

The *Colletotrichum dracaenophilum*, *C. magnum* and *C. orchidearum* species complexes

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Abstract: Although *Glomerella glycines*, *Colletotrichum magnum* and *C. orchidearum* are known as causal agents of anthracnose of soybean, *Cucurbitaceae* and *Orchidaceae*, respectively, their taxonomy remains unresolved. In preliminary analyses based on ITS, strains of these species appear basal in *Colletotrichum* phylogenies, clustering close to *C. cliviae*, *C. brevisporum* and other recently described species from tropical or subtropical regions. Phylogenetic analyses (ITS, *GAPDH*, *CHS-1*, *HIS3*, *ACT*, *TUB2*) of 102 strains previously identified as *Ga. glycines*, *C. magnum* and *C. orchidearum* as well as other related strains from different culture collections and studies placed these taxa in three species complexes, and distinguished at least 24 species, including 11 new species. In this study, *C. magnum*, *C. orchidearum* and *C. piperis* were epitypified and their taxonomy resolved, while *C. clivicola* was proposed as a new name for *C. cliviae*. Furthermore, a sexual morph was observed for *C. yunnanense*, while *C. brevisporum*, *C. clivicola* and *C. tropicicola* were reported from new hosts or countries. Regarding their conidial morphology, species in the *C. dracaenophilum*, *C. magnum* and *C. orchidearum* species complexes are reminiscent of *C. gloeosporioides* or *C. boninense* s. lat., and were likely to be confused with them in the past.

Key words: Anthracnose, Ascomycota, *Colletotrichum*, *Gloeosporium*, *Glomerella*, Phylogeny, Systematics.

Taxonomic novelties: **New name:** *Colletotrichum clivicola* Damm & Crous for *C. cliviae* Yan L. Yang *et al.*; **New species:** *C. cacao* Damm, *C. cattleyicola* Damm & Toy. Sato, *C. coelogyne* Damm, *C. lobatum* Damm, *C. merremiae* Damm, *C. musicola* Damm, *C. okinawense* Damm & Toy. Sato, *C. panamense* Damm, *C. plurivorum* Damm, Alizadeh & Toy. Sato, *C. sojae* Damm & Alizadeh, *C. vittalense* Damm; **Epitypifications (basionyms):** *Glomerella magna* S.F. Jenkins & Winstead, *C. orchidearum* Allesch., *C. piperis* Petch.

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INTRODUCTION

During a systematic study of *Colletotrichum* species, strains were detected that were reminiscent of *C. gloeosporioides* regarding conidial morphology, but did not belong to any of the well-studied species complexes (Cannon *et al.* 2012). Several of these strains were previously identified as *Glomerella glycines*, *Ga. magna* and *C. orchidearum*.

Glomerella glycines is known as the causal agent of anthracnose of soybean. It was described by Lehman & Wolf (1926) from soybean stems as the sexual morph of *Colletotrichum glycines* (Hemmi 1920). The Compendium of Soybean Diseases (Sinclair 1982) lists two species on soybean, the first being *C. dematium* var. *truncatum* (syn. of *C. truncatum*, Damm *et al.* 2009) represented by the line drawing of *C. glycines* by Hemmi (1920), which was apparently regarded as a synonym of *C. truncatum*, and the second being *Ga. glycines*. Further confusion was caused by connecting *C. destructivum* to *Ga. glycines* (Tiffany & Gilman 1954, Manandhar *et al.* 1986). However, a recent molecular study has shown that *C. destructivum* belongs to the *C. destructivum* species complex, while isolates from the study of Manandhar *et al.* (1986) were not closely related to *C. destructivum*, belonging to a different species complex (Damm *et al.* 2014). In contrast, von Arx & Müller (1954) treated *Ga. glycines* as a form of *Ga. cingulata* with large

ascospores. Based on these records, *Ga. glycines* was previously thus connected to at least three different species complexes.

Glomerella magna (syn. *C. magnum*) was described on watermelon (*Citrullus lanatus*) in the USA and is heterothallic (Jenkins & Winstead 1964). According to Jenkins & Winstead (1964), *Ga. magna* is pathogenic to many species of *Cucurbitaceae*, including watermelon, cantaloup (*Cucumis melo*), squash and pumpkin (*Cucurbita* spp.), and sometimes cucumber (*Cucumis sativus*). Grand (1985) lists this species as a pathogen of *Citrullus lanatus*, *Cucumis melo*, *Cucumis sativus*, *Cucurbita pepo*, *Cucurbita* sp. and *Trichosanthes anguina* in North Carolina, USA. Recently, *Ga. magna* was also reported from *Cucumis sativus*, *Lagenaria siceraria* and *Luffa cylindrica* (*Cucurbitaceae*) in Taiwan (Tsay *et al.* 2010), as an anthracnose pathogen of papaya (*Carica papaya*) in Brazil, Mexico and Costa Rica (Nascimento *et al.* 2010, Tapia-Tussel *et al.* 2016, Molina-Chaves *et al.* 2017) and from *Lobelia chinensis* in China (Li *et al.* 2013). Wasilwa *et al.* (1993) found that strains of this species were less aggressive compared with those of *C. orbiculare*. Freeman & Rodriguez (1992, 1993) and Redman *et al.* (1999) studied the lifestyle of this fungus, and were able to disrupt pathogenicity in *C. magnum* using an ultraviolet radiation treatment, transforming it to a non-pathogenic, endophytic mutualist. In the ITS and MAT1-2 phylogenies by Du *et al.* (2005), strain

L2.5 (CBS 519.07) grouped outside any known species complex. The sequence of the mating type protein (MAT1-2) gene is also included in [Marcelino et al. \(2008\)](#), confirming this result. The species was however never included in any of the recent multilocus studies of the genus ([Cannon et al. 2012](#), [Marin-Felix et al. 2017](#)), and its close relatives are unknown.

Colletotrichum orchidearum is known as a causal agent of anthracnose of *Orchidaceae*. The species was described by [Allescher \(1902\)](#) with three *formae* on three different *Orchidaceae* species from the Munich Botanical Garden. Recently, strains from different *Orchidaceae* in China were included in a multilocus analysis of *Orchidaceae* plants from China and identified as *C. orchidearum* ([Yang et al. 2011](#)). [Farr & Rossman \(2017\)](#) list *C. orchidearum* from numerous *Orchidaceae* hosts from Asian, African and Latin American countries. [Xu et al. \(2016\)](#) also reported this species from *Arctium lappa* in China. However, except for [Yang et al. \(2011\)](#) and [Xu et al. \(2016\)](#), these reports originate from checklists or other reports from the pre-molecular era. There are sequences of strains called *C. orchidearum* from two further studies in GenBank, one of them displayed a strain as “type strain of *C. orchidearum*” (Z. Zhang et al., unpubl. data). However, there are no strains available from the original publication. The species was lectotypified recently ([Damm et al. 2012a](#)), but still awaits epitypification to fix the genetic application of the name.

In preliminary analyses based on ITS sequence data, strains of *Ga. glycines*, *C. magnum* and *C. orchidearum* appear basal in *Colletotrichum* phylogenies close to *C. cliviae*, *C. brevisporum* and other recently described species from mainly tropical regions ([Yang et al. 2009](#), [Noireung et al. 2012](#)), and indicating that more than one species complex was involved. The aim of this study was therefore to clarify the systematic position of *Ga. glycines*, *C. magnum* and *C. orchidearum* and related species, resolve the respective species complexes and characterise the species in these complexes morphologically and by means of multilocus sequence analyses.

MATERIALS AND METHODS

Isolates

A total of 102 strains was studied, previously identified as *C. cliviae*, *C. orchidearum*, *C. brevisporum*, *Ga. glycines*, *C. magnum* and *C. dracaenophilum*, as well as other related strains from the culture collections of the Westerdijk Fungal Biodiversity Institute, Utrecht, The Netherlands (CBS), the Genetic Resources Center, National Agriculture and Food Research Organization, Tsukuba, Ibaraki, Japan (MAFF), the University of Tehran, University College of Agriculture and Natural Resources, Tehran, Iran (UTFC) and CABI Europe UK Centre, Egham, UK (IMI) as well as from recent studies in the literature. The Iranian strains were part of recent collections by A. Alizadeh and O. Atghia from cultivated and wild plants in Iran. Type material (holotypes, lectotypes and epitypes) of the species studied are located in the fungaria of the CBS, the US National Fungus Collections, Beltsville, Maryland, USA (BPI), the fungaria based in the Royal Botanic Gardens, Kew, UK (IMI and K(M)), the Botanische Staatssammlung München (M), Germany and the Herbarium Hamburgense (HBG), Germany. All descriptions are based on the ex-holotype or epitype cultures, if not stated otherwise. Features of other

strains are added if deviant. Subcultures of the ex-holotypes and ex-epitypes, respectively, as well as all other isolates used for morphological and sequence analyses are maintained in the culture collections of CBS, IMI, MAFF and UTFC ([Table 1](#)).

Morphological analysis

To enhance sporulation, autoclaved filter paper and double-autoclaved stems of *Anthriscus sylvestris* were placed onto the surface of synthetic nutrient-poor agar medium (SNA; [Nirenberg 1976](#)). SNA and OA (oatmeal agar; [Crous et al. 2009](#)) cultures were incubated at 20 °C under near UV light with a 12 h photoperiod for 10 d. Measurements and photographs of characteristic structures were made according to [Damm et al. \(2007\)](#). Appressoria on hyphae were observed on the reverse side of SNA plates or on slide cultures ([Damm et al. 2013](#)). Microscopic preparations were made in clear lactic acid, with 30 measurements per structure and observed with a Nikon SMZ1000 dissecting microscope (DM), or with a Nikon Eclipse 80i microscope using differential interference contrast (DIC) illumination. Colony characters and pigment production on SNA and OA cultures incubated at 20 °C under near UV light with 12 h photoperiod were determined after 10 d. Colony colours were rated according to [Rayner \(1970\)](#). Growth rates were measured after 7 and 10 d.

Phylogenetic analysis

Genomic DNA of the isolates was extracted using the method of [Damm et al. \(2008\)](#). The 5.8S nuclear ribosomal RNA gene with the two flanking internal transcribed spacers (ITS), a 200-bp intron of the glyceraldehyde-3-phosphate dehydrogenase (GAPDH), partial sequences of the chitin synthase 1 (*CHS-1*), histone H3 (*HIS3*), actin (*ACT*) and beta-tubulin (*TUB2*) genes were amplified and sequenced using the primer pairs ITS-1F ([Gardes & Bruns 1993](#)) + ITS-4 ([White et al. 1990](#)), GDF1 + GDR1 ([Guerber et al. 2003](#)), CHS-354R + CHS-79F ([Carbone & Kohn 1999](#)), CYLH3F + CYLH3R ([Crous et al. 2004b](#)), ACT-512F + ACT-783R ([Carbone & Kohn 1999](#)) and T1 ([O'Donnell & Cigelnik 1997](#)) + Bt-2b ([Glass & Donaldson 1995](#)) or T1 + BT4R ([Woudenberg et al. 2009](#)), respectively. The PCRs were performed in a 2720 Thermal Cycler (Applied Biosystems, Foster City, California) in a total volume of 12.5 µL. The GAPDH, CHS-1, HIS3, ACT and TUB2 PCR mixture contained 1 µL 20× diluted genomic DNA, 0.2 µM of each primer, 1x PCR buffer (Bioline, Luckenwalde, Germany), 2 mM MgCl₂, 20 µM of each dNTP, 0.7 µL DMSO and 0.25 U Taq DNA polymerase (Bioline). Conditions for PCR of these genes constituted an initial denaturation step of 5 min at 94 °C, followed by 40 cycles of 30 s at 94 °C, 30 s at 52 °C and 30 s at 72 °C, and a final denaturation step of 7 min at 72 °C, while the ITS PCR was performed as described by [Woudenberg et al. \(2009\)](#). The DNA sequences generated with forward and reverse primers were used to obtain consensus sequences using Bionumerics v. 4.60 (Applied Maths, St-Marthens-Lathem, Belgium), and the alignment assembled and manually adjusted using Sequence Alignment Editor v. 2.0a11 ([Rambaut 2002](#)).

To determine whether the six sequence datasets were congruent and combinable, tree topologies of 70 % reciprocal Neighbour-Joining bootstrap with Maximum Likelihood distances (10 000 replicates) with substitution models determined separately for each partition using MrModeltest v. 2.3 ([Nylander 2004](#)) were compared visually ([Mason-Gamer & Kellogg 1996](#)).

Table 1. Strains of *Colletotrichum* spp. studied, with collection details and GenBank accession numbers.

Species	Accession no. ¹	Host	Country	GenBank No. ²					
				ITS	GAPDH	CHS-1	HIS3	ACT	TUB2
<i>C. brevisporum</i>	CBS 129957	<i>Anthurium</i> sp.	Thailand	MG600762	MG600822	MG600869	MG600908	MG600966	MG601029
	CBS 129958	<i>Anthurium</i> sp.	Thailand	MG600763	MG600823	MG600870	MG600909	MG600967	MG601030
	CBS 512.75	<i>Carica papaya</i>	Australia	MG600761	MG600821	MG600868	MG600907	MG600965	MG601028
	BCC 38876*	<i>Neoregalia</i> sp.	Thailand	JN050238	JN050227	—	—	JN050216	JN050244
	MFLUCC100182	<i>Pandanus pygmaeus</i>	Thailand	JN050239	JN050228	—	—	JN050217	JN050245
MAFF 305751	<i>Passiflora edulis</i>	Japan	MG600764	MG600824	MG600871	—	MG600968	MG601031	
<i>C. cacao</i>	CBS 119297*	<i>Theobroma cacao</i>	Costa Rica	MG600772	MG600832	MG600878	MG600916	MG600976	MG601039
<i>C. cattleyicola</i>	CBS 170.49*	<i>Cattleya</i> sp.	Belgium	MG600758	MG600819	MG600866	MG600905	MG600963	MG601025
	MAFF 238321	<i>Cattleya</i> sp.	Japan	MG600759	—	—	—	—	MG601026
<i>C. cliviicola</i>	CBS 125375*	<i>Clivia miniata</i>	China	MG600733	MG600795	MG600850	MG600892	MG600939	MG601000
	CSSS2	<i>Clivia miniata</i>	China	GU109480	GU085868	GU085866	—	GU085862	GU085870
	CBS 133705	<i>Clivia</i> sp.	South Africa	MG600732	MG600794	MG600849	MG600891	MG600938	MG600999
<i>C. coelogyne</i>	CBS 132504*	<i>Coelogyne</i> sp.	Germany	MG600713	MG600776	MG600836	MG600882	MG600920	MG600980
	CBS 132515	<i>Coelogyne</i> sp.	Germany	MG600714	MG600777	MG600837	MG600883	MG600921	MG600981
<i>C. dracaenophilum</i>	CBS 121453	<i>Dracaena sanderana</i>	Bulgaria	MG600712	MG600775	MG600835	MG600881	MG600919	MG600979
	CBS 119360	<i>Dracaena sanderana</i>	China	MG600711	MG600774	MG600834	MG600880	MG600918	MG600978
	CBS 118200	<i>Dracaena sanderana</i>	China	MG600710	MG600773	MG600833	MG600879	MG600917	MG600977
	CBS 118199*	<i>Dracaena sanderana</i>	China	JX519222	JX546707	JX519230	JX546756	JX519238	JX519247
<i>C. excelsum-altitudinum</i>	CGMCC 3.15130*	<i>Bletilla ochracea</i>	China	HM751815	KC843502	—	—	KC843548	JX625211
	CGMCC 3.15131	<i>Bletilla ochracea</i>	China	JX625182	KC843503	—	—	KC843549	JX625212
<i>C. gloeosporioides</i>	CBS 112999*	<i>Citrus sinensis</i>	Italy	JQ005152	JQ005239	JQ005326	JQ005413	JQ005500	JQ005587
<i>C. liaoningense</i> 1	CGMCC 3.17616, CAUOS2*	<i>Capsicum annuum</i>	China	KP890104	KP890135	KP890127	—	KP890097	KP890111
<i>C. liaoningense</i> 1	CAUOS6	<i>Capsicum annuum</i>	China	—	—	KP890131	—	—	KP890115
<i>C. liaoningense</i> 2	CAUOS3	<i>Capsicum annuum</i>	China	KP890105	KP890136	KP890128	—	—	KP890112
<i>C. liaoningense</i> 2	CAUOS4	<i>Capsicum annuum</i>	China	KP890106	KP890137	KP890129	—	KP890099	KP890113
<i>C. lobatum</i>	IMI 79736*	<i>Piper cataibaefolium</i>	Trinidad and Tobago	MG600768	MG600828	MG600874	MG600912	MG600972	MG601035
<i>C. magnum</i>	CBS 519.97*	<i>Citrullus lanatus</i>	USA	MG600769	MG600829	MG600875	MG600913	MG600973	MG601036
	IMI 391662	<i>Citrullus lanatus</i>	USA	MG600771	MG600831	MG600877	MG600915	MG600975	MG601038
	CBS 575.97	<i>Citrullus lanatus</i>	USA	MG600770	MG600830	MG600876	MG600914	MG600974	MG601037
<i>C. merremiae</i>	CBS 124955*	<i>Merremia umbellata</i>	Panama	MG600765	MG600825	MG600872	MG600910	MG600969	MG601032
<i>C. musicola</i>	CBS 132885*	<i>Musa</i> sp.	Mexico	MG600736	MG600798	MG600853	MG600895	MG600942	MG601003
	CBS 127557	<i>Musa</i> sp.	Mexico	MG600737	MG600799	MG600854	MG600896	MG600943	MG601004
<i>C. okinawense</i>	MAFF 240517	<i>Carica papaya</i>	Japan	MG600767	MG600827	—	—	MG600971	MG601034
<i>C. orchidearum</i>	CORCX6	<i>Cattleya</i> sp.	China	HM585403	HM585393	HM582027	—	HM581997	HM585419
	UTFC 262	<i>Cordylone terminalis</i>	Iran	MG600742	MG600804	—	—	MG600948	MG601009
	CORCG3	<i>Cymbidium hookerianum</i>	China	HM585402	HM585392	HM582026	—	HM581996	HM585416
	CBS 135131*	<i>Dendrobium nobile</i>	Netherlands	MG600738	MG600800	MG600855	MG600897	MG600944	MG601005
	CBS 136877	<i>Dendrobium nobile</i>	Netherlands	MG600739	MG600801	MG600856	MG600898	MG600945	MG601006
	MAFF 239931	<i>Dendrobium phalaenopsis</i>	Japan	MG600745	MG600807	—	—	MG600951	MG601012
	MAFF 240480	<i>Dendrobium phalaenopsis</i>	Japan	MG600746	MG600808	MG600858	—	MG600952	MG601013
	UTFC 266	<i>Epipremnum aureum</i>	Iran	MG600741	MG600803	—	—	MG600947	MG601008
	MFLUCC 12-0531* (HT of <i>C. hymenocallidicola</i>)	<i>Hymenocallis</i> sp.	Thailand	KT290264	KT290263	KT290262	—	—	—
	CGMCC 3.14982* (HT of <i>C. aracearum</i>)	<i>Monstera deliciosa</i>	China	KX853166	KX893585	—	—	KX893577	KX893581
	CORCX11	<i>Oncidium flexuosum</i>	China	HM585404	HM585394	HM582028	—	HM581998	HM585417
	MAFF 238499	<i>Oncidium</i> sp.	Japan	MG600743	MG600805	—	—	MG600949	MG601010
	MAFF 238779	<i>Oncidium</i> sp.	Japan	MG600744	MG600806	MG600857	—	MG600950	MG601011
	MAFF 306084	<i>Phalaenopsis</i> sp.	Japan	MG600747	—	—	—	—	MG601014
	CGMCC 3.14983	<i>Philodendron selloum</i>	China	KX853167	KX893586	—	—	KX893578	KX893582
	UTFC 265	<i>Philodendron</i> sp.	Iran	MG600740	MG600802	—	—	MG600946	MG601007

(continued on next page)

Table 1. (Continued).

Species	Accession no. ¹	Host	Country	GenBank No. ²					
				ITS	GAPDH	CHS-1	HIS3	ACT	TUB2
	MAFF 240504	<i>Vanda</i> sp.	Japan	MG600748	MG600809	MG600859	—	MG600953	MG601015
<i>C. panamense</i>	CBS 125386*	<i>Merremia umbellata</i>	Panama	MG600766	MG600826	MG600873	MG600911	MG600970	MG601033
<i>C. piperis</i>	IMI 71397, CPC 21195*	<i>Piper nigrum</i>	Malaysia	MG600760	MG600820	MG600867	MG600906	MG600964	MG601027
<i>C. plurivorum</i>	MAFF 306008	<i>Abelmoschus esculentus</i>	Japan	MG600727	MG600790	—	—	MG600933	MG600994
	MAFF 243073	<i>Amorphophallus rivieri</i>	Japan	MG600730	MG600793	MG600847	—	MG600936	MG600997
	CORCX9	<i>Arundina graminifolia</i>	China	HM585398	HM585381	HM582025	—	HM581986	HM585423
	CGMCC 3.17358	<i>Camellia sinensis</i>	China	KJ955215	KJ954916	—	—	KJ954483	KJ955361
	LJTJ30*	<i>Capsicum annuum</i>	China	KP748221	KP823800	—	—	KP823741	KP823853
	(HT of <i>C. sichuanensis</i>)								
	LJTJ3	<i>Capsicum annuum</i>	China	KP748193	KP823773	—	—	KP823738	KP823850
	LJTJ16	<i>Capsicum annuum</i>	China	KP748207	KP823786	—	—	KP823739	KP823851
	LJTJ22	<i>Capsicum annuum</i>	China	KP748213	KP823792	—	—	KP823740	KP823852
	MAFF 238697	<i>Carica papaya</i>	Japan	MG600724	MG600787	—	—	MG600931	MG600991
	CBS 125474*	<i>Coffea</i> sp.	Vietnam	MG600718	MG600781	MG600841	MG600887	MG600925	MG600985
	CBS 125473	<i>Coffea</i> sp.	Vietnam	MG600717	MG600780	MG600840	MG600886	MG600924	MG600984
	CORCG2	<i>Cymbidium hookerianum</i>	China	HM585397	HM585380	HM582024	—	HM581985	HM585422
	MAFF 238875	<i>Glycine max</i>	Japan	MG600725	MG600788	—	—	—	MG600992
	LFN0008	<i>Glycine max.</i>	Brazil	KT696336	KT696289	—	KT696311	KT696275	KT696282
	CBS 132443	<i>Gossypium</i> sp.	Brazil	MG600719	MG600782	MG600842	MG600888	MG600926	MG600986
	CBS 132444	<i>Gossypium</i> sp.	Brazil	MG600720	MG600783	MG600843	MG600889	MG600927	MG600987
	MAFF 306007	<i>Lycopersicon esculentum</i>	Japan	MG600728	MG600791	MG600846	—	MG600934	MG600995
	CMM 3742	<i>Mangifera indica</i>	Brazil	KC702980	KC702941	KC598100	—	KC702908	KC992327
	CMM 3746	<i>Mangifera indica</i>	Brazil	KC702981	KC702942	KC598101	—	KC702909	KC992328
	MAFF 305790	<i>Musa</i> sp.	Japan	MG600726	MG600789	MG600845	—	MG600932	MG600993
	MAFF 238315	<i>Oncidium</i> sp.	Japan	MG600729	MG600792	—	—	MG600935	MG600996
	MAFF 305974	<i>Passiflora edulis</i>	Japan	MG600731	—	MG600848	—	MG600937	MG600998
	CBS 903.69	<i>Phaseolus lunatus</i>	Benin	MG600721	MG600784	MG600844	MG600890	MG600928	MG600988
	UTFC 261	<i>Phaseolus vulgaris</i>	Iran	MG600722	MG600785	—	—	MG600929	MG600989
	UTFC 260	<i>Spathiphyllum wallisii</i>	Iran	MG600723	MG600786	—	—	MG600930	MG600990
<i>C. sojae</i>	SAUCC 1407	<i>Arctium lappa</i>	China	KT362184	KT362188	KT362187	—	KT362189	KT362185
	CGMCC 3.15171	<i>Bletilla ochracea</i>	China	HM751813	KC843501	—	—	KC843550	KC244161
	CAUOS5	<i>Capsicum</i> sp.	China	KP890107	KP890138	KP890130	—	—	KP890114
	LFN0009	<i>Glycine max</i>	Brazil	KT696354	KT696295	—	KT696318	KT696281	KT696288
	UTFC 288	<i>Glycine max</i>	Iran	MG600755	MG600816	—	—	MG600960	MG601022
	CBS 134.87	<i>Glycine max</i>	Italy	MG600752	MG600813	MG600863	MG600902	MG600957	MG601019
	CBS 181.81	<i>Glycine max</i>	Serbia	MG600753	MG600814	MG600864	MG600903	MG600958	MG601020
	CBS 182.81	<i>Glycine max</i>	Serbia	MG600754	MG600815	MG600865	MG600904	MG600959	MG601021
	ATCC 62257*	<i>Glycine max</i>	USA	MG600749	MG600810	MG600860	MG600899	MG600954	MG601016
	IL18A	<i>Glycine max</i>	USA	KC110792	KC110810	—	KC110801	KC110828	KC110819
	IL26A	<i>Glycine max</i>	USA	KC110793	KC110811	—	KC110802	KC110829	KC110820
	ATCC 11871	<i>Medicago sativa</i>	USA	MG600750	MG600811	MG600861	MG600900	MG600955	MG601017
	CBS 128510	<i>Medicago sativa</i>	USA	MG600751	MG600812	MG600862	MG600901	MG600956	MG601018
	UTFC 301	<i>Phaseolus vulgaris</i>	Iran	MG600756	MG600817	—	—	MG600961	MG601023
	UTFC 303	<i>Vigna unguiculata</i>	Iran	MG600757	MG600818	—	—	MG600962	MG601024
<i>C. tropicicola</i> 1	BCC 38877, MFLUCC 110114*	<i>Citrus maxima</i>	Thailand	JN050240	JN050229	—	—	JN050218	JN050246
<i>C. tropicicola</i> 1	CBS 127555, CPC 15927	<i>Citrus</i> sp.	Mexico	MG600715	MG600778	MG600838	MG600884	MG600922	MG600982
<i>C. tropicicola</i> 1	CBS 133174, CPC 15924	<i>Citrus</i> sp.	Mexico	MG600716	MG600779	MG600839	MG600885	MG600923	MG600983
<i>C. tropicicola</i> 2	MFLUCC100167	<i>Paphiopedilum bellatolum</i>	Thailand	JN050241	JN050230	—	—	JN050219	JN050247
<i>C. vittalense</i>	GUFCC 15503	<i>Calamus thwaitesii</i>	India	JN390935	KC790759	KF451996	—	KC790646	KC790892
	CBS 126.25	orchid	unknown	MG600735	MG600797	MG600852	MG600894	MG600941	MG601002
	CBS 181.82*	<i>Theobroma cacao</i>	India	MG600734	MG600796	MG600851	MG600893	MG600940	MG601001
<i>C. yunnanense</i>	CBS 132135, AS3.9617*	<i>Buxus</i> sp.	China	JX546804	JX546706	JX519231	JX546755	JX519239	JX519248
	AS3.9616	<i>Buxus</i> sp.	China	EF369491	—	—	—	—	—

Table 1. (Continued).

Species	Accession no. ¹	Host	Country	GenBank No. ²					
				ITS	GAPDH	CHS-1	HIS3	ACT	TUB2
<i>Colletotrichum</i> sp.	GZAAS5 09545	<i>Citrus medica</i>	China	JQ247623	JQ247599	—	—	JQ247647	JQ247635
	COUFAL7300	<i>Sechium edule</i>	Brazil	KT285378	KT285381	KT285380	—	KT285378	KT285383

¹ ATCC: American Type Culture Collection, Virginia, USA; BCC: BIOTEC culture collection, Bangkok, Thailand; CBS: Culture collection of the Westerdijk Fungal Biodiversity Institute, Utrecht, The Netherlands; CGMCC: China General Microbiological Culture Collection Center, Beijing, China; CMM: Culture Collection of Phyto-pathogenic Fungi Prof. Maria Menezes, Federal Rural University of Pernambuco, Brazil; CPC: Culture collection of Pedro Crous, housed at CBS; COUFAL: Coleção de Culturas de Fungos Fitopatogênicos da Universidade Federal de Alagoas, Brazil; GUFCC: Goa University, Fungal Culture Collection, Taleigao Plateau, Goa, India; GZAAS: Guizhou Academy of Agricultural Sciences, Guiyang, China; IMI: Culture collection of CABI Europe UK Centre, Egham, UK; LARS: Culture collection of Long Ashton Research Station, Bristol, UK (no longer existing); MAFF: MAFF Genebank Project, Ministry of Agriculture, Forestry and Fisheries, Tsukuba, Japan; MFLUCC: Culture collection of the Mae Fah Luang University, Chiang Rai, Thailand; SAUCC: Culture collection of the Department of Plant Pathology, College of Plant Protection, Shenyang Agricultural University, China; STE-U: Culture collection of the Department of Plant Pathology, University of Stellenbosch, South Africa; UFC: Culture collection of the University of Tehran, University College of Agriculture and Natural Resources, University of Tehran, Karaj, Iran.

² ITS: internal transcribed spacers and intervening 5.8S rDNA; GAPDH: partial glyceraldehyde-3-phosphate dehydrogenase gene; CHS-1: partial chitin synthase-1 gene; HIS: partial histone H3 gene; ACT: partial actin gene; TUB2: partial beta-tubulin gene. Sequences generated in this study are emphasised in bold face.

* Ex-holotype or ex-epitype cultures.

Maximum parsimony analyses were performed on the multilocus alignment (ITS, *GAPDH*, *CHS-1*, *HIS3*, *ACT*, *TUB2*) as well as for each gene separately with PAUP (Phylogenetic Analysis Using Parsimony) v. 4.0b10 (Swofford 2003) using the heuristic search option with 100 random sequence additions and tree bisection and reconstruction (TBR) as the branch-swapping algorithm. Alignment gaps were treated as missing and all characters were unordered and of equal weight. No more than 10 trees of score (length) greater than or equal to 10 were saved in each replicate. Tree length, consistency index (CI), retention index (RI), rescaled consistency index (RC) and homoplasy index (HI) were calculated for the resulting tree. The robustness of the trees obtained was evaluated by 10 000 bootstrap replications using the Fast-stepwise addition algorithm (Hillis & Bull 1993). A Markov Chain Monte Carlo (MCMC) algorithm was used to generate phylogenetic trees with Bayesian probabilities using MrBayes v. 3.2.6 (Ronquist & Huelsenbeck 2003) for the combined sequence datasets. Models of nucleotide substitution for each gene determined by MrModeltest v. 2.3 were included for each gene partition. The analyses of two MCMC chains were run from random trees for 10 000 000 generations and sampled every 100 generations. The likelihood score of the two runs were 2630 and 2600 and therefore, the first 2615 (the average of both) trees were discarded as the burn-in phase of the analysis and posterior probabilities determined from the remaining trees. For additional comparison, a Neighbour-Joining analysis was performed on the multigene alignment using PAUP and 1000 bootstrap replications. Sequences derived in this study have been lodged at GenBank, the alignment and trees in TreeBASE (www.treebase.org/treebase-web/home.html), and taxonomic novelties in MycoBank (Crous *et al.* 2004a).

RESULTS

Phylogeny

The six individual datasets did not show any conflicts in tree topology of the 70 % reciprocal bootstrap trees, which allowed us to combine them. In the multigene analyses (gene boundaries of ITS: 1–558, *GAPDH*: 569–900, *CHS-1*: 911–1211, *HIS3*: 1222–1642, *ACT*: 1653–1940, *TUB2*: 1951–2498) of 102

strains previously identified as *C. cliviae*, *C. orchidearum*, *C. brevisporum*, *Ga. glycines*, *C. magnum*, *C. dracaenophilum* as well as other related strains, including the outgroup (*C. gloeosporioides* strain CBS 112999), 2500 characters including the alignment gaps were processed, of which 613 characters were parsimony-informative, 158 parsimony-uninformative and 1729 constant. After a heuristic search using PAUP, the maximum of 1000 equally most parsimonious trees were retained (length = 1470 steps, CI = 0.723, RI = 0.942, RC = 0.681, HI = 0.277), of which one is shown in Fig. 1. The topology of the 1000 trees was similar, which was verified for a large selection of trees. They differed only in the position of taxa within the subclades and in the position of some of the subclades within the main clades. For the Bayesian analyses, a GTR+G model was selected for ITS, a GTR+I+G model for *CHS-1*, a HKY+G model for *GAPDH*, *TUB2* and *HIS3* and a HKY+I model for *ACT*, and incorporated in the analysis. The consensus tree obtained from Bayesian analyses confirmed the tree topology obtained with parsimony. Bayesian posterior probability values agreed with bootstrap support values (Fig. 1).

The analyses resulted in detection of three main clades and 24 subclades, presumably representing different *Colletotrichum* species. The first clade (orchidearum, 99 % bootstrap support) consists of eight subclades, of which three subclades include a large number of strains from several host genera, and five subclades with one to three strains of either the same host genus or the same country. The two subclades on the top of the phylogeny are short-branched with bootstrap support values of 80 % and 94 %, respectively. Except for the single-strain clade of *C. piperis*, all other subclades are longer-branched with bootstrap support values ranging between 82 and 100 %. The second clade (magnum, 99 %) consists of 10 subclades; half of them are single-strain clades. Two further subclades containing five and three strains are on short branches. The remaining three subclades consist of strains from three studies, the sequences of which were downloaded from GenBank; the four strains of *C. liaoningense* form two subclades. There are six subclades in the third clade (dracaenophilum, 86 %); three of them are very long-branched, while the other three subclades are closely related. There was only the ITS sequence available of the second strain of *C. yunnanense*; the bootstrap support value of this long branch is therefore only 87 %. One strain previously identified as *C. tropicicola* (MFLUCC 10-0167) formed a

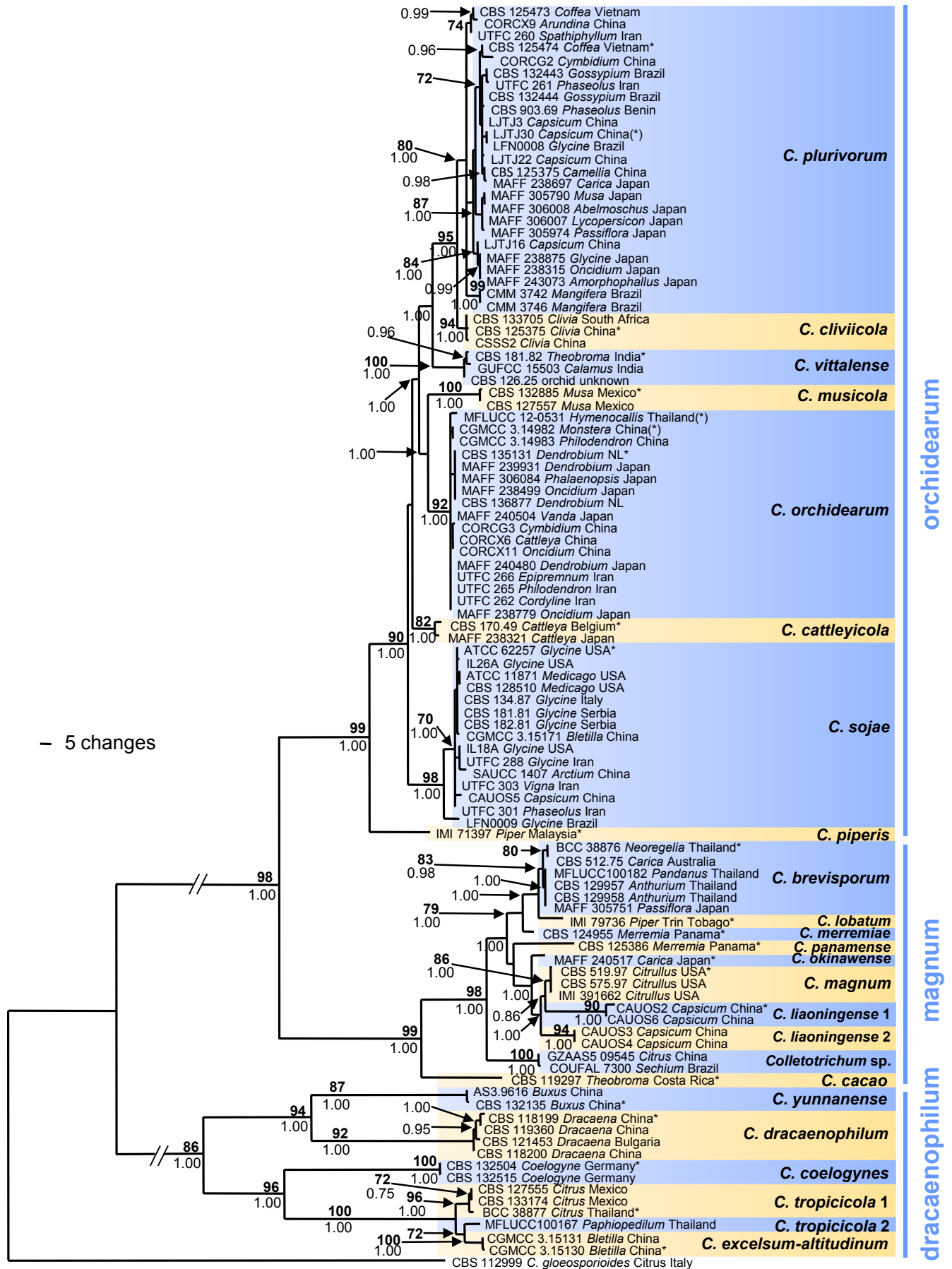


Fig. 1. The first of 1000 equally most parsimonious trees obtained from a heuristic search of the combined ITS, GAPDH, CHS-1, HIS3, ACT and TUB2 sequence alignment of the *Colletotrichum dracaenophilum*, *C. magnum* and *C. orchidearum* species complexes. Bootstrap support values above 70 % (bold) and Bayesian posterior probability values above 0.90 are shown at the nodes. *Colletotrichum gloeosporioides* strain CBS 112999 is used as outgroup. Numbers of ex-holotype and ex-epitype isolates are emphasised with an asterisk. Strain numbers are followed by substrate (host genus) and country of origin, NL = Netherlands, Trin Tobago = Trinidad and Tobago. Species complexes are indicated by blue lines. Branches that are crossed by diagonal lines are shortened by 50 %.

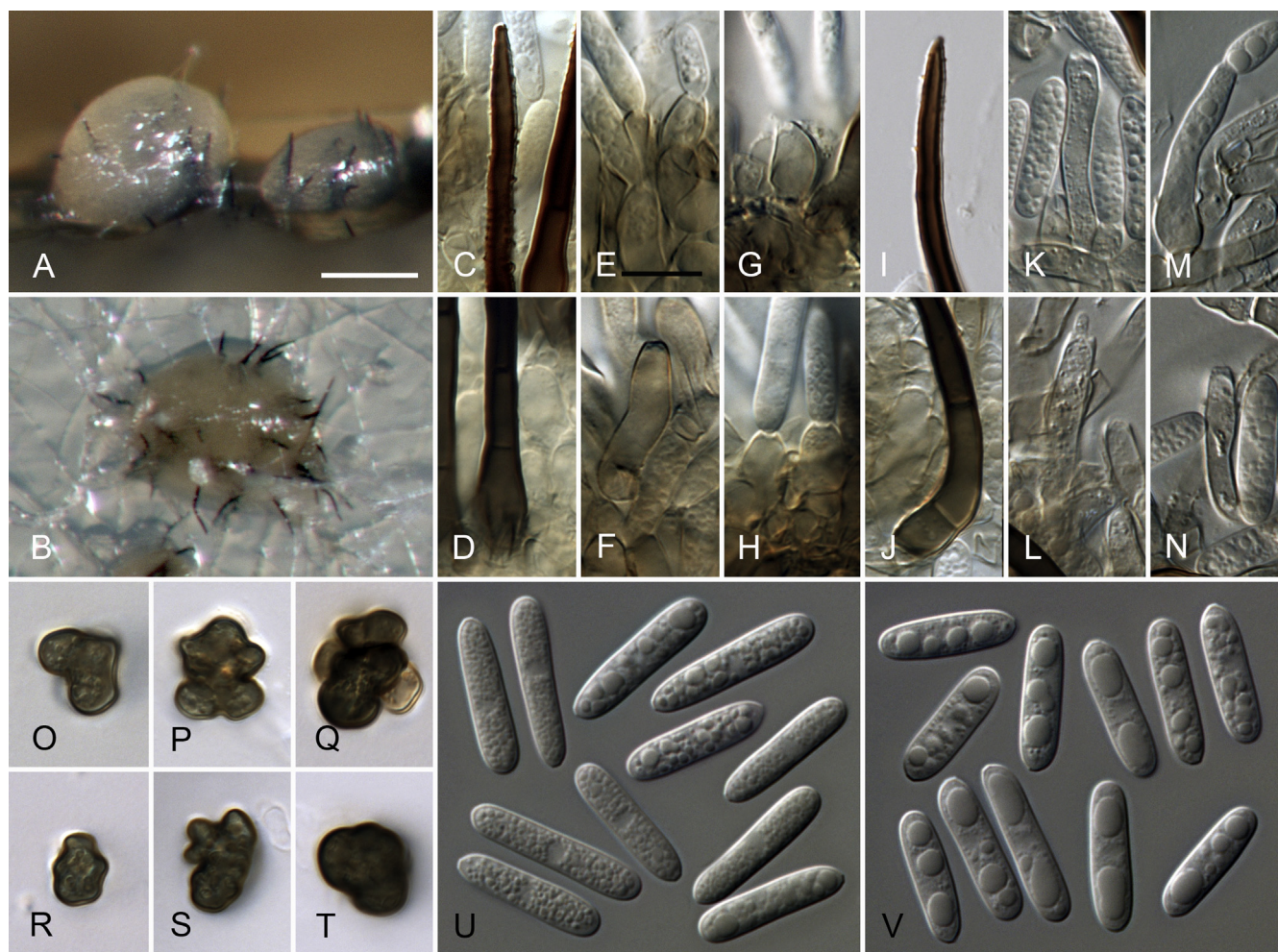


Fig. 2. *Colletotrichum brevisporum* (A–N, U–V. from culture CBS 129957. O–T. from culture CBS 512.75). **A–B.** Conidiomata. **C, I.** Tips of setae. **D, J.** Bases of setae. **E–H, K–N.** Conidiophores. **O–T.** Appressoria. **U–V.** Conidia. **A, C–H, U.** from *Anthriscus* stem. **B, I–T, V.** from SNA. **A–B.** Dissecting microscope (DM). **C–V.** Differential interference contrast illumination (DIC). Scale bars: **A** = 100 μ m, **E** = 10 μ m. Scale bar of **A** applies to **A–B**. Scale bar of **E** applies to **C–V**.

separate lineage between the *C. tropicicola* clade containing the ex-holotype of that species and *C. excelsum-altitudinum*. All six subclades contain strains from only one host genus each.

The three subclades, further referred to as *C. dracaenophilum*, *C. magnum* and *C. orchidearum* species complexes, respectively, are all well supported in the multilocus phylogeny, however, the clades are not supported with some of the single-locus phylogenies (not shown). Isolates can be best assigned to one of these species complexes by using *TUB2* sequence data.

Taxonomy

Based on DNA sequence data and morphology, the 102 strains studied (Table 1) are assigned to 24 species, of which 8, 10 and 6 species, respectively, belong to the *Colletotrichum dracaenophilum*, *C. magnum* and *C. orchidearum* species complexes, including 11 species that proved to be new to science and are described. Five species formed sexual morphs *in vitro*. All species studied in culture are characterised below.

Colletotrichum brevisporum Noireung *et al.*, Cryptog. Mycol. 33: 350. 2012. Fig. 2.

A description of the type specimen is provided by Noireung *et al.* (2012). The description below is based on strains from *Anthurium* sp. in Thailand and *Carica papaya* in Australia.

Sexual morph not observed. *Asexual morph on SNA* (CBS 129957). *Vegetative hyphae* 2–8 μ m diam, hyaline to pale brown, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata*, conidiophores and setae formed directly on hyphae. *Setae* medium brown, verrucose, 60–110 μ m long, 2–4-septate, base pale brown, cylindrical, sometimes slightly inflated, 4–7 μ m diam, tip rounded to \pm acute. *Conidiophores* hyaline to pale brown, smooth-walled, septate, branched, to 40 μ m long. *Conidiogenous cells* (hyaline to) pale brown, smooth-walled, cylindrical to ampulliform, 12–24 \times 3–6 μ m, opening 1–2 μ m diam, collarette 0.5 μ m long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, the apex rounded, the base rounded to truncate, (14–)16.5–19(–19.5) \times (4–)4.5–5(–5.5) μ m, mean \pm SD = 17.7 \pm 1.3 \times 4.8 \pm 0.4 μ m, L/W ratio = 3.7, conidia of strain CBS 512.75 shorter, measuring (10.5–)12.5–14.5(–15.5) \times (3.5–)4–5(–6) μ m, mean \pm SD = 13.4 \pm 1.1 \times 4.6 \pm 0.6 μ m, L/W ratio = 2.9. *Appressoria* not formed by CBS 129957 after > 2 wk, appressoria of strain CBS 129958 single, dark brown, smooth-walled, irregularly roundish outline, with an undulate to lobate margin, (5.5–)8–13(–16) \times (4–)6–10(–12.5) μ m, mean \pm SD = 10.4 \pm 2.5 \times 8.0 \pm 2.2 μ m, L/W ratio = 1.3.

Asexual morph on Anthriscus stem (CBS 129957). *Conidiomata*, conidiophores and setae formed on pale brown, angular cells, 3–8 μ m diam. *Setae* medium brown, verrucose,

50–120(–160) μm long, 1–3-septate, base cylindrical to slightly inflated, 5–6.5 μm diam, tip \pm acute to \pm rounded. *Conidiophores* pale brown, smooth-walled. *Conidiogenous cells* pale brown, smooth-walled, ellipsoidal to cylindrical, 8–22 \times 4–6 μm , opening 1–2 μm diam, conidiogenous cells of strain CBS 512.75 often bent and inflated in the upper part and sometimes extending to form new conidiogenous loci, collarette 0.5 μm long, periclinal thickening visible or distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical, the apex rounded, the base rounded to truncate, (17–)18–20.5(–22) \times (4–)4.5–5(–5.5) μm , mean \pm SD = 19.3 \pm 1.2 \times 4.6 \pm 0.3 μm , LW ratio = 4.2, conidia of strain CBS 512.75 shorter and wider, measuring (11–)12.5–16(–16) \times (4.5–)5–5.5(–6) μm , mean \pm SD = 13.6 \pm 1.3 \times 5.3 \pm 0.4 μm , LW ratio = 2.6.

Cultural characteristics (CBS 129957): Colonies on SNA flat with entire margin, medium hyaline to pale ochreous, filter paper partly olivaceous grey, *Anthriscus* stem, filter paper and medium partly covered with olivaceous grey, iron grey or salmon acervuli and felty whitish aerial mycelium, reverse same colours; 25–27.5 mm in 7 d (\geq 40 mm in 10 d). Colonies on OA flat with entire margin, surface buff to grey olivaceous, covered with pale olivaceous grey, iron grey or salmon acervuli and very short, felty whitish aerial mycelium, reverse buff, pale to olivaceous grey to olivaceous grey; 26–27 mm in 7 d (\geq 40 mm in 10 d). *Conidial mass* salmon.

Materials examined: **Australia**, Victoria, Melbourne, from stem rot of *Carica papaya*, collection date and collector unknown (deposited in CBS collection Oct. 1975 by D.G. Parbery), CBS H-21067, CBS 512.75 = INB 13412. **Thailand**, Chiang Mai, Mesapok waterfall, from leaf spot of *Anthurium* sp., 5 Oct. 2010, P.W. Crous, CBS H-21064, culture CBS 129957; Chiang Mai, Mesapok waterfall, from leaf spot of *Anthurium* sp., 5 Oct. 2010, P.W. Crous, culture CBS 129958.

Notes: *Colletotrichum brevisporum* was described as a causal agent of leaf anthracnose of *Neoregelia* sp. and *Pandanus pygmaeus* in Thailand (Noireung et al. 2012), and has been reported as endophytes and pathogens of several host plants in tropical regions, including *Capsicum chinense* in Brazil (De Almeida et al. 2017), *Capsicum annuum* in China (Liu et al. 2016), *Carica papaya* in Australia (Shivas et al. 2016) and Brazil (Vieira et al. 2013), *Passiflora edulis* in Australia (Shivas et al. 2016), *Citrus medica* in China (Peng et al. 2012), *Lycium chinense* in Korea (Paul et al. 2014) and *Sechium edule* in Brazil (Bezerra et al. 2016).

Although there are only ITS sequences available of the strains from papaya and passion fruit in the paper of Shivas et al. (2016), which is not absolute proof of their identity as *C. brevisporum*, different strains included in this study (CBS 512.75, MAFF 305751) confirm the occurrence of this species on these hosts. However, we also included a strain from papaya in Japan (MAFF 240517), that represents a different species in the *C. magnum* species complex (see *C. okinawense*). We also report here *C. brevisporum* on *Anthurium* in Thailand (Fig. 2A–N, U–V). A different strain from *Anthurium* in Thailand was identified as *C. karstii* (CBS 129927) by Damm et al. (2012b), belonging to the *C. boninense* species complex.

The ITS and *ACT* sequences of *C. brevisporum* are the same as those of *C. merremiae* and *C. lobatum*; the ITS sequence is also identical with that of *C. okinawense*. *Colletotrichum brevisporum* can be identified based on its *GAPDH* sequence, but two groups are resolved. The *TUB2* sequences have only one difference from *C. lobatum*. There are no *CHS-1* and *HIS3* sequences of the ex-type strain available, but based on the strains

included in this study, there is one additional nucleotide difference from *C. lobatum* and *C. panamaense*, and from *C. lobatum* and *C. merremiae*, respectively.

In a blastn search on NCBI GenBank, the *TUB2* sequence of the ex-type strain BCC 38876 is 100 % identical with the two strains of the original paper (Noireung et al. 2012), and with the sequence of *C. brevisporum* strain CCCM12 from *Cucurbita moschata* in China (KY797630, Liu et al. 2018). The only *ACT* and *GAPDH* sequences that are 100 % identical with the ex-type strain are those from the ex-type strain itself. The *ACT* sequence of the strain from *Pandanus* from the original paper as well as *C. brevisporum* strains CCCM12 from *Cucurbita moschata* in China (KY797629, Liu et al. 2018), strain IRA93 from *Capsicum* in Brazil (KU315567, De Almeida et al. 2017), strains CRI-L1 and CRI-N2 (KT185055, KT185056, L. Huang, unpubl. data) and four strains from *Carica papaya* in Brazil (Vieira et al. 2013) are 99 % identical (1 or 2 nucleotides difference). The *GAPDH* sequence of the strain from *Pandanus* is 99 % identical (2 nucleotides difference). The ITS sequences of a large number of unidentified strains and strains identified as *C. brevisporum*, *C. magnum*, *Ga. magna* and *Ga. cingulata* var. *brevispora* are 100 % identical with the ITS sequence of the ex-type strain of *C. brevispora*.

***Colletotrichum cacao* Damm, sp. nov.** MycoBank MB824219. Fig. 3.

Etymology: The species epithet is derived from the host plant, *Theobroma cacao*.

Sexual morph not observed. **Asexual morph on SNA.** *Vegetative hyphae* 1.5–5.5 μm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata*, conidiophores and setae formed directly on hyphae. *Setae* pale to medium brown, verrucose, 35–85 μm long, 1–2(–4)-septate, base cylindrical to somewhat inflated, 4–7.5 μm diam, tip \pm acute. *Conidiophores* pale brown, smooth-walled, septate, sometimes branched, to 45 μm long. *Conidiogenous cells* pale brown, smooth-walled, ellipsoidal, obpyriform to clavate, 9–22 \times (3–)4–6 μm , opening 1.5–2 μm diam, collarette 0.5–1 μm long, periclinal thickening visible, sometimes distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical, the apex and base rounded, (13–)14–15.5(–17) \times 5(–5.5) μm , mean \pm SD = 14.7 \pm 0.8 \times 5.1 \pm 0.2 μm , LW ratio = 2.9. *Appressoria* not formed.

Asexual morph on Anthriscus stem. *Conidiomata*, conidiophores and setae formed directly on hyphae, no basal cells observed, but also formed in medium brown, closed conidiomata. *Setae* medium brown, smooth-walled, verruculose towards the tip, 50–130 μm long, 1–5-septate, base cylindrical, conical to slightly inflated, 4.5–6.5 μm diam, tip \pm acute to \pm rounded or functioning as conidiogenous locus. *Conidiophores* pale brown, smooth-walled to verrucose, septate, branched, to 60 μm long. *Conidiogenous cells* pale brown, smooth-walled to verrucose, cylindrical to clavate, 9–24 \times 3.5–6 μm , opening 1.5–2 μm diam, collarette 0.5–1 μm long, periclinal thickening visible to distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical, the apex and base rounded, (15.5–)16.5–18.5(–20.5) \times 4.5–5.5 μm , mean \pm SD = 17.4 \pm 1.1 \times 5.0 \pm 0.3 μm , LW ratio = 3.5.

Culture characteristics: Colonies on SNA flat with entire margin, agar medium hyaline to pale cinnamon, filter paper, *Anthriscus* stem and agar medium partly covered with isabelline acervuli, aerial mycelium lacking, reverse same colours; 20–25 mm in 7 d

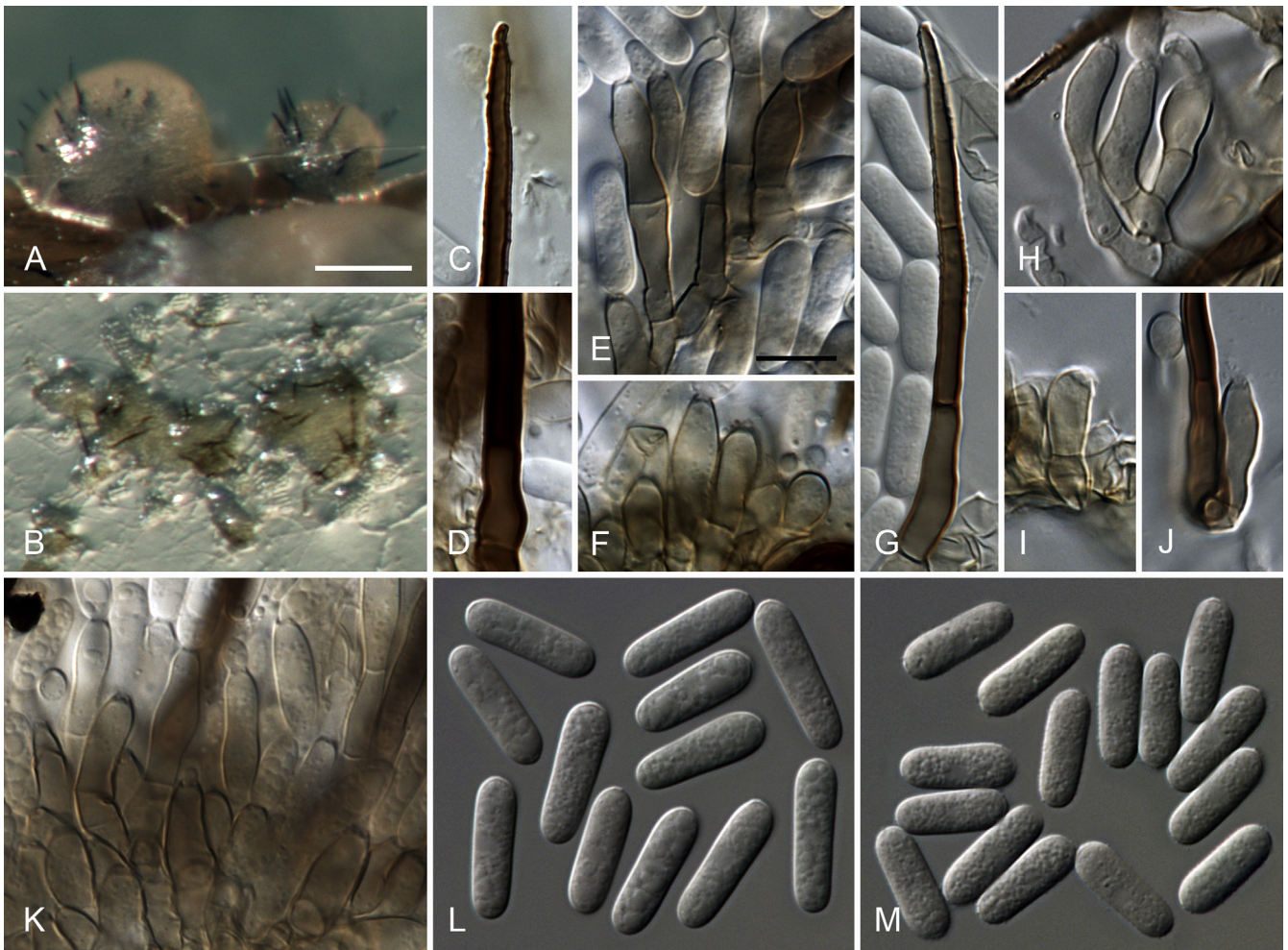


Fig. 3. *Colletotrichum cacao* (from ex-holotype culture CBS 119297). **A–B.** Conidiomata. **C.** Tip of a seta. **D.** Base of a seta. **E–F, H–K.** Conidiophores. **G.** Seta. **L–M.** Conidia. **A, C–F, K–L.** from *Anthriscus* stem. **B, G–J, M.** from SNA. **A–B.** DM. **C–M.** DIC. Scale bars: **A** = 100 μ m, **E** = 10 μ m. Scale bar of **A** applies to **A–B**. Scale bar of **E** applies to **C–M**.

(30–34 mm in 10 d). Colonies on OA flat with entire margin, surface buff, almost entirely covered with small iron grey acervuli, with rosy buff to salmon spore masses towards the centre, whitish towards the margin, aerial mycelium lacking, reverse olivaceous buff to olivaceous grey; 22.5–23 mm in 7 d (34–34.5 mm in 10 d). *Conidial mass* rosy buff to salmon.

Material examined: **Costa Rica**, endophyte of *Theobroma cacao*, collection date and collector unknown (deposited in CBS collection by A. Rossman, INB 13412) (CBS H-21068 **holotype**, culture ex-type CBS 119297 = MCA 2773).

Notes: There are many *Colletotrichum* species occurring on *Theobroma cacao*. For example, *C. ignotum*, *C. theobromicola* and *C. tropicale* were recognised as endophytes of *T. cacao* by [Rojas et al. \(2010\)](#) and described or epitypified in that study; they belong to the *C. gloeosporioides* species complex, that was reviewed recently by [Weir et al. \(2012\)](#). One species from the *C. acutatum* species complex, *C. sloanei*, was described from *Theobroma* in Malaysia, belonging to the *C. acutatum* species complex ([Damm et al. 2012a](#)). A leaf endophyte of *T. cacao* in Panama from the study of [Rojas et al. \(2010\)](#) was re-identified as *C. karstii* (CBS 124951) by [Damm et al. \(2012b\)](#), belonging to the *C. boninense* species complex. In contrast, the species described here, *C. cacao*, belongs to the *C. magnum* species complex. [Rojas et al. \(2010\)](#) noted several further unidentified taxa amongst their collections on *T. cacao* from Panama.

Additional *Colletotrichum* species that have been described on *T. cacao* (see notes under *C. sloanei* in [Damm et al. 2012a](#)) include *C. brachytrichum* and *C. theobromae* from leaves of *T. cacao* in Trinidad and fruits of *T. cacao* in Cameroon that form conidia that are smaller than those of *C. cacao*, measuring 10–13.5 \times 3–3.7 μ m and 9–12 \times 3–5 μ m, respectively ([Saccardo 1906](#)). *Colletotrichum cradwickii*, described from branches of *T. cacao* in Jamaica, forms conidia that are elongate, constricted in the middle, measuring 14–17 \times 5 μ m; while *C. luxificum* was collected from branches, buds and fruits of *T. cacao* in Surinam and Demerara (now Guyana) forming ovoid-oblong conidia with both ends rounded, that are sometimes slightly constricted in the centre, measuring 13–19 \times 4–5 μ m ([Saccardo & Trotter 1913](#)). The conidial dimensions are similar to those of *C. cacao*. However, in both descriptions a constriction in the centre of the conidia is mentioned that was not observed in *C. cacao*.

The formation of setae that function as conidiogenous loci and conidia in closed conidiomata was not observed in any of the other species of the three species complexes studied here. Closed conidiomata are known from the *C. boninense* and *C. gloeosporioides* species complexes ([Damm et al. 2012b](#), B. Weir, unpubl. data), and setae forming conidia is only known from *C. theobromicola* (syn. *C. fragariae*) in the *C. gloeosporioides* species complex ([Villanueva-Arce et al. 2005](#)).

Colletotrichum cacao can be identified with all loci studied. There is no *TUB2* sequence in GenBank that is > 96 % identical, no *ACT* sequence > 97 % identical, no *HIS3* sequence > 91 % identical, no *CHS-1* sequence > 98 % identical and no *GAPDH* sequence > 96 % identical to the respective sequences of *C. cacao*. The ITS sequence of strain CBS 119297 is 100 % identical to that of *Colletotrichum* sp. MCA 2773 (DQ286217), the same strain sequenced by Farr *et al.* (2006), *Colletotrichum* sp. FH2 (FJ919388) from bitter melon, probably from India (V. Jayakumar *et al.*, unpubl. data), fungal endophyte STR1:ICBG-Panama:TK766 from a tropical woody plant (KF436361, Higginbotham *et al.* 2013) and *C. gloeosporioides* isolates S166, S170, S183 and S193 from tissue of *Aristolochia triangularis* in Brazil (MF076612–MF076615, A.K. Stuart *et al.*, unpubl. data).

Colletotrichum cattleyicola Damm & Toy. Sato, **sp. nov.**
Mycobank MB824220. Fig. 4.

Etymology: The species epithet is derived from the host plant, *Cattleya*.

Sexual morph not observed. **Asexual morph on SNA.** **Vegetative hyphae** 1–8 µm diam, hyaline, smooth-walled, septate, branched. **Chlamydospores** not observed. **Conidiomata**, conidiophores and setae formed directly on hyphae. **Setae** medium brown, verruculose to verrucose, 50–80 µm long, 2–3-septate, base cylindrical, slightly inflated to conical, 4.5–6 µm diam, tip ± acute to ± rounded, setae of strain MAFF 238321 up to

280 µm long. **Conidiophores** hyaline to pale brown, smooth-walled, septate, branched, to 35 µm long. **Conidiogenous cells** hyaline to pale brown, smooth-walled, cylindrical to ellipsoidal, 9–35 × 3.5–5.5 µm, opening 1.5–2 µm diam, collarette 0.5–1 µm long, periclinal thickening visible. **Conidia** hyaline, smooth-walled, aseptate, straight, sometimes very slightly curved, cylindrical, the apex and base rounded, (10.5–)14.5–19(–20) × (4–)5–5.5(–6) µm, mean ± SD = 16.9 ± 2.1 × 5.3 ± 0.4 µm, L/W ratio = 3.2, conidia of strain MAFF 238321 longer, measuring (14–)16.5–20.5(–22) × 5–6(–6.5) µm, mean ± SD = 18.7 ± 2.0 × 5.5 ± 0.3 µm, L/W ratio = 3.4. **Appressoria** single, pale to dark brown, smooth-walled, elongate rectangular, clavate to irregular in outline, with an undulate to lobate margin, (6–)8.5–13.5(–16) × (3.5–)4–6.5(–8) µm, mean ± SD = 11.0 ± 2.5 × 5.1 ± 1.3 µm, L/W ratio = 2.2, appressoria of strain MAFF 238321 wider and more variable in size, measuring (5–)6–16.5(–29) × (4.5–)5.5–11.5(–16.5) µm, mean ± SD = 11.3 ± 5.3 × 8.4 ± 2.9 µm, L/W ratio = 1.3.

Asexual morph on Anthriscus stem. **Conidiomata**, conidiophores and setae formed on pale brown, angular cells, 3–7.5 µm diam. **Setae** pale to medium brown, verrucose, 50–100 µm long, 1–3-septate, base conical, to ± inflated, 4.5–7.5 µm diam, tip ± rounded, setae of strain MAFF 238321 up to 330 µm long. **Conidiophores** pale brown, smooth-walled to verruculose, simple or septate and branched, to 50 µm long. **Conidiogenous cells** pale brown, smooth-walled to verruculose,

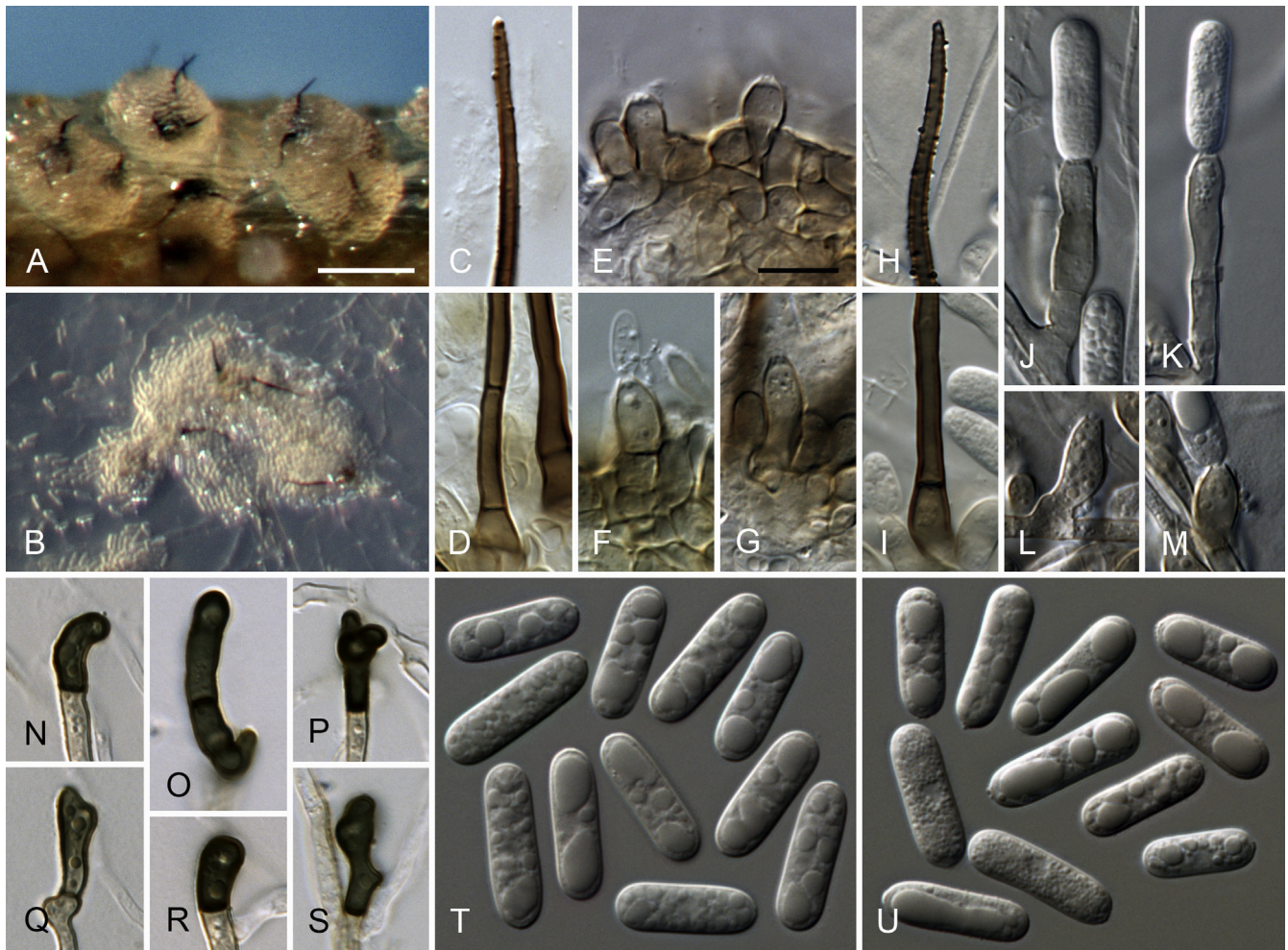


Fig. 4. *Colletotrichum cattleyicola* (from ex-holotype culture CBS 170.49). **A–B.** Conidiomata. **C, H.** Tips of setae. **D, I.** Bases of setae. **E–G, J–M.** Conidiophores. **N–S.** Appressoria. **T–U.** Conidia. **A, C–G, T.** from *Anthriscus* stem. **B, H–S, U.** from SNA. **A–B.** DM. **C–U.** DIC. Scale bars: **A** = 100 µm, **E** = 10 µm. Scale bar of **A** applies to **A–B**. Scale bar of **E** applies to **C–U**.

doliiform to cylindrical, 7–18 × 4.5–5 µm, opening 1–1.5 µm diam, collarete 0.5–1 µm long, periclinal thickening visible, sometimes distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical, the apex and base rounded, (13–)16–19(–20.5) × (5–)5.5–6(–6.5) µm, mean ± SD = 17.6 ± 1.4 × 5.9 ± 0.3 µm, L/W ratio = 3.0, conidia of strain MAFF 238321 longer, measuring (16–)18.5–21.5(–24.5) × (4.5–)5–6(–6.5) µm, mean ± SD = 20.0 ± 1.7 × 5.6 ± 0.4 µm, L/W ratio = 3.6.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline to pale honey, agar medium partly covered with very short whitish aerial mycelium, reverse same colours; growth 30–32.5 mm in 7 d (≥ 40 mm in 10 d). Colonies on OA flat with entire margin; olivaceous buff to primrose, covered with very short whitish aerial mycelium, reverse same colours, growth 31.5–34 mm in 7 d (≥ 40 mm in 10 d). *Conidial mass* whitish to very pale salmon.

Materials examined: **Belgium**, from a root of *Cattleya* sp., collection date and collector unknown (isolated by J. van Holder, identified by A.C. Stolk, deposited in the CBS collection Feb. 1949) (CBS H-21502 **holotype**, culture ex-holotype CBS 170.49). **Japan**, Mie Prefecture, from a lesion on a stem sheath of *Cattleya* sp., unknown collection date, T. Kobayashi (isolated by T. Kobayashi, Jul. 2000), GLM-F111629, culture MAFF 238321 = CBS 143245 = GLMC 1836.

Notes: *Colletotrichum cattleyicola* belongs to the *C. orchidearum* species complex. Based on our study, *C. cattleyicola* is only known from a root of *Cattleya* in Belgium and from lesions on a stem sheath of *Cattleya* sp. in Japan. The strain from Belgium was originally identified as *C. orchidearum*, which is however epitypified in this study and belongs to the *C. dracaenophilum* species complex. The strain from Japan was originally identified as *C. gloeosporioides* (Sato *et al.* 2012) and later re-identified as *C. orchidearum* as well (T. Sato, unpubl. data).

Numerous *Colletotrichum/Gloeosporium* species were described on *Orchidaceae*, among them four species that were described on *Cattleya*. *Colletotrichum cattleyae* Verpl. was described from dead leaves of *Brasso-Cattleya* (*Brassavola* × *Cattleya*) hybrid 'Woluwe' in Belgium with obovate to ovoid conidia that measure 7–10 × 3.5–7 µm, mean ± SD = 9.56 ± 0.18 × 6.22 ± 0.12 µm, L/W ratio = 3.2 (Verplancke 1935b); they are shorter and have a different shape than conidia of *C. cattleyicola* that are cylindrical. *Gloeosporium cattleyae* Henn., Hedwigia 48: 16 (1908) [Nom. illegit., Art. 53.1] was described from *Cattleya leopoldii* in Sao Paulo, Brazil, with ellipsoidal conidia with both ends rounded, that are larger than those of *C. cattleyicola*, measuring 15–22 × 7–11 µm, while *Gl. cattleyae* Henn. var. *macrospora* Verpl. forms conidia that are even larger, measuring 21–31 × 7–10 µm (Verplancke 1935a). The earlier homonym *Gl. cattleyae* Sacc. & D. Sacc. (Saccardo 1906) was described from dead leaves of *Cattleya mossia* in Paris, France, with elongate conidia with both ends rounded, measuring 15–20 × 4–6 µm. They regard this fungus as the asexual morph of *Physalospora cattleyae* Maubl. & Lasnier (Saccardo 1905) that forms ascospores that measure 20–25 × 5–7 µm. The conidial size is similar to that of *C. cattleyicola*; however, we were not able to locate the type specimen in order to verify the morphology of this species. Another species was described from *Cattleya* sp. in Italy, *C. servazzii* (Gallucci-Rangone 1955); conidia are larger than those of *C. cattleyicola*, measuring 26 × 7 µm.

Appressoria of *C. cattleyicola* are narrow and very different in shape (mostly clavate or elongate cylindrical) compared to other species in the *C. orchidearum* complex. *Colletotrichum*

cattleyicola can be identified based on its unique ITS, *HIS3* and *TUB2* sequences, while the *ACT* sequence is the same as that of *C. vittalense* and the *GAPDH* sequence is the same as those of *C. sojae* and *C. orchidearum*. The ITS of strain CBS 170.49 is identical to that of *Colletotrichum* strains ITCC 5213 from *Cattleya* in India (JN390844, Sharma *et al.* 2013b) and *Colletotrichum* sp. strain GLB3 from damaged roots of *Vanilla planifolia* in Mexico (KX953436, M.C.C. Gonzalez-Chavez *et al.*, unpubl. data), indicating possible further occurrences of this species. The closest match with the *TUB2* sequence of strain CBS 170.49 was with 99 % identity (5 nucleotides difference) *Colletotrichum* sp. MST 6-3 from leaves of *Coffea arabica* in Puerto Rico (KJ883603, M.C.C. Gonzalez-Chavez *et al.*, unpubl. data). There is only one nucleotide difference between the *GAPDH* sequence of strain CBS 170.49 and those of three unidentified *Colletotrichum* isolates, C08116, C07004 and C07010 (GU935864–GU935866), probably from Korea (Choi *et al.* 2011). The *ACT* sequence of *C. cattleyicola* is 100 % identical with that of *C. cliviae* strain GUFCC15503 from *Calamus thwaitesii* in India (KC790646, Sharma *et al.* 2013a) that is re-identified as *C. vittalense* in this study.

Colletotrichum cliviicola Damm & Crous, **nom. nov.** MycoBank MB824221. Fig. 5.

Basionym: *Colletotrichum cliviae* Yan L. Yang *et al.*, Fungal Diversity 39: 133. 2009, nom. illeg. [ICN (Melbourne) Art. 53.1], non *Chaetostroma cliviae* Oudem., Verslagen van de Gewone Vergaderingen der Wis- en Natuurkundige Afdeeling: 226. 1896. *Colletotrichum cliviae* (Oudem.) Arnaud, Bulletin de la Société de pathologie végétale de France I: 37. 1914. *Colletotrichum cliviae* (Oudem.) Petr., Sydowia 1 (1–3): 82 (1947), nom. illeg. [ICN (Melbourne) Art. 53.1].

Etymology: The species epithet is derived from the host plant, *Clivia*.

Sexual morph not observed. **Asexual morph on SNA.** **Vegetative hyphae** 1–10 µm diam, hyaline, smooth-walled, septate, branched. **Chlamydospores** not observed. **Conidiomata**, conidiophores formed directly on hyphae. **Setae** (only formed after > 2 wk) pale to dark brown (opaque), sometimes with a pale brown to white tip, smooth-walled to verruculose, 50–130 µm long, 2–4-septate, base cylindrical or slightly inflated, 4.5–5.5 µm diam, tip ± acute. **Conidiophores** hyaline, smooth-walled, septate, branched, to 30 µm long, after 3 wk turning pale brown and elongating up to 70 µm. **Conidiogenous cells** hyaline, smooth-walled, cylindrical to doliiform, often ± flexuous, upper part sometimes surrounded by a mucous sheath, 7.5–23 × 4.5–7.5 µm, opening 1.5–2 µm diam, collarete 0.5–1 µm long, periclinal thickening distinct. **Conidia** hyaline, smooth-walled, aseptate, straight, cylindrical, the apex and base rounded, (11–)15.5–20.5(–26.5) × (4–)5.5–6.5(–7) µm, mean ± SD = 17.9 ± 2.5 × 5.9 ± 0.6 µm, L/W ratio = 3.0, after 3 wk often 1-septate, forming anastomosis or secondary conidia (microcyclic conidiation) from short phialides formed from conidia or anastomosis tubes. **Appressoria** single, medium to dark brown, smooth-walled, elliptical, subcircular or irregular in outline, with an undulate to lobate margin, (7–)8.5–11.5(–12.5) × (4.5–)6.5–8.5(–9.5) µm, mean ± SD = 10.0 ± 1.7 × 7.4 ± 1.1 µm, L/W ratio = 1.3., appressoria of strain CBS 133705 differ in shape and are longer, clavate to navicular in outline, with an undulate to lobate margin, (5.5–)

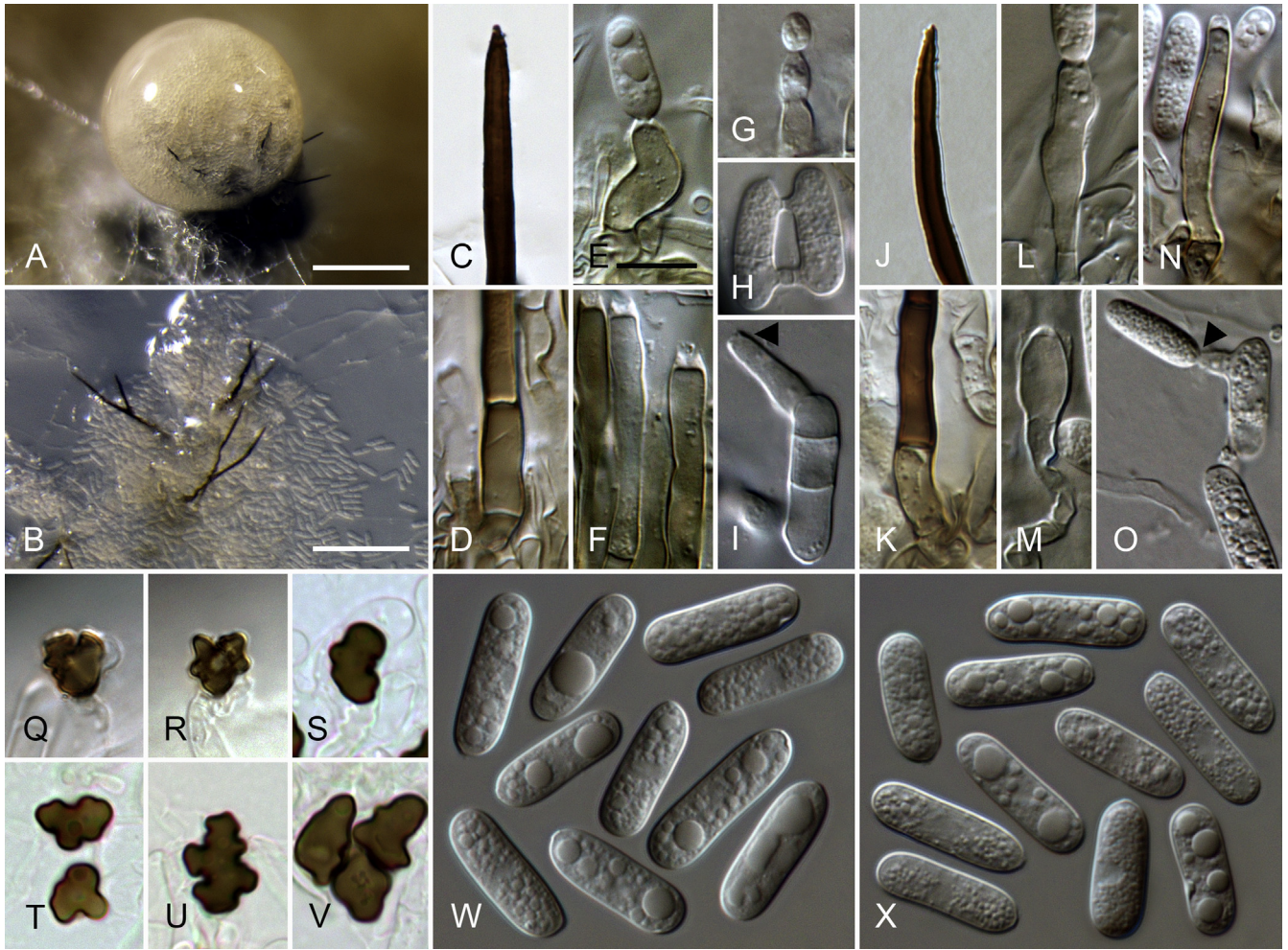


Fig. 5. *Colletotrichum cliviicola* (A–O, W–X. from ex-holotype culture CBS 125375). **A–B.** Conidiomata. **C, J.** Tips of setae. **D, K.** Bases of setae. **E–G, L–N.** Conidiophores. **H.** Two 1-septate conidia forming anastomoses. **I, O.** Aging conidia forming conidiogenous loci (arrow heads). **Q–V.** Appressoria. **W–X.** Conidia. A, C–I, W. from *Anthriscus* stem. B, J–V, X. from SNA. A–B. Dissecting microscope (DM). C–X. Differential interference contrast illumination (DIC). Scale bars: A = 200 μ m, B = 100 μ m, E = 10 μ m. Scale bar of E applies to C–X.

12–21.5(–24) \times (4.5–)5–8(–10.5) μ m, mean \pm SD = 16.6 \pm 4.8 \times 6.4 \pm 1.5 μ m, L/W ratio = 2.6.

Asexual morph on *Anthriscus* stem. **Conidiomata,** conidiophores formed on pale brown, angular cells, 3.5–8.5 μ m diam. **Setae** (only formed after >2 wk) pale to dark brown (opaque), smooth-walled to verruculose, 110–220 μ m long, 2–7-septate, base cylindrical or slightly inflated, 3.5–7.5 μ m diam, tip \pm acute. **Conidiophores** hyaline to pale brown, smooth-walled, septate, to 30 μ m long, after 3 wk elongating up to 80 μ m. **Conidiogenous cells** hyaline to pale brown, smooth-walled, cylindrical to doliiform, often \pm flexuous, occasionally extending to form new conidiogenous loci, 7–19 \times 4.5–7.5 μ m, after 3 wk elongating up to 40 μ m, opening 1.5–2 μ m diam, collarete 0.5–1 μ m long, periclinal thickening distinct. **Conidia** hyaline, smooth-walled, aseptate, straight, cylindrical, the apex and base rounded, (13–)16.5–20.5(–22.5) \times (5–)6–6.5(–7) μ m, mean \pm SD = 18.4 \pm 1.9 \times 6.2 \pm 0.4 μ m, L/W ratio = 3.0, after 3 wk often 1–3-septate, forming anastomosis or secondary conidia (microcyclic conidiation) from short phialides formed from conidia or anastomosis tubes.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline to pale saffron, agar medium and *Anthriscus* stems partly covered with whitish to pale grey aerial mycelium, *Anthriscus* stems also covered with grey to black conidiomata, reverse hyaline

to pale saffron, partial smoke grey to greyish sepia; growth 35–36 mm in 7 d (\geq 40 mm in 10 d). Colonies on OA flat with entire margin; grey olivaceous to olivaceous black, partly covered with floccose whitish to pale grey aerial mycelium, reverse pale olivaceous grey to olivaceous grey, growth 38–40 mm in 7 d (\geq 40 mm in 10 d). **Conidial mass** whitish to very pale salmon.

Materials examined: **China,** Yunnan Province, Kunming, on leaf of *Clivia miniata*, 10 Aug. 2008, Y.L. Yang (GZAAS 080005 **holotype** [not seen], GLM-F112434 isotype, culture ex-holotype CBS 125375 = CSSK4 = GLMC 1861). **South Africa,** Western Cape Province, Stellenbosch, Botanical Garden, on *Clivia* sp., 18. Jul. 2012, P.W. Crous, culture CBS 133705 = CPC 21079.

Notes: **Oudemans (1896)** described a fungus on leaves of *Clivia nobilis* (*Amaryllidaceae*) in the Netherlands as *Chaetostroma cliviae*. **Arnaud (1914)** combined this species in the genus *Colletotrichum*; **Petrak (1947)** did the same, apparently unaware of the publication by **Arnaud (1914)**. Both combinations of *Chaetostroma cliviae* are not listed in Index Fungorum and MycoBank, which was apparently the reason for **Yang et al. (2009)** to overlook them and describe *C. cliviae* as a new species from leaves of *Clivia miniata* in China. *Colletotrichum cliviae* (Oud.) Arnaud has priority over the two later homonyms *C. cliviae* (Oud.) Petr. and *C. cliviae* Yan L. Yang et al.; both are therefore illegitimate names (Art. 53.1). In order to replace the latter name, the new name *C. cliviicola* nom. nov. is provided.

Conidia of *Chaetostroma cliviae* are cylindrical with both ends rounded, measuring $23\text{--}28 \times 5\text{--}7 \mu\text{m}$ (Saccardo and Sydow, 1899), that means they are longer than those of *C. cliviicola*, measuring $(11\text{--})15.5\text{--}20, 5(-26.5) \times (4\text{--})5.5\text{--}6.5(-7) \mu\text{m}$ on SNA and $(13\text{--})16.5\text{--}20.5(-22.5) \times (5\text{--})6\text{--}6.5(-7) \mu\text{m}$ on *Anthriscus* stems. Another species described on *Clivia miniata* in greenhouses in Turnau (today Turnov, Czech Republik), *C. himantophylli* Bubák & Kabát 1907, was regarded as a synonym of *C. cliviae* (Oud.) Arnaud by Arnaud (1914). However, its conidia are narrower than this species, and *C. cliviicola*, measuring $14\text{--}24 \times 4\text{--}4.5 \mu\text{m}$ (Bubák & Kabát 1907). A later homonym, *C. himantophylli* Verpl. & Claess. 1934 (Nom. illegit., Art. 53.1), described from *Clivia nobilis* in Belgium, forms cylindrical but narrower conidia, measuring $15\text{--}23 \times 4\text{--}4.5 \mu\text{m}$ (Trotter & Cash 1972).

Colletotrichum cliviae Yan L. Yang *et al.* was reported as an anthracnose pathogen of *Arundina graminifolia*, *Capsicum* sp., *Clivia miniata*, *Cymbidium hookerianum* and *Zamioculcas zamiifolia* in China (Diao *et al.* 2017, Yang *et al.* 2009, 2011, Zhou & Li 2017) and of soybean, lima bean and grapevine in Brazil (Santos *et al.* 2018, Sousa *et al.* 2018, Barbieri *et al.* 2017), on *Cattleya* sp., *Calamus thwaitesii*, *Phaseolus* sp. and *Saccharum* sp. in India (Sharma *et al.* 2013b, Chowdappa *et al.* 2014), *Myrianthus arboreus* in Cameroon, *Citrus limon* in Vietnam (Douanla-Meli *et al.* 2018) and as an endophyte on *Camellia sinensis* and *Mangifera indica* in Brazil and China, respectively (Vieira *et al.* 2014, Liu *et al.* 2015). However, in this study, only strains from *Clivia* grouped with the ex-holotype strain of *C. cliviicola*, while all “*C. cliviae*” strains from hosts other than *Clivia* (Yang *et al.* 2011, Vieira *et al.* 2014, Liu *et al.* 2015, Barbieri *et al.* 2017), including strains from the MAFF culture collection that were included in our study, were revealed to be mostly *C. plurivorum*, a species closely related to *C. cliviicola*, *C. sojae* or *C. vittalense*.

In a study of Douanla-Meli *et al.* (2018), *C. plurivorum* (as *C. sichuanensis*) was regarded as a synonym of *C. cliviicola* (as *C. cliviae*), although both species formed well supported clades in the phylogeny based on a multilocus data set and there was no indication of discordance between the gene trees. Based on this study, *C. cliviicola* is a distinct species. The *C. cliviae* clade in Douanla-Meli *et al.* (2018) also included strains from an undetermined ornamental plant in India that could also be *Clivia*.

Strains from the studies of Douanla-Meli *et al.* (2018), Liu *et al.* (2015) and Yang *et al.* (2011) previously identified as *C. cliviae* that were re-identified as *C. plurivorum* in this study, formed a sexual morph. However, no sexual morph was observed in strains from *Clivia*, identified as *C. cliviicola* in this study (Yang *et al.* 2009, 2011, this study). Moreover, microcyclic conidiation and the formation of anastomoses were observed in the ex-type strain of *C. cliviicola*, but not in *C. plurivorum*. This species is also the fastest growing species compared to all species treated in this study.

Colletotrichum cliviicola belongs to the *C. orchidearum* species complex and differs from the closely related *C. plurivorum* in its *TUB2*, *HIS* and *GAPDH* sequences, while their *CHS-1* sequences are identical. In the ITS and *ACT* trees (not shown), *C. cliviicola* was also separated from *C. plurivorum*, but forms a subgroup within the *C. plurivorum* clade.

In a pathogenicity test by Yang *et al.* (2011), this species caused symptoms on *Clivia* spp. and *Bletilla striata* (Orchidaceae), but on none of the nine other test plants belonging to *Amaryllidaceae* and other plant families.

***Colletotrichum coelogyne* Damm, sp. nov.** MycoBank MB824222. Fig. 6.

Etymology: Named after the host plant, *Coelogyne*.

Sexual morph not observed. *Asexual morph on SNA*. *Vegetative hyphae* $1.5\text{--}11.5 \mu\text{m}$ diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata*, conidiophores and setae formed directly on hyphae. *Setae* medium brown, smooth-walled, often verruculose towards the tip, $50\text{--}190 \mu\text{m}$ long, $2\text{--}8$ -septate, base cylindrical, $3.5\text{--}5.5 \mu\text{m}$ diam, tip \pm acute. *Conidiophores* pale to medium brown, smooth-walled, septate, branched, to $80 \mu\text{m}$ long. *Conidiogenous cells* pale to medium brown, smooth-walled, cylindrical, $12\text{--}24 \times 3.5\text{--}5.5 \mu\text{m}$, the upper part often surrounded by a gelatinous sheath, opening $1.5\text{--}2.5 \mu\text{m}$ diam, collarete $0.5 \mu\text{m}$ long, periclinal thickening sometimes visible. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical, the apex and base rounded, often with a prominent scar and slightly constricted in the middle, $(15\text{--})15.5\text{--}18(-20) \times (4.5\text{--})5\text{--}6(-6.5) \mu\text{m}$, mean \pm SD = $16.7 \pm 1.2 \times 5.5 \pm 0.4 \mu\text{m}$, LW ratio = 3.0. *Appressoria* single or in loose groups, (pale) medium to dark brown, smooth-walled, navicular, \pm circular or irregular in outline, with an undulate or entire margin, $(8\text{--})10.5\text{--}16.5(-20.5) \times (6.5\text{--})8\text{--}12(-16) \mu\text{m}$, mean \pm SD = $13.4 \pm 3.1 \times 9.8 \pm 2.1 \mu\text{m}$, LW ratio = 1.4.

Asexual morph on Anthriscus stem. *Conidiomata*, conidiophores and setae formed on pale to medium brown, angular cells, $4\text{--}9.5 \mu\text{m}$ diam. *Setae* medium brown, verruculose to verrucose towards the tip, $70\text{--}210 \mu\text{m}$ long, $2\text{--}7$ -septate, base cylindrical to conical, $5\text{--}10 \mu\text{m}$ diam, tip \pm acute, often with a constriction close to the tip. *Conidiophores* pale to medium brown, smooth-walled, septate, branched, to $60 \mu\text{m}$ long. *Conidiogenous cells* pale to medium brown, smooth-walled, cylindrical, $16\text{--}25 \times 3\text{--}5 \mu\text{m}$, opening $1\text{--}1.5 \mu\text{m}$ diam, collarete $0.5 \mu\text{m}$ long, periclinal thickening visible, sometimes distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical, the apex and base rounded, often with a prominent scar and slightly constricted in the middle, $16\text{--}19(-23.5) \times 5\text{--}6 \mu\text{m}$, mean \pm SD = $17.5 \pm 1.6 \times 5.5 \pm 0.3 \mu\text{m}$, LW ratio = 3.2.

Culture characteristics: Colonies on SNA flat with entire margin, medium buff to pale honey, chervil stem, filter paper and SNA medium partly covered with greyish acervuli and short whitish aerial mycelium, reverse buff to pale honey with the grey acervuli shining through; $26\text{--}27.5 \text{ mm}$ in 7 d ($32.5\text{--}35 \text{ mm}$ in 10 d). Colonies on OA flat with entire margin, surface salmon, partly covered with dark grey to orange acervuli and floccose whitish to pale grey aerial mycelium, reverse vinaceous buff, rosy buff to purplish grey; $27.5\text{--}32.5 \text{ mm}$ in 7 d ($\geq 40 \text{ mm}$ in 10 d). *Conidial mass* orange.

Materials examined: **Germany**, Munich, glasshouse, from leaves of *Coelogyne* sp., 20 Nov. 2010, U. Damm (CBS H-21069 **holotype**, culture ex-holotype CBS 132504); Munich, glasshouse, from leaves of *Coelogyne* sp., 20 Nov. 2010, U. Damm, culture CBS 132515.

Notes: Typical for *C. coelogyne* are the large conidiomata and the comparatively high growth rate; *C. coelogyne* is the fastest growing species in the *C. dracaenophilum* complex. In contrast to *C. orchidearum*, *C. coelogyne* forms conidia that often have a prominent scar and are slightly constricted in the middle, as well as have longer setae. See *C. orchidacearum* for other species described and reported from *Orchidaceae*.



Fig. 6. *Colletotrichum coelogyne* (from ex-holotype culture CBS 132504). **A–B.** Conidiomata. **C, H.** Tips of setae. **D, I.** Bases of setae. **E–G, J–K.** Conidiophores. **L–Q.** Appressoria. **R–S.** Conidia. **A, C–G, R.** from *Anthriscus* stem. **B, H–Q, S.** from SNA. **A–B, DM.** C–S. DIC. Scale bars: **A** = 200 μ m, **E** = 10 μ m. Scale bar of **A** applies to **A–B**. Scale bar of **E** applies to **C–S**.

Colletotrichum coelogyne can be identified with all loci studied. Closest matches with the ITS sequence of *C. coelogyne* strain CBS 132504 in GenBank were with 99 % identity (1 and 4 nucleotides difference) endophytic *Colletotrichum* isolates, probably both from *Dendrobium* spp. from China (FJ042517, Yuan *et al.* 2009 and FJ544250, C. Gao & S.X. Guo, unpubl. data). Closest matches with the *TUB2* and the *GAPDH* sequences of strain CBS 132504 were with 92 % and 84 % identity, respectively, the two *C. tropicicola* strains from Noireung *et al.* (2012). Closest matches with the *ACT* and *HIS3* sequences were, both with 92 % identity, *C. tropicicola* strain MFLUCC 11-0114 and the two *C. excelsum-altitudinum* strains (Noireung *et al.* 2012, Tao *et al.* 2013) and *C. pseudomajus* strain CBS 571.88 and *C. radialis* strain CBS 529.93 (KF687864, KF687847, *C. gigasporum* complex, Liu *et al.* 2014), respectively. Closest match with the *CHS-1* sequence of strain CBS 132504 with 95 % identity were *C. yunnanense* strain CBS 132135 (JX519231, Cannon *et al.* 2012) as well as sequences of several species belonging to the *C. gloeosporioides* und *C. gigasporum* complexes.

Colletotrichum dracaenophilum D.F. Farr & M.E. Palm, Mycol. Res. 110: 1401. 2006. Fig. 7.

Sexual morph not observed. Asexual morph on SNA. Vegetative hyphae 1.5–5.5 μ m diam, hyaline, smooth-walled, septate,

branched. *Chlamydospores* not observed. *Conidiomata*, conidiophores and setae formed directly on hyphae. *Setae* medium brown, smooth-walled, verruculose towards the tip, 50–130 μ m long, 2–5-septate, base cylindrical, sometimes slightly inflated, 5–8 μ m diam, tip \pm acute, often ending in a conidiogenous opening. *Conidiophores* hyaline (setae ending in a conidiogenous opening medium brown), smooth-walled, septate, branched. *Conidiogenous cells* hyaline (on setae ending in a conidiogenous opening medium brown), smooth-walled, cylindrical, the upper part sometimes surrounded by a gelatinous sheath, 10–16 \times 5.5–6.5 μ m, opening 1.5–2 μ m diam, collarette 0.5 μ m long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical, the apex rounded, the base rounded or truncate, sometimes tapering to the base and sometimes slightly curved, (15.5–)20–24.5(–28.5) \times (5.5–)6.5–7 μ m, mean \pm SD = 22.2 \pm 2.3 \times 6.6 \pm 0.3 μ m, L/W ratio = 3.4, conidia of strain CBS 121453 shorter, measuring (15.5–)17–21.5(–25.5) \times 6–7(–8) μ m, mean \pm SD = 19.3 \pm 2.4 \times 6.7 \pm 0.4 μ m, L/W ratio = 2.9. *Appressoria* single or in loose groups, dark brown, smooth-walled, navicular, cigar- to bullet-shaped in outline, with an lobate, crenate or undulate margin, (7–)10–18(–22.5) \times (5.5–)6–8.5(–10.5) μ m, mean \pm SD = 13.9 \pm 4.0 \times 7.4 \pm 1.3 μ m, L/W ratio = 1.9, appressoria of strain CBS 121453 wider, measuring (5–)8–19(–27) \times (4.5–)6.5–11.5(–15.5) μ m, mean \pm SD = 13.5 \pm 5.5 \times 9.1 \pm 2.6 μ m, L/W ratio = 1.5.

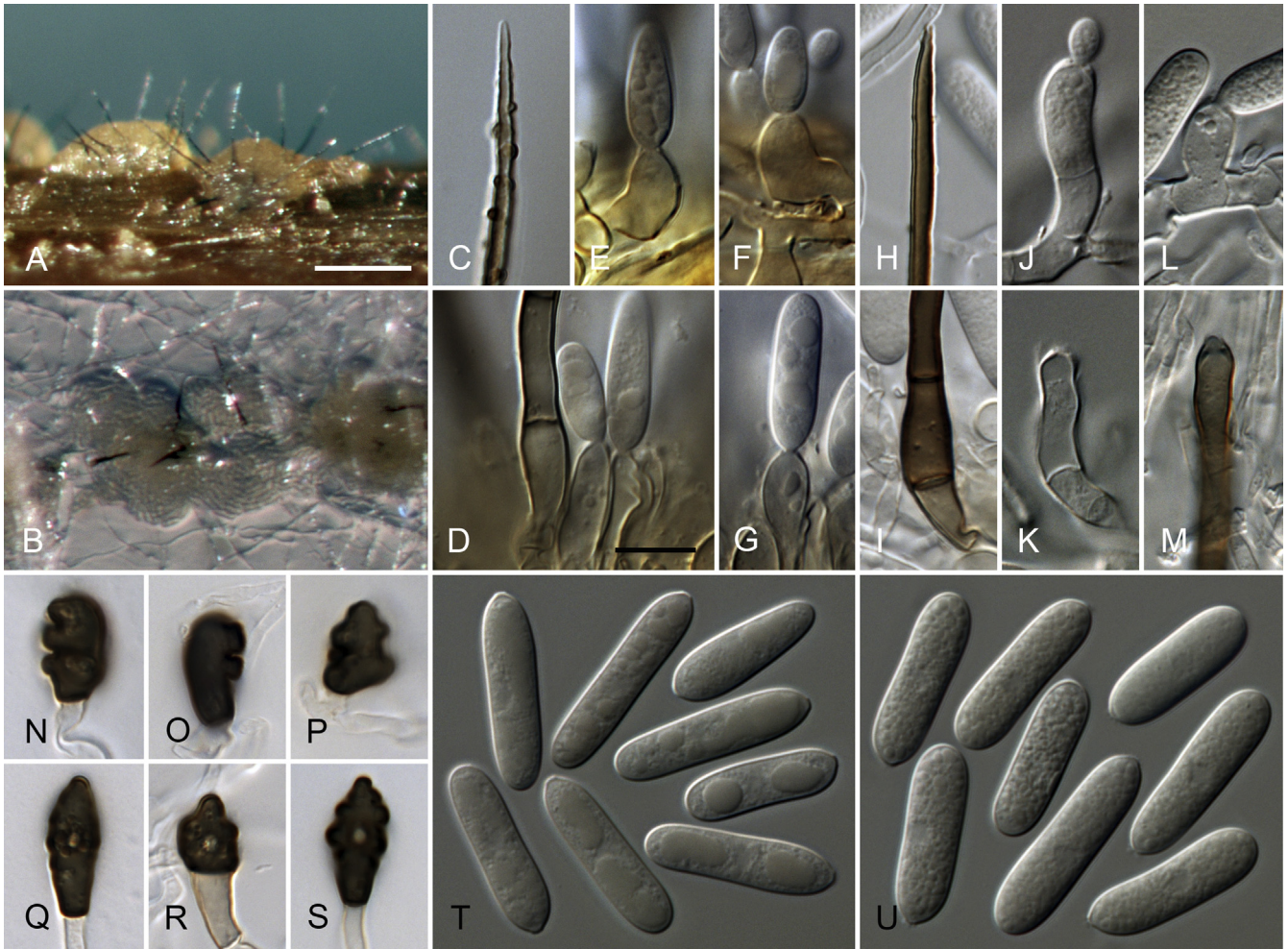


Fig. 7. *C. dracaenophilum* (from ex-holotype culture CBS 118199). A–B. Conidiomata. C, H. Tips of setae. D. Base of a setae and conidiophores. I. Base of a setae. E–G, J–M. Conidiophores. M. Seta ending in a conidiogenous opening. N–S. Appressoria. T–U. Conidia. A, C–G, T. from *Anthriscus* stem. B, H–S, U. from SNA. A–B. DM. C–U. DIC. Scale bars: A = 100 μ m, D = 10 μ m. Scale bar of A applies to A–B. Scale bar of D applies to C–U.

Asexual morph on *Anthriscus* stem. *Conidiomata*, no basal cells were found, on which conidiophores and setae are formed. *Setae* pale to medium brown, smooth-walled, verrucose towards the tip, 60–190 μ m long, 4–6-septate, base cylindrical to \pm inflated, 4–7 μ m diam, very thin towards the tip, tip \pm rounded. *Conidiophores* pale brown, smooth-walled. *Conidiogenous cells* pale brown, smooth-walled, cylindrical to ampulliform, 10–16 \times 5–7 μ m, opening 1–1.5 μ m diam, collarette 0.5 μ m long, rarely observed, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical, the apex rounded, the base rounded or truncate, sometimes with a prominent scar, sometimes tapering towards the base, (17.5–) 20–25(–28) \times 5.5–6.5 μ m, mean \pm SD = 22.4 \pm 2.6 \times 6.1 \pm 0.4 μ m, L/W ratio = 3.7.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline to pale ochreous, filter paper partly pale ochreous, chervil stem, filter paper and SNA medium partly covered with short white aerial mycelium, reverse same colours; 16.5–17 mm in 7 d (24–25.5 mm in 10 d). Colonies on OA flat with entire margin, surface moist, saffron to orange due to sporulation, or with some buff sectors with grey spots, aerial mycelium lacking, reverse saffron to buff; 14.5–15.5 mm in 7 d (25–26.5 mm in 10 d). *Conidial mass* saffron to orange.

Materials examined: **Bulgaria**, Plovdiv, from plants of *Dracaena sanderiana*, bought from the market, collection date unknown, S.G. Bobev, CBS 121453 = AR 4406 = No. 1688/1. **China**, intercepted in San Francisco, California, USA, from dying stems of *Dracaena sanderiana*, 25 Sep. 2002, J.R. Nelson (BPI 871498 **holotype** [not seen], culture ex-holotype CBS 118199 = MEP 1532).

Notes: *Colletotrichum dracaenophilum* was described as a stem pathogen of *Dracaena sanderiana*; it is based on *Dracaena* stems that were intercepted in California, USA, but originated from China (Farr *et al.* 2006). The species is only known from *Dracaena*, from *D. sanderiana* in Australia, Bulgaria, China, Egypt and Florida (USA), and on *D. braunii* in Brazil (Farr *et al.* 2006, Bobev *et al.* 2008, Sharma *et al.* 2014, Macedo & Barreto 2016, Morsy & Elshahawy 2016, Shivas *et al.* 2016). The reports from Bulgaria and Florida (USA) could be debated, as the plants were imported from other countries, probably from Asia (Bobev *et al.* 2008) and could have been infected by the fungus prior to import. The strain from Bobev *et al.* (2008) is included in this study.

Another species on *Dracaena*, *C. petchii*, was found on *D. marginata* and *Dracaena* sp. in Italy and the Netherlands, respectively, and on *D. sanderiana* in China and Australia, and belongs to the *C. boninense* species complex (Damm *et al.* 2012b, Shivas *et al.* 2016). Both species, *C. dracaenophilum* and *C. petchii*, are only known from *Dracaena* spp.

Colletotrichum dracaenophilum can be identified with all loci studied. The closest matches with the sequences of all loci of the ex-type strain CBS 118199 in GenBank are all those of the *C. dracaenophilum* strains included in this study or mentioned above. This species belongs to the *C. dracaenophilum* species complex. Conidia of *C. dracaenophilum* are larger than those of all other species treated in this study.

Colletotrichum excelsum-altitudinum G. Tao et al. [as 'excelsum-altitudum'], *Fungal Diversity* 61: 152. 2013.

Description: See Tao et al. (2013).

Notes: *Colletotrichum excelsum-altitudinum* was described from healthy leaves of *Bletilla ochracea* (Orchidaceae) in Guizhou, China, and reported from this host together with 16 other endophytic species, including a further six new *Colletotrichum* species from the same host (Tao et al. 2013).

Colletotrichum excelsum-altitudinum belongs to the *C. dracaenophilum* species complex. This species forms shorter conidia than the other species in this complex and can be identified with sequences of all loci available (ITS, *GAPDH*, *ACT*, *TUB2*), best with *GAPDH* and *TUB2*. The ITS sequence of the ex-type strain, CGMCC 3.15130, is 100 % identical with the two sequences of *C. excelsum-altitudinum* (Tao et al. 2013) and with that from *C. excelsum-altitudinum* isolate OBitC1 from *Momordica charantia* (Cucurbitaceae) in India (KU239167, P. Chowdappa et al., unpubl. data). The *GAPDH* sequence of the ex-type strain, CGMCC 3.15130, is 100 % identical with the two sequences of *C. excelsum-altitudinum* (Tao et al. 2013); the sequences of all other species are ≤ 96 % identical. The *ACT* sequence of strain CGMCC 3.15130 is 100 % identical with the two sequences of *C. excelsum-altitudinum* (Tao et al. 2013) and 99 % identical (1 and 2 nucleotides difference) with those of the *C. tropicicola* strains from *Citrus* and *Paphiopedilum* (Noireung et al. 2012), while the *TUB2* sequence is 100 % and 99 % identical (1 nucleotides difference) with those of the *C. excelsum-altitudinum* strains and 99 % identical (10 nucleotides difference) with those of both *C. tropicicola* strains.

Colletotrichum liaoningense Y.Z. Diao et al., *Persoonia* 38: 34. 2017.

Description: See Diao et al. (2017).

Notes: This species belongs to the *C. magnum* species complex and is so far only known from *Capsicum* in China (Diao et al. 2017).

There are five strains from *Capsicum* sp. in China cited in Diao et al. (2017) that belong to the species complexes treated in this paper; four strains were described as *C. liaoningense*, while one strain was identified as *C. cliviae*. The *C. cliviae* strain CAUOS5 was re-identified as *C. sojiae* (*C. orchidearum* species complex) in this study. However, there are several irregularities related to the sequence data from Diao et al. (2017). We suspect, for example, that the *ACT* sequence KP890098 is actually from CAUOS5 as well and not from CAUOS3, as it is identical with that of several strains of *C. sojiae*; there is no *ACT* sequence of CAUOS5 listed in the paper. The number of this strain in the strain table is given as CAUOS6. The sequences of the four *C. liaoningense* strains deposited by Diao et al. (2017) also all differ from one another. For example, the ITS sequence of strain CAUOS2, the ex-type strain of *C. liaoningense* differs in numerous positions from those of the other three strains of this

species, while the *TUB2* sequences are identical with *C. magnum* (see notes of this species).

The four strains of *C. liaoningense* form two clades in the phylogeny of this study, suggesting that their identification requires verification.

Colletotrichum lobatum Damm, sp. nov. MycoBank MB824223. Fig. 8.

Etymology: The species epithet is derived from the lobate edge of the appressoria.

Sexual morph not observed.

Asexual morph on SNA. Vegetative hyphae 1–6.5 μm diam, hyaline, smooth-walled, septate, branched. Chlamydospores not observed. Conidiomata, conidiophores and setae formed directly on hyphae. Setae pale to medium brown, verrucose, 35–90 μm long, 1–3-septate, base cylindrical to slightly inflated, 4.5–7 μm diam, tip \pm rounded to \pm acute. Conidiophores hyaline to pale brown, smooth-walled, septate, branched, to 45 μm long. Conidiogenous cells hyaline to pale brown, smooth-walled, cylindrical, 5–30 \times 3–5 μm , opening 1.5–2 μm diam, collarette 0.5–1 μm long, distinct, periclinal thickening distinct. Conidia hyaline, smooth-walled, aseptate, straight, cylindrical, the apex and base rounded, (10.5–)12.5–14.5(–16) \times (4–)4.5–5 μm , mean \pm SD = 13.7 \pm 1.0 \times 4.7 \pm 0.3 μm , L/W ratio = 2.9. Appressoria not formed on the backside of the SNA plate, but in slide culture, single, medium brown, smooth-walled, subglobose, elliptical to irregular in outline, with an lobate or undulate margin, (7–)7.5–15.5(–25) \times (5.5–)6.5–11(–15) μm , mean \pm SD = 11.6 \pm 4.0 \times 8.9 \pm 2.3 μm , L/W ratio = 1.3.

Asexual morph on Anthriscus stem. Conidiomata, conidiophores and setae formed on pale brown, angular cells, 3.5–7 μm diam. Setae medium brown, verrucose, 45–90 μm long, 1–3-septate, base cylindrical, sometimes slightly inflated, 4–6.5 μm diam, tip \pm acute to \pm rounded. Conidiophores hyaline to pale brown, smooth-walled to verruculose, simple or septate, branched, to 30 μm long. Conidiogenous cells pale brown, smooth-walled to verruculose, cylindrical to doliform, 7.5–15 \times 3.5–5.5 μm , opening 1.5–2 μm diam, collarette 0.5 μm long, periclinal thickening distinct. Conidia hyaline, smooth-walled, aseptate, straight, cylindrical, the apex and base rounded, (13.5–)14.5–17(–18) \times (4–)4.5–5(–5.5) μm , mean \pm SD = 15.6 \pm 1.2 \times 4.9 \pm 0.3 μm , L/W ratio = 3.2.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline, honey to pale cinnamon, agar medium, filter paper and *Anthriscus* stem partly covered with tiny grey to salmon acervuli, aerial mycelium lacking, reverse same colours, growth 23–24.5 mm in 7 d (33.5–35 mm in 10 d). Colonies on OA flat with entire margin; cinnamon, entirely covered by tiny grey dots formed by conidiomata, aerial mycelium lacking, reverse buff to vinaceous buff, growth 25.5–27 mm in 7 d (35.5–37.5 mm in 10 d). Conidial mass salmon.

Material examined: Trinidad and Tobago, from *Piper catalpaefolium*, collection date and collector unknown (IMI 79736 holotype, CBS H-21506 isotype, culture ex-holotype IMI 79736 = CPC 21196).

Notes: There are two species on *Piper* spp. treated in this study, *C. lobatum* and *C. piperis*. *Colletotrichum lobatum* belongs to the *C. magnum* species complex, while *C. piperis* belongs to the *C. orchidearum* complex. The conidial sizes and shapes are very similar. In contrast to *C. piperis*, *C. lobatum* forms lobate appressoria and setae that are unbranched, and colonies that

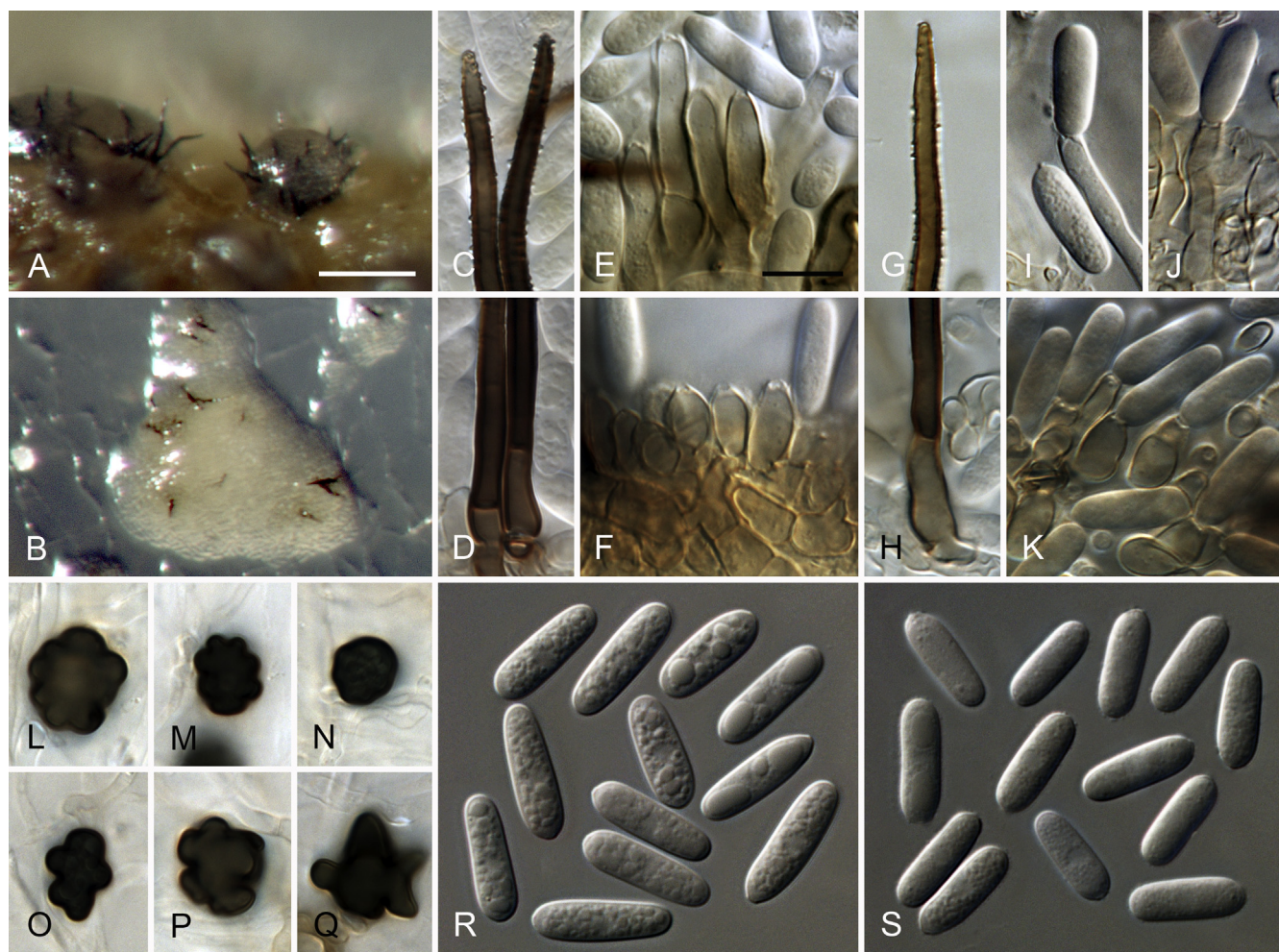


Fig. 8. *Colletotrichum lobatum* (from ex-holotype culture IMI 79736). **A–B.** Conidiomata. **C, G.** Tips of setae. **D, H.** Bases of setae. **E–F, I–K.** Conidiophores. **L–Q.** Appressoria. **R–S.** Conidia. **A, C–F, R.** from *Anthriscus* stem. **B, G–Q, S.** from SNA. **A–B.** DM. **C–S.** DIC. Scale bars: **A** = 100 μ m, **E** = 10 μ m. Scale bar of **A** applies to **A–B**. Scale bar of **E** applies to **C–S**.

grow faster. Moreover, *C. lobatum* strain IMI 79736 originates from Latin America, while *C. piperis* is only known from Asia (Malaysia, Sri Lanka). See *C. piperis* for other species described and reported from *Piper* spp.

The mostly regularly lobed roundish appressoria are also different from the irregular appressoria of the closely related *C. brevisporum* that also has faster growing colonies.

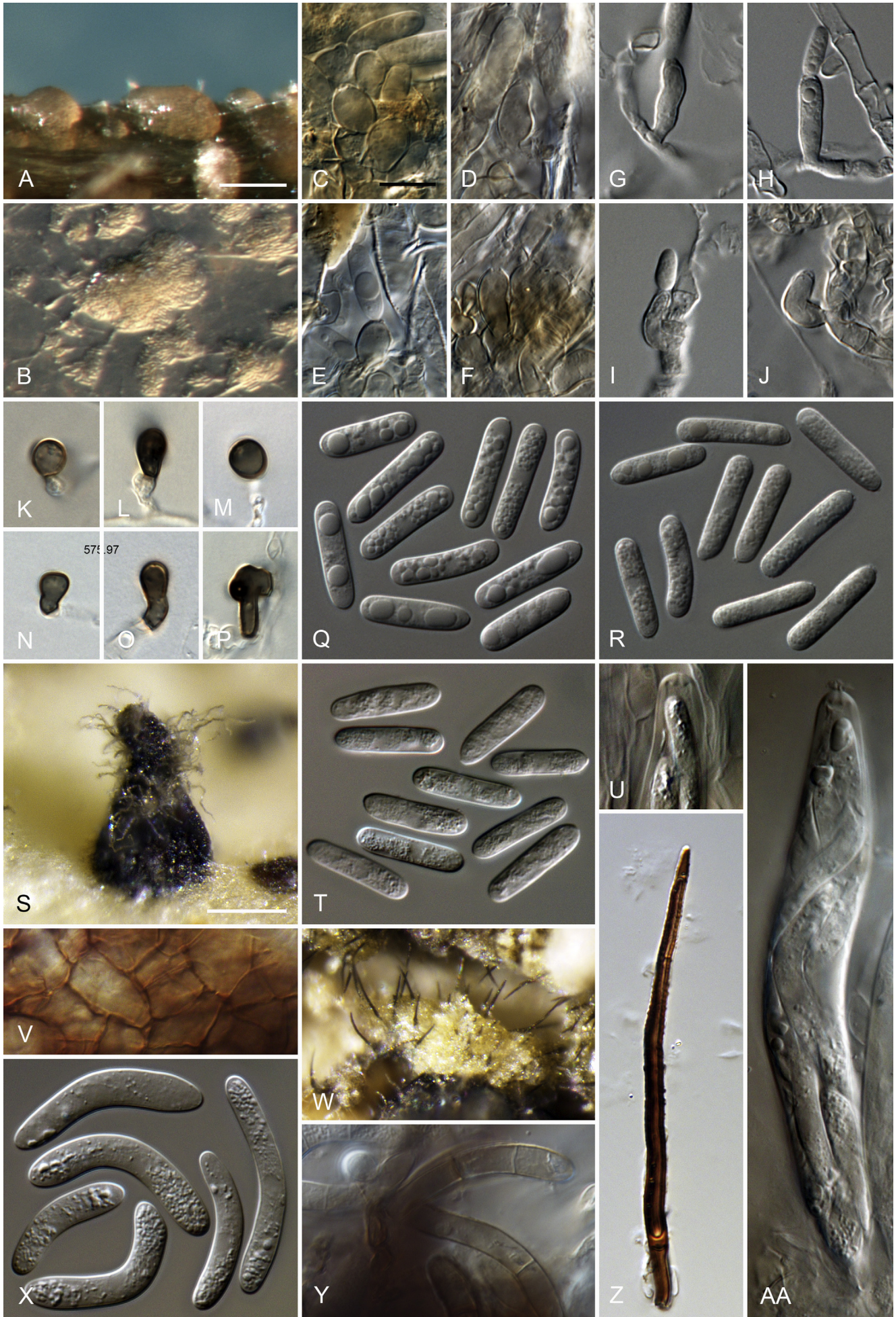
The species can be identified best by its unique *GAPDH* sequence. There is respectively one nucleotide difference in the *TUB2*, *CHS-1* and *HIS3* sequences to those of *C. brevisporum*, while ITS and *ACT* sequences of the two species are identical. The closest matches in a blastn search with the *GAPDH* sequence in GenBank were with 97 % *C. liaoningense* strains CAUOS3 and CAUOS4 (KP890136, KP890137, [Diao et al. 2017](#)), while the closest matches with the *TUB2* sequence were with 99 % identity (1 nucleotide difference) *C. brevisporum* strains L57/LC0600 (ex-holotype strain) and BTL23/LC0870 (JN050244 and JN050245, [Noireung et al. 2012](#)) and strain CCCM12 from *Cucurbita moschata* (KY797630, [Liu et al. 2018](#)). The result of the blastn search with the ITS sequence was the same as that for *C. brevisporum*.

Colletotrichum magnum (S.F. Jenkins & Winstead) Rossman & W.C. Allen, IMA Fungus 7: 4. 2016. [Fig. 9](#).

Basionym: *Glomerella magna* S.F. Jenkins & Winstead, *Phytopathology* 54: 453. 1964.

Sexual morph on filter paper (only observed on the type specimen BPI 596678). *Ascomata* perithecia, solitary, superficial or immersed, non-stromatic, medium to dark brown, subglobose to pyriform, 355–500 \times 200–355 μ m, ostiolate, with a neck. *Peridium* composed of medium brown flattened *textura angularis* with cells 8–17 μ m diam. *Ascogenous hyphae* and *interascal tissue* not observed. *Asci* unitunicate, probably 8-spored, but the number of spores per ascus could not be seen, cylindrical, tapering to apex and base, smooth-walled, 71–122 \times 12–15.5 μ m. *Ascospores* initially hyaline and aseptate but can become pale brown and septate with age, smooth-walled, allantoid, curved most in the middle, with rounded ends, (23–) 27–37(–43.5) \times (4.5–)5–6.5(–7) μ m, mean \pm SD = 32.1 \pm 5.0 \times 5.6 \pm 0.7 μ m, L/W ratio = 5.7.

Asexual morph on filter paper (type specimen BPI 596678). *Conidiomata*, conidiophores (disintegrated) and setae formed on pale brown, angular cells. *Setae* medium brown, verruculose to verrucose, 50–70 μ m long, 1–3-septate, base cylindrical, 3–4 μ m diam, tip rounded. *Conidiophores* and *conidiogenous cells* not observed. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical, the apex and base rounded, (17–)



18–20(–20.5) × 4.5–5(–5.5) µm, mean ± SD = 19.1 ± 1.0 × 4.9 ± 0.3 µm, LW ratio = 3.9.

Asexual morph on SNA (ex-epitype strain CBS 519.97). **Vegetative hyphae** 1.5–11 µm diam, hyaline, smooth-walled, septate, branched. **Chlamydospores** not observed. **Conidiomata**, conidiophores formed directly on hyphae. **Setae** not observed. **Conidiophores** hyaline, smooth-walled, septate, not branched, to 20 µm long, conidiophores of strain CBS 575.97 pale to medium brown, smooth-walled to verruculose, septate, branched, to 50 µm long. **Conidiogenous cells** hyaline, smooth-walled, cylindrical to ellipsoidal, often ± flexuous, 13–20 × 4–5 µm, conidiogenous cells of strain CBS 575.97 pale to medium brown, smooth-walled to verruculose, cylindrical to clavate, opening 1.5–2 µm diam, collarette 0.5 µm long, periclinal thickening visible. **Conidia** hyaline, smooth-walled, aseptate, straight, sometimes very slightly curved, cylindrical, the apex and base rounded, (11–)15.5–19(–20.5) × 4–4.5 µm, mean ± SD = 17.4 ± 1.8 × 4.2 ± 0.2 µm, LW ratio = 4.1. **Appressoria** single or in loose groups, medium to dark brown, smooth-walled, ± circular, elliptical, clavate, spatulate or irregular in outline, with an entire or undulate margin, (5–)6.5–12.5(–16) × (3.5–)4.5–7.5(–10) µm, mean ± SD = 9.4 ± 2.9 × 5.9 ± 1.5 µm, LW ratio = 1.6.

Asexual morph on Anthriscus stem (ex-epitype strain CBS 519.97). **Conidiomata**, conidiophores formed directly on hyphae or on pale brown, angular cells, 3–8.5 µm diam. **Setae** not observed. **Conidiophores** pale brown, smooth-walled, sometimes septate, rarely branched, to 20 µm long. **Conidiogenous cells** pale brown, smooth-walled, subsphaerical to broadly ellipsoidal, sometimes ampulliform, 5.5–12 × 4–7 µm, opening 1.5–2 µm diam, collarette not observed, periclinal thickening visible. **Conidia** hyaline, smooth-walled, aseptate, sometimes very slightly curved, cylindrical, the apex and base rounded, (17–)18–20(–21.5) × 4.5–5(–5.5) µm, mean ± SD = 19.2 ± 1.1 × 4.8 ± 0.3 µm, LW ratio = 4.0, conidia of strain CBS 575.97 narrower, measuring (17–)19–22(–24) × (3.5–)4–4.5(–5) µm, mean ± SD = 20.5 ± 1.4 × 4.3 ± 0.3 µm, LW ratio = 4.8.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline to pale cinnamon, aerial mycelium lacking, in strain CBS 575.97 *Anthriscus* stem and medium partly covered with felty white aerial mycelium, reverse same colours; 24.5–25.5 mm in 7 d (36–36.5 mm in 10 d), strain CBS 575.97 faster growing, 28.5–31.5 mm in 7 d (≥ 40 mm in 10 d). Colonies on OA flat with entire margin, surface isabelline to citrine, towards the margin straw, aerial mycelium lacking, reverse olivaceous buff to olivaceous, 24.5–26 mm in 7 d (36.5 mm in 10 d), strain CBS 575.97 differing in colour, mycelium formation and growth rate: dark olivaceous, olivaceous to olivaceous black, partly covered with short felty whitish aerial mycelium, reverse olivaceous buff, olivaceous grey to iron grey, 25.5–27.5 mm in 7 d (36–≥ 40 mm in 10 d). **Conidial mass** saffron.

Materials examined: USA, from *Citrullus lanatus*, collection date and collector unknown, [BPI 596678 (S120 A × S120 F, dried culture on filter paper) **holotype**]; from *Citrullus lanatus*, collection date and collector unknown (CBS H-21063 **epitype**, here designated MBT380418, culture ex-epitype CBS

519.97 = L2.5 = LARS 688); from *Citrullus lanatus*, collection date and collector unknown, culture CBS 575.97 = DXD = LARS 687; from *Citrullus lanatus*, collection date and collector unknown (deposited in IMI collection by D.S. Freeman), culture IMI 391662 = L2 5 = CPC 19388.

Notes: An anthracnose disease of cucurbits caused by *Ga. magna* was reported from the USA (Jenkins & Winstead 1964). The causal agent was isolated from *Citrullus lanatus* and described as a heterothallic species with very large asci and ascospores that were formed by strains crossed in the laboratory. The species was combined into *Colletotrichum* by Rossman *et al.* (2016).

Compatible strains 120A (=ATCC 15015 = S120A) and 120F (=ATCC 15016 = S120F) that were crossed in the laboratory to produce the sexual morph were deposited in ATCC by Jenkins & Winstead (1964). In the resulting publication, the authors state that they deposited herbarium material in BPI as S 120A and S 120F, apparently two specimens and not indicating it as type material. That would mean the species is not validly published, as it was published after 1 Jan. 1958 without designating a type (Art. 40.1). However, the label on BPI 596678 says “possible type”; further information on the specimen: “S.F.J. & N.N.W. No. S120 A × S120 F, Comm. N.N. Winstead May 10, 1963” clearly reveals that the authors deposited only one specimen, the result of the crossing of the two strains and not two, and that the details of this specimen agree with the information in the original description. BPI 596678 is therefore regarded as the holotype.

The two strains 120A and 120F that were crossed in order to form the sexual morph have no type status, and there is no ex-holotype strain retained. In a subsequent PhD thesis at Cornell University, Ithaca, NY, USA, that was not available to us, S. Brown conducted additional crosses of the two original strains. Strains CBS 519.97 (=LARS 688 = L2.5) and CBS 575.97 (=LARS 687 = DXD) are derived from them (B.G. Turgeon, in litt.). One of these strains, CBS 519.97, was selected as the basis of the epitype.

Conidia of the holotype specimen BPI 596678 measured in this study are smaller than those listed in the original description by Jenkins & Winstead [1964; (24–)28(–40) × (4–)4.5(–6) µm], measuring (17–)18–20(–20.5) × 4.5–5(–5.5) µm]. Conidial measurements from the ex-epitype strain CBS 519.97 agree with those from the holotype. Other features observed on the holotype do not diverge from the original description.

Two further species were described on *Citrullus* in Russia and the USA, respectively. They are possible *Colletotrichum* spp. However, none of them seems to be conspecific with *C. magnum*: *Gloeosporium lagenaria* var. *citrulli* forms shorter conidia (14 × 5 µm, Potebnia 1907) than *C. magnum*, while conidia of *Volutella citrulli* are elliptical or clavate, sometimes slightly curved, measuring 15–20 × 3–4 µm (Stoneman 1898). Conidia of *C. magnum* are wider and not clavate.

Although Jenkins & Winstead (1964) proved the pathogenicity of *Ga. magna* to many species of *Cucurbitaceae*, especially watermelon, squash, pumpkin and cantaloup, strains and specimens from that study are all from watermelon. *Glomerella magna* is reported from other *Cucurbitaceae* in the USA, China

Fig. 9. *Colletotrichum magnum* (A–J, Q–R. from ex-epitype culture CBS 519.97. K–P. from culture CBS 575.97. S–AA. from holotype BPI 596678). **A–B, W.** Conidiomata. **C–J.** Conidiophores. **K–P.** Appressoria. **Q–R, T.** Conidia. **S.** Ascoma. **V.** Outer surface of peridium. **X–Y.** Ascospores. **Z.** Seta. **U, AA.** Asci. A, C–F, Q. from *Anthriscus* stem; B, G–P, R. from SNA. S–AA. from filter paper. A–B, S, W. DM. C–R, T–V. X–AA. DIC. Scale bars: A, S = 100 µm, C = 10 µm. A applies to A–B. S applies to S, W. C applies to C–R, T–V, X–AA.



Fig. 10. *Colletotrichum merremiae* (from ex-holotype culture CBS 124955). **A–B.** Conidiomata. **C.** Tip of a seta. **D.** Base of a seta. **H.** Seta. **E–G, I–L.** Conidiophores. **M–R.** Appressoria. **S–T.** Conidia. **A, C–G, S.** from *Anthriscus* stem. **B, H–R, T.** from SNA. **A–B.** DM. **C–T.** DIC. Scale bars: **A** = 100 μ m, **E** = 10 μ m. Scale bar of **A** applies to **A–B**. Scale bar of **E** applies to **C–T**.

and Taiwan (Grand 1985, Tsay *et al.* 2010), from *Carica papaya* in Brazil, Costa Rica and Mexico (Nascimento *et al.* 2010, Tapia-Tussel *et al.* 2016, Molina-Chaves *et al.* 2017) and *Lobelia chinensis* in China (Li *et al.* 2013), however, most of them either lack molecular data or have ITS data only. By means of sequence comparison, most of the respective strains could be confirmed as belonging to the *C. magnum* species complex. However, there is no species identification possible in this complex based on ITS data.

In contrast, further reports of *Colletotrichum* species on *Citrullus lanatus* include *C. truncatum* (as *C. capsici*) in India, *C. gloeosporioides* and *C. gloeosporioides* f. sp. *cucurbitae* in Brazil, *C. lagenarium* in the USA, Libya and Zimbabwe as well as *C. orbiculare* in several countries worldwide (Farr & Rossman 2017). Probably none of these reports was based on molecular data and some could refer to *C. magnum*. The only strain of a different species from *Citrullus* identified based on molecular data is strain CBS 128524 from *Citrullus lanatus* in New Zealand that was identified as *C. karstii*, belonging to the *C. boninense* species complex (Damm *et al.* 2012b).

Colletotrichum magnum is difficult to differentiate based on sequence data. Of the loci included, only the *GAPDH* and possibly also the *HIS3* sequences are unique. However, *HIS3* sequences are not available of all species that are included in the multilocus phylogeny in this study. The other loci are identical with strains of other species, mainly *C. liaoningense* (Diao *et al.* 2017). Conidia of *C. magnum* are sometimes slightly curved on

both media, having a different shape than those of the closely related *C. okinawense*, and are longer than those of the also closely related *C. liaoningense* (71–122 \times 12–15.5 μ m, Diao *et al.* 2017). The ascospores are curved and larger than those of any other *Colletotrichum* species treated in this study and only exceeded in length by *C. gigasporum* (Rakotoniriana *et al.* 2013) and *C. taiwanense* (Sivanesan & Hsieh 1993), the former belonging to the *C. gigasporum* complex, while the systematic position of the latter is dubious (Liu *et al.* 2014). Both species have filiform, 0–1- or 3–8-septate, respectively, ascospores that are less strongly curved than those of *C. magnum*.

Closest matches with the *GAPDH* sequence of strain CBS 519.97 were with 99 % identity (1 nucleotide difference) *Ga. magna* strain AK7 probably from watermelon in the USA (DQ792850, Liu *et al.* 2007a) and *C. brevisporum* isolate LJTJ59 (KP943513) from *Capsicum* in China (F. Liu & G. Gong, unpubl. data). Based on blastn searches, the ITS sequence of the ex-type strain CBS 519.97 is 100 % identical e.g. to those of *Ga. magna* and *Colletotrichum* sp. strains from *Carica papaya* in Brazil (Nascimento *et al.* 2010), Mexico (E.T. Arechiga-Carvajal *et al.*, unpubl. data) and Malaysia (J.H. Sim *et al.*, unpubl. data). However, the ITS of *C. magnum* is identical with several other species in the *C. magnum* complex.

Colletotrichum magnum was the basis for a number of molecular, morphological and pathogenicity studies on appressorium formation, pathogenic and symbiotic lifestyles of fungi in plants (Bhairi *et al.* 1990, Freeman & Rodriguez 1993, Redman

et al. 1999, Rodriguez et al. 2004). For example, mutation of pathogenic *C. magnum* strains resulted in the loss of a virulence factor and transformation into an endophytic fungus (Freeman & Rodriguez 1993).

Colletotrichum merremiae Damm, sp. nov. MycoBank MB824224. Fig. 10.

Etymology: The species epithet is derived from the host plant, *Merremia*.

Sexual morph not observed. **Asexual morph on SNA.** Vegetative hyphae 1.5–7 µm diam, hyaline to pale brown, smooth-walled, septate, branched. Chlamydospores not observed. Conidiomata, conidiophores and setae formed directly on hyphae. Setae (pale to) medium brown, smooth-walled, verrucose towards the tip, 30–65 µm long, 1–2-septate, base cylindrical or ± inflated, 4–5.5 µm diam, tip ± acute. Conidiophores pale brown, smooth-walled to verruculose, septate, branched, to 40 µm long. Conidiogenous cells pale brown, smooth-walled to verruculose, cylindrical, sometimes flexuous, 10–21 × 3–5 µm, opening 1.5–2 µm diam, collarete 0.5 µm long, periclinal thickening visible, sometimes distinct. Conidia hyaline, smooth-walled, aseptate, straight, cylindrical, the apex rounded, the base rounded to truncate, (12.5–)14–15.5(–16.5) × (4–)4.5–5(–5.5) µm, mean ± SD = 14.8 ± 0.9 × 4.6 ± 0.3 µm, L/W ratio = 3.2. Appressoria single, medium brown, smooth-walled, ± circular to elliptical in outline, with an entire or undulate margin, (4.5–)5–7.5(–10) × (3–)3.5–5(–5.5) µm, mean ± SD = 6.4 ± 1.3 × 4.3 ± 0.7 µm, L/W ratio = 1.5.

Asexual morph on Anthriscus stem. Conidiomata, conidiophores and setae formed directly on hyphae, no basal cells observed. Setae medium brown, verruculose, 45–80 µm long, 1–2-septate, base cylindrical, conical to ± inflated, 4–7.5 µm diam, tip ± acute. Conidiophores pale brown, smooth-walled, septate, rarely branched. Conidiogenous cells pale brown, smooth-walled, cylindrical to ellipsoidal, flexuous and with constrictions, 8–12 × 4.5–6.5 µm, opening 1.5–2 µm diam, collarete 0.5 µm long, periclinal thickening visible. Conidia hyaline, smooth-walled, aseptate, straight, cylindrical, the apex rounded, the base rounded to truncate, (14–)15–16.5(–19) × (4–)4.5–5 µm, mean ± SD = 15.8 ± 0.9 × 4.6 ± 0.2 µm, L/W ratio = 3.4.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline to pale cinnamon, aerial mycelium lacking, reverse same colours, 21.5–22.5 mm in 7 d (31.5–35 mm in 10 d). Colonies on OA flat with entire margin, olivaceous, towards the margin honey to buff, partly covered with short felty whitish aerial mycelium, reverse olivaceous buff to olivaceous grey, 24–24.5 mm in 7 d (35–35.5 mm in 10 d). Conidial mass rosy buff to saffron.

Material examined: Panama, Gamboa, wet lowland forest, leaf endophyte of *Merremia umbellata*, Nov. 2004, S. VanBael & Z. Maynard, D3-1 (CBS H-21065 holotype, culture ex-type CBS 124955 = Q855).

Notes: *Merremia* is a genus of flowering plants in the *Convolvulaceae*; *M. umbellata* is commonly known as hogvine (www.wikipedia.org). No *Colletotrichum* species was previously described from *Merremia* and no strain from this host genus was included in any of the recently studied species complexes. The USDA fungal databases (Farr & Rossman 2017) only list Rojas et al. (2010), the publication where the two strains, CBS 124955 and CBS 125386, described as two different species in this study, *C. merremiae* and *C. panamense*, were derived from. Both species belong to the *C. magnum* species complex.

The conidiogenous cells of *C. merremiae* are usually cylindrical and often flexuous or with constrictions, while those of *C. panamense* are mostly subglobose to ellipsoidal. Conidia of *C. merremiae* are on both media on average at least 2 µm shorter than those of *C. panamense*. Typical are also the small roundish appressoria, that are very different from the compact appressoria of the closely related *C. brevisporum* and *C. lobatum*. According to the measurements in Diao et al. (2017), the appressoria of *C. liaoningense* are even smaller (3.5–5 × 2.5–4.5 µm).

Colletotrichum merremiae can be identified based on its unique *GAPDH*, *HIS3* and *TUB2* sequences. *HIS3* differs in one, *GAPDH* and *TUB2* each in four nucleotides from *C. brevisporum*. The ITS and *ACT* sequences are identical with those of *C. brevisporum* and *C. lobatum*, that of ITS also with *C. okinawense*. The ITS, *GAPDH*, *CHS-1*, *HIS3*, *ACT* and *TUB2* sequences of the two species from *Merremia* differ in 3, 8, 5, 12, 9 and 5 nucleotides, respectively.

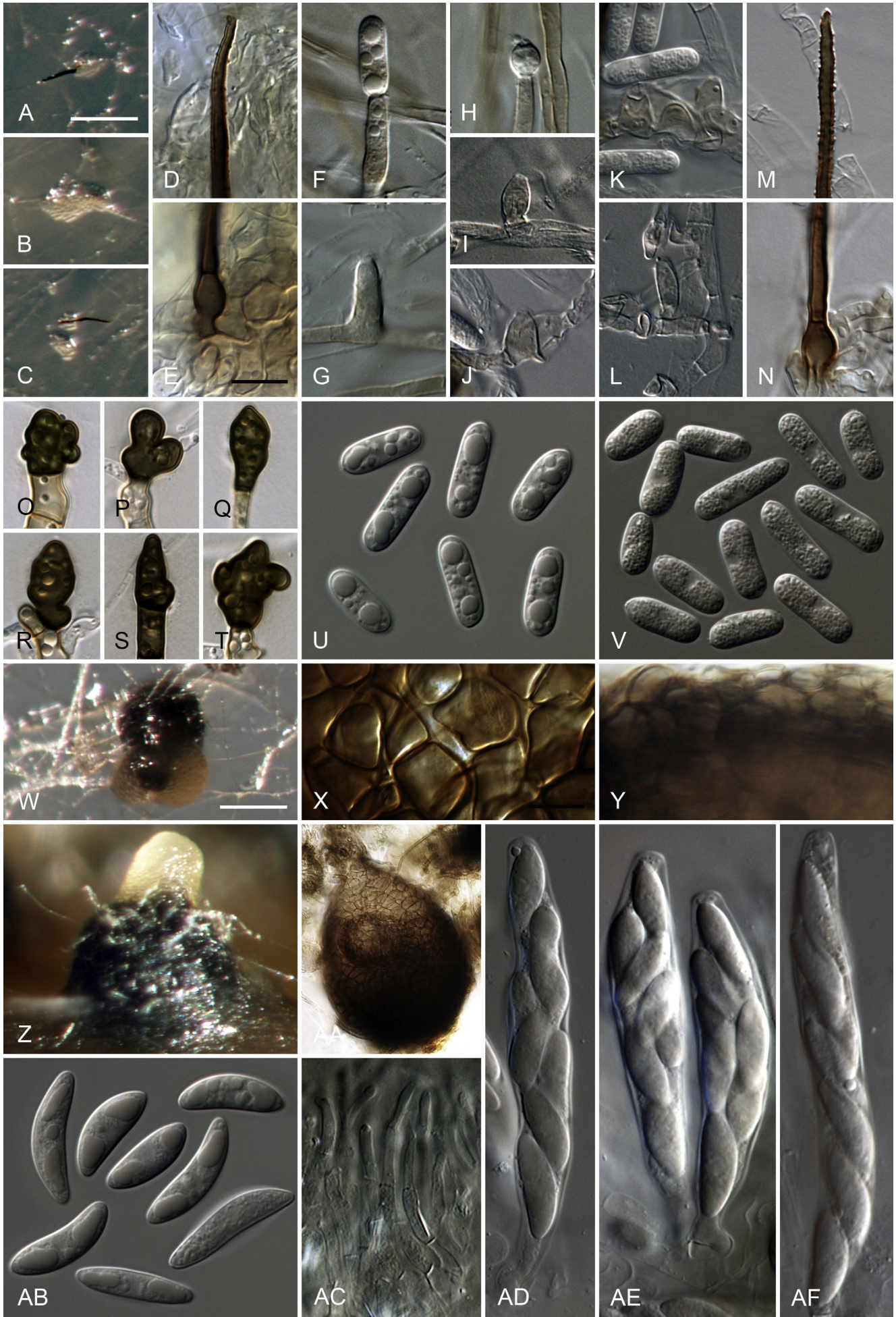
Closest match in a blastn search with the *TUB2* sequence of *C. merremiae* strain CBS 124955 is with 99 % identity (3 nucleotides difference) *C. brevisporum* strain CCCM12 from *Cucurbita moschata* in China (KY797630, Liu et al. 2018) and with the *GAPDH* sequence with 98 % identity the two *C. brevisporum* strains from the paper of Noireung et al. (2012). No *HIS3* sequence in GenBank is more than 91 % identical to that of *C. merremiae*. A blastn search with the ITS sequence of *C. merremiae* resulted in more than 50 identical sequences from strains that were identified as *C. brevisporum*/*Ga. cingulata* var. *brevisporum*, *C. magnum*/*Ga. magna* and unidentified *Colletotrichum* strains including that of the same species sequenced by Rojas et al. (2010, GU994392).

Colletotrichum musicola Damm, sp. nov. MycoBank MB824225. Fig. 11.

Etymology: The species epithet is derived from the host plant, *Musa*.

Sexual morph on Anthriscus stem (only observed in strain CBS 132885). Ascum perithecia, formed after 4 wk, solitary, superficial, non-stromatic, pyriform, ostiolate, glabrous, medium to dark brown, 200–320 × 130–220 µm diam, ostiolate, glabrous; Peridium 5–10 µm thick, composed of 2–4 layers of medium to dark brown flattened *textura angularis* with cells 5–16.5 µm diam. Ascogenous hyphae hyaline, smooth-walled, delicate, rarely visible. Interascal tissue formed of paraphyses, hyaline, smooth-walled, cylindrical, with a round tip, disintegrating quickly, septate, apically free, 40–55 µm long, at the basis 2–6 µm wide. Asci unitunicate, 8-spored, cylindrical to clavate, tapering to apex and base, smooth-walled, 76–91.5 × 9.5–12.5 µm. Ascospores uni- or biserially arranged, aseptate, hyaline, sometimes pale brown, smooth-walled, lunate to fusiform (12.5–)16–21(–25.5) × (4.5–)5.5–6.5(–7) µm, mean ± SD = 18.4 ± 2.4 × 6.0 ± 0.5 µm, L/W ratio = 3.1.

Sexual morph on SNA (only observed in strain CBS 132885). Ascum pyriform to subspherical, 100–370 × 90–300 µm. Peridium 5–10 µm thick, composed of 2–4 layers of pale to medium brown flattened *textura angularis* with cells 4.5–15.5 µm diam. Ascogenous hyphae hyaline, smooth, delicate, rarely visible. Interascal tissue formed of paraphyses, hyaline, smooth-walled, cylindrical, disintegrating quickly, rarely observed. Asci unitunicate, 8-spored, narrowly clavate, cylindrical to flask-shaped, fasciculate, 35–90.5 × 10–13.5 µm. Ascospores uni- or biserially arranged, aseptate, hyaline, sometimes pale brown,



smooth-walled, lunate to fusiform, (15–)17.5–21.5(–24.5) × (5–)5.5–6.5(–8) µm, mean ± SD = 19.5 ± 2.2 × 6.0 ± 0.6 µm, L/W ratio = 3.2.

Asexual morph on SNA. *Vegetative hyphae* 1–10.5 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata*, conidiophores and setae formed directly on hyphae. *Setae* pale to medium brown, verruculose to verrucose, 65–95 µm long, 1–2-septate, base cylindrical to ± inflated, 4.5–6.5 µm diam, tip ± rounded. *Conidiophores* hyaline to pale brown, smooth-walled, single or septate and branched, to 30 µm long. *Conidiogenous cells* hyaline to pale brown, smooth-walled, cylindrical to conical, 7.5–14.5 × 4–6 µm, opening 1–1.5 µm diam, collarette ≤ 0.5 µm long, periclinal thickening observed, collarette of strain CBS 127557 0.5–1 µm long and periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical to ellipsoidal, the apex and base rounded, (10.5–)12.5–16.5(–19) × 4.5–5.5(–6) µm, mean ± SD = 14.5 ± 2.1 × 5.2 ± 0.5 µm, L/W ratio = 2.8, conidia of strain CBS 127557 slightly larger, measuring (13.5–)14.5–17(–19) × 5–5.5(–6) µm, mean ± SD = 15.6 ± 1.2 × 5.3 ± 0.3 µm, L/W ratio = 2.9. *Appressoria* single or in loose groups, medium to dark brown, smooth-walled, elliptical, navicular, bullet-shaped or irregular outline, with undulate or lobate margin, (7.5–)9.5–15(–18.5) × (4.5–)5–7.5(–10) µm, mean ± SD = 12.3 ± 2.8 × 6.4 ± 1.3 µm, L/W ratio = 1.9, appressoria of strain CBS 127557 slightly larger, measuring (9–)11–16.5(–20) × (5–)6–11(–13) µm, mean ± SD = 13.7 ± 2.8 × 8.3 ± 2.5 µm, L/W ratio = 1.6.

Asexual morph on Anthriscus stem not observed in strain CBS 132885, but few conidia and one seta observed in strain CBS 127557. *Seta* medium brown, verruculose, 62 µm long, 2-septate, base slightly inflated, 5.5 µm diam, tip ± acute. *Conidiophores* and *conidiogenous cells* not observed. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical to ellipsoidal, the apex and base rounded, (14–)14.5–17(–17.5) × (5–)5.5–6 µm, mean ± SD = 15.5 ± 1.2 × 5.6 ± 0.3 µm, L/W ratio = 2.8.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline to honey, agar medium, filter paper and *Anthriscus* stem partly covered with felty whitish aerial mycelium and grey to black conidiomata/ascomata, reverse same colours; growth 27.5–29.5 mm in 7 d (≥ 40 mm in 10 d). Colonies on OA flat with entire margin; olivaceous buff, grey olivaceous to olivaceous, partly covered with short felty whitish aerial mycelium and grey conidiomata/ascomata, reverse olivaceous buff to olivaceous grey, growth 28–30 mm in 7 d (≥ 40 mm in 10 d). *Conidial mass* pale salmon.

Materials examined: **Mexico**, from *Musa* sp., 16 Dec. 2008, M. de J. Yanez Morales (CBS H-21500 **holotype**, culture ex-holotype CBS 132885 = CPC 16328); Tapachula, Chiapas, from *Musa* sp., 16 Dec. 2008, M. de J. Yanez Morales, CBS H-21501, culture CBS 127557 = CPC 16329.

Notes: *Colletotrichum musicola* can be identified with all loci studied. Closest matches with the ITS sequence of isolate CBS 132885 were with 99 % identity (1 nucleotide difference) “*C. gloeosporioides*” isolates CG0305 from *Glycine max* in Taiwan (FJ172224, [Chen et al. 2006](#)) and AC4-M-Mexico from

post-harvest fruit of *Musa acuminata* in Mexico (M. Espinoza-Ortega *et al.*, unpubl. data), possibly a similar strain or even one of the strains studied here. Closest matches to the *TUB2* sequence of CBS 132885 are with seven nucleotides difference (99 % identity) *C. orchidearum* strains CORCG3 and CORCX6 from *Cymbidium* and *Cattleya*, respectively, in China (HM585418 and HM585416, [Yang et al. 2011](#)). Closest match with the *GAPDH* sequence of isolate CBS 132885 was with 99 % identity (2 nucleotides difference) “*C. cliviae*” strains LC0551 and LC1238, isolated as endophytes from *Pennisetum purpureum* in Thailand (KC835389, KC835390, [Manamgoda et al. 2013](#)). There is no *ACT* and no *CHS-1* sequence with > 98 % identity and no *HIS3* sequence with > 96 % identity to those of *C. musicola* available in GenBank.

This species belongs to the *C. orchidearum* species complex. Several *Colletotrichum* species are known from *Musa*, for example *C. aotearoa*, *C. chrysophilum*, *C. musae*, *C. siamense*, *C. theobromicola* and *C. tropicale* belonging to the *C. gloeosporioides* complex ([Weir et al. 2012](#), [Sharma et al. 2015](#), [Vieira et al. 2018](#)), *C. karstii*, belonging to the *C. boninense* complex ([Damm et al. 2012b](#)), *C. paxtonii* and *C. scovillei* belonging to the *C. acutatum* complex ([Damm et al. 2012a](#), [Zhou et al. 2017](#)) and *C. gigasporum* belonging to the *C. gigasporum* complex ([Liu et al. 2014](#)). Further *Colletotrichum* species were described on *Musa* spp. without sequence data (see notes under *C. paxtonii* in [Damm et al. 2012a](#)). We could not locate the type material of these species to confirm their taxonomic positions.

One sexual morph, *Ga. musarum*, was described by [Petch \(1917\)](#) on *Musa paradisiaca* in Ceylon (Sri Lanka) as associated with *Gloeosporium musarum* Cooke & Masee; its ascospores are hyaline, aseptate, cymbiform (boat-shaped, navicular), straight or curved, obtuse and measure 14–18 × 3.5–4 µm. Ascospores of *C. musicola* have a different shape and are larger, measuring on average 19.5 × 6 µm (SNA) or 18.4 × 6 µm (*Anthriscus* stem). Ascospore shape and size of strains called *Ga. musae* by [Rodrigues & Owen \(1992\)](#) were again different and cannot be linked either. The sexual morph of the latter species was obtained by means of laboratory crossings, while *C. musicola* formed a sexual morph in pure culture; it is apparently homothallic. Compared to other sexual morphs developed in the *C. orchidearum* complex, *C. musicola* forms ascospores that are similar in length to those of *C. sojiae*, however much wider in the middle and with a different shape (fusiform).

Colletotrichum okinawense Damm & Toy. Sato, **sp. nov.** MycoBank MB824226. [Fig. 12](#).

Etymology: The species epithet is derived from the Japanese island Okinawa, where the species was collected.

Sexual morph not observed. **Asexual morph on SNA.** *Vegetative hyphae* 2–8 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata*, conidiophores formed directly on hyphae. *Setae* not observed. *Conidiophores* hyaline, smooth-walled, septate, branched. *Conidiogenous cells* hyaline, smooth-walled, cylindrical to

Fig. 11. *Colletotrichum musicola* (A–C, I–N, V–AF from ex-holotype culture CBS 132885. D–H, O–U. from culture CBS 127557). **A–C.** Conidiomata. **D, M.** Tips of setae. **E, N.** Bases of setae. **F–L.** Conidiophores. **O–T.** Appressoria. **U–V.** Conidia. **W, Z, AA.** Ascomata. **X.** Outer surface of peridium. **Y.** Peridium in cross section. **AB.** Ascospores. **AC.** Paraphyses. **AD–AF.** Asci. D–E, U, Y–AC, AF. from *Anthriscus* stem. A–C, F–T, V, W–X, AD. from SNA. AE. from OA. A–C, W, Z, AA. DM. D–V, X–Y, AB–AF. DIC. Scale bars: A = 100 µm, E = 10 µm. A applies to A–C, W, Z–AA. E applies to D–V, X–Y, AB–AF.

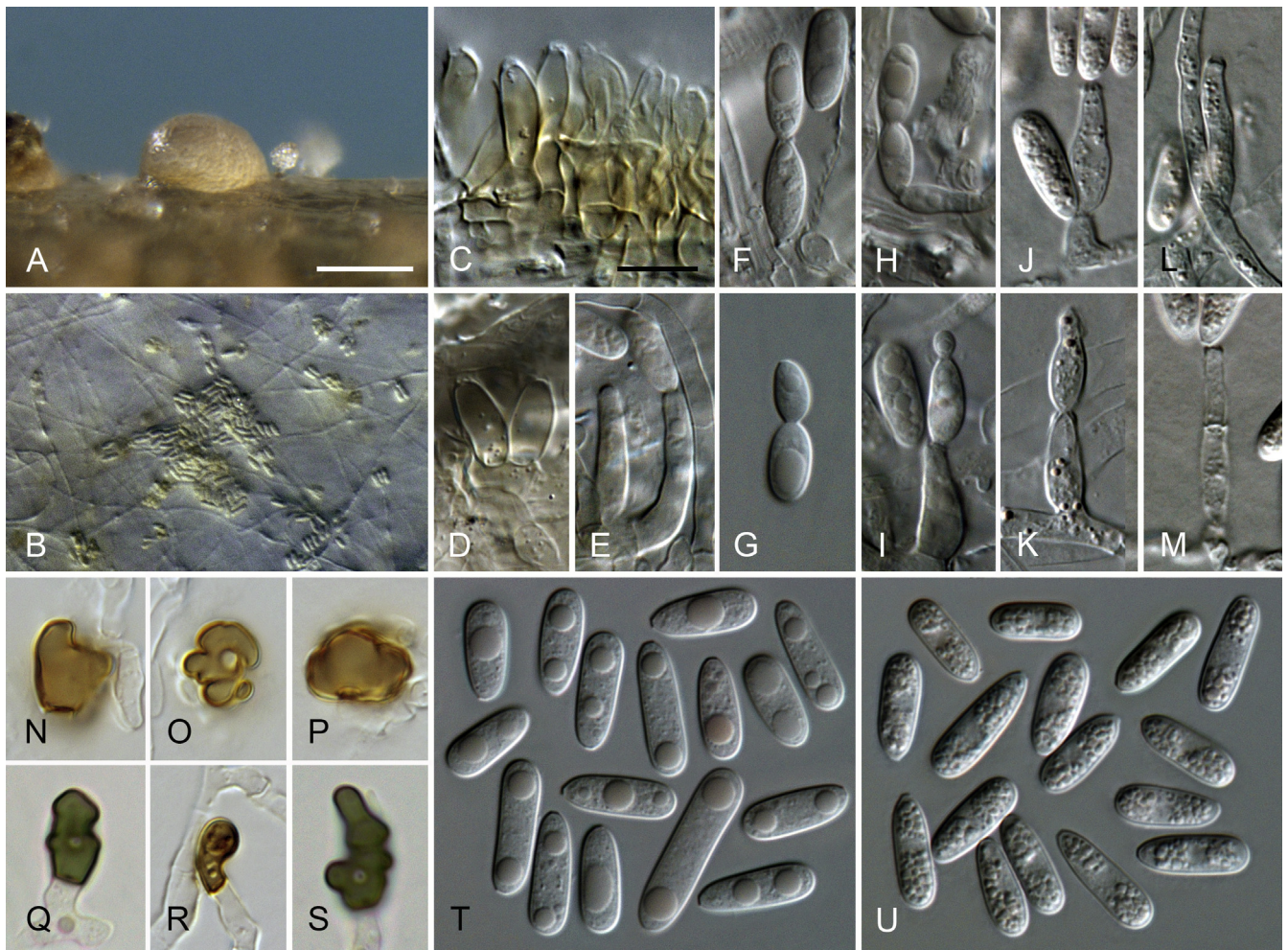


Fig. 12. *Colletotrichum okinawense* (from ex-holotype culture MAFF 240517). **A–B.** Conidiomata. **C–E, J–M.** Conidiophores. **F–I.** Microcyclic conidiation. **N–S.** Appressoria. **T–U.** Conidia. **A, C–I, T.** from *Anthriscus* stem. **B, J–S, U.** from SNA. **A–B.** DM. **C–U.** DIC. Scale bars: **A** = 100 μ m, **C** = 10 μ m. Scale bar of **A** applies to **A–B**. Scale bar of **C** applies to **C–U**.

doliiform, sometimes lacking a basal septum, 8–25 \times 3–6 μ m, opening 1–2 μ m diam, collarete 0.5–1 μ m long, periclinal thickening observed. *Conidia* hyaline, smooth-walled, aseptate, straight, clavate to cylindrical, the apex rounded, the base rounded or truncate, (10.5–)12–14.5(–16.5) \times (3.5–)4.5–5.5 μ m, mean \pm SD = 13.4 \pm 1.3 \times 5.0 \pm 0.4 μ m, L/W ratio = 2.7, few conidia up to 22 μ m long were observed. *Appressoria* single or in loose groups, pale to medium brown, smooth-walled, elliptical, navicular, bullet-shaped or irregular in outline, with undulate or lobate margin, (5.5–)7–15(–23) \times (2.5–)5–10.5(–13) μ m, mean \pm SD = 11.1 \pm 3.9 \times 7.7 \pm 2.6 μ m, L/W ratio = 1.4.

Asexual morph on Anthriscus stem. *Conidiomata*, conidiophores formed on pale to medium brown, angular cells, 3–7 μ m diam. *Setae* not observed. *Conidiophores* hyaline to very pale brown, smooth-walled, septate, branched, to 25 μ m long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical to conical, 4.5–21 \times 3.5–5.5 μ m, opening 1–2 μ m diam, collarete 0.5 μ m long, periclinal thickening observed. Microcyclic conidiation observed, sometimes from conidia still attached to the conidiogenous cell. *Conidia* hyaline, smooth-walled, aseptate, straight, clavate to cylindrical, the apex rounded, the base rounded or truncate, (12–)12.5–15(–16.5) \times (4.5–)5–5.5 μ m, mean \pm SD = 13.9 \pm 1.3 \times 5.1 \pm 0.3 μ m, L/W ratio = 2.7.

Culture characteristics: Colonies on SNA flat with entire margin, medium hyaline, aerial mycelium lacking, reverse same colours;

31.5–34 mm in 7 d (\geq 40 mm in 10 d). Colonies on OA flat with entire margin, surface saffron to salmon, aerial mycelium lacking, reverse salmon; 31.5–34 mm in 7 d (\geq 40 mm in 10 d). *Conidial mass* saffron.

Materials examined: **Brazil**, Minas Gerais, Uberaba, on stems of *Carica papaya*, Jun. 1892, E. Ule n. 1947 (H **holotype** of *Gloeosporium papayae*). **Japan**, Okinawa prefecture, Miyakojima Island, from a petiole of *Carica papaya*, 28 Sep. 2007, S. Sato (isolated Sep. 2007 by T. Sato) (GLM-F 111630 **holotype** of *C. okinawense*, culture ex-holotype MAFF 240517 = NBRC 104626 = CBS 143246 = GLMC 1837).

Notes: This species belongs to the *C. magnum* species complex. Strain MAFF 240517 was originally identified as *C. gloeosporioides* by J. Moriwaki and recently re-identified as *C. brevisporum* by T. Sato. Based on the multilocus phylogeny in this study this species is closely related to *C. brevisporum*, but represents a distinct species.

Many *Colletotrichum* species have been reported or were described on papaya (*Carica papaya*) (Farr & Rossman 2017); a number of them were studied based on molecular data. For example, *C. acutatum* and *C. simmondsii* were described on *Carica papaya* in Australia. They belong to the *C. acutatum* species complex; both species occur on many other host plants as well (Damm et al. 2012a). A strain from *Carica papaya* in Brazil was identified as *C. karstii* (CBS 106.91); this species belongs to the *C. boninense* species complex and also occurs on many host plants (Damm et al. 2012b). *Colletotrichum*

queenslandicum, originally described as *C. gloeosporioides* var. *minus* from *Carica papaya* in Australia, and *C. siamense* strain ICMP 18739 from *Carica papaya* in South Africa belong to the *C. gloeosporioides* species complex (Weir et al. 2012). There are also two other strains from papaya included in this study, one from Japan (MAFF 238697) that is re-identified as *C. plurivorum* (*C. orchidearum* complex), and one from Australia (CBS 512.75) that was re-identified as *C. brevisporum* that belongs to the *C. magnum* complex, too.

Two species were described by Hennings (1895, 1908) from papaya in Brazil: *C. papayae* Henn. 1908 and *Gloeosporium papayae* Henn. 1895. They are not synonyms as listed in Saccardo et al. (1931); Petrak (1953) combined the latter in *Colletotrichum* as *C. papayae* (P. Henn.) Petr. 1953, apparently not being aware of the older homonym (nom. illegit., Art. 53.1). Conidia of *C. papayae* Henn. are cylindrical, straight to curved, measuring 12–20 × 5–7 µm, while those of *Gl. papayae* Henn. are cylindrical to subclavate, obtuse, straight, measuring 11–14 × 5–6 µm according to Hennings (1895) and (12.5–) 13–15(–15.5) × 4.5–6 µm, mean ± SD = 14 ± 1.2 × 5.3 ± 0.5 µm, L/W ratio = 2.7 according to our measurements. The conidia size of strain MAFF 240517 is similar to that of *Gl. papayae*. However, the shape of the conidia observed on the type specimen of *Gl. papayae* was cylindrical with parallel walls or even a constriction at the middle, not distinctly attenuated to the base as those of *C. okinawense*.

GAPDH, *ACT* and *TUB2* sequences of *C. okinawense* differ from all other species treated in this study (no *HIS3* sequence available), while the ITS is identical to that of *C. brevisporum*, *C. merremiae* and *C. lobatum*, and the *CHS-1* sequence to that of *C. brevisporum*. The *ACT* sequence is 100 % identical to those of *C. brevisporum* isolates CMM1672, CMM1702, CMM1822 and CMM2005 from *Carica papaya* in Brazil (KC702903–KC702906, Vieira et al. 2013) that possibly belong to the same species. The closest matches with the *TUB2* sequence are with 99 % identity (6 nucleotides difference) to the four *C. liaoningense* strains from *Capsicum* in China (KP890111–KP890113, KP890115, Diao et al. 2017). The closest matches with the *GAPDH* sequence are with 97 % identity to the *C. liaoningense* strains CAUOS 3 and CAUOS 4 (KP890136, KP890137, Diao et al. 2017). The ITS sequence is 100 % identical to several unidentified isolates and isolates identified as *C. brevisporum*, *C. magnum*, *Ga. magna* and *C. cingulata* var. *brevispora*.

In contrast to all other species in the *C. magnum* complex, conidia of *C. okinawense* are predominantly clavate; it is also the fastest growing species in this complex. Microcyclic conidiation has only rarely been observed in the genus *Colletotrichum*. Only one other species with this feature is known to us, *C. clivicola*, that belongs to the *C. orchidearum* complex. Secondary conidia of *C. okinawense* are formed directly from conidiogenous openings on conidia, and sometimes already when the mother cell itself is still attached to its conidiogenous cell, while secondary conidia of *C. clivicola* are usually formed on short pegs or phialides that appear on older conidia that are sometimes already septate.

Colletotrichum orchidearum Allesch., Rabenh. Krypt.-Fl., Edn 2 (Leipzig) 1(7): 563. 1902 (1903). Fig. 13.

Synonyms: *Colletotrichum hymenocallidicola* Chethana et al., Fungal Diversity 75: 160. 2015.

Colletotrichum aracearum L.W. Hou & L. Cai, Mycosphere 7: 1115. 2016.

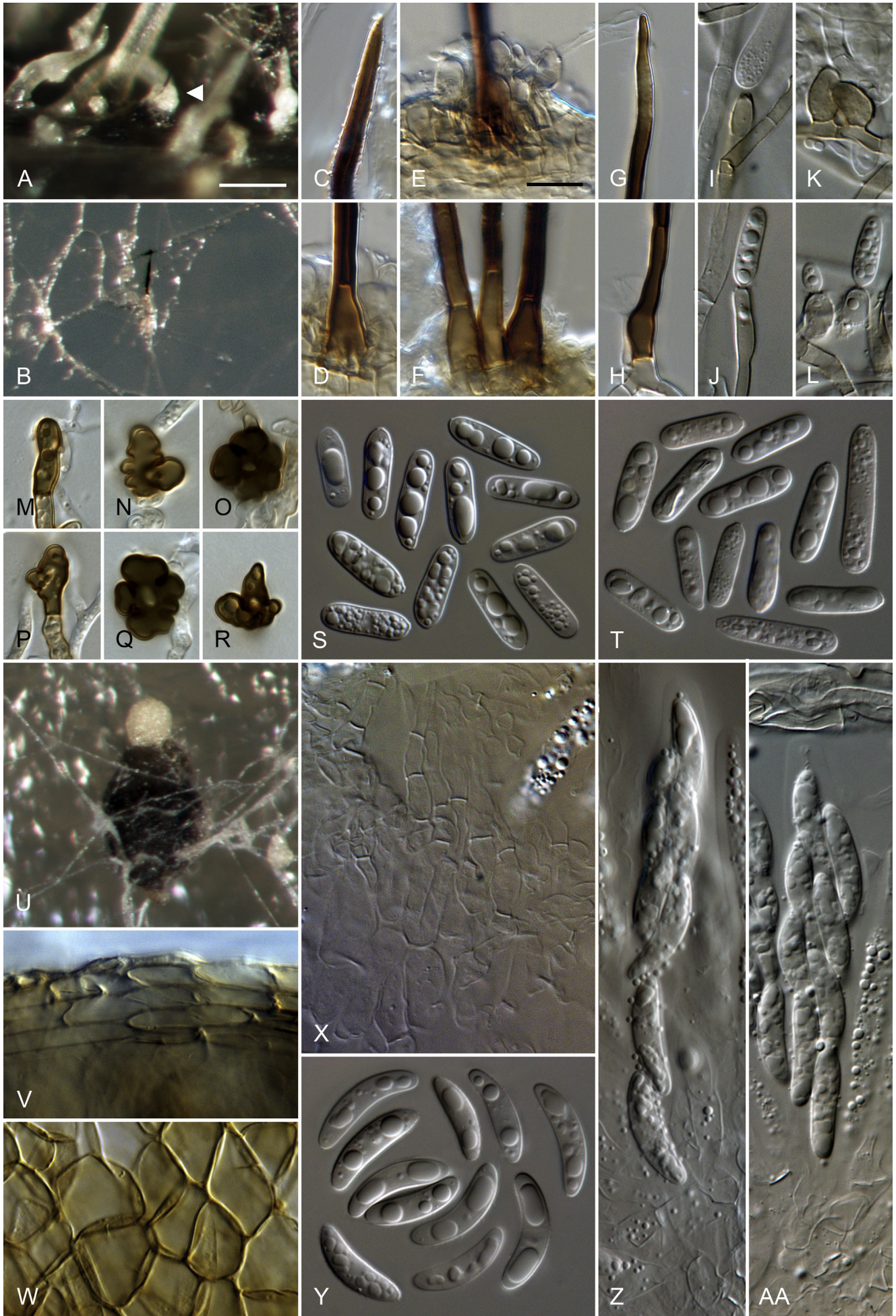
Sexual morph on SNA. *Ascospores* perithecia, formed after 4 wk, solitary, non-stromatic, subglobose, ostiolate, 200–300 × 175–250 µm. *Peridium* 6–15 µm thick, composed of 2–3 layers of medium brown flattened *textura angularis* with cells 5–22 µm diam. *Ascogenous hyphae* hyaline, smooth, delicate. *Interascal tissue* formed of paraphyses, hyaline, smooth-walled, mostly cylindrical but tapering towards the round tip, disintegrating quickly, septate, constricted at the septa, branched, apically free, 40–70 µm long and up to 6–8.5 µm diam. *Asci* unitunicate, 8-spored, fasciculate, smooth-walled, cylindrical to slightly clavate, tapering to apex and base, round tip, no apical apparatus observed, 70–100 × 11–15 µm. *Ascospores* uni- or biserially arranged, aseptate, hyaline, smooth-walled, allantoid, with round ends, (13.5–)16–20(–22) × 5–5.5(–6) µm, mean ± SD = 18.0 ± 1.9 × 5.2 ± 0.3 µm, L/W ratio = 3.5.

Sexual morph on *Anthriscus* stem. *Ascospores* perithecia, formed after 4 wk, solitary, non-stromatic, subglobose to ovoidal, dark brown, ostiolate; outer wall composed of medium brown flattened *textura angularis* with cells 17–22 µm diam. *Asci* 8-spored, cylindrical to clavate, unitunicate, fasciculate, thin-walled, 56–77 × 9–11.5 µm. *Ascospores* uni- or biserially arranged, aseptate, hyaline, smooth-walled, allantoid, with round ends, (13–)15.5–19(–21) × 4.5–5.5(–6) µm, mean ± SD = 17.4 ± 1.8 × 5.1 ± 0.4 µm, L/W ratio = 3.4.

Asexual morph on SNA. *Vegetative hyphae* 1–11 µm diam, hyaline to pale brown, smooth-walled to verruculose, septate, branched. *Chlamydospores* not observed. *Conidiomata*, conidiophores and setae formed directly on hyphae. *Setae* medium brown, verruculose to verrucose, 55–110 µm long, 1–2(–4)-septate, base ± inflated, 5.5–6 µm diam, tip rounded. *Conidiophores* hyaline to pale brown, smooth-walled to verruculose, septate, branched. *Conidiogenous cells* hyaline to pale brown, smooth-walled to verruculose, cylindrical to doliform, 8–40 × 4–5.5 µm, opening 0.5–2 µm diam, collarete 0.5–1 µm long, periclinal thickening sometimes observed. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical, the apex rounded, the base truncate or rounded, (13–)14–20(–28) × 4.5–5.5(–6.5) µm, mean ± SD = 17.0 ± 3.2 × 5.1 ± 0.5 µm, L/W ratio = 3.4, CBS 136877 forms shorter and wider conidia, measuring (12.5–)13–15.5(–17) × 5–6.5(–7) µm, mean ± SD = 14.2 ± 1.2 × 5.7 ± 0.7 µm, L/W ratio = 2.5. *Appressoria* single, medium to dark brown, smooth-walled, clavate, navicular, elliptical or circular in outline, with a lobate or undulate margin, (9–)10.5–17.5(–22.7) × (5–) 6–10.5(–13) µm, mean ± SD = 14.0 ± 3.3 × 8.4 ± 2.3 µm, L/W ratio = 1.7.

Asexual morph on *Anthriscus* stem. *Conidiomata*, conidiophores and setae formed on pale brown, angular cells, 4.5–8 µm diam. *Setae* (few observed) medium to dark brown, verruculose, 75–130 µm long, 1–5-septate, base cylindrical, conical to ± inflated, 4–8 µm diam, tip acute to ± rounded. *Conidiophores* hyaline to pale brown, smooth-walled. *Conidiogenous cells* hyaline to pale brown, smooth-walled, cylindrical to doliform, 7–10 × 4.5–6 µm, opening 1 µm diam, collarete 0.1–1 µm long, periclinal thickening not observed. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical, the apex rounded, the base truncate or rounded, (14.5–) 15.5–17(–17.5) × (4.5–)5–5.5(–6) µm, mean ± SD = 16.2 ± 0.9 × 5.2 ± 0.3 µm, L/W ratio = 3.1.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline to pale honey, agar medium, filter paper and *Anthriscus*



stem partly covered with grey to black fruiting bodies and sparse aerial mycelium, reverse same colours; growth 30–31.5 mm in 7 d (≥ 40 mm in 10 d). Colonies on OA flat with entire margin; buff, honey, grey olivaceous to olivaceous grey, partly covered with short floccose white aerial mycelium, reverse buff to olivaceous grey, growth 30–32 mm in 7 d (≥ 40 mm in 10 d). Conidial mass whitish to pale yellow.

Materials examined: **Germany**, Munich, glasshouses of Botanical Garden, on dead and dying leaves of *Eria javanica* (syn. *E. stellata*), Apr. 1895, J.E. Weiss [M-0140831 **lectotype** of *C. orchidearum* (named as forma *eriae*)]; **Iran**, Golestan province, Gorgan, from leaves of *Epipremnum aureum* (syn. *Scindapsus aureus*), Oct. 2013, A. Alizadeh, strain UTFc 266 = 249C. **Netherlands**, Utrecht (indoor plant), from anthracnose on leaf of *Dendrobium nobile*, Apr. 2013, I. Benoit-Gelber (CBS H-21910 **epitype**, here designated MBT380419, culture ex-epitype CBS 135131); *ibid.*, culture CBS 136877.

Notes: The type specimens of the three forms of *C. orchidearum*, *C. orchidearum* f. *cymbidii*, *C. orchidearum* f. *eriae* and *C. orchidearum* f. *physosiphonis* (Allescher 1902) were recently investigated by Yang *et al.* (2011), and strains from different orchid genera from China clustering in the multilocus phylogeny of that study were identified as *C. orchidearum* based on morphological resemblance. As *C. orchidearum* was described in Europe, the authors were however reluctant to select an epitype from their Asian collection. Damm *et al.* (2012a) studied the specimens as well and lectotypified *C. orchidearum* with the specimen M-0140831 from leaves of *Eria javanica*.

Different collections of *Colletotrichum* species from *Orchidaceae* in Europe were treated in this study, including strains of the species studied by Yang *et al.* (2011), that were isolated from a leaf of *Dendrobium nobile* in the Netherlands cultivated as an indoor plant, confirming the occurrence of this species in Europe. Conidia from the lectotype specimen were measured in Damm *et al.* (2012a): (13.5–)15.5–19.5 \times 5–6 μm , mean \pm SD = 17.2 \pm 1.6 \times 5.6 \pm 0.3 μm , L/W ratio = 3.1. Conidia from one of the strains from the Netherlands, CBS 135131, agree in conidial dimensions, measuring on average (13–)14–20(–28) \times 4.5–5.5(–6.5) μm on SNA and (14.5–)15.5–17(–17.5) \times (4.5–)5–5.5(–6) μm on *Anthriscus* stems. Moreover, conidiomata were minute as observed on the lectotype specimen and the length of the setae was similar (setae from lectotype: 56–120 \times 4.5–6 μm). Strain CBS 135131 was therefore used as basis of the epitype.

Our collection from Munich, Germany, had similar conidial dimensions as *C. orchidearum*; however, conidia often develop a prominent scar and are slightly constricted in the middle. Moreover, the conidiomata of this collection were very large, while those of *C. orchidearum* were small and longer setae were formed. The species collected in Munich belongs to the *C. dracaenophilum* complex and was described as *C. coelogyne* in this study. Another species from orchids described in this study is *C. cattleyicola* that also belongs to the *C. orchidearum* species complex.

There are numerous other *Colletotrichum* species that were described on *Orchidaceae*, including *C. orchidophilum*, belonging to the *C. acutatum* species complex (Damm *et al.* 2012a), *C. cymbidiicola*, *C. oncidii* and *C. karstii*, belonging to the *C. boninense* species complex (Yang *et al.* 2011, Damm *et al.*

2012b), *C. arxii* belonging to the *C. gigasporum* complex (Liu *et al.* 2014), *C. ochracea*, *C. caudasporum*, *C. duyunensis*, *C. endophyllum*, *C. guizhouensis* and *C. bletillum*, belonging to the *C. caudatum*, *C. graminicola* and *C. spaethianum* species complexes, respectively (Tao *et al.* 2013), *C. coelogyne* and *C. excelsum-altitudinum* in the *C. dracaenophilum* species complex (Tao *et al.* 2013, this study).

There are sequences of strains called *C. orchidearum* from three studies in GenBank. Strains from different *Orchidaceae* hosts from the study of Yang *et al.* (2011) and isolate SAUCC 1407 from *Arctium lappa* (Xu *et al.* 2016) both from China were included in our phylogeny. The strains from *Orchidaceae* were confirmed as *C. orchidearum*, while the isolate from *Arctium lappa* was re-identified as *C. sojae*. One of two ITS sequences of “*C. orchidearum*” isolate NW248 from an unpublished and unnamed study was displayed as “type strain of *C. orchidearum*” (EU520211, EU732727; Z. Zhang *et al.*, unpubl. data); it was revealed to be no *Colletotrichum* sp. at all but a species of *Cytospora* (*Diaporthales*).

The description of *C. hymenocallidicola* (Ariyawansa *et al.* 2015) is based on one strain of which five loci were sequenced (ITS, *GAPDH*, *CHS-1*, *ACT*, *TUB2*). Blastn searches on NCBI GenBank with all sequences of this species revealed that the *ACT* and *TUB2* sequences do not conform with the placement of the species based on ITS, *GAPDH* and *CHS-1* sequences. While the closest matches of the ITS, *GAPDH* and *CHS-1* sequences were with 98–99 % identity strains identified as *C. cliviae*, placing the species in the *C. orchidearum* complex, the *ACT* sequence (KT290260) was 93 % identical with those of *C. pseudomajus* and *C. vietnamense* (both *C. gigasporum* complex) and only 83 % identical with strains identified as *C. cliviae*, and the *TUB2* sequence (KT290261) was 100 % identical with the ex-epitype strain of *C. truncatum* (Damm *et al.* 2009). The *ACT* and *TUB2* sequences were possibly mixed-up with those of other strains studied by the authors. Further, the beginning part of the *GAPDH* sequence apparently includes artefacts as it is completely different from all related species. Therefore, *C. hymenocallidicola* and *C. aracearum* were not in the same clade in a recent phylogeny of the genus *Colletotrichum* (Marin-Felix *et al.* 2017). The *ACT* and *TUB2* sequences of *C. hymenocallidicola* as well as the first 22 nucleotides of *GAPDH* were excluded from the alignment in this study. It is highly recommended to re-sequence the ex-type strain of this species, in order to confirm our results with the other loci and establish a solid basis of this apparently common species.

Colletotrichum hymenocallidicola and *C. aracearum* were described recently as pathogens of *Hymenocallis* sp. in Thailand (Ariyawansa *et al.* 2015) and *Monstera deliciosa* and *Philodendron selloum* in China (Hou *et al.* 2016), respectively, and shown to be synonyms of *C. orchidearum* in this study. Based on this study, *C. orchidearum* is known from monocots such as *Hymenocallis* (*Amariyllidaceae*), *Monstera*, *Philodendron*, *Scindapsus* (*Araceae*), *Cordyline* (*Asparagaceae*) as well as many *Orchidaceae*, including *Cattleya*, *Cymbidium*, *Dendrobium*, *Oncidium*, *Phalaenopsis* and *Vanda* in Asia (China, Iran, Japan, Thailand) and Europe (as indoor plant in the Netherlands).

Fig. 13. *C. orchidearum* (A–W, Y–Z. from ex-epitype culture CBS 133131, X, AA. from culture CBS 136877). A–B. Conidiomata, arrow head in A: Conidioma with seta. C, G. Tips of setae. D, F, H. Bases of setae. E, I–L. Conidiophores. M–R. Appressoria. S–T. Conidia. U. Ascoma. V. Peridium in cross section. W. Outer surface of peridium. X. Paraphyses. Y. Ascospores. Z–AA. Asci. A, C–F, S. from *Anthriscus* stem. B, G–R, T–AA. from SNA. A–B, U. DM. C–T, V–AA. DIC. Scale bars: A = 100 μm , E = 10 μm . A applies to A–B. E applies to C–T, V–AA.

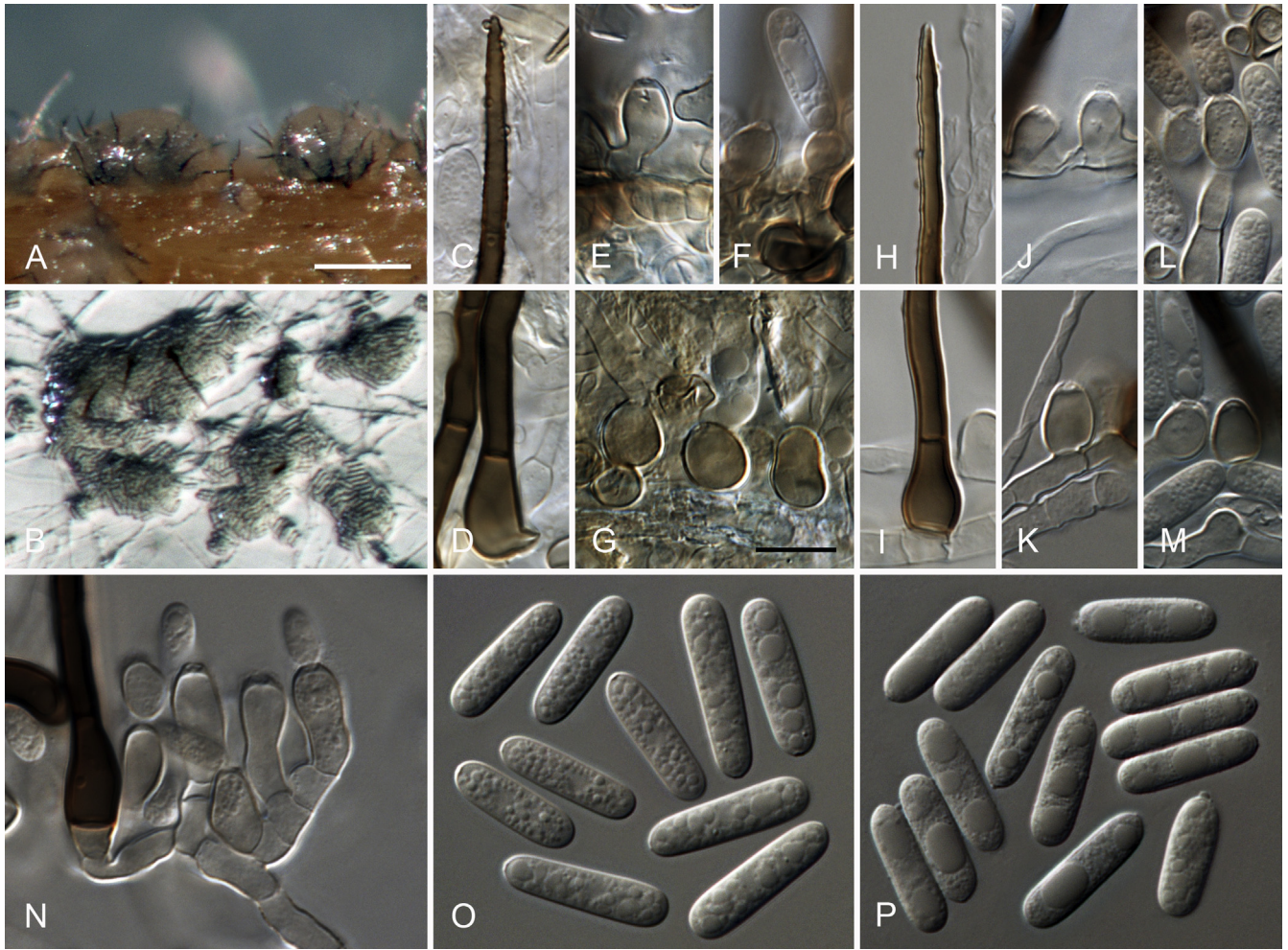


Fig. 14. *Colletotrichum panamense* (from ex-holotype culture CBS 125386). **A–B.** Conidiomata. **C, H.** Tips of setae. **D, I.** Bases of setae. **E–G, J–N.** Conidiophores. **O–P.** Conidia. **A, C–G, O.** from *Anthriscus* stem. **B, H–N, P.** from SNA. **A–B.** DM. **C–P.** DIC. Scale bars: **A** = 100 μ m, **G** = 10 μ m. Scale bar of **A** applies to **A–B**. Scale bar of **G** applies to **C–P**.

Colletotrichum orchidearum can be differentiated with sequences of all loci included, except for *GAPDH*; sequences of *CHS-1* and *HIS3* are only available of part of the strains included. *GAPDH* sequences of *C. orchidearum* and *C. sojiae* are identical. In a blastn search in GenBank, the *TUB2* sequence of strain CBS 135131 was 100 % identical with those of the strains from *Orchidaceae* in China and 99 % identical (one nucleotide difference) with those of the two *C. aracearum* strains, while the two *C. cliviicola* strains CSSS1 and CSSS1 (Yang et al. 2009) differ in eight nucleotides; all are included in this study. In a blastn search with the *ACT* sequence, the two *C. aracearum* strains were identical and the strains from *Orchidaceae* in China differed in one nucleotide; while the *C. cliviicola* strains differed in four nucleotides. The ITS sequence of strain CBS 135131 was identical with those of the two *C. aracearum* (strains, “*C. gloeosporioides*” isolate C10 from *Cymbidium* in China (Yao et al. 2013), *Colletotrichum* sp. strain AR3750 and *Glomerella* sp. strain AR3749 from *Dendrobium* and *Cattleya*, respectively, in Thailand (Farr et al. 2006) and differed in one nucleotide from “*C. gloeosporioides*” isolate C14 from *Cymbidium* in China (?) (J.A. Yao et al., unpubl. data) and the ex-type strain of *C. hymenocallidicola*, while the *C. cliviicola* strains differed in seven nucleotides.

No sexual morph was observed in the strain from *Hymenocallis* (Ariyawansa et al. 2015), but in those from *Monstera*

deliciosa (Hou et al. 2016) and from *Orchidaceae* (Yang et al. 2011, this study). In pathogenicity tests by Yang et al. (2011), strain CORCX6 from *Cattleya* sp. caused lesions on fruits of peppers, apple and tomato by wound/drop inoculation, but none on unwounded fruits.

***Colletotrichum panamense* Damm, sp. nov.** MycoBank MB824227. Fig. 14.

Etymology: The species epithet is derived from the country where the species was collected, Panama.

Sexual morph not observed. **Asexual morph on SNA.** *Vegetative hyphae* 1.5–7.5 μ m diam, hyaline, smooth-walled, septate, branched. *Chlamydoconidia* not observed. *Conidiomata*, conidiophores and setae formed directly on hyphae. *Setae* medium brown, smooth-walled, verrucose towards the tip, 40–100 μ m long, 2(–3)-septate, base inflated, 6–7 μ m diam, tip \pm acute. *Conidiophores* pale brown, smooth-walled, septate or aseptate. *Conidiogenous cells* pale brown, smooth-walled, broadly ellipsoidal, doliiform to cylindrical, 7–16 \times 5.5–7 μ m, often intercalary, opening 1.5–2 μ m diam, collarette 0.5–1 μ m long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical, the apex and base rounded, (14.5–) 15.5–18(–19.5) \times (4.5–)5–5.5 μ m, mean \pm SD = 16.9 \pm 1.2 \times 5.0 \pm 0.3 μ m, L/W ratio = 3.4. *Appressoria* not formed.



Fig. 15. *Colletotrichum piperis* (from ex-epitype culture IMI 71397). **A–B.** Conidiomata. **C, H.** Tips of setae. **D, I.** Bases of setae. **E–G, J–K.** Conidiophores. **L–Q.** Appressoria. **R–S.** Conidia. **A, C–G, R.** from *Anthriscus* stem. **B, H–Q, S.** from SNA. **A–B.** DM. **C–S.** DIC. Scale bars: **A** = 100 μ m, **E** = 10 μ m. Scale bar of **A** applies to **A–B**. Scale bar of **E** applies to **C–S**.

Asexual morph on Anthriscus stem. Conidiomata, conidiophores and setae formed directly on hyphae, no basal cells observed. Setae medium brown, smooth-walled, verrucose towards the tip, 60–100 μ m long, 2–3-septate, base inflated, 5.5–7.5 μ m diam, tip \pm acute to \pm rounded. Conidiophores pale brown, smooth-walled, septate, sometimes branched, to 30 μ m long. Conidiogenous cells pale brown, smooth-walled, ovoidal, broadly ellipsoidal to subspherical, 6–11.5 \times 4.5–7.5 μ m, opening 1.5–2 μ m diam, collarette not observed, periclinal thickening sometimes visible or distinct. Conidia hyaline, smooth-walled, aseptate, straight, cylindrical, the apex and base rounded, (14–)16–20(–22) \times 5–5.5 μ m, mean \pm SD = 18 \pm 2.1 \times 5.3 \pm 0.2 μ m, LW ratio = 3.4.

Culture characteristics: Colonies on SNA flat with entire margin, medium hyaline to pale ochreous to pale luteous, filter paper partly pale luteous, aerial mycelium lacking, reverse same colours; 18.5–20 mm in 7 d (27.5–30 mm in 10 d). Colonies on OA flat with entire margin, surface rosy buff to saffron with small grey dots due to sporulation, aerial mycelium lacking, reverse rosy buff to buff; 22.5–25.5 mm in 7 d (34–33.5 mm in 10 d). Conidial mass saffron.

Material examined: Panama, Gamboa, wet lowland forest, leaf endophyte of *Merremia umbellata*, Nov. 2004, S. Van Bael & Z. Maynard, D2-13 (CBS H-21066 holotype, culture ex-type CBS 125386 = Q882).

Notes: *Colletotrichum panamense* belongs to the *C. magnum* species complex like *C. merremiae* that is also described from *Merremia umbellata* in Panama in this study. In contrast to *C. merremiae*, the conidiogenous cells of *C. panamense* are often subglobose to ellipsoidal, on SNA often also intercalary. Conidia of *C. panamense* are on both media on average at least 2 μ m longer.

Colletotrichum panamense differs with all loci studied from all other species of the genus. The ITS sequence of strain CBS 125386 is 100 % identical to *Colletotrichum* sp. Q882 (GU994392, Rojas *et al.* 2010), which is the same strain. Other sequences have \geq 3 bp differences. Closest matches with the *TUB2* sequence of the ex-type strain of *C. panamense* are with 99 % identity (5 nucleotides difference) the four *C. liaoningense* strains that are included in our study (Diao *et al.* 2017). Closest matches with the *CHS-1* sequence are with 99 % identity (1 nucleotide difference) to those of the ex-type strain of *C. brevisporum* sequenced by Liu *et al.* (2014, KF687760) and *C. brevisporum* strain CCCM12 from *Cucurbita moschata* in China (KY797631, Liu *et al.* 2018). No *ACT* sequence in GenBank is closer than 97 % identical and no *HIS3* sequence closer than 90 % identical to those of *C. panamense*.

Colletotrichum piperis Petch, Ann. R. bot. Gdns Peradeniya 6(3): 239. 1917. Fig. 15.

Sexual morph not observed. *Asexual morph on SNA*. *Vegetative hyphae* 1–8 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata*, conidiophores and setae formed directly on hyphae. *Setae* pale to medium brown, verruculose to verrucose, 30–95 µm long, 1–3-septate, base cylindrical, 4.5–7 µm diam, tip ± acute to ± rounded. *Conidiophores* hyaline to pale brown, smooth-walled to verruculose, septate, branched, to 65 µm long. *Conidiogenous cells* hyaline to pale brown, smooth-walled to verruculose, cylindrical, 10–25 × 3.5–5.5 µm, opening 2–2.5 µm diam, collarette 1–1.5 µm long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical to obclavate, the apex rounded, the base rounded to truncate, (11.5–)13–18.5(–28) × 4–5(–6) µm, mean $15.7 \pm 2.7 \times 4.7 \pm 0.4$ µm, L/W ratio = 3.4. *Appressoria* not formed at the reverse side of SNA plates, but few observed on slide culture after 1 month, single, medium brown, smooth-walled, elliptical, bullet-shaped to rectangular in outline, with an entire margin, (3.5–)6–10(–13) × (3–)4–6(–8.5) µm, mean \pm SD = $7.9 \pm 2.1 \times 5.0 \pm 1.1$ µm, L/W ratio = 1.6.

Asexual morph on Anthriscus stem. *Conidiomata*, conidiophores and setae formed on pale brown, angular cells. *Setae* pale to medium brown, verruculose to verrucose, often branched, 50–120 µm long, 1–3-septate, base cylindrical, sometimes slightly inflated, 4.5–7 µm diam, tip ± acute to ± rounded. *Conidiophores* pale brown, smooth-walled, septate, sometimes branched, to 35 µm long. *Conidiogenous cells* pale brown, smooth-walled, cylindrical to doliform, 8–22 × 4–6.5 µm, opening 1–1.5 µm diam, collarette 0.5–1 µm long, periclinal thickening observed. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical, the apex rounded, the base rounded to truncate, (14–)15.5–17.5(–19.5) × (4–)4.5–5(–5.5) µm, mean \pm SD = $16.6 \pm 1.0 \times 4.7 \pm 0.3$ µm, L/W ratio = 3.6.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline, cinnamon to isabelline in the centre, agar medium, filter paper and *Anthriscus* stem partly covered with grey to salmon acervuli, aerial mycelium lacking, reverse same colours; growth 15.5–16.5 mm in 7 d (26–27.5 mm in 10 d). Colonies on OA flat with entire margin; grey olivaceous, with a buff margin, covered with translucent salmon conidia masses and partly covered with very short aerial mycelium, reverse olivaceous grey to iron-grey, growth 17.5–19 mm in 7 d (26–29 mm in 10 d). *Conidial mass* salmon.

Materials examined: **Malaysia**, from *Piper nigrum*, unknown collection date and collector (IMI history: 1957 P. Holliday HS 134, 1958 CABI) (IMI 71397 **epitype** of *C. piperis* Petch, **here designated**, MBT380420, CBS H-21503 isoeotype, culture ex-epitype IMI 71397). **Puerto Rico**, Caguas, from *Piper umbellatum*, 9 Feb. 1913, FL Stevens, BPI 399521 possible **paratype** of *C. piperis* Stevens. **Sri Lanka**, Medulsima, from leaf of *Piper betle*, T. Petch 4544, 17 Mar. 1915 (K(M) 235609 B, part of **holotype** of *C. piperis* Petch). **Taiwan**, Tainan, from *Piper betle*, 29 Oct. 1907, K. Sawada, BPI 397531 possible **holotype** of *C. geniculatum*.

Notes: There were several species described on *Piper* spp. including *C. dasturii*, *C. geniculatum*, *C. necator*, *C. piperis* Petch and *C. piperis* Stevens. The two species named *C. piperis* were described in the same year (1917), *C. piperis* Petch from leaves of *Piper betle* and *P. nigrum* in Sri Lanka (Ceylon) and *C. piperis* Stevens from *Piper umbellatum* in Puerto Rico, respectively (Petch 1917, Stevens 1917). According to Roy (1948), who investigated the publication dates, the name *C. piperis* Stevens is illegitimate (nom. illegit., Art. 53.1) as it was published between 10th July and 18th August 1917 and it a homonym of the earlier

C. piperis Petch (published 4th July 1917) and was therefore replaced by *C. stevensii*.

Conidia of *C. piperis* Petch measure 12–19 × 3.5–4.5 µm according to Petch (1917) and 10–16 × 4–6 µm and (13.5–)14–16(–17.5) × (4.5–)4.5–5.5(–6) µm, mean \pm SD = $15.1 \pm 1.0 \times 5.1 \pm 0.4$ µm, L/W ratio = 3.0 according to measurements from the type specimen by Roy (1948) and the present study. The conidial size and shape of strain IMI 71397 agree with these measurements and our observations (not shown), respectively. This strain originated from *P. nigrum* in Malaysia, the same region of Asia than the holotype of *C. piperis* Petch (Sri Lanka). Strain IMI 71397 is therefore used as the basis for the epitype of this species. In contrast, conidia of *C. stevensii* (syn. *C. piperis* Stevens) are larger than *C. piperis* Petch, measuring 17–27 × 7 µm (Stevens 1917); which was confirmed by measurements of conidia of a possible paratype specimen of *C. piperis* Stevens in this study: (16.5–)19–23.5(–25.5) × (5–)5.5–7.5(–8.5) µm, mean \pm SD = $21.2 \pm 2.3 \times 6.4 \pm 0.9$ µm, L/W ratio = 3.3. *Colletotrichum necator* that was described from fruit of *Piper* sp. in Singapore by Massee (1912) also forms larger conidia (20–23 × 5–7 µm) than *C. piperis* Petch. Sawada (1959) described *C. geniculatum* from *P. betle* in Taiwan. Conidia from the type specimen measure 12.5–14(–15) × (5–)5.5–6.5(–7) µm, mean \pm SD = $13.3 \pm 0.8 \times 6.2 \pm 0.6$ µm, L/W ratio = 2.2; conidiophores were not observed, setae measure 35–57 × 4–5.5 µm. The conidia size of *C. geniculatum* is similar to that of *C. piperis* Petch. However, the conidia are shorter and wider, resulting in a smaller L/W ratio and a different shape. Roy (1948) described *C. dasturii* from *P. betle* in India, Bengal; its conidia are curved, while *C. piperis* Petch has straight conidia.

Sequence comparison of *Colletotrichum* spp. from *Piper* spp. in GenBank suggests that species from several species complexes can be found on this host genus. For example, strains from a study of leaf endophytes in *Piper hispidum* in Brazil identified by ITS belong to the *C. boninense* and *C. gloeosporioides* species complexes (Orlandelli et al. 2012). A strain from *Piper nigrum* (IMI 324991, unknown location) was recently identified as *C. fioriniae* belonging to the *C. acutatum* species complex (Damm et al. 2012a), while a *C. siamense* strain from a leaf lesion of *P. nigrum* in Australia (James et al. 2014) and two *C. truncatum* strains (CBS 127.57, IMI 63597) from *Peperomia magnoliifolia* (*Piperaceae*) in India (Damm et al. 2009) belong to the *C. gloeosporioides* and *C. truncatum* species complexes, respectively. Farr & Rossman (2017) further list *C. capsici* (syn. of *C. truncatum*), *C. dematium* and *C. gloeosporioides*. However, the respective sources are from the pre-sequence era and therefore need confirmation.

Another species on *Piper*, *C. lobatum*, is described in this study from *Piper catalpaefolium* in Trinidad and Tobago with very similar conidial shape and size, but very different appressoria that are more complex than those of *C. piperis* Petch. *Colletotrichum lobatum* belongs to the *C. magnum* species complex, while *C. piperis* belongs to the *C. orchidearum* complex. Apart from the rather simple appressoria with entire edge, *C. piperis* sometimes forms branched setae, a feature rarely observed in the genus *Colletotrichum*. Moreover, *C. piperis* is the slowest growing species in the *C. orchidearum* complex.

Colletotrichum piperis can be identified with all loci included in this study. Closest matches in a blastn search with the ITS sequence of *C. piperis* strain IMI 71397 on GenBank were with 99 % identity (5 nucleotides difference) several strains identified

as *C. gloeosporioides*, fungal sp., *C. magnum*, *C. orchidearum*, fungal endophyte, *C. trifolii*, *Glomerella glycines*, *Colletotrichum* sp., *C. aracearum* and *Glomerella* sp. There is no *GAPDH* sequence in GenBank with ≥ 96 % identity and no *TUB2* sequence with ≥ 97 % identity to that of strain IMI 71397. The closest match with the *ACT* sequence was with 99 % identity (3 nucleotides difference) *C. cliviae* strain GUFCC15503 from *Calamus thwaitesii* in India (KC790646, Sharma et al. 2013a).

Colletotrichum plurivorum Damm, Alizadeh & Toy. Sato, sp. nov. MycoBank MB824228. Fig. 16.

Synonym: *Colletotrichum sichuanensis* G.S. Gong & F.L. Liu, Scientific Reports 6(32761): 6. 2016. nom. inval., Art. 40.1 (Melbourne).

Etymology: The species epithet is based on the large host range of this species.

Sexual morph on Anthriscus stem (observed in strains CBS 125474 and UTFC 260). *Ascomata* perithecia, formed after 4 wk, solitary, superficial or immersed, non-stromatic, globose to obpyriform, ostiolate, glabrous or covered by sparse white aerial mycelium, medium to dark brown, 100–230 × 95–160 µm, surrounded by pale brown, smooth-walled to verruculose hyphae. *Peridium* 12–18 µm thick, composed of 3–5 layers of pale brown flattened *textura angularis* with cells 5–18 µm diam. *Ascogenous hyphae* hyaline, smooth, delicate, rarely visible. *Interascal tissue* formed of paraphyses, hyaline, smooth-walled, cylindrical, with a rounded tip, disintegrating quickly, septate, apically free, 50–70 µm long, base 4.5–7.5 µm wide, branched at the base. *Asci* unitunicate, 8-spored, cylindrical, smooth-walled, 50–65.5 × 10.5–12.5 µm, the base broadly truncate, asci of strain UTFC 260 larger, measuring 70–90 × 9–13.5 µm. *Ascospores* uni- or biserially arranged, aseptate, in strain UTFC 260 also septate ascospores observed, initially hyaline, turning pale brown with age, smooth-walled, allantoid to fusiform, with both ends rounded, (13–)14.5–18(–22) × (4–)5–6(–7) µm, mean ± SD = 16.4 ± 1.8 × 5.5 ± 0.5 µm, L/W ratio = 3.0.

Sexual morph on SNA (observed in strains CBS 125474, UTFC 260 and UTFC 261). *Ascomata* perithecia, globose to obpyriform, 180–340 × 180–230 µm, ostiolate, medium to dark brown, glabrous. *Peridium* 12–18 µm thick, composed of 4–6 layers of pale brown flattened *textura angularis* with cells 5–19 µm diam. *Interascal tissue* formed of paraphyses, hyaline, smooth-walled, cylindrical with a rounded tip, disintegrating quickly, septate, apically free, 40–70 µm long, base 4.5–6 µm wide, branched at the base. *Asci* unitunicate, 8-spored, cylindrical to clavate, fasciculate, 80.5–93 × 8.5–12 µm. *Ascospores* uni- or biserially arranged, aseptate, initially hyaline, turning pale brown with age, smooth-walled, allantoid to fusiform, with both ends rounded, (13–)15–19(–21) × (5–)5.5–6(–7) µm, mean ± SD = 17.0 ± 2.1 × 5.7 ± 0.4 µm, L/W ratio = 3.0.

Asexual morph on SNA (mostly based on strain CBS 903.69, UTFC 260 and UTFC 261, only few conidia observed in strain CBS 125474). *Vegetative hyphae* 1–8 µm diam, hyaline to pale brown, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata*, conidiophores and setae formed directly on hyphae. *Setae* not observed in strain CBS 125474, setae of strain CBS 903.69 medium brown, verruculose to verrucose, 40–130 µm long, 1–(2)-septate, base cylindrical to slightly inflated, 3–6 µm diam, tip ± rounded to ± acute, setae of strain UTFC 260 2–3-septate. *Conidiophores* and *conidiogenous cells* not observed in strain CBS 125474, conidiophores of strain CBS

903.69 hyaline to pale brown, smooth-walled, septate, branched, to 40 µm long. *Conidiogenous cells* of strain CBS 903.69 hyaline to pale brown, smooth-walled, cylindrical clavate to doliiform, 6.5–19 × 3.5–4.5 µm, often integrated, some polyphialides observed, opening 1–2 µm diam, collarete 0.5–1 µm long, periclinal thickening distinct. *Conidia* (only three observed in strain CBS 125474) hyaline, smooth-walled, aseptate, straight, cylindrical, the apex and base rounded, 15–17 × 5.5 µm, mean ± SD = 16.0 ± 0.9 × 5.6 ± 0.1 µm, L/W ratio = 2.9, conidia of strain CBS 903.69 shorter, measuring (9.5–)11.5–14(–15) × (4.5–)5–6 µm, mean ± SD = 12.7 ± 1.3 × 5.4 ± 0.4 µm, L/W ratio = 2.4, conidia of strain UTFC 261 shorter and narrower, measuring (10–)10.5–11.5(–12.5) × (3.5–)4–4.5(–5) µm, mean ± SD = 11 ± 1.1 × 4.5 ± 0.5 µm, L/W ratio = 2.6, conidia of strains UTFC 260 and UTFC 261 sometimes slightly curved. *Appressoria* single, pale, medium to dark brown, smooth-walled, navicular to bullet-shaped or irregular in outline, with an undulate, crenate to strongly lobate margin, (9–)12.5–18.5(–22.5) × (4.5–)6.5–11.5(–15.5) µm, mean ± SD = 15.4 ± 3.0 × 8.8 ± 2.6 µm, L/W ratio = 1.7, appressoria of strain CBS 903.69 smaller, measuring (5–)8.5–15.5(–24.5) × (5–)6.5–9(–10) µm, mean ± SD = 11.9 ± 3.4 × 7.6 ± 1.3 µm, L/W ratio = 1.6.

Asexual morph on Anthriscus stem. Conidiomata, conidiophores and setae formed on pale brown, angular cells, 2.5–6.5 µm diam. *Setae* medium brown, verruculose to verrucose, 40–95 µm long, 1–2-septate, base conical, slightly inflated, 4.5–8 µm diam, tip ± acute. *Conidiophores* pale brown, smooth-walled, simple or septate and branched, to 30 µm long. *Conidiogenous cells* pale brown, smooth-walled, cylindrical, clavate to doliiform, 7–19 × 4–5.5 µm, opening 1–1.5 µm diam, collarete 0.5–1 µm long, periclinal thickening visible, sometimes distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical, sometimes slightly clavate, the apex and base rounded, (15–)16.5–20(–22.5) × (5–)5.5–6.5(–8) µm, mean ± SD = 18.4 ± 1.8 × 5.9 ± 0.5 µm, L/W ratio = 3.1, conidia of strain CBS 903.69 shorter, measuring (12.5–)13.5–16.5(–16.5) × (5–)5.5–6 µm, mean ± SD = 14.6 ± 1.1 × 5.6 ± 0.2 µm, L/W ratio = 2.6.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline to pale olivaceous grey, agar medium, filter paper and *Anthriscus* stem partly covered with pale olivaceous grey aerial mycelium and grey conidiomata/ascomata, reverse same colours; growth 27.5–31 mm in 7 d (≥ 40 mm in 10 d). Colonies on OA flat with entire margin; olivaceous buff, grey olivaceous to olivaceous, partly covered with short felty whitish aerial mycelium and pale purplish grey to pale olivaceous grey conidiomata/ascomata, reverse pale olivaceous grey to olivaceous grey, growth 28.5–31.5 mm in 7 d (≥ 40 mm in 10 d). *Conidial mass* greyish white to very pale salmon, in strain UTFC 260 pale buff to orange.

Materials examined: **Benin**, Dahomey, Porto Novo, from leaf spot of *Phaseolus lunatus*, collection date and collector unknown (isolated by G. Weststeijn and deposited in CBS collection Oct. 1969 by G. Weststeijn), CBS H-21497, culture CBS 903.69. **Brazil**, from *Gossypium* sp., collection date and collector unknown, culture CBS 132443 = CPC 18211; from *Gossypium* sp., collection date and collector unknown, culture CBS 132444 = CPC 18212. **Iran**, Golestan province, Gorgan, from leaves of *Spathiphyllum wallisii*, May 2013, A. Alizadeh, strain UTFC 260 = 176C; Guilan province, Koochesfahan area, from pods of *Phaseolus vulgaris*, Oct. 2013, O. Atghia & A. Alizadeh, strain UTFC 261 = 513C. **Vietnam**, Da Lat-Lam Dong, from anthracnose on leaf of *Coffea* sp., collection date unknown, P. Nguyen & E. Lijferoth (CBS H-21496 **holotype**, culture ex-holotype CBS 125474 = LD11(L3)); Da Lat-



Lam Dong, from anthracnose on leaf of *Coffea* sp., collection date unknown, P. Nguyen & E. Lijeroth, culture CBS 125473 = LD 33(L1).

Notes: *Colletotrichum plurivorum* was first described as *C. sichuanensis* from *Capsicum annuum* in the Sichuan Province of China (Liu *et al.* 2016). The species is based on four “holotype living cultures”, one of which was designated as holotype; no type specimen has been deposited in a fungarium, and the name is therefore invalid (Art. 40.1). This species is described as a new species based on a strain from *Coffea* in Vietnam (Nguyen *et al.* 2010). In a study of Douanla-Meli *et al.* (2018), *C. sichuanensis* was regarded as a synonym of *C. cliviicola* (as *C. cliviae*), although both species formed well supported clades in the phylogeny of that study based on a multilocus data set and there was no indication of discordance between the gene trees. Based on the data of our study confirming these clades, *C. cliviicola* and *C. plurivorum* are regarded as distinct species.

Colletotrichum plurivorum belongs to the *C. orchidearum* species complex. It has a large host range, including *Anacardiaceae* (*Mangifera*), *Araceae* (*Amorphophallus*, *Spathiphyllum*), *Caricaceae* (*Carica*), *Fabaceae* (*Glycine*, *Phaseolus*), *Malvaceae* (*Abelmoschus*, *Gossypium*), *Musaceae* (*Musa*), *Orchidaceae* (*Arundina*, *Cymbidium*, *Oncidium*), *Passifloraceae* (*Passiflora*), *Rubiaceae* (*Coffea*), *Solanaceae* (*Capsicum*, *Lycopersicon*) and *Theaceae* (*Camellia*). Based on DNA sequence comparisons, strains from *Vitis* spp. (*Vitaceae*) in Brazil (Santos *et al.* 2018) and China (Lei *et al.* 2016), *Dioscorea* (*Dioscoreaceae*) in Puerto Rico (S.E. Fuentes Aponte *et al.*, unpubl. data), *Myrianthus arboreus* (*Urticaceae*) in Cameroon and *Citrus limon* (*Rutaceae*) in Vietnam (Douanla-Meli *et al.* 2018), previously identified as *C. cliviae* or *Colletotrichum* sp. were revealed to be *C. plurivorum* as well. Strains from studies on lima beans (*Phaseolus lunatus*) in Brazil (Sousa *et al.* 2018, Cavalcante *et al.* 2018) probably also belong to this species, based on sequence comparisons of *GAPDH* and *ACT* sequences (*TUB2* was mixed-up with a *C. truncatum* strain) or a multilocus phylogeny, respectively. Many species have been reported or were described from these hosts (Farr & Rossman 2017, this study). It is likely that this species has been described previously in the pre-molecular era based on morphology. Due to the small differences in morphology (e.g. conidial size and shape) between the species of the *C. orchidearum* complex on the one hand and the large interspecific variation on the other, it is hardly possible to link such old species.

Colletotrichum plurivorum formed a sexual morph in culture. However, some strains predominantly formed a sexual morph, while the asexual morph was hardly or not observed; other strains predominantly formed an asexual morph, while the sexual morph was lacking or both morphs were formed. Similar observations were made in other studies. For example, strain CGMCC 3.17358 from *Camellia* in China (Liu *et al.* 2015) was sterile on SNA and PDA, but developed the sexual morph on *Anthriscus* stems; no asexual morph was observed. In contrast, strains from *Orchidaceae* in Yang *et al.* (2011) formed both a sexual and an asexual morph. In the study of Douanla-Meli *et al.* (2018) isolates of *C. plurivorum* (as *C. cliviae*) from *Citrus limon* in Vietnam only produced the sexual morph, while isolates from *Myrianthus arboreus* in Cameroon produced both the asexual and the sexual morph.

In pathogenicity tests by Liu *et al.* (2016) strains described as *C. sichuanensis* from *Capsicum annuum* in China were able to infect fruits of *Capsicum annuum* and *Pyrus pyrifolia*. The pathogenicity of strain UTFC 261 from *Phaseolus vulgaris* in Iran was confirmed by Atghia (2015).

Colletotrichum plurivorum can be identified by *GAPDH*, *HIS3*, and *TUB2* sequences with few nucleotides difference in each gene to the closely related *C. cliviicola*. The asexual morph of the two species is similar. However, *C. plurivorum* is slower growing on SNA and OA than *C. cliviicola*. Moreover, microcyclic conidiation and the formation of anastomoses were observed in the ex-type strain of *C. cliviicola*, but not in *C. plurivorum*, while no sexual morph is so far known in *C. cliviicola*.

In a blastn search in GenBank with the *TUB2* sequence of the ex-type strain CBS 125474 the sequences of several strains were found to be 100 % identical: *C. cliviae* strains AH1B6, AH1B5 (Wang *et al.* 2016b) and LF774 (Liu *et al.* 2015) from tea plants on China, of which the latter was included in this study (as CBS 125375), *Colletotrichum* sp. strain FJ074 from grapevine in China (Lei *et al.* 2016) as well as *Colletotrichum* isolates LJTJ3, LJTJ22 and LJTJ30 that were described by Liu *et al.* (2016) as *C. sichuanensis* and included in this study. The closest matches with the *HIS3* sequence of the ex-type strain are with 99 % identity (1 nucleotide difference) six *C. cliviae* strains from soybeans in Brazil (Barbieri *et al.* 2017), of which one, strain LFN0008, is included in this study. The *GAPDH* sequence of the ex-type strain of *C. plurivorum* is 100 % identical to several strains that were previously identified as *C. cliviae*, including G61B, G14B, F85241C from *Dioscorea alata* in Puerto Rico (S.E. Fuentes Aponte *et al.*, unpubl. data), JQS from *Zamioculcas zamiifolia* in China (Zhou & Li 2017), AV1 from grapevine in Brazil (Santos *et al.* 2018), AH1A2 and AH1B5 from tea plants on China (Wang *et al.* 2016b), HP157 from papaya in Mexico (I. Marquez-Zequera, unpubl. data), CORCG2 from *Cymbidium* in China (Yang *et al.* 2011) that is included in this study, and the six strains from soybeans in Brazil (Barbieri *et al.* 2017). The blastn search with the ITS sequence of strain CBS 125474 resulted in ≥ 40 sequences with 100 % identity. Most, if not all of these strains probably represent *C. plurivorum* as well, but this needs to be confirmed based on *GAPDH*, *HIS3*, or *TUB2* sequences.

The clades representing *C. plurivorum* and *C. sojae* in the phylogeny in this study include strains from *Phaseolus* spp. in Iran and Benin. The well-known anthracnose pathogen of common beans, *C. lindemuthianum* had been reported to form sexual morphs in culture that were called *Ga. lindemuthiana* (Shear & Wood 1913) or *Ga. cingulata* f. sp. *phaseoli* (Kimati & Galli 1970). However, in an extensive study on *C. lindemuthianum* that included the epitypification of this species, several methods were unsuccessfully applied to induce the formation of a sexual morph of this species (Liu *et al.* 2013). Liu *et al.* (2013) assumed the sexual morphs not to be conspecific with *C. lindemuthianum*.

The species studied by Shear & Wood (1913) formed conidia that measure 10.5–16.5 × 4.5–5 µm on corn meal agar and 12–16.5 × 4.5–6 µm on host tissue and curved ascospores that measure 15–22.5 × 4.5–6 µm; it could well be a species of the *C. orchidearum* complex. The ascospores of *C. sojae* studied by us are narrower, while the ascospores of *C. plurivorum* observed

Fig. 16. *Colletotrichum plurivorum* (A, C–H, O–T, V–AD. from ex-holotype culture CBS 125474. B, I–N, U. from culture CBS 903.69). A–B. Conidiomata. C, I. Tips of setae. D, J. Bases of setae. E–H, K–N. Conidiophores. O–S. Appressoria. T–U. Conidia. V–W. Ascomata. X. Paraphyses. Y. Outer surface of peridium. Z. Peridium in cross section. AA–AC. Asci. AD. Ascospores. A, C–H, T, V, X, AA, AD. from *Anthriscus* stem. B, I–S, U, W, Y–Z, AB–AC. from SNA. A–B, V–W. DM. C–U, X–AD. DIC. Scale bars: A = 100 µm, T = 10 µm. A applies to A–B, V–W. T applies to C–U, X–AD.



in this study and the studies of Liu *et al.* (2015) and Yang *et al.* (2011) have a different shape, being only very slightly curved. However, ascospores reported in Liu *et al.* (2016) from *Capsicum* in China have a similar shape, and are similarly arranged in the ascus. It is therefore possible that *C. plurivorum* is the same fungus as "*Ga. lindemuthiana*". In contrast, ascospores of *Ga. lindemuthiana* shown by Rodríguez-Guerra *et al.* (2005) are broader than both species, measuring 15.5–29 × 4.5–7 µm; the size differs from both. Kimati & Galli (1970) observed two types of asci and ascospores of *Ga. cingulata* f. sp. *phaseoli*: (1–) 4(–8)-spored asci with mean ascospores dimensions, 20 × 6.5 µm, and 8-spored asci, with ellipsoidal ascospores, measuring on average 10 × 4 µm, that also do not match with any of the species treated in this study.

While no sequence data were included in these papers, few studies showed that strains from *Phaseolus vulgaris* with sexual morphs and those forming asexual morphs belong to different RAPD groups (Talamini *et al.* 2006) or clades in phylogenies based on ITS and HMG sequence data (Barcelos *et al.* 2011, 2014), one of which clustered with *Ga. magna* strains (Barcelos *et al.* 2014). A blast search with a sequence of strain UFLAG07-3 (KF604738) from that study was 99 % identical (4 nucleotides difference) with *Ga. glycines* strain LFN0009 from soybean in Brazil (Barbieri *et al.* 2017), that is included in the *C. orchidearum* subclade in this study; based on that it is probably none of the species treated in this study. More loci need to be sequenced to resolve the position of this species.

There are also two strains from *Gossypium* in Brazil that were identified as *C. plurivorum*. However, the common causal agents of cotton anthracnose and ramulose, *C. gossypii* var. *gossypii* and *C. gossypii* var. *cephalosporioides*, respectively, belong to the *C. gloeosporioides* complex (Salustiano *et al.* 2014, U. Damm, unpubl. data).

Colletotrichum sojae Damm & Alizadeh **sp. nov.** MycoBank MB824229. Fig. 17.

Non *Vermicularia truncata* Schwein., Trans. Am. phil. Soc. 4(2): 230. 1832. *Glomerella glycines* Lehman & F.A. Wolf, J. Agric. Res., Washington 33(4): 381. 1926. [= *Colletotrichum truncatum* (Schwein.) Andrus & W.D. Moore].

Etymology: The species epithet is derived from the host plant *Glycine max*, soybean.

Sexual morph on Anthriscus stem (observed in strains ATCC 62257, CBS 134.87, UTFC 288, UTFC 301 and UTFC 303). **Ascomata** perithecia, solitary, superficial, non-stromatic, globose to subglobose, ostiolate, pale to medium brown, 80–150 µm diam, glabrous or covered with few stiff hairs, 10–70 µm long. **Peridium** 10–15 µm thick, composed of 3 layers of pale brown flattened *textura angularis*. **Ascogenous hyphae** hyaline, smooth-walled, delicate, rarely visible. **Interascal tissue** not observed. **Asci** mostly immature asci of strain ATCC 62257 observed, mature asci apparently disintegrating quickly, unitunicate, 8-spored, cylindrical to clavate, smooth-walled, the base broadly truncate, mature asci of strain UTFC 288 thin-walled, clavate, measuring 77–80 × 11–11.5 µm. **Ascospores** aseptate, hyaline, smooth-walled, fusiform, curved, sometimes additionally slightly

flexed in the middle, with rounded ends, (14–) 15.5–23(–33.5) × (3.5–)4–5 µm, mean ± SD = 19.3 ± 3.7 × 4.5 ± 0.3 µm, L/W ratio = 4.3, ascospores of strain UTFC 288 wider, measuring 14.5–20 × 5–6.5 µm, mean ± SD = 17 ± 1.49 × 5.5 ± 0.4, L/W ratio = 3.1.

Sexual morph on SNA (only observed in strain CBS 134.87). **Ascomata** perithecia, solitary or in clusters, superficial or immersed in the agar medium, non-stromatic, ± globose, ostiolate, pale to medium brown, glabrous. **Asci** not observed. **Ascospores** aseptate, hyaline, smooth-walled, fusiform, curved, with rounded ends, (18.5–)20–27(–37) × (4–)4.5–5 µm, mean ± SD = 27.7 ± 3.5 × 4.6 ± 0.3 µm, L/W ratio = 5.2.

Asexual morph on SNA. Vegetative hyphae 1–7.5 µm diam, hyaline to pale brown, smooth-walled, septate, branched. **Chlamydospores** not observed. **Conidiomata**, conidiophores and setae formed directly on hyphae. **Setae** medium brown, smooth-walled to verruculose, 30–75 µm long, 2–3-septate, base cylindrical, conical to slightly inflated, 3.5–6 µm diam, tip ± rounded to slightly acute. **Conidiophores** hyaline, smooth-walled, simple, sometimes septate, to 25 µm long. **Conidiogenous cells** hyaline, smooth-walled, cylindrical to ovoidal, often integrated and conical or clavate, 7–22.5 × 3–6.5(–8) µm, opening 1–2 µm diam, collarete 0.5–1 µm long, periclinal thickening distinct. **Conidia** hyaline, smooth-walled, initially aseptate, becoming septate with age, straight, the apex and base rounded, (11–) 14–17(–17.5) × (4.5–)5–6(–6.5) µm, 15.7 ± 1.4 × 5.4 ± 0.4 µm, L/W ratio = 2.9, conidia of strain ATCC 11871 narrower, measuring (14–)15–18(–19.5) × (4–)4.5–5(–5.5) µm, mean ± SD = 16.5 ± 1.5 × 4.9 ± 0.3 µm, L/W ratio = 3.4. **Appressoria** (only few observed) single, medium brown, smooth-walled, navicular, bullet-shaped or irregular in outline, with an undulate to lobate margin, (9–)12–19(–24) × (6–) 8–11.5(–13) µm, mean ± SD = 15.3 ± 3.6 × 9.7 ± 1.8 µm, L/W ratio = 1.6, appressoria of strain UTFC 288 smaller, measuring 11–21 × 5–9.5 µm, mean ± SD = 14.5 ± 3.1 × 7.5 ± 1.4 µm, L/W ratio = 1.9.

Asexual morph on Anthriscus stem. Sporulation sparse. **Conidiomata** not observed in strain ATCC 62257, conidiophores and setae formed by strain ATCC 11871 on pale brown angular cells, 3–8.5 µm diam. **Setae** (few observed) medium to dark brown, smooth-walled or verruculose, 50–130 µm long, 1–12-septate, base cylindrical to conical, or ± inflated, 3–8.5 µm diam, tip ± acute to ± rounded. **Conidiophores** and **conidiogenous cells** not observed in strain ATCC 62257. **Conidiophores** in strain ATCC 11871 hyaline to pale brown, smooth-walled, septate, branched, to 40 µm long. **Conidiogenous cells** in strain ATCC 11871 hyaline to pale brown, smooth-walled, cylindrical, 8–25 × 4–5.5 µm, opening 1–2 µm diam, collarete 0.5 µm long, rarely seen, periclinal thickening observed. **Conidia** hyaline, smooth-walled, aseptate, straight, the apex and base rounded, (12.5–)14–17.5(–18.5) × 5–6(–6.5) µm, mean ± SD = 15.8 ± 1.5 × 5.5 ± 0.4 µm, L/W ratio = 2.9.

Culture characteristics: Colonies on SNA flat, with entire margin, hyaline to honey, covered by thin, floccose, whitish to pale grey, aerial mycelium, reverse same colours; 28–29 mm in 7 d (38.5–≥ 40 mm in 10 d). Colonies on OA flat with entire margin,

Fig. 17. *Colletotrichum sojae* (B–D, I–V, Y–AE. from ex-holotype culture ATCC 62257. A, E–H. from culture ATCC 11871. W–X. from culture CBS 134.87). **A–B.** Conidiomata. **C.** Tip of a seta. **D.** Base of a seta. **I.** Seta. **E–H, J–M.** Conidiophores. **N–S.** Appressoria. **T–U.** Conidia. **V.** Peridium in cross section. **W–X.** Ascomata. **Y.** Outer surface of peridium. **Z.** Ascospores. **AA–AD.** Immature asci. **AE.** Disintegrating apex of an ascus apparently after ascospore release. A, C–H, T, V, X–AE. from *Anthriscus* stem. B, I–S, U, W. from SNA. A–B, W–X. DM. C–V, Y–AE. DIC. Scale bars: A = 100 µm, T = 10 µm, Y = 40 µm. A applies to A–B, W–X. T applies to C–U, V, Y–AE.

buff, olivaceous buff to olivaceous, partly covered with thin, floccose, whitish aerial mycelium, reverse buff to olivaceous grey, 30–32.5 mm in 7 d (≥ 40 mm in 10 d). *Conidial mass* not observed in strain ATCC 62257, those of strain UTFC 288 pale yellow.

Materials examined: Iran, Golestan province, Tooskestan area, isolated from leaves of *Glycine max*, Oct. 2013, A. Alizadeh & O. Atghia, strain UTFC 288 = 442C; Guilan province, Roodsar area, from leaves of *Phaseolus vulgaris*, Oct. 2013, A. Alizadeh & O. Atghia, strain UTFC 301 = 507C; Guilan province, Loolman-Astaneh ashrafie road, from leaves of *Vigna unguiculata*, Oct. 2013, A. Alizadeh & O. Atghia, strain UTFC 303 = 524C. **Italy**, Bologna, from *Glycine max*, unknown collection date and collector (sent to CBS Jan. 1987 for identification by P. Giunchi, Osservatorio Malattie Delle Piante, Bologna, Italy, identification by H.A. van der Aa, No. 9944), CBS H-12958, culture CBS 134.87. **Serbia and Montenegro**, Novi Sad, from *Glycine max*, unknown collection date, Z. Klocokar-Smit (isolated 1980 by Z. Klocokar-Smit and deposited in CBS collection Jan. 1981), CBS H-12907, culture CBS 181.81; Novi Sad, from *Glycine max*, unknown collection date and collector (isolated 1980 by Z. Klocokar-Smit and deposited in CBS collection Jan. 1981), culture CBS 182.81. **USA**, Illinois, from *Glycine max*, unknown collection date, J.B. Manandhar (received from R. O'Connell as *Ga. glycines*, before from J.B. Sinclair) (CBS H-21495 **holotype** of *C. sojae*, culture ex-holotype ATCC 62257 = CPC 19367); Iowa, from stem of *Medicago sativa*, unknown collection date and collector (received from R. O'Connell as *Ga. glycines*, before from L.H. Tiffany), culture ATCC 11871 = CPC 18948; Iowa, from stem of *Medicago sativa* unknown collection date and collector (received from R. O'Connell as *C. destructivum*, before from A. Alfaro, originally from L.H. Tiffany), culture CBS 128510 = LARS 204 = CECT 2873 = Alfaro 212 = ATCC 11871 = DSM 1167 (apparently the same strain as above); North Carolina, Raleigh, from anthracnose of *Glycine max*, unknown collection date, S.G. Lehman & F.A. Wolf [BPI 596658 (dried culture) **holotype** of *Ga. glycines*]; North Carolina, Raleigh, from anthracnose of *Glycine soja* (= *G. max*), unknown collection date and collector (isolated by S.G. Lehman as strain 1936, deposited in CBS collection as *Ga. glycines* in May 1932 by J.A. Stevenson), (strain CBS 195.32 ex-holotype strain of *Ga. glycines*).

Notes: Soybean (*Glycine max*) anthracnose was first reported in 1917 from Korea, where it was attributed to *C. glycines* (Hemmi 1920). Anthracnose occurs in all soybean producing areas and can cause yield losses of up to 100 % (Sinclair 1982). Lehman & Wolf (1926) studied soybean anthracnose in the USA and noticed an asexual morph they identified as *C. glycines* and a sexual morph they regarded as the sexual morph of this species, hence naming it *Ga. glycines*.

The only specimen located that could directly be linked to Lehman & Wolf is BPI 596658. A handwritten note with that specimen reads "ATCC #1936, *G. glycines* (Hori) n.n. (n.n. was later crossed out and replaced by "Lehman & Wolf"), S.G. Lehmann and Frederick A. Wolf, Jour. Agric. Research 33: 381–390, Aug. 15, 1926", referring to the publication of that species. We therefore regard this specimen as the holotype of *Ga. glycines*.

Specimen BPI 596658 contains two dried cultures of *Ga. glycines* strain ATCC 1936 (Label on tubes: *Glomerella glycines*, A.T.C.C. # 1936, 11-19-1929, Vaxter agar on soybean). No conidia or ascospores were observed on these cultures. The same number (1936) appeared with the strain information of strain CBS 195.32 that was isolated by S.G. Lehman from *Glycine max* in Raleigh, North Carolina, USA, originally identified as *Ga. glycines* and deposited to the CBS collection in May 1932 by J.A. Stevenson. This means CBS 195.32 is apparently the same strain as ATCC 1936 and therefore regarded as the ex-holotype strain of *Ga. glycines*. The ATCC collection lists a strain ATCC 1936, but recorded as "unknown". According to a request at ATCC (A. Khashnobish, in lit.), no strain ATCC 1936 exists anymore.

However, strain CBS 195.32 was identified as *C. truncatum* by Damm et al. (2009). Drawings and description of the asexual

morph of *Ga. glycines* observed by Lehman & Wolf (1926) agree with this. *Colletotrichum truncatum* is a common pathogen of soybean (Ramos et al. 2013, Yang et al. 2014, Rogério et al. 2016). However, it is dubious that this soybean pathogen formed a sexual morph in the study of Lehmann & Wolf, as a sexual morph was never observed for any strain of *C. truncatum*, neither in the extensive study of Damm et al. (2009) nor in any other study on this pathogen (e.g. Shenoy et al. 2007, Than et al. 2008, Rogério et al. 2016).

Lehman & Wolf (1926) stated that they made isolations "from diseased stems and pods bearing the conidial stage, from infected seed, and from old, decaying stems bearing the ascogenous stage" and further: "No efforts have been made to make single-spore cultures from either conidia or ascospores..." There is no indication that the authors would have found conidia and ascospores on the same plant parts. They transferred blocks of agar containing several spores each. Although the authors did not observe cultural differences, which was obviously the reason for them to conclude they were studying one species, it is likely that two species were isolated and even mixed cultures were prepared: "Some strains from conidia have born conidia alone, even after repeated transfer and cultivation on a variety of media; other strains from ascospores, however, have consistently yielded both the conidial and ascospore stages when cultivated upon the same kind of media" (Lehman & Wolf 1926). So, it is likely that the sexual morph and the asexual morph observed by them are different species. Yang et al. (2014) reported two species to be common pathogens of soybean in the USA, namely "*Ga. glycines*" and *C. truncatum*. Apparently, Lehman & Wolf never noticed the asexual morph that really belongs to the observed sexual morph.

According to Tiffany & Gilman (1954) and Lin & Wu (1966), the asexual morph of *Ga. glycines* is not *C. glycines*, but a species similar to *C. destructivum*. Manandhar et al. (1986) claimed *C. destructivum* to be the asexual morph of *Ga. glycines* by morphological comparison of strains from *Glycine* forming a sexual morph as described for *Ga. glycines* (Lehman & Wolf 1926) that were therefore considered to be *Ga. glycines*, and strains from *Medicago* that were considered to be *C. destructivum* and gave a detailed description of both morphs. Strains from Manandhar et al. (1986) from both hosts (ATCC 62257 from *Glycine max* and ATCC 11871 from *Medicago*), were included in this study and confirmed to be conspecific. However, these strains are not closely related to *C. destructivum* that was epitypified in a recent study and belongs to the *C. destructivum* complex (Damm et al. 2014).

One of the two strains from Manandhar et al. (1986) easily formed the very typical sexual morph in culture that agrees with the pictures and the description of Lehman & Wolf (1926): perithecia 220–340 μm diam, asci 70–106 \times 9.5–13.5 μm , mean = 80 \times 12 μm ; ascospores in culture were (13.12–) 18.75–28.12(–43.35) μm long. The ascospores of *C. plurivorum*, also occurring on soybeans and also described in this study, have a different shape (see Fig. 16).

The name *Ga. glycines* was applied by Lehman & Wolf (1926) based on the asexual morph that was identified by them as *C. glycines* and the simultaneously observed sexual morph that was apparently wrongly connected to the asexual morph. However, the type specimen of *Ga. glycines* only includes the asexual morph that was re-identified as *C. truncatum* by Damm et al. (2009). *Colletotrichum truncatum* is based on *Vermicularia truncata* (Schweinitz 1832), which has priority over

Ga. glycines. There is no name available for the second species that forms the sexual morph. Consequently, this species is described here as a new species, *C. sojae*.

According to von Arx (1957), *C. glycines* Hori ex Hemmi is a synonym of *C. dematium* f. *truncata*, which is a synonym of *C. truncatum* (Damm et al. 2009). However, von Arx neither saw the type specimen nor a strain of *C. glycines*. In the Compendium of Soybean Diseases, the two species on soybean are treated as *C. truncatum* (= *C. glycines*) and *Ga. glycines* (Sinclair 1982). It is possible that *C. glycines* and *C. truncatum* are synonyms as both types represent species with curved conidia. However, Yang et al. (2014) collected three *Colletotrichum* species with curved conidia on soybeans in the USA, *C. incanum*, *C. chlorophyti* and *C. truncatum*. *Colletotrichum glycines* Hori ex Hemmi could be a synonym of any of these species, or even a different species. We did not study the type of *C. glycines* and there is no ex-type strain of *C. glycines* available for molecular analysis. In order to clarify its systematic position, *C. glycines* would need to be epitypified.

Another species named *C. glycines*, *C. glycines* Gonz. Frag. (González Fragoso 1924) was not described from soybean, but from *Wisteria sinensis* (syn.: *Glycine sinensis*) in Portugal. The name is illegitimate, according to Art. 53.1.

Within the strains of this species there is considerable variation in the formation of sexual and asexual morphs. There are strains that form the asexual morph only and strains that predominantly form the sexual morph. It is very likely the latter case is the reason for Lehman & Wolf (1926) to overlook the asexual morph of this species.

Colletotrichum sojae occurs mainly on *Fabaceae* (*Glycine*, *Medicago*, *Phaseolus*, *Vigna*), but also on *Amaranthaceae* (*Amaranthus*), *Asteraceae* (*Arctium*), *Solanaceae* (*Capsicum*) and *Orchidaceae* (*Bletilla*). There is another species occurring on *Fabaceae* (including *Glycine* and *Phaseolus*) treated in this study (see *C. plurivorum*).

Colletotrichum sojae can be identified by *HIS3*, *ACT* and *TUB2* sequences, while the ITS is identical with that of *C. vittalense*. Closest matches in blastn searches with the *TUB2* sequence of the ex-type strain of *C. sojae*, ATCC 62257, resulted in 100 % matches with *Ga. glycines* strain ATCC 62257 (Yang et al. 2014), *Colletotrichum* strain CGMCC 3.15171 from *Bletilla* in China (Tao et al. 2013), *C. cliviae* strain CAUOS5 from *Capsicum* in China (Diao et al. 2017) and with 99 % identity (1 nucleotide difference) *Ga. glycines* strains IL18A and IL26A (Yang et al. 2014) and *C. orchidearum* isolate SAUCC 1407 (Xu et al. 2016), both included in this study. The *ACT* sequence of strain ATCC 62257 resulted in 100 % identity with the three *Ga. glycines* strains of Yang et al. (2014), *Colletotrichum* strains CGMCC 3.15171 from *Bletilla* (Tao et al. 2013) and CAUGOS3 from *Capsicum* in China (Diao et al. 2017), all included in this study, as well as *Colletotrichum* sp. SKH-2010 isolates C07010 and C08116 (GU944760, GU935805, Choi et al. 2011) and with 99 % identity (1 and 2 nucleotides difference), *C. orchidearum* isolate SAUCC 1407 (Xu et al. 2016) and *Ga. glycines* strain LFN0009 (Barbieri et al. 2017), both included in this study. The *GAPDH* of strain ATCC 62257 is 100 % identical with *Ga. glycines* strains IL26A, ATCC 62257, IL18A (Yang et al. 2014) and LFN0009 (Barbieri et al. 2017) and *C. aracearum* strains LC1033 and LC1041 (Hou et al. 2016), all included in this paper, as well as *Colletotrichum* isolates C08116, C07004 and C07010 (GU935864, GU935865, GU935866, Choi et al. 2011). Closest matches in blastn searches with the ITS sequence of the ex-type strain resulted in a large number of identical sequences from several host plants in different countries.

Colletotrichum orchidearum isolate SAUCC 1407 from *Arc-tium lappa* in China (Xu et al. 2016), *C. cliviae* strains LFN0009 (as *Ga. glycines* in GenBank) from *Glycine max* in Brazil (Barbieri et al. 2017) and CAUOS5 from *Capsicum* in China (Diao et al. 2017), *Colletotrichum* sp. from *Bletilla* in China (CGMCC 3.15171, Tao et al. 2013) as well as *Ga. glycines* isolates IL18A, IL26A from soybean in the USA (Yang et al. 2014) could be re-identified as *C. sojae* based on a sequence comparison in this study. We suspect the *ACT* sequence KP890098 is actually from CAUOS5 as well, and not from CAUOS3. There is no *ACT* sequence of CAUOS5 listed in the paper (Diao et al. 2017). *Colletotrichum* sp. SKH-2010 isolates C07010, C07004 and C08116 were also identified as *C. sojae*. These strains were cited from Choi et al. (2011) in GenBank, but not included in that paper. As there is no strain information, we also did not include the strains in our phylogeny. In contrast, strain MAFF 238875 from *Glycine max* in Japan previously identified as *C. cliviae* was revealed to be *C. plurivorum*. Moreover, the ITS of “*Ga. glycines*” isolate IFO 7384 from an unknown host (GenBank AB057435, Moriwaki et al. 2002) is 100 % identical with that of CBS 127604, the ex-holotype strain of *C. lentis* (Damm et al. 2014).

Colletotrichum tropicicola Phouliv. et al., Cryptog. Mycol. 33(3): 353. 2012. Fig. 18.

A description of the type specimen is provided by Noireung et al. (2012). The description below is based on strains from *Citrus* sp. collected in Mexico.

Sexual morph not observed.

Asexual morph on SNA (CBS 127555). *Vegetative hyphae* 1.5–10.5 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydo-spores* not observed. *Conidiomata*, conidiophores and setae formed directly on hyphae. *Seta* (only one observed) medium brown, verruculose, 81 µm long, 3-septate, base cylindrical, 5.5 µm diam, tip ± rounded. *Conidiophores* hyaline, smooth-walled, septate, branched, to 40 µm long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical, (3–)5–18 × (2–)3–4.5 µm, often extending to form new conidiogenous loci, opening 1.5–2 µm diam, collarette 1 µm long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical, the apex rounded, sometimes tapering to the rounded or truncate base, (13.5–)14–17.5(–22) × 4.5–5(–5.5) µm, mean ± SD = 15.7 ± 1.7 × 4.8 ± 0.3 µm, L/W ratio = 3.3, conidia of strain CBS 133174 wider, measuring (14–)15–17(–18.5) × (5–)5.5–6 µm, mean ± SD = 16.2 ± 1.0 × 5.5 ± 0.3 µm, L/W ratio = 2.9. *Appressoria* single or in loose groups, medium to dark brown, smooth-walled, ellipsoidal to bullet-shaped in outline, with an entire or undulate margin, (7–)8–11(–14.5) × (4–)5.5–7(–7.5) µm, mean ± SD = 9.5 ± 1.5 × 6.2 ± 0.7 µm, L/W ratio = 1.6, appressoria of strain CBS 133174 larger, only few observed, measuring 11.5–20(–24.5) × 5–8(–10) µm, mean ± SD = 15.8 ± 4.1 × 6.7 ± 1.6 µm, L/W ratio = 2.4.

Asexual morph on Anthriscus stem (CBS 127555). *Conidiomata*, conidiophores formed directly on hyphae. *Setae* not observed. *Conidiophores* hyaline, smooth-walled, septate, branched, to 30 µm long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical to ± inflated, 8–25 × 3.5–4.5(–6) µm, opening 1.5–2 µm diam, collarette 0.5 µm long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical, the apex rounded, sometimes tapering to the rounded or

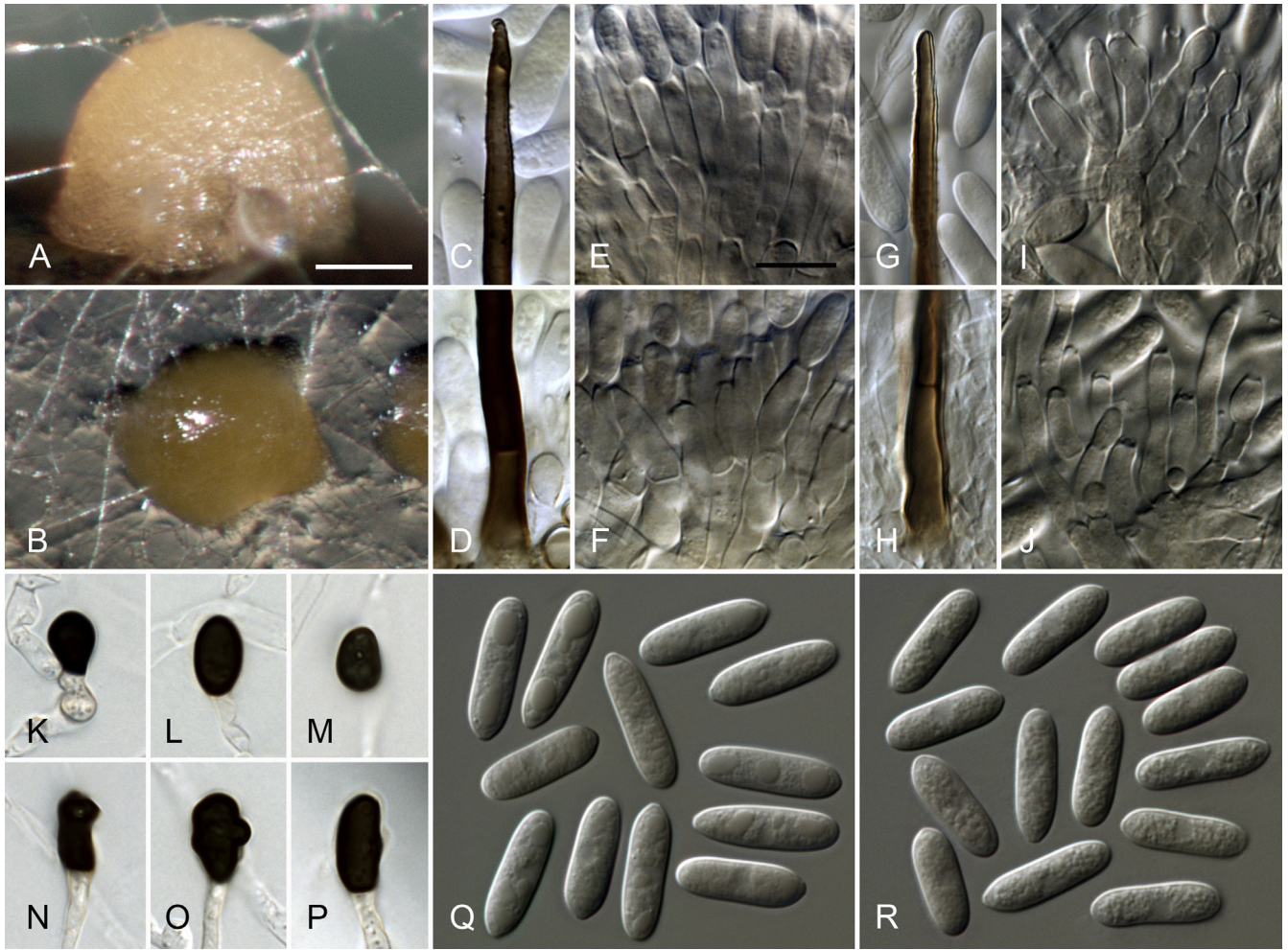


Fig. 18. *Colletotrichum tropicicola* (A–B, E–R. from culture CBS 127555. C–D from culture CBS 133174). **A–B.** Conidiomata. **C, G.** Tips of setae. **D–H.** Bases of setae. **E–F, I–J.** Conidiophores. **K–P.** Appressoria. **Q–R.** Conidia. **A, C–F, Q.** from *Anthriscus* stem. **B, G–P, R.** from SNA. **A–B.** DM. **C–R.** DIC. Scale bars: **A** = 100 μ m, **E** = 10 μ m. **A** applies to **A–B**. **E** applies to **C–R**.

truncate base, (13.5–)15–17(–18) \times 4.5–5(–5.5) μ m, mean \pm SD = 15.9 \pm 1.0 \times 5.0 \pm 0.2 μ m, LW ratio = 3.2, conidia of strain CBS 133174 larger, measuring (15.5–)17–19.5(–20) \times 5–5.5 μ m, mean \pm SD = 18.2 \pm 1.0 \times 5.4 \pm 0.2 μ m, LW ratio = 3.4.

Cultural characteristics (CBS 127555). Colonies on SNA flat with entire margin, medium buff to pale honey, *Anthriscus* stem, filter paper and SNA medium partly covered with greyish to orange acervuli and whitish to grey aerial mycelium, reverse buff to honey with grey to orange acervuli shining through; 15–18 mm in 7 d (28.5–32 mm in 10 d). Colonies on OA flat with entire margin, surface buff, pale olivaceous grey to olivaceous grey, partly covered with floccose to felty pale olivaceous grey to olivaceous grey aerial mycelium and grey to orange acervuli, reverse buff, rosy buff, pale olivaceous grey to olivaceous grey; 16–17.5 mm in 7 d (30–32.5 mm in 10 d). **Conidial mass** orange.

Materials examined: **Mexico**, Tamaulipas, from *Citrus* sp., 16 Oct. 2008, M. de Jesus Yanez-Morales, CBS H-21070, culture CBS 127555 = CPC 15927; Tamaulipas, from *Citrus* sp., 16 Oct. 2008, M. de Jesus Yanez-Morales, culture CBS 133174 = CPC 15924.

Notes: This species belongs to the *C. dracaenophilum* species complex. [Noireung et al. \(2012\)](#) described *C. tropicicola* from leaves of *Citrus maxima* and *Paphiopedilum bellatolum* in Thailand. Further strains from *Citrus* sp. in Mexico could be identified as *C. tropicicola* in this study based on the multilocus

phylogeny. While these two strains formed a well-supported clade with the ex-type strain of *C. tropicicola* in our phylogeny, the strain from *Paphiopedilum* formed a sister clade to *C. excelsum-altitudinum* and could represent a further species (referred to as “*C. tropicicola* 2” in the phylogeny). Thus *C. tropicicola* s. str. only occurs on *Citrus* spp., according to our data.

Colletotrichum tropicicola can be identified with sequences of all loci available (ITS, *GAPDH*, *ACT*, *TUB2*), but best with *GAPDH* and *TUB2*. The ITS sequence of the ex-type strain, MFLUCC 11-0114, is 99 % identical (2, 7 and 6 nucleotides difference) to those of the apparently wrongly identified *C. cordylinicola* strain LC0886 (KC790944, [Sharma et al. 2013a](#)), the two *C. excelsum-altitudinum* isolates ([Tao et al. 2013](#)) and MFLUCC 10-0167, the *C. tropicicola* strain from *Paphiopedilum*, respectively. The *GAPDH* sequence of the ex-type strain is 99 % identical (4 nucleotides difference) to that of the *C. tropicicola* strain from *Paphiopedilum* and 96 % identical with the two *C. excelsum-altitudinum* isolates. The *ACT* sequence of the ex-type strain is 99 % identical (3 and 11 nucleotides difference) to that of the *C. tropicicola* strain from *Paphiopedilum* and the two *C. excelsum-altitudinum* isolates, respectively. The *TUB2* sequence of the ex-type strain is 98 % identical (10 and 8 nucleotides difference) with the two original *C. excelsum-altitudinum* isolates and that of the *C. tropicicola* strain from *Paphiopedilum*, respectively.

***Colletotrichum vittalense* Damm, sp. nov.** MycoBank MB824230. **Fig. 19.**

Etymology: The species epithet is derived from Vittal, the place in Karnataka, India, where the type was collected.

Sexual morph on SNA (only observed in strain CBS 181.82). *Ascomata* perithecia, formed after 4 wk, solitary, superficial or immersed in the agar medium, non-stromatic, globose to obpyriform, ostiolate, glabrous, dark brown, 250–300 × 200–250 µm. *Peridium* 10–15 µm thick, composed of 3–5 layers of medium brown flattened *textura angularis* with cells 5.5–15 µm diam. *Ascogenous hyphae* hyaline, smooth, delicate, rarely visible. *Interascal tissue* formed of paraphyses, hyaline, smooth-walled, cylindrical, disintegrating quickly, septate, apically free. *Asci* unitunicate, 8-spored, cylindrical to clavate, tapering to apex and base, smooth-walled, 53–83 × 9–11 µm, the base broadly truncate. *Ascospores* uni- or biserially arranged, aseptate, hyaline to pale brown, smooth-walled, allantoid, fusiform to ellipsoidal, with both ends rounded, curved or straight, (11.5–)14.5–19(–23.5) × (4–)4.5–5.5(–6) µm, mean ± SD = 16.8 ± 2.3 × 5.1 ± 0.4 µm, L/W ratio = 3.3.

Sexual morph on Anthriscus stem (only observed in strain CBS 181.82). *Ascomata* perithecia, formed after 4 wk, solitary, superficial, non-stromatic, globose to obpyriform, ostiolate, glabrous, dark brown, 150–320 × 130–200 µm diam. *Peridium* 11–13 µm thick, composed of 4–6 layers of medium brown flattened *textura angularis* with cells 5–15.5 µm diam. *Paraphyses* not observed. *Asci* 8-spored, unitunicate, cylindrical to clavate, 53–83 × 9–11 µm. *Ascospores* uni- or biserially arranged, aseptate, hyaline to pale brown, smooth-walled, allantoid, fusiform to ellipsoidal, with both ends rounded, curved or straight, (12–)14–16.5(–17.5) × (4.5–)5–5.5(–6) µm, mean ± SD = 15.1 ± 1.3 × 5.3 ± 0.4 µm, L/W ratio = 2.8.

Asexual morph on SNA. *Vegetative hyphae* 1.5–6.5 µm diam, hyaline to pale brown, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata*, conidiophores and setae formed directly on hyphae. *Setae* medium to dark brown, verruculose to verrucose, 50–120 µm long, 1–3-septate, base cylindrical to conical, 3.5–5.5 µm diam, tip ± acute. *Conidiophores* pale brown, smooth-walled to verruculose, septate, branched, to 60 µm long. *Conidiogenous cells* pale brown, smooth-walled to verruculose, cylindrical to clavate, 7–22.5 × 2.5–6.5 µm, opening 1.5–2 µm diam, collarette 0.5–1 µm long, periclinal thickening distinct, conidiogenous cells of strain CBS 126.25 sometimes integrated. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical, sometimes slightly clavate with the widest part at the base, the apex and base rounded, (11.5–)13.5–16(–18.5) × 5–5.5(–7) µm, mean ± SD = 14.8 ± 1.4 × 5.4 ± 0.4 µm, L/W ratio = 2.8, conidia of strain CBS 126.25 slightly longer, measuring (11–)12.5–15(–18) × 5–5.5 µm, mean ± SD = 13.6 ± 1.2 × 5.2 ± 0.2 µm, L/W ratio = 2.6. *Appressoria* single or in loose groups, medium to dark brown, smooth-walled, navicular, bullet-shaped, elliptical or irregular in outline, with a lobate or undulate margin, (6–)9.5–16.5(–22.5) × (5–)7.5–11(–14.5) µm, mean ± SD = 13.1 ± 3.5 × 9.1 ± 1.7 µm, L/W ratio = 1.4, appressoria of strain CBS 126.25 smaller, measuring (7–)8.5–14.5(–18.5) × (5–)5.5–8(–9.5) µm, mean ± SD = 11.3 ± 3.0 × 6.8 ± 1.1 µm, L/W ratio = 1.7.

Asexual morph on Anthriscus stem. *Conidiomata*, conidiophores and setae formed on medium brown, angular cells, 3–7 µm diam. *Setae* medium brown, verruculose to verrucose, 55–120 µm long, 1–2(–3)-septate, base cylindrical to conical, 4.5–7.5 µm diam, tip ± acute. *Conidiophores* pale brown,

smooth-walled. *Conidiogenous cells* pale brown, smooth-walled, cylindrical to doliform, 7.5–10.5 × 3.5–5.5 µm, opening 1–2 µm diam, collarette ± 0.5 µm long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical, the apex and base rounded, 15–17(–18.5) × 5–5.5(–6) µm, mean ± SD = 16.1 ± 0.9 × 5.3 ± 0.3 µm, L/W ratio = 3.0, conidia of strain CBS 126.25 shorter, measuring (12.5–)13.5–15.5(–17.5) × 5–5.5 µm, mean ± SD = 14.5 ± 1.0 × 5.2 ± 0.2 µm, L/W ratio = 2.8.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline to pale olivaceous grey, agar medium, filter paper and *Anthriscus* stem partly covered with felty white to pale olivaceous grey aerial mycelium and grey to black conidiomata/ascomata, reverse same colours; growth 29–30.5 mm in 7 d (≥ 40 mm in 10 d), strain CBS 126.25 grows more slowly: 22.5–24 mm in 7 d (31–32.5 mm in 10 d). Colonies on OA flat with entire margin; olivaceous buff, grey olivaceous to olivaceous, partly covered with short felty whitish aerial mycelium and pale grey conidiomata/ascomata, reverse olivaceous buff, pale olivaceous grey to olivaceous grey, growth 28.5–30 mm in 7 d (≥ 40 mm in 10 d), strain CBS 126.25 grows more slowly: 24–26 mm in 7 d (28.5–34 mm in 10 d). *Conidial mass* greyish white.

Materials examined: India, Karnataka, Vittal, from *Theobroma cacao* (pathogenic), collection date and collector unknown (isolated and deposited in CBS collection by F.H. Beyma, May 1928) (CBS H-21498 **holotype**, culture ex-holotype CBS 181.82). **Unknown**, from an unknown *Orchidaceae* plant, collection date and collector unknown (isolated and deposited in CBS collection by K.N. Murthy, Mar. 1928), CBS H-21499, culture CBS 126.25.

Notes: *Colletotrichum vittalense* belongs to the *C. orchidearum* species complex and is only known as pathogen of *Theobroma cacao* in India and from an unknown *Orchidaceae* plant.

Several species were described on *Theobroma cacao*, including *C. cacao* in the *C. magnum* complex that is also described in this study. Numerous species were described on *Orchidaceae* hosts, including *C. cattleyicola*, also belonging to the *C. orchidearum* species complex and *C. orchidearum* belonging to the *C. orchidearum* species complex described and epitypified, respectively, in this study. See notes under *C. cacao*, *C. cattleyicola* and *C. orchidearum* for further species and reports on these hosts. The two *C. vittalense* strains from the CBS collection were previously identified as *Ga. cingulata* var. *cingulata* and *C. gloeosporioides*, *Ga. lagenaria* and *Gl. affine*, the latter is a species that was described from *Hoya* (*Apocynaceae*) and *Vanilla* (*Orchidaceae*) from the botanical garden in Padua, Italy, with similar conidial shape (cylindrical with both ends rounded) and size (14–20 × 4–6 µm) as *C. vittalense* (Saccardo 1878). However, we could not locate the type material of this species to confirm its taxonomic position.

A typical feature of *C. vittalense* are the very short ascospores with round ends that vary between straight to strongly curved. This species can be identified by its unique *GAPDH*, *CHS-1*, *HIS3* and *TUB2* sequences. In a blastn search on GenBank with the *GAPDH* sequence of the ex-type strain of *C. vittalense*, CBS 181.82, the only 100 % identical sequence was *C. cliviae* strain GUFCC15503 from *Calamus thwaitesii* in India (KC790759, Sharma et al. 2013a) that was included in the phylogeny of this study and re-identified as *C. vittalense*. Strain GUFCC15503 originates from Netravali in Goa, also in the south-west of India like Vittal. The *GAPDH* sequence of the ex-type strain of *C. clivicola* differs in 2 nucleotides from that of the ex-type strain of *C. vittalense*. Strain GUFCC15503 (KF451996,

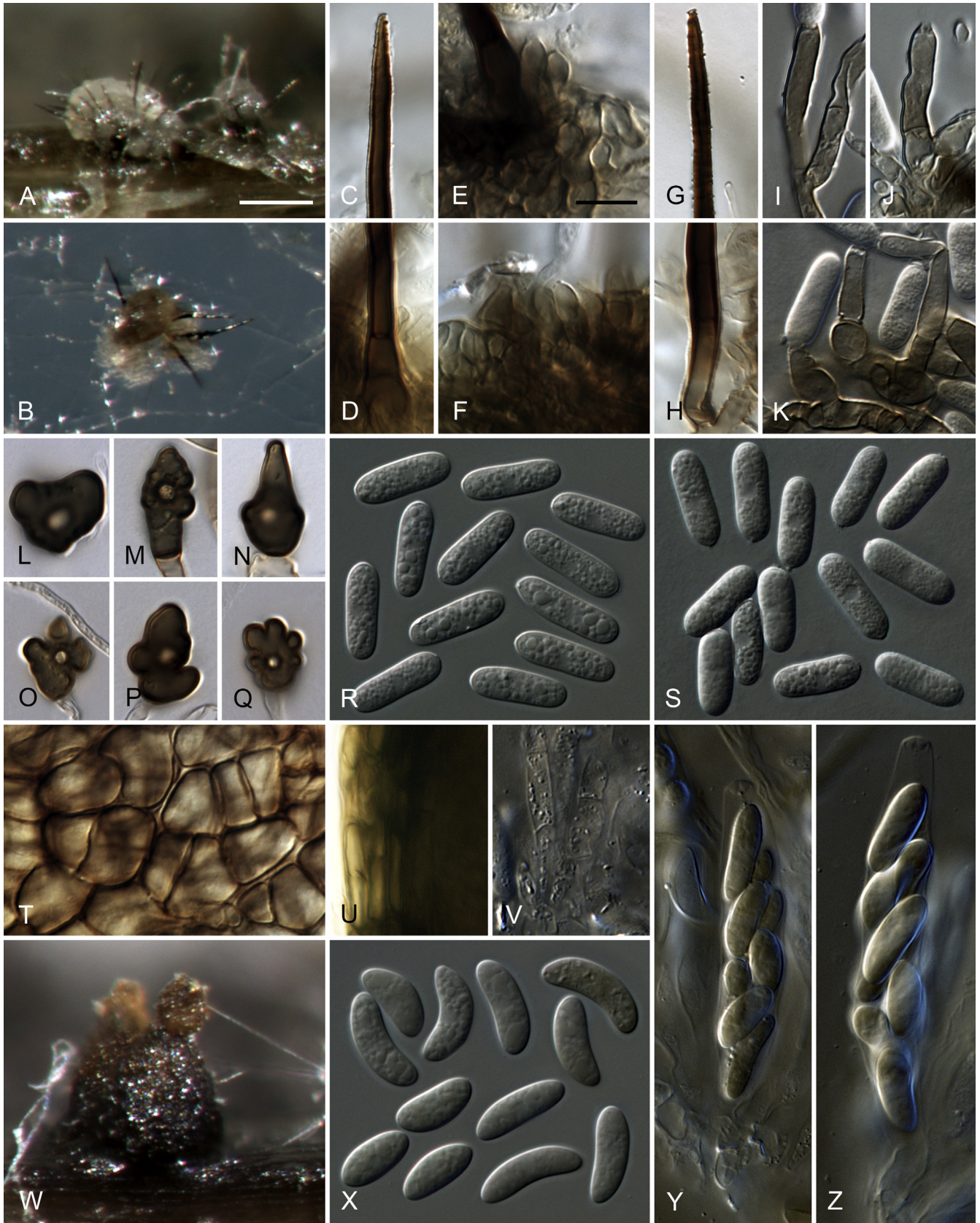


Fig. 19. *Colletotrichum vittalense* (from ex-holotype culture CBS 181.82). **A–B.** Conidiomata. **C, G.** Tips of setae. **D–H.** Bases of setae. **E–F, I–K.** Conidiophores. **L–Q.** Appressoria. **R–S.** Conidia. **T.** Outer surface of peridium. **U.** Peridium in cross section. **V.** Paraphyses. **W.** Ascoma. **X.** Ascospores. **Y–Z.** Asci. **A, C–F, R, U, W–Z.** from *Anthriscus* stem. **B, G–Q, S–T, V.** from SNA. **A–B, W.** DM. **C–V, X–Z.** DIC. Scale bars: **A** = 100 μ m, **E** = 10 μ m. **A** applies to **A–B, W.** **E** applies to **C–V, X–Z.**



Fig. 20. *Colletotrichum yunnanense* (from ex-holotype culture CBS 132135). **A–B.** Conidiomata. **C, G.** Tips of setae. **D–H.** Bases of setae. **E–F, I–K.** Conidiophores. **L–Q.** Appressoria. **R–S.** Conidia. **T.** Ascoma. **U.** Peridium in cross section. **V.** Outer surface of peridium. **W–X.** Asci. **Y.** Tip of an ascus. **Z.** Paraphyses. **AA.** Ascospores. **A, C–F, R.** from *Anthriscus* stem. **B, G–Q, S–AA.** from SNA. **A–B, T.** DM. **C–S, U–AA.** DIC. Scale bars: **A** = 100 μm, **F** = 10 μm. **A** applies to **A–B**, **T, F** applies to **C–S**, **U–AA**.

Sharma *et al.* 2015) was also the closest match in a blast search with the *ACT*, *CHS-1* and *TUB2* sequences of strain CBS 181.82 with none, one or two nucleotides difference, respectively. The ITS sequence of strain CBS 181.82 is 100 % identical with that of strains from various hosts in different countries from different studies, including *C. sojae* strains from *Glycine max* in the USA (Yang *et al.* 2014), that were included in this study. The ITS of the ex-type strain of *C. cliviicola* differs in 3 nucleotides.

Colletotrichum yunnanense Xiao Ying Liu & W.P. Wu, Myco-taxon 100: 139. 2007. Fig. 20.

Sexual morph on SNA. *Ascomata* perithecia, solitary, superficial or immersed in the agar medium, non-stromatic, subglobose, ostiolate, medium to dark brown, 150–200 × 140–260 µm. *Peridium* 10–13 µm thick, composed of 4–6 layers of pale brown *textura angularis*. *Ascogenous hyphae* hyaline, smooth-walled, delicate. *Interascal tissue* formed of paraphyses, hyaline, smooth-walled, cylindrical, apically free, tapering towards the round tip, disintegrating quickly, septate, branched, 50–65 µm long, base 2–2.5 µm diam. *Asci* unitunicate, 8-spored, cylindrical to clavate, tapering to apex and base, smooth-walled, 57–65.5 × 10.5–11.5 µm, the base broadly truncate. *Ascospores* uni- or biserially arranged, aseptate, hyaline, smooth-walled, fusiform with acute ends, slightly curved, (13.5–) 14.5–17.5(–19.5) × 5–5.5(–6) µm, mean ± SD = 16.1 ± 1.7 × 5.4 ± 0.3 µm, L/W ratio = 3.0.

Asexual morph on SNA. *Vegetative hyphae* 1–9 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata*, conidiophores and setae formed directly on hyphae. *Setae* medium brown, verrucose, warts up to 2.5 µm diam, 70–130 µm long, 2–5-septate, base slightly inflated, 4–6.5 µm diam, tip ± acute. *Conidiophores* pale brown, smooth-walled, septate, branched, to 40 µm long. *Conidiogenous cells* pale brown, smooth-walled, clavate, 8–28 × 5–7 µm, the upper part often surrounded by a gelatinous sheath, opening 1.5–2 µm diam, collarete 0.5 µm long, periclinal thickening observed. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical, the apex and base rounded, with a prominent scar, (13–) 15.5–18(–19.5) × 4.5–5(–5.5) µm, rarely up to 29 µm long, mean ± SD = 16.7 ± 1.2 × 5.0 ± 0.2 µm, L/W ratio = 3.4. *Appressoria* in loose groups, medium to dark brown, smooth-walled, subglobose to ellipsoidal in outline, with an entire or lobate margin, (3.5–)5.5–8(–10) × (3–)4.5–7(–7.5) µm, mean ± SD = 6.8 ± 1.3 × 5.8 ± 1.1 µm, L/W ratio = 1.2.

Asexual morph on Anthriscus stem. *Conidiomata*, conidiophores and setae formed on pale brown, angular cells, 3.5–7.5 µm diam. *Setae* medium brown, verrucose, 75–120 µm long, 2–3-septate, base cylindrical, conical to slightly inflated, 5–8 µm diam, tip ± rounded. *Conidiophores* (hyaline to) pale brown, smooth-walled, septate, branched, to 35 µm long. *Conidiogenous cells* (hyaline to) pale brown, smooth-walled, cylindrical, ellipsoidal to doliiform, 9.5–26 × 3.5–6 µm, the upper part often surrounded by a gelatinous sheath, opening 1–1.5 µm diam, collarete 0.5 µm long, periclinal thickening visible, sometimes distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical, the apex and base rounded, with a prominent scar, (16–)17–18.5(–20.5) × 5–5.5 µm, mean ± SD = 17.7 ± 0.9 × 5.2 ± 0.2 µm, L/W ratio = 3.4.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline, filter paper partly straw, agar medium, filter paper and *Anthriscus* stem partly covered with grey acervuli and thin whitish

aerial mycelium, reverse same colours; growth 10–11.5 mm in 7 d (17–17.5 mm in 10 d). Colonies on OA flat with entire margin; buff to grey olivaceous, partly covered with short whitish to grey aerial mycelium and salmon to grey acervuli, reverse buff, honey, olivaceous to olivaceous-grey, growth 11–12.5 mm in 7 d (18–19.5 mm in 10 d). *Conidial mass* salmon.

Material examined: China, Yunnan, Kunming Botanical Garden, from healthy leaves of *Buxus* sp., 5 Nov. 2004, W.P. Wu (WU47182 **holotype** [not seen], culture ex-holotype CBS 132135 = AS 3.9617 = LC1526).

Notes: *Colletotrichum yunnanense* was described from healthy leaves of *Buxus* sp. in Yunnan (China); the species was isolated as an endophyte; no sexual morph was observed by incubating it on PDA at 25 °C in the dark (Holotype WUWP 47182, Liu *et al.* 2007b). The ex-holotype strain was re-examined on SNA and OA in this study, and the formation of a sexual morph was observed on SNA. *Colletotrichum yunnanense* is the only species in the *C. dracaenophilum* complex for which a sexual morph is known. It is the species in this complex with the smallest appressoria; because of their often roundish outline, these appressoria also have the lowest L/W ratio. The growth rate of *C. yunnanense* is the lowest of all species treated in this study.

There are no reports of this species other than that published by Liu *et al.* (2007b). Moreover, only one other *Colletotrichum* species was reported on *Buxus*: *C. theobromicola* on *Buxus microphylla* var. *japonica* in the USA (Singh *et al.* 2015).

Colletotrichum yunnanense can be identified with all loci studied. The closest matches with the sequences of all loci of the ex-type strain CBS 132135 in GenBank are all those of this strain itself and of the ITS sequence of strain AS 3.9616, respectively. One further ITS sequence, LN552210, of the endophytic *Colletotrichum* sp. BS4 from leaves of *Buxus sinica* in Guangzhou, China (Wang *et al.* 2016a) was 99 % identical (6 nucleotides difference) to that of strain CBS 132135. The differences in the sequences are likely to be artefacts, as they are in the beginning of the sequence, where there are several Ns. We assume that this strain is also representative of *C. yunnanense*. The authors discovered three new antibacterial azaphilones, colletotrichones A–C (1–3) and one known compound, chermesinone B (4a). This isolate tested positive against environmental and human pathogenic clinical bacterial strains (Wang *et al.* 2016a). The boxwood plant, *Buxus sinica*, is used in traditional Chinese medicine.

***Colletotrichum* sp. strains GZAAS5.09545 and COUFAL7300**

Notes: Based on our multilocus phylogeny, two strains, GZAAS5.09545 from citron leaves (*Citrus medica*, Rutaceae) in Puer City, Yunnan, China (Peng *et al.* 2012) and COUFAL7300 from anthracnose of chayote fruits (*Sechium edule*, Cucurbitaceae) in Antonio Calos, Santa Catarina State, Brazil (Bezerra *et al.* 2016) formed a clade with high bootstrap support. This clade could represent a further unnamed species in the *C. magnum* species complex. Both strains were originally identified as *C. brevisporum*. The latter strain caused lesions on fruits of *Sechium edule* and *Cucumis melo* (Bezerra *et al.* 2016).

DISCUSSION

All three species complexes treated in this study, namely of *C. dracaenophilum*, *C. magnum* and *C. orchidearum*, form

straight conidia, similar to those in the *C. gloeosporioides* species complex (Weir *et al.* 2012). They could have been regarded as *C. gloeosporioides* in the past. This is corroborated by records in Farr & Rossman (2017), and previous identifications linked to sequences deposited in GenBank.

Except for *C. dracaenophilum* that forms larger conidia, the conidial sizes in all three species complexes differ more within the species (provided that more than one strain was available/measured) than between them. Differences were mainly observed among appressoria and ascospore sizes and shapes. But these structures were not always available as they were not formed by all species and cultures. In this study, nine previously described species were assigned to one of the three species complexes treated in this study. Together with the *C. orbiculare* complex, these species representing the three species complexes constitute the most basal lineages of the genus *Colletotrichum* (Marin-Felix *et al.* 2017).

Many species in the three species complexes are possibly host specific — apparently mainly specialised to monocots, while others occur on many hosts. Most of the species were predominately isolated from plants in tropical or subtropical regions of the world, mainly from Asia and Latin America. The rare collections from the temperate climate in Central-Europe are from ornamental plants.

One of the plant families often found as host plants in the three species complexes is the *Orchidaceae*. This family is often colonised by *Colletotrichum* species. Farr & Rossman (2017) list 34 *Colletotrichum* species on *Orchidaceae*. A number of *Colletotrichum* species were described on *Orchidaceae*, including *C. orchidophilum* in the *C. acutatum* complex (Damm *et al.* 2012a), *C. cymbidiicola* and *C. oncidii* in the *C. boninense* complex (Damm *et al.* 2012b) and *C. arxii* in the *C. gigasporum* complex (Liu *et al.* 2014). There are also several species on *Orchidaceae* treated in this study: *C. excelsum-altitudinum* (Tao *et al.* 2013) and *C. coelogyne* and a possible further *Colletotrichum* species on *Paphiopedilum* in Thailand in the *C. dracaenophilum* species complex, and *C. cattleyicola*, *C. orchidearum*, *C. plurivorum*, *C. sojiae* and *C. vittalense* in the *C. orchidearum* species complex.

The *Colletotrichum dracaenophilum* species complex contains a few apparently host-specific species. Based on the few strains available, these species seem to be uncommon. Most of the species are rather distantly related; it is not a species complex in the strict sense. All species form cylindrical conidia with round ends, some with sometimes truncate bases or with a basal scar. In some species, we also observed conidiogenous cells that are extending to form new conidiogenous loci or mucous layers in the upper parts of the conidiogenous cells, similar to the *C. boninense* complex (Damm *et al.* 2012b). A sexual morph is only known in *C. yunnanense*.

The *Colletotrichum magnum* species complex consists of nine closely related species. Except for *C. brevisporum* and an undescribed species from two independent publications, they are known only from one host species each. However, for some of these species only a single strain is available. A sexual morph is only known from *Ga. magna* that is heterothallic; the sexual morph was the result of a laboratory crossing (Jenkins & Winstead 1964). The ascospores are curved and very large, larger than those of any other *Colletotrichum* species treated in this study and probably only exceeded in length by those of *C. gigasporum* (Rakotoniriana *et al.* 2013) and *C. taiwanense* (Sivanesan & Hsieh 1993), the former belonging to the

C. gigasporum complex, while the systematic position of the latter is dubious (Liu *et al.* 2014).

The *Colletotrichum orchidearum* species complex currently consists of eight closely related species, including three species (*C. orchidearum*, *C. plurivorum*, *C. sojiae*) that are very common and occur on many host species and a number of less common species that seem to be either host-specific (*C. cliviicola*, *C. musicola*, *C. cattleyicola*, *C. piperis*) or restricted to a specific country and region (*C. vittalense*). Sexual morphs were observed in cultures of many of the species of the *C. orchidearum* complex; we assume them to be homothallic. However, this needs to be confirmed.

In some species in the *C. orchidearum* complex we observed different strains that were only/predominantly producing the sexual or the asexual morph, respectively. A dominating sexual morph of one *Colletotrichum* species and another *Colletotrichum* species forming only the asexual morph co-occurring on the same host, is one of the reasons for wrong connections of sexual and asexual morphs of *Colletotrichum* species. This was clearly the case with *Ga. glycines* by Lehman & Wolf (1926). A similar scenario is possible with the sexual morphs ascribed to *C. lindemuthianum* that were called *Ga. lindemuthiana* or *Ga. cingulata* f. sp. *phaseoli* (Shear & Wood 1913, Kimati & Galli 1970). It is also possible that the asexual morphs were just assumed to be *C. lindemuthianum* based on the host plants (common beans) or *C. gloeosporioides* based on conidial morphology, respectively. Epitypifications of the respective species would clarify this situation.

Nothing is known about the infection strategies of the individual species in the three species complexes treated here, and little is known about their distribution, host specificity and their impact on the host plants. The high number of sequences from unidentified or basically only tentatively identified strains in GenBank suggests a larger distribution and probably more species in these complexes than included in the present study.

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