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Hidden diversity behind the Lecanicillium-like white colony-forming mycoparasites on *Hemileia vastatrix* (coffee leaf rust)

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Abstract: During surveys for fungal natural enemies of *Hemileia vastatrix* – the causal agent of coffee leaf rust (CLR) – in its African centre of origin (Cameroon, Ethiopia), as well as in its exotic South American range (Brazil, Paraguay), an eclectic and species-rich mycobiota was encountered. Here, we provide a comprehensive report on an assemblage of "white colony-forming fungi" (WCF), often treated in the earlier literature under the inadequate "label" *Verticillium lecanii* (=*Lecanicillium lecanii*). A total of 265 isolates of WCF were provisionally placed in this arbitrary group. We clarified the identity of our assemblage of Lecanicillium-like fungi using a combination of morphological characteristics and sequence data for the large subunit nuclear ribosomal DNA (LSU), translation elongation factor 1-α (*TEF*) and the largest subunits of RNA polymerase II (*RPB1* and *RPB2*) regions. Fifteen WCF species belonging to eight genera across three hypocrealean families (*Bionectriaceae*, *Clavicipitaceae* and *Cordycipitaceae*) were found parasitizing pustules of CLR. Significantly, *Lecanicillium lecanii* was not found to be present amongst these taxa. Six species belonged to the known genera – *Corniculantispora*, *Gamszarella*, *Lecanicillium, Ovicillium, Pleurodesmospora* and *Simplicillium*. Two new genera are described, *Bettiolomyces* and *Hemileiophthora*, as well as seven new species, *Bettiolomyces urediniophagus*, *Gamszarella uredinophila*, *Hemileiophthora denticulata, H. nodosa, Lecanicillium hemileiae*, *Pleurodesmospora hemileiae* and *Simplicillium hemileiae.* The following known WCF species are recorded here for the first time on pustules of *H. vastatrix*: *Corniculantispora dimorpha*, *Gamszarella buffelskloofina*, *Lecanicillium uredinophilum*, *Ovicillium attenuatum*, *Pleurodesmospora coccorum* and *Simplicillium subtropicum.* Additionally, the new combination *Bettiolomyces epiphytus* is introduced for *Verticillium epiphytum*.

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INTRODUCTION

Coffee leaf rust (CLR), caused by *Hemileia vastatrix*, is the most important disease of coffee worldwide, accounting for annual yield losses of up to 40 % in the Americas (Avelino *et al.* 2015, Talhinhas *et al.* 2017). In the last decade, CLR outbreaks with unexpectedly high intensity have emerged in the highlands of Central America, Colombia, Peru and Ecuador, threatening the livelihoods of smallholder coffee farmers and their dependents in these countries (Avelino *et al.* 2015, McCook & Vandermeer 2015). Coffee leaf rust has now been identified as one of the main causes of mass migration from Latin America – particularly, from Central America – to the USA (Ward *et al.* 2017, Dupre *et al.* 2022).

The use of resistant coffee varieties is the most cost-effective way to control CLR. However, the genetic variability of *H. vastatrix* and the emergence of new races has resulted in resistance genes being overcome, worsening an already difficult situation for farmers and reflecting the difficulties of obtaining varieties with durable resistance (Avelino *et al.* 2015). A particularly worrying example is the breakdown of resistance in the Lempira cultivar, which is widely cultivated in Honduras and other Central American countries (Ward *et al.* 2017). Climate change has played an important role in the increased intensity of CLR since the rust was not problematic above 1000 m.a.s.l. until 2011, when CLR epidemics of equal intensity were observed from 400–1400 m.a.s.l. (Avelino *et. al.* 2015). Chemical control using fungicides, such as copper-based products and triazol, alone or in mixtures with strobilurin (Zambolim 2016), has been equally problematic, due to environmental contamination and pesticide residues, as organic coffee is becoming mainstream.

Biological control offers an environmentally benign and potentially attractive alternative for CLR management, although still relatively unexplored and with few products available for farmers, most of which are based on bacteria of the genus *Bacillus.* Several studies have also demonstrated experimentally the potential of antagonistic bacteria against *H. vastatrix* (Shiomi *et al.* 2006, Haddad *et al.* 2009, Cacefo *et al.* 2016). In contrast, however, searches for antagonistic or mycoparasitic fungi of *H. vastatrix* with biocontrol potential have been limited to a single study undertaken in Mexico, outside the centre of origin of CLR (Carrión & Rico-Gray 2002). These authors catalogued the following fungi in association with CLR pustules: *Acremonium byssoides*, *Calcarisporium arbuscula*, *C. ovalisporum*, *Fusarium pallidoroseum*, *Sporothrix guttuliformis*, and *Verticillium lecanii* (= *Lecanicillium lecanii*; Khonsanit *et al.* 2024).

In 2015, a project was initiated to compare the mycobiota associated with *Hemileia vastatrix* and its *Coffea* hosts in their African centres of origin with that in their exotic South American range. The long-term aim was to identify antagonistic fungi with potential as classical biological control agents. This has resulted in a series of papers cataloguing, describing and assessing the fungi found during the surveys, both as mycoparasites of CLR and as endophytes within wild and cultivated *Coffea* species (Crous *et al.* 2018, Rodríguez *et al.* 2021, Colmán *et al.* 2021, Guterres *et al.* 2021, Salcedo-Sarmiento *et al.* 2021, Kapeua-Ndacnou *et al.* 2023a, b, Pereira *et al.* 2024a, b). The present paper belongs to the series and deals with the biggest group, namely Lecanicillium-like mycoparasites associated with the pustules of CLR.

The most common and noticeable evidence of mycoparasitism of *H. vastatrix* is seen as a complex of "white colony forming fungi" (WCF) overgrowing the rust pustules, usually identified under the generic names *Verticillium* or *Lecanicillium* and, more precisely, as *Verticillium*/*Akanthomyces*/*Lecanicillium lecanii* (*Cordycipitaceae*); depending on the publication chronology (Shaw 1987, Eskes *et al.* 1991, Vélez & Rosillo 1995, Vandermeer *et al.* 2009, Jackson *et al.* 2012, Nicoletti & Becchimanzi 2020, Zewdie *et al.* 2021, Das *et al.* 2024). However, *L. lecanii* is, together with most members of the genus, best known as an insect pathogen. Therefore, the use of this name for mycoparasitic isolates on *H. vastatrix* could be regarded as questionable and it has never been supported by cross-inoculations between rust and arthropod isolates onto each other's arthropod or fungus host. Also, molecular data are lacking in most cases. The recent study of fungi associated with CLR in Mexico and Puerto Rico using single-molecule DNA sequencing (PacBio) of fungal rRNA (James *et al.* 2016) revealed the presence of a hyperdiverse fungal community, but only two species were identified as belonging to the genus *Lecanicillium* and, more significantly, *L. lecanii* was absent. Typically, in coffee plantations, *L. lecanii* is most commonly found attacking the coffee green scale, *Coccus viridis* (Vandermeer *et al.* 2009).

In this paper, we use morphological, ecological and molecular data to elucidate the taxonomic status of the WCF complex, collected and isolated during surveys in Africa and South America, including the centres of origin of *Coffea spp*. in Africa.

MATERIALS AND METHODS

Sample collection, isolation and preservation

The samples included in this study were obtained during surveys conducted between 2015 and 2017, covering localities in Brazil (Minas Gerais, Rio de Janeiro, São Paulo), Paraguay (Central, Cordillera), Cameroon and Ethiopia. The survey included both commercial and abandoned coffee plantations, semi-natural situations where coffee plants grow spontaneously in secondary forest, and "forest coffee": grown with minimal management under the native forest or where it still occurs as a wild species (in Cameroon – *C. canephora*, and Ethiopia – *C. arabica*). Plants bearing CLR symptoms were examined at each locality. Special attention was given to leaves showing signs of mycoparasitized rust pustules, i.e. those exhibiting a white fungal colony cover, and representative samples were collected from these, as well as from leaves with apparently mycoparasite-free pustules for a more detailed examination under a dissecting microscope (Olympus SZ61, Olympus Corporation, Tokyo, Japan) in the laboratory. Isolations were made by transferring conidia or other fungal structures from colonized uredinia onto plates containing potato dextrose agar (PDA) (Hawksworth *et al.* 1996) with a sterilized fine-point needle. For long-term storage, a representative pure culture of each isolate was transferred to flasks containing silica-gel or a 10 % glycerol solution maintained at -80 ºC, as described by Dhingra & Sinclair (1995) and Gonçalves *et al.* (2016). Fungal cultures were deposited in the culture collection "Coleção Octávio de Almeida Drumond" (COAD) of the Universidade Federal de Viçosa (UFV), Viçosa, Minas Gerais, Brazil. Colonies of each isolate were metabolically inactivated and dried cultures were deposited as specimens in the UFV fungarium (VIC). The origin of each isolate, as well as their COAD and VIC codes, are presented in Table 1.

Morphological characterization

Fungal structure from parasitized rust pustules or from potato carrot agar (PCA) (Hawksworth *et al.* 1996) plates were mounted in lactophenol or lactofuchsin for observation under an Olympus BX51 compound microscope equipped with DIC (Olympus, Tokyo, Japan). Micrographs were taken with an Olympus BX53 (Olympus, Tokyo, Japan) compound microscope fitted with a digital camera (OLYMPUSQ-Color 5). Biometric data was taken based on the examination of at least 30 of each taxonomically relevant structures. Ultra-structure was assessed using a Carl-Zeiss LEO VP 1430 scanning electron microscope (SEM) (Carl-Zeiss, Jena, Germany) as follows: aluminium stubs were prepared by covering with double-sided adhesive tape; pieces of coffee leaves with rust pustules colonized by WCF were selected and mounted on the stubs with the abaxial side facing upwards and coated with gold in a sputter apparatus coupled to a freeze-drying unit (FDU010, Oerlykon Balzers, Balzers, Liechtenstein); then examined under the SEM operated at 10 Kv to obtain the electro-micrographs as described in Torres *et al.* (2017).

Culture descriptions were based on observations of the colonies on PDA and PCA plates. These were incubated at 25 °C under a 12 h daily light regime (light provided by two fluorescent daylight lamps and one nuv-lamp placed 35 cm above the plates) for 10 d. Colour terminology followed Rayner (1970).

DNA extraction, sequencing and phylogenetic analysis

In order to obtain representative genomic DNA for each fungal taxon, selected isolates were grown on PDA plates at 25 °C under a 12 h daily light regime for 1 wk. DNA was extracted from approximately 40 mg of fresh mycelium using the Wizard Genomic DNA Purification Kit (Promega Corporation, Madison, USA) following the manufacturer´s protocol.

The following loci were amplified with the respective primers: the large subunit ribosomal RNA (LSU) with primers LROR/LR5 primers (Vilgalys & Sun 1994), the translation elongation factor *1-α* (*TEF*) with primers EF1-983F and EF1-2218R (Rehner & Buckley 2005) and the second largest and largest subunits of RNA polymerase II (*RPB2*) using the primers fRPB2-5f2 and fRPB2-7cR (Liu *et al.* 1999) and (*RPB1*) using the primers RPB1-Cr and RPB1-Ac (Castlebury *et al.* 2004). The PCR amplifications were conducted in a 25 µL volume consisting of 2.5 µL of 10× *Taq* buffer + (NH4)2SO4 (Fermentas, Glen Burnie, MA), 2.0 mM of MgCl2 (25 mM, Fermentas), 0.2 mM of each dNTP, 0.5 µL of each primer at 0.5 mM, 0.2 µL *Taq* DNA Polymerase (recombinant; 5 U/µL, Fermentas) and 0.5 µg of template DNA. The amplification reactions were performed as described by Chirriví-Salomón *et al.* (2015). Sequences were obtained with the same primers employed for the initial amplification; sequencing reactions were conducted at Macrogen Sequencing Service (Seoul, South Korea).

The raw nucleotide sequences (chromatograms as .ab1 files) were manually edited and consensus sequences, based on sequencing both forward and reverse primers, were de novo assembled with Geneious Prime v. 2023.0.3 (https://www.geneious.com). For quality control, the consensus regions obtained were then BLASTed against the GenBank database using Geneious Prime v. 2023.0.3, and sequences belonging to unrelated fungal groups were treated as contaminants. Individual gene alignments were generated by MAFFT (Katoh & Standley 2013). The alignment of every locus was improved manually, annotated and concatenated into a single combined dataset using Geneious Prime v. 2023.0.3. Rare cases of ambiguously aligned regions, meaning unreliable alignment with high variability, multiple gaps or insertions in a specific OTU, were excluded from phylogenetic analysis and gaps were treated as missing data. The final alignment length was 3735 bp: 929 bp for LSU, 1044 bp for *TEF*, 718 bp for *RPB1*, and 1044 for *RPB2*. The Maximum likelihood (ML) analysis was performed with RAxML v. 8.2.12 (Stamatakis 2006) on a concatenated dataset containing all four genes. The dataset consisted of 11 data partitions, these included one each for LSU, and three for each of the three codon positions of the protein coding genes, *TEF*, *RPB1* and *RPB2*. The GTRGAMMA model of nucleotide substitution was employed during the generation of 1000 bootstrap replicates. Branches were considered strongly supported if bootstrap support values were > 70 % (> 50 % is displayed). For this study, we generated 198 new sequences (55 for LSU, 50 for *TEF*, 45 for *RPB1* and 48 for *RPB2*; Table 1).

Sequences derived from this study were deposited in GenBank (http://www.ncbi.nlm.nih.gov/genbank), and the descriptions and nomenclature in MycoBank (Crous *et al.* 2004).

RESULTS

During surveys in South America (Brazil, Paraguay) and Africa (Cameroon, Ethiopia), 265 WCF were isolated from *H. vastatrix* pustules. Many fitted into the subgroup we referred to as Lecanicillium-like. Fifteen species were recognized based on morphology and molecular data, belonging to eight genera; including two that are described here as new, namely: *Bettiolomyces* (*Clavicipitaceae*) and *Hemileiophthora* (*Cordycipitaceae*). We also propose seven new species, based on a combination of morphological and molecular characteristics, which are described below.

Phylogenetic analyses

The results presented in this study recovered the topology presented in previous studies (Kepler *et al.* 2017, Mongkolsamrit *et al.* 2018). Among the WCF genera, the following were found to belong to the *Cordycipitaceae*: *Simplicillium* and *Hemileiophthora* (BP = 92), both forming a monophyletic clade (BP = 92); *Gamszarella* (BP = 98); *Pleurodesmospora* (BP = 100) and *Lecanicillium* (BP = 96) (Fig. 1). In the *Clavicipitaceae*, the three isolates from Brazil and one from Cameroon formed a monophyletic clade with "*Verticillium epiphytum*" CBS 154.61 and CBS 384.81, herein recognized as distinct from *Verticillium* and not related to the *Plectosphaerellaceae* – hence, the new genus *Bettiolomyces* was established to accommodate it (BP = 100) (Fig. 2). *Bettiolomyces* is sister to *Periglandula ipomoeae* and includes two species: *B. epiphytus comb. nov*. and *B.urediniophagus sp. nov*. (Fig. 2).

Simplicillium isolates were obtained from seven specimens belonging to three separate species: *S. hemileiae sp. nov*., *S. subtropicum* and *S. lanosoniveum* (Fig. 1). *Hemileiophthora gen. nov.* formed two well-supported clades (BP = 100), composed of two new species, *H. nodosa* (BP = 99) and *H. denticulata* (BP = 100). In general, *Hemileiophthora nodosa* included isolates from Ethiopia and Brazil, whereas *H. denticulata* comprised exclusively Ethiopian isolates. *Gamszarella* is represented by the type species, *G. buffelskloofina* (two isolates from Ethiopia), and *G. uredinophila sp. nov.* (one isolate from Brazil). In addition, *Pleurodesmospora* formed a monophyletic clade, sister to *Neohyperdermium*. The *Lecanicillium* isolates clustered together and formed a monophyletic clade, sister to *L. uredinophilum*. A novel species is proposed to accommodate them, *L. hemileiae sp. nov.* (Fig. 2). A single member of the family *Bionectriaceae* appeared among the WCF isolates, namely *Ovicillium attenuatum.*

Table 1. GenBank accession numbers for DNA loci of specimens sequenced in this study.

Species	**Voucher numbers**	**GenBank Accession Numbers***				**References**
		LSU	***TEF***	***RBP1***	***RPB2***	
Aciculosporium take	MAFF-241224	LC571753	LC572034	n/a	LC572048	Tanaka *et al.* (2021)
Akanthomyces aculeatus	HUA 186145	MF416520	MF416465	—	—	Kepler *et al.* (2017)
A. cf. *cardinalis*	spat 09-052	MF416527	MF416471	MF416633	MF416435	Kepler *et al.* (2017)
A. cf. *lecanii*	spat 08-146	MF416528	MF416472	MF416634	MF416436	Kepler *et al.* (2017)
A. pistillariaeformis	HUA 186131	MF416521	MF416466	—	—	Kepler *et al.* (2017)
Akanthomyces sp.	spat 09-052	MF416527	MF416471	MF416633	MF416435	Kepler *et al.* (2017)
	spat 09-051	MF416560	MF416507	MF416664	MF416458	Kepler *et al.* (2017)
	TNS 16333	—	MF416505	MF416662	MF416456	Kepler *et al.* (2017)
A. tuberculatus	BCC 16819	MF416546	MF416490	MF416647	MF416444	Kepler *et al.* (2017)
	OSC111002	DQ518767	DQ522338	DQ522384	DQ522435	Kepler *et al.* (2017)
Arachnidicola kanyawimiae	CBS 541.81	MF416553	MF416498	MF416655	MF416449	Kepler *et al.* (2017)
	NHJ6709	EU369042	EU369025	EU369067	EU369086	Johnson *et al.* (2009)
A. sulfurea	NHJ 5112	EU369043	EU369026	EU369066	—	Johnson *et al.* (2009)
Aschersonia marginata	BCC 1765	—	DQ384958	DQ385010	DQ452472	Mongkolsamrit *et al.* Unpublished data 2006
A. marginata	BCC 1713	—	DQ384958	DQ385010	DQ452472	Mongkolsamrit *et al.* Unpublished data 2006
Ascopolyporus polychrous	P.C. 546	DQ118737	DQ118745	DQ127236	—	Chaverri *et al.* (2005)
A. villosus	ARSEF 6355	AY886544	DQ118750	DQ127241	—	Chaverri *et al.* 2006
Atkinsonella hypoxylon	B4728	—	EF689546	—	KP689514	Escobar *et al.* Unpublished data 2015
A. texensis	B6155	—	KP689548	—	KP689516	Schardl. Unpublished data 2015
Balansia epichloë	AEG 96-15a	—	EF468743	EF468851	EF468908	Sung *et al.* (2007)
B. henningsiana	GAM 16112	AY545727	AY489610	AY489643	DQ522413	Castlebury *et al.* (2004)
B. obtecta	B249	—	KP689549	—	—	Schardl (2015)
Beauveria bassiana	ARSEF 1564	—	HQ880974	HQ880833	HQ880905	Kepler *et al.* (2017)
B. blattidicola	MCA 1814	MF416540	MF416484	MF416641	—	Kepler *et al.* (2017)
	MCA 1727	MF416539	MF416483	MF416640	—	Kepler *et al.* (2017)
B. brongniartii	ARSEF 617	AB027381	HQ880991	HQ880854	HQ880926	Kepler *et al.* (2017)
	BCC 16585	JF415967	JF416009	JN049885	JF415991	Kepler *et al.* (2017)
B. caledonica	ARSEF 2567	AF339520	EF469057	EF469086	HQ880961	Kepler *et al.* (2017)

Table 1. (Continued).

Species	Voucher numbers	GenBank Accession Numbers*				References
		LSU	*TEF*	*RBP1*	*RPB2*	
B. diapheromeriphila	QCNE 186272	JQ895534	JQ958610	JX0003848	—	Wang *et al.* (2020)
	MCA1557	MF416529	—	—	—	Kepler *et al.* (2017)
B. locustiphila	CEM 680 (HUA179218)	JQ895535	JQ958619	JX003847	JX003845	Kepler *et al.* (2017)
	CEM 1888(HUA179219)	JQ958598	JQ958597	—	JX003847	Kepler *et al.* (2017)
B. malawiensis	ARSEF 7760	—	DQ376246	HQ880897	HQ880969	Kepler *et al.* (2017)
B. pseudobassiana	ARSEF 3405	—	AY531931	HQ880864	HQ880936	Kepler *et al.* (2017)
B. scarabaeidicola	ARSEF 5689	AF339524	DQ522335	DQ522380	DQ522431	Kepler *et al.* (2017)
Beauveria sp.	BCC23105	MK632107	FJ459793	—	—	Kepler *et al.* (2017)
	ARSEF 2860	—	—	XM_008595357	—	Kepler *et al.* (2017)
B. staphylinidicola	ARSEF 5718	EF468836	EF468776	EF468881	—	Kepler *et al.* (2017)
Bettiolomyces epiphytus	**CBS 384.81**	**AF339547**	**DQ522361**	**DQ522409**	**DQ522469**	Sung *et al.* (2001), Spatafora *et al.* (2007)
	COAD 3299	**PQ962880**	**PV362966**	**PV362917**	**PV987310**	**This study**
	COAD 3297	**PQ962881**	**PV362967**	**PV362918**	**PV987308**	**This study**
	COAD 3298	**PQ962882**	**PV362968**	**PV362919**	**PV987309**	**This study**
Bettiolomyces sp.	**CBS 154.61**	**AF339547**	**EF468802**	—	**EF4688947**	**This study**
B. urediniophagus	**COAD 3296**	**PQ962883**	**PV362969**	**PV362920**	**PV987307**	**This study**
Blackwellomyces cardinalis	OSC 93610	AY184963	EF469059	EF469088	EF469106	Spatafora *et al.* (2007)
B. cardinalis	OSC 93609	AY184962	DQ522325	DQ522370	DQ522422	Spatafora *et al.* (2007)
B. pseudomilitaris	BCC1919	MF416534	MF416478	—	MF416440	Kepler *et al.* (2017)
	BCC2091	MF416535	MF416479	—	MF416441	Kepler *et al.* (2017)
Claviceps fusiformis	ATCC 26019	U17402	DQ522320	DQ522366	—	Spatafora *et al.* (2007)
C. paspali	ATCC 13892	U17398	DQ522321	DQ522367	DQ522416	Spatafora *et al.* (2007)
C. purpurea	GAM 12885	AF543789	AF543778	AY489648	DQ522417	Spatafora *et al.* (2007)
C. purpurea	SA cp11	EF469075	EF469058	EF469087	EF469105	Spatafora *et al.* (2007)
Conoideocrella luteorostrata	NHJ 12516	EF468849	EF468800	EF468905	EF468946	Sung *et al.* (2007)
C. luteorostrata	NHJ 11343	EF468850	EF468801	EF468906	—	Sung *et al.* (2007)
C. tenuis	NHJ 6293	EU369044	EU369029	EU369068	EU369087	Johnson *et al.* (2009)
	NHJ 345.01	EU369045	EU369030	—	EU369088	Johnson *et al.* (2009)

Table 1. (Continued).

Species	Voucher numbers	GenBank Accession Numbers*				References
		LSU	***TEF***	***RBP1***	***RPB2***	
	NHJ 6791	EU369046	EU369028	EU369069	EU369089	Johnson *et al.* (2009)
Cordyceps albocitrina	spat 07-174	—	MF416467	MF416629	—	Kepler *et al.* (2017)
C. bifusispora	EFCC 5690	EF468806	EF468746	EF468854	EF468909	Kepler *et al.* (2017)
	EFCC 8260	EF468807	EF468747	EF468855	EF468910	Kepler *et al.* (2017)
	spat 08-129	MF416523	MF416468	MF416630	—	Kepler *et al.* (2017)
	spat 08-133.1	MF416524	MF416469	MF416631	MF416434	Kepler *et al.* (2017)
C. caloceroides	MCA 2249	MF416525	MF416470	MF416632	—	Kepler *et al.* (2017)
C. cf. *takaomontana*	NHJ12623	EF468838	EF468778	EF468884	EF468932	Kepler *et al.* (2017)
	BCC 12688	MF416545	MF416489	MF416646	—	Kepler *et al.* (2017)
C. cf. *ochraceostromata*	ARSEF 5691	EF468819	EF468759	EF468867	EF468921	Kepler *et al.* (2017)
C. cf. *pruinosa*	spat 08-115	MF416532	MF416476	MF416635	MF416439	Kepler *et al.* (2017)
C. cf. *farinosa*	spat 09-021	MF416533	MF416477	MF416636	—	Kepler *et al.* (2017)
	OSC111004	EF468840	EF468780	EF468886	—	Kepler *et al.* (2017)
C. cicadae	RCEF HP090724-31	MF416552	MF416496	MF416653	MF416447	Kepler *et al.* (2017)
C. coleopterorum	CBS 110.73	JF415988	JF416028	JN049903	JF416006	Kepler *et al.* (2017)
C. exasperata	MCA 2288	MF416538	MF416482	MF416639	—	Kepler *et al.* (2017)
	MCA 2155	MF416542	MF416486	MF416643	—	Kepler *et al.* (2017)
C. farinosa	CBS 111113	MF416554	MF416499	MF416656	MF416450	Kepler *et al.* (2017)
C. kyusyuensis	EFCC 5886	EF468813	EF468754	EF468863	EF468917	Kepler *et al.* (2017)
C. militaris	OSC 93623	AY184966	DQ522332	DQ522377	—	Kepler *et al.* (2017)
C. ninchuckispora	EFCC 5693	EF468821	EF468762	EF468869	—	Kepler *et al.* (2017)
	EFCC 5197	EF468820	EF468760	EF468868	—	Kepler *et al.* (2017)
	NHJ 10627	IEF468822	EF468763	EF468870	—	Kepler *et al.* (2017)
	NHJ 10684	EF468823	EF468761	EF468871	—	Kepler *et al.* (2017)
	EGS 38.165	EF468846	EF468795	EF468900	—	Kepler *et al.* (2017)
	EGS 38.166	EF468847	EF468794	EF468901	—	Kepler *et al.* (2017)
C. polyarthra	MCA 996	MF416543	MF416487	MF416644	—	Kepler *et al.* (2017)
	MCA 1009	MF416544	MF416488	MF416645	—	Kepler *et al.* (2017)

Table 1. (Continued).

Species	Voucher numbers	GenBank Accession Numbers*				References
		LSU	*TEF*	*RBP1*	*RPB2*	
C. rosea	spat 09-053	MF416536	MF416480	MF416637	MF416442	Kepler *et al.* (2017)
C. tenuipes	ARSEF 5135	JF415980	KY973654	JN049896	JF416000	Kepler *et al.* (2017)
	OSC111007	DQ518773	DQ522349	DQ522395	DQ522449	Kepler *et al.* (2017)
Cordyceps sp.	EFCC 2535	EF468835	EF468772	—	—	Kepler *et al.* (2017)
	RCEF HP090724-04C	MF416537	MF416481	MF416638	MF416443	Kepler *et al.* (2017)
C. takaomontana	MCA 1806	MF416541	MF416485	MF416642	—	Kepler *et al.* (2017)
Corniculantispora dimorpha	CBS 363.86	—	AF339559	EF468784	EF468890	Sung *et al.* (2007)
	COAD 3754	**PQ962862**	—	**PV362899**	**PV987291**	**This study**
C. psalliotae	CBS 101270	AF339558	EF469066	EF469095	EF469113	Sung *et al.* (2007)
	CBS 532.81	AF339560	EF469067	EF469096	EF469112	Sung *et al.* (2007)
Dussiella tuberiformis	JFW	—	JQ257027	JQ257015	JQ257020	Kepler *et al.* (2012b)
Epichloe gansuensis	e 7080	—	KP689495	—	KP689494	Schardl (2015)
E. typhina	ATCC 56429	U17396	—	AY489653	DQ522440	Spatafora *et al.* (2007)
Engyodontium aranearum	CBS 309.85	AF339526	DQ522341	DQ522387	DQ522439	Sung *et al.* (2001); Kepler *et al.* (2017)
Flavocillium bifurcatum	YFCC 6101	MN576781	MN576951	MN576841	MN576897	Wang *et al.* (2020)
Gamszarea humicola	LC12462	MK328998	MK336028	—	MK335982	Zhang *et al.* (2021)
G. lunata	CGMCC3.19315	MK328999	MK336029	—	MK335981	Zhang *et al.* (2021)
G. microspora	CGMCC3.19313	MK329001	MK336031	—	MK335983	Zhang *et al.* (2021)
G. wallacei	CBS 101237	AY184967	EF469073	EF469102	EF469119	Sung *et al.* (2007)
Gamszarella antillana	CBS 350.85	AF339536	DQ522350	DQ522396	DQ522450	Spatafora *et al.* (2007)
Gam. buffelskloofina	**COAD 3264**	**PQ962838**	**PV362929**	**PV362880**	**PV987267**	**This study**
	CBS 150062	OR717025	—	OR683715	OR683726	Crous *et al.* (2023)
Gam. uredinophila	**COAD 3263**	**PQ962837**	**PV362928**	**PV362879**	**PV987266**	**This study**
Gibellula clavulifera var. alba	ARSEF1915	DQ518777	DQ522360	DQ522408	DQ522467	Spatafora *et al.* (2007)
G. leiopus	BCC 16025	MF416548	MF416492	MF416649	—	Kepler *et al.* (2017)
G. longispora	NHJ 12014	—	EU369017	EU369055	EU369075	Kepler *et al.* (2017)
G. pulchra	NHJ10808	EU369035	EU369018	EU369056	EU369076	Kepler *et al.* (2017)
Gibellula sp.	DJ29	EU369065	EU369027	—	—	Kepler *et al.* (2017)

Table 1. (Continued).

Species	Voucher numbers	GenBank Accession Numbers*				References
		LSU	*TEF*	*RBP1*	*RPB2*	
	NHJ7859	—	—	EU369064	EU369085	Kepler *et al.* (2017)
	NHJ 10788	EU369036	EU369019	EU369058	EU369078	Kepler *et al.* (2017)
	NHJ 13158	EU369037	EU369020	EU369057	EU369077	Kepler *et al.* (2017)
	NHJ 5401	—	—	EU369059	EU369079	Kepler *et al.* (2017)
Hemileiophthora denticulata	**COAD 3261**	**PQ962833**	**PV362924**	**PV362875**	—	**This study**
	VIC47439	**PQ962834**	**PV362925**	**PV362876**	**PV987263**	**This study**
	COAD 3262	**PQ962835**	**PV362926**	**PV362877**	**PV987264**	**This study**
	COAD 3755	**PQ962836**	**PV362927**	**PV362878**	**PV987265**	**This study**
H. nodosa	**COAD 3258**	**PQ962830**	**PV362921**	**PV362872**	—	**This study**
	COAD 3259	**PQ962831**	**PV362922**	**PV362873**	**PV987262**	**This study**
	COAD 3260	**PQ962832**	**PV362923**	**PV362874**	—	**This study**
Hevansia arachnophilus	NHJ 10469	EU369031	EU369008	EU369047	—	Kepler *et al.* (2017)
H. cf. *novoguineensis*	NHJ 11923	EU369032	EU369013	EU369052	EU369072	Johnson *et al.* (2009); Ridkaew *et al.* Unpublished data 2009
	NHJ 4314	—	EU369012	EU369051	EU369071	Johnson *et al.* (2009); Ridkaew *et al.* Unpublished data 2009
H. nelumboides	TNS 16306	—	MF416475	—	MF416438	Kepler *et al.* (2017)
	BCC 2190	MF416531	MF416474	—	—	Kepler *et al.* (2017)
H. novoguineensis	NHJ 13161	—	EU369011	EU369050	—	Johnson *et al.* (2009); Ridkaew *et al.* Unpublished data 2009
	NHJ 13117	—	EU369010	EU369049	EU369073	Johnson *et al.* (2009); Ridkaew *et al.* Unpublished data 2009
Hevansia sp.	BCC 2093	MF416530	MF416473	—	MF416437	Kepler *et al.* (2017)
Hypocrella citrina	CUP 067825	AY986905	AY986930	DQ000331	—	Chaverri *et al.* (2005)
H. disciformis	ARSEF 7695	AY986913	AY986939	DQ000340	—	Chaverri *et al.* (2005)
H. discoidea	ARSEF 7697	AY986910	AY986936	DQ000337	—	Chaverri *et al.* (2005)
H. hirsuta	CUP 067848	AY986922	AY986949	DQ000350	—	Chaverri *et al.* (2005)
Isaria amoenerosa	CBS 107.73	MF416550	MF416494	MF416651	MF416445	Kepler *et al.* (2017)
I. amoenerosa	CBS 729.73	MF416551	MF416495	MF416652	MF416446	Kepler *et al.* (2017)
	CBS 729.73	MF416551	MF416495	MF416652	MF416446	Kepler *et al.* (2017)

Table 1. (Continued).

Species	Voucher numbers	GenBank Accession Numbers*				References
		LSU	*TEF*	*RBP1*	*RPB2*	
I. farinosa	CBS 240.32	JF 415979	JF416019	JN049895	JF415999	Kepler *et al.* (2017)
	CBS 262.58	AB080087	MF416497	MF416654	MF416448	Kepler *et al.* (2017)
	OSC 111005	DQ518772	DQ522348	DQ522394	—	Kepler *et al.* (2017)
	CBS 240.32	JF 415979	JF416019	JN049895	JF415999	Kepler *et al.* (2017)
	CBS 262.58	AB080087	MF416497	MF416654	MF416448	Kepler *et al.* (2017)
	OSC 111005	DQ518772	DQ522348	DQ522394	—	Kepler *et al.* (2017)
	OSC 111006	EF469080	EF469065	EF469094	—	Kepler *et al.* (2017)
I. fumosorosea	CBS 107.10	MF416556	MF416502	MF416659	MF416453	Kepler *et al.* (2017)
	CBS 375.70	AB083035	MF416501	MF416658	MF416452	Kepler *et al.* (2017)
	CBS 244.31	MF416557	MF416503	MF416660	MF416454	Kepler *et al.* (2017)
	CBS 337.52	MF416555	MF416500	MF416657	MF416451	Kepler *et al.* (2017)
I. javanica	CBS 134.22	MG665231	MF416504	MF416661	MF416455	Kepler *et al.* (2017)
Jenniferia cinerea	NHJ 3510	—	EU369009	EU369048	EU369070	Johnson *et al.* (2009); Ridkaew *et al.* Unpublished data 2009
Jen. thomisidarum	BCC 37881	MZ6840102	MZ707823	MZ707830	MZ707843	Mongkolsamrit *et al.* (2022)
Keithomyces carneus	CBS 239.32	EF468843	EF468789	EF468894	EF468938	Sung *et al.* (2007)
	CBS 399.59	EF468842	EF468788	EF468895	EF468939	Sung *et al.* (2007)
Lecanicillium aranearum	CBS 726.73a	AF339537	AF468781	EF468887	EF468934	Sung *et al.* 2001; Sung *et al.* (2007)
L. attenuatum	CBS 402.78	AF339565	EF468782	EF468888	EF468935	Sung *et al.* (2007)
L. fusisporum	CBS 164.70	AF339549	KM283817	KM283836	KM283858	Sung *et al.* (2007)
L. hemileiae	**COAD 3287**	**PQ962870**	**PV362956**	**PV362906**	**PV9872957**	**This study**
	COAD 3288	**PQ962871**	**PV362957**	**PV362907**	**PV987298**	**This study**
	COAD 3289	—	—	**PV362908**	**PV987299**	**This study**
	COAD 3290	**PQ962872**	**PV362958**	**PV362909**	**PV987300**	**This study**
	COAD 3291	**PQ962873**	**PV362959**	**PV362910**	**PV987301**	**This study**
	COAD 3292	**PQ962874**	**PV362960**	**PV362911**	—	**This study**
	COAD 3293	**PQ962877**	**PV362963**	**PV362914**	**PV987304**	**This study**
	COAD 3294	**PQ962878**	**PV362965**	**PV362915**	**PV987305**	**This study**
	COAD 3295	**PQ962879**	**PV362964**	**PV362916**	**PV987306**	**This study**

Table 1. (Continued).

Species	Voucher numbers	GenBank Accession Numbers*				References
		LSU	*TEF*	*RBP1*	*RPB2*	
	VIC 47468	**PQ962875**	**PV362962**	**PV362912**	**PV987302**	**This study**
	COAD 3752	**PQ962876**	—	**PV362913**	**PV987303**	**This study**
L. lecanii	CBS 101247	AF339555	DQ522359	DQ522407	DQ522466	Kepler *et al.* (2017)
L. uredinophilum	**AC 68**	**PQ962868**	**PV362955**	**PV362905**	**PV9872956**	**This study**
	KUN101466	KM948307	MG948315	MG948311	MG948313	Wei *et al.* (2018)
	KUN101469	KM948308	MG948316	MG948312	MG948314	Wei *et al.* (2018)
	KACC44066	KM283784	KM283808	KM283830	KM283850	Park *et al.* (2015)
	KACC44082	KM283782	KM283806	KM283828	KM283848	Park *et al.* (2015)
	CEP054	OP752150	MH062184	OP762608	OP762612	Manfrino *et al.* (2022)
	CEP057	OP752151	MH062186	OP762609	OP762613	Manfrino *et al.* (2022)
	CEP108	OP752152	MH062188	OP762610	OP762614	Manfrino *et al.* (2022)
	KUN101469	KM948308	MG948316	MG948312	MG948314	Wei *et al.* (2018)
	COAD 3753	**PQ962864**	**PV362951**	**PV362901**	**PV987296**	**This study**
	COAD 3285	**PQ962865**	**PV362952**	**PV362902**	**PV987293**	**This study**
	VIC 47463	**PQ962866**	**PV362953**	**PV362903**	**PV987294**	**This study**
	COAD 3286	**PQ962867**	**PV362954**	**PV362904**	**PV987295**	**This study**
Liangia sinensis	YFCC 3103	MN576782	MN576952	MN576842	MN576898	Wang *et al.* (2020)
Mariannaea pruinosa	ARSEF 5413	AY84968	DQ522351	Q522397	DQ522451	Kepler *et al.* (2017)
Marquandomyces marquandii	CBS 182.27	EF468845	EF468793	EF468899	EF468942	Sung *et al.* (2007)
Metacordyceps sp.	HMAS 199601	JF415978	JF416018	—	JF415998	Kepler *et al.* (2012a)
Metapochonia bulbillosa	CBS 145.70	AF339542	EF468796	EF468902	EF468943	Sung *et al.* (2007)
M. goniodes	CBS 891.72	AF339550	DQ522354	DQ522401	DQ522458	Spatafora *et al.* (2007)
M. parasitica	ARSEF 3436	EF468848	EF468799	EF468904	EF468945	Sung *et al.* (2007)
M. rubescens	CBS 464.88	AF339566	EF468797	EF468903	EF468944	Sung *et al.* (2007)
Metarhizium album	ARSEF 2082	DQ518775	DQ522352	DQ522398	DQ522452	Spatafora *et al.* (2007)
M. anisopliae	ARSEF 3145	AF339530	AF543774	DQ522399	DQ522453	Spatafora *et al.* (2007)
M. atrovirens	TNM F10184	JF415966	—	JN049884	—	Kepler *et al.* (2012a)
M. cylindrosporum	TNS 16371	—	JF415987	JF416027	JN049902	Kepler *et al.* (2012a)

Table 1. (Continued).

Species	**Voucher numbers**	**GenBank Accession Numbers***				**References**
		LSU	***TEF***	***RBP1***	***RPB2***	
	RCEF 3632	JF415987	JF416022	—	—	Kepler *et al.* (2012a)
M. flavoviride	ARSEF 2037	AF339531	DQ522353	DQ522400	DQ522454	Spatafora *et al.* (2007)
	TNS F18554	JF415969	JF416011	JN049887	JF415992	Kepler *et al.* (2012a)
	TNS F18553	JF415968	JF416010	JN049886	JF415992	Kepler *et al.* (2012a)
M. owariensis	NBRC 33258	JF415976	JF416017	—	JF415996	Kepler *et al.* (2012a)
M. pseudoatrovirens	TNSF 16380	JF415977	—	JN049893	JF415997	Kepler *et al.* (2012a)
Metarhizium sp.	OSC 110996	EF468832	EF468773	EF468880	EF468928	Sung *et al.* (2007)
	NHJ 12118	EF468829	EF468768	EF468878	EF468927	Sung *et al.* (2007)
	HMAS 199603	JF415986	JF416026	JN049901	JF416005	Kepler *et al.* (2011)
M. taii	ARSEF 5714	AF543787	AF543775	DQ522383	DQ522434	Spatafora *et al.* (2007)
*Microhilum oncoperae**	ARSEF 4358	AF339532	EF468785	EF468891	EF468936	Kepler *et al.* (2017)
Moelleriella africana	ARSEF 7696	AY986917	AY986943	DQ000344	—	Chaverri *et al.* (2015)
M. basicystis	CUP 067745	AY986903	AY986928	DQ000329	—	Chaverri *et al.* (2015)
	CUP 067747	AY986923	AY986950	DQ000351	—	Chaverri *et al.* (2015)
M. epiphylla	CUP 067754	AY986906	AY986931	DQ000332	—	Chaverri *et al.* (2015)
	CUP 067763	AY986907	AY986932	DQ000333	—	Chaverri *et al.* (2015)
M. evansii	CUP 067764	AY986916	AY986942	DQ000343	—	Chaverri *et al.* (2015)
M. insperata	ARSEF 2396	AY518374	DQ070029	EU392713	—	Chaverri *et al.* (2015)
M. libera	ARSEF 7707	EU392593	EU392664	EU392716	—	Chaverri *et al.* (2015)
M. macrostroma	CUP 067508	AY986919	AY986946	DQ000347	—	Chaverri *et al.* (2015)
	ARSEF 7748	AY986920	AY986947	DQ000348	—	Chaverri *et al.* (2015)
M. madidiensis	CUP 067776	AY986915	AY986941	DQ000342	—	Chaverri *et al.* (2015)
M. ochracea	CUP 067777	AY986901	AY986926	DQ000327	—	Chaverri *et al.* (2015)
M. phyllogena	CUP067790	AY986902	AY986927	DQ000328	—	Chaverri *et al.* (2015)
M. raciborskii	BCC 8238	—	DQ384961	DQ385001	DQ452470	Chaverri *et al.* (2015)
M. reineckiana	BCC 2355	—	DQ384970	DQ385011	DQ452474	Chaverri *et al.* (2015)
M. rhombispora	CUP 067538	AY986908	AY986933	DQ000334	—	Chaverri *et al.* (2015)
M. turbinata	CUP 067860	AY986912	AY986938	DQ000339	—	Chaverri *et al.* (2015)

Table 1. (Continued).

Species	Voucher numbers	GenBank Accession Numbers*				References
		LSU	*TEF*	*RBP1*	*RPB2*	
M. umbospora	CUP 067816	AY986904	AY986929	DQ000330	—	Chaverri *et al.* (2015)
M. zhongdongii	CUP 067823	AY986909	AY986934	DQ000335	—	Chaverri *et al.* (2015)
Myriogenospora atramentosa	AEG 96-32	AY489733	AY489628	AY489665	DQ522455	Spatafora *et al.* (2007)
Neohyperdemium piperis	CBS 116719	AY466442	DQ118749	DQ127240	EU369083	Chaverri *et al.* (2005); Johnson *et al.* (2009)
N. pulvinatum	P.C.602	DQ118738	DQ118746	DQ127237	—	Chaverri *et al.* (2005)
Nigelia martiale	CEM 1190	JF415973	—	JN049891	—	Kepler *et al.* (2011)
N. martiale	EFCC 6863	JF415974	JF416015	—	JF415994	Kepler *et al.* (2011)
	HMAS 197472S	JF415973	—	JN049891	—	Kepler *et al.* (2011)
Niveomyces albus	BCC83025	ON103157	ON125015	ON286876	ON125027	Kobmoo *et al.* (2023)
N. coronatus	NY04434800	ON493606	ON513397	ON513399	ON513400	Araújo *et al.* (2022)
N. formicidarum	BCC79346	ON103160	ON125018	ON286878	ON125030	Kobmoo *et al.* (2023)
N. hirsutellae	BCC36631	ON103164	ON125022	ON286882	ON125033	Kobmoo *et al.* (2023)
N. insectorum	CBS 756.73	ON103169	ON125026	ON286887	ON125038	Kobmoo *et al.* (2023)
N. multisynnematus	BCC 90308	ON103163	ON125021	ON286881	ON125032	Kobmoo *et al.* (2023)
Nomuraea rileyi	CBS 806.71	AY624250	EF468787	EF468893	EF468937	Sung *et al.* (2007)
Orbiocrella petchii	NHJ 6209	EU369039	EU369023	EU369061	EU369081	Johnson *et al.* (2009)
O. petchii	NHJ 5318	EU369040	EU369021	EU369062	EU369080	Johnson *et al.* (2009)
Ovicillium attenuattum	**COAD 3271**	**PQ962846**	**PV362936**	—	**PV987274**	**This study**
	COAD 3272	**PQ962847**	**PV362937**	—	**PV987275**	**This study**
Papiliomyces liangshanensis	EFCC 1452	EF468815	EF468756	—	—	Sung *et al.* (2007)
	EFCC 1523	EF468814	EF468755	—	EF468918	Sung *et al.* (2007)
Periglandula ipomoeae	IasaF13	—	KP689568	—	KP689517	Beaulieu *et al.* (2015)
Pleurodesmospora coccorum	CBS 458.73	MH860741	—	—	—	Vu *et al.* 2019
	CBS 459.74	MH860742	—	—	—	Vu *et al.* 2019
	CBS 460.73	MH860743	—	—	—	Vu *et al.* 2019
	COAD 3275	**PQ962852**	**PV362942**	—	**PV987280**	**This study**
	COAD 3276	**PQ962853**	**PV362943**	**PV362891**	**PV987281**	**This study**
	COAD 3277	**PQ962854**	**PV362944**	**PV362892**	**PV987282**	**This study**

Table 1. (Continued).

Species	**Voucher numbers**	**GenBank Accession Numbers***				**References**
		LSU	*TEF*	*RBP1*	*RPB2*	
	VIC 47456	**PQ962855**	—	**PV362893**	**PV987283**	**This study**
	COAD 3280	**PQ962858**	**PV362946**	**PV362895**	**PV987287**	**This study**
	COAD 3281	**PQ962859**	**PV362947**	**PV362896**	**PV987288**	**This study**
	AC 271	**PQ962857**	**PV362945**	**PV362894**	**PV987286**	**This study**
	COAD 3282	**PQ962860**	**PV362948**	**PV362897**	**PV987289**	**This study**
	COAD 3283	**PQ962861**	**PV362949**	**PV362898**	**PV987290**	**This study**
	COAD 3278	—	—	—	**PX405635**	**This study**
	COAD 3279	**PQ962856**	—	—	**PV987285**	**This study**
P. hemileiae	**VIC 47450**	**PQ962848**	**PV362938**	—	**PV987276**	**This study**
	COAD 3273	**PQ962849**	**PV362939**	**PV362888**	**PV987277**	**This study**
	COAD 3274	**PQ962850**	**PV362940**	**PV362889**	**PV987278**	**This study**
	VIC47453	**PQ962851**	**PV362941**	**PV362890**	**PV987279**	**This study**
P. lepidopterorum	DY10501	—	MW834317	MW843315	MW834316	Chen *et al.* (2021)
	DY10502	—	—	MW834318	MW834319	Chen *et al.* (2021)
Pochonia chlamydosporia	CBS 504.66	AF339544	EF469069	—	EF469120	Spatafora *et al.* (2007)
	CBS 101244	DQ518758	DQ522327	DQ522372	DQ522424	Spatafora *et al.* (2007)
Polystromomyces araneae	BCC93301	—	MZ707825	MZ707832	MZ707845	Mongkolsamrit *et al.* (2022)
Purpureomyces khaoyaiensis	BCC 14290	JF415970	JF416012	—	—	Kepler *et al.* (2012a)
	BCC 12687	JF415971	JF416013	—	—	Kepler *et al.* (2012a)
Pseudoniveomyces blattae	BCC53568	ON103168	ON125025	ON286886	ON125037	Kobmoo *et al.* (2023)
Regiocrella camerunensis	ARSEF 7682	DQ118735	DQ118743	DQ127234	—	Chaverri *et al.* (2005)
Rotiferophthora angustispora	CBS 101437	AF339535	AF543776	DQ522402	DQ522460	Spatafora *et al.* (2007)
Samuelsia rufobrunnea	CUP 067858	AY986918	AY986944	DQ000345	—	Chaverri *et al.* (2005)
Shimizuomyces paradoxus	EFCC 6564	EF469083	EF469072	EF469101	EF469118	Sung *et al.* (2007)
S. paradoxus	EFCC 6279	EF469084	EF469071	—	EF469117	Sung *et al.* (2007)
Simplicillium hemileiae	**COAD 3265**	**PQ962839**	**PV362930**	**PV362881**	**PV987268**	**This study**
S. lamellicola	CBS 116.25	NG_042381	DQ522356	DQ522404	DQ522464	Kepler *et al.* (2017)
S. lanosoniveum	CBS 101267	—	DQ522357	DQ522405	DQ522463	Spatafora *et al.* (2007)

Table 1. (Continued).

Species	Voucher numbers	GenBank Accession Numbers*				References
		LSU	*TEF*	*RBP1*	*RPB2*	
S. lanosoniveum	CBS 704.86	AF339553	DQ522358	DQ522406	DQ522464	Kepler *et al.* (2017)
	COAD 3266	**PQ962840**	**PV362931**	**PV362882**	**PV987269**	**This study**
	COAD 3267	**PQ962841**	**PV362932**	**PV362883**	**PV987270**	**This study**
	COAD 3268	**PQ962842**	—	**PV362884**	**PV987271**	**This study**
	COAD 3269	**PQ962843**	**PV362933**	**PV362885**	**PV987272**	**This study**
	AC 484	**PQ962845**	**PV362935**	**PV362887**	—	**This study**
S. subtropicum	**COAD 3270**	**PQ962844**	**PV362934**	**PV362886**	**PV987273**	**This study**
Sungia yongmunensis	EFCC 2135	EF468834	EF468769	EF468877	—	Sung *et al.* (2007)
	EFCC 2131	EF468833	EF468770	EF468876	—	Sung *et al.* (2007)
Tyrannicordyceps fratricida	TNS 19011	JQ257023	JQ257028	—	JQ257021	Kepler *et al.* (2012b)
Ustilaginoidea dichromenae	IB 9228	JQ257010	JQ257025	JQ257013	JQ257018	Kepler *et al.* (2012b)
U. virens	MAFF 240421	JQ257011	JQ257026	—	JQ257017	Kepler *et al.* (2012b)
Verticillium sp.	CBS 102184	AF339564	EF468803	EF468907	EF468948	Sung *et al.* (2007)
Yosiokobayasia kusanagiensis	TNS F18494	JF415972	JF416014	JN049890	—	Kepler *et al.* (2012a)

*New sequences are in **bold**.

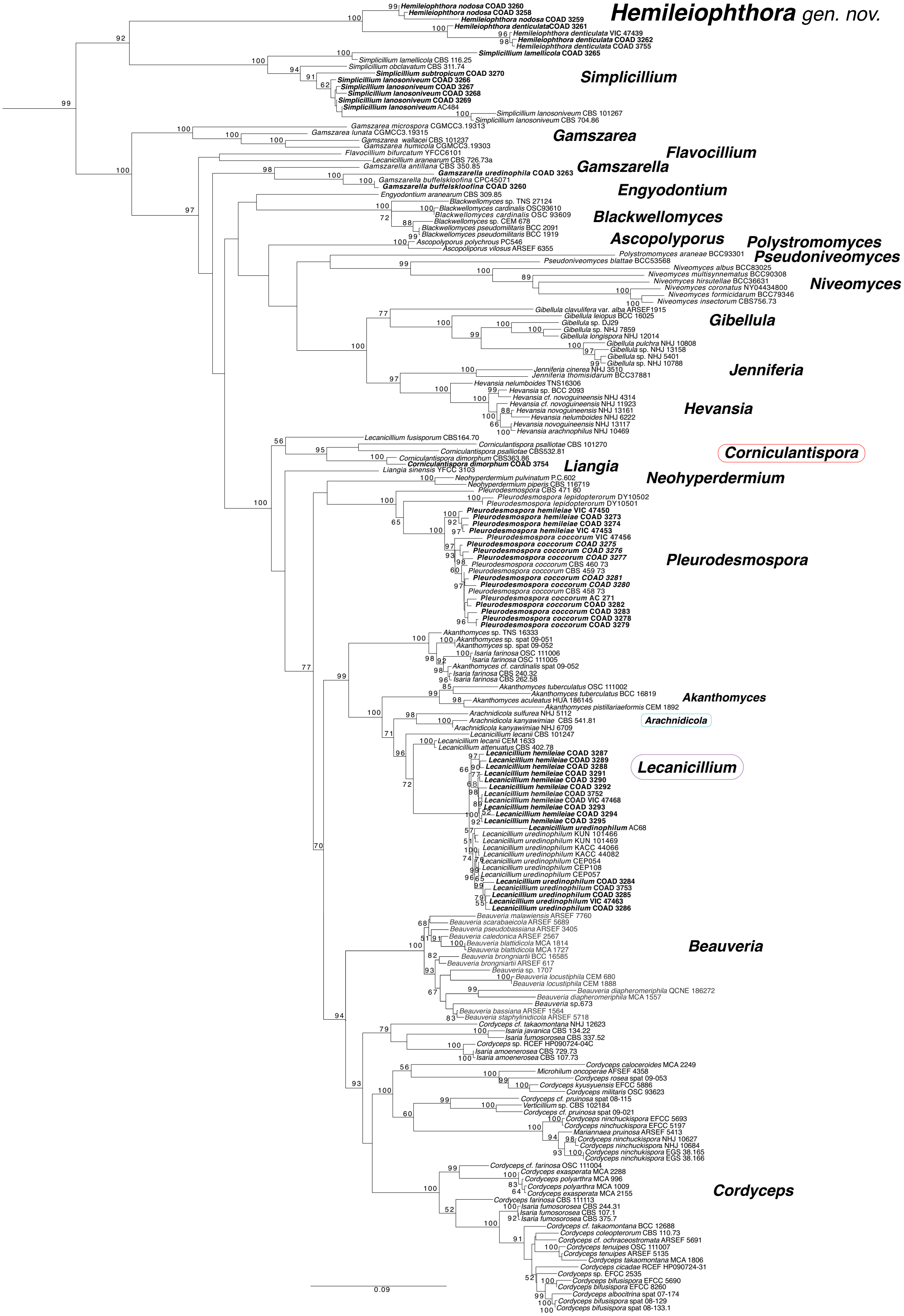

Fig. 1. Phylogenetic relationships of the family *Cordycipitaceae*, including the new genus, *Hemileiophthora* and new species proposed in this study. The tree was obtained from a concatenated dataset of LSU, *TEF*, *RPB1* and *RPB2* using RAxML and nodes with bootstrap support > 70 % are shown.

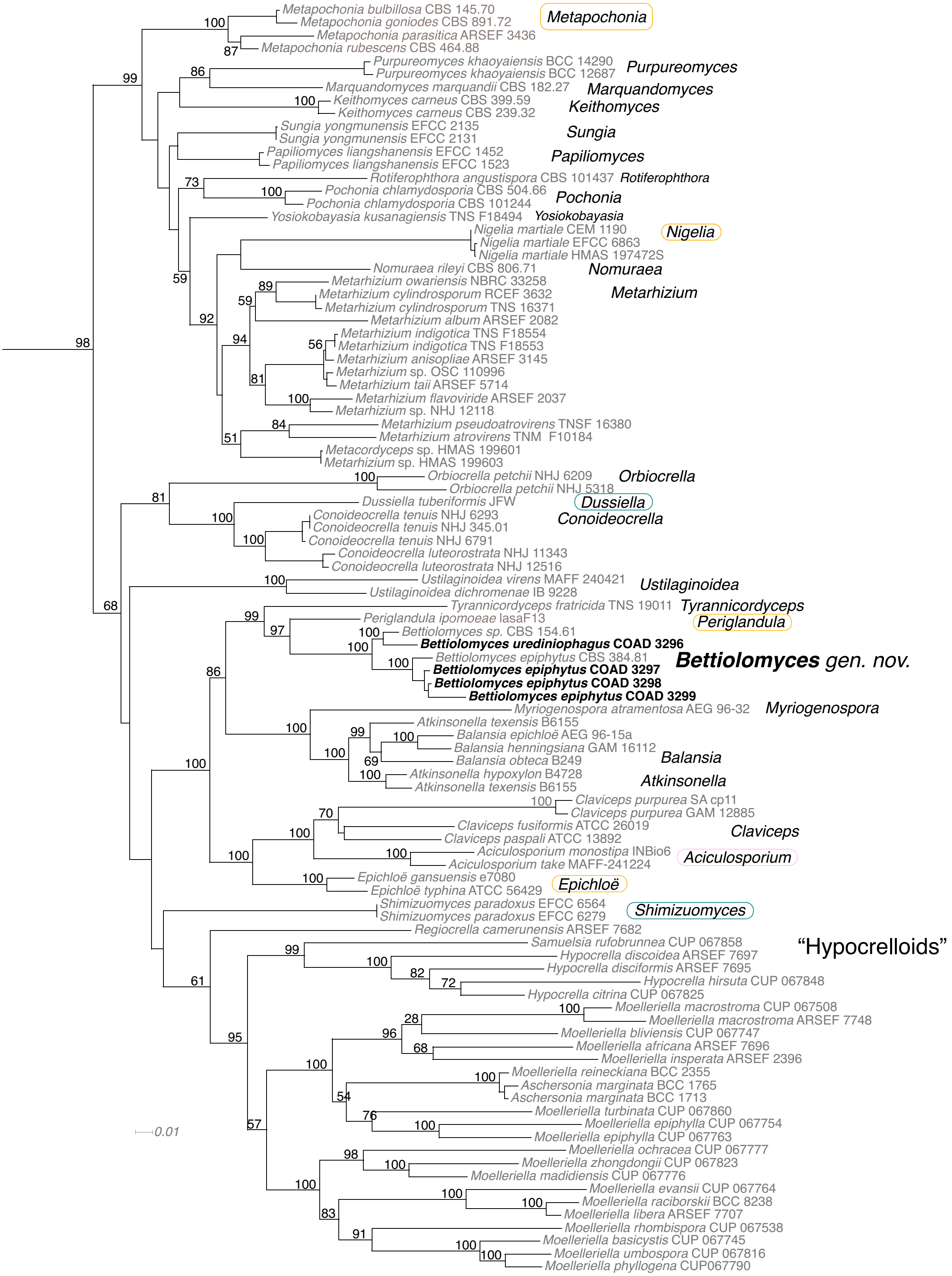

Fig. 2. Phylogenetic relationships of the family *Clavicipitaceae*, including the new genus, *Bettiolomyces* and a new species proposed in this study. The tree was obtained from a concatenated dataset of LSU, *TEF*, *RPB1* and *RPB2* using RAxML and nodes with bootstrap support > 70 % are shown.

TAXONOMY

Bettiolomyces Colmán, H.C. Evans, J.P.M. Araújo & R.W. Barreto, ***gen. nov.*** MB 853084.

Etymology: In reference to Wagner Bettiol, Brazilian plant pathologist and biocontrol scientist.

Description: *Asexual morph* Simplicillium-like. *Phialides* produced from aerial hyphae or short branches, mostly solitary or in whorls, filiform-aculeate, hyaline, smooth. *Conidia* formed in subglobose mucilaginous heads or in fascicles at the phialide tip, sometimes dimorphic: *macroconidia* fusiform to falcate, often with acute ends, aseptate, guttulate, hyaline, smooth; *microconidia* ellipsoidal to slightly falcate, with rounded ends, aseptate, hyaline, smooth. *Sexual morph* unknown.

Type: *Bettiolomyces epiphytus* (Hansf.) Colmán, H.C. Evans, J.P.M. Araújo & R.W. Barreto

Notes: *Bettiolomyces* is a new genus of mycoparasite, erected to accommodate isolates placed originally in *Verticillium epiphytum* and obtained from parasitized *H. vastatrix* pustules from Ethiopia. This species is phylogenetically closely related to *Tyrannnicordyceps fratricida*, a *Claviceps* mycoparasite. On the other hand, the new genus forms a sister clade with the genus *Peringlandula*, but can be easily differentiated from this genus based on contrasting features exclusive of *Periglandula* namely, the seemingly strict symbiotic association with members of the *Convolvulaceae* and the in vitro production of sterile synemata-like structures and only white sterile hyphal mats in vivo on their *Convolvulaceae* hosts (Steiner *et al.* 2011). The genus *Verticillium* s. str. presently includes only plant pathogenic species and belongs to the *Trichosphaeriaceae* as indicated in MycoBank. Zare & Gams (2001) had *V. epyphitum* indicated by those authors as, “in a residual group in need of taxonomy reappraisal”. The morphology of *Bettiolomyces* is dissimilar to *Verticillium* s. str. given the absence of verticillate conidiophores. In *B. epyphitus*, conidiophores are simple as those of *Simplicillium* and related taxa. This genus forms a robust clade within the *Clavicipitaceae* with taxa that have also been found parasitizing fungi.

Bettiolomyces epiphytus (Hansf.) Colmán, H.C. Evans, J.P.M. Araújo & R.W. Barreto, ***comb. nov.*** MB 853085.
Basionym: *Verticillium epiphytum* Hansf., *Proc. Linn. Soc. Lond.* **155**: 41. 1943.

For a complete description see Zare & Gams (2001).

Specimens examined: **Cameroon**, Nguélémendouka, on *Hemileia vastatrix*, 26 Jun. 2017, *M. Kapeua-Ndacnou* (culture COAD 3297). **Ethiopia**, Tepi, on *H. vastatrix*, 20 Sep. 2017, *K. Belachew-Bekele* (VIC 47473, culture COAD 3298); Tepi, on *H. vastatrix*, 20 Sep. 2017, *K. Belachew-Bekele* (VIC 47474, culture COAD 3299).

Notes: This species has been fully described and illustrated by Zare & Gams (2001). It was originally described from Africa (Uganda) as a mycoparasite of *Pseudocercospora triumfettigena* (as *Helminthosporium triumfettae*) by Hansford (1943). It has also been isolated from uredinia of an unidentified rust and from *H. vastatrix* (Sung *et al.* 2001). Our newly collected isolates were also only found in Africa and had a morphology which was recognized as being very close to the earlier published descriptions. In our phylogenetic study it grouped in a clade together with *Verticillium epiphytum* (CBS 154.61). As indicated below, *B. epiphytus* is phylogenetically and morphologically distinct from the second species in the genus proposed herein.

Bettiolomyces urediniophagus Colmán, H.C. Evans, J.P.M. Araújo & R.W. Barreto, ***sp. nov.*** MB 853086. Fig. 3.

Etymology: In reference to its growth on asexual pustules (uredinia) of a rust fungus.

Typus: **Brazil**, Espírito Santo, Sooretama, on *H. vastatrix*, 4 Apr. 2015, *A.A. Colmán* (**holotype** VIC 47472, ex-type culture COAD 3296).

Description: *Colonies* white floccose on pustules with conidia in subglobose heads. *Mycelium* hyaline, branched, septate, 1–1.5 µm wide, thin-walled. *Conidiophores* restricted to conidiogenous cells mostly produced from aerial hyphae. *Conidiogenous cells* enteroblastic phialidic, arising from prostrate hyphae, mostly solitary or in up to 4 whorls, filiform-aculeate, 31–100 × 1–1.5 µm, hyaline, smooth. *Conidia* formed in subglobose mucilaginous heads or in fascicles at the phialide tip, dimorphic: *macroconidia* fusoid to subpyriform, 7–9 × 1.5–2.5 µm, often with acute ends, aseptate, guttulate, hyaline, smooth; *microconidia* ellipsoidal, straight to slightly curved, 4–6 × 1–1.5 µm, with rounded ends, aseptate, hyaline, smooth. *Chlamydospores* often present, terminal or intercalary, globose to subglobose, hyaline, thick-walled.

Culture characteristics: Colonies on PDA 30–40 mm diam. after 10 d at 25 °C; convex, margin entire, aerial mycelium floccose whitish, humid centrally, reverse brownish centrally, sporulation abundant. Colonies on PCA 40–45 mm diam. after 10 d at 25 °C; umbonate, margin entire, aerial mycelium floccose white, reverse brown centrally, sporulation abundant.

Notes: This species has as distinguishing feature dimorphic conidia, which are smaller than those of *B. epiphytus* and less curved than in the type species. Phylogenetically, our isolate grouped with the authentic strain of *Bettiolomyces* (*Verticillium*) *epyphitus* (CBS 384.81), obtained from *P. triumfettigena.* Nevertheless, morphology and geographical distribution justify its recognition as a separate species in the newly proposed genus.

Corniculantispora dimorpha (Treschew) Zare & W. Gams, *Nova Hedwigia* **73**: 21. 2001. MB 484539.

For a complete description see Zare & Gams (2001).

Specimen examined: **Ethiopia**, Agaro-Center, on *H. vastatrix*, 24 Sep. 2017, *K. Belachew-Bekele* (VIC 47459, culture COAD 3754).

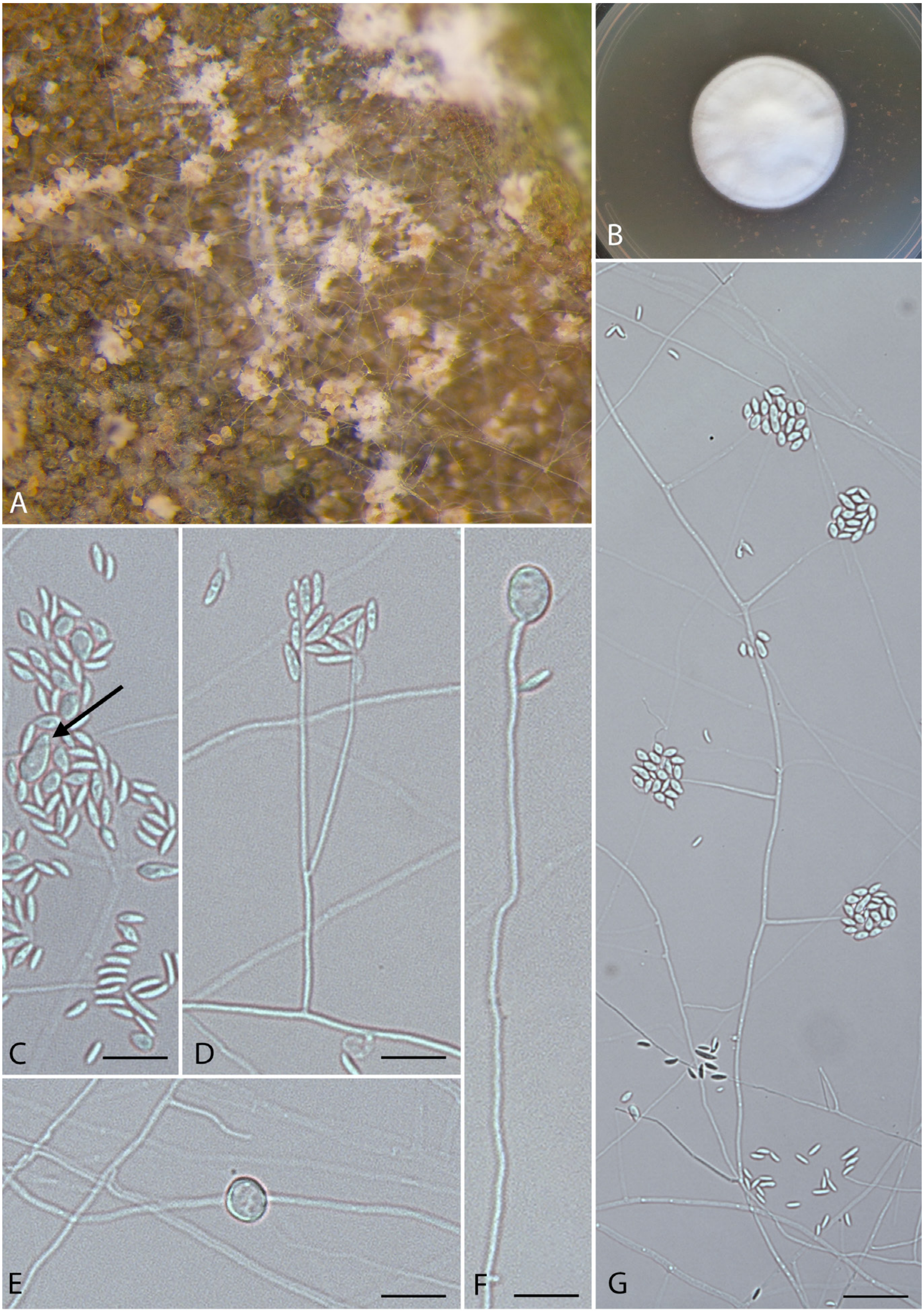

Fig. 3. *Bettiolomycesurediniophagus sp. nov.* **A.** Uredinia of *Hemileia vastatrix* covered and consumed by *B. urediniophagus*. **B.** Colony on potato dextrose agar after 10 d at 25 °C. **C.** Macroconidia and microconidia. **D.** Two filiform phialidic conidiogenous cells. **E.** Chlamydospore formed intercallarly on hyphae. **F.** Chlamydospore formed apically on hyphae. **G.** Conidiogenous cells produced along aerial hyphae. Scale bars = 20 µm.

Notes: The genus *Corniculantispora* has recently been established by Khonsanit *et al.* (2024) to accommodate some species formerly placed in *Lecanicillium* s. lato, which remains phylogenetically unresolved. This new genus includes three species, namely: *C. aranearum*, *C. dimorpha* and *C. psalliotae*. *Corniculantispora dimorpha* is a species morphologically similar to *C. psalliotae*, but differs from this species by having aphanophialides and macroconidia (Zare & Gams 2001). This species was commonly found growing on *Agaricus* spp. and was also recorded on *Puccinia coronata* (Gams 1971). Our isolate was only found on a single sample from Ethiopia. This appears to be the first confirmed report of *C. dimorpha* on *Hemileia* spp. pustules worldwide.

Gamszarella buffelskloofina Crous, *Persoonia* **51**: 391. 2023. MB 850614.

Specimen examined: **Ethiopia**, Sedi-Loya, on *H. vastatrix*, 16 May 2017, *K. Belachew-Bekele* (VIC 47443, culture COAD 3264).

For a complete description see Crous *et al.* (2023).

Notes: The genus *Gamszarella* was established by Crous *et al.* (2023) to accommodate an entomogenous species isolated from a dead insect on leaf litter at the Buffelskloof Nature Reserve, South Africa. The genus belongs to *Cordycipitaceae* and includes a species formerly placed in *Lecanicillium*, *G. antillana*, whereas a second species of *Lecanicillium*, *L. magnispora*, was found to be better accommodated in *Corpulentispora*, rather than *Gamszarella* (Crous *et al.* 2023, Khonsanit *et al.* 2024). Phylogenetically, COAD 3264, isolated from pustules of *H. vastatrix*, grouped with *G. buffelskloofina* with strong support. This is the first report of *G. buffelskloofina* as a mycoparasite. Similarly to other taxa in the *Cordycipitaceae, G. buffelskloofina* appears to have the ability to grow on chitinous substrates including fungi and arthropods.

Gamszarella uredinophila Colmán, H.C. Evans, J.P.M. Araújo & R.W. Barreto, ***sp. nov.*** MB 853082. Fig. 4.

Etymology: In reference to the association with uredinia of *Hemileia*, on which *G. uredinophila* produces its colonies.

Typus: **Brazil**, Minas Gerais, Florestal, on *H. vastatrix*, 16 Jun. 2016, *A.A. Colmán* (**holotype** VIC 47442, ex-type culture COAD 3263).

Description: *Colonies* white, plumose to powdery on rust pustules. *Mycelium* hyaline, smooth, branched, septate, 1.5–2 µm diam. *Conidiophores* erect, branched, verticillate up to 110 × 1.5–2 µm, with 1–6 verticils, each verticil with 2–4 conidiogenous cells. *Conidiogenous cells* holoblastic, monoblastic or polyblastic, filiform, with sympodial and sparingly denticulate fertile apex, slightly swollen at base, gradually tapering towards the apex, 10–22 × 1–2 µm, hyaline, smooth; denticles 1 µm long. *Conidia* ovoid to ellipsoid, 4–11 × 1–2 µm, aseptate to rarely 1-septate, hyaline, thin and smooth-walled.

Culture characteristics: Colonies on PDA 15–17 mm diam. after 10 d at 25 °C; convex, margin entire, aerial mycelium floccose whitish, reverse brownish centrally, sporulation scarce. Colonies on PCA 16–20 mm diam. after 10 d at 25 °C; umbonate, margin entire, aerial mycelium floccose white, reverse brown centrally, sporulation abundant.

Notes: *Gamszarella uredinophila* has a similar morphology to *G. buffelskloofina* but some morphological distinctions are noticeable. It has longer conidiophores (45–110 × 1.5–2 µm) and conidia (4–11 × 1–2 µm) than *G. buffelskloofina*. The morphology of both species of *Gamszarella* resembles that of *Calcarisporium*, a genus including several species that parasitizes other fungi, such as *Cordyceps* and *Xylaria* (Sun *et al.* 2017). Nevertheless, molecular studies have placed *Gamszarella uredinophila* outside *Calcarisporium* (*Calcarisporiaceae*) and within the *Gamszarella* clade (*Cordycipitaceae*) (Fig. 2). *Gamszarella uredinophila* is close to *G. antillana* (Crous *et al.* 2023), but differs morphologically from this species because of the presence of denticulate conidiogenous cells, which are present in most members of *Gamszarella* but not in *G. antillana.* Another taxon which is similar to *G. uredinophila* and was also found on *H. vastatrix* in Mexico by Carrión & Rico-Gray (2002) is *Calcarisporium ovalisporum*. The record of *C. ovalisporum* in Mexico was supported only by morphological data and it is possible that, upon recollection and reexamination under molecular scrutiny, the fungus identified by Carrión & Rico-Gray's will be found to belong to *G. uredinophila.* To our knowledge, this is the first report of the genus *Gamszarella* from Brazil.

Hemileiophthora Colmán, H.C. Evans, J.P.M. Araújo & R.W. Barreto, ***gen. nov.*** MB 853083.

Etymology: In reference to the destruction (from the Greek *phthora* = destruction) of the host, *Hemileia vastatrix*.

Description: *Colonies* white, dense and powdery on rust pustules. *Mycelium* consisting of hyaline, branched, septate 12 µm wide, thin-walled hyphae.. *Conidiophores* erect or prostrate, difficult to distinguish from supporting mycelium, solitary or in groups arising from aerial mycelium laterally or terminally, filiform, mostly unbranched or sparsely branched, septate. *Conidiogenous cells* intercalary or terminal, cylindrical, slightly tapering towards the slightly inflated apex. *Conidia* holoblastic, in apical or lateral tufts or solitary, cylindrical, apex rounded, base acuminate, aseptate, hyaline, smooth. *Sexual morph* unknown.

Type species: *Hemileiophthora nodosa* Colmán, H.C. Evans, J.P.M. Araújo & R.W. Barreto

Notes: *Hemileiophthora* is considered here as representing a new Sporothrix-like genus in the *Cordycipitaceae*, similar to *Niveomyces* (Araújo *et al.* 2022). It is phylogenetically closely related to members of the genus *Simplicillium* (Zare & Gams 2001). Nevertheless, the genus *Simplicillium* is characterized by having predominantly solitary phialides arising from the aerial hyphae and conidial masses which are either in globose slimy heads, or in short chains, or formed

Fig. 4. *Gamszarella uredinophila sp. nov.* **A.** Colony on potato dextrose agar after 10 d at 25 °C. **B.** Uredinia of *Hemileia vastatrix* colonized by *G. uredinophila*. **C, D.** Conidiophores bearing verticillate conidiogenous cells produced along the aerial hyphae with clusters of conidia. Scale bars = 20 µm.

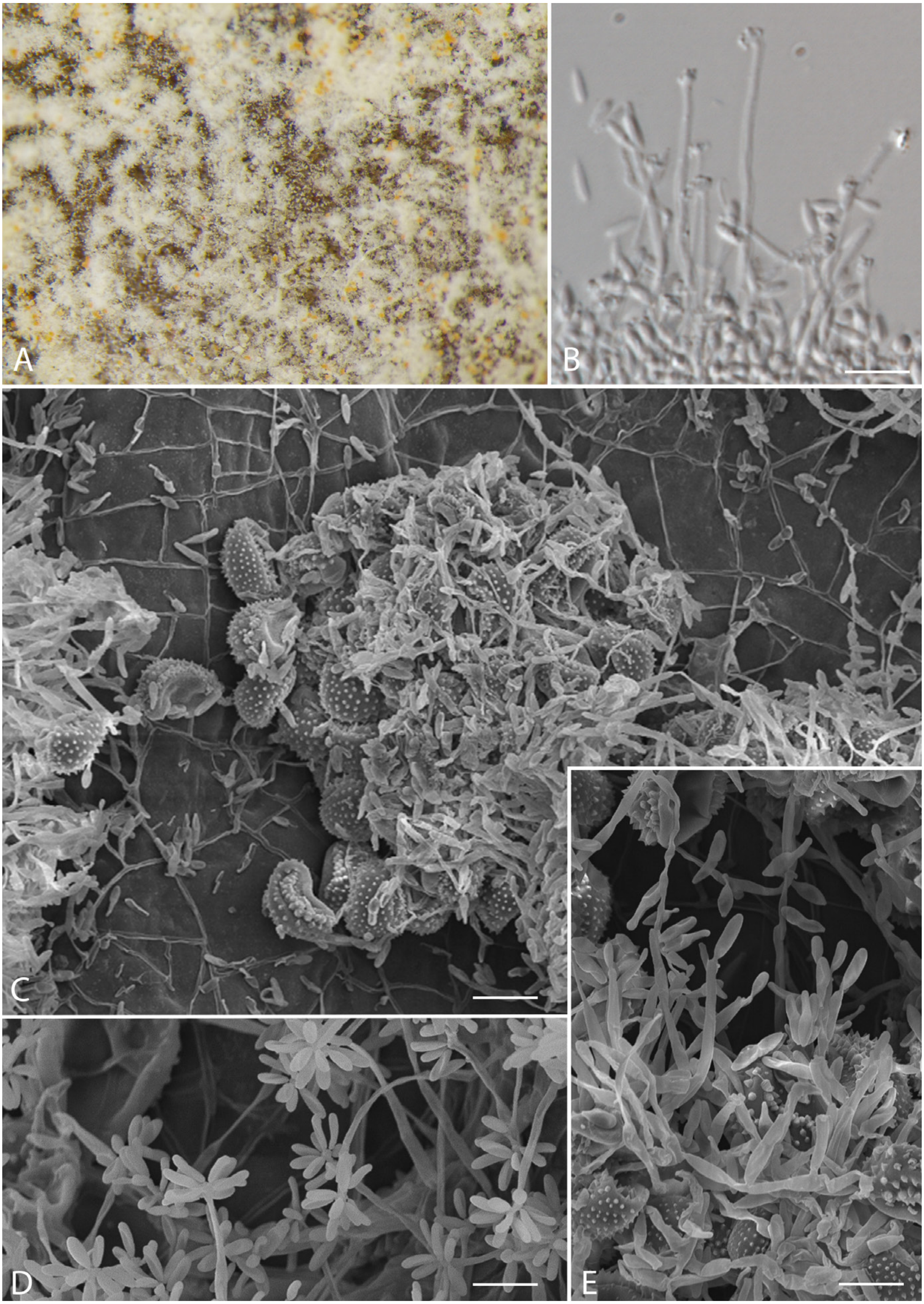

Fig. 5. *Hemileiophthora denticulata*. **A.** Uredia of *Hemileia vastatrix* covered by *H. denticulata*. **B.** Denticulate conidiogenous cells. **C.** *H. denticulata* consuming udiniospores. **D.** Conidial formation at the tips of conidiogenous cells. **E.** Conidiogenous cells and *H. vastatrix* urediniospores. Scale bars: B, D = 5 μm; C, E = 10 μm.

in sympodial succession (Zare & Gams 2001, Nonaka *et al.* 2013). This is in sharp contrast to the morphology of *Hemileiophthora* which has holoblastic, denticulate conidiogenous cells and forms dry tufts of conidia. Another genus resembling the newly proposed genus is *Sporothrix*, of which *S. guttuliformis* has been reported as a mycoparasite of *H. vastatrix* (Carrión & Rico-Gray 2002). Still within *Cordycipitaceae*, the mycoparasitic genus *Niveomyces* also exhibits similar denticles on its conidiogenous cells (Araújo *et al.* 2022). Although *Hemileiophthora* has a similar morphology to *Sporothrix*/*Niveomyces* and related species, the molecular data generated in this study clearly show that it is not closely related to these genera, as *Hemileiophthora* is positioned among the most basal lineages in the family, sister to *Simplicillium*. The new genus belongs to the *Cordycipitaceae* (*Hypocreales*), as well as *Niveomyces*, whereas *Sporothrix s. str.*, and related taxa, belong to the *Ophiostomataceae* (*Ophiostomatales*).

Hemileiophthora denticulata Colmán, H.C. Evans, J.P.M. Araújo & R.W. Barreto, ***sp. nov.*** MB 853066. Fig. 5.

Etymology: In reference to its denticulate conidiogenous cells.

Typus: **Ethiopia**, Gamadro, on *H. vastatrix*, 21 Sep. 2017, *K. Belachew-Bekele* (**holotype** VIC 47438, ex-type culture COAD 3261).

Description: *Colonies* white, floccose and dense on *H. vastatrix* pustules. *Mycelium* consisting of hyaline, smooth, branched, 1.5–2 µm diam., septate hyphae. *Conidiophores* erect, simple, in dense groups formed over infected rust pustules, arising laterally or terminally from aerial hyphae, filiform, 70–82(–96) × 1–2 µm, mostly unbranched or sparsely branched, septate, hyaline, smooth. *Conidiogenous cells* holoblastic, raduliform, intercalary and terminal, cylindrical, 21–32 × 1–1.5 µm, with an apex bearing a cluster of 2–4 blunt denticles, 2–3.5 × 1–2 µm, distance between denticle clusters 2.5–5 µm, hyaline. *Conidiogenous loci* solitary or in groups of 1–3 per conidiogenous cells denticles, blunt, 0.5–1 µm projections, lateral or terminal, either solitary or in groups bearing tufts of conidia. *Conidia* fusiform to subcylindrical, 4–8 × 1–1.5 µm, apex obtuse tapering towards the base, aseptate, hyaline, smooth.

Culture characteristics: Very slow-growing (12–19 mm diam. after 16 d), irregular to convex or flat, raised centrally, with papillate to aculeate projections, undulate to lobate margins, dense cottony to powdery aerial mycelium or mostly immersed and stromatic, white with buff centre, slightly pigmenting the medium in amber (PCA in the dark), reverse either white or pale luteous with cinnamon veins (PDA), or luteous to pale luteous (PCA), colony composed of narrow, thin-walled mycelium; either with no sporulation (under 12 h light-regime) or sporulating abundantly (in the dark).

Specimens examined: **Ethiopia**, Gamadro, on *H. vastatrix*, 21 Sep. 2017, *K. Belachew-Bekele* (VIC 47439); Sheko, on *H. vastatrix*, 19 Sep. 2017, *K. Belachew-Bekele* (VIC 47440, culture COAD 3262); Gimbo, on *H. vastatrix*, 17 Sep. 2017, *K. Belachew-Bekele* (VIC 47441, culture COAD 3755).

Notes: *Hemiliophthora denticulata* is phylogenetically close to *H. nodosa*. However, there are clear morphological differences between the two species: *H. denticulata* has longer conidiophores [70–82(–96) vs 34–62(–80), in *H. nodosa*] and conidia (4–8 × 1–1.5 vs 3.5–6 × 1–2 µm, in *H. nodosa*). Also, the molecular evidence from our phylogenetic results supports the establishment of two distinct species of *Hemiliophthora*.

Hemileiophthora nodosa Colmán, H.C. Evans, J.P.M. Araújo & R.W. Barreto, ***sp. nov.*** MB 853064. Fig. 6.

Etymology: In reference to the nodes from which conidia are produced.

Typus: **Brazil**, Minas Gerais, Viçosa, Infectarium, Departamento de Fitopatologia, Universidade Federal de Viçosa, on *H. vastatrix*, 22 Jun. 2016, *A.A. Colmán* (**holotype** VIC 44431, ex-type culture COAD 3258).

Description: *Colonies* white, downy/powdery, on pustules of *H. vastatrix*. *Mycelium* hyaline, sparingly branched, partly immersed in rust sori but mostly superficial. *Conidiophores* often restricted to long filiform conidiogenous cells, erect, formed singly or in groups over infected rust pustules, arising laterally or terminally from aerial hyphae, 34–62(–80) × 1–2 µm, mostly unbranched, bearing isolate lateral conidiogenous loci on lateral bulges or intercalary or terminal fertile nodes with several conidiogenous loci at 2.5–5 µm intervals at the upper portion. *Conidiogenous loci* solitary or in groups of obtuse projections, 2–3.5 × 1–2 µm. *Conidia* holoblastic, subcylindrical, oblong to fusiform, dry, either solitary or forming apical or intercalary tufts on nodes of conidiogenous cells, 3.5–6 × 1–2 µm, apex rounded attenuated towards the base, aseptate, hyaline, smooth.

Culture characteristics: Colonies on PDA, slow growing 5–15 mm diam. after 30 d; umbonate, margin entire, aerial mycelium scarce floccose, whitish to yellowish, reverse brown at the centre and yellow at periphery, with yellow to orange diffusate, sporulation abundant. Colonies on PCA slow growing 5–10 mm diam. after 30 d; umbonate, margin entire, aerial mycelium floccose whitish to yellowish, reverse brown at the centre to yellow at periphery, soluble yellow to orange pigment present, sporulation abundant.

Specimens examined: **Ethiopia**, Tepi, on *H. vastatrix*, 19 Sep. 2017, *K. Belachew-Bekele* (VIC 47436, culture COAD 3259); Bebeka, on *H. vastatrix*, 17 Sep. 2017, *K. Belachew-Bekele* (VIC 47437, culture COAD 3260).

Notes: *Hemileiophthora nodosa* is phylogenetically close to *H. denticulata* described here. As well as morphological differences (see above), in culture *H. nodosa* produces a yellow to orange diffusive pigment that in the PDA media with abundant sporulation. The clade of *H. nodosa* included isolates from Ethiopia and Brazil, showing that this species can be distributed throughout the main coffee producing regions in both countries.

Lecanicillium hemileiae Colmán, H.C. Evans, J.P.M. Araújo & R.W. Barreto, ***sp. nov.*** MB 853080. Figs 7, 8.

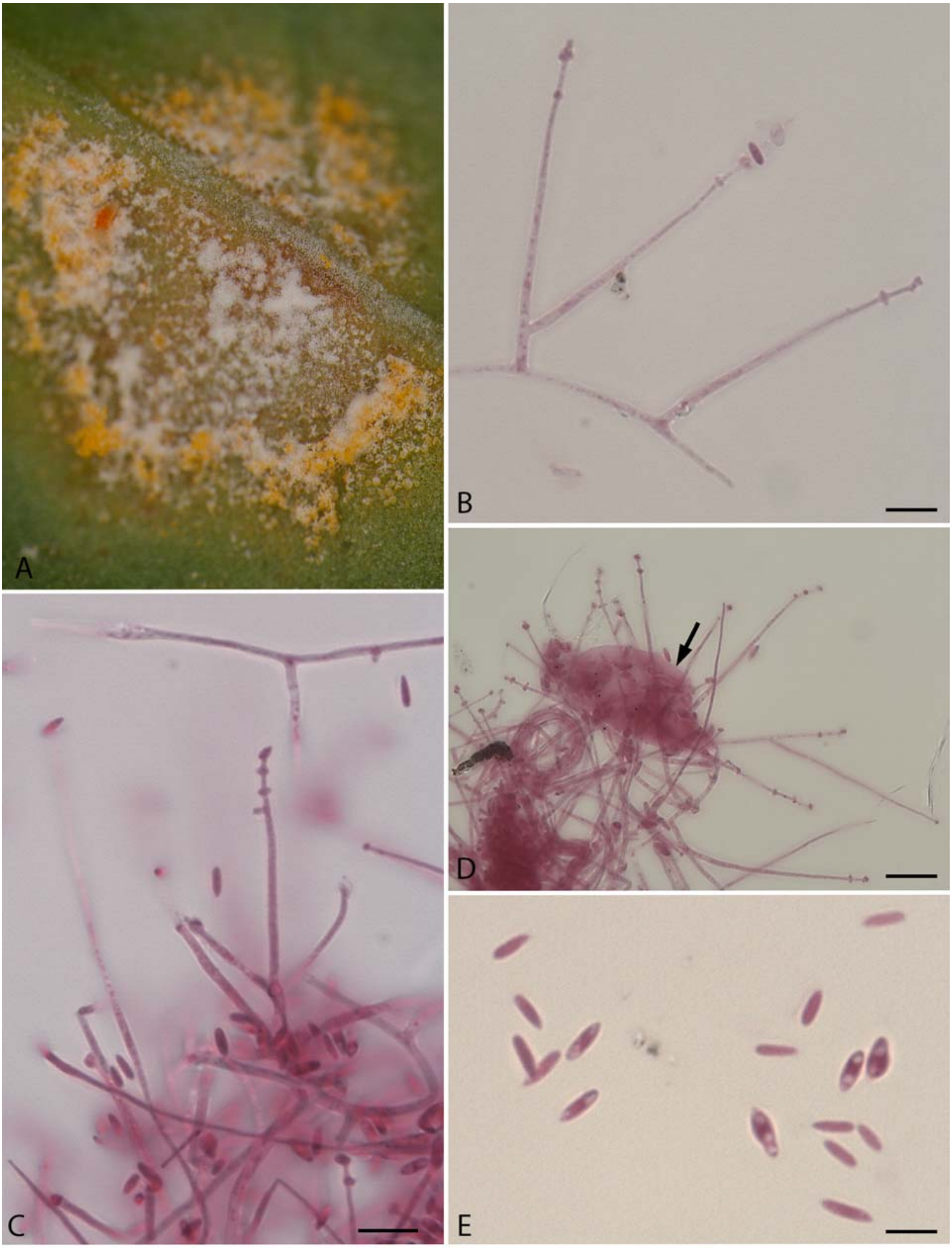

Fig. 6. *Hemileiophthora nodosa*. **A.** *Hemileia vastatrix* uredinia colonized and partially consumed by *H. nodosa* from the centre. **B, C.** Denticulate conidiogenous cells. **D.** Conidiogenous cells emerging from one highly degraded urediniospore (arrowed). **E.** Conidia. Scale bars: B, C = 10 μm; D = 15 μm; E = 5 μm.

Etymology: In reference to the host genus *Hemileia*.

Typus: **Ethiopia**, Dale Mesencho, on *H. vastatrix*, 29 Jul. 2017, *K. Belachew-Bekele* (**holotype** VIC 47467; ex-type culture COAD 3292).

Description: *Colonies* woolly on uredinia, accompanied by abundant small mucilaginous droplets hanging on top of narrow phialides "appearing as if floating" over and between the uredinia of the rust pustules. *Mycelium* slender, branched, 1.5–2 µm diam, hyaline, smooth. *Phialides* filiform, 20–60 × 1–2.5(–3) µm, produced mostly singly or in whorls of 3–4(–5) phialides, on prostrate hyphae. *Conidia* formed in minute mucilaginous heads, enteroblastic, 3–9 × 2–3 µm, cylindrical, oblong, or ellipsoid, mostly aseptate, rarely uniseptate, hyaline, smooth.

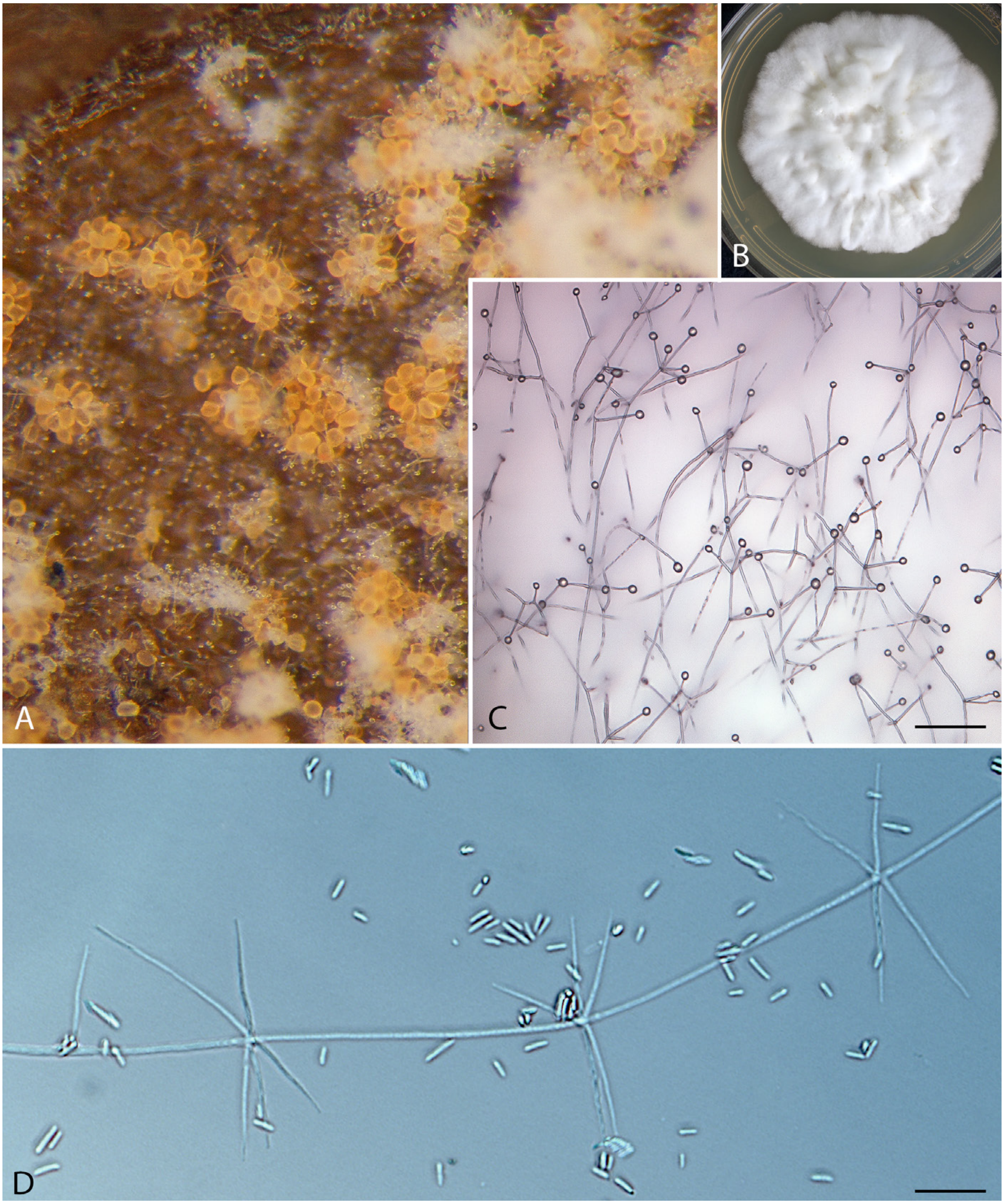

Fig. 7. *Lecanicillium hemileiae*. **A.** *Hemileia vastatrix* uredinia colonized by *L. hemileiae*. **B.** Colony on potato dextrose agar after 10 d at 25 °C. **C.** Conidiogenous cells bearing apical drops of mucilaginous conidia under dissecting microscope. **D.** Prostrate hypha bearing whorls of few phialidic conidiogenous cells and detached conidia. Scale bars: C = 40 µm; D = 10 µm.

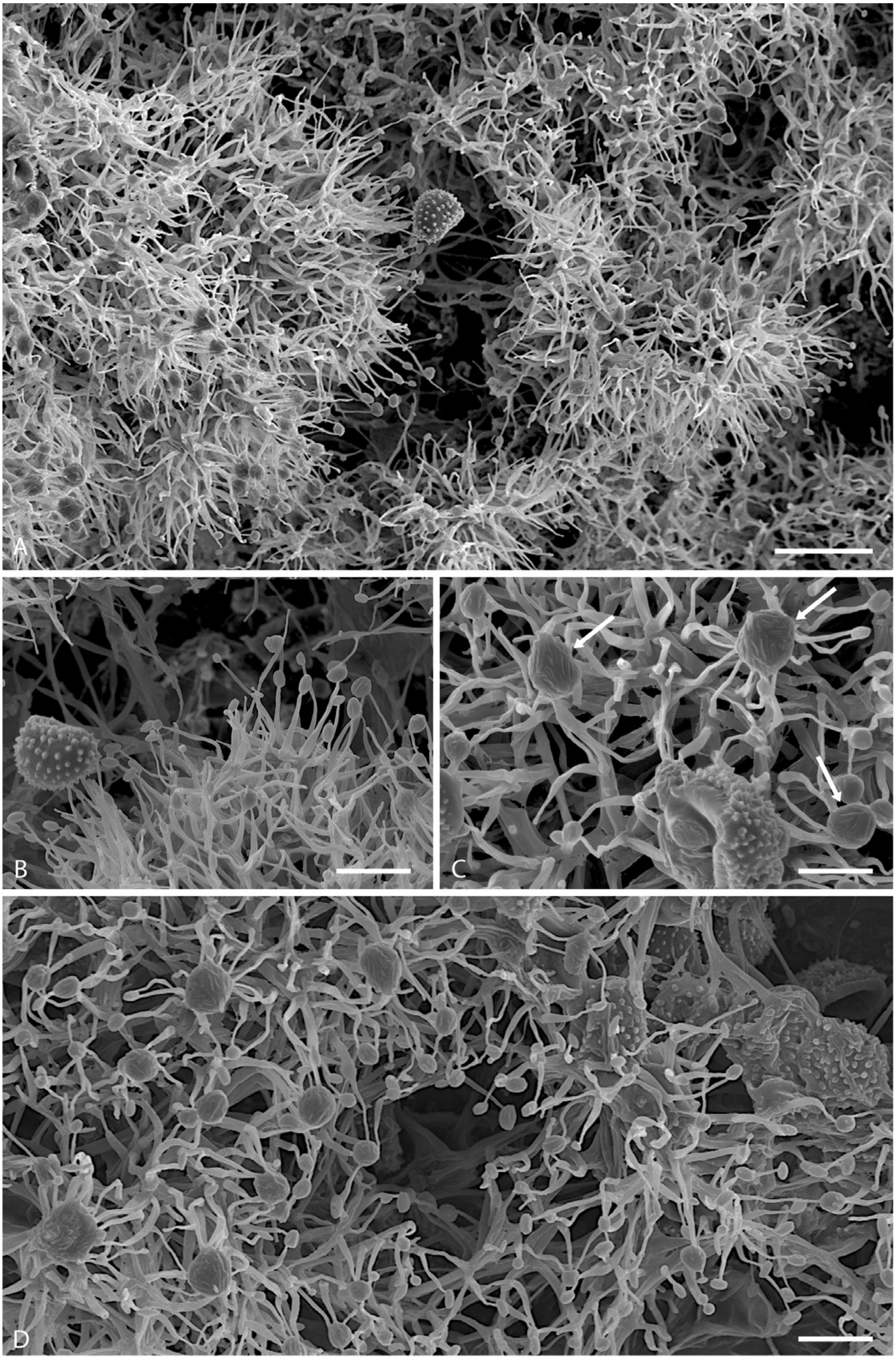

Fig. 8. *Lecanicillium hemileiae* under scanning eletron microscopy. **A.** Single urediniospore of *Hemileia vastatrix* surrounded by extensive colony of *L. hemileiae*. **B.** Close-up of **A** showing detail of apical mucilaginous aggregates of conidia on top of phialides of *L. hemileiae*. **C, D**. *Lecanicillium hemileiae* consuming verrucose urediniospores of *H. vastatrix*. Note mucilaginous aggregates with individual conidia discernible (arrowed) on C. Scale bars: A = 20 µm; B–D = 10 µm.

Culture characteristics: Colony growth slow (30–45 mm diam. after 10 d); convex or umbonate, margin entire, whitish with dense cottony aerial mycelium, humid, reverse brownish centrally, sporulation scarce on PDA, abundant on PCA.

Specimens examined: **Cameroon**, Nguélémendouka, on *H. vastatrix*, 20 Jun. 2017, *M. Kapeua-Ndacnou* (culture COAD 3291). **Ethiopia**, Gore-Hundigda, on *H. vastatrix*, 18 Dec. 2017, *K. Belachew-Bekele* (VIC 474665, culture COAD 3288); Jimma-Eladale, on *H. vastatrix*, 18 Dec. 2017, *J.P.M. Araújo, H.C. Evans & K. Belachew-Bekele* (culture COAD 3287); Haro-Agaro, on *H. vastatrix*, 29 Sep. 2017, *JJ.P.M. Araújo, H.C. Evans & K. Belachew-Bekele* (culture COAD 3289); Shebedino-sedaka, on *H. vastatrix*, 22 Dec. 2017, *J.P.M. Araújo, H.C. Evans & K. Belachew-Bekele* (VIC 47466, culture COAD 3290); Jimma-Farm, on *H. vastatrix*, 22 Dec. 2017, *J.P.M. Araújo, H.C. Evans & K. Belachew-Bekele* (VIC 47468); Dilla Zuria chichu, on *H. vastatrix*, 23 Dec. 2017, *J.P.M. Araújo, H.C. Evans & K. Belachew-Bekele* (VIC 47469, culture COAD 3292); Bebeka, on *H. vastatrix*, 17 Sep. 2017, *J.P.M. Araújo, H.C. Evans & K. Belachew-Bekele* (VIC 47470, culture COAD 3294); Gamadro, on *H. vastatrix*, 21 Sep. 2017, *J.P.M. Araújo, H.C. Evans & K. Belachew-Bekele* (VIC 47471, culture COAD 3295).

Notes: *Lecanicillium hemileiae* has a similar morphology to that described for *L. uredinophilum* (Park *et al.* 2015, Manfrino *et al.* 2022). Nevertheless, it has somewhat longer phialides (20–60 µm) as compared to *L. uredinophilum* (5–50 µm). Based on our phylogenetic results, the two species form sister clades. Although all species of *Lecanicillium* associated with rusts (including those described in this study) form a single clade, they can be distinguished on a combination of morphology, rust host and geographical distribution. *Lecanicillium uredinophilum* was originally isolated from *Coleosporium* sp. and *Pucciniastrum agrimoniae* in Korea whereas all isolates of *L. hemileiae* were from Africa (Cameroon and Ethiopia) on *H. vastatrix*.

Lecanicillium uredinophilum M.J. Park *et al.*, *Mycotaxon* **130**: 997. 2015. MB 814832.

For detailed descriptions see Park *et al.* (2015) and Manfrino *et al.* (2022).

Specimens examined: **Brazil**, Minas Gerais, Viçosa, on *H. vastatrix*, 14 Mar. 2015, *A.A. Colmán* (VIC 47460, culture COAD 3284); Minas Gerais, Universidade Federal de Viçosa, Viveiro do Café, on *H. vastatrix*, 26 Mar. 2015, *A.A. Colmán* (VIC 47461, culture COAD 3754). **Ethiopia**, Aman, on *H. vastatrix*, 17 Sep. 2017, *J.P.M. Araújo, H.C. Evans & K. Belachew-Bekele* (VIC 47462, culture COAD 3285); Sheko, on *H. vastatrix*, 19 Sep. 2017, *J.P.M. Araújo, H.C. Evans & K. Belachew-Bekele*, Bifftu, on *H. vastatrix*, 17 Sep. 2017, *J.P.M. Araújo, H.C. Evans & K. Belachew-Bekele* (VIC 47464, culture COAD 3286).

Notes: *Lecanicillium uredinophilum* is known as a rust mycoparasite but is also capable of colonizing other chitinous hosts such as an undetermined insect in China (Wei *et al.* 2018), and is also known from caterpillars in Tibet (Meng *et al.* 2022). Additionally, Manfrino *et al.* (2022) have isolated this species from other insect hosts, i.e. *Myzus persicae* and *Trialeurodes vaporariorum*, in Argentina. This species was the most frequently collected mycoparasite of *H. vastatrix* in Brazil and was also commonly found in samples from Ethiopia.

Ovicillium attenuatum Zare & W. Gams, *Mycol. Prog.* **15**: 1021. 2016. MB 815496.

For a complete description see Zare & Gams (2016).

Specimens examined: **Ethiopia**, Yebo Mosha, on *Hemileia* sp., 22 Sep. 2017, *J.P.M. Araújo, H.C. Evans & K. Belachew-Bekele* (culture COAD 3271); Agaro Center, on *H. vastatrix*, 22 Sep. 2017, *J.P.M. Araújo, H.C. Evans & K. Belachew-Bekele* (culture COAD 3272).

Notes: The genus *Ovicillium* (*Bionectriaceae*) was proposed by Zare & Gams (2016) to include fungicolous Verticillium-like fungi with erect conidiophores. *Ovicillium* is characterized by its very long, cyanophilic and verticillate conidiophores and globose to short ellipsoidal conidia. The type species of this genus is a mycoparasite which was isolated from *Auricularia* in Cuba (Zare & Gams 2016), whereas our isolates were from Ethiopia on pustules of *H. vastastrix*. Phylogenetic analyses confirmed that these isolates belong to *O. attenuatum*. This is the first report of *O. attenuatum* on *H. vastatrix*, worldwide.

Pleurodesmospora coccorum (Petch) Samson, W. Gams & H.C. Evans., *Persoonia* **11**: 68. 1980. MB 113324. Fig. 9.

For a detailed description see Samson *et al.* (1980).

Description: *Conidiophores* cylindrical, erect or procumbent in groups, hardly differentiated from the vegetative hyphae, 56–20 × 1.5–2 µm, usually branched, smooth, hyaline. *Conidiogenous cells* holoblastic, terminal and intercalary, bearing numerous short-cylindrical, 1–2 µm long and 0.5 µm wide conidiogenous pegs located mainly at the distal cells of the conidiophores or in whorls below the septa. *Conidia* in short chains (7–8 conidia), dacryoid, 3–6(–9) × 2–3 µm, base acuminate, apex rounded, aseptate, hyaline, smooth.

Culture characteristics: Colonies slow growing (18–23 mm diam. after 10 d); flat or umbonate, margin entire, aerial mycelium floccose, powdery at sporulating areas, diurnal zonation present (PCA), white, humid centrally, reverse white to cream, sporulation abundant.

Specimens examined: **Brazil**, Espírito Santo, Sooretama, on *H. vastatrix*, 4 Apr. 2015, *A.A. Colmán* (VIC 47454, culture COAD 3275). **Cameroon**, Foumbot, on *H. vastatrix*, 20 Jun. 2017, *M. Kapeua-Ndacnou* (culture COAD 3280); Nguélémendouka, Kowanbang, on *H. vastatrix*, 23 Jun. 2017, *M. Kapeua-Ndacnou* (VIC 47455, culture COAD 3276); Nguélémendouka, Mbala, on *H. vastatrix*, 21 Jun. 2017, *M. Kapeua-Ndacnou* (culture COAD 3282); Nguélémendouka, Kowanbang, on *H. vastatrix*, 21 Jun. 2017, *M. K.apeua-Ndacnou* (culture COAD 3283); Foumbot, on *H. vastatrix*, 21 Jun. 2017, *M. Kapeua-Ndacnou* (cultures COAD 3277, COAD 3281). **Ethiopia**, Kojja − Yeyebito, on *H. vastatrix*, 28 Sep. 2017, *J.P.M. Araújo, H.C. Evans & K. Belachew-Bekele* (VIC 47456).

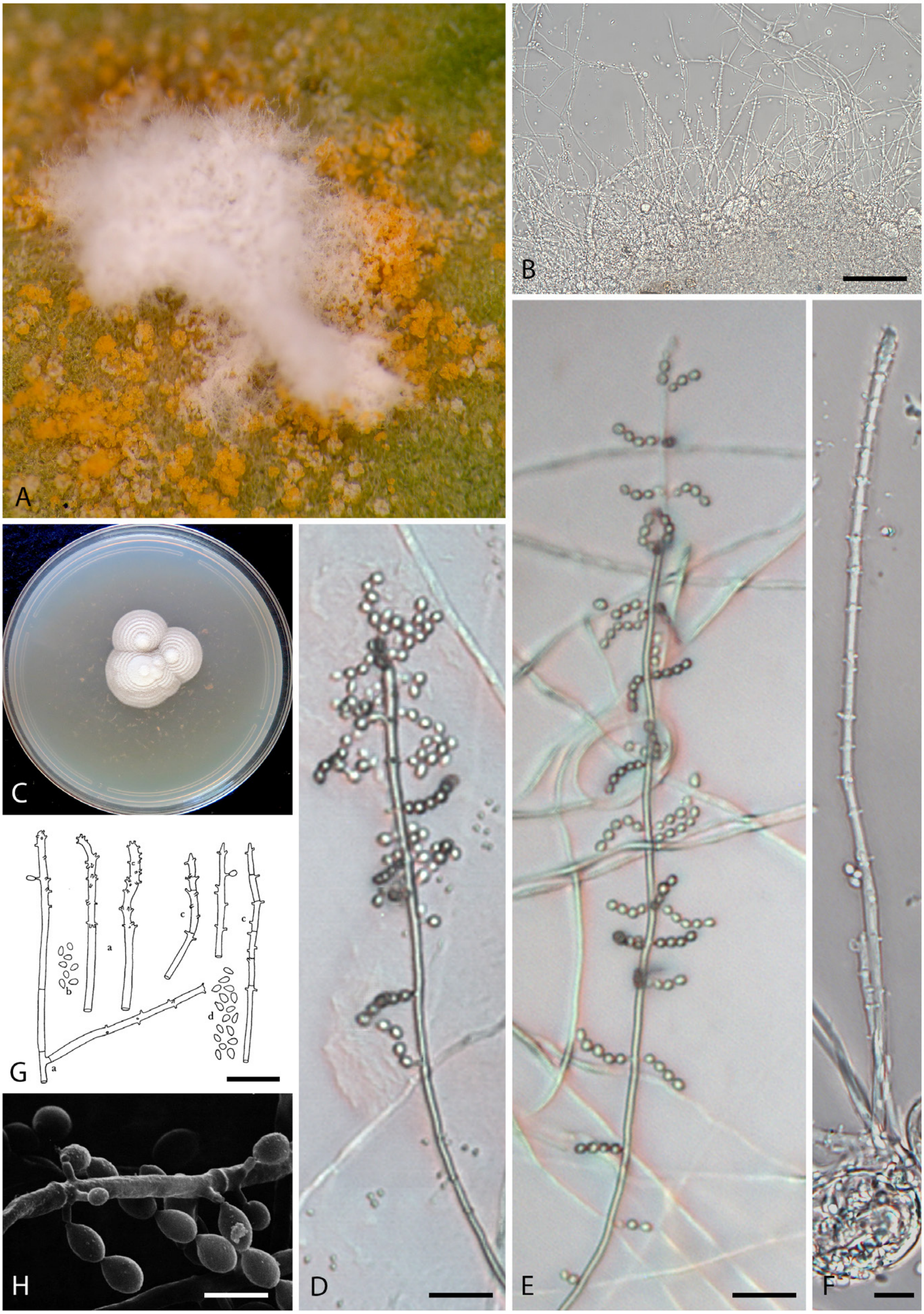

Fig. 9. *Pleurodesmospora coccorum*. **A.** Uredinia of *H. vastatrix* exhibiting colony of *P. coccorum*. **B.** Conidiophores. **C.** Colony on potato dextrose agar after 10 d at 25 °C. **D, E.** Close-up of conidiophore bearing chains of conidia. **F.** Conidiophore and conidia. **G.** Original published line drawing showing *P. coccorum* conidiophores and conidia. **H.** Conidia attached to conidiophore under scanning electron mycroscopy – both G and H by permission (Samson *et al.* 1980). Scale bars: B, D, E, G, H = 10 µm; F = 5 µm.

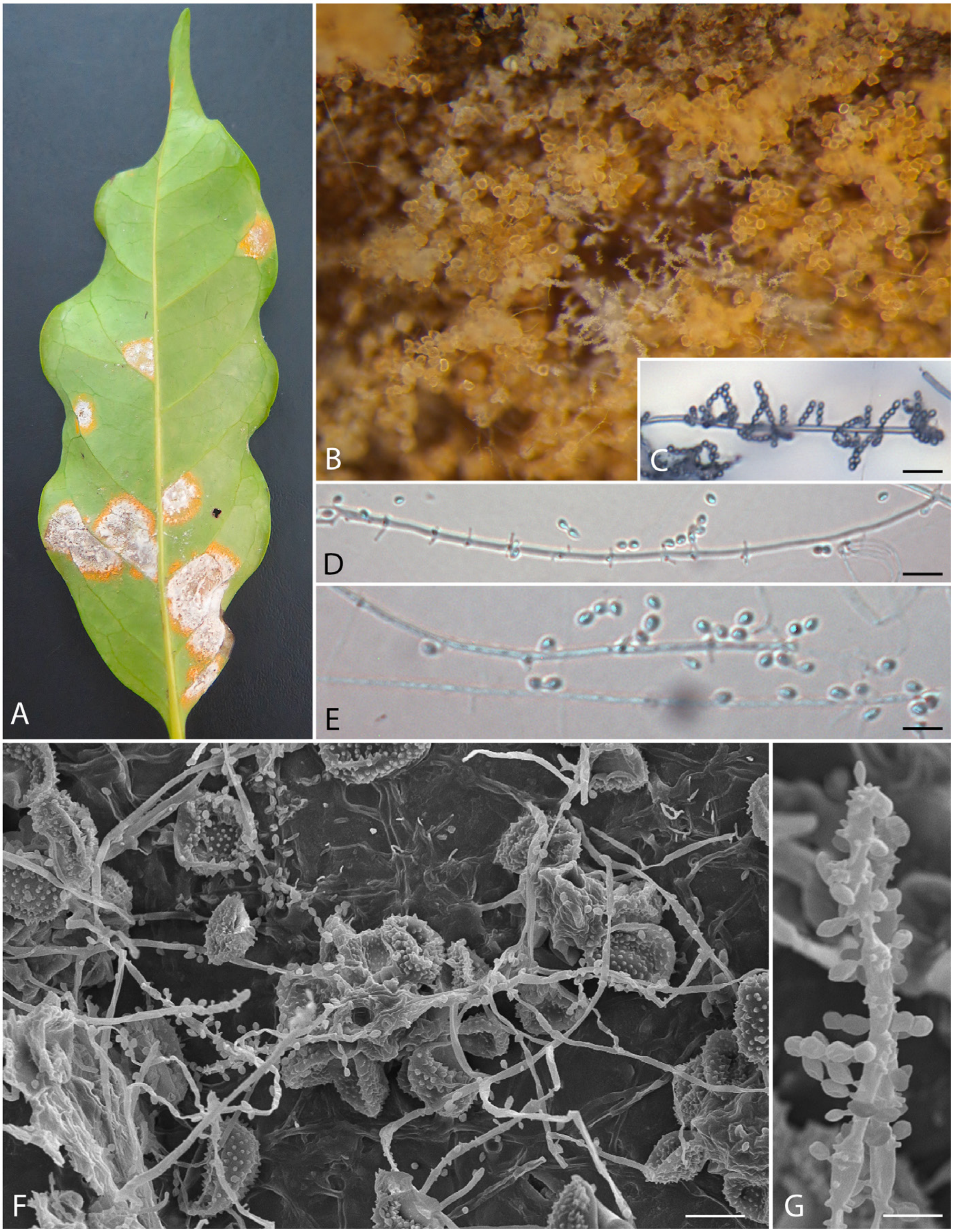

Fig. 10. *Pleurodesmospora hemileiae*. **A.** *Coffea arabica* leaf bearing large lesions due to infection by *Hemileia vastatrix* with extensive white colonies of mycoparasitic *P. hemileiae*. **B.** Close-up under dissecting microscope of a uredinium of *H. vastatrix* bearing hyaline *P. hemileia* structures. **C.** Chain of conidia produced from conidiogenous pegs. **D, E.** Hyphae showing conidiogenous pegs with detached conidia. **F.** Urediniospores being consumed by *P. hemileiae* under scanning eletron microscopy (SEM). **G.** Close-up of conidiogenous cells with attached conidia under SEM. Scale bars: C = 40 µm; D = 20 µm; E, F = 10 µm; G = 5 µm.

Notes: The genus *Pleurodesmospora* was proposed by Samson *et al.* (1980) to accommodate the entomogenous fungus *Pleurodesmospora* (formerly, *Gonatorrhodiella*) *coccorum*. *Pleurodesmospora* species have been isolated from a range of chitinous substrates, such as scale insects, aphids, whiteflies, lepidoptera pupae and mites (Petch 1931, Samson *et al.* 1980, Chen *et al.* 2021). Morphological features of *Pl. coccorum* isolates obtained from *H. vastatrix* pustules are, in general, similar to those given in the original description by Samson *et al.* (1980), although the conidia are slightly longer in our specimens (3–4 × 2–2.8 µm). However, the concatenated sequence analysis combining LSU, *RPB1*, *RPB2* and *TEF* of our isolates from CLR, grouped them with the original isolates of *P. coccorum*. It also seems possible, given the morphological similarity between the two taxa, that the fungus recorded from *H. vastatrix* in Mexico by Carrión & Rico-Gray (2002) as *Sporotrhix guttuliformis* was, in fact, *Pleurodesmospora coccorum*.

Pleurodesmospora hemileiae Colmán, H.C. Evans, J.P.M. Araújo & R.W. Barreto, ***sp. nov.*** MB 853087. Fig. 10.

Etymology: In reference to the host genus *Hemileia*.

Typus: **Brazil**, Minas Gerais, Carmo da Cachoeira, on *H. vastatrix*, 22 Apr. 2015, *A.A. Colmán* (**holotype** VIC 47452; ex-type culture COAD 3274).

Description: *Colonies* dense, powdery, white, starting centrally on pustules of *H. vastatrix* and progressively smothering the older parts of lesions leaving only a rim of younger uredinia at the margin of infected areas on leaves. *Mycelium* branched, thin-walled, septate, smooth 1–1.5 µm wide. *Conidiophores* cylindrical, erect or procumbent, in groups or solitary, hardly differentiated from the vegetative hyphae 70–150 × 1.5–2 µm, usually branched, smooth, hyaline. *Conidiogenous cells* holoblastic, raduliform, terminal and intercalary bearing numerous short-cylindrical, 1–5 µm long and 0.5 µm wide conidiogenous pegs located either at the distal cells of the conidiophores or in whorls below the septa, sometimes branched. *Conidia* in chains (5–9 conidia), subglobose or ellipsoidal, (3.5–)4(–5) × 1.5–2 µm, base truncate, apex rounded, aseptate, hyaline, smooth.

Culture characteristics: Colonies on PDA 20–22 mm diam. after 10 d; convex, margin entire, aerial mycelium floccose, becoming powdery at sporulating areas, whitish, white to cream reverse, sporulation abundant. Colonies on PCA 20–23 mm diam. after 10 d; umbonate, margin entire, aerial mycelium floccose, white, white to cream reverse, becoming powdery due to the abundant conidia.

Specimens examined: **Brazil**, Minas Gerais, Nepomuceno, on *H. vastatrix*, 22 Jun. 2016, *A.A. Colmán* (VIC 47453); Minas Gerais, Viçosa, on *H. vastatrix*, 1 Sep. 2015, *A.A. Colmán* (VIC 47451, culture COAD 3273); Minas Gerais, Lambari, on *H. vastatrix*, 22 Jun. 2016, *A.A. Colmán* (VIC 47450).

Notes: Based on the analysis of combined dataset (LSU, *RPB1*, *RPB2* and *TEF*), *P. hemileiae* is closely related to *P. coccorum*. Morphologically, *P. hemileiae* resembles *P. coccorum* but *P. hemileiae* has shorter conidiophores and broader conidia and differs from *P. lepidopterorum* by the absence of pegs located in the terminal or lateral conidiogenous cells. *Pleurodesmospora hemileiae* is distinguished from *P. acaricola* by its longer conidial chains and absence of solitary conidia and the presence of chlamydospores. Even though both *Pleurodesmospora* spp. were found associated with *H. vastatrix, P. coccorum* was more commonly collected than *P. hemileiae*, occurring in Brazil, Cameroon and Ethiopia, whereas *P. hemileiae* was only found in Brazil. Based on a MegaBLAST search of the NCBI GenBank nucleotide database, *Pleurodesmospora* isolates from CLR are close to several isolates of *Lecanicillium* with more than 98 % identity. Since *Pleurodesmospora* ITS sequences only became available in GenBank in 2019 (Vu *et al.* 2019), it is possible that such “*Lecanicillium*” were misplaced in the genus because of the absence of molecular data. This may have led James *et al.* (2016) to miss the occurrence of *Pleurodesmospora* during their ITS survey of CLR in Mexico and Puerto Rico. Here, we reconstruct the phylogeny of the genus by concatenating the LSU, *RPB1, RPB2* and *TEF* genes of isolates deposited in the Westerdijk Institute (KNAW) and reconfirm the delimitation of species in *Pleurodesmospora* and their placement in the *Cordycipitaceae*.

Simplicillium hemileiae Colmán, H.C. Evans, J.P.M. Araújo & R.W. Barreto, ***sp. nov.*** MB 860218. Figs 11, 12.

Etymology: In reference to the host *Hemileia vastatrix.*

Typus: **Brazil**, Minas Gerais, Viçosa, Mata do Paraíso, on *H. vastatrix*, on spontaneous understory coffee plants, 30 Jun. 2016, *H.C. Evans* (**holotype** VIC 47444; culture ex-type COAD 3265).

Description: *Colonies* starting as powdery white growth intermixed with uredinia, becoming granular in older parts and also appearing as a thin veil over parasitized uredinia bearing abundant tiny mucilaginous drops of conidia in later stages. *Mycelium* 2–3 µm diam., branched, septate, hyaline smooth. *Phialides* arising from prostrate hyphae, solitary, straight or slightly curved, aculeate, 26–55 × 1–1.5 µm, hyaline, smooth. *Conidia* in small mucilaginous globose heads at the apex of the phialides, subglobose to ellipsoidal, 2–5 × 1–2 µm, aseptate, hyaline, smooth. *Perithecia* occasionally formed in older colonies either scattered or forming small groups over a superficial mycelial layer or suspended on the mycelial veil, erect or prostrated, obpyriform or flask-shaped, straight to somewhat curved, 175–210 × 55–80 µm, tapering towards the ostiole, neck 20–33 µm diam., buff becoming amber towards the ostiole, covered with subulate, blunt or pointed bristles (3–13 × 2 µm), some bristles forming apical phialides. *Asci* cylindrical, 90–110 × 2–3 µm, 8-spored, apical cap prominently thickened 1–2 µm, smooth, hyaline. *Ascospores* filiform, densely packed within asci, expanding in length after release, 47–138 × 1 µm, aseptate, hyaline, smooth. Not seen fragmenting into part-spores.

Culture characteristics: Colonies on PDA 30–40 mm diam. after 10 d, convex, aerial mycelium lanose, whitish with floccose aerial mycelium, margin entire, reverse white centrally, sporulation scarce. Colonies on PCA 40–45 mm diam. after 10 d at 25 °C, umbonate, margin entire, aerial mycelium floccose, white, reverse white centrally, sporulation abundant. Perithecia formed regularly on the colony surface.

Notes: The genus *Simplicillium* was introduced by Zare & Gams (2001) and is known to have a wide host range and a cosmopolitan distribution. This genus includes fungi exploiting a diversity of ecological niches, including mycoparasites of rusts, parasites of insects, nematodes, plant endophytes and saprobes (Nonaka *et al.* 2013, Crous *et al.* 2018, Gomes *et al.* 2018, Wei *et al.* 2019). It is characterized by predominantly solitary phialides arising from aerial hyphae and conidia which are arranged either in globose slimy heads, in short chains, or formed in sympodial succession – such as in *S. sympodiophorum* (Zare & Gams 2001, Nonaka *et al.* 2013). Morphologically, *S. hemileiae* resembles *S. lamellicola*, but, contrarily to *S. lamellicola* the new species does not produce spindle-shaped macro-conidia and its conidia are longer than the micro-conidia of *S. lamellicola* which are 2–3 µm as opposed to those of *S. hemileiae* which are 2–5 µm long. Additionally, colonies of *S. hemileiae* have a white reverse instead of brown as in *S. lamellicola*. Although the two species are phylogenetically closely related (Fig. 1) they represent distinct taxa. *Simplicillium hemileiae* produces flask-shapped perithecia both in vivo and in vitro. Although these perithecia-like structures are commonly found to be immature having no differentiated centrum, fertile perithecia were also found. Two distinct features of the sexual morph are recognized here to represent morphological markers for *S. hemileiae*: i) the bristle-like ornaments present on the surface of the perithecia and ii) the aseptate ascospores. *Simplicillium hemileiae* was only obtained from uredinia of *H. vastatrix* in

Fig. 11. *Simplicillium hemileiae*. **A.** Type locality. Spontaneous coffee plants (*Coffea arabica*), infected by coffee leaf rust (*Hemileia vastatrix*), in old coffee plantation overgrown by Atlantic Rainforest – Mata do Paraíso, Universidade Federal de Viçosa, Viçosa, state of Minas Gerais, Brazil. **B.** *Coffea arabica* leaves bearing rust symptoms with uredinia parasitized by the white colony-forming fungus *S. hemileiae* . **C.** Close-up of same. **D.** Colony of *S. hemileiae* over uredinia of *H. vastatrix.* Note few remaining living orange urediniospores and one perithecium of *S. hemileiae* (arrowed). **E.** Loose group of perithecia of *S. hemileiae* (arrowed) scattered on older colony of mycoparasite.

Fig. 12. *Simplicillium hemileiae*. **A.** Curved perithecium surrounded by mycelium and showing bristle-like ornaments under scanning electron microscopy. **B.** Curved perithecium expelling asci and ascospores. Note degraded *Hemileia vastatrix* urediniospores next to perithecium. **C.** Straight perithecium ejecting a single ascus through ostiole. Note degraded *H. vastatrix* urediniospores next to base and abundant bristles on the perithecial walls. **D.** Close-up of ostiole showing phialides bearing single conidia on top (black arrows) and ejecting asci (red arrows). **E.** Hyphae emerging from parasitized urediniospores. Note immature conidium formed at the tip of phialide. **F.** Ascus showing thickened apical cap. Scale bars: A–C, E = 20 µm; D = 10 µm; F = 5 µm.

Brazil. Interestingly this fungus was found repeatedly, but only at a single locality – an Atlantic forest reserve belonging to the UFV (Mata do Paraíso) on remaining plants of an old abandoned coffee plantation (Fig. 11).

Simplicillium lanosoniveum **(**J.F.H. Beyma) Zare & W. Gams, *Nova Hedwigia* **73**: 39. 2001. MB 532459.

For a complete description see Zare & Gams (2001).

Specimens examined: **Brazil**, Minas Gerais, Viçosa, on *H. vastatrix*, 1 Sep. 2015, *A.A. Colmán* (VIC 47448, culture COAD 3269); Minas Gerais, Samambaia, on *H. vastatrix*, 21 Apr. 2015, *A.A. Colmán* (VIC 47447, culture COAD 3268). **Ethiopia**, Dilla Zuria Odomita, on *H. vastatrix*, 23 Dec. 2017, *J.P.M. Araújo, H.C. Evans & K. Belachew-Bekele* (VIC 47445, culture COAD 3266); Tepi, on *H. vastatrix*, 20 Sep. 2017, *J.P.M. Araújo, H.C. Evans & K. Belachew-Bekele* (VIC 47446, culture COAD 3267).

Notes: *Simplicillium lanosoniveum* has been repeatedly found associated with rust fungi and, particularly, with *H. vastatrix* (Zare & Gams 2001) and the soybean rust *Phakopsora pachyrhizi* (Ward *et al.* 2011, Gauthier *et al.* 2014). This species was frequently found in samples from Brazil. Our molecular analyses have demonstrated that cultures obtained from Brazil and Ethiopia grouped together forming a clade near to *S. subtropicum*. This species was the most common species of *Simplicillium* among the three collected during our survey (four isolates from Brazil and Ethiopia). A high frequence of *Simplicillium* spp. associated with CLR has been reported by James *et al.* (2016).

Simplicillium subtropicum Nonaka, Kaifuchi & Masuma., *Mycoscience* **54**: 47. 2013. MB 519349.

For a complete description see Nonaka *et al.* (2013).

Specimen examined: **Paraguay**, Central, San Lorenzo, on *H. vastatrix*, 20 Jun. 2017, *A.A. Colmán* (VIC 47449, culture COAD 3270).

Notes: *Simplicillium subtropicum* was originally isolated from soil samples in Japan, together with four other species of *Simplicillium* (Nonaka *et al.* 2013). Two of those species (*S. cylindrosporum* and *S. minatense*) have also been detected by James *et al.* (2016) during their study of fungi on pustules of *H. vastatrix* in Mexico and Puerto Rico, but not *S. subtropicum*. *Simplicillium subtropicum* has an overall similar morphology to *S. lanosoniveum,* a well-known rust mycoparasite. Nevertheless, molecular phylogenetic results and morphological features – particularly, the subglobose to ellipsoidal conidia of *S. subtropicum* – allow for a clear distinction of this species from *S. lanosoniveum.* It is possible that earlier studies have overlooked the morphological and molecular differences and treated *S. subtropicum* as *S. lanosoniveum.* To our knowledge, this is the first report of *S. subtropicum* associated with *H. vastatrix*, worldwide.

DISCUSSION

Kepler *et al.* (2017) recognized that the taxonomic history within *Cordycipitaceae* is intricate. Khonsanit *et al.* (2024) further refined the delimitation of *Akanthomyces* and *Lecanicillium* but recognized that “further molecular data are necessary for classification within the present system.” The elucidation of the taxonomy of fungi within the broad WCF assemblage has also been challenging. The *Cordycipitaceae* and *Clavicipitaceae* examined here produce simple asexual morphs and present a considerable degree of morphological overlap. Additionally, molecular information for many taxa related to our fungi is lacking. Hopefully, as more isolates are collected and more molecular information becomes available, the taxonomic proposals included in this study will be consolidated or improved.

Isolates placed in *Bettiolomyces*, which was newly proposed here, belonged to two separate species. Interestingly, other isolates of *B. epiphytus* obtained during our surveys form a group including only isolates from Africa, whereas *B. urediniophagus* was found only once in Brazil.

Corniculantispora dimorpha was collected only once on *H. vastatrix* in Ethiopia and was previously found on *Agaricus* spp. and also on another rust (*Puccinia coronata*) by Gams (1971). *Ovicillium attenuatum* is another example of a fungus known from other basidiomycete hosts that was occasionally collected, only in Ethiopia, on *H. vastatrix.* These appear to be broad host-range mycoparasites which may have jumped locally onto *H. vastatrix*.

The genus *Gamszarella* was established by Crous *et al.* (2023) to accommodate an entomogenous fungus found on an insect in South Africa. Of the two isolates found on *H. vastatrix* uredinia, one was identified as *G. buffelskloofina* and the other as the new species, *G. uredinophila.*

Phylogenetic studies, which led to the proposal of *Hemileiophthora* as a novel Sporothrix-like genus, showed that the two species included form a highly-supported (BP = 94), closely related, but distinct, clade to that containing *Simplicillium* (Fig. 1). The genus *Simplicillium* was introduced by Zare & Gams (2001) to accommodate fungicolous or entomogenous fungi with solitary phialides. *Hemileiophthora* forms a monophyletic mycoparasitic clade, which is phylogenetically close to *Simplicillium*, but the new genus has denticulate holoblastic conidiogenous cells. This is in contrast to *Simplicillium* which has enteroblastic phialides. Morphologically, *Hemileiophthora* is closer to *Sporothrix* and related genera.

The molecular taxonomic analysis presented by Kepler *et al.* (2017), concluded that the type species of *Lecanicillium*, *L. lecanii*, is conspecific with *Akanthomyces lecanii* and, thus, the earlier name *Akanthomyces*, was adopted. Subsequently, *Lecanicillium uredinophilum* was recombined as *A. uredinophilus* by Manfrino *et al.* (2022). However, Khonsanit *et al.* (2024) have now shown that the genus *Lecanicllium* should be resurrected, based on a more comprehensive phylogenetic analysis, and they demonstrated that the genus forms a well-supported group within the *Cordycipitaceae*. Consequently, *A. uredinophilus* is now treated as a synonym of *L. uredinophilum*. The new phylogenetic study of Khonsanit *et al.* (2024) has also revealed that *Akanthomyces* is polyphyletic across several clades in the family. Several of the WCF isolates obtained during our surveys belonged to *Lecanicillium* spp. *Lecanicillium hemileiae* is, seemingly common in Ethiopia – only one record in Cameroon – whereas *L. uredinophilum* apparently has a broader geographical distribution.

The recognition that *Pleurodesmospora* includes two mycoparasitic species on *H. vastatrix* was unexpected. *Pleurodesmospora* was, originally, a monotypic genus based on *Pl. coccorum*: a species isolated from various hosts – including both insects and fungi (Samson *et al.* 1980). Two novel species from arthropods have been included in *Pleurodesmospora,* namely: *Pl acaricola* (Yeh *et al.* 2021) and *Pl. lepidopterorum* (Chen *et al.* 2021). Gams (1971) initially transferred a strain, obtained from the black mildew *Meliola* sp., to *Aphanocladium meliolae*, but later corrected his earlier diagnosis, solely based on a key morphological character – the presence of denticles on the conidiophores. The nomenclatural history of *A. meliolae* was reviewed by Samson *et al.* (1980). The latter authors have reported *A. meliolae* as a mycoparasite of *H. vastatrix* in Uganda. It would be interesting, therefore, revisiting the fungus on *Meliola.* It may actually belong to *Pleurodesmospora.* Carrión & Rico-Gray (2002) obtained a fungus from *H. vastatrix* in Mexico which they identified as *Sporothrix guttuliformis.* In their publication, the authors mentioned that *S. guttuliformis* can be mistaken for *Aphanocladium meliolae.* Although some of the isolates of *Pleurodesmospora* collected in our survey had conidial chains smilar to *Sporothrix*, the phylogenetic analyses confirmed that all of our isolates belong to *Pleurodesmospora* – which is a member of the *Cordycipitaceae* (Wan-Hao *et al.* 2021) (Fig. 1). *Sporothrix* s. str., on the other hand, clusters in the *Ophiostomataceae* (De Beer *et al.* 2017). It is possible that the work of Carrión & Rico-Gray (2002), which relied completely on morphological identifications, have mistakenly identified *P. coccorum,* which is rather common both in Africa and in Brazil, as *S. guttuliformis.*

Among the isolates of *Simplicillium* obtained in this survey, *S. lanosoniveum* was the most common species. This species has been reported as mycoparasite of various fungi, including *H. vastatrix* (Zare & Gams, 2001, James *et al.* 2016). It is, therefore, a common and polyphagous mycoparasite. *Simplicillium* spp. are distinguished through a combination of morphological characteristics and ITS sequences (Nonaka *et al.* 2013). Morphological and phylogenetic analyses have shown that *S. hemileiae* differs from *S. coffeicola*, a recently described endophytic species found in *Coffea arabica* in Brazil (Gomes *et al.* 2018). Differently from *Simplicillium*, phylogenetic analyses of *Lecanicillium* have previously been based either solely on ITS (Zare & Gams 2001) or based on multilocus phylogeny using SSU rRNA, LSU rRNA, *TEF, RPB1* and *RPB2* (Park *et al.* 2015, Chiriví-Salomón *et al.* 2015, Chen *et al.* 2017). James *et al.* (2016) performed a single-molecule DNA sequencing study of CLR pustules in Mexico and Puerto Rico and found that *S. lanosoniveum* represented the most abundant Operational Taxonomic Unit (OTUs), concluding that “the antagonist effect of *S. lanosoniveum* on *H. vastatrix* needs to be explored”.

The evidence of mycoparasitism for the WCF assemblage, included in our study, is acknowledged to be mostly circumstantial and based on observation of the overgrowing on rust pustules or formation of sporulating structures on urediniospores. Nevertheless, for *S. lanosoniveum* this has been explored more closely by Gauthier *et al.* (2014) who generated ultrastructural microscopic evidence of the mycoparasitic association with a different rust fungus. His study shows clear penetration of urediniospores of *Phakopsora pachyrhizi* by *S. lanosoniveum* through germ pores of urediniospores and signs of organelle degradation 24 h after inoculation. It is expected that a similar ultrastructural study will generate an equivalent scenario for the association of *S. lanosoniveum* with *H. vastatrix.*

As shown in our previous publications on fungal antagonists of *Hemileia* spp*.,* there are differences between the mycobiotas associated with CLR in the African centres of origin (Cameroon, for *C. canephora*; Ethiopia, for *C. arabica*) of the rust and that found in the exotic range of *H. vastatrix* in the Americas (Brazil, Paraguay). A breakdown of the 15 confirmed WCF taxa shows geographical disparities: six species unique to Africa, six unique to South America and only three common to both continents. Unusually, compared to other taxonomic groups – especially, of course, to *Trichoderma*, as detailed above (Rodríguez *et al.* 2021) – the diversity of WCF associated with CLR is as high in its exotic range as to that in its African centre of origin. Significantly, of the six new taxa described, only two species, *H. denticulata* and *L. hemileiae*, were documented from Africa, whilst four new species were recorded only in South America. This suggests that, as a whole, the WCF may have little host specificity and readily jump from other substrates onto exotic rust species, such as *H. vastatrix* in South America. For example, three species of WCF were found parasitizing CLR pustules in the Galápagos Islands, where coffee is a relatively recently introduced crop (Cannon & Evans 2004).

Until now, the diversity of WCF associated with CLR, would have been “lost” or overlooked, hidden under the *Verticillium/Lecanicillium lecanii*-label. Ironically, *Lecanicillium lecanii* was never found on CLR pustules during our surveys in South America (Brazil, Paraguay) or in Africa (Cameroon, Ethiopia). This reinforces the suspicion that, in previous publications, the name has been incorrectly applied to *H. vastatrix*-associated WCF fungi, which is supported, indirectly, by the study of James *et al.* (2016) which did not find OTUs of this species in their surveys in Latin America. This trend of attributing erroneous CLR biocontrol potential to *L. lecanii* populates the literature until the present day. One recent example is Das *et al.* (2024). In which it was concluded, from their experiments, that their “*L. lecanii*” isolate “could be exploited as a prophylactic biocontrol measure against CLR”, although they did not provide any evidence of the precise identity of their fungus.

The WCF assemblage does include several other genera or groups of fungi in addition to those discussed here. Some of the fungi investigated in our earlier publications, are also seen producing white colonies directly over CLR lesions, namely *Calonectria hemileiae* (Salcedo-Sarmiento *et al.* 2021), *Cordyceps cateniannulata* (Pereira *et al.* 2024b) and *Cryptococcus depauperatus* (Guterres *et al.* 2021).

Additionally, several *Fusarium* spp. and related taxa and several *Acremonium* spp. and Acremonium-like species are also WCF occurring on *H. vastatrix* pustules and are being investigated by our research group.The discovery of so many fungal taxa from such a microhabitat as *H. vastatrix* uredinia is extraordinary and indicates that mycoparasites are a megadiverse group of fungi and possibly an important component of the so-called “dark matter fungi” (Grossart *et al.* 2016). Although relatively little is known about mycoparasites, they may prove to be both a new frontier for the advance of mycology and a valuable resource for plant pathologists and biocontrol scientists.

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Declaration on conflict of interest

The authors declare that there is no conflict of interest.

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