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Camarosporium-like species are polyphyletic in *Pleosporales*; introducing *Paracamarosporium* and *Pseudocamarosporium* gen. nov. in *Montagnulaceae*

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Abstract – *Camarosporium* is a large coelomycetous genus which was formerly recognised as an asexual state in *Botryosphaeriales* and *Cucurbitariaceae*. In the present study, we collected several *Camarosporium*-like taxa in Europe (Germany and Italy) and carried out morpho-molecular analyses. Molecular analyses (maximum likelihood, maximum parsimony and MrBayes) of combined LSU and SSU gene datasets show that the *Camarosporium*-like taxa are polyphyletic in *Pleosporales*. *Camarosporium quaternatum*, the type species of *Camarosporium* clusters in the suborder *Pleosporinae* with five other *Camarosporium* species. This clade is supported by high bootstrap and PP values and is distinct from other well-established families in *Pleosporinae*. Other *Camarosporium*-like taxa grouped in *Montagnulaceae* (*Massarineae*) as two phylogenetically distinct clades and are introduced as two new genera, *viz*. *Paracamarosporium* and *Pseudocamarosporium*. *Paracamarosporium* is morphologically distinct as it has paraphyses and microconidia, while *Pseudocamarosporium* lacks both of these characters. Since *Camarosporium* comprises a large number of species epithets, re-collection and morpho-molecular studies of other *Camarosporium*-like taxa is essential.

Coelomycetes / *Massarineae* / Multi-gene analyses / Phylogeny / *Pleosporinae*

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INTRODUCTION

Camarosporium Schulzer was established by Schulzer (1870) based on *C. quaternatum* (Hazsl.) Schulz. and presently comprises more than 500 species epithets (Index Fungorum, 2014). Members of *Camarosporium* spp. have a worldwide distribution and commonly inhabit branches and leaves as saprobes of a wide range of hosts (Sutton, 1980; Farr & Rossman, 2014). Taylor *et al.* (2001) reported on *Camarosporium* species associated with leaf spots of *Protea cynaroides* but suggested they were not economically important phytopathogens. However, *Camarosporium* has received attention in taxonomic studies as the genus was considered heterogeneous in morphology (Sutton, 1980). Taxonomic notes of *Camarosporium* and other muriform genera (such as *Coryneum*, *Dichomera*), based on morphology, have been undertaken by Sutton & Pollack (1974) and Sutton (1975, 1977, 1980). With the implementation of molecular techniques in fungal taxonomy profound changes have taken place in our understanding of the fungi and are resulting in a natural classification based on morphology as well as molecular data (Chomnunti *et al.,* 2011; Boonmee *et al.,* 2012; Wijayawardene *et al.,* 2014a). Molecular studies on the phylogenetic placement of the genus and species of *Camarosporium* have been carried out by Wijayawardene *et al*., (2014b) and showed that *Camarosporium sensu stricto* belongs to *Pleosporinae* (*Pleosporales*). Since there are several muriform coelomycetes which are morphologically similar to *Camarosporium* (Sutton, 1980) it is important to resolve generic boundaries based on molecular data analyses and incorporate them into a natural classification system (Wijayawardene *et al.,* 2013c).

We collected several *Camarosporium*-like species from Europe (Germany and Italy) and these were subjected to morpho-molecular study. Mega blast searches of LSU and SSU sequence data showed three species were linked with *Camarosporium quaternatum*, the type species of *Camarosporium* (in *Pleosporinae, Pleosporales*), while other strains were related to *Montagnulaceae*, *Massarineae.* In this paper, the placement of *Camarosporium sensu stricto* in *Pleosporinae* is confirmed and the six other *Camarosporium*-like species are placed in the new genera *Paracamarosporium* and *Pseudocamarosporium* in *Montagnulaceae* (*Massarineae, Pleosporales*) which are introduced herein, based on molecular and morphological study.

MATERIALS AND METHODS

Collecting, morphological studies and isolation: Fresh decaying plant materials were collected from several localities in Germany and Italy, placed in paper bags and returned to laboratory. Conidiomata on fresh samples were observed under a stereomicroscope and removed using a sterilised needle and placed in a droplet of distilled water on a clean slide. Conidial structures (i.e. conidiophores, conidiogenous cells and conidia) were examined under a compound microscope (Nikon Eclipse 80i compound microscope fitted with a Canon 450D digital camera). Single conidial isolation was carried out as described in Chomnunti *et al.* (2011). Germinating conidia were transferred aseptically to potato dextrose agar (PDA) plates and grown at 18°C. Colony colour and other characters were

assessed after 1 week. The specimens are deposited in the herbarium of Mae Fah Luang University (MFLU), Chiang Rai, Thailand, New Zealand Fungal & Plant Disease Collection, Landcare Research, New Zealand (PDD) and Guizhou University Fungi Collection (GUFC). Living cultures are deposited at the Culture Collection at Mae Fah Luang University (MFLUCC), Landcare Research, New Zealand (ICPM) and Department of Plant Pathology, Agriculture College, Guizhou University, China (GUCC).

DNA extraction, PCR amplification and sequencing: Colonies generated from single spores were grown on PDA for 7-14 days at 18°C. Fresh fungal mycelia were used to extract genomic DNA by using a BIOMIGA Fungus Genomic DNA Extraction Kit (GD2416) (Wijayawardene *et al.,* 2013a, b). The amplification of rDNA regions of the internal transcribed spacers (ITS), small subunit rDNA (SSU) and large subunit (LSU) genes was carried out by using ITS5 and ITS4, NS1 and NS4 and LROR and LR5 (White *et al.,* 1990; Vilgalys & Hester, 1990) primers. Optimum conditions for amplification of ITS and LSU regions are as described in Alves *et al*. (2004, 2005) and for SSU region as described in Phillips *et al*. (2008). Amplified PCR fragments were checked on 1% agarose electrophoresis gels stained with ethidium bromide. Purified PCR products (by minicolumns, purification resin and buffer according to the manufacturer's protocols Amersham product code: 27-9602-01) were sent to SinoGenoMax Co., Beijing, China for DNA sequencing. The nucleotide sequence data obtained are deposited in GenBank (Table 1).

Table 1. Strains used in this study. Type strains are in bold and newly generated sequences are in bold and marked with an asterisk

Taxon	*Culture collection number*	*GenBank Accession number*		
		LSU	*SSU*	*ITS*
Alternaria alternata	CBS 916.96		KC584507	
Ampelomyces quisqualis	CBS 129.79	EU754128	EU754029	
Bambusicola bambusae	MFLUCC 11-0614	JX442035	JX442039	JX442031
Bambusicola massarinia	MFLUCC 11-0389	JX442037	JX442041	JX442033
Bambusicola splendida	MFLUCC 11-0439	JX442038	JX442042	JX442034
Bimuria novae-zelandiae	CBS 107.79	AY016356	AY016338	
Camarosporium aloes	CPC 21572	KF777198		
Camarosporium clematidis	MFLUCC 13-0336	KJ724249		
Camarosporium elongata	AFTOL-ID 1568	DQ678061	DQ678009	
Camarosporium elongata	MFLUCC 14-0260	KJ724249		
Camarosporium quaternatum	CBS 483.95	GU301806	GU296141	
Camarosporium robinium	MFLUCC 13-0527			
Camarosporium sp.	CPC 12441	DQ377885		
Camarosporium spartii	MFLUCC 13-0548			
Cochliobolus heterostrophus	AFTOL-ID 54	AY544645	AY544727	
Cochliobolus sativus	AFTOL-ID 271	DQ678045	DQ677995	
Coniothyrium palmarum	CBS 400.71	EU754153	EU754054	
Coniothyrium palmarum	CBS 758.73	EU754154	EU754055	
Cucurbitaria berberidis	CBS 394.84	GQ387605	GQ387544	

Table 1. Strains used in this study. Type strains are in bold and newly generated sequences are in bold and marked with an asterisk *(continued)*

Taxon	*Culture collection number*	*GenBank Accession number*		
		LSU	*SSU*	*ITS*
Cucurbitaria berberidis	MFLUCC 11-0384	KC506793		
Cucurbitaria berberidis	MFLUCC 11-0385	KC506794		
Decorospora gaudefroy	CBS 332.63	EF177849	AF394542	
Deniquelata barringtoniae	MFLUCC 110422			
Didymella exigua	CBS 183.55	JX681089	GU296147	GU237794
Didymella pisi	CBS 126.54	GU237968	EU754038	
Didymocrea sadasivanii	CBS 438.65	DQ384103	DQ384074	
Dothidotthia aspera	CPC 12933	EU673276	EU673228	
Dothidotthia symphoricarpi	CPC 12929	EU673273	EU673224	
Halomassarina thalassiae	JK 5385B	GU479804		
Halomassarina thalassiae	JK 5262D	GU301816		
Helicascus nypae	BCC 36752	GU479789	GU479755	
Julella avicenniae	BCC 20173	GU371822	GU371830	
Julella avicenniae	BCC 18422	GU371823	GU371831	
Kalmusia brevispora	KT 1466	AB524600	AB524459	
Kalmusia ebuli	CBS 123120	JN644073	JN851818	
Karstenula rhodostoma	CBS 690.94	GU301821	GU296154	
Lentithecium aquaticum	CBS 123099	GU301823	GU296156	
Lentithecium arundinaceum	CBS 619.86	GU301824	GU296157	
Lentithecium fluviatile	CBS 122367	GU301825	GU296158	
Leptosphaeria doliolum	CBS 541.66	JF740284		
Leptosphaeria doliolum	CBS 155.94	JF740282		
Leptosphaeria doliolum	CBS 125979	JF740283		
Leptosphaeria errabunda	CBS 617.75	JF740289		
Leptosphaeria sydowii	CBS 385.80	JF740313		
Leptosphaerulina australis	CBS 317.83	GU301830	GU296160	
Massarina cisti	CBS 266.62	FJ795447	FJ795490	
Massarina eburnea	CBS 473.64	GU301840	GU296170	
Montagnula anthostomoides	CBS 615.86	GU205223	GU205246	
Montagnula anthostomoides	CBS 615.86	GU205223	GU205246	
Montagnula opulenta	CBS 168.34	NG_027581		
Morosphaeria ramunculicola	JK 5304B	GU479794	GU479760	
Neottiosporina paspali	CBS 331.37	EU754172	EU754073	
Ophiosphaerella herpotricha	AFTOL-ID 1595	DQ767656	DQ767650	
Paracamarosporium psoraleae	CPC 21632	KF777199		KF777143
Paraconiothyrium estuarinum	CBS 109850		AY642522	AY642530
Paraconiothyrium fuscomaculans	CBS 116.16	EU754197	EU754098	
Paraconiothyrium minitans	CBS 122786	EU754174	EU754075	
Paraconiothyrium minitans	CBS 122788	EU754173	EU754074	

Table 1. Strains used in this study. Type strains are in bold and newly generated sequences are in bold and marked with an asterisk *(continued)*

Taxon	*Culture collection number*	*GenBank Accession number*		
		LSU	*SSU*	*ITS*
Paraphaeosphaeria michotii	CBS 652.86	GQ387581	GQ387520	
Paraphaeosphaeria michotii	CBS 652.86	GQ387581	GQ387520	
Paraphaeosphaeria michotii	CBS 591.73	GU456326	GU456305	
Paraphoma fimeti	CBS 170.70	GQ387584	GQ387523	
Peyronellaea zeae-maydis	CBS 588.69	EU754192	EU754093	
Phaeosphaeria nodorum	CBS 110109	EU754175	EU754076	
Phaeosphaeria oryzae	CBS 110110	GQ387591	GQ387530	
Phoma herbarum	CBS 615.75	EU754186	EU754087	
Pleospora calvescens	CBS 246.79	EU754131	EU754032	
Pleospora herbarum	CBS 191.86	GU238160	GU238232	
Pleospora typhicola	CBS 132.69	JF740325	JF740105	
Pseudocamarosporium corni*	**MFLUCC 13-0541**	**KJ813279***	**KJ819946***	**KJ747048***
Pseudocamarosporium lonicerae*	**MFLUCC13-0532**	**KJ813278***	**KJ819947***	**KJ747047***
Pseudocamarosporium piceae*	**MFLUCC14-0192**	**KJ803030***	**KJ819948***	**KJ747046***
Pseudocamarosporium propinquum*	**MFLUCC 13-0544**	**KJ813280***	**KJ819949***	**KJ747049***
Pseudocamarosporium tilicola*	**MFLUCC 13-0550**	**KJ813281***	**KJ819950***	**KJ747050***
Pyrenochaeta acicola	CBS 122789	EU754204	EU754204	
Pyrenochaeta nobilis	CBS 407.76	EU754206	EU754107	
Pyrenochaeta quercina	CBS 115095	GQ387619	GQ387558	
Pyrenochaetopsis decipiens	CBS 343.85	GQ387624	GQ387563	
Pyrenochaetopsis leptospora	CBS 101635	GQ387627	GQ387566	
Pyrenophora phaeocomes	AFTOL-ID 283	DQ499596		
Pyrenophora phaeocomes	AFTOL-ID 283	DQ499596	DQ499595	
Pyrenophora tritici-repentis	AFTOL-ID 173	AY544716	AY544672	
Trematosphaeria pertusa	CBS 122368	FJ201990	FJ201991	
Wojnowicia hirta	CBS 160.73	EU754222	EU754123	

Phylogenetic analyses: A blast search was carried out to reveal the closest taxa to our strains. The sequences were downloaded from GenBank and aligned separately using Bioedit (Hall, 2004), ClustalX v. 1.83 (Thompson *et al.,* 1997) and MEGA 5 (Tamura *et al.,* 2011). Further improvements of the data set were carried out in MAFFTv6 (Katoh *et al.,* 2002; Katoh & Toh, 2008), online sequence alignment editor under the default settings (mafft.cbrc.jp/alignment/server/) and alignments were checked and manual adjustments were made wherever necessary. Then the individual datasets finally combined into one dataset. One hundred thorough maximum likelihood was performed in RAxML 7.2.8 as part of the "RAxML-HPC2 on TG" tool (Stamatakis, 2006) implemented in raxmlGUI v.0.9b2 (Silvestro & Michalak, 2010). Maximum-parsimony (MP) analysis was carried out using PAUP v. 4.0b10 (Swofford, 2002). Posterior probabilities (PP) (Rannala & Yang, 1996; Zhaxybayeva & Gogarten, 2002) were valued by Markov Chain Monte Carlo sampling (BMCMC) in MrBayes v. 3.0b4 (Huelsenbeck & Ronquist, 2001).

RESULTS

Phylogenetic analyses: Combined analyses of LSU and SSU dataset of families in suborders of *Pleosporales* i.e. *Pleosporinae* (*Coniothyriaceae, Cucurbitariaceae, Didymellaceae, Dothidotthiaceae, Leptosphaeriaceae, Phaeosphaeriaceae* and *Pleosporaceae*) and *Massarineae* (*Bambusicolaceae, Lentitheciaceae, Massarinaceae, Montagnulaceae, Morosphaeriaceae, Julellacaeae* and *Trematosphaeriaceae*) (Zhang *et al.,* 2012; Hyde *et al.,* 2013) were used to carry out phylogenetic analyses (Table 1). A separate data set which comprised LSU, SSU and ITS sequence data was used to show the placement of new genera and new species in *Montagnulaceae*. A heuristic search with random addition of taxa (1000 replicates) and gaps are treated as missing characters. Bootstrap support (BS) values of MP and ML (equal or above 50 %) are shown on the upper branches and PP values (equal or above 0.7) from MCMC analyses are shown under the branches.

Combined gene (LSU and SSU) analyses for Pleosporinae: The combined LSU and SSU data set consists of 43 taxa with the outgroup taxa i.e. *Corynespora cassiicola* (CBS 100822) and *C. smithii* (CABI 5649b). The data set consists of 2683 (LSU = 1285 bp and 1390 bp) characters after alignment of which 2642 are included in ML, MP and Bayesian analyses. We have carried out Bayesian analysis for *Pleosporinae* group as some nodes are not supported with higher bootstrap values in MP and ML analyses. Of the included bases, 2350 sites are conserved regions while 292 and 160 sites are variables and parsimony informative respectively.

Camarosporium quaternatum (CBS 483.95), the type species of *Camarosporium* groups with other *Camarosporium* spp. *viz*. *C. aloes* (CPC 21572 *fide* Crous *et al.,* 2013), *C. clematidis* (MFLUCC 13-0336 *fide* Wijayawardene *et al.,* 2014b), *C. robiniicola* (MFLUCC 13-0527 *fide* Wijayawardene *et al.,* 2014b), *C. spartii* (MFLUCC 13-0548 *fide* Wijayawardene *et al.,* 2014b) and *Camarosporium* sp. (CPC 12441 *fide* Crous *et al.,* 2006) in a separate clade. This clade is supported by moderate bootstrap values (75% in ML analysis) and high PP value (1.00). This clade is distinct from *Cucurbitariaceae* and *Leptosphaeriaceae* where *Camarosporium* was previously stated to be the asexual state (Schoch *et al.,* 2009; Doilom *et al.,* 2013). *Cucurbitaria elongata* (AFTOL-ID 1568 *fide* Schoch *et al.,* 2006; MFLUCC 14-0260 *fide* Wijayawardene *et al.,* 2014b) however, also cluster in the *Camarosporium* clade and thus is introduced as a new combination.

Combined gene (LSU and SSU) analyses for Massarineae: The combined LSU and SSU data set consists of 27 taxa with *Pleospora herbarum* (CBS 191.86) as the outgroup taxon. The data set consists of 2819 characters (LSU = 1310 bp and SSU = 1500 bp) after alignment of which 2735 are included in ML and MP analyses. Of the included bases, 2191 sites are conserved regions, while 544 and 261 sites are variables and parsimony informative respectively.

Our new collections of *Camarosporium*-like taxa and *Camarosporium psoraleae* (CPC 21632 *fide* Crous *et al.,* 2013) cluster in *Montagnulaceae* (Fig. 2).

Combined gene (LSU, SSU and ITS) analyses for Montagnulaceae: The combined LSU, SSU and ITS data set used to show the generic placement of *Montagnulaceae*. The data set consists of 22 taxa with *Julella avicenniae* (BCC 18422 and BCC 20173) as the outgroup taxon. The data set consists of 3330 characters (LSU = 1284 bp, SSU = 1501 bp and ITS = 545 bp) after alignment of which 2880 are included in ML and MP analyses. Of the included bases,

2525 sites are conserved regions, while 355 and 175 sites are variables and parsimony informative respectively.

Clade 1 in Figure 3 comprises our five strains of *Camarosporium*-like taxa and this clade is not related with *Camarosporium sensu stricto*. Hence *Pseudocamarosporium* which has high bootstrap values (ML: 99% and MP: 100%) is introduced to accommodate these taxa. *Pseudocamarosporium* comprises with five species *viz*. *P. corni*, *P. lonicerae*, *P. piceae*, *P. propinquum* (≡ *Camarosporium propinquum* (Sacc.) Sacc.) and *P. tiliicola*.

Camarosporium psoraleae (CPC 21632 *fide* Crous *et al.,* 2013) distinct from *Camarosporium sensu stricto* (*Pleosporinae*) is placed in *Montagnulaceae* (Clade 1, Fig. 3). However, it has a distinct phylogenetic lineage from *Pseudocamarosporium*, hence we introduce *Paracamarosporium* as a new genus.

TAXONOMY

In multi-gene analyses of *Pleosporinae* (Fig. 1), *Cucurbitaria elongata* (AFTOL-ID 1568 *fide* Schoch *et al.,* 2006; MFLUCC 14-0260) cluster in *Camarosporium sensu stricto* clade.

Camarosporium elongata (Fr.) Grev. Ex. Wijayawardene & K.D. Hyde **comb. nov.**

Index Fungorum Number: IF550571

≡ *Cucurbitaria elongata* (Fr.) Grev., Scott. crypt. fl. (Edinburgh) 4(37-48): pl. 195 (1826) [1825]

= *Cucurbitaria elongata* var. *coronillae* Fuckel, Jb. nassau. Ver. Naturk. 23-24: 174 (1870) [1869-70]

= *Cucurbitaria elongata* (Fr.) Grev., Scott. crypt. fl. (Edinburgh) 4(37-48): pl. 195 (1826) [1825] var. *elongata*

= *Gibberidea elongata* (Fr.) Kuntze, Revis. gen. pl. (Leipzig) 3(2): 481 (1898)

= *Sphaeria elongata* Fr., Observ. mycol. (Havniae) 1: 175 (1815)

Illustrations: Hyde *et al.,* 2013 (Figure 32, a-i, illustrated as *Cucurbitaria elongata* (Fr.) Grev.)

Notes: Our molecular data analyses (Figs 1 & 2) show *Camarosporium*-like taxa are polyphyletic in *Pleosporales*. *Camarosporium sensu stricto* groups in *Pleosporinae* while other taxa group as two distinct sub-clades in *Massarineae*. One clade comprises five species hence *Pseudocamarosporium* is introduced to accommodate them. The second clade comprises one strain thus *Paracamarosporium* is introduced to accommodate it.

Paracamarosporium Wijayawardene & K.D. Hyde **gen. nov.**

Index Fungorum Number: IF550563

Etymology: Named after its morphological similarity to the genus *Camarosporium*

Saprobic on dead branches and stems of *Psoralea pinnata* (*Fabaceae*). **Sexual state:** Not observed. **Asexual state:** *Conidiomata* immersed to erumpent, solitary, globose, with wall of 3-6 layers of brown cells of *textura angularis*, with central ostiole. *Paraphyses* hyaline, hyphae-like, smooth, intermingled among conidiogenous cells, subcylindrical, with bulbous base, tapering to obtuse apex, 1-4-septate, unbranched or branched at base, and anastomosing. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* lining the inner cavity,

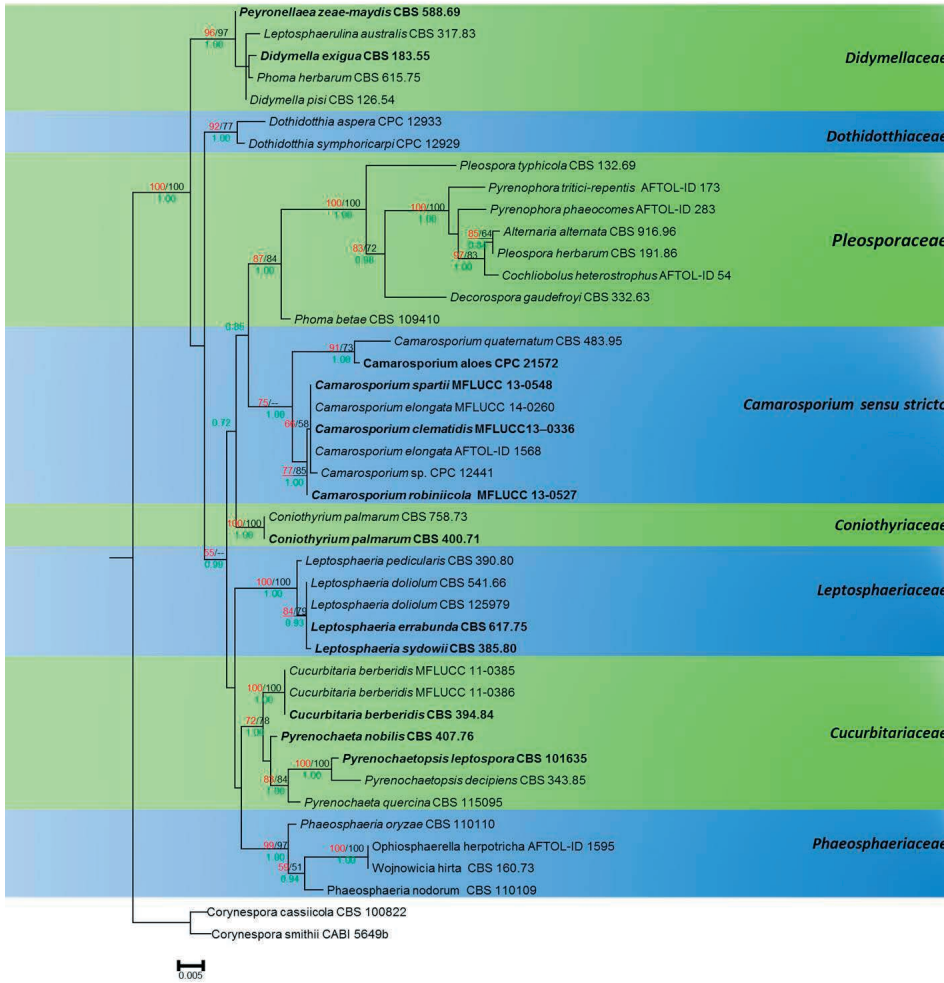

Fig. 1. The best scoring RAxML tree from 43 strains based on combined dataset of LSU and SSU sequences. Bootstrap support values for maximum-likelihood (ML) and maximum-parsimony (MP) greater than 50% are given above the nodes. Posterior Probability values (PP) equal to or greater than 0.7 are given below the nodes. The culture collection numbers are given after the species names. The tree is rooted to *Corynespora smithii* (CABI 5649b) and *C. smithiicola* (CBS 100822). Type and extype strains are in bold.

globose to doliiform, hyaline, smooth, phialidic with prominent periclinal thickening and thick channel (at times also with percurrent proliferation). *Conidia* brown, finely roughened, ellipsoid to ovoid, with obtuse ends, 1-3 transversely septate, developing 1-6 oblique to transverse septa, at times becoming constricted at primary septa. *Microconidiogenous* cells intermingled among macro conidiogenous cells, hyaline, smooth, ampulliform to doliiform to irregular, mono- to polyphialidic, proliferating percurrently, or with periclinal thickening. *Microconidia* hyaline, smooth, guttulate, bacilliform to subcylindrical, apex obtuse, base truncate (Description based on Crous *et al.,* 2013).

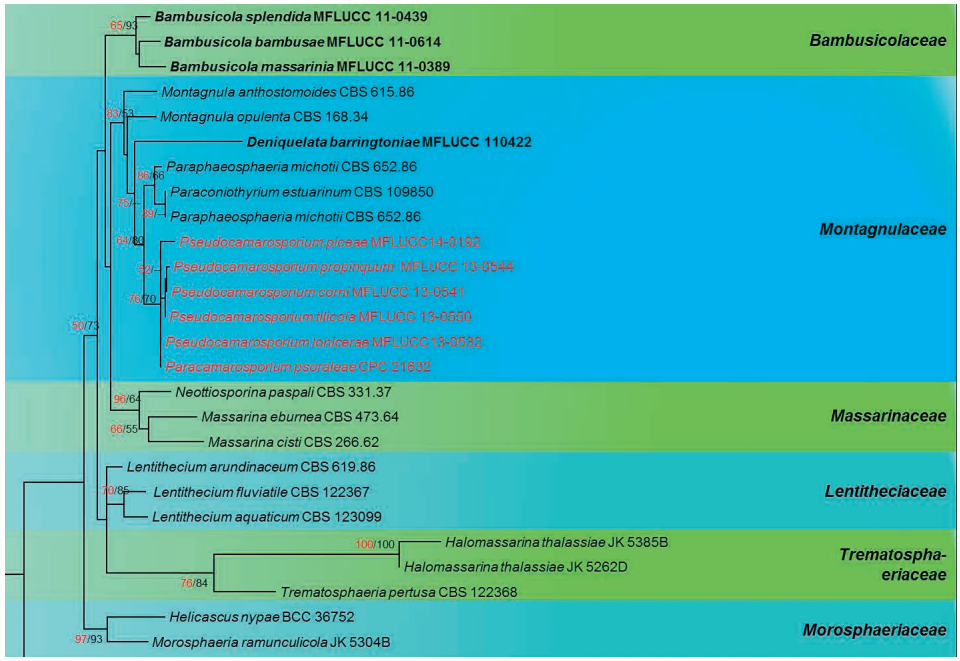

Fig. 2. The best scoring RAxML tree from 27 strains based on combined LSU and SSU dataset. Bootstrap support values for maximum-likelihood (ML) and maximum-parsimony (MP) values equal to greater than 50% are given above the nodes. The culture collection numbers are given after the species names. The tree is rooted to *Pleospora herbarum* (CBS 191.86). Type and extype strains are in bold and newly introduced taxa are in red.

Notes: *Paracamarosporium* shows similar conidial morphology with *Camarosporium sensu stricto* (Crous *et al.*, 2013), but *Camarosporium sensu stricto* lack paraphyses and microconidia (Sutton, 1980; Wijayawardene *et al.*, 2014b). The molecular data (Fig. 3) shows it is unrelated with *Camarosporium sensu stricto* and clusters in *Montagnulaceae*.

Type species: ***Paracamarosporium psoraleae*** (Crous & M.J. Wingf.) Wijayawardene & K.D. Hyde **comb. nov.**

Index Fungorum Number: IF 550562

≡ *Camarosporium psoraleae* Crous & M.J. Wingf., in Crous *et al.* Persoonia, Mol. Phyl. Evol. Fungi 31: 235 (2013)

Type: South Africa, Western Cape Province, Betty's Bay, Harold Porter National Botanical Garden, on stems of *Psoralea pinnata* (*Fabaceae*), 28. October 2012, M.J. Wingfield (holotype CBS H-21440, culture ex-type CPC 21632 = CBS 136628.

Illustrations: Crous *et al.* 2013 (Fungal Planet 181, illustrated as *Camarosporium psoraleae* Crous & M.J. Wingf.)

Pseudocamarosporium Wijayawardene & K.D. Hyde **gen. nov.**

Index Fungorum Number: IF 550556; *Facesoffungi number*: 00007

Etymology. Named after its morphological similarity to the genus *Camarosporium*

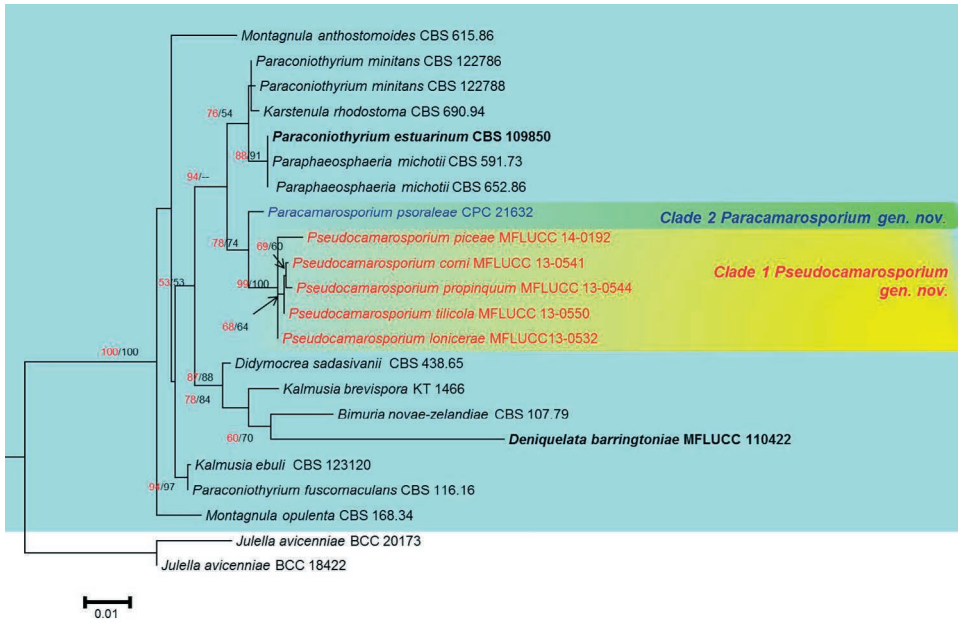

Fig. 3. The best scoring RAxML tree from 22 strains based on LSU, SSU and ITS combined dataset. Bootstrap support values for maximum-likelihood (ML) and maximum-parsimony (MP) values equal to or greater than 50% are given above the nodes. The culture collection numbers are given after the species names. The tree is rooted to *Julella avicenniae* (BCC 18422 and BCC 20173). Type and ex-type strains are in bold and newly introduced taxa are in red (*Pseudocamarosporium*) and blue (*Paracamarosporium*).

Saprobic on dead twigs, branches, cones and stems of various plants. **Sexual state:** Not observed. **Asexual state:** *Conidiomata* pycnidial, black, globose to subglobose, unilocular, immersed, scattered to gregarious, thick-walled, brown to dark brown, with central and papillate ostiole. *Conidiophores* reduced to conidiogenous cell. *Conidiogenous cell* simple, short, hyaline, thin-walled, discrete to integrated, blastic, phialidic with percurrent proliferation. *Conidia* oblong, muriform, with transverse, longitudinal and oblique septa, generally with a truncate base and obtuse apex, varying in shape, brown to dark brown, smooth-walled.

Notes: In conidial morphology, *Pseudocamarosporium* is similar with *Camarosporium sensu stricto* as both genera have muriform conidia and lack pseudoparaphyses. In *Camarosporium*, conidiogenesis is annelidic, while in *Pseudocamarosporium* conidiogenesis is phialidic, but proliferating. Therefore it is quite difficult to distinguish between these two genera based on morphology. *Pseudocamarosporium* is distinct from *Paracamarosporium* in the molecular analyses (Fig. 3) and in morphology. *Paracamarosporium* differs as it has paraphyses and microconidia which are lacking in *Pseudocamarosporium*. We designate *Pseudocamarosporium propinquum* (Sacc.) Sacc. ex. Wijayawardene *et al.* (≡ *Camarosporium propinquum* (Sacc.) Sacc.) as the type species (Saccardo, 1884).

Pseudocamarosporium corni Wijayawardene, E. Camporesi & K.D. Hyde **sp. nov.** **Fig. 4**

Index Fungorum Number: IF 550557; *Facesoffungi number*: 0008
Holotype: MFLU 14-0089
Etymology: Named after the generic name of host, *Cornus*

Saprobic on dead branch of *Cornus sanguinea.* **Sexual state:** Not observed. **Asexual state:** *Conidiomata* pycnidial, 180-270 µm diam., 190-250 µm high, gregarious, dark brown, immersed, unilocular, with centrally located papillate ostiole. *Pycnidial wall* multilayered, outer layer with 1-3 brown walled cells of *textura angularis*, inner wall with 1-4 layers, hyaline. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* enteroblastic, phialidic, percurrently proliferating, smooth, short, hyaline to pale brown. *Conidia* 11-16 × 6-8 µm ($\bar{x}$ = 13.4 × 7.2 µm, n = 20), oblong to ellipsoidal, mostly straight, rarely slight curved, muriform, with 1-3 transverse septa, with 1-2 longitudinal septa, occasionally widest at the middle, brown, smooth-walled.

Culture characteristics: on PDA white from above and very light brown from reverse, with thin mycelium, flat, attaining a diam of 2.5 cm in 7 days at 18°C.

Material examined: Italy, Arezzo Province, Porrena-Poppi, on dead branch of *Cornus sanguinea* L. (*Cornaceae*), 10 March 2013, E. Camporesi, NNW IT 1108 (MFLU 14-0089, **holotype**; isotype PDD 104440), ex-type living culture = MFLUCC 13-0541 = ICMP 20369 = GUCC 0010.

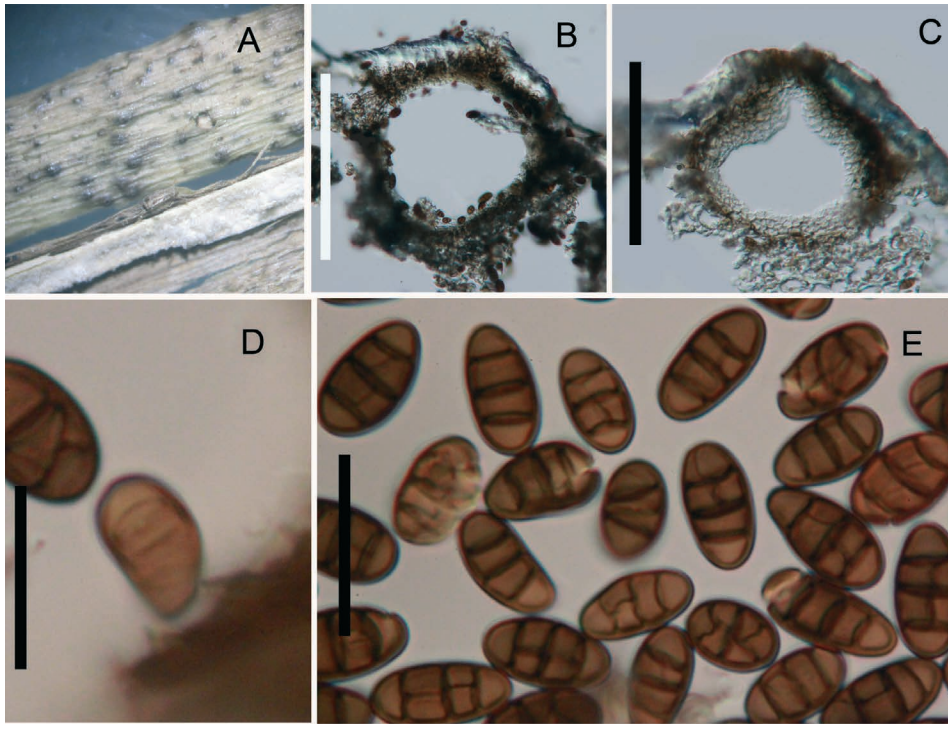

Fig. 4. *Pseudocamarosporium corni* (**holotype**). **A.** Conidiomata on *Cornus sanguinea*. **B, C.** Cross section of pycnidia. **D.** Developing conidium attach to conidiogenous cell. **E.** Conidia. Scale bar: **B, C.** 200 µm; **D, E.** 15 µm.

Notes: Hüseyinov (1968) reported *Camarosporium corni-maris* Hüseyın from *Cornus sanguinea* which has larger conidia (40-64 × 16-23.5 µm). Our collection has smaller conidia and molecular data analyses (Figs 2 & 3) show that, it clusters in *Montagnulaceae* and not *Camarosporium sensu stricto* (Fig. 1). Hence we introduce it as a new species in *Pseudocamarosporium.*

Pseudocamarosporium lonicerae Wijayawardene, E. Camporesi & K.D. Hyde **sp. nov.** **Fig. 5**

Index Fungorum Number: IF 550558; *Facesoffungi number*: 000018

Etymology: Named after the host, *Lonicera*

Holotype: MFLU 14-0091

Saprobic on stems of *Lonicera* sp. **Sexual state:** Not observed. **Asexual state:** *Conidiomata* pycnidial, 160-180 µm diam., 140-160 µm high, solitary, dark brown, immersed, unilocular, with a papillate ostiole. *Pycnidial wall* multilayered, with 3-4 outer layers of brown-walled cells of *textura angularis*, inner layer with hyaline cells. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* enteroblastic, with percurrent phialidic development, hyaline, smooth, formed on the inner layer of pycnidium wall. *Conidia* 12-19 × 5-7 µm ($\bar{x}$ = 15.3 × 4.6 µm, n = 20), oblong, mostly straight, rarely slightly curved at the base, muriform, with 3 transverse septa, with 1-2 longitudinal septa, guttulate when young, pale brown to brown at maturity, smooth-walled.

Culture characteristics: on PDA white from above and pale brown from reverse, cicular, flat, slow growing, attaining a diam of 2 cm in 7 days at 18°C.

Material examined: Italy, Forlì-Cesena Province, Forlì, Via del Partigiano, on stem of *Lonicera* sp. (*Caprifoliaceae*), 09 March 2013, E. Camporesi, NNW IT 1104 (MFLU 14-0091, **holotype**; isotype PDD 104438), living culture MFLUCC 13-0532 = ICMP 20370 = GUCC 0011.

Notes: Several *Camarosporium* species have been recorded from *Lonicera* sp. *viz*. *C. caprifolii* Brunaud (12-15 × 5-6 *fide* Brunaud, 1887), *C. lonicerae* S. Ahmad (22-26 × 7.5-9 µm *fide* Ahmad, 1971), *C. periclymeni* Oudem. (16-20 × 6-7 *fide* Oudemans, 1898), *C. polymorphum* (De Not.) Sacc. (10 × 8 *fide* Saccardo, 1884) and *C. xylostei* Sacc. (18-20 × 8 *fide* Saccardo, 1884). *Camarosporium caprifolii* has conidia of similar size to our collection, but with only one longitudinal septum (Brunaud, 1887). Molecular data analyses show that our taxon is not congeneric with *Camarosporium sensu stricto* (Figs 1 and 2). Hence we introduce our collection as a new species in *Pseudocamarosporium*.

Pseudocamarosporium piceae Wijayawardene, E. Camporesi & K.D. Hyde **sp. nov.** **Fig. 6**

Index Fungorum Number: IF 550559; *Facesoffungi number*: 000019

Etymology: Named after the host genus, *Picea*

Holotype: MFLU 14-0090

Saprobic on cones of *Picea excels.* **Sexual state:** Not observed. **Asexual state:** *Conidiomata* pycnidial, 120-140 µm diam., 110-130 µm high, mostly immersed, unilocular, solitary, scattered, moderately brown, dark brown at ostiolar papilla. *Pycnidial wall* multilayered, with 3-4 outer wall layers of dark brown cells of *textura angularis*, with inner layer with hyaline cells. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* formed from the inner layer of pycnidial wall, enteroblastic, with percurrent phialidic development, smooth, hyaline. *Conidia* 10-13 × 6-7 µm ($\bar{x}$ = 12.2 × 6.4 µm, n = 20), oblong, muriform,

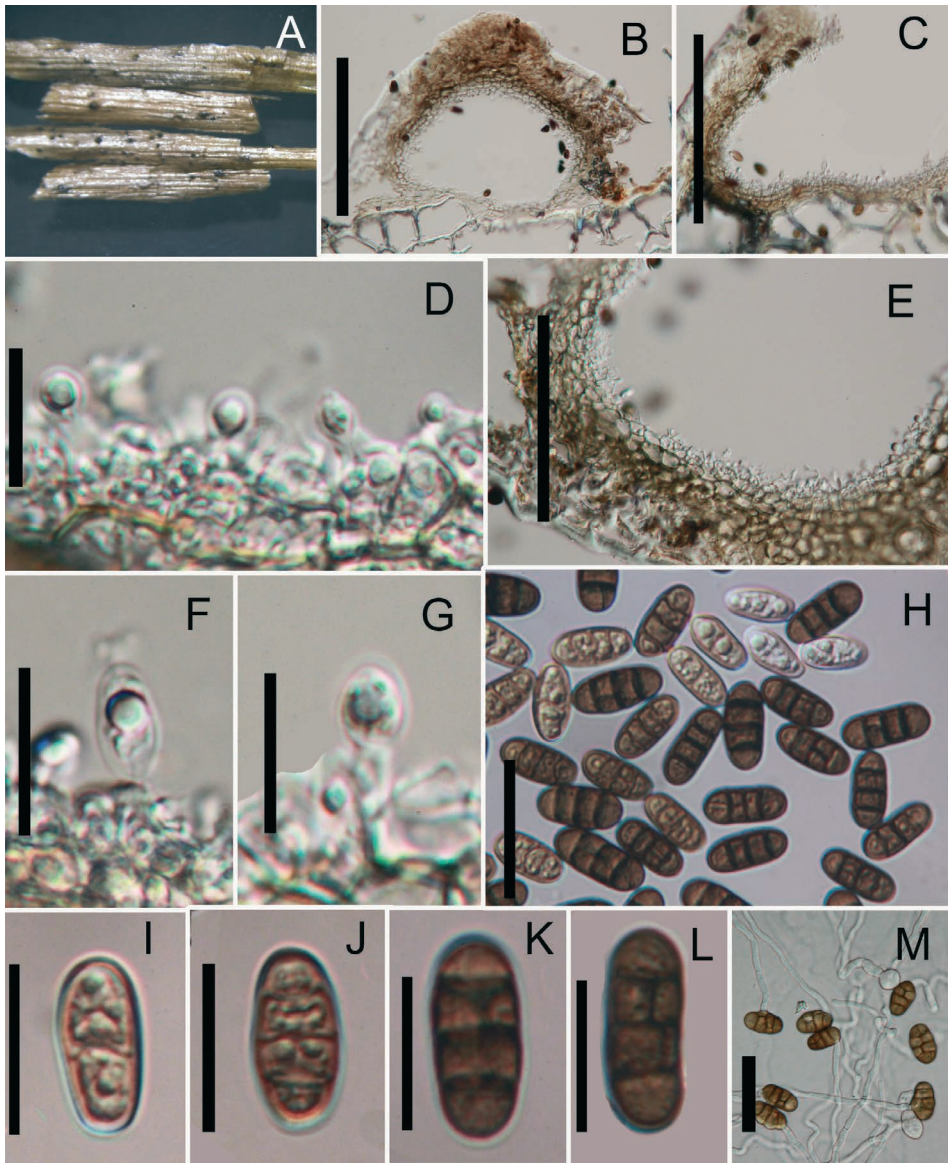

Fig. 5. *Pseudocamarosporium lonicerae* (**holotype**). **A.** Conidiomata on *Lonicera* sp. **B, C.** Cross sections of pycnidium. **D, F, G.** Developing conidia attached to conidiogenous cells. **E.** Pycnidium wall. **H-L.** Conidia. M. Germinating conidia. Scale bar: **B, C.** 150 µm; **D, F, G.** 15 µm; **E** 75 µm; **H.** 20 µm, **I-L.** 15 µm; **M.** 20 µm.

broadly rounded at both ends, with 3 transverse and 1 longitudinal septa, smooth, variable in shape, hyaline when young, dark brown at maturity, smooth-walled.

Cultural characteristics: on PDA white to very light brown from above and reverse, with sparse mycelium, zonate, flat, circular, attaining a diam of 3.5 cm in 7 days at 18°C, reverse become dark green to black in 14 days.

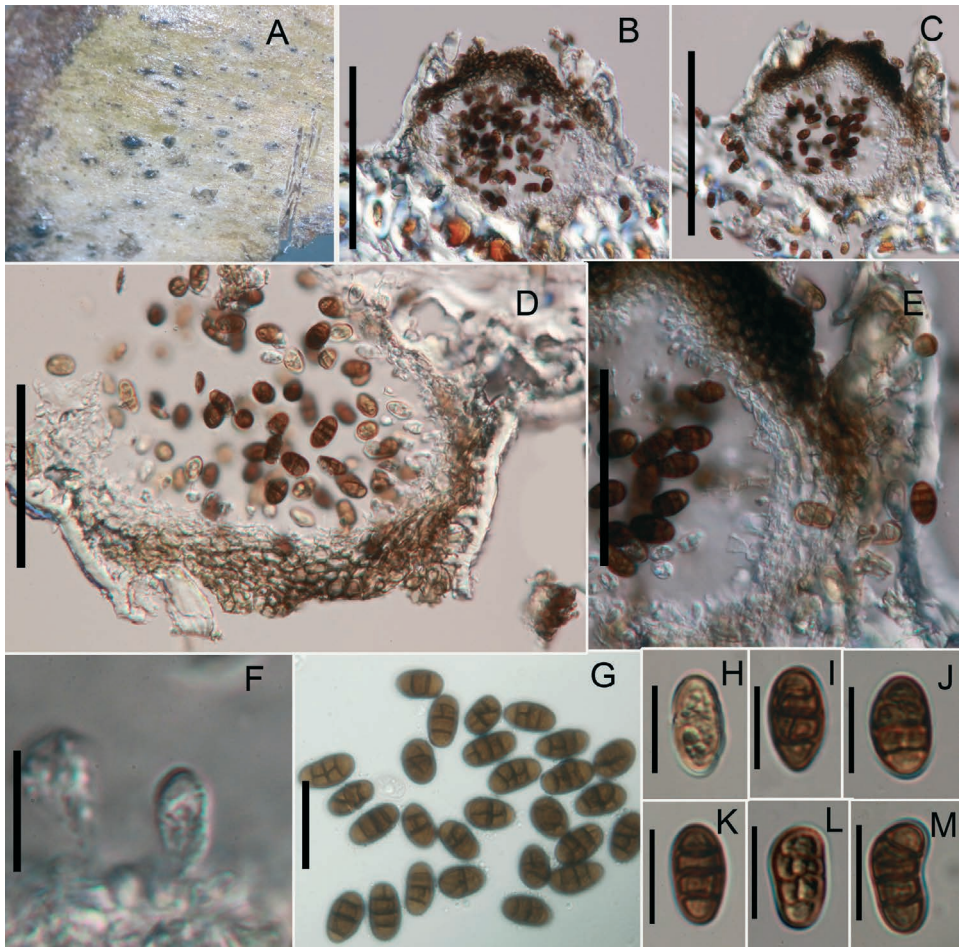

Fig. 6. *Pseudocamarosporium piceae* (**holotype**). **A.** Conidiomata on dead cone of *Picea excels.* **B, C.** Cross sections of pycnidium. **D, E.** Pycnidium wall. **F.** Developing conidia attach to conidiogenous cell. **G-M.** Conidia. Scale bar: **B, C.** 120 µm; **D, E.** 50 µm; **F-M.** 10 µm.

Material examined: Italy, Forlì-Cesena Province, San Martino-Predappio, on dead cones of *Picea excels* (*Pinaceae*), 25 March 2012, E. Camporesi, NNW IT 308 (MFLU 14-0090, **holotype**; isotype PDD 104439), living culture MFLUCC 14-0192 = ICMP 20203 = GUCC 0012.

Notes: There are several coelomycetous taxa that have been recorded from *Picea* spp. (Sutton, 1980; Ellis & Ellis, 1985; Farr & Rossman, 2014), but the only *Camarosporium* species recorded is *C. strobilinum* E. Bommer *et al*. However, the conidial dimensions of these two taxa are distinct. *Camarosporium strobilinum* has smaller conidia (6 × 3-3.5 µm), while *Pseudocamarosporium piceae* has larger conidia (10-13 × 6-7 µm).

Pseudocamarosporium propinquum (Sacc.) Wijayawardene, E. Camporesi & K. D. Hyde **comb. nov.** **Fig. 7**

≡ *Camarosporium propinquum* (Sacc.) Sacc., Syll. fung. (Abellini) 3: 464 (1884)
≡ *Hendersonia propinqua* Sacc., Michelia 1(no. 5): 516 (1879)

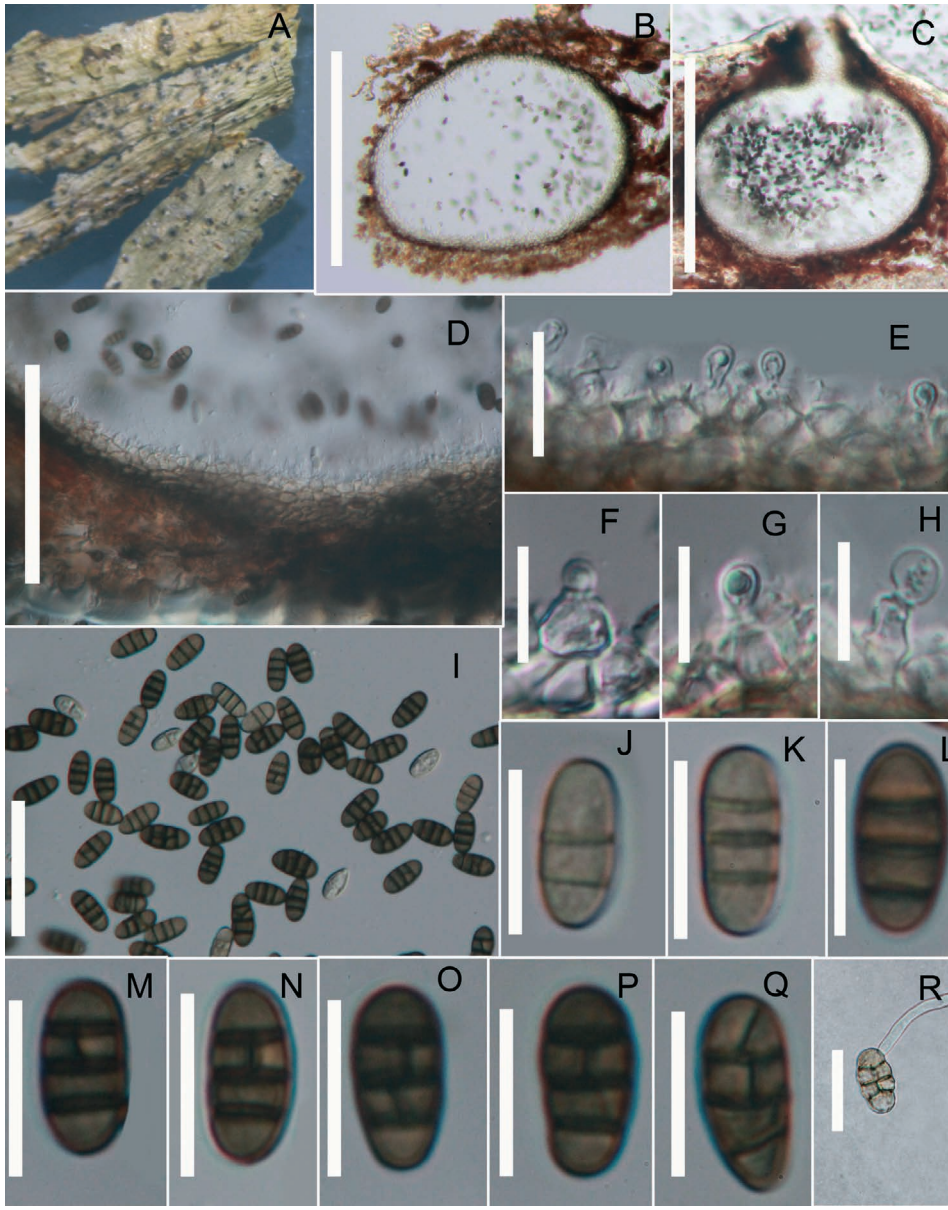

Fig. 7. *Pseudocamarosporium propinquum* (**epitype**). **A.** Conidiomata on *Salix* sp. **B, C.** Cross sections of pycnidia. **D.** Pycnidium wall. **F-H.** Developing conidia attach to conidiogenous cells. **I-Q.** Conidia. **R.** Germinating conidium. Scale bar: **B.** 250 µm; **C.** 350 µm; **D.** 50 µm; **E-H., J-R.** 10 µm; **I** = 20 µm.

Index Fungorum Number: IF 550560; *Facesoffungi number*: 000020

Saprobic on dead branch of *Salix sp*. **Sexual state:** Not observed. **Asexual state:** *Conidiomata* pycnidial, 320-400 µm diam., 250-370 µm high, gregarious, black, immersed, unilocular, ostiole papillate, central. *Pycnidial wall* multilayered, with 1-2 outer wall layers of dark brown to black cells of *textura angularis*, inner wall 3-5 layers, hyaline. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* with percurrent phialidic development, smooth, short, hyaline, formed from the inner layer of the pycnidial wall. *Conidia* 11-14 × 5-7 µm ($\bar{x}$ = 12.2 × 5.5 µm, n = 20), oblong, with truncate base, apex obtuse, straight, muriform, with 3 transverse septa and 1-2 longitudinal septa, pale brown to dark brown, smooth-walled.

Culture characteristics: on PDA white from above and pale brown from reverse, with thin mycelium, irregular, flat, attaining a diam of 2.5 cm in 7 days at 18°C.

Material examined: FRANCE, Rouen, on branch of *Salix vitellina* L. (*Salicaceae*), Letendre (PAD, holotype); ITALY, Firenze Province, Passo Dell'Eremo – Marradi, on dead branch of *Salix* sp. (*Salicaceae*), 12 May 2013, E. Camporesi, NNW IT 1253 (MFLU 14-0092, **epitype** designated here; iso-epitype PDD 104441), ex-type living culture MFLUCC 13-0544 = ICMP 20371 = GUCC 0013.

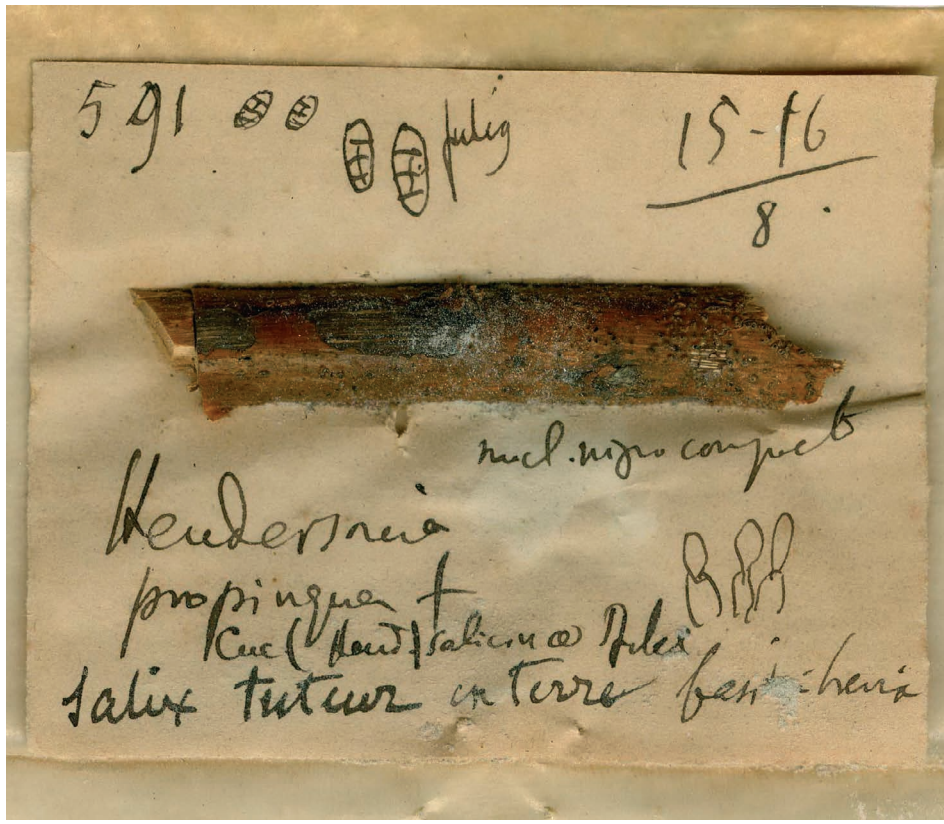

Fig. 8. *Camarosporium propinquum* (holotype).

Notes: Boomer & Rousseau (1884) and Saccardo (1884) described *Camarosporium salicinum* Sacc. *et al.* (conidia 18-20 × 8-10 µm) and *C. propinquum* (conidia 15-16 × 8 µm) from *Salix vitellina*. Our collection is morphologically similar to *C. propinquum.* Our collection shares similar characters i.e. conidiogenesis and conidial dimensions to the iconotype of *C. propinquum* (Fig. 8). In molecular data analyses, *C. propinquum* clusters in *Montagnulaceae* (Figs 2 & 3). Hence, we transfer this species to *Pseudocamarosporium* as a new combination i.e. *Pseudocamarosporium propinquum* and epitypify *Camarosporium propinquum.*

Pseudocamarosporium tiliicola Wijayawardene, R. K. Schumacher & K. D. Hyde **sp. nov.** **Fig. 9**

Index Fungorum Number: IF 550561; *Facesoffungi number*: 000021

Etymology: Named after the host genus *Tilia* from which it was collected

Holotype: MFLU 14-0093

Saprobic in the bark of a dead and corticated branch of *Tilia*. **Sexual state:** Not observed. **Asexual state:** *Conidiomata* pycnidial, 670-700 µm diam., 650-720 µm high, solitary to gregarious, black, semi-immersed to superficial, unilocular, centrally papillate ostiole. *Pycnidial wall* multilayered, with 1-4 outer wall layers of dark brown cells of *textura angularis*, 5-10 cell layers in ostiole

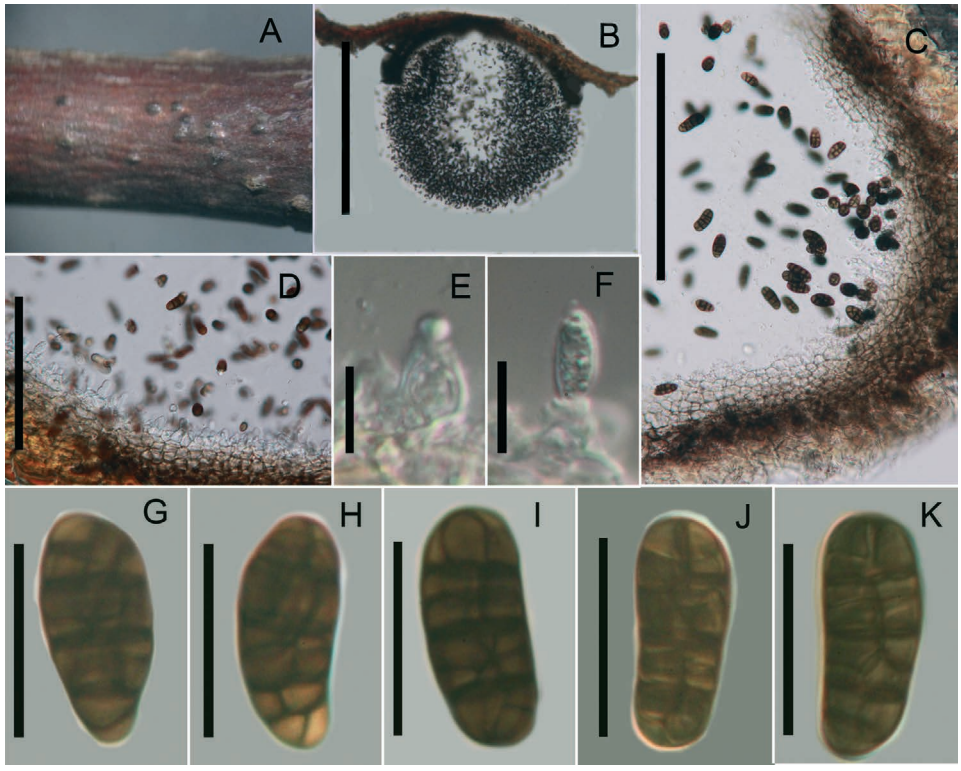

Fig. 9. *Pseudocamarosporium tiliicola* (**holotype**). **A.** Conidiomata on *Tilia* sp. **B.** Spore mass in cross section. **C, D.** Pycnidium wall. **E, F.** Different stages of developing conidia. **G-K.** Conidia. Scale bar: **B.** 650 µm; **C.** 300 µm; **D.** 120 µm; **E, F.** 15 µm; **G-K.** 20 µm.

region, inner wall 2-4 layers, hyaline. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* with percurrent phialidic development, smooth, short, hyaline, segregated, formed from the inner layer of the pycnidial wall. *Conidia* 21-26 × 8-12 µm ($\bar{x}$ = 23.8 × 10.2 µm, n = 20), oblong to ellipsoid, straight to curved, rarely rounded, base tapered and seldom distinctly truncate, muriform, with 3-5 transverse septa and occasionally 2-3 longitudinal septa, brown to dark brown, smooth-walled.

Culture characteristics: on PDA white from above and pale brown from reverse, zonate, with thin mycelium, flat, circular, attaining a diam of 3 cm in 7 days at 18°C.

Material examined: Germany, near Berlin, on a branch of *Tilia* sp. (*Malvaceae*), 31 March 2013, Rene K. Schumacher, NNW G3 (G2/9) (MFLU 14-0093, **holotype**; isotype PDD 104442), living culture MFLUCC 13-0550 = ICMP 20372 = GUCC 0014.

Notes: Saccardo (1882) described *Camarosporium tiliae* Sacc. & Penz. from *Tilia europaea* L., however *Pseudocamarosporium tiliicola* has larger conidia (21-26 × 8-12 µm vs 8-10 × 6-7 µm) and is therefore introduced as a new species.

DISCUSSION

New separate clade in Pleosporinae: The *Pleosporales* is one of the most important and significant orders in *Dothideomycetes* (Schoch *et al.,* 2006, 2009; Hyde *et al.,* 2013) and this order has been the subject of morphological (Sivanesan, 1984) and molecular (Zhang *et al.,* 2012) studies. In their molecular based overview of *Dothideomycetes*, Schoch *et al*. (2009) showed that suborder *Pleosporinae* comprises the families *Didymellaceae*, *Leptosphaeriaceae, Phaeosphaeriaceae* and *Pleosporaceae*. However, Zhang *et al*. (2012) predicted the possibilities of introducing *Cucurbitariaceae* and *Dothidotthiaceae* as families in *Pleosporinae*. Hyde *et al*. (2013) agreed with Zhang *et al*. (2012) and showed *Pleosporinae* comprises *Cucurbitariaceae, Didymellaceae*, *Dothidotthiaceae, Leptosphaeriaceae, Phaeosphaeriaceae* and *Pleosporaceae* and *Coniothyriaceae* (Hyde *et al.,* 2013).

Conventionally, the genus was linked to *Botryosphaeriales incertae sedis* (Kirk *et al.,* 2008; Liu *et al.,* 2012; Wijayawardene *et al.,* 2012a; Hyde *et al.,* 2013) and *Cucurbitariaceae* (Saccardo, 1884; Sivanesan, 1984; Zhang *et al.,* 2012; Doilom *et al.,* 2013). However, Schoch *et al*. (2009) showed that *Camarosporium quaternatum*, the type species of *Camarosporium* groups in *Leptosphaeriaceae*. Furthermore, Ramaley and Barr (1995) stated that *Pleoseptum yuccaesedum* A.W. Ramaley & M.E. Barr, the type species of *Pleoseptum* A.W. Ramaley & M.E. Barr (*Phaeosphaeriaceae fide* Hyde *et al.,* 2013) had asexual states in *Camarosporium* (*viz*. *C. yuccaesedum* Fairm.). Hence this genus is considered to be polyphyletic as predicted by Sutton (1980).

In our multi-gene analyses of *Pleosporinae* (Fig. 1), *Camarosporium quaternatum* groups with *C. aloes*, *C. clematidis, C. robiniicola* and *C. spartii* and forms a distinct clade with high bootstrap values in ML analysis (77%) and in high PP value in Bayesian analysis (1.00). Two strains of *Cucurbitaria elongata* (AFTOL-ID 1568 and MFLUCC 14-0260) also group with these *Camarosporium* strains. However, *Cucurbitaria sensu stricto* (i.e. *Cucurbitariaceae fide* Doilom *et al.,* 2013; Hyde *et al.,* 2013) form a well-supported clade (bootstrap values are 72%

and 78% in ML and MP analyses respectively; 1.00 in Bayesian analysis) including *Cucurbitaria berberidis* (Pers.) Gray, the type species of *Cucurbitaria* (ex-epitype culture MFLUCC11-0384, MFLUCC 11-0385 *fide* Doilom *et al.* 2013, CBS 394.84 *fide* de Gruyter *et al.,* 2009) and *Pyrenochaeta nobilis* De Not., the type species of *Pyrenochaeta* (ex-type strain CBS 407.76 *fide* de Gruyter *et al.,* 2009). *Pyrenochaeta acicola* (CBS 122789 *fide* de Gruyter *et al.,* 2009), *Pyrenochaeta quercina* (CBS 115095 *fide* de Gruyter *et al.,* 2010) and *Pyrenochaetopsis decipiens* (CBS 343.85 *fide* de Gruyter *et al.,* 2010) also clustered in the same clade.

Camarosporium-like *taxa are polyphyletic*: Recent molecular phylogenetic studies reveal that several coelomycetous genera are polyphyletic, *viz. Coniothyrium* and *Phoma* (Verkley *et al.,* 2004, 2014; de Gruyter *et al.,* 2010, 2012). As predicted by Sutton (1980), our molecular based study confirms that *Camarosporium* is also polyphyletic i.e. in *Pleosporinae* (i.e. *Camarosporium sensu stricto*) and in *Massarineae* (i.e. *Montagnulaceae*) (Figs 2 & 3). However, in this study we have not considered the *Camarosporium*-like taxa in *Botryosphaeriales* (Wijayawardene in prep.), where *Camarosporium* species have previously been linked (Liu *et al.,* 2012; Hyde *et al.,* 2013). Since the type species of *Camarosporium*, *C. quaternatum* groups in *Pleosporinae*, we consider that particular clade as *Camarosporium sensu stricto*. The other *Camarosporium*-like taxa in *Montagnulaceae* group as two distinct lineages and are hence considered as two different genera *viz*. *Paracamarosporium* and *Pseudocamarosporium*.

Based on our multi-gene analyses, we conclude that delimitation of *Camarosporium*-like taxa based on morphological characters such as conidiomatal structure, conidiogenesis and conidial morphology have not been successful. Hence it is important to carry out molecular based identification along with morphological studies to place species in genera.

It is important to re-collect *Camarosporium*-like taxa as this group comprises more than 500 names in both Index Fungorum (2014) and Robert *et al.* (2005). In our study, we have confirmed that these taxa are scattered across *Pleosporales* with distinct phylogenetic lineages. Therefore, further re-collecting, isolation and molecular based studies (Wijayawardene *et al.,* 2012c) are essential to interpret correct generic concepts for *Camarosporium*-like taxa.

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