

# Phylogenetic insights resolve *Dacampiaceae* (*Pleosporales*) as polyphyletic: *Didymocyrtis* (*Pleosporales*, *Phaeosphaeriaceae*) with *Phoma*-like anamorphs resurrected and segregated from *Polycoccum* (*Trypetheliales*, *Polycoccaceae* fam. nov.)

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**Abstract** A phylogenetic analysis of nuLSU and ITS sequences representing genera previously included in *Dacampiaceae* indicates that the family is strongly polyphyletic and that the type species of *Dacampia* is placed in *Pleosporales*. The genus *Munkovalsaria* s. str. is placed in *Didymosphaeriaceae* (*Pleosporales*). *Polycoccum* s. str. and two species of *Clypeococcum* are shown to form a new lineage sister to the *Trypetheliaceae* in *Trypetheliales* and described here as *Polycoccaceae*. Other members of *Polycoccum* s. lat. are included in the *Pleosporales* and are closely related to lichenicolous *Phoma*-like species of the family *Phaeosphaeriaceae*. The genus *Didymocyrtis* is resurrected for these species and for lichenicolous species previously assigned to *Diederichia*, *Diederichomyces*, *Leptosphaeria* and *Phoma*. The genera *Diederichia* and

*Diederichomyces* are synonymized with *Didymocyrtis*. The new combinations *Didymocyrtis bryonthae*, *D. cladonicola*, *D. foliaceiphila*, *D. infestans*, *D. kaernefeltii*, *D. melanelixiae*, *D. pseudeverniae*, *D. ramalinae*, *D. slaptoniensis* and *D. xanthomendozae* are made, and the new name *D. epiphyscia* is introduced for *Phoma physciicola*. Some anamorph-teleomorph relationships are resolved, such as *Didymocyrtis ramalinae*–*Phoma ficuzzae* and *Didymocyrtis consimilis*–*Phoma caloplacae*, the phylogenetic results being supported by single ascospore cultures that lead to the asexual stage producing pycnidia and conidia in culture. Speciation by host switching is assumed to be important in the genus *Didymocyrtis*. An identification key to *Didymocyrtis* species is provided.

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## Introduction

The family *Dacampiaceae* Körb. includes lichenicolous, lichenized and saprobic fungi forming blackish, perithecioid ascomata, a pseudoparenchymatous exciple, branched-anastomosing pseudoparaphyses, bitunicate asci, and septate to muriform, usually brown ascospores (Hyde et al. 2013). The family was placed in *Dothideales* in the past (Eriksson and Hawksworth 1986, 1993; Hawksworth and Diederich 1988; Henssen 1995), but is currently considered as ‘*Dothideomycetes*, family *incertae sedis*’ (Hyde et al. 2013; Wijayawardene et al. 2014). *Dacampiaceae* is considered to be a heterogeneous assemblage including about 110 species in 10 genera: *Aaosphaeria*, *Clypeococcum*, *Dacampia*, *Eopyrenula*, *Leptocucurthis*, *Munkovalsaria*, *Polycoccum*, *Pseudonitschkia*, *Pyrenidium* and *Weddellomyces* (Hyde et al. 2013).

Few sequences of *Dacampiaceae* are available in GenBank. One sequenced species is *Munkovalsaria appendiculata* Aptroot, collected on dead culms of *Zea mays* and assigned to *Pleosporales* in a phylogenetic analysis by Aptroot (2004); it also was found to cluster with *Montagnula opulenta* (*Didymosphaeriaceae*) as recently circumscribed by Ariyawansa et al. (2014) in a phylogeny by Wang et al. (2007). Sequences of *M. donacina* (generic type) were generated by Pitt et al. (2014), but not included in a phylogenetic analysis. A 28S rDNA sequence of *Polycoccum vermicularium* was also deposited in GenBank (AY961601), but we found it to be of a poor quality and its reliability is questioned here.

Many described species of *Dacampiaceae* are lichenicolous, but limited sequence data for lichenicolous species means they are not commonly included in cladograms based on molecular data sets (e.g., Lutzoni et al. 2004; Zhang et al. 2009). Despite some recent progress in placing lichenicolous species in *Dothideomycetes* (Lawrey et al. 2011, 2012; Ruibal et al. 2011; Ertz et al. 2013; Pérez-Ortega et al. 2013; Ertz and Diederich 2015), questions remains about whether the placement and content of *Dacampiaceae*, including lichenicolous species, are correct.

*Polycoccum*, the most species-rich genus of *Dacampiaceae* and one that includes only lichenicolous species, has never been adequately studied using molecular data and is here studied in detail. *Polycoccum* had been little used for lichenicolous ascomycetes until its reinstallation by Santesson (1960), but in the past two decades it has become one of the most species-rich genera of lichenicolous fungi, with 57 species accepted by Lawrey and Diederich (2015) and new species described almost every year. A first key was given by Vězda (1969, 10

species). The most complete key so far available is that compiled by Hawksworth and Diederich (1988, 23 species worldwide), and there are additional more recently-published regional keys (e.g., Atienza et al. 2003, 13 species from Spain; Calatayud 2004, 5 species from the Sonoran desert region; Ihlen and Wedin 2008, 14 species from Sweden; Gardiennet 2012, 13 species from France) that illustrate the diversity of this genus in various parts of the world.

The relationship of *Polycoccum* to other members of the *Dothideales* has never been established with certainty. Crivelli (1983: 193) suggested a close relationship among *Dacampia*, *Polycoccum* and *Pyrenidium* (sub *Dacampiosphaeria*). This view was further elaborated by Hawksworth and Diederich (1988), when they proposed to treat these three genera together with *Byssothecium*, *Clypeococcum* and *Weddellomyces* in the family *Dacampiaceae* in the *Dothideales*. However, until now these hypotheses have not been adequately tested.

This paper aims at (1) testing the monophyly of the family *Dacampiaceae*, (2) elucidating the phylogenetic position of the genera *Clypeococcum*, *Diederichia* and *Polycoccum*, (3) testing the monophyly of the genus *Polycoccum*, (4) reinstating the genus *Didymocyrtis*, and (5) testing some anamorph-teleomorph relationships among lichenicolous members of the genera *Polycoccum* s. lat. and *Phoma* s. lat.

## Material and methods

### Morphological study

Herbarium specimens are deposited in BR, CANL, E, GZU, M, NY, UBC and in the private collections of S. Beeching, F. Berger, P. Diederich, J. Hafellner and J. Etayo. External morphology of herbarium specimens was examined and measured under Leica MZ 7.5 (magnification up to  $\times 50$ ), Wild M3 (magnification up to  $\times 40$ ) and Olympus SZX12 (magnification up to  $\times 90$ ) stereomicroscopes. Macroscopic photographs were done using a Canon 40D camera with a Canon MP-E 65 mm lens or a Nikon BD Plan 10 $\times$  microscope objective, StackShot (Cognisys) and Helicon Focus (HeliconSoft) for increasing the depth of field; or with a Color View I digital camera connected to an Olympus SZX12 stereomicroscope. Hand-made sections of ascomata and thallus were studied in water, 5 % KOH (K), or 1 % I<sub>2</sub> Lugol’s reagent without (I) or with KOH pre-treatment (K/I) using Leica DMLB, Leica DMRE and Olympus BX51 microscopes (magnification up to  $\times 1000$ ). Sectioning was performed by one of us (JH) using a freezing microtome (Leitz, sections of 12–15  $\mu\text{m}$ ), but squash preparations were also used, especially for ascus analysis. Conidiogenesis of conidia was studied in water and erythrosin B (ALDRICH 19,826-9) in 10 % ammonia. Measurements of asci, ascospores and conidia all refer to material examined in tap water. Conidial size of a large number of

conidia was measured for some specimens, and the average ( $\bar{X}$ ) and standard deviation (SD) calculated. Such measurements are given as  $\bar{X} \pm \text{SD}$ , surrounded by the extreme values (between parentheses), followed by the number of measurements (n). For the graphical representation of the conidial size distribution (Fig. 6), each specimen is represented by an ellipse, of which the centre represents the average length and breadth, the large radius represents the SD of conidial length and the small radius the SD of conidial breadth. The graphical representation has been done using the PostScript language. Microscopic photographs were prepared using either a Leica DMLB microscope with differential interference contrast and fitted with a Leica EC3 camera, or an Olympus BX51 microscope with interference contrast and connected to a Color View I digital camera.

### Molecular techniques

Cultures were isolated from ascospores (single ascospore cultures for sexual stages of *Didymocyrtis ramalinae*, for *Didymocyrtis* aff. *consimilis* Ertz 17617b, Berger 26876, and for *Didymocyrtis slaptoniensis* MoraA-B; two-ascospores isolate for *Didymocyrtis consimilis* 12041; and multi-ascospores isolate for *Didymocyrtis melanelixiae* and *D. slaptoniensis* 12009), or from conidia (multiconidia cultures) of freshly collected material on malt-yeast extract medium as described by Yoshimura et al. (2002) (Fig. 9). Thin sections were made through ascomata or pycnidia, and the outer wall was removed with a sterile razor blade to expose ascospores or conidia, which were then spread directly on malt-yeast extract agar. Isolated ascospores were immediately transferred to new petri dishes to attain single-spore cultures. Germination of conidia and ascospores was often observed within a day. The cultures were kept at room temperature in the laboratory of the Botanic Garden Meise and exposed to a natural day-light regime. Cultures maintained at George Mason University were kept at 18 °C in 12 h light-12 h dark cycles. No experiments were done to test whether different light or temperature conditions could improve the growth rate. All the strains were fast-growing and therefore only a few weeks were required to obtain sufficient material for DNA extraction. In some cases, hand-made sections of the hymenium or thallus were used for direct PCR as described in Ertz et al. (2014). The outer wall of ascomata was removed with a sterile razor blade to isolate the hymenium. The material was then added to a tube containing the PCR reaction mixture and amplified directly. Genomic DNA was isolated from cultures using the CTAB extraction protocol (Doyle and Doyle 1990). Amplification reactions were prepared for a 50  $\mu\text{l}$  final volume containing 5  $\mu\text{l}$  10 $\times$  DreamTaq Buffer (Fermentas), 1.25  $\mu\text{l}$  of each of the 20  $\mu\text{M}$  primers, 5  $\mu\text{l}$  of 2.5  $\text{mg mL}^{-1}$  bovin serum albumin (Fermentas #B14), 4  $\mu\text{l}$  of 2.5 mM each dNTPs (Fermentas),

1.25 U DreamTaq DNA polymerase (Fermentas), and 1  $\mu\text{l}$  of template genomic DNA or tiny fragments of fungal material. A targeted fragment of about 1.1 kb at the 5' end of the nuLSU rDNA was amplified using primers LIC15R (Miadlikowska et al. 2002) with LR6 (Vilgalys and Hester 1990). A fragment of about 0.6 kb of the nuITS rDNA was amplified using primers ITS1F and ITS4 (White et al. 1990). The yield of the PCRs was verified by running the products on a 1 % agarose gel using ethidium bromide. Both strands were sequenced by MacroGen<sup>®</sup> using amplification primers. Additional primers were used for the sequencing of nuLSU: LR3, more rarely LR3R and LR5 (Vilgalys and Hester 1990) (Vilgalys' website, <http://www.botany.duke.edu/fungi/mycolab>). Sequence fragments were assembled with Sequencher version 4.6 (Gene Codes Corporation, Ann Arbor, Michigan). Sequences were subjected to MEGABLAST searches to verify their closest relatives and to detect potential contaminations.

### Taxon selection and phylogenetic analyses

Although not possible for all taxa, we tried to achieve a sample series with at least two specimens of each newly sequenced species, preferably from different localities, to avoid misidentifications caused by contamination or sequencing errors. Our sample series include sequences obtained from the type species of *Dacampia*, *Didymocyrtis* and *Polycoccum* that are important for taxonomic conclusions. For the nuLSU phylogenetic tree, the closest relatives of the new sequences based on BLAST searches were retrieved from GenBank. Additional taxa were selected from Hyde et al. (2013) and Nelsen et al. (2014) to include a wide array of families belonging to *Dothideomycetes* and an exhaustive list of genera belonging to *Trypetheliales*. The original nuLSU matrix used in Ertz and Diederich (2015) was used as main template. The resulting nuLSU matrix consisted of 109 sequences, mainly from a wide variety of *Dothideomycetes*. Some *Arthoniomycetes* were also included. Three outgroup species were chosen to represent the class *Eurotiomycetes* (*Caliciopsis pinea* and *Capronia munkii*) and the class *Leotiomycetes* (*Lachnum virgineum*). *Caliciopsis pinea* was used as the rooting taxon in the related analyses. The ITS matrix was assembled manually and consisted of 58 sequences, including 52 sequences of *Didymocyrtis* and 6 sequences chosen from the most closely related genera in Trakunyingcharoen et al. (2014). *Phaeosphaeria lycopodina* was used as the rooting taxon in these analyses. The alignments were improved manually using MacClade 4.05 (Maddison and Maddison 2002). Terminal ends of sequences, ambiguous aligned regions and introns were delimited manually and excluded from the nuLSU dataset. The nuLSU data set consisted of 1160 unambiguously aligned characters, of which 463 were variable. The

ITS data set consisted of 594 unambiguously aligned characters, of which 120 were variable.

The best-fit model of DNA evolution GTR+I+G was chosen for the nuLSU data set and the GTR+I for the ITS data set using the Akaike information criterion (AIC; Akaike 1973) as implemented in Modeltest v. 3.7 (Posada and Crandall 1998). Bayesian analyses were carried out using the Metropolis-coupled Markov chain Monte Carlo method (MCMCMC) in MrBayes v. 3.2.3 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003) on the CIPRES portal (Miller et al. 2010). Analyses were run under the selected model of nucleotide substitution with six rate categories. Two parallel MCMCMC runs were performed, with each run using four independent chains and 100,000,000 generations for the nuLSU data set and for the ITS data set, and sampling trees every 1000th generation. Convergence diagnostics were estimated using the PSRF (Potential scale reduction factor) where values closer to one indicated convergence between runs (Gelman and Rubin 1992), and using TRACER v. 1.6 by plotting the log-likelihood values of the sample points against generation time (Rambaut and Drummond 2007). Posterior probabilities (PP) of the nuLSU and ITS matrices were determined by calculating a majority-rule consensus tree generated from the 150,002 post-burnin trees of the 200,002 trees sampled by the two MCMCMC runs using the sumt option of MrBayes. In addition, a Maximum Likelihood (ML) analysis was performed on the nuLSU and ITS data sets using GARLI (Zwickl 2006, v. 0.951 for OSX) with default settings, and a single most likely tree was produced ( $-\ln L=11690.8948$  for the nuLSU tree;  $-\ln L=1941.3522$  for the ITS tree). One thousand bootstrap pseudoreplicates were used to calculate a majority rule consensus tree in PAUP\* 4.0b10 (Swofford 2002) to assess the Maximum Likelihood bootstrap values (ML-bs).  $ML\text{-}bs \geq 70\%$  and  $PP \geq 95\%$  were considered to be significant. Phylogenetic trees were visualized using FigTree v. 1.4.2 (Rambaut 2012).

## Results

We obtained 54 new sequences (20 nuLSU and 34 ITS) belonging to 15 species from Austria, Belgium, Canada, Canary Islands (Gomera), Madeira, France (including Corsica), Iceland, Luxembourg, Scotland, Switzerland and USA (Table 1). The Bayesian nuLSU tree we recovered did not contradict the ML nuLSU tree topology for the strongly supported branches and hence only the ML tree is shown with the branches having  $ML\text{-}bs \geq 70\%$  in bold and with the posterior probabilities of the Bayesian analysis added above the internal branches (Fig. 1). The recovered Bayesian ITS tree did not contradict the ML ITS tree's topology for the strongly supported branches and hence only the ML tree is shown with the branches having  $ML\text{-}bs \geq 70\%$  in bold and with the posterior

probabilities of the Bayesian analysis added above the internal branches (Fig. 2).

The genera *Clypeococcum*, *Dacampia*, *Diederichia* (here synonymized with *Didymocyrtis*, see Taxonomy section) and *Polycoccum* are included in a molecular phylogeny for the first time, all except the first being represented by the type species. The status of *Clypeococcum* remains unclear until the type, *C. cladonema* is sequenced. The backbone of our nuLSU phylogenetic tree is poorly resolved. However, main groups such as *Arthoniales*, *Capnodiales*, *Eremithallales*, *Hysteriales*, *Trypetheliales*, *Tubeufiales* and *Venturiales* are strongly supported by both analyses, even though the relationships among such groups are not supported. *Polycoccum* is resolved as polyphyletic, with species being placed in two main distantly-related lineages corresponding to *Trypetheliales* (as newly defined) and *Pleosporales*. *Trypetheliales* is strongly supported and divided into two strongly supported main lineages corresponding to *Polycoccaceae* (newly described here), and to *Trypetheliaceae*. *Polycoccaceae* includes two genera, *Clypeococcum* and *Polycoccum*, of which the latter is paraphyletic. *Pleosporales* is only supported by the Bayesian analysis (PP=96).

*Dacampia*, the type genus of *Dacampiaceae*, is strongly supported by both analyses (ML-bs=92, PP=100) and placed in *Pleosporales*. It is sister to *Paraleptosphaeria orobanches*, but this relationship is not supported. The relationship of *Dacampiaceae* with other families of *Pleosporales* cannot be resolved with certainty using only nuLSU sequences and the available representatives of *Pleosporales*. *Didymocyrtis* is nested in *Pleosporales* and includes eleven specimens that form a poorly supported clade with very low resolution. Figure 2 presents a more detailed phylogeny of *Didymocyrtis* based on ML analysis of ITS sequence data. According to this analysis, the *Didymocyrtis* clade is strongly supported (ML-bs=72, PP=100) and includes species previously placed in *Diederichia*, *Leptosphaeria*, *Phoma* (or the new genus *Diederichomyces* recently described by Trakuningcharoen et al. 2014) and *Polycoccum*. *Didymocyrtis cladonicola* does not form a monophyletic group, unlike the other species in the clade, which are strongly supported by both analyses. However, relationships among the species are usually poorly supported. In the *Didymocyrtis consimilis* clade, samples from *Caloplaca* hosts cluster together, but this relationship is only supported by the Bayesian analysis (PP=97).

Most taxa now treated in *Didymocyrtis* were previously known either as species of *Leptosphaeria* or *Polycoccum* (sexual stage) or of *Diederichia* or *Phoma* (asexual stage). Co-occurrences of both stages on the same host thallus have rarely been observed and documented until recently. Nevertheless, our phylogenetic analyses clearly show that both stages belong to the same clade, representing the genus *Didymocyrtis* (Figs. 1 and 2), for which the much younger *Diederichia* and *Diederichomyces* are made synonyms.

**Table 1** Specimens and DNA sequences used in this study, with their respective voucher information

Name	Order	Family	Voucher information	Hosts	nuLSU	ITS
<i>Abrothallus parmotremitis</i>	Abrothallales	Abrothallaceae	AB1		KF816231	
<i>Acanthostigma minutum</i>	Tubeufiales	Tubeufiaceae	BBB:MVB 781		JN127360	
<i>Acrospermum compressum</i>	Acrospermales	Acrospermaceae	Vesterholt s.n. (TUR)		EU940084	
<i>Anisomeridium ubianum</i>	Monoblastiales	Monoblastiaceae	Lumbsch; isolate 94		GU327709	
<i>Aptrootia robusta</i>	Trypetheliales	Trypetheliaceae	Lumbsch 20012 (F)		KM453755	
<i>Architrypethelium uberinum</i>	Trypetheliales	Trypetheliaceae	Nelsen s.n. (F)		KM453758	
<i>Arthonia didyma</i>	Arthoniales	Arthoniaceae	Ertz 7587 (BR)		EU704083	
<i>Arthopyrenia cinchonae</i>	Trypetheliales	Trypetheliaceae	Lücking s.n. (F)		KM453759	
<i>Arthopyrenia cf. planorbis</i>	Trypetheliales	Trypetheliaceae	Lücking 29584		JN872352	
<i>Arthopyrenia salicis</i>	Pleosporales	Arthopyreniaceae	CBS 368.94		AY538339	
<i>Asterina weinmanniae</i>	Asterinales	Asterinaceae	Hofmann 592 (M-0141091, PMA)		GU586218	
<i>Astrothelium variolosum</i>	Trypetheliales	Trypetheliaceae	Nelsen s.n. (F)		KM453768	
<i>Bathelium tuberculosum</i>	Trypetheliales	Trypetheliaceae	Lumbsch 19739z (F)		KM453777	
<i>Bimuria novae-zelandiae</i>	Pleosporales	Didymosphaeriaceae	CBS 107.79		AY016356	
<i>Botryosphaeria dothidea</i>	Botryosphaeriales	Botryosphaeriaceae	CBS 115476		DQ678051	
<i>Caliciopsis pinea</i>	Coryneliales	Coryneliaceae	AFTOL-ID 1869		DQ678097	
<i>Capnodium coffeae</i>	Capnodiales	Capnodiaceae	CBS 147.52		DQ247800	
<i>Capronia munkii</i>	Chaetothyriales	Herpotrichiellaceae	AFTOL-ID 656		EF413604	
<i>Clypeococcum placopsiphilum</i>	Trypetheliales	Polycoccaceae	Diederich 17576 (hb. Diederich)	<i>Placopsis gelida</i>	<b>KT383789</b>	
<i>Clypeococcum psoromatis</i>	Trypetheliales	Polycoccaceae	Ertz 19259 (BR)	<i>Squamarina cartilaginea</i>	<b>KT383790</b>	
<i>Coniosporium apollinis</i>	Unknown	Unknown	CBS 109860		GU250899	
<i>Coniothyrium telephii</i>	Pleosporales	Coniothyriaceae	CBS 188.71		GQ387599	
<i>Corynespora cassicola</i>	Pleosporales	Corynesporascaceae	CBS 100822		GU301808	
<i>Cryomyces antarcticus</i>	Unknown	Unknown	CCFEE 536		GU250365	
<i>Cryptothelium pulchrum</i>	Trypetheliales	Trypetheliaceae	Nelsen 4001a (F)		GU327714	
<i>Dacampia engeliana</i>	Pleosporales	Dacampiaceae	Hafellner 72868 (BR)	<i>Solorina saccata</i>	<b>KT383791</b>	
<i>Dacampia hookeri</i>	Pleosporales	Dacampiaceae	Hafellner 73897 (GZU)		<b>KT383792</b>	
<i>Dacampia hookeri</i>	Pleosporales	Dacampiaceae	Hafellner 74269 (GZU)		<b>KT383793</b>	
<i>Dacampia hookeri</i>	Pleosporales	Dacampiaceae	Hafellner 75980 (GZU)		<b>KT383794</b>	
<i>Dacampia hookeri</i>	Pleosporales	Dacampiaceae	Hafellner 81840 (GZU)		<b>KT383795</b>	
<i>Delitschia winteri</i>	Pleosporales	Delitschiaceae	CBS 225.62		DQ678077	
<i>Dendrographa leucophaea</i>	Arthoniales	Roccellaceae	Sparrus 7999 (BR)		AY548810	
<i>Didymella bryoniae</i>	Pleosporales	Didymellaceae	CBS 133.96		GU456335	
<i>Didymocyrtis cladoniicola</i>	Pleosporales	Phaeosphaeriaceae	Ertz 15238 (BR)	<i>Squamarina cartilaginea</i>	JQ238625	JQ238623
<i>Didymocyrtis cladoniicola</i>	Pleosporales	Phaeosphaeriaceae	Ertz 15208 (BR)	<i>Squamarina cartilaginea</i>		JQ238620
<i>Didymocyrtis cladoniicola</i>	Pleosporales	Phaeosphaeriaceae	Diederich 16915 (hb. Diederich)	<i>Cladonia</i> sp.		JQ238626

Table 1 (continued)

Name	Order	Family	Voucher information	Hosts	nuLSU	ITS
<i>Didymocyrtis cladoniicola</i>	Pleosporales	Phaeosphaeriaceae	Diederich 16924 (hb. Diederich)	<i>Parmelina tiliacea</i>		JQ238629
<i>Didymocyrtis cladoniicola</i>	Pleosporales	Phaeosphaeriaceae	Van den Broeck 4662 (BR)	<i>Cladonia</i> sp.		JQ318014
<i>Didymocyrtis cladoniicola</i>	Pleosporales	Phaeosphaeriaceae	Ertz 16072 (BR)	<i>Ramalina pollinaria</i>		JQ318017
<i>Didymocyrtis cladoniicola</i>	Pleosporales	Phaeosphaeriaceae	Ertz 16069 (BR)	<i>Cladonia symphycarpa</i>		JQ318020
<i>Didymocyrtis cladoniicola</i>	Pleosporales	Phaeosphaeriaceae	Ertz 16064 (BR)	<i>Cladonia rangiformis</i>		JQ318023
<i>Didymocyrtis cladoniicola</i>	Pleosporales	Phaeosphaeriaceae	Ertz 16066 (BR)	<i>Cladonia foliacea</i>		JQ318026
<i>Didymocyrtis cladoniicola</i>	Pleosporales	Phaeosphaeriaceae	Ertz 16296 (BR)	<i>Ramalina polymorpha</i>		<b>KT383809</b>
<i>Didymocyrtis cladoniicola</i>	Pleosporales	Phaeosphaeriaceae	Ertz 16464 (BR)	<i>Cladonia foliacea</i>		<b>KT383810</b>
<i>Didymocyrtis consimilis</i>	Pleosporales	Phaeosphaeriaceae	Gardiennet 12041 – asexual stage	<i>Caloplaca cerina</i>		<b>KT383812</b>
<i>Didymocyrtis consimilis</i>	Pleosporales	Phaeosphaeriaceae	Gardiennet 12041 – sexual stage	<i>Caloplaca cerina</i>	<b>KT383796</b>	<b>KT383813</b>
<i>Didymocyrtis consimilis</i>	Pleosporales	Phaeosphaeriaceae	Freebury 1324 – asexual stage	<i>Caloplaca cerina</i>		JQ238635
<i>Didymocyrtis consimilis</i>	Pleosporales	Phaeosphaeriaceae	Freebury 1357 – asexual stage	<i>Caloplaca cerina</i>		JQ238641
<i>Didymocyrtis</i> aff. <i>consimilis</i>	Pleosporales	Phaeosphaeriaceae	Ertz 17617B (BR) – sexual stage	<i>Cladonia</i> cf. <i>pocillum</i>	<b>KT383797</b>	<b>KT383811</b>
<i>Didymocyrtis</i> aff. <i>consimilis</i>	Pleosporales	Phaeosphaeriaceae	Berger 26876 – sexual stage	<i>Melanohalea exasperatula</i>	<b>KT383798</b>	<b>KT383814</b>
<i>Didymocyrtis</i> aff. <i>consimilis</i>	Pleosporales	Phaeosphaeriaceae	Berger 27218 – asexual stage	<i>Melanohalea exasperatula</i>		<b>KT383815</b>
<i>Didymocyrtis</i> aff. <i>consimilis</i>	Pleosporales	Phaeosphaeriaceae	Berger 27251 – asexual stage	<i>Heterodermia</i>		<b>KT383816</b>
<i>Didymocyrtis</i> aff. <i>consimilis</i>	Pleosporales	Phaeosphaeriaceae	Diederich 17465 – asexual stage	<i>Cladonia pocillum</i>		<b>KT383817</b>
<i>Didymocyrtis epiphyscia</i> s. lat.	Pleosporales	Phaeosphaeriaceae	Ertz 17422 (BR)	<i>Xanthoria parietina</i>		<b>KT383818</b>
<i>Didymocyrtis epiphyscia</i> s. lat.	Pleosporales	Phaeosphaeriaceae	Ertz 17615 (BR)	<i>Physcia</i> cf. <i>adscendens</i>		<b>KT383819</b>
<i>Didymocyrtis epiphyscia</i> s. lat.	Pleosporales	Phaeosphaeriaceae	Ertz 17411 (BR)	<i>Physcia adscendens</i>	<b>KT383799</b>	<b>KT383820</b>
<i>Didymocyrtis epiphyscia</i> s. lat.	Pleosporales	Phaeosphaeriaceae	Ertz 17414 (BR)	<i>Xanthoria parietina</i>		<b>KT383821</b>
<i>Didymocyrtis epiphyscia</i> s. lat.	Pleosporales	Phaeosphaeriaceae	Gardiennet 12008-isolate2 (BR)	<i>Xanthoria parietina</i>		<b>KT383822</b>
<i>Didymocyrtis epiphyscia</i> s. lat.	Pleosporales	Phaeosphaeriaceae	Ertz 17461 (BR)	<i>Physcia adscendens</i>		<b>KT383823</b>
<i>Didymocyrtis epiphyscia</i> s. str.	Pleosporales	Phaeosphaeriaceae	Freebury 1411; isolate 512	<i>Physcia aipolia</i>		<b>KT383824</b>
<i>Didymocyrtis epiphyscia</i> s. lat.	Pleosporales	Phaeosphaeriaceae	Ertz 17413 (BR)	<i>Xanthoria parietina</i>		<b>KT383825</b>
<i>Didymocyrtis foliaceiphila</i>	Pleosporales	Phaeosphaeriaceae	Ertz 15257 (BR)	<i>Parmelia sulcata</i>		JQ318002
<i>Didymocyrtis foliaceiphila</i>	Pleosporales	Phaeosphaeriaceae	Ertz 15258 (BR)	<i>Parmelia sulcata</i>	JQ318007	JQ318005
<i>Didymocyrtis foliaceiphila</i>	Pleosporales	Phaeosphaeriaceae	Ertz 15262 (BR)	<i>Cladonia</i> sp.		JQ318008
<i>Didymocyrtis foliaceiphila</i>	Pleosporales	Phaeosphaeriaceae	Ertz 15262bis (BR)	<i>Cladonia</i> sp.		JQ318011
<i>Didymocyrtis foliaceiphila</i>	Pleosporales	Phaeosphaeriaceae	Diederich 17108 (hb. Diederich)	<i>Cladonia squamosa</i>		JQ238638
<i>Didymocyrtis melanelixiae</i>	Pleosporales	Phaeosphaeriaceae	Harris 57475; isolate 551 – sexual stage	<i>Punctelia rudecta</i>		<b>KT383826</b>
<i>Didymocyrtis melanelixiae</i>	Pleosporales	Phaeosphaeriaceae	Harris 57475; isolate 552 – sexual stage	<i>Punctelia rudecta</i>	<b>KT383800</b>	<b>KT383827</b>
<i>Didymocyrtis melanelixiae</i>	Pleosporales	Phaeosphaeriaceae	Harris 57475; isolate 553 – asexual stage	<i>Punctelia rudecta</i>		<b>KT383828</b>
<i>Didymocyrtis melanelixiae</i>	Pleosporales	Phaeosphaeriaceae	Harris 57475B; isolate 555 – asexual stage	<i>Punctelia rudecta</i>		<b>KT383829</b>
<i>Didymocyrtis melanelixiae</i>	Pleosporales	Phaeosphaeriaceae	Harris 57465; isolate 557 – asexual stage	<i>Cetrelia olivetorum</i>		<b>KT383830</b>
<i>Didymocyrtis melanelixiae</i>	Pleosporales	Phaeosphaeriaceae	Harris 57476; isolate 549 – asexual stage	<i>Punctelia rudecta</i>		<b>KT383831</b>

Table 1 (continued)

Name	Order	Family	Voucher information	Hosts	nuLSU	ITS
<i>Didymocyrtis pseudeverniae</i>	Pleosporales	Phaeosphaeriaceae	Diederich 17327a (hb. Diederich)	<i>Pseudevernia furfuracea</i>		<b>KT383832</b>
<i>Didymocyrtis pseudeverniae</i>	Pleosporales	Phaeosphaeriaceae	Diederich 17327b (hb. Diederich)	<i>Pseudevernia furfuracea</i>		<b>KT383833</b>
<i>Didymocyrtis pseudeverniae</i>	Pleosporales	Phaeosphaeriaceae	Diederich 17338 (hb. Diederich)	<i>Pseudevernia furfuracea</i>	<b>KT383801</b>	<b>KT383834</b>
<i>Didymocyrtis ramalinae</i>	Pleosporales	Phaeosphaeriaceae	Paul 13i2013 isolate1 – sexual stage	<i>Ramalina fastigiata</i>		<b>KT383835</b>
<i>Didymocyrtis ramalinae</i>	Pleosporales	Phaeosphaeriaceae	Paul 27i2013 isolate1 – sexual stage	<i>Ramalina fastigiata</i>		<b>KT383836</b>
<i>Didymocyrtis ramalinae</i>	Pleosporales	Phaeosphaeriaceae	Paul 27i2013 isolate2 – sexual stage	<i>Ramalina fastigiata</i>		<b>KT383837</b>
<i>Didymocyrtis ramalinae</i>	Pleosporales	Phaeosphaeriaceae	Ertz 16399 (BR) – sexual stage	<i>Ramalina</i> sp.	<b>KT383802</b>	<b>KT383838</b>
<i>Didymocyrtis ramalinae</i>	Pleosporales	Phaeosphaeriaceae	Paul 10i2013 – asexual stage	<i>Ramalina fastigiata</i>		<b>KT383839</b>
<i>Didymocyrtis ramalinae</i>	Pleosporales	Phaeosphaeriaceae	Van den Broeck 2900 (BR) – asexual stage	<i>Ramalina fastigiata</i>		JQ238614
<i>Didymocyrtis slaptioniensis</i>	Pleosporales	Phaeosphaeriaceae	Gardiennet 12009 – sexual stage	<i>Xanthoria parietina</i>		<b>KT383840</b>
<i>Didymocyrtis slaptioniensis</i>	Pleosporales	Phaeosphaeriaceae	MoraA – sexual stage	<i>Xanthoria parietina</i>	<b>KT383803</b>	<b>KT383841</b>
<i>Didymocyrtis slaptioniensis</i>	Pleosporales	Phaeosphaeriaceae	MoraB – sexual stage	<i>Xanthoria parietina</i>		<b>KT383842</b>
<i>Didymocyrtis xanthomendozae</i>	Pleosporales	Phaeosphaeriaceae	CBS129666	<i>Xanthomendoza hasseana</i>	JQ238634	JQ238632
<i>Dothidea insculpta</i>	Dothideales	Dothideaceae	CBS 189.58		DQ247802	
Dothideomycetes sp.	Unknown	Unknown	AN13		GU250928	
<i>Encephalographa elisae</i>	Eremithallales	Melaspileaceae	EB 0347		GU397343	
<i>Etayoa tryptelii</i>	Lichenostigmatales	Phaeococcomycetaceae	Common 9200-G (MSC, hb. Diederich)		KF176940	
<i>Friedmanniomyces endolithicus</i>	Capnodiales	Teratosphaeriaceae	CCFEE 5180		GU250367	
<i>Geastrumia polystigmatis</i>	Asterinales?	Unknown	NC41.8F1a		KF896877	
<i>Gloniopsis praelonga</i>	Hysteriales	Hysteriaceae	CBS 112415		FJ161173	
<i>Glonium circumserpens</i>	Mytilinidiales	Gloniaceae	CBS 123343; EB 0332		FJ161200	
<i>Halojulella avicenniae</i>	Pleosporales	Halojulellaceae	BCC 18422		GU371823	
<i>Hemigrapha atlantica</i>	Asterinales	Parmulariaceae?	Ertz 14014 (BR)		KP456151	
<i>Hysterium angustatum</i>	Hysteriales	Hysteriaceae	CBS 236.34		FJ161180	
<i>Hysteropatella clavispora</i>	Patellariales	Patellariaceae	CBS 247.34		AY541493	
<i>Jahmula aquatica</i>	Jahmulales	Aliquandostipitaceae	R68-1		EF175655	
<i>Julella fallaciosa</i>	Trypetheliales	Trypetheliaceae	Nelsen s.n. (F)		JN887400	
<i>Kellermania nolinae</i>	Botryosphaeriales	Planistromellaceae	CBS 131717		JX444876	
<i>Lachnum virgineum</i>	Helotiales	Hyaloscyphaceae	AFTOL-ID 49		AY544646	
<i>Laurera megasperma</i>	Trypetheliales	Trypetheliaceae	Ertz 9725 (BR)		FJ267702	
<i>Lepidosphaeria nicotiae</i>	Pleosporales	Testudinaceae	CBS 101341		DQ678067	
<i>Leptosphaeria doliolum</i>	Pleosporales	Leptosphaeriaceae	CBS 125979		JF740283	
<i>Leptosphaeria macrospora</i>	Pleosporales	Leptosphaeriaceae	Kruys 501 (UPS)		DQ384092	
<i>Lichenothelia convexa</i>	Lichenotheliales	Lichenotheliaceae	Diederich 17491 (hb. Diederich)		KF176962	
<i>Lindgomyces ingoldianus</i>	Pleosporales	Lindgomycetaceae	ILLS:A-39-1B		AB521736	
<i>Lophium mytilinum</i>	Mytilinidiales	Mytiliniaceae	CBS 269.34		DQ678081	

**Table 1** (continued)

Name	Order	Family	Voucher information	Hosts	nuLSU	ITS
<i>Marcelaria purpurina</i>	Trypetheliales	Trypetheliaceae	Caceres 2009		KM453790	
<i>Massaria inquinans</i>	Pleosporales	Massariaceae	WU 30527		HQ599402	
<i>Massarina eburnea</i>	Pleosporales	Massarinaceae	CBS 473.64		GU301840	
<i>Melaspilea enteroleuca</i>	Eremithallales	Melaspileaceae	Aptroot 20685 (BR)		KP456160	
<i>Montagnula opulenta</i>	Pleosporales	Didymosphaeriaceae	CBS 168.34		NG027581	
<i>Munkovalsaria appendiculata</i>	Pleosporales	Didymosphaeriaceae	CBS 109027		AY772016	
<i>Munkovalsaria donacina</i>	Pleosporales	Didymosphaeriaceae	Pitt s.n.; HVVV01		KJ628377	
<i>Mycromicrothelia hemispherica</i>	Trypetheliales	Trypetheliaceae	Lücking 28641 (F)		GU327719	
<i>Mycromicrothelia miculiformis</i>	Trypetheliales	Trypetheliaceae	Lücking 28637 (F)		GU327720	
<i>Mycromicrothelia obovata</i>	Trypetheliales	Trypetheliaceae	Nelsen 4007a (F)		GU327721	
<i>Mycosphaerella punctiformis</i>	Capnodiales	Mycosphaerellaceae	CBS 113265		DQ470968	
<i>Myriangium duriaei</i>	Myriangiiales	Myriangiaceae	CBS 260.36		DQ678059	
<i>Myrmaecium rubrum</i>	Valsariales	Valsariaceae	CBS 109505		GU456324	
<i>Neostagonospora caricis</i>	Pleosporales	Phaeosphaeriaceae	CBS 135092			KF251163
<i>Neostagonospora elegiae</i>	Pleosporales	Phaeosphaeriaceae	CBS 135101			KF251164
<i>Paraleptosphaeria orobanches</i>	Pleosporales	Leptosphaeriaceae	CBS 101.638		JF740299	
<i>Paraphoma radicina</i>	Pleosporales	Phaeosphaeriaceae	CBS 111.79		EU754191	
<i>Parastagonospora caricis</i>	Pleosporales	Phaeosphaeriaceae	Quaedvlieg S615			KF251176
<i>Parastagonospora poae</i>	Pleosporales	Phaeosphaeriaceae	CBS 135091			KF251179
<i>Phaeosphaeria lycopodina</i>	Pleosporales	Phaeosphaeriaceae	WA0000019137			JX981471
<i>Phaeosphaeria oryzae</i>	Pleosporales	Phaeosphaeriaceae	CBS110110		GQ387591	
<i>Phaeotrichum benjaminii</i>	Phaeotrichales	Phaeotrichaceae	CBS 541.72		AY004340	
<i>Phyllobathelium anomalum</i>	Strigulales	Strigulaceae	Lücking s.n. (F)		GU327722	
<i>Pleospora fallens</i>	Pleosporales	Pleosporaceae	CBS 284.70		GU238078	
<i>Pleospora herbarum</i>	Pleosporales	Pleosporaceae	CBS 191.86		GU238160	
<i>Polycoccum clauzadei</i>	Trypetheliales	Polycoccaceae	Freebury 2089	<i>Xanthoria elegans</i>	<b>KT383804</b>	
<i>Polycoccum pulvinatum</i>	Trypetheliales	Polycoccaceae	Diederich 17389 (hb. Diederich)	<i>Physcia caesia</i>	<b>KT383805</b>	
<i>Polycoccum pulvinatum</i>	Trypetheliales	Polycoccaceae	Ertz 18114 (BR)	<i>Physcia caesia</i>	<b>KT383806</b>	
<i>Polycoccum trypethelioides</i>	Trypetheliales	Polycoccaceae	Diederich 17508 (hb. Diederich)	<i>Stereocaulon</i>	<b>KT383807</b>	
<i>Polycoccum vermicularium</i>	Trypetheliales	Polycoccaceae	Diederich 17545 (hb. Diederich)	<i>Thamnolia vermicularis</i>	<b>KT383808</b>	
<i>Polymeridium albocinereum</i>	Trypetheliales	Trypetheliaceae	Lücking s.n. (F)		KM453795	
<i>Preussia terricola</i>	Pleosporales	Sporormiaceae	DAOM 230091 (AFTOL-ID 282)		AY544686	
<i>Pseudopyrenula diluta</i>	Trypetheliales	Trypetheliaceae	Lücking 26062 (F)		KM453797	
<i>Pseudotetraploa javanica</i>	Pleosporales	Tetraplophaeriaceae	HHUF: 28596; Tanaka et al.		AB524611	
<i>Pyrenochaeta nobilis</i>	Pleosporales	Cucurbitariaceae	CBS 292.74		GQ387615	
<i>Pyrenochaetopsis decipiens</i>	Pleosporales	Cucurbitariaceae	CBS 343.85		GQ387624	



Table 1 (continued)

Name	Order	Family	Voucher information	Hosts	nuLSU	ITS
<i>Racodium rupestre</i>	Capnodiales	Unknown	L346 - Hatfellner & Muggia (GZU)		EU048583	
<i>Setometanomma holmii</i>	Pleosporales	Phaeosphaeriaceae	CBS 110217		GQ387633	
<i>Stagonospora foliicola</i>	Pleosporales	Massariaceae	CBS 110111		KP456169	KF251256
<i>Stictographa lentiginosa</i>	Asterinales	Unknown	Ertz 17447 (BR)		DQ885904	
<i>Symposventuria capensis</i>	Venturiales	Symposventuriaceae	CBS-H 19757		FJ267701	
<i>Trypethelium nitidiusculum</i>	Trypetheliales	Trypetheliaceae	Ertz 9716 (BR)		KM453819	
<i>Trypethelium tropicum</i>	Trypetheliales	Trypetheliaceae	Nelsen s.n. (F)		DQ470982	
<i>Tubeufia cerea</i>	Unknown	Tubeufiaceae	CBS 254.75		DQ470974	
<i>Tyrannosorus pinicola</i>	Unknown	Unknown	CBS 124.88		GU460205	
<i>Valsaria insitiva</i>	Valsariales	Valsariaceae	CBS 123125		DQ384101	
<i>Venturia chlorospora</i>	Venturiales	Venturiaceae	Kruys 502 (UUPS)		KF176965	
<i>Xanthorhizocola physciae</i>	Capnodiales	Teratosphaeriaceae	Diederich 16713 (hb. Diederich)			

GenBank accession numbers in bold refer to sequences (54) generated by this project. All other sequences (113 GenBank identification numbers) were obtained directly from GenBank

Interestingly, our ITS phylogenetic tree highlights several potential anamorph-teleomorph relationships, as follows: 1. *Phoma ficuzzae* is shown to represent the asexual stage of *Didymocyrtis* (*Leptosphaeria*) *ramalinae*; moreover, an asexual *Phoma*-like stage (with pycnidia and conidia) was obtained in all our cultures of single ascospore isolates of *D. ramalinae*. 2. ITS sequences of the asexual *Phoma*-like stage and the sexual stage of *Didymocyrtis melanelixiae* are identical and both stages clearly represent the same species. 3. ITS sequences of the asexual *Phoma caloplacae* and the sexual *Didymocyrtis consimilis* on *Caloplaca* gr. *cerina* are identical and both stages clearly represent the same species. 4. An asexual *Phoma*-like stage (with pycnidia and conidia) was obtained in our cultures of single ascospore isolates of *Didymocyrtis* aff. *consimilis* (specimen Ertz 17617b, on *Cladonia* cf. *pocillum*, initially identified as *Polycoccum laursenii*), and the corresponding ITS sequence is identical to the one of a *Phoma*-like anamorph collected in the same locality and on the same host, *C. pocillum* (specimen Diederich 17465).

In several other species both sexual and asexual stages sometimes occur on the same host thallus or apothecia, a phenomenon that leads to the following hypotheses: 1. *Phoma denigricans* is the asexual stage of *D. bryonothae* (both confined to *Lecanora epibryon*). 2. An unnamed *Phoma*-like fungus occasionally accompanying perithecia of *D. slaptoniensis* on *Xanthoria parietina* may be the asexual stage of that species. 3. Finally, a sexual stage typical of *Didymocyrtis* has been found growing with *Phoma xanthomendozae*, wherein the perithecia are intimately intermixed with pycnidia and macroscopically indistinguishable from them, and is considered to represent the same species.

## Taxonomy

### Pleosporales Luttr. ex M. E. Barr

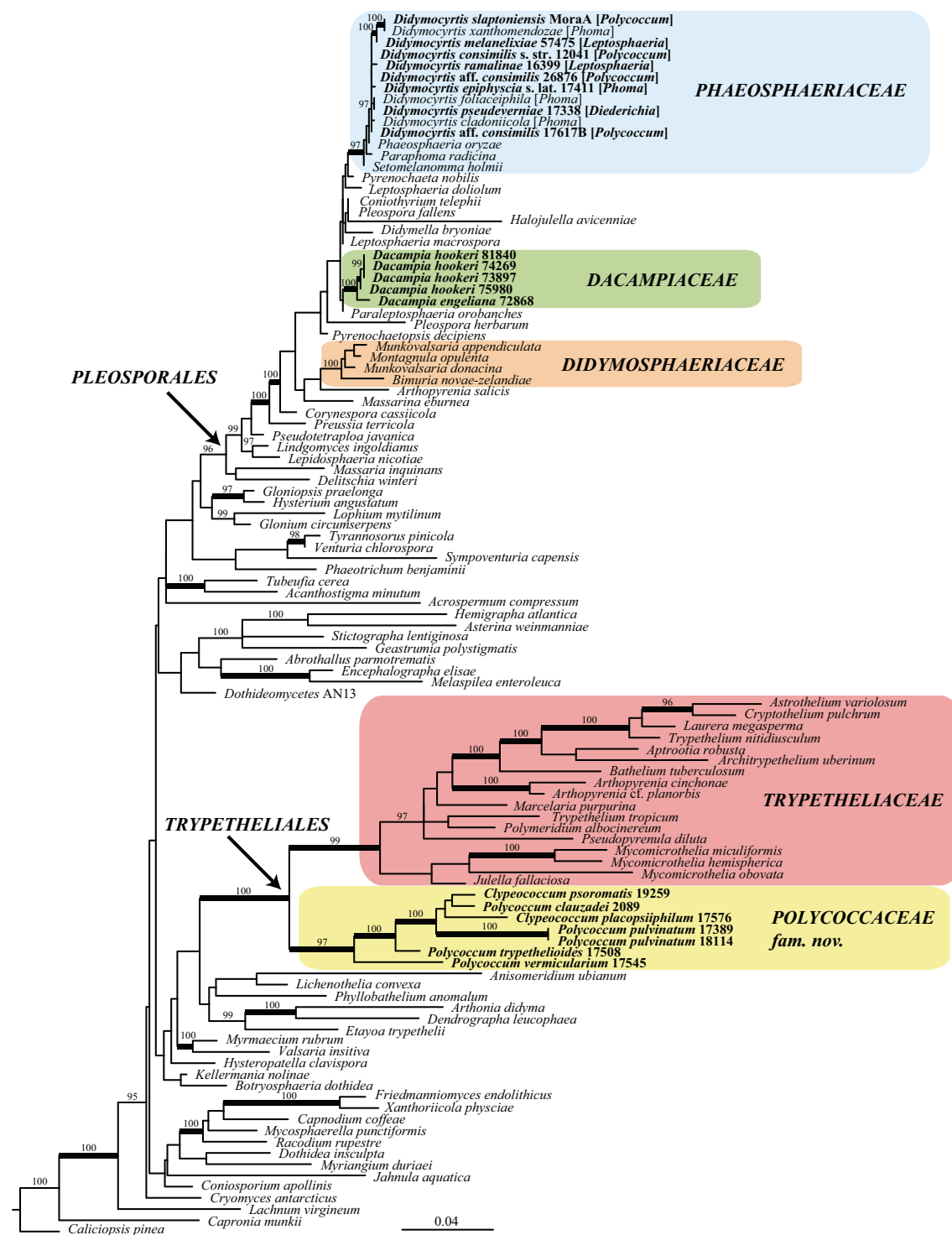
Prodromus to class *Loculoascomycetes* (Amherst) 67 (1987). Type: *Pleospora* Rabenh. ex Ces. & De Not. MycoBank: MB 90563.

Note. *Pleosporales* is the largest order of *Dothideomycetes* with 41 families and includes saprobic fungi on dead plant material, pathogens on living plants, hyperparasites on fungi or insects, and lichenized species (Zhang et al. 2011; Hyde et al. 2013).

### Dacampiaceae Körb.

(as ‘*Dacampieae*’), Syst. Lich. Germ.: 322 (1855). Type: *Dacampia* A. Massal. MycoBank: MB 80680.

Notes. 1. *Dacampiaceae* was considered as a heterogeneous family in the past, with ten genera accepted by Hyde et al. (2013). Our molecular data resolved the family as polyphyletic. The genus *Polycoccum* and members of *Clypeococcum* are accommodated in the new family *Polycoccaceae*, while the genus *Munkovalsaria* is placed in

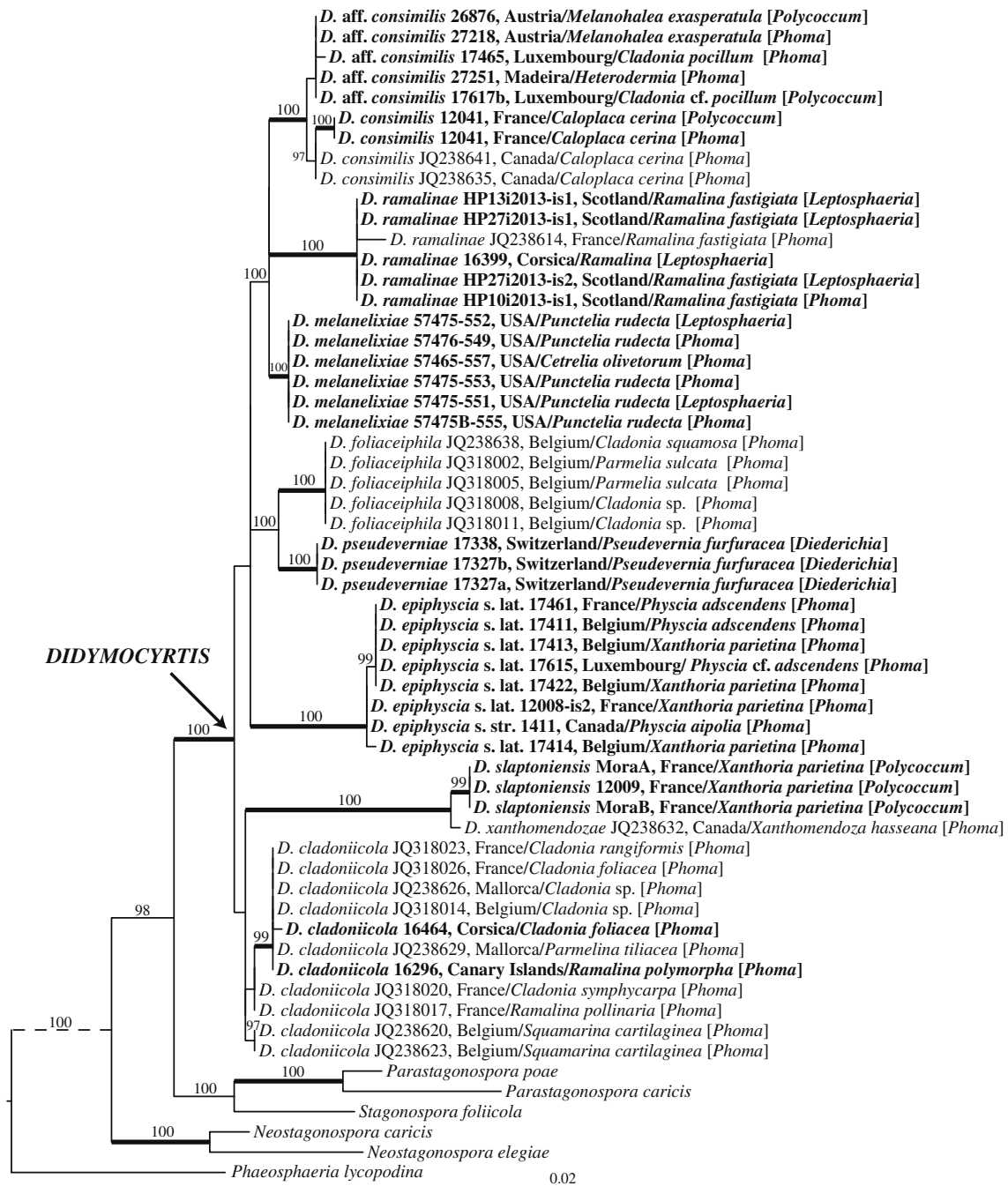


**Fig. 1** Phylogenetic relationships among 109 samples within *Dothideomycetes* (with three outgroup taxa) based on a data set of nuLSU sequences that resulted from a Maximum Likelihood analysis using Garli. Internal branches with Maximum Likelihood bootstrap values  $\geq 70$  obtained from a Garli analysis are considered strongly supported and represented by thicker lines. Posterior probabilities  $\geq 95$

resulting from a Bayesian analysis are shown above internal branches. The newly sequenced specimens are in **bold**. The old and most commonly used generic name is indicated *within brackets* for the species now placed in *Didymocyrtis*. Collecting numbers of the authors following the species names act as specimen and sequence identifiers

*Didymosphaeriaceae* (Fig. 1). No molecular data are available for the other genera currently placed in *Dacampiaceae*, i.e.

*Aaosphaeria*, *Eopyrenula*, *Leptocurthis*, *Pseudonitschka*, *Pyrenidium* and *Weddellomyces*.



**Fig. 2** Phylogenetic relationships among 52 samples of *Didymocyrtis* based on a data set of ITS sequences that resulted from a Maximum Likelihood analysis using Garli. Internal branches with Maximum Likelihood bootstrap values  $\geq 70$  obtained from a Garli analysis are considered strongly supported and represented by thicker lines. Posterior probabilities  $\geq 95$  resulting from a Bayesian analysis are shown above internal branches. The newly sequenced specimens are in

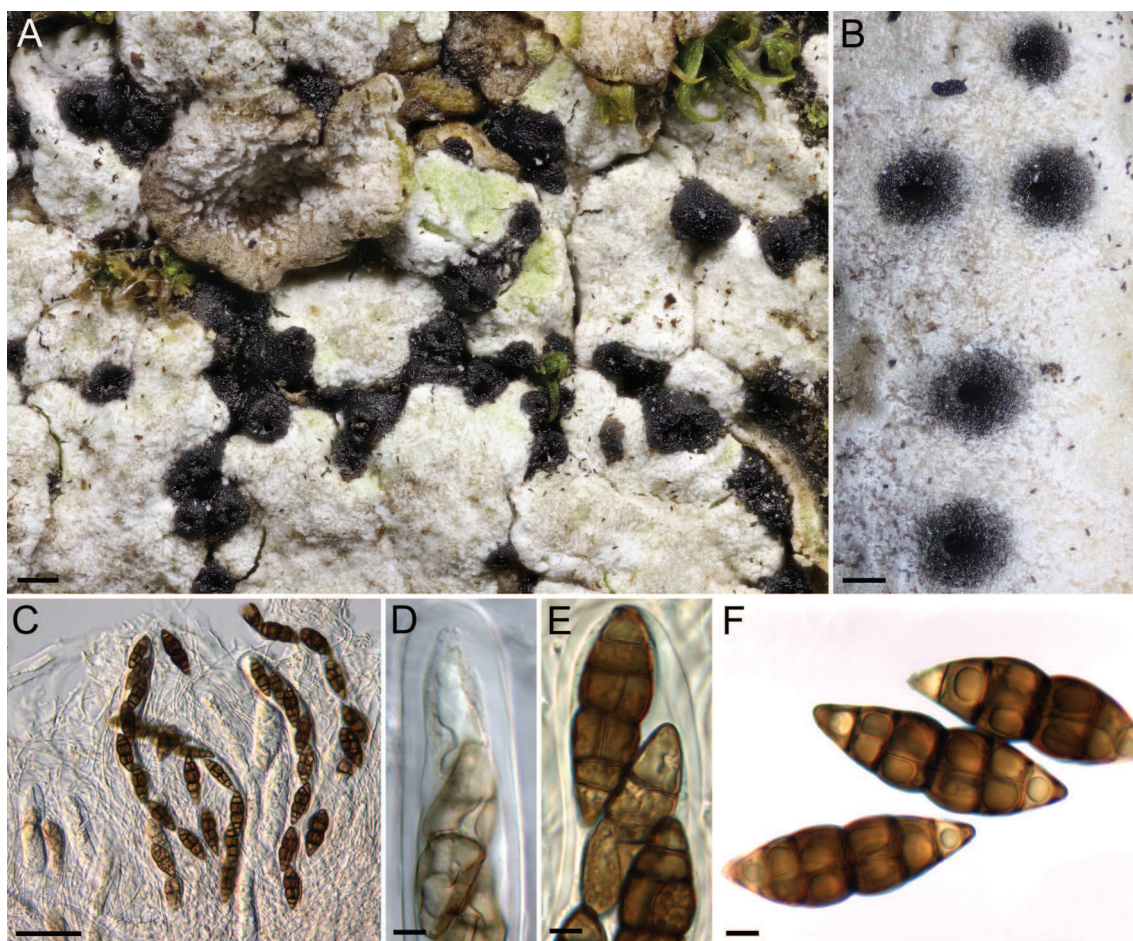
bold. Collecting numbers of the authors following the species names act as specimen and sequence identifiers. The geographical origin and the host lichen species of the sequenced specimens of *Didymocyrtis* are also indicated. The old and most commonly used generic name is indicated within brackets for the species now placed in *Didymocyrtis*. The length of the branch represented by dashed lines was reduced by 50 % for editing reason

2. The genus *Dacampia* is related to members of *Leptosphaeriaceae* in our nuLSU tree (e.g., *Paraleptosphaeria orobanches*, Fig. 1). The relationship of *Dacampiaceae* with other families of *Pleosporales* will require more detailed study. *Leptosphaeriaceae* will become a synonym of

*Dacampiaceae* if *Dacampia* is shown to be nested within it.

**Dacampia A. Massal. (Fig. 3)**

Sulla Lec. Hook. Schaer.: 7 (1853). Type: *Dacampia hookeri* (Borrer) A. Massal. MycoBank: MB 1401.



**Fig. 3** Morphological features of the genus *Dacampia*. **a**, **c**–**f** *Dacampia hookeri* (**a** thallus with marginal ascomata; **c** hymenium; **d**–**e** asci; **f** ascospores; in water; Hafellner 75980). **b** *D. engeliana* on *Solorina*

(Germany, Bad Tölz, 1978, Feuerer). Scale bars: **a**–**b**=200  $\mu$ m; **c**=50  $\mu$ m; **d**–**f**=5  $\mu$ m

Syn.: *Xenosphaeria* Trevis., Conspect. Verruc.: 18 (1860). Type: *Xenosphaeria hookeri* (Schaer.) Trev., lectotypified by Clements and Shear (1931). MycoBank: MB 5823.

Lichenicolous or lichenized with *Coccomyxa* and external cephalodia with *Nostoc*. Ascomata perithecioid, with a central ostiole, lacking setae, black, immersed to semi-immersed, with a pseudoparenchymatic ascomatal wall, in longitudinal section seen as a textura angularis with thick-walled, reddish to dark brown cells. *Hamathecium* of interascal filaments (paraphysoids) with ramifications and anastomoses. *Asci* bitunicate, subcylindrical, apically thickened when mature, with a small, sometimes indistinct, ocular chamber, 8-spored, ascial wall and hymenial gel I–, more rarely K/I+ bluish. *Ascospores* 1–2-seriate, pale brown to dark brown, pigmented from an early stage of development, muriform, ellipsoid to fusiform, often constricted at the septa, smooth, without visible gelatinous sheath. *Asexual stage* unknown.

Note. The genus *Dacampia* includes 15 species, most of them being lichenicolous. The type species, *Dacampia hookeri*, is lichenized (except juvenile stages that might facultatively transform the thallus of *Solorina*

*bispora*), while the lichenicolous *Dacampia engeliana* modifies its host lichen to form a thallus structure similar to that found in *D. hookeri* (Henssen 1995; Hyde et al. 2013; de los Ríos and Grube 2000). The genus might be heterogeneous, as some lichenicolous *Dacampia* species that do not form such thallus structures might be more distantly related, but molecular data are currently missing for them.

#### **Phaeosphaeriaceae M. E. Barr**

*Mycologia* 71: 948 (1979). Type: *Phaeosphaeria* I. Miyake. MycoBank: MB 81637.

Note. *Phaeosphaeriaceae* is a large and important family in the *Pleosporales* (Hyde et al. 2013, Phookamsak et al. 2014). Lawrey et al. (2012) placed all lichenicolous *Phoma* species in *Phaeosphaeriaceae*, while de Gruyter et al. (2009, 2013) stated that *Phoma* s. str. should be restricted only to *Didymellaceae*. Eventually, Trakunyingcharoen et al. (2014) described the new genus *Diederichomyces* to accommodate most of the lichenicolous *Phoma*. But as shown here, several older generic names are available for the lichenicolous *Phoma* species, of which *Didymocyrtis* is the oldest.

**Didymocyrtis Vain.**

Acta Soc. Fauna Flora Fenn. 49(2): 221, 263 (1921). Type: *Didymocyrtis consimilis* Vain., lectotype, selected here. MycoBank: MB 1554.

Syn. nov.: *Diederichia* D. Hawksw., Lichenologist 35: 206 (2003). Type: *Diederichia pseudeverniae* (Etayo & Diederich) D. Hawksw. MycoBank: MB 28744.

Syn. nov.: *Diederichomyces* Crous & Trakunyingcharoen in Trakunyingcharoen et al., IMA Fungus 5: 393 (2014). Type: *Diederichomyces xanthomendozae* (Diederich & Freebury) Crous & Trakunyingcharoen. MycoBank: MB 810828.

*Ascomata* (unknown in some species) perithecioid (pseudothecia); ascomatal wall dark brown, pseudoparenchymatous, in longitudinal section consisting of polyhedral, tangentially flattened cells forming a textura angularis, with the pigment deposited in the hyphal cell walls. *Hamathecial filaments* paraphysoids, persistent, septate, with some branches and anastomoses. *Asci* fissitunicate, narrowly cylindrical, endoascus laterally thickened when young, apically thickened when mature, with a small ocular chamber, ascus wall I- and K/I- except dextrinoid reaction of ascus periplasma, hymenial 'gel' I- and K/I-, 8-spored. *Ascospores* ± uniseriate to half-overlapping, pale brown to brown, usually pigmented from an early stage of development (mature ones pale brown only in some species), relatively thin-walled (compared to those of true *Polycoccum*-species), transversally 1–3-septate, upper half-spore slightly broader than lower one, with rounded ends, most species with a distinct sculpture in light microscopy, a distinct perispore visible in young spores of some species in K.

*Conidiomata* (unknown in some species) *Phoma*-like, with unilocular, ostiolate pycnidia; pycnidia usually undistinguishable from perithecia, except sometimes by the smaller size; pycnidial wall similar to perithecial wall. *Conidiophores* lacking. *Conidiogenous cells* attached to the conidiomal wall and lining the cavity, hyaline; conidiogenesis phialidic, not proliferating. *Conidia* hyaline, simple, smooth-walled, not embedded in a gelatinous matrix, usually with rounded ends.

Notes. 1. Boerema (1997) subdivided the genus *Phoma* into nine sections with sexual stages in the genera *Didymella*, *Leptosphaeria*, *Mycosphaerella* and *Pleospora*. de Gruyter et al. (2009) confirmed the polyphyletic character of *Phoma* in the *Pleosporineae* by the application of molecular methods (see also Zhang et al. 2009). The generic type, *Phoma herbarum*, grouped in the *Didymellaceae*, and therefore, *Phoma* s. str. is considered to be restricted to the *Didymellaceae*. Aveskamp et al. (2010) confirmed that *Phoma* species appear not only in the *Didymellaceae*, but also in the related clades *Leptosphaeriaceae*, *Phaeosphaeriaceae* and *Pleosporaceae*. In a recent phylogenetic study focusing on species of *Sphaerellopsis*, Trakunyingcharoen et al. (2014) described the new genus *Diederichomyces* as including most of the lichenicolous *Phoma* species that had been assigned to the *Phaeosphaeriaceae* by Lawrey et al. (2012). As shown

here, the genus *Diederichia* also belongs to this clade. However, the generic name *Didymocyrtis* Vain., neglected practically from its publication (Vainio 1921), is also available and is here used for this group (see **Taxonomy** section). As a consequence *Diederichia* and *Diederichomyces* are synonymized with *Didymocyrtis*.

2. Vainio (1921) described both the genus *Didymocyrtis* and the species *D. consimilis* in detail, and mentioned *D. physciicola* (Nyl.) Vain. (based on *Mycoporum physciicola* Nyl., a later heterotypic synonym of *Sphaerellothecium parietinarium* (Linds.) Hafellner & V. John) and *Mycoporum epistygium* Nyl. (Vainio 1921: 222) (an ascomycete of unclear relationship on *Melanelia stygia*). *Mycoporum epistygium* was combined into *Didymocyrtis epistygia* (Nyl. ex Vain.) Vain. later in the same publication (Vainio 1921: 263) and, therefore, *Didymocyrtis consimilis* cannot be treated as the holotype and is here selected as lectotype.

3. *Didymocyrtis* differs from *Polycoccum* s. str. mainly by narrowly cylindrical asci, ± monostichously arranged ascospores, thin paraphysoids, thin-walled, medium (reddish)-brown ascospores and a *Phoma*-like anamorphic stage. As well, *Polycoccum* s. str. often induces galls formation on the host lichens, whereas *Didymocyrtis* does not.

4. Many other lichenicolous *Phoma*-like species have been described in the past (Lawrey and Diederich 2015), and some of these will certainly be combined later in *Didymocyrtis*, as soon as sequences of them become available. However, these species should not be combined in this genus, based on morphological characters alone. E.g., sequences of *Phoma puncteliae* Diederich & Lawrey placed this species outside of *Didymocyrtis* (Lawrey et al. 2012) and Trakunyingcharoen et al. (2014) introduced the new genus *Xenophoma* to accommodate the species. Similarly, *Phoma cytospora* (Vouaux) D. Hawksw. has been shown to belong to *Arthoniales*, and the new genus *Briancoppinsia* has subsequently been described for it (Diederich et al. 2011).

5. *Didymocyrtis* is also a generic name used for protists in the family *Coccolidiscidae* (e.g. Gilg et al. 2010).

**Key to species of *Didymocyrtis***

- 1 Fructifications are perithecioid ascomata.....2
- 1 Fructifications are pycnidial conidiomata.....9
- 2 Ascospores predominantly 2- or 3-septate.....3
- 2 Ascospores predominantly 1-septate.....4
- 3 Ascospores predominantly 2-septate, some 1- and 3-septate intermixed, up to 15 µm long; on *Parmeliaceae*.....***D. melanelixiae***
- 3 Ascospores predominantly 3-septate, some 1- or 2-septate ascospores intermixed, usually longer than 15 µm; on *Ramalina* [specimens on *Protousnea*, named *Leptosphaeria protousneae*, will also key out here].....***D. ramalinae***

- 4 Ascospores  $16\text{--}20 \times 8\text{--}10 \mu\text{m}$ ; on *Teloschistes* .....**D. kaernefeltii**
- 4 Ascospores up to  $15 \times 7 \mu\text{m}$  long.....5
- 5 Many asci longer than  $90 \mu\text{m}$ ; ascospores  $13\text{--}15 \times 6\text{--}7 \mu\text{m}$ .....6
- 5 Most asci up to  $90 \mu\text{m}$  long.....7
- 6 Ascospores  $13\text{--}15 \times 6\text{--}7 \mu\text{m}$ ; on *Xanthoria parietina*.....**D. slaptoniensis**
- 6 Ascospores  $11\text{--}13 \times 6\text{--}7 \mu\text{m}$ ; on *Xanthomendoza*.....**D. xanthomendozae**
- 7 All ascospores 1-septate,  $10\text{--}13 \times 4.5\text{--}6 \mu\text{m}$ ; on *Teloschistes*.....**D. infestans**
- 7 Some 2-septate ascospores intermixed; on apothecia of crustose lichens.....8
- 8 Verruculose sculpture of ascospores distinct; ascospores  $11.5\text{--}14 \times 4\text{--}5 \mu\text{m}$ ; on *Lecanora epibryon* [conidia, if present,  $\pm$  ellipsoid,  $7\text{--}8 \times 3\text{--}4 \mu\text{m}$ ].....**D. bryonthae**
- 8 Sculpture of ascospores very minute and often indistinct; ascospores  $12\text{--}15 \times 5\text{--}6 \mu\text{m}$ ; on *Caloplaca* [conidia, if present, broadly ellipsoid,  $4.5\text{--}6.5 \times 2.5\text{--}4.5 \mu\text{m}$ , to subglobose,  $5\text{--}6 \mu\text{m}$  diam.].....**D. consimilis**
- 9 Conidia mostly  $16\text{--}22 \times 6\text{--}9 \mu\text{m}$ , multiguttulate; on *Pseudevernia furfuracea*.....**D. pseudeverniae**
- 9 Conidia smaller, less than  $8 \times 6 \mu\text{m}$ , usually 1–2-guttulate.....10
- 10 Conidia broadly ellipsoid, l/b ratio  $< 1.6$ , mostly 1-guttulate.....11
- 10 Conidia narrowly ellipsoid, l/b ratio  $> 1.4$ , mostly 2-guttulate.....13
- 11 Conidia mostly  $3.8\text{--}5.1 \times 3.2\text{--}3.8 \mu\text{m}$ , with one large guttule; on *Parmeliaceae* [some specimens of *D. consimilis* s. lat. and of *D. ramalinae* may also key out here] .....**D. melanelixiae**
- 11 Conidia at least  $4.5 \times 3.5 \mu\text{m}$ .....12
- 12 Pycnidia (50–)100–150  $\mu\text{m}$  diam.; conidia broadly ellipsoid; on *Physcia aipolia*.....**D. epiphyscia** s. str.
- 12 Pycnidia 70–100(–130)  $\mu\text{m}$  diam.; conidia broadly ellipsoid to subspherical; on *Caloplaca* (gr. *cerina* or gr. *tirolensis*) [*D. consimilis* s. lat. also on *Cladonia pocillum*, *Heterodermia* and *Melanohalea exasperatula*].....**D. consimilis**
- 13 Conidia very narrowly ellipsoid, l/b ratio mainly 2.4–3; on *Cladonia* and *Parmelia* .....**D. foliaceiphila**
- 13 Conidia narrowly ellipsoid, l/b ratio mainly 1.4–2.3.....14
- 14 Conidial breadth mainly  $< 3 \mu\text{m}$ .....15
- 14 Conidial breadth mainly  $> 3 \mu\text{m}$ .....17
- 15 Conidia  $6\text{--}8 \times 2.5\text{--}3.5 \mu\text{m}$ ; on *Xanthoria parietina*.....**D. slaptoniensis**
- 15 Conidia shorter, mainly less than  $6.5 \times 3 \mu\text{m}$  [two genetically distinct species that can hardly be distinguished morphologically].....16
- 16 Pycnidia (50–)100–150  $\mu\text{m}$  diam.; on *Physcia adscendens*, *P. tenella* and *Xanthoria parietina* .....**D. epiphyscia** s. lat.
- 16 Pycnidia (40–)50–100(–140)  $\mu\text{m}$ ; on *Cladonia*, *Ramalina*, *Squamarina* and *Parmeliaceae* .....**D. cladoniicola**
- 17 Conidial l/b ratio  $> 2$ .....18
- 17 Conidial l/b ratio  $< 2$  [two genetically distinct species of which the asexual stages are morphologically very similar].....19
- 18 Conidia mainly  $7\text{--}8 \times 3\text{--}4 \mu\text{m}$ ; on *Lecanora epibryon* (hymenium) [ascospores, if present, mainly  $11.5\text{--}14 \times 4\text{--}5 \mu\text{m}$ ].....**D. bryonthae**
- 18 Conidia mainly  $6\text{--}8 \times 2.5\text{--}3.5 \mu\text{m}$ ; on *Xanthoria parietina* [ascospores, if present, mainly  $13\text{--}15 \times 6\text{--}7 \mu\text{m}$ ].....**D. slaptoniensis**
- 19 Pycnidia 105–135  $\mu\text{m}$  diam.; on *Ramalina* [ascospores, if present, 3-septate].....**D. ramalinae**
- 19 Pycnidia 140–160  $\mu\text{m}$ ; on *Xanthomendoza* [ascospores, if present, 1-septate].....**D. xanthomendozae**

#### **Didymocytis bryonthae (Arnold) Hafellner comb. nov.**

*Endococcus bryonthae* Arnold, Flora (Regensburg) 57: 141 ([21. März] 1874); *Didymosphaeria bryonthae* (Arnold) G. Winter, Rabenh. Krypt.-Fl., 2. Aufl., 1(2): 430 (1885); *Microthelia bryonthae* (Arnold) Kuntze, Revisio generum plantarum 3: 498 (1898); *Mycoporum bryonthae* (Arnold) Jatta, Syll. Lich.: 494 (1900); *Tichothecium bryonthae* (Arnold) Jatta, Fl. Ital. Crypt. Lich.: 841 (1911); *Sphaeria bryonthae* (Arnold) H. Olivier, Bull. Int. Acad. Géogr. Bot. 17: 170 (1907); *Polycoccum bryonthae* (Arnold) Vězda, Česká Mycol. 23: 109 (1969). Type: [Austria, Nordtirol, Serlos-Gruppe], Kalkboden links ober der Ochsenalm, Matreier Grube, Waldrast in Tirol, 6000' [Wiener Fuß = c. 1900 m alt.], on *Lecanora epibryon* (as *Lecanora subfusca* var. *bryontha*), Aug. 1873, F. Arnold (M – holotype!). MycoBank: MB 814022

Syn.?: *Phoma denigricans* Hafellner, Herzogia 10: 18 (1994). Type: Italy: Trentino, Dolomiten, Pordoi-Joch, N-Fuß des Sass Beccle,  $46^{\circ}29'05''$  N,  $11^{\circ}48'40''$  E, c. 2300 m, Hänge mit niedrigen Dolomitschrofen, on *Lecanora epibryon* (apoth.), 25 Oct. 1984, J. Hafellner 11989 (GZU – holotype!). MycoBank: MB 447502

*Ascomata* in dense groups on the apothecia of the host, almost completely immersed in the apothecial hymenium that becomes black and might finally bleach, more protruding when the host hymenium has collapsed, subspherical,  $150\text{--}200$ (–250)  $\mu\text{m}$  diam.; wall dark brown, often somewhat paler towards the base, laterally c.  $12\text{--}15 \mu\text{m}$  diam., of about 4–6 layers of cells. *Paraphysoids*  $1\text{--}1.5 \mu\text{m}$  diam. *Asci*  $60\text{--}80 \times 7\text{--}10 \mu\text{m}$ . *Ascospores*  $\pm$  uniseriate, pale brown, 1-septate, some (less than 5 %)

with an additional septum in the upper cell, (10–)11.5–14(–16)×4–5 µm, often slightly constricted at the septum; septum with externally protruding torus; distinct verruculose sculpture visible in light microscopy.

*Conidiomata* of supposed asexual stage immersed in the hymenium of host apothecia, several per apothecium, blackening the apothecial surface, in longitudinal section broadly oval to subspherical, c. 80–100×100–130 µm diam.; wall dark brown above, paler brown towards the base, of c. 3–5 layers of cells; *conidiogenous cells* broadly pear-shaped, 7–9×4–5 µm. *Conidia* ellipsoid to somewhat tapering towards the lower end to oblong, many biguttulate, (6–)7–8×3–4 µm, l/b ratio 2–2.3.

For further descriptions and illustrations of the teleomorph see Arnold (1874), and of the supposed anamorph see Hafellner (1994).

Distribution and hosts. Taking into consideration published records, and adding the data for the supposed anamorph (*Phoma denigricans*) and of the specimens cited below, the known distribution can be summarized as follows: Europe (Austria, Germany, Italy, Poland, Svalbard, Sweden), Asia (Mongolia, Russia), and North America (Canada, Greenland, USA); in the hymenium of *Lecanora epibryon* (e.g., Arnold 1874; Hafellner 1994; Kukwa and Flakus 2009; Santesson 1993; Triebel and Scholz 2001; Zhurbenko 1996, 2009b).

Notes. 1. The collection Arnold, Lich. exs. 615 sub *Endococcus bryonthae* given as type by various authors (e.g., Aptroot 1995b) is in fact a topotype; that specimen was collected on 4 Sept. 1874 and therefore after the appearance of the protologue (March 1874).

2. Hawksworth and Diederich (1988: 297) and Aptroot (1995b: 59) erroneously described the host of Arnold, Lich. exs. 615 (sec. Arnold duplicates of a later collection from the locus classicus) as *Pertusaria bryontha*; however, according to Arnold and the specimens seen by us, it is *Lecanora epibryon*.

3. Sometimes ascomata of *Didymocyrtis bryonthae* and pycnidia of *Phoma denigricans* can be observed on the same specimen (e.g., Hafellner 38111, 76036, including on one host apothecium). Comparable observations have also been reported from Svalbard and Siberia by Zhurbenko (2009b: 147, 148). Such co-occurrences are one of the arguments for our opinion that the two taxa represent the sexual and asexual stages of the same fungal species.

4. For differences between *Didymocyrtis bryonthae* and *D. consimilis*, see notes below under *D. consimilis*.

5. The record on *Lecanora bryopsora* (Hafellner 2008) could not be confirmed. The specimen, on which this record was based, shows infested *L. epibryon* growing intermingled with an undetermined soresiate crust which evidently is not *L. bryopsora*.

Selected specimens examined (all on *Lecanora epibryon*): Sexual stage: **Austria**: Salzburg, Nationalpark Hohe Tauern, Glockner Gruppe, NW-Grat des Großen Margrötzen Kopfs W ober dem Hochtor, 47°05'10" N, 12°50'10" E, 2620 m, GF 8943/1, 1996, Hafellner 38111 & Wittmann (hb. Hafellner) (with asexual stage). Steiermark, Nordalpen (Nördliche Kalkalpen), Totes Gebirge, Hochangern-Massiv N von Liezen, Nazogl, knapp NE vom Gipfel auf dem Rücken gegen den Angerkogel, 47°36'45" N, 14°13'50" E, 2050 m, GF 8351/3, 2010, Hafellner 76036 & Muggia (GZU) (with asexual stage). **Greenland**: W-Grönland, Gem. Umanak, Hänge über Marmorilik, 50–300 m, 1983, Poelt & Ullrich (GZU). **Italy**: Lombardia, prov. Brescia, Eastern Alps, Central Alps, Ortler-group (Stelvio-group), Cima di Cadi N above Passo del Tonale, N below the summit, 46°16'35" N, 10°34'15" E, 2590 m, 2006, Hafellner 75406 & Muggia (GZU). **Mongolia**: Chubsugul Chimak, Tomim-Brigade, 1983, Huneck MVR 83-43 (GZU). **Russia**: Siberia, Yakutiya (Sakha-Yakutiya Republic), Lena River delta, right bank of Olenek channel/river branch, near fishermans' house Novyi Chai-Tumus, 45 WNW Krest-Tumsa cape and Sokol polar station, 72°22'N, 125°40'E, 10–40 m, 1998, Zhurbenko 9896 (M).

Asexual stage: **Austria**: Steiermark, Zentralalpen, Niedere Tauern, Schladminger Tauern, SE-Abhänge der Steirischen Kalkspitze, W der Giglachseehütte zwischen Preuneggssattel und Akarscharte, 47°16'50"–17'00" N, 13°37'50"–38'10" E, 1970–2080 m, GF 8747/2, 2001, Obermayer 9166 (GZU). **Germany**: Bayern, Landkreis Berchtesgadener Land, Steinernes Meer, Viehkogel, auf dem Gipfel, 2150 m, GF 8543, 1985, Wunder 4030 & Türk (M). **Greenland**: W-Grönland, Gem. Umanak, Marmorilik, N-seitige Hänge S über dem Fjord Qaumarujuk, 5–200 m, 1983, Poelt & Ullrich (GZU).

**Didymocyrtis cladoniicola (Diederich, Kocourk. & Etayo) Ertz & Diederich comb. nov.**

*Phoma cladoniicola* Diederich, Kocourk. & Etayo, Lichenologist 39: 157 (2007); *Diederichomyces cladoniicola* (Diederich, Kocourk. & Etayo) Crous & Trakunyingcharoen in Trakunyingcharoen et al., IMA Fungus 5: 401 (2014). Type: USA, Minnesota, Cottonwood County, 2 miles W of US 71, 14.5 miles N of Windom, 44°06'40" N, 95°04'30" W, 400 m, seasonally dry, flat, Sioux quartzite outcrop on N side of road, on *Cladonia pyxidata*, 28 Sept. 1991, W. R. Buck 20859A (NY – holotypus!; hb. Diederich – isotypus!). MycoBank: MB 814023.

*Ascomata* unknown.

*Conidiomata* immersed in pale necrotic areas of the thallus or partially erumpent, black, subspherical to pyriform, (40–)50–100(–140) µm diam.; pycnidial wall brown, 10–12 µm thick, composed of several layers of cells, outer cells

dark brown, 5–8(–10)  $\mu\text{m}$  diam., inner cells hyaline. *Conidiogenous cells* short-ampulliform, 2.5–4.5  $\mu\text{m}$  high, 2.5–4  $\mu\text{m}$  wide. *Conidia* ellipsoid, biguttulate, with a small guttule near each apex, (3.8–)4.7–5.9(–7.3)  $\times$  (2.0–)2.4–3.0(–3.5)  $\mu\text{m}$ , l/b ratio (1.4–)1.7–2.2(–2.8) ( $n=472$ ) [from Diederich et al. 2007].

For further descriptions and illustrations, see Diederich et al. (2007), Lawrey et al. (2012) and Trakunyingcharoen et al. (2014).

Distribution and hosts (\*confirmed by sequences). Europe (Belgium, Czech Republic, France incl. Corsica, Germany, Spain, Ukraine), Africa (Canary Islands), and North America (USA: Minnesota; Greenland); on *Cladonia cervicornis*, *C. convoluta*, *C. fimbriata*, *C. foliacea*\*, *C. furcata*, *C. phyllophora*, *C. pocillum*, *C. pyxidata*, *C. ramulosa*, *C. rangiformis*\*, *C. symphyrcarpia*\*, *Flavoparmelia caperata*, *Parmelina tiliacea*\*, *Ramalina pollinaria*\*, *R. polymorpha*\* and *Squamarina cartilaginea*\* (Alstrup et al. 2009; Diederich et al. 2007; Etayo 2010a; Lawrey et al. 2012).

Note. This species was originally described from *Cladonia* species. ITS sequences, however, showed that specimens on *Parmelina*, *Ramalina* and *Squamarina* are almost surely conspecific. The four sequences from mainland France originate from the same calcareous outcrop, where the species parasitized *Cladonia foliacea*, *C. rangiformis*, *C. symphyrcarpia* and *Ramalina pollinaria* (all sequenced) and *Squamarina cartilaginea* (not sequenced). This unexpected low host specificity may be explained by the rather aggressive parasitic way of life of this species that eventually kills the host thallus.

Additional specimens examined: **Canary Islands:** Gomera, NW of Imada, Raso Grande, volcanic outcrop, 28°05'36" N, 17°14'52" W, 1288 m, summit of a volcanic outcrop, on *Ramalina polymorpha*, 2011, Ertz 16296 (BR). **France:** Corsica, Saint-Florent, au nord de la route entre Tettola et Santa Maria, 42°41'39" N, 9°19'4" E, pelouse calcaire xérique, sur *Cladonia foliacea*, 2011, Ertz 16464 (BR).

#### ***Didymocyrtis consimilis* Vain.** (Figs. 4a–h and 9a–b)

Acta Soc. Fauna Flora Fenn. 49(2): 221, 263 (1921). Type: [Finland], 'in Selkäsaari in par. Simo in Ostrobotnia bor., on bark of *Sorbus*', on *Caloplaca cerina* (hymenium), Räsänen (TUR-VAIN 32734 – holotype!). MycoBank: MB 431576.

Syn. nov.: *Phoma caloplacae* D. Hawksw., Bull. Br. Mus. nat. Hist. (Bot.) 9: 50 (1981); *Diederichomyces caloplacae* (D. Hawksw.) Crous & Trakunyingcharoen in Trakunyingcharoen et al., IMA Fungus 5(2): 401 (2014). Type: [Russia, Krasnoyarsk Krai], Yeniseysk, Stolba, 60°20' N, on *Caloplaca cerina* (apothecia), 1 July 1876, Brenner 1027b p.p. (UPS – holotype!). MycoBank: MB 112547.

*Ascomata* in dense groups on the apothecia of the host, almost completely immersed in the apothecial hymenium that becomes mis-coloured. *Ascoma* in longitudinal section

subspherical, (70–)100–150  $\mu\text{m}$  diam.; wall medium to dark brown, laterally c. 10–15  $\mu\text{m}$  diam., consisting of c. 3–4 layers of cells. *Paraphysoids* 1–1.5  $\mu\text{m}$  diam. *Asci* 50–70  $\times$  7–10  $\mu\text{m}$ . *Ascospores*  $\pm$  uniseriate or half-overlapping, pale brown, 1-septate, some (less than 5 %) with an additional septum in the upper cell, 12–15  $\times$  (4.5–)5–6(–6.5)  $\mu\text{m}$ , hardly constricted at the septum, externally protruding torus at the septum indistinct, verruculose sculpture hardly visible in light microscopy.

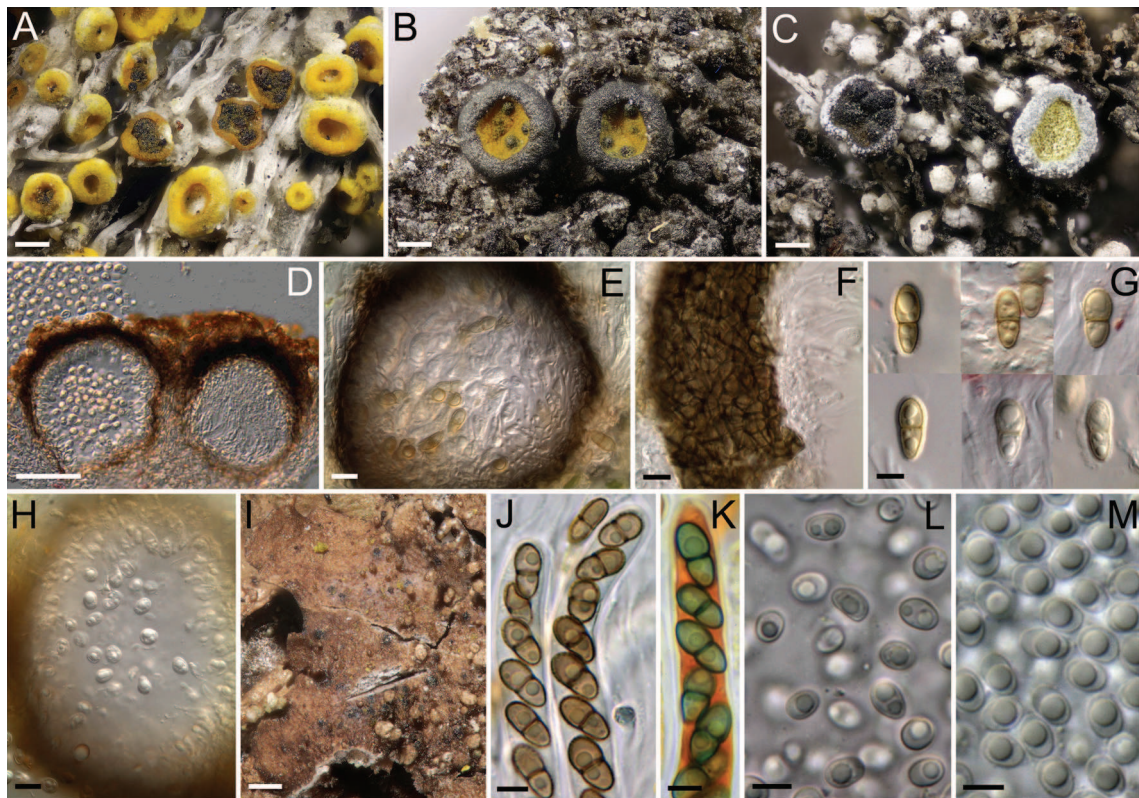
*Conidiomata* several per hymenium, scattered, completely immersed at first, later protruding over the collapsed hymenium, dark brown, somewhat darker as the discoloured hymenial surface of the infested apothecium, in longitudinal section subglobose, 70–100(–130)  $\mu\text{m}$  diam.; wall of conidiomata dark brown in upper part, pale brown to subhyaline towards the base, c. 10–15  $\mu\text{m}$  diam., of c. 3–5 layers of tangentially flattened cells. *Conidiogenous cells* subglobose to broadly obpyriform, 5–6  $\mu\text{m}$  diam. *Conidia* 1–2-guttulate, rather variable in form and size, broadly ellipsoid, 4.5–6.5  $\times$  2.5–4.5  $\mu\text{m}$ , to subglobose, (4–)5–6(–7)  $\mu\text{m}$  diam., l/b ratio < 1.5.

For further descriptions and illustrations of the asexual stage, see Hawksworth (1981), Ihlen and Wedin (2008), Lawrey et al. (2012) and Trakunyingcharoen et al. (2014).

Distribution and hosts. Up to now the sexual stage of the species has not been distinguished from that of *Didymocyrtis bryonthae*, a fungus confined to the *Lecanora subfusca* group (*L. epibryon*). Therefore all reports of '*Polycozum bryonthae*' can be taken as referring to *Didymocyrtis consimilis* as long as a *Caloplaca* of the *C. cerina* or *C. tirolensis* group is given as host for a record. Taking this into consideration and adding data for the asexual stage (*Phoma caloplacae*) and specimens cited below, the known distribution can be summarized as follows: Europe (Austria, Finland, France, Germany, Italy, Poland, Slovakia, Slovenia, Spain, Sweden), Asia (Iran, Israel, Russia, Turkey), and North America (Canada, Greenland); in the hymenium of *Caloplaca cerina*, *C. cerina* var. *muscorum*, *C. stillicidiorum*, *C. tirolensis* (e.g., Alstrup and Hawksworth 1990; Halıcı et al. 2014; Hawksworth 1981; Hawksworth and Diederich 1988; Kondratyuk et al. 2005; Kukwa and Flakus 2009; Lawrey et al. 2012; Magnusson 1952 sub *Phoma physciicola* p. p.; Santesson et al. 2004; Seaward et al. 2008; Wittmann and Türk 1990; Zhurbenko 2009a).

Notes. 1. Two specimens labeled *Didymocyrtis consimilis* are preserved in TUR-VAIN: no. 32734 with locality data as in protologue, hence the type specimen, but with a host different from that given in the protologue, identified as *Placodium gilvum*, 17 June 1916, V. Räsänen; and no. 32733 with locality data differing from that given in the protologue (Finland, Ostrobotnia borealis, Simo, Lammasetto, Pihlajalla), and host as in the protologue, identified as *Placodium gilvum* var. *cyanolepra*, without date, V. Räsänen.





**Fig. 4** *Didymocyrtis consimilis* s. lat. on *Caloplaca* (a–h), on *Melanohalea exasperatula* (i–l) and on *Heterodermia* (m). a on *Caloplaca tirolensis* (Hafellner 83640); b on *C. cerina* (Türk 44065a–7); c on *C. stillicidiorum* (Hafellner 83640); d section through conidioma (left) and ascoma (right) (in water; Gardiennet 12008); e section through overmature ascoma with brown ascospores (in water; Hafellner 41836); f ascomatal wall in surface view (in KOH; Hafellner 41836); g ascospores (in KOH; Hafellner 41836); h section through

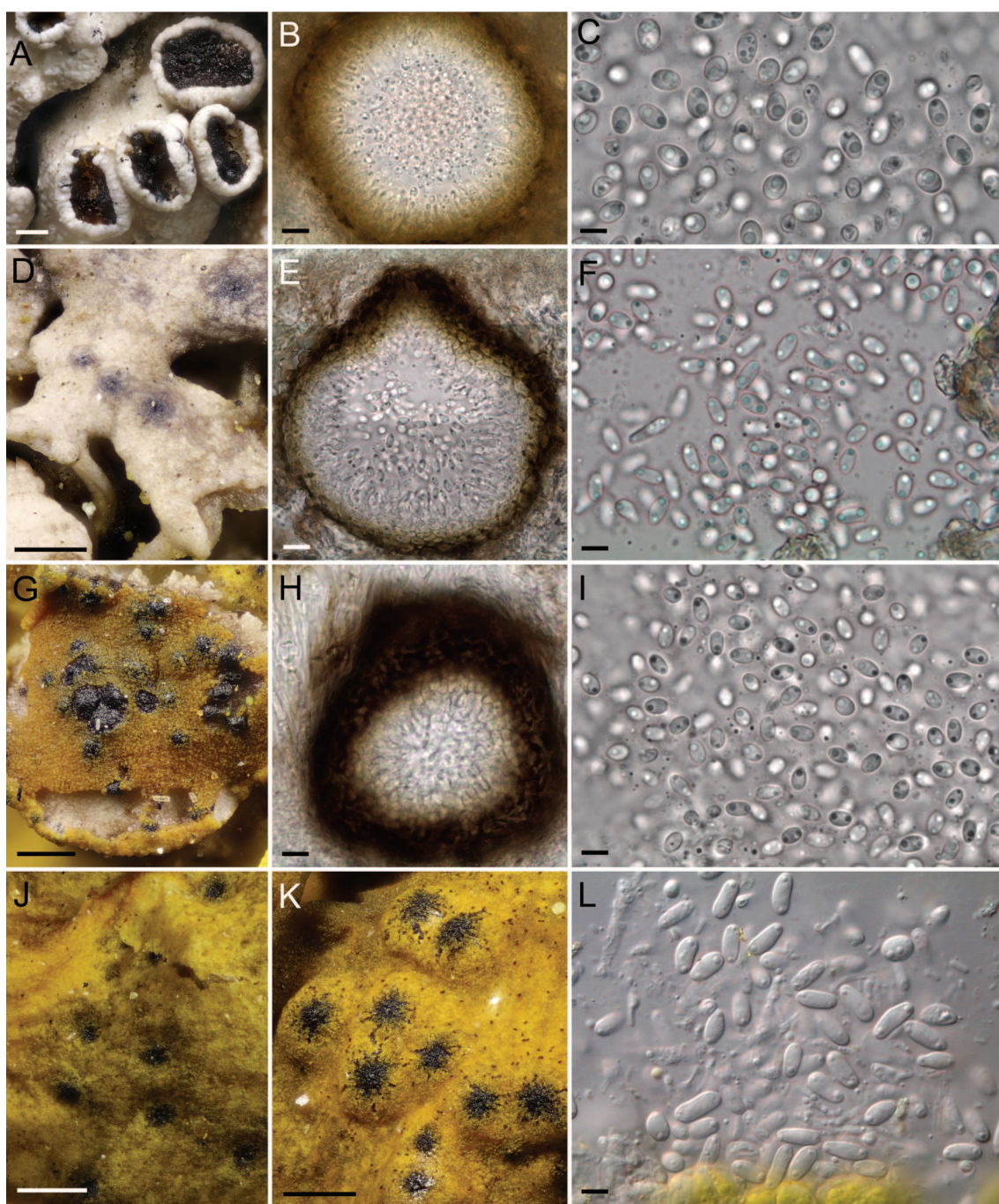
conidioma, showing subspherical conidia (in water; Türk 44065a–7). i black immersed conidiomata on *Melanohalea exasperatula* (Berger 27218); j asci with ascospores in water; k asci with ascospores becoming blue in Lugol's reagent (j–k Berger 26876); l ellipsoid conidia (Berger 27218). m on *Heterodermia*, conidia (in water; Berger 27251). Scale bars: a–c, i=200  $\mu$ m; d=50  $\mu$ m; e–f, h=10  $\mu$ m; g, j–m=5  $\mu$ m

2. In the type specimen, this species is growing on a corticolous *Caloplaca cerina*. Records of this fungus on corticolous *Caloplaca* species are relatively rare but do occur also outside Scandinavia (see below). At least in Central Europe the species is much more common on *Caloplaca* species growing over bryophytes and decaying vascular plants in alpine environments. These populations were usually identified as *Polycoccum bryonthae*, a fungus described from *Lecanora epibryon* and which is treated here as separate species. Both species infest the hymenium of their hosts in which either ascomata or conidiomata, or both develop. Sometimes ascomata (*Didymocyrtis consimilis*) and pycnidia (*Phoma caloplacae*) can be observed on the same specimen (e.g., specimens Wilfling 1847, Hafellner 20068) or even in one host apothecium (e.g., specimens Hafellner 78736, 75304).

3. *Didymocyrtis consimilis* differs from the evidently closely related *D. bryonthae* by smaller ascomata, somewhat broader ascospores, a less conspicuous ascospore sculpture, distinctly broader conidia, and by its host selection.

4. *Didymocyrtis consimilis* has always been considered to be host specific on the *Caloplaca cerina* group, but our nITS

analyses (Fig. 2) revealed the existence of populations on other hosts (*Cladonia pocillum*, *Heterodermia*, *Melanohalea exasperatula*) that have very similar ITS sequences and are morphologically similar (Figs. 4i–m and 9c–d). Some morphological differences were observed, as follows: Conidia on the unusual hosts tend to be more elongate ellipsoid, vs. broadly ellipsoid in *D. consimilis* s. str. on *Caloplaca* gr. *cerina*: specimen Berger 27251 on *Heterodermia* has conidia of 4–5  $\times$  3–3.5  $\mu$ m with one large oil drop (Fig. 4m); specimen Berger 27218 on *Melanohalea exasperatula* has conidia with one large or two small oil drops, 4–6  $\times$  3–4(–5)  $\mu$ m (Fig. 4i); specimen Diederich 17465 on *Cladonia pocillum* has conidia (3.5–)4–4.5  $\times$  2.5–3  $\mu$ m. The sexual stage on *Melanohalea exasperatula* (Berger 26876) has ascospores with a faint and homogeneous amyloid reaction in Lugol (Fig. 4k), (9–)10.5–13(–14)  $\times$  (4–)4.5–5.5(–6)  $\mu$ m; moreover the two isolates on *Melanohalea* produce long yellowish acicular crystals in culture with the agar medium turning dark reddish-brown (Fig. 9d), but as the cultures of *D. consimilis* s. lat. were done in different laboratories and in different conditions, it is unclear if this might be used as a diagnostic character. The sexual



**Fig. 5** *Didymocyrtis epiphyscia* (a–i) and *D. slaptoniensis* (j–l). a–c *D. epiphyscia* s. str. conidiomata on *Physcia aipolia* apothecia (a Freebury 1409; b–c Diederich 17482): habitus, section through conidioma, conidia in water. d–f *D. epiphyscia* s. lat. conidiomata on *P. tenella* thallus (Diederich 17478): habitus, section through conidioma, conidia in water. g–i *D. epiphyscia* s. lat. conidiomata on

*Xanthoria parietina* apothecium (Diederich 17479): habitus, section through conidioma, conidia in water. j–l *D. slaptoniensis* on *X. parietina* thallus (Obermayer 13130): conidiomata, ascomata, conidia in water. Scale bars: a, d, g, j–k=200  $\mu$ m; b, e, h=10  $\mu$ m; c, f, i, l=5  $\mu$ m

stage on *Cladonia* cf. *pocillum* (Ertz 17617b) has smaller ascospores, 8.5–10.5 $\times$ 3.5–4  $\mu$ m, and was thus first identified as *Polycoccum laursenii* Zhurb. (Zhurbenko and Alstrup 2004), a species described from Alaska on *Cladonia pocillum* (but only four ascospores were measured, the specimen being

very tiny). *Phoma heterodermiae* S. Y. Kondr., L. Lökös & J.-S. Hur, described from South Korea on *Heterodermia hypoleuca*, with conidia measuring 3.5–5 $\times$ 3–4(–4.5)  $\mu$ m, might be conspecific with the material studied by us on *Heterodermia*. More studies using a larger taxon sampling

and a multigene approach will be needed to investigate this group in detail.

Selected specimens examined: Sexual stage: **Austria:** Kärnten, Nationalpark Hohe Tauern, [Glockner-Gruppe], Sattelalpe W von Heiligenblut, 1 km SE der Bricciuskapelle, 47°03'01" N, 12°48'10" E, 1600 m, GF 8942/2, on *Caloplaca stillicidiorum*, 1987, Hafellner 20068 & Walther (GZU) (with asexual stage). Salzburg, Pongau, Niedere Tauern, Radstädter Tauern, Kleinarltal, beim Jägersee c. 5 km S von Kleinarl, entlang der Straße am Ostufer des Sees, 47°14'15" N, 13°20'02" E, 1100 m, GF 8746/3, on *C. cerina*, 2006, Hafellner 41836 (GZU). Steiermark, Nordalpen, Mürztaler Alpen, Thalerkogel NE von Trofaiach, kurz N vom Gipfel, 47°28'40" N, 15°03'15" E, 1640 m, GF 8556/1, on *C. stillicidiorum*, 2011, Hafellner 78736 (GZU) (with asexual stage). Steiermark, Nordalpen, Mürzsteger Alpen, Rauschkogel NE von Turnau, 47°36'40" N, 15°22'15" E, 1660 m, GF 8358/3, on *C. tirolensis* and *C. stillicidiorum*, 2005, Hafellner 83640 (GZU). Tirol, Nordalpen, Karwendel, Hinterautal, Umgebung vom Kotwaldsee, 47°22'41" N, 11°21'26" E, 1070 m, GF 8634/1, on *C. cerina*, 2008, Türk 44065a-7 & Pflieger (GZU). **Finland:** Ostrobotnia borealis, Simo, Lammasletto, Pihlajalla, on *C. cerina* (as "*Placodium gilvum* var. *cyanoolepra*") (apoth.), without date, Räsänen (TUR-VAIN 32733). **France:** Côte-d'Or, L'Etang-Vergy, combe Ragon, on *C. cerina*, 2012, Gardiennet 12041 (hb. Gardiennet). **Italy:** Trentino-Alto Adige, prov. Bolzano (Südtirol), Southern Alps, Dolomiti, M. Seceda (Geisler Spitzen) NE of Ortisei (St. Ulrich), on the ridge just W above Forc Pana (Pana Scharte), 46°36'05" N, 11°44'05" E, 2500 m, on *C. tirolensis*, 2002, Hafellner 75196 (GZU).

Asexual stage: **Austria:** Steiermark, Niedere Tauern, Wölzer Tauern, Gumpeneck SE von Gröbming, Gipfelpyramide, NW-seitig, 47°23'50" N, 14°00'50" E, 2180 m, GF 8650/1, on *C. stillicidiorum*/*C. tirolensis*, 1993, Hafellner & Wilfling 1847 (GZU) (with sexual stage). **Canada:** Saskatchewan, RM of Val Marie No. 17, Grasslands National Park, West Block, Frenchman River Valley, Belza's Ranch, 49°9.1' N, 107°31.0' W, 800 m, on bones, on *C. stillicidiorum*, 2010, Freebury 1357 (CANL). **Germany:** Bayern, Nordalpen, Chiemgauer Alpen, Hochgern, 16 km SW von Traunstein, oberste N-Hänge knapp unter dem Gipfel, 47°45'04" N, 12°30'53" E, 1700 m, on *C. stillicidiorum*, 2009, Hafellner 75177 (GZU). **Italy:** Lombardia, prov. Brescia, Eastern Alps, Central Alps, Ortler-group (Stelvio-group), Cima di Cadi N above Passo del Tonale, N below the summit, 46°16'35" N, 10°34'15" E, 2590 m, on *C. cerina* var. *muscorum*, 2006, Hafellner 75407 & Muggia (GZU). **Slovakia:** Carpates, Tatra Magna, pars orientalis, Belanské Tatry, in monte Bujaci, 1900 m, on *C. tirolensis*, 1985, Farkas, Kyselová & Vězda (GZU). **Slovenia:** Southern Alps, Julian Alps, massif of Mangart NE of Bovec, NE slopes of Mali vrh S opposite to Mangartska

koča (Mangart refuge), 46°26'00" N, 13°38'35" E, 1960 m, on *C. cerina* var. *muscorum*, 2003, Hafellner 75304 (GZU). **Spain:** Prov. Barcelona, Sierra de Montseny, Hänge NE der Paßhöhe des Coll Formich, 1200 m, on *C. cerina*, 1983, Hafellner 17354 (GZU). **Sweden:** Torne Lappmark, Umgebung von Abisko, über Kieselkalk auf dem Kliff Paddos S von Abisko, 620–630 m, on *C. tirolensis*, 1967, Poelt (GZU, under the name of the host).

Selected specimens examined on unusual hosts and therefore referred here as *D. aff. consimilis*: Sexual stage: **Austria:** Oberösterreich, Sauwald, Kopfung, 540 m, MTB 7547, auf *Melanohalea exasperatula*, 2012, Berger 26876 (hb. Berger). **Luxembourg:** S of Obercorn, Kiemerchen, 49°30'00" N, 5°53'53" E, 385 m, bois clairs et friches dans une ancienne carrière, sur squamules de *Cladonia* cf. *pocillum* au sol, 2012, Ertz 17617b (BR).

Asexual stage: **Austria:** Bezirk Rohrbach, Neustift, Rannriedl, 300 m N Schloss, 48°29'02" N, 13°46'18" E, 485 m, MTB7548, auf *Juglans regia*, auf *Melanohalea exasperatula*, 2013, Berger 27218 (hb. Berger). **Luxembourg:** SWW de Belvaux, Kiemreech (M8.51), terricole, dans une ancienne exploitation minière, sur *Cladonia pocillum*, 2012, Diederich 17465 (hb. Diederich). **Madeira:** Achada da Madeira, Laurisilva entlang der Levada Rib da Urzal, 32°46'37" N, 16°58'55" W, 655 m, auf *Heterodermia*, 2013, Berger 27251 (hb. Berger).

**Didymocyrtis epiphyscia Ertz & Diederich nom. nov.** (Figs. 5a–c and 6)

*Phoma physciicola* Keissler, Hedwigia 50: 294 (1911). Type: Austria, Steiermark, Gams bei Hieflau, on *Physcia aipolia*, June 1910, K. von Keissler (W 1910/609 – holotype, non vid., examined by Hawksworth 1981). MycoBank: MB 814024

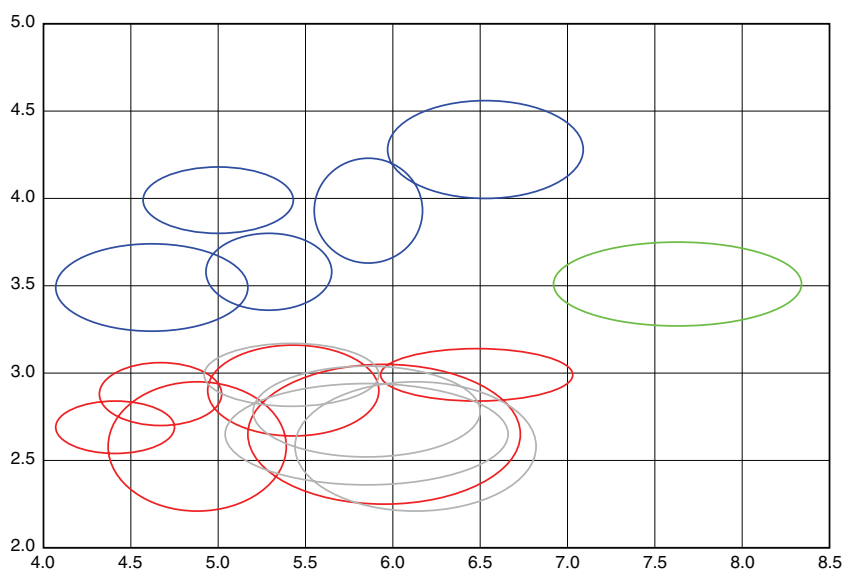
*Ascomata* unknown.

*Conidiomata* immersed in necrotic areas of the host hymenium, more rarely of the thallus, black, subspherical, (50–)100–150 µm diam.; pycnidial wall brown, inner cells paler, darker near the ostiole. *Conidiogenous cells* ampulliform, 4–7 µm diam. *Conidia* ellipsoid, with one or two small guttules, (4.0–)4.6–6.1(–7.8) × (3.2–)3.5–4.2(–5.0) µm, l/b ratio (1.0–)1.2–1.6(–2.0) ( $n=150$ ).

For a description and further illustrations, see Hawksworth (1981).

Distribution and hosts. Europe (Austria, France, Great Britain: Scotland and Luxembourg) and North America (Canada), on *Physcia aipolia* (hymenium, rarely thallus). The species has also been reported on *Physcia stellaris* (Coppins and Coppins 2001), *Physconia distorta* (Hawksworth 1981) and *Phaeophyscia orbicularis* (von Brackel 2011: 82), but we did not examine any material on those last two host genera. The material on *Physcia adscendens* and *P. tenella* with narrower conidia is treated below as *D. epiphyscia* s. lat. Finally, reports from other host

**Fig. 6** Conidial size distribution (length versus breadth, in  $\mu\text{m}$ ) of selected *Didymocyrtis* specimens occurring on *Physcia* and *Xanthoria* (each specimen is represented by an ellipse, based on the measurement of at least 20 conidia from one conidioma; large radius of ellipse = standard deviation (SD) of conidial length; small radius = SD of conidial breadth). Blue = *Didymocyrtis epiphyscia* s. str. on *Physcia aipolia*. Grey = *D. epiphyscia* s. lat. on *P. adscendens* and *P. tenella*. Red = *D. epiphyscia* s. lat. on *Xanthoria parietina*. Green = *D. slaptioniensis* on *X. parietina*



genera, e.g. on *Parmelia sulcata* (von Brackel 2007, 2009; Zhurbenko et al. 2012), almost surely refer to other species.

Notes. 1. This species was originally described as parasitizing the hymenium of *Physcia aipolia*. Although we did not re-examine the holotype, which was carefully studied, described and illustrated by Hawksworth (1981), there is no doubt that our recent specimens in the hymenium of *P. aipolia* belong to the same species. In the description of Hawksworth (1981), conidia were described as slightly narrower [ $4\text{--}5.5(-6)\times 2.5\text{--}3.5(-4)\ \mu\text{m}$ ], but this author regarded the species in a broader sense, also including specimens on *Physconia*. In the original description, conidia were given as ‘ca.  $6\times 4\ \mu\text{m}$ ’, which perfectly agrees with our observations.

2. *Phoma physciicola* Keissler cannot be combined in *Didymocyrtis*, because of the earlier combination *Didymocyrtis physciicola* (Nyl.) Vain., a synonym of *Sphaerellothecium parietinarium* (see Note 2 under *Didymocyrtis*), and a new name for *Phoma physciicola* must therefore be introduced in *Didymocyrtis*. On the other hand, the older name *Phoma epiphyscia* Vouaux is of unknown application and might threaten the current nomenclature of *Didymocyrtis* (see Note under *Didymocyrtis slaptioniensis*) if sequence data become available from a specimen collected close to the neotype locality in Greenland and on the same host *Phaeophyscia sciastra*. To avoid such unwanted future nomenclatural changes, we choose the same epithet ‘*epiphyscia*’ as a *nomen novum* for *Phoma physciicola*.

3. Rather unexpectedly, *Phoma* specimens parasitizing the thallus of *Physcia adscendens* and *P. tenella*, but also the thallus and hymenium of *Xanthoria parietina*, are genetically very close to the specimens on *Physcia aipolia*, suggesting that they might belong to the same species, *Phoma epiphyscia*. However, as conidia on those hosts are constantly much narrower, we treat them below as *D. epiphyscia* s. lat.

Specimens examined (all on *Physcia aipolia*): **Canada:** Quebec, Les Collines-de-l’Outaouais Regional County, Gatineau Park, near Intersection Highway 105 & 366,  $45^{\circ}37'56''\ \text{N}$ ,  $75^{\circ}56'26''\ \text{W}$ , edge of forest near La Pêche River, 2010, Freebury 1119A (CANL); *ibid.*, 2011, Freebury 1409 (CANL). **France:** Côte d’Or, Val-Suzon, En Neudry, 2014, Gardiennet 14079 (hb. Gardiennet). Meuse, SE of Montmédy, Marville, cimetièrre de St Hilaire, 2013, Diederich 17724 (hb. Diederich). **Great Britain:** Scotland, Argyll Main, VC 98, Inverary, Glen Shira, along boundary wall near Allt Buidhe, S of Kilbraan, 1996, Coppins 16745 (E). **Luxembourg:** W of Steinfort, old sandstone quarries, 2012, Diederich 17482 (hb. Diederich); *ibid.*, 2015, Diederich 17766 (hb. Diederich).

***Didymocyrtis epiphyscia* Ertz & Diederich s. lat.** (Figs. 5d–i, 6 and 9g–h)

*Ascomata* unknown.

*Conidiomata* and *conidiogenous cells* as in *Didymocyrtis epiphyscia*, but conidia much narrower, biguttulate or rarely multiguttulate,  $(3.7\text{--})4.6\text{--}6.4(-8.0)\times(2.0\text{--})2.5\text{--}3.1(-3.5)\ \mu\text{m}$ , l/b ratio  $(1.2\text{--})1.6\text{--}2.3(-3.5)$  ( $n=290$ ).

Distribution and hosts. We have seen material from Europe (Belgium, France and Luxembourg), on *Physcia adscendens*, *P. tenella* (thallus) and *Xanthoria parietina* (thallus and apothecia). Specimens likely to be the same species have also been reported from Germany (von Brackel 2007, on *P. tenella*, sub *Phoma physciicola*; von Brackel 2009, on *P. tenella*, sub *Phoma physciicola*; von Brackel 2010, on *P. adscendens*, sub *Phoma epiphyscia*) and Italy (von Brackel 2011, on *P. tenella*, sub *Phoma epiphyscia*). Literature reports on *Xanthoria parietina* are more problematic, as they might as well belong to the putative anamorph of *Didymocyrtis slaptioniensis*.

Notes. 1. As specimens on *Xanthoria parietina* from Belgium, northern France and Luxembourg are genetically and morphologically almost identical to the specimens on

*Physcia adscendens* and *P. tenella*, we consider them as belonging to the same species. Our phylogenetic analyses, using ITS sequences, place these specimens together with *Didymocyrtis epiphyscia* s. str., which differs, however, by constantly much broader conidia.

2. Several asexual specimens from Austria on *Xanthoria parietina* were growing close to *Didymocyrtis slaptoniense*, and we tentatively consider them as representing the asexual stage of that species. Morphologically, conidia from the putative *D. slaptoniense* asexual stage are larger, (5–)6–8(–9) × 2.5–3.5 µm.

3. The name *Phoma epiphyscia* Vouaux was introduced for a species on *Phaeophyscia orbicularis* and *Xanthoria parietina*, collected in northern France (Vouaux 1914). As the type is presumed to be lost (Hawksworth 1981), Alstrup and Hawksworth (1990) neotypified the name on a Greenland specimen on *Phaeophyscia sciastra*. These authors don't describe the neotype, but state that 'The only difference we noted is that the conidia are up to 7 × 3 µm, and not only to 6 × 3 µm as given by Vouaux'. In the identification key (p. 14), they describe the material on *P. sciastra* as 'Conidia 4–6 × 2–3 µm, rounded at the ends; conidiomata immersed'. Following the conidial dimensions, *Phoma epiphyscia* could represent the species we are studying here on *Physcia* and *Xanthoria*. However, sequences from a similar specimen on *P. sciastra* are needed before proposing any conclusions.

4. The material on *Physcia adscendens*, *P. tenella* and *Xanthoria* is morphologically hardly distinguishable from *Didymocyrtis cladoniicola*, of which conidia were given by Diederich et al. (2007) as mainly 4.7–5.9 × 2.4–3.0, l/b ratio 1.7–2.2 ( $n=472$ ). The pycnidia were said to be (40–)50–100(–140) µm in *D. cladoniicola*, slightly smaller than those on *Physcia* and *Xanthoria*. Both species are, however, genetically distinct (see Fig. 2).

Specimens examined: **Belgium**: Rochefort, Ave-et-Auffe, colline schisto-calcaire au centre du village d'Ave, 220 m, on *P. adscendens*, 2012, Ertz 17411 (BR); *ibid.*, on *X. parietina*, Ertz 17413, 17414 (BR). Wibrin, lieu-dit 'Au Bec du Fèyi', rive gauche du ruisseau du Fond de Minée, 440 m, on *X. parietina*, 2012, Ertz 17422 (BR). **France**: Finistère, Camaret-sur-Mer, Pointe de Pen Hir, 48°15'31" N, 4°37'11" W, 35 m, on *P. adscendens*, 2012, Ertz 17461 (BR). Meuse, SE of Montmédy, Marville, cimetière de St Hilaire, on *X. parietina*, 2013, Diederich 17726 (hb. Diederich). Côte d'Or, Saint-Seine-sur-Vingeanne, rive de la Vingeanne au niveau de la D960, sur *X. parietina* sur *Populus*, 2011, Gardiennet 12008 (hb. Gardiennet). **Luxembourg**: S of Obercorn, Kiemerchen, 49°30'00" N, 5°53'53" E, 385 m, on *P. tenella*, 2012, Ertz 17615 (BR). SWW of Belvaux, Kiemreech, on *P. tenella*, 2012, Diederich 17478 (hb. Diederich); *ibid.*, on *X. parietina*, 2012, Diederich 17479 (hb. Diederich). Strassen, Tosseberg, old sandstone quarry, on *X. parietina*, 2014, Diederich 17759 (hb. Diederich).

### ***Didymocyrtis foliaceiphila* (Diederich, Kocourk. & Etayo) Ertz & Diederich comb. nov.**

*Phoma foliaceiphila* Diederich, Kocourk. & Etayo, Lichenologist 39: 159 (2007); *Diederichomyces foliaceiphila* (Diederich, Kocourk. & Etayo) Crous & Trakunyingcharoen in Trakunyingcharoen et al., IMA Fungus 5: 401 (2014). Type: Czech Republic, Central Bohemia, distr. Rakovník, Křivoklátsko protected landscape area, between Nezabudice and Roztoky villages, Nezabudické skály nature reserve, 50°01' N, 13°51' E, 255 m, in *Quercus petraea* forest below steep slope of rocky outcrops, on *Cladonia foliacea*, 2002, J. Kocourková (PRM 896164 – holotypus, non vid.). MycoBank: MB 814025.

*Ascomata* unknown.

*Conidiomata* immersed in pale necrotic areas of the thallus or partially erumpent, black, subspherical to pyriform, 50–100 µm diam.; pycnidial wall brown, 10–12 µm thick, composed of several layers of cells, outer cells dark brown, 5–8(–10) µm diam., inner cells hyaline. *Conidiogenous cells* short-ampulliform, 4–5.5 × 2.5–5 µm. *Conidia* ellipsoid, biguttulate, with a small guttule near each apex, (5.0–)5.8–7.1(–7.5) × (2.0–)2.2–2.7(–3.0) µm, l/b ratio (2.0–)2.4–3.0(–3.5) ( $n=100$ ) [from Diederich et al. 2007].

For further descriptions and illustrations, see Diederich et al. (2007), Lawrey et al. (2012) and Trakunyingcharoen et al. (2014).

Distribution and hosts (\*confirmed by sequences). Europe (Belgium, Czech Republic, France, Germany, Lithuania, Luxembourg, Netherlands, Spain), on *Cladonia fimbriata*, *C. foliacea*, *C. furcata*, *C. rangiformis*, *C. squamosa*\* and *Parmelia sulcata*\* (von Brackel 2010; Diederich et al. 2007; Etayo 2010a; Lawrey et al. 2012; Motiejūnaitė et al. 2011).

Notes. 1. This species was originally described from *Cladonia* species. ITS sequences, however, showed that specimens on *Parmelia sulcata* are almost surely conspecific. The five sequences used in our analysis originate from the same siliceous outcrop in the Belgian Ardennes and obviously represent a genetically uniform population parasitizing both *Cladonia* spp. and *Parmelia sulcata*.

2. Trakunyingcharoen et al. (2014) described the new *Paraphaeosphaeria parmeliae* Crous & Trakunyingcharoen, said to be lichenicolous on *Parmelia sulcata*, and based on a culture (CBS 131728) that 'was originally identified as *Phoma foliaceiphila*'. However, this culture was isolated by us from specimen Ertz 15257, which represents typical *P. foliaceiphila*. Furthermore, our original culture produced pycnidia with typical *P. foliaceiphila* conidia. As a conclusion, it is highly likely that the culture used by Trakunyingcharoen et al. (2014) was contaminated, which would mean that the new *Paraphaeosphaeria parmeliae* is a contaminant obtained in laboratory and therefore of uncertain origin and ecology.

**Didymocyrtis infestans (Speg.) Hafellner comb. nov.**

*Didymosphaeria infestans* Speg., Anal. Soc. Cient. Argentina 12 (4): 176 (1881). *Didymosphaerella infestans* (Speg.) Cooke, Grevillea 18 (86): 29 (1889). *Microthelia infestans* (Speg.) Kuntze, Revisio Generum Plantarum 3: 498 (1898). *Endococcus infestans* (Speg.) Speg., Anales del Museo Nacional de Buenos Aires 19: 369 (1909). *Discothecium infestans* (Speg.) Vouaux, Bull. Soc. Mycol. France 29: 56 (1913). *Polycoccum infestans* (Speg.) Etayo, Bull. Soc. Linn. Provence 47: 105 (1996). Type: Argentina, Buenos Aires, Las Conchas, on apothecia of *Teloschistes chrysophthalmus*, 1 May 1881, C. Spegazzini 5854 (LPS – holotype, non vid., fide Etayo 1996a). MycoBank: MB 814026.

*Ascomata* developing in the hymenium and/or thallus branches of the host, immersed, finally somewhat protruding. Ascoma in longitudinal section subspherical to pyriform, 250–350 µm diam.; wall brown, laterally c. 10–20 µm diam., consisting of about 3–4 layers of cells. *Paraphysoids* 1–1.5 µm diam. *Asci* 70–95×7–9(–10) µm. *Ascospores* ± uniseriate, medium brown, 1-septate (practically no tendency to develop a second septum), 10–13(–14)×4.5–6 µm, not or somewhat constricted at the septum, with distinct verruculose sculpture visible in light microscopy.

*Conidiomata* unknown.

For further descriptions and illustrations of the sexual stage see Spegazzini (1881) and Etayo (1996a).

Distribution and hosts. Africa (Canary Islands) and South America (Argentina); *Teloschistes chrysophthalmus*, *T. flavicans*. The record on *Ramalina* sp. (Etayo 1996a) needs to be revised.

Notes. 1. The host of the type specimen was originally identified as *Teloschistes flavicans*. However, Etayo (1996a: 106) revised it as *Teloschistes chrysophthalmus*.

2. The proposed transfer of the species to *Didymocyrtis* is based on morpho-anatomical characters; molecular data are still lacking.

3. *D. infestans* differs from *D. kaernefeltii*, also occurring upon *Teloschistes*, by its smaller, medium brown ascospores and smaller asci. *Didymocyrtis slaptoniensis* has somewhat longer asci, somewhat larger ascospores with a pale brown spore wall and a more distinct septal torus.

Specimen examined: **Canary Islands:** Gomera, Hermigua, mirador de El Bailadero, bosque de tejos (*Erica scoparia*) en la cresta, 1010 m, on *Teloschistes flavicans*, 1994, Etayo 13142 (hb. Etayo).

**Didymocyrtis kaernefeltii (S. Y. Kondr.) Hafellner comb. nov.**

*Polycoccum kaernefeltii* S. Y. Kondr., Ukr. Bot. Zhurn. 65: 566 (2008). Type: Australia, Victoria, 20 km SW of on the road to Patchewollah, 35°10.52' S, 142°12.32' E, c. 100 m, on *Acacia* and other shrubs along the road, on *Teloschistes chrysophthalmus*,

15 Jan. 1999, I. Kärnefelt 992401 (LD – holotypus, non vid., fide Kondratyuk 2008). MycoBank: MB 814034.

*Ascomata* dispersed, developing in the hymenium of the host apothecia, entirely immersed, only the ostiolar region visible. Ascoma in longitudinal section subspherical, 250–350 µm diam.; wall brown, laterally c. 15–25 µm diam., consisting of about 3–4 layers of cells. *Paraphysoids* 1.5–2 µm diam. *Asci* 90–115×10–13(–15) µm. *Ascospores* ± uniseriate, pale brown, mostly 1-septate, 2-septate intermixed (>10%), 16–20(–23)×8–10 µm, distinctly constricted at the primary septum, with a distinct verruculose sculpture visible in light microscopy.

*Conidiomata* unknown.

For a description and further illustrations of the sexual stage see Kondratyuk (2008).

Distribution and hosts. Australia (South Australia, Victoria, Queensland); on *Teloschistes chrysophthalmus* (Kondratyuk 2008).

Notes. 1. The proposed transfer of the species to *Didymocyrtis* is based on morpho-anatomical characters. Molecular data are still lacking.

2. To date, *Didymocyrtis kaernefeltii* is the most variable known species regarding ascospore septation in the genus. Two-septate spores are quite common (> 10%) in a squash preparation. The additional septum develops more frequently in the upper half of the spore but occasionally also in the lower half. Aseptate and 3-septate spores are rare (< 1%).

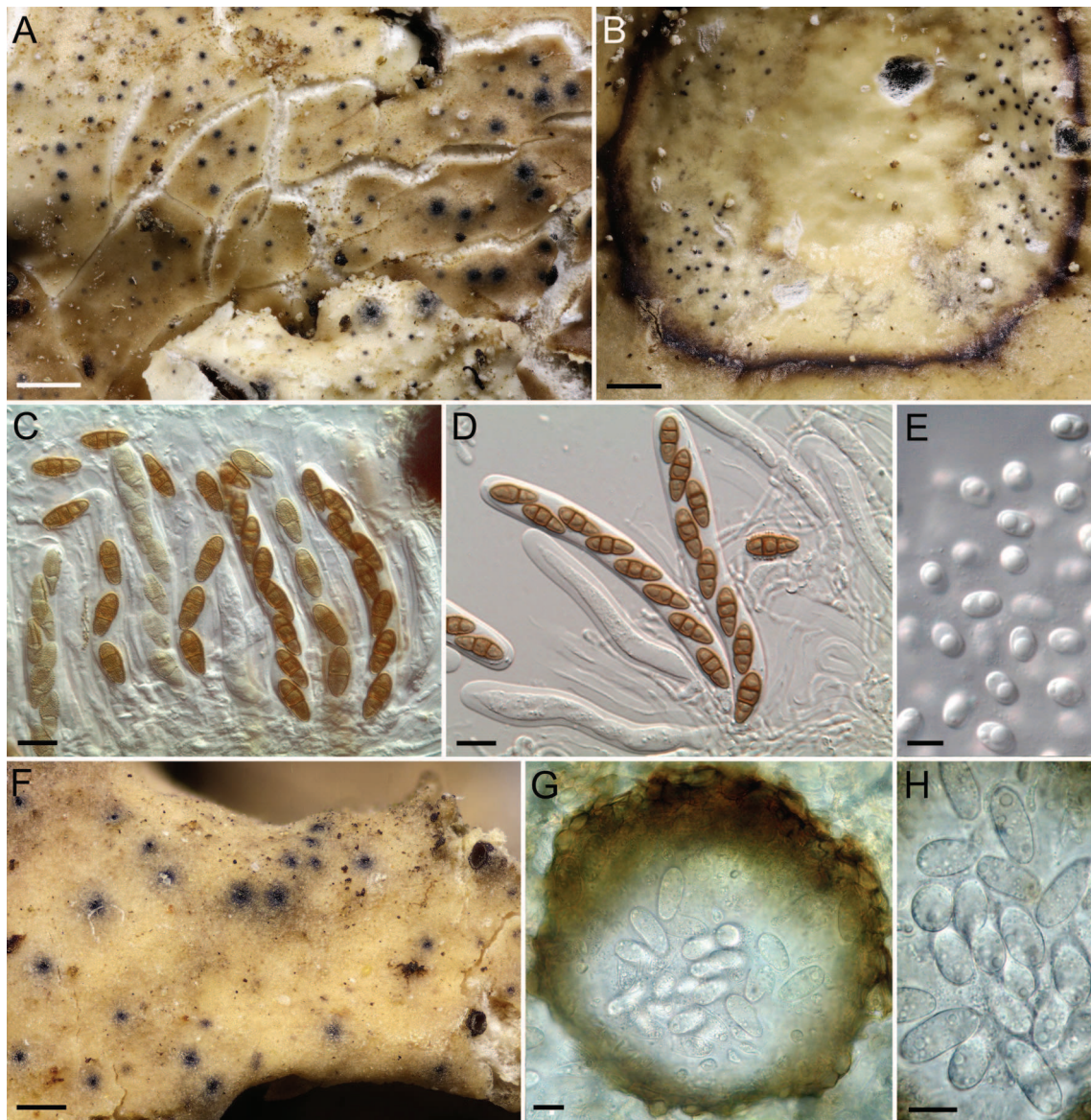
3. According to our data, ascus width measurements given in the protologue are too low, and the indicated average of ascospore length is somewhat too high.

4. *Didymocyrtis kaernefeltii* has also been reported growing on the apothecia of *Caloplaca cerina* from the Caucasus in Russia (Zhurbenko and Kobzeva 2014), but that record needs to be confirmed. We saw another species growing on various *Caloplaca* species (specimens from Afghanistan, Armenia and Cyprus) for which the description provided by Zhurbenko and Kobzeva (2014) fits perfectly. Although the ascospores of this species are surprisingly similar (with some differences in shape and pigmentation), we think that it is neither *Didymocyrtis kaernefeltii* nor *D. consimilis*. With our concept it is not even a *Didymocyrtis*, because the asci are broadly cylindrical to subventricose.

Selected specimens examined (all on *Teloschistes chrysophthalmus*): **Australia:** South Australia, Nairne to Mount Barker road, 2 km S of Nairne, 35°03' S, 138°55' E, 1981, Mayrhofer 2724a (GZU). Queensland, Sellin's Road 1 km E of Mt. Mee State Forest station, 27°05' S, 152°45' E, 500 m, 1986, Hafellner 41806 & Stevens (hb. Hafellner).

**Didymocyrtis melanelixiae (Brackel) Diederich, Harris & Etayo comb. nov. (Fig. 7a–e)**

*Phoma melanelixiae* Brackel, Herzogia 24: 81 (2011). Type: Italy, Basilicata, Prov. di Potenza, Monte Vulture, near “Femmina Morta”, 40°57'24" N, 15°37'17" E, 1145 m, in



**Fig. 7** *Didymocyrtis melanelixiae* (a–e) and *D. pseudeverniae* (f–h). **a** ascomata (right) and conidiomata (left) on *Punctelia rudecta* (Harris 57475); **b** conidiomata on *Cetrelia* (Diederich 9177); **c–d** asci with ascospores (**c** in water; **d** in KOH; Etayo 20035); **e** conidia (in water;

Beeching 15964). **f** *D. pseudeverniae* conidiomata on *Pseudevernia furfuracea* (Etayo 12600); **g** section through conidioma; **h** conidia (**g–h**: in water; Diederich 16755). Scale bars: **a–b**=500  $\mu$ m; **f**=200  $\mu$ m; **c–d**, **g–h**=10  $\mu$ m; **e**=5  $\mu$ m

mixed forest of oaks, elders and maples, on the bark of *Acer pseudoplatanus*, on *Melanelixia glabra*, 22 Aug. 2010, W. & G. v. Brackel 5658 (M – holotypus, non vid.). MycoBank: MB 814027.

*Ascomata* dispersed, developing in necrotic areas of the host thallus, visible as black dots often provided with paler apical dots indicating the ostioles. Ascoma in longitudinal section subspherical or flattened with protruding ostiolar region, 200–250  $\mu$ m diam.; wall brown, laterally c. 15–20  $\mu$ m diam., consisting of about 3–4 layers of cells, cells 5–10  $\mu$ m diam. *Paraphysoids* 1–2.5  $\mu$ m diam. *Asci* 70–100 $\times$ 7.5–10.5  $\mu$ m, 8-spored (but often with fewer spores reaching maturity). *Ascospores*  $\pm$  uniseriate to half-overlapping, medium

to dark brown, (1–)2(–3)-septate, 11.5–15 $\times$ 4–5.5  $\mu$ m, the middle cell slightly wider than the end cells, slightly constricted at the septa, torus indistinct, with a distinct verruculose sculpture visible in light microscopy.

*Conidiomata* immersed in pale necrotic areas of the thallus surrounded by a black line, black, subspherical to ellipsoid, 50–100  $\mu$ m diam.; pycnidial wall brown, dark brown around the ostiole, 9–15  $\mu$ m thick, composed of 3–5 layers of cells 3–9  $\mu$ m diam., inner cells hyaline. *Conidiogenous cells* ampulliform, mainly 5–9 $\times$ 3–4.5  $\mu$ m. *Conidia* broadly ellipsoid to subspherical, with one large guttule or rarely two smaller guttules, (3.5–)3.8–5.1(–6.2) $\times$ (2.8–)3.2–3.8(–4.3)  $\mu$ m, l/b ratio (1.0–)1.1–1.5(–1.8) ( $n$ =140).

Distribution and hosts. Europe (Belgium, France, Italy, Spain, Switzerland, United Kingdom: Scotland), North America (Canada: British Columbia and New Brunswick, USA: Georgia, Maine and North Carolina), South America (Ecuador) and Indian Ocean (La Reunion); on the thallus of Parmeliaceae, including *Canoparmelia*, *Cetrelia*, *Hypotrachyna*, *Melanelixia*, *Parmelia* s. str., *Parmotrema*, *Platismatia*, *Pseudevernia*, *Punctelia* and *Usnea*.

Notes. 1. An unknown *Didymocyrtis* sexual stage had been collected twice on *Punctelia* in the USA, accompanied by a *Phoma*-like asexual stage. A similar *Phoma*-like fungus had been collected on *Cetrelia* in the same locality as one of the two sexual specimens. DNA sequences have shown that both the sexual and asexual stages, collected on *Punctelia* and *Cetrelia*, belong to the same, previously unsequenced species. Subsequently, two further sexual specimens on *Melanelixia* and *Punctelia* became available from Spain and Ecuador. Examination of unidentified *Phoma*-like specimens on diverse parmelioid hosts eventually resulted in a larger number of specimens. Amongst the hitherto described lichenicolous *Phoma* species, *Phoma melanelixiae* has been described on a parmelioid host, and the description perfectly fits the *Phoma*-like asexual stage studied by us. Although neither the type of *P. melanelixiae*, nor any other material from the same host genus, *Melanelixia*, has been sequenced, we believe that there is little doubt that all the material studied by us belongs to *P. melanelixiae*, especially after the recent discovery of the sexual stage on *Melanelixia glabra* in Spain, and the new combination in *Didymocyrtis* is consequently proposed here. A further specimen from Italy on *Parmotrema crinitum*, published by von Brackel (2015) as *Phoma* cf. *melanelixiae*, with a detailed description and illustrations, clearly fits our new species concept of *D. melanelixiae*.

2. The sexual stage of the new species is distinguished from *Didymocyrtis ramalinae* by the smaller and mostly 2-septate ascospores. The asexual stage is distinguished from most lichenicolous *Phoma*-like species by the relatively broad conidia having a single relatively large guttule, often filling more than half of the cell content. Measurements of numerous conidia from all specimens have shown that while the conidial length is rather variable, the breadth is more constant, so that the shape ranges from subspherical to broadly ellipsoid.

3. An undescribed species of *Didymocyrtis*, here treated as *D.* aff. *consimilis*, has been collected by one of us on *Melanohalea exasperatula* (sexual stage: Berger 26876; asexual stage: Berger 27218). That species is genetically only distantly related to *D. melanelixiae*, and the sexual stage is easily distinguished by the 1-septate ascospores. The asexual stage, however, is rather similar to that of *D. melanelixiae*, and further study is needed to better circumscribe the species on *Melanohalea* and to identify if any of the asexual specimens now included in *D. melanelixiae* are, in fact, the undescribed species.

4. *Xenophoma puncteliae* (Diederich & Lawrey) Crous & Trakunyingchaeroen (= *Phoma puncteliae* Diederich & Lawrey), described from *Punctelia rudecta* in the USA, differs by smaller pycnidia, 40–60 µm diam., shorter conidiogenous cells, 2.5–5×3.5–4.5 µm, and much smaller conidia, 2.5–3×2–2.4 µm (Lawrey et al. 2012). The species is known only in the asexual stage.

5. Following the original description of *Phoma fistulata* Etayo and Osorio (2004), this species resembles *Didymocyrtis melanelixiae*. However, re-examination of an isotype (hb. Etayo) showed that the pycnidial wall is very different (composed of well-delimited cells with an irregularly formed margin, similar to pieces of a jigsaw puzzle); the conidiogenesis is difficult to study, but certainly different (no ampulliform or ellipsoid conidiogenous cells were observed); conidia are embedded in a gelatinous matrix (they are free-swimming in microscopical preparations of *Didymocyrtis* species); and the typical guttulation of *Didymocyrtis* conidia could not be observed. As the current specimen is too old to be cultured and sequenced, we can not take a decision on the taxonomic position of this species.

Additional specimens examined: Sexual stage: **Ecuador:** Prov. Tungurahua, Baños de Agua Santa, sendero de la cascada del Bascún, 1760 m, on saxicolous *Punctelia rudecta*, 1999, Etayo 20035 & Palice (QCA, hb. Etayo). **Spain:** Navarra, Carretera de Zabalza a Adoain, N-2103, despoblados de Urraul, viejo camino de Aspuz, on *Melanelixia glabra*, 2015, Etayo 29169 (hb. Etayo). **USA:** Georgia, Murray Co., Chattahoochee National Forest, Cohutta Wilderness, Tearbitches Trail from Forest Serv. Rd. 68 to Bald Mountain, 34°52' N, 84°38' W, 1100–1200 m, on *Punctelia appalachensis*, 1992, Buck 21688 (NY). Maine, Hancock Co., Township of T28 MD, Lead Mountain (Humpback), along trail from parking area to water catchment area, 44°51'28" N, 68°05'52" W, on *P. rudecta*, 2012, Harris 57475 (NY, hb. Diederich).

Asexual stage (sequenced specimens): **USA:** Maine, Hancock Co., Township of T28 MD, Lead Mountain (Humpback), along trail from parking area to water catchment area, 44°51'28" N, 68°05'52" W, on *P. rudecta*, 2012, Harris 57475-B, 57476 (NY); *ibid.*, on *Cetrelia olivetorum*, Harris 57465 (NY).

Asexual stage (non-sequenced specimens, provisionally included in this species; specimens Harris 58925 and Buck 63062 examined by R.C. Harris): **Belgium:** Etalle, SE of Buzenol, vallée de la Rouge-Eau, en aval du passage de la route Etalle – St-Léger, on *Platismatia glauca*, 1984, Diederich 5550 (hb. Diederich). **Canada:** British Columbia, Wells Gray Provincial Park, Clearwater valley, 26 km N of Clearwater, near Kingfishers Wood Cottages, 51°51'23" N, 120°00'52" W, 730 m, on corticolous *Parmelia sulcata*, 2008, Diederich 17272 & Ertz (hb. Diederich). New Brunswick, Albert County, Fundy National Park, Maple



Grove Trail, 45°35'23" N, 64°59'01" W, 225 m, on *P. rudecta*, 2013, Harris 58925 (NY). **France:** Pyrénées-Atlantiques, SW of Larrau, near road to Spain, on *C. olivetorum*, 1990, Diederich 9177 (hb. Diederich). Pyrénées-Atlantiques, à 1 km du Col d'Ibardin, La Redoute des Emigrés, on *Parmotrema reticulatum*, 1995, Etayo 12734 (hb. Etayo). **La Reunion:** Cilaos, Forêt du Grand Matarum, sentier vers le Piton des Neiges, 21°07'13" S, 55°29'03" E, 1550 m, on *Usnea*, 2012, Ertz 18043 (BR). **Switzerland:** Valais, SE of Les Haudères, forêt de Tauge, on *Pseudevernia furfuracea*, 2012, Diederich 17328 (hb. Diederich). **United Kingdom:** Isle of Skye, Broadford, wood near the coast N of Isle Ornsay (NG 70 14), on *Hypotrachyna taylorensis*, 1987, Diederich 8793 (hb. Diederich). **USA:** Georgia, Dekalb Co., Arabia Mt. Park, Vaughtner's Farm, on *Canoparmelia texana*, 2015, Beeching 15964 (hb. Beeching). North Carolina, Camden Co., North River Game Land, E end of Indian Island, N of Indian Island Rd./Sassafras Lane, 3 mi E of Sandy Hook Rd., 36°17'08" N, 75°59'27" W, 1 m, on *P. rudecta*, 2012, Harris 57318-A (NY). North Carolina, Gates Co., Chowan Samp Game Land, E shore of the Chowan River, Buck Rd. 0.9 mi NW of Sandbanks Rd. (CR 1200), 7 mi N of US 13 in Storys, 36°31'15" N, 76°54'09" W, 2 m, on *Quercus*, on *Parmotrema submarginale*, 2012, Harris 57985 (NY). North Carolina, Dare Co., Alligator River National Wildlife Refuge, W of Whipping Creek Road, 0.5 mi N of jct w/ Chip Road, 35°40'31" N, 75°57'45" W, 1 m, on *P. rudecta*, 2014, Buck 63062 (NY).

**Didymocyrtis pseudeverniae (Etayo & Diederich) Ertz & Diederich comb. nov.** (Figs. 7f–h and 9e–f)

*Macrophomina pseudeverniae* Etayo & Diederich, Mycotaxon 60: 419 (1996); *Diederichia pseudeverniae* (Etayo & Diederich) D. Hawksw., Lichenologist 35: 206 (2003). Type: Spain, Huesca, road Sabiñánigo to Boltaña, Perto del Serrablo, Sierra del Gabardón, km 39 near Laguarda, 1200 m, on *Pseudevernia furfuracea*, 5 July 1993, J. Etayo 12597 (MA-Lich – holotype; hb. Etayo – isotype, non vid.). MycoBank: MB 814028

*Ascomata* unknown.

*Conidiomata* immersed in pinkish necrotic areas of the host thallus, dark brown to black, subspherical, 130–170 µm diam.; pycnidial wall brown, inner cells paler, darker near the ostiole. *Conidiogenous cells* ampulliform, 7–10 × 6–7 µm. *Conidia* subcylindrical, ellipsoid or irregular in form, with numerous small guttules, (14–)16–22(–26) × 6–9 µm [from Etayo and Diederich 1996].

For further illustrations, see Etayo and Diederich (1996).

Distribution and hosts. Europe (Great Britain, Italy, Latvia, Lithuania, Spain, Switzerland), on *Pseudevernia furfuracea* (von Brackel 2013; Etayo 2004; Etayo and Diederich 1996; Hitch 1997; Motiejūnaitė and Grochowski 2014; Motiejūnaitė et al. 2011).

Note. This species is distinguished by the particularly large conidia that are multiguttulate, contrary to most other *Didymocyrtis* species, which typically have 1–2-guttulate conidia.

Specimens examined (all on *Pseudevernia furfuracea*): **Spain:** Aragón, Huesca, Araguës del Puerto, 1991, Etayo 770 (hb. Diederich). Sierra de Illón, monte Belbún, Navascués, 2 km from Castillonuevo, 1994, Etayo 12600 (hb. Diederich). **Switzerland:** Valais, Evolène, Les Haudères, Forêt de Tauge, 2008, Diederich 16755 (hb. Diederich). Valais, 3 km S of Haute-Nendaz, road to Siviez, between main road and Planchouet, 2012, Diederich 17327, 17338 (hb. Diederich).

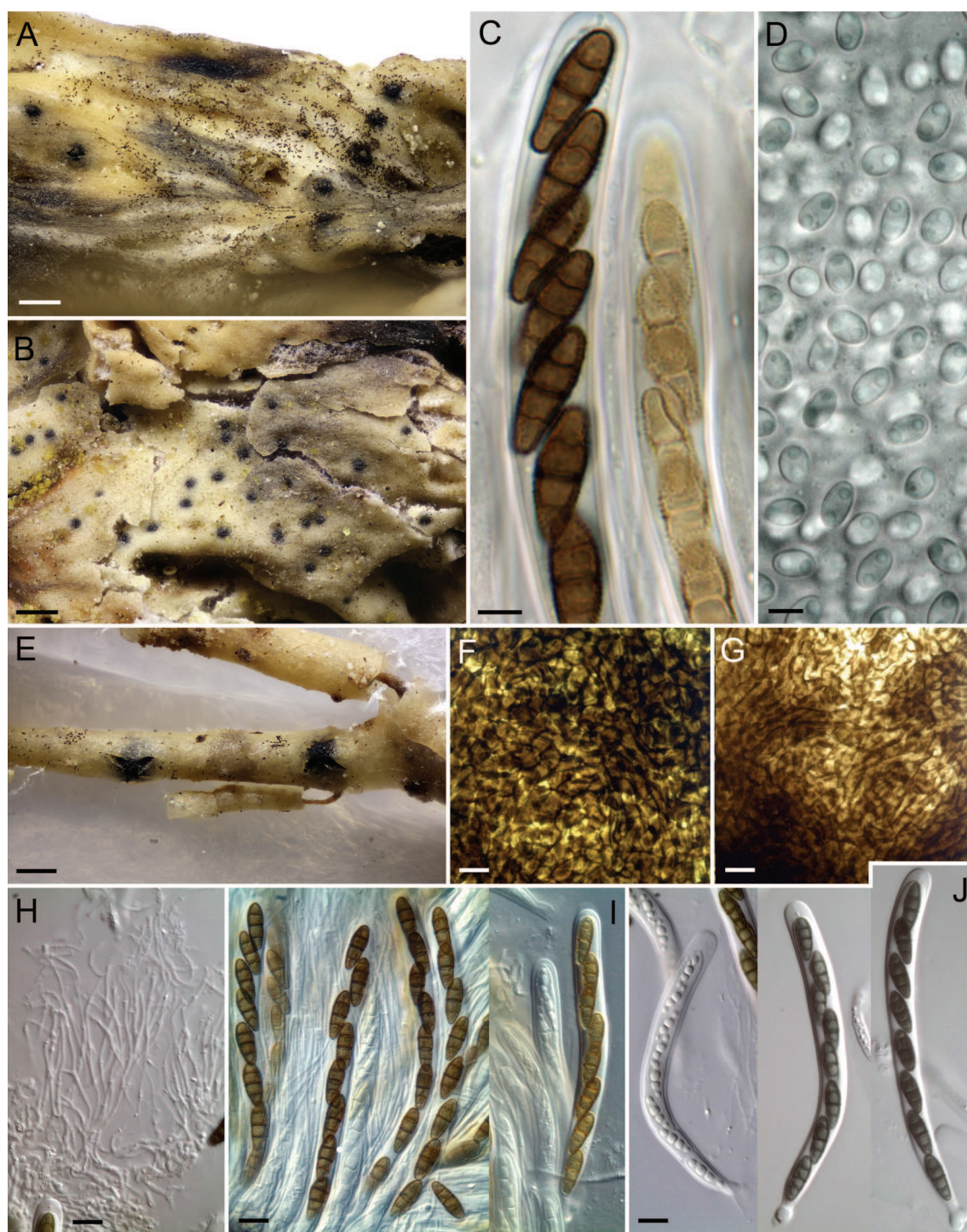
**Didymocyrtis ramalinae (Roberge ex Desm.) Ertz, Diederich & Hafellner comb. nov.** (Figs. 8a–d and 9i)

*Sphaeria ramalinae* Roberge ex Desm., Ann. Sci. Nat., Bot., 3. sér., 11: 354 (1849); *Leptosphaeria ramalinae* (Desm.) Sacc., Syll. Fung. 2: 84 (1883); *Heptameria ramalinae* (Desm.) Cooke, Grevillea 18 (86): 33 (1889); *Phaeospora ramalinae* (Desm.) Vouaux, Bull. Soc. Mycol. France 29: 74 (1913). Type: France, without locality and date, on *Ramalina fastigiata* (thallus), Roberge (?PC – holotypus, non vid.) MycoBank: MB 814029.

Syn. nov.: *Phoma ficuzzae* Brackel, Sauteria 15: 109 (2008); *Diederichomyces ficuzzae* (Brackel) Crous & Trakunyingcharoen, IMA Fungus 5(2): 401 (2014). Type: Italy, Sicily, Prov. Palermo, Bosco della Ficuzza, road from Ficuzza to S, 37°52'00.6" N, 13°23'17.3" E, 910 m, in grazed coppice forest mainly of oaks and ashes, on the bark of *Pyrus amygdaliformis*, on *Ramalina fraxinea*, 9 Aug. 2006, Brackel (hb. IVL 3983 – holotype; M-0044890 – isotype, non vid.). MycoBank: MB 519643.

? Syn.: *Pyrenidium ucrainicum* S. Y. Kondr., L. Lököcs et J.-S. Hur, Acta Bot. Hung. 56: 364 (2014). Type: Ukraine, Crimean AR, Sudak town, “Novy Svit” Botanical Reserve in the vicinity of Novy Svit settlement, SSW slopes of Mt Sykht-Lar, on bark of *Juniperus excelsa*, in thalli of *Ramalina* sp., 44°49'19" N, 34°55'05" E, ca 153 m alt., 17 Nov. 2013, Kondratyuk 21324 & Virchenko (KW-L 70284 – holotype; non vid. [no answer from KW]).

*Ascomata* dispersed, immersed in the apothecial margins, the hymenium and the gradually bleaching branches of the host thallus, visible as black dots, often with paler apical dots indicating the ostioles, more rarely on the apothecial disk and then almost sessile. Ascoma in longitudinal section subspherical with protruding ostiolar region, c. 200–300 µm diam.; wall brown, laterally c. 10–20 µm diam., consisting of c. 3–4 layers of cells. *Paraphysoids* 1–1.5 µm diam. *Asci* 90–110 × 9–12 µm. *Ascospores* ± uniseriate to half-overlapping, dark brown, 3-septate, some only with 1 or 2 septa (<1%), (13–)14–20 × 5–6.5(–7) µm, the upper half

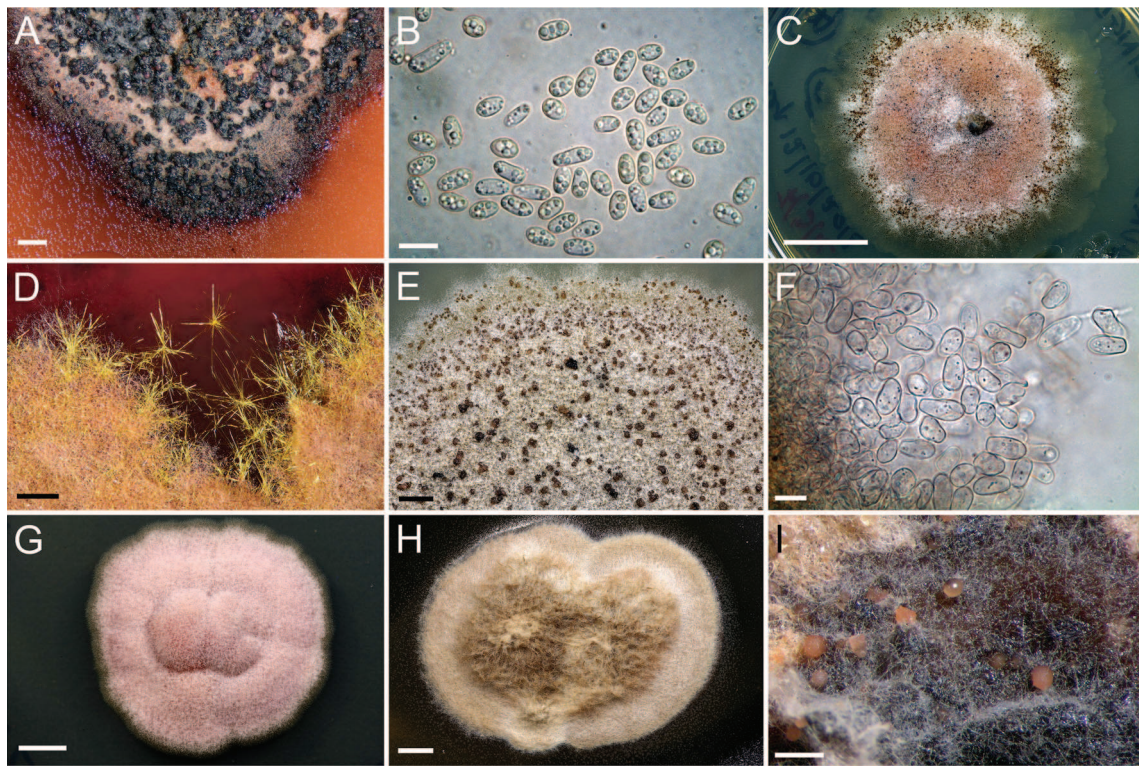


**Fig. 8** *Didymocyrtis ramalinae* (a–d) and *Leptosphaeria protousneae* (e–j). **a** Ascomata on *Ramalina fastigiata* (Santesson *Fungi Lich. Exs.* 318); **b** conidiomata on *R. fastigiata* (Van den Broeck 2900); **c** asci and ascospores (in water; Paul 27i2013); **d** conidia (in water; Van den Broeck 2900). **e–j** *Leptosphaeria protousneae* on *Protousnea* (isotype, hb.

Etayo); **e** immersed ascomata; **f** ascomatal view in surface view showing isodiametric cells (in KOH); **g** id., with elongate cells; **h** hamathecium (in KOH); **i–j** asci (in KOH). Scale bars: **a–b**, **e** = 200  $\mu$ m; **f–j** = 10  $\mu$ m; **c–d** = 5  $\mu$ m

spore (namely second cell) slightly wider than the lower one, not or slightly constricted at the septum, torus indistinct, with distinct verruculose sculpture visible in light microscopy.

*Conidiomata* immersed in pale necrotic areas of the thallus or apothecial margin surrounded by a black line, black, subspherical, 105–135  $\mu$ m diam.; wall brown, dark brown around the ostiole, 7–10  $\mu$ m thick, composed of 2–4(–5)



**Fig. 9** Cultures of *Didymocyrtis* species. **a** *D. consimilis* (Freebury 1357); **b** *D. consimilis* conidia (Freebury 1357); **c** *D. aff. consimilis* on *Cladonia pocillum* (Ertz 17617b); **d** *D. aff. consimilis* on *Melanohalea exasperatula* (Berger 26876); **e** *D. pseudeverniae* (Diederich 17327); **f** *D. pseudeverniae* conidia (Diederich 17338); **g** *D. epiphyscia* s. lat. on

*Physcia tenella* (Ertz 17615); **h** *D. epiphyscia* s. lat. on *Xanthoria parietina* (Gardiennet 12008); **i** *D. ramalinae* (Van den Broeck 2900). Scale bars: **c**=1 cm; **g**=5 mm; **e**, **h**=2 mm; **a**, **d**=1 mm; **i**=500  $\mu$ m; **b**, **f**=10  $\mu$ m

layers of cells  $8\text{--}10 \times 3\text{--}4.5$   $\mu$ m, inner cells hyaline. *Conidiogenous cells* short-ampulliform to subglobose, mainly  $6\text{--}7.5 \times 4\text{--}5.5$   $\mu$ m. *Conidia* ellipsoid, biguttulate, with a small guttule near each apex,  $5\text{--}7 \times 3\text{--}4$   $\mu$ m, l/b ratio 1.5–2 [from von Brackel 2008a and our own observations].

For further descriptions and illustrations of the asexual stage, see von Brackel (2008a) and Lawrey et al. (2012); for the sexual stage, see Vouaux (1913).

Distribution and hosts. Europe (e.g. Denmark, France, Great Britain, Italy, Lithuania, Luxembourg, Poland, Portugal, Spain), Africa (Canary Islands, South Africa), and Australasia (Australia). The sexual stage has been recorded on *Ramalina calicaris*, *R. celastri*, *R. exiguella*, *R. farinacea*, *R. fastigiata*, *R. lacera*, *R. pollinaria*, *R. subgeniculata* and *Ramalina* sp., and the asexual stage on *R. fastigiata* and *R. fraxinea* (e.g., Alstrup et al. 2004; van den Boom and Giralto 2012; von Brackel 2008a; Diederich 1990; Etayo 1996a, b, 2010b; Hafellner 1996; Hitch 2011; Kukwa et al. 2013; Lawrey et al. 2012; Motiejūnaitė et al. 2011, 2012; Vouaux 1913).

Notes. 1. The conidial size is rather variable in this species. In the original description (von Brackel 2008a), conidia were given as  $(5.5\text{--})5.9\text{--}6.8\text{--}(7.6) \times (3.1\text{--})3.5\text{--}3.9\text{--}(4.2)$   $\mu$ m, l/b ratio  $(1.4\text{--})1.6\text{--}1.9\text{--}(2.1)$  ( $n=40$ ). In specimen Van den Broeck

2900 from France, conidia were smaller,  $(4.8\text{--})4.9\text{--}5.4\text{--}(5.8) \times (3.2\text{--})3.2\text{--}3.6\text{--}(4.0)$   $\mu$ m, l/b ratio  $(1.3\text{--})1.4\text{--}1.6\text{--}(1.8)$ . In a culture obtained from Van den Broeck 2900, conidia were  $(5.0\text{--})5.6\text{--}6.4\text{--}(6.7) \times (2.8\text{--})2.9\text{--}3.5\text{--}(3.8)$   $\mu$ m, l/b ratio  $(1.3\text{--})1.7\text{--}2.1\text{--}(2.2)$ . Similarly, the pycnidial diameter is variable, 105–135  $\mu$ m in von Brackel (2008a) and 40–70  $\mu$ m in Van den Broeck 2900, but similar to Brackel's measurements in a culture obtained from Van den Broeck 2900. Lawrey et al. (2012) concluded that the species is probably much more variable than the few specimens examined suggest.

2. *Leptosphaeria protousneae* Etayo (Fig. 8e–j) was described from Chile and is known only from the type locality, where it was found growing as a parasite on the lacinia of the lichen genus *Protousnea* (Etayo and Sancho 2008; known only from sexual stage). *L. protousneae* closely resembles *Didymocyrtis ramalinae*, apart from the perithecial wall cells which were described as elongate in *L. protousneae* and isodiametric in *D. ramalinae*. We, however, found that this character is variable in all *Didymocyrtis* species. The asci and ascospores were also reported to be smaller in *D. ramalinae*, but we have found that the spore dimensions are rather variable within our sequenced specimens of this species, sometimes within a single specimen. The perithecia in *L. protousneae* are breaking through fissures in the cortex

while in *D. ramalinae*, the perithecia usually remain immersed in the thallus, but this might be the results of the thin lacinae of the *Protousnea* host thallus. Although we were unable to find any substantial morphological differences between the taxa, due to the remote geographical distribution of *L. protousneae* and the different host genus, we prefer to wait for molecular data and more material from South America before deciding on a possible synonymy with *Didymocyrtis ramalinae*.

Selected specimens examined (all on *Ramalina*): Sexual stage: **Australia**: Queensland, Tandora about 25 km ENE of Maryborough, 25°27' S, 152°52' E, sea level, on *R. exiguella*, 1986, Hafellner 18174 & Rogers (GZU). **Canary Islands**: Tenerife, Macizo de Anaga, Monte de las Mercedes, NE ober Las Mercedes bei der Abzweigung nach Llano de los Viejos, 28°31'30" N, 16°17' W, 760 m, auf *Ramalina* sp., 1989, Hafellner 35107 (hb. Hafellner). **France**: Corsica, N d'Ajaccio, côte sud du Golfe de Sagone, route à l'est du village de Pevani, Capu di u Monte, 355 m, 42°01'11" N, 8°43'13" E, rocher siliceux exposé, sur *Ramalina* sp., 2011, Ertz 16399 (BR). **Great Britain**: Scotland, VC 95, Moray, Brodie, SE of Plyon Cott, on *R. fastigiata* on *Crataegus* in hedgerow, 18 m, Grid NH973.577, 13 i 2013, Paul s.n. (E); *ibid.*, Forres, Beech Road, on *R. fastigiata* on *Acer pseudoplatanus*, 20 m, Grid NJ04020.57892, 27 i 2013, Paul s.n. (E). **Italy**: Basilicata, Prov. Potenza, NW-Abhänge der Coppola di Paola SE von Rotonda, 1400 m, on *R. fastigiata*, 1979, Hafellner 41837 (hb. Hafellner). **Luxembourg**: Hoscheid, along road, on *R. fastigiata*, 1967, Van Wersch (hb. Diederich). **South Africa**: Cape Province, south coast, about 48 km E of Plettenberg Bay, Tsitsikamma Coastal National Park, along the 'Loerie Trail' N of the camp, 34°30' S, 23°53' E, on *Ramalina* sp., 1987, Wetschnig & Wetschnig (GZU). **Spain**: Castello Prov., Morella, Els Campbello, 40°37' N, 0°06' W, 1000 m, on *R. fastigiata*, 1994, Calatayud, Santesson Fungi Lich. Exs. 318 (hb. Diederich). **Sweden**: Bohuslän, Lysekil commune, Skaftö par., Islandsberg, 1 km S of Grundsund, on trail to Islandsbergs Huvud, c. 50 m, on *R. fastigiata*, 1992, Hafellner 30485 (hb. Hafellner).

Asexual stage (all on *Ramalina*): **France**: Pas-de-Calais, Equihen-Plage, dunes d'Escault, 50°39'55" N, 1°34'37" E, on *Acer*, on *R. fastigiata*, 2009, Van den Broeck 2900 (BR, hb. Diederich) [culture JL334-09, CBS 128019]. **Great Britain**: Scotland, VC 95, Moray, Earlsmill, by Muckle Burn, on *R. fastigiata*, 34 m, Grid NH972.562, 10 i 2013, Paul s.n. (E).

**Didymocyrtis slaptoniensis** (D. Hawksw.) Hafellner & Ertz comb. nov. (Figs. 5j–l and 6)

*Polycoccum slaptoniense* D. Hawksw., Lichenologist 26(4): 342 (1994). Type: Great Britain, England, South Devon, Slapton, Slapton Ley National Nature Reserve, east end of Duck Marsh near The Causeway, on *Sambucus nigra*, on *Xanthoria parietina*, 2 Oct. 1993, D. L. Hawksworth (IMI

359711 – holotype, non vid., fide Hawksworth 1994). MycoBank: MB 814030.

*Ascomata* usually scattered, sometimes in small groups, developing in the hymenium, the apothecial margin and the thallus (when on the thallus, ascomata protruding and surrounded by a thallus collar; when immersed in the hymenium they protrude very little and lack a collar; the thalline collar and the nearest parts of the host thallus may turn purple-red making the infection spot rather conspicuous, with only the ostiolar region becoming exposed and visible as black, somewhat protruding dots). Ascoma in longitudinal section globose to broadly oval, (150–)200–300 µm diam.; wall dark red-brown, laterally c. 15–20 µm diam., up to 40 µm towards the apex, consisting of c. 4–5 layers of cells. *Paraphysoids* 1.5–2 µm diam. *Asci* (80–)90–110 × 7–10 µm. *Ascospores* ± uniseriate, pale brown, 1-septate, (11–)13–15 × (5.5–)6–7 µm, with verruculose sculpture and with torus protruding on the outside in semimature spores (torus of mature spores not protruding any further).

*Conidiomata* of supposed asexual stage on the thallus and occasionally in the hymenium, immersed when young, later protruding. Pycnidia developing on the thallus remain obtected by a thin layer of host plectenchyma forming a more or less distinct collar, very similar to teleomorphic pseudothecia but smaller. Pycnidia in longitudinal section more or less globose, 80–120(–150) µm diam.; wall brown throughout and c. 10 µm diam. *Conidiogenous cells* ellipsoid to flask-shaped, hyaline, 8–10 (–12) × 5–6 µm. *Conidia* ellipsoid to oblong, many somewhat bent, (5–)6–8(–9) × 2.5–3.5 µm, with two small guttules near the ends, l/b ratio c. 2.

For further descriptions and illustrations of the sexual stage, see Hawksworth (1994).

Distribution and hosts. Europe (Austria, Belgium, England, France, Germany, Italy, Liechtenstein, Luxembourg, Portugal, Switzerland), on the thallus and apothecia of *Xanthoria parietina* (van den Boom and Giralt 2012; von Brackel 2008b, 2009; Diederich et al. 2014; Ertz et al. 2008; Gardiennet 2012; Hawksworth 1994; Kocourková and von Brackel 2005; Roux et coll. 2014).

Note. Sometimes ascomata of *Didymocyrtis slaptoniensis* and *Phoma*-like pycnidia can be observed on the same specimen (e.g., Obermayer 13130). This supposed *Phoma*-like anamorph (Fig. 5j, l) fits the description of *Phoma epiphyscia* Vouaux, described from northern France. Vouaux (1914) mentioned two host species in the protologue, namely *Xanthoria parietina* and *Phaeophyscia orbicularis*. As the type is not among the remnants of the Vouaux herbarium (Rondon 1969) and is apparently lost, Alstrup and Hawksworth (1990) designated a neotype originating from Greenland and infesting *Phaeophyscia sciastra*. As the conspecificity of the fungi growing on *Phaeophyscia* and that upon *Xanthoria*

*parietina* is only speculative (no comparable teleomorph is known on *Phaeophyscia*), we hesitate to use Vouaux's name for the fungus growing on *Xanthoria*.

Selected specimens examined (all on *Xanthoria parietina*): Sexual stage: **Austria**: Steiermark, Oststeirisches Riedelland, 5.2 km east of the centre of Graz, Ragnitz, 50 m S of the brook Ragnitzbach (Grazbach), 47°04'24" N, 15°30'26" E, 405 m, GF 8958/2, 2014, Obermayer 13130 (GZU) (with asexual stage). **Belgium**: Hermeton-sur-Meuse, section de 1.5 km de la vallée de l'Hermeton en amont de la confluence avec la Meuse, 100 m, 2005, Ertz 9057 & Duvivier (BR). **France**: Côte d'Or, Véronnes, Combe du Chatelet, vers la chapelle Sainte-Anne, 2012, Gardiennet 12009 (hb. Gardiennet). Ardennes, Fumay, rive droite de la Meuse, entre la carrière du Pont de Fumay et l'ancienne ardoisière de Follemprie, Mora (BR). Rhône-Alpes, Haute-Savoie, Western Alps, Bornes Massif (Le Massif des Bornes), Burzier NW above Sallanches, SE below the parking area at Route de Doran, 45°57'22" N, 6°36'42" E, 935 m, 2011, Hafellner 82564, 82565 (GZU) (with asexual stage). **Liechtenstein**: Eastern Alps, Rätikon, W below the village Triesenberg by the road to Vaduz, 47°06'45" N, 09°32'30" E, 750 m, 2008, Hafellner 83057 (GZU). **Luxembourg**: NW von Ahn, Verbuschung am Wegrand westlich vom Kräizuet, 2014, Cezanne & Eichler 9590 (hb. Diederich) **Switzerland**: canton Bern, municipality of Wengi, 6 km E of Lyss, N of Äschwald (0.6 km NE of the pond Golihuebweiher), 47°05'00" N, 07°22'53" E, 488 m, 2014, Berger & Zimmermann (GZU).

Asexual stage: **Austria**: Burgenland, Südburgenland, Güssing, Schlossberg, Schlossplatz, 47°03'29" N, 16°19'27" E, 310 m, 2012, Berger 26196 (hb. Berger). Steiermark, Nordalpen, Nördliche Kalkalpen, Hochschwab-Gruppe, Seetal W von Seewiesen, 10 km NE von Aflenz, 47°37'15" N, 15°15'20" E, 930 m, GF 8357/4, 2011, Hafellner 78042, 78044 (GZU).

**Didymocyrtis xanthomendozae (Diederich & Freebury) Diederich & Freebury comb. nov.**

*Phoma xanthomendozae* Diederich & Freebury, in Lawrey et al., Fungal Diversity 55: 208 (2012). Type: Canada, Quebec, Les Collines-de-l'Outaouais RCM, Gatineau Park, near Wakefield, grassy ditch beside Route 05, 45°37.8' N, 75°56.4' W, on fallen *Salix*, on *Xanthomendoza hasseana*, 3 May 2010, C. Freebury 1122 (CANL – holotypus; hb. Diederich – isotypus!). Ex-type culture: JL451-10, CBS 129666. MycoBank: MB814031.

Ascomata rare, macroscopically undistinguishable from pycnidia (see description below); globose to broadly oval, 180–250 µm diam.; wall dark red-brown, 20–35 µm diam., consisting of c. 4–5 layers of cells. *Paraphysoids* 1.5–2.5 µm diam. *Asci* c. 75–110×8–9.5 µm. *Ascospores* ± uniseriate, pale

brown, 1-septate, (10.5–)11–13(–14)×(5.5–)6–7(–7.5) µm ( $n=20$ ), with verruculose sculpture and with torus protruding on the outside in semimature spores (not protruding further in mature spores).

*Conidiomata* immersed in the host apothecia, more rarely in the host thallus, black, subspherical, c. 140–160 µm diam.; pycnidial wall brown, 14–17 µm thick, composed of 3–5 layers of cells, outer cells dark brown, 5–7.5 µm diam., inner cells pale brown. *Conidiogenous cells* elongate ampulliform to subcylindrical, 5–10×2.5–3.5 µm. *Conidia* ellipsoid, (1–)2-guttulate, (4.5–)5.6–7.1(–8.6)×(2.9–)3.3–4.3(–4.6) µm, l/b ratio (1.2–)1.4–2.0(–2.5) ( $n=60$ ) [from Lawrey et al. 2012].

For further descriptions and illustrations of the asexual stage and of cultures, see Lawrey et al. (2012).

Distribution and hosts. The species is known from Canada (Quebec and Saskatchewan); it inhabits apothecia and more rarely the thallus of corticolous *Xanthomendoza hasseana* and *X. montana*, and eventually kills the host (Lawrey et al. 2012).

Notes. 1. This species was initially described in *Phoma*, as only pycnidia had been observed. However, a few perithecia have since been observed in one of the specimens, and these are typical for *Didymocyrtis*.

2. Phylogenetically, this species is very close to *Didymocyrtis slaptioniensis*, which also grows on a related host, *Xanthoria parietina*, and therefore we wondered if they were conspecific. However, we decided to treat them as distinct, for several reasons. (1) In Europe, *D. slaptioniensis* appears to be strongly host specific, inhabiting a single species of the genus *Xanthoria*, whilst *D. xanthomendozae* is known only from North America on *Xanthomendoza* species; (2) ascospores of *D. slaptioniensis* (mainly 13–15×5–7 µm) are longer than those of *D. xanthomendozae*; (3) pycnidia of *D. slaptioniensis* are much smaller in diam. than those of *D. xanthomendozae*; (4) conidia in *D. slaptioniensis* (mainly 6–8×2.5–3.5 µm) are slightly longer and distinctly narrower than those of *D. xanthomendozae*; (5) conidiogenous cells in *D. slaptioniensis* (ellipsoid, flask-shaped, mainly 8–10×5–6 µm) are much broader than those of *D. xanthomendozae*, which are mainly subcylindrical.

Sexual stage specimen examined: **Canada**: Quebec, Les Collines-de-l'Outaouais RCM, Gatineau Park, 45°37'56" N, 75°56'26" W, on *Xanthomendoza hasseana*, 2011, Freebury 1413, 1415 (CANL).

**Trypetheliales Lücking, Aptroot & Sipman**

in Aptroot et al., Bibl. Lichenol. 97: 13 (2008). Type: *Trypethelium* Spreng. MycoBank: MB 533049.

Notes. 1. The order *Trypetheliales* was described to accommodate the single family *Trypetheliaceae*, a group of mainly lichenized ascomycetes placed in *Dothideomycetes* in a molecular phylogeny by Del Prado et al. (2006). Species in this order are characterized by perithecioid ascomata appearing solitary or aggregated in pseudostromata, which have either

separate ostioles or with ascomatal chambers laterally fused to share a common ostiole, a dark brown to carbonized perithecial wall, branched and anastomosing paraphysoids embedded in a distinct gelatinous matrix, bitunicate asci, and hyaline or rarely brown ascospores with variously developed endospore thickenings that give the lumina a diamond-shaped or more rarely a round outline (Aptroot et al. 2008; Hyde et al. 2013; Nelsen et al. 2014). The ascospores may be muriform or transversely septate.

2. In the present study, we introduce the new family *Polycoccaceae* for the genera *Polycoccum* and *Clypeococcum*. We provisionally place it in the order *Trypetheliales* based on molecular and morphological data. *Polycoccaceae* species differ from those of *Trypetheliaceae* by their non-lichenized, lichenicolous habit, and 1-septate, brown, usually smaller ascospores; but they are otherwise similar in having perithecioid ascomata, branched and anastomosing paraphysoids in a hymenial gel matrix, and bitunicate asci.

**Polycoccaceae Ertz, Hafellner & Diederich, fam. nov.**

Type: *Polycoccum* Saut. ex Körb., Parerga Lich.: 470 (1865). MycoBank: MB 814032

Lichenicolous fungi, belonging to the *Trypetheliales*. *Ascomata* arising singly, often becoming grouped, sometimes united by a clypeus or enclosed in galls, immersed with only the ostiole visible to erumpent and the upper half exposed when mature, perithecioid, subglobose to obpyriform, dark brown to black, ostiolate, neck not extended and scarcely distinguishable from the ascomatal wall; wall even in thickness or somewhat broader near the ostiole, composed of 3–6 layers of polyhedral pseudoparenchymatous cells, radially compressed in vertical section and roughly isodiametric in surface view, forming a textura angularis; outer layers of cells with  $\pm$  evenly thickened walls, brown to dark brown and continuing below the centrum; inner layers less intensely pigmented to hyaline with thin-walled cells. *Hamathecium* composed of a branched and anastomosing net of thin and regularly septate to remotely septate narrow hyphal filaments, probably trabeculate pseudoparaphyses (paraphysoids); periphyses absent; hymenial gel I+ blue to violet or unchanged. *Asci* broadly cylindrical to subclavate, shortly stalked, bitunicate, fissitunicate, wall thicker in the upper part of mature asci, with a small internal apical beak, 2–8-spored. *Ascospores* irregularly distichously arranged in the asci, ellipsoid, 1-septate (euseptate); cells  $\pm$  equal in size or the upper cell larger and broader, apices generally rounded or rarely attenuated, somewhat constricted at the septum, brown to dark brown when mature, smooth or delicately verruculose, sometimes with a gelatinous sheath.

Note. The family currently includes the genera *Clypeococcum* and *Polycoccum*. It is the sister group to *Trypetheliaceae* in our molecular phylogeny using nuLSU sequences (Fig. 1).

**Polycoccum Saut. ex Körb. (Fig. 10)**

Parerga Lich.: 470 (1865). Type: *Polycoccum sauteri* Körb. [= *Polycoccum trypethelioides* (Th. Fr.) R. Sant., fide Santesson 1960]. MycoBank: MB 4309.

Syn.: *Lophothelium* Stirt., Scott. Naturalist 9: 37 (1887). Type: *Lophothelium acervatum* Stirt. [= *Polycoccum trypethelioides* (Th. Fr.) R. Sant., fide Hawksworth and Diederich 1988]. MycoBank: MB 2945.

Note. The core group of *Polycoccum* is characterized by thick-walled, often distinctly ornamented ascospores. Further characters of *Polycoccum* s. str. are the formation of ascomata on the host thallus, a tendency to induce the formation of galls, and certain features of the ascomatal wall (cells  $\pm$  isodiametric in longitudinal section), the hamathecium (consisting of relatively thick paraphysoids), the ascus (broadly cylindrical to subclavate, generally with irregularly distichously arranged ascospores). Variations exist; for example, the ascospores of the generic type, *Polycoccum trypethelioides*, are often irregularly uniseriate.

**Polycoccum trypethelioides (Th. Fr.) R. Sant. (Fig. 10a–d)**

Svensk Bot. Tidskr. 54: 505 (1960). For synonyms see Hawksworth and Diederich (1988). Type: Norway, Troms Prov., Tromsø, on *Stereocaulon alpinum*, 1857, Fries (UPS, holotype, non vid.) (fide database of UPS herbarium). MycoBank: MB 119595.

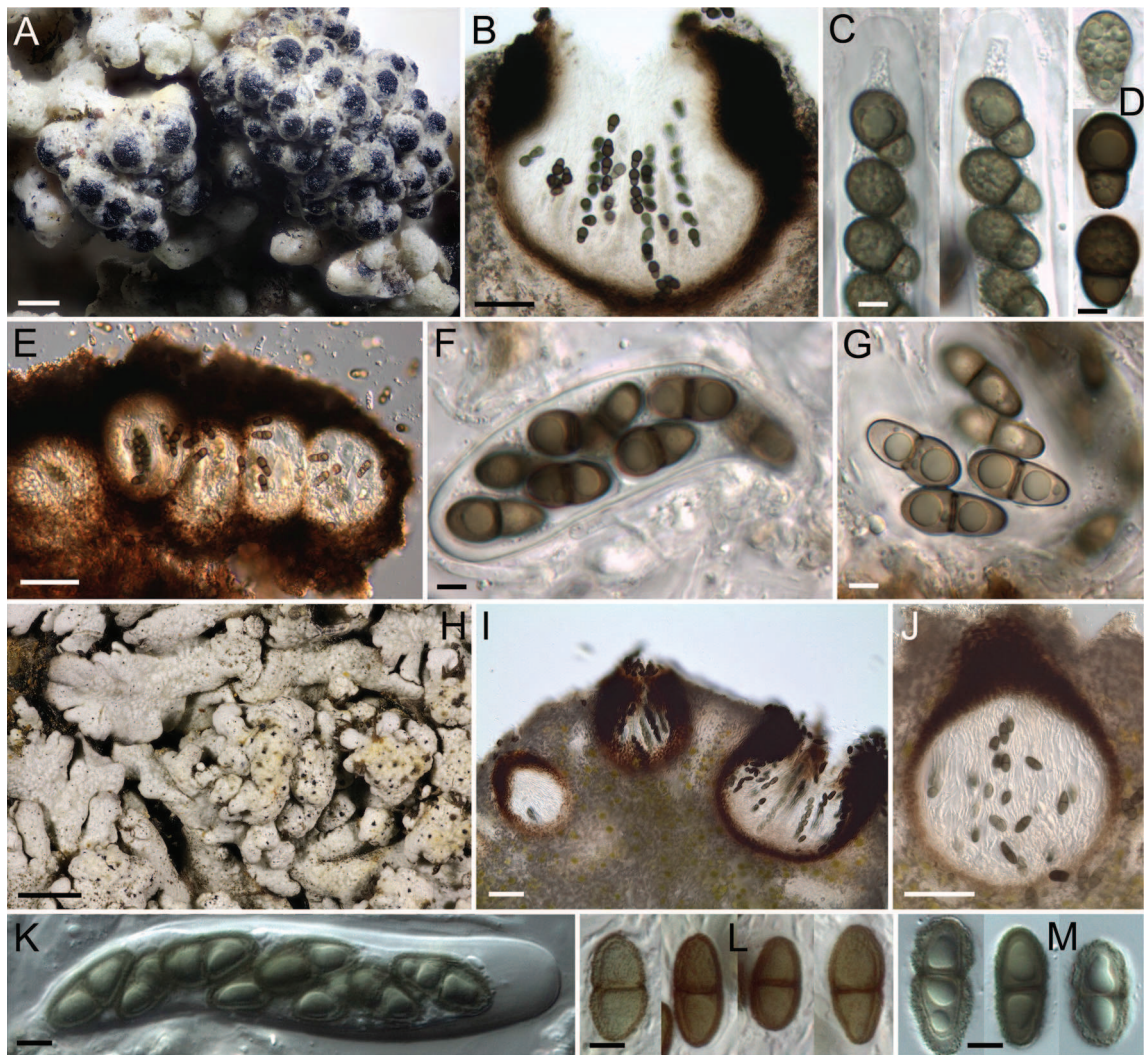
*Ascomata* immersed in subglobose galls on the thallus of the host, 150–250  $\mu\text{m}$  diam. Paraphysoids 1.5–2.5  $\mu\text{m}$  wide. *Asci* elongate-clavate, (75–)80–100 $\times$ (14–)16–19  $\mu\text{m}$ , 8-spored. *Ascospores* overlapping uni- to biseriolate, broadly ellipsoid to soleiform (the upper cell much larger in size, the lower only about 1/3 the length of the spore), brown to dark brown, smooth (according to Hawksworth and Diederich 1988) or verruculose (according to Orange 1990), thick-walled, 14–22 $\times$ 8–10  $\mu\text{m}$ .

*Conidiomata* described by Zhurbenko (2010) as ‘pycnidial, black, subglobose, ostiolate, 50–100  $\mu\text{m}$  diam., immersed to erumpent, crowded and intermixed with the ascomata. Conidiogenous cells holoblastic, arising from the pycnidial wall, subcylindrical to elongate-ampulliform and strongly tapered towards the apex, with 1–2 annulations, c. 14–15 $\times$ 2.5–3.5  $\mu\text{m}$ ; conidia simple, (narrowly) oblong to elliptic, with rounded apex and truncated base, hyaline, smooth-walled, (3.5–)4–5(–7) $\times$ 1.5–2  $\mu\text{m}$ , l/b=(1.8–)2.3–3.4(–4.7) ( $n=47$ ).

For further descriptions, illustrations and synonymy, see Hawksworth and Diederich (1988) and Zhurbenko (2010).

Distribution and hosts. Known from Europe (Austria, British Isles, Canada, Finland, Germany, Iceland, Norway, Russia, Sweden) and North America (Canada, Greenland, USA) (Alstrup 1981; Alstrup and Cole 1998; Alstrup et al. 2008; von Keissler 1930; Hawksworth and Diederich 1988; Körber 1865 [*Polycoccum sauteri*, type of *Polycoccum*, type from Austria]; Orange 1990; Zhurbenko 2007, 2010; Zhurbenko and Santesson 1996) on diverse *Stereocaulon* species.

Selected specimens examined: **Austria:** Tirol, Samnaun-Gruppe, Furgler W ober Serfaus, am Grat zwischen dem



**Fig. 10** Morphological features of the genus *Polycoccum*. **a–d**, *Polycoccum tryphethelioides* (**a** galls on *Stereocaulon* with immersed ascomata; **b** section through ascoma; **c** asci with ascospores; **d** ascospores; in water; **a** Goward 95-282; **b–d** Diederich 17508). **e–g** *P. vermicularium* (**e** section through ascomata in gall; **f** ascus; **g**

ascospores; in water; Diederich 17545). **h–m** *P. pulvinatum* (**h** galls with immersed ascomata on *Physcia caesia*; **i–j** section through ascomata; **k** ascus; **l–m** ascospores; **i–l** in water; **m** in KOH; Diederich 17389). Scale bars: **h**=1 mm; **a**=200  $\mu$ m; **b, e, i–j**=50  $\mu$ m; **c–d, f–g, k–m**=5  $\mu$ m

Furgler Joch und dem Gipfel, 47°02'40" N, 10°30'50" E, 2800–2900 m, GF 8929, on *Stereocaulon*, 1991, Hafellner 30184 (hb. Hafellner). **Canada**: British Columbia, 25 km N of Kispiox, near Skeena River, on *S. tomentosum*, 1995, Goward 95-282 (UBC, hb. Diederich). **Iceland**: SE of Höfn, between road 1 and Jökulsárlón, 1 km W of bridge, 64.04251° N, 16.20525° W, 5 m, terricolous, on *Stereocaulon*, 2013, Diederich 17508 (hb Diederich).

## Discussion

*Polyphyly of Dacampiaceae*. The phylogenetic position of the family *Dacampiaceae* is shown here for the first time by the placement of the genus *Dacampia* in *Pleosporales*. Notably,

while most *Dacampiaceae* species are lichenicolous or saprobic, the type species of *Dacampia*, *D. hookeri*, is lichenized (Henssen 1995; Hyde et al. 2013) (Fig. 3a). *Dacampia hookeri* is also one of the rare lichenized fungi now confirmed in *Pleosporales*, an order that otherwise includes mainly saprobic fungi on dead plant material and pathogens on living plants (Hyde et al. 2013). This species clusters with the lichenicolous *Dacampia engeliana* in our phylogenetic tree (Fig. 1). Atypically for a lichenicolous fungus, *D. engeliana* modifies its host lichen (*Solorina*) to form a thallus structure similar to that found in *D. hookeri* (Henssen 1995; de los Ríos and Grube 2000) (Fig. 3b), a feature supporting their close phylogenetic relationship. Other lichenicolous *Dacampia* species that do not form such thallus structures might therefore be expected to be more distantly

related. *Dacampia* is closely related to members of *Leptosphaeriaceae* (e.g., *Paraleptosphaeria orobanches*, Fig. 1); however, based on the current dataset, the relationship of *Dacampiaceae* with other families of *Pleosporales* is unclear, and resolving this will require more detailed study. Surprisingly, *Dacampiaceae* is strongly polyphyletic since other genera originally assigned to this family, such as *Clypeococcum*, *Polycoccum* and *Munkovalsaria*, are part of other lineages (Fig. 1). Wang et al. (2007) and Hyde et al. (2013) suggested that the family was heterogeneous because it was not strongly characterized morphologically, the only distinguishing characters being multilayered and rather soft ascomatal walls, and relatively wide ostioles.

*Placement of genera previously included in Dacampiaceae.* One of the most striking results of our study is the placement of *Polycoccum* s. str. and two species of *Clypeococcum* as the sister group to the *Trypetheliaceae* (*Trypetheliales*), a family of mainly lichenized tropical fungi. This sister relationship being well-supported, we suggest including *Polycoccum* in *Trypetheliales*, while the position of *Clypeococcum* will need to be confirmed by the sequencing of its type species. We recognize this new, well-supported lineage of lichenicolous fungi as the new family *Polycoccaceae* (see *Taxonomy* section). This relationship is somewhat similar to *Arthoniomycetes*, where the non-lichenized *Lichenostigmatales*, including black yeasts, lichenicolous and rock-inhabiting taxa, are sister to the mainly lichenized *Arthoniales* (Ertz et al. 2013), and it suggests that the lichenicolous life habit might have played a key role in the transition from non-lichenized to lichenized life habits that led to the evolution of some of the main groups of lichenized fungi. The long, isolated branch formed by *Trypetheliaceae* within *Dothideomycetes* (e.g., Muggia et al. 2012; Hyde et al. 2013) is indeed broken by the new lineage of *Polycoccaceae*. The genus *Clypeococcum*, here represented by *C. placopsiophilum* and *C. psoromatis*, is nested within *Polycoccum* and renders this genus paraphyletic. According to Hawksworth and Diederich (1988), *Clypeococcum* differs from *Polycoccum* by the hyphal rather than pseudoparenchymatous ascomatal walls, which are massively thickened around the ostiole, and by the ascomata occurring in groups united by a common clypeus. It is unclear from the data included in our phylogenetic tree whether *Clypeococcum* species need to be included in *Polycoccum* or if *Polycoccaceae* has to be split into several genera. The long branches within *Polycoccaceae* suggest a fast-evolving nuLSU gene contrasting with low morphological variability, which results in few phenotypic characters useful for the recognition of different genera.

Interestingly, several members previously assigned to the genus *Polycoccum* are placed in the *Pleosporales* and are thus distantly related to the *Trypetheliales/Polycoccaceae*. Phenotypic characters such as the ascus type clearly support

the placement of these '*Polycoccum*' species in the *Pleosporales* (see *Taxonomy* section). These '*Polycoccum*' species are closely related to '*Phoma*-like' lichenicolous fungi assigned to the family *Phaeosphaeriaceae* (Lawrey et al. 2012), and all these taxa are treated below as the '*Didymocyrtis* clade'.

Another genus originally assigned to *Dacampiaceae* and included in our phylogenetic tree (Fig. 1) is *Munkovalsaria* [generic type: *M. donacina* (Niessl) Aptroot]. Aptroot (1995a) established this genus to include fungi with a black stroma that forms a clypeus around the ostiole; branched-anastomosing pseudoparaphyses; cylindrical bitunicate asci with eight uniseriate ascospores (K/I-); and reddish to deep brown, euseptate ascospores that are surrounded by a thin gelatinous sheath. Three nuLSU sequences of *Munkovalsaria* were available on GenBank. *Munkovalsaria appendiculata* was already placed in the *Pleosporales* as sister species to *Montagnula opulenta* (*Didymosphaeriaceae*) in a phylogenetic study by Wang et al. (2007). In our nuLSU tree, *Munkovalsaria appendiculata* and *M. donacina* cluster together in *Pleosporales*. Our phylogenetic study shows *M. appendiculata* and *M. donacina* clustered with *Montagnula opulenta* and *Bimuria novae-zelandiae*, which suggests that *Munkovalsaria* does not belong to *Dacampiaceae* as originally classified but to *Didymosphaeriaceae* as recently circumscribed by Ariyawansa et al. (2014). A third species, *Munkovalsaria rubra* Aptroot, van der Aa & Petrini, was found to cluster with *Valsaria insitiva* in a multilocus phylogeny (Zhang et al. 2009), but it was placed outside the order *Pleosporales*. Subsequently, *M. rubra* was accommodated in the new family *Valsariaceae* (*Valsariales*) and combined in the genus *Myrmaecium* (Jaklitsch et al. 2015).

*Anamorph-teleomorph relationships in Didymocyrtis.* Several potential anamorph-teleomorph relationships were highlighted in our ITS phylogenetic tree (e.g. *Phoma ficuzzae/Didymocyrtis ramalinae*, *Phoma caloplacae/Didymocyrtis consimilis*; see *Results* section). Molecular and phylogenetic analyses already suggested anamorph-teleomorph relationships among lichenicolous fungi belonging to other taxonomic groups: in the *Abrothallales* (*Dothideomycetes*), the connection between *Abrothallus* and its anamorph stage *Vouauxiomyces* was established by Denaturing Gradient Gel Electrophoresis (Pérez-Ortega et al. 2011); in the *Lichenostigmatales* (*Arthoniomycetes*) *Phaeosporobolus usneae* was shown to be the anamorphic stage of *Lichenostigma maureri* (Ertz et al. 2013) and in the *Chaetothyriales* (*Eurotiomycetes*), the species *Lichenodiplis lecanorae* and *Muellerella atricola* were suggested to represent, respectively, the anamorph and teleomorph stages of the same fungus (Muggia et al. 2015). The co-occurrence of ascomata and conidiomata on the same lichen thallus often suggests evidence of such relationships. Halıcı and



Hawksworth (2008) and Halıcı et al. (2009) previously suggested the existence of anamorph-teleomorph relationships within the genus *Dacampia*, given the observation of *Phoma*-like conidiomata in intimate association with ascomata of *Dacampia rubra* and *D. muralicola*. The generic position of these two species remains to be confirmed by molecular data, but in the meantime the co-occurrence of *Phoma*-like asexual stages should be considered in support of their placement within the *Pleosporales*, where such anamorphs are frequent.

*Species boundaries and host specificity in Didymocyrtis.* Most lichenicolous fungi are assumed to be highly host specific, confined to a single lichen species or genus. The causes for this are not known, but may involve resistance to lichen secondary metabolites (Merinero et al. 2015) and/or nutritional or mechanical requirements that can be met only by specific lichen hosts (Lawrey and Diederich 2003). Assumptions about host specificity depend heavily on the prevailing species concepts applied to both lichen parasites and their hosts. Since for lichenicolous fungi, species concepts have sometimes been based largely on host ecology, presumed species boundaries and host specificities should be considered as hypotheses to be tested using a combination of morphological, genetic, distributional and ecological information.

In most members of *Didymocyrtis*, species boundaries are relatively well-established and supported by a combination of characters. Some easily distinguished *Didymocyrtis* species can be viewed as narrow specialists, restricted to a single host lichen genus or species. For example, *D. ramalinae* apparently grows only on species of *Ramalina*, while *D. pseudeverniae* is found only on *Pseudevernia furfuracea*. Similarly, *D. slaptioniensis* and *D. xanthomendozae* appear to be closely related sister species that colonize separate hosts and may have arisen as a result of recent host-switching. *Didymocyrtis slaptioniensis*, well-known primarily from the sexual stage, is found only on *Xanthoria parietina*, and *D. xanthomendozae*, known from the sexual and asexual stages, is found only on *Xanthomendoza* spp.

Other morphologically and genetically distinguishable *Didymocyrtis* species appear to have much broader host ecologies, being found on a variety of sometimes unrelated lichen hosts. This situation was first described by Lawrey et al. (2012), who found that *D. cladoniicola* and *D. foliaceiphila*, previously assumed to be restricted to *Cladonia* hosts (Diederich et al. 2007), were also able to infect lichens belonging to other non-related hosts. *Didymocyrtis cladoniicola* is now known from *Cladonia*, *Parmelina*, *Ramalina*, *Squamarina*, and *D. foliaceiphila* is now found on *Cladonia* and *Parmelia*. To these we can also add *D. melanelixiae*, which occurs on many members of *Parmeliaceae*, including *Canoparmelia*, *Cetrelia*, *Hypotrachyna*, *Melanelixia*, *Parmelia* s. str., *Parmotrema*, *Platismatia*, *Pseudevernia* and *Punctelia*.

For other *Didymocyrtis* species, conflicting information blurs species boundaries and makes the assessment of host specificity difficult. For example, *D. consimilis* is well-known mainly from the asexual stage (as syn. *Phoma caloplacae*) and has always been considered to be host specific on the *Caloplaca cerina* group. Our ITS analyses (Fig. 2), however, revealed the existence of populations on other hosts (*Cladonia pocillum*, *Heterodermia*, *Melanohalea exasperatula*) that are genetically almost identical (only one different position in the ITS alignment supports the separation of both groups, *D. consimilis* s. str. and *D. aff. consimilis* in Fig. 2). They are also morphologically similar, although conidia tend to be more elongate ellipsoid on hosts other than *Caloplaca* gr. *cerina*, and in culture some isolates look different from the others. It is impossible to tell if these specimens represent a single parasite species that colonizes a variety of host lichens or several host-specific parasites. Similarly, our ITS tree (Fig. 2) indicates that specimens identified as *Didymocyrtis epiphyscia* are nearly identical genetically but are found on *Physcia aipolia* (host of the type specimen), *P. adscendens*, *P. tenella* and *Xanthoria parietina*. In this species, however, there appear to be two morphologically distinct clusters, with specimens from *P. aipolia* having broad conidia and those from *P. adscendens*, *P. tenella* and *X. parietina* having narrow conidia. In this case, morphology would lead us to recognize two species on different lichen hosts, but the ITS sequencing results suggest that speciation may not yet have taken place.

Although we do not know with certainty the evolutionary processes responsible for the remarkable variation in *Didymocyrtis* host ecology, we assume that speciation by host switching is an important factor. If this is the case, our results appear to include examples of this process at various stages of development. Host switching is known to lead to speciation in mycoparasites (Chaverri and Samuels 2013), including lichenicolous species (Millanes et al. 2014) and is assumed to result from host-specific parasites occasionally exploiting alternative hosts in the habitat. Over time, it is speculated that this could have led to specialization on hosts different from the ancestral species and to the eventual isolation of distinct host-specific species.

Our results include specimens that might represent the earliest stages of this speciation process, most notably *Didymocyrtis epiphyscia* and *D. consimilis*, in which specimens from different hosts can sometimes be distinguished morphologically but with little or no genetic differentiation in ITS. We also recognize species that appear to have resulted from recent speciation initiated by a host switch. These include *D. slaptioniensis* (on *Xanthoria parietina*) and *D. xanthomendozae* (on *Xanthomendoza*), each of which is sufficiently distinct both morphologically and genetically to be recognized as species. Finally, *Didymocyrtis* includes clearly delimited species that are narrowly host-specific

(*D. ramalinae* and *D. pseudeverniae*), and other that are host-generalized (*D. cladoniicola*, *D. foliaceiphila* and *D. melanelixiae*). This wide variety of host-parasite interactions in *Didymocyrtis* species makes them especially attractive for investigations of speciation mechanisms and the causes of high or low host specialization in mycoparasites. Hypotheses based on our findings should be developed and tested with a higher number of specimens and using markers that are more informative than ITS.

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