

# Evolution of lifestyles in *Capnodiales*

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**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), lichenised, epi-, 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 *Racodiales* 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, *Racodiales* Abdollahz. & Crous.

**New families:** *Comminutisporaceae* Abdollahz. & Crous, *Neoantennariellaceae* Abdollahz. & Crous, *Neophaeotheceaceae* Abdollahz. & Crous, *Readeriellipsidaceae* Abdollahz. & Crous.

**New genera:** *Neoantennariella* Abdollahz. & Crous, *Neoasbolisia* Abdollahz. & Crous, *Neophaeothecha* Abdollahz. & Crous.

**New species:** *Capnodium alfenasii* Abdollahz. & Crous, *Capnodium blackwelliae* Abdollahz. & Crous, *Capnodium gamsii* Abdollahz. & Crous, *Capnodium neocoffeicola* Abdollahz. & Crous, *Capnodium paracoffeicola* Abdollahz. & Crous, *Chaetocapnodium summerellii* Abdollahz. & Crous, *Chaetocapnodium indonesiacum* Abdollahz. & Crous, *Chaetocapnodium insulare* Abdollahz. & Crous, *Chaetocapnodium tanzanicum* Abdollahz. & Crous, *Chaetocapnodium thailandense* Abdollahz. & Crous, *Leptoxophium citri* Abdollahz. & Crous, *Neoantennariella phyllicae* Abdollahz. & Crous, *Neoasbolisia phyllicae* Abdollahz. & Crous, *Phaeoxyphiella australiana* Abdollahz. & Crous, *Phaeoxyphiella phyllicae* Abdollahz. & Crous, *Scolecoxyphium blechni* Abdollahz. & Crous, *Scolecoxyphium blechnicola* Abdollahz. & Crous, *Scolecoxyphium leucadendri* Abdollahz. & Crous, *Scolecoxyphium phyllicae* Abdollahz. & Crous, *Scorias aphidis* Abdollahz. & Crous, *Scorias camelliae* Abdollahz. & Crous.

**New combinations:** *Chaetocapnodium philippinense* (Hongsanan & K.D. Hyde) Abdollahz. & Crous, *Chaetocapnodium placitae* (Cheewangkoon & Crous) Abdollahz. & Crous, *Neophaeothecha salicorniae* (Crous & Roets) Abdollahz. & Crous, *Neophaeothecha triangularis* (de Hoog & Beguin) Abdollahz. & Crous, *Phragmocapnias plumeriae* (Hongsanan & K.D. Hyde) Abdollahz. & Crous.

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## 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 Nieuwenhuijzen *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 asci with fissitunicate 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 *Myrangiales* (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 periphyses as a synapomorphic feature (Schoch *et al.* 2006). Taxa in this order lack pseudoparaphyses, but include several species with periphysoids and periphyses (Lumbsch & Lindemuth 2001).

As discussed by Schoch & Grube (2015), the *Capnodiales* was established based on the sooty moulds in three families, *Antennulariaceae*, *Capnodiaceae*, 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

**Table 1.** Details of the sooty mould isolates included in this study. Type cultures and sequences generated in this study are in **bold** face.

Family and Species name	Voucher/Culture <sup>1</sup>	Substrate/Lifestyle <sup>2</sup>	Country/Location	Collector	GenBank accession numbers <sup>3</sup>			
					LSU	ITS	TEF-1 $\alpha$	RPB2
<b>Capnodiaceae</b>								
<i>Capnodium alfenasii</i>	<b>CBS 146151 = CPC 22666</b>	<i>Tabebuia</i> sp.	Brazil	A.C. Alfenas	<b>MN749165</b>	<b>MN749233</b>	<b>MN829346</b>	<b>MN829260</b>
	CBS 146152 = CPC 22667	<i>Tabebuia</i> sp.	Brazil	A.C. Alfenas	<b>MN749166</b>	<b>MN749234</b>	<b>MN829347</b>	<b>MN829261</b>
<i>Ca. blackwelliae</i>	<b>CBS 133588 = CPC 14327</b>	<i>Myrtus communis</i>	USA	P.W. Crous	MH878118	<b>MN749235</b>	GU349054	GU371743
<i>Ca. coartatum</i>	<b>MFLUCC10-0069</b>	<i>Psidium</i> sp.	Thailand	P. Chomnunti	JN832614	–	–	–
	MFLUCC10-0070	–	Thailand	P. Chomnunti	JN832615	–	–	–
	CPC 17779	<i>Alstonia scholaris</i>	Thailand	K.D. Hyde	<b>MN749167</b>	<b>MN749236</b>	<b>MN829348</b>	<b>MN829262</b>
<i>Ca. coffeae</i>	CBS 147.52 = AFTOL-ID 939	<i>Coffea robusta</i>	Zaire	Deposited by J. Nicot/Isolated by A. Saccas	GU214400	DQ491515	DQ471089	KT216519
<i>Ca. coffeicola</i>	<b>MFLUCC15-0206</b>	<i>Coffea</i> sp.	Thailand	S. Hongsanan	KU358920	KU358921	–	–
<i>Ca. gamsii</i>	<b>CBS 892.73</b>	Sooty mould, on unknown leaf	Sri Lanka	W. Gams	GU301847	<b>MN749237</b>	GU349045	GU371736
	CBS 146153 = CPC 17765	<i>Lagerstroemia speciosa</i>	Thailand	K.D. Hyde	<b>MN749168</b>	<b>MN749238</b>	<b>MN829349</b>	<b>MN829263</b>
	MFLUCC10-0066	–	Thailand	S.K. Chandranath	JN832613	–	–	–
	CBS 146154 = CPC 20466 = MFLUCC12-0101	<i>Lagerstroemia floribunda</i>	Thailand	S. Hongsanan	<b>MN749169</b>	<b>MN749239</b>	<b>MN829350</b>	<b>MN829264</b>
	CBS 146155 = CPC 20467 = MFLUCC12-0102	<i>Lagerstroemia floribunda</i>	Thailand	S. Hongsanan	<b>MN749170</b>	<b>MN749240</b>	<b>MN829351</b>	<b>MN829265</b>
	CBS 146156 = CPC 20471 = MFLUCC12-0107	Living leaf of unknown host	Thailand	S. Hongsanan	<b>MN749171</b>	<b>MN749241</b>	<b>MN829352</b>	<b>MN829266</b>
<i>Ca. neocoffeicola</i>	<b>CBS 139614</b> = MFLUCC14-0570	<i>Coffea arabica</i>	Thailand	S. Hongsanan	<b>MN749172</b>	<b>MN749242</b>	<b>MN829353</b>	<b>MN829267</b>
	CBS 139613 = MFLUCC14-0569	<i>Coffea arabica</i>	Thailand	S. Hongsanan	<b>MN749173</b>	<b>MN749243</b>	<b>MN829354</b>	<b>MN829268</b>
<i>Ca. paracoffeicola</i>	<b>CBS 139616</b> = MFLUCC 14-0572	<i>Coffea arabica</i>	Thailand	S. Hongsanan	<b>MN749174</b>	<b>MN749244</b>	<b>MN829355</b>	<b>MN829269</b>
	CBS 139615 = MFLUCC14-0571	<i>Coffea arabica</i>	Thailand	S. Hongsanan	<b>MN749175</b>	<b>MN749245</b>	<b>MN829356</b>	<b>MN829270</b>
<i>Chaetocapnodium indonesiacum</i>	<b>CBS 202.30</b>	<i>Camelia sinensis</i>	Indonesia	Deposited by F.H. van Beyma/Isolated by Steinmann	GU301849	MH855113	GU349060	<b>MN829273</b>
<i>Ch. insulare</i>	<b>CBS 146159 = CPC 19221</b>	<i>Phyllica arborea</i>	South Africa	M.J. Wingfield	<b>MN749178</b>	<b>MN749248</b>	<b>MN829359</b>	<b>MN829274</b>
	CBS 146160 = CPC 19223	<i>Phyllica arborea</i>	South Africa	M.J. Wingfield	<b>MN749179</b>	<b>MN749249</b>	<b>MN829360</b>	<b>MN829275</b>
	CBS 146161 = CPC 19224	<i>Phyllica arborea</i>	South Africa	M.J. Wingfield	<b>MN749180</b>	<b>MN749250</b>	<b>MN829361</b>	<b>MN829276</b>
<i>Ch. philippinense</i>	<b>MFLUCC12-0110</b> = CPC 20474	Palm	Philippines	K.D. Hyde	KP744503	<b>MN749251</b>	<b>MN829362</b>	<b>MN829277</b>
<i>Ch. placitae</i>	<b>CBS 124758 = CPC 13706</b>	<i>Eucalyptus placita</i>	Australia	B.A. Summerell	GQ303299	GQ303268	<b>MN829363</b>	<b>MN829278</b>
<i>Ch. siamensis</i>	<b>MFLUCC13-0778</b>	Leaves of unidentified plant	Thailand	S. Hongsanan	KP744479	–	–	–
	CBS 139815 = MFLUCC13-0096	Leaves of unidentified plant	Thailand	S.C. Karunaratna	<b>MN749181</b>	<b>MN749252</b>	<b>MN829364</b>	<b>MN829279</b>
<i>Ch. summerellii</i>	<b>CBS 146157 = CPC 13654</b>	<i>Eucalyptus placita</i>	Australia	B.A. Summerell	<b>MN749176</b>	<b>MN749246</b>	<b>MN829357</b>	<b>MN829271</b>

Table 1. (Continued).

Family and Species name	Voucher/Culture <sup>1</sup>	Substrate/Lifestyle <sup>2</sup>	Country/Location	Collector	GenBank accession numbers <sup>3</sup>			
					LSU	ITS	TEF-1 $\alpha$	RPB2
	CBS 146158 = CPC 17368	–	Laos	P. Pheng	<b>MN749177</b>	<b>MN749247</b>	<b>MN829358</b>	<b>MN829272</b>
<i>Ch. tanzanicum</i>	<b>CBS 145.79</b>	Lichen	Tanzania	–	<b>MN749182</b>	<b>MN749253</b>	<b>MN829365</b>	<b>MN829280</b>
<i>Ch. thailandense</i>	<b>CBS 139619</b> = MFLUCC13-0787	–	Thailand	S.C. Karunarathna	<b>MN749183</b>	<b>MN749254</b>	<b>MN829366</b>	<b>MN829281</b>
<i>Conidiocarpus asiticus</i>	<b>MFLUCC10-0062</b>	<i>Coffea arabica</i>	Thailand	J.K. Liu	JN832612	KU358924	–	–
<i>Co. caucasicus</i>	<b>GUMH 937</b>	<i>Citrus sinensis</i>	Iran	F. Byrami	KC833050	–	–	–
<i>Co. siamensis</i>	<b>MFLUCC10-0064</b>	<i>Mangifera indica</i>	Thailand	R. Phokhomsak	JN832609	–	–	–
<i>Co. siamensis</i>	MFLUCC10-0061	–	Thailand	P. Chomnunti	JN832607	KU358923	–	–
<i>Co. siamensis</i>	MFLUCC10-0063	<i>Coffea arabica</i>	Thailand	J.K. Liu	JN832608	KU358925	–	–
<i>Conidiocarpus</i> sp.	CPC 17778	<i>Guave</i> sp.	Thailand	K.D. Hyde	<b>MN749185</b>	<b>MN749256</b>	<b>MN829368</b>	<b>MN829283</b>
	CPC 20463 = MFLUCC12-0098	<i>Malus</i> sp.	Thailand	W. Saowanee	<b>MN749187</b>	<b>MN749258</b>	<b>MN829370</b>	<b>MN829285</b>
	CPC 20464 = MFLUCC12-0099	<i>Mimusops elengi</i>	Thailand	S. Hongsanan	<b>MN749194</b>	<b>MN749265</b>	<b>MN829377</b>	<b>MN829292</b>
	CPC 20465 = MFLUCC12-0100	<i>Mimusops elengi</i>	Thailand	S. Hongsanan	<b>MN749191</b>	<b>MN749262</b>	<b>MN829374</b>	<b>MN829289</b>
	CPC 20468 = MFLUCC12-0103	Mango	Thailand	Puttaluk	<b>MN749193</b>	<b>MN749264</b>	<b>MN829376</b>	<b>MN829291</b>
	CPC 20472 = MFLUCC12-0108	Living leaf of unknown host	Thailand	S. Hongsanan	<b>MN749188</b>	<b>MN749259</b>	<b>MN829371</b>	<b>MN829286</b>
	CPC 21380 = MFLUCC12-0404	<i>Malus</i> sp.	Thailand	K.D. Hyde	<b>MN749186</b>	<b>MN749257</b>	<b>MN829369</b>	<b>MN829284</b>
	CBS 139818 = MFLUCC14-0874	<i>Coffea arabica</i>	Thailand	S. Hongsanan	<b>MN749190</b>	<b>MN749261</b>	<b>MN829373</b>	<b>MN829288</b>
	CBS 139819 = MFLUCC14-0875	<i>Coffea arabica</i>	Thailand	S. Hongsanan	<b>MN749192</b>	<b>MN749263</b>	<b>MN829375</b>	<b>MN829290</b>
	CBS 139820 = MFLUCC 14-0876	<i>Coffea arabica</i>	Thailand	S. Hongsanan	<b>MN749184</b>	<b>MN749255</b>	<b>MN829367</b>	<b>MN829282</b>
	CBS 139821 = MFLUCC14-0877	<i>Coffea arabica</i>	Thailand	S. Hongsanan	<b>MN749189</b>	<b>MN749260</b>	<b>MN829372</b>	<b>MN829287</b>
<i>Heteroconium citharexyl</i>	<b>HM628775</b>	<i>Citharexylum ilicifolium</i>	Ecuador	H. Sydow	HM628775	HM628776	–	–
<i>Leptoxyphium cacuminum</i>	<b>MFLUCC10-0059</b>	<i>Gossypium herbaceum</i>	Thailand	S.C. Karunarathna	JN832603	–	–	–
	MFLUCC10-0049	<i>Mimusops elengi</i>	Thailand	P. Chomnunti	JN832602	–	–	–
	MFLUCC10-0086	<i>Ficus</i> sp.	Thailand	K.D. Hyde	JN832604	–	–	–
<i>L. citri</i>	<b>CBS 451.66</b>	<i>Citrus sinensis</i>	Spain	H.A. van der Aa	KF902094	<b>MN749266</b>	GU349039	<b>GU371727</b>
	CBS 146162 = CPC 26196	–	–	V. Guarnaccia	<b>MN749195</b>	<b>MN749267</b>	<b>MN829378</b>	<b>MN829294</b>
<i>L. glochidion</i>	<b>IFRDCC 2651</b>	<i>Glochidion wrightii</i>	China	H. Yang	KF982308	KF982307	–	–
<i>L. kurandae</i>	<b>CBS 129530 = CPC 17274</b>	<i>Eucalyptus</i> sp.	Australia	P.W. Crous & R.G. Shivas	JF951170	JF951150	<b>MN829379</b>	<b>MN829295</b>
<i>L. madagascariense</i>	<b>CBS 124766 = CPC 14623</b>	<i>Eucalyptus camaldulensis</i>	Madagascar	M.J. Wingfield	MH874923	MH863407	<b>MN829380</b>	<b>MN829296</b>
<i>Leptoxyphium</i> sp.	CPC 17767	<i>Gossypium herbaceum</i>	Thailand	K.D. Hyde	<b>MN749203</b>	<b>MN749275</b>	<b>MN829388</b>	<b>MN829304</b>
	CPC 20470 = MFLUCC12-0106	Living leaf of unknown host	Thailand	S. Hongsanan	<b>MN749200</b>	<b>MN749272</b>	<b>MN829385</b>	<b>MN829301</b>

(continued on next page)

Table 1. (Continued).

Family and Species name	Voucher/Culture <sup>1</sup>	Substrate/Lifestyle <sup>2</sup>	Country/Location	Collector	GenBank accession numbers <sup>3</sup>			
					LSU	ITS	TEF-1 $\alpha$	RPB2
	CPC 20473 = MFLUCC12-0109	Living leaf of unknown host	Thailand	S. Hongsanan	MN749197	MN749269	MN829382	MN829298
	CPC 20481 = MFLUCC12-0118	Living leaf of unknown host	Thailand	–	MN749201	MN749273	MN829386	MN829302
	CPC 21382 = MFLUCC12-0406	<i>Heliconia</i> sp.	Thailand	S. Hongsanan	MN749199	MN749271	MN829384	MN829300
	CPC 21383 = MFLUCC12-0407	<i>Ixora chinensis</i>	Thailand	S. Hongsanan	MN749202	MN749274	MN829387	MN829303
	CBS 123.26 = ATCC 11925 = IMI 089363	<i>Hibiscus tiliaceus</i>	Indonesia	Deposited by M.B. Schwarz	GU214430	MH854862	GU349051	GU371741
	CBS 382.87	<i>Citrus aurantium</i>	India	Deposited and isolated by N.D. Sharma	MN749205	MN749277	MN829390	MN829306
	CBS 135836	Insect gut	India	S. Kajale & M. Sonawane	MN749206	MN749278	MN829391	MN829307
	CBS 139617 = MFLUCC13-0781	–	Thailand	S. Hongsanan	MN749196	MN749268	MN829381	MN829297
	CBS 139618 = MFLUCC13-0783	–	Thailand	S. Hongsanan	MN749204	MN749276	MN829389	MN829305
	CBS 139620 = MFLUCC13-0786	–	Thailand	S.C. Karunarathna	MN749207	MN749279	MN829392	MN829308
	CBS 139812 = MFLUCC13-0078	Living leaf of unknown host	Thailand	S.C. Karunarathna	MN749208	MN749280	MN829393	MN829309
	CBS 139814 = MFLUCC13-0790	Living leaf of unknown host	Thailand	S.C. Karunarathna	MN749198	MN749270	MN829383	MN829299
<i>Phragmocarpnias betle</i>	CPC 17762	<i>Mimusops elengi</i> (Bullet wood)	Thailand	K.D. Hyde	MN749221	MN749293	MN829407	MN829323
	CPC 20476 = MFLUCC12-0112	Palm	Philippines	K.D. Hyde	MN749222	MN749294	MN829408	MN829324
	CPC 21379 = MFLUCC12-0403	<i>Malus</i> sp.	Thailand	K.D. Hyde	MN749223	MN749295	MN829409	MN829325
	<b>MFLUCC10-0053</b>	<i>Ixora</i> sp.	Thailand	P. Chomnunti	JN832606	KU358922	–	–
<i>Ph. plumeriae</i>	<b>MFLUCC15-0205</b>	<i>Plumeria</i> sp.	Thailand	C. Singhapop	KU358918	KU358919	–	–
<i>Polychaeton citri</i>	CBS 116435	<i>Citrus aurantium</i>	Iran	R. Zare & W. Gams	GU214469	GU214649	<b>MN829394</b>	<b>MN829310</b>
<b>Neoantennariellaceae</b>								
<i>Fumiglobus pieridicola</i>	<b>UBC F23788</b>	<i>Pieris japonica</i>	Canada	Tanay Bose	KC833052	KF263961	–	–
<i>Neoantennariella phyllicae</i>	CBS 146164 = CPC 19227	<i>Phyllica arborea</i>	South Africa	M.J. Wingfield	<b>MN749209</b>	<b>MN749281</b>	<b>MN829395</b>	<b>MN829311</b>
	CBS 146165 = CPC 19977	<i>Phyllica arborea</i>	UK	P. Ryan	<b>MN749213</b>	<b>MN749285</b>	<b>MN829399</b>	<b>MN829315</b>
	CBS 146166 = CPC 19981	<i>Phyllica arborea</i>	UK	P. Ryan	<b>MN749212</b>	<b>MN749284</b>	<b>MN829398</b>	<b>MN829314</b>
	CBS 146167 = CPC 19985	<i>Phyllica arborea</i>	UK	P. Ryan	<b>MN749210</b>	<b>MN749282</b>	<b>MN829396</b>	<b>MN829312</b>
	CPC 19992	<i>Phyllica arborea</i>	UK	P. Ryan	<b>MN749214</b>	<b>MN749286</b>	<b>MN829400</b>	<b>MN829316</b>
	<b>CBS 146163 = CPC 19989</b>	<i>Phyllica arborea</i>	UK	P. Ryan	<b>MN749211</b>	<b>MN749283</b>	<b>MN829397</b>	<b>MN829313</b>
<i>Neosbolisia phyllicae</i>	<b>CBS 146168 = CPC 19982</b>	<i>Phyllica arborea</i>	UK	P. Ryan	<b>MN749215</b>	<b>MN749287</b>	<b>MN829401</b>	<b>MN829317</b>
<b>Readeriellipsoidaceae</b>								
<i>"Capnodium" salicinum</i>	CBS 131.34 = AFTOL-ID 937	<i>Bursaria spinosa</i>	Indonesia	Deposited by E.E. Fisher	EU019269	AJ244240	DQ677889	KT216553
<i>Phaeoxyphiella australiana</i>	<b>CBS 146169 = CPC 29527</b>	<i>Agonis</i> sp.	Australia	P.W. Crous	<b>MN749220</b>	<b>MN749292</b>	<b>MN829406</b>	<b>MN829322</b>
<i>Ph. phyllicae</i>	CBS 146171 = CPC 19979	<i>Phyllica arborea</i>	UK	P. Ryan	<b>MN749216</b>	<b>MN749288</b>	<b>MN829402</b>	<b>MN829318</b>

Table 1. (Continued).

Family and Species name	Voucher/Culture <sup>1</sup>	Substrate/Lifestyle <sup>2</sup>	Country/Location	Collector	GenBank accession numbers <sup>3</sup>			
					LSU	ITS	TEF-1 $\alpha$	RPB2
	CBS 146172 = CPC 19984	<i>Phyllica arborea</i>	UK	P. Ryan	<b>MN749217</b>	<b>MN749289</b>	<b>MN829403</b>	<b>MN829319</b>
	CBS 146173 = CPC 19987	<i>Phyllica arborea</i>	UK	P. Ryan	<b>MN749218</b>	<b>MN749290</b>	<b>MN829404</b>	<b>MN829320</b>
	<b>CBS 146170 = CPC 19993</b>	<i>Phyllica arborea</i>	UK	P. Ryan	<b>MN749219</b>	<b>MN749291</b>	<b>MN829405</b>	<b>MN829321</b>
<i>Readeriellipsoidis fuscoporiae</i>	<b>CBS 139900 = CPC 24637</b>	<i>Fuscoporia wahlbergii</i>	French Guiana	C. Decock	KR476755	KR476720	<b>MN829410</b>	<b>MN829326</b>
<i>R. guyanensis</i>	CBS 117550 = MUCL 46082	Dead, decaying leaf, unidentified angiosperm in leaf litter	French Guiana	Deposited by C. Decock/Isolated by M.H. de Frahan	FJ493211	MH863023	<b>MN829411</b>	<b>MN829327</b>
<i>Scolecocyphium blechni</i>	<b>CBS 146174 = CPC 19990</b>	<i>Blechnum palmiforme</i>	UK	P. Ryan	<b>MN749224</b>	<b>MN749296</b>	<b>MN829412</b>	<b>MN829328</b>
<i>Sc. blechnicola</i>	<b>CBS 146175 = CPC 19991</b>	<i>Blechnum palmiforme</i>	UK	P. Ryan	<b>MN749225</b>	<b>MN749297</b>	<b>MN829413</b>	<b>MN829329</b>
<i>Sc. leucadendri</i>	<b>CBS 146176 = CPC 18313</b>	<i>Leucadendron</i> sp.	South Africa	P.W. Crous	<b>MN749226</b>	<b>MN749298</b>	<b>MN829414</b>	<b>MN829330</b>
<i>Sc. phyllicae</i>	<b>CBS 146177 = CPC 19219</b>	<i>Phyllica arborea</i>	South Africa	M.J. Wingfield	<b>MN749227</b>	<b>MN749299</b>	<b>MN829415</b>	<b>MN829331</b>
	CBS 146178 = CPC 19225	<i>Phyllica arborea</i>	South Africa	M.J. Wingfield	<b>MN749228</b>	<b>MN749300</b>	<b>MN829416</b>	<b>MN829332</b>
<i>Scorias aphidis</i>	<b>CBS 325.33</b>	Aphid	–	Deposited by L.H. Leonian	MH866910	GU214696	<b>MN829417</b>	KT216542
<i>Sc. camelliae</i>	<b>CBS 201.30</b>	<i>Camellia sinensis</i>	Indonesia	Deposited by F.H. van Beyma/Isolated by Steinmann	MH866560	MH855112	<b>MN829418</b>	<b>MN829333</b>
<i>Sc. leucadendri</i>	<b>CBS 131318 = CPC 18312</b>	<i>Laucadendron muirii</i>	South Africa	P.W. Crous	JQ044456	JQ044437	<b>MN829419</b>	<b>MN829334</b>
	CPC 17088	<i>Callistemon</i> sp.	Australia	P.W. Crous	<b>MN749229</b>	<b>MN749301</b>	<b>MN829420</b>	<b>MN829335</b>
<i>Sc. mangiferae</i>	<b>MFLUCC15-0230</b>	<i>Mangifera indica</i>	Thailand	S. Hongsanan	KT588603	KT588604	–	–
<i>Sc. spongiosa</i>	<b>MFLUCC10-0084</b>	<i>Entada</i> sp.	Thailand	P. Chomnunti	JN832601	–	–	–
<b>Outgroup</b>								
<i>Elsinoe phaseoli</i>	CBS 165.31 = AFTOL-ID 1855 = IMI 303278	<i>Paseolus lunatus</i>	Cuba	Deposited by A.E. Jenkins/Isolated by C. Aguiar	DQ678095	KX887263	DQ677935	KX887144
<i>Myriangium hispanicum</i>	CBS 247.33	<i>Acer monspessulanum</i>	–	Deposited by J.B. Martínez/Isolated by H. Diddens	GU301854	KX887304	GU349055	GU371744

<sup>1</sup> 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, Boreham Lane, United Kingdom; MFLUCC: Mae Fah Luang University Culture Collection, Chiang Rai, Thailand; MUCL: Université Catholique de Louvain, Louvain-la-Neuve, Belgium.

<sup>2</sup> Lifestyle of all sooty mould strains coded as epiphyte.

<sup>3</sup> ITS: internal transcribed spacers and intervening 5.8S nrDNA; LSU: partial 28S large subunit RNA gene; *TEF-1 $\alpha$* : 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*, *Capnodiaceae*, *Euantennariaceae*, *Metacapnodiaceae*), hyperparasites, rock-inhabiting fungi, ectophytes, saprobes, endophytes and pathogens associated with plants and humans (*Cladosporiaceae*, *Cystocoleaceae*, *Dissoconiaceae*, *Extremaceae*, *Mycosphaerellaceae*, *Neodevriesiaceae*, *Schizothyriaceae*, *Phaeothecaceae* (including *Phaeotheca fissurella* and *Phaeotheca shathenatiana*), *Phaeothecoidiaceae*, *Teratosphaeriaceae* (including *Piedraiceae*), *Comminutispora*, *Phaeotheca* (*P. salicorniae* and *P. triangularis*) and lichenised species (*Cystocoleaceae* 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 sampling 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 collections of sooty moulds, thus also providing a more robust phylogeny using four nuclear loci, LSU, ITS, *TEF-1 $\alpha$*  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 collection of Pedro Crous (CPC) housed at the WI (Table 1). Sequences 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 Purification Kit (Promega Corporation, Fitchburg, Wisconsin, USA) following the manufacturer's protocols. The D1/D2 variable domains of the 28S nrDNA (LSU) and the ITS1, 5.8 and ITS2 region of ribosomal DNA and part of RNA polymerase II second largest subunit (*RPB2*) and the translation elongation factor 1- $\alpha$  (*TEF-1 $\alpha$* ) were amplified and sequenced using the following primer pairs: LR0R/LR5 for LSU (Vilgalys & Hester 1990), ITS5/ITS4 for ITS (White *et al.* 1990), fRPB2-5F/fRPB2-7cR for *RPB2* (Liu *et al.* 1999), EF1-983F/EF1-2218R for *TEF-*

*1 $\alpha$*  (Rehner & Buckley 2005). The PCR amplifications were performed in a total volume of 12.5  $\mu$ L containing 1  $\mu$ L genomic DNA, 1  $\times$  NH4 reaction buffer (Bioline, Luckenwalde, Germany), 0.2  $\mu$ M of each primer, 200  $\mu$ M dNTPs, 3 mM MgCl<sub>2</sub>, 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 reaction mixture.

PCR conditions for LSU, ITS and *TEF-1 $\alpha$*  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-1 $\alpha$* ) 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 concatenated 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](http://www.treebase.org); S25414) and taxonomic novelties in MycoBank ([www.Mycobank.org](http://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. Character states were defined as saprobe, epiphyte, parasite or lichen. The character state for taxa with an uncertain lifestyle was coded as “?”.

## Morphology

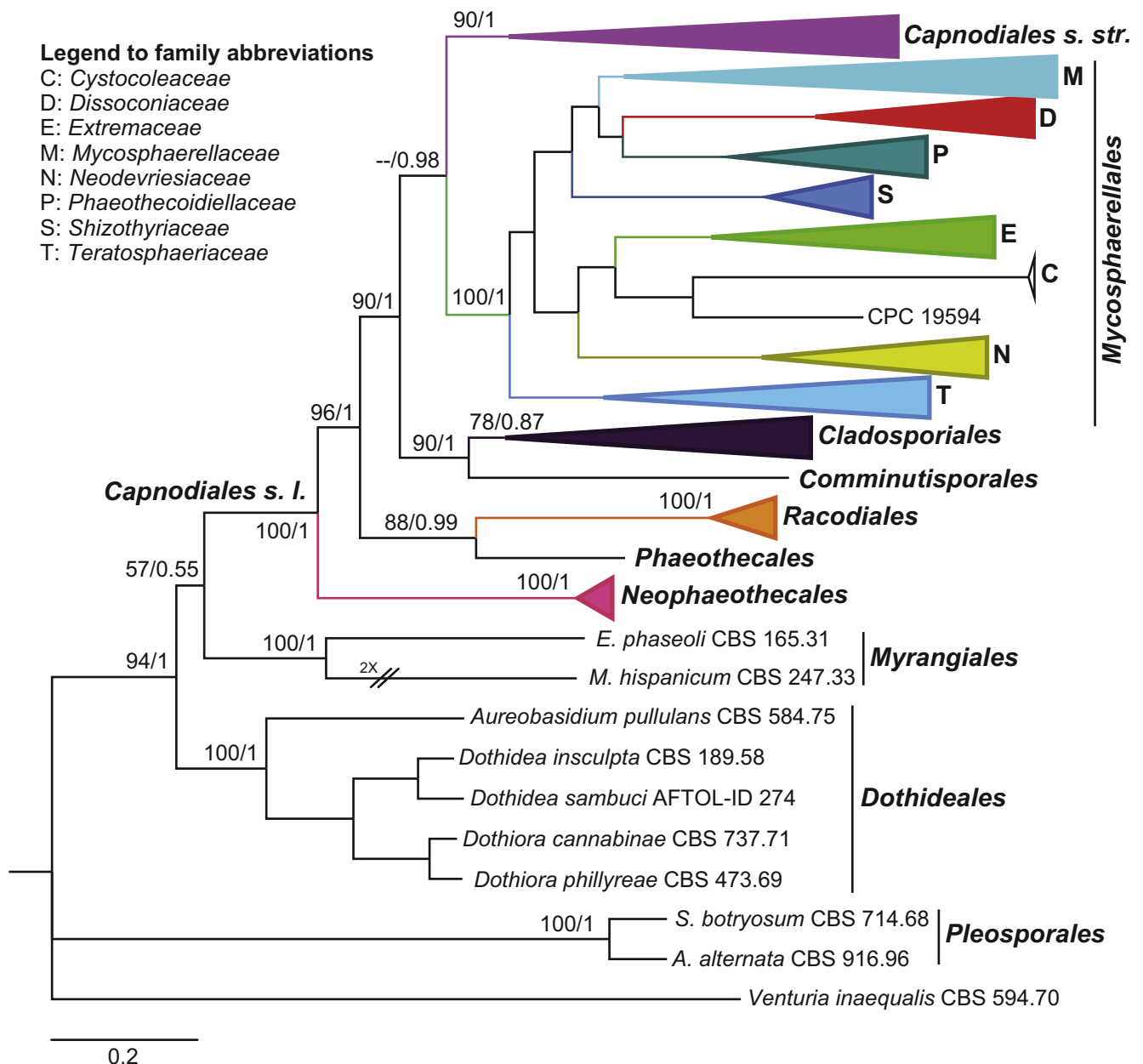
Isolates stored in liquid nitrogen or lyophilised were reactivated on 2 % malt extract agar (MEA) or oatmeal agar (OA). Colonies were sub-cultured onto MEA, OA, cornmeal agar (CMA), potato dextrose agar (PDA), and synthetic nutrient-poor agar (SNA) supplemented with pine needles at room temperature. 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).

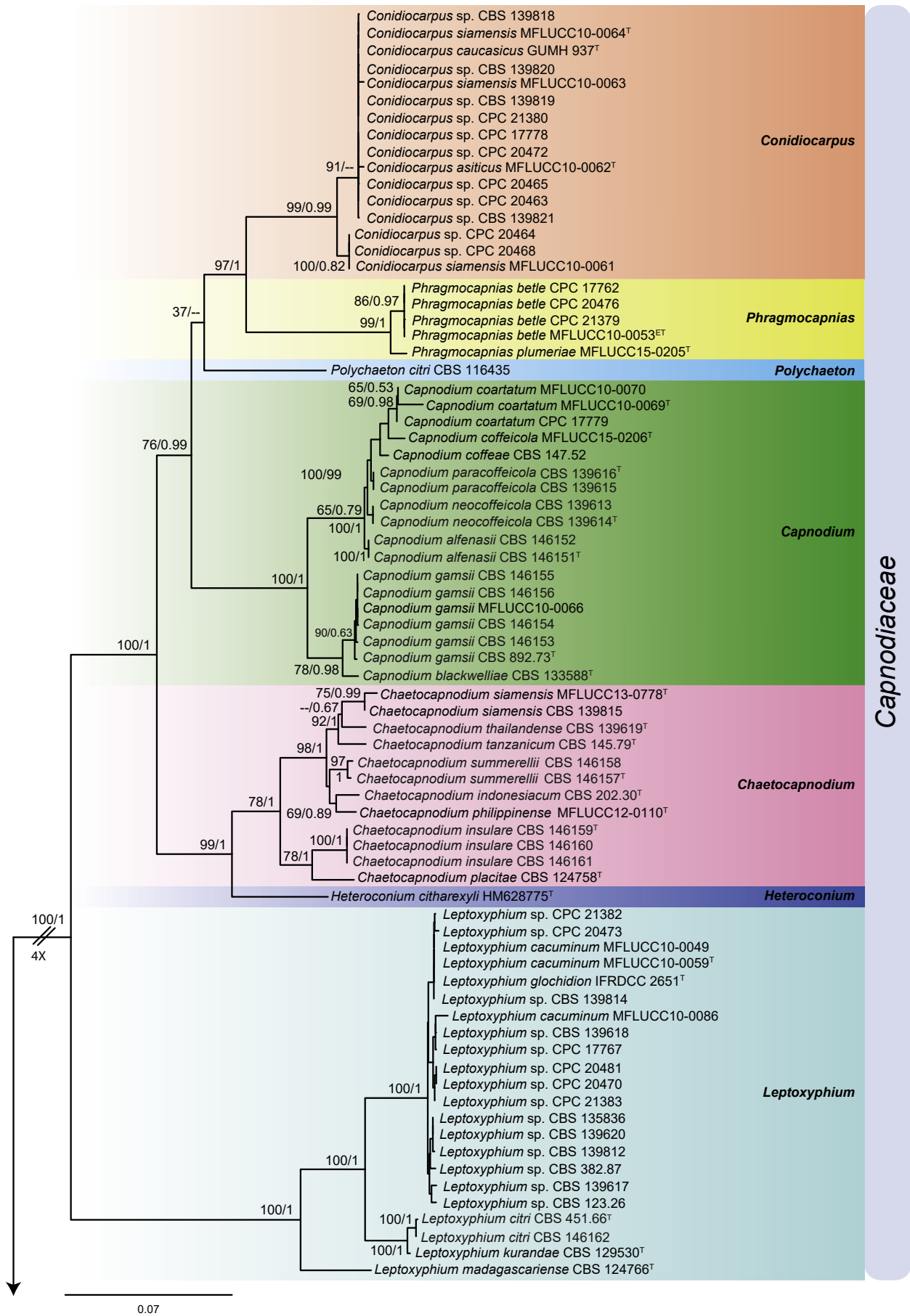
## RESULTS

### Phylogeny

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



**Fig. 1.** Reduced phylogenetic tree inferred from a Bayesian analysis based on a concatenated alignment of LSU, *TEF-1 $\alpha$*  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-1 $\alpha$*  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). <sup>T</sup> Ex-type, <sup>ET</sup> Ex-epitype.



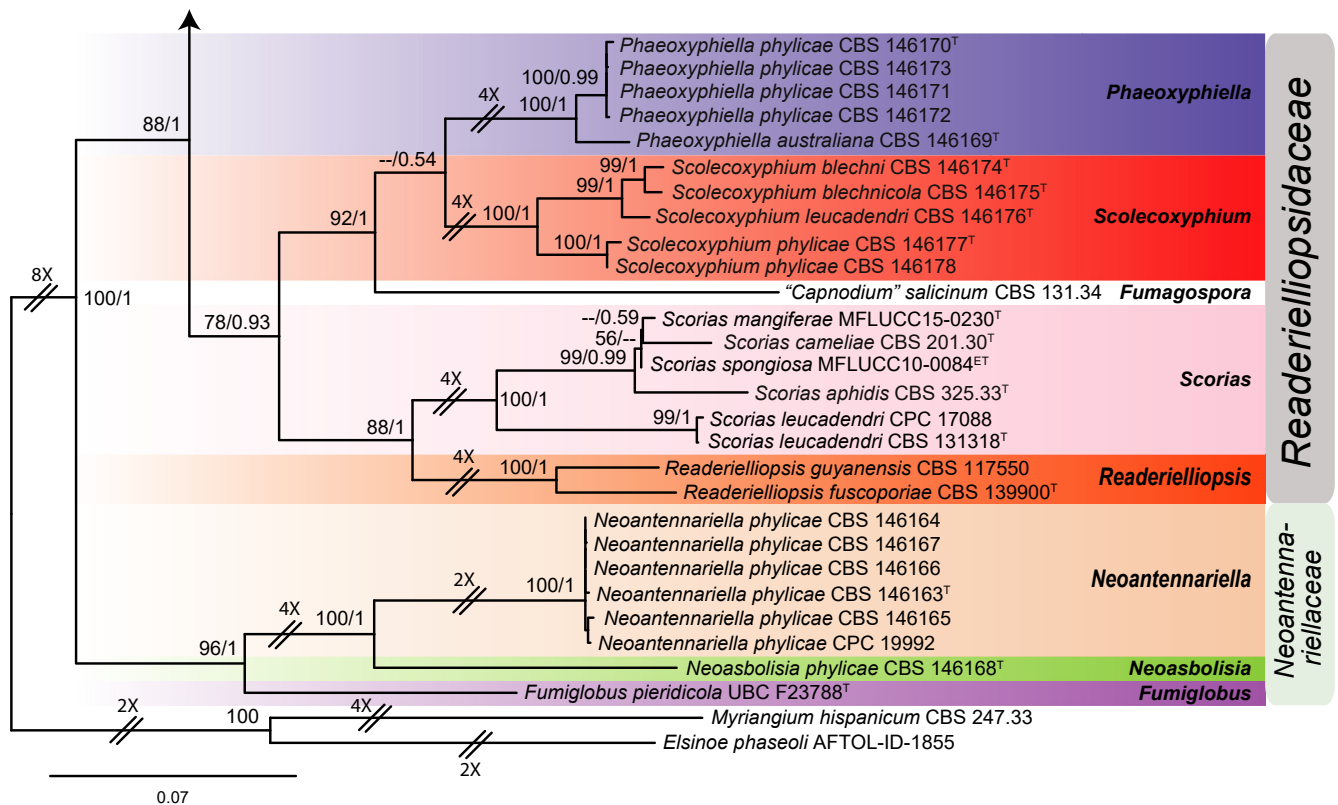


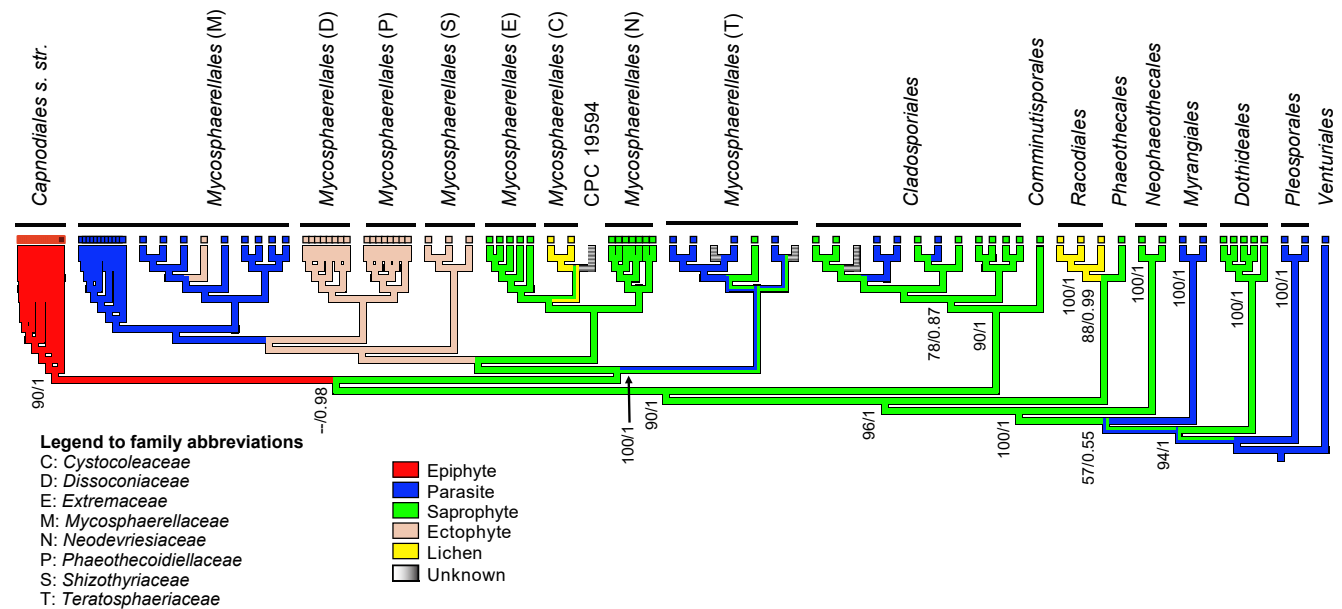
Fig. 2. Continued.

PCR, and therefore a touchdown PCR program was used. For most of the isolates the combination of fRPB2-f5F and fRPB2-7cR primers (Liu *et al.* 1999) was more successful than the primer combination fRPB2-f5F2 and fRPB2-7cR (Sung *et al.* 2007). For a few isolates, we used the forward primer fRPB2-f5F2 instead of fRPB2-f5F.

Two datasets were analysed in this study. The first dataset consisted of combined LSU, *TEF-1 $\alpha$*  and *RPB2*, including 193 taxa representing three orders *Capnodiales s. lat.*, *Myriangiales*, *Dothideales*, with *Venturia inaequalis* (CBS 594.70) as outgroup. After alignment the dataset contained a total of 3168 characters (LSU: 837, *TEF-1 $\alpha$* : 1176, *RPB2*: 1147), including alignment gaps. MrModelTest revealed that the 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-1 $\alpha$*  and *RPB2*). The Bayesian analyses of the concatenated alignments of three loci generated 7292 trees from which 1822 trees were discarded as burn-in. The consensus tree and posterior probability values (PP) were calculated from the remaining 5470 trees. The average standard deviation of split frequencies was 0.009987 at the end of the run. The RAxML search of the dataset with 1767 distinct 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*, *Dissoconiaceae*, *Phaeothecoidiaceae*, *Schizothyriaceae*, *Extremaceae*, *Cystocoleaceae*, *Neodevriesiaceae* and *Teratosphaeriaceae* (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 rupestre*), and *Comminutisporales* (for *Comminutispora agavaciensis*).

The second dataset consisted of aligned sequences of four loci (LSU, ITS, *TEF-1 $\alpha$*  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 3603 characters (LSU: 849, ITS: 553, *TEF-1 $\alpha$* : 1035, *RPB2*: 1154), including alignment gaps. Results from MrModelTest indicated a GTR+I+G as the best fit model for the ITS sequence data, as was the case for three other loci (LSU, *TEF-1 $\alpha$*  and *RPB2*) in dataset 1. The RAxML search of the second dataset detected 1463 distinct alignment patterns and yielded a tree with lnL = -30052.650187 (Fig. 2). The Bayesian analyses generated 4622 trees from which 1154 trees were discarded as burn-in. The consensus tree and posterior probability values (PP) were calculated from the remaining 3468 trees. The average standard deviation of split frequencies was 0.009980 at the end of the run.



**Fig. 3.** Cladogram showing the ancestral state reconstruction and evolution of lifestyles over the tree. Maximum likelihood bootstrap support values (ML-BS) and Bayesian posterior probabilities (PP) are indicated at the nodes (ML-BS/PP).

Posterior probability values were mapped on the ML tree (Fig. 2). Three families, namely *Capnodiaceae*, *Neoantennariellaceae* and *Readeriellipsoidaceae* were recognised in *Capnodiales s. str.* In *Capnodiaceae* seven morphologically and phylogenetically well-supported genera including *Capnodium*, *Chaetocapnodium*, *Conidiocarpus*, *Heteroconium*, *Leptoxyphium*, *Phragmocapnias* and *Polychaeton* were identified. Eleven new species were recognised in this family. *Readeriellipsoidaceae* contained four genera (*Phaeoxyphiella*, *Readeriellipsoidis*, *Scolecoxyphium* and *Scorias*) and *Neoantennariellaceae* three genera (*Fumiglobus*, *Neoantennariella* and *Neosabolisia*).

Ancestral state reconstruction revealed a saprobic lifestyle as the ancestral state of the *Capnodiales s. str.* 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 *Racodiales* 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.

*Etymology:* 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. *Hamathecium* of hyaline, septate, sub-cylindrical pseudoparaphyses. *Asci* 8-spored, bitunicate, fissitunicate, sessile to short-stalked, obovoid to broadly ellipsoid or subcylindrical, straight to slightly curved. *Ascospores* bi- to multi-seriate, or overlapping, hyaline, obovoid to ellipsoid-fusiform, with irregular luminal inclusions. *Asexual morphs* hyphomycetous. *Conidiophores* macronematous, mononematous, simple or branched, brown. *Conidiogenous cells* integrated, terminal and intercalary, sympodial or synchronous, mostly polyblastic, conidiogenous loci conspicuous, darkened-refractive or not. *Conidia* mostly in branched or unbranched acropetal 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.

*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

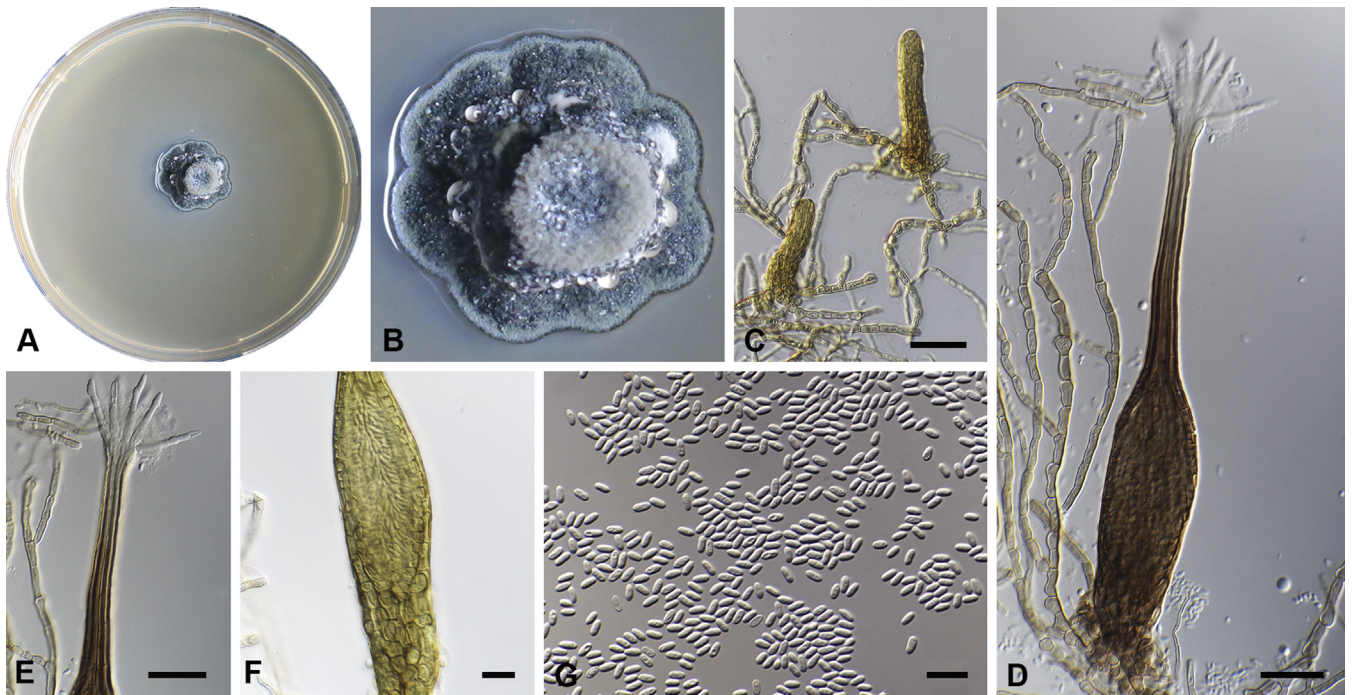


Fig. 4. *Capnodium alfenasii*. A, B. Colony (2-wk-old) on MEA. C. Conidiomata arising from mycelia or immature conidiomata on SNA. D. Conidioma on SNA. E. Ostiole surround by hyaline hyphae. F. Conidia produced in ellipsoidal central part of conidioma. G. Conidia. Scale bars: C = 25  $\mu$ m; D, E =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

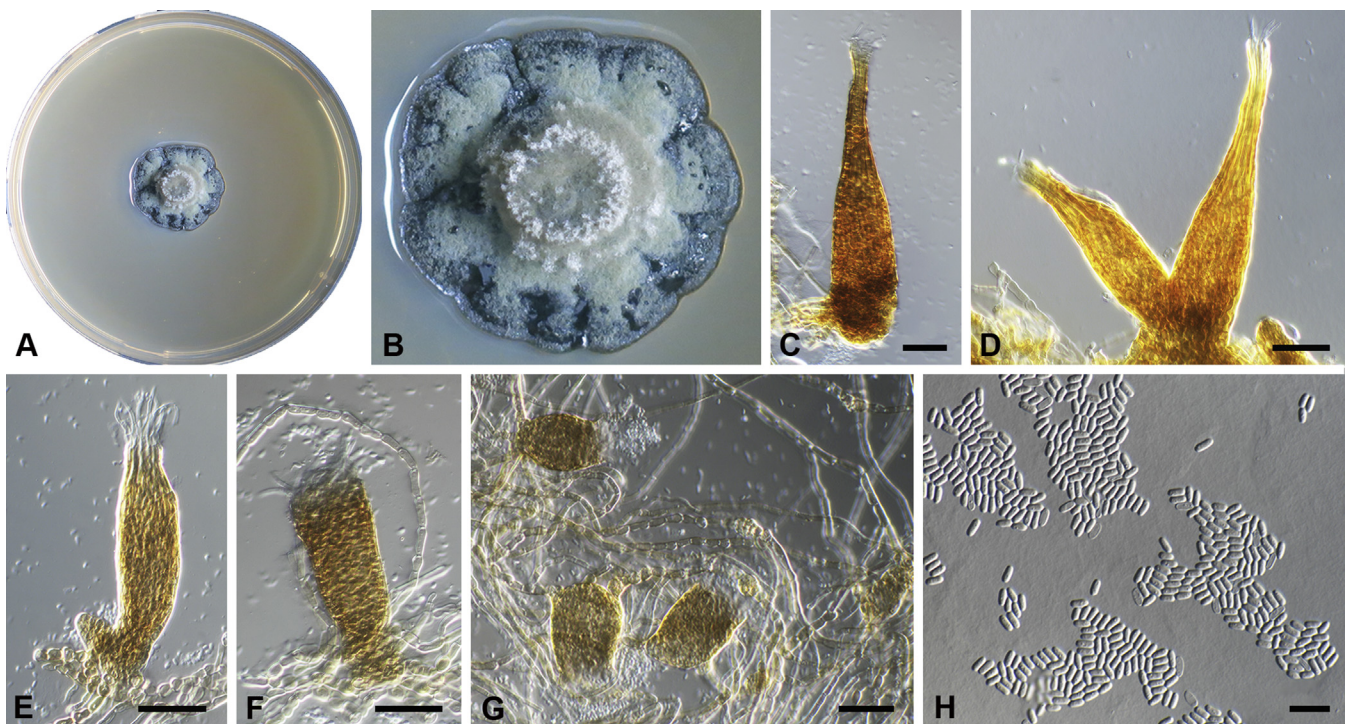


Fig. 5. *Capnodium blackwelliae*. A, B. Colony (2-wk-old) on MEA. C–G. Conidiomata on SNA. H. Conidia. Scale bars: C–G = 25  $\mu$ m; H = 10  $\mu$ m.

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*.

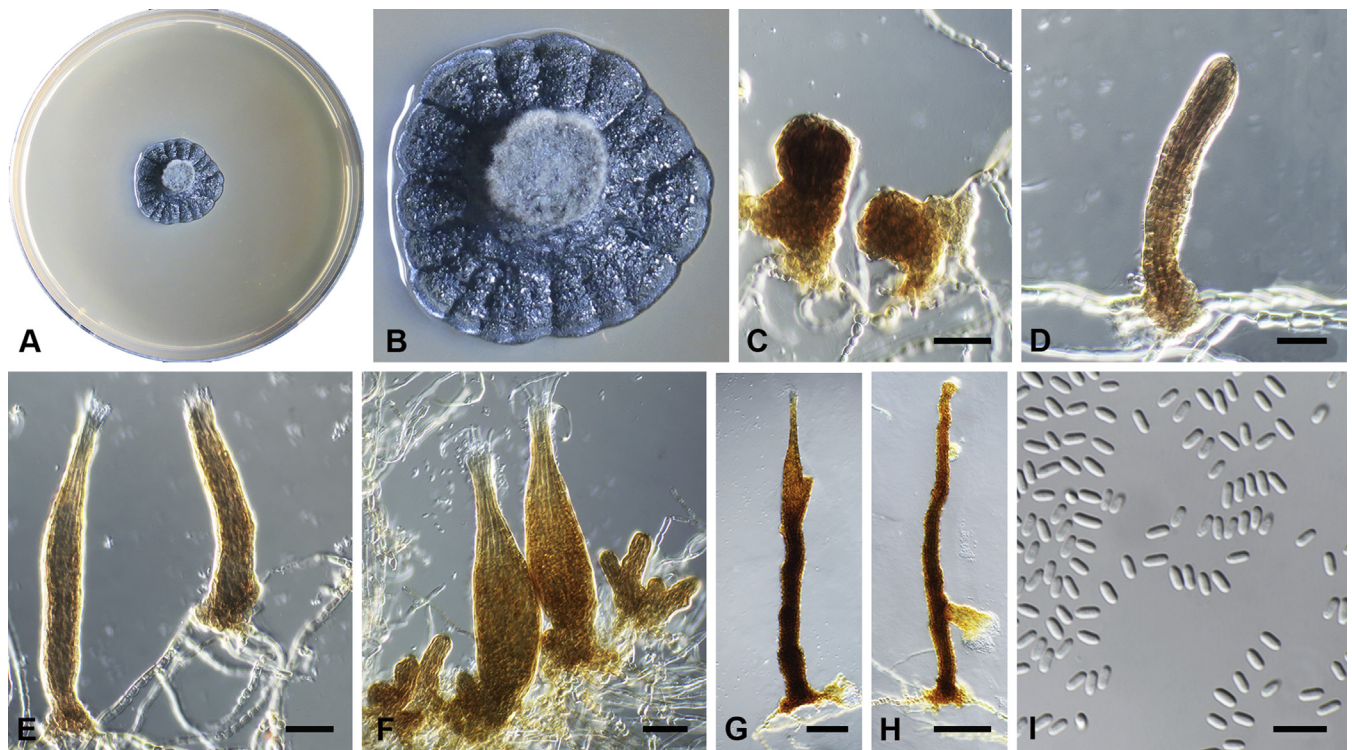
Saprobic. *Ascomata* pseudothecial, immersed, uniloculate, separate. *Asci* bitunicate, 8-spored. *Pseudoparaphyses* absent, hamathecial tissue abundant, ostiolar canal periphysate.

*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** (Nannf.) 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. 6.** *Capnodium gamsii*. **A, B.** Colony (2-wk-old) on MEA. **C, D.** Conidiomata arising from mycelia or immature conidiomata on SNA. **E–H.** Conidiomata on SNA. **I.** Conidia. Scale bars: C–F = 25 µm; G, H = 50 µm; I = 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*), *Dissoconiaceae* (based on *Dissoconium*), *Extremaceae* (based on *Extremus*), *Mycosphaerellaceae* (based on *Mycosphaerella*), *Neodevriesiaceae* (based on *Neodevriesia*), *Phaeothecoidiaceae* (based on *Phaeothecoidiella*), *Schizothyriaceae* (based on *Schizothyrium*, asexual morph *Zygophiala*), *Teratosphaeriaceae* (based on *Teratosphaeria*, asexual morph *Kirramyces*).

***Neophaeothecales*** Abdollahz. & Crous, **ord. nov.** MycoBank MB833143.

*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 obovoid, muriformly septate, bursting open to release endoconidia that are red-brown, verruculose, aseptate, ellipsoid to subglobose or irregular.

***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 obovoid, 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 obovoid, 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.

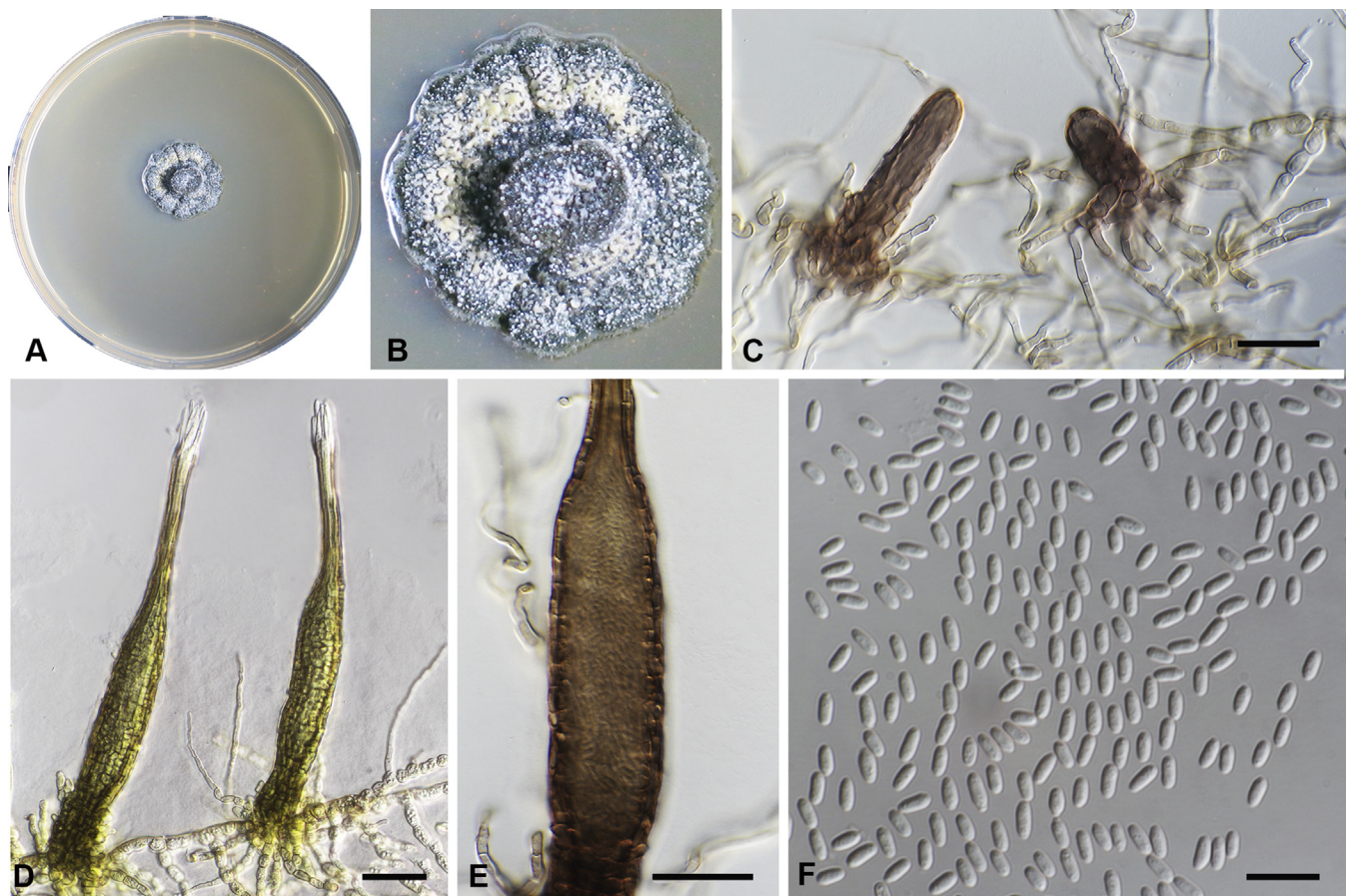
Widespread in tropical and subtropical areas, occurring on honeydew excretions from insects, forming a black, sooty growth on green, healthy leaves, stems and bark. *Ascomata* superficial on mycelium, subglobose to globose, with or without setae, dark brown, with a central ostiole. *Pseudoparaphyses* 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 *Readeriellipsidaceae* (based on *Readeriellipsis*).

**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  $\mu$ m; D = 25  $\mu$ m; F = 10  $\mu$ m.

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. *Asexual morphs*: coelomycetous *Conidiomata* synnematosus 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, paraphysate, 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, ellipsoid, continuous, hyaline, aseptate (adapted from Chomnunti et al. 2011).

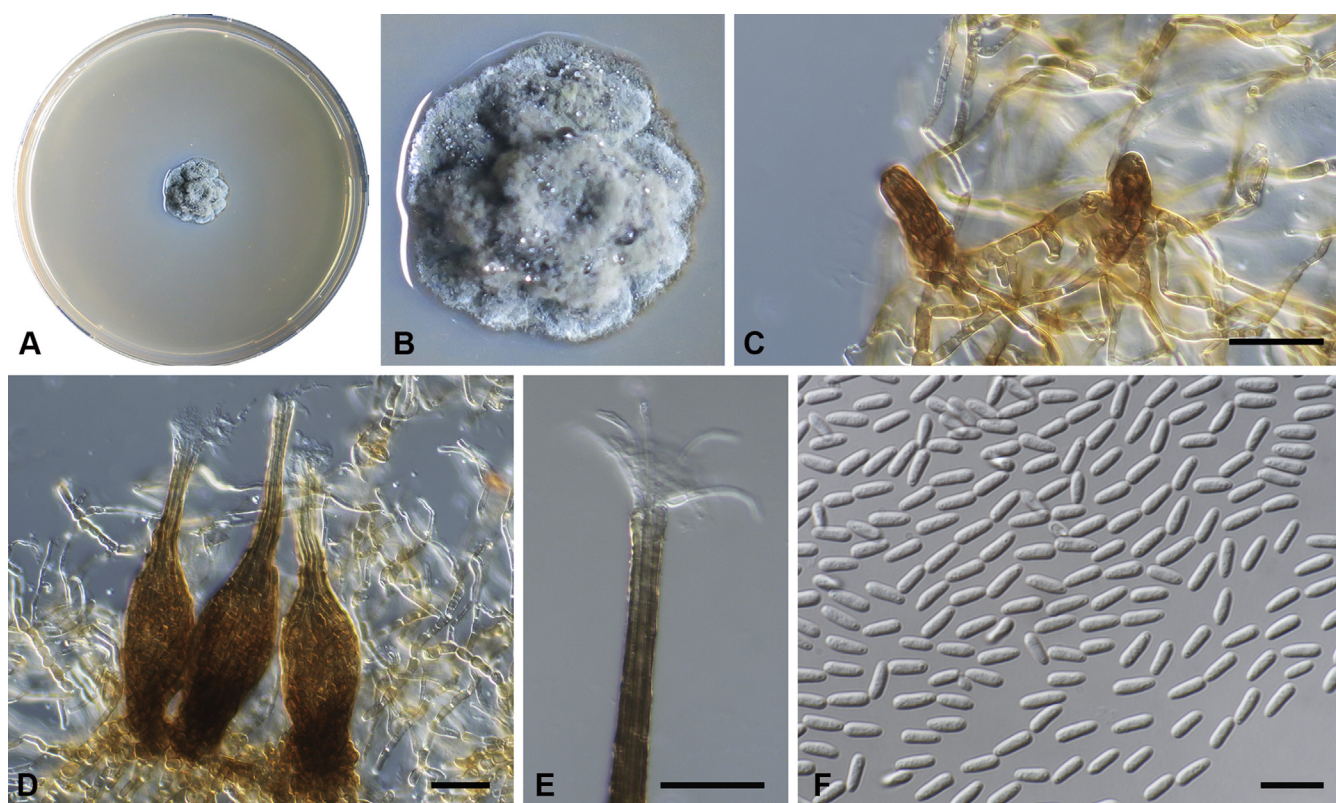
*Type species*: *Capnodium citri* Berk. & Desm.

*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-1 $\alpha$*  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, synnematosus, 113–243  $\mu$ m long (av. = 187  $\mu$ m, n = 20), mostly sessile or with short stalk (25–46  $\times$  18–35  $\mu$ m, av. = 40  $\times$  24  $\mu$ m), oval or ellipsoidal central part (60–124  $\times$  31–46  $\mu$ m, av. = 93  $\times$  34  $\mu$ m), neck (38–118  $\times$  8.8–13.5  $\mu$ m, av. = 70  $\times$  11  $\mu$ m), wall comprising mostly cylindrical cells. *Ostiole* at apex of pycnidia, surrounded by hyaline hyphae. *Conidia* small, hyaline, aseptate, oblong to



**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 surround by hyaline hyphae. **F.** Conidia. Scale bars: C–E = 25  $\mu$ m; F = 10  $\mu$ m.

ellipsoid, continuous, (3.7–)3.9–4.8(–5.1) × (1.4–)1.7–2(–2.2) µm (av. = 4.4 × 1.8 µm, 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 22666).

**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. alfenasii* 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. alfenasii* differs from *Ca. blackwelliae* in having longer pycnidia, from *Ca. neocoffeicola* in having smaller pycnidia, and from *Ca. paracoffeicola* 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, synnematos, 42–116 µm long (av. = 95 µm, n = 20), mostly sessile or with short stalk (25–31 × 17–22 µm, av. = 27 × 19 µm), with or without conspicuous oval or ellipsoidal central region (24–143 × 19–55 µm, av. = 70 × 38 µm), with or without neck (22–102 × 10–37 µm, av. = 38 × 12 µm); 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) × (1.4–)1.6–1.9(–2) µm (av. = 4.2 × 1.7 µm, 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 µm 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 µm high, n = 20) and conidia (3.6–4.6 × 1.7–2.5 µm; av. = 3.9 × 2.25 µm, 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*.

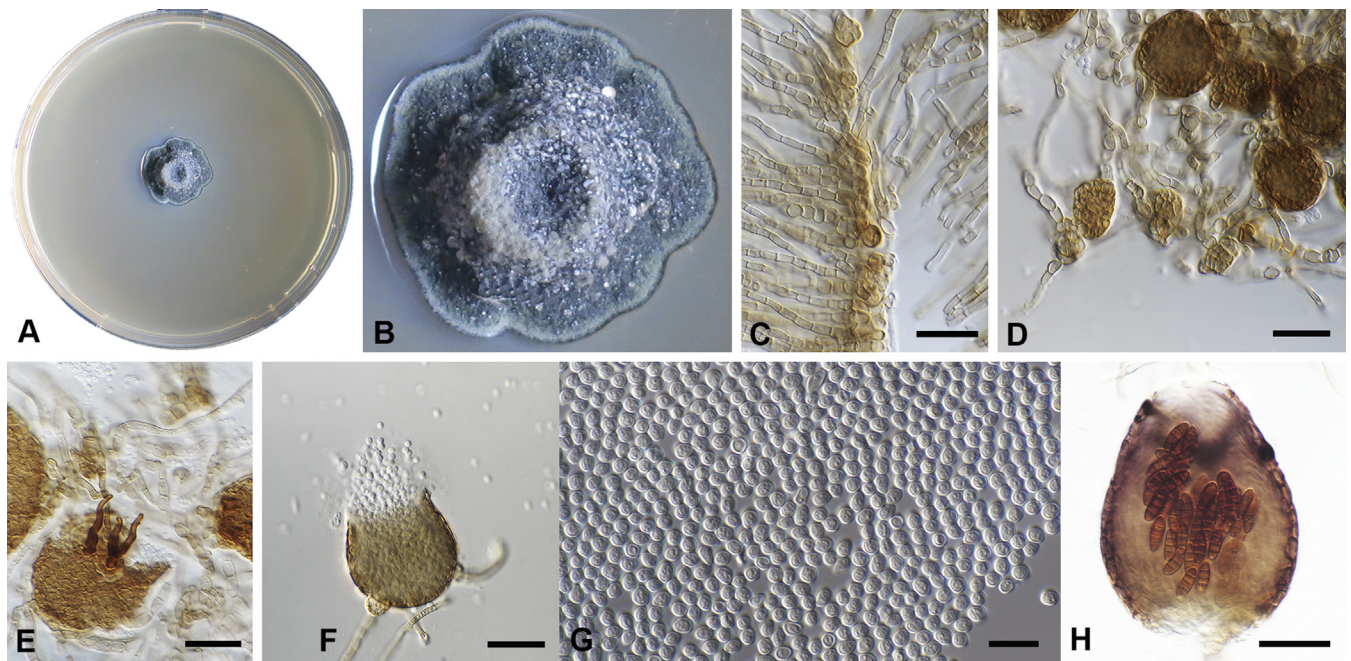
***Capnodium gamsii*** Abdollahz. & Crous, **sp. nov.** MycoBank MB833152. Fig. 6.

**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, synnematos, 97–350 µm long (av. = 185 µm, n = 20), mostly sessile or with short stalk (23–44 × 16–29 µm, av. = 32 × 21 µm), with or without conspicuous oval or ellipsoidal central part, 62–206 × 19–46 µm, av. = 165 × 40 µm, neck present or absent, 15–87 × 9–25 µm, av. = 40 × 16 µm; 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 µm; D = 10 µm.



**Fig. 10.** *Chaetocapnodium insulare*. **A, B.** Colony (2-wk-old) on MEA. **C, D.** Septate hyphae with mucilaginous outer wall layer and immature conidiomata on SNA. **E.** Conidiomata with setae. **F.** Conidia inside conidioma. **G.** Conidia. **H.** Ascoma with 3-septate brown ascospores. Scale bars: C–F, H = 20 µm; G = 10 µm.

at pycnidial apex, surrounded by hyaline hyphae. *Conidia* small, hyaline, aseptate, oblong to ellipsoid, continuous, (3.6–) 4–5.5(–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 floribunda*, 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:** *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,

synnematos, 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, (3.7–) 4–4.7(–5.2) × (1.6–) 1.8–2(–2.3) µm (av. = 4.4 × 1.9 µm, n = 50).

**Culture characteristics:** Colonies leathery, appressed, with fluffy aerial mycelium, with abundant creamy exudates of pycnidia containing conidia, folded, edge sinuate, glaucous grey to pale greenish grey after 2 wk in the dark at 25 °C. Colonies reaching 19–22 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-24267, culture ex-type CBS 139614 = MFLUCC 14-0570).

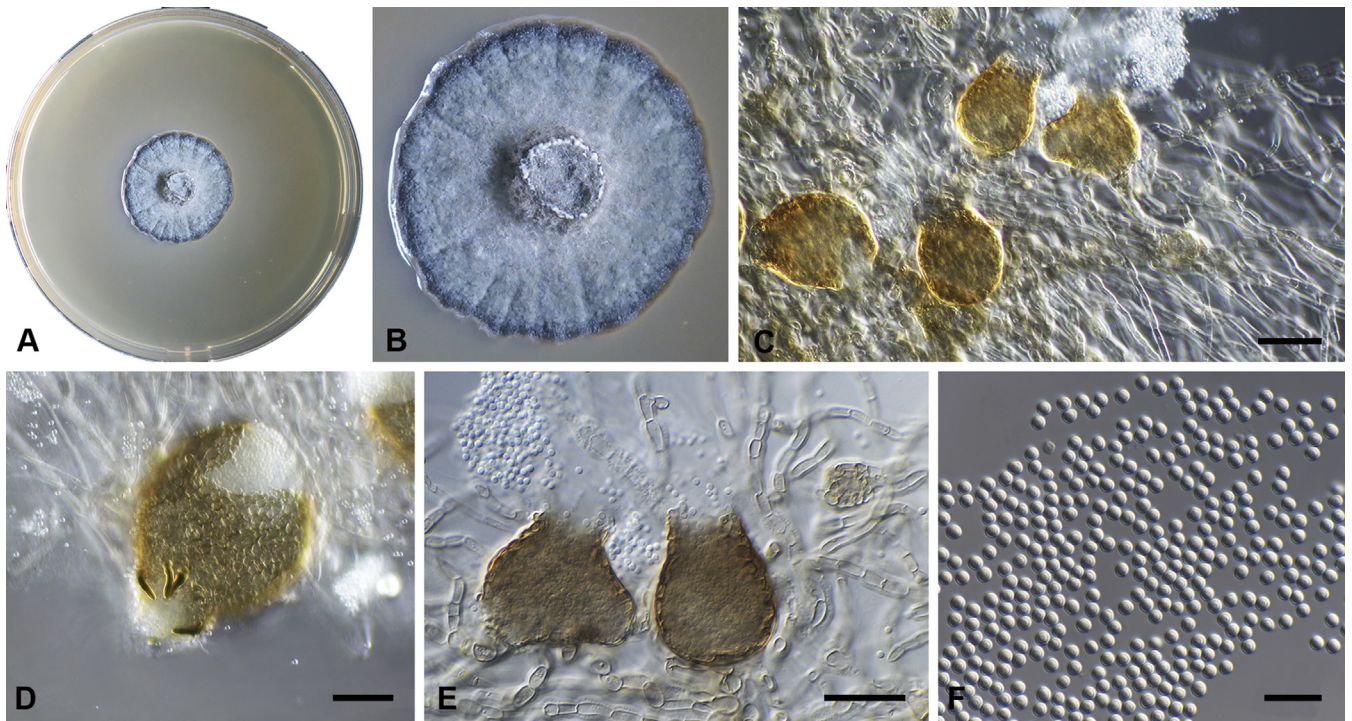
**Additional material examined:** Thailand, Chiang Rai, on living leaves of *Coffea arabica*, 20 Aug. 2014, S. Hongsanan, culture CBS 139613 = MFLUCC 14-0569.

**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. paracoffeicola*, and the longer pycnidia (av. = 230 µm) distinguishes it from other species examined in this study. In *Ca. paracoffeicola*, *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*.





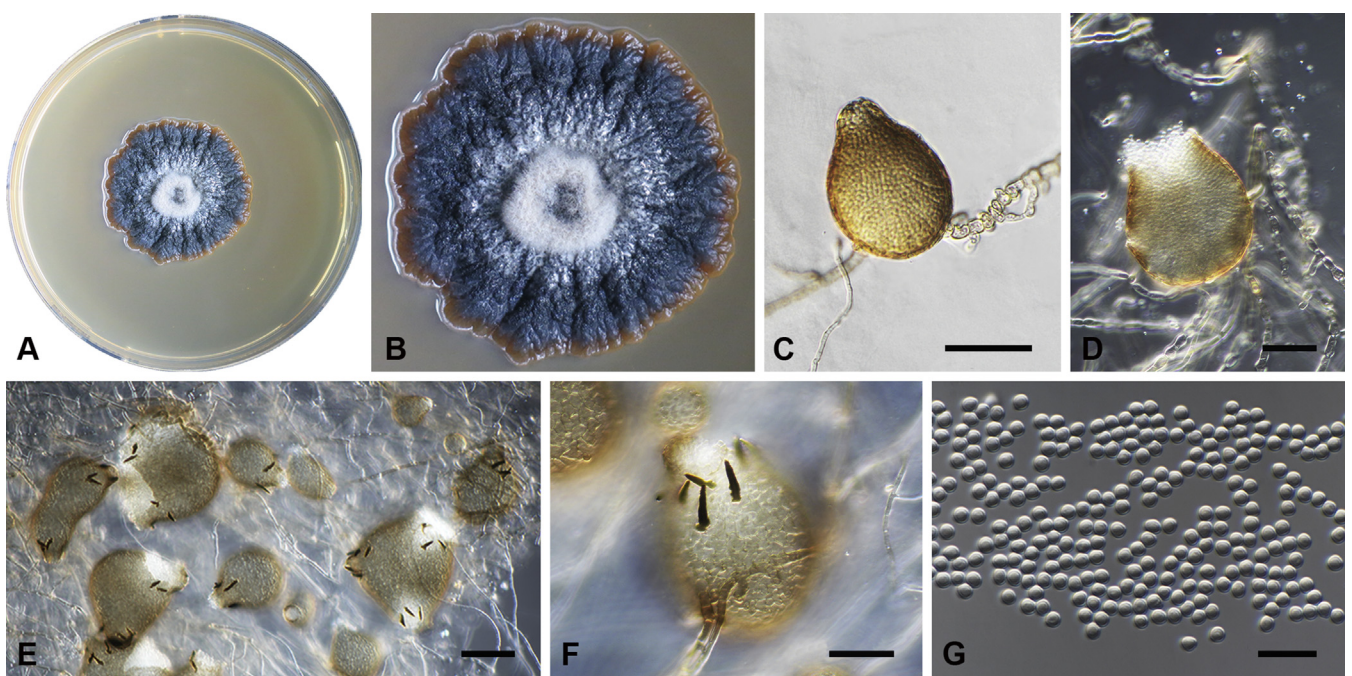
**Fig. 11.** *Chaetocapnodium summerellii*. **A, B.** Colony (2-wk-old) on MEA. **C.** Conidiomata on SNA. **D.** Conidioma with setae. **E.** Conidia inside conidiomata. **F.** Conidia. Scale bars: C, D = 25 µm; E = 20 µm; F = 10 µm.

*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, synnematos, 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).



**Fig. 12.** *Chaetocapnodium tanzanicum*. **A, B.** Colony (2-wk-old) on MEA. **C, D.** Conidia inside conidiomata. **E, F.** Conidiomata with setae on SNA. **G.** Conidia. Scale bars: C, D, F = 25 µm; E = 50 µm; G = 10 µm.

**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. =  $6.4 \times 2.15 \mu\text{m}$ ). Average conidial lengths of the other species studied here are shorter than  $5 \mu\text{m}$ . *Capnodium 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 ( $165\text{--}178 \mu\text{m}$  long), and shorter stalks ( $19\text{--}24 \text{ long} \times 18\text{--}23 \mu\text{m}$  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 *Antenariella 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.

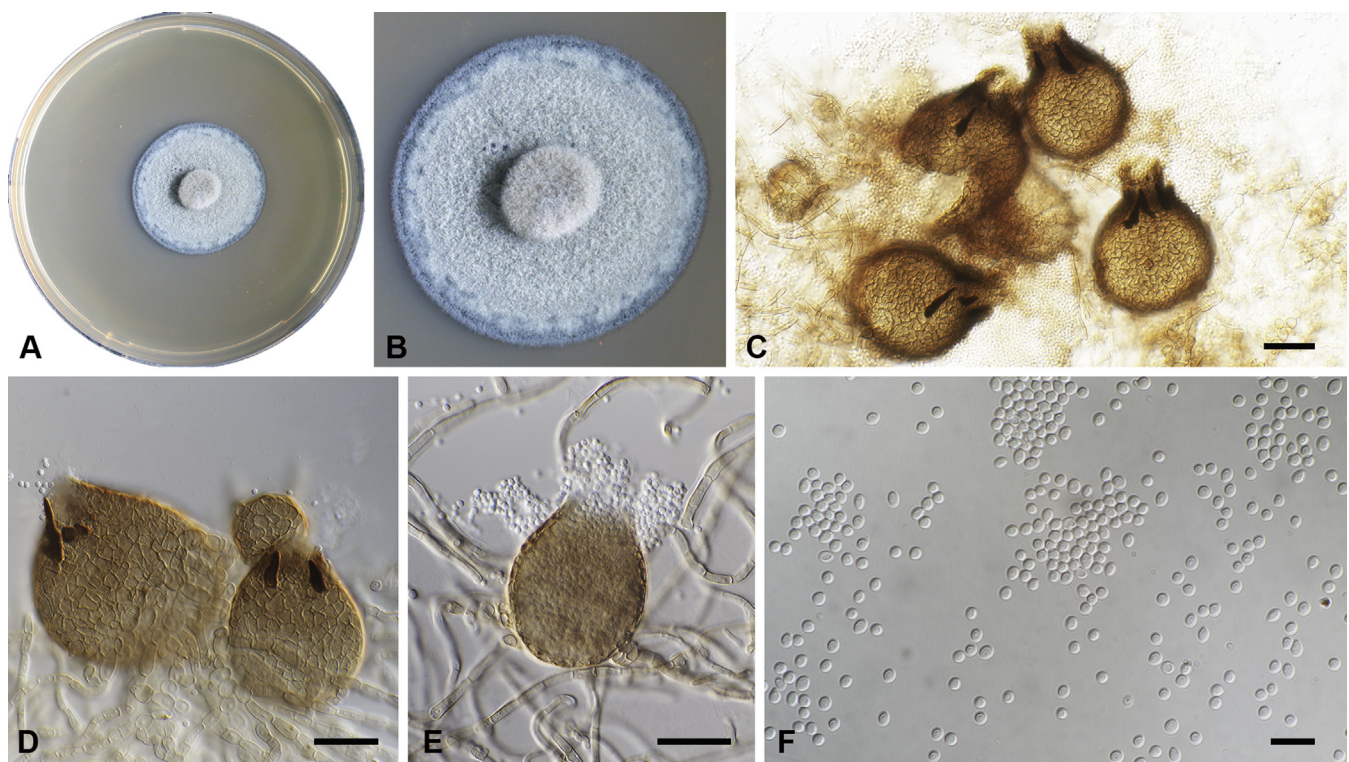
**Etymology:** Name refers to Indonesia where this fungus was collected.

*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)  $\times$  (16–)23–33(–40)  $\mu\text{m}$ . *Setae* not observed. *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–) 2.4–2.8  $\times$  (1.8–)2.2–2.4(–2.6)  $\mu\text{m}$ , (av. =  $2.5 \times 2.2 \mu\text{m}$ , 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-1 $\alpha$*  and *RPB2* loci. *Chaetocapnodium indonesiacum* can be distinguished from all other species by having the smallest pycnidia ( $25\text{--}35 \times 23\text{--}33 \mu\text{m}$ ). 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.



**Fig. 13.** *Chaetocapnodium thailandense*. A, B. Colony (2-wk-old) on MEA. C, D. Conidiomata with setae on SNA. E. Conidia inside conidioma. F. Conidia. Scale bars: C = 25  $\mu\text{m}$ ; D, E = 20  $\mu\text{m}$ ; F = 10  $\mu\text{m}$ .

***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 *Phyllica 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.

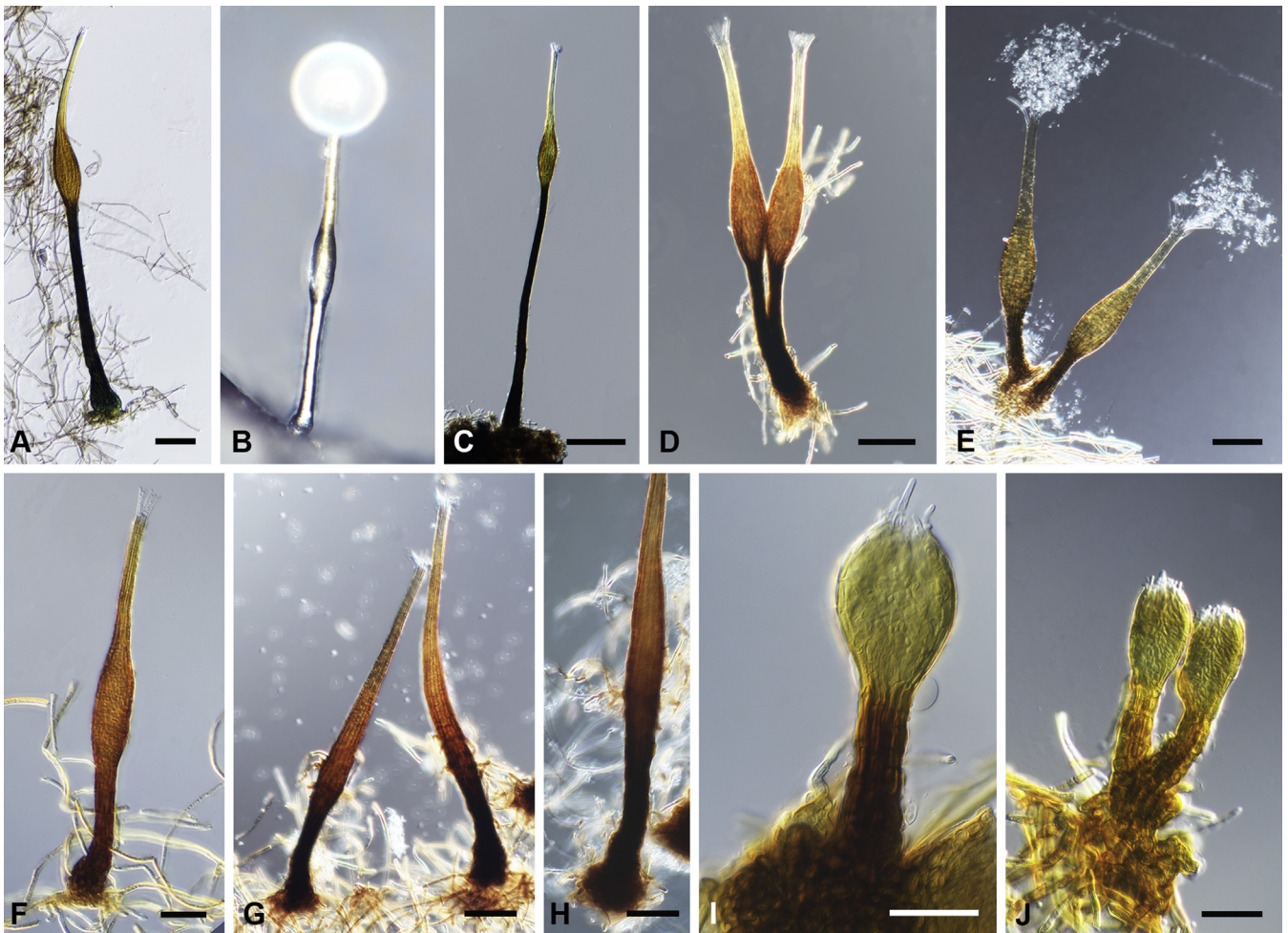
*Notes*: Based on the phylogenetic analyses *Ch. insulare* is related to *Ch. placitae* (Figs S1, 2), but morphologically it is distinct from all *Chaetocapnodium* species examined in this study by producing the largest conidia with average length and width greater than 3 (av. = 3.4 × 3 μm). Moreover, 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.

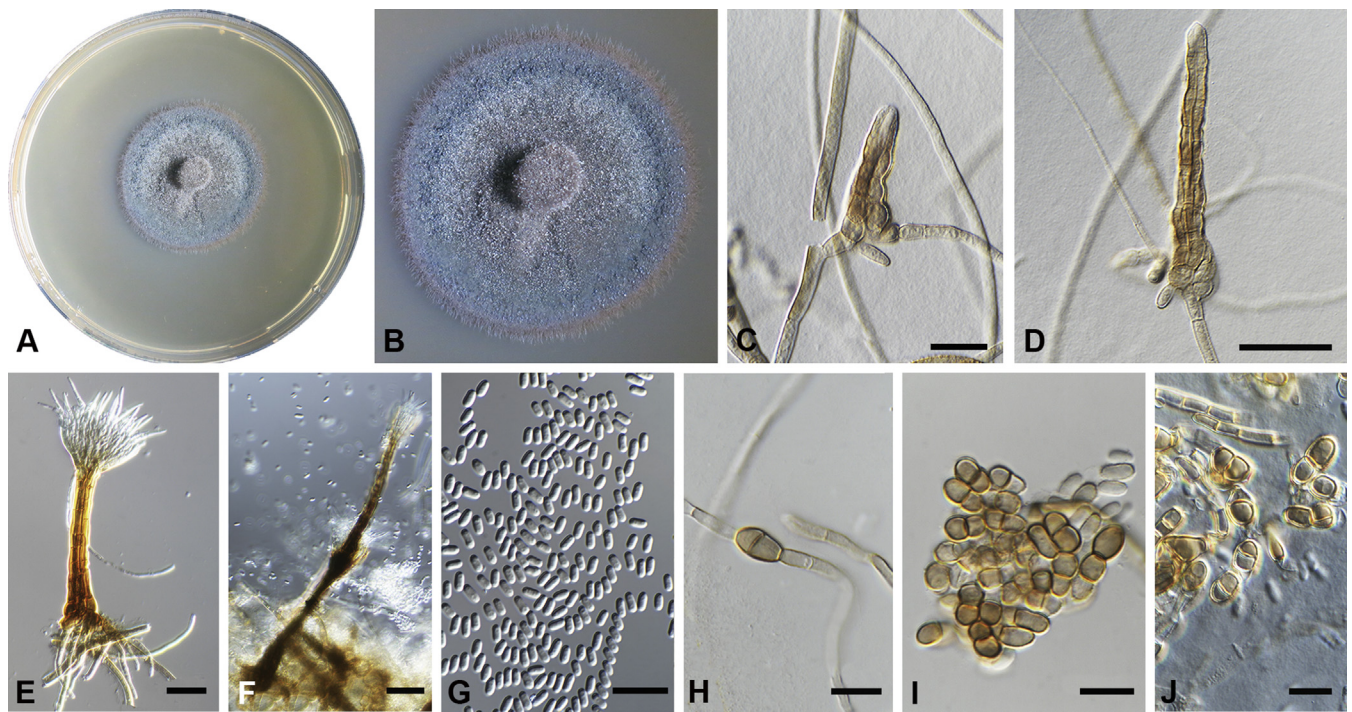
*Basionym*: *Phragmocapnias philippinensis* Hongsanan & K.D. Hyde, Fungal Diversity 72: 69. 2015.

*Description*: Liu *et al.* (2015).

*Typus*: **Philippines**, Laguna, Mount Makiling, on leaves of palm (*Areaceae*), Feb. 2012, K.D. Hyde HSA14/1 (**holotype** MFLU 14-0748, ex-type culture MFLUCC 12-0110 = CPC 20474).



**Fig. 14.** *Conidiocarpus*, *Phragmocapnias* and *Polychaeton* conidiomata. **A, B.** *Conidiocarpus* conidiomata on SNA. **C–E.** *Conidiocarpus* conidiomata on OA. **F.** *Polychaeton* conidioma on SNA. **G, H.** *Polychaeton* conidiomata on OA. **I, J.** *Phragmocapnias* conidiomata on SNA. Scale bars: A, C–E, G, H = 50 μm; F, J = 25 μm; I = 20 μm.



**Fig. 15.** *Leptoxypium citri*. **A, B.** Colony (2-wk-old) on MEA. **C, D.** Conidiomata arising from mycelia on SNA. **E.** Mature funnel-shaped conidioma at apex with hyaline hyphae surrounding the ostiole. **F.** Proliferation through the fertile head of conidioma. **G.** Conidia. **H–J.** Synsexual morph 2-celled conidia. Scale bars: C = 40  $\mu$ m; D = 20  $\mu$ m; E = 25  $\mu$ m; F = 50  $\mu$ m; G–J = 10  $\mu$ m.

***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 intercalary, lateral or terminal on erect hyphal branches, meristogenous in development, pseudoparenchymatous, thin-walled, 1–2 cell layers of *textura angularis*, (36–)45–70(–100)  $\times$  (32–)40–65(–94)  $\mu$ m. *Setae* present, septate or aseptate, pale to dark brown, mostly around ostiole, (13.9–)20–26(–30)  $\mu$ m long (av. = 22.7  $\mu$ m, n = 30). *Ostiole* absent, or not well-developed, mostly releasing conidia by means of irregular rupture. *Conidia* hyaline, septate or aseptate, globose to subglobose, with minute guttules, smooth, thin-walled, (2.1–)2.4–2.8(–3)  $\times$  2–2.4(–2.6)  $\mu$ m (av. = 2.6  $\times$  2.3  $\mu$ m, 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*.

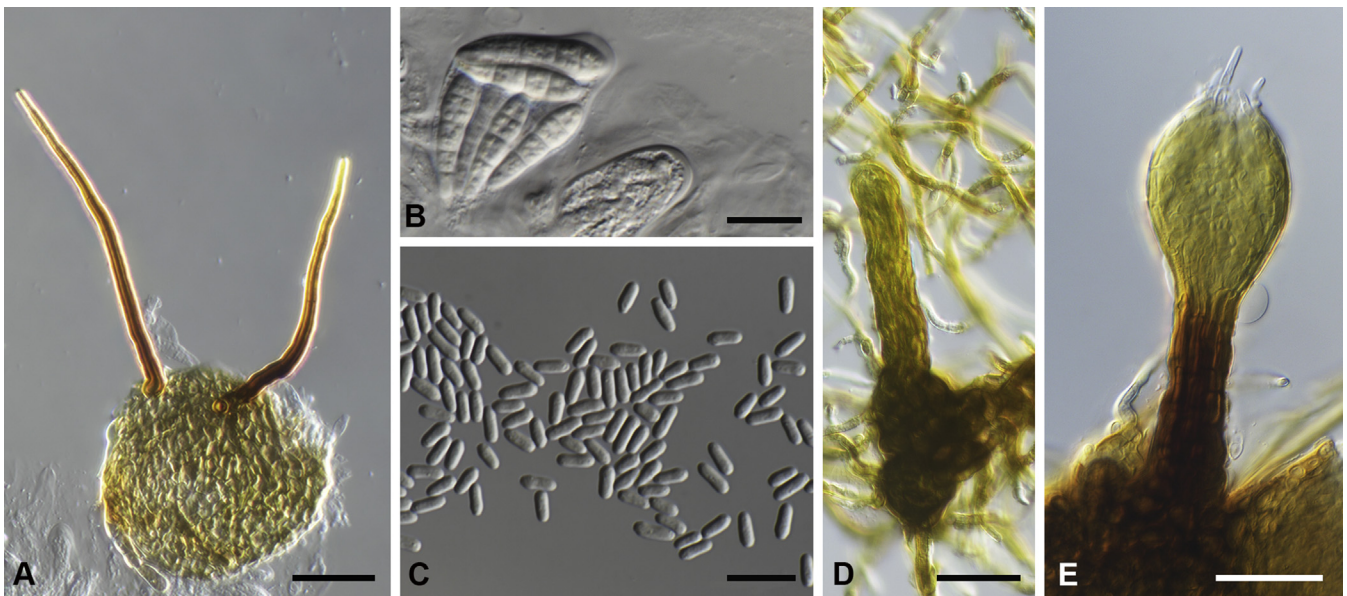
***Chaetocapnodium summerellii*** Abdollahz. & Crous, **sp. nov.** MycoBank MB833155. Fig. 11.

**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, thin-walled, 1–2 cell layers of *textura angularis*, (33–)40–60(–67)  $\times$  (27–)40–55(–60)  $\mu$ m. *Setae* present, septate or aseptate, pale to dark brown, mostly around ostiole, (9–)11–15(–19)  $\mu$ m long (av. = 14.3  $\mu$ m, 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–)2.2–2.5(–2.6)  $\times$  1.9–2.4  $\mu$ m, (av. = 2.3  $\times$  2.1  $\mu$ m, 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).



**Fig. 16.** *Phragmocapnias betle*. **A.** Ascoma with setae on SNA. **B.** Asci and ascospores. **C.** Conidia. **D.** Conidioma arising from mycelium on SNA. **E.** Conidioma on SNA. Scale bars: A, D = 25  $\mu\text{m}$ ; E = 20  $\mu\text{m}$ ; B, C = 10  $\mu\text{m}$ .

*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. 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).

***Chaetocapnodium tanzanicum*** Abdollahz. & Crous, *sp. nov.* MycoBank MB833160. Fig. 12.

*Etymology:* 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–) 55–70(–138)  $\times$  (30–)45–65(–112)  $\mu\text{m}$ . *Setae* present, septate or aseptate, pale to dark brown, mostly around ostiole, (10.5–) 12–17(–23)  $\mu\text{m}$  long (av. = 15.6  $\mu\text{m}$ , 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)  $\times$  (2.3–)2.5–2.8  $\mu\text{m}$ , (av. = 2.8  $\times$  2.6  $\mu\text{m}$ , 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 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. 13.

*Etymology:* 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*, (32–) 40–70(–90)  $\times$  (32–)40–60(–80)  $\mu\text{m}$ . *Setae* present, aseptate, pale to dark brown, mostly around ostiole, (8.7–) 13–19(–26.6)  $\mu\text{m}$  long (av. = 16.1  $\mu\text{m}$ , 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)  $\times$  (1.9–)2–2.7  $\mu\text{m}$  (av. = 2.3  $\times$  2.1  $\mu\text{m}$ , n = 50).

*Culture characteristics:* Colonies, leathery, appressed, with fluffy aerial mycelium, glaucous 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. Karunaratna (**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. tanzanicum* 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, aseptate, 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 *Phragmocapnias* (Hughes 1976). *Phragmocapnias betle* is the type species of *Phragmocapnias*. 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 *Phragmocapnias* to *Conidiocarpus*.

In this study based on phylogenetic analyses, the type species of *Conidiocarpus* and *Phragmocapnias* 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-asexual connections have been confirmed, the pycnidial morphs of *Phragmocapnias* 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 *Phragmocapnias betle*, 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 *Phragmocapnias betle*, 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 *Phragmocapnias* 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. plumeriae* 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 citharexylti* Petr.

*Descriptions:* Hughes (2007), Cheewangkoon 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 *Blastocervulus* (Crous et al. 2019a, b).

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

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

*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, septate, 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 flexuous; 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.

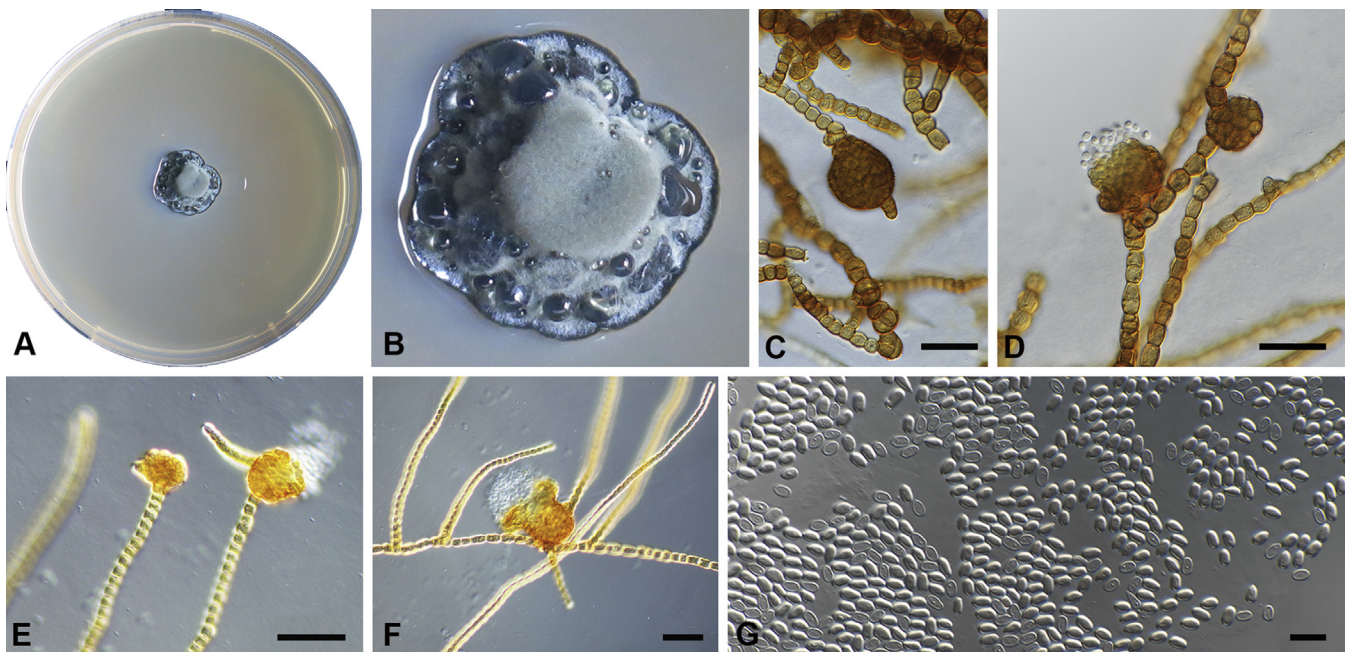


Fig. 17. *Neoantennariella phylicae*. A, B. Colony (2-wk-old) on MEA. C. Septate hyphae and immature conidioma on SNA. D–F. Intercalary, lateral and terminal conidiomata. G. Conidia. Scale bars: C–D = 20  $\mu\text{m}$ ; E–F = 25  $\mu\text{m}$ ; G = 10  $\mu\text{m}$ .

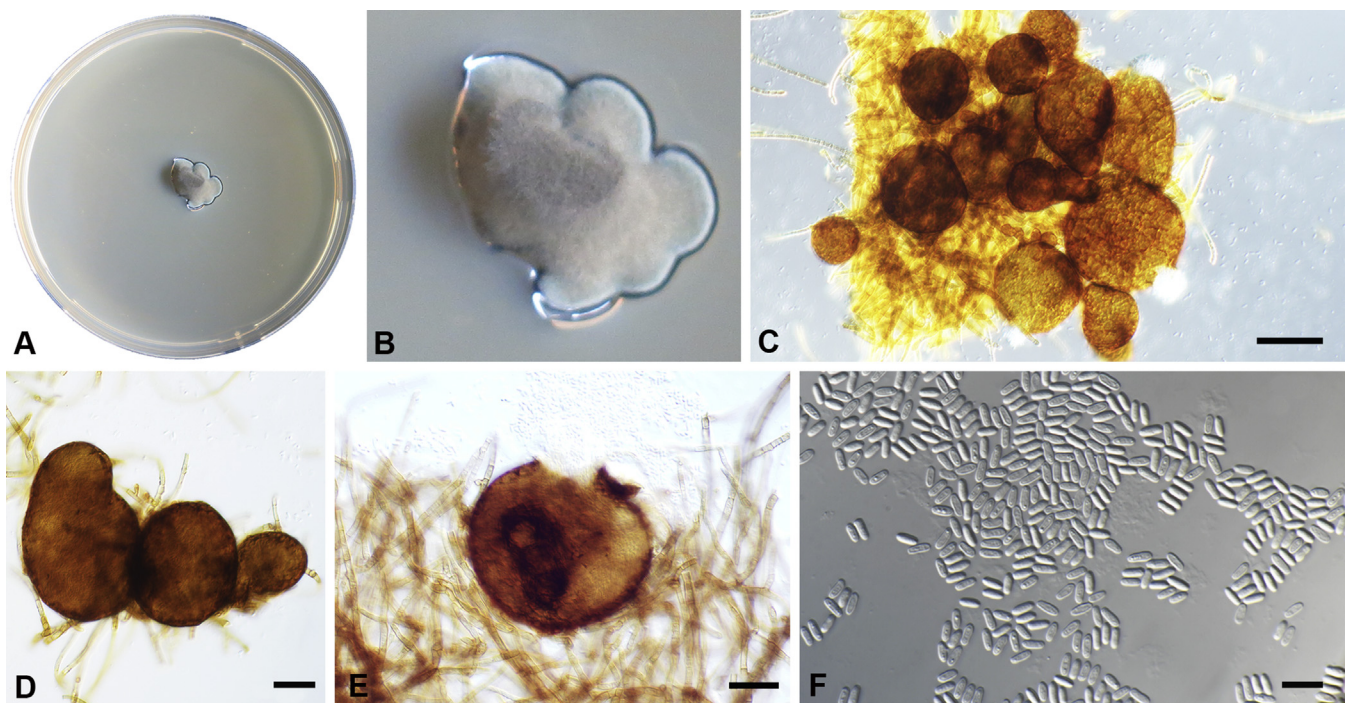


Fig. 18. *Neoasbolisia phylicae*. A, B. Colony (2-wk-old) on MEA. C–E. Conidiomata on SNA. F. Conidia. Scale bars: C = 20  $\mu\text{m}$ ; D–E = 25  $\mu\text{m}$ ; F = 10  $\mu\text{m}$ .

*Conidiophores* subcylindrical to subulate, septate, tightly aggregated in apical part of synnema, among synnematosus 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,  $(3.9\text{--}4.3\text{--}4.9\text{--}5.3) \times (1.9\text{--}2.1\text{--}2.4\text{--}2.6)$   $\mu\text{m}$  (av. =  $4.7 \times 2.2$   $\mu\text{m}$ ,  $n = 50$ ), aggregating in hyaline, slimy masses at apex of synnemata. *Synasexual morph conidia* arthric, single or in chains, frequently around the bulbous base of the synnemata, cylindrical to ellipsoid or ovoid, 1-septate, constricted at septum, smooth, pale to medium brown,  $6\text{--}12 \times 2\text{--}5$   $\mu\text{m}$ .

*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  $^{\circ}\text{C}$ . Colonies reaching 39 mm diam on MEA after 2 wk in the dark at 25  $^{\circ}\text{C}$ .

*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,

*TEF-1 $\alpha$*  and *RPB2* loci, respectively. Conidia of *L. citri* are smaller (4.3–4.9  $\times$  2.1–2.4  $\mu$ m) than those of *L. kurandae* (6–7  $\times$  2–3  $\mu$ m). It is interesting that both isolates of *L. citri* are known from *Citrus* collected in Europe.

***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, hyphae smooth, thin-walled, septate, constricted at septa, with a mucilaginous outer wall layer. *Conidiomata* pycnidial, brown, comprised of cylindrical septate cells, (67–)90–120(–135)  $\mu$ m high (av. = 105  $\mu$ m, n = 20), stalk brown to black, (27–)50–70(–97)  $\mu$ m high (av. = 50  $\mu$ m, n = 20), 12–31 diam (av. = 24  $\mu$ m, n = 20), the oval, swollen part which produces conidia is brown, comprised of cylindrical, septate cells, (37–)50–60(–69)  $\mu$ m high (av. = 48  $\mu$ m, n = 20), (30–)40–55(–75)  $\mu$ m diam (av. = 53  $\mu$ m, 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)  $\times$  (1.4–)1.8–2.2(–2.8)  $\mu$ m (av. = 5.5  $\times$  2  $\mu$ m, 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:* **Philippines**, 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 plumeriae*** (Hongsanan & K.D. Hyde) Abdollahz. & Crous, **comb. nov.** MycoBank MB833164.

*Basionym:* *Conidiocarpus plumeriae* 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 L  veill   (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.) L  v. 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.



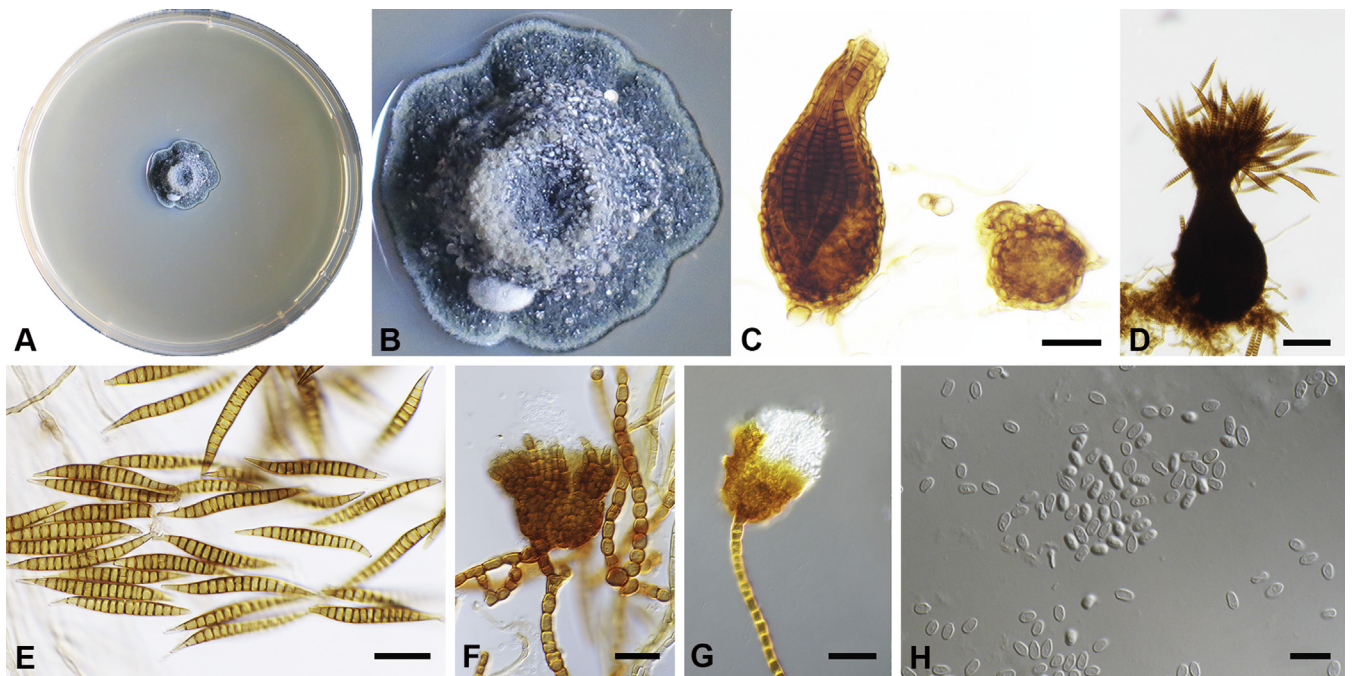


Fig. 19. *Phaeoxyphiella phyllicae*. A, B. Colony (2-wk-old) on MEA. C, D. Conidiomata with conidia on SNA. E. Transversely euseptate brown conidia. F, G. Spermogonia. H. Microconidia. Scale bars: C, E, F = 20  $\mu$ m; D = 50  $\mu$ m; G = 25  $\mu$ m; H = 10  $\mu$ m.

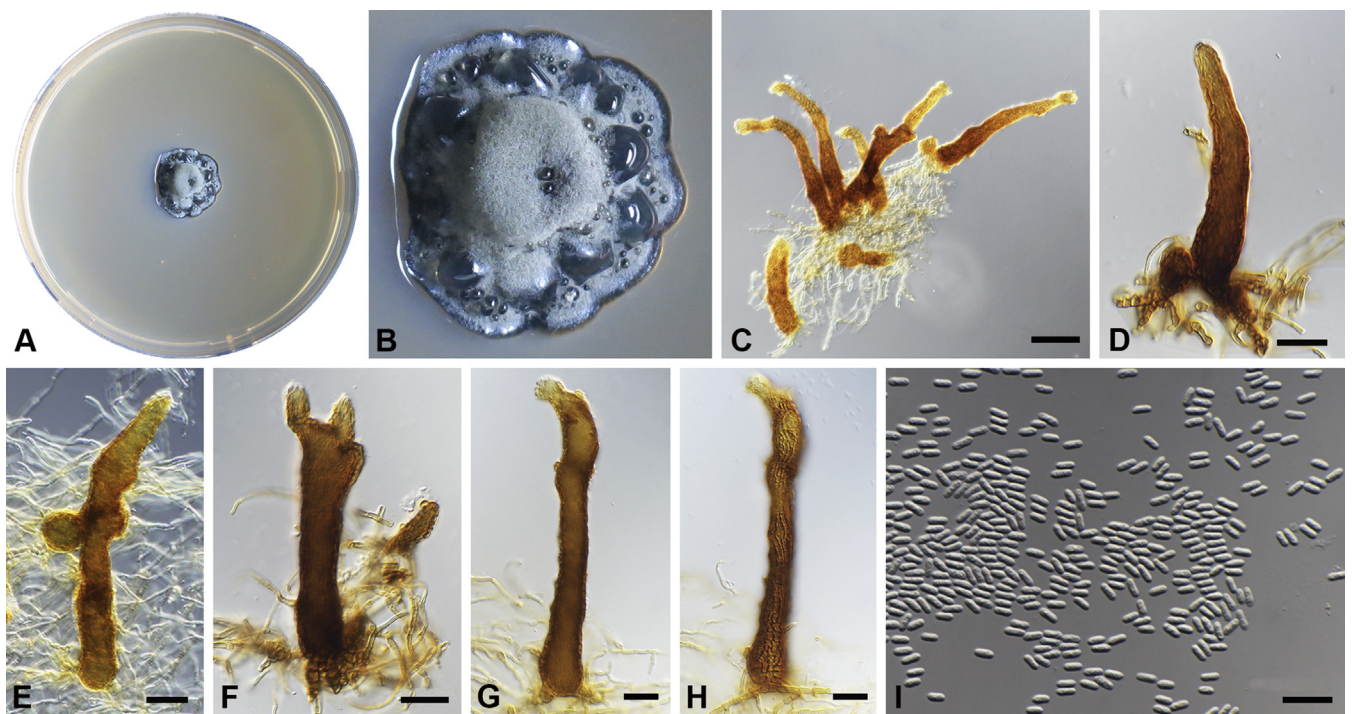


Fig. 20. *Scolecoxyphium blechni*. A, B. Colony (2-wk-old) on MEA. C–H. Irregularly cylindrical-oblong, straight or flexuous, simple or branched conidiomata on SNA. I. Conidia. Scale bars: C = 50  $\mu$ m; D, F–H = 20  $\mu$ m; E = 25  $\mu$ m; I = 10  $\mu$ m.

*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

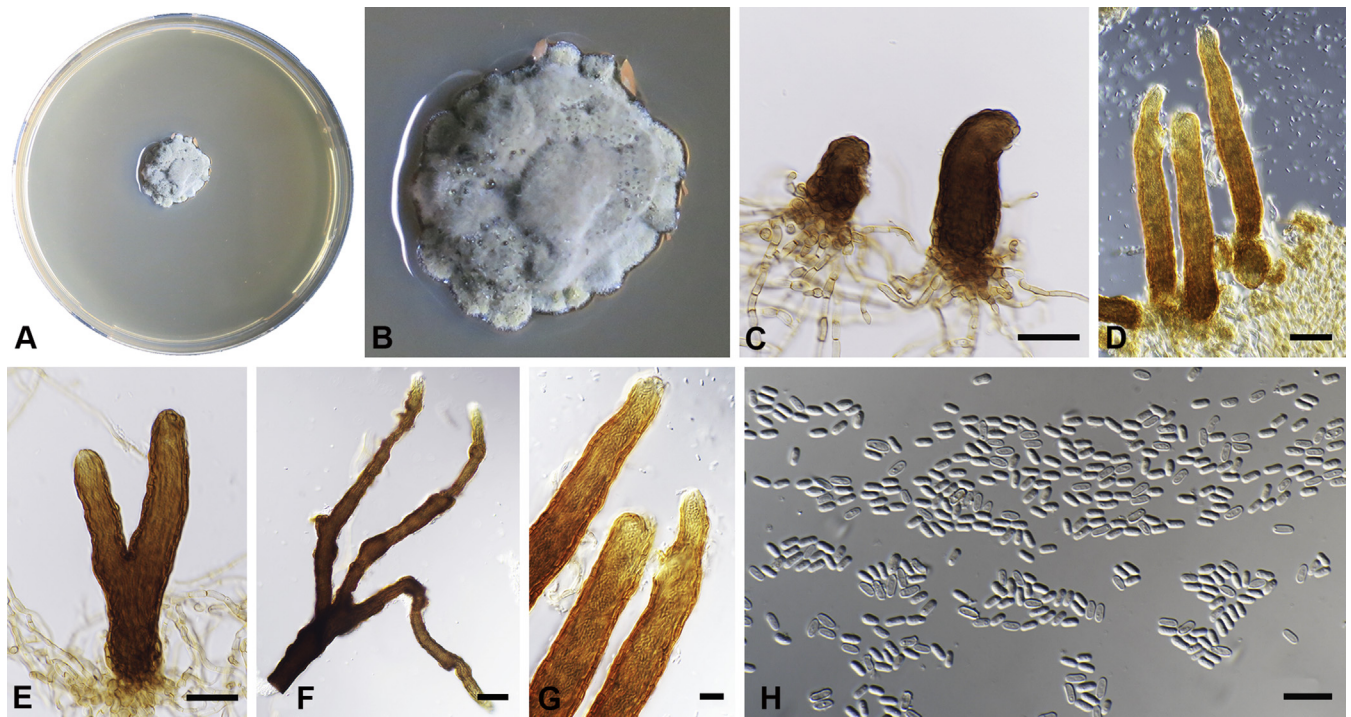
*Fumiglobus* D.R. Reynolds & G.S. Gilbert, *Cryptog. Mycol.* 27: 252. 2006.

*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.



**Fig. 21.** *Scolecoxyphium leucadendri*. **A, B.** Colony (2-wk-old) on MEA. **C.** Immature conidiomata. **D–F.** Irregularly cylindrical-oblong, straight or flexuous, simple or branched conidiomata on SNA. **G.** Conidia inside conidiomata. **H.** Conidia. Scale bars: C, E = 20  $\mu\text{m}$ ; D, F = 25  $\mu\text{m}$ ; G, H = 10  $\mu\text{m}$ .

**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, meristogenous in development, pseudoparenchymatous, thin-walled, 1–2 cell layers of *textura angularis*, (40–)50–65(–85)  $\times$  (30–)50–60(–68)  $\mu\text{m}$  (av. = 45  $\times$  42  $\mu\text{m}$ , n = 20). **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, (3.9–)4.5–5.2(–5.9)  $\times$  2.5–3.2(–3.6)  $\mu\text{m}$  (av. = 4.8  $\times$  2.9  $\mu\text{m}$ , n = 50).

**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 146164. **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.

***Neosbolisia*** 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, meristogenous 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:** *Neosbolisia 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.

***Neosbolisia 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, meristogenous in development, 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, with minute guttules, 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).

**Readeriellipsoidaceae** Abdollahz. & Crous, *fam. nov.* MycoBank MB833170.

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

*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 synnematosus, 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*: *Readeriellipsoidis* 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 *Readeriellipsoidaceae* separate from other *Capnodium* species that grouped in *Capnodium sensu Chomnunti et al. (2011)*. In a study on capnodiaceous 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, multiseptate phragmoconidia. Two species, *Ph. californica* and *Ph. rondeletiae*, have much shorter, oblong to

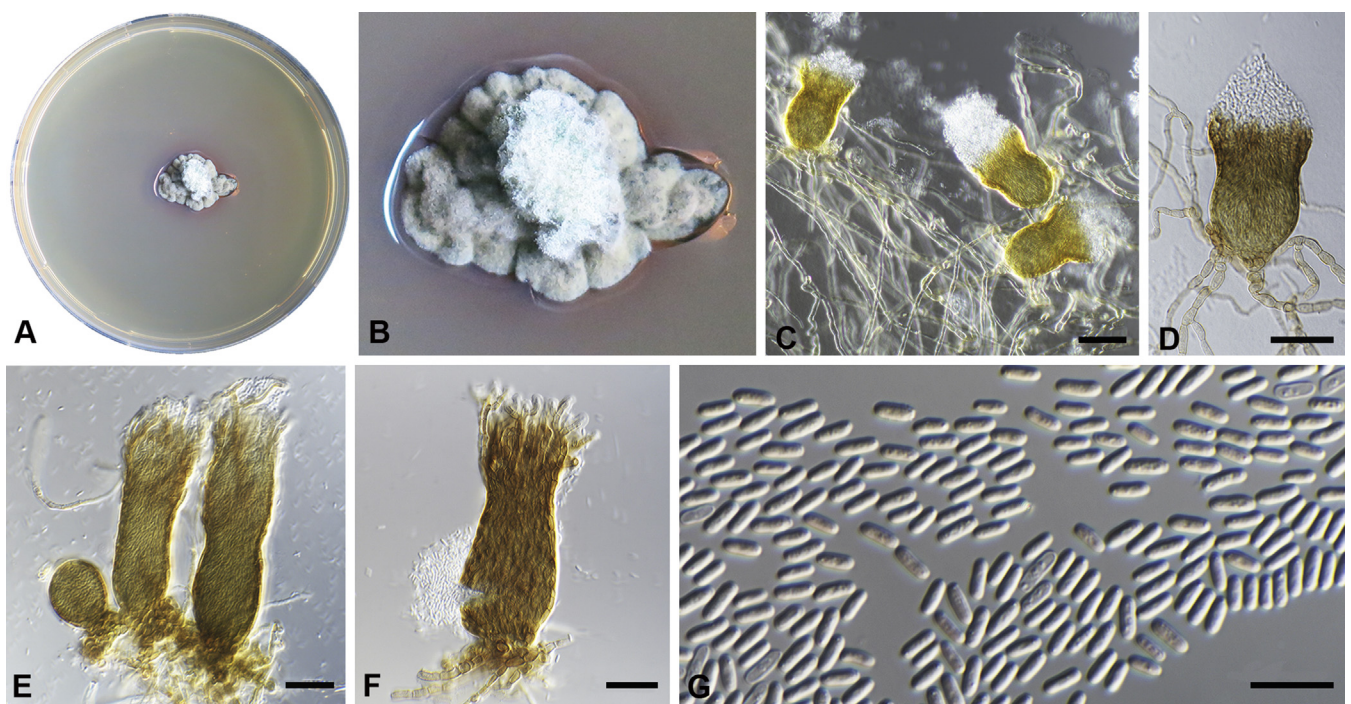
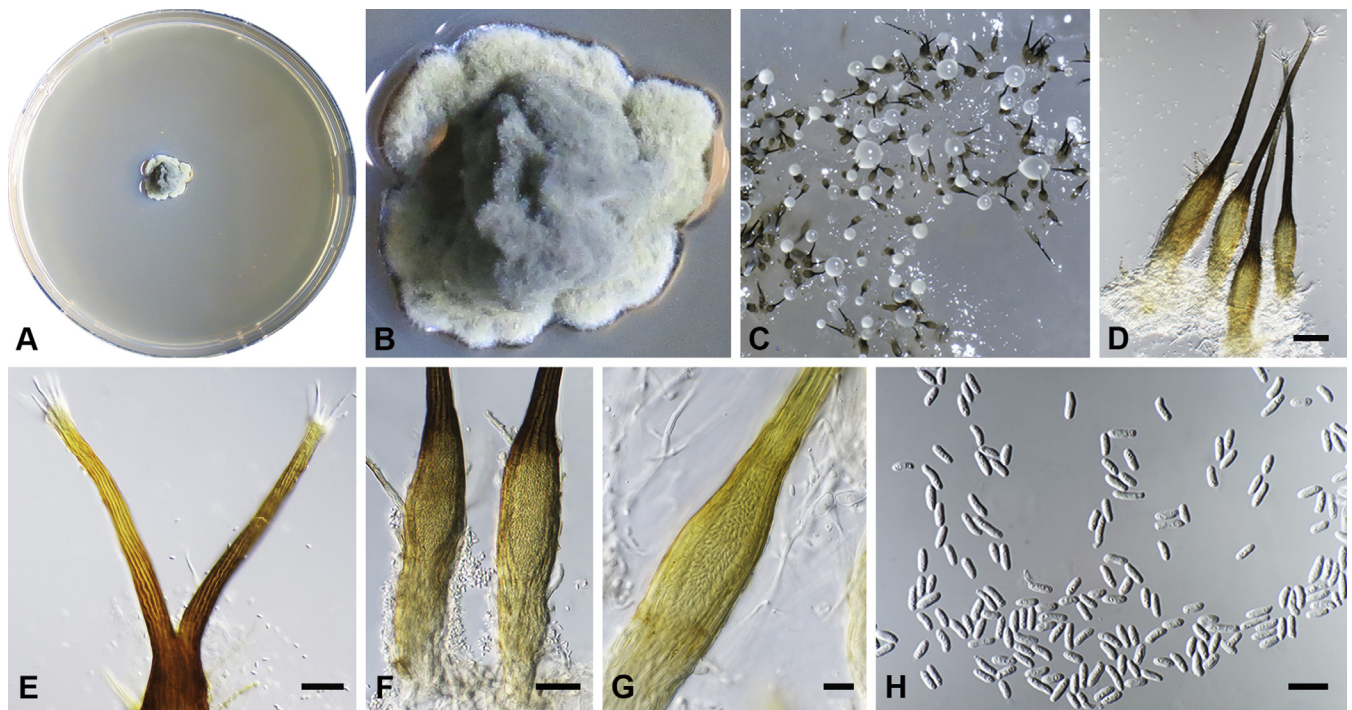


Fig. 22. *Scoleocyphium phylicae*. A, B. Colony (2-wk-old) on MEA. C–F. Cylindrical-oblong, straight, simple conidiomata on SNA. G. Conidia. Scale bars: C = 25 μm; D–F = 20 μm; G = 10 μm.



**Fig. 23.** *Scorias aphidis*. **A, B.** Colony (2-wk-old) on MEA. **C, D.** Flask-shape conidiomata on SNA. **E.** Ostioles surround by hyaline hyphae. **F, G.** Conidia produced in ellipsoidal part of conidiomata. **H.** Conidia. Scale bars: D = 50 µm; E–F = 25 µm; G–H = 10 µm.

ellipsoidal, 3-septate phragmoconidia, which are at first hyaline, slowly becoming brown. The seventh species, *Ph. callitris*, 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), 298(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), 862(C), 881(A), 882(T), 899(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.

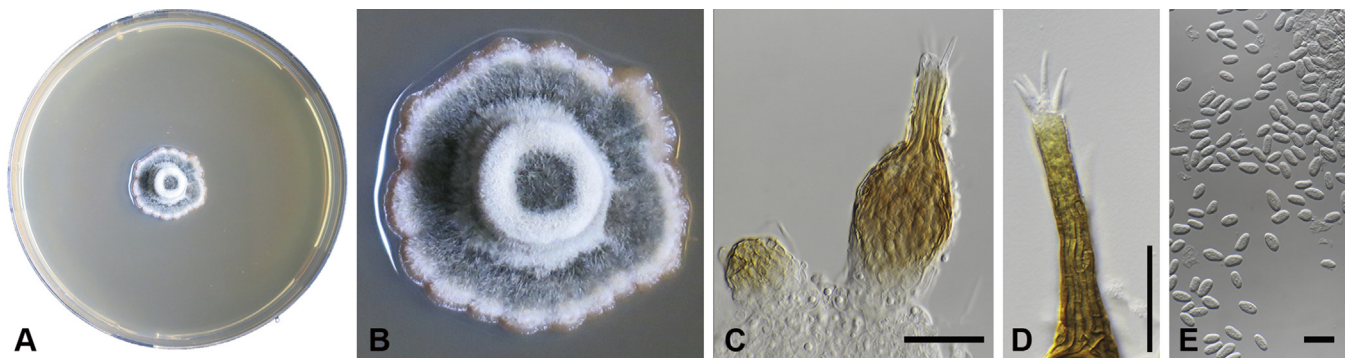
*Etymology:* Name reflects *Phylica*, the host genus from which it was collected.

*Mycelium* superficial or immersed, hyaline to medium brown, branched, hyphae smooth to slightly verruculose, thin-walled, septate, constricted at septa, with a mucilaginous outer layer. *Pycnidia* superficial or immersed, glabrous, sessile, obclavate, pyriform or conoidal, brown, membranous, 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 sinuate, 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.



**Fig. 24.** *Scorias camelliae*. **A, B.** Colony (2-wk-old) on MEA. **C.** Flask-shape conidiomata on SNA. **D.** Ostiole surround by hyaline hyphae. **E.** Conidia. Scale bars: C–D = 20 µm; E = 10 µm.

**Notes:** *Phaeoxyphiella phyllicae* differs from all seven species described by Batista & Ciferri (1963a) by producing 11–19-celled phragmoconidia. Conidial dimensions in *Ph. phyllicae* are close to those of *Ph. walteri*, but conidia are 11–19-celled in *Ph. phyllicae*, and 3–15-celled in *Ph. walteri*.

**Readeriellipsoidis** Crous & Decock, *Persoonia* 34: 195. 2015.

**Type species:** *Readeriellipsoidis fuscoporiae* Crous & Decock

**Description:** See Crous *et al.* (2015).

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

**Scolecoxyphium** Cif. & Bat., *Publicações Inst. Micol. Recife* 47: 5. 1956.

**Type species:** *Scolecoxyphium fraseriae* 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. fraseriae* (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 blechni** Abdollahz. & Crous, *sp. nov.* MycoBank MB833173. 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, synnematosus, 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), 664(G), 667(C), 985(G), 994(C); *TEF-1α* 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-1α* 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, synnematus; 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 ellipsoid, 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:** *Scolecocyphium leucadendri* formed a distinct clade in the phylogenetic trees (Figs S1, 2), but is morphologically similar to *S. blechni*. The two species can be differentiated based on the pycnidial size on OA, geography and substrate.

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

**Etymology:** Name reflects the host genus *Phylica* 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, cylindrical-oblong, straight, short, simple, occur singly or in groups, medium to dark brown, synnematus, 40–65 × 27–37 µm (av. = 52 × 32 µm, n = 20), sessile, without swollen part and neck, wall comprising mostly cylindrical cells. **Ostiole** at apex of pycnidia, surrounded with brown and obtusely rounded hyphae, without hyaline hyphal extensions. **Conidia** small, hyaline, aseptate, oblong to ellipsoid, continuous, (3.6–) 4–4.3(–4.7) × 1.2–1.7 µm (av. = 4.2 × 1.4 µm, n = 50).

**Culture characteristics:** Colonies, leathery, appressed, with fluffy aerial mycelium, folded, edge sinuate, smoke grey to olivaceous grey with a pink pigment after 2 wk in the dark at 25 °C. Colonies reaching 15 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-24303, culture ex-type CPC 19219 = CBS 146177).

**Additional material examined:** **South Africa**, Marion Island, Prince Edward Is., on *P. arborea*, 2011, M.J. Wingfield, culture CPC 19225 = CBS 146178.

**Notes:** Genetically *S. phylicae* constitutes a separate clade within *Scolecocyphium* (Figs S1, 2). It is morphologically distinguishable based on its short cylindrical pycnidia and longer conidia.

***Scorias*** Fr., Syst. Mycol. (Lunde) 3(2): 269. 1832.

**Type species:** *Scorias spongiosa* (Schwein.) Fr.

**Notes:** A search in Index Fungorum and MycoBank (March 2019) revealed 13 names in *Scorias*. Chomnunti et al. (2011) re-examined the type species, *Sc. spongiosa*, and designated an epitype MFLU10-0013 (ex-epitype MFLUCC10-0084) from Thailand. Cultures and molecular data are presently available for three species: *Sc. leucadendri* (LSU, ITS, *TEF-1α* and *RPB2*), *Sc. mangiferae* (LSU and ITS) and *Sc. spongiosa* (LSU). In this study we examined and sequenced isolates CBS 201.30 and CBS 325.33, which are representatives of a new species described here.

***Scorias aphidis*** Abdollahz. & Crous, **sp. nov.** MycoBank MB833177. Fig. 23.

**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, synnematus, 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 ellipsoidal 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(–7.6) × (1.8–)2–2.6 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. mangifera* in 7 bp in LSU and from *Sc. camelliae* in 9 bp in LSU, 8 bp in ITS, 28 bp in *TEF-1α* and 94 bp in *RPB2*. 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, synnematus, 59–163 µm high (av. = 100 µm,

$n = 20$ ), sessile or with short stalk ( $11\text{--}30 \times 12\text{--}24 \mu\text{m}$ , av. =  $15 \times 17 \mu\text{m}$ ), with conspicuous oval or ellipsoidal central part ( $37\text{--}85 \times 16\text{--}57 \mu\text{m}$ , av. =  $45 \times 35 \mu\text{m}$ ), and a long neck ( $19\text{--}77 \times 6\text{--}27 \mu\text{m}$ , av. =  $45 \times 12 \mu\text{m}$ ); wall comprising mostly cylindrical cells. *Ostiole* at apex of pycnidia, surrounded by hyaline hyphae. *Conidia* small, hyaline, aseptate, ellipsoid to ovoid,  $(4.4\text{--})5.3\text{--}5.7(\text{--}7.4) \times (1.9\text{--})2.2\text{--}2.5(\text{--}2.9) \mu\text{m}$  (av. =  $5.6 \times 2.4 \mu\text{m}$ ,  $n = 50$ ).

**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. Steinmann, 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. =  $5.6 \times 2.4 \mu\text{m}$  on SNA) are larger than those of *Sc. spongiosa* (av. =  $3.9 \times 1.9 \mu\text{m}$  on PDA) and smaller than conidia of *Sc. mangiferae* (av. =  $6.7 \times 2.5 \mu\text{m}$  *in vivo*).

## DISCUSSION

The *Capnodiales* was originally established for three families of sooty moulds, namely *Antennariaceae*, *Capnodiaceae* and *Coccodiniaceae* (Woronichin 1925). Schoch *et al.* (2006) transferred *Mycosphaerellaceae* and *Piedraiaceae* 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 saprobes, plant and human pathogens, mycoparasites, lichenised and rock-inhabiting fungi, including epi-, ecto- 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: *Capnodiaceae*, *Cladosporiaceae*, *Cystocoleaceae*, *Dissoconiaceae*, *Extremaceae*, *Mycosphaerellaceae*, *Neodevriesiaceae*, *Phaeothecaceae*, *Phaeothecoidiellaceae*, *Racodiaceae*, *Schizothyriaceae*, *Teratosphaeriaceae* (including *Piedraiaceae*) and two *incertae sedis* genera, *Comminutispora* 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-1 $\alpha$*  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 *Antennariellaceae*, *Capnodiaceae*, *Euantennariaceae* and *Metacapnodiaceae*. Although many studies have focused on the taxonomy of sooty moulds (Hughes 1951, 1966, 1972, 1976,

1981, 2003, 2007, Yamamoto, 1954, Batista & Ciferri 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 *Capnodiaceae*.

In an attempt to explain the high levels of diversity in the *Capnodiales*, the resulting phylogenetic tree (LSU, *TEF-1 $\alpha$*  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*, *Comminutisporiales*, *Neophaeothecales*, *Phaeothecales* and the *Racodiales*.

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 *Capnodiaceae*, *Neoantennariellaceae* and *Readeriellipsidaceae* of which the latter two are newly described. Seven genera are recognised in *Capnodiaceae*: *Capnodium*, *Cheatocapnodium*, *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 asexual morphs.

The *Neoantennariellaceae* is introduced to accommodate *Fumiglobus* and two new monotypic genera, *Neoantennariella* and *Neoasbolisia*. All three genera produce pycnidial conidiomata. In *Readeriellipsidaceae* four coelomycetous genera, namely *Phaeoxyphiella*, *Readeriellipsis*, *Scolecoxyphium* 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-1 $\alpha$*  and *RPB2*) using both RAXML and Bayesian analyses, we found *Mycosphaerellales* to represent a fully supported clade (ML-BS = 100 %, PP = 1) accommodating eight families, namely *Cystocoleaceae*, *Dissoconiaceae*, *Extremaceae*, *Mycosphaerellaceae*, *Neodevriesiaceae*, *Phaeothecoidiellaceae*, *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 ectophytic sooty blotch and flyspeck fungi (*Dissoconiaceae*, *Phaeothecoidiaceae*, *Schizothyriaceae*) have evolved from ancestral phytopathogenic relatives. Lichenisation has occurred once in *Cystocoleaceae*, while plant pathogens are found in *Mycosphaerellaceae*, *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 *Cladosporiaceae* were resolved as a distinct clade apart from *Capnodiaceae*, *Mycosphaerellaceae* and allied families: *Dissoconiaceae*, *Extremaceae*, *Neodevriesiaceae*, *Phaeothecoidiaceae*, *Schizothyriaceae* and *Teratosphaeriaceae* (Crous *et al.* 2009, Schoch *et al.* 2006, 2009, Suetrong *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 *Mycosphaerellales* and *Capnodiales* s. str. and formed a distinct clade sister to *Comminutispora agavaciensis*. Therefore, *Cladosporiaceae* has been elevated to ordinal level as *Cladosporiales*. Morphologically, members of *Cladosporiales* are quite distinct from those of *Mycosphaerellales*, 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 *Mycosphaerellales* are generally slow to reactivate, and far less hardy to extremes in temperature and moisture conditions.

Endoconidial taxa within *Capnodiales* s. lat. that belong to *Comminutispora* and *Phaeotheca* 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 *Comminutisporales*, *Neophaeothecales* and *Phaeothecales*. Furthermore, our results have resolved *Phaeotheca* as polyphyletic, representing two distinct clades. *Phaeotheca fissurella* (*Phaeothecales* ord. nov.) clustered apart from *P. salicornia* 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*, *Mycosphaerellales*), and represents a new order, *Racodiales* 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 *Capnodiales* s. lat., for which we introduced a new genus *Neophaeotheca* (*Neophaeothecaceae* fam. nov. and *Neophaeothecales* ord. nov.). Members of *Phaeothecales*, *Racodiales* and *Neophaeothecales* 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 “*Capnodiales* s. lat.” Many families are not yet represented in our phylogenetic analysis, pending further collections. Although our results revealed *Capnodiales* 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 *Neophaeothecales*; 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.

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## 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 anamorphs 2. Conspectus of mycosphaerella*. CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands: 1–231. CBS Biodiversity Series 5.
- Batista AC, Ciferri R (1963a). *Capnodiales*. *Saccardoia* **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.
- Bezerra 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, unsightly and until now undescribed: *Fumiglobus pieridicola* 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). *Capnodiaceae*. *Fungal Diversity* **51**: 103–134.
- Ciferri R, Batista AC, Nascimento ML (1956). Two new genera of pycnidiaecous sooty-molds associated with *Microxyphium* and *Septonema*. *Publicações do Instituto de Micologia da Universidade do Recife* **47**: 1–7.
- Crous PW, Braun U, Groenewald JZ (2007a). *Mycosphaerella* is polyphyletic. *Studies in Mycology* **58**: 1–32.
- Crous PW, Gams W, Stalpers JA, *et al.* (2004). MycoBank: an online initiative to launch mycology into the 21<sup>st</sup> century. *Studies in Mycology* **50**: 19–22.



- Crous PW, Groenewald JZ, Shivas RG, *et al.* (2011a). Fungal Planet description sheets: 69–91. *Persoonia* **26**: 108–156.
- Crous PW, Luangsa-Ard JJ, Wingfield MJ, *et al.* (2018). Fungal Planet description sheets: 785–867. *Persoonia* **41**: 238–417.
- Crous PW, Mohammed C, Glen M, *et al.* (2007b). *Eucalyptus* microfungi known from culture. 3. *Eucasphaeria* and *Sympoventuria* genera nova, and new species of *Furcasporea*, *Harknessia*, *Heteroconium* and *Phacidiella*. *Fungal Diversity* **25**: 19–36.
- Crous PW, Schoch CL, Hyde KD, *et al.* (2009). Phylogenetic lineages in the Capnodiales. *Studies in Mycology* **64**: 17–47.
- Crous PW, Summerell BA, Shivas RG, *et al.* (2011b). Fungal Planet description sheets: 92–106. *Persoonia* **27**: 130–162.
- Crous PW, Verkley GJM, Groenewald JZ, *et al.* (2019a). *Fungal biodiversity*. Westerdijk Fungal Biodiversity Institute, Utrecht, The Netherlands: 1–425. Westerdijk Laboratory Manual Series 1.
- Crous PW, Wingfield MJ, Cheewangkoon R, *et al.* (2019b). Foliar pathogens of eucalypts. *Studies in Mycology* **94**: 125–298.
- Crous PW, Wingfield MJ, Guarro J, *et al.* (2015). Fungal Planet description sheets: 320–370. *Persoonia* **34**: 167–266.
- Crous PW, Wingfield MJ, Richardson DM, *et al.* (2016). Fungal Planet description sheets: 400–468. *Persoonia* **36**: 316–458.
- de Hoog GS, Beguin H, Batenburg-Van de Vegte WH (1997). *Phaeotheca triangularis*, a new meristematic black yeast from a humidifier. *Antonie van Leeuwenhoek* **71**: 289–295.
- de Hoog GS de, Zalar P, Urzi C, *et al.* (1999). Relationships of dothideaceous black yeasts and meristematic fungi based on 5.8S and ITS2 rDNA sequence comparison. *Studies in Mycology* **43**: 31–37.
- Faull JL, Olejnik I, Ingrouille M, *et al.* (2002). A reassessment of the taxonomy of some tropical sooty moulds. *Tropical Mycology* **2**: 33–40.
- Haridas S, Albert R, Binder M, *et al.* (2020). 101 *Dothideomycetes* genomes: a test case for predicting lifestyles and emergence of pathogens. *Studies in Mycology*. <https://doi.org/10.1016/j.simyco.2020.01.003>.
- Hawksworth DL, Kirk PM, Sutton BC, *et al.* (1995). *Ainsworth and Bisby's Dictionary of the Fungi*, 8th edn. CAB International, Wallingford, UK.
- Hawksworth DL, Santesson R, Tibell L (2011). *Racoleus*, a new genus of sterile filamentous lichen-forming fungi from the tropics, with observations on the nomenclature and typification of *Cystocoleus* and *Racodium*. *IMA Fungus* **2**: 71–79.
- Hongsanan S, Hyde KD, Bahkali AH, *et al.* (2015a). Fungal biodiversity profiles 11–20. *Cryptogamie Mycologie* **36**: 355–381.
- Hongsanan S, Sánchez-Ramírez S, Crous PW, *et al.* (2016). The evolution of fungal epiphytes. *Mycosphere* **7**: 1690–1712.
- Hongsanan S, Tian Q, Hyde KD, *et al.* (2015b). Two new species of sooty moulds, *Capnodium coffeicola* and *Conidiocarpus plumeriae* in Capnodiaceae. *Mycosphere* **6**: 814–824.
- Hongsanan S, Zhao RL, Hyde KD (2017). A new species of *Chaetothyrina* on branches of mango, and introducing *Phaeothecoidiaceae* fam. nov. *Mycosphere* **8**: 137–146.
- Huelsenbeck JP, Ronquist F (2001). MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* **17**: 754–755.
- Hughes SJ (1951). Studies on micro-fungi X. *Zygosporium*. *Mycological Papers* **44**: 1–18.
- Hughes SJ (1966). New Zealand fungi 7. *Capnocybe* and *Capnophialophora*, new form genera of sooty moulds. *New Zealand Journal of Botany* **4**: 333–353.
- Hughes SJ (1972). New Zealand fungi 17. Pleomorphism in *Cuantennariaceae* and *Metacapnodiaceae*, two new families of sooty moulds. *New Zealand Journal of Botany* **10**: 225–242.
- Hughes SJ (1976). Sooty moulds. *Mycologia* **68**: 451–691.
- Hughes SJ (1981). New Zealand fungi 31. *Capnobotrys*, an anamorph of *Metacapnodiaceae*. *New Zealand Journal of Botany* **19**: 193–226.
- Hughes SJ (2003). *Capnofrasera dendryphioides*, a new genus and species of sooty moulds. *New Zealand Journal of Botany* **41**: 139–146.
- Hughes SJ (2007). *Heteroconium* and *Pirozynskiella* n. gen., with comments on conidium transseptation. *Mycologia* **99**: 628–638.
- Hyde KD, Jones EG, Liu JK, *et al.* (2013). Families of *Dothideomycetes*. *Fungal Diversity* **63**: 1–313.
- Ismail SI, Batzer JC, Harrington TC, *et al.* (2016). Ancestral state reconstruction infers phytopathogenic origins of sooty blotch and flyspeck fungi on apple. *Mycologia* **108**: 292–302.
- Jaczewski AA (1917). *Key to Fungi. Vol. II. Fungi Imperfecti*. Publishing House of SL Kind, Petrograd (In Russian).
- Jaklitsch WM, Fournier J, Dai DQ, *et al.* (2015). *Valsaria* and the *Valsariales*. *Fungal Diversity* **73**: 159–202.
- Khodaparast SA, Pourmoghaddam MJ, Amirmijani A, *et al.* (2020). Phylogenetic structure of the Iranian capnodiaceous sooty mould fungi inferred from the sequences of rDNA regions and TEF-1 $\alpha$ . *Mycological Progress* **19**: 155–169.
- Kirk PM, Cannon PF, David JC, *et al.* (2001). *Ainsworth and Bisby's Dictionary of the Fungi*, 9th edn. CAB International, Wallingford, UK.
- Kirk PM, Cannon PF, Minter DW, *et al.* (2008). *Ainsworth and Bisby's Dictionary of the Fungi*, 10th edn. CAB International, Wallingford, UK.
- Léveillé JH (1847). *Mycologie, mycétologie*. In: *Dictionnaire Universel d'Histoire naturelle*, **9**. Victor Masson, Paris: 261–303.
- Liu JK, Hyde KD, Jones EG, *et al.* (2015). Fungal diversity notes 1–110: taxonomic and phylogenetic contributions to fungal species. *Fungal Diversity* **72**: 1–97.
- Liu YJ, Whelen S, Hall BD (1999). Phylogenetic relationships among ascomycetes: evidence from an RNA polymerase II subunit. *Molecular Biology and Evolution* **16**: 1799–1808.
- Lücking R, Hodkinson BP, Leavitt SD (2017). The 2016 classification of lichenized fungi in the *Ascomycota* and *Basidiomycota* - Approaching one thousand genera. *The Bryologist* **119**: 361–417.
- Lumbsch HT, Lindemuth R (2001). Major lineages of *Dothideomycetes* (*Ascomycota*) inferred from SSU and LSU rDNA sequences. *Mycological Research* **105**: 901–908.
- Luttrell ES (1955). The ascstromatic *Ascomycetes*. *Mycologia* **47**: 511–532.
- Maddison WP, Maddison DR (2018). *Mesquite: a modular system for evolutionary analysis*. Version 3.51. <http://www.mesquiteproject.org>.
- Miller MA, Pfeiffer W, Schwartz T (2012). *The CIPRES science gateway: enabling high-impact science for phylogenetics researchers with limited resources*. *Proceedings of the 1st conference of the extreme science and engineering discovery environment: bridging from the extreme to the campus and beyond*. Association for Computing Machinery, USA: 1–8.
- Nylander JAA (2004). *MrModeltest v2*. Evolutionary Biology Centre, Uppsala University, Sweden. Program distributed by the author.
- Quaedvlieg W, Binder M, Groenewald JZ, *et al.* (2014). Introducing the consolidated species concept to resolve species in the *Teratosphaeriaceae*. *Persoonia* **33**: 1–40.
- Ramaley AW (1996). *Comminutispora* gen. nov. and its *Hyphospora* gen. nov. anamorph. *Mycologia* **88**: 132–136.
- Rayner RW (1970). *A mycological colour chart*. Commonwealth Mycological Institute and British Mycological Society, Kew, Surrey, UK.
- Rehner SA, Buckley E (2005). A *Beauveria* phylogeny inferred from nuclear ITS and EF1 $\alpha$  sequences: evidence for cryptic diversification and links to *Cordyceps* teleomorphs. *Mycologia* **97**: 84–98.
- Ren S, Ma J, Zhang X (2012). Two new *Heteroconium* species and two other forest microfungi newly recorded from China. *Mycotaxon* **119**: 361–367.
- Reynolds DR (1975). Observation on growth forms of sooty mold fungi. *Nova Hedwigia* **26**: 179–193.
- Reynolds DR (1979). Follicolous ascomycetes: 3. The stalked capnodiaceous species. *Mycotaxon* **8**: 417–445.
- Reynolds DR (1986). Follicolous ascomycetes 7. Phylogenetic systematics of the *Capnodiaceae*. *Mycotaxon* **27**: 377–403.
- Reynolds DR (1998). Capnodiaceous sooty mold phylogeny. *Canadian Journal of Botany* **76**: 2125–2130.
- Reynolds DR, Gilbert GS (2005). Epifoliar fungi from Queensland, Australia. *Australian Systematic Botany* **18**: 265–289.
- Reynolds DR, Gilbert GS (2006). Epifoliar fungi from Panama. *Cryptogamie Mycologie* **27**: 249–270.
- Rodríguez FJ, Oliver JL, Marín A, *et al.* (1990). The general stochastic model of nucleotide substitution. *Journal of Theoretical Biology* **142**: 485–501.
- Ronquist F, Huelsenbeck JP (2003). MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19**: 1572–1574.
- Ruiz RFC, Iturriga T, Abarca GH, *et al.* (2008). Notes on *Heteroconium* and a new species from Venezuela. *Mycotaxon* **105**: 175–184.
- Ruibal C, Gueidan C, Selbmann L, *et al.* (2009). Phylogeny of rock-inhabiting fungi related to *Dothideomycetes*. *Studies in Mycology* **64**: 123–133.
- Schoch CL, Crous PW, Groenewald JZ, *et al.* (2009). A class-wide phylogenetic assessment of *Dothideomycetes*. *Studies in Mycology* **64**: 1–15.
- Schoch CL, Grube M (2015). *Pezizomycotina: Dothideomycetes* and arthoniomycetes. In: (McLaughlin DJ, Spatafora JW, eds), *The Mycota – systematics and evolution part B, VII*. Springer Verlag, Germany: 143–176.
- Schoch CL, Shoemaker RA, Seifert KA, *et al.* (2006). A multigene phylogeny of the *Dothideomycetes* using four nuclear loci. *Mycologia* **98**: 1041–1052.
- Sigler L, Tsuneda A, Carmichael JW (1981). *Phaeotheca* and *Phaeosclera*, two new genera of dematiaceous hyphomycetes and a redescription of *Sarcinomyces* Lindner. *Mycotaxon* **12**: 449–467.

- 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 *Superstratomyceatales* 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 Russtaupilze 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 *Phaeothea* and *Hyphospora*. *Studies in Mycology* **43**: 49–56.