Evolution of lifestyles in Capnodiales

J. Abdollahzadeh1, J.Z. Groenewald2, M.P.A. Coetzee3, M.J. Wingfield2, and P.W. Crous2,3,4*  

1Department of Plant Protection, Agriculture Faculty, University of Kurdistan, P.O. Box 416, Sanandaj, Iran; 2Westerdijk Fungal Biodiversity Institute, P.O. Box 85167, Utrecht, 3508 AD, the Netherlands; 3Department of Biochemistry, Genetics & Microbiology, Forestry & Agricultural Biotechnology Institute (FABI), University of Pretoria, Pretoria, South Africa; 4Wageningen University and Research Centre (WUR), Laboratory of Phytopathology, Droevendaalsesteeg 1, Wageningen, 6708 PB, the Netherlands

*Correspondence: J. Abdollahzadeh, jabdollahzadeh@uok.ac.ir; P.W. Crous, p.crous@wur.nl

Abstract: The Capnodiales, which includes fungi known as the sooty moulds, represents the second largest order in Dothideomycetes, encompassing morphologically and ecologically diverse fungi with different lifestyles and modes of nutrition. They include saprobes, plant and human pathogens, mycoparasites, rock-inhabiting fungi (RIF), ichenised, ep-, ecto- and endophytes. The aim of this study was to elucidate the lifestyles and evolutionary patterns of the Capnodiales as well as to reconsider their phylogeny by including numerous new collections of sooty moulds, and using four nuclear loci, LSU, ITS, TEF-1α and RPB2. Based on the phylogenetic results, combined with morphology and ecology, Capnodiales s. lat. is shown to be polyphyletic, representing seven different orders. The sooty moulds are restricted to Capnodiales s. str., while Mycosphaerellales is resurrected, and five new orders including Cladosporiales, Comminutisporales, Neophaeothecales, Phaeothecales and Raccodiales are introduced. Four families, three genera, 21 species and five combinations are introduced as new. Furthermore, ancestral reconstruction analysis revealed that the saprobic lifestyle is a primitive state in Capnodiales s. lat., and that several transitions have occurred to evolve lichenised, plant and human parasitic, ectophytic (sooty blotch and flyspeck) and more recently epiphytic (sooty mould) lifestyles.

Key words: Capnodiales, Cladosporium, Mycosphaerella, Multigene phylogeny, Sooty moulds.

Taxonomic novelties: New orders: Cladosporiales Abdollahz. & Crous, Comminutisporales Abdollahz. & Crous, Neophaeothecales Abdollahz. & Crous, Phaeothecales Abdollahz. & Crous, Raccodiales Abdollahz. & Crous.

New families: Comminutisporaceae Abdollahz. & Crous, Neophaeothecaceae Abdollahz. & Crous, Phaeothecaceae Abdollahz. & Crous, Readeriellopsidaceae Abdollahz. & Crous.

New genera: Neocannellaria Abdollahz. & Crous, Neosabolasia Abdollahz. & Crous, Neophaeotheca Abdollahz. & Crous.

New species: Capnodium affinis Abdollahz. & Crous, Capnodium blackwelliae Abdollahz. & Crous, Capnodium gansei Abdollahz. & Crous, Capnodium neocoffeicola Abdollahz. & Crous, Capnodium paracoffeicola Abdollahz. & Crous, Chaetocapnodium summerrelli Abdollahz. & Crous, Chaetocapnodium indonesiacum Abdollahz. & Crous, Chaetocapnodium insulare Abdollahz. & Crous, Chaetocapnodium thailandense Abdollahz. & Crous, Leptosyphium citri Abdollahz. & Crous, Neocannellaria phylicae Abdollahz. & Crous, Neosabolasia phylicae Abdollahz. & Crous, Phaeothyriella australiana Abdollahz. & Crous, Phaeothyriella phylicae Abdollahz. & Crous, Solecoryxophium blechni Abdollahz. & Crous, Solecoryxophium blechnicola Abdollahz. & Crous, Solecoryxophium leucadendri Abdollahz. & Crous, Solecoryxophium phylicae Abdollahz. & Crous, Scoris aphidis Abdollahz. & Crous, Scoris camelliae Abdollahz. & Crous.

New combinations: Chaetocapnodium philippinense (Hongsanan & K.D. Hyde) Abdollahz. & Crous, Chaetocapnodium picta (Cheewangkoon & Crous) Abdollahz. & Crous, Neophaeotheca salicorniae (Crous & Roets) Abdollahz. & Crous, Neophaeotheca triangularis (de Hoog & Begum) Abdollahz. & Crous, Phragmocapnia plumieri (Hongsanan & K.D. Hyde) Abdollahz. & Crous.

Available online 5 March 2020: https://doi.org/10.1016/j.simyco.2020.02.004.

INTRODUCTION

The Dothideomycetes represents a class of ecologically diverse and cosmopolitan fungi from aquatic to terrestrial ecosystems. Diverse lifestyles are found amongst the Dothideomycetes including epiphytes, endophytes, saprobes, plant and animal pathogens, mycoparasites, mycorrhizal, lichenised and rock-inhabiting fungi (Schoch et al. 2009, Schoch & Grube 2015, Ametrano et al. 2019). The Dothideomycetes is divided into two subclasses, Pleosporomycetidae and Dothideomycetidae, and some incertae sedis lineages, accommodating more than 25 orders, 110 families and over 19,000 species, thereby representing the largest class of Ascomycota (Schoch et al. 2009, Hyde et al. 2013, Jaklitsch et al. 2015, Schoch & Grube 2015, Van Nieuwenhuizen et al. 2016, Bezerra et al. 2017, Videira et al. 2017, Wijayawardene et al. 2017). Morphologically they are mostly characterised by ascostromatic development and bitunicate ascii with fissionisticate dehiscence (Schoch & Grube 2015).

The Capnodiales represent the second largest order in Dothideomycetes after the Pleosporales. The Capnodiales is included in the subclass Dothideomycetidae along with the Dothideales and Myriangiales (Crous et al. 2009). The taxonomic concept of this order was expanded from the original description by Luttrell (1955), based on a multigene phylogeny and the presence of ostiolar paraphyses as a synapomorphic feature (Schoch et al. 2006). Taxa in this order lack pseudoparaphyses, but include several species with periphyssoids and paraphyses (Lumbsch & Lindemuth 2001).

As discussed by Schoch & Grube (2015), the Capnodiales was established based on the sooty moulds in three families, Antennulariaceae, Capnodiaeae, and Coccodiniaceae. However, phylogenetic analyses revealed that the sooty moulds are polyphyletic and include species residing in two different classes, Dothideomycetes and Eurotiomycetes (Crous et al. 2007a).

The Capnodiales now includes the epiphytic sooty moulds associated with honeydew produced by insects
| Family and Species name | Voucher/Culture | Substrate/Lifestyle | Country/Location | Collector | GenBank accession numbers | GenBank accession numbers |
|-------------------------|----------------|---------------------|------------------|-----------|--------------------------|--------------------------|
| **Capnodiaceae**        |                |                     |                  |           |                          |                          |
| Capnodium alfenasi       | CBS 146151 = CPC 22666 | Tabebuia sp. | Brazil | A.C. Allenas | MN749165 MN749233 MN829346 MN829260 |                          |
|                         | CBS 146152 = CPC 22667 | Tabebuia sp. | Brazil | A.C. Allenas | MN749166 MN749234 MN829347 MN829261 |                          |
| Ca. blackwelliae         | CBS 133588 = CPC 14327 | Myrtus communis | USA | P.W. Crous | MH878118 MN749235 GU349054 GU371743 |                          |
| Ca. coartatum            | MFLUCC10-0069 | Paidium sp. | Thailand | P. Chomnunti | JN832814 – – – |                          |
|                         | MFLUCC10-0070 | – | Thailand | P. Chomnunti | JN832815 – – – |                          |
|                         | CPC 17779 | Alstonia scholaris | Thailand | K.D. Hyde | – – – |                          |
| Ca. coffeae              | CBS 147.52 = AFTOL-ID 939 | Coffea robusta | Zaire | Deposited by J. Nicot/Isolated by A. Saccas | GU214400 DG491515 DG471089 KT216519 |                          |
| Ca. coffeicola           | MFLUCC15-0206 | Coffea sp. | Thailand | S. Hongsanan | KU358920 KU358921 – – |                          |
| Ca. gamsii               | CBS 89.73 | Sooty mould, on unknown leaf | Sri Lanka | W. Gams | GU301847 MN749237 GU349045 GU371736 |                          |
|                         | CBS 146153 = CPC 17765 | Lagerstroemia speciosa | Thailand | K.D. Hyde | – – – |                          |
|                         | MFLUCC10-0066 | – | Thailand | S.K. Chandranath | JN832813 – – – |                          |
|                         | CBS 146154 = CPC 20466 = MFLUCC12- Lagerstroemia floribunda 0101 | – | Thailand | S. Hongsanan | MN749169 MN749239 MN829350 MN829264 |                          |
|                         | CBS 146155 = CPC 20467 = MFLUCC12- Lagerstroemia floribunda 0102 | – | Thailand | S. Hongsanan | MN749170 MN749240 MN829351 MN829265 |                          |
|                         | CBS 146156 = CPC 20471 = MFLUCC12- Living leaf of unknown host 0107 | – | Thailand | S. Hongsanan | MN749171 MN749241 MN829352 MN829266 |                          |
| Ca. neocoffeicola        | CBS 139614 = MFLUCC14-0570 | Coffea arabica | Thailand | S. Hongsanan | MN749172 MN749242 MN829353 MN829267 |                          |
|                         | CBS 139613 = MFLUCC 14-0569 | Coffea arabica | Thailand | S. Hongsanan | MN749173 MN749243 MN829354 MN829268 |                          |
| Ca. paracoffeicola       | CBS 139616 = MFLUCC 14-0572 | Coffea arabica | Thailand | S. Hongsanan | MN749174 MN749244 MN829355 MN829269 |                          |
|                         | CBS 139615 = MFLUCC14-0571 | Coffea arabica | Thailand | S. Hongsanan | MN749175 MN749245 MN829356 MN829270 |                          |
| Chaetocapnodium           | CBS 202.30 | Camelia sinensis | Indonesia | Deposited by F.H. van Beyma/Isolated by Steinmann | GU301849 MH855113 GU349060 | MN829273                          |
| **indonesiacum**         |                |                     |                  |           |                          |                          |
| Ch. insulare             | CBS 146159 = CPC 19221 | Phyllica arborea | South Africa | M.J. Wingfield | MN749178 MN749248 MN829359 MN829274 |                          |
|                         | CBS 146160 = CPC 19223 | Phyllica arborea | South Africa | M.J. Wingfield | MN749179 MN749249 MN829360 MN829275 |                          |
|                         | CBS 146161 = CPC 19224 | Phyllica arborea | South Africa | M.J. Wingfield | MN749180 MN749250 MN829361 MN829276 |                          |
| Ch. philippinense         | MFLUCC12-0110 = CPC 20474 | Palm | Philippines | K.D. Hyde | KP744503 MN749251 MN829362 MN829277 |                          |
| Ch. placitae             | CBS 124758 = CPC 13706 | Eucalyptus placita | Australia | B.A. Summerell | GQ030326chr02 Q030325chr02 MN829363 MN829278 |                          |
| Ch. siamensis            | MFLUCC13-0778 | Leaves of unidentified plant | Thailand | S. Hongsanan | KP744479 – – – |                          |
|                         | CBS 139815 = MFLUCC13-0096 | Leaves of unidentified plant | Thailand | S.C. Karunathana | MN749181 MN749252 MN829364 MN829279 |                          |
| Ch. summerellii          | CBS 146157 = CPC 13654 | Eucalyptus placita | Australia | B.A. Summerell | MN749176 MN749246 MN829357 MN829271 |                          |
| Family and Species name | Voucher/Culture | Substrate/Lifestyle | Country/Location | Collector | GenBank accession numbers |
|-------------------------|----------------|--------------------|-----------------|----------|--------------------------|
| **Ch. tanzanicum** | CBS 145.79 | Lichen | Tanzania | – | MN749182 MN749253 MN829365 MN829280 |
| **Ch. thailandense** | CBS 139619 = MFLUCC13-0787 | – | Thailand | S.C. Karunarathna | MN749183 MN749254 MN829366 MN829281 |
| **Conidiocarpus asiticus** | MFLUCC10-0062 | Coffea arabica | Thailand | J.K. Liu | JN832612 KU358924 – – |
| **Co. caucasicus** | GUMH 937 | Citrus sinensis | Iran | F. Byrami | KC333050 – – – |
| **Co. siamensis** | MFLUCC10-0064 | Mangifera indica | Thailand | R. Phokhomsak | JN832609 – – – |
| **Co. siamensis** | MFLUCC10-0061 | – | Thailand | P. Chomnunti | JN832607 KU358923 – – |
| **Co. siamensis** | MFLUCC10-0063 | Coffea arabica | Thailand | J.K. Liu | JN832608 KU358925 – – |
| **Conidiocarpus sp.** | CPC 17778 | Guave sp. | Thailand | K.D. Hyde | MN749185 MN749256 MN829368 MN829283 |
| | CPC 20463 = MFLUCC12-0098 | Malus sp. | Thailand | W. Saowanee | MN749187 MN749258 MN829370 MN829285 |
| | CPC 20464 = MFLUCC12-0099 | Mimusops elengi | Thailand | S. Hongsanan | MN749194 MN749265 MN829377 MN829292 |
| | CPC 20465 = MFLUCC12-0100 | Mimusops elengi | Thailand | S. Hongsanan | MN749191 MN749262 MN829374 MN829289 |
| | CPC 20468 = MFLUCC12-0103 | Mango | Thailand | Puttaluk | MN749193 MN749264 MN829376 MN829291 |
| | CPC 20472 = MFLUCC12-0108 | Living leaf of unknown host | Thailand | S. Hongsanan | MN749188 MN749259 MN829371 MN829286 |
| | CPC 21380 = MFLUCC12-0404 | Malus sp. | Thailand | K.D. Hyde | MN749186 MN749257 MN829369 MN829284 |
| | CBS 139618 = MFLUCC14-0874 | Coffea arabica | Thailand | S. Hongsanan | MN749190 MN749261 MN829373 MN829288 |
| | CBS 139619 = MFLUCC14-0875 | Coffea arabica | Thailand | S. Hongsanan | MN749192 MN749263 MN829375 MN829290 |
| | CBS 139820 = MFLUCC 14-0876 | Coffea arabica | Thailand | S. Hongsanan | MN749184 MN749255 MN829367 MN829282 |
| | CBS 139821 = MFLUCC14-0877 | Coffea arabica | Thailand | S. Hongsanan | MN749189 MN749260 MN829372 MN829287 |
| **Heteroconium citharexyli** | HM628775 | Citharexylum ilicifolium | Ecuador | H. Sydow | HM628775 HM628776 – – |
| **Leptoxyphium cacuminum** | MFLUCC10-0059 | Gossypium herbaceum | Thailand | S.C. Karunarathna | JN832603 – – – |
| | MFLUCC10-0049 | Mimusops elengi | Thailand | P. Chomnunti | JN832602 – – – |
| | MFLUCC10-0086 | Ficus sp. | Thailand | K.D. Hyde | JN832604 – – – |
| **L. citri** | CBS 451.66 | Citrus sinensis | Spain | H.A. van der Aa | KF902904 MN749266 GU349039 GU371727 |
| | CBS 146162 = CPC 26196 | – | – | V. Guarnaccia | MN749195 MN749267 MN829378 MN829294 |
| **L. glochidion** | IFRDCC 2651 | Glochidion wrightii | China | H. Yang | KF982308 KF982307 – – |
| **L. kurandae** | CBS 129530 = CPC 17274 | Eucalyptus sp. | Australia | P.W. Crous & R.G. Shivash | JF951170 JF951150 MN829379 MN829295 |
| **L. madagascariense** | CBS 124766 = CPC 14623 | Eucalyptus camaldulensis | Madagascar | M.J. Wingfield | MN874923 MH863407 MN829380 MN829296 |
| **Leptoxyphium sp.** | CPC 17767 | Gossypium herbaceum | Thailand | K.D. Hyde | MN749203 MN749275 MN829388 MN829304 |
| | CPC 20470 = MFLUCC12-0106 | Living leaf of unknown host | Thailand | S. Hongsanan | MN749200 MN749272 MN829385 MN829301 |

(continued on next page)
| Family and Species name | Voucher/Culture | Substrate/Lifestyle | Country/Location | Collector | GenBank accession numbers |
|-------------------------|----------------|--------------------|------------------|----------|-------------------------|
| *Phragmocapnias betle* | CPC 17762      | Mimusops elengi (Bulkt wood) | Thailand | K.D. Hyde | MN749323 MN829307 MN829308 |
|                         | CPC 20476      | Mimusops elengi     | Philippines | K.D. Hyde | MN749304 MN829308 MN829324 |
|                         | CPC 21379      | Malus sp.           | Thailand | K.D. Hyde | MN749223 MN829309 MN829309 |
| *Plumezia citri*        | CBS 116435     | Citrus aurantium    | Iran | R. Zare & W. Gams | GU214649 GU214649 MN829310 |

**Neoantennariellaceae**

| Voucher/Culture | Substrate/Lifestyle | Country/Location | Collector | GenBank accession numbers |
|-----------------|--------------------|------------------|----------|-------------------------|
| Fumiglobus pediculosa | UBC F23788  | Pieria japonica | Canada | Tanay Bose | KC833052 KF263061 – – |
| *Neoantennariella phylicae* | CBS 146164 = CPC 19227 | Phyllica arborea | South Africa | M.J. Wingfield | MN749209 MN749281 MN829315 MN829311 |
|                 | CBS 146165 = CPC 19977 | Phyllica arborea | UK | P. Ryan | MN749213 MN749285 MN829399 MN829315 |
|                 | CBS 146166 = CPC 19981 | Phyllica arborea | UK | P. Ryan | MN749214 MN749284 MN829398 MN829314 |
|                 | CBS 146167 = CPC 19985 | Phyllica arborea | UK | P. Ryan | MN749210 MN749282 MN829396 MN829312 |
|                 | CPC 19992       | Phyllica arborea | UK | P. Ryan | MN749214 MN749286 MN829400 MN829316 |
| *Neoasbolisia phylicae* | CBS 146163 = CPC 19989 | Phyllica arborea | UK | P. Ryan | MN749211 MN749283 MN829397 MN829313 |
|                 | CBS 146168 = CPC 19982 | Phyllica arborea | UK | P. Ryan | MN749215 MN749287 MN829401 MN829317 |

**Readeriellopsidaceae**

| Voucher/Culture | Substrate/Lifestyle | Country/Location | Collector | GenBank accession numbers |
|-----------------|--------------------|------------------|----------|-------------------------|
| "Capnodium" salicinum | CBS 131.34 = AFTOL-ID 937 | Bursaria spinosa | Indonesia | Deposited by E.E. Fisher | EU019269 AJ244240 DQ677889 KT216553 |
| *Phaeoxyphiella australiana* | CBS 146169 = CPC 29527 | Agonis sp. | Australia | P.W. Crous | MN749220 MN749292 MN829406 MN829322 |
| *Phylica phylicae* | CBS 146171 = CPC 19979 | Phyllica arborea | UK | P. Ryan | MN749216 MN749288 MN829402 MN829318 |
| Family and Species name | Voucher/Culture¹ | Substrate/Lifestyle² | Country/Location | Collector | GenBank accession numbers³ |
|------------------------|------------------|----------------------|-----------------|----------|--------------------------|
| **Phylica arborea**    | CBS 146172 = CPC 19984 | UK | P. Ryan | MN749217 MN749289 MN829403 MN829319 |
|                        | CBS 146173 = CPC 19987 | UK | P. Ryan | MN749218 MN749290 MN829404 MN829320 |
|                        | CBS 146170 = CPC 19993 | UK | P. Ryan | MN749219 MN749291 MN829405 MN829321 |
| **Fuscoporia wahlbergii** | CBS 139990 = CPC 24637 | French Guiana | C. Decock | KR476755 KR476720 MN829410 MN829326 |
| **Sclecoxyphium blechni** | CBS 146174 = CPC 19990 | UK | P. Ryan | MN749224 MN749292 MN829412 MN829328 |
| **Phyllactinia leucadendri** | CBS 146176 = CPC 18313 | South Africa | P.W. Crous | MN749226 MN749298 MN829414 MN829330 |
| **Phyllactinia phyllica** | CBS 146177 = CPC 19219 | South Africa | M.J. Wingfield | MN749227 MN749299 MN829415 MN829331 |
| **Phyllactinia spongiosa** | CBS 131318 = CPC 18312 | South Africa | M.J. Wingfield | MN749228 MN749300 MN829416 MN829332 |
| **Scorias aphidis** | CBS 325.33 | Aphid | – | Deposited by L.H. Leonian | MH866910 GU214696 MN829417 KT216542 |
| **Camellia sinensis** | CBS 201.30 | Indonesia | Deposited by F.H. van Beyma/Isolated by Steinmann | MH866560 MH855112 MN829418 MN829333 |
| **Laucadendron muirii** | CBS 131318 = CPC 18312 | South Africa | P.W. Crous | JQ044456 JQ044437 MN829419 MN829334 |
| **Callistemon sp.** | CPC 17088 | Australia | P.W. Crous | MN749229 MN749301 MN829420 MN829335 |
| **Mangifera indica** | MFLUCC15-0230 | Thailand | S. Hongsanan | KT588603 KT588604 – – |
| **Entada sp.** | MFLUCC10-0084 | Thailand | P. Chomnunti | JN832601 – – – |

**Outgroup**

| **Elsinoe phaseoli** | CBS 165.31 = AFTOL-ID 1855 = IMI 303278 | Cuba | Deposited by A.E. Jenkins/Isolated by C. Aguiar | DQ676095 KX887263 DQ677935 KX887144 |
| **Myriangium hispanicum** | CBS 247.33 | Acer monspessulanum | – | Deposited by J.B. Martinez/Isolated by H. Diddens | GU301854 KX887304 GU349055 GU371744 |

¹ ATCC: American Type Culture Collection, Virginia, USA; CBS: Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands; CPC: Culture collection of Pedro Crous, housed at Westerdijk Fungal Biodiversity Institute; IFRDCC: International Fungal Research & Development Centre Culture Collection, Chinese Academy of Forestry, Kunming, China; IMI: International Mycological Institute, CABI-Bioscience, Egham, Wakeham Lane, United Kingdom; MFLUCC: Mae Fah Luang University Culture Collection, Chiang Ria, Thailand; MUCL: Université Catholique de Louvain, Louvain-la-Neuve, Belgium.

² Lifestyle of all sooty mould strains coded as epiphyte.

³ ITS: internal transcribed spacers and intervening 5.8S rDNA; LSU: partial 28S large subunit RNA gene; TEF-1α: partial translation elongation factor 1-alpha gene; RPB2: partial RNA polymerase II second largest subunit gene. Bold GenBank accession numbers for sequences generated in this study; – indicates unavailable sequence.
(Antennariellaceae, Capnodiales, Euantennariaceae, Metacapnodiales), hyperparasites, rock-inhabiting fungi, ecto-
physes, saprobes, endophytes and pathogens associated with
plants and humans (Cladosporiaceae, Cystolecciaceae, Dis-
soconiaciaceae, Extremaceae, Mycosphaerellaceae, Neo-
devriessiaceae, Schizothyriaceae, Phaeothecaceae (including
Phaeotheca fissurella and Phaeotheca shathenatiana), Phaeo-
theoidiellaceae, Teratosphaeraceae (including Pedraziaceae),
Comminutispora, Phaeotheca (P. salicicola and P. triangularis)
and lichenised species (Cystolecciaceae and Racodium)
(Hughes 1976, Aptroot 2006, Crous et al. 2007a, 2009, 2016,
2018, Quaedvlieg et al. 2014, Hongsanan et al. 2017, Lücking
et al. 2017, Videira et al. 2017).

During the course of the past decade, considerable attention
has been paid to the phylogeny and systematics of genera and
families in the Capnodiales. Presently the order accommodates
fungi having highly diverse ecological niches, lifestyles and
modes of nutrition (Crous et al. 2007a, 2009, Ruibal et al. 2009,
Schoch et al. 2009, Hyde et al. 2013, Chomnunti et al. 2014,
Quaedvlieg et al. 2014, Ismail et al. 2016, Hongsanan et al.
2017, Videira et al. 2017, Crous et al. 2018). Although the
Capnodiales s. str. are epiphytic sooty moulds, the presently
applied circumscription also includes ectophytes and plant
pathogens. Previous studies have, however, not addressed this
ecological divergence adequately. This is due to a limited sam-
ping of sooty moulds, and a poorly resolved phylogenetic
backbone mainly based on nuclear ribosomal RNA genes. The
aim of this study was therefore to reconsider the phylogenetic
backbone of the Capnodiales by including numerous new col-
lections of sooty moulds, thus also providing a more robust
phylogeny using four nuclear loci, LSU, ITS, TEF-1α and RPB2.

MATERIALS AND METHODS

Isolates

The sooty mould isolates studied here were obtained from the
culture collection (CBS) of the Westerdijk Fungal Biodiversity
Institute (WI), Utrecht, the Netherlands, and the working collec-
tion of Pedro Crous (CPC) housed at the WI (Table 1). Se-
quences of other strains were retrieved from GenBank (Tables 1,
S1). Representative cultures of the new species described in this
study were deposited in the CBS culture collection.

DNA extraction, PCR amplification and
sequencing

Total genomic DNA was extracted from fresh mycelia grown on
malt extract agar (MEA) using the Wizard® Genomic DNA Pu-
fication Kit (Promega Corporation, Fitchburg, Wisconsin, USA)
following the manufacturer’s protocols. The D1/D2 variable do-
 mains of the 28S rDNA (LSU) and the ITS1, 5.8 and ITS2 re-
gion of ribosomal DNA and part of RNA polymerase II second
largest subunit (RPB2) and the translation elongation factor 1-
alpha (TEF-1α) were amplified and sequenced using the following primer pairs: LR0R/LR5 for LSU (Vilgalys & Hester
1990), ITSS/ITS4 for ITS (White et al. 1990), RPB2-5F/IRPB2-
1α (Rehner & Buckley 2005). The PCR amplifications
were performed in a total volume of 12.5 μL containing 1 μL genomic
DNA, 1 × NH4 reaction buffer (Bioline, Luckenwalde, Germany),
0.2 μM of each primer, 200 μM dNTPs, 3 mM MgCl2, and 0.5 U
Taq DNA polymerase (Bioline). To improve amplification of RPB2
in some difficult DNA templates 4 % Bovine Serum Albumin
(BSA, New England BioLabs, #B9000S) was added to the re-
action mixture.

PCR conditions for LSU, ITS and TEF-1α were: an initial
denaturation step of 5 min at 95 °C followed by 35 cycles of 30 s
at 95 °C, 45 s at 52 °C (ITS, LSU) or 55 °C (TEF-1α) and 1 min
at 72 °C, and a final elongation step of 7 min at 72 °C. Touchdown
PCR was performed for amplification of RPB2 as follows: an initial denaturation at 95 °C for 5 min followed by 35
cycles of 30 s at 95 °C, 30 s at 60 °C (5–10 cycles)/56 °C (5–10
cycles)/52 °C (15–25 cycles) and 1 min at 72 °C, and a final
elongation step of 7 min at 72 °C.

The PCR products were sequenced with both forward and
reverse primers using an Applied Biosystems 3730xl DNA
Analyzer (Thermo Fisher Scientific). The DNASTAR Lasergene
SeqMan Pro v. 8.1.3. software was used to obtain consensus
sequences. All new sequences were submitted to GenBank
(Tables 1, S1).

Phylogenetic analyses

Generated sequences were aligned with sequences retrieved
from GenBank (http://www.ncbi.nlm.nih.gov) using the online
interface of MAFFT v. 7 (http://mafft.cbrc.jp/alignment/server/
index.html), and manually edited in MEGA v. 7.0.21. Maximum
Likelihood (ML) and Bayesian analysis (BA) were implemented
for phylogenetic inferences of both single locus and concate-
nated alignments on the CIPRES Science Gateway portal
(https://www.phylo.org/; Miller et al. 2012) using RAxML-HPC
BlackBox v. 8.2.10 (Stamatakis 2014) and MrBayes v. 3.2.6
(Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003),
respectively. The ML analyses were performed using a
GTR+GAMMA substitution model and four rate classes with
1 000 bootstrap iterations. For the Bayesian analyses the optimal
nucleotide substitution models were determined for each locus
using MrModelTest v. 2.3 (Nylander 2004). Bayesian analyses
were computed under the optimal nucleotide substitution models
with four simultaneous Markov Chain Monte Carlo chains, 10 M
generations and a sampling frequency of 1 000 generations,
ending the run automatically when standard deviation of split
frequencies dropped below 0.01. Burn-in was set to remove
25 % of the first sampled trees, after which the 50 % majority rule
consensus trees and posterior probability (PP) values were
calculated. The resulting trees were plotted using FigTree v.
1.4.3 (http://tree.bio.ed.ac.uk/software/figtree). Alignments
and trees were deposited in TreeBASE (www.treebase.org; S25414)
and taxonomic novelties in MycoBank (www.MycoBank.org;
Crous et al. 2004).

Ancestral states were reconstructed using Mesquite v.3.6
(Maddison & Maddison 2018). Character history was inferred
using the Bayesian tree (see above) as phylogenetic framework.
Ancestral states were determined based on a maximum likelihood
approach with a MK1 model of evolution. Characters states
were defined as saprobe, epiphyte, parasite or lichen. The character
state for taxa with an uncertain lifestyle was coded as “?”. 
Morphology

Isolates stored in liquid nitrogen or lyophilised were reactivated on 2% malt extract agar (MEA) or oatmeal agar (OA). Colonies were sub-cultured onto MEA, OA, cornmeal agar (CMA), potato dextrose agar (PDA), and synthetic nutrient-poor agar (SNA) supplemented with pine needles at room temperature. Culture media were prepared as described by Crous et al. (2019a, b). Cultures were examined periodically for the development of reproductive structures. Slide preparations were made with clear lactic acid or Shear’s mounting fluid. Morphological observations of fungal structures were made using a Nikon SMZ1000 dissecting microscope and a Zeiss Axioscope 2 compound microscope with differential interference contrast (DIC) illumination. Measurements and images were taken using a Nikon DS-Ri2 high definition colour digital camera. Measurements and descriptions of microscopic structures were made from cultures grown on SNA. A few strains that were sterile on SNA were described from other media (indicated in text). The mean, standard deviation, maximum and minimum values of at least 30 fungal structures were calculated where possible. Dimensions are presented as a range with extremes in parentheses. Growth rates were measured on MEA after 2 wk and colony characters were noted. Colony colours were rated according to the colour chart of Rayner (1970).

RESULTS

Phylogeny

Amplification of the partial sequences of LSU, ITS and TEF-1α was successful but RPB2 proved difficult to amplify using normal

---

Legend to family abbreviations

C: Cystocoleaceae
D: Dissoconiaceae
E: Extremaceae
M: Mycosphaerellaceae
N: Neodevriesiaceae
P: Phaeothecoidiellaceae
S: Shizothyriaceae
T: Teratosphaeriaceae

---

Fig. 1. Reduced phylogenetic tree inferred from a Bayesian analysis based on a concatenated alignment of LSU, TEF-1α and RPB2. Bayesian posterior probabilities (PP) and maximum likelihood bootstrap support values (ML-BS) are indicated at the nodes (PP/ML-BS). The scale bar represents the expected number of changes per site. The lineages in Capnodiales s. l. are indicated in different colours. The tree was rooted with Venturia inaequalis (CBS 594.70).
Fig. 2. Phylogenetic tree inferred from a RAxML search of a concatenated alignment of LSU, ITS, TEF-1α and RPB2. Maximum likelihood bootstrap support values (ML-BS) and Bayesian posterior probabilities (PP) are indicated at the nodes (ML-BS/PP). The scale bar represents the expected number of changes per site. Families and orders are highlighted in blocks of different colour and indicated to the right of the tree. The tree was rooted with Myriangium hispanicum (CBS 247.33) and Elsinoe phaseoli (AFTOL-ID-1855). Ex-type, Ex-epitype.
PCR, and therefore a touchdown PCR program was used. For most of the isolates the combination of RPB2-5F and RPB2-7CR primers (Liu et al. 1999) was more successful than the primer combination RPB2-5F2 and RPB2-7CR (Sung et al. 2007). For a few isolates, we used the forward primer RPB2-5F2 instead of RPB2-5F.

Two datasets were analysed in this study. The first dataset consisted of combined LSU, TEF-1α and RPB2, including 193 taxa representing three orders Capnodiales s. lat., Myrangiaceae, Dothideales, with Venturia inaequalis (CBS 594.70) as outgroup. After alignment the dataset contained a total of 3 168 characters (LSU: 837, ITS: 553, TEF-1α: 780.93), with 193 distinctive alignment patterns produced a best-scoring ML tree (lnL = -66287.001595). The bootstrap values equal to or higher than 50 % were mapped on the Bayesian tree (Figs 1, S1). The same phylogenetic tree was obtained from both RAxML and Bayesian analyses. Capnodiales s. lat. was split into seven distinct clades representing seven orders. Sooty mould fungi constituted Capnodiales s. str., a single highly supported clade (ML-BS = 90 %, PP = 1). Mycosphaerellales with high support in both analyses (ML-BS = 100 %, PP = 1) proved clearly distinct from Capnodiales s. str., and was thus resurrected here as a separate order containing eight families: Mycosphaerellaceae, Dissoconiacaeae, Phaeothecoidiellaceae, Schizothyriaceae, Extremaceae, Cystocoleaceae, Neoderviaeasae and Teratosphaeraceae (Figs 1, S1). In the Bayesian analysis Mycosphaerellales grouped with Capnodiales s. str. in a well-supported clade (PP = 0.98), while in the RAxML analysis it was a sister group of Cladosporiaceae with low support (ML-BS < 50 %). Therefore, Cladosporiaceae was elevated to ordinal level, and Cladosporiales introduced. In both RAxML and Bayesian analyses four new orders were recognised: Phaeothecales, Neophaeothecales, Racodiales (for Racodium rupestris), and Comminutisporales (for Comminutispora agavaciensis).

The second dataset consisted of aligned sequences of four loci (LSU, ITS, TEF-1α and RPB2), and included 102 taxa belonging to Capnodiales s. str., and two species, Myriangium hispanicum (CBS 247.33) and Elsinoe phaseoli (AFTOL-ID-1855), as the outgroup taxa. The aligned dataset contained 3 603 characters (LSU: 849, ITS: 553, TEF-1α: 201.30, RPB2: 170.88), including alignment gaps. Results from MrModelTest indicated a general time-reversible model of evolution (Rodríguez et al. 1990), including estimation of invariable sites and assuming a discrete gamma distribution (GTR+I+G) with six rate categories (Isetnst = 6, rates = invgamma) and dirichlet (1,1,1,1) base frequencies is the best nucleotide substitution model for all loci (LSU, TEF-1α and RPB2). The Bayesian analyses of the concatenated alignments of three loci generated 7 292 trees from which 1 463 distinct alignment patterns produced a best-scoring ML tree. The average standard deviation of split frequencies was 0.009987 at the end of the run. The RAxML search of the dataset with 1 767 distinct alignment patterns produced a best-scoring ML tree (lnL = -30052.650187 (Fig. 2). The Bayesian analyses generated 4 622 trees from which 1 463 distinct alignment patterns and yielded a tree with lnL = -30052.650187 (Fig. 2). The Bayesian analyses generated four new orders were recognised: Phaeothecales, Neophaeothecales, Racodiales (for Racodium rupestris), and Comminutisporales (for Comminutispora agavaciensis).
Posterior probability values were mapped on the ML tree (Fig. 2). Three families, namely Capnodiaeae, Neoantennariellaceae and Readerieliopsidaceae were recognised in Capnodiales s. str. In Capnodiaeaceae seven morphologically and phylogenetically well-supported genera including Capnodium, Chaetocapnodium, Conidicarpus, Heteroconium, Leptoxypium, Phragmocapnia and Polychaetum were identified. Eleven new species were recognised in this family. Readerieliopsidaceae contained four genera (Phaseoxyphilina, Readerieliopsis, Scolecoxyphium and Scorias) and Neoantennariellaceae three genera (Fumiglobus, Neoantennariella and Neoasbolisia).

Ancestral state reconstruction revealed a saprobic lifestyle as the ancestral state of the Capnodiales s. lat. included in this study (see Neophaeothecales; Fig. 3), while whole genome sequences of a more diverse set of taxa also supported the ancestral state of Dothideomycetes to be saprobic (Haridas et al. 2020). In the dataset included in the present study the saprobic lifestyle emerged during the evolution of diverse taxa, with several reversals back to parasitism. All Capnodiales emerged from an ancestor that had an ectophytic lifestyle. The analyses also revealed that all Mycosphaerellales shared an ancestor that was saprobic. From this ancestor ectophytes and lichen associated fungi emerged, while the ancestors of several species in this group reverted to a parasitic lifestyle. The ancestor of all Cladosporiales and Comminutisporales were saprobes but some species in the Cladosporiales reverted back to parasitism. Results showed that the ancestor of the Raccoales was a lichen-associated fungus, and that of the Dothideales was a saprobe.

**Taxonomy**

Based on the phylogenetic analyses of the two datasets generated in this study, combined with the differences in morphology and ecology, the Capnodiales requires redefinition, and the Mycosphaerellales must be resurrected. Furthermore, five new orders, four new families, three new genera, 21 new species and five new combinations are introduced below.

**Capnodiales** Woron. Ann. Mycol. 23: 177. 1925.

*Note*: Treated below as Capnodiales s. str.

**Cladosporiales** Abdollahz. & Crous, *ord. nov.* MycoBank MB833140.

*Etyymology*: Name refers to the genus *Cladosporium*.

Saprobic, endophytic, fungicolous, lichenicolous, human and plant pathogen. *Ascomata* pseudothecial, gregarious or scattered, immersed, black to red-brown, globose to subglobose, uniloculate, with 1−3 short, periphysate ostiolar necks. *Ostiole* necks periphysoid. *Hamathecia* of hyaline, septate, subcylindrical pseudoparaphyses. *Asci* 8−spored, bitunicate, fissitunicate, sessile to short-stalked, obvoid to broadly ellipsoid or subcylindrical, straight to slightly curved. *Ascospores* bi- to multi-seriate, or overlapping, hyaline, obvoid to ellipsoid-fusiform, with irregular lumina inclusions. *Asexual morphs* hyphomycetous. *Conidiophores* macroconidial, mononematous, simple or branched, brown. *Conidia* mostly in branched or unbranched acroperal chains, subhyaline to brown, smooth to verrucose or echinulate, ramoconidia present or not, dry, conidium secession schizolytic (adapted from Bensch et al. 2012).

*Type genus*: *Cladosporium* Link (sexual morph Davidiella Crous & U. Braun)

*Family included*: Cladosporiaceae Chalm. & R.G. Archibald (based on Cladosporium).

**Comminutisporales** Abdollahz. & Crous, *ord. nov.* MycoBank MB833141.

*Etyymology*: Name refers to the genus *Comminutispora*.

Saprobic. *Ascomata* pseudothecial, immersed, uniloculate, separate. *Asci* bitunicate, 8−spored. *Pseudoparaphyses* absent, hamathecial tissue abundant, ostiolar canal peripheryste. *Ascospores* muriformly septate, forming secondary ascospores.
within the ascus. Hyphae hyaline, becoming olivaceous, forming hyaline, aseptate endoconidia (adapted from Ramaley 1996).

**Comminutisporaceae** Abdollahz. & Crous, fam. nov. MycoBank MB833142.

**Etymology:** Name refers to the genus *Comminutispora*.

Saprobic. Ascomata pseudothecial, immersed, uniloculate, separate. Asci bitunicate, 8-spored. Pseudoparaphyses absent, hamathecial tissue abundant, ostiolar canal periphysate. Ascospores muriformly septate, forming secondary ascospores within the ascus. Hyphae hyaline, becoming olivaceous, forming hyaline, aseptate endoconidia.

**Type genus:** *Comminutispora* A.W. Ramaley (asexual morph *Hyphospora* A.W. Ramaley).

**Mycosphaerellales** (Nanff.) P.F. Cannon, Ainsworth & Bisby’s Dictionary of the Fungi Ed. 9. 2001.

Saprobic, ectophytic, lichenicolous and phytopathogenic. Ascomata immersed to semi-immersed within the pseudostroma or

---

**Fig. 4.** Capnodium affenasi. A, B. Colony (2-wk-old) on MEA. C. Conidiomata arising from mycelia or immature conidiomata on SNA. D. Conidioma on SNA. E. Ostiole surround by hyaline hyphae. F. Conidia produced in ellipsoidal central part of conidioma. G. Conidia. Scale bars: C = 25 μm; D = 20 μm; F, G = 10 μm.

**Fig. 5.** Capnodium blackwelliae. A, B. Colony (2-wk-old) on MEA. C–G. Conidiomata on SNA. H. Conidia. Scale bars: C–G = 25 μm; H = 10 μm.
clypeus or superficial, solitary, globose to subglobose with protruding central ostiole, dark brown to black, scattered or clustered, gregarious. *Peridium* thin- to thick-walled, of several layers of textura angularis, brown to black. *Hamathecium* present or absent, with cellular pseudoparaphyses, anastomosing, branching, sometimes aparaphysate. *Asci* bitunicate, fissitunicate, 8-spored, cylindrical to cylindrical-clavate, ovoid to saccate, sessile or stipitate, apically rounded with distinct or indistinct ocular chamber. *Ascospores* bi-to multi-seriate, ellipsoidal to obclavate, oblong to cylindrical, hyaline to subhyaline or pale yellowish, mostly 1-septate, constricted or not, smooth or rough-walled. Asexual morphs hyphomycetous or coelomycetous (see Videira et al. 2017 for more details about asexual morphs).

*Type genus:* Ramularia Unger (sexual morph Mycosphaerella Johanson).

**Families included:** Cystocoleaceae (based on Cystocoleus), Dissoconiacaeae (based on Dissoconium), Extremaceae (based on Extremus), Mycosphaerellaceae (based on Mycosphaerella), Neodevriessiaceae (based on Neodevriesia), Phaeothecidiellaceae (based on Phaeothecidiella), Schizothyriaceae (based on Schizothyrium, asexual morph Zygohiphaia), Teratosphaeriaceae (based on Teratosphaeria, asexual morph Kirramyces).

**Neophaeothecaceae** Abdollahz. & Crous, fam. nov. MycoBank MB833144.

*Etymology:* Name refers to the genus *Neophaeotheca*.

*Mycelium* consisting of hyaline, smooth, septate, branched hyphae, that swell in terminal or intercalary cells, developing numerous endoconidia. *Endoconidia* brown, verruculose, globose to ovoid, muriformly septate, bursting open to release endoconidia that are red-brown, verruculose, aseptate, ellipsoid to subglobose or irregular.

**Neophaeotheca** Abdollahz. & Crous, gen. nov. MycoBank MB833145.

*Etymology:* Name refers to its morphological similarity with the genus *Phaeotheca*.

*Mycelium* consisting of hyaline, smooth, septate, branched hyphae, that swell in terminal or intercalary cells, developing numerous endoconidia. *Endoconidia* brown, verruculose, globose to ovoid, muriformly septate, bursting open to release endoconidia that are red-brown, verruculose, aseptate, ellipsoid to subglobose or irregular.

**Type species:** Neophaeotheca salicorniae (Crous & Roets) Abdollahz. & Crous

**Neophaeotheca salicorniae** (Crous & Roets) Abdollahz. & Crous, comb. nov. MycoBank MB833146. Basionym: Phaeotheca salicorniae Crous & Roets, Persoonia 36: 365. 2016.

**Neophaeotheca triangularis** (de Hoog & Beguin) Abdollahz. & Crous, comb. nov. MycoBank MB833147. Basionym: Phaeotheca triangularis de Hoog & Beguin, Antonie van Leeuwenhoek 71: 290. 1997.
**Phaeothecales** Abdollahz. & Crous, *ord. nov.* MycoBank MB833148.

**Etymology:** Name refers to the genus *Phaeotheca*.

*Mycelium* consisting of hyaline to brown, smooth-walled, septate, branched hyphae, terminal or intercalary cells becoming swollen, developing numerous endoconidia. *Endoconidia* brown, smooth to verruculose, thin- to thick-walled, globose to obovoid, aseptate to muriformly septate (from Crous et al. 2018).

**Type genus:** *Phaeotheca* Sigler, Tsuneda & J.W. Carmich.

**Family included:** *Phaeothecaceae* (based on *Phaeotheca*, see Crous et al. 2018).

**Racodiales** Abdollahz. & Crous, *ord. nov.* MycoBank MB833149.

**Etymology:** Name refers to the genus *Racodium*.

*Thallus* filamentous, of elongated, straight hyphae, longitudinally arranged, in close association with photobiont, not corticate, dark brown to black, forming wefts or circular patches, margin not delimited; *hyphae* 4–7 per photobiont filament, straight and parallel, unbranched, non-nodulose. *Ascomata* and *conidiomata* not known (from Smith et al. 2009).

**Type genus:** *Racodium* Fr.

**Family included:** *Racodiaceae* (based on *Racodium*).

**Notes:** The typification of *Racodium* Fr. (based on *R. rupestre* Pers.) was discussed by Hawksworth et al. (2011). Based on the sequences included here, *Racodium* (*Racodiaceae* Link) represents an undescribed order.

**Capnodiales s. str.**

The genera delineated in Fig. 2 are treated alphabetically based on order.

**Capnodiales** Woron. Ann. Mycol. 23: 177. 1925.

Widespread in tropical and subtropical areas, occurring on honeydew excretions from insects, forming a black, sooty growth on green, healthy leaves, stems and bark. *Ascomata* superficial on mycelium, subglobose to globose, with or without setae, dark brown, with a central ostiole. *Pseudoparaphyses* absent. *Asci* bitunicate, saccate, with a short pedicel, lacking an ocular chamber. *Ascospores* multiseptate or muriform, hyaline to brown. *Asexual morphs* pycnidial coelomycetous or hyphomycetous (Hughes 1976, Crous et al. 2009, Chomnunti et al. 2011).

**Type genus:** *Capnodium* Mont.

**Families included:** *Capnodiaceae* (based on *Capnodium*), *Neoantennariellaceae* (based on *Neoantennariella*) and *Readerielliopsidaceae* (based on *Readerielliopsis*).

**Capnodiaceae** Höhn. ex Theiss., Verh. Zool.-Bot. Ges. Wien 66: 363. 1916.

Growing superficially on honeydew excretions from insects, having a black, sooty-like appearance on green leaves, stems and bark; often co-occurring with other fungicolous taxa. *Mycelium* superficial on host surface, black, sooty-like, consisting

---

**Fig. 7.** *Capnodium neocoffeicola*. **A, B.** Colony (2-wk-old) on MEA. **C.** Conidiomata arising from mycelia or immature conidiomata on SNA. **D.** Conidiomata on SNA. **E.** Conidia produced in ellipsoidal central part of conidioma. **F.** Conidia. Scale bars: **C, E** = 20 μm; **D** = 25 μm; **F** = 10 μm.
of septate, branched, brown hyphae. Sexual morph: Ascomata formed in mycelial mass, subglobose to globose, setae present or lacking, dark brown, with central ostiole; peridium brown, thin-walled, cells of textura angularis. Pseudoparaphyses absent. Asci 8-spored, bitunicate, saccate, short pedicellate, generally lacking an ocular chamber. Ascospores bi- to tri-seriate, multi-septate or muriform, hyaline to brown.

Ascomata formed in mycelial mass, subglobose to globose, setae present or lacking, dark brown, with central ostiole; peridium brown, thin-walled, cells of textura angularis. Pseudoparaphyses absent. Asci 8-spored, bitunicate, saccate, short pedicellate, generally lacking an ocular chamber. Ascospores bi- to tri-seriate, multi-septate or muriform, hyaline to brown.

Asexual morphs: coelomycetous

Conidiomata synnematous or pycnidial, globose to pyriform, mostly elongated, with or without necks, and with or without swelling, and central ostiole. Conidia hyaline, aseptate, ellipsoid; hyphomycetous. Conidiophores superficial, erect, brown, cylindrical, septate, proliferating percurrently at apex.

Conidia brown, septate, ellipsoid or subcylindrical, solitary or in chains.

Type genus: Capnodium Mont.

Capnodium Mont., Ann. Sci. Nat. Bot. 11: 233. 1849.

Saprobic on sugary exudates from insects growing on the surface of leaves, fruits, stems and other non-plant objects. Thallus a loose or dense network of pale brown, superficial hyphae or a thick pseudoparenchymatous stromata, with sexual and asexual morphs often growing together. Ascomata superficial on mycelium, brown to dark brown or black, globose to ellipsoidal, short-stalked or sessile, ostiolate at maturity, scattered or in groups, lacking setae. Peridium comprising dark brown to pale brown, thick-walled cells forming a textura angularis. Asci 8-spored, bitunicate, clavate, ovoid or saccate, aparianthoporous, apedicellate. Ascospores brown, oblong or ovoid and some reniform, transversely septate with or without one or more vertical septa. Conidiomata pycnidial, slender to flask-shaped, simple or branched, occur singly or in groups, sessile or with long or short stalk, sometimes on the same base or stalk, with or without conspicuous oval or ellipsoidal part, with short to long or without conspicuous neck, sometimes with two necks, dark brown. Ostiole at apex of pycnidia, hyphae continuing upwards to the tapered neck, terminating in an ostiole which is surrounded by obtusely rounded hyphal ends. Conidia small, ellipsoidal, continuous, hyaline, aseptate (adapted from Chomnunti et al. 2011).

Type species: Capnodium citri Berk. & Desm.

Notes: The taxonomic history of Capnodium was discussed by Chomnunti et al. (2011). Index Fungorum lists 140 species names in Capnodium, while MycoBank lists 168 species names (accessed March 2019). DNA sequence data are available for only two recently published species; Ca. coartatum (LSU) and Ca. coffeicola (LSU/ITS). In the present study we sequenced LSU, ITS, TEF-1α and RPB2 loci for 13 isolates. Phylogenetic analyses revealed that these isolates represent six species, five of which are described as new below.

Capnodium alfenasii Abdollahz. & Crous, sp. nov. MycoBank MB833150. Fig. 4.

Etymology: Named after Prof. Acelino Couto Alfenas, in recognition to his contributions to the study of Brazilian fungal biodiversity.

Mycelium superficial or immersed, hyaline to brown, branched, hyphae smooth, thin-walled, septate, constricted at septa, with a mucilaginous outer wall layer. Pycnidia superficial or immersed, flask-shaped, mostly simple and rarely branched, occur singly or in groups, medium to dark brown, synnematous, 113–243 μm long (av. = 187 μm, n = 20), mostly sessile or with short stalk (25–46 × 18–35 μm, av. = 40 × 24 μm), oval or ellipsoidal central part (60–124 × 31–46 μm, av. = 93 × 34 μm), neck (38–118 × 8.8–13.5 μm, av. = 70 × 11 μm), wall comprising mostly cylindrical cells. Ostiole at apex of pycnidia, surrounded by hyaline hyphae. Conidia small, hyaline, aseptate, oblong to oblong-ellipsoidal.

Fig. 8. Capnodium paracoffeicola. A, B. Colony (2-wk-old) on MEA. C. Conidiomata arising from mycelia or immature conidiomata on SNA. D. Conidiomata on SNA. E. Ostiole surrounded by hyaline hyphae. F. Conidia. Scale bars: C–E = 25 μm; F = 10 μm.
ellipsoid, continuous, \((3.7–)3.9–4.8(–5.1) \times (1.4–)1.7–2(–2.2) \mu m\) (av. = 4.4 × 1.8 \(\mu m\), \(n = 50\)).

**Culture characteristics:** Colonies leathery, appressed, with fluffy aerial mycelium, with creamy exudates of pycnidia containing conidia, folded, edge sinuate, glaucous grey to olivaceous grey after 2 wk in the dark at 25 °C. Colonies reaching 19 mm diam on MEA after 2 wk in the dark at 25 °C.

**Typus:** Brazil, Minas Gerais, Viçosa, on leaves of Tabebuia sp., 1993, A.C. Alfenas (**holotype** CBS H-24256, culture ex-type CBS 146151 = CPC 22667, CBS H-24262).

Additional material examined: Brazil, Minas Gerais, Viçosa, on leaves of Tabebuia sp., 1993, A.C. Alfenas, culture CBS 146152 = CPC 22667, CBS H-24262.

**Notes:** Phylogenetically *Ca. alfensii* forms a distinct clade (Figs S1, 2), but morphologically it is difficult to distinguish from *Ca. gamsii*, despite having smaller conidia and a shorter central pycnidial body. *Ca. alfensii* differs from *Ca. blackwelliae* in having longer pycnidia, from *Ca. neocoffeicola* in having smaller pycnidia and conidia.

*Capnodium blackwelliae* Abdollahz. & Crous, **sp. nov.** MycoBank MB833151. Fig. 5.

**Etymology:** Named after Prof. Meredith Blackwell, who organised the annual meeting of the Mycological Society of America at Baton Rouge, Louisiana in 2007, during which time this fungus was collected.

*Mycelium* superficial or immersed, hyaline to brown, branched, hyphae smooth, thin-walled, septate, constricted at septa, with a mucilaginous outer wall layer. *Pycnidia* superficial or immersed, slender or flask-shaped, simple or branched, occur singly or in groups, medium to dark brown, synnematous, 42–116 \(\mu m\) long (av. = 95 \(\mu m\), \(n = 20\)), mostly sessile or with short stalk (25–31 × 17–22 \(\mu m\), av. = 27 × 19 \(\mu m\)), with or without conspicuous oval or ellipsoidal central region (24–143 × 19–55 \(\mu m\), av. = 70 × 38 \(\mu m\)), with or without neck (22–102 × 10–37 \(\mu m\), av. = 38 × 12 \(\mu m\)); wall comprising mostly cylindrical cells. *Ostiole* at pycnidial apex, surrounded by hyaline hyphae. *Conidia* small, hyaline, aseptate, oblong to ellipsoid, continuous, (3.6–)3.9–4.3(–4.8) \(\times\) (1.4–)1.6–1.9(–2) \(\mu m\) (av. = 4.2 × 1.7 \(\mu m\), \(n = 50\)).

**Culture characteristics:** Colonies, leathery, appressed, with fluffy aerial mycelium, with creamy conidial exudates from pycnidia; surface folded, edge metallic, sinuate, greenish glaucous to olivaceous black after 2 wk in the dark at 25 °C. Colonies reaching 22 mm diam on MEA after 2 wk in the dark at 25 °C.

**Typus:** USA, Louisiana, Baton Rouge, on living leaves of Myrtus communis, 3 Aug. 2007, P.W. Crous (**holotype** CBS H-24266, culture ex-type CBS 133588).

**Notes:** Phylogenetically *Ca. blackwelliae* is closely related to *Ca. gamsii* (Figs S1, 2), but morphologically differs from all other species by having the smallest pycnidial lengths (av. = 95 \(\mu m\) long). Pycnidia in *Ca. blackwelliae* are variable in shape, and range from long and flask-shaped to short and cylindrical.

*Capnodium coartatum* Chomnunti & K.D. Hyde, Fungal Diversity 51: 117. 2011.

Material examined: **Thailand.** Chiang Rai, on living leaves of Alstonia scholaris, 13 Sep. 2009, K.D. Hyde, culture CPC 17779.

**Notes:** We examined isolate CPC 17779 and generated sequences of four loci, namely LSU, ITS, TEF-1α and RPB2. This isolate grouped with two isolates of *Ca. coartatum*, namely MFLUCC10-0069 (ex-type) and MFLUCC10-0070 (Figs S1, 2). There are only LSU sequence data available for both isolates, and they differ at two nucleotide positions. Isolate CPC 17779 is 100 % identical with isolate MFLUCC10-0070 based on LSU sequence data. Morphologically, pycnidia (115–203 \(\mu m\) high, \(n = 20\)) and conidia (3.6–4.6 × 1.7–2.5 \(\mu m\); av. = 3.9 × 2.25 \(\mu m\), \(n = 50\)) of CPC 17779 are both smaller than in *Ca. coartatum* as described by Chomnunti et al. (2011), although measurements in the latter were made from fungal structures in vivo.

*Capnodium gamsii* Abdollahz. & Crous, **sp. nov.** MycoBank MB833152. Fig. 8.

**Etymology:** Named in honour of Prof. K. Walter Gams, who was an avid collector of microfungi, and collected this species in Sri Lanka.

*Mycelium* superficial or immersed, hyaline to brown, branched, hyphae smooth, thin-walled, septate, constricted at septa, with a mucilaginous outer wall layer. *Pycnidia* superficial or immersed, mostly slender or flask-shaped, simple or branched, occur singly or in groups, medium to dark brown, synnematous, 97–350 \(\mu m\) long (av. = 185 \(\mu m\), \(n = 20\)), mostly sessile or with short stalk (23–44 × 16–29 \(\mu m\), av. = 32 × 21 \(\mu m\)), with or without conspicuous oval or ellipsoidal central part, 62–206 × 19–46 \(\mu m\), av. = 165 × 40 \(\mu m\), neck present or absent, 15–87 × 9–25 \(\mu m\), av. = 40 × 16 \(\mu m\); wall comprising mostly cylindrical cells. *Ostiole*

---

**Fig. 9.** Chaetocapnodium indonesiacum. **A, B.** Colony (2-wk-old) on MEA. **C.** Conidiomata on SNA. **D.** Conidia. Scale bars: **C** = 25 \(\mu m\); **D** = 10 \(\mu m\).
Notes: Capnodium gamsii forms a well-supported phylogenetic clade (Figs S1, 2). Morphologically it is distinguishable from other species in having more cylindrical pycnidia with a much longer (av. = 165 × 40 μm, l/w ratio > 4) central region. In other species the average length of the central region is less than 100 μm (l/w ratio < 3).

Capnodium neocoffeicola Abdollahz. & Crous, sp. nov. MycoBank MB833153. Fig. 7.

Etymology: Name refers to the fact that it is related to Ca. coffeicola.

Mycelium superficial or immersed, hyaline to brown, branched; hyphae smooth, thin-walled, septate, constricted at septa, with a mucilaginous outer wall layer. Conidiomata pycnidial, superficial or immersed, flask-shaped, simple and erect, occur singly or in groups, medium to dark brown, synnematous, 134–268 μm long (av. = 230 μm, n = 20), sessile or with short stalk (27–46 × 28–40 μm, av. = 38 × 30 μm), oval or ellipsoidal central part (74–115 × 38–52 μm, av. = 90 × 46 μm), neck (44–136 × 9–12 μm, av. = 110 × 11 μm), wall comprising mostly cylindrical cells. Ostiole at apex of pycnidial neck, surrounded by hyaline hyphae. Conidia small, hyaline, aseptate, oblong to ellipsoid, continuous, (3.6–)4.5–8.1) × (1.6–)1.9–2.4(–2.9) μm (av. = 4.9 × 2.2 μm, n = 50).

Culture characteristics: Colonies leathery, metallic, appressed, with fluffy aerial mycelium at the centre, with creamy exudates of pycnidia containing conidia, folded, edge sinuate, greenish grey to pale greenish grey after 2 wk in the dark at 25 °C. Colonies reaching 20–22 mm diam on MEA after 2 wk in the dark at 25 °C.

Typus: Sri Lanka, Hakgala Botanic Gardens, on leaves of unknown plant, Jan. 1973, W. Gams (holotype CBS H-24296, culture ex-type CBS 892.73).

Additional materials examined: Thailand, Chiang Rai, on Lagerstroemia speciosa, 1 Jan. 2009, P.W. Crous, culture CPC 17765 = CBS 146153; Chiang Rai, on Lagerstroemia Ronkunda, 2009, P.W. Crous, cultures CPC 20466 = CBS 146154 and CPC 20467 = CBS 146155); unknown substrate, 2009, P.W. Crous, culture CPC 20471 = CBS 146156, CBS H-24263).

Notes: In the phylogenetic tree, Ca. neocoffeicola is clearly a distinct species (Figs S1, 2). In terms of morphology, the smaller conidia can differentiate Ca. neocoffeicola from Ca. para-coffeicola, and the longer pycnidia (av. = 230 μm) distinguishes it from other species examined in this study. In Ca. para-coffeicola, Ca. neocoffeicola and Ca. coffeae (CBS 147.52) the average pycnidial length is greater than 200 μm, while in the other species (incl. Ca. coffeicola, 165–178 μm) pycnidia are less than 200 μm long.

Capnodium paracoffeicola Abdollahz. & Crous, sp. nov. MycoBank MB833154. Fig. 8.

Etymology: Name refers to the fact that it is related to Ca. coffeicola.

at pycnidial apex, surrounded by hyaline hyphae. Conidia small, hyaline, aseptate, oblong to ellipsoid, continuous, (3.6–)4.5–8.1) × (1.6–)1.9–2.4(–2.9) μm (av. = 4.9 × 2.2 μm, n = 50).

Culture characteristics: Colonies, leathery, metallic, appressed, with fluffy aerial mycelium at the centre, with creamy exudates of pycnidia containing conidia, folded, edge sinuate, greenish grey to greenish black after 2 wk in the dark at 25 °C. Colonies reaching 20–22 mm diam on MEA after 2 wk in the dark at 25 °C.

Typus: Sri Lanka, Hakgala Botanic Gardens, on leaves of unknown plant, Jan. 1973, W. Gams (holotype CBS H-24296, culture ex-type CBS 892.73).

Additional materials examined: Thailand, Chiang Rai, on Lagerstroemia speciosa, 1 Jan. 2009, P.W. Crous, culture CPC 17765 = CBS 146153; Chiang Rai, on Lagerstroemia Ronkunda, 2009, P.W. Crous, cultures CPC 20466 = CBS 146154 and CPC 20467 = CBS 146155); unknown substrate, 2009, P.W. Crous, culture CPC 20471 = CBS 146156, CBS H-24263).

Notes: In the phylogenetic tree, Ca. neocoffeicola is clearly a distinct species (Figs S1, 2). In terms of morphology, the smaller conidia can differentiate Ca. neocoffeicola from Ca. para-coffeicola, and the longer pycnidia (av. = 230 μm) distinguishes it from other species examined in this study. In Ca. para-coffeicola, Ca. neocoffeicola and Ca. coffeae (CBS 147.52) the average pycnidial length is greater than 200 μm, while in the other species (incl. Ca. coffeicola, 165–178 μm) pycnidia are less than 200 μm long.

Capnodium paracoffeicola Abdollahz. & Crous, sp. nov. MycoBank MB833154. Fig. 8.

Etymology: Name refers to the fact that it is related to Ca. coffeicola.
Mycelium superficial or immersed, hyaline to brown, branched; hyphae smooth, thin-walled, septate, constricted at septa, with a mucilaginous outer wall layer. Pycnidia superficial or immersed, flask-shaped, simple or branched, occurring singly or in groups, medium to dark brown, synnematous, 223–337 μm long (av. = 266 μm, n = 20), sessile or with short stalk (32–87 × 17–28 μm, av. = 70 × 23 μm), oval or ellipsoidal central part (63–160 × 25–40 μm, av. = 90 × 35 μm), neck (82–173 × 8.8–13.9 μm, av. = 120 × 12 μm), wall comprising mostly cylindrical cells. Ostiole at apex of pycnidial neck, surrounded by hyaline hyphae. Conidia small, hyaline, aseptate, oblong to ellipsoid, continuous, (4.9–)5–6.5(–7.7) × (1.8–)1.9–2.3(–2.6) μm (av. = 6.4 × 2.15 μm, n = 50).

Culture characteristics: Colonies leathery, appressed, with fluffy aerial mycelium, folded, edge sinuate, glaucous grey to pale greenish grey after 2 wk in the dark at 25 °C. Colonies reaching 17 mm diam on MEA after 2 wk in the dark at 25 °C.

Typus. Thailand, Chiang Rai, on living leaves of Coffea arabica, 20 Aug. 2014, S. Hongsanan (holotype CBS H-24268, culture ex-type CBS 139616 = MFLUCC 14-0572).
Additional material examined: Thailand. Chiang Rai, on living leaves of Coffea arabica, 20 Aug. 2014, S. Hongsanan, culture CBS 139615 = MFLUCC 14-0571.

Notes: Phylogenetically this species constitutes a distinct clade (Figs S1, 2) that is characterised morphologically by larger conidia (av. = 6.4 × 2.15 μm). Average conidial lengths of the other species studied here are shorter than 5 μm. 

Chaetocapnodium coffeicola was recently described from leaves of Coffea sp. collected in Chiang Rai, Thailand (Hongsanan et al. 2015b). Morphologically it differs from Ca. paracoffeicola in its shorter conidiomata (165–178 μm long), and shorter stalks (19–24 long × 18–23 μm diam; Hongsanan et al. 2015b).

Chaetocapnodium Hongsanan & K.D. Hyde, Fungal Diversity 72: 68. 2015.

Type species: Chaetocapnodium siamensis Hongsanan & K.D. Hyde

Notes: Chaetocapnodium is a hitherto monotypic genus introduced based on the morphology of its sexual morph and supported by LSU sequence data (Liu et al. 2015). The phylogenies generated in the present study (Figs S1, 2), however, revealed that Antennariella placitae and Phragmocapnias philippinensis are congeneric with Chaetocapnodium. Nine other isolates clustered in six distinct clades representing six species, five of which are recognised as taxonomic novelties. Two new combinations are proposed and five new species described in Chaetocapnodium.

Chaetocapnodium indonesiacum Abdollahz. & Crous, sp. nov. MycoBank MB833156. Fig. 9.

Etymology: Name refers to Indonesia where this fungus was collected.

Mycelium superficial or immersed, hyaline to medium brown, branched, hyphae mostly smooth, thin-walled, septate, constricted at septa, with a mucilaginous outer wall layer. Pycnidia superficial or immersed, globose to pyriform, pale to dark brown, mostly intercalary, lateral or terminal on erect hyphal branches, meristogenous in development, pseudoparenchymatous, thin-walled, 1–2 cell layers of textura angularis, (20–) 25–35(–48) × (16–)23–33(–40) μm. Setae not observed. Ostiole absent, or not well-developed, mostly releasing conidia by means of irregular rupture. Conidia hyaline, aseptate, globose to subglobose, smooth, thin-walled, (2–) 2.4–2.8 × (1.8–)2.2–2.4(–2.6) μm, (av. = 2.5 × 2.2 μm, n = 50).

Culture characteristics: Colonies, leathery, appressed, with fluffy aerial mycelium, folded, edge sinuate, smoke grey to pale mouse grey after 2 wk in the dark at 25 °C. Colonies reaching 43 mm diam on MEA after 2 wk in the dark at 25 °C.

Typus: Indonesia, Java Island, Bogor, Buitenzorg, on leaves of Camellia sinensis, 1930?, F.H. van Beyma (holotype CBS H-24269, culture ex-type CBS 202.30).

Notes: Phylogenetically Ch. indonesiacum clusters with Ch. philippinense (Figs S1, 2). Morphologically it is not possible to compare these two species, as the latter is known only from its sexual morph. They are genetically distinct in 1, 1, 9 and 40 bp in LSU, ITS, TEF-1α and RPB2 loci. Chaetocapnodium indonesiacum can be distinguished from all other species by having the smallest pycnidia (25–35 × 23–33 μm). With the exception of Ch. indonesiacum and Ch. placitae, all Chaetocapnodium species have conidiomatal pycnidia with setae. The radial growth rate of Ch. indonesiacum on MEA at 25 °C was more rapid (43 mm diam/2 wk) than that observed in all other species.
Chaetocapnodium insulare Abdollahz. & Crous, sp. nov. MycoBank MB833157. Fig. 10.

Etymology: Name reflects the fact that it was collected from an island.

Mycelium superficial or immersed, hyaline to medium brown, branched, hyphae mostly smooth, thin-walled, septate, constricted at septa, with a mucilaginous outer wall layer. Pycnidia superficial or immersed, globose to pyriform, pale to dark brown, mostly intercalary, lateral or terminal on erect hyphal branches, meristogenous in development, pseudoparenchymatous, thin-walled, 1–2 cell layers of textura angularis, (28–)35–55 × (22–)30–48 μm. Setae present, septate or aseptate, pale to dark brown, mostly around ostiole, (7–)10–13(–19) μm long (av. = 12 μm, n = 30). Ostiole absent, or not well-developed, mostly releasing conidia by means of irregular rupture. Conidia hyaline, aseptate, globose to subglobose, with minute guttules, smooth, thin-walled, (2.8–)3.2–3.6(–4.4) × (2.6–)2.9–3.3(–3.7) μm, (av. = 3.4 × 3 μm, n = 50).

Culture characteristics: Colonies, leathery, appressed, with fluffy aerial mycelium, with creamy conidial exudates, edge sinuate, smoke grey to greenish grey after 2 wk in the dark at 25 °C. Colonies reaching 14 mm diam on MEA after 2 wk in the dark at 25 °C.

Typus: South Africa, Marion Island, Prince Edward Is., on Phylica arborea, 2011, M.J. Wingfield (holotype CBS H-24297, culture ex-type CPC 19221 = CBS 146159).

Additional material examined: South Africa, Marion Island, Prince Edward Is., on P. arborea, 2011, M.J. Wingfield, culture CPC 19223 = CBS 146160; on P. arborea, 2011, M.J. Wingfield, culture CPC 19224 = CBS 146161.

Notes: Based on the phylogenetic analyses Ch. insulare is related to Ch. placitae (Figs S1, 2), but morphologically it is distinct from all Chaetocapnodium species examined in this study by producing the largest conidia with average length and width greater than 3 (av. = 3.4 × 3 μm). Moreover, pycnidia in Ch. insulare are setose with septate or aseptate setae while in Ch. placitae setae are absent. Radial growth rate on MEA at 25 °C is slower (14 mm diam/2 wk) than observed for all other species.

Chaetocapnodium philippinense (Hongsanan & K.D. Hyde) Abdollahz. & Crous, comb. nov. MycoBank MB833158.

Basionym: Phragmocapnias philippinensis Hongsanan & K.D. Hyde, Fungal Diversity 72: 69. 2015.

Description: Liu et al. (2015).

Typus: Philippines, Laguna, Mount Makiling, on leaves of palm (Arecaceae), Feb. 2012, K.D. Hyde HSA14/1 (holotype MFLU 14-0748, ex-type culture MFLUCC 12-0110 = CPC 20474).
**Chaetocapnodium placitae** (Cheewangkoon & Crous) Abdollahz. & Crous, **comb. nov.** MycoBank MB833159.

**Basionym:** *Antennariella placitae* Cheewangkoon & Crous, Persoonia 23: 57. 2009.

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

**Typus:** Australia, New South Wales, Cessnock S 32°50’45”, E 151°17’07”, on Eucalyptus placita, 14 Oct. 2006, coll. B.A. Summerell, isol. P.W. Crous (holotype CBS H-20277, culture ex-type CPC 13706 = CBS 124785).

**Chaetocapnodium siamensis** Hongsanan & K.D. Hyde, Fungal Diversity 72: 69. 2015.

Asexual morph. *Mycelium* superficial or immersed, hyaline to medium brown, branched, hyphae mostly smooth, thin-walled, septate, constricted at septa, with a mucilaginous outer wall layer. *Pycnidia* superficial or immersed, globose to pyriform, pale to dark brown, mostly around ostiole, (9–15) × (36–)45–70(–100) × (32–)40–65(–94) μm. *Setae* present, septate or aseptate, pale to dark brown, mostly around ostiole, (13.9–)20–26(–30) μm long (av. = 22.7 μm, n = 30). *Ostiole* absent, or not well-developed, mostly releasing conidia by means of irregular rupture. *Conidia* hyaline, aseptate, globose to subglobose, with minute guttules, smooth, thin-walled, (2.1–)2.4–2.8(–3) × 2–2.4(–2.6) μm (av. = 2.6 × 2.3 μm, n = 50). For description of sexual morph, see Liu et al. (2015).

Material examined: Thailand, Chiang Rai, Bandu, on leaves of unknown plant host, 2013, S.C. Karunaratna, culture CBS 139815 = MFLUCC 13-0096.

Notes: Isolate CBS 139815 clustered (Figs S1, 2) with the ex-type of *Ch. siamensis* (MFLUCC13-0778, on an unidentified host plant, collected in Chiang Rai). Only LSU sequence data are available for *Ch. siamensis*, which differs from CBS 139815 at two nucleotide positions. We have characterised the asexual morph of CBS 139815, which was not described in the original description of *Ch. siamensis*.

**Chaetocapnodium summerellii** Abdollahz. & Crous, **sp. nov.** MycoBank MB833155. Fig. 11.

**Etymology:** Named in honour of Prof. Brett A. Summerell, Director Research & Chief Botanist at the Royal Botanic Garden Sydney, Australia, who is an active advocate for plant and fungal conservation.

*Mycelium* superficial or immersed, hyaline to medium brown, branched, hyphae mostly smooth, thin-walled, septate, constricted at septa, with a mucilaginous outer wall layer. *Pycnidia* superficial or immersed, globose to pyriform, pale to dark brown, mostly intercalary, lateral or terminal on erect hyphal branches, meristogenous in development, pseudoparenchymatous, thinned, 1–2 cell layers of *textura angularis*, (36–)45–70(–100) × (32–)40–65(–94) μm. *Setae* present, septate or aseptate, pale to dark brown, mostly around ostiole, (9–)11–15(–19) μm long (av. = 14.3 μm, n = 30). *Ostiole* absent or not well-developed, mostly releasing conidia by means of irregular rupture. *Conidia* hyaline, aseptate, globose to subglobose, with minute guttules, smooth, thin-walled, (2.2–)2.5(–2.6) × 1.9–2.4 μm, (av. = 2.3 × 2.1 μm, n = 50).

**Culture characteristics:** Colonies, leathery, appressed, with fluffy aerial mycelium, with creamy conidial exudates in centre of colony; surface folded, edge sinuate, pale mouse grey to olivaceous black after 2 wk in the dark at 25 °C. Colonies reaching 29 mm diam on MEA after 2 wk in the dark at 25 °C.

**Typus:** Australia, New South Wales, on leaves of *Eucalyptus placita* (Myrtaceae), Oct. 2006, B.A. Summerell (holotype CBS H-24257, culture ex-type CPC 13654 = CBS 146157).
Notes: Chaetocapnodium summerellii resembles Ch. thailandense and Ch. tanzanicum in morphology, but is phylogenetically distinct, forming a separate clade (Figs S1, 2). Furthermore, its radial growth rate on MEA at 25 °C (29 mm diam/2 wk) is slower than that of the latter two species (38 mm diam/2 wk).

Additional material examined: Laos, host unknown, 1 Jan. 2009, P. Pheng, culture CPC 17368 = CBS 146158, CBS H-24264.

Notes: Chaetocapnodium summerellii resembles Ch. thailandense and Ch. summerellii. It is distinguishable from Ch. summerellii by having a faster radial growth rate on MEA at 25 °C, and from Ch. thailandense by producing larger conidia.

Chaetocapnodium thailandense Abdollahz. & Crous, sp. nov. MycoBank MB833161. Fig. 12.

Etyymology: Name refers to Thailand where this fungus was collected.

Mycelium superficial or immersed, hyaline to medium brown, branched, hyphae mostly smooth, thin-walled, septate, constricted at septa, with a mucilaginous outer wall layer. Pycnidia superficial or immersed, globose to pyriform, pale to dark brown, mostly intercalary, lateral or terminal on erect hyphal branches, meristogenous in development, pseudoparenchymatous, thin-walled, 1–2 cell layers of textura angularis, (38–) 55–70(–138) × (30–)45–65(–112) μm. Setae present, septate or aseptate, pale to dark brown, mostly around ostiole, (10.5–) 12–17(–23) μm long (av. = 15.6 μm, n = 30). Ostiole absent or not well-developed, mostly releasing conidia by means of irregular rupture. Conidia hyaline, aseptate, globose to subglobose, with minute guttules, smooth, thin-walled, (2.5–) 2.7–2.9(–3.2) × (2.3–)2.5–2.8 μm, (av. = 2.8 × 2.6 μm, n = 50).

Culture characteristics: Colonies, leathery, metallic, appressed, with fluffy aerial mycelium at the centre, with creamy exudates of pycnidia containing conidia, folded, edge sinuate, smoke grey to greenish black, edge sienna to cinnamon after 2 wk in the dark at 25 °C. Colonies reaching 38 mm diam on MEA after 2 wk in the dark at 25 °C.

Typus: Tanzania, on lichen, 1974, M. Dreyfuss (holotype CBS H-24270, culture ex-type CBS 145.79).

Notes: Chaetocapnodium tanzanicum is phylogenetically clearly distinct from other Chaetocapnodium spp. (Figs S1, 2). Morphologically it resembles Ch. thailandense and Ch. summerellii. It is phylogenetically clearly distinct from other Chaetocapnodium spp. (Figs S1, 2).

Chaetocapnodium tanzanicum Abdollahz. & Crous, sp. nov. MycoBank MB833160. Fig. 13.

Etyymology: Name refers to Tanzania where this fungus was collected.

Mycelium superficial or immersed, hyaline to medium brown, branched, hyphae mostly smooth, thin-walled, septate, constricted at septa, with a mucilaginous outer wall layer. Pycnidia superficial or immersed, globose to pyriform, pale to dark brown, mostly intercalary, lateral or terminal on erect hyphal branches, meristogenous in development, pseudoparenchymatous, thin-walled, 1–2 cell layers of textura angularis, (38–) 40–70(–90) × (32–)40–60(–80) μm. Setae present, aseptate, pale to dark brown, mostly around ostiole, (8.7–) 13–19(–26.6) μm long (av. = 16.1 μm, n = 30). Ostiole absent, or not well-developed, mostly releasing conidia by means of irregular rupture. Conidia hyaline, 0(–1)-septate, globose to subglobose, with minute guttules, smooth, thin-walled, (2–) 2.2–2.6(–2.8) × (1.9–)2.7 μm (av. = 2.3 × 2.1 μm, n = 50).

Culture characteristics: Colonies, leathery, metallic, appressed, with fluffy aerial mycelium, glaucoius grey to pale olivaceous grey after 2 wk in the dark at 25 °C. Colonies reaching 38 mm diam on MEA after 2 wk in the dark at 25 °C.

Typus: Thailand, Chiang Rai, host plant unknown, 2013, S.C. Karunarathna (holotype CBS H-24271, culture ex-type CBS 139619 = MFLUCC 13-0787).

Notes: Phylogenetically, Ch. thailandense constitutes a distinct lineage (Figs S1, 2). Morphologically Ch. thailandense resembles Ch. tanzanicum and Ch. summerellii. It is distinguished...
from *Ch. tanzanica* by having smaller conidia, and from *Ch. summerellii* by its faster radial growth rate on MEA at 25 °C. **Conidiocarpus** Woron., Ann. Mycol. 24 (3/4): 250. 1926.

Saprobic on sugary exudates from insects, with dark mycelium forming a soot-like coating on the upper surface of leaves. *Thallus* composed of black, pelliculose, reticulately branched, dense, cylindrical, radiating, septate hyphae. *Ascomata* not observed. *Conidiomata* pycnidial, supported on black, long, narrow, cylindrical stalks composed of tightly compacted, anastomosed, synnematous cylindrical hyphae, lageniform with a brown oval or ellipsoid part, which produces a long neck and conidia. The pycnidium wall is composed of two or more layers, the outer one being more or less pseudoparenchymatous although the short cells tend to be arranged linearly, indicating their origin from longitudinally fused hypha. *Ostiole* surrounded by hyaline, subulate, hyphal extensions. *Conidia* small, ellipsoid, continuous, asceptate, hyaline, smooth-walled, arranged in a droplet at the apex of pycnidial neck (adapted from Hughes 1976, Chomnunti et al. 2011).

Type species: *Conidiocarpus caucasicus* Woron.

Notes: *Conidiocarpus* with the type species *Co. caucasicus* was introduced by Woronichin in Jaczewski (1917). However, Hughes (1976) stated that Batista & Ciferri (1963a) considered *Co. penzigii*, the second oldest species introduced in 1926, as the type species. *Conidiocarpus* has been reported as the asexual morph of *Phragmocapnia* (Hughes 1976). *Phragmocapnia bettle* is the type species of *Phragmocapnia*. Following the ICN code based on the priority rule and one fungus = one name principles, Bose et al. (2014) chose *Conidiocarpus* and transferred species of *Phragmocapnia* to *Conidiocarpus*.

In this study based on phylogenetic analyses, the type species of *Conidiocarpus* and *Phragmocapnia* clustered in two distinct clades representing two different genera (Figs S1, 2). As discussed by Hughes (1976), pycnidia of *Co. caucasicus* are elongated, 540–650 μm long including a stalk, swollen part and a neck. In morphological studies, we found that all of the species that grouped with *C. caucasicus* produced a *Conidiocarpus* pycnidial type, typified by having a long neck (Fig. 14).

Hughes (1976) mentioned that in cases where the sexual-axexual connections have been confirmed, the pycnidial morphs of *Phragmocapnia* were the tall *Conidiocarpus* conidiomata that lacked necks (Figs 14, 16), Chomnunti et al. (2011) designated an epitype (MFLU09-0650, living culture MFLUCC10-0053) for the type species *Phragmocapnia bettle*, and re-described this species based on the sexual morph. They did not observe the asexual morph. Based on Hughes (1976), asexual conidiomata are *Conidiocarpus* pycnidia (150–700 μm long) that lack a neck. To observe the pycnidial morph of *Phragmocapnia bettle*, we used different culture media and were able to introduce the asexual morph on PDA, PCA and CMA. Conidiomata were pycnidia with short stalks, ellipsoidal swellings, and lacking necks. Therefore, following the views of Hughes (1976), we chose to resurrect *Phragmocapnia* for species with conidiocarpus-like pycnidia lacking necks.

A search of Index Fungorum and MycoBank (March 2019) revealed 12 names in *Conidiocarpus*, of which six species, *Co. asiaticus*, *Co. betle*, *Co. caucasicus*, *Co. philippinensis*, *Co. plumerieae* and *Co. siamensis* have DNA sequence data.

In our phylogenetic analyses based on four loci (LSU, ITS, TEF-1α and RPB2), *Conidiocarpus* isolates clustered in two subclades (Figs S1, 2). The ex-type isolates of *Co. asiaticus* and *Co. siamensis* together with *Co. caucasicus* and the nine isolates sequenced in this study clustered in the first subclade strongly supported in the RAxML analysis, but with no support from the Bayesian analyses. These species are morphologically different but phylogenetically unresolved, which may be due to missing data. Only LSU sequence data are available for the ex-type strains of *Co. caucasicus* (GUMH937) and *Co. siamensis* (MFLUCC10-0064), and LSU/ITS sequences for *Co. asiaticus* (MFLUCC10-0062). Two isolates CPC 20464 and CPC 20468 for which four genes sequenced in this study and an isolate belonging to *Co. siamensis* (MFLUCC10-0061) with LSU and ITS sequences clustered in the second sub-clade, representing a putatively new *Conidiocarpus* species supported by both RAxML and Bayesian analyses (ML-BS = 100 %, PP = 0.82). However, the identity of the other *Conidiocarpus* isolates included in this study can only be resolved once additional gene regions have been sequenced.

**Heteroconium** Petr., Sydowia 3: 264. 1949.

Type species: *Heteroconium citarexfyli* Petr.

Descriptions: Hughes (2007), Cheewangkoont et al. (2012).

Notes: A search of Index Fungorum and MycoBank (March 2019) lists 25 and 28 names in *Heteroconium*, respectively. However, only LSU sequence data are available for the type species and no sequence data are available for other species in the genus. *Heteroconium kleinzeense* was recently transferred to *Blastacervulus* (Crous et al. 2019a, b).

**Leptoxyphium** Spec., Phys. Rev. Soc. Arg. Cienc. Nat. 4 (17): 294. 1918.

Type species: *Leptoxyphium graminum* (Pat.) Spec.

Notes: A search in Index Fungorum and MycoBank (March 2019) listed 18 names in *Leptoxyphium*. However, sequence data are available only for the types of four species; *L. cacuminum* MFLUCC10-0059 (LSU), *L. glochidion* IFRDCC 2651 (LSU/ITS), *L. kurandae* CBS 129530 (LSU, ITS/TEF-1α/ RPB2) and *L. madagascariense* CBS 124766 (LSU, ITS/TEF-1α/ RPB2). *Leptoxyphium cacuminum* and *L. glochidion* are identical based on LSU sequences, but they are morphologically different. These species clustered in the same clade together with 14 isolates considered in this study (Figs S1, 2). Some variation in nucleotide sequences (especially RPB2) was observed within this clade, which may indicate intra- or interspecific variation. Isolates CBS 451.66 and CPC 26196 clustered in a distinct clade (Figs S1, 2) representing a new species described below.

**Leptoxyphium citri** Abdollahz. & Crous, *sp. nov.* MycoBank MB833163. Fig. 15.

Etymology: Name refers to *Citrus*, the host genus from which it was collected.

*Mycelium* superficial or immersed, grey to pale brown, branched, smooth to finely verruculose, thick-walled, septic, constricted at septa, with a mucilaginous outer wall layer, forming hyphal ropes. *Conidiomata* synnematous, simple or successively proliferating through the fertile head to produce another conidiogenous apex at a higher level, single or in groups, erect, straight to slightly flexuose; bulbous base medium to dark brown, cylindrical part dark olivaceous brown, 53–153 × 6–12 μm, expanding to a funnel-shaped hyphal apex, 20–40 μm high, 15–46 μm wide.
Conidiophores subcylindrical to subulate, septate, tightly aggregated in apical part of synnema, among synnematous hyphae that diverge close to apex. Conidiogenous cells integrated, terminal, phialidic, tapering to a truncate apex. Conidia broadly ellipsoid with rounded ends, aseptate, eguttulate, hyaline, smooth, (3.9–)4.3–4.9(-5.3) × (1.9–)2.1–2.4(-2.6) μm (av. = 4.7 × 2.2 μm, n = 50), aggregating in hyaline, slimy masses at apex of synnemata. Synasexual morph conidia arthric, single or in chains, frequently around the bulbous base of the synnema, cylindrical to ellipsoid or ovoid, 1-septate, constricted at septum, smooth, pale to medium brown, 6–12 × 2–5 μm.

Culture characteristics: Colonies, appressed, with fluffy aerial mycelium, with creamy conidial exudates, smoke grey to pale olivaceous grey after 2 wk in the dark at 25 °C. Colonies reaching 39 mm diam on MEA after 2 wk in the dark at 25 °C.

Typus: Spain, on fruit of Citrus sinensis. Jan. 1966, H.A. van der Aa (holotype CBS H-14520, culture ex-type CBS 451.66).

Additional material examined: Italy, on Citrus sp., 2015, V. Guarnaccia, culture CPC 26196 = CBS 146162, CBS H-24265.

Notes: Phylogenetically, L. citri is closely related to L. kurandae (Figs S1, 2). These two species differ in 1, 4 and 10 bp in LSU,
**Phragmocapnias** Theiss. & Syd., Ann. Mycol. 15: 480. 1918.

Saprobic on sugary exudates from insects, dark mycelium forming a soot-like coating on the upper surface of leaves. Thallus composed of black, pelliculose, reticulately branched, dense, cylindrical, radiating, septate hyphae. Ascomata scattered, subglobose to broadly ellipsoidal, barely stalked, firmly attached to the basal hyphae, dark brown, thick-walled, ostiolate, with setae. Peridium consisting of pale to dark brown cells forming a textura angularis. Asci bitunicate, 8-spored, broadly clavate, with short pedicle. Ascospores cylindrical-clavate, hyaline, 4-septate and constricted at the septum (Chomnunti et al. 2011). Conidiomata pycnidial, similar to Conidiocarpus, but with a short stalk and oval or ellipsoid part and ostiole, lacking a neck. Ostiole surrounded by hyaline, subulate hyphal extensions. Conidia small, ellipsoid, continuous, aseptate, hyaline, smooth-walled, arranged in a droplet at the apex of pycnidium (Figs 14, 16).

**Type species:** *Phragmocapnias betle* (Syd. et al.) Theiss. & Syd.

**Notes:** Of the six Conidiocarpus species for which DNA sequence data are available, two species, *Co. betle* and *Co. plumeriae*, clustered in *Phragmocapnias* (Figs S1, 2). *Phragmocapnias betle* is consequently resurrected, and a new combination is introduced for *Conidiocarpus plumeriae*.

**Phragmocapnias betle** (Syd. et al.) Theiss. & Syd., Ann. Mycol. 15: 480. 1918. Fig. 16.

**Descriptions:** Hughes (1976), Chomnunti et al. (2011).

**Notes:** Chomnunti et al. (2011) provided a detailed description for *P. betle* based on the sexual morph, and designated an epitype for the species. The following description is provided for the asexual morph:

**Mycelium** superficial or immersed, hyaline to brown, branched, hyphal smooth, thin-walled, septate, constricted at septa, with a mucilaginous outer wall layer. *Conidiocarpus pycnidial*, brown, comprised of cylindrical septate cells, (67–90)–120(–135) μm high (av. = 105 μm, n = 20), stalk brown to black, (27–) 50–70(–97) μm high (av. = 50 μm, n = 20), 12–31 diam (av. = 24 μm, n = 20), the oval, swollen part which produces conidia is brown, comprised of cylindrical, septate cells, (37–) 50–60(–69) μm high (av. = 48 μm, n = 20), (30–) 40–55(–75) μm diam (av. = 53 μm, n = 20). Ostiole surrounded by hyaline hyphae. *Conidiogenous cells* formed on the inner layer of the oval part. *Conidia* oblong to ellipsoid, aseptate, hyaline, continuous, (4–)5–6(–7.9) × (1.4–)1.8–2.2(–2.8) μm (av. = 5.5 × 2 μm, n = 50).

**Culture characteristics:** Colonies leathery, appressed, with fluffy aerial mycelium, somewhat folded at the middle, pale olivaceous grey to pale greenish grey after 2 wk in the dark at 25 °C. Colonies reaching 32–34 mm diam on MEA after 2 wk in the dark at 25 °C.

**Materials examined:** *Philippinipes*, on living leaf of unidentified palm, 2009, K.D. Hyde, culture CPC 20476. Thailand, Chiang Rai, on living leaves of unknown plant, 1 Jan. 2009, P.W. Crous, culture CPC 17762; Chiang Rai, house of K.D. Hyde, living leaves of Malus sp., 2009, P.W. Crous, culture CPC 21379.

**Phragmocapnias plumerieae** (Hongsanan & K.D. Hyde) Abdollahz. & Crous, comb. nov. MycoBank MB833164.

**Basionym:** *Conidiocarpus plumerieae* Hongsanan & K.D. Hyde, Mycosphere 6: 820. 2015.

**Description:** Hongsanan et al. (2015b).

**Notes:** This species was recently described by Hongsanan et al. (2015b) based on its sexual morph. Phylogenetically, it is closely related to *P. betle* (Figs S1, 2).

**Polychaeton** (Pers.) Lév., In: Orbigny, Dict. Univ. Hist. Nat. 8: 493. 1846.

**Mycelium** superficial or immersed, hyaline to brown, branched, consisting of smooth, thin-walled, septate hyphae, constricted at septa, with a mucilaginous outer wall layer. *Conidiomata* pycnidial, supported on a black mycelial network, narrow and cylindrical stalks composed of tightly compacted, anastomosed, synnematous cylindrical hyphae, lageniform with a brown oval or ellipsoid part which produces conidia and a long neck. The pycnidium wall is composed of two or more layers, the outer one being more or less pseudoparenchymatous although the short cells tend to be arranged linearly, indicating their origin from longitudinally fused hypha. Ostiole surrounded by hyaline, subulate, hyphal extensions. Conidia small, oblong to ellipsoid, continuous, aseptate, hyaline, smooth-walled, arranged in a droplet at the apex of pycnidium.

**Type species:** *Polychaeton quercinum* (Pers.) Kuntze

**Notes:** *Polychaeton* was introduced by Persoon as a sub-genus in *Fumago*, and raised to generic rank by Léveillé (1847). The taxonomy of *Polychaeton* was discussed by Hughes (1976) and Chomnunti et al. (2011). Hughes (1976) considered *Po. citri* and *Po. quercinum* suitable as generic types, and designated *Po. quercinum* as lectotype species of *Polychaeton*. Chomnunti et al. (2011) regarded *Capnodium* as sexual morph of *Polychaeton*, and chose *Capnodium* following the one fungus = one name concept. A search of Index Fungorum and MycoBank (March 2019) revealed several names in *Polychaeton* including *Po. citri*. In this study, we examined isolate CBS 116435 deposited in CBS as *Po. citri* (Pers.) Lév. from Iran on *Citrus aurantium*, isolated by Walter Gams. In the phylogenetic analyses (Figs S1, 2) this isolate clustered in a distinct clade close to *Conidiocarpus* and *Phragmocapnias*. Hughes (1976) mentioned that in *Polychaeton* pycnidia are supported on a stalk, have an ellipsoidal pycnidial cavity, with no conspicuous swelling, and terminate in a neck with hyaline hyphal extensions. On SNA isolate CBS 116435 produced pycnidia with a swollen body, a long neck, and a short stalk. On OA pycnidia tended to have much longer necks with no conspicuous swelling, while in *Conidiocarpus* pycnidia have a conspicuous swelling, a long neck, and are supported on a long stalk on both OA and SNA (Fig. 14). Therefore, we designate this clade as *Polychaeton*, although further studies are required to resolve the taxonomy of the various species described in the genus.

**Neoantennariellaceae** Abdollahz. & Crous, fam. nov. MycoBank MB833165.

**Etymology:** Name refers to the genus *Neoantennariella*.

**Mycelium** superficial or immersed, pale brown to brown, branched, consisting of smooth, thin-walled, septate hyphae, constricted at septa, with a mucilaginous outer wall layer.
Pycnidia superficial or immersed, mostly globose or cylindrical, pale to dark brown, intercalary, lateral or terminal on erect hyphal branches. Ostiole absent, or not well-developed, mostly releasing conidia by means of irregular rupture. Conidia hyaline, aseptate, ellipsoid to ovoid, with minute guttules, smooth, thin-walled.

**Type genus:** Neoantennariella Abdollahz. & Crous

**Fumiglobus** D.R. Reynolds & G.S. Gilbert, Cryptog. Mycol. 27: 252. 2006.

**Type species:** *F. ficinus* (Bat. et al.) D.R. Reynolds & G.S. Gilbert

**Description:** Reynolds & Gilbert (2006).

**Note:** According to Index Fungorum and MycoBank (March 2019), *Fumiglobus* presently contains 10 names, of which LSU and ITS sequences data are only available for *F. pieridicola*.

**Neoantennariella** Abdollahz. & Crous, *gen. nov.* MycoBank MB833166.
Etymology: Name reflects its morphological similarity to the genus *Antennariella*.

*Mycelium* superficial or immersed, pale brown to brown, branched, consisting of smooth, thin-walled, septate hyphae, constricted at septa, with a mucilaginous outer wall layer. *Pycnidia* superficial or immersed, mostly globose or cylindrical, pale to dark brown, mostly intercalary, lateral or terminal on erect hyphal branches. Ostiole absent, or not well-developed, mostly releasing conidia by means of irregular rupture. *Conidia* hyaline, aseptate, ellipsoid to ovoid, with minute guttules, smooth, thin-walled.

Type species: *Neoantennariella phylicae* Abdollahz. & Crous

Note: Morphologically similar to *Antennariella* (see Hughes 1976, fig. 11), but different in conidiomatal and conidium morphology.

*Neoantennariella phylicae* Abdollahz. & Crous, sp. nov. MycoBank MB833167. Fig. 17.

Etymology: Name reflects the host genus *Phylica* from which it was isolated.

*Mycelium* superficial or immersed, pale brown to brown, branched, consisting of smooth, thin-walled, septate hyphae, constricted at septa, with a mucilaginous outer wall layer. *Pycnidia* superficial or immersed, mostly globose or cylindrical, pale to dark brown, mostly intercalary, lateral or terminal on erect hyphal branches, meristogenously in development, pseudoparenchymatous, thin-walled. Ostiole absent or not well-developed, mostly releasing conidia by means of irregular rupture. *Conidia* hyaline, aseptate, oblong to ellipsoid, with minute guttules, smooth, thin-walled.

Type species: *Neoasbolisia phylicae* Abdollahz. & Crous

Note: Morphologically similar to *Asbolisia* Bat. & Cif. (*Nom. illegit.*, Art. 53.1), but as the latter is illegitimate, a new genus is introduced.

Culture characteristics: Colonies leathery, appressed, with fluffy aerial mycelium; surface folded, edge sinuate, smoke grey to glaucous grey after 2 wk in the dark at 25 °C. Colonies reaching 17 mm diam on MEA after 2 wk in the dark at 25 °C.

Typus: UK, Inaccessible Island, on *Phylica arborea*, 30 Sep. 2011, P. Ryan (holotype CBS H-24298, culture ex-type CPC 19989 = CBS 146163).

Additional materials examined: South Africa, Marion Island, Prince Edward Is., on *P. arborea*, 2011, M.J. Wingfield, culture CPC 19227 = CBS 146146, UK, Inaccessible Island, on *P. arborea*, 30 Sep. 2011, P. Ryan, cultures CPC 19977 = CBS 146165, CPC 19981 = CBS 146166, CPC 19985 = CBS 146167, CPC 19992.

*Neoasbolisia* Abdollahz. & Crous, gen. nov. MycoBank MB833168.

Etymology: Name reflects its morphological similarity to the genus *Asbolisia* Bat. & Cif.

*Mycelium* superficial or immersed, pale brown to brown, branched, consisting of smooth, thin-walled, septate hyphae, constricted at septa, with a mucilaginous outer wall layer. *Pycnidia* superficial or immersed, mostly globose or pyriform, brown to dark brown, intercalary, meristogenously in development, pseudoparenchymatous, thin-walled. Ostiole absent or not well-developed, mostly releasing conidia by means of irregular rupture. *Conidia* hyaline, aseptate, oblong to ellipsoid, with minute guttules, smooth, thin-walled.

Type species: *Neoasbolisia phylicae* Abdollahz. & Crous

Note: Morphologically similar to *Asbolisia* Bat. & Cif. (*Nom. illegit.*, Art. 53.1), but as the latter is illegitimate, a new genus is introduced.

Culture characteristics: Colonies leathery, appressed, with fluffy aerial mycelium; surface folded, edge sinuate, smoke grey to glaucous grey after 2 wk in the dark at 25 °C. Colonies reaching 17 mm diam on MEA after 2 wk in the dark at 25 °C.

Typus: UK, Inaccessible Island, on *Phylica arborea*, 30 Sep. 2011, P. Ryan (holotype CBS H-24298, culture ex-type CPC 19989 = CBS 146163).

Additional materials examined: South Africa, Marion Island, Prince Edward Is., on *P. arborea*, 2011, M.J. Wingfield, culture CPC 19227 = CBS 146146, UK, Inaccessible Island, on *P. arborea*, 30 Sep. 2011, P. Ryan, cultures CPC 19977 = CBS 146165, CPC 19981 = CBS 146166, CPC 19985 = CBS 146167, CPC 19992.

*Neoasbolisia* Abdollahz. & Crous, gen. nov. MycoBank MB833168.

Etymology: Name reflects its morphological similarity to the genus *Asbolisia* Bat. & Cif.

*Mycelium* superficial or immersed, pale brown to brown, branched, consisting of smooth, thin-walled, septate hyphae, constricted at septa, with a mucilaginous outer wall layer. *Pycnidia* superficial or immersed, mostly globose or pyriform, brown to dark brown, intercalary, meristogenously in development, pseudoparenchymatous, thin-walled. Ostiole absent or not well-developed, mostly releasing conidia by means of irregular rupture. *Conidia* hyaline, aseptate, oblong to ellipsoid, with minute guttules, smooth, thin-walled.

Type species: *Neoasbolisia phylicae* Abdollahz. & Crous

Note: Morphologically similar to *Asbolisia* Bat. & Cif. (*Nom. illegit.*, Art. 53.1), but as the latter is illegitimate, a new genus is introduced.
Neoasbolisia phylicae Abdollahz. & Crous, sp. nov. MycoBank MB833169. Fig. 18.

Etymology: Name reflects the host genus Phylica from which it was isolated.

Mycelium superficial or immersed, pale brown to brown, branched, consisting of smooth, thin-walled, septate hyphae, constricted at septa, with a mucilaginous outer wall layer. Pycnidia superficial or immersed, mostly globose or pyriform, brown to dark brown, intercalary, meristogenously developing, pseudoparenchymatous, thin-walled, 1–2 cell layers of textura angularis, (63–)80–140(–180) × (56–)70–100(–148) μm (av. = 110 × 90 μm, n = 20). Ostiole absent or not well-developed, mostly releasing conidia by means of irregular rupture. Conidia hyaline, aseptate, oblong to ellipsoid, smooth, thin-walled, (4.5–)4.6–5.2(–5.9) × (1.6–)1.8–2(–2.3) μm (av. = 5.2 × 2 μm, n = 50).

Culture characteristics: Colonies leathery, appressed, with fluffy aerial mycelium, edge sinuate, glaucous grey to olivaceous grey after 2 wk in the dark at 25 °C. Colonies reaching 14 mm diam on MEA after 2 wk in the dark at 25 °C.

Typus: UK. Inaccessible Island, on Phylica arborea, 30 Sep. 2011, P. Ryan (holotype CBS H-24299, culture ex-type CPC 19982 = CBS 146168).

Readerielliopsidaceae Abdollahz. & Crous, fam. nov. MycoBank MB833170.

Etymology: Name refers to the genus Readerielliopsis.

Mycelium superficial or immersed, hyaline to pale brown, branched, hyphae smooth, thin-walled, septate, constricted at septa, with a mucilaginous outer wall layer. Pycnidia superficial, globose to pyriform, cylindrical to flask-shaped, short to long, straight to irregular, occurring singly or in groups, medium to dark brown, if synnematous, then with a hyaline to pale brown stalk forming a long neck. Ostiole absent, or present, with or without hyphal hairs. Conidia small, hyaline, smooth, aseptate, oblong to ellipsoid or obdeltoid, or pale to medium brown, transversely euseptate, filiform, fusoid-ellipsoidal.

Type genus: Readerielliopsis Crous & Decock

Fumagospora G. Arnaud, Ann. École Nat. Agric. Montpellier, Sér. 2 10: 326. 1911.

Type species: Fumagospora capnodioides G. Arnaud

As discussed by Hughes (1976) Fumagospora with hyaline and continuous conidia that become brown and transversely septate with one or more longitudinally septate cells, is the asexual morph of some Capnodium species (e.g. Capnodium salicinum). In this study Ca. salicinum (CBS 131.34) constitutes a distinct clade in Readerielliopsidaceae separate from other Capnodium species that grouped in Capnodium sensu Chomnunti et al. (2011). In a study on capnodioaceous sooty molds in Iran, phylogenetic analysis based on ITS sequence data placed isolate GUM 1315 with Fumagospora morphology (fig. 2, Khodaparast et al. 2020) close to Ca. salicinum CBS 131.34. Therefore, we designated Fumagospora as a generic name for this clade.

Phaeoxyphiella Bat. & Cif., Quad. Lab. Crittogam., Pavia 31: 145. 1963.

Type species: Ph. morototoni Bat. & Cif.

Notes: A search in Index Fungorum and MycoBank (March 2019) revealed seven names in Phaeoxyphiella. As discussed by Hughes (1976), Batista & Ciferri proposed this generic name for seven species, which fall into two groups based on conidial morphology. Four species, Ph. bahiensis, Ph. fischeri, Ph. morototoni and Ph. walteri, have long, fusoid or spindle-shaped, deeply pigmented, multisepate phragmoconidia. Two species, Ph. californica and Ph. rondeletiae, have much shorter, oblong to

Fig. 22. Scalecoxyphium phylicae. A, B. Colony (2-wk-old) on MEA. C–F. Cylindrical-oblong, straight, simple conidiomata on SNA. G. Conidia. Scale bars: C = 25 μm; D–F = 20 μm; G = 10 μm.
ellipsoidal, 3-septate phragmoconidia, which are at first hyaline, slowly becoming brown. The seventh species, *Ph. calitis*, has 5-septate conidia, but is a nomen nudum because it lacks a Latin diagnosis. There are no cultures or sequences available for any of these species. In this study, we examined five isolates which based on phylogenetic inference clustered in two distinct clades (Figs S1, 2).

**Phaeoxyphiella australiana** Abdollahz. & Crous, sp. nov. MycoBank MB833171. 

**Etymology**: Name reflects the country where it was collected, Australia.

Culture sterile. *Phaeoxyphiella australiana*, differs from its closest phylogenetic neighbour, *Ph. phylicae*, by unique alleles in four loci based on alignments of the separate loci deposited in TreeBASE as Study S25414: RPB2 positions 52(G), 55(G), 70(A), 91(C), 112(A), 136(G), 151(C), 178(A), 238(G), 259(G), 268(T), 288(T), 334(C), 346(A), 349(T), 367(T), 379(C), 382(T), 386(C), 388(G), 520(C), 529(T), 532(A), 535(C), 551(C), 586(C), 595(C), 607(T), 661(A), 667(C), 736(G), 805(A), 826(C), 828(T), 881(A), 882(T), 8899(C), 904(C), 907(A), 937(C), 979(T), 988(A), 994(C), 1007(C), 1009(A), 1027(T), 1042(C), 1054(C), 1075(T); TEF-1α positions 60(C), 282(T), 283(T), 450(C), 489(T), 578(C), 596(C), 662(T), 674(G), 755(A), 788(T), 824(T), 848(C), 1011(A); ITS positions 67(C), 81(C), 149(T), 164(C), 412(A); LSU positions 414(T), 415(C), 609(C).

**Typus**: Australia, Western Australia, Denmark, Mount Lindesay Walk Trail, on Agonis sp., 19 Sep. 2015, P.W. Crous (*holotype* CBS H-24258, culture ex-type CPC 29527 = CBS 146169).

**Note**: *Phaeoxyphiella australiana* differs phylogenetically from *Ph. phylicae* in 3, 5, 14 and 50 bp in the LSU, ITS, TEF-1α and RPB2 sequences.

*Phaeoxyphiella phylicae* Abdollahz. & Crous, sp. nov. MycoBank MB833172. Fig. 19.

**Etymology**: Name reflects *Phylica*, the host genus from which it was collected.

**Mycelium** superficial or immersed, hyaline to medium brown, branched, hyphae smooth to slightly verruculose, thin-walled, septate, constricted at septa, with a mucilaginous outer wall layer. **Pycnidia** superficial or immersed, glutinous, sessile, obclavate, pyriform or conoidal, brown, membraneous, thin-walled, 105–200 × 60–130 μm. **Ostiole** present, simple, without hyphal extensions. **Conidia** pale to medium brown, transversely euseptate, not constricted at septa, 11–19-celled, filiform, fusoid-ellipsoidal, straight to somewhat curved, ends rounded, often with a truncate base, smooth, (43–)67–80(–90) × (5.9–)6–9(–9.8) μm, (av. = 75 × 7.7 μm, n = 50). **Spermatogonia** superficial or immersed, globose to subglobose, pale to dark brown, mostly intercalary, lateral or terminal on erect hyphal branches, 49–69 × 43–62 μm. **Ostiole** absent, releasing microconidia by means of irregular rupture. **Microconidia** hyaline, aseptate, ellipsoid to ovoid, continuous, with minute guttules, smooth, thin-walled, (3.6–)4.2–4.9(–5.1) × (2–)2.2–2.7(–2.9) μm, (av. = 4.5 × 2.4 μm, n = 50).

**Culture characteristics**: Colonies, leathery, appressed, with fluffy aerial mycelium, folded, edge sinate, glaucous grey to pale olivaceous grey after 2 wk in the dark at 25 °C. Colonies reaching 18 mm diam on MEA after 2 wk in the dark at 25 °C.

**Typus**: UK, Inaccessible Island, on *Phylica arborea*, 30 Sep. 2011, P. Ryan (*holotype* CBS H-24300, culture ex-type CPC 19993 = CBS 146170).

**Additional material examined**: UK, Inaccessible Island, on *P. arborea*, 30 Sep. 2011, P. Ryan cultures CPC 19979 = CBS 146171, CBS H-24259, CPC 19984 = CBS 146172, CPC 19987 = CBS 146173, CBS H-24260.
Notes: Phaeoxyphiella phylicae differs from all seven species described by Batista & Ciferri (1963a) by producing 11–19-celled phragmoconidia. Conidial dimensions in Ph. phylicae are close to those of Ph. walteri, but conidia are 11–19-celled in Ph. phylicae, and 3–15-celled in Ph. walteri.

Readerielliopsis Crous & Decock, Persoonia 34: 195. 2015.
Type species: Readerielliopsis fuscoporiae Crous & Decock

Description: See Crous et al. (2015).

Note: Readerielliopsis includes two species, R. fuscoporiae (isolated from basidiomata of Fuscoporia wahlbergii) and R. guayanensis (isolated from the decaying leaf of an angiosperm).

Scolecoxyphium Cif. & Bat., Publicações Inst. Micol. Recife 47: 5. 1966.

Type species: Scolecoxyphium fraserae Cif. & Bat.

Mycelium superficial or immersed, hyaline to brown, branched, hyphae smooth, thin-walled, septate, constricted at septa, with a mucilaginous outer wall layer. Pycnidia irregularly cylindrical, straight or flexuous, short or long, sessile, with no swollen part to indicate the location of the pycnidial cavity; wall is composed of linearly arranged, fused hyphae. Ostiole present, without hyaline hyphal extensions; around the ostiole the hyphae are brown and obtusely rounded. Conidia ellipsoidal, hyaline and continuous (adapted from Hughes 1976).

Notes: A search in Index Fungorum and MycoBank (March 2019) revealed four names in Scolecoxyphium. This genus was established by Ciferri and Batista based on the type species, S. fraserae (Ciferri et al. 1956). Three additional species were introduced by Batista & Ciferri (1963a). No cultures or sequence data exist for any of these species. In the phylogenies generated here, a highly supported clade was resolved resembling Scolecoxyphium (Figs S1, 2). The taxa studied here differed from all previously described species of Scolecoxyphium, and are therefore described as new.

Scolecoxyphium blechini Abdollahz. & Crous, sp. nov. MycoBank MB833174. Fig. 20.

Etymology: Name reflects the host genus Blechnum from which it was isolated.

Mycelium superficial or immersed, hyaline to brown, branched, hyphae smooth, thin-walled, septate, constricted at septa, with a mucilaginous outer wall layer. Pycnidia superficial or immersed, irregularly cylindrical-oblong, straight or flexuous, long, simple or branched, occurring singly or in groups, medium to dark brown, synnematos, on SNA 80–225 × 18–40 μm (av. = 160 × 24 μm, n = 20), on OA 180–420 × 30–57 μm (av. = 225 × 38 μm, n = 20), sessile, without swollen part and neck; wall comprising mostly of cylindrical cells. Ostiole at apex of pycnidia, without hyaline hyphal extensions. Conidia small, hyaline, aseptate, oblong to ellipsoid, continuous, (3.3–)3.5–4(–4.4) × 1.3–1.7 μm (av. = 3.8 × 1.5 μm, n = 50).

Culture characteristics: Colonies, leathery, appressed, with fluffy aerial mycelium, folded, edge sinuate, glaucous grey to pale olivaceous grey after 2 wk in the dark at 25 °C. Colonies reaching 11 mm diam on MEA after 2 wk in the dark at 25 °C.

Typus: UK, Inaccessible Island, on Blechnum palmiforme, 30 Sep. 2011, P. Ryan (holotype CBS H-24301, culture ex-type CPC 19990 = CBS 146174).

Notes: Phylogenetically (Figs S1, 2) S. blechni is closely related to S. blechnicola. Morphologically S. blechni resembles S. leucadendri, but pycnidia of S. leucadendri (av. = 500 × 30 μm) on OA are much longer than those of S. blechni (av. = 225 × 38 μm). Moreover, these two species differ in their geographical origin (S. blechni from UK, S. leucadendri from South Africa) and substrate (S. blechni on Blechnum palmiforme, S. leucadendri on Leucadendron sp.).

Scolecoxyphium blechnicola Abdollahz. & Crous, sp. nov. MycoBank MB833174.

Etymology: Name reflects the host genus Blechnum from which it was isolated.

Culture sterile. Scolecoxyphium blechnicola differs from its closely related species, Scolecoxyphium blechni by unique alleles in four loci based on alignments of the separate loci deposited in TreeBASE as Study S25414: RPB2 positions 58(T), 82(T), 133(G), 355(T), 397(T), 403(C), 472(C), 475(C), 481(A), 551(T), 577(G), 580(A), 864(G), 867(C), 985(G), 984(C); TEF-1a positions 447(C), 683(G), 737(T), 761(C), 803(T), 878(T), 969(T), 1023(C), ITS positions 92(T), 93(C), 180(C), 515(T).

Typus: UK, Inaccessible Island, on Blechnum palmiforme, 30 Sep. 2011, P. Ryan (holotype CBS H-24261, culture ex-type CPC 19991 = CBS 146175).

Note: S. blechnicola differs from S. blechni by 4, 8 and 17 nucleotides in ITS, TEF-1a and RPB2 loci, respectively.

Scolecoxyphium leucadendri Abdollahz. & Crous, sp. nov. MycoBank MB833175. Fig. 21.
**Etymology:** Name reflects the host genus *Leucadendron* from which it was isolated.

*Mycelium* superficial or immersed, hyaline to brown, branched, consisting of smooth, thin-walled, septate hyphae, constricted at septa, with a mucilaginous outer wall layer. *Pycnidia* superficial or immersed, irregularly cylindrical-oblong, straight or flexuous, long, simple or branched, occurring singly or in groups, medium to dark brown, synnematous; on SNA 104–178 × 20–37 μm (av. = 150 × 25 μm, n = 20), on OA 350–700 × 18–39 μm (av. = 500 × 30 μm, n = 20), sessile, without swelling part and neck, wall comprising mostly cylindrical cells. Ostiole at apex of pycnidia, without hyaline hyphal extensions. *Conidia* small, hyaline, aseptate, oblong to elliptoid, continuous, 3–4 × 1.3–1.6 μm (av. = 3.5 × 1.5 μm, n = 50).

**Culture characteristics:** Colonies, leathery, appressed, with fluffy aerial mycelium, folded, edge sinuate, smoke grey to olivaceous grey after 2 wk in the dark at 25 °C. Colonies reaching 12 mm diam on MEA after 2 wk in the dark at 25 °C.

**Typus:** South Africa, Western Cape Province, Hermanus, Fernkloof, on leaves of *Leucadendron* sp., 2 May 2010, P.W. Crous (holotype CBS H-24302, culture ex-type CPC 18313 = CBS 146176).

**Notes:** *Scolecoxyphium leucadendri* formed a distinct clade in the phylogenetic trees (Figs S1, 2), but is morphologically similar to *S. blechini*. The two species can be differentiated based on the pycnidial size on OA, geography and substrate.

*Scolecoxyphium phylicae* Abdollahz. & Crous, *sp. nov.* MycoBank MB833176. Fig. 22.

**Etymology:** Name reflects the fact that it was isolated from an aphid.

*Mycelium* superficial or immersed, hyaline to pale brown, branched, hyphae smooth, thin-walled, septate, constricted at septa, with a mucilaginous outer wall layer. *Pycnidia* superficial, flask-shape, simple, occurring singly or in groups, medium to dark brown, synnematous, 200–505 μm high (av. = 395 μm, n = 20), with a hyaline to pale brown stalk (50–108 × 32–74 μm, av. = 80 × 50 μm), conspicuous oval or ellipsoid central part (90–260 × 42–135 μm, av. = 210 × 80 μm), and a long neck (50–185 × 15–60 μm, av. = 115 × 20 μm); wall comprising mostly cylindrical cells. Ostiole at pycnidial apex, surrounded by hyaline hyphae. *Conidia* small, hyaline, aseptate, oblong to ellipsoid, (4.9–) 5.5–6.5(–7.8) × (1.8–)2.6–2.8 μm (av. = 6.2 × 2.2 μm, n = 50).

**Culture characteristics:** Colonies leathery, appressed, with fluffy aerial mycelium and creamy exudates conidia; surface folded, edge sinuate, glaucous grey to olivaceous grey after 2 wk in the dark at 25 °C. Colonies reaching 18 mm diam on MEA after 2 wk in the dark at 25 °C.

**Typus:** Country unknown, on aphid, 1933, dep. L.H. Leonian (holotype CBS H-24272, culture ex-type CBS 325.33).

**Notes:** Phylogenetically (Figs S1, 2) *Sc. aphidis* clustered in a clade containing *Sc. mangiferae*, *Sc. spongiosa* and *Sc. camelliae*, but differs from *Sc. mangiferae* in 8 bp in LSU and 7 bp in ITS, from *Sc. mangiferae* in 7 bp in LSU and from *Sc. camelliae* in 9 bp in LSU, 8 bp in ITS, 28 bp in 5EF-1a and 94 bp in RP2. Morphologically, conidia of *Sc. aphidis* (av. = 6.2 × 2.2 μm, on SNA) are larger than those of *Sc. spongiosa* (av. = 3.9 × 1.9 μm on PDA) and *Sc. camelliae* (av. = 5.6 × 2.4 μm on SNA), but similar to conidia of *Sc. mangiferae* (av. = 6.7 × 2.5 μm in vivo). Moreover, pycnidia of *Sc. camelliae* (av. = 100 μm) are much shorter than those of *Sc. aphidis* (av. = 395 μm).

*Scorias camelliae* Abdollahz. & Crous, *sp. nov.* MycoBank MB833178. Fig. 24.

**Etymology:** Name reflects the host genus *Camillia* from which it was collected.

*Mycelium* superficial or immersed, hyaline to pale brown, branched, hyphae smooth, thin-walled, septate, constricted at septa, with a mucilaginous outer wall layer. *Pycnidia* superficial, flask-shape, simple, occurring singly or in groups, medium to dark brown, synnematous, 59–163 μm high (av. = 100 μm,
n = 20), sessile or with short stalk (11–30 × 12–24 μm, av. = 15 × 17 μm), with conspicuous oval or ellipsoidal central part (37–85 × 16–57 μm, av. = 45 × 35 μm), and a long neck (19–77 × 6–27 μm, av. = 45 × 12 μm); wall comprising mostly cylindrical cells. Ostiole at apex of pycnidia, surrounded by hyaline hyphae. Conidia small, hyaline, aseptate, ellipsoidal to ovoid, (4.4–)5.3–5.7(–7.4) μm × (1.9–)2.2–2.5(–2.9) μm (av. = 5.6 × 2.4 μm, n = 50).

Culture characteristics: Colonies, leathery, appressed, with fluffy aerial mycelium; surface folded, edge sinuate, dirty white to olivaceous grey after 2 wk in the dark at 25 °C. Colonies reaching 20 mm diam on MEA after 2 wk in the dark at 25 °C.

Typus: Indonesia, Java island, Bogor, Buitenzorg, on Camellia sinensis leaves, 1930, isol. Steinhann, dep. F.H. van Beyma (holotype CBS H-24273, culture ex-type CBS 201.30).

Notes: In the phylogenetic analyses (Fig. 2), Sc. camelliae clustered with Sc. spongiosa and Sc. mangiferae, but differs from Sc. spongiosa in 8 bp in LSU and from Sc. mangiferae in 10 bp in LSU and 1 bp in ITS. Morphologically, conidia of Sc. camelliae (av. = 5.6 × 2.4 μm on SNA) are larger than those of Sc. spongiosa (av. = 3.9 × 1.9 μm on PDA) and smaller than conidia of Sc. mangiferae (av. = 6.7 × 2.5 μm in vivo).

DISCUSSION

The Capnodiales was originally established for three families of sooty moulds, namely Antennariariaceae, Capnodicaceae and Coccodiniaceae (Woronichin 1925). Schoch et al. (2006) transferred Mycosphaerellaceae and Piedraeiaceae to the Capnodiales and recognised the Cladosporiaceae (= Davidiellaceae), thereby expanding the concept of the order. Subsequent phylogenetic studies further expanded the concept of Capnodiales, making it the second largest order of Dothideomycetes. These included fungi with a broad spectrum of morphology, life-styles and modes of nutrition, accommodating saprobic, plant and human pathogens, mycoparasites,lichenised and rock-inhabiting fungi, including epi-, endo- and endophytes (Crous et al. 2009, Schoch et al. 2006, 2009, Schoch & Grube 2015). Based on this broad definition, we have included a collection of isolates representing 11 families: Capnodicaceae, Cladosporiaceae, Cystocoleaceae, Dissorconiaaceae, Extermaceae, Mycosphaerellaceae, Neodevriesiaceae, Phaeotheciadiaceae, Phaeothecidiellaceae, Racodiaceae, Schizothyriaceae, Teratosphaeriaceae (including Piedraeiaceae) and two incertae sedis genera, Communitispor and Phaeotheca.

Previous phylogenetic studies on Capnodiales all suffered from a limited sampling of true sooty moulds, an aspect that we have addressed in the present study. In addition, we have included two protein-coding genes (TEF-1α and RPB2) together with rDNA sequence data (LSU and ITS) to achieve a more stable and robustly supported phylogeny for this extremely diverse group of fungi.

Sooty moulds are presently classified in seven families, with some miscellaneous genera in either Dothideomycetes or Eurotiomycetes (Chomnunti et al. 2014). Dothideomycetous sooty moulds belong to four families, namely Antennariariaceae, Capnodicaceae, Euantennariaceae and Metacapnodicaceae. Although many studies have focused on the taxonomy of sooty moulds (Hughes 1951, 1966, 1972, 1976, 1981, 2003, 2007, Yamamoto, 1954, Batista & Ciferni 1963a, b, Reynolds, 1975, 1979, 1986, 1998, Faull et al. 2002, Reynolds & Gilbert, 2005, 2006, Crous et al. 2007b, 2011a, b, Ruiz et al. 2008, Cheewangkoon et al. 2009, Chomnunti et al. 2011, 2014, Ren et al. 2012, Bose et al. 2014, Yang et al. 2014, Hongsanan et al. 2015a, b, Liu et al. 2015), cultures for inclusion in the present study were available only for Capnodiales.

In an attempt to explain the high levels of diversity in the Capnodiales, the resulting phylogenetic tree (LSU, TEF-1α and RPB2) revealed Capnodiales s. lat. as polyphyletic, representing seven orders. As a result, Capnodiales s. str. was redefined, the Mycosphaerellales was resurrected, and five new orders were introduced. These include the Cladosporiales, Communitisporales, Neophaeothecales, Phaeothecales and the Racoidiales.

All sooty mould isolates in both the RAxML and Bayesian analyses, constituted a well-supported monophyletic clade thus defining Capnodiales s. str. (ML-BS = 90 %, PP = 1). The monophyly of the sooty moulds was also supported by their unique morphology, ecology and mode of nutrition. Sooty moulds are epiphytes usually with dark-coloured and mucilaginous hyphae, occurring superficially on living plants. They are often associated with insects producing honeydew, and derive nutrients from the excretion of these insects, but they can occur also without insects and absorb other nutrients (Hughes 1976, Crous et al. 2009, Chomnunti et al. 2014). In the present study three families are recognised in Capnodiales s. str., namely Capnodicaceae, Neoaatennariellaceae and Readerielliposidaceae of which the latter two are newly described. Seven genera are recognised in Capnodiales: Capnodium, Chetacapnodium, Conidiocarpus, Heterconium, Leptoxyphium, Phragmocapnias and Polychaeton. Based on morphology and phylogenetic analyses Phragmocapnias has been resurrected and a further 11 new species have been introduced in the family, which includes both hyphomycetous and coelomycetous assexual morphs.

The Neoaatennariellaceae is introduced to accommodate Fumiglobus and two new monotypic genera, Neoaatennariella and Neosboliosis. All three genera produce pycnidial conidiodia. In Readerielliposidaceae four coelomycetous genera, namely Phaeoxyphelia, Readeriellipsis, Solecoryphium and Scorias, and eight new species have been recognised.

Hawksworth et al. (1995) introduced Mycosphaerellaceae in the Dothideales, while Kirk et al. (2001) elevated this family to the order Mycosphaerellales, and Schoch et al. (2006) and Kirk et al. (2008) again placed it as a family in the Capnodiales. Despite high support values obtained in subsequent phylogenetic studies (Crous et al. 2009, Schoch et al. 2009, Suetrong et al. 2009, Hyde et al. 2013), the Mycosphaerellales was never resurrected, and the Capnodiales was applied in a broad sense beyond the original concept presented by Woronichin (1926) to accommodate the sooty moulds. In our multigene phylogeny (LSU, TEF-1α and RPB2) using both RAxML and Bayesian analyses, we found Mycosphaearella to represent a fully supported clade (ML-BS = 100 %, PP = 1) accommodating eight families, namely Cystocoleaceae, Dissorconiaaceae, Extermaceae, Mycosphaerellaceae, Neodevriesiaceae, Phaeotheciidiellaceae, Schizothyriaceae and Teratosphaeriaceae. We have consequently resurrected Mycosphaerellales as a separate order and provided an amended description for it. Although the Mycosphaerellales includes species that are saprobes, ectophytes, plant pathogens and lichenised fungi, this order is mainly characterised by plant pathogenic fungi that are commonly
isolated as endophytes, being ecologically distinct from the sooty moulds, which are epiphytes. Xu et al. (2017) and Ismail et al. (2016) showed that the ecophytic sooty blotch and flyspeck fungi (Dissoconiaeae, Pheothecidiellaeae, Schizothyriaceae) have evolved from ancestral phytopathogenic relatives. Lichenisation has occurred once in Cystocoleaceae, while plant pathogens are found in Mycosphaerellaeae, Neodevriesiaceae, and Teratosphaeriaceae and human pathogens have evolved in Teratosphaeriaceae. To better elucidate the general evolutionary pattern, a greater number of samples and genome-wide comparative analyses will be conducted in future studies.

Members of Cladosporiaceae are chiefly saprobic and endophytic, with a few species that are fungicolous, lichenicolous, or plant pathogenic. In a series of phylogenetic studies, members of Cladosporiales were resolved as a distinct clade apart from Capnodiaceae, Mycosphaerellaceae and allied families: Dissoconiaeae, Extremaceae, Neodevriesiaceae, Pheothecidiellaeae, Schizothyriaceae and Teratosphaeriaceae (Crous et al. 2009, Schoch et al. 2006, 2009, Suertong et al. 2009, Bensch et al. 2012, Hyde et al. 2013, Van Nieuwenhuijzen et al. 2016, Videira et al. 2017). In the present study, Cladosporiaceae clustered apart from Mycosphaerellaceae and Capnidiaceae s. str. and formed a distinct clade sister to Committinsopora agavaciensis. Therefore, Cladosporiaceae has been elevated to ordinal level as Cladosporiales. Morphologically, members of Cladosporiales are quite distinct from those of Mycosphaerellaceae, having long, solitary, flexuous conidiophores with chains of dry, pigmented conidia. Ecologically, conidia of Cladosporiales can rehydrate, germinate and grow within hours, while members of Mycosphaerellaceae are generally slow to reanimate, and far less hardy to extremes in temperature and moisture conditions.

Endocodial taxa within Capnidiaceae s. lat. that belong to Committinsopora and Pheotheca have received considerable attention (Sigler et al. 1981, Ramaley 1996, de Hoog et al. 1997, 1999, Zalar et al. 1999, Crous et al. 2009, 2016, 2018). These saprobic fungi (de Hoog et al. 1999, Crous et al. 2009) were found to occupy a basal position in the phylogenetic tree (Figs S1, 1, 3), representing three new orders, namely Committinsoporales, Neophaeothecales and Pheothecales. Furthermore, our results have resolved Pheotheca as polyphyletic, representing two distinct clades. Pheotheca fissurella (Pheothecaceae ord. nov.) clustered apart from P. salicinia and P. triangularis in a clade together with the lichen Racodium rupestre. Racodium rupestre clusters in a separate clade apart from another lichen species, Cystocoleus ebeneus (Cystocoleaceae, Mycosphaerellaceae), and represents a new order, Racoziosiales ord. nov. Phaeotheca salicornia and P. triangularis occupied the basal position in the phylogenetic tree (Figs S1, 1, 3) as one of the earliest lineages in Capnidiaceae s. lat., for which we introduced a new genus Neophaeotheca (Neophaeothecaceae fam. nov. and Neophaeothecaceae ord. nov.). Members of Phaeothecaceae, Racoziosiales and Neophaeothecaceae are commonly isolated under more dry, extreme conditions.

The present study has provided a more stable backbone for the phylogeny of sooty moulds and allied taxa formerly classified in what was circumscribed as “Capnidiaceae s. lat.” Many families are not yet represented in our phylogenetic analysis, pending further collections. Although our results revealed Capnidiaceae s. lat. as polyphyletic, including seven different orders, this remains a work in progress. Furthermore, phylogenetic ancestral reconstruction analysis has revealed the saprobic lifestyle to be a primitive state in Capnodiales s. lat. (see Neophaeothecaceae; Fig. 3), while Haridas et al. (2020) also showed the ancestral state of Dothideomycetes to be saprobic. Several transitions have occurred to evolve lichenised, epiphytic and plant and human pathogenic lifestyles (Hongsanan et al. 2016, Ametrano et al. 2019), with the sooty mould ecology apparently having evolved more recently. A more robust sampling of the unexplored or little-known clades of Dothideomycetes, and genome-wide comparative analyses will provide greater clarity on the evolutionary patterns of lifestyles and modes of nutrition, that has made it possible for communities of Dothideomycetes to adapt to changing environmental conditions.

ACKNOWLEDGEMENTS

Jafar Abdollahzadeh was supported by the University of Kurdistan, Sanandaj, Kurdistan Province, Iran during his sabbatical leave at the Westerdijk Fungal Biodiversity Institute.

APPENDIX A. SUPPLEMENTARY DATA

Supplementary data to this article can be found online at https://doi.org/10.1016/j.simyco.2020.02.004.

REFERENCES

Ametrano CG, Grewe F, Crous PW, et al. (2019). Genome-scale data resolve ancestral rock-inhabiting lifestyle in Dothideomycetes (Ascomycota). IMA Fungus 10: 19.

Aptroot A. (2006). Mycosphaerella and its anamorph 2. Conspectus of mycosphaerella. CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands: 1–231. CBS Biodiversity Series 5.

Batista AC, Ciferri R (1963a). Capnidiaceae. Saccardia 2: 1–296.

Batista AC, Ciferri R (1963b). The sooty-molds of the family Asbolisiaceae. Quaderno del Laboratorio Crittogamico del Istituto Botanico dell’Università di Pavia 31: 1–229.

Bensch K, Braun U, Groenewald JZ, et al. (2012). The genus Cladosporium. Studies in Mycology 72: 1–401.

Bezerromycetales

Cheez JD, Oliveira RJ, Paiva LM, et al. (2017). Bezerromycetales and Wiesneriomycetales ord. nov. (class Dothideomycetes), with two novel genera to accommodate endophytic fungi from Brazilian cactus. Mycological Progress 16: 297–309.

Bose T, Reynolds DR, Berbee ML (2014). Common, unsuspected and until now undescribed: Fumiglobus pleistocenicus sp. nov., a sooty mold infesting Pieris japonica from western North America. Mycologia 106: 746–756.

Cheewangkoon R, Groenewald JZ, Hyde KD, et al. (2012). Chocolate spot disease of Eucalyptus. Mycological Progress 11: 61–69.

Cheewangkoon R, Groenewald JZ, Summerell BA, et al. (2009). Myrtaceae, a cache of fungal biodiversity. Persoonia 23: 55–85.

Chomnunti P, Hongsanan S, Aguirre-Hudson B, et al. (2014). The sooty moulds. Fungal Diversity 66: 1–36.

Chomnunti P, Schoch CL, Aguirre-Hudson B, et al. (2011). Capnodiales. Fungal Diversity 51: 102–134.

Ciferri R, Batista AC, Nascimento ML (1956). Two new genera of pycnidiaceous Asbolisiaceae. Mycospharella and its anamorphs 2. Conspectus of mycosphaerella. Aptroot A (2006). Dothideomycetes (Ascomycota) ancestral rock-inhabiting lifestyle in Dothideomycetes (Ascomycota). IMA Fungus 10: 19.

Aptroot A. (2006). Mycosphaerella and its anamorph 2. Conspectus of mycosphaerella. CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands: 1–231. CBS Biodiversity Series 5.

Batista AC, Ciferri R (1963a). Capnidiaceae. Saccardia 2: 1–296.

Batista AC, Ciferri R (1963b). The sooty-molds of the family Asbolisiaceae. Quaderno del Laboratorio Crittogamico del Istituto Botanico dell’Università di Pavia 31: 1–229.

Bensch K, Braun U, Groenewald JZ, et al. (2012). The genus Cladosporium. Studies in Mycology 72: 1–401.

Bezerromycetales

Cheez JD, Oliveira RJ, Paiva LM, et al. (2017). Bezerromycetales and Wiesneriomycetales ord. nov. (class Dothideomycetes), with two novel genera to accommodate endophytic fungi from Brazilian cactus. Mycological Progress 16: 297–309.

Bose T, Reynolds DR, Berbee ML (2014). Common, unsuspected and until now undescribed: Fumiglobus pleistocenicus sp. nov., a sooty mold infesting Pieris japonica from western North America. Mycologia 106: 746–756.

Cheewangkoon R, Groenewald JZ, Hyde KD, et al. (2012). Chocolate spot disease of Eucalyptus. Mycological Progress 11: 61–69.

Cheewangkoon R, Groenewald JZ, Summerell BA, et al. (2009). Myrtaceae, a cache of fungal biodiversity. Persoonia 23: 55–85.

Chomnunti P, Hongsanan S, Aguirre-Hudson B, et al. (2014). The sooty moulds. Fungal Diversity 66: 1–36.

Chomnunti P, Schoch CL, Aguirre-Hudson B, et al. (2011). Capnodiales. Fungal Diversity 51: 102–134.

Ciferri R, Batista AC, Nascimento ML (1956). Two new genera of pycnidiaceous Asbolisiaceae. Mycosphaerella and its anamorphs 2. Conspectus of mycosphaerella. Aptroot A (2006). Dothideomycetes (Ascomycota) ancestral rock-inhabiting lifestyle in Dothideomycetes (Ascomycota). IMA Fungus 10: 19.
Smith CW, Aptroot A, Coppins BJ, et al. (2009). The Lichens of Great Britain and Ireland. British Lichen Society, London.

Stamatakis A (2014). RAxML Version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30: 1844–1849.

Suetrong S, Schoch CL, Spatafora JW, et al. (2009). Molecular systematics of the marine Dothideomycetes. Studies in Mycology 64: 155–173.

Sung G-H, Sung J-M, Hywel-Jones NL, et al. (2007). A multigene phylogeny of Clavicipitaceae (Ascomycota, Fungi): identification of localized incongruence using a combinational bootstrap approach. Molecular Phylogenetics and Evolution 44: 1204–1223.

Van Nieuwenhuijzen EJ, Miadlikowska JM, Houbraken JA, et al. (2016). Wood staining fungi revealed taxonomic novelties in Pezizomycotina: new order Superstratomycetales and new species Cyanodermella oleoligni. Studies in Mycology 85: 107–124.

Videira SI, Groenewald JZ, Nakashima C, et al. (2017). Mycosphaerellaceae – chaos or clarity? Studies in Mycology 87: 257–421.

Vilgalys R, Hester M (1990). Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several Cryptococcus species. Journal of Bacteriology 172: 4238–4246.

White TJ, Bruns T, Taylor J (1990). Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: A guide to molecular methods and applications (Innis MA, Gelfand DH, Sninsky JJ, White JW, eds). Academic Press, New York: 315–322.

Wijayawardene NN, Hyde KD, Tibpromma S, et al. (2017). Towards incorporating asexual fungi in a natural classification: checklist and notes 2012–2016. Mycosphere 8: 1457–1555.

Woronichin NN (1926). Zur Kenntnis der Morphologie und Systematik der Russtaulzle Transkaukasiens. Annales Mycologici 24: 231–264.

Woronichin NN (1925). Über die Capnodiales. Annales Mycologici 23: 174–178.

Yamamoto W (1954). Taxonomic studies on the Capnodiaceae 2. On the species of the Eucapnodiae. Annals of Phytopathological Society of Japan 19: 1–5.

Xu C, Zhang R, Sun G, et al. (2017). Comparative genome analysis reveals adaptation to the ectophytic lifestyle of sooty blotch and flyspeck fungi. Genome Biology and Evolution 9: 3137–3151.

Yang H, Ariyawansa HA, Wu HX, et al. (2014). The genus Leptoxyphium (Capnodiaceae) from China. Phytotaxa 176: 174–183.

Zalar P, de Hoog GS, Gunde-Cimerman N (1999). Taxonomy of the endoconidial black yeast genera Phaeotheca and Hyphospora. Studies in Mycology 43: 49–56.