



# One stop shop III: taxonomic update with molecular phylogeny for important phytopathogenic genera: 51–75 (2019)

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## Abstract

This is a continuation of a series focused on providing a stable platform for the taxonomy of phytopathogenic fungi and organisms. This paper focuses on 25 phytopathogenic genera: *Alternaria*, *Capnodium*, *Chaetothyria*, *Cytospora*, *Cyphellophora*, *Cyttaria*, *Dactylonectria*, *Diplodia*, *Dothiorella*, *Entoleuca*, *Eutiarosporella*, *Fusarium*, *Ilyonectria*, *Lasiodiplodia*, *Macrophomina*, *Medeolaria*, *Neonectria*, *Neopestalotiopsis*, *Pestalotiopsis*, *Plasmopara*, *Pseudopestalotiopsis*, *Rosellinia*, *Sphaeropsis*, *Stagonosporopsis* and *Verticillium*. Each genus is provided with a taxonomic background, distribution, hosts, disease symptoms, and updated backbone trees. A new database (Onestopshopfungi) is established to enhance the current understanding of plant pathogenic genera among plant pathologists.

**Keywords** Classification · Database · Plant pathology · Phylogeny · Taxonomy · Symptoms · Systematics

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## Contents and contributors (main contributors underlined)

51. *Capnodium*–P Chomnunti, RS Jayawardena
52. *Chaetothyria*–S Hongsanan, RS Jayawardena
53. *Cytospora*–C Norphanphoun, RS Jayawardena, KD Hyde
54. *Cyphellophora*–Q Tian, RS Jayawardena
55. *Cyttaria*–AH Ekanayake
56. *Dactylonectria*–RH Perera
57. *Entoleuca*–MC Samarakoon
58. *Eutiarospora*–RS Brahmanage, AJL Phillips, RS Jayawardena
59. *Ilyonectria*–RH Perera
60. *Macrophomina*–DS Tennakoon, AJL Phillips
61. *Medeolaria*–AH Ekanayake
62. *Neonectria*–RH Perera, F. Halleen
63. *Neopestalotiopsis*–NI de Silva, SSN Maharachchikumbura, RS Jayawardena
64. *Plasmopara*–IS Manawasinghe, EHC McKenzie
65. *Pseudopestalotiopsis*–NI de Silva, SSN Maharachchikumbura, RS Jayawardena
66. *Rosellinia*–MC Samarakoon
67. *Sphaeropsis*–DS Tennakoon, AJL Phillips

## Updated genera

68. *Alternaria*–RS Jayawardena, KD Hyde
69. *Diplodia*–AJ Dissanayake, AJL Phillips
70. *Dothiorella*–RS Jayawardena, AJL Phillips
71. *Fusarium*–RH Perera
72. *Lasiodiplodia*–AJL Phillips, RS Jayawardena
73. *Pestalotiopsis*–NI de Silva, SSN Maharachchikumbura
74. *Stagonosporopsis*–SC Jayasiri, RS Jayawardena
75. *Verticillium*–CG Lin

## Introduction

One stop shop (OSS) is a series of papers focused on providing a stable platform for the taxonomy of plant pathogenic fungi and organisms. Genera included in these paper series are associated with plant diseases. However, some may not be well-known plant pathogens and Kochs' postulates might have not been conducted in order to establish their pathogenicity. When this series was launched in 2014, its specific aims were mentioned (Hyde et al. 2014). Two issues of OSS have been published in which 50 genera were treated (Hyde et al. 2014; Jayawardena et al. 2019). In this study we treat 25 genera of plant pathogens as well as establish a new website, [www.onestopshopfungi.org](http://www.onestopshopfungi.org), to host a database for plant pathogenic fungi and

organisms. This fungal database allows mycologists and plant pathologists to understand disease symptoms, host distribution, classification, morphology and provides an updated phylogeny which will enhance current understanding of plant pathogens and gain better insights into the current fungal classification system. The Onestopshopfungi webpage is an output funded by the Mushroom Research Foundation, Thailand, which is a non-government and non-profit organization. We invite all mycologists to contribute to make this a success. The outcome of this series provides a stable taxonomy and phylogeny for plant pathogens that can provide a reliable platform for mycologists and plant pathologists to accurately identify causal organisms.

## Material and methods

Photo plates of the symptoms of the disease and morphological characters are given, when available. Classification follows Wijayawardene et al. (2018).

Sequence data from ex-type, ex-epitype or authentic strains for each species were retrieved from GenBank. Sequence data from single gene regions were aligned using Clustal X1.81 (Thompson et al. 1997) and further alignment of the sequences were carried out by using the default settings of MAFFT v.7 (Katoh and Toh 2008; <http://mafft.cbrc.jp/alignment/server/>), and manual adjustment was conducted using BioEdit where necessary. Gene regions were also combined using BioEdit v.7.0.9.0 (Hall 1999). Primers for each gene locus can be found in the bibliography related to the phylogeny presented for each genus. Phylogenetic analyses consisted of maximum likelihood (ML), maximum parsimony (MP) and Bayesian inference (BYPP). Maximum parsimony analysis was performed using PAUP (Phylogenetic Analysis Using Parsimony) v. 4.0b10 (Swofford 2002) to obtain the most parsimonious trees. Maximum likelihood analyses were also performed in raxmlGUIv.0.9b2 (Silvestro and Michalak 2012) or RAxML-HPC2 on XSEDE (8.2.8) in the CIPRES science gateway platform (Miller et al. 2010) using GTR+I+G model of evolution. Bayesian inference was used to construct the phylogenies using Mr. Bayes v.3.1.2 (Ronquist and Huelsenbeck 2003). MrModeltest v. 2.3 (Nylander et al. 2008) was used for statistical selection of best-fit model of nucleotide substitution and was incorporated into the analyses.

## Results

*Capnodium* Mont., *Annls Sci. Nat., Bot*, sér. 3, 11: 233 (1849)

The genus *Capnodium* was introduced by Montagne (1849) to accommodate *C. salicinum*. *Capnodium* is one of the most commonly found sooty moulds in gardens and landscapes (Laemmlen 2011). *Capnodium* has a saprobic association with sap-feeding insects in the Order Homoptera, which includes aphids, whiteflies, soft scale, mealy bugs, leafhoppers and psyllids (Barr 1987). Gavrilov-Zimin (2017) reported that the larvae and female of a new species and a new monotypic genus of legless mealybug, *Orbuspedum machinator*, from bamboo twigs in southern Thailand are covered with densely packed fungal hyphae of the sooty mould *Capnodium* sp. Herath et al. (2012) reported that a tropical sooty mould (*Capnodium* sp.) is known to produce antibiotics such as tetramic acid, methiosetin and epicorazin A.

*Capnodium* species grow on honeydew, gradually covering the surface of the plant part affected by insects, colouring it with various shades of black. These fungi do not colonize the plant tissues or trigger symptoms. However, they alter the ability of the plant to perform photosynthesis and exchange of gases with the atmosphere. Severely affected leaves may die and fall, thereby affecting plant growth and survival. Therefore, we treat *Capnodium* as a main plant pathogenic group.

**Classification**—Dothideomycetes, Dothideomycetidae, Capnodiales, Capnodiaceae

**Type species**—*Capnodium salicinum* Mont., Anns Sci. Nat., Bot, sér. 3 11:234 (1849)

**Distribution**—Species of *Capnodium* have a wide distribution but are most common in tropical and subtropical

regions (Chomnunti et al. 2014). They can be found on plants that have been previously fed upon by insects.

**Disease symptoms**—Dark mycelium coating surface of host can cause chlorosis and reduce photosynthetic ability of plants, which effects plant growth, reduces yield, and leading to marketability problems (Chomnunti et al. 2014; Fig 1). In higher latitudes, *Capnodium* spp. are scarce during the winter; the most common being *C. salicinum* in the UK (Cannon et al. 1985; Royal Botanic Gardens, Kew, UK National Collection of Dried Fungi, unpublished data). Warm-temperate climates in Australia and the Mediterranean countries provide an abundance of perennial foliage on which sooty moulds are able to establish themselves during the winter, and so persist from one season to the next (Fraser 1935; Reynolds and Gilbert 2005). In northern Thailand, most of the sooty mould infections are caused by *Capnodium* species (Chomnunti et al. 2014).

**Hosts**—Many plants when colonised by insects that produce honeydew. Species of *Annona*, *Camellia*, *Citrus*, *Coffea*, *Chrysophyllum*, *Ficus*, *Malus*, *Mangifera*, *Olea*, *Populus*, *Prunus*, *Psidium*, *Rhododendron* and *Salix* (Farr and Rossman 2019)

### Morphological based identification and diversity

The asexual morph forms elongated pycnidia that develop from a superficial mycelium on living plant surfaces and produce tiny, hyaline conidia on top of the pycnidia (Chomnunti et al. 2011). Persoon (1822) mention that *Fumago citri* is the sooty mould but it was not well described and completed; therefore it was transferred to genus *Polychaeton* by Lévillé (1847). Later, Berkeley-

**Fig. 1** Sooty moulds on various host plants associated with insects. **a** On a hardwood tree, **b** on guava, **c** on coffee, **d–f** on mango



Desmazieres (1849) transferred all species once known in the genus *Fumago* to *Capnodium*. Molecular evidence revealed that *Polychaeton* is an asexual stage of *Capnodium*, therefore, both are the same organism. According to “one fungus one name” and the Melbourne Code under Art. 57.2, *Capnodium* was considered for conservation as it has a larger number of epithets and is more widely used in this group of fungi, even though *Polychaeton* is the older name (Chomnunti et al. 2011, 2014; McNeill et al. 2012; Hyde et al. 2013; Wijayawardene et al. 2014, 2017, 2018; Liu et al. 2015; Hongsanan et al. 2015).

The morphology of *Capnodium* species can be recognised by black mycelial growth spreading on the host surface, which produces superficial colonies with septate, dark brown hyphae and cylindrical and bitunicate asci. On host surface *Capnodium* species share the same ecological niche and are similar in appearance to other genera and families of sooty moulds; often found with sexual and asexual states growing together and living in complex communities (Faull et al. 2002; Hughes 2003; Hughes and Seifert 2012; Chomnunti et al. 2014; Hongsanan et al. 2015).

#### Molecular based identification and diversity

DNA sequencing data of *Capnodium coffeae*, *C. coartatum*, *C. salicinum*, *C. coffeicola* and *C. dematum* and eleven unidentified *Capnodium* spp. are available in GenBank, including sequence data for LSU, SSU and ITS (4/7/2019). Hongsanan et al. (2015) introduced a new species *Capnodium coffeicola*. It differs from other *Capnodium* species in having pycnidia with short and black stalks at the base and is swollen at the central part, and it has cylindrical to oblong conidia, but its placement is supported with phylogenetic analysis using LSU and ITS sequence data.

Sooty moulds often grow in colonies of more than one species, and taxonomic descriptions thus often unknowingly combine elements of different genera and species. Identification based on morphology only is difficult as there are overlapping morphological characters among many taxa (Chomnunti et al. 2011, 2014). To achieve accurate generic and species identification and taxonomic placements, phylogenetic studies using large subunit ribosomal RNA (LSU rRNA) gene sequences and the internal transcribed spacer regions and 5.8S nrDNA gene (ITS) were performed (Crous et al. 2009; Chomnunti et al. 2011, 2014; Liu et al. 2015; Hongsanan et al. 2015).

This study reconstructs the phylogeny of *Capnodium* based on analyses of ITS sequence data (Table 1, Fig. 2) and corresponds with previous studies (Chomnunti et al. 2011, 2014; Hongsanan et al. 2015). This can be used as a backbone tree in the identification of *Capnodium* species (Fig. 3).

**Table 1** Details of *Capnodium* isolates used in the phylogenetic analyses

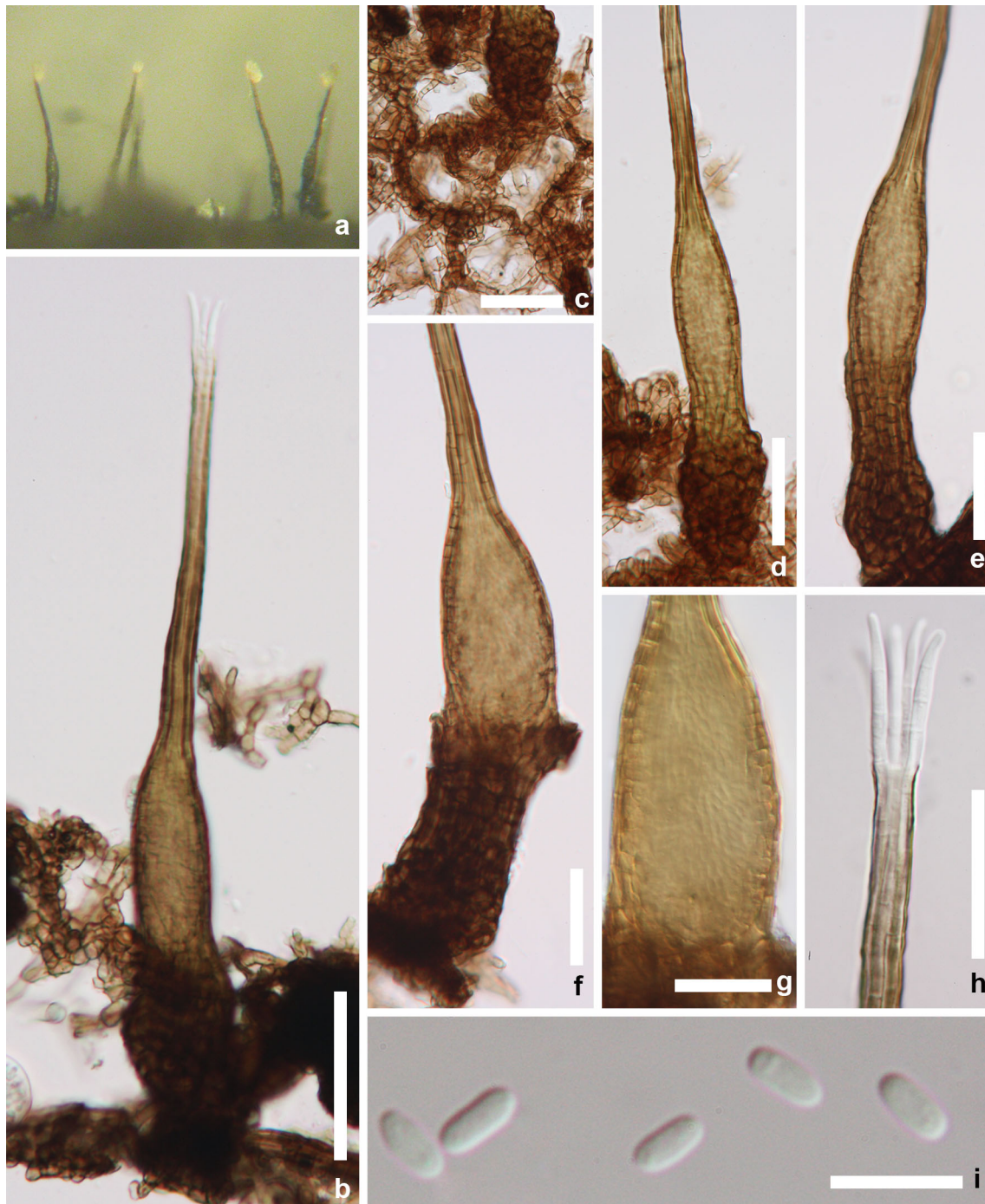
| Species                               | Isolate/voucher no        | ITS             |
|---------------------------------------|---------------------------|-----------------|
| <i>C. coffeae</i>                     | AFTOL-ID 939              | DQ491515        |
| <i>C. coffeae</i>                     | CBS 147.52                | AJ244239        |
| <i>Capnodium coffeae</i>              | CTQE057                   | KX893384        |
| <b><i>Capnodium coffeicola</i></b>    | <b>MFLUCC 15-0206*</b>    | <b>KU358921</b> |
| <i>Capnodium salicinum</i>            | CBS 131.34                | AJ244240        |
| <i>Capnodium</i> sp.                  | SZ-F22                    | KT443921        |
| <i>Capnodium</i> sp.                  | S80                       | MH633887        |
| <i>Capnodium</i> sp.                  | CP1                       | MH629975        |
| <i>Capnodium</i> sp.                  | OUCMBI101100              | HQ914834        |
| <i>Capnodium</i> sp.                  | ELM115                    | KU556052        |
| <i>Capnodium</i> sp.                  | GPO-CO-02                 | KC180729        |
| <i>Capnodium</i> sp.                  | agrFF1633                 | HE584839        |
| <i>Capnodium</i> sp.                  | agrFF1683                 | HE584838        |
| <i>Capnodium</i> sp.                  | agrFF1681                 | HE584837        |
| <i>Capnodium</i> sp.                  | agrFF1679                 | HE584836        |
| <i>Capnodium</i> sp.                  | agrFF1678                 | HE584835        |
| <i>Capnodium</i> sp.                  | agrFF1639                 | HE584834        |
| <b><i>Capnodium</i> sp.</b>           | <b>agrFF1638</b>          | <b>HE584833</b> |
| <i>Capnodium</i> sp.                  | agrFF1614                 | HE584832        |
| <i>Capnodium</i> sp.                  | agrFF1613                 | HE584831        |
| <i>Capnodium</i> sp.                  | agrFF0153                 | HE584830        |
| <i>Capnodium</i> sp.                  | agrFF1634                 | HE584829        |
| <i>Capnodium</i> sp.                  | agrFF1631                 | HE584828        |
| <i>Capnodium</i> sp.                  | agrFF0180                 | HE584822        |
| <i>Capnodium</i> sp.                  | agrFF1690                 | HE584823        |
| <b>Species</b>                        | <b>Isolate/Voucher no</b> | <b>ITS</b>      |
| <i>Capnodium</i> sp.                  | agrFF0045                 | HE584825        |
| <i>Capnodium</i> sp.                  | agrFF0207                 | HE584826        |
| <i>Capnodium</i> sp.                  | TMS-2011                  | HQ631045        |
| <i>Capnodium</i> sp.                  | TTI-247                   | KU985278        |
| <b><i>Conidiocarpus plumeriae</i></b> | <b>MFLUCC 15-0205</b>     | <b>KU358919</b> |
| <i>Conidiocarpus siamensis</i>        | MFLUCC 10-0053            | KU358922        |
| <i>Co. siamensis</i>                  | MFLUCC 10-0061            | KU358923        |
| <i>Co. siamensis</i>                  | MFLUCC 10-0062            | KU358924        |
| <b><i>Co. siamensis</i></b>           | <b>MFLUCC 10-0063</b>     | <b>KU358925</b> |
| <i>Co. siamensis</i>                  | MFLUCC 10-0064            | KU358926        |
| <i>Co. siamensis</i>                  | MFLUCC 10-0065            | KU358927        |
| <i>Co. siamensis</i>                  | MFLUCC 10-0074            | KU358928        |
| <i>Scoria leucadendri</i>             | CBS 131318                | JQ044437        |

Ex-type (or ex-epitype) strains are in bold and marked with an asterisk\* and voucher strains are in bold

*Recommended genetic marker (genus level)*—LSU

*Recommended genetic markers (species level)*—LSU, ITS

Sequence data of LSU, SSU and ITS are available for five species of *Capnodium* in GenBank but none of them has complete sequence data. LSU is useful for preliminary

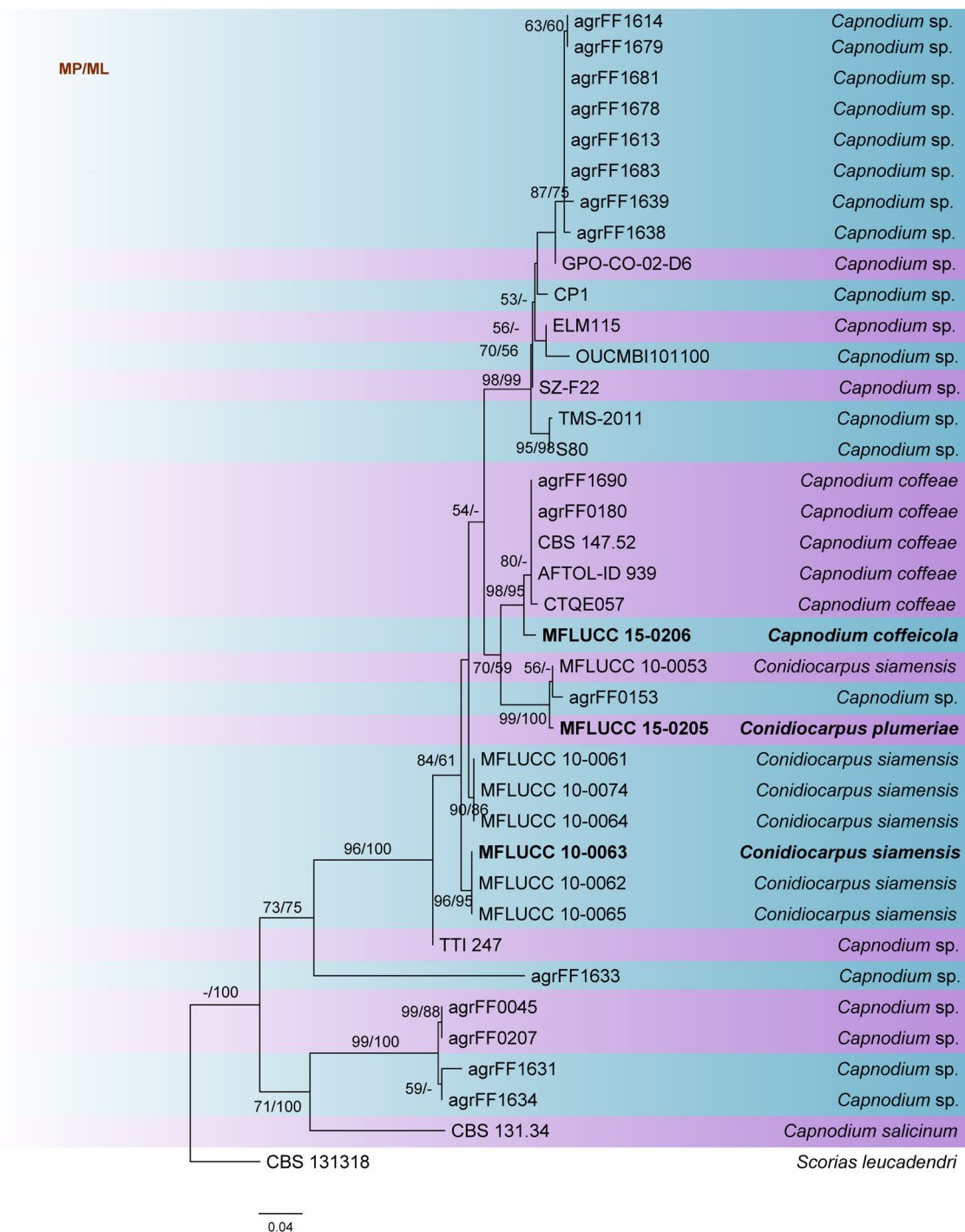


**Fig. 2** Morphology of *Capnodium* sp. **a** pycnidia on the host. **b, d, e, f** stalked pycnidia **c** mycelium network, **g** conical pycnidium and pycnidial wall, **h** ostiole surrounded by hyaline hyphae, **i** conidia. Scale bars: **b, d–f** = 100  $\mu$ m, **c, g** = 50  $\mu$ m, **h**, = 20  $\mu$ m, **i** = 10  $\mu$ m

identification at the generic level (Chomnunti et al 2011, 2014; Quaedvlieg et al 2014). Hongsanan et al. (2015) recommended the use of combined LSU and ITS sequence data to identify the species. More protein-coding gene loci should be sequenced to clarify the taxonomic problems in this genus. In the current analyses, *C. cortatum* was not included due to lack of ITS sequences in GenBank.

A revision of this genus is needed as it may reveal many new species. Re-sequencing of species as well as designating epitypes or representative species is also important.

*Accepted number of species:* There are 140 epithets in Index Fungorum (2019), however only **four** species have DNA sequence data.



**Fig. 3** Phylogenetic tree generated by maximum likelihood analysis of ITS sequence data of *Capnodium* species. Related sequences were obtained from GenBank. Thirty-eight strains are included in the analyses, which comprise 512 characters including gaps. The tree was rooted with *Scoria leucadendri* (CBS 131318). Tree topology of the ML analysis was similar to the MP analysis. The best scoring RAxML tree with a final likelihood value of  $-2398.970137$  is presented. The matrix had 236 distinct alignment patterns, with 16.01% of undetermined characters or gaps. Estimated base frequencies were as follows; A = 0.285338, C = 0.285338, G = 0.241464, T = 0.238894;

substitution rates AC = 1.204962, AG = 1.857184, AT = 2.642904, CG = 1.319860, CT = 4.051266, GT = 1.000000; gamma distribution shape parameter  $\alpha = 0.287147$ . The maximum parsimonious dataset consisted of constant 327, 125 parsimony-informative and 60 parsimony-uninformative characters. The parsimony analysis of the data matrix resulted in the maximum of two equally most parsimonious trees with a length of 358 steps (CI = 0.735, RI = 0.875, RC = 0.630, HI = 0.265) in the first tree. RAxML and maximum parsimony bootstrap support value  $\geq 50\%$  are shown, respectively, near the nodes. Ex-type strains are in bold

**References:** Chomnunti et al 2011, 2014; Quaedvlieg et al 2014; Hongsanan et al. 2015 (morphology, phylogeny).

***Chaetothyria*** Theiss., *Annls mycol.* 11(6):495 (1913)

The genus *Chaetothyria* was established by Theissen (1913), with *C. musarum* (Speg.) Theiss as the type species. *Chaetothyria* was placed in *Micropeltidaceae* based on its superficial, flattened base, poorly developed thyriothecium and irregular meandering arrangement of compact hyphae of walled cells. Singtripop et al. (2016) provided molecular data of one reference specimen and one new species. Hongsanan et al. (2017) established a new species of *Chaetothyria* and introduced a new family *Phaeothecoidiaceae* to accommodate species of *Chaetothyria*, *Houjia* and *Phaeothecoidiella* in Capnodiales. Based on its placement in phylogenetic trees and the morphological uniqueness, *Micropeltidaceae* was excluded from Microthyriales and treated as family *incertae sedis* in Lecanoromycetes (Hongsanan et al. 2017; Zeng et al. 2019) (Fig. 4).

**Classification**—Dothideomycetes, *incertae sedis*, Capnodiales, Phaeothecoidiaceae

**Type species**—*Chaetothyria musarum* (Speg.) Theiss., *Annls mycol.* 11(6):495 (1913)

**Distribution**—Known from Brazil, Cook Islands, Dominican Republic, India, Mexico, Pakistan, Panama, Thailand, US

**Disease symptoms**—Sooty blotch and flyspeck

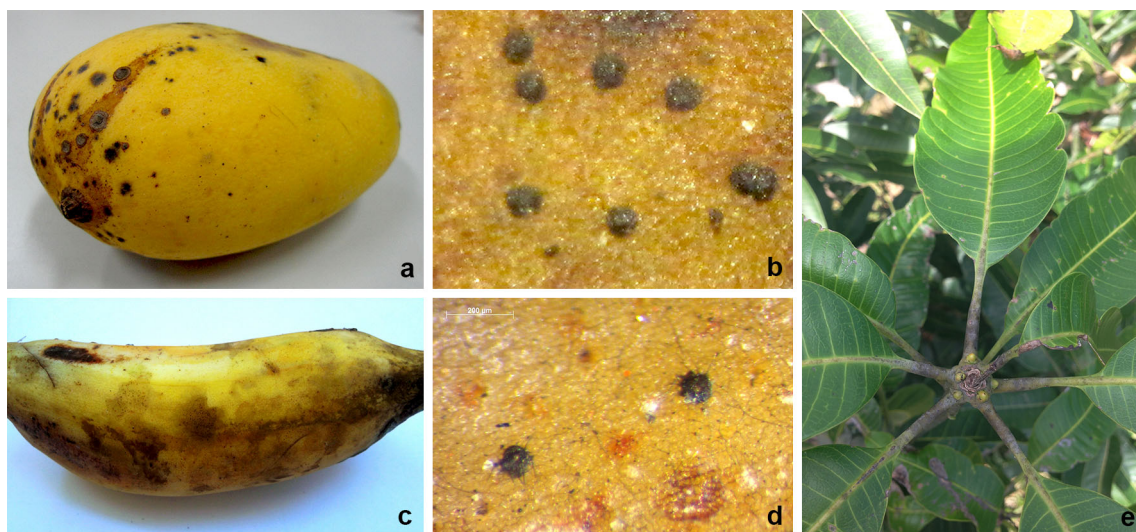
Species in this genus cause flyspeck disease on various plants, such as *C. musarum* on *Musa* sp. and *C. panamensis* (F. Stevens & Dorman) Arx on *Oncoba laurina*. Sooty blotch and flyspeck (SBFS) is a disease complex caused by nearly 80 fungal species (Singtripop et al. 2016) that are epiphytes which blemish the epicuticular wax layer of several fruit crops, such as apple, pear, orange, persimmon,

banana and grape worldwide (Gleason et al. 2011; Gao et al. 2014), cutting sale price and limiting the growth rate of fruit production (Williamson and Sutton 2000; Gao et al. 2014). ‘Sooty blotch’ is characterized by colonies produced on host tissues from superficial, spreading, dark irregular blotches of mycelium with or without sclerotium-like structures or fruiting bodies. On the other hand, ‘flyspeck’ defines clusters of shiny, small, black sclerotium-like structures or fruiting bodies, lacking visible intercalary mycelium (Gleason et al. 2011; Mayfield et al. 2012; Singtripop et al. 2016).

**Hosts**—Species of *Anacardium*, *Anodendron*, *Anogeisus*, *Carallia*, *Cassia*, *Chonemorpha*, *Dalbergia*, *Dianella*, *Euonymus*, *Hevea*, *Iiana*, *Magnifera*, *Magnolia*, *Mammea*, *Maytenus*, *Memecylon*, *Mitragyna*, *Musa*, *Myrcia*, *Ochrocarpos*, *Olea*, *Oncoba*, *Phoebe*, *Similax*, *Streblus* and *Vochysia*.

### Morphological based identification and diversity

*Chaetothyria* is characterized by superficial, flattened thyriothecia, with base poorly developed, with thyriothecial setae and 1-septate ascospores (Reynolds and Gilbert 2005; Singtripop et al. 2016; Hongsanan et al. 2017). *Chaetothyria* can be distinguished from other species in *Micropeltidaceae* on the basis of thyriothecial setae appearance, shape and septation of the ascospores (Singtripop et al. 2016; Hongsanan et al. 2017). Twenty-three species of *Chaetothyria* epithets are listed in Index Fungorum (2019), but sequence data are available for only two species (4/7/2019). *Chaetothyria* is a poorly studied genus. Fresh collections and sequence data are needed for this genus. The disease cycle of this genus is yet to be established (Fig. 5).

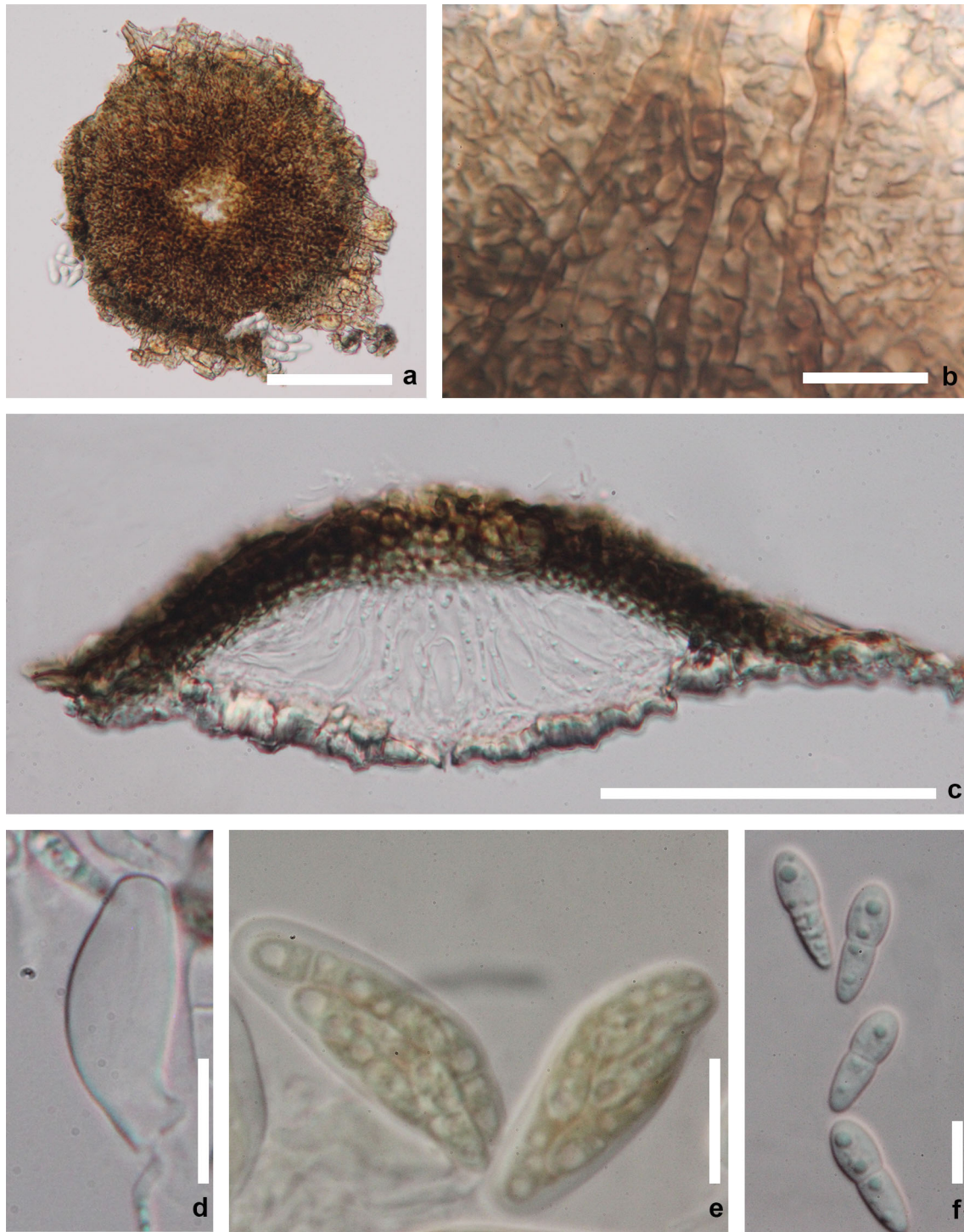


**Fig. 4** Disease symptoms caused by *Chaetothyria* spp. **a** on mango, **b, d** appearance of thyriothecia on hosts, **c** on a banana, **e** on mango leaves

### Molecular based identification and diversity

Singtripop et al. (2016) provided a reference type specimen of *C. musarum* with sequence data. Using combined LSU,

SSU and ITS sequence data, *Chaetothyrina* clustered as a sister genus to *Houjia* and *Phaeothecoidiella* within Capnodiales (Hongsanant et al. 2017; Table 2, Fig. 6).



**Fig. 5** *Chaetothyrina guttulata* **a** Thyriotheceum when viewed in squash mount. **b** Surface of thyriotheceum. **c** Section through thyriotheceum. **d** Ascus when immature. **e** Asci at maturity. **f** Ascospores. Scale bars: **a** = 50  $\mu\text{m}$ , **b**, **d**, **e** = 10  $\mu\text{m}$ , **c** = 100  $\mu\text{m}$ , **f** = 5  $\mu\text{m}$



*Recommended genetic markers (genus level)*—LSU and SSU

*Recommended genetic markers (species level)*—ITS and RPB2

*Accepted number of species:* There are 23 epithets in Index Fungorum (2019). However, only two species have molecular data.

*References:* Reynolds and Gilbert 2005; Singtripop et al. 2016; Hongsanan et al. 2017 (morphology, phylogeny)

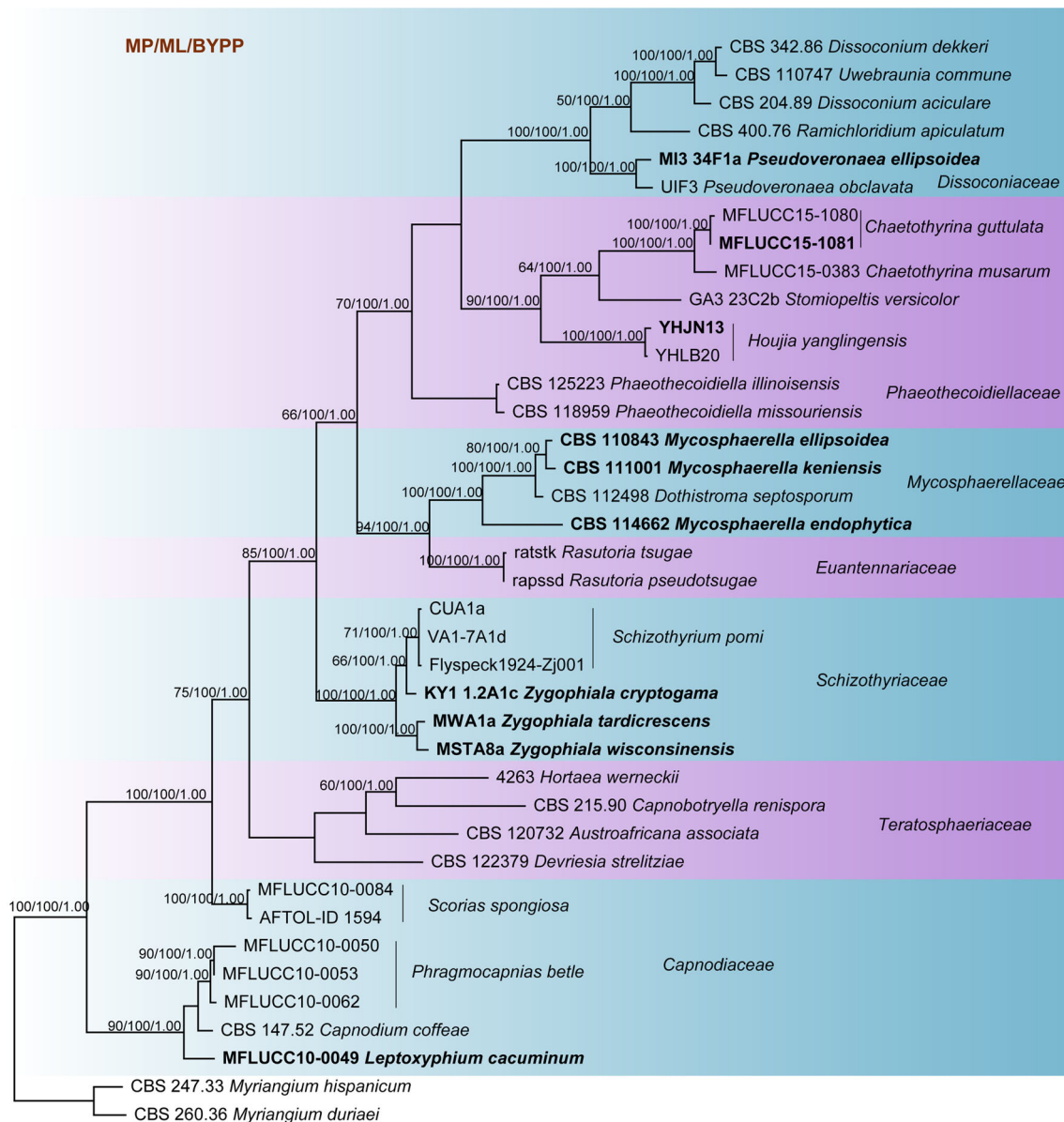
*Cytospora* Ehrenb., Sylv. mycol. berol.: 28 (1818)

*Cytospora* was introduced by Ehrenberg (1818) as the type genus of the family *Cytosporaceae* in Diaporthales (Wehmeyer 1975; Barr 1978; Eriksson et al. 2001; Castlebury et al. 2002). The genus is an important

**Table 2** Details of *Chaetothyria* isolates used in the phylogenetic analyses

| Species                                  | Isolate/voucher no    | LSU      | SSU      | ITS      |
|--|-----------------------|----------|----------|----------|
| <i>Austroafricana associata</i>          | CBS 120732            | KF901829 | –        | KF901512 |
| <i>Capnobotryella renispora</i>          | CBS 215.90            | GU214399 | AY220613 | AY220613 |
| <i>Capnodium coffeae</i>                 | CBS 147.52            | GU214400 | DQ247808 | AJ244239 |
| <i>Chaetothyria guttulata</i>            | MFLUCC15-1080         | KU358917 | KU358916 | KX372277 |
| <b><i>C. guttulata</i></b>               | <b>MFLUCC15-1081*</b> | KU358914 | KU358915 | KX372276 |
| <i>C. musarum</i>                        | MFLUCC15-0383         | KU710171 | KU710174 | KX372275 |
| <i>C. musarum</i>                        | MFLUCC15-0383         | KU710171 | KU710174 | KX372275 |
| <i>Devriesia strelitziae</i>             | CBS 122379            | GU301810 | GU296146 | EU436763 |
| <i>Dissoconium aciculare</i>             | CBS 204.89            | GU214419 | GU214523 | AY725520 |
| <i>D. dekkeri</i>                        | CBS 342.86            | JN232431 | –        | –        |
| <i>Dothistroma septosporum</i>           | CBS:112498            | GQ852597 | JX901744 | JX901744 |
| <i>Hortaea werneckii</i>                 | 4263                  | JX141471 | JX141470 | DQ336709 |
| <i>Houjia yanglingensis</i>              | YHLB20                | GQ433630 | –        | GQ433629 |
| <b><i>H. yanglingensis</i></b>           | <b>YHJN13*</b>        | GQ433631 | –        | GQ433628 |
| <b><i>Leptoxyphium cacuminum</i></b>     | <b>MFLUCC10-0049*</b> | JN832602 | JN832587 | –        |
| <b><i>Mycosphaerella ellipsoidea</i></b> | <b>CBS:110843*</b>    | GQ852602 | AY725545 | AY725545 |
| <b><i>M. endophytica</i></b>             | <b>CBS:114662*</b>    | GQ852603 | DQ302953 | DQ302953 |
| <b><i>M. keniensis</i></b>               | <b>CBS:111001*</b>    | GQ852610 | –        | –        |
| <i>Myriangium duriaei</i>                | CBS 260.36            | NG027579 | AF242266 | –        |
| <i>M. hispanicum</i>                     | CBS 247.33            | GU301854 | GU296180 | –        |
| <i>Phaeothecoidiella illinoisensis</i>   | CBS:125223            | GU117901 | –        | GU117897 |
| <i>P. missouriensis</i>                  | CBS:118959            | GU117903 | –        | GU117899 |
| <i>Phragmocapnias asiticus</i>           | MFLUCC10-0062         | JN832612 | JN832597 | –        |
| <i>P. betle</i>                          | MFLUCC10-0053         | JN832606 | JN832591 | –        |
| <i>P. betle</i>                          | MFLUCC10-0050         | JN832605 | JN832590 | –        |
| <b><i>Pseudoveronaea ellipsoidea</i></b> | <b>MI3 34F1a*</b>     | JQ622103 | –        | FJ425205 |
| <i>P. obclavata</i>                      | UIF3                  | AY598916 | –        | AY598877 |
| <i>Ramichloridium apiculatum</i>         | CBS 400.76            | EU041851 | EU041794 | EU041794 |
| <i>Rasutoria pseudotsugae</i>            | rapssd                | EF114704 | EF114729 | EF114687 |
| <i>R. tsugae</i>                         | ratsk                 | EF114705 | EF114730 | EF114688 |
| <i>Schizothyrium pomi</i>                | CUA1a                 | AY598895 | –        | EF164898 |
| <i>S. pomi</i>                           | Flyspeck1924-Zj001    | AY598894 | –        | AY598848 |
| <i>Scorias spongiosa</i>                 | MFLUCC10-0084         | JN832586 | JN832601 | –        |
| <i>S. spongiosa</i>                      | AFTOL-ID 1594         | DQ678075 | DQ678024 | –        |
| <i>Stomiopeltis versicolor</i>           | GA3 23C2b             | FJ147163 | –        | FJ438375 |
| <b><i>Zygothiala cryptogama</i></b>      | <b>KY1 1.2A1c*</b>    | EF164902 | –        | EF164900 |
| <b><i>Z. tardicrescens</i></b>           | <b>MWA1a*</b>         | EF164901 | –        | AY598856 |
| <b><i>Z. wisconsinensis</i></b>          | <b>MSTA8a*</b>        | AY598897 | –        | AY598853 |

Ex-type (or ex-epitype) strains are in bold and marked with an asterisk\* and voucher strains are in bold



10

**Fig. 6** Phylogenetic tree generated by maximum parsimony analysis of combined LSU, SSU and ITS sequence data. Thirty-nine strains are included in the analyses, which comprised 2225 characters including gaps. The tree was rooted with *Myriangium duriaei* (CBS 260.36) and *M. hispanicum* (CBS 247.33). The maximum parsimonious dataset consisted of 1645 constant, 461 parsimony-informative and 119

parsimony-uninformative characters. The parsimony analysis of the data matrix resulted in the maximum of ten equally most parsimonious trees with a length of 1637 steps (CI = 0.549, RI 0.736, RC = 0.404, HI = 0.451) in the first tree. MP and ML bootstrap values  $\geq 50\%$  and bayesian posterior probabilities  $\geq 0.90$  (BYPP) are shown respectively near the nodes. Ex-type strains are in bold

pathogenic fungus, causing canker and dieback on branches of a wide range of hosts with a wide distribution (Adams et al. 2005, 2006; Hyde et al. 2017, 2018; Norphanphoun et al. 2017, 2018).

**Classification**—Sordariomycetes, Diaporthomycetidae, Diaporthales, Valsaceae

**Type species**—*Cytospora chrysosperma* (Pers.) Fr. 1823

**Distribution**—Worldwide

**Disease symptoms**—Canker and dieback disease on branches

**Hosts**—Species of *Abies*, *Acer*, *Berberis*, *Betula*, *Ceratonia*, *Cornus*, *Cotinus*, *Crataegus*, *Elaeagnus*, *Eriobotrya*, *Eucalyptus*, *Juniperus*, *Lummitzera*, *Malus*, *Picea*, *Pinus*, *Platanus*, *Platyclusus*, *Populus*, *Prunus*, *Pyrus*, *Quercus*, *Rosa*, *Salix*, *Sequoia*, *Sibiraea*, *Sorbaronia*, *Sorbus*,

*Spiraea*, *Styphnolobium*, *Syringa*, *Syzygium*, *Tibouchina*, *Ulmus*, *Vitis* and *Xylocarpus* (Norphanphoun et al. 2018).

### Morphological based identification and diversity

*Cytospora* is characterized by multi-loculate conidiomata with ostiolar necks and unicellular, elongate-allantoid to subcylindrical, hyaline conidia (Fan et al. 2015a, b; Norphanphoun et al. 2017, 2018; Fig. 7). The genus which was reported as causing canker diseases in many woody plants was established in 1818 and studied in detail by taxonomists (Fries 1823; Saccardo 1884). *Valsa* Fr. was reported as the sexual stage of this genus and therefore, *Valsa* was treated as a synonym of *Cytospora* (1818) based on The International Code of Nomenclature for Algae, Fungi, and Plants (ICN, McNeill et al. 2012), with *Cytospora* being the oldest and most widely used name (Adams et al. 2005; Fotouhifar et al. 2010; Fan et al. 2014; Rossman et al. 2015). Previously, the conventional identification of species in *Cytospora* was based on their host association, often with vague morphological descriptions. Mycologists began to elucidate the relationships between *Cytospora* species and their hosts, with morphological observations combined with phylogenetic analyses using internal transcribed spacer (ITS) regions as an effective fungal DNA barcode (Adams et al. 2005, 2006; Fotouhifar et al. 2010; Schoch et al. 2012). The establishment of multi-gene analyses using ITS, LSU, ACT, RPB2, TUB2 has proved comprehensive for the species level (Fan et al. 2015a, b, 2020; Liu et al. 2015; Yang et al. 2015; Hyde et al. 2016; Li et al. 2016; Norphanphoun et al. 2017, 2018; Phookamsak et al. 2019).

### Molecular based identification and diversity

Comprehensive multigene phylogenetic analyses for this genus were performed by Fan et al. (2015a, b, 2020) and Norphanphoun et al. (2017, 2018).

This study reconstructs the phylogeny of *Cytospora* based on analyses of a combined ITS, LSU, ACT and RPB2 sequence data (Table 3, Fig 8). The phylogenetic tree is updated with recently introduced *Cytospora* species and corresponds to previous studies (Norphanphoun et al. 2018).

*Recommended genetic markers (genus level)*—LSU, ITS  
*Recommended genetic markers (species level)*—ITS, ACT and RPB2

*Accepted number of species:* There are 630 species in Index Fungorum (2019) and 110 species have molecular data.

*References:* Fan et al. 2015a, b, Lawrence et al. 2016, Senanayake et al. 2017, 2018 (morphology), Norphanphoun et al. 2017, 2018 (morphology, phylogeny).

***Cyphellophora*** G.A. de Vries, Mycopath. Mycol. appl. 16(1):47(1962)

*Cyphellophora* is cosmopolitan, comprising species distributed from a broad range of environmental sources as human and animal disease, saprobes, epiphytes and plant pathogens (de Hoog et al. 1999, 2000; Jacob and Bhat 2000; Decock et al. 2003; Crous et al. 2007; Zhuang et al. 2010; Feng et al. 2014; Mayfield et al. 2012; Gao et al. 2014; Phookamsak et al. 2019). Most species, including the type species, *C. laciniata*, were isolated from nails or skin of humans, resulting in clinical symptoms (Feng et al. 2014). Phylogenetically, *C. phyllostachydis* clustered with *C. europaea*, a human or mammal infection of hyperkeratosis (de Hoog et al. 2000). In contrast, *C. phyllostachydis* causes sooty blotch and flyspeck (SBFS) of bamboo and is not found on humans (Gao et al. 2014). The sooty mould species *C. jingdongensis* was introduced with a sexual morph; it reduces plant photosynthesis but does not damage or cause disease of the plant (Chomnunti et al. 2014; Yang et al. 2018).

*Classification*—Eurotiomycetes, Chaetothyriomycetidae, Chaetothyriales, Cyphellophoraceae

*Type species*—***Cyphellophora laciniata*** G.A. de Vries, Mycopath. Mycol. appl. 16(1):47(1962)

*Distribution*—Australia, Brazil, China, Germany, India, Israel, Korea, Taiwan

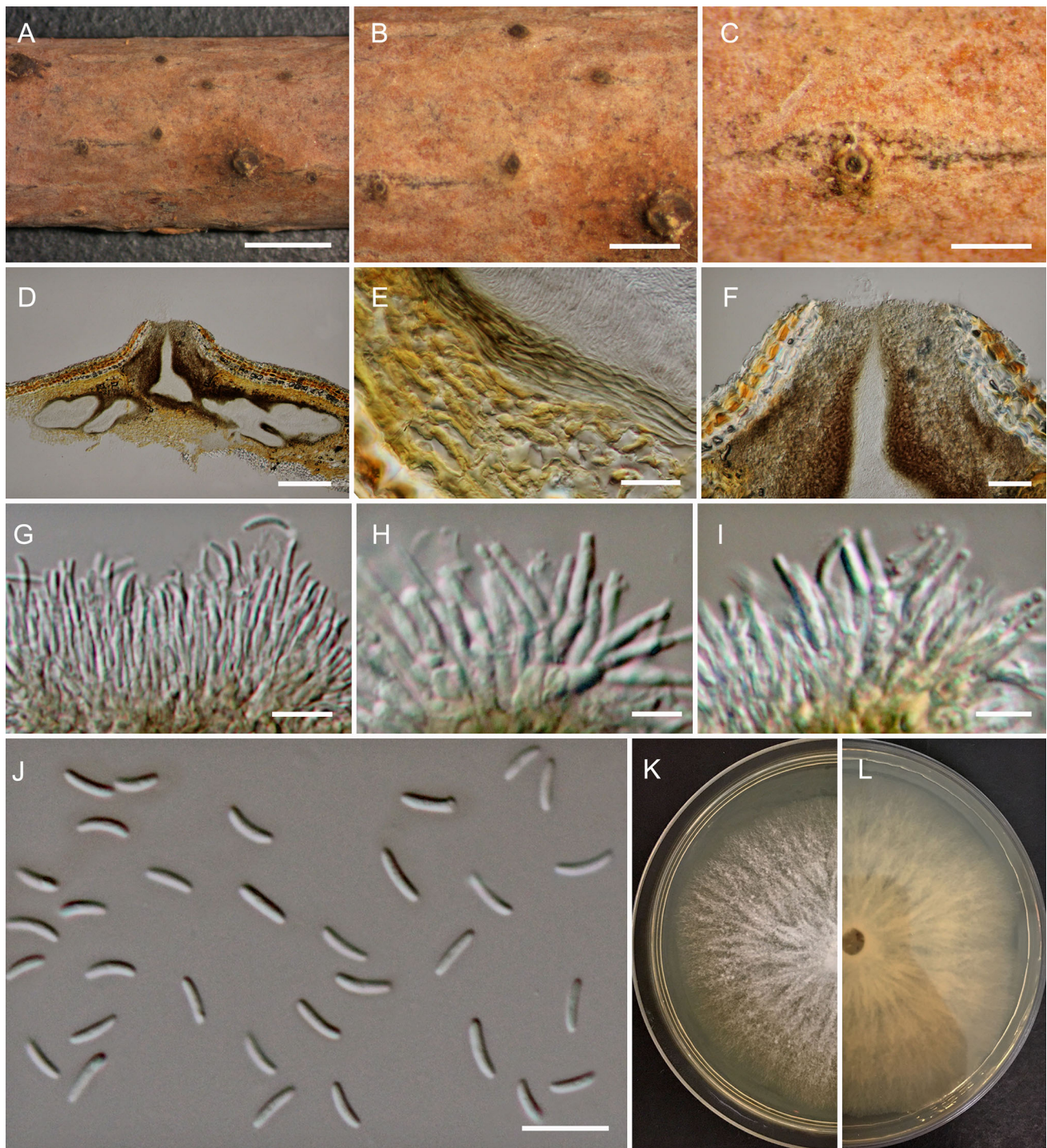
*Disease symptoms*—Sooty blotch and flyspeck (main symptoms of this disease are given under *Chaetothyria*).

To date, *C. artocarpi*, *C. guyanensis*, *C. jingdongensis*, *C. musae*, *C. olivacea*, *C. oxyspora*, *C. phyllostachydis* and *C. sessilis* have been isolated from plant materials (Gams and Holubová-Jechová 1976; de Hoog et al. 1999; Decock et al. 2003; Gao et al. 2014; Yang et al. 2018). *Cyphellophora artocarpi*, *C. musae*, *C. phyllostachydis* and *C. sessilis* were reported to cause sooty blotch and flyspeck from apple, jackfruit (*Artocarpus heterophyllus*) and bamboo (*Phyllostachys heterocycla*, *Sinobambusa tootsik*), resulting in significant economic damage (Zhuang et al. 2010; Mayfield et al. 2012; Gao et al. 2014).

*Hosts*—*Artocarpus heterophyllus*, *Dendrocalamus strictus*, *Eucalyptus* sp., *Helomeco velane*, *Hylomecon verlane*, *Malus domestica*, *Musa* sp., *Phyllostachys* sp., *Sinobambusa tootsik* and *Stenocalyx uniflorus*.

### Morphological based identification and diversity

It is difficult to identify this black yeast-like genus based solely on morphological characters since the characters are very similar to those of other black yeast-like fungi, such as *Phialophora* and *Pseudomicrodochium*. Species of *Cyphellophora* resemble those of *Phialophora* in having melanized thalli with intercalary or terminal phialides bearing collarettes, but *Phialophora* has aseptate conidia whereas *Cyphellophora* produces larger, fusiform to



**Fig. 7** *Cytospora ampulliformis* **a** stromatal habit in wood. **b** fruiting bodies on the substrate. **c** Surface of fruiting bodies. **d** Cross-section of the stroma showing conidiomata. **e** Peridium, **f** ostiolar neck. **g–i** Conidiogenous cells with attached conidia. **j** Mature conidia. **k**,

**l** Colonies on MEA (**k**-from above, **l**-from below). Scale bars: **a** = 2 mm, **b** = 1 mm, **c** = 500  $\mu$ m, **d**, **f** = 200  $\mu$ m, **e** = 50  $\mu$ m, **g**, **h** = 10  $\mu$ m, **i**, **j** = 5  $\mu$ m

sigmoid, aseptate to multi-septate conidia (Réblová et al. 2013). *Cyphellophora* can also be compared to *Pseudomicrodochium*, the former having melanized thalli while they are hyaline in *Pseudomicrodochium* (Decock et al. 2003; de Hoog et al. 2000, 2011). Yang et al. (2018)

introduced *C. jingdongensis* as the first sexual morph, which is characterized by subglobose to globose, non-ostiolate ascomata, ellipsoidal to cylindrical asci and fusoid, 1–3 septate ascospores. However, the asexual morph of *C. jingdongensis* was difficult to observe in culture to

**Table 3** Details of *Cytospora* isolates used in the phylogenetic analyses

| Species                    | Isolate no      | GenBank accession numbers |          |          |          |             |          |
|----------------------------|-----------------|---------------------------|----------|----------|----------|-------------|----------|
|                            |                 | ITS                       | LSU      | ACT      | RPB2     | <i>tefl</i> | TUB2     |
| <i>Cytospora acacia</i>    | CBS 468.69      | DQ243804                  | –        | –        | –        | –           | –        |
| <i>C. ailianthicola</i>    | CFCC 89970*     | MH933618                  | MH933653 | MH933526 | MH933592 | MH933494    | MH933565 |
| <i>C. abyssinica</i>       | CMW 10181*      | AY347353                  | –        | –        | –        | –           | –        |
| <i>C. ampulliformis</i>    | MFLUCC 16-0583* | KY417726                  | KY417760 | KY417692 | KY417794 | –           | –        |
| <i>C. amygdali</i>         | CBS 144233*     | MG971853                  | –        | MG972002 | –        | –           | –        |
| <i>C. atrocirrhatta</i>    | CFCC 89615      | KR045618                  | KR045700 | KF498673 | KU710946 | KP310858    | KR045659 |
| <i>C. austromontana</i>    | CMW 6735*       | AY347361                  | –        | –        | –        | –           | –        |
| <i>C. beilinensis</i>      | CFCC 50493*     | MH933619                  | MH933654 | MH933527 | –        | MH933495    | MH933561 |
| <i>C. berberidis</i>       | CFCC 89927*     | KR045620                  | KR045702 | KU710990 | KU710948 | KU710913    | KR045661 |
| <i>C. berkeleyi</i>        | StanfordT3*     | AY347350                  | –        | –        | –        | –           | –        |
| <i>C. brevispora</i>       | CBS 116811*     | AF192315                  | –        | –        | –        | –           | –        |
| <i>C. bungeanae</i>        | CFCC 50495*     | MH933621                  | MH933656 | MH933529 | MH933593 | MH933497    | MH933563 |
| <i>C. californica</i>      | CBS 144234*     | MG971935                  | –        | MG972083 | –        | MG971645    | –        |
| <i>C. carbonacea</i>       | CFCC 89947      | MH933622                  | MH933657 | MH933530 | MH933594 | MH933498    | MH933564 |
| <i>C. carpobroti</i>       | CMW 48981*      | MH382812                  | MH411216 | –        | –        | MH411212    | MH411207 |
| <i>C. cedri</i>            | CBS 196.50      | AF192311                  | –        | –        | –        | –           | –        |
| <i>C. celtidicola</i>      | CFCC 50497*     | MH933623                  | MH933658 | MH933531 | MH933595 | MH933499    | MH933566 |
| <i>C. centravillosa</i>    | MFLUCC 16-1206* | MF190122                  | MF190068 | –        | MF377600 | –           | –        |
| <i>C. ceratosperma</i>     | CBS 116.21      | AY347335                  | –        | –        | –        | –           | –        |
| <i>C. ceratospermopsis</i> | CFCC 89626*     | KR045647                  | KR045726 | KU711011 | KU710978 | KU710934    | KR045688 |
| <i>C. chrysosperma</i>     | CFCC 89981      | MH933625                  | MH933660 | MH933533 | MH933597 | MH933501    | MH933568 |
| <i>C. cinereostroma</i>    | CMW 5700*       | AY347377                  | –        | –        | –        | –           | –        |
| <i>C. cotini</i>           | MFLUCC 14-1050* | KX430142                  | KX430143 | –        | KX430144 | –           | –        |
| <i>C. curvata</i>          | MFLUCC 15-0865* | KY417728                  | KY417762 | KY417694 | KY417796 | –           | –        |
| <i>C. davidiana</i>        | CXY 1350*       | KM034870                  | –        | –        | –        | –           | –        |
| <i>C. diatrypelloidea</i>  | CMW 8549*       | AY347368                  | –        | –        | –        | –           | –        |
| <i>C. elaeagni</i>         | CFCC 89632      | KR045626                  | KR045706 | KU710995 | KF765708 | KU710918    | KR045667 |
| <i>C. eriobotryae</i>      | IMI 136523*     | AY347327                  | –        | –        | –        | –           | –        |
| <i>C. erumpens</i>         | MFLUCC 16-0580* | KY417733                  | KY417767 | KY417699 | KY417801 | –           | –        |
| <i>C. eucalypti</i>        | LSEQ            | AY347340                  | –        | –        | –        | –           | –        |
| <i>C. eucalypticola</i>    | ATCC 96150*     | AY347358                  | –        | –        | –        | –           | –        |
| <i>C. eucalyptina</i>      | CMW 5882        | AY347375                  | –        | –        | –        | –           | –        |
| <i>C. eugeniae</i>         | CMW 7029        | AY347364                  | –        | –        | –        | –           | –        |
| <i>C. euonymicola</i>      | CFCC 50499*     | MH933628                  | MH933662 | MH933535 | MH933598 | MH933503    | MH933570 |
| <i>C. euonymina</i>        | CFCC 89993*     | MH933630                  | MH933664 | MH933537 | MH933600 | MH933505    | MH933590 |
| <i>C. fraxinigena</i>      | MFLUCC 14-0868* | MF190133                  | MF190078 | –        | –        | –           | –        |
| <i>C. friesii</i>          | CBS 194.42      | AY347328                  | –        | –        | –        | –           | –        |
| <i>C. fugax</i>            | CBS 203.42      | AY347323                  | –        | –        | –        | –           | –        |
| <i>C. germanica</i>        | CXY 1322        | JQ086563                  | JX524617 | –        | –        | –           | –        |
| <i>C. gigalocus</i>        | CFCC 89620*     | KR045628                  | KR045708 | KU710997 | KU710957 | KU710920    | KR045669 |
| <i>C. granati</i>          | CBS 144237*     | MG971799                  | –        | MG971949 | –        | MG971514    | MG971664 |
| <i>C. hippophaës</i>       | CFCC 89639      | KR045632                  | KR045712 | KU711001 | KU710961 | KU710924    | KR045673 |
| <i>C. japonica</i>         | CBS 375.29      | AF191185                  | –        | –        | –        | –           | –        |
| <i>C. joaquinensis</i>     | CBS 144235*     | MG971895                  | –        | MG972044 | –        | MG971605    | MG971761 |
| <i>C. junipericola</i>     | MFLU 17-0882*   | MF190125                  | MF190072 | –        | –        | MF377580    | –        |
| <i>C. juniperina</i>       | CFCC 50501*     | MH933632                  | MH933666 | MH933539 | MH933602 | MH933507    | –        |
| <i>C. kantschavelii</i>    | CXY 1383        | KM034867                  | –        | –        | –        | –           | –        |

**Table 3** (continued)

| Species                     | Isolate no             | GenBank accession numbers |          |          |          |             |          |
|-----------------------------|------------------------|---------------------------|----------|----------|----------|-------------|----------|
|                             |                        | ITS                       | LSU      | ACT      | RPB2     | <i>tefl</i> | TUB2     |
| <i>C. kunzei</i>            | CBS 118556             | DQ243791                  | –        | –        | –        | –           | –        |
| <i>C. leucosperma</i>       | CFCC 89622             | KR045616                  | KR045698 | KU710988 | KU710944 | KU710911    | KR045657 |
| <i>C. longiostiolata</i>    | <b>MFLUCC 16-0628*</b> | KY417734                  | KY417768 | KY417700 | KY417802 | –           | –        |
| <i>C. longispora</i>        | <b>CBS 144236*</b>     | MG971905                  | –        | MG972054 | –        | MG971615    | MG971764 |
| <i>C. lumnitzericola</i>    | <b>MFLUCC 17-0508*</b> | MG975778                  | MH253453 | MH253457 | MH253461 | –           | –        |
| <i>C. mali</i>              | CFCC 50028             | MH933641                  | MH933675 | MH933548 | MH933606 | MH933513    | MH933577 |
| <i>C. melnikii</i>          | <b>MFLUCC 15-0851*</b> | KY417735                  | KY417769 | KY417701 | KY417803 | –           | –        |
| <i>C. mougeotii</i>         | ATCC 44994             | AY347329                  | –        | –        | –        | –           | –        |
| <i>C. multicollis</i>       | <b>CBS 105.89*</b>     | DQ243803                  | –        | –        | –        | –           | –        |
| <i>C. myrtagena</i>         | <b>CBS 116843*</b>     | AY347363                  | –        | –        | –        | –           | –        |
| <i>C. nitschkii</i>         | <b>CMW 10180*</b>      | AY347356                  | –        | –        | –        | –           | –        |
| <i>C. nivea</i>             | MFLUCC 15-0860         | KY417737                  | KY417771 | KY417703 | KY417805 | –           | –        |
| <i>C. oleicola</i>          | <b>CBS 144248*</b>     | MG971944                  | –        | MG972098 | –        | MG971660    | MG971752 |
| <i>C. palm</i>              | <b>CXY 1280*</b>       | JN411939                  | –        | –        | –        | KJ781297    | –        |
| <i>C. parakantschavelii</i> | <b>MFLUCC 15-0857*</b> | KY417738                  | KY417772 | KY417704 | KY417806 | –           | –        |
| <i>C. parapersoonii</i>     | <b>T28.1*</b>          | AF191181                  | –        | –        | –        | –           | –        |
| <i>C. parapistaciae</i>     | <b>CBS 144506*</b>     | MG971804                  | –        | MG971954 | –        | MG971519    | MG971669 |
| <i>C. paratranslucens</i>   | <b>MFLUCC 16-0506*</b> | KY417741                  | KY417775 | KY417707 | KY417809 | –           | –        |
| <i>C. pini</i>              | <b>CBS 224.52*</b>     | AY347316                  | –        | –        | –        | –           | –        |
| <i>C. pistaciae</i>         | <b>CBS 144238*</b>     | MG971802                  | –        | MG971952 | –        | MG971517    | MG971667 |
| <i>C. platanicola</i>       | <b>MFLU 17-0327*</b>   | MH253451                  | MH253452 | MH253449 | MH253450 | –           | –        |
| <i>C. platycladi</i>        | <b>CFCC 50504*</b>     | MH933645                  | MH933679 | MH933552 | MH933610 | MH933516    | MH933581 |
| <i>C. platycladicola</i>    | <b>CFCC 50038*</b>     | KT222840                  | MH933682 | MH933555 | MH933613 | MH933519    | MH933584 |
| <i>C. plurivora</i>         | <b>CBS 144239*</b>     | MG971861                  | –        | MG972010 | –        | MG971572    | MG971726 |
| <i>C. populicola</i>        | <b>CBS 144240*</b>     | MG971891                  | –        | MG972040 | –        | MG971601    | MG971757 |
| <i>C. populina</i>          | CFCC 89644             | KF765686                  | KF765702 | KU711007 | KU710969 | KU710930    | KR045681 |
| <i>C. predappioensis</i>    | <b>MFLUCC 17-2458*</b> | MG873484                  | MG873480 | –        | –        | –           | –        |
| <i>C. predappioensis</i>    | MFLU 17-0327           | MH253451                  | MH253452 | MH253449 | MH253450 | –           | –        |
| <i>C. prunicola</i>         | <b>MFLU 17-0995*</b>   | MG742350                  | MG742351 | MG742353 | MG742352 | –           | –        |
| <i>C. pruinopsis</i>        | <b>CFCC 50034*</b>     | KP281259                  | KP310806 | KP310836 | KU710970 | KP310849    | KP310819 |
| <i>C. pruinosa</i>          | CBS 201.42             | DQ243801                  | –        | –        | –        | –           | –        |
| <i>C. punicae</i>           | CBS 144244             | MG971943                  | –        | MG972091 | –        | MG971654    | MG971798 |
| <i>C. quercicola</i>        | <b>MFLUCC 14-0867*</b> | MF190129                  | MF190073 | –        | –        | –           | –        |
| <i>C. rhizophorae</i>       | MUCC302                | EU301057                  | –        | –        | –        | –           | –        |
| <i>C. ribis</i>             | CBS 187.36             | DQ243810                  | –        | –        | –        | –           | –        |
| <i>C. rosae</i>             | <b>MFLUCC 14-0845*</b> | MF190131                  | MF190075 | –        | –        | –           | –        |
| <i>C. rostrata</i>          | <b>CFCC 89909*</b>     | KR045643                  | KR045722 | KU711009 | KU710974 | KU710932    | KR045684 |
| <i>C. rusanovii</i>         | <b>MFLUCC 15-0854*</b> | KY417744                  | KY417778 | KY417710 | KY417812 | –           | –        |
| <i>C. salicacearum</i>      | <b>MFLUCC 16-0509*</b> | KY417746                  | KY417780 | KY417712 | KY417814 | –           | –        |
| <i>C. salicicola</i>        | <b>MFLUCC 14-1052*</b> | KU982636                  | KU982635 | KU982637 | –        | –           | –        |
| <i>C. salicina</i>          | <b>MFLUCC 15-0862*</b> | KY417750                  | KY417784 | KY417716 | KY417818 | –           | –        |
| <i>C. salicina</i>          | <b>MFLUCC 15-0862*</b> | KY417750                  | KY417784 | KY417716 | KY417818 | –           | –        |
| <i>C. schulzeri</i>         | CFCC 50040             | KR045649                  | KR045728 | KU711013 | KU710980 | KU710936    | KR045690 |
| <i>C. sibiraeae</i>         | <b>CFCC 50045*</b>     | KR045651                  | KR045730 | KU711015 | KU710982 | KU710938    | KR045692 |
| <i>C. sophorae</i>          | CFCC 89598             | KR045654                  | KR045733 | KU711018 | KU710985 | KU710941    | KR045695 |
| <i>C. sophoricola</i>       | <b>CFCC 89595*</b>     | KR045655                  | KR045734 | KU711019 | KU710986 | KU710942    | KR045696 |
| <i>C. sophoriopsis</i>      | <b>CFCC 89600*</b>     | KR045623                  | KP310804 | KU710992 | KU710951 | KU710915    | KP310817 |

**Table 3** (continued)

| Species                   | Isolate no             | GenBank accession numbers |          |          |          |             |          |
|---------------------------|------------------------|---------------------------|----------|----------|----------|-------------|----------|
|                           |                        | ITS                       | LSU      | ACT      | RPB2     | <i>tefl</i> | TUB2     |
| <i>C. sorbi</i>           | <b>MFLUCC 16-0631*</b> | KY417752                  | KY417786 | KY417718 | KY417820 | –           | –        |
| <i>C. sorbicola</i>       | <b>MFLUCC 16-0584*</b> | KY417755                  | KY417789 | KY417721 | KY417823 | –           | –        |
| <i>C. spiraeae</i>        | <b>CFCC 50049*</b>     | MG707859                  | MG707643 | MG708196 | MG708199 | –           | –        |
| <i>C. tamaricicola</i>    | <b>CFCC 50508*</b>     | MH933652                  | MH933687 | MH933560 | MH933617 | MH933523    | MH933588 |
| <i>C. tanaitica</i>       | <b>MFLUCC 14-1057*</b> | KT459411                  | KT459412 | KT459413 | –        | –           | –        |
| <i>C. thailandica</i>     | <b>MFLUCC 17-0262*</b> | MG975776                  | MH253455 | MH253459 | MH253463 | –           | –        |
| <i>C. tibouchinae</i>     | <b>CPC 26333*</b>      | KX228284                  | KX228335 | –        | –        | –           | –        |
| <i>C. translucens</i>     | CXY 1351               | KM034874                  | –        | –        | –        | –           | KM034895 |
| <i>C. ulmi</i>            | <b>MFLUCC 15-0863*</b> | KY417759                  | –        | –        | –        | –           | –        |
| <i>C. valsoidea</i>       | <b>CMW 4309*</b>       | AF192312                  | –        | –        | –        | –           | –        |
| <i>C. variostromatica</i> | <b>CMW 6766*</b>       | AY347366                  | –        | –        | –        | –           | –        |
| <i>C. vinacea</i>         | <b>CBS 141585*</b>     | KX256256                  | –        | –        | –        | KX256277    | KX256235 |
| <i>C. viticola</i>        | <b>CBS 141586*</b>     | KX256239                  | –        | –        | –        | KX256260    | KX256218 |
| <i>C. xylocarpi</i>       | <b>MFLUCC 17-0251*</b> | MG975775                  | MH253462 | MH253462 | MH253462 | –           | –        |

Ex-type (or ex-epitype) strains are in bold and marked with an asterisk\* and voucher strains are in bold

compare with other species in *Cyphellophora* (Yang et al. 2018). There are 26 epithets of *Cyphellophora* in Index Fungorum (2019). Yang et al. (2018) clarified 23 species in this genus. To properly delineate these species, phylogenetic studies using multi-loci sequences (ITS, LSU, RPB1 and TUB2) and the secondary structures of ITS analyses are needed (Réblová et al. 2013; Feng et al. 2014; Gao et al. 2014; Yang et al. 2018).

### Molecular based identification and diversity

Based on SSU and LSU sequence data, *Cyphellophora* clustered in a well-supported clade within the Chaetothyriales (Feng et al. 2014). Generic and species delimitation with morphological characters, ecological traits, host distribution and phylogenetic analyses using the internal transcribed spacer region (ITS), the partial  $\beta$ -tubulin gene (TUB2), the nuclear large subunit rDNA gene (LSU) and the DNA dependent RNA polymerase II largest subunit (RPB1) were recently performed (Feng et al. 2014; Gao et al. 2014). The present study reconstructs the phylogeny of *Cyphellophora* based on analyses of a combined ITS, TUB2, LSU and RPB1 sequence data (Table 4, Fig. 9). The phylogenetic tree in this study is updated with recently introduced *Cyphellophora* species and corresponds to previous studies (Feng et al. 2014; Gao et al. 2014). *Cyphellophora indica* and *C. taiwanensis* lack sequences in GenBank (4/7/2019). *Cyphellophora hylomeconis* was synonymized as *Camptophora hylomeconis* and *C. eugeniae* was synonymized as *Aphanophora eugeniae* (Réblová et al. 2013). *Cyphellophora eucalypti*

were synonymized as *C. guyanensis* (Feng et al. 2014). Therefore, these species were not included in the present phylogenetic analyses (Fig. 9).

*Recommended genetic markers (genus level)*—LSU and SSU

*Recommended genetic markers (species level)*—ITS, LSU, TUB2, RPB1 and secondary (2D) structure of ITS analyses

LSU is useful for preliminary identification at the generic level (Feng et al. 2014). Réblová et al. (2013) resolved *Cyphellophora* and *Phialophora* as close relatives within the Chaetothyriales, although both genera were paraphyletic based on analysis of ITS, TUB2 and nuc28S rDNA sequence data. It is recommended to use a combination of ITS, LSU, TUB2, RPB1 and secondary (2D) structure of ITS analyses (Réblová et al. 2013; Feng et al. 2014; Gao et al. 2014) in order to identify to the species level.

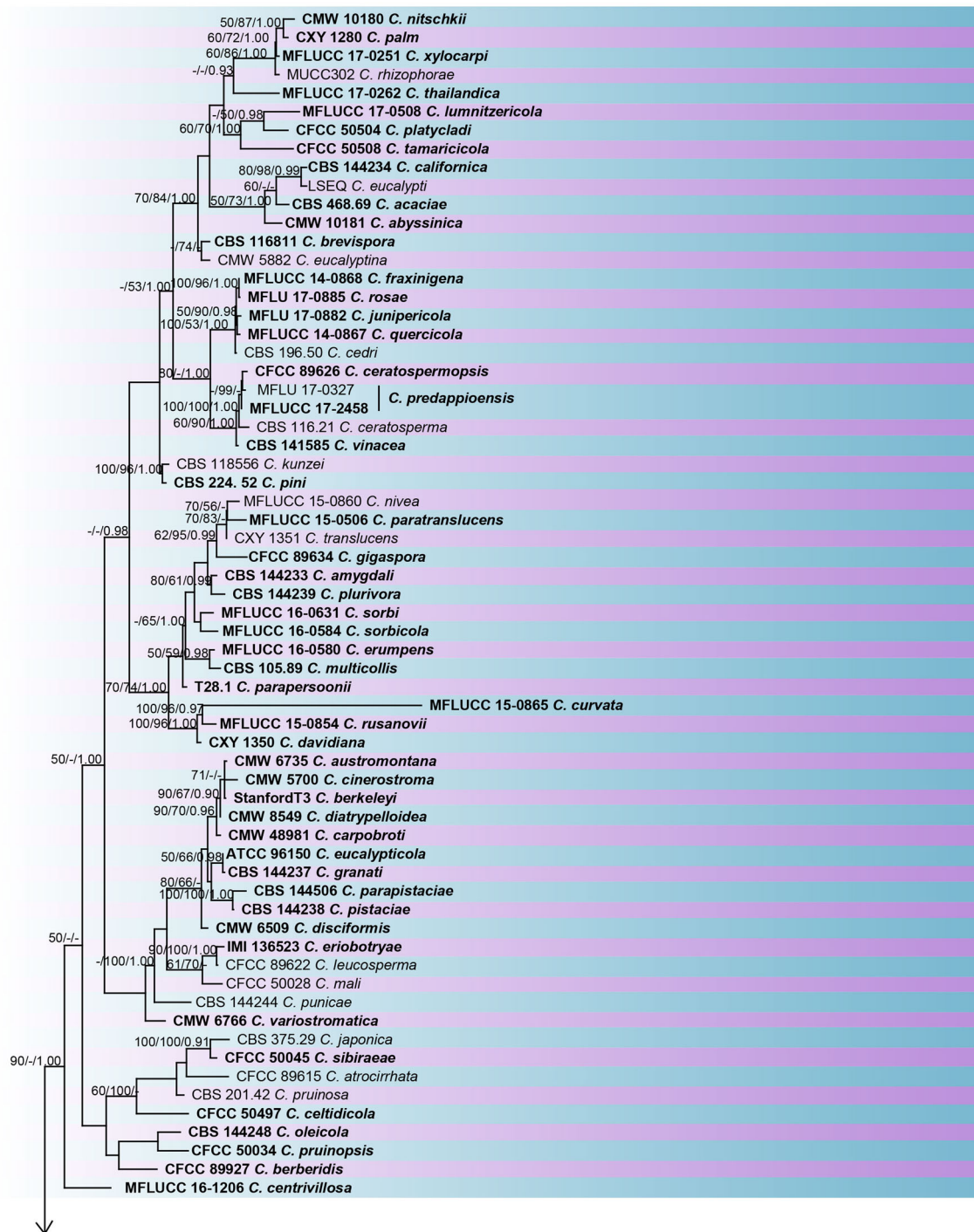
*Accepted number of species: 24 species*

*References:* Vries 1962, 1986; Matsushima 1987; Walz and de Hoog 1987; Decock et al. 2003; Crous et al. 2013, 2016; Réblová et al. 2013; Feng et al. 2014; Gao et al. 2014; Madrid et al. 2016; Yang et al. 2018 (morphology, phylogeny)

*Cyttaria* Berk., Trans. Linn. Soc. London 19:40 (1842)

This genus is geographically restricted to South America (Argentina and Chile) and Southeastern Australasia (including Tasmania, and New Zealand) (Peterson and Pfister 2010). *Cyttaria* species are found in the secondary phloem and xylem, cambium and cortex of the hosts. They produce

## MP/ML/BYPP



**Fig. 8** Phylogenetic tree generated by maximum parsimony analysis of combined ITS, LSU, ACT and RPB2 sequence data of *Cytospora* species. Related sequences were obtained from GenBank. One hundred and eleven strains are included in the analyses, which comprised 2266 characters including gaps. The tree was rooted with *Diaporthe vaccinii* (CBS 160.32). The maximum parsimonious dataset consisted of 1358 constant, 596 parsimony-informative and

312 parsimony-uninformative characters. The parsimony analysis of the data matrix resulted in the maximum of ten equally most parsimonious trees with a length of 3836 steps (CI = 0.364, RI 0.649, RC = 0.236, HI = 0.636) in the first tree. MP and ML bootstrap values  $\geq 50\%$  and Bayesian posterior probabilities  $\geq 0.90$  are shown respectively near the nodes. The scale bar indicates 10 changes per site. Ex-type strains are in bold



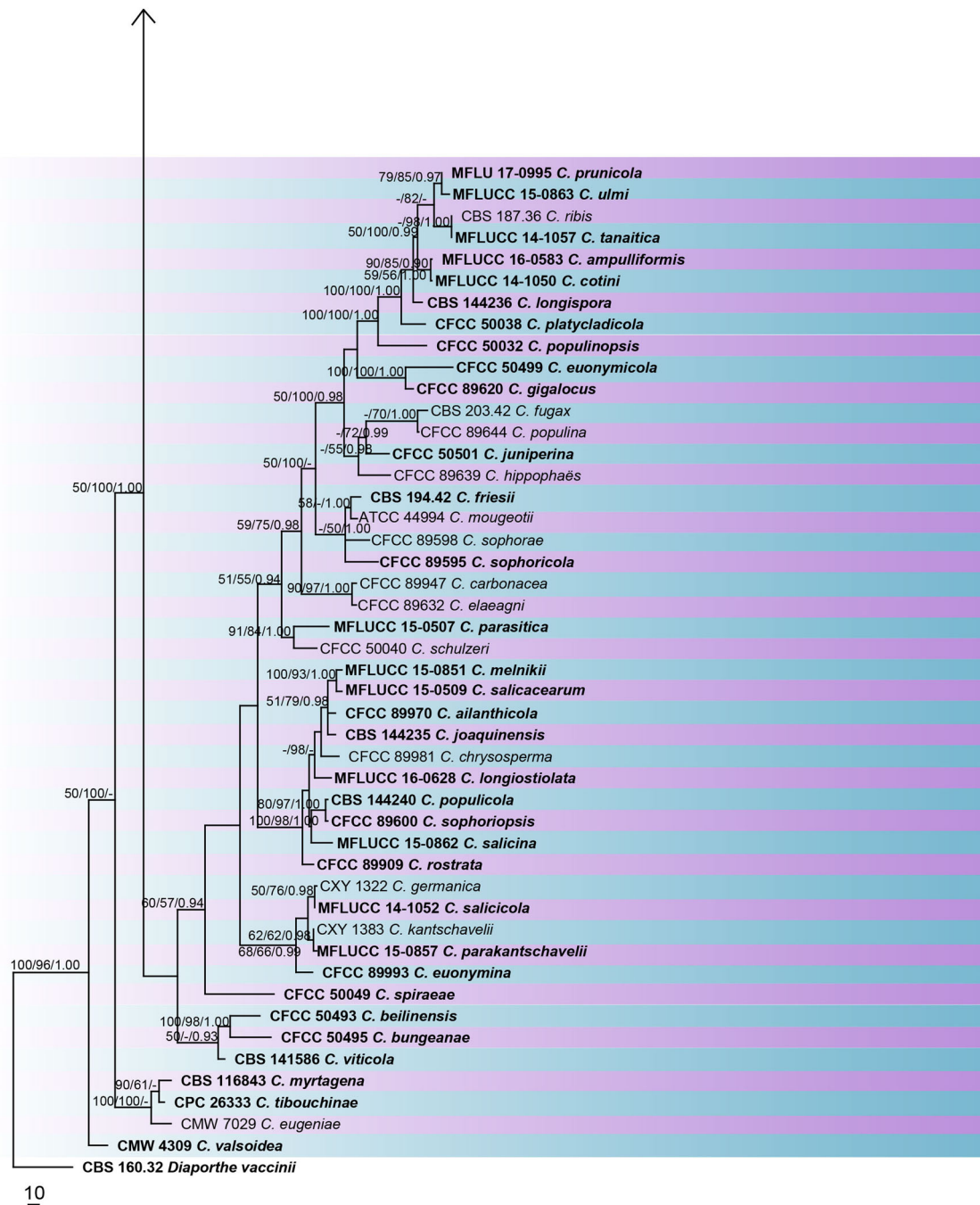


Fig. 8 continued

trunk and branch cankers that arise due to localized, stimulated cambial activity attributed to the presence of hyphae of *Cyttaria* (Wilson 1907; Gutierrez de Sanguinetti 1988). *Cyttaria* species are considered as weak parasites (Gamundí and De Lederkremer 1989).

**Classification**—Leotiomyces, Leotiomycetidae, Cyttariales, Cyttariaceae

**Type species**—*Cyttaria darwinii* Berk., Trans. Linn. Soc. London 19:40 (1842)

**Distribution**—Argentina, Australia, Chile, New Zealand, Tasmania.

**Disease symptoms**—Canker, galls

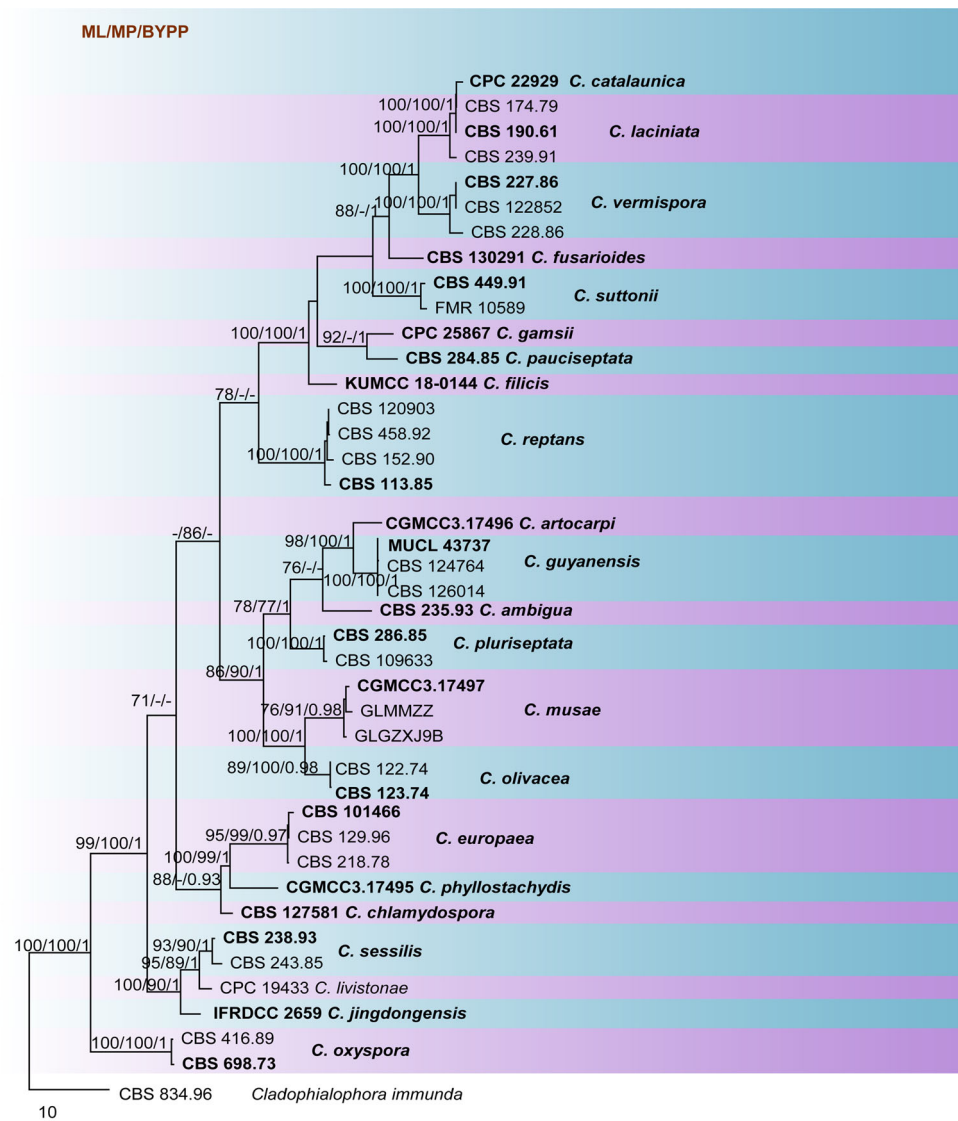
These species are known to cause two types of cankers: globose and longitudinal. Globose cankers arise from

**Table 4** Details of the *Cyphellophora* isolates used in the phylogenetic analyses

| Species                         | Isolate/voucher no                | ITS      | LSU      | RPB1     | TUB2     |
|---------------------------------|-----------------------------------|----------|----------|----------|----------|
| <i>Cyphellophora ambigua</i>    | <b>CBS 235.93*</b>                | JQ766431 | JQ766480 | JQ766386 | JQ766340 |
| <i>C. artocarp</i>              | <b>CGMCC3.17496*</b>              | KP010367 | KP122930 | KP122920 | KP122925 |
| <i>C. catalaunica</i>           | <b>CPC 22929*</b>                 | HG003670 | HG003673 | –        | –        |
| <i>C. chlamyospora</i>          | <b>CBS 127581 (= FMR 10878) *</b> | HG003674 | HG003675 | –        | –        |
| <i>C. europaea</i>              | <b>CBS 101466*</b>                | JQ766443 | KC455259 | JQ766395 | JQ766365 |
| <i>C. europaea</i>              | CBS 218.78                        | JQ766441 | JQ766488 | JQ766393 | JQ766366 |
| <i>C. europaea</i>              | CBS 129.96                        | JQ766440 | JQ766487 | JQ766392 | JQ766364 |
| <i>C. filicis</i>               | KUMCC 18-0144                     | MK404056 | MK404052 | –        | –        |
| <i>C. fusarioides</i>           | <b>CBS 130291*</b>                | JQ766439 | KC455252 | JQ766391 | JQ766363 |
| <i>C. gamsii</i>                | <b>CPC 25867*</b>                 | KX228255 | KX228307 | –        | KX228381 |
| <i>C. guyanensis</i>            | <b>MUCL 43737*</b>                | KC455240 | KC455253 | –        | KC455223 |
| <i>C. guyanensis</i>            | CBS 124764                        | GQ303274 | GQ303305 | –        | –        |
| <i>C. guyanensis</i>            | CBS 126014                        | JQ766434 | JQ766483 | JQ766389 | JQ766339 |
| <i>C. jingdongensis</i>         | <b>IFRDCC 2659*</b>               | MF285234 | MF285236 | –        | –        |
| <i>C. laciniata</i>             | <b>CBS 190.61*</b>                | JQ766423 | JQ766472 | JQ766378 | JQ766329 |
| <i>C. laciniata</i>             | CBS 174.79                        | JQ766422 | JQ766471 | JQ766377 | JQ766328 |
| <i>C. laciniata</i>             | CBS 239.91                        | JQ766424 | JQ766473 | JQ766379 | JQ766330 |
| <i>C. livistonae</i>            | CPC19433                          | KC005774 | KC005796 | –        | –        |
| <i>C. musae</i>                 | <b>CGMCC3.17497*</b>              | KP010370 | KP122932 | KP122922 | KP122927 |
| <i>C. musae</i>                 | GLGZXJ9B                          | KP010368 | KP122931 | KP122923 | KP122926 |
| <i>C. musae</i>                 | GLMMZZ4                           | KP010369 | KP122934 | KP122921 | KP122928 |
| <i>C. olivacea</i>              | <b>CBS 123.74*</b>                | KC455248 | KC455261 | –        | KC455231 |
| <i>C. olivacea</i>              | CBS 122.74                        | KC455247 | KC455260 | –        | KC455230 |
| <i>C. oxyspora</i>              | <b>CBS 698.73*</b>                | JQ766450 | KC455262 | JQ766402 | KC455232 |
| <i>C. oxyspora</i>              | CBS 416.89                        | JQ766449 | JQ766497 | JQ766401 | JQ766374 |
| <i>C. pauciseptata</i>          | <b>CBS 284.85*</b>                | JQ766466 | JQ766515 | JQ766415 | JQ766360 |
| <i>C. phyllostachidis</i>       | <b>CGMCC3.17495*</b>              | KP010371 | KP122933 | KP122924 | KP122929 |
| <i>C. pluriseptata</i>          | <b>CBS 286.85*</b>                | JQ766429 | KC455255 | JQ766384 | JQ766335 |
| <i>C. pluriseptata</i>          | CBS 109633                        | JQ766430 | JQ766479 | JQ766385 | JQ766336 |
| <i>C. reptans</i>               | <b>CBS 113.85*</b>                | JQ766445 | JQ766493 | JQ766397 | JQ766370 |
| <i>C. reptans</i>               | CBS 152.90                        | JQ766446 | JQ766494 | JQ766398 | JQ766371 |
| <i>C. reptans</i>               | CBS 458.92                        | JQ766447 | JQ766495 | JQ766399 | JQ766372 |
| <i>C. reptans</i>               | CBS120903                         | JQ766448 | JQ766496 | JQ766400 | JQ766373 |
| <i>C. sessilis</i>              | <b>CBS 243.85*</b>                | EU514700 | EU514700 | –        | KC455234 |
| <i>C. sessilis</i>              | CBS 238.93                        | AY857541 | KF928523 | –        | KF928587 |
| <i>C. suttonii</i>              | <b>CBS 449.91*</b>                | JQ766459 | KC455256 | –        | KC455226 |
| <i>C. suttonii</i>              | FMR 10589                         | KU705828 | KU705845 | –        | –        |
| <i>C. vermispota</i>            | <b>CBS 228.86*</b>                | KC455244 | KC455257 | JQ766381 | JQ766332 |
| <i>C. vermispota</i>            | CBS 122852                        | JQ766427 | JQ766476 | JQ766382 | JQ766333 |
| <i>C. vermispota</i>            | CBS 227.86                        | JQ766425 | JQ766474 | JQ766380 | JQ766331 |
| <i>Cladophialophora immunda</i> | CBS 834.96                        | EU137318 | KC809990 | –        | EU137203 |

Ex-type (or ex-epitype) strains are in bold and marked with an asterisk\* and voucher strains are in bold

**Fig. 9** Phylogram generated from RAxML analysis based on combined sequences of ITS, LSU, RPB1 and TUB2 sequences of all accepted species of *Cyrtophthora*. Forty-one strains are included in the analyses, which comprise 2514 characters including gaps. The tree was rooted with *Cladophialophora immunda* (CBS 834.96). Tree topology of the ML analysis was similar to the MP and BYPP analyses. The best scoring RAxML tree with a final likelihood value of  $-5928.387430$  is presented. The matrix had 337 distinct alignment patterns, with 12.44% of undetermined characters or gaps. Estimated base frequencies were as follows; A = 0.234866, C = 0.250597, G = 0.284325, T = 0.230211; substitution rates AC = 1.492532, AG = 2.025910, AT = 2.769660, CG = 1.674732, CT = 8.545312, GT = 1.000000; gamma distribution shape parameter  $\alpha = 0.136482$ . RAxML and maximum parsimony bootstrap support value  $\geq 50\%$  are shown respectively near the nodes. Bayesian posterior probabilities  $\geq 0.95$  (BYPP) indicated as thickened black branches. Ex-type strains are in bold



growth mainly in the transverse axis of the branch while longitudinal cankers arise from growth mainly along the long axis (Rawlings 1956; Gamundi 1971). Development of perennial galls on branches and stems may lead to malformation and occasional death of branches (Gadgil 1985).

*Hosts*—*Nothofagus* spp.

### Morphological based identification and diversity

Ascomata of *Cyrtaria* species are orange, pitted apothecia similar to deeply dimpled golf balls. Each fruiting body is composed of 1–200 apothecia immersed in a sterile fleshy-gelatinous stroma. Asci are 8-spored, inoperculate and amyloid. Ascospores are uninucleate, subglobose to ovoid, smooth to rugulose, at first hyaline to yellowish but later becoming pigmented (Mengoni 1986; Peterson et al 2010).

### Molecular based identification and diversity

The first phylogenetic analysis which included *Cyrtaria* was done by Gargas and Taylor (1995) showing its relationship with other discomycetes. Wang et al. (2006) showed its placement within Leotiomycetes using combined analysis of SSU, LSU and 5.8S rDNA gene sequence data and then confirmed by Ekanayaka et al. (2017). Peterson and Pfister (2010) did large scale phylogeny for *Cyrtaria* including all accepted 12 species in the genus using sequence data of partial nucSSU, nucLSU and mtSSU rRNA, as well as *tefl*. They found *Cyrtaria* to be a strongly supported clade and suggested a close relationship between *Cyrtaria* and some members of the Helotiales (*Cordierites*, *Encoelia*, *Ionomidotis* and *Chlorociboria*) (Peterson and Pfister 2010). The present study reconstructs the phylogeny of *Cyrtaria* based on analyses of a combined

**Table 5** Details of *Cyttaria* isolates used in the phylogenetic analyses

| Species                   | Isolate/voucher no | LSU      | SSU      | mtSSU    |
|---------------------------|--------------------|----------|----------|----------|
| <i>C. berteroi</i>        | Isolate 16         | EU107205 | EU107178 | EU10723  |
| <i>C. darwinii</i>        | Isolate 40         | EU107207 | EU107180 | EU107236 |
| <i>C. darwinii</i>        | Isolate 14         | EU107208 | EU107181 | –        |
| <i>C. darwinii</i>        | Isolate 57         | EU107206 | EU107179 | EU107235 |
| <i>C. darwinii</i>        | Isolate 45         | EU107209 | –        | –        |
| <i>C. darwinii</i>        | Isolate 50         | EU107211 | –        | –        |
| <i>C. darwinii</i>        | Isolate 49         | EU107210 | –        | –        |
| <i>C. espinosae</i>       | Isolate 187        | –        | EU107183 | EU107238 |
| <i>C. espinosae</i>       | Isolate 92         | EU107212 | EU107182 | EU107237 |
| <i>C. exigua</i>          | Isolate 77         | EU107214 | EU107185 | EU107240 |
| <i>C. exigua</i>          | Isolate 76         | EU107213 | EU107184 | EU107239 |
| <i>C. gunnii</i>          | Isolate 138        | –        | EU107189 | EU107242 |
| <i>C. gunnii</i>          | Isolate 127        | EU107215 | EU107186 | EU107241 |
| <i>C. gunnii</i>          | Isolate 136        | –        | EU107188 | –        |
| <i>C. gunnii</i>          | Isolate 132        | –        | EU107187 | –        |
| <i>C. hariotii</i>        | Isolate 44         | EU107217 | EU107194 | EU107245 |
| <i>C. hariotii</i>        | Isolate 55         | EU107218 | EU107195 | EU107246 |
| <i>C. hariotii</i>        | Isolate 65         | EU107223 | –        | –        |
| <i>C. hariotii</i>        | Isolate 64         | EU107222 | –        | –        |
| <i>C. hariotii</i>        | Isolate 63         | EU107221 | –        | –        |
| <i>C. hariotii</i>        | Isolate 62         | EU107220 | –        | –        |
| <i>C. hariotii</i>        | Isolate 51         | EU107219 | –        | –        |
| <i>C. hookeri</i>         | Isolate 60         | EU107227 | –        | –        |
| <i>C. hookeri</i>         | Isolate 59         | EU107226 | –        | –        |
| <i>C. hookeri</i>         | Isolate 80         | EU107228 | –        | –        |
| <i>C. hookeri</i>         | Isolate 61         | EU107225 | EU107197 | –        |
| <i>C. hookeri</i>         | Isolate 58         | EU107224 | EU107196 | –        |
| <i>C. johowii</i>         | Isolate 73         | EU107229 | EU107198 | –        |
| <i>C. johowii</i>         | Isolate 74         | EU107230 | EU107199 | –        |
| <i>C. nigra</i>           | Isolate 100        | EU107232 | EU107201 | EU107248 |
| <i>C. nigra</i>           | Isolate 97         | EU107231 | EU107200 | EU107247 |
| <i>C. septentrionalis</i> | Isolate 199        | –        | EU107203 | EU107249 |
| <i>C. septentrionalis</i> | Isolate 85         | –        | EU107202 | –        |

LSU, SSU and mtSSU sequence data (Table 5, Fig. 10). The phylogenetic tree is updated with recently introduced *Cyttaria* species and corresponds to previous studies (Feng et al. 2014; Gao et al. 2014).

*Recommended genetic markers (genus level)*—ITS, LSU  
*Recommended genetic markers (species level)*—nucSSU, nucLSU, mitSSU rRNA, and *tefl*

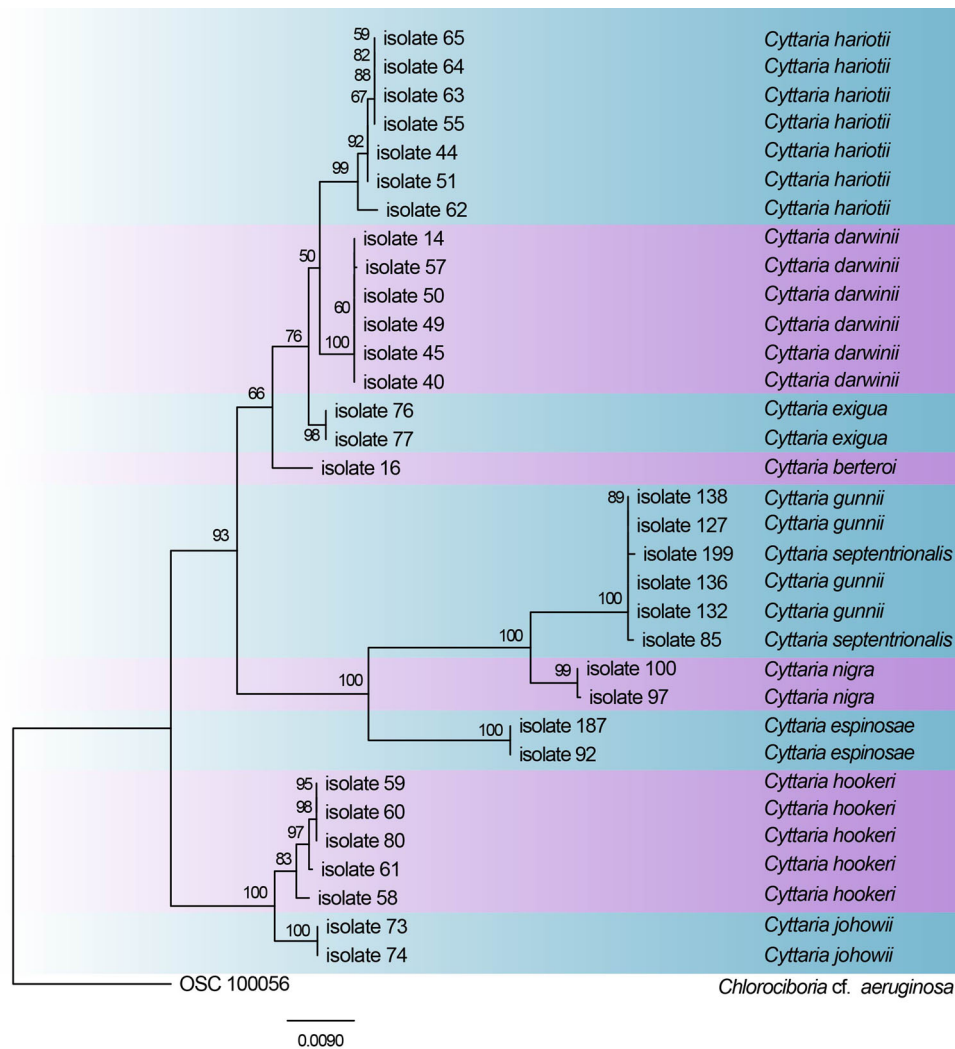
Combined nucSSU, nucLSU, mitSSU rRNA, and *tefl* can resolve almost all species of *Cyttaria* currently known from sequence data (Peterson et al 2010).

*Accepted number of species:* There are 21 epithets in Index Fungorum (2019). However, **12 species have molecular data and are treated as accepted.**

*References:* Mengoni 1986, Peterson et al 2010 (morphology); Peterson and Pfister (2010), Ekanayaka et al. 2017 (morphology, phylogeny).

*Dactylonectria* L. Lombard & Crous, in Lombard et al., Phytopath. Mediterr. 53(3): 523 (2014)

The genus *Dactylonectria* was introduced by Lombard et al. (2014) for a group of species which were previously treated in *Ilyonectria* (Chaverri et al. 2011; Cabral et al. 2012a, b, c). In morphology, *Dactylonectria* resembles *Ilyonectria* and *Neonectria* but can be distinguished by their characteristic ovoid to obpyriform, smooth to finely warted, dark-red ascomata with a papillate ostiolar region at the apex (Lombard et al. 2014; Gordillo and Decock



**Fig. 10** Phylogram generated from RAxML analysis based on combined sequences of LSU, SSU and mtSSU sequences of all the accepted species of *Cyttaria*. Related sequences were obtained from GenBank. Thirty-four strains are included in the analyses, which comprise 3480 characters including gaps. Single gene analyses were carried out and compared with each species, to compare the topology of the tree and clade stability. The tree was rooted with *Chlorociboria cf. aeruginosa* (OSC 100056). The best scoring RAxML tree with a

final likelihood value of  $-7505.900855$  is presented. The matrix had 360 distinct alignment patterns, with 39.17% of undetermined characters or gaps. Estimated base frequencies were as follows; A = 0.256, C = 0.214, G = 0.280, T = 0.250; substitution rates AC = 1.190197, AG = 1.207782, AT = 0.373130, CG = 0.681125, CT = 3.724394, GT = 1.000000; gamma distribution shape parameter  $\alpha = 0.020000$ . RAxML and maximum parsimony bootstrap support value  $\geq 50\%$  (BT) are shown respectively near the nodes

2018). Species of this genus are mostly associated with *Vitis* sp., while some species are also recorded from other hosts (Farr and Rossman 2019).

**Classification**—Sordariomycetes, Hypocreomycetidae, Hypocreales, Nectriaceae

**Type species**—*Dactylonectria macrodidyma* (Hallen, Schroers & Crous) L. Lombard & Crous, in Lombard et al., Phytopath. Mediterr. 53(3): 527 (2014)

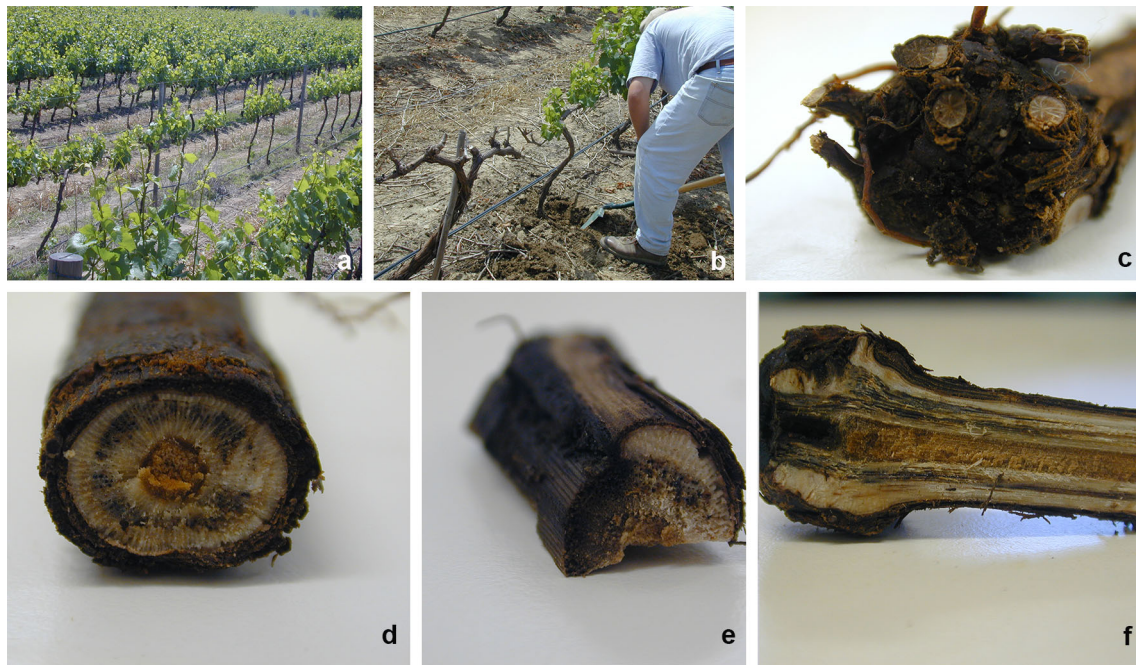
**Distribution**—Worldwide

**Disease symptoms**—Black foot disease, black root rot

Characteristic symptoms of black foot disease include a reduction in root biomass and root hairs with sunken and necrotic lesions (Halleen et al. 2006). Severe necrosis of

the root system results in stunting, wilting, leaf chlorosis, browning and leaf drop prior to death (Parkinson et al. 2017). *Dactylonectria alcacerensis*, *D. estremocensis*, *D. macrodidyma*, *D. novozelandica*, *D. pauciseptata*, *D. pinicola*, *D. torresensis* and *D. vitis* are associated with black foot disease of grapevine (Cabral et al. 2012a; Lombard et al. 2014) (Fig. 11).

**Hosts**—*Abies* sp., *Annona cherimola*, *Anthrrium* sp., *Arbutus unedo*, *Cistus albidus*, *Crataegus azalosa*, *Erica melanthera*, *Eriobotrya japonica*, *Ficus* sp., *Fragaria* sp., *Hordeum vulgare*, *Ilex aquifolium*, *Juglans regia*, *Juniperus phoenicea*, *Lonicera* sp., *Myrtus communis*, *Persea americana*, *Picea glauca*, *Pinus* sp., *Pistacia lentiscus*,



**Fig. 11** Symptoms of black foot disease on *Vitis* spp. **a, b** dead plants and stunted growth of grapevine. **c, e** Infection of rootstock. **d** Blocked xylem vessels. **f** Black streak (Courtesy of Halleen)

*Prunus domestica*, *Pyracantha* sp., *Quercus* sp., *Rosmarinus officinalis*, *Santolina chamaecyparissus* and *Vitis* sp.

#### Morphological based identification and diversity

Lombard et al. (2014) accepted ten species in *Dactylonectria* based on ITS, LSU, TUB2 and *tefl* sequence data and morphological characters. Later, Gordillo and Decock (2018) introduced another four species to the genus based on morphology and sequence data.

Fourteen *Dactylonectria* species have been described with DNA sequence data in GenBank. *Dactylonectria* species produce cylindrocarpon-like asexual morphs, several of which were previously treated in *Ilyonectria* (Lombard et al. 2014). *Dactylonectria* species were distinguished mainly by phylogenetic inference and using unique fixed single nucleotide polymorphisms (SNP's) rather than morphological characters (Lombard et al. 2014; Gordillo and Decock 2018).

#### Molecular based identification and diversity

Lombard et al. (2014) re-evaluated genera with cylindrocarpon-like asexual morphs based on multi-gene phylogeny of ITS, LSU, TUB2 and *tefl* genes. Gordillo and Decock (2018) analysed His3 together with latter gene regions, for delimiting the species in *Dactylonectria*. Lombard et al. (2015) also supported the fact that *Dactylonectria* is monophyletic and distinct from *Ilyonectria*. In this study, we reconstruct the phylogeny of *Dactylonectria* based on analyses of a combined ITS, LSU, TUB2 and *tefl* sequence

data (Table 6, Fig. 12). The phylogenetic tree is updated with recently introduced *Dactylonectria* species and corresponds to previous studies (Lombard et al. 2014, 2015; Gordillo and Decock 2018).

*Recommended genetic markers (genus level)*—ITS, LSU, TUB2, *tefl*

*Recommended genetic markers (species level)*—TUB, *tefl*

*Accepted number of species: 14 species*

*References:* Cabral et al. 2012a, b; Halleen et al. 2004, Schroers et al. 2008; Lombard et al. 2014; Gordillo and Decock 2018 (morphology, phylogeny).

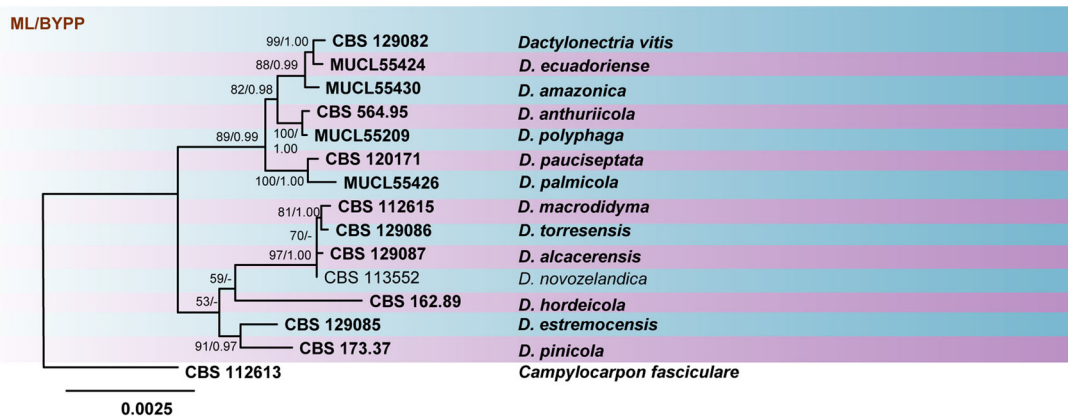
*Entoleuca* Syd., Annl. mycol. 20(3/4):186 (1922)

The genus *Entoleuca* Syd. (*Xylariaceae*) consists of saprobic and plant pathogenic species distributed in Europe. *Entoleuca mammata* causes canker diseases (commonly known as Hypoxylon canker) on *Malus* sp. (*Rosaceae*), *Populus* sp., *Salix* sp. (*Salicaceae*) and *Sorbus* sp. (*Rosaceae*) (Shaw 1973; Callan 1998; Kasanen et al. 2004; Eriksson 2014) and also occurs as a saprobe on decaying tree trunks. The species are distributed in terrestrial habitats in temperate regions. The genus is characterized by its known sexual morph. It is characterized by partially embedded solitary or aggregated orbicular stroma, that has a whitish surface when young and dark surface at maturity, papillate ostiole; multiple, monostichous and embedded ascomata in stromata; 8-spored, unitunicate asci that are cylindrical, long pedicellate, with J+ apical ring bluing in Melzer's reagent and uniseriate, unicellular,

**Table 6** Details of the *Dactylonectria* isolates used in the phylogenetic analyses

| Species                            | Isolate/voucher no | ITS      | LSU      | TUB2     | <i>tefl</i> |
|------------------------------------|--------------------|----------|----------|----------|-------------|
| <i>Campylocarpon fasciculare</i>   | <b>CBS 112613*</b> | AY677301 | HM364313 | AY677221 | JF735691    |
| <i>Dactylonectria alcacerensis</i> | <b>CBS 129087*</b> | JF735333 | KM231629 | AM419111 | JF735819    |
| <i>D. anthuriicola</i>             | <b>CBS 564.95*</b> | JF735302 | KM515897 | JF735430 | JF735768    |
| <i>D. amazonica</i>                | <b>MUCL55433*</b>  | MF683707 | MF683727 | MF683644 | MF683665    |
| <i>D. ecuadoriense</i>             | <b>MUCL55424*</b>  | MF683704 | MF683724 | MF683641 | MF683662    |
| <i>D. estremocensis</i>            | <b>CBS 129085*</b> | JF735320 | KM231630 | JF735448 | JF735806    |
| <i>D. hordeicola</i>               | <b>CBS 162.89*</b> | AM41906  | KM515898 | AM419084 | JF735799    |
| <i>D. macrodidyma</i>              | <b>CBS 112615*</b> | AY677290 | KM515900 | AY677233 | JF735836    |
| <i>D. novozelandica</i>            | <b>CBS 112608*</b> | AY677288 | KM515901 | AY677235 | JF735821    |
| <i>D. palmicola</i>                | <b>MUCL55426*</b>  | MF683708 | MF683728 | MF683645 | MF683666    |
| <i>D. pauciseptata</i>             | <b>CBS 120171*</b> | EF607089 | KM515903 | EF607066 | JF735776    |
| <i>D. pinicola</i>                 | <b>CBS 173.37*</b> | JF735319 | KM515905 | JF735447 | JF735803    |
| <i>D. polyphaga</i>                | <b>MUCL55209*</b>  | MF683689 | MF683710 | MF683626 | MF683647    |
| <i>D. torresensis</i>              | <b>CBS 129086*</b> | JF735362 | KM231631 | JF735492 | JF735870    |
| <i>D. vitis</i>                    | <b>CBS 129082*</b> | JF735303 | KM515907 | JF735431 | JF735769    |

Ex-type (or ex-epitype) strains are in bold and marked with an asterisk\* and voucher strains are in bold



**Fig. 12** Phylogram generated from RAxML analysis based on combined sequences of ITS, LSU, TUB and *tefl* sequences of all the accepted species of *Dactylonectria*. Related sequences were obtained from GenBank. Fifteen taxa are included in the analyses, which comprise 2460 characters including gaps. Single gene analyses were carried out and compared with each species, to compare the topology of the tree and clade stability. The tree was rooted with *Campylocarpon fasciculare* (CBS 112613). Tree topology of the ML analysis was similar to the BI. The best scoring RAxML tree with a final likelihood value of  $-6772.195394$  is presented. The matrix had

261 distinct alignment patterns, with 0.96% of undetermined characters or gaps. Estimated base frequencies were as follows; A = 0.230657, C = 0.279364, G = 0.252128, T = 0.237852; substitution rates AC = 1.388608, AG = 2.845402, AT = 2.389715, CG = 0.838197, CT = 7.220493, GT = 1.000000; gamma distribution shape parameter  $\alpha = 0.650385$ . RAxML and maximum parsimony bootstrap support value  $\geq 50\%$  are shown respectively near the nodes. Bayesian posterior probabilities  $\geq 0.95$  (BYPP) indicated as thickened black branches. Ex-type strains are in bold

ellipsoidal inequilateral, brown, with straight to oblique germ slit ascospores (Rogers and Ju 1996; Daranagama et al. 2018). Daranagama et al. (2018) provided an identification key with emphasis on the coarsely papillate ostiole in *Entoleuca*.

Sydow and Petrak (1922) introduced the genus with *E. callimorpha* as the type species. Until 1994, *Hypoxyton mammatum* was considered a similar taxon to *E. callimorpha*. However, Læssøe and Spooner (1994) and Læssøe (1994) treated *H. mammatum* as a separate,

synonym to *Rosellinia*. Based on these taxonomic confusions, Rogers and Ju (1996) revised the type, authentic and other specimens and re-established the genus *Entoleuca*.

**Classification**—Sordariomycetes, Xylariomycetidae, Xylariales, Xylariaceae

**Type species**—*Entoleuca callimorpha* Syd., in Sydow & Petrak, Annl. mycol. 20(3/4):186 (1922)

**Distribution**—Austria, Canada, Poland, Sweden, USA

**Disease symptoms**—Canker

Symptoms may vary on the stage of disease development. Young cankers appear as slightly sunken, yellowish orange areas with irregular margins. Later, the outer-most bark within the canker breaks out in blisters exposing a powdery grey mat of fungal tissue and conidia. Then the patches of bark start to flake off making the canker rough and black in the centre. Advancing margins of the enlarging cankers become yellowish orange (Ostry 2013). *Hosts*—Known from *Malus sylvestris*, *Populus* sp., *Salix* sp. and *Sorbus aucuparia*.

### Morphological based identification and diversity

Currently, the genus comprises three species: *E. callimorpha*, *E. ellisii* and *E. mammata* (Sydow and Petrak 1922; Rogers and Ju 1996; Ju et al. 2004; Index Fungorum 2019). Due to the presence of clear papillate ostioles, they have been distinguished from closely related genera such as *Amphirosellinia*, *Nemania*, and *Rosellinia*. Molecular data are only available for *E. mammata*, which is the most important species in the genus as a pathogen. Rogers and Ju (1996) observed that there are no distinguishing morphological differences among *E. mammata* isolates from different hosts. However, there is a high polymorphism, but no major phylogenetic differences among the isolates from Europe (Kasanen et al. 2004). Ju et al. (2004) introduced *E. ellisii* based on characterizations of ascospore and germ slit. Therefore, a combination of morphological and phylogenetic analyses are needed for species delimitation of *Entoleuca*.

### Molecular based identification and diversity

Several recent studies have focused on the molecular phylogeny of *Entoleuca*, especially *E. mammata*. Phylogenetic based population studies revealed that higher polymorphism occurs in North American than in Europe (Kasanen et al. 2004). The sterile mycelia associated with *Pinus tabulaeformis* and its ITS-based phylogenetic analyses revealed that the genus *Entoleuca* clusters in *Xylariaceae* and is closely related to *Nemania* (Guo et al. 2003). Daranagama et al. (2018) revisited the family *Xylariaceae* and due to the morphological differences and conidial state characters, they suggested that it is useful to maintain the taxa as distinct genera. Daranagama et al. (2018) and Wendt et al. (2018) conducted multi-gene phylogenetic analyses using ITS, LSU, RPB2 and TUB2 and revealed that *E. mammata* clusters with *Rosellinia corticium* with high support. Due to the lack of molecular data from other species and other gene regions, it is difficult to place *Entoleuca* in an appropriate family.

In this study, we included the available sequences of *Entoleuca* in the analysis done for *Rosellinia* (Table 7, Fig 13).

*Recommended genetic markers (genus level)*—LSU and ITS

*Recommended genetic markers (species level)*—RPB2 and TUB2

Combined LSU, ITS, RPB2 and TUB2 provide a satisfactory resolution for resolving species.

*Accepted number of species:* **Three species**

*References:* Sydow and Petrak 1922; Rogers and Ju 1996; Ju et al. 2004 (morphology), Daranagama et al. 2018 (morphology, phylogeny).

*Eutiarosporella* Crous, in Crous et al., Phytotaxa 202(2): 85 (2015)

*Eutiarosporella* was introduced by Crous et al. (2015) and is typified by *Eutiarosporella tritici* (B. Sutton & Marasas) Crous on *Triticum aestivum* from South Africa. The genus was named on account of its similarity to *Tiarosporella* Höhn. (Crous et al. 2006). *Eutiarosporella* species are coelomycetes that are saprobes or pathogens which occur in terrestrial habitats (Crous et al. 2015; Thynne et al. 2015; Li et al. 2016). *Eutiarosporella* species have been reported from *Celtis africana* (Rosales), *Triticum aestivum* (Poales), *Acacia karroo* (Fabales) and *Dactylis glomerata* (Poales) (Thambugala et al. 2014; Crous et al. 2015). On wheat, it causes the economically important disease known as white grain disorder (Thynne et al. 2015). Several studies have reported this genus on woody hosts as a saprobe (Jami et al. 2012, 2014; Dissanayake et al. 2016).

*Classification*—*Dothideomycetes*, *incertae sedis*, *Botryosphaeriales*, *Botryosphaeriaceae*  
*Type species*—*Eutiarosporella tritici* (B. Sutton & Marasas) Crous, in Crous et al., Phytotaxa 202(2):85 (2015)

*Distribution*—Worldwide

*Disease symptoms*—White grain disorder of wheats

White grain disorder shrivels and discolours (white to light grey) wheat grain (Thynne et al. 2015). Affected grains are more brittle and can break during harvesting. Infected spikelets of green heads may show bleaching appearance or grey discolouration. At first, the bleached florets may show blue-gray ‘highlights’. Rachis of affected heads and the upper peduncle may show a brownish discolouration (Thynne et al. 2015).

Even though species of this genus have been found to be associated with several hosts other than wheat, their diseases have not been described.

*Hosts*—*Acacia karroo*, *Arrhenatherum elatius*, *Avenella flexuosa*, *Celtis africana*, *Dactylis glomerata*, *Triticum aestivum* and *Vachelloa karroo* (Farr and Rossman 2019).

### Morphological based identification and diversity

*Eutiarosporella* is characterized by hairy conidiomata with long necks, and holoblastic conidiogenesis, features which



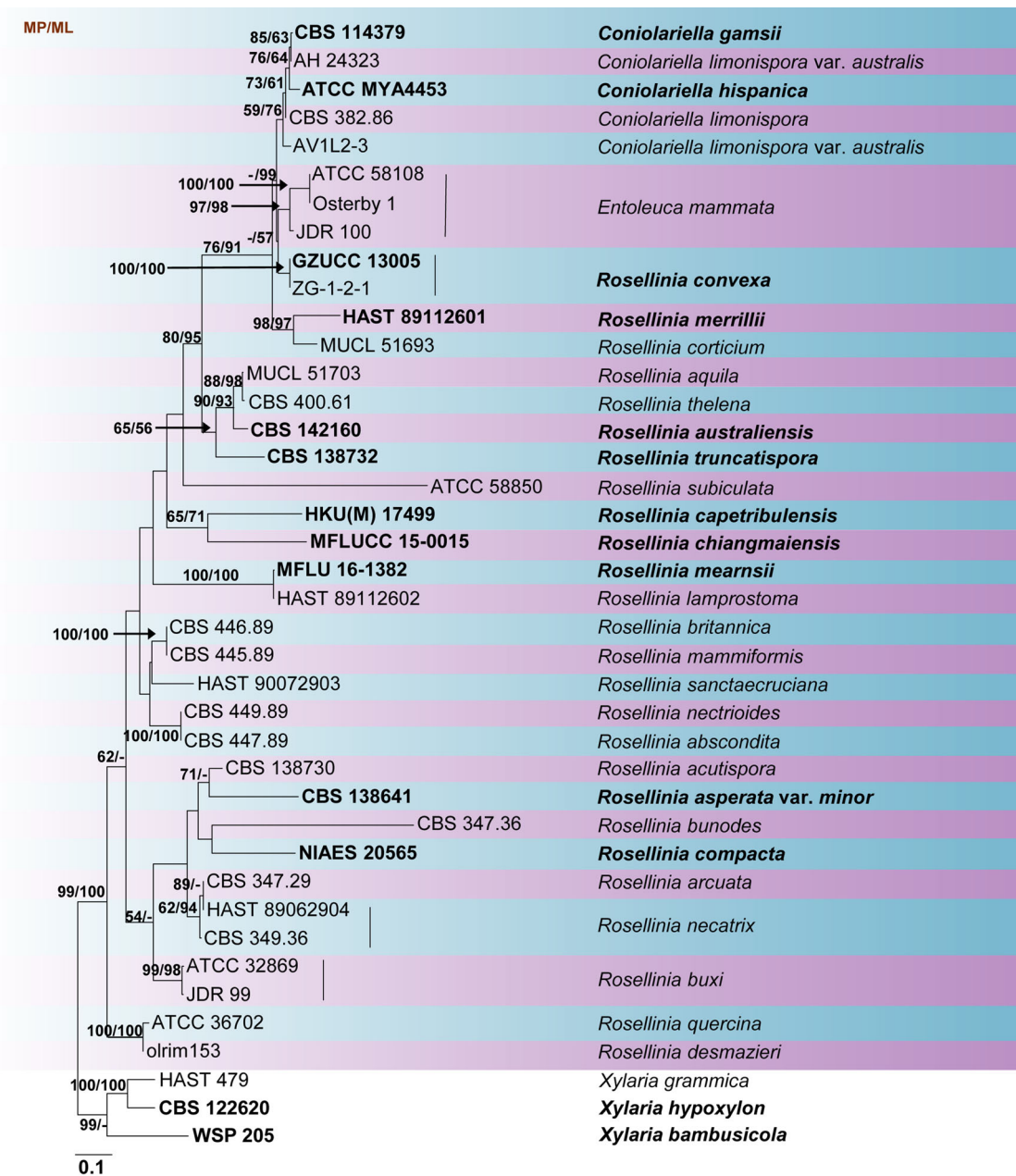
**Table 7** Details of the *Entoleuca* and *Rosellinia* isolates used in the phylogenetic analyses

| Species                                     | Isolate/voucher no    | ITS      | LSU      | RPB2     |
|---|-----------------------|----------|----------|----------|
| <i>Coniolaria gamsii</i>                    | <b>CBS 114379*</b>    | GU553325 | GU553329 | N/A      |
| <i>C. hispanica</i>                         | <b>ATCC MYA4453*</b>  | GU553323 | GU553353 | N/A      |
| <i>C. limonispota</i>                       | CBS 382.86            | KF719199 | KF719211 | N/A      |
| <i>C. limonispota</i> var. <i>australis</i> | AV1L2-3               | KP101193 | N/A      | N/A      |
| <i>C. limonispota</i> var. <i>australis</i> | AH24323               | AY908997 | N/A      | N/A      |
| <i>Entoleuca mammata</i>                    | JDR 100               | GU300072 | N/A      | GQ844782 |
| <i>E. mammata</i>                           | ATCC 58108            | AF201713 | N/A      | N/A      |
| <i>E. mammata</i>                           | Osterby 1             | AF176983 | N/A      | N/A      |
| <i>Rosellinia abscondita</i>                | CBS 447.89            | FJ175180 | KF719208 | N/A      |
| <i>R. aquila</i>                            | MUCL 51703            | KY610392 | KY610460 | KY624285 |
| <i>R. arcuate</i>                           | CBS347.29             | AB017660 | N/A      | N/A      |
| <i>R. asperata</i> var. <i>minor</i>        | <b>CBS 138641*</b>    | KY941107 | N/A      | N/A      |
| <i>R. australiensis</i>                     | <b>CBS 142160*</b>    | KY979742 | KY979797 | N/A      |
| <i>R. britannica</i>                        | CBS 446.89            | FJ175182 | KF719209 | N/A      |
| <i>R. bunodes</i>                           | CBS 347.36            | AB609598 | KF719205 | N/A      |
| <i>R. buxi</i>                              | JDR 99                | GU300070 | N/A      | GQ844780 |
| <i>R. buxi</i>                              | ATCC 32869            | AY909000 | EF489467 | N/A      |
| <i>R. capetribulensis</i>                   | <b>HKU(M) 17499*</b>  | AY862570 | N/A      | N/A      |
| <i>R. acutispota</i>                        | CBS 138730            | KY941108 | N/A      | N/A      |
| <i>R. chiangmaiensis</i>                    | <b>MFLU 15-3524*</b>  | KU246226 | KU246227 | N/A      |
| <i>R. compacta</i>                          | <b>NIAES:20565*</b>   | AB430457 | N/A      | N/A      |
| <i>R. convexa</i>                           | <b>GZUCC 13005*</b>   | KF614036 | N/A      | KP876561 |
| <i>R. convexa</i>                           | ZG-1-2-1              | KR822145 | N/A      | N/A      |
| <i>R. corticium</i>                         | MUCL 51693            | KC477236 | KY610461 | KY624229 |
| <i>R. desmazieri</i>                        | olrim153              | AY805591 | N/A      | N/A      |
| <i>R. lamprostoma</i>                       | HAST 89112602         | EF026118 | N/A      | GQ844778 |
| <i>R. mammiformis</i>                       | CBS 445.89            | KF719200 | KF719212 | N/A      |
| <i>R. mearnsii</i>                          | <b>MFLU 16-1382*</b>  | KY514059 | KY514060 | KY514061 |
| <i>R. merrillii</i>                         | <b>HAST 89112601*</b> | GU300071 | N/A      | GQ844781 |
| <i>R. necatrix</i>                          | HAST 89062904         | EF026117 | AY083824 | GQ844779 |
| <i>R. necatrix</i>                          | CBS 349.36            | AY909001 | KF719204 | N/A      |
| <i>R. nectrioides</i>                       | CBS 449.89            | FJ175181 | KF719213 | N/A      |
| <i>R. quercina</i>                          | ATCC 36702            | AB017661 | N/A      | N/A      |
| <i>R. sanctaeruciana</i>                    | HAST 90072903         | GU292824 | N/A      | GQ844777 |
| <i>R. subiculata</i>                        | ATCC 58850            | AY909002 | EF489468 | N/A      |
| <i>R. thelena</i>                           | CBS 400.61            | KF719202 | KF719215 | N/A      |
| <i>R. truncatispora</i>                     | <b>CBS 138732*</b>    | KY941109 | N/A      | N/A      |
| <i>Xylaria bambusicola</i>                  | <b>WSP 205*</b>       | EF026123 | AB376825 | GQ844802 |
| <i>X. grammica</i>                          | HAST 479              | GU300097 | N/A      | GQ844813 |
| <i>X. hypoxylon</i>                         | <b>CBS 122620*</b>    | AM993141 | KM186301 | KM186302 |

Ex-type (or ex-epitype) strains are in bold and marked with an asterisk\* and voucher strains are in bold

are clearly distinguishable from *Tiarosporella* (Höhnelt 1919; Crous et al. 2015). This genus is morphologically similar to *Marasasiomyces* (long-necked, hairy conidiomata, and holoblastic conidiogenesis), except that it forms conidiomata in clusters, which are not found in *Marasasiomyces* (Crous et al. 2015). Li et al. (2016) reported the sexual morph of *Eutiarosporella* in *E.*

*dactylidis* for the first time from *Avenella flexuosa* (Poales). The sexual morph is characterised by globose ascomata, with a central ostiole, a two-layered peridium, hyphae-like pseudoparaphyses and hyaline, aseptate, fusoid to ovoid ascospores, with a mucilaginous sheath (Thambugala et al. 2014).



**Fig. 13** Phylogenetic tree generated by maximum likelihood analysis of combined ITS, LSU and RPB2 sequence data of *Entoleuca* and *Rosellinia* species. Related sequences were obtained from GenBank. Forty strains are included in the analyses, which comprise 2336 characters including gaps. Single gene analyses were carried out and compared with each species, to compare the topology of the tree and clade stability. The tree was rooted with *Xylaria bambusicola* (WSP 205), *X. grammica* (HAST 479) and *X. hypoxylon* (CBS 122620). Tree topology of the ML analysis was similar to the MP. The best scoring RAxML tree with a final likelihood value of  $-12521.202450$  is presented. The matrix had 793 distinct alignment patterns, with 51.67% of undetermined characters or gaps. Estimated base

frequencies were as follows; A = 0.241655, C = 0.263843, G = 0.260086, T = 0.234416; substitution rates AC = 1.764265, AG = 4.237635, AT = 0.953946, CG = 1.541272, CT = 8.643978, GT = 1.000000; gamma distribution shape parameter  $\alpha = 1.105097$ . The maximum parsimonious dataset consisted of constant 1567, 629 parsimony-informative and 140 parsimony-uninformative characters. The parsimony analysis of the data matrix resulted in the maximum of two equally most parsimonious trees with a length of 2112 steps (CI = 0.545, RI = 0.668, RC = 0.364, HI = 0.455) in the first tree. RAxML and maximum parsimony bootstrap support value  $\geq 50\%$  are shown respectively near the nodes. Ex-type strains are in bold

Based on ITS and LSU sequence data, three species were initially included in this genus, *E. africana* (Jami et al.) Crous, *E. tritici* (B. Sutton & Marasas) Crous and *E. urbis-rosarum* (Jami et al.) Crous by Crous et al. (2015). Subsequently, *E. darliae* E. Thynne et al., *E. tritici-austriaca* E. Thynne, et al. and *E. dactylidis* (Thambug., Camporesi & K.D. Hyde) Dissan., Camporesi & K.D. Hyde were accommodated in the genus (Crous et al. 2015; Thynne et al. 2015; Li et al. 2016), which now comprises seven species (Dissanayake et al. 2016; Wijayawardene et al. 2017).

Colony and conidial morphology are the primary characters to identify species within this genus. Colonies on nutrient-rich media (PDA or V8-OMA) grow rapidly (Thynne et al. 2015). However, we consider morphological characters alone are inadequate to identify species due to plasticity and overlapping of conidial dimensions. Therefore, incorporation of molecular data together with morphology is recommended.

### Molecular based identification and diversity

Taxonomy of *Eutiarospora* is largely based on DNA sequence data to reveal the phylogenetic relationships between the species (Crous et al. 2015; Thynne et al. 2015; Dissanayake et al. 2016; Li et al. 2016). According to studies by Crous et al. (2015), Thynne et al. (2015) and Li et al. (2016), ITS and LSU are the most suitable loci for delineation of species within the genus. The phylogram generated with sequences available in GenBank including ex-epitype sequences is provided in Fig. 14 (Table 8). Our phylogenetic analyses are in accordance with previous studies by Crous et al. (2015), Thynne et al. (2015), Dissanayake et al. (2016) and Li et al. (2016).

*Recommended genetic markers (genus level)*—LSU and SSU

*Recommended genetic markers (species level)*—ITS and LSU

*Accepted number of species:* **Seven species.**

*References:* Crous et al. (2015), Thynne et al. (2015), Dissanayake et al. (2016), Li et al. 2016 (morphology, phylogeny).

***Ilyonectria*** P. Chaverri & Salgado, in Chaverri et al., Stud. Mycol. 68:69 (2011)

Species of *Ilyonectria* (Nectriaceae, Hypocreales) are important soil-borne pathogens of various woody and herbaceous plant hosts. *Ilyonectria* species are cosmopolitan and are found on a wide range of hosts (Chaverri et al. 2011). They are mostly associated with root diseases and stem cankers (Seifert et al. 2003; Halleen et al. 2004, 2006; Chaverri et al. 2011; Cabral et al. 2012a, b, c; Vitale et al. 2012; Lombard et al. 2013; Aiello et al. 2014). There are 23 species of *Ilyonectria*, all associated with

disease symptoms of their original plant hosts (Chaverri et al. 2011; Cabral et al. 2012a,c; Lombard et al. 2013, 2014; Aiello et al. 2014). *Ilyonectria* is a well-known genus causing black foot rot of grapevines in various countries (Halleen et al. 2003, 2004, 2006; Chaverri et al. 2011; Cabral et al. 2012a, b, c; Lombard et al. 2014).

*Classification*—Sordariomycetes, Hypocreomycetidae, Hypocreales, Nectriaceae

*Type species*—***Ilyonectria radicola*** (Gerlach & L. Nilsson) P. Chaverri & Salgado, in Chaverri et al., Stud. Mycol. 68:71 (2011)

*Distribution*—Worldwide

*Disease symptoms*—Black foot disease, black root rot

Symptoms are given under the genus *Dactylonectria*

*Hosts*—Wide host range including plant genera in *Amaryllidaceae*, *Aracaceae*, *Araliaceae*, *Cupressaceae*, *Fagaceae*, *Liliaceae*, *Myrtaceae*, *Pinaceae*, *Proteaceae*, *Rosaceae*, *Strelitziaceae* and *Vitaceae* (Farr and Rossman 2019).

### Morphological based identification and diversity

The genus *Ilyonectria* was introduced based on *I. radicola* as the type species, to accommodate *Neonectria* species belonging to the “*N. radicola*” group (Booth 1959). This genus has asexual morphs and belonged to Booth’s Group 3 (chlamydospores and microconidia present, Booth 1966; Chaverri et al. 2011; Lombard et al. 2014). Molecular phylogenetic studies revealed that *Ilyonectria*, as originally conceived, was paraphyletic (Cabral et al. 2012a, c; Lombard et al. 2013, 2014). Conidial size, culture characters and molecular data enabled the separation of *Ilyonectria* species (Cabral et al. 2012a, c; Lombard et al. 2013, 2014).

### Molecular based identification and diversity

Delineating between species of *Ilyonectria* can be achieved with histone (His3) gene region. The topologies of the phylogenetic tree (Fig. 15, Table 9) is similar to previous studies done on this genus (Cabral et al. 2012a; Lombard et al. 2014).

*Recommended genetic markers (genus level)*—ITS, LSU, *tef1*, TUB2

*Recommended genetic markers (species level)*—*tef1*, TUB2, His3

*Accepted number of species:* **23 species**

*References:* Booth 1959, 1966 (morphology), Cabral et al. 2012a, b, c; Lombard et al. 2013, 2014 (morphology, phylogeny).

***Macrophomina*** Petr., Anns mycol. 21: 314 (1923)

Species of *Macrophomina* are mostly pathogens that cause damping-off, seedling blight, collar rot, stem rot, charcoal rot, basal stem rot and root rot in many plant

species (Arora et al. 2001; Pal et al. 2001; Gupta et al. 2002; Sarr et al. 2014; Wijayawardene et al. 2017). The type species, *Macrophomina phaseolina* (Tassi) Goid., is a seed-borne polyphagous pathogen that affects more than 500 crop and non-crop species, including economically important crops, such as soybean, sunflower, common bean, peanut, corn, sorghum, cowpea and cotton (Gupta et al. 2002; Ndiaye et al. 2010; Sarr et al. 2014).

**Classification**—*Dothideomycetes*, *incertae sedis*, *Botryosphaerales*, *Botryosphaeriaceae*

**Type species**—*Macrophomina phaseolina* (Tassi) Goid., *Annali Sper. agr.*, N.S. 1(3): 457 (1947)

**Distribution**—Worldwide

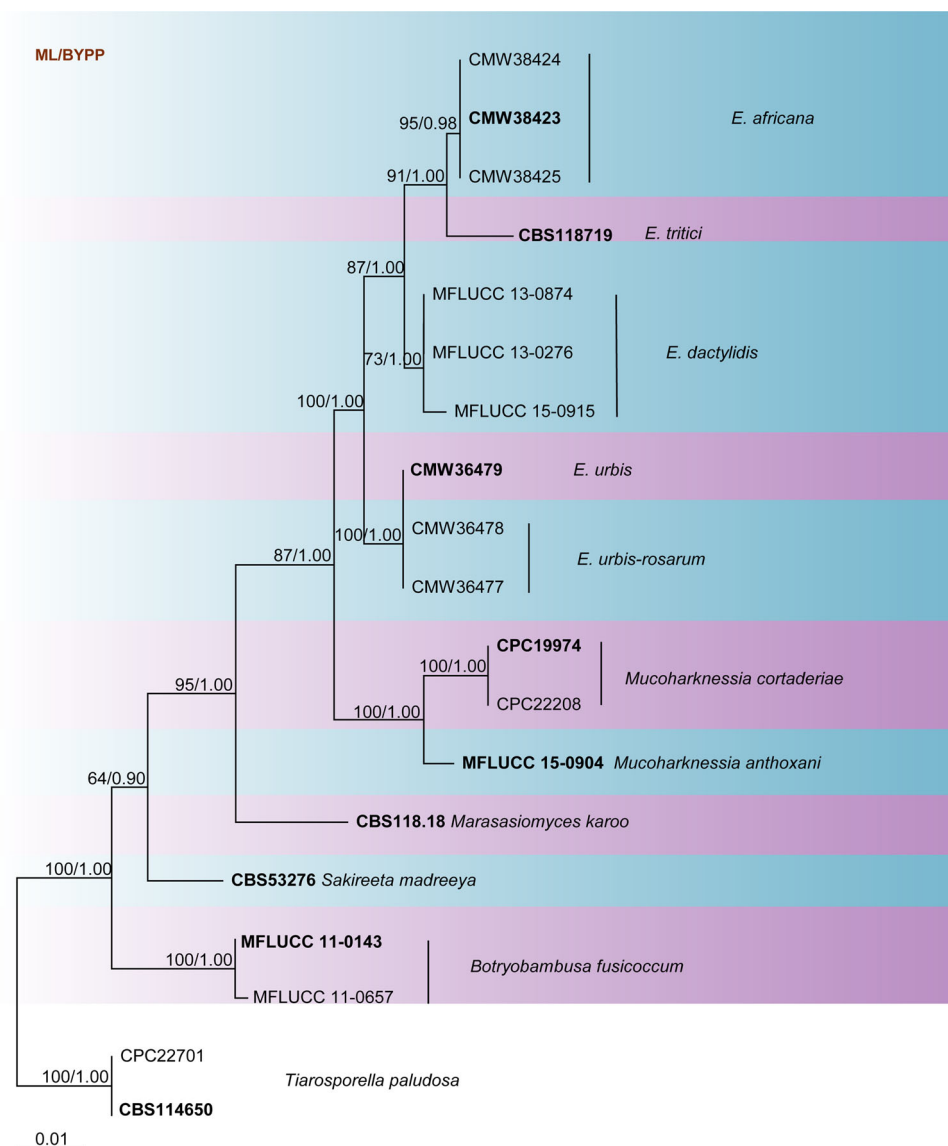
**Disease symptoms**—Charcoal rot, collar rot, damping off, root rot, seedling blight, stem rot, wilt

Seedling damage can occur when infected seeds are planted. Infected plants may produce slightly smaller

leaflets than healthy plants and have reduced vigour. As the disease advances, leaflets turn yellow, wilt and turn brown (Adorada et al. 2018). A grey/silver discoloration can be observed in the roots and lower stem when the plants split open (Romero Luna et al. 2017; Koehler and Shew 2018; Meena et al. 2018). In charcoal rot, the abundant production of minute black sclerotia by the fungus causes the rotted tissues to become blackened. Infections on soybean lead to early maturation and incomplete pod filling (ElAraby et al. 2003; Yang and Navi 2005; Sarr et al. 2014). In peanut, it causes seed and seedling rots, wilt, root and stem rots, leaf spot and rotting of developing pods and seeds (Gupta et al. 2002; Deshwal et al. 2003).

**Hosts**—This soil-borne fungus can infect more than 500 agricultural crops and weed species including, *Fragaria*, *Glycine*, *Helianthus*, *Sorghum* and *Zea*.

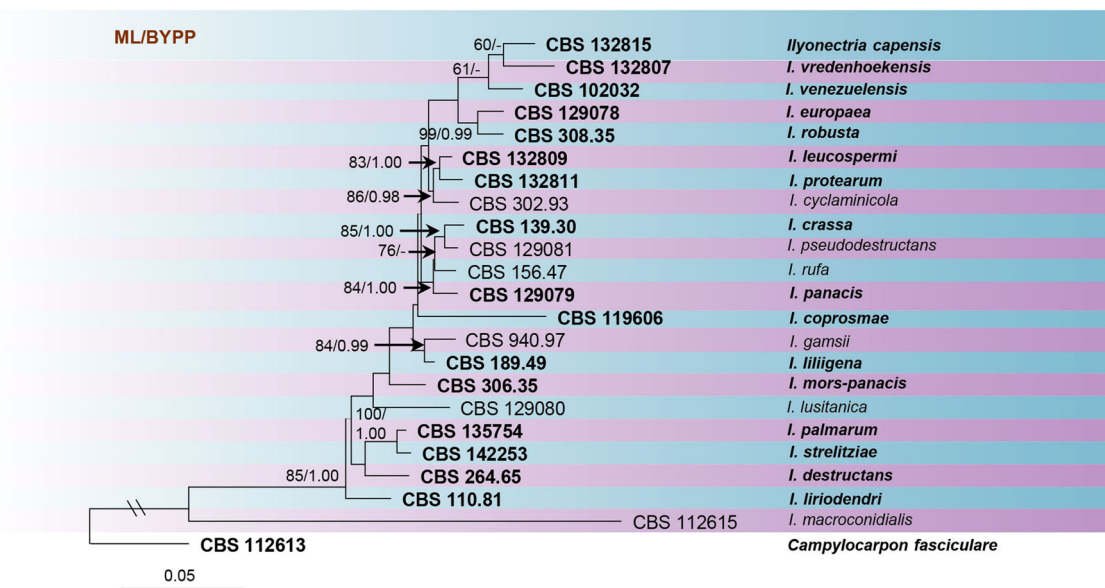
**Fig. 14** Phylogram generated from maximum likelihood analysis based on combined LSU and ITS sequence data retrieved from GenBank. The tree is rooted in *Tiarospora paludosa* (CPC 22701 and CBS 114650). Tree topology of the ML analysis was similar to the Bayesian analysis. The best scoring RAXML tree with a final likelihood value of  $-7055.996836$  is presented. The matrix had 380 distinct alignment patterns, with 40.12% of undetermined characters or gaps. Estimated base frequencies were as follows; A = 0.229604, C = 0.264209, G = 0.282595, T = 0.223593; substitution rates AC = 1.357965, AG = 1.612491, AT = 0.913118, CG = 2.194420, CT = 5.121479, GT = 1.000000; gamma distribution shape parameter  $\alpha = 0.137391$ . Maximum likelihood bootstrap support values greater than 60% are indicated above the nodes. Ex-type (ex-epitype) and voucher strains are in bold



**Table 8** Details of the *Eutiarosporella* isolates used in the phylogenetic analyses

| Species                           | Isolate/voucher no     | LSU             | ITS             |
|-----------------------------------|------------------------|-----------------|-----------------|
| <i>Botryobambusa fusicoccum</i>   | MFLUCC 11-0657         | JX646810        | JX646793        |
| <b><i>B. fusicoccum</i></b>       | <b>MFLUCC 11-0143*</b> | <b>JX646809</b> | <b>NR111793</b> |
| <i>Eutiarosporella africana</i>   | <b>CMW 38423*</b>      | <b>KC769990</b> | <b>KC769956</b> |
| <i>E. dactylidis</i>              | MFLUCC 15-0915         | KU246380        | NR148093        |
| <i>Eutiarosporella dactylidis</i> | MFLUCC 13-0874         | KM978948        | KM978945        |
| <b><i>E. dactylidis</i></b>       | <b>MFLUCC 13-0276*</b> | <b>KM978949</b> | <b>KM978944</b> |
| <b><i>E. urbis</i></b>            | <b>CMW 36477*</b>      | <b>JQ239420</b> | <b>NR111705</b> |
| <i>E. urbis-rosarum</i>           | CMW 36479              | JQ239422        | JQ239409        |
| <i>E. urbis-rosarum</i>           | CMW 36478              | JQ239421        | JQ239408        |
| <i>Marasasiomyces karoo</i>       | <b>CBS 1187.18*</b>    | <b>DQ377939</b> | <b>KF531828</b> |
| <i>Mucoharknessia anthoxanthi</i> | <b>MFLUCC 15-0904*</b> | <b>KU246379</b> | <b>NR148092</b> |
| <i>M. cortaderiae</i>             | CPC 22208              | KM108402        | KM108375        |
| <b><i>M. cortaderiae</i></b>      | <b>CPC 19974*</b>      | <b>KM108401</b> | <b>NR148075</b> |
| <i>Sakireeta madreeya</i>         | <b>CBS 532.76*</b>     | <b>DQ377940</b> | <b>KC769960</b> |
| <i>Tiarosporella africana</i>     | CMW 38425              | KC769992        | KC769958        |
| <i>T. africana</i>                | CMW 38424              | KC769991        | KC769957        |
| <i>T. paludosa</i>                | CPC 22701              | KM108404        | NR132907        |
| <b><i>T. paludosa</i></b>         | <b>CBS 114650*</b>     | <b>KM108403</b> | <b>KM108377</b> |
| <b><i>T. tritici</i></b>          | <b>CBS 118719*</b>     | <b>DQ377941</b> | <b>KC769961</b> |

Ex-type (or ex-epitype) strains are in bold and marked with an asterisk\* and voucher strains are in bold



**Fig. 15** Phylogenetic tree generated by maximum likelihood analysis of combined ITS, TEF, TUB, and His3 sequence data of *Ilyonectria* species. Twenty-three strains are included in the analyses, which comprise 2242 characters including gaps. The tree is rooted in *Campylocarpon fasciculare*. Tree topology of the ML analysis was similar to the one generated from BI (Figure not shown). The best scoring RAxML tree with a final likelihood value of  $-9669.617830$  is presented. The matrix had 507 distinct alignment patterns, with

5.11% of undetermined characters or gaps. Estimated base frequencies were as follows; A = 0.219321, C = 0.325516, G = 0.222910, T = 0.230587; substitution rates AC = 0.215721, AG = 0.328038, AT = 0.225653, CG = 0.615208, CT = 5.798530, GT = 1.000000; gamma distribution shape parameter  $\alpha = 0.518017$ . Maximum likelihood bootstrap support values  $\geq 60\%$  and bayesian posterior probabilities  $\geq 95$  (BYPP) are indicated above or near the nodes. Ex-type strains are in bold

### Morphological based identification and diversity

Eight species names are recorded in Index Fungorum (2019), however, sequences are available for only two

species *Macrophomina phaseolina* and *M. pseudophaseolina* (Sarr et al. 2014). Morphological characteristics of *M.*

*phaseolina* are mostly similar to *M. pseudophaseolina*, except that conidia of the latter are shorter.

Colony and conidial morphology are the primary characters used to identify species within this genus (Ellis 1971, 1976; Simmons 1992). However, the connectivity of sexual and asexual morphs is not proven, as no sexual morph has been obtained from nature or culture (Crous et al. 2006; Wijayawardene et al. 2017, 2018). According to the morphological identifications, *Macrophomina phaseolina* has conidia with apical mucoid appendages as found in *Tiarosporella* (Sutton and Marasas 1976). Nevertheless, it can be distinguished from *Tiarosporella* in having conidia with apical mucoid appendages, per currently proliferating conidiogenous cells and dark brown (at maturity) conidia (Crous et al. 2006; Phillips et al. 2013). Morphologically *M. phaseolina* is similar to *M. pseudophaseolina*, except that conidia of the latter are shorter.

### Molecular based identification and diversity

Phillips et al. (2013) suggested that phylogenetic analysis of a combined SSU, LSU, ITS, *tef1* and TUB2 genes provide better resolution. Sarr et al. (2014) used ITS, *tef1*, ACT, CAL and TUB2 sequence data representing a large

sample of *Macrophomina* isolates from many hosts. According to the multi-gene analysis of SSU, LSU, ITS, *tef1* and TUB2 genes in this study (Fig. 16, Table 10), the two species cluster in a well-supported clade with high bootstrap values (100% ML, 1.00 BYPP). The overall topology of our phylogeny tree is similar to previous studies.

*Recommended genetic markers (genus level)*—cosmopolitan genus, and—LSU and SSU

*Recommended genetic markers (species level)*—ITS, *tef1*, ACT, CAL and TUB2

*Accepted number of species:* There are eight epithets in Index Fungorum (2019) However, **two** species have molecular data.

*References:* Crous et al. 2006; Phillips et al. 2013; Sarr et al. 2014, Wijayawardene et al. 2017 (morphology, phylogeny).

*Medeolaria* Thaxt., Proc. Amer. Acad. Arts & Sci. 57(17): 432 (1922)

The genus *Medeolaria* belongs to the family *Medeolariaceae* (Medeolariales, Leotiomyces, Ascomycota).

**Table 9** Details of the *Ilyonectria* isolates used in the phylogenetic analyses

| Species                          | Isolate/voucher no  | ITS      | <i>tef1</i> | tub2     | His3     |
|----------------------------------|---------------------|----------|-------------|----------|----------|
| <i>Campylocarpon fasciculare</i> | CBS 112613          | AY677301 | JF735691    | AY677221 | JF735502 |
| <i>Ilyonectria capensis</i>      | <b>CBS 132815*</b>  | JX231151 | JX231119    | JX231103 | JX231135 |
| <i>I. coprosmae</i>              | <b>CBS 119606*</b>  | JF735260 | JF735694    | JF735373 | JF735505 |
| <i>I. crassa</i>                 | <b>CBS 139.30*</b>  | JF735275 | JF735723    | JF735393 | JF735534 |
| <i>I. cyclaminicola</i>          | <b>CBS 302.93*</b>  | JF735304 | JF735770    | JF735432 | JF735581 |
| <i>I. destructans</i>            | <b>CBS 264.65*</b>  | AY677273 | JF735695    | AY677256 | JF735506 |
| <i>I. europaea</i>               | <b>CBS 129078*</b>  | JF735294 | JF735756    | JF735421 | JF735567 |
| <i>I. gamsii</i>                 | CBS 940.97          | AM419065 | JF735766    | AM419089 | JF735577 |
| <i>I. leucospermi</i>            | <b>CBS 132809*</b>  | JX231161 | JX231129    | JX231113 | JX231145 |
| <i>I. liliigena</i>              | <b>CBS 189.49*</b>  | JF735297 | JF735762    | JF735425 | JF735573 |
| <i>I. liriiodendri</i>           | <b>CBS 110.81*</b>  | DQ178163 | JF735696    | DQ178170 | JF735507 |
| <i>I. lusitanica</i>             | CBS 129080          | JF735296 | JF735759    | JF735423 | JF735570 |
| <i>I. macroconidialis</i>        | CBS 112615          | AY677290 | JF735836    | AY677233 | JF735647 |
| <i>I. mors-panacis</i>           | <b>CBS 306.35*</b>  | JF735288 | JF735746    | JF735414 | JF735557 |
| <i>I. palmarum</i>               | <b>CBS 135754*</b>  | HF937431 | HF922614    | HF922608 | HF922620 |
| <i>I. panacis</i>                | <b>CBS 129079*</b>  | AY295316 | JF735761    | JF735424 | JF735572 |
| <i>I. protearum</i>              | <b>CBS 132811*</b>  | JX231157 | JX231125    | JX231109 | JX231141 |
| <i>I. pseudodestructans</i>      | CBS 129081          | AJ875330 | JF735752    | AM419091 | JF735563 |
| <i>I. robusta</i>                | <b>CBS 308.35*</b>  | JF735264 | JF735707    | JF735377 | JF735518 |
| <i>I. rufa</i>                   | CBS 156.47          | AY677272 | JF735730    | AY677252 | JF735541 |
| <i>I. strelitziae</i>            | <b>CBS 142253 *</b> | KY304649 | KY304727    | KY304755 | KY304621 |
| <i>I. venezuelensis</i>          | <b>CBS 102032 *</b> | AM419059 | JF735760    | AY677255 | JF735571 |
| <i>I. vredenhoekensis</i>        | <b>CBS 132807*</b>  | JX231155 | JX231123    | JX231107 | JX231139 |

Ex-type (or ex-epitype) strains are in bold and marked with an asterisk\* and voucher strains are in bold

*Medeolaria* was introduced by Thaxter (1922) and typified with *Medeolaria farlowii*. *Medeolaria* species are pathogens of *Medeola virginiana* (Liliaceae). Currently, the known distribution of this genus is only from America.

**Classification**—Leotiomycetes, Medeolariales, Medeolariaceae

**Type species**—*Medeolaria farlowii* Thaxt., Proc. Amer. Acad. Arts & Sci. 57(17): 432 (1922)

**Distribution**—America

**Disease symptoms**—This fungus causes gall-like deformations on thickened, hypertrophic 9 parts below leaf whorls of herbaceous stems of the host tissue, in autumn. However, they are present not only in stem lesions of the host plant but in uninfected leaves, stems and rhizomes (Pfister et al 2013). Pfister et al. (2013) also showed the long-term perpetuation of the fungus in populations of the plant. They suggested the fungus remains as a systemic infection of vegetative plant parts and when the plant reproduces clonally, this infection is carried in populations of the host plant (Pfister et al 2013).

**Hosts**—*Magnolia* spp.

### Morphological based identification and diversity

This genus contains only a single species, *Medeolaria farlowii* Thaxter (1922), described from material collected from *Magnolia*. It produces erumpent, indefinite apothecia with a palisade layer of asci and paraphyses. An excipulum is absent or is a very thin layer. The hymenium layer forms fusiform swellings below and/or between the shortened internodes of the host plant. Ascospores are large, fusiform to naviculate, with a dark, striate outer wall. The asexual morph of this fungus is unknown (Korf 1973; Pfister and LoBuglio 2009; Ekanayaka et al 2017).

### Molecular based identification and diversity

The first stable taxonomic placement for this genus was provided by Korf (1973) under the family Medeolariaceae, order Medeolariales within Leotiomycetes, according to its morphology. Recent phylogenetic studies (LoBuglio and Pfister 2010; Pfister et al 2013; Ekanayaka et al. 2017) confirmed its phylogenetic relationship with Leotiomycetes (Fig. 10), but the phylogenetic position within the class is unresolved.

**Recommended genetic marker (genus level)**—ITS

**Recommended genetic marker (species level)**—ITS

ITS is the best single genetic marker for the genus *Medeolaria* (Pfister et al 2013). Pfister et al. (2013) provided primers, designed to specifically amplify ITS rDNA regions of *Medeolaria farlowii*.

**Accepted number of species: One species**

**References:** Korf 1973; LoBuglio and Pfister 2010; Pfister et al. 2013(morphology, phylogeny).

*Neonectria* Wollenw., Annls mycol. 15(1/2):52 (1917)

*Neonectria* is a cosmopolitan genus, and their asexual morphs are common in tropical and temperate regions (Chaverri et al. 2011). *Neonectria* species can be found on the bark of recently dead woody plants and sometimes on decaying herbaceous material (Samuels and Brayford 1990; Samuels and Brayford 1990, 1993, 1994; Rossman et al. 1999; Castlebury et al. 2006; Chaverri et al. 2011). Some species of *Neonectria* are plant pathogens causing cankers and other diseases on hardwood and coniferous trees (Castlebury et al. 2006; Rossman and Palm-Hernández 2008; Crane et al. 2009; Chaverri et al. 2011; Schmitz et al. 2017; Wenneker et al. 2017). *Neonectria neomacrospora* has been added to the European and Mediterranean Plant Protection Organization (EPPO) alert list (EPPO, 2019).

**Classification**—Sordariomycetes, Hypocreomycetidae, Hypocreales, Nectriaceae

**Type species**—*Neonectria ramulariae* Wollenw., Annls mycol. 15(1/2):52 (1917)

**Distribution**—Worldwide

**Disease symptoms**—Canker

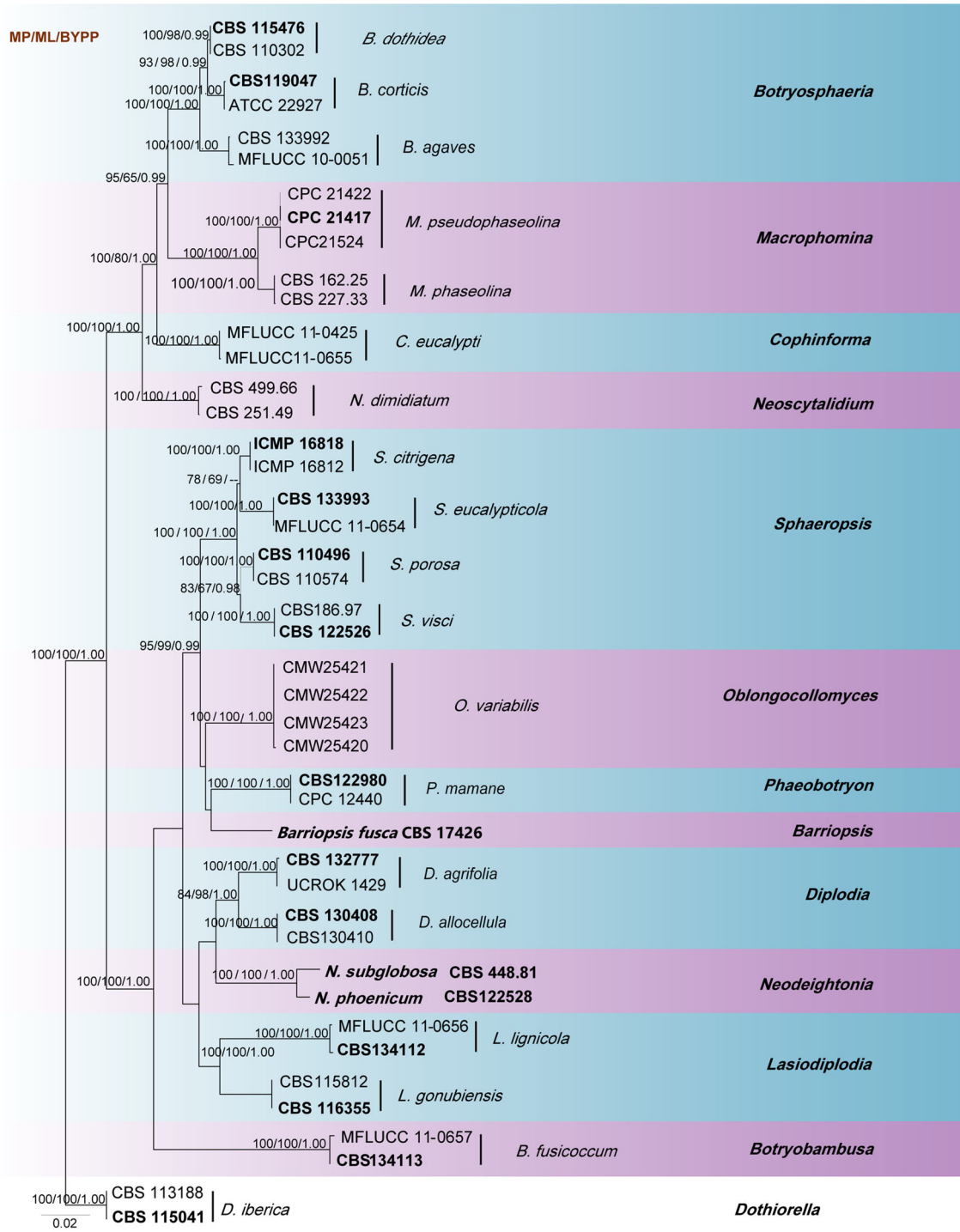
Dead shoots can be observed in the lower branches or all over the affected tree. Affected branches or trunks show canker and some may have abundant resin flow. When the canker girdles the affected area, part of the tree above the canker dies. Under humid conditions characteristic small, red fruiting bodies will be formed. Badly affected trees will eventually die (Castlebury et al. 2006).

Beech (*Fagus*) bark disease is caused by *N. coccinea*, *N. ditissima*, *N. fuckeliana* and *N. faginata*. Cankers of fruit trees are caused by *N. rugulosa* and *N. ditissima*. Shoot dieback of *Abies* species are caused by *N. neomacrospora* (Castlebury et al. 2006; Rossman et al. 2008; Crane et al. 2009; Chaverri et al. 2011; Schmitz et al. 2017; Wenneker et al. 2017).

**Hosts**—Wide host range including plant genera in Amaryllidaceae, Aracaceae, Araliaceae, Betulaceae, Ericaceae, Fagaceae, Lauraceae, Myrtaceae, Pinaceae, Proteaceae, Rosaceae, Sapindaceae and Vitaceae (Farr and Rossman 2019).

### Morphological based identification and diversity

The genus *Neonectria* was established by Wollenweber (1917). The generic concept of *Neonectria* has been revised by different authors (Booth 1959; Samuels and Brayford 1994; Rossman et al. 1999). Rossman et al. (1999) accepted only three species (*N. coccinea*, *N. galligena* and *N. ramulariae*) in *Neonectria*. Subsequently, species were added to the genus based on morphology and/or phylogeny (Hirooka et al. 2005; Castlebury et al. 2006; Luo and Zhuang 2010a, b; Zhao et al. 2011; Lombard et al. 2014, 2015). However, some unrelated species were transferred to other genera based on molecular analyses





◀**Fig. 16** Phylogenetic tree generated by maximum likelihood analysis of combined ITS, LSU, SSU, *tef1* and TUB2 sequences. Related sequences were obtained from GenBank. Forty-four strains are included in the analyses, which comprise 3477 characters including gaps. Single gene analyses were carried out and compared with each species, to compare the topology of the tree and clade stability. The tree was rooted with *Dothiorella iberica* (CBS 113188 and CBS 115041). Tree topology of the ML analysis was similar to the MP and BI. The best scoring RAxML tree with a final likelihood value of  $-12764.659013$  is presented. The matrix had 898 distinct alignment patterns, with 28.31% of undetermined characters or gaps. Estimated base frequencies were as follows; A = 0.238049, C = 0.253522, G = 0.272022, T = 0.236408; substitution rates AC = 1.121500, AG = 2.393284, AT = 1.053637, CG = 1.711098, CT = 4.682724, GT = 1.000000; gamma distribution shape parameter  $\alpha = 0.545763$ . The maximum parsimonious dataset consisted of constant 2820, 575 parsimony-informative and 82 parsimony-uninformative characters. The parsimony analysis of the data matrix resulted in the maximum of two equally most parsimonious trees with a length of 1490 steps (CI = 0.626, RI = 0.861, RC = 0.539, HI = 0.374) in the first tree. RAxML, maximum parsimony bootstrap support values  $\geq 65\%$  and Bayesian posterior probabilities  $\geq 0.95$  (BYPP) are shown respectively near the nodes. Ex-type strains are in bold

and morphological data (Lombard et al. 2014, 2015). There are 31 species recognised in the genus, while 23 species have sequence data in GenBank (4/7/2019). Morphological characters (perithecial morphology, ascospore size, macroconidial morphology, presence or absence of microconidia and chlamydospores) along with DNA sequence analysis are appropriate for identification of *Neonectria* species (Brayford et al. 2004).

#### Molecular based identification and diversity

Since 2001, DNA sequence analysis has been used to clarify the taxonomy of *Neonectria* (Mantiri et al. 2001; Brayford et al. 2004; Halleen et al. 2004; Hirooka et al. 2005; Chaverri et al. 2011). Mantiri et al. (2001) and Brayford et al. (2004) used mtSSU rDNA sequence data to infer intragenetic relationships of some *Neonectria* and *Cylindrocarpon* species. Later, Halleen et al. (2004) used mtLSU rDNA, TUB2 and nrDNA ITS regions to separate some *Cylindrocarpon* species included in the *N. mammoidea* group. Chaverri et al. (2011) approached a comprehensive treatment of *Cylindrocarpon* and *Neonectria* based on combined loci analyses and morphological data. Chaverri et al. (2011) defined *Neonectria sensu stricto* within *Nectriaceae* with *Cylindrocarpon sensu stricto* based on multi-gene phylogeny of ITS, LSU, *tef1*, TUB2, ACT, and RPB1. The ITS, *tef1* and TUB2 loci possess highly variable regions (Chaverri et al. 2011) and are important in species delimitation of *Neonectria*. Rossman et al. (2013) proposed to protect generic name *Neonectria* over *Cylindrocarpon*. Maharachchikumbura et al. (2015) considered *Cylindrodendrum* not to be congeneric with *Neonectria* and accepted *Neonectria* over *Cylindrocarpon*.

This study reconstructs the phylogeny of *Neonectria* based on analyses of a combined ITS, LSU, *tef1* and TUB2 sequence data (Table 11, Fig. 17). The phylogenetic tree is updated with recently introduced *Neonectria* species and corresponds to previous studies (Chaverri et al. 2011; Lombard et al. 2014; Mantiri et al. 2001).

*Recommended genetic markers (genus level)*—LSU, ITS, *tef1* and TUB2

*Recommended genetic markers (species level)*—ITS, *tef1* and TUB2

*Accepted number of species: 28 species*

*References:* Rossman et al. 1999 (morphology), Brayford et al. 2004; Hirooka and Kobayashi 2007; Chaverri et al. 2011; Lombard et al. 2014 (morphology, phylogeny).

*Neopestalotiopsis* Maharachch., K.D. Hyde & Crous (2014), in Maharachchikumbura et al., Stud. Mycol. 79:147 (2014a)

*Neopestalotiopsis* is an important plant pathogenic, saprobic and endophytic genus commonly present in tropical and subtropical ecosystems. The genus was introduced by Maharachchikumbura et al. (2014b). Species of *Neopestalotiopsis* are appendage-bearing asexual coelomycetes in the family *Sporocadaceae* (Jayawardena et al. 2016). *Classification*—*Sordariomycetes*, *Xylariomycetidae*, *Amphisphaerales*, *Sporocadaceae*

*Type species*—*Neopestalotiopsis protearum* (Crous & L. Swart) Maharachch. et al., in Maharachchikumbura et al., Stud. Mycol. 79:147 (2014a)

*Distribution*—Worldwide

*Disease symptoms*—Canker, dieback, fruit rots, leaf spot

Pathogenic *Neopestalotiopsis* are recorded in post-harvest fruit rots of grapes, trunk diseases in grapevine in China, India and France, leaf spot disease of grapevine in China and leaf blights in many plant species worldwide (Hyde et al. 2014; Jayawardena et al. 2015, 2016; Maharachchikumbura et al. 2017).

*Neopestalotiopsis* species infect a variety of grapevine cultivars, causing diseases including grapevine dieback, fruit rot, postharvest disease and severe defoliation. Initial symptoms of fruit rot disease are mostly observed at the splits between the pedicel and the berry and at the wounds of the fruits and severely infected fruits become rotten and separate completely from the pedicel (Jayawardena et al. 2015). *Neopestalotiopsis asiatica* and *N. javaensis* are associated with grapevine trunk disease (Maharachchikumbura et al. 2017). Grapevine trunk diseases reduce the yield and quality of grapes, even leading to partial or total death of individual plants.

*Neopestalotiopsis clavisporea* and *N. surinamensis* cause guava scab (Solarte et al. 2018). *Neopestalotiopsis ellipsozona* causes leaf spot on sweet potatoes

**Table 10** Details of *Macrophomina* and *Sphaeropsis* isolates used in the phylogenetic analyses

| Species                             | Isolate/voucher no     | SSU      | ITS      | LSU      | tef1     | TUB2     |
|-------------------------------------|------------------------|----------|----------|----------|----------|----------|
| <i>Barriopsis fusca</i>             | <b>CBS 174.26*</b>     | EU673182 | EU673330 | DQ377857 | EU673296 | EU673109 |
| <i>Botryobambusa fusicoccum</i>     | <b>CBS 134113*</b>     | JX646826 | JX646792 | JX646809 | JX646857 | N/A      |
|                                     | MFLUCC 11-0657         | JX646827 | JX646793 | JX646810 | JX646858 | N/A      |
| <i>Botryosphaeria agaves</i>        | <b>CBS 133992*</b>     | JX646825 | JX646791 | JX646808 | JX646856 | JX646841 |
|                                     | MFLUCC 10-0051         | JX646824 | JX646790 | JX646807 | JX646855 | JX646840 |
| <i>B. corticis</i>                  | <b>CBS 119047*</b>     | EU673175 | DQ299245 | EU673244 | EU017539 | EU673107 |
|                                     | ATCC 22927             | EU673176 | DQ299247 | EU673245 | EU673291 | EU673108 |
| <i>B. dothidea</i>                  | <b>CBS 115476 *</b>    | EU673173 | AY236949 | AY928047 | AY236898 | AY236927 |
|                                     | CBS 110302             | EU673174 | AY259092 | EU673243 | AY573218 | EU673106 |
| <i>Cophinforma atrovirens</i>       | <b>MFLUCC 11-0425*</b> | JX646833 | JX646800 | JX646817 | JX646865 | JX646848 |
|                                     | MFLUCC 11-0655         | JX646834 | JX646801 | JX646818 | JX646866 | JX646849 |
| <i>Dothiorella iberica</i>          | <b>CBS 115041*</b>     | EU673155 | AY573202 | AY928053 | AY573222 | EU673096 |
|                                     | CBS 113188             | EU673156 | AY573198 | EU673230 | EU673278 | EU673097 |
| <i>Diplodia allocellula</i>         | <b>CBS 130408*</b>     | N/A      | JQ239397 | JQ239410 | JQ239384 | JQ239378 |
|                                     | CBS 130410             | N/A      | JQ239399 | JQ239412 | JQ239386 | JQ239380 |
| <i>D. agrifolia</i>                 | <b>CBS 132777*</b>     | N/A      | JN693507 | N/A      | JQ517317 | JQ411459 |
|                                     | UCROK 1429             | N/A      | JQ411412 | N/A      | JQ512121 | JQ411443 |
| <i>Lasiodiplodia gonubiensis</i>    | <b>CBS 115812*</b>     | EU673193 | AY639595 | DQ377902 | DQ103566 | DQ458860 |
|                                     | CBS 116355             | EU673194 | AY639594 | EU673252 | DQ103567 | EU673126 |
| <i>L. lignicola</i>                 | <b>CBS 134112*</b>     | JX646830 | JX646797 | JX646814 | JX646862 | JX646845 |
|                                     | MFLUCC 11-0656         | JX646831 | JX646798 | JX646815 | JX646863 | JX646846 |
| <i>Neoscytalidium hyalinum</i>      | CBS 499.66             | KF531818 | KF531820 | DQ377925 | KF531798 | KF531800 |
|                                     | CBS 251.49             | KF531817 | KF531819 | DQ377923 | KF531797 | KF531799 |
| <i>Neodeightonia subglobosa</i>     | <b>CBS 448.81*</b>     | EU673202 | EU673337 | DQ377866 | EU673306 | EU673137 |
| <i>N. phoenicum</i>                 | <b>CBS 122528*</b>     | EU673205 | EU673340 | EU673261 | EU673309 | EU673116 |
| <i>Macrophomina phaseolina</i>      | CBS 227.33             | KF531823 | KF531825 | DQ377906 | KF531804 | KF531806 |
|                                     | CBS 162.25             | KF531824 | KF531826 | DQ377905 | KF951996 | KF531805 |
| <i>M. pseudophaseolina</i>          | CPC 21422              | N/A      | KF951792 | N/A      | KF952154 | KF952234 |
|                                     | <b>CPC 21417*</b>      | N/A      | KF951791 | N/A      | KF952153 | KF952233 |
|                                     | CPC 21524              | N/A      | KF951799 | N/A      | KF952161 | KF952240 |
| <i>Phaeobotryon mamane</i>          | <b>CBS 122980*</b>     | EU673184 | EU673332 | EU673248 | EU673298 | EU673121 |
|                                     | CPC 12442              | EU673185 | EU673333 | DQ377899 | EU673299 | EU673124 |
| <i>Oblongocollomyces variabilis</i> | CMW 25420              | N/A      | EU101313 | N/A      | EU101358 | N/A      |
|                                     | CMW 25421, CBS 121775  | N/A      | EU101314 | N/A      | EU101359 | N/A      |
|                                     | CMW 25422, CBS 121776  | N/A      | EU101326 | N/A      | EU101371 | N/A      |
|                                     | CMW 25423              | N/A      | EU101327 | N/A      | EU101372 | N/A      |
| <i>Sphaeropsis citrigena</i>        | <b>ICMP 16812*</b>     | EU673180 | EU673328 | EU673246 | EU673294 | EU673140 |
|                                     | ICMP 16818             | EU673181 | EU673329 | EU673247 | EU673295 | EU673141 |
| <i>S. eucalypticola</i>             | <b>CBS 133993*</b>     | JX646835 | JX646802 | JX646819 | JX646867 | JX646850 |
|                                     | MFLUCC 11-0654         | JX646836 | JX646803 | JX646820 | JX646868 | JX646851 |
| <i>S. porosa</i>                    | <b>CBS 110496*</b>     | EU673179 | AY343379 | DQ377894 | AY343340 | EU673130 |
|                                     | CBS 110574             | N/A      | AY343378 | N/A      | AY343339 | N/A      |
| <i>S. visci</i>                     | <b>CBS 122526 *</b>    | N/A      | EU673324 | N/A      | EU673292 | N/A      |
|                                     | CBS 186.97             | EU673178 | EU673325 | DQ377868 | EU673293 | EU673128 |

Ex-type (or ex-epitype) strains are in bold and marked with an asterisk\* and voucher strains are in bold

**Table 11** Details of the *Neonectria* isolates used in the phylogenetic analyses

| Species                               | Isolates/voucher no                      | ITS             | LSU             | TUB             | <i>tefl</i>     |
|---------------------------------------|--|-----------------|-----------------|-----------------|-----------------|
| <i>Neonectria austroradicicola</i>    | PDD 46334 G.J.S. 83-154                  | EF607077        | –               | –               | –               |
| <i>N. candida</i>                     | CBS 151.29/IMI 113894/MUCL 28083         | AY677291        | AY677333        | DQ789863        | DQ789723        |
| <i>N. coccinea</i>                    | CBS 119158/GJS 98-114                    | JF268759        | KC660620        | KC660727        | JF268734        |
| <b><i>N. confusa</i></b>              | CBS 127485/HMAS 99197*                   | <b>FJ560437</b> | <b>KM515934</b> | <b>FJ860054</b> | –               |
| <i>N. confusa</i>                     | CBS 127484/HMAS 99198                    | KM515889        | KM515933        | KM515886        | –               |
| <i>N. ditissima</i>                   | CBS 100318                               | KM515890        | KM515935        | DQ789858        | KM515944        |
| <i>N. ditissima</i>                   | CBS 100317                               | KM515891        | KM515936        | KM515887        | KM515945        |
| <b><i>N. ditissimopsis</i></b>        | <b>HMAS 98329*</b>                       | <b>JF268764</b> | –               | <b>JF268729</b> | <b>JF268745</b> |
| <b><i>N. faginata</i></b>             | <b>CBS 217.67/IMI 105738/ATCC 16547*</b> | <b>HQ840385</b> | <b>HQ840382</b> | <b>JF268730</b> | <b>JF268746</b> |
| <i>N. faginata</i>                    | CBS 119160/GJS 04-159                    | HQ840384        | HQ840383        | DQ789883        | DQ789740        |
| <i>N. fuckeliana</i>                  | CBS 239.29/IMI 039700                    | HQ840386        | HQ840377        | DQ789871        | JF268748        |
| <b><i>N. hederæ</i></b>               | <b>IMI 058770a/ATCC 16543*</b>           | –               | <b>KC660617</b> | <b>DQ789895</b> | <b>DQ789752</b> |
| <i>N. hederæ</i>                      | CBS 714.97/PD 97/1932                    | –               | KC660616        | DQ789878        | KC660461        |
| <i>N. lugdunensis</i>                 | CBS 125485/DAOM 235831/TG 2008-07        | KM231762        | KM231625        | KM232019        | KM231887        |
| <b><i>N. major</i></b>                | <b>CBS 240.29/IMI 113909*</b>            | <b>JF735308</b> | <b>KM515942</b> | <b>DQ789872</b> | <b>JF735782</b> |
| <i>N. microconidia</i>                | HMAS 98294                               | KC660530        | KC660587        | –               | –               |
| <i>N. neomacrospora</i>               | CBS 198.62/BBA 9628/IMI 113890           | AJ009255        | HM364316        | HM352865        | HM364351        |
| <i>N. neomacrospora</i>               | CBS 324.61/DSM 62489/IMB 9628            | JF735312        | HM364318        | DQ789875        | –               |
| <i>N. obtusispora</i>                 | CBS 183.36/IMI 113895                    | AM419061        | KM515943        | AM419085        | JF735796        |
| <i>N. punicea</i>                     | CBS 242.29                               | KC660522        | KC660565        | DQ789873        | DQ789730        |
| <i>N. shennongjiana</i>               | HMAS 183185                              | FJ560440        | –               | FJ860057        | –               |
| <b><i>N. tsugæ</i></b>                | <b>CBS 788.69*</b>                       | <b>KM231763</b> | <b>HQ232146</b> | <b>KM232020</b> | –               |
| <b><i>Thelonectria gongylodes</i></b> | <b>CBS 12511/GJS 90-48</b>               | <b>JQ403330</b> | <b>JQ403369</b> | <b>HM352870</b> | <b>HM364357</b> |

Ex-type (or ex-epitype) strains are in bold and marked with an asterisk\* and voucher strains are in bold

(Maharachchikumbura et al. 2016). *Neopestalotiopsis clavispora* causes crown and root rot of strawberry worldwide while *N. iranensis* infects leaves and fruits of strawberry (Ayoubi and Soleimani 2016), with the pathogen initially developing circular, black, and slightly sunken spots that expand outwards on the surface. Droplets of spores are scattered over the white aerial mycelial area and later cause soft decay of the fruit flesh (Ayoubi and Soleimani 2016). Canker and dieback on blueberry in Chile and Uruguay are also caused by *N. clavispora* (Espinoza et al. 2008; González et al. 2012; Chamorro et al. 2016). *Neopestalotiopsis samarangensis* has been described from wax apple fruit rot in Thailand (Maharachchikumbura et al. 2013a, b). In fruit rots, the initial symptom is small, circular, black, slightly sunken spots on fruits. Later, the spots enlarged rapidly, become sunken and result in a soft decay of the fruit flesh (Maharachchikumbura et al. 2013a, b). **Hosts**—Species of *Fragaria* × *ananassa*, *Ipomoea*, *Malus*, *Psidium*, *Vaccinium* and *Vitis*

### Morphological based identification and diversity

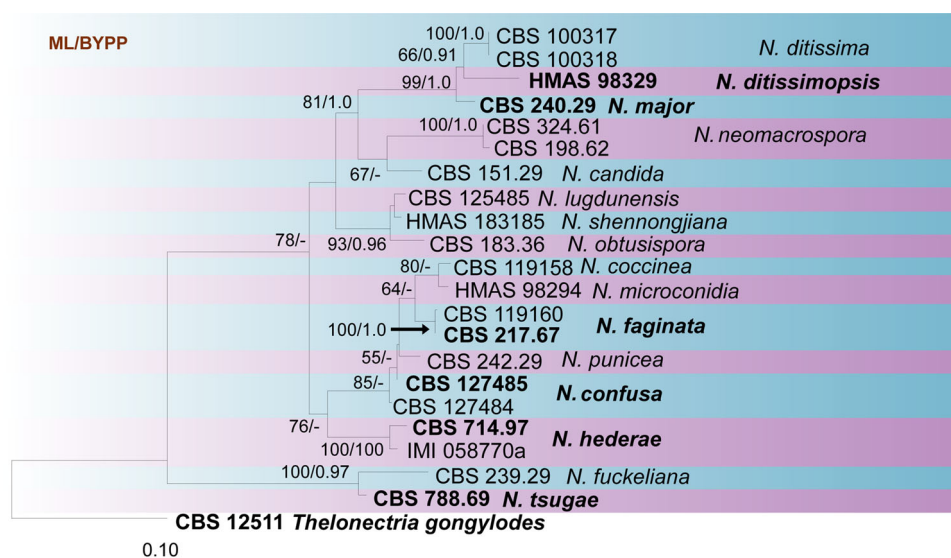
*Neopestalotiopsis* species can be differentiated using morphology and molecular phylogeny (Maharachchikumbura

et al. 2014b). There are 36 species epithets listed in Index Fungorum (2019). *Neopestalotiopsis* species differ from *Pestalotiopsis* and *Pseudopestalotiopsis* in having somewhat versicolorous median cells (Maharachchikumbura et al. 2014b) whereas both *Pestalotiopsis* and *Pseudopestalotiopsis* have concolourous median cells (Maharachchikumbura et al. 2014b) as well as its conidiophores which are indistinct and often reduced to conidiogenous cells (Maharachchikumbura et al. 2014b).

Conidial morphology is widely used in taxonomy in pestalotioid fungi (Steyaert 1949; Guba 1961; Nag Raj 1993; Maharachchikumbura et al. 2012, 2014b). Species delimitation based on morphological characters is limited as these characters are plastic and vary between hosts and environments (Maharachchikumbura et al. 2011, 2016). Therefore, phylogenetic species recognition is an effective method to identify different pestalotioid species (Maharachchikumbura et al. 2016).

### Molecular based identification and diversity

*Neopestalotiopsis* species can be roughly separated from *Pestalotiopsis* and *Pseudopestalotiopsis* based on the total number of base pairs in the ITS region



**Fig. 17** Phylogenetic tree generated by maximum likelihood analysis of combined ITS, LSU, *tef1* and TUB sequence data of *Neonectria* species. Related sequences were obtained from GenBank. Twenty-three strains are included in the analyses, which comprise 2336 characters including gaps. Tree topology of the ML analysis was similar to the one generated from BI (figure not shown). The best scoring RAxML tree with a final likelihood value of  $-7942.756270$  is presented. The matrix had 525 distinct alignment patterns, with 18.13% of undetermined characters or gaps. Estimated base

frequencies were as follows; A = 0.223071, C = 0.285136, G = 0.261197, T = 0.230596; substitution rates AC = 1.213729, AG = 2.500008, AT = 1.727890, CG = 0.720430, CT = 6.191594, GT = 1.000000; gamma distribution shape parameter  $\alpha = 0.749195$ . Maximum likelihood bootstrap support ( $\geq 55\%$ ) and posterior probabilities (BYPP  $\geq 0.90$ ) from Bayesian inference analysis are indicated respectively near the nodes. Ex-type strains are in bold. The tree is rooted in *Thelonectria gonyolodes*

(Maharachchikumbura et al. 2014b). However, the use of ITS sequences alone does not resolve *Neopestalotiopsis* species (Maharachchikumbura et al. 2012). Therefore, Maharachchikumbura et al. (2014b) suggested using combined ITS, TUB2 and *tef1* genes to provide a better resolution in phylogenetic analyses. This study reconstructs the phylogeny of *Neopestalotiopsis* based on a combined ITS, TUB2 and *tef1* sequence data (Fig 18, Table 12) and reveals similar phylogenetic relationships to previous studies by Maharachchikumbura et al. (2014b, 2016).

*Recommended genetic marker (genus level)*—LSU

*Recommended genetic markers (Species level)*—ITS, TUB2 and *tef1*

*Accepted number of species:* **41 species.**

*References:* Maharachchikumbura 2012, 2014b (morphology, phylogeny); Maharachchikumbura et al. 2016 (morphology, phylogeny); Jayawardena et al. 2015, 2016 (morphology, phylogeny, pathogenicity)

***Plasmopara*** J. Schröt., in Cohn, Krypt.-Fl. Schlesien 3.1(9–16): 236 (1886) [1889]

The genus *Plasmopara* belongs to the family *Peronosporaceae* of the *Peronosporales* in *Oomycetes* (Riethmüller et al. 2002; Görg et al. 2017). This genus is included in this study as it is an important plant pathogen on many economically important crops. *Plasmopara* was introduced by

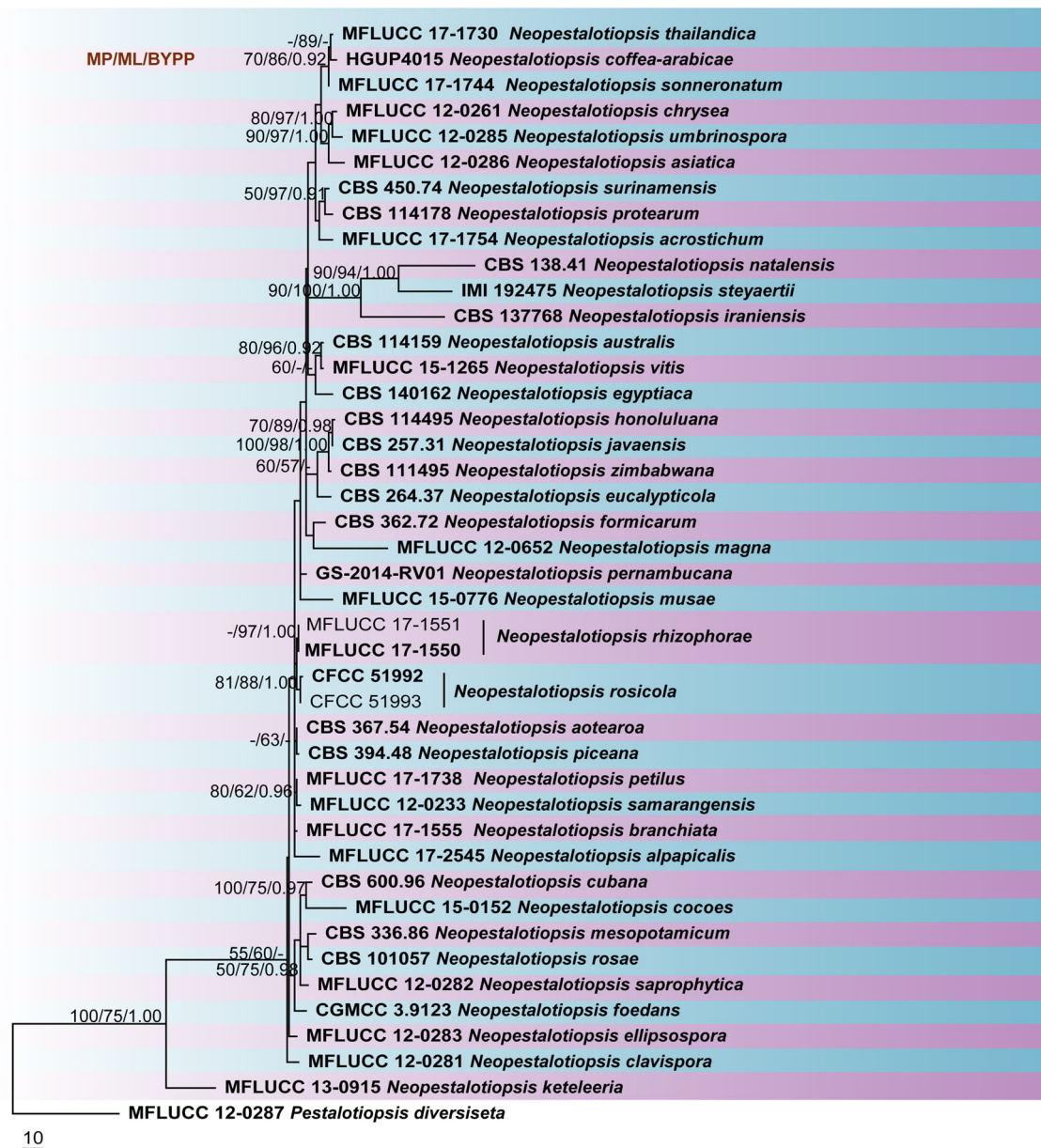
Schröter (1886), but no species was assigned as a type for the genus (Constantinescu et al. 2005). *Plasmopara nivea* is considered as the type species of this genus (Constantinescu et al. 2005). *Plasmopara* species are commonly known as downy mildew pathogens. There are 2064 records in USDA fungal database under genus *Plasmopara* (Farr and Rosman 2019). Downy mildew has become one of the most troublesome diseases in agriculture including *P. viticola* on grape, *P. geranii* on geranium and *P. halstedii* on sunflower (McTaggart et al. 2015). Kamoun et al. (2015) categorized *P. viticola* among the top ten Oomycetes pathogens in plant pathology. Current interest in this genus is to understand the co-evolution with the host and effective disease management (Thines and Kamoun 2010). Taxonomically useful morphological or ecological characters are few for the downy mildews and this makes identification of synapomorphic states impossible (Göker et al. 2003).

*Classification*—*Oomycota incertae sedis*, *Peronosporae*, *Peronosporidae*, *Peronosporales*, *Peronosporaceae*  
*Type species*—***Plasmopara nivea*** (Unger) J. Schröt.

*Distribution*—Worldwide

*Disease symptoms*—Downy mildew

*Hosts*—Species belonging to this genus are obligate biotrophs on a wide range of hosts including *Acanthaceae*, *Asteraceae*, *Balsaminaceae*, *Geraniaceae*, *Malvaceae*, *Onagraceae*, *Orobanchaceae*, *Violaceae* and *Vitaceae*



**Fig. 18** Phylogram generated from maximum likelihood analysis based on combined ITS, TUB2 and *tefl* sequence data of *Neopestalotiopsis* species. Related sequences were obtained from GenBank. Forty-three strains are included in the combined sequence analyses, which comprise 1391 characters with gaps. *Pestalotiopsis diversiseta* (MFLUCC 12-0287) is used as the outgroup taxa. The best scoring RAxML tree with a final likelihood value of  $-5457.035085$  is presented. The matrix had 409 distinct alignment patterns, with 6.30% of undetermined characters or gaps. Estimated base frequencies were as follows; A = 0.231067, C = 0.270889, G = 0.213946, T = 0.284098; substitution rates AC = 0.847461, AG = 2.876343,

AT = 1.282349, CG = 0.723831, CT = 3.850003, GT = 1.000000; gamma distribution shape parameter  $\alpha = 0.235476$ . The maximum parsimonious dataset consisted of 1026 constant, 177 parsimony-informative and 188 parsimony-uninformative characters. The parsimony analysis of the data matrix resulted in the maximum of ten equally most parsimonious trees with a length of 650 steps (CI = 0.688, RI = 0.609, RC = 0.419, HI = 0.312) in the first tree. RAxML and maximum parsimony bootstrap support value  $\geq 50\%$  and posterior probabilities BYPP  $\geq 0.90$  from Bayesian inference analysis are indicated respectively near the nodes, are shown respectively near the nodes. Ex-type strains are in bold

(Voglmayr et al. 2004; Thines and Kamoun 2010; McTaggart et al. 2015).

### Morphological based identification and diversity

Wilson (1907) was the first to consider *P. pygmaea* as the type of *Plasmopara*. However, even after a century of

discussion of nomenclatural and taxonomic problems of this genus, *Plasmopara* was segregated in two different groups by morphology and phylogeny (Constantinescu et al. 2005). Constantinescu et al. (2005) proposed to introduce a new generic name for *P. pygmaea* and for six

**Table 12** Details of the *Neopestalotiopsis* isolates used in the phylogenetic analyses

| Species                              | Isolate no                  | ITS      | TUB2     | <i>tefl</i> |
|--------------------------------------|-----------------------------|----------|----------|-------------|
| <i>Neopestalotiopsis acrostichum</i> | <b>MFLUCC 17-1754*</b>      | MK764272 | MK764338 | MK764316    |
| <i>N. alapicalis</i>                 | <b>MFLUCC 17-2544*</b>      | MK357772 | MK463545 | MK463547    |
| <i>N. aotearoa</i>                   | <b>MFLUCC 17-1754</b>       | MK764272 | MK764338 | MK764316    |
| <i>N. asiatica</i>                   | <b>MFLUCC12-0286*</b>       | JX398983 | JX399018 | JX399049    |
| <i>N. australis</i>                  | <b>CBS 114159*</b>          | KM199348 | KM199432 | KM199537    |
| <i>N. brachiata</i>                  | <b>MFLUCC 17-1555*</b>      | MK764274 | MK764340 | MK764318    |
| <i>N. chrysea</i>                    | <b>MFLUCC12-0261*</b>       | JX398985 | JX399020 | JX399051    |
| <i>N. clavispora</i>                 | <b>MFLUCC 12-0281*</b>      | JX398979 | JX399014 | JX399045    |
| <i>N. cocoes</i>                     | <b>MFLUCC 15-0152*</b>      | KX789687 | –        | KX789689    |
| <i>N. coffeae-arabicae</i>           | <b>HGUP 4019*</b>           | KF412647 | –        | –           |
| <i>N. cubana</i>                     | <b>CBS 600 96*</b>          | KM199347 | KM199438 | KM199521    |
| <i>N. egyptiaca</i>                  | <b>CBS 140162*</b>          | KP943747 | KP943746 | KP943748    |
| <i>N. ellipospora</i>                | <b>MFLUCC 12-0283*</b>      | JX398980 | JX399016 | JX399047    |
| <i>N. eucalypticola</i>              | <b>CBS 264 37*</b>          | KM199376 | KM199431 | KM199551    |
| <i>N. foedans</i>                    | <b>CGMCC3 9123*</b>         | JX398987 | JX399022 | JX399053    |
| <i>N. formicarum</i>                 | <b>CBS 362 72*</b>          | KM199358 | KM199455 | KM199517    |
| <i>N. honoluluana</i>                | <b>CBS 114495*</b>          | KM199364 | KM199457 | KM199548    |
| <i>N. iraniensis</i>                 | <b>CBS 137768*</b>          | KM074048 | KM074057 | KM074051    |
| <i>N. javaensis</i>                  | <b>CBS 257 31*</b>          | KM199357 | KM199437 | KM199543    |
| <i>N. keteleeria</i>                 | <b>MFLUCC 13-0915*</b>      | KJ503820 | KJ503821 | KJ503822    |
| <i>N. macadamiae</i>                 | <b>BRIP 63738B*</b>         | KX186604 | KX186654 | KX186627    |
| <i>N. magna</i>                      | <b>MFLUCC12-652*</b>        | KF582795 | KF582793 | KF582791    |
| <i>N. mesopotamica</i>               | <b>CBS 336 86*</b>          | KM199362 | KM199441 | KM199555    |
| <i>N. musae</i>                      | <b>MFLUCC 15-0776*</b>      | KX789683 | KX789686 | KX789685    |
| <i>N. natalensis</i>                 | <b>CBS 138 41*</b>          | KM199377 | KM199466 | KM199552    |
| <i>N. pernambucana</i>               | <b>GS-2014 strain RV01*</b> | KJ792466 | –        | KU306739    |
| <i>N. petila</i>                     | <b>MFLUCC 17-1738*</b>      | MK764275 | MK764341 | MK764319    |
| <i>N. piceana</i>                    | <b>CBS 394 48*</b>          | KM199368 | KM199453 | KM199527    |
| <i>N. protearum</i>                  | <b>CBS 114178*</b>          | JN712498 | KM199463 | KM199542    |
| <i>N. rhizophorae</i>                | <b>MFLUCC 17-1550*</b>      | MK764277 | MK764343 | MK764321    |
| <i>N. rosae</i>                      | <b>CBS 101057*</b>          | KM199359 | KM199429 | KM199523    |
| <i>N. rosicola</i>                   | <b>CFCC 51992</b>           | KY885239 | KY885245 | KY885243    |
| <i>N. samarangensis</i>              | <b>MFLUCC 12-0233*</b>      | JQ968609 | JQ968610 | JQ968611    |
| <i>N. saprophytica</i>               | <b>MFLUCC 12-0282*</b>      | KM199345 | KM199433 | KM199538    |
| <i>N. sonneratae</i>                 | <b>MLFUCC 17-1745*</b>      | MK764279 | MK264345 | MK264323    |
| <i>N. steyaertii</i>                 | <b>IMI192475*</b>           | KF582796 | KF582794 | KF582792    |
| <i>N. surinamensis</i>               | <b>CBS 450.74*</b>          | KM199351 | KM199465 | KM199518    |
| <i>N. thailandica</i>                | <b>MFLUCC 17-1730*</b>      | MK764281 | MK764347 | MK754325    |
| <i>N. umbrinospora</i>               | <b>MFLUCC 12-0285*</b>      | JX398984 | JX399019 | JX399050    |
| <i>N. vitis</i>                      | <b>MFLUCC 15-1265*</b>      | KU140694 | KU140685 | KU140676    |
| <i>N. zimbabweana</i>                | <b>CBS 111495*</b>          | –        | KM199456 | KM199545    |

Ex-type (or ex-epitype) strains are in bold and marked with an asterisk\* and voucher strains are in bold

other related species and they have established the current classification for *Plasmopara*.

Species belonging to *Plasmopara* have the following characters. Hyphae are intercellular, haustoria are intracellular, as obpyriform, globose, or slightly elongated

vesicles (Göker et al. 2003; Voglmayr et al. 2004; Constantinescu et al. 2005). A callose sheath often surrounds haustoria. Sporangiohores are mostly present on the under leaf surface of the host, but sometimes also on other parts of the plant (eg. *P. viticola* produces sporangiohores on inflorescences and young berries, Zhang et al. 2017). Sporangiohores are colourless, branched in the upper part. They branch monopodially, in two to more orders (Göker et al. 2003; Constantinescu et al. 2005). Branches are more or less divergent, ending in a number of elongated ultimate branchlets. The newly formed wall closing the tip after sporangium discharge (Constantinescu et al. 2005). Callose plugs usually present in trunk and/or branches. Sporangiohorogenesis is holoblastic. These species produce sporangia synchronously, which vary in shape, sporangia wall is colourless, appearing smooth in light microscopy but showing various types of ornamentations in the electron microscope (Constantinescu et al. 2005). There are 199 epithets listed in Index Fungorum (2019), however, 40 of them do not belong to *Plasmopara* based on phylogenetic evidence (Figs. 19, 20).

Oospores develop a single germ tube, terminating with sporangium, once a sporangium disseminated, by rain flash or wind, it releases zoospores (Ash 2000; Rossi et al. 2008; Carisse 2016; Kamoun et al. 2015; Wilcox et al. 2015).

#### Molecular based identification and diversity

Molecular and phylogenetic studies have shown that *Plasmopara* is polyphyletic (Riethmüller et al. 2002; Göker et al. 2003, 2007; Voglmayr et al. 2004; Voglmayr and Constantinescu 2008). Even though Wilson (1907) proposed *P. pygmaea* as the type species of the genus *Plasmopara*, it has a close relationship with *Bremia*, *Paraperonospora* and *Basidiophora* (Göker et al. 2003). With these morphological and phylogenetic aspects, many species that are traditionally included in *Plasmopara* have moved into new genera. The newly introduced genera are *Viennotia* (Göker et al. 2003), *Protobremia* (Voglmayr et al. 2004), and *Plasmoverna* (Constantinescu et al. 2005). Constantinescu et al. (2005) resolved *Plasmopara* phylogeny, introducing *Plasmoverna* as a new genus to accommodate the morphologically dissimilar and polyphyletic taxa belonging to previous classifications. Voglmayr and Constantinescu (2008) re-classified three species of *Plasmopara* into new genus *Novotelnova* Voglmayr & Constant. The species belonging to *Novotelnova* were identical in the analyses of the nuLSU and nuSSU-ITS1-5.8S datasets. Therefore, in the present study, we follow Voglmayr and Constantinescu (2008) to provide a backbone tree for *Plasmopara* using combined nuLSU sequence data (Fig. 21, Table 13).

The downy mildew pathogens have been studied extensively to understand their host specificity and co-

evolution with the host plants. The grape downy mildew has been identified as a host-specific cryptic species (Rouxel et al. 2013; Zhang et al. 2017). Rouxel et al. (2013) considered the cryptic species as formae speciales: *P. viticola* f. sp. *riparia* (lineage A occurring on *V. riparia* and some hybrids); *P. viticola* f. sp. *aestivalis* (lineage B found on *V. aestivalis*, *V. labrusca*, *V. vinifera* and some hybrids); *P. viticola* f. sp. *vinifera* (lineage C occurring on *V. vinifera* and some hybrids); *P. viticola* f. sp. *quinquefolia* (lineage D found on *V. quinquefolia*). To understand the cryptic lineages genealogical concordance phylogenetic species recognition (GCPSR) approach is currently accepted (Taylor et al. 2000; Rouxel et al. 2013). GCPSR facilitate the most convenient analysis for species that cannot be cultivated or mate in control conditions (O'Donnell et al. 2000; Steenkamp et al. 2002; Rouxel et al. 2013).

*Recommended genetic marker (genus level)*—LSU

*Recommended genetic marker (species level)*—LSU

The universal barcode for the Oomycetes, the cytochrome oxidase subunit 1 and 2 genes (cox 1 and cox 2) are used. However Choi et al. (2015) suggested cox2 is better suited to this because of its ease of amplification among oomycete lineages, better performance on herbarium specimens, higher discriminatory power at the species level and the availability of a large taxonomically diverse database that already includes many species of oomycetes, especially the downy mildew. In previous studies, nuLSU gene regions (D1–D3 and D7–D8 sequences) were widely used (Riethmüller et al. 2002; Göker et al. 2003, 2007; Voglmayr et al. 2004; Voglmayr and Constantinescu 2008). Branch supports of the backbone tree was often higher in the nuLSU data, which resulted in a larger data matrix and a higher number of parsimony-informative characters than when ITS was used (Voglmayr and Constantinescu 2008). No study has combined these gene regions or any other gene regions as the marker to understand the phylogenetic relationship within the genus.

*Accepted number of species:* There are 199 species in Index Fungorum (2019) and only 19 species have molecular data in this genus.

*References:* Riethmüller et al. 2002; Göker et al. 2003; 2007; Voglmayr et al. 2004; Voglmayr and Constantinescu 2008; Rouxel et al. 2013; Zhang et al. 2017 (morphology, phylogeny).

*Pseudopestalotiopsis* Maharachch., K.D. Hyde & Crous (2014), in Marachchikumbura et al., in Maharachchikumbura et al., Stud. Mycol. 79:180 (2014a)

The genus was introduced by Maharachchikumbura et al. (2014b) with *Pseudopestalotiopsis theae* (Sawada) Maharachch., K.D. Hyde & Crous as the type species. Species of *Pseudopestalotiopsis* are appendage-bearing phenotypically diverse coelomycetes in the family



**Fig. 19** Grape downy mildew disease symptoms. **a** Infected grapevines, **b–c** appearance of oil spot on the upper leaf surface. **d** Sporulation on the lower leaf surface. **e** Young infected berries with sporulation. **f** Infection on fruits

*Sporocadaceae* and are commonly found in tropical and subtropical ecosystems (Jaklitsch et al. 2016; Maharachchikumbura et al. 2016). *Pseudopestalotiopsis* is characterized by brown to dark brown or olivaceous median cells and knobbed or not knobbed apical appendages (Maharachchikumbura et al. 2014b, 2016). The epitype of *Pseudopestalotiopsis theae* (Sawada) Steyaert was designated from fresh leaves of *Camellia sinensis* collected in Thailand (Maharachchikumbura et al. 2013a, b). *Pseudopestalotiopsis* has been studied for the production of various secondary metabolites with diverse structural features, with antitumour, antifungal, antimicrobial and other activities (Ding et al. 2008; Maharachchikumbura et al. 2011, 2016).

*Pseudopestalotiopsis theae* is economically significant as it has been identified as a pathogen in major tea-growing areas in the world (Maharachchikumbura et al. 2016). *Pseudopestalotiopsis theae* causes grey blight of tea and reduces yield (Maharachchikumbura et al. 2011, 2013a, b, 2016). *Pseudopestalotiopsis theae* was also isolated as an endophyte from different hosts (*Camellia nitidissima*, *C. sinensis*, *Holarrhena antidysenterica*, *Podocarpus macrophyllus*, *Terminalia arjuna*) or as a saprobe (seeds of *Diospyros crassiflora*) (Maharachchikumbura et al. 2011, 2013a, b, 2016).

**Classification**—*Sordariomycetes*, *Xylariomycetidae*, *Amphisphaeriales*, *Sporocadaceae*

**Type species**—*Pseudopestalotiopsis theae* (Sawada) Maharachch., in Maharachchikumbura et al., Stud. Mycol. 79:183 (2014a)

**Distribution**—China, India, Indonesia, Malaysia, Thailand (Maharachchikumbura et al. 2016)

**Disease symptoms**—*Pseudopestalotiopsis theae* causes grey blight in major tea growing areas in the world (Horikawa 1986, Maharachchikumbura et al. 2013a, b, 2016). The pathogen develops circular to irregular leaf spots initially and grey, brown margins when mature, covering up to half of the leaf with acervuli (Maharachchikumbura et al. 2016). *Pseudopestalotiopsis ixorae* and *P. taiwanensis* cause a leaf spot which initially develops small, circular, ash-coloured spots which later turn into brown spots (Tsai et al. 2018).

**Hosts**—*Averrhoa carambola*, *Camellia* sp., *Cinnamomum* sp., *Cocos nucifera*, *Diospyros crassiflora*, *Fragaria* sp., *Hibiscus rosa-sinensis*, *Holarrhena antidysenterica*, *Ixora* sp., *Kandelia obovate*, *Macaranga* sp., *Pandanus odoratissimus*, *Podocarpus macrophyllus*, *Prunus* sp., *Terminalia arjuna* and *Thea sinensis*



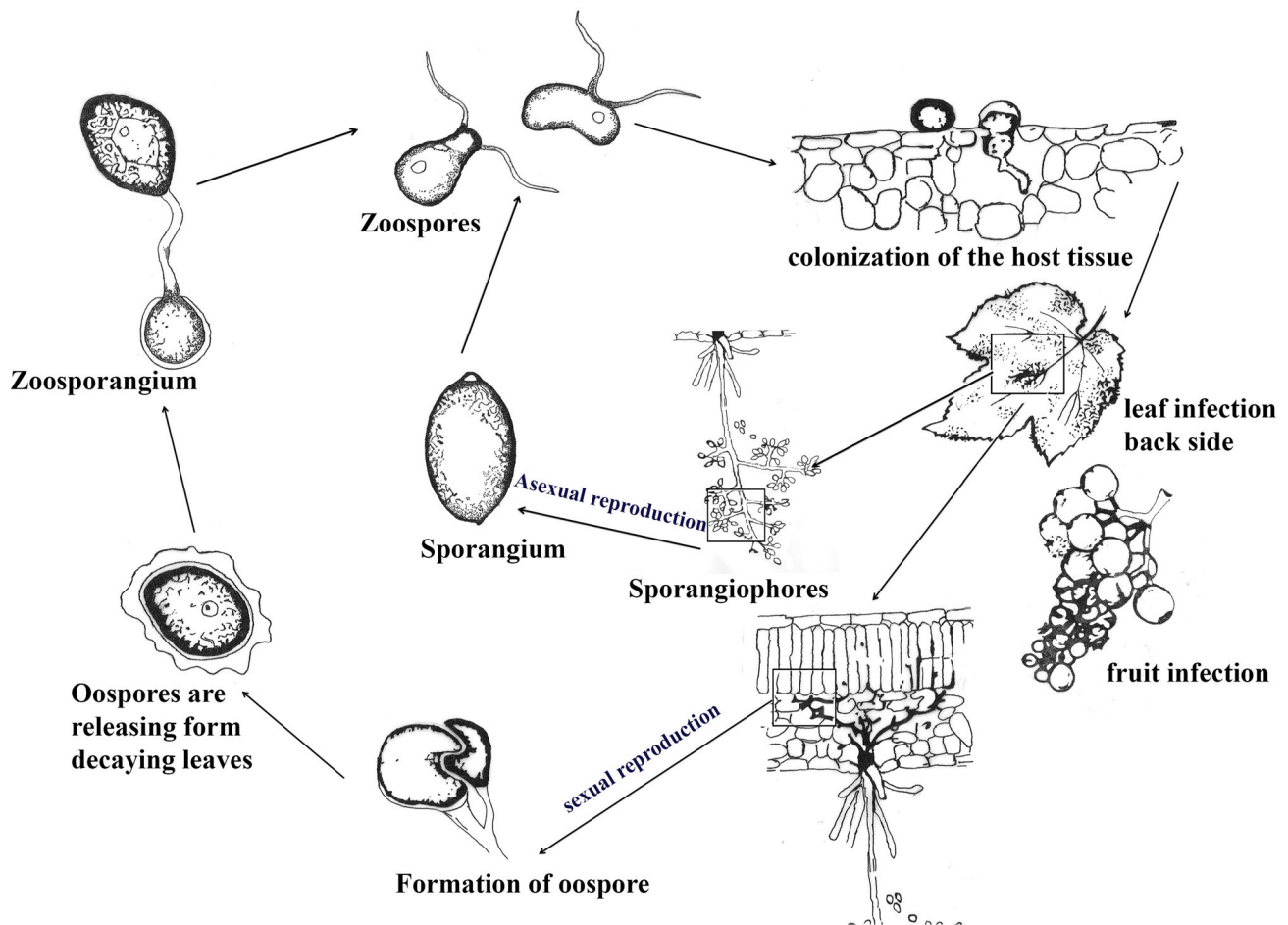


Fig. 20 Disease cycle of grape downy mildew. Redrawn from Kassemeyer (2017)

### Morphological based identification and diversity

*Pseudopestalotiopsis* can be distinguished from *Neopestalotiopsis* and *Pestalotiopsis* by dark concolourous median cells with indistinct conidiophores (Maharachchikumbura et al. 2014b, 2016). However, there could be a wide host range for *Pseudopestalotiopsis* species and the actual number of species could be much higher than presently known (Maharachchikumbura et al. 2011, 2016).

Conidial morphology is widely used in taxonomy in pestalotioid fungi (Steyaert 1949; Guba 1961; Nag Raj 1993; Maharachchikumbura et al. 2011, 2012, 2014b). Species delimitation based on morphological characters is limited as these characters are plastic and vary between hosts and environments (Maharachchikumbura et al. 2011, 2016). Therefore, phylogenetic species recognition is an effective method to identify different pestalotioid species (Maharachchikumbura et al. 2016).

### Molecular based identification and diversity

ITS sequence data alone is not sufficient for species delimitation of *Pseudopestalotiopsis*. Therefore, Maharachchikumbura et al. (2012) suggested a phylogenetic analysis of combined ITS, TUB2 and *tefl* genes provide better resolution as compared to single gene phylogeny (Fig. 22, Table 14).

*Recommended genetic markers (genus level)*—LSU (as outlined in Maharachchikumbura et al. 2012)

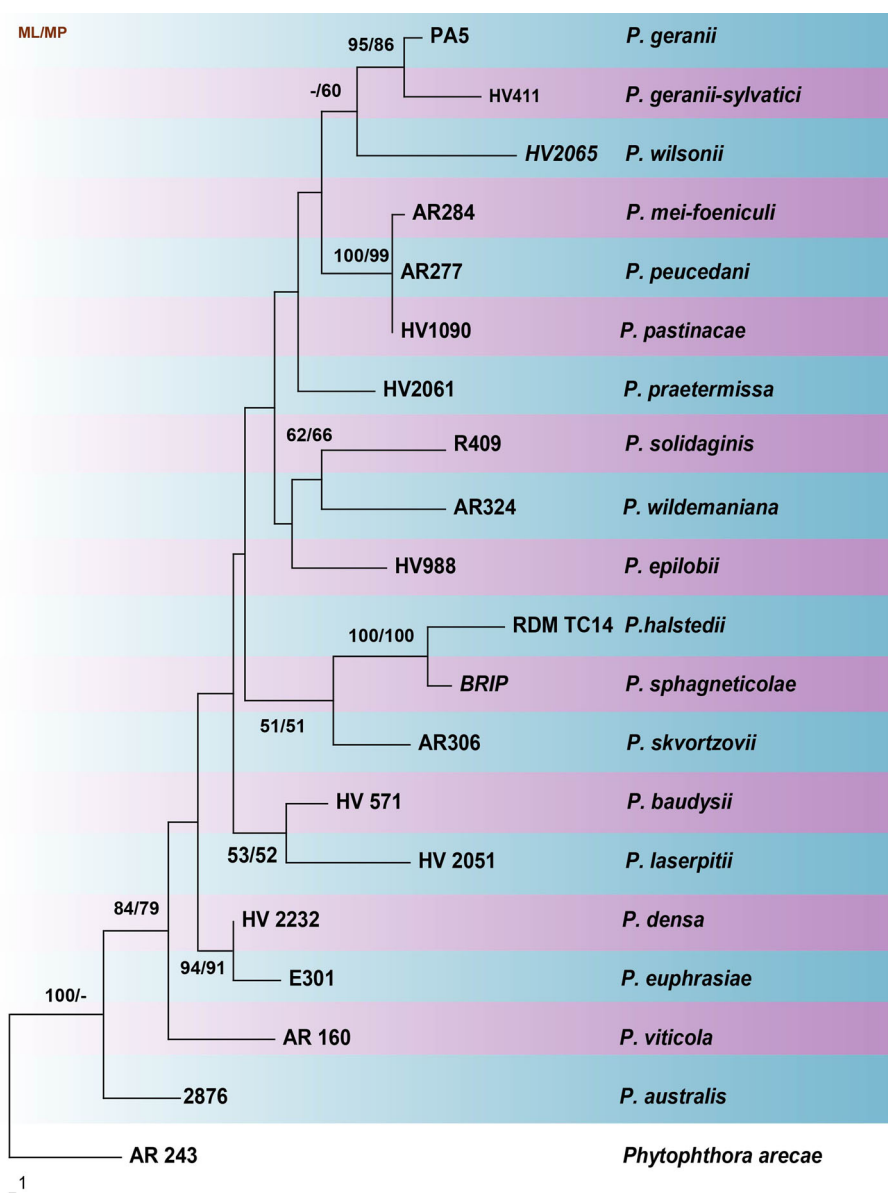
*Recommended genetic markers (species level)*—ITS, TUB2 and *tefl* (as outlined in Maharachchikumbura et al. 2012)

*Accepted number of species: 20 species*

*References:* Maharachchikumbura 2013a, b, 2014b, 2016b (morphology, phylogeny)

*Rosellinia* De Not., G. bot. ital.1 (1): 334(1844)

*Rosellinia* (*Xylariaceae*) species are characterized mainly as saprobes, some endophytes and occasionally as pathogens. They have a worldwide distribution and common in both temperate and tropical regions (Petrini



**Fig. 21** Phylogenetic tree generated by maximum parsimony analysis of LSU sequence data of *Plasmopara* species. Related sequences were obtained from GenBank. Nineteen strains are included in the analyses, which comprise 1263 characters including gaps. The tree was rooted with *Phytophthora arecae* (AR 234). Tree topology of the MP analysis was similar to the ML. The maximum parsimonious dataset consisted of constant 1053, 110 parsimony-informative and 100 parsimony-uninformative characters. The parsimony analysis of the data matrix resulted in the maximum of two equally most parsimonious trees with a length of 365 steps (CI = 0.641, RI =

0.539, RC = 0.345, HI = 0.359) in the first tree. The best scoring RAxML tree with a final likelihood value of  $-3660.849005$  is presented. The matrix had 254 distinct alignment patterns, with 30.91% of undetermined characters or gaps. Estimated base frequencies were as follows; A = 0.229156, C = 0.177763, G = 0.308486, T = 0.284595; substitution rates AC = 0.706031, AG = 4.368078, AT = 1.048734, CG = 0.141039, CT = 7.063364, GT = 1.000000; gamma distribution shape parameter  $\alpha = 0.163551$ . RAxML and maximum parsimony bootstrap support value  $\geq 50\%$  (BT) are shown respectively near the nodes

1993, 2013; ten Hoopen and Krauss 2006). Plant pathogenic *Rosellinia* species play a vital role in economically important crops, trees and ornamental plants. *Rosellinia desmazieresii* and *R. necatrix* are mostly known from temperate regions, while *R. bunodes* is known only from the tropics causing root rot on fruit trees and vines (Agris 2005; ten Hoopen and Krauss 2006). Among the root

diseases cause by *Rosellinia* species, *R. bunodes* is responsible for black root rot, *R. necatrix* for white root rot and *R. pepo* for stellate root rot (Castro et al. 2013). Species of this genus can survive as microsclerotia in wood, roots and soil and the infection spreads through feeder roots when they contact hyphae or microsclerotia (Ploetz et al. 2003).

**Table 13** Details of the *Plasmopara* isolates used in the phylogenetic tree

| Species                     | Isolate/voucher no | Host                           | LSU      |
|-----------------------------|--------------------|--------------------------------|----------|
| <i>Plasmopara australis</i> | HV 2867            | <i>Luffa cylindrica</i>        | KT159461 |
| <i>P. baudysii</i>          | HV 571             | <i>Berula erecta</i>           | AY035517 |
| <i>P. densa</i>             | HV 2232            | <i>Rhinanthus minor</i>        | EF553463 |
| <i>P. epilobii</i>          | HV988              | <i>Epilobium parviflorum</i>   | AY250178 |
| <i>P. euphrasiae</i>        | EV 301             | <i>Euphrasia rostkoviana</i>   | EF553467 |
| <i>P. geranii</i>           | PA5                | <i>Geranium maculatum</i>      | DQ148397 |
| <i>P. geranii-sylvatici</i> | HV411              | <i>Geranium sylvaticum</i>     | DQ148398 |
| <i>P. halstedii</i>         | RDM TC14           | <i>Rudbeckia fulgida</i>       | KP164999 |
| <i>P. laserpitii</i>        | HV2051             | <i>Laserpitium latifolium</i>  | KC495034 |
| <i>P. mei-foeniculi</i>     | AR284              | <i>Meum athamanticum</i>       | AY250160 |
| <i>P. pastinacae</i>        | HV1090             | <i>Pastinaca sativa</i>        | AY250157 |
| <i>P. peucedani</i>         | AR277              | <i>Peucedanum palustre</i>     | AY250154 |
| <i>P. praetermissa</i>      | HV2061             | <i>Geranium sylvaticum</i>     | DQ148396 |
| <i>P. skvortzovii</i>       | AR306              | <i>Abutilon theophrasti</i>    | AY250179 |
| <i>P. solidaginis</i>       | R409               | <i>Solidago virgaurea</i>      | AY250144 |
| <i>P. sphagnetocolae</i>    | BRIP               | <i>Sphagneticola trilobata</i> | KM085176 |
| <i>P. viticola</i>          | AR 160             | <i>Vitis vinifera</i>          | AY035524 |
| <i>P. wildemaniana</i>      | AR324              | <i>Hypoestes</i> sp.           | AY250180 |
| <i>P. wilsonii</i>          | HV2065             | <i>Geranium nepalense</i>      | DQ148408 |
| <i>Phytophthora arecae</i>  | AR 243             | Unknown                        | AY035530 |

*Rosellinia* was introduced to accommodate species which are characterized by uniascomatal and carbonaceous stromata that develop within a subiculum. There have been different contradiction placements of *Rosellinia*. Miller (1928) placed it in the family *Xylariaceae* and this was confirmed in morphology and phylogeny-based studies later (Hsieh et al. 2010; Daranagama et al. 2015). Daranagama et al. (2018) and Wendt et al. (2018) revealed that *Rosellinia* is closely related to *Entoleuca* and *Nemania*.

**Classification**—*Sordariomycetes*, *Xylariomycetidae*, *Xylariales*, *Xylariaceae*

**Type species**—*Rosellinia aquila* (Fr.) Ces. & De Not., G. bot. ital.1 (1): 334(1844)

**Distribution**—Worldwide

**Disease symptoms**—Root rots

Black root rot is characterized by the occurrence in patches that extend in a circular pattern. *Rosellinia bunodes* the main causal agent of black root rot typically shows black branching strands that are firmly attached to the roots and may form condensed irregular knots and chlorotic leaves may shed gradually (Sivanesan and Holiday 1972; Oliverira et al. 2008).

The symptoms of white root rot caused by *R. necatrix* in the upper parts of the plants (such as yellow foliage, shrivelled fruits, no new growth) cannot be recognized in early stages of root infection. Cottony, white mycelia cover feeder roots of a tree and decay sets in. Mycelia grow into the soil and upward in the tree forming small, pale patches under or in the bark of major roots, root crown and lower

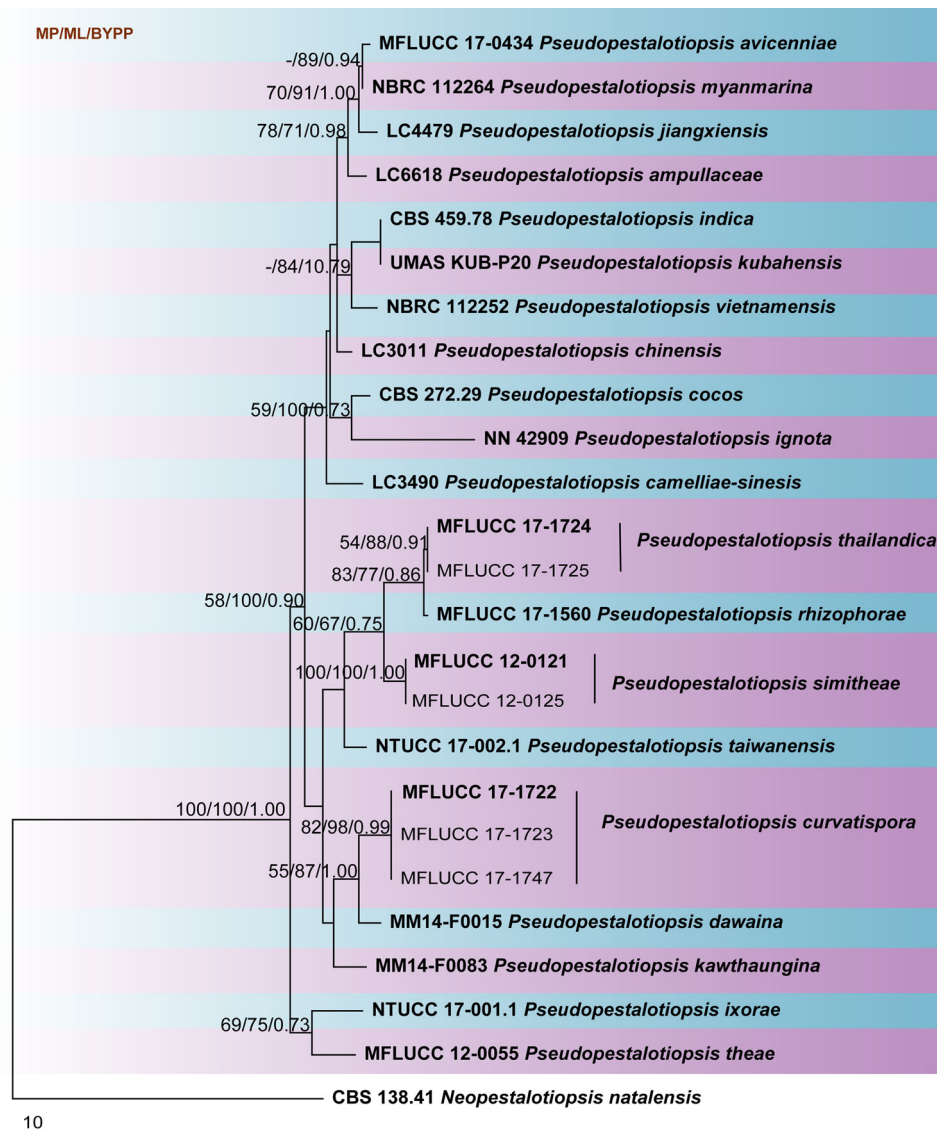
trunk which eventually decay. A purple canker in wood at the root crown of young trees can also be caused by the fungus. Diseased trees will defoliate and premature death may occur (Pérez-Jiménez 2006; Pasini et al. 2016).

**Hosts**—This genus has a wide range of hosts including *Adoxaceae*, *Annonaceae*, *Apiaceae*, *Asteraceae*, *Betulaceae*, *Celastraceae*, *Convolvulaceae*, *Euphorbiaceae*, *Fabaceae*, *Fagaceae*, *Grossulariaceae*, *Juglandaceae*, *Lauraceae*, *Moraceae*, *Myrtaceae*, *Oleaceae*, *Pinaceae*, *Poaceae*, *Rosaceae*, *Rutaceae*, *Salicaceae*, *Sapindaceae*, *Scrophulariaceae*, *Tamaricaceae*, *Verbenaceae*, *Vitaceae* and *Zingiberaceae*.

### Morphological based identification and diversity

The genus is characterized by globose-subglobose, uni- to multiloculate, often collapsed ascomata, mostly detached from the stroma wall.; septate, hyaline paraphyses, asci that are 8-spored, unitunicate, cylindrical to clavate, long pedicellate, rounded at the apex, with J + apical ring bluing in Melzer's reagent, massive barrel-shaped with distinctive rings ascospores that are uniseriate, unicellular, elongated ellipsoidal-fusiform, light to dark brown, with germ slits, cellular appendages and/or may be slimy sheaths or caps and a dematophora-like or geniculosporium-like asexual morphs (Daranagama et al. 2018).

*Rosellinia* is a large genus with 483 epithets in MycoBank, 517 in Index Fungorum and 311 in Global Biodiversity Information Facility (GBIF); there are currently 158 accepted species (Petrini 2013; Li and Guo 2015; Li et al.



**Fig. 22** Phylogram generated from maximum likelihood analysis based on combined ITS, TUB2 and *tefl* sequence data of *Pseudopestalotiopsis* species. Related sequences were obtained from GenBank. Twenty-five strains are included in the combined sequence analyses, which comprise 1404 characters with gaps. *Neopestalotiopsis natalensis* (CBS 138.41) was used as the outgroup taxa. The best scoring RAxML tree with a final likelihood value of  $-4028.799660$  is presented. The matrix had 274 distinct alignment patterns, with 6.34% of undetermined characters or gaps. Estimated base frequencies were as follows; A = 0.235765, C = 0.270775, G = 0.213073, T = 0.280387; substitution rates AC = 1.242401, AG = 3.217138,

AT = 1.272343, CG = 0.837226, CT = 4.463116, GT = 1.000000; gamma distribution shape parameter  $\alpha = 0.229606$ . The maximum parsimonious dataset consisted of 1122 constant, 79 parsimony-informative and 203 parsimony-uninformative characters. The parsimony analysis of the data matrix resulted in the maximum of four equally most parsimonious trees with a length of 386 steps (CI = 0.832, RI = 0.737, RC = 0.613, HI = 0.168) in the first tree. RAxML and maximum parsimony bootstrap support value  $\geq 50\%$  are shown respectively near the nodes. Bayesian posterior probabilities  $\geq 0.95$  (BYPP) indicated as thickened black branches. Ex-type strains are in bold

2015, 2016; Su et al. 2016; Crous et al. 2017; Fournier et al. 2017a, b; Tibpromma et al. 2017). Petrini (2013) found seven morphologically distinct groups with distinguishing morphological characters associated with the shape, size and orientations of stroma, ostiole, ascospores and germ slit, which can be used for species delimitation (Fig. 23).

### Molecular based identification and diversity

Protein coding gene sequences are available for nine species of *Rosellinia*, mostly with only ITS and LSU sequence data. However, with the limited data, Daranagama et al. (2018) provided an updated backbone tree for genera in *Xylariaceae*, and *Rosellinia* clustered with *Nemania* and *Entoleuca*. Several phylogenetic studies have focused on

**Table 14** Details of the *Pseudopezalotiopsis* isolates used in the phylogenetic analyses

| Species                               | Isolates               | ITS      | TUB2     | <i>tefl</i> |
|---------------------------------------|------------------------|----------|----------|-------------|
| <i>Pseudopezalotiopsis ampullacea</i> | <b>LC6618*</b>         | KX895025 | KX895358 | KX895244    |
| <i>P. avucenniae</i>                  | <b>MFLUCC 17-0434*</b> | MK764287 | MK764353 | MK764331    |
| <i>P. camelliae-sinensis</i>          | <b>LC3490*</b>         | KX894985 | KX895316 | KX895202    |
| <i>P. chinensis</i>                   | <b>LC3011*</b>         | KX894937 | KX895269 | KX895154    |
| <i>P. cocos</i>                       | <b>CBS 272.29*</b>     | KM199378 | KM199467 | KM199553    |
| <i>P. dawaina</i>                     | <b>MM14-F0015*</b>     | LC324750 | LC324751 | LC324752    |
| <i>P. curvatispora</i>                | <b>MFLUCC 17-1722*</b> | MK764288 | MK764354 | MK764332    |
| <i>P. ignota</i>                      | <b>NN 42909*</b>       | KU500020 | –        | KU500016    |
| <i>P. indica</i>                      | <b>CBS 459.78*</b>     | KM199381 | KM199470 | KM199560    |
| <i>P. ixorae</i>                      | <b>NTUCC 17-001.1*</b> | MG816316 | MG816326 | MG816336.   |
| <i>P. jiangxiensis</i>                | <b>LC 4479*</b>        | KX895034 | KX895343 | KX895229    |
| <i>P. kawthaungina</i>                | <b>MM14-F0083</b>      | LC324753 | LC324754 | LC324755    |
| <i>P. kubahensis</i>                  | <b>UMAS KUB-P20*</b>   | KT006749 | –        | –           |
| <i>P. myanmarina</i>                  | <b>NBRC 112264*</b>    | LC114025 | LC114045 | LC114065    |
| <i>P. rhizophorae</i>                 | <b>MFLUCC 17-1560*</b> | MK764291 | MK764357 | MK764335    |
| <i>P. smithae</i>                     | <b>MFLUCC 12-0121*</b> | KJ503812 | KJ503815 | KJ503818    |
| <i>P. thailandica</i>                 | <b>MFLUCC 17-1724*</b> | MK764292 | MK764358 | MK764336    |
| <i>P. taiwanensis</i>                 | <b>NTUCC 17-002.1*</b> | MG816319 | MG816329 | MG816339    |
| <i>P. theae</i>                       | <b>MFLUCC 12-0055*</b> | JQ683727 | JQ683711 | JQ683743    |
| <i>P. vietnamensis</i>                | <b>NBRC 112252*</b>    | LC114034 | LC114054 | LC114074    |

Ex-type (ex-epitype) strains are in bold and marked with an asterisk\* and voucher stains are in bold

pathogenic species such as *R. bunodes* and *R. pepo*. Castro et al. (2013) investigated *R. bunodes* and *R. pepo* isolated from *Coffea arabica* (Rubiaceae), *Hevea brasiliensis* (Euphorbiaceae), *Macadamia integrifolia* (Proteaceae), *Psidium guajava* (Myrtaceae) and *Theobroma cacao* (Malvaceae) using ITS based phylogenetic analyses from Colombia. Another ITS-based phylogenetic study identified *R. necatrix*, the pathogen responsible for white root disease on *Aronia melanocarpa* (Rosaceae) in Korea (Choi et al. 2017).

This study reconstructs the phylogeny of *Rosellinia* based on analyses of combined ITS, LSU and RPB2 sequence data (Table 7, Fig. 13). The phylogenetic tree is updated with recently introduced *Rosellinia* species and corresponds to previous studies (Li et al. 2015, 2016; Su et al. 2016; Crous et al. 2017; Fournier et al. 2017a, b; Tibpromma et al. 2017).

**Recommended genetic markers (genus level)**—LSU, ITS  
**Recommended genetic marker (species level)**—ITS

Based on several studies and the availability of sequence data, ITS based phylogenetic studies are sufficient to identify *Rosellinia* to species level. There are few other studies carried out using LSU, ITS and RPB2 sequences. With a lack of sequence data for most species, there are some contradictions for the species and generic delimitation.

**Accepted number of species:** 158 with only **26 species with molecular data**

**References:** Petrini 2013; Li and Guo 2015; (morphology), Castro et al. 2013; Li et al. 2015, 2016; Crous et al. 2017; Fournier et al. 2017a, b; Tibpromma et al. 2017, Daranagama et al. 2018 (morphology, phylogeny), Shimizu et al. 2012; dos Santos et al. 2017; Arjona-Girona and López-Herrera 2018; Kleina et al. 2018 (pathogenicity).

**Sphaeropsis** Sacc., *Michelia* 2: 105. 1880.

The genus *Sphaeropsis* was introduced by Saccardo (1880) (for species of *Diplodia* with brown, aseptate conidia), with *S. visci* as the type species. *Sphaeropsis* is the asexual morph of *Phaeobotryosphaeria* (Phillips et al. 2008, 2013; Wijayawardene et al. 2017). Species in *Sphaeropsis* seem to be cosmopolitan in distribution since they have been recorded from both temperate and tropical countries (i.e. Germany, New Zealand, South Africa, Thailand (Phillips et al. 2013; Slippers et al. 2014; Farr and Rossman 2019). Host specificity of *Sphaeropsis* has not yet been clarified and species have been recorded from various plant families.

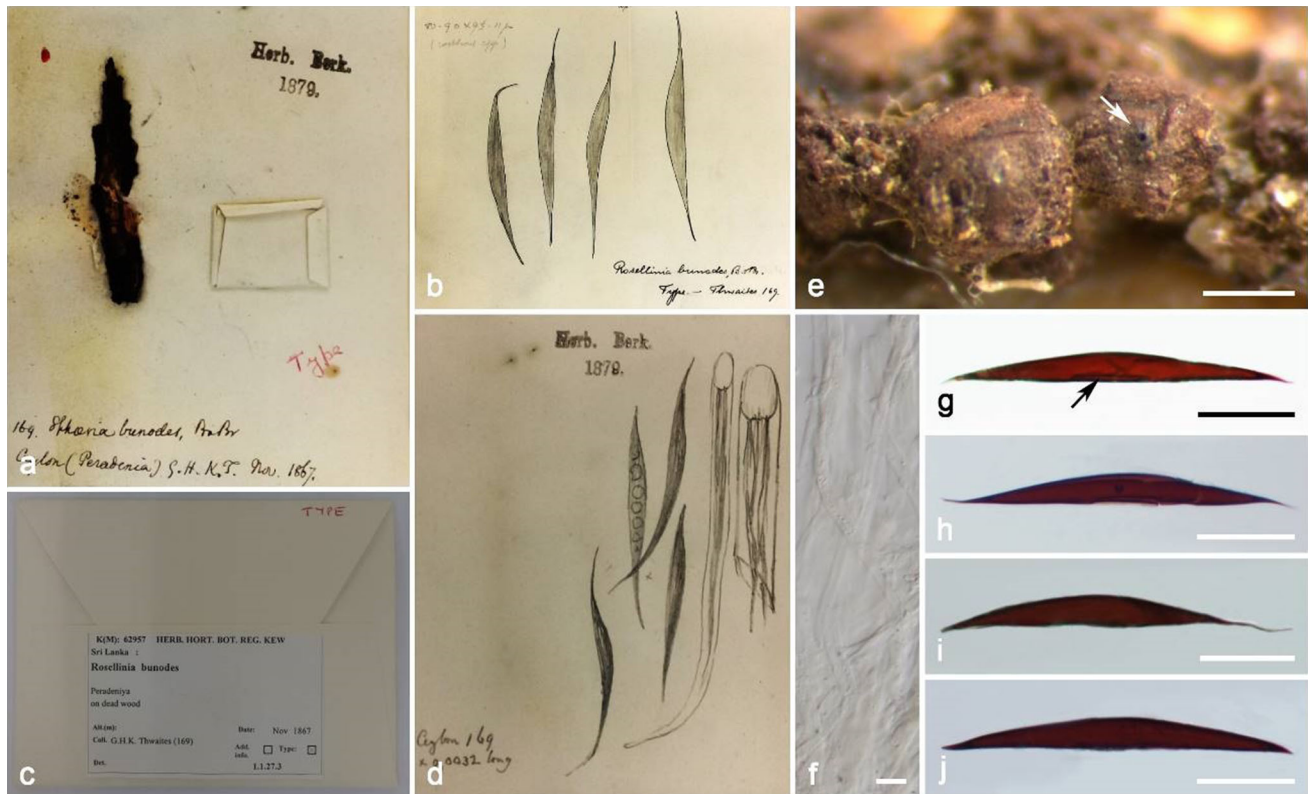
**Classification**—Dothideomycetes, incertae sedis, Botryosphaeriales, Botryosphaeriaceae

**Type species**—*Sphaeropsis visci* (Alb. & Schwein.) Sacc.

**Distribution**—Worldwide

**Disease symptoms**—calyx-end rot, stem end rot

The decayed tissues in rot diseases are firm or spongy and brown in colour. The skin of decayed areas generally remains brown or dark brown but may appear dark in aged areas (Kim et al. 2005).



**Fig. 23** *Rosellinia bunodes* (holotype, K(M) 62957, Sri Lanka, Peradeniya, on dead wood, November 1867, G.H.K. Thwaites) **a**, **e** Stromata (**e** ostiole white arrow). **b–d** Herbarium details.

**Hosts**—Broad range of hosts, including *Myrtaceae*, *Rutaceae*, *Santalaceae* and *Vitaceae*.

#### Morphological based identification and diversity

Over 600 species names are listed in Index Fungorum (2019), but few of them are currently in use and for most species cultures are not available except for *S. citrigena* (A.J.L. Phillips et al.) A.J.L. Phillips & A. Alves, *S. eucalypti* Berk. & Broome, *S. porosa* (Van Niekerk & Crous) A.J.L. Phillips & A. Alves, and *S. visci* (Alb. & Schwein.) Sacc. Pycnidial paraphyses in *Sphaeropsis* species distinguish this genus from *Diplodia* species, which do not have paraphyses. The aseptate, smooth-walled conidia of *Sphaeropsis* species differentiate them from *Lasiodiplodia* species, which have 1-septate, striate conidia. Recently, *S. variabilis* was transferred to a separate genus, *Oblongocollomyces* due to distinct morphological differences (Yang et al. 2017).

Colony and conidial morphology are the primary characters to identify species within this genus (Ellis 1971, 1976; Simmons 1992). The sexual and asexual morphs connection of *Sphaeropsis* was established by Phillips et al. (2008) who obtained coelomycetes with large, brown, aseptate conidia typical of *Sphaeropsis* from *Phaeobotryosphaeria* culture. Four *Sphaeropsis* species

**f** Paraphyses. **g–j** Ascospores (**g** germ slit black arrow). Scale bars: **e** = 500  $\mu$ m, **g–j** = 20  $\mu$ m, **f** = 5  $\mu$ m

have been identified from culture. *Sphaeropsis porosa* differs from other species in having distinct pitted conidial walls. *Sphaeropsis visci* and *S. citrigena* can be distinguished from each other with their conidial pigmentation and swollen paraphyses tips (Phillips et al. 2013).

#### Molecular based identification and diversity

Phillips et al. (2013) suggested that phylogenetic analysis of combined SSU, LSU, ITS, *tef1* and TUB2 genes provide better resolution compared to ITS alone. This study provides the phylogenetic analyses of combined ITS, LSU, SSU, *tef1* and TUB2 sequence data (Table 10, Fig. 16). The topology of the *Sphaeropsis* species tree is identical to the phylogeny tree of Phillips et al. (2013).

**Recommended genetic markers (genus level)**—LSU and SSU

**Recommended genetic markers (species level)**—ITS, *tef1* and TUB2

**Accepted number of species:** There are 624 species epithets in Index Fungorum (2019) under this genus. However, only **four** species have sequence data.

**References:** Phillips et al. 2013; Yang et al. 2017 (morphology, phylogeny).

## Updates on important phytopathogens

*Alternaria* Nees, Syst. Pilze (Würzburg): 72 (1816)

Species of *Alternaria* are saprotrophs on dead vegetation and are frequently isolated from soil, air, dust and water-damaged buildings (Ellis 1971, 1976; De Hoog and Horré 2002; Runa et al. 2009; Woudenberg et al. 2013; Lawrence et al. 2016). The majority of species, however, are pathogens, infecting a vast array of host species (Jayawardena et al. 2019). A detailed background, diseases and the symptoms, morphological characters is discussed in Jayawardena et al. (2019). In this paper, we provide an update for the sections in *Alternaria* based on six gene combination analyses (Al Ghafri et al. 2019; Table 15, Fig. 24).

*Diplodia* Fr., in Montagne, Anns Sci. Nat., Bot., sér. 2 1: 302 (1834)

The genus *Diplodia* was introduced by Montagne (1834) and comprises species with hyaline or dark brown, aseptate or 1-septate, thick-walled conidia (Phillips et al. 2005). *Diplodia* is defined by having unilocular, solitary or aggregated conidiomata lined with conidiogenous cells that form conidia at their tips (Phillips et al. 2005). The type species of *Diplodia* is *Diplodia mutila* (Montagne 1834; Fries 1849), but there are no living cultures linked to the holotype of this species. As this has severely hampered studies on taxonomy and phylogeny of *Diplodia*, Alves et al. (2004) provided a detailed description of *D. mutila* based on an isolate from grapevines in Portugal (CBS 112553). Alves et al. (2014) designated an epitype for *Diplodia mutila*, with associated ex-epitype cultures. This epitype confirmed in all ways with the isotype of *D. mutila* and with the asexual morph on BPI 599153 as described by Alves et al. (2004). *Diplodia mutila* has hyaline conidia that become brown and one-septate after discharge from the pycnidia. Species of *Diplodia* can be differentiated on slight differences in conidial dimensions (Alves et al. 2014).

*Classification*—Dothideomycetes, incertae sedis, Botryosphaerales, Botryosphaeriaceae

*Type species*—*Diplodia mutila* (Fr. : Fr.) Fr., Summa Veg. Scand. 2:417 (1849)

*Distribution*—Worldwide

*Disease symptoms*—Diebacks, cankers, fruit rots.

*Hosts*—Plurivorous on woody hosts.

## Morphological based identification and diversity

*Diplodia* is a large genus and a search in MycoBank (2019) revealed 1398 names while Index Fungorum (2019) has 1268 names. Cryptic speciation is common in the genus, which makes species identification difficult if based only on morphological characters (Phillips et al. 2012, 2013).

Dissanayake et al. (2016) included 26 *Diplodia* species in their phylogeny. Recently, a novel species *Diplodia eriobotryicola* on *Eriobotrya japonica* from Spain was introduced by González-Domínguez et al. (2016). Yang et al. (2017) introduced *D. pyri* on *Pyrus* sp., the Netherlands, *D. citricarpa* on *Citrus* sp., Iran, and *D. gallae* on galls of *Quercus* sp. However, the ITS and *tefl* of the novel species, *D. citricarpa* are not available in GenBank and hence we could not include this species in our phylogeny. The genus now comprises 30 species known from culture.

## Molecular based identification and diversity

Earlier taxonomic studies on *Diplodia* using molecular data employed ITS rDNA, but this single marker can underestimate species diversity among closely related or cryptic species. Multiple gene sequence concordance phylogenies have therefore been applied to identify cryptic or previously overlooked species of *Diplodia* (Slippers et al. 2004a, b, c; Burgess et al. 2006; Phillips et al. 2005, 2012, 2013; Hyde et al. 2014; Dissanayake et al. 2016). As the *tefl* gene is considerably more variable than the ITS rDNA region in these taxa, data from *tefl* have been combined with ITS sequence data. Unfortunately, no single gene region is sufficient to distinguish all species in this genus. The present phylogenetic analysis was performed based on up to date ex-holotype or ex-epitype sequence data available in GenBank (Fig. 25, Table 16).

*Recommended genetic markers (genus level)*—SSU and LSU

*Recommended genetic markers (species level)*—ITS, *tefl*, TUB2

*Accepted number of species: 30 species*

*References:* Phillips et al. 2013 (morphology, phylogeny, distribution, hosts); Dissanayake et al. 2016 (phylogeny).

*Dothiorella* Sacc., Melichia 2(6): 5 (1880)

*Dothiorella* was proposed by Saccardo to accommodate *D. pyrenophora* (Hyde et al. 2014). Members of this genus are pathogens, endophytes and saprobes (Phillips et al. 2013; Dissanayake et al. 2016). Taxonomy of this genus has been in a state of flux for decades (Phillips et al. 2013). Sivanesan (1984) treated *D. pyrenophora* as a synonym of *Dothichiza sorbi* (asexual morph of *Dothiora pyrenophora*). However, Sivanesan (1984) was referring to *Dothiorella pyrenophora* Sacc. (1884) which, according to Sutton (1977), is a later homonym of *Dothiorella pyrenophora* Sacc. (1880). Crous and Palm (1999) studied the holotype of *D. pyrenophora* and considered it a synonym of *Diplodia*. However, Phillips et al. (2005) based on both morphological and molecular data revived the genus *Dothiorella* for species in which the conidia become brown and 1-septate while attached to the conidiogenous cells.

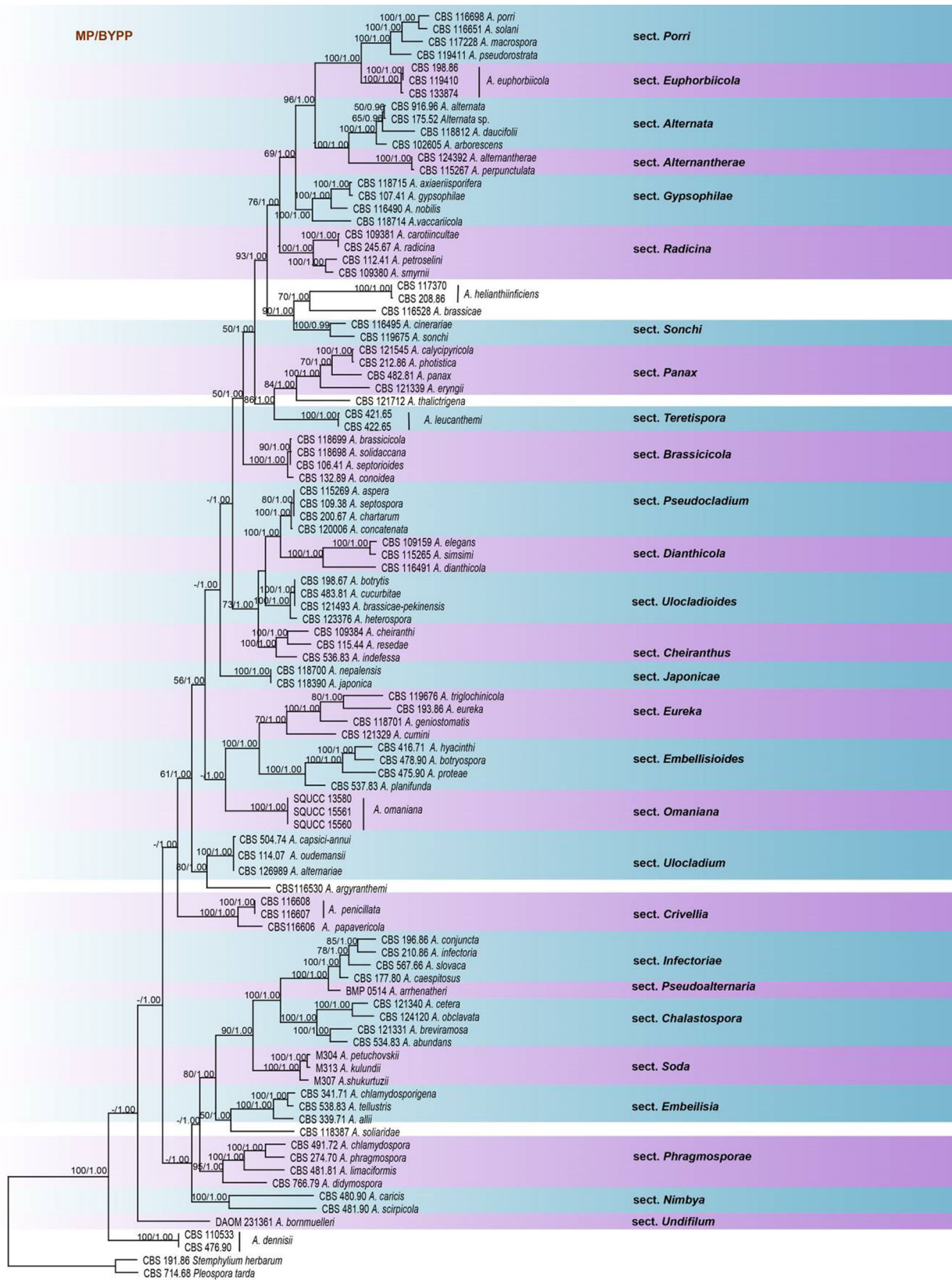
**Table 15** Details of the *Alternaria* isolates used in the phylogenetic analyses

| Species name                   | Strain number | GenBank accession numbers |          |          |          |          |             |
|--------------------------------|---------------|---------------------------|----------|----------|----------|----------|-------------|
|                                |               | SSU                       | LSU      | RPB2     | ITS      | GPDH     | <i>tef1</i> |
| <i>Alternaria abundans</i>     | CBS 534.83    | KC584581                  | KC584323 | KC584448 | JN383485 | KC584154 | KC584707    |
| <i>A. alternantherae</i>       | CBS 124392    | KC584506                  | KC584251 | KC584374 | KC584179 | KC584096 | KC584633    |
| <i>A. alternariae</i>          | CBS 126989    | KC584604                  | KC584346 | KC584470 | AF229485 | AY278815 | KC584730    |
| <i>A. alternata</i>            | CBS 916.96    | KC584507                  | DQ678082 | KC584375 | AF347031 | AY278808 | KC584634    |
| <i>A. arborescens</i>          | CBS 102605    | KC584509                  | KC584253 | KC584377 | AF347033 | AY278810 | KC584636    |
| <i>A. argyranthemii</i>        | CBS 116530    | KC584510                  | KC584254 | KC584378 | KC584181 | KC584098 | KC584637    |
| <i>A. arrhenatheri</i>         | BMP 0514      | –                         | –        | –        | JQ693680 | JQ693629 | –           |
| <i>A. aspera</i>               | CBS 115269    | KC584607                  | KC584349 | KC584474 | KC584242 | KC584166 | KC584734    |
| <i>A. atra</i>                 | CBS 195.67    | KC584608                  | KC584350 | KC584475 | AF229486 | KC584167 | KC584735    |
| <i>A. axiaeriisporifera</i>    | CBS 118715    | KC584513                  | KC584257 | KC584381 | KC584184 | KC584101 | KC584640    |
| <i>A. bornmueller</i>          | DAOM 231361   | KC584624                  | KC584366 | KC584491 | FJ357317 | FJ357305 | KC584751    |
| <i>A. botryospora</i>          | CBS 478.90    | KC584594                  | KC584336 | KC584461 | AY278844 | AY278831 | KC584720    |
| <i>A. botrytis</i>             | CBS 197.67    | KC584609                  | KC584351 | KC584476 | KC584243 | KC584168 | KC584736    |
| <i>A. brassicae</i>            | CBS 116528    | KC584514                  | KC584258 | KC584382 | KC584185 | KC584102 | KC584641    |
| <i>A. brassicae-pekinensis</i> | CBS 121493    | KC584611                  | KC584353 | KC584478 | KC584244 | KC584170 | KC584738    |
| <i>A. brassicicola</i>         | CBS 118699    | KC584515                  | KC584259 | KC584383 | JX499031 | KC584103 | KC584642    |
| <i>A. breviramosa</i>          | CBS 121331    | KC584574                  | KC584318 | KC584442 | FJ839608 | KC584148 | KC584700    |
| <i>A. calycipyricola</i>       | CBS 121545    | KC584516                  | KC584260 | KC584384 | KC584186 | KC584104 | KC584643    |
| <i>A. capsici-annui</i>        | CBS 504.74    | C584517                   | KC584261 | KC584385 | KC584187 | KC584105 | KC584644    |
| <i>A. caricis</i>              | CBS 480.90    | KC584600                  | KC584342 | KC584467 | Y278839  | AY278826 | C584726     |
| <i>A. carotiincultae</i>       | CBS 109381    | KC584518                  | KC584262 | KC584386 | KC584188 | KC584106 | KC584645    |
| <i>A. cetera</i>               | CBS 121340    | KC584573                  | KC584317 | KC584441 | JN383482 | AY562398 | KC584699    |
| <i>A. chartarum</i>            | CBS 200.67    | KC584614                  | KC584356 | KC584481 | AF229488 | KC584172 | KC584741    |
| <i>A. cheiranthi</i>           | CBS 109384    | C584519                   | C584263  | C584387  | F229457  | C584107  | C584646     |
| <i>A. chlamydospora</i>        | CBS 491.72    | KC584520                  | KC584264 | KC584388 | KC584189 | KC584108 | KC584647    |
| <i>A. chlamydosporigena</i>    | CBS 341.71    | KC584584                  | KC584326 | KC584451 | KC584231 | KC584156 | KC584710    |
| <i>A. cinerariae</i>           | CBS 116495    | KC584521                  | KC584265 | KC584389 | KC584190 | KC584109 | KC584648    |
| <i>A. concatenate</i>          | CBS 120006    | KC584613                  | KC584355 | KC584480 | KC584246 | AY762950 | KC584740    |
| <i>A. conjuncta</i>            | CBS 196.86    | KC584522                  | KC584266 | KC584390 | J266475  | Y562401  | KC584649    |
| <i>A. conoidea</i>             | CBS 132.89    | KC584585                  | KC584327 | KC584452 | AF348226 | FJ348227 | KC584711    |
| <i>A. consortialis</i>         | CBS 104.31    | KC584615                  | KC584357 | KC584482 | KC584247 | KC584173 | KC584742    |
| <i>A. cucurbitae</i>           | CBS 483.81    | KC584616                  | KC584358 | KC584483 | FJ266483 | AY562418 | KC584743    |
| <i>A. cumini</i>               | CBS 121329    | KC584523                  | KC584267 | KC584391 | KC584191 | KC584110 | KC584650    |
| <i>A. daucifolii</i>           | CBS 118812    | KC584525                  | KC584269 | KC584393 | KC584193 | KC584112 | KC584652    |
| <i>A. dennisii</i>             | CBS 110533    | KC584586                  | KC584328 | KC584453 | KC584232 | KC584157 | KC584712    |
| <i>A. dennisii</i>             | CBS 476.90    | KC584587                  | KC584329 | KC584454 | JN383488 | JN383469 | KC584713    |
| <i>A. dianthicola</i>          | CBS 116491    | KC584526                  | KC584270 | KC584394 | KC584194 | KC584113 | KC584653    |
| <i>A. didymospora</i>          | CBS 766.79    | KC584588                  | KC584330 | KC584455 | FJ357312 | FJ357300 | KC584714    |
| <i>A. elegans</i>              | CBS 109159    | KC584527                  | KC584271 | KC584395 | KC584195 | KC584114 | KC584654    |
| <i>A. embellisia</i>           | CBS 339.71    | KC584582                  | KC584324 | KC584449 | KC584230 | KC584155 | KC584708    |
| <i>A. eryngii</i>              | CBS 121339    | KC584529                  | KC584273 | KC584397 | Q693661  | Y562416  | KC584656    |
| <i>A. eureka</i>               | CBS 193.86    | KC584589                  | KC584331 | KC584456 | JN383490 | JN383471 | KC584715    |
| <i>A. geniostomatis</i>        | CBS 118701    | KC584532                  | KC584276 | KC584400 | KC584198 | KC584117 | KC584659    |
| <i>A. gypsophilae</i>          | CBS 107.41    | KC584533                  | KC584277 | KC584401 | KC584199 | KC584118 | KC584660    |
| <i>A. helianthiinficiens</i>   | CBS 117370    | KC584534                  | KC584278 | KC584402 | KC584200 | KC584119 | KC584661    |
| <i>A. helianthiinficiens</i>   | CBS 208.86    | KC584535                  | KC584279 | KC584403 | JX101649 | KC584120 | EU130548    |
| <i>A. heterospora</i>          | CBS 123376    | KC584621                  | KC584363 | KC584488 | KC584248 | KC584176 | KC584748    |



**Table 15** (continued)

| Species name              | Strain number | GenBank accession numbers |          |          |          |          |             |
|---------------------------|---------------|---------------------------|----------|----------|----------|----------|-------------|
|                           |               | SSU                       | LSU      | RPB2     | ITS      | GPDH     | <i>tef1</i> |
| <i>A. hyacinthi</i>       | CBS 416.71    | KC584590                  | KC584332 | KC584457 | KC584233 | KC584158 | KC584716    |
| <i>A. indefessa</i>       | CBS 536.83    | KC584591                  | KC584333 | KC584458 | KC584234 | KC584159 | KC584717    |
| <i>A. infectoria</i>      | CBS 210.86    | KC584536                  | KC584280 | KC584404 | DQ323697 | AY278793 | KC584662    |
| <i>A. japonica</i>        | CBS 118390    | KC584537                  | KC584281 | KC584405 | KC584201 | KC584121 | KC584663    |
| <i>A. kulundii</i>        | M313          | KJ443087                  | KJ443132 | KJ443176 | KJ443262 | KJ649618 | -           |
| <i>A. leucanthemi</i>     | CBS 421.65    | KC584605                  | KC584347 | KC584472 | KC584240 | KC584164 | KC584732    |
| <i>A. leucanthemi</i>     | CBS 422.65    | KC584606                  | KC584348 | KC584473 | KC584241 | KC584165 | KC584733    |
| <i>A. limaciformis</i>    | CBS 481.81    | KC584539                  | KC584283 | KC584407 | KC584203 | KC584123 | KC584665    |
| <i>A. macrospora</i>      | CBS 117228    | KC584542                  | KC584286 | KC584410 | KC584204 | KC584124 | KC584668    |
| <i>A. nepalensis</i>      | CBS 118700    | KC584546                  | KC584290 | KC584414 | KC584207 | KC584126 | KC584672    |
| <i>A. nobilis</i>         | CBS 116490    | KC584547                  | KC584291 | KC584415 | KC584208 | KC584127 | KC584673    |
| <i>A. obclavata</i>       | CBS 124120    | KC584575                  | FJ839651 | KC584443 | KC584225 | KC584149 | KC584701    |
| <i>A. oudemansii</i>      | CBS 114.07    | KC584619                  | KC584361 | KC584486 | FJ266488 | KC584175 | KC584746    |
| <i>A. omaniana</i>        | SQUCC 13580   | MK878559                  | MK878556 | MK880893 | MK878562 | MK880899 | MK880896    |
| <i>A. omaniana</i>        | SQUCC 15560   | MK878560                  | MK878557 | MK880894 | MK878563 | MK880900 | MK880897    |
| <i>A. omaniana</i>        | SQUCC 15561   | MK878561                  | MK878558 | MK880895 | MK878564 | MK880901 | MK880898    |
| <i>A. panax</i>           | CBS 482.81    | KC584549                  | KC584293 | KC584417 | KC584209 | KC584128 | KC584675    |
| <i>A. papavericola</i>    | CBS 116606    | KC584579                  | KC584321 | KC584446 | FJ357310 | FJ357298 | KC584705    |
| <i>A. penicillata</i>     | CBS 116608    | KC584572                  | KC584316 | KC584440 | FJ357311 | FJ357299 | KC584698    |
| <i>A. penicillata</i>     | 116607        | KC584580                  | KC584322 | KC584447 | KC584229 | KC584153 | KC584706    |
| <i>A. perpunctulata</i>   | CBS 115267    | KC584550                  | KC584294 | KC584418 | KC584210 | KC584129 | KC584676    |
| <i>A. petroselini</i>     | CBS 112.41    | KC584551                  | KC584295 | KC584419 | KC584211 | KC584130 | KC584677    |
| <i>A. petuchovskii</i>    | M304          | KJ443079                  | KJ443124 | KJ443170 | KJ443254 | KJ649616 | -           |
| <i>A. photistica</i>      | CBS 212.86    | KC584552                  | KC584296 | KC584420 | KC584212 | KC584131 | KC584678    |
| <i>A. phragmospora</i>    | CBS 274.70    | KC584595                  | KC584337 | KC584462 | JN383493 | JN383474 | KC584721    |
| <i>A. porri</i>           | CBS 116698    | KC584553                  | KC584297 | KC584421 | DQ323700 | KC584132 | KC584679    |
| <i>A. proteae</i>         | CBS 475.90    | KC584597                  | KC584339 | KC584464 | AY278842 | KC584161 | KC584723    |
| <i>A. pseudorostrata</i>  | CBS 119411    | KC584554                  | KC584298 | KC584422 | JN383483 | AY562406 | KC584680    |
| <i>A. radicina</i>        | CBS 245.67    | KC584555                  | KC584299 | KC584423 | KC584213 | KC584133 | KC584681    |
| <i>A. scirpicola</i>      | CBS 481.90    | KC584602                  | KC584344 | KC584469 | KC584237 | KC584163 | KC584728    |
| <i>A. septorioides</i>    | CBS 106.41    | KC584559                  | KC584303 | KC584427 | KC584216 | KC584136 | KC584685    |
| <i>A. septospora</i>      | CBS 109.38    | KC584620                  | KC584362 | KC584487 | FJ266489 | FJ266500 | KC584747    |
| <i>A. shukurtuzii</i>     | M307          | KJ443082                  | KJ443127 | KJ443172 | KJ443257 | KJ649620 | -           |
| <i>A. simsimi</i>         | CBS 115265    | KC584560                  | KC584304 | KC584428 | JF780937 | KC584137 | KC584686    |
| <i>A. slovacca</i>        | CBS 567.66    | KC584576                  | KC584319 | KC584444 | KC584226 | KC584150 | KC584702    |
| <i>A. smyrnii</i>         | CBS 109380    | KC584561                  | KC584305 | KC584429 | AF229456 | KC584138 | KC584687    |
| <i>A. solani</i>          | CBS 116651    | KC584562                  | KC584306 | KC584430 | KC584217 | KC584139 | KC584688    |
| <i>A. soliaridae</i>      | CBS 118387    | KC584563                  | KC584307 | KC584431 | KC584218 | KC584140 | KC584689    |
| <i>A. solidaccana</i>     | CBS 118698    | KC584564                  | KC584308 | KC584432 | KC584219 | KC584141 | KC584690    |
| <i>A. sonchi</i>          | CBS 119675    | KC584565                  | KC584309 | KC584433 | KC584220 | KC584142 | KC584691    |
| <i>Alternaria</i> sp.     | CBS 175.52    | KC584577                  | KC584320 | KC584445 | KC584227 | KC584151 | KC584703    |
| <i>A. tagetica</i>        | CBS 479.81    | KC584566                  | KC584310 | KC584434 | KC584221 | KC584143 | KC584692    |
| <i>A. tellustris</i>      | CBS 538.83    | KC584598                  | KC584340 | KC584465 | FJ357316 | AY562419 | KC584724    |
| <i>A. thalictorigena</i>  | CBS 121712    | KC584568                  | KC584312 | KC584436 | EU040211 | KC584144 | KC584694    |
| <i>A. triglochinicola</i> | CBS 119676    | KC584569                  | KC584313 | KC584437 | KC584222 | KC584145 | KC584695    |
| <i>A. vaccariae</i>       | CBS 116533    | KC584570                  | KC584314 | KC584438 | KC584223 | KC584146 | KC584696    |
| <i>A. vaccariicola</i>    | CBS 118714    | KC584571                  | KC584315 | KC584439 | KC584224 | KC584147 | KC584697    |



◀**Fig. 24** Phylogenetic tree generated by maximum parsimony analysis of combined SSU, LSU, ITS, GPDH, *tefl* and RPB2 sequence data of *Alternaria* species. One hundred strains are included in the analyses, which comprised 4056 characters including gaps. The tree was rooted with *Stemphylium herbarium* (CBS 191.86) and *Pleospora tarda* (CBS 714.68). The maximum parsimonious dataset consisted of 3091 constant, 852 parsimony-informative and 113 parsimony-uninformative characters. The parsimony analysis of the data matrix resulted in the maximum of ten equally most parsimonious trees with a length of 4520 steps (CI = 0.335, RI 0.708, RC = 0.237, HI = 0.665) in the first tree. MP and ML bootstrap values  $\geq 50\%$  and Bayesian posterior probabilities  $\geq 0.90$  are shown respectively near the nodes. Ex-type strains are in bold

*Classification*—Dothideomycetes, incertae sedis, Botryosphaerales, Botryosphaeriaceae

*Type species*—*Dothiorella pyrenophora* Berk. ex Sacc., *Michelia* 2 (6): 5 (1880) (1909)

*Distribution*—Worldwide

*Disease symptoms*—Diebacks, cankers, fruit rots.

*Hosts*—Plurivorous on woody hosts.

### Morphological based identification and diversity

Species of this genus were mostly described based on host association, which has led to the introduction of many species names and currently there are 393 epithets in Index Fungorum (2019). Slippers et al. (2013) suggested that host association cannot be considered as an important factor in species delimitation, many names are likely to be synonyms. Phillips et al. (2008) introduced a new genus *Spencermartinsia* to accommodate dothiorella-like species with apiculate ascospores. However, Yang et al. (2017) based on six-gene phylogeny and a broad taxon sampling considered that *Spencermartinsia* should be treated as a synonym of *Dothiorella*. Phillips et al. (2013) listed all cultures available for this genus and provided a phylogenetic tree and a key to the species. In that study 13 species names and 16 unnamed lineages were listed. Hyde et al. (2014), Dissanayake et al. (2016) and Yang et al. (2017) provided updates for the genus. Hyde et al. (2014) accepted 19 species and Dissanayake et al. (2016) accepted 30 species in the genus. After making *Spencermartinsia* a synonym of *Dothiorella* Yang et al. (2017) accepted 36 species in this genus.

Phillips et al. (2013) differentiated 13 *Dothiorella* species on the basis of conidiomata and conidial dimensions. However, the dimensions of these characters overlap between species. Therefore, using morphology alone without molecular data is not suitable to define species.

### Molecular based identification and diversity

Recent studies have re-evaluated this genus based on multi-gene phylogeny of ITS, TUB2 and *tefl* sequence data. We reconstruct the phylogeny of *Dothiorella* based on analyses of a combined ITS and *tefl* sequence data (Table 17,

Fig. 26). The phylogenetic tree is updated with recently introduced *Dothiorella* species and corresponds to previous studies (Dissanayake et al. 2016; Yang et al. 2017; Hyde et al. 2018; Phookamsak et al. 2019). In the analyses, it appears that several species are synonyms, such as *D. parva*/*D. guttulata* and *D. rhamnii*/*D. eriobotryae* and possibly others. Therefore, a thorough revision of the genus is recommended to clarify the status of these dubious species.

*Recommended genetic markers (genus level)*—SSU and LSU

*Recommended genetic markers (species level)*—ITS and *tefl*

*Accepted number of species*: Currently, 393 species names are listed for *Dothiorella* in Index Fungorum (2019). Cultures and DNA sequences are available for 46 species, therefore **46 species are currently accepted in *Dothiorella***.

*References*: Phillips et al. 2013; Dissanayake et al. 2016 (morphology, phylogeny, distribution, hosts), Yang et al. 2017 (morphology and phylogeny)

*Fusarium* Link, Mag. Gesell. naturf. Freunde, Berlin 3(1-2): 10 (1809)

*Fusarium* is a genus with 20 monophyletic species complexes (Rana et al. 2017).

Species formerly belonged to *F. solani* species complex were transferred to genus *Neocosmospora* based on sexual morph characters and molecular phylogeny (Lombard et al. 2015; Sandoval-Denis and Crous (2018). *Fusarium* species are saprobes, parasites, endophytes, soil-borne or isolated from water (Rana et al. 2017). Species of *Fusarium* are economically important fungi as they are responsible for blights, cankers, rots, and wilts of horticultural, ornamental and forest crops in both agricultural and natural ecosystems, worldwide, and also human infections (Rana et al. 2017; Varela et al. 2013; Peraldi et al. 2014; Al-Hatmi et al. 2019; Maryani et al. 2019a, b). In nature, sexual morphs of *Fusarium* occur less commonly than the asexual morphs (Gräfenhan et al. 2011; Rossmann et al. 1999).

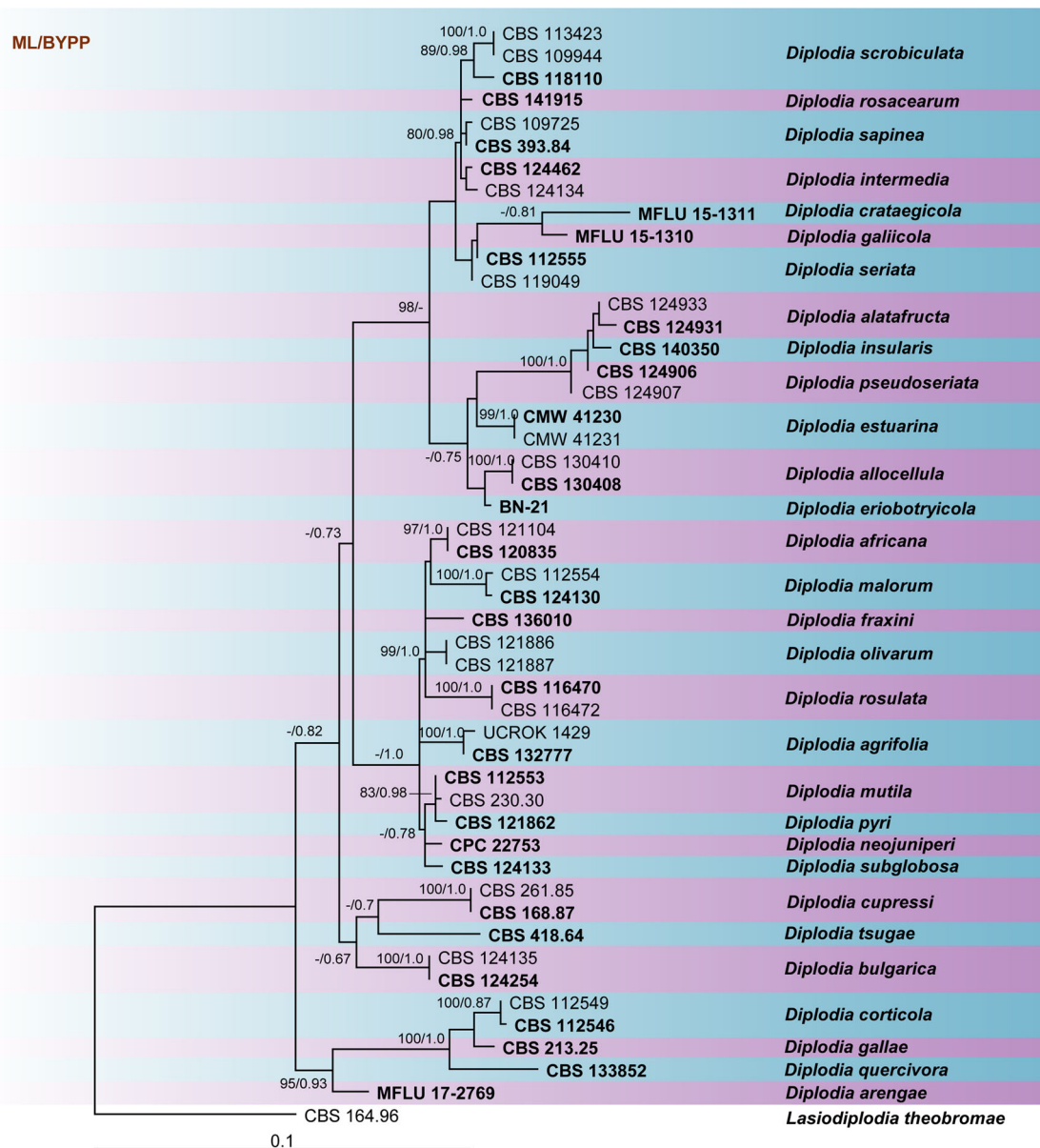
*Classification*—Sordariomycetes, Hypocreomycetidae, Hypocreales, Nectriaceae

*Type species*—*Fusarium sambucinum* Fuckel, Hedwigia 2: 135.1863.

*Distribution*—Worldwide

*Disease symptoms*—blights, cankers, rots, and wilts

Plant pathogenic species of this genus have the capability to change their lifestyle to saprotrophic and can survive for long periods as chlamydospores in host tissues. *Fusarium* species damage their hosts by systemically colonizing and occluding the host xylem (Ploetz et al. 2003). *Hosts*—Known from many host plant families.



**Fig. 25** Phylogenetic tree generated by maximum likelihood analysis of combined ITS and *tefl* sequence data of *Diplodia* species. Related sequences were obtained from GenBank. Forty nine strains are included in the analyses, which comprise 866 characters including gaps. The tree was rooted with *Lasiodiplodia theobromae* (CBS 164.96). Tree topology of the ML analysis was similar to the BYPP. The best scoring RAxML tree with a final likelihood value of  $-3342.903931$  is presented. The matrix had 278 distinct alignment patterns, with 9.02% of undetermined characters or gaps.

Estimated base frequencies were as follows; A = 0.207781, C = 0.297582, G = 0.261770, T = 0.232868; substitution rates AC = 0.993193, AG = 3.566477, AT = 0.787748, CG = 1.607220, CT = 4.471399, GT = 1.000000; gamma distribution shape parameter  $\alpha = 1.224079$ . RAxML bootstrap support values  $\geq 80\%$  (BT) are shown respectively near the nodes. Bayesian posterior probabilities  $\geq 0.5$  (PP) indicated as thickened black branches. Ex-type strains are in bold

### Morphological based identification and diversity

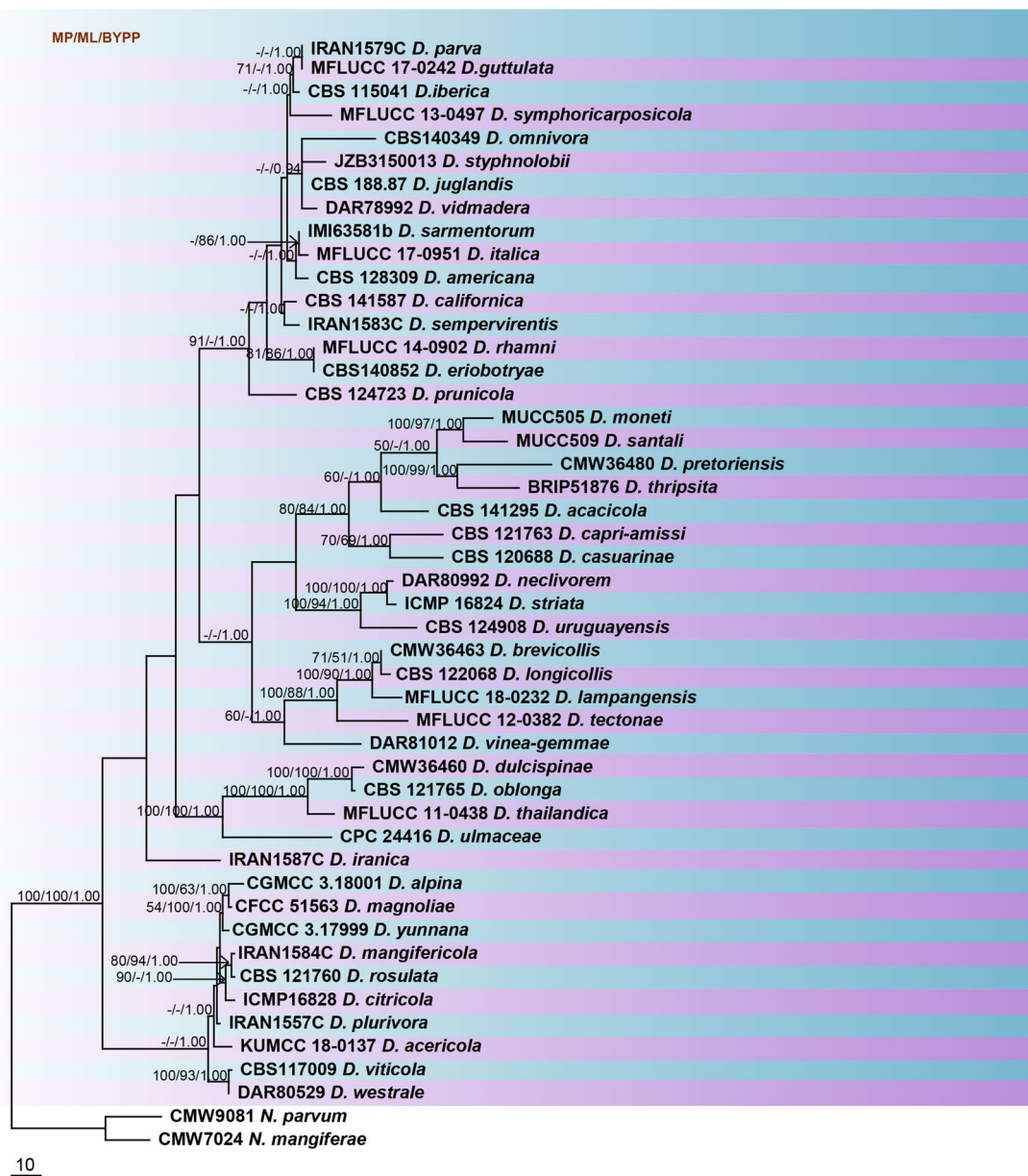
*Fusarium* was also known from the sexual morphic fungus name *Gibberella*, which was suppressed in favour of *Fusarium* by Rossman et al. (2013). Variation and mutation in culture and lack of clear morphological characters for separating species are the main problems which make the

species concept of *Fusarium* much broader (Geiser et al. 2004). It leads to the incorrect and confusing application of species names to toxigenic and pathogenic isolates (Geiser et al. 2004). Species boundaries have been inferred using multi-gene phylogenetic methods, reflecting the species diversity more than morphological treatments (Aoki and O'Donnell 1999; Geiser et al. 2004; O'Donnell 2000;

**Table 16** Details of the *Diplodia* isolates used in the phylogenetic analyses

| Species                              | Isolate/voucher no   | ITS             | <i>tefl</i>     |
|--------------------------------------|----------------------|-----------------|-----------------|
| <b><i>Diplodia africana</i></b>      | <b>CBS 120835*</b>   | <b>EF445343</b> | <b>EF445382</b> |
| <i>Diplodia africana</i>             | CBS 121104           | EF445344        | EF445383        |
| <b><i>Diplodia agrifolia</i></b>     | <b>CBS 132777*</b>   | <b>JN693507</b> | <b>JQ517317</b> |
| <i>Diplodia agrifolia</i>            | UCROK1429            | JQ411412        | JQ512121        |
| <b><i>Diplodia alatafructa</i></b>   | <b>CBS 124931*</b>   | <b>FJ888460</b> | <b>FJ888444</b> |
| <i>Diplodia alatafructa</i>          | CBS 124933           | FJ888478        | FJ888446        |
| <b><i>Diplodia allocellula</i></b>   | <b>CBS 130408*</b>   | <b>JQ239397</b> | <b>JQ239384</b> |
| <i>Diplodia allocellula</i>          | CBS 130410           | JQ239399        | JQ239386        |
| <b><i>Diplodia arengae</i></b>       | <b>MFLU 17-2769</b>  | MG762771        | MG762774        |
| <b><i>Diplodia bulgarica</i></b>     | <b>CBS 124254*</b>   | <b>GQ923853</b> | <b>GQ923821</b> |
| <i>Diplodia bulgarica</i>            | CBS 124135           | GQ923852        | GQ923820        |
| <b><i>Diplodia corticola</i></b>     | <b>CBS 112549*</b>   | <b>AY259100</b> | <b>AY573227</b> |
| <i>Diplodia corticola</i>            | CBS 112546           | AY259110        | DQ458872        |
| <b><i>Diplodia crataegicola</i></b>  | <b>MFLU 15-1311*</b> | <b>KT290244</b> | <b>KT290248</b> |
| <b><i>Diplodia cupressi</i></b>      | <b>CBS 168.87*</b>   | <b>DQ458893</b> | <b>DQ458878</b> |
| <i>Diplodia cupressi</i>             | CBS 261.85           | DQ458894        | DQ458879        |
| <b><i>Diplodia estuarina</i></b>     | <b>CMW41231*</b>     | <b>KP860831</b> | <b>KP860676</b> |
| <i>Diplodia estuarina</i>            | CMW41230             | KP860830        | KP860675        |
| <b><i>Diplodia fraxinii</i></b>      | <b>CBS 136010*</b>   | <b>KF307700</b> | <b>KF318747</b> |
| <b><i>Diplodia gallicola</i></b>     | <b>MFLU 15-1310*</b> | <b>KT290245</b> | <b>KT290249</b> |
| <b><i>Diplodia insularis</i></b>     | <b>CBS 140350*</b>   | <b>KX833072</b> | <b>KX833073</b> |
| <b><i>Diplodia intermedia</i></b>    | <b>CBS 124462*</b>   | <b>GQ923858</b> | <b>GQ923826</b> |
| <i>Diplodia intermedia</i>           | CBS 124134           | HM036528        | GQ923851        |
| <b><i>Diplodia malorum</i></b>       | <b>CBS 124130*</b>   | <b>GQ923865</b> | <b>GQ923833</b> |
| <i>Diplodia malorum</i>              | CBS 112554           | AY259095        | DQ458870        |
| <b><i>Diplodia mutila</i></b>        | <b>CBS 112553*</b>   | <b>AY259093</b> | <b>AY573219</b> |
| <i>Diplodia mutila</i>               | CBS 230.30           | DQ458886        | DQ458869        |
| <b><i>Diplodia neojuniperi</i></b>   | <b>CPC 22753*</b>    | <b>KM006431</b> | <b>KM006462</b> |
| <b><i>Diplodia olivarum</i></b>      | <b>CBS 121887*</b>   | <b>EU392302</b> | <b>EU392279</b> |
| <i>Diplodia olivarum</i>             | CBS 121886           | EU392297        | EU392274        |
| <b><i>Diplodia pseudoseriata</i></b> | <b>CBS 124906*</b>   | <b>EU080927</b> | <b>EU863181</b> |
| <i>Diplodia pseudoseriata</i>        | CBS 124907           | EU080922        | EU863179        |
| <b><i>Diplodia quercivora</i></b>    | <b>CBS 133852*</b>   | <b>JX894205</b> | <b>JX894229</b> |
| <b><i>Diplodia rosacearum</i></b>    | <b>CBS 141915*</b>   | <b>KT956270</b> | <b>KU378605</b> |
| <b><i>Diplodia rosulata</i></b>      | <b>CBS 116470*</b>   | <b>EU430265</b> | <b>EU430267</b> |
| <i>Diplodia rosulata</i>             | CBS 116472           | EU430266        | EU430268        |
| <b><i>Diplodia sapinea</i></b>       | <b>CBS 393.84*</b>   | <b>DQ458895</b> | <b>DQ458880</b> |
| <i>Diplodia sapinea</i>              | CBS 109725           | DQ458896        | DQ458881        |
| <b><i>Diplodia scrobiculata</i></b>  | <b>CBS 118110*</b>   | <b>AY253292</b> | <b>AY624253</b> |
| <i>Diplodia scrobiculata</i>         | CBS 109944           | DQ458899        | DQ458884        |
| <i>Diplodia scrobiculata</i>         | CBS 113423           | DQ458900        | DQ458885        |
| <b><i>Diplodia seriata</i></b>       | <b>CBS 112555*</b>   | <b>AY259094</b> | <b>AY573220</b> |
| <i>Diplodia seriata</i>              | CBS 119049           | DQ458889        | DQ458874        |
| <b><i>Diplodia subglobosa</i></b>    | <b>CBS 124133*</b>   | <b>GQ923856</b> | <b>GQ923824</b> |
| <b><i>Diplodia tsugae</i></b>        | <b>CBS 418.64*</b>   | <b>DQ458888</b> | <b>DQ458873</b> |

Ex-type (ex-epitype) strains are in bold and marked with an asterisk\* and voucher stains are in bold



**Fig. 26** Phylogenetic tree generated by maximum parsimony analysis of combined ITS and *tef1* sequence data of *Dothiorella* species. Related sequences were obtained from GenBank. Forty eight strains are included in the analyses, which comprised 873 characters including gaps. The tree was rooted with *Neofusicoccum parvum* (CMW9081) and *N. mangiferae* (CMW7024). The maximum parsimonious dataset consisted of 572 constant, 204 parsimony-

informative and 97 parsimony-uninformative characters. The parsimony analysis of the data matrix resulted in the maximum of ten equally most parsimonious trees with a length of 891 steps (CI = 0.532, RI 0.738, RC = 0.393, HI = 0.468) in the first tree. MP and ML bootstrap values  $\geq 50\%$  and Bayesian posterior probabilities  $\geq 0.90$  are shown respectively near the nodes. The scale bar indicates 10 changes per site. Ex-type strains are in bold

O'Donnell et al. 1998a, b; Ward et al. 2002). A combined phylogenetic analysis of LSU, ITS, RPB2 and new phylogenetic marker *acl1* by Gräfenhan et al. (2011), revealed that the early concept of *Fusarium* is not monophyletic. *Fusarium sensu* Wollenweber divided into two large groups, basal '*Fusarium*-like clades', and the other one terminal '*Fusarium* clade' in the *Nectriaceae* (Gräfenhan et al. 2011) (Fig. 27).

### Molecular based identification and diversity

ITS and LSU are least informative in species-level identification of *Fusarium* (O'Donnell et al. 1998a; Hyde et al. 2014). Moreover, non-orthologous copies of the ITS2, which can lead to wrong phylogenetic inferences, can be detected in many species of *Fusarium* (Geiser et al. 2004; O'Donnell et al. 1998a, b). Generally, for the species-level identification of fungi intron-rich regions of protein-coding

**Table 17** Details of the *Dothiorella* isolates used in the phylogenetic analyses

| Species                       | Isolate/voucher no     | ITS      | <i>tefl</i> |
|-------------------------------|------------------------|----------|-------------|
| <i>Dothiorella acacicola</i>  | <b>CBS 141295</b>      | KX228269 | KX228376    |
| <i>D. acericola</i>           | <b>KUMCC 18-0137*</b>  | MK359449 | MK361182    |
| <i>D. alpina</i>              | <b>CGMCC 3.18001*</b>  | KX499645 | KX499651    |
| <i>D. americana</i>           | <b>CBS 128309*</b>     | HQ288218 | HQ288262    |
| <i>D. brevicollis</i>         | <b>CBS 130411*</b>     | JQ239403 | JQ239390    |
| <i>D. californica</i>         | <b>CBS 141587*</b>     | KX357188 | KX357211    |
| <i>D. capri-amissi</i>        | <b>CMW 25403*</b>      | EU101323 | EU101368    |
| <i>D. casuarinae</i>          | <b>CBS 120688*</b>     | DQ846773 | DQ875331    |
| <i>D. citricola</i>           | <b>ICMP16828*</b>      | EU673323 | EU673290    |
| <i>D. dulcispinae</i>         | <b>CBS 130413*</b>     | JQ239400 | JQ239387    |
| <i>D. eriobotryae</i>         | <b>CBS 140852*</b>     | KT240287 | KT240262    |
| <i>D. guttulata</i>           | <b>MFLUCC 17-0242</b>  | KY797637 | –           |
| <i>D. iberica</i>             | <b>CBS 115041*</b>     | AY573202 | AY573222    |
| <i>D. iranica</i>             | <b>IRAN1587C*</b>      | KC898231 | KC898214    |
| <i>D. italica</i>             | <b>MFLUCC 17-0951</b>  | MG828897 | MG829267    |
| <i>D. juglandis</i>           | <b>CBS 188.87</b>      | EU673316 | EU673283    |
| <i>D. lampangensis</i>        | <b>MFLUCC 18-0232</b>  | MK347758 | MK340869    |
| <i>D. longicollis</i>         | <b>CBS 122068*</b>     | EU144054 | EU144069    |
| <i>D. magnoliae</i>           | <b>CFCC 51563</b>      | KY111247 | KY213686    |
| <i>D. mangifericola</i>       | <b>IRAN1584C*</b>      | KC898221 | KC898204    |
| <i>D. moneti</i>              | <b>MUCC505*</b>        | EF591920 | EF591971    |
| <i>D. neclivorem</i>          | <b>DAR80992*</b>       | KJ573643 | KJ573640    |
| <i>D. oblonga</i>             | <b>CMW 25407*</b>      | EU101300 | EU101345    |
| <i>D. omnivora</i>            | <b>CBS 140349*</b>     | KP205497 | KP205470    |
| <i>D. parva</i>               | <b>IRAN1579C*</b>      | KC898234 | KC898217    |
| <i>D. plurivora</i>           | <b>IRAN1557C*</b>      | KC898225 | KC898208    |
| <i>D. pretoriensis</i>        | <b>CBS 130404*</b>     | JQ239405 | JQ239392    |
| <i>D. prunicola</i>           | <b>CBS 124723*</b>     | EU673313 | EU673280    |
| <i>D. rhamnii</i>             | <b>MFLUCC 14-0902*</b> | KU246381 | –           |
| <i>D. rosulata</i>            | <b>CBS 121760*</b>     | EU101290 | EU101335    |
| <i>D. santali</i>             | <b>MUCC 509*</b>       | EF591924 | EF591975    |
| <i>D. sarmentorum</i>         | <b>IMI63581b*</b>      | AY573212 | AY573235    |
| <i>D. sempervirentis</i>      | <b>IRAN1583C*</b>      | KC898236 | KC898219    |
| <i>D. striata</i>             | <b>ICMP16824*</b>      | EU673320 | EU673287    |
| <i>D. styphnolobii</i>        | <b>JZB3150013*</b>     | MH880849 | MK069594    |
| <i>D. symphoricarposicola</i> | <b>MFULCC 13-0497*</b> | KJ742378 | KJ742381    |
| <i>D. tectonae</i>            | <b>MFLUCC12-0382*</b>  | KM396899 | KM409637    |
| <i>D. thailandica</i>         | <b>CBS 133991*</b>     | JX646796 | JX646861    |
| <i>D. thripsita</i>           | <b>BRIP 51876*</b>     | FJ824738 | KJ573639    |
| <i>D. ulmacea</i>             | <b>CBS 138855*</b>     | KR611881 | KR611910    |
| <i>D. uruguayensis</i>        | <b>CBS 124908*</b>     | EU080923 | EU863180    |
| <i>D. vidmadera</i>           | <b>DAR78992*</b>       | EU768874 | EU768881    |
| <i>D. vinea-gemmae</i>        | <b>DAR81012*</b>       | KJ573644 | KJ573641    |
| <i>D. viticola</i>            | <b>CBS 117009*</b>     | AY905554 | AY905559    |
| <i>D. westrale</i>            | <b>DAR80529*</b>       | HM009376 | HM800511    |
| <i>D. yunnana</i>             | <b>CGMCC 3.17999*</b>  | KX499643 | KX499649    |

Ex-type (ex-epitype) strains are in bold and marked with an asterisk\* and voucher stains are in bold  
 a the *tefl* sequence of *D. guttulata* in GenBank is incorrect, therefore was not included in the analyses

genes are used as the markers (Geiser et al. 2004). The translation elongation factor 1-a (*tef1*), which lacks non-orthologous copies of the gene, is highly informative at the species level in *Fusarium* (Geiser et al. 2004). RPB1 and RPB2 are also very informative gene regions for species identification of *Fusarium* (O'Donnell et al. 2013; Hyde et al. 2014). Lombard et al. (2018) observed that *tef1* and RPB2 genes provide better resolution of the species in the *F. oxysporum* complex than *cmdA* and *tub2* (Fig. 28, Table 18).

**Recommended genetic markers (genus level)**—ATP citrate lyase (*ac11*), *tef1* and ITS

**Recommended genetic markers (species level)**—calmodulin-encoding gene (*cmdA*), *tub2*, *tef1*, RPB1 and RPB2

**Accepted number of species:** There are 1552 species epithets in Index Fungorum (2019) under this genus. More than 175 species have DNA sequence data.

**References:** Booth 1971, Rossman et al. 1999 (morphology), Rana et al. 2017, Gräfenhan et al. 2011; Laurence et al. 2014; Lombard et al. 2018, 2019; Maryani et al. 2019a, b; Wang et al. 2019; Nalim et al. 2011 (morphology, phylogeny).

***Lasiodiplodia*** Ellis & Everh., Bot. Gaz. 21:92 (1896)

According to Clendenin (1896), a fungus causing rot of sweet potatoes imported from Java was identified by Ellis in 1894 as a new genus and he named the fungus *Lasiodiplodia tuberculata*. However, Ellis (1894) did not describe the fungus or publish the new genus. Clendenin (1896) provided a description of the genus and the species, attributing both to Ellis and Everhardt. Griffin and Maublanc (1909) considered that on account of the pycnidial paraphyses, *Botryodiplodia theobromae*, described by Patouillard and de Lagerheim (1892), was more suitably accommodated in *Lasiodiplodia*. Since the epithet *theobromae* (1892) is older than *tuberculata* (1896), *L. theobromae* should be regarded as the type species of *Lasiodiplodia*. Neither Patouillard and de Lagerheim (1892) nor Clendenin (1896) referred to any type or other specimens of the genus or species. Pavlic et al. (2004) could not locate the types, and they could not find any specimens from the original hosts or origins. Phillips et al. (2013) designated CBS H-21411 as neotype with CBS 164.96 as culture ex-neotype.

The sexual morph has been reported for *L. theobromae*, but the connection with the asexual morph has not been confirmed (Phillips et al. 2013). Sexual morphs have also been reported for *L. pseudotheobromae* (Tennakoon et al. 2016), *L. gonubiensis* (Trakunyingcharoen et al. 2015) and *L. lignicola* (Phillips et al. 2013) with clear evidence that connects sexual with asexual morphs.

**Classification**—*Dothideomycetes*, *incertae sedis*, *Botryosphaeriales*, *Botryosphaeriaceae*

**Type species**—*Lasiodiplodia theobromae* (Pat.) Griffon & Maubl., Bull. Soc. mycol. Fr. 25: 57 (1909)

**Distribution**—Worldwide, mostly confined to tropical and sub-tropical regions, but becoming increasingly more common in warm temperate regions.

**Disease symptoms**—Diebacks, cankers, fruit rots.

**Hosts**—Plurivorous on woody hosts

### Morphological based identification and diversity

The pigmented, 1-septate conidia with longitudinal striations together with the pycnidial paraphyses distinguish *Lasiodiplodia* from all other genera in *Botryosphaeriaceae* (Phillips et al. 2013). Striations on the conidia distinguish it from *Diplodia*, the conidiomata paraphyses distinguish it from *Neodeightonia*, which also has striate conidia. Although *Barriopsis* has striate conidia and paraphyses, *Lasiodiplodia* is unique in the *Botryosphaeriaceae* because striations are visible on immature, hyaline conidia. Although Phillips et al. (2013) differentiated 18 species in *Lasiodiplodia* on the basis of conidial morphology (especially dimensions) and morphology of the paraphyses, in reality, species in *Lasiodiplodia* cannot be identified with any confidence from their morphology and molecular data are necessary for definitive identifications.

### Molecular based identification and diversity

Denman et al. (2000) suggested that *Lasiodiplodia* could be a synonym of *Diplodia*. When Crous et al. (2006) re-organized *Botryosphaeria* on the basis of LSU phylogeny they split the genus into 10 genera, but could not resolve the position of *Lasiodiplodia* or separate it from *Diplodia*. Following a multi-locus approach (SSU, ITS, LSU, *tef1* and TUB2) Phillips et al. (2008) showed that *Lasiodiplodia* constitutes a clear phylogenetic lineage.

For many years, only the type species of *Lasiodiplodia* (*L. theobromae*) was mentioned in the phytopathological and mycological literature, and it was regarded as a cosmopolitan, plurivorous pathogen restricted mainly to tropical and sub-tropical regions (Punithalingam 1976, 1980). Soon after the widespread application of DNA-based phylogenies, Pavlic et al. (2004) introduced *L. gonubiensis* as a new species on the basis of conidial morphology and ITS sequence data. Soon after, Burgess et al. (2006) described three new species (*L. crassispora*, *L. venezuelensis* and *L. rubropurpurea*) from the tropics based on ITS and *tef1* sequence data and morphological characters. Alves et al. (2008) also used ITS and *tef1* sequence data to reveal two cryptic species in the *L. theobromae* complex. Over the years more species were introduced and Phillips et al. (2013) listed 18 species and Dissanayake et al. (2016) listed 31 species known from culture. Today





**Fig. 27** Sexual morph of a *Fusarium* sp. **a** Herbarium material. **b** Ascomata on the host. **c** Section of ascomata. **d** Section of the ostiolar region. **e** Peridium in face view. **f–h** Asci (**h** in Melzer's

reagent). **i, j** Ascospores. **k** Germinating ascospore. **l, m** Colony on MEA. Scale bars: **c** = 100  $\mu\text{m}$ , **d** = 50  $\mu\text{m}$ , **e–k** = 20  $\mu\text{m}$

the figure stands at 40 (Fig. 29). Apart from *L. theobromae*, all species have been introduced almost entirely on the basis of DNA sequence phylogenies. Although the phylogenies were derived from analysis of multiple loci (mostly ITS, *tef1* and TUB2 and sometimes RPB2) the genealogical concordance phylogenetic species recognition concept (Taylor et al. 2000) has not always been strictly applied and species have been introduced on the basis of minor differences in only one locus. The result is that some species are not well separated phylogenetically (Fig. 29, Table 19), such as *L. hyalina* and *L. thailandica*, *L.*

*chinensis*, *L. sterculiae*, *L. pseudotheobromae*, *L. pyriformis* and *L. crassispora*. In a detailed study of five loci of 19 *Lasiodiplodia* species, Cruywagen et al. (2017) concluded that several accepted species (*L. viticola*, *L. missouriana*, *L. laeliocattleyae*, *L. brasiliense*) may, in fact, be hybrids. There has been no such study of the 16 species introduced after the work of Cruywagen et al. (2017). In view of the questionable status of several species in *Lasiodiplodia*, there is an urgent need to re-assess all of the species currently accepted in this genus.



◀**Fig. 28** Phylogram generated from RAxML analysis based on combined RPB1, RPB2 and *tef1* sequences of accepted species of *Fusarium*. Related sequences were obtained from GenBank. One hundred sixty-five taxa are included in the analyses, which comprise 3980 characters including gaps. Single gene analyses were carried out and compared with each species, to compare the topology of the tree and clade stability. The tree was rooted in *Fusicolla aquaeductum* (NRRL 20696). Tree topology of the ML analysis was similar to the BYPP. The best scoring RAxML tree with a final likelihood value of  $-63956.723151$  is presented. The matrix had 2254 distinct alignment patterns, with 25.13% of undetermined characters or gaps. Estimated base frequencies were as follows; A = 0.257298, C = 0.251723, G = 0.248896, T = 0.242083; substitution rates AC = 1.366599, AG = 4.760724, AT = 1.266971, CG = 0.903914, CT = 9.564945, GT = 1.000000; gamma distribution shape parameter  $\alpha = 1.089091$ . Maximum likelihood bootstrap support values  $\geq 70\%$  (BT) and Bayesian posterior probabilities  $\geq 0.99$  (PP) are given near the nodes respectively

*Recommended genetic markers (genus level)*—SSU and LSU

*Recommended genetic markers (species level)*—ITS, *tef1*, TUB2

*Accepted number of species:* Currently, 51 species names are listed for *Lasiodiplodia* in MycoBank and Index Fungorum (2019). Cultures and DNA sequences are available for 43 species, three of which have been reduced to synonymy under existing names. **Thus, 40 species are currently recognised in *Lasiodiplodia*.**

*References:* Phillips et al. 2013 (morphology, phylogeny, distribution, hosts); Dissanayake et al. 2016 (species).

***Pestalotiopsis*** Steyaert, Bull. Jard. bot. État Brux. 19: 300 (1949)

*Pestalotiopsis* is an appendage-bearing, 5-celled conidia (asexual coelomycetes) in the family *Sporocadaceae* (Maharachchikumbura et al. 2014a, b; Jayawardena et al. 2016). The genus was introduced by Steyaert (1949). *Pestalotiopsis* species are widely distributed throughout tropical and temperate regions (Guba 1961; Maharachchikumbura et al. 2012, 2014a). *Pestalotiopsis* species have been isolated from dead leaves, bark, twigs, soil, polluted stream water, wood, paper, fabrics, and wool (Guba 1961; Maharachchikumbura et al. 2012, 2014a). Some species have been associated with human and animal infections, and others (e.g. *P. guepinii* and *P. microspora*) have also been isolated from extreme environments (Maharachchikumbura et al. 2014b).

*Classification*—Sordariomycetes, Xylariomycetidae, Amphisphaerales, Sporocadaceae

*Type species*—***Pestalotiopsis guepinii*** (Desm.) Steyaert [as ‘guepini’], Bull. Jard. bot. État Brux. 19(3): 312 (1949)

*Distribution*—Worldwide

*Disease symptoms*—Species of *Pestalotiopsis* cause a variety of diseases in plants including canker lesions, shoot dieback, leaf spots, needle blight, tip blight, grey blight, scabby canker, severe chlorosis, fruit rots and various post-harvest diseases (Maharachchikumbura et al. 2013a, b, 2014a, b). These pathogens reduce production and cause economic loss in apple, blueberry, coconut, chestnut, ginger, grapevine, guava, hazelnut, lychee, mango, orchid, peach, rambutan, tea and wax apple due to diseases (Maharachchikumbura et al. 2013a, b, 2014a, b). Grapevine trunk diseases are the most destructive diseases of grapevines that impact the economic production and longevity of vineyards and even leading to partial or total death of individual plants. Therefore, the initial identification of the causal agent is essential for early control of these diseases (Jayawardene et al. 2015; Maharachchikumbura et al. 2017). Pestalotoid fungi have been reported as pathogens on a variety of grapevine cultivars, causing diseases including grapevine dieback, fruit rot, postharvest disease and severe defoliation and they infect all plant parts including leaves, canes, wood, berries and flowers (Jayawardene et al. 2015; Maharachchikumbura et al. 2017). *Pestalotiopsis menezesiana* (Bres. & Torr.) Bissett. and *P. uvicola* (Spegazzini) Bissett, are the most common species recorded from grapevine around the world and especially *P. biciliata* are associated with trunk grapevine disease (Jayawardene et al. 2015; Maharachchikumbura et al. 2017).

*Hosts*—Broad range of hosts including members of *Altingiaceae*, *Arecaceae*, *Bromeliaceae*, *Euphorbiaceae*, *Myrtaceae*, *Poaceae*, *Proteaceae*, *Rosaceae*, *Rutaceae*, *Theaceae* and *Vitaceae*.

### Morphological based identification and diversity

There are around 250 species, most of which were named according to their host associations (Maharachchikumbura et al. 2014a, b). However, *Pestalotiopsis* species are not hosted specific and are found on a wide range of plants and substrates (Jeewon et al. 2003; Lee et al. 2006; Maharachchikumbura et al. 2014a, b). They exhibit considerable diversity in phenotype, and group together based on similarities in conidial morphology (Jeewon et al. 2003; Maharachchikumbura et al. 2012, 2013a, b, 2014a, b). Considering morphology, conidial length, width, median cell length, the colour of median cells and length of the apical appendages appear to be stable characters within *Pestalotiopsis* (Jeewon et al. 2003; Maharachchikumbura et al. 2014b).

*Pestalotiopsis guepinii* was considered to be the type species of the genus described from stems and leaves of *Camellia japonica* collected in France, and is characterised by 5-celled conidia with three concolourous median cells, hyaline terminal cells and simple or unbranched

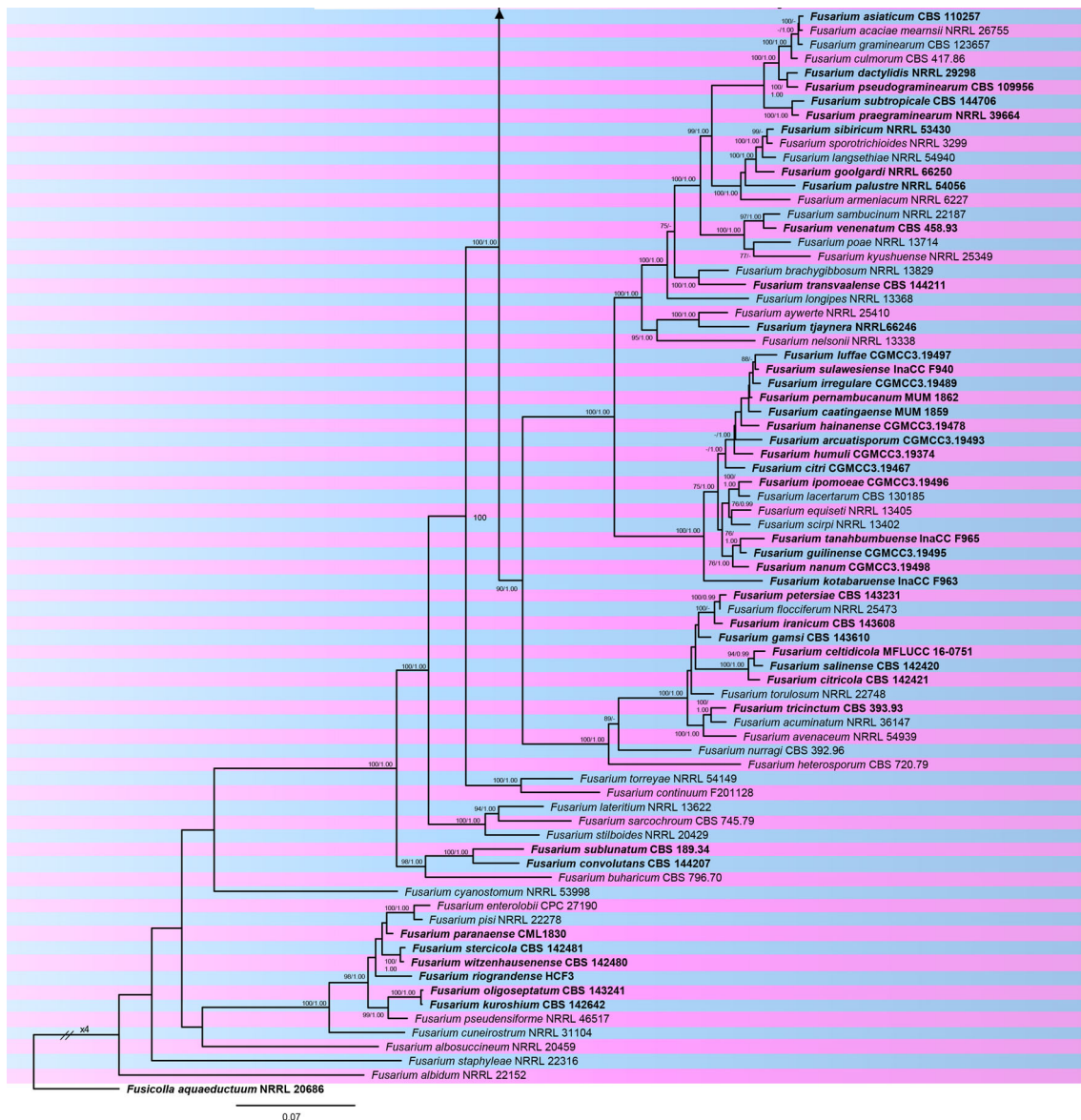


Fig. 28 continued

appendages arising from the apex of the apical cell (Steyaert 1949; Maharachchikumbura et al. 2014b). Nag Raj (1985) regarded *P. maculans* as the type species of *Pestalotiopsis* with *P. guepinii* as a synonym. Jeewon et al. (2003) also accepted *P. maculans* clusters with species having concolourous median cells based on phylogenetic analysis of ITS sequence data and that *P. karstenii* might be a synonym of *P. maculans* (Maharachchikumbura et al. 2014b).

Most *Pestalotiopsis* species lack sexual morphs. The sexual morph of *Pestalotiopsis* was treated as *Pestalospaeria* Barr, with the type species *Pestalospaeria concentrica* collected from grey-brown spots on living leaves

of *Rhododendron maximum* in North Carolina, USA (Maharachchikumbura et al. 2014b). *Pestalospaeria concentrica* is characterised by immersed, subglobose ascomata and unitunicate, cylindrical asci with a J + apical ring; ascospores uniseriate in the ascus, ellipsoid, pale dull brown and 2-septate (Maharachchikumbura et al. 2014b).

*Pestalotiopsis* species have the ability to switch life-modes as endophytes, pathogens and saprobes (Hu et al. 2007; Maharachchikumbura et al. 2012). Therefore, many endophytic and plant pathogenic *Pestalotiopsis* species persist as saprobes and have been isolated from dead leaves, bark and twigs (Maharachchikumbura et al. 2012, 2013a, b, 2014b).

**Table 18** Details of the *Fusarium* isolates used in the phylogenetic analyses

| Species                    | Isolate/voucher no                | RPB1     | RPB2     | <i>tefl</i> |
|----------------------------|-----------------------------------|----------|----------|-------------|
| <i>Fusarium anguioides</i> | NRRL 25385*; ATCC 66485           | JX171511 | JX171624 | MH742689    |
| <i>F. acaciae-mearnsii</i> | NRRL 26755                        | KM361640 | KM361658 | AF212449    |
| <i>F. acuminatum</i>       | NRRL 36147; CBS 109232            | HM347174 | GQ505484 | GQ505420    |
| <i>F. agapanthi</i>        | NRRL 54463*                       | KU900620 | KU900625 | KU900630    |
| <i>F. albidum</i>          | NRRL 22152                        | JX171492 | JX171605 | –           |
| <i>F. albosuccineum</i>    | NRRL 20459                        | JX171471 | JX171585 | –           |
| <i>F. algeriense</i>       | NRRL 66647*; CBS 142638; IL-79    | MF120488 | MF120499 | –           |
| <i>F. ananatum</i>         | CBS 118516*                       | LT996188 | LT996137 | KU604416    |
| <i>F. andiyazi</i>         | NRRL 31727; CBS 119857            | LT996189 | LT996138 | KP662901    |
| <i>F. anthophilum</i>      | NRRL 13602; CBS 737.97            | LT996190 | LT996139 | KU711685    |
| <i>F. arcuatisporum</i>    | CGMCC3.19493*; LC12147            | MK289799 | MK289739 | MK289584    |
| <i>F. armeniacum</i>       | NRRL 6227                         | JX171446 | JX171560 | HM744692    |
| <i>F. asiaticum</i>        | NRRL 13818*; CBS 110257           | JX171459 | JX171573 | AF212451    |
| <i>F. avenaceum</i>        | NRRL 54939                        | JX171551 | JX171663 | MH582391    |
| <i>F. aywerte</i>          | NRRL 25410                        | JX171513 | JX171626 | KU171717    |
| <i>F. babinda</i>          | NRRL 25539; CBS 396.96            | JX171519 | JX171632 | MH742712    |
| <i>F. begoniae</i>         | CBS 403.97*; NRRL 25300           | LT996191 | LT996140 | AF160293    |
| <i>F. beomiforme</i>       | NRRL 25174; CBS 740.97            | –        | JX171619 | –           |
| <i>F. brachygibbosum</i>   | NRRL 13829                        | JX171460 | JX171574 | –           |
| <i>F. buharicum</i>        | NRRL 13371; CBS 796.70            | JX171449 | JX171563 | –           |
| <i>F. bulbicola</i>        | NRRL 13618*; CBS 220.76           | KF466394 | KF466404 | KF466415    |
| <i>F. burgessii</i>        | CBS 125537*; RBG 5319             | KJ716217 | HQ646393 | HQ667149    |
| <i>F. callistephi</i>      | CBS 187.53*                       | –        | MH484905 | MH484966    |
| <i>F. carminascens</i>     | CBS 144738*; CPC 25800            | –        | MH484937 | MH485028    |
| <i>F. celtidicola</i>      | MFLUCC 16-0751*                   | –        | MH576580 | –           |
| <i>F. citri</i>            | CGMCC3.19467*; LC6896             | MK289828 | MK289771 | MK289617    |
| <i>F. citricola</i>        | CBS 142421*; CPC 27805            | LT746290 | LT746310 | LT746197    |
| <i>F. coicis</i>           | NRRL 66233*; RBG5368              | KP083269 | KP083274 | KP083251    |
| <i>F. commune</i>          | NRRL 28387                        | –        | JX171638 | KU171720    |
| <i>F. concentricum</i>     | NRRL 25181*; CBS 450.97           | LT996192 | JF741086 | AF160282    |
| <i>F. concolor</i>         | NRRL 13459*; CBS 961.87           | JX171455 | JX171569 | MH742681    |
| <i>F. contaminatum</i>     | CBS 114899*                       | –        | MH484901 | MH484992    |
| <i>F. continuum</i>        | F201128                           | KM520389 | KM236780 | KM236720    |
| <i>F. convolutans</i>      | CBS 144207*; CPC 33733            | LT996193 | LT996141 | LT996094    |
| <i>F. cugenangense</i>     | InaCCF984*                        | LS479560 | LS479308 | –           |
| <i>F. culmorum</i>         | NRRL 25475; CBS 417.86            | JX171515 | JX171628 | KY873384    |
| <i>F. cuneirostrum</i>     | NRRL 31104                        | –        | EU329558 | EF408413    |
| <i>F. curvatum</i>         | CBS 238.94; NRRL 26422; PD 94/184 | –        | MH484893 | MH484984    |
| <i>F. cyanostomum</i>      | NRRL 53998                        | JX171546 | JX171658 | –           |
| <i>F. dactylidis</i>       | NRRL 29298*                       | KM361654 | KM361672 | DQ459748    |
| <i>F. denticulatum</i>     | NRRL 25302; CBS 735.97            | LT996195 | LT996143 | AF160269    |
| <i>F. desaboruense</i>     | InaCC F950                        | LS479870 | LS479852 | –           |
| <i>F. dlamini</i>          | NRRL 13164*; CBS 119860           | KU171681 | KU171701 | MK639039    |
| <i>F. duoseptatum</i>      | InaCC F916*                       | LS479495 | LS479239 | –           |
| <i>F. elaeidis</i>         | CBS 217.49*; NRRL 36358           | –        | MH484870 | MH484961    |
| <i>F. enterolobii</i>      | CPC 27190                         | –        | LT746312 | LT746199    |
| <i>F. equiseti</i>         | NRRL 13405                        | –        | GQ915491 | GQ915507    |
| <i>F. fabacearum</i>       | CBS 144743*; CPC 25802            | –        | MH484939 | MH485030    |

Table 18 (continued)

| Species                  | Isolate/voucher no                      | RPB1     | RPB2     | <i>tefl</i> |
|--------------------------|---|----------|----------|-------------|
| <i>F. ficrescens</i>     | <b>CBS 125178*</b>                      | –        | KT154002 | KP662899    |
| <i>F. flocciferum</i>    | NRRL 25473                              | JX171514 | JX171627 | –           |
| <i>F. foetens</i>        | NRRL 38302                              | JX171540 | JX171652 | GU170559    |
| <i>F. fracticaudum</i>   | CMW 252374                              | LT996196 | LT996144 | KJ541059    |
| <i>F. fractiflexum</i>   | <b>NRRL 28852*</b>                      | –        | LT575064 | AF160288    |
| <i>F. fredkrugeri</i>    | <b>CBS 144209*</b> ; CPC 33747          | LT996199 | LT996147 | LT996097    |
| <i>F. fujikuroi</i>      | NRRL 13566                              | JX171456 | JX171570 | –           |
| <i>F. gaditjirrii</i>    | NRRL 45417                              | –        | JX171654 | KU171724    |
| <i>F. gamsi</i>          | <b>CBS 143610*</b> ; CPC 30862; OrSaAg4 | –        | LT970760 | LT970788    |
| <i>F. globosum</i>       | <b>NRRL 26131*</b> ; CBS 428.97         | KF466396 | KF466406 | KF466417    |
| <i>F. glycines</i>       | <b>CBS 144746*</b> ; CPC 25808          | –        | MH484942 | MH485033    |
| <i>F. gossypinum</i>     | <b>CBS 116613*</b>                      | –        | MH484909 | MH485000    |
| <i>F. graminearum</i>    | NRRL 31084; CBS 123657                  | JX171531 | JX171644 | HM744693    |
| <i>F. grosnichelii</i>   | <b>InaCC F833*</b>                      | LS479548 | LS479295 | LS479744    |
| <i>F. guilinense</i>     | <b>CGMCC3.19495*</b> ; LC12160          | MK289831 | MK289747 | MK289594    |
| <i>F. guttiforme</i>     | NRRL 22945                              | JX171505 | JX171618 | –           |
| <i>F. hainanense</i>     | <b>CGMCC3.19478*</b> ; LC11638          | MK289833 | MK289735 | MK289581    |
| <i>F. heterosporum</i>   | NRRL 20693; CBS 720.79                  | JX171480 | JX171594 | –           |
| <i>F. hexaseptatum</i>   | <b>InaCC F866*</b>                      | –        | LS479359 | LS479805    |
| <i>F. hoodiae</i>        | <b>CBS 132474*</b>                      | –        | MH484929 | MH485020    |
| <i>F. hostae</i>         | NRRL 29889                              | JX171527 | JX171640 | AY329034    |
| <i>F. inflexum</i>       | NRRL 20433                              | –        | JX171583 | AF008479    |
| <i>F. ipomoeae</i>       | <b>CGMCC3.19496*</b> ; LC12165          | MK289859 | MK289752 | MK289599    |
| <i>F. iranicum</i>       | <b>CBS 143608*</b> ; CPC 30860; OrSaAg2 | –        | LT970757 | LT970785    |
| <i>F. irregulare</i>     | <b>CGMCC3.19489*</b> ; LC7188           | MK289863 | MK289783 | MK289629    |
| <i>F. kalimantanense</i> | <b>InaCC F917*</b>                      | LS479497 | LS479241 | LS479690    |
| <i>F. konzum</i>         | <b>CBS 119849*</b>                      | LT996200 | LT996148 | LT996098    |
| <i>F. kotabaruense</i>   | <b>InaCC F963*</b>                      | LS479875 | LS479859 | LS479445    |
| <i>F. kuroshium</i>      | <b>CBS 142642*</b> ; UCR3641            | KX262236 | KX262256 | KX262216    |
| <i>F. kyushuense</i>     | NRRL 25349                              | –        | GQ915492 | GQ915508    |
| <i>F. lacertarum</i>     | NRRL 20423; CBS 130185                  | HM347137 | JX171581 | GQ505593    |
| <i>F. lactis</i>         | <b>NRRL 25200*</b> ; CBS 411.97         | LT996201 | LT996149 | AF160272    |
| <i>F. langsethiae</i>    | NRRL 54940                              | JX171550 | JX171662 | –           |
| <i>F. languescens</i>    | <b>CBS 645.78*</b> ; NRRL 36531         | –        | MH484880 | MH484971    |
| <i>F. lateritium</i>     | NRRL 13622                              | JX171457 | JX171571 | AY707173    |
| <i>F. libertatis</i>     | <b>CBS 144749*</b> ; CPC 28465          | –        | MH484944 | MH485035    |
| <i>F. longipes</i>       | NRRL 13368                              | JX171448 | JX171562 | –           |
| <i>F. luffae</i>         | <b>CGMCC3.19497*</b> ; LC12167          | MK289869 | MK289754 | MK289601    |
| <i>F. lumajangense</i>   | <b>InaCC F872*</b>                      | –        | LS479850 | LS479441    |
| <i>F. lyarnte</i>        | NRRL 54252; CBS 125536                  | JX171549 | JX171661 | –           |
| <i>F. mangiferae</i>     | <b>NRRL 25226*</b> ; BBA 69662          | JX171509 | JX171622 | –           |
| <i>F. miscanthi</i>      | NRRL 26231                              | –        | JX171634 | KU171725    |
| <i>F. mundagurra</i>     | <b>NRR L66235*</b> ; RBG5717            | KP083272 | KP083276 | MK639058    |
| <i>F. nanum</i>          | <b>CGMCC3.19498*</b> ; LC12168          | MK289871 | MK289755 | MK289602    |
| <i>F. napiforme</i>      | <b>CBS 748.97*</b> ; NRRL 13604         | HM347136 | EF470117 | KU604409    |
| <i>F. nelsonii</i>       | NRRL 13338                              | JX171447 | JX171561 | GQ505402    |
| <i>F. newnesense</i>     | NRRL 66237; RBG5443                     | KP083271 | KP083277 | KJ397074    |
| <i>F. nirenbergiae</i>   | <b>CBS 840.88*</b>                      | –        | MH484887 | MH484978    |

**Table 18** (continued)

| Species                      | Isolate/voucher no  | RPB1     | RPB2     | <i>tefl</i> |
|------------------------------|---|----------|----------|-------------|
| <i>F. nisikadoi</i>          | NRRL 25179; CBS 742.97                                    | JX171507 | JX171620 | –           |
| <i>F. nurragi</i>            | NRRL 36452; CBS 392.96                                    | JX171538 | JX171650 | –           |
| <i>F. nygamai</i>            | <b>NRRL 13448*</b> ; CBS 749.97                           | LT996202 | EF470114 | AF160273    |
| <i>F. odoratissimum</i>      | <b>InaCC F822*</b>  | LS479618 | LS479386 | –           |
| <i>F. oligoseptatum</i>      | <b>NRRL 62579*</b> ; FRC S- 2581; MAFF 246283; CBS 143241 | KC691596 | KC691656 | KC691538    |
| <i>F. oxysporum</i>          | <b>CBS 144134*</b>  | –        | MH484953 | MH485044    |
| <i>F. palustre</i>           | <b>NRRL 54056*</b>  | KT597718 | KT597731 | –           |
| <i>F. paranaense</i>         | <b>CML1830*</b>   | –        | KF680011 | KF597797    |
| <i>F. parvisorum</i>         | <b>CBS 137236*</b> ; FCC 5407; CMW 25267                  | –        | LT996150 | KJ541060    |
| <i>F. pernambucanum</i>      | <b>MUM 1862*</b> ; URM 7559                               | MH668869 | –        | –           |
| <i>F. petersiae</i>          | <b>CBS 143231*</b>  | MG386139 | MG386150 | MG386159    |
| <i>F. pharetrum</i>          | <b>CBS 144751*</b> ; CPC 30824                            | –        | MH484952 | MH485042    |
| <i>F. phialophorum</i>       | <b>InaCC F971*</b>  | LS479545 | LS479292 | LS479741    |
| <i>F. phyllophilum</i>       | <b>NRRL 13617*</b> ; CBS 216.76                           | KF466399 | KF466410 | KF466421    |
| <i>F. pisi</i>               | NRRL 22278  | –        | EU329501 | AF178337    |
| <i>F. poae</i>               | NRRL 13714  | JX171458 | JX171572 | –           |
| <i>F. praegraminearum</i>    | <b>NRRL 39664*</b>  | KX260125 | KX260126 | KX260120    |
| <i>F. proliferatum</i>       | NRRL 22944; CBS 217.76                                    | JX171504 | JX171617 | –           |
| <i>F. pseudensiforme</i>     | NRRL 46517  | KC691615 | KC691645 | KC691555    |
| <i>F. pseudocircinatum</i>   | <b>NRRL 22946*</b> ; CBS 449.97                           | LT996204 | LT996151 | AF160271    |
| <i>F. pseudograminearum</i>  | <b>NRRL 28062*</b> ; CBS 109956                           | JX171524 | JX171637 | AF212468    |
| <i>F. pseudonygamai</i>      | <b>NRRL 13592*</b> ; CBS 417.97                           | LT996205 | LT996152 | AF160263    |
| <i>F. purpurascens</i>       | <b>InaCC F886*</b>  | –        | LS479385 | LS479827    |
| <i>F. ramigenum</i>          | <b>NRRL 25208*</b> ; CBS 418.98                           | KF466401 | KF466412 | KF466423    |
| <i>F. redolens</i>           | NRRL 22901; CBS 743.97                                    | –        | KU171708 | KU171728    |
| <i>F. riograndense</i>       | <b>HCF3*</b>  | –        | KX534003 | KX534002    |
| <i>F. roseum</i>             | NRRL 22187  | JX171493 | JX171606 | –           |
| <i>F. sacchari</i>           | NRRL 13999; CBS 223.76                                    | JX171466 | JX171580 | KU711669    |
| <i>F. salinense</i>          | <b>CBS 142420*</b> ; CPC 26973                            | LT746286 | LT746306 | LT746193    |
| <i>F. sangayamense</i>       | <b>InaCC F960*</b>  | LS479537 | LS479283 | –           |
| <i>F. sarcochrom</i>         | NRRL 20472; CBS 745.79                                    | JX171472 | JX171586 | –           |
| <i>F. scirpi</i>             | NRRL 13402  | JX171452 | JX171566 | GQ505592    |
| <i>F. sibiricum</i>          | <b>NRRL 53430*</b>  | –        | HQ154472 | HM744684    |
| <i>F. siculi</i>             | <b>CBS 142422*</b> ; CPC 27188                            | LT746299 | LT746327 | LT746214    |
| <i>F. sororula</i>           | <b>CBS 137242*</b>  | LT996206 | LT996153 | –           |
| <i>F. sporotrichioides</i>   | NRRL 3299   | JX171444 | JX171558 | HM744665    |
| <i>F. staphyleae</i>         | NRRL 22316  | JX171496 | JX171609 | MH582426    |
| <i>F. stercicola</i>         | <b>CBS 142481*</b> ; DSM 106211                           | –        | KY556552 | KY556524    |
| <i>F. stilboides</i>         | NRRL 20429; ATCC 15662                                    | JX171468 | JX171582 | –           |
| <i>F. subglutinans</i>       | <b>NRRL 22016*</b> ; CBS 747.97                           | JX171486 | JX171599 | HM057336    |
| <i>F. sublunatum</i>         | <b>NRRL 13384*</b> ; CBS 189.34                           | JX171451 | JX171565 | –           |
| <i>F. subtropicale</i>       | <b>NRRL 66764*</b> ; CBS 144706                           | MH706972 | MH706973 | MH706974    |
| <i>F. succisae</i>           | NRRL 13613; CBS 219.76                                    | LT996207 | LT996154 | AF160289    |
| <i>F. sudanense</i>          | <b>CBS 454.97*</b> ; NRRL 25451                           | LT996208 | LT996155 | KU711697    |
| <i>F. sulawesiense</i>       | <b>InaCC F940*</b>  | –        | LS479855 | LS479443    |
| <i>F. tanahbumbuense</i>     | <b>InaCC F965*</b>  | LS479877 | LS479863 | LS479448    |
| <i>F. tardichlamyosporum</i> | <b>InaCC F958*</b>  | –        | LS479280 | LS479729    |
| <i>F. tardicrescens</i>      | <b>NRRL 36113*</b>  | LS479474 | LS479217 | LS479665    |

**Table 18** (continued)

| Species                       | Isolate/voucher no              | RPB1     | RPB2     | <i>tefl</i> |
|-------------------------------|---------------------------------|----------|----------|-------------|
| <i>F. terricola</i>           | <b>CBS 483.94*</b>              | LT996209 | LT996156 | KU711698    |
| <i>F. thapsinum</i>           | NRRL 22045; CBS 733.97          | JX171487 | JX171600 | AF160270    |
| <i>F. tjaetaba</i>            | <b>NRRL66243*</b> ; RBG5361     | KP083267 | KP083275 | KP083263    |
| <i>F. tjaynera</i>            | <b>NRRL66246*</b> ; RBG5367     | KP083268 | KP083279 | –           |
| <i>F. torreyae</i>            | NRRL 54149                      | JX171548 | HM068359 | HM068337    |
| <i>F. torulosum</i>           | NRRL 22748; NRRL 13919          | JX171502 | JX171615 | –           |
| <i>F. transvaalense</i>       | <b>CBS 144211*</b> ; CPC 30923  | LT996210 | LT996157 | LT996099    |
| <i>F. tricinatum</i>          | <b>NRRL 25481*</b> ; CBS 393.93 | JX171516 | HM068327 | MH582379    |
| <i>F. triseptatum</i>         | <b>CBS 258.50*</b> ; NRRL 36389 | –        | MH484873 | MH484964    |
| <i>F. udum</i>                | NRRL 22949; CBS 178.32          | LT996220 | LT996172 | AF160275    |
| <i>F. venenatum</i>           | <b>CBS 458.93*</b>              | –        | KM232382 | KM231942    |
| <i>F. verrucosum</i>          | NRRL 22566, BBA 64786           | –        | JX171613 | –           |
| <i>F. verticillioides</i>     | NRRL 20956                      | JX171485 | JX171598 | –           |
| <i>F. veterinarium</i>        | <b>CBS 109898*</b> ; NRRL 36153 | –        | MH484899 | MH484990    |
| <i>F. volatile</i>            | <b>CBS 143874*</b>              | –        | LR596006 | LR596007    |
| <i>F. witzenhauseense</i>     | <b>CBS 142480*</b>              | –        | KY556553 | KY556525    |
| <i>F. xylarioides</i>         | NRRL 25486; CBS 258.52          | JX171517 | JX171630 | AY707136    |
| <i>F. caatingaense</i>        | <b>MUM 1859*</b> ; URM 6779     | MH668845 | LS398495 | LS398466    |
| <i>F. goolgardi</i>           | <b>NRRL 66250*</b> ; RBG5411    | KP083270 | KP083280 | KP101123    |
| <i>F. humuli</i>              | <b>CGMCC3.19374*</b> ; CQ1039   | MK289840 | MK289724 | MK289570    |
| <i>Fusicolla aquaeductuum</i> | <b>NRRL 20686*</b>              | JX171476 | JX171590 | –           |

Ex-type (ex-epitype) strains are in bold and marked with an asterisk\* and voucher stains are in bold

*Pestalotiopsis* species that were isolated as endophytes are important in the discovery of novel compounds with medicinal, agricultural and industrial applications (Maharachchikumbura et al. 2014b; Xu et al. 2010, 2014). *Pestalotiopsis* species are a rich source for bioprospecting compared to other fungal genera, and more than 100 compounds have been isolated from *Pestalotiopsis* (Maharachchikumbura et al. 2014b; Xu et al. 2010, 2014).

#### Molecular based identification and diversity

Maharachchikumbura et al. (2012) tested with 10 gene regions to resolve species boundaries in *Pestalotiopsis* (actin, calmodulin, glutamine synthase, glyceraldehyde-3-phosphate dehydrogenase, ITS, LSU, 18S nrDNA, RNA polymerase II, *tefl* and TUB2). Maharachchikumbura et al. (2014b) used phylogenetic analysis of combined ITS, TUB2 and *tefl* genes to successfully resolve *Pestalotiopsis* species (Fig. 30, Table 20).

*Recommended genetic marker (genus level)*—LSU (as outlined in Maharachchikumbura et al. 2012)

*Recommended genetic markers (species level)*—ITS, TUB2 and *tefl* (as outlined in Maharachchikumbura et al. 2012)

*Accepted number of species:* There are 360 epithets in Index Fungorum in this genus, however, **75 species** with DNA sequence data are accepted.

*References:* Maharachchikumbura et al. 2013a, b, 2014b, 2016 (morphology, phylogeny)

*Stagonosporopsis* Died. emend. Aveskamp et al., Stud. Mycol. 65: 44. 2010

*Stagonosporopsis* is a coelomycetous genus in the family *Didymellaceae* (de Gruyter et al. 2013), accommodating several important phytopathogenic species. Some of the species have described sexual forms in *Didymella* (Diedicke 1912; Aveskamp et al. 2010). Some *Stagonosporopsis* species have quarantine importance. *Stagonosporopsis andigena* is listed in Annex IAI by European Union (EU), meaning its introduction to EU is prohibited. This pathogen is also listed in the A1 list by the European and Mediterranean Plant Protection Organization (EPPO 2019). *Stagonosporopsis chrysanthemi* is another species listed in A2 list by EPPO (EPPO 2019).

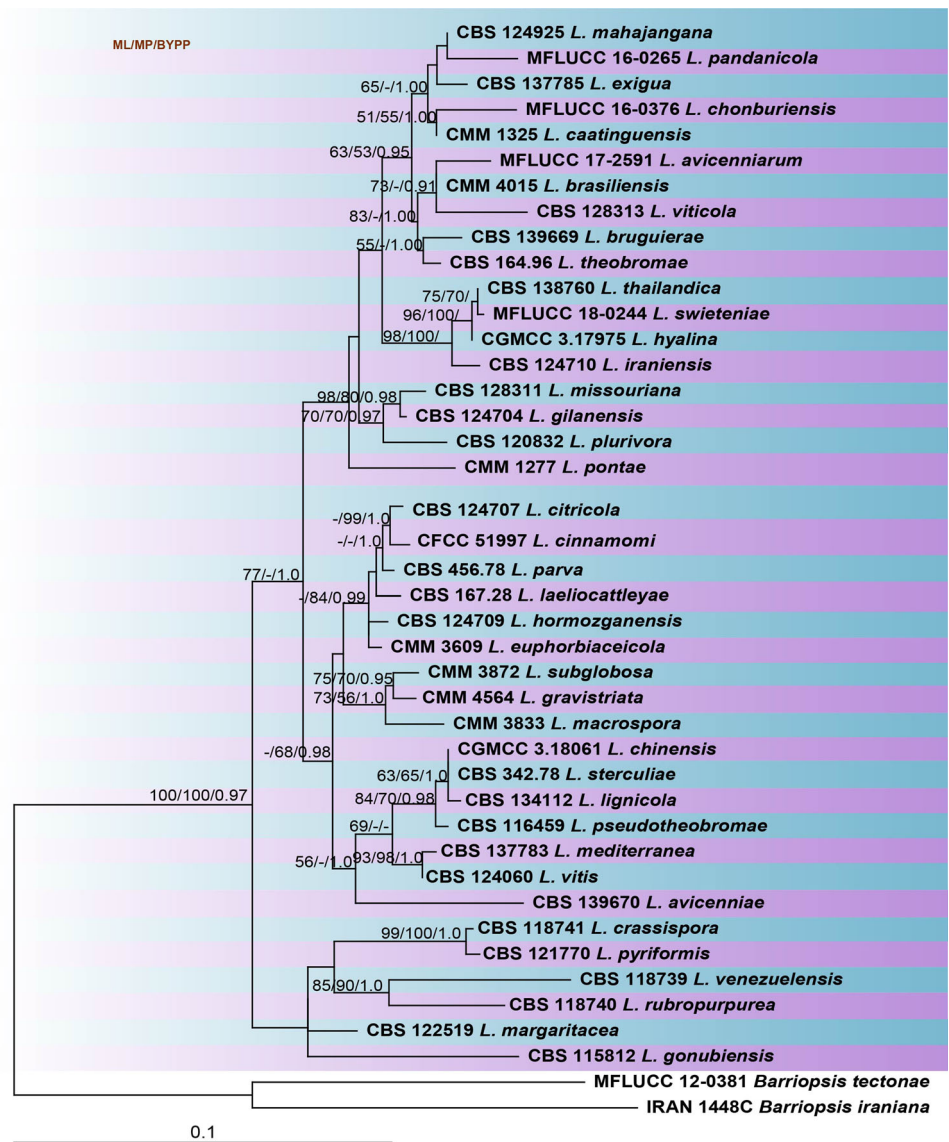
*Classification*—*Dothideomycetes*, *Pleosporomycetidae*, *Pleosporales*, *Didymellaceae*

*Type species*—*Stagonosporopsis boltshauseri* (Sacc.) Died. 1912

*Distribution*—Worldwide



**Fig. 29** Phylogenetic tree generated by maximum likelihood analysis of combined ITS and *tef1* sequence data of *Lasiodiplodia* species. Related sequences were obtained from GenBank. Forty nine strains are included in the analyses, which comprise 866 characters including gaps. The tree was rooted with *Barriopsis tectonae* and *B. iraniana*. Tree topology of the ML analysis was similar to MP and BYPP. The best scoring RAXML tree with a final likelihood value of  $-3733.342990$  is presented. The matrix had 253 distinct alignment patterns, with 4.41% of undetermined characters or gaps. Estimated base frequencies were as follows; A = 0.211797, C = 0.285190, G = 0.260783, T = 0.242230; substitution rates AC = 0.983905, AG = 3.303939, AT = 1.281593, CG = 0.950258, CT = 5.553417, GT = 1.000000; gamma distribution shape parameter  $\alpha = 0.221126$ . RAXML bootstrap support values  $\geq 80\%$  are shown respectively near the nodes. Bayesian posterior probabilities  $\geq 0.5$  (BYPP) indicated as thickened black branches. Ex-type strains are in bold



**Disease symptoms**—the Black blight of potato, gummy stem blight, ray blight

All plant parts may be attacked by *S. chrysanthemi* and *S. inoxydabilis*, however, flowers and cuttings are highly susceptible. Death of flowers and buds, a necrotic lesion on leaves and peduncles of unopened buds, soft rot of cortex of roots and discolouration of bark are the main symptom of the disease. Eventually, plant death occurs (Fox 1998; Pethybridge et al. 2008). In gummy stem blight of cucurbits, symptoms can be observed on all above ground and reproductive parts. Leaf spots are the main diagnostic character of this disease. Most of the circular or triangular shaped spots start at the margin of the leaf or extend towards the margin. The centre of the leaf spot is a lighter shade of brown than the surrounding portion. As leaf spots coalesce leaf blights occur. Actively expanding lesions on

leaves, petioles, and pedicels often appear as water-soaked. Cankers may form on crowns, main stems and vines (Keinath 2013). *Stagonosporopsis andigena* the black blight of potato causal agent affects leaves, petioles and stems causing lesions and premature leaf drop, but does not infect the underground parts. On leaves, the pathogen causes small, blackish concentric lesions. The initial symptoms can be observed on the lower leaves, however, as the disease progresses lesions may also develop in upper leaves as well. Lesions may coalesce and severely affected leaves may turn blackish giving a scorched appearance (EFSA panel on plant health 2019).

**Hosts**—*Amaranthaceae*, *Asteraceae*, *Campanulaceae*, *Caryophyllaceae*, *Cucurbitaceae*, *Fabaceae*, *Lamiaceae*, *Pinaceae*, *Ranunculaceae*, *Solanaceae* and *Valerianaceae*.

**Table 19** Details of the *Lasiodiplodia* isolates used in the phylogenetic analyses

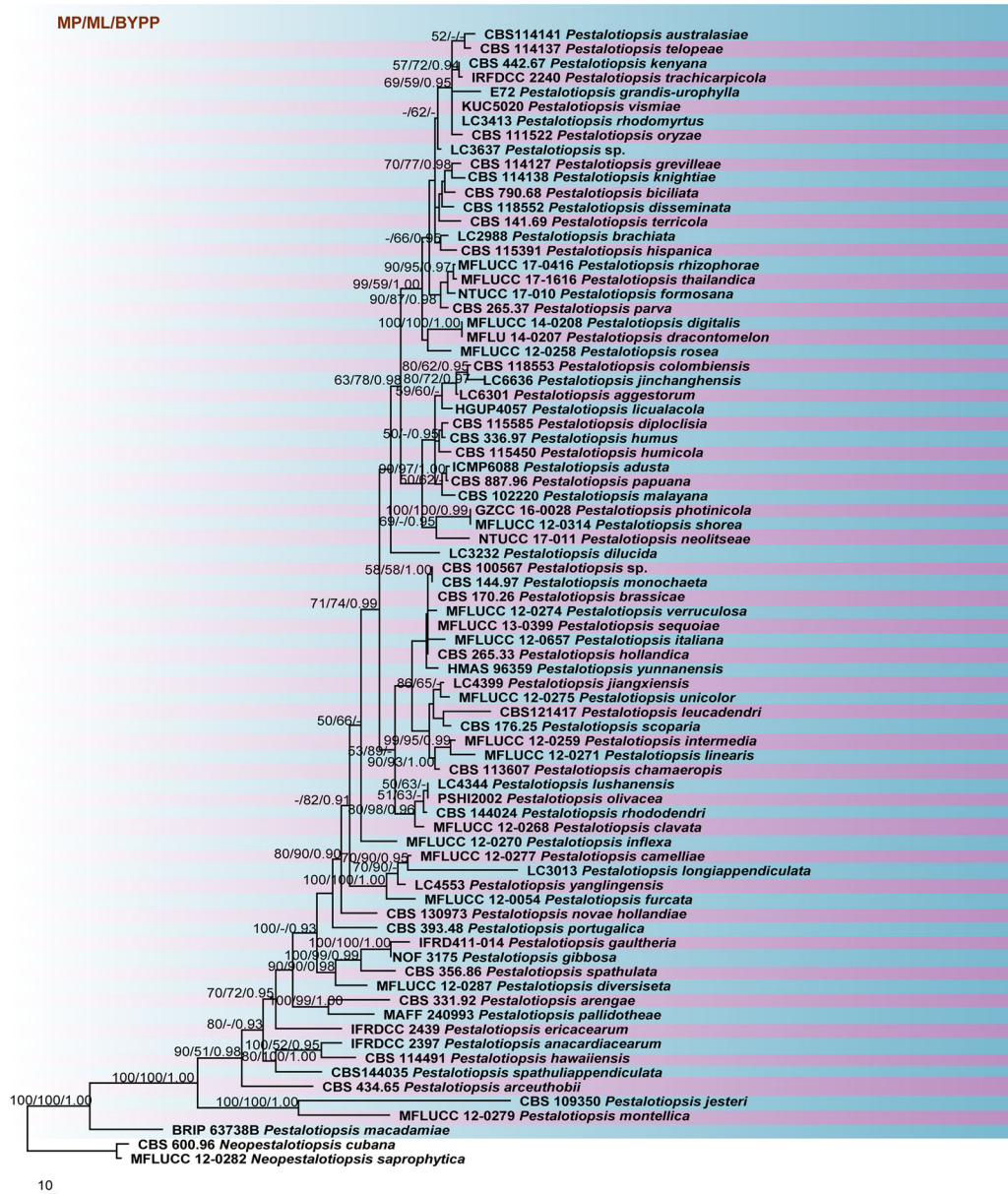
| Species                         | Isolate/voucher no     | ITS      | <i>tef1</i> |
|---------------------------------|------------------------|----------|-------------|
| <i>Lasiodiplodia avicenniae</i> | <b>CBS 139670*</b>     | KP860835 | KP860680    |
| <i>L. avicenniarum</i>          | <b>MFLUCC 17-2591*</b> | MK347777 | MK340867    |
| <i>L. brasiliense</i>           | <b>CMM 4015*</b>       | JX464063 | JX464049    |
| <i>L. bruguierae</i>            | <b>CBS 139669*</b>     | KP860832 | KP860677    |
| <i>L. caatinguensis</i>         | <b>CMM 1325*</b>       | KT154760 | KT008006    |
| <i>L. chinensis</i>             | <b>CGMCC 3.18061*</b>  | KX499889 | KX499927    |
| <i>L. chonburiensis</i>         | <b>MFLUCC 16-0376*</b> | MH275066 | MH412773    |
| <i>L. cinnamomi</i>             | <b>CFCC 51997*</b>     | MG866028 | MH236799    |
| <i>L. citricola</i>             | <b>CBS 124707*</b>     | GU945354 | GU945340    |
| <i>L. crassispora</i>           | <b>CBS 118741*</b>     | DQ103550 | EU673303    |
| <i>L. euphorbiicola</i>         | <b>CMM 3609*</b>       | KF234543 | KF226689    |
| <i>L. exigua</i>                | <b>CBS 137785*</b>     | KJ638317 | KJ638336    |
| <i>L. gilanensis</i>            | <b>CBS 124704*</b>     | GU945351 | GU945342    |
| <i>L. gonubiensis</i>           | <b>CBS 115812*</b>     | AY639595 | DQ103566    |
| <i>L. gravistriata</i>          | <b>CMM 4564*</b>       | KT250949 | KT250950    |
| <i>L. hormozganensis</i>        | <b>CBS 124709*</b>     | GU945355 | GU945343    |
| <i>L. hyalina</i>               | <b>CGMCC 3.17975*</b>  | KX499879 | KX499917    |
| <i>L. iraniensis</i>            | <b>CBS 124710*</b>     | GU945346 | GU945334    |
| <i>L. laeliocattleyae</i>       | <b>CBS 167.28*</b>     | KU507487 | KU507454    |
| <i>L. lignicola</i>             | <b>CBS 134112*</b>     | JX646797 | KU887003    |
| <i>L. macrospora</i>            | <b>CMM 3833*</b>       | KF234557 | KF226718    |
| <i>L. mahajangana</i>           | <b>CBS 124925*</b>     | FJ900595 | FJ900641    |
| <i>L. margaritacea</i>          | <b>CBS 122519*</b>     | EU144050 | EU144065    |
| <i>L. mediterranea</i>          | <b>CBS 137783*</b>     | KJ638312 | KJ638331    |
| <i>L. missouriana</i>           | <b>CBS 128311*</b>     | HQ288225 | HQ288267    |
| <i>L. pandanicola</i>           | <b>MFLUCC 16-0265*</b> | MH275068 | MH412774    |
| <i>L. parva</i>                 | <b>CBS 456.78*</b>     | EF622083 | EF622063    |
| <i>L. plurivora</i>             | <b>CBS 120832*</b>     | EF445362 | EF445395    |
| <i>L. pontae</i>                | <b>CMM 1277*</b>       | KT151794 | KT151791    |
| <i>L. pseudotheobromae</i>      | <b>CBS 116459*</b>     | EF622077 | EF622057    |
| <i>L. pyriformis</i>            | <b>CBS 121770*</b>     | EU101307 | EU101352    |
| <i>L. rubropurpurea</i>         | <b>CBS 118740*</b>     | DQ103553 | EU673304    |
| <i>L. sterculiae</i>            | <b>CBS 342.78*</b>     | KX464140 | KX464634    |
| <i>L. subglobosa</i>            | <b>CMM 3872*</b>       | KF234558 | KF226721    |
| <i>L. swieteniae</i>            | <b>MFLUCC 18-0244*</b> | MK347789 | MK340870    |
| <i>L. thailandica</i>           | <b>CBS 138760*</b>     | KJ193637 | KJ193681    |
| <i>L. theobromae</i>            | <b>CBS 164.96*</b>     | AY640255 | AY640258    |
| <i>L. venezuelensis</i>         | <b>CBS 118739*</b>     | DQ103547 | EU673305    |
| <i>L. viticola</i>              | <b>CBS 128313*</b>     | HQ288227 | HQ288269    |
| <i>L. vitis</i>                 | <b>CBS 124060*</b>     | KX464148 | KX464642    |

Ex-type (ex-epitype) strains are in bold and marked with an asterisk\* and voucher stains are in bold

### Morphological based identification and diversity

*Stagonosporopsis* is characterized by ellipsoidal to subglobose, aseptate to 3 septate conidia and sexual morph with ellipsoidal, fusiform or obovoid, 1 septate ascospore (Aveskamp et al. 2010; Chen et al. 2015). *Stagonosporopsis* was originally separated from *Ascochyta*

by Diedicke (1912) based on the occasional formation of multi-septate (*Stagonospora*-like) conidia. In the phylogenetic reassessment of *Didymellaceae* (Aveskamp et al. 2010) based on the sequences LSU and ITS of the nrDNA and TUB2 region, multiple *Phoma* species, including *P. ligulicola*, were recovered in a high supported clade with the interpretive types of the genus *Stagonosporopsis*; *S.*



**Fig. 30** Phylogram generated from RAxML analysis based on combined ITS, TUB2 and *tefl* sequences of all the accepted species of *Pestalotiopsis*. Related sequences were obtained from GenBank. Seventy-nine taxa are included in the analyses, which comprise 1581 characters including gaps. The tree was rooted in *Neopestalotiopsis cubana* (CBS 600.96) and *N. saprophytica* (MFLUCC 12-0282). Tree topology of the ML analysis was similar to the BYPP and MP. The best scoring RAxML tree with a final likelihood value of -12269.881063 is presented. The matrix had 763 distinct alignment patterns, with 15.79% of undetermined characters or gaps. Estimated base frequencies were as follows; A = 0.234129, C = 0.293516,

G = 0.211518, T = 0.260837; substitution rates AC = 1.189917, AG = 3.402399, AT = 1.153875, CG = 1.001451, CT = 4.301074, GT = 1.000000; gamma distribution shape parameter  $\alpha$  = 0.283001. The maximum parsimonious dataset consisted of 948 constant, 450 parsimony-informative and 183 parsimony-uninformative characters. The parsimony analysis of the data matrix resulted in the maximum of ten equally most parsimonious trees with a length of 1962 steps (CI = 0.498, RI = 0.697, RC = 0.347, HI = 0.502) in the first tree. RAxML and maximum parsimony bootstrap support value  $\geq 50\%$  and BYPP  $\geq 0.90$  values are shown near the nodes. The scale bar indicates 10 changes per site. The ex-type strains are in bold

*actaeae* (Boerema 1997, Boerema et al. 2004). In addition, *S. tanacetii* shows morphological similarity to *S. inoxydabilis* but can be differentiated by the faster growth rate, larger conidia, presence of chlamydospores, and lack of ascumata in culture (Vaghefi et al. 2012). Morphological

characters overlap between the species in this genus and species are primarily separated based on molecular data.

### Molecular based identification and diversity

Most comprehensive multigene phylogeny analyses for this genus were performed by Aveskamp et al. (2010), Vaghefi

**Table 20** Details of *Pestalotiopsis* the isolates used in the phylogenetic analyses

| Species                      | Isolate/voucher no | ITS        | TUB2     | <i>tefl</i> |
|------------------------------|--------------------|------------|----------|-------------|
| <i>Pestalotiopsis adusta</i> | ICMP 6088*         | JX399006   | JX399037 | JX399070    |
| <i>P. aggestorum</i>         | LC6301*            | KX895015   | KX895348 | KX895234    |
| <i>P. anacardiacearum</i>    | IFRDCC 2397*       | NR120255.1 | KC247155 | KC247156    |
| <i>P. arceuthobii</i>        | CBS 434.65*        | NR147561   | KM199427 | KM199516    |
| <i>P. arengae</i>            | CBS 331.92*        | NR147560   | KM199426 | KM199515    |
| <i>P. australasiae</i>       | CBS 114126*        | NR147546   | KM199409 | KM199499    |
| <i>P. australis</i>          | CBS 114193*        | KM199332   | KM199383 | KM199475    |
| <i>P. biciliata</i>          | CBS 124463*        | KM199308   | KM199399 | KM199505    |
| <i>P. brachiata</i>          | LC2988*            | KX894933   | KX895265 | KX895150    |
| <i>P. brassicae</i>          | CBS170.26*         | NR147562   | –        | KM199558    |
| <i>P. camelliae</i>          | MFLUCC12-0277*     | NR120188   | JX399041 | JX399074    |
| <i>P. chamaeropsis</i>       | CBS 186.71*        | KM199326   | KM199391 | KM199473    |
| <i>P. clavata</i>            | MFLUCC12-0268*     | JX398990   | JX399025 | JX399056    |
| <i>P. colombiensis</i>       | CBS 118553*        | NR147551   | KM199421 | KM199488    |
| <i>P. digitalis</i>          | ICMP 5434*         | KP781879   | KP781883 | –           |
| <i>P. dilucida</i>           | LC3232*            | KX894961   | KX895293 | KX895178    |
| <i>P. diplocisiae</i>        | CBS 115587*        | NR147552   | KM199419 | KM199486    |
| <i>P. diversiseta</i>        | MFLUCC12-0287*     | NR120187   | JX399040 | JX399073    |
| <i>P. dracontomelon</i>      | MFUCC 10-0149*     | KP781877   | –        | KP781880    |
| <i>P. ericacearum</i>        | IFRDCC 2439*       | KC537807   | KC537821 | KC537814    |
| <i>P. formosana</i>          | NTUCC 17-009*      | MH809381   | MH809385 | MH809389    |
| <i>P. furcata</i>            | MFLUCC12-0054*     | JQ683724   | JQ683708 | JQ683740    |
| <i>P. gaultheria</i>         | IFRD 411-014*      | KC537805   | KC537819 | KC537812    |
| <i>P. gibbosa</i>            | NOF3175*           | LC311589   | LC311590 | LC311591    |
| <i>P. grevilleae</i>         | CBS 114127*        | NR147548   | KM199407 | KM199504    |
| <i>P. hawaiiensis</i>        | CBS 114491*        | NR147559   | KM199428 | KM199514    |
| <i>P. hollandica</i>         | CBS 265.33*        | KM199328   | KM199388 | KM199481    |
| <i>P. humus</i>              | CBS 336.97*        | KM199317   | KM199420 | KM199484    |
| <i>P. inflexa</i>            | MFLUCC12-0270*     | JX399008   | JX399039 | JX399072    |
| <i>P. intermedia</i>         | MFLUCC12-0259*     | JX398993   | JX399028 | JX399059    |
| <i>P. italiana</i>           | MFLUCC12-0657*     | KP781878   | KP781882 | KP781881    |
| <i>P. jester</i>             | CBS 109350*        | KM199380   | KM199468 | KM199554    |
| <i>P. jiangxiensis</i>       | LC4399*            | KX895009   | KX895341 | KX895227    |
| <i>P. jinchangensis</i>      | LC6636*            | KX895028   | KX895361 | KX895247    |
| <i>P. kenya</i>              | CBS 442.67*        | KM199302   | KM199395 | KM199502    |
| <i>P. knightiae</i>          | CBS 114138*        | KM199310   | KM199408 | KM199497    |
| <i>P. licualacola</i>        | HGUP 4057*         | KC492509   | KC481683 | KC481684    |
| <i>P. linearis</i>           | MFLUCC12-0271*     | JX398992   | JX399027 | JX399058    |
| <i>P. longiappendiculata</i> | LC3013*            | KX894939   | KX895271 | KX895156    |
| <i>P. lushanensis</i>        | LC4344*            | KX895005   | KX895337 | KX895223    |
| <i>P. macadamiae</i>         | BRIP 63738b*       | KX186588   | KX186680 | KX186621    |
| <i>P. malayana</i>           | CBS 102220*        | NR147550   | KM199411 | KM199482    |
| <i>P. monochaeta</i>         | CBS 144.97*        | KM199327   | KM199386 | KM199479    |
| <i>P. montellica</i>         | MFLUCC12-0279*     | JX399012   | JX399043 | JX399076    |
| <i>P. neolütseae</i>         | NTUCC 17-011*      | MH809383   | MH809387 | MH809391    |
| <i>P. novae-hollandiae</i>   | CBS 130973*        | NR147557   | KM199425 | KM199511    |
| <i>P. olivaceae</i>          | PSHI2002*          | AY687883   | DQ333580 | –           |
| <i>P. oryzae</i>             | CBS 353.69*        | KM199299   | KM199398 | KM199496    |
| <i>P. pallidotheae</i>       | MAFF 240993*       | NR111022   | LC311584 | LC311585    |
| <i>P. papuana</i>            | CBS 887.96*        | KM199318   | KM199415 | KM199492    |

**Table 20** (continued)

| Species                   | Isolate/voucher no    | ITS      | TUB2     | <i>tefl</i> |
|---------------------------|-----------------------|----------|----------|-------------|
| <i>P. parva</i>           | <b>CBS 265.37*</b>    | KM199312 | KM199404 | KM199508    |
| <i>P. photinicola</i>     | <b>GZCC 16-0028*</b>  | KY092404 | KY047663 | KY047662    |
| <i>P. portugalia</i>      | <b>CBS 393.48*</b>    | KM199335 | KM199422 | KM199510    |
| <i>P. rhizophorae</i>     | <b>MFLUCC17-0416*</b> | MK764283 | MK764349 | MK764327    |
| <i>P. rhododendri</i>     | <b>IFRDCC 2399*</b>   | NR120265 | KC537818 | KC537811    |
| <i>P. rhodomyrtus</i>     | <b>HGUP 4230*</b>     | KF412648 | KF412642 | KF412645    |
| <i>P. rosea</i>           | <b>MFLUCC12-0258*</b> | JX399005 | JX399036 | JX399069    |
| <i>P. scoparia</i>        | <b>CBS 176.25*</b>    | KM199330 | KM199393 | KM199478    |
| <i>P. shorea</i>          | <b>MFLUCC12-0314*</b> | KJ503811 | KJ503814 | KJ503817    |
| <i>P. spathulata</i>      | <b>CBS 356.86*</b>    | NR147558 | KM199423 | KM199513    |
| <i>P. telopeae</i>        | <b>CBS 114161*</b>    | NR147545 | KM199403 | KM199500    |
| <i>P. thailandica</i>     | <b>MFLUCC17-1616*</b> | MK764285 | MK764351 | MK764329    |
| <i>P. trachicarpicola</i> | <b>IFRDCC 2440*</b>   | NR120109 | JQ845945 | JQ845946    |
| <i>P. unicolor</i>        | <b>MFLUCC12-0276*</b> | JX398999 | JX399030 | –           |
| <i>P. verruculosa</i>     | <b>MFLUCC12-0274*</b> | NR120185 | –        | JX399061    |
| <i>P. yanglingensis</i>   | <b>LC4553*</b>        | KX895012 | KX895345 | KX895231    |
| <i>P. yunnanensis</i>     | <b>HMAS 96359*</b>    | AY373375 | –        | –           |

Ex-type (ex-epitype) strains are in bold and marked with an asterisk\* and voucher stains are in bold

et al. (2012), Hyde et al. (2014), Chen et al. (2015, 2017) and Jayasiri et al. (2019). Five-marker phylogeny of the *Stagonosporopsis* spp. for which these DNA sequence data are available is shown (Table 21).

Identification of *Stagonosporopsis* species associated with ray blight of *Asteraceae* can be achieved through multi-locus sequence typing (Aveskamp et al. 2010; Vaghefi et al. 2012) and also with a species-specific multiplex PCR assay developed by Vaghefi et al. (2016). This assay is based on a four-primer PCR that targets the intergenic spacer of the nrDNA of the ray blight pathogens, producing species-specific amplicons of ~ 560 in *S. chrysanthemi*, ~ 630 bp in *S. inoxydabilis* and ~ 400 bp in *S. tanacetii*, which can be easily differentiated on an agarose gel (Vaghefi et al. 2016).

This study reconstructs the phylogeny of *Stagonosporopsis* based on analyses of a combined ITS, LSU, RPB2 and TUB2 sequence data (Fig. 31). The phylogenetic tree is updated with recently introduced *Stagonosporopsis* species and corresponds to previous studies (Chen et al. 2017, Jayasiri et al. 2019).

*Recommended genetic marker (genus level)*—ITS

*Recommended genetic markers (species level)*—TUB2 and RPB2

*Accepted number of species:* There are 55 species in Index Fungorum (2019) and only 24 species are accepted/ have molecular data in this genus.

*References:* Chen et al. 2015, 2017, Jayasiri et al. 2019 (morphology, phylogeny).

*Verticillium* Nees, Syst. Pilze (Würzburg): 57 (1816) [1816-17]

The genus *Verticillium* Nees was introduced by Nees von Esenbeck (1816) for a single saprotrophic species, *V. tenerum* Nees, which was proposed as the type species. Zare et al. (2004) synonymized *V. tenerum* under *Acrostalagmus luteoalbus* (Link) Zare, W. Gams & Schroers, and Gams et al. (2005) proposed *V. dahliae* Kleb. as the conserved type of the genus *Verticillium*.

*Verticillium* includes several plant pathogenic species that infect trees, insects, mushrooms and, in particular, dicotyledonous plants: *V. dahliae* Kleb., *V. albo-atrum* Reinke et Berth., *V. nigrescens* Pethybr., *V. nubilum* Pethybr., *V. tricorpus* Isaac., *V. theobromae* (Turc.) Mas. & Hughes and *V. fungicola* (Preuss) Hassebrauk (Pegg and Brady 2002). Zare et al. (2007) assigned *V. nigrescens* to the genus *Gibellulopsis* and *V. theobromae* to *Musciellium*. Zare and Gams (2008) assigned *V. fungicola* to the genus *Lecanillium*. *Verticillium dahliae* and *V. albo-atrum* are the two most notorious species which cause *Verticillium* wilt diseases in a wide range of mainly dicotyledonous hosts and result in billions of dollars of damage annually in crop losses worldwide (Pegg and Brady 2002; Barbara and Clewes 2003; Inderbitzin et al. 2011).

*Verticillium* species, in particular, *V. dahliae* and *V. albo-atrum*, can infect a wide range of plant species. Many hosts of *Verticillium* species were given by different mycologists, e.g., Van der Meer (1925); Rudolph (1931); Engelhard and Carter (1956); Parker (1959); Stark (1961); Devaux and Sackston (1966); Himelick (1969), including

high-value crop plants, e.g., cotton (Land et al. 2016), lettuce (Garibaldi et al. 2007; Powell et al. 2013), mango (Baeza-Montanez et al. 2010; Ahmed et al. 2014), gold kiwifruit (Auger et al. 2009), bean (Berbegal and Armen-gol 2009; Sun et al. 2016; Blomquist et al. 2017), water-melon (Bruton et al. 2007), olive tree (Lo Giudice et al. 2010; Kaliterna et al. 2016), potato (Pace-Lupi et al. 2006), pumpkin (Rampersad 2008). The most comprehensive hosts' list was provided by Pegg and Brady (2002).

**Classification**—Sordariomycetes, Hypocreomycetidae, Glomerellales, Plectosphaerellaceae

**Type species**—*Verticillium dahliae* Kleb., Mykol. Zentbl. 3: 66 (1913)

**Distribution**—Worldwide

**Disease symptoms**—Wilt

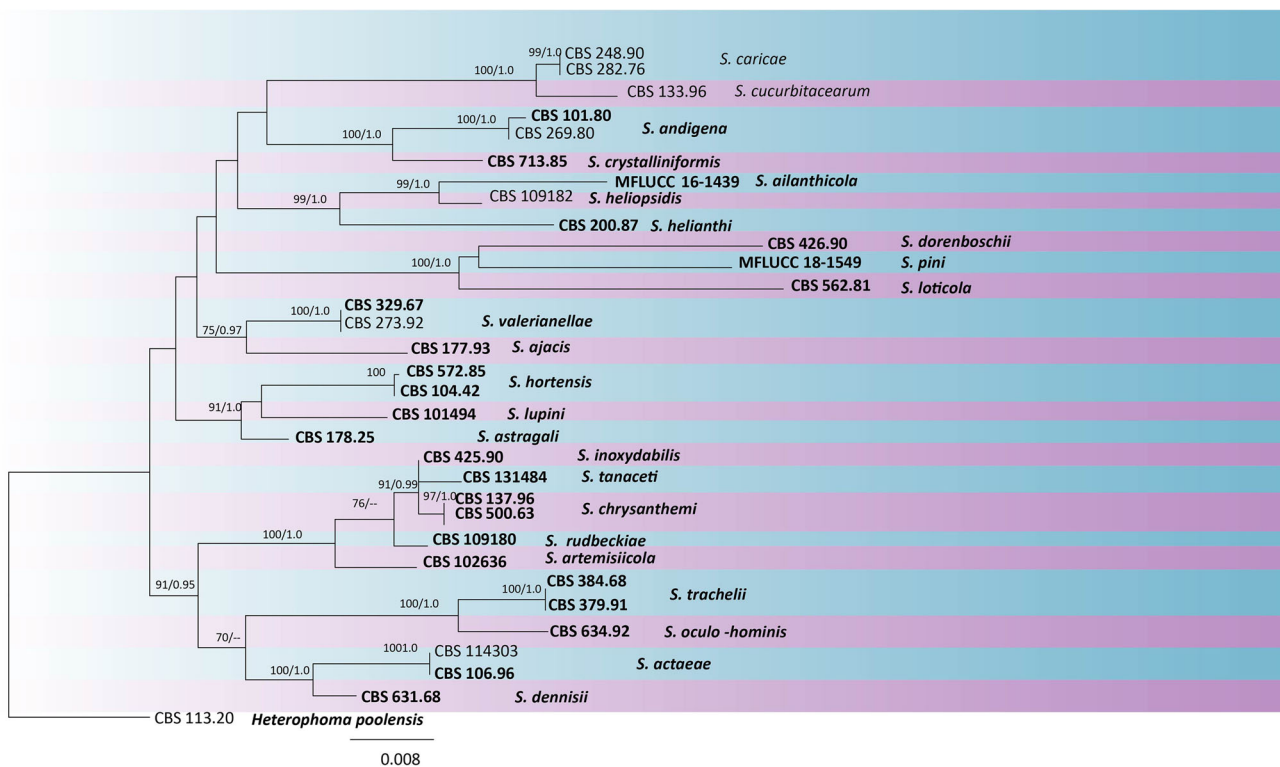
Wilt caused by *Verticillium* species is a serious fungal disease that causes injury or death to many plant species. Symptoms of this disease vary according to the host species and to environmental conditions including sudden wilting of small branches, yellowing of foliage, stunt

growth and premature defoliation. Olive- green to black streaks can be observed in the sapwood of infected branches. In cross sections, vascular tissue appears as a dark ring or pinpoint dark spots. Initial symptoms can occur on one side of the tree or the entire plant (Fradin and Thomma 2006; Blum et al. 2018).

**Hosts**—Species of this genus have a broad host range including members of *Amaranthaceae*, *Amaryllidaceae*, *Asteraceae*, *Brassicaceae*, *Musaceae*, *Pinaceae*, *Rosaceae*, *Rubiaceae*, *Sapindaceae*, *Solanaceae*, *Theaceae*, *Vitaceae* and *Zingiberaceae* (Farr and Rossman 2019).

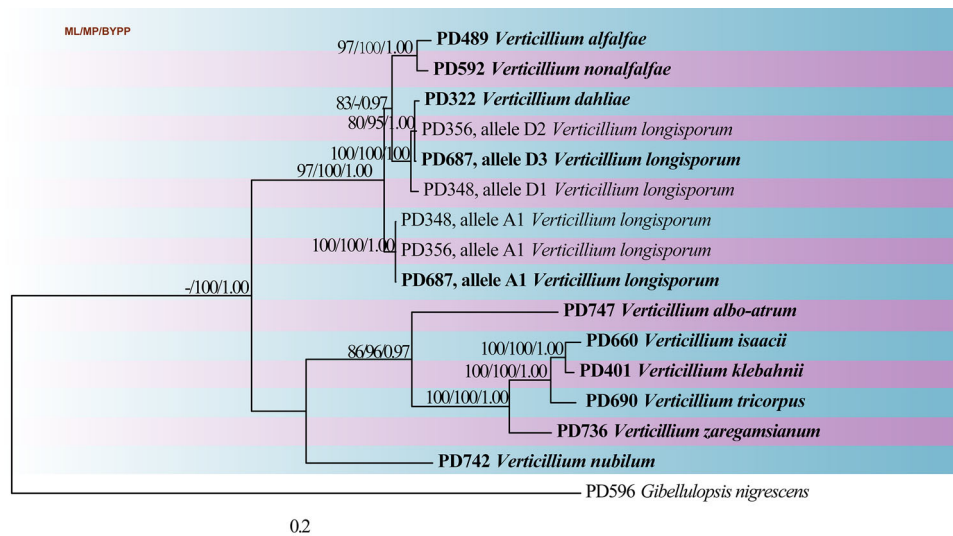
### Morphological based identification and diversity

There are 270 records in Index Fungorum (2019) and 288 records in MycoBank (Crous et al. 2004) in this genus. Most of the species have been transferred to other genera, e.g., *Gibellulopsis* (Zare et al. 2007), *Haptocillium* (Zare and Gams 2001b), *Lecanicillium* (Zare and Gams 2001a), *Musiccillium* (Zare et al. 2007), *Pochonia* (Zare and Gams 2001a, b), *Simplicillium* (Zare and Gams 2001a). Only ten



**Fig. 31** Phylogenetic tree generated by maximum likelihood analysis of combined ITS, LSU, RPB2 and TUB2 sequence data of *Stagonosporopsis* species. Related sequences were obtained from GenBank. Thirty-two are included in the analyses, which comprise 2756 characters including gaps. Single gene analyses were carried out and compared with each species, to compare the topology of the tree and clade stability. The tree was rooted with *Heterophoma poolensis* (CBS 113.20). Tree topology of the ML analysis was similar to the MP. The best scoring RAxML tree with a final likelihood value of

– 8386.622374 is presented. The matrix had 388 distinct alignment patterns, with 11.83% of undetermined characters or gaps. Estimated base frequencies were as follows; A = 0.245798, C = 0.237676, G = 0.273178, T = 0.243348; substitution rates AC = 1.882600, AG = 4.123164, AT = 2.015920, CG = 0.907833, CT = 12.626910, GT = 1.000000; gamma distribution shape parameter  $\alpha = 1.105097$ . RAxML bootstrap support values  $\geq 50\%$  and Bayesian posterior probabilities  $\geq 0.95$  (BYPP) are shown respectively near the nodes. Ex-type strains are in bold



**Fig. 32** Phylogenetic tree generated from Bayesian analysis based on combined ACT, *tef1*, GPD and TS sequence data for the genus *Verticillium*. Sixteen strains are included in the combined genes sequence analyses which comprise total of 2597 characters (609 characters for the ACT, 620 characters for *tef1*, 744 characters for GPD, 624 characters for TS) after alignment. For the Bayesian analysis, two parallel runs with six chains were run for 1,000,000 generations and trees were sampled every 100th generation, resulted

in 20,002 trees from two runs of which 15,002 trees were used to calculate the posterior probabilities (each run resulted in 10,001 trees of which 7501 trees were sampled). Bootstrap support values for maximum likelihood (ML, first set) and maximum parsimony (MP, second set) greater than 75% and Bayesian posterior probabilities greater than 0.95 are indicated above or below the nodes. Ex-type strains are in bold. The tree is rooted with *Gibellulopsis nigrescens* (PD596)

species, *V. albo-atrum*, *V. alfalfae*, *V. dahliae*, *V. isaacii*, *V. klebahnii*, *V. longisporum*, *V. nonalfalfae*, *V. nubilum*, *V. tricorpus* and *V. zaregamsianum*, were accepted within *Verticillium sensu stricto* (Inderbitzin et al. 2011). No sexual states are known. Descriptions and a key to these ten species were provided by Inderbitzin et al. (2011).

### Molecular based identification and diversity

The first phylogenetic analysis of *Verticillium* species was made by Morton et al. (1995) to analysis the relationship between *V. albo-atrum* and *V. dahliae* based on the internal transcribed spacer regions and intervening 5.8S rDNA (ITS) sequences data (Fig. 32, Table 22). Subsequently, SSU, LSU, RNA polymerase II largest subunit gene

(RPB1), the cytochrome oxidase subunit III gene (*cox3*), the small ribosomal rRNA subunit (*rns*), NADH dehydrogenase subunit genes (*nad1* and *nad3*) were used (Barbara and Clewes 2003; Pantou et al. 2005; Zare and Gams 2008, 2016).

*Recommended genetic marker (genus level)*—LSU

*Recommended genetic marker (species level)*—ITS

*Accepted number of species: 10 species.*

*References:* Inderbitzin et al. 2011 (morphology and phylogeny); Barbara and Clewes 2003, Morton et al. 1995, Pantou et al. 2005, Zare and Gams 2008, 2016 (phylogeny); Fradin and Thomma 2006, Blum et al. 2018 (pathogenicity)

**Table 21** Details of the *Stagonosporopsis* isolates used in the phylogenetic analyses

| Species                         | Culture                | LSU      | GenBank Accession numbers |          | TUB2     |
|---------------------------------|------------------------|----------|---------------------------|----------|----------|
|                                 |                        |          | ITS                       | RPB2     |          |
| <i>Stagonosporopsis actaeae</i> | <b>CBS 106.96*</b>     | GU238166 | GU237734                  | KT389672 | GU237671 |
|                                 | CBS 114303             | KT389760 | KT389544                  | –        | KT389847 |
| <i>S. ailanthicola</i>          | <b>MFLUCC 16-1439*</b> | KY100874 | KY100872                  | KY100876 | KY100878 |
| <i>S. ajacis</i>                | <b>CBS 177.93*</b>     | GU238168 | GU237791                  | KT389673 | GU237673 |
| <i>S. andigena</i>              | CBS 269.80             | GU238170 | GU237817                  | –        | GU237675 |
|                                 | <b>CBS 101.80</b>      | GU238169 | GU237714                  | –        | GU237674 |
| <i>S. artemisiicola</i>         | <b>CBS 102636</b>      | GU238171 | GU237728                  | KT389674 | GU237676 |
| <i>S. astragali</i>             | <b>CBS 178.25</b>      | GU238172 | GU237792                  | –        | GU237677 |
| <i>S. caricae</i>               | CBS 248.90             | GU238175 | GU237807                  | –        | GU237680 |
|                                 | CBS 282.76             | GU238177 | GU237821                  | –        | GU237682 |
| <i>S. chrysanthemi</i>          | <b>CBS 500.63</b>      | GU238190 | GU237871                  | –        | GU237695 |
|                                 | <b>CBS 137.96</b>      | GU238191 | GU237783                  | –        | GU237696 |
| <i>S. crystalliniformis</i>     | <b>CBS 713.85*</b>     | GU238178 | GU237903                  | KT389675 | GU237683 |
| <i>S. cucurbitacearum</i>       | CBS 133.96             | GU238181 | GU237780                  | KT389676 | GU237686 |
| <i>S. dennisii</i>              | <b>CBS 631.68*</b>     | GU238182 | GU237899                  | KT389677 | GU237687 |
| <i>S. dorenboschii</i>          | <b>CBS 426.90*</b>     | GU238185 | GU237862                  | KT389678 | GU237690 |
| <i>S. helianthi</i>             | <b>CBS 200.87*</b>     | KT389761 | KT389545                  | KT389683 | KT389848 |
| <i>S. heliopsisidis</i>         | <b>CBS 109182</b>      | GU238186 | GU237747                  | KT389679 | GU237691 |
| <i>S. hortensis</i>             | <b>CBS 104.42</b>      | GU238198 | GU237730                  | KT389680 | GU237703 |
|                                 | <b>CBS 572.85</b>      | GU238199 | GU237893                  | KT389681 | GU237704 |
| <i>S. inoxydabilis</i>          | <b>CBS 425.90*</b>     | GU238188 | GU237861                  | KT389682 | GU237693 |
| <i>S. loticola</i>              | <b>CBS 562.81*</b>     | GU238192 | GU237890                  | KT389684 | GU237697 |
| <i>S. lupini</i>                | <b>CBS 101494*</b>     | GU238194 | GU237724                  | KT389685 | GU237699 |
| <i>S. oculohominis</i>          | <b>CBS 634.92*</b>     | GU238196 | GU237901                  | KT389686 | GU237701 |
| <i>S. pini</i>                  | <b>MFLUCC 18-1549*</b> | MK348019 | MK347800                  | MK434860 | –        |
| <i>S. rudbeckiae</i>            | <b>CBS 109180</b>      | GU238197 | GU237745                  | –        | GU237702 |
| <i>S. tanacetii</i>             | <b>CBS 131484*</b>     | JQ897461 | NR_111724                 | –        | JQ897496 |
| <i>S. trachelii</i>             | <b>CBS 379.71</b>      | GU238173 | GU237850                  | KT389687 | GU237678 |
|                                 | <b>CBS 384.68</b>      | GU238174 | GU237856                  | –        | GU237679 |
| <i>S. valerianellae</i>         | CBS 273.92             | GU238200 | GU237819                  | –        | GU237705 |
|                                 | <b>CBS 329.67*</b>     | GU238201 | GU237832                  | –        | GU237706 |



**Table 22** GenBank accession numbers of *Verticillium* isolates included in this study

| Taxa                           | Strains | Haplotype | ACT      | <i>tefl</i> | GPD      | TS       |
|--------------------------------|---------|-----------|----------|-------------|----------|----------|
| <i>Verticillium albo-atrum</i> | PD747   |           | JN188144 | JN188272    | JN188208 | JN188080 |
| <i>V. alfalfa</i>              | PD489   |           | JN188097 | JN188225    | JN188161 | JN188033 |
| <i>V. dahlia</i>               | PD322   |           | HQ206921 | HQ414624    | HQ414719 | HQ414909 |
| <i>V. isaacii</i>              | PD660   |           | HQ206985 | HQ414688    | HQ414783 | HQ414973 |
| <i>V. klebahnii</i>            | PD401   |           | JN188093 | JN188221    | JN188157 | JN188029 |
| <i>V. longisporum</i>          | PD348   | a1        | HQ206930 | HQ414633    | HQ414728 | HQ414918 |
| <i>V. longisporum</i>          | PD348   | d1        | HQ206931 | HQ414634    | HQ414729 | HQ414919 |
| <i>V. longisporum</i>          | PD356   | a1        | HQ206934 | HQ414637    | HQ414732 | HQ414922 |
| <i>V. longisporum</i>          | PD356   | d2        | HQ206935 | HQ414638    | HQ414733 | HQ414923 |
| <i>V. longisporum</i>          | PD687   | a1        | HQ206993 | HQ414696    | HQ414791 | HQ414981 |
| <i>V. longisporum</i>          | PD687   | d2        | HQ206994 | HQ414697    | HQ414792 | HQ414982 |
| <i>V. nonalfalfae</i>          | PD592   |           | JN188099 | JN188227    | JN188163 | JN188035 |
| <i>V. nubilum</i>              | PD742   |           | JN188139 | JN188267    | JN188203 | JN188075 |
| <i>V. tricorpus</i>            | PD690   |           | JN188121 | JN188249    | JN188185 | JN188057 |
| <i>V. zaregamsianum</i>        | PD736   |           | JN188133 | JN188261    | JN188197 | JN188069 |

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