidiophores, macro- and microconidium morphology. Some of these could be linked to older names, or taxa long regarded as potential synonyms of “destructans”, which could now be resurrected. These taxa are treated below:

*Ilyonectria anthuricola* A. Cabral & Crous, sp. nov. (Fig. 2)

MycoBank 560108.

**Etymology** Named after its host, *Anthurium*.

*Cylindrocarpi destructantis* morphologic simile, sed longitudine media conidiorum longiore, 29.5–32.2 μm, distinguishur.

*Conidiophores* simple or complex to sporodochial. Simple conidiophores arising laterally or terminally from aerial mycelium, solitary to loosely aggregated, unbranched or sparsely branched bearing up to three phialides, 1–3-septate, 40–95 μm long; phialides monophialidic, more or less cylindrical but slightly tapering towards the tip, 10.5–20.5 μm long, 2.5–3.5 μm wide at the base, 3.0–4.5 μm at widest point, 1.5–2.5 μm near the aperture. Conidiophores giving rise to microconidia, formed on mycelium at agar surface, penicillately mono- or bi-verticillate; phialides monophialidic, narrowly flask-shaped, typically with widest point near the middle, 8–15 μm long, 2.0–3.0 μm wide at the base, 2.5–4.5 μm at widest point, 1.0–2.0 μm near the apex. Sporodochial conidiophores irregularly branched; phialides cylindrical, mostly widest near the middle. *Macroconidia* formed in flat domes of slimy masses, (1–)
3-septate, straight or minutely curved, cylindrical with both ends more or less obtusely rounded, mostly without a visible hilum; 1-septate, (20.0)23.5–26.7(29.0)×(5.5)5.9–6.8(7.0) μm (average=25.1×6.4 μm), with a length:width ratio of 3.6–4.8; 2-septate, (25.0)26.6–29.3(32.0)×(6.5)6.8–7.8(8.5) μm (av. = 27.9×7.3 μm), with a length:width ratio of 3.2–4.8; 3-septate, (25.0)29.5–32.2(38.0)×(6.0)7.5–8.1(9.0) μm (av. = 30.8×7.8 μm) with a length:width ratio of 3.1–5.2. Microconidia 0(−1)-septate, subglobose to ovoid, rarely ellipsoid, mostly with a visible centrally located or slightly laterally displaced hilum; aseptate microconidia, (4.9)5.0–8.1(12.0)×(4.0)4.3–5.5(6.5) μm (av. = 6.5×4.9 μm), with a length:width ratio of 1.0–1.8; 1-septate, (11.0)11.6–16.7(18.0)×(5.0)5.4–6.1(6.0) μm (av. = 14.1×5.8 μm), with a length:width ratio 1.8–3.0. Chlamydospores globose to subglobose to ellipsoid, 8–14×7–12 μm, smooth, but often appearing rough due to deposits, thick-walled, formed intercalary in chains or in clumps and also in the cells of macroconidia, hyaline, becoming golden-brown.

Holotype: Netherlands, Bleiswijk, root rot of Anthurium sp., 1995, coll./isol. R. Pieters, holotype CBS H-20555, culture ex-type CBS 564.95.

Culture characteristics: Mycelium felty with average density. Surface on OA chestnut, with aerial mycelium sparse, saffron; margin pure yellow to orange. Surface on PDA, chestnut with saffron aerial mycelium, growth at margin luteous; zonation absent, transparency homogeneous, margin

Fig. 2 Ilyonectria anthuriicola (CBS 564.95). a–c Simple conidio- phores on aerial mycelium. d–g Conidiophores giving rise to micro- conidia, formed on mycelium at agar surface, penicillately mono- or bi-verticillate. h–l Micro- and macroconidia. m Chlamydospores in mycelium. Bars 10 μm
Isolate studied: CBS 564.95 (Table 1).

Host and distribution: Roots of Anthurium sp. (Netherlands).

*Ilyonectria crassa* (Wollenw.) A. Cabral & Crous, comb. et stat. nov (Fig. 3)

MycoBank 560109.

*Basionym: Cylindrocarpon radicicola var. crassum* Wollenw., Z. Parasitenkunde 3: 495. 1931.
≡ *Cylindrocarpon destructans* var. *crassum* (Wollenw.) C. Booth, Mycol. Pap. 104: 37. 1966.

Conidiophores simple or complex, to sporodochial. Simple conidiophores arising laterally or terminally from aerial mycelium, solitary to loosely aggregated, unbranched or sparsely branched bearing up to two phialides, rarely consisting only of phialides, 1–4-septate, 40–180 μm long; phialides monophialidic, cylindrical to subulate, 20–55 μm long, 2.5–4.0 μm wide at the base, 1.5–2.0 μm near the apex. Complex conidiophores aggregated in small sporodochia (on carnation leaf), repeatedly and irregularly branched; phialides more or less cylindrical, but tapering slightly in the upper part towards the apex, or narrowly flask-shaped, mostly with widest point near the middle, 17–24 μm long, 2.0–3.0 μm wide at the base, 2.5–3.5 μm at the widest point, and 1.5–2.5 μm wide near the apex. *Macroconidia* predominating, formed on both type of conidiophores, on SNA formed in flat domes of slimy masses, 1–3-septate, straight, cylindrical, but may narrow towards the tip, more or less broadly rounded, and the base appearing somewhat acute due to the presence of the hilum, mostly centrally located; 1-septate, (21.0)25.7–27.3(34.0)×(4.5)5.0–5.3(6.5) μm (av. = 26.5×5.1 μm), with a length:width ratio of 3.8–6.7; 2-septate, (23.0)28.5–30.3(37.0)×(4.5)5.3–5.6(6.5) μm (av. = 29.4×5.4 μm) with a length:width ratio of 4.2–6.7; 3-septate, (29.0)34.1–36.0(49.0)×(5.0)5.6–5.8(7.0) μm (av. = 35.1×5.7 μm), with a length:width ratio of 4.8–8.9. *Microconidia* 0–1-septate, ellipsoid to subcylindrical, more or less straight, with a visible, truncate hilum; aseptate microconidia, (7.0)9.7–10.9 (15.0)×(3.0)3.3–3.6(4.5) μm (av. = 10.3×3.5 μm), with a length:width ratio of 1.8–4.3; 1-septate, (12.0)14.2–15.2 (19.0)×(3.0)3.8–4.2(5.0) μm (av. = 14.7×4.0 μm), with a length:width ratio 2.7–5.0. *Conidia* formed in heads on simple conidiophores or as white (OA) or unpigmented (SNA) masses. *Chlamydospores* globose to subglobose to cylindrical, 7–15×6–10 μm, smooth, but often appearing rough due to deposits, thick-walled, terminal on short

Fig. 3 *Ilyonectria crassa* (CBS 129083). a–c Simple conidiophores on aerial mycelium. d–g Micro- and macroconidia. h–i Chlamydospores and macroconidia. Bars 10 μm
lateral branches, rarely intercalary, single, in chains or in clumps, and also in the cells of the macroconidia, hyaline, becoming pale brown.

*Lectotype*: The Netherlands, on *Lilium* bulbs, Dec. 1930, coll./isol. W.F. van Hell, lectotype designated here CBS H-20556, culture ex-lectotype CBS 139.30.

*Culture characteristics*: Mycelium cottony to felty with average to strong density. Surface on OA cinnamon, with aerial mycelium sparse, buff. Surface on PDA saffron with aerial mycelium sparse buff to saffron to pale luteous. No zonation was observed, transparency was homogeneous and growth at margin even. Reverse similar to surface, except in colour, saffron to cinnamon on OA, and chestnut to sienna on PDA. Colonies on PDA grow 5–8 mm diam at 4°C after 7 days. Optimum temperature at 20°C, when colonies reach 31–46 mm diam, after 7 days. Colony diam was 19–34 mm at 25°C, after 7 days. No growth was observed at 30°C.

*Isolates studied*: CBS 139.30; CBS 158.31; CBS 129083; NSAC-SH-2; NSAC-SH-2.5 (Table 1).

*Hosts and distribution*: *Lilium* sp. (bulbs), *Narcissus* sp. (roots) (Netherlands), *Panax quinquefolium* (roots) (Canada).

*Notes*: In the original description, Wollenweber (1931) cites *Cylindrocarpon radicicola* var. *crassum* as occurring on roots of *Ulmus, Taxus* and *Lilium* in Europe (Germany and the Netherlands). He did not designate any type specimen. However, he specifically refers to a culture sent to him by Prof. J. Westerdijk on *Lilium* from the CBS in the Netherlands in 1930, which was regarded as authentic for the species. This culture is represented by CBS 139.30 (accessioned in 1930, from *Lilium*, the Netherlands), and thus we designate a dried, sporulating culture as lectotype for the species.

*Ilyonectria cyclaminicola* A. Cabral & Crous, sp. nov. (Fig. 4)

MycoBank 560110.

*Etymology*: Named after the host from which it was isolated, *Cyclamen* sp.

*Cylindrocarpi destructantis* morphologicis simile, sed longitudine media conidiorum longiore, 26.9–31.9 μm, distinguetur.

*Conidiophores* simple or complex to sporodochial. *Simple conidiophores* arising laterally or terminally from aerial mycelium, solitary to loosely aggregated, unbranched or sparsely branched, bearing up to two phialides, 1–3-septate, 60–120 μm long; phialides monophialidic, more or less cylindrical but slightly tapering towards the tip, 20–60 μm long, 2.0–4.0 μm wide at the base, 3.0–4.5 μm at widest point, 1.5–2.5 μm near the aperture. Conidiophores giving rise to microconidia formed by mycelium at agar surface, penicillate to mono-verticillate; phialides monophialidic, more or less cylindrical, but with slight taper towards the tip, 19–34 μm long, 1.5–2.5 μm wide at the base, 2.0–3.0 μm

![Fig. 4 Ilyonectria cyclaminicola (CBS302.93). a, b Simple conidiophores on aerial mycelium. c Penicillate conidiophores with aseptate microconidia. d Sporodochial conidiophore on carnation leaf agar. e Isolated chlamydospores formed in lateral branches. f–j Micro- and macroconidia. Bars 10 μm](image-url)
Sporodochial conidiophores irregularly branched; phialides more or less cylindrical, but slightly tapering towards the tip, or narrowly flask-shaped, with widest point near the base, 14–26 μm long, 2.5–3.5 μm wide at the base 3.0–4.0 μm at widest point, 1.0–2.0 μm near the apex. Macroconidia formed in flat domes of slimy masses, 1(−3)-septate, straight or minutely curved, cylindrical with both ends more or less broadly rounded, sometimes with a constriction at the septa, mostly without a visible hilum; 1-septate, (19.2)21.3–23.6 (29.8)×(4.4)5.4–6.0(7.3) μm (av. = 22.5×5.7 μm), with a length:width ratio of 3.4–5.5; 2-septate, (23.8)24.0–28.4 (29.8)×(5.0)5.5–7.3(8.0) μm (av. = 26.2×6.4 μm), with a length:width ratio of 3.1–5.1; 3-septate, (25.3)26.9–31.9 (33.6)×(5.8)5.9–6.5(6.9) μm (av. = 29.4×6.2 μm), with a length:width ratio of 3.7–5.6. Microconidia formed in heads or on the agar surface, 0–1-septate, subglobose to ovoid to subcylindrical, mostly with a visible, centrally located or slightly laterally displaced hilum; aseptate microconidia, (3.9)7.6–8.9(12.9)×(2.2)3.6–3.9(5.4) μm (av. = 8.2×3.7 μm), with a length:width ratio of 1.2–3.4; 1-septate, (11.5)13.8–15.2(17.5)×(3.7)4.6–4.9(5.5) μm (av. = 14.5×4.7 μm), with a length:width ratio of 2.3–3.9.

Chlamydospores globose to subglobose, 10–18×10–16 μm, smooth, but often appearing rough due to deposits, thick-walled, formed in lateral branches, rarely intercalary, mostly isolated, hyaline, becoming medium brown.

**Holotype:** Netherlands, Roelofarendsveen, NAKS laboratory, *Cyclamen* bulb, May 1993, coll./isol. M. Hooftman, iden. E.J. Hermanides-Nijhof, holotype CBS H-20557, culture ex-type CBS 302.93.

**Culture characteristics:** Mycelium felty with average density. Surface on OA sepia to chestnut. Surface on PDA sepia to chestnut, with sparse, rust, aerial mycelium; no zonation was observed, and transparency was homogeneous; margins predominantly even. Reverse similar to surface, except in colour, sepia to dark brick on OA and chestnut on PDA. Colonies on PDA do not grow at 4°C after 7 days. Optimum temperature at 22°C, when colonies reach 68–70 mm diam, after 7 days. Colony diam was 63–64 mm at 25°C, after 7 days. No growth was observed at 30°C.

**Isolate studied:** CBS 302.93 (Table 1).

**Host and distribution:** Bulb of *Cyclamen* sp. (Netherlands).

**Ilyonectria europaea** A. Cabral, Rego & Crous, sp. nov. (Fig. 5)

MycoBank 560103.

**Etymology:** Named after the European continent, where this fungus appears to be widely distributed.

![Fig. 5 Ilyonectria europaea (CBS 129078). a–c Simple conidiophores on aerial mycelium. d Sporodochial conidiophore on carnation leaf agar. e Chlamydospores in aerial mycelium. f–i Micro- and macroconidia. Bars 10 μm](image_url)
**Ilyonectriae robustae** morphologice similis, sed longitutine media macroconidiorum breviore, 29.7–31.5 μm, distinguitur. 

Conidiophores simple or complex to sporodochial. Simple conidiophores arising laterally or terminally from aerial mycelium, solitary or loosely aggregated, unbranched or sparsely branched, bearing up to three phialides, 1–3-septate, 50–120 μm long; phialides monophialidic, cylindrical to subulate, 26–60 μm long, 2.5–3.5 μm wide at the base, 1.5–2.5 μm near the apex. Complex conidiophores aggregated in small sporodochia (on carnation leaf), repeatedly and irregularly branched. Macroconidia predominating, formed on both type of conidiophores, on SNA formed in flat domes of slimy masses, 1(–3)-septate, straight or minutely curved, cylindrical with both ends more or less broadly rounded, but may narrow towards the tip, mostly without a visible hilum; 1-septate, (16.4)21.9–23.4(34.0)×(4.0)5.2–5.6(7.8) μm (av. = 22.7×5.4 μm), with a length:width ratio of 3.2–5.4; 2-septate, (22.0)26.4–28.1(34.0)×(4.4)5.9–6.4(8.0) μm (av. = 27.2×6.1 μm), with a length:width ratio of 3.4–6.4; 3-septate, (22.0)29.7–31.5(40.0)×(5.0)6.5–6.9 (8.6) μm (av. = 30.6×6.7 μm), with a length:width ratio of 3.5–6.0. Microconid 0–1-septate, ellipsoid to ovoid, more or less straight, without a visible hilum; asceptate microconidia sometimes curved towards one end, (3.0) 8.5–9.8(17.0)×(1.7)3.3–3.5(5.0) μm (av. = 9.1×3.4 μm), with a length:width ratio of 1.5–3.4; 1-septate, (9.2)13.4–14.6(18.9)×(3.0)4.0–4.4(5.9) μm (av. = 14.0×4.2 μm), with a length:width ratio 2.6–4.0. Conidia formed in heads or on simple conidiophores as white (OA) or unpigmented (SNA) masses. *Chlamydosporae* globose to subglobose, 9–14×7–14 μm, smooth, but often appearing rough due to deposits, thick-walled, terminal on short or long lateral branches or intercalary, single, in chains or in clumps, golden-brown.

**Holotype**: Portugal, Vidigueira, at basal end of a 2-year-old *Vitis vinifera* plant; scion Petit Verdot, rootstock 110R, 2008, coll./isol. C. Rego, holotype CBS H-20558, culture ex-type CBS 129078=Cy241=CPC 19165.

**Culture characteristics**: Mycelium felty with average density. Surface on OA cotton, with saffron aerial mycelium. Sienna to saffron on PDA, with luteous aerial mycelium. Concentric zonation, with homogeneous transparency, margins predominantly even. Reverse similar to surface, except in the colour; sepia on OA, and chestnut to brown on PDA. Colonies on PDA grow poorly, 1–5 mm diam at 4°C after 7 days. Optimum temperature for growth is 22°C, when colonies reach 43–57 mm diam, after 7 days. Colony diam was 37–47 mm at 25°C, after 7 days. No growth was observed at 30°C.

**Isolates studied**: Cy131; Cy155; CBS 537.92; CBS 102892; CBS 129078 (Table 1).

**Hosts and distribution**: *Actinidia chinensis* ‘Hayward’ (internal lesion of stem) (France), *Aesculus hippocastanum* (wood) (Belgium), *Phragmites australis* (stem) (Germany), *Vitis vinifera* (Portugal).

**Ilyonectria gamsii** A. Cabral & Crous, sp. nov. (Fig. 6) MycoBank 560112.

**Etymology**: Named after Prof. dr. Walter Gams, who has made a major contribution to our knowledge of Hypocrelean soil fungi.

**Ilyonectriae panacis** morphologice similis, sed longitutine media macroconidiorum breviore, 34.3–38.5 μm, distinguitur.

Conidiophores simple or complex to sporodochial. Simple conidiophores arising laterally or terminally from aerial mycelium, solitary to loosely aggregated, unbranched or sparsely branched, bearing up to two phialides, 1–3-septate, 50–150 μm long; phialides monophialidic, cylindrical to subulate, 30–60 μm long, 2.5–3.5 μm wide at the base, 1.5–2.0 μm near the aperture. Sporodochial conidiophores irregularly branched; phialides cylindrical, mostly widest near the base. Macroconidia predominating, formed on simple conidiophores, on SNA formed in flat domes of slimy masses, 1–3-septate, straight, cylindrical with both ends broadly rounded, with mostly visible, centrally located hilum; 1-septate, (22.0)25.7–27.9(33.0)×(4.0)5.1–5.5(6.0) μm (av. = 26.8×5.3 μm), with a length:width ratio of 4.3–6.2; 2-septate, (25.0)28.2–31.7(39.0)×(5.0)5.5–5.9(6.5) μm (av. = 29.9×5.7 μm), with a length:width ratio of 4.2–7.1; 3-septate, (24.0)34.3–38.5(44.0)×(5.0)5.9–6.3(7.0) μm (av. = 36.4×6.1 μm), with a length:width ratio of 4.3–7.3. Microconid 0–1-septate, ellipsoid to subcylindrical, more or less straight, mostly with a visible hilum; asceptate microconidia (4.0)6.9–8.0(10.0)×(3.0)4.0–4.5(5.0) μm (av. = 7.4×4.3 μm), with a length:width ratio of 1.3–2.9; 1-septate, (8.0)12.9–15.7(18.0)×(4.0)4.2–4.7(5.5) μm (av. = 14.3×4.4 μm), with a length:width ratio 1.8–4.0. *Chlamydosporae* globose to subglobose to ellipsoidal, 8–14×7–12 μm, smooth, but often appearing rough due to deposits, thick-walled, mostly intercalary, rarely terminal on short lateral branches, single, in chains or in clumps, hyaline, becoming medium brown.

**Holotype**: Netherlands, Lelystad, soil, June 1997, coll./isol. J.T. Poll, iden. W. Gams, holotype CBS H-20559, culture ex-type CBS 940.97.

**Culture characteristics**: Mycelium cottony, dense. Surface on OA cinnamon, with sparse, buff aerial mycelium, on PDA umber to chestnut, with buff to saffron aerial mycelium; zonation absent, transparency homogeneous, margin even; reverse similar to surface, but chestnut on PDA. Colonies on PDA grow 6–7 mm diam at 4°C after 7 days. Optimum temperature at 22°C when colonies reach...
– 45 mm diam, after 7 days. Colony diam is 22–24 mm at 25°C, after 7 days. No growth observed at 30°C.

Isolate studied: CBS 940.97 (Table 1).

Habitat and distribution: Soil (Netherlands).

Ilyonectria liliigena A. Cabral & Crous, sp. nov. (Fig. 7)

MycoBank 560114.

Etymology: Named after its host, Lilium regale.

Ilyonectria panacis morphologicæ similis, sed longitudine media macroconidiorum 3-septatorum breviore, 27.9–29.8 μm, distinguitur.

Conidiophores simple or complex or sporodochial. Simple conidiophores arising laterally or terminally from aerial mycelium, solitary to loosely aggregated, unbranched or sparsely branched, bearing up to two phialides, 1–4-septate, 50–170 μm long; phialides monophialidic, cylindrical to subulate, 30–65 μm long, 2.0–3.5 μm wide at the base, 1.5–2.0 μm near the apex. Sporodochial conidiophores irregularly branched; phialides cylindrical, mostly widest near the base. Macroconidia predominating, formed on simple conidiophores, on SNA formed in flat domes of slimy masses, 1(−3)-septate, straight or frequently minutely curved, cylindrical or sometimes typically minutely widening towards the tip, therefore appearing somewhat clavate, mostly without a visible hilum; 1-septate, (19.0)22.9–24.6 (30.0)×(3.3)4.2–4.5(5.2) μm (av. = 23.8×4.3 μm), with a length:width ratio of 4.0–7.0; 2-septate, (21.0)26.1–27.7 (32.1)×(4.0)4.7–5(5.7) μm (av. = 26.9×4.9 μm) with a length:width ratio of 3.8–7.0; 3-septate, (23.9)27.9–29.8 (35.0)×(3.9)4.7–5.1(6.0) μm (av. = 28.9×4.9 μm), with a length:width ratio of 4.0–8.3. Microconidia 0–1-septate, ellipsoidal to subcylindrical, more or less straight, mostly with a visible hilum; aseptate, microconidia (5.9)8.9–10.3 (17.0)×(2.5)3.0–3.2(4.4) μm (av. = 9.6×3.1 μm), with a length:width ratio of 2.0–4.6; 1-septate, (10.0)12.9–14.3 (18.0)×(2.5)3.3–3.6(4.5) μm (av. = 13.6×3.4 μm), with a length:width ratio 2.8–5.6. Conidia formed in heads on simple conidiophores or as white (OA) or unpigmented (SNA) masses. Chlamydosporæ globose to subglobose, 6–14×5–12 μm, smooth but often appearing rough due to deposits, thick-walled, mostly in terminal on short lateral branches or rarely intercalary, single, in chains or in clumps, hyaline, becoming slightly brown at margins.

Holotype: Netherlands, Hoorn, bulb rot of Lilium regale, 1949, coll./isol. M.A.A. Schipper, holotype CBS H-20560, culture ex-type CBS 189.49.

Culture characteristics: Mycelium felty, with an average to strong density. Surface on OA sienna, with sparse, saffron, aerial mycelium. Surface on PDA sepia to cinnamon, with saffron to buff aerial mycelium. Zonation absent or concentric, with homogeneous transparency. Margins were even, or sometimes slightly uneven. Reverse similar to surface, except in colour; on OA pale vinaceous
to cinnamon; on PDA buff to saffron to chestnut. Colonies on PDA grew poorly (1–4 mm diam) at 4°C after 7 days. Optimum temperature at 22°C, when colonies reach 34–45 mm diam, after 7 days. Colony diam was 16–29 mm at 25°C, after 7 days. No growth was observed at 30°C.

**Isolates studied:** CBS 189.49; CBS 732.74; CBS 304.85; CBS 305.85 (Table 1).

**Host and distribution:** *Lilium regale* bulbs (Netherlands).

*Ilyonectria lusitanica* A. Cabral, Rego & Crous, sp. nov. (Fig. 8)

MycoBank 560105.

**Etymology:** Named after the Latin name for the country from which it was collected, Portugal.

*Ilyonectriae europaeae* morphologice similis, sed longitudine media macroconidiorum breviore, 25–28.4 μm, distinguetur.

**Conidiophores** simple or complex, sporodochial. *Simple conidiophores* arising laterally or terminally from aerial mycelium, solitary to loosely aggregated, unbranched or sparsely branched, bearing up to two phialides, 1–4-septate, 60–220 μm long; phialides monophialidic, cylindrical to subulate, 20–70 μm long, 2.5–3.5 μm wide at the base, 1.5–2.5 μm near the aperture. *Complex conidiophores* aggregated in small sporodochia, repeatedly and irregularly branched. *Macroconidia* predominating, formed by both type of conidiophores, on SNA formed in flat domes of slimy masses, 1(–3)-septate, straight or minutely curved, cylindrical with both ends more or less broadly rounded, but may narrow towards the tip, without a visible hilum, and may have a constriction on the septa in older cultures; 1-septate, (14.0) 17.3–18.8(21.0)×(4.0)6–5(5.5) μm (av. = 18.1×4.8 μm), with a length:width ratio of 2.8–4.8; 2-septate, (18.0)20.5–22.1(27.0)×(4.0)9–5.2(6.0) μm (av. = 21.3×5.1 μm), with a length:width ratio of 3.5–5.4; 3-septate, (18.0)25.0–28.4 (38.0)×(4.5)5–5.5(6.0) μm (av. = 26.7×5.4 μm), with a length:width ratio of 3.6–6.8. *Microconidia* 0–1-septate, ellipsoid to ovoid, more or less straight, without a visible hilum, and may have a constriction at the septum; aseptate, (5.0)6.9–8.2(10.0)×(2.5)3.0–3.3(4.0) μm (av. = 7.6×3.2 μm), with a length:width ratio of 1.7–3.3; 1-septate, (8.0)10.0–11.0 (14.0)×(3.0)3.4–3.7(4.0) μm (av. = 10.5×3.6 μm), with a length:width ratio 2.0–3.7. *Conidia* formed in heads on simple conidiophores or as white (OA) or unpigmented (SNA) masses. *Chlamydospores* rarely observed, globose to subglobose to cylindrical, 9–13×7–11 μm, smooth, but often appearing rough due to deposits, thick-walled, intercalary, hyaline, becoming slightly brown at the margin.

![Fig. 7 Ilyonectria liligena (CBS 189.49). a–d Simple conidiophores on aerial mycelium. e Chlamydospores on mycelium. f–i Micro- and macroconidia. Bars 10 μm](image-url)
Holotype: Portugal, Melgaço, Alvaredo, on *Vitis vinifera*, below grafting zone, 6–year-old plant; scion Alvarinho on rootstock 196–17, 2005, coll./isol. N. Cruz, holotype CBS H-20563, culture ex-type CBS 129080=Cy197=CPC 19166.

Culture characteristics: Mycelium felty with average density. Surface on OA cinnamon, with aerial mycelium sparse, buff. Surface on PDA, cinnamon, with sparse, ochreous to buff aerial mycelium. Zonation absent, transparency homogeneous, margin even. Reverse similar to surface but buff to cinnamon on OA, and chestnut to cinnamon on PDA. Colonies on PDA grow 5–6 mm at 4°C after 7 days. Optimum temperature between 20 and 22°C, with colonies reaching 42–46 mm and 43–46 mm, respectively, after 7 days. Colony diam was 31–32 mm at 25°C, after 7 days. No growth observed at 30°C.

Isolate studied: CBS 129080 (Table 1).

Host and distribution: *Vitis vinifera* (Portugal).

*Ilyonectria mors-panacis* (A.A. Hildebr.) A. Cabral & Crous, comb. nov. (Fig. 9)

MycoBank 560115.

*Basionym:* *Ramularia mors-panacis* A.A. Hildebr., Can. J. Res. 12: 101. 1935.

≡ *Cylindrocarpon destructans* f.sp. *panacis* Matuo & Miyaz., Ann. Phytopath. Soc. Japan 50: 390. 1984.

*Conidiophores* simple or complex, sporodochial. *Simple conidiophores* arising laterally or terminally from aerial mycelium, solitary to loosely aggregated, unbranched or sparsely branched, rarely consisting only of phialides, 1–3-septate, 45–170 μm long; phialides monophialidic, cylindrical to subulate, 23–55 μm long, 2.0–3.0 μm wide at the base, 1.5–3.0 μm near the apex. *Complex conidiophores* aggregated in small sporodochia, repeatedly and irregularly branched. *Macroconidia* predominating, formed on simple conidiophores, on SNA formed in flat domes of slimy masses, 1(–3)-septate, straight, cylindrical with both ends more or less broadly rounded, mostly without a hilum; 1-septate, (21.0)28.2–31.6(40.0)×(5.0)5.8–6.3(7.5) μm (av. = 29.9×6.1 μm), with a length:width ratio of 3.3–7.0; 2-septate, (28.0)30.5–38.4(42.0)×(5.0)5.9–6.4–7.0(7.1) μm (av. = 34.4×6.4 μm), with a length:width ratio of 4.0–6.0; 3-septate, (37.8)39.0–44.2(45.0)×(6.9)7.0–7.5(7.5) μm (av. = 41.0×7.2 μm), with a length:width ratio of 5.3–6.0. *Microconidia* 0–1-septate, ellipsoid to subcylindrical, more or less straight, without a visible hilum; aseptate, (5.0)8.9–10.4(17.0)×(2.5)3.6–3.9(5.0) μm (av. = 9.6×3.8 μm), with a length:width ratio of 1.3–3.4; 1-septate, (9.0)12.5–14.1(19.0)×(3.5)4.4–4.8(5.5) μm (av. = 13.3×4.6 μm), with a length:width ratio 2.0–4.0. Conidia

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**Fig. 8** *Ilyonectria lusitanica* (CBS 129080). a–c Simple conidiophores of the aerial mycelium. d Chlamydospores on mycelium. e–g Micro- and macroconidia. Bars (a) 20 μm, (b–g) 10 μm
formed in heads on simple conidiophores or as white, creamy (OA) or hyaline (SNA) masses. *Chlamydosporae* globose to subglobose, 8–16×7–15 μm, smooth, but often appearing rough due to deposits, thick-walled, terminal on short lateral branches or intercalary, single, in chains or in clumps, hyaline, becoming medium brown.

**Lectotype**: Canada, Ontario, on living roots of *Panax quinquefolium*, June 1935, A.A. Hildebrand, lectotype designated here CBS H-20561, culture ex-lectotype CBS 306.35.

**Culture characteristics**: Mycelium felty with an average density. Surface on OA and PDA chestnut, with sparse, buff to rosy-buff to cinnamon or saffron aerial mycelium. Concentric zonation, with homogeneous transparency, and even margins. Reverse similar to surface, ochreous to fulvous, or sepia to dark vinaceous on OA, and chestnut to sienna on PDA. Colonies on PDA grow 3–9 mm diam at 4°C after 7 days. Optimum temperature for growth is 18°C, when colonies reach 22–40 mm diam, after 7 days. Colony diam was 31–40 mm at 25°C after 7 days. No growth was observed at 30°C.

**Isolates studied**: CBS 306.35; CBS 307.35; CBS 120359; CBS 120360; CBS 120361; CBS 120362; CBS 120363; CBS 120364; CBS 120365; CBS 120366; CBS 120367; CBS 120368; CBS 120369; CBS 124662; CPC 13535; CPC 13537 (Table 1).

**Hosts and distribution**: *Panax ginseng* (Japan), *P. quinquefolium* (Canada).

**Notes**: *Ilyonectria mors-panacis* is distinct from “C.” *destructans* (anamorph: “C”. *destructans*, neotype CUP-011985, conidia (18.0)23.0–30.0(35.0) × (6.0)6.5(7.0) μm) in having larger conidia, and indistinct hila (being prominent, flat, 2 μm diam in *I. radicicola*; see also Samuels and Brayford 1990, Fig. 1). “Ramularia” *panacicola* is distinct by also having shorter conidia than *I. mors-panacis*, 5.5–34.2 × 2.5–7.2 μm (Zinssmeister 1918), and appears to be another potential synonym of “C.” *destructans*. However, no authentic material could be located of “R.” *panacicola*, and the only isolate deposited under this name was a Canadian strain collected by Hildebrand (1935), which in fact represented *I. mors-panacis* (Fig. 1). The oldest name for the species on Panax treated here, therefore, is *R. mors-panacis* (CBS 306.35), with the Japanese collections (“C.” *panacis ≡ “C.” destructans* f.sp. *panacis*, CBS 124662=NBRC 31881) being later synonyms (see Fig. 1).

**Ilyonectria panacis** A. Cabral & Crous, sp. nov. (Fig. 10)

**Etymology**: Named after its host, *Panax quinquefolium*.

**Conidiophores** simple or complex, sporodochial. Simple conidiophores arising laterally or terminally from aerial mycelium, solitary to loosely aggregated, unbranched or sparsely branched bearing up to three phialides, 1–5-septate, 60–220 μm long; phialides monophialidic, cylindrical to

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**Fig. 9** *Ilyonectria mors-panacis* (CBS120363). a, b Simple conidiophores on aerial mycelium. c–g Micro- and macroconidia. h–j Chlamydospores on mycelium. Bars 10 μm.
subulate, 20–65 μm long, 2.5–3.0 μm wide at the base, 1.5–2.0 μm near the aperture. Complex conidiophores aggregated in small sporodochia, repeatedly and irregularly branched. Macroconidia predominating, formed on both type of conidiophores, on SNA formed in flat domes of slimy masses, 1(−3)-septate, straight, cylindrical with both ends more or less broadly rounded, mostly with a visible centrally located hilum; 1-septate, (20.0)23.7–25.9(32.0)×(4.0)4.7–5.0(5.5) μm (av. = 24.8×4.8 μm), with a length:width ratio of 4.0–6.0; 2-septate, (23.0)27.0–30.3(37.0)×(4.8)5.0–5.4(6.0) μm (av. = 28.7×5.2 μm), with a length:width ratio of 4.6–6.7; 3-septate, (27.0)31.2–35.0(49.0)×(5.0)5.4–5.8(6.0) μm (av. = 33.1×5.6 μm), with a length:width ratio of 4.9–8.2. Microconidia 0–1-septate, ellipsoid to ovoid to subcylindrical, more or less straight, mostly with a visible hilum; aseptate, (6.0)8.0–9.8(13.0)×(3.5)3.7–3.9(4.0) μm (av. = 8.9×3.8 μm), with a length:width ratio of 1.7–3.3; 1-septate, (8.0)11.3–13.7(16.0)×(3.5)3.8–4.2(4.5) μm (av. = 12.5×4.0 μm), with a length:width ratio 1.8–4.3. Conidia formed in heads on simple conidiophores or as white (OA) or unpigmented (SNA) masses. Chlamydospores globose to subglobose to ellipsoidal, 8–14×6–10 μm, smooth, but often appearing rough due to deposits, thick-walled, terminal on short lateral branches or intercalary, single, in chains or in clumps, hyaline, becoming medium brown.

Holotype: Canada, Alberta, Panax quinquefolium, 1998, coll./isol. K. F. Chang, holotype CBS H-20562, culture ex-type CBS 129079=CDC-N-9A=CPC 19167.

Culture characteristics: Mycelium felty with strong density. Surface on OA chestnut to sienna, with aerial mycelium sparse, vinaceous-buff. Surface on PDA chestnut to cinnamon, with aerial mycelium sparse, buff to saffron. No zonation was observed, and transparency was homogeneous; margins predominantly even. Reverse similar to surface, except in the colour, fawn to cinnamon on OA, and chestnut on PDA. Colonies on PDA grow 5 mm diam at 4°C after 7 days. Optimum temperature at 20°C, with colonies reaching 40–42 mm diam, after 7 days. Colony diam was 15 mm at 25°C after 7 days. No growth observed at 30°C.

Isolate studied: CBS 129079 (Table 1).

Host and distribution: Panax quinquefolium (Canada).

Notes: Several species have in the past been described on Panax in the genera Ramularia and Cylindrocarpon. The only unresolved species is “C.” destructans (and its potential synonym, “Ramularia” panacicola, see above). “Cylindrocarpon” destructans is clearly different from I.
panacis, which has larger conidia, (27.0)31.2–33.1–35.0 (49.0)×(5.0)5.4–5.6–5.8(6.0) μm.

_Ilyonectria pseudodestructans_ A. Cabral, Rego & Crous, sp. nov. (Fig. 11)

MycoBank 560106.

Etymology: Named after its morphological similarity to "Cylindrocarpon" destructans.

_Ilyonectriae crassae_ morphologice similis, sed macroconidis clavatis distinguatur.

Conidiophores simple or complex, sporodochial. Simple conidiophores arising laterally or terminally from aerial mycelium, solitary to loosely aggregated, unbranched or sparsely branched, bearing up to two phialides, 1–3-septate, 50–180 μm long; phialides monophialidic, cylindrical to subulate, 30–58 μm long, 2.5–3.5 μm wide at the base, 1.5–2.0 μm near the aperture. Complex conidiophores aggregated in small sporodochia, repeatedly and irregularly branched. Macroconidia predominating, formed by simple conidiophores, on SNA formed in flat domes of slimy masses, 1–3(–4)-septate, straight, typically clavate, mostly centrally located hilum; 1-septate, (19.0)25.8–27.5(35.0)×(4.0)5.0–5.3(6.5) μm (av. = 26.7×5.2 μm), with a length:width ratio of 3.8–6.6; 2-septate, (23.0)30.0–31.7(38.0)×(5.0)5.3–5.5(6.0) μm (av. = 30.9×5.4 μm), with a length:width ratio of 4.3–7.4; 3-septate, (28.0)34.2–36.2(48.0)×(5.0)5.9–6.2(7.0) μm (av. = 35.2×6.0 μm), with a length:width ratio of 4.6–7.4. Microconidia 0–1-septate, ellipsoid to ovoid to subcylindrical, more or less straight, with a visible, centrally located hilum; aseptate (6.0)10.5–11.8 (15.0)×(3.0)3.6–3.8(4.5) μm (av. = 11.2×3.7 μm), with a length:width ratio of 1.5–4.3; 1-septate, (10.0)14.6–15.6 (18.0)×(3.0)4.1–4.4(5.0) μm (av. = 15.1×4.2 μm), with a length:width ratio of 2.4–5.0. Conidia formed in heads on simple conidiophores or as white (OA) or unpigmented (SNA) masses. Chlamydospores globose to subglobose to ellipsoid, 9–18×8–14 μm, smooth but often appearing rough due to deposits, thick-walled, terminal on short lateral branches or intercalary, in chains or in clumps, and also in the cells of macroconidia, hyaline, becoming medium brown.

Holotype: Portugal, São Paio, Gouveia, _Vitis vinifera_, 4-year-old, showing decline symptoms, scion Malvasia fina; rootstock 1103P, 1996, coll./isol. C. Rego, holotype CBS H-20564, culture ex-type CBS 129081=Cy20=CPC 19164.

Culture characteristics: Mycelium felty, with average to strong density. Surface on OA cinnamon, with sparse, buff

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Fig. 11 _Ilyonectria pseudodestructans_ (all from CBS 129081, except _g_ and _e_ from CBS117824). _a–d_ Simple, unbranched or sparsely branched conidiophores on aerial mycelium. _e–g_ Chlamydospores on mycelium and macroconidia. _h–l_ Micro- and macroconidia. Bars 10 μm
to saffron or chestnut to sienna aerial mycelium. Surface on PDA cinnamon to vinaceous, with sparse, saffron to buff or chestnut to sienna aerial mycelium. Zonation absent, with homogeneous transparency; margins even. Reverse similar to surface, except in colour, sepia to cinnamon on OA and chestnut to cinnamon on PDA. Colonies on PDA grow poorly (4–6 mm diam), at 4°C after 7 days. Optimum temperature between 20–22°C, when colonies reach 32–44 mm and 37–41 mm diam, respectively, after 7 days. Colony diam was 22–29 mm at 25°C after 7 days. No growth was observed at 30°C.

**Isolates studied:** CPC 13534; CBS 117812; CBS 117824; CBS 129081; Cy22 (Table 1).

**Hosts and distribution:** Poa pratensis (Canada), Quercus sp. (Austria), Vitis vinifera (Portugal).

**Notes:** Ilyonectria pseudodestructans is reminiscent of "Cylindrocarpon" destructans, in having a similar conidial morphology (3-septate, with central, truncate hilum). However, conidia of I. pseudodestructans are somewhat longer than those of I. radicicola.

**Fig. 12** Ilyonectria robusta (a, b from CPC 13532×CBS 308.35; c–k from CPC 13532×CBS 117813). a, b Development of perithecia on the surface of a birch toothpick or agar. c–e Perithecia mounted in lactic acid. d Ostiolar area. e Surface view of perithecia wall region. f–h Longitudinal sections of perithecia showing details of ostiole and wall. i–k Asci and ascospores. Bars (a–c) 50 μm; (d, f) 20 μm; (e, g–k) 10 μm

**Ilyonectria robusta** (A.A. Hildebr) A. Cabral & Crous, **comb. nov** (Figs. 12 and 13)

MycoBank 560113.

**Basionym:** Ramularia robusta A.A. Hildebr. Can. J. Res. 12: 102. 1935.

Perithecia formed heterothallically in vitro, disposed solitarily or in groups, developing directly on the agar surface or on sterile pieces of birch wood, ovoid to obpyriform, with a flattened apex, up to 70 μm wide, orange to red, becoming purple-red in 3 % KOH (positive colour reaction), smooth to warted, up to 250 μm diam and high; perithecial wall consisting of two regions; outer region 11–36 μm thick, composed of 1–3 layers of angular to subglobose cells, 10–30×6–24 μm; cell walls up to 1 μm thick; inner region 8–14 μm thick, composed of cells that are flat in transverse optical section and angular to oval in subsurface optical face view, 5–11×2.5–5 μm; Asc narrowly clavate to cylindrical, 40–50×4.5–6 μm, 8-spored; apex subtruncate, with a minutely visible ring.
Ascospores medianly 1-septate, ellipsoid to oblong-ellipsoidal, somewhat tapering towards both ends, smooth to finely warted, frequently guttulate, hyaline, (8.2)9.4–9.7–10.0(11.5)×(2.5)2.9–3.0–3.1(3.7) μm. Conidiophores simple or complex or sporodochial. Simple conidiophores arising laterally or terminally from aerial mycelium, solitary to loosely aggregated, unbranched or sparsely branched, bearing up to three phialides, 1–4-septate, 55–160 μm long; phialides monophialidic, cylindrical to subulate, 20–60 μm long, 2.0–3.0 μm wide at the base, 1.5–2.0 μm near the apex. Complex conidiophores aggregated in small sporodochia (on carnation leaf agar; Crous et al. 2009b), repeatedly and irregularly branched; phialides more or less cylindrical, but tapering slightly in the upper part towards the apex, 15–20 μm long, 2.5–3.5 μm wide at the base, 3.0–4.0 μm at the widest point, and 1.0–2.0 μm wide near the apex. Macroconidia predominating, formed on simple conidiophores, on SNA formed in flat domes of slimy masses, 1–3-septate, straight, minutely curved or sometimes distorted, cylindrical with both ends more or less broadly rounded, but may narrow towards the tip, mostly without a visible hilum; 1-septate, (15.0)22.8–24.6(35.0)×(4.5)6.3–6.7(8.0) μm (av. = 23.7×6.5 μm), with a length:width ratio of 2.7–5.2; 2-septate, (20.0)26.2–28.1(38.0)×(5.0)6.9–7.2(8.0) μm (av. = 27.2×7.0 μm), with a length:width ratio of 2.9–5.2; 3-septate, (24)32.3–34.7(58)×(6.0)7.2–7.5(9.0) μm (av. = 33.5×7.4 μm), with a length:width ratio of 3.1–7.3. Microconidia 0–1-septate, ellipsoid to ovoid to subcylindrical, more or less straight, without a visible hilum; aseptate, (4.0)8.0–9.3(14.0)×(2.5)3.6–4.0(5.5) μm (av. = 8.7×3.8 μm), with a length:width ratio of 1.3–4.0; 1-septate, (9.0)13.5–14.7(18.0)×(3.5)4.7–5.1(6.0) μm (av. = 14.1×4.9 μm), with a length:width ratio 1.5–4.5. Conidia formed in heads on simple conidiophores or as white (OA) or unpigmented (SNA) masses. Chlamydospores globose to subglobose, 7–14×6–13 μm, smooth, but often appearing rough due to deposits, thick-walled, mostly occurring intercalary in chains, hyaline, becoming golden-brown.

Lecto- and teleotype: Canada, Ontario, on living roots of Panax quinquefolium, 1935, A.A. Hildebrand, lectotype designated here CBS H-20565, as dried culture of CBS 308.35; teleotype designated here CBS H-20566, including fertile perithecia of the teleomorph (CPC 13532×CBS 308.35), culture ex-lectotype CBS 308.35.

Fertile matings: Perithecia observed after 4 wk in crossings of strains: CPC 13532×CBS 308.35, CPC 13532×CBS 773.83, CPC 13532×CBS 605.92, CPC 13532×CBS 117813, CBS 129084×CBS 308.35, CBS 129084×CBS 605.92, CBS 129084×CBS 117813.
Culture characteristics: Mycelium felty with an average density. Surface on OA sienna to sepia with aerial mycelium sparse, buff. Surface on PDA cinnamon, with aerial mycelium buff to cinnamon, or rosy buff on PDA. Zonation absent to concentric, with homogeneous transparency; margins predominantly even, but sometimes uneven. Reverse similar to surface, except in the colour, sienna on OA and chestnut at the centre, and sienna to orange towards the margin on PDA. Colonies on PDA grow 4–7 mm at 4°C after 7 days. Optimum temperature at 22°C when colonies reach 40–52 mm diam, after 7 days. Colony diam was 35–48 mm at 25°C after 7 days. No growth to slight growth (0–2 mm) was observed at 30°C.

Isolates studied: CBS 321.34; CBS 308.35; CBS 773.83; CBS 605.92; CBS 117813; CBS 117814; CBS 117815; CBS 117817; CBS 117818; CBS 117819; CBS 117820; CBS 117821; CBS 117822; CBS 117823; CBS 129084; CD1666; CPC 13532; Cy23; Cy158; Cy231 (Table 1).

Hosts and distribution: Loroglossum hircinum (root) (Tunisia), Panax quinquefolium (root) (Canada), Prunus cerasus, Thymus sp., Vitis vinifera (basal end of rootstock) (Portugal), Quercus robur (root), Quercus sp. (root) (Austria), Tilia petiolaris (rootstock) (Germany), water (in aquarium with Anodonta sp.) (Netherlands).

Notes: When Hildebrand (1935) described Ramularia robusta from living roots of Panax quinquefolium in Ontario, Canada, he did not indicate a type specimen. However, he deposited an original culture in the CBS. A sporulating, dried-down culture is thus herewith designated as lectotype, and a new name proposed in Ilyonectria, with a teleotype represented by a fertile mating between CPC 13532×CBS 308.35.

Ilyonectria rufa A. Cabral & Crous, sp. nov (Fig. 14)

MycoBank 560116.

Etymology: The epithet “rufa” referring to “Coleomyces rufus”, a provisional name proposed for this species by Moreau and Moreau (1937).

Ilyonectriae crassae morphologicse similis, sed macroconidis brevioribus, 28–31.2 μm longis, distinguitur.

Conidiophores simple or complex, sporodochial. Simple conidiophores arising laterally or terminally from aerial mycelium, solitary to loosely aggregated, unbranched or sparsely branched, bearing up to two phialides, 1–5-septate, 55–210 μm long; phialides monophialidic, cylindrical to subulate, 20–57 μm long, 2.5–3.5 μm wide at the base, 1.5–2.0 μm near the aperture. Complex conidiophores aggregated in small sporodochia, repeatedly and irregularly branched. Macroconidia predominating, formed on both types of conidiophores, on SNA formed in flat domes of slimy masses, 1(–3)-septate, straight, cylindrical with both

Fig. 14 Ilyonectria rufa (All from CBS 156.47, except e from CBS 120372). a–c Simple, sparsely branched conidiophores on aerial mycelium. d–f Chlamydospores in mycelium and in macroconidia. g–k Micro- and macroconidia. Bars 10 μm
ends broadly round, mostly centrally located hilum; 1-septate, (17.0)22.3–23.8(29.0)×(4.0)5.1–5.4(6.0) μm (av. = 23.1×5.3 μm), with a length:width ratio of 3.1–5.6; 2-septate, (19.0)24.5–26.6(32.0)×(4.0)5.2–5.5(6.5) μm (av. = 25.5×5.4 μm), with a length:width ratio of 3.4–6.0; 3-septate, (23.0)28.6–31.2(37.0)×(5.0)5.5–5.9(7.0) μm (av. = 29.9×5.7 μm), with a length:width ratio of 3.4–7.2. *Microconidia* 0–1-septate, ellipsoid to subcylindrical, more or less straight, with a visible, centrally located hilum; aseptate, (4.0)8.4–9.8 (15.0)×(3.0)3.5–3.8(5.0) μm (av. = 9.1×3.6 μm), with a length:width ratio of 1.3–4.0; 1-septate, (9.0)12.1–13.3 (17.0)×(3.0)4.2–4.6(5.5) μm (av. = 12.7×4.4 μm), with a length:width ratio 2.2–3.8. *Conidia* formed in heads on simple conidiophores or as white (OA) or unpigmented (SNA) masses. *Chlamydosporides* globose to subglobose to cylindrical, 7–12×6–9 μm, smooth, but often appearing rough due to deposits, thick-walled, terminal on short, lateral branches, or intercalary, single, in chains or in clumps, and also in the cells of the macroconidia, hyaline, becoming slightly brown in the outer wall.

**Holotype:** France, dune sand, Feb. 1937, coll./isol. F. Moreau, holotype CBS H-20567, culture ex-type CBS 153.37.

**Culture characteristics:** For CBS 153.37, CBS 156.47, CPC 13536 and 94–1628: Mycelium feltly with average to strong density. Surface on OA buff to saffron, aerial mycelium sparse, buff. On PDA rosy-buff to cinnamon, slightly brown in the outer wall. For CBS 640.77, CBS 120371 and CBS 120372: Mycelium felty with average to strong density. Surface on OA cinnamon to sienna, aerial mycelium sparse, buff. On PDA cinnamon to sienna, V enezuela. Hosts and distribution: *Azalea indica* (Belgium), dune sand (France), *Picea glauca, Pseudotsuga menziesii* (Canada).

**Notes:** The genus *Coleomyces* represents a later synonym of *Cylindrocarpon* (Booth 1966). However, *Coleomyces*, which is based on *C. rufus* (Moreau and Moreau 1937), was published as “ad interim”, suggesting that Moreau and Moreau were planning to validate the name later, which was not the case. Based on the International Code of Botanical Nomenclature (Art. 34.1, Ex. 6), Chaverri et al. (2011) correctly chose to ignore the name. However, an original strain of *C. rufus* was deposited in the CBS (CBS 153.37), and the species epithet is herewith validated for the species.

*Ilyonectria venezuelensis* A. Cabral & Crous, sp. nov. (Fig. 15)

MycoBank 560117.

**Etymology:** Named after the country from where it was collected, Venezuela.

*Ilyonectriae robustae* morphologicie similis, sed conidiophoris cum verticillo terminali phialidium distinguetur.

*Conidiophores* simple or complex, sporodochial. *Simple conidiophores* arising laterally or terminally from aerial mycelium or from agar surface, solitary to loosely aggregated, unbranched, or bearing terminal, penicillate phialides, 1–4-septate, 35–200 μm long; phialides monophialidic, cylindrical to subulate, 40–60 μm long, 2.5–3.5 μm wide at the base, 1.5–2.5 μm near the apex, or narrowly flask-shaped, 16–40 μm long, 2.0–3.0 μm wide at the base, 3.0–4.0 μm at the widest point, 1.5–2.5 μm near the apex. *Complex conidiophores* aggregated in small sporodochia, repeatedly and irregularly branched. *Macroconidia* predominating, formed by both types of conidiophores, on SNA formed in flat domes of slimy masses, 1–3-septate, straight or minutely curved, cylindrical with both ends more or less broadly rounded, but may narrow towards the tip, mostly without a visible hilum; 1-septate, (22.0)24.6–27.3(35.0)×(5.0)5.3–5.7(6.5) μm (av. = 26.0×5.5 μm), with a length:width ratio of 3.8–7.0; 2-septate, (25.0)26.3–37.4(44.0)×(5.9)6.0–6.6(7.0) μm (av. = 31.9×6.3 μm), with a length:width ratio of 4.2–6.8; 3-septate, (28.0)36.5–41.7(50.0)×(6.0)6.9–7.5(8.0) μm (av. = 39.1×7.2 μm), with a length:width ratio of 4.0–6.7. *Microconidia* 0–1-septate, ellipsoid to ovoid, more or less straight, without a visible hilum; aseptate, (5.0)8.4–10.5(13.0)×(3.0)3.3–3.7(4.0) μm (av. = 9.5×3.5 μm), with a length:width ratio of 1.7–3.4; 1-septate, (11.0)14.5–16.3(19.0)×(3.5)3.9–4.3(5.0) μm (av. = 15.4×4.1 μm), with a length:width ratio 2.8–4.8. *Conidia* formed in heads on simple conidiophores or as white (OA) or unpigmented (SNA) masses. *Chlamydosporides* ovoid to ellipsoidal, 6–13×5–7 μm, smooth, but often appearing rough due to deposits, thick-walled, terminal on short lateral branches or intercalary, single, in chains or in clumps, hyaline, becoming slightly brown at the margin.

**Holotype:** V enezuela, Amazonas, Cerro de la Neblina, tree bark, 1985, coll./isol. A. Rossman, holotype CBS H-20568, culture ex-type CBS 102032.

**Culture characteristics:** Mycelium cottony with average to strong density. Surface on OA saffron, with aerial...
mycelium sparse, buff, on PDA buff to saffron, with aerial mycelium saffron to pale luteous; zonation absent, transparency homogeneous, margin even; reverse similar to surface, but saffron to cinnamon on PDA. Colonies on PDA grow poorly (2–3 mm) at 4°C, after 7 days. Optimum temperature at 20°C, with colonies reaching 49 mm diam, after 7 days. Colony diam was 35–36 mm at 25°C after 7 days. No growth was observed at 30°C.

Isolate studied: CBS 102032 (Table 1).

Host and distribution: Tree bark (Venezuela).

Ilyonectria vitis A. Cabral, Rego & Crous, sp. nov.
(Fig. 16)

MycoBank 560107.

Etymology: Named after the host from which it was collected, Vitis vinifera.

Ilyonectriae anthuricolae morphologicae similis, sed longitudine media macroconidiorum longiore, 41.6–43.5 μm, distinguitur.

Conidiophores simple or complex or sporodochial. Simple conidiophores arising laterally or terminally from aerial mycelium, solitary to loosely aggregated, unbranched or sparsely branched, bearing up to three phialides, 1–3 septate, 30–70 μm long; monophialides more or less cylindrical, but tapering slightly towards the tip, 11–21 μm long, 2.0–3.0 μm wide at the base, 3.0–4.5 μm at widest point, 1.5–2.5 μm near the apex. Conidiophores forming microconidia arising from mycelium at agar surface, reduced to monophialides, or a stipe with a terminal arrangement of phialides, ranging from 2 to a dense cluster; sparsely branched or penicillate; monophialides narrowly flask-shaped, typically with widest point near the middle, 10–17 μm long, 1.5–3.0 μm wide at the base, 2.5–4.0 μm at widest point, 1.0–2.0 μm near the apex. Sporodochial conidiophores irregularly branched; phialides more or less cylindrical but slightly tapering towards the tip, or narrowly flask-shaped, with widest point near the middle, 14–20 μm long, 2.5–3.5 μm wide at the base, 3.0–4.5 μm at widest point, 1.5–2.5 μm near the apex. Macroconidia formed in flat domes of slimy masses, predominantly 3-septate, rarely 1–2- or 4-septate, straight or minutely curved, cylindrical with both ends more or less broadly rounded, mostly without a visible hilum; 3-septate conidia (34.9)41.6–43.5(51.6)×(6.2)7.9–8.2(9.5) μm (av. =42.5×8.0 μm), with a length:width ratio of 3.9–6.7. Microconidia on SNA formed in heads, aseptate, subglobose to ovoid, rarely ellipsoid, mostly with a visible, centrally located or slightly laterally displaced hilum, (3.7)4.9–5.4(6.7)×(3.2)3.7–4.0(4.6) μm (av. = 5.1×3.9 μm), with a length:width ratio of 1.1–1.7. Chlamydospores globose to subglobose to ellipsoid, 9–18×6–13 μm, smooth, but often appearing...
rough due to deposits, thick-walled, formed intercalary in chains or in clumps, and also in the cells of macroconidia, hyaline, becoming golden-brown.

**Holotype:** Portugal, Vidigueira, *Vitis vinifera*, basal end of a 2-year-old plant; scion Touriga Nacional; rootstock 110R, 2008, coll./isol. C. Rego, holotype CBS H-20569, culture ex-type CBS 129082=Cy233=CPC 19168.

**Culture characteristics:** Mycelium felty with density low to average. Surface on OA sienna, with sparse, saffron aerial mycelium, and luteous growth at margin. Surface on PDA chestnut, with sienna aerial mycelium, and luteous growth at margin. Zonation was absent (OA) or concentric (PDA), transparency was homogeneous (PDA) or not (OA). Growth at margin even to uneven. Reverse similar to surface, except in colour, sienna to saffron on OA, and chestnut to umber on PDA. Colonies on PDA do not grow at 4°C after 7 days. Optimum temperature at 20°C, when colonies reach 29–30 mm diam, after 7 days. Colony diam was 39–40 mm at 25°C and 8–9 mm at 30°C after 7 days. No growth was observed at 35°C.

**Isolate studied:** CBS 129082 (Table 1).

**Host and distribution:** *Vitis vinifera* (Portugal).

**Key to species treated**

1. Growth at margin on OA after 14 days at 20°C, lacking yellow pigmentation
2. Colony diameter on PDA after 7 days at 25°C<30 mm
3 Macroconidia forming chlamydospores
4 Macroconidia 1–3-septate, 3-septate macroconidia mean range 34.1–36.2 μm long
5 Macroconidia cylindrical, with the base appearing somewhat acute I. crassa
5* Macroconidia clavate I. pseudodestructans
4* Macroconidia predominantly 1-septate; 3-septate macroconidia smaller, mean range 28–31.2 μm long I. rufa
3* Macroconidia lacking chlamydospores
6 Macroconidia predominantly curved I. liliigena
6* Macroconidia straight
7 Macroconidia lacking visible hilum I. mors-panacis
7* Macroconidia with a visible, centrally located hilum
8 Three-septate macroconidia mean range 31.0–35.0 μm long I. panacis
8* Three-septate macroconidia mean range 34.3–38.5 μm long I. gamsii
2* Colony diameter after 7 days at 25°C>30 mm
9 Colony diameter after 7 days at 25°C, >50 mm I. cyclaminicola
9* Colony diameter after 7 days at 25°C, 30–50 mm
10 Conidiophores bearing a terminal whorl of phialides I. venezuelensis
10* Conidiophores unbranched, or different from above
11 Teleomorph known, and can be induced in culture
12 Three-septate macroconidia mean range 32.3–34.7 μm long; ascospores mean range 9.4–10.0 μm long I. robusta
12* Three-septate macroconidia mean range 30.0–36.0 μm long; ascospores mean range longer, 10–13 μm long I. radicicola
11* Teleomorph unknown
13 Mean range of 3-septate macroconidia, 29.7–31.5 × 6.5–6.9 μm I. europaea
13* Mean range of 3-septate macroconidia smaller, 25.0–28.4 × 5.2–5.5 μm I. lusitanica
1* Yellow pigmentation present at margin
14 Macroconidia 3-septate, mean range 29.5–32.2 μm long I. anthuricola
14* Macroconidia 3-septate, mean range 41.6–43.5 μm long I. vitis

*aNo authentic cultures of “C.” destructans, conidia (18.0–23.0–30.0(–35.0) × (6.0–6.5(–7.0) μm, are presently available.

Discussion

“Cylindrocarpon” destructans is a cosmopolitan soil-borne pathogen causing disease on a wide number of herbaceous and woody plant species (Samuels and Brayford 1990). The wide morphological and pathogenic amplitude of “C.” destructans makes it a commonly identified species, with many diseases from the Cylindrocarpon-complex being attributed to it, and ranking at the top of all “Cylindrocarpon” spp. deposited in the NCBI nucleotide database.

In this study, “C.” destructans isolates from the CBS culture collection (deposited under the wider concept of the species) were analysed using a multigene approach in order to clarify taxonomic aspects of this species complex. Molecular analyses show that these isolates cluster in various clades supported by high bootstrap support values. A previous study (Seifert et al. 2003) included a subset of the strains used here, and already highlighted the existence of unexpected divergence in “C.” destructans, as opposed to a large homogeneity in e.g. Neonectria ditissima. Several species have in recent years been separated from the “C.” destructans complex, including “C.” macroconidialis, “C.” coprosmae and “C.” austoradicalis based on morphological (Samuels and Brayford 1990) and molecular characters (Schröers et al. 2008; Seifert et al. 2003). Furthermore, several isolates causing black foot disease of grapevine, previously considered as “C.” destructans, were recently identified as I. liriodendri (Chaverri et al. 2011; Halleen et al. 2006), along with the ex-type strain from Liriodendron tulipifera (CBS 110.81) and a strain from Cyclamen (CBS 301.93). In this study, two further strains isolated from young Malus domestica and Quercus suber trees showing decline symptoms were also identified as I. liriodendri.

Altogether, we analysed 68 strains putatively belonging to “C.” destructans, but none of them clustered together with the ex-type culture of I. radicicola (CBS 264.65), suggesting that this species may not be as common as previously accepted. Halleen et al. (2006) identified a single strain (IMI 313237, isolated from arecoid palm) clustering with CBS 264.65. This also raises questions relating to the correlation between the anamorph, “C.” destructans, and its purported teleomorph, I. radicicola.

“Nectria” radicicola was described by Gerlach and Nilson (1963) from decayed leaves, flowers stalks and corms of Cyclamen persicum collected in Sweden, with a “Cylindrocarpon” anamorph they identified as “C.” radicicola.

In 1924, Wollenweber introduced “C.” radicicola (McAlpine) Wollenw. as a new combination, based on Septocylindrium radicicola McAlpine (1899), described from Citrus trees in Australia. Later, Wollenweber (1928) noted that Septocylindrium radicicola, with catenulate conidia, was different from “C.” radicicola, and the name was therefore based on Wollenweber’s (1928) description. Because of this confusion in names, Booth (1966) suggested that “C.” radicicola should be dropped, and that the name to be used as anamorph for I. radicicola should be “C.” destructans [originally described by Zinssmeister (1918) on Panax quinquefolia from Wisconsin, USA].
Furthermore, Booth (1966) designated a neotype for “C.” destructans, obtained from *P. quinquefolia* in USA, KY, Washington Co., Springfield; collected by W.B. Edwards in 1922, available as herbarium material in Cornell Plant Pathology Herbarium, CUP-011985. This specimen was re-examined in the present study [conidia (18.0)23.0–30.0(35.0) × (6.0)6.5(7.0) μm] [original description by Zinssmeister (1918), 9.0–32.4×3.2–8.1 μm], thus revealing conidia to be smaller than those formed by *I. radicicola*, which are (24.0)33.1(47.0) × (4.9)6.4(7.8) μm. From these observations, we conclude that “C.” destructans, which occurs on *P. quinquefolia* in the USA, represents yet another species distinct from *I. radicicola*, which is not yet represented in our phylogenetic tree (Fig. 1).

A strain deposited in CBS culture collection by Hildebrand in 1935, as “Ramularia” mors-panacis, was found to represent original material (ex-type CBS 306.35), collected from living roots of *Panax quinquefolium* in Ontario, Canada. The epithet “mors-panacis” is therefore resurrected for this clade, while the Japanese collection identified as “Cylindrocarpon destructans” f. sp. panacis (ex-type CBS 124662=NBRC 31881), isolated from *Panax ginseng* in Japan, is treated as synonym.

The ex-type strain of “Ramularia” robusta (CBS 308.35), isolated from living roots of *Panax quinquefolium* in Ontario, Canada, can be resurrected for a large clade representing isolates from a range of hosts and continents. Similarly, an authentic strain of “C.” destructans var. crassum (Booth 1966; Wollenweber 1931) is available for a species occurring on *Panax* and *Pseudotsuga* in Canada, *Lilium* and *Narcissus* in the Netherlands, and can thus be resurrected as *I. crassa*. Although strain CBS 120370 clustered together with other strains of *I. crassa* for most genes (no nucleotide differences in ITS and TEF, two nucleotide differences in HIS), this strain was not included in that species because of an 8-bp difference in TUB, a slower growth rate (e.g., 21 mm colony diam at 20°C for 7 days, as opposed to 31–46 mm for other isolates), a lower conidial length:width ratio [e.g. for 3-septate conidia 4.0–6.5, as opposed to 4.8–8.9 and smaller conidia (e.g. 3-septate conidia ranging from (26.0)31.2–34.0(40.0) × (6.0)6.6–7.1(8.0) μm (av. 32.6×6.9 μm), as opposed to (29.0)34.1–36(49.0) × (5.0)5.6–5.8(7.0) μm (av. 35.1×5.7 μm)]. Further studies should thus be conducted in order to clarify the taxonomy of this strain.

*Ilyonectria anthuriicola* and *I. vitis* are very similar in morphology to “C.” paeuseptatum. These species all have predominantly 3-septate macroconidia after 10 days in culture. *Ilyonectria anthuriicola* is easier to distinguish than “C.” paeuseptatum as the 3-septate conidia are smaller and narrower, (25.0)29.5–32.2(38.0) × (6.0)7.5–8.1(9.0) μm, while in “C.” paeuseptatum they are (37.0)42.0–47.0 (54.0) × (7.0)8.5–9.5(10.0) (Schroers et al. 2008). For *I. vitis* 3-septate macroconidia are of similar size to those of “C.” paeuseptatum, (34.9)41.6–43.5(51.6) × (6.2)7.9–8.2 (9.5), making it difficult to distinguish them based on this character. Growth rate at 20°C is slower in *I. vitis* than in “C.” paeuseptatum, and they also differ regarding colony characteristics and colours. Morphologically, however, they remain difficult to distinguish.

In this study, the genetic structure of the *I. radicicola* complex was analysed using a multi-locus approach along with morphological and culture characters. Three major groups were identified based on this approach, each group containing several species. Although we have been able to clarify several aspects related to the host range and distribution of taxa in the *I. radicicola* species complex, further collections, especially from *Panax* in the USA, will be essential to elucidate the status of “C.” destructans.

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