

All that glitters is not Ramularia

S.I.R. Videira^{1,2}, J.Z. Groenewald¹, U. Braun³, H.D. Shin⁴, and P.W. Crous^{1,2,5*}

¹CBS-KNAW Fungal Biodiversity Centre, Uppsalalaan 8, 3584 CT Utrecht, The Netherlands; ²Wageningen University and Research Centre (WUR), Laboratory of Phytopathology, Droevendaalsesteeg 1, 6708 PB Wageningen, The Netherlands; ³Martin-Luther-Universität, Institut für Biologie, Bereich Geobotanik und Botanischer Garten, Herbarium, Neuwerk 21, D-06099 Halle (Saale), Germany; ⁴Division of Environmental Science and Ecological Engineering, Korea University, Seoul 02841, Korea; ⁵Department of Microbiology and Plant Pathology, Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, Pretoria 0002, South Africa

*Correspondence: P.W. Crous, p.crous@cbs.knaw.nl

Abstract: Ramularia is a species-rich genus that harbours plant pathogens responsible for yield losses to many important crops, including barley, sugar beet and strawberry. Species of Ramularia are hyphomycetes with hyaline conidiophores and conidia with distinct, thickened, darkened, refractive conidiogenous loci and conidial hila, and Mycosphaerella sexual morphs. Because of its simple morphology and general lack of DNA data in public databases, several allied genera are frequently confused with Ramularia. In order to improve the delimitation of Ramularia from allied genera and the circumscription of species within the genus Ramularia, a polyphasic approach based on multilocus DNA sequences, morphological and cultural data were used in this study. A total of 420 isolates belonging to Ramularia and allied genera were targeted for the amplification and sequencing of six partial genes. Although Ramularia and Ramulariopsis proved to be monophyletic, Cercosporella and Pseudocercosporella and Pseudocercosporella isolates that were not congeneric with the ex-type strains of the type species of those genera were assigned to existing genera or to the newly introduced genera Teratoramularia and Xenoramularia, respectively. Teratoramularia is a genus with ramularia-like morphology belonging to the Teratosphaeriaceae, and Xenoramularia was introduced to accommodate hyphomycetous species closely related to Zymoseptoria. The genera Apseudocercosporella, Epicoleosporium, Filiella, Fusidiella, Neopseudocercosporella, and Mycosphaerelloides were also newly introduced to accommodate species non-congeneric with their purported types. A total of nine new combinations and 24 new species were introduced in this study.

Key words: Barcoding, Cercosporoid, Multilocus phylogeny, Mycosphaerella, Plant pathogen.

Taxonomic novelties: New genera: Apseudocercosporella Videira & Crous, Epicoleosporium Videira & Crous, Filiella Videira & Crous, Fusoidiella Videira & Crous, Mycosphaerelloides Videira & Crous, Neopseudocercosporella Videira & Crous, Teratoramularia Videira, H.D. Shin & Crous, Xenoramularia Videira, H.D. Shin & Crous; New combinations: Filiella pastinacae (P. Karst.) Videira & Crous, Fusoidiella depressa (Berk. & Broome) Videira & Crous, Mycosphaerelloides madeirae (Crous & Denman) Videira & Crous, Neopseudocercosporella brassicae (Chevall.) Videira & Crous, Neopseudocercosporella capsellae (Ellis & Event.) Videira & Crous, Ramularia cerastiicola (Crous) Videira & Crous, Ramularia stellariicola (M.J. Park et al.) Videira, H.D. Shin & Crous, Sphaerulina chaenomelis (Y. Suto) Videira, U. Braun, H.D. Shin & Crous, Sphaerulina koreana (Crous et al.) Videira, H.D. Shin & Crous; New names: Ramularia alangiicola Videira, H.D. Shin & Crous, Ramularia veronicicola Videira & Crous; New species: Acrodontium fagicola Videira & Crous, Acrodontium luzulae Videira & Crous, Acrodontium pigmentosum Videira & Crous, Apseudocercosporella trigonotidis Videira, H.D. Shin & Crous, Cercosporella catenulata Videira & Crous, Epicoleosporium ramularioides Videira, H.D. Shin & Crous, Ramularia euonymicola Videira, H.D. Shin, U. Braun & Crous, Ramularia gaultheriae Videira & Crous, Ramularia geraniicola Videira & Crous, Ramularia malicola Videira & Crous, Ramularia neodeusta Videira & Crous, Ramularia osterici Videira, H.D. Shin & Crous, Ramularia rumicicola Videira, H.D. Shin & Crous, Ramularia trigonotidis Videira, H.D. Shin & Crous, Ramularia weberiana Videira & Crous, Ramulariopsis pseudoglycines Videira, Crous & Braun, Teratoramularia infinita Videira & Crous, Teratoramularia kirschneriana Videira & Crous, Teratoramularia persicariae Videira, H.D. Shin & Crous, Teratoramularia rumicicola Videira, H.D. Shin & Crous, Xenoramularia arxii Videira & Crous, Xenoramularia neerlandica Videira & Crous, Xenoramularia polygonicola Videira, H.D. Shin & Crous; Typifications: Epitypifications: Cercosporella gossypii Speg., Cylindrosporium heraclei Oudem., Fusoma inaequale Preuss, Ovularia tovarae Sawada, Ramularia acroptili Bremer, Ramularia aplospora Speg., Ramularia armoraciae Fuckel, Ramularia beticola Fautrey & Lambotte, Ramularia geranii Fuckel, Ramularia Iamii Fuckel var. Iamii, Ramularia pusilla Unger, Ramularia vallisumbrosae Cavara, Ramularia variabilis Fuckel; Neotypifications: Crocysporium rubellum Bonord., Ramularia collo-cygni B. Sutton & J.M. Waller; Lectotypification: Ramularia kriegeriana Bres.

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INTRODUCTION

Ramularia (Unger 1833) is a species-rich genus (1 220 names listed in MycoBank, accessed 6 Nov. 2015) that belongs to the family *Mycosphaerellaceae* in the order *Capnodiales*. *Ramularia* species are mostly phytopathogenic and associated with leaf spots, necrosis or chlorosis, but some species can be saprobic or even mycophylic. The genus was monographed by Braun (1995, 1998) who defined *Ramularia* as genus of hyphomycetous species with hyaline conidiophores and conidia with distinct, thickened, darkened and refractive conidiogenous loci and conidial hila. *Ramularia* and allied genera were traditionally described based on the colour (hyaline or pigmented) and the structure of conidiophores (simple or branched), the structure of

conidiogenous loci and conidial hila (conspicuous or inconspicuous, by being thickened and darkened or not). Genera with hyaline structures and conspicuous conidial loci include *Cercosporella*, *Hawksworthiana*, *Neoovularia*, *Phacellium*, *Pseudodidymaria*, *Ramularia* and *Ramulariopsis*, while genera with inconspicuous conidial loci include *Monodidymaria*, *Neoramularia* and *Pseudocercosporella*.

Although these morphological characters have been considered important to define these genera, molecular studies have indicated that they are not always phylogenetically informative, and that the generic concepts need to be revised (Crous *et al.* 2001, Verkley *et al.* 2004, Kirschner 2009). The genus *Cercosporella* was usually distinguished from *Ramularia* by having bulging and hyaline conidiogenous loci. However, these characters are minute

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and difficult to observe with light microscopy, resulting in frequent transfers of species between both genera. Based on 28S nrDNA sequence data the type species of *Cercosporella* (*C. virgaureae*) was shown to cluster in a sister clade to *Ramularia s. str.* (Kirschner 2009), and two additional characters were observed: *Cercosporella* has flat conidiogenous loci shaped as a truncated cone and produces cup-shaped appressoria. In contrast, *Ramularia* has conidiogenous loci with a raised rim with a tall central dome and a crater in between (resembling *Cladosporium*, see Bensch *et al.* 2012), and does not form appressoria.

Species of Ramularia have Mycosphaerella sexual morphs, but only a few lifecycles have been experimentally proven, and some species may be asexual holomorphs (Braun 1995, 1998, Verkley et al. 2004, Videira et al. 2015b). Mycosphaerella s. lat. species have been associated with more than 30 genera, including both hyphomycetes and coelomycetes (Mycosphaerellaceae) (Crous 2009). Mycosphaerella s. str., however, was shown to be confined to taxa with Ramularia asexual morphs (Verkley et al. 2004, Crous et al. 2009b, Videira et al. 2015b). In agreement with the new rules for naming of pleomorphic fungi in the International Code of Nomenclature for algae, fungi and plants (ICN: Hawksworth 2011, Hawksworth et al. 2011, Wingfield et al. 2012, Crous et al. 2015), the older name Ramularia was selected over that of Mycosphaerella (see Videira et al. 2015b for more details), and is included in a list of protected generic names (Kirk et al. 2013, Wijayawardene et al. 2014, Rossman et al. 2015).

The genus *Ramularia* includes important plant pathogens such as *R. collo-cygni* and *R. beticola* that cause severe economic losses to barley and sugar beet crops, respectively. Protecting crops from damage by weeds, animal pests and pathogens is a major prerequisite to increase productivity to meet the global increase in demand for food, feed and bioenergy. *Ramularia collocygni* is responsible for yield losses of 15–25 % in winter barley in northern European countries and New Zealand (Cromey *et al.* 2004). Yield losses in sugar beet due to plant pathogens and pests are estimated in general to be 26 % with, and more than 80 % without, crop protection (Oerke & Dehne 2004).

As plant pathogens, some cercosporoid species have shown potential as biocontrol agents of weeds, but no commercial application is yet available. *Acroptilon repens* and *Centaurea solstitiales* are both invasive weeds in the eastern USA. The fungi *Cercosporella acroptili* and *Cercosporella centaureicola* cause significant damage to *A. repens* and *C. solstitiales*, respectively (Berner *et al.* 2005). *Crupina vulgaris* is an invasive weed of pastures in the western USA that is susceptible to leaf blight caused by *Ramularia crupinae*. *Myrica faya* is considered an invasive plant in Hawaii but, in its natural habitat, is susceptible to *Ramularia* dieback caused by *Phacellium rufibasis* (= *Ramularia destructiva*) (Gardner & Hodges 1990). The necrotrophic fungus *Ramularia rubella* is also effective against *Rumex obtusifolius*, an invasive plant of pastures, by causing severe defoliation, shoot and root weight loss (Zaller 2004).

Plant pathogenic fungi are known to produce toxic metabolites that contribute to symptom development in the host. Some phytotoxins induce the formation of reactive oxygen molecules in the plant cells such as superoxide, hydrogen peroxide or hydroxyl radicals that induce oxidative processes of membrane fatty acids. The phytopathogenic species *Ramularia rubella* was the first species of this genus observed producing rubellin metabolites (Arnone *et al.* 1986), a photodynamically active anthraquinone derivative (Heiser *et al.* 2003). More recently, also *Ramularia collo-cygni* (Miethbauer *et al.* 2003) and the mycophylic species *R. uredinicola* (Khodaparast & Braun 2005) were documented as producing rubellins, with *R. rosea* also being a candidate for rubellin biosynthesis. Although a few *Ramularia* species use the photodynamically active rubellins as non-hostspecific phytotoxins, most of the species in this genus are unable to produce these compounds (Miethbauer *et al.* 2006).

Given the importance of the genus *Ramularia* to agriculture as outlined above, the aims of the present study were: (i) to resolve the phylogenetic placement of *Ramularia* and allied genera within the order *Capnodiales*, and (ii) to apply a polyphasic approach based on multilocus DNA sequence, morphological and cultural data to delimit species within the genus *Ramularia* and allied genera.

MATERIALS AND METHODS

Isolates

Isolates included in this study were obtained from the culture collection of the CBS-KNAW Fungal Biodiversity Centre (CBS), Utrecht, the Netherlands, from the working collection of Pedro Crous (CPC), housed at CBS, or were freshly isolated from a range of different plant hosts (Table 1). Single-conidium and ascospore cultures were obtained using the techniques described for species of *Mycosphaerella* and its asexual morphs (Crous *et al.* 1991, Crous 1998). Representative cultures of the new species delineated in this study were deposited in the CBS culture collection.

DNA extraction, amplification and sequencing

Fungal mycelia of strains (Table 1) were harvested with a sterile scalpel and the genomic DNA isolated using the UltraClean[™] Microbial DNA Isolation Kit (MoBio Laboratories, Inc., Solana Beach, CA, USA) following the manufacturers' protocols. The DNA was initially targeted for the amplification and sequencing of 11 partial nuclear genes: 28S nrRNA gene (LSU), internal transcribed spacer regions and intervening 5.8S nrRNA gene (ITS) of the nrDNA operon, actin (actA), translation elongation factor 1-a (tef1-a), histone H3 (his3), glyceraldehyde-3phosphate dehydrogenase (gapdh), RNA polymerase II second largest subunit (*rpb2*), calmodulin (*cmdA*), β-tubulin (*tub2*), chitinsynthase 1 (chs-1) and a gene encoding a minichromosome maintenance protein (mcm7). The primers employed for PCR amplification of each partial gene region are listed in Table 2, with the respective annealing temperatures used. During the course of this study, new primers were designed to amplify rpb2. The primer positions based on GenBank accession KT216537.1 are: Rpb2-F4 34-56, Rpb2-F1 247-266, Rpb2-R1 937-959. A new forward primer was also designed for the amplification of gapdh and its position based on GenBank accession KJ504580.1 is: Gapdh-F1 14-32. The PCR amplifications were performed on a GeneAmp[®] PCR System 9700 (Applied Biosystems, Foster City, CA, USA). The PCR mixtures consisted of 1 µL genomic DNA, 1× NH4 reaction buffer (Bioline, Luckenwalde, Germany), 2 mM MgCl₂, 40 µM of each dNTP, 0.2 µM of each primer and 0.5 U Taq DNA polymerase (Bioline) in a total volume of 12.5 µL. The PCR mixtures for his3, gapdh, rpb2, cmdA and tub2 contained 2 µL genomic DNA. The general PCR conditions were: initial

Table 1. Collectio	n details and	GenBank accessi	on numbers of isola	ates included in the	nis study. ³										
Species ⁴	Culture number ^{1,2}	Previous name ⁴	Host	Country	Collector	LSU	ITS	actA	tef1-α	gapdh	rpb2	his3	cmdA	tub2	chs-1
Acrodontium crateriforme	CBS 144.33^T; ATCC 15679; MUCL 15748; MUCL 8978		Associated with <i>Tuberculina</i> maxima	Netherlands	-	KX286952	FN666565	-	-	-	KX288399) _	-	_	-
	CBS 151.58; MUCL 15750		Human sputum	Netherlands	-	KX286953	KX287266	-	-	-	KX288400) —	-	-	-
	CBS 985.70		Fraxinus excelsior	UK, Westmorland	J.C. Frankland	KX286954	KX287267	-	-	-	KX288401	-	-	-	-
	CBS 840.71		Foodstuff	Netherlands	-	KX286955	KX287268	-	-	-	KX288402	2 -	-	-	-
	CBS 842.71		Citrus sp.	Indonesia, Java	J.H. van Emden	KX286956	KX287269	-	-	-	KX288403	3 —	-	-	-
	CPC 11509	P. fraxini	Fraxinus rhynchophylla	South Korea	H.D. Shin	GU214682	GU214682	(GU320413)	(GU384425)	-	KX288404	KX288727	KX289011	-	-
	CPC 11519	Pseudocercosporella sp.	Agrimonia pilosa	South Korea	H.D. Shin	KX286957	KX287270	KX287558	-	KX288123	KX288405	5 KX288728	KX289012	-	-
	CPC 25894		Ranunculus sp.	Germany	W. Quaedvlieg	KX286958	KX287271	KX287559	-	KX288124	KX288406	6 KX288729	-	-	-
	CPC 25895		<i>Betula</i> sp.	Germany	W. Quaedvlieg	KX286959	KX287272	KX287560	-	-	KX288407	′ KX288730	-	-	-
	CBS 137975; CPC 22172	A. neolitsiae	Neolitsea australiensis	Australia	B.A. Summerell	KJ869184	KJ869127	-	-	-	KX288408	3 -	-	-	-
A. fagicola	CBS 714.79 [⊤]	Acrodontium sp.	Fagus sylvatica	Germany	-	KX286960	-	-	-	-	KX288409) _	-	-	-
A. luzulae	CBS 841.71	A. crateriforme	<i>Puccinia</i> sp., on leaf of <i>Carex</i> sp.	Netherlands	-	KX286961	KX287273	-	-	-	KX288410) –	-	-	-
	CBS 839.71 [⊤]	A. crateriforme	Luzula sylvatica	UK, England	-	KX286962	KX287274	-	-	-	KX288411	-	-	-	-
A. pigmentosum	CBS 111111 ^T	A. griseum	Outdoor air	Finland	S. Haatainen	KX286963	KX287275	-	-	-	KX288412	2 -	-	-	-
Apseudocercosporella trigonotidis	CPC 10865	Pseudocercosporella sp.	Trigonotis peduncularis	South Korea	H.D. Shin	KX286964	KX287276	KX287561	-	-	KX288413	8 –	-	-	-
	CBS 131890^T; CPC 10864	Pseudocercosporella sp.	Trigonotis peduncularis	South Korea	H.D. Shin	JQ324972	GU269858	(JQ325029)	(GU384569)	-	KX288414	+ _	-	-	-
Caryophylloseptoria lychnidis	CBS 109102		Silene pratensis	Austria	G. Verkley	KF251793	KF251289	(KF253598)	(KF253237)	-	KX348048	3 -	(KF253952)	(KF252771)	-
Ca. pseudolychnidis	CBS 128614; KACC 42904; SMKC 22691		Lychnis cognata	South Korea	-	KF251794	KF251290	(KF253599)	(KF253238)	-	KX348049) _	(KF253953)	(KF252772)	-
Cercospora campi-silii	CBS 132625; CPC 14585		Impatiens noli-tangere	South Korea	H.D. Shin	KX286965	JX143561	(JX143069)	(JX143315)	-	KX288415	5 (JX142577)	(JX142823)	-	-
Cercospora cf. chenopodii	CBS 132677; CPC 15599	Ce. chenopodii	Chenopodium sp.	Mexico	M. de Jesús Yáñez-Morales	KX286966	JX143573	(JX143083)	(JX143329)	-	KX288416	6 (JX142591)	(JX142837)	-	-
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Species ⁴	Culture number ^{1,2}	Previous name ⁴	Host	Country	Collector	LSU	ITS	actA	tef1-α	gapdh	rpb2	his3	cmdA	tub2	chs-1
	CPC 12450	Pa. dubia	Chenopodium ficifolium	South Korea	H.D. Shin	KX286967	JX143574	(JX143084)	(JX143330)	-	KX288417	7 (JX142592)	(JX142838)	-	-
Ce. dubia	CPC 15600	Cercosporella sp.	Chenopodium sp.	Mexico	M. de Jesús Yáñez-Morales	KX286968	KX287277	-	-	-	KX288418	3 -	-	-	-
Ce. sojina	CBS 132615^{№T} ; CPC 11353		Glycine soja	South Korea	H.D. Shin	KX286969	JX143659	(JX143173)	(JX143419)	-	KX288419	9 (JX142681)	(JX142927)	-	-
Ce. sorghi	CBS 478.92; INIFAT C91/204	Ramulispora sorghi	-	-	-	KX286970	KX287278	-	-	-	KX288420) –	-	-	-
Cercospora sp.	CBS 220.31	Pa. personata	-	-	-	KX286971	KX287279	-	-	-	KX288421	-	-	-	-
Cercospora sp.	CPC 11422	Pa. sojina	Glycine soja	South Korea	H.D. Shin	KX286972	KX287280	-	-	-	KX288422	2 -	-	-	-
Cercosporella dolichandrae	CBS 138101^T ; CPC 22948		Dolichandra unguiscati	South Africa	A. King	KJ869197	KJ869140	KX287562	-	-	KX288423	3 –	-	-	-
C. catenulata	CBS 355.73 ^T	R. deusta var. alba	Phaseolus vulgaris	Rwanda	D. Froment	KX286973	KX287281	KX287563	-	-	KX288424	KX288731	KX289013	-	-
C. virgaureae	CPC 11456		Erigeron annuus	South Korea	H.D. Shin	KX286974	_	KX287564	KX287838	KX288125	KX348050) KX288732	KX289014	-	-
	CPC 11457		Erigeron annuus	South Korea	H.D. Shin	KX286975	KX287282	KX287565	KX287839	KX288126	KX288425	5 KX288733	KX289015	-	-
	CPC 11460		Erigeron annuus	South Korea	H.D. Shin	KX286976	KX287283	KX287566	KX287840	KX288127	KX288426	6 KX288734	KX289016	-	-
	CPC 11461		Erigeron annuus	South Korea	H.D. Shin	KX286977	KX287284	KX287567	KX287841	-	KX288427	7 KX288735	KX289017	-	-
	CPC 10286		Erigeron annuus	South Korea	H.D. Shin	KX286978	KX287285	KX287568	KX287842	KX288128	KX288428	8 KX288736	KX289018	-	-
	CPC 10287		Erigeron annuus	South Korea	H.D. Shin	KX286979	KX287286	KX287569	KX287843	KX288129	KX288429) KX288737	KX289019	-	-
	CPC 10288		Erigeron annuus	South Korea	H.D. Shin	KX286980	KX287287	KX287570	KX287844	-	KX288430) KX288738	-	-	-
	CBS 113304		Erigeron annuus	-	H.D. Shin	KF251805	GU214658	(KF253610)	(KF253249)	KX288130	KX348051	KX288739	(KF253964)	-	-
	CPC 19492	Cercosporella sp.	Conyza canadensis	Brazil	B.S. Vieira	KX286981	KX287288	KX287571	KX287845	KX288131	KX288431	KX288740	KX289020	-	-
Cladosporium cladosporioides	CBS 112388 ^{NT}		Indoor air	Germany	Ch. Traumann	KX286982	HM148003	3 (HM148490)	(HM148244)) —	KX288432	2 -	-	-	-
Epicoleosporium ramularioides	CBS 141103^T ; CPC 10672	R. coleosporii	Coleosporium phellodendrion on Phellodendron amurense	South Korea	H.D. Shin	GU214688	GU214688	8 –	KX287846	-	KX288433	3 -	-	-	-
	CPC 10673	R. coleosporii	Coleosporium phellodendrion on Phellodendron amurense	South Korea	H.D. Shin	-	KX287289	-	KX287847	-	KX288434	 -	-	-	KX289242
Dissoconium aciculare	CBS 204.89		Astragalus sp.	Germany	T. Hijwegen	GU214419	AY725520	-	-	-	KX288435	5 –	-	-	-
Dothistroma pini	CBS 121005; CMW 24852		Pinus pallasiana	Russia	T.S. Bulgakov	KF251659	KF251155	(JX902075)	(KF253115)	-	KX348052	2 -	(JX901514)	(KF252653)	-
	CBS 116486		Pinus nigra	USA, Michigan	G. Adams	JX901823	JX901735	(JX902070)	(JX901621)	-	KX348053	3 -	(JX901509)	(JX902192)	-

Table 1. (Continue	ed).														
Species ⁴	Culture number ^{1,2}	Previous name ⁴	Host	Country	Collector	LSU	ITS	actA	tef1-α	gapdh	rpb2	his3	cmdA	tub2	chs-1
D. septosporum	CBS 128782; CPC 16798		Pinus mugo subsp. rostrata	Netherlands	W. Quaedvlieg	JX901829	JX901741	(JX902076)	(JX901627)	-	KX348054	ŧ –	(JX901515)	(JX902198)	-
Fusoidiella depressa	CBS 141335; CPC 14915	Pa. depressa	Angelica gigas	South Korea	H.D. Shin	KF251813	KF251309	-	(KF253256)	-	KX348055	5 –	(KF253972)) (KF252788) —
Filiella pastinacae	CBS 114116; UPSC 2633	P. pastinacae	Laserpitium latifolium	Sweden	K. & L. Holm	KF251832	KF251328	(KF253633)	(KF253275)	-	KX348056	6 –	(KF253980)) (KF252803)) —
Microcyclosporella mali	CBS 126136^T ; CPC 16184; HJS 300-07		Malus domestica	Slovenia	J. Frank	GU570547	GU570535	KX287572	(HM177424)	-	KX288436	ð –	-	-	-
Microcyclosporella sp.	CBS 118960; CUD3b	Pseudocercosporella sp.	-	USA, Illinois	J. Batzer	KX286985	KX287290	KX287573	KX287848	KX288132	KX288437	7 KX288741	-	-	-
	CBS 125654; RH7; GA3 3D1b	Pseudocercosporella sp.	<i>Malus</i> sp.	USA, Georgia	M. Wheeler	FJ031995	FJ425202	KX287574	KX287849	KX288133	KX288438	3 KX288742	-	-	-
	CBS 119461; RH2.2	Pseudocercosporella sp.	-	USA, Illinois	J. Batzer	KX286986	KX287291	KX287575	KX287850	KX288134	KX288439) KX288743	KX289021	-	-
	CBS 125653; RH6; MI3 20F1a	Pseudocercosporella sp.	<i>Malus</i> sp.	USA, Michigan	G. Sundin	FJ031994	FJ425201	KX287576	KX287851	KX288135	KX288440) _	-	-	-
	CBS 118969; UMD1a	Pseudocercosporella sp.	-	USA, Missouri	J. Batzer	KX286987	KX287292	KX287577	KX287852	KX288136	KX288441	KX288744	-	-	-
	CBS 125651; RH1; OH1 34D2a	Pseudocercosporella sp.	Malus sp.	USA, Ohio	M. Ellis	FJ031989	FJ425196	KX287578	KX287853	KX288137	KX288442	2 KX288745	KX289022	-	-
Mycosphaerelloides madeirae	CBS 112895^T ; CMW 14458; CPC 3745	M. madeirae	Eucalyptus globulus	Portugal	S. Denman	KF902017	AY725553	-	(KF903109)	-	KX348057	7 KX288746	(KF902545) –	-
	CBS 115936	<i>Ramularia</i> sp.	-	Netherlands	-	KX286988	AY853187	KX287579	KX287854	KX288138	KX288443	3 –	KX289023	-	-
	CBS 116066	<i>Ramularia</i> sp.	Quercus robur	Netherlands	-	KX286989	AY853188	KX287580	KX287855	KX288139	KX288444	4 KX288747	KX289024	-	-
	CBS 116068	<i>Ramularia</i> sp.	Quercus robur	Netherlands	-	KX286990	AY853189	KX287581	KX287856	KX288140	KX288445	5 KX288748	KX289025	-	-
Neocercospora ammicola	CBS 136450 ^T ; CCTU 1186	Cercospora sp.	Ammi majus	Iran	M. Arzanlou	KR232405	KR232407	(KR232411)	(KR232409)	-	KX288446	6 (KR232413)) —	-	-
Neopseudocercosporella brassicicola	a CBS 228.32	M. brassicicola	Brassica oleraceae	Denmark	-	KF251808	KF251304	(KF253613)	(KF253252)	-	KX348058	3 —	(KF253967)) (KF252783)) —
	CBS 173.88	M. brassicicola	Brassica oleracea	Germany	-	KX286991	KX287293	KX287582	KX287857	-	KX288447	7 _	-	_ (continued or	– n next page)

Table 1. (Conunu	ea).														
Species ⁴	Culture number ^{1,2}	Previous name ⁴	Host	Country	Collector	LSU	ITS	actA	tef1-α	gapdh	rpb2	his3	cmdA	tub2	chs-1
	CBS 267.53	M. brassicicola	Brassica oleraceae var. acephala subvar. sabelica	Netherlands	-	KF251809	KF251305	(KF253614)	(KF253253)	-	KX348059) _	(KF253968)	(KF252784) –
N. capsellae	CBS 135464; CPC 11677	<i>Mycosphaerella</i> sp.	Draba nemorosa var. hebecarpa	South Korea	H.D. Shin	KX286992	DQ303091	(KF253616)	KX287858	-	KX288448	8 -	(KF253970)	(KF252786)) –
	CPC 14774	P. capsellae	Raphanus sativus	South Korea	H.D. Shin	KX286993	KX287294	KX287583	KX287859	KX288141	KX288449) _	-	-	-
	CBS 131896; CPC 14773	P. capsellae	Raphanus sativus	South Korea	H.D. Shin	GU253714	GU269666	6 (GU320372)) (GU384383)) KX288142	KX288450) KX288749	-	-	-
	CBS 112032; HJS 601	P. capsellae	Brassica sp.	-	-	KF251824	KF251320	(KF253627)	(KF253267)	-	KX348060) _	(KF253975)	(KF252797)) –
	CBS 112033; HJS 600	P. capsellae	Brassica sp.	-	-	KF251810	KF251306	(KF253615)	(KF253254)	-	KX348061	-	(KF253969)	(KF252785) –
	CPC 12518		Capsella bursa-pastoris	South Korea	H.D. Shin	KX286994	KX287295	KX287584	KX287860	-	KX288451	KX288750	-	-	-
	CPC 12519		Capsella bursa-pastoris	South Korea	H.D. Shin	KX286995	KX287296	KX287585	KX287861	-	KX288452	2 KX288751	-	-	-
Pallidocercospora acaciigena	CBS 112515^T; CPC 3837		Acacia mangium	Venezuela	M.J. Wingfield	KF902166	KF901805	(KF903455)	(KF903125)	-	KX348062	2 –	(KF902564)	(KF902828) –
Pal. crystallina	CBS 111045; CPC 1179		Eucalyptus grandis	South Africa	M.J. Wingfield	KF902051	KF901704	(KF903424)	(KF903129)	-	KX348063	8 —	(KF902568)	(KF902832)) –
Pal. heimii	CPC 11716	M. parkii	-	Brazil	A.C. Alfenas	KF901937	KF901612	(KF903605)	(KF903134)	-	KX348064	+ _	(KF902573)	(KF902837) –
Pal. irregulariramosa	CBS 111211; CPC 1362		Eucalyptus saligna	South Africa	M.J. Wingfield	KF902053	KX287297	(KF903441)	(KF903139)	-	KX348065	ō —	(KF902578)	(KF902842)) –
Pal. konae	CBS 111028; CPC 2125; JT 526		<i>Leucadendron</i> cv. Safari Sunset	USA, Hawaii	P.W. Crous	KF902158	KF901798	(KF903422)	(KF903140)	-	KX348066	6 –	-	(KF902843)) –
Parapenidiella pseudotasmaniensis	CBS 111681; CPC 1539	<i>Mycovellosiella</i> sp.	-	-	-	KX286996	KX287298	-	-	-	KX288453	8 —	-	-	-
	CBS 124991[⊤]; CPC 12400		Eucalyptus globulus	Australia	I.W. Smith	KF901844	KF901522	(KF903562)	(KF903152)	-	KX348067	′ _	(KF902589)	(KF902855) –
Pp. tasmaniensis	CBS 111687^T; CMW 14780; CPC 1555		Eucalyptus nitens	Australia	-	KF901843	DQ267591	(KF903451)	(KF903150)	-	KX348068	3 —	(KF902587)	(KF902853)) –
Pseudocercospora dingleyae	CBS 114645	P. dingleyae	Haloragis erecta	New Zealand	-	KX286997	KX287299	-	-	-	KX288454	l –	-	-	-
Ps. eucalyptorum	CBS 132015; CPC 11713		Eucalyptus globulus	Spain	P. Mansilla	KF902096	KF901743	(KF903604)	(GU384523)) —	KX348069) _	(KF902615)	(KF902884) –
	CBS 114866; CPC 11		Eucalyptus nitens	South Africa	P.W. Crous	KF902067	KF901720	(KF903474)	(KF903195)	-	KX348070) _	(KF902627)	(KF902897) –

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Table 1. (Continue	ed).														
Species ⁴	Culture number ^{1,2}	Previous name ⁴	Host	Country	Collector	LSU	ITS	actA	tef1-α	gapdh	rpb2	his3	cmdA	tub2	chs-1
Ps. flavomarginata	CBS 124990; CPC 13492		Eucalyptus camaldulensis	Thailand	W. Himaman	GU253817	KF251323	(KF253629)	(KF253270)	-	KX34807	1 –	-	(JX902274)	-
Ps. fori	CBS 113286; CMW 9096		Eucalyptus sp.	South Africa	J. Roux	KF902068	KF901721	(KF903463)	(KF903197)	-	KX348072	2 –	(KF902628) (KF902899) —
Ps. macadamiae	CBS 133432^{ET}; BRIP 55526a		Macadamia integrifolia	Australia, Queensland	O.A. Akinsanmi	KX286998	KX287300	-	-	-	KX288455	5 –	-	-	-
Ps. metrosideri	CBS 114294	P. metrosideri	Metrosideros excelsa	New Zealand	-	KX286999	KX287301	-	-	-	KX288456	ô –	-	-	-
Ps. myopori	CBS 114644	Cercospora sp.	Myoporum laetum	New Zealand	-	KX287000	KX287302	-	-	-	KX288457	7 –	-	-	-
Ps. norchiensis	CBS 120738^T; CPC 13049		Eucalyptus sp.	Italy	W. Gams	GU253780	KF901665	(KF903531)	(GU384464)	-	KX348073	3 –	(KF902633) (KF902906) —
Ps. pistacina	CPC 23118	Pseudocercospora-like sp.	Pistacia vera	Turkey	K. Sarpkaya	KF442674	KF442647	-	KF442637	-	KX348074	4 —	-	(KF442733) —
Ps. robusta	CBS 111175^T; CMW 5151; CPC 1269		Eucalyptus robur	Malaysia	M.J. Wingfield	KF902020	KF442500	(JX902150)	(JX901694)	-	KX348075	5 –	(KF902640) (KF442463) —
Pseudocercospora sp.	CPC 19535	Cercosporella sp.	Eichhornia azurea	Brazil	D.J. Soares	KX287001	KX287303	-	-	-	KX288458	8 –	-	-	-
	CBS 113386	<i>Mycovellosiella</i> sp.	Chromolaena odorata	Guatemala	M.J. Morris	KX287002	DQ676532	2 -	-	-	KX288459	9 (DQ676557) –	-	-
	CPC 19537	Cercosporella sp.	Eichhornia azurea	Brazil	D.J. Soares	KX287003	KX287304	-	-	-	KX288460) –	-	-	-
	CBS 110780; CPC 204	Pseudocercosporella sp.	Syzygium cordatum	South Africa	P.W. Crous	KX287004	KX287305	-	-	-	KX28846 ⁻	1 –	-	-	-
Ps. vitis	CBS 132012; CPC 11595		Vitis vinifera	South Korea	-	KF902011	KF901669	(KF903603)	(GU384541)	-	KX348076	6 –	(KF902649) (KF902927) —
Pseudocercosporella bakeri	CBS 119488; Lynfield 1252		lpomoea indica	New Zealand	C.F. Hill	KX287005	KX287306	KX287586	KX287862	-	KX288462	2 –	-	-	-
	CBS 125685^{ET}; CPC 17570		lpomoea aquatica	Laos	P. Phengsintham	GU570553	GU570542	2 KX287587	KX287863	-	KX288463	3 KX288752	-	-	-
Ramichloridium apiculatum	CBS 400.76; IMI 088021		Soil	Pakistan	-	EU041851	EU041794	-	-	-	KX348077	7 –	-	-	-
	CBS 156.59^T; ATCC 13211;		Forest soil	USA, Georgia	-	EU041848	EU041791	-	-	-	-	-	-	-	-
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Table 1. (Continu	ed).														
Species ⁴	Culture number ^{1,2}	Previous name ⁴	Host	Country	Collector	LSU	ITS	actA	<i>tef1-</i> α	gapdh	rpb2	his3	cmdA	tub2	chs-1
	IMI 100716; JCM 6972; MUCL 15753; MUCL 7991; QM 7716						_			_			_	_	
Ramichloridium sp.	CPC 12310	Pseudocercosporella sp.	Vicia amurensis	South Korea	H.D. Shin	GU214687	GU214687	' _	-	-	KX28846	4 —	-	-	-
Ramularia abscondita	CBS 114727; UPSC 3341		Arctium tomentosum	Sweden	E. Gunnerbeck	KX287006	KX287307	KX287588	KX287864	KX288143	KX28846	5 KX288753	KX289026	KX289126	-
R. acris	CPC 25898		Ranunculus acris	Netherlands	S.I.R. Videira	KX287007	KX287308	KX287589	KX287865	KX288144	KX28846	6 KX288754	-	-	-
	CPC 25899		Ranunculus acris	Netherlands	S.I.R. Videira	KX287008	KX287309	KX287590	KX287866	KX288145	KX28846	7 KX288755	-	-	-
	CPC 25900		?Ranunculus sp.	Netherlands	U. Damm	KX287009	KX287310	KX287591	KX287867	KX288146	KX28846	8 KX288756	-	-	-
	CBS 109794	R. didyma var. didyma	a Ranunculus sp.	Netherlands	G. Verkley	KX287010	KX287311	KX287592	KX287868	KX288147	KX28846	9 KX288757	-	KX289127	-
R. acroptili	CPC 18723	Ramularia sp.	Cynara cardunculus	USA, California	L. Davenport	KX287011	KX287312	KX287593	KX287869	KX288148	KX28847	0 KX288758	-	KX289128	-
	CPC 18724	<i>Ramularia</i> sp.	Cynara cardunculus	USA, California	L. Davenport	KX287012	KX287313	KX287594	KX287870	KX288149	KX28847	1 KX288759	-	KX289129	-
	CBS 120252^{ET} ; 98-001		Acroptilon repens	Turkey	R. Sobhian	GU214689	GU214689	KX287595	KX287871	KX288150	KX28847	2 KX288760	KX289027	-	-
	CBS 120253; 04-011	C. centaureicola	Centaurea solstitialis	Greece	D. Berner	EU019257	EU019257	KX287596	KX287872	KX288151	KX28847	3 KX288761	KX289028	KX289130	-
R. actinidiae	CPC 11674*	Ramularia sp.	Actinidia polygama	South Korea	H.D. Shin	KX287013	KX287314	-	-	-	-	-	-	-	-
	CPC 11675	Ramularia sp.	Actinidia polygama	South Korea	H.D. Shin	KX287014	KX287315	KX287597	KX287873	KX288152	KX288474	4 KX288762	-	-	-
R. agastaches	CPC 10819	R. lamii	Agastache rugosa	South Korea	H.D. Shin	KX287015	KX287316	KX287598	KX287874	KX288153	KX28847	5 KX288763	-	KX289131	-
	CPC 10820	R. lamii	Agastache rugosa	South Korea	H.D. Shin	KX287016	KX287317	KX287599	KX287875	KX288154	KX28847	6 KX288764	KX289029	KX289132	-
	CPC 10821	R. lamii	Agastache rugosa	South Korea	H.D. Shin	KX287017	KX287318	KX287600	KX287876	KX288155	KX28847	7 KX288765	KX289030	KX289133	-
R. agrimoniae	CPC 11450	Ramularia sp.	Agrimonia pilosa	South Korea	H.D. Shin	KX287018	KX287319	KX287601	KX287877	KX288156	KX28847	8 KX288766	-	KX289134	-
	CPC 11451	Ramularia sp.	Agrimonia pilosa	South Korea	H.D. Shin	KX287019	KX287320	KX287602	KX287878	KX288157	KX28847	9 KX288767	-	KX289135	-
	CPC 11452	Ramularia sp.	Agrimonia pilosa	South Korea	H.D. Shin	KX287020	KX287321	KX287603	KX287879	KX288158	KX28848	0 KX288768	-	KX289136	-
	CPC 11651		Agrimonia pilosa	South Korea	H.D. Shin	KX287021	KX287322	KX287604	KX287880	KX288159	KX28848	1 KX288769	-	KX289137	KX289243
	CPC 11652		Agrimonia pilosa	South Korea	H.D. Shin	KX287022	KX287323	KX287605	KX287881	KX288160	KX28848	2 KX288770	-	KX289138	-

Table 1. (Continu	ued).														
Species ⁴	Culture number ^{1,2}	Previous name⁴	Host	Country	Collector	LSU	ITS	actA	tef1-α	gapdh	rpb2	his3	cmdA	tub2	chs-1
	CPC 11653		Agrimonia pilosa	South Korea	H.D. Shin	KJ504743	KJ504784	KJ504448	KJ504699	KJ504567	KJ504655	6 KJ504611	-	KJ504481	-
R. alangiicola	CPC 10299	Ph. alangii	Alangium platanifolium var. macrophylum	South Korea	H.D. Shin	KX287023	KX287324	-	KX287882	KX288161	KX288483	3 KX288771	-	-	-
R. aplospora	CBS 545.82 ^{ET}	Cladosporium sp.	Mildew on Alchemilla vulgaris	Germany	-	KP894110	EU040238	KP894325	KP894435	KP894545	KP894656	6 KP894767	KP894878	KP894965	-
	CBS 109120		Alchemilla vulgaris	Austria	G. Verkley	KP894108	KP894217	KP894323	KP894433	KP894543	KP894654	1 KP894765	KP894876	-	-
	CBS 109121		Alchemilla vulgaris	Austria	G. Verkley	KX287024	KX287325	KX287606	KX287883	KX288162	KX288484	4 KX288772	KX289031	-	-
	CBS 237.73; CCM F-367		Alchemilla xanthochlora	former Czechoslovakia	-	KX287025	KX287326	KX287607	KX287884	KX288163	KX28848	5 KX288773	KX289032	KX289139	-
	CBS 109013		Alchemilla vulgaris	Austria	G. Verkley	KX287026	KX287327	KP894322	KX287885	KX288164	KX288486	6 KX288774	KX289033	KX289140	-
	CBS 109014		Alchemilla vulgaris	Austria	G. Verkley	KP894107	KP894216	KP894322	KP894432	KP894542	KP894653	3 KP894764	KP894875	-	-
	CBS 114118; UPSC 2679		Alchemilla vulgaris	Sweden	E. Gunnerbeck	KP894109	KP894218	KP894324	KP894434	KP894544	KP894655	5 KP894766	KP894877	-	-
R. archangelicae	CBS 108991		Angelica sylvestris	Austria	G. Verkley	KX287027	KX287328	KX287608	KX287886	KX288165	KX288487	7 KX288775	KX289034	-	-
	CBS 108992		Angelica sylvestris	Austria	G. Verkley	KX287028	KX287329	KX287609	KX287887	KX288166	KX288488	3 KX288776	KX289035	-	-
	CBS 109011		Angelica sylvestris	Austria	G. Verkley	KX287029	KX287330	KX287610	KX287888	KX288167	KX288489) KX288777	KX289036	-	KX289244
	CBS 109012		Angelica sylvestris	Austria	G. Verkley	KX287030	KX287331	KX287611	KX287889	KX288168	KX288490) KX288778	KX289037	-	KX289245
	CBS 288.49	M. rubella	Angelica sylvestris	Austria	-	KX287031	AY490767	KX287612	KX287890	KX288169	KX28849 ⁻	1 KX288779	KX289038	-	-
R. armoraciae	CBS 241.90 ^{ET}		Armoracia rusticana	Germany	S. Petzoldt	KX287032	KX287332	KX287613	KX287891	KX288170	KX288492	2 KX288780	-	-	-
	CBS 253.28		Armoracia rusticana	Netherlands	-	KX287033	KX287333	KX287614	KX287892	KX288171	KX288493	3 KX288781	-	KX289141	KX289246
R. asteris	CBS 131.21; ATCC 44003		Aster tripolium	Netherlands	-	KX287034	KX287334	KX287615	KX287893	KX288172	KX288494	4 KX288782	KX289039	KX289142	-
R. bellunensis	CBS 118417		Argyranthemum frutescens	New Zealand	-	KX287035	KX287335	KX287616	KX287894	KX288173	KX348078	3 KX288783	-	-	-
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Species ⁴	Culture number ^{1,2}	Previous name ⁴	Host	Country	Collector	LSU	ITS	actA	tef1-α	gapdh	rpb2	his3	cmdA	tub2	chs-1
	CBS 116.43		Chrysanthemum frutescens	Netherlands	-	KX287036	KX287336	KX287617	KX287895	KX288174	KX288495	5 KX288784	-	-	-
R. beticola	CPC 30065		Beta vulgaris	Denmark	A.L. Hansen	KX287037	KX287337	KX287618	KX287896	KX288175	KX288496	6 KX288785	KX289040	-	-
	CBS 141109^{ET}; CPC 30066		Beta vulgaris	France	A. Champeil	KX287038	KX287338	KX287619	KX287897	KX288176	KX288497	7 KX288786	KX289041	-	-
	CPC 30067		Beta vulgaris	Netherlands	S.I.R. Videira	KX287039	KX287339	KX287620	KX287898	KX288177	KX288498	3 KX288787	KX289042	-	-
	CPC 30063		Beta vulgaris	Netherlands	S.I.R. Videira	KX287040	KX287340	KX287621	KX287899	KX288178	KX288499	9 KX288788	KX289043	-	-
	CPC 30064		Beta vulgaris	Netherlands	-	KX287041	KX287341	KX287622	KX287900	KX288179	KX288500) KX288789	KX289044	-	-
	CBS 341.29	R. betae	-	Germany	-	KX287042	KX287342	KX287623	KX287901	KX288180	KX288501	1 KX288790	KX289045	-	-
	CBS 113540; UPSC 1612		Beta vulgaris	Sweden	O. Constantinescu	KX287043	KX287343	KX287624	KX287902	KX288181	KX288502	2 KX288791	KX289046	-	-
	CBS 151.67		Beta vulgaris	Switzerland	-	KX287044	KX287344	KX287625	KX287903	KX288182	KX288503	3 KX288792	KX289047	-	-
R. bosniaca	CBS 123880; V6024.2	<i>Ramularia</i> sp.	Scabiosa ochroleuca	Czech Republic	G. Verkley	KX287045	KX287345	KX287626	KX287904	KX288183	KX288504	4 KX288793	-	KX289143	-
	CBS 123881; V6024.1	<i>Ramularia</i> sp.	Scabiosa ochroleuca	Czech Republic	G. Verkley	KX287046	KX287346	KX287627	KX287905	KX288184	KX288505	5 KX288794	-	KX289144	-
R. buniadis	CBS 114301; UPSC 2718		Bunias orientalis	Sweden	E. Gunnerbeck	KX287047	KX287347	KX287628	KX287906	KX288185	KX288506	6 KX288795	KX289048	KX289145	-
R. calcea	CBS 101612		Symphytum sp.	Germany	G. Arnold	KP894111	KP894219	KP894326	KP894436	KP894546	KP894657	7 KP894768	KP894879	KP894966	-
	CBS 101613		Symphytum sp.	Germany	G. Arnold	KP894112	KP894220	KP894327	KP894437	KP894547	KP894658	3 KP894769	-	KP894967	-
	CBS 114442; UPSC 2727	R. lactea	Viola hirta	Sweden	E. Gunnerbeck	KP894122	KP894229	KP894337	KP894447	KP894557	KP894668	3 KP894779	KP894884	KP894972	-
R. carneola	CBS 108975		Scrophularia nodosa	Netherlands	G. Verkley	KX287048	KX287348	KX287629	KX287907	KX288186	KX288507	7 KX288796	KX289049	KX289146	-
	CBS 108976		Scrophularia nodosa	Netherlands	G. Verkley	KX287049	KX287349	KX287630	KX287908	KX288187	KX288508	3 KX288797	KX289050	KX289147	KX289247
	CBS 108977		Scrophularia nodosa	Netherlands	G. Verkley	KX287050	KX287350	KX287631	KX287909	KX288188	KX288509	9 KX288798	KX289051	KX289148	-
	CBS 108978		Scrophularia nodosa	Netherlands	G. Verkley	KX287051	KX287351	KX287632	KX287910	KX288189	KX288510) KX288799	KX289052	KX289149	-
	CBS 109847		Scrophularia nodosa	Netherlands	G. Verkley	KX287052	KX287352	KX287633	KX287911	KX288190	KX288511	1 KX288800	KX289053	KX289150	-
R. cerastiicola	CBS 115913^T; CPC 11290	M. cerastiicola	Cerastium semidecandrum	Netherlands	A. Aptroot	KF251727	KF251224	KX287634	KF253180	KX288191	KX348079	9 KX288801	-	-	-
R. chamaedryos	CBS 116577; UPSC 2322		Veronica chamaedrys	Sweden	E. Gunnerbeck	KX287053	KX287353	KX287635	KX287912	KX288192	KX288512	2 KX288802	KX289054	-	-
	CBS 113307	<i>Ramularia</i> sp.	Veronica didyma	South Korea	H.D. Shin	KX287054	KX287354	KX287636	KX287913	KX288193	KX288513	3 KX288803	-	KX289151	-

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Table 1. (Continu	ied).														
Species ⁴	Culture number ^{1,2}	Previous name ⁴	Host	Country	Collector	LSU	ITS	actA	tef1-α	gapdh	rpb2	his3	cmdA	tub2	chs-1
	CBS 131773; KACC 42885		Veronica persica	South Korea	H.D. Shin & M.J. Park	. KX287055	KX287355	KX287637	KX287914	KX288194	KX288514	4 KX288804	-	KX289152	-
	CBS 118794	R. veronicae	Veronica persica	New Zealand	-	KX287056	KX287356	KX287638	KX287915	KX288195	KX288515	5 KX288805	KX289055	-	-
	CBS 114731; UPSC 3243	R. anagallidis	Veronica anagallis-aquatica	Sweden	E. Gunnerbeck	KX287057	KX287357	KX287639	KX287916	KX288196	KX288516	6 KX288806	-	-	-
R. chelidonii	CPC 12208		Hylomecon vernalis	South Korea	H.D. Shin	KX287058	KX287358	KX287640	KX287917	KX288197	KX288517	7 KX288807	KX289056	-	-
	CPC 12209		Hylomecon vernalis	South Korea	H.D. Shin	KX287059	KX287359	KX287641	KX287918	KX288198	KX288518	3 KX288808	-	-	-
	CBS 113317	<i>Ramularia</i> sp.	Hylomecon vernalis	South Korea	H.D. Shin	KX287060	KX287360	KX287642	KX287919	KX288199	KX288519) KX288809	-	-	-
R. coleosporii	CPC 10653	<i>Ramularia</i> sp.	Coleosporium eupatorii on Eupatorium japonicum	South Korea	H.D. Shin	KX287061	KX287361	-	KX287920	-	KX288520) –	-	-	-
	CPC 10669	<i>Ramularia</i> sp.	Coleosporium eupatorii on Eupatorium japonicum	South Korea	H.D. Shin	KX287062	KX287362	KX287643	KX287921	KX288200	KX288521	KX288810	-	KX289153	-
	CPC 10731	<i>Ramularia</i> sp.	Coleosporium clematidis- apiifoliae on Clematis apiifolia	South Korea	H.D. Shin	KX287063	KX287363	KX287644	KX287922	KX288201	KX288522	2 KX288811	-	KX289154	-
	CPC 10732	<i>Ramularia</i> sp.	Coleosporium clematidis- apiifoliae on Clematis apiifolia	South Korea	H.D. Shin	KX287064	KX287364	KX287645	KX287923	KX288202	KX288523	3 KX288812	-	KX289155	-
	CPC 10733	<i>Ramularia</i> sp.	Coleosporium clematidis-apiifoliae on Clematis apiifolia	South Korea	H.D. Shin	KX287065	KX287365	KX287646	KX287924	KX288203	KX288524	¥ KX288813	-	-	-
	CPC 10746	<i>Ramularia</i> sp.	Coleosporium eupatorii on Eupatorium lindleyanum	South Korea	H.D. Shin	KX287066	KX287366	KX287647	KX287925	KX288204	KX288525	5 KX288814	-	KX289156	-
	CPC 10747	<i>Ramularia</i> sp.	Coleosporium eupatorii on Eupatorium lindleyanum	South Korea	H.D. Shin	KX287067	KX287367	KX287648	KX287926	KX288205	KX288526	6 KX288815	-	KX289157	-
	CPC 10748	<i>Ramularia</i> sp.	Coleosporium eupatorii on Eupatorium lindleyanum	South Korea	H.D. Shin	KX287068	KX287368	KX287649	KX287927	KX288206	KX288527	7 KX288816	-	KX289158	-

Table 1 (Continued)

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Species ⁴	Culture number ^{1,2}	Previous name ⁴	Host	Country	Collector	LSU	ITS	actA	<i>tef1-</i> α	gapdh	rpb2	his3	cmdA	tub2	chs-1
	CPC 11516		Coleosporium plectranthi on Plectranthus japonicus	South Korea	H.D. Shin	KX287069	KX287369	KX287650	KX287928	KX288207	KX288528	3 KX288817	-	KX289159	-
	CBS 131753; KACC 42483		Coleosporium perillae on Perilla frutescens var. japonica	South Korea	H.D. Shin & M.J. Park	KX287070	KX287370	KX287651	KX287929	KX288208	KX288529) KX288818	-	KX289160	-
	CBS 131754; KACC 43177		Coleosporium asterum on Aster pilosus	South Korea	H.D. Shin & M.J. Park	KX287071	KX287371	KX287652	KX287930	KX288209	KX288530) KX288819	-	KX289161	-
	CBS 131755; KACC 43977		Coleosporium asterum on Aster pilosus	South Korea	H.D. Shin & M.J. Park	KX287072	KX287372	KX287653	KX287931	KX288210	-	KX288820	-	KX289162	-
	CBS 131756; KACC 43200		Coleosporium clematidis-apiifoliae on Clematis apiifolia	South Korea	H.D. Shin & M.J. Park	KX287073	KX287373	KX287654	KX287932	KX288211	KX288531	KX288821	-	KX289163	-
	CBS 131757; KACC 43185		Coleosporium horianum on Codonopsis Ianceolata	South Korea	H.D. Shin & M.J. Park	KX287074	KX287374	KX287655	KX287933	KX288212	KX288532	2 KX288822	-	-	KX289248
	CBS 131758; KACC 44854		Coleosporium cacaliae on Syneilesis palmata	South Korea	H.D. Shin & M.J. Park	KX287075	KX287375	KX287656	KX287934	KX288213	KX288533	8 KX288823	-	-	-
	CBS 131759; KACC 44073		Coleosporium horianum on Codonopsis lanceolata	South Korea	H.D. Shin & M.J. Park	KX287076	KX287376	KX287657	KX287935	KX288214	KX288534	KX288824	-	-	-
	CBS 131760; KACC 44081		Coleosporium horianum on Codonopsis lanceolata	South Korea	H.D. Shin & M.J. Park	KX287077	KX287377	KX287658	KX287936	KX288215	KX288535	5 KX288825	-	KX289164	-
	CBS 131761; KACC 44855		Coleosporium saussureae on Saussurea pulchella	South Korea	H.D. Shin & M.J. Park	KX287078	KX287378	KX287659	KX287937	KX288216	KX288536	6 KX288826	-	KX289165	-
	CBS 131762; KACC 44860		Coleosporium sp. on Solidago serotina	South Korea	H.D. Shin & M.J. Park	KX287079	KX287379	KX287660	KX287938	KX288217	KX288537	7 KX288827	-	KX289166	-

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Table 1. (Continu	ed).														
Species ⁴	Culture number ^{1,2}	Previous name ⁴	Host	Country	Collector	LSU	ITS	actA	<i>tef1-</i> α	gapdh	rpb2	his3	cmdA	tub2	chs-1
	CBS 131763; KACC 42484		Coleosporium eupatorii on Eupatorium japonicum	South Korea	H.D. Shin & M.J. Park	KX287080	KX287380	KX287661	KX287939	KX288218	KX288538	KX288828	KX289057	KX289167	KX289249
	CBS 131764; KACC 43182		Coleosporium eupatorii on Eupatorium lindleyanum	South Korea	H.D. Shin & M.J. Park	KX287081	KX287381	KX287662	KX287940	KX288219	KX288539	KX288829	-	KX289168	-
	CBS 131765; KACC 42635		Coleosporium asterum on Aster pilosus	South Korea	H.D. Shin & M.J. Park	KX287082	KX287382	KX287663	KX287941	KX288220	KX288540	KX288830	-	KX289169	-
	CBS 131766; KACC 43058		Coleosporium clerodendr on Clerodendron trichotomum	i South Korea	H.D. Shin & M.J. Park	KX287083	KX287383	KX287664	KX287942	KX288221	KX288541	KX288831	-	KX289170	-
	CBS 131767; KACC 44053		Pileolaria shiraiana on Rhus trichocarpa	South Korea	H.D. Shin & M.J. Park	KX287084	KX287384	KX287665	KX287943	KX288222	KX288542	KX288832	-	KX289171	-
R. collo-cygni	CBS 101180 ^{№™}		Hordeum vulgare	Austria	Züchtungsfirma Saatbau Linz	KX287085	KX287385	KX287666	KX287944	KX288223	KX288543	KX288833	-	KX289172	-
	CBS 101181		Hordeum vulgare	Germany, Bavaria	E. Sachs	KJ504745	KJ504786	KJ504450	KJ504701	KJ504569	KJ504657	KJ504613	KJ504513	KJ504483	-
	CBS 101182		Hordeum vulgare	Germany, Bavaria	E. Sachs	KX287086	KX287386	KX287667	KX287945	KX288224	KX288544	KX288834	KX289058	KX289173	-
	CBS 119442; CPC 12688; V22	2	Hordeum vulgare	Norway	S. Salamati	KX287087	KX287387	KX287668	KX287946	KX288225	KX288545	KX288835	-	-	-
	CBS 119441; CPC 12690; V40)	Hordeum vulgare	Norway	S. Salamati	KX287088	KX287388	KX287669	KX287947	KX288226	KX288546	KX288836	-	-	-
	CBS 119440; CPC 12692; V58	3	Hordeum vulgare	Norway	S. Salamati	KX287089	KX287389	KX287670	KX287948	KX288227	KX288547	KX288837	KX289059	-	-
	CBS 119439; CPC 12693; V74	ļ	Hordeum vulgare	Norway	S. Salamati	KX287090	KX287390	KX287671	KX287949	KX288228	KX288548	KX288838	KX289060	-	-
R. coryli	CBS 117800; CPC 12090	R. endophylla	Corylus avellana	Netherlands	G. Verkley	KX287091	KX287391	KX287672	KX287950	KX288229	KX288549	KX288839	KX289061	-	KX289250
R. cupulariae	CBS 235.73		<i>Inula</i> sp.	former Czechoslovakia	L. Marvanová	KX287092	KX287392	KX287673	KX287951	KX288230	KX288550	KX288840	-	KX289174	-
R. cyclaminicola	CBS 399.51		Cyclamen persicum	USA	-	KX287093	KX287393	KX287674	KX287952	KX288231	KX288551	KX288841	-	-	-
R. cynarae	CPC 18427		Cynara cardunculus	USA, California	S.T. Koike	KX287094	KX287394	KX287675	KX287953	KX288232	KX288552	KX288842	-	KX289175	-
													(continued or	n next page)

Table 1. (Continu	led).														
Species ⁴	Culture number ^{1,2}	Previous name ⁴	Host	Country	Collector	LSU	ITS	actA	<i>tef1-</i> α	gapdh	rpb2	his3	cmdA	tub2	chs-1
	CBS 128779; CPC 18725		Carthamus tinctorius	USA, California	S.T. Koike	KX287095	HQ728118	3 KX287676	KX287954	KX288233	KX288553	3 KX288843	-	KX289176	-
	CBS 128912^{ET}; CPC 18426		Cynara cardunculus	USA, California	S.T. Koike	KX287096	HQ728117	7 KX287677	KX287955	KX288234	KX288554	4 KX288844	-	KX289177	-
	CBS 114728; UPSC 3248	R. cirsii	Cirsium arvense	Sweden	E. Gunnerbeck	KX287097	KX287395	KX287678	KX287956	KX288235	KX288555	5 KX288845	-	KX289178	-
	CPC 25896		Carex acutiformis	Netherlands	S.I.R. Videira	KX287098	KX287396	KX287679	KX287957	KX288236	KX288556	6 KX288846	-	-	-
	CPC 25897		Carduus sp.	Netherlands	S.I.R. Videira	KX287099	KX287397	KX287680	KX287958	KX288237	KX288557	7 KX288847	-	KX289179	-
	CBS 114729; UPSC 3338	R. cardui	Carduus crispus	Sweden	E. Gunnerbeck	KX287100	KX287398	KX287681	KX287959	KX288238	KX288558	3 KX288848	-	KX289180	-
R. deusta	CBS 473.50; IMI 099672	R. deusta f. latifolia	Lathyrus latifolius	Guadeloupe	-	KX287101	KX287399	KX287682	KX287960	KX288239	KX288559) KX288849	KX289062	KX289181	-
R. didyma var. didyma	CBS 114299; UPSC 2746	R. didyma	Ranunculus repens	Sweden	E. Gunnerbeck	KX287102	KX287400	KX287683	KX287961	KX288240	KX288560) KX288850	-	KX289182	-
	CBS 420.67	R. didyma	Ranunculus repens	UK, England	-	KX287103	KX287401	KX287684	KX287962	KX288241	KX28856	1 KX288851	-	KX289183	-
	CBS 431.67*	R. didyma	Ranunculus repens	Luxembourg	-	KX287104	KX287402	KX287685	KX287963	KX288242	-	KX288852	-	-	-
R. diervillae	CPC 16860	<i>Ramularia</i> sp.	Diervilla lonicera	Canada	K.A. Seifert	KX287105	KX287403	KX287686	KX287964	KX288243	KX288562	2 KX288853	-	KX289184	-
	CPC 16864	<i>Ramularia</i> sp.	Diervilla lonicera	Canada	K.A. Seifert	KX287106	KX287404	KX287687	KX287965	KX288244	KX288563	3 KX288854	-	KX289185	-
	CPC 16859	<i>Ramularia</i> sp.	Diervilla lonicera	Canada	K.A. Seifert	KX287107	KX287405	KX287688	KX287966	KX288245	KX288564	1 –	-	KX289186	-
	CPC 16863	<i>Ramularia</i> sp.	Diervilla lonicera	Canada	K.A. Seifert	KX287108	KX287406	KX287689	KX287967	KX288246	KX288565	5 KX288855	-	KX289187	-
R. digitalis-ambiguae	CBS 434.67	R. variabilis	Digitalis purpurea	Luxembourg	-	KX287109	KX287407	KX287690	KX287968	KX288247	KX288566	6 KX288856	KX289063	-	-
	CBS 297.37 ^T	R. variabilis	Digitalis sp.	Netherlands	-	KX287110	KX287408	KX287691	KX287969	KX288248	KX288567	7 KX288857	-	-	-
R. endophylla	CBS 113871		Quercus robur	Netherlands	G. Verkley	KP894130	KP894237	KP894345	KP894455	KP894566	KP894677	7 KP894787	KP894891	KP894977	-
	CBS 113265 ^{ET}		Quercus robur	Netherlands	G. Verkley	AY490776	AY490763	KF903461	KF253276	KP894562	KP894673	3 KP207603	KF253981	KP894975	-
	CBS 101680		Castanea sativa	Netherlands	A. Aptroot	KP894126	KP894233	KP894341	KP894451	KP894561	KP894672	2 KP894783	KP894887	KP894974	-
	CBS 115303		Quercus robur	Netherlands	-	KP894133	KP894240	KP894348	KP894458	KP894569	KP894680) KP894790	KP894894	-	-
	CBS 113869		Quercus robur	Netherlands	G. Verkley	KP894128	KP894235	KP894343	KP894453	KP894564	KP894675	5 KP894785	KP894889	-	-
	CBS 115302		Quercus robur	Netherlands	-	KP894132	KP894239	KP894347	KP894457	KP894568	KP894679) KP894789	KP894893	KP894978	-
R. eucalypti	CBS 120728; CPC 13304		Eucalyptus sp.	Australia, Queensland	P.W. Crous	KJ504751	KJ504793	KJ504457	KJ504708	KJ504576	KJ504664	KJ504620	KJ504520	-	-
	CPC 19188	<i>Ramularia</i> sp.	Phragmites sp.	Netherlands	P.W. Crous	KJ504756	KJ504798	KJ504462	KJ504713	KJ504581	KJ504669	KJ504625	KJ504524	KJ504491	-
	CBS 120726^T ; CPC 13043		Corymbia grandifolia	Italy	W. Gams	KF251834	KJ504792	KJ504456	KJ504707	KJ504575	KJ504663	KJ504619	KJ504519	-	KJ504542
R. euonymicola	CBS 113308 ^T	Ramularia sp.	Euonymus alatus	South Korea	H.D. Shin	KX287111	KX287409	KX287692	KX287970	KX288249	KX288568	3 KX288858	_	KX289188	_

KX287112 KX287410 KX287693 KX287971 KX288250 KX288569 KX288859 -

Italy

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Gaultheria shallon

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R. gaultheriae

CBS 299.80^T

Ramularia sp.

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Table 1. (Contin	ued).														
Species ⁴	Culture number ^{1,2}	Previous name ⁴	Host	Country	Collector	LSU	ITS	actA	tef1-α	gapdh	rpb2	his3	cmdA	tub2	chs-1
R. gei	CBS 344.49		Geum urbanum	Netherlands	J.A. von Arx	KX287113	KX287411	KX287694	KX287972	KX288251	KX288570) KX288860	KX289064	-	-
	CBS 113977; UPSC 2323		Geum sp.	Sweden	E. Gunnerbeck	KX287114	KX287412	KX287695	KX287973	KX288252	KX28857	KX288861	KX289065	KX289189	-
R. geranii	CBS 159.24		Geranium pyrenaicum	France	-	KX287115	6 KX287413	KX287696	KX287974	KX288253	KX288572	2 KX288862	KX289066	KX289190	KX289251
	CBS 160.24 ^{ET}		Geranium sylvaticum	France	C. Killian	KX287116	6 KX287414	KX287697	KX287975	KX288254	KX288573	3 KX288863	KX289067	KX289191	-
R. geraniicola	CPC 25912 [™]		Geranium sp.	Netherlands	U. Damm	KX287117	KX287415	KX287698	KX287976	KX288255	KX288574	KX288864	-	-	-
R. glechomatis	CBS 343.49	R. calcea	Glechoma hederacea	Netherlands	-	KX287118	KX287416	KX287699	KX287977	KX288256	KX288575	5 KX288865	-	KX289192	-
	CBS 108979		Glechoma hederacea	Netherlands	G. Verkley	KJ504757	KJ504799	KJ504463	KJ504714	KJ504582	KJ504670	KJ504626	-	KJ504492	KJ504543
	CBS 108980		Glechoma hederacea	Netherlands	G. Verkley	KX287119	KX287417	KX287700	KX287978	KX288257	KX288576	6 KX288866	-	KX289193	-
R. glennii	CBS 129441^T; det. 11-013M		Human bronchial alveolar lavage	Netherlands	-	KJ504728	KJ504769	KJ504433	KJ504684	KJ504552	KJ504640	KJ504596	KJ504500	-	-
	CBS 122989; CPC 15195		Human skin	Netherlands	-	KJ504727	KJ504768	KJ504432	KJ504683	KJ504551	KJ504639	KJ504595	KJ504499	-	-
	CPC 18468	R. eucalypti	Rubber of refrigerator	USA, Athens	A.E. Glenn	KJ504734	KJ504775	KJ504439	KJ504690	KJ504558	KJ504646	KJ504602	KJ504503	-	-
	CBS 120727; CPC 13046		Corymbia grandifolia	Italy	W. Gams	KJ504726	KJ504767	KJ504431	KJ504682	-	KJ504638	KJ504594	KJ504498	KJ504474	KJ504530
	CPC 16560	<i>Ramularia</i> sp.	Eucalyptus camaldulensis	Iraq	A. Saadoon	KJ504731	KJ504772	KJ504436	KJ504687	KJ504555	KJ504643	KJ504599	KJ504501	KJ504475	KJ504532
	CPC 16565	<i>Ramularia</i> sp.	Eucalyptus camaldulensis	Iraq	A. Saadoon	KJ504733	KJ504774	KJ504438	KJ504689	KJ504557	KJ504645	KJ504601	-	KJ504477	KJ504533
R. grevilleana	CBS 259.36	M. fragariae	-	Netherlands	-	KP894114	KP894222	KP894329	KP894439	KP894549	KP894660) KP894771	-	-	-
	CBS 719.84	M. fragariae	<i>Fragaria</i> × <i>ananassa</i> Tioga	New Zealand	-	KP894116	EU167605	KP894331	KP894441	KP894551	KP894662	2 KP894773	KP894881	-	-
	CBS 298.34	M. fragariae	-	Netherlands	-	KP894115	KP894223	KP894330	KP894440	KP894550	KP89466	KP894772	KP894880	KP894969	-
	CBS 114732; UPSC 3244		Fragaria ananassa	Sweden	E. Gunnerbeck	KP894113	KP894221	KP894328	KP894438	KP894548	KP894659) KP894770	-	KP894968	-
R. haroldporteri	CPC 16297	<i>Ramularia</i> sp.	Unidentified bulb plant	South Africa	P.W. Crous	KX287120	KX287418	KX287701	KX287979	KX288258	KX288577	7 KX288867	-	-	-
	CBS 137272^т; СРС 16296		Unidentified bulb plant	South Africa	P.W. Crous	KJ504725	KJ504766	KJ504430	KJ504681	(KJ504549) KJ504637	KJ504593	KJ504497	-	-
R. heraclei	CBS 108969 ^{ET}		Heracleum sphondylium	Netherlands	G. Verkley	KX287121	KX287419	KX287702	KX287980	KX288259	KX288578	3 –	KX289068	-	-

(continued on next page)

All that glitters is not Ramularia

Species ⁴	Culture number ^{1,2}	Previous name ⁴	Host	Country	Collector	LSU	ITS	actA	tef1-α	gapdh	rpb2	his3	cmdA	tub2	chs-1
	CBS 108972		Heracleum sphondylium	Netherlands	G. Verkley	KX287122	KX287420	KX287703	KX287981	KX288260	KX288579	9 –	KX289069	-	-
	CBS 108987		Heracleum sp.	Austria	G. Verkley	KX287123	KX287421	KX287704	KX287982	KX288261	KX288580) KX288868	-	-	KX289252
	CBS 108988		Heracleum sp.	Austria	G. Verkley	KX287124	KX287422	KX287705	KX287983	KX288262	KX288581	1 KX288869	KX289070	-	-
	CPC 11505	<i>Ramularia</i> sp.	Heracleum moellendorffii	South Korea	H.D. Shin	KX287125	KX287423	KX287706	KX287984	KX288263	KX288582	2 KX288870	KX289071	-	KX289253
	CPC 11506	<i>Ramularia</i> sp.	Heracleum moellendorffii	South Korea	H.D. Shin	KX287126	KX287424	KX287707	KX287985	KX288264	KX288583	3 KX288871	KX289072	-	-
	CPC 11507	<i>Ramularia</i> sp.	Heracleum moellendorffii	South Korea	H.D. Shin	KX287127	KX287425	KX287708	KX287986	KX288265	KX288584	4 KX288872	KX289073	-	-
	CBS 113976; UPSC 2344		Heracleum sphondylium	Sweden	E. Gunnerbeck	KX287128	KX287426	KX287709	KX287987	KX288266	KX288585	5 KX288873	KX289074	-	-
	CBS 194.25		Pastinaca sativa	-	-	KX287129	KX287427	KX287710	KX287988	KX288267	KX288586	6 KX288874	KX289075	-	-
R. hieracii-umbellati	CPC 10690	R. inaequalis	Hieracium umbellatum	South Korea	H.D. Shin	KX287130	KX287428	KX287711	KX287989	KX288268	KX288587	7 KX288875	-	-	-
	CPC 10691	R. inaequalis	Hieracium umbellatum	South Korea	H.D. Shin	KX287131	KX287429	KX287712	KX287990	KX288269	KX288588	3 KX288876	-	-	-
	CPC 10692	R. inaequalis	Hieracium umbellatum	South Korea	H.D. Shin	KX287132	KX287430	KX287713	KX287991	KX288270	KX288589	9 KX288877	-	-	-
	CPC 10788	R. inaequalis	Hieracium umbellatum	South Korea	H.D. Shin	KX287133	KX287431	KX287714	KX287992	KX288271	KX288590) KX288878	-	-	-
	CPC 10789	R. inaequalis	Hieracium umbellatum	South Korea	H.D. Shin	KX287134	KX287432	KX287715	KX287993	KX288272	KX288591	1 KX288879	KX289076	-	-
R. hydrangeae- macrophyllae	CBS 122273^T ; 2007/2068		Hydrangea macrophylla	New Zealand	C.F. Hill	KX287135	KX287433	KX287716	KX287994	KX288273	KX288592	2 KX288880	KX289077	-	-
	CPC 25908		Laurus sp.	Netherlands	W. Quaedvlieg	KX287136	KX287434	KX287717	KX287995	KX288274	KX288593	3 KX288881	-	-	-
	CBS 118410	<i>Ramularia</i> sp.	Ligularia clivorum	New Zealand	-	KX287137	KX287435	KX287718	KX287996	KX288275	KX288594	4 KX288882	KX289078	KX289194	-
	CPC 25905		Carex sp.	Netherlands	W. Quaedvlieg	KX287138	KX287436	KX287719	KX287997	KX288276	KX288595	5 KX288883	-	-	-
	CBS 122625; CPC 14811; 2007/3485-B	R. rollandii	<i>lris × hollandica</i> hybrid	New Zealand	C.F. Hill	KX287139	KX287437	KX287720	KX287998	KX288277	KX288596	6 KX288884	KX289079	KX289195	-
	CBS 122272; 2007/2973	<i>Ramularia</i> sp.	<i>lri</i> s sp.	New Zealand	C.F. Hill	KX287140	KX287438	KX287721	KX287999	KX288278	KX288597	7 KX288885	KX289080	KX289196	-
	CPC 25902		Aesculus hippocastanum	Netherlands	S.I.R. Videira	KX287141	KX287439	KX287722	KX288000	KX288279	KX288598	3 KX288886	KX289081	-	-
	CPC 25906		Carex sp.	Netherlands	W. Quaedvlieg	KX287142	KX287440	KX287723	KX288001	KX288280	KX288599	9 KX288887	-	-	-
	CPC 19854	<i>Ramularia</i> sp.	Feijoa sellowiana	Italy	G. Polizzi	KX287143	KX287441	KX287724	KX288002	KX288281	KX288600) KX288888	KX289082	-	-
	CPC 19026	Ramularia sp.	Phragmites sp.	Netherlands	P.W. Crous	KX287144	KX287442	KX287725	KX288003	KX288282	KX288601	1 KX288889	-	-	-

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Table 1. (Continu	ued).														
Species ⁴	Culture number ^{1,2}	Previous name ⁴	Host	Country	Collector	LSU	ITS	actA	tef1-α	gapdh	rpb2	his3	cmdA	tub2	chs-1
	CPC 19027	<i>Ramularia</i> sp.	Phragmites sp.	Netherlands	P.W. Crous	KX287145	KX287443	KX287726	KX288004	KX288283	KX288602	2 KX288890	KX289083	-	-
	CBS 341.49	R. archangelicae	Angelica sylvestris	Netherlands	-	KX287146	KX287444	KX287727	KX288005	KX288284	KX288603	3 KX288891	KX289084	KX289197	-
	CPC 25907		Juncus sp.	Netherlands	U. Damm	KX287147	KX287445	KX287728	KX288006	KX288285	KX288604	KX288892	-	-	-
	CPC 20406	Ramularia sp.	Eucalyptus caesia	USA, California	P.W. Crous	KX287148	KX287446	KX287729	KX288007	KX288286	KX288605	5 KX288893	-	-	-
	CPC 20484	<i>Ramularia</i> sp.	Iris foetidissima	Netherlands	-	KX287149	KX287447	KX287730	KX288008	KX288287	KX288606	6 KX288894	-	-	-
	CPC 25901		Platanus sp.	Netherlands	S.I.R. Videira	KX287150	KX287448	KX287731	KX288009	KX288288	KX288607	′ KX288895	KX289085	-	KX289254
	CBS 766.84	R. deusta var. alba	Ulex europaeus	UK, England	-	KX287151	KX287449	KX287732	KX288010	KX288289	KX288608	3 KX288896	-	KX289198	-
	CBS 159.82	R. sparganii	Sparganium ramosum	Netherlands	W. Gams	KX287152	KX287450	KX287733	KX288011	KX288290	KX288609) KX288897	KX289086	KX289199	-
	CPC 19030	Ramularia sp.	<i>Iris</i> sp.	UK	P.W. Crous	KX287153	KX287451	KX287734	KX288012	KX288291	KX288610) KX288898	KX289087	KX289200	-
	CBS 114117; UPSC 2662	R. butomi	Filipendula vulgaris	Sweden	E. Gunnerbeck	KX287154	KX287452	KX287735	KX288013	KX288292	KX288611	KX288899	KX289088	KX289201	-
	CPC 25904		Potentilla sp.	Netherlands	U. Damm	KX287155	KX287453	KX287736	KX288014	KX288293	KX288612	2 KX288900	-	-	-
	CBS 113614	<i>Ramularia</i> sp.	Sparganium ramosum	Netherlands	-	KX287156	KX287454	KX287737	KX288015	KX288294	KX288613	8 KX288901	KX289089	-	-
	CPC 25903		<i>Typha</i> sp.	Netherlands	S.I.R. Videira	KX287157	KX287455	KX287738	KX288016	KX288295	KX288614	KX288902	KX289090	KX289202	-
	CBS 118408	R. hellebori	Helleborus niger	New Zealand	C.F. Hill	KX287158	KX287456	KX287739	KX288017	KX288296	KX288615	5 KX288903	KX289091	-	-
R. inaequalis	CPC 15815	Cercosporoid sp.	<i>Taraxacum</i> sp.	Mexico	M. de Jesús Yáñez-Morales	KX287159	KX287457	KX287740	KX288018	KX288297	KX288616	6 KX288904	KX289092	KX289203	-
	CBS 250.96	R. inaequalis	Taraxacum officinale	Canada, Nova Scotia	S. Green	KP894117	KP894224	KP894332	KP894442	KP894552	KP894663	8 KP894774	KP894882	KP894970	-
	CPC 15752	<i>Ramularia</i> sp.	Taraxacum sp.	Mexico	M. de Jesús Yáñez-Morales	KP894118	KP894225	KP894333	KP894443	KP894553	KP894664	KP894775	-	-	-
	CPC 15753	<i>Ramularia</i> sp.	<i>Taraxacum</i> sp.	Mexico	M. de Jesús Yáñez-Morales	KP894119	KP894226	KP894334	KP894444	KP894554	KP894665	5 KP894776	KP894883	KP894971	-
	CBS 141111^{ET}; CPC 25741		Taraxacum officinale	Netherlands	U. Damm	KP894120	KP894227	KP894335	KP894445	KP894555	KP894666	6 KP894777	-	-	-
	CPC 25742; X4	0	Corylus avellana	Netherlands	S.I.R. Videira	KP894121	KP894228	KP894336	KP894446	KP894556	KP894667	′ KP894778	-	-	-
R. interstitialis	CBS 120.68	R. primulae	Primula variabilis	UK	S.A.J. Tarr	KX287160	KX287458	-	-	-	-	-	-	-	-
R. kriegeriana	CPC 10825		Plantago asiatica	South Korea	H.D. Shin	KX287161	KX287459	KX287741	KX288019	KX288298	KX288617	KX288905	-	KX289204	KX289255
	CPC 10826		Plantago asiatica	South Korea	H.D. Shin	KX287162	KX287460	KX287742	KX288020	KX288299	KX288618	3 KX288906	-	KX289205	KX289256
	CPC 10827		Plantago asiatica	South Korea	H.D. Shin	KX287163	KX287461	KX287743	KX288021	KX288300	KX288619	KX288907	-	KX289206	KX289257
R. lamii var. lamii	CBS 108970 ^{ET}		Lamium album	Netherlands	G. Verkley	KX287164	KX287462	KX287744	KX288022	KX288301	KX288620) KX288908	KX289093	-	KX289258
	CBS 108971		Lamium album	Netherlands	G. Verkley	KX287165	KX287463	KX287745	KX288023	KX288302	KX288621	KX288909	KX289094 (_ continued or	– n next page)

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Species ⁴	Culture number ^{1,2}	Previous name ⁴	Host	Country	Collector	LSU	ITS	actA	tef1-α	gapdh	rpb2	his3	cmdA	tub2	chs-1
R. leonuri	CPC 11312	R. lamii var. lamii	Leonurus sibiricus	South Korea	H.D. Shin	KF251835	KF251331	KF253636	KF253178	KX288303	KX348080) KX288910	KF253983	KF252711	-
	CPC 11313	R. lamii var. lamii	Leonurus sibiricus	South Korea	H.D. Shin	KX287166	KX287464	KX287746	KX288024	KX288304	KX288622	2 KX288911	-	KX289207	-
	CPC 11314	R. lamii var. lamii	Leonurus sibiricus	South Korea	H.D. Shin	KX287167	KX287465	KX287747	KX288025	KX288305	KX288623	3 KX288912	KX289095	KX289208	-
	CPC 11411	R. lamii var. lamii	Leonurus sibiricus	South Korea	H.D. Shin	KX287168	KX287466	KX287748	KX288026	KX288306	KX288624	KX288913	KX289096	KX289209	-
	CPC 11412	R. lamii var. lamii	Leonurus sibiricus	South Korea	H.D. Shin	KX287169	KX287467	KX287749	KX288027	KX288307	KX288625	5 KX288914	-	KX289210	-
	CPC 11413	R. lamii var. lamii	Leonurus sibiricus	South Korea	H.D. Shin	KX287170	KX287468	KX287750	KX288028	KX288308	KX288626	6 KX288915	-	KX289211	-
	CBS 141112; CPC 14570	R. lamii var. lamii	Leonurus sibiricus	South Korea	H.D. Shin	KX287171	KX287469	KX287751	KX288029	KX288309	KX288627	7 KX288916	-	KX289212	-
	CPC 14571	R. lamii var. lamii	Leonurus sibiricus	South Korea	H.D. Shin	KX287172	KX287470	KX287752	KX288030	KX288310	KX288628	3 KX288917	-	KX289213	-
	CPC 14572	R. lamii var. lamii	Leonurus sibiricus	South Korea	H.D. Shin	KX287173	KX287471	KX287753	KX288031	KX288311	KX288629) KX288918	-	KX289214	-
R. lethalis	CBS 141113; CPC 25910		Acer pseudoplatanus	Netherlands	S.I.R. Videira	KX287174	KX287472	KX287754	KX288032	KX288312	KX288630) KX288919	KX289097	-	-
R. ligustrina	CBS 379.52		Ligustrum vulgare	Italy	-	KX287175	KX287473	KX287755	KX288033	KX288313	KX288631	KX288920	KX289098	-	-
R. macrospora	CBS 109015		-	-	-	KX287176	KX287474	-	-	-	KX288632	2 KX288921	-	-	-
R. major	CBS 141114; CPC 12542		Petasites japonicus	South Korea	H.D. Shin	KX287177	KX287475	KX287756	KX288034	KX288314	KX288633	3 KX288922	-	KX289215	-
	CPC 12543		Petasites japonicus	South Korea	H.D. Shin	KJ504758	KJ504800	KJ504464	KJ504715	KJ504583	KJ504671	KJ504627	-	KJ504493	-
	CPC 12544		Petasites japonicus	South Korea	H.D. Shin	KX287178	KX287476	KX287757	KX288035	KX288315	KX288634	KX288923	-	KX289216	-
R. mali	CBS 129581 ^T		Apple in cold storage	Italy	-	KJ504737	KJ504778	KJ504442	KJ504693	KJ504561	KJ504649	KJ504605	KJ504506	KJ504478	KJ504534
R. malicola	CBS 119227^т; Р5	<i>Ramularia</i> sp.	<i>Malus</i> sp.	USA, Missouri	J. Batzer	AY598910	AY598873	KX287758	KX288036	KX288316	KX288635	5 KX288924	KX289099	KX289217	-
R. miae	CBS 120121^T ; CPC 12736		Wachendorfia thyrsifolia	South Africa	M.K. & P.W. Crous	DQ885902	KJ504801	KJ504465	KJ504716	KJ504584	KJ504672	KJ504628	KJ504525	-	KJ504544
	CPC 21692	<i>Ramularia</i> sp.	Wachendorfia thyrsifolia	South Africa	M.J. Wingfield	KX287179	KX287477	KX287759	KX288037	KX288317	KX288636	6 KX288925	-	-	-
	CPC 19770	Teratosphaeria sp.	Leonotis leonurus	South Africa	P.W. Crous	KJ504762	KJ504805	KJ504469	KJ504720	KJ504588	KJ504676	KJ504632	KJ504528	-	-
	CPC 19835	<i>Ramularia</i> sp.	Gazania rigens var. uniflora	South Africa	P.W. Crous	KJ504761	KJ504804	KJ504468	KJ504719	KJ504587	KJ504675	KJ504631	KJ504527	-	-
R. neodeusta	CPC 13568	R. deusta var. alba	Lathyrus odoratus	New Zealand	C.F. Hill	KX287180	KX287478	KX287760	KX288038	KX288318	KX288637	7 KX288926	KX289100	-	-
	CBS 141115^T; CPC 13567	<i>Ramularia</i> sp.	Vicia faba	New Zealand	C.F. Hill	KX287181	KX287479	KX287761	KX288039	KX288319	KX288638	3 KX288927	KX289101	-	-
R. helminthiae	CPC 11502	R. inaequalis	Picris hieracioides var. glabrensis	South Korea	H.D. Shin	KX287182	KX287480	KX287762	KX288040	KX288320	KX288639) KX288928	KX289102	-	-
	CPC 11504	R. inaequalis	Picris hieracioides var. glabrensis	South Korea	H.D. Shin	KX287183	KX287481	KX287763	KX288041	KX288321	KX288640) KX288929	KX289103	-	-
	CBS 118418	R. inaequalis	Picris echioides	New Zealand	-	KX287184	KX287482	KX287764	KX288042	KX288322	KX288641	KX288930	KX289104	KX289218	-

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Table 1. (Continu	ied).														
Species ⁴	Culture number ^{1,2}	Previous name ⁴	Host	Country	Collector	LSU	ITS	actA	tef1-α	gapdh	rpb2	his3	cmdA	tub2	chs-1
R. nyssicola	CBS 127665^{ET}; AR 4656; DM 2		Nyssa ogeche × sylvatica hybrid	a USA, Maryland	R. Olsen	KJ504724	KJ504765	KJ504429	KJ504680	KJ504548	KJ504636	KJ504592	KJ504496	KJ504473	-
	CBS 127664; AR 4629	M. nyssicola	<i>Nyssa ogeche × sylvatica</i> hybrid	a USA, Maryland	R. Olsen	KP894124	KP894231	KP894339	KP894449	KP894559	KP894670) KP894781	KP894885	-	-
R. osterici	CBS 141116 [⊤] ; CPC 10750	R. archangelicae	Ostericum koreanum	South Korea	H.D. Shin	KX287185	KX287483	KX287765	KX288043	KX288323	KX288642	2 KX288931	KX289105	-	-
	CPC 10751	R. archangelicae	Ostericum koreanum	South Korea	H.D. Shin	KX287186	KX287484	KX287766	KX288044	KX288324	KX288643	3 KX288932	KX289106	-	-
	CPC 10752	R. archangelicae	Ostericum koreanum	South Korea	H.D. Shin	KX287187	KX287485	KX287767	KX288045	KX288325	KX288644	KX288933	KX289107	-	-
R. parietariae	CBS 123730; V6019.1		Parietaria officinalis	Czech Republic	G. Verkley	KX287188	KX287486	KX287768	KX288046	KX288326	KX288645	5 KX288934	KX289108	-	-
	CBS 123731; V6019.2		Parietaria officinalis	Czech Republic	G. Verkley	KX287189	KX287487	KX287769	KX288047	KX288327	KX288646	6 KX288935	KX289109	-	-
R. phacae-frigidae	CBS 234.55 [⊤]	M. phacae-frigidae	Phaca frigida	Switzerland	E. Müller	KP894125	KP894232	KP894340	KP894450	KP894560	KP894671	KP894782	KP894886	-	-
R. plurivora	CBS 118743^т; СРС 12207		Human bone marrow	Netherlands	-	KJ504739	KJ504780	KJ504444	KJ504695	KJ504563	KJ504651	KJ504607	KJ504508	KJ504479	KJ504536
	CPC 16123	Cladosporium-like sp.	Melon in storage	Netherlands	J.H. Houbraken	KJ504741	KJ504782	KJ504446	KJ504697	KJ504565	KJ504653	KJ504609	KJ504510	-	KJ504538
	CBS 118693; CPC 12206		Human skin	Netherlands	-	KJ504738	KJ504779	KJ504443	KJ504694	KJ504562	KJ504650	KJ504606	KJ504507	-	-
	CPC 16124	Cladosporium-like sp.	Melon in storage	Netherlands	J.H. Houbraken	KJ504742	KJ504783	KJ504447	KJ504698	KJ504566	KJ504654	KJ504610	KJ504511	-	-
R. pratensis var. pratensis	CBS 122105; RoKi 3045	R. pratensis	Rumex sp.	Taiwan	R. Kirschner & CJ. Chen	KX287190	KX287488	KX287770	KX288048	KX288328	KX288647	7 KX288936	KX289110	-	-
	CPC 16868	<i>Ramularia</i> sp.	Verbascum sp.	Canada	K.A. Seifert	KX287191	KX287489	KX287771	KX288049	KX288329	KX288648	3 KX288937	-	-	KX289259
	CPC 19448	Ramularia sp.	Prunus domestica	-	-	KX287192	KX287490	KX287772	KX288050	KX288330	KX288649) KX288938	-	KX289219	-
R. proteae	CBS 112161^T; CPC 3075		Protea longifolia	Australia, Tasmania	A. Macfadyen	EU707899	EU707899	-	-	-	KX288650) KX288939	-	-	-
R. pusilla	CBS 124973^{ет}; RoKi 3143		Poa annua	Germany	R. Kirschner	KP894141	KP894248	KP894356	KP894466	-	KP894687	7 KP894798	KP894901	-	-
R. rhabdospora	CBS 312.92		-	Germany	S. Petzoldt	KX287193	KX287491	KX287773	KX288051	KX288331	KX288651	KX288940	-	KX289220	-
	CBS 118415		Plantago lanceolata	New Zealand	-	KX287194	KX287492	KX287774	KX288052	KX288332	KX288652	2 KX288941	-	-	-
R. rubella	CPC 15748	<i>Ramularia</i> sp.	Rumex sp.	Mexico	M. de Jesús Yáñez-Morales	KX287195	KX287493	KX287775	KX288053	KX288333	KX288653	3 KX288942	-	-	-
	CPC 15749	<i>Ramularia</i> sp.	Rumex sp.	Mexico	M. de Jesús Yáñez-Morales	KX287196	KX287494	KX287776	KX288054	KX288334	KX288654	4 KX288943	-	KX289221	-
	CPC 15750	<i>Ramularia</i> sp.	Rumex sp.	Mexico	M. de Jesús Yáñez-Morales	KX287197	KX287495	KX287777	KX288055	KX288335	KX288655	5 KX288944	-	KX289222	-
	CBS 120161		Rumex obtusifolius	New Zealand	-	KX287198	KX287496	KX287778	KX288056	KX288336	KX288656	6 KX288945	KX289111	-	-
	CBS 114440; UPSC 2857		Rumex longifolius	Sweden	E. Gunnerbeck	KX287199	KX287497	KX287779	KX288057	KX288337	KX288657	7 KX288946	KX289112	-	KX289260

(continued on next page)

Table 1. (Contin	nued).														
Species ⁴	Culture number ^{1,2}	Previous name ⁴	Host	Country	Collector	LSU	ITS	actA	tef1-α	gapdh	rpb2	his3	cmdA	tub2	chs-1
	CPC 19471	Cercosporella sp.	Prunus sp.	Netherlands	W. Quaedvlieg	KX287200	KX287498	KX287780	KX288058	KX288338	KX288658	3 KX288947	KX289113	-	-
	CPC 19472	Cercosporella sp.	Prunus sp.	Netherlands	W. Quaedvlieg	KX287201	KX287499	KX287781	KX288059	KX288339	KX288659	9 KX288948	-	-	-
	CPC 15821	<i>Ramularia</i> sp.	Rumex sp.	Mexico	M. de Jesús Yáñez-Morales	KX287202	KX287500	KX287782	KX288060	KX288340	KX288660) KX288949	KX289114	KX289223	-
	CBS 141117^{№†} ; CPC 25911		Rumex sp.	Netherlands	U. Damm	KX287203	KX287501	KX287783	KX288061	KX288341	KX28866 ²	1 KX288950	-	-	-
R. rufibasis	CBS 114567; UPSC 3339	Ph. rufibasis	Myrica gale	Sweden	E. Gunnerbeck	KX287204	KX287502	KX287784	KX288062	KX288342	KX288662	2 KX288951	-	KX289224	-
R. rumicicola	CBS 141118^T; CPC 11294	R. pratensis var. pratensis	Rumex crispus	South Korea	H.D. Shin	KF902111	KF901756	KF903599	KX288063	KX288343	KX348087	1 KX288952	-	(KF902946) —
	CPC 11295	R. pratensis var. pratensis	Rumex crispus	South Korea	H.D. Shin	KX287205	KX287503	KX287785	KX288064	KX288344	KX288663	3 KX288953	KX289115	-	KX289261
	CPC 11296	R. pratensis var. pratensis	Rumex crispus	South Korea	H.D. Shin	KX287206	KX287504	KX287786	KX288065	KX288345	KX288664	4 KX288954	-	-	-
R. rumicis	CBS 114300; UPSC 2724	R. decipiens	Rumex aquaticus	Sweden	E. Gunnerbeck	KJ504746	KJ504787	KJ504451	KJ504702	KJ504570	KJ504658	8 KJ504614	KJ504514	-	KJ504539
<i>Ramularia</i> sp. A	CBS 114566; UPSC 3340		Geranium pusillum	Sweden	E. Gunnerbeck	KX287207	KX287505	KX287787	KX288066	KX288346	KX288665	5 KX288955	KX289116	-	-
<i>Ramularia</i> sp. B	CBS 114568; UPSC 3246	<i>Ramularia</i> sp.	Epilobium hirsutum	Sweden	E. Gunnerbeck	KJ504747	KJ504788	KJ504452	KJ504703	KJ504571	KJ504659	KJ504615	KJ504515	-	KJ504540
<i>Ramularia</i> sp. C	CBS 299.49		Symphytum officinale	Netherlands	-	KX287208	KX287506	KX287788	KX288067	KX288347	KX288666	6 KX288956	-	-	-
<i>Ramularia</i> sp. D	CBS 135.23	R. lactea	Viola odorata	-	-	KP894123	KP894230	KP894338	KP894448	KP894558	KP894669	9 KP894780	-	KP894973	-
<i>Ramularia</i> sp. E	CPC 14767	<i>Ramularia</i> sp.	Hydrangea serrata	South Korea	H.D. Shin	KX287209	KX287507	KX287789	KX288068	KX288348	KX288667	7 KX288957	-	-	-
	CPC 14768	<i>Ramularia</i> sp.	Hydrangea serrata	South Korea	H.D. Shin	KX287210	KX287508	KX287790	KX288069	KX288349	KX288668	8 KX288958	-	-	-
	CPC 14769	<i>Ramularia</i> sp.	Hydrangea serrata	South Korea	H.D. Shin	KX287211	KX287509	KX287791	KX288070	KX288350	KX288669	9 KX288959	-	-	-
	CPC 14832	Ramularia sp.	Hydrangea serrata	South Korea	H.D. Shin	KX287212	KX287510	KX287792	KX288071	KX288351	KX288670) KX288960	-	-	-
	CPC 14833	<i>Ramularia</i> sp.	Hydrangea serrata	South Korea	H.D. Shin	KX287213	KX287511	KX287793	KX288072	KX288352	KX28867	1 KX288961	-	-	-
	CPC 14834	<i>Ramularia</i> sp.	Hydrangea serrata	South Korea	H.D. Shin	KX287214	KX287512	KX287794	KX288073	KX288353	KX288672	2 KX288962	-	-	-
R. sphaeroidea	CBS 112891; CPC 5242		Vicia villosa subsp. varia	USA, California	S.T. Koike	KX287215	AY352584	KX287795	KX288074	KX288354	KX288673	3 KX288963	KX289117	-	-
R. stellariicola	CPC 11298	Cercosporella sp.	Stellaria aquatica	South Korea	H.D. Shin	KX287216	KX287513	KX287796	KX288075	KX288355	KX288674	4 KX288964	-	-	-
	CBS 130592[⊤]; CPC 11297; KACC 42363	P. stellariicola	Stellaria aquatica	South Korea	H.D. Shin & M.J. Park	. GU214693	GU214693	8 KX287797	KX288076	KX288356	KX288675	5 KX288965	KX289118	-	-

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Table 1. (Continu	ued).														
Species ⁴	Culture number ^{1,2}	Previous name ⁴	Host	Country	Collector	LSU	ITS	actA	<i>tef1-</i> α	gapdh	rpb2	his3	cmdA	tub2	chs-1
R. stellenboschensis	CBS 130600^T ; CPC 18294		Protea sp., with Vizella interupta	South Africa	P.W. Crous	JN712566	JN712499	KX287798	_	KX288357	KX288676	6 KX288966	-	_	_
R. tovarae	CBS 113305 ^{ET}	<i>Ramularia</i> sp.	Polygonum filiforme	South Korea	H.D. Shin	KJ504764	KJ504807	KJ504471	KJ504722	KJ504590	KJ504678	3 KJ504634	KJ504529	KJ504494	-
R. tricherae	CBS 108973		Knautia arvensis	Netherlands	G. Verkley	KP894142	2 KP894249	KP894357	KP894467	KP894577	KP894688	8 KP894799	KP894902	KP894985	-
	CBS 108974		Knautia arvensis	Netherlands	G. Verkley	KX287217	′ KX287514	KX287799	KX288077	KX288358	KX28867	7 KX288967	KX289119	KX289225	KX289262
	CBS 108994		Knautia arvensis	Netherlands	G. Verkley	KP894145	5 KP894252	KP894360	KP894470	KP894580	KP89469	1 KP894802	KP894905	KP894987	-
	CBS 108995		Knautia arvensis	Netherlands	G. Verkley	KX287218	8 KX287515	KX287800	KX288078	KX288359	KX288678	8 KX288968	KX289120	KX289226	-
	CBS 108989		Knautia dipsacifolia	Austria	G. Verkley	KP894143	KP894250	KP894358	KP894468	KP894578	KP89468	9 KP894800	KP894903	KP894986	-
	CBS 108990		Knautia dipsacifolia	Austria	G. Verkley	KP894144	KP894251	KP894359	KP894469	KP894579	KP894690	0 KP894801	KP894904	-	-
	CBS 236.73; CCM F-369		Knautia drymeia	former Czechoslovakia	-	KP894146	6 KP894253	KP894361	KP894471	KP894581	KP894692	2 KP894803	KP894906	-	-
R. trigonotidis	CBS 141119^T; CPC 14764	<i>Ramularia</i> sp.	Trigonotis nakaii	South Korea	H.D. Shin	KX287219) KX287516	KX287801	KX288079	KX288360	KX288679	9 KX288969	-	-	-
	CPC 14765	<i>Ramularia</i> sp.	Trigonotis nakaii	South Korea	H.D. Shin	KX287220) KX287517	KX287802	KX288080	KX288361	KX288680	0 KX288970	-	-	-
	CPC 14766	<i>Ramularia</i> sp.	Trigonotis nakaii	South Korea	H.D. Shin	KX287221	KX287518	KX287803	KX288081	KX288362	KX28868	1 KX288971	-	-	-
R. trollii	CBS 109118	P. trollii	Trollius europaeus	Austria	G. Verkley	KX287222	2 KX287519	KX287804	KX288082	KX288363	KX288682	2 KX288972	-	KX289227	-
	CBS 109119	P. trollii	Trollius europaeus	Austria	G. Verkley	KX287223	8 KX287520	KX287805	KX288083	KX288364	KX288683	3 KX288973	-	-	-
R. unterseheri	CBS 124846	R. endophylla	Fagus sylvatica	Germany	M. Unterseher	KP894160) KP894267	KP894375	KP894485	KP894595	KP894706	6 KP894817	KP894920	KP894999	-
	CBS 124838; li-26.4	R. endophylla	Fagus sylvatica	Germany	M. Unterseher	KP894158	8 KP894265	6 KP894373	KP894483	KP894593	KP894704	4 KP894815	KP894918	-	-
	CBS 130721	R. endophylla	Room inside a castle	Germany	-	KP894164	KP894271	KP894379	KP894489	KP894599	KP894710	0 KP894821	KP894924	-	-
	CBS 117879; CPC 11207	R. endophylla	Acer pseudoplatanus	Netherlands	G. Verkley	KP894150) KP894257	KP894365	KP894475	KP894585	KP894696	6 KP894807	KP894910	-	-
	CBS 124884 ^T	R. endophylla	Fagus sylvatica	Germany	M. Unterseher	KP894163	KP894270	KP894378	KP894488	KP894598	KP894709	9 KP894820	KP894923	KP895002	-
R. uredinicola	CBS 141120^T; CPC 11852		Melampsora sp. on Salix babylonica	Iran	S.A. Khodaparast	KX287224	KX287521	KX287806	KX288084	KX288365	KX288684	4 KX288974	-	KX289228	-
	CBS 179.68	R. uredinis	<i>Melampsora</i> sp. on <i>Populus</i> sp.	Italy	-	KX287225	5 KX287522	KX287807	KX288085	KX288366	KX28868	5 KX288975	-	-	-
	CPC 12491	<i>Ramularia</i> sp.	<i>Melampsora</i> sp. on <i>Salix</i> sp.	South Korea	H.D. Shin	KX287226	6 KX287523	KX287808	KX288086	KX288367	KX288686	6 KX288976	-	KX289229	-
	CPC 12492	<i>Ramularia</i> sp.	<i>Melampsora</i> sp. on <i>Salix</i> sp.	South Korea	H.D. Shin	KX287227	KX287524	KX287809	KX288087	KX288368	KX28868	7 KX288977	-	KX289230	-
	CPC 12493	<i>Ramularia</i> sp.	<i>Melampsora</i> sp. on <i>Salix</i> sp.	South Korea	H.D. Shin	KX287228	8 KX287525	KX287810	KX288088	KX288369	KX288688	8 KX288978	-	KX289231	-
	CPC 11481	<i>Ramularia</i> sp.	<i>Melampsora</i> sp. on <i>Salix</i> sp.	South Korea	H.D. Shin	KX287229) KX287526	KX287811	KX288089	KX288370	KX288689	9 KX288979	-	KX289232	-
														(continued or	n next page)

All that glitters is not Ramularia

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Table 1 (Continued)

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Species ⁴	Culture number ^{1,2}	Previous name ⁴	Host	Country	Collector	LSU	ITS	actA	<i>tef1-</i> α	gapdh	rpb2	his3	cmdA	tub2	chs-1
	CPC 11482	<i>Ramularia</i> sp.	<i>Melampsora</i> sp. on <i>Salix</i> sp.	South Korea	H.D. Shin	KX287230	KX287527	KX287812	KX288090	KX288371	KX288690) KX288980	-	KX289233	-
	CBS 131769; KACC 42535		<i>Melampsora</i> sp. on <i>Salix gracilistyla</i>	South Korea	H.D. Shin & M.J. Park	KX287231	KX287528	KX287813	KX288091	KX288372	KX28869 ⁻	KX288981	-	KX289234	-
	CBS 131770; KACC 44864		Melampsora sp. on Populus alba × glandulosa	South Korea	H.D. Shin & M.J. Park	KX287232	KX287529	KX287814	KX288092	KX288373	KX288692	2 KX288982	-	KX289235	-
	CBS 131771; KACC 44215		Melampsora sp. on Salix koreensis	South Korea	H.D. Shin & M.J. Park	KX287233	KX287530	KX287815	KX288093	KX288374	KX288693	3 KX288983	-	KX289236	-
	CBS 131772; KACC 44218		Melampsora sp. on Salix matsudana for. tortuosa	South Korea	H.D. Shin & M.J. Park	KX287234	KX287531	KX287816	KX288094	KX288375	-	KX288984	-	KX289237	-
R. urticae	CBS 105.26	An. pulmonalis	-	-	-	KP894169	KP894276	KP894384	KP894494	KP894604	KP89471	5 KP894826	-	-	-
	CBS 113974; UPSC 2359		Urtica dioica	Sweden	E. Gunnerbeck	KP894168	KP894275	KP894383	KP894493	KP894603	KP894714	KP894825	KP894926	KP895005	-
	CBS 162.91	Ramulariopsis sp.	Urtica dioica	Germany, Thüringen	G. Arnold	KP894170	KP894277	KP894385	KP894495	KP894605	KP894716	6 KP894827	-	KP895006	-
	CPC 14807	<i>Ramularia</i> sp.	Aconitum pseudo-laeve var. erectum	South Korea	H.D. Shin	KX287235	KX287532	KX287817	KX288095	KX288376	KX288694	4 KX288985	-	-	-
R. valerianae var. valerianae	CBS 109122		<i>Valeriana</i> sp.	Austria	G. Verkley	KX287237	KX287534	KX287818	KX288096	-	KX288696	6 KX288986	-	-	-
	CBS 109123		Valeriana sp.	Austria	G. Verkley	KX287238	KX287535	KX287819	KX288097	KX288377	KX288697	7 KX288987	-	KX289238	-
R. vallisumbrosae	CBS 271.38		<i>Narcissus</i> cv. Victoria	UK, England	-	KX287239	KX287536	KX287820	KX288098	KX288378	KX288698	3 KX288988	KX289121	KX289239	-
	CBS 272.38 ^{ET}		<i>Narcissus</i> cv. Golden Spur	UK, England	-	KX287240	KX287537	KX287821	KX288099	KX288379	KX288699) KX288989	KX289122	KX289240	-
R. variabilis	CPC 16865	<i>Ramularia</i> sp.	Verbascum sp.	Canada	K.A. Seifert	KP894171	KP894278	KP894386	KP894496	KP894606	KP894717	7 KP894828	-	KP895007	-
	CPC 16866	<i>Ramularia</i> sp.	Verbascum sp.	Canada	K.A. Seifert	KP894172	KP894279	KP894387	KP894497	KP894607	KP894718	3 KP894829	-	KP895008	-
	CBS 141121^{ET}; CPC 25967		Verbascum sp.	Germany	C. Scheuer	KP894173	KP894280	KP894388	KP894498	KP894608	KP894719) KP894830	-	-	-
R. veronicicola	CBS 113981; UPSC 2320	Ph. veronicae	Veronica spicata	Sweden	E. Gunnerbeck	KX287241	KX287538	KX287822	KX288100	KX288380	KX288700) KX288990	-	KX289241	-
R. vizellae	CBS 130601^T ; CPC 18283		<i>Protea</i> sp., in association with <i>Vizella</i> <i>interupta</i>	South Africa	P.W. Crous	JN712567	KJ504808	KJ504472	KJ504723	KJ504591	KJ504679	KJ504635	-	KJ504495	-
	CBS 117798; CPC 12088	R. endophylla	Carpinus betulus	Netherlands	G. Verkley	KP894182	KP894289	KP894397	KP894507	KP894617	KP894728	3 KP894839	-	-	-

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Table 1. (Continue	ed).														
Species ⁴	Culture number ^{1,2}	Previous name ⁴	Host	Country	Collector	LSU	ITS	actA	tef1-α	gapdh	rpb2	his3	cmdA	tub2	chs-1
	CBS 115981	R. endophylla	<i>Malus</i> dead leaf litter	Netherlands	-	KP894176	KP894283	KP894391	KP894501	KP894611	KP894722	2 KP894833	KP894928	KP895010	-
	CBS 115982	R. endophylla	<i>Malus</i> dead leaf litter	Netherlands	-	KP894177	KP894284	KP894392	KP894502	KP894612	KP894723	8 KP894834	KP894929	KP895011	-
	CBS 117871; CPC 11194	R. endophylla	Quercus rubra	Netherlands	G. Verkley	KP894188	KP894295	KP894403	KP894513	KP894623	KP894734	KP894845	KP894939	KP895021	-
	CBS 117872; CPC 11197	R. endophylla	Amelanchier Iamarckii	Netherlands	G. Verkley	KP894189	KP894296	KP894404	KP894514	KP894624	KP894735	5 KP894846	KP894940	KP895022	-
R. weberiana	CBS 136.23 ^T	R. pratensis	-	-	-	KJ504763	KJ504806	KJ504470	KJ504721	KJ504589	KJ504677	KJ504633	-	-	KJ504547
R. weigelae	CBS 113309	Phaeoramularia weigelicola	Weigela subsessilis	South Korea	H.D. Shin	KX287242	KX287539	-	KX288101	-	KX288701	-	-	-	-
Ramulariopsis gossypii	CBS 141099^{ет}; CPC 25909		Gossypium sp.	Brazil	-	KX287243	KX287540	KX287823	KX288102	KX288381	KX288702	2 KX288991	-	-	-
Rp. pseudoglycines	CPC 20036	Rp. gossypii	Gossypium barbadense	Тодо	M. Piatek	KX287244	KX287541	KX287824	KX288103	-	KX288703	8 KX288992	KX289123	-	-
	CPC 18241	Rp. gossypii	Gossypium sp.	Brazil	-	KX287245	KX287542	KX287825	KX288104	-	KX288704	KX288993	KX289124	-	-
	CBS 141100^т ; CPC 18242	Rp. gossypii	Gossypium sp.	Brazil	-	KX287246	KX287543	KX287826	KX288105	-	KX288705	5 KX288994	-	-	-
Readeriella angustia	CBS 124998; CPC 13618		Eucalyptus delegatensis	Australia, Tasmania	B.A. Summerell	KF902113	KF901758	(KF903567)	(KF903245)	-	KX348082	2 -	(KF902668)	(KF902949)) —
Re. eucalyptigena	CBS 124999^т; CPC 13026		Eucalyptus dives	Australia, New South Wales	B.A. Summerell	KF901868	KF901546	(KF903568)	(KF903254)	-	KX348083	3 —	(KF902676)	(KF902957)) —
Re. menaiensis	CBS 125003^T ; CPC 14447		Eucalyptus oblonga	Australia, New South Wales	B.A. Summerell	KF901870	KF901548	(KF903572)	(KF903256)	-	KX348084	+ _	(KF902678)	(KF902959)) —
Re. pseudocallista	CBS 125001^T; CPC 13599		Eucalyptus prominula	Australia, New South Wales	B.A. Summerell	KF901861	KF901539	(KF903570)	(KF903239)	-	KX348085	5 –	(KF902664)	(KF902943)) —
Re. tasmanica	CBS 125002^т; CPC 13631		Eucalyptus delegatensis	Australia, Tasmania	B.A. Summerell	KF902116	KF901761	(KF903656)	(KF903264)	-	KX348086	6 –	(KF902687)	(KF902967)) —
Septoria cerastii	CBS 132028; CPC 12343		Cerastium holosteoides var. hallaisanense	South Korea	H.D. Shin	GU253869	KF251366	(KF253670)	(KF253313)	-	KX348087	· _	(KF254018)	(KF252838) –
S. dysentericae	CBS 131892; CPC 12328		Inula britannica var. chinensis	South Korea	H.D. Shin	GU253866	KF251406	(KF253710)	(KF253353)	-	KX348088	8 –	(KF254058)	(KF252877)) —
S. lamiicola	CBS 123882; V6020.2		<i>Lamium</i> sp.	Czech Republic	G. Verkley	KF251951	KF251447	(KF253751)	(KF253395)	-	KX348089) _	(KF254099)	(KF252919)) —
S. leucanthemi	CBS 353.58; BBA 8504; IMI 091322		Chrysanthemum maximum	Germany, Hamburg	R. Schneider	KF251962	KF251458	(KF253762)	(KF253406)	-	KX348090) _	(KF254110)	(KF252930) continued or) – n next page)

All that glitters is not Ramularia

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Table 1. (Continu	ed).														
Species ⁴	Culture number ^{1,2}	Previous name ⁴	Host	Country	Collector	LSU	ITS	actA	tef1-α	gapdh	rpb2	his3	cmdA	tub2	chs-1
S. lycopersici	CBS 128654; KACC 42519; SMKC 22002		Lycopersicum esculentum	South Korea	-	KF251966	KF251462	(KF253766)	(KF253410)	_	KX348091	_	(KF254114)) (KF252934	4) —
S. paridis	CBS 109110		Paris quadrifolia	Austria	G. Verkley	KF251995	KF251490	(KF253794)	(KF253439)	-	KX348092	2 -	(KF254143)) (KF252960)) —
Sphaerulina chaenomelis	CBS 131897; CPC 14795	P. chaenomellis	Chaenomeles speciosa	South Korea	H.D. Shin	GU253834	4 GU269817	(GU320520)) (GU384530)) —	KX288706	8 –	-	-	-
Sp. berberidis	CBS 324.52	M. berberidis	Berberis vulgaris	Switzerland	E. Müller	KF252106	KF251601	(KF253903)	(KF253548)	-	KX348093	3 –	(KF254253)) (KF253067	7) —
Sp. betulae	CBS 128597; KACC 43119; SMKC 23059		Betula schmidtii	South Korea	-	KF252109	KF251604	(KF253906)	(KF253551)	-	KX348094	1 –	(KF254256)) (KF253070)) –
Sp. gei	CBS 128632; KACC 44051; SMKC 23686		Geum japonicum	South Korea	-	KF252120	KF251615	(KF253917)	(KF253562)	-	KX348095	5 –	(KF254267)) (KF253081	I) —
Sp. koreana	CBS 135462[⊤]; CPC 11414	P. koreana	Vicia amurensis	South Korea	H.D. Shin	GU214683	3 GU269852	2 (GU320556)) (GU384564)) —	KX288707	7 _	-	-	-
	CBS 131898; CPC 11415	Sp. viciae	Vicia amurensis	South Korea	H.D. Shin	KF252144	KF251639	(KF253940)	(KF253586)	-	KX348096	6 –	(KF254291)) (KF253101	I) —
Sphaerulina sp.	CPC 13566		Haloragis erecta	New Zealand	C.F. Hill	KX287247	' _	-	-	-	KX288708	3 –	-	-	-
Sp. tirolensis	CBS 109018 ^T		Rubus idaeus	Austria	G. Verkley	KF252143	KF251638	(KF253939)	(KF253585)	-	KX348097	7 _	(KF254290)) (KF253100)) –
Stromatoseptoria castaneicola	CBS 102322		Castanea sativa	Netherlands	G. Verkley	KF251774	KF251271	-	(KF253219)	-	KX348098	3 –	-	(KF252752	2) –
	CBS 102377		Castanea sativa	Netherlands	G. Verkley	KF251775	KF251272	-	(KF253220)	-	KX348099) _	-	(KF252753	3) —
Teratoramularia infinita	CBS 120815	Cercosporella sp.	Thladiantha punctata	Taiwan	R. Kirschner & CJ. Chen	KX287248	8 KX287544	KX287827	KX288106	KX288382	KX288709) KX288995	-	-	-
	CBS 141104^T; CPC 19488	Cercosporella sp.	Conyza canadensis	Brazil	-	KX287249	KX287545	KX287828	KX288107	KX288383	KX288710) –	KX289125	-	-
Tr. persicariae	CPC 11408	<i>Ramularia</i> sp.	Persicaria nepalensis	South Korea	H.D. Shin	KX287250) KX287546	KX287829	KX288108	KX288384	KX288711	KX288996	-	-	-
	CPC 11409	<i>Ramularia</i> sp.	Persicaria nepalensis	South Korea	H.D. Shin	KX287251	KX287547	KX287830	KX288109	KX288385	KX288712	2 KX288997	-	-	-
	CBS 141105^T; CPC 11410	<i>Ramularia</i> sp.	Persicaria nepalensis	South Korea	H.D. Shin	KX287252	2 KX287548	KX287831	KX288110	KX288386	KX288713	3 KX288998	-	-	-
	CBS 195.27	R. anomala	Fagopyrum esculentum	-	-	KX287253	8 –	-	KX288111	KX288387	KX288714	4 KX288999	-	-	-
Tr. rumicicola	CPC 14652	R. pratensis var. pratensis	Rumex crispus	South Korea	H.D. Shin	KX287254	KX287549	_	KX288112	KX288388	KX288715	5 KX289000	-	-	-
	CBS 141106^T; CPC 14653	R. pratensis var. pratensis	Rumex crispus	South Korea	H.D. Shin	KX287255	6 KX287550	-	KX288113	KX288389	KX288716	6 KX289001	-	-	-

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Table 1. (Continued).															
Species ⁴	Culture number ^{1,2}	Previous name ⁴	Host	Country	Collector	LSU	ITS	actA	tef1-α	gapdh	rpb2	his3	cmdA	tub2	chs-1
	CPC 14654	R. pratensis var. pratensis	Rumex crispus	South Korea	H.D. Shin	KX287256	KX287551	-	KX288114	KX288390	KX288717	KX289002	-	-	-
Tr. kirschneriana	CBS 113093[⊤]; RoKi 1144	Ph. paspali	Setaria palmifolia	Taiwan	R. Kirschner & CJ. Chen	GQ852627	GU214669	KX287832	KX288115	KX288391	KX288718	3 KX289003	-	-	-
Teratosphaeria biformis	CBS 124578^T; MUCC 693		Eucalyptus globulus	Australia, Queensland	G. Whyte	KF901887	KF901564	(KF903551)	(KF903287)	-	KX348100) _	(KF902703)	(KF902987)) —
T. cryptica	CBS 111663; CPC 1558		-	-	_	KF901823	KF901506	(KF903449)	(KF903300)	-	KX348101	-	(KF902715)	(KF902999)) —
T. eucalypti	CPC 12552	Phaeophleospora eucalypti	Eucalyptus nitens	Australia	C. Mohammed	KF901900	KF901576	(KF903619)	(KF903303)	-	KX348102	2 -	(KF902718)	(KF903002)) —
T. gauchensis	CBS 119465; CMW 17545		Eucalyptus grandis	Uruguay	M.J. Wingfield	KF902145	KF901787	(KF903509)	(KF903312)	-	KX348103	3 -	(KF902726)	(KF903010)) —
T. molleriana	CBS 118359; CMW 11560		Eucalyptus globulus	Australia, Tasmania	-	KF902120	KF901764	(KF903490)	(KF903327)	-	KX348104	+ _	(KF902740)	(KF903024)) —
Uwebraunia australiensis	CBS 120729; CPC 13282	U. australiensis	Eucalyptus platyphylla	Australia, Queensland	P.W. Crous	KF442553	EF394854	-	(JQ622129)	-	KX348105	i –	-	(KF442475)) —
U. commune	CPC 12397	M. lateralis	Eucalyptus globulus	Australia	I. Smith	KF251740	KF251237	-	(KF253190)	-	KX348106	6 –	-	(KF252724)) —
U. musae	CBS 122453[™]; X1021		<i>Musa acuminata</i> cv. Nendran	India	I. Buddenhagen	JQ739816	EU514225	(EU514296)	-	-	KX348107	' (EU514349)	-	-	-
	CBS 122454; X1022		<i>Musa acuminata</i> cv. Grande Naine	Indonesia	I. Buddenhagen	KX287257	EU514226	(EU514297)	-	-	KX288719	9 (EU514350)	-	-	-
Xenoramularia arxii	CBS 342.49 [⊤]	R. aromatica	Acorus calamus	Netherlands	J.A. von Arx	KX287258	KX287552	KX287833	KX288116	KX288392	KX288720	KX289004	-	-	-
X. neerlandica	CBS 113615	Pseudocercosporella sp.	Sparganium ramosum	Netherlands	-	KX287259	KX287553	KX287834	KX288117	KX288393	KX288721	KX289005	-	-	-
	CBS 141101^T ; CPC 18377	Pseudocercosporella sp.	Iris pseudacorus	Netherlands	P.W. Crous	KX287260	KX287554	KX287835	KX288118	KX288394	KX288722	2 KX289006	-	-	-
	CPC 18378	Pseudocercosporella sp.	Iris pseudacorus	Netherlands	P.W. Crous	KX287261	-	KX287836	KX288119	KX288395	KX348108	3 KX289007	-	-	-
X. polygonicola	CBS 141102[⊤]; CPC 10852	<i>Ramularia</i> sp.	Polygonum sp.	South Korea	H.D. Shin	GU214695	GU214695	KX287837	KX288120	KX288396	KX288723	3 KX289008	-	-	-
	CPC 10853	<i>Ramularia</i> sp.	Polygonum sp.	South Korea	H.D. Shin	KX287262	KX287555	-	KX288121	KX288397	KX288724	KX289009	-	-	-
	CPC 10854	<i>Ramularia</i> sp.	Polygonum sp.	South Korea	H.D. Shin	KX287263	KX287556	-	KX288122	KX288398	KX288725	5 KX289010	-	-	-
Zymoseptoria brevis	CBS 128853^T; CPC 18106; no. 8S		Phalaris minor	Iran	M. Razavi	JQ739833	JF700867	(JF701036)	(JQ739777)	-	KX348109) _	(JF701104)	(JF700968)	-

ALL THAT GLITTERS IS NOT RAMULARIA (continued on next page)

Table 1. (Continued).

Species ⁴	Culture number ^{1,2}	Previous name ⁴	Host	Country	Collector	LSU	ITS	actA	tef1-α	gapdh	rpb2	his3	cmdA	tub2	chs-1
Z. halophila	CBS 128854 ^T ; CPC 18105; IRAN1483C; GLS1		Hordeum glaucum	Iran	M. Razavi	KF252150	KF251645	(KF253946)	(KF253592)	-	KX348110	-	(KF254297)	(JF700977)	-
Z. passerinii	CBS 120382^{ET}; P 83		Hordeum vulgare	USA, North Dakota	S. Goodwin	JQ739843	JF700877	(JF701046)	(JQ739787)	(KP894652)	KP894763	(KP894874)	(JF701114)	(JF700978)	-
Z. tritici	CPC 18116	Septoria sp.	Avena sp.	Iran	Amir	KX287264	JF700884	(JF701053)	-	-	KX348111	-	(JF701121)	(JF700985)	-
	CBS 115943 ^{ET} ; IPO 323	M. graminicola	Triticum aestivum	Netherlands	R. Daamen	GU214436	AF181692	(JF701061)	-	-	KX348112	-	(JF701129)	(JF700993)	-
Z. verkleyi	CBS 133618^T CBS 136761		Poa annua Poa annua	Netherlands Netherlands	S.I.R. Videira U. Damm	KF442686 KX287265	KC005781 KX287557	-	-	-	KX348113 KX288726	-	-	-	-

* Strains not included in the phylogenetic analyses for lack of complete dataset. Species identification is based on the available data.

¹ AR: Personal culture collection of Amy Rossman; ATCC: American Type Culture Collection, Virginia, USA; BRIP: Plant Pathology Herbarium, Department of Primary Industries, Queensland, Australia; CBS: CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands; CCM: Czech Collection of Microorganisms, Masaryk University, Brno, Czech Republic; CMW: Culture Collection of the Forestry and Agricultural Biotechnology Institute (FABI) of the University of Pretoria, Pretoria, South Africa; CPC: Personal culture collection of Pedro Crous, housed at CBS; IMI: International Mycological Institute, CABI-Bioscience, Egham, Bakeham Lane, United Kingdom; INIFAT: Alexander Humboldt Institute for Basic Research in Tropical Agriculture, Ciudad de La Habana, Cuba; JCM: Japan Collection of Microorganism, RIKEN BioResource Center, Japan; JT: Personal number of J.E. Taylor; KACC: Korean Agricultural Culture Collection, National Institute of Agricultural Biotechnology, Rural Development Administration, Suwon, Republic of Korea; MUCL: Université Catholique de Louvain, Louvain-la-Neuve, Belgium; QM: Quartermaster Research and Development Center, U.S. Army, Massachusetts, USA; RoKI: Personal culture collection of Roland Kirschner; UPSC: Uppsala University Culture Collection of Fungi, Botanical Museum University of Uppsala, Uppsala, Sweden.

² Status of the strains: (T) ex-type, (ET) ex-epitype, (NT) ex-neotype.

³ LSU: large subunit (28S) of the nrRNA gene operon; ITS: internal transcribed spacers and intervening 5.8S nrDNA; *actA*: partial actin gene; *tef1-a*: partial translation elongation factor 1-alpha gene; *gapdh*: partial glyceraldehyde-3-phosphate dehydrogenase (GAPDH) gene; *rpb2*: partial RNA polymerase II second largest subunit gene; *his3*: partial histone H3 gene; *cmdA*: partial calmodulin gene; *tub2*: partial beta-tubulin gene; *chs-1*: partial chitin synthase-1 gene; "–" represents missing data.

⁴ A. = Acrodontium; An. = Antennaria; C. = Cercosporella; Ca. = Caryophylloseptoria; Ce. = Cercospora; D. = Dothistroma; N. = Neopseudocercosporella; M. = Mycosphaerella; P. = Pseudocercosporella; Pa. = Passalora; Pal. = Pallidocercospora;

Ph. = Phacellium; Pp. = Parapenidiella; Ps. = Pseudocercospora; R. = Ramularia; Re. = Readeriella; Rp. = Ramulariopsis; S. = Septoria; Sp. = Sphaerulina; T. = Teratosphaeria; Tr. = Teratoramularia; U. = Uwebraunia; X. = Xenoramularia; Z. = Zymoseptoria.

Table 2. Details of primers used and/or developed in this study for the PCR amplification and sequencing of different loci.									
Locus ¹	Primer Name	Sequence $5' \rightarrow 3'$	Annealing temperature (°C)	Orientation	Reference				
actA	ACT-2Rd	ARR TCR CGD CCR GCC ATG TC	55	Reverse	Groenewald et al. (2013)				
	ACT-512F	ATG TGC AAG GCC GGT TTC GC	55	Forward	Carbone & Kohn (1999)				
	ACT-783R	TAC GAG TCC TTC TGG CCC AT	55	Reverse	Carbone & Kohn (1999)				
chs-1	CHS-354R	TGG AAG AAC CAT CTG TGA GAG TTG	52	Reverse	Carbone & Kohn (1999)				
	CHS-79F	TGG GGC AAG GAT GCT TGG AAG AAG	52	Forward	Carbone & Kohn (1999)				
cmdA	CAL-228F	GAG TTC AAG GAG GCC TTC TCC C	58	Forward	Carbone & Kohn (1999)				
	CAL-737R	CAT CTT TCT GGC CAT CAT GG	58	Reverse	Carbone & Kohn (1999)				
	Cal2Rd	TGR TCN GCC TCD CGG ATC ATC TC	58	Reverse	Groenewald et al. (2013)				
gapdh	Gapdh-F1	ATY GTC TTC CGC AAY GCGT	56	Forward	This study				
	gpd1	CAA CGG CTT CGG TCG CAT TG	58	Forward	Berbee et al. (1999)				
	gpd2	GCC AAG CAG TTG GTT GTG C	58	Reverse	Berbee et al. (1999)				
his3	CylH3F	AGG TCC ACT GGT GGC AAG	52	Forward	Crous et al. (2004b)				
	CylH3R	AGC TGG ATG TCC TTG GAC TG	52	Reverse	Crous et al. (2004b)				
ITS	ITS4	TCC TCC GCT TAT TGA TAT GC	52	Reverse	White et al. (1990)				
	V9G	TTA CGT CCC TGC CCT TTG TA	52	Forward	De Hoog & Gerrits van den Ende (1998)				
LSU	LR5	TCC TGA GGG AAA CTT CG	52	Reverse	Vilgalys & Hester (1990)				
	LSU1Fd	GRA TCA GGT AGG RAT ACC CG	52	Forward	Crous et al. (2009c)				
mcm7	Mcm7-1348rev	GAY TTD GCI ACI CCI GGR TCW CCC AT	56	Reverse	Schmitt et al. (2009)				
	Mcm7-709for	ACI MGI GTI TCV GAY GTH AAR CC	56	Forward	Schmitt et al. (2009)				
rpb2	RPB2-5f2	GGG GWG AYC AGA AGA AGG C	$60 \rightarrow 58 \rightarrow 54$	Forward	Sung et al. (2007)				
	RPB2-7cR	CCC ATR GCT TGY TTR CCC AT	$60 \rightarrow 58 \rightarrow 54$	Reverse	Liu et al. (1999)				
	Rpb2-F1	GGTGTCAGTCARGTGYTGAA	$60 \rightarrow 58 \rightarrow 54$	Forward	This study				
	Rpb2-F4	GAY YTB GCI GGI CCI YTI ATG GC	$60 \rightarrow 58 \rightarrow 54$	Forward	This study				
	RPB2-f5f	GAY GAY MGW GAT CAY TTY GG	$60 \rightarrow 58 \rightarrow 54$	Forward	Liu et al. (1999)				
	Rpb2-R1	TCC TCN GGV GTC ATG ATR ATC AT	$60 \rightarrow 58 \rightarrow 54$	Reverse	This study				
tef1-a	EF-2	GGA RGT ACC AGT SAT CAT GTT	54	Reverse	O'Donnell et al. (1998)				
	EF1-728F	CAT CGA GAA GTT CGA GAA GG	54	Forward	Carbone & Kohn (1999)				
	TEF-1R	CTT GAT GAA ATC ACG GTG ACC	54	Reverse	Videira <i>et al.</i> (2015a)				
tub2	Bt-2a	GGT AAC CAA ATC GGT GCT GCT TTC	52	Forward	Glass & Donaldson (1995)				
	Bt-2b	ACC CTC AGT GTA GTG ACC CTT GGC	52	Reverse	Glass & Donaldson (1995)				
	T1 β-Sandy-R	AAC ATG CGT GAG ATT GTA AGT GCR CGN GGV ACR TAC TTG TT	52 52	Forward Reverse	O'Donnell & Cigelnik (1997) Stukenbrock <i>et al.</i> (2012)				

¹ actA: partial actin gene; *chs-1*: partial chitin synthase-1 gene; *cmdA*: partial calmodulin gene; *gapdh*: partial glyceraldehyde-3-phosphate dehydrogenase gene; *his3*: partial histone H3 gene; ITS: internal transcribed spacer regions and intervening 5.8S nrRNA gene of the nrDNA operon; LSU: partial 28S nrRNA gene; *mcm7*: partial gene encoding a minichromosome maintenance protein gene; *rpb2*: partial RNA polymerase II second largest subunit gene; *tef1-α*: partial translation elongation factor 1-α gene; *tub2*: partial β-tubulin gene.

denaturation (94 °C, 3 min); 35 cycles amplification [denaturation 94 °C, 30 s; locus-specific annealing temperature (Table 2), 30 s; extension 72 °C, 45 s], and final extension (72 °C, 5 min). For *gapdh* and *his3*, 40 amplification cycles were used. To obtain the partial *rpb2*, a touchdown PCR protocol was used: initial denaturation (94 °C, 3 min), 5 amplification cycles (denaturation 94 °C, 45 s; annealing 60 °C, 45 s; extension 72 °C, 2 min), 5 amplification cycles (denaturation 94 °C, 45 s; annealing 60 °C, 45 s; extension 72 °C, 2 min), 5 amplification cycles (denaturation 94 °C, 45 s; annealing 58 °C, 45 s; extension 72 °C, 2 min), 30 amplification cycles (denaturation 94 °C, 45 s; extension 72 °C, 2 min) and a final extension (72 °C, 8 min). In a few cases that double bands were obtained in the amplification of *gapdh* and *his3*, the band of correct size was purified from the agarose gel using the QlAquick[®] Gel Extraction Kit (Qiagen) according to the

manufacturer's instructions. These purified samples underwent a second round of PCR amplification following the protocol originally used to amplify that fragment. The amplified DNA fragments were sequenced in both directions using the PCR primers and the BigDye[®] Terminator v. 3.1 Cycle Sequencing Kit (Applied Biosystems Life Technologies, Carlsbad, CA, USA). DNA sequencing amplicons were purified through Sephadex G-50 Superfine columns (Sigma-Aldrich, St. Louis, MO) in MultiScreen HV plates (Millipore, Billerica, MA). Purified sequence reactions were analysed on an Applied Biosystems 3730xl DNA Analyzer (Life Technologies, Carlsbad, CA, USA). The DNA sequences generated were analysed and consensus sequences were computed using the BioNumerics v. 4.61 software package (Applied Maths, St-Martens-Latem, Belgium).

Phylogenetic analyses

The generated sequences for each gene were aligned with the online version of MAFFT v. 7 (Katoh & Standley 2013). The alignments were manually checked and improved where necessary using MEGA v. 5 (Tamura et al. 2011) and were concatenated with Mesquite v. 2.75 (Maddison & Maddison 2011). From the strains listed in Table 1, only those with the complete dataset of genes were used in the subsequent phylogenetic analyses, with the exception of R. pusilla (missing gapdh sequence) and R. primulae (missing rpb2 sequence), in which cases they were considered as missing data in the alignments. The phylogenetic methods used in this study included Neighbour-Joining and Parsimony analyses, both performed with PAUP v. 4.0b10 (Swofford 2003), a Maximum-Likelihood analysis performed with RAxML v. 8 (Stamatakis 2014) and a Bayesian analysis performed with MrBayes v. 3.2 (Ronquist et al. 2011). The Neighbour-Joining analysis using the HKY85 substitution model was applied to each gene partition individually in order to manually check the congruency among the genes (data not shown, trees deposited in TreeBASE S19315). Alignment gaps were treated as missing data and all characters were unordered and of equal weight. Any ties were broken randomly when encountered. For parsimony analysis, alignment gaps were treated as fifth character state and all characters were unordered and of unequal weight. Maximum parsimony analysis was performed in PAUP using the heuristic search option with 100 random taxon additions and tree bisection and reconnection (TBR) as the branch-swapping algorithm. Branches of zero length were collapsed and all multiple, equally most parsimonious trees were saved. The robustness of the trees obtained was evaluated by 1 000 bootstrap replications (Hillis & Bull 1993). Other measures calculated included tree length (TL), consistency index (CI), retention index (RI) and rescaled consistency index (RC). MrModeltest v. 2.2 (Nylander 2004) was used to determine the best nucleotide substitution model settings for each data partition in order to perform a model-optimised Bayesian phylogenetic reconstruction. The Markov Chain Monte Carlo (MCMC) analysis of four chains started in parallel from a random tree topology, the heat parameter was set at 0.1 and trees were saved every 100 (overview phylogeny) or 1 000 (Ramularia species phylogeny) generations until the average standard deviation of split frequencies reached 0.01 (stop value). Burn-in was set to 25 % after which the likelihood values were considered to be stationary. The Maximum-Likelihood analysis used the GTRGAMMA model and included 1 000 bootstrap replicates. All resulting trees were printed with Geneious v. 7.0.6 (Kearse et al. 2012). All new sequences generated in this study were deposited in NCBI's GenBank nucleotide database (www.ncbi.nlm.nih.gov) and the accession numbers are listed in Table 1. The alignments and respective phylogenetic trees were deposited in TreeBASE S19315 (www.TreeBASE.org).

Kimura-2-parameter values

To evaluate the ability of each gene for species resolution, interand intra-specific distance matrixes were calculated based on each gene's individual alignment using MEGA v. 5 (Tamura *et al.* 2011). Single strain species were excluded from the analyses. The matrixes were generated using the Kimura-2-parameter model, with substitutions including transitions and transversions, using uniform rates among sites and treating gaps as complete deletion. The obtained distance values were sorted into frequency distribution bins using Microsoft Excel 2007. The frequency distribution mean was calculated according to the formula $x = \Sigma(f.b) / \Sigma(f)$, in which the "f" is the frequency and "b" is the bin. The distance between the mean of the inter- and intraspecific distance distributions represents the barcoding gap (Hebert *et al.* 2003).

Taxonomy

Isolates were cultivated for 7-15 d at 21 °C in a regular day/night regime. Morphological observations of reproductive structures were determined using a Nikon Eclipse 80i compound microscope with differential interference contrast (DIC) illumination. Slides were prepared using the inclined coverslip method (Kawato & Shinobu 1959, revised in Nugent et al. 2006) and also transparent adhesive tape (Titan Ultra Clear Tape, Conglom Inc., Toronto, Canada) (Bensch et al. 2012). Clear lactic acid was used as mounting medium for microscopic observations of structures in vivo while Shear's solution was used for structures from herbarium material. The morphological structure terminology followed those used for Ramularia species by Crous et al. (2011). The observed isolates were cultivated on synthetic nutrient-poor agar (SNA) for the observation and measurement of conidiogenous structures (recipes according to Crous et al. 2009e). The recorded measurements represent the minimum value followed by the 95 % confidence interval of 30 individual measurements and the maximum value, for both length and width. For culture characterisation the isolates were inoculated on 2 % potato dextrose agar (PDA), oatmeal agar (OA) and 2 % malt extract agar (MEA) (recipes according to Crous et al. 2009e), and incubated in the dark at 25 °C. After 14 d, the colony diameter was measured and the colony colour described according to the mycological colour charts of Rayner (1970). Nomenclatural novelties and descriptions were deposited in MycoBank (Crous et al. 2004a).

RESULTS

The PCR amplification and sequencing of actA, gapdh, his3, ITS, LSU, rpb2 and tef1-a was successful for most of the isolates included in this study. The amplification of cmdA and tub2 often resulted in multiple bands, despite the attempts of protocol optimisation, and were therefore excluded from the phylogenetic analysis. The amplification of the partial genes chs-1 and mcm7 was unsuccessful for most of the strains tested and were therefore not targeted for the complete dataset. The amplification of gapdh and his3 of a few isolates resulted in double bands from which the band with the correct size was subsequently purified from the agarose gel and re-amplified using the same primers to obtain a single band. All the obtained sequences were deposited in GenBank (Table 1). The individual gene trees based on Neighbour-Joining analysis using the HKY85 substitution model (data not shown, available in TreeBASE S19315) showed that: 1) ITS was able to discriminate several clades but some species could not be distinguished; 2) actA, gapdh, rpb2 and tef1-a each supported the same general species clades and were suitable to use in a multigene analysis, and 3) the his3 phylogenetic tree was not congruent with the other genes trees and these sequences were therefore not used in the multigene analysis. Based on the *his3* gene, clades were split apart and closely related species based on the other gene trees were positioned far apart (e.g. Fig. 1, clades 19-20, 21, 23-25).

LSU & rpb2 phylogeny: The concatenated alignment of two loci (LSU and rpb2) was used to build a phylogeny that resolved the phylogenetic position of Ramularia and allied genera known from culture within the Dissoconiaceae, Mycosphaerellaceae and Teratosphaeriaceae. A strain of Cladosporium cladosporioides (CBS 112388) was used as outgroup. Based on the results of MrModelTest the Bayesian (BA) analysis was performed with the GTR+I+G substitution model, with inverse gamma rates and with dirichlet base frequencies for both genes (LSU and rpb2). The alignment contained a total of 625 unique site patterns: 200 (LSU) and 425 (rpb2). The analysis generated 9 222 trees from which 6 918 were sampled and 2304 were discarded (25 % burnin) and the consensus tree is depicted in Fig. 1. The Maximum-Likelihood (ML) analysis detected 625 distinct patterns and reached a final ML optimisation likelihood of -31995.929951. The bootstrap support values from the best-scoring tree were mapped on the Bayesian tree as the second value in the tree nodes (Fig. 1; bootstrap values \geq 80 %). The **Parsimony** (PA) analysis generated the maximum of 1 000 equally most parsimonious trees. From the total of 1 367 characters analysed, 745 were constant, 62 were variable and parsimony-uninformative and 560 were parsimony-informative. The robustness of the trees obtained was evaluated by 1000 bootstrap replications. The bootstrap support values were mapped on the Bayesian tree as the third value in the tree nodes (Fig. 1, bootstrap values \geq 80 %). A parsimony strict consensus tree was calculated from the equally most parsimonious trees and the branches were mapped with a thicker stroke on the Bayesian tree (Fig. 1). The additional parameters calculated were TL = 7149, CI = 0.167, RI = 0.793, RC = 0.132.

The phylogenetic trees generated using the three phylogenetic methods separated the strains into the same genus clades (Fig. 1). Clades I to XXII belong to Mycosphaerellaceae, clades XXIII to XXV to Dissoconiaceae and clades XXVI to XXX to Teratosphaeriaceae. Within these families we observed wellknown and highly supported clades (Bayesian posterior probability/Maximum Likelihood bootstrap support/Parsimony bootstrap support) such as Cercospora (clade VI, 1/100/100), Septoria (clade VII, 1/97/100), Sphaerulina (clade VIII, 1/100/ 100), Caryophylloseptoria (clade IX, 1/100/100), Cercosporella (clade X, 0.99/86/-), Ramulariopsis (clade XI, 1/99/93), Pseudocercospora (clade XII, 1/89/94), Pallidocercospora (clade XIII, 1/100/100), Ramularia (clade XIV, 1/100/100), Zymoseptoria (clade XVI, 0.92/-/-), Dothistroma (clade XVII, 1/100/99), Stromatoseptoria (clade XVIII, 1/100/100), Pseudocercosporella (clade XIX, 1/100/100), Microcyclosporella (clade XX, 1/98/100), Uwebraunia (clade XXIII, 1/100/99), Ramichloridium (clade XXV, 1/100/99), Acrodontium (clade XXVI, 1/99/100), Parapenidiella (clade XXVII, 1/100/100), Teratosphaeria (clade XXVIII, 1/100/ 100) and Readeriella (clade XXIX, 1/100/100). In this phylogeny, the genera Neocercospora (clade V) and Dissoconium (clade XXIV) are represented as single lineages (Fig. 1). Additional distinct clades with high support values were observed and are described as new genera in the Taxonomy section below, namely, Neopseudocercosporella (clade I, 1/100/100), Apseudocercosporella (clade IV, 1/100/100), Xenoramularia (clade XV, 0.57/–), *Mycosphaerelloides* (clade XXI, 1/100/100), *Epi-coleosporium* (clade XXII, 1/100/100) and *Teratoramularia* (clade XXX, 1/100/98). The genera *Fusoidiella* (clade II) and *Filiella* (clade III) are represented as single lineages and are described as new genera based on both molecular and morphological differences.

Multigene phylogeny of Ramularia s. str.: The concatenated alignment of five loci was used to build a phylogeny that revealed the species diversity within the genus Ramularia for species known from culture. A strain of Zvmoseptoria halophila (CBS 128854) was used as outgroup. The final alignment included 300 taxa and contained 2689 characters (including alignment gaps) divided into five partitions: 664 (rpb2), 529 (ITS), 263 (actA), 633 (gapdh) and 580 (tef1-α) characters respectively. The five characters artificially introduced as spacers between partitions were excluded from the phylogenetic analysis (see alignment in TreeBASE S19315). The following characters were also excluded as ambiguously aligned regions: 1053-1059 (ITS), 1391-1400 (actA), 1545-1560 and 1686-1720 (gapdh), 2255-2276, 2369-2376 and 2426-2506 (tef1-α). Based on the results of MrModelTest the Bayesian analysis was performed with the GTR+I+G substitution model, with inverse gamma rates and with dirichlet base frequencies for actA, gapdh and rpb2. The ITS partition was analysed with a SYM+I+G substitution model with fixed frequencies and with inverse gamma rates while the tef1-a partition was analysed with the HKY+I+G substitution model with inverse gamma rates and with dirichlet base frequencies. The alignment contained a total of 1 476 unique site patterns: 374 (rpb2), 178 (ITS), 191 (actA), 354 (qapdh), and 379 $(tef1-\alpha)$. The analysis generated 17 232 trees from which 12 924 were sampled and 4 308 were discarded (25 % burnin) and the final tree is depicted in Fig. 2. The Maximum Likelihood analysis using the GTRGAMMA model detected 1415 distinct patterns and reached a final ML optimisation likelihood of -62205.001171. The bootstrap support values from the best-scoring tree were mapped on the Bayesian tree as the second value in the tree nodes (Fig. 2; bootstrap values >80 %). The parsimony analysis generated the maximum of 1000 equally most parsimonious trees. From the 2499 characters analysed, 1068 were constant, 182 were variable and parsimony-uninformative and 1 249 were parsimony-informative. The robustness of the trees obtained was evaluated by 1000 bootstrap replications. The bootstrap support values were mapped on the Bayesian tree as the third value in the tree nodes (Fig. 2, bootstrap values > 80 %). A consensus parsimony tree was calculated from the equally most parsimonious trees and the branches were mapped with a thicker stroke on the Bayesian tree (Fig. 2). The additional parameters calculated were TL = 14589, CI = 0.213, RI = 0.827 and RC = 0.176.

The phylogenetic trees based on the multigene dataset (Fig. 2) that were generated with BA, ML and PA separated the strains into similar species clades. The phylogeny distributed the species into three main clades, and the position of single species clades varied with each gene and each phylogenetic method. The tree depicted a total of 86 clades, of which 30 are single lineages (clades 4, 6, 11, 12, 14, 18, 22, 25, 26, 33, 34, 36, 37, 39, 43, 44, 48, 51, 62–64, 69, 73, 75, 77, 80, 82–84, 88), 20 clades represent new species (clades 1, 5, 7, 15, 20, 24, 25, 44, 51, 56, 58, 70, 76, 77, 80, 83, 84, 88), and 12 clades contained good candidates for epitypification for existing species (clades 3, 16, 27, 38–40, 48, 50, 52, 67, 78, 79). These are discussed in further detail in the Taxonomy section below.



Fig. 1. Phylogenetic tree resulting from a Bayesian analysis on the combined alignment of LSU and *rpb2*. Bayesian posterior probabilities (BPP), maximum likelihood bootstrap support values (\geq 80 %; MLBS) and parsimony bootstrap support values (\geq 80 %; PBS) are indicated at the nodes (BPP/MLBS/PBS). Values of BPP/MLBS/PBS equal to 1/100/100 were replaced with a hash (#). The scale bar represents the expected number of changes per site. Branches in a thicker stroke represent the branches present in the strict consensus parsimony tree. Species names are written in black text, host names in green and country of origin in brown. In the species names, in descending order on the tree, the genus is abbreviated as: *N. = Neopseudocercosporella*; *F. = Flieilla*; *A. = Apseudocercosporella*; *Ne. = Neocercospora*; *C. = Cercospora*; *S. = Septoria*; *Sp. = Sphaerulina*; *Ca. = Caryophylloseptoria*; *Ce. = Cercospora*; *R. = Ramulariopsis*; *P. = Pseudocercosporella*; *M. = Microcyclosporella*; *M. = Teratoramularia*; *X. = Zernoamularia*; *X. = Zarapenidiella*; *T. = Teratosphaeria*; *R. = Readeriella*; *R. = Teratoramularia*; *C. = Cladosporium*; *U. = Uwebrawnia*; *Di. = Dissoconium*; *Ram. = Ramichloridium*; *Ac. = Acrodontium*; *Par. = Parapenidiella*; *T. = Teratosphaeria*; *R. = Teratoramularia*. Genus clades are delimited in coloured blocks, with genus names and clade numbers indicated to the right of the tree together with the family they belong to. Type strains are represented in **bold**. The tree was rooted to *Cladosporium cladosporioides* (CBS 112388).



Fig. 1. (Continued).





Fig. 1. (Continued).

Kimura-2-parameter values: The individual loci showed varying degrees of effectiveness in their ability to separate species (Fig. 3). In these datasets, *rpb2* and *gapdh* showed the best barcode gap distances between the inter- and intraspecific distances, followed by *actA*, *tef1*- α and *his3*. The ITS lacked a significant barcode gap, which indicates that this gene performs poorly for species resolution in the genus *Ramularia*. The *gapdh* and *rpb2* also showed the lowest overlap between the intra- and interspecific distances, followed by *tef1*- α , *actA* and ITS, respectively. A good barcode should be easily amplifiable by PCR, have a large barcode gap and a small overlap between intra- and interspecific distances (Schoch *et al.* 2012, Stielow *et al.* 2015). Based on these characteristics, both *rpb2* and *actA* make good secondary barcode loci for *Ramularia* species.

Taxonomy

In this study we applied the Consolidated Species Concept (Quaedvlieg *et al.* 2014), a polyphasic approach combining the concordance of multiple gene genealogies with morphological and ecological information to improve fungal species delimitation. The genera mapped in Fig. 1 are discussed by clade order followed by a section describing and illustrating the allied genera of *Ramularia* for which only herbarium specimens were available. The species of *Ramularia* resolved in Fig. 2 are discussed in alphabetical order in a third section to which a few important species not known from culture but of phytopathological importance were added.

Clade I: *Neopseudocercosporella* Videira & Crous, gen. nov. MycoBank MB816820.

Etymology: Named after the similarity with Pseudocercosporella.

Phytopathogenic, causing leaf spots. Mycelium internal, hyaline, septate, branched, stromata almost absent to welldeveloped. Ascomata pseudothecial, mycosphaerelloid, single to aggregated, black, immersed, becoming erumpent, globose, with an apical ostiole; wall of medium brown textura angularis. Asci aparaphysate, fasciculate, bitunicate, subsessile, obovoid to narrowly ellipsoid. Ascospores, straight to fusoid-ellipsoid, hyaline, guttulate, thin-walled, with subobtuse ends, medianly 1septate. Conidiophores solitary or grouped, erumpent through the cuticle or emerging through stomata, hyaline, sometimes faintly pigmented, smooth, simple, straight, slightly curved or geniculate-sinuous, usually aseptate, i.e. reduced to conidiogenous cells, thin-walled, smooth. Conidiogenous cells hyaline, subcylindrical to geniculate-sinuous, with inconspicuous conidiogenous loci, unthickened, neither darkened nor refractive, mostly truncate. Conidia solitary, hyaline or rarely slightly pigmented, thin-walled, smooth, straight to flexuous, subcylindrical to obclavate, with apex obtuse to subacute and base truncate, sometimes somewhat obconically, one- to multiseptate, hilum not thickened or darkened.

Type species: Neopseudocercosporella capsellae (Ellis & Everh.) Videira & Crous.



Fig. 2. Phylogenetic tree resulting from a Bayesian analysis on the combined alignment of five genes (*rpb2*, ITS, *actA*, *gapdh*, *tef1*- α). Bayesian posterior probabilities (BPP), maximum likelihood bootstrap support values (\geq 80 %; MLBS) and parsimony bootstrap support values (\geq 80 %; PBS) are indicated at the nodes (BPP/MLBS/PBS). Values of BPP/MLBS/PBS equal to 1/100/100 were replaced with a hash (#). The scale bar represents the expected number of changes per site. Branches in a thicker stroke represent the branches present in the strict consensus parsimony tree. Species clades are delimited in coloured blocks, where strain numbers are written in black, host names in blue and country of origin in brown. The current species name and clade number are indicated to the right of the tree. Type strains are represented in **bold**. The tree was rooted to *Zymoseptoria halophila* (CBS 128854).



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Fig. 2. (Continued).



Fig. 2. (Continued).



Fig. 2. (Continued).


Fig. 2. (Continued).

Notes: This genus currently accommodates two species, Neopseudocercosporella capsellae (syn. Pseudocercosporella capsellae/Mycosphaerella capsellae) and Neopseudocercosporella brassicae (syn. Mycosphaerella brassicicola) (Fig. 1, clade I; Fig. 4) which are not congeneric with the type species of Pseudocercosporella. Both are considered as important pathogens of Brassica species, especially in the Brassica oleraceae group that includes broccoli, cauliflower and Brussel sprouts, and have been reported worldwide. Neopseudocercosporella capsellae is the causative agent of White Leaf Spot disease while Neopseudocercosporella brassicae causes Ringspot disease. In literature, these pathogens are usually distinguished based on their disease symptoms, morphology of their ascospores, and culture characteristics (Inman et al. 1991). Both pathogens cause symptoms on leaves, stems and pods. The lesions caused by N. capsellae are round to angular and tan to light grey while the lesions caused by N. brassicae expand in a pattern of concentric rings with shades of grey. The ascomata, asci and ascospores of N. capsellae and N. brassicae are very similar in size and shape. The ascospores in both species are 1-septate and not constricted at the septa but the ascospores of N. brassicae typically have one cell that is broader than the other while in N. capsellae they are of similar size and shape. In culture, N. capsellae isolates produced spermogonia and conidia and also secreted a pink pigment into the media, while N. brassicae isolates produced no spermogonia, conidia or pigment. The similarity between these two diseases is high and White Leaf Spot disease was previously misdiagnosed as Ringspot in Canada, since both diseases produce slate grey lesions with spermogonia and pseudothecia on stems and pods (Rimmer et al. 2007). The

character used to distinguish these two species that is most emphasised in literature is their ascospore morphology (Inman et al. 1991, Rimmer et al. 2007). The production of pigment into the media should be considered a poor character to distinguish these species since it has been observed that, among a large number of isolates of *N. capsellae*, only a small percentage could produce pigment and this ability was highly dependant on the media used (Gunasinghe et al. 2016). Although these are economically important fungi, only a few isolates are available in culture collections and mostly of N. capsellae. The sequences of five gene regions of strains deposited in the culture collection as N. capsellae and N. brassicae used in this study showed only 6-8 unique nucleotide differences in a concatenated alignment containing about 3 000 nucleotides. None of these are from extype cultures or specimens and only N. capsellae ITS and LSU sequences were available on GenBank for comparison. Based on molecular data there is a distinct possibility that these two species might be synonymous but for now we prefer to keep them separate pending the recollection of fresh material. Neopseudocercosporella capsellae has a predominantly asexual life cycle and the sexual morph is produced at the end of the season to enable survival. Neopseudocercosporella brassicae has no recorded asexual morph other than spermatogonia in vivo. Ascomata can be produced all year round and the fungus is homothallic, meaning ascomata can be produced without the need for two complementary mating types (Rimmer et al. 2007).

Neopseudocercosporella brassicae (Chevall.) Videira & Crous, comb. nov. MycoBank MB817145.





Fig. 3. Frequency distribution graph of the Kimura-2-parameter distance test for the five individual gene loci (actaA; gapdh; ITS; rpb2; tef1-a). Barcoding gap calculated based on the frequency distributions. Percentage of overlap between the inter- and intra-specific distances based on the frequency distributions.

Basionym: Asteroma brassicae Chevall., Fl. gén. env. (Paris) 1: 449. 1826.

- *≡ Asteromella brassicae* (Chevall.) Boerema & Kesteren, Persoonia 3: 18. 1964.
- = Sphaeria brassicicola Duby, as "brassicaecola", Bot. gall., Edn 2 (Paris) 2: 712. 1830.
 - ≡ *Depazea brassicicola* (Duby) Klotzsch, in Klotzsch, Herb. Viv. Mycol.: no. 1142. 1848.
 - ≡ *Mycosphaerella brassicicola* (Duby) Lindau, in Engler & Prantl, Nat. Pflanzenfam. 1(1): 424. 1897.
 - ≡ *Sphaerella brassicicola* (Duby) Ces. & De Not., Comment. Soc. Crittog. Ital. 1(4): 238. 1863.
- = Dothidea brassicae Desm., Ann. Sci. Nat., Bot., ser. 2 17: 113. 1842.
- = Phyllosticta brassicicola Grove, J. Roy. Hort. Soc. 40: 76. 1914.

Specimens examined: **Denmark**, on *Brassica oleraceae*, date and collector unknown, isol. and dep. by C.A. Jörgensen, Feb. 1932, culture CBS 228.32. **Netherlands**, Berlikum, on *Brassica oleraceae* var. *acephala* subvar. *sabelica*, date and collector unknown, isol. and dep. by F. Quak, Nov. 1953, culture CBS 267.53. **Germany**, Schleswig-Holstein, Marne, on *Brassica oleracea*, date and collector unknown, isol. by W. Zornbach, Aug. 1986, dep. by W. Zornbach, Mar. 1988, culture CBS 173.88.

Substrate and distribution: On various Brassica oleraceae subspecies and varieties (Brussels sprouts, broccoli, cauliflower and cabbage) and other cruciferous species such as oilseedrape, rutabanga and kale. Notes: Boerema & van Kesteren (1964) addressed the nomenclatural history of *Mycosphaerella brassicicola*. *Mycosphaerella brassicicola* (1897) is based on *Sphaeria brassicicola* (1830) from *Brassica oleraceae* from France, Germany, Italy and Belgium. It is hereby transferred to the genus *Neopseudocercosporella*. Although the isolates used in this study match this host and localities, they were unfortunately sterile in culture (Fig. 1, clade I). Fresh cultures need to be collected from plants exhibiting typical disease symptoms and included in a molecular phylogeny.

Neopseudocercosporella capsellae (Ellis & Everh.) Videira & Crous, comb. nov. MycoBank MB817119. Fig. 4.

Basionym: Cylindrosporium capsellae Ellis & Everh., J. Mycol. 3(11): 130. 1887.

- ≡ Cercoseptoria capsellae (Ellis & Everh.) H.C. Greene, Trans. Wisconsin Acad. Sci. 47: 127. 1959.
 - ≡ Pseudocercosporella capsellae (Ellis & Everh.) Deighton, Mycol. Pap. 133: 42. 1973.
 - ≡ Cercoseptoria capsellae (Ellis & Everh.) Arx, Proc. Kon. Ned. Akad. Wetensch. C 86(1): 35. 1983.
- = Mycosphaerella capsellae A.J. Inman & Sivan., Mycol. Res. 95: 1339. 1991.

For additional synonyms see Braun (1995) or MycoBank.



Fig. 4. Neopseudocercosporella capsellae (A-D. CPC 14774; E-I. CPC 12518; J-N. CPC 11677). A, E. Leaf spot symptoms on hosts. B-D, F. Conidiogenous cell and conidia from herbarium material. G, H, J, K, L. Conidiogenous cells and conidia from culture. I, M, N. Conidia from culture. Scale bars = 10 µm.

Description in vivo: See Braun (1995).

Specimens examined: **South Korea**, Hongcheon, on *Capsella bursa-pastoris*, 4 Nov. 2005, H.D. Shin, culture CPC 12519; on *Draba nemorosa*, 30 Oct. 2004, H.D. Shin, culture CBS 135464 = CPC 11677; Inje, on *Trigonotis peduncularis*, 14 Sep. 2003, H.D. Shin, culture CPC 10865; Namyangju, on *Raphanus sativus*, 22 Oct. 2007, H.D. Shin, culture CBS 131896 = CPC 14773. **New Zealand**, Auckland, Mt. Albert, on *Brassica* sp., unknown date and collector, isol. C.F. Hill, Jul. 2005, culture CBS 118412. **Unknown country**, on *Brassica* sp., unknown date and collector, isol. R. Evans, 28 Aug. 2002, cultures CBS 112032, CBS 112033. **USA**, Columbia, Missouri, Boone Co., on *Capsella bursa-pastoris*, May 1887, Galloway 253 (**holotype** NY 883641, **isotype** BPI 399944).

Substrate and distribution: Various cruciferous species (*Brassicaceae*), circumglobal (host list and detailed distribution see Braun 1995).

Notes: Pseudocercosporella capsellae (1973) is based on *Cylindrosporium capsellae* (1887) from *Capsella bursa-pastoris* from the USA (Columbia, Missouri). It is hereby combined in the new genus *Neopseudocercosporella. Neopseudocercosporella capsellae* causes White Leaf Spot disease, an important disease of cruciferous species worldwide (Fig. 1, Clade I; Fig. 4). The strains CPC 12518 and CPS 12519 were isolated from this host but originated from South Korea. *Mycosphaerella*

capsellae (1991) is described from *Brassica napus* in the UK and linked to *Pseudocercosporella capsellae*. The isolates CBS 112032 and 112033 are listed from the UK but with *Brassica* sp. as host and were deposited by R. Evans who also at approximately the same time deposited IMI 389562, which is listed in the IMI database as being from *Brassica napus*. Based on ITS and partial LSU, an isolate from ATCC (38562 from *Brassica rapa*, USA, California; GenBank JX499036) which is listed in ATCC as *Pseudocercosporella capsellae*, also belongs to this clade. Unfortunately no other sequences were available for this isolate. Fresh cultures need to be collected from plants exhibiting typical disease symptoms and included in a molecular phylogeny.

Clade II: Fusoidiella Videira & Crous, gen. nov. MycoBank MB816818.

Etymology: Named after the fusiform-shaped conidia of the type species.

Phytopathogenic, causing small yellow to olivaceous green spots on leaves. *Mycelium* internal. *Conidiophores* aggregated in dense fascicles, arising through stomata, aseptate, i.e. usually reduced to conidiogenous cells, smooth, brown, subcylindrical to clavate, straight to curved due to thickening of the wall on one side, not geniculate, one to multiple conidiogenous loci located laterally or apically, loci conspicuous, thickened and broad, areolate, darkened and refractive. *Conidia* solitary, smooth, light brown, thin-walled, fusiform to obclavate-fusiform, straight to somewhat curved, septate, not constricted at the septa, apex obtuse and base truncate, hilum flattened, thickened, darkened and refractive.

Type species: Fusoidiella depressa (Berk. & Broome) Videira & Crous.

Notes: The morphology of the type species is quite unique and different from the closest phylogenetic species, *Neopseudocercosporella capsellae*. *Fusoidiella depressa* forms a single lineage in the phylogenetic analysis (Fig. 1, clade II).

Fusoidiella depressa (Berk. & Broome) Videira & Crous, comb. nov. MycoBank MB817146. Fig. 5.

Basionym: Cladosporium depressum Berk. & Broome, Ann. Mag. Nat. Hist. 7: 99, t. 5: 8. 1851.

≡ Passalora depressa (Berk. & Broome) Sacc., Nuovo Giorn. Bot. Ital. 8(2): 187. 1876.

≡ *Fusicladium depressum* (Berk. & Broome) Roum., Fungi Sel. Gall. Exs.: No. 86. 1879.

≡ Cercospora depressa (Berk. & Broome) Vassiljevsky, Fungi imperfecti Parasitici. I. Hyphomycetes: 385. 1937.

Ξ Cercosporidium depressum (Berk. & Broome) Deighton, Mycol. Pap. 112: 37. 1967.

For additional synonyms see Deighton (1967), Crous & Braun (2003) and MycoBank.

Specimen examined: **South Korea**, Bonghwa, on *Angelica gigas*, 18 Oct. 2007, H.D. Shin, KUS-F23064 = CBS H-22632, culture CBS 141335 = CPC 14915.

Notes: The specimen studied here (KUS-F23064) was initially identified as *Passalora depressa* and both the symptoms on the host and morphological characters (Fig. 5) are similar to those described from the authentic specimen (herb. K(M) 29181, on *Angelica sylvestris*, Great Britain; Deighton 1967). The conidiophores of the herbarium specimen observed are slightly smaller $[(10.5-)20-23(-29) \times (3-)4-5(-6) \mu m]$ than those described for the type $[20-70(-120) \times 4-8 \mu m]$. Similarly, the observed conidia were also slightly smaller $[(17.5-)32-38(-47) \times (4.5-)5-6(-8) \mu m]$ than those described for the type $[20-78 \times 6.5-11 \mu m]$. This species forms a single lineage in the phylogenetic analysis (Fig. 1, clade II). Fresh collections of *Passalora depressa* on *Angelica sylvestris* from the UK are required to facilitate an epitypification, and to fix the application of the name.

Clade III: *Filiella* Videira & Crous, gen. nov. MycoBank MB816823.

Etymology: Named after the filiform-shaped conidia of the type species.

Phytopathogenic. Mycelium internal, hyaline, septate, branched, forming well-developed stromata composed of swollen hyphae. *Conidiophores* emerging in dense fascicles from stromata, through the cuticle or through stomata, subcylindrical, straight to flexuous, geniculate-sinuous, aseptate, i.e. usually reduced to conidiogenous cells, rarely 1septate near the base, hyaline to pale yellow at the base, thin-walled, smooth, with inconspicuous conidiogenous loci, unthickened, neither darkened nor refractive. *Conidia* solitary, acicular, subcylindrical, filiform, narrowly obclavate, hyaline, discretely septate, thin-walled, smooth, apex subacute, base truncate, hila unthickened, not darkened (adapted from Braun 1993).

Type species: Filiella pastinacae (P. Karst.) Videira & Crous.

Notes: This monotypic genus (Fig. 1, Clade III) was established to accommodate *Pseudocercosporella pastinacae*, since it is not congeneric with *Pseudocercosporella s. str.* based on *P. bakeri* (Fig. 1, clade XIX). This species is represented by a single lineage in the phylogenetic analysis (Fig. 1, clade III). It is closely related to *Neopseudocercosporella* and *Fusoidiella*, but can be distinguished by the acicular-filiform conidia instead of the sub-cylindrical conidia of *N. capsellae*, or pigmented, fusiform conidia of *F. depressa*.

Filiella pastinacae (P. Karst.) Videira & Crous, comb. nov. MycoBank MB817147.

Basionym: Cercosporella pastinacae P. Karst., Hedwigia 23: 63. 1884.

≡ *Ramularia pastinacae* (P. Karst.) Lindr. & Vestergr., Acta Soc. Fauna FI. Fenn. 22(1): 8. 1902.

≡ *Pseudocercosporella pastinacae* (P. Karst.) U. Braun, Nova Hedwigia 56(3-4): 444. 1993.

- = *Phyllosticta umbellatarum* Rabenh., Fungi Eur. Exs., Cent. XII: no. 1262. 1869.
- = Phloeospora laserpitii Bres., Fungi trident. 2(8–10): 45. 1892.

= Cylindrosporium septatum Romell, Syll. Fung. 10: 503. 1892.

For additional synonyms see Braun (1995) and MycoBank.

Specimens examined: Germany, Dresden, on *Pastinaca sativa*, 1866, Rabenh., Fungi Eur. Exs. 1262 (neotype, designated in Braun 1995, HAL). Sweden, Uppland, Uppsala Näs, Vreta, on *Laserpitium latifolium*, 2 Jun. 1988, K. & L. Holm, culture CBS 114116.

Substrate and distribution: On Angelica, Apium, Archangelica, Astrantia, Eremodaucus, Heracleum, Laserpitium, Libanotis, Pastinaca, and other hosts (Apiaceae); Caucasus, Central Asia, Europe, N. America and S. Africa (see Braun 1995).

Notes: Cercosporella pastinacae was transferred to Pseudocercosporella by Braun (1993). It was originally described on Pastinaca sativa from Finland. The type material was not preserved and a neotype specimen on Pastinaca sativa from Germany was selected (Braun 1995; neotype in HAL). This species is known for causing cercosporoid leaf blight of parsnip that is characterised by the formation of yellow-brown spots on leaves and petioles that later become necrotic and lead to plant defoliation. Filiella pastinacae (= P. pastinacae) is often found in mixed infections with R. heraclei (= R. pastinacae-sativa) and they have been often confused. Filiela pastinacae also infects celery, and Angelica species and seeds contaminated with this pathogen must be discarded. The disease has been reported from Europe and Central Asia (Braun 1995) and is susceptible to various fungicides (Davis & Raid 2002). This species is represented by a single lineage in the phylogenetic analyses (Fig. 1, clade III).



Fig. 5. Fusoidiella depressa (CBS 141335). A–H. Observations from herbarium material. A. Leaf spot symptoms on the host. B–D. Conidia. E. Conidia and conidiophores. F–H. Conidiophores. Scale bars = 10 µm.

Clade IV: Apseudocercosporella Videira & Crous, gen. nov. MycoBank MB816816.

Etymology: Named after the similarity with the genus *Pseudocercosporella*.

Phytopathogenic. *Mycelium* composed of hyaline, septate, branched, thin-walled, smooth hyphae. *Conidiophores* arising from hyphae, simple, and occasionally branched, straight and subcylindrical to flexuous, geniculate-sinuous, septate or aseptate, hyaline, thin-walled, smooth. *Conidiogenous cells* integrated, terminal or conidiophores often reduced to conidiogenous cells, subcylindrical to geniculate-sinuous, conidiogenous loci slightly thickened and darkened. *Conidia* formed singly, filiform, or subcylindrical, hyaline, thin-walled, smooth, septate or aseptate, base more or less truncate, hilum slightly thickened and darkened.

Type species: Apseudocercosporella trigonotidis Videira, H.D. Shin & Crous.

Notes: This monotypic genus (Fig. 1, Clade IV) was established to accommodate a pseudocercosporella-like species, since it is not congeneric with *Pseudocercosporella s. str.* based on *P. bakeri* (Fig. 1, clade XIX). This genus clade is highly supported in the phylogenetic analysis (Fig. 1, clade IV, 1/100/100). It is closely related to *Filiella* and *Neopseudocercosporella*, but can be distinguished by the conidial hila and conidiogenous loci that are slightly thickened and darkened instead of inconspicuous.

Apseudocercosporella trigonotidis Videira, H.D. Shin & Crous, **sp. nov.** MycoBank MB816845. Fig. 6.

Etymology: Named after the host on which it was observed, *Trigonotis*.

Mycelium composed of hyaline, septate, branched, hyphae, 1–2 µm diam. *Conidiophores* arising from hyphae, simple, occasionally branched, straight and subcylindrical to flexuous, geniculate-sinuous, $(5.5-)11-16(-32) \times 1-1.5$ µm, aseptate to 1(–2)-septate, hyaline, thin-walled, smooth. *Conidiogenous cells* integrated, terminal or conidiophores often reduced to conidiogenous cells, subcylindrical to geniculate-sinuous, (4–) $6.5-8(-13) \times 1-2$ µm; conidiogenous loci slightly thickened and darkened, 1–2 µm diam. *Conidia* formed singly, filiform, or subcylindrical, (11–)19–22(–30) × 1 µm, hyaline, thin-walled, smooth, aseptate or 1–4-septate, apex obtuse, base more or less truncate, 1 µm diam, hilum slightly thickened and darkened.

Culture characteristics: On MEA, 32 mm diam, surface low convex, smooth, white with a greyish tinge, with margins undulate, colony reverse ochraceous; on OA, 20 mm diam, surface flat, white, sparse aerial mycelium in the colony centre, fluffy, with margins crenate, colony reverse buff; on PDA, 29 mm diam, surface low convex, white, sparse aerial mycelium in the colony centre, fluffy, with margins entire, colony reverse buff.

Specimen examined: **South Korea**, Jeju, on *Trigonotis peduncularis*, 12 Nov. 2003, H.D. Shin (**holotype** KUS-F20054, isotype CBS H-22515, culture ex-type CBS 131890 = CPC 10864); *idem*. CPC 10865.

Notes: Apseudocercosporella is the first cercosporoid species isolated from *Trigonotis.* It differs from the closest species in the phylogenetic tree (Fig. 1) by the slightly darkened conidiogenous loci and hila (Fig. 6). The clade is highly supported by BA and ML phylogenetic analysis (Fig. 1, clade IV, 1/100/100).

Clade V: *Neocercospora* M. Bakhshi *et al.*, Phytotaxa 213: 28. 2015.

Note: See Bakshi et al. (2015a).



Fig. 6. Apseudocercosporella trigonotidis (CPC 10865). A–D. Observations from herbarium material. E–G. Structures formed in culture. A. Leaf spot symptoms on the host. B, C, E–G. Conidiophores, conidiogenous cells and conidia. D. Conidium. Scale bars = 10 µm.

Clade VI: Cercospora Fresen. ex Fuckel, Fungi Rhen. Exs., Fasc. II: no. 117, 1863.

Note: See Groenewald et al. (2013), Bakshi et al. (2015b) and Braun et al. (2015).

Clade VII: Septoria Sacc., Syll. Fung. 3: 474. 1884.

Note: See Verkley et al. (2013) and Quaedvlieg et al. (2013).

Clade VIII: Sphaerulina Sacc., Michelia 1(4): 399. 1878.

Note: See Quaedvlieg et al. (2013).

Sphaerulina chaenomelis (Y. Suto) Videira, U. Braun, H.D. Shin & Crous, **comb. nov.** MycoBank MB817148.

Basionym: Cercosporella chaenomelis Y. Suto, Mycoscience 40: 513. 1999.

≡ *Pseudocercosporella chaenomelis* (Y. Suto) C. Nakash. *et al.*, Stud. Mycol. 75: 70. 2013.

Specimens examined: Japan, Mie Pref., Tsu, on leaves of *Chaenomeles* sinensis, 29 Oct. 2011, C. Nakashima (epitype TFM: FPH-8101, culture exepitype CBS 132131 = MUCC 1510). South Korea, Kimhae, on *Chaenomeles* speciosa, 14 Nov. 2007, H.D. Shin, CBS H-20844 = KUS-F23225, culture CBS 131897 = CPC 14795.

Notes: Chaenomeles sinensis is a deciduous tree native to China that is planted as ornamental in Japan. It is susceptible to a leaf spot disease commonly called frosty mildew caused by *Cercosporella chaenomelis* (Horie & Kobayashi 1982). Disease symptoms include large coalescing leaf spots, the development of white tufts of conidiophores on the lower surfaces, and tree defoliation. This species has been linked to the sexual morph *Mycosphaerella chaenomelis* (Suto 1999) that forms ascomata on fallen overwintered leaves providing inoculum for new infections. Crous et al. (2013) considered that the fungus would be better placed in Pseudocercosporella due to the hyaline conidia with unthickened conidial hila and proposed a new combination in that genus. Based on DNA sequence data from the ITS and actA gene regions, strains from Japan and South Korea are identical (Crous et al. 2013, unpubl. data). Pseudocercosporella chaenomelis is morphologically comparable only with Pseudocercosporella gei, known on Geum spp. in North America and the Far East of Russia (Braun 1995). In this study, based on LSU and rpb2, this species falls in the Sphaerulina clade (Fig. 1, clade VIII), and a new combination is therefore proposed. In the genus Sphaerulina, there is also Sphaerulina gei, on Geum japonicum from South Korea, and one could speculate that Pseudocercosporella gei may be a synonym of the latter, but no molecular data are presently available for this species, which could of course also be a different fungus.

Sphaerulina koreana (Crous *et al.*) Videira, H.D. Shin & Crous, **comb. nov.** MycoBank MB817149.

Basionym: Pseudocercosporella koreana Crous et al., Stud. Mycol. 75: 71. 2013 (2012).

= Sphaerulina viciae Quaedvl. et al., Stud. Mycol. 75: 348. 2013.

Specimen examined: South Korea, Hoengseong, on Vicia amurensis, 4 Aug. 2004, H.D. Shin (holotype CBS H-20845, isotypes HAL 1850 F, KUS-F20554, culture ex-type CBS 135462 = CPC 11414; CPC 11415).

Notes: This isolate was described as a new species in two different papers in the same journal volume (Studies in Mycology 75). The name *Pseudocercosporella koreana* (Crous *et al.* 2013) was published online earlier than the name *Sphaerulina viciae* (Quaedvlieg *et al.* 2013). Therefore, the name *Pseudocercosporella koreana* is retained as basionym with *Sphaerulina viciae* as later synonym.

Clade IX: Caryophylloseptoria Verkley et al., Stud. Mycol. 75: 233. 2013.

Note: See Verkley et al. (2013) and Quaedvlieg et al. (2013).

Clade X: Cercosporella Sacc., Michelia 2(6): 20. 1880.

Phytopathogenic, mostly causing leaf spots. *Hyphae* restricted to intercellular spaces and forming cup- or bowl-shaped appresoria, 7–17 µm diam that attach to walls of mesophyll cells. *Conidiophores* emerging through stomata or erumpent through the cuticle, straight, subcylindrical to geniculate-sinuous, hyaline, sometimes lightly pigmented near the base, more or less thinwalled and smooth. *Conidiogenous cells* integrated, terminal, polyblastic, sympodial, mostly conspicuously geniculate, conidiogenous loci conspicuous, hyaline but refractive, thickened and raised in the shape of a truncated cone (ultrastructure). *Conidia* formed singly, hyaline, subcylindrical to obclavate, sometimes fusiform, 1- to multi-septate, usually thin-walled and smooth, apex obtuse, base often rounded to truncate or obconically truncate, hilum thickened, not darkened but refractive. Description adapted from Braun (1995) and Kirschner (2009).

Type species: Cercosporella virgaureae (Thüm.) Allesch. [= *Cercosporella cana* (Sacc.) Sacc. (designated by Deighton 1973)].

Notes: Cercosporella species are phytopathogenic and mostly cause leaf spots. The genus was first described by Saccardo (1880) on Solidago virgaurea, Austria, and was later redescribed by Deighton (1973). Species with consistently internal mycelium in vivo are allocated to Cercosporella subgen. Cercosporella (type species C. virgaureae) and species with superficial mycelium in vivo to Cercosporella subgen. Pseudovellosiella (type species C. crataevae) (Braun 1995). Morphologically, Cercosporella differs from Ramularia by producing cup-shaped appressoria and by having flat conidial loci in the shape of a truncated cone (Kirschner 2009). Conidiogenous loci of Ramularia spp. have a raised rim with a central dome that is cladosporium-like and does not produce appressoria. A representative of the type species of the genus, C. virgaureae, was recently recollected but unfortunately not deposited in a culture collection (Kirschner 2009). A LSU sequence retrieved from the Cercosporella strain clustered in a sister clade to Ramularia (Kirschner 2009, this study). The LSU sequence of this isolate (GenBank EU710894) is 100 % identical to the LSU sequence of the South Korean isolates used in this study (Fig. 1, clade X). The recently described species C. dolichandrae belongs to Cercosporella as currently circumscribed (Crous et al. 2014). A first report of the leaf spot disease caused by Cercosporella pfaffiae on Brazilian Ginseng was published, with the closest match on LSU data (GenBank JQ990330) being Cercosporella virgaureae (CBS 113304; GenBank GU214658) (Machado et al. 2012), but due to the lack of an rpb2 sequence it was not included in the phylogeny created in this study. There are a total of 50 species described in the genus Cercosporella (Braun 1995, Seifert et al. 2011) but very few are available as cultures, and many are not congeneric with Cercosporella s. str. (e.g. Fig. 1, clades XII, XIV, XXX). A particularly important species cited in literature is Cercosporella rubi (G. Winter) Plakidas (= Fusisporium rubi G. Winter), the causal agent of the Blackberry rosette disease, a major disease of blackberries in the Southeastern USA. It infects the axillary buds and induces them to germinate as leafy bunches called rosettes. The disease causes reduced yield, poor quality fruit and in severe cases, cane death (Ellis & Converse 1991). Braun (1995) re-examined type material of this species and described and discussed this fungus under "Excluded, doubtful and insufficiently known species". Unfortunately no cultures of this species were available for study.

Cercosporella catenulata Videira & Crous, **sp. nov.** MycoBank MB816846. Fig. 7.

Etymology: Named after the unusual production of short conidial chains.

Mycelium composed of hyaline, septate, branched hyphae, 1-2 µm diam. Conidiophores arising from hyphae, simple or branched, straight and subcylindrical to flexuous or geniculatesinuous, (8.5-)37-50(-77) × (1-)1.5-2 µm, 2-6-septate, hyaline, thin-walled, smooth. Conidiogenous cells integrated, terminal or lateral, subcylindrical to geniculate-sinuous, (4-) $8.5-10.5(-15) \times (1-)1.5(-2) \mu m$, with a single to multiple conidiogenous loci, conspicuous, thickened but not darkened. Conidia hyaline, smooth, formed singly or in very short chains, aseptate but rarely 1-septate, with hila thickened but not 1 µm diam. Ramoconidia fusoid, darkened. (5-) $9-11(-15) \times 2-2.5(-3) \mu m$, with two apical hila. Intercalary conidia fusoid, $(7-)9.5-11(-14) \times 2-2.5(-3) \mu m$, in branched chains of up to two conidia. Terminal conidia fusoid to obovoid, $(3.5-)6-7.5(-12) \times 2-2.5(-3) \mu m.$

Culture characteristics: On MEA, 5 mm diam, surface raised, erumpent aerial mycelium, buff, with margins undulate, colony reverse hazel; on OA, 5 mm diam, surface low convex, erumpent aerial mycelium, buff, with margins crenate, feathery, colony reverse hazel; on PDA, 11 mm diam, surface convex, erumpent aerial mycelium, rosy buff, with margins entire and with sparse mycelium, colony reverse honey in the centre and buff at the margin.

Specimen examined: Rwanda, Rubona, on leaves of *Phaseolus vulgaris*, 10 Jan. 1973, D. Froment (holotype CBS H-17715, culture ex-type CBS 355.73).

Substrate and distribution: Only known from the type host and location.

Notes: Cercosporella catenulata is an unusual member of the genus, since it produces catenate conidia (Fig. 7). This species is represented by a single lineage in the phylogenetic analysis (Fig. 1, clade X).

Cercosporella virgaureae (Thüm.) Allesch., Hedwigia 34: 286. 1895. Fig. 8.

Basionym: Ramularia virgaureae Thüm., Fungi Austr. Exs., Cent. 11: no. 1072. 1874.

- ≡ Ovularia virgaureae (Thüm.) Sacc., Syll. Fung. 4: 142. 1886.
- ≡ Cylindrosporium virgaureae (Thüm.) J. Schröt., Krypt.-Fl. Schlesien 3-2(10): 489. 1897.
- ≡ *Cercospora virgaureae* (Thüm.) Oudem., Ned. Kruidk. Arch. 2: 315. 1901.

For additional synonyms see Braun (1995) or MycoBank.



Fig. 7. Cercosporella catenulata (CBS 355.73). A-H. Structures observed in culture. A, B, D, E, H. Conidiophores, conidiogenous cells and conidia. C, F. Conidia. G. Conidiophore. Scale bars = 10 µm.



Fig. 8. Cercosporella virgaureae (CPC 11461). A. Leaf spot symptoms on the host in herbarium material. B-F. Structures observed in culture. B-D. Conidiophores and conidiogenous cells. E, F. Conidia. Scale bars = 10 µm.

Description in vivo: See Braun (1995).

Specimens examined: Austria, Krems, on Solidago virgaurea, 1871 [Thüm., Fungi Austr. Exs. 1072] (lectotype K). Brazil, Guimarania, Minas Gerais, on *Conyza canadensis*, unknown date, B.S. Vieira, culture CPC 19492. South Korea, Jinju, on *Erigeron annuus*, 1 Jul. 2004, H.D. Shin, cultures CPC 11456, CPC 11457, CPC 11460, CPC 11461; Namyangju, on *Erigeron annuus*, 9 Oct. 2002, H.D. Shin, cultures CPC 10286–10288; Chuncheon, on *Erigeron annuus*, 21 May 2003, H.D. Shin, culture CBS 113304.

Notes: Cercosporella virgaureae has a nearly circumglobal distribution and has been isolated from several hosts in the Asteraceae (Braun 1995), although it was originally described on Solidago virgaurea, Austria. Deighton (1973) reduced numerous Cercosporella species to synonymy with *C. virgaureae*. Kirschner (2009) collected representative strains of the type species of *Ramularia* (*R. pusilla*) and *Cercosporella* (*C. virgaureae*) and compared them based on LSU sequences, light microscopy and scanning electron microscopy, confirming them to represent two separate genera. The phylogenetic analysis in this study also supports the separation of *Cercosporella* (Fig. 1, clade X) from *Ramularia* (Fig. 1, clade XIV).

Clade XI: Ramulariopsis Speg., Anales Mus. Nac. Hist. Nat. Buenos Aires 20(13): 421 [ser. 3, 13]. 1910. Fig. 9.

Phytopathogenic on vascular plants and usually forming leaf spots. *Mycelium* internal. *Conidiophores* fasciculate, arising through stomata or erumpent, hyaline, septate, thin-walled, smooth, simple or often branched. *Conidiogenous cells* integrated, terminal, intercalary as well as pleurogenous (as short nodulose protuberances or subcylindrical branchlets), polyblastic, sympodial, with thickened and darkened conidiogenous loci. *Conidia* catenate, in simple as well as branched chains, ellipsoid-ovoid, subcylindrical-fusiform, 0–1- to multi-euseptate, thin-walled, hyaline, with thickened and darkened hila; conidial secession schizolytic. Description adapted from Braun (1998).



Fig. 9. Ramulariopsis cnidoscoli (LPS herbarium Nº12.850, type specimen). A-C. Conidiophores. D-F, H, I, Conidia. G. Conidiogenous cell. Scale bars = 10 µm.

Type species: Ramulariopsis cnidoscoli Speg.

Specimen examined: Argentina, Salta, Orán, on *Cnidoscolus vitifolius* var. *cnicodendron* (= *C. cnicodendron*), Apr. 1905, C. Spegazzini (lectotype, designated by Deighton 1972, LPS 12.850) (Fig. 9).

Notes: Ramulariopsis species have frequently branched conidiophores with integrated, terminal, intercalary and pleurogenous conidiogenous cells with thickened and darkened conidiogenous loci. The conidia are catenate in simple or branched chains. *Ramularia* is very similar to the present genus, but differs in having simple conidiophores with consistently terminal conidiogenous cells. *Ramulariopsis* was described by Spegazzini (1910) and emended by Deighton (1972). The type species, *R. cnidoscoli*, was collected on *Cnidoscolus vitifolius* in Argentina, and is only known from herbarium material (Fig. 9). This genus currently accommodates four species (Seifert *et al.* 2011) that are phytopathogenic, and usually cause leaf spots (Braun 1998). The most widespread and economically important species is *R. gossypii*, known to be the causal agent of areolate mildew of cotton.

Ramulariopsis gossypii (Speg.) U. Braun, Nova Hedwigia 56: 432. 1993. Fig. 10.

Basionym: Cercosporella gossypii Speg., Anales Soc. Ci. Argent. 22(4): 208. 1886.

≡ Ramularia gossypii (Speg.) Cif., Quad. Lab. Crittog. Ist. Bot. Univ. Pavia 19: 124. 1962.

≡ Septocylindrium gossypii (Speg.) Subram., Hyphomycetes (New Delhi): 309. 1971.

- = Ramularia areola G.F. Atk., Bot. Gaz. 15: 168. 1890.
- = Mycosphaerella areola Ehrlich & F.A. Wolf, Phytopathology 22: 238. 1932.

Description in vivo: See Braun (1998: 314).

Mycelium composed of hyaline, septate, branched hyphae, $1-3 \mu m$ diam. *Conidiophores* hyaline, thin-walled, smooth, erect, subcylindrical to geniculate-sinuous, simple or sometimes

branching from the base to the apex, septate, (18-)27-35(-46) × $(1.5-)2-3 \mu m$. *Conidiogenous cells* hyaline, smooth, integrated, terminal or pleurogenous, formed as short lateral branchlets, subcylindrical to geniculate-sinuous, (15-)17-19(-20) × $(2-)2.5-3 \mu m$, with conidiogenous loci slightly thickened and darkened. *Ramoconidia* hyaline, thin-walled, smooth, subcylindrical-fusiform, 0-3-septate, (12-) 16-19(-23) × $(1.5-)2-3(-4) \mu m$. *Intercalary conidia* hyaline, smooth, fusiform, 0-3-septate, $(7.5-)11.5-13(-17) \times (1.5-)$ 2-3 μm . *Terminal conidia* hyaline, smooth, catenate, 0-1septate, fusiform, obovoid, $(3-)9-11(-16) \times (1-)2-3(-4) \mu m$, hila slightly thickened and darkened.

Culture characteristics: On MEA, 8 mm diam, surface raised, lumpy, hairy, iron-grey and olivaceous grey, with margins crenate, convex, colony reverse iron-grey and olivaceous grey; on OA, 8 mm diam, surface irregular, patches with pale olivaceous grey erumpent mycelium and others naked and iron-grey, with margins undulate, with sparse mycelium and hazel, colony reverse olivaceous grey; on PDA, 8 mm diam, surface raised, lumpy, hairy in the centre with iron-grey and pale olivaceous grey patches, with margins crenate and convex, colony reverse olivaceous grey.

Specimens examined: Brazil, Paraguari, on Gossypium sp., May 1883, Balansa 3856 (lectotype, designated in Braun (1998), LPS). Brazil, on Gossypium sp., Oct. 2000, collector unknown (epitype designated here CBS H-22535, MBT204824, culture ex-epitype CBS 141099 = CPC 25909).

Notes: Ramulariopsis gossypii is the causal agent of a major disease of cotton known as cotton areolate mildew. In countries like Madagascar and India, yield losses due to the disease can reach up to 60 % of the crop (Kirkpatrick & Rothrock 2001). In Brazil it was considered a minor disease but the expansion of the cultivated area on cotton and the introduction of susceptible varieties increased the disease incidence and yield losses now reach 30 % of crop production (Lima *et al.* 2010). *Ramulariopsis*



Fig. 10. Ramulariopsis gossypii (CBS 141099). A, C, D. Observations from herbarium material. B, E–H. Structures formed in culture. A. Leaf spot symptoms on the host. B, E. Conidiophores and conidia. C, D. Conidiophores. F–H. Conidia. Scale bars = 10 µm.

gossypii was originally described on *Gossypium* sp. from Brazil (lectotype in LPS) but the species has a worldwide distribution wherever cotton is cultivated (Braun 1998). Therefore, strain CPC 25909, which is from the same host and country and conforms to the morphological description of this species (Fig. 10), is herewith designated as epitype. This species is represented by a single lineage in the phylogenetic analysis (Fig. 1, clade XI).

Ramulariopsis pseudoglycines Videira, Crous & Braun, **sp. nov.** MycoBank MB816926. Fig. 11.

Etymology: Named after its morphological similarity to the species *Ramulariopsis glycines*.

Mycelium composed of hyaline, septate, branched, hyphae, 1.5–3 µm diam. *Conidiophores* hyaline, thin-walled, smooth, erect, subcylindrical to geniculate-sinuous, simple or sometimes branching from the base to the apex, septate, (67–) 121–175(–226) × 2 µm. *Conidiogenous cells* hyaline, smooth, terminal or formed as short lateral branchlets, subcylindrical to geniculate-sinuous, sometimes integrated in the mycelium, pleurogenous, $(14-)21-25(-33) \times (1.5-)2(-3)$ µm, with conidiogenous loci slightly thickened and darkened. *Ramoconidia* hyaline, smooth, 0–3-septate, (9–)14–17(–21) × (2–)2.5–3 µm. *Intercalary conidia* hyaline, smooth, fusiform, 0–2-septate, (7–) 12–15(–23) × (1.5–)2–3(–3.5) µm. *Terminal conidia* hyaline, smooth, catenate, aseptate, fusiform to obovoid, (4.5–) 6.5–8(–12) × (2–)2.5–3 µm; hila slightly thickened and darkened.

Culture characteristics: On MEA, 10 mm diam, surface raised, lumpy, smooth, pale olivaceous grey with whitish areas, with margins undulate and fimbriate, colony reverse iron-grey; on OA, 10 mm diam, surface low convex, smooth, smoke grey in the centre and a pale olivaceous margin, with margins entire, colony reverse iron-grey; on PDA, 10 mm diam, surface low

convex, lumpy, olivaceous grey with pale olivaceous grey patches, with margins undulate, colony reverse olivaceous grey.

Specimens examined: Brazil, on Gossypium sp., 2000, unknown collector (holotype CBS H-22546, culture ex-type CBS 141100 = CPC 18242); *idem*. CPC 18241. Togo, Kara region, on Gossypium barbadense, 31 Oct. 2011, M. Piatek, culture CPC 20036.

Notes: These strains were initially identified as *R. gossypii* but observations of the conidiogenous structures in culture and in the herbarium specimen revealed this species to have very long conidiophores, rather similar to *Ramulariopsis glycines* but much longer (Fig. 11). *Ramulariopsis glycines*, however, was originally described from *Glycine javanica*, Zambia, and has not been previously reported on *Gossypium* from Brazil (Braun 1998). This species clade is highly supported by the phylogenetic analysis (Fig. 1, clade XI, 1/100/100).

Clade XII: *Pseudocercospora* Speg., Anales Mus. Nac. Buenos Aires, Ser. 3, 20: 437. 1910.

Notes: Pseudocercospora was established by Spegazzini (1910) to accommodate species that produce pigmented conidiophores and conidia with neither thickened nor darkened conidiogenous loci and conidial hila (Braun 1995, Crous *et al.* 2013). The genus was based on the type species *P. vitis*, a foliar pathogen of grapevines, but also includes species that are endophytes or saprobes. The generic circumscription of *Pseudocercospora* has been emended in recent years due to the publication of DNA sequence data of various gene regions (Crous *et al.* 2000, 2001, 2013). Based on these studies the genera *Cercostigmina*, *Phaeoisariopsis* and *Pseudocercospora* and the name *Pseudocercospora* was conserved over *Stigmina*, which represented an older generic name (Braun & Crous 2006).



Fig. 11. Ramulariopsis pseudoglycines (CBS 141100). A–D. Observations from herbarium material. E–G. Structures formed in culture. A. Leaf spot symptoms on the host. B–G. Conidiophores, conidiogenous cells and conidia. Scale bars = 10 µm.

Clade XIII: Pallidocercospora Crous, Stud. Mycol. 75: 73. 2013.

Note: See Crous et al. (2013).

Clade XIV: *Ramularia* Unger, Exanth. Pflanzen (Wien): 169. 1833. emend. U. Braun (nom. cons.).

= Didymaria Corda, Icon. fung. (Prague) 5: 9. 1842.

≡ Septocylindrium Bonord. ex Sacc., Michelia 2: 15. 1880.

= Acrotheca Fuckel, Jahrb. Vereins Naturk. Herzogth. Nassau 15: 43. 1860.

= *Phacellium* Bonord., in Rabenh., Fungi Eur. Exs., Edn. 2, ser. 2: no. 288. 1860.

= Ovularia Sacc., Michelia 2: 17. 1880.

= Ophiocladium Cav., Z. Pflanzenkrankh. 3: 26. 1893.

= *Pseudovularia* Speg., Anales Mus. Nac. Buenos Aires, Ser. 3, 20: 418. 1910.

For additional synonyms see Braun (1998).

Mostly phytopathogenic (leaf spots, chlorosis or necrosis), sometimes saprobic or mycophylic. Conidiophores individual or synnematous, sometimes forming small to sporodochial caespituli, emerging through stomata or through the cuticle, straight, subcylindrical to geniculate-sinuous, continuous or septate, hyaline or in some species with a faintly reddish tinge, occasionally branched, thin-walled, usually smooth but rarely rough. Conidiogenous cells integrated, terminal, polyblastic, sympodially elongating, straight to geniculate-sinuous, conidiogenous loci conspicuously thickened, darkened and refractive, coronate (cladosporoid). Conidia consistently solitary or in simple or branched chains, solitary conidia 0-1-septate, catenate conidia aseptate to multiseptate (mostly 1-4 eusepta), hyaline, in a few species with a faintly reddish tinge, usually ellipsoid-ovoid, cylindrical-fusiform, rarely filiform, occasionally constricted at the septa, thin-walled, smooth to verruculose-echinulate, hila distinct, slightly to conspicuously thickened, darkened, refractive; conidial secession schizolytic.

Type species: Ramularia pusilla Unger.

Notes: The genus Ramularia was described by Unger (1833) to include two species R. pusilla and R. didyma, of which R. pusilla on Poa nemoralis, Austria, was later designated as lectotype (Unger 1836). The confused taxonomic history of Ramularia has been addressed by several authors (Hughes 1949, Braun 1988, Sutton & Waller 1988), and the genus was monographed by Braun (1995, 1998). Ramularia species are usually described as hyphomycetes with hyaline conidiophores and conidia with distinct, thickened, darkened and refractive conidial loci and hila. Braun (1998) divided the genus Ramularia in two morphologically circumscribed subgenera, one with conidia consistently solitary (Ramularia subgen. Ramularia) and another with catenate conidia (Ramularia subgen. Septocylindrium, type species R. septata). Within Ramularia subgen. Ramularia, two sections were established, one with conidiogenous cells straight to geniculous-sinuous (Sect. Ramularia, type Ramularia pusilla) and one with conidiogenous cells strongly curved like a swan's neck (Sect. Ophiocladium, type species R. collo-cygni).

Ramularia species are phytopathogenic and mostly cause leaf spots but they can also be endophytic, saprophytic and mycophylic. There are about 325 species accepted in this genus (Braun 1998, or MycoBank) of which only six have thus far been experimentally linked to a *Mycosphaerella* sexual morph (Videira *et al.* 2015b). Currently *Ramularia* is accepted as being a hostspecific genus of phytopathogenic fungi (Braun 1998), although some exceptions are known (e.g. *R. vizellae*, Videira *et al.* 2015b).

Phacellium was described by Bonorden (1861) and currently includes 27 species (Braun 1998, Seifert *et al.* 2011 or Myco-Bank). The type species, *Ph. alborosellum* (Fig. 12) was described from *Cerastium holosteoides* in France and is



Fig. 12. Phacellium alborosellum (PC herbarium PC0084649, type specimen). A. Disease symptom on host leaf. B, C. Synnematous conidiophores, conidiogenous cells and conidia. D–G. Single and multiseptate conidia. Scale bars = 10 µm.

characterised by forming synnematous conidiomata that can be hyaline or slightly pigmented. The *Phacellium* strains in this study cluster within *Ramularia* (Fig. 1, clade XIV; Fig. 2, clade 64, clade 82) and a new *Ramularia* species that forms synnemata is described (Fig. 2, clade 76). These results support the hypothesis that, as in *Pseudocercospora*, synnematous conidiophores is a feature that is unreliable at generic level. Therefore, the genus *Phacellium* is tentatively synonymised with *Ramularia* until the exact phylogenetic position of its type species becomes known.

Clade XV: Xenoramularia Videira, H.D. Shin & Crous, gen. nov. MycoBank MB816822.

Etymology: Named after its morphological similarity to the genus *Ramularia*, composed of xeno- (xenos, Greek for strange) and the latter genus name.

Phytopathogenic, causing leaf spots. *Mycelium* composed of hyaline, septate, branched hyphae. *Conidiophores* hyaline to pigmented, solitary, simple, straight or slightly curved, often reduced to conidiogenous cells, thin-walled, smooth. *Conidiogenous cells* hyaline, integrated in the mycelium or terminal in the conidiophores, subcylindrical to geniculate-sinuous, with one or multiple thickened but not darkened conidiogenous loci. *Conidia* hyaline, thin-walled, smooth, formed singly or catenate, aseptate or 1-septate, subcylindrical, apex obtuse to subacute, base truncate; hila thickened but not darkened.

Type species: Xenoramularia polygonicola Videira, H.D. Shin & Crous.

Notes: The genus Xenoramularia (Fig. 1, clade XV, 0.59/-/-) is very close to Zymoseptoria (Fig. 1, clade XVI, 0.92/-/-) and

their individual support by the phylogeny is low but they are maintained apart due to morphological differences. Morphologically *Xenoramularia* is similar to *Ramularia* but can be distinguished by the following set of characters: it tends to have reduced conidiophores that are mostly solitary (always solitary in culture, rarely with weakly developed fascicles on host tissue), hyaline, but at times somewhat pigmented, and conidial hila and conidiogenous loci that are thickened, but not darkened and refractive as in *Ramularia*.

Xenoramularia arxii Videira & Crous, **sp. nov.** MycoBank MB816927. Fig. 13.

Etymology: Named after Josef Adolf von Arx, who collected this species.

Mycelium consisting of hyaline, septate, branched hyphae, 1–3 µm diam. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* integrated in the mycelium, hyaline, thinwalled, smooth, subcylindrical, $(4-)8-10(-14) \times 1.5-2$ µm, with single or multiple conidiogenous loci that are thickened but not darkened. *Conidia* formed singly, aseptate or 1-septate, hyaline, thin-walled, smooth, subcylindrical, with a rounded apex and an acute base, $(5-)9-12(-21) \times (1.5-)2(-3)$ µm; hila thickened but not darkened.

Culture characteristics: On MEA, 47 mm diam, surface raised, smooth mycelium, white with buff tinge with margins entire and feathery, colony reverse iron grey in the centre and ochreous towards the margin; on OA, 45 mm diam, surface flat, feathery white mycelium in the centre becoming sparse and hazel towards the margin, margin undulate, almost naked, colony reverse hazel; on PDA, 50 mm diam, surface low convex, centre



Fig. 13. Xenoramularia arxii (CBS 342.49). A-E. Conidiogenous cells and conidia formed in culture. Scale bars = 10 µm.

white turning pale olivaceous grey and erumpent towards the margin, with margin olivaceous grey and sparse mycelium, colony reverse olivaceous black in the centre and olivaceous towards the buff margin.

Specimen examined: Netherlands, Utrecht Prov., Baarn, Eemufer, on leaf spot of *Acorus calamus*, 5 Sep. 1949, J.A. von Arx (holotype CBS H-4925, culture ex-type CBS 342.49).

Notes: Xenoramularia arxii (Fig. 13) forms a basal single lineage to other taxa in the genus (Fig. 1, clade XV), but is retained in *Xenoramularia* as it is morphologically similar. For a morphological comparison see notes under *X. polygonicola*.

Xenoramularia neerlandica Videira & Crous, **sp. nov.** Myco-Bank MB816928. Fig. 14.

Etymology: Named after the country from where it was collected, the Netherlands.

Mycelium consisting of hyaline, septate, branched, hyphae, 0.5–1 µm diam. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* integrated in the mycelium, hyaline, thinwalled, smooth, subcylindrical, (8–)11–13.5(–16) × (1–) 1.5(–2) µm, with single or multiple conidiogenous loci that are thickened but not darkened. *Conidia* formed singly or catenate and ramoconidia scarce. *Ramoconidia* hyaline, thin-walled, smooth, aseptate or 1-septate, subcylindrical to fusiform, (9–) 13.5–18(–23) × (0.5–)1(–1.5) µm. *Intercalary conidia* hyaline, smooth, aseptate or 1-septate, subcylindrical to fusiform, (7–) 10–12(–19) × (0.5–)1 µm. *Terminal conidia* hyaline, smooth, aseptate or 1-septate, subcylindrical to fusiform, (3–) 11–17(–32) × (0.5–)1(–2) µm; hila thickened but not darkened.

Culture characteristics: On MEA, 20 mm diam, surface raised, smooth, white with pale grey and olivaceous grey tinge, margins

undulate, colony reverse olivaceous grey; on OA, 22 mm diam, surface with fluffy mycelium pale grey and olivaceous grey, margins undulate and with sparse aerial mycelium, reverse irongrey; on PDA, 18 mm diam, surface flat, smooth aerial mycelium, centre white turning pale olivaceous grey towards the margin, margin undulate with sparse mycelium, reverse olivaceous grey.

Specimens examined: Netherlands, Utrecht Prov., Breukelen, on Sparganium ramosum, Sep. 2003, W. Gams, culture CBS 113615; Utrecht, De Uithof, on Iris pseudacorus, 26 Jun. 2006, P.W. Crous (holotype CBS H-22540, culture ex-type CBS 141101 = CPC 18377); idem. CPC 18378.

Notes: Xenoramularia neerlandica (Fig. 14) is highly supported in the phylogenetic analysis (Fig. 1, clade XV, 1/100/100). For morphological comparison with the other species in this genus see notes under *X. polygonicola*.

Xenoramularia polygonicola Videira, H.D. Shin & Crous, **sp. nov.** MycoBank MB 816929. Fig. 15.

Etymology: Named after the host genus from which it was described, *Polygonum*.

Mycelium consisting of hyaline, septate, branched, hyphae, 0.5–1 µm diam. *Conidiophores* hyaline, thin-walled, smooth, solitary, simple, sometimes branched, straight to slightly curved, sometimes reduced to conidiogenous cells, (13.5–) 23–29(–42) × (0.5–)1 µm. *Conidiogenous cells* integrated in the mycelium, lateral or terminal in the conidiophores, subcylindrical to geniculate-sinuous, (6.5–)9–11(–17) × (0.5–)1 µm, with conidiogenous loci thickened but not darkened. *Conidia* formed singly or catenate, but no ramoconidia were observed. *Intercalary conidia* hyaline, smooth, subcylindrical, aseptate or 1-septate, (6–)8.5–11(–16) × (0.5–)1 µm. *Terminal conidia* hyaline, smooth, formed singly or catenate, aseptate or 1-septate,



Fig. 14. Xenoramularia neerlandica (CBS 113615). A-G. Structures formed in culture. A, C-G. Conidiogenous cells and conidia. B. Conidia. Scale bars = 10 µm.



Fig. 15. Xenoramularia polygonicola (CBS 141102). A–C. Observations from herbarium material. D–G. Structures formed in culture. A. Leaf spot symptoms on host. B–F. Conidiophores, conidiogenous cells and conidia. G. Conidiophore. Scale bars = 10 µm.

subcylindrical, apex obtuse to subacute, base truncate, (4-) 6.5-8(-11) × (0.5-)1 µm; hila thickened but not darkened.

Culture characteristics: On MEA, 8 mm diam, surface raised, lumpy, smooth mycelium, pale olivaceous grey, with margins undulate, buff, convex, colony reverse iron grey; on OA, 8 mm diam, surface flat, smooth mycelium, pale olivaceous grey, with margins entire, with sparse aerial mycelium, colony reverse olivaceous grey; on PDA, 10 mm diam, surface low convex,

smooth, grey olivaceous, radially striated and cutting into the agar, with margins undulate, convex and buff, colony reverse olivaceous grey.

Specimens examined: South Korea, Pyeongchang, on *Polygonum* sp., 20 Sep. 2003, H.D. Shin (holotype KUS-F19688, isotype CBS H-22541, culture ex-type CBS 141102 = CPC 10852); *idem.* CPC 10853, CPC 10854.

Notes: The species *X. polygonicola* is highly supported in the phylogenetic analysis (Fig. 1, clade XV, 1/100/100).

Xenoramularia polygonicola (Fig. 15) forms conidiophores while X. arxii (Fig. 13) and X. neerlandica (Fig. 14) have conidiophores reduced to conidiogenous cells. Xenoramularia polygonicola and X. arxii do not produce ramoconidia and in X. neerlandica they were rarely observed. Xenoramularia polygonicola and X. neerlandica produce both single and catenate conidia while X. arxii produces only single, wider conidia.

Clade XVI: *Zymoseptoria* Quaedvl. & Crous, Persoonia 26: 64. 2011.

Note: See Quaedvlieg *et al.* (2011) and Stukenbrock *et al.* (2012).

Clade XVII: Dothistroma Hulbary, Bull. Illinois Nat. Hist. Surv. 21: 235. 1941.

Note: See Barnes et al. (2004).

Clade XVIII: Stromatoseptoria Quaedvl., Verkley & Crous, Stud. Mycol. 75: 353. 2013.

Note: See Quaedvlieg et al. (2013).

Clade XIX: *Pseudocercosporella* Deighton, Mycol. Pap. 133: 38. 1973.

Colonies in vivo. Mycelium consisting of hyaline to pale brown, septate and smooth hyphae. *Conidiophores* solitary to fasciculate, emerging through stomata or through the cuticle, arising from inner hyphae or from stromata, sometimes arising from superficial hyphae or forming subglobose sporodochia, aseptate or septate, straight and subcylindrical to geniculate-sinuous, rarely branched, mostly hyaline but occasionally faintly pigmented, thin-walled, mostly more or less smooth. *Conidiogenous cells* integrated, terminal or conidiophores reduced to conidiogenous cells, mono- to polyblastic, sympodial; conidiogenous loci inconspicuous, unthickened and hyaline. *Conidia* formed singly, subcylindrical, filiform to obclavate, 1- multi-euseptate, hyaline, thin-walled, mostly smooth, apex obtuse to subacute, base subtruncate, hilum unthickened, not darkened nor refractive. Adapted from Frank *et al.* (2010).

Type species: Pseudocercosporella bakeri (Syd. & P. Syd.) Deighton (= *Pseudocercosporella ipomoeae* Deighton).

Notes: Pseudocercosporella was described by Deighton (1973), and is characterised by solitary conidia, rarely in chains, with unthickened, inconspicuous conidial loci (Braun 1995). Braun (1990) confined Pseudocercosporella to species with solitary conidia and the species with catenate conidia were transferred to Thedgonia. However, the conidial ontogeny in Thedgonia is thallic (i.e. conidia form in disarticulating chains) while the species in question had polyblastic conidiogenesis and conidia in acropetal chains (Crous et al. 2009a). Braun (1995) placed these species back in Pseudocercosporella under a different subgenus: Pseudocercosporella subgen. Pseudocercocatenella (type: Pseudocercosporella dioscoriae). Braun (1995) also established another subgenus based on morphology to include species with superficial secondary mycelium and solitary conidiophores: Pseudocercosporella subgen. Cercovellosiella (type: Pseudocercosporella crataegi). The type species Pseudocercosporella *bakeri* (= *P. ipomoea*) has recently been epitypified (on *Ipomoeae* sp., Philippines, ex-epitype culture CBS 125685; Frank *et al.* 2010) and forms a single species clade (Fig. 1, clade XIX) that clusters close to *Dothistroma* (Fig. 1, clade XVII) and *Stromatoseptoria* (Fig. 1, clade XVIII). The pseudocercosporella-like morphology is polyphyletic (see Frank *et al.* 2010, Crous *et al.* 2011, 2012), and new taxonomically useful morphological features will need to be found to delineate all the genera presently accommodated in other clades.

Clade XX: *Microcyclosporella* J. Frank *et al.*, Persoonia 24: 101. 2010.

Mycelium consisting of pale brown, smooth to finely verruculose, branched, septate hyphae, sometimes covered in a mucoid layer. *Conidiophores* mostly reduced to conidiogenous cells. *Conidiogenous cells* integrated in hyphae, cylindrical to doliiform, pale brown to hyaline if occurring in yeast-like sectors of colonies, thin-walled, smooth, mono- or polyblastic, proliferating sympodially; conidiogenous loci lateral, inconspicuous, truncate, unthickened, not darkened. *Conidia* hyaline, thin-walled, smooth, subcylindrical to narrowly obclavate or narrowly fusoid with acutely rounded apex and obconically truncate base, guttulate, 0–6 transversely septate; microcyclic conidiation common. Adapted from Frank *et al.* (2010).

Type species: Microcyclosporella mali J. Frank, Schroers & Crous.

Specimens examined: Slovenia, Senozeti, Dolsko, on fruit surface Malus domestica, 7 Aug. 2007, J. Frank (holotype CBS H-20413, culture ex-type 300-07 = CBS 126136 = CPC 16184). USA, Georgia, Ellijay, on Malus sp., 29 Aug. 2005, M. Wheeler, culture CBS 125654; Illinois, Chester, on unknown host, Sep. 2000, J. Batzer, culture CBS 119461; Illinois Rockford, Illinois, on unknown host, Sep. 2000, J. Batzer, culture CBS 118960; Michigan, Fennville, on Malus sp., 1 Sep. 2005, G. Sundin, culture CBS 125653; Missouri, New Franklin, on unknown host, Sep. 2000, J. Batzer, culture CBS 118969; Ohio, Wooster on Malus sp., 5 Sep. 2005, M. Ellis, culture CBS 125651.

Notes: Microcyclosporella was described by Frank *et al.* (2010) to accommodate species with hyaline conidiophores and long scolecosporous conidia with inconspicuous conidiogenous loci and unthickened, non-pigmented hila, resembling *Pseudo-cercosporella*, but also displaying microcyclic conidiation. More work needs to be done in this genus since the variation observed in the phylogeny (Fig. 1, clade XX) indicates that more than one species may be present.

Clade XXI: Mycosphaerelloides Videira & Crous, gen. nov. MycoBank MB816819.

Etymology: Named after the morphological similarity to the genus *Mycosphaerella*.

Ascomata pseudothecial, single, black, immersed, becoming erumpent, globose, apical ostiole, wall with medium brown *textura angularis. Asci* aparaphysate, fasciculate, bitunicate, subsessile, obovoid to narrowly ellipsoid. Ascospores, straight to fusoid-ellipsoid, hyaline, guttulate, thin-walled, with subobtuse ends, medianly 1-septate, widest in the middle of the apical cell. Ascospore germination from both ends, with germ tubes parallel to the long axis of the spore. Mycelium consisting of smooth, branched, septate, pale to medium brown hyphae. *Conidiomata* fasciculate, medium brown. *Conidiophores* arising from mycelium or from the upper cells of a brown stroma, pale to medium brown, smooth, unbranched or branched, subcylindrical, straight to variously curved. *Conidiogenous cells* terminal or lateral, solitary, pale brown, smooth, proliferating sympodially or percurrently; conidiogenous loci inconspicuous. *Conidia* smooth, subcylindrical, multiseptate; hila neither thickened nor darkened-refractive. Adapted from Crous *et al.* (2004b).

Type species: Mycosphaerelloides madeirae (Crous & Denman) Videira & Crous.

Notes: The strains in this genus represent a mycosphaerella-like species lacking a ramularia-like asexual morph, and also not being congeneric with *Ramularia* based on *R. pusilla* (Fig. 1, clade XIV). This monotypic genus is highly supported by the phylogenetic analysis (Fig. 1, clade XXI, 1/100/100).

Mycosphaerelloides madeirae (Crous & Denman) Videira & Crous, **comb. nov.** MycoBank MB817150.

Basionym: Mycosphaerella madeirae Crous & Denman, Stud. Mycol. 50: 204. 2004.

Specimens examined: **Portugal**, Madeira, Party Farm, on leaves of *Eucalyptus globulus*, Apr. 2000, S. Denman (**holotype** CBS H-9898, culture ex-type CBS 112895 = CPC 3745); *idem*. CBS 112301 = CPC 3747. **Netherlands**, Utrecht, Soest, endophytic on green leaves of *Quercus robur*, 2002, G. Verkley, cultures CBS 115936, CBS 116068, CBS 116066.

Notes: Mycosphaerelloides madeirae was isolated from *Eucalyptus globulus* collected in Madeira (Portugal), and is very similar to *M. heimioides* (Crous 1998), but can be distinguished by its ascospore germination pattern as well as its cultural characteristics.

Clade XXII: *Epicoleosporium* Videira & Crous, gen. nov. MycoBank MB816817.

Etymology: Named after the host its type species was isolated from, *Coleosporium*.

Colonies growing on uredinia of *Coleosporium*, mycophylic. *Mycelium* superficial, consisting of hyaline, septate, thin-walled, smooth hyphae. *Conidiophores* hyaline, loose, straight, sub-cylindrical, unbranched, septate, thin-walled, smooth. *Conidiogenous cells* hyaline, terminal in the conidiophore, cylindrical-oblong, proliferation sympodial, with conspicuous conidiogenous loci, thickened, darkened and refractive. *Conidia* hyaline, smooth, solitary or in short chains, cylindrical-oblong, clavate, obovate, aseptate, thin-walled, smooth, with hila thickened, darkened and refractive.

Type species: Epicoleosporium ramularioides Videira, H.D. Shin & Crous.

Notes: This monotypic genus is highly supported by the phylogenetic analysis (Fig. 1, clade XXII, 1/100/100) and represents a mycophylic species that is ramularia-like in its morphology but is not congeneric with *Ramularia* based on *R. pusilla* (Fig. 1, clade XIV). *Epicoleosporium ramularioides* Videira, H.D. Shin & Crous, **sp. nov.** MycoBank MB816847. Fig. 16.

Etymology: Named after its morphological similarity with the genus *Ramularia*.

Colonies on uredinia of Coleosporium, mycophylic, whitish. Mycelium superficial, consisting of hyaline, septate, thin-walled, smooth hyphae, 1.5-2 µm diam. Conidiophores hyaline, loose, straight. subcvlindrical. unbranched. erect. (37 -)65-83(-129) × 2-3 µm, septate, thin-walled, smooth. Conidiogenous cells hyaline, integrated, terminal on the conidiophore, cylindrical-oblong, $(9-)11-13(-15) \times 1.5-2(-2.5) \mu m$, conidiogenous loci thickened, darkened and refractive, 1 µm diam. Conidia hyaline, thin-walled, smooth, solitary or in short chains, cylindrical-oblong, clavate, obovate, aseptate, (6-) $10-13(-21) \times (2.5-)3-4(-5) \mu m$, apex obtuse, base obtuse to slightly elongated, with hila thickened, darkened and refractive. 1 um diam.

Specimens examined: **South Korea**, Pyeongchang, on *Coleosporium phellodendri* on leaves of *Phellodendron amurense*, 4 Sep. 2003, H.D. Shin (**holotype** KUS-F19603, isotype CBS H-22542, culture ex-type CBS 141103 = CPC 10672); *idem*. CPC 10673.

Notes: *Epicoleosporium ramularioides* is morphologically ramularia-like (Fig. 16) and represents another addition to the list of known mycophylic cercosporoid species. It differs from *R. coleosporii* that produces conidiophores occasionally branched, longer and wider $[(20-)30-200(-270) \times 3-6 \mu m]$. In addition, the conidia of *R. coleospori* are catenate, ellipsoid-ovoid, smooth to rough, longer and wider $[8-35(-45) \times 3-8 \mu m]$ and 0-1(-3)-septate (Braun 1998). The development of the conidial structures of *E. ramularioides* in culture is unusual (Fig. 16).

Clade XXIII: Uwebraunia Crous & M.J. Wingf., Mycologia 88: 446. 1996.

Note: See Crous and Wingfield (1996) and Li et al. (2012).

Clade XXIV: Dissoconium de Hoog et al., Proc. Kon. Ned. Akad. Wetensch. C 86(2): 198. 1983.

Note: See Crous *et al.* (1999), Jakson *et al.* (2004) and Li *et al.* (2012).

Clade XXV: *Ramichloridium* Stahel ex de Hoog, Stud. Mycol. 15: 59. 1977.

Note: See Arzanlou et al. (2007).

Clade XXVI: Acrodontium de Hoog, Stud. Mycol. 1: 23. 1972.

Saprobic or mycophylic. *Mycelium* consisting of subhyaline, brownish or olivaceous, smooth, thin-walled, septate hyphae. *Conidiophores* when present arising from hyphae, erect or procumbent, sometimes thick-walled and dark brown at the base, paler brown towards the apex, branched verticillately or dichotomously. *Conidiogenous cells* integrated, terminal in conidiophores and often forming whorls or conidiophores reduced to conidiogenous cells, arising from hyphae, basal part flask-



Fig. 16. Epicoleosporium ramularioides (CBS 141103). A–F. Observations from herbarium material. G, H. Structures formed in culture. A. Leaf spot symptoms on host. B. Conidiophores. C, D, F–H. Conidiophore and conidia. E. Conidia. Scale bars = 10 µm.

shaped or elongate, tapering towards the tip forming a sympodial denticulate rachis, straight to flexuous. *Conidia* formed singly, hyaline or pigmented, smooth, subglobose to fusiform, with an apiculate base. Adapted from De Hoog (1972).

Type species: Acrodontium crateriforme (J.F.H. Beyma) de Hoog.

Notes: The genus *Acrodontium* was introduced by De Hoog (1972), and currently accommodates 10 species varying in lifestyle from saprobic to mycophylic (Seifert *et al.* 2011). *Acrodontium* species have conidiogenous cells that bear conidia on a sympodially proliferating rachis, straight or slightly flexuous, bearing alternating denticles at regular intervals (De Hoog 1972). According to the present study, the type species of the genus, *A. crateriforme* (CBS 144.33), belongs to the *Teratosphaeriaceae* (Fig. 1, clade XXVI, 1/100/100). The LSU sequences of isolates belonging to *A. antarcticum*, *A. abietis*, *A. griseum*, *A. hydnicola*, *A. salmoneum*, *A. simplex* and *A. virelum* currently housed in the CBS collection (data not shown) place them in different orders (e.g. *Sordariomycetes* and *Leotiomycetes*) and will not be treated here.

Acrodontium crateriforme (J.F.H. Beyma) de Hoog, Stud. Mycol. 1: 26. 1972. Fig. 17.

Basionym: Chloridium crateriforme J.F.H. Beyma, Zentralbl. Bakteriol., 2 Abt., 89: 241. 1933.

- ≡ *Tritirachium crateriforme* (J.F.H. Beyma) Matsush., Icon. microfung. Matsush. lect.: 160. 1975.
- = Acrodontium neolitseae Crous & Summerell, Persoonia 32: 209. 2014.

Description in vitro: See De Hoog (1972: 26)

Specimens examined: Australia, Nightcap National Park, on *Neolitsea australiensis*, 9 Mar. 2013, B. Summerell, culture CBS 137975 = CPC 22172. Germany, Hesse, Schlangenbad, on leaves of *Betula* sp., 2012, W. Quaedvlieg, culture CPC 25895; on leaves of *Ranunculus* sp., 2012, W. Quaedvlieg, culture CPC 25894. **Java**, Tjibodas Hortus Botanicus, on leaf of *Citrus* sp., 1969, J.H. van Emden, culture CBS 842.71. **South Korea**, Hoengseong, on *Agrimonia pilosa*, 21 Ago. 2004, H.D. Shin, culture CPC 11519; Hongcheon, on *Fraxinus chinensis* subsp. *rhynchophylla* (\equiv *F. rhynchophylla*), 11 Aug. 2004, H.D. Shin, culture CPC 11509. **Netherlands**, on foodstuff, unknown collector and date, isol. M. van Schothorst, dep. RIV, Bilthoven, Oct. 1971, culture CBS 840.71; Baarn, isolated from sputum, unknown collector and date, isol. G.A. de Vries, dep. Jul. 1958, culture CBS 151.58; Baarn, associated with *Tuberculina maxima*, unknown collector and date, isol. 15748 = MUCL 8978). **UK**, Westmorland, Meathop Wood, on living leaflet of *Fraxinus excelsior*, unknown date, J.C. Frankland, culture CBS 985.70.

Notes: The recently described species A. neolitseae (CPC 22172) is 100 % identical to A. crateriforme on LSU but differs on 3 nucleotides on ITS and 7 nucleotides on rpb2. The morphological description of A. neolitseae also fits with A. crateriforme (Fig. 17) since this taxon can sometimes have slightly pigmented conidiophores and conidia. At the time A. neolitsiae was described, the ITS BLAST resulted in a 99 % similarity to a strain identified as Pseudocercosporella fraxini (GenBank GU214682; CPC 11509) and Acrodontium crateriforme (GenBank FN666566), which we show here to represent the same species (Fig. 1, clade XXVI). Since the strain CPC 11509 was not used in a morphological study before two scenarios are possible, namely that the fungus isolated from the specimen was the wrong one or that the culture was contaminated previous to storage and is no longer P. fraxini but A. crateriforme. The phylogenetic analysis strongly supports this species clade (Fig. 1, clade XXVI, 1/100/ 100).

Acrodontium fagicola Videira & Crous, sp. nov. MycoBank MB817151. Fig. 18.

Etymology: Named after the host genus *Fagus*, from which it was collected.



Fig. 17. Acrodontium crateriforme (CBS 144.33). A-E. Structures formed in culture. A-D. Conidiophores, conidiogenous cells and conidia. E. Conidia. Scale bars = 10 µm.

Mycelium hyaline, consisting of septate, branched, smooth, 1–1.5 µm diam hyphae. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* hyaline, thin-walled, smooth, subulate to slightly ampulliform, sometimes with a transverse septum, straight to flexuous, proliferating sympodially and forming a rachis in the upper part, (16.5–) $31-38(-61) \times (1-)1.5-2$ µm, with multiple conidiogenous loci slightly thickened but not darkened. *Conidia* hyaline, thinwalled, smooth, solitary, ellipsoid with obtuse apex, (2–) $2.5-3 \times 1.5-2$ µm; hilum slightly thickened but not darkened.

Culture characteristics: On MEA, 10 mm diam, surface raised, smooth, with erumpent aerial mycelium, olivaceous, margins undulate, reverse sepia; on OA, 11 mm diam, surface raised, smooth, with erumpent aerial mycelium, olivaceous and sepia, margins undulate, reverse umber; on PDA, 10 mm diam, surface flat, smooth, with erumpent aerial mycelium, olivaceous and sepia, margins entire, reverse sepia.

Specimen examined: Germany, on Fagus sylvatica, isol. G. Arnold, Oct. 1978, dep. G. Arnold, Dec. 1979 (holotype CBS H-8534, culture ex-type CBS 714.79).

Note: This species is represented by a single lineage in the phylogenetic analysis (Fig. 1, clade XXVI) and differs from *A. crateriforme* by having longer conidiogenous cells and smaller conidia (Fig. 18).

Acrodontium luzulae Videira & Crous, sp. nov. MycoBank MB816844. Fig. 19.

Etymology: Named after the host genus *Luzula*, from which the ex-type strain was collected.

Mycelium consisting of hyaline, septate, branched, smooth, $1-2 \mu m$ diam hyphae. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* hyaline, thin-walled, smooth, elongate ampulliform, straight to flexuous, proliferating sympodially and forming a rachis in the upper part, $(23-)44-56(-98) \times (1.5-)$ $2(-3) \mu m$, with multiple conidiogenous loci slightly thickened but not darkened. *Conidia* hyaline, thin-walled, smooth, solitary,

ellipsoid with obtuse apex, $(2.5-)3-4(-5) \times (1-)2(-2.5) \mu m$, hilum slightly thickened but not darkened.

Culture characteristics: On MEA, 10 mm diam, surface flat, smooth, with sparse erumpent aerial mycelium, buff, margins entire, reverse umber; on OA, 10 mm diam, surface flat, smooth, greyish sepia, margins undulate, reverse fawn; on PDA, 10 mm diam, surface flat, smooth, with sparse erumpent aerial mycelium, buff, margins entire, reverse sepia.

Specimens examined: England, Devon, East Lyn River, on dead leaf of *Luzula* sylvatica, unknown collector and date, isol. W. Gams, Sep. 1971, dep. Nov. 1971, (holotype CBS H-8529, culture ex-type CBS 839.71). Netherlands, Beerze, near Campina, on leaf of *Carex* sp., unknown collector and date, isol. W. Gams, Apr. 1968, dep. Nov. 1971, culture CBS 841.71.

Notes: Although initially identified as *A. crateriforme*, these strains are not conspecific with the type species, and the phylogenetic analysis strongly supports this clade (Fig. 1, clade XXVI, 1/97/100). Morphologically it differs from *A. pigmentosum* by having longer conidiogenous cells and conidia (Fig. 19).

Acrodontium pigmentosum Videira & Crous, sp. nov. Myco-Bank MB817152. Fig. 20.

Etymology: Named after its pigmented mycelium.

Mycelium consisting of hyaline to slightly olivaceous, septate, branched, thin-walled, smooth hyphae, 0.8–1.5 µm diam. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* hyaline, thin-walled, smooth, subulate, sometimes with a transverse septum, arising from the mycelium or from a subtending cell in groups of two, straight to flexuous, proliferating sympodially and forming a rachis in the upper part, (9.5–) $15.5-19(-31) \times (1-)1.5-2$ µm, with multiple conidiogenous loci slightly thickened but not darkened. *Conidia* hyaline, thin-walled, smooth, solitary, subglobose to broadly ellipsoidal, $2-3 \times 1-2$ µm, hilum slightly thickened but not darkened.

Culture characteristics: On MEA, 8 mm diam, surface raised, smooth, with erumpent aerial mycelium, smoke-grey, margins



Fig. 18. Acrodontium fagicola (CBS 714.79). A-F. Conidiophores, conidiogenous cells and conidia formed in culture. Scale bars = 10 µm.



Fig. 19. Acrodontium luzulae (CBS 839.71). A–F. Structures formed in culture. A. Conidiogenous loci in the rachis. B–F. Conidiophores, conidiogenous cells and conidia. Scale bars = 10 µm.

entire, reverse iron grey; on OA, 11 mm diam, surface raised, smooth, with erumpent aerial mycelium, greyish sepia, margins undulate, reverse fuscous black; on PDA, 10 mm diam, surface flat, smooth, with erumpent aerial mycelium, olivaceous and greyish sepia, margins entire, reverse olivaceous black.

Specimen examined: Finland, from outdoor air, unknown date, S. Haatainen (holotype CBS H-22637, culture ex-type CBS 11111).

Notes: Initially identified as *A. griseum*, the micro- and macromorphology of *A. pigmentosum* differs significantly from *A. griseum* by not forming markedly differentiated conidiophores with a thick stalk, smooth and thick-walled, bearing multiple brown conidiogenous cells in side branches and also by not forming olivaceous conidia (De Hoog 1972). This species is represented by a single lineage in the phylogenetic analysis (Fig. 1, clade XXVI) and differs from the closest species, *A. fagicola* by having wider conidiogenous cells, larger



Fig. 20. Acrodontium pigmentosum (CBS 11111). A-G. Conidiophores, conidiogenous cells and conidia formed in culture. Scale bars = 10 µm.

conidiophores and pigmented mycelium (Fig. 20), as well as 47 nucleotides in *rpb2*, and 5 in LSU.

Clade XXVII: *Parapenidiella* Crous & Summerell, Persoonia 29: 185. 2012.

Note: See Crous et al. (2012).

Clade XXVIII: Teratosphaeria Syd. & P. Syd., Ann. Mycol. 10: 39. 1912.

Note: See Crous et al. (2009c) and Quaedvlieg et al. (2014).

Clade XXIX: Readeriella Syd. & P. Syd., Ann. Mycol. 6: 484. 1908.

Note: See Crous et al. (2009c).

Clade XXX: *Teratoramularia* Videira, H.D. Shin & Crous, gen. nov. MycoBank MB816821.

Etymology: composed of *Terato-* from *Teratosphaeriaceae* and *Ramularia*.

Mycelium consisting of smooth, branched, septate, hyaline hyphae, or swollen pale to brown hyphae. *Conidiophores* at times synnematal, but mostly reduced to conidiogenous cells or consisting of one supporting cell and conidiogenous cell. *Conidiogenous cells* hyaline, thin-walled, smooth, terminal or lateral, subcylindrical, straight, proliferating sympodially; conidiogenous loci conspicuous, thickened and darkened. *Conidia* are catenate, forming ramoconidia, intercalary conidia and terminal conidia. *Conidia (type I)* hyaline, thin-walled, smooth, subcylindrical, long, aseptate to 1-septate, with conspicuous hila, thickened and darkened. *Conidia (type II)*, sometimes formed, brown, multiseptate, constricted at the septa, with

thickened and darkened hila, germinating to form pigmented mycelium.

Type species: Teratoramularia persicariae Videira, H.D. Shin & Crous.

Notes: This is the first time that the ramularia-like morphology is observed outside the *Mycosphaerellaceae*. Like in *Ramularia*, species of *Teratoramularia* produce catenate, hyaline conidia with conspicuous hila, but differ by having conidiophores mostly reduced to conidiogenous cells, and by producing very long intercalary conidia and ramoconidia that usually appear immediately next to the conidiogenous cell. In addition, on OA, sometimes pigmented mycelium as well as conidia are observed, that are brown, multiseptate and constricted at their septa. The pigmented conidia were not observed in association with the hosts in the herbarium material. The phylogenetic analysis strongly supports this genus clade (Fig. 1, clade XXX, 1/100/98).

Teratoramularia infinita Videira & Crous, **sp. nov.** MycoBank MB817153. Fig. 21.

Etymology: The epithet "*infinita*" indicates its ability to infect a wide host range.

Mycelium consisting of hyaline, septate, branched, thin-walled, smooth, 1–1.5 µm diam hyphae. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* hyaline, thin-walled, smooth, integrated in hyphae, cylindrical-oblong, (6.5–) $11.5-14(-19) \times 1-1.5(-2)$ µm, with 1 thickened and darkened apical locus, 1 µm diam. *Conidia* are catenate, forming ramoconidia, intercalary conidia and terminal conidia. *Conidia (type I)* hyaline, thin-walled, smooth, aseptate, *hila* thickened and darkened, 1 µm diam; *ramoconidia* subcylindrical to fusiform, (4.5–) $8.5-11(-17) \times (1-)1.5-2$ µm, with two apical hila; *intercalary conidia*, subcylindrical to fusiform, sometimes curved, (5–)



Fig. 21. Teratoramularia infinita (CBS 120815). A-H. Conidiophores, conidiogenous cells and conidia observed in culture. Scale bars = 10 µm.

 $10-14.5(-25.5) \times (1-)1.5-2 \mu m$, in chains of up to 11 conidia; terminal conidia obovoid, $(3-)4(-6) \times (1-)1.5-2 \mu m$. Conidia (type II) not observed.

Culture characteristics: On MEA, 18 mm diam, surface raised, folded, smooth, pale grey, with margins crenate, convex, underneath olivaceous grey; on OA, 14 mm diam, surface flat, smooth, pale olivaceous grey, with margins undulate, with sparse olivaceous grey mycelium, reverse iron-grey; on PDA, 15 mm diam, surface, smooth, pale olivaceous grey, with margins crenate, reverse olivaceous grey.

Specimens examined: **Brazil**, on *Conyza canadensis*, 2000, unknown collector (**holotype** CBS H-22536, culture ex-type CBS 141104 = CPC 19488). **Taiwan**, Chiayi, Meishan, Taixingcun, on living leaves of *Thladiantha punctata*, unknown date, R. Kirschner & C.-J. Chen, culture CBS 120815.

Notes: The two strains in this clade have been isolated from two very distinct hosts, *Conyza canadensis* (*Asteraceae*) and *Thladiantha punctata* (*Cucurbitaceae*), and from two very distinct locations, Brazil and Taiwan, respectively. Nevertheless, they are identical on five genes suggesting this species has a wide host range and distribution. The phylogeny supports their separation from the closest neighbour, *T. rumicicola* (Fig. 1, clade XXX, 1/ 100/100) from which it also differs morphologically by producing longer conidiogenous cells, shorter and slightly narrower ramoconidia and terminal conidia (Fig. 21).

Teratoramularia persicariae Videira, H.D. Shin & Crous, **sp. nov.** MycoBank MB817154. Fig. 22.

Etymology: Named after the host genus *Persicaria*, from which the ex-type strain of this taxon was collected.

Mycelium consisting of hyaline, septate, branched, thin-walled, smooth, $1-2 \mu m$ diam hyphae, but on OA also brown,

pigmented hyphae are formed. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* hyaline, thin-walled, smooth, integrated in hyphae, cylindrical-oblong, (4.5–) $9-11(-15) \times (1-)1.5(-2) \mu m$, with one thickened and darkened conidiogenous locus, 1 μm diam. *Conidia* are catenate, forming ramoconidia, intercalary conidia and terminal conidia. *Conidia (type 1)* hyaline, thin-walled, smooth, aseptate, with *hila* thickened and darkened, 1 μm diam; *ramoconidia* subcylindrical to fusiform, (9.5–)17–20(–30) × (1.5–)2(–2.5) μm , with 2 apical hila; *intercalary conidia* subcylindrical to fusiform, sometimes curved, (8.5–)14–18(–30) × (1–)1.5–2(–2.5) μm , in chains of up to eight conidia; *terminal conidia* hyaline, smooth, aseptate, subcylindrical, (3–)7–8(–10) × (1.5–)2(–3) μm . *Conidia (type II)* not observed.

Culture characteristics: On MEA, 15 mm diam, surface smooth, raised, lumpy, olivaceous grey with buff and white patches, with margins crenate and convex, reverse iron-grey with ochreous patches; on OA, 10 mm diam, surface concave, smooth, pale olivaceous grey, with margins raised, undulate, with sparse aerial mycelium, reverse olivaceous grey; on PDA, 13 mm diam, surface smooth, lumpy, irregular, iron-grey with pale vinaceous patches, margins undulate, reverse rosy buff and olivaceous grey.

Specimens examined: South Korea, Hongcheon, on *Persicaria nepalensis*, 29 Jul. 2004, H.D. Shin (holotype KUS-F20536, isotype CBS H-22537, culture extype CBS 141105 = CPC 11410); *idem*. CPC 11408, CPC 11409. **Unknown country**, on leaf spot of *Fagopyrum esculentum*, isol. and dep. M.W. Gardner, Jul. 1927, culture CBS 195.27.

Notes: The host species, *Persicaria nepalensis*, is distributed worldwide but a broader sampling is required to show whether the fungal species follows this distribution. The phylogenetic analysis supports the separation of *Teratoramularia persicariae* from *T. rumicicola* (Fig. 1, clade XXX, 0.99/95) and,



Fig. 22. Teratoramularia persicariae (CBS 141105). A–D. Observations from herbarium material. E–J. Structures formed in culture. A. Leaf spot symptoms on the host. B, C. Conidiophores and conidiogenous cells. D–H. Conidiophores, conidiogenous cells and conidia. H, J. Pigmented conidiogenous structures developed on OA culture medium. Scale bars = 10 µm.

morphologically, *T. persicariae* (Fig. 22) produces longer conidia than *T. rumicicola*.

Teratoramularia rumicicola Videira, H.D. Shin & Crous, **sp. nov.** MycoBank MB817155. Fig. 23.

Etymology: Named after the host genus *Rumex*, from which it was collected.

Mycelium consisting of hyaline, septate, branched, thin-walled, smooth, 1-2 µm diam hyphae. Conidiophores reduced to conidiogenous cells. Conidiogenous cells hyaline, thin-walled, smooth, integrated in hyphae, cylindrical-oblong, (5-) $10-12.5(-16.5) \times (1-)1.5(-2) \mu m$, with 1 thickened and darkened apical locus, 1 µm diam. Conidia are catenate, forming ramoconidia, intercalary conidia and terminal conidia. Conidia (type I) hyaline, thin-walled, smooth, catenate, aseptate or occasionally 1-septate, with hila conspicuous, thickened and darkened, 1 µm diam; ramoconidia subcylindrical to fusiform, (8.5-) $12-15(-23) \times (1.5-)2(-2.5) \mu m$, with 2 apical hila; intercalary conidia subcylindrical, sometimes slightly curved, (6.5-) $10-13(-20) \times (1.5-)2(-2.5) \mu m$, in chains of up to five conidia; terminal conidia subcylindrical obovoid. to (3-) $5.5-6(-8) \times (1.5-)2(-3) \mu m$. Conidia (type II) brown, smooth, catenate, 1-4-septate, constricted at the septa, (5-)11.5-14.5(-18.5) × (2-)2.5-3 µm, with hila thickened and darkened.

Culture characteristics: On MEA, 20 mm diam, surface raised, strongly folded, smooth, white with greyish tinge in the centre, with margins crenate, convex, olivaceous grey, reverse iron-grey; on OA, 15 mm diam, surface flat, smooth, pale olivaceous grey, with margins undulate, with sparse olivaceous grey mycelium, reverse iron-grey; on PDA, 16 mm diam, surface with smooth

and folded portions, pale olivaceous grey, with margins crenate and smoke grey, reverse olivaceous grey.

Specimens examined: South Korea, Jecheon, on Rumex crispus, 19 Oct. 2007, H.D. Shin (holotype KUS-F23080, isotype CBS H-22538, culture ex-type CBS 141106 = CPC 14653); *idem.* CPC 14652, CPC 14654.

Notes: A total of seven Ramularia species have been described from Rumex worldwide (Braun 1998) and two of these species form filiform, long conidia, i.e. R. pseudodecipiens and R. pratensis. Ramularia pseudodecipiens is only known from the type collection in the USA (Wyoming), has larger conidia $[(10-)25-45(-55) \times 2-5 \mu m]$ that are consistently septate and, although sometimes constricted at the septa, they are always hyaline. Ramularia pratensis has a worldwide distribution and produces conidia of approximately the same size, $(6-)8-25(-35) \times (1.5-)$ 2-4(-5) µm, but they are never constricted at the septa or pigmented. In addition, the conidiophores in T. rumicicola (Fig. 23) were consistently reduced to conidiogenous cells while both R. pseudodecipiens and R. pratensis produce long conidiophores. The phylogenetic analysis supports this species clade (Fig. 1, clade XXX, 1/100/100).

Teratoramularia kirschneriana Videira & Crous, **sp. nov.** MycoBank MB817156. Fig. 24.

Etymology: Named after the mycologist Roland Kirschner, who has contributed greatly to our knowledge of cercosporoid fungi.

Mycelium consisting of hyaline, septate, branched, thin-walled, smooth, 0.5–1.5 µm diam hyphae. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* hyaline, smooth, integrated in hyphae, cylindrical-oblong, (13.5–) $14-15(-16) \times 1(-1.5)$ µm, with 1 thickened and darkened



Fig. 23. Teratoramularia rumicicola (CBS 141106). A–B. Observations from herbarium material. C–I. Structures formed in culture. B. Conidia. C–G. Conidiophores, conidiogenous cells and conidia. H, I. Pigmented conidiogenous structures and conidia formed on OA culture medium. Scale bars = 10 µm.



Fig. 24. Teratoramularia kirschneriana (CBS 113093). A-G. Structures formed in culture. A, C-G. Conidiogenous cells and conidia. B. Conidia. Scale bars = 10 µm.

apical locus, 1 µm diam. *Conidia* are catenate, forming ramoconidia, intercalary conidia and terminal conidia. *Conidia* (*type I*) hyaline, thin-walled, smooth, aseptate, *hila* thickened and darkened, 1 µm diam.; *ramoconidia* subcylindrical to fusiform, $(7-)8.5-10(-15) \times (1-)1.5-2$ µm, with two apical hila; *intercalary conidia*, fusiform, $(6-)8-10(-17) \times (1-)$ 1.5-2 µm, in chains of up to five conidia; *terminal conidia*, fusiform to obovoid, $(3.5-)5-6(-7) \times (1-)1.5-2$ µm. *Conidia* (*type II*) not observed.

Culture characteristics: On MEA, 16 mm diam, surface folded, smooth, pale grey, with margins crenate, convex, colony reverse iron-grey; on OA, 15 mm diam, surface flat, smooth, pale grey, with margins undulate, colony reverse iron-grey; on PDA, 13 mm diam, surface smooth, pale grey, with margins crenate, colony reverse iron-grey.

Specimen examined: Taiwan, Tahsuehshan, on leaves of Setaria palmifolia, 13 Apr. 2002, R. Kirschner & C.-J. Chen (holotype TNM No. F0016568, isotype CBS H-22539, culture ex-type CBS 113093).

Notes: The strain representing this species was originally identified as *Phacellium paspali*. The characteristic *Phacellium* synnemata are sometimes also formed in culture. This species is represented by a single basal lineage in the *Teratoramularia* clade in the phylogenetic analysis (Fig. 1, clade XXX). Morphologically (Fig. 24), it is nearly impossible to distinguish it from the closest sister species *T. infinita*.

Genera allied to Ramularia lacking cultures

Hawksworthiana U. Braun, Int. J. Mycol. Lichenol. 3: 276. 1988. Fig. 25.

Lichenicolous, forming gall-like deformations. *Mycelium* consisting of hyaline, septate, sparsely branched, thin-walled hyphae. *Conidiophores* reduced to the conidiogenous cells, erumpent, usually ampulliform but sometimes subcylindrical, aseptate, hyaline, thin-walled, mono- or polyblastic, sympodial, conidiogenous loci conspicuous, thickened and darkened. *Conidia* formed singly, acrogenous, oblong-clavate to subcylindrical, hyaline, thin-walled, smooth, aseptate or 1-septate, hilum conspicuous, thickened and darkened.

Type species: Hawksworthiana peltigericola (D. Hawksw.) U. Braun.

Specimens examined: Luxembourg, on lichen Peltigera rufescens, 7 May 2008, P. Diederich. Scotland, Isle of Mull, Killiemore, on *Peltigera polydactyla*, 16 Jun. 1979, Clark (holotype K(M) IMI 239715a).

Notes: Hawksworthiana is monotypic and was described based on *H. peltigericola* on a specimen of *Peltigera polydactyla* from the Isle of Mull in Scotland. It forms gall-like deformations on lichens of the genus *Peltigera*, and has been reported from Europe and North America. *Hawksworthiana* differs from *Ramularia* by its lichenicolous habit and morphological characters such as the wide ampulliform conidiogenous cells, the conidiogenous loci and hila are not refractive, the absence of stroma-like structures and the symptoms caused on the host (Fig. 25). All attempts to culture this fungus from fresh collections have thus far proven unsuccessful.

Monodidymaria U. Braun, Nova Hedwigia 58: 195. 1994. Fig. 26.

Phytopathogenic, causing leaf spots. *Mycelium* consisting of hyaline, septate, branched, thin-walled hyphae; stromata absent or small. *Conidiophores* macronematous, solitary or in fascicles, arising from internal hyphae or hyphal aggregations, emerging through stomata or erumpent through the cuticle, filiform and straight or flexuous to sinuous, but not geniculate, usually aseptate, thin-walled, hyaline and smooth, sometimes reduced to conidiogenous cells. *Conidiogenous cells* integrated, terminal, monophialidic. *Conidia* formed singly, ellipsoid-ovoid, obovoid, subcylindrical, fusoid or subclavate, aseptate or 1(-3)-septate, hyaline, thin-walled, smooth to rough, base rounded to truncate.

Type species: Monodidymaria canadensis (Ellis & Everh.) U. Braun.

Specimens examined: Canada, Ontario, London, on Carex conoidea, Aug. 1890, Dearness (lectotype NY 01293230, syntypes NY 01293231, 01293232 and 01293233).

Notes: While *Ramularia* has polyblastic, sympodial and cicatrised conidiogenous cells, *Monodidymaria* has monophialidic conidiogenous cells (Fig. 26). This character excludes *Monodidymaria* from the *Cercosporella/Ramularia* complex, but due to their common taxonomical history, they are still studied together. *Monodidymaria* is in fact morphologically more similar to *Cephalosporiopsis*, but the latter genus comprises saprophytic soil hyphomycetes and its taxonomic status is not yet certain (Braun 1998). As a consequence, the genus is maintained until more data is available to clarify its taxonomic position (Braun 1998). Five species are known to belong in this genus and were isolated from several hosts (*Chenopodium, Equisetum, Scirpus* and *Vitex*) from Asia, Europe, North and South America (Braun 1998, Seifert *et al.* 2011).

Neoovularia U. Braun, Nova Hedwigia 54: 473. 1992. Fig. 27.

Phytopathogenic, causing leaf spots. *Caespituli* amphigenous, whitish to pink or ochraceous. *Mycelium* consisting of hyaline to faintly pigmented, septate, branched, thin-walled hyphae forming well-developed stromata. *Conidiophores* arising from stromata, emerging through stomata or erumpent through the cuticle, often forming sporodochia, subcylindrical, subclavate, simple, thin-walled, smooth, hyaline or lightly pigmented, continuous or septate. *Conidiogenous cells* integrated, terminal, straight to moderately geniculate-sinuous, polyblastic and sympodial, conidiogenous loci numerous, conspicuous, bulging, papilla-like, but not thickened and darkened, at most slightly refractive. *Conidia* formed singly, subglobose, obovoid, ellipsoid, aseptate, hyaline to faintly pigmented, thin-walled, smooth to verruculose; basal hilum not thickened or darkened; conidial secession schizolytic. Adapted from Braun (1998).

Type species: Neoovularia nomuriana (Sacc.) U. Braun.

Specimens examined: Hungary, Sükösd, on leaves of Astragalus cicer, Sep. 1913, leg. F. Greinich, det. G. Moesz., Flora Hungarica exsiccata 106, cent. II, Fungi 16, M-0177904. Japan, Mino Prov., Kawanye-mura, on Astragalus sinicus, May 1912, leg. K. Hara, com. P. Sydow, Kabát et Bubák: Fungi Imperfecti exsiccati 835, M-0177907; Kikotaru, on Astragalus sinicus, 1903, Nomura (holotype PAD). Russia, Ufa, Jabalakly, on leaves of Astragali cicer, 29 Jun. 1910, leg. Serebrianikow, Tranzschel et Serebrianikow Mycotheca Rossica 195, M-0177906, M-0177905.

Notes: *Neoovularia* species are characterised by having unthickened but bulging and refractive conidiogenous loci, and by producing single, subglobose conidia with unthickened but refractive hila (Fig. 27). There are six species described in this genus that are phytopathogenic and cause distinct lesions on leaves and stems (Braun 1998). They have been observed from hosts belonging to four different families (*Asteraceae, Fabaceae, Lamiaceae* and *Malvaceae*) and located in Europe, Asia, Caucasus and N. America.

Neoramularia U. Braun, Nova Hedwigia 53: 291. 1991. Fig. 28.

Phytopathogenic, causing leaf spots. *Mycelium* consisting of hyaline or subhyaline, septate, branched, thin-walled hyphae forming stromata or not. *Conidiophores* macronematous, usually in large fascicles, sometimes forming sporodochial and



Fig. 25. Hawksworthiana peltigericola (herbarium Paul Diederich). A-I. Observations from herbarium material. A, D. Conidiogenous structures developing on the host. B, C. Conidia. E, H, I. Conidiophores and conidia. F, G. Conidiophores. Scale bars = 10 µm.



Fig. 26. Monodidymaria canadensis (NY herbarium, 01293230, lectotype specimen). A. Leaf spot lesion on the host. B-E, I. Conidia. F-H. Conidiophores. Scale bars = 10 µm.

basistromatic conidiomata, emerging through stomata or erumpent through the cuticle, straight, subcylindrical to geniculatesinuous, simple, hyaline or faintly pigmented, continuous or septate, thin-walled, smooth or occasionally rough. *Conidiogenous cells* integrated, terminal, polyblastic, percurrent and sympodial, conidiogenous loci inconspicuous, not thickened or darkened. *Conidia* solitary or catenate, ellipsoid-ovoid, subcylindrical or fusoid, hyaline or slightly pigmented, aseptate to 3septate, thin-walled, smooth or almost so, hila unthickened and hyaline, conidial secession schizolytic.

Type species: Neoramularia eurotiae (Gamalizk.) U. Braun [= *N. kochiae* (Woron.) U. Braun].

Specimen examined: Russia, Central Tien-Shan, 5 Jun. 1958, Gamalitzkaja (holotype of Ramularia eurotiae LE 41968).

Notes: The genus *Neoramularia* was introduced by Braun (1991) to include species with inconspicuous, unthickened, hyaline conidiogenous loci and hila. The circumscription of *Neoramularia* was later modified to include species forming catenate conidia such as *Neoramularia esfandiarii* (Braun 1992). Ten species are currently known in this genus and have been isolated from different hosts in Asia, Europe and North America (Braun 1998, Seifert *et al.* 2011). The type species is known from *Kochia* sp., Azerbaijan, and a photoplate based on the holotype of *R. eurotia*, a synonym of *Neoramularia kochiae* is presented (Fig. 28).

Pseudodidymaria U. Braun, Cryptog. Bot. 4: 110. 1993. Fig. 29.

Phytopathogenic, causing leaf spots. *Mycelium* consisting of hyaline or faintly pigmented, septate, thin-walled and branched



Fig. 27. Neovularia nomuriana (M-0177907). A. Leaf spot lesion on the host. B, E, F. Conidiophores and conidia. C, D. Conidiogenous cells. G, H. Conidia. Scale bars = 10 µm.



Fig. 28. Neoramularia eurotiae (No. 41968, LE herbarium, holotype of Ramularia eurotiae). A-K. Observations from herbarium material. A. Leaf spot symptoms on the host. B-D, G. Conidiogenous cells and conidia. E, F, H-K. Conidia. Scale bars = 10 µm.

hyphae, forming well developed stromata. *Conidiomata* basistromatic and sporodochial. *Conidiophores* arranged in palisadelike fascicles, subcylindrical, subclavate, straight to flexuous, sinuous, rarely septate, hyaline to faintly pigmented, thin-walled, smooth, sometimes reduced to conidiogenous cells. *Conidiogenous cells* integrated, terminal, polyblastic, sympodial, conidiogenous loci bulging, unthickened or with a thickened rim, not darkened but refractive. *Conidia* formed singly, ellipsoidobovoid, subclavate, aseptate to 2-septate, base rounded to broadly truncate, hyaline to faintly pigmented, thin-walled, smooth to verruculose, hilum unthickened, not darkened but refractive, conidial secession schizolytic.



Fig. 29. Pseudodidymaria wyethiae (NY herbarium 01087025, lectotype specimen). A. Leaf spot lesion on the host. B, C. Conidiogenous cells and conidia. D–G. Conidia. Scale bars = 10 µm.

Type species: Pseudodidymaria wyethiae (Ellis & Everh.) U. Braun.

Specimens examined: **USA**, California, Santa Rosa, on leaves of *Wyethia glabra*, 25 May 1894, WC Blasdale (**lectotype** NY 01087025, **isolectotypes** NY 01087026, 01087027, 01087028).

Notes: Pseudodydimaria was established to accommodate *Didymaria wyethiae*, since it did not fit comfortably with the description of *Ramularia*, *Pseudocercosporidium* or *Neoovularia*. *Pseudocercosporidium* differs by having very long, branched conidiophores, formed singly or loosely grouped. *Neoovularia* differs by having aseptate, subglobose to ovoid conidia with narrow, darkened, refractive hila. Two species are currently known to belong to this genus, *P. wyethiae* (Fig. 29) and *P. clematidis*, reported from North America (Braun 1998).

Tretovularia Deighton, Trans. Brit. Mycol. Soc. 82: 743. 1984. Fig. 30.

Phytopathogenic, causing leaf spots. *Mycelium* consisting of hyaline, septate, branched, thin-walled hyphae; stromata absent or small. *Conidiophores* macronematous, growing singly or in fascicles, arising from internal hyphae or stromata, emerging through stomata, subcylindrical to sinuous, fertile part usually strongly geniculate-sinuous, hyaline, continuous or sometimes septate, thin-walled, smooth. *Conidiogenous cells* integrated, terminal, sometimes becoming intercalary, polytretic, indeterminate, proliferation sympodial, conidiogenous loci are minute pores located in small shoulders that are later covered by a colourless cap. *Conidia* solitary, subglobose, broad ellipsoid-ovoid, pyriform, aseptate, hyaline, base rounded or with a small protrusion. Type species: Tretovularia villiana (Magnus) Deighton.

Specimen examined: Germany, Unterfranken, Hassfurt near Nürnberg, on *Vicia cassubica*, Sep. 1898, A. Vill [Allesch. & Schn., Fungi bavar. 691], ex-herb. P. Magnus acc.1918 (holotype HBG).

Notes: This monotypic genus was established to accommodate *Ovularia villiana* (Fig. 30), a phytopathogenic species that forms polytretic conidiogenous cells with sympodial proliferation, a characteristic very different from *Ramularia* and other similar genera.

Ramularia sensu stricto

Ramularia abscondita (Fautrey & F. Lamb.) U. Braun, Int. J. Mycol. Lichenol. 3: 280. 1988. Fig. 31.

Basionym: Ovularia abscondita Fautrey & F. Lamb., Rev. Mycol. (Toulouse) 18: 144. 1896.

- = Ramularia filaris f. lappae Sacc., Syll. Fung. 4: 210. 1886.
- = Ramularia filaris var. lappae Bres., Hedwigia 36: 200. 1896.
- ≡ Ramularia lappae (Bres.) Ferraris, Fl. Ital. Crypt., Fungi 1(6): 837. 1913.

Mycelium consisting of hyaline, septate, branched, smooth, 1–2 µm diam hyphae. *Conidiophores* hyaline, thin-walled, smooth, erect, septate, cylindrical-oblong, straight to geniculatesinuous, unbranched, (10–)15.5–20.5(–44.5) × (1.5–)2 µm, or reduced to conidiogenous cells. *Conidiogenous cells* integrated in the mycelium or terminal on the conidiophore, cylindrical-oblong to geniculate-sinuous, (7–)11–14(–22.5) × (1–)1.5–2(–3) µm, with multiple conidiogenous loci almost flat to protuberant, thickened, darkened and refractive. *Conidia* hyaline, thin-walled, smooth to slightly verruculose, catenate, with *hila* thickened, darkened and refractive. *Ramoconidia* cylindrical-oblong, clavate,



Fig. 30. Tretovularia viliana (holotype, HBG). A. Leaf spot lesion on the host. B, F, G. Conidiogenous cells and conidia. C-E. Conidia. Scale bars = 10 µm.



Fig. 31. Ramularia abscondita (CBS 114727). A–J. Structures formed in culture. A, C, E, G. Conidia. B, D, F, I, J. Conidiophores, conidiogenous cells and conidia. H. Conidiophore. Scale bars = 10 µm.

sometimes curved, oval, $(5.5-)8-9.5(-15) \times 2-2.5(-3) \mu m$, aseptate, with 2-3 apical hila. *Intercalary conidia* cylindrical-oblong, oval, ellipsoid, aseptate, (4.5-) $6.5-7(-10) \times 2(-2.5) \mu m$, in branched chains of up to five conidia. *Terminal conidia* obovoid, aseptate, $(4-)5(-6) \times (1.5-)$ $2-2.5 \mu m$ (on SNA, CBS 114727). *Culture characteristics*: On MEA, 8 mm diam, surface raised, fluffy aerial mycelium, dirty white, with margins undulate, colony reverse ochreous; on OA, 8 mm diam, surface raised, folded, fluffy aerial mycelium, white, margins undulate, colony reverse buff; on PDA, 8 mm diam, surface raised, folded, fluffy aerial mycelium pale grey, with margins undulate, colony reverse buff.

Description in vivo: See Braun (1998: 84).

Specimens examined: France, Viserny, Côte-d'Or, on Arctium lappa, 1896, Fautrey [Roum., Fungi Sel. Gall. Exs. 7245] (lectotype, designated in Braun 1998, PC). Sweden, Uppland, Dalby, on leaves of Arctium tomentosum, 20 Sep. 1990, E. Gunnerbeck, culture CBS 114727.

Substrate and distribution: On Arctium spp. (Asteraceae); Caucasus, Central Asia, Europe.

Notes: Ramularia abscondita was originally described on Arctium lappa from France (lectotype in PC). It has a wide geographical distribution but has only been isolated from hosts belonging to the genus Arctium (Asteraceae), a plants genus commonly known as thistle burdock. Burdock root was used as bittering agent of beer before the introduction of hop and is very much used in Asian cuisine. Ramularia abscondita has been reported on Arctium tomentosum from Sweden (Braun 1998). The morphological description of this strain (Fig. 31) differs from the one in literature (Braun 1998) based on collections in vivo by having longer conidiophores and narrower conidiophores and conidia. These differences may be related to the fungus growing in culture and not being associated with its host. This strain forms a single lineage in the phylogenetic analysis (Fig. 2, clade 43) but will be tentatively considered as a good representative of this species until material from the type host and location is collected and cultured.

Ramularia acris Lindr., Acta Soc. Fauna Fl. Fenn. 22(1): 14. 1902.

= Septocylindrium ranunculi Peck, Rep. (Annual) New York State Mus. Nat. Hist. 34: 46. 1881.

= Ramularia aequivoca f. *ranunculi-acris* C. Massal., Atti Mem. Accad. Agric. Sci. Art. Verona: 156. 1902.

= Ramularia aequivoca var. andrei M. Morelet, Bull. Soc. Sci. Nat. Archéol. Toulon Var: 9. 1967.

Description in vivo: See Braun (1998: 234).

Specimens examined: **Netherlands**, Gelderland Prov., Wageningen, on living leaves of *Ranunculus acris*, Aug. 2012, S.I.R. Videira, cultures CBS 141107 = CPC 25899 and CPC 25898; Utrecht Prov., Utrecht, Rhijnauwen, on living leaves of *?Ranunculus* sp., May 2013, U. Damm, culture CPC 25900; Zeeland Prov., Borsele, Vladijk near Nisse, on *Ranunculus* sp., 27 Aug. 2001, G. Verkley, culture CBS 109794.

Substrate and distribution: On Ranunculus (Ranunculaceae); Asia, Europe and N. America.

Notes: The strains in this clade were previously identified as *R. didyma*. Authentic strains of *R. didyma* cluster in clade 72 (Fig. 2) and, besides *R. didyma*, *R. acris* is also common on *Ranunculus acris*. Since the strains were sterile in culture and no herbarium specimens were preserved, the morphological characters could not be compared with the description available in literature. The strains in this clade cluster in a highly supported clade (Fig. 2, clade 7, 1/100/100) and are tentatively treated as *R. acris*.

Ramularia acroptili Bremer, Sydowia 2: 315. 1984.

- ≡ Cercosporella acroptilli (Bremer) U. Braun, Nova Hedwigia 56: 439. 1993.
- = Cercosporella centaureicola D. Berner et al., Mycologia 97: 1122. 2006.

Description in vivo: See Braun (1995: 72).

Specimens examined: Greece, Macedonia region, Kozani, on leaves of *Centaurea solstitialis*, 28 Apr. 2004, D. Berner, culture CBS 120253 = BPI 844247. Turkey, Ankara, on *Acroptilon repens*, 14 Jul 1947, Bremer [Reliquiae Petrakianae 363] (lectotype W, No. 11177); near Isparta, on *Acroptilon repens*, 1 Sep. 1997, R. Sobhian (epitype designated here BPI 745883, MBT130827, culture ex-epitype CBS 120252). USA, California, on *Cynara cardunculus*, Oct. 2010, L. Davenport, cultures CPC 18723, CPC 18724.

Substrate and distribution: On Acroptilon repens, Centaurea solstitiales and Cynara cardunculus (Asteraceae); Central Asia, Europe and N. America.

Notes: Russian knapweed (Acroptilon repens) and yellow starthistle (Centaurea solstitialis) are invasive weeds in the western USA. Berner et al. (2005) studied two potential biological control agents for these weeds namely Cercosporella acroptili for A. repens, and a morphologically similar Cercosporella sp. on Centaurea solstitialis. The culture of Cercosporella acroptili (CBS 120252) from the same host and country as the type (Acroptilon repens, Turkey) was compared with the herbarium type material and found to be identical. Both Cercosporella acroptili (CBS 120252) and Cercosporella sp. (CBS 120253) were morphologically cryptic, the infection symptoms were phenotypically similar and the ITS sequences were 99 % similar with only 3 base pairs difference. Pathogenicity tests showed they were only pathogenic to their respective hosts, growth studies showed some culture morphology differences, and that they were vegetatively incompatible (Berner et al. 2006). At the time, the combination of these minor differences in morphology, pathogenicity, growth and genetics (ITS sequences) between C. acroptili and Cercosporella sp. were found sufficient to describe the new species as Cercosporella centaureicola (CBS 120253). However, previous studies have shown that a strain isolated from one host that was not able to colonise the other host did not necessarily mean they were different species; they can be the same species with different physiological specialisations to the host in which case a forma specialis is usually proposed (Macedo et al. 2013). In this study, the strains CBS 120252 and CBS 120253 show minimal nucleotide differences for the six genes amplified: 0 (LSU), 5 (ITS), 3 (rpb2), 2 (actA), 2 (gapdh) and 5 (tef1- α). We propose that this is the same species and synonymise Cercosporella centaureicola and C. acroptili under R. acroptili, since this is the older name. These strains fall in the Ramularia clade (Fig. 1, clade XIV, 1/100) and cluster in a highly supported clade based on BA, ML and PA phylogenetic analysis (Fig. 2, clade 2, 1/100).

Ramularia actinidiae Ablak., Bot. Mater. Otd. Sporov. Rast. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 13: 244. 1960. Fig. 32.

Mycelium consisting of hyaline, septate, branched, smooth, 1–2 µm diam hyphae. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* hyaline, thin-walled, smooth, intermediate in the mycelium, cylindrical-oblong, (6–) 11.5–15(–20) × (1.5–)2(–3) µm, with one *conidiogenous locus*, almost flat to protuberant, thickened, darkened and refractive. *Conidia* hyaline, thin-walled, smooth, catenate, with *hila* thickened, darkened and refractive. *Ramoconidia* subcylindrical, fusoid, (15–) 18–20(–28) × (1.5–)2–3 µm, 0–1-septate, with two apical hila. *Intercalary conidia* subcylindrical, fusoid, 0–1-septate, slightly narrower at the septa, (11–)17–20(–27) × 2–3 µm, in branched chains of up to four conidia. *Terminal conidia* subcylindrical, obovoid, aseptate, (7–)10–12.5(–20) × (1.5–)2(–3) µm (on SNA).



Fig. 32. Ramularia actinidiae (CBS 141108). A-F. Observations from herbarium material. G-I. Structures formed in culture. A. Leaf spot lesion on the host. B, D, F, H, I. Conidiophores and conidia. C, E, G. Conidia. Scale bars = 10 µm.

Culture characteristics: On MEA, 17 mm diam, surface convex, pale olivaceous grey, smooth flat mycelium, radially striated close to the margin, margins white and lobate, colony reverse olivaceous grey with a buff margin and radially striated; on OA, 15 mm diam, surface flat, short and uniform aerial mycelium, livid vinaceous in the centre and smoke-grey towards margin, with margins olivaceous grey, undulate and with scarce aerial mycelium, colony reverse iron-grey; on PDA, 18 mm diam, surface low convex, short and uniform aerial mycelium, pale olivaceous grey, with margins undulate, feathery, white, colony reverse iron-grey.

Description in vivo: See Braun (1998: 46).

Specimen examined: **South Korea**, Yangpyeong, on *Actinidia polygama*, 24 Oct. 2004, H.D. Shin, KUS-F20880, CBS H-22543, cultures CBS 141108 = CPC 11675, and CPC 11674.

Substrate and distribution: On Actinidia polygama; Russia and South Korea.

Notes: The description of R. actinidiae available in literature includes grevish caespituli, conidiophores, hyaline, simple, 20-40 µm long, conidia cylindrical, aseptate, 10.5-17 × 3 µm. The specimen observed has short conidiophores (12-) $19-23(-35) \times (1.5)-2-2.5(-3) \mu m$ and conidial dimensions matching the ones in culture $(5-)10-12(-21) \times (1.5-)2(-3) \mu m$. Ramularia actinidiae was originally described on Actinidia polygama from Russia. Braun (1998) commented on this species being insufficiently known, and that the type material was not available for study. The strain used in this study is from a different location to that of R. actinidiae but the description of the morphology is quite similar (Fig. 32). It forms a single lineage supported by the Bayesian multigene analysis (Fig. 2, clade 77) and is tentatively maintained as Ramularia actinidiae until fresh material from the same location and host as the type has been recollected (Actinidia polygama, Russia).

Ramularia agastaches Sawada, Bull. Gov. Forest Exp. Sta., Meguro 105: 85. 1958. Fig. 33.

Mycelium consisting of hyaline, septate, branched, smooth, 1–2 µm diam hyphae. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* hyaline, thin-walled, smooth, terminal or intermediate in the mycelium, cylindrical-oblong, (8.5–) 11–13(–16) × 1.5–2(–2.5) µm, with one or two conidiogenous loci, thickened, darkened and refractive. *Conidia* hyaline, thin-walled, smooth, catenate, with hila thickened, darkened and refractive. *Ramoconidia* subcylindrical, clavate, ovoid, (11–) 15–18(–27) × (2.5–)3–3.5(–4) µm, 0–1-septate, with two apical hila. *Intercalary conidia* subcylindrical, 0–1-septate, (11–) 13.5–15.5(–21) × 3(–4) µm, in branched chains of up to six conidia. *Terminal conidia* subcylindrical, obovoid, aseptate, (4–) 8–10(–13) × (2–)3(–4) µm (on SNA).

Culture characteristics: On MEA, 12 mm diam, surface raised, strongly folded, pale olivaceous grey, smooth, with margins crenate, reverse olivaceous grey; on OA, 10 mm diam, surface convex, pale olivaceous grey, fluffy aerial mycelium, with margins undulate, reverse olivaceous grey; on PDA, 10 mm diam, surface raised, pale olivaceous grey with white patches, fluffy aerial mycelium, with margins undulate, reverse rosy buff with olivaceous grey patches.

Specimen examined: South Korea, Hoengseong, on Agastache rugosa, 10 Oct. 2003, H.D. Shin, KUS-F19865, cultures CPC 10819–10821.

Substrate and distribution: On Agastache rugosa, East Asia (Japan, South Korea).

Notes: Ramularia agastaches was originally described on Agastache rugosa from Japan and was synonymised with *R. lamii* var. *lamii* by Braun (1998) who was not able to examine the type specimen. The strains in this clade were previously



Fig. 33. Ramularia agastaches (CPC 10820). A-C. Observations from herbarium material. D-H. Structures formed in culture. A. Leaf spot symptoms on the host. B, G, H. Conidiophores, conidiogenous cells and conidia. C, D, F. Conidia. E. Conidiophore. Scale bars = 10 µm.



Fig. 34. Ramularia alangiicola (CPC 10299). A, C. Observations from herbarium material. B, D–G. Structures formed in culture. A. Leaf spot symptoms on the host. B, C, D. Conidiophores and conidia. E–G. Conidia. Scale bars = 10 µm.

identified as *R. lamii*, which is now restricted to species in clade 67 (Fig. 2). The strains in this clade form a highly supported clade by all three methods of phylogenetic analysis (Fig. 2, clade 46, 1/100/100). Morphologically (Fig. 33) the description does not match that of *R. lamii* available in literature (Braun 1998).

Ramularia agrimoniae Sacc., Malpighia 10: 277. 1896.

Leaf spots almost absent to subcircular, pale to brownish occasionally with reddish border. *Mycelium* consisting of hyaline, branched, smooth, septate hyphae, sometimes forming small stromata internally. *Conidiophores* in loose fascicles arising from stromata, through stomata, or solitary arising from secondary hyphae, straight, subcylindrical to geniculate-sinuous, simple, $4-30 \times 1.5-4 \mu m$, 0-1(-2)-septate, hyaline, thin-walled,

smooth; *conidiogenous loci* slightly thickened and darkened. *Conidia* formed in chains, occasionally branched, ellipsoid-ovoid, fusiform, subcylindrical, $6-19.5 \times 1.5-3.5(-5) \mu m$, 0-1-septate, hyaline, thin-walled, smooth to faintly rough, ends obtuse to subacute; *hila* minute, slightly thickened and darkened. Adapted from Braun (1998).

Specimens examined: South Korea, Hoengseong, on Agrimonia pilosa, 4 Aug. 2004, H.D. Shin, KUS-F20540, cultures CPC 11450–11452, CPC 11651–11653. Russia, Siberia, Paseka, on Agrimonia sp., 19 Jun., herb. Saccardo (holotype PAD).

Substrate and distribution: On Agrimonia spp. (Rosaceae), Asia, Caucasus, Europe.

Note: Ramularia agrimoniae was originally described on *Agrimonia* sp. from Siberia, Russia. Despite the reported distribution of this species across Europe and Asia, the available strains in this study all originate from South Korea (Fig. 2, clade 8, 1/100/100).

Ramularia alangiicola Videira, H.D. Shin & Crous, nom. nov. MycoBank MB817157. Fig. 34.

Basionym: Phacellium alangii H.D. Shin & J.D. Kim, Mycotaxon 81: 341. 2002, non Ramularia alangii Hasija, 1962.

Mycelium consisting of hyaline, septate, branched, smooth, 1-2 µm diam hyphae. Conidiophores hyaline, thin-walled, smooth, erect, septate, cylindrical-oblong, straight, unbranched, $(11-)24.5-35.5(-67) \times (1.5-)2(-3)$ µm, or reduced to conidiogenous cells. Conidiogenous cells integrated in the mycelium or terminal on the conidiophore, cylindrical-oblong, (6-) $11-15.5(-27) \times (1.5-)2(-3) \mu m$, with 1-2 conidiogenous loci almost flat to protuberant, thickened, darkened and refractive. Conidia hyaline, thin-walled, smooth to slightly verruculose, catenate, aseptate, with hila thickened, darkened and refractive. Ramoconidia cylindrical-oblong to clavate. (10-)12.5-14(-19) × (1.5-)2(-2.5) µm, with 2-3 apical hila. Intercalary conidia cylindrical-oblong, $(8.5-)11-12(-16) \times (1.5-)$ 2(-2.5) µm, in branched chains of up to five conidia. Terminal conidia obovoid, (6-)8.5-9.5(-11.5) × (1.5-)2 µm.

Specimens examined: **South Korea**, Chuncheon, on leaves of *Alangium platanifolium* var. *macrophyllum*, 11 Oct. 2002, H.D. Shin, KUS-F19227, culture CPC 10299; Chuncheon, on living leaves of *Alangium platanifolium* var. *macrophyllum*, 29 Sep. 2000, H.D. Shin (**holotype** KUS-F17673, **isotype** HAL 1656 F).

Substrate and distribution: Only known from the type collection.

Notes: Phacellium alangii was originally described on Alangium platanifolium var. macrophyllum from South Korea (holotype in KUS). In vivo, this species produced long and septate conidiophores grouped in synnemata ($90-340 \times 20-50 \mu$ m) and conidia solitary or in short chains ($5-42 \times 2-5 \mu$ m) (Shin & Kim 2002). At the time it was described (Shin & Kim 2002), it was compared with Ramularia alangii but found different since the later has short and aseptate conidiophores ($10-35 \times 3-6.5 \mu$ m) and longer and wider catenate conidia ($20-45 \times 3-4.5 \mu$ m). Ramularia alangii was only known from the type location (on Alangium salviifolium [= A. lamarckii] from India) and this fact, together with the morphological differences, supported Phacellium alangii as a new species. In the herbarium specimen from which isolate CPC 10299 was derived, we observed that the conidiophores grow in synnemata that are hyaline to pale brown

(Fig. 34, C). In culture, the synnemata were not observed, the conidiophores and conidia were shorter and narrower than the ones described in the original publication (Shin & Kim 2002). Since the species formed a distinct single lineage in the *Ramularia* clade (Fig. 1, clade XIV) and the production of synnemata is no longer considered a reliable character to separate *Ramularia* from *Phacelium*, a new combination is proposed. Because the epithet "*alangii*" is already occupied in *Ramularia* for a different species, the new epithet "*alangiicola*" is introduced.

Ramularia aplospora Speg., Dec. Mycol. Ital. no. 105. 1879. Fig. 35.

≡ Ovularia aplospora (Speg.) Magnus, Hedwigia 44: 17. 1904.

= Ramularia schroeteri J.G. Kühn, Hedwigia 20: 147. 1881.

≡ Ovularia schroeteri (J.G. Kühn) Sacc., Syll. Fung. 4: 140. 1886.

Mycelium consisting of hyaline, septate, branched, smooth, 1-2 µm diam hyphae. Conidiophores hyaline, thin-walled, smooth, erect, 1-3(-5)-septate, cylindrical-oblong, straight and apically geniculate-sinuous, unbranched (22 -) $40-60(-135) \times (1-)2(-3) \mu m$. Conidiogenous cells terminal in conidiophores, cylindrical-oblong to sinuous, narrower at the top, $(10.5-)19-24(-40) \times (1-)1.5-2(-2.5) \mu m$, with multiple conidiogenous loci almost flat to protuberant in a terminal and lateral position, thickened, darkened, refractive. Conidia hyaline, thinwalled, smooth to slightly verruculose, catenate, with hila thickened, darkened and refractive. Ramoconidia ellipsoidal to oval, $(8.5-)10-11(-13) \times (3.5-)5-6(-7) \mu m$, aseptate, with 2 apical hila. Intercalary conidia ellipsoidal to oval, 0-1-septate, (8-) $10-11(-14) \times (4-)5-5.5(-7) \mu m$, in branched chains of up to five conidia. Terminal conidia ellipsoidal to obovoid, aseptate, $(5.5-)7.5-8.5(-11) \times (3.5-)4.5-5.5(-6.5) \mu m.$

Culture characteristics: On MEA, 20 mm diam, surface low convex, smooth, greenish grey, producing small droplets of hyaline exudate on top of the mycelium, radially striated with margins undulate and concave, colony reverse olivaceous grey, broken radially; on OA, 16 mm diam, surface low convex, smooth, pale olivaceous grey producing small droplets of hyaline exudate on top of the mycelium, with margins with an entire edge and with sparse buff mycelium, with a discolouration halo in the media around the colony margins, colony reverse buff and olivaceous grey; on PDA, 18 mm diam, surface low convex, smooth, grey olivaceous, margins feathery with an entire edge, colony reverse olivaceous grey.

Description in vivo: See Braun (1998: 242).

Specimens examined: Austria, Tirol, Ober Inntal, Samnaum Gruppe, Lazidalm near Serfaus, on leaf spot from *Alchemilla vulgaris*, 8 Aug. 2000, G. Verkley, cultures CBS 109120, CBS 109121; Ötztal, Hoch-Sölden, on leaf spot from *Alchemilla vulgaris*, 25 Jul. 2000, G. Verkley, cultures CBS 109013, CBS 109014. Former Czechoslovakia, on *Alchemilla xanthochlora*, unknown collector and date, isol. L. Marvanová, Nov. 1972, dep. L. Marvanová, Jan. 1973, culture CBS 237.73. Germany, Gössweinstein, Ober-Franken, on *Alchemilla vulgaris*, unknown collector and date, isol. T. Hijwegen, 3 Aug. 1982, dep. T. Hijwegen, Oct. 1982 (epitype, designated here, CBS H-1743, MBT204828, culture ex-epitype CBS 545.82). Italy, on *Alchemilla vulgaris* L., Speg., Decad. Mycol. Ital. 105 (lectotype designated in Braun 1998, PAD). Sweden, Uppland, Haga, Årtopet, on *Alchemilla vulgaris*, 14 Aug. 1988, E. Gunnerbeck, culture CBS 114118.

Substrate and distribution: On Alchemilla and Aphanes (Rosaceae); Asia, Caucasus, Europe.



Fig. 35. Ramularia aplospora (CBS 545.82). A-F. Structures formed in culture. A-C, E, F. Conidiophores, conidiogenous cells and conidia. D. Conidia. Scale bars = 10 µm.



Fig. 36. Ramularia archangelicae (CBS 108991). A–F. Structures formed in culture. A–C. Conidiophores, conidiogenous cells and conidia. D, F. Conidia. E. Conidiogenous cell and conidia. Scale bars = 10 µm.

Notes: In literature, *R. aplospora* is linked to the sexual morph named *Mycosphaerella alchemillicola* (Vassiljevsky 1925, Braun 1998), but experimental proof is still lacking (Videira *et al.* 2015b). The strain CBS 545.82 has previously been indicated as the type strain of the latter (Crous *et al.* 2007) but this was not formally proposed. Therefore, and since the morphological characteristics are in agreement with the original description

(Fig. 35), we formally designate CBS 545.82 as the ex-epitype strain of *R. aplospora*. This species formed a highly supported clade (Fig. 2, clade 27, 1/100/100). *Ramularia aplospora* is the only species in this genus known from the host *Alchemilla* (*Rosaceae*). *Alchemilla* plants are herbaceous perennials commonly known as "lady's mantle" and highly appreciated in gardens for their flowers and foliage (Hawke 2004).

Ramularia archangelicae Lindr., Acta Soc. Fauna FI. Fenn. 23: 22. 1902. Fig. 36.

- = Ramularia angelicae Höhn., Hedwigia 42: 178. 1903.
- = Cylindrosporium vaccarianum Sacc., Nuovo Giorn. Bot.
- Ital., N.S., 24: 41. 1917. = *Ramularia grantii* Dearn., Mycologia 21: 326. 1929.
- = Septocylindrium angelicae Katsuki, Kyushu Agric. Res. 6: 42. 1953.

Mycelium consisting of hyaline, septate, branched, smooth, 0.5-2 µm diam hyphae. Conidiophores hyaline, thin-walled, smooth, erect, septate, straight, cylindrical-oblong, unbranched, (11.5-)26.5-36(-46.5) × 1.5-2(-2.5) µm or reduced to conidiogenous cells. Conidiogenous cells integrated in mycelium or conidiophores, terminal in cylindrical-oblong, (5.5-) $9.5-12(-16) \times (1-)1.5-2 \mu m$, with 1-2 apical conidiogenous loci, almost flat to short cylindrical thickened, darkened, refractive. Conidia hyaline, thin-walled, smooth, with hila thickened, darkened and refractive. Ramoconidia subcylindrical to clavate, (15-)22-25(-35) × (1.5-)2-2.5(-3) µm, 0-3-septate. with 2-3 apical hila. Intercalary conidia aseptate or 0-1(-2)-septate, subcylindrical, sometimes curved, $(14-)18-22(-37) \times (1.5-)$ 2(-2.5) µm, in branched chains of up to seven conidia. Terminal conidia aseptate. subcvlindrical to obovoid. (6-) $10-12(-16) \times 1.5-2(-2.5)$ µm, hila thickened, darkened, refractive.

Culture characteristics: On MEA, 13 mm diam, surface raised, folded, smooth, light smoke grey with pale vinaceous tinge with margins undulate, convex, feathery, colony reverse brick and with dark vinaceous patches; on OA, 16 mm diam, surface low convex, fluffy aerial mycelium, dirty white to smoke-grey, with margins crenate, producing a brick coloured pigment imbued in the agar forming a 13 mm band surrounding the colony, colony reverse dark vinaceous centre; on PDA, 16 mm diam, surface flat, smooth, pale smoke-grey with pale vinaceous tinge, forming tiny droplets of pale vinaceous exudate, with margins undulate, colony reverse pale vinaceous centre turning lighter shade towards the margin. Strains CBS 108992 and CBS 288.49 did not produce any pigment.

Description in vivo: See Braun (1998: 55).

Specimens examined: Austria, Ötztal, Ötz near Habichen, on leaf spot of *Angelica sylvestris*, 24 Jul. 2000, G. Verkley, cultures CBS 108991, CBS 108992, CBS 109011, CBS 109012; on stem of *Angelica sylvestris*, unknown collector and date, isol. and dep. J.A. von Arx, Jun. 1949, culture CBS 288.49. **Sweden**, Lapponia Lulensis, Sarvestjakko, on *Angelica archangelica*, 12 Aug. 1900 [Verstergr., Micromyc. Rar. Sel. Praec. Scand. 549] (neotype, designated in Braun 1998, B).

Substrate and distribution: On Angelica (Apiaceae); Asia, Europe, North America.

Notes: This species was described from *Argelica archangelica* collected in Sweden (neotype at B). The representative strains of this species cluster in a clade highly supported by BA and ML phylogenetic analyses (Fig. 2, clade 19, 1/100/100). Morphologically, the structures observed in culture (Fig. 36) are slightly narrower than those described in literature based on material *in vivo* (Braun 1998) but similar in all other characters. The strain CBS 288.49 was initially identified as *Mycosphaerella rubella*, and the type of this species was isolated from *Angelica sylvestris* from Germany. However, there is no evidence in literature of a link between these sexual and asexual names, and further

studies are necessary to evaluate whether these species are conspecific.

Ramularia armoraciae Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 361 "1869" (1870) emend. U. Braun (1998). Fig. 37.

- ≡ Ovularia armoraciae (Fuckel) Massee, Brit. Fung.-Fl. 3: 321: 1893.
 ≡ Cylindrospora armoraciae (Fuckel) J. Schröt., in Cohn, Krypt.-Fl. Schlesien, 3.2(4): 485: 1897.
- = Entylomella armoraciae (Fuckel) Cif., Ann. Mycol. 26: 17. 1928.
- = Ramularia matronalis Sacc., Michelia 2(6): 123. 1880.
- = Ramularia cochleariae Cooke, Grevillea 11(60): 155. 1883.
- = Ramularia hesperidis Săvul. & Sandu, Mem. Sect. Şti. Acad. Română, Ser. 3, 15: 477. 1940.

For additional synonyms see Braun (1998).

Mycelium consisting of hyaline, septate, branched, smooth, 1.5–3 µm diam hyphae. *Conidiophores* hyaline, thin-walled, smooth, erect, septate, straight, cylindrical-oblong, geniculate-sinuous, unbranched, $(12-)20-29(-41) \times (1.5-)2(-3)$ µm or reduced to conidiogenous cells. *Conidiogenous cells* integrated in mycelium or terminal in conidiophores, cylindrical-oblong, geniculate-sinuous, $(2-)12-17(-30) \times (1-)1.5-2.0(-3)$ µm, with one to multiple apical conidiogenous loci, almost flat or slightly protuberant, thickened, darkened and refractive. *Conidia* hyaline, thinwalled, smooth, catenate, aseptate, with hila thickened, darkened and refractive. *Ramoconidia* subcylindrical to clavate, (10.5–) 13–14.5(–18.5) × (2.5–)3(–4) µm, with two apical hila. *Intercalary conidia* fusoid, ovoid, ellipsoid, (8–)10.5–12(–16) × (2.5–) 3–3.5(–4) µm, in branched chains of up to ten conidia. *Terminal conidia* obovoid, (5–)7–8(–10) × (2–)3–3.5(–4) µm (on SNA).

Culture characteristics: On MEA, 13 mm diam, surface irregular, raised, smooth, white, with margins crenate feathery and olivaceous green, colony reverse olivaceous green; on OA, 14 mm diam, surface flat, smooth, with sparse aerial mycelium, white with olivaceous green patches, with margin irregular, with sparse aerial mycelium, colony reverse iron-grey; on PDA, 13 mm diam, surface flat, smooth, white with pale olivaceous grey patches, margins undulate, colony reverse olivaceous grey.

Description in vivo: See Braun (1998: 120).

Specimens examined: Germany, on Armoracia rusticana [Fuckel, Fungi Rhen. Exs. 133; lectotype, designated in Braun (1998), HAL]; on Armoracia rusticana, S. Petzoldt, unknown date (epitype designated here, CBS H-22518, MBT204829, culture ex-epitype CBS 241.90). Netherlands, on Armoracia rusticana, unknown collector and date, isol. and dep. A.L. Houwink, Nov. 1928, culture CBS 253.28.

Substrate and distribution: On various crucifers (*Brassicaceae*); Asia, Caucasus, Europe, Africa (Kenya), N. America.

Notes: Ramularia armoraciae was first described on *Armoracia rusticana* from Germany (lectotype in HAL). Strain CBS 241.90 originates from the same country and was isolated from the same host as the holotype, and is therefore chosen as ex-epitype (Fig. 37). Phylogenetically, this species is highly supported by the BA and ML analysis (Fig. 2, clade 55).

Ramularia asteris (W. Phillips & Plowr.) Bubák, in Kabát & Bubák, Fungi Imperf. Exs., Fasc. 8, no. 388. 1906. *Basionym: Fusidium asteris* W. Phillips & Plowr., Grevillea 6: 23. 1877.



Fig. 37. Ramularia armoraciae (CBS 241.90). A-G. Structures formed in culture. A, C-E, G. Conidiophores, conidiogenous cells and conidia. B, F. Conidia. Scale bars = 10 µm.

= *Ramularia rudbeckiae* Peck, Rep. (Annual) New York State Mus. Nat. Hist. 34: 47. 1881.

= *R. macrospora* var. *asteris* Trel., Preliminary list of the parasitic fungi of Winsconsin: 13. 1884.

= *Ramularia asteris-tripolii* Jaap, Verh. Bot. Vereins Prov. Brandenburg 50: 48. 1908.

= *R. serotina* var. *stomaticola* U. Braun, Nova Hedwigia 58: 199. 1994. For additional synonyms see Braun (1998) or MycoBank.

Description in vivo: See Braun (1998: 259).

Specimens examined: **Netherlands**, on *Aster tripolium*, unknown collector and date, isol. v.d. Molen, dep. Oct. 1921, culture CBS 131.21. **UK**, Kings Lynn, on *Aster tripolium*, 10/5, Plowright (**holotype** K).

Substrate and distribution: On Aster, Galatella, Grindelia, Heteropappus, Rudbeckia, Solidago (Asteraceae); Asia, Europe, N. America.

Notes: Ramularia asteris was first observed on Aster tripolium from England (holotype in K). There are specimens of Ramularia asteris with narrow conidia $(3-5 \ \mu\text{m})$ that are referred to as *R. asteris* var. asteris, and broader conidia $(5-7 \ \mu\text{m})$ that are usually referred to as *R. asteris* var. latispora (Braun 1998). Only one isolate was available in this study (CBS 131.21) and it forms a single lineage (Fig. 2, clade 11). The culture was unfortunately sterile and no morphological observations could be made.

Ramularia bellunensis Speg., Michelia 1(5): 475. 1879.

Description in vivo: See Braun (1998: 95).

Specimens examined: Italy, Belluno, on *Tanacetum parthenium*, Oct. 1878, Spegazzini [lectotype, designated in Braun (1998), PAD]. Netherlands, on *Argyranthemum frutescens* (≡ *Chrysanthemum frutescens*), unknown collector and date, isol. H.C. Koning, dep. Dutch Plant Protection Services, Jan. 1943, culture CBS 116.43. New Zealand, Auckland, Grey Lynn, on *A. frutescens*, unknown collector and date, isol. C.F. Hill, Jun. 2005, dep. C.F. Hill, culture CBS 118417. Substrate and distribution: On Argyranthemum, Chrysanthemum, Leucanthemum, Tanacetum (Asteraceae); Africa, Asia, Caucasus, Europe.

Notes: Ramularia bellunensis was described in 1879 from Tanacetum parthenium, from Italy [lectotype, designated in Braun (1998), in PAD]. This species is represented in a single lineage (Fig. 2, clade 75). This is a new report for the Netherlands and New Zealand, as well as a first report on the host *Argyr*anthemum frutescens (Braun 1998). Although strain CBS 118417 is not in the phylogenetic trees, it is identical to CBS 116.43, except on one nucleotide in *gapdh* and one nucleotide in *tef1*- α . It was not included because at the time the trees were prepared we did not possess all the gene sequences. No ex-type strain of this species is available, and collections on *Tanacetum* from Italy are required to resolve its identity.

Ramularia beticola Fautrey & Lambotte, Rev. Mycol. (Toulouse) 19: 54. 1897. Fig. 38.

= Ramularia betae Rostr., Bot. Tidskr. 22: 272. 1898 (1899).

Mycelium consisting of hyaline, septate, branched, smooth, 1–2 µm diam hyphae. *Conidiophores* hyaline, thin-walled, smooth, erect, 1–2(-4)-septate, straight to sinuous, cylindricaloblong, unbranched (19.5–)43–58(–83) × 2–2.5(–3) µm or reduced to conidiogenous cells. *Conidiogenous cells* integrated in mycelium or terminal in conidiophores, cylindrical-oblong and narrower at the top, (7–)16.5–20(–30) × 2–2.5(–3) µm, with 1–4 apical conidiogenous loci, almost flat or protuberant, thickened, darkened and refractive. *Conidia* hyaline, thin-walled, smooth to slightly verruculose, catenate, with hila thickened, darkened and refractive. *Ramoconidia* subcylindrical to clavate, (8–)12–14.5(–22) × 3–4 µm, 0–1-septate, with two apical hila. *Intercalary conidia* subcylindrical, sometimes curved, ovoid, 0–1septate, (8.5–)10.5–12.5(–20) × (2.5–)3(–4) µm, in branched



Fig. 38. Ramularia beticola (CBS 141109). A. Observations from herbarium material. B-H. Structures formed in culture. A. Leaf spot symptoms on the host. B, G, H. Conidiophores and conidiogenous cells. C, D, I. Conidiophores, conidiogenous cells and conidia. E, F. Conidia. Scale bars = 10 µm.

chains of up to eight conidia. *Terminal conidia* subcylindrical to obovoid, aseptate, $(3.5-)6.5-8(-11) \times (2-)3(-5) \mu m$ (on SNA).

Culture characteristics: On MEA, 13 mm diam, surface irregular, raised, smooth, white, with margins crenate feathery and olivaceous green, colony reverse olivaceous green; on OA, 14 mm diam, surface flat, smooth, with sparse aerial mycelium white with olivaceous green patches, with margin irregular, with sparse aerial mycelium, colony reverse iron-grey; on PDA, 13 mm diam, surface flat, smooth, with white to pale olivaceous grey patches, margins undulate, colony reverse olivaceous grey.

Description in vivo: See Braun (1998: 136).

Specimens examined: **Denmark**, Holeby, on leaf spot on *Beta vulgaris*, 2011, A.L. Hansen, culture CPC 30065; Jungshoved, on leaf spot on *Beta vulgaris*, 2011, A.L. Hansen, culture CPC 30653. **France**, Dumont, on *Beta vulgaris* L., 1896, Fautrey [Roum., Fungi Sel. Exs. 7261; **lectotype**, designated in Braun (1998), PC]; Fresneyl'Évêque, on leaf spot on *Beta vulgaris*, 2011, A. Champeil, **epitype designated here** CBS H-22519, MBT204830, culture CBS 141109 = CPC 30066). **Germany**, Bonn, on unknown host, unknown collector and date, isol. and dep. H.A. Diddens, Jan. 1929, culture CBS 341.29. **Netherlands**, Groningen, leaf spot on *Beta vulgaris*, 2011, S.I.R. Videira, culture CPC 30067; Steenbergen, leaf spot on *Beta vulgaris*, 2011, S.I.R. Videira, cultures CPC 30063, CPC 30064. **Switzerland**, Nyon, on *Beta vulgaris*, unknown collector and date, isol. B. Lieberherr, dep. R. Corbaz, Feb. 1967, culture CBS 151.67.

Substrate and distribution: On Beta (Chenopodiaceae); Asia, Europe, North America.

Notes: Ramularia beticola (Fig. 38) is the causal organism of Ramularia leaf spot disease in sugar beet, table beet and fodder beet. The fungus forms pale brown leaf spots and affected leaves turn yellow, become necrotic and die. The impact of Ramularia leaf spot disease can vary significantly from season to season. Conditions of high humidity, moderate temperature (17–20 °C), high plant density and sulphur deficiency usually

increase disease intensity and damage. It has been reported from North America (Oregon, Washington, California and Colorado), Europe (Ireland, UK, the Scandinavian countries, Belgium, France, Germany) and Russia (Harveson et al. 2009), Worldwide, yield losses in sugar beet due to plant pathogens and pests are estimated in general to be 26 % with, and more than 80 % without crop protection (Oerke & Dehne 2004). In the Netherlands, in spite of crop protection measures, the yield losses due to pests and diseases for top growers were 37.1 and 16.7 % on sandy and clay soils respectively (Hanse et al. 2011). When treatments are applied timely, programmes of disease control in Denmark increased sugar yield by 10 %. Thus far, R. beticola has not shown signs of developing resistance to either strobilurin or triazol fungicides, but it remains important to apply fungicides efficiently by following monitoring programmes and respecting the recommended thresholds (www.FRAC.info) (Thach et al. 2013). Ramularia beticola was described on Beta vulgaris from France in 1896. The strains used in this study clustered together in a single and highly supported clade (Fig. 2, clade 52, 1/100/100).

Ramularia bosniaca Bubák, Österr. Bot. Z. 53: 49. 1903. Fig. 39.

= Ramularia scabiosae Rostr. ex Lind, Danish Fungi: 511. 1913.

= Ramularia scabiosae Jaap, Ann. Mycol. 15: 122. 1917.

Mycelium consisting of hyaline, septate, branched, smooth, 1–3 µm diam hyphae. *Conidiophores* hyaline, thin-walled, smooth, erect, 1–2(–4)-septate, straight to geniculatesinuous, cylindrical-oblong, unbranched, (20–) $41-60(-119) \times 2-2.5(-3)$ µm or reduced to conidiogenous cells. *Conidiogenous cells* integrated in mycelium or terminal in conidiophores, cylindrical-oblong and narrower at the top, geniculate-sinuous, (14–)19–23(–35) × 2–2.5(–3) µm, with 1–4 apical conidiogenous loci, almost flat or protuberant,


Fig. 39. Ramularia bosniaca (CBS 123880). A-H. Structures formed in culture. A, F. Conidia. B, G. Conidiophores. C, D, E, H. Conidiophores and conidia. Scale bars = 10 µm.

thickened, darkened and refractive. *Conidia* hyaline, thinwalled, smooth, solitary or catenate, aseptate, with hila thickened, darkened and refractive. *Ramoconidia* subcylindrical to ovoid, $(7.5-)10-11(-14) \times (3-)4-4.5(-5) \mu m$, with two apical hila. *Intercalary conidia* ovoid, 0-1-septate, $(8-)9.5-10.5(-13) \times (3-)4-5(-7) \mu m$, in branched chains of up to four conidia. *Terminal conidia* obovoid, (5-) $7-8(-10) \times (2.5-)4(-5) \mu m$ (on SNA).

Culture characteristics: On MEA, 13 mm diam, surface irregular, raised, smooth, white, with margins crenate, feathery and olivaceous green, colony reverse olivaceous green; on OA, 14 mm diam, surface flat, smooth, with sparse aerial mycelium white with olivaceous green patches, with margin irregular, with sparse aerial mycelium, colony reverse iron-grey; on PDA, 13 mm diam, surface flat, smooth, with white with pale olivaceous grey patches, margins undulate, colony reverse olivaceous grey.

Description in vivo: See Braun (1998: 143).

Specimen examined: Czech Republic, Moravia, Pavlov, forest around the ruin, leaf spot on *Scabiosa ochroleuca*, 18 Nov. 2008, G. Verkley, cultures CBS 123880, CBS 123881.

Substrate and distribution: On *Scabiosa* (*Dipsacaceae*); Central Asia, Caucasus, Europe.

Notes: Ramularia bosniaca was originally described on the host Scabiosa columbaria in Bosnia (holotype BPI 416442 [the neotype designated in Braun (1998), BPI 416443, is obsolete since holotype material has been traced in BPI]) and is the only species of Ramularia known to infect Scabiosa (Braun 1998). Ramularia bosniaca has been reported from several European countries but this is the first time it is reported from the Czech

Republic. The description of these collections fit that of *R. bosniaca* (Braun 1998), except that conidia were shorter than 28 μ m (Fig. 39). Additional collections from Montenegro may well reveal the strains from the Czech Republic to represent a new species. The phylogenetic analysis provides good support to this species clade (Fig. 2, clade 60, 1/100/100).

Ramularia buniadis Vestergr., Jahreskat. Wiener Kryptog. Tauschanst.: 4. 1897.

Specimens examined: Sweden, Uppsala, Skottsbacke, X. 1897 [Vestergr., Micromyc. Rar. Sel. Praec. Scad. 73; lectotype, designated in Braun (1998), S-F57272]. Sweden, Uppland, Haga, Årtopet, on *Bunias orientalis*, 16 Sep. 1988, E. Gunnerbeck, culture CBS 114301 = UPSC 2718.

Substrate and distribution: On Bunias orientalis (Brassicaceae); Caucasus, Europe.

Notes: This species was described on *Bunias orientalis* collected in Sweden (lectotype in S). *Ramularia buniadis* (among other names) was synonymised with *R. armoraciae*, but since *R. armoraciae* clusters in clade 55 (Fig. 2), the name *R. buniadis* is again resurrected for this isolate (Fig. 2, clade 48). Although this isolate could be considered a good representative for epitypification, it is sterile in culture and no herbarium material of the CBS isolate was preserved.

Ramularia calcea Ces., in Rabenhorst, Klotzschii Herb. Viv. Mycol., Ed. 1, Cent. 17: no. 1681, Dresden 1852, emend. U. Braun (1998). Fig. 40.

- = Hormodendrum farinosum Bonord., Bot. Zeitung 19: 196. 1861.
- = Ovularia symphyti-cordati Săvul. & Sandu, Hedwigia 73: 107. 1933.
- = Ramularia trachystemonis Siemaszko, Mat. Mikol. Fitopatol. Ross., I, 3: 39. 1915.
- = Ramularia noneae Lobik, Bolez. Rast. 17: 190. 1928.

For additional synonyms see Braun (1998).

Mycelium consisting of hyaline, septate, branched, smooth, 0.5-1.5 µm diam hyphae. Conidiophores reduced to conidiogenous cells. Conidiogenous cells hvaline. thin-walled. smooth, intermediate in the mycelium, cylindrical-oblong, (5.5-)10.5-13(-17) × 1-1.5(-2) µm, with one or two conidiogenous loci, almost flat to protuberant, thickened, darkened and refractive, 1 µm diam. Conidia hyaline, thin-walled, smooth, catenate, with hila thickened, darkened and refractive. Ramoconidia cylindrical-oblong to oval, $(7-)9.5-12(-23) \times (1.5-)$ 2(-2.5) um, 0-1-septate, with 2-4 apical hila. Intercalary conidia cylindrical-oblong, ellipsoid or fusoid, aseptate, (4.5-) $7-8(-11) \times (1.5-)2(-2.5) \mu m$, in branched chains of up to seven Terminal conidia obovoid, conidia. aseptate, (3-)4-4.5(-6) × (1-)1.5-2 µm (on SNA, CBS 101613).

Culture characteristics: On MEA, 17 mm diam, surface raised, folded, erumpent aerial mycelium, vinaceous-buff, with margins lobate, convex, feathery, colony reverse brown-vinaceous and fawn margin; on OA, 15 mm diam, surface raised, folded, erumpent aerial mycelium, vinaceous-buff, with margins undulate, rosy-vinaceous and no aerial mycelium, colony surrounded by a 0.5 cm discoloured halo, colony reverse vinaceous; on PDA, 14 mm diam, surface greyish lilac, erumpent, convex, with margins pale vinaceous, undulate, colony surrounded by pale vinaceous pigment diffusing into the media, colony reverse vinaceous.

Description in vivo: See Braun (1998: 112).

Specimens examined: Germany, Thüringen, Weimar, brown leaf spot on Symphytum sp., 1999, G. Arnold, cultures CBS 101612, CBS 101613. Italy, Vercellis, 1851, Cesatis [Rabenh., Klotzschii Herb. Viv. Mycol. 1681; lectotype, designated in Braun (1998), HAL]. Sweden, Uppland, Vassunda, on Viola hirta, 11 Sep. 1988, E. Gunnerbeck, culture CBS 114442.

Substrate and distribution: On Nonea, Symphytum, and Trachystemon spp. (Boraginaceae); Asia, Caucasus, Europe.

Notes: Ramularia calcea is a species with a wide distribution within Europe that was originally described on Symphytum officinale from Italy. Morphologically, the strains in this clade have conidiophores reduced to conidiogenous cells and narrower conidia (Fig. 40) than the in vivo description of R. calcea found in literature (Braun 1998), in which the conidiophores are small and sometimes deeply forked $[10-80 \times (2-)]$ 3 - 6(-7)µm]. and conidia are wider [(5-)] $8-24(-26.5) \times (2.5-)3-7(-8) \mu$ m]. Unfortunately, the herbarium specimen from which the culture was retrieved was not preserved which made it impossible to assess the morphological characters of this species on host tissue. The clade formed by these two strains is highly supported by the phylogenetic analysis (Fig. 2, clade 42). Strain CBS 299.49 (Fig. 2, clade 36) is also under the name *R. calcea* in the CBS database, but since this is sterile it will be treated as Ramularia sp. C. Therefore, the correct phylogenetic placement of this species remains unresolved until material from the type host and location is recollected. Ramularia calcea has been reported on Symphytum officinale in both Germany and the Netherlands, among other countries. The morphological characteristics of CBS 114442 are identical to CBS 102612 and 102613, therefore, until more collections become available, these strains will be treated as R. calcea here.

Ramularia carneola (Sacc.) Nannf., in Lundell & Nannf., Fungi Exs. Suec., Fasc. XXXIX–LX, Sched.: 25. 1950.

Basionym: Ovularia carneola Sacc., Fungi ital. Del., Tab. 975. 1881.

- = Ovularia duplex Sacc., Fungi ital. Del., Tab. 876. 1881.
- = Ramularia scrophulariae Fautery & Roum., Revue Mycol. (Toulouse): 81. 1891
- = R. nicolai Bubák, Sitzungsber. Königl. Böhm. Ges. Wiss. Prag: 19. 1903.
- = R. borghettiana C. Massal., Malpighia 25: 14. 1912.
- = R. nodosa Tho, Novosti Sist. Nizsh. Rast. 9: 204. 1972.

Description in vivo: See Braun (1998: 264).

Specimens examined: France, Rouen, on Scrophularia nodosa, Letendre, herb. Saccardo (holotype PAD). Netherlands, Utrecht Prov., Baarn, de Hooge Vuursche, leaf spot on Scrophularia nodosa, 22 Jun. 2000, G. Verkley, cultures CBS 108975–108978; Goedereede, Kwade Hoek nature reserve parking, leaf spot on Scrophularia nodosa, 13 Sep. 2001, G. Verkley, culture CBS 109847.

Substrate and distribution: On Scrophularia (Scrophulariaceae); Asia, Caucasus, Armenia, Europe, N. America.

Notes: Ramularia carneola is a pathogen of *Scrophularia* spp. that are commonly known as figworts. It was first described on *Scrophularia nodosa* from France (holotype in PAD). Although *R. carneola* has a broad geographical distribution, this is the first record for the Netherlands. The strains of this species cluster together in a clade highly supported by the BA and ML phylogenetic analyses (Fig. 2, clade 49, 1/100).

Ramularia cerastiicola (Crous) Videira & Crous, comb. nov. MycoBank MB816933.

Basionym: Mycosphaerella cerastiicola Crous, IMA Fungus 2: 55. 2011.

Specimen examined: Netherlands, Flevoland, on *Cerastium semidecandrum*, 2 May 2004, A. Aptroot (holotype CBS H-20549, culture ex-type CBS 115913 = CPC 11290).

Notes: When this species was initially described, both the ITS and LSU sequences placed it within the genus *Ramularia* but the cryptic nature of the asexual morph, with its septoria- to pseudocercosporella-like morphology, baffled the researchers (Crous *et al.* 2011). Based on all three phylogenetic analyses performed on the five-gene alignment, this species forms a single lineage (Fig. 2, clade 14) closely related to *Ramularia* stellariicola.

Ramularia chamaedryos (Lindr.) Gunnerb., Svensk Bot. Tidskr. 61: 135. 1967. Fig. 41.

Basionym: Ovularia chamaedryos Lindr., Acta Soc. Fauna Fl. Fenn. 23: 7. 1902.

- = ?*Ramularia veronicae* Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 361. 1869. (1870)
- ≡ Ovularia veronicae (Fuckel) Sacc., Fungi ital. Del., t. 974. 1881.
- = ?Ramularia beccabungae Fautrey, Revue Mycol. (Toulouse) 14: 10. 1892.

Mycelium consisting of hyaline, septate, branched, smooth, 1–2 µm diam hyphae. *Conidiophores* hyaline, thin-walled, smooth, erect, septate, straight, cylindrical-oblong, unbranched, $(24.5-)60-92(-230) \times 1.5-2(-3)$ µm or reduced to conidiogenous cells. *Conidiogenous cells* integrated in mycelium or terminal in conidiophores, cylindrical-oblong, geniculate-sinuous,



Fig. 40. Ramularia calcea (CBS 101613). A–I. Structures formed in culture. A, E, I. Conidia. B, F. Conidiophore reduced to conidiogenous cell. C, D, G, H. Conidiophore and conidia. Leaf spot symptoms on the host. Scale bars = 10 μ m.



Fig. 41. Ramularia chamaedryos (CBS 116577). A-G. Conidiophores, conidiogenous cells and conidia formed in culture. Scale bars = 10 µm.

(14–)20–26(–44) × 2–3 µm, with 1–4 apical conidiogenous loci, almost flat or protuberant, thickened, darkened and refractive. *Conidia* hyaline, thin-walled, smooth, aseptate, catenate, with hila thickened, darkened and refractive. *Ramoconidia* subcylindrical, clavate, ovoid, (9.5–)15–19(–31.5) × (3–) 3.5-4(-5) µm, with two apical hila. *Intercalary conidia* subcylindrical, fusoid, ovoid, (9–)11–13(–22) × (3–) 3.5-4(-4.5) µm, in branched chains of up to five conidia.

Terminal conidia obovoid, $(6.5-)8-9(-11) \times (3.5-)4(-5) \mu m$ (on SNA, CBS 116577).

Culture characteristics: On MEA, 8 mm diam, surface smooth, smoke-grey, with margins undulate, feathery and olivaceous grey, colony reverse olivaceous grey; on OA, 10 mm diam. Surface smooth, with fuffy aerial mycelium, light grey with olivaceous green patches, with margin irregular, with sparse

aerial mycelium, colony reverse iron-grey; on PDA, 9 mm diam, surface smooth, buff to smoke-grey, margins crenate, colony reverse olivaceous.

Description in vivo: See Braun (1998: 258).

Specimens examined: Latvia, Vidzeme, on Veronica chamaedrys, 1936, Smarods [neotype, designated in Braun (1998), JE]. Sweden, Uppland, Uppsala Näs parish, Vängelstra, on Veronica chamaedrys, 29 Sep. 1986, E. Gunnerbeck, culture CBS 116577. New Zealand, Auckland, St. Johns, on Veronica persica, unknown collector and date, isol. C.F. Hill, Oct. 2005, dep. C.F. Hill, culture CBS 118794. South Korea, Samcheok, on Veronica didyma, 8 May 2003, H.D. Shin, KUS-F19441, culture CBS 113307; Taean, on Veronica persica, 17 Apr. 2007, H.D. Shin & M.J. Park, KUS-F22542, culture CBS 131773 = KACC 42885. Sweden, Uppland, Knivsta, on Veronica anagallisaquatica, 22 Sep. 1989, E. Gunnerbeck, culture CBS 114731.

Substrate and distribution: On Veronica (Scrophulariaceae); Europe, Korea, New Zealand.

Notes: The description of CBS 116577 fits the morphology of R. chamaedryos. Ramularia veronicae and R. beccabungae are similar, but differ in vivo in having septate conidia. Ramularia chamaedryos is only known from Veronica chamaedryos (Scrophulariaceae) and was originally described from Finland [type not preserved, neotype designated in Braun (1998), in JE]. Ramularia veronicae is known from several Veronica spp. worldwide with the exception of Australia and Antartica. Ramularia beccabungae has been described from several Veronica spp. in Europe and Asia. Some Ramularia species have been shown to be plurivorous while others can be seen as host specific. Phylogeny based on five partial gene sequences places sequences retrieved from Ramularia on Veronica chamaedrys (as ?R. chamaedryos), V. persica (as ?R. veronicae, but not the type host) and V. anagallis-aquatica (as ?R. beccabungae) in the same clade (Fig. 2, clade 61, 1/100/100), suggesting that a single species is involved. However, this assumption is still vague and unproven since the description of the sporulation in vitro is only based on a culture of R. chamaedryos on Veronica chamaedrys (Fig. 41). Sporulating cultures of R. veronicae and R. beccabungae based on isolations from the type hosts are necessary for comparison and to evaluate and explain possible differences in the conidial septation between in vivo and in vitro material. Therefore, a final taxonomic conclusion is not yet possible.

Ramularia chelidonii (Jacz.) Karak., Fungi Imperfecti Parasitici. I. Hyphomycetes: 123. 1937.

Basionym: Didymaria chelidonii Jacz., Fungi Ross. Exs. 349. 1899.

= *Ramularia hylomeconis* Naumov, Bull. Trimestriel Soc. Mycol. France 30: 80. 1914.

Description in vivo: See Braun (1998: 197).

Specimens examined: Russia, Far East, Amur, near Radde Station, on *Hylomecon japonica* (≡ *Chelidonium japonicum*), 28 May/9 Jun. 1895, Komarov [Jacz. et al., Fungi Ross. Exs. 349; **lectotype**, designated in Braun (1998), LE 40741]. **South Korea**, Hongcheon, on *Hylomecon vernalis*, 6 Jun. 2005, H.D. Shin, KUS-F21198, cultures CPC 12208, CPC 12209; Yangpyeong, on *Hylomecon vernalis*, 4 Jun. 2003, H.D. Shin, KUS-F19550, culture CBS 113317.

Substrate and distribution: On Chelidonium and Hylomecon (Papaveraceae); Asia, Caucasus, Europe (Ukraine).

Notes: Ramularia chelidonii was originally described on *Chelidonium japonicum* from Russia (lectotype in LE). The strains of *R. chelidonii* used in this study cluster in a highly supported clade (Fig. 2, clade 71, 1/100/100). This is the first report of this species from South Korea and on *Hylomecon*.

Ramularia coleosporii Sacc., Michelia 2(6): 170. 1880.

≡ Cylindrosporium coleosporii (Sacc.) J. Schröt., Krypt.-Fl. Schlesien, Pilze, 3.2(4): 493. 1897.

= Ramularia clerodendri Sawada, Rep. Dept. Agric. Gov. Res. Inst. Formosa 87: 71. 1944, nom. inval.

= R. fagarae Sawada, Rep. Dept. Agric. Gov. Res. Inst. Formosa 87: 72. 1944, nom. inval.

Description in vivo: See Braun (1998: 39).

Specimens examined: France, Lyon, on Coleosporium melampyri on Melampyrum nemorosum, Sep. 1879, Therry [Thüm., Mycoth. Univ. 1566; lectotype, designated in Braun (1998), HAL]. South Korea, Hongcheon, on Coleosporium horianum on Codonopsis lanceolata, 9 Oct. 2007, H.D. Shin & M.J. Park, culture CBS 131757 = KACC 43185; same location, date and collectors, on Coleosporium eupatorii on Eupatorium lindlevanum, culture CBS 131764 = KACC 43182; Incheon, on Coleosporium sp. on Solidago gigantea, 24 Sep. 2009, H.D. Shin & M.J. Park, culture CBS 131762 = KACC 44860; Inje, on Coleosporium asterum on Aster pilosus, 3 Oct. 2008, H.D. Shin & M.J. Park, culture CBS 131755 = KACC 43977; Jinju, on Coleosporium horianum on Codonopsis lanceolata, 13 Oct. 2008, H.D. Shin & M.J. Park, culture CBS 131759 = KACC 44073; Jecheon, on Coleosporium clematidis-apiifoliae on Clematis apiifolia, 19 Oct. 2007, H.D. Shin & M.J. Park, culture CBS 131756 = KACC 43200; Namyangju, on Coleosporium perillae on Perilla frutescens var. japonica, 21 Aug. 2006, H.D. Shin & M.J. Park, culture CBS 131753 = KACC 42483; Pocheon, on Coleosporium asterum on Aster pilosus, 22 Sep. 2006, H.D. Shin & M.J. Park, culture CBS 131765 = KACC 42635; Pocheon, on Coleosporium eupatorii on Eupatorium japonicum, 2 Sep. 2003, H.D. Shin, culture CPC 10669; Pocheon, on Coleosporium eupatorii on Eupatorium japonicum, 20 Aug. 2006, H.D. Shin & M.J. Park, culture CBS 131763 = KACC 42484; Pocheon, on Aster ageratoides, 23 Oct. 2002, H.D. Shin, culture CPC 10085; Pyeongchang, on Coleosporium clematidis-apiifoliae on Clematis apiifolia, 20 Sep. 2003, H.D. Shin, cultures CPC 10731-10733; Pyeongchang, on Pileolaria shiraiana on Rhus trichocarpa, 22 Sep. 2008, H.D. Shin & M.J. Park, culture CBS 131767 = KACC 44053; Pyeongchang, on Coleosporium eupatorii on Eupatorium lindleyanum, 20 Sep. 2003, H.D. Shin, cultures CPC 10746-10748; Pyeongchang, on Coleosporium cacaliae on Syneilesis palmata, 14 Sep. 2009, H.D. Shin & M.J. Park, culture CBS 131758 = KACC 44854; same location, date and collectors, on Coleosporium saussureae on Saussurea pulchella, culture CBS 131761 = KACC 44855: Seoul. on Coleosporium clerodendri on Clerodendron trichotomum. 2 Sep. 2007, H.D. Shin & M.J. Park, culture CBS 131766 = KACC 43058; Suwon, on Coleosporium asterum on Aster pilosus, 1 Oct. 2007, H.D. Shin & M.J. Park, culture CBS 131754 = KACC 43177; Ulleung, on Coleosporium horianum on Codonopsis lanceolata, 21 Oct. 2008, H.D. Shin & M.J. Park, culture CBS 131760 = KACC 44081; Pocheon, on Coleosporium eupatorii on Eupatorium japonicum, 2 Sep. 2003, H.D. Shin, culture CPC 10653; Pyeongchang, on Coleosporium phellodendri on Phellodendron amurense, 4 Sep. 2003, H.D. Shin, cultures CPC 10672, CPC 10673; Hoengseong, on Coleosporium plectranthi on Plectranthus japonicus, 21 Aug. 2004, H.D. Shin, culture CPC 11516.

Substrate and distribution: Mycophylic on Chrysomyxa, Coleosporium (Coleosporiaceae, Pucciniales), Pileolaria (Pileolariaceae, Pucciniales); Asia, Europe, N. America (USA), West Indies (Puerto Rico).

Notes: Only six species of *Ramularia* have been classified as mycophylic (*R. butomi*, *R. coleosporii*, *R. cylindriopsis*, *R. dichosciadii*, *R. uredinearum*, and *R. uredines*). Kirulis (1942) stated that *R. coleosporii* does not parasitise *Coleosporium* directly but that it is confined to the weakened tissue around the sori and that it is unrelated to other foliicolous species on the same hosts. Braun (1998) hypothesised that *R. coleosporii* could be a

separate species or a collective species composed of various races since on some hosts there are morphologically similar phytopathogenic species and in other hosts this species was morphologically distinguishable from other phytopathogenic species. Ramularia coleosporii was originally described parasitising Coleosporium melampyri on Melampyrum nemorosum from France (lectotype in HAL). All the strains of R. coleosporii used in this study cluster together in the same clade (Fig. 2, clade 66, 1/ 100/100) and are clearly separated from the other Ramularia spp., supporting the hypothesis that this is indeed a unique species. They were, however, all collected from South Korea, and a few isolates from other countries should be analysed to determine if it is a global species. It was the first time that this species was observed in association with the host Pileoaria shiraiana. To determine if R. coleosporii is truly mycophylic more studies need to be done to understand the biology and ecology of this species.

Ramularia collo-cygni B. Sutton & J.M. Waller, Trans. Brit. Mycol. Soc. 90: 57. 1988.

≡ Ophiocladium hordei Cav., Z. Pflanzenkr. 3: 26. 1893.

≡ Ovularia hordei (Cav.) R. Sprague, Mycologia 38: 63. 1946.

≡ *Ramularia hordeicola* U. Braun, Int. J. Mycol. Lichenol. 3 (2–3): 281. 1988.

For additional synonyms see Braun (1998) or MycoBank.

Description in vivo: See Braun (1998: 202).

Specimens examined: Austria, Reichersberg am Inn, on Hordeum vulgare, unknown date, Züchtungsfirma Saatbau Linz (neotype designated here: CBS H-22641, MBT371836, culture ex-neotype CBS 101180). Germany, Bavaria, Aspachhof, Uffenheim, on Hordeum vulgare, 1998, E. Sachs, CBS H-17711, cultures CBS 101181, CBS 101182. Norway, Central Norway, on Hordeum vulgare, unknown date, S. Salamati, cultures CBS 119439 = CPC 12693, CBS 119440 = CPC 12692, CBS 119441 = CPC 12690, CBS 119442 = CPC 12688.

Substrate and distribution: On Bromus, Festuca, Glyceria, Leucopoa, Lolium, Phalaris, and Triticale (Poaceae) and Cannabis (Cannabaceae); Europe, N. America (Canada, Mexico, USA), S. America (Chile, Colombia), Asia (Japan, Russia), Australia and New Zealand.

Notes: Ramularia collo-cygni was originally isolated from the host Hordeum vulgare collected in Italy, but the type specimen is presumed missing (Braun 1998). The strains used in this study cluster together in a highly supported clade (Fig. 2, clade 38, 1/100/100) and a strain isolated from the same host that was collected in Austria is designated as neotype. Ramularia collo-cygni is the causal agent of Ramularia leaf spot disease on barley, a disease that has been known for more than 100 years but of which the importance has only been recognised in the last 30 years. The disease has been reported worldwide and on various cereals and grasses. On barley, the symptoms appear late in the season as reddish brown necrotic spots that lead to premature leaf senescence and subsequent grain yield loss. Environmental conditions such as temperature and humidity are key factors in activating the production of rubellin, a non-host specific toxin, by the fungus. The development of molecular diagnostic tools has improved the detection of the pathogen in plant tissue and seeds before symptom development. Vertical transmission of the fungus in barley has been confirmed (Havis et al. 2015) and further evidence points to the existence of an endophytic life-style that shifts towards necrotrophy depending on plant health. Population studies using simple-sequence repeat markers and sequence analyses of housekeeping genes revealed a high genetic diversity in R. collo-

cygni isolates (Piotrowska 2014, Havis et al. 2015). A high level of genotypic diversity is usually indicative of sexual recombination, but the sexual morph of R. collo-cygni is yet to be identified. Control of the disease can be accomplished by timely fungicide application between the Zadoks growth stages (ZGS) 30 and ZGS 49, well before the symptoms develop that usually happens at stage ZGS 70. Ramularia collo-cygni has lost sensitivity to strobilurin-based fungicides due to the development of the G143A point mutation in the cytochrome b gene, which is now prevalent in most populations. The introduction of a new generation of SDHI fungicide has brought some leverage in disease control, but the rapid evolutionary potential displayed by this fungus suggests it can adapt to new control strategies quickly. Despite all the research performed so far several questions still need to be addressed to fully understand the biology of this species in order to develop appropriate control measures (Havis et al. 2015). Ramularia collocygni also causes Tan Leaf Spot on turfgrass. Turfgrasses are used to control water and wind erosion of soil, and are used as ornamental plants and as ground cover of playing fields in many sports. The disease has been reported from Australia, Japan, New Zealand and North America (Smiley et al. 1983).

Ramularia coryli Chevassut, in Braun, Monograph Cercosporella, Ramularia Allied Genera (Phytopath. Hyphom.) 2: 140. 1998.

Description in vivo: See Braun (1998: 140).

Specimen examined: Netherlands, Utrecht, Rhijnauwen, on dead leaves of Corylus avellana, G. Verkley, 25 Apr. 2005, culture CBS 117800 = CPC 12090.

Substrate and distribution: On Corylus avellana; Europe (France, Netherlands).

Notes: Ramularia coryli was originally described on *Coryllus avellana* from France, and is currently the only *Ramularia* species known to infect this host (Braun 1998). The strain used in this study forms a single lineage (Fig. 2, clade 83), and is positioned on a very long branch, which supports this species as unique. Unfortunately, this strain proved to be sterile, and thus we could not compare it morphologically. This clade is for now maintained as representative of *R. coryli* until fresh material is collected and more information becomes available.

Ramularia cupulariae Pass., Hedwigia 15: 107. 1876.

- = Ovularia inulae Sacc., Fungi ital., Tab. 971. 1881.
 - ≡ *Ramularia inulae* (Sacc.) Höhn., in Kab. & Bub., Fungi Imperf. Exs. no. 389. 1906.
- = Ovularia inulae f. major Brunaud, Actes Soc. Linn. Bordeaux 1890: 46. 1890.
- = Ramularia inulae-britannicae Allesch., in Jaap, Abh. Bot. Ver. Prov. Brandenb. 47: 98. 1905.
- = R. codonocephali Annaliev, Novosti Sist. Nizsh. Rast. 15: 74. 1978.

Description in vivo: See Braun (1998: 81).

Specimens examined: Former Czechoslovakia, on *Inula* sp., unknown date, L. Marvanová, culture CBS 235.73. **Italy**, Vigheffio near Parma, Oct. 1874, Passerini [Rahenh., Fungi Eur. Exs. 2065; **lectotype**, designated in Braun (1998), HAL].

Substrate and distribution: On Carpesium, Codonocephalum, Inula, and Pulicaria (Asteraceae); Asia, Caucasus, Europe.

Notes: Two varieties are known for this species, *R. cupulariae* var. *cupulariae* (lectotype on *Inula viscosa*, Italy, in HAL) and

R. cupulariae var. *britannicae* (holotype on *Inula britannica*, Germany, in HBG). Specimens of var. *britannicae* have very long and filiform conidiophores ($20-100 \times 2.5-5 \mu m$) when compared to var. *cupulariae* ($5-30 \times 2-5 \mu m$). This species has been reported from four different host genera within the family *Asteraceae* (*Carpesium, Codonocephalum, Inula* and *Pulicaria*) from Asia, Caucasus and Europe. The strain used in this study forms a single lineage (Fig. 2, clade 6).

Ramularia cyclaminicola Trel., Trans. Illinois Acad. Sci. 9: 145. 1916.

= *Cladosporium cyclaminis* Massey & Tilford, Phytopathology 22(1): 19. 1932.

Description in vivo: See Braun (1998: 226).

Specimen examined: USA, on stunted Cyclamen persicum, unknown collector and date, isolated and deposited by K.F. Baker, 1951, culture CBS 399.51; Illinois, Urbana, University, north greenhouse, 14 Jan. 1914, Trelease (holotype ILL 14246).

Substrate and distribution: On Cyclamen (Primulaceae); N. America.

Notes: Ramularia cyclaminicola causes both a leaf spot disease and a stunt or wilt through systemic invasion of vascular tissue in Cyclamen persicum. Cyclamen plants, grown for their flowers, were imported into America from Germany and the Netherlands. No disease was reported from these countries and it is likely that R. cyclaminicola is native to North America, perhaps infecting other members of the Primulaceae (Baker et al. 1950). The disease may be confused with a physiological problem or with Fusarium wilt or Phialophora wilt, and was more common in the first half of the 20th century than it is today (Daughtrey et al. 1995). Ramularia cyclaminicola was originally described on Cyclamen persicum from Illinois, USA (holotype in ILL). In the present study, Ramularia cyclaminicola is represented by a single lineage (Fig. 2, clade 18). Strain CBS 399.51 was isolated by Baker and deposited at CBS in 1951, which means this is likely an authentic strain of this species.

Ramularia cynarae Sacc., Michelia 1: 536. 1879.

= R. cardui P. Karst, Meddeland. Soc. Fauna Fl. Fenn. 14: 109. 1888.

- = *R. cirsii* Allesch., Ber. Bayr. Bot. Ges. 2: 18. 1892.
- = R. jurineae Hollós, Ann. Hist.-Nat. Mus. Natl. Hung. 5: 467. 1907.
- = *R. carthami* Zaprom., Bolez. Rast. 15(3): 142. 1926, and Mater. Mikofl. Sredn. Azii I: 32. 1926.

For additional synonyms see Braun (1998) or MycoBank.

Description in vivo: See Braun (1998: 101).

Specimens examined: France, Saintes, Brunaud, herb. Saccardo (holotype PAD). Netherlands, Gelderland Prov., Hoge Veluwe Nat. Park, on *Carduus* sp., 2012, S.I.R. Videira culture CPC 25897; Nijmegen, on *Carex acutiformis*, Jul. 2012, S.I.R. Videira, culture CPC 25896. Sweden, Uppland, Haga, Årtopet, on *Cirsium arvense*, 4 Oct. 1989, E. Gunnerbeck, culture CBS 114728; Uppland, Dalby, on leaves of *Carduus crispus*, 29 Aug. 1989, E. Gunnerbeck, culture CBS 114729. USA, California, Monterey County, Castrovill, on leaves of *Cynara cardunculus*, 10 Aug. 2010, S.T. Koike (epitype CBS H-20514, culture ex-epitype CBS 128912 = CPC 18426); *idem*. CPC 18427; California Santa Clara County, Morgan Hill, on leaves of *Carthamus tinctorius*, 19 Oct. 2010, S.T. Koike, cultures CBS 128779 = CPC 18725, CPC 18726.

Substrate and distribution: On Carduus, Carthamus, Cirsium, Cousinia, Cynara, Echinops, Jurinea, Onopordum, Saussurea, and Silybum (Asteraceae); worldwide.

Notes: Ramularia cynarae was originally described on Cynara scolymus from France (holotype in PAD), but the species has a wide host range within the Asteraceae (Braun 1998). This species was epitypified by Koike et al. (2011), who reported the pathogen R. cynarae as the causal agent of leaf spot symptoms on Carthamus tinctorius (spineless safflower) in California, USA. Spineless safflower is grown as commercial cut flower crops in coastal California. The isolates collected from both Cynara and Carthamus were identical in morphology and ITS sequences (GenBank HQ728117, HQ728118). This supports the hypothesis that R. cynarae has a broad host range on Asteraceae hosts instead of being a species complex. Ramularia carthami was previously reported from agronomic safflower grown for oil production in Northern California (Hostert et al. 2006). The ITS sequence of this isolate (DQ466083) is 100 % similar to the ITS sequence of the R. cynarae ex-epitype culture (CBS 128912), indicating that these are likely the same species. In this study, strains of R. cynarae clustered in a highly supported clade (Fig. 2, clade 9, 1/100/100). Some internal variation was observed and the transition from concordance to conflict determined the phylogenetic limit of this species (Taylor et al. 2000). This intraspecific variation may be the reason that this species is able to colonise a broad host range or indicate that it is undergoing sexual reproduction, as can be observed with R. vizellae (Videira et al. 2015b).

Ramularia deusta (Fuckel) Karak. var. *deusta*, Fungi Imperfecti Parasitici. I. Hyphomycetes: 116. 1937.

Basionym: Scolicotrichum deustum Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 357. 1870

Description in vivo: See Braun (1998: 156).

Specimens examined: Germany, near Eberbach, on Lathyrus linifolius [Fuckel, Fungi Rhen. Exs. 2206; lectotype, designated in Braun (1998), HAL]. Guadeloupe, on Lathyrus latifolius, unknown collector and date, dep. K.F. Baker & W.C. Snyder, Oct. 1950, culture CBS 473.50.

Host and distribution: On Lathyrus (Fabaceae); Asia, Europe, N. and S. America, New Zealand.

Notes: Ramularia deusta is distributed worldwide in temperate and subtropical climates on nine species of Lathyrus, including the cultivated sweet pea (L. odoratus) and perennial pea (L. latifolius). The first pathological study was conducted in England on sweet pea (Dowson 1924), and since then it has been reported from several countries around the world. The economical impact of this disease was considered minor on this crop (Baker et al. 1950). Two physiological forms were recognised by Baker et al. (1950) from collections in California, R. deusta f. odorati as pathogenic on the host Lathyrus odoratus, and R. deusta f. latifolii as pathogenic on the host L. latifolius. Braun (1998) divided Ramularia deusta into three varieties. Ramularia deusta var. alba (on Lathyrus odoratus, Denmark, holotype in B) has whitish caespituli while R. deusta var. deusta (on Lathyrus linifolius, Germany, lectotype in HAL) has yellowish ochraceous or pink to reddish caespituli. Ramularia deusta var. lathyri-maritimi (on Lathyrus maritimus, Sweden, holotype in BPI) has longer and mostly septate conidia (15-30 × 2.5-5 µm), while R. deusta var. deusta has shorter and mostly aseptate conidia, (5-) 8-20(-23) × 2.5-5 µm. Although R. deusta f. odorati was synonymised under R. deusta var. alba (Braun 1998), R. deusta f.

latifolii does not appear as synonym of any of the other varieties and should, therefore, be considered as a synonym of *R. deusta* var. *deusta*. The strain used in this study (CBS 473,50; Fig. 2, clade 62) was previously identified as *R. deusta* f. *latifolii* and was deposited by Baker and Snyder in 1950, which makes it an authentic strain and a reliable representative of the species *Ramularia deusta* var. *deusta* until fresh material from the same location and host as the type material is recollected.

Ramularia didyma Unger var. didyma, Exanth. Pfl.: 169. 1833.

- ≡ Didymaria ungeri Corda, Icon. fung. (Prague) 1: 32. 1837.
- ≡ D. didyma (Unger) Pond, Amer. Naturalist 23: 163. 1889.
- = Fusisporium aequivocum Ces., Bot. Zeitung (Berlin) 15: 43. 1857.
- ≡ Ramularia aequivoca (Ces.) Sacc., Fungi ital. Del., Tab.: 994. 1881.= Ramularia ovularioides H.C. Greene, Trans. Wisconsin Acad. Sci. 38: 246.
- 1946 (1947).

For additional synonyms see Braun (1998).

Description in vivo: See Braun (1998: 239).

Specimens examined: Luxembourg, Kantenbach, on leaf spot on *Ranunculus repens*, unknown collector and date, isol. L. Marvanová, 25 Sep. 1967, dep. L. Marvanová, Oct. 1967, culture CBS 431.67. Sweden, Uppland, Haga par., Årtopet, on *Ranunculus repens*, 23 Oct. 1988, E. Gunnerbeck, culture CBS 114299 = UPSC 2746. UK, South West England, Exeter, on leaf spot from *Ranunculus repens*, unknown collector and date, isol. S.A.J. Tarr, 30 Apr. 1967, dep. S.A.J. Tarr, Sep. 1967, culture CBS 420.67.

Substrate and distribution: On Anemone and Ranunculus (Ranunculaceae); Asia, Caucasus, Europe, N. and S. America, New Zealand.

Notes: There are three varieties of this species, namely R. didvma var. didvma [neotype on Ranunculus nemorosus. Switzerland, designated in von Arx (1983), in ZT], R. didyma var. exigua (holotype on Ranunculus uncinatus, USA, Oregon, WSP) and R. didyma var. pulsatillae [neotype on Pulsatilla pratensis, Denmark, designated in Braun (1998), in Cl. While R. didyma var. didyma conidiophores emerge through stromata and form catenate conidia, R. didyma var. exigua exhibits conidiophores erumpent through the cuticle, and R. didyma var. pulsatillae frequently forms solitary conidia. Ramularia didyma var. didyma has a wider distribution than the other two varieties (Braun 1998). Ramularia didyma was identified as the causal agent of leaf spotting symptoms on Persian buttercups (Ranunculus asiaticus) in USA. California. These are colourful, cool-season perennials or annuals grown for the flowers and bulbs. Introduction of this pathogen into commercial production fields could cause significant economic loss (Blomquist & Warfield 2011). The ITS sequence (GenBank HQ442297) generated at that time is 100 % similar to the ITS sequence of the strains in this clade. Based on phylogenetic analyses in this study, this species forms a highly supported clade (Fig. 2, clade 72, 1/100/100). The morphology could not be observed since the cultures were sterile and no herbarium materials corresponding to the strains were preserved. This clade is tentatively maintained as a representative of this species until fresh material from the type host and location is recollected.

Ramularia diervillae Peck, Rep. (Annual) New York State Mus. Nat. Hist. 38: 99. 1885. Fig. 42.

= Ramularia umbrosa Davis, Trans. Brit. Mycol. Soc. 19: 714. 1919.

Mycelium consisting of hyaline, septate, branched, smooth, 1-2 µm diam hyphae. Conidiophores hyaline, thin-walled, smooth, erect, 1-2-septate, cylindrical-oblong, straight to sinuous, unbranched, $(10-)26.5-35(-54) \times (1-)1.5-2(-3) \mu m$, or reduced to conidiogenous cells, terminal on conidiophores or intermediate in the mycelium, cylindrical-oblong, narrower at the top, $(5.5-)14.5-19(-29) \times 1.5-2(-3) \mu m$, with one or two conidiogenous loci almost flat to protuberant; conidiogenous loci thickened, darkened and refractive. Conidia hyaline, thin-walled, smooth, catenate, with hila thickened, darkened and refractive. Ramoconidia cylindrical-oblong, sometimes sinuous or curved, $(9.5-)14-17(-26.5) \times (1.5-)2-2.5(-3) \mu m, 0-1$ -septate, with 2 apical hila. Intercalary conidia cylindrical-oblong, fusoid, sometimes curved, aseptate, $(8-)11-13(-19.5) \times (1.5-)2(-3) \mu m$, in branched chains of up to seven conidia. Terminal conidia cylindrical-oblong to obovoid, aseptate, $(5-)7-8(-11) \times (1.5-)$ 2(-2.5) µm. Sporulating on SNA.

Culture characteristics: On MEA, 11 mm diam, surface raised, folded, with sparse aerial mycelium, smooth, rosy buff, with margins crenate and convex, colony reverse cinnamon with olivaceous grey patches; on OA, 9 mm diam, surface smooth, low convex, white with pale olivaceous grey tinge, with margins undulate, colony reverse fawn; on PDA, 10 mm diam, surface low convex, pale olivaceous grey, smooth, producing tiny transparent exudate droplets, with margins lobate, colony reverse olivaceous grey with a buff margin.

Description in vivo: See Braun (1998: 130).

Specimens examined: Canada, Quebec, La Peche, Lac Bernard, on Diervilla Ionicera, 5 Jul. 2009, K.A. Seifert, cultures CPC 16859, CPC 16860, CPC 16863, CPC 16864. USA, New York, Adirondack Mt., on Diervilla Ionicera, Peck (holotype NYS).

Substrate and distribution: On Diervilla (Caprifoliaceae); N. America (Canada, USA).

Notes: Ramularia diervilla was originally described on Diervilla Ionicera from New York, USA (holotype in NYS), and is the only species of Ramularia known to infect this host. Although it has been previously reported from North America, this is the first report from Canada. This species formed a highly supported clade (Fig. 2, clade 41, 1/100/100). Braun (1998) reported that when associated with its host, R. diervilla produces simple, straight to geniculate-sinuous conidiophores. 5-25 × 1.5-3.5 µm, and catenate, cylindrical-fusiform conidia, $5-25(-30) \times 1.5-4 \mu m$. The conidiophores described in culture are longer and the conidia are slightly narrower than what is described in vivo (Fig. 42). In the herbarium specimen corresponding to the isolate CPC 16859, the conidiophores are shorter than in culture [(25-)28-30(-33) × (1.5-)2(-3) µm] but more similar to the description provided by Braun (1998), while the conidial dimensions $[(4-)8-9(-12) \times (1.5-)2(-3) \mu m]$ are smaller than in culture, but still narrower than in Braun (1998). The cultures and specimens represented in this clade are considered here as representative material of the species until collections from the type location are examined.

Ramularia digitalis-ambiguae Arx, Sydowia 3: 93. 1949.

Mycosphaerella digitalis-ambiguae Arx, Sydowia 3: 92. 1949.
 Asteromella digitalis-ambiguae Arx, Sydowia 3: 94. 1949.



Fig. 42. Ramularia diervillae (CPC 16859). A–C. Observations from herbarium material. D–I. Structures formed in culture. A. Leaf spot symptoms on the host. B, E. Conidiophores. C, D. Conidia. F–I. Conidiophores and conidia. Scale bars = 10 µm.

Specimens examined: Luxembourg, Kantenbach, on leaf spot on *Digitalis purpurea*, unknown collector and date, isol. L. Marvanová, 25 Sep. 1967, dep. L. Marvanová, Oct. 1967, culture CBS 434.67. Netherlands, on *Digitalis* sp., unknown collector and date, isol. F. Hespe, dep. Jul. 1937, culture ex-type CBS 297.37.

Notes: Although these isolates were originally identified as R. variabilis, the latter species clusters in clade 50 (Fig. 2; 1/100/ 100), in contrast to the Digitalis isolates (Fig. 2, clade 58, 1/100/100), which clearly represents a different species. Since collections of Ramularia on Digitalis and Verbascum spp. are in vivo morphologically barely distinguishable, Braun (1998) assigned them to a single species, R. variabilis, and reduced Mycosphaerella digitalisambiguae and Ramularia digitalis-ambiguae to synonym under R. variabilis. Although not yet phylogenetically proven, R. digitalisambiguae is available for the Digitalis Ramularia and can at least tentatively be used for this taxon until sporulating cultures retrieved from Ramularia lesions on Digitalis ambigua and D. purpurea are available for comparison. The connection of Mycosphaerella digitalis-ambiguae and the two syn-asexual morphs, Ramularia digitalis-ambiguae and Asteromella digitalis-ambiguae, has only been observed in vivo (von Arx 1949), but not vet verified in vitro or by means of molecular methods. Aptroot (2006) referred to the strong morphological similarity between M. digitalis-ambiguae and the saprobic M. subradians (Fr. : Fr.) J. Schröt. Mycosphaerella digitalis (Ferraris) Tomilin (≡ Sphaerella digitalis Ferraris; Ferraris 1902: 451, and plate X, fig. II), on dry stems of Digitalis lutea, described from North Italy, is quite distinct from *M. digitalis-ambiguae*, differing in having much larger asci, 60 × 20-21 µm, and longer, wider ascospores, 18–10 × 5–6 µm without constrictions at the septa (vs. asci 32-42 × 7-9 µm, ascospores 11-15 × 3.5-4.5 µm, constricted at the septa in M. digitalis-ambiguae).

Ramularia endophylla Verkley & U. Braun, Mycol. Res. 108: 1276. 2004.

= Sphaeria punctiformis Pers., Ann. Bot. (Usteri) 11: 26. 1794, non Ramularia punctiformis Sacc., 1904.

≣ Mycosphaerella punctiformis (Pers.) Starbäck, Bih. Kongl. Svenska Vetensk.-Akad. Handl., Afd. 3, 15(no. 9): 163. 1889.
 For additional synonyms see Verkley *et al.* (2004).

Specimens examined: Netherlands, Utrecht Prov., Baarn, Groeneveld, on dead leaves of *Castanea sativa*, 23 Feb. 1999, A. Aptroot, culture CBS 101680; De Stompert, Soest, on fallen leaves of *Quercus robur*, G. Verkley, culture CBS 113871; same location, on dead fallen leaves of *Quercus robur*, Apr. 2003, G. Verkley (holotype CBS H-7949, culture ex-epitype CBS 113265, previously *Mycosphaerella punctiformis*); same location, on green leaf (endophytic) of *Quercus robur*, unknown collector and date, isol. G. Verkley, Aug. 2002, CBS 115302, CBS 115303; same location, on living leaves (endophytic) of *Quercus robur*, G. Verkley, CBS 113869.

Substrate and distribution: On Quercus and Castanea (Fagaceae); Europe (Belgium, Netherlands), Asia (South Korea).

Notes: See Verkley *et al.* (2004) and Videira *et al.* (2015b). The phylogenetic analyses provide high support for this species clade (Fig. 2, clade 87, 1/100/100). The host range and distribution of this species is insufficiently known and only those of existing strains were considered above.

Ramularia eucalypti Crous, Fungal Diversity 26: 174. 2007.

Specimens examined: Australia, Queensland, Cairns, Kuranda, Karoomba River Walk, on leaves of *Eucalyptus* sp., 19 Aug. 2006, P.W. Crous, culture CBS 120728 = CPC 13304. Italy, Norcia, on *Corymbia grandifolia*, 10 May 2006, W. Gams (holotype CBS H-19832, ex-type culture CBS 120726 = CPC 13043). Netherlands, Gelderland, Wageningen, *Phragmites* sp., 19 Feb. 2011, P.W. Crous, culture CPC 19188.

Substrate and distribution: On Carex (Cyperaceae), Corymbia and Eucalyptus (Myrtaceae), Geranium (Geraniaceae), Malus (Rosaceae), Phragmites (Poaceae), and Pinus spp. (Pinaceae); Australia and Europe. *Notes*: See Crous *et al.* (2007), Videira *et al.* (2015a). The phylogenetic analyses provide high support for this species clade (Fig. 2, clade 31, 1/100/100).

Ramularia euonymicola Videira, H.D. Shin, U. Braun & Crous, **sp. nov.** MycoBank MB816848. Fig. 43.

Etymology: Named after the host genus from which it was isolated, *Euonymus* (inhabitant of *Euonymus*).

In planta: Leaf spots subcircular to irregular, white to ochraceous. Caespituli emerging through stomata, hyaline to buff. Conidiophores hyaline, thin-walled, slightly verruculose, erect, fasciculate, septate, cylindrical-oblong, straight to sinuous, unbranched, $(31-)48.5-56(-73) \times (2.5-)3-3.5(-4.5) \ \mum.$ Conidiogenous cells hyaline, slightly verruculose, terminal or intermediate in the conidiophore, cylindrical-oblong or geniculate-sinuous, $(8-)13-16(-27) \times 2-3(-4.5) \ \mum$, with one or two conidiogenous loci almost flat to protuberant; conidiogenous loci thickened, darkened and refractive. Conidia hyaline, thin-walled, slightly verruculose, solitary or in short chains, rarely branched, cylindrical-oblong to obovate, (1-)3-4-septate, $(20.5-)30-35.5(-51) \times (3-)3.5-4(-5) \ \mum$ with hila thickened, darkened and refractive.

Specimen examined: South Korea, Hongcheon, on *Euonymus alatus*, 16 May 2003, H.D. Shin, (holotype KUS-F19467, isotypes HAL 1869 F and CBS H-22520, culture ex-type CBS 113308).

Substrate and distribution: On Euonymus alatus (Celastraceae); Asia (South Korea).

Notes: Presently only *Ramularia celastri* has been described from *Euonymus alatus* (USA). It was described as having simple and straight to geniculate-sinuous conidiophores measuring $10-40(-60) \times 1.5-4.5(-5.5)$ µm, and catenate conidia that are fusiform to subcylindrical, 0-2(-3)-septate, $8-35 \times 2-4.5$ µm (Braun 1998). *Ramularia euonymicola* was collected in South Korea and differs from *R. celastri* by producing slightly longer conidiophores and much longer conidia that are often 3–4septate (Fig. 43). This species is represented by a single lineage in the phylogenetic analyses (Fig. 2, clade 73).

Ramularia gaultheriae Videira & Crous, **sp. nov.** MycoBank MB817158. Fig. 44.

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

Mycelium hyaline, septate, branched. Conidiophores and conidiogenous cells scarce and insufficient for complete description. *Conidia* hyaline, smooth to slightly verruculose, catenate, consistently aseptate, ellipsoid-ovoid, subcylindrical, obovoid $(4-)5.5-6.5(-11) \times (1.5-)2-2.5(-3.5) \ \mu m.$

Sterile in culture/*in vitro. Ramularia gaultheriae* (Fig. 2, clade 88), differs from its closest phylogenetic neighbour, *R. endophylla* (Fig. 2, clade 87), by unique allelles in five loci based on alignments of the separate loci deposited in TreeBASE as Study S19315: *rpb2* positions 3(C), 15(C), 24(G), 33(C), 48(T), 69(C), 78(C), 87(T), 96(T), 99(C), 102(A), 108(G), 138(T), 157(T), 195(C), 196(C), 198(C), 204(C), 219(T), 234(C), 240(A), 249(C),

252(T), 261(A), 291(T), 297(G), 318(A), 324(T), 330(A), 333(C), 336(A), 339(A), 342(T), 345(C), 346(C), 366(C), 369(T), 372(A), 393(A), 402(T), 409(C), 420(C), 429(T), 453(A), 468(C), 471(T), 472(T), 474(C), 475(G), 477(T), 480(C), 483(C), 487(G), 495(C), 498(C), 500(A), 504(A), 511(A), 516(A), 522(T), 525(A), 531(T), 537(A), 541(T), 543(A), 549(C), 552(C), 555(C), 558(T), 559(A), 564(C). 570(G), 573(G), 577(A), 578(A), 583(C), 585(A), 606(C), 607(T), 613(G), 614(G), 627(C), 630(A), 639(T), 642(C), 645(A), 654(A); ITS positions 33(T), 45(A), 46(G), 48(A), 49(A), 50(T), 76(G), 81(A), 421(C), 422(T), 423(T), 425(A), 427(T), 428 insertion (C), 429(A), 430(A), 431(T), 465(A), 466(A), 478(A), 479(A), 480(A); actA positions 31(T), 34(C), 47(G), 49(C), 50(T), 62(C), 63(T), 68(C), 69(T), 71(C), 72(G), 73(G), 82(G), 83(C), 87(C), 88(A), 95(G), 98(T), 101(A), 104(G), 105(C), 107(T), 115(C), 118(A), 138(C), 165(T), 166(A), 168(T), 175(T), 177(T), 178(C), 179(A), 180(T), 182(T), 185(A), 186(C), 187 insertion (T), 209(A), 210(C), 212(G), 214(G), 218(C), 220(A), 245(A); gapdh positions 17(C), 18(T), 19(C), 21(T), 54-58 insertion (ATGTG), 59(G), 61(T), 64(G), 65(A), 93(T), 94(G), 99(T), 101(G), 107(A), 108(C), 109(A), 111(A), 119(A), 120(C), 121(A), 122(G), 124(A), 156(C), 158(C), 161(T), 207(C), 208(A), 209(G), 210(C), 212(T), 257(C), 259(T), 263(A), 269(G), 271(A), 272(T), 282(C), 284(T), 287(A), 288(C), 289(C), 290(T), 297(C), 298(A), 301(G), 303(C), 304(C), 308(C), 309(A), 310 insertion (A), 311(T), 312(C), 313(C), 353(T), 389(C), 404(C), 405(A), 411(G), 442(A), 449(A), 461(T), 521(C), 557(C), 566(C), 569(C), 575(T), 587(C), 593(T), 617(T); tef1-a positions 15(C), 16(T), 22(G), 23(C), 24(T), 25-26 insertion (CC), 59(T), 69(C), 72(G), 78(C), 95(C), 96(A), 107(G), 183(T), 196(C), 205(C), 223(T), 225(A), 233(T), 243(T), 275(C), 277(A), 284(T), 286(T), 294(G), 296(C), 303-304 insertion (GC), 305(G), 313(A), 315(G), 316(T), 399(C), 401(G), 402(C), 404(G), 405(A), 408(A), 410(G), 412(T), 413 insertion (T), 423(A), 424(A), 425(A), 427(T), 429(T), 430(G), 431(C), 444(C).

Specimen examined: **Italy**, on healthy leaf of *Gaultheria shallon*, unknown collector and date, isol. and dep. O. Petrini, May 1980, (**holotype** CBS H-17765, extype culture CBS 299.80).

Substrate and distribution: On Gaultheria shallon (Ericaceae); Europe (Italy).

Notes: The strain used in this study forms a single lineage (Fig. 2, clade 88), basal to *R. endophylla*, and is positioned on a very long branch, which supports this species as unique. No *Ramularia* species is currently known from *Gaultheria*. Unfortunately, the culture was sterile and the herbarium material is an old dried culture on which some conidiophores and conidiogenous cells could be observed but were not sufficient to warrant a full description. (Fig. 44), so the molecular differences based on the sequence data are also provided.

Ramularia gei (A.G. Eliasson) Lindr., Acta Soc. Fauna Fl. Fenn. 23: 26. 1902.

Basionym: Ovularia gei A.G. Eliasson, Bih. Kongl. Svenska Vetensk.-Akad. Handl. 22(12): 19. 1897.

≡ Ramularia gei (A.G. Eliasson) Höhn., Ann. Mycol. 2: 57. 1904, homonym!

≡ Ramularia gei (Fuckel) Lindau, in Rabenh., Krypt.-Fl., 2. Aufl., 1 Bd.,
 Pilze IX. Abt., Fungi Imperfecti, Hyphomycetes: 766. 1920, homonym!
 ≡ Pseudocercospora gei (Fuckel) Y.-L. Guo & X.-J. Liu, Acta Mycol. Sin.:
 344. 1986.

= *Acrotheca gei* Fuckel, Jahrb. Nassauischen Vereins Naturk. 15: 43. 1860. For additional synonyms see Braun (1998).



Fig. 43. Ramularia euonymicola (CBS 113308). A–I. Observations from herbarium material. A. Leaf spot symptoms on the host. B, C, F, I. Conidiophores and conidiogenous cells. D. Conidiogenous cell and conidia. E, G, H. Conidia. Scale bars = 10 µm.



Fig. 44. Ramularia gaultheriae (CBS 299.80). A-F. Observations from herbarium material. B, D. Conidiophore reduced to conidiogenous cell. C, E, F. Conidia. Scale bars = 10 µm.

Description in vivo: See Braun (1998: 246).

Specimens examined: Netherlands, Baarn, Loenen, Overholland, on Geum urbanum, 12 Apr. 1969, J.A. von Arx, CBS H-4927, culture CBS 344.49. Sweden, Uppland, Danmark par., Bergsbrunna, on Geum sp., 25 Sep. 1986, E. Gunnerbeck, culture CBS 113977; near Uppsala, on Geum urbanum, 4 Sep. 1895, Eliasson (holotype S-F-58091).

Substrate and distribution: On Geum (Rosaceae); Asia, Caucasus, Europe, Iceland, N. America.

Notes: Ramularia gei was originally described on Geum urbanum from Sweden (holotype in S). The similarities between Acrotheca gei and Ramularia gei were discussed by Hughes (1953) and those between R. gei and R. submodesta were pointed out by von Höhnel (1904). The strains included here form a highly supported clade (Fig. 2, clade 74, 1/100/100), but

were sterile in culture and the herbarium specimen is depauperate.

Ramularia geranii Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 361. 1870. Fig. 45.

= Fusidium geranii Westend., Bull. Acad. Belg. 18: 413. 1851.

≡ Cylindrospora geranii (Westend.) J. Schröt., Krypt.-FI. Schlesien 3.2(4): 486. 1897.

For additional synonyms see Braun (1998) or MycoBank.

Mycelium consisting of hyaline, septate, branched, smooth, 1.5–3 µm diam hyphae. *Conidiophores* hyaline, thin-walled, erect, septate, straight to geniculate-sinuous, cylindrical-oblong, unbranched, $(65-)82-100(-150) \times 2-2.5(-3)$ µm or reduced to conidiogenous cells, hyaline, smooth, integrated in mycelium or terminal in conidiophores, cylindrical-oblong, (14.5–) 19–22(–28) × 2–3 µm, with one apical *conidiogenous locus*,



Fig. 45. Ramularia geranii (CBS 160.24). A-G. Structures formed in culture. A. Conidiophore, conidiogenous cell and conidia. B-G. Conidia. Scale bars = 10 µm.

thickened and darkened. *Conidia* hyaline, thin-walled, smooth, with hila thickened and darkened. *Ramoconidia* subcylindrical to clavate, 1–4-septate, $(23-)28-30(-35) \times (3-)4-4.5(-5) \mu m$, with 2–3 conidiogenous apical hila. *Intercalary conidia*, 0–3-septate, subcylindrical to clavate, straight or slightly curved, narrower at the centre and broader at the apices, (17-) 22–25(–30) × $(2.5-)3.5-4(-5) \mu m$, in chains of up to five conidia. *Terminal conidia* 0–1-septate, obovoid, clavate, phalangoid, $(11-)15.5-18(-25) \times (3-)4(-5) \mu m$.

Culture characteristics: On MEA, 11 mm diam, surface rosy vinaceous to pale vinaceous grey, strongly folded, raised with margins crenate, colony reverse cinamon with iron grey patches. On OA, 10 mm diam, surface rosy buff, flat, sparse aerial mycelium with margins undulate and sparse aerial mycelium, colony reverse rosy buff with brown vinaceous patches. On PDA, 11 mm diam, surface folded, rosy buff to pale olivaceous grey, raised, with margins undulate, concave, colony reverse olivaceous.

Description in vivo: See Braun (1998: 164).

Specimens examined: France, on Geranium pyrenaicum, collector and date unknown, isol. and dep. C. Killian, Jun. 1924, culture CBS 159.24; on Geranium sylvaticum, unknown date, C. Killian (epitype designated here CBS H-17726, MBT371838, culture ex-epitype CBS 160.24). Poland, on Geranium pusillum [Schneider, Herb. Schles. Pilze 898; neotype, designated in Braun (1998), HAL].

Substrate and distribution: On Erodium and Geranium (Geraniaceae); Asia, Caucasus, Europe, N. America.

Notes: Two varieties are known for *Ramularia geranii*, *R. geranii* var. *geranii* (on *Geranium pusillum*, Poland, neotype in HAL) and *R. geranii* var. *erodii* (on *Erodium cicutarium*, Germany, neotype in B). The latter differs from the first by having long slender

conidia with up to four septa. They are distributed in the northern hemisphere and R. gerani var. gerani has also been reported from Erodium. The strains representing Ramularia geranii in this study clustered separately with CBS 259.24 and CBS 160.20 forming one clade (Fig. 2, clade 3) and CBS 114566 forming a single lineage on a long branch (Fig. 2, clade 4). The strains CBS 159.24 and CBS 160.24 produce very large conidia fitting with the original description and were isolated from the same host genus, but from a different species and country. Strain CBS 114566 was isolated from the same host as the type but from a different European country. Unfortunately it was sterile and morphological comparison with the original description was not possible. Strains CBS 159.24 and CBS 160.24 (Fig. 2, in clade 3, 1/100/100; Fig. 45) are considered good representatives of R. geranii both morphologically and phylogenetically, and CBS 160.24 is therefore chosen as ex-epitype. The strain CBS 114566 appears as R. geranii in the CBS database but it is not conspecific with the species in this clade and will be treated as a Ramularia sp. A for the time being.

Ramularia geraniicola Videira & Crous, **sp. nov.** MycoBank MB816849. Fig. 46.

Etymology: Named after the host genus, *Geranium*, from which it was collected.

Mycelium consisting of hyaline, septate, branched, smooth, 1–2.5 µm diam hyphae. *Conidiophores* hyaline, thin-walled, smooth, emerging from hyphae or dark hyphal spherical aggregates, erect, 1-2(-4)-septate, straight to sinuous, cylindrical-oblong, unbranched (22.5–)35.5–44(–66.5) × (1.5–) 2–3(–4) µm or reduced to conidiogenous cells. *Conidiogenous cells*, integrated, cylindrical-oblong and narrower at the top, geniculate-sinuous, (12–)18–22(–33) × 2–2.5(–3) µm, with 1–4 apical conidiogenous loci, almost flat or protuberant;



Fig. 46. Ramularia geraniicola (CBS 141110). A-F. Conidiophores, conidiogenous cells and conidia formed in culture. Scale bars = 10 µm.

conidiogenous loci thickened, darkened and refractive. Conidia hyaline, thin-walled, smooth, catenate, with hila thickened, darkened and refractive. Ramoconidia subcylindrical to clavate, $(10-)13.5-16(-22.5) \times (2-)3(-4) \mu m$, 0–1-septate, with two apical hila. Intercalary conidia subcylindrical, fusoid, 0–1-septate, $(8.5-)12.5-14.5(-21.5) \times (2.5-)3(-4) \mu m$, in branched chains of up to eight conidia. Terminal conidia subcylindrical to obovoid, aseptate, $(3-)6.5-8.5(-13) \times (2-) 2.5-3(-3.5) \mu m$ (on SNA).

Culture characteristics: On MEA, 15 mm diam, raised, folded, smooth, radially striated, olivaceous grey, with margins pale olivaceous grey and lobate, colony reverse olivaceous grey; on OA, 13 mm diam, flat, sparse aerial mycelium, smooth, olivaceous grey with some tufts pale olivaceous grey, with margins with sparse aerial mycelium and entire edge, colony reverse olivaceous grey; on PDA, 16 mm diam, flat, olivaceous grey, fluffy aerial mycelium, pale olivaceous grey, with margins undulate, colony reverse olivaceous grey and buff margin.

Specimen examined: Netherlands, Utrecht, Rhijnauwen, on *Geranium* sp., May 2013, U. Damm (holotype CBS H-22521, culture ex-type CBS 141110 = CPC 25912).

Substrate and distribution: On Geranium sp. (Geraniaceae); Europe (Netherlands).

Notes: Two Ramularia species (*R. geranii* var. geranii, *R. pseudogeranii*) and two ramularia-like species (*Phacellium geranii* and *Pseudocercosporella magnusiana*) have thus far been described from *Geranium* (Braun 1998). *Ramularia geranii* var. *geranii* produces conidia that are smooth to verruculose, ellipsoid-ovoid to fusiform, 0–3-septate and 10–40(–55) × (2–) 2.5-6(-7) µm. *Ramularia pseudogeranii* produces solitary

obovoid conidia, $14-25 \times 6-12 \mu m$. The synnematous *Phacellium geranii* produces catenate conidia, ellipsoid-ovoid to fusoid, $12-28 \times 4-7 \mu m$. *Pseudocercosporella magnusiana* produces solitary conidia, subcylindrical-filiform to acicular (30-) $40-100(-120) \mu m$, 2-8-septate, with hyaline, unthickened hilum. The morphological characters of *R. geraniicola* (Fig. 46) are also distinct from the closest species, *R. variabilis* that produces shorter conidiophores and narrower fusiform to obovoid conidia (Fig. 2, clade 50). *Ramularia geraniicola* has unique morphological characters and forms a single lineage in the phylogenetic analysis (Fig. 2, clade 51).

Ramularia glechomatis U. Braun, Nova Hedwigia 56: 426. 1993. Fig. 47.

= Fusisporium calceum Desm., Ann. Sci. Nat., Bot., 2 Sér., 17: 95. 1842.
≡ Cylindrospora calcea (Desm.) J. Schröt., in Cohn, Krypt.-FI. Schles.
3.2(4): 491. 1897.

For additional synonyms see Braun (1998) or MycoBank.

Mycelium consisting of hyaline, septate, branched, smooth, 1-2 µm diam hyphae. Conidiophores hyaline, smooth, thinwalled, erect, septate, cylindrical-oblong, straight to sinuous, unbranched (15-)28-36(-61) × (1.5-)2 µm, or reduced to conidiogenous cells, terminal in conidiophores or intermediate in the mycelium, cylindrical-oblong to geniculate-sinuous, (4-) $11-13(-18) \times 1.5- 2(-3) \mu m$, with up to three protuberant conidiogenous loci; conidiogenious loci thickened, darkened and refractive. Conidia hyaline, thin-walled, slightly verruculose, catenate, with hila thickened, darkened and refractive. Ramoconidia cylindrical-oblong, $(8-)11-13(-17) \times 2(-3) \mu m$, 0-1septate, with two apical hila. Intercalary conidia cylindricaloblong, fusoid, aseptate, $(6.5-)8.5-10(-14) \times 2(-3) \mu m$, in branched chains of up to seven conidia. Terminal conidia cylindrical-oblong to obovoid, aseptate, $(3-)5-6.5(-9) \times (1-)$ 2(-3) µm (on SNA).



Fig. 47. Ramularia glechomatis (CBS 108980). A–G. Structures formed in culture. A, C, E. Conidia. B, F, G. Conidiophores, conidiogenous cells and conidia. D. Conidiophore. Scale bars = 10 µm.

Culture characteristics: On MEA, 10 mm diam, surface raised, smooth, white with a greyish tinge, with margins lobate, colony reverse iron-grey; on OA, 12 mm diam, surface flat, smooth, pale grey, with margins entire, colony reverse iron-grey; on PDA, 11 mm diam, surface flat, smooth, white with greyish patches, with margins entire, colony reverse iron-grey.

Description in vivo: See Braun (1998: 180).

Specimens examined: Germany, Brandenburg, Nedlitz near Potsdam, on *Glechoma hederacea*, 7 Sep. 1919 [Sydow, Mycoth. Germ. 1757] (holotype JE). Netherlands, Utrecht Prov., Baarn, de Hooge Vuursche, on leaf spot on *G. hederacea*, 22 Jun. 2000, G. Verkley, cultures CBS 108979, CBS 108980; Utrecht Prov., Nieuwersluis, Overholland, on leaf spot on *Glechoma hederacea*, unknown collector and date, isol. and dep. J.A. von Arx, Nov. 1949, culture CBS 343.49.

Substrate and distribution: On Glechoma hederacea (Lamiaceae); Asia, Caucasus, Europe.

Notes: Ramularia glechomatis was originally described on *Glechoma hederaceae* from Germany (holotype in JE) but it has been reported on this host from almost all countries in Europe including the Netherlands (Braun 1998). The strains used in this study cluster in a highly supported clade (Fig. 2, clade 45, 1/100/100). Morphologically, they are similar to the description available in literature (Braun 1998) except for producing narrower conidia, but our observations are based on cultures on SNA (Fig. 47).

Ramularia glennii Videira & Crous, Persoonia 34: 55. 2015.

Specimens examined: Iraq, Al-Kora, Basrah, on leaves of *Eucalyptus camaldulensis*, 1 Mar. 2009, A. Saadoon, cultures CPC 16560, CPC 16565. Italy, Viterbo, on leaves of *Corymbia grandifolia*, 1 Apr. 2006, W. Gams, culture CBS 120727 = CPC 13047. **Netherlands**, on human bronchial alveolar lavage, Rotterdam, Maasstad Ziekenhuis (Clara), on human bronchial alveolar lavage, 2011, unknown collector, dep. A. van Duin (**holotype** CBS H-21617, ex-type culture CBS 129441); Rotterdam Maasstad Ziekenhuis (Clara), on human skin tissue, 29 April 2008, unknown collector, dep. H. Naaktgeboren, culture CBS 122989. **USA**, Athens, on rubber of refrigerator, Sep. 2010, A. Glenn, culture CPC 18468.

Substrate and distribution: On Corymbia grandifolia and Eucalyptus camaldulensis (Myrtaceae), human and environmental samples; Western Asia (Iraq), Europe, USA.

Notes: See Videira *et al.* (2015a). The phylogenetic analyses provide good support for this species clade (Fig. 2, clade 32, 1/ 100/96).

Ramularia grevilleana (Oudem.) Jørst., Meld. Stat. Plantepatol. Inst. 1: 17. 1945, emend. U. Braun, A monograph of *Cerco-sporella*, *Ramularia* and allied genera (Phytopathogenic Hyphomycetes) 2: 68. 1998.

Basionym: Cylindrosporium grevilleanum Oudem., Arch. Néerl. Sci. Exact. Nat. 8: 392. 1873.

= Cylindrosporium sp., in Tul. & C. Tul., Select. fung. carpol. 2: 288. 1863.

- = Mycosphaerella fragariae (Tul. & C. Tul.) Lindau, in Engler & Prantl, Nat. Pflanzenfam., ed.1, Sphaeriales, 1(1): 424. 1897.
- = Ramularia tulasnei Sacc., Michelia 1: 536. 1879, nom. superfl.!
- = Ramularia fragariae Peck, Annual Rep. (Annual) New York State Mus. Nat. Hist. 32: 43. 1879.
- = R. modesta Sacc., Fungi ital. Del., Tab. 999. 1881.

For additional synonyms see Braun (1998) or MycoBank.

Description in vivo: See Braun (1998: 248).

Specimens examined: Netherlands, unknown host, date and collector, isol. Moll, dep. Oct. 1934, cultures CBS 298.34; unknown host, date and collector, isol. van Egmond, dep. Aug. 1936, CBS 259.36; Heemstede, on *Fragaria vesca*, Jul. 1872, Oudemans [lectotype, designated by Braun & Pennycook (2003), L 371868]. New Zealand, Auckland, on *Fragaria* sp., unknown date and collector, isol. and dep. W.F. Hartill, Dec. 1983, culture CBS 719.84. Sweden, Uppland, Alsike, on *Fragaria ananassa*, 4 Oct. 1989, E. Gunnerbeck, culture CBS 114732.

Substrate and distribution: On Duchesnea, Fragaria, Horkelia, Potentilla, and Waldsteinia (Rosaceae); almost circumglobal.

Notes: The valid publication of Cylindrosporium grevilleanum, the basionym of Ramularia grevilleana, dates back to Oudemans (1873). A detailed discussion of the complicated nomenclature of this species and its lectotypification has been published by Braun & Pennycook (2003). The phylogenetic analyses provide high support for this species clade (Fig. 2, clade 28, 1/100/100). Ramularia grevilleana causes Ramularia leaf spot disease of strawberry and other hosts of the Rosaceae. The most conspicuous symptoms are leaf lesions but symptoms can also develop on fruits, calyxes, fruit trusses, petioles and stolons. It occurs worldwide on cultivated varieties as well as wild strawberry species. In earlier years, the economic impact of the disease was so great that Ramularia leaf spot was considered the most important strawberry disease. With increased emphasis on the development and use of resistant cultivars, Ramularia leaf spot disease, although still an important foliar disease is now of less concern (Maas 1984). The link between the sexual morph Mycosphaerella fragariae and the asexual morph R. grevilleana has been experimentally proven (Dudley 1889).

Ramularia haroldporteri Videira & Crous, Persoonia 34: 58. 2015.

Specimen examined: South Africa, unidentified bulb plant, 14 Jan. 2009, P.W. Crous (holotype CBS H-21616, ex-type cultures CBS 137272 = CPC 16296, CPC16297).

Substrate and distribution: Thus far only known from South Africa.

Notes: See Videira *et al.* (2015a). The phylogenetic analyses provide high support for this species clade (Fig. 2, clade 30, 1/ 100/100).

Ramularia helminthiae Bremer & Petr., Sydowia 1: 259. 1947. Fig. 48

= *Ramularia helminthiae* T.M. Achundov, Novosti Sist. Nizsh. Rast. 20: 59. 1983, nom. illeg.

Mycelium consisting of hyaline, septate, branched, smooth, 1-3 µm diam hyphae. Conidiophores hyaline, thin-walled, smooth, erect, 1-3-septate, straight to flexuous, cylindricaloblong, unbranched (19-)41-53(-82) × (1.5-)2-2.5(-3) µm or reduced to conidiogenous cells. Conidiogenous cells integrated in mycelium or terminal on conidiophores, cylindricaloblong, (15-)21.5-25.5(-36) × 2.0-2.5(-3) µm, with 1-2 apical conidiogenous loci almost flat to short cylindrical, thickened, darkened, refractive. Conidia hyaline, thin-walled, smooth to slightly verruculose, with hila thickened, darkened and refractive. Ramoconidia subcylindrical to clavate, (14-) 21-27(-44) × (2.5-)3-3.5(-4) µm, 0-3-septate, with 2-3 apical hila. Intercalary conidia hyaline, smooth, 0-3-septate, subcylindrical with apices rounded and broader, (14-) $19-25(-50) \times (2.5-)3-4(-4.5) \mu m$, in branched chains of up to four conidia. Terminal conidia aseptate, subcylindrical to obovoid, (5.5-)13-16.5(-25.5) × (2-)3-3.5(-4.5) μm.

Culture characteristics: On MEA, 15 mm diam, surface raised, folded, smooth mycelium, smoke-grey with olivaceous tinge,

with small buff droplets, with margins lobate, convex, feathery, colony reverse olivaceous grey and ochraceous patches; on OA, 15 mm diam, surface low convex, smooth mycelium, white, with margins buff, naked, undulate, colony reverse rosybuff; on PDA, 20 mm diam, surface low convex, smooth mycelium, white with greyish tinge with margins undulate, feathery, colony reverse rosy-buff and iron-grey patches.

Specimens examined: Azerbaijan, Talysh, district Massalli, Kyzylagadzh, on Helminthotheca echioides (≡ Picris echioides), 2 Jun. 1974, T.M. Achundov (isotype of *R. helminthiae* T.M. Achundov LE 41974). South Korea, Hongcheon, on Picris hieracioides var. glabrescens, 9 Jul. 2004, H.D. Shin, KUS-F20442, culture CPC 11502, CPC 11504. New Zealand, Auckland, Mt. Albert, on *H. echioides*, unknown collector and date, isol. C.F. Hill, Jul. 2005, det. C.F. Hill, culture CBS 118418. Turkey, Adana, Terliksiz, on *H. echioides*, 8 Jun. 1943, G. Karel [lectotype of *R. helminthiae* Bremer & Petr., designated in Braun (1998), W 15449].

Notes: These strains were initially identified as R. inaequalis, but this species clusters in clade 40 (Fig. 2). Several names have been synonymised with R. inaequalis that refer to species isolated from different hosts and locations. These need to be recollected and re-examined since it appears that R. inaequalis is a species complex. Helminthotheca echioides is of Mediterranean origin, but now with a widespread, almost cosmopolitan neophytic distribution. The descriptions of both species named R. helminthiae are from the neophytic area of the host, but the origin of the species concerned is probably Mediterranean as well. A sporulating culture based on material collected on *H. echioides* in Turkey or adjacent countries should serve as epitype for this species, but is not yet available. Therefore, the name R. helminthiae is only tentatively used for the present strains until appropriate cultures will be available. Ramularia helminthiae (Fig. 48) is supported as distinct from other included species by the phylogenetic analyses (Fig. 2, clade 5, 1/100/100). The strain CBS 118418 did not sporulate in culture.

Ramularia heraclei (Oudem.) Sacc., Fungi ital. Del., Tab. 1008. 1881, emend. U. Braun, A monograph of *Cercosporella*, *Ramularia* and allied genera (Phytopathogenic Hyphomycetes) 2: 68. 1998. Fig. 49.

Basionym: Cylindrosporium heraclei Oudem., Arch. Néerl. Sci. Exact. Nat. 8: 383. 1873.

- = Ramularia cicutae P. Karst., Hedwigia 23: 7. 1884.
- = R. levistici Oudem., Ned. Kruidk. Arch., 2 ser., IV: 540. 1886.
- = R. pastinacae Bubák, Sitzungsber. Königl. Böhm. Ges. Wiss., Math.-nat. Kl., 1903: 19. 1903.
- = R. coriandri Moesz & Smarods, Magyar Bot. Lapok 1/12: 37. 1930.
- For additional synonymies see Braun (1998).

Description in vivo: See Braun (1998: 58).

Specimens examined: Austria, Ötztal, Ötz near Habichen, on leaf spot of *Heracleum* sp., 24 Jul. 2000, G. Verkley, cultures CBS 108987, CBS 108988. Netherlands, Bloemendaal, on *Heracleum sphondylium*, Aug. 1871, Oudemans [lectotype, designated in Braun (1998), in L]; Limburg Prov., Gerendal, on leaf spot of *Heracleum sphondylium*, 28 Jun. 2000, G. Verkley (epitype designated here CBS H-22638, MBT371839, culture ex-epitype CBS 108969); *idem*. CBS 108972. South Korea, Yangpyeong, on *Heracleum moellendorffii*, 24 Jun. 2004, H.D. Shin, cultures CPC 11505–11507. Sweden, Uppland, Danemora par., Andersby, on *Heracleum sphondylium*, 31 Aug. 1987, E. Gunnerbeck, culture CBS 113976 = UPSC 2344. Unknown country, on *Pastinaca sativa*, unknown collector and date, isol. and dep. J.E.V. Smith, Apr. 1923, culture CBS 194.25.



Fig. 48. Ramularia helminthiae (CPC 11504). A, D, E. Observations from herbarium material. B, C, F, G. Structures formed in culture. A. Leaf spots on the host. D, F, G. Conidiophores and conidia. B, C, E. Conidia. Scale bars = 10 µm.



Fig. 49. Ramularia heraclei (CBS 108972, CBS 108988). A–K. Observations from herbarium material A–F. CBS 108972. G–K. CBS 108988. A, G. Leaf spot symptoms on the host. B, H. Conidiophores, conidiogenous cells and conidia. F, K. Conidiogenous cells. C–E, I–J. Conidia. Scale bars = 10 µm.

Substrate and distribution: On Apium, Cicuta, Conium, Coriandrum, Hansenia, Heracleum, Levisticum, Malabaila, and Pastinaca (Apiaceae); Asia, Africa, Caucasus, Europe, New Zealand, N. America and West Indies.

Notes: Ramularia heraclei was originally described on Heracleum sphondylium from the Netherlands (lectotype in L). Strains of *Ramularia heraclei* used in this study formed two sister clades that are both highly supported in the multigene phylogeny (Fig. 2, clade 78, 1/100/100). In literature (Braun 1998), the description of this species is quite broad including conidiophores in fascicles or forming crustose-like layers, erect and simple, cylindrical to geniculate-sinuous and variable in length, $5-80(-110) \times 2-6 \mu m$ and conidia which are catenate, 0-3-septate, smooth to

verruculose, $(8-)10-35(-45) \times 2-6 \mu m$. The herbarium material corresponding to strain CBS 108972 has short conidiophores, $(5-)12-17(-20) \times 2-3 \mu m$ and conidia which are catenate, verruculose, 0-1-septate, (6-)11-14(-25) × (2-) 3(-6) µm. The herbarium material corresponding to the strain CBS 108988 has longer conidiophores, (29-) $49-59(-82) \times 2-3 \mu m$ and longer conidia, catenate, smooth to sliahtly verruculose. (0-)1-3-septate and (6.5-)15.5-20(-36) × (2.5-)3.5-4(-6) µm. They both fit the morphological description in literature and strain CBS 108969. which was collected from the Netherlands and isolated from Heracleum sphondylium, the same location and host as the type species, and is herewith designated as epitype (Fig. 49). The morphology of Ramularia collections from hosts of Apiaceae that are preserved in herbaria are difficult to distinguish and several names were synonymised with R. heraclei (Braun 1998). The variation in morphology and the phylogeny indicate that this may be a species complex that needs further study and comparison with collections from other apiaceous hosts.

Ramularia hieracii-umbellati A.G. Eliasson, Svensk. Bot. Tidskr. 9: 412. 1915. Fig. 50.

In planta: Leaf spots rectangular, following the leaf nerves, yellowish to brown. *Caespituli* emerging through stomata, hyaline to buff. *Conidiophores* hyaline, thin-walled, smooth, erect, septate, cylindrical-oblong, straight to geniculate-sinuous, rarely branched, $(14-)27-32(-41.5) \times (2-)3(-4) \mu m$. *Conidiogenous cells* terminal or intermediate in the conidiophore, cylindrical-oblong or geniculate-sinuous, $(7-)10-13(-22) \times (2-)3(-4) \mu m$, with multiple *conidiogenous loci* almost flat to protuberant, thickened, darkened and refractive. *Conidia* hyaline, thinwalled, smooth, solitary or in short chains unbranched, cylindrical-oblong to obovate, (0-)1-2-septate, $(8-)15-20(-25) \times (2-)2.5-3 \mu m$ with hila thickened, darkened and refractive.

Culture characteristics: On MEA, 13 mm diam, surface raised, olivaceous grey fluffy aerial mycelium, droplets of iron-grey, margins undulate, convex, feathery, colony reverse undulate, convex, feathery, iron-grey; on OA, 15 mm diam, surface low convex, smooth, pale olivaceous grey, with margins with entire edge, colony reverse olivaceous grey; on PDA, 14 mm diam, surface raised, greenish grey, with olivaceous grey droplets exudate, radially striated, with margins lobate, convex, feathery, colony reverse iron-grey.

Specimens examined: **South Korea**, Pocheon, on *Hieracium umbellatum*, 2 Sep. 2003, H.D. Shin, KUS-F19596, cultures CPC 10690–10692; Pyeongchang, on *Hieracium umbellatum*, 4 Sep. 2003, H.D. Shin, KUS-F19601, cultures CPC 10788, CPC 10789; **Sweden**, Smolandiae, Lofthammer, on *Hieracium umbellatum*, 12 Jul. 1912, A.G. Eliasson (**holotype** UPS).

Substrate and distribution: On Hieracium umbellatum (Asteraceae); Asia (South Korea), Europe (Sweden).

Notes: Previously identified as *Ramularia inaequalis* these strains in fact represent a separate species (Fig. 50), since they do not cluster together with the type of *R. inaequalis* (Fig. 2, clade 40). The morphology agrees well with *R. hieracii-umbellati* described on *Hieracium umbellatum* from Sweden. Cultures and sequences based on collections from Sweden are not available for comparison, but since the Korean material might belong to

this species, we prefer to apply the latter name, at least tentatively. *Hieracium umbellatum* is a widespread circumpolar species. Strains of *R. hieracii-umbellati* form a highly supported clade (Fig. 2, clade 56, 1/100/100). *Ramularia hieracii-umbellati* formed a sister clade to *R. rhabdospora*, but the latter produces wider conidiophores $[10-50(-115) \times 2-8 \ \mu\text{m}]$ and larger catenate conidia $[(10-)15-40(-50) \times 3-7 \ \mu\text{m}]$, echinulate, ellipsoidovoid to cylindrical, and 0-3(-4)-septate (Braun 1998).

Ramularia hydrangeae-macrophyllae U. Braun & C.F. Hill, Australas. Mycol. 27: 53. 2008. Fig. 51.

In planta: Leaf spots variable, from angular-irregular speckles to large brown leaf blotches. Mycelium internal and external but lacking stromata. Conidiophores arising from internal hyphae, emerging through stomata or from superficial hyphae, straight, simple, thin-walled, smooth, subcylindrical to moderately geniculous-sinuous, 4-35 × 1.5-3.5 µm, 0-1-septate, or reduced to conidiogenous cells, 4-20 µm long; conidiogenous loci conspicuous, thickened and darkened. Conidia catenate, sometimes in branched chains, ellipsoid-ovoid to fusiformsubcylindrical. 4-18 × 1.5-2.5 µm. 0-1-septate. hvaline. thinwalled, smooth to verruculose, hila thickened and darkened. Description adapted from Braun & Hill (2008). Ascomata pseudothecial, single, brown, immersed, becoming erumpent, globose, apical ostiole. Asci aparaphysate, fasciculate, bitunicate, subsessile, obovoid to narrowly ellipsoid. Ascospores, straight to fusoid-ellipsoid, hyaline, thin-walled, with subobtuse ends, medianly 1-septate, symmetrical or with one side slightly larger than the other, sometimes slightly constricted at the septa, $(4.5-)5-6(-7.5) \times (1-)1.5-2(-2.5) \mu m.$

Specimens examined: Italy, Grancarlo, on Feijoa sellowiana, unknown date, G. Polizzi, culture CPC 19854. Netherlands, Flevoland Prov., Lelystad, Hollandse Hout, on Platanus sp., Apr. 2012, S.I.R. Videira, culture CPC 25901; same prov., Kortenhoefse Plassen, on a dead leaf of Sparganium ramosum, Jan. 1982, W. Gams, culture CBS 159.82; Utrecht prov., Bilthoven, on Phragmites sp., 6 Jan. 2011, P.W. Crous, cultures CPC 19026, CPC 19027; Breukelen, on Sparganium ramosum, unknown collector and date, isol. W. Gams, Sep. 2003, culture CBS 113614; Houten, on Typha sp., Jul. 2012, S.I.R. Videira, cultures CPC 25903; Nieuwersluis, Overholland, from leaf spot on Angelica sylvestris, unknown collector and date, dep. Nov. 1949, culture CBS 341.49; Utrecht, Botanical Garden, on Aesculus hippocastanum, Apr. 2012, S.I.R. Videira, cultures CPC 25902; Utrecht, Botanical Garden, on Iris foetidissima, collector and date unknown, culture CPC 20484: Utrecht, on Juncus sp., May 2013 U. Damm, culture CPC 25907; Utrecht, on Potentilla sp., Oct. 2012, U. Damm, cultures CPC 25904; Utrecht, on Laurus sp., May 2013, W. Quaedvlieg, culture CPC 25908; Veenendaal, on Carex sp., May 2013, W. Quaedvlieg, cultures CPC 25905, CPC 25906; New Zealand, Auckland, Grey Lynn, on Helleborus niger, 1 May 2005, C.F. Hill, culture CBS 118408; Mt. Albert, Rurangi Road, on the underside of the leaf of Hydrangea macrophylla, 2 Jul. 2007, C.F. Hill (holotype HAL 2103 F, culture ex-type CBS 122273); Grafton, Park Road, The Auckland Domain, on dead leaves of Iris ×hollandica hybrid, 28 Oct. 2007, C.F. Hill, culture CBS 122625 = CPC 14811; Grey Lynn, Great North Road, Western Springs, on leaf lesion from Iris sp., 23 Sep. 2007, C.F. Hill, culture CBS 122272; Grey Lynn, on Ligularia clivorum, unknown collector and date, isol. C.F. Hill, 13 Jun, 2005, dep. C.F. Hill, culture CBS 118410. Sweden, Uppland, Dalby par., Jerusalem, on Filipendula vulgaris, 12 Jul. 1988, E. Gunnerbeck, culture CBS 114117. UK, England, Basingstoke, Upton Grey, Weston Road, on Iris sp., 25 Dec. 2010, P.W. Crous, culture CPC 19030; Exeter, endophyte on Ulex europaeus, unknown collector and date, isol. and dep. J. Fisher, Nov. 1984, culture CBS 766.84. USA, California, Walnut Creek, Ruth Bancroft Botanical Garden, on Eucalyptus caesia, 20 Mar. 2012, P.W. Crous, culture CPC 20406.

Substrate and distribution: Aesculus (Sapindaceae), Angelica (Apiaceae), Carex (Cyperaceae), Eucalyptus, Feijoa (Myrtaceae), Filipendula, Potentilla (Rosaceae), Helleborus



Fig. 50. Ramularia hieracii-umbelati (CPC 10690). A-H. Observations from herbarium material. A. Leaf spot symptoms on the host. B. Conidia. C-H. Conidiophores and conidiogenous cells. Scale bars = 10 µm.



Fig. 51. Ramularia hydrangeae-macrophyllae (CPC 25902). A-D. Observations from herbarium material. E-H. Structures formed in culture. A. Leaf spot symptoms on the host. B, C. Asci and ascospores. D. Ascospores. E, F. Germinating ascospores. G, H. Conidia. Scale bars = 10 µm.

(Ranunculaceae), Hydrangea (Hydrangeaceae), Iris (Iridaceae), Laurus (Lauraceae), Ligularia (Asteraceae), Phragmites (Poaceae), Platanus (Platanaceae), Sparganium, Typha (Typhaceae), and Ulex spp. (Fabaceae); Europe, N. America, New Zealand.

Notes: The species epithet of Ramularia hydrangeae-macrophyllae reflects the name of the host on which it was first observed, *Hydrangea macrophylla*, from New Zealand (holotype in HAL). Within this clade the phylogenetic structure was not resolved consistently in all gene trees (data not shown; Fig. 2, clade 21) and, in accordance with the Genealogical Concordance Phylogenetic Species Recognition (GCPSR) concept, the transition from concordance to conflict determined the limit of these species (Taylor *et al.* 2000). *Ramularia sparganii* was described from *Sparganium emersum* from Sweden (holotype in

C) and has not been reported from the Netherlands (Braun 1998). The species produces conidiophores that are subcylindrical to geniculate-sinuous, 5-40(-60) × 1-3 µm, catenate ellipsoid-fusoid, 0-1-septate, conidia. smooth. 8-30(-33) × 1.5-3 µm and with minute hila. The strain CBS 159.82 was possibly misidentified based on the host but was sterile in culture and morphological characters were not observed. Ramularia hellebori was described from Helleborus foetidus from Germany (lectotype in HAL), and was firstly reported from New Zealand on Helleborus orientalis (Braun & Hill 2002) and later on Helleborus niger (CBS 118408) (Braun et al. 2006), but no ex-type culture was designated. This species description includes conidiophores that are subcylindrical to geniculate sinuous, $10-45 \times 1.5-5 \mu m$, conidia catenate, ellipsoid-ovoid to fusiform, verruculose, 0-1-septate, 6-20(-30) × 2-4 µm and minute hila. Ramularia rollandii was described from Iris pseudacorus from France (lectotype in PC) and the species was reported from New Zealand on an Iris × hollandica hybrid (CBS 122625) (Braun & Hill 2008), but no ex-type culture is known. This species produces conidiophores that are cylindrical to geniculate-sinuous, apically minutely subdenticulate, $5-15(-20) \times 2-3 \mu m$, conidia solitary or in short chains, smooth to faintly verruculose, filiform to acicular, $15-40(-60) \times 1-2 \mu m$, 1-4-septate, with minute hila. Ramularia butomi is mycophylic and was originally described overgrowing ascomycetous stromata on dead leaves of Butomus umbellatus in Sweden (lectotype in B), but the strain CBS 114117 is not documented as hyperparasite in the database. This species produces conidiophores that are simple, subcylindrical to geniculate-sinuous, $8-60 \times 1-4 \mu m$, conidia catenate, narrowly ellipsoid-ovoid subcylindrical-fusiform, (5-)to $8-16(-24) \times (1.5-)2-3(-4) \mu m$, 0-1(-2)-septate, vertuculose and with minute hila. Ramularia deusta var. alba is not reported from Ulex and the representative clade for this species has been designated in this study (Fig. 2, clade 62). All the species mentioned above have in common that the conidia are catenate and slightly verruculose to verruculose, with minute hila, but size and septation vary among them. It is necessary to collect fresh material from the type location and host for further observations. The only ex-type culture present in this clade is that of Ramularia hydrangeae-macrophyllae (CBS 122273) (Braun & Hill 2008), and in accordance with the GCPST concept, we accept that name for this clade. This species, now with a broad host range and wide geographical distribution, forms a highly supported clade (Fig. 2, clade 21, 1/100/100). Similar intraspecific variation, wide host range and geographical distribution have been observed before for Ramularia vizellae (Videira et al. 2015b; Fig. 2, clade 85). Strains CPC 25901 and CPC 25902 were isolated using the method developed for single ascospore isolation for Mycosphaerella (Crous et al. 1991, Crous 1998), which means this species has a sexual morph (Fig. 51).

Ramularia hydrangeicola J.H. Park & H.D. Shin, Mycotaxon 131: 97. 2016

Substrate and distribution: Only known from South Korea.

Notes: This species has been recently described (Park & Shin 2016) and is only known from South Korea. Until now, only two *Ramularia* species were known to infect *Hydrangea* hosts, *R. hydrangeae* Y.L. Guo & U. Braun (on *Hydrangea bretschneideri*, China, holotype in HMAS) and *Ramularia hydrangeae*-macrophyllae U. Braun & C.F. Hill (on *Hydrangea-macrophylla*, New Zealand, holotype in HAL). The isolates of *Ramularia hydrangeicola* cluster in a highly supported clade (Fig. 2, clade 70, 1/100/100) and are not conspecific with *R. hydrangeae-macrophyllae* (Fig. 2, clade 21).

Ramularia inaequalis (Preuss) U. Braun, Monogr. *Cercosporella*, *Ramularia Allied Genera (Phytopath. Hyphom.)* 2: 68. 1998. Fig. 52.

Basionym: Fusoma inaequale Preuss, Linnaea 26: 706. 1855. 1853.

= *Ramularia lineola* Peck, Rep. (Annual) New York State Mus. Nat. Hist. 32: 43. 1879.

= *R. traxaci* P. Karst., Hedwigia 23: 7. 1884.

For additional synonyms see Braun (1998).

Mycelium consisting of hyaline, septate, branched, smooth, 1-2 µm diam hyphae. Conidiophores hyaline, thin-walled, smooth, erect, 1-2-septate, cylindrical-oblong, straight to (25-)40-50(-70)sinuous. unbranched х (1.5-)2-2.5(-3) um, or reduced to conidiogenous cells, Conidiogenous cells terminal on conidiophores or intermediate in the mycelium, cylindrical-oblong, $(7.5-)16.5-20(-28) \times (1.5-)$ 2(-2.5) µm, with one conidiogenous locus almost flat to protuberant, thickened, darkened and refractive. Conidia catenate, hyaline, thin-walled, smooth with hila thickened, darkened and refractive. Ramoconidia cylindrical-oblong, sometimes with the apices broader than the centre, $(14.5-)18-20.5(-27) \times (1.5-)$ 2-2.5(-3) µm, 0-1(-3)-septate, with two apical hila. Intercalary conidia cylindrical-oblong, fusoid or clavate, 0-1septate, slightly narrower at the septa, (10.5-) $14-16.5(-26.5) \times (1.5-)2(-2.5) \mu m$, in branched chains of up to five conidia. Terminal conidia cylindrical-oblong to obovoid, aseptate, (5.5-)10.5-13(-19) × (1-)1.5-2(-3) µm.

Culture characteristics: On MEA, 25 mm diam, surface with convex centre, smooth, with rosy-buff centre turning buff and white towards the raised margin, undulate and feathery, colony reverse olivaceous grey in the centre and ochreous margin; on OA, 25 mm diam, surface flat, smooth, white with a greyish tinge, with margins undulate, naked, buff, colony reverse olivaceous grey centre and cinnamon towards the margin; on PDA, 22 mm diam, surface flat, short and uniform aerial mycelium, pale olivaceous grey, margins naked, entire, buff, colony reverse olivaceous grey centre and buff margin.

Specimens examined: Austria, Krems, on *Taraxacum officinale*, 1870 [Thüm, Fungi Austr. Exs. 888; neotype, designated in Braun (1998), in HAL]. Canada, Nova Scotia, Truro, on *Taraxacum officinale*, unknown date, S. Green, culture CBS 250.96. Mexico, Montecillo, on *Taraxacum* sp., 1 Oct. 2008, M. de Jesús Yáñez-Morales, culture CPC 15815; Montecillo, on *Taraxacum* sp., 22 Sep. 2008, M. de Jesús Yáñez-Morales, cultures CPC 15752, CPC 15753. Netherlands, Utrecht, Rhijnauwen, on *Taraxacum officinale*, May 2013, U. Damm, (epitype designated here: CBS H-22544, MBT204826, culture ex-epitype CBS 141111 = CPC 25741); *idem*. CPC 25742.

Substrate and distribution: On Andryala, Cichorium, Crepis, Hedypnois, Hieracium, Hyoseris, Hypochoeris, ?Lactuca,

Specimens examined: South Korea, Yangpyeong, on *Hydrangea serrata*, 18 Oct. 2007, H.D. Shin, holotype KUS-F23039, ex-type culture KACC43597; *idem.* cultures CPC 14767–14769; Jeju, on *Hydrangea serrata*, 2 Nov., H.D. Shin, KUS-F23141, cultures CPC 14832–14834.



Fig. 52. Ramularia inaequalis (CPC 15752). A-G. Structures formed in culture. A, B, D, F, G. Conidiophores and conidia. C, E. Conidia. Scale bars = 10 µm.



Fig. 53. Ramularia interstitialis (CBS 120.68). A-F. Observations from herbarium material. B-F. Conidia. Scale bars = 10 µm.

Leontodon, Picris, Reichardia, Rhagadiolus, Scorzonera, Sonchus, Taraxacum, and Tolpis (Asteraceae); circumglobal.

Notes: Braun (1998) synonymised several names with *R. inaequalis* since the specimens available on numerous hosts belonging to the *Asteraceae* were morphologically very uniform. *Ramularia inaequalis* was originally described on *Taraxacum officinale* from Austria (neotype in HAL) but it is a commonly reported species worldwide and in a wide range of hosts. The strains originally identified as *R. inaequalis* used in this study fell in three different clades (Fig. 2, clades 5, 40 and 56). Only in clade 40 (Fig. 2) are strains collected from Europe that were suitable for epitypification (Fig. 52); the other strains are tentatively considered as *R. hieracii-umbellati* (Fig. 2, clade 56) and as *R. helminthiae* (Fig. 2, clade 5). The clade representing *R. inaequalis* is highly supported (Fig. 2, clade 40, 1/100/100). *Ramularia inaequalis* has a very wide host range and distribution.

Ramularia interstitialis (Berk. & Broome) Gunnerb. & Constant., Thunbergia 15: 50. 1991. Fig. 53.

Basionym: Peronospora interstitialis Berk. & Broome, Ann. Mag. Nat. Hist. 15: 34. 1875.

- ≡ Ovularia interstitialis (Berk. & Broome) Massee, British Fungus-Flora 3: 322. 1893.
- = Ramularia primulana P. Karst., Hedwigia 23 (1): 7. 1884.
- = Ovularia corcellensis Sacc. & Berl., Atti Ist. Veneto Sci. Lett. Arti 3: 731. 1885.

Mycelium hyaline, septate, branched. *Conidiophores* and *conidiogenous cells* scarce and insufficient for complete description. *Conidia* hyaline, smooth to slightly verruculose, catenate, branching chains, consistently aseptate, ellipsoid-ovoid, occasionally subcylindrical, obovoid $(3.5-)6-8(-20) \times (2.5-)$ $3.5-4(-5) \mu m$.

Description in vivo: See Braun (1998: 225).

Specimen examined: UK, Southwestern England, Exeter, on Primula vulgaris × vernalis, S.A.J. Tarr, CBS H-17746, culture CBS 120.68.

Substrate and distribution: On Primula (Primulaceae); Europe.

Notes: Two species have been described from hosts of the genus Primula, Ramularia primulae and R. interstitialis, that have a broad distribution in Europe. Ramularia primulae produces catenate conidia, $(8-)10-35(-40) \times 3-6 \mu m$, that are 0-2(-3)-septate. Ramularia interstitialis produces very distinctive conidiophores, erect or decumbent to repent, long and strongly geniculate-sinuous, the conidia are produced singly, occasionally in short chains, are aseptate and $(6-)8-16(-21) \times (4-)5-8(-10)\mu m$. In the observed specimen (Fig. 53), the conidiogenous structures observed were too scarce for a proper analysis and the conidia were slightly narrower than in the description of R. interstitialis found in literature (Braun 1998). However, the name is tentatively used for this isolate pending the collection of fresh material since in vitro measurement can vary when compared to in vivo. The strain used in this study originated from the UK and falls in the Ramularia clade (Fig. 1, clade XIV), but was not used in the multigene phylogeny because it was not possible to amplify the partial genes of gapdh and rpb2.

Ramularia kriegeriana Bres., Hedwigia 39: 328. 1900.

= Ramularia plantaginis Ellis & G. Martin, Amer. Naturalist 16: 1003. 1882, nom. illeg., non *R. plantaginis* Peck, 1880.

Specimens examined: Germany, Saxony, Königstein, Pfaffendorf, on *Plantago* major, 17 Jul. 1895 [Krieger, Fungi Saxon Exs. 1630; lectotype of *R. kriegeriana*, designated in Braun (1998), in JE]. South Korea, Hoengseong, on *Plantago* asiatica, 10 Oct. 2003, H.D. Shin, KUS-F19845, culture CPC 10825–10827. USA, Kentucky, Lexington, on *Plantago* major, Jul. 1882, Kellerman s.n.; type of *R. plantaginis* Ellis & G. Martin, in BPI 418612.

Substrate and distribution: On Plantago spp. (Plantaginaceae); Asia, Europe, N. America.

Notes: Braun (1998) used the name Ramularia plantaginis Ellis & G. Martin for Ramularia on Plantago major and other species characterised by verruculose conidia. This was based on the wrong assumption that R. plantaginis Peck was also published in 1882, which is, however, not correct since the latter name was published in 1880, which makes R. plantaginis Ellis & G. Martin an illegitimate homonym. Thus, R. kriegeriana is the oldest valid name for this fungus. This species has previously been reported from South Korea on Plantago asiatica, and is known from several Plantago species in Asia, Europe and N. America, including P. asiatica from China (Braun 1998). The strains in this study cluster together in a highly supported clade (Fig. 2, clade 65, 1/100/100) although a collection from Germany is required to fix the application of this name. Plantago asiatica is phylogenetically close to P. major, the principal host of Ramularia kriegeriana. The two species belong in Plantago subgen. Plantago, in contrast to P. lanceolata, the principal host of R. rhabdospora, which belongs in subgen. Psyllium (Rønsted et al. 2002).

Ramularia lamii Fuckel var. *lamii*, Jahrb. Nassauischen Vereins Naturk. 23–24: 361. 1870. Fig. 54.

≡ *Ovularia lamii* (Fuckel) Sacc., Syll. ung. 6: 144. 1886. For additional synonyms see Braun (1998).

Mycelium consisting of hyaline, septate, branched, smooth, 1–3 µm diam hyphae. *Conidiophores* hyaline, thin-walled, smooth, erect, septate, straight to geniculate-sinuous, cylindrical-oblong, unbranched, $(8-)10-50(-80) \times 1.5-2(-3)$ µm or reduced to

conidiogenous cells. *Conidiogenous cells* integrated in mycelium or terminal on conidiophores, cylindrical-oblong, (7.5–) $18.5-24.5(-33) \times 1.5-2(-2.5) \mu m$, with 1–3 apical conidiogenous loci almost flat, thickened, darkened and refractive. *Conidia* hyaline, thin-walled, smooth, catenate, with hila thickened, darkened and refractive. *Ramoconidia* subcylindrical to clavate, sometimes with broader apexes and narrower at the centre, (9–) $14-18(-28) \times (2.5-)3-3.5(-4) \mu m$, 0–1-septate, with two apical hila. *Intercalary conidia* subcylindrical, sometimes slightly curved, ovoid, (8.5–)11.5–13(–19) × (2.5–)3(–4) µm, in branched chains of up to six conidia. *Terminal conidia* obovoid, aseptate, (4.5–) $7-8(-11.5) \times (2-)2.5-3(-5) \mu m$ (on SNA, CBS 108971).

Culture characteristics: On MEA surface strongly folded, rosybuff with smoke-grey areas, low convex with margins concave and crenate, colony reverse fawn to cinnamon, folded, grows 1.7 mm after 2 wk at 25 °C. On OA surface flat, aerial mycelium white with a rose tinge raised in the centre, produces a transparent exudate, with margins undulate, sparse aerial mycelium, rosy-buff, colony reverse saffron, grows 1.8 mm after 2 wk at 25 °C. On PDA, surface low convex, white with a light grey tinge, fluffy, with margins slightly undulate, colony reverse salmon with olivaceous grey patches, grows 1.8 mm after 2 wk at 25 °C.

Specimens examined: Germany, on Lamium album [Fuckel, Fungi Rhen. Exs. 136; lectotype, designated in Braun (1998), in HAL]. Netherlands, Utrecht Prov., Baarn, de Hooge Vuursche, leaf spot of Lamium album, 22 Jun. 2000, G. Verkley (epitype designated here CBS H-22639, MBT371840, culture ex-epitype CBS 108970); *idem.* CBS 108971.

Description in vivo: See Braun (1998: 183).

Substrate and distribution: on Lamium (Lamiaceae); Asia, Caucasus, Europe, N. Africa, N. America.

Notes: There are two varieties of *R. lamii*, namely *R lamii* var. *lamii* (on *Lamium album*, Germany, lectotype in HAL), and *R. lamii* var. *minor* (on *Prunella vulgaris*, USA, Winsconsin, holotype in NY). The latter variety has smaller conidiophores and smaller and narrower conidia. Strains originally identified as *R. lamii* appeared in three distinct clades in the phylogeny (Fig. 2, clades 1, 46 and 67) showing that more than one species is present in this complex. The strains in clade 67 (Fig. 2) were collected in the Netherlands and are morphologically good representatives of *R. lamii* (Fig. 54), and are therefore designated as ex-epitype strains, whereas the other strains are assigned to *R. leonuri* and *R. agastaches*, respectively. All three phylogenetic analyses provided high support to this species clade (Fig. 2, clade 67, 1/100/100).

Ramularia leonuri Sorokīn, Trudy Obshch. Estestvoisp. Imp. Kazansk. Univ. 2: 30. 1872. Fig. 55.

≡ Ramularia sorokinii Sacc. & Syd., Syll. fung. 14: 1065. 1899, nom. illeg. (superfl.).

= Ramularia leonuri Sacc. & Penz., Michelia 2: 638. 1882.

Mycelium consisting of hyaline, septate, branched, smooth, 1–1.5 µm diam hyphae. *Conidiophores* hyaline, thin-walled, smooth, erect, 1–3-septate, straight, cylindrical-oblong, unbranched, (11.5–)20–25.5(–28) × 1.5–2 µm or reduced to conidiogenous cells. *Conidiogenous cells* integrated in mycelium, cylindrical-oblong, (4–)11–15(–19) × 1–2(–3) µm, with one conidiogenous locus, thickened and darkened. *Conidia* hyaline,



Fig. 54. Ramularia lamii var. lamii (CBS 108971). A-E. Structures formed in culture. A, E. Conidia. B-D. Conidiophores, conidiogenous cells and conidia. Scale bars = 10 µm.



Fig. 55. Ramularia leonuri (CPC 11314). A–D. Observations from herbarium material. E–G. Structures formed in culture. A. Leaf spot symptoms on the host. B, E. Conidia. C, D. Conidiophores and conidiogenous cells. F, G. Conidiophores and conidia. Scale bars = 10 μm.

thin-walled, smooth, catenate, with hila thickened and darkened. *Ramoconidia* subcylindrical to clavate, aseptate to 1-septate and narrower at the septa, $(18-)21-23.5(-28) \times (2-)2.5-3 \mu m$, with two conidiogenous apical hila. *Intercalary conidia*, aseptate to 1-septate, subcylindrical, sometimes curved, $(14.5-)18.5-21(-28) \times (1.5-)2.5-3(-3.5) \mu m$, in chains of up to five conidia. *Terminal conidia*, aseptate, subcylindrical to obovoid, $(6.5-)13-15(-25) \times (2-)2.5-3(-4) \mu m$. *Culture characteristics*: On MEA, 27 mm diam, surface smooth, low convex, radially striated, cracking in the centre, with entire margins, convex and feathery, colony reverse iron-grey with ochreous margin; on OA, 20 mm diam, surface flat, fluffy uniform, white with buff tinge, with margins buff and with no aerial mycelium, undulate, colony reverse buff; on PDA, 25 mm diam, surface concave, smooth and white, margins entire, feathery and low convex, colony reverse olivaceous grey and buff.

Specimens examined: France, Rouen, on *Leonurus cardiaca*, Letendre, herb. Saccardo (holotype of *R. leonuri* Sacc. & Syd. PAD); Russia, Jaroslavl, Bernichino, on *Leonurus cardiaca*, 22 Aug. 1909, Serebrianikov [Tranz. & Serebr., Mycoth. Ross. 48; neotype of *R. leonuri* Sorokin, designated in Braun (1998), in LE 200619]; South Korea, Hongcheon, on *Leonurus sibiricus*, 9 Oct. 2007, H.D. Shin, KUS-F22992, CBS H-22522, culture CBS 141112 = CPC 14570; *idem*. CPC 14571, CPC 14572; Jinju, on *Leonurus sibiricus*, 14 May 2004, H.D. Shin, KUS-F20195, cultures CPC 11312–11314; Yangpyeong, on *Leonurus sibiricus*, 23 Jul. 2004, H.D. Shin, KUS-F20502, cultures CPC 11411–11413.

Notes: Ramularia leonuri on Leonurus cardiaca, reduced to synonymy under *R. lamii* var. *lamii* by Braun (1998), is morphologically indistinguishable from the Korean material on *L. sibirica*. Therefore, we prefer to apply this name to this collection, at least tentatively, although cultures of *R. leonuri* from France and Russia are not yet available for comparison. The *R. leonuri* clade was highly supported by phylogenetic analyses (Fig. 2, Clade 1, 1/100/100) and is currently known only from South Korea. These strains were previously identified as *R. lamii* var. *lamii* but the type of *R. lamii* clusters in a different clade (Fig. 2, clade 67). *Ramularia leonuri* and *Ramularia lamii* var. *lamii* are morphologically very similar but *R. leonuri* produces shorter conidiophores, smaller conidiogenous cells and longer terminal conidia (Fig. 55).

Ramularia lethalis Ellis & Everh., Proc. Acad. Nat. Sci. Philadelphia 43: 86. 1891. Fig. 56.

Mycelium consisting of hyaline, septate, branched, smooth, 1–2 µm diam hyphae. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* hyaline, thin-walled, smooth, integrated in mycelium, cylindrical-oblong to geniculate-sinuous, $(6-)10-12(-15) \times 1-2$ µm, with 1–3 apical conidiogenous loci almost flat to protuberant, thickened and darkened. *Conidia* hyaline, thin-walled, smooth to verruculose, catenate, mostly aseptate and rarely 1-septate, with hila thickened and darkened. *Ramoconidia* subcylindrical to ellipsoid, $(4-)6-7(-12) \times (1.5-)$ 2.5-3 µm, with 2–3 conidiogenous apical hila. *Intercalary conidia*, fusoid-ellipsoid, $(4-)5(-6.5) \times (1.5-)2-3$ µm, in chains of up to three conidia. *Terminal conidia*, aseptate, ellipsoid-obovoid, $(2-)3-4 \times (1-)2-2.5$ µm.

Culture characteristics: On MEA, 8 mm diam, surface raised, irregular, mycelium smooth and white, with entire margin, convex and feathery, colony reverse ochraceous; on OA, 10 mm diam, surface raised, irregular, mycelium smooth, white with buff tinge, margins undulate, colony reverse buff; on PDA, 9 mm diam, surface smooth, mycelium flat and white, entire margins, colony reverse buff with olivaceous patches.

Description in vivo: See Braun (1998: 46).

Specimens examined: Netherlands, Utrecht, Hollandse Hout, on leaves of Acer pseudoplatanus, 5 Apr. 2012, S.I.R. Videira, cultures CBS 141113 = CPC 25910. Canada, Ontario, London, on Acer rubrum, Oct. 1890, Dearness [Ellis & Everh., N. Amer. Fungi 2596; lectotype, designated in Braun (1998), in NY 830534].

Substrate and distribution: On *Acer*, Caucasus, Europe (the Netherlands) and North America.

Notes: Three species of *Ramularia* are known from *Acer*, namely *R. lethalis*, *R. unterseheri* and *R. vizellae*. *Ramularia lethalis* (Fig. 56) was originally described on *Acer rubrum* from Canada (lectotype in NY). The strain used in this study forms a single

lineage and is positioned in a very long branch, which supports this species as unique (Fig. 2, clade 84). Morphological characters of the isolate used in this study agree with the description of *R. lethalis* from literature (Braun 1998). This is a first report of this pathogen in Europe and on *Acer pseudoplatanus*.

Ramularia ligustrina Maubl., Bull. Trimestriel Soc. Mycol. France 22: 70. 1906.

Specimen examined: Italy, Torino, on living leaf of *Ligustrum vulgare*, unknown collector and date, isol. and dep. M. Ribaldi, Oct. 1952, culture CBS 379.52.

Substrate and distribution: On *Ligustrum vulgare*; Caucasus (Armenia), Europe (Bulgaria, France, Germany, Italy and Moldova).

Notes: Ramularia ligustrina was described as a pathogen on *Ligustrum vulgare* in France, but was considered doubtful by Braun (1998) since type material or other collections agreeing with the description could not be traced. The species is insufficiently known but the name is tentatively accepted here given its distinct phylogeny (Fig. 2, clade 69), pending further collections.

Ramularia macrospora Fresen., Beitr. Mykol. 3: 88. 1863.

- ≡ Cylindrosporium macrosporum (Fresen.) J. Schröt., Krypt.-Fl. Schlesien 3.2(4): 490. 1897.
- = Scolicotrichum ochraceum Fuckel, Fungi Rhen. Exs., Cent. 22: no. 2108. 1868.
- = Ramularia prismatocarpi Oudem., Ned. Kruidk. Arch. 3: 155. 1877.
- = Cercospora phyteumatis A.B. Frank, Krankh. Pfl., 1. Aufl.: 601. 1880.
- = Ramularia adenophorae Moesz, Bot. Közlem. 35 (1-2): 67. 1938.
- *= Ramularia rapunculoidis* Nannf., in Lundell & Nannfeldt, Fungi Exs. Suec. 39–40: 31. 1950.

For additional synonyms see (Braun 1998)

Description in vivo: See Braun (1998: 125).

Specimen examined: Austria, Ötztal, Sölden, Hoch-Sölden, alt. 1800 m., on leafspots of *Phyteuma betonicifolium*, 25 Jul. 2000, G. Verkley, No. 1011.1, cultures CBS 109015, 109016.

Substrate and distribution: On Adenophora, Asyneuma, Campanula, Gadellia, Legousia, and Phyteuma (Campanulaceae), Aristolochia punjabensis (Aristolochiaceae); Asia, Caucasus, Europe, N. America, Pakistan.

Notes: Ramularia macrospora was described as a pathogen on Campanula pyramidalis from Germany (iconotype Pl. XI, figs 29–32). The strains used in this study cluster in the Ramularia clade (Fig. 1, clade XIV) but were not used in the multigene analysis because it was not possible to amplify and sequence the *tef1-* α partial gene. Although *R. macrospora* is usually associated with members of the Campanulaceae (Braun 1998), it was recently observed infecting a host from the Aristolociaceae (Mukhtar *et al.* 2012).

Ramularia major (Unger) U. Braun, Nova Hedwigia 47: 340. 1988.

Basionym: Cylindrospora major Unger, Exanth. Pfl.: 168: 1833.

- = Fusidium petasitidis Pass., in Thüm., Mycoth. Univ. 1473. 1879.
- = Ramularia cervina Speg., Dec. Mycol. Ital.: 107. 1879.
- ≡ *Cylindrospora cervina* (Speg.) J. Schöt., in Cohn, Krypt.-Fl. Schlesien 3.2(4): 488. 1897.
- = R. variegata Ellis & Holw., in Arth., Rep. Bot. Minnesota: 34. 1886.



Fig. 56. Ramularia lethalis (CBS 141113). A-I. Structures formed in culture. A, F. Conidiophores reduced to conidiogenous cells and conidia. B-E, G, H, I. Conidia. Scale bars = 10 µm.

= R. petasitis-tomentosae Săvul. & Sandu, Hedwigia 73: 121. 1933. For additional synonyms see Braun (1998) or MycoBank.

Description in vivo: See Braun (1998: 86).

Specimens examined: Germany, Thuringia, Erfurt, on *Petasites hybridus*, 7 Oct. 1910, Diedicke [neotype, designated in Braun (1998), in JE]. South Korea, Chuncheon, on *Petasites japonicus*, 25 Oct. 2005, H.D. Shin, KUS-F21578, CBS H-22523, cultures CBS 141114 = CPC 12542; *idem*. CPC 12543, CPC 12544.

Substrate and distribution: On Adenostyles, Homogyne, and Petasites (Asteraceae); Asia, Caucasus, Europe, N. America.

Notes: Ramularia major was originally described on *Petasites hybridus* from Germany (neotype in JE) and is a common pathogen associated with a few related hosts of the family *Asteraceae* worldwide (Braun 1998). The strains used in this study form a highly supported clade (Fig. 2, clade 10, 1/100/100), which is tentatively maintained as representative of the species until material from the type host and location are recollected and examined.

Ramularia mali Videira & Crous, Persoonia 34: 58. 2015.

Specimen examined: Italy, Piemont, on Malus domestica fruit in cold storage, May 2011, unknown collector, dep. R. Piemonte & G. Michelatti (holotype CBS H-21618, culture ex-type CBS 129581).

Substrate and distribution: Thus far only known from the type collection.

Notes: See Videira *et al.* (2015a). This species formed a single lineage (Fig. 2, clade 33) basal to the *R. glenii* clade (Fig. 2, clade 32). In a single lineage next to *R. mali* we can observe *Ramularia* sp. B, which is sterile in culture and could not be described.

Ramularia malicola Videira & Crous, **sp. nov.** MycoBank MB816850. Fig. 57.

Etymology: Named after the host it was isolated from, Malus.

Mycelium consisting of hyaline, septate, branched, smooth, $2-4 \mu m$ diam hyphae. *Conidiophores* hyaline, thin-walled, smooth, erect, multiseptate, straight, cylindrical-oblong, unbranched, (45–) $100-120(-158) \times (2.5-)4-5(-6) \mu m$ or reduced to conidiogenous cells. *Conidiogenous cells* integrated in mycelium, cylindrical-oblong, $(16.5-)25-32(-42) \times (3-)4(-5) \mu m$, with one apical conidiogenous locus, thickened and darkened. *Conidia* formed singly, hyaline, thin-walled, smooth, aseptate, ellipsoid, obovoid, (11–) $21-27(-40) \times (4.5-)6-7(-8) \mu m$, with hila thickened and darkened.

Culture characteristics: On MEA, 15 mm diam, surface raised and strongly folded, rosy-vinaceous with erumpent white mycelium, with small ochreous droplets, with margins crenate, colony reverse ochreous; on OA, 10 mm diam, surface raised, folded, rosy-vinaceous with erumpent white mycelium, with margins crenate, feathery, colony reverse brick; on PDA, 15 mm diam, surface raised and strongly folded, rosy-vinaceous with erumpent white mycelium, with small buff droplets, with margins crenate, colony reverse ochreous.

Specimen examined: USA, Missouri, New Franklin, on *Malus* sp., Sep. 2000, J. Batzer (holotype CBS H-22524, ex-type culture CBS 119227).

Note: Ramularia malicola formed a single lineage (Fig. 2, clade 80) that is sister to *R. rubella* (Fig. 2, clade 79). This species is morphologically similar to *R. rubella* but differs by forming wider conidia (Fig. 57). Ramularia malicola was first isolated in a study related to sooty blotch and flyspeck on



Fig. 57. Ramularia maliicola (CBS 119227). A-H. Structures formed in culture. A-D. Conidiophores and conidia. E-G. Conidia. H. Conidiogenous cells. Scale bars = 10 µm.

apple in the USA (Batzer *et al.* 2005). It was present in samples collected from two orchards and caused punctate symptoms on the fruit. It was described as *Ramularia* sp. P5 based on the morphological characteristics that included hyaline, single-celled, ovularia-type conidia, irregular in shape, $5.2-14.5 \times 1.5-7 \mu m$ (CLA media), produced on brown conidiophores that had dendritic branches with a single central basal cell. In this study, the conidiophores observed were always hyaline but a different culture medium was used to that of Batzer *et al.* (2005).

Ramularia miae Crous, Fungal Planet No. 3. 2006.

Specimens examined: South Africa, on Wachendorfia thyrsiflora, 4 Jan. 2006, M.K. Crous & P.W. Crous (holotype CBS H-19763, ex-type culture CBS 120121 = CPC 12736), idem. cultures CPC 12737, CPC 12738; on Gazania rigens var. uniflora, 9 Aug. 2011, P.W. Crous, culture CPC 19835; on Leonotis leonurus, 30 Jul. 2011, P.W. Crous, culture CPC 19770; on Wachendorfia thyrsiflora, 28 Oct. 2012, M.J. Wingfield, culture CPC 21692.

Substrate and distribution: On Gazania rigens var. uniflora (Asteraceae), Leonotis leonurus (Lamiaceae) and Wachendorfia thyrsiflora (Haemodoraceae); South Africa.

Notes: See Crous and Groenewald (2006) and Videira *et al.* (2015a). The phylogenetic analyses provide high support for this species clade (Fig. 2, clade 29, 1/100/100).

Ramularia neodeusta Videira & Crous, **sp. nov.** MycoBank MB817159.

Etymology: Named after its morphological similarity to *Ramularia deusta*.

Cultures sterile. Ramularia neodeusta (Fig. 2, clade 15), differs from its closest phylogenetic neighbour, *R. vallisumbrosae* (Fig. 2, clade 16), by unique allelles in five loci based on alignments of the separate loci deposited in TreeBASE as Study S19315: rpb2 positions 12(C), 15(A), 27(G), 39(A), 45(G), 54(C), 63(G), 75(A), 87(A), 99(C), 120(G), 135(C), 150(C), 151(T), 165(C), 168(T), 171(T), 186(G), 189(C), 195(T), 201(G), 204(T), 234(C), 240(G), 246(C), 252(C), 253(T), 264(A), 285(T), 297(G), 303(G), 318(C), 321(G), 324(C), 327(A), 330(G), 333(A), 336(A), 354(A), 357(A), 363(G), 375(G), 378(C), 387(T), 405(G), 411(T), 420(T), 441(G), 447(G), 456(T), 468(T), 478(G), 480(G), 483(C), 489(C), 492(T), 499(T), 504(C), 505(A), 507(T), 511(G), 519(G), 524(A), 532(C), 540(C), 546(A), 570(A), 576(T), 582(G), 591(C), 597(A), 630(A), 639(T), 642(A), 651(A); ITS positions 77(A), 81(T), 82(C), 108(G), 109(A), 110-111 deletion (TC), 342(A), 419(A), 420(G), 472(G), 500(C); actA positions 19(T), 31(G), 34(T), 49(C), 59(C), 61(A), 62(T), 63-67 insertion (GAGCA), 68(G), 69(C), 73(C), 82-83 deletion (AC), 86-88 deletion (CGA) 95(A), 96(G), 98(A), 99(A), 101(C), 108(T), 115(T), 116(T), 121(A), 122(T), 153(C), 164(C), 167(T), 182(T), 186(T), 208(C), 210(A), 211(T), 233(A), 238(C); gapdh positions 13(G), 18(A), 30(C), 39(A), 41(A), 42(C), 44(G), 47(G), 49(C), 60(G), 65(A), 66(G), 68(C), 101(G), 106(A), 113 deletion (C), 114(C), 116(G), 131(C), 140(C), 167(C), 200(C), 206(T), 207(C), 208(G), 210(T), 258(T), 259(C), 260(C), 262-263 insertion (TA), 264(C), 265 insertion (A), 267 insertion (G), 268(A), 269(A), 270(T), 271(A), 281(G), 282(G), 284(C), 286(C), 287(C), 288(G), 290(T), 292(C), 298(T), 299(T), 305(T), 307(T), 308(C), 313 deletion (G), 314(C), 315(C), 374(C), 389(C), 431(T), 449(A), 455(C), 506(T), 548(C), 554(C), 566(T), 584(T), 593(T), 614(C), 623(T), 626(T); tef1-a positions 14(T), 15(T), 16(T), 20(T), 22(C), 23(C), 24(T), 26 deletion (C), 27(T), 29 deletion (T), 45 deletion (CTC), 48(A), 49(C), 52(A), 57(G), 58(C), 86(C), 95(A), 99(T), 107(A), 129(T), 145(T), 178 deletion (T), 195(C), 212(T), 226-228 insertion (TAA), 232(A), 241(A), 242(A), 247(T), 255(C), 256(C), 257(A), 269(A), 271(T), 291(C), 292(C), 294(A), 304(T), 307-310 insertion (CTAT), 311(G), 313(A), 316(C), 398(T), 400(C), 401(T), 404(A), 406(C), 407(A), 409(A), 410(C), 411-424

insertion (TTCTCAACAAACTT), 427(T), 431(A), 432(A), 434(T), 447(C), 448(A), 450(T), 455(C), 578(T).

Specimens examined: **New Zealand**, on leaf of *Vicia faba*, 25 Oct. 2005, C.F. Hill (**holotype** CBS H-22525, culture ex-type CBS 141115 = CPC 13567); on leaf of *Lathyrus odoratus*, 23 Oct. 2005, C.F. Hill, culture CPC 13568.

Notes: This strain was initially identified as *R. deusta* var. *alba*, a species that was previously reported from New Zealand on *Lathyrus pratensis* and *L. latifolius*. However, an authentic strain of *R. deusta* can be found in clade 62 (Fig. 2). Therefore, the strains in this clade represent a new species that is highly supported (Fig. 2, clade 15, 1/100/100). Unfortunately the strains were sterile and therefore a molecular description is provided.

Ramularia nyssicola (Cooke) Videira & Crous, Persoonia 34: 60. 2015.

Basionym: Sphaerella nyssicola Cooke, Hedwigia 17: 40. 1878. ≡ Mycosphaerella nyssicola (Cooke) F.A. Wolf, Mycologia 32: 333. 1940.

Description: See Minnis et al. (2011).

Specimens examined: **USA**, Maryland, Prince George's County, Glen Dale, on overwintered leaves *Nyssa ogeche* × *sylvatica* hybrid, R.T. Olsen, culture CBS 127664; same location, substrate and collector, 18 Jun. 2009 (**epitype** BPI 880897, AR 4656, culture ex-epitype CBS 127665).

Substrate and distribution: On Nyssa (Cornaceae); N. America (eastern USA).

Notes: See Minnis *et al.* (2011), who designated an epitype for the species, and Videira *et al.* (2015a) who reassigned the species to the genus *Ramularia*. The phylogenetic analyses provide high support to this species clade (Fig. 2, clade 81, 1/100/100).

Ramularia osterici Videira, H.D. Shin & Crous, **sp. nov.** MycoBank MB816851. Fig. 58.

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

Mycelium consisting of hyaline, septate, branched, smooth, 1-2.5 µm diam hyphae. Conidiophores hyaline, erect, 1-3(-5)septate, straight, cylindrical-oblong, unbranched (13-) 34-51(-140) × (1.5-)2-2.5(-3) µm or reduced to conidiogenous cells. Conidiogenous cells hyaline, smooth, integrated in mycelium or terminal in conidiophores, cylindrical-oblong, (10-) 17.5-21(-30) × (2-)2.5-3(-4) µm, with one apical conidiogenous locus, almost flat, thickened, darkened, refractive. Conidia hyaline, smooth, catenate, with hila thickened, darkened, refractive. Ramoconidia subcylindrical, clavate, with broader apices and narrower centre, $(10-)14.5-17.5(-30) \times (2-)$ 3(-4) µm, 0-1-septate, with two apical hila. Intercalary conidia subcylindrical, fusoid, sometimes curved, 0-1-septate, (9.5-) $12.5-14(-18) \times (2.5-)3(-4) \mu m$, in branched chains of up to eight conidia. Terminal conidia subcylindrical to obovoid, (4.5-) 8-9.5(-14.5) × (2-)2.5-3(-3.5) µm.

Culture characteristics: On MEA, 10 mm diam, surface raised, strongly folded, smooth, pale smoke-grey with margins undulate, colony reverse iron-grey; on OA, 13 mm diam, surface convex, fluffy aerial mycelium, white to buff, with margins undulate, colony reverse buff; on PDA, 14 mm diam, surface raised, folded,

with fluffy aerial mycelium white to buff, with margins undulate, colony reverse buff with iron-grey patches.

Specimens examined: **South Korea**, Pyeongchang, on Ostericum grosseserratum (≡ Angelica grosseserrata, = Ostericum koreanum), 20 Sep. 2003, H.D. Shin (**holotype** KUS-F19687, **isotype** CBS H-22545, culture ex-type CBS 141116 = CPC 10750); *idem*. CPC 10751, CPC 10752.

Substrate and distribution: On Ostericum (Apiaceae); Asia (South Korea).

Notes: Ramularia osterici is morphologically similar to *R. archangelicae*, but with shorter and broader ramoconidia, intercalary and terminal conidia (Fig. 58), and it does not produce any pigment in culture. Strains CBS 108991 (*R. archangelicae*) and CPC 10751 (*R. osterici*) are identical based on their ITS sequences but differ in several nucleotides in the other six genes amplified: 1 (LSU), 24 (actA), 32 (gapdh), 45 (tef1-α), 25 (his3), 26 (*cmdA*). The *R. osterici* clade is highly supported (Fig. 2, clade 20, 1/100/100). This is the first *Ramularia* species described on *Ostericum (Apiaceae*).

Ramularia parietariae Pass., in Rabenh., Fungi Eur. Exs., Ed. nov., Ser. sec., Cent. 2 (resp. Cent. 21), no. 2066: 1876.

- ≡ *Cylindrospora parietariae* (Pass.) J. Schröt., in Cohn, Krypt.-Fl. Schlesien 3.2(4): 493: 1897.
- = Ramularia parietariae var. minor Bubák, Bull. Herb. Boiss., 2 Sér., 6: 486. 1906.

Description in vivo: See Braun (1998: 274).

Specimens examined: Czech Republic, Moravia, Pavlov, forest around the ruin, on leaf spot on *Parietaria officinalis*, 18 Sep. 2008, G. Verkley, cultures CBS 123730, CBS 123731. Italy, Parma, Gajone, on *Parietaria officinalis*, Oct. 1874, Passerini [Rabenh., Fungi Eur. Exs. 2066; lectotype, designated in Braun (1998), in HAL].

Substrate and distribution: On Parietaria (Urticaceae); Central Asia, Caucasus, Europe, Israel, N. Africa, N. America.

Notes: Ramularia parietariae was originally described on Parietaria officinalis from Italy (lectotype in HAL), but it is also pathogenic to other species of the genus Parietaria. Phylogenetic analyses showed that these strains cluster together in a highly supported clade (Fig. 2, clade 47, 1/100/100).

Ramularia phacae-frigidae (E. Müll. & Wehm.) Videira & Crous, Fungal Biol. 119: 836. 2015.

Basionym: Mycosphaerella phacae-frigidae E. Müll. & Wehm., Sydowia 8: 190. 1954.

Specimen examined: Switzerland, Corveglia, above St. Moritz, on dead leaves of *Phaca frigida*, 20 Jul. 1953, E. Müller (holotype in ZT, ex-type culture CBS 234.55).

Substrate and distribution: On Phaca frigida (Fabaceae), Europe (Switzerland).

Notes: Ramularia phacae-frigidae was originally described as Mycosphaerella phacae-frigidae, a pathogen infecting Phaca frigida from Helvetia (holotype in ZT). Although Müller & Wehmeyer (1954) mentioned the presence of Ramularia and Asteromella morphs in his description of Mycosphaerella phacae-frigidae, he refrained from naming them. The allocation to



Fig. 58. Ramularia osterici (CPC 10751). A, B. Observations from herbarium material. C-G. Structures formed in culture. A. Leaf spot symptoms on the host. B-D, F, G. Conidiophores, conidiogenous cells and conidia. E. Conidia. Scale bars = 10 µm.

Ramularia was based on the phylogenetic position of the ex-type culture (Videira *et al.* 2015b), which in this study is located in clade 63 (Fig. 2).

Ramularia plurivora Videira & Crous, Persoonia 34: 60. 2015.

Description: Videira et al. (2015a).

Specimens examined: Netherlands, Den Haag, Laboratory of Medical Microbiology, Hospital Leyenburg, from human bone marrow, 2005 (holotype CBS H-21619, culture ex-type CBS 118743 = CPC 12207); Hilversum, Central Biological and Serological Laboratory, on human skin from neck, 20 May 2005, culture CBS 118693 = CPC 12206; on melon in storage, 1 Jan. 2008, J.H. Houbraken, culture CPC 16123, CPC 16124. Korea, on *Coleosporium plectranthi* on *Plectranthus excisus*, 2004, H.D. Shin, CPC 11517.

Substrate and distribution: On human samples, on *Cucumis* sp., on *Coleosporium plectranthi on Plectranthus excisus*; in Europe (Netherlands) and East Asia (South Korea).

Notes: See Videira *et al.* (2015a). Phylogenetic analyses provided high support for this species clade (Fig. 2, clade 35, 1/100/100).

Ramularia pratensis Sacc. var. *pratensis*, Fungi ital. Del., Tab. 998. 1881, and Michelia 2: 550. 1882 emend. U. Braun, 1998. Fig. 59.

- = Ramularia rhei Allesch., Hedwigia 35: 34. 1896.
- = Ovularia rumicis A. G. Eliasson, Bih. Kungl. Svenska Vetenskapsakad. Handl. 22, Afd. 3, 12: 18. 1897.
- = Ramularia rumicis-crispi Sawada, Rep. Dept. Agric. Gov. Res. Inst. Formosa 85: 89. 1943.
- = Ramularia oxyriae-digynae Gjaerum, Norweg. J. Bot. 18: 110. 1971.

Mycelium consisting of hyaline, septate, branched, smooth, $1-2 \mu m$ diam hyphae. *Conidiophores* reduced to *conidiogenous cells*, hyaline, thin-walled, smooth, integrated in mycelium or

terminal in conidiophores, cylindrical-oblong and narrower at the top, $(5.5-)12-15(-27) \times (1.5-)2(-3) \mu m$, with 1–2 apical conidiogenous loci almost flat to short cylindrical; *conidiogenous loci* thickened, darkened, refractive, 1 μ m diam. *Ramoconidia* hyaline, thin-walled, smooth, subcylindrical to obclavate, (5-) 8.5–11(–19) × (2–)2.5–3(–4) μ m, aseptate to 1–3-septate, with 2–3 apical hila. *Intercalary conidia* hyaline, smooth, aseptate or 1–3-septate, subcylindrical with apices rounded and broader, $(5-)7-8(-11.5) \times 2-2.5(-3) \mu$ m, in branched chains of up to seven conidia. *Terminal conidia*, hyaline, smooth, aseptate, obovoid, $(3-)4.5-5(-6) \times 2-2.5(-3) \mu$ m, *hila* thickened, darkened, refractive, 1 μ m diam.

Culture characteristics: On MEA, 18 mm diam, surface low convex, folded, fluffy aerial mycelium, pale olivaceous grey and dirty white, with margins undulate, convex, feathery, colony reverse iron-grey and buff margin; on OA, 30 mm diam, surface flat, smooth aerial mycelium, dirty white, transparent exudate small droplets, margins with entire edge with no aerial mycelium, colony reverse violet slate; on PDA, 30 mm diam, surface flat, fluffy aerial mycelium, pale olivaceous grey and olivaceous grey, with margins crenate, with sparse aerial mycelium, colony reverse slate blue with buff margin.

Description in vivo: See Braun (1998: 123).

Specimens examined: Canada, Stittsville, Ontario, on Verbascum sp., 12 Jul. 2009, K.A. Seifert, culture CPC 16868. Italy, Padova, on *Rumex acetosa*, herb. Saccardo (holotype PAD); Taiwan, Hualian County, Hehuanshan, on living leaves of *Rumex* sp., 3 Apr. 2007, R. Kirschner & C.-J. Chen, culture CBS 122105. Unknown country and collection details, culture CPC 19448.

Substrate and distribution: On Oxyria, Rheum, and Rumex (Polygonaceae), and Verbascum (Scrophulariaceae); Asia, Caucasus, Europe, N. and S. America.



Fig. 59. Ramularia pratensis var. pratensis (CBS 122105). A–C. Observations from herbarium material. D–H. Structures formed in culture. A. Leaf spot symptoms on the host. B. Conidiogenous cells and conidia. D, G, H. Conidiophores, conidiogenous cells and conidia. C, E, F. Conidia. Scale bars = 10 µm.

Notes: Two varieties of Ramularia pratensis have been described, R. pratensis var. pratensis (on numerous Rumex species) with broader conidia, (6-)8-25(-35) × (1.5-)2-4(-5) µm), and R. pratensis var. angustiformis (Rumex acetosella, USA, holotype in NY) with very narrow conidia, 10-35 × 1.5-2 µm. It is the first time R. pratensis var. pratensis is reported from the host Verbascum (Scrophulariaceae). Ramularia rhei, currently a synonym of R. pratensis var. pratensis, has been reported as the causal agent of rhubarb leaf and petiole spot disease in the UK (Zhao et al. 2002). Rhubarb (Rheum rhaponticum) is a perennial crop that that is largely grown in northern Europe, the USA and Canada. Rhubarb petioles are mainly used in domestic food and in processed products such as jams, syrups and wine (Foust & Marshall 1991). Since the disease is not yet a problem of economic importance to rhubarb production in Europe, little research and investigation have been conducted on its biology and epidemiology, besides the work of Zhao et al. (2006) comparing the effect of temperature on conidial germination. This species clade is highly supported by the phylogenetic analyses (Fig. 2, clade 23, 1/100/100), and the strain CBS 122105 is considered a good representative of the species based on its morphological characters (Fig. 59).

Ramularia proteae Crous & Summerell, Austral. Pl. Pathol. 29: 277. 2000.

Specimen examined: Australia, Tasmania, on Protea Iongifolia, Aug. 1999, A. Macfadyen (holotype DAR 74883, culture ex-type CBS 112161 = CPC 3075).

Substrate and distribution: Thus far only known from the type location.

Notes: Ramularia proteae was the first Ramularia species reported from a Protea host. It was observed causing a leaf spot disease on *P. longifolia* in Tasmania (Crous *et al.* 2000). Ramularia proteae is morphologically similar to

R. stellenboschensis, described from South Africa but with smaller and fusoid conidia. This species clusters very close to *R. stellenbochensis* in the phylogenetic analyses (Fig. 1, clade XIV) and was not included in the multigene phylogeny because it was not possible to amplify the *tef1*- α partial gene.

Ramularia pusilla Unger, Exanth. Pfl.: 169. 1833. Fig. 60. *Caeoma pusilla* (Unger) Bonord., Handb. Mykol.: 41. 1851. *Ovularia pusilla* (Unger) Sacc., Syll. Fung. 4: 140. 1886. *Ramularia pulchella* Ces., Bot. Zeitung (Berlin) 11: 238. 1853.
For additional synonyms see Braun (1998) or MycoBank.

Mycelium consisting of hyaline, septate, branched, smooth, 0.5-1 µm diam hyphae. Conidiophores hyaline, thin-walled, smooth, erect, 1-3-septate, cylindrical-oblong, straight apically geniculate-sinuous, and unbranched (7.5-) $37-50(-96) \times (1-)2(-3)$ µm. Conidiogenous cells terminal on conidiophores, cylindrical-oblong to geniculate-sinuous, narrower at the top, $(6.0-)19-23(-37) \times (1-)2(-3) \mu m$, with multiple conidiogenous loci almost flat to protuberant and in a terminal or lateral position, thickened, darkened, refractive. Conidia formed singly, hyaline, thin-walled, smooth to verruculose, aseptate, ellipsoidal to obovoid, $(5-)8-10(-15) \times (3-)$ 5-6(-8) µm, hila thickened, darkened, refractive. Sporulating on SNA.

Culture characteristics: On MEA, 12 mm diam, surface raised, with white fluffy mycelium with a rosy-buff tinge, margins lobate, feathery and convex, colony reverse buff; on OA, 15 mm diam, surface wavy, smooth, with white to buff aerial mycelium, margins entire, colony reverse fawn; on PDA, 12 mm diam, surface flat, smooth, with fluffy white to buff mycelium, with margins entire, colony reverse buff.

Description in vivo: See Braun (1998: 205).



Fig. 60. Ramularia pusilla (CBS 124973). A-H. Structures formed in culture. A-C, F. Conidiophores and conidia. D, G. Conidia. E, H. Conidiophores. Scale bars = 10 µm.

Specimens examined: Austria, on *Poa nemoralis*, Unger, Exanth. Pfl., Pl. II, fig. 12, lectotype (iconotype, see Braun 1998). Germany, Frankfurt am Main, Botanical Garden, on leaves of *Poa annua*, 25 Feb. 2008, R. Kirschner (epitype designated here CBS H-22527, MBT204832, culture ex-epitype CBS 124973).

Substrate and distribution: Agropyrum, Agrostis, Alopecurus, Anthoxanthum, Arctagrostis, Arrhenatherum, Bromus, Calamagrostis, Cinna, Cynosurus, Dactylis, Deschampsia, Elymus, Eremopyrum, Festuca, Glyceria, Helictotrichon, Hierochloë, Hordeum, Lolium, Melica, Muhlenbergia, Phalaris, Phleum, Poa, Puccinellia, Trisetum, Triticum, Vulpia, and other undetermined grasses (Poaceae), almost circumglobal.

Notes: Ramularia pusilla is the type species of the genus Ramularia and has a broad host range within the family Poaceae and a worldwide distribution (Braun 1998). Two varieties of Ramularia pusilla are known, R. pusilla var. pusilla (on Poa nemoralis, Austria, iconotype) with conidiophores in small fascicles of 2-6, and R. pusilla var. baldingerae (on Phalaris arundinacea, Sweden, holotype in UPS), forming large tufts of conidiophores of 5-20. Strain CBS 124973 was examined by means of morphology and LSU sequence data in a previous study (Kirschner 2009), and was considered to be a good representative of the type species of the genus. In this study this strain forms a single lineage (Fig. 1, clade XIV; Fig. 2, clade 39) and is closely related to R. collo-cygni. The existing type material of this species consists of the original illustration (iconotype) since the original type material was not preserved and appropriate material for a neotypification could not be traced (Braun 1998). We hereby designate the strain CBS 124973 as exepitype culture of R. pusilla (Fig. 60).

Ramularia rhabdospora (Berk. & Broome) Nannf., Fungi Exs.. Suec. Fasc. 39–40, Sched.: 32. 1950. Basionym: Cylindrosporium rhabdosporum Berk. & Broome, Ann. Mag. Nat. Hist. 15: 34. 1875.

- = Ramularia plantaginis Peck, Rep. (Annual) New York State Mus. Nat. Hist. 32: 43. 1879 (1880).
- ≡ *Ramularia peckii* Sacc. & P. Syd., Syll. Fung. 14: 1065. 1899, nom. illeg. (superfl.).

For additional synonyms see Braun (1998) or MycoBank.

Description in vivo: See Braun (1998: 197).

Specimens examined: Germany, on unknown host, unknown date, S. Petzoldt, culture CBS 312.92. New Zealand, Auckland, Grey Lynn, on *Plantago lanceolata*, unknown collector and date, isol. C.F. Hill, Jul. 2005, dep. C.F. Hill, culture CBS 118415. UK, Glamis, on *Plantago lanceolata*, Berkeley (holotype K).

Substrate and distribution: On Plantago (Plantaginaceae); Asia, Caucasus, Europe, N. and S. America, New Zealand.

Notes: Ramularia rhabdospora was originally described on Plantago lanceolata from England (holotype in K) but has since been reported from several other countries (Braun 1998). Two species have been described from the host Plantago, R. rhabdospora and R. kriegeriana. Traditionally, these species are distinguished by the ornamentation of the conidia that is echinulate in R. rhabdospora and verruculose in R. kriegeriana, which is correlated with the phylogenetic affinity of the host species. Plantago lanceolata, the principal host of R. rhabdospora belongs in Plantago subgen. Psyllium, and P. major, the principal host of R. kriegeriana, is a species of Plantago subgen. Plantago (Rønsted et al. 2002). Phylogenetically, these two strains cluster apart, with R. rhabdospora in clade 57 and R. kriegeriana in clade 65 (Fig. 2) and are morphologically easily distinguishable.

Ramularia rubella (Bonord.) Nannf., in Lundell & Nannf., Fungi Exs.. Suec., Fasc. 39–40: 33. 1950. Fig. 61.



Fig. 61. Ramularia rubella (CBS 120161). A-J. Structures formed in culture. A, D. Conidiophore and conidia. B, C, F. Conidiophores. E, G-J. Conidia. Scale bars = 10 µm.

Basionym: Crocysporium rubellum Bonord., Bot. Zeitung (Berlin) 19: 201. 1861.

- ≡ Ovullaria rubella (Bonord.) Sacc., Syll. Fung. 4: 145. 1886.
- = Oidium monosporium Westend., Bull. Soc. Roy. Bot. Belgique 2: 252. 1863.
- = Ramularia obovata Fuckel, Hedwigia. 5: 50. 1866.
- = Ramularia circumfusa Ellis & Everh., Proc. Acad. Nat. Sci. Philadelphia 47: 437. 1895.
- For additional synonyms see Braun (1998).

Mycelium consisting of hyaline, septate, branched, smooth to verruculose, $1.5-3 \mu m$ diam hyphae. *Conidiophores* hyaline, thin-walled, smooth to verruculose, erect, multiseptate, cylindrical-oblong, straight, unbranched (31–) 73–115(–282) × (2–)2.5–3(–5) μm . *Conidiogenous cells* terminal on conidiophores, cylindrical-oblong, $16-40 \times 2-3 \mu m$, with one conidiogenous locus, almost flat and in a terminal or lateral position thickened, darkened, refractive. *Conidia* formed singly, hyaline, thin-walled, smooth to verruculose, mostly aseptate and rarely 1-septate, ellipsoid to obovoid, (15–) 26–35(–54) × (5–)6–7(–9) μm ; *hila* thickened, darkened, refractive.

Culture characteristics: On MEA, 7 mm diam, surface raised, irregular, with flat mycelium, white, with undulate margins and colony reverse olivaceous; on OA, 8 mm diam, surface raised in the centre and flattening towards the edge, smooth rosy-buff mycelium, radially striated, producing tiny droplets of exudate in the centre, with undulate edge and colony reverse ochraceous; on PDA, 9 mm diam, surface raised, irregular, smooth mycelium, white to rosy-buff, producing tiny droplets of exudate, with crenate margins, colony reverse iron-grey.

Description in vivo: See Braun (1998: 210).

Specimens examined: [Germany, Guestphalia, On *Rumex aquaticus*, Bonorden, holotype not preserved]. Luxembourg, Kantenbach, on leaf spot on *Rumex obtusifolius*, unknown collector and date, isol. L. Marvanová, 25 Sep. 1967, dep. L. Marvanová, Oct. 1967, culture CBS 433.67. Mexico, Montecillo, on *Rumex* sp., 22 Sep. 2008, M. de Jesús Yáñez-Morales, cultures CPC 15748–15750; Montecillo, on *Rumex* sp., 1 Oct. 2008, M. de Jesús Yáñez-Morales, culture CPC 15821. Netherlands, Utrecht, on *Rumex* sp., May 2013, U. Damm, (neotype designated here, herbarium CBS H-22528, MBT204835, culture ex-neotype CBS 141117 = CPC 25911); Gelderland Prov., Wageningen, on *Prunus* sp., 23 May 2011, W. Quaedvlieg, cultures CPC 19471, CPC 19472. New Zealand, Auckland, Mt. Albert, on *Rumex obtusifolius*, unknown collector and date, isol. C.F. Hill, Jul. 2005, dep. C.F. Hill, culture CBS 120161. Sweden, Uppland, Haga, Årtopet, on *Rumex longifolius*, 16 Sep. 1988, E. Gunnerbeck, culture CBS 114440.

Substrate and distribution: On Polygonum s. lat. and Rumex (Polygonaceae); almost circumglobal.

Notes: Ramularia rubella was originally described on *Rumex aquaticus* from Germany, but it has a wide geographical distribution in association with the host *Rumex*, while it is very rarely observed infecting *Polygonum s. lat.* (Braun 1998). As a necrotroph, *Ramularia rubella* shows promise as a biological control agent against *Rumex obtusifolius* by causing severe defoliation, shoot and root weight loss (Huber-Meinicke *et al.* 1989). The available strains form a highly supported clade based on the employed phylogenetic methods (Fig. 2, clade 79, 1/100/100). The morphological description of the isolates (Fig. 61) in this clade is in agreement with the one presented in literature (Braun 1998), except the conidiophores were reduced to conidiogenous cells in culture. Because of the long, solitary conidia and sometimes broad conidiogenous loci and hila, some of the strains were initially confused with *Cercosporella*.

Ramularia rufibasis (Berk. & Broome) Gunnerb. & Constant., Thunbergia 15: 77. 1991.

Basionym: Peronospora rufibasis Berk. & Broome, Ann. Mag. Nat. Hist. 15: 34. 1875.

- *Ovularia rufibasis* (Berk. & Broome) Massee, Brit. fung.-fl. 3: 322. 1893.
 Phacellium rufibasis (Berk. & Broome) U. Braun, Nova Hedwigia 54: 471. 1992.
- = Ramularia destructiva W. Phillips & Plowr., Grevillea 6(37): 22. 1877.
- = Ovularia monilioides Ellis & G. Martin, Amer. Naturalist 19: 76. 1885.

Description in vivo: See Braun (1998: 328).

Specimens examined: Sweden, Uppland, Järlåsa, on leaves of *Myrica gale*, 17 Sep. 1990, E. Gunnerbeck, culture CBS 114567. UK, Glamis, on *Myrica gale*, herb. Berkeley (holotype of *Peronospora rufibasis* in K); King's Lynn, on *Myrica gale*, May 1876, Plowright [Rabenh., Fungi. Eur. Exs. 2267; lectotype of *Ramularia destructiva*, designated in Braun (1998), in HAL]. USA, Massachusetts, Magnolia, *Myrica gale*, Jun. 1884, C.H. Clarke [lectotype of *Ovularia monilioides*, designated in Braun (1998), in NY 938246].

Substrate and distribution: On Comptonia and Myrica (Myricaceae); Asia, Canary Islands, Europe, N. America)

Notes: Ramularia destructiva, described on Myrica gale from England (holotype in K), was reassigned to the genus Phacellium as Phacellium rufibasis (Braun 1992) due to the production of synnematous conidiophores. The genus Phacellium is now considered a synonym of Ramularia as the production of synnemata was deemed as an unreliable character to separate these two genera. The strain used in this study clusters within the genus Ramularia (Fig. 1, clade XIV), and formed a single lineage (Fig. 2, clade 82) basal to R. nyssicola (clade 81), but positioned on a very long branch, which supports this species as unique. Unfortunately, the strain was sterile in culture and morphological data could not be evaluated. This lineage is for now maintained as a representative of R. rufibasis, until fresh material is collected and more information becomes available. This species causes the Ramularia dieback disease of Myrica faya in its natural habitat, affecting young shoots and causing leaf spots (Gardner & Hodges 1990). Myrica faya is considered an invasive plant in Hawaii and this pathogen represents a potentially good biocontrol agent, but no studies for field applications have been conducted thus far.

Ramularia rumicicola Videira, H.D. Shin & Crous, **sp. nov.** MycoBank MB816852. Fig. 62.

Etymology: Named after the host genus from which it was collected, *Rumex*.

Mycelium consisting of hyaline, septate, branched, smooth, 1–2 µm diam hyphae. *Conidiophores* hyaline, thin-walled, smooth, erect, septate, straight, cylindrical-oblong, unbranched, (11.5–)33.5–50(–74) × (1.5–)2(–3) µm or reduced to conidiogenous cells. *Conidiogenous cells* integrated in mycelium or terminal in conidiophores, cylindrical-oblong to geniculatesinuous, (8–)10.5–13(–18) × (1.5–)2(–3) µm, with 1–2 apical conidiogenous loci, thickened, darkened, refractive. *Conidia* hyaline, thin-walled, smooth, catenate, with hila thickened, darkened and refractive. *Ramoconidia* subcylindrical, (8.5–) 13.5–16(–20) × 2–2.5(–3) µm, 0–1-septate, with 2–3 apical hila. *Intercalary conidia* subcylindrical to fusoid, 0–1-septate, (7.5–)11–13(–19) × 2–2.5(–3) µm, in branched chains of up to seven conidia. *Terminal conidia* subcylindrical to obovoid, aseptate, (5–)7.5–9(–13) × 2–2.5(–3) µm. *Culture characteristics*: On MEA, 30 mm diam, surface concave, radially striated, smooth mycelium, white with greyish tinge, with margins undulate and feathery, colony reverse iron grey; on OA, 35 mm diam, surface flat and buff with a purplish grey centre except for a slice of white and grey olivaceous fluffy mycelium, margins entire, colony reverse buff with iron grey centre; on PDA, 40 mm diam, surface flat with short hairy mycelium, dark grey olivaceous, with margins entire, sparse in mycelium and feathery, colony reverse iron grey at the centre and grey olivaceous margin.

Specimen examined: **South Korea**, Jinju, on *Rumex crispus*, 14 May 2004, H.D. Shin (**holotype** KUS-F20194, isotype CBS H-22529, culture ex-type CBS 141118 = CPC 11294); *idem*. CPC 11295, CPC 11296.

Notes: Ramularia rumicicola formed a highly supported clade (Fig. 2, clade 24, 1/100/100). It differs from *R. pratensis* by having larger ramo-, intercalary and terminal conidia, and by culture characteristics (Fig. 62).

Ramularia rumicis Kalchbr. & Cooke, Grevillea 8: 23. 1880. = Ramularia decipiens Ellis & Everh., J. Mycol. 1: 70. 1885.

Description in vivo: See Braun (1998: 216).

Specimens examined: South Africa, Cape, Somerset-East, on *Rumex obtusifolius*, MacOwan 1180 [lectotype, designated in Braun (1998), in B]. Sweden, Uppland, Dalby, Jerusalem, on *Rumex aquaticus*, 7 Sep. 1988, E. Gunnerbeck, culture CBS 114300.

Substrate and distribution: On Rumex (Polygonaceae); Asia, Caucasus, Europe, Africa, N. America.

Notes: Ramularia rumicis was originally described on Rumex obtusifolius from South Africa (lectotype in B) and has a very wide geographical distribution (Braun 1998). This species forms a single lineage (Fig. 2, clade 26). In literature (Braun 1998), a total of seven Ramularia species, including four varieties, have been described from Rumex. Ramularia rubella (Fig. 2, clade 79) and *R. pratensis* var. pratensis (Fig. 2, clade 23) have a circumglobal distribution. Ramularia bulgarica (on Rumex alpinus, Bulgaria, holotype in BPI) is only known from Europe. Ramularia occidentalis var. occidentalis (on Rumex britannica, lectotype in NY), Ramularia pseudodecipiens (on Rumex venosus, holotype in NY) and *R. pratensis* var. angustifolia (on Rumex acetosella, holotype in NY) are only known from the USA. Braun (1998) stated that *R. bulgarica* is closely related to *R. pratensis* but no culture was available for this study.

Ramularia sp. D Fig. 63

Mycelium consisting of hyaline, septate, branched, smooth, $1-2 \mu m$ diam hyphae. *Conidiophores* hyaline, thin-walled, smooth, erect, septate, cylindrical-oblong, straight, unbranched (44–) $71-92(-129) \times 2 \mu m$, or reduced to conidiogenous cells. *Conidiogenous cells* integrated in the mycelium or terminal in the conidiophore, cylindrical-oblong, $(24-)26.5-30(-35) \times 2(-2.5) \mu m$, with one *conidiogenous locus* almost flat, thickened, darkened and refractive. *Conidia* hyaline, thin-walled, smooth, catenate, aseptate, with *hila* thickened, darkened and refractive. *Ramoconidia* cylindrical-oblong, sometimes curved, $(16-)21-24(-34) \times (1.5-)$



Fig. 62. Ramularia rumicicola (CBS 141118). A–D. Observations from herbarium material. E–H. Structures formed in culture. A. Leaf spot symptoms on the host. B, C, E, F. Conidiophores and conidia. D. Conidiophores and conidiogenous cells. G. Conidia. H. Conidiogenous cell and conidia. Scale bars = 10 µm.



Fig. 63. Ramularia sp. D (CBS 135.23). A-F. Structures formed in culture. A, B, E. Conidia. C, D, F. Conidiophores, conidiogenous cells and conidia. Scale bars = 10 µm.

2(-3) μ m, with two protruding apical hila. *Intercalary conidia* cylindrical-oblong, apical apex sometimes curved, (14–) 20–22(–30) × (1.5–)2(–3) μ m, in branched chains of up to five conidia. *Terminal conidia* cylindrical-obovoid, (7.5–) 14–16(–22) × (1.4–)2–2.5 μ m (on SNA, CBS 135.23).

Culture characteristics: On MEA, 10 mm diam, surface raised, fluffy aerial mycelium, white-buff, with margins lobate, colony reverse ochreous; on OA, 12 mm diam, surface flat, ochreous,

with sparse white aerial mycelium, margins lobate, colony reverse cinnamon; on PDA, 11 mm diam, surface flat, fluffy white aerial mycelium, with margins lobate, colony reverse buff.

Specimen examined: Unknown country, on Viola odorata, unknown collector and date, isol. and dep. L. Solberg, May 1923, culture CBS 135.23.

Notes: Although this isolate was originally identified as *R. lactea*, the morphological characteristics of this strain (Fig. 63) do not match with that of the original description of *R. lactea* (Braun

1998). Ramularia lactea has shorter conidiophores $(5-50 \times 1.5-4 \mu m)$, and smooth to vertuculose conidia (5-) $8-18(-25) \times (1.5-)2-5(-6) \mu m$. Three other Ramularia species have been described from Viola, namely *R. coleosporii* (Fig. 2, clade 66), *R. agrestis* and *R. biflorae*. Ramularia agrestis var. agrestis, *R. agrestis* var. deflectans and *R. biflorae* all produce septate conidia that are longer and wider than Ramularia sp. D. Ramularia sp. D (Fig. 2, clade 44) formed a single lineage closely related to *R. abscondita*. Although we suspect this culture to represent a new species, more material of other taxa occurring on Viola is required to make a suitable comparison.

Ramularia sphaeroidea Sacc., Michelia 1: 130. 1878. emend. U. Braun (1998: 151).

= Ovularia sphaeroidea (Sacc.) Sacc., Fungi ital. Del., Tab. 979. 1881.

= Ramularia viciae A.B. Frank, Krankh. Pfl., 1. Aufl.: 600. 1880.

= *Peronospora exigua* W.G. Smith, Diseases of Field and Garden Crops: 13. 1884.

= Ovularia lotophaga Ellis & Everh., Proc. Acad. Nat. Sci. Phil. 47: 432. 1895.

= *Pseudovularia trifolii* Speg., Anales Mus. Nac. Hist. Nat. Buenos Aires 20: 418. 1910.

For additional synonyms see Braun (1998) or MycoBank.

Description in vivo: See Braun (1998: 151).

Specimens examined: Germany, Berlin, Spandau, on *Lotus uliginosus*, Jul. 1875, Magnus (holotype PAD). USA, California, on *Vicia villosa* subsp. *varia*, Apr. 2002, S.T. Koike, culture CBS 112891.

Substrate and distribution: On Chesneya, Glycyrrhiza, Lotus, Trifolium, and Vicia (Fabaceae); Central Asia, Caucasus, Europe, N. and S. America, Australia, New Zealand.

Notes: Ramularia sphaeroidea was originally described on Lotus uliginosus from Germany (holotype in PAD), but it is able to infect other hosts from Fabaceae worldwide. Vetches (Vicia spp.) are planted alone or in combination with other plants as cover crops in vegetable production areas in California. From 2001 to 2003, purple vetches (V. benhalensis) and lana woollypod vetches (V. villosa subsp. varia) in the Salinas Valley (Monterey county, California) developed a foliar disease. Based on morphological and molecular (ITS) data (CBS 112891, GenBank AY352584), the fungus was identified as Ramularia sphaeroidea. Pathogenicity was confirmed by spraying healthy plants with a conidial suspension in water (Koike et al. 2004). This strain formed a single lineage (Fig. 2, clade 12), but positioned on a long branch, which supports this species as unique. This clade is tentatively maintained as representative of the species until material from the type host and location are recollected and examined.

Ramularia stellariicola (M.J. Park *et al.*) Videira, H.D. Shin & Crous, **comb. nov.** MycoBank MB817160

Basionym: Pseudocercosporella stellariicola M.J. Park et al., Mycotaxon 119: 270. 2012.

Specimen examined: **South Korea**, Namyangju, Korea University, on *Stellaria aquatica*, 3 May 2006, H.D. Shin & M.J. Park (**holotype** KUS-F21740, culture ex-type KACC 42363 = CBS 130592 = CPC 11297, CPC 11298).

Substrate and distribution: On Stellaria aquatica (Caryophyllaceae); Asia (South Korea). *Notes*: At the time *Pseudocercosporella stellariicola* was described the ITS sequence placed it within the genus *Ramularia*, but morphologically it was better accommodated in *Pseudocercosporella*. However, this species is not congeneric with the type of *Pseudocercosporella*, *P. bakeri* (Fig. 1, clade XIX). Therefore, we propose a new combination in *Ramularia*. This species clusters in a highly supported clade (Fig. 2, clade 13, 1/ 100/100). No sexual morph of this species is known. Although it formed a sister clade to "*Mycosphaerella cerastiicola*", the latter species displays a cryptic septoria-like to pseudocercosporella-like asexual morph and differs in several nucleotides in the seven genes amplified: 2 (LSU), 9 (*rpb2*), 10 (ITS), 5 (*actA*), 9 (*gapdh*), 5 (*tef1*- α), 11 (*his3*). These taxa are maintained as separate species until further studies are conducted.

Ramularia stellenboschensis Crous, Persoonia 27: 37. 2011.

Specimen examined: South Africa, Western Cape Province, Stellenbosch, J.S. Marais Botanical Garden, on leaves of *Protea* sp., associated with leaf spots of *Vizella interrupta*, 6 May 2010, P.W. Crous (holotype CBS H-20678, cultures extype CBS 130600 = CPC 18294).

Substrate and distribution: On Protea sp. (Proteaceae); Africa (South Africa).

Notes: Protea species are very popular due to their brightly coloured and textured flowers and fungal pathogens that damage the blooms are highly undesirable. *Ramularia stellenboschensis* was the first species of *Ramularia* described from *Proteaceae* in South Africa. This species formed a single lineage (Fig. 2, clade 22), but positioned in a long branch, basal to *R. hydrangeae-macrophyllae* (clade 21). It is closely related to *R. proteae* (Fig. 1, clade XIV) but differs from it by forming larger sudcylindrical conidia and by several nucleotides among the seven genes amplified: 16 (*rpb2*), 4 (ITS), 9 (*actA*), 12 (*gapdh*), 14 (*tub2*), 2 (*his3*), 20 (*cmdA*).

Ramularia tovarae (Sawada) U. Braun, Internat. J. Mycol. Lichenol. 3: 283. 1988.

Basionym: Ovularia tovarae Sawada, Bull. Gov. Forest. Exp. Stat. Tokyo 105: 83. 1958.

Description in vivo: See Braun (1998: 212).

Specimens examined: Japan, on Polygonum filiforme [Antenoron filiforme, Tovara filiforme] (Polygonaceae), syntypes, 26 May 1948, 16 Jun 1948 and 7 Nov. 1947, Sawada (not seen!). South Korea, Hongcheon, on Antenoron filiforme (≡ Polygonum filiforme), 16 May 2003, H.D. Shin, KUS-F19471 (epitype designated here, MBT204827, HAL 1849 F, culture ex-epitype CBS 113305).

Substrate and distribution: Thus far only known from East Asia (Japan and South Korea), on *Polygonum filiforme* (*Polygonaceae*).

Notes: Ramularia tovarae was originally described on *Poly-gonum filiforme* from Japan and its distribution was limited to the type location. The only strain available representative of this species formed a single lineage (Fig. 2, clade 37), but positioned on a long branch that supports this species as unique. Although the strain did not sporulate in culture, the morphology observed in vivo corresponded to that described in literature (Braun 1998). Therefore, this specimen is considered as a good representative

of the species and, despite being originary from South Korea, it is hereby designated as epitype.

Ramularia tricherae Lindr., Acta Soc. Fauna Fl. Fenn. 23: 38. 1902.

- = Ramularia succisae var. knautiae C. Massal., Nuovo Giorn. Bot. Ital. 21: 169. 1889.
- ≡ Ramularia knautiae (C. Massal.) Bubák, Österr. Bot. Z. 53: 50. 1903.
- = Ovularia tricherae Vestergr., Bot. Not. 1899: 169. 1899.
- = Ramularia knautiae var. arvensis C. Massal., Malpighia 20: 169. 1906.

Description in vivo: See Braun (1998: 144).

Specimens examined: Austria, Ötztal, Ötz near Habichen, on leaf spot on Knautia dipsacifolia, 24 Jul. 2000, G. Verkley, culture CBS 108989, CBS 108990. Former Czechoslovakia, on Knautia drymeia, unknown collector and date, isol. L. Marvanová, Nov. 1972, dep. L. Marvanová, Jan. 1973, culture CBS 236.73. Netherlands, Limburg Prov., Gerendal, on leaf spot on Knautia arvensis, 28 Jun. 2000, G. Verkley, cultures CBS 108973, CBS 108974, CBS 108994, CBS 108995.

Substrate and distribution: On Knautia (Dipsacaceae); Caucasus, Europe.

Notes: Ramularia tricherae was originally described on *Knautia arvensis* from Finland [syntypes not seen by Braun (1998)] and has been reported from many European countries. In literature, this species is associated with the sexual morph *Sphaerella sylvatica* Sacc. & Speg. (Saccardo 1878) [syn. *Mycosphaerella scabiosae* Tomilin (Tomilin 1971)] but this connection has not been experimentally proven (Laibach 1921, Braun 1998, Aptroot 2006, Videira *et al.* 2015b). Phylogenetic analyses provided high support for this species clade (Fig. 2, clade 59, 1/ 100/100).

Ramularia trigonotidis Videira, H.D. Shin & Crous, **sp. nov.** MycoBank MB816853. Fig. 64.

Etymology: Named after the host genus from which it was collected, *Trigonotis*.

Mycelium consisting of hyaline, septate, branched, smooth, 1-2 µm diam hyphae. Conidiophores hyaline, thin-walled, smooth, septate, straight, cylindrical-oblong, geniculate-sinuous, unbranched, (16-) $36-48(-94) \times (1.5-)2(-3) \mu m$, or reduced to conidiogenous cells. Conidiogenous cells terminal in conidiophores or intermediate in the mycelium, cylindrical-oblong, $(7-)13-16.5(-31) \times (1.5-)2(-3) \mu m$, with one conidiogenous locus, almost flat to protuberant, thickened, darkened and refractive. Conidia hyaline, thin-walled, smooth, aseptate, catenate, with hila thickened, darkened and refractive. Ramoconidia subcylindrical, (12-)15-17(-25)x (2-) $2.5-3(-4) \mu m$, 0-1-septate, with two flat to protruding apical hila. Intercalary conidia subcylindrical, sometimes curved, (11-) $14.5-16(-18) \times (2-)2.5-3(-3.5) \mu m$, in branched chains of up to five conidia. Terminal conidia cylindrical-oblong to ovoid, (4.5-) 10.5-12.5(-16) × (2-)2.5-3(-4) µm (on SNA).

Culture characteristics: On MEA, 13 mm diam, surface convex, smooth, smoke grey with a rosy tinge, with margins undulate, white, convex, feathery, colony reverse iron grey; on OA, 9 mm diam, surface convex, fluffy aerial mycelium, white in centre pale vinaceous towards the edges, margins olivaceous grey, feathery, colony reverse olivaceous grey; on PDA, 12 mm diam, surface

convex, pale vinaceous grey, smooth and uniform, with margins undulate, feathery, hazel, colony reverse brown vinaceous and buff at margin.

Specimens examined: **South Korea**, Hoengseong, on *Trigonotis radicans* subsp. sericea (= *T. nakaii*), 15 Oct. 2007, H.D. Shin (**holotype** KUS-F23007, isotype CBS H-22530, culture ex-type CBS 141119 = CPC 14764); *idem.* CPC 14765, CPC 14766.

Substrate and distribution: On Trigonotis radicans subsp. sericea (Boraginaceae); Asia (South Korea).

Notes: Ramularia trigonotidis (Fig. 64) is the first species of *Ramularia* described on *Trigonotis*, and the available strains form a highly supported clade (Fig. 2, clade 76, 1/100/100). In the phylogeny it is closely related to *R. actinidiae* (Fig. 2, clade 77), but the latter species produces conidiophores that are reduced to conidiogenous cells, and subcylindrical to fusoid conidia that are slightly narrower.

Ramularia trollii Iwanoff, Trudy Imp. S.-Peterburgsk. Obshch. Estestvoisp., Vyp. 3, Otd. Bot. 30(3): 12. 1900. Fig. 65.

= Didymaria trollii Jacz., Bull. Soc. Imp. Naturalistes Moscou, n.s., 3: 435. 1898.

Description in vivo: See Braun (1998: 233).

Specimens examined: Austria, Tirol, Ober Inntal, Serfaus, Komperdell Alm near Kölnerhaus, on leaf spot on *Trollius europaeus*, 10 Aug. 2000, G. Verkley, cultures CBS 109118, CBS 109119. Russia, Prov. Vjatka, Distr. Kotelnitsh, on *Trollius europaeus*, 19 Jul 1921, Chochjakov, ex herb. Vjatskogo Obl. Mus. 78 [neotype, designated in Braun (1998), in LEP].

Substrate and distribution: On Trollius (Ranunculaceae); Europe, Asia.

Notes: The type material of *R. trollii* was not preserved and a neotype was proposed by Braun (1998) on the host *Trollius europaeus* from Russia (neotype in LEP). Thus far it has only been reported infecting *Trollius* hosts and is known from Asia and several European countries (Braun 1998). The representative isolates of this species clustered within the *Ramularia* clade (Fig. 1, clade XIV) and formed a highly supported clade based on the multigene phylogeny (Fig. 2, clade 17, 1/100/100). These strains were originally identified as *Pseudocercosporella trollii* but they produce catenate conidia with conspicuous hila that are consistent with the *R. trollii* description from literature (Braun 1998) (Fig. 65).

Ramularia unterseheri Videira & Crous, Fungal Biology 119: 836. 2015.

Specimens examined: **Germany**, Greifswald, Elisenhain, on leaf litter of *Fagus sylvatica*, 4 Jan. 2008, M. Unterseher (**holotype** CBS H-22285, culture ex-type CBS 124884); Greifswald, Elisenhain, on living leaves from the understorey of *Fagus sylvatica*, 8 Jan. 2008, M. Unterseher, cultures CBS 124826, CBS 124838; Munich, in room inside a castle, May 2011, unknown collector, dep. A. Klein-Vehne, culture CBS 130721. **Netherlands**, Utrecht Prov., Baarn, on decaying leaves of *Acer pseudoplatanus*, 26 Apr. 2004, G. Verkley, culture CBS 117879 = CPC 11207.

Substrate and distribution: On Fagus (Fagaceae) and Acer (Sapindaceae); Europe (Germany, Netherlands).



Fig. 64. Ramularia trigonotidis (CPC 14765). A-H. Structures formed in culture. A, C-E. Conidia. B. Conidiophore. F-H. Conidiophores, conidiogenous cells and conidia. Scale bars = 10 µm.



Fig. 65. Ramularia trollii (CBS 109118). A-E. Observations from herbarium material. F-G. Structures formed in culture. A. Leaf spot symptoms on the host. B, C, E. Conidiophores and conidia. D, F, G. Conidia. Scale bars = 10 µm.

Notes: See Videira *et al.* (2015b). The phylogenetic analyses places all the representatives of this species in one clade (Fig. 2, clade 86) closely related to *R. vizellae*.

Ramularia uredinicola Khodap. & U. Braun, Mycotaxon 91: 358. 2005.

Specimens examined: Iran, Guilan Prov., on *Melampsora* sp. on *Salix bab-ylonica*, 3 Jul 2004, S.A. Khodaparast (holotype IRAN 12316 F, isotype CBS H-22531, culture ex-type CBS 141120 = CPC 11852). Italy, Roma, on leaf *Mel-ampsora* sp. on *Populus* sp., unknown collector and date, isol. and dep. G. Magnani, Mar. 1968, culture CBS 179.68. South Korea, Hoengseong, on *Mel-ampsora* sp. on *Salix* sp., 21 Aug. 2004, H.D. Shin, culture CPC 11481, CPC 11482; Hoengseong, on *Melampsora* sp. on *Salix* sp., 21 Aug. 2004, H.D. Shin, culture CPC 11481, CPC 11482; Hoengseong, on *Melampsora* sp. on *Salix* sp., 21 Aug. 2004, H.D. Shin, culture CPC 106, H.D. Shin & M.J. Park, culture CBS 131769 = KACC 42535; Hongcheon, on

Melampsora sp. on *Populus alba* × *glandulosa*, 18 Oct. 2009, H.D. Shin & M.J. Park, culture CBS 131770 = KACC 44864; Hongcheon, on *Melampsora* sp. on *Salix pierotii* (= *S. koreensis*), 26 Oct. 2008, H.D. Shin & M.J. Park, culture CBS 131771 = KACC 44215; Suwon, on *Melampsora* sp. on *Salix matsudana* cv. *Tortuosa*, 30 Oct. 2008, H.D. Shin, M.J. Park, culture CBS 131772 = KACC 44218.

Substrate and distribution: Hyperparasite of Melampsora sp.; Asia (Iran, South Korea), Europe (Italy).

Notes: Ramularia uredinicola and R. rosea are closely related species (Khodaparast & Braun 2005) that form reddish or pink caespituli with age, probably due to the production of rubellins (Arnone *et al.* 1986, Miethbauer *et al.* 2003). However, they can be distinguished based on morphology and have different life-styles. Ramularia uredinicola is mycophylic and has longer and branched conidiophores, while R. rosea causes leaf spots on leaves. Ramularia uredinis is also mycophylic but the caespitulli do not turn reddish with age and the conidiophores are shorter and unbranched. Ramularia coleosporii and R. uredinearum are also mycophylic, but the caespitulli are always hyaline (Braun 1998, Khodaparast & Braun 2005). The strains used in this study from South Korea clustered in a highly supported clade (Fig. 2, clade 68, 1/100/100).

Ramularia urticae Ces., in Rabenh., Herb. Viv. Mycol., Cent. XVII, no. 1680. 1852.

- ≡ *Cylindrospora urticae* (Ces.) J. Schröt., in Cohn, Krypt.-FI. Schlesien 3.2(4): 492: 1897.
- ≡ Septocylindrium urticae (Ces.) Subram., Hyphomycetes: 310: 1971.
- = Sphaerella superflua Fuckel, Jahrb. Nassauischen Vereins Naturk. 23-24:

102. 1870 (1869–1870). ≡ Mycosphaerella superflua (Fuckel) Petr., Ann. Mycol. 38: 235. 1940.

Description in vivo: See Braun (1998: 273).

Specimens examined: Germany, Weimar, Belvedere, leaf spot on *Urtica dioica*, 8 Oct. 1990, G. Arnold, culture CBS 162.91. **Italy**, Vercellis, on *Urtica dioica*, 1851, Cesati [Rabenh., Herb. Viv. Mycol. 1680; **lectotype**, designated in Braun (1998), in HAL]. **South Korea**, Hoengseong, on *Aconitum pseudo-laeve* var. *erectum*, 15 Oct. 2007, H.D. Shin, culture CPC 14807. **Sweden**, Uppland, Haga par., Årtopet, on *Urtica dioica*, 29 Sep. 1987, E. Gunnerbeck, culture CBS 113974. **Unknown country**, on unknown host, unknown collector and date, dep. P. Redaelli, Mar. 1926, culture CBS 105.26.

Substrate and distribution: On Urtica (Urticaceae); Asia Caucasus, Europe, N. America.

Notes: Ramularia urticae was originally described on *Urtica dioica* from Italy (lectotype in HAL). It has a broad geographical distribution but it is thus far only known from the host *Urtica*. Since the morphological characters of the strains CBS 105.26 and CPC 14807 were not observed, and they clustered close to strains of *R. urticae* in a well-supported clade (Fig. 2, clade 53, 1/94/91), they are tentatively considered as the same species. However, we refrain to expand the host range and geographical distribution of the species until further evidence is available.

Ramularia valerianae (Speg.) Sacc. var. *valerianae*, Fungi ital. Del., Tab. 1007. 1881.

Basionym: Cylindrosporium valerianae Speg., Michelia 1: 475. 1879.

= Ramularia valerianae var. valerianae-montanae Săvul. & Sandu, Hedwigia 73: 120. 1933.

= Ramularia eamesii Dearn & House, Bull. New York State Mus. Nat. Hist. 233-234: 39. 1920.

= Ramularia basarabica Săvul. & Sandu, Hedwigia 73: 120. 1933.

Description in vivo: See Braun (1998: 276).

Specimens examined: Austria, Tirol, Ötztal, Horlachtal near Umhausen, forest near Stuibenfalle, on leaf spot on *Valeriana* sp., 3 Aug. 2000, G. Verkley, cultures CBS 109123, CBS 109122. Italy, Conegliano, on *Valeriana officinalis*, herb. Saccardo (holotype PAD).

Substrate and distribution: On Valeriana (Valerianaceae), Asia, Caucasus, Europe, N. America.

Notes: Two varieties of *R. valerianae* have been described thus far, *R. valerianae* var. *centranthi* (type on *Centranthus ruber*, France) and *R. valerianae* var. *valerianae* (on *Valeriana officinalis*, Italy, holotypus in PAD). They differ in the type of lesions they form on plant hosts that are angular-irregular, sometimes vein delimited, pale greenish to reddish brown in *R. valerianae* var. *valerianae* and subcircular to irregular, pale brown with greyish white centre and purple brown margins in *R. valerianae* var. *centranthi. Ramularia valerianae* var. *valerianae* also produces longer and wider conidia $[(8-)10-50(-55) \times (-1.5) 2-5.5(-7) \mu m]$ than *R. valerianae* var. *centranthi* [(6-) 12–35 × 2–4 µm]. Strains of this species cluster in a highly supported clade (Fig. 2, clade 54, 1/100/100). Unfortunately these strains proved to be sterile in culture.

Ramularia vallisumbrosae Cavara, Rev. Mycol. (Toulouse) 21: 101. 1899.

= Ramularia narcissi Chittenden, Gard. Chron. 39: 277. 1906.

= Ramularia ucrainica Petr., Ann. Mycol. 19 (1-2): 78. 1921.

Description in vivo: See Braun (1998: 48).

Specimens examined: Italy, Vallombrosa, Orto botanico, on *Narcissus* sp., 1899, Cavara [lectotype, designated in Braun (1998), PAD]. UK, Southwestern England, Cornwall, on *Narcissus* var. Victoria, unknown collector and date, isol. P.H. Gregory, dep. A. Beaumont, May 1938, culture CBS 271.38; Scilly Island, on *Narcissus* var. Golden Spur, unknown collector and date, isol. P.H. Gregory, Apr. 1938, dep. P.H. Gregory, Dec. 1938 (epitype designated here CBS H-22532, MBT204833, culture ex-epitype CBS 272.38).

Substrate and distribution: On Leucojum, Narcissus, and Pancratium (Amaryllidaceae); Europe, N. America.

Notes: Ramularia vallisumbrosae is the causal agent of white mould disease on leaves of daffodils (*Narcissus* cultivars) in commercial plantations in England and Scotland. The disease is not believed to be bulb-borne (Moore 1979), but poses a serious threat in these regions causing early defoliage die-down and associated reductions in bulb yield (O'Neill *et al.* 2002). This species formed a highly supported clade (Fig. 1, clade XIV; Fig. 2, clade 16, 1/100/100).

Ramularia variabilis Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 361. 1870. Fig. 66.

≡ *Ovularia variabile* (Fuckel) E. Bommer & M. Rousseau, Bull. Soc. Roy. Bot. Belgique 23(1): 274. 1884.

≡ Cylindrosporium variabilis (Fuckel) J. Schröt., Krypt.-Fl. Schlesien 3.2(4): 490. 1897.

≡ Entylomella variabilis (Fuckel) Cif., Ann. Mycol. 26 (1-2): 17. 1928.

= Sphaerella mariae Sacc. & E. Bommer, Bull. Soc. Roy. Bot. Belgique 25(1): 173. 1886



Fig. 66. Ramularia variabilis (CBS 141121). A, C, D. Observations from herbarium material. B, E–H. Structures formed in culture. A. Leaf spot symptoms on the host. B, D, E. Conidia. C, G. Conidiogenous cells and conidia. F, H. Conidiophores and conidia. Scale bars = 10 µm.

≡ Mycosphaerella mariae (Sacc. & E. Bommer) Lindau, Hilfsb. Sammeln Ascomyc.: 37. 1903.

Mycelium consisting of hyaline, septate, branched, smooth, 1-2 µm diam hyphae. Conidiophores hyaline, thin-walled, smooth, erect, 1-2-septate, cylindrical-oblong, straight to sinuous, unbranched, (10-)26.5-35(-54) × (1-)1.5-2(-3) µm, or reduced to conidiogenous cells. Conidiogenous cells terminal in conidiophores or intermediate in the mycelium, cylindrical-oblong, (5.5-)14.5-19(-29) × 1.5-2(-3) µm, with 1-3 conidiogenous loci almost flat to cylindrical-protuberant, thickened, darkened and refractive. Conidia hyaline, thin-walled, smooth to slightly verruculose, catenate, with hila thickened, darkened and refractive. Ramoconidia fusiform, (9.5-)14-17(-26.5)х (1.5-)2-2.5(-3) µm, 0-1-septate, with 2-3 apical hila. Intercalary conidia fusiform to oval, aseptate, $(8-)11-13(-19.5) \times (1.5-)$ 2(-3) µm, in branched chains of up to five conidia. Terminal conidia obovoid, aseptate, (5-)7-8(-11) × (1.5-)2(-2.5) µm (on SNA).

Culture characteristics: On MEA, 11 mm diam, surface raised, folded, with sparse aerial mycelium, smooth, rosy-buff, with margins crenate and convex, colony reverse cinnamon with olivaceous grey patches; on OA, 9 mm diam, surface smooth, low convex, white with pale olivaceous grey tinge, with margins undulate, colony reverse fawn; on PDA, 10 mm diam, surface low convex, pale olivaceous grey, smooth, producing tiny transparent exudate droplets, with margins lobate, colony reverse olivaceous grey with a buff margin.

Description in vivo: See Braun (1998: 263).

Specimens examined: Austria, Graz, on Verbascum sp., Oct. 2012, C. Scheuer (epitype designated here CBS H-22533, MBT204834, culture ex-epitype CBS 141121 = CPC 25967). Canada, Stittsville, Ontario, on Verbascum sp., K.A. Seifert, 12 Jul. 2009, cultures CPC 16865, CPC 16866. Germany, on Verbascum thapsus [Fuckel, Fungi Rhen. Exs. 135; lectotype, designated in Braun (1998), in HAL].

Substrate and distribution: On Digitalis, Verbascum (Scrophulariaceae); Asia, Caucasus, Europe, N. America.

Notes: Ramularia variabilis has a broad geographical distribution and has been reported to infect plants from the genera *Digitalis* and *Verbascum*. In this study, the strains isolated from *Digitalis* and *Verbascum* were separated into distinct clades (Fig. 2), namely clades 50 and 58, respectively, clearly suggesting that two different species are involved (see *Ramularia digitalis-ambiguae*). Strain CPC 25967 was isolated from the same host and from a neighbouring country as the type, and is morphologically a good representative of this species (Fig. 66). All three phylogenetic methods applied to this dataset gave high support to this clade (Fig. 2, clade 50, 1/100/100). This species has been experimentally linked to the sexual morph *Mycosphaerella mariae* (Sacc. & Bommer) Lindau (von Arx 1949; Videira *et al.* 2015b).

Ramularia veronicicola Videira & Crous, **nom. nov.** MycoBank MB817161.

Basionym: Stysanus veronicae Pass., Hedwigia 16(6): 123. 1877 (1876), non Ramularia veronicae Fuckel, 1870.

- ≡ Isariopsis veronicae (Pass.) Savile, Canad. J. Bot. 46: 465. 1968.
- ≡ Phacellium veronicae (Pass.) U. Braun, Nova Hedwigia 50: 511. 1990.

Description in vivo: See Braun (1998: 337).

Specimens examined: Italy, Parma, botanical garden, on Veronica longifolia, 1875/76, Passerini [Rabenh., Fungi Eur. Exs. 2268; lectotype, designated in Braun (1998), HAL]. Sweden, Uppland, Danmark par., Bergsbrunna, on Veronica spicata, 25 Sep. 1987, E. Gunnerbeck, culture CBS 113981.

Substrate and distribution: On Veronica (Scrophulariaceae); Europe, N. America.

Notes: Previously named Phacellium veronicae, this species was originally isolated on Veronica longifolia from Italy
(lectotype in HAL). Based on phylogenetic analyses in this study, strain CBS 113981 clustered within the Ramularia clade (Fig. 1, clade XIV) and formed a single lineage (Fig. 2, clade 64) in the multigene phylogeny. Since Phacellium is now considered a synonym of Ramularia, a new combination is proposed. Because the epithet "veronicae" is already occupied in Ramularia for a different species (Fig. 2, clade 64) the new epithet "veroniciola" is introduced. Ramularia veroniciola is the causative agent of leaf spot disease on Veronica species that are perennial plants used as ornamentals. The pathogen causes brown roundish spots and develops conidiophores aggregated in synnemata. This species has been observed in several European countries and also in North America (Canada) (Braun 1998). It has recently been reported from China infecting V. sibirica and, although the disease incidence was low, it may become significant with the increase of the cultivated area (Bai et al. 2013; ITS sequence GenBank HE995799). During recent field surveys in Hungary, the disease incidence affecting V. spicata and V. spuria varied between 90-100 %, and reached a severity between 30-60 % (Horvát et al. 2015; ITS sequences GenBank HQ690097 and JQ920427). The ITS sequence of the isolate CBS 113981 is identical to GenBank JQ920427, and differs from GenBank HQ690097 in 1 nucleotide and from GenBank HE995799 in 10 nucleotides. Unfortunately this strain did not sporulate in culture, and the corresponding herbarium specimen was not preserved.

Ramularia vizellae Crous, Persoonia 27: 37. 2011.

Specimens examined: Netherlands, Gelderland, Randwijk, on dead leaf litter from *Malus* sp., unknown collector and date, isol. G. Verkley, 26 Jun 2004, cultures CBS 115981, CBS 115982; Utrecht, Rhijnawen forest, on fruit scales of *Carpinus betulus*, 25 Apr. 2005, G. Verkley, culture CBS 117798; Utrecht Prov., Baarn, Park Groeneveld, on decaying leaves of *Quercus rubra*, collection date unknown, G. Verkley, culture CBS 117871; Utrecht Prov., Baarn, Park Kasteel Groeneveld, on *Amelanchier lamarckii*, 26 Apr. 2004, G. Verkley, culture CBS 117872. **South Africa**, Western Cape Prov., Hermanus Fernkloof Nature Reserve, on leaves of *Protea* sp., in association with *Vizella interupta*, 2 May 2010, P.W. Crous (holotype CBS H-20679, culture ex-type CBS 130601 = CPC 18283).

Substrate and distribution: On Lotus, Phaseolus (Fabaceae), Acer, Aesculus (Sapindaceae), Protea (Proteaceae), Carpinus, Corylus (Betulaceae), Fagus, Quercus (Fagaceae), Amelanchier, Malus (Rosaceae), Brassica (Brassicaceae), and Tilia spp. (Malvaceae); Europe (France, Germany, Netherlands, Switzerland, Germany), South Africa.

Notes: See Videira *et al.* (2015b). The phylogenetic analyses provide high support to this species clade (Fig. 2, clade 85, 1/ 100/99).

Ramularia weberiana Videira & Crous, **sp. nov.** MycoBank MB817162.

Etymology: Named after the depositor of the strain, A. Weber.

Culture sterile. *Ramularia weberiana* (Fig. 2, clade 25), differs from its closest phylogenetic neighbour, *R. rumicicola* (Fig. 2, clade 24), by unique allelles in five loci based on alignments of the separate loci deposited in TreeBASE as Study S19315: *rpb2* positions 15(C), 57(G), 63(C), 102(A), 117(G), 196(C), 228(C), 249(T), 267(A), 327(C), 330(G), 348(T), 357(T),

358(C), 378(T), 402(T), 414(T), 435(C), 445(T), 459(T), 493(A), 519(A), 531(T), 588(T), 591(C), 594(T), 606(T), 615(T), 627(G), 633(C), 636(C), 654(G), 657(G); ITS positions 33(G), 47(A), 167(T); actA positions 83(T), 96(C), 98(T), 121(A), 164(A), 166(A), 185(T), 186(C), 211(C), 212(C); gapdh positions 14(A), 29 deletion (C), 38(G), 39(T), 43(A), 45(C), 120(T), 131(A), 132(T), 158(T), 167(T), 185(C), 208(C), 257(A), 258(T), 259(A), 260(C), 262(A), 281(T), 286(G), 287(T), 289(T), 291(A), 293–295 insertion (CCA), 315(A), 347(T), 380(T), 431(C), 438(T), 440(T), 446(T), 479(C), 524(C), 572(C), 593(T); tef1- α positions 8(T), 15(T), 17(C), 18(T), 48(C), 56(T), 59(T), 145(C), 196(C), 233(G), 248(C), 284(C), 286(T), 289(T), 290(T), 294(A), 295(C), 296(T), 401(C), 409(A), 425(T), 430(A), 578(T).

Specimen examined: Unknown country, on unknown host, unknown collector and date, isol. and dep. by A. Weber, Aug. 1923 (holotype CBS H-22534, culture ex-type CBS 136.23).

Notes: The strain in this clade represents a new species that is clearly distinct from other species based on the phylogenetic analyses (Fig. 2, clade 25). Unfortunately this strain did not sporulate in culture and a comparison with the descriptions available in literature was not possible.

Ramularia weigelae Speg. (as *weigeliae*), Michelia 1(5): 475. 1879. Fig. 67.

≡ *Phaeoramularia weigelicola* H.D. Shin & U. Braun, Mycotaxon 58: 163. 1996.

≡ *Passalora weigelicola* (H.D. Shin & U. Braun) U. Braun & Crous, Mycosphaerella and its anamorphs: 1. Names published in Cercospora and Passalora: 475. 2003.

Description in vivo: See Braun (1998: 389).

Specimen examined: South Korea, on Weigela subsessilis, 4 Jun. 2003, H.D. Shin, KUS-F19549, culture CBS 113309.

Substrate and distribution: On Weigela (Diervillaceae); Asia, Europe.

Notes: Ramularia weigelae was originally described on *Weigela florida* from Italy (holotype). Braun (1998) stated that the type material of *R. weigelae* is probably not preserved but a specimen collected from South Korea corresponded to the description of the species. Since the conidiophores were pigmented, the species was transferred to *Phaeoramularia* as *P. weigelicola*. However, isolate CBS 113309 (Fig. 67), previously identified as *Phaeoramularia weigelicola*, clustered within the genus *Ramularia* (Fig. 1, clade XIV). The strain was not used in the multigene analysis since it lacked the *rpb2* partial gene sequence at the time the tree was run.

Important phytopathogenic *Ramularia* species lacking cultures in this study

Ramularia cercosporelloides U. Braun & Crous, Monogr. *Cercosporella*, *Ramularia* Allied Genera (Phytopath. Hyphom.) 2: 419. 1998.

≡ Cercosporella carthami Murashk., Izv. Zapadno-Sibirsk. Otd. Russk. Geogr. Obshch 5: 4. 1926.

Description in vivo: See Braun (1998: 419).



Fig. 67. Ramularia weigelae (CBS 113309). A–C. Observations from herbarium material. D–I. Structures formed in culture. A. Leaf spot symptoms on the host. B, D, E, G–I. Conidiophores and conidia. C, F. Conidia. Scale bars = 10 µm.

Substrate and distribution: On Carthamus (Asteraceae), Asia, Caucasus, Europe.

Notes: The type material of this species, on Carthamus tinctorius from Russia (near Omsk), could not be traced by Braun (1998) and the placement of the species in the genus Ramularia was based on the observation of a fresh specimen from the Netherlands on Carthamus tinctorius that is currently deposited in HAL. Some studies point to this pathogen as the causative agent of leaf spot disease on safflower in Sonora. Mexico. leading to severe yield losses on this crop. Morphological identification followed by pathogenicity tests of the isolates was performed by Huerta-Espino et al. (2006). However, in a more recent study (Quintana-Obregón et al., 2013), isolates of the false mildew of safflower collected from the field were morphologically identified as R. cercosporelloides but, based on DNA sequences of the LSU and ITS regions, they were similar to Cercosporella acroptili (= Ramularia acroptili). Other studies point to R. carthami (now R. cynarae) as the causative agent (Montoya-Coronado et al. 2008, Borbon-Garcia et al. 2011). More work needs to be done to understand which fungus is causing the disease.

Ramularia oryzae Deighton & D.E. Shaw, Trans. Brit. Mycol. Soc. 43: 516. 1960.

≡ Mycovellosiella oryzae (Deighton & D.E. Shaw) Deighton, Mycol. Pap. 144: 25. 1979.

Description in vivo: See Braun (1998: 201).

Substrate and distribution: On Oryza (Poaceae); Asia and Africa.

Notes: Ramularia oryzae was described on Oryza sativa from Papua New Guinea [holotype in K(IMI)] and has been reported from Asia and Africa (Braun 1998). White leaf streak, caused by Mycovellosiella oryzae (= Ramularia oryzae) was observed in Louisiana, USA, in 1996, developing on leaves of the rice cultivar Lemont. Pathogenicity tests were performed on the rice cultivars Lemont and Cypress by spraying a conidial suspension onto leaves at boot stage. Many elongated lesions were produced 3-4 wk after inoculation. With the same method, 45 other cultivars were tested. Most of the cultivars grown in southern US were moderately susceptible to susceptible. Foreign cultivars tested (BR-7, BR-11, Cica-4, Cica-7 to Cica-9, Oryzica Ilanos, Rax clear, Tequing, and Tetep) were resistant. As symptoms of both white leaf streak and narrow brown leaf spot were observed on the same leaf it is possible that the disease was present but not identified separately because of the similarity of the symptoms of the two diseases. At present it appears to be a minor problem for rice cultivation in Louisiana. White leaf streak has previously been reported from Papua New Guinea on cultivated Oryza sativa, and from the Solomon Islands, Sabah, Nigeria, and Sierra Leone on cultivated O. glabberima, and on wild perennial rice O. berthii (Webster & Gunnell 1992, Shahjahan et al. 1998, Zhou et al. 2010).

Ramularia phaseoli (O.A. Drumm.) Deighton, Trans. Brit. Mycol. Soc. 50: 125. 1967.

Basionym: Ovularia phaseoli O.A. Drumm., Revista Ceres 6(33): 169. 1945.

- ≡ Mycovellosiella phaseoli (O.A. Drumm.) Deighton, Mycol. Pap. 137: 70. 1974.
- = Ramularia phaseolina Petr., Sydowia 4(1-6): 584. 1950.

Description in vivo: See Braun (1998: 128).

Substrate and distribution: Asia, Africa, S. America on *Glycine* and *Phaseolus* (*Fabaceae*).

Notes: Ramularia phaseoli is a pathogen that was first observed on *Phaseolus vulgaris* from Brazil (lectotype in CUP). This species is the causative agent of floury leaf spot disease on leaves of dry beans. Leaf spots usually appear first on older leaves, progresses to new foliage, and a severe infection may cause plant defoliation. Conidiophores and conidia develop mostly on the lower surface of the leaf in white, floury mats. It is among the more serious diseases of common bean at relatively high altitudes in the tropics and has been reported from Eastern and Central Africa, Europe, Malaysia, Papua New Guinea, South and Central America. It is usually controlled with chemical sprays with benomyl and thiophanate methyl and by rotation with non-host crops such as cereals and corn (Schwartz *et al.* 2005).

Ramularia primulae Thüm., Oesterr. Bot. Z. 28(5): 147. 1878. ≡ Cylindrosporium primulae (Thüm.) J. Schröt., Krypt.-Fl. Schlesien 3.2(4): 492. 1897.

Description in vivo: See Braun (1998: 228).

Substrate and distribution: On Primula (Primulaceae); Asia, Caucasus, Europe, N. and S. America, Australia, New Zealand.

Notes: Ramularia primulae was originally described on Primula elatior from Germany (neotype in PAD), but it has a worldwide distribution and has been reported infecting other species of the genus Primula (Braun 1998). This species is responsible for the Ramularia leaf spot disease on Primula spp. It is able to infect both Primula × pruhonicensis (polyanthus) and P. malacoides (fairy primrose) leaves creating tan or brown leaf spots that may be accompanied by chlorosis. Conidiophores and conidia develop preferentially on the lower surface of lesions forming white spore masses under humid conditions. It is a disease mainly prevalent in the USA, but easily controlled by removing infected plants from the general population and keeping the seedlings away from older plants to avoid inoculum transfer (Daughtrey et al. 1995).

DISCUSSION

The genera covered in the present study include species with very diverse lifestyles that sometimes have a negative impact on the crops we depend on for food, feed and bioenergy. Although some species may cause significant yield losses, none of them are included in plant protection quarantine lists. The identification of species of *Ramularia* and allied genera has thus far mainly relied on host taxonomy and morphological characters such as the shape, size and septation of conidia and the type of conidiogenous loci and conidial hila. Reliable identification of these species based on morphological characters alone is difficult since their morphology is rather reduced. In order to improve the identification of cryptic species, the use of DNA phylogenetic markers, also known as DNA barcoding, is becoming an increasingly popular tool (Crous *et al.* 2009b, 2013, Groenewald *et al.* 2013, Verkley *et al.* 2013).

The present study provides a broad phylogenetic overview of *Ramularia* and allied genera, thereby establishing a foundation of reference sequences in public databases that can be used for species identification, and at the same time promote further research. The phylogenetic analysis of *Ramularia* allied genera generally provided good resolution with maximum to high bootstrap and posterior probability values for almost all terminal nodes and several of the deeper nodes. Phylogenetic support

based on three different methods facilitated the resolution of several genera based on their type species, such as Ramularia and Ramulariopsis. The genus Ramularia proved to be polyphyletic, and not monophyletic as previously thought, and the species non-congeneric with the type R. pusilla were assigned to the new genera Xenoramularia, Epicoleosporium and Teratoramularia. This was also the first time species with a ramularialike morphology were observed in the Teratosphaeriaceae, which renders morphology-based identifications more difficult, and underlines the necessity of molecular data for accurate identification. The genus Cercosporella, although not epitypified, was analysed in two different studies (Kirschner 2009; present study), and based on its phylogenetic position and morphology, is considered to be reliably represented by the species used in this study. The phylogenetic position of Pseudocercosporella was reiterated as confined to its type species, P. bakeri, and the pseudocercosporella-like species not congeneric with the type were reassigned to new or existing genera such as Apseudocercosporella. Filiella, Microcyclosporella, Neopseudocercosporella, Pseudocercospora, Ramularia and Sphaerulina. An isolate previously identified as representative of Pseudocercosporella fraxinea was found to belong to the genus Acrodontium, typified by A. crateriforme, which prompted a short review of this genus, with the eventual description of three new species.

Although many more genera allied to Ramularia are treated in literature, most have not yet been preserved in culture, such as Hawksworthiana, Neoovularia, Neoramularia, Monodidymaria, Pseudodidymaria and Tretovularia. These genera need to be recollected, cultured and compared by means of DNA sequence analysis. In order to facilitate their identification, photoplates of their type specimens or representative species were produced in this study. The relationship between these genera and Ramularia is based on morphological characters but their phylogenetic position is still unknown and they may even not belong to the Mycosphaerellaceae. One example of this relates to the genus Thedgonia that was morphologically related to Pseudocercosporella, and later found to belong to Helotiales (Crous et al. 2013). Ramularia and allied genera are much undersampled and are frequently described without culture or DNA sequence data. In the last 15 years, among the 41 novel Ramularia names released on MycoBank, only 13 included cultures and DNA sequence data while the rest relied only on morphological descriptions based on herbarium specimens.

The present study includes the largest number of Ramularia isolates and species ever subjected to DNA sequence analysis. Combined with a recent classic monograph of the genus (Braun 1998), it provides powerful tools to better understand and promote further research on these species. The phylogenetic overview of the species belonging to Ramularia generally provided good resolution with maximum to high bootstrap and posterior probability values for almost all terminal nodes, while several of the deeper nodes were only supported by the Bayesian analysis. Several species were morphologically and molecularly characterised, two new combinations and two new names were proposed, nine new species were described, and 12 species epitypified. The type species of Ramularia, R. pusilla, was epitypified providing a reliable phylogenetic anchor for this genus. The Ramularia species analysed in this study generally agree with the concept presented in literature (Braun 1998), which regards them as being host-specific. Of the 88 taxa subjected to analysis 39 were found to occur in only one host

genus, a number that rises to 60 when the single lineages are also considered. With the phylogeny we observed that some species previously thought to have a broad host range and geographical distribution were in fact different species (e.g. R. lamii var. lamii, R. agastaches, R. leonuri). While some species are reported to have a broad host range in literature (Braun 1998), this was not observed in the phylogeny, which could be due to undersampling (e.g. R. asteris, R. belunensis, R. collocygni, R. grevilleana, R. heraclei, R. inaequalis, R. macrospora, R. pusilla and R. sphaeroidea). Only six of the 88 taxa analysed proved to have a broad host range (e.g. R. cynarae, R. hydrangeae-macrophyllae, R. vizellae, R. unterseheri, R. glennii and R. eucalypti). The clades representing R. hydrangeae-macrophyllae, R. vizellae, R. endophylla, R. unterseheri and R. cynarae show some intraspecific variation in the genes investigated. Among these, only R. cynarae has not been observed to develop a sexual morph. Although in literature 20 connections between asexual and sexual morphs are reported for Ramularia species alone, only seven have been proven thus far, including the newly observed R. hydrangeaemacrophyllae. Sexual reproduction is known to introduce variability in the genes and this may explain the variation observed.

The gene regions used in this study were selected based on their extensive use in fungal phylogenetic studies. They have proved suitable to explore phylogenetic relationships within and between genera of the Mycosphaerellaceae (Crous et al. 2013, Groenewald et al. 2013, Verkley et al. 2013). Based on the individual genes, ITS was able to discriminate 58 % of the species while *tef1*-α recognised 62 %, actA 72%, gapdh 76 % and rpb2 84 %. The K2P results show that the ITS barcode has a lower ability to discriminate species than protein-coding genes, since it displayed the smallest barcode gap and highest overlap percentage of inter-intra specific distances among all genes. The gapdh, with its big barcode gap and low overlap would be a good candidate for a secondary barcode gene, but its amplification proved to be challenging. The rpb2 gene displayed the widest barcode gap of all genes, but it had a relatively higher overlap percentage when compared to the other genes. Nevertheless, it was able to discriminate 84 % of the Ramularia species studied here, and the amplification of *rpb2* with the primers developed in this study was successful for all the isolates. The best statistical support for each genus was obtained using rpb2, therefore this locus should in future be more extensively used to determine relations within Mycosphaerellaceae. A recent publication on fungal barcoding genes recommends tef1-a as a secondary universal DNA barcode for the fungal kingdom (Stielow et al. 2015). However, the fragment amplified by the primers used in that study is different from the fragment amplified in this study, and therefore cannot be compared directly.

Genomic studies of *Ramularia* species are presently unavailable but the amplification of the complete genome of two *Ramularia* species, *R. endophylla* (Grigoriev *et al.* 2013) and *R. collo-cygni* (Havis *et al.* 2015), are underway. They are likely to provide valuable insights into the genetic diversity of these species, their biological cycles and their hability to produce secondary metabolites that influence pathogenesis. *Ramularia collo-cygni*, *R. rubella* and *R. uredinicola* are able to produce a non-host specific phytotoxin, rubellin. They appear quite separate in the phylogenetic analysis suggesting this is a trait that evolved multiple times and is not confined to a single lineage. In this study, the species *R. archangelicae* and *R. calcea* have been observed to produce pigments of pink and brick colours, respectively, that diffused into the culture media, suggesting these species may also be able to produce rubellins. Besides the rubellins, no other secondary metabolites have been attributed to *Ramularia* and allied genera species, which indicates this is a fairly unexplored research line in this group of agricultural important species.

The present study includes several taxa that are of major concern for agriculture such as Neopseudocercosporella capsellae and N. brassicicola (Brassica spp.), Ramulariopsis gossypii (cotton), Ramularia collo-cygni (barley) and Ramularia beticola (sugar beet), since they affect important crops planted worldwide. We believe that this study serves as a backbone for future studies on the taxonomy of Ramularia and allied genera. Although many important species have been reliably identified and epitypified, many puzzles remain unsolved (e.g. the identity of R. cercosporelloides). More than 1000 names are known in Ramularia alone and this study covered only 88 taxa, which means many species still need to be recollected and characterised based on their DNA sequence data. With the reference cultures that this study has now made available to the community, further genomic research on the more important agricultural pathogens may shed some light on the mechanisms driving their evolution, and allow the development of more appropriate control measures.

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