Persoonia 22, 2009: 139–161
www.persoonia.org

RESEARCH ARTICLE

doi:10.3767/003158509X461701

Phylogeny and taxonomy of obscure genera of microfungi

P.W. Crous[1], U. Braun[2], M.J. Wingfield[3], A.R. Wood[4], H.D. Shin[5], B.A. Summerell[6], A.C. Alfenas[7], C.J.R. Cumagun[8], J.Z. Groenewald[1]

Key words

Brycekendrickomyces
Chalastospora
Cyphellophora
Dictyosporium
Edenia
phylogeny
taxonomy
Thedgonia
Trochophora
Verrucisporota
Vonarxia
Xenostigmina

Abstract The recently generated molecular phylogeny for the kingdom *Fungi*, on which a new classification scheme is based, still suffers from an under representation of numerous apparently asexual genera of microfungi. In an attempt to populate the Fungal Tree of Life, fresh samples of 10 obscure genera of hyphomycetes were collected. These fungi were subsequently established in culture, and subjected to DNA sequence analysis of the ITS and LSU nrRNA genes to resolve species and generic questions related to these obscure genera. *Brycekendrickomyces* (*Herpotrichiellaceae*) is introduced as a new genus similar to, but distinct from *Haplographium* and *Lauriomyces*. *Chalastospora* is shown to be a genus in the *Pleosporales*, with two new species, *C. ellipsoidea* and *C. obclavata*, to which *Alternaria malorum* is added as an additional taxon under its oldest epithet, *C. gossypii*. *Cyphellophora eugeniae* is newly described in *Cyphellophora* (*Herpotrichiellaceae*), and distinguished from other taxa in the genus. *Dictyosporium* is placed in the *Pleosporales*, with one new species, *D. streliziae*. The genus *Edenia*, which was recently introduced for a sterile endophytic fungus isolated in Mexico, is shown to be a hyphomycete (*Pleosporales*) forming a pyronellea-like synanamorph in culture. *Thedgonia* is shown not to represent an anamorph of *Mycosphaerella*, but to belong to the *Helotiales*. *Trochophora*, however, clustered basal to the *Pseudocercospora* complex in the *Mycosphaerellaceae*, as did *Verrucisporota*. *Vonarxia*, a rather forgotten genus of hyphomycetes, is shown to belong to the *Herpotrichiellaceae* and *Xenostigmina* is confirmed as synanamorph of *Mycopappus*, and is shown to be allied to *Seifertia* in the *Pleosporales*. Dichotomous keys are provided for species in the various genera treated. Furthermore, several families are shown to be polyphyletic within some orders, especially in the *Capnodiales*, *Chaetothyriales* and *Pleosporales*.

Article info Received: 2 April 2009; Accepted: 23 April 2009; Published: 9 June 2009.

INTRODUCTION

The recent 'Deep Hypha' issue of Mycologia (vol. 98, 2006) included 21 phylogenetic studies employing multi-gene phylogenies to resolve major groups of *Fungi*. These papers provided the foundation for the study of James et al. (2006), in which six genes (SSU, LSU, 5.8S rRNA, rpb1, rpb2 and tef1) for approximately 200 fungal taxa were used to present the first kingdom-level phylogeny, and a new classification for the *Fungi* (Hibbett et al. 2007). These studies also illustrated clearly that it was merely the 'tip of the iceberg', and that numerous genera must now be accommodated in this phylogenetic framework.

A major problem encountered during the Assembling the Fungal Tree of Life (AFTOL, www.aftol.org) project, was that many genera are insufficiently known, and have never been cultured, or subjected to DNA analyses. This is especially true for the majority of apparently asexual microfungi, namely the coelomycetes (Sutton 1980, Nag Raj 1993) and hyphomycetes (Ellis 1971, 1976, Carmichael et al. 1980). The only means to deal with this problem is, therefore, to encourage mycologists to recollect these genera and species, to establish cultures for them and to ultimately generate DNA sequence data (Shenoy et al. 2007), a process which can be described as 'leafing out the fungal tree of life'.

Ten genera of hyphomycetes not previously known from culture, or for which the phylogenetic classification is uncertain, are treated in the present study. These fungi were collected from diverse hosts from various continents, isolated in axenic culture, and subjected to DNA sequence analysis. They are shown to belong to the *Chaetothyriales* (*Brycekendrickomyces*, *Cyphellophora*, *Vonarxia*), *Pleosporales* (*Chalastospora*, *Dictyosporium*, *Edenia*, *Xenostigmina*), *Helotiales* (*Thedgonia*), and the *Capnodiales*, *Mycosphaerellaceae* (*Trochophora*, *Verrucisporota*).

The present paper represents a further contribution in a series aiming to clarify the morphology and DNA phylogeny of obscure genera of microfungi. Other than resolving their phylogenetic relationships, several novelties are described, and keys are provided to the accepted species in these genera.

MATERIAL AND METHODS

Isolates

Symptomatic leaves and leaf litter were collected on various continents, and sent to the Centraalbureau voor Schimmelcultures (CBS) for isolation of microfungi. Leaves with visible fruiting were immediately subjected to direct isolation of hyphomycetes, or alternatively were first incubated in moist chambers to

[1] CBS Fungal Biodiversity Centre, Uppsalalaan 8, 3584 CT Utrecht, The Netherlands; corresponding author e-mail: p.crous@cbs.knaw.nl.
[2] Martin-Luther-Universität, Institut für Biologie, Bereich Geobotanik und Botanischer Garten, Herbarium, Neuwerk 21, D-06099 Halle (Saale), Germany.
[3] Department of Genetics, Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, Pretoria 0002, South Africa.
[4] ARC – Plant Protection Research Institute, P. Bag X5017, Stellenbosch, 7599, South Africa.
[5] Division of Environmental Science & Ecological Engineering, Korea University, Seoul 136-701, Korea.
[6] Royal Botanic Gardens and Domain Trust, Mrs. Macquaries Road, Sydney, NSW 2000, Australia.
[7] Departamento de Fitopatologia, Universidade Federal de Viçosa, 36.570 Viçosa, MG, Brazil.
[8] Crop Protection Cluster, College of Agriculture, University of the Philippines, Los Baños College, Laguna 4031, Philippines.

Table 1 Collection details and GenBank accession numbers for fungal species included in this study.

Species	Strain no.[1]	Substrate	Country	Collector(s)	GenBank Accession no.[2]	
					ITS	LSU
Brycekendrickomyces acaciae	CBS 124104; CPC 15078	*Acacia auriculiformis*	Indonesia	M.J. Wingfield	FJ839606	FJ839641
Chalastospora cetera	CBS 121340; E.G.S. 41.072	*Elymus scabrus*	Australia	R.G. Rees	FJ839607	FJ839642
Chalastospora ellipsoidea	CBS 121331; E.G.S. 22.060	*Triticum* sp.	Australia	H.L. Harvey & S. Perth	FJ839608	FJ839643
Chalastospora gossypii	CBS 112844; CPC 4571	*Bromus tectorum*	USA	F.M. Dugan	AY251081	AY251081
	CBS 114005; CPC 4572	*Festuca idahoensis*	USA	F.M. Dugan	AY251079	AY251079
	CBS 114809; MAF 943	Leaves of *Anethum graveolens* (dill) along with *Itersonilia perplexans*	New Zealand	J. Pike	FJ839609	FJ839644
	CBS 114810; MAF 954	*Quercus robur* (oak) leaves in association with *Tubakia dryina*	New Zealand	H. Nettleton	FJ839610	FJ839645
	CBS 148.66; CPC 3690; NRRL W 52-29	—	USA	C.W. Hesseltine	FJ839611	FJ839646
	CBS 173.80; ATCC 200939; CPC 3685	Agricultural soil	Syria	M.I.A. Abdel-Kader	—	FJ839647
	CBS 216.65; NRRL A-13702	*Triticum aestivum* grain	USA	C.W. Hesseltine	FJ839612	DQ008142
	CBS 266.75; ATCC 28332; CPC 3680; IMI 165252; PRE 44703	Wheat stubble	South Africa	W.F.O. Marasas	FJ839613	FJ839648
	CBS 900.87; ATCC 200938	Soil	Lebanon	F. Seigle-Murandi	FJ839614	FJ839649
	CPC 15567; C.F. Hill 2008/3899	Wood and wallpaper from inside walls of a dwelling	New Zealand	D. De Vanny	FJ839615	FJ839650
Chalastospora gossypii var. *polymorpha*	CBS 112048; CPC 4570	Dormant buds (overwintered) of *Vitis vinifera*	USA	F.M. Dugan	AY251080	AY251080
Chalastospora obclavata	CBS 124120; E.G.S. 12.128	Air	USA	C.T. Rogerson	FJ839616	FJ839651
Cyphellophora eugeniae	CBS 124105; CPC 15172	Living leaves of *Stenocalyx uniflorus*	Brazil	A.C. Alfenas	FJ839617	FJ839652
Dictyosporium strelitziae	CBS 123359; CPC 15359	Dead leaves of *Strelitzia nicolai*	South Africa	A. Wood	FJ839618	FJ839653
Edenia gomezpompae	CBS 124106; CPC 15689	*Senna alata*	Phillippines	C.J.R. Cumagun	FJ839619	FJ839654
Haplographium catenatum	CBS 196.73	Decaying wood	Germany	W. Gams	FJ839620	FJ839655
	CBS 482.67; CMW 754	Decaying wood	Germany	W. Gams	FJ839621	FJ839656
	CBS 739.68; CMW 755	Decaying wood	Netherlands	H.A. van der Aa	FJ839622	FJ839657
Lauriomyces bellulus	CBS 517.93	Cupule of *Castanea sativa*	Switzerland	P.W. Crous	FJ839623	FJ839658
Lauriomyces heliocephalus	CBS 112054; INIFAT CO2/59	Decaying leaf	Brazil	A. Stchigel & J. Guarro	FJ839624	FJ839659
Mycopappus aceris	CBS 124109; CPC 14379	Fallen leaves of *Acer macrophyllum*	Canada	B. Callan	FJ839625	FJ839660
Mycosphaerella lupini	CPC 1661	*Lupinus* sp.	USA	W. Kaiser	AF362050	FJ839661
Stenella anthuriicola	CBS 118742	*Anthurium* leaf	Thailand	C. F. Hill	FJ839626	FJ839662
Stigmina platani	CBS 110755; CPC 4299; IMI 136770	*Platanus orientalis*	India	—	AY260090	FJ839663
Thedgonia ligustrina	CPC 10019	*Ligustrum ovalifolium*	South Korea	H.-D. Shin	FJ839627	FJ839664
	CPC 10530	*Ligustrum ovalifolium*	Netherlands	P.W. Crous	FJ839628	FJ839665
	CPC 10861	*Ligustrum ovalifolium*	South Korea	H.-D. Shin	FJ839629	FJ839666
	CPC 14754	*Ligustrum obtusifolium*	South Korea	H.-D. Shin	FJ839630	FJ839667
	CPC 4298; W1877	*Ligustrum* sp.	Asia	H. Evans	EU040242	EU040242
Trochophora fasciculata	CPC 10281	Leaves of *Daphniphyllum macropodum*	South Korea	H.-D. Shin	FJ839631	—
	CPC 10282	Leaves of *Daphniphyllum macropodum*	South Korea	H.-D. Shin	FJ839632	FJ839668
Verrucisporota daviesiae	CBS 116002; VPRI 31767	Living leaves of *Daviesia mimosoides*	Australia	V. & R. Beilharz	FJ839633	FJ839669
Verrucisporota grevilleae	CBS 124107; CPC 14761	Leaves of *Grevillia decurrens*	Australia	B. Summerell	FJ839634	FJ839670
Verrucisporota proteacearum	CBS 116003; VPRI 31812	*Grevillea* sp.	Australia	V. Beilharz	FJ839635	FJ839671
Vonarxia vagans	CBS 123533; CPC 15151	*Stenocalyx uniflorus*	Brazil	A.C. Alfenas	FJ839636	FJ839672
	CPC 15152	*Stenocalyx uniflorus*	Brazil	A.C. Alfenas	FJ839637	FJ839673
Xenostigmina zilleri	CBS 115685; CPC 4011	Living leaves of *Acer* sp.	Canada	K.A. Seifert	FJ839638	FJ839674
	CBS 124108; CPC 14376	Fallen leaves of *Acer macrophyllum*	Canada	B. Callan	FJ839639	FJ839675
	CBS 115686; CPC 4010	Living leaves of *Acer* sp.	Canada	K.A. Seifert	FJ839640	FJ839676

[1] ATCC: American Type Culture Collection, Virginia, USA; C.F. Hill: Culture collection of C.F. Hill, housed at MAF, New Zealand; CBS: CBS Fungal Biodiversity Centre, Utrecht, The Netherlands; CMW: Culture collection of M.J. Wingfield, housed at FABI, Pretoria, South Africa; CPC: Culture collection of P.W. Crous, housed at CBS; E.G.S.: Culture collection of E.G. Simmons, Indiana USA; IMI: International Mycological Institute, CABI-Bioscience, Egham, Bakeham Lane, U.K.; INIFAT: Alexander Humboldt Institute for Basic Research in Tropical Agriculture, Ciudad de La Habana, Cuba; MAF: Ministry of Agriculture and Forestry, New Zealand; NRRL: National Center for Agricultural Utilization Research, Peoria, USA; PRE: National collection of fungi, Pretoria, South Africa; VPRI: Victorian Department of Primary Industries, Knoxfield, Australia.

[2] ITS: Internal transcribed spacers 1 and 2 together with 5.8S nrDNA; LSU: 28S nrDNA.

stimulate sporulation. Single-conidial isolates were established on malt extract agar (MEA; 20 g/L Biolab malt extract, 15 g/L Biolab agar) using the technique outlined in Crous (1998). Cultures were later plated on fresh MEA, 2 % water agar (WA) supplemented with sterile pine needles, 2 % potato-dextrose agar (PDA), synthetic nutrient agar (SNA) and/or oatmeal agar (OA) (Crous et al. 2009), and subsequently incubated at 25 °C under near-ultraviolet light to promote sporulation. Reference strains are maintained in the culture collection of the CBS, Utrecht, the Netherlands (Table 1). Descriptions, nomenclature, and illustrations were deposited in MycoBank (www.mycobank.org, Crous et al. 2004b).

DNA isolation, amplification and analyses

Genomic DNA was isolated from fungal mycelium grown on MEA, using the UltraClean™ Microbial DNA Isolation Kit (Mo Bio Laboratories, Inc., Solana Beach, CA, USA) according to the manufacturer's protocols. The Primers V9G (de Hoog & Gerrits van den Ende 1998) and LR5 (Vilgalys & Hester 1990) were used to amplify part of the nuclear rDNA operon spanning the 3' end of the 18S rRNA gene (SSU), the first internal transcribed spacer (ITS1), the 5.8S rRNA gene, the second ITS region (ITS2) and the first 900 bases at the 5' end of the 28S rRNA gene (LSU). The primers ITS4 (White et al. 1990) and LR0R (Rehner & Samuels 1994) were used as internal sequence primers to ensure good quality sequences over the entire length of the amplicon. The PCR conditions, sequence alignment and subsequent phylogenetic analysis followed the methods of Crous et al. (2006b). Alignment gaps were treated as new character states. Sequence data were deposited in GenBank (Table 1) and alignments in TreeBASE (www.treebase.org). The ITS sequences were compared with those sequences available in NCBI's GenBank nucleotide database using a megablast search and the results are discussed where applicable under the taxonomic notes. Because the genus *Chalastospora* is relatively novel, species in this genus were supported by a separate phylogenetic tree.

Morphology

Fungal descriptions were based on cultures sporulating in vitro (media indicated). Wherever possible, 30 measurements (× 1 000 magnification) were made of structures mounted in lactic acid, with the extremes of spore measurements given in parentheses. Colony colours (surface and reverse) were assessed after 2–4 wk on different media at 25 °C in the dark, using the colour charts of Rayner (1970).

RESULTS

Phylogenetic analysis

Amplification products of approximately 1 700 bases were obtained for the isolates listed in Table 1. The LSU region of the sequences was used to obtain additional sequences from GenBank, which were added to the alignment. Due to the inclusion of the shorter LSU sequences of *Dictyosporium alatum* (GenBank accession DQ018101), *Dictyosporium elegans* (GenBank accession DQ018100) and *Dictyosporium toruloides* (GenBank accession DQ018104) in the alignment, it was not possible to subject the full length of the determined LSU sequences (Table 1) to analyses. The manually adjusted LSU alignment contained 115 sequences (including the two outgroup sequences) and, of the 568 characters used in the phylogenetic analyses, 267 were parsimony informative, 30 were variable and parsimony uninformative, and 271 were constant. Neighbour-joining analyses using three substitution models on the sequence data yielded trees supporting the same tree topology to one another but differed from the most parsimonious tree shown in Fig. 1 with regard to the placement of the clade containing *Ochroconis* and *Fusicladium* (in the distance analyses, this clade moves to a more basal position). Forty equally most parsimonious trees (TL = 1 039 steps; CI = 0.477; RI = 0.833; RC = 0.397), the first of which is shown in Fig. 1, were obtained from the parsimony analysis of the LSU alignment.

The manually adjusted ITS alignment contained 28 sequences (including the outgroup sequence) and, of the 521 characters used in the phylogenetic analyses, 97 were parsimony informative, 91 were variable and parsimony uninformative, and 333 were constant. Neighbour-joining analyses using three substitution models on the sequence data yielded trees supporting the same tree topology to one another but differed from the most parsimonious tree shown in Fig. 2 with regard to the placement of *Chalastospora ellipsoidea* (in the distance analyses, this taxon moves to a more basal position in *Chalastospora*). Six equally most parsimonious trees (TL = 253 steps; CI = 0.913; RI = 0.938; RC = 0.856), the first of which is shown in Fig. 2, were obtained from the parsimony analysis of the ITS alignment. The results of the phylogenetic analyses are highlighted below under the taxonomic notes, or in the Discussion, where applicable.

Taxonomy

Brycekendrickomyces Crous & M.J. Wingf., *gen. nov*. — MycoBank MB509515

Mycelium ex hyphis ramosis, septatis, laevibus, pallide brunneis, 1–2 µm latis compositum. Conidiophora solitaria, erecta, cylindrica, recta vel leviter flexuosa, cellula basali bulbosa, sine rhizoideis, stipite modice brunneo vel atro-brunneo, laevi, transverse euseptato, ad apicem cum (1–)2–4(–6) cellulis conidiogenis. Cellulae conidiogenae subcylindricae, allontoides vel doliiformes, rectae vel leviter curvatae, pallide brunneae, polyblasticae, sympodialiter proliferantes. Conidia hyalina, mucilagine aggregata (sed non catenata), ellipsoidea, apice subobtuso, basi subtruncata.

Type species. Brycekendrickomyces acaciae Crous & M.J. Wingf.

Etymology. Named for Bryce Kendrick, husband of Laurie Kendrick, for which *Lauriomyces* was named and that resembles the current genus.

Mycelium consisting of branched, septate, smooth, pale brown, 1–2 µm wide hyphae. *Conidiophores* solitary, erect, cylindrical, straight to somewhat flexuous, basal cell bulbous, without rhizoids; stalk medium to dark brown, smooth, transversely euseptate; upper cell giving rise to (1–)2–4(–6) conidiogenous cells. *Conidiogenous cells* subcylindrical to allantoid or doliiform, straight to gently curved, pale brown, polyblastic, proliferating sympodially. *Conidia* hyaline, aggregating in slimy mass (never in chains), ellipsoid, apex subobtuse, base subtruncate.

Brycekendrickomyces acaciae Crous & M.J. Wingf., *sp. nov*. — MycoBank MB509517; Fig. 3

Maculae modice brunneae vel atro-brunneae, margine elevato, rubro-purpureo, oblongae vel ellipticae, ad 7 mm diam, in consortione '*Phaeotrichoconis' crotalariae*. In vitro (MEA): Mycelium ex hyphis ramosis, septatis, laevibus, pallide brunneis, 1–2 µm latis compositum. Conidiophora ex hyphis oriunda, solitaria, erecta, cylindrica, recta vel leviter flexuosa, cellula basali bulbosa, sine rhizoideis, 4–6 µm lata, ad basim 10–15 µm lata, stipite modice brunneo vel atro-brunneo, laevi, transverse 2–5-euseptato, (15–)30–50(–60) µm longo, (3–)4(–5) µm lato, ad apicem cum (1–)2–4(–6) cellulis conidiogenis. Cellulae conidiogenae subcylindricae, allontoides vel doliiformes, rectae vel leviter curvatae, pallide brunneae, 5–8 × 2–2.5 µm, polyblasticae, sympodialiter proliferantes. Conidia hyalina, mucilagine aggregata (sed non catenata), ellipsoidea, apice subobtuso, basi subtruncata, latitudine maxima in parte centrali vel in parte supra centrum, saepe leviter asymmetrica, (3.5–)4(–4.5) × 2(–2.5) µm.

Etymology. Named after the host genus on which the fungus occurs, *Acacia*.

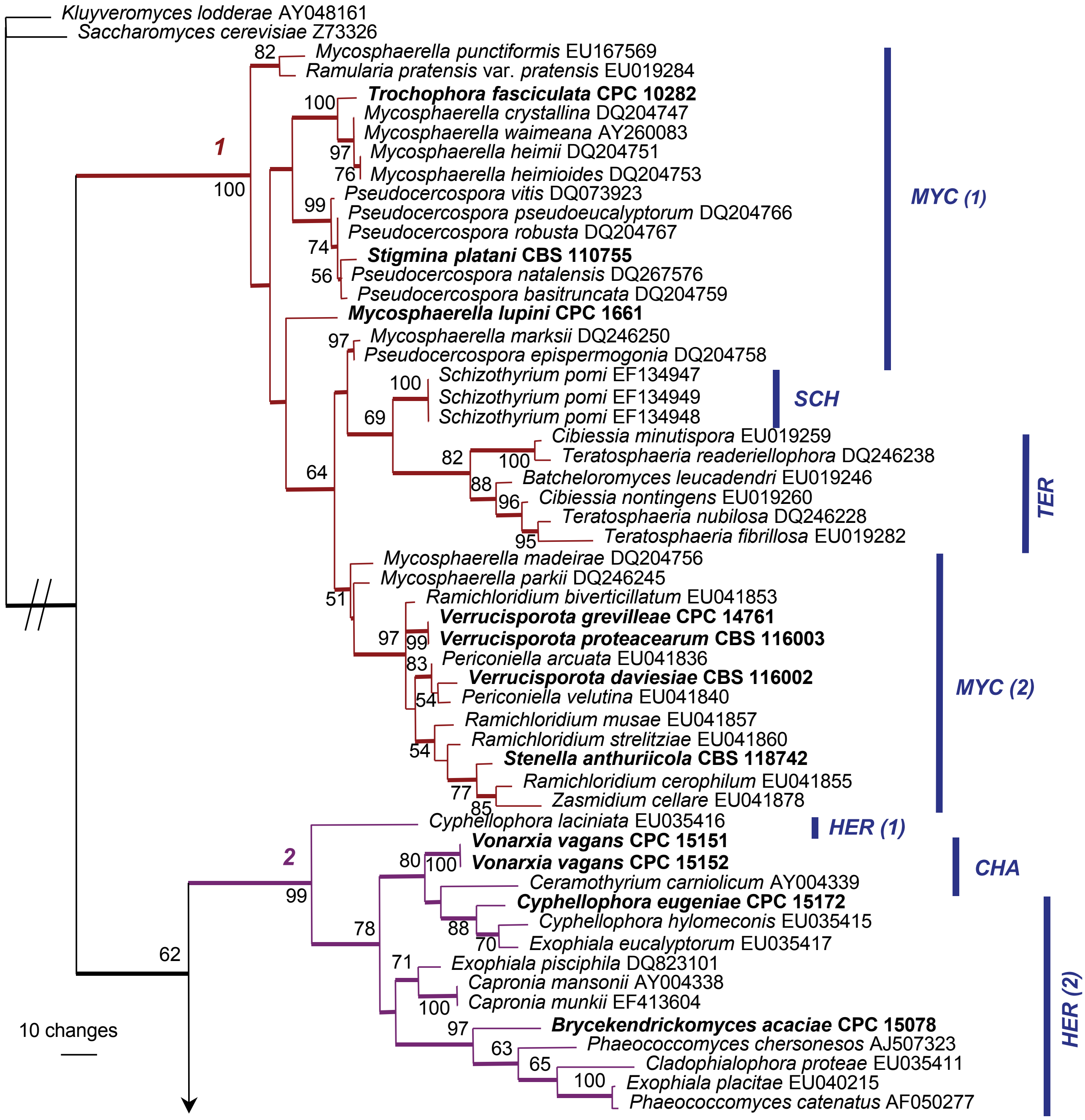


Fig. 1 The first of 1 000 equally most parsimonious trees obtained from a heuristic search with 100 random taxon additions of the LSU sequence alignment. The scale bar shows 10 changes, and bootstrap support values from 1 000 replicates are shown at the nodes. Novel sequences generated for this study are shown in **bold**. Branches present in the strict consensus tree are thickened. Orders and families are coded as indicated in the legends. The tree was rooted to a sequence of *Kluyveromyces lodderae* (GenBank accession AY048161) and *Saccharomyces cerevisiae* (GenBank accession Z73326).
Abbreviations used: **Families**: AMO = *Amorphothecaceae*, CHA = *Chaetothyriaceae*, HEL = *Helotiaceae*, HER = *Herpotrichiellaceae*, HYA = *Hyaloscyphaceae*, IC = Incertae cedis: LEP = *Leptosphaeriaceae*, LOP = *Lophiostomataceae*, MEL = *Melanommataceae*, MYC = *Mycosphaerellaceae*, PHA = *Phaeosphaeriaceae*, PLE = *Pleosporaceae*, PSE = *Pseudeurotiaceae*, RHY = *Rhytismataceae*, SCH = *Schizothyriaceae*, TER = *Teratosphaeriaceae*. **Orders**: 1 = *Capnodiales*, 2 = *Chaetothyriales*, 3 = Incertae cedis, 4 = *Rhytismatales*, 5 = *Helotiales*, 6 = *Hypocreales*, 7 = *Pezizales*, 8 = *Pleosporales*.

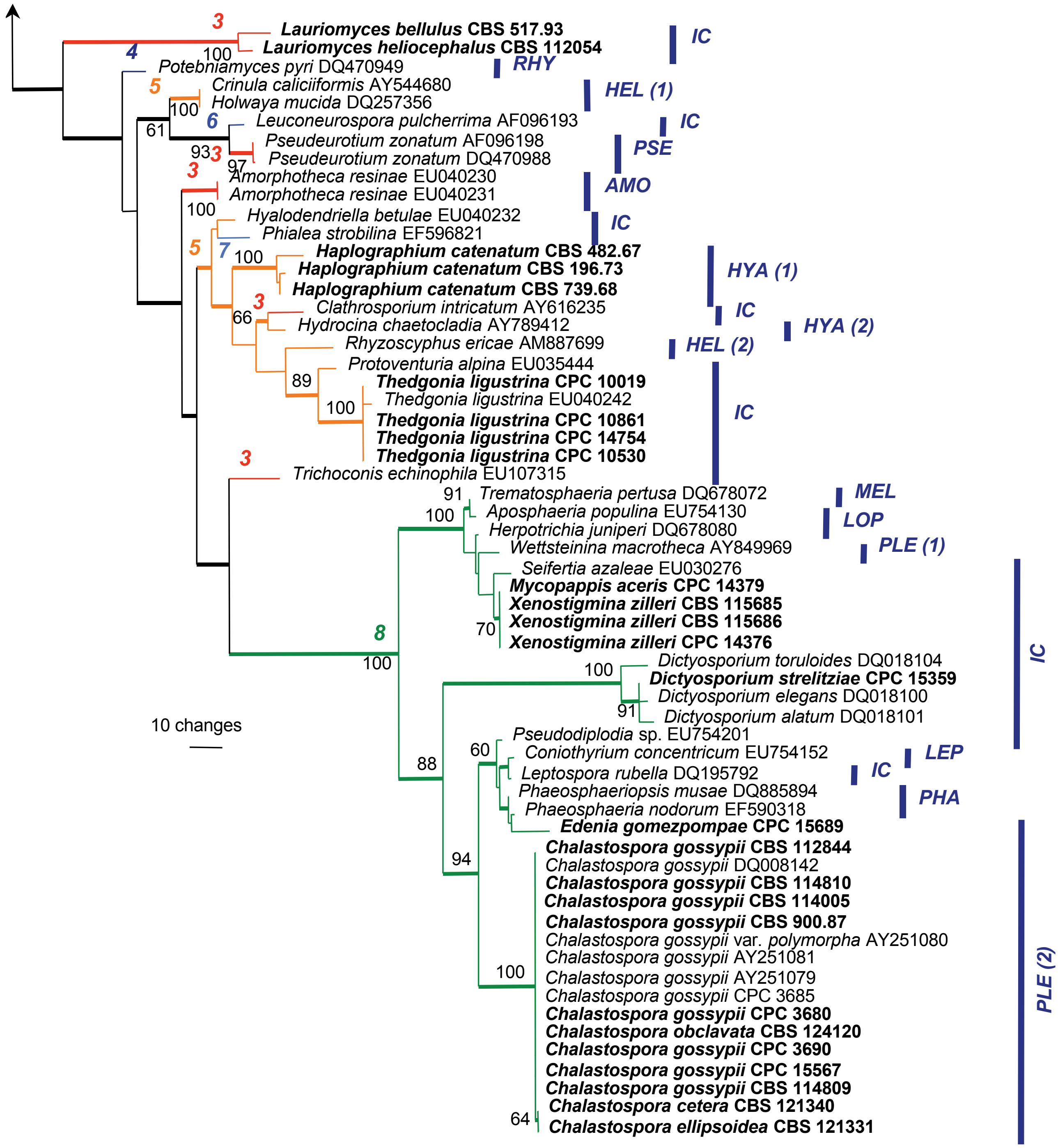
Leaf spots medium to dark brown, margin raised, red-purple, oblong to ellipsoid, up to 7 mm diam, associated with '*Phaeotrichoconis' crotalariae*. Description based on culture on MEA: *Mycelium* consisting of branched, septate, smooth, pale brown, 1–2 µm wide hyphae. *Conidiophores* arising from mycelium, solitary, erect, cylindrical, straight to somewhat flexuous; basal cell bulbous, without rhizoids, 4–6 µm wide in upper part, but becoming 10–15 µm wide at basal part; stalk medium to dark brown, smooth, transversely 2–5-euseptate, (15–)30–50(–60) µm tall, (3–)4(–5) µm wide in the middle part; upper cell giving rise to (1–)2–4(–6) conidiogenous cells. *Conidiogenous cells* subcylindrical to allantoid or doliiform, straight to gently curved, pale brown, 5–8 × 2–2.5 µm; polyblastic, proliferating sympodially. *Conidia* hyaline, aggregating in slimy mass (never in chains), ellipsoid, apex subobtuse, base subtruncate, widest in the middle or upper third of the conidium, frequently somewhat asymmetrical, (3.5–)4(–4.5) × 2(–2.5) µm.

Characteristics in culture — Colonies on MEA erumpent, spreading, with moderate aerial mycelium; surface folded, margin lobate, smooth; surface olivaceous-grey, outer margin iron-grey; reverse iron-grey; colonies reaching up to 20 mm after 1 mo. Colonies fertile on SNA, OA and MEA.

Specimen examined. Indonesia, Pelalawan, living leaves of *Acacia auriculiformis*, Mar. 2008, leg. *M.J. Wingfield*, isol. *P.W. Crous*, holotype CBS H-20198, culture ex-type CPC 15078 = CBS 124104.

Notes — Castañeda & Kendrick (1990) established the genus *Lauriomyces*, characterised by dark brown conidiophores,

Fig. 1 (cont.)



and a series of branches, giving rise to chains of hyaline conidia via sympodial conidiogenesis. *Brycekendrickomyces* is morphologically similar to *Lauriomyces*, which in turn resembles *Haplographium*. The genus *Haplographium* is based on *H. delicatum*. Its confused history is discussed in detail by Zucconi & Pagano (1993). *Haplographium delicatum* was originally described by Berkeley & Broome as having conidia in chains (Mason 1933), which Saccardo (1886) also reported for the type species. Hughes (1958) noted that *Stilbum catenatum* was an older name for *H. delicatum*, which led Holubová-Jechová (1973) to place this species in *Haplographium*, while Castañeda & Kendrick (1990) placed it in *Lauriomyces*. If *Haplographium* and *Lauriomyces* are synonymous, the older name, *Haplographium*, would have preference. However, as shown here, '*Lauriomyces*' *catenatus* is not congeneric with other species of *Lauriomyces*, such as *L. heliocephalus* (Rao & de Hoog 1986, Castañeda & Kendrick 1990) and *L. bellulus* (Crous & Wingfield 1994), suggesting that the two genera are distinct, and that the name *Haplographium catenatum* should be resurrected. Data from this study, furthermore, suggest that the strains of *H. catenatum* included here, probably represent a species complex.

Brycekendrickomyces differs from *Haplographium* and *Lauriomyces* by the absence of an intricate conidiophore branching system, and in having conidia produced in slimy heads rather than in chains. Furthermore, it is not phylogenetically related to species of *Lauriomyces* or *Haplographium* presently known from culture (Fig. 1). *Brycekendrickomyces* is somewhat similar to *Argopericonia* (Sutton & Pascoe 1987), although the latter fungus produces hyaline, apical conidiogenous heads, and it has ellipsoidal, single to short catenate conidia, each with a prominent, globose guttule.

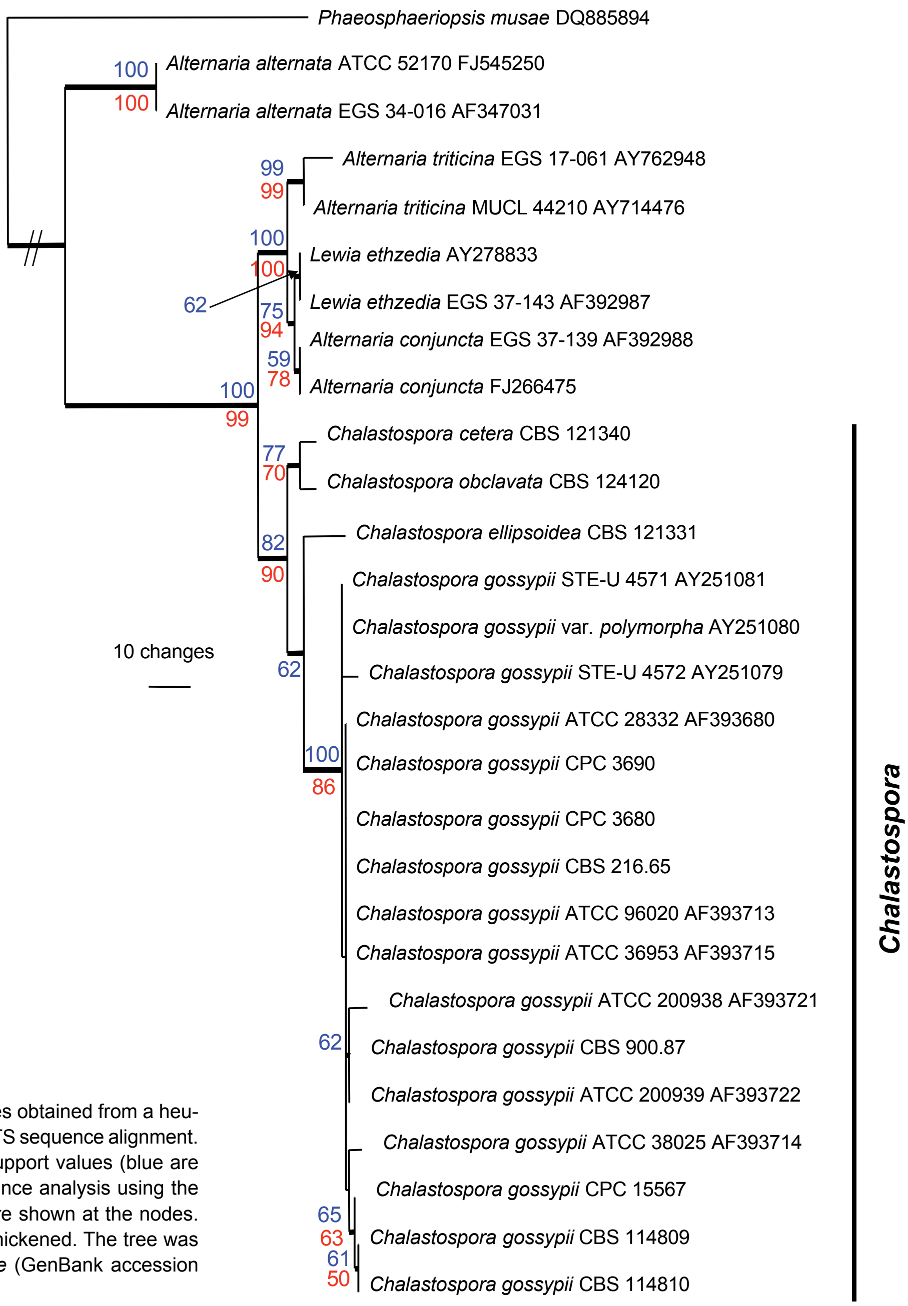


Fig. 2 The first of 6 equally most parsimonious trees obtained from a heuristic search with 100 random taxon additions of the ITS sequence alignment. The scale bar shows 10 changes, and bootstrap support values (blue are from the parsimony analysis and red from the distance analysis using the HKY85 substitution model) from 1 000 replicates are shown at the nodes. Branches present in the strict consensus tree are thickened. The tree was rooted to a sequence of *Phaeosphaeriopsis musae* (GenBank accession DQ885894).

Chalastospora E.G. Simmons, Alternaria. An identification manual: 668. 2007

Type species. Chalastospora cetera (E.G. Simmons) E.G. Simmons.

Conidiophores solitary, brown, smooth, arising from surface hyphae or as short, lateral branches from ropes of aerial hyphae; short, subcylindrical to flask-shaped, 0–2-transversely euseptate, seldom once geniculate or branched. *Conidiogenous cells* integrated, terminal or conidiophores reduced to conidiogenous cells, monotretic, determinate to polytretic, sympodial, conidiogenous loci visible as minute pores, without or with somewhat darkened and slightly thickened rim. *Conidia* in acropetal, branched chains, narrowly ellipsoid to narrowly ovoid, pale to medium brown, rarely 1–3 transversely euseptate, generally lacking longitudinal or oblique septa; conidial apex functioning as secondary conidiophore, proliferating laterally.

Chalastospora gossypii (Jacz.) U. Braun & Crous, *comb. nov.* — MycoBank MB509518; Fig. 4

Basionym. Cladosporium gossypii Jacz., Holopkovoe Delo 1929, 5–6: 564. 1929 and Trudy Byuro Priklad. Bot. 24 (5): 181–182. 1931.

= *Cladosporium malorum* Rühle, Phytopathology 21: 1146. 1931.

≡ *Alternaria malorum* (Rühle) U. Braun, Crous & Dugan, Mycol. Progr. 2: 5. 2003.

= *Phaeoramularia kellermaniana* Marasas & I.H. Bredell, Bothalia 11: 217. 1974.

= *Cladophialophora kellermaniana* (Marasas & I.H. Bredell) U. Braun & Feiler, Microbiol. Res. 150: 83, 1995.

≡ *Pseudocladosporium kellermanianum* (Marasas & I.H. Bredell) U. Braun, A monograph of *Cercosporella*, *Ramularia* and allied genera 2: 393. 1998.

= *Cladosporium porophorum* Matsush., Icones Microfungorum a Matsushima lectorum: 36. 1975.

Characteristics in culture — See Braun et al. (2003).

Specimens examined. Canada, Saskatchewan, Matador, from grass litter, 27 May 1968, *G.C. Bhatt* 255, IMI 144487 = ATCC 38025 = CBS 597.69; from (?) soil, 18 Sept. 1973, *H.A.H. Wallace*, IMI 179345; Alberta, from *Bromus inermis*, 1994, *R.J. Howad* 397, IMI 360655, HAL. – Central Asia (without detailed locality), on fibres of *Gossypium* sp., 1927 and 1928, *V.S. Fedorov*, LEP, syntypes of *Cladosporium gossypii*. – Lebanon, from soil, July 1987, *F. Seigle-Murandi*, ATCC 200938 = CBS 900.87. – Libya, from *Prunus persica*, April 1975, *Casay*, IMI 194863. – New Zealand, Wellington, 40 Epuni Street, Te Aro Valley, wood and wallpaper from inside walls of a dwelling, 5 Sept. 2008, leg. *D. De Vanny*, isol. *C.F. Hill* 2008/3899, CPC 15567; Auckland, Henderson Valley Road, Henderson, leaves of *Anethum graveolens* (dill)

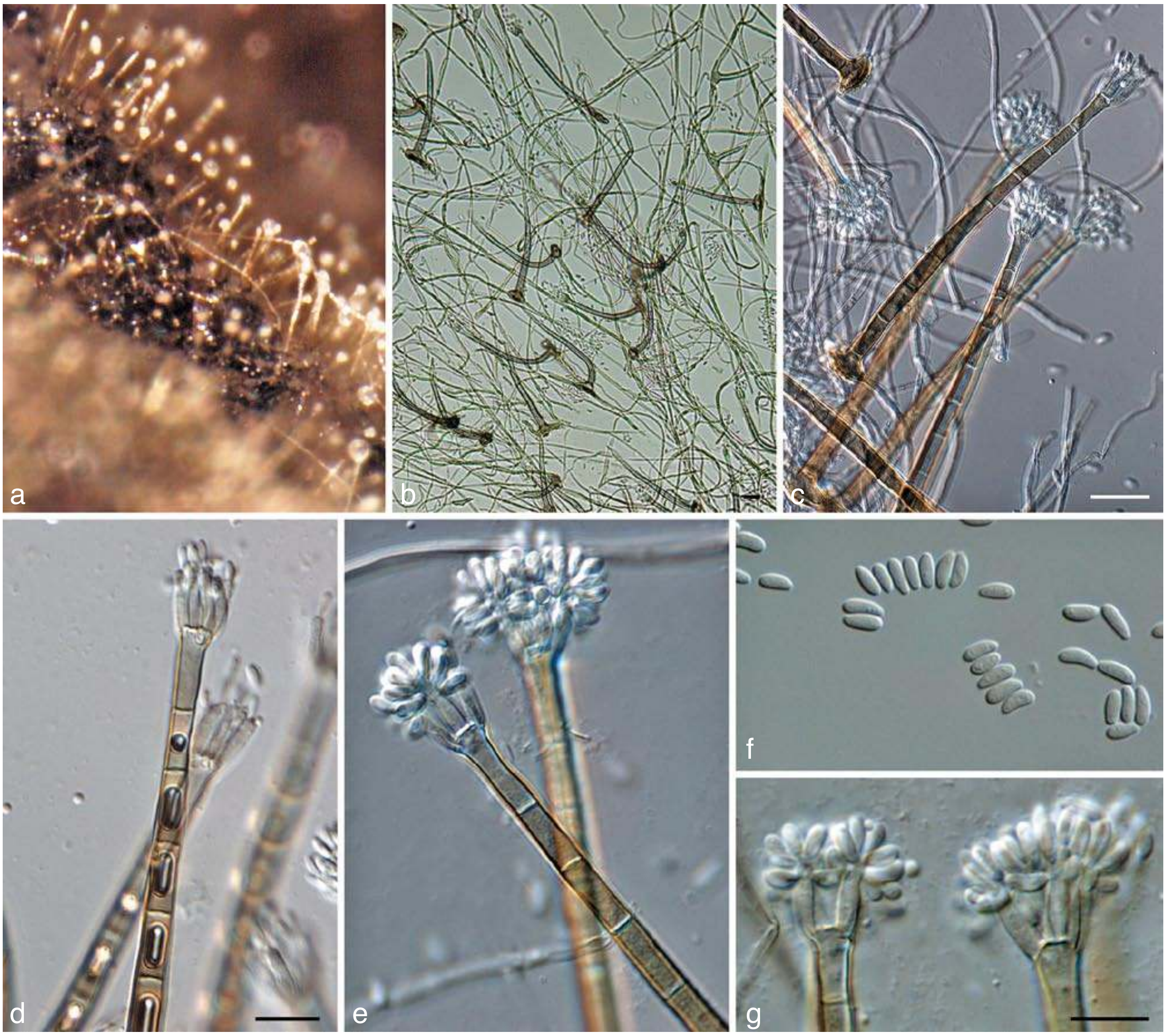


Fig. 3 *Brycekendrickomyces acaciae* (CBS 124104). a. Colonies sporulating on MEA; b. colonies on SNA; c–e, g. conidiophores with conidiogenous apparatus; f. conidia. — Scale bars = 10 µm.

along with *Itersonilia perplexans*, 1 Dec. 2003, leg. *J. Pike*, isol. *C.F. Hill*, MAF 943 = CBS 114809; Auckland, 90 Aberdeen Road, Castor Bay, isolated from *Quercus robur* (oak) leaves in association with *Tubakia dryina*, 5 Sept. 2008, leg. *H. Nettleton*, isol. *C.F. Hill*, MAF 954 = CPC 15567 = CBS 114810. – Pakistan, Karachi, from stored grains, 5 Jan. 1967, *S.S. Hussain*, IMI 124270. – South Africa, Western Cape Province, Kopgat, Calvinia, from wheat stubble, Feb. 1972, *W.F.O. Marasas* OP-76, PREM 44703, IMI 165252, cultures ATCC 28332 = IMI 165252 = PRE 44703 = CPC 3680 = CBS 266.75, ex-type cultures of *Phaeoramularia kellermaniana*. – Syria, from agricultural soil, Feb. 1980, *M.I.A. Abdel-Kader*, CPC 3685 = ATCC 200939 = CBS 173.80. – Turkey, Manisa, from *Hordeum* sp., 16 June 1971, *Maksu & Selçuc*, IMI 159198; *Gossypium* seeds, *M. Esentepe*, CBS 540.75. – USA, New Mexico, Red River, from a polypore on *Picea* sp., 4 Sept. 1996, *D. Wicklow*, IMI 386094; Washington State, from Bing cherry fruit, June 1992, *F.M. Dugan*, ATCC 96020; from fruits of *Malus domestica*, *F.D. Heald*, ATCC 36953; Washington State, *Festuca idahoensis*, F.M. Dugan, STE-U 4572 = CBS 114005; Pacific Northwest, Feb. 1966, *C.W. Hesseltine*, NRRL W 52-29 = CPC 3690 = CBS 148.66; Oregon, Portland, *Triticum aestivum* grain, June 1965, *C.W. Hesseltine*, NRRL A-13702 = CBS 216.65; *Malus sylvestris* fruit, Jan. 1931, *F.D. Head*, ATCC 36953 = MUCL 10096 = CBS 135.31; Washington State, *Bromus tectorum*, *F.M. Dugan*, CPC 4571 = CBS 112844; Washington State, Roza Canal near Prosser, isolated from dormant buds (overwintered) of *Vitis vinifera*, Mar. 2001, *F.M. Dugan*, holotype WSP 70286, cultures ex-type STE-U 4570 = CBS 112048 (var. *polymorpha*). – Uzbekistan, Bukhara, Experiment Station, on fibres of *Gossypium hirsutum*, 1928, *V.S. Zelenetzi*, LEP, lectotype of *Cladosporium gossypii* (selected here) (isolectotype in LEP); Bukhara, Shafrikanskoje, on fibres of *Gossypium hirsutum*, 1928, *V.S. Zelenetzi*, LEP, syntype of *Cladosporium gossypii*.

Notes — The genus *Chalastospora* appears to represent an anamorph lineage in the *Pleosporales* (Fig. 1). *Chalastospora cetera* and *C. gossypii* are clearly congeneric (Fig. 2). Based on the ITS data, there are some point mutations among strains of *C. gossypii*, suggesting that other genes need to be sequenced to fully elucidate the variation within this species (Fig. 2). On SNA, ramoconidia of CBS 114810 were 10–17 × 3–5 µm, and conidia narrowly ellipsoid-ovoid, cylindrical to fusiform, 6–10 × 2–2.5 µm, thus much smaller than that reported by Braun et al. (2003) on PDA. Jaczewski introduced the name *Cladosporium gossypii* in 1929, and provided a brief Russian description, including shape and size of conidia. This description, published before 1935, is, however, valid. In his paper of 1931, he re-introduced *C. gossypii* together with a Latin description and a micrograph of conidia. Type material of *C. gossypii* was re-examined and it is identical to *C. malorum*. However, *C. gossypii* is an older name than *C. malorum*, which was published in 1931, and has priority.

Chalastospora ellipsoidea Crous & U. Braun, *sp. nov*. — MycoBank MB509519; Fig. 5

Chalastosporae gossypii similis, sed conidiis ellipsoideis, longioribus et leviter latioribus, (8–)10–15(–17) × 3(–3.5) µm.

Etymology. Named after its ellipsoid conidia.

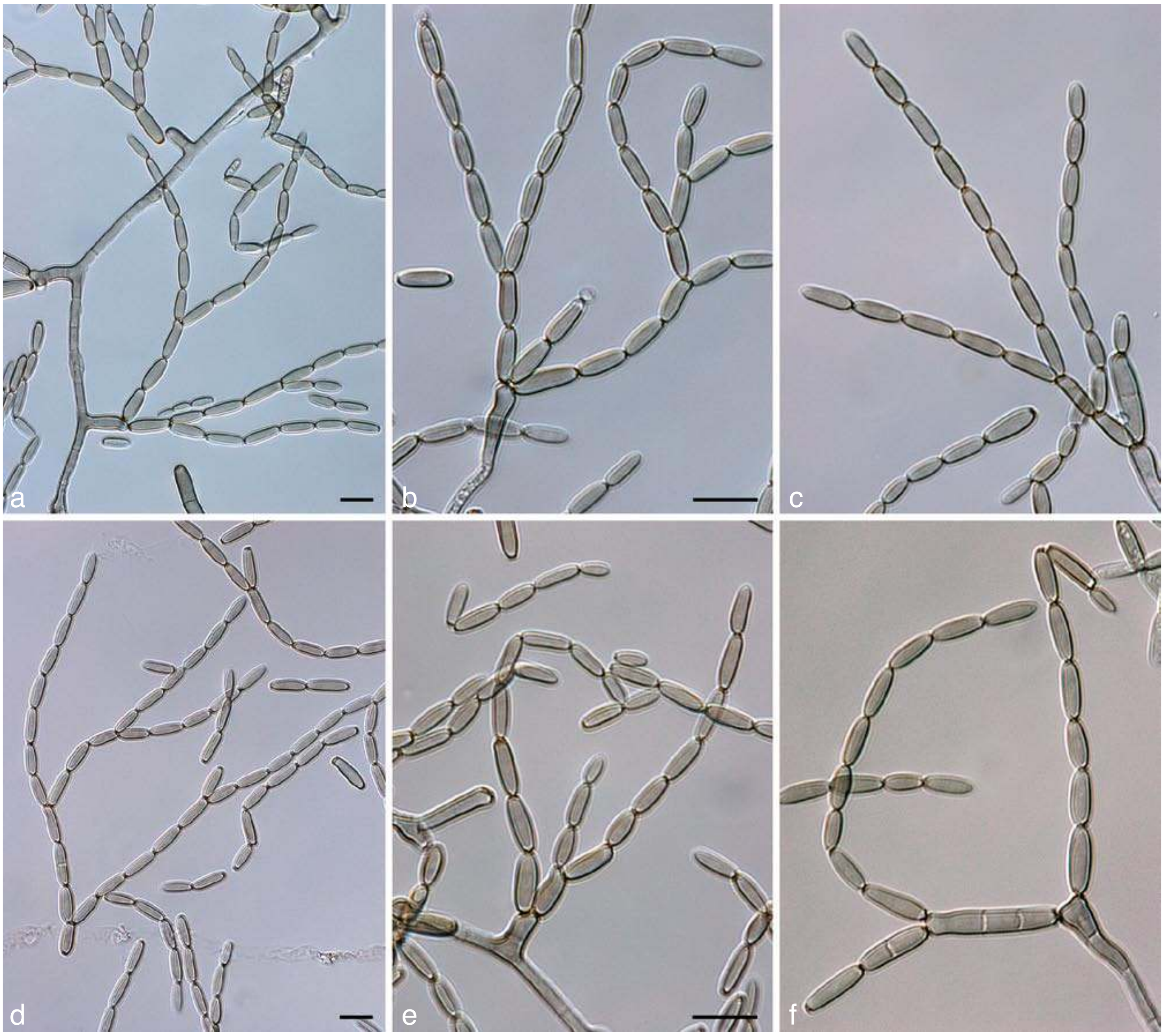


Fig. 4 *Chalastospora gossypii* (CBS 114810). a–f. Superficial mycelium on SNA showing conidiophores with branched conidial chains. — Scale bars = 10 µm.

On SNA: *Conidiophores* arising singly from aerial and creeping hyphae; subcylindrical, erect, medium brown, smooth, up to 25 × 3 µm, frequently reduced to conidiogenous cells, 5–13 × 3 µm; seldom once geniculate, mostly straight, with a slight swelling in the apical conidiogenous region; conidiogenous loci 1–3 per conidiogenous cell, medium brown, slightly thickened, darkened, up to 1 µm wide. *Ramoconidia* (0–)1–3-septate, ellipsoid-ovoid, subcylindrical or fusiform, smooth, medium brown, (12–)15–18(–30) × 3(–4) µm; apex at times with short beak, giving rise to lateral branch. *Conidia* ellipsoid to fusoid, medium brown, smooth, in long acropetal chains, simple, or branched with short apical or basal, lateral branches, (8–)10–15(–17) × 3(–3.5) µm, 0–1(–2)-septate; hila thickened and darkened, 0.5–1 µm wide.

Characteristics in culture — Colonies on OA spreading, with moderate, flattened aerial mycelium, smoke-grey. On MEA cinnamon with patches of hazel on surface and reverse. On PDA olivaceous-grey, with moderate aerial mycelium; iron-grey in reverse.

Specimen examined. Australia, on *Triticum*, *H.L. Harvey & S. Perth*, holotype CBS H-20199, culture ex-type E.G.S. 22.060 = CBS 121331.

Notes — The most characteristic features of this species are its short lateral branches, and ellipsoid conidia. It is clearly distinct from *C. cetera* and *C. gossypii* based on ITS sequence data (Fig. 2).

Chalastospora obclavata Crous & U. Braun, *sp. nov*. — MycoBank MB509520; Fig. 6

Differt ab omnibus specibus *Chalastosporae* conidiis intercalaribus obclavatis.

Etymology. Named after its obclavate conidia.

Sporulating poorly on SNA. *Conidiophores* 17–30 × 3–4 µm, arising singly from aerial and creeping hyphae; subcylindrical, somewhat clavate near apex of conidiogenous region, erect, straight to once geniculate, medium brown, smooth, frequently reduced to conidiogenous cells, 5–10 × 3–4 µm; conidiogenous loci medium brown, slightly thickened, darkened, 1–1.5 µm wide. *Ramoconidia* medium brown, smooth, developing short lateral beaks at apex that give rise to lateral chains (verticillate-like appearance), obclavate, widest at base, 0–3-septate, (28–)30–35 × (3.5–)4–5(–6) µm. *Conidia* obclavate, widest at base, (23–)26–30(–35) × (3.5–)4 µm, 0–3-septate; hila thickened, darkened, 1–1.5 µm wide.

Characteristics in culture — Colonies on OA spreading, with moderate, white aerial mycelium, grey-olivaceous to smoke grey; reverse grey-olivaceous. On MEA cream with dense aerial mycelial mat.

Specimen examined. USA, Kansas, Manhattan, ex air, Jan. 1958, *C.T. Rogerson*, holotype CBS H-20200, culture ex-type E.G.S. 12.128 = CBS 124120.

Fig. 5 *Chalastospora ellipsoidea* (CBS 121331). a–f. Superficial mycelium on SNA showing conidiophores with conidial chains; g, h. microconidiophores; i, j. conidia in chains. — Scale bars = 10 μm.

Notes — The most characteristic features of this species are its conidial branching pattern and conidial shape. This strain was discussed by Simmons under *Alternaria cetera* (Simmons 1996), and under *Chalastospora* in Simmons (2007). It is clearly distinct from *C. cetera* (ex-type CBS 121340, Fig. 7), *C. ellipsoidea* and *C. gossypii* based on ITS sequence data (Table 1, Fig. 2).

KEY TO SPECIES OF *CHALASTOSPORA*[1]

1. Intercalary conidia usually longer than 20 μm 2
1. Intercalary conidia shorter than 20 μm 3

2. Intercalary conidia narrowly ellipsoid to narrowly ovoid, widest in middle or lower third, (10–)19–24(–30) × 3(–4) μm, 0–3-septate . . . . *C. cetera*
2. Intercalary conidia obclavate, widest at base, (23–)26–30 (–35) × (3.5–)4 μm, 0–3-septate . . . . *C. obclavata*

3. Intercalary conidia narrowly ellipsoid-ovoid to cylindrical or fusiform, 6–10 × 2–2.5 μm, mostly aseptate . . *C. gossypii*
3. Intercalary conidia ellipsoid, not cylindrical nor fusiform, (8–)10–15(–17) × 3(–3.5) μm, 0(–2)-septate *C. ellipsoidea*

[1] Colonies cultivated on SNA.

Cyphellophora G.A. de Vries, Mycopathol. Mycol. Appl. 16: 47. 1962

Type species. Cyphellophora laciniata G.A. de Vries.

Hyphae fertile, pale brown, 1.5–3 μm wide, at times constricted at septa. *Conidiogenous cells* phialidic, intercalary, at times on short lateral branches, with a prominent to indistinct collarette. *Conidia* sickle-shaped, brown, smooth-walled, 1–3-septate, adhering in bundles.

Cyphellophora eugeniae Crous & Alfenas, *sp. nov*. — MycoBank MB509521; Fig. 8

Cyphellophorae taiwanensis similis, sed conidiis valde longioribus, (40–)60–75(–90) × 2–2.5(–3) μm.

Etymology. Named after the host on which it occurs, *Eugenia*.

On PDA. *Mycelium* consisting of branched, greenish brown, septate, smooth, 3–5 μm wide hyphae, constricted at septa. *Conidiogenous cells* phialidic, intercalary, inconspicuous to subdenticulate, 1 μm wide, with minute collarettes, with several loci aggregated at hyphal swellings. *Conidia* subcylindrical, tapering towards obtuse ends, curved, smooth, hyaline to olivaceous,

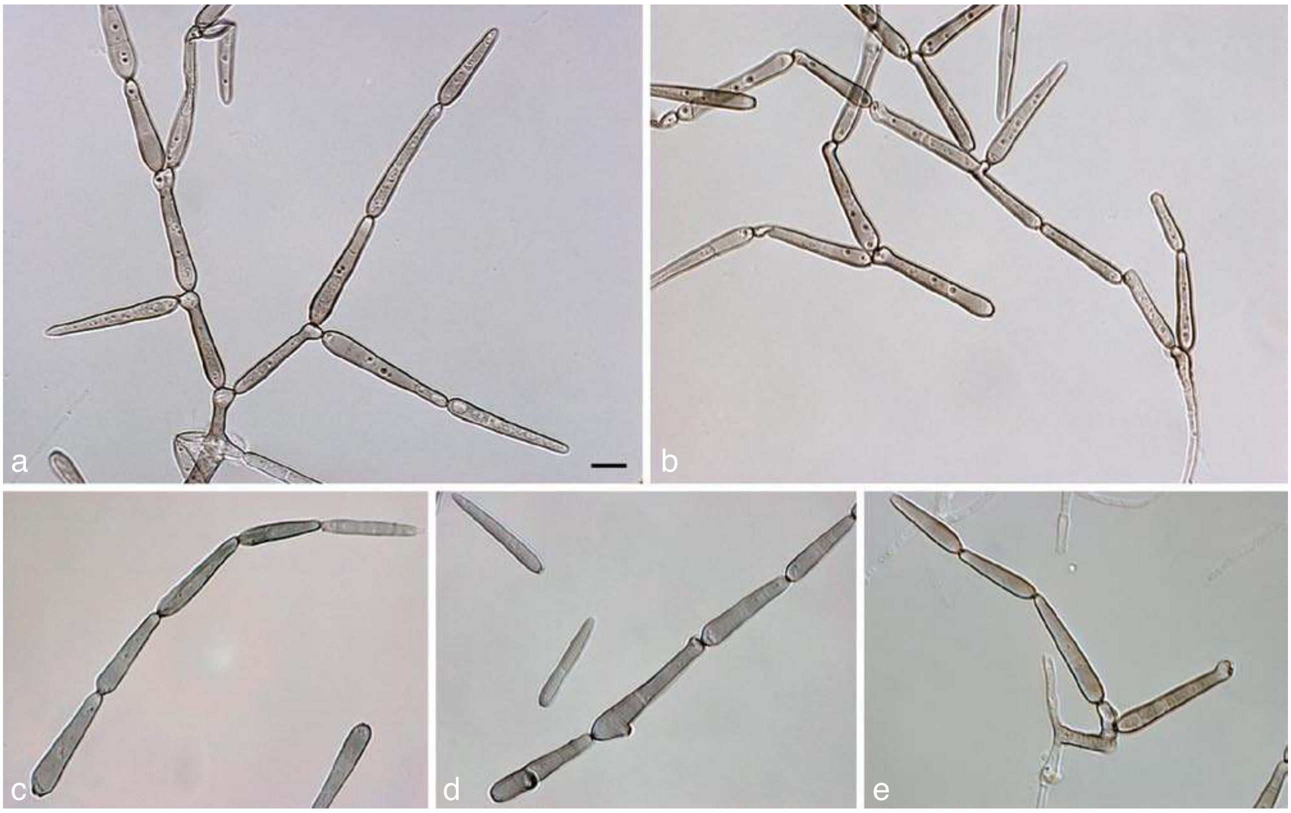


Fig. 6 *Chalastospora obclavata* (CBS 124120). a, b. Superficial mycelium on SNA showing conidiophores with branched conidial chains; c–e. conidia in chains. — Scale bar = 10 µm.

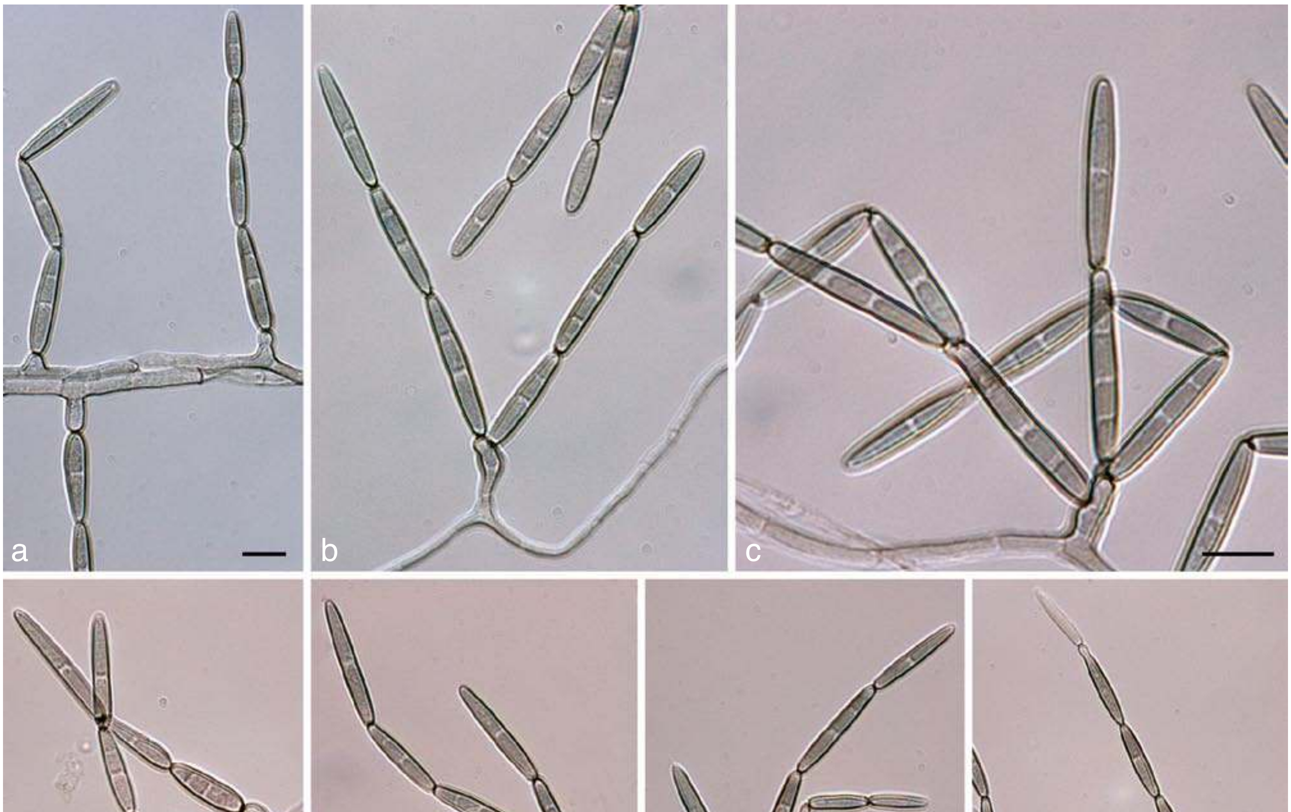


Fig. 7 *Chalastospora cetera* (CBS 121340). a–g. Superficial mycelium on SNA showing conidiophores with conidial chains. — Scale bars = 10 µm.

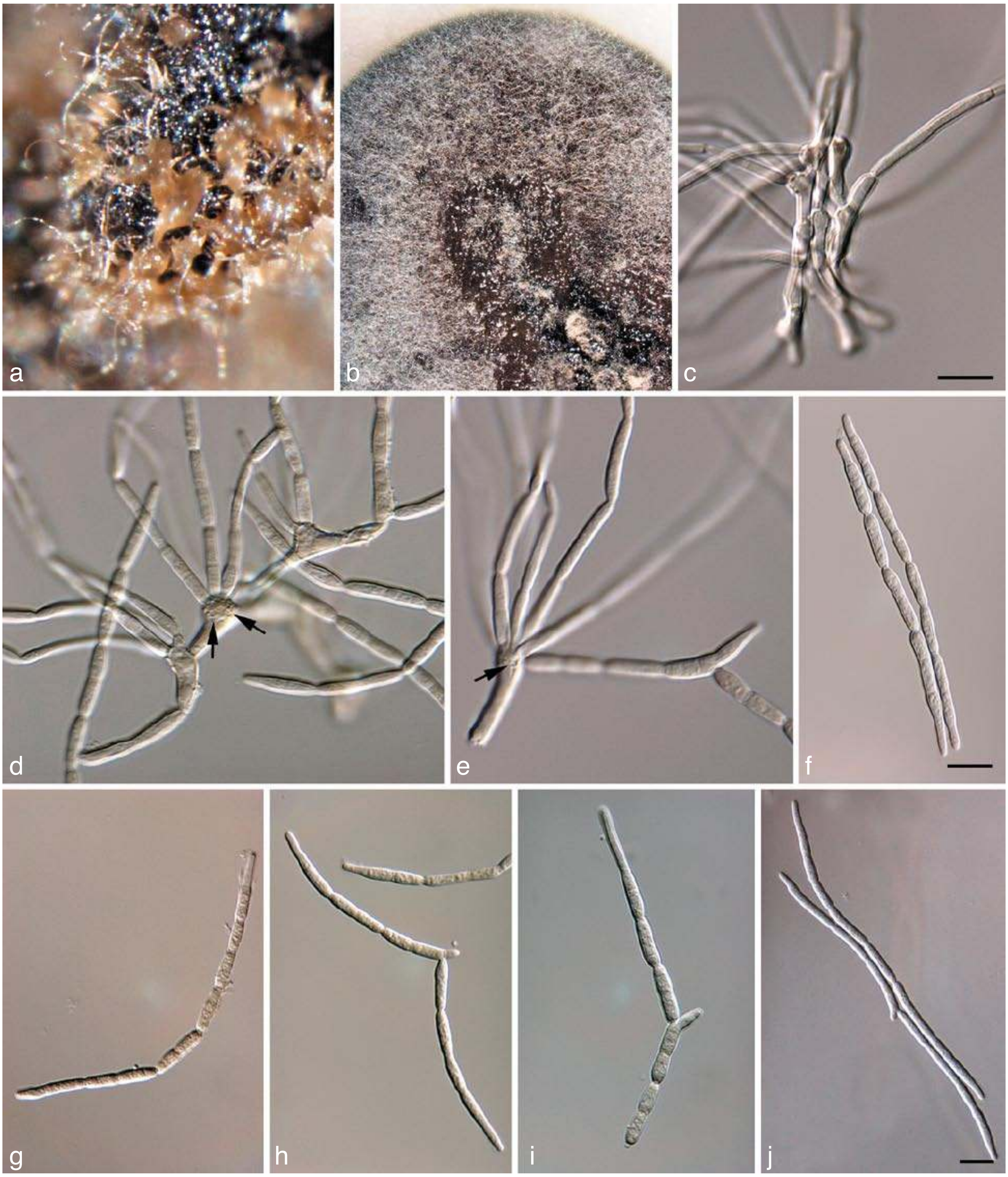


Fig. 8 *Cyphellophora eugeniae* (CBS 124105). a, b. Colonies sporulating on OA; c–e. conidia attached to conidiogenous cells (arrows denote loci); f–j. conidia. — Scale bars = 10 µm.

finely guttulate, 4–6(–10)-septate, prominently constricted at septa, widest in the middle of conidium, (40–)60–75(–90) × 2–2.5(–3) µm; conidia also anastomose and undergo microcyclic conidiation in culture.

Characteristics in culture — Colonies on PDA erumpent, with sparse aerial mycelium and even margins; surface olivaceous-grey, with patches of iron-grey; reverse iron-grey. On MEA erumpent, with folded surface and smooth, lobate margin, and sparse aerial mycelium; surface pale olivaceous-grey to olivaceous-grey; reverse iron-grey. On OA spreading, flat, with even, smooth margins and sparse aerial mycelium, olivaceous-grey. Colonies reaching 15 mm diam after 1 mo at 25 °C, fertile, sporulating in slimy sporodochial masses.

Specimen examined. Brazil, Rio Grande do Sul, Guaiba, living leaves of *Stenocalyx uniflorus*, 1 Apr. 2008, leg. *A.C. Alfenas*, isol. *P.W. Crous*, holotype CBS H-20201, culture ex-type CPC 15172 = CBS 124105.

Notes — The indistinct conidiogenous loci of *C. eugeniae* are reminiscent of those of *C. taiwanensis* (Matsushima 1985). The two species can be distinguished by the much longer conidia in *C. eugeniae*. Based on the key provided by Decock et al. (2003), *C. eugeniae* appears to represent a new species. Further collections of this complex are required to confirm the synonymy of the genera *Cyphellophora* with *Pseudomicrodochium* and *Kumbhayama* (Decock et al. 2003, Crous et al. 2007b), which were originally distinguished based on the absence of conidial pigmentation. The ITS sequence of *C. eugeniae* has 89 % similarity to that of *Cyphellophora hylomeconis* (GenBank accession EU035415).

KEY TO SPECIES OF *CYPHELLOPHORA* (adapted from Decock et al. 2003)

1. Phialides intercalary, reduced to a sessile locus with collarette 2
1. Phialides prominent, cylindrical, flask-shaped, sessile or with an elongated base 6

2. Conidia 1–3-septate 3
2. Conidia usually more than 3-septate 4

3. Conidia up to 2.5 μm wide (11–20 × 2–2.5 μm), 1(–2)-septate . . . . *C. fusarioides*
3. Conidia up to 5 μm wide (11–25 × 2–5 μm), 1–3-septate . . . . *C. laciniata*

4. Conidia up to 2 μm wide, 3–6-septate, sigmoid (16–35 × 1.5–2 μm) . . . . *C. taiwanensis*
4. Conidia wider than 2 μm 5

5. Conidia subcylindrical, 4–6(–10)-septate, (40–)60–75(–90) × 2–2.5(–3) μm . . . . *C. eugeniae*
5. Conidia sigmoid, 1–5-septate, (15–)25–35(–55) × (2.5–)3(–4) μm . . . . *C. hylomeconis*

6. Phialides short to long and cylindrical; conidia 1–1.2 μm wide, 2–3-septate . . . . *C. suttonii*
6. Phialides prominent, flask-shaped, sessile or with an elongated base 7

7. Conidia mainly straight, on average smaller than 20 μm, 1–5-septate . . . . *C. pluriseptata*
7. Conidia straight to more commonly falcate, curved, or sigmoid, on average longer than 20 μm 8

8. Conidia (1–)3-septate, wider than 3 μm, 25–40 × 3.5–5.5 μm; phialides commonly with an elongated base *C. indica*
8. Conidia 2–8-septate, narrower than 3 μm; phialides without elongated base 9

9. Conidia vermiform, mostly curved, mostly 4–8-septate, 30–55 × 1.2–1.5 μm. . . . . *C. vermispora*
9. Conidia straight, falcate or slightly sigmoid, (2–)3–6-septate, (18–)19.5–28(–29) × 1.5–2 μm . . . . *C. guyanensis*

Dictyosporium Corda, in Weitenweber, Beitr. Gesammten Natur-Heilwiss., Prag 1: 87. 1836

Type species. *Dictyosporium elegans* Corda.

Conidiomata sporodochial, black, scattered. *Mycelium* predominantly immersed, consisting of branched, septate, smooth, thin-walled hyphae. *Conidiophores* micronematous, mononematous, pale brown, smooth to finely verruculose, thin-walled, septate, cylindrical. *Conidiogenous cells* monoblastic, integrated, pale to medium brown, smooth to finely verruculose, cylindrical, determinate; at times remaining attached to released conidium. *Conidia* cheiroid, medium to dark brown, smooth, euseptate, one cell-layer thick, cells arranged in 1–2 planes, fan-shaped; cell rows originating from a central basal cell; rows usually attached along their length; outer rows usually shorter than inner rows, at times paler in colour than central rows, and with or without hyaline, thin-walled, 1–2-celled appendages that are allantoid, clavate to globose, or fusoid to cylindrical.

Dictyosporium strelitziae Crous & A.R. Wood, *sp. nov*. — MycoBank MB509522; Fig. 9

Dictyosporii bulbosi valde simile, sed conidiis leviter longioribus, (30–)40–46(–55), et phylogenetice manifeste divergens.

Etymology. Named after the host genus *Strelitzia*, on which it occurs.

Leaf spots absent, colonies occurring on dead leaf tissue. Description based on colonies sporulating on WA with pine nee-

Fig. 9 *Dictyosporium strelitziae* (CBS 123359). a. Colony sporulating on PDA; b, c. conidia attached to conidiogenous cells; d–h. conidia with hyaline, apical appendages. — Scale bars = 10 μm.

dles (colonies also sporulate well on OA and MEA): *Mycelium* predominantly internal in host tissue, consisting of branched, septate, smooth, brown, 2–2.5 µm wide hyphae. *Conidiomata* sporodochial, scattered, black, up to 170 µm diam. *Conidiophores* subcylindrical, darker brown than hyphae, at times slightly verruculose, irregularly curved to geniculate-sinuous, 1–3-septate, 10–25 × 2–2.5 µm; older conidiophores curved like sheperd's crook. *Conidiogenous cells* terminal, medium brown, verruculose, subcylindrical, curved (semi-circular), 5–10 × 2–2.5 µm. *Conidia* solitary, complanante, cheiroid, smooth-walled, uniformly pale brown, becoming uniformly medium brown at maturity; cells arranged in (4–)5(–6) rows, meeting at basal cell; outer rows with 8–10 cells, with a hyaline, globose, apical appendage, 5–10 µm diam; outer rows shorter than inner rows; inner rows with 7–11 cells; central row with 6–10 cells; conidia (30–)40–46(–55) × (20–)21–23(–25) µm.

Characteristics in culture — *Colonies* on OA flat, spreading, without aerial mycelium, and with regular, even margin; on MEA flat, spreading, with moderate aerial mycelium and regular, smooth margin; surface buff, reverse cinnamon; colonies on both media reaching 30 mm diam after 1 mo at 25 °C.

Specimen examined. South Africa, KwaZulu-Natal, Skyline Nature Reserve, Uvongo, on dead leaves of *Strelitzia nicolai*, 29 May 2008, leg. *A. Wood*, isol. *P.W. Crous*, CBS H-20202 holotype, cultures ex-type CPC 15359–15361, CBS 123359.

Notes — The genus *Dictyosporium* is well defined, and separated from similar genera by having smooth-walled, euseptate conidia produced from determinate conidiogenous cells (Sutton et al. 1996, Tsui et al. 2006). Based on the key provided by Cai et al. (2003b), *D. strelitziae* is morphologically most similar to *D. bulbosum* (conidia 27–46 × 11–30 µm), but its conidia are somewhat longer, and there is a 10 bp difference between the ITS sequences of *D. strelitziae* and *D. bulbosum* (DQ018086). Phylogenetically, *D. strelitziae* is closest to *D. elegans* (conidia 44–80 × 24–36 µm; appendages absent) (5 bp difference in the ITS sequence, DQ018087), but it has smaller conidia than the latter species. Furthermore, it also appears distinct from all species not occurring in the key of Cai et al. (2003b) (Arambarri et al. 2001, Cai et al. 2003a, Zhao & Zhang 2003, Kodsueb et al. 2006, Cai & Hyde 2007, McKenzie 2008).

KEY TO SPECIES OF *DICTYOSPORIUM* (adapted from Cai et al. 2003b)

1. Conidia with appendages 2
1. Conidia lacking appendages 13
2. Appendages apical 3
2. Appendages not apical 4
3. Apical appendages aseptate 6
3. Apical appendages frequently 1-septate, cylindrical, 24–51 × 6–10.5 µm; conidia 27.5–47.5 × 20–25 µm, complanate, with 4–5 rows of cells . . . . *D. canisporum*
4. Appendages subapical, cylindrical to clavate; conidia 52.5–72.5 × 18.5–26.5 µm, not complanate, with 5 rows of cells . . . . *D. tetraploides*
4. Appendages not subapical, but central or basal 5
5. Appendages central, hyaline, thin-walled, clavate to obovoid; conidia 36–45 × 16–21 µm, not complanate, mostly 7 rows of cells . . . . *D. musae*
5. Appendages basal, fusoid to cylindrical; conidia 22–28 × 12.5–18 µm, complanate, with 3 rows of cells . . *D. manglietiae*
6. Conidia with 3 rows of cells, (27–)31–43 × 10–12 µm . . . . *D. freycinetiae*
6. Conidia with more than 3 rows of cells 7
7. Conidia mostly with 4 rows of cells 8
7. Conidia with 5 or more rows of cells 10
8. Conidia with darker colour at apex of inner rows; apical cells of outer rows each bearing a hyaline, cylindrical appendage . . . . *D. nigroapice*
8. Conidia concolorous 9
9. Conidia 24–40 × 14–20 µm; appendages clavate . . . . *D. tetraseriale*
9. Conidia 36–45 × 16–21 µm; appendages tapering . . . . *D. palmae*
10. Conidia mostly comprising 5 rows of cells 11
10. Conidia mostly comprising 6–8 rows, 46–88 × 26–46 µm; appendages hyaline, curved . . . . *D. digitatum*
11. Conidia longer than 32 µm, appendages globose to obovoid 12
11. Conidia shorter than above, 26–32 × 15–24 µm; appendages cylindrical to clavate . . . . *D. alatum*
12. Conidia up to 46 µm long, and 30 µm wide, 27–46 × 11–30 µm; appendages globose to obovoid . . . . . *D. bulbosum*
12. Conidia longer than 46 µm, but not wider than 25 µm, (30–)40–46(–55) × (20–)21–23(–25) µm; appendages globose . . . . *D. strelitziae*
13. Conidia complanate, one cell layer thick 14
13. Conidia not complanate, more than one cell layer thick 24
14. Conidia regularly consisting of 3 rows of cells 15
14. Conidia consisting of at least 4 rows of cells 16
15. Conidia 15–22.5 × 10–16.5 µm . . . . *D. lakefuxianensis*
15. Conidia 26–32 × 16–18 µm . . . . *D. triseriale*
16. Conidia curved, with 5–7 rows of cells, each curving in the same direction, 34–56 × 20–38 µm . . . . *D. foliicola*
16. Conidia not curved 17
17. Conidia less than 25 µm long 18
17. Conidia more than 25 µm long 19
18. Conidia 18–24 × 13–19 µm . . . . . . *D. brahmaswaroopii*
18. Conidia 15–17 × 11–12 µm . . . . . . *D. schizostachyfolium*
19. Conidia with paler outer rows 20
19. Conidia concolorous 21
20. Conidia 25–45 × 22–38 µm, with (5–)6(–7) rows . . . . *D. yunnanensis*[1]
20. Conidia 26–40 × 13–25 µm, mostly with 5 rows . . . . *D. zeylanicum*
21. Conidia with 4 rows, 23.5–40 × 16–21.5 µm . . . . *D. tetrasporum*
21. Conidia with more than 4 rows 22
22. Conidia 40–80 × 24–36 µm, mostly with 5 rows, slightly constricted at septa . . . . *D. elegans*
22. Conidia mostly with more than 5 rows, strongly constricted at septa 23
23. Conidia 26–34 × 23–34 µm, mostly with 7–9 rows of cells; conidiomata sporodochial . . . . *D. polystichum*
23. Conidia 38–56 × 25–32 µm, mostly 6–8 rows of cells; conidiomata not sporodochial . . . . *D. toruloides*
24. Conidia campaniform, with a darker base; with 12–16 rows of cells, 22–40 × 20–30 µm . . . . *D. campaniforme*
24. Conidia more or less cylindrical, concolorous, comprising 3–7 rows of cells 25
25. Conidia regularly with 3 rows of cells; usually 13.5 µm or less wide 26
25. Conidia mostly with 4–7 rows of cells; more than 13.5 µm wide 28

[1] Appearing morphologically similar to *D. taishanensis*, also described from China; conidia with (3–)5(–7) cell layers, 27–43 × 15–30 µm (Zhao & Zhang 2003). *Dictyosporium taishanensis* (22 February 2003) is older than *D. yunnanensis* (March 2003), and would have priority if these fungi are shown to be synonymous.

26. Conidia 40–60 × 10–13.5 µm . . . . *D. triramosum*
26. Conidia shorter than 43 µm 27
27. Conidia 36–43 × 11–12 µm; sporodochia usually covered with gelatinous matrix . . . . *D. australiense*
27. Conidia 20–30 × 10–12 µm; sporodochia not as above . . . . *D. micronesicum*
28. Conidia 40–50 × 18–25 µm, with 4–6 rows of cells, muriform, with hyaline, subglobose conidiogenous cell remaining attached as basal appendage . . . . *D. gauntii*
28. Conidial morphology not as above 29
29. Conidia with rows of cells that are distinctly incurved or hook-like at the apex 30
29. Conidia with more or less straight rows of cells at the apex 32
30. Conidia 105–121 × 25–32 µm . . . . *D. giganticum*
30. Conidia up to 80 µm long 31
31. Conidia 50–80 × 20–30 µm . . . . *D. heptasporum*
31. Conidia 33–42 × 16–20 µm . . . . *D. subramanianii*
32. Colonies effuse, not sporodochial; conidia irregularly cylindrical or oblong, strongly constricted at septa; 30–50 × 12–30 µm . . . . *D. oblongum*
32. Colonies sporodochial; conidia more or less cylindrical, slightly constricted at septa, 53–76 × 19–22 µm . . . . *D. cocophilum*

Edenia M.C. González, Anaya, Glenn, Saucedo & Hanlin, Mycotaxon 101: 254. 2007.

Type species. *Edenia gomezpompae* M.C. González, Anaya, Glenn, Saucedo & Hanlin.

Conidiophores fasciculate, subcylindrical, medium brown, finely roughened, 3–15-septate, straight to variously curved or geniculate-sinuous, irregular in width, constricted at some septa, with percurrent rejuvenation in upper part, situated on a submerged, brown stroma. *Conidiogenous cells* terminal, integrated, becoming paler brown towards apex, tapering to a subtruncate tip, with several lateral loci that are somewhat thickened and protruding (pimple-like), giving rise to conidia

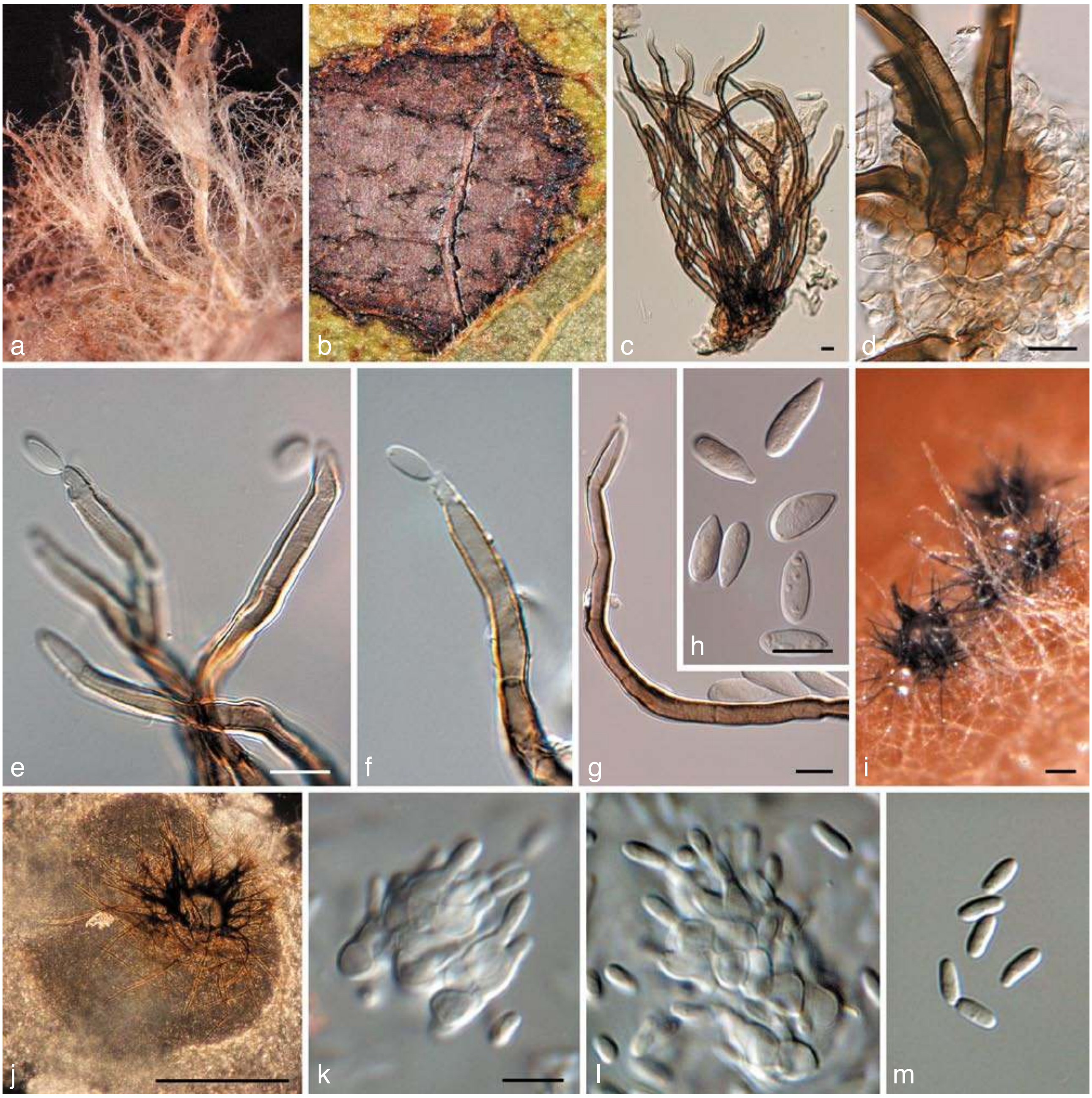


Fig. 10 *Edenia gomezpompae* (CBS 124106). a. Hyphal tufts visible when cultivated on MEA; b. leaf spot with conidiophores; c. fasciculate conidiophores; d. conidiophores arising from conidioma; e–g. conidiophores and conidiogenous cells; h. conidia; i. conidiomata forming on OA; j. conidioma with ostiolar setae; k, l. conidiogenous cells; m. conidia. — Scale bars = 10 µm.

via sympodial proliferation near apex. *Conidia* 11–16 × 3.5–6 µm, subhyaline, smooth, thin-walled, finely guttulate, fusoid-ellipsoidal with obtuse apex and tapering from its widest point in the middle towards a subtruncate base, 1–1.5 µm wide.

Edenia gomezpompae M.C. González, Anaya, Glenn, Saucedo & Hanlin, Mycotaxon 101: 254. 2007 — Fig. 10

Leaf spots subcircular, 3–12 mm diam, grey-brown, with a dark brown, raised border, surrounded by a diffuse, black halo (absent in smaller spots). *Conidiophores* in fascicles of 5–30, subcylindrical, medium brown, finely roughened, 3–15-septate, straight to variously curved or geniculate-sinuous, 50–170 × 4–6 µm, irregular in width, constricted at some septa, with percurrent rejuvenation in upper part; fascicles randomly distributed over lesion, amphigenous, visible as erect, dark brown to black tufts on lesions, situated on a submerged, brown stroma, up to 60 µm wide and 40 µm high, intermingled among leaf trichomes (fruiting structures of a *Ramularia* sp. and ascomata of another fungus also present in some lesions). *Conidiogenous cells* 15–30 × 3–4 µm, terminal, integrated, becoming paler brown towards apex, tapering to a subtruncate tip, with several lateral loci that are somewhat thickened and protruding (pimple-like), up to 1 µm diam, giving rise to conidia via sympodial proliferation near apex, but some conidiogenous cells also show signs of percurrent proliferation, but this appears to be linked to rejuvenation, not conidiogenesis. *Conidia* (11–)13–15(–16) × (3.5–)4.5–5.5(–6) µm, subhyaline, smooth, thin-walled, finely guttulate, fusoid-ellipsoidal with obtuse apex and tapering from its widest point in the middle towards a subtruncate base, 1–1.5 µm wide.

Characteristics in culture — Colonies fluffy, with white hyphal strands that turn brown with age; surface woolly with abundant aerial mycelium; margins uneven. On MEA buff to rosy-buff (surface), brick to dark brick (reverse); on PDA fluffy, cream to buff (surface), dark brick to buff (reverse); on OA brick with patches of cream to buff. Colonies reaching 25 mm diam after 2 wk at 25 °C, becoming fertile on OA.

Specimens examined. Mexico, Quintana Roo, Isla Mujeres Municipality, El Eden Ecological reserve, from leaves of *Callicarpa acuminata* (*Lamiaceae*), May 2002, *A. Saucedo-García* & *A.L. Anaya*, holotype MEXU 25346. – Philippines, on *Senna alata* (≡ *Cassia alata*) (*Caesalpiniaceae*), Oct. 2008, leg. *C.J.R. Cumagun*, isol. *P.W. Crous*, epitype designated here CBS H-20203, cultures CPC 15689 = CBS 124106, CPC 15690, 15691.

Notes — The genus *Edenia* was originally introduced for a sterile fungus (suspected to be a member of the *Pleosporaceae*), isolated as an endophyte from leaves of *Callicarpa acuminata* in Mexico (González et al. 2007). The genus was characterised by producing numerous sterile, whitish mycelial strands and coils on PDA. The present collection from *Cassia alata* in the Philippines has the same colony characteristics, and based on its identical DNA sequence data (GenBank EF565744.1), we believe that this is the same fungus. What is interesting, however, is the fact that the latter collection was made from conidia of a dematiaceous hyphomycete sporulating on leaf spots of *C. alata*. As other fungi were also present on these spots, its potential role as pathogen remains uncertain. On host tissue, however, some conidiophores were associated with a weakly developed layer of pale brown stromatic cells. On OA, cultures became fertile, and conidiophores were arranged around well-developed ostioles of submerged pycnidia (with a similar pale brown stromatic wall to that observed on the host). It is possible, therefore, that if the field material had been placed in moist chambers, the pycnidial state would have developed. The latter state resembles species that are pyronellea-like in morphology. Morphologically, the hyphomycete state of *Edenia* resembles genera such as *Digitopodium*, although species of this genus have rhizoids, and 1-septate, pale brown conidia that can also occur in short chains (Heuchert et al. 2005). It also shares some similarities with *Blastophorum* (Matsushima 1971), although the latter fungus is distinct in having solitary conidiophores with rhizoids, and a hyaline, upper conidiogenous region.

Thedgonia B. Sutton, Trans. Brit. Mycol. Soc. 61: 426. 1973

Type species. *Thedgonia ligustrina* (Boerema) B. Sutton.

Conidiomata fasciculate, punctiform. *Mycelium* internal, hyphae subhyaline, septate, branched, forming substomatal stromata, hyaline to pale brown. *Conidiophores* fasciculate, arising from stromata, simple, rarely branched, subcylindrical, straight to geniculate-sinuous, continuous to septate, smooth, hyaline to pale yellowish green. *Conidiogenous cells* integrated, terminal, occasionally conidiophores reduced to conidiogenous cells, sympodial, conidiogenous loci more or less planate, unthickened, non-pigmented. *Conidia* in disarticulating chains, rarely in branched chains, subcylindrical to obclavate, with one to several transverse eusepta, hyaline or almost so, apex rounded to truncate, base truncate, hila flat, unthickened, hyaline.

Thedgonia ligustrina (Boerema) B. Sutton, Trans. Brit. Mycol. Soc. 61: 428. 1973 — Fig. 11

Basionym. *Cercospora ligustrina* Boerema, Tijdschr. Plantenziekten 68: 117. 1962.

≡ *Cercoseptoria ligustrina* (Boerema) Arx, Genera of Fungi Sporulating in Pure Culture, ed. 3: 306, Lehre 1981.

Characteristics in culture — On MEA erumpent, slow growing, 5–8 mm after 2 wk, with moderate, white aerial mycelium and smooth, lobate margins; umber in reverse. On OA 5–8 mm diam after 2 wk, submerged to flattened on surface, sparse aerial mycelium, and smooth, even margins; umber on surface.

Specimens examined. Asia, on *Ligustrum* sp., *H. Evans*, CPC 4296 = W2072, CPC 4297 = W 2073, CPC 4298 = W 1877. – Netherlands, Eefde, on *Ligustrum ovalifolium*, 23 Mar. 1959, *G.H. Boerema*, holotype L, ex-type culture CBS 148.59; Bilthoven, on *L. ovalifolium*, 2003, *P.W. Crous*, CPC 10530 = CBS 124332, CPC 10532, 10533. – South Korea, Namyangju, on *L. ovalifolium*, 9 Oct. 2002, leg. *H.D. Shin*, isol. *P.W. Crous*, CBS H-20204, CPC 10019, 10861–10863; Suwon, on *L. obtusifolium*, 2 Oct. 2007, leg. *H.D. Shin*, isol. *P.W. Crous*, CBS H-20207, CPC 14754–14756.

Notes — Kaiser & Crous (1998) linked '*Thedgonia*' *lupini* as anamorph to *Mycosphaerella lupini*, and thus suggested that *Thedgonia* belongs in the *Mycosphaerellaceae*. Results of this study (Fig. 1), however, show that *Thedgonia* s.str. belongs to the *Helotiales*, and is unrelated to the *Mycosphaerellaceae*. Furthermore, there is presently no separate anamorph genus in the *Mycosphaerellaceae* to accommodate '*T.' lupini*. Although '*T.' lupini* resembles species of *Pseudocercosporella* (Braun 1995), it appears to represent a separate phylogenetic lineage.

Trochophora R.T. Moore, Mycologia 47: 90. 1955

Type species. *Trochophora fasciculata* (Berk. & M.A. Curtis) Goos (syn. *T. simplex* (Petch) R.T. Moore).

Colonies hypophyllous, medium to dark brown, consisting of numerous synnemata. *Stroma* absent, but a superficial network of hyphae linking the various synnemata. *Conidiophores* synnematous, mostly unbranched and straight, or with 1–2 short branches, straight or curved, cylindrical, individual conidiophores tightly aggregated, but separating near the apex, pale to medium brown, smooth. *Conidiogenous cells* polyblastic, integrated, terminal, determinate to sympodial, with visible

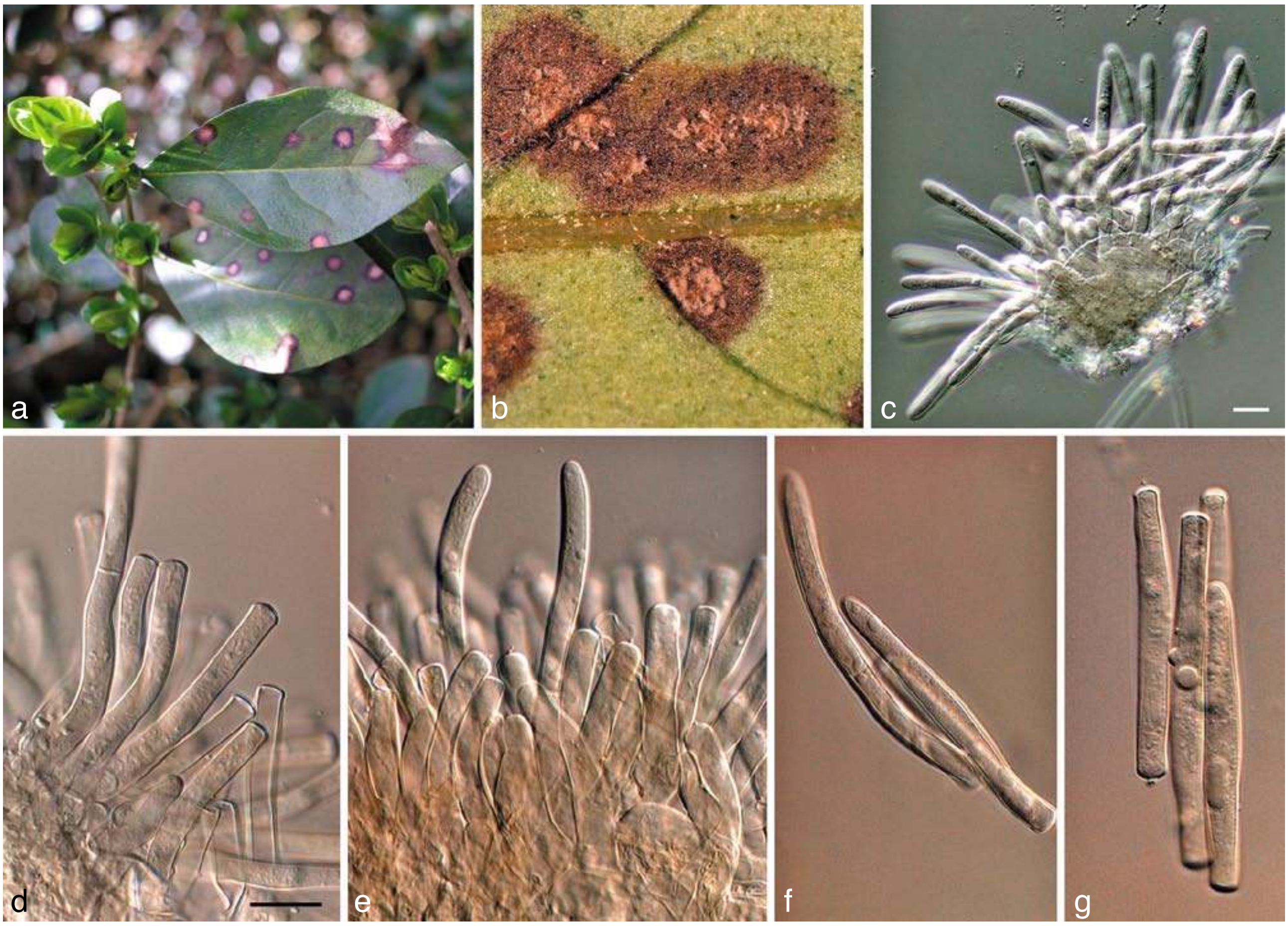


Fig. 11 *Thedgonia ligustrina* (CBS 124332). a, b. Leaf spots on *Ligustrum*; c. fasciculate conidiophores; d, e. conidiophores; f, g. conidia. — Scale bars = 10 µm.

unthickened scar, clavate. *Conidia* solitary, terminal or lateral on conidiogenous cells, prominently curved to helicoid, pale to medium brown, smooth, transversely septate with a darkened, thickened band at the septa.

Trochophora fasciculata (Berk. & M.A. Curtis) Goos (as '*fasciculatum*'), Mycologia 78: 759. 1986 — Fig. 12

Basionym. *Helicoma fasciculatum* Berk. & M.A. Curtis, U.S. North Pacific Exped.: 142. (1853–1856) 1853.

≡ *Helicosporium fasciculatum* (Berk. & M.A. Curtis) Sacc., Syll. fung. 4: 560. 1886.

≡ *Helicomyces fasciculatus* (Berk. & M.A. Curtis) Pound & Clem., Minnesota Bot. Stud. 1: 658. 1896.

= *Helicosporium simplex* Syd., Mém. Herb. Boissier 4: 7. 1900.

≡ *Helicoma simplex* (Syd.) Linder, Ann. Missouri Bot. Gard. 16: 315. 1929.

= *Helicostilbe simplex* Petch, Ann. Roy. Bot. Gard. Peradeniya 7: 321. 1922.

≡ *Trochophora simplex* (Petch) R.T. Moore, Mycologia 47: 90. 1955.

Specimen examined. Korea, Pusan, on leaves of *Daphniphyllum macropodum*, 13 Nov. 2002, leg. *H.D. Shin*, isol. *P.W. Crous*, KUS-F19414, cultures CPC 10280–10282.

Notes — Two species have been described in the genus, namely *T. fasciculata* and *T. simplex*; the latter recognised as a synonym of the former (Zhao et al. 2007). Within the *Mycosphaerellaceae*, pseudocercospora-like species cluster in two well-defined clades, namely the *P. vitis* clade (*Pseudocercospora* s.str.), and the *P. heimii* clade (pseudocercospora-like). Based on LSU DNA phylogeny (Fig. 1), *Trochophora* clusters basal to the pseudocercospora-like clade. Although it is tempting to use the name *Trochophora* for this clade, further collections of *Trochophora* are required to clarify the morphological variation among taxa with this unique conidial morphology. Using sequence data of the ITS gene, the closest taxa obtained from a BLAST search is the *Mycosphaerella heimii* species complex (96 % similarity).

Zhao et al. (2007) consider *T. fasciculata* as a pathogen of *Daphniphyllum*, and report it from this host in several Asian countries, namely Sri Lanka, China (incl. Hong Kong and Taiwan) and India.

Verrucisporota D.E. Shaw & Alcorn, Austral. Syst. Bot. 6: 273. 1993

≡ *Verrucispora* D.E. Shaw & Alcorn, Proc. Linn. Soc. New South Wales 92: 171. 1967. (nom. illegit.).

Type species. *Verrucisporota proteacearum* (D.E. Shaw & Alcorn) D.E. Shaw & Alcorn.

Mycelium consisting of pale brown, septate, verrucose hyphae. *Stroma* forming in substomatal cavities, cells brown-walled, pseudoparenchymatous. *Conidiophores* macronematous, mononematous, simple, flexuous, often geniculate, septate, mainly smooth, pale to dark brown, tapering towards the apex, but often becoming more swollen, and also verruculose to verrucose at the apex. *Conidiogenous cells* cylindrical, becoming geniculate, integrated, terminal, becoming intercalary, polyblastic, proliferating sympodially, cicatrised; conidiogenous loci planate, conspicuous, protuberant, thickened and darkened. *Conidia* cylindrical, narrowing slightly to an obtuse apex and with a truncate base with a distinctly thickened hilum, medium brown, straight or curved, transversely septate, verrucose to verruculose.

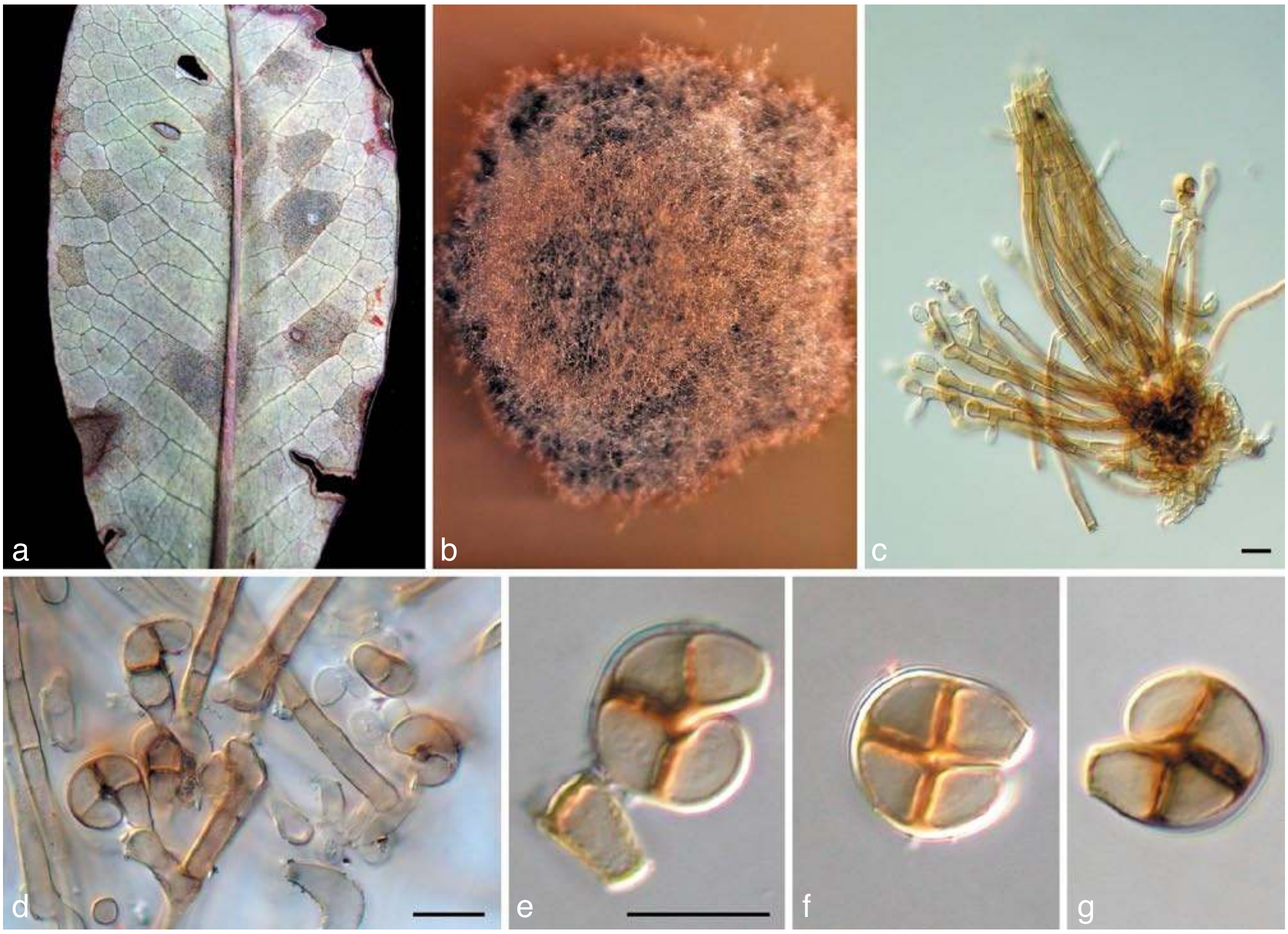


Fig. 12 *Trochophora fasciculata* (CPC 10280). a. Leaf spots on *Daphniphyllum*; b. colony on MEA; c. fasciculate conidiophores; d. conidiophores and conidiogenous cells; e–g. conidia. — Scale bars = 10 µm.

Verrucisporota daviesiae (Cooke & Massee) Beilharz & Pascoe, Mycotaxon 82: 360. 2002

Basionym. *Cercospora daviesiae* Cooke & Massee, Grevillea 18: 7. 1889.

Teleomorph. *Mycosphaerella daviesiicola* Beilharz & Pascoe, Mycotaxon 82: 364. 2002.

Characteristics in culture — On MEA erumpent, spreading with folded surface, and sparse aerial mycelium and even, lobate margin; surface iron-grey to olivaceous-grey; reverse iron-grey; colonies reaching 7 mm diam after 2 wk. On PDA erumpent, spreading, with moderate aerial mycelium and uneven margins; surface white in middle, olivaceous-grey in outer region, iron-grey underneath; colonies reaching 8 mm diam after 2 wk. On OA erumpent, spreading, with moderate aerial mycelium and uneven margin; surface white in middle, olivaceous-grey in outer region; colonies reaching 8 mm diam after 2 wk.

Specimen examined. Australia, Victoria, on living leaves of *Daviesia mimosoides* (≡ *D. cormybosa* var. *mimosoides*), *V. & R. Beilharz*, VPRI 31767 = CBS 116002.

Notes — The type species of the genus *Stenella*, *S. araguata*, clusters in the *Teratosphaeriaceae* (Crous et al. 2007a), and thus the majority of the stenella-like anamorphs in the *Mycosphaerellaceae*, will need to be placed in another genus. One option would be *Zasmidium* (Arzanlou et al. 2007), which clusters in the *Mycosphaerellaceae*, along with *Verrucisporota* (Fig. 1). This clade, however, is neither morphologically nor phylogenetically well resolved, and taxa need to be added to improve the phylogeny before a reasonable assessment can be made. The ITS sequence of this species is distinct from the other two species of this genus treated in this paper (Table 1).

Verrucisporota grevilleae Crous & Summerell, *sp. nov.* — MycoBank MB509523; Fig. 13

Differt a *Verrucisporota protearum* conidiis angustioribus et longioribus, (30–)50–65(–80) × (5–)6–7 µm, et conidiophoris brevioribus, (35–)80–120(–160) × (5–)6–7 µm.

Etymology. Named after the host genus on which it occurs, *Grevillea*.

Leaf spots angular, elongated, amphigenous, 1–2 mm wide, 3–10 mm long, medium to dark brown to black, discrete. *Mycelium* immersed and superficial, hyphae medium brown, septate, verrucose, 1.5–3 µm wide. *Stroma* up to 60 µm wide and 40 µm high, forming in substomatal cavities, becoming erumpent, cells brown, thick-walled, pseudoparenchymatous. *Conidiophores* macronematous, mononematous, caespitose, emerging through the stomata, simple, flexuous, often geniculate-sinuous, 4–7-septate, mainly smooth, dark brown, from a bulbous base tapering towards the apex, but often becoming more swollen, and also verrucose at the apex, (35–)80–120(–160) × (5–)6–7 µm. *Conidiogenous cells* cylindrical, becoming geniculate, integrated, terminal, polyblastic, proliferating sympodially, 20–45 × 5–7 µm, with conspicuous, cicatrised, protuberant, conidiogenous loci, 3 µm diam. *Conidia* subcylindrical, narrowing slightly to an obtuse apex (frequently swollen), and with a truncate base with a distinctly thickened, darkened, somewhat refractive hilum, 3 µm wide, red-brown, straight or curved, with 3–7(–12) mainly unconstricted eusepta, thick-walled, verrucose, (30–)50–65(–80) × (5–)6–7 µm. Conidiophores frequently arising from brown, erumpent spermatogonia, up to 150 µm wide. *Spermatia* hyaline, smooth, bacilliform, 4–6 × 1–1.5 µm.

Characteristics in culture — Colonies on MEA erumpent, with sparse aerial mycelium; margins feathery, crenate; surface

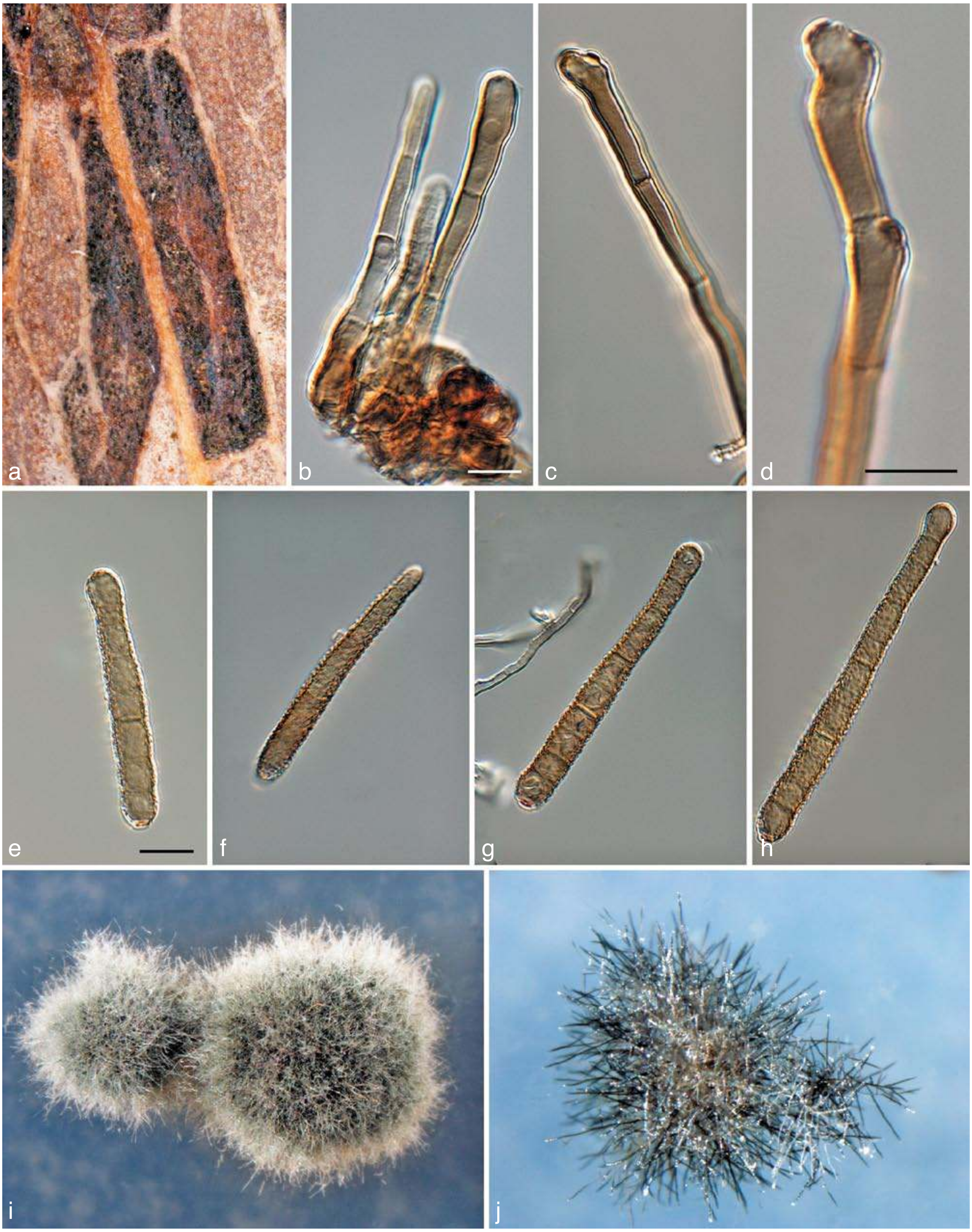


Fig. 13 *Verrucisporota grevilleae* (CBS 124107). a. Leaf spots on *Grevillea*; b. conidiophores; c, d. conidiophores and conidiogenous cells; e–h. conidia; i. colony on PDA; j. colony on SNA. — Scale bars = 10 µm.

folded, with zones of salmon or smoke-grey mycelium; outer region and reverse olivaceous-grey; colonies reaching 10 mm diam after 1 mo.

Specimen examined. Australia, Northern Territory, Emerald Springs (13°37'13.3" 131°36'40"), on leaves of *Grevillea decurrens*, 22 Sept. 2007, leg. *B. Summerell*, isol. *P.W. Crous*, CBS H-20205, cultures CPC 14761 = CBS 124107, CPC 14762, 14763.

Notes — Conidia of *V. grevilleae* are narrower and longer, and conidiophores shorter than those of *V. protearum* (conidia 23–51 × 5.6–10.5 µm, conidiophores up to 290 µm long, 4.5–8.5 µm wide; Shaw & Alcorn 1967). South African specimens from the genus *Protea* have conidia that are (20–)31–36(–49) × (7–)8.5–9.5(–12) µm (Crous et al. 2004a). These findings suggest that the fungus treated as *V. protearum* on *Proteaceae* (Shaw & Alcorn 1967, 1993, Beilharz & Pascoe 2002, Crous et al. 2004a), probably represents a complex of several taxa.

Verrucisporota proteacearum (D.E. Shaw & Alcorn) D.E. Shaw & Alcorn, Austral. Syst. Bot. 6: 273. 1993

Basionym. *Verrucispora proteacearum* D.E. Shaw & Alcorn, Proc. Linn. Soc. New South Wales 92: 171. 1967.

Characteristics in culture — On MEA erumpent with sparse aerial mycelium; surface cream to pale olivaceous-grey, folded, with smooth, even margin; reverse brown-vinaceous; reaching 8 mm diam after 2 wk. On PDA erumpent with sparse aerial mycelium and smooth to feathery margin; surface cream to pale olivaceous-grey; reverse olivaceous-grey, reaching 8 mm diam after 2 wk. On OA erumpent, with moderate aerial mycelium and uneven margin, pale white in middle, pale olivaceous-grey in outer region; reaching 10 mm diam after 2 wk.

Specimen examined. Australia, *Grevillea* sp., *V. Beilharz*, VPRI31812 = CBS 116003.

Notes — Because *V. proteacearum* was originally described from *Finschia* (conidia 23–51 × 5.6–10.5 µm; Shaw & Alcorn 1967), there is a strong possibility that the strain listed here from *Grevillea* (conidia 30–45 × 10–12 µm on OA) may represent a different taxon to the one occurring on *Finschia.* Although apparently identical based on the LSU phylogeny (see Fig. 1), the ITS sequence of this isolate is different to that of *V. grevilleae* (95 % similarity and 4 % gaps).

KEY TO SPECIES OF *VERRUCISPOROTA*

1. Conidia wider than 4.5 µm 2
1. Conidia narrower than 4.5 µm 3
2. Conidia up to 56 µm long 4
2. Conidia longer than 56 µm, 3–7(–12)-septate, (30–)50–65(–80) × (5–)6–7 µm; on *Grevillea* . . . . *V. grevilleae*
3. Conidia mostly up to 30 µm long, (0–)2–3(–7)-septate, 13–30(–70) × 2.75–4 µm; on *Capparis* . *V. kimberleyana*
3. Conidia longer, mostly up to 77 µm long, 1–11-septate, (10–)27–77(–108) × 3–4.5 µm; on *Struthanthus* . . . . *V. struthanthicola*
4. Conidia up to 3-septate, obclavate, 1–3-septate, 32.5–55 × 7–10.5 µm; on *Celastrus* . . . . *V. indica*
4. Conidia more than 3 septa 5
5. Conidia up to 32 µm long; (1–)3–4(–5)-septate, 20–32 × 6–10 µm; on *Bridelia* . . . . *V. brideliae*
5. Conidia frequently longer than above 6
6. Conidia 0–6-septate, 18–56 × 4.5–7 µm; on *Daviesia* (Beilharz & Pascoe 2002) . . . .*V. daviesiae*
6. Conidia 3–7-septate, 23–51 × 5.6–10.5 µm; on *Finschia* . . . . *V. proteacearum*

Vonarxia Bat., Publ. Inst. Micol. Univ. Fed. Pernambuco 283: 5. 1960

Type species. *Vonarxia anacardii* Bat. & J.L. Bezerra.

Mycelium immersed and superficial, composed of branched, septate, pale to medium brown, smooth to finely roughened hyphae. *Conidiomata* sporodochial; basal stroma composed of globose-ellipsoidal, brown, slightly roughened cells. *Setae* irregularly scattered throughout colony, simple, subulate with a bulbous base, straight to slightly curved, dark brown, smooth to slightly roughened, thick-walled, 5–16-euseptate, septa rather thick, but becoming thinner towards apex. *Conidiogenous cells* arise from upper cells of the stroma, tightly aggregated, doliiform to ellipsoid, pale brown to subhyaline or hyaline, smooth, giving rise to a cluster of conidia by means of sympodial proliferation, with successive conidia forming at a higher level. *Conidia* hyaline, smooth-walled, tetraradiate, basal cell subcylindrical to clavate to doliiform, 0–1-septate; upper three arms arise from the apical part of the basal cell, 3–10-septate, subcylindrical to cylindrical, apex subobtuse.

Vonarxia vagans (Speg.) Aa, Persoonia 13: 128. 1986 — Fig. 14

Basionym. *Ypsilonia vagans* Speg., Revista Mus. La Plata, Secc. Bot. 15: 35. 1908.
≡ *Kazulia vagans* (Speg.) Nag Raj, Canad. J. Bot. 55: 1621. 1977.

On PDA. *Mycelium* immersed and superficial, composed of branched, septate, pale to medium brown, smooth to finely roughened, 3–5 µm wide hyphae. *Conidiomata* sporodochial, flattened to erect and globose (especially on WA, not so on MEA or PDA, tending to be more flattened, and more hemispherical on OA), up to 300 µm diam; basal stroma up to 70 µm thick, composed of globose-ellipsoidal, brown, slightly roughened cells, 5–10 µm diam. *Setae* irregularly scattered throughout colony, simple, subulate with a bulbous base, straight to slightly curved, dark brown, smooth to slightly roughened, thick-walled (1–1.5 µm diam), (5–)10–12(–16)-septate, septa rather thick, but becoming thinner towards apex, basal cell 10–13 µm wide, with slight taper towards bluntly rounded, obtuse apex, (120–)150–200(–220) µm; width at basal septum (5–)6(–7) µm; width at apical septum, 2–3(–5) µm; apical two cells frequently pale brown; individual cells 10–25 µm long. *Conidiogenous cells* arise from upper cells of the stroma, tightly aggregated, doliiform to ellipsoid, pale brown to subhyaline or hyaline, smooth, 8–10 × 3–5 µm, giving rise to a cluster of conidia by means of sympodial proliferation, with successive conidia forming at a higher level. *Conidia* hyaline, smooth-walled, tetraradiate, basal cell subcylindrical to clavate to doliiform, 0–1-septate, 10–15 × (1.5–)2–3 µm (10–18 µm long on OA); upper three arms arise from the apical part of the basal cell, 3–5-septate (prominently constricted at septa on WA and MEA, up to 10-septate on these media), subcylindrical to cylindrical, apex subobtuse, arms 20–55 µm long (20–90 µm on OA), 1.5–2 µm wide (2–3 µm wide on OA).

Characteristics in culture — Colonies on OA spreading, with sparse aerial mycelium, and uneven, striate surface, with crenate margin; surface black, with patches of mouse-grey, reaching up to 25 mm diam after 1 mo; on PDA spreading, with sparse aerial mycelium and crenate margins; surface pale mouse-grey, outer region grey-olivaceous; reverse grey-olivaceous, reaching up to 25 mm diam after 1 mo; on MEA spreading, erumpent with sparse aerial mycelium; surface prominently striate, margin crenate; centre black, outer region mouse-grey; reverse black; colonies reaching up to 20 mm diam after 1 mo.

Specimens examined. Brazil, São Paulo Horto Botanico, leaves of *Spiraea cantoniensis*, Sept. 1905, leg. *Usteri* no. 15 bis, holotype LPS 12280; Rio Grande do Sul, Guaiba, living leaves of *Stenocalyx uniflorus*, 1 Apr. 2008, leg. *A.C. Alfenas*, isol. *P.W. Crous*, epitype designated here CBS H-20206, culture ex-type CPC 15151 = CBS 123533, CPC 15152.

Notes — The holotype specimen (LPS 12280) was described and illustrated in detail by Nag Raj (1977). The species was originally described from leaves of *Spiraea cantoniensis* collected in the São Paulo Botanical Garden, where it occurred on leaves of several tree species, suggesting that it is not host specific. The present collection was obtained by incubating *Eugenia* leaves with leaf spots of *Phaeophleospora eugeniae* in moist chambers, which resulted in a few conidiophores of *Vonarxia vegans* developing.

Nag Raj (1977) erected *Kazulia* for a genus of hyphomycetes with dark brown, septate setae, and tetraradiate conidia, which he regarded as morphologically distinct, and a probable anamorph of the *Chaetothyriaceae*. The fact that he did not compare *Kazulia* with *Vonarxia* is not surprising, because

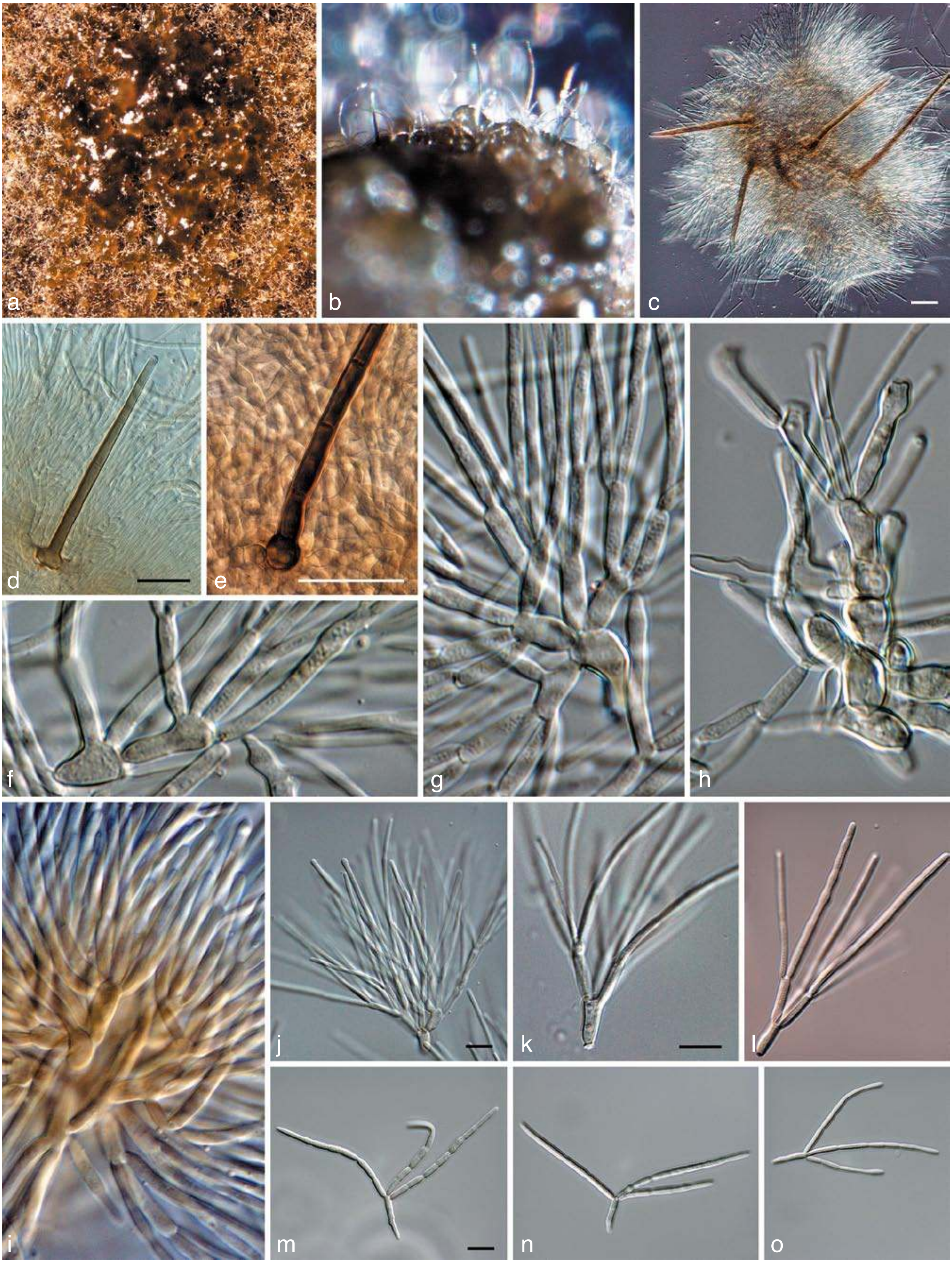


Fig. 14 *Vonarxia vagans* (CBS 123533). a, b. Colony on PDA; c. colony with setae; d, e. setae with rounded apices and swollen bases, lacking rhizoids; f–i. conidiogenous cells giving rise to conidia; j–o. conidia. — Scale bars = 10 µm.

Batista et al. (1960) who initially described *Vonarxia*, showed setae on the outside of the pycnidia, and thus this fungus was regarded as a coelomycete. Later comments from Nag Raj (1977) (as *Kazulia*) suggest, however, that these bodies are perithecia of a probable teleomorph. In a subsequent study Van der Aa & Van Oorschot (1985) and Van der Aa & Von Arx (1986) showed that *Kazulia* is a synonym of *Vonarxia*. Wu & Sutton (1995) were not convinced of the distinction between *Vonarxia* and another hyphomycete genus, *Fumagopsis*, due to insufficient material, and chose to use the name *Fumagopsis* for *F. complexa*, which they described from *Eugenia* leaves collected in India. Based on the present collection of *V. vagans*, it is apparent, that these are two distinct genera. In *Fumagopsis* the setae are aseptate, arranged around the sporodochium, and taxa have rhizoid-like structures. In contrast, the setae of *Vonarxia* are septate, irregularly distributed and do not surround the sporodochium, and have a simple, bulbous base.

KEY TO SPECIES OF *VONARXIA*

1. Setae 87–155 µm long; apical conidial arms 12–35 µm long . . . . *V. anacardii*
1. Setae and conidial arms longer; setae 120–220 µm long; apical conidial arms 20–55(–90) µm long . . . . *V. vagans*

Xenostigmina Crous, Mycol. Mem. 21: 154. 1998

Type species. Xenostigmina zilleri (A. Funk) Crous.

Associated with leaf spots. *Mycelium* internal, consisting of hyaline to pale brown, septate, branched, smooth hyphae. *Conidiomata* sporodochial, brown to black. *Conidiophores* densely aggregated, arising from the upper cells of a pale brown stroma, finely verruculose, hyaline to pale brown, multiseptate, subcylindrical, straight to variously curved, branched. *Conidiogenous cells* terminal and intercalary, hyaline to pale brown, finely verruculose, doliiform to subcylindrical, tapering to flat tipped loci, proliferating sympodially and percurrent; loci not thickened or conspicuous. *Conidia* solitary, pale to medium brown, with pale brown apical and basal regions, finely verruculose, mostly straight, ellipsoidal, apex subobtuse, frequently extending into a beak; base truncate at dehiscence, inner part extending later to form a short, subobtuse basal appendage; septation muriform; basal marginal frill present.

Xenostigmina zilleri (A. Funk) Crous, Mycol. Mem. 21: 155. 1998 — Fig 15

Basionym. *Stigmina zilleri* A. Funk, Canad. J. Bot. 65: 482. 1987.

Synanamorph. *Mycopappus aceris* (Dearn. & Barthol.) Redhead & G.P. White, Canad. J. Bot. 63: 1430. 1985.

Basionym. *Cercosporella aceris* Dearn. & Barthol., Mycologia 9: 362. 1917.

Teleomorph. ? *Didymella mycopappi* (A. Funk & Dorworth) Crous, Mycol. Mem. 21: 152. 1998.

Basionym. *Mycosphaerella mycopappi* A. Funk & Dorworth, Canad. J. Bot. 66: 295. 1988.

Characteristics in culture — Colonies spreading on PDA with moderate to abundant aerial mycelium, and feathery margins; olivaceous-grey with patches of iron-grey and pale olivaceous-grey; iron-grey in reverse. On OA spreading, with abundant aerial mycelium, olivaceous-grey with patches of pale olivaceous-grey. On MEA erumpent, spreading, with abundant aerial mycelium, pale olivaceous-grey with patches of olivaceous-grey and iron-grey; reverse iron-grey.

Specimens examined. CANADA, British Columbia, 15 km east of Sardis, on living leaves of *Acer macrophyllum*, 22 Oct. 1985, *A. Funk & C.E. Dorworth*, holotype DAVFP 23272; British Columbia, on living leaves of *Acer* sp., 2002, leg. *K.A. Seifert*, isol. *P.W. Crous*, CBS 115686 = CPC 4010, CBS 115685 = CPC 4011; Victoria BC, 48°30'25.63"N, 123°30'46.99"W, 115 m, fallen leaves of *Acer macrophyllum*, 6 Sept. 2007, leg. *B. Callan*, isol. *P.W. Crous*, CBS H-20208, CPC 14376 = CBS 124108, CPC 14377, 14378 (*Xenostigmina zilleri*), CPC 14379 = CBS 124109, CPC 14380, 14381 (*Mycopappus aceris*).

Notes — Although *Stigmina* s.str. has been shown to reside in *Pseudocercospora* s.str. (Crous et al. 2006a, Braun & Crous 2006, 2007), this is not the case for *Xenostigmina* (Crous 1998), which appears to be related to *Seifertia* (Seifert et al. 2007) in the *Dothideomycetes*. Isolates of the *Xenostigmina* state are shown here (Fig. 1) to be identical to those of the *Mycopappus* state, which proves that these two genera are indeed synanamorphs. No ascospore isolates were obtained, however, to confirm their relationship to '*Mycosphaerella*' *mycopappi*, though this species is clearly not a member of the *Mycosphaerellaceae*. *Xenostigmina wolfii* (Crous & Corlett 1998), which is the anamorph of *Mycosphaerella stigmina-platani*, and a *Pseudocercospora* synanamorph, is not congeneric with *X. zilleri*, and would be better accommodated in *Pseudocercospora* (Crous et al. 2006a) than in *Xenostigmina*.

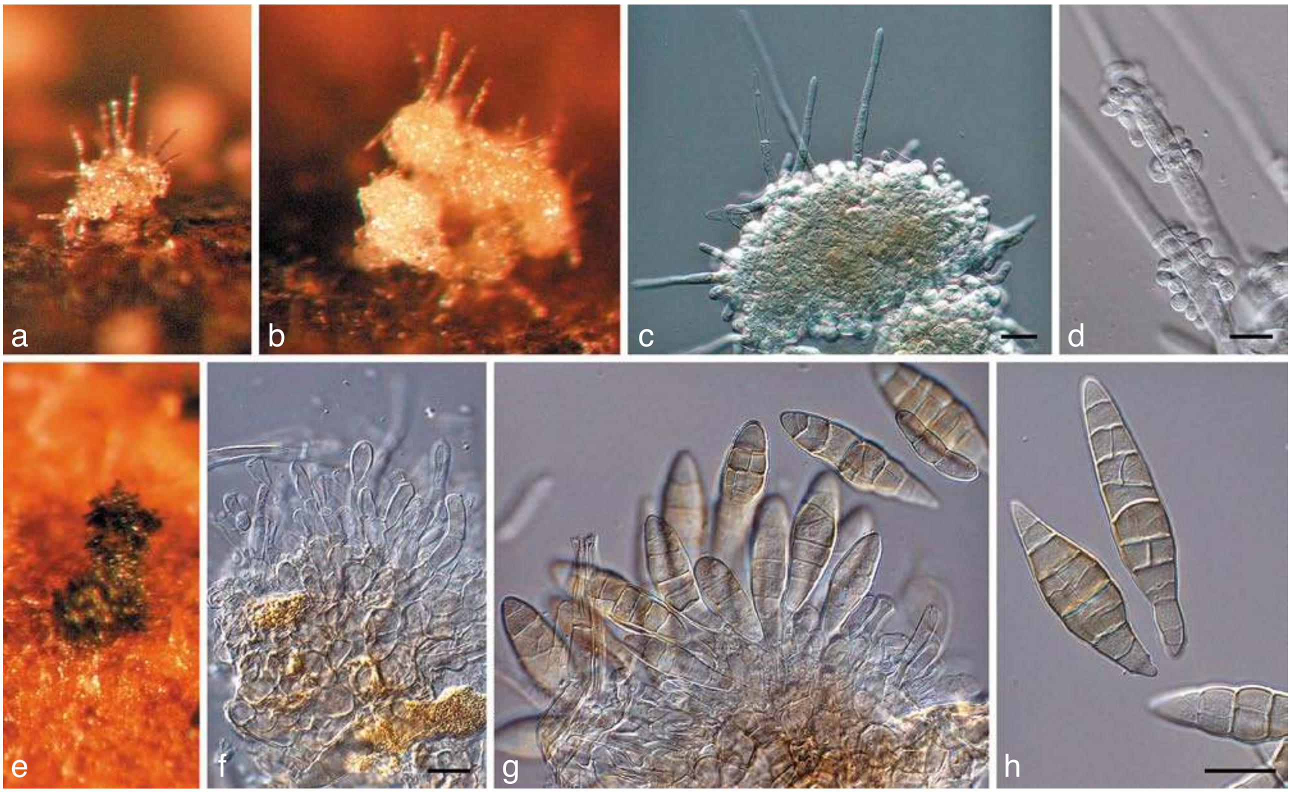


Fig. 15 *Xenostigmina zilleri* (CBS 124108). a–c. Conidial propagules of *Mycopappus aceris*; d. setae on the surface of conidial propagules; e. colony of *Xenostigmina zilleri*; f, g. fasciculate conidiophores; h. conidia. — Scale bars = 10 µm.

Acknowledgements We acknowledge Drs B.E. Callan (Canadian Forest Service, Natural Resources Canada), F. Dugan (Washington State University, Pullman), H. Evans (CABI, UK) and V. Beilharz (Department of Primary Industries, Knoxfield, Victoria, Australia), who provided valuable specimens for study. We are grateful to the technical staff including A. van Iperen, M. Vermaas, and M. Starink for providing assistance with cultures, photoplates and DNA sequencing, respectively. Dr E.G. Simmons (Crawfordsville, Indiana, USA) is acknowledged for bringing to our attention the problem of *Alternaria malorum* and for providing strains representing related novel taxa known to him, for inclusion in this study.

REFERENCES

Aa HA van der, Arx JA von. 1986. On Vonarxia, Kazulia and other fungi with stauroconidia. Persoonia 13: 127–128.

Aa HA van der, Oorschot CAN van. 1985. A redescription of some genera with staurospores. Persoonia 12: 415–425.

Arambarri AM, Cabello MN, Cazau MC. 2001. Dictyosporium triramosum, a new hyphomycete from Argentina. Mycotaxon 78: 185–189.

Arzanlou M, Groenewald JZ, Gams W, Braun U, Shin HD, Crous PW. 2007. Phylogenetic and morphotaxonomic revision of Ramichloridium and allied genera. Studies in Mycology 58: 57–93.

Batista AC, Bezerra JL, Maia, Silva H da. 1960. Vonarxia n. gen. e outros imperfecti fungi. Publicaçao Instituto de Micologia Universidade de Recife 283: 1–32.

Beilharz V, Pascoe I. 2002. Two additional species of Verrucisporota, one with a Mycosphaerella teleomorph, from Australia. Mycotaxon 82: 357–365.

Braun U. 1995. A monograph of Cercosporella, Ramularia and allied genera (phytopathogenic hyphomycetes). Vol. 1. IHW-Verlag, Eching, Germany.

Braun U, Crous PW. 2006. (1732) Proposal to conserve the name Pseudocercospora against Stigmina and Phaeoisariopsis (Hyphomycetes). Taxon 55: 803.

Braun U, Crous PW. 2007. The diversity of cercosporoid hyphomycetes – new species, combinations, names and nomenclatural clarifications. Fungal Diversity 26: 55–72.

Braun U, Crous PW, Dugan F, Groenewald JZ, Hoog SG de. 2003. Phylogeny and taxonomy of Cladosporium-like hyphomycetes, including Davidiella gen. nov., the teleomorph of Cladosporium s.str. Mycological Progress 2: 3–18.

Cai L, Hyde KD. 2007. Anamorphic fungi from freshwater habitats in China: Dictyosporium tetrasporum and Exserticlava yunnanensis spp. nov., and two new records for Pseudofuscophialis lignicola and Pseudobotrytis terrestris. Mycoscience 48: 290–296.

Cai L, Zhang K, McKenzie EHC, Hyde KD. 2003a. New species of Dictyosporium and Digitodesmium from submerged wood in Yunnan, China. Sydowia 55: 129–135.

Cai L, Zhang K, McKenzie EHC, Lumyong S, Hyde KD. 2003b. New species of Canalisporium and Dictyosporium from China and a note on the differences between these genera. Cryptogamie Mycologie 24: 3–11.

Carmichael JW, Kendrick BW, Conners IL, Sigler L. 1980. Genera of Hyphomycetes. Edmonton, University of Alberta Press, Canada.

Castañeda RF, Kendrick B. 1990. Conidial fungi from Cuba II. University of Waterloo Biological Series 33: 1–61.

Crous PW. 1998. Mycosphaerella spp. and their anamorphs associated with leaf spot diseases of Eucalyptus. Mycologia Memoir 21: 1–170.

Crous PW, Braun U, Groenewald JZ. 2007a. Mycosphaerella is polyphyletic. Studies in Mycology 58: 1–32.

Crous PW, Corlett M. 1998. Reassessment of Mycosphaerella spp. and their anamorphs occurring on Platanus. Canadian Journal of Botany 76: 1523–1532.

Crous PW, Denman S, Taylor JE, Swart L, Palm ME. 2004a. Cultivation and diseases of Proteaceae: Leucadendron, Leucospermum and Protea. CBS Biodiversity Series 2: 1–228.

Crous PW, Gams W, Stalpers JA, Cannon PF, Kirk PM, David JC, Triebel D. 2004b. An online database of names and descriptions as an alternative to registration. Mycological Research 108: 1236–1238.

Crous PW, Liebenberg MM, Braun U, Groenewald JZ. 2006a. Re-evaluating the taxonomic status of Phaeoisariopsis griseola, the causal agent of angular leaf spot of bean. Studies in Mycology 55: 163–173.

Crous PW, Schubert K, Braun U, Hoog GS de, Hocking AD, Shin H-D, Groenewald JZ. 2007b. Opportunistic, human-pathogenic species in the Herpotrichiellaceae are phenotypically similar to saprobic or phytopathogenic species in the Venturiaceae. Studies in Mycology 58: 185–217.

Crous PW, Slippers B, Wingfield MJ, Rheeder J, Marasas WFO, Philips AJL, Alves A, Burgess T, Barber P, Groenewald JZ. 2006b. Phylogenetic lineages in the Botryosphaeriaceae. Studies in Mycology 55: 235–253.

Crous PW, Verkley GJM, Groenewald JZ, Samson RA (eds). 2009. Fungal Biodiversity. CBS Laboratory Manual Series 1. Centraalbureau voor Schimmelcultures, Utrecht, Netherlands.

Crous PW, Wingfield MJ. 1994. Sporendocladia fumosa and Lauriomyces bellulus sp. nov. from Castanea cupules in Switzerland. Sydowia 46: 193–203.

Decock C, Delgado-Rodríguez G, Buchet S, Seng JM. 2003. A new species and three new combinations in Cyphellophora, with a note on the taxonomic affinities of the genus, and its relation to Kumbhamaya and Pseudomicrodochium. Antonie van Leeuwenhoek 84: 209–216.

Ellis MB. 1971. Dematiaceous hyphomycetes. Commonwealth Mycological Institute, Kew, UK.

Ellis MB. 1976. More dematiaceous hyphomycetes. Commonwealth Mycological Institute, Kew, UK.

González MC, Anaya AL, Glenn AE, Saucedo-García A, Macías-Rubalcava ML, Hanlin RT. 2007. A new endophytic ascomycete from El Eden Ecological reserve, Quintana Roo, Mexico. Mycotaxon 201: 251–260.

Heuchert B, Braun U, Schubert K. 2005. Morphotaxonomic revision of fungicolous Cladosporium species (Hyphomycetes). Schlechtendalia 13: 1–78.

Hibbett DS, Binder M, Bischoff JF, Blackwell M, Cannon PF, et al. 2007. A higher-level phylogenetic classification of the Fungi. Mycological Research 111: 509–547.

Holubová-Jechová V. 1973. Lignicolous hyphomycetes from the Netherlands. Koninklijke Nederlandse Akademie van Wetenschappen, Ser. C, 76: 297–302.

Hoog GS de, Gerrits van den Ende AHG. 1998. Molecular diagnostics of clinical strains of filamentous Basidiomycetes. Mycoses 41: 183–189.

Hughes SJ. 1958. Revisiones hyphomycetum aliquot cum appendice de nominibus rejiciendis. Canadian Journal of Botany 36: 727–836.

James TY, Kauff F, Schoch CL, Matheny PB, Hofstetter V, et al. 2006. Reconstructing the early evolution of the fungi using a six gene phylogeny. Nature 443: 818–822.

Kaiser W, Crous PW. 1998. Mycosphaerella lupini sp. nov., a serious leaf spot disease of perennial lupin in Southcentral Idaho, USA. Mycologia 90: 726–731.

Kodsueb R, Lumyong S, Hyde KD, Lumyong P, McKenzie EHC. 2006. Acrodictys micheliae and Dictyosporium manglietiae, two new anamorphic fungi from woody litter of Magnoliaceae in northern Thailand. Cryptogamie Mycologie 27: 111–119.

McKenzie EHC. 2008. Two new dictyosporous hyphomycetes on Pandanaceae. Mycotaxon 104: 23–28.

Mason EW. 1933. Annotated account of fungi received at the Imperial Mycological Institute. Mycological Papers 3: 61–63.

Matsushima T. 1971. Microfungi of the Solomon Islands and Papua New Guinea. Matsushima, Kobe, Japan.

Matsushima T. 1985. Matsushima Mycological Memoirs No. 4. Matsushima, Kobe, Japan.

Nag Raj TR. 1977. Ypsilonia, Acanthotheciella, and Kazulia gen. nov. Canadian Journal of Botany 55: 1599–1622.

Nag Raj TR. 1993. Coelomycetous anamorphs with appendage-bearing conidia. Mycologue Publications, Waterloo, Ontario, Canada.

Rao V, Hoog GS de. 1986. New or critical Hyphomycetes from India. Studies in Mycology 28: 1–84.

Rayner RW. 1970. A mycological colour chart. Commonwealth Agricultural Bureau, Kew, UK.

Rehner SA, Samuels GJ. 1994. Taxonomy and phylogeny of Gliocladium analysed from nuclear large subunit ribosomal DNA sequences. Mycological Research 98: 625–634.

Saccardo PA. 1886. Sylloge fungorum omnium hucusque cognitorum. Vol. IV. Pavia, Italy.

Seifert KA, Hughes SJ, Boulay H, Louis-Seize G. 2007. Taxonomy, nomenclature and phylogeny of three cladosporium-like hyphomycetes, Sorocybe resinae, Seifertia azalea and the Hormoconis anamorph of Amorphotheca resinae. Studies in Mycology 58: 235–245.

Shaw DE, Alcorn JL. 1967. The genus Verrucispora gen. nov. (Fungi Imperfecti) on Proteaceae in New Guinea and Queensland. Proceedings of the Linnean Society of New South Wales 92: 171–173.

Shaw DE, Alcorn JL. 1993. New names for Verrucispora and its species. Australian Systematic Botany 6: 273–276.

Shenoy BD, Jeewon R, Hyde KD. 2007. Impact of DNA sequence-data on the taxonomy of anamorphic fungi. Fungal Diversity 26: 1–54.

Simmons EG. 1996. Alternaria themes and variations (145–149). Mycotaxon 57: 391–409.

Simmons EG. 2007. Alternaria. An identification manual. CBS Biodiversity Series 6: 1–775.

Sutton BC. 1980. The coelomycetes. Fungi imperfecti with pycnidia, acervuli and stromata. Commonwealth Mycological Institute, Kew, UK.

Sutton BC, Carmarán CC, Romero AI. 1996. Ramoconidiifera, a new genus of hyphomycetes with cheiroid conidia from Argentina. Mycological Research 100: 1337–1340.
Sutton BC, Pascoe IG. 1987. Argopericonia and Thyssglobulus, new hyphomycete genera from Banksia leaves. Transactions of the British Mycological Society 88: 41–46.
Tsui CKM, Berbee ML, Jeewon R, Hyde KD. 2006. Molecular phylogeny of Dictyosporium and allied genera inferred from ribosomal DNA. Fungal Diversity 21: 157–166.
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, Lee S, Taylor J. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (eds), PCR Protocols: a guide to methods and applications: 315–322. Academic Press, USA.
Wu WP, Sutton BC. 1995. Fumagopsis complexa sp. nov., a species with complicated conidial morphology. Mycological Research 99: 1450–1452.
Zhao GZ, Liu XZ, Wu WP. 2007. Helicosporous hyphomycetes from China. Fungal Diversity 26: 313–524.
Zhao GZ, Zhang TY. 2003. Notes on dictyosporic hyphomycetes from China 1. The genus Dictyosporium. Mycosystema 22: 19–22.
Zucconi L, Pagano S. 1993. Concerning the generic limits in Haplographium. Mycotaxon 46: 11–18.