

## The Genera of Fungi – G 4: *Camarosporium* and *Dothiora*

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**Abstract:** The current paper represents the fourth contribution in the Genera of Fungi series, linking type species of fungal genera to their morphology and DNA sequence data. The present paper focuses on two genera of microfungi, *Camarosporium* and *Dothiora*, which are respectively epi- and neotypified. The genus *Camarosporium* is typified by *C. quaternatum*, which has a karstenula-like sexual morph, and phoma-like synasexual morph. Furthermore, *Camarosporomyces*, *Foliophoma* and *Hazslinszkyomyces* are introduced as new camarosporium-like genera, while *Querciphoma* is introduced as a new phoma-like genus. *Libertasomycetaceae* is introduced as a new family to accommodate *Libertasomyces* and *Neoplatysporoides*. *Dothiora*, which is typified by *D. pyrenophora*, is shown to produce dothichiza- and hormonema-like synasexual morphs in culture, and *D. cactacearum* is introduced as a new species. In addition to their typification, ex-type cultures have been deposited in the Westerdijk Fungal Biodiversity Institute (CBS Culture Collection), and species-specific DNA barcodes in GenBank. Authors interested in contributing accounts of individual genera to larger multi-authored papers in this series should contact the associate editors listed on the List of Protected Generic Names for Fungi.

### Key words:

DNA Barcodes  
fungal systematics  
ITS  
LSU  
typification  
[www.GeneraofFungi.org](http://www.GeneraofFungi.org)

**Article info:** Submitted: 15 April 2017; Accepted: 19 May 2017; Published: 23 May 2017.

## INTRODUCTION

The present paper clarifies two generic names in the Genera of Fungi project ([www.GeneraOfFungi.org](http://www.GeneraOfFungi.org); Crous *et al.* 2014a), which has the aim to revise the generic names of fungi accepted in Kirk *et al.* (2013). The two genera treated are supplemented with recently collected epi- or neotypes, which have been registered in MycoBank (Robert *et al.* 2013). Furthermore, in keeping with the one fungus = one name initiative for fungi (Hawksworth *et al.* 2011, Crous *et al.* 2015a), a single name is indicated for each genus.

The aim of the present contribution was to treat two problematic genera, namely *Camarosporium*, and *Dothiora*. In recent years, it has become clear that the *Camarosporium* morphology has evolved several times within *Dothideomycetes*, and that camarosporium-like morphs have phoma-like synasexual morphs, and pleospora-like sexual morphs. An additional complication lies in that some taxa only produce a single morph (e.g. see below in the present study), and thus it is almost impossible to clarify the generic identification without molecular data. Furthermore, the treatment of *Phoma* by Boerema *et al.* (2004) placed genetically distinct genera into one genus, while the same was true for the treatment of *Pleospora* by De Gruyter *et al.* (2013), and the assumption that the reference strains of *Camarosporium* included in Crous *et al.* (2006) were authentic for the name.

The genus *Dothiora* (based on *D. pyrenophora*) produces a *Dothichiza* asexual morph in culture, but the *Dothideaceae* has several genera that are dothiora-like in morphology, and that produce dothichiza-like asexual morphs in culture. Although we address the status of *Dothiora* in the present study, many additional collections are still required to resolve the generic boundaries of other old generic names in this family, particularly as we have observed hyaline, 1-septate ascospores to become muriformly septate with age, and eventually to even become pigmented. Given that these characters have traditionally been used to separate genera in the family (Sivanesan 1984, Thambugala *et al.* 2014), it now appears likely that there are far fewer genera in *Dothideaceae* than previously assumed (Crous & Groenewald 2016).

## MATERIALS AND METHODS

### Isolates

Freshly collected twigs were placed in damp chambers, and incubated at room temperature (ca. 20 °C) for 1–2 d. Single conidial or ascospore colonies were established from sporulating conidiomata or ascomata in Petri dishes containing 2 % malt extract agar (MEA) as described earlier (Crous *et al.* 1991). After 1–2 d, single spores were picked up and transferred to fresh MEA plates. Colonies were sub-

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cultured onto 2 % potato dextrose agar (PDA), oatmeal agar (OA), MEA (Crous *et al.* 2009), autoclaved pine needles on 2 % tap water agar (PNA) (Smith *et al.* 1996), and incubated at 25 °C under continuous near-ultraviolet light to promote sporulation. Reference strains and specimens are maintained at the Westerdijk Fungal Biodiversity Institute (CBS Culture Collection) in Utrecht, The Netherlands.

### DNA isolation, amplification and analyses

Genomic DNA was extracted from fungal colonies growing on MEA using the Wizard® Genomic DNA purification kit (Promega, Madison, WI), according to the manufacturer's protocol. The primers V9G (de Hoog & Gerrits van den Ende 1998) or ITS5 (White *et al.* 1990) and LR5 (Vilgalys & Hester 1990) were used to amplify for all isolates part of the nuclear rDNA operon (ITS) spanning the 3' end of the 18S nrRNA gene, the first internal transcribed spacer (ITS1), the 5.8S nrRNA gene, the second ITS region (ITS2) and approximately 900 bp of the 5' end of the 28S nrRNA gene. The primers ITS4 (White *et al.* 1990) and LR0R (Vilgalys & Hester 1990) were used as internal sequence primers to ensure good quality sequences over the entire length of the amplicon. Part of the beta-tubulin gene (*tub2*) was amplified and sequenced for selected isolates using T1 (O'Donnell & Cigelnik 1997) or Bt-2a and Bt-2b (Glass & Donaldson 1995). In addition, part of the first or second half of the translation elongation factor 1-alpha gene (*tef1*) was amplified and sequenced for selected isolates using EF1-728F (Carbone & Kohn 1999) and EF2 (O'Donnell *et al.* 1998), and EF1-983F and EF1-2218R (Rehner & Buckley 2005), respectively. Part of the 18S small subunit nrRNA gene (SSU) was amplified and sequenced for selected isolates using NS1 and NS4 (White *et al.* 1990). Amplification conditions followed Cheewangkoon *et al.* (2008) and Quaedvlieg *et al.* (2012). The programme SeqMan Pro v. 13.0.0 (DNASTAR, Madison, WI) was used to obtain consensus sequences of each isolate. Blast searches using ITS and LSU sequences were performed for each isolate and the closest matches were retrieved from GenBank and included in the phylogenetic analyses. The SSU, *tef1* and *tub2* sequences were not included in phylogenetic analyses but were used in blast searches to confirm the species identification where possible. Multiple sequence alignments for ITS and LSU were generated using the online version of MAFFT (<http://mafft.cbrc.jp/alignment/software/>) and subsequent phylogenetic analyses were conducted using parsimony in PAUP v. 4.0b10 (Swofford 2003) as described by Cheewangkoon *et al.* (2008). Sequence data were deposited in GenBank (Table 1) and the alignments and trees in TreeBASE (<http://www.treebase.org>).

### Morphology

Slide preparations were mounted in clear lactic acid or water from colonies sporulating on the media previously mentioned. Sections of sporocarps were made by hand for examination purposes. Observations were made with a Nikon SMZ25 stereo-microscope, and with a Zeiss Axio Imager 2 light microscope using differential interference contrast (DIC) illumination and a Nikon DS-Ri2 camera and software. Colony characters and pigment production were noted after 2 wk of growth on MEA, PDA and OA (Crous *et al.* 2009) incubated

at 25 °C. Colony colours (surface and reverse) were rated according to the colour charts of Rayner (1970). Taxonomic novelties and new typifications were deposited in MycoBank ([www.MycoBank.org](http://www.MycoBank.org); Crous *et al.* 2004).

## RESULTS

### Phylogeny

Four analyses were performed in this study; the first was based on a partial alignment of LSU (Fig. 1) to provide an overview phylogeny of the species and genera treated in the present study, whereas the remaining three alignments were ITS alignments representing *Camarosporium* and allied genera (Fig. 2), *Dothidea* and *Dothiora* (Fig. 3), and *Paracamarosporium* and *Pseudocamarosporium* (Fig. 4), respectively. The statistical parameters for these four phylogenies are summarised in Table 2.

The overview LSU phylogeny (Fig. 1) shows that *Dothiora pyrenophora* is nested inside the *Dothiora* clade. Based on this LSU phylogeny, the *Dothidea* clade has a bootstrap support value of 99 %, but the *Dothiora* clade did not receive any bootstrap support. *Libertasomyces* and *Neoplatysporoides* formed a lineage distinct from other families included in the phylogeny and therefore a family name is introduced below to accommodate these genera. *Camarosporium quaternatum* clustered with *Ochrocladosporium*, but without any bootstrap support. Megablast searches of the NCBI GenBank nucleotide database failed to reveal any closer matches. Strains previously published as *Camarosporium quaternatum* (CBS 134.97 and CBS 483.95) proved to be neither conspecific nor congeneric with *C. quaternatum* and therefore new combinations are proposed to accommodate these two strains in *Libertasomyces* and the new genus *Hazslinszkyomyces*. Two species of *Pleospora*, *P. flavigena* and *P. fallens*, were not congeneric with *Pleospora* (based on *P. herbarum*) and therefore the new genera *Camarosporomyces* and *Foliophoma* are introduced to accommodate these taxa. The genus *Hazslinszkyomyces* is erected below to accommodate "*Camarosporium*" *aloes*, while *Querciphoma* is erected to accommodate "*Coniothyrium*" *carteri*. Several species treated until now as belonging to *Camarosporium* represent yet another new genus and family, which will be treated in elsewhere.

The ITS phylogeny of *Camarosporium* and allied genera (Fig. 2) resolved most of the included species, except for those in the "*Camarosporium*" clade where the ITS sequences were highly similar (97 % similar and higher when compared to "*Camarosporium*" sp. 1 strain CPC 12441; a maximum of 14 nucleotides differences). *Neoplatysporoides aloicola* (GenBank KR476719) clustered inside *Libertasomyces*, compared to the LSU phylogeny (Fig. 1) where it was basal to the clade. The sister placement of *N. aloicola* (conidia brown, 1-septate) to *L. myopori* (conidia hyaline, aseptate) did not receive any bootstrap support and this species is therefore not combined into *Libertasomyces*. In the LSU phylogeny (Fig. 1), *Camarosporomyces flavigenus* clustered as a basal lineage in the *Hazslinszkyomyces* clade, and based on this position was first considered to be a species of that genus. However, the ITS sequence was clearly not congeneric with

*Hazslinszkyomyces* (Fig. 2) and a new generic name is therefore introduced to accommodate it. Both the ITS and LSU sequences of this strain were confirmed by two independent DNA isolations, and subsequent PCR and sequencing.

The ITS phylogeny of *Dothidea* and *Dothiora* (Fig. 3) resolved the included species, although the lineages in *Dothiora* were poorly supported. Crous & Groenewald (2016) used a combination of ITS, *tef1* and *tub2* to resolve the species in this genus. *Dothiora cactacearum* is introduced below as a new species related to *D. buxi* while the generic type species, *D. pyrenophora*, is shown to be sister to *D. sorbi*. In the *Dothidea* clade, three isolates representing *D. ribesia* were not conspecific with two isolates published by Thambugala *et al.* (2014) as *Plowrightia ribesia* and which are indicated in our phylogeny as “*Dothidea* sp.” pending further elucidation.

The ITS phylogeny of *Paracamarosporium* and *Pseudocamarosporium* (Fig. 4) resolved most of the included *Paracamarosporium* species, but did not resolve species in the *Pseudocamarosporium* clade where the ITS sequences were highly similar (99 % similar and higher when compared to *Pseudocamarosporium* sp. 1 strain CPC 25926; a maximum of five nucleotides differences). “*Camarosporium*” *mamanes* (GenBank DQ885900) clustered as sister to *Paracamarosporium psoraleae* and therefore a new combination is provided for it in that genus.

## THE GENERA

### *Camarosporium* complex

**Coniothyriaceae** W.B. Cooke, *Revista de Biol.* **12**: 289 (1983) [“1980–1983”].

*Type species: Coniothyrium palmarum* Corda 1840.

*Genera included: Camarosporium, Camarosporomyces, Coniothyrium, Dimorphosporicola, Foliophoma, Hazslinszkyomyces, Neocamarosporium, Ochrocladosporium, Pseudo-leptosphaeria.*

*Note: Camarosporiaceae* Locq. 1984 is not validly published (Art. 39.1) in lacking a Latin diagnosis. However, the genus *Camarosporium* s. str. on which this family was based, falls in *Coniothyriaceae* (see De Gruyter *et al.* 2013) in our analysis, thus we refrain from validating *Camarosporiaceae* to accommodate *Camarosporium*.

***Camarosporium*** Schulzer, *Verh. K.K. Zool.-Bot. Ges. Wien* **17**: 717 (1867).

*Classification: Coniothyriaceae, Pleosporales, Dothideomycetes.*

*Current generic circumscription: Ascumata* pseudothecial, single or in clusters, subcorticolous, +/- globose, black, ostiolum central, short papillate and terete, without setae; *ascumatal wall* of *textura angularis*. *Pseudoparaphyses* numerous, filiform, cellular, multi-celled, branched, anasto-

mosing, hyaline, smooth. *Asci* 8-spored, cylindrical, apically rounded, pedicel short and furcate, thick-walled, bitunicate, fissitunicate, inamyloid. *Ascospores* 6-celled, ellipsoidal, straight, muriform, golden, with 1–3 longitudinal septa, eguttulate, without a gelatinous sheath and appendages. *Conidiomata* dimorphic, pycnidial, subcorticolous, single to gregarious, partly caespitose, globose, ostiole central, terete, short papillate; conidiomatal wall few-layered, consisting of a *textura globulosa-angularis* with red brown, thick-walled, and smooth cells. *Paraphyses* and *conidiophores* absent. *Conidiogenous cells* formed from the inner cells of the pycnidial wall, doliiform, hyaline, thin-walled, annellidic. *Conidia* multi-celled, muriformly septate, with one longitudinal or diagonal septum per cell and 1–2 per conidium, ellipsoidal, pyriform, clavate, straight to slightly curved, yellowish not brown, basal cell often paler or hyaline, wall golden. *Synasexual morph: conidiomata* separate, pycnidial, immersed to superficial on PNA, brown, globose, with 1–2 papillate ostioles, exuding a crystalline conidial mass. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* lining the inner cavity, hyaline, smooth, ampulliform. *Conidia* solitary, hyaline, smooth, subcylindrical, straight, rarely curved, apex obtuse, base truncate.

*Type species: Camarosporium quaternatum* (Hazsl.) Schulzer 1867.

***Camarosporium quaternatum*** (Hazsl.) Schulzer, *Verh. K.K. Zool.-Bot. Ges. Wien* **17**: 717 (1867).

(Fig. 5)

*Basionym: Clinterium quaternatum* Hazsl., *Verh. K.K. Zool.-Bot. Ges. Wien* **15**: 450 (1865); as “*Clinterium (quaternatum)*”; type: Hazslinszky (1865: figs 9–12 – **lectotype designated here**, MBT376246; **Hungary**: near Budapest, private garden, on twigs of *Lycium barbarum* (*Solanaceae*), attached, corticated, 2 May 2016, L. Bartalos, det. R.K. Schumacher (CBS H-23064 – **epitype designated here**, MBT376247; CPC 31081 = CBS 142616 – culture epitype, CPC 31518).

*Synonyms: Cucurbitaria varians* Hazsl., *Verh. K.K. Zool.-Bot. Ges. Wien* **15**: 451 (1865); type: Hazslinszky (1865: figs 13–24 — **lectotype designated here**, MBT376243).

*Karstenula varians* (Hazsl.) Sacc., *Syll. Fung.* **2**: 241 (1883).

*Pleomassaria varians* (Hazsl.) G. Winter, *Rabenh. Krypt.-Fl.*, 2<sup>nd</sup> edn **1**(2): 552 (1886).

*Camarosporium hendersonia* Schulzer, *Verh. K.K. Zool.-Bot. Ges. Wien* **17**: 716 (1867), nom. illegit. (Art. 53.1, based on *C. quaternatum* (Hazsl.) Schulzer 1867).

*Camarosporium hazslinszkyi* Sacc., *Syll. Fung.* **3**: 468 (1884), nom. illegit. (Art. 53.1, based on *C. quaternatum* (Hazsl.) Schulzer 1867).

*Additional material examined: Germany*: Berlin, mixed forest, about 50 m asl, sand, acid, fresh, mesotroph, on twig of *Daphne mezereum* (*Thymelaeaceae*), 18 May 2013, R. Jarling, det. R.K. Schumacher (CBS H-23063, culture CPC 23216 = CBS 142617).

*Description: Ascumata* pseudothecial, single or in clusters, subcorticolous, +/- globose with a flattened base, black, smooth, soft, thick, ostiole central, short papillate and terete,

Table 1. Details of the strains included in the taxonomic treatments or for which novel sequences were deposited in GenBank.

Species name	Strain accession number <sup>1,2</sup>	Collector and collection date	Host or substrate	Country	ITS	LSU	GenBank accession number <sup>3</sup>		
							tef1 (first part)	tef1 (second part)	tub2
" <i>Camarosporium</i> " <i>arezzoensis</i>	CPC 31420	R.K. Schumacher, 22 Jul. 2016	<i>Cytisus borysthenticus</i> , branch	Ukraine	KY929127	KY929163	–	–	–
" <i>Camarosporium</i> " sp. 1	CPC 12441	W. Gams, Aug. 2005	<i>Sophora chrysophylla</i>	USA: Hawaii	KY929128	DQ377885	–	–	–
" <i>Camarosporium</i> " sp. 2	CPC 25960	R.K. Schumacher, 21 Dec. 2014	<i>Caregana</i> sp., twig	Finland	KY929129	KY929164	–	KY929198	–
" <i>Camarosporium</i> " sp. 3	CPC 25962	R.K. Schumacher, 1 Dec. 2014	<i>Caregana</i> sp., twig	Finland	KY929130	KY929165	–	KY929199	–
" <i>Camarosporium</i> " sp. 4	CPC 31031	R.K. Schumacher, 10 May 2016	<i>Elaeagnus rhamnoides</i> , twig	Germany	KY929131	KY929166	–	–	–
" <i>Camarosporium</i> " sp. 5	CPC 31632	R.K. Schumacher, 12 Oct. 2016	<i>Ulmus laevis</i> , twig	Ukraine	KY929132	KY929167	–	–	–
" <i>Camarosporium</i> " sp. 6	CPC 27667	A. Usichenko, 25 May 2015	<i>Robinia pseudoacacia</i> , dead branch	Ukraine	KY929133	KY929168	–	–	–
" <i>Camarosporium</i> " sp. 7	CPC 30379	R.K. Schumacher, 2 Apr. 2016	<i>Philadelphus coronarius</i> , twig	Germany	KY929134	KY929169	–	–	–
" <i>Camarosporium</i> " sp. 8	CPC 23216	R.K. Schumacher, 18 May 2013	<i>Daphne mezereum</i> , twig	Germany	KY929135	KY929170	–	KY929200	KY929122
" <i>Camarosporium</i> " sp. 9	CPC 31081 <sup>1ET</sup> or <i>Clinium quaternarium</i>	R.K. Schumacher, 2 May 2016	<i>Lycium barbarum</i> , twig	Hungary	KY929136	KY929171	–	KY929201	KY929123
" <i>Camarosporium</i> " sp. 10	CPC 31518	R.K. Schumacher, 2 May 2016	<i>Lycium barbarum</i> , twig	Hungary	KY929137	KY929172	–	KY929202	KY929124
" <i>Camarosporium</i> " sp. 11	CBS 314.80 <sup>T</sup>	K. Fodor, 1980	Water	Romania	KY929138	GU238076	–	–	GU238217
" <i>Camarosporium</i> " sp. 12	CBS 193.58	–	<i>Viburnum lantana</i>	Switzerland	KY929139	AY004342	–	–	–
" <i>Camarosporium</i> " sp. 13	CPC 30638	R.K. Schumacher	<i>Ribes uva-crispa</i> , stem	Germany	KY929140	KY929173	KY929192	–	KY929205
" <i>Camarosporium</i> " sp. 14	CPC 30689	R.K. Schumacher, 4 May 2016	<i>Ribes rubrum</i> , twig	Germany	KY929141	KY929174	KY929193	–	KY929206
" <i>Camarosporium</i> " sp. 15	CPC 30713	R.K. Schumacher, 4 May 2016	<i>Ribes rubrum</i> , twig	Germany	KY929142	KY929175	KY929194	–	KY929207
" <i>Camarosporium</i> " sp. 16	CBS 142492 = CPC 15585	P.W. Crous, 2013	Cactaceae (ornamental)	USA	KY929143	KY929176	KY929195	–	KY929208
" <i>Camarosporium</i> " sp. 17	CPC 15587	P.W. Crous, 2013	Cactaceae (ornamental)	USA	KY929144	KY929177	KY929196	–	KY929209
" <i>Camarosporium</i> " sp. 18	CPC 30632 <sup>NT</sup>	R.K. Schumacher, 27 Apr. 2016	<i>Sorbus aucuparia</i> , twig	Germany	KY929145	KY929178	–	KY929203	KY929210
" <i>Camarosporium</i> " sp. 19	CPC 30634	R.K. Schumacher, 27 Apr. 2016	<i>Sorbus aucuparia</i> , twig	Germany	KY929146	KY929179	–	KY929204	KY929211
" <i>Camarosporium</i> " sp. 20	CBS 161.78	G.F. Laundon, 1978	<i>Olea europaea</i> , leaf spot	New Zealand	KY929147	GU238074	–	–	GU238215



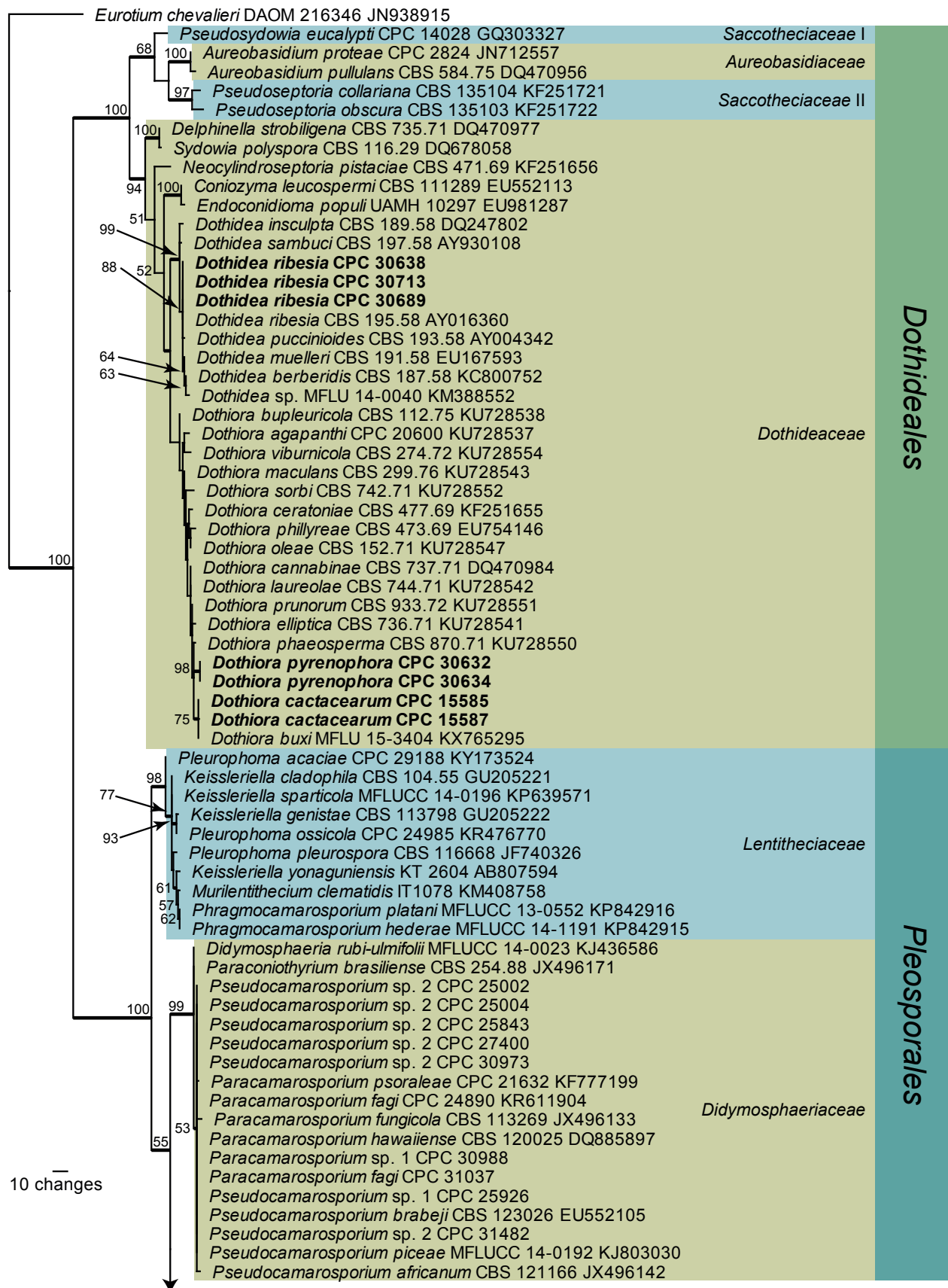
Table 1. (Continued).

Species name	Strain accession number <sup>1,2</sup>	Collector and collection date	Host or substrate	Country	ITS	LSU	GenBank accession number <sup>3</sup>		
							tef1 (first part)	tef1 (second part)	SSU
	CBS 284.70	H.A. van der Aa, Apr. 1970	<i>Nerium oleander</i> , leaf spot	Italy	KY929148	GU238078	–	–	GU238218
<i>Hazslinszyomyces aloes</i>	CBS 136437 = CPC 21572 <sup>1</sup>	M.J. Wingfield, Sept. 2012	<i>Aloe dichotoma</i> , dead bark	South Africa	KF777142	KF777198	–	–	–
<i>Hazslinszyomyces aptrootii</i>	CBS 483.95 <sup>1</sup>	A. Aptroot, 17 Mar. 1995	<i>Lycium</i> sp.	Netherlands	KY929149	DQ377884	–	GU349044	GU296141
<i>Hazslinszyomyces lycii</i>	CPC 30998 <sup>1</sup>	R.K. Schumacher, 2 May 2016	<i>Lycium barbarum</i> , twig	Hungary	KY929150	KY929180	–	–	–
	CPC 31014	R.K. Schumacher, 1 May 2016	<i>Lycium barbarum</i> , twig	Hungary	KY929151	KY929181	–	–	–
<i>Libertasomyces quercus</i>	CBS 134.97 = INIFAT C96/108 <sup>1</sup>	R.F. Castañeda, 20 Jul. 1996	<i>Quercus ilex</i> , leaf litter	Spain	KY929152	DQ377883	KY929197	–	KY929212
<i>Neocamarosporium chersinae</i>	CPC 27298 <sup>1</sup>	P.W. Crous, 25 May 2015	Dead angulate tortoise shell	South Africa	KY929153	KY929182	–	–	–
<i>Paracamarosporium fagi</i>	CPC 31037	R.K. Schumacher, 10 May 2016	<i>Elaeagnus rhamnoides</i> , twig	Germany	KY929154	KY929183	–	–	–
<i>Paracamarosporium</i> sp. 1	CPC 30988	R.K. Schumacher, 1 May 2016	<i>Tilia platyphyllos</i> , twig	Germany	KY929155	KY929184	–	–	–
<i>Pseudocamarosporium</i> sp. 1	CPC 25926	M.J. Wingfield, Nov. 2014	<i>Erica</i> sp.	South Africa	KY929156	KY929185	–	–	–
<i>Pseudocamarosporium</i> sp. 2	CPC 25002	R.K. Schumacher	<i>Platanus</i> sp., branch	Switzerland	KY929157	KY929186	–	–	–
	CPC 25004	R.K. Schumacher	<i>Platanus</i> sp., branch	Switzerland	KY929158	KY929187	–	–	–
	CPC 25843	R.K. Schumacher, 17 Dec. 2014	<i>Betula pendula</i> , twig	Germany	KY929159	KY929188	–	–	–
	CPC 27400	R.K. Schumacher, 27 May 2015	<i>Frangula alnus</i>	Germany	KY929160	KY929189	–	–	–
	CPC 30973	R.K. Schumacher, 10 May 2016	<i>Elaeagnus rhamnoides</i> , thorn and twig	Germany	KY929161	KY929190	–	–	–
	CPC 31482	R.K. Schumacher, 22 Jul. 2016	<i>Malus domestica</i> , twig	Ukraine	KY929162	KY929191	–	–	–
<i>Querciphoma carteri</i>	CBS 101633 = PD 84174	PD Lisse	<i>Quercus</i> sp.	Netherlands	KF251210	GQ387593	KF253166	–	KF252701 GQ387532
	CBS 105.91	H. Schill	<i>Quercus robur</i> , leaves and twigs	Germany	KF251209	GQ387594	KF253165	–	KF252700 GQ387533

<sup>1</sup> CBS: Westerdijk Fungal Biodiversity Institute, Utrecht, The Netherlands; CPC: Culture collection of Pedro Crous housed at CBS, INIFAT: Alexander Humboldt Institute for Basic Research in Tropical Agriculture, Ciudad de La Habana, Cuba; PD: Plant Protection Service, nVWA, Division Plant, Wageningen, The Netherlands.

<sup>2</sup> ET: ex-epitype culture; NT: ex-neotype culture; T: ex-type culture.

<sup>3</sup> ITS: internal transcribed spacers and intervening 5.8S nrDNA; LSU: partial 28S nrDNA; SSU: partial 18S nrDNA; tef1: partial translation elongation factor 1-alpha gene; tub2: partial beta-tubulin gene.



**Fig. 1.** One of 1 000 equally most parsimonious trees obtained from a maximum parsimony analysis of the LSU sequence alignment. The scale bar shows 10 changes, and parsimony bootstrap support values > 49 % from 1 000 replicates are shown at the nodes. Thickened lines represent those branches also present in the strict consensus tree and families are indicated with coloured blocks and the taxonomic novelties, or species treated in the present paper, are in **bold** text. Orders are indicated on the right side of the tree. The tree was rooted to *Eurotium chevalieri* (GenBank accession number JN938915).

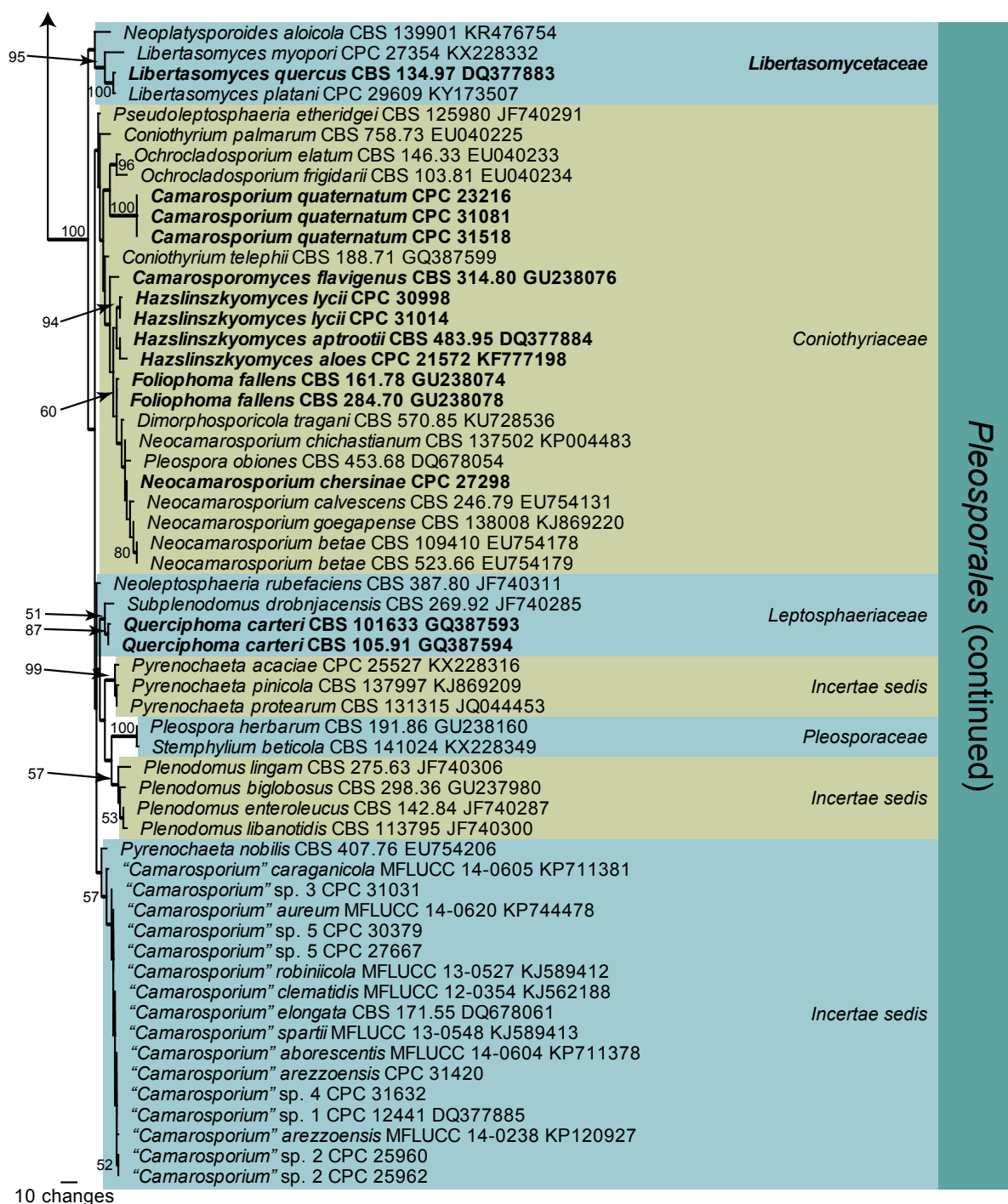
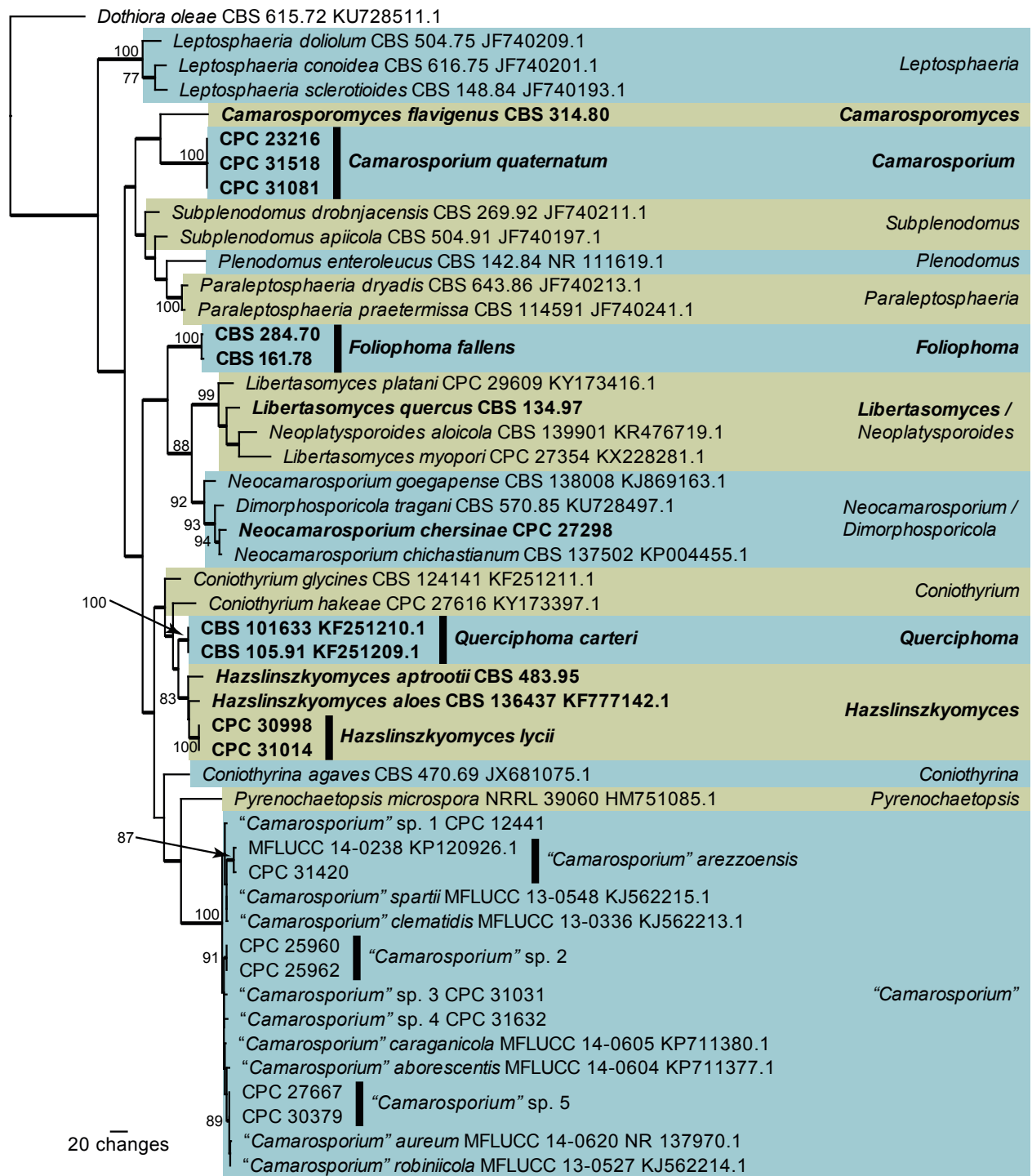


Fig. 1. (Continued).

basally with a few red-brown, smooth, thick-walled and eguttulate hyphae, without setae; ascomatal wall consisting of a *textura angularis* with red-brown, thick-walled, smooth and eguttulate cells. *Pseudoparaphyses* numerous, cellular, filiform, multi-celled, short celled, branched, anastomosing, hyaline, smooth, thin-walled, eguttulate,  $3.5 \times 4 \mu\text{m}$  diam. *Asci* 8-spored, cylindrical, apically rounded, pedicel short and furcate, thick-walled, bitunicate, fissitunicate, inamyloid (water plus Lugol), spores oblique uniseriate,  $153\text{--}172 \times 16 \times 18.5 \mu\text{m}$ . *Ascospores* (4–)6-celled, ellipsoidal, straight, muriformly septate, golden, faintly thick-walled and smooth, septa in the middle constricted otherwise +/-

faintly constricted, mostly the middle cells and seldom both end cells with 1–3 longitudinal septa, eguttulate, without a gelatinous sheath and appendages, rehydrated and examined in water, mature (20–)22.5(–26.5)  $\times$  (10–)11.5(–13)  $\mu\text{m}$ , (1.79–)1.99(–2.2) (l/b). *Conidiomata* pycnidial, saprobic, subcorticolous, single to gregarious, partly caespitose, globose seldom broad pyriform with a flattened base, ostiole centrally, terete, short papillate, and somewhat erumpent, black, soft, +/-thin, covered with hyaline to ochre and smooth hyphae, to 0.8 mm diam; conidiomatal wall few-layered, consisting of a *textura globulosa-angularis* with red brown, thick-walled, and smooth cells. *Paraphyses*



**Fig. 2.** One of 284 equally most parsimonious trees obtained from a maximum parsimony analysis of the ITS sequence alignment of *Camarosporium* and allied genera. The scale bar shows 20 changes, and parsimony bootstrap support values > 74 % from 1 000 replicates are shown at the nodes. Thickened lines represent those branches also present in the strict consensus tree and genera are indicated with coloured blocks and the taxonomic novelties, or species treated in the present paper, are in bold text. The tree was rooted to *Dothiora oleae* (GenBank accession number KU728511).

and *conidiophores* absent. *Conidiogenous cells* formed from the inner cells of the pycnidial wall, doliiform, hyaline, thin-walled, smooth, eguttulate, annellidic, secession apically and singly. *Conidia* as brownish, dark olive to black drops in mass, (3–)4(–6)-celled, muriformly septate, with one longitudinal or diagonal septum per cell and 1–2 per conidium, ellipsoidal, pyroid, clavate, straight to slightly

curved, apically rounded, base often tapered but never truncate, always yellowish, but never brown, both end cells but mostly the basal cell often paler or hyaline, wall golden, thin and smooth, septa golden, thick-walled and smooth to slightly constricted, eguttulate at maturity, examined in water, living and mature, (18–)26.5(–34) × (9–)12(–16) µm, (1.19–)2.26(–3.32) (l/b). *Synasexual morph in culture:*





**Fig. 3.** One of 140 equally most parsimonious trees obtained from a maximum parsimony analysis of the ITS sequence alignment of *Dothidea* and *Dothiora*. The scale bar shows 10 changes, and parsimony bootstrap support values > 74 % from 1 000 replicates are shown at the nodes. Thickened lines represent those branches also present in the strict consensus tree and genera are indicated with coloured blocks and the taxonomic novelties, or species treated in the present paper, are in bold text. The tree was rooted to *Pezicula cinnamomea* (GenBank accession number KR859133).

*Conidiomata* separate, pycnidial, immersed to superficial on PNA, brown, globose, 150–200 µm diam, with 1–2 papillate ostioles, exuding a crystalline conidial mass. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* lining the inner cavity, hyaline, smooth, ampulliform, with periclinal thickening at apex, 3–5 × 4–5 µm. *Conidia* solitary, hyaline, smooth, aseptate, subcylindrical, straight, rarely curved, apex obtuse, base truncate, (3–)4–5(–6) × 1.5 µm.

**Culture characteristics:** On MEA spreading, with fluffy aerial mycelium and feathery margin; surface dirty white with patches of olivaceous grey. On PDA surface and reverse olivaceous grey. On OA surface olivaceous grey with patches of dirty white and umber.

**Notes:** Single conidial colonies of *C. quaternatum* formed a phoma-like fungus in culture. The single conidial isolation step was redone three times on different media, with the same result. It was only once colonies were subcultured onto SNA plates supplemented with autoclaved pieces of banana leaf, that a few typical *Camarosporium* conidiomata again developed on leaf pieces. The trigger influencing which morph develops in culture, however, remains unknown, with the phoma-like morph being most commonly encountered, and the *Camarosporium* morph extremely rare.

Ascospores of *Camarosporium quaternatum* studied here agree with those of the original description of *Cucurbitaria varians* (figs 13–24), and conidia that of its asexual morph, *Clinterium quaternatum* (figs 9–12) (Hazslinszky 1865). Because the holotype material could not be traced, the original illustrations are designated as lectotypes, to facilitate epitypification.

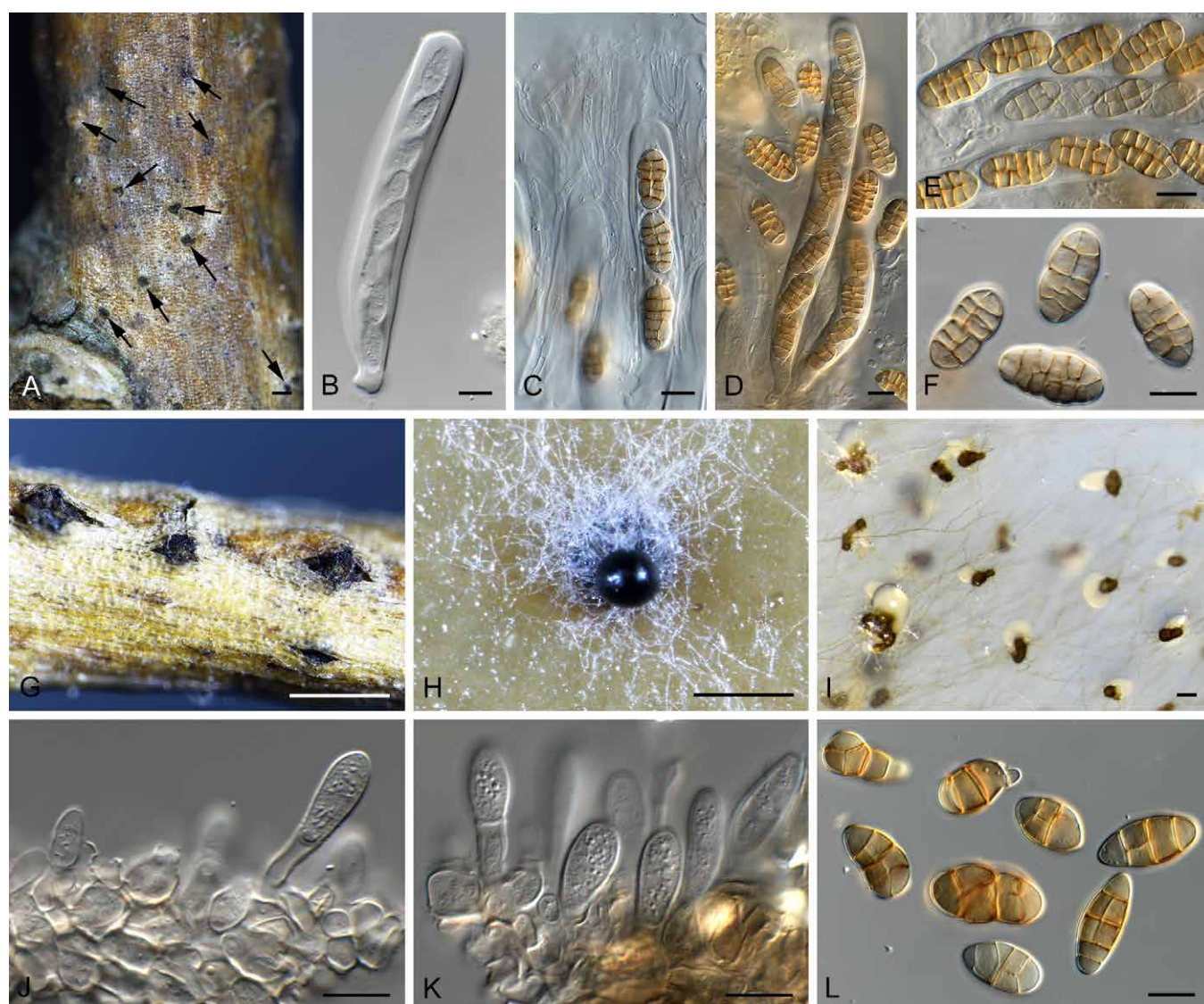


**Fig. 4.** One of 16 equally most parsimonious trees obtained from a maximum parsimony analysis of the ITS sequence alignment of *Paracamarosporium* and *Pseudocamarosporium*. The scale bar shows 10 changes, and parsimony bootstrap support values > 69 % from 1 000 replicates are shown at the nodes. Thickened lines represent those branches also present in the strict consensus tree and genera are indicated with coloured blocks and the taxonomic novelties, or species treated in the present paper, are in bold text. The tree was rooted to *Keissleriella trichophorica* (GenBank accession number KJ869113).

**Table 2.** Statistical information on the individual alignments and number of equally most parsimonious trees saved for each dataset analysed<sup>1</sup>.

	LSU overview	<i>Camarosporium</i> ITS	<i>Dothidea</i> ITS	<i>Paracamarosporium</i> ITS
Aligned characters (including gaps)	722	554	530	523
Parsimony-informative characters	192	242	109	45
Variable and parsimony-uninformative characters	55	88	107	143
Constant characters	475	224	314	335
Equally most parsimonious trees obtained	1 000	284	140	16
Tree length	673	1 247	470	249
Consistency index (CI)	0,551	0,499	0,691	0,912
Retention index (RI)	0,948	0,764	0,832	0,891
Rescaled Consistency index (RC)	0,522	0,381	0,575	0,812

<sup>1</sup> ITS: internal transcribed spacers and intervening 5.8S nrDNA; LSU: partial 28S nrDNA.



**Fig. 5.** *Camarosporium quaternatum* (CPC 31081). **A.** Immersed ascomata on twig (arrows). **B–E.** Asci and pseudoparaphyses. **F.** Ascospores. **G.** Conidiomata on twig. **H.** *Camarosporium* conidioma on OA. **I.** Phoma-like conidiomata on SNA. **J–K.** Conidiogenous cells giving rise to *Camarosporium* conidia. **L.** Conidia. Bars: A, I = 200  $\mu\text{m}$ , G = 800  $\mu\text{m}$ , H = 300  $\mu\text{m}$ , all others = 10  $\mu\text{m}$ .

Saccardo (1883) reported the fungus to occur on *Lycium barbarum* in Hungary and Germany. In the present study, we also found the sexual morph on *Daphne mezereum*, a new host for *C. quaternatum*. The two cultures used in previous studies as representative of this fungus (CBS 483.95, CBS 134.97) (e.g. Crous *et al.* 2006) represent two camarosporium-like fungi that are morphologically distinct from *C. quaternatum*.

Sutton (1980) stated that the genus *Camarosporium*, which contains several hundred species, is polyphyletic and in need of revision. As we have shown here, *Camarosporium s. str.* is distinct from other taxa that have been treated as representative of or similar in some respects to *Camarosporium*, viz. *Henfellra*, *Neocamarosporium*, *Paracamarosporium*, or *Xenocamarosporium* (Crous *et al.* 2013, 2014b, 2015b, Wijayawardene *et al.* 2014, 2016, Hawksworth *et al.* 2016). Further studies are underway to treat those taxa that are presently known from culture.

During the course of evaluating the status of *Camaro-*

*sporium s. str.*, several other camarosporium-like or pleospora-like isolates also had to be examined and were found to be undescribed. These are treated below:

***Camarosporomyces* Crous, gen. nov.**  
Mycobank MB820901

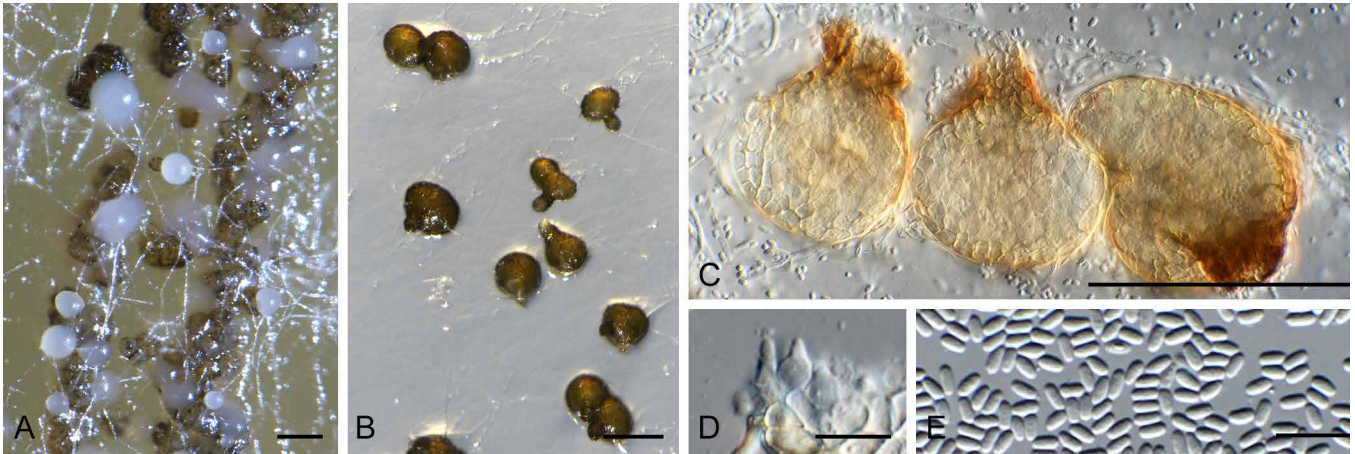
*Etymology:* Named after its morphological similarity to *Camarosporium* and its phoma-like synasexual morph.

*Diagnosis:* Distinct from phoma-like genera in having pycnidial conidiomata with prominent papillate dark brown periphysate ostiole, and thicker wall at apex.

*Type species:* *Camarosporomyces flavigenus* (Constantinou & Aa) Crous 2017.

*Description:* Conidiomata pycnidial, solitary to aggregated, obovoid, medium brown, with prominent papillate ostiole,





**Fig. 6.** *Camarosporomyces flavigenus* (CBS 314.80). **A.** Conidiomata on PDA. **B.** Conidiomata on SNA. **C.** Conidiomata showing darker ostiolar area. **D.** Conidiogenous cells. **E.** Phoma-like conidia. Bars: A–C = 90  $\mu$ m, D–E = 10  $\mu$ m.

dark brown, with extra 1–2 layers of wall at the apex (thicker than pycnidial body), periphysate. *Conidiophores* reduced to conidiogenous cells lining inner cavity, hyaline, smooth, ampulliform; phialidic with periclinal thickening. *Conidia* solitary, hyaline, smooth, aseptate, subcylindrical, straight, apex obtuse, base truncate.

***Camarosporomyces flavigenus*** (Constant. & Aa)  
Crous, **comb. nov.**

Mycobank MB820902

(Fig. 6)

*Basionym:* *Phoma flavigena* Constant. & Aa, *Trans. Brit. Mycol. Soc.* **79**: 343 (1982).

*Synonym:* *Pleospora flavigena* (Constant. & Aa) Gruyter & Verkley, *Stud. Mycol.* **75**: 25 (2013) ["2012"].

*Type:* **Romania:** Bucharest, station for water treatment, from water, 1980, K. Fodor (CBS H-23067 – holotype; CBS 314.80 – culture ex-type).

*Description:* *Conidiomata* pycnidial, solitary to aggregated, obovoid, medium brown, 50–90  $\mu$ m diam, with prominent papillate ostiole, dark brown, 10–25  $\mu$ m diam with extra 1–2 layers of wall at the apex (thicker than pycnidial body), periphysate. *Conidiophores* reduced to conidiogenous cells lining inner cavity, hyaline, smooth, ampulliform, 4–5  $\times$  3–4  $\mu$ m; phialidic with periclinal thickening. *Conidia* solitary, hyaline, smooth, aseptate, subcylindrical, straight, apex obtuse, base truncate, (2.5–)3  $\times$  1.5  $\mu$ m.

*Culture characteristics:* Colonies flat, spreading, with sparse aerial mycelium, margins smooth, lobate, reaching 30 mm diam after 2 wk. On OA surface umber with diffuse yellow pigment. On PDA surface umber, outer region pale luteous, reverse umber.

*Note:* *Camarosporomyces flavigenus* is a phoma-like fungus which was originally described as *Phoma flavigena*, and later placed in *Pleospora* by De Gruyter *et al.* (2013), who used a much wider circumscription of the genus *Pleospora* than applied here.

***Foliophoma*** Crous, **gen. nov.**

Mycobank MB820903

*Etymology:* Named after its association with leaf spots, and its morphological similarity to *Phoma*.

*Diagnosis:* Distinct from phoma-like genera in having eustromatic conidiomata, uni- to multi-loculate with 1–3 ostioles. *Conidiogenous* cells with periclinal thickening or percurrent proliferation at apex.

*Type species:* *Foliophoma fallens* (Sacc.) Crous 2017.

*Description:* *Conidiomata* globose, eustromatic, uni- to multi-locular with 1–3 ostioles, medium brown, outer surface smooth; wall of 3–6 layers of brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells lining inner cavity, hyaline, smooth, doliiform to subcylindrical; phialidic with periclinal thickening or percurrent proliferation at apex. *Conidia* aseptate, solitary, hyaline, smooth, guttulate to granular, broadly ellipsoidal, thick-walled, apex obtuse, base truncate to bluntly rounded.

***Foliophoma fallens*** (Sacc.) Crous, **comb. nov.**

Mycobank MB820904

(Fig. 7)

*Basionym:* *Phoma fallens* Sacc., *Syll. Fung.* **10**: 146 (1892).

*Synonyms:* *Pleospora fallens* (Sacc.) Gruyter & Verkley, *Stud. Mycol.* **75**: 25 (2013) ["2012"].

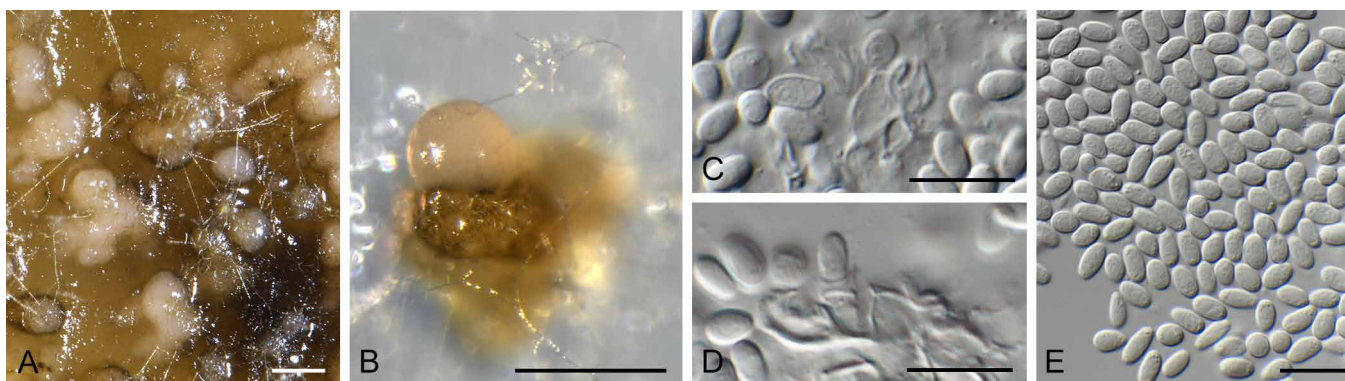
*Phyllosticta glaucispora* Delacr., *Bull. Soc. Mycol. France* **9**: 266 (1893).

*Phoma glaucispora* (Delacr.) Noordel. & Boerema, *Versl. Meded. Plantenziektenk. Dienst Wageningen* **166**: 108 (1989) ["1988"].

*Phyllosticta oleandri* Gutner, *Trudy Bot. Inst. Akad. Nauk S.S.S.R., ser. 2, Sporov. Rast.* **1**: 306 (1933).

*Description:* *Conidiomata* globose, eustromatic, uni- to multi-locular with 1–3 ostioles, 120–250  $\mu$ m diam, medium brown, outer surface smooth; wall of 3–6 layers of brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells lining inner cavity, hyaline, smooth, doliiform to subcylindrical,





**Fig. 7.** *Foliophoma fallens* (CBS 284.70). **A.** Conidiomata on PDA. **B.** Conidiomata on SNA. **C–D.** Conidiogenous cells. **E.** Conidia. Bars: A–B = 250 µm, all others = 10 µm.

5–7 × 4–5 µm; phialidic with periclinal thickening or percurrent proliferation at apex. *Conidia* aseptate, solitary, hyaline, smooth, guttulate to granular, broadly ellipsoidal, thick-walled, apex obtuse, base truncate to bluntly rounded, (5–)5.5–6(–7) × (3–)4(–5) µm (based on CBS 284.70).

**Culture characteristics:** Colonies flat, spreading, with moderate aerial mycelium and even, lobate margins, reaching 50 mm diam after 2 wk. On PDA surface sepia to umber, reverse dark mouse grey. On OA surface greyish sepia.

**Material examined:** **Italy:** Capri, Villa Jovis, leaf spot on *Nerium oleander* (*Apocynaceae*), Apr. 1970, H.A. van der Aa (CBS H-16639, 23066, culture CBS 284.70). – **New Zealand:** Levin, from leaf spot of *Olea europaea* (*Oleaceae*), 1978, G.F. Laundon (CBS 161.78 = LEV 1131).

**Notes:** *Phoma fallens* is associated with leaf spots of *Olea europaea* in Europe (conidia 7–9 × 3–4 µm), while *Phoma glaucispora* (conidia 5–8 × 2.5–4.5 µm) is associated with leaf spots on *Nerium oleander* in Europe (Boerema *et al.* 2004). Phylogenetically, however, De Gruyter *et al.* (2013) found these two species to be closely related, and therefore treated them as a single species, placing them in *Pleospora* based on the larger circumscription used at the time. However, the present fungus is not congeneric with *Stemphylium herbarum* (syn. *Pleospora herbarum*; Rossman *et al.* 2015), and therefore a new generic name is introduced to accommodate it.

**Hazslinszkyomyces** Crous & R.K. Schumach., **gen. nov.**

MycoBank MB820905

**Etymology:** Named after Friedrich August Hazslinszky von Hazslin (1818–1896), in recognition for his work on camarosporium-like fungi.

**Diagnosis:** Morphologically similar to *Camarosporium*, but distinct as conidia are uniformly brown in colour, those of *Camarosporium* having paler end cells.

**Type species:** *Hazslinszkyomyces aloes* (Crous & M.J. Wingf.) Crous 2017.

**Description:** *Ascomata* pseudothecial, saprobic, subcorticolous, densely crowded, erumpent, globose to pyriform with a flattened base, ostiole central, terete, and short papillate, black, periphysate; ascomatal wall multi-layered, consisting of a *textura angularis*. *Pseudoparaphyses* numerous, basally moniliform, upwards filiform, multi-celled, hyaline, thin-walled, smooth. *Asci* 8-spored, cylindrical, thick-walled, apically rounded and with an ocular chamber, pedicel short and furcate, bitunicate, fissitunicate. *Ascospores* transversely septate, constricted at the median septum, becoming muriformly septate, ellipsoidal, golden brown. Phoma-like morph: *Conidiomata* pycnidial, solitary, brown, globose, with central ostiole; wall of 2–3 layers of brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells lining the inner cavity, hyaline, smooth, doliiform to subcylindrical. *Conidia* solitary, hyaline, smooth, guttulate, subcylindrical, straight, aseptate. Camarosporium-like morph: Occurring in the same or separate conidioma with a phoma-like morph. *Conidiogenous cells* lining the inner cavity, doliiform to subcylindrical, hyaline, smooth, proliferating percurrently at apex. *Conidia* solitary, brown, smooth, broadly ellipsoidal to obovoid, transversely septate, becoming muriformly septate.

**Hazslinszkyomyces aloes** (Crous & M.J. Wingf.)

Crous, **comb. nov.**

MycoBank MB820906

**Basionym:** *Camarosporium aloes* Crous & M.J. Wingf., *Persoonia* **31**: 247 (2013).

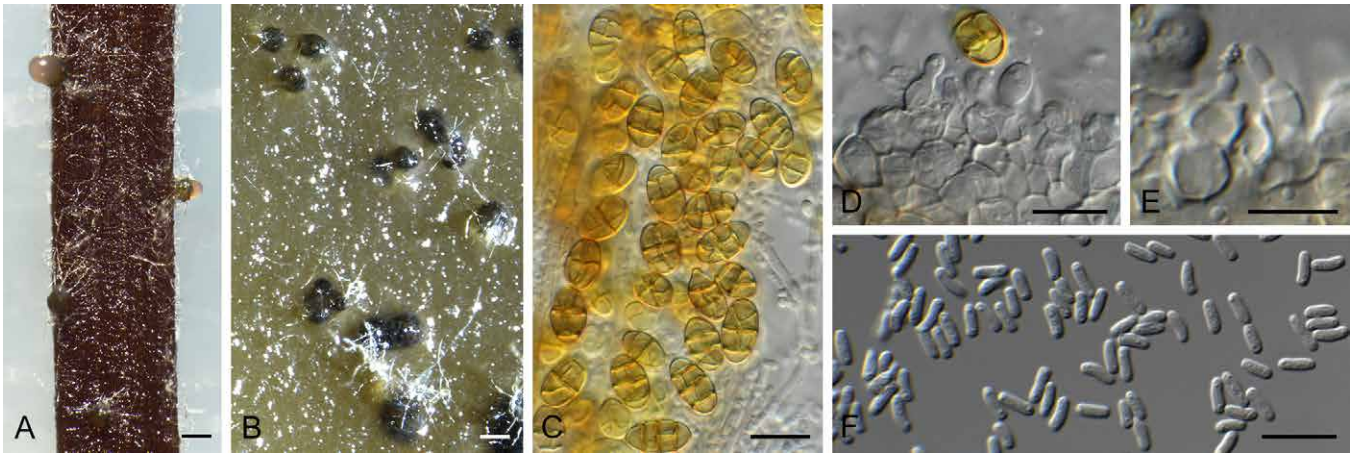
**Type:** **South Africa:** *Western Cape Province:* Clanwilliam, on dark lesions on dead bark of *Aloe dichotoma* (*Xanthorrhoeaceae*), Sept. 2012, M.J. Wingfield (CBS H-21446 – holotype; CPC 21572 = CBS 136437 – culture ex-type).

**Hazslinszkyomyces aptrootii** Crous, **sp. nov.**

MycoBank MB820908

(Fig. 8)

**Etymology:** Named after André Aptroot, who collected this fungus in The Netherlands.



**Fig. 8.** *Hazslinszkyomyces aptrootii* (CBS 483.95). **A.** Conidiomata on PNA. **B.** Conidiomata on PDA. **C.** *Hazslinszkyomyces* and phoma-like conidia. **D–E.** Conidiogenous cells. **F.** Phoma-like conidia. Bars: A–B = 170  $\mu\text{m}$ , all others = 10  $\mu\text{m}$ .

**Diagnosis:** Similar to *Hazslinszkyomyces aloes* [conidia (9–)11–13(–14)  $\times$  (4–)6–7(–8)  $\mu\text{m}$ ], but distinct in having larger conidia.

**Type:** **The Netherlands:** Province of Noord-Holland: Egmond, on *Lycium* sp., 17 Mar. 1995, A. Aptroot (CBS H-23068 – holotype; CBS 483.95 – culture ex-type).

**Description:** *Conidiomata* separate, erumpent, pycnidial, globose, brown, 130–170  $\mu\text{m}$  diam, with central, non-papillate ostiole, 10  $\mu\text{m}$  diam, exuding a creamy conidial mass; wall of 3–6 layers of brown *textura angularis*. Conidia dimorphic. Phoma-like morph: *Conidiophores* reduced to conidiogenous cells lining the inner cavity, ampulliform to subcylindrical, hyaline, smooth, phialidic with periclinal thickening at apex, becoming percurrent with age, 5–7  $\times$  3–6  $\mu\text{m}$ . *Conidia* solitary, hyaline, smooth, guttulate, subcylindrical, aseptate, straight to curved, apex obtuse, base truncate, (4–)5–6  $\times$  2  $\mu\text{m}$ . Camarosporium-like morph: Occurring in the same conidiomata as the phoma-like morph. *Conidiophores* reduced to conidiogenous cells, hyaline, smooth, doliiform to subcylindrical, proliferating percurrently at apex, 5–7  $\times$  4–6  $\mu\text{m}$ . *Conidia* solitary, broadly ellipsoidal, apex subobtusely rounded, base truncate, hilum 2  $\mu\text{m}$  diam, medium brown, smooth, muriformly septate, with 3 transverse septa, and 1–3 oblique septa, (11–)13–14(–16)  $\times$  (7–)8(–9)  $\mu\text{m}$ .

**Culture characteristics:** Colonies flat, spreading, with sparse to moderate aerial mycelium, covering dish in 2 wk, with even, lobate margins. On PDA surface umber, reverse brown vinaceous. On OA surface chestnut to brown vinaceous.

**Notes:** This collection was originally identified as *Camarosporium quaternatum*, based on its general morphology, and the fact that it occurred on *Lycium*. Morphologically, however, the conidia are much smaller than those of *C. quaternatum*, and thus it is described as a new species of *Hazslinszkyomyces*. Phylogenetically the two genera are also quite distinct.

### *Hazslinszkyomyces lycii* Crous & R.K. Schumach., sp. nov.

Mycobank MB820909

(Fig. 9)

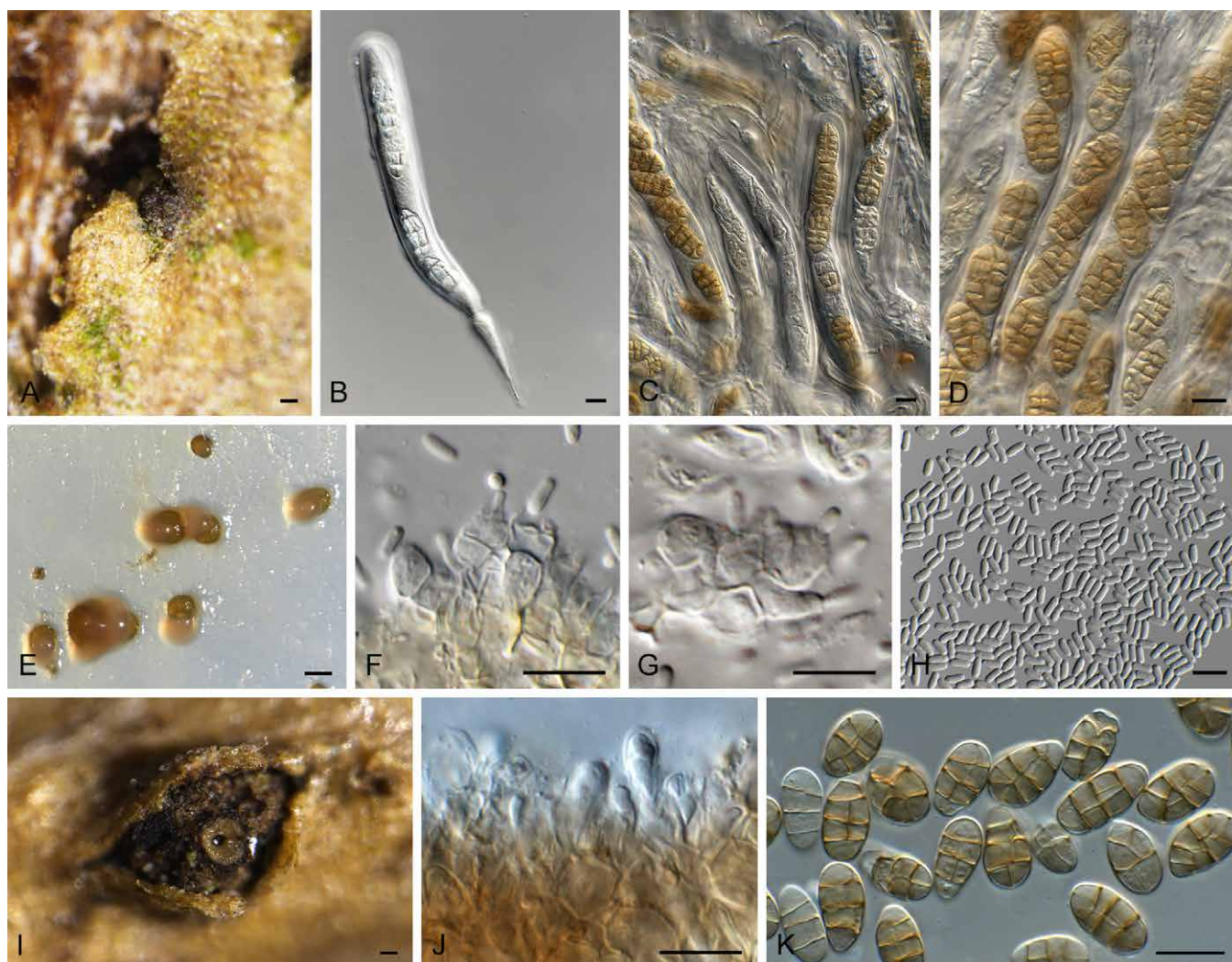
**Etymology:** Named after the host genus from which it was isolated, *Lycium*.

**Diagnosis:** Similar to *Hazslinszkyomyces aptrootii* [conidia (11–)13–14(–16)  $\times$  (7–)8(–9)  $\mu\text{m}$ ], but distinct in having larger conidia.

**Type:** **Hungary:** near Budapest, on twig of *Lycium barbarum* (*Solanaceae*), 2 May 2016, L. Bartalos (CBS H-23069 – holotype; CPC 30998 = CBS 142619 – culture ex-type).

**Description:** *Ascomata* pseudothecial, saprobic, subcorticolous, densely crowded, erumpent, globose to pyriform with a flattened base, ostiole central, terete, and short papillate, black, soft, thick, to 130  $\mu\text{m}$  diam, periphysate; ascomatal wall multi-layered, consisting of a *textura angularis* with red-brown, thick-walled, smooth and small cells. *Pseudoparaphyses* numerous, basally moniliform, upwards filiform, multi-celled, short-celled, branched, with anastomoses, gnarled, hyaline, thin-walled, smooth. *Asci* 8-spored, cylindrical, thick-walled, apically rounded and with an ocular chamber, 2–3  $\mu\text{m}$  diam, pedicel short and furcate, bitunicate, fissitunicate, 185–214  $\times$  14.5  $\times$  15.5  $\mu\text{m}$ , ascospores oblique uniseriate. *Ascospores* initially with three transverse septa, constricted at the median septum, developing up to five transverse septa, becoming muriformly septate, 1–2 longitudinal or diagonal septa per cell, ellipsoidal, straight, the upper part often wider, end cells mostly bluntly rounded seldom conical, wall faintly thick and smooth, golden brown, septa red-golden and faintly thick, median septum constricted otherwise faintly constricted, eguttulate at maturity, no mucilaginous sheath in all stages of development, in lactic acid (18–)20–21(–23)  $\times$  (8.5–)9–10(–12)  $\mu\text{m}$ , in water 20.5–30.5  $\times$  10–15  $\mu\text{m}$ . Phoma-like morph: *Conidiomata* pycnidial, solitary, brown, globose, 180–250  $\mu\text{m}$  diam, with central ostiole, 20–30  $\mu\text{m}$  diam; wall of 2–3 layers of brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells lining the inner cavity, hyaline,





**Fig. 9.** *Hazslinszkyomyces lycii* (CPC 30998). **A.** Ascoma immersed in twig. **B–D.** Asci and pseudoparaphyses. **E.** Phoma-like conidiomata on SNA. **F–G.** Conidiogenous cells. **H.** Conidia. **I.** *Hazslinszkyomyces* conidioma on twig. **J.** Conidiogenous cells. **K.** Conidia. Bars: A = 130  $\mu\text{m}$ , I = 250  $\mu\text{m}$ , all others = 10  $\mu\text{m}$ .

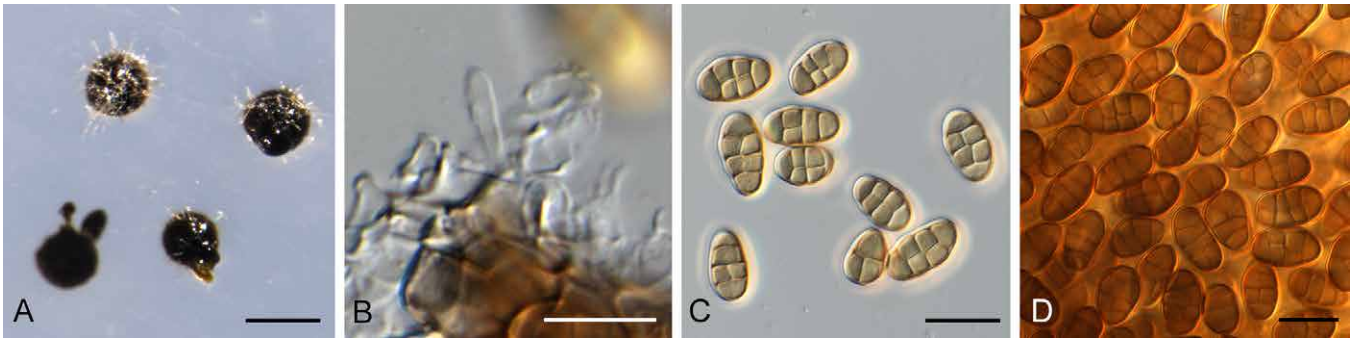
smooth, doliiform to subcylindrical, 4–7  $\times$  4–5  $\mu\text{m}$ ; phialidic, with periclinal thickening at apex. *Conidia* solitary, hyaline, smooth, guttulate, subcylindrical, straight, aseptate, apex obtuse, base truncate, hilum 1.5  $\mu\text{m}$  diam, (3.5–)4–5(–6)  $\times$  2  $\mu\text{m}$ . Camarosporium-like morph: *Conidiomata* pycnidial, solitary, gregarious, brown, globose, with central ostiole, wall few-layered of brown *textura globulosa-angularis*, completely covered with hyaline to brownish and short hyphae, to 800  $\mu\text{m}$  diam. *Conidiogenous cells* lining the inner cavity, doliiform to subcylindrical, hyaline, smooth, 6–7  $\times$  5–7  $\mu\text{m}$ ; annellidic, proliferating percurrently at apex. *Conidia* solitary, pale yellowish with a golden wall, smooth, broadly ellipsoidal to obovoid but also clavate, seldom cylindrical, straight, seldom slightly curved, apex obtuse, base sometimes tapered and never truncate, 4–5  $\mu\text{m}$  diam, transversely (2–)3(–4–5)-septate, becoming muriformly septate, with vertical and oblique septa, septa smooth to slightly constricted and thick, eguttulate, (15–)16–18(–20)  $\times$  (8–)9(–10)  $\mu\text{m}$  *in vitro*, 18–34  $\times$  9–16  $\mu\text{m}$  *in vivo*.

**Culture characteristics:** Colonies covering dish in 2 wk, with moderate aerial mycelium, and smooth, lobate margins. On

PDA surface fawn to hazel, reverse fawn. On OA surface ochreous to umber.

**Other material examined:** **Hungary:** near Budapest, on twig of *Lycium barbarum* (Solanaceae), 1 May 2016, L. Bartalos (HPC 1029 = CPC 31014 = CBS 142618).

**Notes:** *Hazslinszkyomyces lycii* occurred in association with a camarosporium-like morph which, when cultured, proved to be identical based on DNA sequence data. The sexual morph also produced a phoma-like synasexual morph in culture. *Pyrenophora lycii* (syn. *Pleospora lycii*), also described from *Lycium barbarum* in Hungary, has setose pseudothecia and ascospores that are transversely 5-septate with only one longitudinal septum per cell, 26–30  $\times$  8  $\mu\text{m}$ , and is distinct from the present fungus. A further name to consider is “*Hendersonia lycii* Hazsl”. Hazslinszky (1865) referred to a *Hendersonia* form on *Lycium barbarum*, but the name *Hendersonia lycii* was never validly published with any description, and has crept into literature in error, and is thus unavailable for this collection. The taxon is therefore described here as new.



**Fig. 10.** *Neocamarosporium chersinae* (CPC 27298). **A.** Conidiomata on SNA. **B.** Conidiogenous cells. **C–D.** Conidia. Bars: A = 300 µm, all others = 10 µm.

***Neocamarosporium chersinae* Crous, sp. nov.**

MycoBank MB820910

(Fig. 10)

**Etymology:** Named after the angulate tortoise or “rooipens” (*Chersina angulata*), a tortoise species found in dry areas and scrub forest in South Africa. The angulate tortoise is used as a food source by people in rural areas, and is also often kept as a pet.

**Diagnosis:** Similar to *Neocamarosporium chichastianum* [conidia (11–)15–19(–22) × (6–)8–9(–11) µm], but conidia smaller.

**Type:** **South Africa:** *Western Cape Province:* Robben Island, on dead angulate tortoise shell, 25 May 2015, *P.W. Crous* (CBS H-23070 – holotype; CPC 27298 = CBS 142620 – culture ex-type).

**Description:** *Conidiomata* solitary, pycnidial, immersed to erumpent, golden brown, 200–300 µm diam, with central ostiole, 25–35 µm diam; wall of 2–3 layers of brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells, hyaline, smooth, subcylindrical, 3–6 × 2–4 µm; proliferating several times percurrently at apex (conidiogenous cells dissolve at maturity). *Conidia* solitary, golden brown, thick-walled, smooth, broadly ellipsoidal to subcylindrical or irregular, transverse 3-septate, with 0–3 oblique septa, (10–)12–13(–15) × (5–)6(–7) µm.

**Culture characteristics:** Colonies covering the dish in 2 wk, with fluffy aerial mycelium. On OA, MEA and PDA surface olivaceous grey to pale olivaceous grey, reverse olivaceous grey.

**Notes:** *Neocamarosporium chersinae* is introduced as a new species of *Neocamarosporium* (Crous *et al.* 2014b). *Neocamarosporium* is camarosporium-like in morphology, and can only be safely distinguished from this genus based on DNA data.

***Libertasomycetaceae* Crous, fam. nov.**

MycoBank MB820911

**Etymology:** Named after the genus *Libertasomyces*.

**Classification:** *Libertasomycetaceae*, *Pleosporales*, *Dothiideomycetes*.

**Diagnosis:** Similar to *Coniothyriaceae*, but distinct in that ascomata are immersed in a brown stroma, and conidiomata are stromatic in culture.

**Type genus:** *Libertasomyces* Crous & Roets 2016.

**Description:** *Ascomata* immersed in a brown stroma, becoming erumpent, breaking through the host surface, aggregated in clusters, with a central ostiole; wall of 6–10 layers of brown *textura angularis*. *Pseudoparaphyses* hyphal-like, intermingled among asci, hyaline, smooth, septate, anastomosing. *Asci* fasciculate, stipitate, hyaline, smooth, subcylindrical, bitunicate with ocular chamber, containing 8 ascospores. *Ascospores* fusoid-ellipsoidal, brown, verruculose with obtuse ends, muriformly septate, encased in a mucoid sheath. *Conidiomata* unilocular, stromatic, separate, globose, immersed, brown, opening via a central ostiole, exuding a brown conidial mass; wall of 3–6 layers of brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* lining the inner cavity, hyaline, smooth, ampulliform to doliiform, with prominent periclinal thickening at the apex, or with tightly aggregated percurrent proliferations at the apex. *Conidia* solitary, golden brown, subcylindrical to ellipsoidal, straight to curved, 0–1-septate, constricted at median septum, apex obtuse, base truncate, with marginal frill, and longitudinal striations, or hyaline, smooth, granular, thin-walled, ellipsoidal, apex obtuse, base truncate to bluntly rounded, aseptate.

**Genera included:** *Libertasomyces* and *Neoplatysporoides*.

***Libertasomyces quercus* Crous, sp. nov.**

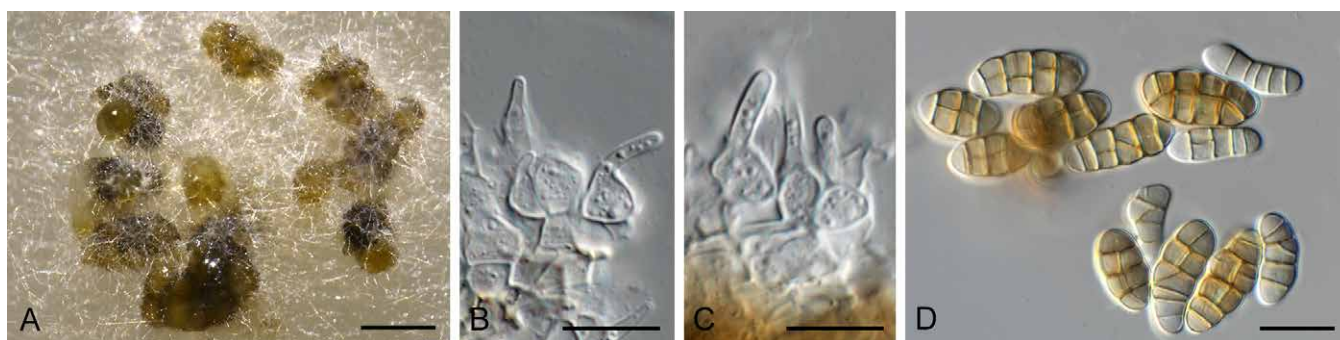
MycoBank MB820912

(Fig. 11)

**Etymology:** Named after the genus from which it was isolated, *Quercus*.

**Diagnosis:** Similar to *Camarosporium quaternatum* (conidia 18–34 × 9–16 µm), but distinct in having smaller, uniformly brown conidia (15–21 × 6–10 µm).





**Fig. 11.** *Libertasomyces quercus* (CBS 134.97). **A.** Conidiomata on OA. **B, C.** Conidiogenous cells. **D.** Conidia. Bars: A = 200  $\mu\text{m}$ , all others = 10  $\mu\text{m}$ .

**Type:** **Spain:** location unknown, on leaf litter of *Quercus ilex* (Fagaceae), 20 Jul. 1996, R.F. Castañeda (CBS H-23065 – holotype; CBS 134.97 = INIFAT C96/108 – culture ex-type).

**Description:** *Conidiomata* brown, solitary or aggregated in clusters, stromatic, obovoid, 120–180  $\mu\text{m}$  diam, with paler brown papillate ostiole, outer region covered with brown hyphae; wall of 6–12 layers of brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells lining the inner cavity, hyaline, smooth, doliiform to ampulliform, 5–7  $\times$  4–6  $\mu\text{m}$ ; proliferating percurrently at apex. *Conidia* solitary, brown, smooth, subcylindrical to broadly ellipsoidal, apex obtuse, base truncate to bluntly rounded, transversely 3–7-septate, becoming muriformly septate with vertical and oblique septa, (15–)17–19(–21)  $\times$  (6–)7–8(–10)  $\mu\text{m}$ .

**Culture characteristics:** Colonies flat, spreading, reaching 40 mm diam after 2 wk with sparse to moderate aerial mycelium and even, lobate margins. On PDA surface umber with patches of salmon, reverse hazel. On OA surface dirty white with patches of umber.

**Notes:** *Libertasomyces quercus* (conidia 15–21  $\times$  6–10  $\mu\text{m}$ ) was originally identified as *Camarosporium quaternatum* (conidia 18–34  $\times$  9–16  $\mu\text{m}$ , see above), but differs in conidial dimensions. Phylogenetically, it is better accommodated in *Libertasomyces* (based on *L. myopori*; Crous *et al.* 2016), which is pleomorphic, having a sexual morph, a camarosporium-like and a phoma-like synsexual morph.

**Leptosphaeriaceae** M.E. Barr, *Mycotaxon* **29**: 503 (1987).

**Type genus:** *Leptosphaeria* Ces. & De Not. 1863.

**Querciphoma** Crous, **gen. nov.**  
Mycobank MB820913

**Etymology:** Named after the host on which it occurs, *Quercus*, and its phoma-like morphology.

**Diagnosis:** Morphologically similar to *Phoma*, but distinct in that conidiomata are eustromatic, uni- to multi-locular, and conidia become brown and verruculose with age.

**Type species:** *Querciphoma carteri* (Gruyter & Boerema) Crous 2017.

**Description:** *Conidiomata* pycnidial, globose, eustromatic, uni- to multi-locular, with 1–3 papillate ostioles, medium brown, outer surface covered in short, brown, verruculose, septate setae with obtuse ends; wall of 3–6 layers of brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells lining inner cavity, hyaline, smooth, doliiform; phialidic with periclinal thickening at the apex. *Conidia* solitary, hyaline, smooth, guttulate, broadly ellipsoidal, aseptate, becoming brown, verruculose with age.

**Querciphoma carteri** (Gruyter & Boerema) Crous, **comb. nov.**

Mycobank MB820914  
(Fig. 12)

**Basionym:** *Phoma carteri* Gruyter & Boerema, *Persoonia* **17**: 547 (2002) [“2001”].

**Synonyms:** *Coniothyrium carteri* (Gruyter & Boerema) Verkley & Gruyter, *Stud. Mycol.* **75**: 23 (2013) [“2012”].

*Pyrenochaeta minuta* J.C. Carter, *Bull. Illinois Nat. Hist. Surv.* **21**: 214 (1941).

**Description:** *Conidiomata* pycnidial, globose, eustromatic, uni- to multi-locular, with 1–3 papillate ostioles, 150–250  $\mu\text{m}$  diam, medium brown, outer surface covered in short, brown, verruculose, septate setae with obtuse ends, to 80  $\mu\text{m}$  tall; wall of 3–6 layers of brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells lining inner cavity, hyaline, smooth, doliiform, 4–6  $\times$  4–5  $\mu\text{m}$ ; phialidic with periclinal thickening at apex. *Conidia* solitary, hyaline, smooth, guttulate, broadly ellipsoidal, aseptate, becoming brown, verruculose with age, apex obtuse, base truncate to bluntly rounded, (3.5–)4–5(–6)  $\times$  3(–3.5)  $\mu\text{m}$ .

**Culture characteristics:** Colonies flat, spreading, reaching 50 mm diam after 2 wk, with sparse to moderate aerial mycelium, and smooth, lobate margins. On PDA surface umber, reverse chestnut. On OA surface umber.

**Material examined:** **Germany:** former West-Germany: on leaves and twigs of *Quercus robur* (Fagaceae), H. Schill (CBS H-23071, culture CBS 105.91). – **The Netherlands:** PD Lisse, on *Quercus* sp., date and collector unknown (PD 84/74 = CBS 101633).



**Fig. 12.** *Querciphoma carteri* (CBS 105.91). **A.** Conidiomata on PDA. **B.** Conidiomata on SNA. **C.** Setae. **D.** Conidiogenous cells. **E.** Conidia. Bars: A, B = 250  $\mu$ m, all others = 10  $\mu$ m.

**Notes:** This isolate was deposited as *Phoma* sp., and reclassified as *Coniothyrium carteri* (based on *Phoma carteri*; see Boerema *et al.* 2004) by De Gruyter *et al.* (2013). However, as shown here, it clusters separately from *Coniothyrium* s.str. (having brown, 1-septate conidia), and is best placed in a separate genus.

**Didymosphaeriaceae** Munk, *Dansk bot. Ark.* **15**: 128 (1953).

*Type genus:* *Didymosphaeria* Fuckel 1870.

**Paracamarosporium mamanan** (Crous) Crous, **comb. nov.**

Mycobank MB820916

*Basionym:* *Camarosporium mamanan* Crous, *Fungal Planet* No. 5: 1 (2006).

**Type:** **USA:** *Hawaii:* Saddle Road, on stems of *Sophora chrysophylla* (*Leguminosae*), Aug. 2005, W. Gams & Y. Degawa (CBS H-19775 – holotype; CPC 12252 = CBS 120031, CPC 12253–12254 – cultures ex-type).

**Notes:** *Camarosporium mamanan* is allocated to the genus *Paracamarosporium* based on its phylogenetic position. However, the distinction between *Paracamarosporium* and *Pseudocamarosporium* is highly debatable (Wijayawardene *et al.* 2014), and although we could separate them here based on ITS sequence data, the genera cannot be separated based on LSU data, and appear to represent a single genus, *Paracamarosporium*. Furthermore, there have also been an excessive number of species introduced in the genus, which are not supported based on their DNA barcodes.

## **DOTHIORA COMPLEX**

**Dothideaceae** Chevall., *Fl. gén. env. Paris* **1**: 446 (1826); as “*Dothideae*”.

*Type genus:* *Dothidea* Fr. 1818.

**Dothiora** Fr., *Summa veg. Scand.* **2**: 418 (1849).

*Synonyms:* *Dothichiza* Lib. ex Roum., *Fungi Selecti Gallici* Exs. cent. 7, no. 627 (1880).

*Coleonaema* Höhn., *Mitt. Bot. Lab. TH Wien* **1**(3): 95 (1924).  
*Cylindroseptoria* Quaedvl., *et al.*, *Stud. Mycol.* **75**: 358 (2013).

*Additional synonyms:* See Crous & Groenewald (2016).

*Classification:* *Dothideaceae*, *Dothideales*, *Dothideomycetes*.

**Current generic circumscription:** *Ascostromata* immersed to erumpent, pulvinate to globose, black, multi-loculate; wall of dark brown *textura angularis*. *Locules* globose to subglobose, broadly rounded or papillate with central ostiole. *Pseudoparaphyses* absent. *Asci* 8- or more spored, bitunicate, fissitunicate, oblong to clavate, pedicellate, with a small ocular chamber. *Ascospores* biseriate to multi-seriate, septate, constricted at the primary median septum, at times with a vertical septum, hyaline, rarely pale brown, obovate to ellipsoidal to fusoid, often inequilateral or slightly curved, smooth, at times with a thin mucoid sheath. *Conidiomata* pycnidial, separate, or aggregated in a stroma. *Conidiophores* reduced to conidiogenous cells lining the inner cavity, hyaline, smooth, ampulliform to doliiform, phialidic. *Conidia* aseptate, hyaline, smooth, subcylindrical to ovoid or oblong. *Hyphae* becoming brown, verruculose and constricted at septa, giving rise to a hormonema-like synasexual morph.

*Type species:* *Dothiora pyrenophora* (Fr.) Fr. 1849.

**Dothiora cactacearum** Crous, **sp. nov.**

Mycobank MB820917

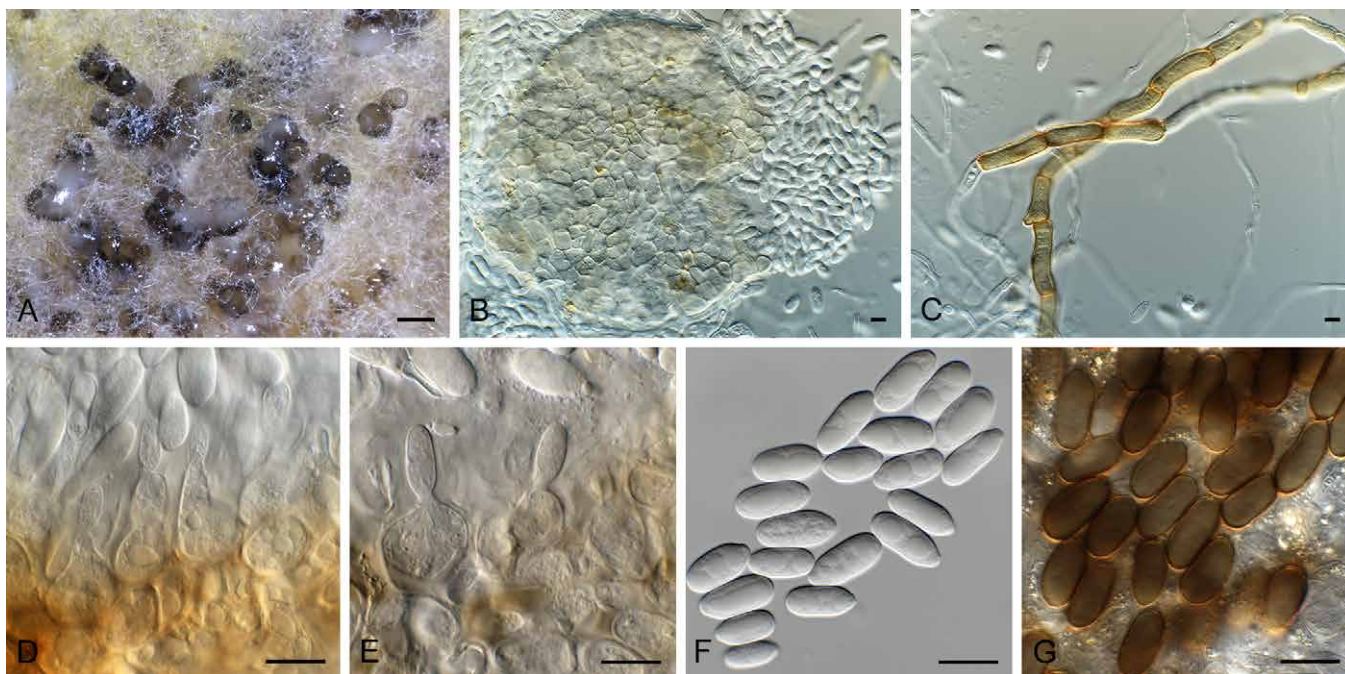
(Fig. 13)

**Etymology:** Named after the host family from which the fungus was isolated, *Cactaceae*.

**Diagnosis:** Morphologically distinct from other species of *Dothiora* in that conidia become brown and roughened with age.

**Type:** **USA:** *Texas:* Austin, on phyllodes of *Cactaceae*, 2013, P.W. Crous (CBS H-23074 – holotype; CPC 15585 = CBS 142492 – culture ex-type, CPC 15587).





**Fig. 13.** *Dothiora cactacearum* (CPC 15585). **A.** Conidiomata on OA. **B.** Conidioma. **C.** Brown hyphae forming on SNA. **D, E.** Conidiogenous cells. **F.** Conidia. **G.** Conidia turning brown and verruculose with age. Bars: A = 150  $\mu$ m, all others = 10  $\mu$ m.

**Description:** *Conidiomata* separate, erumpent, pycnidial, globose, medium brown, 150–300  $\mu$ m diam, with a central ostiole, exuding a creamy conidial mass; wall of 3–6 layers of brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells lining the inner cavity, hyaline, smooth, ampulliform to doliiform, 7–15  $\times$  7–15  $\mu$ m, phialidic, at times with percurrent proliferation and prominent collarette. *Conidia* hyaline, smooth, guttulate, subcylindrical to broadly ellipsoidal, apex obtuse, tapering to a truncate, protruding hilum, 2–3  $\mu$ m diam, (12–)14–17(–19)  $\times$  (5–)6–7.5(–8)  $\mu$ m (av. 15  $\times$  7  $\mu$ m); conidia becoming brown and roughened with age. *Hyphae* becoming brown, verruculose and constricted at the septa.

**Culture characteristics:** Colonies flat, spreading, with sparse to moderate aerial mycelium, and even, lobate margin, reaching 40 mm diam after 2 wk at 25  $^{\circ}$ C. On MEA surface umber, reverse luteous; on PDA surface fawn, reverse isabelline; on OA surface isabelline.

***Dothiora pyrenophora* (Fr.) Fr., *Summa veg. Scand.* 2: 418 (1849). (Fig. 14)**

**Basionym:** *Dothidea pyrenophora* Fr., *Kongl. Vetensk. Acad. Handl.* 40: 88 (1819); Fr., *Syst. mycol.* 2(2): 552 (1823).

**Type: Sweden:** without locality, on dead branches of *Sorbus* sp. (*Rosaceae*), E.M. Fries (no original material found). – **Germany:** on twig of *Sorbus aucuparia*, 27 Apr. 2016, R.K. Schumacher (CBS H-23073 – **neotype designated here**, MBT376258; CPC 30634, CPC 30632 = CBS 142621–cultures ex-neotype).

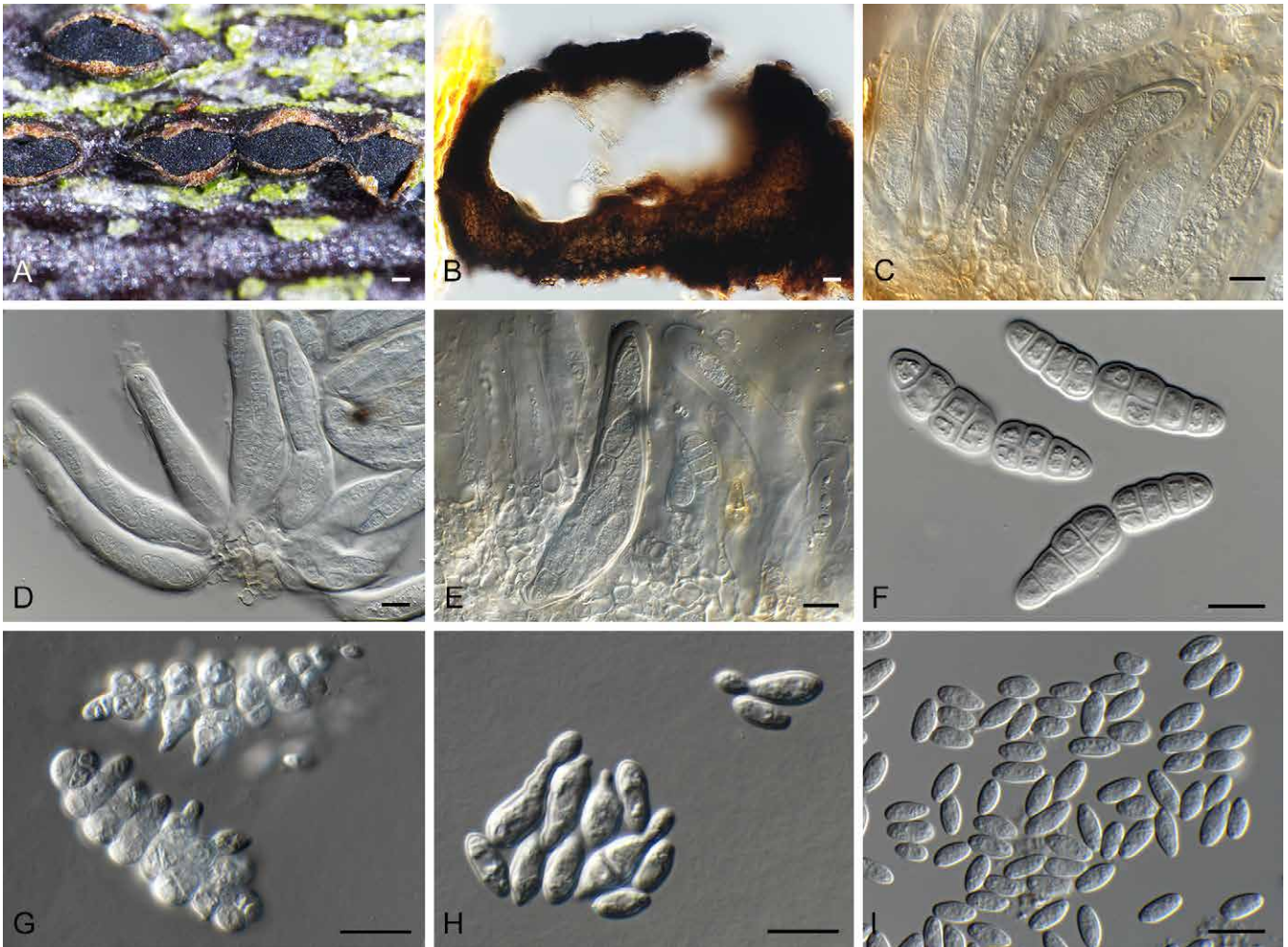
**Description:** *Ascostromata* solitary to aggregated, black, immersed to erumpent, unilocular, to 400  $\mu$ m diam, elliptical,

pulvinate, opening by an irregular pore, upper layer dissolving with age; wall of 6–10 layers of brown *textura angularis*. *Asci* bitunicate, hyaline, oblong to subcylindrical, short stipitate, 8-spored, with apical apiculus, 2–3  $\mu$ m diam, 90–120  $\times$  14–17  $\mu$ m. *Ascospores* bi- to triseriate in ascus, hyaline, smooth, at times turning yellow-brown with age, fusiform, inequilateral, slightly curved, with prominent mucoid sheath when young (in water), dissolving at maturity, (5–)5(–8) transversely septate, prominently constricted at primary septum, with oblique or vertical septa in central cells, (22–)25–30(–35)  $\times$  (7–)8  $\mu$ m; ascospores directly giving rise to asexual morph via budding, with ascomata transforming with age into large conidiomata, with apical opening completely dissolving. *Conidiomata* immersed to erumpent, pycnidial, black, globose, to 300  $\mu$ m diam, separate or gregarious, unilocular; wall of 3–6 layers of brown *textura angularis*. *Conidiophores* lining the inner cavity, reduced to conidiogenous cells. *Conidiogenous cells* hyaline, smooth, doliiform to ampulliform, 4–9  $\times$  4–6  $\mu$ m, with minute periclinal thickening at apex. *Conidia* solitary, aseptate, hyaline, smooth, ovate to ellipsoidal, with minute guttules, subobtuse apex, and truncate hilum, (5–)7–8(–9)  $\times$  (3–)4  $\mu$ m.

**Culture characteristics:** Colonies flat, spreading, with sparse aerial mycelium and feathery, undulate margins. On PDA, MEA and OA surface and reverse iron-grey.

**Other material examined: Germany:** on twig of *Sorbus aucuparia*, 27 Apr. 2016, R.K. Schumacher (CBS H-23072).

**Notes:** The taxonomic position of the several species occurring on *Sorbus* require further clarification based on fresh material. One culture identified as *Dothiora sorbi* (CBS 742.71) was included in this study, and clustered slightly apart from *D. pyrenophora* (nine bp different on ITS), suggesting



**Fig. 14.** *Dothiora pyrenophora* (CPC 30632). **A.** Ascostroma on twig. **B.** Section through ascoma. **C–E.** Asci. **F.** Ascospores. **G.** Ascospores undergoing microcyclic conidiation. **H.** Conidia undergoing budding. **I.** Conidia. Bars: A, B = 200  $\mu\text{m}$ , all others = 10  $\mu\text{m}$ .

that these may very well be two closely related, but distinct species.

Genera such as *Sydowia* Bres.1895 and *Pringsheimia* Schulzer 1866 appear to represent younger generic names within *Dothideaceae*, based on their morphological similarity, and the formation of *Dothichiza* and hormonema-like morphs in culture, which are commonly observed in the family (Froidevaux 1972, Sivanesan 1984, Crous & Groenewald 2016). Another confusing aspect of many of the taxa in this family is that young ascospores can be hyaline and uniseptate, but become brown and muriformly septate with age (e.g. *Dothidea ribesia*, Fig. 15), which complicate the generic delimitation within the family (Thambugala *et al.* 2014), and identification keys based on immature material.

Species of *Dothiora* are commonly isolated from dead branches of woody hosts (Sivanesan 1984), while Crous & Groenewald (2016) also reported some species from dead leaves and fruit of diverse hosts, suggesting that it is a saprobe, possibly acting as a weak pathogen on stressed plant tissues.

## ACKNOWLEDGEMENTS

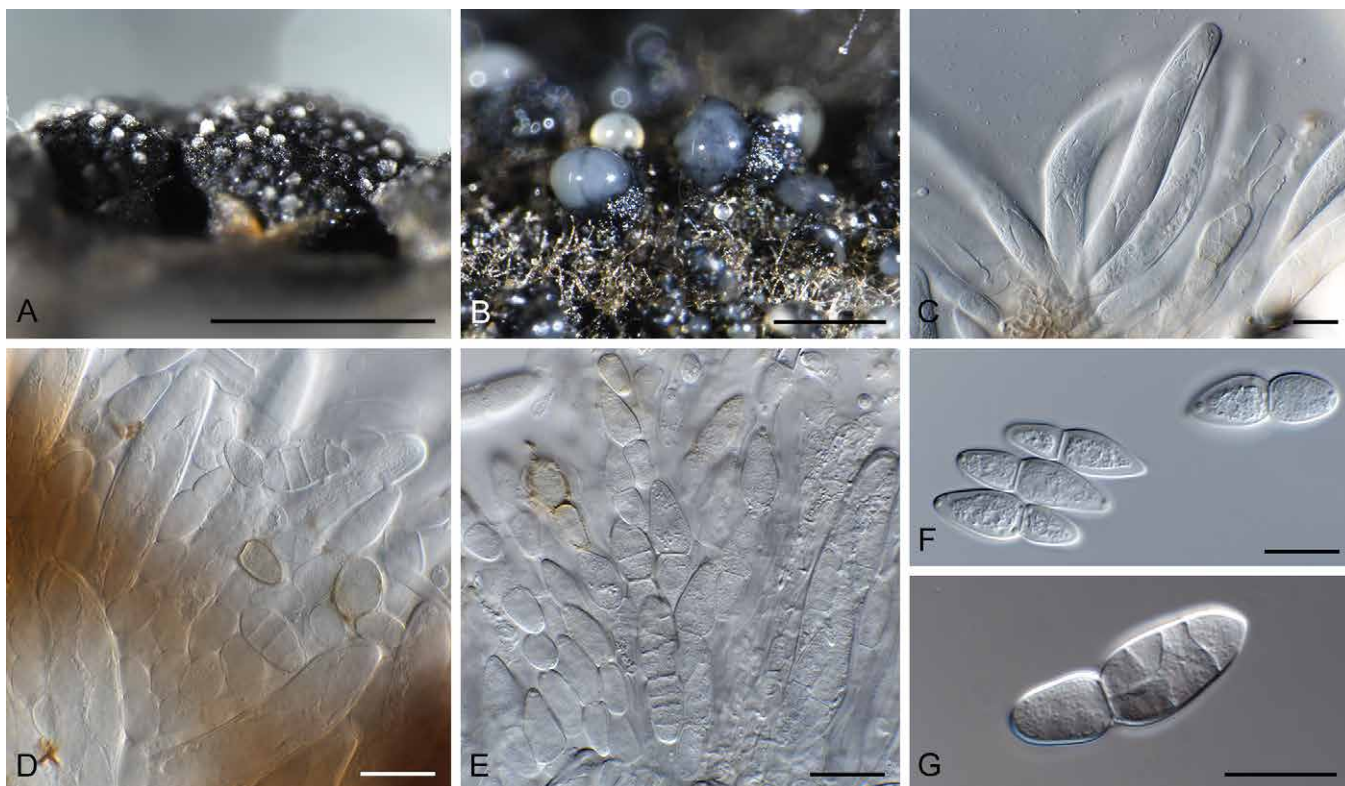
We acknowledge Laszlo Bartalos and René Jarling for sending us specimens of *Camarosporium* and similar taxa examined in the

present study. We are also thankful to René K. Schumacher for making many valuable collections available to be included in this study, and for bringing the problem related to the nomenclature of *Camarosporium* to our attention.

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**Fig. 15.** *Dothidea ribesia* (CPC 30638). **A.** Ascostromata on twig. **B.** Ostioles with exuding ascospores. **C–E.** Asci with ascospores that become muriformly septate. **F.** One-septate ascospores. **G.** Muriformly septate ascospore. Bars: A = 3 mm, B = 100  $\mu$ m, all others = 10  $\mu$ m.

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