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Colletotrichum: complex species or species complexes?

Ulrike Damm, Paul F. Cannon and Pedro W. Crous, editors

CBS-KNAW Fungal Biodiversity Centre,
Utrecht, The Netherlands
An institute of the Royal Netherlands Academy of Arts and Sciences

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Cover: Top from left to right: Conidia of *Colletotrichum beeveri* on SNA, anthracnose of strawberry fruit caused by *C. nymphaeae*, conidia of *C. gloeosporioides* on *Anthriscus* stem. Bottom from left to right: culture of *C. alatae* on PDA, conidia of *C. fioriniae* on *Anthriscus* stem, conidioma of *C. novae-zelandiae* on *Anthriscus* stem.

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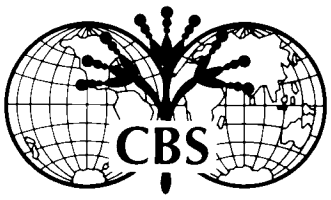

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DEDICATION

This volume is dedicated to Brian C. Sutton, fungal systematist *non plus ultra* and Chief Mycologist at the International Mycological Institute (IMI) until his retirement in 1995.

After arrival at IMI straight from university in 1959, Brian was faced with the choice of specialising in rusts or coelomycetes (fungi forming conidia within fruit-bodies). His courageous decision to work with the then almost unknown coelomycete group paved the way for a long and diverse career. Many of the fungi he worked with are minute and require patient and meticulous analytical microscopy. Brian's ability to see almost invisible details of conidiomatal anatomy, conidiogenesis and conidium morphology, and to translate these observations into detailed descriptions and beautiful line drawings, made him one of the most celebrated fungal systematists of the pre-molecular era. He has a voluminous publication record, and his 1980 monograph "*The Coelomycetes – Fungi imperfecti with pycnidia, acervuli and stromata"* is still the basic standard morphological reference work for this group of fungi.

The diversity of his output can be judged by the list of 990 fungal names he authored or co-authored. Some of these were imaginatively named, including the genera *Satchmopsis* (in honour of his jazz hero Louis Armstrong) and *Omega* (the final taxon published in *Transactions of the British Mycological Society*, of which he was Senior Editor between 1977 and 1988). Brian was always generous with his time in support of fellow mycologists and students from all over the globe, who sent him numerous collections of "troublesome" coelomycetes. On many occasions, these initial requests for help led on to mentoring of the developing scientific careers of his correspondents, and to continuing collaborations in fungal systematics.

Brian Sutton working in his office (1992), in the final days of the International Mycological Institute at Kew (photo by David Minter).

Brian's involvement with *Colletotrichum* began with a paper on *C. dematium* and *C. trichellum* in 1962, and developed as the subject for his PhD thesis which focused on the morphology and ontogeny of species associated with grasses. His were the first scientific contributions that established the importance of appressorium morphology in *Colletotrichum* systematics. After studies of conidial fungi in almost all the branches and bywaters of the *Ascomycota*, his second major contribution was to provide a user-friendly guide to *Colletotrichum* in the 1980 *Coelomycetes* monograph, which built on von Arx's work to provide a framework for morphology-based identification that still has value today. This was followed by a further systematic account in 1992, which increased the number of accepted species to 39.

Brian retired shortly before the fungal molecular phylogenetic revolution gained pace. Although the classification he developed in *The Coelomycetes* was unavoidably artificial, it continues to play a major role in ground-truthing of the results of new phylogenetic research, through integration with recent studies that add molecular data to Brian's original morphological observations.

Other than his love for fungi, Brian's love for jazz music is well known among his mycological colleagues. Our decision to dedicate this volume to him comes with the expectation that he will be paging through it with something soothing playing in the background. Although the backbone of *Colletotrichum* systematics remains unaltered more than thirty years after *The Coelomycetes* was published, we hope that recognition of the cryptic lineages within the species complexes included in this volume goes some way towards explanation of their extraordinary variation.

"And it feels like rain "ing species" – Buddy Guy

The Editors September 2012

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The *Colletotrichum boninense* species complex

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Abstract: Although only recently described, *Colletotrichum boninense* is well established in literature as an anthracnose pathogen or endophyte of a diverse range of host plants worldwide. It is especially prominent on members of *Amaryllidaceae*, *Orchidaceae*, *Proteaceae* and *Solanaceae*. Reports from literature and preliminary studies using ITS sequence data indicated that *C. boninense* represents a species complex. A multilocus molecular phylogenetic analysis (ITS, ACT, TUB2, CHS-1, GAPDH, HIS3, CAL) of 86 strains previously identified as *C. boninense* and other related strains revealed 18 clades. These clades are recognised here as separate species, including *C. boninense s. str.*, *C. hippeastri*, *C. karstii* and 12 previously undescribed species, *C. annellatum*, *C. beeveri*, *C. brassicicola*, *C. brasiliense*, *C. colombiense*, *C. constrictum*, *C. cymbidiicola*, *C. dacrycarpi*, *C. novae-zelandiae*, *C. oncidii*, *C. parsonsiae* and *C. torulosum.* Seven of the new species are only known from New Zealand, perhaps reflecting a sampling bias. The new combination *C. phyllanthi* was made, and *C. dracaenae* Petch was epitypified and the name replaced with *C. petchii*. Typical for species of the *C. boninense* species complex are the conidiogenous cells with rather prominent periclinal thickening that also sometimes extend to form a new conidiogenous locus or annellations as well as conidia that have a prominent basal scar. Many species in the *C. boninense* complex form teleomorphs in culture.

Key words: anthracnose, *Ascomycota, Colletotrichum boninense*, *Glomerella*, phylogeny, systematics.
Taxonomic novelties: New combination - *Colletotrichum phyllanthi* (H. Surendranath Pai) Damm, P.F. Cannon & Crous. **Name replacement -** *C. petchii* Damm, P.F. Cannon & Crous. **New species -** *C. annellatum* Damm, P.F. Cannon & Crous, *C. beeveri* Damm, P.F. Cannon, Crous, P.R. Johnst. & B. Weir, *C. brassicicola* Damm, P.F. Cannon & Crous, *C. brasiliense* Damm, P.F. Cannon, Crous & Massola, *C. colombiense* Damm, P.F. Cannon, Crous, *C. constrictum* Damm, P.F. Cannon, Crous, P.R. Johnst. & B. Weir, *C. cymbidiicola* Damm, P.F. Cannon, Crous, P.R. Johnst. & B. Weir, *C. dacrycarpi* Damm, P.F. Cannon, Crous, P.R. Johnst. & B. Weir, *C. novae-zelandiae* Damm, P.F. Cannon, Crous, P.R. Johnst. & B. Weir, *C. oncidii* Damm, P.F. Cannon & Crous, *C. parsonsiae* Damm, P.F. Cannon, Crous, P.R. Johnst. & B. Weir, *C. torulosum* Damm, P.F. Cannon, Crous, P.R. Johnst. & B. Weir. **Typifications: Epitypifications** - *C. dracaenae* Petch.

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INTRODUCTION

Colletotrichum boninense was first described from *Crinum asiaticum* var. *sinicum* (*Amaryllidaceae*) collected in the Bonin Islands, Japan (Moriwaki *et al.* 2003). According to these authors, the species was associated with a variety of host plants in Japan, including *Clivia miniata* (*Amaryllidaceae*), *Cucumis melo* (*Cucurbitaceae*), *Cattleya* sp., *Cymbidium* sp. and *Dendrobium kingianum* (*Orchidaceae*), *Passiflora edulis* (*Passifloraceae*) and *Prunus mume* (*Rosaceae*). Since 2003, *C. boninense* (in its wide sense prior to our research) has frequently been identified as a pathogen causing fruit and leaf anthracnose, as well as an endophyte of a range of host plants worldwide, especially belonging to *Amaryllidaceae*, *Orchidaceae*, *Proteaceae* and *Solanaceae*. For example, *C. boninense* was found to be associated with diseases of *Leucospermum* and *Protea cynaroides* in Australia and Zimbabwe and with *Eucalyptus* in South Africa (Lubbe *et al.* 2004). In pathogenicity studies it was shown to infect *Protea* leaves and stems (Lubbe *et al.* 2006). Farr *et al.* (2006) reported *C. boninense* on *Dracaena* and *Pachira* in China, *Passiflora* in New Zealand and *Hippeastrum* in Brazil and the Netherlands. According to Johnston & Jones (1997) and Johnston *et al.* (2005), *C. boninense* (= *C. gloeosporioides* groups E–I in Johnston & Jones 1997) occurs on a range of hosts including *Capsicum*, *Citrus*, *Cucurbita* and *Solanum* species in New Zealand. *Colletotrichum boninense* was reported as the cause of anthracnose of pepper (*Capsicum annuum*) in Brazil (Tozze *et al.* 2009), of passion fruit (*Passiflora*) in Florida (Tarnowski & Ploetz 2010) and Brazil (Tozze *et al.* 2010) and of *Crinum asiaticum* in China (Yang *et al.* 2009). Lee *et al.* (2005a, b) observed leaf anthracnose on Japanese spindle tree (*Euonymus japonica*) in Korea and demonstrated the pathogenicity of *C. boninense*. Nguyen *et al.* (2009) reported *C. boninense* as a pathogen of berries and twigs of *Coffea* in Vietnam. Recently, *C. boninense* was identified as one of the causal agents of anthracnose in avocado (*Persea americana*) in Mexico (Silva-Rojas & Ávila-Quezada 2011).

Lu *et al.* (2004) detected probable *C. boninense* isolates as endophytes in leaves of several tree species in the Iwokrama Forest Reserve in Guyana. Other reports of *C. boninense* as endophytes include Pileggi *et al.* (2009), who isolated it from leaves of the medicinal plant *Maytenus ilicifolia* in Brazil. Joshee *et al.* (2009) studied foliar endophytes of *Podocarpaceae* and *Myrtaceae* trees in New Zealand and identified several of them as belonging to the *C. boninense* group. Several other isolates causing anthracnose on tamarillo, *Passiflora* and mango from Colombia (Afanador-Kafuri *et al.* 2003) and endophytes in coffee plants from Colombia and Hawaii (Vega *et al.* 2010) belonging to the *C. boninense* species

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

				GenBank No.						
Species	**Accession No.[1]**	**Host/Substrate**	**Country**	**ITS**	**GAPDH**	**CHS-1**	**HIS3**	**ACT**	**TUB2**	**CAL**
C. annellatum	CBS 129826, CH1*	*Hevea brasiliensis*, leaf	Colombia	JQ005222	JQ005309	JQ005396	JQ005483	JQ005570	JQ005656	JQ005743
C. beeveri	CBS 128527, ICMP 18594*	*Brachyglottis repanda*	New Zealand	JQ005171	JQ005258	JQ005345	JQ005432	JQ005519	JQ005605	JQ005692
C. boninense	CBS 128547, ICMP 10338	*Camellia* sp.	New Zealand	JQ005159	JQ005246	JQ005333	JQ005420	JQ005507	JQ005593	JQ005680
	CBS 123756, MAFF 306094	*Crinum asiaticum* var. *sinicum*	Japan	JQ005154	JQ005241	JQ005328	JQ005415	JQ005502	JQ005589	JQ005675
	CBS 123755, MAFF 305972*	*Crinum asiaticum* var. *sinicum*	Japan	JQ005153	JQ005240	JQ005327	JQ005414	JQ005501	JQ005588	JQ005674
	MAFF 306162, ICMP 18596	*Crinum asiaticum* var. *sinicum*, leaf	Japan	JQ005155	JQ005242	JQ005329	JQ005416	JQ005503	-	JQ005676
	CBS 128526, ICMP 18591	*Dacrycarpus dacrydioides*, leaf endophyte	New Zealand	JQ005162	JQ005249	JQ005336	JQ005423	JQ005510	JQ005596	JQ005683
	CBS 112115, STE-U 2966	*Leucospermum* sp.	Australia	JQ005160	JQ005247	JQ005334	JQ005421	JQ005508	JQ005594	JQ005681
	CBS 129831, STE-U 2965	*Leucospermum* sp.	Australia	JQ005161	JQ005248	JQ005335	JQ005422	JQ005509	JQ005595	JQ005682
	CBS 128549, ICMP 15444	*Solanum betaceum*, flowers	New Zealand	JQ005156	JQ005243	JQ005330	JQ005417	JQ005504	JQ005590	JQ005677
	CBS 128506, ICMP 12950	*Solanum lycopersicum*, fruit rot	New Zealand	JQ005157	JQ005244	JQ005331	JQ005418	JQ005505	JQ005591	JQ005678
	CBS 128546, ICMP 18595	*Tecomanthe speciosa*	New Zealand	JQ005158	JQ005245	JQ005332	JQ005419	JQ005506	JQ005592	JQ005679
C. brasiliense	CBS 128501, ICMP 18607, PAS12*	*Passiflora edulis*, fruit anthracnose	Brazil	JQ005235	JQ005322	JQ005409	JQ005496	JQ005583	JQ005669	JQ005756
	CBS 128528, ICMP 18606, PAS10	*Passiflora edulis*, fruit	Brazil	JQ005234	JQ005321	JQ005408	JQ005495	JQ005582	JQ005668	JQ005755
C. brassicicola	CBS 101059, LYN 16331*	*Brassica oleracea* var. *gemmifera*, leaf spot	New Zealand	JQ005172	JQ005259	JQ005346	JQ005433	JQ005520	JQ005606	JQ005693
C. colombiense	CBS 129817, G1	*Passiflora edulis*, leaf	Colombia	JQ005173	JQ005260	JQ005347	JQ005434	JQ005521	JQ005607	JQ005694
	CBS 129818, G2*	*Passiflora edulis*, leaf	Colombia	JQ005174	JQ005261	JQ005348	JQ005435	JQ005522	JQ005608	JQ005695
C. constrictum	CBS 128504, ICMP 12941*	*Citrus limon*, fruit rot	New Zealand	JQ005238	JQ005325	JQ005412	JQ005499	JQ005586	JQ005672	JQ005759
	CBS 128503, ICMP 12936	*Solanum betaceum*, fruit rot	New Zealand	JQ005237	JQ005324	JQ005411	JQ005498	JQ005585	JQ005671	JQ005758
C. cymbidiicola	CBS 123757, MAFF 306100	*Cymbidium* sp.	Japan	JQ005168	JQ005255	JQ005342	JQ005429	JQ005516	JQ005602	JQ005689
	IMI 347923*	*Cymbidium* sp., leaf lesion	Australia	JQ005166	JQ005253	JQ005340	JQ005427	JQ005514	JQ005600	JQ005687
	CBS 128543, ICMP 18584	*Cymbidium* sp., leaf spot	New Zealand	JQ005167	JQ005254	JQ005341	JQ005428	JQ005515	JQ005601	JQ005688
C. dacrycarpi	CBS 130241, ICMP 19107*	*Dacrycarpus dacrydioides*, leaf endophyte	New Zealand	JQ005236	JQ005323	JQ005410	JQ005497	JQ005584	JQ005670	JQ005757
C. gloeosporioides	CBS 112999, STE-U 4295*	*Citrus sinensis*	Italy	JQ005152	JQ005239	JQ005326	JQ005413	JQ005500	JQ005587	JQ005673
C. hippeastri	CBS 241.78, IMI 304052	*Hippeastrum* sp.	Netherlands	JQ005232	JQ005319	JQ005406	JQ005493	JQ005580	JQ005666	JQ005753
	CBS 125377, CSSK4	*Hippeastrum vittatum*	China	JQ005230	JQ005317	JQ005404	JQ005491	JQ005578	JQ005664	JQ005751
	CBS 125376, CSSG1*	*Hippeastrum vittatum*, leaf	China	JQ005231	JQ005318	JQ005405	JQ005492	JQ005579	JQ005665	JQ005752
C. karstii	CBS 128500, ICMP 18585	*Annona cherimola*, fruit	New Zealand	JQ005202	JQ005289	JQ005376	JQ005463	JQ005550	JQ005636	JQ005723
	CBS 128550, ICMP 17896	*Annona cherimola*, fruit anthracnose	Mexico	JQ005219	JQ005306	JQ005393	JQ005480	JQ005567	JQ005653	JQ005740
	CBS 129927	*Anthurium* sp.	Thailand	JQ005206	JQ005293	JQ005380	JQ005467	JQ005554	JQ005640	JQ005727
	CBS 861.72	*Bombax aquaticum*	Brazil	JQ005184	JQ005271	JQ005358	JQ005445	JQ005532	JQ005618	JQ005705
	CBS 128545, ICMP 18587	*Capsicum annuum*	New Zealand	JQ005207	JQ005294	JQ005381	JQ005468	JQ005555	JQ005641	JQ005728

Table 1. (Continued).

Species	Accession No.[1]	Host/Substrate	Country	GenBank No.						
				ITS	GAPDH	CHS-1	HIS3	ACT	TUB2	CAL
C. karstii	CBS 106.91	*Carica papaya*, fruit spots	Brazil	JQ005220	JQ005307	JQ005394	JQ005481	JQ005568	JQ005654	JQ005741
	CBS 128524, ICMP 18588	*Citrullus lanatus*, rotten fruit	New Zealand	JQ005195	JQ005282	JQ005369	JQ005456	JQ005543	JQ005629	JQ005716
	CBS 126532, STE-U 6830	*Citrus* sp.	South Africa	JQ005209	JQ005296	JQ005383	JQ005470	JQ005557	JQ005643	JQ005730
	CBS 128551, ICMP 12065	*Citrus* sp.	New Zealand	JQ005208	JQ005295	JQ005382	JQ005469	JQ005556	JQ005642	JQ005729
	MAFF 306204, ICMP 18597	*Clivia miniata*, leaf	Japan	JQ005196	JQ005283	JQ005370	JQ005457	JQ005544	JQ005630	JQ005717
	CBS 125468	*Coffea* sp., berry tissue	Vietman	JQ005197	JQ005284	JQ005371	JQ005458	JQ005545	JQ005631	JQ005718
	MAFF 305998, ICMP 18599	*Cucumis melo*	Japan	JQ005191	JQ005278	JQ005365	JQ005452	JQ005539	JQ005625	JQ005712
	CBS 127597, BRIP 29085a	*Diospyros australis*, calyx necrosis	Australia	JQ005204	JQ005291	JQ005378	JQ005465	JQ005552	JQ005638	JQ005725
	CBS 110779	*Eucalyptus grandis*	South Africa	JQ005198	JQ005285	JQ005372	JQ005459	JQ005546	JQ005632	JQ005719
	CBS 127535, STE-U 193	*Eucalyptus grandis*	South Africa	JQ005199	JQ005286	JQ005373	JQ005460	JQ005547	JQ005633	JQ005720
	CBS 129830, STE-U 195B	*Eucalyptus grandis*	South Africa	JQ005200	JQ005287	JQ005374	JQ005461	JQ005548	JQ005634	JQ005721
	CBS 127536, STE-U 196	*Eucalyptus grandis*	South Africa	JQ005201	JQ005288	JQ005375	JQ005462	JQ005549	JQ005635	JQ005722
	CBS 127552	*Eugenia uniflora*	Brazil	JQ005217	JQ005304	JQ005391	JQ005478	JQ005565	JQ005651	JQ005738
	CBS 129829	*Gossypium hirsutum*	Germany	JQ005189	JQ005276	JQ005363	JQ005450	JQ005537	JQ005623	JQ005710
	CBS 130235	*Gossypium hirsutum*	Germany	JQ005190	JQ005277	JQ005364	JQ005451	JQ005538	JQ005624	JQ005711
	CBS 111860, STE-U 2193	*Leucospermum* sp.	USA, Hawaii	JQ005211	JQ005298	JQ005385	JQ005472	JQ005559	JQ005645	JQ005732
	CBS 111998, STE-U 2999	*Leucospermum* sp.	Australia	JQ005212	JQ005299	JQ005386	JQ005473	JQ005560	JQ005646	JQ005733
	CBS 112762, STE-U 3000	*Leucospermum* sp.	Australia	JQ005213	JQ005300	JQ005387	JQ005474	JQ005561	JQ005647	JQ005734
	CBS 486.97	*Lupinus albus*, cv. Lu Blanc	Germany	JQ005182	JQ005269	JQ005356	JQ005443	JQ005530	JQ005616	JQ005703
	CBS 113087, STE-U 5288	*Malus* sp.	USA	JQ005181	JQ005268	JQ005355	JQ005442	JQ005529	JQ005615	JQ005702
	CBS 127596, BRIP 28443a	*Mangifera indica*, stem, endophyte	Australia	JQ005203	JQ005290	JQ005377	JQ005464	JQ005551	JQ005637	JQ005724
	CBS 129832	*Musa* sp.	Mexico	JQ005177	JQ005264	JQ005351	JQ005438	JQ005525	JQ005611	JQ005698
	CBS 129833	*Musa* sp.	Mexico	JQ005175	JQ005262	JQ005349	JQ005436	JQ005523	JQ005609	JQ005696
	CBS 129834	*Musa* sp.	Mexico	JQ005176	JQ005263	JQ005350	JQ005437	JQ005524	JQ005610	JQ005697
	CBS 129824, B1	*Musa* AAA, fruit	Colombia	JQ005215	JQ005302	JQ005389	JQ005476	JQ005563	JQ005649	JQ005736
	CBS 127595	*Musa banksii*	Australia	JQ005178	JQ005265	JQ005352	JQ005439	JQ005526	JQ005612	JQ005699
	CBS 118401	*Pachira* sp., living leaves	China	JQ005192	JQ005279	JQ005366	JQ005453	JQ005540	JQ005626	JQ005713
	MAFF 305973, ICMP 18598	*Passiflora edulis*	Japan	JQ005194	JQ005281	JQ005368	JQ005455	JQ005542	JQ005628	JQ005715
	CBS 129822, G7	*Passiflora edulis*, leaf	Colombia	JQ005218	JQ005305	JQ005392	JQ005479	JQ005566	JQ005652	JQ005739
	CBS 112982, STE-U 2289	*Protea cynaroides*	Zimbabwe	JQ005183	JQ005270	JQ005357	JQ005444	JQ005531	JQ005617	JQ005704
	CBS 115535, STE-U 5210	*Protea obtusifolia*	Portugal, Madeira	JQ005214	JQ005301	JQ005388	JQ005475	JQ005562	JQ005648	JQ005735

Table 1. (Continued).

Species	Accession No.[1]	Host/Substrate	Country	GenBank No.						
				ITS	GAPDH	CHS-1	HIS3	ACT	TUB2	CAL
C. karstii	CBS 124969, LCM 232	*Quercus salicifolia*, leaf endophyte	Panama	JQ005179	JQ005266	JQ005353	JQ005440	JQ005527	JQ005613	JQ005700
	CBS 127591	*Sapium integerrimium*	Australia	JQ005186	JQ005273	JQ005360	JQ005447	JQ005534	JQ005620	JQ005707
	CBS 129815, T.A.7	*Solanum betaceum*, fruit	Colombia	JQ005187	JQ005274	JQ005361	JQ005448	JQ005535	JQ005621	JQ005708
	CBS 128548, ICMP 18589	*Solanum lycopersicum*	New Zealand	JQ005205	JQ005292	JQ005379	JQ005466	JQ005553	JQ005639	JQ005726
	CBS 508.97, LARS 168	*Stylosanthes sympodialis*	Australia	JQ005193	JQ005280	JQ005367	JQ005454	JQ005541	JQ005627	JQ005714
	CBS 128552, ICMP 18276	*Synsepalum dulcificum*, leaves	Taiwan	JQ005188	JQ005275	JQ005362	JQ005449	JQ005536	JQ005622	JQ005709
	CBS 124951	*Theobroma cacao*, leaf endophyte	Panama	JQ005180	JQ005267	JQ005354	JQ005441	JQ005528	JQ005614	JQ005701
	CBS 128540, STE-U 698	*Triticum* sp.	South Africa	JQ005210	JQ005297	JQ005384	JQ005471	JQ005558	JQ005644	JQ005731
	CBS 124956	*Zamia obliqua*, leaf endophyte	Panama	JQ005216	JQ005303	JQ005390	JQ005477	JQ005564	JQ005650	JQ005737
	CBS 124956	*Zamia obliqua*, leaf endophyte	Panama	JQ005216	JQ005303	JQ005390	JQ005477	JQ005564	JQ005650	JQ005737
	CBS 125388	*Zamia obliqua*, leaf endophyte	Panama	JQ005185	JQ005272	JQ005359	JQ005446	JQ005533	JQ005619	JQ005706
C. novae-zelandiae	CBS 128505, ICMP 12944*	*Capsicum annuum*, fruit rot	New Zealand	JQ005228	JQ005315	JQ005402	JQ005489	JQ005576	JQ005662	JQ005749
	CBS 130240, ICMP 12064	*Citrus* sp. (grapefruit)	New Zealand	JQ005229	JQ005316	JQ005403	JQ005490	JQ005577	JQ005663	JQ005750
C. oncidii	CBS 129828*	*Oncidium* sp., leaf	Germany	JQ005169	JQ005256	JQ005343	JQ005430	JQ005517	JQ005603	JQ005690
	CBS 130242	*Oncidium* sp., leaf	Germany	JQ005170	JQ005257	JQ005344	JQ005431	JQ005518	JQ005604	JQ005691
C. parsonsiae	CBS 128525, ICMP 18590*	*Parsonsia capsularis*, leaf endophyte	New Zealand	JQ005233	JQ005320	JQ005407	JQ005494	JQ005581	JQ005667	JQ005754
C. petchii	CBS 378.94*	*Dracaena marginata*, spotted leaves	Italy	JQ005223	JQ005310	JQ005397	JQ005484	JQ005571	JQ005657	JQ005744
	CBS 379.94	*Dracaena marginata*, spotted leaves	Italy	JQ005224	JQ005311	JQ005398	JQ005485	JQ005572	JQ005658	JQ005745
	CBS 118193, AR 3658	*Dracaena sanderana*, living leaves	China	JQ005227	JQ005314	JQ005401	JQ005488	JQ005575	JQ005661	JQ005748
	CBS 118774, AR 3751	*Dracaena sanderana*, living stems	China	JQ005225	JQ005312	JQ005399	JQ005486	JQ005573	JQ005659	JQ005746
	CBS 125957, NB 145	*Dracaena*, leaf spots	Netherlands	JQ005226	JQ005313	JQ005400	JQ005487	JQ005574	JQ005660	JQ005747
C. phyllanthi	CBS 175.67, MACS 271*	*Phyllanthus acidus*, anthracnose	India	JQ005221	JQ005308	JQ005395	JQ005482	JQ005569	JQ005655	JQ005742
C. torulosum	CBS 128544, ICMP 18586*	*Solanum melongena*	New Zealand	JQ005164	JQ005251	JQ005338	JQ005425	JQ005512	JQ005598	JQ005685
	CBS 102667	*Passiflora edulis*, leaf blotch	New Zealand	JQ005165	JQ005252	JQ005339	JQ005426	JQ005513	JQ005599	JQ005686
***Colletotrichum* sp.**	CBS 123921, MAFF 238642	*Dendrobium kingianum*	Japan	JQ005163	JQ005250	JQ005337	JQ005424	JQ005511	JQ005597	JQ005684

[1]CBS: Culture collection of the Centraalbureau voor Schimmelcultures, Fungal Biodiversity Centre, Utrecht, The Netherlands; IMI: Culture collection of CABI Europe UK Centre, Egham, UK; MAFF: MAFF Genebank Project, Ministry of Agriculture, Forestry and Fisheries, Tsukuba, Japan; BRIP: Plant Pathology Herbarium, Department of Employment, Economic, Development and Innovation, Queensland, Australia; ICMP: International Collection of Microorganisms from Plants, Auckland, New Zealand; STE-U: Culture collection of the Department of Plant Pathology, University of Stellenbosch, South Africa; MACS: MACS Collection of Microorganisms, Pune, India; * ex-holotype or ex-epitype cultures.

complex were detected in blastn searches in GenBank. Yang *et al.* (2011) recently reported *C. boninense* from *Pleione bulbocodioides* and *Oncidium flexuosum* (*Orchidaceae*) in China and described a related species, *C. karstii* that occurs on several orchids in China.

Conidia of *C. boninense s. lat.* are similar to those of *C. gloeosporioides*, differing only slightly in length/width ratio and in the presence of a prominent scar at the base of the conidium (Moriwaki *et al.* 2003). Isolates of *C. boninense* have often been identified as *C. gloeosporioides* in the past (Moriwaki *et al.* 2002, 2003, Johnston *et al.* 2005). Von Arx (1957) listed approximately 600 synonyms of *C. gloeosporioides* and nine *formae speciales*, and it is likely that some of these refer to *C. boninense*.

The ITS1 phylogeny in the paper of Moriwaki *et al.* (2003) shows considerable infraspecific variation. Some of the strains accepted by these authors as *C. boninense* are referable to the segregate species recognised in this paper. Lubbe *et al.* (2004) recognised two subgroups but considered both as *C. boninense*. Grouping within *C. boninense* was also detected by phylogenies of strains from New Zealand (Johnston & Jones 1997, Johnston *et al.* 2005) showing several clades, with some developing sexual morphs (see Hyde *et al.* 2009). These data indicate that *C. boninense* represents a species complex. In this paper, we characterise species within the *C. boninense* species complex morphologically and by means of multi-gene analysis.

MATERIALS AND METHODS

Isolates

Isolates comprised those previously identified as *C. boninense* as well as other related cultures from the CBS culture collection. The type specimens of the species studied are located in the fungaria (dried fungus collections) of the Centraalbureau voor Schimmelcultures (CBS), Utrecht, The Netherlands, the Botanische Staatssammlung München (M), Germany and the Royal Botanic Gardens, Kew (K(M)), United Kingdom which now incorporates the CABI dried collection (IMI). The culture dried down to serve as epitype specimen of *C. petchii,* was selected from the culture collection of the CBS. All descriptions are based on either the ex-holotype or ex-epitype culture. Features of other isolates are added if they deviated from the ex-holotype and ex-epitype isolates. Subcultures of the types and epitypes, as well as all other isolates used for morphological and sequence analyses, are maintained in the culture collections of CBS, IMI and/or ICMP (International Collection of Microorganisms from Plants, Landcare Research, Auckland, New Zealand), and their data are presented in Table 1.

Morphological analysis

To enhance sporulation, 5-mm-diam plugs from the margin of actively growing cultures were transfered to the centre of 9-cm-diam Petri dishes containing synthetic nutrient-poor agar medium (SNA; Nirenberg 1976) amended with autoclaved filter paper and double-autoclaved stems of *Anthriscus sylvestris* placed onto the agar surface. The strains were also studied after growth on OA (oatmeal agar, Crous *et al.* 2009) or 2 % PDA (Difco potato-dextrose agar). 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 methods described by Damm *et al.* (2007). Appressoria on hyphae were observed on the reverse side of colonies grown on SNA plates. 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 incubated at 20 °C were noted 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 gene with the two flanking internal transcribed spacers (ITS), a 200-bp intron of the glyceraldehyde-3-phosphate dehydrogenase (GAPDH), and partial sequences of the actin (ACT), chitin synthase 1 (CHS-1), beta-tubulin (TUB2), histone3 (HIS3) and calmodulin (CAL) genes were amplified and sequenced using the primer pairs ITS-1F (Gardes & Bruns 1993) + ITS-4 (White *et al.* 1990) or V9G (de Hoog & Gerrits van den Ende 1998) + ITS-4, GDF1 + GDR1 (Guerber *et al.* 2003), ACT-512F + ACT-783R (Carbone & Kohn 1999), CHS-354R + CHS-79F (Carbone & Kohn 1999), BT2Fd + BT4R (Woudenberg *et al.* 2009) or T1 (O'Donnell & Cigelnik 1997) + Bt-2b (Glass & Donaldson 1995), CYLH3F + CYLH3R (Crous *et al.* 2004b) and CAL 228F + CAL 737R (Carbone & Kohn 1999), 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, ACT, CHS-1, TUB2, HIS3 and CAL PCR mixture contained 1 µL 20x diluted genomic DNA, 0.2 µM of each primer, 1x PCR buffer (Bioline, Luckenwalde, Germany), 2 mM $MgCl_2$, 20 µM of each dNTP, 0.7 µL DMSO and 0.25 U Taq DNA polymerase (Bioline). Conditions for amplification were 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. The ITS PCR was performed as described by Woudenberg *et al.* (2009). The DNA sequences obtained from forward and reverse primers were used to obtain consensus sequences using Bionumerics v. 4.60 (Applied Maths, St-Martens-Latem, Belgium), which were added to the outgroup (*C. gloeosporioides* CBS 112999) and the alignment assembled and manually adjusted using Sequence Alignment Editor v. 2.0a11 (Rambaut 2002).

To determine whether the seven sequence datasets were congruent and combinable, tree topologies of 70 % reciprocal Neighbour-Joining bootstrap with Maximum Likelihood distances (10000 replicates) with substitution models determined separately for each partition using MrModeltest v. 2.3 (Nylander 2004) were compared visually (Mason-Gamer & Kellogg 1996). A maximum parsimony analysis was performed on the multilocus alignment (ITS, ACT, TUB2, CHS-1, GAPDH, HIS3, CAL) with PAUP (Phylogenetic Analysis Using Parsimony) v. 4.0b10 (Swofford, 2000) 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. The robustness of the trees obtained was evaluated by 500 bootstrap replications with two random sequence additions (Hillis & Bull 1993). Tree length, consistency index (CI), retention index (RI), rescaled consistency index (RC) and homoplasy index (HI) were calculated for the resulting tree. A Markov Chain Monte Carlo (MCMC) algorithm was used to generate phylogenetic trees with Bayesian probabilities using MrBayes v. 3.1.1 (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 one million generations and sampled every 100 generations. The likelihood score of the two runs were 2 730 and 2 170 and therefore, the first 2 450 (the average of both) trees were discarded as the burn-in phase of the analysis and posterior probabilities determined from the remaining trees. Sequences derived in this study were lodged at GenBank, the alignment in TreeBASE (www.treebase.org), and taxonomic novelties in MycoBank (Crous *et al.* 2004a).

RESULTS

Phylogeny

The seven sequence datasets did not show any conflicts in tree topology for the 70 % reciprocal bootstrap trees, which allowed us to combine them. In the multigene analyses (gene boundaries of ITS: 1–561, GAPDH: 572–864, CHS-1: 875–1154, HIS3: 1164–1562, ACT: 1573–1851, TUB2: 1862–2363, CAL: 2374–2823) of 87 isolates of *C. boninense* and related *Colletotrichum* species including the outgroup, 2 823 characters including the alignment gaps were processed, of which 572 characters were parsimony-informative, 247 parsimony-uninformative and 2004 constant. After a heuristic search using PAUP, 958 most parsimonious trees were retained (length = 1423 steps, CI = 0.740, RI = 0.927, RC = 0.686, HI = 0.260) of which one is shown in Fig. 1. The topology of the 958 trees was similar, which was verified for a large selection of trees. They differed in the position of taxa within the subclades and in the position of strain CBS 130241. For Bayesian analysis, a HKY+G model was selected for ACT and CAL, SYM+I+G for ITS, K80+I+G for CHS-1, GTR+I+G for HIS3, and HKY+I for GAPDH and TUB2, and incorporated in the analysis. The consensus tree obtained from Bayesian analyses confirmed the tree topology obtained with parsimony as well as the bootstrap support (Fig. 1).

The analyses resulted in the detection of 18 clades, which we accept as representing different *Colletotrichum* species. More than half of all strains included cluster in the first clade (*C. karstii*) with a bootstrap support of 96 % and a Bayesian posterior probability value of 1.00. Two single strain clades, representing *C. phyllanthi* and *C. annellatum,* group with this big clade with a bootstrap support/Bayesian posterior probability value of 96/0.99 and 100/1.00, respectively. The *C. petchii* clade is well supported (100/1.00) and forms a sister clade to the first three species. The clade representing *C. novae-zelandiae* consists of two strains on a long branch (100/1.00). In contrast, the following five clades are short-branched, namely *C. boninense s. str.* (95/1.00), *C. torulosum* (100/1.00), *C. cymbidiicola* (96/1.00), *C. oncidii* (100/1.00) and a clade containing an unnamed single strain (CBS 123921). These five species form a sister clade (100/1.00) to another well supported (100/1.00) clade formed by two single strain clades, *C. beeveri* and *C. brassicicola*, and the *C. colombiense* clade (100/1.00) containing two strains. The clades representing *C. hippeastri* and *C. brasiliense* consist of three and two strains respectively, and are well supported (100/1.00). They group (100/1.00) with a single strain clade (*C. parsonsiae*). The *C. constrictum* clade (100/1.00) containing two strains and the single strain clade representing *C. dacrycarpi* are on very long branches and group with a Bayesian posterior probability value of 1.00.

The individual alignments and trees of the seven single genes were compared as well with respect to their performance in species recognition. With ITS and CHS-1 only 7 and 9 species can be recognised, with TUB2 some species close to *C. boninense* can not be separated, while with HIS3 and CAL some species only differ in one or two bp and form no or only short-branched clades. With GAPDH all clades are recognised, but some are also short-branched, especially the single strain clades *C. beeveri* and *C. brassicicola* that are well differentiated with almost all other genes except for ITS. With ACT the intraspecific variability is very high in some species, which could lead to misidentifications.

Taxonomy

The 86 isolates studied (Table 1) are assigned to 18 species within the *Colletotrichum boninense* complex based on DNA sequence data and morphology, including 12 species that are new to science. Ten species form teleomorph stages *in vitro*, four species have known anamorphs described in *Colletotrichum*, while one species, *G. phyllanthi*, has a known teleomorph and is shown here as belonging to the *Colletotrichum boninense* species complex. All species studied in culture are characterised below.

Species of *Colletotrichum* represent anamorphic stages of *Glomerella*. Anamorph and telemorph names of fungi will have equal status under the *International Code of Nomenclature for algae, fungi, and plants* (formerly the *International Code for Botanical Nomenclature*), with the deletion of Art. 59, which takes effect on 1 Jan. 2013. The decision was qualified by a stipulation that uptake of names of anamorphic genera that predate well-known competing teleomorphic names should be ratified by a committee of the International Commission for the Taxonomy of Fungi. The name *Colletotrichum* (Corda 1831) predates *Glomerella* (Spauld. & H. Schrenk 1903) and is more commonly used. Consequently we name the new holomorphs as species of *Colletotrichum* and we do not name the new sexual morphs separately. Furthermore, *G. phyllanthi* is combined in *Colletotrichum* as *C. phyllanthi*. There is precedent for this as Rojas *et al.* (2010) described *Colletotrichum ignotum* as having a teleomorph (see Rojas *et al.* 2010: figs 44–47, table III), although the teleomorphic structures were not included in the formal species diagnosis.

Colletotrichum annellatum Damm, P.F. Cannon & Crous, **sp. nov.** MycoBank MB560734. Fig. 2.

Etymology: The name refers to the proliferation of conidiogenous cells, which appear annellate.

Teleomorph developed on SNA. *Ascomata* ovoid to obpyriform, medium to dark brown, 180–220 × 100–150 µm, glabrous, ostiolate, neck hyaline to pale brown, wall 5–10 µm thick, outer layer composed of flattened medium brown angular cells, 5–10 µm diam. *Interascal tissue* composed of paraphyses, hyaline, septate, branched at the base, disintegrating quickly, 35–55 µm long, base 3–4.5 µm diam, apically free, the apex rounded. *Asci* cylindrical to clavate, 58–74 × 11–16 µm, 8-spored. *Ascospores* arranged biseriately, hyaline, smooth-walled, aseptate, cylindrical to narrowly fabiform, straight or rarely very slightly curved, both sides rounded, (13.5–)15–17(–18.5) × 5–6 µm, mean ± SD = 16.0 ± 1.1 × 5.6 ± 0.4 µm, L/W ratio = 2.9.

Teleomorph developed on *Anthriscus stem*. *Ascomata* ovoid to obpyriform, medium brown. *Asci* cylindrical to clavate, 60–70

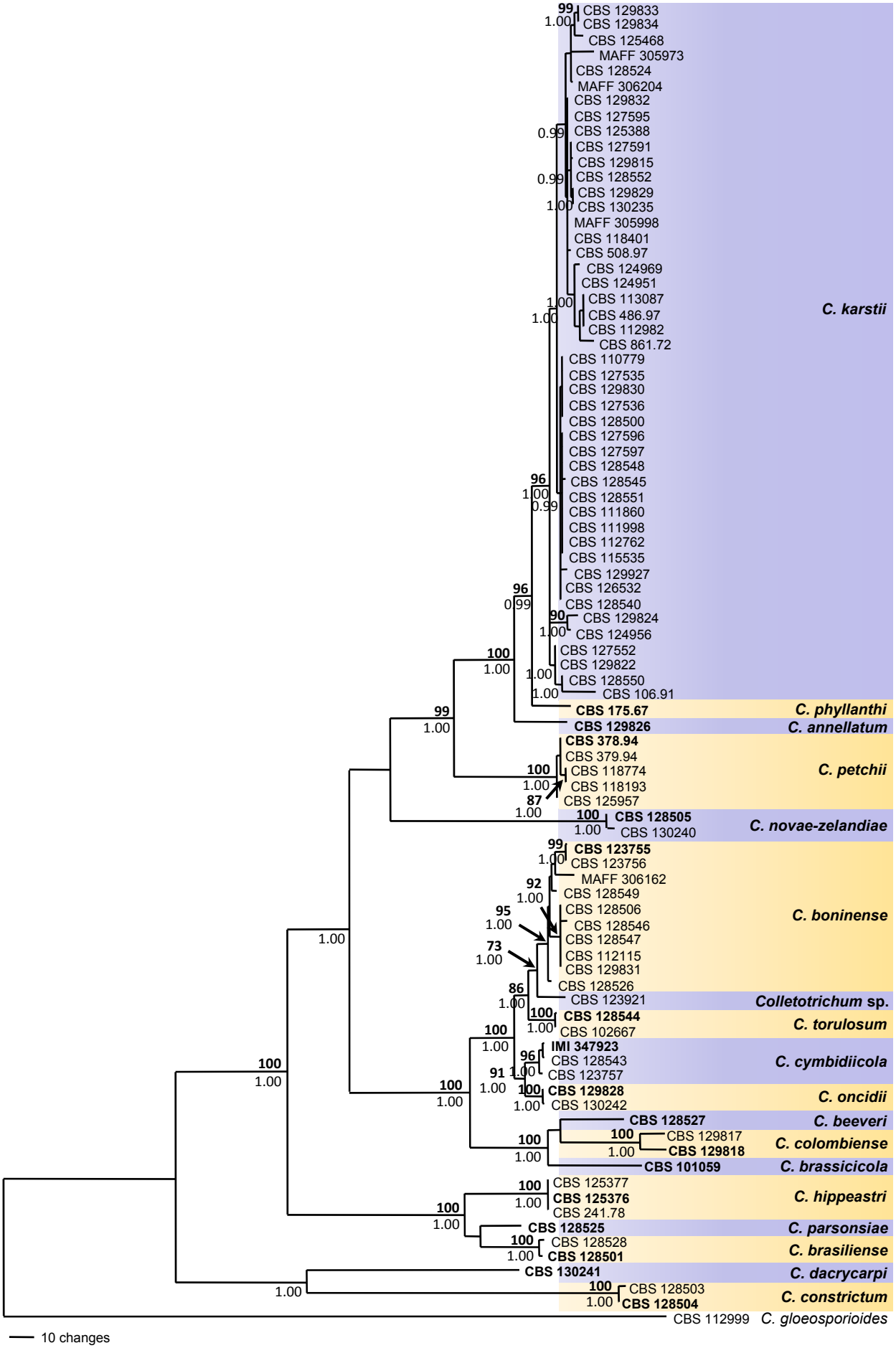

Fig. 1. One of 958 most parsimonious trees obtained from a heuristic search of the combined ITS, GAPDH, CHS-1, ACT, HIS3, TUB2 and CAL sequences alignment of the *Colletotrichum boninense* species complex. Bootstrap support values (500 replicates) above 70 % (bold) and Bayesian posterior probability values above 0.95 are shown at the nodes. *Colletotrichum gloeosporioides* CBS 112999 is used as outgroup. Numbers of ex-type and ex-epitype strains are emphasised in bold.

Fig. 2. *Colletotrichum annellatum* (from ex-holotype strain CBS 129826). A–B. Conidiomata. C–E. Conidiophores. F. Basis of seta and conidiophores. G. Tip of seta. H–I. Conidiophores. J–K. Conidia. L–M. Ascomata. N. Ascospores. O. Paraphyses. P–R. Asci. S. Peridium in cross section. T. Outer surface of peridium. A, C–E, J. from *Anthriscus* stem; B, F–I, K–T. from SNA. A–B, L. Dissecting microscope (DM), C–K, M–T. Differential interference contrast illumination (DIC), Scale bars: A, L = 100 µm, M = 50 µm, C, N = 10 µm. Scale bar of A applies to A–B. Scale bar of C applies to C–K. Scale bar of N applies to N–T.

× 11–14 µm, 8-spored. *Ascospores* arranged biseriately, hyaline, smooth-walled, aseptate, cylindrical, straight or rarely very slightly curved, both sides rounded (13.5–)14.5–17(–19.5) × (5–)5.5–6(–6.5) µm, mean ± SD = 15.8 ± 1.4 × 5.8 ± 0.4 µm, L/W ratio = 2.7.

Anamorph developed on SNA. Vegetative hyphae 1.5–9 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* absent, conidiophores and setae formed directly from vegetative hyphae or on a small cushion of hyaline to pale brown, angular cells 3–6 µm diam. *Setae* pale to medium brown, smooth to verruculose, especially towards the tip, 2–4-septate, 70–160 µm long, the base cylindrical, sometimes slightly inflated, 3.5–5.5 µm diam, the tip ± rounded. *Conidiophores* hyaline to very pale brown, smooth-walled, septate, branched, to 80 µm long. *Conidiogenous cells* hyaline to very pale brown, smooth-walled, cylindrical, sometimes extending to form new conidiogenous loci, 4–22 × 4–5 µm, opening 1–2 µm diam, collarette < 0.5 µm long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, cylindrical, the apex and base rounded, with a prominent scar, contents granular or guttulate, often with two big guttules, (11.5–)13–15(–15.5) × (5–)5.5–6 µm, mean ± SD = 14.0 ± 0.9 × 5.7 ± 0.2 µm, L/W ratio = 2.4. *Appressoria* rare (only 8 observed) single, medium brown, roundish, elliptical or with a bullet-shaped outline, the margin entire to undulate, 5.5–9(–11) × (4–)4.5–6.5 µm, mean ± SD = 7.3 ± 1.6 × 5.7 ± 1.0 µm, L/W ratio = 1.3.

Anamorph on Anthriscus stem. Conidiomata acervular, conidiophores formed on a cushion of pale brown, thick-walled, angular cells, 5–10 µm diam. *Setae* not observed. *Conidiophores* pale brown, smooth-walled, septate, branched, to 35 µm long. *Conidiogenous cells* pale brown, smooth-walled, cylindrical, annellations frequently observed, 7–21 × 3.5–5 µm, opening 1.5–2 µm diam, collarette 0.5–1 µm long. *Conidia* hyaline, smooth-walled, aseptate, cylindrical, the apex and base rounded, with a prominent scar, contents granular or guttulate, often with two big guttules, (13–)14–15.5(–16.5) × 5.5–6(–6.5) µm, mean ± SD = 14.7 ± 1.0 × 5.8 ± 0.3 µm, L/W ratio = 2.6.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline to pale honey-coloured. On medium with *Anthriscus* stem and filter paper, partly covered with short floccose, white aerial mycelium and grey to black conidiomata; reverse same colours, 17.5–19.5 mm in 7 d (28–29.5 mm in 10 d). Colonies on OA flat with entire margin, buff, pale mouse-grey to greyish sepia, partly covered with floccose white aerial mycelium and salmon to black conidiomata; reverse buff, olivaceous buff to olivaceous grey, 19–20 mm in 7 d (30–31 mm in 10 d). *Conidia in mass* salmon.

Material examined: **Colombia**, Meta, Villavicencio, from a leaf of *Hevea brasiliensis*, 13 Aug. 2010, Olga Castro, (CBS H-20693 **holotype**, culture ex-type CBS 129826 = CH1).

Notes: This species is sister to a clade that contains *C. karstii* and *C. phyllanthi*. *Colletotrichum annellatum* has rather longer asci compared with *C. karstii* (58–74 µm versus 31.5–56 µm), ascospores that tend to be wider, and smaller appressoria (though these are rarely formed in *C. annellatum*). *Colletotrichum phyllanthi* did not produce anamorphic or teleomorphic structures under our growth conditions, so direct comparison of morphological characters was problematic. As its name suggests, *C. annellatum* frequently produces conidiogenous cells that have annellide-like proliferations on *Anthriscus* stem, while on SNA conidiogenous cells with a distinct periclinal thickening were predominant.

Two species referable to *Colletotrichum* have previously been described from *Hevea*. *Colletotrichum heveae* Petch (Petch 1906) has longer and wider conidia than *C. annellatum* (measured as 18–24 × 7.5–8 µm by its author), and seems to be similar in morphological terms to the *C. crassipes* group as accepted by Sutton (1980). There are a number of distantly related *Colletotrichum* taxa with broad conidia and more revisionary work is needed; see also Lubbe *et al.* (2004) and Cannon *et al.* (2012, this issue). A further species was published in the same article, *Gloeosporium heveae* Petch. Many species described in that genus now belong in *Colletotrichum*, differing only in having sparse or absent setae (von Arx 1970). From its description, *G. heveae* belongs to the *C. gloeosporioides* aggregate; as it has conidia that measure 12–17 × 3.5–5 µm (*i.e.* narrower than those of *C. annellatum*) and conidiogenous cells ("basidia") measuring 20–34 × 2 µm. Typification of neither species is easy. The only potential type material of either species in K contains a single packet labelled in Petch's handwriting with "*Gloeosporium brunneum* Petch & *Colletotrichum heveae* Petch, no. 2228. On *Hevea*, 7 Oct. 1905; type of *Colletotrichum heveae*". The packet contains two young leaves, apparently with only one fungus, corresponding to the description of *G. heveae* rather than *C. heveae*. The name *G. brunneum* Petch was apparently never published (it would be a later homonym of *G. brunneum* Ellis & Everh. 1889) and it seems most likely that Petch changed the name of this species between collection and publication. Petch's names cannot therefore be unequivocally typified, but it seems certain that neither provides an earlier name for *C. annellatum*.

Most *Colletotrichum* isolates derived from *Hevea* plants have been found to belong to the *C. gloeosporioides* and *C. acutatum* species complexes (Jayasinghe *et al.* 1997, Saha *et al.* 2002, Gazis & Chaverri 2010, Gazis *et al.* 2011, Damm *et al.* 2012, this issue). However, one isolate from *Hevea guianensis* in Peru has an ITS sequence placing it in the *C. boninense* species complex, within *C. karstii* or *C. phyllanthi* (Gazis *et al.* 2011; GenBank HQ022474). The ITS sequence of *C. annelatum* differs in two bp from *C. karstii* and *C. phyllanthi.* Further research is needed to clarify the placement of the strain from Peru.

Colletotrichum beeveri Damm, P.F. Cannon, Crous, P.R. Johnst. & B. Weir, **sp. nov.** MycoBank MB560735. Fig. 3.

Etymology: Named after Ross Beever, New Zealand mycologist and fungal geneticist, who collected the plant material from which this species was isolated.

Teleomorph not observed. On SNA, *Anthriscus* stem/filterpaper and OA closed round structures were observed that could be undeveloped ascomata, neither conidia nor ascospores were produced.

Anamorph developed on SNA. Vegetative hyphae 1.5–7 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* absent, conidiophores and setae formed directly from vegetative hyphae or on pale brown, thick-walled angular cells 3–6.5 µm diam. *Setae* dark brown, smooth-walled, 1–3-septate, 50–100 µm long, base conical to ± inflated, 5–6.5 µm diam, tip ± acute. *Conidiophores* pale brown, smooth-walled, septate, branched, to 50 µm long. *Conidiogenous cells* pale brown, smooth-walled, cylindrical to ampulliform, 9–30 × 03.5–6.5 µm, opening 1–1.5 µm diam, collarette ≤ 0.5 µm long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, cylindrical, the apex and base rounded, with a prominent scar, contents granular or guttulate, often

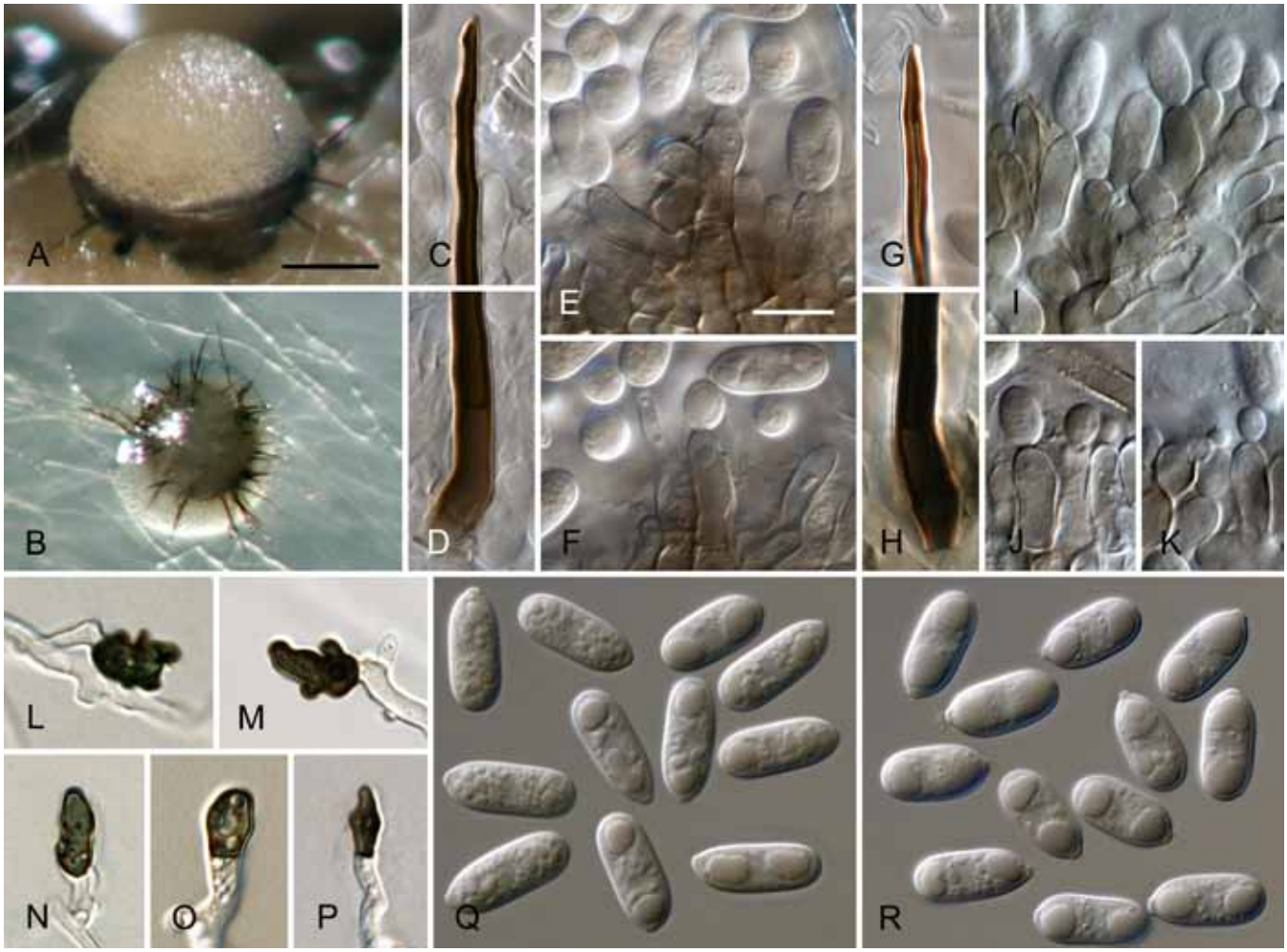

Fig. 3. *Colletotrichum beeveri* (from ex-holotype strain CBS 128527). A–B. Conidiomata. C.Tip of seta. D. Basis of seta. E–F. Conidiophores. G. Tip of seta. H. Basis of seta. I–K. Conidiophores. L–P. Appressoria. Q–R. Conidia. A, C–F, Q. from *Anthriscus* stem. B, G–P, R. from SNA. A–B, DM, C–R. DIC, Scale bars: A = 100 µm, E = 10 µm. Scale bar of A applies to A–B. Scale bar of E applies to C–R.

with two big guttules, (11.5–)12–14(–16) × 5.5–6.5 µm, mean ± SD = 13.2 ± 1.0 × 6.0 ± 0.3 µm, L/W ratio = 2.2. *Appressoria* single, dark brown, irregular, but often elliptical to navicular in outline, the margin lobate, (5.5–)7.5–12.5(–14.5) × (4–)5.5–8.5(–9) µm, mean ± SD = 10.1 ± 2.5 × 7.1 ± 1.4 µm, L/W ratio = 1.4.

Anamorph on Anthriscus stem. Conidiomata acervular, conidiophores and setae formed on a cushion of medium brown, thick-walled angular cells, 3–10 µm diam. *Setae* (only a few observed at the margin of acervuli) dark brown, smooth-walled, 2–3-septate, 80–95 µm long, base conical to cylindrical, 4.5–6 µm diam, tip roundish to ± acute. *Conidiophores* pale to medium brown, smooth-walled, septate, branched, to 20 µm long. *Conidiogenous cells* pale to medium brown, smooth-walled, short cylindrical to ampulliform, sometimes extending to form new conidiogenous loci, 9–15 × 4.5–5.5 µm, opening 1–1.5 µm diam, collarette < 0.5 µm long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, cylindrical, the apex and base rounded, with a prominent scar, contents granular or guttulate, sometimes with two big guttules, (12.5–)12–14(–15.5) × 5.5–6.5 µm, mean ± SD = 14.3± 0.8 × 6.0± 0.4 µm, L/W ratio = 2.4.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline, with filter paper, *Anthriscus* stem and partly agar medium covered with orange to black conidiomata and filter paper partly with white mycelium; reverse hyaline with black spots mainly under the filter paper, 22.5–24 mm in 7 d (32.5–37 mm in 10 d). Colonies on OA flat with entire margin, buff, primrose to greenish olivaceous with orange, dark grey to black conidiomata or ascomata and partly with short floccose white aerial mycelium; reverse buff, pale purplish grey, primrose, greenish olivaceous to iron-grey with olivaceous grey spots due to the conidiomata/ascomata shining through, 26.5–29 mm in 7 d (39–40 mm in 10 d). *Conidia in mass* salmon to orange.

Material examined: **New Zealand**, Great Barrier Island, from brown lesions on a leaf of *Brachyglottis repanda*, R.E. Beever, 23 Mar. 2006, (CBS H-20694 **holotype**, culture ex-type CBS 128527 = ICMP 18594).

Notes: This species is characterised by wide conidia and complex appressoria. It forms a sister group to *C. brassicicola* (from *Brassica*, also from New Zealand) and *C. colombiense* (from *Passiflora* leaves in Colombia), which have similarly sized and shaped conidia. It differs from *C. colombiense* by its acute, ± smooth-walled setae and its more elongate conidiogenous cells. In common with *C. brassicicola*, *C. beeveri* can produce pycnidium-like structures in culture, but none produced spores.

No species of *Colletotrichum* has been previously described from *Brachyglottis*, and none of those species described from members of the *Asteraceae* originate from Australasia. According to sequence comparisons with six genes, *C. beeveri* (identified as *C. boninense*) was isolated as an endophyte of healthy roots of *Pleione bulbocodioides* (*Orchidaceae*) in China (Yang *et al.* 2011). Several endophytic strains from *Podocarpaceae* leaves from New Zealand have the same or similar ITS sequences as *C. beeveri* (*e.g.* EU482210, EU482288 and EU482283; Joshee *et al.* 2009).

Colletotrichum boninense Moriwaki, Toy. Sato & Tsukib., *Mycoscience* 44(1): 48. 2003. Fig. 4.

Teleomorph developed on OA (CBS 123756). *Ascomata* perithecia, variable in shape but usually subglobose to pyriform, glabrous, medium brown, 100–300 × 100–200 µm, ostiolate, periphysate, neck hyaline to pale brown, to 100 µm in length, outer wall composed of flattened angular cells 4–15 µm diam. Interascal tissue composed of rather irregular thin-walled hyaline septate paraphyses. *Asci* in a basal fascicle, cylindric-clavate, 45–60 × 12.5–17 µm, 8-spored, with a ± truncate apex and a small refractive apical ring. *Ascospores* initially hyaline and aseptate, becoming 1–3-septate, septation sometimes occurring inside the ascus, light to medium brown-pigmented, sometimes verruculose prior to the start of germination, allantoid, (12.5–)14–17(–18) × (4–)5–6(–6.5) µm, mean ± SD = 15.6 ± 1.4 × 5.4 ± 0.5 µm, L/W ratio = 2.9.

Anamorph developed on SNA (CBS 123755). *Vegetative hyphae* 1–6 µm diam, hyaline or pale brown, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* poorly or not developed, conidiophores and setae formed directly on hyphae. *Setae* rare, medium brown, smooth to verruculose, 1–2-septate, 20–60 µm long, base cylindrical, conical or slightly inflated, 3–7 µm diam at the widest part, tip ± rounded. *Conidiophores* hyaline or pale brown, simple or septate, branched or unbranched, to 40 µm long. *Conidiogenous cells* hyaline or pale brown, cylindrical, 6–15 × 3–5 µm, opening 1–2 µm diam, collarette 0.5–1.5 µm long, periclinal thickening conspicuous. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical, apex round, base round with a prominent hilum, often containing two big polar guttules, (8.5–)11–14.5(–17.5) × (4–)5–6(–6.5) µm, mean ± SD = 12.8 ± 1.6 × 5.4 ± 0.4 µm, L/W ratio = 2.4. *Appressoria* solitary or in short chains, medium brown, thick-walled, entire edge or crenate, rarely lobate, smooth-walled, irregular in shape, but often bullet-shaped or navicular with an acute tip, (4.5–)7–14(–18) × (4–)5–8(–11) µm, mean ± SD = 10.5 ± 3.3 × 6.4 ± 1.5 µm, L/W ratio = 1.6.

Anamorph developed on Anthriscus stem (CBS 123755). *Conidiomata* acervular, conidiophores and setae formed from a cushion of pale brown, roundish to angular cells, 3–9 µm diam. *Setae* rare, medium brown, basal cell often paler, verruculose, 1–2-septate, 30–70 µm long, base cylindrical, conical or slightly inflated, 3.5–6.5 µm diam, tip ± round to ± acute. *Conidiophores* pale brown, septate, branched or unbranched, to 40 µm long. *Conidiogenous cells* pale brown, cylindrical to ellipsoidal, 5.8–17 × 3.5–6 µm, opening 0.5–1.5 µm diam, collarette ≤ 0.5 µm long, periclinal thickening visible to conspicuous. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical to clavate, apex round, base round with a prominent hilum, sometimes with two big polar guttules, (9–)12–14.5(–16.5) × (4–)5.5–6.5 µm, mean ± SD = 13.2 ± 1.4 × 5.8 ± 0.5 µm, L/W ratio = 2.3. The conidia of CBS 129831 are longer (up to 20 µm) with an average L/W ratio of 2.6.

Culture characteristics: Colonies on SNA flat with slightly undulate margin, hyaline with felty white aerial mycelium on filter paper; reverse filter paper partly pale cinnamon to pale hazel; 25.5–29 mm in 7 d (37.5–40 mm in 10 d). Colonies on OA flat with entire margin; surface covered with felty white, rosy buff or very pale glaucous grey aerial mycelium, in the centre pale luteous aerial mycelium; reverse buff, rosy buff, pale luteous to honey-coloured; 27.5–32.5 mm in 7 d (39–40 mm in 10 d). *Conidia in mass* salmon. CBS 102667 is slower growing: SNA 18–21 mm in 7 d (29–29.5 mm in 10 d), OA 21.3–22.5 mm in 7 d (31.5–32.5 mm in 10 d).

Material examined: **Japan**, Bonin Islands, from a diseased leaf of *Crinum asiaticum* var. *sinicum*, 1988, T. Sato, culture **ex-holotype** CBS 123755 = MAFF 305972; Bonin Islands, from *Crinum asiaticum* var. *sinicum*, 1990, T. Sato, culture CBS 123756 = MAFF 306094. **Australia**, from *Leucospermum* sp., culture CBS 129831 = STE-U 2965. **New Zealand**, Northland, Kaipara, from flowers of *Solanum betaceum*, 1 Feb. 2004, M. Manning, culture CBS 128549 = ICMP 15444.

Notes: Conidia of *C. boninense* are similar to those of *C. karstii*, although the ascospores of *C. boninense* are more uniform with rounded ends, becoming brown and septate with age and the asci are longer and wider.

We recognise that there is significant genetic variation in *C. boninense*. Host plants of *C. boninense s. str.* are very diverse including *Amaryllidaceae*, *Bignoniaceae*, *Podocarpaceae*, *Proteaceae*, *Solanaceae* and *Theaceae*. Several ITS sequences, for example HM044131 (Yuan *et al.*, unpubl. data) from *Oryza granulata*, and FJ449913 (Hu & Guo, unpubl. data) from *Dendrobium* sp., both presumably from China, are similar to the ITS of *C. boninense*, *C. oncidii* and *C. cymbidiicola,* but these species can not be separated from each other by comparison of ITS sequences.

Colletotrichum brasiliense Damm, P.F. Cannon, Crous & Massola, **sp. nov.** MycoBank MB560736. Fig. 5.

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

Teleomorph not observed. *Anamorph on SNA. Vegetative hyphae* 1–5.5 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* acervular, conidiophores and setae formed on a cushion of pale brown, ± thin-walled, angular cells 3–9 µm diam, however, in strain CBS 128528 conidiophores and setae are formed directly on hyphae. *Setae* sparse, pale to medium brown, basal cell usually paler, smooth to finely verruculose, 2–4-septate, 50–60 µm long, base cylindrical to conical, 6–8 µm diam, tip ± acute to slightly roundish or zig-zag-shaped. *Conidiophores* hyaline to pale brown, smooth-walled, simple or septate and branched, to 30 µm long. *Conidiogenous cells* hyaline to pale brown, smooth-walled, cylindrical to ellipsoidal, encased in a mucous sheath, sometimes extending to form new conidiogenous loci, 7–14 × 4.5–7.5 µm, opening 1–2 µm diam, collarette visible, ≤ 0.5 µm long, periclinal thickening visible, in strain CBS 128528 conidiogenous cells longer (12–25 µm) and periclinal thickening conspicuous. *Conidia* hyaline, smooth-walled, aseptate, cylindrical, the apex and base rounded, with a prominent scar, contents granular or guttulate, (11.5–)13–16(–18) × 5–5.5(–6) µm, mean ± SD = 14.6 ± 1.6 × 5.4 ± 0.2 µm, L/W ratio = 2.7, conidia of strain CBS 128528 longer, measuring (13.5–)14–19(–22.5) × (4.5–)5–5.5(–6) µm, mean ± SD = 16.5 ± 2.4 × 5.3 ± 0.3 µm, L/W ratio = 3.1. *Appressoria* medium to dark brown, smooth-walled, lobed, often with a roundish outline, sometimes also triangular, SNA (5.5–)7–16(–32) × (4–)6.5–13(–24) µm, mean ± SD = 11.5 ± 4.5 × 9.7 ± 3.3 µm, L/W ratio = 1.2.

Anamorph on Anthriscus stem. Conidiomata acervular, conidiophores and setae formed on a cushion of pale brown, angular cells, 3–8 µm diam. *Setae* (only one observed) medium brown, smooth-walled, 3-septate, 65 µm long, base cylindrical, 4.5 µm diam, tip ± acute and zig-zag-shaped. *Conidiophores* hyaline to pale brown, smooth-walled, simple or septate and branched, to 20 µm long. *Conidiogenous cells* hyaline to pale brown, smooth-walled, cylindrical to ellipsoidal, sometimes extending to form new conidiogenous loci, 6–12 × 3.5–7.5 µm, opening 1–2 µm diam, collarette 1 µm long, periclinal thickening visible, in strain CBS

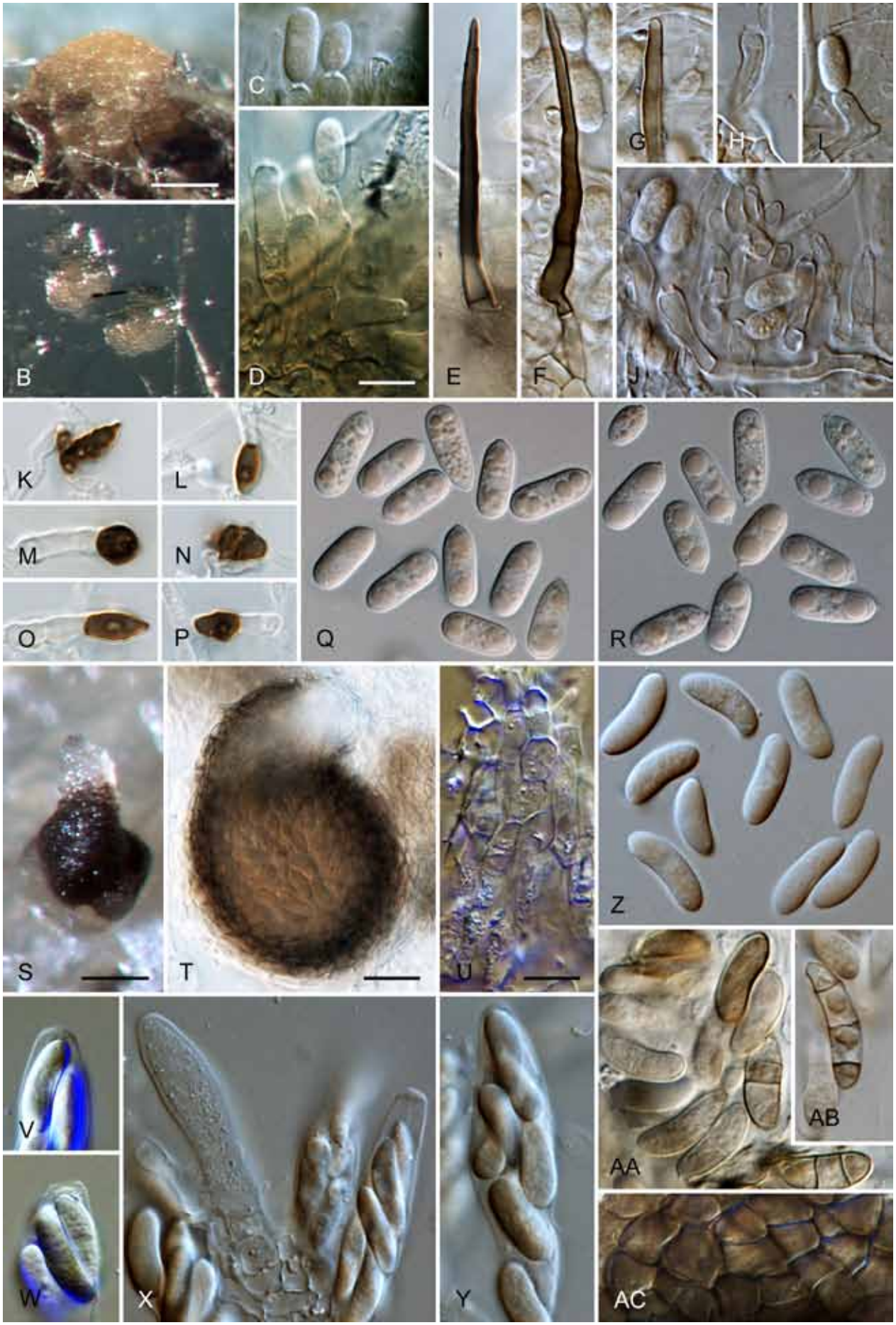

Fig. 4. *Colletotrichum boninense*. A–B. Conidiomata. C–D. Conidiophores. E–F. Setae. G. Tip of seta. H–J. Conidiophores. K–P. Appressoria. Q–R. Conidia. S–T. Ascomata. U. Paraphyses. V–W. Apical regions of asci. X–Y. Asci. Z, AA–AB. Ascospores. AC. Outer surface of peridium. A–R. from ex-holotype strain CBS 123755. S–AC. from strain CBS 123756. A, C–E, Q. from *Anthriscus* stem. B, F–P, R. from SNA. A–B, S. DM, C–R, T–AC. DIC, Scale bars: A, S = 100 µm, T = 25 µm, D, U = 10 µm. Scale bar of A applies to A–B. Scale bar of D applies to C–R. Scale bar of U applies to U–AC.

Fig. 5. *Colletotrichum brasiliense* (from ex-holotype strain CBS 128501). A–B. Conidiomata. C.Tip of seta. D. Basis of seta. E–F. Conidiophores. G. Seta. H–I. Conidiophores. J–O. Appressoria. P– Q . Conidia. A, C–F, P. from *Anthriscus* stem. B, G–O, Q. from SNA. A–B. DM, C–Q. DIC, Scale bars: A = 100 µm, E = 10 µm. Scale bar of A applies to A–B. Scale bar of E applies to C–Q.

128528 conspicuous. *Conidia* hyaline, smooth-walled, aseptate, cylindrical, the apex and base rounded, with a prominent scar, contents granular or guttulate, (13–)13.5–16(–19) × (4.5–)5–5.5(–6) µm, mean ± SD = 14.8 ± 1.3 × 5.3 ± 0.3 µm, L/W ratio = 2.8, conidia of strain CBS 128528 longer, measuring (13–)14–19(–22.5) × (4–)4.5–5.5(–6) , mean ± SD = 16.7 ± 2.5 × 5.1 ± 0.5 µm, L/W ratio = 3.3.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline, pale cinnamon close to *Anthriscus* stem, on *Anthriscus* stem covered with orange to black conidiomata, filter paper partly rosy buff, grey to black, covered with white mycelium and grey to black conidiomata; reverse same colours, with black spots mainly under the filter paper, 21–21.5 mm in 7 d (32.5–33.5 mm in 10 d). Colonies on OA flat with entire margin, buff, towards the centre greenish olivaceous with orange to black conidiomata, aerial mycelium lacking; reverse buff, grey olivaceous to olivaceous grey towards the centre, 21.5 mm in 7 d (32–33.5 mm in 10 d). *Conidia in mass* orange.

Material examined: **Brazil**, Sao Paulo, Bauru City, from fruit anthracnose of *Passiflora edulis f. flavicarpa*, 1 June 2006, N. Massola and H.J.Tozze Jr., (CBS H-20697 **holotype**, culture ex-type CBS 128501 = ICMP 18607 = PAS12); Sao Paulo, Bauru City, from fruit of *Passiflora edulis*, 1 June 2006, N. Massola and H.J.Tozze Jr., CBS H-20696, culture CBS 128528 = ICMP 18606 = PAS10.

Notes: There are four species in the *C. boninense* species complex known to occur on *Passiflora*: *C. brasiliense* from Brazil (on fruits), *C. colombiense* from Colombia (on leaves), *C. torulosum* from New Zealand (on leaves) and *C. karstii* from Japan and Colombia (on leaves) and from Brazil (on fruits). According to Johnston & Jones (1997), *C. gloeosporioides* Group E (= *C. novae-zelandiae*) and *C. gloeosporioides* Group I (= *C. constrictum*) have also been isolated from *Passiflora*, although this has not been confirmed by molecular methods. *Colletotrichum brasiliense* and *C. colombiense* are at this stage known only from *Passiflora*. *Colletotrichum brasiliense* is known only from Brazil where it causes anthracnose of yellow passion fruit (*Passiflora edulis f. flavicarpa*; Tozze *et al.* 2010). *Colletotrichum brasiliense* is closely related to *C. parsonsiae* and *C. hippeastri*. *Colletotrichum brasiliense* is distinguished from these species with most of the genes, including ITS, although the CHS-1 sequence of one isolate was the same as that of *C. parsonsii*. Appressoria have a lower L/W ratio (1.2) than other species in this group.

There are numerous records of *Colletotrichum*, *Gloeosporium* and *Glomerella* species on *Passiflora* (Farr & Rossman 2011). Two *Colletotrichum* and two *Gloeosporium* species have been previously described from *Passiflora*. *Gloeosporium passiflorae* Speg., described from *Passiflora* sp. in Argentina, forms longer conidia (20–30 × 5–6 µm) than any of the species in the *C. boninense* species complex known from *Passiflora* (Spegazzini 1899). Conidia of *C. passiflorae* Siemaszko, which was described on leaves of *Passiflora edulis* in Transcaucasia (today belonging to Armenia, Azerbaijan, and Georgia) are smaller, measuring 14–25 × 4–6 µm (Siemaszko 1923). Most of the species treated here have shorter conidia. Only conidia of *C. brasiliense* isolate CBS

128528 sometimes exceed 20 µm, but their average length is 16.5 µm and their L/W ratio is 3.3 rather than 3.5–4.25 as implied by Siemaszko's measurements.

Colletotrichum passiflorae F. Stevens & P.A. Young (Stevens 1925), described on fruits of *P. laurifolia* and leaves of *P. edulis* from Hawaii, U.S.A., might be an earlier name for several of the species of the *boninense* complex, but von Arx (1957) treated it as a synonym of the *gloeosporioides* complex and its description ("Acervuli black, numerous, 90–225 µ in diameter. Setae brown, 50–75 by 5 µm. Conidia granular, cylindrical 11–18 by 3.5–6 µm," Stevens 1925) is inadequate to make an assessment of its identity. Setae of *C. constrictum*, *C. novae-zelandiae*, *C. karstii* and *C. torulosum* are longer than the length quoted for *C. passiflorae* by Stevens, but the different growth conditions makes such a comparison unreliable. No living cultures of *C. passiflorae* appear to have been maintained, so we are forced to regard the name as of uncertain application. The name is not available for any of the species of the *C. boninense* complex as it is a later homonym of *C. passiflorae* Siemaszko.

The name *Gloeosporium passifloricola* Sawada [as "*passifloricolum*"], was introduced for a fungus on *Passiflora quadrangularis* in Taiwan (Sawada 1943), but the name was invalidly published and cannot threaten any of the species presented in our paper.

Colletotrichum brassicicola Damm, P.F. Cannon & Crous, **sp. nov.** MycoBank MB560737. Fig. 6.

Etymology: Named after the host plant genus, *Brassica*.

Teleomorph developed on Anthriscus stem. Ascomata globose to subglobose, pale brown, 100–250 × 90–150µm, glabrous, ostiolate, neck hyaline to pale brown, outer wall composed of flattened angular cells 8–19.5 × 5.5–15.5 µm in size. Interascal tissue composed of paraphyses; hyaline, septate, branched, 55–100 × 4–8 µm. Asci cylindrical, 65–105 × 12–13.5 µm, 8-spored. Ascospores (only 7 observed) arranged biseriately, hyaline and aseptate, fusiform, sometimes broader towards one side, sometimes curved, smooth, (15–)17.3–21(–24) × (3.5–)4–5.5(–7) µm, mean ± SD = 19.1 ± 1.8 × 4.8± 0.8 µm, L/W ratio = 4.0. *On filterpaper* ascospores (16.5–) 18–22.5(–23.5) × 4.5–5.5(–6.5) µm, mean ± SD = 20.3 ± 2.4 × 5.1± 0.5 µm, L/W ratio = 4.0**.**

Anamorph developed on SNA. Vegetative hyphae 1–5 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* poorly developed, conidiophores and setae formed directly on hyphae. *Setae* medium brown, verruculose, 1–3-septate, 30–70 µm long, base cylindrical, conical or slightly inflated, 4–6.5 µm diam at the widest part, tip round. *Conidiophores* pale brown, septate, unbranched or branched, to 30 µm long. *Conidiogenous cells* hyaline or pale brown, smooth to verruculose, clavate, cylindrical or doliiform, sometimes lacking a basal septum and continuous with the conidiophore, 7–14 × 4–5.5 µm, opening 1.5–2 µm diam, collarette 0.5–1(–1.5) µm long, periclinal thickening conspicuous. *Conidia* hyaline, smooth-walled, aseptate, straight, ovoid, apex round, base round, sometimes with prominent scar, sometimes containing one or two big guttules, (9.5–)11–13.6(–17.5) × (4.5–)5–6(–6.5) µm, mean ± SD = 12.2 ± 1.4 × 5.6 ± 0.4 µm, L/W ratio = 2.2. *Appressoria* pale to dark brown, crenate to lobed, (5.5–)7.5–14.5(–21) × (4.5–)6–9.5(–12.5) µm, mean ± SD = 11.1 ± 3.6 × 7.8 ± 1.7 µm, L/W ratio = 1.4.

Anamorph developed on Anthriscus stem. Conidiomata acervular, conidiophores and setae formed from a cushion of hyaline to pale brown, angular cells, 3–9 µm diam. *Setae* medium brown, base often paler, smooth to verruculose, 1–2-septate, 25–60 µm long, base cylindrical to conical, often slightly inflated, 4–7.5 µm diam, tip round. *Conidiophores* pale brown, septate, branched, to 30 µm long. *Conidiogenous cells* hyaline to pale brown, smooth-walled, cylindrical, clavate to ellipsoidal, 5–16 × 3.5–5 µm, opening 1.5–2 µm diam, collarette 0.5–1 µm long, periclinal thickening visible to conspicuous. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical to clavate, apex round, base round with a prominent scar, guttulate, sometimes with one or two big guttules, (9–)11.5–13.5(–14.5) × (5–)5.5–6 µm, mean ± SD = 12.4 ± 1 × 5.6 ± 0.3 µm, L/W ratio = 2.2. *On filter paper* (less often observed on *Anthriscus* stem) dark brown to black, roundish closed conidiomata are formed, to 400 µm diam, opening by irregular rupture. *Conidia* hyaline, smooth-walled, aseptate, irregularly shaped, possibly deformed due to pressure inside the conidiomata, (7.5–)10–14.5(–18) × (4.5–)5–7(–8.5) µm, mean ± SD = 12.2 ± 2.3 × 6.2 ± 0.9 µm, L/W ratio = 2.0.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline with felty white aerial mycelium on *Anthriscus* stem and filter paper and salmon to orange acervuli and black sclerotia/ascomata on filter paper; reverse filter paper rosy buff to hazel with black sclerotia/ascomata shining through; 17.5–21 mm in 7 d (27.5–31.5 mm in 10 d). Colonies on OA flat with entire margin; surface buff, pale luteous to greenish olivaceous, partly covered with olivaceous grey structures, orange spore masses and with felty white to pale olivaceous grey aerial mycelium, reverse honey-coloured, pale luteous to isabelline; 19–22.5 mm in 7 d (29–32.5 mm in 10 d). *Conidia in mass* salmon to orange.

Material examined: **New Zealand**, Manawatu-Wanganui, Ohakune, from leaf spot of *Brassica oleracea* var. *gemmifera*, unknown collection date (July 1998 deposited in CBS collection), B. Thrupp, (CBS H-20698 **holotype**, culture ex-type CBS 101059 = LYN 16331).

Notes: The conidia of *C. brassicicola* are very short, while ascospores and asci are longer than those of the other four species in the *C. boninense* species complex with a known sexual morph. Farr & Rossman (2011) list six *Colletotrichum* taxa associated with *Brassica* species: *C. truncatum, C. capsici* (treated as a synonym of *C. truncatum* by Damm *et al.* 2009), *C. dematium*, *C. gloeosporioides*, *C. gloeosporioides* var. *minor* and *C. higginsianum*. *Colletotrichum truncatum* and *C. dematium* have curved conidia, and belong to separate clades that are not closely related to *C. boninense* (Damm *et al.* 2009). *Colletotrichum gloeosporioides* has noticeably longer conidia than species in the *C. boninense* complex (Sutton 1980, 1992; Weir *et al.* 2012). *Colletotrichum gloeosporioides* var. *minor* was reported on *Brassica oleracea* in Australia (Simmonds 1966) with narrower conidia (11.1–17.7 × 3.1–5.0 µm) and shorter ascospores (13.5–16.8 × 3.5–4.9 µm) (Simmonds 1968) than *C. brassicicola*. Weir *et al.* (2012) confirm *C. gloeosporioides* var. *minor* as belonging to the *C. gloeosporioides* species complex, and describe it as a new species, *C. queenslandicum*. *Colletotrichum higginsianum* (O'Connell *et al.* 2004) is part of the *C. destructivum* complex (Cannon *et al.* 2012, this issue) and has longer conidia that tend to be inaequilateral.

Vassiljewski and Karakulin (1950) described *Colletotrichum brassicae* on *Brassica* as having slightly curved, fusoid conidia that are longer (19–24 µm) than those of *C. brassicicola*. *Colletotrichum brassicae* was regarded as a synonym of *C. dematium* (von Arx 1957), but no authentic material has been seen.

Fig. 6. *Colletotrichum brassicicola* (from ex-holotype strain CBS 101059). A–B. Conidiomata. C. Setae. D–H. Conidiophores. I. Seta and conidiophores. J–O. Appressoria. P–Q. Conidia. R–S. Ascomata. T. Conidia formed in closed conidiomata. U. Ascospores. V. Asci and paraphyses. W. Apical region of an ascus. X. Paraphyses. Y. Outer surface of peridium. Z. Peridium in cross section. A, C–E, P, R–S, U–Z. from *Anthriscus* stem. B, F–O, Q. from SNA. T. from filter paper. A–B, R. DM, C–Q, T–Z. DIC, Scale bars: A, R = 100 µm, S = 50 µm, D, T = 10 µm. Scale bar of A applies to A–B. Scale bar of D applies to C–Q. Scale bar of T applies to T–Z.

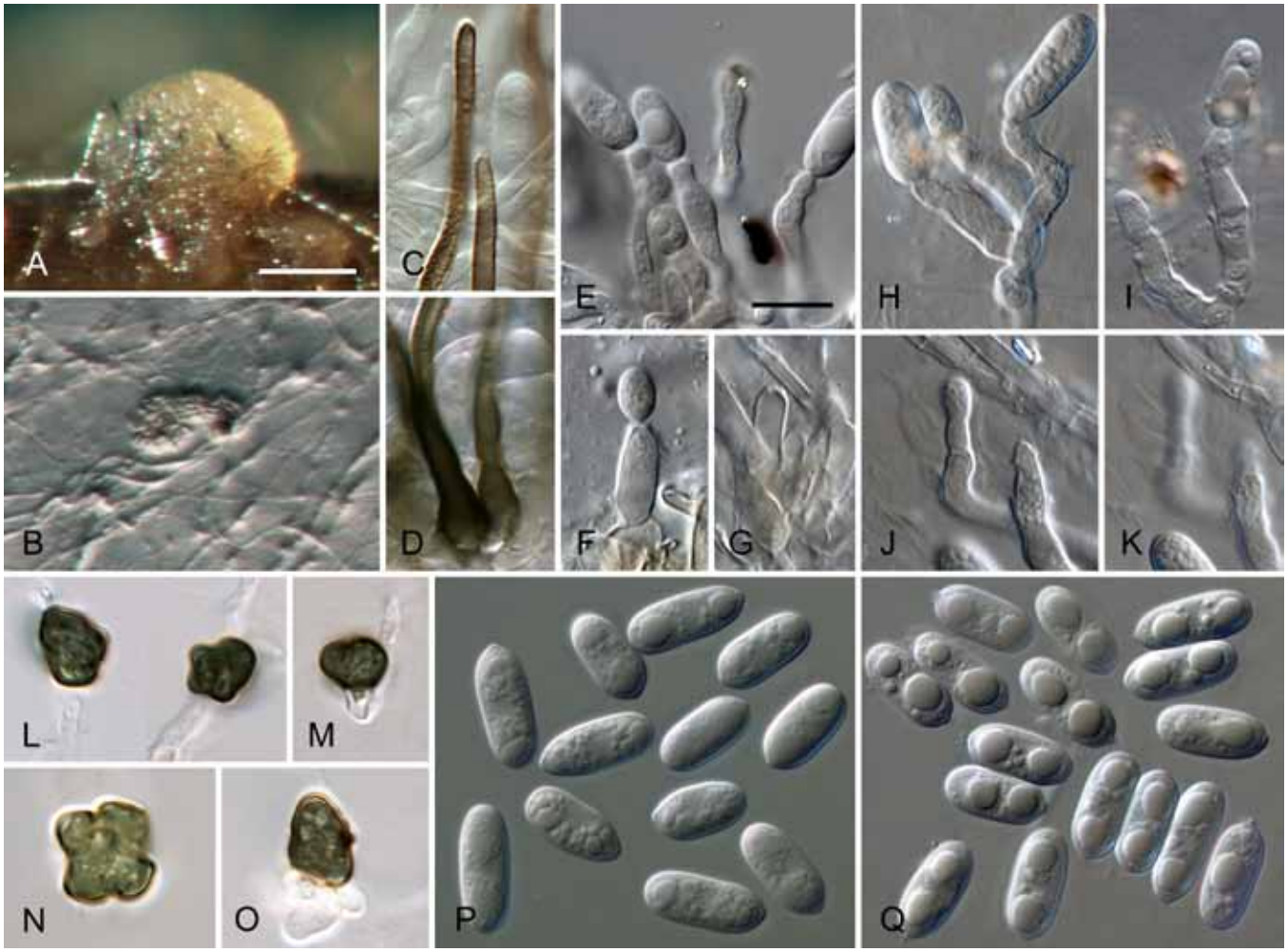

Fig. 7. *Colletotrichum colombiense* (from ex-holotype strain CBS 129818). A–B. Conidiomata. C.Tips of setae. D. Bases of setae. E–K. Conidiophores. L–O. Appressoria. P–Q. Conidia. A, C–G, P. from *Anthriscus* stem. B, H–K, Q. from SNA. A–B. DM, C–Q. DIC, Scale bars: A = 100 µm, E = 10 µm. Scale bar of A applies to A–B. Scale bar of E applies to C–Q.

An isolate on *Passiflora* sp. from Colombia (Pass-65, Afanador-Kafuri *et al.* 2003) has the same ITS sequence as *C. brassicicola,* and isolates from leaves of *Podocarpus totara* and *Prumnopitys ferruginea* in New Zealand (Joshee *et al.* 2009) differ by only two or three substitutions in ITS sequences. We cannot be sure whether these strains belong to *C. brassicicola* or to other segregates of the *C. boninense* group.

Colletotrichum colombiense Damm, P.F. Cannon & Crous, **sp. nov.** MycoBank MB560738. Fig. 7.

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

Teleomorph not observed, but on OA spherical structures on the agar surface and within the medium that lack any conidia or ascospores. *Anamorph on SNA. Vegetative hyphae* 1–6 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* absent, conidiophores formed directly from vegetative hyphae. *Setae* not observed. *Conidiophores* hyaline, smooth-walled, septate, branched, to 50 µm long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical, sometimes slightly inflated, surrounded by several mucous layers, often extending to form new conidiogenous loci, 7–18 × 3.5–5 µm, opening 1–1.5 µm diam, collarette and periclinal thickening not observed. *Conidia* hyaline, smooth-walled, aseptate, cylindrical, the apex and base rounded, with a prominent scar, contents granular or guttulate, often with two big guttules (11.5–)12–14(–15.5) × (4.5–) 5–6(–6.5) µm, mean ± SD = 13.1 ± 1.0 × 5.7 ± 0.4 µm, L/W ratio = 2.3. *Appressoria* single, medium to dark brown, roundish to elliptical in outline, the margin undulate to lobate, (5.5–)6–10(–12.5) × (3.5–)4.5–7.5(–10) µm, mean ± SD = 7.8 ± 2.0 × 6.0 ± 1.5 µm, L/W ratio = 1.3, appressoria of strain CBS 129817 larger, (7–) 7.5–14.5(–21.5) × (5–)6–10(–12.5) µm, mean ± SD = 11.0 ± 3.5 × 8.1 ± 1.9 µm, L/W ratio = 1.3.

Anamorph on Anthriscus stem. Conidiomata acervular, conidiophores and setae formed on a cushion of pale brown, angular cells, 3–8 µm diam. *Setae* medium brown, verruculose, 1–3-septate, 35–110 µm long, base cylindrical to strongly inflated, 3.5–8.5 µm diam, tip rounded. *Conidiophores* hyaline, smooth-walled, septate, branched, to 40 µm long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical, sometimes surrounded by a gelatinous sheath, sometimes extending to form new conidiogenous loci, 7–26 × 3–5.5 µm, opening 1–1.5 µm diam, collarette < 0.5 µm long, periclinal thickening observed. *Conidia* hyaline, smooth-walled, aseptate, cylindrical, the apex and base rounded, with a prominent scar, contents granular or guttulate, (11–)12–14.5(–15) × (5–)5.5–6 µm, mean ± SD = 13.1 ± 1.1 × 5.7 ± 0.3 µm, L/W ratio = 2.3.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline to pale honey-coloured, with medium containing *Anthriscus* stem and filter paper partly covered with very short, white aerial mycelium; reverse same colours, 24–25 mm in 7 d (34–35 mm in 10 d). Colonies on OA flat with entire margin, buff, honey to

isabelline, partly covered with salmon, grey to black conidiomata, aerial mycelium lacking; reverse buff to olivaceous grey, 26–26.5 mm in 7 d (37–39 mm in 10 d). *Conidia in mass* salmon.

Material examined: **Colombia**, Cundinamarca, Tibacuy, from a leaf of *Passiflora edulis*, 22 Jan. 2010, D. Riascos, (CBS H-20699 **holotype**, culture ex-type CBS 129818 = G2); Cundinamarca, Tibacuy, from a leaf of *Passiflora edulis*, 5 Nov. 2009, D. Riascos, CBS H-20700, culture CBS 129817 = G1.

Notes: Sequences of *C. colombiense* form a sister group to *C. beeveri* and *C. brassicicola*. It differs from *C. beeveri* in morphology by setae that are verrucose and rounded, and shorter conidiogenous cells. Other species isolated from *Passiflora* have pigmented conidiogenous cells (*C. brasiliense* and *C. karstii* on the media used here) or much more complex appressoria (*C. torulosum*). See under *C. brasiliense* for a discussion of previously published *Colletotrichum* taxa associated with *Passiflora*.

Many other isolates from *Passiflora* sp. from Colombia in the study by Afanador-Kafuri *et al.* (2003) have the same or similar ITS sequence as *C. colombiense*, but cannot be identified on the basis of ITS only because of the close relationship of the three species.

Colletotrichum constrictum Damm, P.F. Cannon, Crous, P.R. Johnst. & B. Weir, **sp. nov.** MycoBank MB560739. Fig. 8.

Etymology: Name refers to the shape of the ascospores, which are often constricted.

Teleomorph on *SNA*. *Ascomata* perithecia, formed after 4 wk, solitary, non-stromatic, ovoid to obpyriform, ostiolate, glabrous, medium brown, 120–200 × 90–150 µm. *Peridium* 6–10 µm thick, composed of medium brown, flattened angular cells, 7–15 µm diam. *Ascogenous hyphae* hyaline, smooth-walled, delicate, rarely visible. *Interascal tissue* formed of paraphyses, hyaline, smooth-walled, mostly cylindrical but tapering towards the round tip, disintegrating quickly, septate, branched, very variable, slightly constricted at the septa, apically free, 40–95 × 5–7 µm. Asci unitunicate, 8-spored, cylindrical to clavate, tapering to apex and base, 50–95 × 15–20 µm, the base broadly truncate. *Ascospores* biseriately arranged, aseptate, hyaline, smooth-walled, (almost) straight, base and apex uniformly broadly rounded, often ± constricted in the centre, therefore broadest close to the ends, (14–)16–20(–23) × (6–)6.5–8(–9) µm, mean ± SD = 17.9 ± 2.1 × 7.1 ± 0.7 µm, L/W ratio = 2.5.

Teleomorph on Anthriscus stem. *Ascomata* perithecia, formed after 4 wk. Asci unitunicate, 8-spored, cylindrical to clavate, tapering to apex and base, smooth-walled, 60–75 × 15–17 µm, the base broadly truncate. *Ascospores* biseriately arranged, aseptate, hyaline, smooth-walled, same shape as formed on SNA, (13–)16.5–19.5(–21) × (6.5–)7–8(–9) µm, mean ± SD = 18.0 ± 1.7 × 7.6 ± 0.6 µm, L/W ratio = 2.4.

Anamorph on SNA. *Vegetative hyphae* 1–8 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* absent, conidiophores and setae formed directly from vegetative hyphae or from a reduced cushion of pale brown, angular cells 3–9 µm diam. *Setae* pale to medium brown, verruculose, 1–4-septate, 65–130 µm long, base cylindrical, sometimes slightly inflated, 4.5–6.5 µm diam, tip ± acute. *Conidiophores* hyaline to pale brown, smooth-walled, aseptate or septate and branched, to 70 µm long. *Conidiogenous cells* hyaline to pale brown, smooth-walled, cylindrical to ampulliform, often extending to form new conidiogenous loci, 8–20 × 3–7.5 µm, opening 1–2 µm diam, collarette ≤ 0.5 µm, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical, the apex and base rounded, with a prominent scar, contens granular (8.5–)12–15(–16) × (5–)5.5–6(–6.5) µm, mean ± SD = 13.3 ± 1.5 × 5.7 ± 0.4 µm, L/W ratio = 2.3, in strain CBS 128503 occationally also globose to subglobose conidia observed, 9–13 × 7–13 µm. *Appressoria* single or in small groups of 2–3, medium to dark brown, smooth-walled, ovate, bullet-shaped, navicular or clavate in outline, the margin undulate to lobate, (5–)7.5–12(–14.5) × (5–)5.5–7.5(–9.5) µm, mean ± SD = 9.7 ± 2.4 × 6.5 ± 1.1 µm, L/W ratio = 1.5.

Anamorph on Anthriscus stem. *Conidiomata* acervular, conidiophores and setae formed from a cushion of pale brown, thick-walled, angular cells 2.5–8 µm diam. *Setae* medium brown, basal cell often paler, verruculose, 2–4-septate, 70–150 µm long, base cylindrical, conical to ± inflated, 3.5–6.5 µm diam, tip acute. *Conidiophores* hyaline to pale brown, smooth-walled, aseptate or septate, branched, to 30 µm long. *Conidiogenous cells* hyaline to pale brown, smooth-walled, cylindrical to ampulliform, often extending to form new conidiogenous loci, 7–15 × 3.5–7 µm, opening 1–2 µm diam, collarette < 0.5 µm long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical, apex round, base round with a prominent hilum, the contents appearing granular to guttulate, (13–)14–15.5(–16) × 5–5.5(–6) µm, mean ± SD = 14.6 ± 0.7 × 5.4 ± 0.3 µm, L/W ratio = 2.7.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline, pale cinnamon close to *Anthriscus* stem, with *Anthriscus* stem covered with orange to black conidiomata and ascomata, filter paper partly rosy buff, grey to black, covert with white mycelium and grey to black conidiomata/ascomata; reverse same colours, with black spots mainly under the filter paper, 15–21 mm in 7 d (30.5–32.5 mm in 10 d). Colonies on OA flat with entire margin, rosy buff, olivaceous to black with dark grey to black conidiomata or ascomata, in the centre orange due to sporulation and partly covert with short white aerial mycelium; reverse buff, vinaceous buff to dark mouse-grey, 24–28 mm in 7 d (35–37.5 mm in 10 d). *Conidia in mass* orange.

Material examined: **New Zealand**, AK, Auckland, from fruit of *Citrus limon* (lemon), 1 Dec. 1988, P.R. Johnston, (CBS H-20701 **holotype**, culture ex-type CBS 128504 = ICMP 12941); from ripe fruit rot of *Solanum betaceum* (tamarillo) 1 June 1988, P.R. Johnston, CBS H-20702, culture CBS 128503 = ICMP 12936.

Notes: *Colletotrichum constrictum* differs from all other species in this complex by the shape and size of the ascospores, which are broader than those of the other species (av. ≥ 7 µm) and have a small L/W ratio (≤ 2.5). In contrast to the other species, the ascospores of *C. constrictum* are almost straight and often constricted at the centre. Consequently, the asci are also broader than those of other species in the *C. boninense* complex. The species forms a distinct cluster within all single-gene phylogenies. In the multi-gene phylogeny, *C. constrictum* and *C. dacrycarpi* form a sister clade to all other taxa within the *C. boninense* aggregate. In blastn searches no ITS sequence was found with more than 96 % identity; matches with other genes were ≤ 93 % identical. The lack of matches may indicate that *C. constrictum* has a restricted distribution.

Colletotrichum constrictum was previously referred to as *C. gloeosporioides* group I by Johnston & Jones (1997) and is only known from New Zealand. Isolates studied here are from *Citrus* sp. and *Solanum betaceum*. According to Johnston & Jones (1997), the species also occurs on *Passiflora edulis* and *P. mollissima*, although this has not been confirmed by molecular methods.

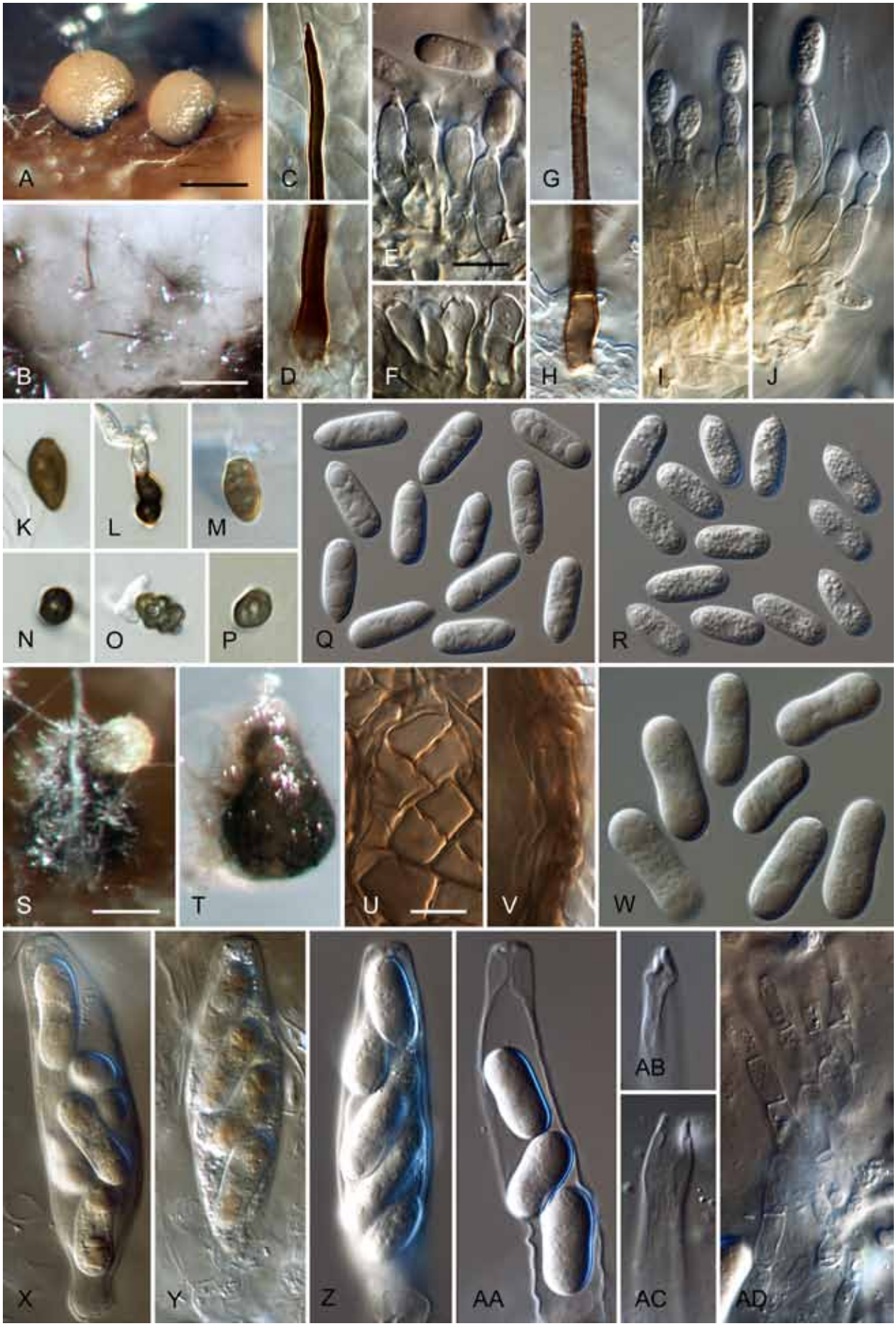

Fig. 8. *Colletotrichum constrictum* (from ex-holotype strain CBS 128504). A–B. Conidiomata. C. Tip of seta. D. Basis of seta. E–F. Conidiophores. G. Tip of seta. H. Basis of seta. I–J. Conidiophores. K–P. Appressoria. Q–R. Conidia. S–T. Ascomata. U. Outer surface of peridium. V. Peridium in cross section. W. Ascospores. X–AA. Asci. AB–AC. Apical regions of asci. AD. Paraphyses. A, C–F, Q, S, Z–AC. from *Anthriscus* stem. B, G–P, R, T–Y, AD. from SNA. A–B, S–T. DM, C–R, U–AD. DIC, Scale bars: A = 200 µm, B, S = 100 µm, E, U = 10 µm. Scale bar of E applies to C–R. Scale bar of S applies to S–T. Scale bar of U applies to U–AD.

Colletotrichum cymbidiicola Damm, P.F. Cannon, Crous, P.R. Johnst. & B. Weir, **sp. nov.** MycoBank MB560740. Fig. 9.

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

Teleomorph on *SNA*. *Ascomata* perithecia, formed after 4 wk, solitary, semi-immersed or immersed in the agar medium, non-stromatic, subspherical to ovoid, ostiolate, glabrous, medium brown, 130–160 × 170–220 µm. *Peridium* 10–12 µm thick, composed of pale to medium brown flattened angular cells 3.5–15 µm diam. *Ascogenous hyphae* hyaline, smooth-walled, delicate, rarely visible. *Interascal tissue* not observed. *Asci* unitunicate, 8-spored, cylindrical, tapering to apex and base, smooth-walled, 40–48 × 9.5–11 µm, the base truncate, apex 3.5–4 µm wide. *Ascospores* biseriately arranged, aseptate, hyaline, smooth-walled, fusiform, slightly curved, base rounded, apex acute or rounded, (12.5–)15–18(–21) × 5–6 (–6.5) µm, mean ± SD = 16.5 ± 1.6 × 5.6 ± 0.4 µm, L/W ratio = 3.0.

Teleomorph on Anthriscus stem. *Ascomata* perithecia, formed after 4 wk, superficial, non-stromatic, ovoid to obpyriform, ostiolate, glabrous, medium brown, 200–300 × 200–400 µm. *Interascal tissue* formed of paraphyses, hyaline, smooth-walled, cylindrical, disintegrating quickly, septate, branched, to 70 µm long, 3–5.5 µm wide. Asci unitunicate, 8-spored, cylindrical, tapering to apex and base, smooth-walled, 55–77 × 11.5–13.5 µm, the base truncate. *Ascospores* biseriately arranged, aseptate, hyaline, smooth-walled, cylindrical to fusiform, slightly curved, usually one end broadly rounded, the other end (which is widest and more curved) often ± acute, giving the ascospores a footprint-like appearence, (15–)17.5–25(–31) × 5–6(–7) µm, mean ± SD = 21.2 ± 3.9 × 5.5 ± 0.6 µm, L/W ratio = 3.9.

Anamorph on SNA. Vegetative hyphae 1.5–7.5 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* absent, conidiophores and setae formed directly from medium brown, verruculose hyphae or formed on a cushion of medium brown angular cells, 3–6.5 µm diam. *Setae* medium brown, verruculose, 1–4-septate, 50–150 µm long, base cylindrical to conical, 5–7 µm diam, tip ± acute to rounded, often also with a constriction. *Conidiophores* hyaline, smooth-walled, septate, branched, to 50 µm long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical, often extending to form new conidiogenous loci, 7.5–17 × 3–5.5 µm, opening 1–2 µm diam, collarette ≤ 0.5 µm diam, periclinal thickening conspicuous. *Conidia* hyaline, smooth-walled, aseptate, cylindrical, the apex and base rounded, with a prominent scar, contents granular, (12.5–)14–15.5(–16.5) × 5.5–6 µm, mean ± SD = 14.6 ± 0.8 × 5.8 ± 0.2 µm, L/W ratio = 2.5. *Appressoria* medium to dark brown, outline very variable, the margin lobate, single or in loose groups, (6.5–)8–14.5(–18.5) × (3.5–)4.5–8(–11.5) µm, mean ± SD = 11.2 ± 3.2 × 6.3 ± 1.9 µm, L/W ratio = 1.8.

Anamorph on Anthriscus stem. Conidiomata acervular, conidiophores and setae formed on a cushion of pale brown angular cells, 3–8 µm diam. *Setae* medium brown, verruculose to verrucose, 1–4-septate, 75–180 µm long, base cylindrical to strongly inflated, 4–10 µm diam, tip ± rounded to ± acute. *Conidiophores* hyaline to pale brown, smooth-walled, septate, branched. *Conidiogenous cells* hyaline, smooth-walled, cylindrical to ampulliform, sometimes extending to form new conidiogenous loci, 8–13 × 5.5–7 µm, opening 1.5–2 µm diam, collarette ≤ 0.5 µm diam, periclinal thickening conspicuous. *Conidia* hyaline, smooth-walled, aseptate, cylindrical, the apex and base rounded, with a prominent scar, contents guttulate, (11.5–)13.5–15.5(–16.5) × (5–)5.5–6(–6.5) µm, mean ± SD = 14.6 ± 0.9 × 5.7 ± 0.3 µm, L/W ratio = 2.6.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline to honey, partly covered with floccose-felty white aerial mycelium, *Anthriscus* stem and filter paper partly covered with grey to black conidiomata partly oozing salmon to orange conidia; reverse hyaline to honey, filter paper with grey to black spots due to conidiomata shining through, 25–26.5 mm in 7 d (37.5–40 mm in 10 d). Colonies on OA flat with entire margin, buff to straw, sectors covert either with granular white aerial mycelium or black conidiomata, oozing salmon to orange conidia; reverse buff, straw, honey, isabelline, olivaceous grey to iron-grey, 25–27.5 mm in 7 d (40 mm in 10 d). *Conidia in mass* salmon to orange.

Material examined: **Australia**, Western Australia, Perth, Fremantle, from leaf lesion of *Cymbidium* sp., 27 Mar. 1991, P.M. Wood, (CBS H-20703 **holotype**, culture ex-type IMI 347923). **New Zealand**, AK, Mangere, from leaf spot of *Cymbidium* sp., 22 Mar. 1990, P. Broadhurst, CBS H-20704, culture CBS 128543 = ICMP 18584. **Japan**, Ibaraki Pref., from *Cymbidium* sp., 1989, T. Sato, culture CBS 123757 = MAFF 306100.

Notes: *Colletotrichum cymbidiicola* occupies one of several clades of the *C. boninense* aggregate associated with orchids, and is a sister group to *C. oncidii*, another clade of orchid pathogens. From the limited number of samples available, both species appear host-specific at plant genus level. A curious feature of *C. cymbidiicola* is the size and shape of the ascospores and conidia which both differ considerably when grown on *Anthriscus* stem, compared with those derived from cultures on SNA. *Colletotrichum oncidii* did not produce a telemorph under our culture growth conditions; its conidia are also longer in relation to their width when grown on *Anthriscus* stem compared to SNA cultures, but the difference is not as prominent. *Colletotrichum cymbidiicola* differs from *C. boninense* in the shape of the appressoria that are usually lobate with irregular shapes in *C. cymbidiicola*, while those of *C. boninense* are typically bullet-shaped to navicular with entire edge or crenate.

Colletotrichum dacrycarpi Damm, P.F. Cannon, Crous, P.R. Johnst. & B. Weir, **sp. nov.** MycoBank MB560741. Fig. 10.

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

Teleomorph not observed.

On SNA. Vegetative hyphae 1–6 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* globose to flask-shaped, apparently opening by rupture, wall cells medium brown, angular; conidiophores formed from a cushion of medium brown, angular cells 3–7.5 µm diam. *Setae* not observed. *Conidiophores* hyaline, smooth-walled, septate, branched, to 60 µm long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical to ampulliform, sometimes extending to form new conidiogenous loci, sometimes annelides observed, 11–28 × 2.5–4.5 µm, the opening 2–3 µm diam, collarette ≤ 0.5 µm, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical, the apex and base rounded, guttulate, (17–)18.5–21.5(–22.5) × (5–)5.5–6(–6.5) µm, mean ± SD = 19.9 ± 1.7 × 5.7 ± 0.3 µm, L/W ratio = 3.5. *Appressoria* not observed after 3 wk.

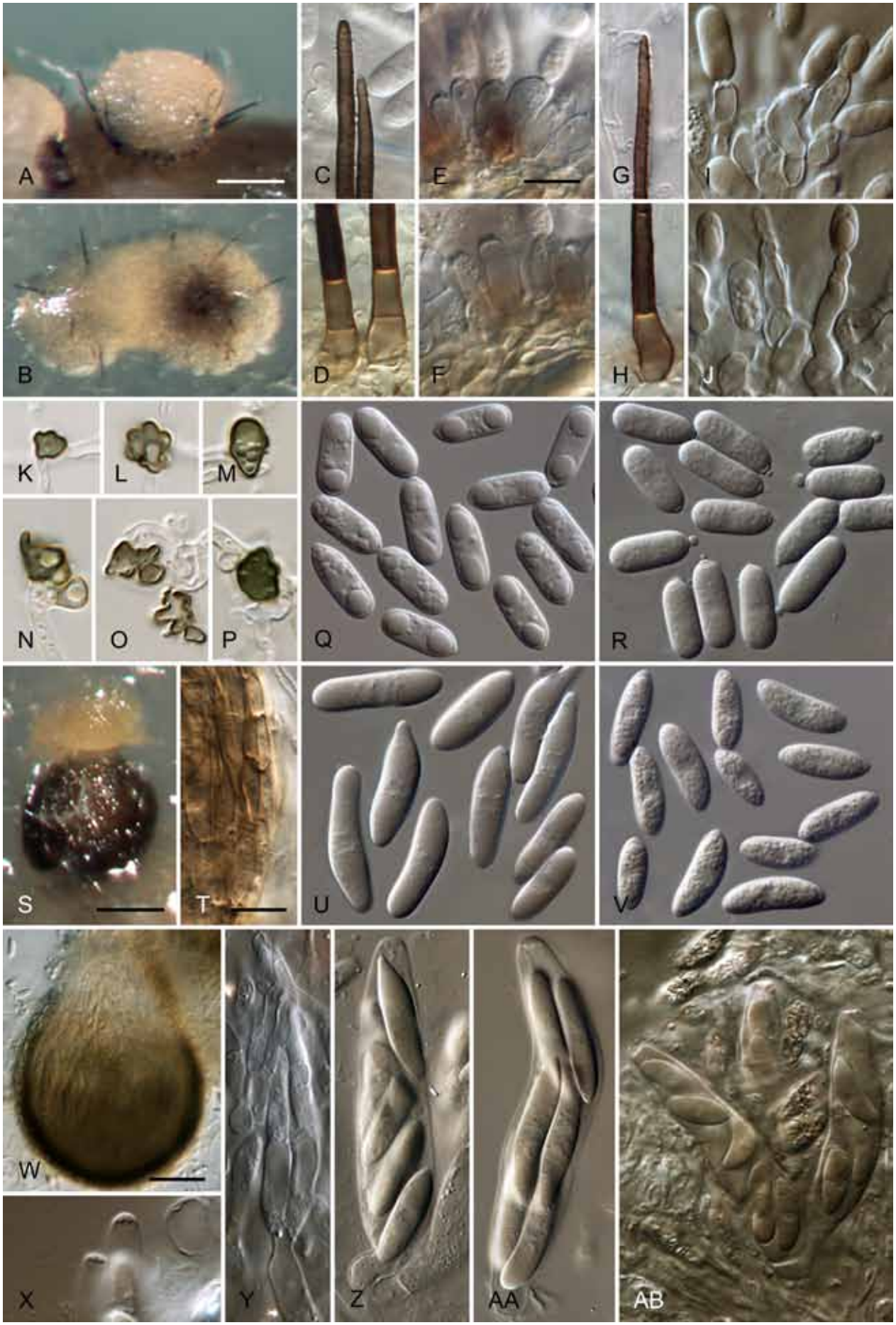

Fig. 9. *Colletotrichum cymbidiicola* (from ex-holotype strain IMI 347923). A–B. Conidiomata. C. Tips of setae. D. Bases of setae. E–F. Conidiophores. G. Tip of seta. H. Basis of seta. I–J. Conidiophores. K–P. Appressoria. Q–R. Conidia. S, W. Ascomata. T. Peridium in cross section. U–V. Ascospores. X. Apical regions of asci. Y. Paraphyses. Z–AB. Asci. A, C–F, Q, U, X–AA. from *Anthriscus* stem. B, G–P, R, T, V–W, AB. from SNA. S. from filter paper. A–B, S. DM, C–R, T–AB. DIC, Scale bars: A, S = 100 µm, W = 50 µm, E, T = 10 µm. Scale bar of A applies to A–B. Scale bar of E applies to C–R. Scale bar of T applies to T–V and X–AB.

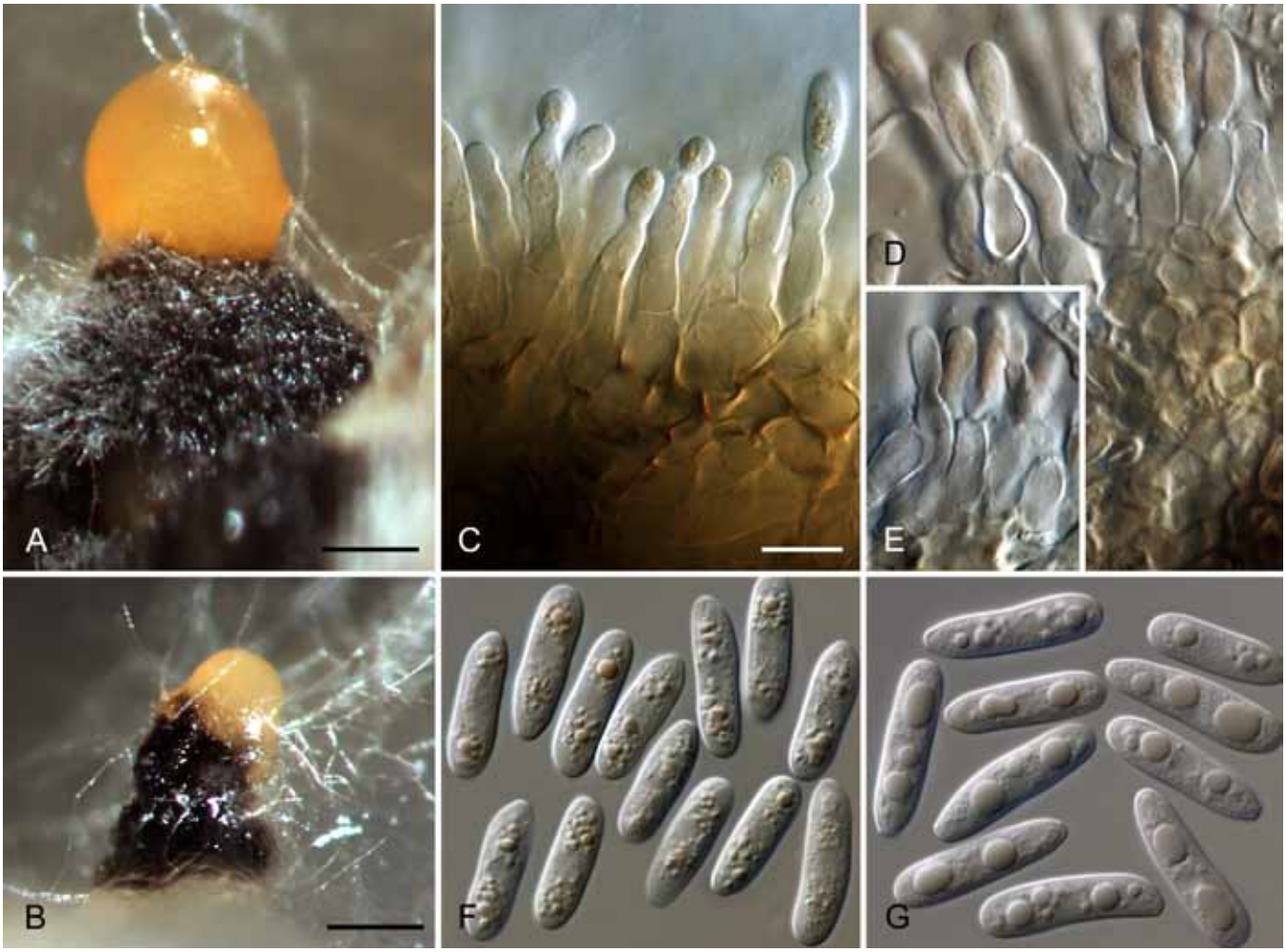

Fig. 10. *Colletotrichum dacrycarpi* (from ex-holotype strain CBS 130241). A–B. Conidiomata. C–E. Conidiophores. F–G. Conidia. A, C, F. from *Anthriscus* stem. B, D–E, G. from SNA. A–B. DM, C–G. DIC, Scale bars: A = 100 µm, B = 200 µm, C = 10 µm. Scale bar of C applies to C–Q.

On Anthriscus stem. Conidiomata globose, apparently opening by rupture, wall cells medium brown, angular, 7–20 µm diam. *Setae* not observed. *Conidiophores* hyaline, smooth-walled, septate, branched, to 50 µm long, developing from a cushion of medium brown, angular to rounded cells, 3.5–12 µm diam. *Conidiogenous cells* hyaline to pale brown, smooth-walled, cylindrical, surrounded by a gelatinous sheath, sometimes extending to form new conidiogenous loci, 7.5–23 × 3–5 µm, the opening 1.5–2.5 µm diam, collarette not observed, periclinal thickening observed. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical, apex round, base round, granular to guttulate content, (13–)15.5–19.5(–24) × 5–6(–6.5) µm, mean ± SD = 17.3 ± 2.0 × 5.5 ± 0.3 µm, L/W ratio = 3.2.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline to honey-coloured, with *Anthriscus* stem, filter paper and medium partly covered white floccose aerial mycelium and grey structures, orange conidial masses in the centre; reverse hyaline, honey to pale salmon, with dark grey spots due to conidiomata or ascomata shining through, 10.5–12.5 mm in 7 d (17.5–20 mm in 10 d). Colonies on OA flat with entire margin, rosy buff to pale flesh with a buff margin, covert with sepia to black conidiomata or ascomata and orange conidia masses in the centre and very sparse white aerial mycelium; reverse buff to rosy buff, 11–12.5 mm in 7 d (16–17.5 mm in 10 d). *Conidia in mass* orange.

Material examined: **New Zealand**, Auckland, Wenderholm Regional Park, leaf endophyte from *Dacrycarpus dacrydioides* (kahikatea), 16 Oct. 2009, G. Carroll, (CBS H-20705 **holotype**, culture ex-type CBS 130241 = ICMP 19107).

Notes: There were no *Colletotrichum* species described from *Dacrycarpus* species (*Podocarpaceae*) prior to this study. *Colletotrichum dacrycarpi* does not look like a typical member for the genus, with its slow growth and the production of conidia within closed fruit-bodies with walls that rupture. These closed fruit-bodies have been observed in several other species within the *C. boninense* complex, and the extension of conidiogenous cells to form a new conidiogenous locus is typical of species within the *C. boninense* complex. *Colletotrichum dacrycarpi* is one of the most basal members of the overall clade, and forms a sister group to the morphologically distinct *C. constrictum*. With all single gene phylogenies, *C. dacrycarpi* is situated on a long branch. Blastn searches with the ITS sequences found no close match.

Colletotrichum hippeastri Yan L. Yang, Zuo Y. Liu, K.D. Hyde & L. Cai, Fungal Diversity 39: 133. 2009. Fig 11.

Teleomorph not observed. *On SNA. Vegetative hyphae* 1–6 µm diam, hyaline to pale brown, usually smooth-walled, sometimes warted, septate, branched. *Chlamydospores* not observed. *Conidiomata* absent, conidiophores and setae formed directly on hyphae. *Setae* medium brown, verruculose, 2–7-septate, 70–200 µm long, the base cylindrical or inflated, 4–7 µm diam, the tip rounded. *Conidiophores* pale to medium brown, septate,

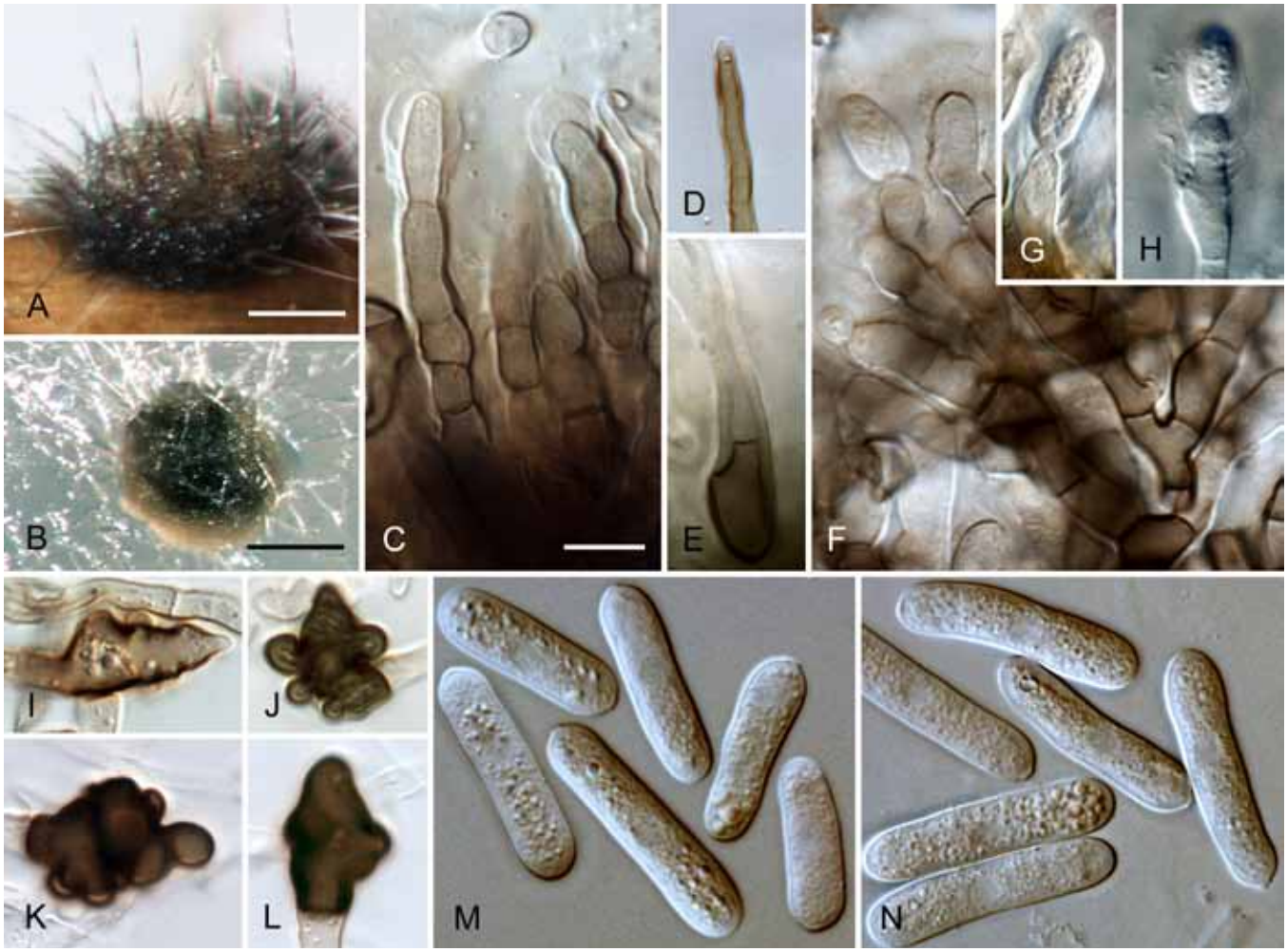

Fig. 11. *Colletotrichum hippeastri* (from ex-holotype strain CBS 125377). A–B. Conidiomata. C. Conidiophores. D. Tip of seta. E. Basis of seta. F–H. Conidiophores. I–L. Appressoria. M–N. Conidia. A, C–F, M. from *Anthriscus* stem. B, F–L, N. from SNA. A–B. DM, C–N. DIC, Scale bars: A = 100 µm, B = 200 µm, C = 10 µm. Scale bar of C applies to C–Q.

branched, to 50 µm long. *Conidiogenous cells* pale brown, hyaline towards the tip, smooth or verruculose, cylindrical, the upper part surrounded by a gelatinous sheath of several layers, 13–27.5 × 4–6.5 µm, the opening 1.5–2.5 µm diam, collarette and periclinal thickening not visible. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical, the apex and base rounded, cytoplasm appearing granular, (19–)24.5–32.5(–37.5) × (5.5–)6–7.5(–8.5) µm, mean ± SD = 28.5 ± 4.1 × 6.8 ± 0.6 µm, L/W ratio = 4.2. Strain CBS 241.78 differs in forming shorter and broader conidia, measuring (10.5–)17–31.5(–40) × (6–)6.5–8(–8.5) µm, mean ± SD = 24.4 ± 7.3 × 7.2 ± 0.7 µm, L/W ratio = 3.4. *Appressoria* dark brown, irregular in shape and strongly nodose, (8.5–)10–20(–32) × (5.5–)7.5–12.5(–15) µm, mean ± SD = 14.9 ± 5.0 × 10.0 ± 2.5 µm, L/W ratio = 1.5.

On Anthriscus stem. Conidiomata acervular, conidiophores and setae formed from a cushion of medium brown, angular to rounded cells, 3.5–12 µm diam. *Setae* pale brown, darker towards the base, smooth and very thick-walled, 1–6-septate, the septa concentrated towards the base, 50–150 µm long, the base cylindrical, conical or inflated, 5.5–10 µm diam, the tip rounded. *Conidiophores* pale to medium brown, septate, branched, to 70 µm long. *Conidiogenous cells* sometimes extending to form new conidiogenous loci, pale to medium brown, smooth, cylindrical, the upper part surrounded by a gelatinous sheath, 12–28 × 4.5–5.5 µm, the opening 1.5–2 µm diam, collarette and periclinal thickening not observed. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical, apex round, base round, granular content, (14.5–)18.5–30(–39) × (5–)6–8(–9) µm, mean ± SD = 24.2 ± 5.8 × 6.9 ± 0.9 µm, L/W ratio = 3.5.

Culture characteristics: Colonies on SNA flat with fimbriate margin (individual hyphae visible at the margin), hyaline with floccose white to very pale grey aerial mycelium on *Anthriscus* stem and filter paper medium with black structures (non-functional ascomata?) visible in the centre and on *Anthriscus* stem; 29–34 mm in 7 d (35–38 mm in 10 d). Colonies on OA flat with entire margin; surface covered with floccose pale olivaceous grey aerial mycelium, mainly at the margin, and grey to black structures, mainly in the centre; reverse smoke grey to olivaceous grey; 30–33 mm in 7 d (40 mm in 10 d). *Conidia in mass* salmon to orange.

Growth rates for CBS 125377 are SNA: 28 mm in 7 d (37 mm in 10 d), OA: SNA: 30.8 mm in 7 d (40 mm in 10 d).

Material examined: **China**, Guizhou Province, Guiyang, isolated from leaf of *Hippeastrum vittatum*, 23 May 2009, Y.L. Yang, culture **ex-holotype** CBS 125376 = CSSG1. **Netherlands**, isolated from leaf of *Hippeastrum* sp., deposited in CBS from Plantenziektenkundige Dienst Wageningen in May 1978, culture CBS 241.78 = IMI 304052.

Notes: *Colletotrichum hippeastri* is an outlying species in the *C. boninense* clade and is distinguished from related species by its large conidia as well as elongate and complex appressoria. A feature that is common with others of the complex is conidiogenous cells that are covered in a gelatinous sheath (not mentioned in the original description by Yang *et al.* 2009). Phylogenetically

informative sequence differences were not detected in the strains studied, and the species forms a distinct cluster within all single-gene phylogenies.

All isolates of *C. hippeastri* are from *Hippeastrum*, which is a genus of bulb-forming plants native to tropical and subtropical regions of the Americas from Argentina north to Mexico and the Caribbean (www.wikipedia.org). Strain CBS 119185 from *Hippeastrum* sp. in Brazil, which was unfortunately lost, is the only record of *C. hippeastri* from the Americas, as determined by the ITS sequence generated by Farr *et al.* (2006). Isolates included in this study are from China and the Netherlands.

Colletotrichum karstii Y.L. Yang, Zuo Y. Liu, K.D. Hyde & L. Cai, Cryptogamie Mycologie 32: 241. 2011. Fig. 12.

Teleomorph on *SNA*. *Ascomata* perithecia, formed after 4 wk, solitary, superficial or immersed in the agar medium, non-stromatic, globose to obpyriform, ostiolate, periphysate, glabrous, medium brown, paler towards the ostiole, 90–130 × 90–200 µm, with a neck to 90 µm, but usually much shorter. *Peridium* 6–10 µm thick, composed of 3–5 layers of pale to medium brown flattened *textura angularis* with cells 3.5–12 µm diam. *Ascogenous hyphae* hyaline, smooth, delicate, rarely visible. *Interascal tissue* formed of paraphyses, hyaline, smooth-walled, mostly cylindrical but tapering towards the round tip, disintegrating quickly, septate, constricted at the septa, apically free, 30–50 × 4.5–7 µm. Asci unitunicate, 8-spored, cylindrical to clavate, tapering to apex and base, smooth-walled, 37–56 × 9–12 µm (asci of isolate CBS 128550 up to 65 µm long), the base broadly truncate, basal septum 3.5–5.5 µm diam. *Ascospores* uni- or biseriately arranged, initially aseptate but often septate with age, hyaline, smooth-walled, variable in shape, fusiform to ovoid, slightly curved, (11.5–)13–16.5(–18.5) × (4–)4.5–5.5(–6.5) µm, mean ± SD = 14.7 ± 1.8 × 5.0 ± 0.7 µm, L/W ratio = 2.9. Ascospores of isolate CBS 128550 larger, measuring (14.5–)16–18(–18.5) × (3.5–)4.5–6(–6.5) µm.

Teleomorph on PDA. Ascomata ± globose to obpyriform, to *ca.* 275 µm diam, ostiolate, periphysate, reddish brown, glabrous; outer wall composed of irregular reddish brown polyhedral cells 10–20 µm diam. *Asci* 8-spored, narrowly clavate, unitunicate, fasciculate. *Ascospores* allantoid to pyriform, inaequilateral, often straight on inner side, apices rounded, tapered towards base, 14–19 × 4.0–7.5 µm, 1-celled, hyaline, arranged biseriately.

Anamorph on SNA. Vegetative hyphae 1–5 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* absent, the conidiophores formed directly from vegetative hyphae. CBS 129833 forms brown, roundish closed conidiomata, opening by irregular rupture, the wall composed of *textura intricata*, covered with brown, verrucose to warted hairs/hyphae, 3–3.5 µm wide, conidiophores lining the inner wall. *Setae* not observed. *Conidiophores* hyaline to pale brown, smooth, septate, strongly branched, to 100 µm long. *Conidiogenous cells* hyaline or pale brown, smooth, cylindrical to elongate-ampulliform, sometimes extending to form new conidiogenous loci, 9–20 × 3–5 µm, opening 1–1.5 µm diam, collarette < 0.5 µm diam, periclinal thickening conspicuous. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical, the apex and base rounded, with a prominent hilum *ca*. 1 µm diam, < 0.3 µm long, the contents appearing granular, (11.5–)12.5–14(–14.5) × (5–)5.5–6(–6.5) µm, mean ± SD = 13.1 ± 0.7 × 5.8 ± 0.4 µm, L/W ratio = 2.2, conidia of CBS 111998 sometimes longer (up to 18.5 µm, L/W ratio = 2.8). *Appressoria* single or in small groups of 2–3, pale to medium brown, often navicular to bullet-shaped, not nodose, smooth-walled to undulate, (4.5–)6–12(–16.5) × (2.5–)4–7(–10) µm, mean ± SD = 8.9 ± 2.9 × 5.4 ± 1.5 µm, L/W ratio = 1.7, appressoria of CBS 129833 larger, measuring (5.5–)7.5–13(–17) × (4.5–)5.5–8.5(–10.5) µm, mean ± SD = 10.3 ± 2.6 × 7.1 ± 1.5 µm, L/W ratio = 1.4.

Anamorph on Anthriscus stem. Conidiomata acervular, conidiophores and setae formed from a cushion of pale brown, angular cells, 3–10 µm diam. *Setae* rare, medium to dark brown, verruculose, 2–3-septate, 80–120 µm long, base conical to slightly inflated, 4.5–5.5 µm diam, tip rounded, setae of isolate CBS 128550 more frequent, pale to medium brown, 2–7-septate, 60–160 µm long, base cylindrical-conical to slightly inflated, 4–7 µm diam, tip acute. *Conidiophores* hyaline to pale brown, aseptate or septate, branched, to 80 µm long. *Conidiogenous cells* hyaline to pale brown, smooth-walled, cylindrical to ampulliform, sometimes extending to form new conidiogenous loci, 4.5–15 × 3–6 µm, opening 1–2 µm diam, collarette < 0.5 µm long, periclinal thickening conspicuous. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical, apex round, base round with a prominent hilum, the contents appearing granular, (12–)13–15(–16.5) × 5.5–6(–6.5) µm, mean ± SD = 14.0 ± 1.1 × 5.7 ± 0.3 µm, L/W ratio = 2.4, conidia of CBS 111998 sometimes longer (up to 17) and L/W ratio = 2.6.

Anamorph on PDA after 4 wk under near UV light. *Conidia* straight, cylindrical, rounded at both ends, with a hilum-like protuberance at the base, somewhat larger than on SNA, measuring 14.5–17.0 × 5.0–6.5 µm.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline, with filter paper and *Anthriscus* stem covered with orange conidiomata and partly with white mycelium; reverse hyaline with grey flecks mainly under the filter paper, 23.0–27.5 mm in 7 d (36.5–40 mm in 10 d). Colonies on OA flat with entire margin, buff to rosy buff to pale salmon, covered with orange to grey conidiomata, lacking aerial mycelium; reverse buff, rosy buff to honey, 23.0–26.5 mm in 7 d (35.5–38 mm in 10 d). Colonies on PDA after 4 wk under near UV light with grey to white aerial mycelium at the centre and in dispersed tufts, with numerous dark conidiomata scattered over the surface, reverse colourless to pale orange with numerous dark flecks corresponding to the ascomata. *Conidia in mass* orange.

Material examined: **Australia**, QLD, Palmwoods, latitude 26° 41' S, longitude 152° 57' E, from calyx necrosis of *Diospyros australis*, 1 May 2002, H. Drew, CBS H-20712, culture CBS 127597 = BRIP 29085a (strain described); New South Wales, from *Leucospermum* sp., Aug. 1999, P.W. Crous, culture CBS 111998 = STE-U 1999. **Mexico**, Villahermosa, Tabasco, from *Musa* sp., 18 Dec. 2008, M. de Jesus Yarez-Morales, CBS H-20714, culture CBS 129833; Cooitepec Harinas, from fruit anthracnose of *Annona cherimola*, 1 July 2003, R. Villanueva-Arce, culture CBS 128550 = ICMP 17896.

Notes: Based on sequence comparison with six genes (ITS, GAPDH, ACT, CAL, TUB2, CHS-1), 46 of the isolates in this study group with *C. karstii* (not shown). *Colletotrichum karstii* was recently described from a leaf of *Vanda* sp. (*Orchidaceae*) in China and reported on several other orchids (Yang *et al.* 2011). It occurs on many host plants and is the most common and geographically diverse species in the *C. boninense* complex. *Colletotrichum karstii* was referred to as *C. gloeosporioides* groups F and G by Johnston & Jones (1997) who also listed *Persea americana* and *Cucurbita* spp. as host plants. Many earlier works have cited isolates of *C. boninense* that are identified here as *C. karstii*, including some of those detailed in the original description (Morikawi *et al.* 2003), some in Farr *et al.* (2006) and all those in Lubbe *et al.* (2004). Some isolates from *Passiflora edulis* in Brazil that caused anthracnose on passion

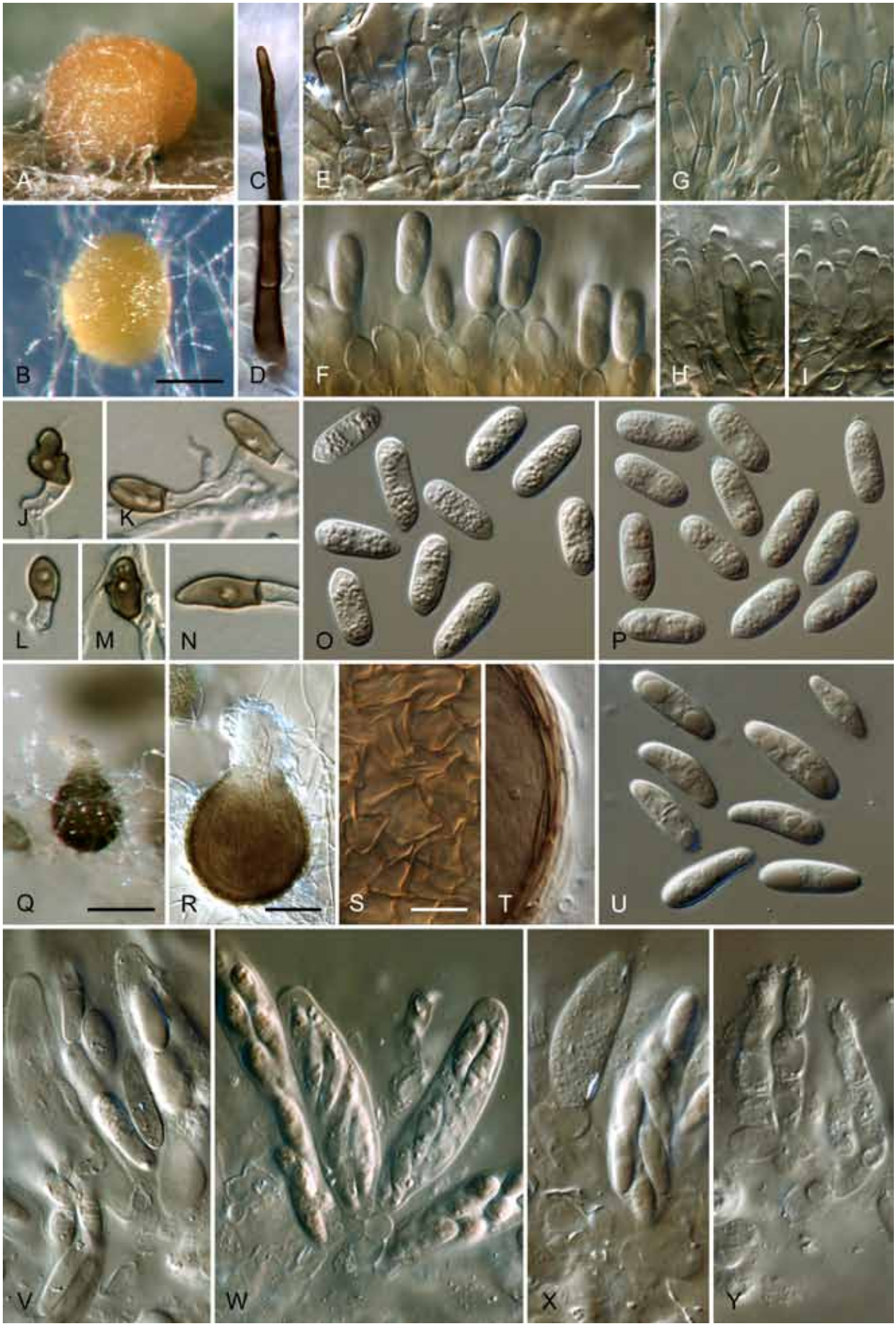

Fig. 12. *Colletotrichum karstii* (from strain CBS 127597). A–B. Conidiomata. C. Tip of seta. D. Basis of seta. E–I. Conidiophores. J–N. Appressoria. O–P. Conidia. Q–R. Ascomata. S. Outer surface of peridium. T. Peridium in cross section. U. Ascospores. V–X. Asci. Y. Paraphyses. A, C–F, O. from *Anthriscus* stem. B, G–N, P–Y. from SNA. A–B, Q. DM, C–P, R–Y. DIC, Scale bars: A = 200 µm, B, Q = 100 µm, R = 50 µm, E, S = 10 µm. Scale bar of E applies to C–P. Scale bar of S applies to S–Y.

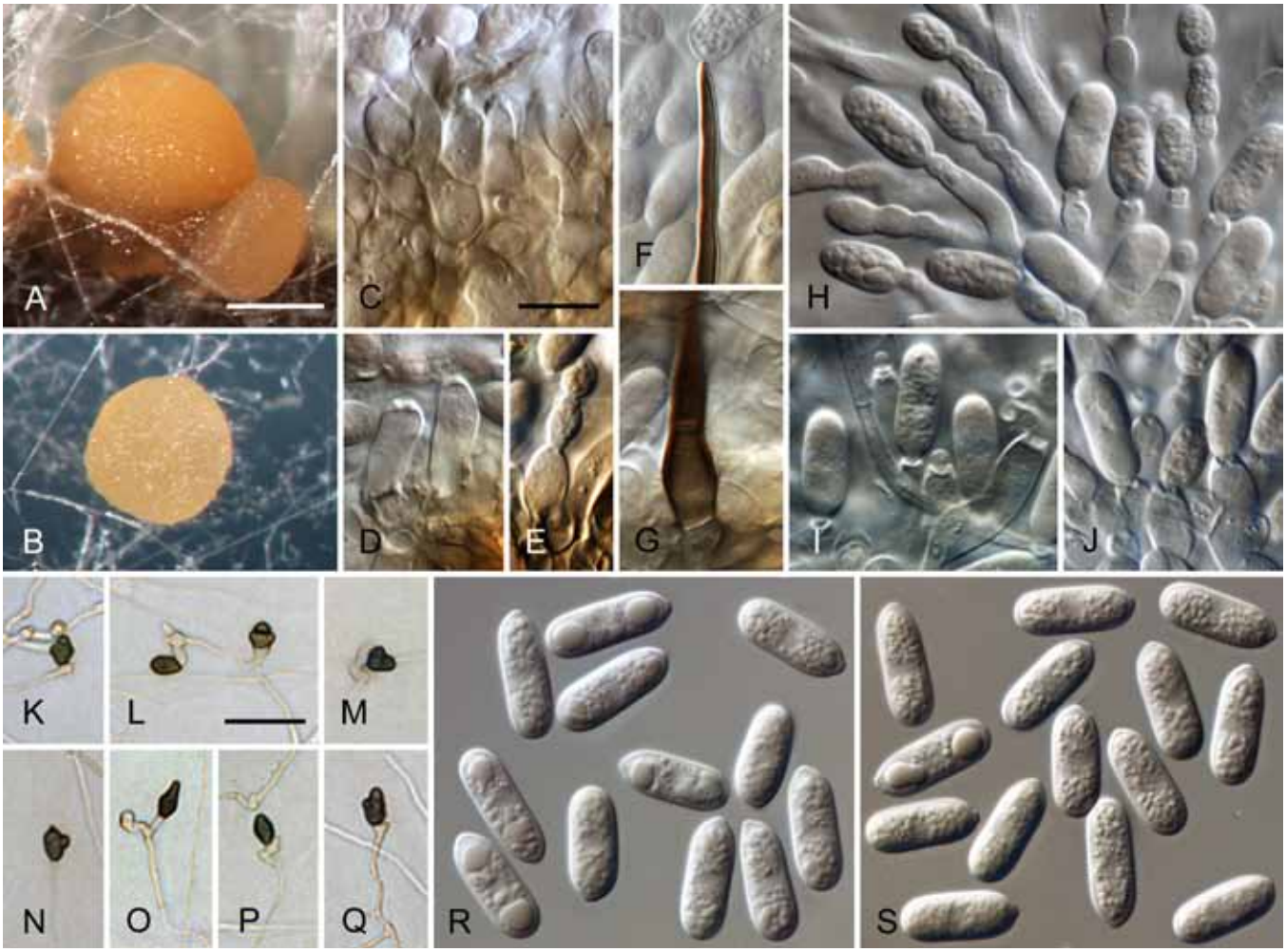

Fig. 13. *Colletotrichum novae-zelandiae* (from ex-holotype strain CBS 128505). A–B. Conidiomata. C–E. Conidiophores. F. Tip of seta. G. Basis of seta. H–J. Conidiophores. K–Q. Appressoria. R–S. Conidia. A, C–G, R. from *Anthriscus* stem. B, H–Q, S. from SNA. A–B. DM, C–S. DIC, Scale bars: A = 200 µm, C = 10 µm, L = 25 µm. Scale bar of A applies to A–B. Scale bar of C applies to C–J and R–S. Scale bar of L applies to K–Q.

fruits (Tozze *et al.* 2010) were identified as *C. karstii* by GAPDH sequences (GenBank accessions FJ949450 and FJ949452, not included in phylogeny). ITS sequences of endophytic strains of *C. gloeosporioides* "group 2" from *Musa acuminata* from Thailand (Photita *et al.* 2005) as well as *C. boninense* isolates from *Persea americana* from Mexico (Silva-Rojas & Ávila-Quezada 2011), *Maytenus ilicifolia* from Brazil (Pileggi *et al.* 2009) and *Passiflora* sp. in Florida, U.S.A. (Tarnowski & Ploetz 2010) are identical or similar to those of *C. karstii* (and *C. phyllanthi*).

Sequence and morphological variability is high, with differences in conidium size and conidiomatal structures ranging from sporodochial to acervular to closed. This makes identification difficult if based on morphology alone. The conidia of *C. karstii* are smaller than those of *C. hippeastri* and *C. dracaenae*, and broader than those of *C. phyllanthi*. The asci are shorter than those of *C. brassicicola* and *C. dracaenae*, and the shape of the ascospores differs from *C. boninense*, being slightly wider and less tapered in that species.

Some strains have morphological features that are slightly different from those of strain CBS 127597 described above. Strain CBS 129833 forms rather larger asci (190–220 × 140–170 µm) and brown, roundish closed conidiomata that open by irregular rupture, and covered with brown, verrucose to warted hairs/hyphae, 3–3.5 µm wide. In addition, the setae are more frequent, shorter (40–80 µm long) and broader at the base (5–7.5 µm diam). The appressoria are larger, measuring (5.5–)7.5–13(–17) × (4.5–)5.5–8.5(–10.5) µm, mean ± SD = 10.3 ± 2.6 × 7.1 ± 1.5 µm, L/W ratio = 1.4. This strain and CBS 111998 are also slower-growing than the type; on SNA: 20–22.5 mm in 7 d (32–34.5 mm in 10 d) and 20.5–22.5 mm in 7 d (30.5–31.5 mm in 10 d), and on OA: 21.5–23.5 mm in 7 d (33.5–35 mm in 10 d) and 15.5–16.5 mm in 7 d (25–27 mm in 10 d). There are some indications that CBS 129833 is distinct phylogenetically from the main body of *C. karstii* strains, but the sequence differences are slight.

Colletotrichum novae-zelandiae Damm, P.F. Cannon, Crous, P.R. Johnst. & B. Weir, **sp. nov.** MycoBank MB560742. Fig. 13.

Etymology: Named after the country from which it was collected, New Zealand.

Teleomorph not observed. *Anamorph on SNA. Vegetative hyphae* 1.5–10 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* absent, conidiophores formed directly from vegetative hyphae or from angular to roundish, hyaline, thick-walled cells, 3–8 µm diam. *Setae* not observed. *Conidiophores* hyaline, smooth-walled, septate, branched, to 50 µm long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical to more or less inflated, often extending to form new conidiogenous loci, making the conidiogenous cell appear catenate, sometimes polyphialidic, 4.5–20 × 4–6 µm, opening 1.5–2 µm diam, collarette

to 1 µm diam, periclinal thickening conspicuous. *Conidia* hyaline, smooth-walled, aseptate, cylindrical, the apex and base rounded, with a prominent scar, contents granular or guttulate, (12.5–)13–14.5(–15.5) × 5–5.5(–6) µm, mean ± SD = 13.8 ± 0.7 × 5.4 ± 0.2 µm, L/W ratio = 2.6. *Appressoria* only very few (8) observed, medium to dark brown, roundish with an undulate margin, single or in small clusters, 3.5–8 × 4–5.5 µm, mean ± SD = 5.9 ± 1.5 × 5.1 ± 0.6 µm, L/W ratio = 1.1. Appressoria of strain CBS 130240 are larger, also only very few (8) observed, measuring 7–12.5 × 5.5–7.5 µm, mean ± SD = 10.2 ± 2.0 × 6.7 ± 0.9 µm, L/W ratio = 1.5.

Anamorph on Anthriscus stem. Conidiomata acervular, conidiophores and setae formed on a cushion of pale brown, thick-walled, angular cells 3.5–7 µm diam. *Setae* dark brown, smooth to finely verruculose close to the tip, 2–3-septate, 90–140 µm long, base cylindrical, conical or inflated, usually paler, 4.5–6.5 µm diam, tip ± acute to rounded. *Conidiophores* pale brown, smooth-walled, septate, branched, to 30 µm long. *Conidiogenous cells* pale brown, smooth-walled, (broadly) cylindrical, often extending to form new conidiogenous loci, 8–15 × 4–6 µm, opening 1–1.5 µm diam, collarette 1 µm diam, periclinal thickening conspicuous. *Conidia* hyaline, smooth-walled, aseptate, cylindrical, the apex and base rounded, with a prominent scar, contents granular or guttulate, (12–)13–15(–15.5) × (4–)5–6 µm, mean ± SD = 14.1 ± 0.8 × 5.4 ± 0.4 µm, L/W ratio = 2.6.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline to pale luteous, filter paper partly pure yellow to luteous on both sides, filter paper, *Anthriscus* stem and partly agar medium covered with orange to black conidiomata/ascomata and filter paper and agar medium partly covered with white aerial mycelium, 24–25 mm in 7 d (35–37.5 mm in 10 d). Colonies on OA flat with entire margin, buff, honey, saffron, pure yellow to isabelline, partly coverd with floccose white aerial mycelium and with orange to black conidiomata/ascomata; reverse buff, vinaceous buff, pale luteous, luteous to isabelline, 24.5–27.5 mm in 7 d (36–39 mm in 10 d). *Conidia in mass* orange.

Material examined: **New Zealand**, GB, Gisborne, from ripe fruit rot of *Capsicum annuum* (sweet pepper), 1 Mar. 1990, P.R. Johnston, (CBS H-20706 **holotype**, culture ex-type CBS 128505 = ICMP 12944); AK, Auckland, from fruit *Citrus* sp. (grapefruit), 2 Aug. 1988, P.R. Johnston, CBS H-20707, culture CBS 130240 = ICMP 12064.

Notes: *Colletotrichum novae-zelandiae* is morphologically indistinguishable from other species of the *C. boninense* species complex. It forms a separate lineage/cluster in all single gene phylogenies, as sister to a group including *C. karstii*, *C. petchii*, *C. annellatum* and *C. phyllanthi*. This species is only known from New Zealand where it has been isolated from ripe fruit of *Capsicum* and *Citrus*. Johnston & Jones (1997) identified this species as *C. gloeosporioides* group E, and indicated that it was frequently isolated from *Citrus* fruits and also found on *Passiflora edulis*, although there was no molecular confirmation.

The only close match in blastn searches (99 % identity) was EU670082, the ITS sequence of "*Glomerella acutata"* strain S43 from *Prunus dulcis* (almond) in Australia. That strain was isolated together with *C. acutatum* and was shown to cause lesions on amond fruits in a pathogenicity test (McKay *et al.* 2009). It was first morphologically identified as *C. acutatum* by the authors and recognised later as *C. boninense* using molecular data.

Teleomorphic structures were observed in mated cultures of some strains from *Citrus* spp. that probably belong to *C. novae-zelandiae*, but their identity has not been confirmed by sequencing. *Ascomata* develop on PDA after 14 d in tight clumps of 4–5, along margins between colonies, mostly lacking an obvious neck or with a short, broad, hyaline ostiolar neck. *Asci* not observed. *Ascospores* aseptate, hyaline, smooth-walled, fusiform to ovoid, usually straight but sometimes slightly curved, measurements range from 12.5–19 × 5.5–7 µm (C1019.1 × C1041.19) to 16–22.5 × 4.5–7 µm (C1010.18 × C1015.3). No teleomorphic structures were observed in cultures derived from single conidia.

Colletotrichum oncidii Damm, P.F. Cannon & Crous, **sp. nov.** MycoBank MB560743. Fig. 14.

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

Anamorph on SNA. Vegetative hyphae 1–7.5 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* absent, conidiophores and setae formed directly from hyphae. *Setae* medium brown, basal cell paler, verruculose, 2–5-septate, 65–120 µm long, sometimes branched, base cylindrical, 3.5–5.5 µm diam, tip ± acute to ± rounded. *Conidiophores* hyaline, smooth-walled, septate, branched, to 75 µm long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical, often extending to form new conidiogenous loci, 8–23 × 3.5–5.5 µm, opening 1–2 µm diam, collarette ≤ 0.5 µm diam, periclinal thickening conspicuous. *Conidia* hyaline, smooth-walled, aseptate, cylindrical, the apex and base rounded, with a prominent scar, contents granular, (11.5–)13–15.5(–17.5) × 5–5.5(–6) µm, mean ± SD = 14.4 ± 1.3 × 5.5 ± 0.3 µm, L/W ratio = 2.6. *Appressoria* medium to dark brown, outline variable, usually lobate, single or in loose groups, (5.5–)8.5–16(–21) × (4–)5.5–10(–13) µm, mean ± SD = 12.2 ± 3.8 × 7.8 ± 2.2 µm, L/W ratio = 1.6.

Anamorph on Anthriscus stem. Conidiomata acervular, conidiophores and setae formed on a cushion of pale to medium brown, angular cells, 3–9 µm diam. *Setae* medium brown, verruculose, 2–5-septate, 75–210 µm long, base cylindrical to ± inflated, 3.5–7 µm diam, tip ± rounded to ± acute. *Conidiogenous cells* disintegrating quickly, their structure difficult to determine. *Conidia* hyaline, smooth-walled, aseptate, cylindrical, the apex and base rounded, with a prominent scar, contents granular to guttulate, (14–)15–17(–17.5) × 5–5.5(–6) µm, mean ± SD = 16.0 ± 0.8 × 5.4 ± 0.2 µm, L/W ratio = 3.0.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline to honey, with filter paper and *Anthriscus* stem partly covered with floccose white, rosy buff to olivaceous buff aerial mycelium, grey to salmon conidiomata; reverse hyaline to honey, filter paper partly pale saffron with dark grey spots due to conidiomata/ascomata shining through, 26.5–29 mm in 7 d (37.5–39 mm in 10 d). Colonies on OA flat with entire margin, surface buff to honey, some sectors covered with orange to black conidiomata and lacking aerial mycelium, some with granulose to floccose white to pale olivaceous grey aerial mycelium; reverse buff, honey, cinnamon, olivaceous gey to iron grey, 30–31.5 mm in 7 d (39–40 mm in 10 d). *Conidia in mass* salmon to orange.

Material examined: **Germany**, Munich, greenhouse, from leaf of *Oncidium* sp., 20 Nov. 2010, U. Damm, (CBS H-20709 **holotype**, culture ex-type CBS 129828); Munich, greenhouse, from leaf of *Oncidium* sp., 20 Nov. 2010, U. Damm, CBS H-20708, culture CBS 130242.

Notes: *Colletotrichum oncidii* forms a sister group to *C. cymbidiicola*, also orchid pathogens but recorded from the Asia-Pacific region

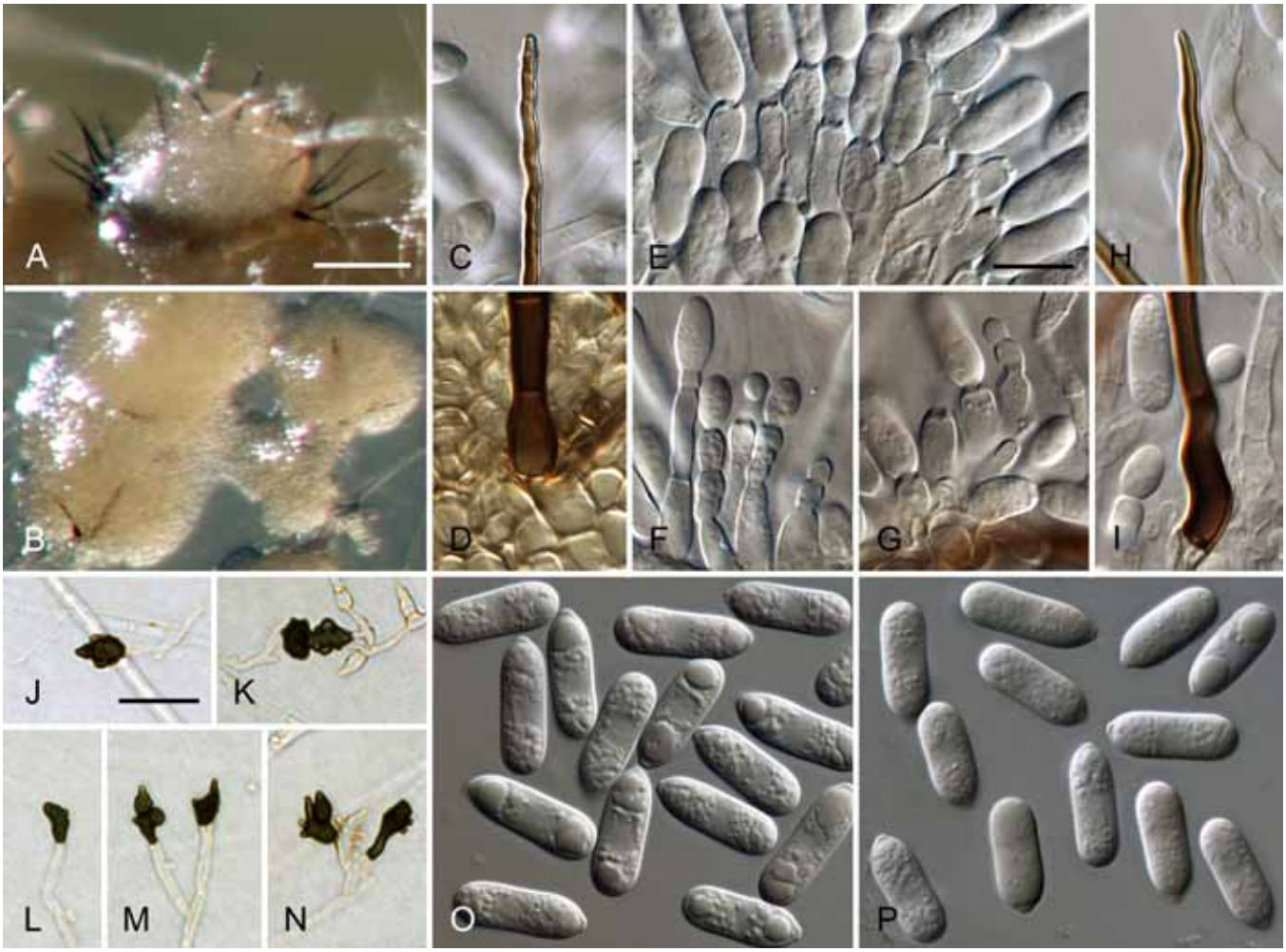

Fig. 14. *Colletotrichum oncidii* (from ex-holotype strain CBS 129828). A–B. Conidiomata. C. Tip of seta. D. Basis of seta. E–G. Conidiophores. H. Tip of seta. I. Basis of seta. J–N. Appressoria. O–P. Conidia. A, C–D, O. from *Anthriscus* stem. B, E–N, P. from SNA. A–B. DM, C–P. DIC, Scale bars: A = 100 µm, E = 10 µm, J = 25 µm. Scale bar of A applies to A–B. Scale bar of E applies to C–I and O–P. Scale bar of J applies to J–N.

rather than Europe. The known isolates of *C. oncidii* were from plants in greenhouses, and the ultimate origin of the species is uncertain. It has well-developed strongly setose conidiomata in culture, pale conidia and conidiogenous cells that extend to form new conidiogenous loci.

Colletotrichum oncidii differs from the closely related *C. boninense* in forming appressoria that are larger and lobate, while those of *C. boninense* are entire or crenate. *Colletotrichum oncidii* also has longer setae (SNA: 65–120, *Anthriscus* stem: 75–210) that are 2–5-septate on both media, while those of *C. boninense* are only 20–60 or 30–70 µm long, and 1–2-septate. No teleomorph is known.

Colletotrichum parsonsiae Damm, P.F. Cannon, Crous, P.R. Johnst. & B. Weir, **sp. nov.** MycoBank MB560744. Fig. 15.

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

Teleomorph on *SNA*. *Ascomata* perithecia, formed after 4 wk, obpyriform, ostiolate, glabrous, 100–170 × 120–220 µm. *Peridium* composed of pale to medium brown, flattened *textura angularis* with cells 5–16 µm diam. *Interascal tissue* formed of paraphyses, hyaline, smooth-walled, mostly cylindrical but tapering towards the rounded tip, disintegrating quickly, septate, apically free, 50–70 × 3–4 µm. *Asci* unitunicate, 8-spored, cylindrical to clavate, tapering to apex and base, smooth-walled, 70–80 × 10–13 µm. *Ascospores* biseriately arranged, aseptate, hyaline, smooth-walled, broadly allantoid with rounded ends, (12.5–)14–17(–18) × (5–)5.5–6(–6.5) µm, mean ± SD = 15.7 ± 1.4 × 5.8 ± 0.4 µm, L/W ratio = 2.7.

Anamorph on SNA. *Vegetative hyphae* 1–7 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* acervular, conidiophores and setae formed on a cushion of pale brown, angular cells, 3–7 µm diam. *Setae* pale to medium brown, basal cell often paler, smooth-walled, 2–4-septate, 50–150 µm long, base cylindrical to conical, 4–6 µm diam, tip ± acute to rounded. *Conidiophores* hyaline to pale brown, smooth-walled, septate, branched, to 45 µm long. *Conidiogenous cells* hyaline to pale brown, smooth-walled, cylindrical to ampulliform, surrounded by a gelatinous sheath, sometimes extending to form new conidiogenous loci, 10–25 × 3–5.5 µm, opening 1–2 µm diam, collarette ≤ 0.5 µm long, periclinal thickening sometimes distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical, apex and base rounded, hilum visible, the contents guttulate, (12.5–)16.5–20.5(–21.5) × 5–6(–6.5) µm, mean ± SD = 18.5 ± 1.8 × 5.4 ± 0.3 µm, L/W ratio = 3.4. *Appressoria* in loose groups to dense clusters, medium to dark brown, navicular, bullet-shaped to ellipsoidal in outline, smooth, crenulate to lobate, (7.5–)10–16.5(–22.5) × (4.5–)5.5–8(–10.5) µm, mean ± SD = 13.2 ± 3.3 × 6.6 ± 1.3 µm, L/W ratio = 2.0.

Anamorph on Anthriscus stem. *Conidiomata* acervular, conidiophores and setae formed from a cushion of pale brown,

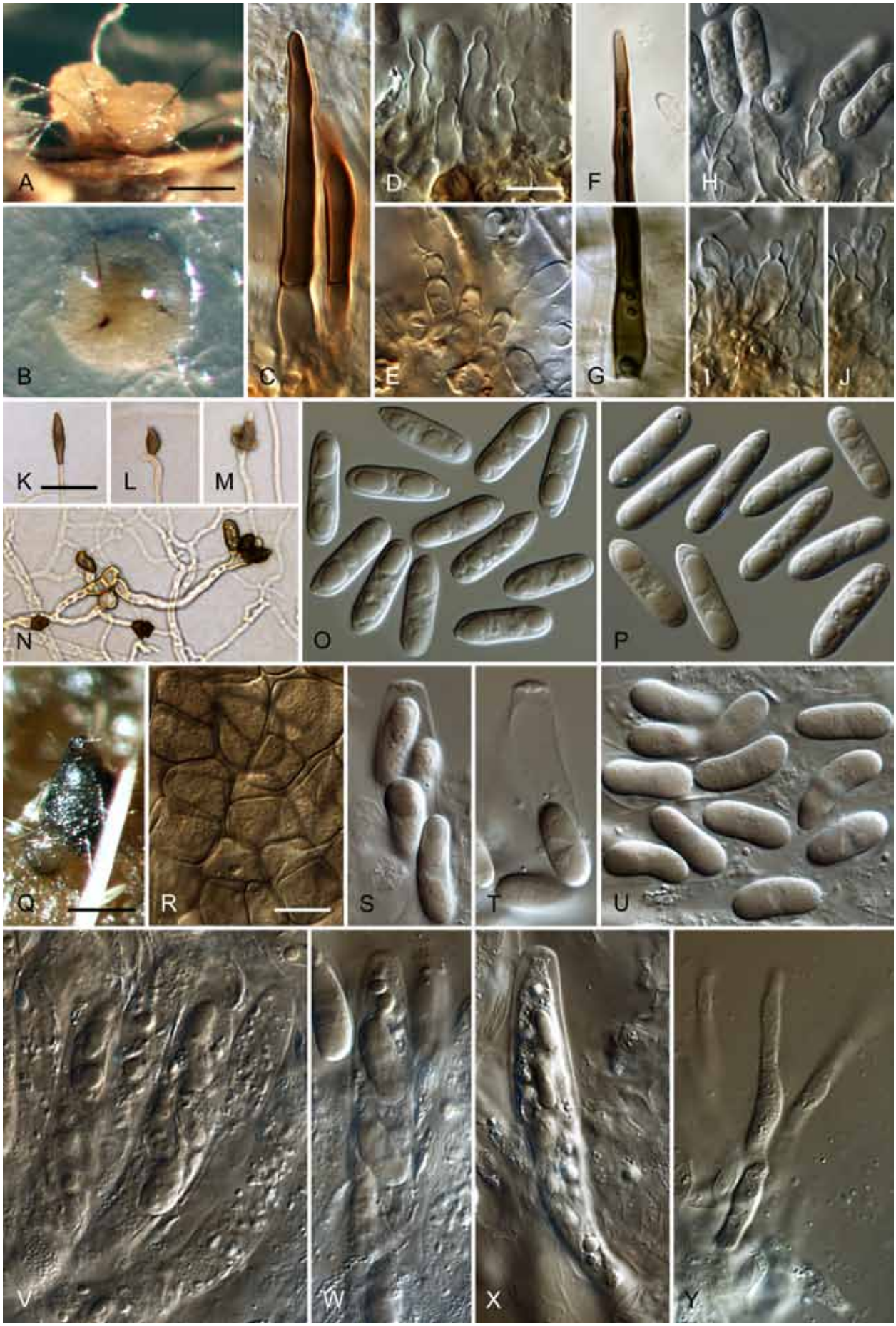

Fig. 15. *Colletotrichum parsonsiae* (from ex-holotype strain CBS 128525). A–B. Conidiomata. C. Setae. D–E. Conidiophores. F. Tip of seta. G. Basis of seta. H–J. Conidiophores. K–N. Appressoria. O–P. Conidia. Q. Ascomata. R. Outer surface of peridium. S–T. Apical region of ascus. U. Ascospores. V–X. Asci. Y. Paraphyses. A, C–E, O, Q. from *Anthriscus* stem. B, F–N, P, R–Y. from SNA. A–B, Q. DM, C–P, R–Y. DIC, Scale bars: A, Q = 100 µm, D, R = 10 µm, K = 25 µm. Scale bar of A applies to A–B. Scale bar of D applies to C–J and O–P. Scale bar of K applies to K–N. Scale bar of R applies to R–Y.

angular, thick-walled cells, 4–10.5 µm diam. *Setae* dark brown, basal cell sometimes paler, smooth-walled to verruculose, 2–4-septate, 60–200 µm long, base cylindrical to conical, 4.5–7.5 µm diam, tip rounded. *Conidiophores* hyaline to pale brown, smooth-walled, septate, branched, to 50 µm long. *Conidiogenous cells* hyaline to pale brown, smooth-walled, surrounded by a gelatinous sheath, sometimes extending to form new conidiogenous loci, 4–16 × 3–4.5 µm, opening 1–2 µm diam, collarette ≤ 0.5 µm long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical, apex round, base round, hilum visible, the contents guttulate, (15–)16.5–19(–20) × (4.5–)5–6(–6.5) µm, mean ± SD = 17.6 ± 1.3 × 5.4 ± 0.5 µm, L/W ratio = 3.2.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline, with filter paper and medium partly covered with salmon to grey conidiomata and *Anthriscus* stem covered with white aerial mycelium; reverse hyaline to honey with salmon to grey flecks, 20–24 mm in 7 d (32.5–34 mm in 10 d). Colonies on OA flat with entire margin, buff, fawn to rosy buff with dark grey to black conidiomata or ascomata and partly with floccose white aerial mycelium; reverse buff to fawn with olivaceous grey spots due to the conidiomata/ascomata shining through, 22–26.5 mm in 7 d (35–37.5 mm in 10 d). *Conidia in mass* salmon to orange.

Material examined: **New Zealand**, Auckland, leaf endophyte from *Parsonsia capsularis*, 1 Dec. 2009, G. Carroll, (CBS H-20710 **holotype**, culture ex-type CBS 128525 = ICMP 18590).

Notes: *Colletotrichum parsonsiae* is known from a single collection on *Parsonsia capsularis* from New Zealand. There are no *Colletotrichum* species described on *Parsonsia* and no record of any *Colletotrichum* sp. on *Parsonsia* in the USDA Fungus-Host database (Farr & Rossman 2011). The shape and size of conidia differ from other species in the *C. boninense* complex. Conidia are shorter than those of the closely related *C. hippeastri*, but longer than those of all other species. The conidial width is the same or less, resulting in comparatively high L/W ratios, especially on *Anthriscus stem* (L/W ratio = 3.7).

Colletotrichum petchii Damm, P.F. Cannon & Crous, **nom. nov.** MycoBank MB560745. Fig. 16.

Basionym: *Colletotrichum dracaenae* Petch, Annls Roy. Bot. Gdn Peradeniya 9: 325. 1925, nom. illeg. (Art. 53.1).

≠ *Colletotrichum dracaenae* Allesch., in Rabenhorst, Rabenh. Krypt.-Fl. (Leipzig) 7: 560. 1902.

Etymology: Named after Thomas Petch (1870–1948), an English mycologist and plant pathologist who discovered this species but described it under a previously existing name, *Colletotrichum dracaenae*.

Teleomorph on Anthriscus stem: Ascomata perithecia, globose to subglobose, *ca.* 200 × 150 µm, ostiolate, glabrous, the neck short, hyaline to pale brown, outer wall composed of medium to dark brown verruculose angular cells 6.5–11(–17) × 9–16(–20) µm in size. Interascal tissue composed of paraphyses; hyaline, septate, apparently unbranched, the basal cells strongly inflated, 45–50 × 13–15.5 µm. *Asci* clavate, the apex ± truncate with a well-developed refractive apical ring, 45–85 × 12–15.5 µm, 8-spored. *Ascospores* arranged biseriately, hyaline to pale brown, aseptate, narrowly ovoid to fusiform and slightly inaequilateral, smooth, without a gelatinous sheath, (14.5–)16–18.5(–20) × (4.5–)5–6(–6.5) µm, mean ± SD = 17.2 ± 1.3 × 5.7 ± 0.5 µm, L/W ratio = 3.0.

Anamorph on SNA. Vegetative hyphae 1–8 µm diam, hyaline to pale brown, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* acervular, conidiophores and setae formed on a cushion of pale brown, roundish cells, 4.5–9 µm diam. *Setae* medium to dark brown, basal cell sometimes lighter, verruculose, 1–2(–3)-septate, 40–110 µm long, the base somewhat bulbous, 6–9 µm diam, tip round to somewhat acute. *Conidiophores* pale brown, septate, branched, surrounded by a slimy gelatinous coating, to 50 µm long. *Conidiogenous cells* pale brown, paler towards the tip, smooth, cylindrical to ampulliform, with a gelatinous coating, sometimes extending to form new conidiogenous loci, 11–16 × 3.5–5 µm, opening 1–1.5 µm diam, collarette and periclinal thickening inconspicuous. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical, sometimes slightly constricted in the middle of the conidium, apex round, base round with a short prominent hilum, guttulate, sometimes containing two big polar guttules, (14.5–)15–17.5(–18.5) × (5.5–)6–6.5 µm, mean ± SD = 16.3 ± 1.1 × 6.1 ± 0.3 µm, L/W ratio = 2.7. *Appressoria* irregular in shape, dark brown, sometimes nodose, not formed in chains, (4.5–)8.5–15.5(–19) × (5–)6–10(–13) µm, mean ± SD = 12.0 ± 3.4 × 7.9 ± 2.0 µm, L/W ratio = 1.5.

Anamorph on Anthriscus stem. Conidiomata acervular, conidiophores and setae formed on a cushion of pale brown, angular cells cells 3–10 µm diam. *Setae* medium to dark brown, the base often paler, smooth to finely verruculose, 1–2(–3)-septate, 50–130 µm long, base conical or inflated, 5–10 µm wide, tip round to somewhat acute. *Conidiophores* pale brown, septate, branched, to 30 µm long. *Conidiogenous cells* pale brown, smooth, cylindrical or conical, annellations observed on some cells, 9–16 × 4.5–6 µm, opening 1–2 µm diam, collarette ≤ 0.5–1 µm long, periclinal thickening conspicuous. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical, sometimes slightly constricted in the middle of the conidium, apex round, base round with a short, prominent hilum, sometimes guttulate, (12.3–)14.5–18(–21.1) × (5–)5.5–6.5 µm, mean ± SD = 16 ± 1.8 × 6 ± 0.3 µm, L/W ratio = 2.7.

Culture characteristics: Colonies on SNA flat with entire to slightly undulate margin, hyaline with woolly white aerial mycelium on filter paper and SNA medium and salmon to orange acervuli on filter paper and SNA medium and black ascomata on *Anthriscus* stem; reverse filter paper buff to pale cinnamon with acervuli shining through medium; 23.8–25 mm in 7 d (33–35.5 mm in 10 d). Colonies on OA flat with entire to slightly undulate margin; surface buff to rosy buff, with sectors covered with grey to black structures or orange spore masses and with woolly white aerial mycelium in the centre, reverse buff to cinnamon, with grey to black structures shining through medium; 20–25 mm in 7 d (33–36.3 mm in 10 d). *Conidia in mass* salmon to orange.

Material examined: **Sri Lanka**, Peradeniya, from dark brown patches on leaves of *Dracaena braunii* (syn. *D. sanderiana*), May 1924, collector not named, no. 6775 (K(M) 125641, **holotype** of *C. dracaenae* Petch. **Italy**, from spotted leaves of *Dracaena fragrans* (syn. *D. deremensis*), P. Di Lenna (from Università degli Studi, Padova), deposited in June 1994, CBS-H 20711, **epitype** of *C. dracaenae* Petch, here designated, culture ex-epitype CBS 378.94. **China**, from living leaves of *Dracaena sanderiana*, 30 Apr. 2001, P. Milicia, culture CBS 118193 = AR 3658. **Netherlands**, from leaf spots of *Dracaena* sp., received from Naktuinbouw Roelofarendsveen, culture CBS 125957. **Germany**, Munich, greenhouses of the botanical garden, from wilting leaves of *Dracaena aletriformis* (syn. *D. latifolia*), Apr. 1895, J.E. Weiss, M-0090064, **holotype** of *C. dracaenae* Allescher.

Notes: Conidia of *C. petchii* are larger than those of *C. boninense* and *C. brassicicola*. Conidia, ascospores and asci are usually

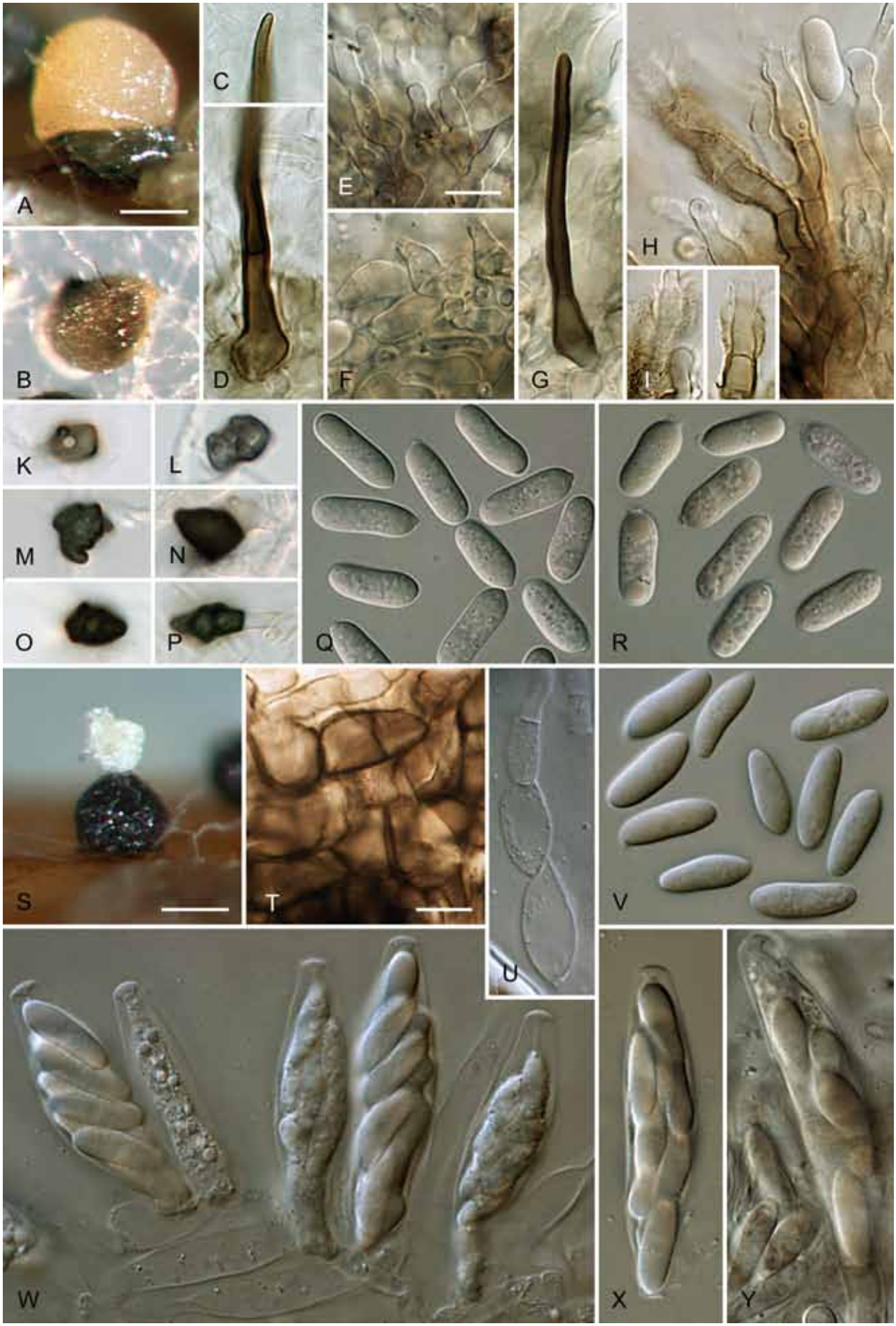

Fig. 16. *Colletotrichum petchii* (from ex-epitype strain CBS 378.94). A–B. Conidiomata. C. Tip of seta. D. Basis of seta. E–F. Conidiophores. G. Seta. H–J. Conidiophores. K–P. Appressoria. Q–R. Conidia. S. Ascomata. T. Outer surface of peridium. U. Paraphysis. V. Ascospores. W–Y. Asci. A, C–F, Q, S–T, V, Y. from *Anthriscus* stem. B, G–P, R, U, W–X. from SNA. A–B, S. DM, C–R, T–Y. DIC, Scale bars: A, S = 100 µm, E, T = 10 µm. Scale bar of A applies to A–B. Scale bar of E applies to C–R. Scale bar of T applies to T–Y.

also larger than those of *C. karstii* and C. *phyllanthi*. Conidia of *C. hippeastri* are larger, while *C. dracaenophilum* occurs on *Dracaena* spp. as well, but is not closely related to *C. petchii* as demonstrated by Farr *et al.* (2006). Their study included CBS 118193 and CBS 118774 (*C. petchii*). Another species from *Dracaena*, *C. dracaenae-fragrantis*, has narrower conidia, measuring 5–12 × 2.5–3.5 µm (Saccardo 1895); its affinities are unclear.

Colletotrichum dracaenicola (syn. *C. dracaenae* Trinchieri 1909, *non* Allesch.) may be a synonym of *C. dracaenae*. The conidial size was given as 12–19 × 2–7 µm by Saccardo & Trotter (1913), which is an unusually wide range, but which overlaps with that of *C. dracaenae* Allesch. Farr *et al.* (2006) could not locate the type specimen (it was not present in NAP, PORUN or PAD), and the name therefore remains uncertain.

Von Arx (1957) considered both *C. dracaenae* Allesch. and *C. dracaenae* Petch to be synonyms of *C. gloeosporioides*. Farr *et al.* (2006) agreed with this conclusion concerning *C. dracaenae* Allesch. after studying type material, although their focus was on the need to demonstrate distinctions between *C. dracaenae* and their new species *C. dracaenophilum*. The shape of the conidia of *C. dracaenae* is similar to *C. gloeosporioides*, including the overall length and the constriction in the central part. The conidia were found to be noticeably wider in *C. dracaenae* compared with "typical" *C. gloeosporioides.*

The original description (Allescher 1902) of the conidia of *C. dracaenae* Allesch. (14–18 × 5–7 µm, elongate-cylindrical, both sides round) fits well with the species as circumscribed here. Most features of the setae also agree (40–60 µm long, obtuse tip, few septa, appearing late at the margins of conidiomata), apart from their diameter (2.5–3.5 µm according to Allescher, 5–10 µm diam as measured here in the CBS strains). In the type material, we found that the conidia measured (12.5–)13.5–16 × 5–6 µm (n = 20, mean ± SD = 15.2 ± 1.1 × 5.4 ± 0.3 µm, L/W ratio 2.8), which is smaller than those of the epitype of *C. petchii* but with a comparable L/W ratio. Few conidia had a noticeably prominent hilum, and the setae were found to be narrow (as observed by Allescher) and slightly verruculose. It is not certain that Allescher's collection and the CBS isolates represent the same species, as comparisons with dried material and living cultures are difficult. As the conidial hilum morphology seems to diverge from that seen in *C. petchii* (a diagnostic feature of the *C. boninense* aggregate) we have chosen not to use Allescher's name.

Part of the type of *C. dracaenae* Petch was examined by Farr *et al.* (2006), who noted that the fruit bodies had a very thin subhymenial layer that is only one or two layers thick. No other observations were made, and it is possible that the material they examined was effete. We re-examined the type and found conidiomata typical of the *C. boninense* aggregate. In concordance with Petch's original description, the setae are strongly curved and tapering, and strongly verruculose towards the tip. Few conidia were seen and those present were variable in shape and length/width ratio. The majority of those examined were 14–16 × 5–6.5 µm in size, and were cylindrical to doliiform with a rather prominent hilum. We place Petch's illegitimate taxon with confidence in the *C. boninense* aggregate, and it is not unreasonable to suppose that it is synonymous with *C. dracaenae* Allesch. Petch (1925) contrasted his species with *C. cordylines* Pollacci but was evidently unaware of Allescher's work.

In contrast to other species in the *C. boninense* complex, *C. dracaenae* may be host-specific to *Dracaena*. The majority of *Dracaena* species are native to Africa, with a few in southern Asia and one in tropical Central America, and they are often grown as pot plants or in greenhouses. The host species of the isolates studied here are popular houseplants. *Colletotrichum dracaenae* was mostly isolated from leaves, where it caused leaf spots as indicated in the sampling details of some of the isolates (Di Lenna & Montecchio 1995). Within the species there is only low sequence variability, and separate clusters are obtained with all phylogenies employing single genes.

Colletotrichum phyllanthi (H. Surendranath Pai) Damm, P.F. Cannon & Crous, **comb. nov.** MycoBank MB560746.
Basionym: *Glomerella phyllanthi* H. Surendranath Pai, Mycopath. Mycol. appl. 42: 70. 1970.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline, lacking aerial mycelium; reverse filter paper very pale luteous; 21.3–23.8 mm in 7 d (32.5–33.8 mm in 10 d). Colonies on OA flat with entire to slightly undulate margin; surface buff to saffron, lacking aerial mycelium, reverse same colours; 19–23 mm in 7 d (30.8–35 mm in 10 d). *Anamorph and teleomorphic structures* not observed in the culture available.

Material examined: **India**, Maharashtra, Poona, from leaf anthracnose on *Phyllanthus acidus*, 10 Feb. 1966, H. Surendranath Pai, IMI 122826, **holotype**; Maharashtra, Poona, isolated from anthracnose symptoms on leaves of *Phyllanthus acidus*, 10 Feb. 1966, H. Surendranath Pai, CBS H-7188, **isotype**, dried culture (PDA) of ascigerous stage, culture ex-isotype CBS 175.67 = MACS 271.

Notes: *Glomerella phyllanthi* is known only from the original collection taken from leaves of *Phyllanthus acidus* in India. The ex-type strain CBS 175.67, deposited in the CBS collection, did not sporulate under standard growth conditions. The description below is derived from the original publication (Pai 1970).

"Perithecia isolated or gregarious, dark brown, 159–190.8 µm with long beaks measuring 47.7–150 µm. Ostiolar threads absent. Asci numerous, unitunicate, clavate, octosporous, arising in basal layers, sessile to subsessile, 43.2–56.6 × 8.6–10.8 µm. Paraphyses abundant in early stages but disintegrating at maturity. Ascospores uniseriate or irregularly biseriate, elliptical to slightly curved, hyaline with oil globules at both ends, 12.9–17.28 × 2.1–6.4 µm." Ascospore measurements from the isotype (CBS H-7188) agree with those of the original description: (14–)14.5–17(–18) × (4–)4.5–5.5(–6) µm, mean ± SD = 15.7 ± 1.1 × 5.1 ± 0.6 µm, L/W ratio = 3.1. Pai (1970) assumed that *G. phyllanthi* was the teleomorph of *Colletotrichum heveae*, and did not provide a complete description of the anamorph, providing the following information: acervuli 113–159 µm, setae (only formed in old cultures) 63–143 µm, conidia cylindrical, oblong, 14–17 × 3–5 µm. No anamorph structures could be observed in the holotype or isotype specimens.

According to its original description, conidia of *Glomerella phyllanthi* are narrower than the other species within the *C. boninense* complex and none formed ascomata with a long beak as reported from *G. phyllanthi*, though it must be recognised that culture medium and growth conditions were not the same. According to the multigene phylogeny, *G. phyllanthi* forms a separate lineage close to *C. karstii*. This was the situation also in 5 of 7 single-gene phylogenies.

Glomerella phyllanthi causes an anthracnose disease on leaves of *Phyllanthus acidus* in India (Pai 1966) but has not been reported since. Farr & Rossman (2011) list *C. gloeosporioides* from *Phyllanthus emblica* in China (Zhuang 2001) and *P. reticulatus* in Myanmar (Thaung 2008) as well as an unidentified *Colletotrichum* sp. from *P. acidus* in India (Mathur 1979), of which at least the latter could be identical with *G. phyllanthi*.

Fig. 17. *Colletotrichum torulosum*. A–B. Conidiomata. C. Setae. D–F. Conidiophores. G. Seta. H. Conidiophores. I–N. Appressoria. O–P. Conidia. A–B, D–P. from ex-holotype strain CBS 128544. C. from strain CBS 102667. A, C–F, O. from *Anthriscus* stem. B, G–N, P. from SNA. A–B. DM, C–P. DIC, Scale bars: A = 100 µm, D = 10 µm. Scale bar of A applies to A–B. Scale bar of D applies to C–P.

Pai (1970) regarded *C. heveae* Petch as the anamorph of *G. phyllanthi* on the basis of the telemorph strain being pathogenic to four of six *Euphorbiaceae* plant species tested, including *Hevea brasiliensis*, along with general morphological similarity. The conidium size of *C. heveae* was given as 18–24 × 7.5–8 µm by Petch (1906), wrongly cited by Pai (1970) as 18–24 × 5–8 µm.

Type material of *Colletotrichum heveae* (Sri Lanka, on *Hevea*, 7 Oct. 1905, Petch 2228, K(M) 167287) is in poor condition with the *Colletotrichum* colonies overrun by saprobic species. The packet indicates that two species are present, *Gloeosporium brunneum* and *C. heveae.* Apart from the saprobic fungi the only species now present is a *Colletotrichum*-like fungus that lacks setae, but with rather variable ± cylindrical conidia with rounded ends that are mostly 14.5–16 × 4–6 µm in size. These are wider than typical *C. gloeosporioides* conidia and are reminiscent in some features of the *C. boninense* aggregate, so it is possible that the anamorph-teleomorph connection assumed by Pai (1970) is correct. However, there are no authentic cultures of *C. heveae* and the type material is in a poor state. *Gloeosporium brunneum* Ellis & Everh. is considered to be the anamorph of *Drepanopeziza punctiformis* Gremmen (von Arx 1970), a north temperate pathogen of *Populus* and most unlikely to be present on a *Hevea* leaf from Sri Lanka. Use of that name by Petch remains a mystery. According to a note in the CBS database von Arx did not support the teleomorph/anamorph connection assumed by Pai (1970), and we can see no clear reason why the two taxa should be linked in this way.

Diseases of *Hevea* in south India caused by *Colletotrichum* species are attributable to the *C. gloeosporioides* and *C. acutatum* aggregates (*e.g.* Saha *et al.* 2002; unpublished ITS sequences from this research deposited in GenBank confirm these identifications to species aggregate level). A species on *Hevea* from Colombia closely related to *C. phyllanthi* is described in this paper (see *C. annellatum*).

Colletotrichum torulosum Damm, P.F. Cannon, Crous, P.R. Johnst. & B. Weir, **sp. nov.** MycoBank MB560747. Fig. 17.

Etymology: Named in recognition of the highly convoluted nature of its appressoria.

Anamorph on SNA. Vegetative hyphae 1–7.5 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* absent and conidiophores and setae formed directly from hyphae. *Setae* medium brown, basal cell paler, verruculose, 2–5-septate, 65–120 µm long, sometimes branched, base cylindrical, 3.5–5.5 µm diam, tip ± acute to ±rounded. *Conidiophores* hyaline, smooth-walled, septate, branched, to 75 µm long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical, 8–23 × 3.5–5.5 µm, opening 1–2 µm diam, collarette ≤ 0.5 µm diam, periclinal thickening conspicuous. *Conidia* hyaline, smooth-walled, aseptate, cylindrical, the apex and base rounded, with a prominent scar and an apparently verrucose vesicle attached to

it, contents granular, (13–)14–17(–21) × 5.5–6.5(–7.5) µm, mean ± SD = 15.5 ± 1.5 × 6.0 ± 0.4 µm, L/W ratio = 2.6, conidia of strain CBS 102667 are shorter, measuring (10.5–)12–14.5(–17.5) × (4.5–)5.5–6.5 µm, mean ± SD = 13.4 ± 1.2 × 5.8 ± 0.5 µm, L/W ratio = 2.3. *Appressoria* medium to dark brown, outline variable, the margin lobate, single or in loose groups, (5.5–)8.5–14.5(–16.5) × (4.5–)6–9.5(–13) µm, mean ± SD = 11.4 ± 2.9 × 7.7 ± 1.9 µm, L/W ratio = 1.5.

Anamorph on Anthriscus stem. Conidiomata acervular, conidiophores formed on a cushion of pale brown, angular cells, 3–10 µm diam. *Setae* not observed in strain CBS 128544. Setae of strain CBS 102667 medium brown, basal cell paler, verruculose, sometimes verrucose, 0–2-septate, 20–60 µm long, base cylindrical, conical or slightly inflated, 4.5–6.5 µm diam, tip rounded. *Conidiophores* hyaline to pale brown, smooth-walled, septate, branched, to 60 µm long. *Conidiogenous cells* hyaline to pale brown, smooth-walled, cylindrical, often extending to form new conidiogenous loci, 9–23 × 4.5–6.5 µm, opening 1.5–2.5 µm diam, collarette ≤ 0.5 µm diam, periclinal thickening conspicuous. *Conidia* hyaline, smooth-walled, aseptate, cylindrical, the apex and base rounded, with a prominent scar, contents guttulate, (13.5–)14.5–16.5(–17.5) × (5–)5.5–6(–6.5) µm, mean ± SD = 15.5 ± 0.9 × 5.8 ± 0.3 µm, L/W ratio = 2.7, conidia of strain CBS 102667 are shorter, measuring 12–14.5(–18) × (5–)5.5–6(–6.5) µm, mean ± SD = 13.4 ± 1.3 × 5.7 ± 0.4 µm, L/W ratio = 2.3.

Material examined: **New Zealand**, GB, Gisborne, Allen Park Gardens, from *Solanum melongena* (eggplant), 6 Mar. 1990, P.R. Johnston, (CBS H-20715 **holotype**, culture ex-type CBS 128544 = ICMP18586); Auckland, Mount Albert, from leaf bloch of *Passiflora edulis*, May 2000, C.F. Hill, CBS H-20716, culture CBS 102667.

Notes: *Colletotrichum torulosum* occupies a minor clade as sister to a group containing *C. boninense s. str.* and an unnamed taxon that occurs on orchids (CBS 123921). It has significantly longer conidia than *C. boninense* with a larger L/W ratio. The conidia formed on SNA have hyaline, faintly verrucose vesicles attached to the base adjacent to the conidial scar. The function of these structures is unclear and they may be artefacts. These vesicles also occur on conidia of *C. cymbidiicola* (Fig. 9R).

Colletotrichum torulosum is known from two New Zealand collections, on *Solanum* and *Passiflora*. Endophytic strains from *Dacrycarpus dacrydioides* (*Podocarpaceae*) and *Kunzea ericoides* (*Myrtaceae*) leaves from New Zealand have the same ITS sequences as *C. torulosum* (EU482212, EU482213; Joshee *et al.* 2009), although their identity needs to be confirmed by comparison with sequences of other genes. *Colletotrichum torulosum* is not host-specific. It is not clear whether it is a native New Zealand species that has jumped onto cultivated exotic plants, or has been imported on diseased plant material.

DISCUSSION

Moriwaki *et al.* (2003) differentiated *C. boninense* from *C. gloeosporioides* based on its wider conidia (L/W ratio = (1.8–)2–3(–3.3), the prominent scar at the conidial base and cream to orange coloured colonies on PDA. The L/W ratio of conidia of *C. boninense s. str.* and *C. karstii* (included in *C. boninense* by Moriwaki *et al.* 2003) are variable, ranging from 2.1 to 2.8 depending on isolate (and medium), while conidia of *C. gloeosporioides* have a L/W ratio of 2.6 to 3.0 (Cannon *et al.* 2008, Weir *et al.* 2012). According to Moriwaki *et al.* (2003), the shape of the appressoria in *C. boninense* differs from that seen in *C. gloeosporioides*, and setae are rarely produced in *C. boninense*. Many strains belonging to the *C. boninense* aggregate have more complex appressoria than those typical for *C. gloeosporioides*.

None of the morphological characters of *C. boninense* enables unequivocal identification and misplacement of strains based on morphology alone is common. For example, Lu *et al.* (2004) classified one isolate as *C. gloeosporioides* according to morphological characters but re-identified it as *C. boninense* using molecular techniques. *Colletotrichum dracaenae* Petch (here epitypified and renamed as *C. petchii*) was considered as a synonym of *C. gloeosporioides* by von Arx (1957). Our study shows that *C. petchii* does not belong to *C. gloeosporioides s. lat.,* but to the *C. boninense* species complex, although the conidia are largely typical of *C. gloeosporioides* with their relatively large length/width ratio.

Conidiogenesis in the *C. gloeosporioides* and *C. boninense* species complexes is usually percurrent, but more variable in *C. boninense*, depending on the site of septation in the conidiogenous cell that results in a prominent periclinal thickening. Sometimes distinct annellations are formed, which are common in *C. annelatum* and occasionally occur in *C. dacrycarpi* and *C. petchii*. After producing a number of conidia the conidiogenous cells of many species extend without forming a septum and form a new conidiogenous locus at the tip. These processes can alternate, making the conidiogenous cell appear catenate, *e.g.* in *C. constrictum*, *C. novae-zelandiae* and *C. oncidii*. Additionally, several species had an apparent gelatinous multi-layered coating around the conidiogenous cells.

Differentiation between the two species complexes using morphological methods is problematic, but the diagnostic characters established by Morikawi *et al.* (2003) can be used reliably to identify many isolates. A distinctive feature of the *C. boninense* complex in morphological terms is the conidiogenous cell with prominent periclinal thickening that extends to form a new conidiogenous locus. This feature is unknown in species of the *C. gloeosporioides* complex (Weir *et al.* 2012). Another distinctive feature of the *C. boninense* complex is the prominent scar (hilum) at the base of the conidia.

Species of the *C. boninense* complex appear to be concentrated in certain regions of the world, and prefer certain host plants. Isolates treated in this paper and found by nucleotide blastn searches of GenBank originate mainly from New Zealand/Australia, South and East Asia (Japan, China, Taiwan, Thailand, Vietnam, India), South and Central America (Columbia, Brazil, Panama, Mexico, Guyana) and South and East Africa (South Africa, Zimbabwe, Kenya). A number of isolates from Europe (Italy, Netherlands, Germany and probably Hungary) have been associated with indoor/greenhouse plants (*Dracaena*, *Hippeastrum* and *Gossypium* species and several orchids) or air from greenhouses with orchids (Magyar *et al.* 2011). A few samples from *Coffee arabica* and *Leucospermum* originated from U.S.A. (Hawaii) and one from *Protea obtusifolia* from Madeira (Portugal).

Four of the species in the *C. boninense* complex have only been found in New Zealand (two on indigenous plants), and three only from Colombia or Brazil (two of these from *Passiflora*). The species richness in New Zealand is surprising as no *Colletotrichum* taxon has previously been described from this country, apart from the *formae speciales C. acutatum f. sp. pineum* and *C. gloeosporioides f. sp. camelliae*. Compared with many countries, plant biosecurity is well supported in New Zealand, and both exotic and indigenous species are likely to be surveyed more intensively for pathogens

than in many other regions of the world. Sampling bias is likely an explanation for this phenomenon.

In some *Colletotrichum* species complexes there is little or no evidence of host specificity even at species level (*e.g.* Johnston & Jones 1997, Damm *et al.* 2009), while others appear to be associated with single host genera and/or families, *e.g.* in the *C. graminicola* and *C. orbiculare* species complexes (Crouch *et al.* 2009, Liu *et al.* 2007). There are indications that a few of the segregate taxa within the *C. boninense* complex are host-specific, or at least show preference for hosts from particular plant groups. Morikawi *et al.* (2003) detected four molecular subgroups within the species as they defined it, using ITS1 data. The primary branch separated strains from monocotyledonous (monocot) and dicotyledonous (dicot) plant hosts. The dicot clade did not show any clear host-linked substructure, but the monocot clade contained three subclades with one restricted to *Orchidaceae* and the other two containing strains from *Crinum* (*Amaryllidaceae*). The dicot clade corresponds to *C. karstii* as recognised in this paper, while the monocot clade contains *C. boninense s. str*. Our research does not support this split. While occuring on a wide range of dicots, *C. karstii* was also described on *Orchidaceae* and occurs on other monocots as well, especially *Musa* spp. Of the other segregate species that we recognise, *C. dracaenae* and *C. hippeastri* seem to be specific at host genus level, although the number of strains that we have examined is insufficient to confirm these indications.

A feature of many strains of the *C. boninense* aggregate is the production of a teleomorph. The *Glomerella* morphs of *Colletotrichum* have been inadequately studied in comparison to the anamorphs. Von Arx & Müller (1954) carried out a global revision using morphological characters and Uecker (1994) completed an ontogenetic study of one *C. gloeosporioides* isolate. We know that at least some strains of most of the principal species aggregates can undergo meiosis, including the *C. acutatum* group (Guerber & Correll 2001, Guerber *et al.* 2003, Marcelino *et al.* 2008), the *C. destructivum* group (Armstrong-Cho & Banniza 2006, linked to an anamorph misidentified as *C. truncatum*), the *C. orbiculare* group (Rodriguez-Guerra *et al.* 2005) and the *C. graminicola* group (Crouch *et al.* 2009).

The *Glomerella* morphs of *Colletotrichum* species are morphologically uniform, with ascospore size and shape the only feature that has been credited with any diagnostic value. There is much overlap in published dimensions and it is not practical to distinguish sexual structures of the *C. boninense* aggregate from those of the other groups using morphological methods alone.

Lu *et al.* (2004) observed high genetic variability among *Colletotrichum* strains, including some from the *C. boninense* complex, from trees in the Iwokrama Forest Reserve in Guyana by means of ISSR-PCR, RAPD PCR and ITS rDNA sequencing. Almost no two strains were genetically identical, and this variability was postulated to be due to meiosis. Comparing about 80 isolates from different tree species in the same area, they also did not detect host specificity, neither at species nor population level. Those cultures were not available to us, but some of their ITS sequences diverge from those of the main body of the *C. boninense* species complex and may represent further segregate taxa. The relationship between endophytic and pathogenic isolates of *Colletotrichum* needs more research, as some endophytes may be latent pathogens (Lu *et al.* 2004), while others appear exclusively endophytic (Rojas *et al.* 2010). In both studies, endophytes did not appear to be strongly host-specific. Most of the species in our study of the *C. boninense* species complex are known only from a few isolates, either from a single host genus or from more than one host genus and then with a limited distribution. However, two species were represented by many isolates, *C. karstii* and *C. boninense*, of which *C. karstii* has the widest host range and distribution. Almost all strains that were isolated as endophytes belong to *C. karstii*, although that species also includes strains derived from diseased plant tissues. More research is needed into the life strategies and host-parasite relations of the fungi belonging to this clade.

Detailed study of the *C. boninense* complex has demonstrated that even recently recognised species of *Colletotrichum* may mask extensive variation at the molecular level, and can contain multiple taxa with distinct evolutionary origins. The arguments as to whether these segregate taxa should be recognised at species or infraspecific level (Cannon *et al.* 2008) have still not been laid to rest, but recent trends are to consider them as independent species. This has the benefit of simplicity when referring to them, but in many cases the name does not infer host specificity or nutritional/biological strategy and is thus of limited practical value to the applied mycologist and plant pathologist. Unfortunately, many of these species cannot be reliably identified at this time using single diagnostic (barcoding) sequences, and this aspect of their systematics must obtain a high priority for the future. On a positive note, we now have substantially more information about the *C. boninense* complex in terms of its phylogenetic constituents.

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REFERENCES

Afanador-Kafuri L, Minz D, Maymon M, Freeman S (2003). Characterization of *Colletotrichum* isolates from tamarillo, passiflora, and mango in Colombia and identification of a unique species from the genus. *Phytopathology* **93**: 579–587.

Allescher A (1902). *Rabenhorst's Kryptogamen-Flora*. Pilze - Fungi Imperfecti vol. **1**(7): 385–704. Edn 2.

Armstrong-Cho CL, Banniza S (2006). *Glomerella truncata* sp. nov., the teleomorph of *Colletotrichum truncatum*. *Mycological Research* **110**: 951–956.

Arx JA von (1957). Die Arten der Gattung *Colletotrichum* Cda. *Phytopathologische Zeitschrift* **29**: 413–468.

Arx JA von (1970). A revision of the fungi classified as *Gloeosporium*. *Bibliotheca Mycologica* **24**: 1–203.

Arx JA von, Müller E (1954). Die Gattungen der amerosporen Pyrenomyceten. *Beiträge zur Kryptogamenflora der Schweiz* **11** (1): 1–434.

Cannon PF, Buddie AG, Bridge PD (2008). The typification of *Colletotrichum gloeosporioides*. *Mycotaxon* **104**: 189–204.

Cannon PF, Damm U, Johnston PR, Weir BS (2012). *Colletotrichum* – current status and future directions. *Studies in Mycology* **73**: 181–213.

Carbone I, Kohn LM (1999). A method for designing primer sets for speciation studies in filamentous ascomycetes. *Mycologia* **91**: 553–556.

Crouch JA, Clarke BB, White JW, Hillman BI (2009). Systematic analysis of the falcate-spored graminicolous *Colletotrichum* and a description of six new species of the fungus from warm-season grasses. *Mycologia* **101**: 717–732.

Crous PW, Gams W, Stalpers JA, Robert V, Stegehuis G (2004a). MycoBank: an online initiative to launch mycology into the 21st century. *Studies in Mycology* **50**: 19–22.

Crous PW, Groenewald JZ, Risede JM, Hywel-Jones NL (2004b). *Calonectria* species and their *Cylindrocladium* anamorphs: species with sphaeropedunculate vesicles. *Studies in Mycology* **50**: 415–430.

Crous PW, Verkleij GJM, Groenewald JZ, Samson RA (eds) (2009). *Fungal Biodiversity*. CBS Laboratory Manual Series 1. Centraalbureau voor Schimmelcultures, Utrecht, Netherlands.

Damm U, Crous PW, Fourie PH (2007). *Botryosphaeriaceae* as potential pathogens of *Prunus* species in South Africa, with descriptions of *Diplodia africana* and *Lasiodiplodia plurivora* spp. nov. *Mycologia* **99**: 664–680.

Damm U, Mostert L, Crous PW, Fourie PH (2008a). Novel *Phaeoacremonium* species associated with necrotic wood of *Prunus* trees. *Persoonia* **20**: 87–102.

Damm U, Woudenberg JHC, Cannon PF, Crous PW (2009). *Colletotrichum* species with curved conidia from herbaceous hosts. *Fungal* Diversity **39**: 45–87.

Damm U, Cannon PF, Woudenberg JHC, Crous PW (2012). The *Colletotrichum acutatum* species complex. *Studies in Mycology* **73**: 37–113.

Farr DF, Rossman AY (2011). Fungal Databases, Systematic Mycology and Microbiology Laboratory, ARS, USDA. Retrieved October 18, 2011, from http://nt.ars-grin.gov/fungaldatabases.

Farr DF, Aime MC, Rossman AY, Palm ME (2006). Species of *Colletotrichum* on *Agavaceae*. *Mycological Research* **110**: 1395–1408.

Di Lenna P, Montecchio L (1995). Gravi danni da antracnosi (*Colletotrichum gloeosporioides*) su colture di *Dracaena deremensis* in serra. *Informatore Fitopatologico* **4**: 24–26.

Gardes M, Bruns TD (1993). ITS primers with enhanced specificity for basidiomycetes - application to the identification of mycorrhizae and rusts. *Molecular Ecology* **2**: 113–118.

Gazis R, Chaverri P (2010). Diversity of fungal endophytes in leaves and stems of wild rubber trees (*Hevea brasiliensis*) in Peru. *Fungal Ecology* **3**: 240–254.

Gazis R, Rehner S, Chaverri P (2011). Species delimitation in fungal endophyte diversity studies and its implications in ecological and biogeographic inferences. *Molecular Ecolology* **20**: 3001–3013.

Glass NL, Donaldson G (1995). Development of primer sets designed for use with PCR to amplify conserved genes from filamentous ascomycetes. *Applied and Environmental Microbiology* **61**: 1323–1330.

Guerber JC, Correll JC (2001). Characterization of *Glomerella acutata*, the teleomorph of *Colletotrichum acutatum*. *Mycologia* **93**: 216–229.

Guerber JC, Liu B, Correll JC, Johnston PR (2003). Characterization of diversity in *Colletotrichum acutatum sensu lato* by sequence analysis of two gene introns, mtDNA and intron RFLPs, and mating compatibility. *Mycologia* **95**: 872–895.

Hillis DM, Bull JJ (1993). An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. *Systematic Biology* **42**: 182–192.

Hoog GS de, Gerrits van den Ende AHG (1998). Molecular diagnostics of clinical strains of filamentous basidiomycetes. *Mycoses* **41**: 183–189.

Hyde KD, Cai L, Cannon PC, Crouch JA, Crous PW, *et al.* (2009). *Colletotrichum* – names in current use. *Fungal Diversity* **39**: 147–182.

Jayasinghe CK, Fernando THPS, Priyanka UMS (1997). *Colletotrichum acutatum* is the main cause of *Colletotrichum* leaf disease of rubber in Sri Lanka. *Mycopathologia* **137**: 53–56.

Johnston PR, Jones D (1997). Relationships among *Colletotrichum* isolates from fruit-rots assessed using rDNA sequences. *Mycologia* **89**: 420–430.

Johnston PR, Pennycook SR, Manning MA (2005). Taxonomy of fruit-rotting fungal pathogens: what's really out there? *New Zealand Plant Protection* **58**: 42–46.

Joshee S, Paulus BC, Park D, Johnston PR (2009). Diversity and distribution of fungal foliar endophytes in New Zealand *Podocarpaceae*. *Mycological Research* **113** (9): 1003–1015.

Lee HB, Park JY, Jung HS (2005a). First report of leaf anthracnose caused by *Colletotrichum boninense* on spindle trees. *Plant Pathology* **54**: 254.

Lee HB, Park JY, Jung HS (2005b). Identification, growth and pathogenicity of *Colletotrichum boninense* causing leaf anthracnose on spindle tree. *Plant Pathology Journal* **21**: 27–32.

Liu B, Wasilwa LA, Guerber JC, Morelock TE, O'Neill NR, Correll JC (2007). Comparison of *Colletotrichum orbiculare* and allied *Colletotrichum* species for mtDNA RFLPs, intron RFLPs, sequence variation, vegetative compatibility, and host specificity. *Phytopathology* **97**: 1305–1314.

Lu G, Cannon PF, Reid A, Simmons CM (2004). Diversity and molecular relationships of endophytic *Colletotrichum* isolates from the Iwokrama Forest Reserve, Guyana. *Mycological Research* **108**: 53–63.

Lubbe CM, Denman S, Cannon PF, Groenewald JZ, Lamprecht SC, Crous PW (2004). Characterization of *Colletotrichum* species associated with diseases of *Proteaceae*. *Mycologia* **96**: 1268–1279.

Lubbe CM, Denman S, Lamprecht SC, Crous PW (2006). Pathogenicity of *Colletotrichum* species to *Protea* cultivars. *Australasian Plant Pathology* **35**: 37–41.

Magyar D, Eszéki ER, Oros G, Szécsi A, Kredics L, *et al.* (2011). The air spora of an orchid greenhouse. *Aerobiologia* **27**: 121–134.

Marcelino J, Giordano R, Gouli S, Gouli V, Parker BL, *et al.* (2008). *Colletotrichum acutatum* var. *fioriniae* (teleomorph: *Glomerella acutata* var. *fioriniae* var. nov.) infection of a scale insect. *Mycologia* **100**: 353–374.

Mason-Gamer RJ, Kellogg EA (1996). Chloroplast DNA analysis of the monogenomic *Triticeae*: phylogenetic implications and genome-specific markers. In: *Methods of Genome Analysis in Plants (*Jauhar PP, ed.), CRC Press, Boca Raton: 301–325.

Mathur RS (1979). *The Coelomycetes of India*. Bishen Singh Mahendra Pal Singh, Delhi, India.

McKay SF, Freeman S, Minz D, Maymon M, Sedgley M, *et al.* (2009). Morphological, genetic, and pathogenic characterization of *Colletotrichum acutatum*, the cause of anthracnose of almond in Australia. *Phytopathology* **99**: 985–995.

Moriwaki J, Sato T, Tsukiboshi T (2003). Morphological and molecular characterization of *Colletotrichum boninense* sp. nov. from Japan. *Mycoscience* **44**: 47–53.

Moriwaki J, Tsukiboshi T, Sato T (2002). Grouping of *Colletotrichum* species in Japan based on rDNA sequences. *Journal of General Plant Pathology* **68**: 307–320.

Nguyen PTH, Pettersson OV, Olsson P, Liljeroth E (2009). Identification of *Colletotrichum* species associated with anthracnose disease of coffee in Vietnam. *European Journal of Plant Pathology* **127**: 73–87.

Nirenberg HI (1976). Untersuchungen über die morphologische und biologische Differenzierung in der *Fusarium*-Sektion *Liseola*. *Mitteilungen aus der Biologischen Bundesanstalt für Land- und Forstwirtschaft Berlin-Dahlem* **169**: 1–117.

Nylander JAA (2004). *MrModeltest v.2*. Program distributed by the author. Evolutionary Biology Centre, Uppsala University.

O'Connell R, Herbert C, Sreenivasaprasad S, Khatib M, Esquerré-Tugayé M-T, Dumas B (2004). A novel *Arabidopsis-Colletotrichum* pathosystem for the molecular dissection of plant-fungal interactions. *Molecular Plant-Microbe Interactions* **17**: 272–282.

O'Donnell K, Cigelnik E (1997). Two divergent intragenomic rDNA ITS2 types within a monophyletic lineage of the fungus *Fusarium* are nonorthologous. *Molecular Phylogenetics and Evolution* **7**:103–116.

Pai HS (1966). A new anthracnose disease of *Phyllanthus acidus* from India. *Plant Disease Reporter* **50**: 313–314.

Pai HS (1970). Life cycle of *Colletotrichum heveae* inciting spot anthracnose of *Phyllanthus acidus*. *Mycopathologia et Mycologia applicata* **42**: 65–72.

Petch T (1906). Descriptions of new Ceylon fungi. *Annals of the Royal Botanical Gardens Peradeniya* **3**(1): 1–10.

Petch T (1925). Additions to Ceylon fungi. III. *Annals of the Royal Botanic Gardens, Peradeniya* **9** (3): 313–328.

Photita W, Taylor PWJ, Ford R, Lumyong P, McKenzie HC, Hyde KD (2005). Morphological and molecular characterization of *Colletotrichum* species from herbaceous plants in Thailand. *Fungal Diversity* **18**: 117–133.

Pileggi SA, Vieira de Oliveira SF, Andrade CW, Vicente VA, Dalzoto Pdo R, *et al.* (2009). Molecular and morphological markers for rapid distinction between two *Colletotrichum* species. *Canadian Journal of Microbiology* **55**: 1076–1088.

Rambaut A (2002). *Sequence Alignment Editor*. Version 2.0. University of Oxford, Oxford.

Rayner RW (1970). *A Mycological Colour Chart*. Commonwealth Mycological Institute, Kew, UK.

Rodríguez-Guerra R, Ramírez-Rueda MT, Cabral-Enciso M, García-Serrano M, Lira-Maldonado Z, *et al.* (2005). Heterothallic mating observed between Mexican isolates of *Glomerella lindemuthiana*. *Mycologia* **97**: 793–803.

Rojas EI, Rehner SA, Samuels GJ, Van Bael S, Herre EA, *et al.* (2010). *Colletotrichum gloeosporioides s.l.* associated with *Theobroma cacao* and other plants in Panamá: multilocus phylogenies distinguish host-associated pathogens from asymptomatic endophytes. *Mycologia* **102**: 1318–1338.

Ronquist F, Huelsenbeck JP (2003). MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19**: 1572–1574.

Saccardo PA (1895). *Sylloge Fungorum* vol. 11. Padova, Italy.

Saccardo PA, Trotter A (1913). *Sylloge Fungorum* vol. 22. Padova, Italy.

Saha T, Kumar A, Ravindran M, Jacobs K, Roy B, Nazeer MA (2002). Identification of *Colletotrichum acutatum* from rubber using random amplified polymorhic DNAs and ribosomal DNA polymorphisms. *Mycological Research* **106**: 215–221.

Sawada K (1943). Descriptive catalogue of the Formosan fungi. Part VIII. *Report of the Department of Agriculture, Government Research Institute of Formosa* **85**: 1–130.

Siemaszko W (1923). Fungi caucasici novi vel minus cogniti. II. Diagnoses specierum novarum ex Abchazia. Adzariaque provenientium. *Acta Societatis Botanicorum Poloniae* **1**: 1–10.

Silva-Rojas HV, Ávila-Quezada GD (2011). Phylogenetic and morphological identification of *Colletotrichum boninense*: a novel causal agent of anthracnose in avocado. *Plant Pathology* **60**: 899–908.

Simmonds JH (1966). *Host index of plant diseases in Queensland*. Queensland Department of Primary Industries, Brisbane: 111 pp.

Simmonds JH (1968). Type specimens of *Colletotrichum gloeosporioides* var. *minor* and *Colletotrichum acutatum*. *Queensland Journal of Agricultural and Animal Science* **25**: 178A.

Spegazzini C (1899). Fungi Argentini novi vel critici. *Anales del Museo nacional de Historia natural, Buenos Aires* **6**, Series: Ser. 2: 289–365.

Stevens FL (1925). Hawaiian fungi. *Bulletin of the Bernice Bishop Museum* **19**: 1–189.

Sutton BC (1980). *The Coelomycetes. Fungi Imperfecti with Pycnidia, Acervuli and Stromata*. Commonwealth Mycological Institute, Kew, UK.

Sutton BC (1992). The genus *Glomerella* and its anamorph *Colletotrichum*. In: *Colletotrichum: Biology, Pathogenicity, and Control* (Bailey JA , Jeger MJ, eds). CAB International, Wallingford, UK: 1–26.

Swofford DL (2000). *PAUP* 4.0: phylogenetic analysis using parsimony (* and other methods)*. Sinauer Associates, Sunderland, MA.

Tarnowski TLB, Ploetz RC (2010). First report of *Colletotrichum boninense*, *C. capsici*, and a *Glomerella* sp. as causes of postharvest anthracnose of passion fruit in Florida. *Plant Disease* **94**: 786.

Thaung MM (2008). Biodiversity survey of coelomycetes in Burma. *Australasian Mycologist* **27**: 74–110.

Tozze Jr HJ, Massola Jr NM, Camara MPS, Gioria R, Suzuki O, Brunelli KR, Braga RS, Kobori RF (2009). First report of *Colletotrichum boninense* causing anthracnose on pepper in Brazil. *Plant Disease* **93**: 106.

Tozze Jr HJ, Fischer IH, Camara MPS, Massola Jr NS (2010). First report of *Colletotrichum boninense* infecting yellow passion fruit (*Passiflora edulis f. flavicarpa*) in Brazil. *Australasian Plant Disease Notes* **5**: 70–72

Uecker FA (1994). Ontogeny of the ascoma of *Glomerella cingulata*. *Mycologia* **86**: 82–88.

Vassiljevski NI, Karakulin BP (1950). *Fungi imperfecti Parasitici*. Pars II. *Melanconiales*. Academiae Scientiarum URSS, Moscow and Leningrad.

Vega FE, Simpkins A, Aime MC, Posada F, Peterson SW, *et al.* (2010). Fungal endophyte diversity in coffee plants from Colombia, Hawai'i, Mexico and Puerto Rico. *Fungal Ecology* **3**: 122–138.

Weir BS, Johnston PR, Damm U (2012). The *Colletotrichum gloeosporioides* species complex. *Studies in Mycology* **73**: 115–180.

White TJ, Bruns T, Lee S, Taylor J (1990). Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: PCR Protocols: a guide to methods and applications (Innis MA, Gelfand DH, Sninsky JJ, White TJ, eds), Academic Press, San Diego: 315–322.

Woudenberg JHC, Aveskamp MM, Gruyter J de, Spiers AG, Crous PW (2009). Multiple *Didymella* teleomorphs are linked to the *Phoma clematidina* morphotype. *Persoonia* **22**: 56–62.

Yang YL, Liu ZY, Cai L, Hyde KD, Yu ZN, McKenzie EHC (2009). *Colletotrichum* anthracnose of *Amaryllidaceae*. *Fungal Diversity* **39**: 123–146.

Yang YL, Cai L, Yu ZN, Liu ZY, Hyde KD (2011). *Colletotrichum* species on *Orchidaceae* in southwest China. *Cryptogamie Mycologie* **32**: 229–253.

Yuan ZL, Su ZZ, Mao LJ, Peng YQ, Yang GM (2011). Distinctive endophytic fungal assemblage in stems of wild rice *(Oryza granulata)* in China with special reference to two species of *Muscodor* (*Xylariaceae*). *Journal of Microbiology* **49**: 15–23.

Zhuang W-Y, Ed. (2001). *Higher Fungi of Tropical China*. Mycotaxon, Ltd., Ithaca, NY.

The *Colletotrichum acutatum* species complex

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Abstract: *Colletotrichum acutatum* is known as an important anthracnose pathogen of a wide range of host plants worldwide. Numerous studies have reported subgroups within the *C. acutatum* species complex. Multilocus molecular phylogenetic analysis (ITS, ACT, TUB2, CHS-1, GAPDH, HIS3) of 331 strains previously identified as *C. acutatum* and other related taxa, including strains from numerous hosts with wide geographic distributions, confirmed the molecular groups previously recognised and identified a series of novel taxa. Thirty-one species are accepted, of which 21 have not previously been recognised. *Colletotrichum orchidophilum* clusters basal to the *C. acutatum* species complex. There is a high phenotypic diversity within this complex, and some of the species appear to have preferences to specific hosts or geographical regions. Others appear to be plurivorous and are present in multiple regions. In this study, only *C. salicis* and *C. rhombiforme* formed sexual morphs in culture, although sexual morphs have been described from other taxa (especially as laboratory crosses), and there is evidence of hybridisation between different species. One species with similar morphology to *C. acutatum* but not belonging to this species complex was also described here as new, namely *C. pseudoacutatum*.

Key words: anthracnose, *Ascomycota, Colletotrichum acutatum*, *Gloeosporium*, *Glomerella*, phylogeny, systematics.
Taxonomic novelties: New combinations - *Colletotrichum limetticola* (R.E. Clausen) Damm, P.F. Cannon & Crous, *C. lupini* (Bondar) Damm, P.F. Cannon & Crous, *C. salicis* (Fuckel) Damm, P.F. Cannon & Crous. **New species -** *C. acerbum* Damm, P.F. Cannon & Crous, *C. australe* Damm, P.F. Cannon & Crous, *C. brisbanense* Damm, P.F. Cannon & Crous, *C. cosmi* Damm, P.F. Cannon & Crous, *C. costaricense* Damm, P.F. Cannon & Crous, *C. cuscutae* Damm, P.F. Cannon & Crous, *C. guajavae* Damm, P.F. Cannon & Crous, *C. indonesiense* Damm, P.F. Cannon & Crous, *C. johnstonii* Damm, P.F. Cannon & Crous, *C. kinghornii* Damm, P.F. Cannon & Crous, *C. laticiphilum* Damm, P.F. Cannon & Crous, *C. melonis* Damm, P.F. Cannon & Crous, *C. orchidophilum* Damm, P.F. Cannon & Crous, *C. paxtonii* Damm, P.F. Cannon & Crous, *C. pseudoacutatum* Damm, P.F. Cannon & Crous *C. pyricola* Damm, P.F. Cannon & Crous, *C. rhombiforme* Damm, P.F. Cannon & Crous, *C. scovillei* Damm, P.F. Cannon & Crous, *C. sloanei* Damm, P.F. Cannon & Crous, *C. tamarilloi* Damm, P.F. Cannon & Crous, *C. walleri* Damm, P.F. Cannon & Crous. **Typifications: Epitypifications -** *C. acutatum* J.H. Simmonds, *C. limetticola* (R.E. Clausen) Damm, P.F. Cannon & Crous, *C. nymphaeae* (Pass.) Aa, *C. phormii* (Henn.) D.F. Farr & Rossman, *C. salicis* (Fuckel) Damm, P.F. Cannon & Crous. **Lectotypifications -** *C. nymphaeae* (Pass.) Aa, *C. orchidearum* Allesch.

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INTRODUCTION

Colletotrichum acutatum is one of the most frequently reported species of the genus and causes diseases commonly known as anthracnose on numerous host plants worldwide (Farr & Rossman 2012). Originally described from diseased tissues of *Carica papaya*, *Capsicum frutescens* and *Delphinium ajacis* in Australia by Simmonds (1965), the *C. acutatum* species complex is today known as especially destructive on fruits like strawberry (Garrido *et al.* 2009), citrus (Peres *et al.* 2008), apple (Lee *et al.* 2007), olive (Talhinhas *et al.* 2011), cranberry (Polashock *et al.* 2009) and blueberry (Wharton & Schilder 2008). It is also implicated in the "terminal crook" disease of pine (Dingley & Gilmour 1972) and in the anthracnose of leather leaf fern (Schiller *et al.* 2006). There are also reports of a disseminated infection of a sea turtle (Manire *et al.* 2002) and the infection of a scale insect (Marcelino *et al.* 2008). Reviews of the species in its broad sense and its pathology were published by Wharton & Diéguez-Uribeondo (2004) and Peres *et al.* (2005).

On strawberry, *C. acutatum* mainly causes black spot of fruit but can also attack crowns, roots and leaves (Freeman & Katan 1997), and is one of the most serious diseases in commercial fruit production. Largely due to its economic importance as a strawberry pathogen, *C. acutatum* was treated for many years as a regulated plant quarantine pest by the European and Mediterranean Plant Protection Organization (EPPO), though it is absent from the current list (EPPO 2011) – presumably due to its now widespread distribution in Europe. Inoculum sources are frequently transplant material, mostly with quiescent infections (Rahman & Louws 2008), infected plants, weeds and other hosts (McInnes *et al.* 1992, Parikka *et al.* 2006), while the survival rate of conidia in natural field soil is low (Freeman *et al.* 2002).

The most well-known morphological feature of *C. acutatum* (*s. lat.*) is the shape of its conidia, which have acute ends (Simmonds 1965). However, other conidial shapes, especially ± cylindrical with only one acute end, are frequently encountered, especially in strains that have been repeatedly subcultured, but these conidial shapes can also occur in species outside the *C. acutatum* species complex. Even the differentiation between *C. acutatum* (*s. lat.*) and *C. gloeosporioides* (*s. lat.*) is difficult, because many intermediate strains exist with a restricted number of typical fusiform conidia and many cylindrical ones (Van der Aa *et al.* 1990). On the host, conidia are formed in acervuli; in culture, conidia are often also produced in the aerial mycelium (Johnston & Jones 1997). *Colletotrichum acutatum* has also been observed to form secondary conidia on the surface of living strawberry leaves (Leandro *et al.* 2001) that were

stimulated by strawberry plant extracts, especially flower extracts (Leandro *et al.* 2003). According to Buddie *et al.* (1999) secondary conidia may be produced directly from germinating primary conidia, and are smaller and more variable in shape, thus obscuring differences between taxa. Additionally, *C. acutatum* forms simple pigmented appressoria, but few or no setae (Simmonds 1965).

Guerber & Correll (1997, 2001) described *Glomerella acutata*, the sexual morph of *C. acutatum*, as the product of mating experiments, while some related species are homothallic, including *Ga. acutata* var. *fioriniae* (Marcelino *et al.* 2008), later regarded as a separate species (*C. fioriniae*, Shivas & Tan 2009) and an isolate of a *Glomerella* species related to *C. acutata* from *Acer platanoides* in the USA (LoBuglio & Pfister 2008). Talgø *et al.* (2007) observed the sexual morph *Ga. acutata* on naturally infected fruits of highbush blueberry in Norway. Numerous studies have shown that *C. acutatum* is morphologically and phylogenetically diverse (Sreenivasaprasad *et al.* 1994, Johnston & Jones 1997, Lardner *et al.* 1999, Freeman *et al.* 2001a, Nirenberg *et al.* 2002, Talhinhas *et al.* 2002, Guerber *et al.* 2003, Lubbe *et al.* 2004, Du *et al.* 2005, Peres *et al.* 2005, Sreenivasaprasad & Talhinhas 2005, Talhinhas *et al.* 2005, Johnston *et al*. 2008). Sreenivasaprasad *et al.* (1996) were the first to recognise that *C. acutatum* was unusually diverse, with strains showing divergence of 5.8 % in ITS-1 sequence compared with levels of 2–4 % frequently found within other fungal species, and they suggested splitting *C. acutatum* into two species. Johnston & Jones (1997) recognised four morphological groups, *C. acutatum* A–C and *Glomerella miyabeana.* Three of these groups were supported by 28S nuclear ribosomal large subunit rRNA (LSU) sequence data. Lardner *et al.* (1999), using a combination of RAPDs and morphological/cultural data, identified seven subordinate groups within *C. acutatum*. Sequences of a 200-bp intron of the glyceraldehyde-3-phosphate dehydrogenase (GAPDH) and a 900-bp intron of the glutamine synthetase GS distinguished seven main clades and several subclades within strains that originated mainly from North America and New Zealand (Guerber *et al.* 2003). The recognition of infraspecific groups was more firmly established by Sreenivasaprasad & Talhinhas (2005), who distinguished clades A1 to A8 based on rDNA ITS and beta-tubulin DNA (TUB2) sequences. These clades were mostly correlated with the groups that had been distinguished previously. Whitelaw-Weckert *et al.* (2007) recognised an additional group A9.

At this point, it was widely presumed that *C. acutatum* was a species complex containing a number of constituent taxa, but there was substantial reluctance to recognise the clades involved as independent species. This was due to the lack of differential morphological and cultural characters. For example, *C. lupini* was not recognised as formally separate from *C. acutatum* by Talhinhas *et al.* (2002) or by Sreenivasaprasad & Talhinhas (2005). There were some attempts to address these concerns via adoption of *formae speciales* e.g. *C. acutatum f. sp. pineum* (Dingley & Gilmour 1972), *C. acutatum f. sp. hakeae* (Lubbe *et al.* 2004) and *C. acutatum f. sp. fioriniae* (Marcelino *et al.* 2008), but this mechanism for recognition of pathology-related taxa is now rarely used.

Gradually, separate species were recognised or accepted as part of the *C. acutatum* species complex, *e.g. C. lupini* (Nirenberg *et al.* 2002) and *C. phormii* (Farr *et al.* 2006). In a study using two genes, ITS and TUB2, combined with morphological data, Shivas & Tan (2009) recognised three distinct groups within *C. acutatum* strains from Australia and accepted two new species, *C. simmondsii* and *C. fioriniae* (formerly *C. acutatum f. sp. fioriniae*) for groups A2 and A3. Recently, a new species was described for group A4, *C. clavatum* (Faedda *et al.* 2011).

Our research aims to present a comprehensive revision of the *C. acutatum* species complex. We thoroughly survey the constituent taxa and delineate additional species where needed. We have examined a large number of *C. acutatum s. lat.* strains, isolated from various hosts and in various geographic areas. Multi-locus molecular analysis is the basis of species recognition, but morphological and cultural characters allowing alternative means of species recognition are given where possible.

MATERIALS AND METHODS

Isolates

A total of 331 strains have been studied, mostly previously identified as *C. acutatum*, as well as other related strains from the CBS, IMI and other culture collections. Type material (holotypes and epitypes) of the species studied are located in the Herbarium of the Centraalbureau voor Schimmelcultures (CBS), Utrecht, The Netherlands, in the IMI Fungarium, which is based in the Royal Botanic Gardens, Kew (IMI and K(M)), UK, US National Fungus Collections (BPI), Beltsville, Maryland, USA, the Botanic Garden and Botanical Museum Berlin-Dahlem, Freie Universität Berlin (B), Germany and in the dried collection of the Botanische Staatssammlung München (M), Germany. All descriptions are based on the ex-type, ex-epitype or ex-neotype culture as appropriate. Features of other strains are added if deviant. Subcultures of the types, epitypes and neotypes, respectively, as well as all other isolates used for morphological and sequence analyses are maintained in the culture collections of CBS and IMI (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 oatmeal agar (OA; Crous *et al.* 2009) cultures were incubated at 20 °C under near UV light with 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. 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. In the *C. acutatum* species complex, conidia are usually formed in acervular conidiomata and additionally in the aerial mycelium. Unless mentioned otherwise, only conidia from conidiomata were used in this study for morphological examination.

Colony characters and pigment production on SNA and OA cultures incubated at 20 °C under near UV light with 12 h photoperiod were noted 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 gene with the two flanking internal transcribed spacers (ITS), a 200-bp intron of the glyceraldehyde-3-phosphate dehydrogenase (GAPDH), and partial

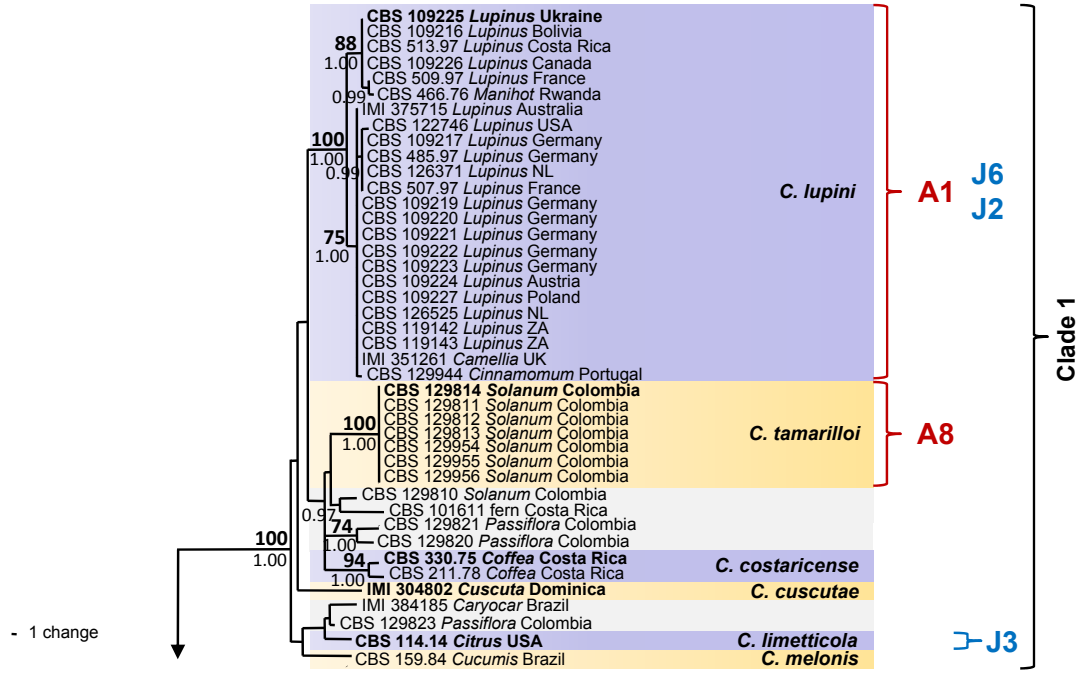

Fig. 1. One of 830 most parsimonious trees obtained from a heuristic search of the combined ITS, GAPDH, CHS-1, ACT, HIS3 and TUB2 sequences alignment of the *Colletotrichum acutatum* species complex. Bootstrap support values above 70 % (bold) and Bayesian posterior probability values above 0.95 are shown at the nodes. *Colletotrichum orchidophilum* CBS 632.80, CBS 631.80, IMI 309357 and CBS 119291 are used as outgroup. Numbers of ex-holotype, ex-neotype and ex-epitype strains are emphasised in bold. Strain numbers are followed by substrate (host genus) and country of origin, NL = Netherlands, NZ = New Zealand, ZA = South Africa. Branches that are crossed by diagonal lines are shortened by 50 %. Corresponding groups of Sreenivasaprasad & Talhinhas 2005 are emphasised in red, mtDNA RFLP haplotypes of Guerber *et al.* (2003) are emphasised in blue.

sequences of the chitin synthase 1 (CHS-1), histone3 (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) or V9G (de Hoog & Gerrits van den Ende 1998) + ITS-4, 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 BT2Fd + BT4R (Woudenberg *et al.* 2009) or T1 (O'Donnell & Cigelnik 1997) + Bt-2b (Glass & Donaldson 1995), 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 20x diluted genomic DNA, 0.2 µM of each primer, 1x PCR buffer (Bioline, Luckenwalde, Germany), 2 mM $MgCl_2$, 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). A maximum parsimony analysis was 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 2000) 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. The robustness of the trees obtained was evaluated by 10 000 bootstrap replications using the Fast-stepwise addition algorithm (Hillis & Bull 1993). Tree length, consistency index (CI), retention index (RI), rescaled consistency index (RC) and homoplasy index (HI) were calculated for the resulting tree. A Markov Chain Monte Carlo (MCMC) algorithm was used to generate phylogenetic trees with Bayesian probabilities using MrBayes v. 3.1.1 (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 1000 000 generations and sampled every 100 generations. The likelihood score of the two runs were 2 500 and 2 200 and therefore, the first 2 350 (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 in TreeBASE (www.treebase.org/treebase-web/home.html), and taxonomic novelties in MycoBank (Crous *et al.* 2004a).

RESULTS

Phylogeny

The six sequence data sets did not show any conflicts in tree topology for the 70 % reciprocal bootstrap trees, which allowed us

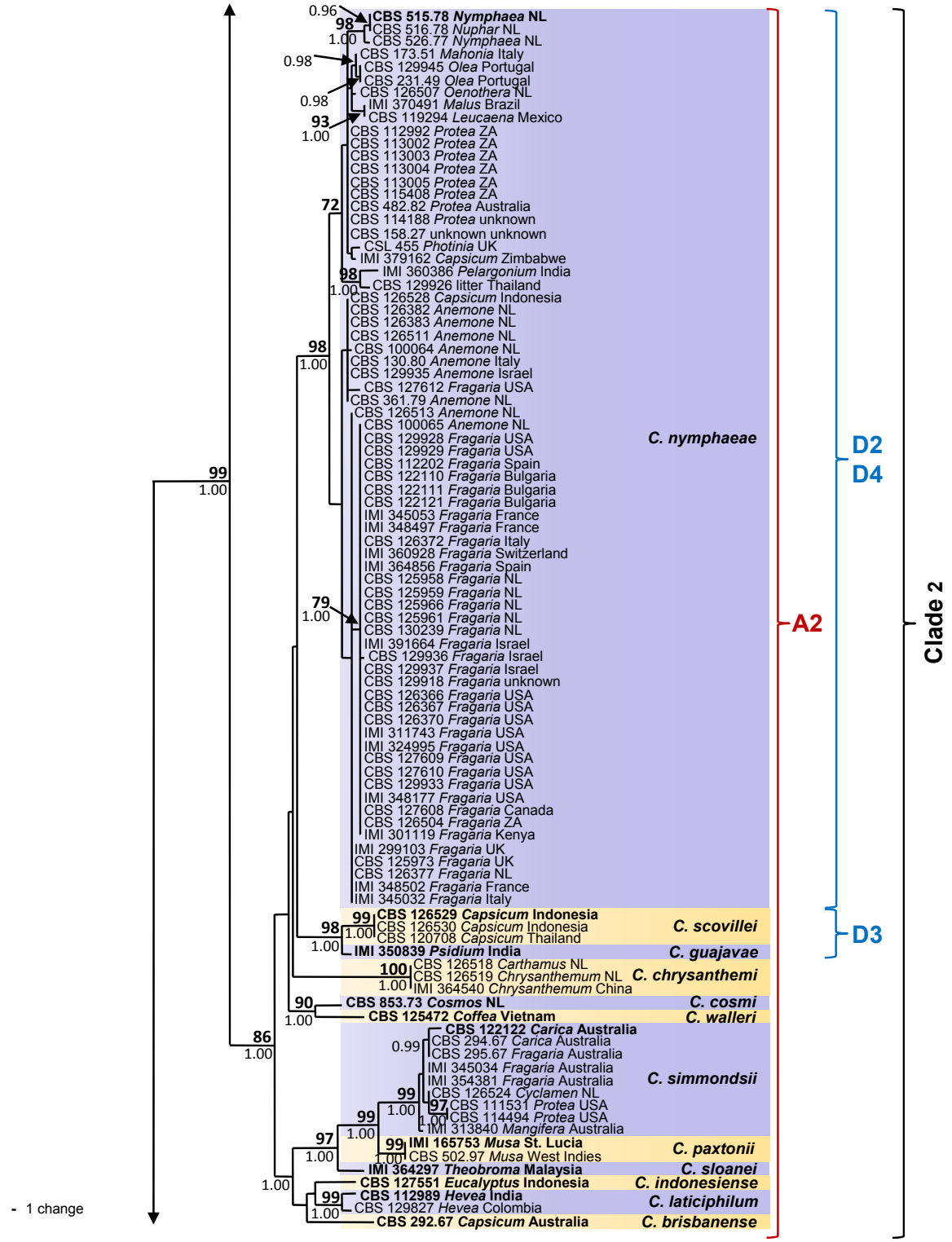

Fig. 1. (Continued).

to combine them. In the multigene analyses (gene boundaries of ITS: 1–546, GAPDH: 557–829, CHS-1: 840–1121, HIS3: 1131–1519, ACT: 1530–1786, TUB2: 1797–2290) of 330 isolates of *C. acutatum* and related *Colletotrichum* species including the outgroup (*C. orchidophilum* strains CBS 631.80, CBS 632.80, CBS 119291, IMI 309357), 2290 characters including the alignment gaps were processed, of which 468 characters were parsimony-informative, 65 parsimony-uninformative and 1757 constant. One strain that was revealed as not belonging to the *C. acutatum* species complex (CBS 436.77, *C. pseudoacutatum*) was not included in the analysis presented in Fig. 1. After a heuristic search using PAUP, 830 most parsimonious trees were retained (length = 1008 steps, CI = 0.643, RI = 0.981, RC = 0.681, HI = 0.357) of which one is shown in Fig. 1. The topology of the 830 trees was similar, which was verified for a large selection of trees. They differed only in the position of taxa within the subclades. For Bayesian analysis, a HKY+I model was selected for ITS, a HKY+G model for GAPDH and TUB2, a K80+I+G model for CHS-1, a HKY+I+G model for HIS3, a GTR+G model for ACT, and incorporated in the analysis. The consensus tree obtained from Bayesian analyses and the NJ tree (not shown) confirmed the tree topology obtained with parsimony. Bayesian posterior probability values agreed with bootstrap supports (Fig. 1).

Fig. 1. (Continued).

The analyses resulted in detection of five main clades and 29 subclades within *C. acutatum s. lat.*, which we accept as representing different *Colletotrichum* species. The corresponding groups according to Sreenivasaprasad & Talhinhas (2005, numbers beginning with A) and Guerber *et al.* (2003, mtDNA RFLP haplotypes, numbers beginning with C...K), which are the most differential and comparable studies, are listed in brackets below and are indicated in the phylogenetic tree (Fig. 1). The

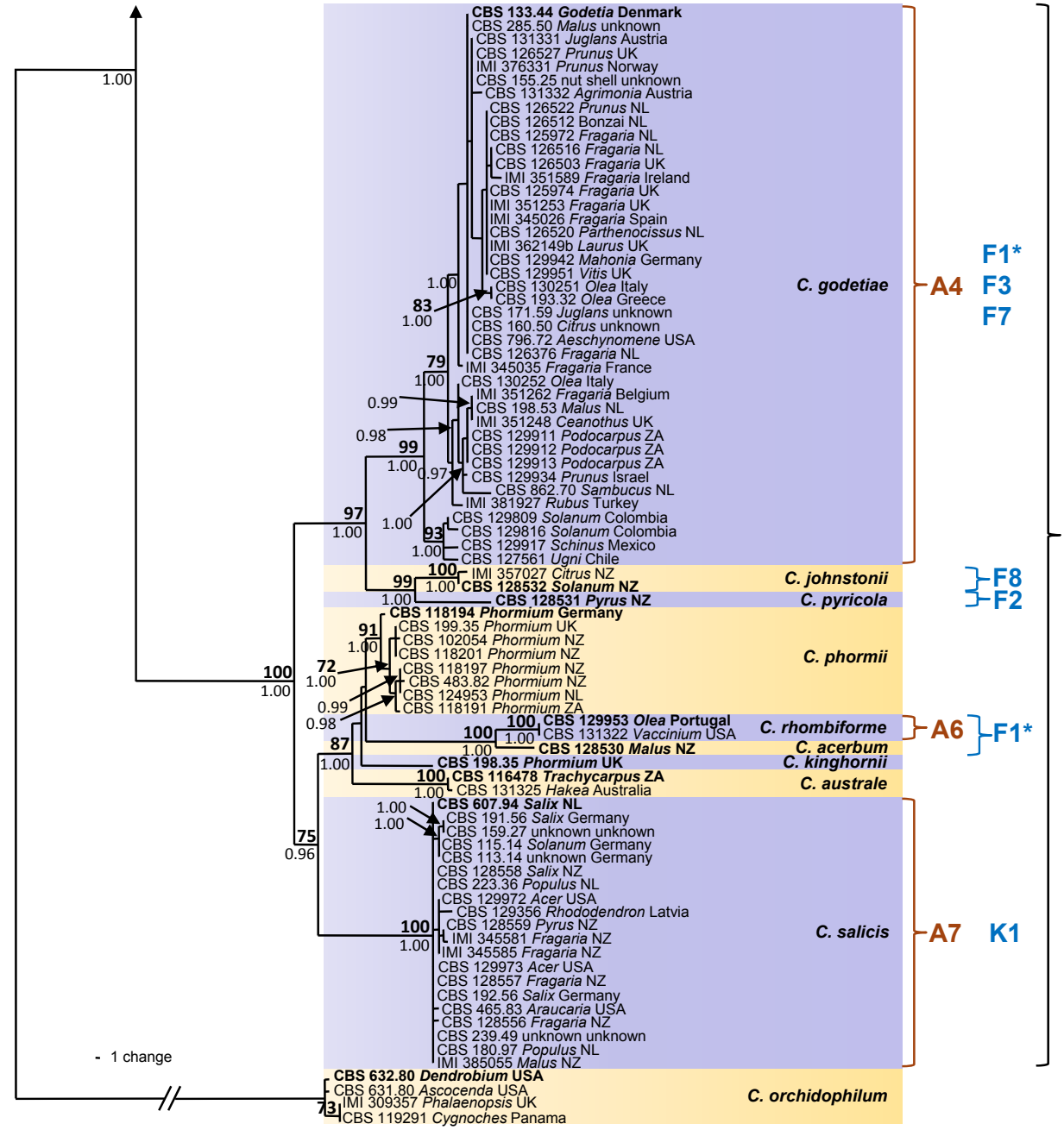

Fig. 1. (Continued).

first clade is well supported with a bootstrap support of 100 % and a Bayesian posterior probability value of 1.00. It consists of two frequently isolated, well-supported clades (bootstrap support/ Bayesian posterior probability value of both 100/1.00) comprising several strains each, representing *C. lupini* (A1, J2/J6) and *C. tamarilloi* (A8). Other less frequently encountered subclades in the first clade include *C. costaricense* (94/1.00) with two strains, *C. cuscutae* and *C. melonis* both represented by single-strain clades on long branches, and several short-branched single-strain clades, including the known species *C. limetticola* (J3) and six further unnamed strains. The majority of strains in clade 2 (A2, 86/1.00) belong to *C. nymphaeae* (98/1.00, D2/D4), while most of the other 11 subclades of this clade are occupied by only one or few strains. The clade representing *C. scovillei* (99/1.00) consists of three strains and groups (98/1.00) with a single-strain clade formed by *C. guajavae*. These two adjacent clades probably correspond to clade D3 in Guerber *et al.* (2003). The other sister clades represent *C. simmondsii* (99/1.00), *C. chrysanthemi* (100/1.00), *C. paxtonii* (99/1.00), *C. laticiphilum* (99/1.00), *C. cosmi*, *C. walleri*, *C. sloanei*, *C. indonesiense* and *C. brisbanense,* the last five of which consist of single-strain clades. Clades 3 and 4 are well-supported (100/1.00 and 100/0.87) and on long branches; they represent *C. fioriniae* (A3, C1/C2/C3) and *C. acutatum* (A5, J4). Clade 5 consists of two sister clades. *Colletotrichum godetiae* (A4, F1*, 99/1.00), formed by a large number of strains, belongs to the first sister clade and groups (97/1.00) with *C. johnstonii* (F8, 100/1.00) and a single-strain clade representing *C. pyricola* (F2). The other sister clade (75/1.00) consists of six subclades: a large, long-branched and almost homogenous subclade representing *C. salicis* (A7, K1, 100/1.00); a short-branched subclade representing *C. phormii* (91/1.00); *C. rhombiforme* (A6, 100/1.00), which groups with a single-strain clade representing *C. acerbum* on a long branch (F1*, 100/1.00); plus *C. australe* (100/1.00) and *C. kinghornii* on long branches. Strains named F1 appear in the phylogeny of Guerber *et al.* (2003) in different subclades, corresponding to *C. acerbum*, *C. godetiae* and probably also *C. rhombiforme*. *Colletotrichum pseudoacutatum*

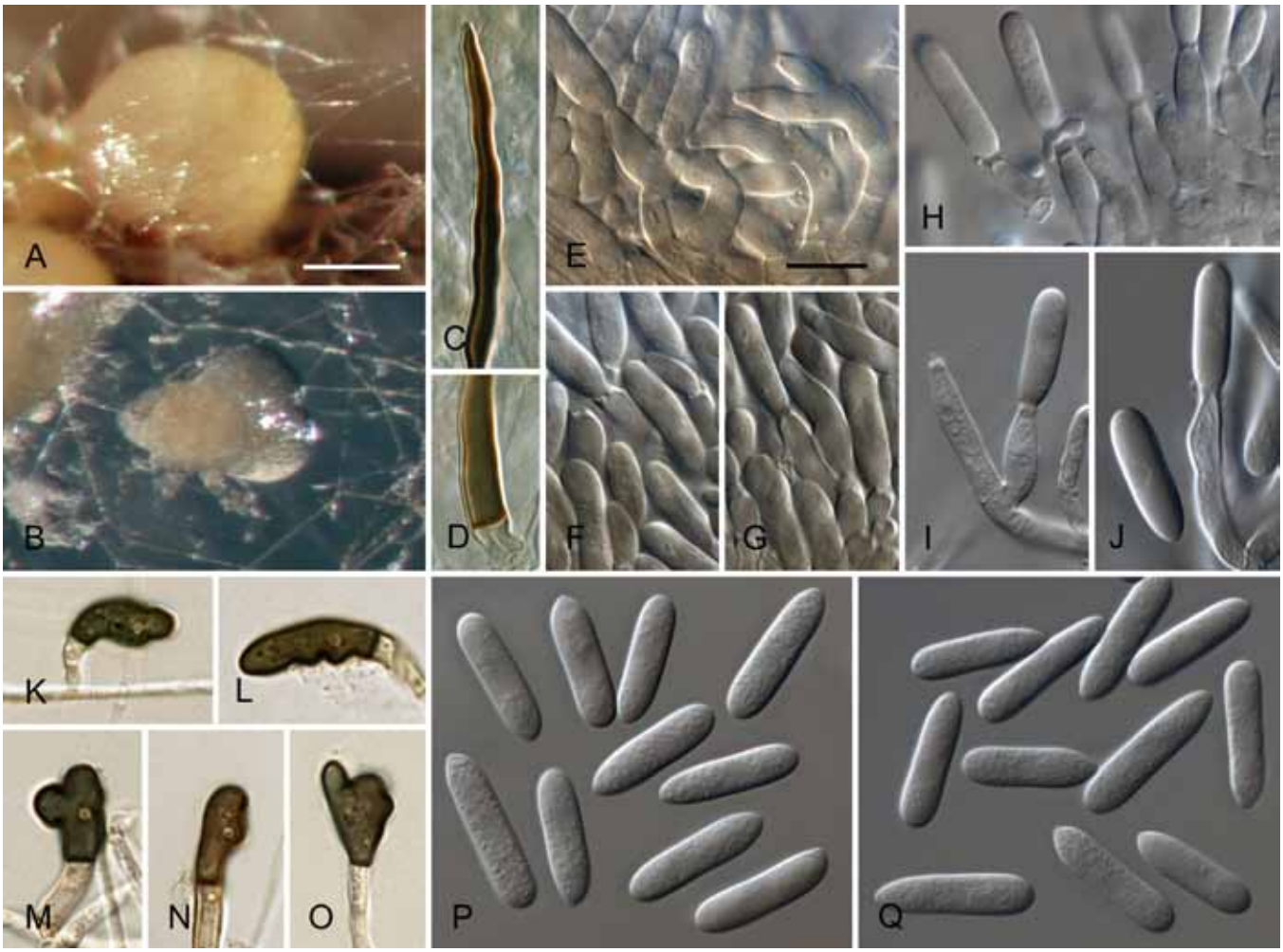

Fig. 2. *Colletotrichum acerbum* (from ex-holotype strain CBS 128530). A–B. Conidiomata. C. Tip of a seta. D. Basis of a seta. E–J. Conidiophores. K–O. Appressoria. P–Q. Conidia. A, C–G, P. from *Anthriscus* stem. B, H–O, Q. from SNA. A–B. DM, C–Q. DIC, Scale bars: A = 100 µm, E = 10 µm. Scale bar of A applies to A–B. Scale bar of E applies to C–Q.

is only distantly related to the *C. acutatum* complex and is therefore not included in the phylogeny, while *C. orchidophilum* was found to be more closely related and was therefore used as outgroup. The phylogenetic position of these and all other species included here is exhibited in fig. 1 and 2 of Cannon *et al.* (2012, this issue).

The individual alignments and maximum parsimony analyses of the six single genes were compared with respect to their performance in species recognition. With ITS and CHS-1, only 11 and 13 species, respectively, can be recognised. All subclades are recognised with TUB2 and GAPDH. TUB2 performs better than GAPDH due to higher numbers of base pair differences, but even with TUB2 there are clades with differerences of only 1 bp, which suggests that both genes should be used for identification. The performance of the other two genes is intermediate between ITS and TUB2/GAPDH.

Taxonomy

Based on DNA sequence data and morphology, the 331 strains studied (Table 1) are assigned to 31 species, of which 29 species are within the *C. acutatum* species complex and two outside this group, including 21 species that proved to be new to science. Two species formed sexual morphs *in vitro*. All species studied in culture are characterised below.

Colletotrichum acerbum Damm, P.F. Cannon & Crous, **sp. nov.** MycoBank MB800494. Fig. 2.

Etymology: *acerbus* = Latin for bitter; referring to bitter rot, the vernacular name for *Colletotrichum* disease of apple.

Sexual morph not observed. *Asexual morph on SNA. Vegetative hyphae* 1–6 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* absent, 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 ampulliform, sometimes lacking a basal septum and continuous with the conidiophore, sometimes extending to form new conidiogenous loci, polyphialides sometimes observed, discrete phialides measure 7–18 × 3–4.5 µm, opening 1.5–2 µm diam, collarette 0.5–1.5 µm long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical to clavate with one end round and one end slightly acute or both ends round, 15.5–20.5(–29) × (4–) 4.5–5 µm, mean ± SD = 17.9 ± 2.4 × 4.7 ± 0.2 µm, L/W ratio = 3.8. *Appressoria* single or in loose groups, medium to dark brown, smooth-walled, clavate, ovate or irregular outline, the edge entire or undulate, sometimes lobate, (8–)9–14(–16.5) × (4–)5–7.5(–9.5) µm, mean ± SD = 11.3 ± 2.4 × 6.2 ± 1.2 µm, L/W ratio = 1.8.

Asexual morph on Anthriscus stem. Conidiomata acervular, conidiophores formed on a cushion of pale brown angular cells,

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

Species	Accession No.[1]	Host/Substrate	Country	GenBank No.					
				ITS	GAPDH	CHS-1	HIS3	ACT	TUB2
C. acerbum	CBS 128530, ICMP 12921, PRJ 1199.3*	*Malus domestica*, bitter rot of fruit	New Zealand	JQ948459	JQ948790	JQ949120	JQ949450	JQ949780	JQ950110
C. acutatum	CBS 126521, PD 87/639	*Anemone* F1 hybride, cv. Melisande, curled leaf, constriction of the stem	Netherlands	JQ948366	JQ948697	JQ949027	JQ949357	JQ949687	JQ950017
	IMI 223120, CPC 18870	*Anemone* sp., stem	Australia	JQ948353	JQ948684	JQ949014	JQ949344	JQ949674	JQ950004
	CBS 127539, CPC 11738	*Aspalathus linearis*, anthracnose on stems and leaves	South Africa	JQ948377	JQ948708	JQ949038	JQ949368	JQ949698	JQ950028
	CBS 127542, CPC 13880	*Aspalathus linearis*, anthracnose on stems and leaves	South Africa	JQ948379	JQ948710	JQ949040	JQ949370	JQ949700	JQ950030
	CBS 129921, CPC 13881	*Aspalathus linearis*, anthracnose on stems and leaves	South Africa	JQ948380	JQ948711	JQ949041	JQ949371	JQ949701	JQ950031
	CBS 129922, CPC 13885	*Aspalathus linearis*, anthracnose on stems and leaves	South Africa	JQ948381	JQ948712	JQ949042	JQ949372	JQ949702	JQ950032
	CBS 127543, CPC 13886	*Aspalathus linearis*, anthracnose on stems and leaves	South Africa	JQ948382	JQ948713	JQ949043	JQ949373	JQ949703	JQ950033
	CBS 127545, CPC 13947	*Aspalathus linearis*, anthracnose on stems and leaves	South Africa	JQ948383	JQ948714	JQ949044	JQ949374	JQ949704	JQ950034
	CBS 129914, CPC 15490	*Aspalathus linearis*, anthracnose on stems and leaves	South Africa	JQ948384	JQ948715	JQ949045	JQ949375	JQ949705	JQ950035
	CBS 129915, CPC 15512	*Aspalathus linearis*, anthracnose on stems and leaves	South Africa	JQ948385	JQ948716	JQ949046	JQ949376	JQ949706	JQ950036
	CBS 129925, CPC 18023	*Aspalathus linearis*, anthracnose on stems and leaves	South Africa	JQ948386	JQ948717	JQ949047	JQ949377	JQ949707	JQ950037
	CBS 127541, CPC 11751	*Aspalathus linearis*, anthracnose on stems and leaves	South Africa	JQ948378	JQ948709	JQ949039	JQ949369	JQ949699	JQ950029
	CBS 127540, CPC 11749	Water that was used to irrigate *Aspalathus linearis* seedlings in a nursery	South Africa	JQ948373	JQ948704	JQ949034	JQ949364	JQ949694	JQ950024
	CBS 129923, CPC 13887	Water that was used to irrigate *Aspalathus linearis* seedlings in a nursery	South Africa	JQ948374	JQ948705	JQ949035	JQ949365	JQ949695	JQ950025
	CBS 129924, CPC 13891	Water that was used to irrigate *Aspalathus linearis* seedlings in a nursery	South Africa	JQ948375	JQ948706	JQ949036	JQ949366	JQ949696	JQ950026
	CBS 127546, CPC 13950	Water that was used to irrigate *Aspalathus linearis* seedlings in a nursery	South Africa	JQ948376	JQ948707	JQ949037	JQ949367	JQ949697	JQ950027
	CBS 144.29	*Capsicum annuum*, fruit	Sri Lanka	JQ948401	JQ948732	JQ949062	JQ949392	JQ949722	JQ950052
	CBS 112996, ATCC 56816, STE-U 5292*	*Carica papaya*	Australia	JQ005776	JQ948677	JQ005797	JQ005818	JQ005839	JQ005860
	IMI 216370, CPC 18869	*Coffea arabica*, berry lesion	Tanzania	JQ948398	JQ948729	JQ949059	JQ949389	JQ949719	JQ950049
	CBS 979.69	*Coffea arabica*	Kenya	JQ948400	JQ948731	JQ949061	JQ949391	JQ949721	JQ950051
	IMI 319423, CPC 18877	*Coffea arabica*, berry lesion	Kenya	JQ948399	JQ948730	JQ949060	JQ949390	JQ949720	JQ950050
	CBS 127602, BRIP 52691a, WAC 5416	*Fragaria* × *ananassa*, fruit rot	Australia	JQ948359	JQ948690	JQ949020	JQ949350	JQ949680	JQ950010
	CBS 111993, STE-U 3037	*Grevillea* sp.	Australia	JQ948349	JQ948680	JQ949010	JQ949340	JQ949670	JQ950000
	CBS 113599, STE-U 3038	*Grevillea* sp.	Australia	JQ948347	JQ948678	JQ949008	JQ949338	JQ949668	JQ949998
	CBS 113600, STE-U 3039	*Grevillea* sp.	Australia	JQ948348	JQ948679	JQ949009	JQ949339	JQ949669	JQ949999
	CBS 112759, STE-U 4470	*Hakea sericea*	South Africa	JQ948391	JQ948722	JQ949052	JQ949382	JQ949712	JQ950042
	CBS 112760, STE-U 4468	*Hakea sericea*	South Africa	JQ948392	JQ948723	JQ949053	JQ949383	JQ949713	JQ950043
	CBS 112993, STE-U 4469	*Hakea sericea*	South Africa	JQ948394	JQ948725	JQ949055	JQ949385	JQ949715	JQ950045

Table 1. (Continued).

Species	Accession No.[1]	Host/Substrate	Country	GenBank No.					
				ITS	GAPDH	CHS-1	HIS3	ACT	TUB2
C. acutatum	CBS 113007, STE-U 4462	*Hakea sericea*	South Africa	JQ948395	JQ948726	JQ949056	JQ949386	JQ949716	JQ950046
	CBS 113009, STE-U 4467	*Hakea sericea*	South Africa	JQ948397	JQ948728	JQ949058	JQ949388	JQ949718	JQ950048
	CBS 113008, STE-U 4463	*Hakea sericea*	South Africa	JQ948396	JQ948727	JQ949057	JQ949387	JQ949717	JQ950047
	CBS 112761, STE-U 4461	*Hakea sericea*	South Africa	JQ948393	JQ948724	JQ949054	JQ949384	JQ949714	JQ950044
	CBS 129919, CPC 13876	*Hoodia* sp.	South Africa	JQ948370	JQ948701	JQ949031	JQ949361	JQ949691	JQ950021
	CBS 129920, CPC 13877	*Hoodia* sp.	South Africa	JQ948371	JQ948702	JQ949032	JQ949362	JQ949692	JQ950022
	CBS 127544, CPC 13945	*Hoodia* sp.	South Africa	JQ948372	JQ948703	JQ949033	JQ949363	JQ949693	JQ950023
	CBS 112990, STE-U 4448	*Leucadendron* sp., cv. Safari Sunset	South Africa	JQ948360	JQ948691	JQ949021	JQ949351	JQ949681	JQ950011
	CBS 115202, STE-U 5233	*Leucadendron* sp., cv. Safari Sunset	South Africa	JQ948362	JQ948693	JQ949023	JQ949353	JQ949683	JQ950013
	CBS 112994, STE-U 5122	*Leucospermum* sp.	South Africa	JQ948361	JQ948692	JQ949022	JQ949352	JQ949682	JQ950012
	CBS 126505, PD 97/4384	*Lobelia* sp., cv. Blue Moon, leaf spots	Netherlands	JQ948387	JQ948718	JQ949048	JQ949378	JQ949708	JQ950038
	CBS 369.73, NRCC 10081	*Lupinus angustifolius*	New Zealand	JQ948350	JQ948681	JQ949011	JQ949341	JQ949671	JQ950001
	CBS 115393, STE-U 5433	*Mimetes* sp.	South Africa	JQ948365	JQ948696	JQ949026	JQ949356	JQ949686	JQ950016
	IMI 384175, CPC 18936	*Nerium oleander*, leaf	New Zealand	JQ948369	JQ948700	JQ949030	JQ949360	JQ949690	JQ950020
	CBS 127598, 223/09	*Olea europaea*	South Africa	JQ948363	JQ948694	JQ949024	JQ949354	JQ949684	JQ950014
	CBS 129952, PT227, RB015	*Olea europaea*	Portugal	JQ948364	JQ948695	JQ949025	JQ949355	JQ949685	JQ950015
	CBS 126506, PD 90/443	*Phlox* sp., leaf spots	Netherlands	JQ948388	JQ948719	JQ949049	JQ949379	JQ949709	JQ950039
	CBS 110735, Lundquist 256, STE-U 163	*Pinus radiata*	South Africa	JQ948354	JQ948685	JQ949015	JQ949345	JQ949675	JQ950005
	CBS 112979, Lundquist 258, STE-U 160	*Pinus radiata*	South Africa	JQ948355	JQ948686	JQ949016	JQ949346	JQ949676	JQ950006
	CBS 112980, STE-U 164	*Pinus radiata*	South Africa	JQ948356	JQ948687	JQ949017	JQ949347	JQ949677	JQ950007
	CBS 112981, Lundquist 253, STE-U 162	*Pinus radiata*	South Africa	JQ948357	JQ948688	JQ949018	JQ949348	JQ949678	JQ950008
	CBS 127534, Lundquist 257, STE-U 161	*Pinus radiata*	South Africa	JQ948358	JQ948689	JQ949019	JQ949349	JQ949679	JQ950009
	CBS 370.73, NRCC 10088	*Pinus radiata*	New Zealand	JQ948351	JQ948682	JQ949012	JQ949342	JQ949672	JQ950002
	CBS 371.73, NRCC 10086	*Pinus radiata*	New Zealand	JQ948352	JQ948683	JQ949013	JQ949343	JQ949673	JQ950003
	IMI 336479, CPC 18881	*Pistacia vera*, pericarp	Australia	JQ948367	JQ948698	JQ949028	JQ949358	JQ949688	JQ950018
	CBS 113006, STE-U 4460	*Protea cynaroides*	South Africa	JQ948390	JQ948721	JQ949051	JQ949381	JQ949711	JQ950041
	CBS 128499, ICMP 17992, PRJ 10.208	*Pyrus pyrifolia*, black spot on fallen, immature fruit	New Zealand	JQ948368	JQ948699	JQ949029	JQ949359	JQ949689	JQ950019
	CSL 287, RB117	*Statice* sp.	UK	JQ948389	JQ948720	JQ949050	JQ949380	JQ949710	JQ950040
C. australe	CBS 116478, HKUCC 2616*	*Trachycarpus fortunei*	South Africa	JQ948455	JQ948786	JQ949116	JQ949446	JQ949776	JQ950106
	CBS 131325, CPC 19820	*Hakea* sp.	Australia	JQ948456	JQ948787	JQ949117	JQ949447	JQ949777	JQ950107
C. brisbanense	CBS 292.67, DPI 11711*	*Capsicum annuum*	Australia	JQ948291	JQ948621	JQ948952	JQ949282	JQ949612	JQ949942
C. chrysanthemi	IMI 364540, CPC 18930	*Chrysanthemum coronarium*, leaf spot	China	JQ948273	JQ948603	JQ948934	JQ949264	JQ949594	JQ949924
	CBS 126518, PD 84/520	*Carthamus* sp., twisted stem	Netherlands	JQ948271	JQ948601	JQ948932	JQ949262	JQ949592	JQ949922

Table 1. (Continued).

Species	Accession No.[1]	Host/Substrate	Country	GenBank No.					
				ITS	GAPDH	CHS-1	HIS3	ACT	TUB2
C. chrysanthemi	CBS 126519, PD 85/694	*Chrysanthemum coronarium*, vascular discoloration	Netherlands	JQ948272	JQ948602	JQ948933	JQ949263	JQ949593	JQ949923
C. cosmi	CBS 853.73, PD 73/856*	*Cosmos* sp., seed	Netherlands	JQ948274	JQ948604	JQ948935	JQ949265	JQ949595	JQ949925
C. costaricense	CBS 330.75*	*Coffea arabica,* cv. Typica, berry	Costa Rica	JQ948180	JQ948510	JQ948841	JQ949171	JQ949501	JQ949831
	CBS 211.78, IMI 309622	*Coffea* sp., twig	Costa Rica	JQ948181	JQ948511	JQ948842	JQ949172	JQ949502	JQ949832
C. cuscutae	IMI 304802, CPC 18873*	*Cuscuta* sp.	Dominica	JQ948195	JQ948525	JQ948856	JQ949186	JQ949516	JQ949846
	CBS 128498, ICMP 17991, PRJ 10.207	*Actinidia* sp., fruit rot of ripe fruit	New Zealand	JQ948337	JQ948667	JQ948998	JQ949328	JQ949658	JQ949988
	CBS 126523, PD 88/642	*Berberis* sp., tips with black discolouration	Netherlands	JQ948322	JQ948652	JQ948983	JQ949313	JQ949643	JQ949973
	IMI 363003, CPC 18928	*Camellia reticulata*	China	JQ948339	JQ948669	JQ949000	JQ949330	JQ949660	JQ949990
	CBS 981.69	*Coffea arabica*, branch	Angola	JQ948327	JQ948657	JQ948988	JQ949318	JQ949648	JQ949978
	CBS 125970, NB 852	*Cyclamen* sp., bulb, symptoms	Italy	JQ948341	JQ948671	JQ949002	JQ949332	JQ949662	JQ949992
	CBS 128517, ARSEF 10222, ERL 1257, EHS 58*	*Fiorinia externa* (elongate hemlock scale, insect)	USA	JQ948292	JQ948622	JQ948953	JQ949283	JQ949613	JQ949943
	IMI 345578, CPC 19393, RB148	*Fragaria* × *ananassa*	New Zealand	JQ948334	JQ948664	JQ948995	JQ949325	JQ949655	JQ949985
	IMI 345583, CPC 18889	*Fragaria* × *ananassa*, lesion	New Zealand	JQ948333	JQ948663	JQ948994	JQ949324	JQ949654	JQ949984
	IMI 345575, CPC 18888	*Fragaria* × *ananassa*, lesion	New Zealand	JQ948332	JQ948662	JQ948993	JQ949323	JQ949653	JQ949983
	CBS 128529, ICMP 1701, PRJ 659	*Fragaria* × *ananassa*, root	New Zealand	JQ948331	JQ948661	JQ948992	JQ949322	JQ949652	JQ949982
	CSL 1259, RB057	*Fragaria* × *ananassa*, petiole	UK	JQ948330	JQ948660	JQ948991	JQ949321	JQ949651	JQ949981
	CBS 127611, DAOM 213703, CF-132	*Fragaria* × *ananassa*	USA	JQ948328	JQ948658	JQ948989	JQ949319	JQ949649	JQ949979
	CBS 127614, DAOM 213712	*Fragaria* × *ananassa*	USA	JQ948329	JQ948659	JQ948990	JQ949320	JQ949650	JQ949980
	CBS 129940	*Grevillea* sp.	Germany	JQ948335	JQ948665	JQ948996	JQ949326	JQ949656	JQ949986
	CBS 129941	*Grevillea* sp.	Germany	JQ948336	JQ948666	JQ948997	JQ949327	JQ949657	JQ949987
	IMI 384569, CPC 18938	*Kalmia* sp.	USA	JQ948340	JQ948670	JQ949001	JQ949331	JQ949661	JQ949991
	CSL 473, RB131	*Liriodendron tulipifera*	UK	JQ948345	JQ948675	JQ949006	JQ949336	JQ949666	JQ949996
	CSL 318, RB132	*Magnolia* sp.	UK	JQ948346	JQ948676	JQ949007	JQ949337	JQ949667	JQ949997
	CBS 786.86,	*Malus sylvestris*, fruit	Italy	JQ948303	JQ948633	JQ948964	JQ949294	JQ949624	JQ949954
	CBS 126381	*Malus domestica*, cv. Junami, fruit	Netherlands	JQ948302	JQ948632	JQ948963	JQ949293	JQ949623	JQ949953
	CBS 129930, 2.7.3(T1326), ICMP 1791	*Malus domestica*	New Zealand	JQ948304	JQ948634	JQ948965	JQ949295	JQ949625	JQ949955
	CBS 128555, ICMP 12923, PRJ 839-1	*Malus domestica*, bitter rot of fruit	New Zealand	JQ948305	JQ948635	JQ948966	JQ949296	JQ949626	JQ949956
	CBS 129931, 1.4.51a(T1166)	*Malus domestica*	USA	JQ948294	JQ948624	JQ948955	JQ949285	JQ949615	JQ949945
	CBS 129932, 5.7.52	*Malus domestica*	USA	JQ948295	JQ948625	JQ948956	JQ949286	JQ949616	JQ949946
	CBS 112995, STE-U 5287	*Malus domestica*	USA	JQ948298	JQ948628	JQ948959	JQ949289	JQ949619	JQ949949
	CBS 127538, STE-U 5290	*Malus domestica*	USA	JQ948300	JQ948630	JQ948961	JQ949291	JQ949621	JQ949951
	ATCC 28992, CPC 19391	*Malus domestica*	USA	JQ948297	JQ948627	JQ948958	JQ949288	JQ949618	JQ949948
	CBS 129938, APPY3	*Malus domestica*	USA	JQ948296	JQ948626	JQ948957	JQ949287	JQ949617	JQ949947

Table 1. (Continued).

Species	Accession No.[1]	Host/Substrate	Country	GenBank No.					
				ITS	GAPDH	CHS-1	HIS3	ACT	TUB2
C. fioriniae	CBS 125396, GJS 08-140A	*Malus domestica*, fruit lesion	USA	JQ948299	JQ948629	JQ948960	JQ949290	JQ949620	JQ949950
	IMI 324996, CPC 18880	*Malus pumila*	USA	JQ948301	JQ948631	JQ948962	JQ949292	JQ949622	JQ949952
	CBS 235.49	*Malus* sp.	USA	JQ948325	JQ948655	JQ948986	JQ949316	JQ949646	JQ949976
	CBS 127601, BRIP 28761a	*Mangifera indica*, stem endophyte	Australia	JQ948311	JQ948641	JQ948972	JQ949302	JQ949632	JQ949962
	CBS 167.86	*Myriophyllum spicatum*, submerged stem	USA	JQ948324	JQ948654	JQ948985	JQ949315	JQ949645	JQ949975
	CBS 129946, PT170, RB021	*Olea europaea*	Portugal	JQ948342	JQ948672	JQ949003	JQ949333	JQ949663	JQ949993
	CBS 126509, PD 92/1060	*Parthenocissus* sp., cv. Disci, soft rot	Netherlands	JQ948316	JQ948646	JQ948977	JQ949307	JQ949637	JQ949967
	CBS 125956 , NB 112	*Penstemon* sp., symptoms in the bottom part of the plant	Netherlands	JQ948321	JQ948651	JQ948982	JQ949312	JQ949642	JQ949972
	CBS 293.67, DPI 13120	*Persea americana*	Australia	JQ948310	JQ948640	JQ948971	JQ949301	JQ949631	JQ949961
	CBS 127600, BRIP 20127a	*Persea americana*, fruit rot	Australia	JQ948308	JQ948638	JQ948969	JQ949299	JQ949629	JQ949959
	CBS 127599, BRIP 29284a	*Persea americana*, fruit rot	Australia	JQ948309	JQ948639	JQ948970	JQ949300	JQ949630	JQ949960
	IMI 324991, CPC 18878	*Piper nigrum*	Unknown	JQ948338	JQ948668	JQ948999	JQ949329	JQ949659	JQ949989
	CBS 126526, PD 93/1373, BBA 70343	*Primula* sp., leaf spots	Netherlands	JQ948323	JQ948653	JQ948984	JQ949314	JQ949644	JQ949974
	CBS 124958	*Pyrus* sp., fruit rot	USA	JQ948306	JQ948636	JQ948967	JQ949297	JQ949627	JQ949957
	ATCC 12097, CPC 19392	*Rhododendron* sp.	USA	JQ948307	JQ948637	JQ948968	JQ949298	JQ949628	JQ949958
	CBS 200.35	*Rubus* sp.	USA	JQ948293	JQ948623	JQ948954	JQ949284	JQ949614	JQ949944
	CBS 490.92, ATCC 60260	*Solanum lycopersicum*	New Zealand	JQ948326	JQ948656	JQ948987	JQ949317	JQ949647	JQ949977
	CBS 124962	*Solanum lycopersicum*, fruit rot	USA	JQ948319	JQ948649	JQ948980	JQ949310	JQ949640	JQ949970
	CBS 124963	*Solanum lycopersicum*, fruit rot	USA	JQ948320	JQ948650	JQ948981	JQ949311	JQ949641	JQ949971
	CBS 129948, RB128	*Tulipa* sp.	UK	JQ948344	JQ948674	JQ949005	JQ949335	JQ949665	JQ949995
	CBS 126508, PD 92/906, BBA 70339	*Vaccinium corymbosum* (blueberry), fruit rot	Netherlands	JQ948315	JQ948645	JQ948976	JQ949306	JQ949636	JQ949966
	CBS 119293, MEP 1322	*Vaccinium corymbosum* (blueberry), fruit	New Zealand	JQ948314	JQ948644	JQ948975	JQ949305	JQ949635	JQ949965
	CBS 119186, MEP 1325	*Vaccinium* sp., fruit	New Zealand	JQ948312	JQ948642	JQ948973	JQ949303	JQ949633	JQ949963
	CBS 119292, MEP 1323	*Vaccinium* sp., fruit	New Zealand	JQ948313	JQ948643	JQ948974	JQ949304	JQ949634	JQ949964
	CBS 127537, STE-U 5289	*Vaccinium* sp. (blueberry)	USA	JQ948318	JQ948648	JQ948979	JQ949309	JQ949639	JQ949969
	CBS 129916, CPC 16823	*Vaccinium* sp. (blueberry)	USA	JQ948317	JQ948647	JQ948978	JQ949308	JQ949638	JQ949968
	CBS 129947, CR46, RB022	*Vitis vinifera*	Portugal	JQ948343	JQ948673	JQ949004	JQ949334	JQ949664	JQ949994
C. godetiae	CBS 796.72	*Aeschynomene virginica*	USA	JQ948407	JQ948738	JQ949068	JQ949398	JQ949728	JQ950058
	CBS 131332	*Agrimonia eupatoria*, leaf spot	Austria	JQ948429	JQ948760	JQ949090	JQ949420	JQ949750	JQ950080
	CBS 126512, PD 88/958	Bonzai, sunken brown spots on fruit	Netherlands	JQ948412	JQ948743	JQ949073	JQ949403	JQ949733	JQ950063
	IMI 351248, CPC 18894	*Ceanothus* sp.	UK	JQ948433	JQ948764	JQ949094	JQ949424	JQ949754	JQ950084
	CBS 160.50	*Citrus aurantium*, fruit rot	Unknown	JQ948406	JQ948737	JQ949067	JQ949397	JQ949727	JQ950057
	CBS 133.44*	*Clarkia hybrida*, cv. Kelvon Glory, seed	Denmark	JQ948402	JQ948733	JQ949063	JQ949393	JQ949723	JQ950053

Table 1. (Continued).

Species	Accession No.[1]	Host/Substrate	Country	GenBank No.					
				ITS	GAPDH	CHS-1	HIS3	ACT	TUB2
C. godetiae	IMI 351262, CPC 18897	*Fragaria* × *ananassa*	Belgium	JQ948422	JQ948753	JQ949083	JQ949413	JQ949743	JQ950073
	IMI 345035, CPC 18885	*Fragaria vesca*	France	JQ948425	JQ948756	JQ949086	JQ949416	JQ949746	JQ950076
	IMI 351589, CPC 18921	*Fragaria* × *ananassa*	Ireland	JQ948423	JQ948754	JQ949084	JQ949414	JQ949744	JQ950074
	CBS 125972, PD 85/456	*Fragaria* × *ananassa*	Netherlands	JQ948416	JQ948747	JQ949077	JQ949407	JQ949737	JQ950067
	CBS 126376, PD 95/5903	*Fragaria* × *ananassa*	Netherlands	JQ948417	JQ948748	JQ949078	JQ949408	JQ949738	JQ950068
	CBS 126516, PD 88/548	*Fragaria* × *ananassa*, fruit rot	Netherlands	JQ948418	JQ948749	JQ949079	JQ949409	JQ949739	JQ950069
	IMI 345026, CPC 18882	*Fragaria* × *ananassa*	Spain	JQ948424	JQ948755	JQ949085	JQ949415	JQ949745	JQ950075
	CBS 125974, PD 88/858	*Fragaria* × *ananassa*	UK	JQ948419	JQ948750	JQ949080	JQ949410	JQ949740	JQ950070
	CBS 126503, PD 88/859, BBA 70342	*Fragaria* × *ananassa*	UK	JQ948420	JQ948751	JQ949081	JQ949411	JQ949741	JQ950071
	IMI 351253, CPC 18895	*Fragaria* × *ananassa*	UK	JQ948421	JQ948752	JQ949082	JQ949412	JQ949742	JQ950072
	CBS 171.59	*Juglans regia*	Unknown	JQ948405	JQ948736	JQ949066	JQ949396	JQ949726	JQ950056
	CBS 131331	*Juglans regia*, leaf spot	Austria	JQ948404	JQ948735	JQ949065	JQ949395	JQ949725	JQ950055
	IMI 362149b, CPC 18927	*Laurus nobilis*, dead fallen leaf	UK	JQ948427	JQ948758	JQ949088	JQ949418	JQ949748	JQ950078
	CBS 129942	*Mahonia aquifolium*, leaf spots	Germany	JQ948428	JQ948759	JQ949089	JQ949419	JQ949749	JQ950079
	CBS 198.53	*Malus sylvestris*, fruit	Netherlands	JQ948432	JQ948763	JQ949093	JQ949423	JQ949753	JQ950083
	CBS 285.50	*Malus sylvestris*, fruit	Unknown	JQ948403	JQ948734	JQ949064	JQ949394	JQ949724	JQ950054
	CBS 155.25	Nut shell	Unknown	JQ948410	JQ948741	JQ949071	JQ949401	JQ949731	JQ950061
	CBS 193.32	*Olea europaea*	Greece	JQ948415	JQ948746	JQ949076	JQ949406	JQ949736	JQ950066
	CBS 130251, OL 10, IMI 398854	*Olea europaea*	Italy	JQ948413	JQ948744	JQ949074	JQ949404	JQ949734	JQ950064
	CBS 130252, IMI 398855, OL 20	*Olea europaea*	Italy	JQ948414	JQ948745	JQ949075	JQ949405	JQ949735	JQ950065
	CBS 126520, PD 87/383	*Parthenocissus* sp., leaf and stem spots	Netherlands	JQ948426	JQ948757	JQ949087	JQ949417	JQ949747	JQ950077
	CBS 129911, CPC 15124	*Podocarpus* sp.	South Africa	JQ948434	JQ948765	JQ949095	JQ949425	JQ949755	JQ950085
	CBS 129912, CPC 15125	*Podocarpus* sp.	South Africa	JQ948435	JQ948766	JQ949096	JQ949426	JQ949756	JQ950086
	CBS 129913, CPC 15126	*Podocarpus* sp.	South Africa	JQ948436	JQ948767	JQ949097	JQ949427	JQ949757	JQ950087
	CBS 126527, PD 93/1748	*Prunus avium*	UK	JQ948408	JQ948739	JQ949069	JQ949399	JQ949729	JQ950059
	CBS 126522, PD 88/472, BBA 70345	*Prunus cerasus*, fruit, die-back	Netherlands	JQ948411	JQ948742	JQ949072	JQ949402	JQ949732	JQ950062
	CBS 129934, ALM-IKS-7Q	*Prunus dulcis*	Israel	JQ948431	JQ948762	JQ949092	JQ949422	JQ949752	JQ950082
	IMI 376331, CPC 18933	*Prunus* sp., fruit	Norway	JQ948409	JQ948740	JQ949070	JQ949400	JQ949730	JQ950060
	IMI 381927, CPC 18935	*Rubus idaeus*, cane	Turkey	JQ948438	JQ948769	JQ949099	JQ949429	JQ949759	JQ950089
	CBS 862.70	*Sambucus nigra*, fruit	Netherlands	JQ948437	JQ948768	JQ949098	JQ949428	JQ949758	JQ950088
	CBS 129951, RB118	*Vitis* sp.	UK	JQ948430	JQ948761	JQ949091	JQ949421	JQ949751	JQ950081
	CBS 129917, CPC 16002	*Schinus molle*	Mexico	JQ948441	JQ948772	JQ949102	JQ949432	JQ949762	JQ950092
	CBS 129809, T.A.1	*Solanum betaceum*, fruit, anthracnose	Colombia	JQ948439	JQ948770	JQ949100	JQ949430	JQ949760	JQ950090

Table 1. (Continued).

Species	Accession No.[1]	Host/Substrate	Country	GenBank No.					
				ITS	GAPDH	CHS-1	HIS3	ACT	TUB2
C. godetiae	CBS 129816, T.A.8	*Solanum betaceum*, fruit, anthracnose	Colombia	JQ948440	JQ948771	JQ949101	JQ949431	JQ949761	JQ950091
	CBS 127561, CPC 16426	*Ugni molinae*, twig, tip necrosis	Chile	JQ948442	JQ948773	JQ949103	JQ949433	JQ949763	JQ950093
C. guajavae	IMI 350839, CPC 18893*	*Psidium guajava*, fruit	India	JQ948270	JQ948600	JQ948931	JQ949261	JQ949591	JQ949921
C. indonesiense	CBS 127551, CPC 14986*	*Eucalyptus* sp.	Indonesia	JQ948288	JQ948618	JQ948949	JQ949279	JQ949609	JQ949939
C. johnstonii	IMI 357027, CPC 18924, PRJ 1125.005	*Citrus* sp.	New Zealand	JQ948443	JQ948774	JQ949104	JQ949434	JQ949764	JQ950094
	CBS 128532, ICMP 12926, PRJ 1139.3*	*Solanum lycopersicum*, fruit rot	New Zealand	JQ948444	JQ948775	JQ949105	JQ949435	JQ949765	JQ950095
C. kinghornii	CBS 198.35*	*Phormium* sp.	UK	JQ948454	JQ948785	JQ949115	JQ949445	JQ949775	JQ950105
C. laticiphilum	CBS 112989, IMI 383015, STE-U 5303*	*Hevea brasiliensis*	India	JQ948289	JQ948619	JQ948950	JQ949280	JQ949610	JQ949940
	CBS 129827, CH2	*Hevea brasiliensis*, leaf, anthracnose	Colombia	JQ948290	JQ948620	JQ948951	JQ949281	JQ949611	JQ949941
C. limetticola	CBS 114.14*	*Citrus aurantifolia*, young twig	USA, Florida	JQ948193	JQ948523	JQ948854	JQ949184	JQ949514	JQ949844
C. lupini	IMI 351261, CPC 18896	*Camellia* sp.	UK	JQ948177	JQ948507	JQ948838	JQ949168	JQ949498	JQ949828
	CBS 129944, CMG12, RB042	*Cinnamomum verum*	Portugal	JQ948178	JQ948508	JQ948839	JQ949169	JQ949499	JQ949829
	IMI 375715, CPC 19390	*Lupinus albus*	Australia	JQ948161	JQ948491	JQ948822	JQ949152	JQ949482	JQ949812
	CBS 109224, BBA 70399	*Lupinus albus*	Austria	JQ948172	JQ948502	JQ948833	JQ949163	JQ949493	JQ949823
	CBS 109216, BBA 63879	*Lupinus mutabilis*	Bolivia	JQ948156	JQ948486	JQ948817	JQ949147	JQ949477	JQ949807
	CBS 109226, BBA 71249	*Lupinus albus*	Canada	JQ948158	JQ948488	JQ948819	JQ949149	JQ949479	JQ949809
	CBS 513.97, LARS 401	*Lupinus polyphyllus*	Costa Rica	JQ948157	JQ948487	JQ948818	JQ949148	JQ949478	JQ949808
	CBS 509.97, LARS 178	*Lupinus albus*	France	JQ948159	JQ948489	JQ948820	JQ949150	JQ949480	JQ949810
	CBS 507.97, LARS 163	*Lupinus albus*	France	JQ948166	JQ948496	JQ948827	JQ949157	JQ949487	JQ949817
	CBS 109220, BBA 70317	*Lupinus albus*	Germany	JQ948168	JQ948498	JQ948829	JQ949159	JQ949489	JQ949819
	CBS 109221, BBA 70352	*Lupinus albus*	Germany	JQ948169	JQ948499	JQ948830	JQ949160	JQ949490	JQ949820
	CBS 109222, BBA 70358	*Lupinus albus*	Germany	JQ948170	JQ948500	JQ948831	JQ949161	JQ949491	JQ949821
	CBS 485.97	*Lupinus albus*, cv. Minori	Germany	JQ948164	JQ948494	JQ948825	JQ949155	JQ949485	JQ949815
	CBS 109223, BBA 70385	*Lupinus angustifolius*	Germany	JQ948171	JQ948501	JQ948832	JQ949162	JQ949492	JQ949822
	CBS 109219, BBA 70073	*Lupinus polyphyllus*	Germany	JQ948167	JQ948497	JQ948828	JQ949158	JQ949488	JQ949818
	CBS 109217, BBA 68334	*Lupinus* sp.	Germany	JQ948163	JQ948493	JQ948824	JQ949154	JQ949484	JQ949814
	CBS 126525, PD 89/1303, BBA 70346	*Lupinus* sp., leaf spots	Netherlands	JQ948174	JQ948504	JQ948835	JQ949165	JQ949495	JQ949825
	CBS 126371, PD 93/1436, BBA 70344	*Lupinus* sp., petiole with sunken spots	Netherlands	JQ948165	JQ948495	JQ948826	JQ949156	JQ949486	JQ949816
	CBS 109227, BBA 71310	*Lupinus luteus*	Poland	JQ948173	JQ948503	JQ948834	JQ949164	JQ949494	JQ949824
	CBS 119142, CMW 9931	*Lupinus albus*, anthracnose	South Africa	JQ948175	JQ948505	JQ948836	JQ949166	JQ949496	JQ949826
	CBS 119143, CMW 9933	*Lupinus albus*, anthracnose	South Africa	JQ948176	JQ948506	JQ948837	JQ949167	JQ949497	JQ949827
	CBS 122746, BPI 871840, AR 2826	*Lupinus* sp., Russell hybrid mix	USA	JQ948162	JQ948492	JQ948823	JQ949153	JQ949483	JQ949813
	CBS 109225, BBA 70884*	*Lupinus albus*	Ukraine	JQ948155	JQ948485	JQ948816	JQ949146	JQ949476	JQ949806

Table 1. (Continued).

Species	Accession No.[1]	Host/Substrate	Country	GenBank No.					
				ITS	GAPDH	CHS-1	HIS3	ACT	TUB2
C. lupini	CBS 466.76	*Manihot utilissima*, leaf	Rwanda	JQ948160	JQ948490	JQ948821	JQ949151	JQ949481	JQ949811
C. melonis	CBS 159.84*	*Cucumis melo*, peel of fruit	Brazil	JQ948194	JQ948524	JQ948855	JQ949185	JQ949515	JQ949845
C. nymphaeae	CBS 100064	*Anemone* sp.	Netherlands	JQ948224	JQ948554	JQ948885	JQ949215	JQ949545	JQ949875
	CBS 100065	*Anemone* sp.	Netherlands	JQ948225	JQ948555	JQ948886	JQ949216	JQ949546	JQ949876
	CBS 130.80	*Anemone* sp.	Italy	JQ948226	JQ948556	JQ948887	JQ949217	JQ949547	JQ949877
	CBS 129935, ANE-4	*Anemone* sp.	Israel	JQ948227	JQ948557	JQ948888	JQ949218	JQ949548	JQ949878
	CBS 361.79	*Anemone coronaria*	Netherlands	JQ948248	JQ948578	JQ948909	JQ949239	JQ949569	JQ949899
	CBS 126383, PD 84/121	*Anemone coronaria,* cv. de Caen group	Netherlands	JQ948221	JQ948551	JQ948882	JQ949212	JQ949542	JQ949872
	CBS 126382, PD 79/648	*Anemone coronaria*, cv. de Caen group, curl disease	Netherlands	JQ948220	JQ948550	JQ948881	JQ949211	JQ949541	JQ949871
	CBS 126511, PD 88/673	*Anemone coronaria,* cv. de Caen group, stengeltop, curled stengeltop	Netherlands	JQ948222	JQ948552	JQ948883	JQ949213	JQ949543	JQ949873
	CBS 126513, PD 91/1282, BBA 70350	*Anemone* sp., stem, curl disease	Netherlands	JQ948223	JQ948553	JQ948884	JQ949214	JQ949544	JQ949874
	CBS 126528, PD 94/921-2, BBA 70348	*Capsicum* sp.	Indonesia	JQ948219	JQ948549	JQ948880	JQ949210	JQ949540	JQ949870
	IMI 379162, CPC 18934	*Capsicum annuum*, seed	Zimbabwe	JQ948218	JQ948548	JQ948879	JQ949209	JQ949539	JQ949869
	CBS 122110, AR 4455	*Fragaria* × *ananassa*, cv. Redchief, fruit rot	Bulgaria	JQ948235	JQ948565	JQ948896	JQ949226	JQ949556	JQ949886
	CBS 122111, AR 4456	*Fragaria* × *ananassa*, cv. Redchief, fruit rot	Bulgaria	JQ948236	JQ948566	JQ948897	JQ949227	JQ949557	JQ949887
	CBS 122121, AR 4457	*Fragaria* × *ananassa*, cv. Redchief, fruit rot	Bulgaria	JQ948237	JQ948567	JQ948898	JQ949228	JQ949558	JQ949888
	CBS 127608, DAOM 212589, 89M-112	*Fragaria* × *ananassa*	Canada	JQ948264	JQ948594	JQ948925	JQ949255	JQ949585	JQ949915
	IMI 348497, CPC 18891	*Fragaria* × *ananassa*, crown	France	JQ948240	JQ948570	JQ948901	JQ949231	JQ949561	JQ949891
	IMI 345053, CPC 18887	*Fragaria* × *ananassa*	France	JQ948239	JQ948569	JQ948900	JQ949230	JQ949560	JQ949890
	IMI 348502, CPC 18892	*Fragaria* × *ananassa*, crown	France	JQ948238	JQ948568	JQ948899	JQ949229	JQ949559	JQ949889
	IMI 391664, CPC 18940	*Fragaria* × *ananassa*	Israel	JQ948251	JQ948581	JQ948912	JQ949242	JQ949572	JQ949902
	CBS 129936, TUT137A	*Fragaria* × *ananassa*	Israel	JQ948252	JQ948582	JQ948913	JQ949243	JQ949573	JQ949903
	CBS 129937, TUT5954	*Fragaria* × *ananassa*	Israel	JQ948253	JQ948583	JQ948914	JQ949244	JQ949574	JQ949904
	CBS 126372, PD 93/1666A	*Fragaria* × *ananassa*, cv. Idea	Italy	JQ948242	JQ948572	JQ948903	JQ949233	JQ949563	JQ949893
	IMI 345032, CPC 18883	*Fragaria* × *ananassa*, fruit	Italy	JQ948241	JQ948571	JQ948902	JQ949232	JQ949562	JQ949892
	IMI 301119, CPC 18872	*Fragaria vesca*	Kenya	JQ948266	JQ948596	JQ948927	JQ949257	JQ949587	JQ949917
	CBS 125966, NB 732	*Fragaria* × *ananassa*	Netherlands	JQ948247	JQ948577	JQ948908	JQ949238	JQ949568	JQ949898
	CBS 126377, PD 95/9269	*Fragaria* × *ananassa*	Netherlands	JQ948233	JQ948563	JQ948894	JQ949224	JQ949554	JQ949884
	CBS 130239	*Fragaria* × *ananassa*, fruit anthracnose	Netherlands	JQ948250	JQ948580	JQ948911	JQ949241	JQ949571	JQ949901
	CBS 125961, NB 559	*Fragaria* × *ananassa*, root discoloration	Netherlands	JQ948249	JQ948579	JQ948910	JQ949240	JQ949570	JQ949900
	CBS 125958, NB 155	*Fragaria* × *ananassa*, seed	Netherlands	JQ948245	JQ948575	JQ948906	JQ949236	JQ949566	JQ949896
	CBS 125959, NB 156	*Fragaria* × *ananassa*, seed	Netherlands	JQ948246	JQ948576	JQ948907	JQ949237	JQ949567	JQ949897

Table 1. (Continued).

Species	Accession No.[1]	Host/Substrate	Country	GenBank No.					
				ITS	GAPDH	CHS-1	HIS3	ACT	TUB2
C. nymphaeae	CBS 126504, C 105	*Fragaria* × *ananassa*	South Africa	JQ948265	JQ948595	JQ948926	JQ949256	JQ949586	JQ949916
	CBS 112202	*Fragaria* sp., fruit lesions	Spain	JQ948234	JQ948564	JQ948895	JQ949225	JQ949555	JQ949885
	IMI 364856, CPC 18931	*Fragaria* × *ananassa*, crown	Spain	JQ948244	JQ948574	JQ948905	JQ949235	JQ949565	JQ949895
	IMI 360928, CPC 18926	*Fragaria* × *ananassa*, fruit lesion	Switzerland	JQ948243	JQ948573	JQ948904	JQ949234	JQ949564	JQ949894
	IMI 299103, CPC 18871	*Fragaria vesca*	UK	JQ948231	JQ948561	JQ948892	JQ949222	JQ949552	JQ949882
	CBS 125973, PD 88/857	*Fragaria* × *ananassa*	UK	JQ948232	JQ948562	JQ948893	JQ949223	JQ949553	JQ949883
	CBS 129918, MUCL 44838	*Fragaria* sp.	Unknown	JQ948254	JQ948584	JQ948915	JQ949245	JQ949575	JQ949905
	IMI 311743, CPC 18874	*Fragaria* sp., fruit lesion	USA	JQ948258	JQ948588	JQ948919	JQ949249	JQ949579	JQ949909
	CBS 127612, DAOM 213709, H-1984	*Fragaria* × *ananassa*	USA	JQ948230	JQ948560	JQ948891	JQ949221	JQ949551	JQ949881
	CBS 129928, 216	*Fragaria* × *ananassa*	USA	JQ948228	JQ948558	JQ948889	JQ949219	JQ949549	JQ949879
	CBS 129929, 2.6.23	*Fragaria* × *ananassa*	USA	JQ948229	JQ948559	JQ948890	JQ949220	JQ949550	JQ949880
	CBS 126366, PD 92/785	*Fragaria* × *ananassa*	USA	JQ948255	JQ948585	JQ948916	JQ949246	JQ949576	JQ949906
	CBS 126367, PD 92/786	*Fragaria* × *ananassa*	USA	JQ948256	JQ948586	JQ948917	JQ949247	JQ949577	JQ949907
	CBS 126370, PD 92/790	*Fragaria* × *ananassa*	USA	JQ948257	JQ948587	JQ948918	JQ949248	JQ949578	JQ949908
	IMI 324995, CPC 18879	*Fragaria* × *ananassa*	USA	JQ948259	JQ948589	JQ948920	JQ949250	JQ949580	JQ949910
	CBS 127609, DAOM 213394, CA-37-2-2	*Fragaria* × *ananassa*	USA	JQ948260	JQ948590	JQ948921	JQ949251	JQ949581	JQ949911
	CBS 127610, DAOM 213395, CA-37-2-4	*Fragaria* × *ananassa*	USA	JQ948261	JQ948591	JQ948922	JQ949252	JQ949582	JQ949912
	CBS 129933, Goff99	*Fragaria* × *ananassa*	USA	JQ948262	JQ948592	JQ948923	JQ949253	JQ949583	JQ949913
	IMI 348177, CPC 18890	*Fragaria* × *ananassa*, crown	USA	JQ948263	JQ948593	JQ948924	JQ949254	JQ949584	JQ949914
	CBS 119294, MEP 1534	*Leucaena* sp., fruit	Mexico	JQ948205	JQ948535	JQ948866	JQ949196	JQ949526	JQ949856
	CBS 129926, CPC 18719	Litter	Thailand	JQ948216	JQ948546	JQ948877	JQ949207	JQ949537	JQ949867
	CBS 173.51	*Mahonia aquifolium*, leaf	Italy	JQ948200	JQ948530	JQ948861	JQ949191	JQ949521	JQ949851
	IMI 370491, CPC 18932	*Malus pumila*, fruit	Brazil	JQ948204	JQ948534	JQ948865	JQ949195	JQ949525	JQ949855
	CBS 516.78, IAM 14670	*Nuphar luteum*, leaf spot	Netherlands	JQ948198	JQ948528	JQ948859	JQ949189	JQ949519	JQ949849
	CBS 526.77	*Nymphaea alba*, leaf	Netherlands	JQ948199	JQ948529	JQ948860	JQ949190	JQ949520	JQ949850
	CBS 515.78*	*Nymphaea alba*, leaf spot	Netherlands	JQ948197	JQ948527	JQ948858	JQ949188	JQ949518	JQ949848
	CBS 126507, PD 91/1392	*Oenothera* sp., black staining of stem	Netherlands	JQ948203	JQ948533	JQ948864	JQ949194	JQ949524	JQ949854
	CBS 129945, PT135, RB012	*Olea europaea*	Portugal	JQ948201	JQ948531	JQ948862	JQ949192	JQ949522	JQ949852
	CBS 231.49	*Olea europaea*	Portugal	JQ948202	JQ948532	JQ948863	JQ949193	JQ949523	JQ949853
	IMI 360386, CPC 18925	*Pelargonium graveolens*, petiole, leaf and twig	India	JQ948206	JQ948536	JQ948867	JQ949197	JQ949527	JQ949857
	CSL 455, RB126	*Photinia* sp.	UK	JQ948217	JQ948547	JQ948878	JQ949208	JQ949538	JQ949868
	CBS 482.82	*Protea* sp.	Australia	JQ948213	JQ948543	JQ948874	JQ949204	JQ949534	JQ949864
	CBS 115408, STE-U 5357	*Protea cynaroides*	South Africa	JQ948212	JQ948542	JQ948873	JQ949203	JQ949533	JQ949863

Table 1. (Continued).

Species	Accession No.[1]	Host/Substrate	Country	GenBank No.					
				ITS	GAPDH	CHS-1	HIS3	ACT	TUB2
C. nymphaeae	CBS 112992, STE-U 4452	*Protea magnifica*	South Africa	JQ948207	JQ948537	JQ948868	JQ949198	JQ949528	JQ949858
	CBS 113002, STE-U 4456	*Protea repens*	South Africa	JQ948208	JQ948538	JQ948869	JQ949199	JQ949529	JQ949859
	CBS 113003, STE-U 4457	*Protea* sp.	South Africa	JQ948209	JQ948539	JQ948870	JQ949200	JQ949530	JQ949860
	CBS 113004, STE-U 4458	*Protea* sp.	South Africa	JQ948210	JQ948540	JQ948871	JQ949201	JQ949531	JQ949861
	CBS 113005, STE-U 4459	*Protea* sp.	South Africa	JQ948211	JQ948541	JQ948872	JQ949202	JQ949532	JQ949862
	CBS 114188, STE-U 2971	*Protea* sp., cv. Pink Ice	Unknown	JQ948214	JQ948544	JQ948875	JQ949205	JQ949535	JQ949865
	CBS 158.27	*Phaseolus* sp.	Netherlands	JQ948215	JQ948545	JQ948876	JQ949206	JQ949536	JQ949866
C. orchidophilum	CBS 631.80	*Ascocenda* sp.	USA	JQ948152	JQ948482	JQ948813	JQ949143	JQ949473	JQ949803
	CBS 119291, MEP 1545	*Cycnoches aureum*	Panama	JQ948154	JQ948484	JQ948815	JQ949145	JQ949475	JQ949805
	CBS 632.80*	*Dendrobium* sp.	USA	JQ948151	JQ948481	JQ948812	JQ949142	JQ949472	JQ949802
	IMI 309357, CPC 16815	*Phalaenopsis* sp.	UK	JQ948153	JQ948483	JQ948814	JQ949144	JQ949474	JQ949804
C. paxtonii	CBS 502.97, LARS 58	*Musa nana*	"West Indies"	JQ948286	JQ948616	JQ948947	JQ949277	JQ949607	JQ949937
	IMI 165753, CPC 18868*	*Musa* sp.	Saint Lucia	JQ948285	JQ948615	JQ948946	JQ949276	JQ949606	JQ949936
C. phormii	CBS 102054	*Phormium* sp., leaf spot	New Zealand	JQ948448	JQ948779	JQ949109	JQ949439	JQ949769	JQ950099
	CBS 118201, MEP 1334	*Phormium* sp., leaf	New Zealand	JQ948449	JQ948780	JQ949110	JQ949440	JQ949770	JQ950100
	CBS 199.35, DSM 1168	*Phormium* sp.	UK	JQ948447	JQ948778	JQ949108	JQ949438	JQ949768	JQ950098
	CBS 118191, AR 3787	*Phormium* sp., leaf	South Africa	JQ948453	JQ948784	JQ949114	JQ949444	JQ949774	JQ950104
	CBS 118197, AR 3389	*Phormium* sp.	New Zealand	JQ948450	JQ948781	JQ949111	JQ949441	JQ949771	JQ950101
	CBS 124953	*Phormium* sp., leaf	Netherlands	JQ948452	JQ948783	JQ949113	JQ949443	JQ949773	JQ950103
	CBS 483.82	*Phormium tenax*	New Zealand	JQ948451	JQ948782	JQ949112	JQ949442	JQ949772	JQ950102
	CBS 118194, AR 3546*	*Phormium* sp.	Germany	JQ948446	JQ948777	JQ949107	JQ949437	JQ949767	JQ950097
C. pseudoacutatum	CBS 436.77*	*Pinus radiata*	Chile	JQ948480	JQ948811	JQ949141	JQ949471	JQ949801	JQ950131
C. pyricola	CBS 128531, ICMP 12924, PRJ 977.1*	*Pyrus communis*, fruit rot	New Zealand	JQ948445	JQ948776	JQ949106	JQ949436	JQ949766	JQ950096
C. rhombiforme	CBS 129953, PT250, RB011*	*Olea europaea*	Portugal	JQ948457	JQ948788	JQ949118	JQ949448	JQ949778	JQ950108
	CBS 131322, DAOM 233253, C10, MS1L34	*Vaccinium macrocarpum*	USA	JQ948458	JQ948789	JQ949119	JQ949449	JQ949779	JQ950109
C. salicis	CBS 129972, MP1, RB096	*Acer platanoides*, symptomatic leaves	USA	JQ948466	JQ948797	JQ949127	JQ949457	JQ949787	JQ950117
	CBS 129973, MP2, RB097	*Acer platanoides*, symptomatic leaves	USA	JQ948467	JQ948798	JQ949128	JQ949458	JQ949788	JQ950118
	CBS 465.83	*Araucaria excelsa*, anthracnose and dieback	USA	JQ948468	JQ948799	JQ949129	JQ949459	JQ949789	JQ950119
	IMI 345585, CPC 19376	*Fragaria* × *ananassa*, petiole spot	New Zealand	JQ948476	JQ948807	JQ949137	JQ949467	JQ949797	JQ950127
	CBS 128556, ICMP 12954, PRJ 11071	*Fragaria* × *ananassa*, fruit rot	New Zealand	JQ948473	JQ948804	JQ949134	JQ949464	JQ949794	JQ950124
	CBS 128557, ICMP 12955, PRJ 1115.1	*Fragaria* × *ananassa*, fruit rot	New Zealand	JQ948474	JQ948805	JQ949135	JQ949465	JQ949795	JQ950125
	IMI 345581, CPC 19377	*Fragaria* × *ananassa*, lesion	New Zealand	JQ948475	JQ948806	JQ949136	JQ949466	JQ949796	JQ950126
	CBS 113.14	*Malus domestica*, cv. Manks Küchenapfel, fruit	Germany	JQ948478	JQ948809	JQ949139	JQ949469	JQ949799	JQ950129

Table 1. (Continued).

Species	Accession No.[1]	Host/Substrate	Country	GenBank No.					
				ITS	GAPDH	CHS-1	HIS3	ACT	TUB2
C. salicis	IMI 385055, CPC 18939	*Malus domestica*, fruit	New Zealand	JQ948472	JQ948803	JQ949133	JQ949463	JQ949793	JQ950123
	CBS 180.97, PD 96003647	*Populus canadensis*, cv. Dorschkamp	Netherlands	JQ948464	JQ948795	JQ949125	JQ949455	JQ949785	JQ950115
	CBS 223.36	*Populus* sp.	Netherlands	JQ948465	JQ948796	JQ949126	JQ949456	JQ949786	JQ950116
	CBS 128559, ICMP 12957, PRJ 1160.1	*Pyrus pyrifolia*, fruit rot	New Zealand	JQ948471	JQ948802	JQ949132	JQ949462	JQ949792	JQ950122
	CBS 129356, MSCL 850	*Rhododendron* sp.	Latvia, Riga	JQ948470	JQ948801	JQ949131	JQ949461	JQ949791	JQ950121
	CBS 191.56	*Salix* sp.	Germany	JQ948461	JQ948792	JQ949122	JQ949452	JQ949782	JQ950112
	CBS 192.56	*Salix* sp., tissue	Germany	JQ948462	JQ948793	JQ949123	JQ949453	JQ949783	JQ950113
	CBS 607.94*	*Salix* sp., leaf, spot	Netherlands	JQ948460	JQ948791	JQ949121	JQ949451	JQ949781	JQ950111
	CBS 128558, ICMP 12956, PRJ 1117.4	*Salix* sp., twig, lesion	New Zealand	JQ948463	JQ948794	JQ949124	JQ949454	JQ949784	JQ950114
	CBS 159.27	*Salix* sp.	UK	JQ948479	JQ948810	JQ949140	JQ949470	JQ949800	JQ950130
	CBS 115.14	*Solanum lycopersicum*, fruit	Germany	JQ948477	JQ948808	JQ949138	JQ949468	JQ949798	JQ950128
	CBS 239.49	Unknown	Unknown	JQ948469	JQ948800	JQ949130	JQ949460	JQ949790	JQ950120
C. scovillei	CBS 126529, PD 94/921-3, BBA 70349*	*Capsicum* sp.	Indonesia	JQ948267	JQ948597	JQ948928	JQ949258	JQ949588	JQ949918
	CBS 126530, PD 94/921-4	*Capsicum* sp.	Indonesia	JQ948268	JQ948598	JQ948929	JQ949259	JQ949589	JQ949919
	CBS 120708, HKUCC 10893, Mj6	*Capsicum annuum*	Thailand	JQ948269	JQ948599	JQ948930	JQ949260	JQ949590	JQ949920
C. simmondsii	CBS 294.67, DPI 13483	*Carica papaya*	Australia	JQ948277	JQ948607	JQ948938	JQ949268	JQ949598	JQ949928
	CBS 122122, BRIP 28519*	*Carica papaya*, fruit	Australia	JQ948276	JQ948606	JQ948937	JQ949267	JQ949597	JQ949927
	CBS 126524, PD 89/582	*Cyclamen* sp., deformations and brown staining of stem tip	Netherlands	JQ948281	JQ948611	JQ948942	JQ949272	JQ949602	JQ949932
	CBS 295.67, DPI 16518	*Fragaria* sp., fruit	Australia	JQ948278	JQ948608	JQ948939	JQ949269	JQ949599	JQ949929
	IMI 345034, CPC 18884	*Fragaria* × *ananassa*, fruit	Australia	JQ948279	JQ948609	JQ948940	JQ949270	JQ949600	JQ949930
	IMI 354381, CPC 18923	*Fragaria* × *ananassa*, fruit rot	Australia	JQ948280	JQ948610	JQ948941	JQ949271	JQ949601	JQ949931
	IMI 313840, CPC 18875	*Mangifera indica*	Australia	JQ948284	JQ948614	JQ948945	JQ949275	JQ949605	JQ949935
	CBS 111531, STE-U 2090	*Protea cynaroides*	USA	JQ948282	JQ948612	JQ948943	JQ949273	JQ949603	JQ949933
	CBS 114494, STE-U 2964, STE-U 2088	*Protea cynaroides*	USA	JQ948283	JQ948613	JQ948944	JQ949274	JQ949604	JQ949934
C. sloanei	IMI 364297, CPC 18929*	*Theobroma cacao*, leaf	Malaysia	JQ948287	JQ948617	JQ948948	JQ949278	JQ949608	JQ949938
C. tamarilloi	CBS 129814, T.A.6*	*Solanum betaceum*, fruit, anthracnose	Colombia	JQ948184	JQ948514	JQ948845	JQ949175	JQ949505	JQ949835
	CBS 129811, T.A.3	*Solanum betaceum*, fruit, anthracnose	Colombia	JQ948185	JQ948515	JQ948846	JQ949176	JQ949506	JQ949836
	CBS 129813, T.A.5	*Solanum betaceum*, fruit, anthracnose	Colombia	JQ948187	JQ948517	JQ948848	JQ949178	JQ949508	JQ949838
	CBS 129812, T.A.4	*Solanum betaceum*, fruit, anthracnose	Colombia	JQ948186	JQ948516	JQ948847	JQ949177	JQ949507	JQ949837
	CBS 129954, Tom-21, RB017	*Solanum betaceum*	Colombia	JQ948188	JQ948518	JQ948849	JQ949179	JQ949509	JQ949839
	CBS 129955, Tom-12, RB018	*Solanum betaceum*	Colombia	JQ948189	JQ948519	JQ948850	JQ949180	JQ949510	JQ949840
	CBS 129956, Tom-9, RB112	*Solanum betaceum*	Colombia	JQ948190	JQ948520	JQ948851	JQ949181	JQ949511	JQ949841

Table 1. (Continued).

Species	Accession No.[1]	Host/Substrate	Country	GenBank No.					
				ITS	GAPDH	CHS-1	HIS3	ACT	TUB2
C. walleri	CBS 125472, BMT(HL)19*	*Coffea* sp., leaf tissue	Vietnam	JQ948275	JQ948605	JQ948936	JQ949266	JQ949596	JQ949926
***Colletotrichum* sp.**	CBS 129820, G5	*Passiflora edulis*, fruit, scab	Colombia	JQ948183	JQ948513	JQ948844	JQ949174	JQ949504	JQ949834
	CBS 129821, G6	*Passiflora edulis*, fruit, scab	Colombia	JQ948182	JQ948512	JQ948843	JQ949173	JQ949503	JQ949833
	CBS 129823, G8	*Passiflora edulis*, leaf, anthracnose	Colombia	JQ948192	JQ948522	JQ948853	JQ949183	JQ949513	JQ949843
	IMI 384185, CPC 18937	*Caryocar brasiliense*	Brazil	JQ948191	JQ948521	JQ948852	JQ949182	JQ949512	JQ949842
	CBS 101611	Fern	Costa Rica	JQ948196	JQ948526	JQ948857	JQ949187	JQ949517	JQ949847
	CBS 129810, T.A.2	*Solanum betaceum*, fruit, anthracnose	Colombia	JQ948179	JQ948509	JQ948840	JQ949170	JQ949500	JQ949830

[1]CBS: Culture collection of the Centraalbureau voor Schimmelcultures, Fungal Biodiversity Centre, Utrecht, The Netherlands; IMI: Culture collection of CABI Europe UK Centre, Egham, UK; MAFF: MAFF Genebank Project, Ministry of Agriculture, Forestry and Fisheries, Tsukuba, Japan; BRIP: Plant Pathology Herbarium, Department of Employment, Economic, Development and Innovation, Queensland, Australia; ICMP: International Collection of Microorganisms from Plants, Auckland, New Zealand; STE-U: Culture collection of the Department of Plant Pathology, University of Stellenbosch, South Africa; HKUCC: The University of Hong Kong Culture Collection, Hong Kong, China; PD: Plantenziektenkundige Dienst Wageningen, Nederland; * ex-holotype or ex-epitype cultures.

3–8.5 µm diam. *Setae* very few, medium brown, basal cell pale, smooth-walled, 1–2-septate, 45–85 µm long, base cylindrical, 3–4 µm diam, tip ± acute. *Conidiophores* hyaline to pale brown, smooth-walled, septate, branched, to 30 µm long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical to ampulliform, 9–20 × 3.5–5 µm, opening 1–1.5 µm diam, collarette 0.5–1 µm long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical with one end round and one end slightly acute, (12.5–)15–18.5(–20.5) × (4–)4.5–5 µm, mean ± SD = 16.8 ± 1.7 × 4.7 ± 0.3 µm, L/W ratio = 3.6.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline to pale cinnamon, on filter paper, *Anthriscus* stem and medium partly covered with short floccose-felty white aerial mycelium and salmon, orange to olivaceous grey acervuli, reverse same colours, growth rate 20–21.5 mm in 7 d (32–33 mm in 10 d). Colonies on OA flat with entire margin; surface buff to honey, almost entirely covered with floccose-felty white to pale olivaceous grey aerial mycelium and olivaceous grey to salmon acervuli, reverse buff, pale olivaceous grey, grey olivaceous to iron-grey, growth rate 17.5–20 mm in 7 d (27.5–30 mm in 10 d). *Conidia in mass* salmon to orange.

Material examined: **New Zealand,** Nelson, from bitter rot on fruit of *Malus domestica*, 1 Aug. 1987, P.R. Johnston, (CBS H-20725 **holotype**, culture ex-type CBS 128530 = ICMP 12921 = PRJ 1199.3).

Notes: Bitter rot has been considered an economically signficant disease of apple for many years (Schrenk & Spaulding 1903b), and was initially ascribed to *Gloeosporium fructigenum* (Berkeley 1856). However, Berkeley's type was examined by Vinnere (2004) and found to have falcate conidia, thus excluding it from the *C. acutatum* species complex. Currently, bitter rot is known to be caused primarily by fungi from the *C. gloeosporioides* species complex (González *et al*. 2006); that study focused on strains from the USA and Brazil, and we do not know whether their *C. acutatum s. lat.* strains are conspecific with *C. acerbum*. Those of Lee *et al*. (2007) from Korea are referable to *C. acutatum* clades 2 (*C. nymphaeae* and related species) and 3 (*C. fioriniae*), so the host certainly appears susceptible to a wide range of *Colletotrichum* pathogens.

The ex-type strain of *C. acerbum* is the only strain we included in our study that represents *C. acutatum* group B as delineated by Lardner *et al.* (1999). It may be common on *Malus* in New Zealand, but Lardner *et al*. (1999) found that more strains from fruit rot of apple, as well as from feijoa and fig, belonged to group C and had similar RAPD banding patterns (Lardner *et al.* 1999). It is possible that their group C includes more than one species. The GAPDH sequence of strain PJ9 (= PRJ 819 in Lardner *et al.* 1999), which was isolated from apple in New Zealand and was sequenced by Guerber *et al.* (2003), is identical to that of CBS 128530, the ex-type strain of *C. acerbum*.

Colletotrichum acerbum is distinguishable from *C. rhombiforme* and all other species in all gene sequences analysed except for CHS-1, and is most effectively distinguished with TUB2 and ITS. In morphological terms its conidia are longer and the appressoria are shorter and wider than those of *C. rhombiforme*. Based on our studies and blastn searches in GenBank, it seems that *C. acerbum* could be endemic to New Zealand. The closest match based on TUB2 sequence that we could find (with 99 % identity, 5 bp differences) was AJ748624 from isolate PT250 (= CBS 129953), derived from olive in Portugal (Talhinhas *et al.* 2005), which we assign to *C. rhombiforme*. The closest matches for the ITS

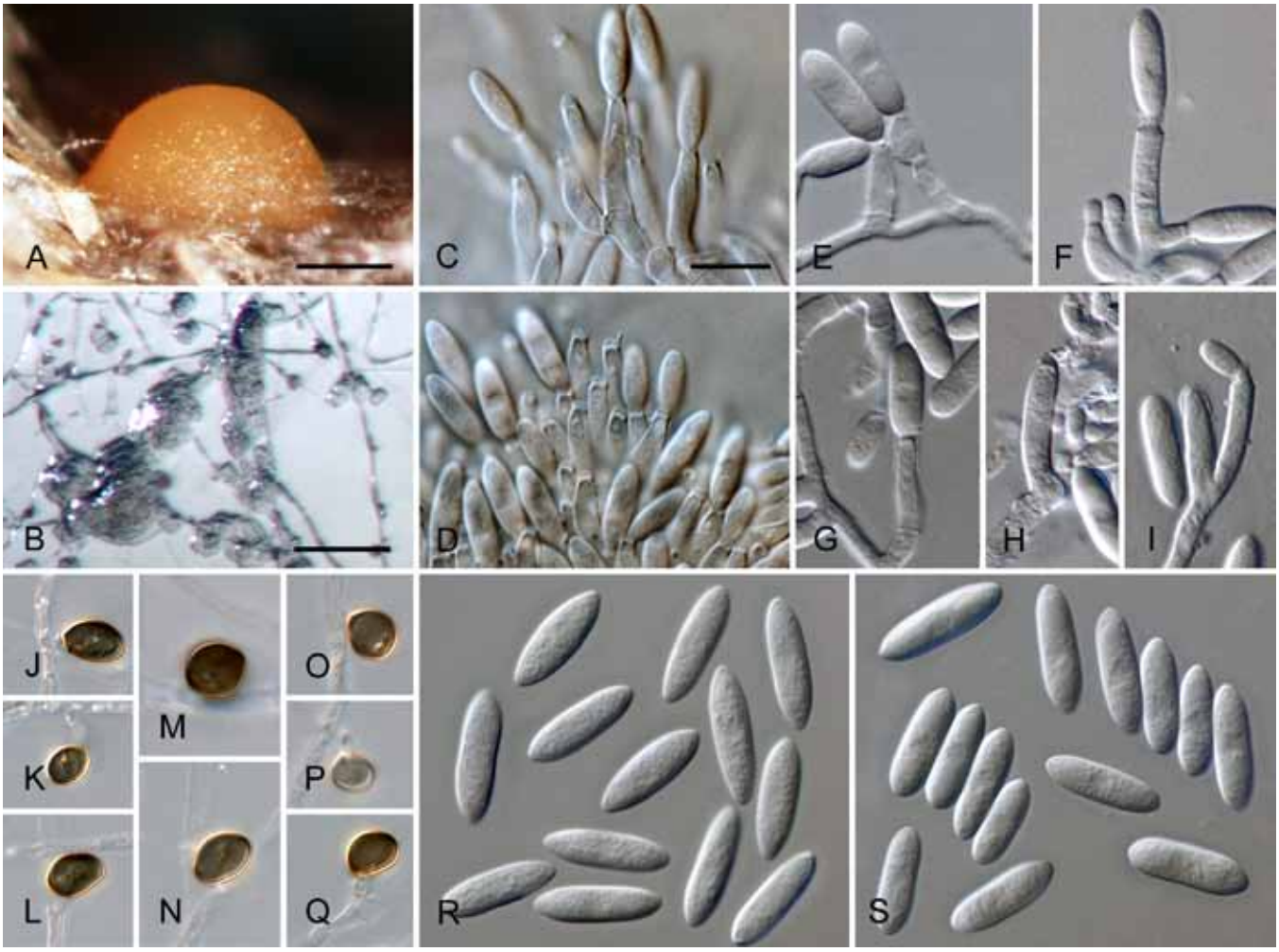

Fig. 3. *Colletotrichum acutatum* (from ex-epitype strain CBS 112996). A–B. Conidiomata. C–I. Conidiophores. J–Q. Appressoria. R–S. Conidia. A, C–D, R. from *Anthriscus* stem. B, E–Q, S. from SNA. A–B. DM, C–S. DIC, Scale bars: A = 200 µm, B = 100 µm, C = 10 µm. Scale bar of C applies to C–S.

sequence of *C. acerbum* (with 99 % identity, 3 bp differences), were with the ITS of *C. phormii* and *C. salicis*, which are all members of the same major clade.

Colletotrichum acutatum J.H. Simmonds, Queensland J. agric. Anim. Sci. 25: 178A. 1968. Fig. 3.

≡ *Colletotrichum acutatum* J.H. Simmonds, Queensland J. agric. Anim. Sci. 22: 458. 1965, nom. inval., Art. 37.1.

Sexual morph not observed. *Asexual morph on SNA. Vegetative hyphae* 1–5.5 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* absent, conidiophores formed directly on vegetative hyphae. *Setae* not observed. *Conidiophores* hyaline, smooth-walled, mostly simple, sometimes septate and branched, to 25 µm long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical to slightly inflated, often not clearly separated from subtending hyphae by a septum, 3.5–20 × 2–3.5 µm, opening 1–1.5 µm diam, collarette distinct, 1–1.5 µm long, periclinal thickening conspicuous. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical to fusiform with both ends acute, (7.5–)11–14.5(–19) × 3.5–4(–4.5) µm, mean ± SD = 12.6 ± 1.8 × 3.9 ± 0.3 µm, L/W ratio = 3.2, conidia of strains CBS 112759, CBS 112979 and CBS 979.69 differ in being cylindrical to clavate and having one round and one acute end, *e.g.*, conidia of strain CBS 112759 are smaller, measuring (6.5–)8.5–12(–13) × (2.5–)3–4 µm, mean ± SD = 10.3 ± 1.9 × 3.4 ± 0.5 µm, L/W ratio = 3.1. *Appressoria* solitary, medium brown, smooth-walled, ellipsoidal to obovate, entire edge, sometimes undulate, (4–)5.5–9(–13) × (3–)4–6.5(–9.5) µm, mean ± SD = 7.3 ± 2.0 × 5.4 ± 1.2 µm, L/W ratio = 1.3.

Asexual morph on Anthriscus stem. Conidiomata acervular, conidiophores formed on a cushion of pale brown angular cells, 2–7 µm diam. *Setae* not observed. *Conidiophores* hyaline, septate, branched, smooth-walled, to 50 µm long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical, 9–18 × 3–3.5 µm, opening 1–1.5 µm diam, collarette distinct, 0.5 µm long, periclinal thickening conspicuous. *Conidia* hyaline, smooth-walled, aseptate, straight, fusiform to cylindrical, apex and base uniformly acute, (8.5–)12–16.5(–17.5) × (3–)3.5–4.5(–5) µm, mean ± SD = 14.3 ± 2.1 × 4.1 ± 0.4 µm, L/W ratio = 3.5, conidia of strains CBS 112759, CBS 370.73 and CBS 112979 differ in being cylindrical to clavate and in having one round and one acute end, conidia of strain CBS 370.73 are smaller, measuring (5–)6.5–11(–12.5) × (2–)2.5–3.5(–4.5) µm, mean ± SD = 8.8 ± 2.1 × 3.2 ± 0.5 µm, L/W ratio = 2.7.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline with white aerial mycelium on *Anthriscus* stem and filter paper, reverse of filter paper partly pale ochreous; growth rate 21–24.5 mm in 7 d (30–36.5 mm in 10 d). Colonies on OA flat with entire margin; surface buff, rosy buff, salmon to peach due to sporulation, with olivaceous sectors in the centre, partly covered by white floccose aerial mycelium, reverse rosy buff to flesh, smoke grey to olivaceous grey in the centre; growth rate 20–25 mm in 7 d (31–33.5 mm in 10 d). *Conidia in mass* saffron to orange.

Material examined: **Australia**, Queensland, Ormiston, Redlands Research Station, from fruit rot of *Carica papaya*, 1 Oct. 1965, J.H. Simmonds (IMI 117617 = QDPI&F plant disease log book no. 16741B1 **holotype**, BRIP 4693, isotype of *C. acutatum*); Queensland, Brisbane, Ormiston, from fruit rot of *Carica papaya*, 5 Jul. 1965, J.H. Simmonds (deposited in CBS collection 2002 by P.W. Crous), (CBS-H 20723, **epitype** here designated, culture ex-epitype (and ex-paratype IMI 117620 of *C. acutatum*) CBS 112996 = ATCC 56816 = ICMP 1783 = STE-U 5292); New South Wales; Mount Annari, from *Grevillea* sp., 12 Oct. 1999, P.W. Crous, culture CBS 111993 = STE-U 3037; Western Australia, Wanneroo, from *Fragaria* × *ananassa*, 8 Aug. 1988, R.M. Floyd, culture CBS 127602 = BRIP 52691a = WAC 5416; from seedling of *Pinus radiata*, collection date and collector unknown (isolated Apr. 1971, deposited in CBS collection Sep. 1972 from Forest Research Institut Rotorua as *C. acutatum f. sp. pineum*), culture CBS 797.72. **South Africa**, from *Leucadendron* sp. cv. Safari Sunset, collection date unknown, J.E. Taylor, culture CBS 112990 = STE-U 4448; from *Aspalathus linearis*, collection date unknown, S. Lamprecht, culture CBS 129915 = CPC 15512; Southern Cape, Kruisfontein, from *Pinus radiata*, collection date unknown, Lundquist, culture CBS 110735 = STE-U 163; Kruisfontein, from *Pinus radiata*, collection date unknown, Lundquist, culture CBS 112979 = STE-U 160; Eastern Cape, Langkloof, from *Hakea sericea*, collector unknown (deposited in CBS collection 2002 by P.W. Crous), culture CBS 112759 = STE-U 4470; from *Hakea sericea*, collection date unknown (deposited in CBS collection 2002 by P.W. Crous), K. Lubbe, culture CBS 112761 = STE-U 4461. **New Zealand**, Tokoroa, from *Pinus radiata*, unknown collection date and collector (deposited in CBS collection Jan 1973 by J.M. Dingley), culture CBS 370.73 = NRCC 10088; **Kenya**, Yala, from berry of *Coffea arabica*, collection date unknown, D.M. Masaba, culture IMI 319423 = CPC 18877; from *Coffea arabica*, unknown collection date and collector (deposited in CBS collection Nov. 1969 by H. Vermeulen), culture CBS 979.69.

Notes: *Colletotrichum acutatum* was described by Simmonds (1965) from a range of different hosts from Australia. No type was designated, and the name was validated three years later (Simmonds 1968) with designation of a holotype, IMI 117617 from *Carica papaya*, and paratypes from *C. papaya* (IMI 117618 - IMI 117621), *Capsicum frutescens* (IMI 117622), and *Delphinium* sp. (IMI 117623).

Vinnere *et al.* (2002) sequenced the ITS region of the holotype specimen (AF411700) and one paratype specimen IMI 117619 (AF411701) and found morphological and cultural differences between Simmonds's six holotype/paratype specimens of *C. acutatum*. There is no living ex-holotype culture available, but two ex-paratype strains, one from *Carica papaya* (IMI 117620 = QDPI&F plant disease log book no. 16633D = ATCC 56816 = CBS 112996 = STE-U 5292) and one from *Capsicum frutescens* (IMI 117622 = QDPI&F plant disease log book no. 11711A = CBS 292.67, see *C. brisbanense*) and an ex-topotype strain from *Carica papaya* (QDPI&F plant disease log book no. 13483-0 = CBS 294.67, see *C. simmondsii*) do exist in a living state.

Than *et al.* (2008b) epitypified *C. acutatum* with a strain from *Carica papaya* from the region in which the species was first collected (BRIP 28519 = CBS 122122). Not only was this action inadvisable bearing in mind that living cultures from two paratypes still exist, it was regrettable as it was subsequently discovered that their epitype was not conspecific with the type. Following an ITS and TUB2 analysis of the clade, Shivas & Tan (2009) described *C. acutatum sensu* Than *et al.* (2008b) as a separate species, *C. simmondsii*. They did not designate a further epitype for *C. acutatum*, but bearing in mind that only the ITS region of the holotype was sequenced, we feel that it is important to fix the application of that species name with an appropriate epitype that can be subject to multigene analysis. This has been done above, with one of Simmond's original paratypes chosen for this purpose.

Colletotrichum acutatum s. str. causes diseases of a wide range of unrelated plants, some of which are economically significant, including papaya (*Carica papaya*), strawberry (*Fragaria* × *ananassa*), pine (*Pinus* spp.), *Hakea* spp. and rooibos (*Aspalathus linearis*). Two of these are associated with recognition of *formae speciales*. These are not accepted as a taxonomic rank in the International Code of Nomenclature for Algae, Fungi and Plants (ICN) as they are based on fungus/plant interactions rather than single species, and formal ICN-compliant taxa cannot use *formae speciales* as basionyms for new combinations.

Colletotrichum acutatum f. sp. pinea (Dingley & Gilmour 1972) was described for a malady of pines called terminal crook disease, with the fungus apparently causing malformation of growing tips. We have examined authentic cultures derived from Dingley & Gilmour's work, which were also used by von Arx. Most of these cannot be distinguished in morphological or molecular terms from *C. acutatum s. str.*, but strain CBS 436.77 (from Chile, not from New Zealand as are the authentic cultures of *C. acutatum f. sp. pinea*), belongs to a quite different species outside of the *C. acutatum* species complex (see *C. pseudoacutatum*). CBS 797.72 appears to show evidence of hybrid origin and is not included in the molecular analyses (see below).

Colletotrichum acutatum f. sp. hakeae (Lubbe *et al.* 2004) was introduced for an apparently strongly host-specific set of strains, one of which was being used as a potential biological control agent (Morris 1982, Gordon & Fourie 2011), but we have not found any morphological differences and there are few sequence-based differences (1 bp difference in ITS, 2 bp differences in HIS3) between these and other *C. acutatum s. str.* strains. We therefore do not feel confident to recognise this *forma specialis* on that basis as a segregate species. *Colletotrichum acutatum f. sp. chromogenum* was described by Baxter *et al*. (1983), based on strains from olive referred to as *Gloeosporium fructigenum f. sp. chromogenum* by Gorter (1962), for strains producing pink to purple pigments in culture. Such pigment production is common throughout the *C. acutatum* complex (*e.g.* Polashock *et al.* 2009) and is especially prominent in *C. acutatum s. str.* (as their clade A5) according to Sreenivasaprasad & Talhinhas (2005). In fact the only strain from olive in South Africa included in this study (CBS 127589) belongs to this species and could represent *C. acutatum f. sp. chromogenum*. But whatever the case, the rank used is inappropriate for this purpose.

A variety of *C. acutatum*, described on *Fiorinia externa* (a scale insect), *C. acutatum* var. *fioriniae* (Marcelino *et al.* 2008), was recognised as the separate species *C. fioriniae* by Shivas & Tan (2009) and is included below in this study.

A *sexual morph* was described for *C. acutatum* (Guerber & Correll 1997, 2001), based on mating compatible strains in the laboratory. The cross designated as type of *Glomerella acutata* was based on two cultures, ATCC 56816 and ATCC MYA-662. The first of these is derived from one of Simmonds' original Queensland collections from papaya, IMI 117620 (here designated as epitype of *C. acutatum*). There is ongoing confusion regarding the provenance of this strain, however; Guerber & Correll (2001) and Than *et al.* (2008b) wrongly equated ATCC 56816 with IMI 117617, the holotype, and that congruence is recorded as such in the ATCC catalogue. The second strain ATCC MYA-662 was isolated from apple in Louisiana, USA (Guerber & Correll 2001), and is here assigned to *C. fioriniae* in clade 3. Fertile sexual morphs were also produced by Guerber & Correll (2001) and Guerber *et al.* (2003) by mating a series of different strains, including crosses between parents that are both assigned to *C. fioriniae*. None of the strains tested was self-fertile.

The holotype of *Glomerella acutata* is therefore an interspecific hybrid between *C. acutatum* and *C. fioriniae*. This might be construed as strong evidence that these two taxa constitute a single biological species, and therefore that the species concepts used in this paper are much too narrow. However, the parent strains of the holotype

originate from highly distant populations in geographical terms, and there are instances in other fungal groups (*e.g. Neurospora*) where non-sympatric populations lose post-mating reproductive isolation barriers (Turner *et al.* 2010, 2011). Further research on population structures and mating-type barriers would be instructive.

Colletotrichum acutatum has subsequently been reported to produce a sexual morph in nature, on *Vaccinium corymbosum* (highbush blueberry) in Norway (Talgø *et al.* 2007). Sequence-based identification was apparently not carried out and so the identity of this population remains uncertain, however the blueberry pathogen is usually *C. fioriniae*, which has a known sexual morph (Marcelino *et al.* 2008). Its origin is also unknown; the crop is not native to Norway and the fungus may have been introduced from the USA along with planting material. The *Glomerella* sexual morph described from *Acer platanoides* in Massachusetts, USA is homothallic (LoBuglio & Pfister 2008), and belongs to *C. salicis*, not *C. acutatum s. str*. Two strains from this research are included in our study. Further discussion may be found in Cannon *et al.* (2012, this issue).

A further twist in the story may be provided by CBS 797.72; this is one of the strains on which *C. acutatum f. sp. pinea* was based (Dingley & Gilmour 1972). Sequences of three of the six genes sampled (ACT, HIS3 and CHS-1) indicate affinities with *C. acutatum* (clade 4) but the other three (ITS, GAPDH and TUB2) suggest that the strain belongs to *C. fioriniae* (clade 3). This was confirmed by repeating sequencing from a new subculture from the CBS collection and after re-singlesporing of one of the single spore isolates. This too may be of hybrid origin. The phylogeny by Guerber *et al.* (2003) includes strains from *Pinus* in New Zealand in both species (as groups J4 and C1). We do not know if they should be assigned to *C. fioriniae*, or are hybrids as well.

The widespread geographical range and economic importance of *C. acutatum* makes it likely that an earlier name exists for the species, probably listed as a synonym of *C. gloeosporioides* by von Arx (1957). Walker *et al.* (1991) noted that *C. xanthii* (Halsted 1893) is such a candidate based on the fusiform shape of conidia found on the type material, but no authentic cultures exist and no other strain from *Xanthium* with fusiform conidia was available to us. It is therefore impossible to determine whether this species provides an earlier name for *C. acutatum s. str.*, for another species within the *C. acutatum* complex or belongs to the *C. acutatum* species complex at all (see *C. pseudoacutatum*).

Apart from *C. acutatum* and *C. simmondsii*, there have been other *Colletotrichum* and *Gloeosporium* species described on *Carica papaya*, all from Brazil. Conidia of *C. papayae* Henn. described from branches and petioles of papaya in Sao Paulo, are larger and differ in shape from *C. acutatum s. str.*; they are cylindrical, straight to curved, hyaline, and measure 12–20 × 5–7 µm (Saccardo *et al.* 1931), while those of *C. acutatum* measure on average 8.8–15.5 × 3.2–4.5 µm, depending on strain and medium. *Gloeosporium papayae* Henn., described from stems of papaya in Uberaba, Minas Gerais, forms cylindrical-oblong to subclavate, obtuse, straight, hyaline to pale yellowish conidia that measure 11–14 × 5–6 µm (Hennings 1895); conidia of *C. acutatum* are hyaline and broader. A presumed isotype in K(M) of *G. papayae*, "E. Ule n. 1947", collected in June 1892, is actually a species of *Phomopsis*. *Gloeosporium fructus-caricae* Henn. forms conidia that overlap in size with those of *C. acutatum*, however their shape is described as oblong-cylindrical with both ends rounded, while conidia of *C. acutatum* usually have both ends acute. Even if the description matches completely with that of *C. acutatum* we could not be sure they are the same species; the morphology of most species in the *C. acutatum* species complex is highly variable and overlapping. There is no strain from papaya in Brazil included in this study, and there is no report of *C. acutatum s. lat.* from Brazil listed in Farr & Rossman (2012). We have tried to draw a reasonable balance between respect for the rules of priority and the need for nomenclatural stability, and in this case we feel that Simmonds' name should be conserved if such a synonymy is established.

Colletotrichum acutatum is separated from other species by all genes. Closest matches in a blastn search with the TUB2 sequence of strain CBS 112996, with 100 % identity, were GU183307–GU183309 and GU183311–GU183314, from *Boronia*, *Anemone*, *Fragaria*, *Pistacia*, *Anemone*, *Olea*, *Ranunculus* and *Mangifera* in Australia (Shivas & Tan 2009), FJ788419 from Simmonds' specimen 16633D from *Carica papaya* in Australia (Weir & Johnston, unpubl. data), AY376546–AY376549 and AY376558–AY376568 from *Pinus*, *Leucadendron* and *Carica* (STE-U 5292 = CBS 112996) and *Hakea* (Lubbe *et al.* 2004), AJ748627 and AJ748630 from *Phlox* and *Statice* (Talhinhas *et al.* 2005), HE573032 from *Arbutus unedo* (strawberry tree) (Polizzi *et al.* 2011) and with 99 % identity (1 or 2 bp difference) AY376550 and AY376545 from *Protea* and *Leucospermum* (Lubbe *et al.* 2004) and AJ748618 from *Olea* (Talhinhas *et al.* 2005). *Colletotrichum acutatum s. str.* can therefore be assumed to be a widespread species that causes disease symptoms on a wide range of plants.

Colletotrichum australe Damm, P.F. Cannon & Crous, **sp. nov.** MycoBank MB800495. Fig. 4.

Etymology: derived from the localities of collection in the Southern Hemisphere.

Sexual morph not observed. *Asexual morph on SNA. Vegetative hyphae* 1–5 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* absent, conidiophores and setae formed directly on hyphae. *Setae* rarely observed, pale to medium brown, smooth-walled to finely verruculose, 1–3-septate, 30–90 µm long, base cylindrical to conical, 3.5–5.5 µm diam, tip ± roundish and bent and function as a conidiogenous locus. *Conidiophores* hyaline to pale brown, smooth-walled, simple or septate and branched, to 30 µm long. *Conidiogenous cells* hyaline to pale brown, smooth-walled, conical to ampulliform, 4.5–15 × 2.5–5.5 µm, opening 0.5–1 µm diam, collarette 0.5–1.5 µm long, periclinal thickening visible. *Conidia* hyaline, smooth-walled, aseptate, become septate with age, straight, cylindrical, with one end round and one end slightly acute to truncate, (10–)14.5–19.5(–25) × (3.5–)4–5(–6) µm, mean ± SD = 17.0 ± 2.4 × 4.4 ± 0.5 µm, L/W ratio = 3.9. *Appressoria* single or in small groups, medium brown, smooth-walled, outline mostly subglobose to elliptical, sometimes clavate, the edge entire or undulate, sometimes slightly lobate, (5–)6–11(–14) × (4–)4.5–7(–8.5) µm, mean ± SD = 8.5 ± 2.6 × 5.8 ± 1.1 µm, L/W ratio = 1.5.

Asexual morph on Anthriscus stem. Conidiomata acervular where present, conidiophores and setae formed directly on hyphae or on a cushion of pale brown angular cells. *Setae* pale to medium brown, smooth-walled to finely verruculose, 2–7-septate, 40–130 µm long, base cylindrical to conical, 3–5 µm diam, tip broadly rounded to somewhat acute, and may function as a conidiogenous locus. *Conidiophores* hyaline to pale brown, smooth-walled, septate, little branched, to 50 µm long. *Conidiogenous cells* hyaline to pale brown, smooth-walled, cylindrical to ampulliform, 8–19 × 3–5 µm, opening 1–2.5 µm diam, collarette 0.5–1 µm

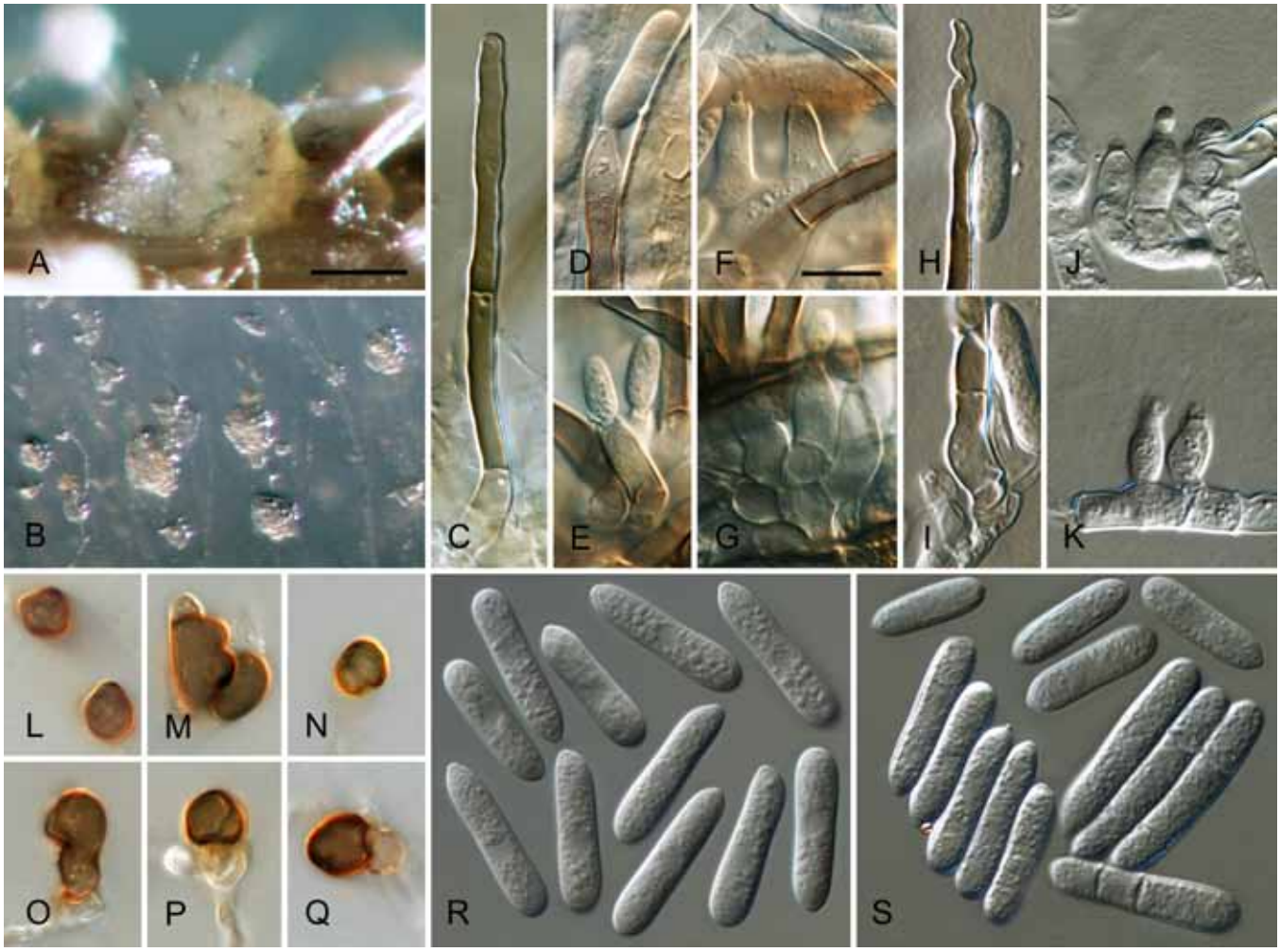

Fig. 4. *Colletotrichum australe* (from ex-holotype strain CBS 116478). A–B. Conidiomata. C. Seta. D–G. Conidiophores. H. Tip of seta. I. Basis of seta. J–K. Conidiophores. L–Q. Appressoria. R–S. Conidia. A, C–G, R. from *Anthriscus* stem. B, H–Q, S. from SNA. A–B. DM, C–S. DIC, Scale bars: A = 100 µm, F = 10 µm. Scale bar of A applies to A–B. Scale bar of F applies to C–S.

long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical, sometimes slightly constricted in the middle, with one end round and one end slightly acute to truncate, (16–)17–20(–22) × (4–)4.5–5(–5.5) µm, mean ± SD = 18.6 ± 1.6 × 4.7 ± 0.4 µm, L/W ratio = 4.0, conidia of strain CBS 131325 smaller, measuring (13.5–)15–17.5(–18) × (3.5–)4–5(–5.5) µm, mean ± SD = 16.3 ± 1.1 × 4.4 ± 0.4 µm, L/W ratio = 3.7.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline to honey, filter paper straw to pale olivaceous grey, aerial mycelium lacking, reverse same colours, growth rate 16–18 mm in 7 d (28.5–30 mm in 10 d). Colonies on OA flat with entire margin; surface pale luteous to amber, in the centre covered with floccose white aerial mycelium, reverse pale luteous to salmon, growth rate 16–20 mm in 7 d (25–29.5 mm in 10 d). *Conidia in mass* salmon.

Material examined: **South Africa**, Stellenbosch, university campus, from *Trachycarpus fortunei*, 2 Jan. 1998, J.E. Taylor, (CBS-H 20721 **holotype**, culture ex-type CBS 116478 = HKUCC2616). **Australia**, Western Australia, Alcoa, from *Hakea* sp., 12 Jul. 2011, W. Gams, culture CBS 131325.

Notes: *Colletotrichum australe* belongs to the clade that includes *C. phormii, C. kinghornii, C. rhombiforme* and *C. acerbum*. Setae are better developed (in cultures on *Anthriscus* stem) and conidia are larger than in most other species in the *C. acutatum* species complex. Only *C. phormii* forms larger conidia, which are fusiform, while those of *C. australe* are cylindrical. Additionally, appressoria of *C. australe* are shorter than those of *C. phormii*. Conidia of *C. rhombiforme* are shorter, while those of *C. kinghornii* are narrower.

It is possible that *Fusarium hakeae* (Hennings 1898), described from leaves of *Hakea saligna* from the Botanic Garden in Berlin, Germany, is the same species as *C. australe*. The description is short but largely corresponds with our species, but bearing in mind that most *Colletotrichum* species show a lack of host specificity, there is no strong reason to equate the two taxa in the absence of sequenceable material of *F. hakeae*. Wollenweber (1916) transferred *F. hakeae* to *Gloeosporium*, and von Arx (1957, 1970) included the name as a synonym of *C. gloeosporioides*. Bondarzeva-Monteverde *et al.* (1936) described a separate fungus as *Gloeosporium hakeae* from greenhouses in St Petersburg; this was reported to have straight to curved conidia and is unlikely to be a synonym of Hennings' fungus. Lubbe *et al.* (2004) published *C.acutatum f. sp. hakeae* for isolates that caused a distinctive disease of *Hakea* in South Africa; these have shorter conidia than those of *C. australe* and group in *C. acutatum s. str. Colletotrichum acutatum* has been reported from *Trachycarpus fortunei* in Australia and Switzerland by Taylor & Hyde (2003); we do not know whether these collections represent further records of *C. australe*.

Colletotrichum australe is separated from other species by all gene sequences surveyed except for CHS-1, which is the same as that of *C. phormii*, and most effectively separated by HIS3. The closest match in a blastn search with the TUB2 sequence of strain

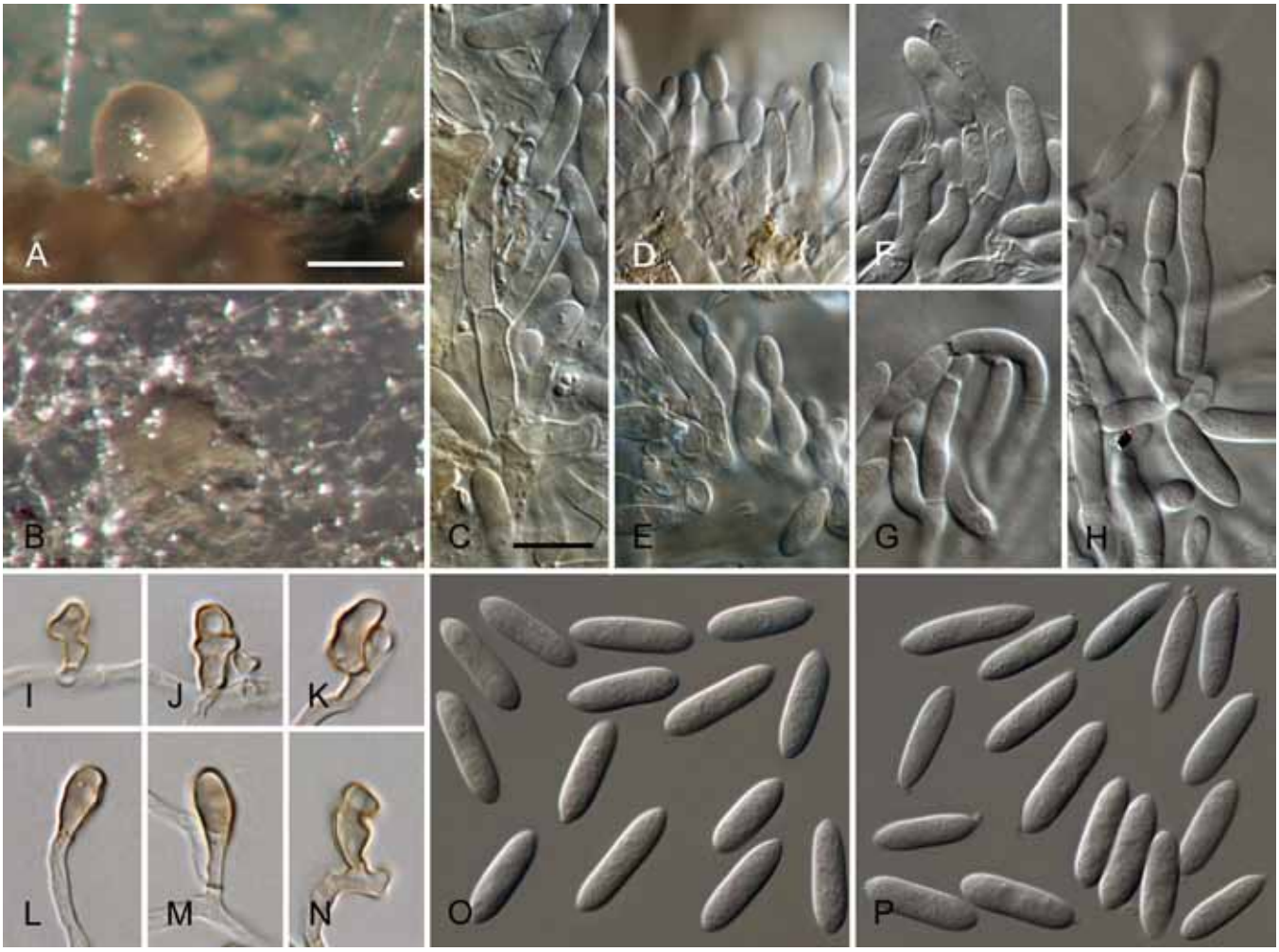

Fig. 5. *Colletotrichum brisbanense* (from ex-holotype strain CBS 292.67). A–B. Conidiomata. C–H. Conidiophores. I–N. Appressoria. O–P. Conidia. A, C–E, O. from *Anthriscus* stem. B, F–N, P. from SNA. A–B. DM, C–P. DIC, Scale bars: A = 100 µm, C = 10 µm. Scale bar of A applies to A–B. Scale bar of C applies to C–P.

CBS 116478 (with 98 % identity, 8 and 9 bp differences) were isolates PCF 459 (EU635504) from strawberry in Belgium (Debode *et al.* 2009) and PT250 (= CBS 129953, see *C. rhombiforme*), and AJ748624 from olive, Portugal (Talhinhas *et al.* 2005). We do not think that any of these sequences are derived from strains that are conspecific with *C. australe*. With the GAPDH sequence there was no closer match than 87 % identity. The closest matches with ITS sequence, with 99 % sequence identity, include *Glomerella cingulata* BBA 70991 from *Salix* (AJ301952, Nirenberg *et al.* 2002) and *Glomerella* sp. strain MP3 from *Acer platanoides* (EU622052, LoBuglio & Pfister 2008), which are both likely to be *C. salicis*. Other strains with 99 % ITS sequence homology include that deposited as *Fusarium phormii* strain CBS 198.35 (DQ286144, Farr *et al.* 2006) which we assign to *C. kinghornii*, and *Ga. acutata* PT715 from *Olea europaea* in Portugal (AM991135, Talhinhas *et al.* 2009).

Colletotrichum brisbanense Damm, P.F. Cannon & Crous, **sp. nov.** MycoBank MB800497. Fig. 5.

Etymology: Named after Brisbane, the city in Queensland, Australia where the species was collected.

Sexual morph not observed. *Asexual morph on SNA. Vegetative hyphae* 1–8 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* not developed, 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 slightly inflated, sometimes lacking a basal septum and continuous with the conidiophore, sometimes proliferating and extending to form a new conidiogenous locus, discrete phialides measure 8.5–21 × 2.5–4 µm, opening 1–1.5 µm diam, collarette 1–1.5 µm long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical with both ends slightly acute or one end round and one end slightly acute, (12–)12–17.5(–25) × (3–) 3.5–4(–5) µm, mean ± SD = 14.8 ± 2.8 × 3.8 ± 0.5 µm, L/W ratio = 3.9. *Appressoria* single or in loose groups, pale brown, smooth-walled, mostly clavate, the edge entire to undulate, (5–)7.5–14.5(–18) × (2.5–)3.5–5(–6) µm, mean ± SD = 11.1 ± 3.4 × 4.3 ± 0.9 µm, L/W ratio = 2.6.

Asexual morph on Anthriscus stem. Conidiomata possibly acervular, but no basal cells observed. *Setae* not observed. *Conidiophores* hyaline to pale brown, smooth-walled, septate, branched, to 30 µm long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical to ampulliform, sometimes proliferating and extending to form a new conidiogenous locus, sometimes polyphialidic, 8.5–23 × 2.5–4.5 µm, opening 1–2 µm diam, collarette 0.5–1 µm long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical with both ends slightly acute, (9.5–)12–15(–17) × (3–)3.5–4 µm, mean ± SD = 13.5 ± 1.4 × 3.9 ± 0.3 µm, L/W ratio = 3.5.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline to pale cinnamon, on filter paper partly pale saffron, agar medium partly covered with very short white aerial mycelium,

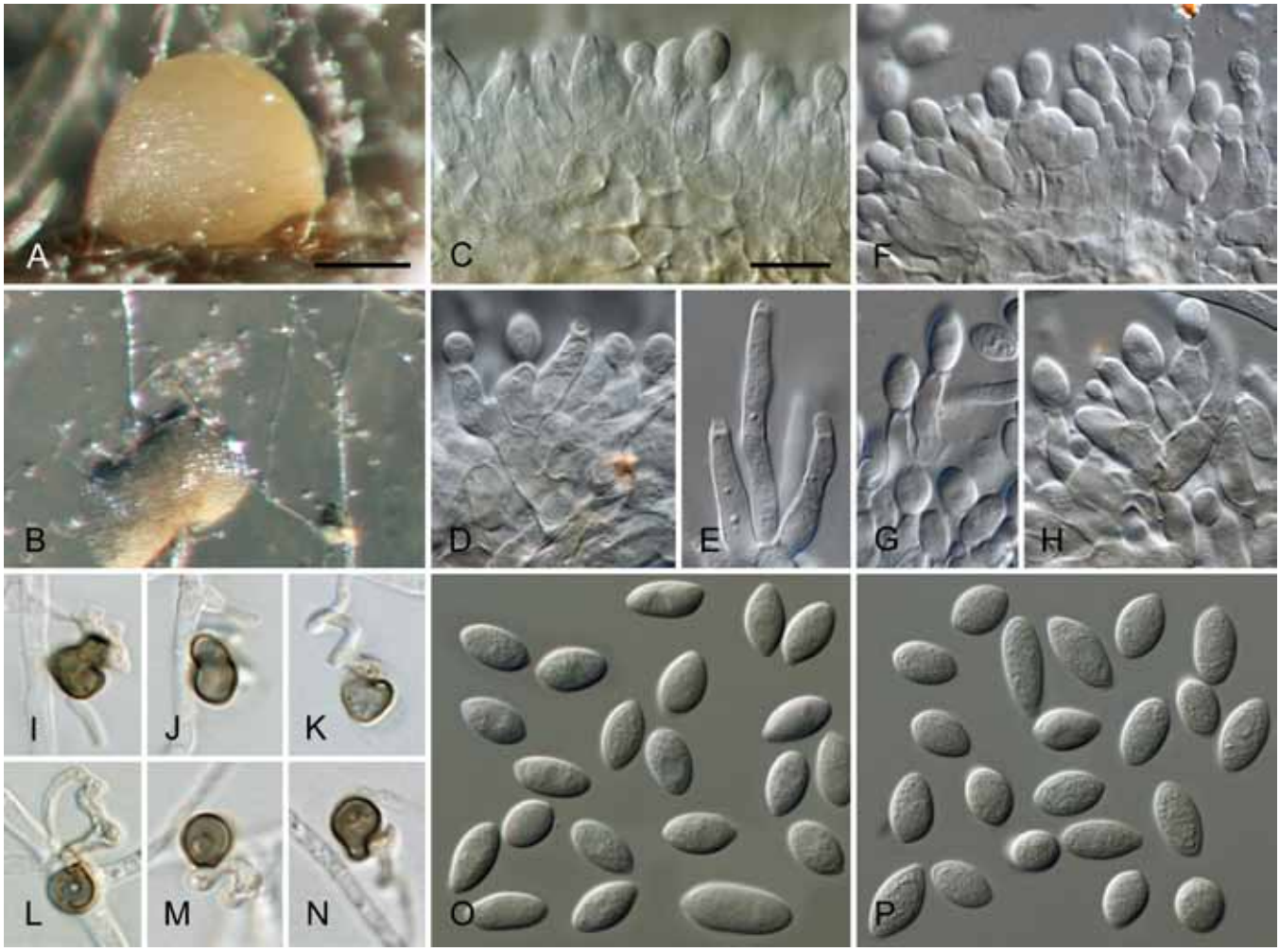

Fig. 6. *Colletotrichum chrysanthemi* (from strain CBS 126518). A–B. Conidiomata. C–H. Conidiophores. I–N. Appressoria. O–P. Conidia. A, C–E, O. from *Anthriscus* stem. B, F–N, P. from SNA. A–B. DM, C–P. DIC, Scale bars: A = 100 µm, C = 10 µm. Scale bar of A applies to A–B. Scale bar of C applies to C–P.

reverse same colours; growth rate 18–20 mm in 7 d (26–29 mm in 10 d). Colonies on OA flat with entire margin; surface buff, rosy buff to pale saffron, covered with short white aerial mycelium, reverse same colours; growth rate 17.5–18.5 mm in 7 d (27.5–28.5 mm in 10 d). *Conidia in mass* salmon.

Material examined: **Australia**, Queensland, Brisbane, Eight Mile Plains, from fruit rot of *Capsicum annuum*, 14 Jul. 1955, J.H. Simmonds, (IMI 117622 **holotype** of *C. brisbanense* (also paratype of *C. acutatum*), CBS H-20801 isotype, culture ex-type CBS 292.67 = BRIP 4684).

Notes: The type and only confirmed strain of *C. brisbanense* was cited as one of the paratype strains of *C. acutatum* by Simmonds (1968), and assigned to *C. simmondsii* by Shivas & Tan (2009). Conidia and appressoria of *C. brisbanense* are larger overall than those of *C. simmondsii* as accepted in this treatment. The two species are easily separable using all sequence data except for ITS, and most effectively with TUB2 and GAPDH sequences. There is only one bp difference in CHS-1 sequence between *C. brisbanense* and *C. indonesiense.* There is a further species in clade 2 associated with *Capsicum annuum*, *C. scovillei*, possibly a species endemic to Southeast Asia. *Colletotrichum brisbanense* can be separated easily from *C. scovillei* based on appressorium measurements, as well as by most DNA data. See *C. scovillei* for further information.

A blastn search with the TUB2 sequence of strain CBS 292.67 resulted in a 100 % match with GU183275, the sequence of the same strain generated by Shivas & Tan (2009); next closest was DQ454064 from isolate S6 from *Fragaria* in Thailand with 99 % identity (four differences; Sang *et al.* 2011). With the GAPDH sequence there was no match with more than 95 % identity. The ITS sequence of strain CBS 292.67 matched 100 % with GU183315, a sequence of the same isolate generated by Shivas & Tan (2009).

Colletotrichum chrysanthemi (Hori) Sawada, Rep. Govt Res. Inst. Dep. Agric., Formosa 85: 81. 1943. Fig. 6.

≡ *Gloeosporium chrysanthemi* Hori, in Takimoto, Jour. Hort. Japan 36(9): 27. 1924.

Sexual morph not observed. *Asexual morph on SNA* (CBS 126518). *Vegetative hyphae* 1.5–9 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* absent, conidiophores formed directly on hyphae. *Setae* not observed. *Conidiophores* hyaline to pale brown, smooth-walled, septate and branched, to 55 µm long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical to ampulliform, 7–15 × 3–4.5 µm, opening 1.5–2 µm diam, collarette distinct, 0.5–1 µm long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, broadly ellipsoidal to ovoid, with both ends acute, rarely clavate to cylindrical with one round end one acute end, (6–)7–9.5(–12) × (3–)4–5.5(–6) µm, mean ± SD = 8.3 ± 1.3 × 4.8 ± 0.6 µm, L/W ratio = 1.7, conidia from aerial mycelium shorter, measuring (3.5–)4.5–9(–15) × 3–5(–6.5) µm, mean ± SD = 6.7 ± 2.3 × 4.1 ± 0.8 µm, L/W ratio = 1.6. *Appressoria* single, medium brown, smooth-walled,

subglobose, elliptical or irregular in outline, with entire, undulate or lobate margin, (5–)5.5–9.5(–11.3) × (3–)4.5–6.5(–7.5) µm, mean ± SD = 7.5 ± 1.8 × 5.4 ± 1.1 µm, L/W ratio = 1.4.

Asexual morph on Anthriscus stem (CBS 126518). *Conidiomata* acervular, conidiophores formed on a cushion of angular cells 3–8.5 µm diam. *Setae* not observed. *Conidiophores* hyaline to pale brown, smooth-walled, septate, branched, to 40 µm long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical, 7–16.5 × 3.5–4.5 µm, opening 1–2 µm diam, collarette distinct, 0.5–1 µm long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, subglobose, broadly ellipsoidal to oval, with both ends ± acute, (3.5–)6.5–10.5(–13.5) × (3.5–)4–5(–5.5) µm, mean ± SD = 8.5 ± 1.8 × 4.5 ± 0.5 µm, L/W ratio = 1.9.

Culture characteristics (CBS 126518): Colonies on SNA flat with entire margin, hyaline to pale honey, on filter paper, *Anthriscus* stem and medium partly covered with floccose white aerial mycelium, reverse hyaline to pale honey; growth rate 14–17.5 mm in 7 d (23.5–27.5 mm in 10 d). Colonies on OA umbonate with entire margin; surface rosy buff to pale purplish grey, covered with woolly to floccose-felty white to pale grey aerial mycelium, reverse rosy buff, olivaceous grey to iron grey; growth rate 16–17.5 mm in 7 d (27.5–28 mm in 10 d). *Conidia in mass* pale salmon.

Material examined: **Netherlands**, Emmeloord, from twisted stem of *Carthamus* sp., unknown collection date and collector, culture CBS 126518 = PD 84/520; from vascular discoloration of *Glebionis carinata*, collection date and collector unknown, culture CBS 126519 = PD 85/694. **China**, Hong Kong, from leaf spot of *Glebionis coronaria*, (deposited in IMI 1994 by Wan-chi Ko as culture no. 1964), culture IMI 365540.

Notes: *Gloeosporium chrysanthemi* was described by Hori as causing severe anthracnose disease in *Chrysanthemum coronarium* (= *Glebionis coronaria*) in the Fukuoka prefecture in Japan (Takimoto 1924) and transferred to *Colletotrichum* by Sawada (1943). A pathogen of another *Asteraceae* plant, *Carthamus tinctorius*, was described in Japan by Fukui as *Marssonia carthami* (Fukui 1916, see also Tanaka 1917). The fungus was transferred to *Gloeosporium* by Hori & Hemmi.

Uematsu *et al.* (2012) re-examined authentic specimens of *C. chrysanthemi* collected by Takimoto in 1919 and of *G. carthami* collected by Hemmi in 1915 and sequenced the ITS1 and TUB2 regions of these specimens as well as of isolates from *Carthamus*, *Chrysanthemum* and *Calendula* species from Japan. The resulting sequences place the two species in the *C. acutatum* species complex. While all specimens and strains had almost identical ITS sequences, there were two groups in the TUB2 phylogeny, placing most of the *Calendula* isolates with the authentic specimen of *Gm. carthami* and the *Chrysanthemum* and *Carthamus* isolates as well as two *Calendula* isolates with the authentic specimen of *Gm. chrysanthemi*, suggesting the two species to be separate. In spite of this, the authors regard *C. chrysanthemi* as synonym of the older species *G. carthami*. Based on TUB2 sequences of the authentic specimens (AB696992, AB696993) and some of the strains from *Calendula* (AB688785, AB688787), *Carthamus* (AB688807, AB688811) and *Chrysanthemum* (AB688791) included in our alignment (not shown), isolates studied here group with the Japanese isolates from *Carthamus* and *Chrysanthemum* and the authentic specimen of *Gm. chrysanthemi*, and we therefore treat them here as *C. chrysanthemi* . The TUB2 sequences of the *Calendula* isolates and the authentic material of *Gm. carthami* appear to belong to a different clade that is not included in our study.

There are few additional reports of *Colletotrichum* on *Carthamus*, *Chrysanthemum* and *Calendula*. Sette *et al.* (1999) report *C. acutatum* on *Carthamus tinctorius* in Korea; the fungus formed strongly fusiform conidia (see fig. 2 in Sette *et al.* 1999), and formed setae at least occasionally on host plant and PDA medium. Vichova *et al.* (2011) found *C. simmondsii* on *Carthamus tinctorius* in the Czech Republic. There is another species that was also described on *Chrysanthemum* and *Dahlia* in Portugal, *C. dahliae*; this species however forms larger conidia with round ends, measuring 16–19 × 5.3–7 µm (Costa & Sousa da Câmara 1953).

Colletotrichum chrysanthemi is separated from other species by all diagnostic genes applied in this study except for ITS, best with TUB2, GAPDH and HIS3, and its very short acute-ended conidia differ from those of other species of the *C. acutatum* species complex. The ITS sequence of strain CBS 126518 matches with 100 % identity with AB042306 and AB042307 from isolates from *Carthamus* and *Chrysanthemum* in Japan (Moriwaki J, Tsukiboshi T, Sato T, Uematsu S, unpubl. data), and also with AJ749675 from isolates PD85/694 (= CBS 126519), sequenced by Talhinhas *et al.* (2005) and AY376508 *Ga. acutata* strain STE-U 5303 (= CBS 112989, *C. laticiphilum*) from *Hevea* (Lubbe *et al.* 2004). Closest match in a blastn search with the TUB2 sequence of strain CBS 126518 with 100 % identity was AJ748632 from isolate PD85/694 (= CBS 126519, included in this study), sequenced by Talhinhas *et al.* (2005). Closest matches with the GAPDH sequence with 95 % identity (12 and 13 differences) were HM038336 from isolate MFU09 0628 from *Mangifera indica* and HM038337 from isolate MFU09 0624 from *Ziziphus mauritiana*, both from Laos (Phoulivong *et al.* 2010).

Colletotrichum cosmi Damm, P.F. Cannon & Crous, **sp. nov.** MycoBank MB800498. Fig. 7.

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

Sexual morph not observed. *Asexual morph on SNA. Vegetative hyphae* 1–7.5 µm diam, hyaline, sometimes pale brown, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* not developed, conidiophores formed directly on hyphae. *Setae* not observed. *Conidiophores* hyaline to pale brown, smooth-walled, septate, branched, to 40 µm long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical, sometimes slightly inflated, 9–17 × 2.5–3.5 µm, opening 1–1.5 µm diam, collarette 1 µm long, periclinal thickening visible. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical to clavate with both ends slightly acute or one end round, (7–)13–18.5(–19.5) × (3–)3.5–4.5 µm, mean ± SD = 15.8 ± 2.5 × 4.0 ± 0.4 µm, L/W ratio = 4.0. *Appressoria* very few, mostly single, pale to medium brown, smooth-walled, subglobose, elliptical or clavate, the edge entire, (5–)5.5–8(–11.5) × (4–)4.5–5.5 µm, mean ± SD = 6.8 ± 1.2 × 4.9 ± 0.4 µm, L/W ratio = 1.4.

Asexual morph on Anthriscus stem. Conidiomata either not developed, conidiophores formed directly on hyphae, or acervular, conidiophores formed on pale brown, angular, basal cells, 3–9 µm diam. *Setae* not observed. *Conidiophores* hyaline to pale brown, smooth-walled, septate, branched, to 40 µm long. *Conidiogenous cells* hyaline to pale brown, smooth-walled, cylindrical, 9–24 × 3–3.5 µm, opening 1–1.5 µm diam, collarette 1–1.5 µm long, periclinal thickening conspicuous. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical to fusiform with both ends ± acute, (12–)14–16.5(–18) × (3.5–)4–4.5 µm, mean ± SD = 15.3 ± 1.4 ×

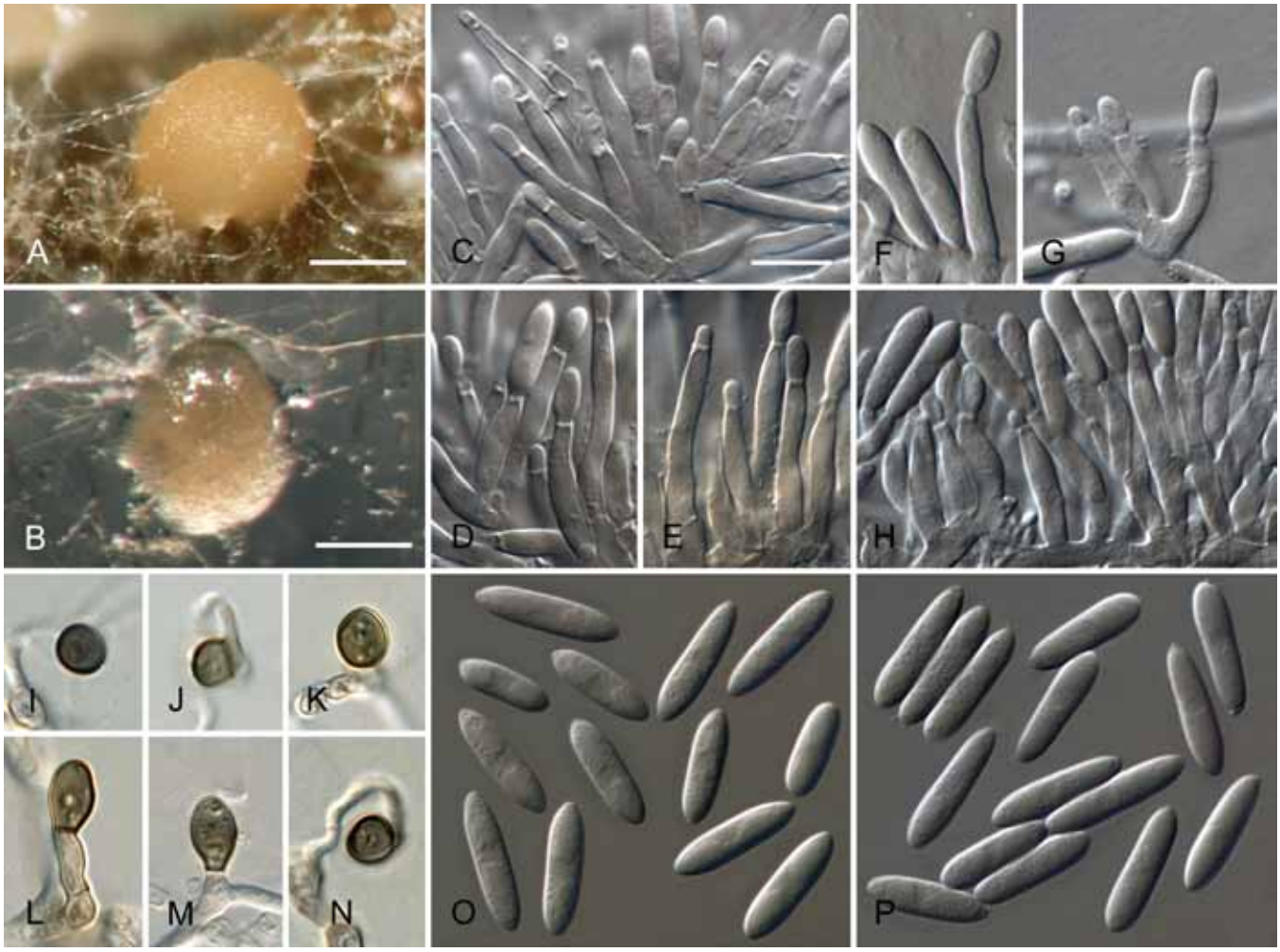

Fig. 7. *Colletotrichum cosmi* (from ex-holotype strain CBS 853.73). A–B. Conidiomata. C–H. Conidiophores. I–N. Appressoria. O–P. Conidia. A, C–E, O. from *Anthriscus* stem. B, F–N, P. from SNA. A–B. DM, C–P. DIC, Scale bars: A = 200 µm, B = 100 µm, C = 10 µm. Scale bar of C applies to C–P.

4.0 ± 0.3 µm, L/W ratio = 3.8.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline, buff to pale honey, on filter paper partly pale olivaceous grey, the medium, filter paper and *Anthriscus* stem partly covered with floccose-felty whitish to pale olivaceous grey aerial mycelium and orange acervuli, reverse of filter paper partly pale cinnamon, pale olivaceous grey to olivaceous grey; growth rate 23–24 mm in 7 d (33.5–34 mm in 10 d). Colonies on OA flat with entire margin; surface entirely covered with thin floccose-felty white to pale olivaceous grey aerial mycelium and orange acervuli, reverse vinaceous buff, purplish grey to fuscous black; growth rate 23–25 mm in 7 d (33.5–37.5 mm in 10 d). *Conidia in mass* orange.

Material examined: **Netherlands**, Wageningen, from seed of *Cosmos* sp., collection date and collector unknown (deposited in CBS collection in Nov. 1973 by G.H. Boerema), (CBS H-20794 **holotype**, culture ex-type CBS 853.73 = PD 73/856).

Notes: Kwon *et al.* (1999) report *C. acutatum* (*s. lat.*) to cause sunken brownish spots on stems, as well as symptoms on leaves, flowers and floral axes of *Cosmos bipinnatus* in Korea. Morphological characters (conidia, appressoria) are similar to those of strain CBS 853.73, except for setae, which our strain did not develop in our standard culture conditions. It is therefore possible that the collection from Korea represents *C. cosmi*. *Colletotrichum acutatum* (*s. lat.*) is also known as an anthracnose pathogen of flowers and flower buds of *Cosmos bipinnatus* in Japan (Yaguchi *et al.* 1996). The shape of conidia and appressoria of the Japanese fungus are similar to our strain, but the conidia are smaller, measuring 11–14 × 2.8–3.5 µm. Two other species are reported from *Cosmos bipinnatus* in India, *C. truncatum* (as *C. capsici*) associated with seeds and causing seed and seedling rot (Srivastava *et al.* 1981) and *C. gloeosporioides* associated with leaves (Kumari *et al.* 1981). When strain CBS 853.73 was first accessed into CBS, von Arx identified it as *C. gloeosporioides*, but with the remark "deviating by longer, slender conidia". Molecular data do not support this identification; the strain belongs to the *C. acutatum* complex, but it is possible that reports of *C. gloeosporioides* refer to this species.

Colletotrichum cosmi is part of clade 2. It can be separated from other species by all gene sequences, but mostly with only 1 bp divergence. There are more sequence divergences in GAPDH and HIS3; however, with these genes individually, the species sits within the very variable *C. nymphaeae* clade. The closest match in a blastn search with the TUB2 sequence of strain CBS 853.73 (with 99 % identity, 4 bp differences) was GU246633 from isolate R14 from *Capsicum annuum* from South Korea (Sang *et al.* 2011), while the closest match with the GAPDH sequence covering ± the full length sequence (with 98 % identity, 4 bp differences) was HQ846724 from isolate OBP6 from an unknown plant, probably from India (P. Chowdappa, C.S. Chethana, S. Madhura, unpubl. data). We do not consider that these data in isolation are sufficient evidence to identify these sequences as originating from *C. cosmi*. There are 22 sequences in GenBank that match the ITS sequence of strain CBS 853.73 with 99 % identity, all with 2 bp differences.

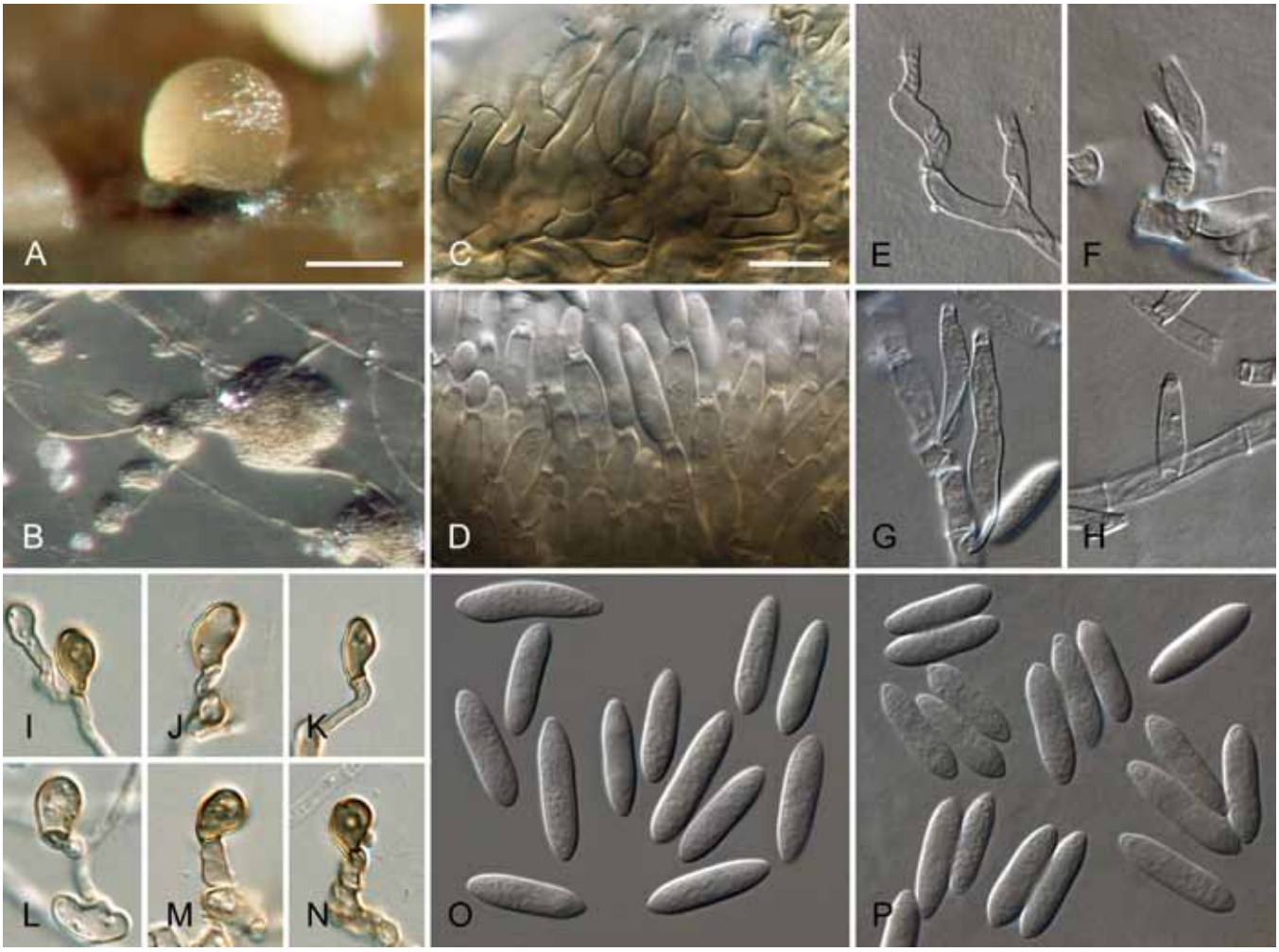

Fig. 8. *Colletotrichum costaricense* (from ex-holotype strain CBS 330.75). A–B. Conidiomata. C–H. Conidiophores. I–N. Appressoria. O–P. Conidia. A, C–D, O. from *Anthriscus* stem. B, E–N, P. from SNA. A–B. DM, C–P. DIC, Scale bars: A = 100 µm, C = 10 µm. Scale bar of A applies to A–B. Scale bar of C applies to C–P.

Colletotrichum costaricense Damm, P.F. Cannon & Crous, **sp. nov.** MycoBank MB800499. Fig. 8.

Etymology: Named after the country where it was collected, Costa Rica.

Sexual morph not observed. *Asexual morph on SNA. Vegetative hyphae* 1–9.5 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* not developed, conidiophores formed directly on hyphae. *Setae* not observed. *Conidiophores* hyaline, smooth-walled, simple or septate and branched. *Conidiogenous cells* hyaline, smooth-walled, cylindrical to ampulliform, polyphialides observed, 4.5–24 × 2–3.5 µm, opening 0.5–1.5 µm diam, collarette 0.5–1.5 µm long, periclinal thickening visible. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical with both ends acute, (9–)11.5–18(–28) × (3–)3.5–4(–4.5) µm, mean ± SD = 14.6 ± 3.1 × 3.7 ± 0.3 µm, L/W ratio = 4.0. *Appressoria* sparse, single or in small groups, pale brown, smooth-walled, subglobose to elliptical, the edge entire to undulate, (4.5–)6–8.5(–10) × (3–)4–6(–6.5) µm, mean ± SD = 7.1 ± 1.2 × 4.9 ± 0.9 µm, L/W ratio = 1.4, appressoria of strain CBS 211.78 are medium brown.

Asexual morph on Anthriscus stem. Conidiomata not developed, conidiophores and setae formed directly on hyphae. *Setae* medium to dark brown, smooth-walled to finely verruculose, 0–2-septate, 50–60 µm long, base cylindrical, 3.5–4.5 µm diam, the tip ± acute. *Conidiophores* hyaline to pale brown, smooth-walled, septate, branched, to 40 µm long. *Conidiogenous cells* hyaline to pale brown, smooth-walled, cylindrical to ampulliform, 8–22 × 3–5 µm, opening 1–1.5 µm diam, collarette 1–1.5 µm long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical with both ends acute, (12.5–)13.5–16(–18) × 3.5–4 µm, mean ± SD = 14.8 ± 1.4 × 3.8 ± 0.3 µm, L/W ratio = 3.9.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline to pale cinnamon, on *Anthriscus* stem partly olivaceous grey to iron-grey, on filter paper pale olivaceous grey to olivaceous grey, with short or woolly white aerial mycelium and few salmon acervuli on filter paper and on *Anthriscus* stem, reverse of filter paper same colours; growth rate 19–22.5 mm in 7 d (31–34 mm in 10 d). Colonies on OA flat with entire margin; surface olivaceous with pale olivaceous grey to olivaceous grey sectors, the sectors covered with short white aerial mycelium and salmon acervuli or culture completely covered with short felty whitish aerial mycelium, reverse honey, olivaceous grey to iron-grey, growth rate 22–23 mm in 7 d (28.5–34.5 mm in 10 d). *Conidia in mass* salmon to saffron.

Material examined: **Costa Rica**, Meseta Central, from berry of *Coffea arabica* cv. Typica, collection date and collector unknown (deposited in CBS collection Jun. 1975 by D. Mulder, Wageningen), (CBS H-20811 **holotype**, culture ex-type CBS 330.75); Turrialba, from twig of *Coffea* sp., collection date and collector unknown (deposited in CBS collection Apr. 1978 by C. Bianchini), culture CBS 211.78 = IMI 309622.

Notes: Von Arx (in litt.) identified the strain CBS 330.75 as *C. acutatum* but with the remark "deviating by lack of pigment and less fusiform conidia". While the main causal agent of coffee berry disease (CBD) is *C. kahawae* (Waller *et al.* 1993) that belongs to the *C. gloeosporioides* species complex (Weir *et al.* 2012, this issue), strains from the *C. acutatum* aggregate are not frequently encountered associated with coffee. Hindorf (1973) studied *Colletotrichum* populations from *Coffea arabica* in Kenya and illustrated conidia or ascospores of some strains diverging from each other in morphology and culture appearance, including a strain identified as *C. acutatum* and another as *C. gloeosporioides* with conidia some of which are ellipsoidal and acute-ended. One of the two strains from western Kenya that are assigned to *C. acutatum s. str.* is derived from a suspected disease symptom on a coffee berry from Kenya that did not cause CBD (Gielink & Vermeulen, 1983). One of the endophytic strains from *Coffea robusta* in Brazil studied by Sette *et al.* (2006) showing antimicrobial activity against *Staphylococcus aureus* belongs to the *C. acutatum* species complex; since only a short ITS sequence of this strain was generated (DQ123614), the species cannot be identified. *Colletotrichum walleri* (clade 2) is known from a single strain from coffee, from Vietnam. *Colletotrichum costaricense* is quite distinct from either of these taxa based on molecular sequence data.

Two *Colletotrichum* species have previously been described from leaves of *Coffea* sp. in Costa Rica, *C. brachysporum* and *C. coffeophilum*. Conidia of the first are smaller than those of *C. costaricense* and have a different shape; they are subglobose-ovoid and measure 7–8 × 4–6 µm (Saccardo *et al*. 1931), while those of *C. costaricense* measure on average 14.6 × 3.7 µm or 14.8 × 3.8 µm depending on the medium. Conidia of *C. coffeophilum* are wider than those of *C. costaricense*, being ellipsoidal and straight or slightly curved (navicular), and measuring 13–15 × 6–8 µm (Saccardo *et al*. 1931).

Colletotrichum costaricense may be differentiated from the other species accepted here by TUB2, GAPDH and ACT sequences, and most effectively with TUB2. The ACT sequences of the two strains differ by 2 bp, but have only 1 bp in common to separate them from *C. lupini* and some of the unnamed single strains. The closest match in a blastn search with the TUB2 sequence of strain CBS 330.75 with 99 % identity (3 bp differences) was FN611028 from a *Citrus sinensis* isolate (Ramos *et al.* 2006), while the closest matches with the GAPDH sequence with 99 % identity (2 differences) were EU647322 and EU647324 from leatherleaf fern isolates (MacKenzie *et al.* 2009). All isolates were from Florida, USA. The closest matches with the ITS sequence with 100 % identity were FN566877 from isolate DPI from *Citrus aurantifolia* in Florida, USA (Ramos *et al.* 2006) and isolate c2 from *Citrus* sp. in Brazil (Giaretta *et al.* 2010).

Colletotrichum cuscutae Damm, P.F. Cannon & Crous, **sp. nov.** MycoBank MB800500. Fig. 9.

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

Sexual morph not observed. *Asexual morph on SNA. Vegetative hyphae* 1–5.5 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* not developed, conidiophores formed directly on hyphae. *Setae* not observed. *Conidiophores* hyaline, smooth-walled, simple or septate and branched, to 35 µm long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical to ampulliform, often integrated, polyphialides occationally observed, discrete phialides measuring 4–14.5 × 2.5–4.5 µm, opening 1.5–2 µm diam, collarette 0.5–1.5 µm long, periclinal thickening conspicuous. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical with both ends acute, (15.5–)17.5–21(–27) × (3–)3.5–4.5 µm, mean ± SD = 19.2 ± 1.7 × 4.0 ± 0.3 µm, L/W ratio = 4.8. *Appressoria* single or in loose clusters, pale brown, smooth-walled, elliptical to clavate, entire edge (3.5–)5.5–11.5(–15.5) × (2–)3.5–5.5(–6.5) µm, mean ± SD = 8.5 ± 3.2 × 4.6 ± 0.9 µm, L/W ratio = 1.8.

Asexual morph on Anthriscus stem. Conidiomata acervular, conidiophores formed on pale brown angular basal cells, 3–8 µm diam. *Setae* not observed. *Conidiophores* hyaline to pale brown, smooth-walled, septate, branched, to 40 µm long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical to fusiform with both ends acute, 8–21 × 2–3.5 µm, opening 1–2 µm diam, collarette 0.5–1 µm long, periclinal thickening conspicuous. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical with both ends acute, (15–)17–20(–21) × (3.5–)4–4.5 µm, mean ± SD = 18.6 ± 1.5 × 4.2 ± 0.2 µm, L/W ratio = 4.5.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline to buff, on filter paper and *Anthriscus* stem partly covered with woolly to felty white to pale grey aerial mycelium and orange acervuli, reverse hyaline to buff, under filter paper pale olivaceous grey; growth 20 mm in 7 d (30 mm in 10 d). Colonies on OA flat to raised with entire margin; surface partly covered with woolly white to pale olivaceous grey aerial mycelium and olivaceous grey to orange acervuli appearing in rings, reverse buff, pale olivaceous grey to olivaceous grey with orange sectors; growth 19–21 mm in 7 d (27.5–31 mm in 10 d). *Conidia in mass* orange.

Material examined: **Dominica,** Castle Comfort, from *Cuscuta* sp., 1986, C. Prior (IMI 304802 **holotype**, CBS H-20784 isotype, culture ex-type IMI 304802).

Notes: *Colletotrichum cuscutae* is known from a single strain, reported from Dominica. The multigene analysis indicates that it occupies a single subclade within clade 1, quite distinct from the principal subclade of *C. lupini*. Its conidia are substantially longer than is typical for *C. lupini* (mean length 18.6 µm as opposed to 12 µm for *C. lupini*), though the length range for the latter species is considerable. The appressoria of *C. cuscutae* are narrower than those of *C. lupini* and also greater in length/width ratio.

Colletotrichum species have been reported previously as parasitising *Cuscuta* species, which are themselves non-photosynthetic parasites of other plants. *Colletotrichum destructivum* was found to affect *Cuscuta campestris* parasitising alfalfa crops in NW USA (Leach 1958). A strain identified as *C. gloeosporioides f. sp. cuscutae* was apparently used widely as a biological control agent "Lu Bao no. 1" of *Cuscuta* in China after its adoption in the 1960s (Zhang 1985, Gao & Gan 1992), but its current commercial status is unknown and it may no longer be in production (Watson *et al.* 2000). According to Watson *et al.* (2000) and Dinoor *et al.* (2009) the Lu Bao strain belongs to *C. acutatum* rather than *C. gloeosporioides*. However, no detailed morphological data are available and the identification as *C. acutatum* was made by means of primers that at that time were considered to be species-specific for the two species that are both now recognised as species complexes.

Guerber *et al.* (2003) studied isolates from *Cuscuta* in the USA and China that belong to two different species, neither of which

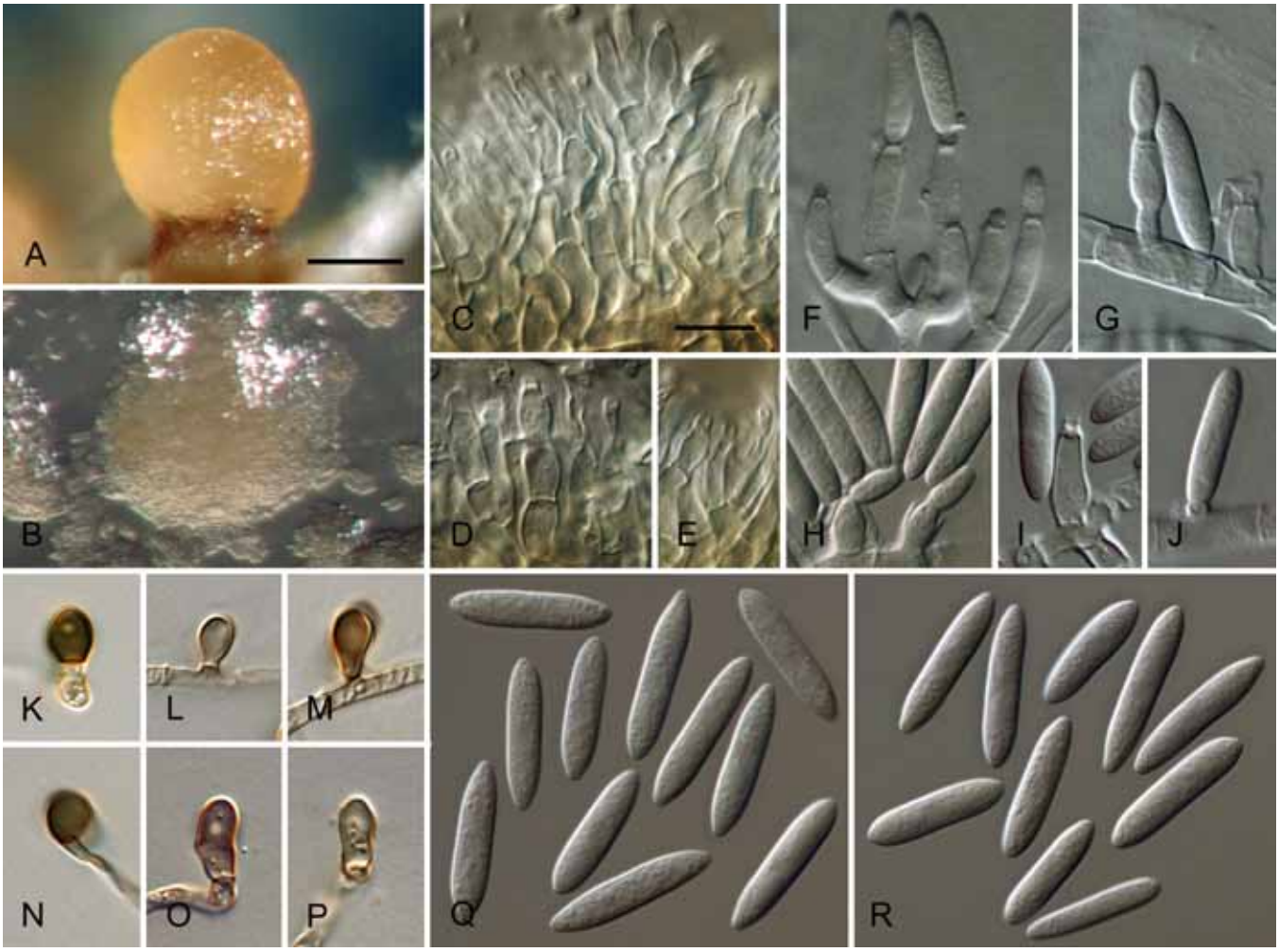

Fig. 9. *Colletotrichum cuscutae* (from ex-holotype strain IMI 304802). A–B. Conidiomata. C–J. Conidiophores. K–P. Appressoria. Q–R. Conidia. A, C–E, Q. from *Anthriscus* stem. B, F–P, R. from SNA. A–B. DM, C–R. DIC, Scale bars: A = 100 µm, C = 10 µm. Scale bar of A applies to A–B. Scale bar of C applies to C–R.

is conspecific with *C. cuscutae*. Based on GAPDH sequences (Guerber *et al.* 2003), isolates FRC2 and FRC7 from dodder in the USA are *C. fioriniae*, while strain 783 from China (apparently identical with strain Lu Bao no. 1) belongs to a subclade of clade 2 that is not included in this study. Strain 783 was found to have a haplotype of *Msp*I mtDNA identical to those of two Australian strains causing terminal crook disease of pine, and distinct from those of other *Cuscuta* strains.

In an attempt to compare endophytes of a *Cuscuta* parasite and its hosts in India, Suryanarayanan *et al.* (2000) isolated 44 fungal endophytes from *Cuscuta reflexa*, including *C. gloeosporioides*, *C. truncatum* and a "*Colletotrichum* sp." that was not further characterised. None of the strains is included in this study, and there are no corresponding sequences available on GenBank.

Colletotrichum cuscutae is separated from other species by all genes studied except for ITS, most effectively by TUB2 and ACT. In blastn searches with the ITS, TUB2 and GAPDH sequences of the ex-type strain IMI 304802, no sequence matched with 100 % homology. Closest matches with the TUB2 sequence (with 98 % identity, 8 bp differences) were FN611029 and FN611028 from *Citrus aurantifolia* and *Citrus sinensis* from Florida, USA (Ramos *et al.* 2006) and the closest matches with the GAPDH sequence (with 98 % identity and 4 bp differences) were EU168905, EU647318 and EU647319 from sweet orange (Peres *et al.* 2008, MacKenzie *et al.* 2009). In a blastn search with the ITS sequence a large number of strains were 99 % identical with that of strain IMI 304802 including several ITS sequences from Key lime isolates, *e.g.* EU647307 and EU647308 (MacKenzie *et al.* 2009).

Colletotrichum fioriniae (Marcelino & Gouli) R.G. Shivas & Y.P. Tan, Fungal Diversity 39: 117. 2009. Fig. 10.

Basionym: *Colletotrichum acutatum* var. *fioriniae* Marcelino & Gouli, Mycologia 100: 362. 2008.

≡ *Glomerella fioriniae* (Marcelino & Gouli) R.G. Shivas & Y.P. Tan, Fungal Diversity 39: 117. 2009.

≡ *Glomerella acutata* var. *fioriniae* Marcelino & Gouli, Mycologia 100: 362. 2008.

Sexual morph not observed. *Asexual morph on SNA. Vegetative hyphae* 1.5–7.5 µm diam, hyaline to pale brown, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* conidiophores formed directly on hyphae. *Setae* not observed. *Conidiophores* hyaline to pale brown, smooth-walled, septate, branched, up to 35 µm long. *Conidiogenous cells* hyaline to pale brown, smooth-walled, cylindrical to ampulliform, sometimes lacking a basal septum and continuous with the conidiophore, sometimes covert with a mucous coating, discrete phialides measure 4–12 × 2.5–3.5 µm, opening 1–2 µm diam, collarette 1 µm long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, fusiform to cylindrical with both ends acute, (10–)13.5–16.5(–19.5) × 4–5(–5.5) µm, mean ± SD = 15.0 ± 1.6 × 4.5 ± 0.3 µm, L/W ratio = 3.3 µm, conidia of strain CBS 129947 are smaller, measuring (10.5–)12–15(–17) × 3.5–5(–6) µm, mean ± SD = 13.5 ± 1.7 × 4.1 ± 0.8 µm, L/W ratio = 3.3 µm. *Appressoria* solitary or in loose groups, pale to medium brown, smooth-walled, ellipsoidal,

Fig. 10. *Colletotrichum fioriniae* (from ex-holotype strain CBS 128517). A–B. Conidiomata. C–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 = 200 µm, B = 100 µm, C = 10 µm. Scale bar of C applies to C–T.

clavate to irregular outline, entire edge or undulate, (4.5–)7–11.5(–15.5) × (4–)4.5–7(–10.5) µm, mean ± SD = 9.2 ± 2.2 × 5.6 ± 1.2 µm, L/W ratio = 1.6.

Asexual morph on Anthriscus stem. Conidiomata forming a cushion of pale brown, thick-walled, angular cells, 3–6.5 µm diam. *Setae* not observed. *Conidiophores* hyaline to pale brown, smooth-walled, septate, branched, up to 35 µm long. *Conidiogenous cells* hyaline to pale brown, smooth-walled, cylindrical, 10–22 × 3–4 µm, opening 1.5–2 µm diam, collarette 0.5–1 µm long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, fusiform to cylindrical with both ends acute, (12.5–)14–18.5(–24.5) × 4–5 µm, mean ± SD = 16.1 ± 2.2 × 4.4 ± 0.4 µm, L/W ratio = 3.6, conidia of CBS 200.35 differ in sometimes having one round and one slightly acute end, conidia of strain CBS 129947 are smaller, measuring (13–)14–16(–17) × (3.5–)4–4.5(–5) µm, mean ± SD = 15.0 ± 1.0 × 4.3 ± 0.4 µm, L/W ratio = 3.5 µm.

Culture characteristics: Colonies on SNA filter paper, *Anthriscus* stem covered with orange acervuli, on filter paper covered with white to pale olivaceous grey aerial mycelium and partly with salmon to orange acervuli, reverse filter paper with pale olivaceous grey to olivaceous grey patches and spots, growth rate 22.5–23 mm in 7 d (32.5–34 mm in 10 d). Colonies on OA flat with entire margin; surface saffron with olivaceous spots (mottled), covered with salmon acervuli, aerial mycelium lacking, reverse salmon, pale vinaceous, olivaceous to purplish grey, growth rate 22–22.5 mm in 7 d (34–35 mm in 10 d). *Conidia in mass* salmon to orange

Material examined: **USA**, New York, Ward Pound Ridge Reserve, on mummified adult *Fiorinia externa* (elongate hemlock scale, insect), 2005, J.A.P. Marcelino and S. Gouli, **culture ex-holotype** of *C. fioriniae* CBS 128517 = EHS_{58} = ARSE 10222; Michigan, from *Vaccinium* sp. (blueberry), collection date and collector unknown (isolated by A. Schilder), culture CBS 129916 = CPC 16823; **Unknown country (probably USA),** from *Rubus* sp., collection date and collector unknown (deposited in CBS collection Apr. 1935 by K.J. Kadow as *Glomerella rubicola*), culture CBS 200.35. **Australia**, Queensland, Mount Tamborine, from fruit rot of *Persea americana*, 4 Sep. 2002, K.G. Pegg, culture CBS 127599 = BRIP 29284a; Queensland, Brisbane, from *Persea americana*, collection date and collector unknown (isolated J.H. Simmonds, No. 13120, 25 Jun 1958) culture CBS 293.67 = DPI 13120; Queensland, Yarwun, endophytic from stem of *Mangifera indica*, 16 Feb. 1994, G.I. Johnson, culture CBS 127601 = BRIP 28761a. **Portugal**, Lisbon, from *Vitis vinifera*, 2000, collector unknown, culture CBS 129947.

Notes: *Colletotrichum fioriniae* is the only representative of clade 3, which is supported by all six genes individually (including ITS). The clade has been recognised as distinct within the *C. acutatum* species complex for some years now (Sreenivasaprasad & Talhinhas 2005), and was accepted as a separate species by Shivas & Tan (2009).

In the current study, a large number of strains (over 50) has been found to belong to this species. They were isolated from a wide variety of host plants, primarily in the temperate zones. There is some evidence of heterogeneity within the species, as two subclades are apparent in the phylogenetic analysis, but neither bootstrap support nor Bayesian probability values are sufficiently high to justify their recognition at species level. Also, strains from the major hosts and countries appear throughout the clade.

The name *C. fioriniae* is based on *C. acutatum* var. *fioriniae* (Marcelino *et al*. 2008), named for a series of strains isolated from an epizootic infection of the exotic scale insect *Fiorinia externa* in the New England region. Implication of *Colletotrichum* species as entomopathogens might be considered surprising. However, the insects in question are sap-suckers and *C. fioriniae* was found to occur widely as an endophyte (Marcelino *et al*. 2009), both in the host plant of the scale insect (*Tsuga canadensis*) and in a phylogenetically diverse set of associated plants. This appears to represent a further case of mutualism between *Colletotrichum* and its host plants, with endophytic strains acting as natural protectants against insect herbivory. A similar case was reported for a strain labelled *C. gloeosporioides f. sp. ortheziidae* (probably belonging to *C. nymphaeae*, see notes there) parasitising the economically important citrus scale insect *Orthezia praelonga* in Brazil (Cesnik *et al*. 1996). Endophytic *Colletotrichum* strains have been demonstrated to protect *Theobroma cacao* plants against *Phytophthora* pathogens (Arnold *et al*. 2003, Mejía *et al*. 2008, Rojas *et al*. 2010).

Strains referred to as *C. acutatum* and identified here as *C. fioriniae* have been implicated in fruit rot of cranberry and blueberry throughout the northern USA and in British Columbia (MacKenzie *et al.* 2009, Polashock *et al*. 2009).

In fruit-rot assays by Freeman & Shabi (1996), isolates from apple and peach (based on ITS sequence, probably identifiable as *C. fioriniae*) produced lesions on many different fruits, "suggesting that isolates of this group have the ability to cross-infect fruit from multiple hosts". All of the fruits tested in the study (almond, apple, avocado, mango, nectarine) are host plants of *C. fioriniae* (Guerber *et al.* 2003, Table 1). In pathogenicity tests MacKenzie *et al.* (2009) showed that isolates from blueberry (= *C. fioriniae*) did not cause lesions on strawberry leaves but caused anthracnose on strawberry fruits, though lesions were smaller than those caused by isolates from strawberry (= *C. nymphaeae*). MacKenzie *et al.* (2009) concluded that therefore the probability of an epidemic on strawberry in Florida caused by blueberry isolates is rather low, but added that the climate could also play a role; in Florida, ripe rot of blueberry fruits is predominantly caused by *C. gloeosporioides* (*s. lat.*), while further north in temperate regions, it is most frequently caused by *C. acutatum* (*s. lat.*) (Smith *et al.* 1996). According to our study, both species occur on strawberry, but based on the number of strains we have seen, *C. fioriniae* seems to be of rather minor importance compared to *C. nymphaeae*.

Marcelino *et al.* (2008) found that strains of *C. fioriniae* could be crossed to form a sexual morph and that some appeared to be self-fertile, though it is not clear whether the self-fertile strains were derived from single spores. We did not see sexual production in the strains examined during the present study.

An earlier name may exist for *C. fioriniae*, in *Gnomoniopsis rubicola* (Stoneman 1898), one of a group of five species (including *Ga. cingulata*) on which the genus *Glomerella* was based (Schrenk & Spaulding 1903a, b). That species was described from diseased leaves of *Rubus strigosus* in West Virginia. No cultures are available and the description of the asexual morph is not detailed, but Marcelino *et al.* (2009) showed that *C. fioriniae* is widespread in the region and both taxa produce a sexual morph. Kadow (1935) ascribed a disease of raspberry from the same region to *Ga. rubicola*, and a culture derived from his work (CBS 200.35) has been examined in the current study and confirmed as belonging to *C. fioriniae*. Without sequence-based evidence from type material, however, we are reluctant to adopt this earlier name. As far as we can tell, a combination into *Colletotrichum* has never formally been made. The name *C. rubicola* was cited on herbarium labels by Ellis & Everhart but only as an asexual name for *Glomerella rubicola*; apparently it was never accompanied by a description.

Colletotrichum fioriniae is separated from other species by all gene sequences studied. The closest matches in a blastn search with the TUB2 sequence of strain CBS 128517 with 100 % identity were AY376557 (from apple in the USA, strain STE-U 5287; Lubbe *et al.* 2004) and AJ748628 from *Liriodendron tulipifera* in the UK (Talhinhas *et al.* 2005). With 99 % identity (and 1–3 bp differences) a series of matches could be made, including AJ748610 and AJ748623 from olive in Portugal, AJ748626 from *Nandina domestica* and AJ748634 from *Magnolia* in the UK (Talhinhas *et al.* 2005). Further sequences with the same level of homology include AJ311668 from *Vitis vinifera* (Talhinhas *et al.* 2002), EF593320–EF593326 from *Fiorinia externa*, EF593329 from blueberry and EF593330 tomato (all from the USA; Marcelino *et al.* 2008), GU183274 from *Acacia acuminata*, GU183273, GU183270, and GU183268 from *Persea americana*, GU183267 *Actinidia chinensis* and GU183269 from *Mangifera indica* (all from Australia; Shivas & Tan 2009), AB618092 from *Apium graveolens* var. *dulce* (celery) in Japan (Fujinaga *et al.* 2011) and AB273716 from grape in Japan (Nakaune & Nakano 2007). All of these are likely to represent strains of *C. fioriniae*, further emphasising its widespread distribution and presumably also its wide host range as a pathogen.

Colletotrichum godetiae Neerg., *Friesia* 4: 72. 1950. Fig. 11.

≡ *Colletotrichum godetiae* Neerg., Aarsberetn. J. E. Ohlens Enkes plantepatol. Lab. 1 April 1942–31 Marts 1943: 8. 1943, nom. inval., Art. 36.1.

= *Colletotrichum clavatum* Agosteo, Faedda & Cacciola, *Fungal Diversity* 50: 292. 2011.

Sexual morph not observed. *Asexual morph on SNA. Vegetative hyphae* 1–7 µm diam, hyaline to pale brown, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* absent, conidiophores formed directly on hyphae. *Setae* not observed. *Conidiophores* hyaline, smooth-walled, simple, to 14 µm long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical, often with only short necks, 4–14 × (1.5–)3–6 µm, opening 1.5–2 µm diam, collarette 0.5 µm long, periclinal thickening observed. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical to fusiform with both ends acute or one end round and one end slightly acute, (7–)10.5–14.5(–15.5) × (3.5–)4–5(–5.5) µm, mean ± SD = 12.4 ± 2.0 × 4.3 ± 0.5 µm, L/W ratio = 2.9, strains CBS 127561, CBS 129917, CBS 193.32 and CBS 129951 differ in forming cylindrical to clavate conidia with one round and one acute end, conidia of strain CBS 862.70 are larger, measuring (8–)14–19(–24) × (4–)4.5–5(–5.5) µm, mean ± SD = 16.4 ± 2.4 × 4.9 ± 0.4 µm, L/W ratio = 3.4. *Appressoria* solitary, medium brown, smooth-walled, clavate to elliptical, the edge entire or undulate (8–)9–12.5(–14.5) × (3–)4–5.5(–6) µm, mean ± SD = 10.7 ± 1.9 × 4.7 ± 0.7 µm, L/W ratio = 2.3.

Asexual morph on Anthriscus stem. Conidiomata absent, conidiophores formed directly on hyphae in aerial mycelium (in strain CBS 125972 present as a cushion of angular to roundish cells 4–10 µm diam). *Setae* not observed (in strain CBS 125972 very few setae present, medium brown, smooth-walled, 2–3-septate, 70–110 µm long, base cylindrical, 4–5 µm diam, tip ± acute). *Conidiophores* hyaline, septate, branched, smooth-walled. *Conidiogenous cells* hyaline, smooth-walled, cylindrical, 9–20 × 3 µm, opening 1.5 µm diam, collarette < 0.5 µm long, periclinal

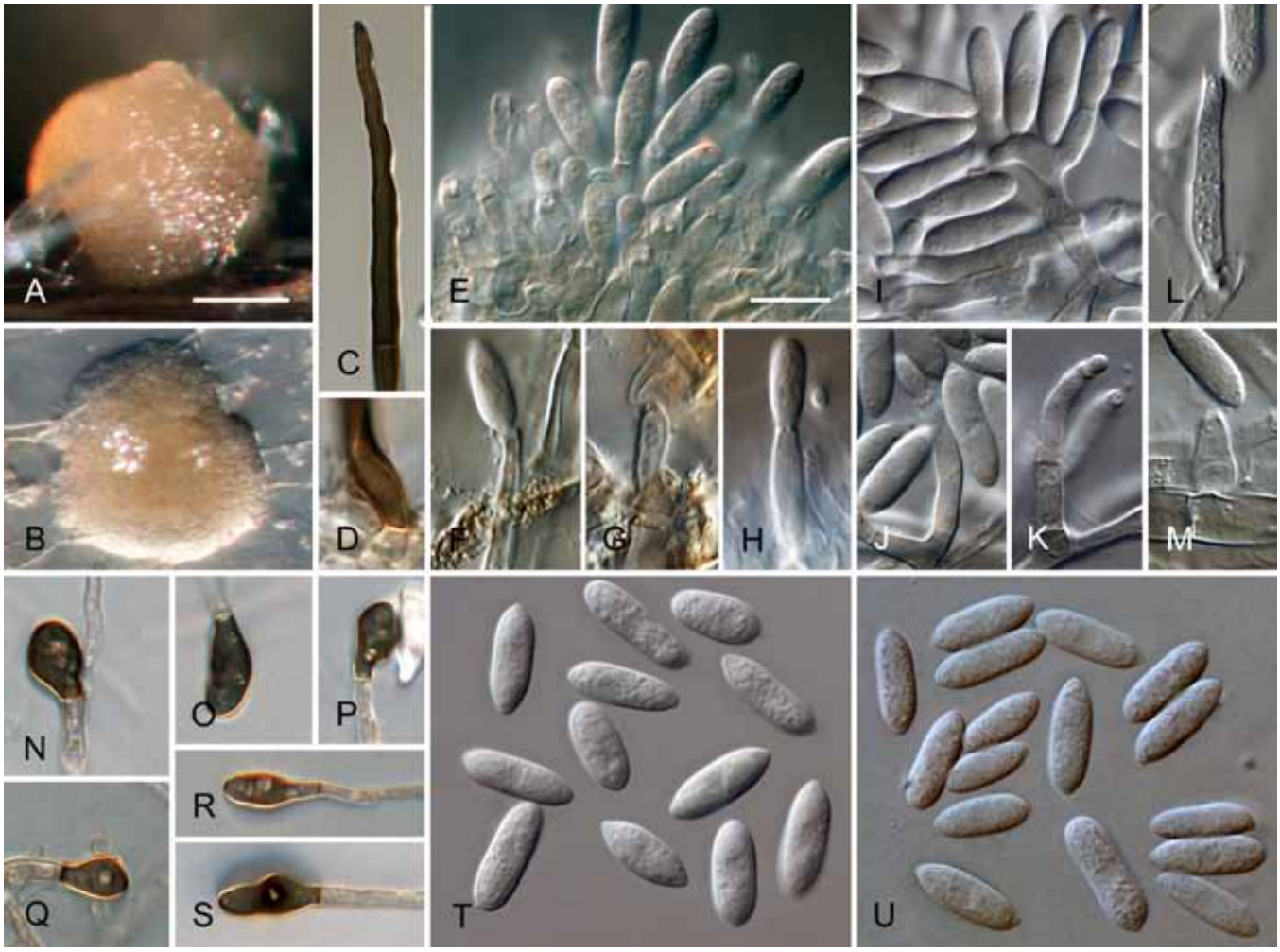

Fig. 11. *Colletotrichum godetiae* (F–G, L–M, T–U from ex-holotype strain CBS 133.44. A–E, H–K, N–S from strain CBS 125972). A–B. Conidiomata. C. Tip of a seta. D. Basis of a seta. E–M. Conidiophores. N–S. Appressoria. T–U. Conidia. A, C–H, T. from *Anthriscus* stem. B, I–S, U. from SNA. A–B. DM, C–U. 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.

thickening visible. *Conidia* hyaline, smooth-walled, aseptate, cylindrical to fusiform with both ends acute, (9.5–)10.5–15(–20.5) × 4–5 µm, mean ± SD = 12.8 ± 2.3 × 4.5 ± 0.4 µm, L/W ratio = 2.8, strain CBS 127561 differs in forming clavate conidia with one round and one acute end and strains CBS 129917, CBS 193.32 and CBS 129911 in forming cylindrical to clavate conidia with one round and one acute end, conidia of strain CBS 862.70 are larger, measuring (12.5–)15.5–18(–19.5) × 4.5–5(5.5) µm, mean ± SD = 16.8 ± 1.4 × 4.9 ± 0.2 µm, L/W ratio = 3.4, conidia of strain CBS 129911 are smaller, measuring (7–)9–13(–15.5) × (2.5–)3–4 µm, mean ± SD = 11.0 ± 2.0 × 3.5 ± 0.3 µm, L/W ratio = 3.1.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline, with little low white aerial mycelium, on *Anthriscus* stem growth rate 21–21.5 mm in 7 d (30.5–31.5 mm in 10 d). Colonies on OA flat with entire margin; surface salmon to hazel, no aerial mycelium, reverse salmon to vinaceous buff; growth rate 21–24 mm in 7 d (30–33.5 mm in 10 d). *Conidia in mass* not observed in strain CBS 133.44, but in strain CBS 125972 orange.

Material examined: **Denmark**, from seed of *Clarkia* (syn. *Godetia*) hybrida cv. Kelvedon Glory 463 C in seed disinfection experiment, 17 Jun. 1943, P. Neergaard, **culture ex-holotype** of *C. godetiae* CBS 133.44. **Italy**, Calabria, Rizziconi, from rotten fruit of *Olea europaea*, Oct. 1992, G.E. Agosteo and G. Magnano di San Lio, **culture ex-holotype** of *C. clavatum* CBS 130251 = OL10 = IMI 398854. **Greece**, from *Olea europaea*, collection date and collector unknown (deposited in CBS collection Jan. 1932 by L. Petri), culture CBS 193.32. **Netherlands**, Tilburg, from *Fragaria* × *ananassa*, collection date and collector unknown, culture CBS 125972 = PD 85/456; near Meerssen, from fruit of *Sambucus nigra*, collection date and collector unknown (deposited in CBS collection Oct. 1970), culture CBS 862.70. **South Africa**, from *Podocarpus* sp., collection date unknown, A. Wood, culture CBS 129911. **Colombia**, Cundinamarca, from fruit anthracnose of *Solanum betaceum*, 13 Aug. 2010, J. Molina, culture CBS 129809 = T.A.1; Cundinamarca, from fruit anthracnose of *Solanum betaceum*, 13 Aug. 2010, J. Molina, culture CBS 129816 = T.A.8. **Chile**, Puerto Saavedra, from tip necrosis on twig of *Ugni molinae*, 1 Oct. 2008, A. Schilder, culture CBS 127561. **Mexico**, Montecillo, from *Schinus molle*, unknown collection date, M. de Jesus Yarez-Morales, culture CBS 129917. **USA**, Arkansas, Fayetteville, from *Aeschynomene virginica* (but see notes), collection date and collector unknown (deposited in CBS collection Aug. 1972 by G.E. Templeton as *C. gloeosporioides f. sp. aeschynomenes*), G.E. Templeton, culture CBS 796.72.

Notes: *Colletotrichum godetiae* was described from seed of *Clarkia* (syn. *Godetia*) hybrida cv. Kelvedon Glory by Neergard (1943), and validated with a Latin description seven years later (Neergard 1950). *Colletotrichum godetiae* corresponds to *C. acutatum* group A4 as recognised by Sreenivasaprasad & Talhinhas (2005) and to part of clade F as defined by Guerber *et al.* (2003). According to Sreenivasaprasad & Talhinhas (2005), group A4 corresponds to group B from New Zealand (Lardner *et al.* 1999). However, the only *C. acutatum* group B strain from New Zealand that we have studied belongs to *C. acerbum* (A6-2). Faedda *et al.* (2011) described strains from group A4 that cause olive anthracnose in Italy as *C. clavatum*, not knowing that an older name for this species exists, of which the ex-holotype culture is available in the CBS culture collection. The ex-holo- and ex-paratype strains are included in this

study (Fig. 1). Von Arx (1957) regarded *C. godetiae* as a synonym of *Ga. cingulata.*

Colletotrichum godetiae also occurs on hosts such as *Fragaria*, *Malus*, and *Prunus*, mainly in Europe and the Near East, causing fruit, leaf or stem (cane, twig) diseases. Most of the isolates of *C. acutatum s. lat.* from *Rhododendron* in Sweden and Latvia (Vinnere *et al.* 2002) belong to this species, based on ITS data. One of their strains (S1) is included in Guerber *et al.* (2003); its GAPDH sequence groups with *C. godetiae*, thus confirming this placement. Additionally, several strains from Latin America have been studied. These occupy a subclade that has comparitively high bootstrap support, but as the subclades cannot be separated using any single gene of the set we have used, we amalgamate them into the one species.

Faedda *et al.* (2011) named *C. clavatum* to highlight the shape of the conidia in the constituent strains. However, conidia of the ex-type strain of *C. godetiae*, CBS 133.44, are rarely clavate and mostly fusiform or short cylindrical. Additionally, conidia of CBS 125972 from strawberry on SNA are uniformly fusiform, while those of CBS 193.32 from olive are mainly clavate, and those of CBS 129911 from *Podocarpus* are fusiform on SNA and mainly clavate on *Anthriscus* stem. According to Vinnere *et al.* (2002) isolates from *Rhododendron* in Sweden and Latvia also form mainly clavate conidia. The conidial shape is therefore an unreliable character for species recognition and seems to depend on the host/origin of the isolate or the growth medium.

One of the isolates we studied, CBS 796.72, was deposited in the CBS collection in August 1972 by G.E. Templeton as *C. gloeosporioides f. sp. aeschynomenes* and would appear to be an authentic strain of this *forma specialis* (Daniel e*t al.* 1973). *Colletotrichum gloeosporioides f. sp. aeschynomenes* caused an epidemic anthracnose disease of northern jointvetch (*Aeschynomene virginica*) in 1969 in Arkansas, USA and was in the following years successfully applied as a biological control agent against this weed. According to our multigene phylogeny, this isolate belongs to the *C. godetiae* clade. According to Daniel e*t al.* (1973) *C. gloeosporioides f. sp. aeschynomenes* is specific for *Aeschynomene* species, was considered to be more virulent to *A. virginica* than to *A. indica* and did not affect rice, soybeans, cotton or 12 other common crops tested. The fungus developed as the weed biocontrol agent Collego (TeBeest 1988, Ditmore *et al.* 2008) against *A. virginica* was also named as *C. gloeosporioides f. sp. aeschynomenes*, and is genetically distinct from *C. godetiae*. It belongs to the *C. gloeosporioides* species complex and is newly described in this volume as *C. aeschynomenes* (Weir *at al.* 2012, this issue). This is probably the reason for differences noted in the host range by TeBeest (1988). There is also some confusion about the host plant. *Aeschynomene virginica* as a weed of soybean and rice fields is actually misidentified *A. indica*, while the true *A. virginica* is rare and threatened and became a federally listed threatened species in the United States in 1992 (www. wikipedia. org).

Colletotrichum godetiae is separated from other species in the *C. acutatum* species complex by all genes except CHS-1, which has the same sequence as in *C. johnstonii*; TUB2, ACT and HIS3 separate the species best. With all genes, the interspecific variation is high. Blastn searches with the TUB2 seqence of CBS 133.44 resulted in 100 % identity with several GenBank accessions from olive isolates studied by Talhinhas *et al.* (2005) and one (AJ409294) from a *Fragaria* isolate (Talhinhas *et al.* 2002), followed with 99 % identity by AJ409302 from a *Ceanothus* isolate in France (Talhinhas *et al.* 2002). These are all probably referable to *C. godetiae*.

Colletotrichum guajavae Damm, P.F. Cannon & Crous, **sp. nov.** MycoBank MB800501. Fig. 12.

Etymology: Named after the host plant, *Psidium guajava.*

Sexual morph not observed. *Asexual morph on SNA. Vegetative hyphae* 1–6 µm diam, hyaline to pale brown, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* not developed, conidiophores formed directly on hyphae. *Setae* not observed. *Conidiophores* hyaline to pale brown, smooth-walled, septate, branched, to 30 µm long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical, some polyphialides observed, 7–19 × 3–4 µm, opening 1–1.5 µm diam, collarette 0.5–1 µm long, periclinal thickening visible. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical to fusiform with both ends slightly acute, (6–)10.5–16.5(–23.5) × (2.5–)3–4(–5) µm, mean ± SD = 13.4 ± 3.0 × 3.5 ± 0.5 µm, L/W ratio = 3.8. *Appressoria* formed singly, medium brown, smooth-walled, subglobose or elliptical to clavate, the outline entire, (4.5–)5–8(–10.5) × (3.5–)4.5–6(–6.5) µm, mean ± SD = 6.6 ± 1.4 × 5.2 ± 0.7 µm, L/W ratio = 1.3.

Asexual morph on Anthriscus stem. Conidiomata acervular, conidiophores formed on pale brown, angular, basal cells 2.5–8 µm diam. *Setae* medium brown, smooth-walled, 0–2-septate, 40–75 µm long, base cylindrical, sometimes inflated, 3–6 µm diam at the widest part, tip ± acute. *Conidiophores* hyaline to pale brown, smooth-walled, septate, branched, to 40 µm long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical, sometimes extending to form a new conidiogenous locus, 7–18 × 2–3.5 µm, opening 1–1.5 µm diam, collarette 0.5–1.5 µm long, periclinal thickening conspicuous. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical to fusiform with both ends ± acute, (11–)13–16(–17) × (3–)3.5–4 µm, mean ± SD = 14.6 ± 1.7 × 3.8 ± 0.3 µm, L/W ratio = 3.9.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline, buff to pale honey, on filter paper partly pale olivaceous grey, on medium, filter paper and *Anthriscus* stem partly covered with whitish to pale olivaceous grey floccose-felty aerial mycelium, reverse of filter paper smoke grey to grey olivaceous; growth rate 22–24 mm in 7 d (31.5–34 mm in 10 d). Colonies on OA flat with entire margin; surface white, pale olivaceous grey to rosy buff, covered with thin floccose-felty whitish to pale olivaceous grey aerial mycelium, reverse rosy buff, grey olivaceous to olivaceous black; growth rate 24–26.5 mm in 7 d (35.5–37 mm in 10 d). *Conidia in mass* salmon.

Material examined: **India**, Assam, Silchar, from fruit of *Psidium guajava*, collection date and collector unknown (deposited in IMI 1991 by M. Das as isolate India No. 1), (IMI 350839 **holotype**, CBS H-20793 isotype, culture ex-type IMI 350839).

Notes: Anthracnose and fruit canker of guava are serious diseases in the Indian subcontinent, and according to Misra (2004) are caused in part by *C. psidii*. However, the identity of the guava pathogen in the sense of Misra is unclear as the conidia are described as sickle-shaped. Curzi (1927) described the conidia of *C. psidii* as cylindrical with both ends rounded, straight, sometimes slightly curved and measuring 12–15 × 3.5–4.5 µm. Based on study of an authentic strain from *Psidium* sp. from Italy, *C. psidii* belongs to the *C. gloeosporioides* species complex (Weir *et al.* 2012, this issue). A separate taxon, *Glomerella psidii* (apparently based on *Gloeosporium psidii*), causing the "mummy disease" of guava, has uncertain relationships. The sexual morph was formed on apple

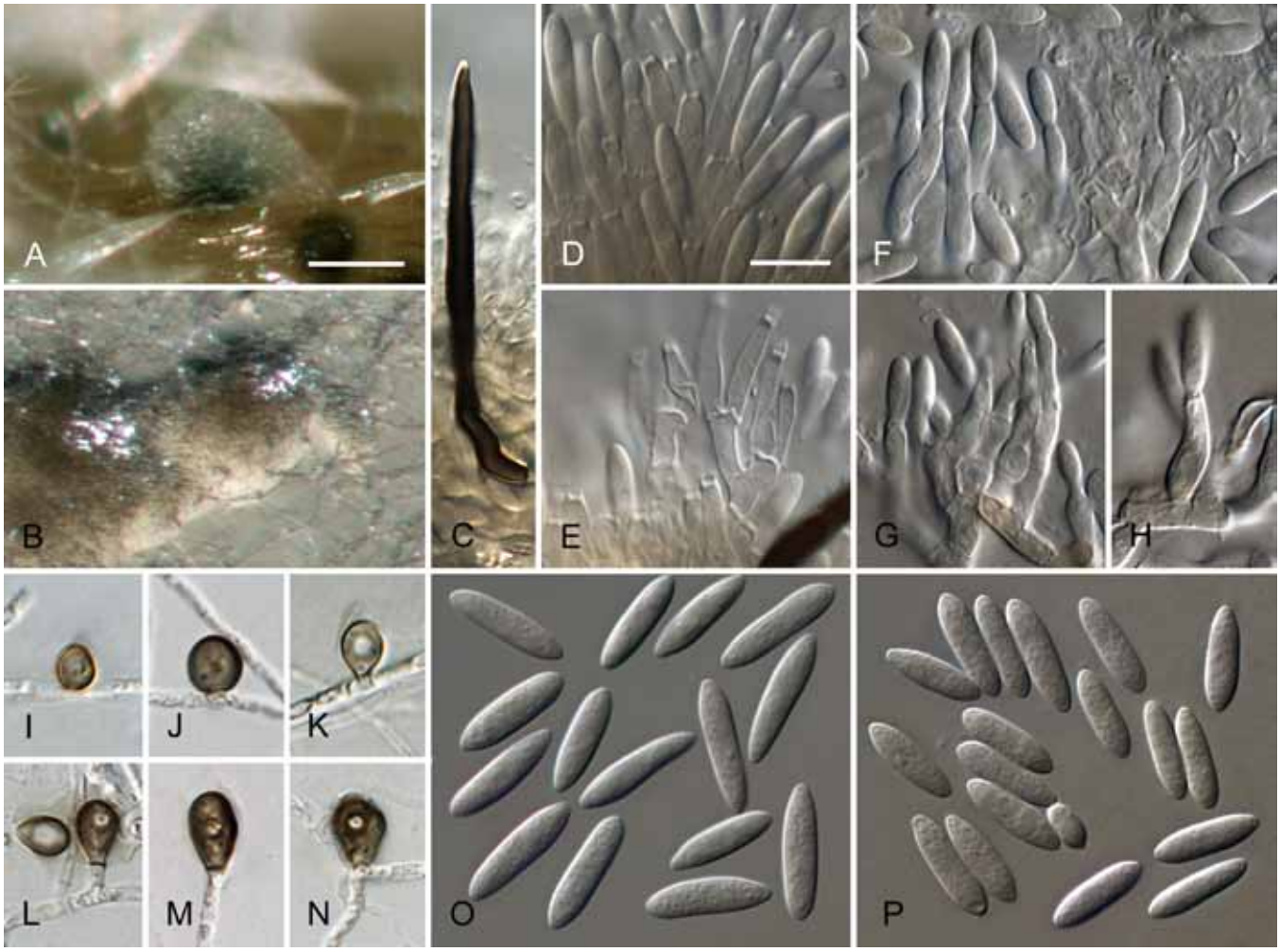

Fig. 12. *Colletotrichum guajavae* (from ex-holotype strain IMI 350839). A–B. Conidiomata. C. Seta. D–H. Conidiophores. I–N. Appressoria. O–P. Conidia. A, C–E, O. from *Anthriscus* stem. B, F–N, P. from SNA. A–B. DM, C–P. DIC, Scale bars: A = 100 µm, D = 10 µm. Scale bar of A applies to A–B. Scale bar of D applies to C–P.

agar and resembled *Glomerella*. The *Gloeosporium* stage it links to may well fall within the *C. acutatum* complex: *Gm. psidii*, described from *Psidium pomiferi* (= *Psidium guajava*) in Mexico, forms ellipsoidal-ovoid conidia measuring 10–16 × 4–6 µm (Saccardo 1906); its conidia are thus broader than those of *C. guajavae*. *Gloeosporium fructus-psidii* was found on fruits of *Psidium* in Sao Paulo, Brazil, and was described as forming oblong, subfusoid to clavate, hyaline conidia, measuring 14–20 × 5–6 µm (Saccardo *et al.* 1931). The shape of the conidia of that species points also at the *C. acutatum* complex, however, there is no species in this complex with conidia on average generally wider than 5 µm. Conidia of *C. guajavae* are substantially smaller, measuring on average 13.4 × 3.5 µm on SNA and 14.6 × 3.8 µm on *Anthriscus* stem.

Peres *et al.* (2002) isolated *C. acutatum* (*s. lat.*) from a guava fruit in Brazil. It caused lesions on guava fruits that were slightly larger than those caused by a *C. acutatum* (*s. lat.*) isolate from strawberry. Based on the ITS sequences they generated, the isolates from guava and strawberry from Brazil belong to the same major clade as *C. guajavae*; the ITS sequence is in fact identical to that of *C. guajavae*, but also the same as a number of other species in this complex, making an identification to species level impossible without additional information. Based on a phylogeny from combined GAPDH and GS sequences in the study by Guerber *et al.* (2003), both strains belong to clade D (= clade 2 in this study), but not to the same subclade. The GAPDH sequence generated in Guerber *et al.* (2003) differs in 5 bp from that of *C. guajavae* ex-holotype strain IMI 350839. A strain from guava from New Zealand, included in the same study, belongs to clade J3 *sensu* Guerber *et al.* (2003) (= *C. acutatum s. str.*). Apart from *C. acutatum s. lat.* and *C. psidii*, Farr & Rossman (2012) list reports from *Psidium* for *C. coccodes* in Myanmar, *C. gloeosporioides* in Brazil, China, Cuba, India, Mexico, Puerto Rico, South Africa, USA, Virgin Islands and Mexico, and *Colletotrichum* sp. in Brazil, Jamaica and Mexico; it is possible that some of these reports should be referred to *C. guajavae.*

Colletotrichum guajavae can be distinguished from other species of clade 2 of the *C. acutatum* complex using TUB2, GAPDH and ACT sequences, most effectively with GAPDH. With data from GAPDH alone the species sits within the very variable *C. nymphaeae* cluster. With TUB2 and ACT there is only 1 bp difference between *C. guajavae* and *C. scovillei*, while CHS-1 and HIS3 sequences are the same as those of *C. scovillei. Colletotrichum guajavae* is not reliably distinguishable from these species using morphological characteristics. Blastn searches with the GAPDH sequence of strain CBS 853.73 shows 100 % identity with HM038337 from *Colletotrichum* sp. isolate MFU 09 0624 from *Ziziphus mauritiana* (jujube) from Laos (Phoulivong *et al.* 2010), and it is therefore probable that this strain also belongs to *C. guajavae*. The closest match with the TUB2 sequence of strain CBS 853.73, with 100 % identity, was GU246633 from isolate R14 from *Capsicum annuum* from South Korea (Sang *et al.* 2011). We identify that isolate as *C. scovillei*; the available sequence does not include the region containing the single nucleotide polymorphism that distinguishes TUB2 sequences of *C. guajavae* and *C. scovillei*.

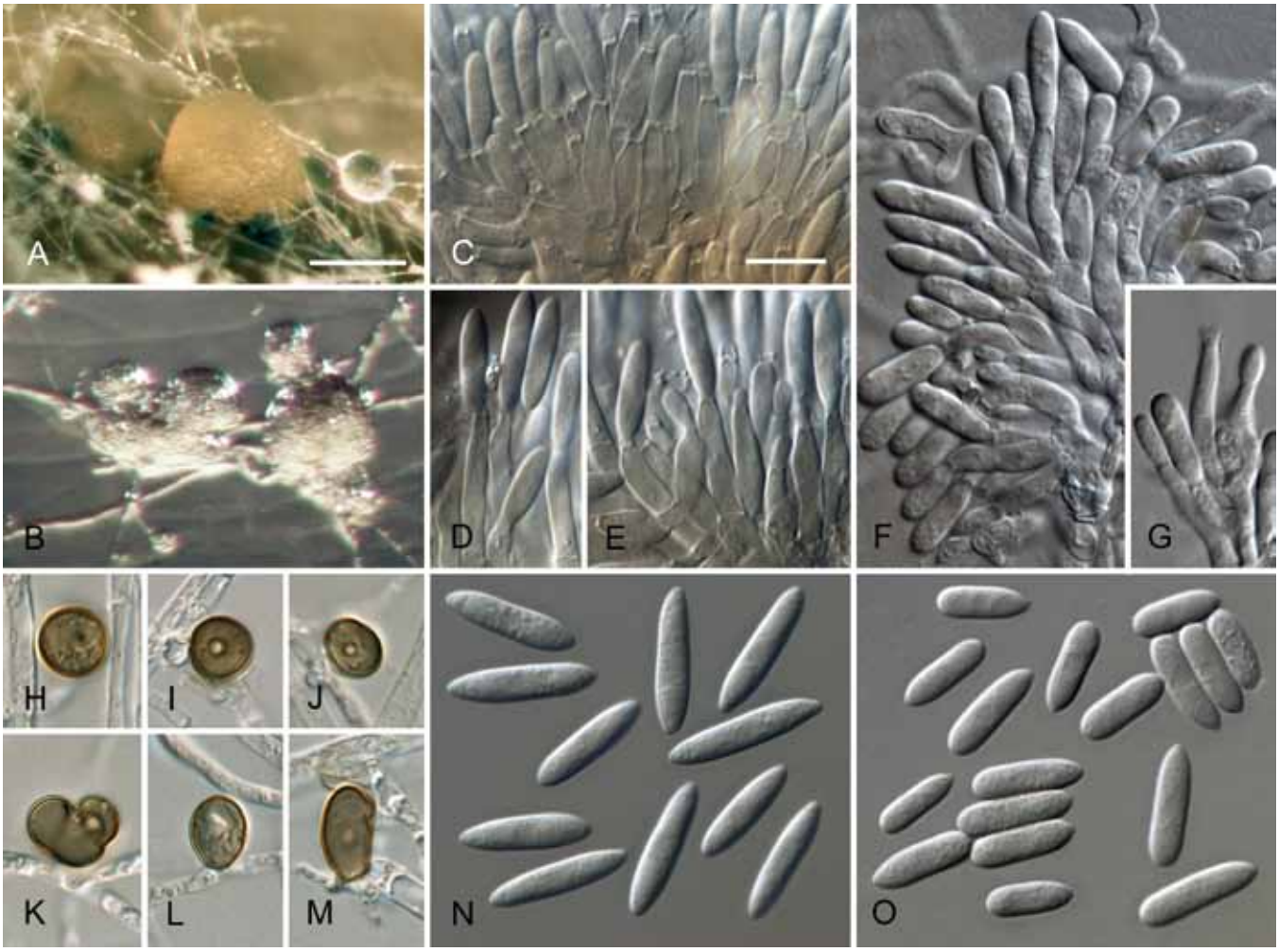

Fig. 13. *Colletotrichum indonesiense* (from ex-holotype strain CBS 127551). A–B. Conidiomata. C–G. Conidiophores. H–M. Appressoria. N–O. Conidia. A, C–E, N. from *Anthriscus* stem. B, F–M, O. from SNA. A–B. DM, C–O. DIC, Scale bars: A = 100 µm, C = 10 µm. Scale bar of A applies to A–B. Scale bar of C applies to C–O.

Colletotrichum indonesiense Damm, P.F. Cannon & Crous, **sp. nov.** MycoBank MB800502. Fig. 13.

Etymology: Named after the country of origin, Indonesia.

Sexual morph not observed. *Asexual morph on SNA. Vegetative hyphae* 1–7 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* not developed, conidiophores formed directly on hyphae. *Setae* not observed. *Conidiophores* hyaline, smooth-walled, simple or septate and branched, to 40 µm long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical to ± inflated, 8–21 × 2–3.5 µm, opening 1–1.5 µm diam, collarette 1–1.5 µm long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical with one end round and one end acute, (8–)10–14.5(–18) × (2.5–)3.5–4(–4.5) µm, mean ± SD = 12.3 ± 2.4 × 3.8 ± 0.3 µm, L/W ratio = 3.2. *Appressoria* single, pale to medium brown, smooth-walled, elliptical, to subglobose in outline, the edge entire, sometimes undulate, 5.5–9(–14.5) × (5–)5.5–7.5(–9) µm, mean ± SD = 7.5 ± 1.8 × 6.3 ± 1.0 µm, L/W ratio = 1.2.

Asexual morph on Anthriscus stem. Conidiomata acervular, conidiophores formed on pale brown, angular, basal cells 2.5–6 µm diam. *Setae* not observed. *Conidiophores* hyaline to pale brown, smooth-walled, septate, branched, to 60 µm long. *Conidiogenous cells* hyaline to pale brown, smooth-walled, cylindrical, sometimes ± inflated, 9–25 × 2–4 µm, opening 1–1.5 µm diam, collarette 1–1.5 µm long, periclinal thickening visible. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical to fusiform with both ends acute, (10.5–)13–17.5(–19) × (3–)3.5–4 µm, mean ± SD = 15.4 ± 2.2 × 3.7 ± 0.2 µm, L/W ratio = 4.1.

Culture characteristics: Colonies on SNA flat, partly raised with entire margin, hyaline, buff to pale honey, on medium, filter paper and *Anthriscus* stem partly covered with irregular white aerial mycelium, *Anthriscus* stem partly covered with orange acervuli, reverse hyaline, white, buff to cinnamon, filter paper partly olivaceous grey; growth rate 18.5–20 mm in 7 d (30–31 mm in 10 d). Colonies on OA flat, partly raised with entire margin; surface covered with irregular floccose to woolly white to olivaceous grey aerial mycelium and few orange acervuli, reverse buff, cinnamon to dark purplish grey; growth rate 22.5–24 mm in 7 d (32.5–34 mm in 10 d). *Conidia in mass* orange.

Material examined: **Indonesia**: Sumatra, Tele, from leaf spots developing after herbicide treatment of *Eucalyptus* sp., 1 Jan. 2008, M.J. Wingfield, (CBS H-20798 **holotype**, culture ex-type CBS 127551 = CPC 14986).

Notes: *Eucalyptus* is not a well-known disease reservoir for *Colletotrichum* species. *Colletotrichum eucalypti* was described from Brazil by Bitancourt (1927) and noted again by Viégas (1946) from the Campinas region, causing anthracnose of *Eucalyptus* leaves. Viégas described the species as having conidia that are elongate-fusiform to oblong and 10–20 × 3–5 µm in size; the

description is reminiscent of the *C. acutatum* species complex, but cultures are not available, we have not seen type material, and the species was described from a different continent.

There is a number of *Gloeosporium* species that were described on *Eucalyptus* spp. in different countries, but none was described in Asia, and most differ considerably from *C. indonesiense*. *Gloeosporium eucalypti* was described on *E. corynocalyx* in Australia, and forms shorter conidia than *C. indonesiense*, measuring 8–10 × 3–4 µm (Saccardo 1906) compared to those of *C. indonesiense* that average 12.3 × 3.8 µm and 15.4 × 3.7 µm on SNA and *Anthriscus* stem, respectively. *Gloeosporium eucalyptorum*, described on leaves and twigs of *Eucalyptus* spp. in Italy, has larger conidia, measuring 18–26 × 5–6 µm. They have a different shape, cylindrical to cylindric-clavate, straight to slightly curved, with both ends obtuse (see Tavola VIII, fig. 5 in Turconi 1924), while conidia of *C. indonesiense* are straight and cylindrical, with one acute end when formed on SNA and both ends acute when formed on *Anthriscus* stem. *Gloeosporium capsularum* was described on *Eucalyptus* sp. in California, USA; it has longer and narrower conidia, measuring 18–20 × 2.5 µm. They are straight and cylindrical with both sides obtuse (Saccardo 1884). Conidia of *Gm. nigricans* described from leaves of *E. pauciflora* in Australia are ovoid and wider than those of *C. indonesiense*, measuring 12 × 7 µm (Cooke 1891). *Gloeosporium ochrostictum* from *E. rostrata* in Australia has oblong-clavate, inaequilateral conidia measuring 9–12 × 4–5 µm (Saccardo 1899); conidia of *C. indonesiense* are narrower and aequilateral. We have not examined authentic material of any of these taxa, but bearing in mind that none have associated cultures and that type material would be too old to yield multigene sequences, we prefer to leave them in obscurity.

There are *Colletotrichum* species in the *C. boninense* species complex known on *Eucalyptus*: *C. boninense* and *C. karstii* have both been found on *Eucalyptus* in South Africa, and *C. karstii* also occurs on the related host genus *Eugenia* in Brazil (Damm *et al.* 2012, this issue).

Colletotrichum indonesiense is separated from other species by TUB2, ACT, GAPDH and CHS-1 sequences, and most effectively with TUB2. With CHS-1 there is only one bp difference from *C. laticiphilum*, and the HIS3 sequence is the same as that of that species. The closest match in a blastn search with the TUB2 sequence of strain CBS 127551 with 99 % identity (6 differences) was GU246633 from isolate R14 from *Capsicum annuum* from South Korea (Sang *et al.* 2011; identified by us as *C. scovillei*). The closest match with the GAPDH sequence (with 97 % identity, 7 bp differences) is isolate OCC95 from an unspecified crop in India (HQ846719; P. Chowdappa, C.S. Chethana, S. Madhura, unpubl. data). There are more than 40 ITS sequences in GenBank with 99 % identity (1 bp difference) to the ITS sequence of *C. indonesiense*.

Colletotrichum johnstonii Damm, P.F. Cannon & Crous, **sp. nov.** MycoBank MB800503. Fig. 14.

Etymology: Named after Peter R. Johnston (Landcare Research), a major contributor to recent improvements in *Colletotrichum* systematics.

Sexual morph not observed. *Asexual morph on SNA. Vegetative hyphae* 1–7 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* not developed, conidiophores formed directly on hyphae. *Setae* not observed in type, but present in strain IMI 357027, medium brown, basal cell sometimes pale brown, smooth-walled, 0–1-septate, 35–55 µm long, base cylindric-conical, often constricted at septum, 3.5–4 µm diam, the tip ± acute. *Conidiophores* hyaline, smooth-walled, septate, branched. *Conidiogenous cells* hyaline smooth-walled, cylindrical, sometimes slightly inflated, sometimes lacking a basal septum and continuous with the conidiophore, some polyphialides observed, discrete phialides measure 6–27 × 2.5–4 µm, opening 1–2 µm diam, collarette 1–1.5 µm long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical to fusiform with one end slightly acute and one end round or slightly acute, (13.5–)14.5–19(–21.5) × (3.5–)4.5–5(–6) µm, mean ± SD = 16.7 ± 2.1 × 4.7 ± 0.4 µm, L/W ratio = 3.6. *Appressoria* sparse, single or in loose groups, pale to medium brown, smooth-walled, elliptical to clavate or irregular, the outline undulate or entire, (6–)8–11.5(–14) × (2–)4–7.5(–10.5) µm, mean ± SD = 9.6 ± 1.7 × 5.8 ± 1.9 µm, L/W ratio = 1.7.

Asexual morph on Anthriscus stem. Conidiomata acervular, conidiophores formed on pale brown, angular, basal cells, 3.5–7.5 µm diam. *Setae* not observed in type, but present in strain IMI 357027, medium brown, basal cell pale brown, smooth-walled, 0–1-septate, 40–60 µm long, base cylindric-conical to slightly inflated, 2.5–5 µm diam, the tip ± acute to ± roundish, sometimes with a constriction. *Conidiophores* hyaline, smooth-walled, septate, branched, to 60 µm long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical, 11–26 × 2.5–4 µm, opening 1–2 µm diam, collarette 1 µm long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical to fusiform with one end slightly acute and one end round or slightly acute, (14.5–)15.5–17(–18) × 4.5–5(–5.5) µm, mean ± SD = 16.3 ± 1.0 × 4.9 ± 0.3 µm, L/W ratio = 3.3.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline; medium, filter paper and *Anthriscus* stem partly covered with thin floccose white to pale grey aerial mycelium and orange acervuli, reverse hyaline with orange to grey acervuli shining through; growth rate 23–24.5 mm in 7 d (36–37 mm in 10 d). Colonies on OA flat to raised, with entire margin; surface covered with floccose whitish to pale olivaceous grey aerial mycelium and orange acervuli, reverse rosy buff, olivaceous grey to iron-grey in the centre; growth rate 22.5–24.5 mm in 7 d (37.5–39 mm in 10 d). *Conidia in mass* orange.

Material examined: **New Zealand**, AK, Auckland, from fruit rot of *Solanum lycopersicum*, 29 Feb. 1990, J.M. Dingley, (CBS H-20809 **holotype**, culture ex-type CBS 128532 = ICMP 12926 = PRJ 1139.3); Takaka, from fruit rot of *Citrus* sp., 1989, collector unknown (deposited in IMI 1993 by P.R. Johnston, No. 1125.5), culture IMI 357027 = PRJ 1125.5.

Notes: *Colletotrichum johnstonii* is part of clade 4 but has slightly longer conidia than those of *C. godetiae*, and can be separated from other species on the basis of ACT, HIS3, TUB2, and GAPDH sequences. The gene that performs best as a differential test is ACT. The GAPDH sequence is only 1 bp different from that of *C. godetiae*, while the CHS-1 sequences of both species are the same. The two *C. johnstonii* strains from citrus and tomato and a strain from pear that is newly described here as *C. pyricola* were included in *C. acutatum* group C by Lardner *et al.* (1999). Two of their tamarillo strains, also in Lardner's group C, had near-identical RAPD banding patterns to that of the ex-type strain of *C. johnstonii*. There are two strains from citrus (PJ50 = PRJ 1125.5 and PJ49 = PRJ 1124.5) and one from tamarillo (Pj18 = PRJ 979.9) from New Zealand included in the study of Guerber *et al.* (2003) that have the

Fig. 14. *Colletotrichum johnstonii* (A–B, D–G, I–R. from ex-holotype strain CBS 128532. C, H. from IMI 357027). A–B. Conidiomata. C, H. Setae. D–G, I–J. Conidiophores. K–P. Appressoria. Q–R. Conidia. A, C–G, Q. from *Anthriscus* stem. B, H–P, R. from SNA. A–B. DM, C–R. DIC, Scale bars: A = 100 µm, B = 200 µm, D = 10 µm. Scale bar of D applies to C–R.

same GAPDH sequence, and these strains also were assigned to to group C in Lardner *et al.* (1999). From the evidence we have to date, *C. johnstonii* appears to be endemic to New Zealand, but is not host-specific.

The closest matches from GenBank with the TUB2 sequence of strain CBS 128532 with (98 % identity, 10 bp differences) were AJ409294 from *Fragaria* in the UK (Talhinhas *et al.* 2002) as well as AJ748609, AJ748612-AJ748614, AJ748619–AJ748622 and AJ748625, isolates from olive (Talhinhas *et al.* 2005). We do not believe that any of these sequences represent further records of *C. johnstonii*. With the GAPDH sequence of strain CBS 128532, there was no closer match than 88 % identity. The ITS sequence of strain CBS 128532 is identical to those of *C. salicis*, *C. pyricola* and *C. phormii*.

Colletotrichum kinghornii Damm, P.F. Cannon & Crous, **sp. nov.** MycoBank MB800504. Fig. 15.

Etymology: Named after W.O. Kinghorn, who previously studied this fungus.

Sexual morph not observed. *Asexual morph on SNA. Vegetative hyphae* hyaline, smooth-walled, septate, branched, 1–6 µm diam. *Chlamydospores* not observed. *Conidiomata* absent, conidiophores formed directly on hyphae. *Setae* not observed. *Conidiophores* hyaline, smooth-walled, simple or septate and branched, up to 45 µm long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical, conical or ± inflated, 5.5–18 × 2–3.5 µm, opening 1–1.5 µm diam, collarette 0.5–1.5, periclinal thickening visible. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical to fusiform with one round and one truncate end, (11–)15.5–21(–22.5) × (3–)3.5–4(–4.5) µm, mean ± SD = 18.3 ± 2.9 × 3.8 ± 0.4 µm, L/W ratio = 4.9. *Appressoria* not observed.

Asexual morph on Anthriscus stem. Conidiomata absent, conidiophores formed directly on hyphae. *Setae* not observed. *Conidiophores*, hyaline, smooth-walled, septate, sometimes branched, up to 50 µm long. *Conidiogenous cells*, hyaline, smooth-walled, cylindrical to clavate, 20–27 × 2.5–4 µm, opening 1–1.5 µm diam, collarette 1 µm, periclinal thickening visible. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical to fusiform with one round and one truncate end, (n = 18) measure (15–)16–20.5(–23) × 3.5–4.5 µm, mean ± SD = 18.1 ± 2.3 × 4.0 ± 0.4 µm, L/W ratio = 4.6.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline, medium partly covert with very short white aerial mycelium, reverse same colours; 14.5–15.5 mm in 7 d (21–24 mm in 10 d). Colonies on OA flat with entire margin, white, pale olivaceous grey to greyish sepia, surface covert with thin, short floccose white aerial mycelium, reverse white to pale olivaceous grey; 11–16.5 mm in 7 d (16–24 mm in 10 d). *Conidia in mass* not observed.

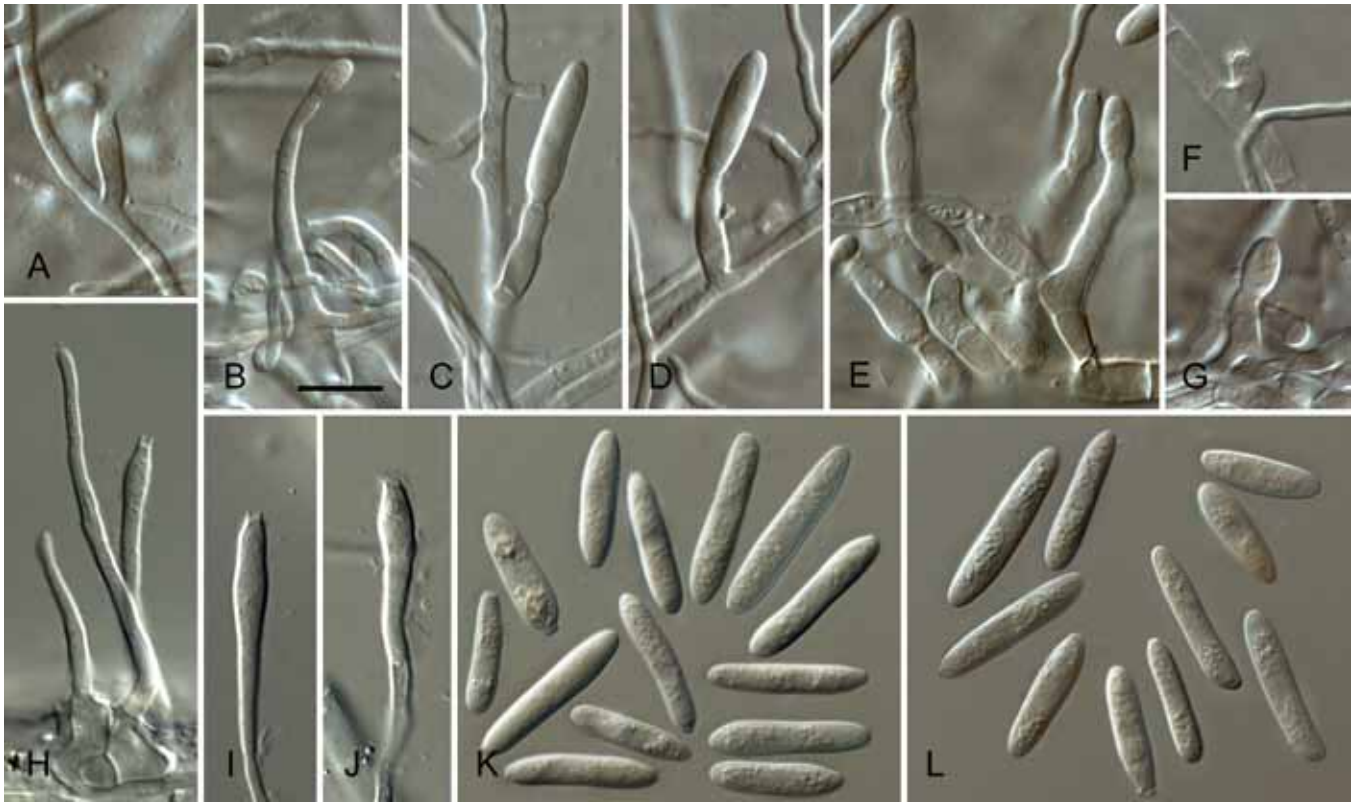

Fig. 15. *Colletotrichum kinghornii* (from ex-holotype strain CBS 198.35). A–J. Conidiophores. K–L. Conidia. H–K. from *Anthriscus* stem. A–G, L. from SNA. A–L. DIC, Scale bars: B = 10 µm. Scale bar of B applies to A–L.

Material examined: **UK**, Scotland, from *Phormium tenax*, unknown collection date, N.L. Alcock (deposited in CBS collection Feb. 1935 by W.O. Kinghorn as *Glomerella phacidiomorpha*), (CBS H-20909 **holotype**, culture ex-type CBS 198.35).

Notes: Kinghorn (1936) worked on two strains isolated from *Phormium* from material collected in Scotland by N.L. Alcock. Both of these were identified as *C. phormii* by Farr *et al.* (2006). One of these is confirmed as *C. phormii* in this study, but we have found the other (CBS 198.35) to be distinct in molecular terms. Kinghorn named his material *Glomerella phacidiomorpha*, but Farr *et al.* (2006) examined the type of that name and found it to be a species of *Phaeosphaeriopsis*.

Colletotrichum kinghornii is one of the two species in the *C. acutatum* complex with the largest conidia; only those of *C. phormii* are bigger. However, strain CBS 198.35 hardly sporulates, and the conidia measured were mostly formed in the aerial mycelium. According to the molecular analyses, strain CBS 198.35 must be considered separate at species rank from *C. phormii*, with several sequence differences in almost every gene, and a single bp difference in the ITS sequence (this was not detected in the Farr *et al.* study). *Colletotrichum kinghornii* is most effectively separated from other species using HIS3.

Closest match in blastn searches with the TUB2 sequence of strain CBS 198.35 (with 98 % identity, 7 bp differences) was *Glomerella acutata* isolate PCF 459 (EU635504) from strawberry in Belgium (Debode *et al.* 2009) and with 98 % identity (8 bp differences) isolate PT250 (= CBS 129953) AJ748624 from olive in Portugal (see A6-1) (Talhinhas *et al.* 2005). This last strain is assigned to *C. rhombiforme* in this study. With the GAPDH sequence of strain CBS 198.35 there was no closer match from GenBank than with 86 % identity.

Colletotrichum laticiphilum Damm, P.F. Cannon & Crous, **sp. nov.** MycoBank MB800505. Fig. 16.

Etymology: *latex* = Greek for milk, latex and *-philus* = Greek for loving; referring to the economically significant feature of the host plant.

Sexual morph not observed. *Asexual morph on SNA. Vegetative hyphae* 1–7.5 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* not developed, conidiophores formed directly on hyphae. *Setae* not observed. *Conidiophores* hyaline, smooth-walled, simple or septate and branched. *Conidiogenous cells* hyaline, smooth-walled, ampulliform to conical, sometimes lacking a basal septum and continuous with the conidiophore, discrete phialides measuring 6.5–15 × 3–4.5 µm, opening 1–1.5 µm diam, collarette 0.5–1.5 µm long, periclinal thickening visible. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical with both ends ± acute or one end round and one end slightly acute, (9.5–)13.5–19.5(–25.5) × (3–)3.5–4(–4.5) µm, mean ± SD = 16.6 ± 3.1 × 3.8 ± 0.4 µm, L/W ratio = 4.4, conidia of CBS 129827 smaller, measuring (5–)8–15(–18.5) × (1.5–)2.5–4.5(–5.3) µm, mean ± SD = 11.5 ± 3.4 × 3.6 ± 0.9 µm, L/W ratio = 3.2. *Appressoria* single, medium brown, smooth-walled, subglobose, elliptical to clavate, the edge entire or rarely slightly undulate, (5–)6.5–12(–16) × (4–)6–8(–8.5) µm, mean ± SD = 9.2 ± 2.8 × 7.2 ± 1.0 µm, L/W ratio = 1.3, appressoria of CBS 129827 smaller, measuring (4–)5–7(–8) × (2.5–)3.5–5.5(–6) µm, mean ± SD = 6.0 ± 1.1 × 4.5 ± 0.8 µm, L/W ratio = 1.3.

Asexual morph on Anthriscus stem. Conidiomata possibly acervular, but no basal cells observed. *Setae* not observed. *Conidiophores* hyaline to pale brown, smooth-walled, simple or septate and branched, to 25 µm long. *Conidiogenous cells* hyaline

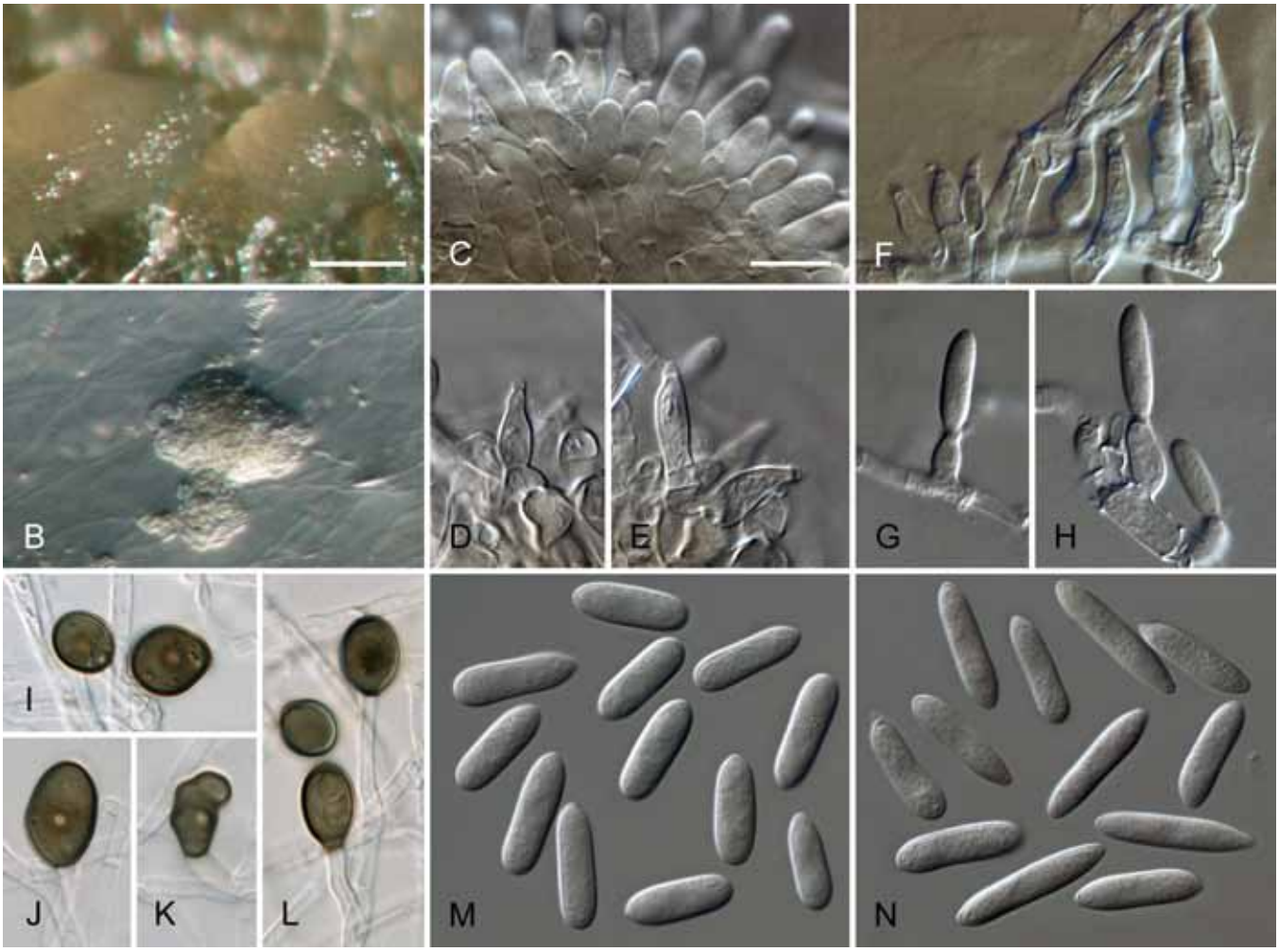

Fig. 16. *Colletotrichum laticiphilum* (from ex-holotype strain CBS 112989). A–B. Conidiomata. C–H. Conidiophores. I–L. Appressoria. M–N. Conidia. A, C–E, M. from *Anthriscus* stem. B, F–L, N. from SNA. A–B. DM, C–N. DIC, Scale bars: A = 100 µm, C = 10 µm. Scale bar of A applies to A–B. Scale bar of C applies to C–N.

to pale brown, smooth-walled, ampulliform to cylindrical, 9–15 × 3.5–5.5 µm, opening 1–1.5 µm diam, collarette 0.5–1 µm long, periclinal thickening visible. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical with one end round and one end slightly acute, (10–)12–15(–19.5) × 4–5(–5.5) µm, mean ± SD = 13.6 ± 1.7 × 4.5 ± 0.3 µm, L/W ratio = 3.0.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline to pale honey, filter paper pale olivaceous grey; growth rate 22.5 mm in 7 d (33.5 mm in 10 d). Colonies on OA flat with entire margin; surface white, buff to pale isabelline, covered with short felty white aerial mycelium, reverse buff to honey; growth rate 22.5–23 mm in 7 d (32.5–35 mm in 10 d). *Conidia in mass* whitish.

Material examined: **India**, Kerala, Kottayam, Rubber Research Institute campus, from raised spots on leaf of *Hevea brasiliensis*, 1999, unknown collector, (CBS H-20799 **holotype**, culture ex-type CBS 112989 = IMI 383015 = STE-U 5303 = CG_6). **Colombia**, Meta, Villavicencio, from leaf, anthracnose of *Hevea brasiliensis*, 14 Aug. 2010, O. Castro, culture CBS 129827 = CH2.

Notes: *Colletotrichum* leaf disease (CLD) has been considered to be a major cause of declining yields of *Hevea brasiliensis* in Southeast Asia (Brown & Soepena 1994, Jayasinghe *et al*. 1997, Saha *et al.* 2002). The pathogen was at first routinely identified as *C. heveae* (Petch 1906) and then assumed to be *C. gloeosporioides* (*s. lat.*) (Carpenter & Stevenson 1954, von Arx 1957).

Jayasinghe and colleagues found that the majority of strains examined from Sri Lanka belonged to *C. acutatum* (*s. lat*.), and Saha *et al.* (2002) reported this species from India as well; it is likely that similar strains are widespread in the region. Saha *et al.* (2002) revealed that *C. acutatum* (*s. lat*.) causes the raised spot symptom, while *C. gloeosporioides* (*s. lat*.) causes both anthracnose and papery lesions on *Hevea* leaves in India. In a study from Sri Lanka, Thambugala & Deshappriya (2009) found that *C. acutatum* causes larger lesions and can act synergistically in combination with *C. gloeosporioides* to cause CLD. Strain IMI 383015 is one of the strains causing the raised spots on *Hevea* leaves in India. It was included in the study of Saha *et al.* (2002) and also in the study of Lubbe *et al.* (2004), who generated its ITS and TUB2 sequences. The TUB2 sequence of strain IMI 383015 (AY376556) was also included in the TUB2 phylogeny by Shivas & Tan (2009); the strain was identified there as *C. simmonsii.*

It is necessary to consider the possible conspecificity of *C. laticiphilum* with three previously described taxa, all published by Petch in the same paper (Petch 1906) from collections made from *Hevea* in Sri Lanka. These were named as *C. heveae*, *Gloeosporium heveae* [nomenclaturally unrelated to *C. heveae*] and *Gm. alborubrum*. All three species were regarded as synonyms of *C. gloeosporioides* by von Arx (1957).

Colletotrichum heveae was described with very wide conidia, measuring 18–24 × 7.5–8 µm (Petch 1906), larger than any of the species in the *C. acutatum* species complex, and possibly

belonging to the *C. crassipes* group as accepted by Sutton (1980). No type details were given in the original description. There is a probable type specimen of *C. heveae* in K(M), collected from leaves of *Hevea* (Petch 2228) on 7 Oct. 1905, presumably from Sri Lanka. It is fragmentary and also contains a fungus identified on the label as *Gloeosporium brunneum*. According to Petch (1927), *C. heveae* causes an indeterminate leaf spot, and is perhaps an invader following mechanical damage; it was not considered to be a significant disease of rubber at that time. No fungus corresponding to the description of *C. heveae* was found on the type specimen, and a slide previously made from this material (IMI 80135) also does not contain this species. *Glomerella phyllanthi* (from the related plant *Phyllanthus acidus*) was initially regarded as the sexual morph of *C. heveae* (Pai 1970), but was later revealed to belong to the *C. boninense* species complex, as was another species on *Hevea*, *C. annellatum* (Damm *et al.* 2012, this issue).

The conidia of *Gm. heveae* are about the same size as those of *C. laticiphilum* (12–17 × 3.5–5 µm); however the spores extrude in a pale brown mass, which would be unusual for a *Colletotrichum*. Also the size range of the "basidia" (= conidiogenous cells) is given as 20–34 × 2 µm; corresponding structures of *C. laticiphilum* are shorter and much wider. There is no material in K(M) identified as *Gm. heveae*. It is possible that the fungus identified as *Gm. brunneum* in the type collection of *C. heveae* is actually *Gm. heveae*, as *Gm. brunneum* is a completely unrelated fungus originating from *Populus* leaves in the USA (Ellis & Everhart 1889). Petch could have realised after writing the packet label, but before publication, that naming his fungus *Gm. brunneum* would create a later homonym. Petch (1927) indicated that *Gm. heveae* was found only in one isolated instance in 1905, when it caused leaf fall in young nursery-grown plants and resulted in general discoloration and death of the whole leaf blade. The disease was successfully controlled by reducing exposure to shade. Synonymy of *Gm. heveae* with our fungus would not affect the naming of *C. laticiphilum* as a combination into *Colletotrichum* based on *Gm. heveae* would be a later homonym of *C. heveae*.

It seems possible that *Gm. alborubrum* might be referable to the species described here. According to Saha *et al.* (2002) a symptom consisting of raised spots had been attributed to this species. The fungus was originally described from green stems of *Hevea brasiliensis*, but Petch (1927) stated that it caused abnormal leaf fall and appeared to spread to green ends of the branches to cause dieback. He thought that it might be a secondary invader following *Phytophthora* infection. These symptoms do not seem to correspond well with those described by Saha and colleagues. The conidia of *Gm. alborubrum* were measured as 15–20 × 3–4 µm, and described as oblong with rounded ends, straight or slightly curved, issuing in thick pink or white tendrils (Petch 1906). The size is similar to *C. laticiphilum*; we also observed slightly curved conidia, especially in the isolate from Colombia (CBS 129827). The conidial shape of both *C. laticiphilum* isolates on *Anthriscus* stem is not fusiform, but cylindrical with one end round and one end only slightly acute. Therer are three specimens in K(M) identified by Petch as belonging to *Gm. alborubrum*, but none can be type material as they were all collected after publication of the name.

Bearing in mind that definite type material of all three names is either missing or fragmentary and that none of the authentic material would be likely to yield good sequences, we think that it is more practical to publish a new taxon rather than to epitypify or neotypify one of the earlier names with a specimen that we are not confident is conspecific with the type.

Colletotrichum laticiphilum is separated from other species by its TUB2, GAPDH and CHS-1 sequences, and most differentially with TUB2. With CHS-1 there is only one bp difference from *C. indonesiense*, while the HIS3 sequence is the same as that of that species. The closest match with the GAPDH sequence (with 99 % identity, 1 bp difference) was HQ846719 from an unnamed plant, probably from India (P. Chowdappa, C.S. Chethana, S. Madhura, unpubl. data). The ITS sequence of strain CBS 112989 matches 100 % with AB042306 and AB042307 from isolates from *Carthamus* and *Glebionis* from Japan (J. Moriwaki, T. Tsukiboshi, T. Sato, S. Uematsu, unpubl. data), with AJ749675 from isolate PD85/694 (= CBS 126519, *C. chrysanthemi*), and with AB219024 from strawberry in Japan (Chung *et al.* 2006).

Colletotrichum limetticola (R.E. Clausen) Damm, P.F. Cannon & Crous, **comb. nov.** MycoBank MB455483. Fig. 17.
Basionym: *Gloeosporium limetticola* [as *Gm. limetticolum*] R.E. Clausen, Phytopathology 2: 231. 1912.

Sexual morph not observed. *Asexual morph on leaf of Citrus aurantifolia* (BPI 394978). *Conidiomata* conidiophores formed on a cushion of pale brown angular cells 3–6 µm diam. *Setae* not observed. *Conidiophores* hyaline, smooth-walled, septate and branched, up to 75 µm. *Conidiogenous cells* hyaline, smooth-walled, cylindrical, sometimes slightly inflated, 10–18 × 2.5–4 µm, opening 1–1.5 µm diam, collarette 0.5–1 µm long, periclinal thickening visible, sometimes distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, sometimes slightly flexuous, cylindrical with one end round and one end slightly acute to truncate, or both ends slightly acute, (10–)12.5–17.5(–20) × (3.5–)4–4.5(–4.5) µm, mean ± SD = 15.1 ± 2.4 × 4.1 ± 0.3 µm, L/W ratio = 3.7. *Appressoria* few observed on specimen, pale to medium brown, smooth-walled, subglobose, ovoid to ellipsoidal outline, entire edge.

Asexual morph on SNA (CBS 114.14). *Vegetative hyphae* 1–8.5 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* not developed, conidiophores formed directly on hyphae. *Setae* not observed. *Conidiophores* hyaline, smooth-walled, simple or septate and branched, up to 45 µm. *Conidiogenous cells* hyaline, smooth-walled, cylindrical to ampulliform, sometimes integrated (not separated from fertile hyphae by a septum, polyphialides rarely observed, 8.5–20 × 3–5.5 µm, opening 1–1.5 µm diam, collarette 0.5–1 µm long, periclinal thickening visible, sometimes distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, sometimes slightly curved, cylindrical to clavate with one end round and one end slightly acute to truncate, or both ends slightly acute, sometimes slightly constricted in the middle, (9–)12–20.5(–29) × (3–)4–5(–6) µm, mean ± SD = 16.3 ± 4.2 × 4.5 ± 0.6 µm, L/W ratio = 3.6. *Appressoria* single or in loose groups, pale to medium brown, smooth-walled, subglobose, ovoid to ellipsoidal outline, entire or undulate edge (5–)6–8.5(–11) × (4–)4.5–6(–7) µm, mean ± SD = 7.4 ± 1.3 × 5.3 ± 0.7 µm, L/W ratio = 1.4.

Asexual morph on Anthriscus stem (CBS 114.14). *Conidiomata* conidiophores formed directly on hyphae or on a cushion of pale brown angular cells 3.5–6.5 µm diam. *Setae* not observed. *Conidiophores* hyaline, smooth-walled, septate, branched, to 80 µm long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical slightly inflated, 6–13 × 2.5–4.5 µm, opening 1–1.5 µm diam, collarette 0.5–1 µm long, periclinal thickening visible. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical, clavate, cylindrical to fusiform with one end round and one end (often only

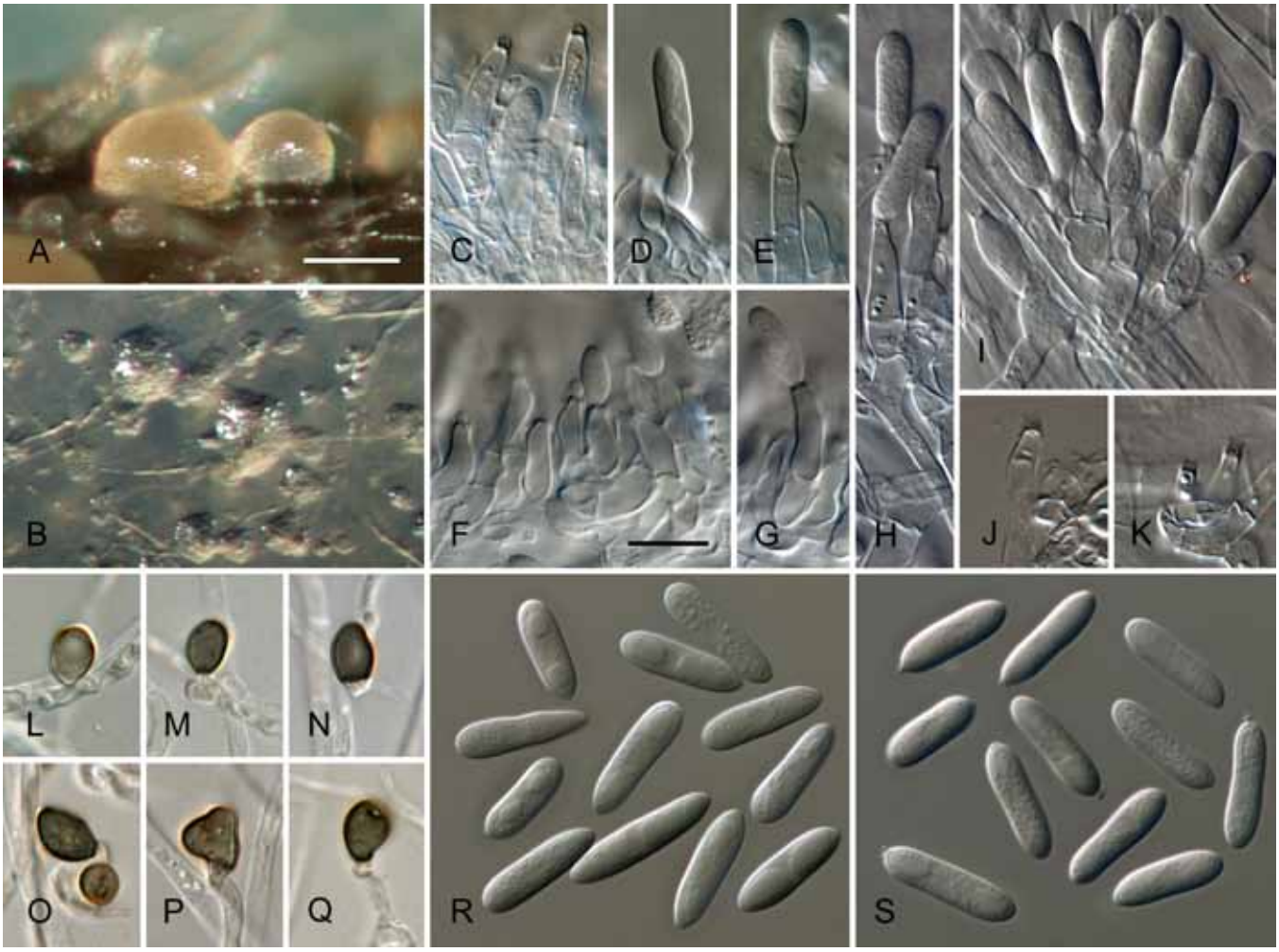

Fig. 17. *Colletotrichum limetticola* (from ex-epitype strain CBS 114.14). A–B. Conidiomata. C–K. Conidiophores. L–Q. Appressoria. R–S. Conidia. A, C–G, R. from *Anthriscus* stem. B, H–Q, S. from SNA. A–B. DM, C–S. DIC, Scale bars: A = 100 µm, F = 10 µm. Scale bar of A applies to A–B. Scale bar of F applies to C–S.

slightly) acute or both ends acute, (12–)13–18(–24) × (3.5–)4–4.5(–5.5) µm, mean ± SD = 15.5 ± 2.3 × 4.3 ± 0.4 µm, L/W ratio = 3.6.

Culture characteristics: Colonies on SNA flat to low convex with entire margin, hyaline, filter paper partly pale salmon to straw, partly covered with felty white aerial mycelium, reverse hyaline to pale ochreous, filter paper partly straw; 18.5–20 mm in 7 d (26–30.5 mm in 10 d). Colonies on OA flat with entire margin; surface moist, white to pale luteous, saffron towards the centre due to sporulation, aerial mycelium lacking, reverse whitish, buff to rosy buff, 18–21.5 mm in 7 d (26–29 mm in 10 d). *Conidia in mass* salmon.

Material examined: **Cuba**, Herradura, inoculation experiment XV in Berkeley, Alameda Co., California, from twig of *Citrus medica* var. *acida* (= *Citrus aurantifolia*), unknown collection date, (inoculated 30 Jan. 1912, photographed 20 Mar. 1912 by R.E. Clausen), Earle (UC 302386 **lectotype** [not seen], BPI 394978 **isolectotype**). **USA**, Florida, from young twig of *Citrus aurantifolia*, collection date and collector unknown (deposited in CBS collection Feb. 1914 by R.E. Clausen as *Gloeosporium limetticola*), (CBS H-20910 **epitype**, here designated, culture ex-epitype CBS 114.14).

Notes: *Gloeosporium limetticola* was described by Clausen (1912) following pathogenicity trials in California on young sour lime (*Citrus medica* var. *acida* = *Citrus aurantifolia*, Key lime) trees inoculated with strains from sour lime from Cuba and with strains from orange, lemon, pomelo and tangerine from Cuba, California, and Florida. The Cuban sour lime strain from Herradura consistently caused wither tip disease symptoms on tester plants from that species, and another Cuban strain (from Santiago de las Vegas) caused broadly similar symptoms on both sour lime and lemon (*Citrus limon*) trees. Clausen stated that a virulent form of wither tip occurred in Florida also, but this author was unable to access diseased material to compare with the Cuban pathogen.

Type material of *Gm. limetticola* was deposited by Clausen in the dried fungus collections at the University of California (UC) and Washington DC (BPI). However, its identity (in particular its local geographical origin, i.e. from Herradura or Santiago de las Vegas) was not specified in the original paper. The species was described [translated from the Latin] as occurring "in young leaves and stems of *Citrus medica* var. *acida*, acting as a pathogen naturally in Cuba, and also artificially inoculated in greenhouses in California on leaves and stems of *C. medica* var. *acida*, *C. limetta* and *C. limon*)".

The relevant accession at UC consists of a single packet (UC 302386) containing three further packets. One is from Clausen's Experiment XV and is marked "lime type"; another is from lemon (Experiment XXVII) and Cuban lime material (presumably the original diseased sample) and is marked "type material". The lemon sample is definitely from a genetic source different from that of the lime collections, and, it was not marked as type material. The two lime samples may well be genetically identical and could be regarded collectively as the holotype, but on balance we feel that treating them as two syntypes is more reasonable. That conclusion was also reached by Tavares *et al.* (1997), who designated the collection from Experiment XV in UC as lectotype of *Gm. limetticola*.

Cultures from the type material have not been preserved. However, strain CBS 114.14 from Florida was deposited in the CBS collection in Feb. 1914 by R.E. Clausen, as *Gm. limetticola*. The strain was not specified as being an ex-type strain, and we suppose that it was one of the samples requested by Clausen from wither tip of lime in Florida. It is reasonable to consider the culture as authentic material, and we therefore designate a dried subculture as epitype for *Gm. limetticola*.

The wither tip disease of *Citrus aurantifolia* is apparently identical with Key lime anthracnose (KLA), a specific disease of leaves, twigs, flowers and fruits of Key lime (*Citrus aurantifolia*) and has been well studied in recent years (Brown *et al*. 1996, Agostini *et al.* 1992, Timmer & Brown 2000, Peres *et al*. 2008, MacKenzie *et al.* 2009). While the causal organism of KLA was identified as *C. gloeosporioides* by Agostini *et al.* (1992), following von Arx (1957) who listed the fungus as a synonym of that taxon, Brown *et al*. (1996) assigned the fungus to *C. acutatum* based on ITS sequence data. According to Farr & Rossman (2012), *Gm. limetticola* has been reported from *Citrus aurantifolia* in Barbados, California, Cuba, Fiji, Florida, Hawaii, India, Jamaica, Philippines and Tanzania.

Colletotrichum strains from anthracnose on leaves of Key lime in Florida, USA (KLA-Anderson, HM-1, Ss) and MTR-KLA-A1 (Belize) included in the study of Peres *et al.* (2008) and MacKenzie *et al.* (2009) have the same ITS and GAPDH sequences as strain CBS 114.14. Additionally, the ITS sequences of isolates DPI from *Citrus aurantifolia* in Florida, USA (FN566877, Ramos *et al.* 2006) and c2 from *Citrus* sp. in Brazil (EU008878, Giaretta *et al.* 2010) match that of CBS 144.14 with 100 % identity. Probable *C. limetticola* strains are also included in Guerber *et al.* (2003) as mtDNA RFLP haplotype J3; the GAPDH sequences of two Key lime strains (MD33, MD15) are almost identical to that of CBS 114.14. The closest match with the TUB2 sequence of strain CBS 114.14 with 100 % identity is GenBank accession FN611029 from isolate DPI as well (Ramos *et al.* 2006). In their study on *Citrus* in Portugal, Ramos *et al.* (2006) did not find any *C. acutatum s. lat.*; *C. gloeosporioides* (*s. lat.*) seems to be the major anthracnose pathogen.

According to MacKenzie *et al.* (2009), Key lime isolates differ significantly from isolates from flowers of postbloom fruit drop (PFD) affecting sweet orange (*Citrus sinensis*) in Florida, USA (STF-FTP-10, OCO-ARC-4, ALB-IND-25). The differences are found in their ITS, GAPDH and GS sequences. Based on ITS and GAPDH sequences of 69 PFD and KLA strains from different countries (Belize, Brazil, Costa Rica, Dominican Republic, USA (Florida), Mexico), Peres *et al.* (2008) recognised the causal agents of the two citrus diseases as two distinct phylogenetic lineages of *C. acutatum* with few or no sequence differences in both the ITS and GAPDH genes. We did not include PFD isolates in our study, but according to ITS and GAPDH sequences, PFD and KLA strains are related to each other, but seem to belong to different species. Agostini *et al.* (1992) noticed morphological and cultural differences between PFD and KLA isolates: appressoria of PFD isolates were clavate and deeply pigmented and those of KLA isolates round, smaller and less pigmented. Also, KLA strains grew slightly more slowly than PFD isolates.

Pathogenicity tests by MacKenzie *et al.* (2009) had basically the same results as those by Clausen (1912); only *Colletotrichum* isolates from key lime caused leaf necrosis on key lime, while isolates from PFD, strawberry (= *C. nymphaeae*, according to this study), blueberry (= *C. fioriniae*, according to this study) and leatherleaf fern did not. Key lime isolates caused necrosis of flowers on Orlando tangelo flower clusters as well, but the percentage of affected flowers was lower than those inoculated with PFD isolates. Chen *et al.* (2005) identified a gene (*KLAP1* gene) that was required for causing KLA, particularly for the infection of Key lime leaves, but not for the infection of flower petals.

Colletotrichum limetticola is distinguished from other species by TUB2, GAPDH and HIS3, most effectively with TUB2, which is only 2 bp different from the sequence seen in CBS 129823 (*Colletotrichum* sp. from *Passiflora* in Colombia, occupying an unnamed subclade within Clade 1).

Colletotrichum lupini (Bondar) Damm, P.F. Cannon & Crous, **comb. nov.** MycoBank MB800519. Fig. 18.

Basionym: *Gloeosporium lupini* [as *Gm. lupinus*] Bondar, Boln Agric., São Paulo 13: 427. 1912.

≡ *Colletotrichum lupini* (Bondar) Nirenberg, Feiler & Hagedorn, Mycologia 94(2): 309. 2002, *nom. inval.* (Art. 33.3).

≡ *Colletotrichum lupini* var. *setosum* Nirenberg, Feiler & Hagedorn, Mycologia 94(2): 309. 2002, *nom. inval.* (Art. 43.1).

Sexual morph not observed. *Asexual morph on SNA. Vegetative hyphae* 1–6.5 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* absent, conidiophores formed directly on hyphae on the surface of the medium and in the aerial mycelium. *Setae* not observed. *Conidiophores* hyaline, smooth-walled, simple or septate and branched, rapidly degenerating. *Conidiogenous cells* hyaline, smooth-walled, cylindrical, 2.5–20 × 1.5–2.5 µm, often integrated (not separated from fertile hyphae by a septum), opening 0.5 µm diam, collarette 0.5 µm long, periclinal thickening visible. *Conidia* hyaline, smooth-walled, aseptate, straight, rather variable in shape, usually cylindrical to clavate with one end round and one end acute, 9–15(–26.5) × (3–)3.5–4.5(–6) µm, mean ± SD = 12.0 ± 3.2 × 4.1 ± 0.6 µm, L/W ratio = 2.9, conidia of strain CBS 109221 are slightly larger, measuring 11.5–15.5(–19) × (3.5–)4–4.5(–5) µm, mean ± SD = 13.5 ± 1.9 × 4.3 ± 0.4 µm, L/W ratio = 3.2. *Appressoria* single or in small dense clusters, medium brown, round to elliptical in outline with an undulate to lobate margin, (4–)6–12(–20.5) × (4.5–)6–9(–11.5) µm, mean ± SD = 9.0 ± 2.8 × 7.4 ± 1.7 µm, L/W ratio = 1.2. Appressoria of strain CBS 109221 differ in being arranged singly or in rows along hyphae and mostly having an entire margin (rarely undulate to lobate).

Asexual morph on Anthriscus stem. Conidiomata acervular, conidiophores formed on a cushion of pale brown angular cells 3–6.5 µm diam. *Setae* not observed in the ex-neotype strain, but in strain CBS 109221 where a few setae were observed. *Conidiophores* hyaline to pale brown, smooth-walled, septate, branched, to 30 µm long. *Conidiogenous cells* hyaline to pale brown, smooth-walled, cylindrical, sometimes ± inflated, 7–15 × 2.5–3.5 µm, opening 1–1.5 µm diam, collarette 0.5 µm long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical to clavate with one end round and one end acute, (10–)12.5–16(–18.5) × (3–)3.5–4.5 µm, mean ± SD = 14.2 ± 1.7 × 4.0 ± 0.3 µm, L/W ratio = 3.6.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline, on filter paper and on *Anthriscus* stem partly covered with short white to pale grey aerial mycelium, reverse of filter paper white to pale luteous; growth 15–21 mm in 7 d (25–31 mm in 10 d). Colonies on OA flat with entire margin; surface covered with felty to woolly white to pale olivaceous grey aerial mycelium, reverse buff to smoke grey; growth 15–19 mm in 7 d (24–27 mm in 10 d), strain CBS 466.76 grows faster 23.5–27.5 mm in 7 d (36–37.5 mm in 10 d). *Conidia in mass* salmon.

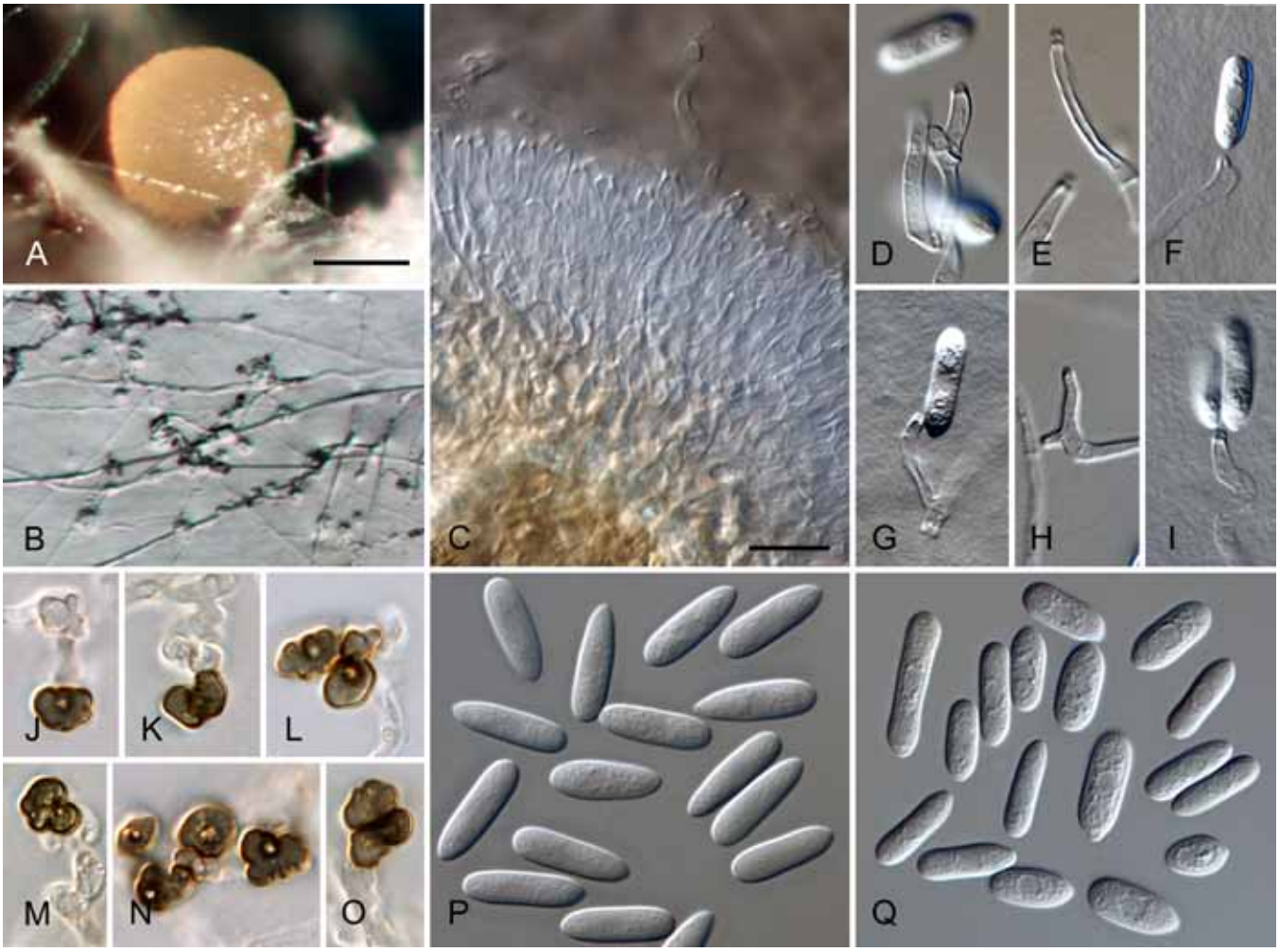

Fig. 18. *Colletotrichum lupini* (from ex-neotype strain CBS 109225). A–B. Conidiomata. C–I. Conidiophores. J–O. Appressoria. P–Q. Conidia. A, C, P. from *Anthriscus* stem. B, D–O, Q. from SNA. A–B. Dissecting microscope (DM), C–Q. Differential interference contrast illumination (DIC), Scale bars: A = 100 µm, C = 10 µm. Scale bar of A applies to A–B. Scale bar of C applies to C–Q.

Material examined: **Ukraine**, from seed of *Lupinus albus*, unknown date, H.I. Nirenberg, culture **ex-neotype** of *C. lupini*, CBS 109225 = BBA 70884. **Germany**, from *Lupinus albus*, unknown date, U. Feiler, culture **ex-holotype** of *C. lupini* var. *setosum*, CBS 109221 = BBA 70352.

Notes: Two studies on the causal agent of lupin anthracnose published in 2002 arrived at different results: while Talhinhas *et al.* (2002) regarded the causal agent of lupin anthracnose as *C. acutatum*, Nirenberg *et al.* (2002) concluded that the causal isolates belonged to a separate species, *C. lupini.* Nirenberg and her colleagues based this new name on *Gloeosporium lupini* (Bondar 1912), but their combination is invalid because the basionym was not cited correctly according to the ICBN. We therefore validate the combination here. Nirenberg *et al.* (2002) designated a dried culture derived from BBA 70884 (= CBS 109225) as a neotype of *Gm. lupini,* since no type material was designated by Bondar (1912); this action is nomenclaturally correct.

Nirenberg *et al.* (2002) additionally described a variety of the lupin pathogen, *C. lupini* var. *setosum*. They noted few morphological and physiological differences between the two varieties: strains of var. *lupini* were observed to produce more conidia than var. *setosum* in the aerial mycelium, as well as to grow slightly slower on PDA and to have a lower optimum growth temperature. In addition, var. *lupini* isolates usually formed concentric growth rings in culture, while var. *setosum* did not. The authors rarely observed setae in var. *lupini*, but these were regularly seen in var. *setosum*. In our study, the ex-holotype strain of *C. lupini* var. *setosum* formed a few setae. Nirenberg and colleagues indicated that the ITS sequences of the two varieties differ in only one base. Our study, based on analysis of six genes, showed few other bp differences, blurring the distinction between the two varieties. The name *C. lupini* var. *setosum* was also invalidly published (Art. 43.1). As the species name *C. lupini* was invalid itself at the time, and as we do not accept the variety as a distinct taxon, we do not validate the name here.

According to Nirenberg *et al.* (2002), a typical feature of *C. lupini* is the conidial morphology, with spores having one end pointed and one rounded. We also observed this feature clearly when the fungus was growing on *Anthriscus* stem. However, the conidia of the ex-neotype strain observed in this study on SNA are from simple or branched conidiophores at the agar surface and from the aerial mycelium rather than from conidiomata, because the strain no longer produces defined acervuli on this medium. Conidia from aerial mycelium are ± cylindrical, sometimes with both ends rounded. They are very variable in size (Nirenberg *et al.* 2002).

Colletotrichum lupini was originally described from *Lupinus albus* in the São Paulo region of Brazil, presumably introduced to South America along with its host plant, which is native to the Mediterranean region (Kurlovich 2002). The only isolates from South and Central America (Bolivia and Costa Rica) included in our study have sequences identical to that of the ex-neotype strain of *C. lupini*. The same is true for the strains studied from Europe and elsewhere. The species now appears to have no restriction to particular continents or climatic zones.

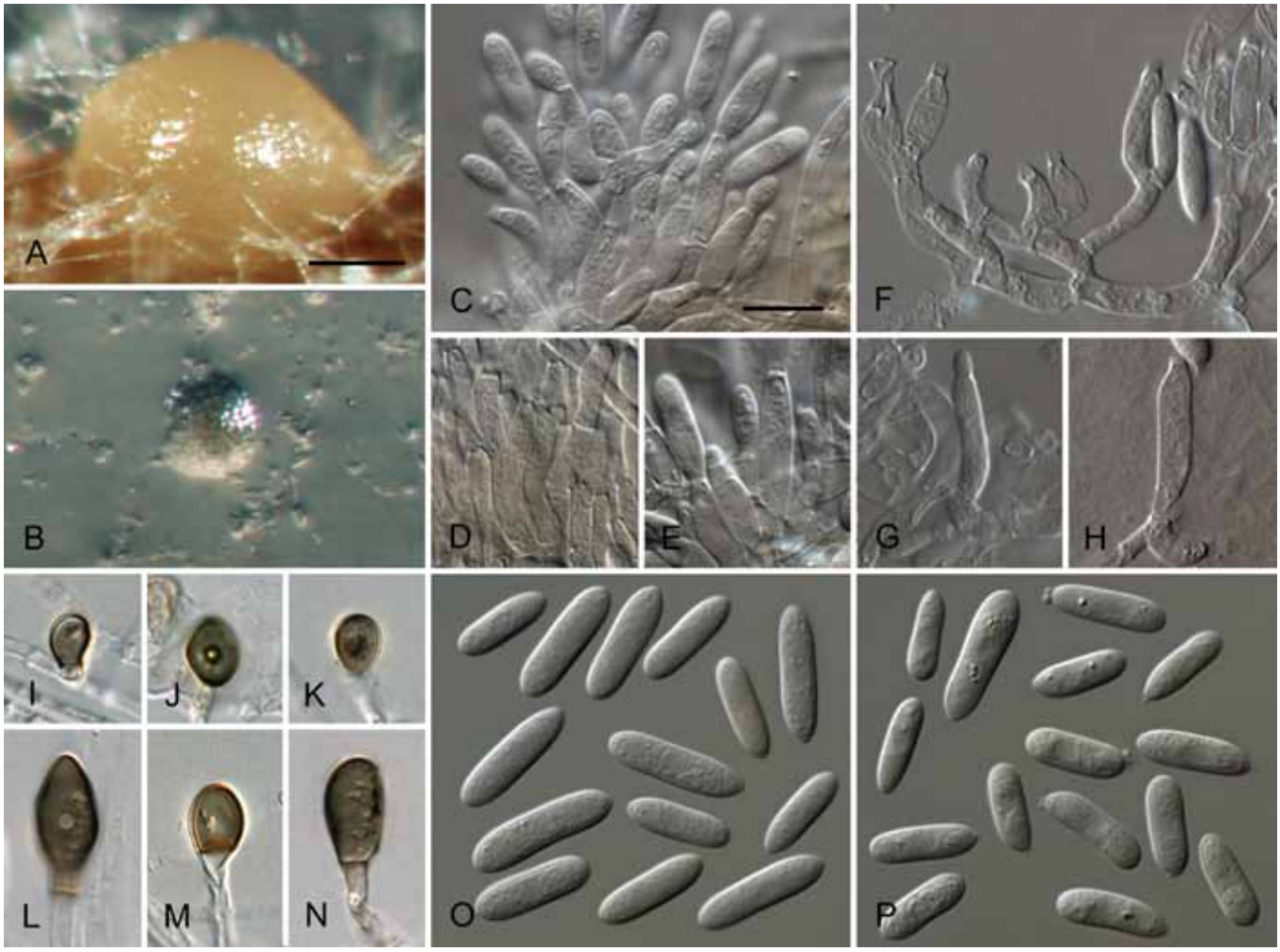

Fig. 19. *Colletotrichum melonis* (from ex-holotype strain CBS 159.84). A–B. Conidiomata. C–H. Conidiophores. I–N. Appressoria. O–P. Conidia. A, C–E, O. from *Anthriscus* stem. B, F–N, P. from SNA. A–B. DM, C–P. DIC, Scale bars: A = 100 µm, C = 10 µm. Scale bar of A applies to A–B. Scale bar of C applies to C–P.

Colletotrichum lupini is an economically significant pathogen of lupin crops worldwide, and there is substantial interest in breeding resistant host cultivars (*e.g.* Adhikari *et al*. 2011). While *C. lupini* shows a clear host preference based on the strains we have examined, a few cultures were derived from hosts other than lupins, namely from *Manihot*, *Camellia* and *Cinnamomum*. Sreenivasaprasad & Talhinhas (2005) also listed *Urtica dioica* as a host. A study by Nirenberg & Gerlach (2000) showed that a strain of *C. lupini* var. *setosum* was able to infect *Bergenia* in greenhouse tests. Pathogenicity tests by Sreenivasaprasad & Talhinhas (2005) also failed to show host specificity of *C. acutatum* strains from lupins (= *C. lupini*), though Lardner *et al*. (1999) found that the strains they placed in *C. acutatum* Group D (now known to belong to *C. lupini*) did not infect pine seedlings in the manner of *C. acutatum f.* sp. *pineum* (now regarded as *C. acutatum s. str.*). The strain from *Camellia* in the UK (IMI 351261) was deposited 1992 in IMI by R. Cook and is most likely one of the avirulent *C. acutatum* strains reported from ornamental *Camellia* species by Dickens and Cook (1989).

Our phylogeny clearly supports *C. lupini* as a distinct species within the *C. acutatum* species complex. *Colletotrichum lupini* is separated from other species by all genes included, except for ACT, with TUB2 providing the best differential test.

Colletotrichum melonis Damm, P.F. Cannon & Crous, **sp. nov.** MycoBank MB800506. Fig. 19.

Etymology: Named after host plant, *Cucumis melo.*

Sexual morph not observed. *Asexual morph on SNA. Vegetative hyphae* 1–6.5 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* not developed, conidiophores formed directly from vegetative hyphae. *Setae* not observed. *Conidiophores* hyaline, smooth-walled, septate, branched, degenerating rapidly. *Conidiogenous cells* hyaline, smooth-walled, cylindrical to ampulliform, 7–19 × 2.5–4 µm, opening 1–1.5 µm diam, collarette 1–1.5 µm long, periclinal thickening visible. *Conidia* hyaline, smooth-walled, aseptate, straight, some slightly curved, cylindrical with one end round and one end slightly acute to round, rarely both ends acute, (7–)9–16.5(–23.5) × (3–)3.5–4.5(–5) µm, mean ± SD = 12.8 ± 3.6 × 3.9 ± 0.4 µm, L/W ratio = 3.3 µm, L/W ratio = 3.7. *Appressoria* formed singly, medium brown, smooth-walled, subglobose, elliptical or clavate, the edge entire, rarely slightly undulate, (4.5–)6–11(–13.5) × (3.5–)4.5–6.5(–7.5) µm, mean ± SD = 8.3 ± 2.4 × 5.5 ± 1.0 µm, L/W ratio = 1.5.

Asexual morph on Anthriscus stem. Conidiomata acervular, conidiophores formed on pale brown angular basal cells, 3–7 µm diam. *Setae* not observed. *Conidiophores* hyaline to pale brown, smooth-walled, septate, branched, to 50 µm long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical to ampulliform, sometimes

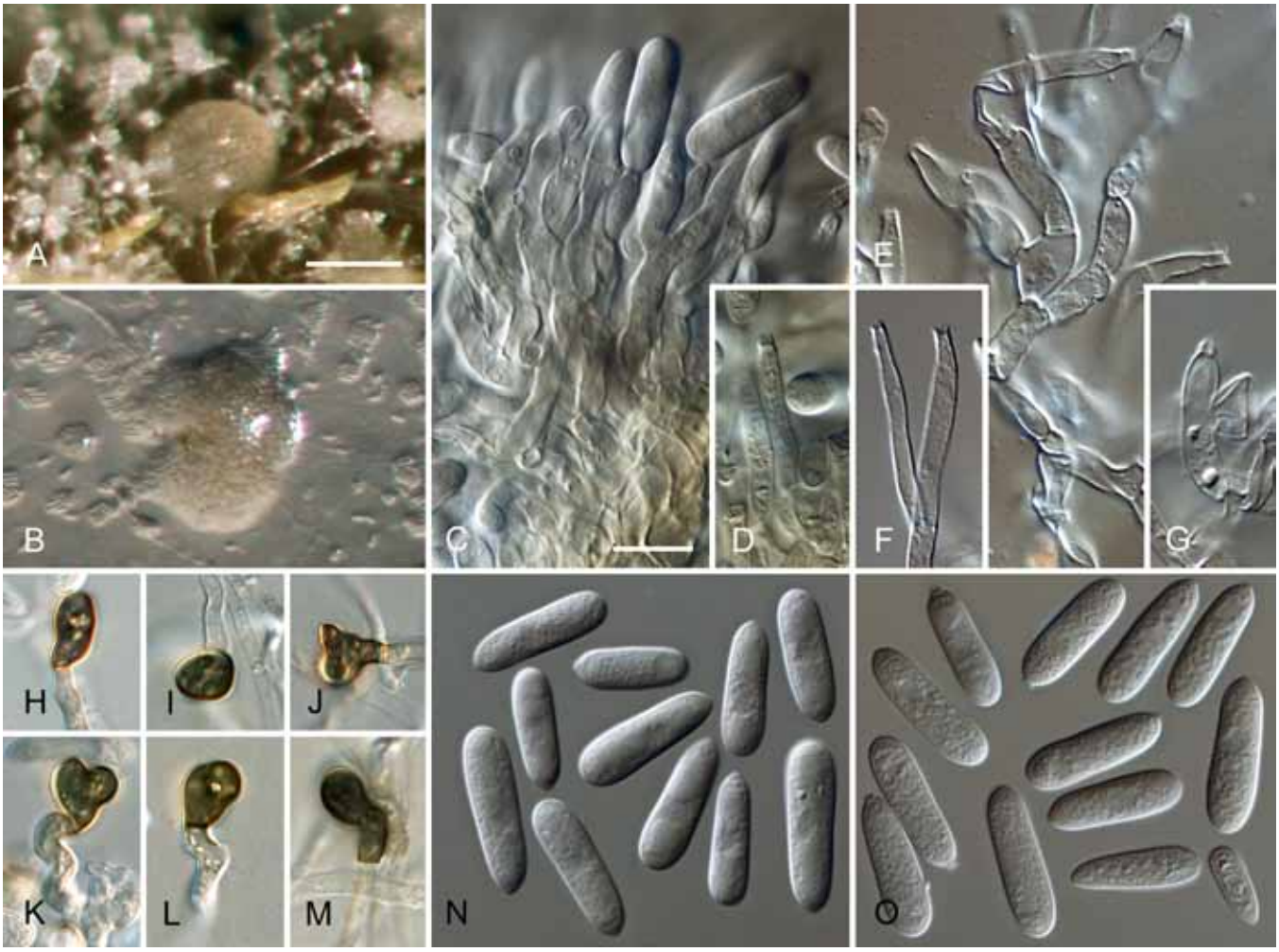

Fig. 20. *Colletotrichum nymphaea* (from ex-epitype strain CBS 515.78). A–B. Conidiomata. C–G. Conidiophores. H–M. Appressoria. N–O. Conidia. A, C–D, N. from *Anthriscus* stem. B, E–M, O. from SNA. A–B. DM, C–O. DIC, Scale bars: A = 100 µm, C = 10 µm. Scale bar of A applies to A–B. Scale bar of C applies to C–O.

polyphialidic, 10–20 × 3–4.5 µm, opening 1–2 µm diam, collarette 0.5–1(–1.5) µm long, periclinal thickening visible, sometimes distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical with one end round and one end slightly acute to round, (9–)12–17(–20) × (3.5–)4–4.5(–5) µm, mean ± SD = 14.5 ± 2.3 × 4.2 ± 0.3 µm, L/W ratio = 3.5.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline to pale honey, on filter paper and *Anthriscus* stem partly covered with floccose-felty white aerial mycelium, reverse same colours; growth 20.5–21.5 mm in 7 d (27.5–32 mm in 10 d). Colonies on OA flat with entire margin; surface buff, honey to saffron, partly covered with floccose-felty white aerial mycelium and saffron to isabelline acervuli, reverse buff, honey to rosy buff; growth 22–24 mm in 7 d (34–34.5 mm in 10 d). *Conidia in mass* saffron.

Material examined: **Brazil**, from peel of fruit of *Cucumis melo*, unknown collector and collection date (isolated by H.A. van der Aa, No. 9014 and deposited in CBS collection 1 Mar. 1984), (CBS H-20785 **holotype**, culture ex-type CBS 159.84).

Notes: *Colletotrichum melonis* belongs to clade 1 of the *C. acutatum* species complex but occupies a distinct subclade that is supported by multiple genes. The sole strain that we are aware of has appressoria with a significantly larger length/width ratio than those of *C. lupini* (mean L/W = 1.5 versus 1.2), the most frequently encountered species of clade 1. These appressoria form singly rather than in clusters.

The pathogenicity of *C. melonis* is not known. This appears to be the first report of a *Colletotrichum* species from the *C. acutatum* species complex as an associate of cucurbits. There are various reports of disease caused by members of the *C. boninense* and *C. gloeosporioides* clades, but the principal cucurbit pathogens appear to be *Glomerella magna* and *C. orbiculare* (von Arx & van der Velden 1961, Jenkins & Winstead 1964, Du *et al.* 2005, Hyde *et al.* 2009, Cannon *et al.* 2012, this issue).

Colletotrichum melonis is separated from other species by GAPDH, ACT and HIS3 sequences, with GAPDH performing best as a differential gene, while the TUB2 sequence is the same as that of strain IMI 384185 (unnamed strain in clade 1). Closest matches in blastn search with the GAPDH sequence of strain CBS 159.84 (with 97 % identity, 6 bp differences) were EU168905, EU647318 and EU647319 from sweet orange (Peres *et al.* 2008, MacKenzie *et al.* 2009), while the closest published matches with the TUB2 sequence (with 99 % identity, 4 bp differences) were FN611029 and FN611028 from *Citrus aurantifolia* and *Citrus sinensis* from USA, Florida (Ramos *et al.* 2006). The ITS sequence matched 100 % with EU008864–EU008866 from *Malus domestica* in Brazil (Giaretta *et al.* 2010).

Colletotrichum nymphaeae (Pass.) Aa, Netherlands J. Pl. Pathol., Supplement 1 84: 110. 1978. Fig. 20.
Basionym: *Ascochyta nymphaeae* Pass., in Rabenh., Fungi Europaei edn 2: 2251 (1876, in sched.); Hedwigia 16: 120. 1877.

= *Colletotrichum mahoniae* Fabric., Atti Imp. Regia Accad. Rovereto, ser. 3, 6: 139. 1950.

Sexual morph not observed. *Asexual morph on SNA. Vegetative hyphae* 1.5–5 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* absent, conidiophores formed directly on hyphae. *Setae* not observed. *Conidiophores* hyaline to pale brown, smooth-walled, septate and branched, to 60 µm long. *Conidiogenous cells* hyaline to pale brown, smooth-walled, cylindrical, 10.5–20 × 2–4 µm, opening 1 µm diam, collarette distinct, 1–1.5 µm long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical to cylindric-clavate with one end round and one end rounded to ± acute, (10–)14–18.5(–19.5) × (3–)4–5.5(–6) µm, mean ± SD = 16.1 ± 2.3 × 4.9 ± 0.7 µm, L/W ratio = 3.3. Strain CBS 526.77 has smaller conidia, measuring (8.5–)9–13(–16) × (3–)3–4.5(–5) µm, mean ± SD = 11.0 ± 2.0 × 3.8 ± 0.6 µm, L/W ratio = 2.9, while conidia of strain CBS 112202 differ in being cylindrical to fusiform with both ends acute. *Appressoria* single, medium brown, smooth-walled, elliptical, clavate or irregular in outline, entire, undulate to lobate margin, (4.5–)6–11(–15) × (3–)4.5–6.5(–8) µm, mean ± SD = 8.7 ± 2.5 × 5.5 ± 1.0 µm, L/W ratio = 1.6.

Asexual morph on Anthriscus stem. Conidiomata absent, conidiophores formed directly on hyphae. *Setae* not observed. *Conidiophores* hyaline to pale brown, smooth-walled, septate, branched, to 60 µm long. *Conidiogenous cells* hyaline to pale brown, smooth-walled, ± cylindrical, sometimes polyphialidic, 12–30 × 2.5–3.5 µm, opening 0.5 µm diam, collarette distinct, 0.5 µm long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical to cylindric-clavate with one end round and one end rounded to ± acute, (12.5–)14–18.5(–22.5) × (4–)4.5–5.5(–6) µm, mean ± SD = 16.3 ± 2.1 × 4.8 ± 0.5 µm, L/W ratio = 3.4. Strain CBS 526.77 has wider conidia, measuring (9.5–)13.5–19(–21.5) × (3.5–)5–6(–6.5) µm, mean ± SD = 16.1 ± 2.7 × 5.6 ± 0.7 µm, L/W ratio = 2.9, while conidia of strain 173.51 are smaller, measuring (7.5–)10–14.5(–16) × (3–)3.5–4.5 µm, mean ± SD = 12.3 ± 2.0 × 3.9 ± 0.4 µm, L/W ratio = 3.2, conidia of most of the isolates studied differ in shape from the ex-epitype strain, being cylindrical to fusiform with both ends acute, *e.g.* CBS 173.51 and CBS 112202.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline with low white aerial mycelium on filter paper and *Anthriscus* stem, on filter paper partly pale olivaceous grey on both sides; growth rate 16.5 mm in 7 d (20 mm in 10 d); some strains grow faster, *e.g.* CBS 126382 25–26 mm in 7 d (35–37 mm in 10 d). Colonies on OA flat with entire margin; surface isabelline, cinnamon to honey, white at the margin, aerial mycelium lacking, reverse greyish sepia to buff; growth rate 14.5 mm in 7 d (20 mm in 10 d); some other strains grow faster, *e.g.* CBS 126382 23.5–29 mm in 7 d (37.5–40 mm in 10 d). Colony surface of strains CBS 516.78 and CBS 526.77 is dark olivaceous to iron-grey. *Conidia in mass* pale salmon.

Material examined: **Italy**, Parma, in horto botanico, from leaf of *Nymphaea alba*, summer 1875, G. Passerini, in Rabenhorst, Fungi Europaei exsiccati edn 2: 2251 (holotype not selected by the original author and location uncertain; K(M) 176820 **isotype**, here designated as **lectotype**; K(M) 99741 isolectotype; CBS H-00769 isolectotype). **Netherlands**, Oude Waal near Nijmegen, Gem. Ubbergen, from leaf spots of *Nymphaea alba*, 7 Aug. 1978, G. van der Velde, (CBS H-20787 **epitype**, here designated, culture ex-epitype CBS 515.78 = van der Aa No. 6573); Kortenhoefse Plassen from leaf of *Nymphaea alba*, collection date and collector unknown (isolated Aug. 1977 by H.A. van der Aa), culture CBS 526.77; from curl disease of *Anemone coronaria* De Caen, collection date and collector unknown, CBS 126382 = PD 79/648. **Italy**, Rome, from leaf of *Mahonia aquifolium*, collection date and collector unknown (deposited in CBS collection Jun. 1951 by R. Ciferri), culture CBS 173.51; Rome, from *Fragaria* x *ananassa*, cv. Idea, collection date and collector unknown (send to Plantenziektenkundige Dienst Wageningen by L Corazza), culture CBS 126372 = PD 93/1666A. **South Africa** Western Cape, Stellenbosch, Elsenberg Farm, from *Protea magnifica*, 1 Apr. 2001, K. Lubbe, culture CBS 112992 = STE-U 4452. **Spain**, from fruit lesions of *Fragaria* sp., Mar. 2002, H.A. van der Aa, culture CBS 112202.

Notes: *Colletotrichum nymphaeae* was described in detail in morphological and pathological terms by van der Aa (1978). Its basionym *Ascochyta nymphaeae* was first validly published in 1876 in Rabenhorst's *Fungi Europaei* edn nova, exsiccatum no. 2251 (Stevenson 1971), and the label data was published in the journal *Hedwigia* in the following year. The name *A. nymphaeae* was ascribed to Passerini on the exsiccatum label as an unpublished herbarium name. Individuals of this exsiccatum can therefore be regarded as type material, but it is not clear where the holotype resides. We interpret individuals of *Fungi Europaei* no. 2251 as isotypes, and select one of the three examples in Kew, K(M) 176820 (labelled as purchased 1/1886) as lectotype of *A. nymphaeae*. We also designate an epitype with a living culture from the material studied by van der Aa.

Van der Aa (1978) investigated possible synonyms of *C. nymphaeae*, finding that *Ramularia nymphaeae* (syn. *Ovularia nymphaeae*) was conspecific with that species. *Gloeosporium nymphaearum* (Allescher 1895) is the type of the genus *Ovulariella* (considered as a *nom. nud*. by von Arx (1970) but with an indirect reference to a description in the original publication). Von Arx considered it to be a later synonym of *Ramularia nymphaeae*, and van der Aa (1978) confirmed the synonymy. To our knowledge, there are no living cultures derived from authentic material of either of these taxa. We have no reason to doubt van der Aa's synonymy, but we have not examined type material and there is no strong reason to designate epitypes.

We have examined a culture from *Mahonia aquifolia* from Italy, which was sent to CBS by R. Ciferri as *C. mahoniae* the year after the species had been described, and this could have been derived from the type of *C. mahoniae*, but we do not have enough information to be sure. Another species from *Mahonia*, *Gloeosporium japonicum* (Hemmi 1920), was described as having wider conidia (10–18 × 5–7 µm) with a different shape (ellipsoidal, short-cylindrical or ovoidal, both ends rounded). However, Hemmi mentioned that conidia in culture have very variable size and shape, measuring 9–20 × 3.6–6 µm in size. We have not located authentic material for this taxon, but even if it were conspecific with *C. nymphaeae* its name would not have priority. Von Arx (1957) considered *Gm. japonicum* to be a synonym of *C. gloeosporioides*.

Another possible synonym of *C. nymphaeae* is *C. nymphaeicola* (Kelkar 1972, as *C.* "*nymphicola*"). Judging from the description and illustration this is certainly a species of *Colletotrichum*, but the conidia were claimed to be oblong and to measure 5–15 × 1.5–3 µm. This wide variation in size makes it impossible to attempt a placement in any species as currently circumscribed. The type was reputedly deposited in HCIO but apparently no cultures were obtained. *Gloeosporium nymphaeae* (Hemmi & Kawase 1954) causes symptoms similar to those of *C. nymphaeae*, but setae were found to be present. These were not seen in *C. nymphaeae* either by ourselves or by van der Aa (1978). The conidia of *Gm. nymphaeae* were described as rounded at both ends, 9–17 × 3–6 µm. We have not been able to locate type material or living cultures of this fungus.

A further species of *Colletotrichum* associated with waterlilies, *C. nupharicola*, was described by Johnson *et al.* (1997). This species appears to have substantially longer and wider conidia

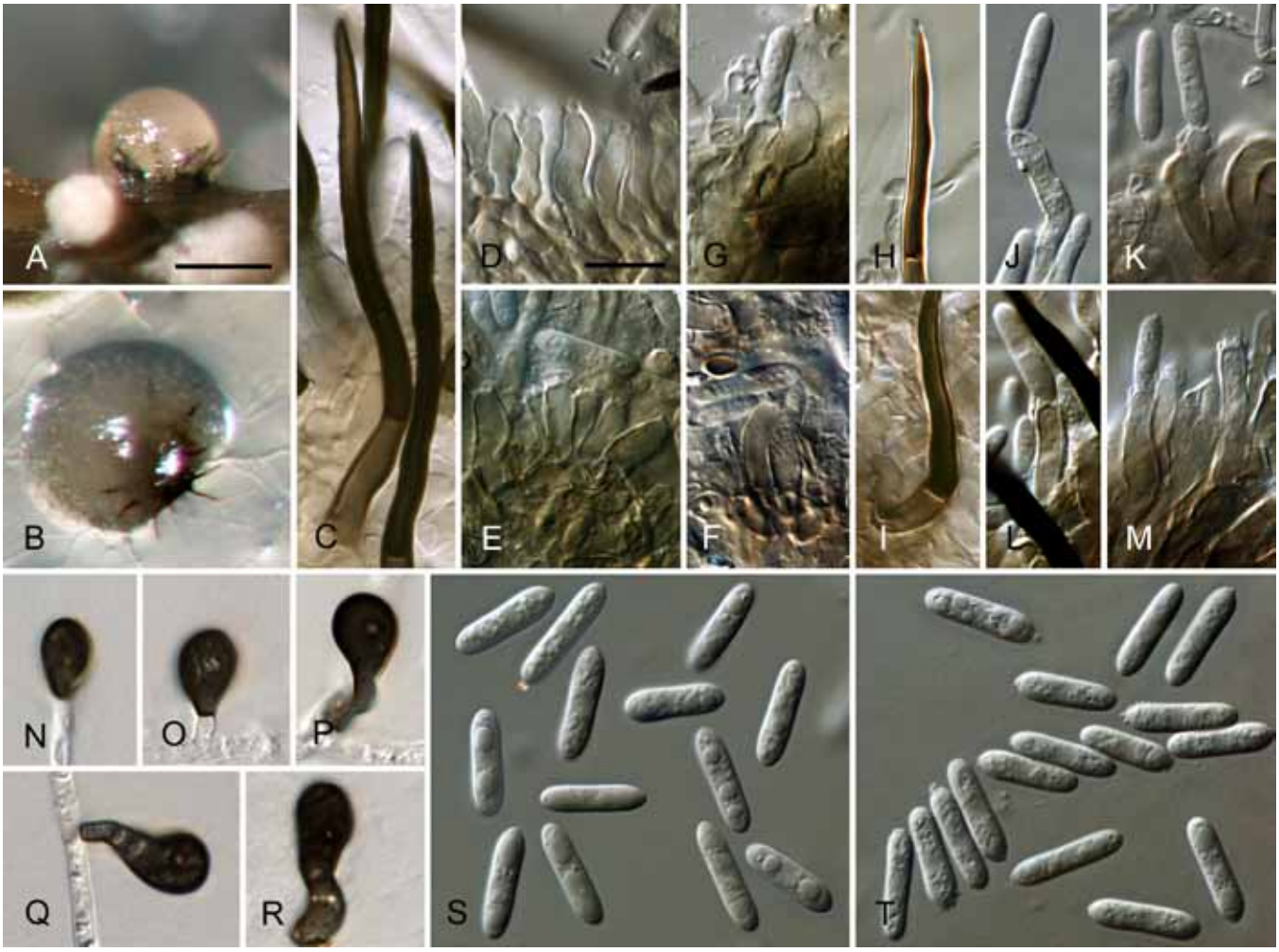

Fig. 21. *Colletotrichum orchidophilum* (A–M, S–T from ex-holotype strain CBS 632.80. N–R from IMI 305357). A–B. Conidiomata. C. Setae. D–F. Conidiophores. H. Tip of seta. I. Basis of seta. J–M. Conidiophores. N–R. Appressoria. S–T. Conidia. A, C–F, S. from *Anthriscus* stem. B, H–R, T. from SNA. A–B. DM, C–T. DIC, Scale bars: A = 100 µm, D = 10 µm. Scale bar of A applies to A–B. Scale bar of D applies to C–T.

than *C. nymphaeae* with mean widths of individual strains ranging between 6.5 and 7.5 µm (the figures are difficult to interpret and the overall range of conidial size in the discription surprising). It has been found to belong within the *C. gloeosporioides* complex (Weir *et al.* 2012, this issue).

In pathogenicity tests MacKenzie *et al.* (2009) showed that *Colletotrichum* isolates from petiole, fruit and crown of strawberry with anthracnose from Florida, USA (based on ITS and GAPDH: *C. nymphaeae*) caused anthracnose on strawberry fruits. Lesions were larger than those caused by isolates from blueberry (based on ITS and GAPDH: *C. fioriniae*). These differences in virulence should be attributed to the different species the pathogens belong to rather than to the different host plants; both species occur on strawberries, but based on the number of strains in this study, *C. nymphaeae* seems to be the more important strawberry anthracnose pathogen within the *C. acutatum* species complex.

Colletotrichum nymphaeae is well separated from other species with TUB2, but not in its ITS. With all other genes the intraspecific variability is very high. The closest matches (100 % identity) in a blastn search using the TUB2 sequence of the ex-epitype strain were AB618090 from *Apium* in Japan (Fujinaga *et al.* 2011); AY376551–AY376555 from *Protea* (Lubbe *et al.* 2004); AJ409296, AJ314716, AJ314718 from *Fragaria* in USA, Portugal and Australia; AJ314722, AJ409300, AJ748636 from *Lupinus* and *Anemone* (Talhinhas *et al.* 2002, 2005); and DQ454063, DQ454064 from *Fragaria* in Thailand (Than *et al.* 2008a). With 99 % identity reflecting 1 bp difference, the search yielded AJ748605, AJ748607, AJ748608, AJ748611, AJ748615 from olive; AM992148, AM992147 probably also from olive; AJ748633 from *Photinia* (Talhinhas *et al.* 2005, 2009); and GQ369612 from a strain identified as *C. caudatum* (Chen H, Feng Y and Hyde KD, unpubl. data). With 99 % identity reflecting 2 bp differences, we got EF593327 and EF593328 from strains ARSEF4360 and EMA26, respectively, from *Orthezia praelonga* in Brazil (Marcelino *et al.* 2008). These two strains were identified as *C. gloeosporioides f. sp. ortheziidae* and have entomopathogenic activity to the scale insect *Orthezia praelonga*. They are apparently being used effectively as a biological control agent against this insect in Brazil (Cesnik *et al*. 1996, Cesnik & Ferraz 2000). Several of these strains listed above are included in this study.

Colletotrichum orchidophilum Damm, P.F. Cannon & Crous, **sp. nov.** MycoBank MB800507. Fig. 21.

Etymology: Named for the host plants from which the species is known, all of which belong to the *Orchidaceae*.

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* not developed, conidiophores and setae formed directly on hyphae. *Setae* abundant, medium brown, basal cell often paler, smooth-

walled, 1–2-septate, 40–80 µm long, base cylindrical, 2–4.5 µm diam, tip somewhat acute. *Conidiophores* pale to medium brown, septate, branched, smooth-walled, to 60 µm long. *Conidiogenous cells* hyaline to medium brown, usually smooth-walled, but some warted conidiogenous cells observed, cylindrical with a slime sheath, 7–18 × 2.5–5 µm, opening 1–1.5 µm diam, collarette 0.5 µm long, periclinal thickening conspicuous. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical with one end round and one end somewhat acute, (10.5–)11.5–14(–16.5) × (2–)3–3.5(–4) µm, mean ± SD = 12.7 ± 1.1 × 3.1 ± 0.3 µm, L/W ratio = 4.1, conidia of strain CBS 631.80 are larger, measuring (13–)13.5–17.5(–19) × 2.5–3.5 µm, mean ± SD = 15.4 ± 2.1 × 3.0 ± 0.3 µm, L/W ratio = 5.1. *Appressoria* not observed in type, but present in strain IMI 305357, single or in periodic intervals along hyphae, dark brown, smooth-walled, elliptical, pyriform or spathulate, (5.5–)7.5–15.5(–20.5) × (4.5–)5.5–8.5(–12) µm, mean ± SD = 11.6 ± 3.9 × 7.0 ± 1.6 µm, L/W ratio = 1.6, appressoria of strain CBS 631.80 smaller, measuring (4.5–)5.5–11(–18) × (4–)4.5–6(–7) µm, mean ± SD = 8.2 ± 2.8 × 5.2 ± 0.8 µm, L/W ratio = 1.6. In SNA cultures of strains IMI 305357 and CBS 119291 no setae were observed.

Asexual morph on Anthriscus stem. Conidiomata acervular, conidiophores and setae formed directly on hyphae or on pale brown basal cells 3–6 µm diam. *Setae* abundant, dark brown, basal cell often paler, smooth-walled, 0–2-septate, 40–70 µm long, base cylindrical to conical, sometimes inflated, 3–6.5 µm wide, tip somewhat acute, setae of strain CBS 631.80 only up to 40 µm long, with a round tip or functioning as conidiogenous cells. *Conidiophores* pale brown, septate, branched, to 40 µm long. *Conidiogenous cells* hyaline to pale brown, smooth-walled, cylindrical, 7–16 × 3–5 µm, opening 1.5–2 µm diam, collarette 0.5–1 µm long, distinct, periclinal thickening conspicuous. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical with one end round and one end somewhat acute, (11.5–)12.5–14(–15.5) × (2.5–)3–3.5(–4) µm, mean ± SD = 13.2 ± 0.9 × 3.3 ± 0.3 µm, L/W ratio = 4.0.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline, aerial mycelium lacking, medium, filter paper and on *Anthriscus* stem partly covered with acervuli appearing as tiny black spots, which are also visible from the reverse side; growth rate 17.5–22.5 mm in 7 d (32.5–36 mm in 10 d). Colonies on OA flat with entire margin; surface olivaceous to grey olivaceous, covered with black or salmon acervuli, aerial mycelium lacking, reverse olivaceous to olivaceous grey; growth rate 18–26 mm in 7 d (30–37.5 mm in 10 d). *Conidia in mass* salmon. Colonies of isolate IMI 309357 differ in forming felty white to olivaceous buff or grey aerial mycelium on OA and *Anthriscus* stem.

Material examined: **USA**, Hawaii, Oahu, Manoa, from *Dendrobium* sp., unknown collection date and collector (deposited in CBS collection Oct. 1980 by M. Aragaki, isolated 1978 as No. 826), (CBS H-20718 **holotype**, culture ex-type CBS 632.80); Hawaii, Kona, from × *Ascocenda* sp., unknown collection date and collector (deposited in CBS collection Oct. 1980 by M. Aragaki, isolated 1978 as No. 828), culture CBS 631.80. **UK**, from *Phalaenopsis* sp., unknown collection date and collector, culture IMI 305357. **Panama**, APHIS interception Miami 223820, from *Cycnoches aureum*, collection date unknown (isolated 11 Apr. 2003 by M.E. Palm), D. Begley, culture CBS 119291 = MEP1545. **Germany**, Munich, glasshouses of Botanical Garden, on dead and dying leaves of *Eria javanica* (syn. *E. stellata*), April 1895, J.E. Weiss (M-0140831 **syntype** of *C. orchidearum* (named as forma *eriae*) and **lectotype** of *C. orchidearum*, here designated); Munich, glasshouses of Botanical Garden, on both sides of dying leaves of *Cymbidium aloifolium* (syn. *C. pendulum*), Apr. 1895, J.E. Weiss (M-0140830 **syntype** of *C. orchidearum* (named as *C. orchidearum* forma *cymbidii*)); Munich, glasshouses of Botanical Garden, on dead and dying leaves of *Stelis emarginata* (syn. *Physosiphon loddigesii*), April 1895, J.E. Weiss (M-0140832 **syntype** of *C. orchidearum* (named as forma *physosiphonis*)).

Notes: Diagnostic features for *C. orchidophilum* include its very narrow (usually 3–3.5 µm wide) cylindrical conidia, abundantly formed setae and dark brown, uniformly shaped, pyriform to spathulate appressoria. *Colletotrichum orchidophilum* is basal to the *C. acutatum* species complex (fig. 1 in Cannon *et al.* 2012, this issue) and therefore used as outgroup in the phylogeny of the *C. acutatum* complex (Fig. 1). The species is associated with a range of genera in the *Orchidaceae.* According to blastn searches with ITS sequences, *C. orchidophilum* has possibly also been found on other orchids and in other countries: on *Cycnoches aureum* in Panama (DQ286148, Farr *et al.* 2006), on *Pleione* sp. (AJ301980, Nirenberg *et al.* 2002) and as an endophyte of *Dendrobium nobile* in China (FJ042519, Yuan *et al.* 2009). As far as we can tell, *C. orchidophilum* is restricted to the *Orchidaceae*.

The description of *C. cinctum* provided by Stoneman (1898), with its narrow conidia and abundant setae, seems similar to that of the strains we have identified as *C. orchidophilum*, and her strain originated from the same habitat and geographical region as Berkeley & Curtis's fungus *Gloeosporium cinctum* (Berkeley 1874). Stoneman referred to the binomial *C. cinctum* but only in synonymy with the sexual morph *Gnomoniopsis cincta* (= *Glomerella cincta*), and it is therefore invalidly published. The connection between *Gloeosporium cinctum* and *Gnomoniopsis cincta* does seem to be doubtful; Stoneman referred to the *Colletotrichum* morph "found associated with a pycnidial stage and also a minute pyrenomycetous form". The former was not described (and is presumably a co-coloniser rather than genetically linked), and the latter was described as having spores measuring only 6–7 × 2–3 µm – much smaller than typical *Glomerella* ascospores. This contrasts with the *Gnomoniopsis* morph described by Stoneman from old cultures of the asexual morph, which had ascospores measuring 15–20 × 3 µm; we interpret this as the true sexual morph. We have not seen a sexual morph associated with *C. orchidophilum*, and we think it is more likely that Stoneman's fungus (and that of Berkeley & Curtis) belong to the *C. gloeosporioides* species complex.

Colletotrichum orchidophilum differs from *C. orchidearum* in forming much narrower conidia; those of the type of *C. orchidearum* forma *eriae* measure (13.5–)15.5–19.5 × 5–6 µm, mean ± SD = 17.2 ± 1.6 × 5.6 ± 0.3 µm, L/W ratio = 3.1, n = 20, and those of forma *physosiphonis* measure (14–)16–18.5 × 5–6 µm, mean ± SD = 17.2 ± 1.1 × 5.5 ± 0.3 µm, L/W ratio = 3.1, n = 20. *Colletotrichum orchidearum* was described by Allescher (1902) from three diseased orchid plants in the glasshouses of the Munich botanic garden. Each of the collections was given a separate name at forma rank, as listed above, and while no forma *orchidearum* was listed, that name automatically comes into existence on description of the other forms (Art. 26). The species account included a description of the overall taxon, and compared it with *C. macrosporum*, another species from orchids described by Saccardo (1896) from a Brazilian collection. That species was found by Saccardo to have substantially larger conidia than those of *C. orchidearum* (measurements of 28–32 × 8–10 µm were given), and its affinities are currently unknown. One of the forms introduced by Allescher, forma *cymbidii*, is invalidly published as no description was given.

There are three dried specimens in the Allescher collections in M, all gathered by Dr J.E. Weiss in April 1895, which clearly constitute type material; M-0140830 named as *C. orchidearum* forma *cymbidii* from *Cymbidium aloifolium* (syn. *C. pendulum*), M-0140831 named as forma *eriae* from *Eria javanica* (syn. *E. stellata*), and M-0140832 named as forma *physosiphonis* from

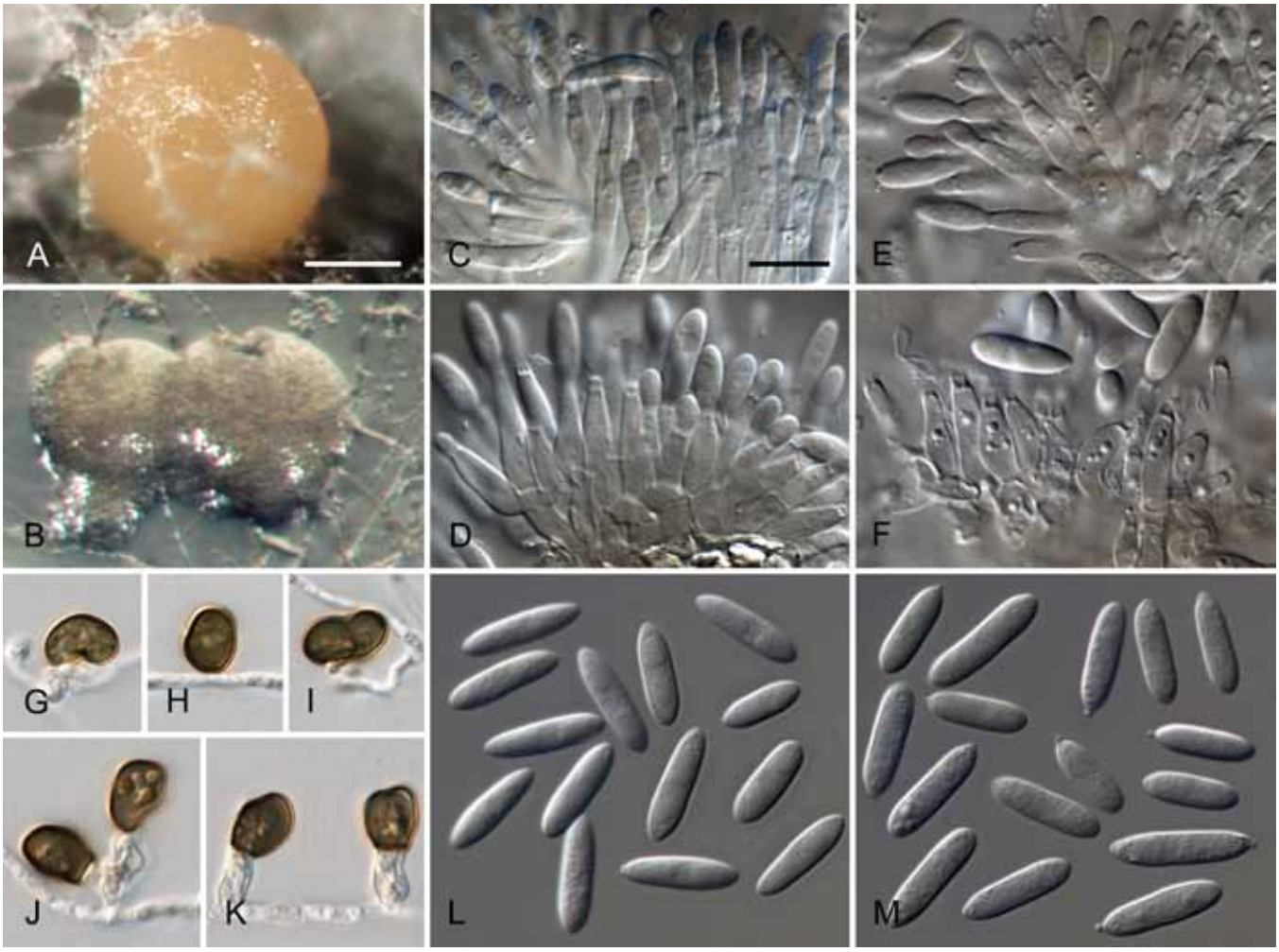

Fig. 22. *Colletotrichum paxtonii* (from ex-holotype strain IMI 165753). A–B. Conidiomata. C–F. Conidiophores. G–K. Appressoria. L–M. Conidia. A, C–D, L. from *Anthriscus* stem. B, E–K, M. from SNA. A–B. DM, C–M. DIC, Scale bars: A = 100 µm, C = 10 µm. Scale bar of A applies to A–B. Scale bar of C applies to C–M.

Stelis emarginata (syn. *Physosiphon loddigesii*). The collection on *Cymbidium* appears to be effete, and while a few of the conidiomata contained setae, no conidia or conidiogenous cells were seen. This may be why *C. orchidearum* forma *cymbidii* was not described in the original publication. It is necessary to designate one of these authentic collections as lectotype of *C. orchidearum* in order to fix the application of that name, and we therefore choose M-0140831 for this purpose as M-0140830 is effete and M-0140832 is rather depauperate. That has the effect that *C. orchidearum* forma *eriae* becomes an obligate synonym of *C. orchidearum* forma *orchidearum*. There are no significant morphological differences between the material from *Eria* and that from *Physosiphon*. The conidiomata of the invalid forma *cymbidii* are substantially larger than those of the two validly published forms, and the host plant material is strongly blackened in their immediate vicinity. We are unable to establish the significance of this distinction; it may be host- rather than fungus-related.

Yang *et al.* (2011) reviewed species of *Colletotrichum* from orchids in south-western China. They identified one clade as *C. orchidearum*, and their Chinese strain does seem to have close similarities with the type of that species. None of the species treated in Yang *et al.* (2011) belong to the *C. acutatum* complex.

Colletotrichum paxtonii Damm, P.F. Cannon & Crous, **sp. nov.** MycoBank MB800508. Fig. 22.

Etymology: Named after Sir Joseph Paxton, gardener to William Spencer Cavendish, 6th Duke of Devonshire, who first brought the Cavendish banana into cultivation.

Sexual morph not observed. *Asexual morph on SNA. Vegetative hyphae* 1–8 µm diam, hyaline to pale brown, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* not developed, 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, 5–10 × 2–4 µm, opening 1–1.5 µm diam, collarette 1–1.5 µm long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical with one end round and one end slightly acute both ends slightly acute, (5–)10.5–15.5(–19.5) × (2.5–)3.5–4(–4.5) µm, mean ± SD = 13.0 ± 2.6 × 3.7 ± 0.3 µm, L/W ratio = 3.5. *Appressoria* single or in loose groups, medium brown, smooth-walled, subglobose, elliptical or clavate, the edge undulate or entire, (5–)6–11.5(–16.5) × (3.5–)5.5–7.5(–8.5) µm, mean ± SD = 8.8 ± 2.7 × 6.5 ± 1.1 µm, L/W ratio = 1.4, strain CBS 502.97 forms smaller appressoria, measuring (3.5–)4.5–7.5(–10.5) × (3–)3.5–5(–5.5) µm, mean ± SD = 6.0 ± 1.7 × 4.2 ± 0.7 µm, L/W ratio = 1.4.

Asexual morph on Anthriscus stem. Conidiomata acervular, conidiophores formed on pale brown, angular, basal cells 3.5–7.5

µm diam. *Setae* not observed. *Conidiophores* hyaline to pale brown, smooth-walled, septate, branched, to 30 µm long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical, 7–19 × 2–3 µm, opening 1–1.5 µm diam, collarette 1–1.5 µm long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical to fusiform with both ends ± acute, sometimes one end round, (6.5–)12–15.5(–17) × (3–)3.5–4 µm, mean ± SD = 13.7 ± 1.8 × 3.8 ± 0.3 µm, L/W ratio = 3.6.

Culture characteristics: Colonies on SNA flat to raised with entire margin, hyaline, on filter paper partly pale olivaceous grey, on medium, filter paper and *Anthriscus* stem partly covered with thin, floccose white to pale olivaceous grey aerial mycelium and orange acervuli, reverse hyaline to pale cinnamon, filter paper partly pale olivaceous grey; 23–24.5 mm in 7 d (34–36.5 mm in 10 d). Colonies on OA flat with entire margin; surface covered with floccose rosy buff to pale olivaceous grey aerial mycelium and orange acervuli, reverse pale vinaceous, hazel, olivaceous grey to iron grey; growth rate 22.5–23 mm in 7 d (33.5–35.5 mm in 10 d). *Conidia in mass* orange.

Material examined: **St. Lucia**, from *Musa* sp., 1972, P. Griffee (IMI 165753 **holotype**, CBS H-20797 isotype, culture ex-type IMI 165753). **Unknown country (West Indies),** from *Musa nana*, unknown collection date (deposited in CBS collection Feb. 1997 by J.A. Bailey), P. Spencer-Phillips, CBS 502.97 = LARS 58 [sterile on receipt at CBS, judging from information in Sherriff *et al*. (1994) these two strains originate from the same isolate].

Notes: The most prominent species of *Colletotrichum* associated with *Musa* species is *C. musae*, a central species in one of the major clades of the *C. gloeosporioides* species complex (Weir *et al*. 2012, this issue). It was recently epitypified with a strain from Florida (Su *et al*. 2011). One of the strains (CBS 502.97 = LARS 58) that we have examined of *C. paxtonii* was first studied by Sherriff *et al.* (1994) using the misapplied name *C. musae*; however, Johnston & Jones (1997) confirmed that it was a member of the *C. acutatum* complex. *Colletotrichum paxtonii* does not appear to produce setae at all, while *C. musae* rarely does so, and this may have led to confusion between the two species in the past.

There are no records of *C. acutatum* (*s. lat.*) on *Musa* in Farr & Rossman (2012); however, some other species have been described on *Musa* spp. *Colletotrichum cavendishii* was described by Petrak (1925) with "elongated oblong, ellipsoid, oblong or ovate, almost cylindrical" conidia that measure 10–19 × 4.5–7 µm. This certainly suggests that Petrak's species belongs to the *C. acutatum* species complex and it could provide an earlier name for *C. paxtonii*, but its conidia are described as substantially wider than those of that the latter species - conidia in the *C. acutatum* species complex are rarely wider than 5 µm (Table 2). No cultures are available to allow evaluation of the synonymy.

Another species on banana was described by Sawada (1959), *C. liukiuensis*, on leaves of *Musa liukiuensis* in Taiwan. The conidia of this species are described as ellipsoid or oblong-ellipsoid with rounded ends, measuring 12–14 × 4.8–5.5 µm. The fungus forms dark brown 1–2-septate setae, which seem to be prominent, because they were included in the sketchy drawing (Pl. II: 30-31 of the publication) Sawada provided. This drawing showed a seta present as well as conidia with broadly rounded ends. Together with the width of the conidia, these characters exclude the name of this fungus from contention as an earlier synonym of *C. paxtonii.*

Additional species on *Musa* have been described in *Gloeosporium*. *Gloeosporium musarum* Cooke & Massee has elongate-ellipsoidal conidia with both ends rounded, measuring 12 × 4 µm. It was collected from ripe bananas in Brisbane, Australia (Cooke 1887). Apart from the rounded ends of the conidia, the fungus has features that tend to place it in the *C. acutatum* complex. *Glomerella musarum* was described from *Musa paradisiaca* in Sri Lanka and was observed to be associated with *Gm. musarum* and other fungi (Petch 1917). We could not locate the type material of either of these species to confirm their taxonomic positions. *Gloeosporium musarum* var. *importatum*, described in 1910 on fruits of *Musa sapinea* in Germany, has conidia larger than those of *C. paxtonii*, measuring 9–24 × 5–7 µm (Saccardo 1913). *Gloeosporium lagenaria* var. *musarum* was published without any morphological information; the paper merely stated that this fungus did not differ from the forms found on *Cucurbitaceae* (Ellis & Everhart 1889). The lack of description means that the name is invalidly published. *Gloeosporium lagenaria* var. *lagenaria* again has conidia larger than those of *C. paxtonii*, measuring 16–18 × 5–6 µm. It is widely believed to be a synonym of *C. orbiculare* (Cannon *et al.* 2012, this issue).

Colletotrichum paxtonii is separated from other species by TUB2 and GAPDH, with TUB2 performing best as a diagnostic sequence. With the GAPDH sequence there is only one bp difference from *C. sloanei*, while ACT, HIS3 and CHS-1 sequences are the same as *C. simmondsii.* The closest matches in a blastn search with the TUB2 sequence of strain IMI 165753 (with 99 % identity, 2 bp differences) were AJ748635 from isolate PD 89/582 (= CBS 126524, *C. simmondsii*) from *Cyclamen* in the Netherlands (Talhinhas *et al.* 2005), EU635505 from isolate DAR 32068 (as A9 from Whitelaw-Weckert *et al.* 2007) from *Fragaria* in Australia (Debode *et al.* 2009), EF143968 from isolate BRIP 4704a from *Fragaria* in Australia (Than *et al.* 2008a) and FJ907443 from isolate BRIP 28519 (ex-holotype culture of *C. simmondsii*) from *Carica papaya* in Australia (Prihastuti *et al.* 2009). With the GAPDH sequence of strain IMI 165753 there are no closer matches than 97 % identity covering ± the full of the length sequence. Since the ITS sequence of *C. paxtonii* strain IMI 165753 is the same as that of several other *Colletotrichum* spp., there is a long list of 100 % matching sequences in GenBank. These sequences, however, are all from isolates with hosts other than *Musa*.

Colletotrichum phormii (Henn.) D.F. Farr & Rossman, Mycol. Res. 110(12): 1403. 2006. Fig. 23.

Basionym: *Fusarium phormii* Henn., Verh. bot. Ver. Prov. Brandenb. 40: 175. 1898. [1899].

≡ *Gloeosporium phormii* (Henn.) Wollenw., Fus. Auto Delin. no. 498. 1916, non Sacc. 1915.

= *Gloeosporium phormii* Sacc., Nuovo Giorn. Bot. Ital. n.s. 22: 67. 1915.

= *Cryptosporium rhodocyclum* Mont. ex Almeida & Souza da Camara, Bol. Soc. Brot. 25: 190. 1909.

≡ *Gloeosporidium rhodocyclum* (Mont. ex Almeida & Souza da Camara) Höhn., Annls mycol. 18(1/3): 92. 1920.

≡ *Colletotrichum rhodocyclum* (Mont. ex Almeida & Souza da Camara) Petr., Annls mycol. 25(3/4): 251. 1927.

= *Physalospora phormii* J. Schröt., in Cohn, Krypt.-Fl. Schlesien (Breslau) 3.2(3): 347. 1894.

≡ *Hypostegium phormii* (J. Schröt.) Theiss., Verh. zool.-bot. Ges. Wien 66: 384. 1916.

≡ *Glomerella phormii* (J. Schröt.) D.F. Farr & Rossman, Mycol. Res. 110(12): 1403. 2006.

Sexual morph not observed. *Asexual morph on SNA. Vegetative hyphae* 1–5 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* absent, conidiophores formed directly on hyphae. *Setae* not observed. *Conidiophores* hyaline to very pale brown, smooth-walled to finely verruculose,

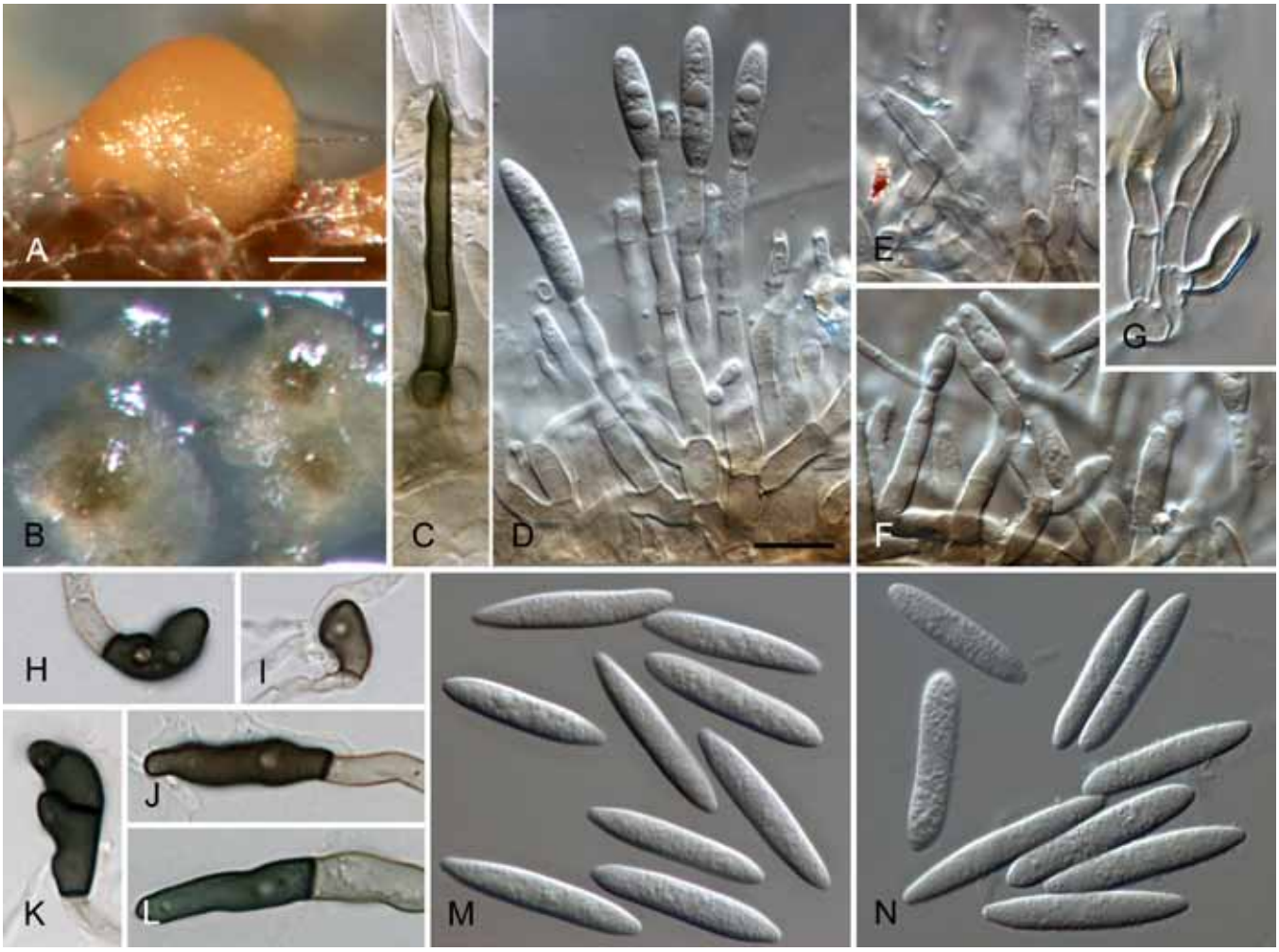

Fig. 23. *Colletotrichum phormii* (from ex-epitype strain CBS 118194). A–B. Conidiomata. C. Seta. D–G. Conidiophores. H–L. Appressoria. M–N. Conidia. A, C–D, M. from *Anthriscus* stem. B, E–L, N. from SNA. A–B. DM, C–N. DIC, Scale bars: A = 100 µm, D = 10 µm. Scale bar of A applies to A–B. Scale bar of D applies to C–N.

simple or septate and branched, to 40 µm in length. *Conidiogenous cells* hyaline to pale brown, smooth-walled to finely verruculose, cylindrical, elongate ampulliform to ampulliform, 7.5–16.5 × 2.2–4.5 µm, opening 1–1.5 µm diam, collarette 1–2 µm long, periclinal thickening visible. *Conidia* hyaline, smooth-walled or verruculose, aseptate, straight, cylindrical to fusiform with both ends acute or one end round and one end acute, (17–)20–26(–35.5) × 4–5(–6.5) µm, mean ± SD = 23.0 ± 3.2 × 4.6 ± 0.6 µm, L/W ratio = 5.1. *Appressoria* single or in loose groups, medium to dark brown, outline mostly oblong to irregular, the edge entire or undulate, rarely lobate, (4–)8.5–20.5(–32) × (2.5–)4–6(–8) µm, mean ± SD = 14.5 ± 6.2 × 5.1 ± 1.0 µm, L/W ratio = 2.9, appressoria of strain CBS 102054 are shorter, measuring (5.5–)8–13(–14.5) × 5–6.5(–8) µm, mean ± SD = 10.4 ± 2.4 × 5.8 ± 0.8 µm, L/W ratio = 1.8.

Asexual morph on Anthriscus stem. Conidiomata acervular, conidiophores and setae formed on a cushion of pale brown roundish to angular cells, 2.5–10 µm diam. *Setae* few, hyaline to medium brown, smooth-walled, 0–1-septate, 25–70 µm long, base cylindrical, to 5 µm diam, tip ± roundish to ± acute. *Conidiophores* pale brown, smooth-walled, septate, branched, to 50 µm long. *Conidiogenous cells* pale brown, smooth-walled, usually cylindrical, sometimes elongate ampulliform to ampulliform , 8–25 × 2.5–3.5(–5.5) µm, opening 1–1.5 µm diam, collarette 1 µm long, periclinal thickening visible. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical to fusiform with both ends acute, (14–)20–24.5(–25.5) × 4–4.5(–5) µm (one conidium measured 47 × 5 µm), mean ± SD = 22.3 ± 2.3 × 4.3 ± 0.2 µm, L/W ratio = 5.2, conidia of most other strains are slightly broader and those of strain CBS 118191 are additionally shorter than conidia of the ex-epitype strain, measuring (14–)18.5–22(–24) × (4–)4.5–5(–5.5) µm, mean ± SD = 20.3 ± 1.9 × 4.9 ± 0.4 µm, L/W ratio = 4.1.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline with felty white aerial mycelium on *Anthriscus* stem and filter paper, filter paper on both sides partially olivaceous to pale olivaceous grey; growth rate 15–19 mm in 7 d (27.5–32.5 mm in 10 d). Colonies on OA flat with entire margin; surface buff, with olivaceous to grey olivaceous sectors, and roundish olivaceous grey structures embedded in the medium, surface partly covered with floccose-felty white to pale olivaceous grey aerial mycelium, reverse buff with pale to dark olivaceous grey sectors; growth rate 15–21 mm in 7 d (27.5–33.5 mm in 10 d). *Conidia in mass* salmon.

Material examined: **Germany**, Berlin, Botanical garden, Kalthaus, from *Phormium tenax*, Apr. 1889, P. Hennings, (B 70 0005220 **holotype** of *Fusarium phormii* [not seen]); APHIS interception Port Orlando 007160, from *Phormium* sp., 6 Nov. 2000, W. Sheta, (CBS-H 20720 **epitype**, here designated, culture ex-epitype CBS 118194 = AR 3546). **New Zealand,** Auckland, Blockhouse Bay, from leaf spot of *Phormium* sp., Jun. 1999, C.F. Hill, culture CBS 102054; from leaf of *Phormium* sp., APHIS interception Los Angeles, California 134866, 1 May 1997, M.A. Abdelshife, culture CBS 118197 = AR 3389; APHIS interception Los Angeles, California 105828), from leaf of *Phormium* sp., 4 May 1993, N. Suzuki, culture CBS 118201 = MEP 1334; from *Phormium tenax*, unknown collection date and collector (deposited in CBS 1 Aug. 198), culture CBS 483.82. **South Africa,** from leaf of *Phormium sp*., APHIS interception Miami, Florida, 223143, 26 Feb. 2002, H. Ruiz, culture CBS 118191 = AR 3787. **Netherlands**, from leaf of *Phormium* sp., unknown collection date and collector, culture CBS 124953.

Table 2. Conidia measurements of *Colletotrichum* strains studied.

Species	Accession No.	Conidia on SNA			Conidia on *Anthriscus* stem		
		length × width (µm)²	length × width (µm) mean ± stdev	L/W ratio	length × width (µm)²	length × width (µm) mean ± stdev	L/W ratio
C. acerbum	CBS 128530*	15.5–20.5(–29) × (4–)4.5–5	17.9 ± 2.4 × 4.7 ± 0.2	3.8	(12.5–)15–18.5(–20.5) × (4–)4.5–5	16.8 ± 1.7 × 4.7 ± 0.3	3.6
C. acutatum	CBS 112996*	(7.5–)11–14.5(–19) × 3.5–4(–4.5)	12.6 ± 1.8 × 3.9 ± 0.3	3.2	(8.5–)12–16.5(–17.5) × (3–)3.5–4.5(–5)	14.3 ± 2.1 × 4.1 ± 0.4	3.5
	CBS 111993	(10.5–)12–16(–20) × (3–)3.5–4.5(–5)	14.0 ± 1.8 × 4.0 ± 0.5	3.5	(12.5–)14–17(–18) × (3.5–)4–4.5(–5)	15.5 ± 1.3 × 4.2 ± 0.3	3.7
	CBS 127602	(8–)11.5–14.5(–15) × (2.5–)3.5–4	13.0 ± 1.5 × 3.8 ± 0.4	3.5	(8–)12.5–18.5(–22) × 4–4.5	15.5 ± 2.9 × 4.2 ± 0.3	3.7
	CBS 112990	(8.5–)12.5–15.5(–17.5) × (2.5–)4–5	14.1 ± 1.6 × 4.3 ± 0.5	3.3	(8.5–)11.5–15.5(–17) × (3.5–)4–4.5(–5)	13.5 ± 1.8 × 4.2 ± 0.3	3.2
	CBS 129915	(7–)12–15.5(–16.5) × (3.5–)4–4.5(–5)	13.8 ± 1.9 × 4.1 ± 0.3	3.3	(6.5–)11–14.5(–15.5) × (3.5–)4–4.5(–5)	12.8 ± 2.0 × 4.3 ± 0.3	2.9
	CBS 112759	(6.5–)8.5–12(–13) × (2.5–)3–4	10.3 ± 1.9 × 3.4 ± 0.5	3.1	(8–)11–15(–19) × (3–)4–5	12.9 ± 1.9 × 4.5 ± 0.4	2.9
	CBS 112761	(7.5–)10–15.5(–20.5) × (3–)3.5–4.5(–6)	12.7 ± 2.7 × 4.1 ± 0.5	3.1			
	CBS 370.73				(5–)6.5–11(–12.5) × (2–)2.5–3.5(–4.5)	8.8 ± 2.1 × 3.2 ± 0.5	2.7
	CBS 797.72	(6–)8.5–13(–18) × 3.5–4.5(–5)	10.8 ± 2.3 × 4.0 ± 0.3	2.7	(5.5–)10–14(–15.5) × (3–)4–5	12.0 ± 2.2 × 4.4 ± 0.5	2.7
	CBS 110735	(7.5–)11–16.5(–21) × (3–)3.5–4(–4.5)	13.7 ± 2.5 × 3.8 ± 0.4	3.6	(12.5–)14–17(–17.5) × (3.5–)4–4.5(–5)	15.5 ± 1.5 × 4.4 ± 0.3	3.5
	CBS 112979	(7.5–)9–13(–15) × (2–)3–3.5(–4)	11 ± 2.0 × 3.3 ± 0.4	3.3	(9–)10.5–15.5(–16.5) × (3–)3.5–4.5(–5)	13.1 ± 2.4 × 4.2 ± 0.5	3.1
	CBS 979.69	(5–)8.5–14.5(–16.5) × (2.5–)3–4(–4.5)	11.5 ± 3.1 × 3.5 ± 0.4	3.3	(12–)13–15.5(–17) × (3.5–)4–4.5(–5)	14.1 ± 1.3 × 4.1 ± 0.3	3.4
	IMI 319423	(8–)11.5–14.5(–16) × (3–)3.5–4.5	13.2 ± 1.5 × 4.0 ± 0.3	3.3	(7.5–)11.5–15.5(–19.5) × (3–)3.5–4.5	13.6 ± 2.0 × 4.0 ± 0.4	3.4
C. australe	CBS 116478*	(10–)14.5–19.5(–25) × (3.5–)4–5(–6)	17.0 ± 2.4 × 4.4 ± 0.5	3.9	(16–)17–20(–22) × (4–)4.5–5(–5.5)	18.6 ± 1.6 × 4.7 ± 0.4	4.0
	CBS 131320	(14–)15–19(–26) × (3.5–)4–5(–5.5)	17.0 ± 2.0 × 4.5 ± 0.3	3.8	(13.5–)15–17.5(–18) × (3.5–)4–5(–5.5)	16.3 ± 1.1 × 4.4 ± 0.4	3.7
C. brisbanense	CBS 292.67*	(12–)12–17.5(–25) × (3–)3.5–4(–5)	14.8 ± 2.8 × 3.8 ± 0.5	3.9	(9.5–)12–15(–17) × (3–)3.5–4	13.5 ± 1.4 × 3.9 ± 0.3	3.5
C. chrysanthemi	CBS 126518	(6–)7–9.5(–12) × (3–)4–5.5(–6)	8.3 ± 1.3 × 4.8 ± 0.6	1.7	(3.5–)6.5–10.5(–13.5) × (3.5–)4–5(–5.5)	8.5 ± 1.8 × 4.5 ± 0.5	1.9
	CBS 126518[1]	(3.5–)4.5–9(–15) × 3–5(–6.5)	6.7 ± 2.3 × 4.1 ± 0.8	1.6			
	CBS 126519[1]	(4–)5–10(–14) × (3–)3.5–5(–6)	7.4 ± 2.6 × 4.1 ± 0.6	1.8	(6.5–)8–10.5(–14.5) × (3–)4–5(–5.5)	9.2 ± 1.4 × 4.5 ± 0.4	2
	IMI 364540	(4.5–)6.5–13(–26) × (3–)3.5–5(–11)	9.8 ± 3.2 × 4.3 ± 0.9	2.3	(5–)6.5–12.5(–21) × (2–)3.5–5(–6)	9.4 ± 2.9 × 4.3 ± 0.7	2.2
C. cosmi	CBS 853.73*	(7–)13–18.5(–19.5) × (3–)3.5–4.5	15.8 ± 2.5 × 4.0 ± 0.4	4.0	(12–)14–16.5(–18) × (3.5–)4–4.5	15.3 ± 1.4 × 4.0 ± 0.3	3.8
C. costaricense	CBS 330.75*	(9–)11.5–18(–28) × (3–)3.5–4(–4.5)	14.6 ± 3.1 × 3.7 ± 0.3	4.0	12.5–)13.5–16(–18) × 3.5–4	14.8 ± 1.4 × 3.8 ± 0.3	3.9
	CBS 211.78	(11.5–)12–16(–20) × (3.5–)4–4.5	13.9 ± 1.9 × 4.3 ± 0.2	3.2	(12–)14–16.5(18.5) × (3.5–)4–4.5	15.2 ± 1.4 × 4.2 ± 0.2	3.6
C. cuscutae	IMI 304802*	(15.5–)17.5–21(–22.5) × (3–)3.5–4.5	19.2 ± 1.7 × 4.0 ± 0.3	4.8	(15–)17–20(–21) × (3.5–)4–4.5	18.6 ± 1.5 × 4.2 ± 0.2	4.5
C. fioriniae	CBS 128517*	(10–)13.5–16.5(–19.5) × 4–5(–5.5)	15.0 ± 1.6 × 4.5 ± 0.3	3.3	(12.5–)14–18.5(–24.5) × 4–5	16.1 ± 2.2 × 4.4 ± 0.4	3.6
	CBS 200.35	(8–)10.5–17.5(–30.5) × 3.5–5(–6.5)	14.1 ± 3.4 × 4.3 ± 0.6	3.3	(9–)12.5–17.5(–23) × (3.5–)4–5	15.0 ± 2.3 × 4.4 ± 0.4	3.4
	CBS 127599	(7.5–)12–16.5(–17) × (2.5–)4–5(–5.5)	14.4 ± 2.4 × 4.5 ± 0.6	3.2	(10.5–)13.5–17(–17.5) × (3.5–)4–5	15.1 ± 1.7 × 4.4 ± 0.4	3.4
	CBS 129916	(6.5–)11.5–16 × (3–)3.5–4.5(–5)	13.8 ± 2.2 × 3.9 ± 0.4	3.5	(10–)13–16.5(–18) × (4–)4.5–5(–5.5)	14.8 ± 1.7 × 4.7 ± 0.3	3.2
	CBS 127601	(4.5–)10.5–18(–20) × (3.5–)4–5(–5.5)	14.2 ± 4.0 × 4.5 ± 0.4	3.2	(7–)13.5–18.5(–19) × (3.5–)4–4.5(–5)	15.9 ± 2.3 × 4.4 ± 0.4	3.6
	CBS 129947	(10.5–)12–15(–17) × 3.5–5(–6)	13.5 ± 1.7 × 4.1 ± 0.8	3.3	(13–)14–16(–17) × (3.5–)4–4.5(–5)	15.0 ± 1.0 × 4.3 ± 0.4	3.5
	CBS 293.67	(8.5–)12.5–16(–17.5) × (3–)3.5–4.5(–5)	14.4 ± 1.7 × 4.0 ± 0.5	3.6	(13–)14–16.5(–18) × (4–)4.5–5(–5.5)	15.2 ± 1.3 × 4.7 ± 0.3	3.2
C. godetiae	CBS 133.44*	(7–)10.5–14.5(–15.5) × (3.5–)4–5(–5.5)	12.4 ± 2.0 × 4.3 ± 0.5	2.9	(9.5–)10.5–15(–20.5) × 4–5	12.8 ± 2.3 × 4.5 ± 0.4	2.8
	CBS 125972	(5.5–)12–16.5(–17) × (3.5–)4–4.5(–5)	14.2 ± 2.2 × 4.3 ± 0.4	3.3	(13.5–)14–16(–17) × (4–)4.5–5	15.1 ± 0.9 × 4.7 ± 0.3	3.2

Table 2. (Continued).

Species	Accession No.	Conidia on SNA			Conidia on *Anthriscus* stem		
		length × width (µm)²	length × width (µm) mean ± stdev	L/W ratio	length × width (µm)²	length × width (µm) mean ± stdev	L/W ratio
C. godetiae	CBS 193.32	(8–)11.5–15(–19.5) × (2.5–)3.5–4.5(–5)	13.2 ± 1.9 × 4.2 ± 0.5	3.1	(6.5–)9.5–14(–15.5) × (3–)3.5–4.5(–5.5)	11.8 ± 2.2 × 4.1 ± 0.6	2.9
	CBS 129911	(10.5–)12.5–15.5(–17.5) × (3–)4–5(–6.5)	13.9 ± 1.4 × 4.5 ± 0.6	3.1	(7–)9–13(–15.5) × (2.5–)3–4	11.0 ± 2.0 × 3.5 ± 0.3	3.1
	CBS 862.70	(8–)14–19(–24) × (4–)4.5–5(–5.5)	16.4 ± 2.4 × 4.9 ± 0.4	3.4	(12.5–)15.5–18(–19.5) × 4.5–5(5.5)	16.8 ± 1.4 × 4.9 ± 0.2	3.4
	CBS 129809	(10.5–)13.5–17(–22.5) × (3.5–)4–5(–5.5)	15.3 ± 1.9 × 4.4 ± 0.3	3.4	(14–)14–17.5(–23) × 4–4.5(–5)	15.8 ± 1.6 × 4.4 ± 0.3	3.6
	CBS 129816	(13–)13.5–16.5(–20.5) × 4–4.5(–5)	15.1 ± 1.4 × 4.4 ± 0.3	3.4	(13–)14–16(–17.5) × 4.5–5	15.1 ± 1.1 × 4.7 ± 0.2	3.2
	CBS 127561	(12.5–)14–15.5(–16.5) × 4.5–5(–5.5)	14.7 ± 0.9 × 4.9 ± 0.3	3.0	(11.5–)13.5–17.5(–20) × (4–)4.5–5.5	15.5 ± 1.8 × 5.0 ± 0.4	3.1
	CBS 129917	(8–)10–15(–18.5) × 3–4.5(–5.5)	12.5 ± 2.3 × 3.8 ± 0.6	3.3	(9.5–)13–16(–17) × (4–)4.5–5.5(–6)	14.6 ± 1.5 × 4.9 ± 0.5	3.0
C. guajavae	IMI 350839*	(6–)10.5–16.5(–23.5) × (2.5–)3–4(–5)	13.4 ± 3.0 × 3.5 ± 0.5	3.8	(11–)13–16(–17) × (3–)3.5–4	14.6 ± 1.7 × 3.8 ± 0.3	3.9
C. indonesiense	CBS 127551*	(8–)10–14.5(–18) × (2.5–)3.5–4(–4.5)	12.3 ± 2.4 × 3.8 ± 0.3	3.2	(10.5–)13–17.5(–19) × (3–)3.5–4	15.4 ± 2.2 × 3.7 ± 0.2	4.1
C. johnstonii	CBS 128532*	(13.5–)14.5–19(–21.5) × (3.5–)4.5–5(–6)	16.7 ± 2.1 × 4.7 ± 0.4	3.6	(14.5–)15.5–17(–18) × 4.5–5(–5.5)	16.3 ± 1.0 × 4.9 ± 0.3	3.3
	IMI 357027	(13–)14.5–17(–19) × (4–)4.5–5(–5.5)	15.6 ± 1.3 × 4.7 ± 0.3	3.3	(8.5–)14.5–17.5(–19) × (3–)4–5	15.9 ± 1.6 × 4.6 ± 0.4	3.8
C. kinghornii	CBS 198.35*	(11–)15.5–21(–22.5) × (3–)3.5–4(–4.5)	18.3 ± 2.9 × 3.8 ± 0.4	4.9	(15–)16–20.5(–23) × 3.5–4.5	18.1 ± 2.3 × 4.0 ± 0.4	4.6
C. laticiphilum	CBS 112989*	(9.5–)13.5–19.5(–25.5) × (3–)3.5–4(–4.5)	16.6 ± 3.1 × 3.8 ± 0.4	4.4	(10–)12–15(–19.5) × 4–5(–5.5)	13.6 ± 1.7 × 4.5 ± 0.3	3.0
	CBS 129827	(5–)8–15(–18.5) × (1.5–)2.5–4.5(–5.3)	11.5 ± 3.4 × 3.6 ± 0.9	3.2	(10–)12.5–17.5(–20) × 4–4.5(–5)	15.1 ± 2.5 × 4.4 ± 0.3	3.4
C. limetticola	CBS 114.14*	(9–)12–20.5(–29) × (3–)4–5(–6)	16.3 ± 4.2 × 4.5 ± 0.6	3.6	(12–)13–18(–24) × (3.5–)4–4.5(–5.5)	15.5 ± 2.3 × 4.3 ± 0.4	3.6
C. lupini	CBS 109225*	9–15(–26.5) × (3–)3.5–4.5(–6)	12.0 ± 3.2 × 4.1 ± 0.6	2.9	(10–)12.5–16(–18.5) × (3–)3.5–4.5	14.2 ± 1.7 × 4.0 ± 0.3	3.6
	IMI 375715	(7.5–)9.5–16(–25) × 3.5–5(–6.5)	12.8 ± 3.3 × 4.3 ± 0.6	3.0	(10–)11.5–15(–17) × (3.5–)4–4.5(–5)	13.3 ± 1.8 × 4.2 ± 0.3	3.1
	CBS 109221	11.5–15.5(–19) × (3.5–)4–4.5(–5)	13.5 ± 1.9 × 4.3 ±0 .4	3.2	(11.5–)13.5–16.5(–18.5) × (3.5–)4–4.5	15.0 ± 1.5 × 4.3 ± 0.3	3.5
C. melonis	CBS 159.84*	(7–)9–16.5(–23.5) × (3–)3.5–4.5(–5)	12.8 ± 3.6 × 3.9 ± 0.4	3.3	(9–)12–17(–20) × (3.5–)4–4.5(–5)	14.5 ± 2.3 × 4.2 ± 0.3	3.5
C. nymphaeae	CBS 173.51	(6–)9.5–13.5(–15) × (2–)3–4.5	11.5 ± 1.8 × 3.7 ± 0.5	3.1	(7.5–)10–14.5(–16) × (3–)3.5–4.5	12.3 ± 2.0 × 3.9 ± 0.4	3.2
	CBS 112992	(5.5–)8–14.5(–20.5) × (2.5–)3–4(–4.5)	11.2 ± 3.4 × 3.5 ± 0.5	3.2	(7.5–)11–16(–20) × (2.5–)3.5–4(–4.5)	13.6 ± 2.7 × 3.8 ± 0.4	3.6
	CBS 126372	(9.5–)13–17.5(–21.5) × (2.5–)3.5–4.5(–5.5)	15.3 ± 2.4 × 3.9 ± 0.7	3.9	(12.5–)13.5–17(–18.5) × (3.5–)4–4.5	15.3 ± 1.7 × 4.2 ± 0.3	3.7
	CBS 112202	(10–)14–17(–18.5) × (3–)4–4.5	15.7 ± 1.6 × 4.1 ± 0.3	3.8	(12–)13.5–17.5(–19.5) × (3.5–)4(–4.5)	15.5 ± 1.8 × 4.0 ± 0.2	3.9
	CBS 126382	(3–)7.5–14(–17.5) × 3–4(–5)	10.8 ± 3.4 × 3.6 ± 0.5	3.0	(11–)12.5–16(–18) × (3–)3.5–4.5	14.4 ± 1.8 × 4.0 ± 0.3	3.6
	CBS 515.78*	(10–)14–18.5(–19.5) × (3–)4–5.5(–6)	16.1 ± 2.3 × 4.9 ± 0.7	3.3	(12.5–)14–18.5(–22.5) × (4–)4.5–5.5(–6)	16.3 ± 2.1 × 4.8 ± 0.5	3.4
	CBS 526.77	(8.5–)9–13(–16) × (3–)3–4.5(–5)	11.0 ± 2.0 × 3.8 ± 0.6	2.9	(9.5–)13.5–19(–21.5) × (3.5–)5–6(–6.5)	16.1 ± 2.7 × 5.6 ± 0.7	2.9
C. orchidophilum	CBS 632.80*	(10.5–)11.5–14(–16.5) × (2–)3–3.5(–4)	12.7 ± 1.1 × 3.1 ± 0.3	4.1	(11.5–)12.5–14(–15.5) × (2.5–)3–3.5(–4)	13.2 ± 0.9 × 3.3 ± 0.3	4.0
	IMI 305357	(8.5–)11.5–17(–25) × (1.5–)2.5–4(–4.5)	14.2 ± 2.7 × 3.3 ± 0.6	4.4	(10–)12–14.5(–15) × 3–3.5(–4)	13.3 ± 1.0 × 3.5 ± 0.3	3.8
	CBS 119291	(13.5–)14–15.5(–16) × 3–3.5(–4)	14.8 ± 0.7 × 3.3 ± 0.3	4.5	(10.5–)11.5–13.5(–14.5) × 3–4	12.7 ± 1.0 × 3.5 ± 0.3	3.6
	CBS 631.80	(13–)13.5–17.5(–19) × 2.5–3.5	15.4 ± 2.1 × 3.0 ± 0.3	5.1	(10.5–)11.5–13.5(–14.5) × (3–)3.5–4	12.4 ± 0.9 × 3.6 ± 0.3	3.4
C. paxtonii	IMI 165753*	(5–)10.5–15.5(–19.5) × (2.5–)3.5–4(–4.5)	13.0 ± 2.6 × 3.7 ± 0.3	3.5	(6.5–)12–15.5(–17) × (3–)3.5–4	13.7 ± 1.8 × 3.8 ± 0.3	3.6
C. phormii	CBS 118194*	(17–)20–26(–35.5) × 4–5(–6.5)	23.0 ± 3.2 × 4.6 ± 0.6	5.1	(14–)20–24.5(–25.5) × 4–4.5(–5)	22.3 ± 2.3 × 4.3 ± 0.2	5.2
	CBS 102054	(180.5–)20–24(–29) × (4–)4.5–5(–5.5)	22.1 ± 2.1 × 4.8 ± 0.4	4.6	(19–)20.5–24(–25) × (4–)4.5–5.5	22.2 ± 1.6 × 4.9 ± 0.4	4.5
	CBS 118197	19.5–25(–33.4) × (3.5–)4–5(–6)	22.3 ± 2.6 × 4.5 ± 0.4	5.0	21.5–26(–30) × (4–)4.5–5(–6)	23.7 ± 2.1 × 4.9 ± 0.4	4.9

Table 2. (Continued).

Species	Accession No.	Conidia on SNA			Conidia on *Anthriscus* stem		
		length × width (µm)[2]	length × width (µm) mean ± stdev	L/W ratio	length × width (µm)[2]	length × width (µm) mean ± stdev	L/W ratio
C. phormii	**CBS 118201**	(21–)21.5–24(–24.5) × 4–4.5	22.9 ± 1.2 × 4.4 ± 0.3	5.2	(20–)20.5–23.5(–25) × 4.5–5(–5.5)	21.9 ± 1.4 × 4.8 ± 0.2	4.5
	CBS 118191	(18–)18.5–30(–39.5) × (3–)3.5–4.5(–5)	24.1 ± 5.5 × 4.2 ± 0.3	5.7	(14–)18.5–22(–24) × (4–)4.5–5(–5.5)	20.3 ± 1.9 × 4.9 ± 0.4	4.1
	CBS 124953	(13.5–)18–26.5(–28) × 4–4.5(–5)	22.3 ± 4.2 × 4.4 ± 0.3	5.0	(20.5–)21–23(–23.5) × 4.5–5	22.0 ± 1.2 × 4.9 ± 0.2	4.5
	CBS 483.82	(18–)19–28(–33.5) × 4–5(–6.5)	23.3 ± 4.5 × 4.5 ± 0.6	5.2	(19–)20–22(–23) × 4.5–5(–5.5)	20.9 ± 1.0 × 4.7 ± 0.3	4.4
C. pseudoacutatum	**CBS 436.77***	(9.5–)11.5–13.5(–14.5) × 3.5–4	12.7 ± 1.1 × 3.8 ± 0.2	3.4	(9.5–)11.5–13.5(–14.5) × 3.5–4	15.0 ± 1.2 × 4.2 ± 0.3	3.5
C. pyricola	**CBS 128531***	(10–)14.5–18.5(–24) × (3.5–)4.5–5(–5.5)	16.7 ± 2.1 × 4.7 ± 0.4	3.5	(9.5–)14–17(–18.5) × (4–)4.5–5(–5.5)	15.4 ± 1.6 × 4.8 ± 0.4	3.2
C. rhombiforme	**CBS 129953***	(12–)12.5–17(–24) × (4–)4.5–5.5(–6)	14.7 ± 2.1 × 5.0 ± 0.7	2.9	(7.5–)10.5–17.5(–21) × (3.5–)4–5.5(–6)	14.1 ± 3.5 × 4.8 ± 0.6	2.9
C. salicis	**CBS 607.94***	(8.5–)10.5–15.5(–19.5) × (3.5–)3–4.5(–5)	13.0 ± 2.4 × 4.0 ± 0.5	3.2	(14.5–)16–18.5(–20) × (4–)4.5–5(–5.5)	17.1 ± 1.3 × 4.9 ± 0.3	3.5
	CBS 115.14	(9–)10.5–15(–17) × 2.5–3.5(–4)	12.7 ± 2.3 × 3.1 ± 0.5	4.1	(9.5–)11.5–16(–18.5) × (2.5–)3–4(–4.5)	14.0 ± 2.3 × 3.3 ± 0.4	4.2
	CBS 465.83	(7.5–)9.5–15.5(–22) × 3–3.5(–4.5)	12.4 ± 3.1 × 3.3 ± 0.4	3.8	not observed		
C. scovillei	**CBS 126529***	(10.5–)12.5–15(–16.5) × (3–)3.5–4(–4.5)	13.7 ± 1.3 × 3.8 ± 0.3	3.6	(9–)14.5–18(–19.5) × 3.5–4.5	16.0 ± 1.8 × 4.0 ± 0.3	4
	CBS 120708	(11.5–)12.5–14.5(–15) × 3–3.5	13.5 ± 0.8 × 3.3 ± 0.2	4.1	(12.5–)13–16(–18) × (3–)3.5–4	14.6 ± 1.4 × 3.6 ± 0.3	4.1
C. simmondsii	**CBS 122122*[1]**	(4.5–)6.5–10(–11.5) × (2–)2.5–3.5(–4)	8.1 ± 1.7 × 2.9 ± 0.4	2.7	(6–)7–10(–12.5) × (2–)2.5–3.5(–4.5)	8.4 ± 1.5 × 3.0 ± 0.5	2.8
	CBS 294.67	(6–)10.5–14(–16.5) × 3.5–4.5(–5.5)	12.3 ± 1.8 × 4.0 ± 0.4	3.0	(11–)12–14.5(–15.5) × (3–)4–4.5(–5)	13.3 ± 1.2 × 4.1 ± 0.4	3.2
	CBS 114494	(6–)9.5–14.5(–15.5) × (2.5–)3–4(–4.5)	12.1 ± 2.7 × 3.6 ± 0.5	3.3	(10–)13–17(–18) × (3–)3.5–4.5(–5)	14.9 ± 1.9 × 3.8 ± 0.4	3.9
	IMI 354381	(8.5–)11–15(–16) × (3.5–)4–4.5	13.0 ± 1.8 × 4.2 ± 0.2	3.1	(12–)13.5–17(–19) × (3.5–)4–4.5(–5)	15.4 ± 1.7 × 4.2 ± 0.3	3.7
C. sloanei	**IMI364297***	(8.5–)12–17(–22) × (3–)3.5–4(–4.5)	14.4 ± 2.5 × 3.7 ± 0.3	3.9	(9–)11.5–15.5(–19.5) × (3–)3.5–4(–4.5)	13.4 ± 1.8 × 3.9 ± 0.3	3.5
C. tamarilloi	**CBS 129814***	(8.5–)11.5–14.5(–15) × (2.5–)3–4(–4.5)	13.0 ± 1.4 × 3.5 ± 0.4	3.7	(10.5–)12–16(–22) × (3–)3.5–4.5(–5)	14.0 ± 1.9 × 4.0 ± 0.4	3.5
	CBS 129811	(9.5–)12–15.5(–19.5) × (3–)3.5–4(–4.5)	13.7 ± 1.6 × 3.7 ± 0.3	3.7	(12.5–)13.5–16.5(–17.5) × (3–)3.5–4	15.1 ± 1.4 × 3.8 ± 0.3	4.0
	CBS 129955	(10.5–)11.5–14.5(–17.5) × 3–4(–5)	13.2 ± 1.5 × 3.6 ± 0.4	3.6	(11.5–)13.5–17(–18.5) × 3.5–4(–4.5)	15.3 ± 1.7 × 3.8 ± 0.3	4.0
C. walleri	**CBS 125472***	(6–10.5)15.5–(–19.5) × (3–)3.5–4.5(–5.5)	13.0 ± 2.7 × 4.0 ± 0.5	3.3	(10.5–)12–16(–18.5) × 3.5–4(–4.5)	13.9 ± 1.8 × 4.0 ± 0.3	3.5
Colletotrichum sp.	**CBS 129821**	(9–)12–14.5(–15.5) × (3–)3.5–4.5(–5.5)	13.2 ± 1.4 × 4.0 ± 0.5	3.3	(10–)13–17(–20) × 3.5–4(–4.5)	14.9 ± 2.0 × 4.0 ± 0.2	3.8
	CBS 129820	(9.5–)11–15(–19.5) × (2.5–)3.5–4(–4.5)	13.1 ± 1.9 × 3.7 ± 0.4	3.5	(9.5–)12–14.5(–16) × (3–)4–4.5	13.3 ± 1.3 × 4.0 ± 0.2	3.3
	CBS 129823	(7–)10.5–15.5(–18) × (2.5–)3–4(–4.5)	13.1 ± 2.3 × 3.5 ± 0.6	3.7	(9–)12–15.5(–17) × (2.5–)3.5–4(–4.5)	14.0 ± 1.8 × 3.8 ± 0.4	3.7
	IMI 384185	(9–)12–14(–14.5) × (2.5–)3–4(–4.5)	12.3 ± 1.5 × 3.6 ± 0.4	3.4	(6–)10–16.5(–19.5) × (3–)3.5–4.5(–6)	13.5 ± 3.2 × 4.0 ± 0.6	3.4
	CBS 101611	(13–)15–19(–22) × (3.5–)4–5(–5.5)	16.9 ± 2.0 × 4.5 ± 0.4	3.7	(14–)16.5–20(–23.5) × (4–)4.5–5(–5.5)	18.3 ± 1.8 × 4.6 ± 0.3	4
	CBS 129810	(12.5–)13–17(–23.5) × (2.5–)3.5–4(–4.5)	15.1 ± 2.1 × 3.9 ± 0.3	3.9	(7.5–)9.5–12.5(–15) × 2.5–3.5(–4)	10.8 ± 1.5 × 2.9 ± 0.5	3.7

*ex-type strain

[1]aerial mycelium

[2](min–)min-stdev–max-stdev(–max)

Notes: The synonymy given for this species follows Farr *et al.* (2006), and this work should be consulted for details. *Fusarium phormii* was described by Hennings (1898) on leaves of *Phormium tenax* in the Botanical Garden in Berlin, Germany, as forming sporodochia with oblong-cylindrical to fusoid, straight to slightly curved, multiguttulate, hyaline conidia, measuring 18–25 × 4–6 µm. Hennings (1898) found this fungus together with *Physalospora phormii*, and assumed the two belonged together. *Fusarium phormii* is formed on the leaf surface, while the perithecia of *P. phormii* appear on the undersurface. Kinghorn (1936) observed structures considered to be the sexual morph of *C. phormii* on leaves of *Phormium* plants but not in culture, as did von Arx (in litt.). We have found, however, that Kinghorn was looking at two species; part of this material belongs to a species that is named in the present publication as *C. kinghornii*. The sexual morph, originally named as *Physalospora phormii*, was originally found by Schröter (1894) on dead leaves of *Phormium tenax* in Breslau, Germany (today: Wrocław, Poland).

The sexual morph was not observed in our study. Farr *et al.* (2006) gave the following description: "Ascomata on upper and lower surface of leaves in large, elliptical, discoloured areas similar to those bearing acervuli, with or without a narrow, black margin, subepidermal, sometimes partially erumpent, solitary, scattered to crowded or aggregated, black, shiny when exposed, globose to ellipsoid, flattened. Ascomatal walls of thin-walled, brown cells, 9–15 µm diam. Paraphyses sparse, inflated, hyaline. Asci unitunicate, narrowly clavate with a rounded apex and short stipe, 56–70 × 15–20 µm, with an indistinct apical ring in immature asci, 8-spored, obliquely seriate. Ascospores hyaline, non-septate, ellipsoidal, 15–22 × 4.5–6 µm."

Von Arx (1957) regarded *Gloeosporium phormii* as a synonym of *C. gloeosporioides*. However in the phylogeny of Farr *et al.* (2006), strains of this species cluster with *C. acutatum* and *C. lupini*. Morphological and cultural differences revealed *C. phormii* as a distinct lineage. We have confirmed this in our study. *Colletotrichum phormii* can be distinguished from the closely related *C. salicis* (and indeed from all other species in the *C. acutatum* complex) by its elongate, large conidia and large appressoria (Tables 2, 3). The species appears to be host-specific to *Phormium* spp. Recently, Takeuchi & Hori (2006) reported *C. gloeosporioides* from *Phormium* in Japan. However, based on dimensions of conidia (10–16.5 × 4–6 µm) and appressoria (7–17 × 4–11.5 µm) and the shape of the conidia – cylindrical with broadly rounded ends – (fig. 3 of that paper), the fungus seems to be a species in the *C. gloeosporioides* complex rather than one of the two *C. acutatum* complex members from *Phormium* treated in this study.

Colletotrichum phormii is separated from other species by TUB2, GAPDH, HIS3 and ACT sequences, and most effectively with HIS3. The CHS-1 sequence is the same as that of *C. australe*. The closest matches in a blastn search with the TUB2 sequence of strain CBS 118194 (with 99 % identity, 4 bp differences) was *Ga. acutata* isolate PCF 459 (EU635504) from strawberry in Belgium (Debode *et al.* 2009) and with 99 % identity (5 bp differences), isolate PT250 (= CBS 129953) AJ748624 from olive, Portugal (Talhinhas *et al.* 2005), which is here referred to *C. rhombiforme*. With the GAPDH sequence of strain CBS 118194 there was no match closer than 89 % identity. The closest matches in a blastn search with the ITS sequence with 100 % identity were the same GenBank accessions as those obtained in blastn searches of *C. salicis*, *C. pyricola* and *C. johnstonii*.

Colletotrichum pseudoacutatum Damm, P.F. Cannon & Crous, **sp. nov.** MycoBank MB800509. Fig. 24.

Etymology: Named refers to the morphology that is similar to *C. acutatum*, which is not closely related.

Sexual morph not observed. *Asexual morph on SNA. Vegetative hyphae* 1–5 µm diam, hyaline to pale brown, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* acervular, conidiophores and setae formed on a cushion of pale brown angular cells 3–8 µm diam. *Setae* rare (only one found), medium brown, smooth-walled, 2-septate, 57 µm long, base cylindrical, constricted at basal septum, 4 µm diam, tip somewhat round. *Conidiophores* hyaline to pale brown, smooth-walled, septate, branched, to 50 µm long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical, often ± bent or partly inflated, 9–22 × 2–3.5 µm, opening 1 µm diam, collarette distinct, 0.5–1 µm long, periclinal thickening conspicuous. *Conidia* hyaline, smooth-walled, aseptate, straight, fusiform to cylindrical with both ends acute, (9.5–)11.5–13.5(–14.5) × 3.5–4 µm, mean ± SD = 12.7 ± 1.1 × 3.8 ± 0.2 µm, L/W ratio = 3.4. *Appressoria* in loose groups to dense clusters, pale brown, verruculose, irregular shape, (3–)5.5–18.5(–25) × (2.5–)3.5–7(–9.5) µm, mean ± SD = 12.0 ± 6.3 × 5.1 ± 1.7 µm, L/W ratio = 2.3.

Asexual morph on Anthriscus stem. Conidiomata acervular, conidiophores and setae formed on a cushion of pale brown angular cells 4–10 µm diam. *Setae* abundant, medium brown, basal cell often paler, smooth-walled, 65–130 µm long, mostly with one septum close to the base, (0–)1(–2)-septate, base cylindrical to conical, often ± bent, often looking like an outgrowth or like beginning to branch, 3–5 µm wide, tip somewhat acute to slightly roundish. *Conidiophores* hyaline, septate, branched, smooth-walled, to 30 µm long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical to elongate ampulliform, 5.5–17 × 2.5–4(–5) µm, opening 1 µm diam, collarette distinct, 0.5–1 µm long, periclinal thickening visible, sometimes conspicuous. *Conidia* hyaline, smooth-walled, aseptate, straight, fusiform to cylindrical with both ends acute, (9.5–)11.5–13.5(–14.5) × 3.5–4 µm, mean ± SD = 15.0 ± 1.2 × 4.2 ± 0.3 µm, L/W ratio = 3.5.

Culture characteristics: Colonies on SNA flat with undulate to lobate margin, hyaline, pale honey in the centre, aerial mycelium lacking, filter paper grey and mottled, on *Anthriscus* stem partly covered with salmon to apricot acervuli; growth rate 13.5–17.5 mm in 7 d (23–26 mm in 10 d). Colonies on OA flat with undulate to lobate margin; surface buff, sectors isabelline mottled and covered with salmon to apricot acervuli, aerial mycelium lacking, reverse salmon and mottled olivaceous grey, centre iron-grey; growth rate 15–21 mm in 13.5–21 mm in 7 d (21–27.5 mm in 10 d). *Conidia in mass* salmon to apricot.

Material examined: **Chile**, Valdivia, San Patricio forest nursery of the Corporación Nacional Forestal near San José de la Mariquina, from seedlings of *Pinus radiata*, between Dec 1976 and Feb 1977, unknown collector (isolated and deposited in CBS collection Aug. 1977 by H. Peredo López), (CBS H-20729 **holotype**, culture ex-holotype CBS 436.77).

Notes: Peredo *et al.* (1979) reported a disease of *Pinus radiata* seedlings in a nursery in Chile. The seedlings bent leaders in a similar manner to the "terminal crook" disease in New Zealand (Dingley & Gilmor 1972) and the affected part of the stem became pinkish. The disease resulted in small seedlings with a thick stem,

Table 3. Appressoria measurements of *Colletotrichum* strains studied.

Species	Accession No.	Appressoria on SNA		
		length × width (µm)[1]	length × width (µm) mean ± stdev	L/W ratio
C. acerbum	**CBS 128530***	(8–)9–14(–16.5) × (4–)5–7.5(–9.5)	11.3 ± 2.4 × 6.2 ± 1.2	1.8
C. acutatum	**CBS 112996***	(4–)5.5–9(–13) × (3–)4–6.5(–9.5)	7.3 ± 2.0 × 5.4 ± 1.2	1.3
	CBS 111993	(3–)5–8.5(–10.5) × (2–)4–6(–7)	6.7 ± 1.8 × 4.9 ± 1.0	1.4
	CBS 112759	(4–)5–7.5(–10) × (3.5–)4–6(–8)	6.3 ± 1.1 × 5.0 ± 1.0	1.3
	IMI 319423	(5.5–)6–13(–19.5) × (4–)5–6(–7.5)	9.5 ± 3.6 × 5.5 ± 0.7	1.7
C. australe	**CBS 116478***	(5–)6–11(–14) × (4–)4.5–7(–8.5)	8.5 ± 2.6 × 5.8 ± 1.1	1.5
	CBS 131320	(5–)7–10(–11) × (4.5–)5–7(–9)	8.6 ± 1.6 × 6.1 ± 1.1	1.4
C. brisbanense	**CBS 292.67***	(5–)7.5–14.5(–18) × (2.5–)3.5–5(–6)	11.1 ± 3.4 × 4.3 ± 0.9	2.6
C. chrysanthemi	**CBS 126518**	(5–)5.5–9.5(–11.5) × (3–)4.5–6.5(–7.5)	7.5 ± 1.8 × 5.4 ± 1.1	1.4
	IMI 364540	(5.5–)6–10(–14) × (4.5–)5–6.5(–7.5)	7.8 ± 2.0 × 5.5 ± 0.8	1.4
C. cosmi	**CBS 853.73***	(5–)5.5–8(–11.5) × (4–)4.5–5.5	6.8 ± 1.2 × 4.9 ± 0.4	1.4
C. costaricense	**CBS 330.75***	(4.5–)6–8.5(–10) × (3–)4–6(–6.5)	7.1 ± 1.2 × 4.9 ± 0.9	1.4
	CBS 211.78	(4–)5.5–9(–11) × (3–)4–6(–6.5)	7.3 ± 1.8 × 4.9 ± 1.2	1.5
C. cuscutae	**IMI 304802***	(3.5–)5.5–11.5(–15.5) × (2–)3.5–5.5(–6.5)	8.5 ± 3.2 × 4.6 ± 0.9	1.8
C. fioriniae	**CBS 128517***	(4.5–)7–11.5(–15.5) × (4–)4.5–7(–10.5)	9.2 ± 2.2 × 5.6 ± 1.2	1.6
	CBS 200.35	(6–)7.5–10.5(–12) × (4–)5–7(–9)	8.8 ± 1.5 × 6.0 ± 1.0	1.5
	CBS 129916	(5–)5.5–11.5(–18) × (4–)4.5–6.5(–8)	8.5 ± 3.1 × 5.4 ± 0.8	1.6
C. godetiae	**CBS 133.44***	(8–)9–12.5(–14.5) × (3–)4–5.5(–6)	10.7 ± 1.9 × 4.7 ± 0.7	2.3
	CBS 125972	(6–)8–13(–17) × (3.5–)5–6.5(–7)	10.3 ± 2.4 × 5.8 ± 0.7	1.8
	CBS 129911	(6–)7–10.5(–14.5) × (4.5–)5–7(–9)	9.0 ± 1.7 × 6.1 ± 1.0	1.5
	CBS 862.70	(4–)5.5–12.5(–17.5) × (3.5–)4–6(–8)	9.0 ± 3.4 × 5.1 ± 1.2	1.8
	CBS 129809	(6–)7.5–12(–15) × (4–)5–8(–11.5)	9.6 ± 2.2 × 6.5 ± 1.5	1.5
	CBS 127561	(6–)7–12(–16.5) × 4–6(–6.5)	9.4 ± 2.5 × 5.0 ± 0.9	1.9
C. guajavae	**IMI 350839***	(4.5–)5–8(–10.5) × (3.5–)4.5–6(–6.5)	6.6 ± 1.4 × 5.2 ± 0.7	1.3
C. indonesiense	**CBS 127551***	5.5–9(–14.5) × (5–)5.5–7.5(–9)	7.5 ± 1.8 × 6.3 ± 1.0	1.2
C. johnstonii	**CBS 128532***	(6–)8–11.5(–14) × (2–)4–7.5(–10.5)	9.6 ± 1.7 × 5.8 ± 1.9	1.7
	IMI 357027	(4.5–)6.5–10.5(–14) × (3–)4–7(–9.5)	8.4 ± 1.9 × 5.4 ± 1.6	1.6
C. laticiphilum	**CBS 112989***	(5–)6.5–12(–16) × (4–)6–8(–8.5)	9.2 ± 2.8 × 7.2 ± 1.0	1.3
	CBS 129827	(4–)5–7(–8) × (2.5–)3.5–5.5(–6)	6.0 ± 1.1 × 4.5 ± 0.8	1.3
C. limetticola	**CBS 114.14***	(5–)6–8.5(–11) × (4–)4.5–6(–7)	7.4 ± 1.3 × 5.3 ± 0.7	1.4
C. lupini	**CBS 109225***	(4–)6–12(–20.5) × (4.5–)6–9(–11.5)	9.0 ± 2.8 × 7.4 ± 1.7	1.2
	CBS 109221	(4.5–)5.5–11.5(–19.5) × (3.5–)5–7.5(–8.5)	8.6 ± 3.0 × 6.2 ± 1.1	1.4
C. melonis	**CBS 159.84***	(4.5–)6–11(–13.5) × (3.5–)4.5–6.5(–7.5)	8.3 ± 2.4 × 5.5 ± 1.0	1.5
C. nymphaeae	**CBS 173.51**	(4–)5.5–11(–17) × (3–)4–6.5(–9)	8.2 ± 2.7 × 5.2 ± 1.3	1.6
	CBS 112992	(4.5–)6–11(–16.5) × (4–)4.5–6(–7.7)	8.5 ± 2.3 × 5.2 ± 0.9	1.6
	CBS 112202	(5–)6.5–10(–13.5) × (4–)5–6.5(–8)	8.2 ± 1.9 × 5.8 ± 0.8	1.4
	CBS 126382	(5.5–)5.5–10(–17.5) × (3.5–)4.5–6.5(–9)	7.8 ± 2.4 × 5.5 ± 1.1	1.4
	CBS 515.78*	(4.5–)6–11(–15) × (3–)4.5–6.5(–8)	8.7 ± 2.5 × 5.5 ± 1.0	1.6
	CBS 526.77	(4.5–)6–9(–12) × (3.5–)4.5–6.5(–7.5)	7.4 ± 1.6 × 5.6 ± 1.1	1.3
C. orchidophilum	**IMI 305357**	(5.5–)7.5–15.5(–20.5) × (4.5–)5.5–8.5(–12)	11.6 ± 3.9 × 7.0 ± 1.6	1.6
	CBS 631.80	(4.5–)5.5–11(–18) × (4–)4.5–6(–7)	8.2 ± 2.8 × 5.2 ± 0.8	1.6
C. paxtonii	**IMI 165753***	(5–)6–11.5(–16.5) × (3.5–)5.5–7.5(–8.5)	8.8 ± 2.7 × 6.5 ± 1.1	1.4
	CBS 502.97	(3.5–)4.5–7.5(–10.5) × (3–)3.5–5(–5.5)	6.0 ± 1.7 × 4.2 ± 0.7	1.4
C. phormii	**CBS 118194***	(4–)8.5–20.5(–32) × (2.5–)4–6(–8)	14.5 ± 6.2 × 5.1 ± 1.0	2.9
	CBS 102054	(5.5–)8–13(–14.5) × 5–6.5(–8)	10.4 ± 2.4 × 5.8 ± 0.8	1.8
C. pseudoacutatum	**CBS 436.77***	(3–)5.5–18.5(–25) × (2.5–)3.5–7(–9.5)	12.0 ± 6.3 × 5.1 ± 1.7	2.3
C. pyricola	**CBS 128531***	(4.5–)6–16(–22) × (3.5–)4.5–7(–8.5)	11.1 ± 5.1 × 5.7 ± 1.2	2.0
C. rhombiforme	**CBS 129953***	(5.5–)8–13(–17.5) × (4.5–)6–8(–9.5)	10.6 ± 2.4 × 7.0 ± 1.1	1.5
C. salicis	**CBS 607.94***	(6–)8–15(–19.5) × (5–)6.5–8.5(–9.5)	11.5 ± 3.5 × 7.6 ± 1.0	1.5
	CBS 115.14	(3.5–)6.5–12(–16.5) × (3–)4–5.5(–7.5)	9.3 ± 2.7 × 4.9 ± 0.9	1.9

Table 3. (Continued).

Species	Accession No.	Appressoria on SNA		
		length × width (µm)[1]	length × width (µm) mean ± stdev	L/W ratio
C. salicis	**CBS 465.83**	(7–)8–14(–18) × (5–)5.5–8(–11)	11.1 ± 2.9 × 6.9 ± 1.3	1.6
C. scovillei	**CBS 126529***	(3.5–)5–7.5(–10.5) × (3.5–)5–6.5(–7)	6.3 ± 1.2 × 5.6 ± 0.8	1.1
	CBS 120708	(4.5–)6.5–9(–10.5) × (4.5–)6–7.5(–7.5)	7.7 ± 1.2 × 6.7 ± 0.7	1.2
C. simmondsii	**CBS 122122***	(4.5–)6–9.5(–11.5) × (3.5–)4–6.5(–9.5)	7.8 ± 1.9 × 5.3 ± 1.1	1.5
	CBS 294.67	(6–)6.5–10(–14) × (4.5–)5–7(–8.5)	8.3 ± 1.8 × 6.0 ± 0.8	1.4
	CBS 114494	(4–)5.5–9.5(–12.5) × (3–)4–6(–8)	7.5 ± 1.8 × 5.0 ± 1.1	1.5
C. sloanei	**IMI 364297***	(4–)5–11(–17.5) × (4–)4.5–6.5(–8)	8.0 ± 3.0 × 5.4 ± 0.9	1.5
C. tamarilloi	**CBS 129814***	(4–)5–10.5(–16) × (3.5–)4.5–6.5(–8)	7.8 ± 2.6 × 5.5 ± 0.9	1.4
	CBS 129811	(4–)5–10(–15) × (3.5–)4.5–6(–7)	7.5 ± 2.4 × 5.2 ± 0.9	1.5
C. walleri	**CBS 125472***	(4.5–)5.5–12.5(–18.5) × (3.5–)4.5–7.5(–10.5)	9.0 ± 3.3 × 5.9 ± 1.4	1.5
Colletotrichum sp.	**CBS 129821**	(5.5–)6.5–9(–11) × (4.5–)5.5–7.5(–8.5)	7.9 ± 1.3 × 6.5 ± 0.9	1.2
	CBS 129820	(6.5–)8.5–11.5(–13.5) × (5–)6–8.5(–10.5)	10.0 ± 1.6 × 7.2 ± 1.2	1.4
	CBS 129823	(5–)5.5–10.5(–15.5) × (3.5–)4.5–6.5(–8)	7.9 ± 2.4 × 5.4 ± 1.1	1.5
	IMI 384185	(4.5–)5.5–9.5(–12.5) × (4.5–)5–7(–8)	7.6 ± 2.1 × 6.0 ± 0.8	1.3
	CBS 101611	(5.5–)6.5–10(–14) × (5–)6–8(–8.5)	8.2 ± 1.8 × 6.8 ± 1.0	1.2
	CBS 129810	(6–)6.5–9(–10.5) × (5.5–)6–7(–7.5)	7.8 ± 1.1 × 6.3 ± 0.6	1.2

* ex-type strain

[1](min–)min-stdev–max-stdev(–max)

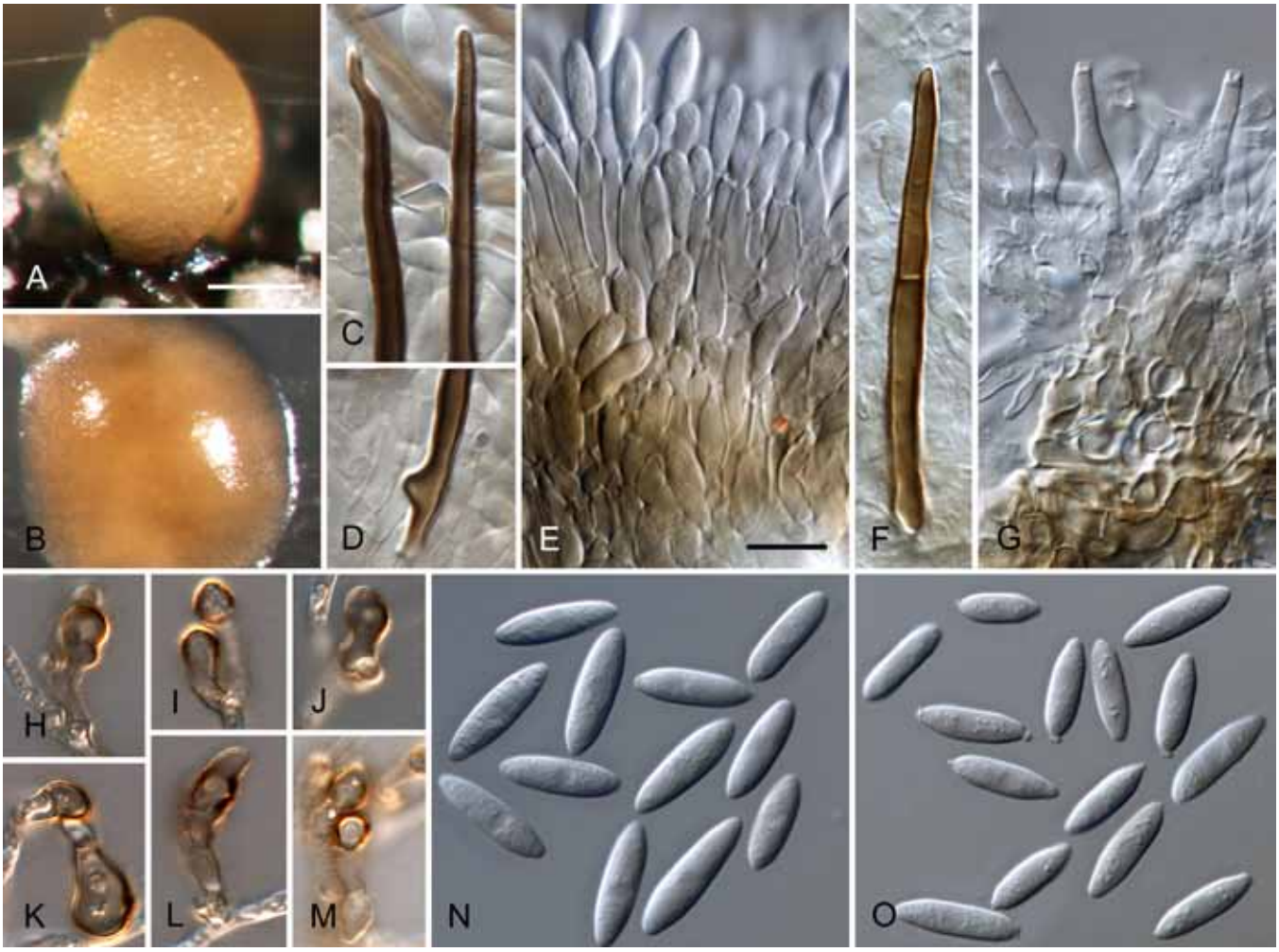

Fig. 24. *Colletotrichum pseudoacutatum* (from ex-holotype strain CBS 436.77). A–B. Conidiomata. C. Tips of setae. D. basis of seta. E. Conidiophores. F. Seta. G. Conidiophores. H–M. Appressoria. N–O. Conidia. A, C–E, N. from *Anthriscus* stem. B, F–M, O. from SNA. A–B. DM, C–O. DIC, Scale bars: A = 100 µm, B = 200 µm, E = 10 µm. Scale bar of E applies to C–O.

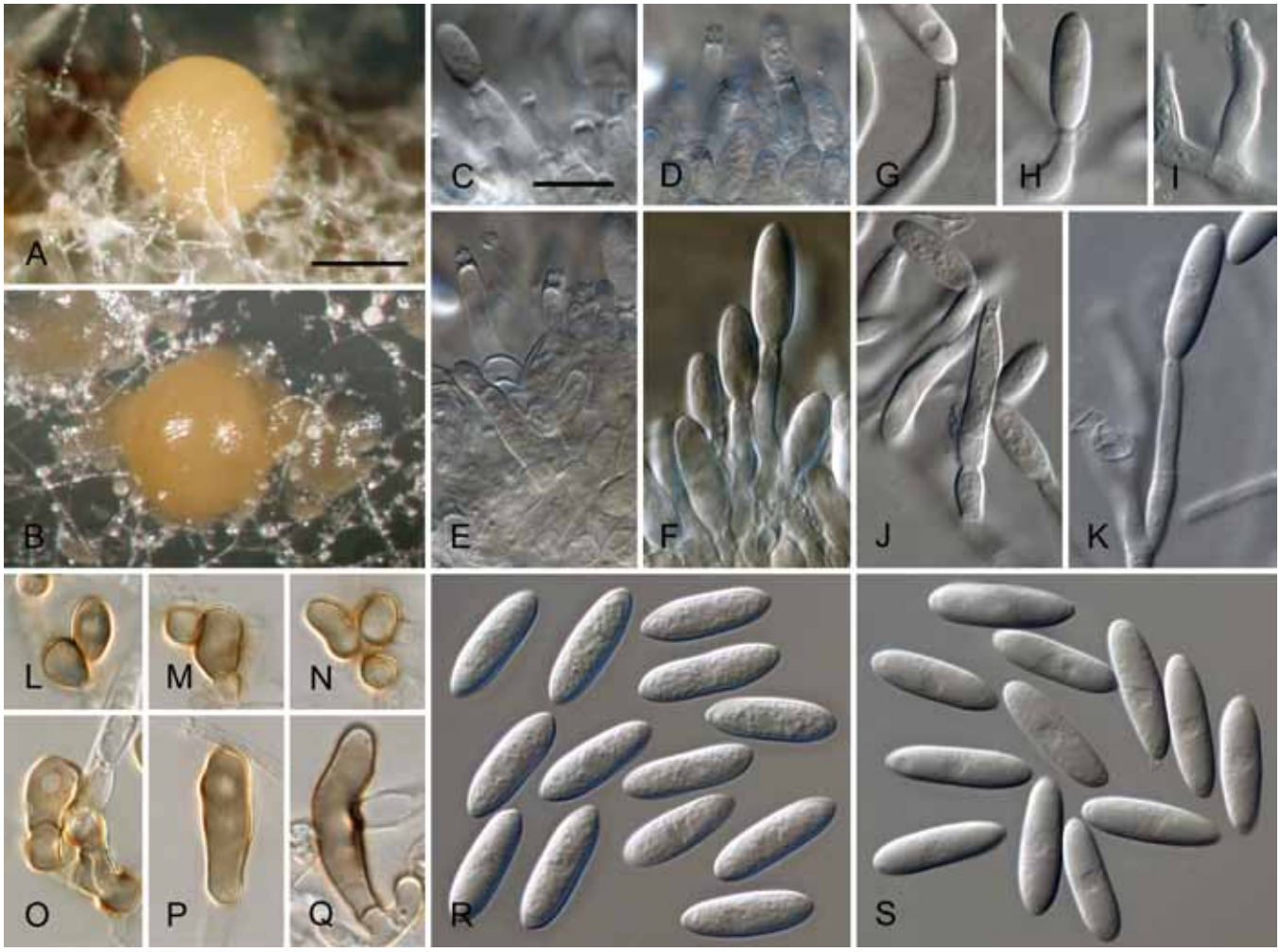

Fig. 25. *Colletotrichum pyricola* (from ex-holotype strain CBS 128531). A–B. Conidiomata. C–K. Conidiophores. L–Q. Appressoria. R–S. Conidia. A, C–F, R. from *Anthriscus* stem. B, G–Q, S. from SNA. A–B. DM, C–S. DIC, Scale bars: A = 200 µm, C = 10 µm. Scale bar of A applies to A–B. Scale bar of C applies to C–S.

restricted terminal growth and increased growth of lateral shoots. Two strains with differing colony characteristics were isolated and were used in pathogenicity tests on 4-month-old seedlings of *Pinus radiata*; 11.5 % of the seedlings inoculated with the salmon orange culture and 92 % of the seedlings with the grey culture showed the symptoms. The two strains were sent to CBS, and both were identified as *C. acutatum f. pineum* by von Arx, presumably because of the identity of the host plant and some of their morphological features, especially the conidia with acute ends typical for *C. acutatum*. One of the strains was kept in the CBS collection as CBS 436.77; unfortunately we can only suppose it was the salmon orange culture.

Strain CBS 436.77 turns out not to be closely related to *C. acutatum f. pineum*, which belongs to *C. acutatum s. str.* (Fig. 1). *Colletotrichum pseudoacutatum* is at best basal to the *C. acutatum* species complex and forms a sister group to a clade containing the *C. acutatum* complex and *C. orchidophilum* (fig. 2 in Cannon *et al.* 2012, this issue). The closest matches in a blastn search on the ITS sequence of strain CBS 436.77 (with only 94 % identity) are unidentified *Colletotrichum* isolates, *e.g.* from *Podocarpaceae* in New Zealand (Joshee *et al.* 2009), plus several *C. coccodes* strains including the ex-epitype strain CBS 164.49 (HM171678, Liu *et al.* 2011), *C. trichellum* strains MEP1535 (= CBS 118198, DQ286152, Farr *et al.* 2006) and DAOM 188792 (= CBS 125343, EU400142, wrongly identified as *C. dematium,* Chen YY, Conner R, Babcock C, Penner W, unpubl. data) and "*C. gloeosporioides*" strains DAOM 183087 (EU400145, probably *C. coccodes*, Chen YY, Conner R, Babcock C, Penner W, unpubl. data) and BBA 71369 from *Pleione* (AJ301980, probably *C. orchidophilum*, Nirenberg *et al.* 2002). The closest matches with the TUB2 sequence showed only 82 % identity, including *C. trichellum* strains HKUCC 10378, CBS 217.64 and CBS 118198 (GQ849447, Yang *et al.* 2009, GU228106, GU228107, Damm *et al.* 2009). There is no match over the whole span of the GAPDH sequence of this species.

In morphological terms, *C. pseudoacutatum* mainly differs from species in the *C. acutatum* complex by the formation of pale brown, verruculose, irregular shaped appressoria, and also by the more abundant formation of setae.

Colletotrichum pyricola Damm, P.F. Cannon & Crous, **sp. nov.** MycoBank MB800510. Fig. 25.

Etymology: Named after the host plant *Pyrus communis.*

Sexual morph not observed. *Asexual morph on SNA. Vegetative hyphae* 1–8 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* not developed, conidiophores formed directly on hyphae. *Setae* not observed. *Conidiophores* hyaline, smooth-walled, septate, branched. *Conidiogenous cells* hyaline smooth-walled, cylindrical, 9–25 × 2.5–3.5 µm, opening 1–1.5 µm diam, collarette 1–1.5 µm long, periclinal thickening visible. *Conidia* hyaline, smooth-walled,

aseptate, straight, fusiform to cylindrical with one end slightly acute and one end round or slightly acute, (10–)14.5–18.5(–24) × (3.5–)4.5–5(–5.5) µm, mean ± SD = 16.7 ± 2.1 × 4.7 ± 0.4 µm, L/W ratio = 3.5. *Appressoria* single or in small dense clusters, pale brown, smooth-walled, ellipsoidal, clavate to cylindrical, the edge entire or undulate, (4.5–)6–16(–22) × (3.5–)4.5–7(–8.5) µm, mean ± SD = 11.1 ± 5.1 × 5.7 ± 1.2 µm, L/W ratio = 2.0.

Asexual morph on Anthriscus stem. Conidiomata acervular, conidiophores formed on pale brown, angular, basal cells 3–7 µm diam. *Setae* not observed. *Conidiophores* hyaline, smooth-walled, septate, branched, to 40 µm long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical, 11–20 × 3–4 µm, opening 1.5–2 µm diam, collarette 0.5–2 µm long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, fusiform to cylindrical with both ends acute, (9.5–)14–17(–18.5) × (4–)4.5–5(–5.5) µm, mean ± SD = 15.4 ± 1.6 × 4.8 ± 0.4 µm, L/W ratio = 3.2.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline, on medium, filter paper and *Anthriscus* stem partly covered with thin floccose white to pale grey aerial mycelium and orange acervuli, reverse hyaline with orange to grey acervuli shining through; growth rate 24–25 mm in 7 d (35–37 mm in 10 d). Colonies on OA flat to raised with entire margin; surface partly covered with floccose to woolly whitish to pale olivaceous grey aerial mycelium and orange acervuli mainly appearing in growth rings, reverse buff, olivaceous buff to grey olivaceous with olivaceous grey to iron grey rings; growth rate 21.5–22.5 mm in 7 d (35–37.5 mm in 10 d). *Conidia in mass* orange.

Material examined: **New Zealand**, WO, Waikato, from fruit rot of *Pyrus communis*, 1 Jun. 1988, unknown collector (deposited in ICMP collection by P.R. Johnston), (CBS H-20810 **holotype**, culture ex-type CBS 128531 = ICMP 12924 = PRJ 977.1).

Notes: This is a third species within clade 4, not clearly distinct from *C. johnstonii* using morphological or cultural characteristics but with unique ACT, TUB2, CHS-1, GAPDH and HIS3 sequences. The ITS sequence of *C. pyricola* is identical with those of *C. salicis*, *C. johnstonii* and *C. phormii*.

As with *C. johnstonii*, *C. pyricola* appears to be endemic to New Zealand, but more data are needed to confirm its distribution. Strain CBS 128531 (= PRJ 977.1) is the only strain of this species available to us and was included in C. *acutatum* group C by Johnston & Jones (1997) and Lardner *et al.* (1999) and in group F2 by Guerber *et al.* (2003). In the combined GS and GAPDH phylogeny in Guerber *et al.* (2003), there is a second strain grouping with *C. pyricola* that they assigned as the only representative of their F5 group. This strain (PRJ 823) however belongs to group B in Lardner *et al.* (1999), with a completely different RAPD banding pattern.

In contrast to apple, for which *Colletotrichum* species are listed as major pathogens causing bitter rot (González *et al*. 2006), pear trees seem to be rarely affected by anthracnose. *Colletotrichum piri* Noack was actually described from apple (listed as *Pyrus malus*, a synonym of *Malus pumila*) in Brazil, rather than from pear as its name suggests.

The closest match in a blastn search with the TUB2 sequence of strain CBS 128531 (with 98 % identity, 10 bp differences) were AJ409294 isolate 90 from *Fragaria* in the UK (Talhinhas *et al.* 2002) as well as AJ748609, AJ748612–AJ748614, AJ748619–AJ748622, AJ748625 from olive isolates (Talhinhas *et al.* 2005). With the GAPDH sequence there was no closer match than 89 % identity.

Colletotrichum rhombiforme Damm, P.F. Cannon & Crous, **sp. nov.** MycoBank MB800511. Fig. 26.

Etymology: Named after the shape of the ascospores, which can be rhomboidal.

Sexual morph developed on *Anthriscus stem*. Ascomata globose to subglobose, pale brown, 300–400 × 400–500 µm, glabrous, ostiolate. Peridium 8–14 µm thick, composed of pale to medium brown flattened angular cells, 6–16 µm diam. *Ascogenous hyphae* hyaline, smooth-walled, delicate. *Interascal tissue* composed of paraphyses, hyaline, septate, branched at the base, 35–80 × 3–5 µm, widest part at the base, tips round. *Asci* cylindrical, 55–73 × 9–11 µm, 8-spored. *Ascospores* arranged uni-to bi-seriately, aseptate, hyaline, smooth-walled, oval, fusiform, or rhomboidal, one end ± acute and one end round or both ends round, sometimes slightly curved, (11–)12.5–16(–17) × 4–)4.5–6(–7.5) µm, mean ± SD = 14.1 ± 1.6 × 5.2 ± 0.8 µm, L/W ratio = 2.7.

Asexual morph on SNA. Vegetative hyphae 1–8 µm diam, hyaline to pale brown, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* absent, conidiophores formed directly on hyphae. *Setae* not observed. *Conidiophores* hyaline to pale brown, smooth-walled, septate and branched, to 50 µm long. *Conidiogenous cells* hyaline to pale brown, smooth-walled, cylindrical to ampulliform, often lacking a basal septum and continuous with the conidiophore, discrete phialides measure 4–13 × 3–5 µm, opening 1–2 µm diam, collarette distinct, 1–2 µm long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight cylindrical with one end round and one end slightly acute or both ends round, (12–)12.5–17(–24) × (4–)4.5–5.5(–6) µm, mean ± SD = 14.7 ± 2.1 × 5.0 ± 0.7µm, L/W ratio = 2.9. *Appressoria* single or in loose groups, medium to dark brown, smooth-walled, the outline mostly clavate, elliptical or ovate, the edge entire or undulate, rarely lobate, (5.5–)8–13(–17.5) × (4.5–)6–8(–9.5) µm, mean ± SD = 10.6 ± 2.4 × 7.0 ± 1.1 µm, L/W ratio = 1.5.

Asexual morph on Anthriscus stem. Conidiomata acervular, conidiophores formed on a cushion of pale brown angular cells 4–9 µm diam. *Setae* very few, pale brown, smooth-walled, 3–4-septate, 50–80 µm long, base cylindrical, 3–3.5 µm diam, tip ± rounded or ending with a conidiogenous locus. *Conidiophores* pale brown, smooth-walled, septate, branched, to 40 µm long. *Conidiogenous cells* pale brown, smooth-walled, cylindrical, sometimes polyphialides, 12–28 × 2–3.5 µm, opening 1–2 µm diam, collarette 0.5–1.5 µm long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, very variable in shape, cylindrical, clavate, ellipsoidal or limoniform with one end round and one end slightly acute to truncate, (7.5–)10.5–17.5(–21) × (3.5–)4–5.5(–6) µm, mean ± SD = 14.1 ± 3.5 × 4.8 ± 0.6 µm, L/W ratio = 2.9.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline to pale cinnamon, on filter paper, *Anthriscus* stem and medium covered with short floccose-felty pale olivaceous grey aerial mycelium, on *Anthriscus* stem covered with pale grey to black structures, reverse medium hyaline to pale cinnamon, filter paper pale cinnamon to olivaceous grey, growth rate 20–22.5 mm in 7 d (32.5–37.5 mm in 10 d). Colonies on OA flat with entire margin; surface honey, pale olivaceous grey, grey olivaceous to olivaceous, almost entirely covered with floccose-felty pale olivaceous grey aerial mycelium, reverse pale olivaceous grey, grey olivaceous

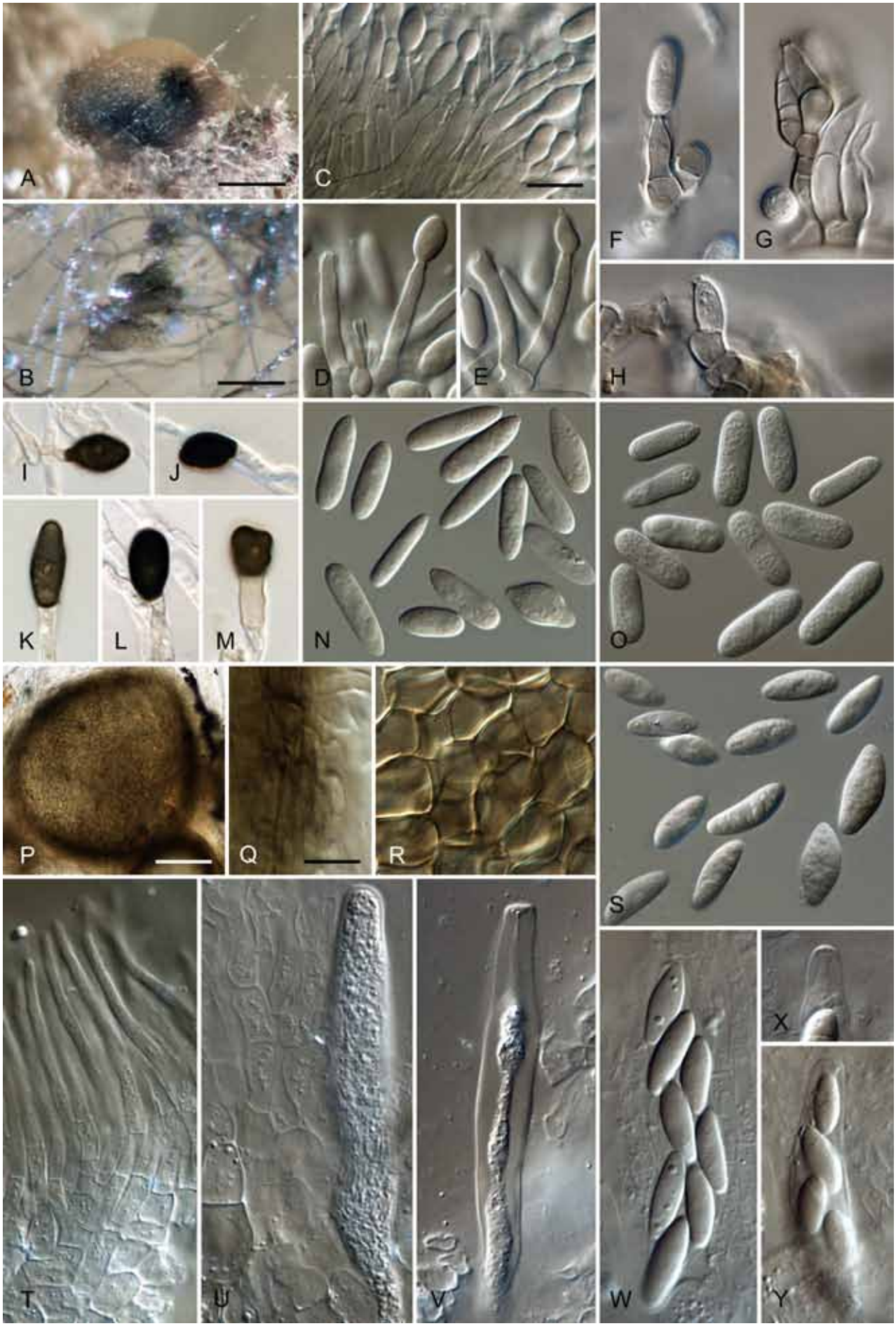

Fig. 26. *Colletotrichum rhombiforme* (from ex-holotype strain CBS 129953). A–B. Conidiomata. C–H. Conidiophores. I–M. Appressoria. N–O. Conidia. P. Ascomata. Q. Peridium in cross section. R. Outer surface of peridium. S. Ascospores. T. Paraphyses. U–W, Y. Asci. X. Apical region of ascus. A, C–E, N, P–Y. from *Anthriscus* stem. B, F–M, O. from SNA. A–B. DM, C–Y. DIC, Scale bars: A = 200 µm, B, P = 100 µm, C, Q = 10 µm. Scale bar of C applies to C–O. Scale bar of Q applies to Q–Y.

to iron grey, growth rate 19–21 mm in 7 d (29–32.5 mm in 10 d). *Conidia in mass* whitish to pale salmon.

Material examined: **Portugal**, Mirandela, Torre de D. Chama, from anthracnose on fruit of *Olea europaea*, Dec. 2003, P. Talhinhas (CBS H-20724 **holotype**, culture ex-type CBS 129953 = PT250). **USA**, Washington, Long Beach, from *Vaccinium macrocarpon*, 1993, Carris, culture CBS 131322 = DAOM 233523.

Notes: Talhinhas *et al.* (2005, 2009, 2011) found a diverse range of *C. acutatum* isolates from olive fruit with anthracnose symptoms in Portugal. One of these strains, PT250 (=CBS 129953) was found to be significantly divergent from other groups within *C. acutatum* based on ITS and beta-tubulin sequences, and was placed in the new clade A6. Talhinhas's olive strain here forms the type of *C. rhombiforme*. A second strain that we identified as *C. rhombiforme* and included here was isolated from *Vaccinium macrocarpon* (American cranberry) in the USA, and was studied by Robideau *et al.* (2008). Further representatives of this clade are likely to be some of those isolated from *Rhododendron* in Sweden and Latvia (strains S2, L3, L4, L5, L6) by Vinnere *et al.* (2002) that were reported to belong to clade A6 by Sreenivasaprasad & Talhinhas (2005) based on ITS sequencing. Since ITS does not distinguish between all species, sequences of additional genes would be necessary to confirm this placement.

A variety of *Glomerella rufomaculans*, *Ga. rufomaculans* var. *vaccinii* Shear was described from leaves of *Vaccinium macrocarpon* in New Jersey, USA with conidia and ascospores that agree in size with *C. rhombiforme*. Its conidia were described as oblong-cylindric, subclavate, sometimes slightly curved (Shear 1907). The variety was wrongly listed as *Ga. fructigena* var. *vaccinii* in Sylloge Fungorum (Saccardo & Trotter 1913); MycoBank and Index Fungorum list this taxon as separate species, *Ga. rufomaculans-vaccinii* Shear, MycoBank also as *Ga. rufomaculansvaccinii* (orthographic variant) and additionally as *Ga. fructigena* var. *vaccinii.* However a strain (CBS 124.22) deposited 1922 in the CBS collection by L.C. Shear as *Ga. rufomaculans* var. *vaccinii* is lacking host information and belongs to the *C. gloeosporioides* complex (Weir *et al*. 2012, this issue).

Colletotrichum rhombiforme is closely related to *C. acerbum*, *C. australe*, *C. kinghornii* and *C. phormii*, which together form a sister clade to *C. salicis*. In this study, only strains of *C. rhombiforme* and *C. salicis* formed sexual morphs in culture. The ascospores of the two species have the same size, but differ in shape. Additionally, conidia of *C. salicis* formed on SNA are smaller than those of *C. rhombiforme*, and conidia of *C. rhombiforme* formed on *Anthriscus stem* are sometimes ellipsoidal or limoniform while those of *C. salicis* are uniformly cylindrical.

Colletotrichum rhombiforme is separated from other species by all sequences studied except the CHS-1 sequence, which is the same as that of *C. acerbum*. It can best be identified with TUB2 and ITS. The closest match in a blastn search with the TUB2 sequence of CBS 129953 with 100 % identity was AJ748624, the sequence generated from the same isolate by Talhinhas *et al.* (2005), all other isolates showed ≤ 97 % sequence identity. With the GAPDH sequence there was no closer match than 88 % identity. Closest matches with the ITS sequence (with 100 % identity) were AJ749700 from isolate PT250 (= CBS 129953) (Talhinhas *et al.* 2005), AF411704, AF411706, AF411707 and AF411719 from *Rhododendron* isolates L3, L5, L6, S2 from Latvia and Sweden (Vinnere *et al.* 2002) and with 99 % identity (1 bp difference) AF411705 from *Rhododendron* isolate L4 (Vinnere *et al.* 2002) and EF672241 from *Vaccinium* isolate DAOM 233253 (= CBS 131322, the other isolate of *C. rhombiforme* included in this study) (Robideau *et al.* 2008).

Colletotrichum salicis (Fuckel) Damm, P.F. Cannon & Crous, **comb. nov.** MycoBank MB800518. Fig. 27.

Basionym: *Sphaeria salicis* Fuckel, Jahrb. nass. Ver. Naturk. 23–24: 115. 1870.

≡ *Sphaeria salicis* Auersw., in Fuckel, Fungi Rhen. no. 913, in sched. 1864, nom. nud.

≡ *Physalospora salicis* (Fuckel) Sacc., Syll. fung. (Abellini) 1: 439. 1882.

≡ *Physosporella salicis* (Fuckel) Höhn., Annls mycol. 16: 58. 1918.

≡ *Anisostomula salicis* (Fuckel) Petr., Hedwigia 65: 198. 1925.

≡ *Plectosphaera salicis* (Fuckel) Arx & E. Müll., Beitr. Kryptfl. Schweiz 11 (no. 1): 204. 1954.

≡ *Glomerella salicis* (Fuckel) L. Holm, in Holm & Ryman, Thunbergia 30: 6. 2000.

= *Phyllachora amenti* Rostr., Skr. Christiana Vidensk.-Selsk. Forhandl. 9: 5. 1891.

≡ *Haplothecium amenti* (Rostr.) Theiss. & Syd., Annls Mycol. 13: 615. 1915.

≡ *Glomerella amenti* (Rostr.) Arx & E. Müll., Beitr. Kryptfl. Schweiz 11 (no. 1): 197. 1954.

= *Glomerella lycopersici* F. Krüger, Arbeiten Kaiserl. Biol. Anst. Land- Forstw. 9: 308. 1913.

≡ *Gloeosporium lycopersici* F. Krüger, Arbeiten Kaiserl. Biol. Anst. Land-Forstw. 9: 308. 1913.

≡ *Colletotrichum kruegerianum* Vassiljevsky, Fungi Imperfecti Parasitici 2: 321. 1950 [non *C. lycopersici* Chester 1891].

= *Physalospora miyabeana* Fukushi, Annls phytopath. *Soc. Japan* 1 (no. 4): 7. 1921.

≡ *Glomerella miyabeana* (Fukushi) Arx, Phytopath. Z. 29: 448. 1957.

Sexual morph developed on *Anthriscus stem*. Ascomata globose to pyriform, ostiolate, medium brown, darker towards the ostiole, 150–200 × 185–250 µm. *Peridium* 10–15 µm thick, composed of pale to medium brown flattened angular cells 5–15 µm diam. *Ascogenous hyphae* hyaline, smooth-walled, delicate. *Interascal tissue* composed of paraphyses, hyaline, septate, 30–80 × 2–3.5 µm, widest part at the base, tips round. *Asci* cylindrical, 55–88 × 8–12 µm, 8-spored. *Ascospores* arranged uni- to biseriately, aseptate, hyaline, smooth-walled, ovoid, fusiform, cigar-shaped or cylindrical, one end acute and one end obtuse or both ends obtuse, sometimes very slightly curved, (12.5–)13–15(–17) × (4.5–)5–6(–6.5) µm, mean ± SD = 14.1 ± 1.1 × 5.4 ± 0.5 µm, L/W ratio = 2.6.

Asexual morph on SNA. Vegetative hyphae 1–8 µm diam, hyaline to pale brown, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* absent, conidiophores formed directly on hyphae. *Setae* not observed. *Conidiophores* hyaline, smooth-walled, simple or septate and branched. *Conidiogenous cells* hyaline, smooth-walled, cylindrical to elongate ampulliform, sometimes intercalary (necks not separated from hyphae by a septum), 5–20 × 2–3.5 µm, opening 1–1.5 µm diam, collarette 0.5–1 µm long, periclinal thickening visible. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical to clavate with one end round and one end ± acute to truncate, (8.5–)10.5–15.5(–19.5) × (3.5–)3–4.5(–5) µm, mean ± SD = 13.0 ± 2.4 × 4.0 ± 0.5 µm, L/W ratio = 3.2, conidia of strains CBS 115.14 and CBS 465.83 narrower, measuring (9–)10.5–15(–17) × 2.5–3.5(–4) µm, mean ± SD = 12.7 ± 2.3 × 3.1 ± 0.5 µm, L/W ratio = 4.1 and (7.5–)9.5–15.5(–22) × 3–3.5(–4.5) µm, mean ± SD = 12.4 ± 3.1 × 3.3 ± 0.4 µm, L/W ratio = 3.8. *Appressoria* single or in small groups, medium brown, outline mostly clavate, elliptical or ovate, the edge entire or undulate, rarely lobate, (6–)8–15(–19.5) × (5–)6.5–8.5(–9.5) µm, mean ± SD = 11.5 ± 3.5 × 7.6 ± 1.0 µm, L/W ratio = 1.5.

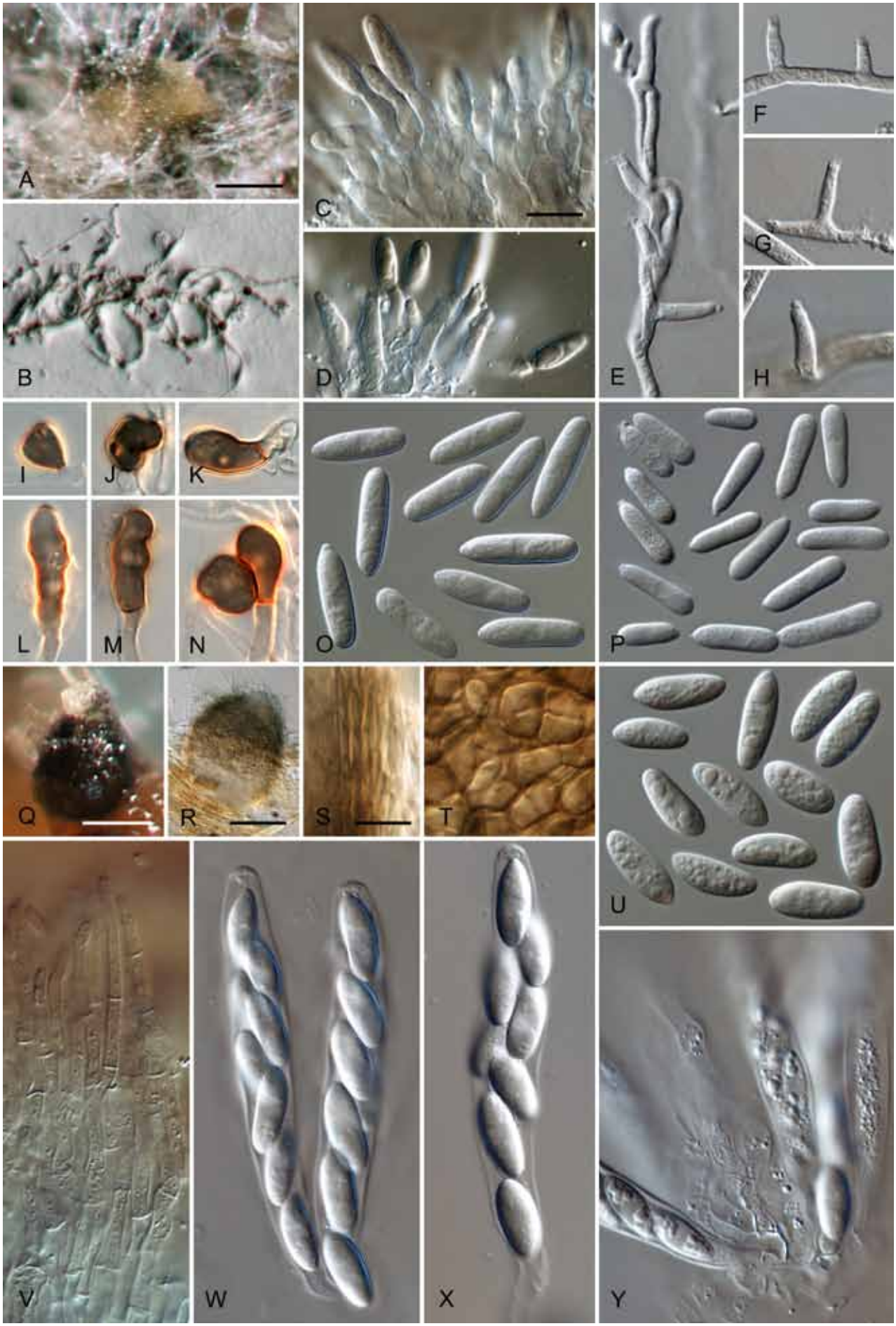

Fig. 27. *Colletotrichum salicis* (from ex-epitype strain CBS 607.94). A–B. Conidiomata. C–H. Conidiophores. I–N. Appressoria. O–P. Conidia. Q–R. Ascomata. S. Peridium in cross section. T. Outer surface of peridium. U. Ascospores. V. Paraphyses. W–Y. Asci. A, C–D, O, Q–Y. from *Anthriscus* stem. B, E–N, P. from SNA. A–B, Q. DM, C–P, R–Y. DIC, Scale bars: A, Q, R = 100 µm, C, S = 10 µm. Scale bar of A applies to A–B. Scale bar of C applies to C–P. Scale bar of S applies to S–Y.

Asexual morph on Anthriscus stem. Conidiomata acervular, only formed after *ca.* 14 d, the conidiophores, formed on a cushion of pale brown angular cells, 3.5–8.5 µm diam. *Setae* not observed. *Conidiophores* hyaline, smooth-walled, simple or septate and branched, to 30 µm long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical, 11–18 × 2.5–4 µm, opening 1–2 µm diam, collarette 0.5 µm long, periclinal thickening visible. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical with one end round and one end slightly acute to truncate, (14.5–)16–18.5(–20) × (4–)4.5–5(–5.5) µm, mean ± SD = 17.1 ± 1.3 × 4.9 ± 0.3 µm, L/W ratio = 3.5, conidia of strain CBS 115.14 smaller, measuring (9.5–)11.5–16(–18.5) × (2.5–)3–4(–4.5) µm, mean ± SD = 14.0 ± 2.3 × 3.3 ± 0.4 µm, L/W ratio = 4.2.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline, filter paper rose to iron-grey, with felty to woolly, white to olivaceous grey aerial mycelium on *Anthriscus* stem and filter paper, reverse same colours; growth rate 18–24 mm in 7 d (32.5–36 mm in 10 d). Colonies on OA flat with entire margin; surface pale amber, ochraceous to apricot, almost entirely covered by felty to floccose-felty, white, pale luteous to very pale olivaceous aerial mycelium, reverse rosy buff, ochraceous, cinnamon to buff; growth rate 21–27 mm in 7 d (34–37.5 mm in 10 d). *Conidia in mass* pale salmon.

Material examined: **Germany**, Hessen, near Oestrich (Hostrichia), on dry branches of *Salix fragilis*, collection date and collector unknown (Fuckel, *Fungi Rhenani* no. 913 (G **holotype** [not seen], K(M) **isotype** of *Sphaeria salicis*). **Netherlands**, Z.-Flevoland, *Salix* forest near Blocq van Kuffeler, from leaf spot of *Salix* sp., 11 Sep. 1994, H.A. van der Aa, (CBS H-20730 **epitype** of *Sphaeria salicis*, here designated, culture ex-epitype CBS 607.94). **Sweden**, Uppland, Uppsala, Bondkyrka parish, Nåsten forest, between Lurbo bridge and Predikstolen cliff, 22 Jun. 1946, S. Lundell (*Fungi exsiccati Suecici, praesertim Upsalienses* no. 3613a; K(M) 85441), stated by L. Holm to "agree perfectly" with the type of *Sphaeria salicis*. **Germany**, Berlin, Dahlem, from fruit of *Solanum lycopersicum,* collection date and collector unknown (deposited in CBS collection Feb. 1914 by F. Krüger), culture **ex-syntype** of *Glomerella lycopersici* CBS 115.14. **Japan**, Sapporo, on stems of *Salix purpurea*, 20 Oct. 1920, Fukushi (K(M) 110218), authentic and **possible type material** of *Physalospora miyabeana*, sent to Kew via R.M. Nattrass. **USA**, Ithaca, New York State College of Agriculture, in office, Plant Sci. Bldg, Cornell Univ., from anthracnose and dieback of *Araucaria excelsa*, 22 Apr. 1983, J. E. Carol, culture CBS 465.83.

Notes: *Colletotrichum salicis* is unusual among *Colletotrichum* species in the prominence of sexual structures relative to asexual structures; it is one of the few species to produce fertile ascomata in culture. The ascomata are not infrequently encountered on dead and dying, weakly lignified tissues including young stems, bracts and flower/fruit stalks of *Salix* species. A lack of distinctive features has caused this species to be described as new several times.

Colletotrichum salicis was first described as *Sphaeria salicis* by Fuckel (1870), based on an exsiccatum in his series *Fungi Rhenani* issued in 1864. Its label ascribed the species name to Auerswald, but no description was provided and Auerswald was not credited with the name when it was subsequently validly published.

Sphaeria salicis has been transferred to a range of different sexual morph genera. In 1954, it was moved to the rather confused genus *Plectosphaera* (von Arx & Müller 1954, Cannon 1991) and later, in 2000, to *Glomerella* (Holm & Ryman 2000).

Phyllachora amenti was described from *Salix reticulata* in Dovre, Norway by Rostrup (1891). Von Arx & Müller (1954) transferred the species to *Glomerella* (apparently not noticing the similarities with *Plectosphaera salicis*). We have not seen Rostrup's type, but his description and that of von Arx & Müller are highly reminiscent of *C. salicis* and we are confident of the synonymy. Rostrup also described a putative asexual morph of *Phyllachora amenti* with filiform septate conidia, 35–45 × 1 µm in size, formed in pycnidia. This is most likely to be an accompanying species rather than a genetically linked morph. It may be *Septoria didyma*.

Physalospora miyabeana was described from *Salix purpurea* var. *angustifolia* in Japan by Fukushi (1921), and combined into *Glomerella* by von Arx (1957) as *Glomerella miyabeana*. The pathology of this fungus was described in detail by Nattrass (1928) based on British collections from *Salix viminalis*. He noted that the species showed similarities to *Physalospora salicis*. He identified his collections as *P. miyabeana* due to the presence of a *Gloeosporium* (i.e. *Colletotrichum*) asexual morph as noted by Fukushi (1921), and considered that the species was more closely related to *Glomerella* than to *Physalospora*. Further information on pathology has been contributed by Butin (1960).

Glomerella lycopersici was described from a mummified fruit of *Solanum lycopersicum* (= *Lycopersicon esculentum*) in Germany. The ex-syntype strain CBS 115.14 hardly sporulates and did not form a sexual morph in culture, but molecular data confirm the synonymy. The ascospore measurements (15–17.3 × 5.8–6.9 µm) in the original description by Krüger (1913) differ somewhat from our measurements, and those of conidia differ even more (20–22 × 4.7–6.9 µm) from our own; the discrepancy could be due to the use of different growth media. However, the shapes of the ascospores (one side often nearly straight and one side convex or irregularly biconvex) and of the conidia (often clavate) correspond to those of strain CBS 607.94. A further synonym may be *Guignardia salicina* (syn. *Physalospora salicina*, *Glomerella salicina*), but we have not been able to source the original description or examine type material.

Colletotrichum lucidae was described on living leaves *Salix lucida* in Wisconsin, USA by Greene (1956). It forms obtuse cylindrical conidia (13–19 × 4–6.5 µm) and 1–2-septate setae (50–65 × 4–5 µm). It might also be a synonym of *C. salicis*. Greene (1964) also found the species a few years later on *S. pyrifolia*. The strains we studied did not form setae, but if *C. lucidae* is conspecific, it will just be a later synonym of *C. salicis*.

Johnston & Jones (1997) found that *C. salicis* (as *Ga. miyabeana*) had a close genetic affinity to *C. acutatum*. Vinnere (2004) regarded *Ga. miyabeana* as the sexual morph of one of the biological groups within *C. acutatum s. lat.*, and suggested that it should be recognised as a separate species. This is confirmed by our study. *Colletotrichum salicis* forms a sister clade to a clade formed by *C. phormii*, *C. rhombiforme*, *C. acerbum*, *C. australe* and *C. kinghornii*.

Fruit-inhabiting strains of *C. salicis* (as *Ga. miyabeana*) are known to be homothallic (Johnston & Jones 1997), and those from *Acer platanoides* in USA (which also belong here), were also determined as homothallic by LoBuglio & Pfister (2008). In this study, only strains of *C. salicis* and *C. rhombiforme* formed sexual morphs in culture. The ascospores of the two species are the same size, but differ in shape. Conidia of *C. salicis* formed on SNA are smaller than those of *C. rhombiforme*, and those formed on *Anthriscus stem* are uniformly cylindrical, with no ellipsoidal or limoniform conidia as found in *C. rhombiforme*. Other closely related species i.e. *C. acerbum*, *C. australe*, *C. kinghornii* and *C. phormii* form conidia on SNA, measuring on average 17.9 × 4.7 µm, 17 × 4.4 µm and 18.3 × 3.8 µm and 23 × 4.6 µm respectively, that are larger than those of *C. salicis*, measuring 13.0 × 4.0 µm.

According to our study, *C. salicis* is not restricted to a single host genus but seems to have a preference for woody hosts *(Acer*, *Araucaria*, *Malus, Populus*, *Pyrus* and especially *Salix*). According to Farr & Rossman (2012), *Glomerella amenti* has been recorded

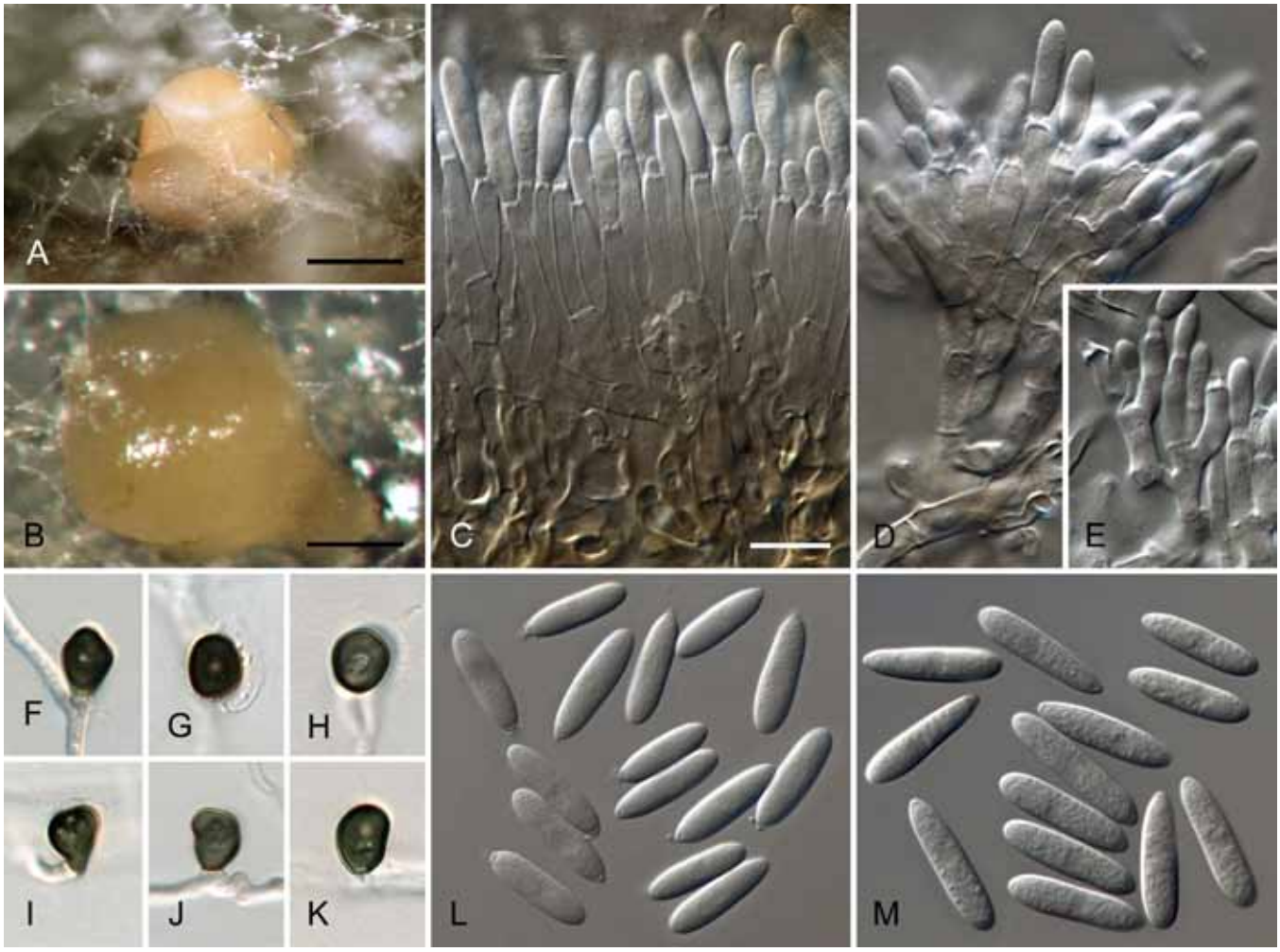

Fig. 28. *Colletotrichum scovillei* (from ex-holotype strain CBS 126529). A–B. Conidiomata. C–E. Conidiophores. F–K. Appressoria. L–M. Conidia. A, C, L. from *Anthriscus* stem. B, D–K, M. from SNA. A–B. DM, C–M. DIC, Scale bars: A = 200 µm, B = 100 µm, C = 10 µm. Scale bar of C applies to C–M.

on *Salix polaris* and *S. reticulata* in Norway (Holm & Holm 1994) and *Ga. miyabeana* was recorded on *Salix amygdaloides*, *S. babylonica*, *S. daphnoides*, *S. fragilis*, *S. gooddingii*, *S. lasiolepis*, *S.* × *alba-matsudana*, *Fragaria* × *ananassa*, *Malus domestica* and *Pyrus pyrifolia* in New Zealand (Pennycook 1989, Guerber *et al.* 2003, Gadgil 2005) on *Salix* sp. in Poland (Mulenko *et al.* 2008) and UK (Dennis 1986) and on *Acer truncatum* in China (Sun *et al.* 2011). The species is also reported from leaf lesions of *Salix fragilis*, *S. alba* var. *vitellina*, *S. cinerea* in Australia (Cunnington *et al.* 2007). Johnston & Jones (1997) suggested that *Ga. miyabeana* which causes the distinctive disease "twig canker" on *Salix* spp., only occurs on fruits (strawberry, apple, nashi, tomato) as an opportunistic secondary invader, becoming infected from willow trees that, in New Zealand, are commonly used as orchard shelter belts. Cunnington *et al.* (2007) therefore tested the pathogenicity of strains from *Salix* spp. in Australia on apple and nashi fruits. They were shown to be positive for pathogenicity but less aggressive than a different *C. acutatum s. lat.* strain that originated from an apple fruit. All *Colletotrichum* strains from *Salix* spp. in the CBS collection belong to the former species.

Colletotrichum salicis is separated from other species by all genes, except for ITS; it forms a well-supported clade (bootstrap support 98–99 %) with little sequence variation in HIS3, TUB2, GAPDH and ACT. The closest match in a blastn search with the TUB2 sequence of CBS 607.94 (with 97 % identity, 13 bp differences) was *Ga. acutata* isolate PCF 459 (EU635504) from strawberry in Belgium (Debode *et al.* 2009). With the GAPDH sequence of CBS 607.94 no match closer than 87 % identity was found. In blastn searches with the ITS sequence, numerous matches with 100 % identity were found, some of which we know to belong to distinct species.

Colletotrichum scovillei Damm, P.F. Cannon & Crous, **sp. nov.** MycoBank MB800512. Fig. 28.

Etymology: Named after Wilbur Lincoln Scoville (1865–1942) who devised the Scoville scale for measuring the "hotness" of chilli peppers, the host plant of this species.

Sexual morph not observed. *Asexual morph on SNA. Vegetative hyphae* 1–5.5 µm diam, hyaline to pale brown, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* absent, acervuli not developed, conidiophores formed directly on hyphae. *Setae* not observed. *Conidiophores* hyaline to pale brown, smooth-walled to verruculose, septate, branched, to 50 µm long. *Conidiogenous cells* hyaline smooth-walled, cylindrical to slightly inflated, 8–18 × 3–4 µm, opening 1–2 µm diam, collarette 1–1.5(–2) µm long, periclinal thickening conspicuous. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical to clavate with one end round and one end ± acute, (10.5–)12.5–15(–16.5) × (3–)3.5–4(–4.5) µm, mean ± SD = 13.7 ± 1.3 × 3.8 ± 0.3 µm, L/W ratio = 3.6, conidia of strain CBS 120708

narrower, measuring (11.5–) 12.5–14.5(–15) × 3–3.5 µm, mean ± SD = 13.5 ± 0.8 × 3.3 ± 0.2 µm, L/W ratio = 4.1. *Appressoria* single or in loose groups, medium to dark brown, smooth-walled, subglobose, ovoid to ellipsoidal, the outline entire, sometimes undulate, (3.5–)5–7.5(–10.5) × (3.5–)5–6.5(–7) µm, mean ± SD = 6.3 ± 1.2 × 5.6 ± 0.8 µm, L/W ratio = 1.1.

Asexual morph on Anthriscus stem. Conidiomata acervular, conidiophores formed on pale brown, angular, basal cells 3–8.5 µm diam. *Setae* not observed in strain CBS 126529, however in strain CBS 120708 medium brown, smooth-walled, 1–2-septate, 40–60 µm long, base cylindrical to inflated, 3.5–8 µm diam, rounded. *Conidiophores* hyaline to pale brown, smooth-walled, septate, branched, to 30 µm long. *Conidiogenous cells* hyaline to pale brown, smooth-walled, cylindrical, 9–23 × 2.5–3.5 µm, opening 1.5–2 µm diam, collarette 1 µm long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical to fusiform with both ends slightly acute or one end round, (9–)14.5–18(–19.5) × 3.5–4.5 µm, mean ± SD = 16.0 ± 1.8 × 4.0 ± 0.3 µm, L/W ratio = 4.0, conidia of strain CBS 120708 smaller, measuring (12.5–)13–16(–18) × (3–)3.5–4 µm, mean ± SD = 14.6 ± 1.4 × 3.6 ± 0.3 µm, L/W ratio = 4.1.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline, on filter paper pale olivaceous grey, on medium, filter paper and *Anthriscus* stem partly covered with floccose whitish to pale olivaceous grey aerial mycelium and on *Anthriscus* stem with few orange acervuli, reverse hyaline, rosy buff to greyish sepia, on filter paper and *Anthriscus* stem partly fuscous black; growth rate 22–22.5 mm in 7 d (33.5–35 mm in 10 d). Colonies on OA flat with entire margin; surface covered with short floccose whitish to pale olivaceous grey aerial mycelium, margin rosy buff, reverse rosy buff, olivaceous grey to iron grey in the centre; growth rate19–20 mm in 7 d (33–35 mm in 10 d). *Conidia in mass* salmon.

Material examined: **Indonesia**, from *Capsicum* sp., collection date and collector unknown, (CBS H-20792 **holotype**, culture ex-type CBS 126529 = BBA 70349 = PD 94/921-3). **Thailand**, Chiang Mai, Sansai, from anthracnose on fruit of *Capsicum annuum* (chilli), 2005, P.P. Than, culture CBS 120708 = HKUCC 10893.

Notes: *Colletotrichum scovillei* belongs to clade 2 of the *C. acutatum* species complex, and can be separated from other species by TUB2, GAPDH and ACT sequences, (with GAPDH being most clearly differential), while CHS-1 and HIS3 sequences are the same as those of *C. guajavae*. The conidia are slightly longer than is typical for *C. simmondsii* and *C. nymphaeae*, with a larger length/width ratio. However, those characters are variable within the clade, and sequence data are required to distinguish between the constituent taxa on a reliable basis.

The ex-type strain was included in the study of Nirenberg *et al.* (2002) as *C. acutatum*, and one of the strains studied (CBS 120708) was included in a paper on *Colletotrichum* diseases of chilli in Thailand (Than *et al.* 2008a), in which ITS and TUB2 sequences were generated. The strain was identified there as *C. acutatum*, a representative of one of two clades of that species complex associated with chilli. In drop inoculation tests, strains from that clade were found to cause typical anthracnose symptoms on chilli fruits. Two other species (or species complexes) were reported to cause disease of chilli by Than *et al.* (2008a), with isolates identified also as *C. gloeosporioides* and *C. capsici*. The latter taxon was found to be a synonym of *C. truncatum* by Damm *et al.* (2009). Other *Colletotrichum* species were also reported from the *C. boninese* species complex, namely *C. novae-zelandiae* and *C. karstii* in New Zealand, both occuring also on other host plants (Damm *et al.* 2012, this issue). There are several reports of *C. coccodes*, inclusive of its synonym *C. atramentarium* and of *C. nigrum*, on *Capsicum* in different countries (Farr & Rossman 2012). These species do not belong to the *C. acutatum* complex. *Colletotrichum coccodes* is more closely related to some of the curved-spored species (fig. 1 in Cannon *et al.* 2012, this issue). The identity of *C. nigrum* has not been studied recently, and it is most probably either a further synonym of *C. coccodes* or a member of the *C. gloeosporioides* complex. Another species on *Capsicum annuum* from Australia belonging to the *C. acutatum* species complex*, C. brisbanense*, is described above. Apart from earlier reports of the strains included in this study, *C. acutatum* (*s. lat.*) has also been reported on *Capsicum* in Bulgaria (Jelev *et al.* 2008), India (Kaur & Singh 1990), Korea (Cho & Shin 2004) and Taiwan (Liao *et al.* 2012).

The closest match in a blastn search with the GAPDH sequence of strain CBS 126529 (with 100 % identity) was HM038335 from *Colletotrichum* sp. isolate MFU 090619 from *Capsicum annuum* (chilli) from Laos (Phoulivong *et al.* 2010). Among the closest matches with the TUB2 sequence were 100 % identity matches with DQ454059–DQ454060 from *Capsicum annuum* isolates obtained in Thailand (Than *et al.* 2008a). One of these isolates is included in this study. Another 100 % match was with GU246633 from isolate R14 from *Capsicum annuum* in South Korea (Sang *et al.* 2011). All of these strains are likely to belong to *C. scovillei*. Based on the GAPDH sequence of strain LLB17, *C. scovillei* also occurs on *Capsicum annuum* in Taiwan (as part of group D3 in Guerber *et al.* 2003).

Colletotrichum simmondsii R.G. Shivas & Y.P. Tan, Fungal Diversity 39: 119. 2009. Fig. 29.

Sexual morph not observed. *Asexual morph on SNA. Vegetative hyphae* 1–5 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* absent, conidiophores formed directly on hyphae on the surface of the medium and in the aerial mycelium. *Setae* not observed. *Conidiophores* hyaline, smooth-walled, rather irregular in form, sometimes septate. *Conidiogenous cells* formed singly or in clusters of 2–3 apically or as lateral branches of conidiophores, hyaline, smooth-walled, cylindrical, thread-like, 7–23 × 1–2.2 µm, opening 0.5 µm diam, collarette sometimes visible, < 0.5 µm long, periclinal thickening not observed, conidiogenous cells of other strains differ, *e.g.* conidiophores of CBS 294.67 are cylindrical, sometimes slightly inflated and usually wider than the ex-type strain, measuring 4.5–18 × 1.5–4 µm, opening 1–1.5 µm diam, collarette 0.5–1 µm long, periclinal thickening visible. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical with one end round and one end acute or both ends acute, (4.5–)6.5–10(–11.5) × (2–)2.5–3.5(–4) µm, mean ± SD = 8.1 ± 1.7 × 2.9 ± 0.4 µm, L/W ratio = 2.7, conidia of other strains differ in shape and size from the ex-type strain, *e.g.* conidia of CBS 294.67 are cylindrical to fusiform with both ends acute and measure (6–)10.5–14(–16.5) × 3.5–4.5(–5.5) µm, mean ± SD = 12.3 ± 1.8 × 4.0 ± 0.4 µm, L/W ratio = 3. *Appressoria* in loose groups or dense clusters of 2–6, medium brown, round, elliptical to clavate in outline, the margine entire to undulate, (4.5–)6–9.5(–11.5) × (3.5–)4–6.5(–9.5) µm, mean ± SD = 7.8 ± 1.9 × 5.3 ± 1.1 µm, L/W ratio = 1.5.

Asexual morph on Anthriscus stem. Conidiomata not observed, conidiophores formed on aerial hyphae only. *Setae* not observed in the ex-type strain, but few setae observed in

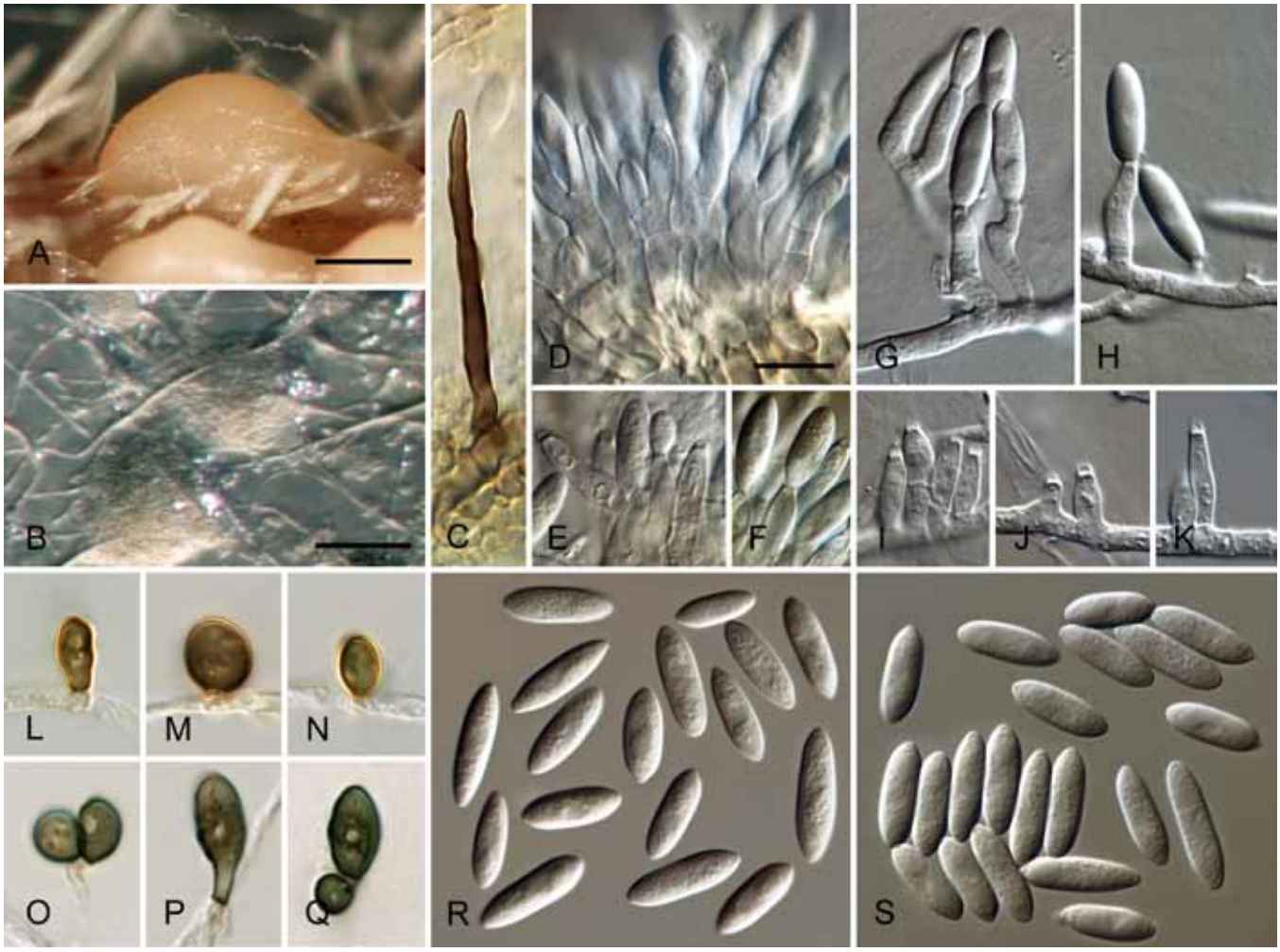

Fig. 29. *Colletotrichum simmondsii* (A–K, R-S from strain CBS 294.67. L–Q from ex-holotype strain CBS 122122). A–B. Conidiomata. C. Seta. D–K. Conidiophores. L–Q. Appressoria. R–S. Conidia. A, C–F, R. from *Anthriscus* stem. B, G–Q, S. from SNA. A–B. DM, C–S. DIC, Scale bars: A = 200 µm, B = 100 µm, D = 10 µm. Scale bar of D applies to C–S.

strain CBS 294.67, medium brown, smooth-walled, 0–1-septate, 20–40 µm long, base 2–3 µm diam, cylindrical, tip ± acute. *Conidiophores* hyaline, smooth-walled, septate, branched, to 65 µm long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical, thred-like, 19–30 × 1 µm, opening 0.5 µm diam, collarette < 0.5 µm long, periclinal thickening not observed, conidiogenous cells of other strains differ, *e.g.* conidiophores of CBS 294.67 are cylindrical to slightly inflated and usually wider than the ex-type strain, measuring 5–18 × 2.5–4.5 µm, opening 1–1.5 µm diam, collarette 0.5–1 µm long, periclinal thickening visible. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical to fusiform with both ends acute or one end round and one end acute, (6–)7–10(–12.5) × (2–)2.5–3.5(–4.5) µm, mean ± SD = 8.4 ± 1.5 × 3.0 ± 0.5 µm, L/W ratio = 2.8, conidia of other strains differ in shape and size from the ex-type strain, *e.g.* conidia of CBS 294.67 are cylindrical to fusiform with both ends acute and (11–)12–14.5(–15.5) × (3–)4–4.5(–5) µm, mean ± SD = 13.3 ± 1.2 × 4.1 ± 0.4 µm, L/W ratio = 3.2.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline to to pale isabelline, on filter paper and on *Anthriscus* stem partly covered with short white to pale grey felty aerial mycelium, reverse of filter paper white to olivaceous grey, growth 10–16 mm in 7 d (16–26 mm in 10 d), other strains differ from the type strain by growing faster, *e.g.* CBS 294.67 grows 20.5–31 mm in 7 d (34–40 mm in 10 d). Colonies on OA flat with entire margin; surface covered with felty white aerial mycelium, becoming pale olivaceous grey towards the centre, margin white or rosy buff, reverse dark olivaceous grey or salmon and purplish to iron-grey towards the margin, growth 10–16 mm in 7 d (14–24 mm in 10 d), other strains differ from the type strain by growing faster, *e.g.* CBS 294.67 grows 21–27 mm in 7 d (32.5–40 mm in 10 d). *Conidia in mass* not observed in the ex-type strain, those of other strains are salmon-orange.

Material examined: **Australia**, Queensland, Yandina, from fruit anthracnose of of *Carica papaya*, May 1987, L.M. Coates, culture **ex-holotype** CBS 122122 = BRIP 28519 = BCC 28680 = HKUCC 10928 = ICMP 17298 = KACC 43258; Queensland, Brisbane, Ormiston, from fruit rot of *Carica papaya*, 1959, J.H. Simmonds, culture ex-topotype of *C. acutatum* CBS 294.67 = BRIP 11084; Queensland, Brisbane, Nambour, from fruit rot of *Fragaria* × ananassa, 30 Mar. 1965, J.H. Simmonds, (according to BRIP database: K.G. Pegg), culture CBS 295.67 = BRIP 11086; Western Australia, Wanneroo, from rotting fruit of *Fragaria* × *ananassa*, collection date and collector unknown (deposited in IMI in 1992 by R.M. Floyd, Western Australia Department of Agriculture, Australia, No. WA 2768), culture IMI 354381 = CPC 18923. **USA**, Hawaii, from *Protea cynaroides*, 8 Dec. 1998, P.W. Crous & M.E. Palm, culture CBS 114494 = STE-U 2964 = STE-U 2088.

Notes: *Colletotrichum simmondsii* was described by Shivas & Tan (2009) to accommodate strains of the *C. acutatum* aggregate assigned to group A2 by Sreenivasaprasad & Talhinhas (2005). The type of *C. simmondsii* was erroneously designated as an epitype of *C. acutatum* (*i.e. s.str.*) by Than *et al.* (2008b), before Shivas & Tan (2009) recognised that the two taxa are not conspecific. In

this paper *C. simmondsii* is accepted in a more restricted sense. According to the TUB2 phylogeny in Shivas & Tan (2009, see fig. 2 of that paper), *C. simmondsii* includes strain BRIP 4684 from *Capsicum*, here identified as *C. brisbanense*, and sequences from GenBank belonging to strains of *C. laticiphilum* (AY376556) and *C. nymphaeae* (AY376551, AJ748607), as well as some strains from *Litchi* and *Persea* that could represent further segregate species of the *C. acutatum* species complex.

Conidial measurements of the type of *C. simmondsii* by Shivas & Tan (2009) are considerably larger (10–16 × 3.5–4.5 µm) than ours. It is possible that this discrepancy could be due to the different growth medium that they used (PDA) or the age of the culture. Measurements of all other strains studied in culture, including strain CBS 294.67, also from papaya in Australia, more closely approximate to the measurements for *C. simmondsii* given by Shivas & Tan (2009).

The ex-holotype strain (CBS 122122) of *C. simmondsii* has restricted growth; all other isolates studied are much faster growing, especially CBS 294.67 on OA. Than *et al.* (2008b) also remarked on the slow growth rate of CBS 122122 (as BRIP 28519), giving measurements of 2.3–2.6 mm (presumably per day). CBS 111531 also differs, showing buff to olivaceous pigmentation on OA, and white aerial mycelium.

Pigments produced in PDA cultures may differ among species in the *C. acutatum* complex. According to Shivas & Tan (2009) the reverse of *C. acutatum* cultures are intensely carmine-red without flecking, while those of *C. fioriniae* pale pink with flecking. Reverses in *C. simmondsii* appear pale orange or yellow, without flecking. We did not use PDA as a diagnostic growth medium, so a direct comparison cannot be made among studies, but we did not observe substantial differences in colony reverse colours in OA cultures. It appears that culture pigmentation may change with extended storage or subculturing, and we would be cautious about using these characters as diagnostic tools. In a study on *C. acutatum s. lat.* from grape in Australia, Whitelaw-Weckert *et al.* (2007) established a further molecular group beyond those recognised by Sreenivasaprasad & Talhinhas (2005), designated as A9. We have not examined their cultures, and the TUB2 sequences generated in Whitelaw-Weckert *et al.* (2007) are from a different region of the gene and could therefore not be compared with our TUB2 sequence data, but we suspect that their strains may be referable to *C. simmondsii*. The TUB2 sequence of the ex-type strain of *C. simmondsii*, CBS 122122, is identical with that of strain DAR32068 (group A9 in Whitelaw-Weckert *et al.* 2007) from strawberry in Australia as sequenced by Debode *et al.* (2009, EU635505), which supports this hypothesis.

Colletotrichum simmondsii is separable from other species by GAPDH and TUB2 sequencing, with TUB2 more strongly diagnostic, while ACT, HIS3 and CHS-1 sequences are the same as those of *C. paxtonii.* A blastn search with the TUB2 sequence of CBS 122122 resulted in 100 % matches with a number of different sequences, including some from the main clade of *C. simmondsii* seen in the phylogeny of Shivas & Tan (2009, see fig. 2 of that paper), HE573031 from strain ITEM 13492 from *Arbutus unedo* in Italy (Polizzi *et al.* 2011), AJ748635 from strain PD 89/582 (= CBS 126524) from *Cyclamen* sp. Netherlands (Talhinhas *et al.* 2005), and FJ907443 from strain BRIP 28519 (= CBS 122122, ex-holotype) as generated by Prihastuti *et al.* (2009).

Colletotrichum sloanei Damm, P.F. Cannon & Crous, **sp. nov.** MycoBank MB800515. Fig. 30.

Etymology: Named after Sir Hans Sloane (1660–1753), physician and noted natural history collector. His specimens formed a major part of the original collections of the Natural History Museum in London, his Jamaican material of the host plant became Linnaeus's type of *Theobroma cacao*, and his recipe for a milk chocolate drink was commercialised by the Cadbury brothers (Natural History Museum, 2011).

Sexual morph not observed. *Asexual morph on SNA. Vegetative hyphae* 1–8.5 µm diam, hyaline to pale brown, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* not developed, conidiophores formed directly on hyphae. *Setae* not observed. *Conidiophores* hyaline to pale brown, smooth-walled, simple or septate and branched. *Conidiogenous cells* hyaline to pale brown, smooth-walled, cylindrical to conical, sometimes lacking a basal septum and continuous with the conidiophore, polyphialides also sometimes observed, discrete phialides measuring 8–24 × 2–3.5 µm, opening 1 µm diam, collarette 1–1.5 µm long, periclinal thickening visible. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical to clavate with one end round and one end ± acute, sometimes both ends ± acute, (8.5–)12–17(–22) × (3–)3.5–4(–4.5) µm, mean 14.4 ± SD = 3.7 ± 2.5 × ± 0.3 µm, L/W ratio = 3.9. *Appressoria* single or in loose groups, medium brown, smooth-walled, elliptical, subglobose to clavate in outline, entire, the edge undulate or lobate, (4–)5–11(–17.5) × (4–)4.5–6.5(–8) µm, mean ± SD = 8.0 ± 3.0 × 5.4 ± 0.9 µm, L/W ratio = 1.5.

Asexual morph on Anthriscus stem. Conidiomata either not developed, conidiophores formed directly on hyphae or formed on a cushion of pale brown, angular, basal cells 2.5–6 µm diam. *Setae* not observed. *Conidiophores* hyaline to pale brown, smooth-walled, septate, branched, to 40 µm long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical to ± inflated, 9–18 × 2.5–4 µm, opening 1–1.5 µm diam, collarette 1–1.5 µm long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, fusiform to cylindrical with both ends acute, (9–)11.5–15.5(–19.5) × (3–)3.5–4(–4.5) µm, mean ± SD = 13.4 ± 1.8 × 3.9 ± 0.3 µm, L/W ratio = 3.5.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline buff to pale honey, on filter paper and *Anthriscus* stem partly pale olivaceous grey to olivaceous grey, the medium, filter paper and *Anthriscus* stem partly covered with thin white aerial mycelium, reverse same colours; growth rate 21–24 mm in 7 d (31–34 mm in 10 d). Colonies on OA flat with entire margin; surface iron-grey to black with a buff margin, partly covered with thin felty white aerial mycelium and orange acervuli arranged in a few rings at the margin, reverse olivaceous grey with a buff margin; growth rate 21–22.5 mm in 7 d (31–32.5 mm in 10 d). *Conidia in mass* salmon to orange.

Material examined: **Malaysia**, Borneo, Sabah, Tuaran, from leaf of *Theobroma cacao*, 1994, A.R. Rossman and C.L. Bong, (IMI 364297 **holotype**, CBS H-20796 isotype, culture ex-type IMI 364297).

Notes: A representative of the *C. acutatum* species complex does not previously appear to have been associated with *Theobroma cacao*. Three species from the *C. gloeosporioides* species complex, *C. ignotum*, *C. theobromicola* and *C. tropicale* were recognised as endophytes of *T. cacao* by Rojas *et al*. (2010). Two of these

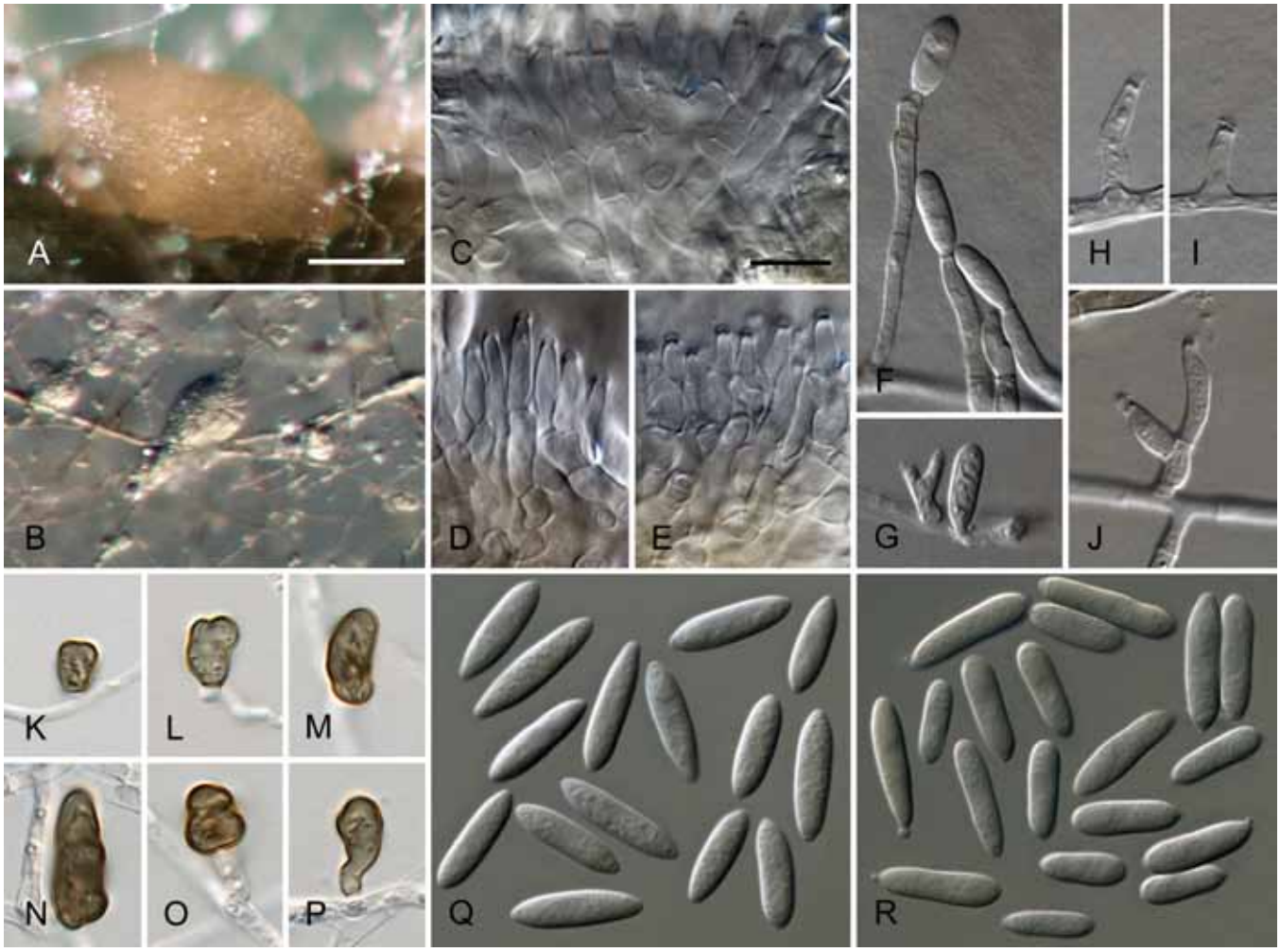

Fig. 30. *Colletotrichum sloanei* (from ex-holotype strain IMI 364297). A–B. Conidiomata. C–J. Conidiophores. K–P. Appressoria. Q–R. Conidia. A, C–E, Q. from *Anthriscus* stem. B, F–P, R. from SNA. A–B. DM, C–R. DIC, Scale bars: A = 100 µm, C = 10 µm. Scale bar of A applies to A–B. Scale bar of C applies to C–R.

species were considered to have potential to protect host plants from *Phytophthora* diseases. All have been reviewed by Weir *et al.* (2012, this issue).

Further *Colletotrichum* species have been described from *T. cacao*, including *C. brachytrichum* from leaves of *T. cacao* in Trinidad. This species has conidia that are ovoid-cylindrical with an attenuated base and a round apex, measuring 10–13.5 × 3–3.7 µm; it produces sparse setae that are dark brown, aseptate, slightly flexuous and 40 × 3.5 µm, as well as conidiogenous cells measuring 4 × 2 µm (Saccardo 1906). In contrast, *C. sloanei* forms larger conidia averaging 14.4 × 3.7 µm on SNA and 13.4 × 3.9 µm on *Anthriscus* stem. No setae were found in cultures of *C. sloanei* (though these may only form on host material) and its conidiogenous cells are much longer than those of *C. brachytrichum*.

Colletotrichum cradwickii, described from branches of *T. cacao* in Jamaica, forms conidia that are hyaline (red in mass), elongate, constricted in the middle, and 14–17 × 5 µm, with setae that are straight, rigid, acute, 2–3-septate, purplish and 70–100 × 4–6 µm in size (Saccardo & Trotter 1913). *Colletotrichum luxificum* was collected from branches, buds and fruits of *T. cacao* in Surinam and Demerara (now Guyana). It formed ovoid-oblong conidia, sometimes slightly constricted in the centre, with both sides rounded, smooth, and 13–19 × 4–5 µm. Setae were formed that were described as 2–4-septate, 50–120 × 3.5–4.5 µm (Saccardo & Trotter 1913). Although the larger size is discrepant, the constriction of the conidia and the formation of setae described for these two species is reminiscent of species in the *C. gloeosporioides* complex.

Colletotrichum theobromae forms oblong, straight conidia with obtuse ends, measuring 9–12 × 3–5 µm, and dark-brown, pluriseptate, acute setae measuring 60–75 × 3 µm (Saccardo 1906). It was found on fruits of *T. cacao* in Cameroon, and also does not agree in character with *C. sloanei*. *Gloeosporium theobromicola* [as "*theobromicolum*"], from fruits of *T. cacao* in Brazil, forms conidia that are hyaline, fusoid and 6–9 × 2–2.5 µm, (Saccardo *et al*. 1931). These are considerably smaller than those of *C. sloanei*. This organism may not be a species of *Colletotrichum*.

None of the species previously described on *T. cacao* originates from Asia, and all known species from other parts of the world differ from *C. sloanei*. Rojas *et al.* (2010) noted several unidentified taxa amongst their collections from *T. cacao* from Panama, but based on ITS sequence data, none of them belongs to the *C. acutatum* species complex. They also isolated C*. gloeosporioides s. lat*. and a strain belonging to the *C. boninense* species complex (CBS 124951); the latter was identified as *C. karstii* by Damm *et al.* (2012, this issue).

Colletotrichum sloanei may be separated from other species by TUB2, ACT, GAPDH and HIS3 sequences. It is most easily distinguished with TUB2, HIS3 and ACT. With GAPDH there is only one bp difference from *C. paxtonii*, while the CHS-1 sequence is the same as that of *C. walleri.* Closest matches in a blastn search with the TUB2 sequence of strain IMI 364297 (with 99 % identity,

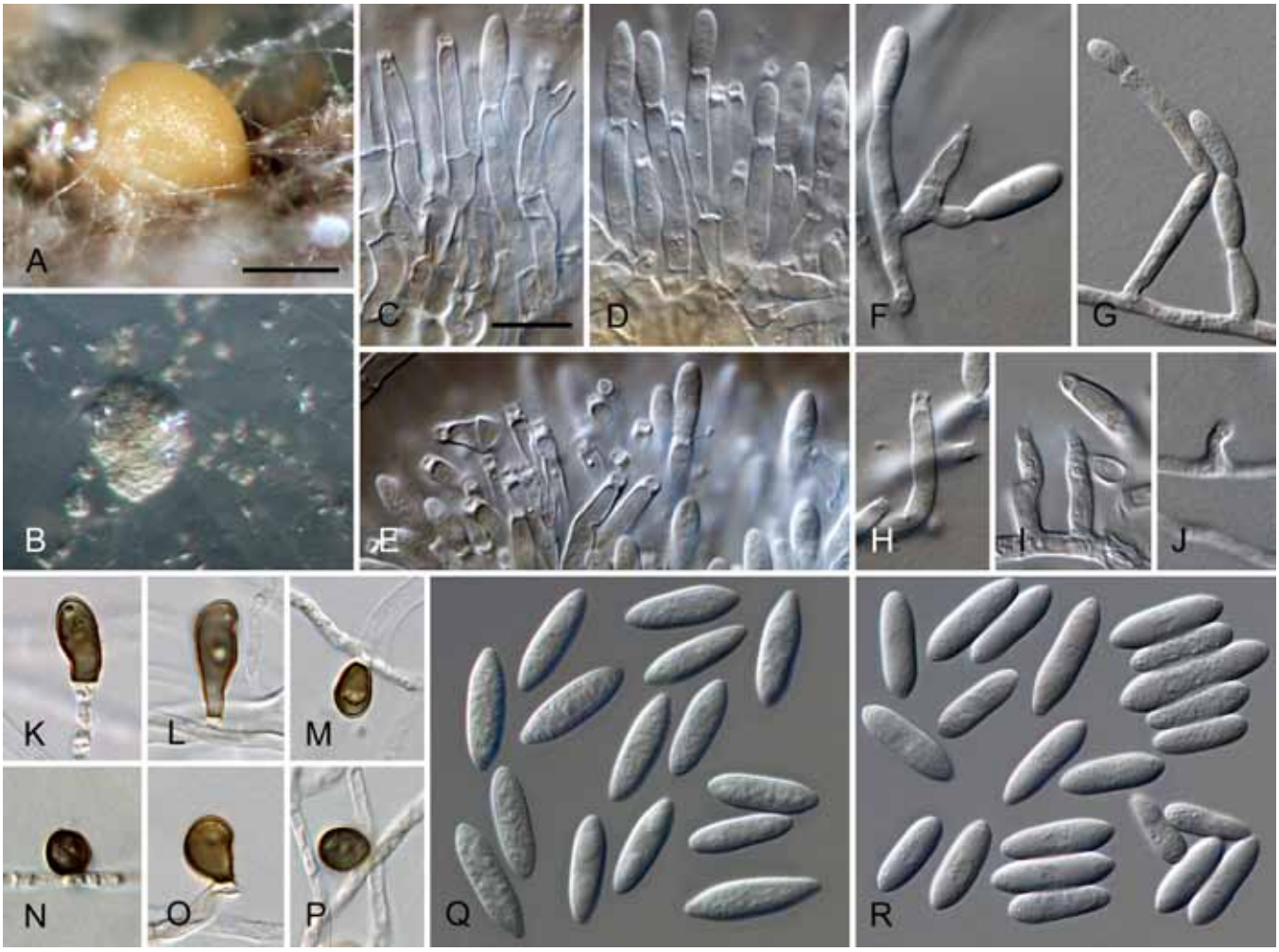

Fig. 31. *Colletotrichum tamarilloi* (from ex-holotype strain CBS 129814). A–B. Conidiomata. C–J. Conidiophores. K–P. Appressoria. Q–R. Conidia. A, C–E, Q. from *Anthriscus* stem. B, F–P, R. from SNA. A–B. DM, C–R. DIC, Scale bars: A = 100 µm, C = 10 µm. Scale bar of A applies to A–B. Scale bar of C applies to C–R.

2 or 3 bp differences) were GU183300, GU183299 and GU183295 from *C. simmondsii* strains from *Litchi chinensis* in Australia (Shivas & Tan 2009). There are no strains from *Litchi* included in our analyses, but according to the TUB2 tree in Shivas & Tan (2009), they probably belong to *C. simmondsii s. str*. The closest match with the GAPDH sequence of strain IMI 364297 covering ± the full length sequence (with 98 % identity, 6 bp differences) was HQ846719 from an unnamed plant, probably from India (Chowdappa P, Chethana CS, Madhura S, unpubl. data). Closest matches with the ITS sequence (with 99 % identity, 1 bp difference) were 25 sequences, that are not listed here.

Colletotrichum tamarilloi Damm, P.F. Cannon & Crous, **sp. nov.** MycoBank MB800516. Fig. 31.

Etymology: Named after the host plant tamarillo (*Solanum betaceum*).

Sexual morph not observed (structures that are possibly immature ascomata were seen on *Anthriscus* stem). *Asexual morph on SNA. Vegetative hyphae* 1–5.5 µm diam, hyaline to pale brown, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* not developed, 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, often integrated, discrete phialides measure 8–18 × 2.5–3.5 µm, opening 1–1.5 µm diam, collarette distinct, 1–1.5 µm long, periclinal thickening conspicuous. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical to fusiform with both ends acute, sometimes clavate with one round and one acute end, (8.5–)11.5–14.5(–15) × (2.5–)3–4(–4.5) µm, mean ± SD = 13.0 ± 1.4 × 3.5 ± 0.4 µm, L/W ratio = 3.7. *Appressoria* single, medium brown, smooth-walled, subglobose, elliptical or clavate, the edge entire, rarely slightly undulate, (4–)5–10.5(–16) × (3.5–)4.5–6.5(–8) µm, mean ± SD = 7.8 ± 2.6 × 5.5 ± 0.9 µm, L/W ratio = 1.4.

Asexual morph on Anthriscus stem. Conidiomata acervular, conidiophores formed on thick-walled, pale brown, angular, basal cells 4–8 µm diam. *Setae* not observed. *Conidiophores* hyaline to pale brown, smooth-walled, septate, branched, to 50 µm long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical, sometimes polyphialidic, 10–21 × 2–4 µm, opening 1–1.5 µm diam, collarette distinct, 1–2 µm long, periclinal thickening conspicuous. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical to fusiform with both ends acute, (10.5–)12–16(–22) × (3–)3.5–4.5(–5) µm, mean ± SD = 14.0 ± 1.9 × 4.0 ± 0.4 µm, L/W ratio = 3.5. Conidia of CBS 129955 and CBS 129811 differ in having slightly longer conidia, measuring (11.5–)13.5–17(–18.5) × 3.5–4(–4.5) µm, mean ± SD = 15.3 ± 1.7 × 3.8 ± 0.3 µm, L/W ratio = 4.0.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline to pale honey, on filter paper partly pale olivaceous grey

to olivaceous grey, filter paper *Anthriscus* stem and medium partly covered with felty white aerial mycelium (and salmon acervuli), reverse same colours; growth rate 17.5–21.5 mm in 7 d (28.5–31.5 mm in 10 d). Colonies on OA flat with entire margin; surface honey, isabelline to olivaceous, almost entirely covered by felty white to pale olivaceous grey aerial mycelium, reverse buff, olivaceous, pale olivaceous grey, olivaceous grey to iron-grey, growth rate 16–18 mm in 7 d (26–29 mm in 10 d). *Conidia in mass* salmon.

Material examined: **Colombia**, Cundinamarca, from fruit anthracnose of *Solanum betaceum*, 13 Aug. 2010, J. Molina, (CBS H-20726 **holotype**, culture ex-type CBS 129814 = T.A.6); Cundinamarca, from anthracnose on a fruit of *Solanum betaceum*, 13 Aug. 2010, J. Molina, culture CBS 129811 = T.A.3; Antioquia, Santa Rosa, from a flower of *Solanum betaceum*, 1998, collector unknown, CBS H-20728, culture CBS 129955 = Tom-12.

Notes: Afanador-Kafuri *et al.* (2003) identified several strains from tamarillo in Colombia as *C. acutatum*, three of which are included in this study. Sreenivasaprasad & Talhinhas (2005) recognised these strains as a separate molecular group, A8, closely related to A1 (*C. lupini*).

Colletotrichum tamarilloi can be separated from other species using CHS-1, HIS3, TUB2 and GAPDH sequences, most effectively with GAPDH, and forms a uniform cluster even with six genes (Fig. 1). Afanador-Kafuri *et al.* (2003) observed uniformity of banding patterns with apPCR, RAPD-PCR and A+T-rich DNA analyses of the strains they studied. They speculated that selection for clonality and homogeneity had occurred among the isolates, all of which were collected in one region in Colombia where only one cultivar of the host was cultivated. Conidia of *C. tamarilloi* are uniformly fusiform on SNA, and almost so on *Anthriscus* stem, while *C. lupini* forms conidia that are usually clavate on SNA and cylindrical on the stems. Additionally, we found that appressoria of *C. lupini* have an undulate to lobate margin, while those of *C. tamarilloi* have an entire or rarely slightly undulate edge.

This species is only known on *Solanum betaceum* in Colombia. There are no previously described species associated with this host. Three *Colletotrichum* species are reported from tamarillo in the USDA fungal databases (Farr & Rossman 2012): *C. acutatum* (Guerber *et al.* 2003, Gadgil 2005) and *C. gloeosporioides* (Gadgil 2005) in New Zealand and *C. simmondsii* in Australia (Shivas & Tan 2009). None of these species/groups is identical with *C. tamarilloi*. While *C. lupini* and *C. tamarilloi* form well-supported clusters, there are several additional species and unnamed strains from various hosts in Central and South America, as well as in Florida that are closely related to *C. lupini* and *C. tamarilloi*. One of these is from tamarillo in the same locality in Colombia (CBS 129810).

A recently reported anthracnose pathogen of tamarillo in the USA (Jones & Perez 2012) probably belongs to *C. fioriniae* according to its ITS sequence (JN863589). The *Colletotrichum* strains available to us from tamarillo in Colombia and New Zealand belong to *C. godetiae*, *C. tamarilloi* and an unnamed strain related to *C. tamarilloi* (this study), as well as *C. boninense*, *C. constrictum* and *C. karstii* belonging to the *C. boninense* species complex (Damm *et al.* 2012, this issue). Yearsley *et al.* (1988) report *C. acutatum* (*s. lat.*) infections of tamarillo in New Zealand; however none of our tamarillo strains isolated from New Zealand belongs to the *C. acutatum* group. The strains from this host included in Guerber *et al.* (2003) and assigned to group F2 formed a clade with strains described as *C. johnstonii* in this study. We did not find any species on tamarillo occurring in both Colombia and New Zealand.

Falconi & van Heusden (2011) studied *Colletotrichum* isolates collected from *Lupinus mutabilis* and tamarillo in the Ecuadorian Andes. They formed two different subgroups within *C. acutatum* based on ITS sequence data. The isolates from lupins were pathogenic to tamarillo and *vice versa*, but lupin and tamarillo isolates were each more virulent to their own hosts. ITS sequence of the ex-type strain of *C. tamarilloi*, CBS 129814, matched with 100 % identity with JN543070 from isolate Tam7 from tamarillo, as well as JN543066 from isolate Lup28 from *L. mutabilis* in Ecuador (Falconi *et al.* 2012).

The closest TUB2 blastn matches for CBS 129814 (with 99 % identity, 4 bp differences) were FN611029 and FN611028 from isolates DPI and CS-1 from *Citrus aurantifolia* and *Citrus sinensis* from USA, Florida (Ramos *et al.* 2006). The closest GAPDH matches (with 97 % identity) were EU647323 from leatherleaf fern and EU168905, EU647318 and EU647319 from sweet orange isolates, all from Florida, USA (Peres *et al.* 2008, MacKenzie *et al.* 2009).

Colletotrichum walleri Damm, P.F. Cannon & Crous, **sp. nov.** MycoBank MB800517. Fig. 32.

Etymology: Named after J.M. Waller, tropical pathologist *extra-ordinaire* and a key worker on the most important *Colletotrichum* pathogen of coffee.

Sexual morph not observed. *Asexual morph on SNA. Vegetative hyphae* 1–6 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* not developed, conidiophores formed directly on hyphae. *Setae* not observed. *Conidiophores* hyaline, smooth-walled, septate, branched, to 70 µm long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical to ampulliform, 10–14 × 3–4 µm, opening 1–1.5 µm diam, collarette 0.5–1 µm long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical to fusiform with both ends slightly acute or one end round, (6–10.5)15.5–(–19.5) × (3–)3.5–4.5(–5.5) µm, mean ± SD = 13.0 ± 2.7 × 4.0 ± 0.5 µm, L/W ratio = 3.3. *Appressoria* single, medium brown, smooth-walled, elliptical, clavate, sometimes irregularly shaped, the edge entire or undulate, (4.5–)5.5–12.5(–18.5) × (3.5–)4.5–7.5(–10.5) µm, mean ± SD = 9.0 ± 3.3 × 5.9 ± 1.4 µm, L/W ratio = 1.5.

Asexual morph on Anthriscus stem. Conidiomata either not developed, conidiophores formed directly on hyphae, or acervular, conidiophores formed on pale brown, angular, basal cells 3.5–7 µm diam. *Setae* not observed. *Conidiophores* hyaline to pale brown, smooth-walled, septate, branched, to 70 µm long. *Conidiogenous cells* hyaline to pale brown, smooth-walled, cylindrical, 12–23 × 2.5–3 µm, opening 1–1.5 µm diam, collarette 0.5–1 µm long, periclinal thickening visible to distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, sometimes slightly curved, cylindrical to fusiform with both ends ± acute or one end round, (10.5–)12–16(–18.5) × 3.5–4(–4.5) µm, mean ± SD = 13.9 ± 1.8 × 4.0 ± 0.3 µm, L/W ratio = 3.5.

Culture characteristics: Colonies on SNA flat with entire margin, hyaline, filter paper pale olivaceous grey, medium, filter paper and *Anthriscus* stem covert with fely white aerial mycelium, reverse same colours; 21–24 mm in 7 d (31–34 mm in 10 d). Colonies on OA flat with entire margin; surface covert with felty or short floccose white to pale olivaceous grey aerial mycelium, reverse olivaceous grey to iron grey, olivaceous in the centre and white towards the margin; 20–26 mm in 7 d (30.5–37.5 mm in 10 d). *Conidia in mass* salmon.

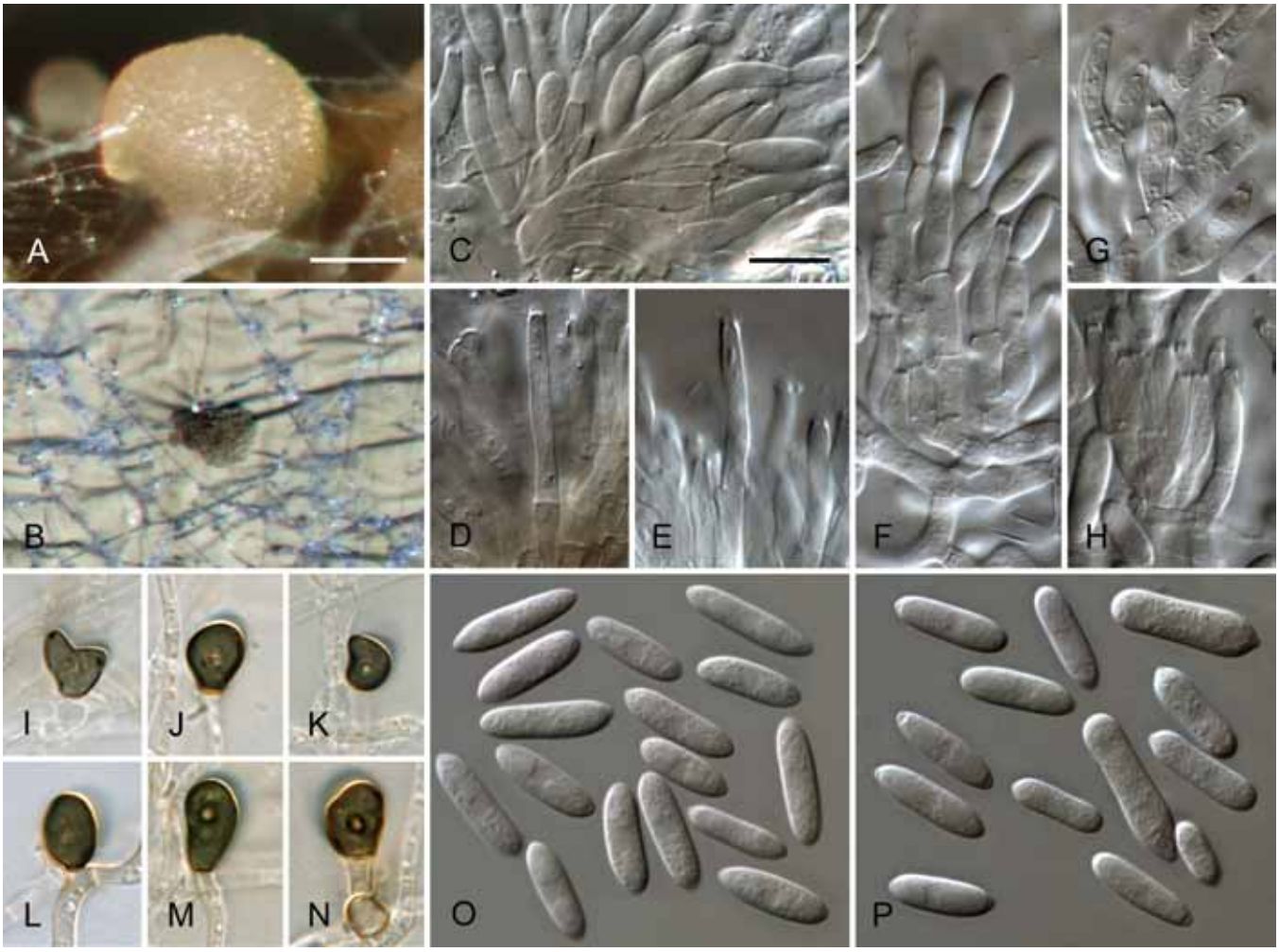

Fig. 32. *Colletotrichum walleri* (from ex-holotype strain CBS 125472). A–B. Conidiomata. C–H. Conidiophores. I–N. Appressoria. O–P. Conidia. A, C–E, O. from *Anthriscus* stem. B, F–N, P. from SNA. A–B. DM, C–P. DIC, Scale bars: A = 100 µm, C = 10 µm. Scale bar of A applies to A–B. Scale bar of C applies to C–P.

Material examined: **Vietnam**, Buon Ma Thuot-Dak Lac, from leaf tissue of *Coffea arabica*, unknown collection date, H. Nguyen, (CBS H-20795 **holotype**, culture ex-type CBS 125472 = BMT(HL)19).

Notes: Species of the *C. gloeosporioides* species complex are well-known as pathogens of *Coffea*, especially the African coffee berry disease pathogen *C. kahawae* (Waller *et al*. 1993). Additional *Coffea*-associated components of this species complex from Vietnam and Thailand have been studied by Nguyen *et al.* (2009) and Prihastuti *et al.* (2009); see Weir *et al*. (2012, this issue) for further review.

Masaba & Waller (1992) commented that strains identified as *C. acutatum* may cause minor disease of ripening coffee berries. Kenny *et al*. (2006) and Nguyen *et al.* (2010) respectively isolated, in Papua New Guinea and Vietnam, taxa in this species complex from coffee leaves, twigs and fruits. None of the Vietnamese isolates could infect undamaged coffee berries (Nguyen *et al.* 2010). One of the *C. acutatum* cultures studied by Nguyen *et al.* (BMT(HL)19) was sent to CBS and a dried sample of this strain is here designated as holotype of *C. walleri*. In this study, this is the only coffee isolate from Asia, while six other isolates from coffee, originating from Africa and Central America, belong to three other species within the *C. acutatum* species complex (*C. fioriniae*, *C. acutatum s. str.* and *C. costaricense*). Two of these strains were included in the study by Waller *et al.* (1993).

Colletotrichum walleri is separated from other species by almost all genes. It is most easily distinguished using HIS3 and ITS sequences, while sequences of other genes differ by only one bp from those of other species. The CHS-1 sequence is the same as that of *C. sloanei*. The closest TUB2 blastn match for CBS 125472 (with 99 % identity, 5 bp differences) was GU246633 from isolate R14 from *Capsicum annuum* from South Korea (Sang *et al.* 2011). The closest GAPDH match for a sequence covering ± the full gene length (with 98 % identity, 4 bp differences) was HQ846724 from isolate OBP6 from an unnamed plant, probably from India (Chowdappa P, Chethana CS, Madhura S, unpubl. data). The only 100 % match with the ITS sequence was FJ968601, the sequence of the same isolate previously sequenced by Nguyen *et al.* (2009).

DISCUSSION

Colletotrichum acutatum (in the broad sense) was originally distinguished using morphological characteristics. The primary diagnostic feature was given as the possession of fusiform conidia with acute ends (Simmonds 1965). More detailed research has however shown that this characteristic is not absolute; while most strains of species within the *C. acutatum* complex have at least a proportion of conidia with at least one acute end, it is common to find significant variation in conidial shape within species and even within individual strains. Conidia that are more or less cylindrical are frequently encountered. The variation may have multiple causes; in some circumstances it seems that secondary conidia

are formed directly from the germ tube of a germinating primary conidium, and these are smaller and more irregular in form than those from which they are derived (Buddie *et al.* 1999). Additionally, older strains, especially if they have been frequently subcultured, may have conidia that are more variable in appearance than those derived from recent stock. Nirenberg *et al.* (2002) observed that shapes differed among conidia formed in acervuli and in the aerial mycelium. The variation in conidial shape has led to species within the *C. acutatum* complex being incorrectly placed into synonymy with other *Colletotrichum* species, primarily *C. gloeosporioides* – a legacy of the revision of the genus by von Arx (1957). His work marked a new era in the understanding of *Colletotrichum* systematics (Cannon *et al.* 2012, this issue), but many of the synonymies proposed were inaccurate.

In this study we found many species that had been considered as synonyms of *C. gloeosporioides* by von Arx (1957) actually belong to the *C. acutatum* species complex, including *C. mahoniae*, *C. godetiae*, *Gm. phormii*, *Gm. lycopersici*, and *Gm. limetticola*. *Glomerella miyabeana*, here treated as a synonym of the older *C. salicis*, was regarded as a *forma specialis* of *Ga. cingulata* by von Arx (1957). Species treated as synonyms of *C. gloeosporioides* by von Arx (1957) have also been found in the *C. boninense* species complex (Damm *et al.* 2012, this issue). There were 39 strains included in this study that had previously been identified as *C. gloeosporioides* or *Ga. cingulata*, based on morphology. These strains in fact belong to 14 species in or closely related to the *C. acutatum* species complex, including *C. acutatum*, *C. australe*, *C. cosmi*, *C. costaricense*, *C. fioriniae*, *C. godetiae*, *C. limetticola*, *C. lupini*, *C. melonis*, *C. nymphaeae*, *C. phormii*, *C. rhombiforme*, *C. salicis* and *C. orchidophilum*.

Not all species of *Colletotrichum* with acute-ended conidia belong to the *C. acutatum* complex. There are species with falcate conidia that belong to the *C. graminicola* species complex (Crouch *et al.* 2009). Also outside the *C. acutatum* complex are species from herbaceous hosts with more or less curved conidia; these were previously regarded as *C. dematium* (Damm *et al*. 2009). In addition, the newly described *C. pseudoacutatum* forms straight conidia with acute ends but appears not to belong to the *C. acutatum* species complex (Cannon *et al.* 2012, this issue). Conidial shape is therefore not a uniform feature of the *C. acutatum* species complex.

Bearing in mind the frequency with which strains from the *C. acutatum* species complex are encountered and their pathogenicity to a wide range of crop plants, it would be surprising if earlier names for *C. acutatum* did not exist. Walker *et al*. (1991) found that *C. xanthii* (Halsted 1893) was synonymous with *C. acutatum* based on morphological criteria, but no authentic sequences are available and it is not clear at present in which clade this species fits. There was no interest at the time amongst *Colletotrichum* researchers to replace the name *C. acutatum*, and now the name is so widely used that a name change would be unlikely to gain recognition. Other older taxa have been recognised as belonging to the *C. acutatum* complex, but as close relatives rather than formal synonyms. *Colletotrichum lupini* was found to be an independent taxon within the *C. acutatum* complex by Nirenberg *et al*. (2002), rather than belonging to the *C. gloeosporioides* aggregate as assumed by Yang & Sweetingham (1998) and Elmer *et al.* (2001). Farr *et al.* (2006) found *C. phormii* (based on *Fusarium phormii*, Hennings 1898) to be closely related to *C. acutatum* and stated that older reports of *C. gloeosporioides* as pathogens of *Phormium* could actually refer to *C. phormii* as well.

Sreenivasaprasad & Talhinhas (2005) distinguished eight distinct molecular groups within *C. acutatum*, A1–A8 (based on ITS and TUB2 DNA sequences), each of which was recognised here as comprising one or more separate species. These authors listed previously described groups that corresponded to their own groups, including the seven groups recognised by Lardner *et al.* (1999), A, B, C, D, E, *Ga. miyabeana* and *C. acutatum f. pineum*. The Lardner *et al.* groups were mainly distinguished by morphology, partial LSU sequences and RAPD banding patterns. Some of the strains from Lardner *et al.* (1999) are included in the present study and we found that only some of them corresponded with the groups adopted by Sreenivasaprasad & Talhinhas (2005). *Colletotrichum acutatum* group A from Lardner *et al.* (1999) was regarded as corresponding to group A5, but in our study, three of the four included strains of *C. acutatum* group A – ICMP 1701, ICMP 12923 and ICMP 17991 – belonged to *C. fioriniae* (= group A3) and only one, ICMP 17992, belonged to *C. acutatum* (= group A5). At the same time, the three strains of *C. acutatum* group C, which was supposed to correspond to Sreenivasaprasad & Talhinhas group A3, were shown to belong to *C. johnstonii*, in the case of ICMP 12926 and IMI 357027, and to *C. pyricola* in the case of ICMP 12924. *Colletotrichum acutatum* group B was listed as corresponding to group A4, but the only strain included here, ICMP 12921, is now the ex-type of *C. acerbum*. ICMP strains regarded as *Ga. miyabeana,* that is ICMP 12954–12957, were confirmed here as *C. salicis* (= *Ga. miyabeana*). Our phylogenetic tree (see Fig. 1) attempts to portray the groupings of some of these earlier studies, mapped on to our own phylogeny. This illustrates the problems encountered when one compares groups established by different studies using different criteria for characterisation.

Differences in pathogenicity of strains from different hosts have been observed in several studies. Some fruit diseases caused by the *C. acutatum* complex have been shown to be caused by distinct phylogenetic lineages (Peres *et al.* 2008), and strawberry fruit rot in particular was rarely found to be caused by isolates from heterogeneous hosts (Mackenzie *et al.* 2009). Cross-infection potential was tested by, to give a few examples, Bernstein *et al.* (1995), Freeman and Shabi (1996), Freeman *et al.* (2001b) and Mackenzie *et al*. (2007). Cross-infection may occur in the field as well as in the laboratory (Afanador-Kafuri *et al.* 2003). Freeman *et al.* (2001a) found that *C. acutatum* from strawberry is able to cause lesions on various fruits, both when the fruits are wounded and when they are intact. *In vitro* infection studies by Whitelaw-Weckert *et al.* (2007) revealed low host specificity among isolates that can be assigned here to *C. acutatum*, *C. simmondsii* and *C. fioriniae*.

The lack of perceived host specificity in the *C. acutatum* complex probably has multiple causes, but much of the difficulty rests with poor identification practice in pathology studies. Many investigations even now avoid the inclusion of sequence-based evidence, or only use ITS sequences, and only a few deposit adequate voucher material. This means that name use is much less rigorous than it should be, leading to misleading results and poor comparability between studies. That said, it has to be acknowledged that many, if not most of the species we now recognise via multigene analyses appear not to be restricted to particular plants.

One factor making interpretation of pathogenicity data difficult may be incomplete or misleading information on pathology for the strains we have studied. The stated plant/fungus association does not necessarily involve a pathogenic relationship: strains could be isolated as benign endophytes or as secondary pathogens. There is much further work needed on the mechanisms of pathogenicity and on evolution at the population level, but it does appear that many *Colletotrichum* species are unusually successful in overcoming multiple host barriers.

There is limited evidence of restricted geographical range for some of the species we accept here. For most species, the number of strains available is too small to allow us to draw definite conclusions. For example, except for *C. lupini*, all isolates of clade 1 (some of which are not recognised as separate species) appear to have an origin restricted to Central and South America and the southern USA. The globalisation of agriculture has in all probability led to frequent unrecognised introductions to new regions. The baseline information we have on native versus exotic taxa is inadequate to allow introductions to be mapped. However, some of the apparently specific host-fungus connections could be supported further by tracing more strains from the respective hosts in future blastn searches, *e.g.* for *C. scovillei* and *C. limetticola*.

Colletotrichum acutatum has been regarded as a pathogen of countless host plant species, and also as occurring everywhere. Sreenivasaprasad & Talhinhas (2005) discovered that *C. acutatum* group A5, here accepted as *C. acutatum s. str.*, occurs only on certain hosts, mostly in the southern hemisphere. This study confirms that *C. acutatum s. str.* does in fact have multiple hosts, but the known host spectrum is much smaller than previously accepted.

Some host plants appear to be particularly susceptible to infection by multiple *Colletotrichum* taxa. Occurrence of species on strawberry has been particularly well researched due to the former status of *C. acutatum* as a regulated quarantine pathogen. We have found that strains from this host belong to six different clades within the *C. acutatum* species complex, namely *C. simmondsii* (three strains from Australia), *C. nymphaeae* (38 strains, mostly from Europe and the USA), *C. fioriniae* (seven strains from New Zealand, UK and USA), *C. godetiae* (10 strains, all from Europe), *C. acutatum s. str.* (one strain from Australia) and *C. salicis* (four strains from New Zealand). In a study by MacKenzie *et al.* (2009), strains from strawberry were shown to be more aggressive to strawberry than strains from *Vaccinium*. Based on TUB2 sequences generated by those authors, the strains from strawberry were assigned to *C. nymphaeae*, and the strains from *Vaccinium* to *C. fioriniae.* Possibly the reason for apparent differences in pathogenicity, lie not in the different hosts, but in the fact that the strains studied belong to different species. To our knowledge, *C. acutatum s. str.* has rarely been found in Europe, and then mostly on ornamental plants. So far, it has been isolated from strawberry only in Australia. In pathogenicity tests by Talhinhas *et al.* (2005), an isolate of *C. acutatum s. str*. from olive caused anthracnose symptoms on strawberry fruits; the virulence of this isolate was not different from that of of group A2 (*C. nymphaeae* and related species), A3 (*C. fioriniae*) or A4 (*C. godetiae*). If further quarantine regulation is to take place, other than generalised prohibition of contamination by any and all members of the *C. acutatum* species complex, then more rigorous diagnostic methods will be needed.

Other hosts that are attacked by more than one species of the *C. acutatum* species complex include apple, citrus, olive, cranberry and blueberry. For example the causal organisms of bitter rot of apple in Korea belong to *C. acutatum* clades 2 (*C. nymphaeae* and related species) and 3 (*C. fioriniae*) (Lee *et al.* 2007). In our study there are strains from *Malus* belonging to five species, namely *C. acerbum* (one strain), *C. fioriniae* (13 strains), *C. godetiae* (two strains), *C. nymphaeae* (one strain) and *C. salicis* (two strains). Talhinhas *et al.* (2005) found five groups, now recognised as species, within *C. acutatum s. lat*. occurring on olives in Portugal: A2 (actually *C. nymphaeae*), A3 (*C. fioriniae*), A4 (*C. godetiae*), A5 (*C. acutatum*) and A6 (*C. rhombiforme*).

Our study emphasises the complex nature of the evolutionary pathways that have been traversed within the *C. acutatum* species complex. Speciation has taken place much more prolifically than has been suspected so far. It seems likely that the *C. acutatum* species complex is still evolving rapidly. The emergence of new species is doubtless encouraged by the opportunities for mixing of gene pools that are provided by modern global agricultural practices combined with imperfect phytosanitary regulation.

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REFERENCES

Aa HA van der (1978). A leaf spot of *Nymphaea alba* in the Netherlands. *Netherlands Journal of Plant Pathology* **84**: 109–115.

Aa HA van der, Noordeloos ME, Gruyter J de (1990). Species concepts in some larger genera of the coelomycetes. *Studies in Mycology* **32**: 3–19.

Adhikari KN, Thomas G, Buirchell BJ, Sweetingham MW (2011). Identification of anthracnose resistance in yellow lupin (*Lupinus luteus* L.) and its incorporation into breeding lines. *Plant Breeding* **130**: 660–664.

Afanador-Kafuri L, Minz D, Maymon M, Freeman S (2003). Characterization of *Colletotrichum* isolates from tamarillo, *Passiflora*, and mango in Colombia and identification of a unique species from the genus. *Phytopathology* **93**: 579–587.

Agostini JP, Timmer LW, Mitchell DJ (1992). Morphological and pathological characteristics of strains of *Colletotrichum gloeosporioides* from citrus. *Phytopathology* **82**: 1377–1382.

Albrectsen BR, Björkén L, Varad A, Hagner Å, Wedin M, Karlsson J, Jansson S (2010). Endophytic fungi in European aspen (*Populus tremula*) leaves-diversity, detection, and a suggested correlation with herbivory resistance. *Fungal Diversity* **41**: 17–28.

Allescher A (1895). Mykologische Mittheilungen aus Süd-Bayern. *Hedwigia* **34**: 256–290.

Allescher A (1902). Fungi Imperfecti. In: *Rabenhorst's Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz*. 2d edn.**1**(7): 385–704.

Arnold AE, Mejía LC, Kyllo D, Rojas EI, Maynard Z, Robbins N, Herre EA (2003). Fungal endophytes limit pathogen damage in a tropical tree. *Proceedings of the National Academy of Science, USA* **100**: 15649–15654.

Arx JA von (1957). Die Arten der Gattung *Colletotrichum* Cda. *Phytopathologische Zeitschrift* **29**:413–468.

Arx JA von (1970). A revision of the fungi classified as *Gloeosporium*. *Bibliotheca Mycologica* **24**: 1–203.

Arx JA von (1981). *The Genera of Fungi Sporulating in Pure Culture*. 3d edn. J. Cramer, Vaduz, Lichtenstein.

Arx JA von, Müller E (1954). Die Gattungen der amerosporen Pyrenomyceten. *Beiträge zur Kryptogamenflora der Schweiz* **11** (1): 1–434.

Arx JA von, Velden FJJA van der (1961). Das *Colletotrichum* der Gurkengewächse. *Phytopathologische Zeitschrift* **41**: 228–235.

Baxter AP, Westhuizen GCA van der, Eicker A (1983). Morphology and taxonomy of South African isolates of *Colletotrichum*. *South African Journal of Botany* **2**: 259–289.

Berkeley MJ (1856). *Gloeosporium fructigenum*. *Gardeners' Chronicle* **1856**: 245.

Berkeley MJ (1874). Notices of North American fungi. *Grevillea* **3**(25): 1–17.

Bernstein B, Zehr EI, Dean RA (1995). Characteristics of *Colletotrichum* from peach, apple, pecan and other hosts. *Plant Disease* **79**: 478–482.

Bitancourt AA (1927). Uma doença do eucalipto. *Revista de Agricultura (Piracicaba)* **2**: 32–39.

Bondar G (1912). Tremoco branco e suas molestias. *Boletim de Agricultura* São Paulo **13**: 427–432.

Bondarzeva-Monteverde VN, Gutner LS, Novoselova ED (1936). [The parasitic fungi in the greenhouse of the Botanical Institutes of the Academy of Sciences of the USSR]. *Acta Instituti Botanici Nomine V.L. Komarovii Academiae Scientiarum Unionis Rerum Publicarum Soveticarum Socialisticarum* Series II, Fasc. **3**: 715–801.

Brown AE, Soepena H (1994). Pathogenicity of *Colletotrichum acutatum* and *C. gloeosporioides* on leaves of *Hevea* spp. *Mycological Research* **98**: 264–266.

Brown AE, Sreenivasaprasad S, Timmer LW (1996). Molecular characterization of slow-growing orange and key lime anthracnose strains of *Colletotrichum* from citrus as *C. acutatum*. *Phytopathology* **86**: 523–527.

Butin H (1960). Die Krankheiten der Weide und deren Erreger. *Mitteilungen aus der Biologischen Bundesanstalt* **98**: 1–46.

Cannon PF (1991). A monograph of the species of *Phyllachora* on the host family *Leguminosae*. *Mycological Papers* **163**: 1–302.

Cannon PF, Damm U, Johnston PR, Weir BS (2012). *Colletotrichum* – current status and future directions. *Studies in Mycology* **73**: 181–213.

Carbone I, Kohn LM (1999). A method for designing primer sets for speciation studies in filamentous ascomycetes. *Mycologia* **91**: 553–556.

Carpenter JB, Stevenson JA (1954). A secondary leaf spot of the *Hevea* rubber tree caused by *Glomerella cingulata*. *Plant Disease Reporter* **38**: 494–499.

Cesnik R, Ferraz JNG (2000). *Orthezia praelonga*, 1891 (*Hemiptera*, *Ortheziidae*) biologia, controle químico e biológico. Jaguariúna: embrapa meio ambiente. *Boletim Pesquisa* **9**: 27.

Cesnik R, Ferraz JNG, Oliveira RCAL, Arellano F, Maia AH (1996). Controle de *Orthezia praelonga* com o fungo *Colletotrichum gloeosporioides* isolado *Orthezia*, na regiao de Limeira, SP. *Proceedings, 5 Simpósio de Controle Biológico,* Foz de Iguaçu, Brazil.

Chen HQ, Cao L, Dekkers K, Chung KR (2005). A gene with domains related to transcription regulation is required for pathogenicity in *Colletotrichum acutatum* causing Key lime anthracnose. *Molecular Plant Pathology* **6**: 513–525.

Chung WH, Ishii H, Nishimura K, Fukaya M, Yano K, Kajitani Y (2006). Fungicide sensitivity and phylogenetic relationship of anthracnose fungi isolated from various fruit crops in Japan. *Plant Disease* **90**: 506–512.

Clausen RE (1912). A new fungus concerned in whiter tip of varieties of *Citrus medica*. *Phytopathology* **2**: 217–236.

Cooke MC (1887). New Australian fungi. *Grevillea* **16**(77): 1–6.

Cooke MC (1891). Australian fungi. *Grevillea* **19**(92): 89–92.

Costa ME, Souza da Camara M de (1953). Species aliquae mycologicae Lusitaniae. II. *Portugaliae Acta Biologica* **4**, Sér. B (1–2): 162–176.

Crouch JA, Clarke BB, White JF, Hillman BI (2009). Systematic analysis of the falcate-spored graminicolous *Colletotrichum* and a description of six new species from warm-season grasses. *Mycologia* **101**: 717–732.

Crous PW, Gams W, Stalpers JA, Robert V, Stegehuis G (2004a). MycoBank: an online initiative to launch mycology into the 21st century. *Studies in Mycology* **50**: 19–22.

Crous PW, Groenewald JZ, Risede JM, Hywel-Jones NL (2004b). *Calonectria* species and their *Cylindrocladium* anamorphs: species with sphaeropedunculate vesicles. *Studies in Mycology* **50**: 415–430.

Crous PW, Verkleij GJM, Groenewald JZ, Samson RA (eds) (2009). *Fungal Biodiversity.* CBS Laboratory Manual Series 1. Centraalbureau voor Schimmelcultures, Utrecht, Netherlands.

Cunnington JH, Powney RA, Adair RJ Finlay KJ (2007). *Glomerella miyabeana* on willows in Australia. *Australasian Mycologist* **25**: 69–72.

Curzi M (1927). De novis eumycetibus. *Atti dell'Istituto Botanico della Università e Laboratorio Crittogamico di Pavia* **3**, Ser. 3: 203–208.

Damm U, Crous PW, Fourie PH (2007). *Botryosphaeriaceae* as potential pathogens of *Prunus* species in South Africa, with descriptions of *Diplodia africana* and *Lasiodiplodia plurivora* spp. nov. *Mycologia* **99**: 664–680.

Damm U, Mostert L, Crous PW, Fourie PH (2008). Novel *Phaeoacremonium* species associated with necrotic wood of *Prunus* trees. *Persoonia* **20**: 87–102.

Damm U, Woudenberg JHC, Cannon PF, Crous PW (2009). *Colletotrichum* species with curved conidia from herbaceous hosts. *Fungal Diversity* **39**: 45–87.

Damm U, Cannon PF, Woudenberg JHC, Johnston PR, Weir BS, Tan YP, Shivas RG, Crous PW (2012). The *Colletotrichum boninense* species complex. *Studies in Mycology* **73**: 1–36.

Daniel JT, Tempelton GE, Smith RJ, Fox WT (1973). Biological control of northern jointvetch in rice with an endemic fungal disease. *Weed Science* **21**: 303–307.

Debode J, Van Hemelrijck W, Baeyen S, Creemers P, Heungens K, Maes M (2009). Quantitative detection and monitoring of *Colletotrichum acutatum* in strawberry leaves using real-time PCR. *Plant Pathology* **58**: 504–514.

Dennis RWG (1986). *Fungi of the Hebrides*. Royal Botanic Gardens, Kew, UK.

Dickens JSW, Cook RTA (1989). *Glomerella cingulata* on *Camellia*. *Plant Pathology* **38**: 75–85.

Dingley JM, Gilmour JW (1972). *Colletotrichum acutatum* Simmds. *f. sp. pineum* associated with terminal crook disease of *Pinus* spp. *New Zealand Journal of Forestry Science* **2**: 192–201.

Dinoor A, Rubin B, Nof E (2009). Epidemiological aspects of trilateral relationships between higher plants, a parasitic plant and a fungal pathogen. In Gadoury DM, Seem RC, Moyer MM & Fry WE (eds), *Proceedings of the 10th International Epidemiology Workshop* Geneva, New York: 38–40.

Ditmore M, Moore JW, TeBeest DO (2008). Interactions of two selected field isolates of *Colletotrichum gloeosporioides f. sp. aeschynomene* on *Aeschynomene virginica*. *Biological Control* **47**: 298–308.

Du M, Schardl CL, Vaillancourt LJ (2005). Using mating-type gene sequences for improved phylogenetic resolution of *Colletotrichum* species complexes. *Mycologia* **97**: 641–658.

Ellis JB, Everhart BM (1889). New and rare species of North American fungi (*Sphaeropsideae*). *Journal of Mycology* **5**(3): 145–157.

Elmer WH, Yang HA, Sweetingham MW (2001). Characterization of *Colletotrichum gloeosporioides* isolates from ornamental lupins in Connecticut. *Plant Disease* **85**: 216–219.

EPPO (2011). *EPPO A1 and A2 Lists of Pests Recommended for Regulation as Quarantine Pests*. EPPO, Paris.

Fabricatore JM (1950). *Colletotrichum mahoniae* n. sp. parassita su foglie di *Mahonia aquifolium*. *Bollettino della Stazione di Patologia Vegetale* Roma Ser. 3, **6**: 133–139.

Faedda R, Agosteo GE, Schena L, Mosca S, Frisullo S, Magnano di San Lio G, Cacciola SO (2011). *Colletotrichum clavatum* sp. nov. identified as the causal agent of olive anthracnose in Italy. *Phytopathologia Mediterranea* **50**: 283–302.

Falconi CE (2012). *Lupinus mutabilis in Ecuador with special emphasis on anthracnose resistance.* Ph.D. dissertation. Department of Plant Breeding, WageningenUniversity, The Netherlands.

Farr DF, Aime, MC, Rossman AY, Palm ME (2006). Species of *Colletotrichum* on *Agavaceae*. *Mycological Research* **110**: 1395–1408.

Farr DF, Rossman AY (2012). Fungal Databases, Systematic Mycology and Microbiology Laboratory, ARS, USDA. Retrieved February 28, 2012, from http://nt.ars-grin.gov/fungaldatabases/

Freeman S, Horowitz S, Sharon A (2001a). Pathogenic and non-pathogenic lifestyles in *Colletotrichum acutatum* from strawberry and other plants. *Phytopathology* **91**: 986–992.

Freeman S, Katan T (1997). Identification of *Colletotrichum* species responsible for anthracnose and root necrosis of strawberry in Israel. *Phytopathology* **87**: 516–521.

Freeman S, Minz D, Maymon M, Zveibil A (2001b). Genetic diversity within *Colletotrichum acutatum sensu* Simmonds. *Phytopahology* **91**: 586–592.

Freeman S, Shalev Z, Katan T (2002). Survival in soil of *Colletotrichum acutatum* and *C. gloeosporioides* pathogenic on strrawberry. *Plant Disease* **86**: 965–970.

Freeman S, Shabi E (1996). Cross-infection of subtropical and temperate fruits by *Colletotrichum* species from various hosts. *Physiological and Molecular Plant Pathology* **49**: 395–404.

Fuckel L (1870). Symbolae mycologicae. Beiträge zur Kenntnis der rheinischen Pilze. *Jahrbücher des Nassauischen Vereins für Naturkunde.* **23–24**: 1–459.

Fujinaga M, Yamagishi N, Ogiso H, Takeuchi J, Moriwaki J, Sato T (2011). First report of celery stunt anthracnose caused by *Colletotrichum simmondsii* in Japan. *Journal of General Plant Pathology* **77**: 243–247.

Fukui T (1916). On some fungi of the useful plants in Japan. *Journal of the Scientific Agricultural Society* No. **166**: 375–386. (in Japanese)

Fukushi T (1921). A willow-canker disease caused by *Physalospora miyabeana* and its conidial form *Gloeosporium*. *Annals of the Phytopathological Society of Japan* **1**: 1–11.

Gadgil PD (2005). *Fungi on Trees and Shrubs in New Zealand*. Fungi of New Zealand Volume 4. Fungal Diversity Press, Hong Kong. Gao ZY, Gan J (1992).

Biological control of dodder - a review on research progress of the bioherbicide "Lu Bao No. 1". *Chinese Journal of Biological Control* **8**: 173–175.

Gardes M, Bruns TD (1993). ITS primers with enhanced specificity for basidiomycetes - application to the identification of mycorrhizae and rusts. *Molecular Ecology* **2**: 113–118.

Garrido C, Carbú M, Fernández-Acero FJ, Vallejo I, Cantoral JM (2009). Phylogenetic relationships and genome organisation of *Colletotrichum acutatum* causing anthracnose in strawberry. *European Journal of Plant Pathology* **125**: 397–411.

Giaretta DR, Bogo A, Coelho CMM, Guidolin AF, Dantas ACM, Gomes EA (2010). ITS-rDNA phylogeny of *Colletotrichum* spp., causal agent of apple glomerella leaf spot. *Ciência Rural* **40**: 806–812.

Gielink AJ, Vermeulen H (1983). The ability of American and African *Colletotrichum* isolates to cause coffee berry disease symptoms and the association of some isolates with *Glomerella cingulata*. *European Journal of Plant Pathology* **89**: 188–190.

Glass NL, Donaldson G (1995). Development of primer sets designed for use with PCR to amplify conserved genes from filamentous ascomycetes. *Applied and Environmental Microbiology* **61**: 1323–1330.

González E, Sutton TB, Correll JC (2006). Clarification of the etiology of *Glomerella* leaf spot and bitter rot of apple caused by *Colletotrichum* spp. based on morphology and genetic, molecular and pathogenicity tests. *Phytopathology* **96**: 982–992.

Gordon AJ, Fourie A (2011). Biological control of *Hakea sericea* Schrad. and J.C.Wendl. and *Hakea gibbosa* (Sm.) Cav. (*Proteaceae*) in South Africa. *African Entomology* **19**: 303–314.

Gorter GJMA (1962). The identity of the fungus causing anthracnose of olives in South Africa. *Bothalia* **7**: 769–778.

Greene HC (1956). Notes on Wisconsin parasitic fungi. XXII. *Transactions of the Wisconsin Academy of Science* **45**: 177–191.

Greene HC (1964). Notes on Wisconsin parasitic fungi. XXXI. *Transactions of the Wisconsin Academy of Science* **53**: 197–215.

Guerber JC, Correll JC (1997). The first report of the teleomorph of *Colletotrichum acutatum* in the United States. *Plant Disease* **81**: 1334.

Guerber JC, Correll JC (2001). Characterization of *Glomerella acutata*, the teleomorph of *Colletotrichum acutatum*. *Mycologia* **93**: 216–229.

Guerber JC, Liu B, Correll, JC, Johnston PR (2003). Characterization of diversity in *Colletotrichum acutatum sensu lato* by sequence analysis of two gene introns, mtDNA and intron RFLPs, and mating compatibility. *Mycologia* **95**: 872–895.

Halsted BD (1893). Some new weed fungi. *Bulletin of the Torrey Botanical Club* **20**: 250–252.

Hemmi T (1919). Vorläufige Mitteilung über eine Anthraknose von *Carthamus tinctorius*. *Annals of the Phytopathological Society of Japan* **1**(2): 1–11.

Hemmi T (1920). Kurze Mitteilung über drei Fälle von Anthracnose auf Pflanzen. *Annals of the Phytopathological Society of Japan* **1**(3): 13–21.

Hemmi T, Kawase Y (1954). On a new anthracnose of water-lily caused by *Gloeosporium nymphaeae* sp.n. *Bulletin of Naniwa University* Ser. B **4**: 1–6.

Hennings P (1895). Fungi goyazenses. *Hedwigia* **34**: 88–116.

Hennings P (1898). Die in den Gewächshäusern des Berliner Botanischen Gartens beobachteten Pilze. *Verhandlungen des Botanischen Vereins der Provinz Brandenburg* **40**: 109–177.

Hillis DM, Bull JJ (1993). An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. *Systematic Biology* **42**: 182–192.

Hindorf H (1973). *Colletotrichum*-Population auf *Coffea arabica* L. in Kenia II. Qualitative und quantitative Unterschiede in der *Colletotrichum*-Population. *Phytopathologische Zeitschrift* **77**: 216–234

Holm L, Holm K (1994). Svalbard Pyrenomycetes. An annotated checklist. *Karstenia* **34**: 65–78.

Holm L, Ryman S (2000). Fungi exsiccati suecici. Fascicle 73 (Nos 3601-3650). *Thunbergia* **30**: 1–21.

Hoog GS de, Gerrits van den Ende AHG (1998). Molecular diagnostics of clinical strains of filamentous Basidiomycetes. *Mycoses* **41**: 183–189.

Hyde KD, Cai L, Cannon PC, Crouch JA, Crous PW, *et al*. (2009). *Colletotrichum* – names in current use. *Fungal Diversity* **39**: 147–182.

Jayasinghe CK, Fernando THPS, Priyanka UMS (1997). *Colletotrichum acutatum* is the main cause of *Colletotrichum* leaf disease of rubber in Sri Lanka. *Mycopathologia* **137**: 53–56.

Jenkins SF, Winstead NN (1964). *Glomerella magna*, cause of a new anthracnose of cucurbits. *Phytopathology* **54**: 452–454.

Johnson DA, Carris LM, Rogers JD (1997). Morphological and molecular characterization of *Colletotrichum nymphaeae* and *C. nupharicola* sp. nov. on water-lilies (*Nymphaea* and *Nuphar*). *Mycological Research* **101**: 641–649.

Johnston P, Dodd S, Park D, Massey B, Charuchinda B, *et al*. (2008). Are stable, consistant, reliable, and useful species names possible within *Colletotrichum*? In: *Colletotrichum Diseases of Fruit Crops* (Peres NA, Timmer LW, eds). Pre-Congress workshop, ICPP 2008, August 24, Torino, Italy: 1–7.

Johnston PR, Jones D (1997). Relationships among *Colletotrichum* isolates from fruit-rots assessed using rDNA sequences. *Mycologia* **89**: 420–430.

Jones RW, Perez FG (2012). First report of anthracnose caused by *Colletotrichum acutatum* on tamarillo in the United States. *Plant Disease* **96**: 587.

Joshee S, Paulus BC, Park D, Johnston PR (2009). Diversity and distribution of fungal foliar endophytes in New Zealand Podocarpaceae. *Mycological Research* **113**: 1003–1015.

Kadow KJ (1935). The raspberry white-bud disease and its relation to bitter rot of apple. *Phytopathology* **25**: 91–104.

Kelkar PV (1972). A new species of *Colletotrichum* Corda from Maharashtra, India. *Maharashtra Vidnyan Mandir Patrika* **7**: 47–48.

Kenny MK, Galea VJ, Scott PT, Price TV (2006). A comparison of *Colletotrichum* species associated with berry diseases of *Coffea arabica* L. pest and disease incursion: risk, threats and management in Papua New Guinea. *ACIAR Technical Reports* **62**: 192–199.

Kim WG, Moon YG, Cho WD, Park SD (1999). Anthracnose of safflower caused by *Colletotrichum acutatum*. *Plant Pathology Journal* **15**: 62–67.

Kinghorn WO (1936). *Glomerella phacidiomorpha* (Ces.) Pet. on *Phormium tenax* in Britain. *Annals of Applied Biology* **23**: 30–44.

Krüger F (1913). Beiträge zur Kenntnis einiger Gloeosporien. *Arbeiten aus der Kaiserlichen Biologischen Anstalt für Land- u. Forstwirtschaft* **9**: 233–323.

Kumari PS, Nair MC (1981). Some new host records for *Colletotrichum gloeosporioides* in India. *Indian Phytopathology* **34**: 402–403.

Kurlovich BS (2002). *Lupins. Geography, classification, genetic resources and breeding*. St. Petersburg: Intan.

Kwon J-H, Kang S-W, Son KE, Park C-S (1999). Anthracnose of cosmos caused by *Colletotrichum acutatum* in Korea. *The Plant Pathology Journal* **15**: 172–174.

Lardner R, Johnston PR, Plummer KM, Pearson MN (1999). Morphological and molecular analysis of *Colletotrichum acutatum sensu lato*. *Mycological Research* **103**, 275–285.

Leach CM (1958). A disease of dodder caused by the fungus *Colletotrichum destructivum. Plant Disease Reporter* **42**: 827–829.

Leandro LFS, Gleason ML, Nutter FW Jr., Wegulo SN, Dixon PM (2001). Germination and sporulation of *Colletotrichum acutatum* on symptomless strawberry leaves. *Phytopathology* **91**: 659–664.

Leandro LFS, Gleason ML, Nutter FW Jr, Wegulo SN, Dixon PM (2003). Strawberry plant extracts stimulate secondary conidiation by *Colletotrichum acutatum* on symptomless leaves. *Phytopathology* **93**: 1285–1291.

Lee DH, Kim DH, Jeon YA, Uhm JY, Hong SB (2007). Molecular and cultural characterization of *Colletotrichum* spp. causing bitter rot of apples in Korea. *Plant Pathology Journal* **23**: 37–44.

Liao CY, Chen MY, Chen YK, Wang TC, Sheu ZM, Kuo KC, Chang PFL, Chung KR, Lee MH (2012). Characterization of three *Colletotrichum acutatum* isolates from *Capsicum* spp. *European Journal of Plant Pathology* **133**: 599–608

Liu F, Hyde KD, Cai L (2011). Neotypification of *Colletotrichum coccodes*, the causal agent of potato black dot disease and tomato anthracnose. *Mycology* **2**: 248–254.

LoBuglio KF, Pfister DH (2008). A *Glomerella* species phylogenetically related to *Colletotrichum acutatum* on Norway maple in Massachusetts. *Mycologia* **100**: 710–715.

Lotter HC, Berger DK (2005). Anthracnose of lupins in South Africa is caused by *Colletotrichum lupini* var. *setosum*. *Australasian Plant Pathology* **34**: 385–392.

Lubbe CM, Denman S, Cannon PF, Groenewald JZ, Lamprecht SC, Crous PW (2004). Characterization of *Colletotrichum* species associated with diseases of Proteaceae. *Mycologia* **96**: 1268–1279.

McInnes TB, Black LL, Gatti JM Jr. (1992). Disease-free plants for management of strawberry anthracnose crown rot disease. *Plant Disease* **76**: 260–264.

MacKenzie SJ, Peres NA, Barquero MP, Arauz LF, Timmer LW (2009). Host range and genetic relatedness of *Colletotrichum acutatum* isolates from fruit crops and leatherleaf fern in Florida. *Phytopathology* **99**: 620–631.

MacKenzie SJ, Seijo TE, Legard DE, Timmer LW, Peres NA (2007). Selection for pathogenicity to strawberry in populations of *Colletotrichum gloeosporioides* from native plants. *Phytopathology* **97**: 1130–1140.

Manire CA, Rhinehart HL, Sutton DA, Thompson EH, Rinaldi MG, Buck JD, Jacobson E (2002). Disseminated Mycotic Infection Caused by *Colletotrichum acutatum* in a Kemp's Ridley Sea Turtle (*Lepidochelys kempi*). Journal of Clinical Microbiology **40**: 4273–4280.

Marcelino J, Giordano R, Gouli S, Gouli V, Parker BL, Skinner M, TeBeest D, Cesnik R (2008). *Colletotrichum acutatum* var. *fioriniae* (teleomorph: *Glomerella acutata* var. *fioriniae* var. nov.) infection of a scale insect. *Mycologia* **100**: 353–374.

Marcelino JAP, Gouli S, Parker BL, Skinner M, Schwarzberg L, Giordano R (2009). Host plant associations of an entomopathogenic variety of the fungus, *Colletotrichum acutatum,* recovered from the elongate hemlock scale, *Fiorinia externa*. 11 pp. *Journal of Insect Science* **9**: 25, available online: insectscience.org/9.25

Martinez-Culebras PV, Querol AA, Suarez-Fernandez MB, Garcia-Lopez MD, Barrio E (2003). Phylogenetic relationship among *Colletotrichum* pathogens of stawberry and design of PCR primers for their identification. *Journal of Phytopathology* **151**: 135–143.

Masaba DM, Waller JM (1992). Coffee berry disease: The current status. In JA Bailey & MJ Jeger (Eds.), *Colletotrichum: Biology, Pathology and Control*: 237–249. Wallingford: CAB International.

Mason-Gamer RJ, Kellogg EA (1996). Testing for phylogenetic conflict among molecular data sets in the tribe *Triticeae* (*Gramineae*). *Systematic Biology* **45**: 524–545.

Mejía LC, Enith I, Rojas EI, Maynard Z, Van Bael S, Arnold AE, Hebbar P, Samuels GJ, Robbins N, Herre EA (2008). Endophytic fungi as biocontrol agents of *Theobroma cacao* pathogens. *Biological Control* **46**: 4–14.

Misra AK (2004). Guava diseases – their symptoms, causes and management. In: *Diseases of fruits and vegetables. Diagnosis and management Volume 2*. (Naqvi SAMH. ed.). Kluwer Academic Publishers, Dordrecht: 81–119.

Morris MJ (1982). Biological control of *Hakea* by a fungus.*Veld & Flora* **68**: 51–52.

Mułenko W, Majewski T, Ruszkiewicz-Michalska M (2008). A preliminary checklist of micromycetes in Poland. W. Szafer Institute of Botany. *Polish Academy of Sciences* **9**: 1–752.

Nakaune R, Nakano M (2007). Benomyl resistance of *Colletotrichum acutatum* is caused by enhanced expression of beta-tubulin 1 gene regulated by putative leucine zipper protein CaBEN1. *Fungal Genetics and Biology* **44**: 1324–1335.

Nattrass RM (1928). The *Physalospora* disease of the basket willow. *Transactions of the British Mycological Society* **13**: 286–304.

Natural History Museum (2011). http://www.nhm.ac.uk/research-curation/research/projects/sloane-herbarium/hanssloane.htm, accessed 21/12/2011.

Neergaard P (1943). *8. Aarsberetning fra J. E. Ohlens Enkes Plantepatologiske Laboratorium 1. April 1942–31. Marts 1943.* J. D. Qvist & Komp. Bogtrykkeri Akts., København, Danmark.

Neergaard P (1950). Mycological Notes III. 7. *Colletotrichum godetiae* Neerg. 8. *Phoma bellidis* Neerg. 9. *Zygosporium parasiticum* (Grove) Bunting & Mason. 10. *Peronospora dianthicola* Barthelet. *Friesia* **4**: 72–80.

Nguyen PTH, Vinnere Pettersson O, Olsson P, Liljeroth E (2010). Identification of *Colletotrichum* species associated with anthracnose disease of coffee in Vietnam. *European Journal of Plant Pathology* **127**: 73–87.

Nguyen THP, Säll T, Bryngelsson T, Liljeroth E (2009). Variation among *Colletotrichum gloeosporioides* isolates from infected coffee berries at different locations in Vietnam. *Plant Pathology* **58**: 898–909.

Nirenberg HI (1976). Untersuchungen über die morphologische und biologische Differenzierung in der Fusarium-Sektion Liseola. *Mitteilungen aus der Biologischen Bundesanstalt für Land- und Forstwirtschaft Berlin-Dahlem* **169**: 1–117.

Nirenberg HI, Feiler U, Hagedorn G (2002). Description of *Colletotrichum lupini* comb. nov. in modern terms. *Mycologia* **94**: 307–320.

Nirenberg HI, Gerlach W. (2000). Bestimmung und Pathogenitätsnachweis des Erregers der Anthraknose an Bergenien. *Nachrichtenblatt des Deutschen Pflanzenschutzdienstes* **52**: 1–4.

Nylander JAA (2004). MrModeltest v2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University.

O'Donnell K, Cigelnik E (1997). Two divergent intragenomic rDNA ITS2 types within a monophyletic lineage of the fungus *Fusarium* are nonorthologous. *Molecular Phylogenetics and Evolution* **7**:103–116.

Parikka P, Pääskynkivi E, Lemmetty A (2006). *Colletotrichum acutatum*: survival in plant debris and infection on alternate hosts. NJF Report **2**(10): 37.

Pennycook SR (1989). *Plant diseases recorded in New Zealand Vol. 3*, Plant Diseases Division, DSIR, Auckland, New Zealand.

Peredo HL, Osorio M, Santamaría A (1979). *Colletotrichum acutatum f. sp.pinea*, a new pathogen of *Pinus radiata* on nurseries in Chile. *Plant Disease Reporter* **63**: 121–122.

Peres NAR, Kuramae EE, Dias MSC, Souza NL de (2002). Identification and characterization of *Colletotrichum* spp. affecting fruit after harvest in Brazil. *Journal of Phytopathology* **150**: 128–134.

Peres NA, MacKenzie SJ, Peever TL, Timmer LW (2008). Postbloom fruit drop of citrus and Key lime anthracnose are caused by distinct populations of *Colletotrichum acutatum*. *Phytopathology* **98**: 345–352.

Peres NA, Timmer LW, Adaskaveg JE, Correll JC (2005). Life styles of *Colletotrichum acutatum*. *Plant Disease* **89**: 784–796.

Petch T (1906). Descriptions of new Ceylon fungi. *Annals of the Royal Botanical Gardens, Peradeniya* **3**(1): 1–10.

Petch T (1917). Additions to Ceylon fungi. *Annals of the Royal Botanic Gardens*, *Peradeniya* **6**(3): 195–256.

Petch T (1927). *Diseases and Pests of the Rubber Tree*. Macmillan, London, UK.

Petrak F (1925). Mykologische Notizen. VIII. *Annales Mycologici* **23**: 1–143.

Phoulivong S, Cai L, Chen H, McKenzie EHC, Abdelsalam K, Hyde KD, Chukeatirote E (2010). *Colletotrichum gloeosporioides* is not a common pathogen on tropical fruits. *Fungal Diversity* **44**: 33–43.

Polashock JJ, Oudemans PV, Caruso FL, Mcmanus P, Crouch J (2009). Population structure of the North American cranberry fruit rot complex. *Plant Pathology* **58**: 1116–1127.

Polizzi G, Aiello D, Guarnaccia V, Vitale A, Perrone G, Stea G (2011). First report of damping-off on strawberry tree caused by *Colletotrichum acutatum* and *C. simmondsii* in Italy. *Plant Disease* **95**: 1588.

Prihastuti H, Cai L, Chen H, McKenzie EHC, Hyde KD (2009). Characterization of *Colletotrichum* species associated with coffee berries in northern Thailand. *Fungal Diversity* **39**: 89–109.

Rahman M, Louws FJ (2008). *Colletotrichum gloeosporioides* on strawberry: From nursery to fruiting field. In: *Colletotrichum Diseases of Fruit Crops* (Peres NA, Timmer LW, eds). Pre-Congress workshop, ICPP 2008, August 24, Torino, Italy: 54.

Rambaut A (2002). *Sequence Alignment Editor. Version 2.0.* University of Oxford, Oxford, UK.

Ramos AP, Merali Z, Talhinhas P, Sreenivasaprasad S, Oliveira H (2006). Molecular and morphological characterisation of *Colletotrichum* species involved in citrus anthracnose in Portugal. *IOBC/WPRS Bulletin* **29**: 317–326.

Rayner RW (1970). *A mycological colour chart.* Commonwealth Mycological Institute, Kew, UK.

Robideau GP, Caruso FL, Oudemans PV, McManus PS, Renaud M-A, Auclair M-E, Bilodeau GJ, Yee D, Désaulniers NL, DeVerna JW, Lévesque CA (2008). Detection of cranberry fruit rot fungi using DNA array hybridization. *Canadian Journal of Plant Pathology* **30**: 226–240.

Rojas EI, Rehner SA, Samuels GJ, Van Bael SA, Herre EA, Cannon PF, Chen R, Pang J-f, Wang R-w, Zhang Y-p, Sha T (2010). *Colletotrichum gloeosporioides* s.l. associated with *Theobroma cacao* and other plants in Panama: multilocus phylogenies distinguish pathogen and endophyte clades. *Mycologia* **102**: 1318–1338.

Ronquist F, Huelsenbeck JP (2003). MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19**: 1572–1574.

Rostrup FGE (1891). Bidrag til kundskaben om Norges soparter. II. Ascomycetes fra Dovre. *Christiana Videnskabs-Selskabs Forhandlinger* **9**: 1–14.

Saccardo PA (1884). *Sylloge Fungorum* vol. 3. Padova, Italy.

Saccardo PA (1896). Fungi aliquot Brasilienses phyllogeni. *Bulletin de la Société Royale de Botanique Belgique* **35**: 127–132.

Saccardo PA (1899). *Sylloge Fungorum* vol. 14. Padova, Italy.

Saccardo PA (1906). *Sylloge Fungorum* vol. 18. Padova, Italy.

Saccardo PA, Trotter A (1913). *Sylloge Fungorum* vol. 22. Padova, Italy.

Saccardo PA, Saccardo D, Traverso JB, Trotter A (1931). *Sylloge Fungorum* vol. 25. Padova, Italy.

Saha T, Kumar A, Ravindran M, Jacobs K, Roy B, Nazeer MA (2002). Identification of *Colletotrichum acutatum* from rubber using random amplified polymorhic DNAs and ribosomal DNA polymorphisms. *Mycological Research* **106**: 215–221.

Sang MK, Kim JD, Kim BS, Kim KD (2011). Root treatment with rhizobacteria antagonistic to *Phytophthora* blight affects anthracnose occurrence, ripening, and yield of pepper fruit in the plastic house and field. *Phytopathology* **101**: 666–678.

Sawada K (1943). Descriptive catalogue of the Formosan fungi. Part VIII. *Report of the Department of Agriculture, Government Research Institute of Formosa* **85**: 1–130.

Sawada K (1959). Descriptive catalogue of Taiwan (Formosan) fungi. XI. *Special Publication, College of Agriculture, National Taiwan University* **8**: 1–268.

Schiller M, Lübeck M, Sundelin T, Meléndez LFC, Danielsen S, Jensen DF, Ordeñana KM (2006). Two subpopulations of *Colletotrichum acutatum* are responsible for anthracnose in strawberry and leatherleaf fern in Costa Rica. *European Journal of Plant Pathology* **116**: 107–118.

Schrenk H von, Spaulding P (1903a). The bitter rot fungus. *Science n.s.* **17**: 750–751.

Schrenk H von, Spaulding P (1903b). The bitter rot of apples. *United States Department of Agriculture Bureau of Plant Industry Bulletin* **44**: 1–54, 9 plates.

Schroeter J (1894). Die Pilze Schlesiens. In: *Kryptogamen-Flora von Schlesien 2* (Cohn F, ed). J.U. Kern's Verlag, Breslau: 257–384.

Sette LD, Passarini MRZ, Delarmelina C, Salati F, Duarte MCT. (2006). Molecular characterization and antimicrobial activity of endophytic fungi from coffee plants. *World Journal of Microbiology and Biotechnology* **11**: 1185–1195.

Shear CL (1907). New species of fungi. *Bullentin of the Torrey Botanical Club* **34** (6): 305–317.

Sherriff C, Whelan MJ, Arnold GM, Lafay JF, Brygoo Y, Bailey JA (1994). Ribosomal DNA sequence analysis reveals new species groupings in the genus *Colletotrichum*. *Experimental Mycology* **18**: 121–138.

Shivas RG, Tan YP (2009). A taxonomic re-assessment of *Colletotrichum acutatum*, introducing *C. fioriniae comb. et stat. nov.* and *C. simmondsii sp. nov. Fungal Diversity* **39**: 111–122.

Simmonds JH (1965). A study of the species of *Colletotrichum* causing ripe fruit rots in Queensland. *Queensland Journal of Agricultural and Animal Science* **22**: 437–459.

Simmonds JH (1968). Type specimens of *Colletotrichum gloeosporioides* var. *minor* and *Colletotrichum acutatum*. *Queensland Journal of Agricultural and Animal Science* **25**: 178A.

Smith BJ, Magee JB, Gupton CL (1996). Susceptibility of rabbiteye blueberry cultivars to postharvest diseases. *Plant Disease* **80**: 215–218.

Sreenivasaprasad S, Mills PR, Brown AE (1994). Nucleotide sequence of the rDNA spacer 1 enables identification of isolates of *Colletotrichum* as *C. acutatum*. *Mycological Research* **98**: 186–188.

Sreenivasaprasad S, Mills PR, Meehan BM, Brown AE (1996). Phylogeny and systematics of 18 *Colletotrichum* species based on ribosomal DNA spacer sequences. *Genome* **39**: 499–512

Sreenivasaprasad S, Talhinhas P (2005). Genotypic and phenotypic diversity in *Colletotrichum acutatum*, a cosmopolitan pathogen causing anthracnose on a wide range of hosts. *Molecular Plant Pathology* **6**: 361–378.

Srivastava RN, Gupta JS (1981). Seed mycoflora from Indian seed lots of *Cosmos bipinnatus* and their control. *Indian Phytopathology* **34**: 402–403.

Stevenson JA (1971). An account of fungus exsiccati containing material from the Americas. *Beihefte zur Nova Hedwigia* **36**: 563 pp.

Stoneman B (1898). A comparative study of the development of some anthracnoses. *Botanical Gazette Chicago* **26**: 69–120.

Su YY, Noireung P, Liu F, Hyde KD, Moslem MA, Bahkali AH, Abd-Elsalam KA, Cai L (2011). Epitypification of *Colletotrichum musae*, the causative agent of banana anthracnose. *Mycoscience* **52**: 376–382.

Sun X, Guo L-D, Hyde KD (2011). Community composition of endophytic fungi in *Acer truncatum* and their role in decomposition. *Fungal Diversity* **47**: 85–95.

Suryanarayanan TS, Senthilarasu G, Muruganandam V (2000). Endophytic fungi from *Cuscuta reflexa* and its host plants. *Fungal Diversity* **4**: 117–123.

Swofford DL (2000). *PAUP* 4.0: phylogenetic analysis using parsimony (* and other methods)*. Sinauer Associates, Sunderland, MA.

Takeuchi J, Horie H (2006). First report of anthracnose of *Phormium tenax* and *Chimonanthus praecox f. concolor by Colletotrichum gloeosporioides* occurring in Japan. *Annual Report of the Kanto-Tosan Plant Protection Society* **53**: 83–85.

Takimoto K (1924). Anthracnose of crown daisy. *Japanese Journal of Horticulture (Nihon-Engei Zasshi)* **36**(9): 27–29.

Talgø V, Aamot HU, Strømeng GM, Klemsdal SS, Stensvand A (2007). *Glomerella acutata* on highbush blueberry (*Vaccinium corymbosum* L.) in Norway. Online. *Plant Health Progress* doi:10.1094/PHP-2007-0509-01-RS.

Talhinhas P, Sreenivasaprasad S, Neves-Martins J, Oliveira H (2002). Genetic and morphological characterization of *Colletotrichum acutatum* causing anthracnose of lupin. *Phytopathology* **92**: 986–996.

Talhinhas P, Sreenivasaprasad, S, Neves-Martins J, Oliveira H (2005). Molecular and phenotypic analyses reveal association of diverse *Colletotrichum acutatum* groups and a low level of *C. gloeosporioides* with olive anthracnose. *Applied and Environmental Microbiology* **71**: 2987–2998.

Talhinhas P, Neves-Martins J, Oliveira H, Sreenivasaprasad S (2009). The distinctive population structure of *Colletotrichum* species associated with olive anthracnose in the Algarve region of Portugal reflects a host-pathogen diversity hot spot. *FEMS Microbiology Letters* **296**: 31–38.

Talhinhas P, Mota-Capitão C, Martins S, Ramos AP, Neves-Martins J, Guerra-Guimarães L, Várzea V, Silva MC, Sreenivasaprasad S, Oliveira H (2011). Epidemiology, histopathology and aetiology of olive anthracnose caused by *Colletotrichum acutatum* and *C. gloeosporioides* in Portugal. *Plant Pathology* **60**: 483–495.

Tanaka T (1917). New Japanese fungi. Notes and translations – 1. *Mycologia* **9**: 249–253.

Taylor JE, Hyde KD (2003). *Microfungi of Tropical and Temperate Palms*. Fungal Diversity Press, Hong Kong.

TeBeest DO (1988). Additions to host range of *Colletotrichum gloeosporioides f. sp. aeschynomenes*. *Plant Disease* **72**: 16–18.

Thambugala TADP, Deshappriya N (2009). The role of *Colletotrichum* species on the *Colletotrichum* leaf disease of *Hevea brasiliensis* – a preliminary study. *Journal of the National Science Foundation* Sri Lanka **37**: 135–138.

Than PP, Jeewon R, Hyde KD, Pongsupasamit S, Mongkolporn O, Taylor PWJ (2008a). Characterization and pathogenicity of *Colletotrichum* species associated with anthracnose on chilli (*Capsicum* spp.) in Thailand. *Plant Pathology* **57**: 562–572.

Than PP, Shivas RG, Jeewon R, Pongsupasamit S, Marney TS, Taylor PWJ, Hyde KD (2008b). Epitypification and phylogeny of *Colletotrichum acutatum* J.H. Simmonds. *Fungal Diversity* **28**: 97–108.

Timmer LW, Brown GE (2000). Biology and control of anthracnose diseases of citrus. In: *Host Specificity, Pathology, and Host-Pathogen Interactions of Colletotrichum* (Prusky D, Freeman S, Dickman MB eds) American Phytopathological Society, St. Paul, MN, USA: 300–316.

Turconi M (1924). Una moria di giovani piante di Eucalipti. *Atti dell'Istituto Botanico della Università e Laboratorio Crittogamico di Pavia* **1**, Ser. 3: 125–135.

Turner E, Jacobson DJ, Taylor JW (2010). Biogeography of postmating reproductive isolation barriers is consistent with reinforcement selection in *Neurospora*, a model microbial eukaryote. *Journal of Evolutionary Biology* **23**: 1642–1656.

Turner E, Jacobson DJ, Taylor JW (2011). Genetic architecture of a reinforced, postmating, reproductive isolation barrier between *Neurospora* species indicates evolution via natural selection. *PLoS Genetics* **7**: e1002204. doi:10.1371/journal.pgen.1002204.

Uematsu S, Kageyama K, Moriwaki J, Sato T (2012). *Colletotrichum carthami* comb nov., an anthracnose pathogen of safflower, garland chrysanthemum and pot marigold, revived by molecular phylogeny with authentic herbarium specimens. *Journal of General Plant Pathology*. doi: 10.1007/s10327-012-0397-3

Vichova J, Vejrazka K, Cholastova T, Pokorny R, Hrudova E (2011). *Colletotrichum simmondsii* causing anthracnose on safflower in the Czech Republic. *Plant Disease* **95**: 79.

Viégas AP (1946). Alguns fungos do Brasil XII. Fungi imperfecti – Melanconiales. *Bragantia* **6**: 1–37.

Vinnere O (2004). *Approaches to Species Delineation in Anamorphic (Mitosporic) Fungi: A Study on Two Extreme Cases*. Ph.D. dissertation. Department of Evolutionary Biology, Uppsala University, Sweden.

Vinnere O, Fatehi J, Wright SAI, Gerhardson B (2002). The causal agent of anthracnose of *Rhododendron* in Sweden and Latvia. *Mycological Research* **106**: 60–69.

Walker J, Nikandrow A, Millar GD (1991). Species of *Colletotrichum* on *Xanthium* (Asteraceae) with comments on some taxonomic and nomenclatural problems in the genus *Colletotrichum*. *Mycological Research* **95**: 1175–1193.

Waller JM, Bridge PD, Black B, Hakiza G (1993). Characterization of the coffee berry disease pathogen *Colletotrichum kahawae* sp. nov. *Mycological Research* **97**: 989–994.

Watson AK, Gressel J, Sharon A, Dinoor A (2000). *Colletotrichum* strains for weed control. In: *Colletotrichum*. *Host Specificity, Pathology and Host-Pathogen Interaction* (Prusky D, Freeman S & Dickman MB, eds). APS Press, St Paul, USA: 245–265.

Weir BS, Johnston PR, Damm U (2012). The *Colletotrichum gloeosporioides* species complex. *Studies in Mycology* **73**: 115–180.

Wharton PS, Diéguez-Uribeondo J (2004). The biology of *Colletotrichum acutatum*. *Anales del Jardín Botánico de Madrid* **61**: 3–22.

Wharton PS, Schilder AMC (2008) Novel infection strategies of *Colletotrichum acutatum* on ripe blueberry fruit. *Plant Pathology* **57**: 122–134.

White TJ, Bruns T, Lee S, Taylor J (1990). Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: *PCR Protocols: a guide to methods and applications* (Innis MA, Gelfand DH, Sninsky JJ, White TJ, eds). Academic Press, San Diego, USA: 315–322.

Whitelaw-Weckert MA, Curtin SJ, Huang R, Steel CC, Blanchard CL, Roffey PE. (2007). Phylogenetic relationships and pathogenicity of *Colletotrichum acutatum* isolates from grape in subtropical Australia. *Plant Pathology* **56**: 448–463.

Wollenweber HW (1916). *Fusaria Autographice Delineata* **1**, 1 edn., Berlin, Germany.

Woudenberg JHC, Aveskamp MM, Gruyter J de, Spiers AG, Crous PW (2009). Multiple *Didymella* teleomorphs are linked to the *Phoma clematidina* morphotype. *Persoonia* **22**: 56–62.

Yaguchi Y, Suyama K, Ushiyama K, Kobayashi M, Saito T, Nakamura S (1996). Anthracnose of *Cosmos bipinnatus* caused by *Colletotrichum acutatum* Simmonds ex Simmonds. *Annales of the Phytopathological Society of Japan* **62**: 433–436.

Yang HA, Sweetingham MW (1998). The taxonomy of *Colletotrichum* isolates associated with lupin anthracnose. *Australian Journal of Agricultural Research* **49**: 1213–1223.

Yang YL, Cai L, Yu ZN, Liu ZY, Hyde KD (2011). *Colletotrichum* species on *Orchidaceae* in southwest China. *Cryptogamie Mycologie* **32**: 229–253.

Yang YL, Liu ZY, Cai L, Hyde KD, Yu ZN, McKenzie EHC (2009). *Colletotrichum* anthracnose of *Amaryllidaceae*. *Fungal Diversity* **39**: 123–146.

Yearsley CW, Huang BY, McGrath HJ, Fry J, Stec MGH, Dale JR (1988). Red tamarillos (*Cyphomandra betacea*): comparison of two postharvest dipping strategies for the control of fungal storage disorders. *New Zealand Journal of Experimental Agriculture* **16**: 359–366.

Yuan ZL, Chen YC, Yang Y (2009). Diverse non-mycorrhizal fungal endophytes inhabiting an epiphytic, medicinal orchid (*Dendrobium nobile*): estimation and characterization. *World Journal of Microbiology and Biotechnology* **25**: 295–303.

Zhang TY (1985). A forma specialis of *Colletotrichum gloeosporioides* on *Cuscuta* spp. *Acta Mycologica Sinica* **4**: 234–239.

Studies in Mycology 73: 115–180.

The *Colletotrichum gloeosporioides* species complex

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Abstract: The limit of the *Colletotrichum gloeosporioides* species complex is defined genetically, based on a strongly supported clade within the *Colletotrichum* ITS gene tree. All taxa accepted within this clade are morphologically more or less typical of the broadly defined *C. gloeosporioides*, as it has been applied in the literature for the past 50 years. We accept 22 species plus one subspecies within the *C. gloeosporioides* complex. These include *C. asianum*, *C. cordylinicola*, *C. fructicola*, *C. gloeosporioides*, *C. horii*, *C. kahawae* subsp. *kahawae*, *C. musae*, *C. nupharicola*, *C. psidii*, *C. siamense*, *C. theobromicola*, *C. tropicale*, and *C. xanthorrhoeae*, along with the taxa described here as new, *C. aenigma*, *C. aeschynomenes*, *C. alatae*, *C. alienum*, *C. aotearoa*, *C. clidemiae*, *C. kahawae* subsp. *ciggaro*, *C. salsolae*, and *C. ti*, plus the nom. nov. *C. queenslandicum* (for *C. gloeosporioides* var. *minus*). All of the taxa are defined genetically on the basis of multi-gene phylogenies. Brief morphological descriptions are provided for species where no modern description is available. Many of the species are unable to be reliably distinguished using ITS, the official barcoding gene for fungi. Particularly problematic are a set of species genetically close to *C. musae* and another set of species genetically close to *C. kahawae*, referred to here as the Musae clade and the Kahawae clade, respectively. Each clade contains several species that are phylogenetically well supported in multi-gene analyses, but within the clades branch lengths are short because of the small number of phylogenetically informative characters, and in a few cases individual gene trees are incongruent. Some single genes or combinations of genes, such as glyceraldehyde-3-phosphate dehydrogenase and glutamine synthetase, can be used to reliably distinguish most taxa and will need to be developed as secondary barcodes for species level identification, which is important because many of these fungi are of biosecurity significance. In addition to the accepted species, notes are provided for names where a possible close relationship with *C. gloeosporioides sensu lato* has been suggested in the recent literature, along with all subspecific taxa and *formae speciales* within *C. gloeosporioides* and its putative teleomorph *Glomerella cingulata*.

Key words: anthracnose, *Ascomycota,* barcoding, *Colletotrichum gloeosporioides*, *Glomerella cingulata*, phylogeny, systematics.
Taxonomic novelties: Name replacement - *C. queenslandicum* B. Weir & P.R. Johnst. **New species -** *C. aenigma* B. Weir & P.R. Johnst., *C. aeschynomenes* B. Weir & P.R. Johnst., *C. alatae* B. Weir & P.R. Johnst., C. *alienum* B. Weir & P.R. Johnst, *C. aotearoa* B. Weir & P.R. Johnst., *C. clidemiae* B. Weir & P.R. Johnst., *C. salsolae* B. Weir & P.R. Johnst., *C. ti* B. Weir & P.R. Johnst. **New subspecies -** *C. kahawae* subsp. *ciggaro* B. Weir & P.R. Johnst. **Typification: Epitypification -** *C. queenslandicum* B. Weir & P.R. Johnst.

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INTRODUCTION

The name *Colletotrichum gloeosporioides* was first proposed in Penzig (1882), based on *Vermicularia gloeosporioides*, the type specimen of which was collected from *Citrus* in Italy. Much of the early literature used this name to refer to fungi associated with various diseases of *Citrus*, with other species established for morphologically similar fungi from other hosts. However, several early papers discussed the morphological similarity between many of the *Colletotrichum* spp. that had been described on the basis of host preference, and used inoculation tests to question whether or not the species were distinct. Some of these papers investigated in culture the link between the various *Colletotrichum* species and their sexual *Glomerella* state (*e.g.* Shear & Wood 1907, Ocfemia & Agati 1925). Authors such as Shear & Wood (1907, 1913) and Small (1926) concluded that many of the species described on the basis of host preference were in fact the same, rejecting apparent differences in host preference as a basis for taxonomic segregation. Small (1926) concluded that the names *Glomerella cingulata* and *Colletotrichum gloeosporioides* should be used for the sexual and asexual morphs, respectively, of the many *Colletotrichum* spp. they regarded as conspecific. *Colletotrichum gloeosporioides* was stated to be the earliest name with a proven link to what they regarded as a biologically diverse *G. cingulata*. The studies of von Arx & Müller (1954) and von Arx (1957, 1970) taxonomically formalised this concept.

The "von Arxian" taxonomic concept for *Colletotrichum* saw large numbers of species synonymised with the names *C. graminicola* (for grass-inhabiting species) and *C. gloeosporioides* (for non-grass inhabiting species with straight conidia). The genetic and biological diversity encompassed by these names was so broad that they became of little practical use to plant pathologists, conveying no information about pathogenicity, host range, or other attributes. The von Arx & Müller (1954) and von Arx (1957) studies were not based on direct examination of type material of all species and some of the synonymy proposed in these papers has subsequently been found to be incorrect. Examples include the segregation of *C. acutatum* (Simmonds 1965) and *C. boninense* (Moriwaki *et al.* 2003) from *C. gloeosporioides sensu* von Arx (1957). Other studies published elsewhere in this volume (Damm *et al*. 2012a, b) show that several species regarded as synonyms of *C. gloeosporioides* by von Arx (1957) are members of the *C. acutatum* complex (*e.g. C. godetiae*, *Gloeosporium limetticola*, *G. lycopersici*, and *G. phormii*) or the *C. boninense* complex (*e.g. C. dracaenae*). Recent molecular studies have resulted in a much better understanding of phylogenetic relationships amongst the

grass-inhabiting species of the *C. graminicola* group and the development of a more useful taxonomy for this group of fungi (*e.g.* Hsiang & Goodwin 2001, Du *et al.* 2005, and Crouch *et al.* 2006). This group is now recognised as comprising several host-specialised, genetically well characterised species, but a modern taxonomy for *C. gloeosporioides* has yet to be resolved.

Von Arx (1970) and Sutton (1980) distinguished the *C. gloeosporioides* group using conidial shape and size. A few apparently host-specialised, *C. gloeosporioides*-like taxa were retained by these authors, but the basis of their identification was often difficult to understand. Prior to the availability of DNA sequence data, taxonomic concepts within *Colletotrichum* were based on features such as host species, substrate, conidial size and shape, shape of appressoria, growth rate in culture, colour of cultures, presence or absence of setae, whether or not the teleomorph develops, etc. Some studies have found characters such as these useful for distinguishing groups within *C. gloeosporioides* (*e.g.* Higgins 1926, Gorter 1956, Hindorf 1973, and Johnston & Jones 1997). However, problems arise because many of these morphological features change under different conditions of growth (dependent upon growth media, temperature, light regime, etc.), or can be lost or change with repeated subculturing. Host preference is poorly controlled — even good, well-defined pathogens causing a specific disease can be isolated by chance from other substrates (*e.g.* Johnston 2000). *Colletotrichum* conidia will germinate on most surfaces, form an appressorium, remain attached to that surface as a viable propagule or perhaps as a minor, endophytic or latent infection, and grow out from there into senescing plant tissue or onto agar plates if given the opportunity. In addition, the same disease can be caused by genetically distinct sets of isolates, the shared pathogenicity presumably independently evolved, *e.g.* the bitter rot disease of apple is caused by members of both the *C. acutatum* and *C. gloeosporioides* species complexes (Johnston *et al.* 2005).

Sutton (1992) commented on *C. gloeosporioides* that "No progress in the systematics and identification of isolates belonging to this complex is likely to be made based on morphology alone". A start was made towards a modern understanding of this name with the designation of an epitype specimen with a culture derived from it to stabilise the application of the name (Cannon *et al.* 2008). Based on ITS sequences, the ex-epitype isolate belongs in a strongly supported clade, distinct from other taxa that have been confused with *C. gloeosporioides* in the past, such as *C. acutatum* and *C. boninense* (*e.g.* Abang *et al.* 2002, Martinez-Culebras *et al.* 2003, Johnston *et al*. 2005, Chung *et al.* 2006, Farr *et al.* 2006, Than *et al.* 2008). However, biological and genetic relationships within the broad *C. gloeosporioides* clade remain confused and ITS sequences alone are insufficient to resolve them.

In this study we define the limits of the *C. gloeosporioides* species complex on the basis of ITS sequences, the species we accept within the complex forming a strongly supported clade in the ITS gene tree (fig. 1 in Cannon *et al.* 2012, this issue). In all cases the taxa we include in the *C. gloeosporioides* complex would fit within the traditional morphological concept of the *C. gloeosporioides* group (*e.g.* von Arx 1970, Mordue 1971, and Sutton 1980). Commonly used species names within the *C. gloeosporioides* complex include *C. fragariae*, *C. musae*, and *C. kahawae*. Since the epitype paper (Cannon *et al.* 2008), several new *C. gloeosporioides*-like species have been described in regional studies, where multi-gene analyses have shown the new species to be phylogenetically distinct from the ex-epitype strain of *C. gloeosporioides* (*e.g.* Rojas *et al.* 2010, Phoulivong *et al.* 2011, and Wikee *et al.* 2011).

The regional nature of most of these studies, the often restricted genetic sampling across the diversity of *C. gloeosporioides* globally, and the minimal overlap between isolates treated and gene regions targeted in the various studies, means that the relationship between the newly described species is often poorly understood.

While some authors have embraced a genetically highly restricted concept for *C. gloeosporioides*, many applied researchers continue to use the name in a broad, group-species concept (*e.g.* Bogo *et al.* 2012, Deng *et al.* 2012, Kenny *et al.* 2012, Parvin *et al.* 2012, and Zhang *et al.* 2012). In this paper we accept both concepts as useful and valid. When used in a broad sense, we refer to the taxon as the *C. gloeosporioides* species complex or *C. gloeosporioides s. lat*.

This paper aims to clarify the genetic and taxonomic relationships within the *C. gloeosporioides* species complex using a set of isolates that widely samples its genetic, biological and geographic diversity. Type specimens, or cultures derived from type specimens, have been examined wherever possible. Although we do not treat all of the names placed in synonymy with *C. gloeosporioides* or *Glomerella cingulata* by von Arx & Müller (1954) and von Arx (1957, 1970), we treat all names for which a possible close relationship with *C. gloeosporioides* has been suggested in the recent literature, along with all subspecific taxa and *formae speciales* within *C. gloeosporioides* and *G. cingulata*.

ITS sequences, the official barcoding gene for fungi (Seifert 2009, Schoch *et al.* 2012), do not reliably resolve relationships within the *C. gloeosporioides* complex. We define species in the complex genetically rather than morphologically, on the basis of phylogenetic analyses of up to eight genes. Following Cannon *et al.* (2012, this issue) the generic name *Colletotrichum* is used as the preferred generic name for all species wherever possible throughout this paper, whether or not a *Glomerella* state has been observed for that fungus, and whether or not the *Glomerella* state has a formal name.

MATERIALS AND METHODS

Specimen isolation and selection

An attempt was made to sample the genetic diversity across *C. gloeosporioides* as widely as possible, with isolates from diverse hosts from around the world selected for more intensive study. A BLAST search of GenBank using the ITS sequence of the epitype culture of *C. gloeosporioides* (Cannon *et al*. 2008) provided a coarse estimate for the genetic limit of the *C. gloeosporioides* complex and ITS diversity across the complex was used to select a genetically diverse set of isolates. Voucher cultures were obtained from the research groups who deposited the GenBank records. To these were added isolates representing the known genetic and morphological diversity of *C. gloeosporioides* from New Zealand, isolated from rots of native and introduced fruits, from diseased exotic weeds, and as endophytes from leaves of native podocarps. Additional isolates representing ex-type and authentic cultures of as many named taxa and *formae speciales* within the *C. gloeosporioides* complex as possible were obtained from international culture collections. Approximately 400 isolates belonging to the *C. gloeosporioides* complex were obtained. GAPDH gene sequences were generated for all isolates as an initial measure of genetic diversity. A subset of 156 isolates, selected to represent the range of genetic, geographic, and host plant diversity,

was used in this research (Table 1).

Most of the New Zealand isolates had been stored as conidial suspensions made from single conidium or ascospore cultures and then stored at -80 °C in a 5 % glycerol/water suspension. Additional isolates from New Zealand were obtained from the ICMP culture collection, where isolates are stored as lyophilised (freeze-dried) ampoules or in a metabolically inactive state in liquid nitrogen at -196 °C. The storage history of most of the isolates received from other research groups is not known. Table 1 lists the isolates studied. All those supplying cultures are acknowledged at the end of this manuscript, and additional details on each culture are available on the ICMP website (http://www.landcareresearch.co.nz/resources/collections/icmp).

Culture collection and fungal herbarium (fungarium) abbreviations used herein are: CBS = Centraalbureau voor Schimmelcultures (Netherlands), ICMP = International Collection of Microorganisms from Plants, MFLU = Mae Fah Luang University Herbarium (Thailand) MFLUCC = Mae Fah Luang University Culture Collection (Thailand), GCREC = University of Florida, Gulf Coast Research and Education Centre (USA), HKUCC = The University of Hong Kong Culture Collection (China), IMI = CABI Genetic Resource Collection (UK), MAFF = Ministry of Agriculture, Forestry and Fisheries (Japan), DAR = Plant Pathology Herbarium (Australia), NBRC = Biological Resource Center, National Institute of Technology and Evaluation (Japan), BCC = BIOTEC Culture Collection (Thailand), GZAAS = Guizhou Academy of Agricultural Sciences herbarium (China), MUCL = Belgian Co-ordinated Collections of Micro-organisms, (agro)industrial fungi & yeasts (Belgium), BRIP = Queensland Plant Pathology Herbarium (Australia), PDD = New Zealand Fungal and Plant Disease Collection (New Zealand), BPI = U.S. National Fungus Collections (USA), STE-U = Culture collection of the Department of Plant Pathology, University of Stellenbosch (South Africa), and MCA = M. Catherine Aime's collection series, Louisiana State University (USA).

DNA extraction, amplification, and sequencing

Mycelium was collected from isolates grown on PDA agar, and manually comminuted with a micropestle in 420 µL of Quiagen DXT tissue digest buffer; 4.2 µL of proteinase K was added and incubated at 55 °C for 1 h. After a brief centrifugation 220 µL of the supernatant was placed in a Corbett X-tractorGene automated nucleic acid extraction robot. The resulting 100 µL of pure DNA in TE buffer was stored at -30 °C in 1.5 mL tubes until use.

Gene sequences were obtained from eight nuclear gene regions, actin (ACT) [316 bp], calmodulin (CAL) [756 bp], chitin synthase (CHS-1) [229 bp], glyceraldehyde-3-phosphate dehydrogenase (GAPDH) [308 bp], the ribosomal internal transcribed spacer (ITS) [615 bp], glutamine synthetase (GS) [907 bp], manganese-superoxide dismutase (SOD2) [376 bp], and β-tubulin 2 (TUB2) [716 bp].

PCR Primers used during this study are shown in Table 2. The standard CAL primers (O'Donnell *et al*. 2000) gave poor or non-specific amplification for most isolates, thus new primers (CL1C, CL2C) were designed for *Colletotrichum* based on the *C. graminicola* M1.001 genome sequence. The standard GS primers (Stephenson *et al*. 1997) sequenced poorly for some isolates due to an approx. 9 bp homopolymer T run 71 bp in from the end of the GSF1 primer binding site. A new primer, GSF3, was designed 41 bp downstream of this region to eliminate the homopolymer slippage error from sequencing. The reverse primer GSR2 was designed in the same location as GSR1 with one nucleotide change. Both new GS primers were based on similarity with a *C. theobromicola* UQ62 sequence (GenBank L78067, as *C. gloeosporioides*).

The PCRs were performed in an Applied Biosystems Veriti Thermal Cycler in a total volume of 25 µL. The PCR mixtures contained 15.8 µL of UV-sterilised ultra-filtered water, 2.5 µL of 10× PCR buffer (with 20 mM $MgCl_2$), 2.5 µL of dNTPs (each 20 µM), 1 µL of each primer (10 µM), 1 µL of BSA, 1 µL of genomic DNA, and 0.2 µL (1 U) of Roche FastStart Taq DNA Polymerase.

The PCR conditions for ITS were 4 min at 95 °C, then 35 cycles of 95 °C for 30 s, 52 °C for 30 s, 72 °C for 45 s, and then 7 min at 72 °C. The annealing temperatures differed for the other genes, with the optimum for each; ACT: 58 °C, CAL: 59 °C, CHS-1: 58 °C, GAPDH: 60 °C, GS: 54 °C, SOD2: 54 °C, TUB2: 55 °C. Some isolates required altered temperatures and occasionally gave multiple bands, which were excised separately from an electrophoresis gel and purified. PCR Products were purified on a Qiagen MinElute 96 UF PCR Purification Plate.

DNA sequences were obtained in both directions on an Applied Biosystems 3130*xl* Avant Genetic analyzer using BigDye v. 3.1 chemistry, electropherograms were analysed and assembled in Sequencher v. 4.10.1 (Gene Codes Corp.).

Phylogenetic analyses

Multiple sequence alignments of each gene were made with ClustalX v. 2.1 (Larkin *et al*. 2007), and manually adjusted where necessary with Geneious Pro v. 5.5.6 (Drummond *et al*. 2011).

Bayesian inference (BI) was used to reconstruct most of the phylogenies using MrBayes v. 3.2.1 (Ronquist *et al*. 2012). Bayesian inference has significant advantages over other methods of analysis such as maximum likelihood and maximum parsimony (Archibald *et al*. 2003) and provides measures of clade support as posterior probabilities rather than random resampling bootstraps. jModelTest v. 0.1.1 (Posada 2008) was used to carry out statistical selection of best-fit models of nucleotide substitution using the corrected Akaike information criteria (AICc) (Table 3). Initial analyses showed that individual genes were broadly congruent, thus nucleotide alignments of all genes were concatenated using Geneious, and separate partitions created for each gene with their own model of nucleotide substitution. Analyses on the full data set were run twice for 5 x 10^7 generations, and twice for 2 x 10^7 generations for the clade trees. Samples were taken from the posterior every 1000 generations. Convergence of all parameters was checked using the internal diagnostics of the standard deviation of split frequencies and performance scale reduction factors (PSRF), and then externally with Tracer v. 1.5 (Rambaut & Drummond 2007). On this basis the first 25 % of generations were discarded as burn-in.

An initial BI analysis treated all 158 isolates using a concatenated alignment for five of the genes, ACT, CAL, CHS-1, GAPDH, and ITS. *Colletotrichum boninense* and *C. hippeastri* were used as outgroups. A second BI analysis, restricted to ex-type or authentic isolates of each of the accepted species, was based on a concatenated alignment of all eight genes. A third set of BI analyses treated focussed on taxa within the Musae clade and the Kahawae clade. For each clade, the ex-type or authentic isolates, together with 2–3 additional selected isolates of each accepted taxon where available, were analysed using a concatenated alignment of all eight genes, with *C. gloeosporioides* used as the outgroup for both analyses.

Table 1. A list of strains used in this study.

Species	Culture*	Host	Country	GenBank accession number							
				ITS	GAPDH	CAL	ACT	CHS-1	GS	SOD2	TUB2
C. aenigma	ICMP 18608*	*Persea americana*	Israel	JX010244	JX010044	JX009683	JX009443	JX009774	JX010078	JX010311	JX010389
	ICMP 18686	*Pyrus pyrifolia*	Japan	JX010243	JX009913	JX009684	JX009519	JX009789	JX010079	JX010312	JX010390
C. aeschynomenes	ICMP 17673*, ATCC 201874	*Aeschynomene virginica*	USA	JX010176	JX009930	JX009721	JX009483	JX009799	JX010081	JX010314	JX010392
C. alatae	CBS 304.67*, ICMP 17919	*Dioscorea alata*	India	JX010190	JX009990	JX009738	JX009471	JX009837	JX010065	JX010305	JX010383
	ICMP 18122	*Dioscorea alata*	Nigeria	JX010191	JX010011	JX009739	JX009470	JX009846	JX010136	JX010371	JX010449
C. alienum	IMI 313842, ICMP 18691	*Persea americana*	Australia	JX010217	JX010018	JX009664	JX009580	JX009754	JX010074	JX010307	JX010385
	ICMP 18703	*Persea americana*	New Zealand	JX010252	JX010030	JX009656	JX009528	JX009885			
	ICMP 12071*	*Malus domestica*	New Zealand	JX010251	JX010028	JX009654	JX009572	JX009882	JX010101	JX010333	JX010411
	ICMP 17972	*Diospyros kaki*	New Zealand	JX010247	JX009944	JX009655	JX009497	JX009750			
	ICMP 18704	*Persea americana*	New Zealand	JX010253	JX010045	JX009658	JX009456	JX009886			
	ICMP 18621	*Persea americana*	New Zealand	JX010246	JX009959	JX009657	JX009552	JX009755	JX010075	JX010308	JX010386
	ICMP 12068	*Malus domestica*	New Zealand	JX010255	JX009925	JX009660	JX009492	JX009889			
	ICMP 18725	*Malus domestica*	New Zealand	JX010254	JX009943	JX009659	JX009530	JX009887			
C. aotearoa	ICMP 18532	*Vitex lucens*	New Zealand	JX010220	JX009906	JX009614	JX009544	JX009764	JX010108	JX010338	JX010421
	ICMP 18734	*Agathis australis*	New Zealand	JX010211	JX010004	JX009627	JX009569	JX009878			
	ICMP 18528	*Berberis glaucocarpa*	New Zealand	JX010199	JX009977	JX009615	JX009527	JX009879			
	ICMP 17324	*Kunzea ericoides*	New Zealand	JX010198	JX009991	JX009619	JX009538	JX009770	JX010109	JX010344	JX010418
	ICMP 18533	*Prumnopitys ferruginea*	New Zealand	JX010197	JX010026	JX009624	JX009522	JX009769	JX010110	JX010340	JX010416
	ICMP 18535	*Dacrycarpus dacrydioides*	New Zealand	JX010201	JX009968	JX009617	JX009545	JX009766	JX010107	JX010364	JX010423
	ICMP 18577	*Coprosma* sp.	New Zealand	JX010203	JX009978	JX009612	JX009567	JX009851	JX010111	JX010360	JX010417
	ICMP 18529	*Acmena smithii*	New Zealand	JX010222	JX009956	JX009618	JX009539	JX009883			
	ICMP 18537*	*Coprosma* sp.	New Zealand	JX010205	JX010005	JX009611	JX009564	JX009853	JX010113	JX010345	JX010420
	ICMP 18536	*Coprosma* sp.	New Zealand	JX010204	JX009907	JX009610	JX009577	JX009852			
	ICMP 18748	*Ligustrum lucidum*	New Zealand	JX010209	JX009918	JX009613	JX009453	JX009858			
	ICMP 17326	*Podocarpus totara*	New Zealand	JX010202	JX010049	JX009616	JX009578	JX009768	JX010106	JX010341	JX010422
	ICMP 18540	*Geniostoma ligustrifolium*	New Zealand	JX010207	JX010043	JX009622	JX009514	JX009855			
	ICMP 18541	*Coprosma* sp.	New Zealand	JX010208	JX009960	JX009607	JX009513	JX009856			
	ICMP 18742	*Meryta sinclairii*	New Zealand	JX010210	JX010025	JX009626	JX009477	JX009862			
	ICMP 18740	*Dysoxylum spectabile*	New Zealand	JX010218	JX009988	JX009625	JX009517	JX009763	JX010135	JX010368	JX010446
	ICMP 18530	*Vitex lucens*	New Zealand	JX010268	JX009911	JX009623	JX009521	JX009884	JX010112	JX010339	JX010419
	ICMP 18735	*Hedychium gardnerianum*	New Zealand	JX010221	JX010023	JX009620	JX009500	JX009880	JX010115	JX010343	JX010424

Table 1. (Continued).

Species	Culture*	Host	Country	GenBank accession number							
				ITS	GAPDH	CAL	ACT	CHS-1	GS	SOD2	TUB2
	ICMP 18736	*Lonicera japonica*	New Zealand	JX010200	JX009912	JX009608	JX009454	JX009894			
	ICMP 18548	*Coprosma* sp.	New Zealand	JX010206	JX009961	JX009609	JX009854	JX009445	JX010114	JX010342	JX010425
	ICMP 18543	*Melicytus ramiflorus*	New Zealand	JX010156	JX009983	JX009621	JX009524	JX009859			
C. asianum	IMI 313839, ICMP 18696	*Mangifera indica*	Australia	JX010192	JX009915	JX009723	JX009576	JX009753	JX010073	JX010306	JX010384
	MAFF 306627, ICMP 18603	*Mangifera indica*	Philippines	JX010195	JX009938	JX009725	JX009579	JX009825			
	HKUCC 10862, ICMP 18605	*Mangifera indica*	Thailand	JX010194	JX010021	JX009726	JX009465	JX009787			
	ICMP 18580*, CBS 130418	*Coffea arabica*	Thailand	**FJ972612**	JX010053	**FJ917506**	JX009584	JX009867	JX010096	JX010328	JX010406
	CBS 124960, ICMP 18648	*Mangifera indica*	Panama	JX010193	JX010017	JX009724	JX009546	JX009871			
C. boninense	MAFF 305972*, ICMP 17904, CBS 123755	*Crinum asiaticum* var. *sinicum*	Japan	JX010292	JX009905		JX009583	JX009827			
C. clidemiae	ICMP 18706	*Vitis* sp.	USA	JX010274	JX009909	JX009639	JX009476	JX009777	JX010128	JX010353	JX010439
	ICMP 18658*	*Clidemia hirta*	USA, Hawaii	JX010265	JX009989	JX009645	JX009537	JX009877	JX010129	JX010356	JX010438
C. cordylinicola	MFLUCC 090551*, ICMP 18579	*Cordyline fruticosa*	Thailand	JX010226	JX009975	**HM470238**	**HM470235**	JX009864	JX010122	JX010361	JX010440
C. fructicola	ICMP 12568	*Persea americana*	Australia	JX010166	JX009946	JX009680	JX009529	JX009762			
	ICMP 17787	*Malus domestica*	Brazil	JX010164	JX009958	JX009667	JX009439	JX009807			
	ICMP 17788	*Malus domestica*	Brazil	JX010177	JX009949	JX009672	JX009458	JX009808			
	IMI 345051, ICMP 17819	*Fragaria* × *ananassa*	Canada	JX010180	JX009997	JX009668	JX009469	JX009820			
	ICMP 18613	*Limonium sinuatum*	Israel	JX010167	JX009998	JX009675	JX009491	JX009772	JX010077	JX010310	JX010388
	ICMP 18698	*Limonium* sp.	Israel	JX010168	JX010052	JX009677	JX009585	JX009773			
	ICMP 18667	*Limonium* sp.	Israel	JX010169	JX009951	JX009679	JX009464	JX009775			
	ICMP 18615	*Limonium* sp.	Israel	JX010170	JX010016	JX009678	JX009511	JX009776			
	ICMP 18610	*Pyrus pyrifolia*	Japan	JX010174	JX010034	JX009681	JX009526	JX009788			
	ICMP 18120	*Dioscorea alata*	Nigeria	JX010182	JX010041	JX009670	JX009436	JX009844	JX010091	JX010323	JX010401
	CBS 125395, ICMP 18645	*Theobroma cacao*	Panama	JX010172	JX009992	JX009666	JX009543	JX009873	JX010098	JX010330	JX010408
	ICMP 18581*, CBS 130416	*Coffea arabica*	Thailand	JX010165	JX010033	**FJ917508**	**FJ907426**	JX009866	JX010095	JX010327	JX010405
	ICMP 18727	*Fragaria* × *ananassa*	USA	JX010179	JX010035	JX009682	JX009565	JX009812	JX010083	JX010316	JX010394
	CBS 120005, ICMP 18609	*Fragaria* × *ananassa*	USA	JX010175	JX009926	JX009673	JX009534	JX009792			
	ICMP 17789	*Malus domestica*	USA	JX010178	JX009914	JX009665	JX009451	JX009809			
	ICMP 18125	*Dioscorea alata*	Nigeria	JX010183	JX010009	JX009669	JX009468	JX009847			
C. fructicola (syn. *C. ignotum*)	CBS 125397(*), ICMP 18646	*Tetragastris panamensis*	Panama	JX010173	JX010032	JX009674	JX009581	JX009874	JX010099	JX010331	JX010409
C. fructicola (syn. *Glomerella cingulata* var. *minor*)	CBS 238.49(*), ICMP 17921	*Ficus edulis*	Germany	JX010181	JX009923	JX009671	JX009495	JX009839	JX010090	JX010322	JX010400

Table 1. (Continued).

Species	Culture*	Host	Country	GenBank accession number							
				ITS	GAPDH	CAL	ACT	CHS-1	GS	SOD2	TUB2
C. gloeosporioides	DAR 76936, ICMP 18738	*Carya illinoinensis*	Australia	JX010151	JX009976	JX009730	JX009542	JX009797			
	IMI 356878*, ICMP 17821, CBS 112999	*Citrus sinensis*	Italy	JX010152	JX010056	JX009731	JX009531	JX009818	JX010085	JX010365	JX010445
	ICMP 12939	*Citrus* sp.	New Zealand	JX010149	JX009931	JX009728	JX009462	JX009747			
	ICMP 12066	*Ficus* sp.	New Zealand	JX010158	JX009955	JX009734	JX009550	JX009888			
	ICMP 18730	*Citrus* sp.	New Zealand	JX010157	JX009981	JX009737	JX009548	JX009861			
	ICMP 12938	*Citrus sinensis*	New Zealand	JX010147	JX009935	JX009732	JX009560	JX009746			
	ICMP 18694	*Mangifera indica*	South Africa	JX010155	JX009980	JX009729	JX009481	JX009796			
	CBS 119204, ICMP 18678	*Pueraria lobata*	USA	JX010150	JX010013	JX009733	JX009502	JX009790			
	ICMP 18695	*Citrus* sp.	USA	JX010153	JX009979	JX009735	JX009494	JX009779			
	ICMP 18697	*Vitis vinifera*	USA	JX010154	JX009987	JX009736	JX009557	JX009780			
C. gloeosporioides (syn. *Gloeosporium pedemontanum*)	CBS 273.51(*), ICMP 19121	*Citrus limon*	Italy	JX010148	JX010054	JX009745	JX009558	JX009903			
C. hippeastri	CBS 241.78, ICMP 17920	*Hippeastrum* sp.	Netherlands	JX010293	JX009932	JX009740	JX009485	JX009838			
C. horii	ICMP 12942	*Diospyros kaki*	New Zealand	**GQ329687**	**GQ329685**	JX009603	JX009533	JX009748	JX010072	JX010296	JX010375
	ICMP 12951	*Diospyros kaki*	New Zealand	**GQ329689**	**GQ329683**	JX009602	JX009466	JX009751			
	NBRC 7478*, ICMP 10492	*Diospyros kaki*	Japan	**GQ329690**	**GQ329681**	JX009604	JX009438	JX009752	JX010137	JX010370	JX010450
	ICMP 17968	*Diospyros kaki*	China	JX010212	**GQ329682**	JX009605	JX009547	JX009811	JX010068	JX010300	JX010378
	MAFF 306429, ICMP 17970	*Diospyros kaki*	Japan	JX010213	**GQ329686**	JX009606	JX009467	JX009824			
C. kahawae subsp. *ciggaro*	ICMP 18539*	*Olea europaea*	Australia	JX010230	JX009966	JX009635	JX009523	JX009800	JX010132	JX010346	JX010434
	ICMP 18728	*Miconia* sp.	Brazil	JX010239	JX010048	JX009643	JX009525	JX009850			
	ICMP 18741	*Kunzea ericoides*	New Zealand	JX010229	JX010039	JX009631	JX009472	JX009767			
	ICMP 18534	*Kunzea ericoides*	New Zealand	JX010227	JX009904	JX009634	JX009473	JX009765	JX010116	JX010351	JX010427
	ICMP 18544	*Toronia toru*	New Zealand	JX010240	JX009920	JX009632	JX009430	JX009860			
	ICMP 18531	*Persea americana*	New Zealand	JX009463	JX009999	JX009647	JX009463	JX009749			
	ICMP 12952	*Persea americana*	New Zealand	JX010214	JX009971	JX009648	JX009431	JX009757	JX010126	JX010348	JX010426
	ICMP 12953	*Persea americana*	New Zealand	JX010215	JX009928	JX009646	JX009499	JX009758			
	CBS 112984, ICMP 17932	*Dryandra* sp.	South Africa	JX010237	JX009973	JX009633	JX009434	JX009833			
	IMI 359911, ICMP 17931, CBS 12988	*Dryas octopetala*	Switzerland	JX010236	JX009965	JX009637	JX009475	JX009832	JX010121	JX010354	JX010428
C. kahawae subsp. *ciggaro* (syn. *Glomerella cingulata* var. *migrans*)	CBS 237.49(*), ICMP 17922	*Hypericum perforatum*	Germany	JX010238	JX010042	JX009636	JX009450	JX009840	JX010120	JX010355	JX010432

Table 1. (Continued).

Species	Culture*	Host	Country	GenBank accession number							
				ITS	GAPDH	CAL	ACT	CHS-1	GS	SOD2	TUB2
C. kahawae subsp. *ciggaro* (syn. *Glomerella rufomaculans* var. *vaccinii*)	CBS 124.22(*), ICMP 19122	*Vaccinium* sp.	USA	JX010228	JX009950	JX009744	JX009536	JX009902	JX010134	JX010367	JX010433
C. kahawae subsp. *kahawae*	CBS 982.69, ICMP 17915	*Coffea arabica*	Angola	JX010234	JX010040	JX009638	JX009474	JX009829	JX010125	JX010352	JX010435
	IMI 361501, ICMP 17905	*Coffea arabica*	Cameroon	JX010232	JX010046	JX009644	JX009561	JX009816	JX010127	JX010349	JX010431
	IMI 319418*, ICMP 17816	*Coffea arabica*	Kenya	JX010231	JX010012	JX009642	JX009452	JX009813	JX010130	JX010350	JX010444
	CBS 135.30, ICMP 17928	*Coffea* sp.	Kenya	JX010235	JX010037	JX009640	JX009554	JX009831			
	IMI 301220, ICMP 17811	*Coffea arabica*	Malawi	JX010233	JX009970	JX009641	JX009555	JX009817	JX010131	JX010347	JX010430
C. musae	CBS 192.31, ICMP 17923	*Musa* sp.	Indonesia	JX010143	JX009929	JX009690	JX009587	JX009841			
	IMI 52264, ICMP 17817	*Musa sapientum*	Kenya	JX010142	JX010015	JX009689	JX009432	JX009815	JX010084	JX010317	JX010395
	ICMP 12931	*Musa* sp.	New Zealand (imported)	JX010140	JX009995	JX009688	JX009442	JX009756			
	ICMP 18600	*Musa* sp.	Philippines	JX010144	JX010038	JX009686	JX009556	JX009848			
	ICMP 12930	*Musa* sp.	New Zealand	JX010141	JX009986	JX009685	JX009566	JX009881			
	ICMP 18701	*Musa* sp.	Philippines	JX010145	JX010047	JX009687	JX009551	JX009849			
	CBS 116870*, ICMP 19119	*Musa* sp.	USA	JX010146	JX010050	JX009742	JX009433	JX009896	JX010103	JX010335	**HQ596280**
C. nupharicola	CBS 469.96, ICMP 17938	*Nuphar lutea* subsp. *polysepala*	USA	JX010189	JX009936	JX009661	JX009486	JX009834	JX010087	JX010319	JX010397
	CBS 470.96*, ICMP 18187	*Nuphar lutea* subsp. *polysepala*	USA	JX010187	JX009972	JX009663	JX009437	JX009835	JX010088	JX010320	JX010398
	CBS 472.96, ICMP 17940	*Nymphaea ordorata*	USA	JX010188	JX010031	JX009662	JX009582	JX009836	JX010089	JX010321	JX010399
C. psidii	CBS 145.29*, ICMP 19120	*Psidium* sp.	Italy	JX010219	JX009967	JX009743	JX009515	JX009901	JX010133	JX010366	JX010443
C. queenslandicum	ICMP 1778*	*Carica papaya*	Australia	JX010276	JX009934	JX009691	JX009447	JX009899	JX010104	JX010336	JX010414
	ICMP 1780	*Carica* sp.	Australia	JX010186	JX010010	JX009693	JX009504	JX009900			
	ICMP 12564	*Persea americana*	Australia	JX010184	JX009919	JX009692	JX009573	JX009759			
	ICMP 18705	*Coffea* sp.	Fiji	JX010185	JX010036	JX009694	JX009490	JX009890	JX010102	JX010334	JX010412
C. salsolae	ICMP 19051*	*Salsola tragus*	Hungary	JX010242	JX009916	JX009696	JX009562	JX009863	JX010093	JX010325	JX010403
	CBS 119296, ICMP 18693	*Glycine max* (inoculated)	Hungary	JX010241	JX009917	JX009695	JX009559	JX009791			
C. siamense	ICMP 12567	*Persea americana*	Australia	JX010250	JX009940	JX009697	JX009541	JX009761	JX010076	JX010309	JX010387
	DAR 76934, ICMP 18574	*Pistacia vera*	Australia	JX010270	JX010002	JX009707	JX009535	JX009798	JX010080	JX010313	JX010391
	ICMP 12565	*Persea americana*	Australia	JX010249	JX009937	JX009698	JX009571	JX009760			
	CBS 125379, ICMP 18643	*Hymenocallis americana*	China	JX010258	JX010060	**GQ849451**	**GQ856776**	**GQ856729**			
	ICMP 18121	*Dioscorea rotundata*	Nigeria	JX010245	JX009942	JX009715	JX009460	JX009845	JX010092	JX010324	JX010402
	ICMP 18118	*Commelina* sp.	Nigeria	JX010163	JX009941	JX009701	JX009505	JX009843			

Table 1. (Continued).

Species	Culture*	Host	Country	GenBank accession number							
				ITS	GAPDH	CAL	ACT	CHS-1	GS	SOD2	TUB2
	ICMP 18117	*Dioscorea rotundata*	Nigeria	JX010266	JX009954	JX009700	JX009574	JX009842			
	ICMP 18739	*Carica papaya*	South Africa	JX010161	JX009921	JX009716	JX009484	JX009794			
	ICMP 18570	*Persea americana*	South Africa	JX010248	JX009969	JX009699	JX009510	JX009793			
	ICMP 18569	*Persea americana*	South Africa	JX010262	JX009963	JX009711	JX009459	JX009795			
	ICMP 18578*, CBS 130417	*Coffea arabica*	Thailand	JX010171	JX009924	**FJ917505**	**FJ907423**	JX009865	JX010094	JX010326	JX010404
	HKUCC 10884, ICMP 18575	*Capsicum annuum*	Thailand	JX010256	JX010059	JX009717	JX009455	JX009785			
	HKUCC 10881, ICMP 18618	*Capsicum annuum*	Thailand	JX010257	JX009945	JX009718	JX009512	JX009786			
	ICMP 18572	*Vitis vinifera*	USA	JX010160	JX010061	JX009705	JX009487	JX009783			
	ICMP 18571	*Fragaria* × *ananassa*	USA	JX010159	JX009922	JX009710	JX009482	JX009782			
	ICMP 18573	*Vitis vinifera*	USA	JX010271	JX009996	JX009712	JX009435	JX009784			
	ICMP 17795	*Malus domestica*	USA	JX010162	JX010051	JX009703	JX009506	JX009805	JX010082	JX010315	JX010393
	ICMP 17791	*Malus domestica*	USA	JX010273	JX009933	JX009708	JX009508	JX009810			
	ICMP 17797	*Malus domestica*	USA	JX010263	JX009984	JX009704	JX009461	JX009806			
	ICMP 17785	*Malus domestica*	USA	JX010272	JX010051	JX009706	JX009446	JX009804			
C. siamense (syn. *C. hymenocallidis*)	CBS 125378(*), ICMP 18642	*Hymenocallis americana*	China	JX010278	JX010019	JX009709	**GQ856775**	**GQ856730**	JX010100	JX010332	JX010410
C. siamense (syn. *C. jasmini-sambac*)	CBS 130420(*), ICMP 19118	*Jasminum sambac*	Vietnam	**HM131511**	**HM131497**	JX009713	**HM131507**	JX009895	JX010105	JX010337	JX010415
C. theobromicola	MUCL 42295, ICMP 17958, CBS 124250	*Stylosanthes guianensis*	Australia	JX010291	JX009948	JX009598	JX009498	JX009822	JX010067	JX010303	JX010381
	ICMP 18566	*Olea europaea*	Australia	JX010282	JX009953	JX009593	JX009496	JX009801	JX010071	JX010297	JX010376
	ICMP 18565	*Olea europaea*	Australia	JX010283	JX010029	JX009594	JX009449	JX009802	JX010070	JX010298	JX010374
	ICMP 18567	*Olea europaea*	Australia	JX010287	JX009985	JX009599	JX009457	JX009803	JX010069	JX010299	JX010377
	ICMP 18576	*Limonium* sp.	Israel	JX010279	JX010022	JX009595	JX009532	JX009771			
	ICMP 17895	*Annona diversifolia*	Mexico	JX010284	JX010057	JX009600	JX009568	JX009828	JX010066	JX010304	JX010382
	ICMP 15445	*Acca sellowiana*	New Zealand	JX010290	JX010027	JX009601	JX009509	JX009893			
	CBS 125393, ICMP 18650	*Theobroma cacao*	Panama	JX010280	JX009982	JX009590	JX009503	JX009872			
	CBS 124945*, ICMP 18649	*Theobroma cacao*	Panama	JX010294	JX010006	JX009591	JX009444	JX009869	JX010139	JX010372	JX010447
	ICMP 17099	*Fragaria* × *ananassa*	USA	JX010285	JX009957	JX009588	JX009493	JX009778			
	ICMP 17100	*Quercus* sp.	USA	JX010281	JX009947	JX009596	JX009507	JX009781			
	IMI 348152, ICMP 17814	*Fragaria vesca*	USA	JX010288	JX010003	JX009589	JX009448	JX009819	JX010062	JX010301	JX010379
C. theobromicola (syn. *C. fragariae*)	CBS 142.31(*), ICMP 17927	*Fragaria* × *ananassa*	USA	JX010286	JX010024	JX009592	JX009516	JX009830	JX010064	JX010295	JX010373
C. theobromicola (syn. *C. gloeosporioides* f. *stylosanthis*)	MUCL 42294(*), ICMP 17957, CBS 124251	*Stylosanthes viscosa*	Australia	JX010289	JX009962	JX009597	JX009575	JX009821	JX010063	JX010302	JX010380

Table 1. (Continued).

Species	Culture*	Host	Country	GenBank accession number							
				ITS	GAPDH	CAL	ACT	CHS-1	GS	SOD2	TUB2
C. ti	ICMP 5285	*Cordyline australis*	New Zealand	JX010267	JX009910	JX009650	JX009553	JX009897	JX010124	JX010363	JX010441
	ICMP 4832*	*Cordyline* sp.	New Zealand	JX010269	JX009952	JX009649	JX009520	JX009898	JX010123	JX010362	JX010442
C. tropicale	MAFF 239933, ICMP 18672	*Litchi chinensis*	Japan	JX010275	JX010020	JX009722	JX009480	JX009826	JX010086	JX010318	JX010396
	CBS 124949*, ICMP 18653	*Theobroma cacao*	Panama	JX010264	JX010007	JX009719	JX009489	JX009870	JX010097	JX010329	JX010407
	CBS 124943, ICMP 18651	*Annona muricata*	Panama	JX010277	JX010014	JX009720	JX009570	JX009868			
C. xanthorrhoeae	BRIP 45094*, ICMP 17903, CBS 127831	*Xanthorrhoea preissii*	Australia	JX010261	JX009927	JX009653	JX009478	JX009823	JX010138	JX010369	JX010448
	IMI 350817a, ICMP 17820	*Xanthorrhoea* sp.	Australia	JX010260	JX010008	JX009652	JX009479	JX009814			
Glomerella cingulata "f.sp. *camelliae*"	ICMP 10643	*Camellia* × *williamsii*	UK	JX010224	JX009908	JX009630	JX009540	JX009891	JX010119	JX010358	JX010436
	ICMP 18542	*Camellia sasanqua*	USA	JX010223	JX009994	JX009628	JX009488	JX009857	JX010118	JX010357	JX010429
	ICMP 10646	*Camellia sasanqua*	USA	JX010225	JX009993	JX009629	JX009563	JX009892	JX010117	JX010359	JX010437

* = ex-type or authentic culture, (*) = ex-type or authentic culture of synonymised taxon. Sequences downloaded from GenBank, not generated as part of this project are in bold font. Collection abbreviations are listed in the methods.

Several species-trees analyses were conducted using BEAST v. 1.7.1 (Drummond *et al*. 2012). Species-trees combine multi-gene and multiple isolate data to reconstruct the evolutionary history of hypothesised species, rather than individual isolates. BEAST does not use concatenation, but rather co-estimates the individual gene trees embedded inside the summary species tree. It also estimates the time since each species shared a common ancestor (divergence times). For these analyses the species tree ancestral reconstruction option was selected (Heled & Drummond 2010), the gene data partitioned as for BI and the substitution model for each gene was selected based on the models selected using jModelTest. The individual isolates were grouped into sets of species by setting species names as trait values. A strict clock was used for the GAPDH gene (as an all intronic sequence it was assumed to be accumulating mutations at a steady rate) and the other gene clock rates were estimated relative to GAPDH, using an uncorrelated lognormal relaxed clock. The species tree prior used for all genes was the Yule process, with the ploidy type set to nuclear autosomal. Uninformative priors were used for all parameters, and were allowed to auto optimise.

The first species-tree analysis was conducted using the 158 isolate, five gene dataset, with *C. boninense* and *C. hippeastri* as the outgroups. The MCMC chain was set to 1×10^8 generations for the species complex tree and samples were taken from the posterior every 1000 generations. The analysis was run twice independently. The effective sample size (ESS) and traces of all parameters and convergence of the two runs was checked with Tracer and a summary maximum clade credibility species tree was built with TreeAnnotator v. 1.7.1 (Drummond *et al*. 2012) using a 10 % burn-in and a posterior probability limit of 0.5, setting the heights of each node in the tree to the mean height across the entire sample of trees for that clade. Separate analyses were conducted using all eight genes and the same restricted set of isolates chosen to represent taxa within the Musae clade and the Kahawae clade as were used for the BI analyses of the eight gene concatenated analyses outlined above. For each of the Musae and Kahawae clade analyses, the MCMC chain was set to 5×10^7 generations, but otherwise run as for the five gene dataset.

To illustrate the potential limitations of ITS to discriminate species within the *C. gloeosporioides* complex, an UPGMA tree was built of all 158 ITS sequences, using the Geneious tree builder tool. A UPGMA tree visually approximates a BLAST search, which is based on distances (and sequence length) rather than corrected nucleotide substitutions of more sophisticated, model-based analyses.

Sequences derived in this study were lodged in GenBank (Table 1), the concatenated alignment and trees in TreeBASE (www.treebase.org) study number S12535, and taxonomic novelties in MycoBank (Crous *et al.* 2004).

Morphology

Detailed morphological descriptions are provided only for those species with no recently published description. Few specimens were examined from infected host material; the descriptions provided are mostly from agar cultures. Cultures were grown on Difco PDA from single conidia, or from single hyphal tips for the few specimens where no conidia were formed, with culture diameter measured and appearance described after 10 d growth at 18–20 °C under mixed white and UV fluorescent tubes, 12 h light/12 h dark. Colour codes follow Kornerup & Wanscher (1963).

Table 2. Primers used in this study, with sequences and sources.

Gene	Product name	Primer	Direction	Sequence (5'–3')	Reference
ACT	Actin	ACT-512F	Foward	ATG TGC AAG GCC GGT TTC GC	Carbone & Kohn 1999
		ACT-783R	Reverse	TAC GAG TCC TTC TGG CCC AT	Carbone & Kohn 1999
CAL	Calmodulin	CL1	Foward	GAR TWC AAG GAG GCC TTC TC	O'Donnell *et al.* 2000
		CL2A	Reverse	TTT TTG CAT CAT GAG TTG GAC	O'Donnell *et al.* 2000
		CL1C	Foward	GAA TTC AAG GAG GCC TTC TC	This study
		CL2C	Reverse	CTT CTG CAT CAT GAG CTG GAC	This study
CHS-1	Chitin synthase	CHS-79F	Foward	TGG GGC AAG GAT GCT TGG AAG AAG	Carbone & Kohn 1999
		CHS-345R	Reverse	TGG AAG AAC CAT CTG TGA GAG TTG	Carbone & Kohn 1999
GAPDH	Glyceraldehyde-3-phosphate dehydrogenase	GDF	Foward	GCC GTC AAC GAC CCC TTC ATT GA	Templeton *et al.* 1992
		GDR	Reverse	GGG TGG AGT CGT ACT TGA GCA TGT	Templeton *et al.* 1992
GS	Glutamine synthetase	GSF1	Foward	ATG GCC GAG TAC ATC TGG	Stephenson *et al.* 1997
		GSF3	Foward	GCC GGT GGA GGA ACC GTC G	This study
		GSR1	Reverse	GAA CCG TCG AAG TTC CAG	Stephenson *et al.* 1997
		GSR2	Reverse	GAA CCG TCG AAG TTC CAC	This study
ITS	Internal transcribed spacer	ITS-1F	Foward	CTT GGT CAT TTA GAG GAA GTA A	Gardes & Bruns 1993
		ITS-4	Reverse	TCC TCC GCT TAT TGA TAT GC	White *et al.* 1990
SOD2	Manganese-superoxide dismutase	SODglo2-F	Foward	CAG ATC ATG GAG CTG CAC CA	Moriwaki & Tsukiboshi 2009
		SODglo2-R	Reverse	TAG TAC GCG TGC TCG GAC AT	Moriwaki & Tsukiboshi 2009
TUB2	β-Tubulin 2	T1	Foward	AAC ATG CGT GAG ATT GTA AGT	O'Donnell & Cigelnik 1997
		T2	Reverse	TAG TGA CCC TTG GCC CAGT TG	O'Donnell & Cigelnik 1997
		Bt2b	Reverse	ACC CTC AGT GTA GTG ACC CTT GGC	Glass & Donaldson 1995

Table 3. Nucleotide substitution models used in phylogenetic analyses.

Gene	All taxa	Musae clade	Kahawae clade
ITS	TrNef+G	TrNef+G	TrNef
GAPDH	HKY+G	TPM1uf+G	TrN
CAL	TIM1+G	TIM1+G	TrN+G
ACT	HKY+G	TrN	JC
CHS-1	TrNef+G	TrNef+G	K80
GS		TIM2+G	TIM3+G
SOD2		HKY+G	GTR+I+G
TUB2		TrN+G	HKY+G

Conidia were measured and described using conidia taken from the conidial ooze on acervuli and mounted in lactic acid, at least 24 conidia were measured for each isolate, range measurements are provided in the form (lower extreme–) 25 % quartile – 75 % quartile (–upper extreme), all ranges were rounded to the nearest 0.5 µm. Cultures were examined periodically for the development of perithecia. Ascospores were measured and described from perithecia crushed in lactic acid.

Appressoria were producing using a slide culture technique. A small square of agar was inoculated on one side with conidia and immediately covered with a sterile cover slip. After 14 d the cover slip was removed and placed in a drop of lactic acid on a glass slide.

All morphological character measurements were analysed with the statistical programme "R" v. 2.14.0 (R Development Core Team 2011). The R package ggplot2 (Wickham 2009) was used for graphical plots. The box plots show the median, upper and lower quartiles, and the 'whisker' extends to the outlying data, or to a maximum of 1.5× the interquartile range, individual outliers outside this range are shown as dots.

Taxa treated in the taxonomic section

Species, subspecific taxa, and *formae speciales* within the *C. gloeosporioides* species complex are treated alphabetically by epithet. The names of *formae speciales* are not governed by the International Code of Botanical Nomenclature (ICBN) (McNeill *et al.* 2006, Art. 4, Note 4), and are hence enclosed in quotation marks to indicate their invalid status. Other invalid names that are governed by the ICBN are also enclosed in quotation marks. Accepted names are marked with an asterisk (*). The breadth of the taxonomic names treated includes:

all taxonomic names with DNA sequence data in GenBank that place them in the *C. gloeosporioides* complex as it has been defined here on the basis of the ITS gene tree. The sense that the names were used in GenBank may have been misapplied;

names that have been used in the literature in recent years for which a possible relationship to *C. gloeosporioides* has been suggested;

all subspecific taxa and *formae speciales* within *C. gloeosporioides* and *Glomerella cingulata*.

We have not considered the full set of species in *Colletotrichum*, *Gloeosporium* and *Glomerella* that were placed in synonymy with *C. gloeosporioides* or *Glomerella cingulata* by von Arx & Müller (1954) or von Arx (1957, 1970).

For each accepted species, comments are provided regarding the limitations of ITS, the official barcoding gene for fungi, to distinguish that species from others within the *C. gloeosporioides* complex.

RESULTS

Phylogenetics

DNA sequences of five genes were obtained from all 158 isolates included in the study and concatenated to form a supermatrix of 2294 bp. The gene boundaries in the alignment were: ACT: 1–316, CAL: 317–1072, CHS-1: 1073–1371, GAPDH: 1372–1679, ITS: 1680–2294. A BI analysis of the concatenated dataset is presented in Fig.1. This tree is annotated with the species boundaries of the taxa that we accept in the *C. gloeosporioides* complex, and the clades representing these taxa formed the basis for investigating the morphological and biological diversity of our species. Ex-type and authentic isolates are highlighted in bold and labelled with the names under which they were originally described. The posterior probability (PP) support for the grouping of most species ranges from 1 to 0.96, however support for deeper nodes is often lower, *e.g.* 0.53 for the root of *C. ti* and *C. aotearoa,* indicating that the branching may be uncertain for the root of these species. Branch lengths and node PP are typically lower within a species than between species.

The large number of taxa in Fig. 1 makes it difficult to visualise the interspecific genetic distance between the recognised species. The unrooted tree in Fig. 2 represents the results of a BI analysis based on a concatenation of all eight genes, but restricted to the ex-type or authentic cultures from each of the accepted taxa. The analysis was done without out-group taxa and clearly shows two clusters of closely related species that we informally label the Musae clade, and the Kahawae clade.

To better resolve relationships within the Musae and Kahawae clades a further set of BI analyses included eight genes and, wherever possible, several representative isolates of each of the accepted species. All eight gene sequences were concatenated to form a supermatrix for each clade. For the Musae clade of 32 isolates the alignment was 4199 bp and the gene boundaries were: ACT: 1–292, TUB2: 293–1008, CAL: 1009–1746, CHS-1: 1747–2045, GAPDH: 2046–2331, GS: 2332–3238, ITS: 3239–3823, SOD2: 3824–4199. For the Kahawae clade of 30 isolates the alignment was 4107 bp and the gene boundaries were: ACT: 1–281, TUB2: 282–988, CAL: 989–1728, CHS-1: 1729–2027, GAPDH: 2028–2311, GS: 2312–3179, ITS: 3198–3733, SOD2: 3734–4107. The additional genes sequenced provided additional support for our initial species delimitations with better resolution for some closely related species. For example, the highly pathogenic coffee berry isolates (referred to here as *C. kahawae* subsp. *kahawae*) were distinguished from other *C. kahawae* isolates.

Analyses based on concatenated data sets can mask incongruence between individual gene trees. The low levels of support within some parts of the species-tree analysis (Fig. 3), in part reflects incongruence between gene trees. The levels of support for the Kahawae clade and for the Musae clade are strong (PP=1) but the species that we accept within these clades have lower levels of support than is shown between the other species outside of the clades. The scale bar in Fig. 3 represents a time scale, calibrated at zero for the present day, and at 1 for the last common ancestor (LCA) of the *C. gloeosporioides* and *C. boninense* species complexes. The separate species-tree analyses for the Musae and Kahawae clades provide a finer resolution of evolutionary history within each clade, the time scale based on the same calibration as Fig. 3.

The UPGMA-based ITS gene tree (Fig 6). shows that *C. theobromicola*, *C. horii*, *C. gloeosporioides, G. cingulata* "f. sp. *camelliae*"*, C. asianum, C. musae, C. alatae, C. xanthorrhoeae* all form monophyletic clades and may be distinguished with ITS, but many species are unable to be discriminated using this gene alone. Note that *C. cordylinicola* and *C. psidii* are represented by a single isolate, meaning that variation within ITS sequences across these species has not been tested.

Morphology and biology

Brief morphological descriptions, based on all specimens examined, are provided for only those species with no recently published description. Conidial sizes for all accepted species are summarised in Fig. 7. Within a species, conidial sizes are reasonably consistent across isolates, independent of geographic origin or host. However, differences between species are often slight and size ranges often overlap (Fig. 7). The shape of appressoria is generally consistent within a species, some being simple in outline, others complex and highly lobed.

Several species are characterised in part by the development of perithecia in culture. These include four species in the Musae clade (*C. alienum*, C. *fructicola*, *C. queenslandicum*, and *C. salsolae*) and three in the Kahawae clade (*C. clidemiae*, *C. kahawae* subsp. *ciggaro*, and *C. ti*). Ascospore size and shape can be a useful species-level diagnostic feature (Fig. 8). In most species the ascospores are strongly curved and typically tapering towards the ends, but in *C. clidemiae* and *C. ti*, they are more or less elliptic with broadly rounded ends and not, or only slightly, curved. Individual isolates within any of these species may lose the ability to form perithecia, perhaps associated with cultural changes during storage.

Large, dark-walled stromatic structures are present in the cultures of some species not known to form perithecia. Often embedded in agar, less commonly on the surface or amongst the aerial mycelium, these structures differ from perithecia in comprising a compact tissue of tightly tangled hyphae rather than the pseudoparenchymatous, angular cells typical of perithecial walls. They have a soft, leathery texture compared to the more brittle perithecia. These stromatic structures sometimes develop a conidiogenous layer internally, and following the production of conidia they may split open irregularly, folding back to form a stromatic, acervulus-like structure. These kind of structures are also formed by some species in the *C. boninense* species complex (Damm *et al.* 2012b, this issue).

The macroscopic appearance of the cultures is often highly divergent within a species (*e.g. C. fructicola* and *C. theobromicola),* in most cases probably reflecting different storage histories of the isolates examined. Prolonged storage, especially with repeated subculturing, results in staling of the cultures, the aerial mycelium often becoming dense and uniform in appearance and colour, and a loss of conidial and perithecial production, and variable in growth rate (Fig. 9). In some species, individual single ascospore or single conidial isolates show two markedly different cultural types, see notes under *C. kahawae* subsp. *ciggaro*.

Some species appear to be host specialised, *e.g. C. horii, C. kahawae* subsp. *kahawae, C. nupharicola, C. salsolae, C. ti*, and *C. xanthorrhoeae*, but those most commonly isolated have broad host and geographic ranges, *e.g. C. fructicola, C. kahawae* subsp. *ciggaro, C. siamense,* and *C. theobromicola*. *Colletotrichum gloeosporioides s. str.* is commonly isolated from *Citrus* in many

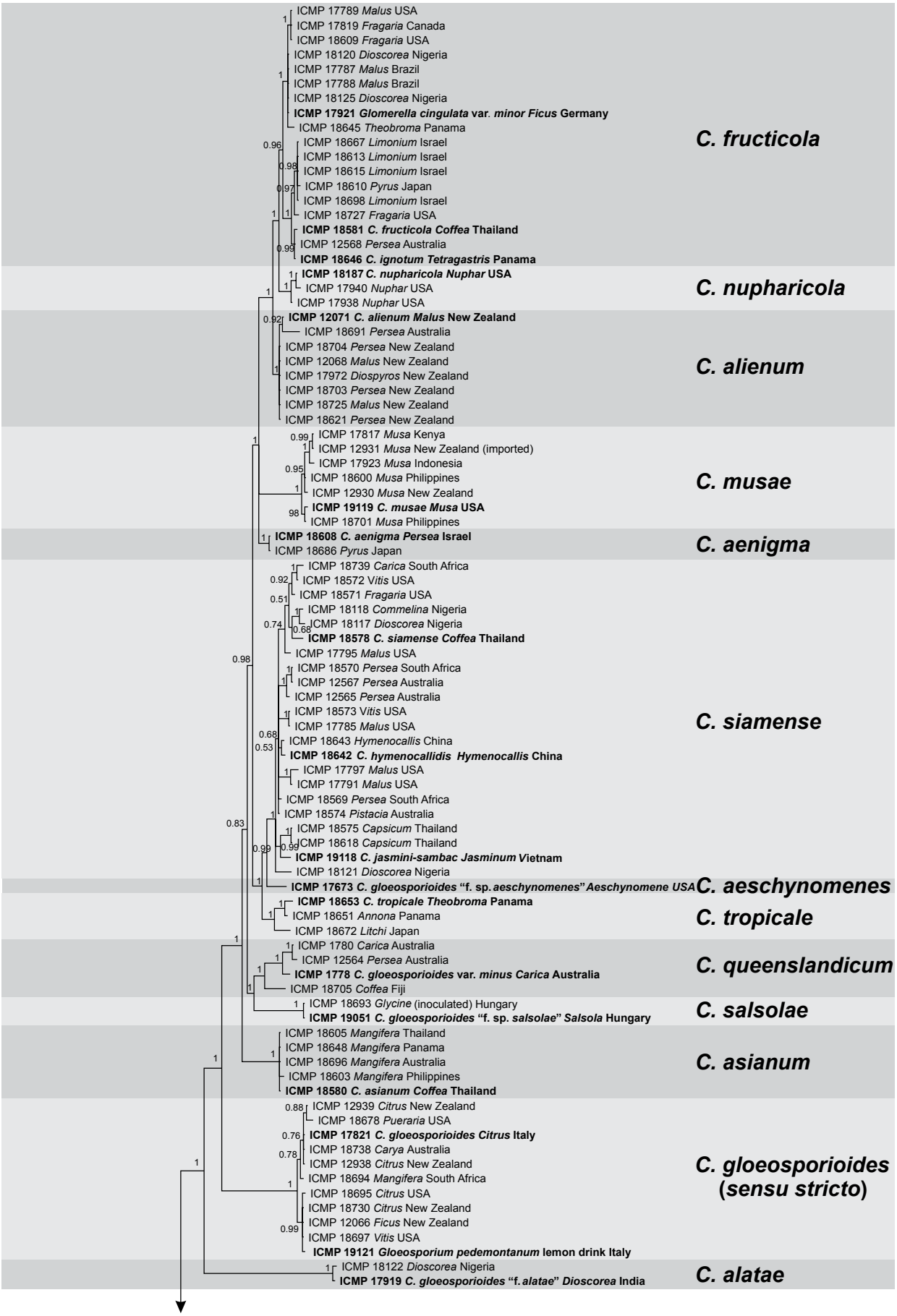


Fig. 1. A Bayesian inference phylogenetic tree of 156 isolates in the *Colletotrichum gloeosporioides* species complex. The tree was built using concatenated sequences of the ACT, CAL, CHS-1, GAPDH, and ITS genes each with a separate model of DNA evolution. Bayesian posterior probability values ≥ 0.5 are shown above nodes. Culture accession numbers are listed along with host plant genus and country of origin. Ex-type and authentic cultures are emphasised in bold font, and include the taxonomic name as originally described. Species delimitations are indicated with grey boxes. *Colletotrichum boninense* and *C. hippeastri* isolates are used as outgroups. The scale bar indicates the number of expected changes per site.

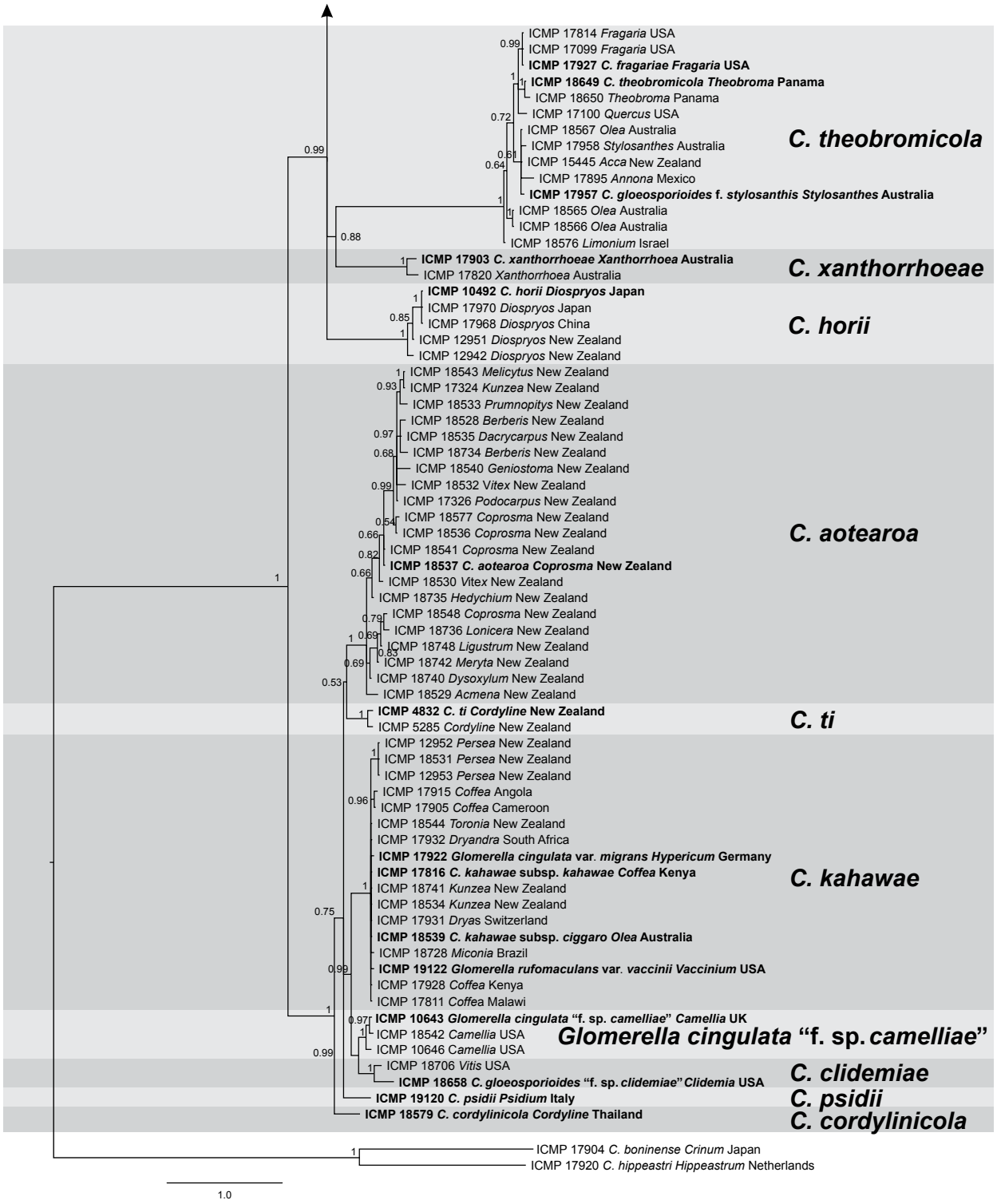


Fig. 1. (Continued).

parts of the world, but has been isolated from other hosts as well, such as *Ficus*, *Mangifera*, *Pueraria*, and *Vitis*. Not all of the species with a broad host range are found everywhere, for example in New Zealand *C. alienum* is commonly associated with cultivated fruits, whereas species such as *C. siamense* and *C. fructicola*, common on these same cultivated fruits in other parts of the world, have not been reported from New Zealand.

Taxonomy

Based on results of the multigene concatenated BI phylogenies, we accept 22 species plus one subspecies within the *C. gloeosporioides* complex. Isolates authentic for *G. cingulata* "f. sp. *camelliae*" form a genetically distinct group, but this is not formally named because of doubts over its relationship to *C. camelliae*. Based on DNA sequence comparisons, a few other isolates almost certainly represent additional unnamed species. We do not formally describe them because most are known from a single isolate, often stale, with little understanding of either their morphological or biological diversity. In the Musae clade these include ICMP 18614 and ICMP 18616, both from grape from Japan, and ICMP 18726 from pawpaw from the Cook Islands, and in the Kahawae clade ICMP 18699 from chestnut from Japan. These isolates are not included in the phylogenies in this study,

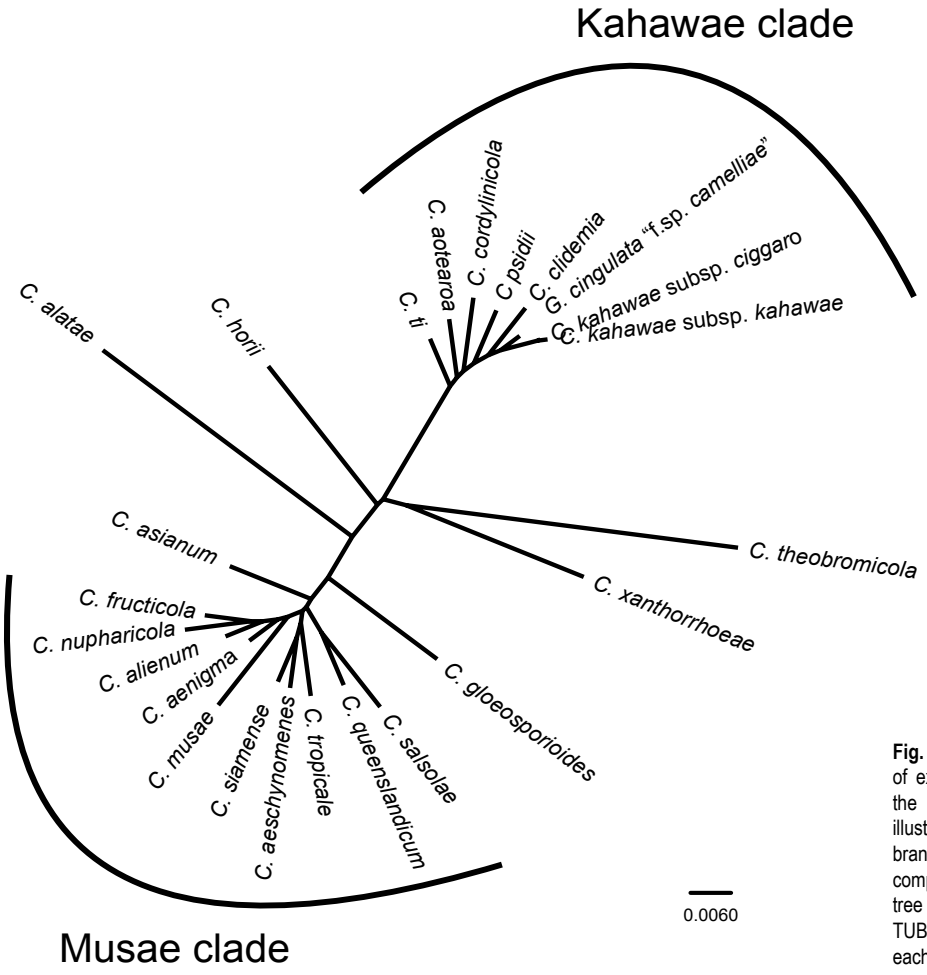


Fig. 2. An unrooted Bayesian inference phylogenetic tree of ex-type and authentic cultures of the 24 taxa within the *Colletotrichum gloeosporioides* species complex, illustrating their relative genetic distances, as indicated by branch lengths. There are two clusters within the species complex, the 'Musae clade' and the 'Kahawae clade'. The tree was build using concatenated sequences of the ACT, TUB2, CAL, CHS-1, GAPDH, GS, ITS, and SOD2 genes each with a separate model of DNA evolution.

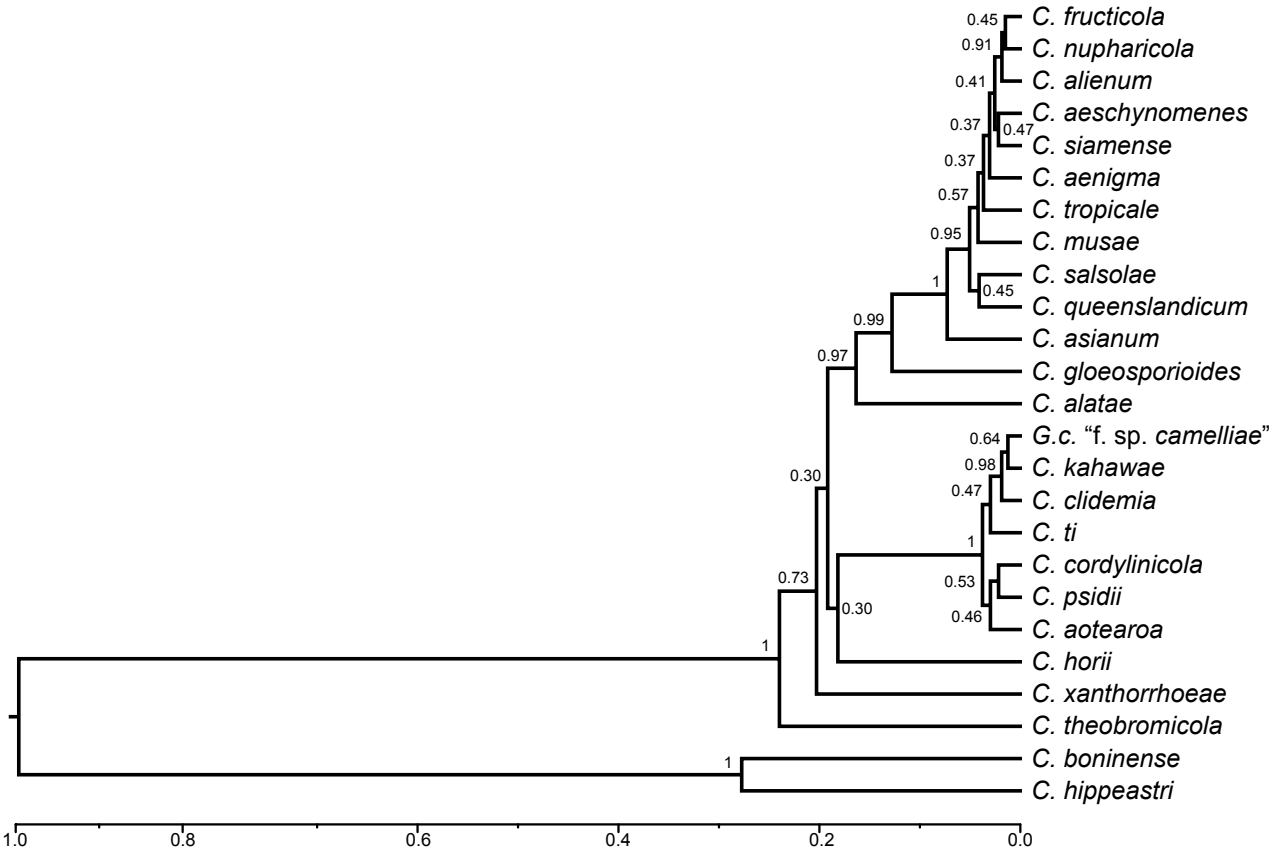


Fig. 3. A Bayesian inference species-tree of the *C. gloeosporioides* species complex. The tree was built by grouping all 158 isolates into species and simultaneously estimating the individual five gene trees (ACT, CAL, CHS-1, GAPDH, and ITS) and the summary species tree using BEAST. The scale is an uncalibrated clock set relative to the last common ancestor of the *C. gloeosporioides* and *C. boninense* species complexes.

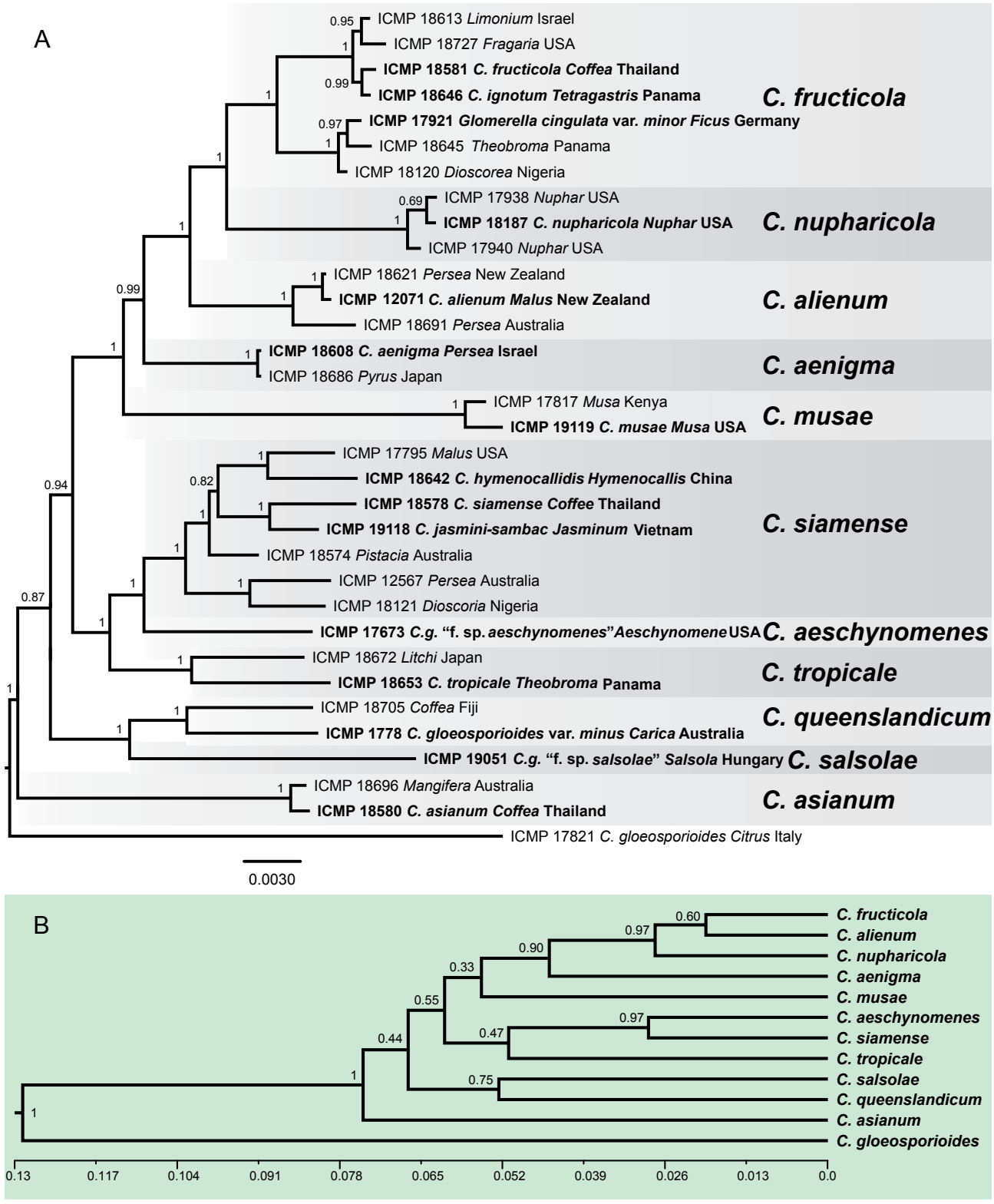


Fig. 4. A Bayesian inference phylogenetic tree of 32 selected isolates in the Musae clade of the *Colletotrichum gloeosporioides* species complex. The tree was build using concatenated sequences of the ACT, TUB2, CAL, CHS-1, GAPDH, GS, ITS, and SOD2 genes each with a separate model of DNA evolution. Other details as per Fig.1. B. A species-tree constructed from the same data, the scale is an clock set relative to the last common ancestor of the Musae clade and *C. gloeosporioides s. str.*, as calibrated in Fig. 3.

but DNA sequences from these isolates have been accessioned into GenBank (ITS: JX009423–JX009428, GAPDH: JX009416–JX009422, ACT: JX009404–JX009407, CAL: JX009408–JX009411, CHS-1: JX009412–JX009415).

Many of the species that we recognise fall into one of two clades, the informally named Musae clade and Kahawae clade (Fig. 2). Each clade contains several species that are phylogenetically well supported in multi-gene analyses, but within the clades branch lengths are short because of the small number of phylogenetically informative characters. This is reflected in the low support values in the gene tree analyses for the species we accept within that clade (Figs 3, 4). Both the Musae and Kahawae clades contain ex-type or authentic cultures from several long accepted species. In this work we have made a pragmatic decision to minimise taxonomic disruption, so that monophyletic subclades within the Kahawae and Musae clades are accepted as species where they include

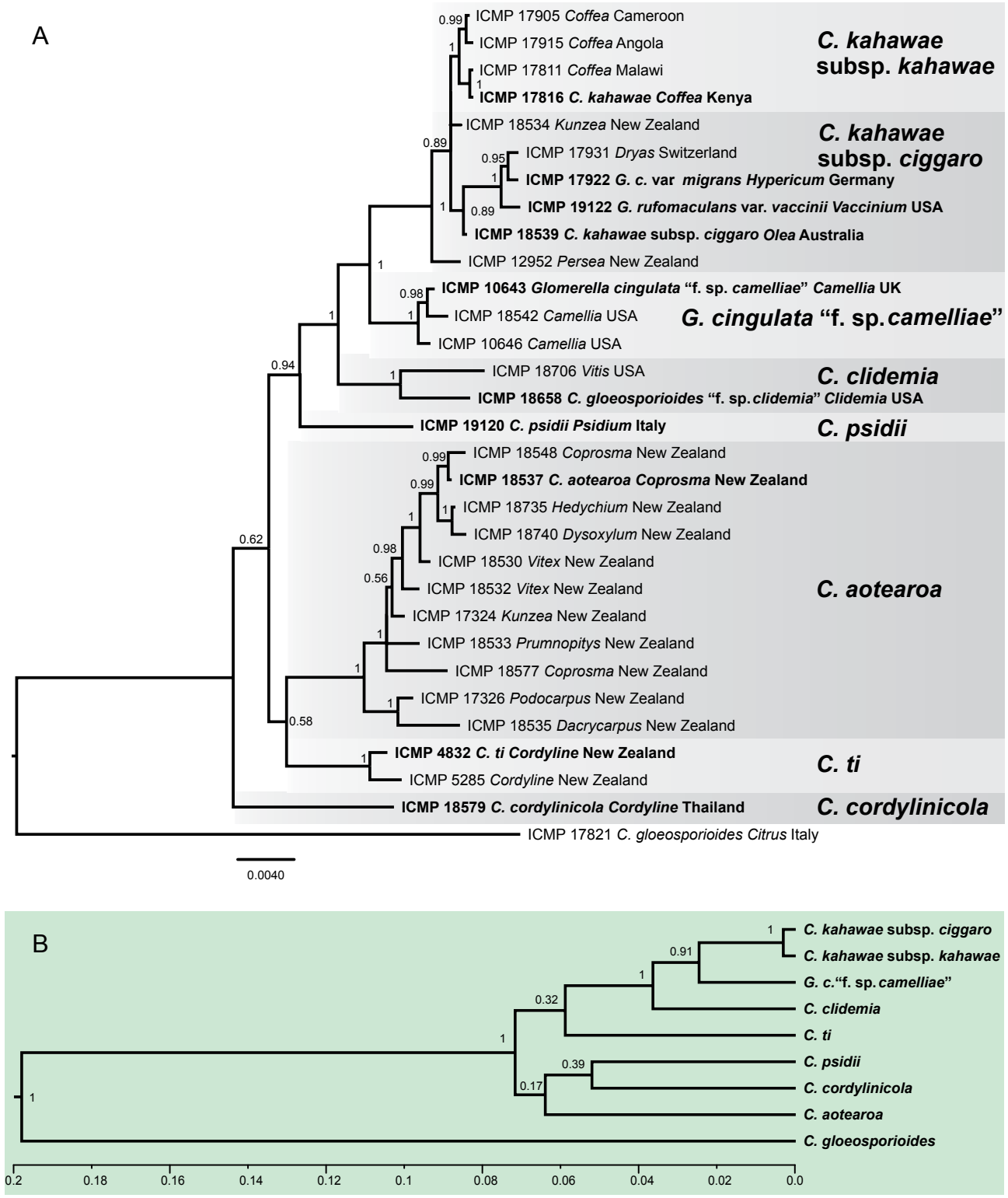


Fig. 5. A Bayesian inference phylogenetic tree of 30 selected isolates in the Kahawae clade of the *Colletotrichum gloeosporioides* species complex. The tree was build using concatenated sequences of the ACT, TUB2, CAL, CHS-1, GAPDH, GS, ITS, and SOD2 genes each with a separate model of DNA evolution. Other details as per Fig.1. B. A species-tree constructed from the same data, the scale is a clock set relative to the last common ancestor of the Kahawae clade and *C. gloeosporioides s. str.*, as calibrated in Fig. 3.

ex-type or authentic cultures. The Musae clade thus includes *C. fructicola*, *C. musae*, *C. nupharicola*, *C. siamense*, and *C. tropicale*; and the Kahawae clade includes *C. cordylinicola*, *C. psidii*, and *C. kahawae*. Also belonging in the latter is *Glomerella cingulata* "f. sp. *camelliae*". To provide a consistent taxonomic treatment of the subclades resolved within the Musae and Kahawae clades, several new species and one new subspecies are proposed. In the Musae clade these are *C. aenigma*, *C. aeschynomenes*, *C. alienum*, *C. queenslandicum*, and *C. salsolae*; in the Kahawae clade *C. aotearoa*, *C. clidemiae*, *C. kahawae* subsp. *ciggaro*, and *C. ti*. The other accepted species, well resolved in all of the gene trees, are *C. alatae, C. asianum*, *C. gloeosporioides*, *C. horii*, *C. theobromicola*, and *C. xanthorrhoeae*.

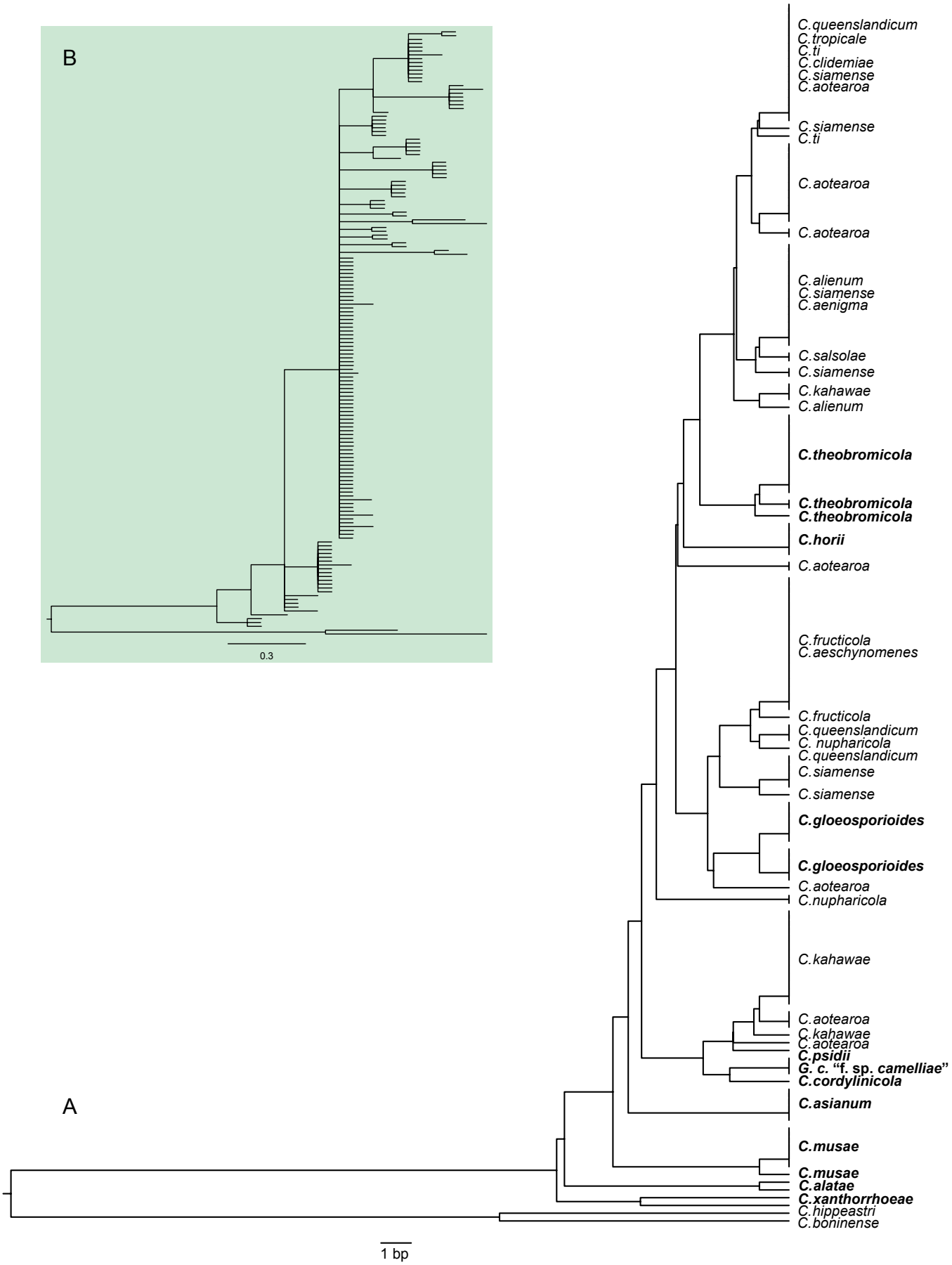
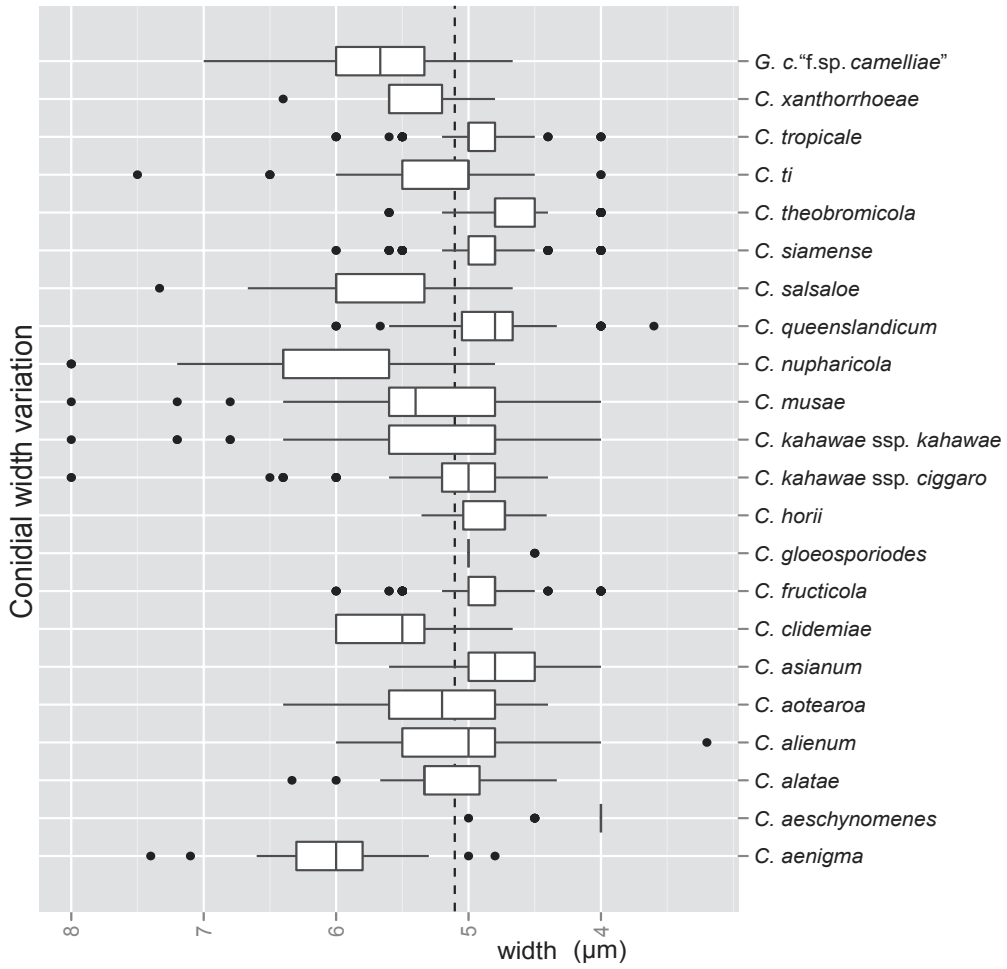


Fig. 6. An UPGMA tree of ITS sequences from 156 isolates in the *Colletotrichum gloeosporioides* species complex. Isolate names have been replaced with species present in each clade. Species that are in monophyletic clades are emphasised in bold font to indicate those for which ITS barcoding is likely to work well. B: A 50 % majority-rule consensus Bayesian inference tree of the same data, showing the collapse of structure when analysed with a more robust method.



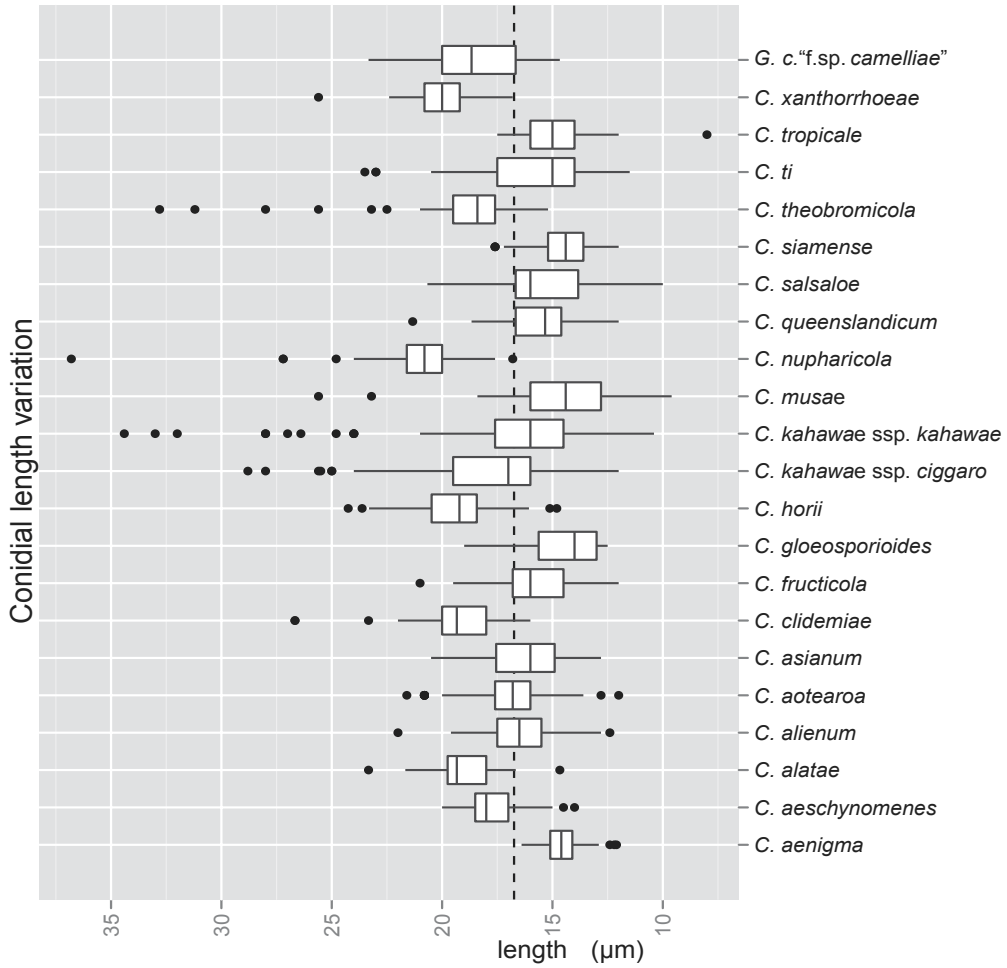
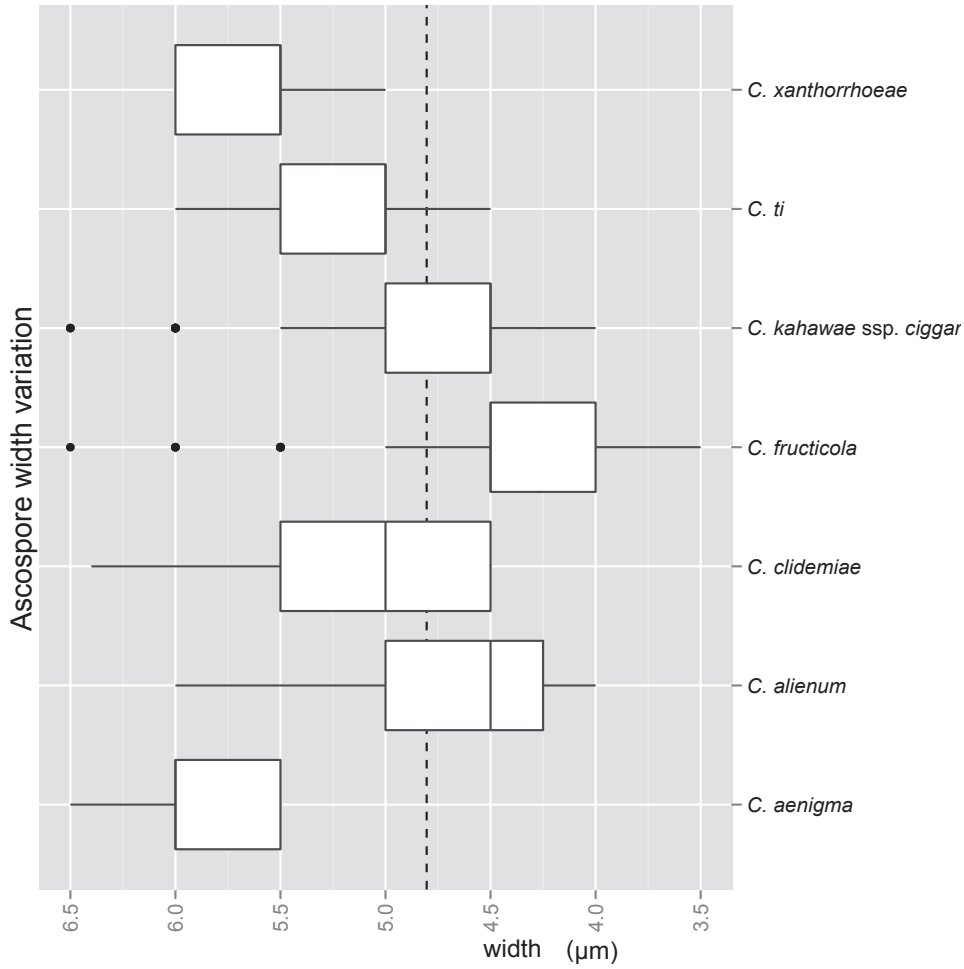


Fig. 7. Box plots showing the variation in length and width of conidia produced by the cultures examined in this study. The dashed lines show the mean length (16.74 µm) and width (5.1 µm) across the species complex (n = 1958).



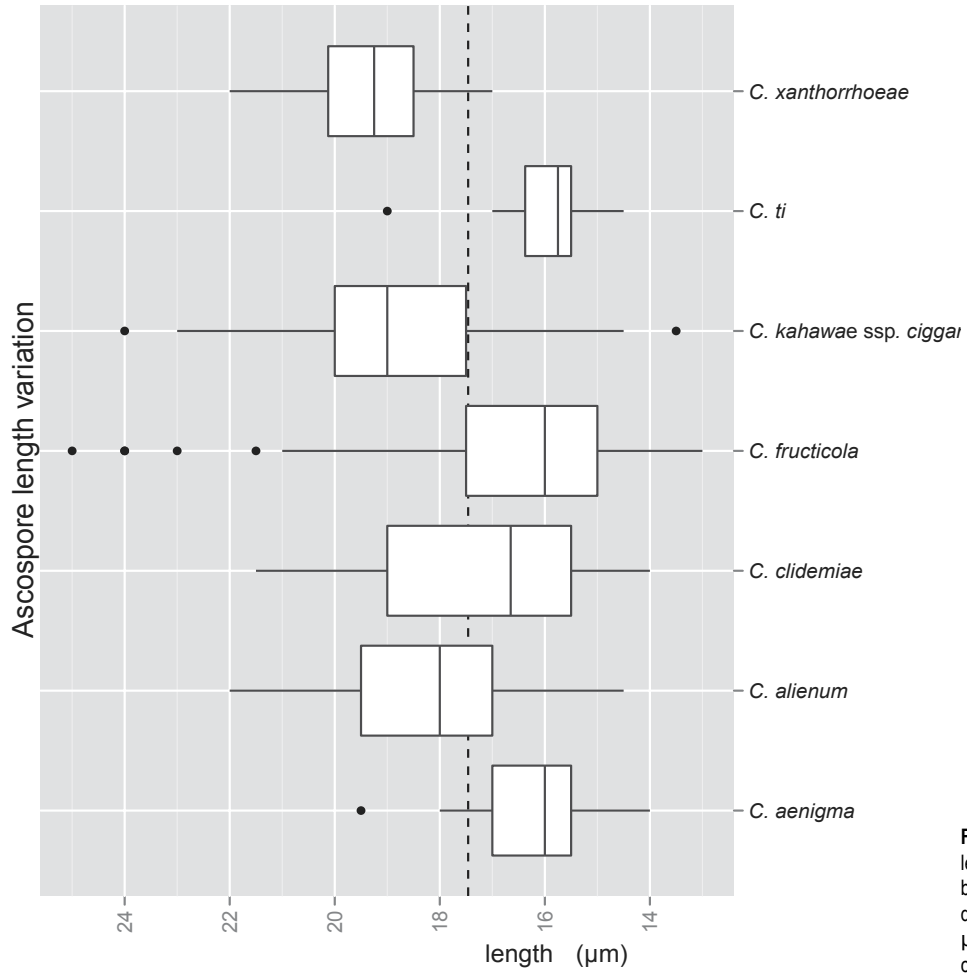


Fig. 8. Box plots showing the variation in length and width of ascospores produced by the cultures examined in this study. The dashed lines show the mean length (17.46 µm) and width (4.8 µm) across the species complex (n = 452).

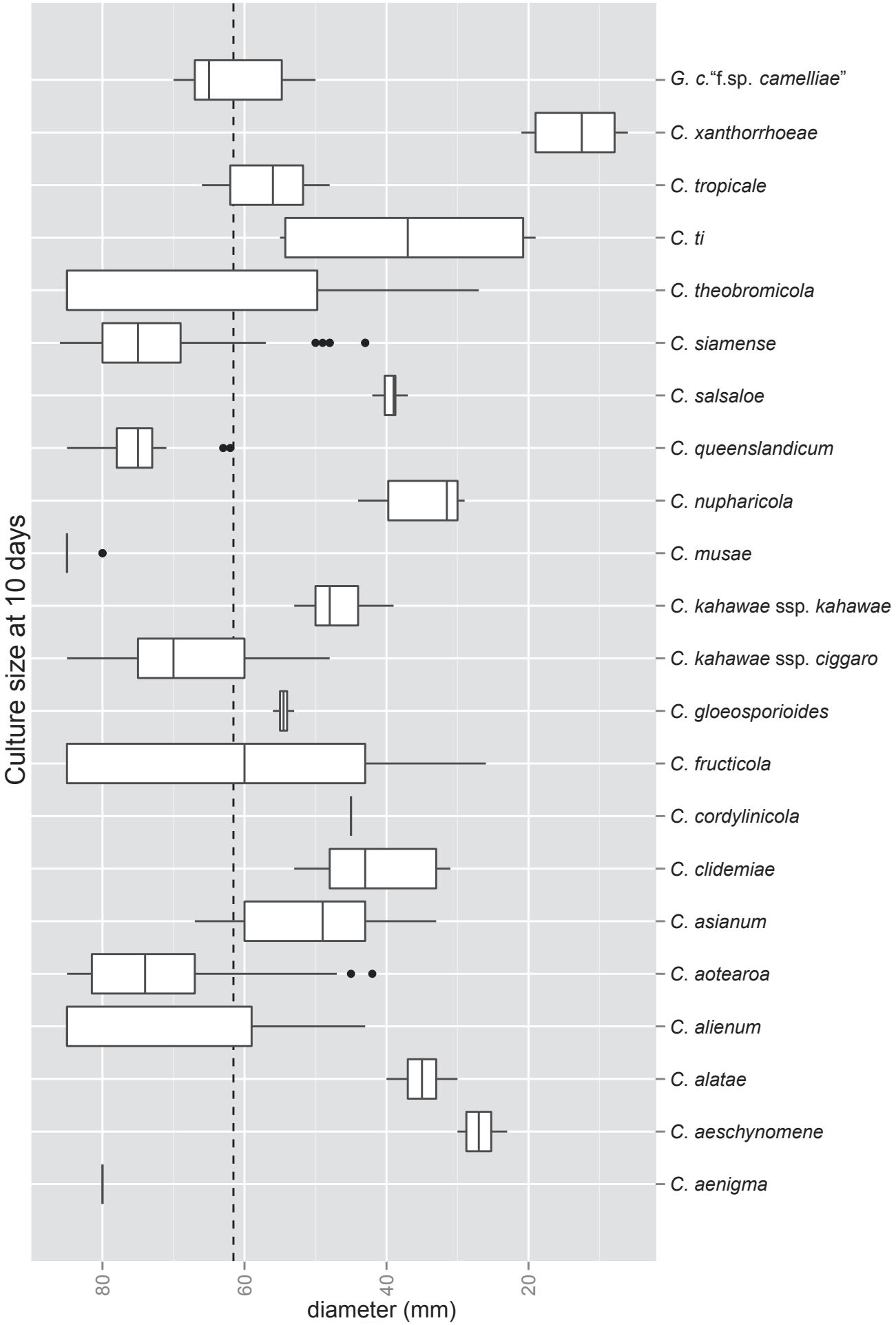


Fig. 9. A box plot of the diameter of cultures grown on PDA agar at 18 °C for 10 d. The dashed line shows the mean culture size (61.56 mm) across the species complex (n = 719). Note that the data is skewed by some fast growing cultures that reached the agar plate diam (85 mm) in under 10 d.

*** *Colletotrichum aenigma*** B. Weir & P.R. Johnst., **sp. nov.** MycoBank MB563759. Fig. 10.

Etymology: from the Latin *aenigma*, based on the enigmatic biological and geographic distribution of this species.

Holotype: **Israel**, on *Persea americana*, coll. S. Freeman Avo-37-4B, PDD 102233; ex-holotype culture ICMP 18608.

Colonies grown from single conidia on Difco PDA 30–35 mm diam after 10 d. Aerial mycelium sparse, cottony, white, surface of agar uniformly pale orange (7A5) towards centre, more or less colourless towards edge, conidia not associated with well differentiated acervuli and no masses of conidial ooze. In reverse pale orange towards centre. *Conidiogenous cells* arising haphazardly from dense, tangled hyphae across agar surface, short-cylindric with a poorly differentiated conidiogenous locus. *Conidia* often germinating soon after release, sometimes forming appressoria, so forming a thin, compact, layer of germinated, septate conidia, germ tubes, and appressoria across the central part of the colony surface. Conidia (12–)14–15(–16.5) × (5–)6–6.5(–7.5) µm (av. 14.5 × 6.1 µm, n = 53), cylindric with broadly rounded ends. *Appressoria* 6–10 µm diam, subglobose or with a few broad lobes.

Geographic distribution and host range: known from only two collections, one from *Pyrus pyrifolia* from Japan, the other from *Persea americana* from Israel.

Genetic identification: ITS sequences are insufficient to separate *C. aenigma* from *C. alienum* and some *C. siamense* isolates. These taxa are best distinguished using TUB2 or GS.

Notes: Although the biology of this species is more or less unknown, it has been found in two widely separate regions and is, therefore, likely to be found to be geographically widespread in the future. Genetically distinct within the Musae clade, this species has a distinctive appearance in culture with sparse, pale aerial mycelium and lacking differentiated acervuli.

Other specimen examined: **Japan**, on *Pyrus pyrifolia*, coll. H. Ishii Nashi-10 (ICMP 18686).

*** *Colletotrichum aeschynomenes*** B. Weir & P.R. Johnst., **sp. nov.** MycoBank MB563590. Fig. 11.

= *C. gloeosporioides* "f. sp. *aeschynomenes*" (Daniel *et al.* 1973, as *aeschynomene*).

Etymology: Based on *C. gloeosporioides* "f. sp. *aeschynomenes*", referring to the host from which this species was originally described.

Holotype: **USA**, Arkansas, on *Aeschynomene virginica* stem lesion, coll. D. TeBeest 3-1-3, PDD 101995; ex-type culture ICMP 17673 = ATCC 201874.

Colonies grown from single conidia on Difco PDA 25–35 mm diam after 10 d, aerial mycelium sparse, cottony, white, surface of colony with numerous acervuli, some with dark bases, with orange conidial ooze; in reverse more or less colourless apart from the dark acervuli and orange conidial masses showing through the agar. *Conidia* (14–)17–18.5(–20) × 4(–5) µm (av. 17.6 × 4.1 µm, n = 30), cylindric, straight, tapering slightly near both ends. *Appressoria* mostly elliptic to subfusoid, deeply lobed. Perithecia not seen.

Geographic distribution and host range: Reported only from USA, pathogenic to *Aeschynomeme.*

Genetic identification: ITS sequences do not distinguish *C. aeschynomenes* from *C. fructicola*. These taxa are best distinguished using TUB2, GAPDH, or GS.

Notes: *Colletotrichum gloeosporioides* "f. sp. *aeschynomenes*" has been used to refer to isolates pathogenic to *Aeschynomene virginica*, later developed as the weed biocontrol agent Collego (references in Ditmore *et al.* 2008). It has also been reported from a range of other hosts (TeBeest 1988). Our analyses, based on a single, authentic strain of *C. gloeosporioides* "f. sp. *aeschynomenes*" (TeBeest 3.1.3, apparently the source of the single spore isolate originally used in the development of Collego, Ditmore *et al.* (2008)) show it to be genetically distinct within the Musae clade of the *C. gloeosporioides* complex. Genetically close to the geographically and biologically diverse *C. siamense*, it differs morphologically from this species in having slightly longer and narrower conidia which taper slightly toward the ends, and in having larger, strongly lobed appressoria.

An isolate deposited as *C. gloeosporioides* f. sp. *aeschynomenes* in CBS (CBS 796.72) by G.E. Templeton, one of the early *C. gloeosporioides* f. sp. *aeschynomenes* researchers (Daniel *et al.* 1973), is genetically distinct to TeBeest 3.1.3 and has been identified by Damm *et al.* (2012a, this issue) as *C. godetiae*, a member of the *C. acutatum* complex. The strain that we examined (Te Beest 3.1.3) matches genetically another strain often cited in the *C. gloeosporioides* f. sp. *aeschynomenes* literature (Clar-5a = ATCC 96723) (GenBank JX131331). It is possible that two distinct species, both highly pathogenic to *Aeschynomene* in Arkansas, have been confused. A survey of additional isolates of *Colletotrichum* highly virulent to *Aeschynomene* in Arkansas would clarify the interpretation of the past literature on this pathogen. For example, *C. gloeosporioides* "f. sp. *aeschynomenes*" was initially reported as specific to *Aeschynomene virginica* (Daniel *et al.* 1973), while later studies reported isolates putatively of the same taxon, to have a wider host range (TeBeest 1988).

Cisar *et al.* (1994) reported fertile ascospores from crosses between isolates identified as *C. gloeosporioides* "f. sp. *aeschynomenes*" and isolates of *C. gloeosporioides* "f. sp. *jussiaeae*", a pathogen of *Jussiaea decurrens*. The position of *C. gloeosporioides* "f. sp. *jussiaeae*" within our phylogeny is not known, but these taxa could prove useful for better understanding of the biological differences between phylogenetically defined species of *Colletotrichum*.

Specimen examined: **USA**, Arkansas, on *Aeschynomene virginica* stem lesion, coll. D. TeBeest 3.1.3 (ICMP 17673 = ATCC 201874).

*** *Colletotrichum alatae*** B. Weir & P.R. Johnst., **sp. nov.** MycoBank MB563747. Fig. 12.

= *Colletotrichum gloeosporioides* "f. *alatae*" R.D. Singh, Prasad & R.L. Mathur, Indian Phytopathol. 19: 69. 1966. [nom. inval., no Latin description, no type designated].

Etymology: Based on the invalid name *C. gloeosporioides* "f. *alatae*" (Singh *et al.* 1966), referring to *Dioscorea alata*, the scientific name for yam.

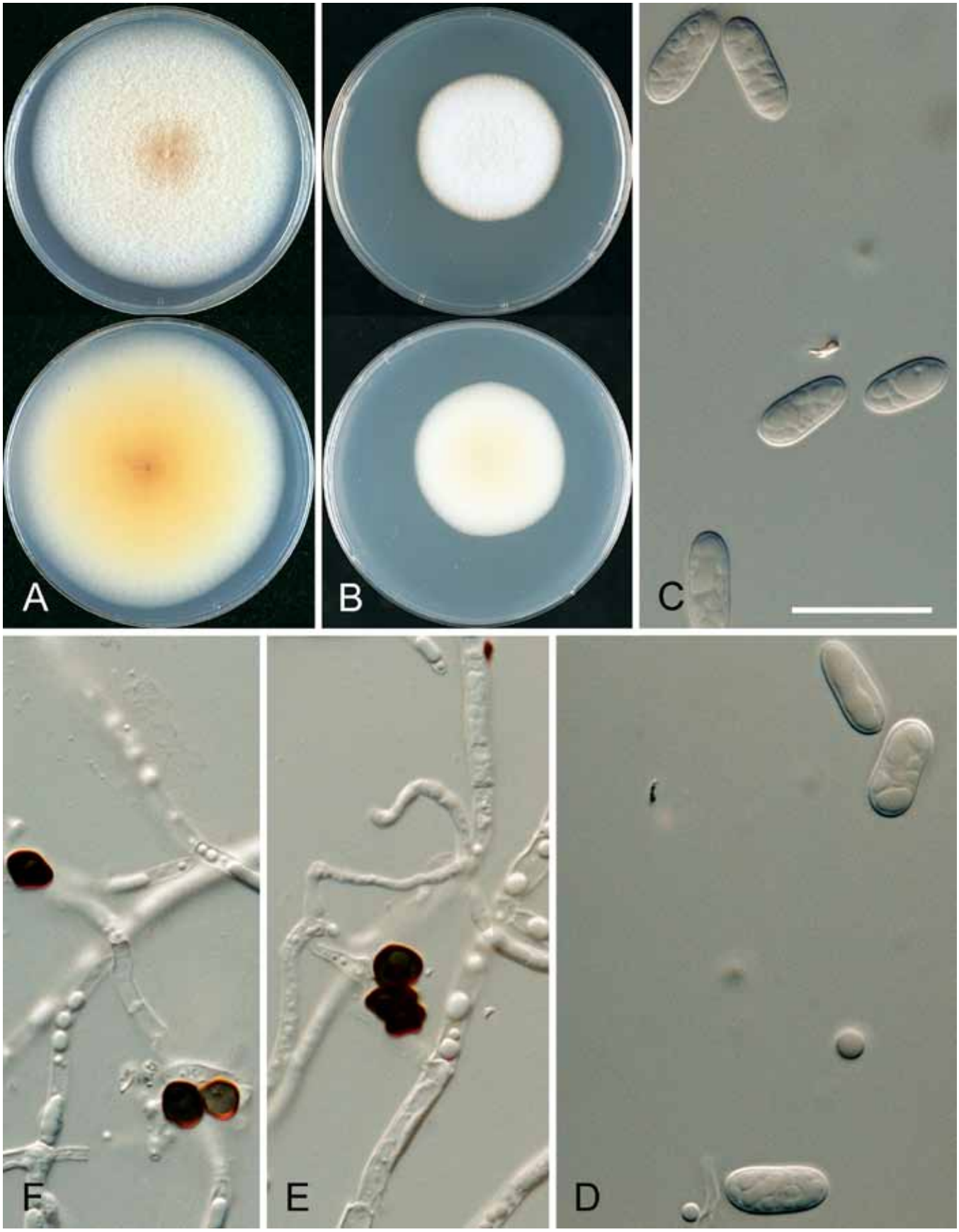


Fig. 10. *Colletotrichum aenigma*. A, C, D, E, F. ICMP 18608 – ex-holotype culture. B. ICMP 18616. A–B. Cultures on PDA, 10 d growth from single conidia, from above and below. C–D. Conidia. E–F. Appressoria. Scale bar C = 20 µm. Scale bar of C applies to C–F.

Holotype: **India**, Rajasthan, Udaipur, on *Dioscorea alata* leaves and stems, coll. K.L. Kothari & J. Abramham, 1959, CBS H-6939; ex-type culture and putatively authentic isolate of *C. gloeosporioides* f. *alatae* CBS 304.67 = ICMP 17919.

Colonies grown from single conidia on Difco PDA 30–40 mm diam after 10 d. Ex-holotype culture looks "stale", with low, felted, dense, pale grey aerial mycelium, orange agar surface showing through near the margin, scattered dark based acervuli with orange conidial

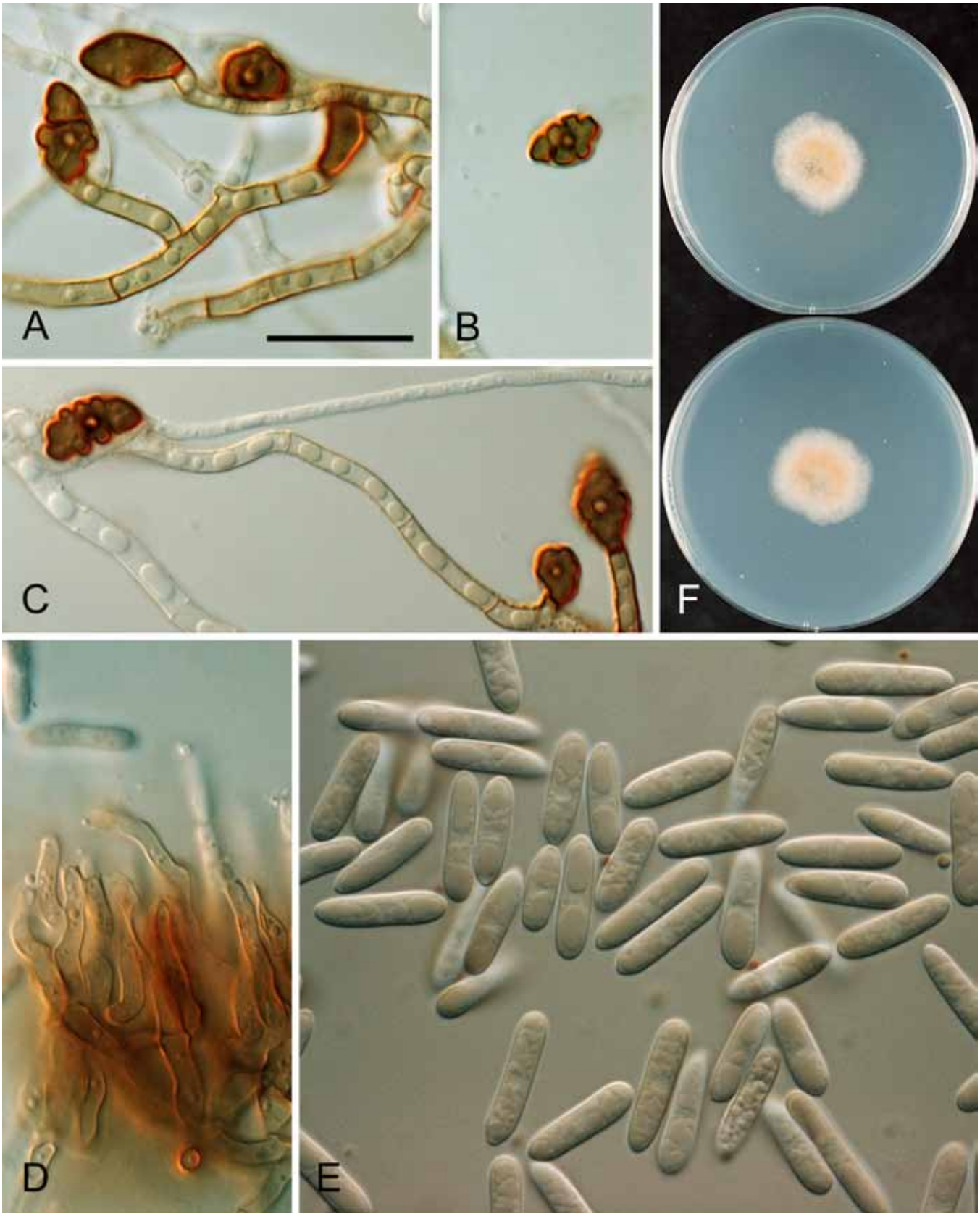


Fig. 11. *Colletotrichum aeschynomenes*. ICMP 17673 – ex-holotype culture. A–C. Appressoria. D. Conidiogenous cells. E. Conidia. F. Cultures on PDA, 10 d growth from single conidia, from above and below. Scale bar of A = 20 µm. Scale bar of A applies to A–E.

masses near centre; in reverse deep pinkish orange with patches of grey pigment near centre. ICMP 18122 with aerial mycelium sparse, colony surface with numerous discrete, dark-based acervuli with bright orange conidial ooze, margin of colony feathery; in reverse irregular sectors with pale grey pigment within the grey, otherwise colourless apart from the colour of the acervuli and conidial masses. *Conidia* (14.5−)18–19.5(−23.5) × (4.5−)5−5.5(−6.5) µm (av. 18.9 × 5.2 µm, n = 40), cylindric, straight, ends rounded, a few tapering towards the basal end. *Appressoria* mostly simple, elliptic to fusoid in shape, sometime developing broad, irregular lobes, about 7–13.5 × 5–10.5 µm. Perithecia not seen.

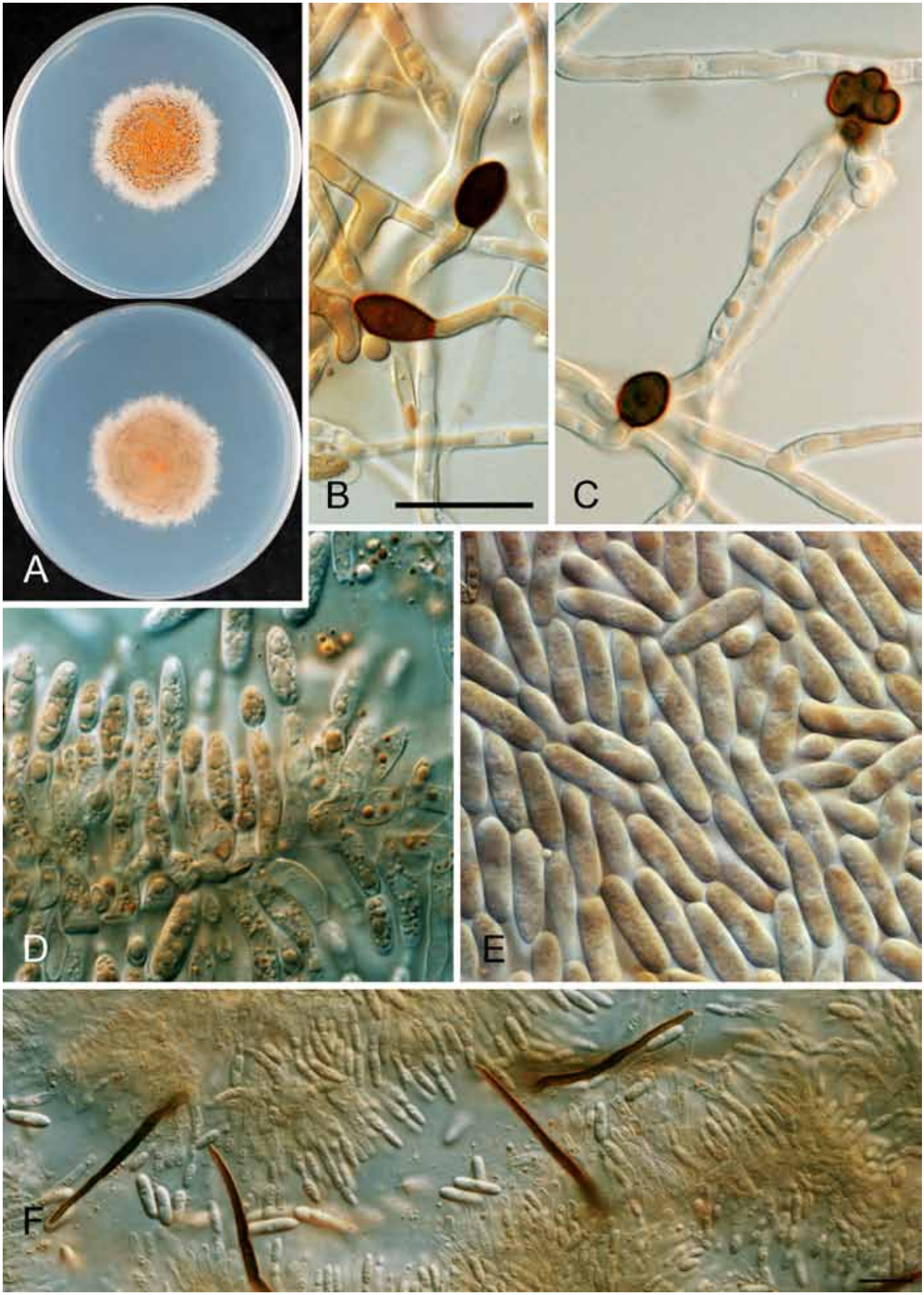


Fig. 12. *Colletotrichum alatae*. ICMP 18122. A. Cultures on PDA, 10 d growth from single conidia, from above and below. B–C. Appressoria. D. Conidiogenous cells and conidia. E. Conidia. F. Setae. Scale bars B, F = 20 µm. Scale bar of B applies to B–E.

Geographic distribution and host range: Known only from yam (*Dioscorea alata*), from Nigeria, Barbardos, India, Guadeloupe.

Genetic identification: ITS sequences distinguish *C. alatae* from all other taxa.

Notes: Anthracnose diseases of yam are found throughout the regions where the host is grown (*e.g.* Winch *et al.* 1984, Prasad & Singh 1960, Singh *et al.* 1966, Abang *et al.* 2002, 2003). Isolates from diseased yam leaves are morphologically (Winch *et al.* 1984) and genetically (Abang *et al.* 2002) diverse. Both of these authors used a broad species concept, grouping all isolates sourced from yam under the single name *C. gloeosporioides*. In this paper we accept part of that diversity to represent a distinct species, newly described here as *C. alatae*. The type specimen of *C. alatae* matches the SGG (slow growing grey) group of Abang *et al.* (2002), the group that these authors found to be more pathogenic to yam than the other morphological and genetic groups they recognised within *C. gloeosporioides*. In addition to the Nigerian isolates of Abang *et al.* (2002), isolates from yam from Barbados (isolates SAS8 and SAS9 from Sreenivasaprasad *et al.* 1996), Guadeloupe (GenBank accession GQ495617) and India (CBS 304.67 and GenBank accession FJ940734) belong in this clade, while no isolates from other hosts have been found.

Other isolates from yam that we sequenced included some representing the Abang *et al.* (2002) FGS group (Abang Cg22 = ICMP 18120, Abang Cg13 = ICMP 18125, Abang CgS6 = ICMP 18117, Abang CgS2 = ICMP 18121), a group distinguished from the highly pathogenic SGG isolates by faster growth in culture and shorter conidia (Abang *et al.* 2002). Two of these isolates (ICMP 18120, 18125) genetically match *C. fructicola*, the others match *C. siamense*.

Several names have been applied to *Colletotrichum* specimens from anthracnose of yam stems and leaves, including *Gloeosporium pestis* Massee, *G.* "*dioscoreae*" Sawada (nom. inval.; no Latin diagnosis), *Colletotrichum dioscoreae* Av.-Saccá 1917, and C. *dioscoreae* Tehon 1933. In addition, *Gloeosporium bomplandii* Speg. was described from a host doubtfully identified as *Dioscorea*. Because of the broad genetic diversity of *Colletotrichum* spp. associated with diseased yam, the lack of cultures from any of these early type specimens, and the uncertainty to which part of the yam-associated diversity they correspond, we have chosen not to use these names for our newly recognised, yam-specialised pathogen. Whether the post-harvest tuber rot referred to as dead skin disease of yam (Abang *et al.* 2003, Green & Simmons 1994) is caused by the same *Colletotrichum* population as associated with diseased foliage is not known.

Other specimen examined: **Nigeria**, Kpite, on *Dioscorea alata* leaf, coll. M.M. Abang Cg25, 2001 (ICMP 18122).

*** *Colletotrichum alienum*** B. Weir & P.R. Johnst., **sp. nov.** MycoBank MB563591. Figs 13, 14.

Etymology: Based on the biology of this species, confined to exotic hosts and presumed to be a recent introduction to Australasia.

Holotype: **New Zealand**, Auckland, Kumeu research orchard, *Malus domestica* fruit rot, coll. P.R. Johnston C824, 14 Aug. 1987, PDD 101996; ex-type culture ICMP 12071.

Colonies grown from single conidia on Difco PDA 85 mm diam after 10 d. Colonies often with distinct sectors; some with cottony, grey aerial mycelium with numerous dark-based acervuli and orange conidial ooze visible through the mycelium; others with dense, cottony to felted mycelium, fewer acervuli and these hidden by the dense mycelium. In reverse, irregular dark grey patches and sectors masking the pale orange coloured pigmentation. ICMP 18691 looks "stale" with slow growth, dense, pale aerial mycelium and sparse conidial production and no perithecia. *Conidia* (12.5–) 15.5–17.5(–22) × (3–)5–5.5(–6) µm (av. 16.5 × 5.0 µm, n = 70), cylindric with broadly rounded ends. *Appressoria* mostly simple, globose to short-cylindric, a few with broad, irregular lobes; ICMP 18691 has mostly lobed appressoria. *Perithecia* forming in most cultures after about 10 d, dark-walled, globose with short, narrow ostiolar neck. *Ascospores* (14.5–)17–19.5(–22) × 4–5(–6) µm (av. 18.1 × 4.6 µm, n = 55), cylindric, curved, tapering slightly to each end.

Geographic distribution and host range: Known only from Australia and New Zealand, common on a wide range of introduced fruit crops.

Genetic identification: ITS sequences do not separate *C. alienum* from some *C. siamense* isolates. These taxa are best distinguished using CAL or GS.

Notes: Common on commercial fruit crops, this fungus was referred to as *C. gloeosporioides* Group A by Johnston & Jones (1997) and Johnston *et al.* (2005).

Other specimens examined: **Australia**, New South Wales, Murwillumbah, on *Persea americana* (DAR 37820 = IMI 313842 = ICMP 18691). **New Zealand**, Auckland, Oratia, Shaw Rd, on *Malus domestica* fruit rot, coll. P.R. Johnston C938.5, 14 Apr. 1988 (ICMP 18725); Bay of Plenty, Katikati, on *Diospyros kaki* ripe fruit rot, coll. M.A. Manning, Jun. 1989 (ICMP 17972); Bay of Plenty, Te Puke, on *Persea americana* ripe fruit rot, coll. W.F.T. Hartill, 2 Feb. 1988 (ICMP 18704); Bay of Plenty, Te Puna, on *Persea americana* ripe fruit rot, coll. W.F.T. Hartill, 25 Jan. 1988 (ICMP 18703); Bay of Plenty, on *Persea americana* ripe fruit rot, coll. W.F.T. Hartill, Feb. 1991 (ICMP 18621); Waikato, Hamilton, on *Malus domestica* fruit rot, coll. G.I. Robertson, May 1988 (ICMP 12068).

*** *Colletotrichum aotearoa*** B. Weir & P.R. Johnst., **sp. nov.** MycoBank MB800213. Figs 15, 16.

Etymology: Based on the Maori name for New Zealand; most isolates from native New Zealand plants belong here.

Holotype: **New Zealand**, Auckland, Glen Innes, Auckland University campus, on *Coprosma* sp. incubated berries, coll. B. Weir C1282.4, 30 Apr 2009, PDD 101076; ex-type culture ICMP 18537.

Colonies grown from single conidia on Difco PDA 70–85 mm diam after 10 d, several isolates with restricted growth, 50–55 mm diam with an irregularly scalloped margin. Aerial mycelium cottony to dense cottony, tufted near centre, grey to dark grey, scattered, small, dark-based acervuli and large, globose, stromatic structures partially embedded in agar, these sometimes splitting apart and forming conidia. In reverse typically with pinkish-orange pigments, variable in intensity, in some isolates this colour partially hidden by more or less concentric bands of dark grey pigment. *Conidia* (12–)16–17.5(–21.5) × (4.5–)5–5.5(–6.5) µm (av. 16.9 × 5.2 µm, n = 216), cylindric, straight, apex broadly rounded, often tapering slightly towards subtruncate base, 0-septate, hyaline. *Appressoria*

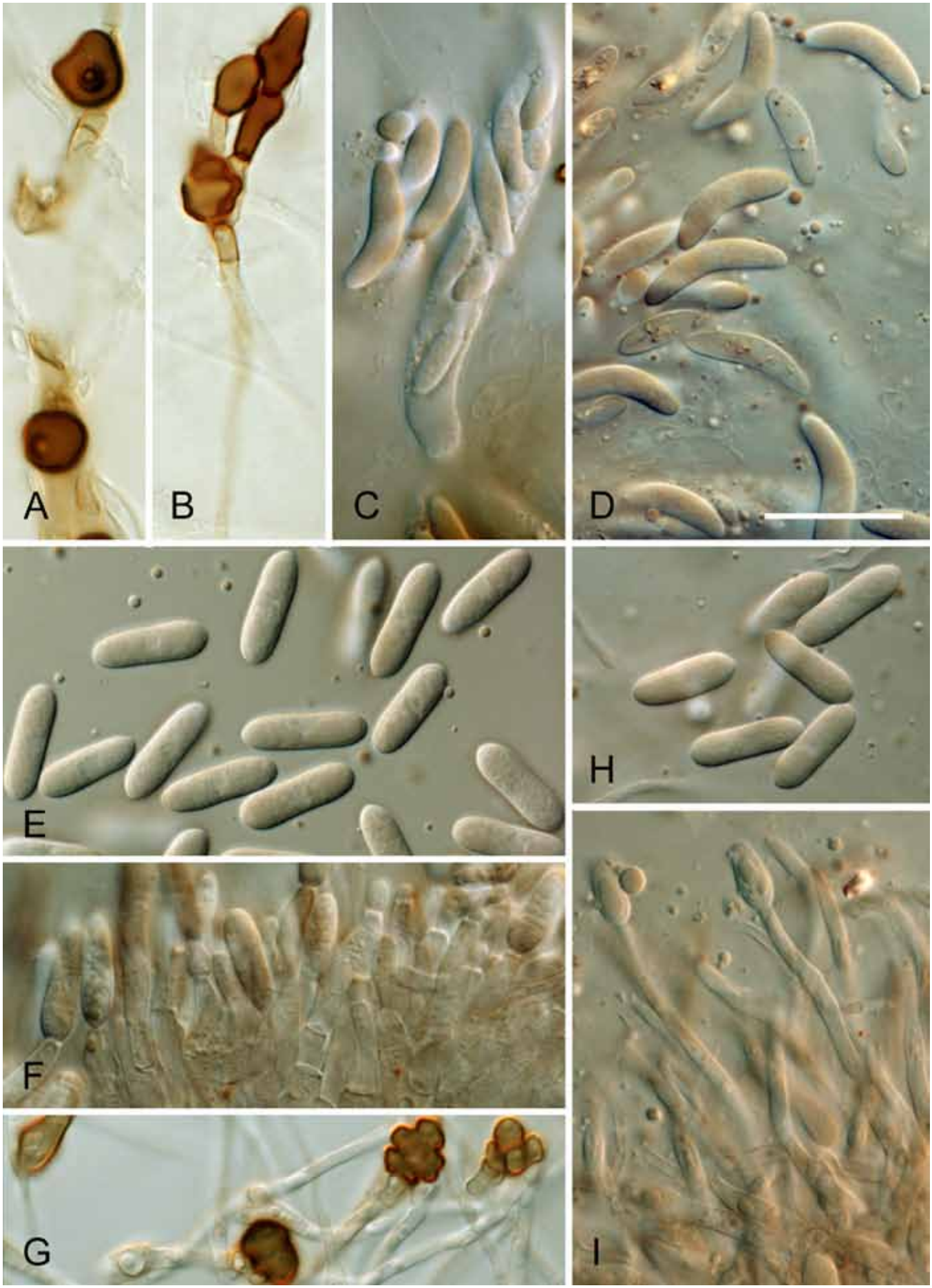


Fig. 13. *Colletotrichum alienum*. A, E, F. ICMP 12071 – ex-holotype culture. B. ICMP 18703. C–D. ICMP 12068. G–I. ICMP 18691 (ex DAR 37820). A–B. Appressoria. C–D. Asci and ascospores. E. Conidia. F. Conidiogenous cells. G. Appressoria. H. Conidia. I. Conidiogenous cells. Scale bar D = 20 µm. Scale bar of D applies to A–I.

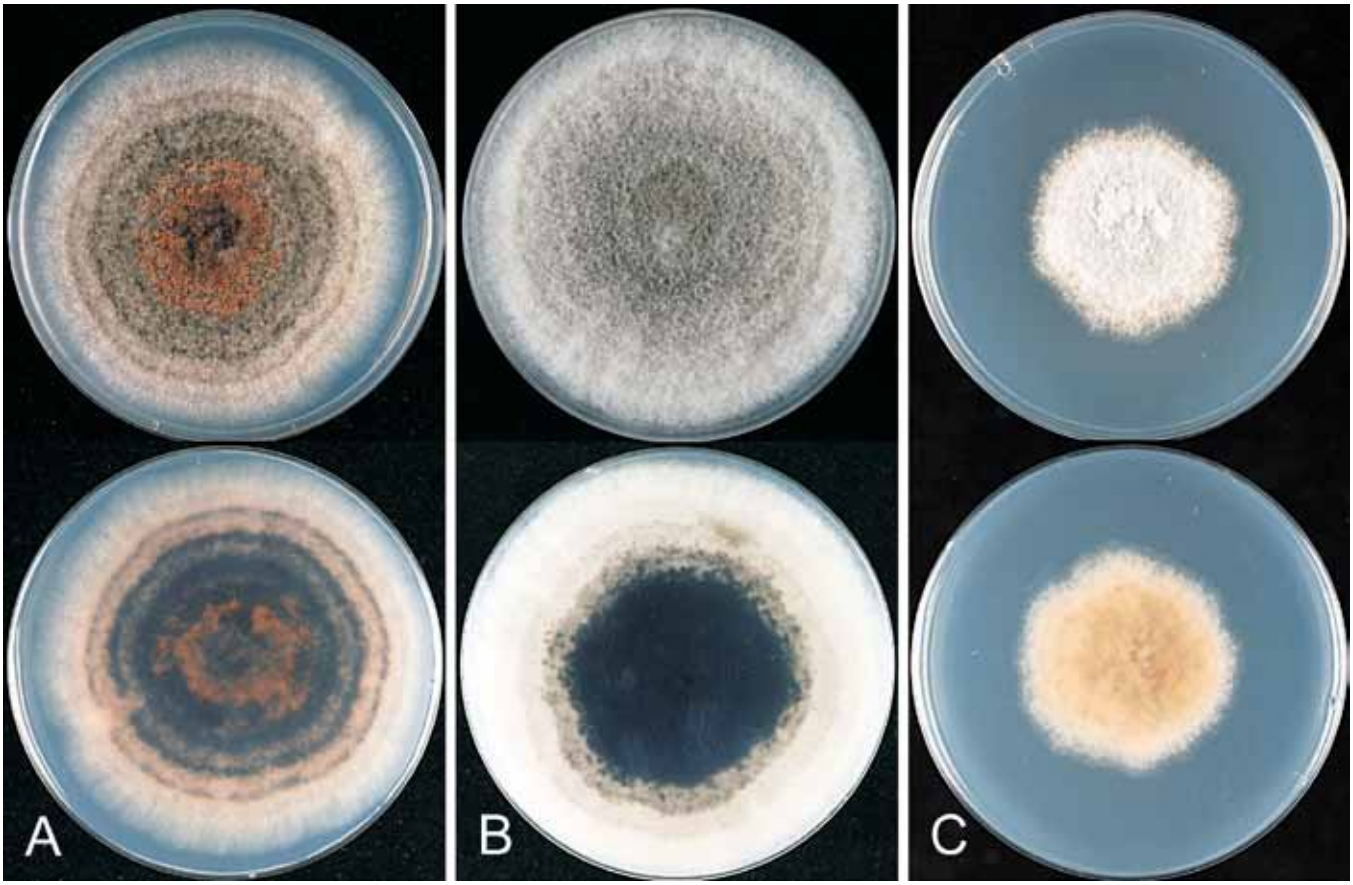


Fig. 14. *Colletotrichum alienum*. A. ICMP 12071 – ex-holotype culture. B. ICMP 12068. C. ICMP 18691 (ex DAR 37820). A–C. Cultures on PDA, 10 days growth from single conidia, from above and below.

variable in shape, simple to broadly lobed, sometimes in groups, sometimes intercalary, about 7–17 × 4–9.5 µm. *Perithecia* not seen in culture.

Geographic distribution and host range: Confirmed only from New Zealand, but GenBank records suggest *C. aotearoa* also occurs in China (see below). In New Zealand this species is common on a taxonomically diverse set of native plants, as both a fruit rot and a leaf endophyte, and has also been isolated from leaves of several species of naturalised weeds.

Genetic identification: ITS sequences do not separate *C. aotearoa* from several taxa in the Kahawae and Musae clades. This species can be distinguished using several other genes, including TUB2, CAL, GS, and GAPDH.

Notes: All isolates in the *C. gloeosporioides* complex from New Zealand native plants studied here belong in the Kahawae clade, and most of these are *C. aotearoa*; a small number of leaf endophyte isolates from New Zealand native trees are *C. kahawae* subsp. *ciggaro*. The *C. aotearoa* isolates have been isolated as endophytes from symptomless leaves as well as from rotting fruit from native trees. Morphologically indistinguishable from isolates of *C. kahawae* subsp. *ciggaro*, this species is distinguished genetically with all genes sampled, except ITS. The GAPDH gene tree splits *C. aotearoa* into two well supported clades, but these do not correlate to any other features, either geographic or biological. Isolates associated with distinctive and common leaf spots on *Meryta sinclairii*, first recorded by Beever (1984), belong in this species. Whether isolates of *C. aotearoa* from other hosts are able to cause the same disease on *Meryta* is not known.

Also in *C. aotearoa* are a range of isolates from weeds that have become naturalised in New Zealand. We assume that *C. aotearoa* is a New Zealand native species. It has a broad host range amongst native plants and has apparently jumped host to some weeds. It has never been found associated with cultivated plants or as a rot of cultivated fruit.

Colletotrichum aotearoa may also occur in China. ITS sequences from isolates from *Boehmeria* from China (GenBank records GQ120479 and GQ120480) from Wang *et al.* (2010) match exactly a set of *C. aotearoa* isolates. ITS between-species differences within the *C. gloeosporioides* complex are very small, so this match needs confirming with additional genes. *C. aotearoa* was referred to as Undescribed Group 2 by Silva et al. (2012b).

Other specimens examined: **New Zealand**, Auckland, Freemans Bay, on *Vitex lucens* fruit, coll. P.R. Johnston C1252.1, 26 Aug. 2007 (ICMP 18532; PDD 92930). on *Berberis* sp. leaf spot, coll. N. Waipara C69 (ICMP 18734); Auckland, Mangere, on *Berberis glaucocarpa* leaf spot, coll. N. Waipara C7, Jun. 2007 (ICMP 18528); Auckland, Waitakere Ranges, on *Kunzea ericoides* leaf endophyte, coll. S. Joshee 7Kun3.5, Jan. 2004 (ICMP 17324); Auckland, Waitakere Ranges, on *Prumnopitys ferruginea* leaf endophyte, coll. S. Joshee 8Mb5.1, Jan. 2004 (ICMP 18533); Auckland, Waitakere Ranges, on *Dacrycarpus dacrydioides* leaf endophyte, coll. S. Joshee 5K5.9, Jan. 2004 (ICMP 18535); Auckland, St Johns, Auckland University campus, on *Coprosma* sp. incubated berries, coll. B. Weir C1282.1, 30 Apr. 2009 (ICMP 18577); Auckland, Mt Albert, on *Acmena smithii* lesions fruit, coll. P.R. Johnston C847, 9 Sep. 1987 (ICMP 18529); Auckland, Glen Innes, Auckland University campus, on *Coprosma* sp. incubated berries, coll. B. Weir C1282.3, 30 Apr. 2009 (ICMP 18536); Auckland, Orakei, on *Ligustrum lucidum* leaf spot, coll. C. Winks & D. Than M136.3 (ICMP 18748); Auckland, Waitakere Ranges, on *Podocarpus totara* leaf endophyte, coll. S. Joshee 3T5.6, Jan. 2004 (ICMP 17326); Auckland, Waitakere Ranges, Huia, on *Geniostoma ligustrifolium* leaf endophyte, coll. S. Bellgard M128, 8 Jul. 2010 (ICMP 18540); Auckland, Waitakere Ranges, Huia, on *Coprosma* sp. rotten berry, coll. S. Bellgard M130-2, 8 Jul. 2010 (ICMP 18541); Auckland, Waiheke Island, Palm Beach, on *Meryta sinclairii* leaf spot, coll. P.R. Johnston C1310.1, 21 Mar. 2010 (PDD 99186; ICMP 18742); Auckland, Tiritiri Island, on *Dysoxylum spectabile* fruit rot, coll. P.R.

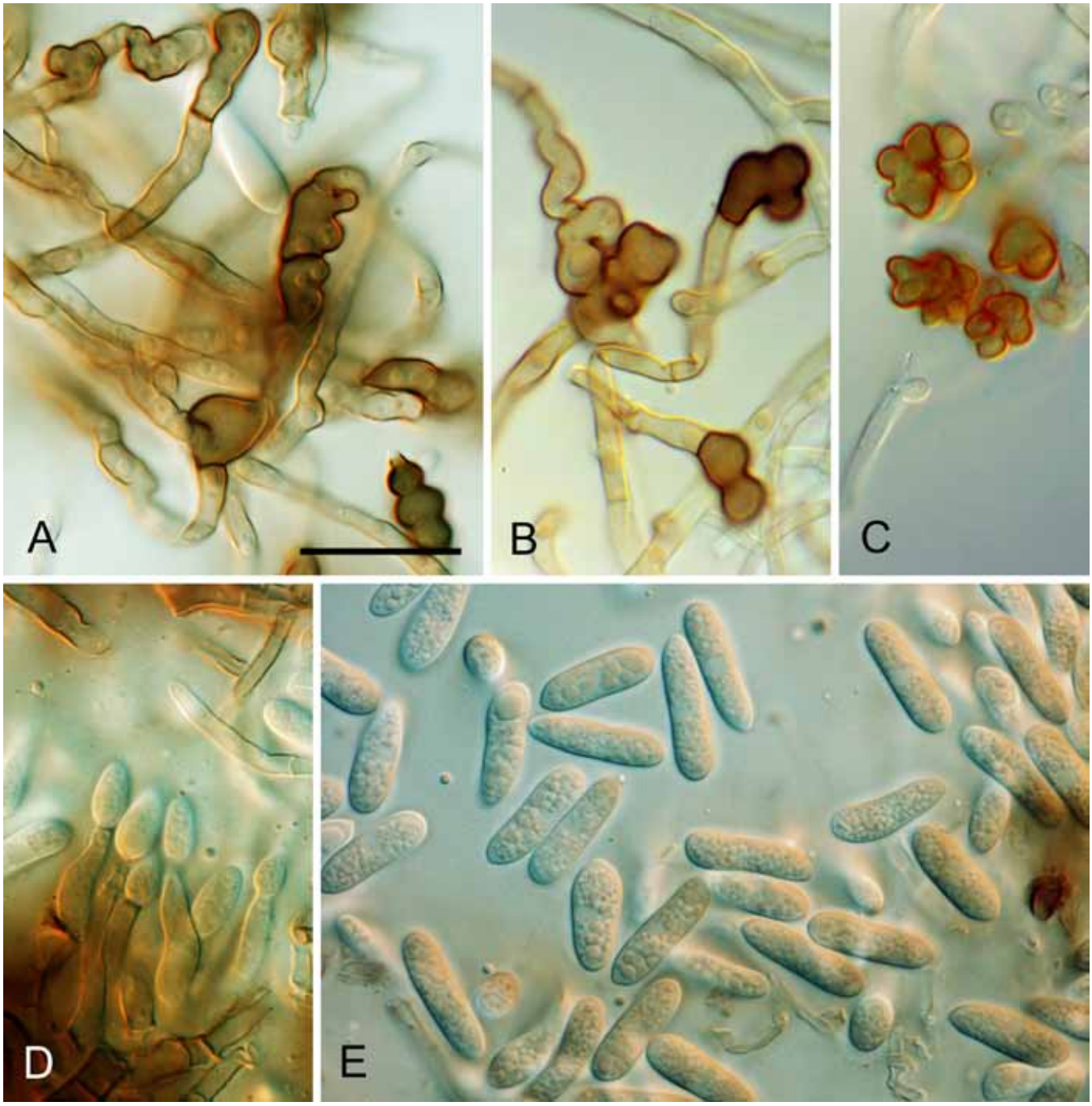


Fig. 15. *Colletotrichum aotearoa*. A. ICMP 17324. B. ICMP 18529. C. ICMP 18548. D. 18532. E. ICMP 18540. A–C. Appressoria. D. Conidiogenous cells. E. Conidia. Scale bar A = 20 µm. Scale bar of A applies to A–E.

Johnston C1220, 12 Feb. 1997 (PDD 67042; ICMP 18740); Northland, Whangaruru, on *Vitex lucens* fruit rot, coll. P.R. Johnston C880.1, L. Brako, P. Berry, 28 Jan. 1988 (PDD 48408; ICMP 18530); on *Berberis* sp. leaf spot, coll. N. Waipara C77 (ICMP 18735), on *Lonicera japonica* leaf spot, coll. N. Waipara J3 (ICMP 18736); Wellington, Waikanae, on *Coprosma* sp. leaf, coll. B. Weir C1285, 14 May 2009 (ICMP 18548); Auckland, Wenderholm Regional Park, on *Melicytus ramiflorus* leaf endophyte, coll. G.C. Carroll MELRA, 16 Sep. 2009 (ICMP 18543).

*** *Colletotrichum asianum*** Prihastuti, L. Cai & K.D. Hyde, Fungal Diversity 39: 96. 2009. Fig. 17.

Prihastuti *et al.* (2009) provide a description of this species.

Geographic distribution and host range: Known on *Mangifera indica* from Australia, Colombia, Japan, Panama, Philippines, and Thailand; also reported on *Coffea arabica* from Thailand.

Genetic identification: *Colletotrichum asianum* is distinguished from all other taxa using any of the genes tested, including ITS.

Notes: Although the type specimen is from coffee, this fungus is isolated commonly from mango (*Mangifera indica*) (*e.g.* Morphological Group 1 from Than *et al.* 2008; IMI 313839 from Australia; MAFF 306627 from Japan). Isolates referred to *Colletotrichum* indet. sp. 1 by Rojas *et al.* (2010), also associated with mango fruit rots, again match *C. asianum*. Based on ITS sequences, isolates Man-63 and Man-69 cited by Afanador-Kafuri *et al.* (2003) from mango from Colombia, are probably also *C. asianum*. Several papers have reported genetically uniform populations of *C. gloeosporioides* associated with *M. indica* around the world (*e.g.* Hodson *et al.* 1993, Alahakoon *et al.* 1994, Sanders & Korsten 2003) and these perhaps also represent *C. asianum*, although DNA sequences are not available to confirm this.

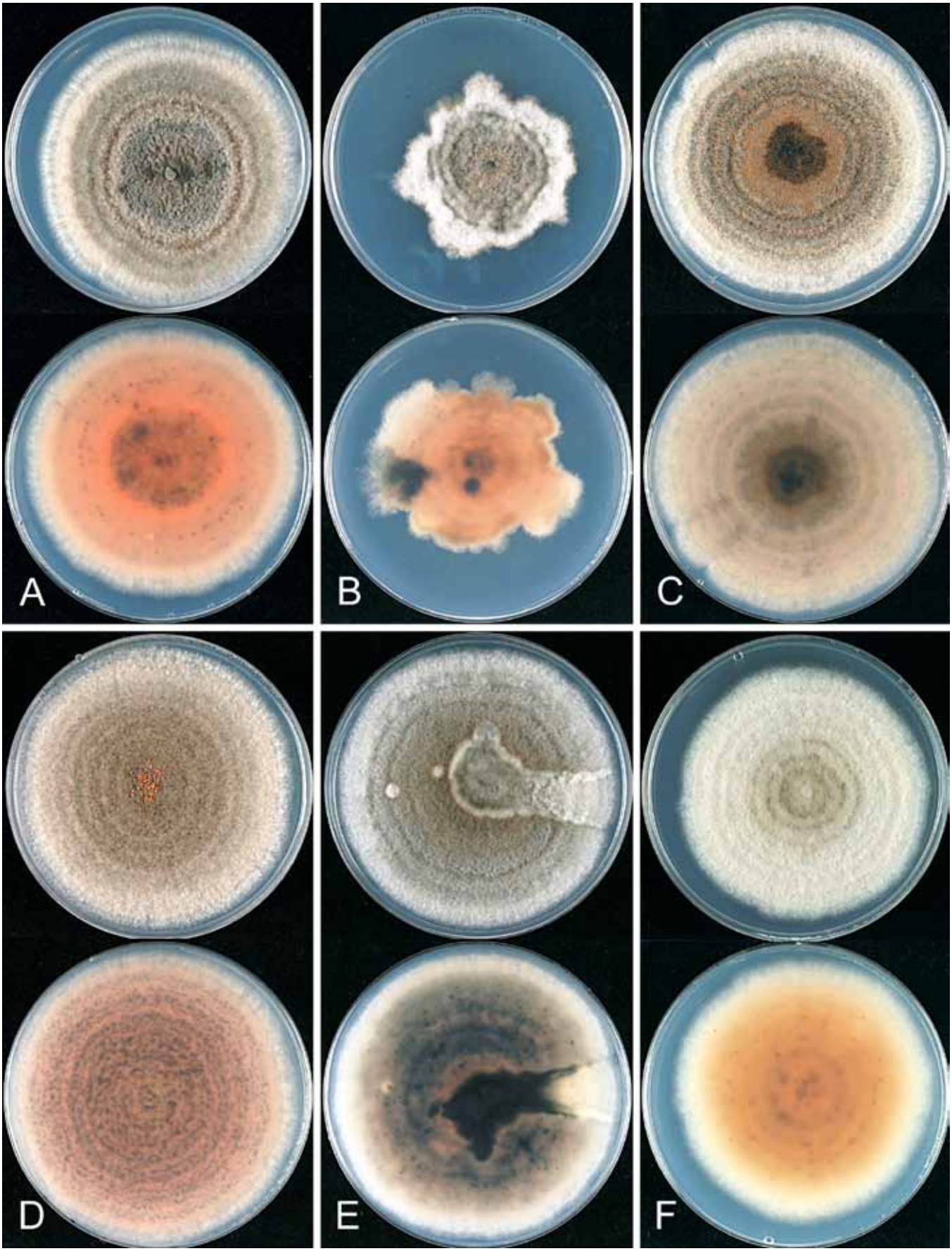


Fig. 16. *Colletotrichum aotearoa*. A. ICMP 18537 – ex-holotype culture. B. ICMP 18548. C. ICMP 18532. D. ICMP 18740. E. ICMP 18533. F. ICMP 18530. A–F. Cultures on PDA, 10 d growth from single conidia, from above and below.

Three earlier species, originally described from leaves rather than fruit of *Mangifera*, may provide earlier names for *C. asianum* but type material for these species has not been examined in this study; *C. mangiferae* Kelkar, *Gloeosporium mangiferae* Henn. 1898, and *G. mangiferae* Racib. 1900. As with most substrates, several different species of *Colletotrichum* often occur on the same host.

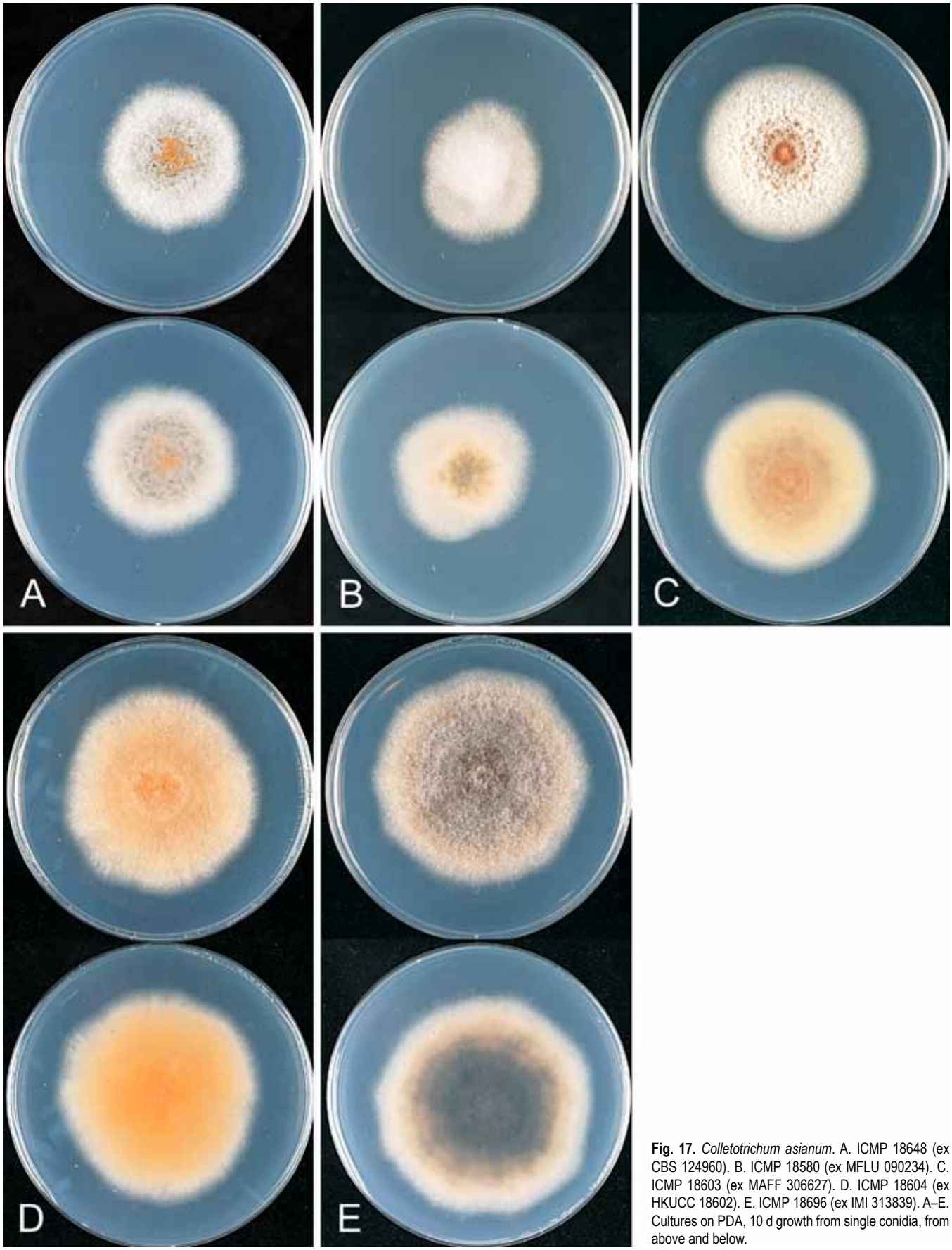


Fig. 17. *Colletotrichum asianum*. A. ICMP 18648 (ex CBS 124960). B. ICMP 18580 (ex MFLU 090234). C. ICMP 18603 (ex MAFF 306627). D. ICMP 18604 (ex HKUCC 18602). E. ICMP 18696 (ex IMI 313839). A–E. Cultures on PDA, 10 d growth from single conidia, from above and below.

For example, Damm *et al.* (2012a, b, this issue) report members of the *C. acutatum* and *C. boninense* species complexes, *C. simmondsii*, *C. fioriniae*, and *C. karstii*, from mango from Australia.

Isolates from *Capsicum* reported by Than *et al.* (2008) as *C. gloeosporioides* Morphological Group 2 (*e.g.* isolates Ku4 = ICMP 18575 and Ku8 = ICMP 18618), were referred to as *C. asianum* by Hyde *et al.* (2009), however they are genetically distinct from *C. asianum* and belong to *C. siamense* based on our analyses.

The *C. asianum* protologue designates the holotype as MFLU 090234, and the culture derived from the holotype as "BCC" with

no strain number. The ex-holotype culture is listed as BDP-I4 in the Prihastuti *et al.* (2009) Table 1, but this number is not mentioned in the description. Culture BDP-I4 was obtained from the authors (Prihastuti *et al.* 2009) for this study.

Specimens examined: **Australia**, New South Wales, Sextonville, on *Mangifera indica*, 1987 (IMI 313839 = ICMP 18696). **Philippines**, on *Mangifera indica* (MAFF 306627 = ICMP 18603). **Thailand**, Chiang Mai, on *Mangifera indica* fruit, coll. P.P. Than M3 (HKUCC 10862 = ICMP 18605); Chiang Mai, on *Mangifera indica* fruit, coll. P.P. Than M4 (HKUCC 10863 = ICMP 18604); Mae Lod Village, Mae Taeng District, Chiang Mai, on *Coffea arabica* berries, coll. H. Prihastuti BPD-I4, 16 Jan. 2008 (**ex-holotype culture** of *C. asianum* from specimen MFLU 090234 = ICMP 18580 = CBS 130418). **Panama**, Gamboa, on *Mangifera indica* fruit rot, coll. S. Van Bael GJS 08-144, Jul 2008 (CBS 124960 = ICMP 18648).

Colletotrichum boehmeriae Sawada, Hakubutsu Gakkwai Kwaihô (Trans. Nat. Hist. Soc. Formosa) 17: 2. 1914.

Notes: Sawada (1922) provided an English translation of his original description. This species was described as a stem pathogen of *Boehmeria nivea*, and remains in use in this sense (*e.g.* Li & Ma 1993). Wang *et al.* (2010) cite several GenBank accessions from isolates they identify as *C. gloeosporioides* that cause severe disease of *Boehmeria*. Based on a comparison of the GenBank data with our ITS gene tree, these and other isolates from the same host deposited by the same authors (GQ120479–GQ120499), appear to represent three different taxa within the *C. gloeosporioides* complex — *C. gloeosporioides s. str.*, *C. aotearoa*, and *C. fructicola*. Isolates representative of all three taxa are reportedly pathogenic on *Boehmeria* (Wang *et al.* 2010). The genetic relationship of these fungi needs to be confirmed using additional genes.

Colletotrichum camelliae Massee, Bull. Misc. Inform. Kew. 1899: 91. 1899.

Notes: *Colletotrichum camelliae* was described by Massee (in Willis 1899) from the living leaves of tea (*Camellia sinensis*) from Sri Lanka. It was placed in synonymy with *C. gloeosporioides* by von Arx (1957). Although not listed by Hyde *et al.* (2009), the name is widely used in the trade and semi-popular literature as the causal agent of the brown blight disease of tea (*e.g.* Sosa de Castro *et al.* 2001, Muraleedharan & Baby 2007).

We have been unable to sample *Colletotrichum* isolates from tea with typical brown blight symptoms. There are four GenBank accessions of *Colletotrichum* from tea, two from China (EU732732, FJ515007), one from Japan (AB218993), and another from Iran (AB548281), referred variously to *C. camelliae*, *C. crassipes* and *C. gloeosporioides*. Although ITS sequences only are available for these geographically widespread isolates, the DNA sequence of the Iranian isolate appears to match *C. gloeosporioides s. str.*, while those from the other three isolates are all very similar to each other. The ITS sequence from these isolates matches that of CBS 232.79, from tea shoots from Java (GenBank JX009429). GAPDH and ITS sequences from CBS 232.79 (GenBank JX009417, JX009429) place this isolate in *C. fructicola*. Note that CBS 571.88, isolated from tea from China and deposited as *Glomerella cingulata*, is a *Colletotrichum* sp. outside *C. gloeosporioides s. lat.*, based on ITS sequences (GenBank JX009424).

We tested the pathogenicity of CBS 232.79 and isolates of *G. cingulata* "f. sp. *camelliae*" (see below) using detached tea leaves and found that only the *G. cingulata* "f. sp. *camelliae*" isolates were strong pathogens (unpubl. data).

The genetic relationship between the pathogen of ornamental *Camellia* (here referred to *G. cingulata* "f. sp. *camelliae*"), isolates from tea with DNA sequence data in GenBank, and isolates associated with brown blight symptoms of tea remain unresolved. Additional isolates with known pathogenicity, collected from typical brown blight symptoms from the field, are required to determine whether or not there are two distinct pathogens of *Camellia*, one of tea, the other of ornamental varieties.

Other *Colletotrichum* species reported from tea include *C.* "*theae-sinensis*", an invalid recombination of *Gloeosporium theae-sinensis* I. Miyake, proposed by Yamamoto (1960). Moriwaki and Sato (2009) summarised the taxonomic history of this name and transferred *G. theae-sinensis* to *Discula* on the basis of DNA sequences. *Sphaerella camelliae* Cooke and its recombination *Laestadia camelliae* (Cooke) Berl. & Voglino were listed by von Arx & Müller (1954) as synonyms of *Glomerella cingulata*. This species is now accepted as *Guignardia camelliae* (Cooke) E.J. Butler ex Petch and is regarded as the causal agent of copper blight disease of tea (Spaulding 1958).

Thang (2008) placed *C. camelliae* in synonymy with *C. coccodes*, presumably on the basis of the Species Fungorum synonymy (www.speciesfungorum.org, website viewed 6 Oct 2010). Thang (2008) questioned the synonymy, noting differences between the descriptions of the two species provided by Massee (in Willis 1899) and Sutton (1980) respectively.

Colletotrichum caricae F. Stevens & J.G. Hall, Z. Pflanzenkrankh., 19: 68. 1909.

Notes: Placed in synonymy with *C. gloeosporioides* by von Arx (1957), *C. caricae* was listed as a separate species by Sutton (1992). It was described from fruits and leaves of *Ficus carica* from the USA (Stevens & Hall 1909) but is poorly understood both morphologically and biologically. Its genetic relationship to and within the *C. gloeosporioides* species complex, and to other *Ficus*-associated species such as *Colletotrichum ficus* Koord. and *Glomerella cingulata* var. *minor* (here placed in synonymy with *C. fructicola*) is unknown.

Glomerella cingulata (Stonem.) Spauld. & H. Schrenk, Science, n.s. 17: 751. 1903.

Basionym: *Gnomoniopsis cingulata* Stonem., Bot. Gaz. 26: 101. 1898.

= *Gloeosporium cingulatum* G.F. Atk., Bull. Cornell Univ. Agric. Exp. Sta. 49: 306. 1892. [fide Stoneman 1898]

Notes: Stoneman (1898) described *Glomerella cingulata* from diseased stems of *Ligustrum vulgare* from the USA and reported the development of perithecia in cultures initiated from conidia of what she considered its asexual morph, *Gloeosporium cingulatum*. There are recent reports of anthracnose diseases of *Ligustrum* (*e.g.* Alfieri *et al.* 1984, Vajna & Bagyinka 2002) but the relationship of isolates causing this disease to the *C. gloeosporioides* complex is not known.

Glomerella cingulata is often linked taxonomically to the anamorph *Colletotrichum gloeosporioides*, and the name has in the past been applied in an equally broad sense to *C. gloeosporioides s. lat.* (*e.g.* Small 1926, von Arx & Müller 1954). However, it is unlikely that the type specimen of *G. cingulata* represents the same species as *C. gloeosporioides s. str.* (see notes under *C. gloeosporioides*). *Colletotrichum gloeosporioides s. str.* is not known to form perithecia in culture, and there are no isolates of *C. gloeosporioides s. str.* known to us that are associated with a *Glomerella* state on diseased stems of *Ligustrum,* An isolate of *C.*

Fig. 18. *Glomerella cingulata* "f. sp. *camelliae*". A, C, D. ICMP 10643. B, E. ICMP 10646. A–B. Appressoria. C. Conidiogenous cells. D–E. Conidia. Scale bar A = 20 µm. Scale bar of A applies to A–E.

aotearoa (ICMP 18748) was isolated from *Ligustrum lucidum* in New Zealand, but it was not associated with a stem lesion and no *C. aotearoa* isolates were observed forming perithecia.

Glomerella cingulata* var. *brevispora Wollenw., Z. Parasitenk. (Berlin) 14: 260. 1949.

Notes: Described from fruit rots from Germany, this name has not been used since. No cultures are available and its relationship to and within the *C. gloeosporioides* complex is not known.

*** *Glomerella cingulata*** "**f. sp. *camelliae***" (Dickens & Cook 1989). Figs 18, 19.

Notes: Dickens & Cook (1989) proposed the name *Glomerella cingulata* "f. sp. *camelliae*" for isolates morphologically typical of *C. gloeosporioides s. lat.* that were highly pathogenic to leaves and shoots of ornamental *Camellia saluenensis* hybrids, causing the disease *Camellia* twig blight. These authors reported the fungus from plants imported into the UK from New Zealand and noted that a similar disease had been reported from plants grown in the UK,

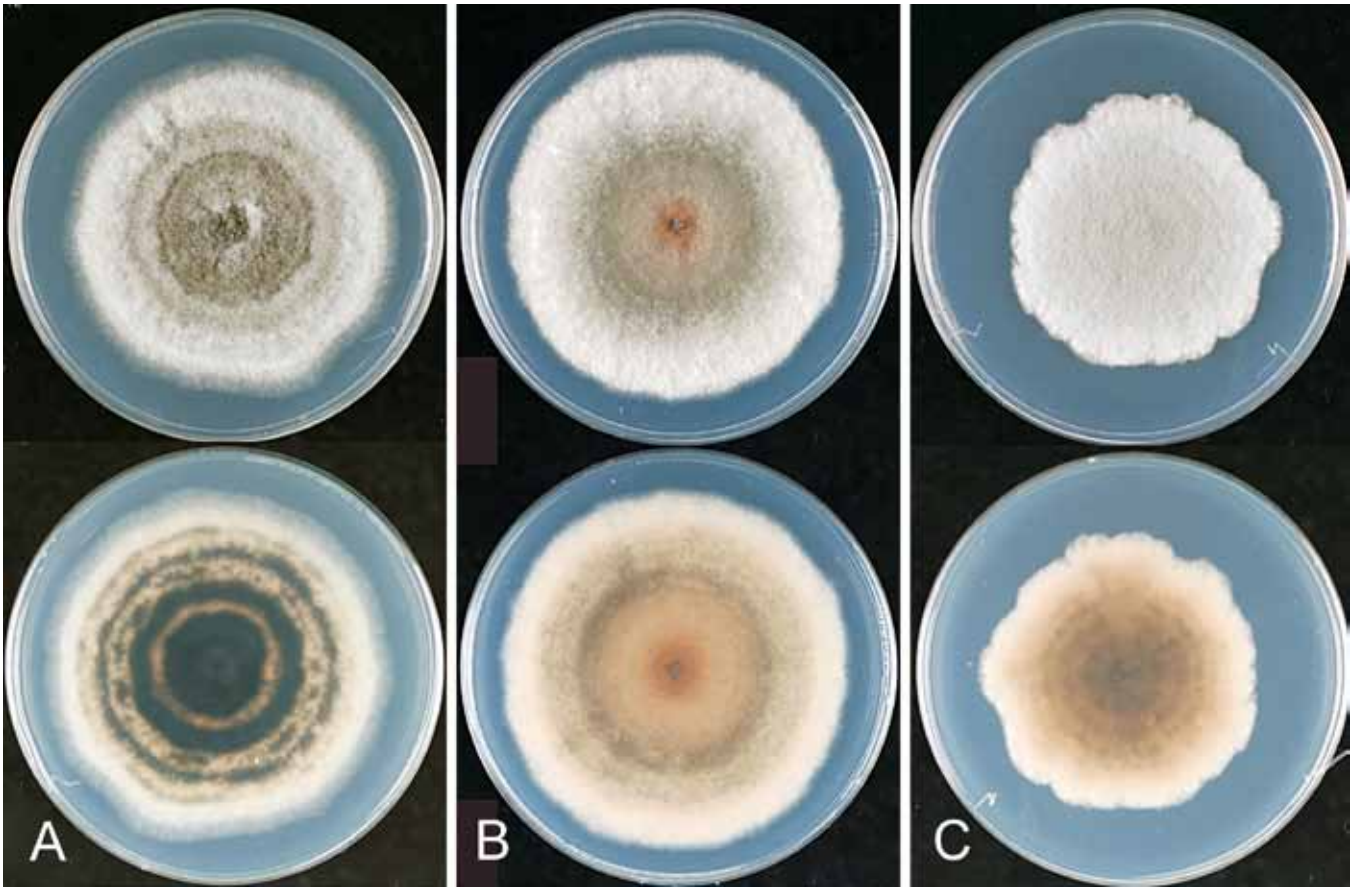


Fig. 19. *Glomerella cingulata* "f. sp. *camelliae*". A. ICMP 18542. B. ICMP 10643. C. ICMP 10646. A–C. Cultures on PDA, 10 d growth from single conidia, from above and below.

USA, Australia, France, and Italy. The disease has been reported from *Camellia japonica*, *C. reticulata*, and *C. sasanqua*. Although isolated in the UK from plants imported from New Zealand, this pathogen has not yet been found on *Camellia* plants growing in New Zealand.

We have sequenced authentic isolates cited by Dickens & Cook (1989) as well as isolates pathogenic to *Camellia saluenensis* collected from the USA. They are similar to each other genetically as well as biologically and morphologically. ITS sequences alone distinguish *G. cingulata* "f. sp. *camelliae*" from all other taxa in the *C. gloeosporioides* complex, and there is good genetic evidence to consider these isolates to be representative of a distinct species within the *C. kahawae* clade. A new species is not proposed here because the relationship between the *G. cingulata* "f. sp. *camelliae*" isolates and *C. camelliae*, the fungus causing brown blight of tea, remains uncertain.

Dickens & Cook (1989) also reported two *C. acutatum* strains from ornamental *Camellia* species that were avirulent in tests with detached *Camellia* cv. Donation leaves. Strain IMI 351261, deposited 1992 in IMI by R. Cook, is likely to be one of them. This strain was confirmed as belonging to the *C. acutatum* species complex and identified as *C. lupini*, which causes lupin anthracnose and is occasionally found on other hosts (Damm *et al.* 2012a, this issue). Another strain from *Camellia reticulata* from China belongs to *C. fioriniae*, also a species in the *C. acutatum* complex, while a strain from New Zealand (ICMP 10338) is *C. boninense s. str.* (Damm *et al.* 2012a, b, this issue).

See notes under *C. camelliae*.

Specimens examined: **UK**, plants imported from New Zealand, on *Camellia* × *williamsii*, coll. Dickens & Cook 82/437, 1982 (**authentic culture** of *Glomerella cingulata* "f. sp. *camelliae*" – ICMP 10643; dried culture PDD 56488). **USA**, Mississippi, on *Camellia sasanqua* twig blight, coll. W.E. Copes CG02g, May 2002 (ICMP 18542); South Carolina, on *Camellia* sp., coll. G. Laundon 20369, 1 Jan. 1982 (ICMP 10646).

Glomerella cingulata* var. *crassispora Wollenw., Z. Parasitenk. (Berlin) 14: 260. 1949.

Notes: Described from *Coffea arabica* from a glasshouse in Germany, this name has not been used since. No cultures are available and its relationship to and within the *C. gloeosporioides* complex is not known.

Glomerella cingulata "**f. sp. *manihotis***" (Chevaugeon 1956)

Notes: See notes under *Colletotrichum manihotis*.

Glomerella cingulata* var. *minor Wollenw., Z. Parasitenk. (Berlin) 14: 261. 1949.

= *Gloeosporium elasticae* Cooke & Massee, Grevillea 18: 74. 1890. [fide Wollenweber & Hochapfel 1949]

Notes: Placed here in synonymy with *C. fructicola*.

Glomerella cingulata var. *minor* was described from *Ficus* from Germany, but Wollenweber & Hochapfel (1949) noted that the same fungus occurred also on other hosts in Europe, Africa, and America, including *Malus* and *Coffea*. Genetically the ex-holotype culture of *G. cingulata* var. *minor* (CBS 238.49) matches the type specimen of *C. fructicola*, although the culture itself appears to be stale, with slow growth and an irregularly scalloped margin (see

images under *C. fructicola*). Wollenweber & Hochapfel (1949) used the name *Gloeosporium elasticae* Cooke & Massee for the conidial state of *G. cingulata* var. *minor*, the type specimens for both names being from *Ficus*.

See also notes under *C. queenslandicum*.

Specimen examined: **Germany,** Berlin-Dahlem, from *Ficus edulis* leaf spot, May 1936 (**ex-holotype culture** of *G. cingulata* var. *minor* – CBS 238.49 = ICMP 17921).

Glomerella cingulata* var. *migrans Wollenw., Z. Parasitenk. (Berlin) 14: 262. 1949.

Notes: Placed here in synonymy with *C. kahawae* subsp. *ciggaro*, see notes under this species.

Specimen examined: **Germany**, Berlin-Dahlem, on stem of *Hypericum perforatum*, Jun. 1937 (**ex-holotype culture** of *Glomerella cingulata* var. *migrans* – CBS 237.49 = ICMP 17922).

Glomerella cingulata "**var. *orbiculare***" Jenkins & Winstead, *Phytopathology* 52: 15. 1962.

Notes: Listed in Index Fungorum, this name was mentioned in an abstract, but is invalid (no Latin description) and never formally published. It was being used to refer to the teleomorph of *Colletotrichum orbiculare*, not part of the *C. gloeosporioides* complex (Cannon *et al.* 2012, this issue). *Glomerella lagenaria* (Pass.) F. Stevens, a recombination of the anamorphic name *Fusarium lagenarium* Pass., has also been used to refer to this teleomorph. Correll *et al.* (1993) comment on the pathogenicity of cucurbit-associated strains that form a *Glomerella* state in culture, suggesting a degree of confusion around the application of these names.

Glomerella cingulata "**f. sp. *phaseoli***" (Kimati & Galli 1970).

Notes: Both *G. cingulata* "f. sp. *phaseoli*" (*e.g.* Castro *et al.* 2006) and *Glomerella lindemuthiana* (*e.g.* Rodríguez-Guerra *et al.* 2005, as *G. lindemuthianum*) have been used for the teleomorph of *Colletotrichum lindemuthianum* in the recent literature, the two names placed in synonymy by Sutton (1992). This fungus is not part of the *C. gloeosporioides* complex (Cannon *et al*. 2012, this issue).

Glomerella cingulata* var. *sorghicola Saccas, Agron. Trop. (Maracay). 9: 171. 1954.

Notes: Not a member of the *C. gloeosporioides* complex. Sutton (1992) suggested using this name to refer to the teleomorph of *Colletotrichum sublineola*, although Crouch *et al.* (2006) note that *C. sublineola* has no known teleomorph.

*** *Colletotrichum clidemiae*** B. Weir & P.R. Johnst. **sp. nov.** MycoBank MB563592. Figs 20, 21.

= *Colletotrichum gloeosporioides* "f. sp. *clidemiae*" (Trujillo *et al.* 1986).

Etymology: Based on the host reportedly susceptible to this species.

Holotype: **USA**, Hawai'i, Aiea, on *Clidemia hirta* leaf spot, coll. S.A. Ferreira & K. Pitz, 14 May 2010, PDD 101997; ex-type culture ICMP 18658.

Colonies grown from single conidia on Difco PDA 25 mm diam after 10 d, aerial mycelium grey, cottony, sparse, surface of colony with numerous small, dark-based acervuli with deep orange conidial ooze and scattered setae, in reverse more or less colourless except for the acervuli and masses of conidial ooze showing through. After 18 d numerous globose, pale walled protoperithecia developing near centre of colony. *Conidia* (16−)18−20(−26.5) × (4.5−)5.5−6 µm (av. 19.3 × 5.5 µm, n = 48), broad-cylindric, ends broadly rounded, longer conidia sometimes tapering slightly towards the base. *Appressoria* variable in shape, some simple, subglobose, but often with a small number of broad, irregular lobes. *Perithecia* mature after about 21 d, dark-walled, about 200–250 µm diam with short ostiolar neck, perithecial wall of 3–4 layers of angular cells 10–15 µm diam with walls thin, pale brown to brown. *Asci* 8-spored 60–67 × 10–14 µm. *Ascospores* (14–)15.5–19(–21.5) × 4.5–5.5(–6.5) µm (av. 17.2 × 5.0 µm, n = 46), oblong-elliptic, tapering to rounded ends, widest point toward one end, in side view flat on one side, rarely curved and if so, then slightly.

Geographic distribution and host range: First reported from *Clidemia*, native to Panama, and subsequently introduced to Hawai'i as a pathogen of that host. Genetically matching isolates occur on native *Vitis* and *Quercus* spp. in Florida (see notes below).

Genetic identification: ITS sequences do not separate *C. clidemiae* from *C. aotearoa*. The two species are best distinguished using ACT, GAPDH, or GS.

Notes: Isolates referred to *C. gloeosporioides* "f. sp. *clidemiae*" by Trujillo *et al.* (1986) were highly pathogenic to *Clidemia*, but not to the other species of *Melastomataceae* tested. No voucher cultures of the original isolates collected from Panama were kept, but recent specimens isolated from naturalised *Clidemia hirta* plants in Hawai'i with typical disease symptoms are genetically uniform and distinct within the Kahawae clade. Phylogenetic, biological, and morphological evidence support this fungus being described as a new species within the *C. gloeosporioides* complex.

A fungus isolated from a *Vitis* sp. in Florida and referred to as "*Glomerella cingulata* native host" by MacKenzie *et al.* (2007), is genetically close to our isolates from *Clidemia* and is here referred to the same species. Data in MacKenzie *et al.* (2007) shows the same fungus occurs on both *Vitis* and *Quercus* in Florida. Micro-morphologically the isolates from *Clidemia* and from *Vitis* that we examined are similar with respect to the size and shape of appressoria, conidia, and ascospores. They are distinct in cultural appearance, the cultures of the *Vitis*-associated fungus having aerial mycelium darker and more dense, and a faster growth rate. Similar variation in cultural appearance is present in several of the phylogenetically defined species that we recognise. Whether or not the *Clidemia*-associated isolates are biologically distinct from the *Vitis*- and *Quercus*-associated isolates from Florida requires pathogenicity tests to determine.

Other specimens examined: **USA,** Florida, Sarasota, on *Vitis* sp. leaf, coll. S. MacKenzie SS-Grape-12, 2002 (ICMP 18706); Hawai'i, Aiea, on *Clidemia hirta* leaf spot, coll. S.A. Ferreira & K. Pitz, 14 May 2010 (ICMP 18659, ICMP 18660, ICMP 18661, ICMP 18662, ICMP 18663).

Colletotrichum coffeanum F. Noak, Z. Pflanzenkrankh. 11: 202. 1901.

Notes: Waller *et al.* (1993) discussed the use of the names *Colletotrichum coffeanum* and *Gloeosporium coffeanum* Delacr. and the geographic and biological differences between these

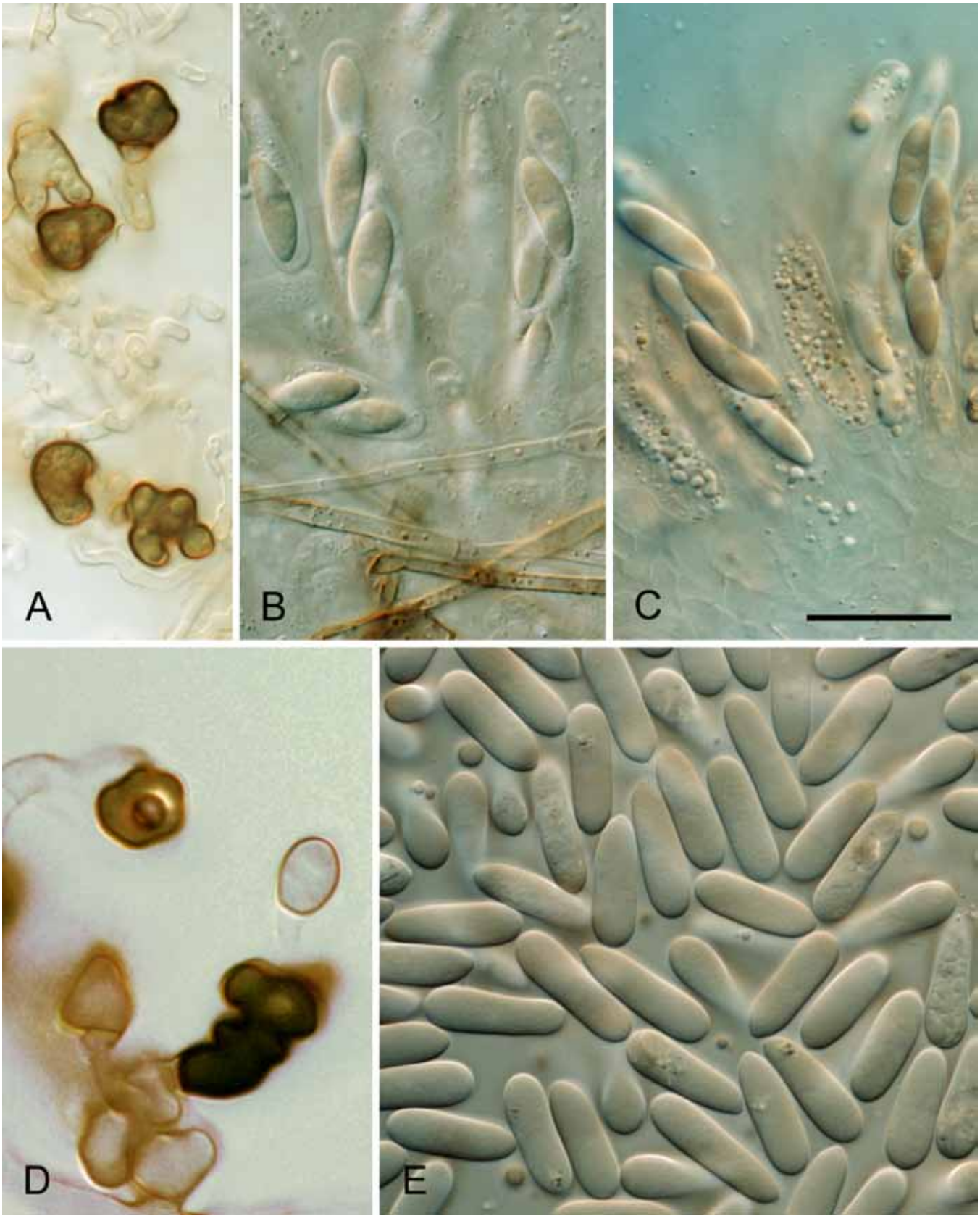


Fig. 20. *Colletotrichum clidemiae*. A, B, E. ICMP 18658 – ex-holotype culture. C, D. ICMP 18706. A, D. Appressoria. B, C. Asci and ascospores. E. Conidia. Scale bar C = 20 µm. Scale bar of C applies to A–E.

species and the pathogen of coffee berries, *C. kahawae*. Both *C. coffeanum* and *G. coffeanum* were described from leaves of coffee, the two species distinguished by Noak (1901) by the presence or absence of setae in the acervuli. There is a wide range of *C. gloeosporioides*-like species on coffee plants (see Waller *et al.* 1993 and notes under *C. kahawae*) and the relationships of *C. coffeanum* and *G. coffeanum* within the *C. gloeosporioides* species complex remain uncertain.

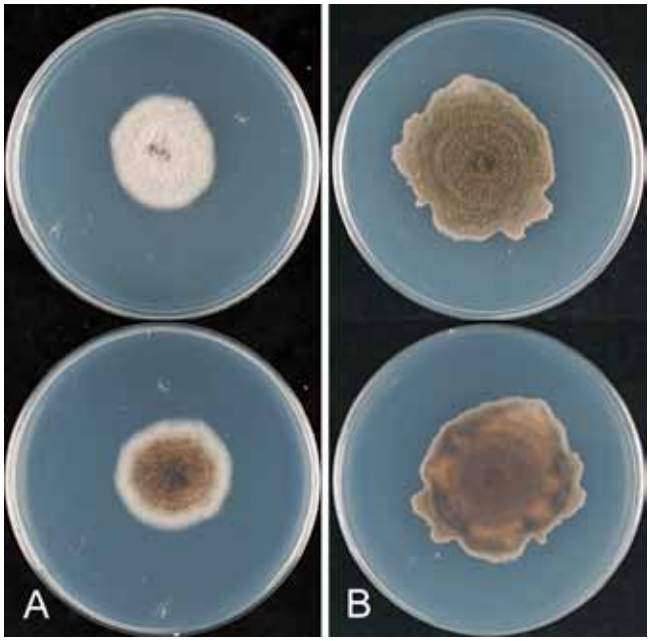


Fig. 21. *Colletotrichum clidemiae*. A. ICMP 18658 – ex-holotype culture. ICMP 18706. Cultures on PDA, 10 d growth from single conidia, from above and below.

Colletotrichum cordylines Pollacci, Atti Ist. Bot. Univ. Pavia, Serie 2, 5: 44. 1899.

Notes: Described from leaves of *Cordyline indivisa* from a botanical garden in Italy, the genetic and biological status of this species is not known. Two *Cordyline*-associated species are accepted in this study, *C. cordylinicola* from Thailand and the newly described *C. ti* from New Zealand. The original description of *C. cordylines* is brief (Pollacci 1899) but it specifically mentions setae more than 100 µm long. *Colletotrichum cordylinicola* is described as lacking setae (Phoulivong *et al.* 2011) and in *C. ti* they are rare and when present much less than 100 µm long. The phylogenetic significance of this apparent difference and confirmation that these names represent different fungi requires DNA sequences to be generated from type material of *C. cordylines*.

*** *Colletotrichum cordylinicola*** Phoulivong, L. Cai & K.D. Hyde, Mycotaxon 114: 251. 2011 ["2010"]. Fig. 22.

Phoulivong *et al.* (2011) provide a description.

Geographic distribution and host range: Known only from *Cordyline* from Thailand and *Eugenia* from Laos.

Genetic identification: ITS sequences separate *C. cordylinicola* from all other species.

Notes: Phoulivong *et al.* (2011) report *C. cordylinicola* from *Cordyline* (*Agavaceae*) and *Eugenia* (*Myrtaceae*). They noted that the isolate from *Eugenia* was not pathogenic to *Cordyline* and vice versa, and they also showed that the specimens from the two hosts are genetically somewhat distinct, although forming a sister relationship amongst the taxa included in their analysis. The calmodulin gene tree generated from our sequence data together with the sequences provided by Phoulivong *et al.* (2011) (GenBank accession HM470236) supports placing the isolates from *Eugenia* and from *Cordyline* in the same species (unpubl. data).

Colletotrichum cordylinicola is genetically distinct from a species associated with *Cordyline* leaf spots from New Zealand, described here as *C. ti*. See also notes under *C. cordylines*.

Specimen examined: **Thailand,** Chiang Mai, Sam Sai District, Maejo Village, on *Cordyline fruticosa*, coll. S. Phoulivong, 15 Mar. 2009 (**ex-holotype culture** – MFLUCC 090551 = ICMP 18579). Note that the ex-holotype culture was mistakenly cited as MFUCC 090551 by Phoulivong *et al.* (2011).

Colletotrichum crassipes (Speg.) Arx, Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Sect. 2, 51(3): 77. 1957.
Basionym: *Gloeosporium crassipes* Speg., Rivista Vitic. Enol. 2: 405. 1878.

Notes: Several isolates identified as *Colletotrichum crassipes* that have sequences accessioned to GenBank belong in *C. gloeosporioides s. lat*. GenBank accessions identified as *C. crassipes* that have a publically available culture include *C. kahawae* subsp. *ciggaro* (STE-U 5302 = CBS 112988 – AY376529, AY376577, FN557348, FN557538, and FN599821; STE-U 4445 = CBS 112984 – AY376530, AY376578, – FN557347, FN557537, and FN599820), along with several other species outside of the *C. gloeosporioides* complex (CBS 169.59 = IMI 309371 – AJ536230, FN557344, and FN599817; CBS 159.75 – FN557345 and FN599818; CBS 109355 – FN557346 and FN599819). Those with no isolates in a public collection include *C. kahawae* subsp. *ciggaro* (CORCS3 cited in Yang *et al.* (2011), HM584410, HM582002, HM585412), *C. fructicola* (strain 080912009 Jining, unpubl. data, FJ515007), and a possibly undescribed species within the Kahawae clade (strain SYJM02, unpubl. data, JF923835). Originally described from the berries of *Vitis vinifera* from Italy (Spegazzini 1878), the identity of *C. crassipes* remains unresolved. There is confusion regarding its morphology. Von Arx (1970) uses the name *C. crassipes* for fungi in which setae are rare, conidia are 22–34 × 6–8 µm (more or less matching the original description), and the lobed appressoria are distinctively globose in shape. Sutton (1980) uses a different morphological concept – setae common (according to Sutton these are rare in the otherwise morphologically similar *C. musae*), conidia 10–15 × 4.5–6.5 µm (Sutton's concept of *C. gloeosporioides* is characterised by narrower conidia), and the appressoria deeply lobed. The conidial width cited for *C. gloeosporioides* by Sutton (1980), 3–4.5 µm, is narrower than we have found for all the taxa we accept within *C. gloeosporioides s. lat.*, whereas his *C. crassipes* measurement of 4.5–6.5 µm matches many of the taxa we recognise. Several of these taxa also have deeply lobed appressoria.

Colletotrichum dracaenae Allesch., *Rabenhorst's Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz*, Ed. 2, 1(7): 560. 1902.

Notes: Farr *et al.* (2006) examined the type specimen of this species and concluded it was a member of *C. gloeosporioides s. lat.*, based on conidial size and shape. Genetic data is not available to confirm this. See also discussion under *C. petchii* in Damm *et al.* (2012b, this issue)

Colletotrichum fragariae A.N. Brooks, Phytopathology 21: 113. 1931.

Notes: Placed here in synonymy with *C. theobromicola*. See notes and additional specimens examined under *C. theobromicola*.

The name *C. fragariae* was originally applied to isolates associated with a disease of strawberry (*Fragaria* × *ananassa*) runners (stolons) and petioles in Florida (Brooks 1931). Although the name was placed in synonymy with *C. gloeosporioides* by

Fig. 22. *Colletotrichum cordylinicola*. ICMP 18579 (ex MFLUCC 090551 – ex-holotype culture). A. Cultures on PDA, 10 d growth from single conidia, from above and below.

von Arx (1957), it has continued to be used in the literature for strawberry-associated *Colletotrichum* isolates. It was accepted as distinct by Sutton (1992), although he noted confusion surrounding application of the name. Designation of one of Brook's cultures (CBS 142.31 = IMI 346325) as the epitype of *C. fragariae* by Buddie *et al.* (1999) has allowed a modern, genetic basis for this name to be fixed. The ex-epitype culture of *C. fragariae* sits in a strongly supported clade containing isolates from a wide range of hosts from many parts of the world, including the ex-epitype culture of *C. theobromicola*, an earlier name for *C. fragariae* in the sense that we accept these species in this paper.

There are several species from the *C. gloeosporioides* complex which inhabit diseased strawberry plants, and as shown by MacKenzie *et al.* (2007, 2008) isolates that genetically match the epitype of *C. fragariae* have a wide host range. Despite its name MacKenzie *et al.* (2007, 2008) regarded this fungus as simply one of a group of several species sometimes found on strawberry. Our study confirms that members of the *C. fragariae*/*theobromicola* clade occur throughout the world on a wide range of hosts. Within the diversity of the *C. fragariae*/*theobromicola* clade, there is a subclade consisting of the *C. fragariae* epitype and two contemporary ex-strawberry isolates from the USA (Fig. 1), further work will be needed to establish if the strawberry stolon disease is restricted to this subclade. Despite regular surveys this disease has not been found on strawberries in New Zealand.

Xie *et al.* (2010b) provides a good example of the confusion that continues to surround the application of *Colletotrichum* names to isolates from strawberry. These authors noted that putative *C. gloeosporioides* and *C. fragariae* isolates were difficult to distinguish using ITS sequences, the only sequences that they generated. Xie *et al.* (2010b) found 4 groups of isolates, each with a slightly different ITS sequence, two of those groups they considered to be *C. fragariae* and two to be *C. gloeosporioides*. To classify their isolates as either *C. fragariae* of *C. gloeosporioides* they used a restriction enzyme method based on Martinez-Culebras *et al.* (2000). Incorporating their ITS sequences into our ITS alignment, one of their groups genetically matches *C. tropicale*, one matches *C. gloeosporioides s. str.*, one matches *C. fructicola*, and one matches *C. siamense*. These relationships are based on ITS sequences only — the genetic differences between some of these species are small and are indicative only of possible relationships. However, it is clear that none of the Xie *et al.* (2010b) sequences match those of the epitype of *C. fragariae*. There are also several species within the *C. acutatum* species complex associated with *Fragaria* (Damm *et al.* 2012, this issue).

Specimen examined: **USA**, Florida, on *Fragaria* × *ananassa*, coll. A.N. Brooks, 1931 (**ex-epitype culture** – CBS 142.31 = ICMP 17927).

*** *Colletotrichum fructicola*** Prihastuti, L. Cai & K.D. Hyde, Fungal Diversity 39: 158. 2009. Fig. 23.

= *Colletotrichum ignotum* E.I. Rojas, S. A. Rehner & Samuels, Mycologia 102: 1331. 2010.

= *Glomerella cingulata* var. *minor* Wollenw., Z. Parasitenk. (Berlin) 14: 261. 1949.

Prihastuti *et al.* (2009) and Rojas *et al.* (2010) provide descriptions.

Geographic distribution and host range: Originally reported from coffee berries from Thailand (as *C. fructicola*) and as a leaf endophyte from several plants in Central America (as *C. ignotum*), isolates that we accept as *C. fructicola* are biologically and geographically diverse. Known from *Coffea* from Thailand, *Pyrus pyrifolia* from Japan, *Limonium* from Israel, *Malus domestica* and *Fragaria* × *ananassa* from the USA, *Persea americana* from Australia, *Ficus* from Germany, *Malus domestica* from Brazil, *Dioscorea* from Nigeria, and *Theobroma* and *Tetragastris* from Panama.

Genetic identification: ITS sequences do not separate *C. fructicola* from *C. aeschynomenes* and some *C. siamense* isolates. These taxa are best distinguished using GS or SOD2.

Notes: Rojas *et al.* (2010) noted the occurrence of two distinct haplotype subgroups (A4-3 and A5-4) within their concept of *C. ignotum*. Our genetic analyses resolve the two clades representative of these two subgroups. However, together they are monophyletic within the Musae clade of the *C. gloeosporioides* complex, and we retain them here as a single species. Both clades include isolates from a wide range of hosts from many countries, and both are similar in morphology and cultural appearance. The types of both *C. fructicola* and *C. ignotum* are in the same haplotype subgroup.

The *C. fructicola* protologue designates the holotype as MFLU 090228, but the culture derived from holotype as "BCC" with no specimen number. The ex-holotype culture is listed as BDP-I16 in Table 1 of Prihastuti *et al.* (2009) but this number is not mentioned in the description. Culture BDP-I16 was obtained from the authors (Prihastuti *et al.* 2009) for this study and deposited as ICMP 18581.

See also notes under *G. cingulata* var. *minor*.

Specimens examined: **Australia,** Queensland, Bli-Bli, on *Persea americana* fruit rot, coll. L. Coates 24154 (ICMP 12568). **Brazil,** Rio Grande do Sul State, on *Malus domestica* leaf, coll. T. Sutton BR 8 2001, Jan. 2001 (ICMP 17787); Santa Catarina State, on *Malus domestica* leaf, coll. T. Sutton BR 21 2001, Jan. 2001 (ICMP 17788).

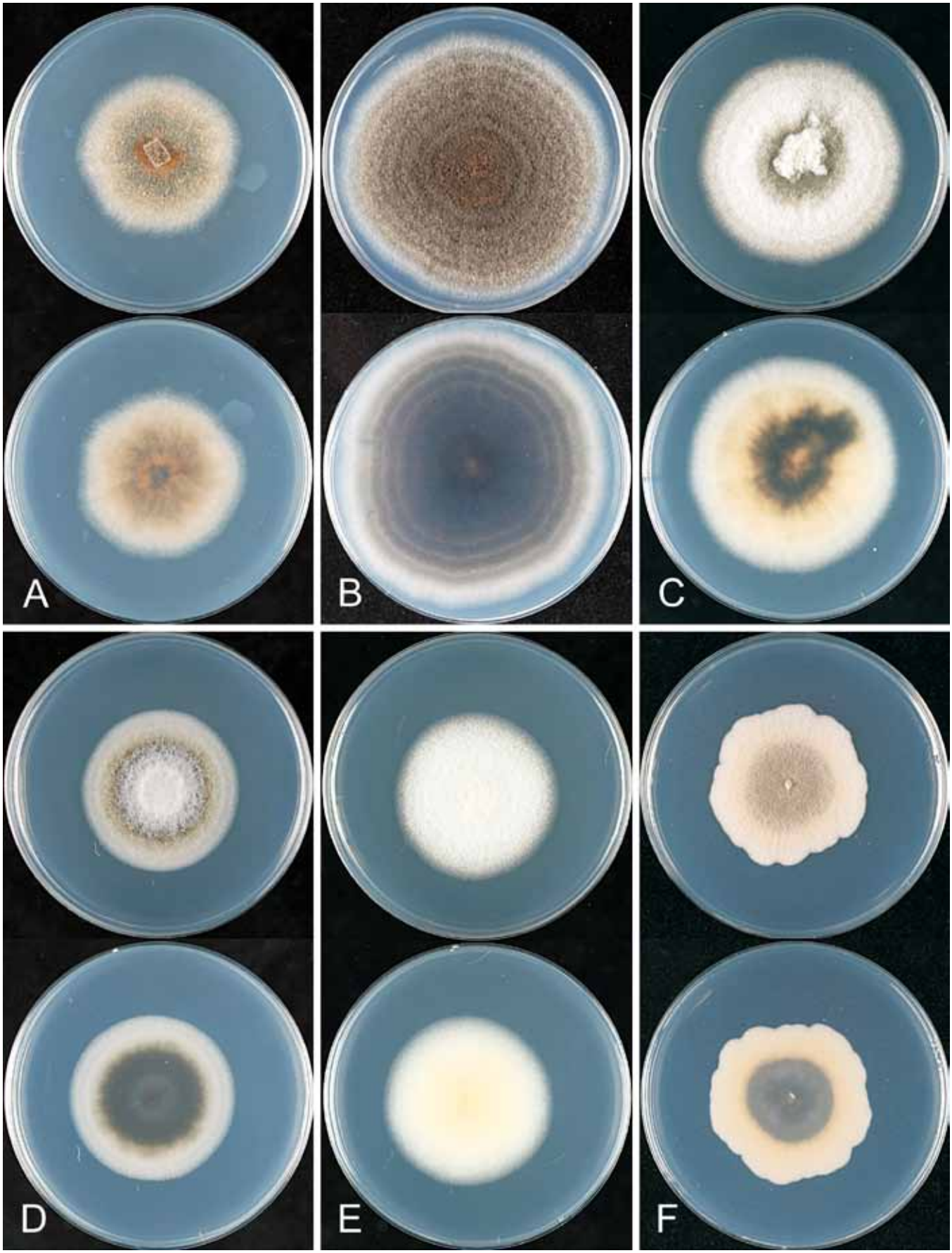


Fig. 23. *Colletotrichum fructicola*. A. ICMP 12568. B. ICMP 18615. C. ICMP 18581 (ex MFLU 090228 – ex-holotype culture of *C. fructicola*). D. ICMP 18610. E. ICMP 18646 (ex CBS 125379 – ex-holotype culture of *C. ignotum*). F. ICMP 17921 (ex CBS 238.49 – ex-holotype culture of *G. cingulata* var. *minor*). A–F. Cultures on PDA, 10 d growth from single conidia, from above and below.

Canada, Ontario, on *Fragaria* × *ananassa*, Jan. 1991 (IMI 345051 = ICMP 17819). **Germany**, Berlin-Dahlem Botanical Garden, on *Ficus edulis* leaf spot, (**ex-holotype culture** of *Glomerella cingulata* var. *minor* – CBS 238.49 = ICMP 17921). **Indonesia,** Java, Bandung, Pangheotan Estate, on *Camellia sinensis* shoots, coll. H. Semangun, Apr. 1979 (CBS 232.79 = ICMP 18656). **Israel**, on *Limonium sinuatum* leaf lesion, coll. S. Freeman L32 (cited in Moriwaki *et al.* 2006) (ICMP 18613); on *Limonium* sp. leaf

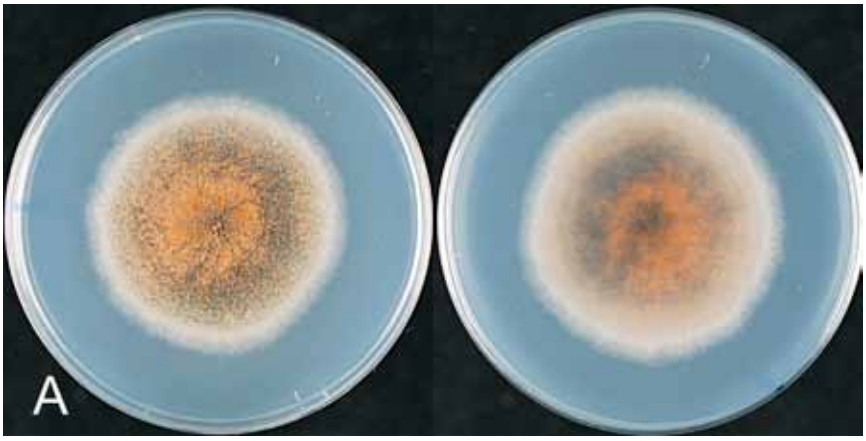


Fig. 24. *Colletotrichum gloeosporioides*. A. ICMP 17821 (ex IMI 356878 – ex-epitype culture). A. Cultures on PDA, 10 d growth from single conidia, from above and below.

lesion, coll. S. Freeman L50 (cited in Maymon *et al.* 2006) (ICMP 18698); on *Limonium* sp. leaf lesion, coll. S. Freeman Cg2 (cited in Maymon *et al.* 2006) (ICMP 18667); on *Limonium sinuatum*, coll. S. Freeman L11 (cited in Maymon *et al.* 2006) (ICMP 18615). **Japan**, Saga, on *Pyrus pyrifolia*, coll. H. Ishii sA02-5-1 (cited in Chung *et al.* 2006) (ICMP 18610). **Nigeria**, Ibadan, on *Dioscorea alata* leaf spot, M. Abang Cg13 (cited in Abang *et al.* 2002) (ICMP 18125); Ilesha, *Dioscorea rotundata* leaf spots, coll. M. Abang Cg22 (cited in Abang *et al.* 2002) (ICMP 18120). **Panama**, Barro Colorado Monument, *Tetragastris panamensis* leaf endophyte, coll. E.I. Rojas E886, 1 Jun. 2004 (**ex-holotype culture** of *C. ignotum* – CBS 125397 = ICMP 18646); *Theobroma cacao* leaf endophyte, coll. E. Rojas E183 (CBS 125395 = ICMP 18645). **Thailand**, Chiang Mai, Pa Daeng Village, on *Coffea arabica* berry, coll. H. Prihastuti BPD-I16, 12 Dec. 2007 (**ex-holotype culture** of *C. fructicola*, from specimen MFLU 090228 – ICMP 18581 = CBS 130416). **USA**, on *Fragaria* × *ananassa* crown, F. Louws 9, (ICMP 18727); Florida, on *Fragaria* × *ananassa*, coll. F.A. Ueckes FAU552 (CBS 120005 = BPI 747977 = ICMP 18609); North Carolina, Lincoln County, on *Malus domestica* fruit, coll. T. Sutton CROTTS 13 2001, Jan. 2001 (ICMP 17789).

*** *Colletotrichum gloeosporioides*** (Penz.) Penz. & Sacc., Atti Reale Ist. Veneto Sci. Lett. Arti., Serie 6, 2: 670. 1884. Fig. 24.

Basionym: *Vermicularia gloeosporioides* Penz., Michelia 2: 450. 1882.

= *Gloeosporium pedemontanum* Pupillo, Ann. Sperim. Agrar. n.s. 6: 57. 1952.

Cannon *et al.* (2008) provide a description of the species.

Geographic distribution and host range: Most isolates of *C. gloeosporioides* are associated with *Citrus*, and in many parts of the world this fungus is common on *Citrus*, but it also occurs on other hosts including *Ficus*, *Mangifera*, *Pueraria*, and *Vitis*. The isolate reported as a pathogen of paper mulberry (*Broussonetia papyrifera*) by Yan *et al.* (2011) matches *C. gloeosporioides s. str.* genetically.

Genetic identification: ITS separates *C. gloeosporioides* from all other species.

Notes: The name *Colletotrichum gloeosporioides* is currently in common use in two senses, one a genetically and biologically broad sense more or less following von Arx (1957, 1970) and Sutton (1992), including the whole species complex, the other a strict sense, encompassing only those specimens genetically matching the epitype selected for this name by Cannon *et al.* (2008). Depending on the context, use of the name in either sense can be useful. When used in a broad sense in this paper, it is referred to as the *C. gloeosporioides* species complex or *C. gloeosporioides s. lat*.

Colletotrichum gloeosporioides is often linked taxonomically to the teleomorph *Glomerella cingulata*, see notes under *G. cingulata*.

Specimens examined: **Australia**, New South Wales, Tamworth, on *Carya illinoinensis* (DAR 76936; ICMP 18738). **Italy**, Calabria, on *Citrus sinensis*, (**ex-epitype culture** of *C. gloeosporioides* – IMI 356878 = CBS 112999 = ICMP 17821); on *Citrus limon* juice, coll. G. Goidánich, 1951 (**ex-holotype culture** of *Gloeosporium pedemontanum* – CBS 273.51 = ICMP 19121). **New Zealand**, Auckland, Sandringham, on *Citrus* sp. fruit, coll. P.R. Johnston C1014.6, 2 May 1988 (ICMP 12939); Auckland, Sandringham, on *Ficus* sp. fruit, coll. P.R. Johnston C945.2, 9 May 1988 (ICMP 12066); Auckland, on Citrus sp. fruit, coll. G. Caroll, Feb 2010 (ICMP 18730); Northland, Kerikeri, Kapiro Rd, on *Citrus sinensis* fruit, coll. P.R. Johnston C1009.2, 10 Aug. 1988 (ICMP 12938). **South Africa**, on *Mangifera indica*, coll. L. Korsten Cg68 (ICMP 18694). **USA**, Georgia, on *Pueraria lobata* (AR2799 = CBS 119204 = BPI 871837 = ICMP 18678); Florida, on *Citrus* sp. leaf lesion, coll. N. Peres SRL-FTP-9 (ICMP 18695); Florida, on *Vitis vinifera* leaf lesion, coll. N. Peres LAGrape8 (ICMP 18697).

Colletotrichum gloeosporioides "**f. sp. *aeschynomenes***" (Daniel *et al.* 1973, as *aeschynomene*).

Notes: See *Colletotrichum aeschynomenes.*

Colletotrichum gloeosporioides "**f. *alatae***" R.D. Singh, Prasad & R.L. Mathur, Indian Phytopathol. 19: 69. 1966. [nom. inval., no Latin description, no type designated]

Notes: See *Colletotrichum alatae*.

Colletotrichum gloeosporioides* var. *aleuritis Saccas & Drouillon [as "aleuritidis"], Agron. Trop. (Nogent-sur-Marne) 6: 249. 1951.

≡ *Glomerella cingulata* var. *aleuritis* Saccas & Drouillon [as "aleuritidis"], Agron. Trop. (Nogent-sur-Marne) 6: 251. 1951.

Notes: Originally described from *Aleurites fordii* and *A. montaba* from French Equatorial Africa, these names have not been used since being described and the genetic relationship of this fungus to and within the *C. gloeosporioides* species complex is unknown. Although the original publications have not been seen, both names were tagged as invalid in the Index of Fungi 2: 53, 57 (1952).

Colletotrichum gloeosporioides "**f. sp. *clidemiae***" (Trujillo *et al.* 1986).

Notes: See *Colletotrichum clidemiae*.

Colletotrichum gloeosporioides "**f. sp. *cucurbitae***" (Menten *et al.* 1980).

Notes: First described from cucumber, this fungus is widely regarded as a synonym of *C. orbiculare* in the plant pathology literature (*e.g.* Snowdon 1991, da Silva *et al.* 2011).

Colletotrichum gloeosporioides "**f. sp. *cuscutae***" (Zhang 1985).

Notes: A strain identified by this name was developed as a mycoherbicide against dodder (*Cuscuta chinensis* in China (Zhang 1985). This strain referred to as "Lu Bao No.1" is apparently included in the study of Guerber *et al.* (2003) as strain 783 and belongs to the *C. acutatum* species complex. Other strains from dodder in the USA included in the same study were revealed to be *C. fioriniae*, while a strain from Dominica was found to represent a new species, both belonging to the *C. acutatum* species complex as well (Damm *et al.* 2012, this issue).

Colletotrichum gloeosporioides **var. *gomphrenae*** Perera, Revista Fac. Agron. Univ. Nac. La Plata 41: 12. 1965.

Notes: Originally described from *Gomphrena globosa*, the name has not been used since it was described and its genetic relationship to and within the *C. gloeosporioides* species complex is unknown.

Colletotrichum gloeosporioides **var. *hederae*** Pass., Atti Reale Accad. Italia, Rendiconti., Serie 4, 6: 469. 1889.

Notes: The original description of this *Hedera*-inhabiting species, with fusiform, straight to curved conidia suggests that it is a synonym of the *Hedera* pathogen *C. trichellum*.

Colletotrichum gloeosporioides **f. *heveae*** (Petch) Saccas, Agron. Trop. (Nogent-sur-Marne) 14: 430. 1959.
Basionym: *Colletotrichum heveae* Petch, Ann. Roy. Bot. Gard. Peradeniya 3(1): 8. 1906.

Notes: Originally described from the leaves of seedlings of *Hevea brasiliensis* from Sri Lanka, this fungus was described with very broad conidia, 18–24 × 7.5–8 µm. Carpenter & Stevenson (1954) considered this, and several other *Colletotrichum*, *Gloeosporium* and *Glomerella* species described from rubber, to be synonyms of *C. gloeosporioides*. The genetic relationship of these species to and within the *C. gloeosporioides* species complex is unknown. See also notes in Damm *et al.* (2012b, this issue) under *Colletotrichum annelatum*.

Colletotrichum gloeosporioides "**f. sp. *hyperici***" (Harris 1993).

Notes: This name was first used by Harris (1993) for strains of *C. gloeosporioides* pathogenic to *Hypericum perforatum*. Earlier studies by Hildebrand & Jensen (1991) had found the *Hypericum* pathogen to be pathogenic also on several other plants. The genetic relationship of the *Hypericum* pathogen to and within the *C. gloeosporioides* species complex is unknown. Note that the ex-holotype culture of *G. cingulata* var. *migrans*, a variety here placed in synonymy with *C. kahawae* subsp. *ciggaro*, was also isolated from *Hypericum*.

Colletotrichum gloeosporioides "**f. sp. *jussiaeae***" (Boyette *et al*. 1979).

Notes: Strains identified as *C. gloeosporioides* "f. sp. *jussiaeae*" are highly pathogenic, specialised pathogens of *Jussiaea decurrens* (Boyette *et al.* 1979). The genetic relationship of this taxon to and within the *C. gloeosporioides* species complex, or to *Colletotrichum jussiaeae* Earle, is unknown. Isolates pathogenic to *Jussiaea* have a similar conidial germination self-inhibitor profile to another isolate identified as *C. fragariae* (Tsurushima *et al.* 1995). The authentic isolate of *C. gloeosporioides* "f. sp. *jussiaeae*" deposited as ATCC 52634, is not included in this study.

Colletotrichum gloeosporioides "**f. sp. *malvae***" (Makowski & Mortensen 1989).

Notes: Strains identified as *C. gloeosporioides* "f. sp. *malvae*" were registered as a bioherbicide against round leafed mallow in Canada (Makowski & Mortensen 1989). The fungus was subsequently recognised as belonging to the *C. orbiculare* species complex (Bailey *et al.* 1996).

Colletotrichum gloeosporioides "**f. sp. *manihotis***" (Chevaugeon 1956).

Notes: See *Colletotrichum manihotis*.

Colletotrichum gloeosporioides **f. *melongenae*** Fournet, Ann. Mus. Civico Storia Nat. Genova 5: 13. 1973.

Notes: In addition to *C. gloeosporioides* f. *melongenae*, the names *C. gloeosporioides* "f. sp. *melongenae*", *C. melongenae* Av.-Saccá 1917, and *C. melongenae* Lobik 1928 have been used to refer to fungi associated with anthracnose diseases of *Solanum melongena* (*e.g.* Sherf & McNab 1986, Kaan 1973). Other names used for isolates from the same host have included *Gloeosporium melongenae* Ellis & Halst. 1891 and *G. melongenae* Sacc. 1916. The genetic relationships of these eggplant-associated taxa to and within the *C. gloeosporioides* species complex remain unknown. *Solanum melongena* associated species are known also from the *C. boninense* species complex (Damm *et al*. 2012b, this issue).

Colletotrichum gloeosporioides "**f. sp. *miconiae***" (Killgore *et al.* 1999).

Notes: Killgore *et al.* (1999) reported that the isolates they recognised as *C. gloeosporioides* "f. sp. *miconiae*" were highly specialised pathogens of *Miconia calvescens*, unable to infect the closely related *Clidemia hirta*. The original voucher cultures are no longer available (pers. comm., Robert Barreto). Recently collected isolates from *Miconia* from the type locality in Brazil have proved to be genetically diverse across the *C. gloeosporioides* species complex, with isolates in both the Kahawae and Musae clades (unpubl. data). For now the genetic position of this pathogen remains unresolved.

Colletotrichum gloeosporioides **var. *minus*** Simmonds, Queensland J. Agric. Anim. Sci. 25: 178A. 1968.

Notes: See *Colletotrichum queenslandicum*.

Colletotrichum gloeosporioides* var. *nectrioidea Gonz. Frag., Bol. Soc. Brot., 2: 52. 1924.

Notes: Originally described from *Citrus aurantium* from Portugal, the name has not been used since it was described and its genetic relationship to and within the *C. gloeosporioides* species complex is unknown.

Colletotrichum gloeosporioides "**f. sp. *ortheziidae***" (Marcelino *et al.* 2008).

Notes: Marcelino *et al.* (2008) clearly show that the *Orthezia praelonga* pathogen belongs in the *C. acutatum* species complex, despite referring to the fungus only as *C. gloeosporioides* "f. sp. *ortheziidae*". See also notes under *C. nymphaeae* in Damm *et al.* (2012a, this issue).

Colletotrichum gloeosporioides "**f. sp. *pilosae***" (Singh 1974).

Notes: First described from leaves of *Bidens pilosa*, this name has not been used since it was described and its genetic relationship to and within the *C. gloeosporioides* species complex is unknown.

Colletotrichum gloeosporioides* f. *stylosanthis Munaut, Mycol. Res. 106: 591. 2002.

Notes: Placed here in synonymy with *C. theobromicola*; see notes under *C. theobromicola*.

Irwin & Cameron (1978) and Munaut *et al.* (2002) described different diseases of *Stylosanthes* associated with Type A and Type B isolates of *C. gloeosporioides* f. *stylosanthis*, the two groups of isolates distinguished morphologically by growth rate in culture and by conidial morphology. Compared with Type A, the Type B isolates had a slower growth rate on PDA, and conidia more variable in size and shape (Irwin & Cameron 1978). They were also distinguished genetically using RFLP and similar methods (*e.g.* Munaut *et al.* 1998, 2002). Munaut *et al.* (2002) used ITS1 sequences to show the *C. gloeosporioides* f. *stylosanthis* to be related to an isolate they identified as *C. fragariae*. We regard *C. fragariae* to be a synonym of *C. theobromicola*, with putatively authentic Type A (HM335, *C. gloeosporioides* f. *stylosanthis* "f. sp. *guianensis*") and Type B (HM 336, *C. gloeosporioides* f. *stylosanthis* "f. sp. *stylosanthis*") isolates both also belonging to this species. From the ITS1 sequence data available, isolates regarded as typical of Type A (RAPD cluster I) and of Type B (RAPD cluster II) by Munaut *et al.* (1998) all belong in *C. theobromicola* in the sense that we are using the name; their RAPD cluster III isolate could be *C. tropicale*, and their RAPD cluster IV isolates are probably *C. fructicola*.

The cultures of *C. gloeosporioides* f. *stylosanthis* that we used were originally studied by Irwin & Cameron (1978), and selected as the "types" of "f. sp. *guianensis*" and "f. sp. *stylosanthis*" by Munaut *et al.* (2002). Both isolates have a 'stale' growth form, no longer forming conidia in culture and with aerial mycelium closely appressed to the agar surface, resulting in an almost slimy colony surface. Both isolates had a slow growth rate, similar to that reported for Type B isolates by Irwin & Cameron (1978). Genetically both isolates were identical for all the genes we sequenced. This identity should be checked against additional isolates, especially some matching Type A *sensu* Irwin & Cameron (1978) with respect to both pathogenicity and growth form.

Sherriff *et al.* (1994), using ITS2 and partial 28S rDNA sequences, found isolates they considered to represent *C. gloeosporioides* f. *stylosanthis* Type A and Type B respectively to be genetically distinct. However, their ITS2 sequences show that the putative Type B isolate in their study was in fact a member of the *C. boninense* species complex.

Specimens examined: **Australia**, Queensland, Townsville, on *Stylosanthes viscosa*, coll. J.A.G. Irwin 21365 (HM335), 1976 (**ex-holotype culture** of *C. gloeosporioides* f. *stylosanthis* – MUCL 42294 = ICMP 17957 = CBS 124251); Samford, on *Stylosanthes guianensis*, coll. J.A.G. Irwin 21398 (HM336), 1979 (MUCL 42295 = ICMP 17958 = CBS 124250).

Colletotrichum gloeosporioides* f. *stylosanthis "**f. sp. *guianensis***" (Munaut *et al.* 2002)

≡ *Colletotrichum gloeosporioides* "f. sp. *guianensis*" (Vinijsanum *et al.* 1987).

Notes: See notes and specimens examined under *C. gloeosporioides* f. *stylosanthis*.

Colletotrichum gloeosporioides* f. *stylosanthis "**f. sp. *stylosanthis***" (Munaut *et al.* 2002).

Notes: See notes and specimens examined under *C. gloeosporioides* f. *stylosanthis*.

Colletotrichum gloeosporioides "**f. sp. *uredinicola***" (Singh 1975).

Notes: Described from uredinia and telia of *Ravenelia sessilis* on pods of *Albizia lebbek*, this name has not been used since it was described and its genetic relationship to and within the *C. gloeosporioides* species complex is unknown.

Colletotrichum gossypii Southw., J. Mycol. 6: 100. 1891.

= *Glomerella gossypii* Edgerton, Mycologia 1: 119. 1909.

Notes: This species was originally described from the USA and was reported to cause disease symptoms on all parts of cotton plants, but especially the bolls (Southworth 1891, Edgerton 1909). Isolates identified as *C. gossypii* by Shear & Wood (1907) were reportedly associated with a *Glomerella* state in culture, and Edgerton (1909) described *Glomerella gossypii* from diseased, mature cotton plants in the USA Edgerton (1909) discussed differences in ascospore shape between *G. gossypii* and fruit-rotting isolates of *G. cingulata*, with *G. gossypii* having elliptic, not curved ascospores. Von Arx (1957) considered *C. gossypii* to be a synonym of *C. gloeosporioides* and von Arx & Müller (1954) regarded *G. gossypii* to be a synonym of *G. cingulata*.

Modern authors have recognised two pathogens of cotton, *C. gossypii* and *C. gossypii* var. *cephalosporioides*. *Colletotrichum gossypii* is reportedly the cause of cotton anthracnose, a damping-off disease of cotton seedlings, and *C. gossypii* var. *cephalosporioides* the cause of ramulosis, a disease causing abnormal branching of mature plants (Bailey *et al.* 1996, Silva-Mann *et al.* 2005). In a study based on ITS2 sequences, Bailey *et al.* (1996) found *C. gossypii* and *C. gossypii* var. *cephalosporioides* to be genetically distinct but with both belonging to the *C. gloeosporioides* species complex. Silva-Mann *et al.* (2005) also distinguished the two taxa genetically, based on an AFLP analysis. The only DNA sequences available for isolates identified as *C. gossypii* and *C.*

gossypii var. *cephalosporioides* are ITS2 and the D2 region of the rDNA LSU, neither of which resolves their relationships within the *C. gloeosporioides* complex. Whether the seedling pathogen regarded by Silva-Mann *et al.* (2005) and Bailey *et al.* (1996) to be *C. gossypii* represents the species first described from cotton in the USA is not known. The genetic relationship of these apparently biologically specialised fungi requires additional sequences to be generated from authentic isolates with known pathogenicity.

Colletotrichum gossypii* var. *cephalosporioides A.S. Costa, Bragantia 6: 5. 1946.

≡ *Colletotrichum gloeosporioides* "var. *cephalosporioides*" (A.S. Costa) Follin & Mangano, Coton et fibres tropicales 37: 209. 1983. [comb. inval., no full reference to basionym]

Notes: See notes under *Colletotrichum gossypii*.

*** *Colletotrichum horii*** B. Weir & P.R. Johnst., Mycotaxon 111: 21. 2010.

Weir & Johnston (2010) and Xie *et al.* (2010a) provide descriptions.

Geographic distribution and host range: Associated with fruit and stem disease of *Diospyros kaki* from China, Japan, and New Zealand. Xie *et al.* (2010a) noted minor symptoms on inoculated fruit of *Capsicum annuum*, *Musa acuminata*, and *Cucurbita pepo*, but noted that the fungus had never been associated with disease symptoms on these hosts from the field.

Genetic identification: ITS distinguishes *C. horii* from all other species.

Specimens examined: See Weir & Johnston (2010).

Colletotrichum hymenocallidis Yan L. Yang, Zuo Y. Liu, K.D. Hyde & L. Cai, Fungal Diversity 39: 138. 2009.

Notes: Placed here in synonymy with *Colletotrichum siamense*. See notes and additional specimens examined under *C. siamense*. Yang *et al.* (2009) reported this species as a leaf pathogen of *Hymenocallis americana*. They distinguished *C. hymenocallidis* from *C. siamense*, also described from *Hymenocallis*, primarily on the basis of a multi-gene phylogeny and differences in colony colour. Although gene selection was appropriate for resolving genetic relationships within the *C. gloeosporioides* group, Yang *et al.* (2009) included only five isolates of the *C. gloeosporioides* complex in their phylogeny. Based on this isolate selection, the *C. hymenocallidis* isolates were genetically distinct from the *C. siamense* isolates. However, in our analysis, in which the *C. siamense*/*C. hymenocallidis* group is represented by 30 isolates from a wide range of hosts from all over the world, authentic isolates of the two species fall within a monophyletic clade that cannot be further subdivided phylogenetically.

The Latin part of the *C. hymenocallidis* protologue designates a culture ("Holotypus: Cultura (CSSN2)") as the holotype but the English citation of the type specimen corrects this apparent mistake, citing CSSN2 as an ex-holotype culture, with the herbarium specimen GZAAS 080001 as the holotype.

Specimen examined: **China**, Guangxi, Nanning, on *Hymenocallis americana* leaf spot, coll. Y.L. Yang GZAAS 080001, 19 Jun 2008 (**ex-holotype culture** of *C. hymenocallidis* − CBS 125378 = ICMP 18642).

Colletotrichum ignotum E.I Rojas, S.A. Rehner & Samuels, Mycologia 102: 1331. 2010.

Notes: Placed here in synonymy with *Colletotrichum fructicola*. See notes and additional specimens examined under *C. fructicola*.

Specimen examined: **Panama**: Barro Colorado Monument, *Tetragastris panamensis* leaf endophyte, coll. E.I. Rojas E886, 1 Jun 2004 (**ex-holotype culture** of *C. ignotum* − CBS 125397 = ICMP 18646).

Colletotrichum jasmini-sambac Wikee, K.D. Hyde, L. Cai & McKenzie, Fungal Diversity 46: 174. 2011.

Notes: Placed here in synonymy with *Colletotrichum siamense* based on the ITS, GAPDH, CAL, TUB2, and ACT gene sequences from the ex-holotype culture, deposited in GenBank by Wikee *et al.* (2011).

Wikee *et al.* (2011) discussed similarities between *C. jasmini-sambac*, *C. siamense* and *C. hymenocallidis*, three species genetically close in their phylogenetic analysis. The broader range of isolates representing *C. siamense* in our analysis shows that these species form a single, monophyletic clade that cannot be sensibly subdivided (see notes under *C. siamense*).

Specimen examined: **Vietnam**, Cu Chi District, Trung An Ward, on living leaves of *Jasminum sambac*, Jan. 2009, coll. Hoa Nguyen Thi LLTA–01 (**ex-holotype culture** of C. *jasmini-sambac* – CBS 130420 = ICMP 19118).

*** *Colletotrichum kahawae*** J.M. Waller & Bridge subsp. ***kahawae***, Mycol. Res. 97: 993. 1993. Fig. 25.

Waller *et al.* (1993) provide a description.

Geographic distribution and host range: Known only from *Coffea* from Africa.

Genetic identification: ACT, CAL, CHS-1, GAPDH, TUB2, SOD2, and ITS sequences are the same as those from *C. kahawae* subsp. *ciggaro*. The two subspecies can be distinguished by GS sequences; *C. kahawae* subsp. *kahawae* has a 22 bp deletion and a single C to T transition. Collectively, the two subspecies can be distinguished from all other species using ITS sequences alone.

Notes: *Colletotrichum kahawae* was proposed by Waller *et al.* (1993) as a name to refer specifically to *Colletotrichum* isolates causing Coffee Berry Disease (CBD), to taxonomically distinguish these disease-causing isolates from the several other *Colletotrichum* spp. that can be isolated from coffee plants, including *C. coffeanum* (see notes under *C. coffeanum*). *Colletotrichum kahawae* is an apparently clonal population (Varzea *et al.* 2002), widespread on coffee in Africa, and with a distinctive growth form and biology (Waller *et al.* 1993).

In this paper *C. kahawae sensu* Waller *et al.* (1993) is reduced to subspecies. Based on ACT, CAL, CHS-1, GAPDH, TUB2, SOD2, and ITS gene sequences the coffee berry pathogen cannot be distinguished from isolates from a wide range of other hosts that are not pathogenic to coffee. Those other isolates are referred to here as *C. kahawae* subsp. *ciggaro*. We retain a distinct taxonomic label for the coffee berry pathogen to reflect its biosecurity importance. In addition to its biology, *C. kahawae* subsp. *kahawae* can be distinguished metabolically, and genetically using GS gene sequences. Waller *et al.* (1993) used a metabolic test, an inability

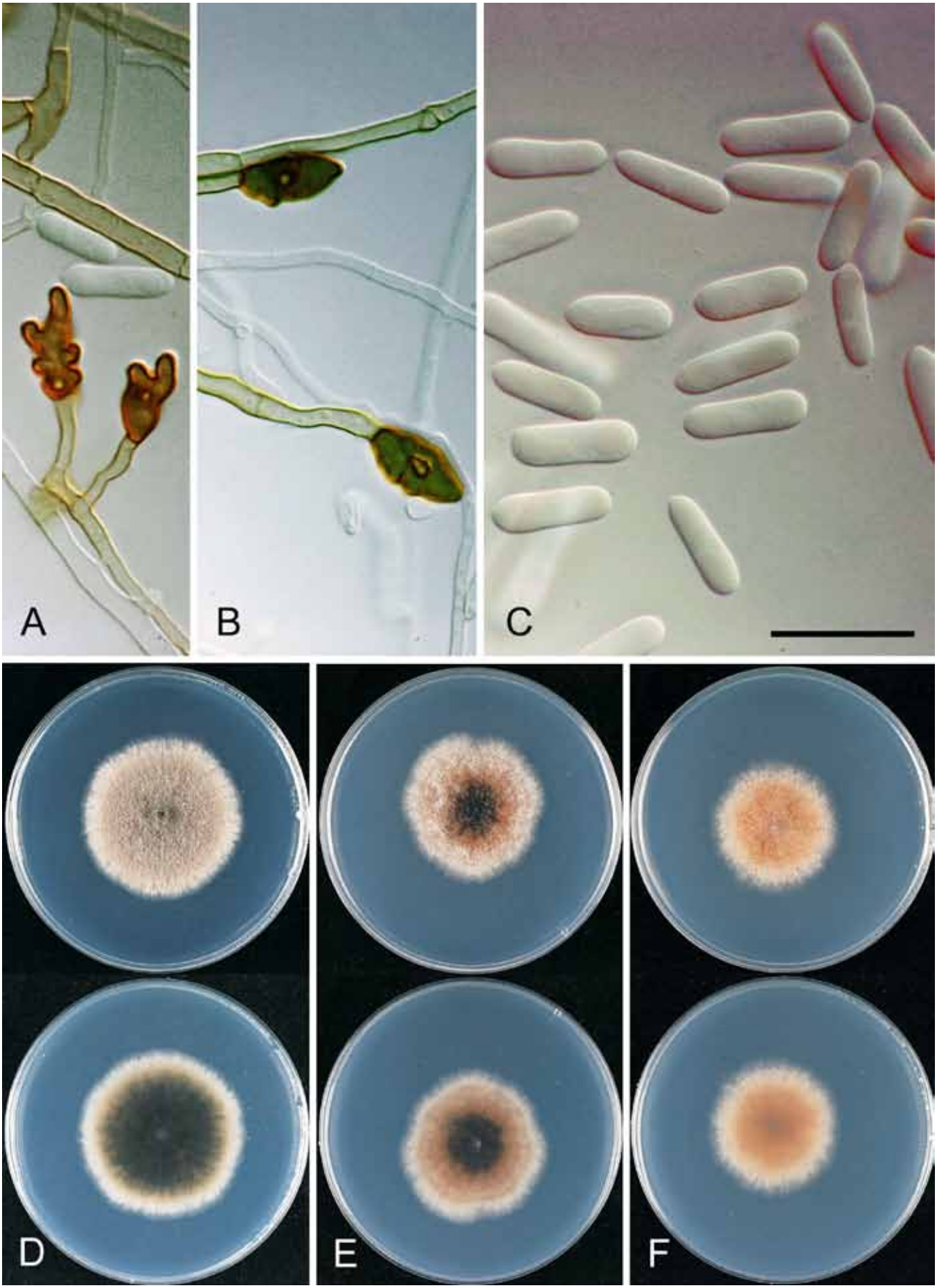


Fig. 25. *Colletotrichum kahawae* subsp. *kahawae*. A, E. ICMP 17905 (ex IMI 361501). B–C. ICMP 17816 (ex IMI 319418 – ex-holotype culture). C. ICMP 17915 (ex CBS 982.69). A–B. Appressoria. C. Conidia. D–E. Cultures on PDA, 10 d growth from single conidia, from above and below. Scale bar C = 20 µm. Scale bar of C applies to A–C.

to utilise either citrate or tartrate as a sole carbon source, to help characterise isolates as *C. kahawae*. None of our *C. kahawae* subsp. *kahawae* isolates were able to utilise either citrate or tartrate, whereas all of the *C. kahawae* subsp. *ciggaro* isolates were able to utilise one or both of these carbon sources (Weir & Johnston 2009). All of the *C. kahawae* subsp. *kahawae* isolates share a 22 bp deletion in the glutamine synthetase gene, lacking in the *C. kahawae* subsp. *ciggaro* isolates. Note that one of the isolates metabolically and genetically typical *C. kahawae* subsp. *kahawae* (CBS 982.69) was reported by Gielink & Vermeulen (1983) to be non-pathogenic to coffee, but we have not independently checked this result.

The isolates we accept as *C. kahawae* subsp. *kahawae* show two cultural types, one matching the description of Waller *et al.* (1993), slow growing, darkly pigmented cultures with conidia developing mostly in the aerial mycelium. The second cultural type grew even more slowly, had little or no pigmentation within the agar, and the colony surface was covered with numerous acervuli and orange conidial masses. Metabolically and genetically both cultural types were the same, and pathogenicity tests showed that the non-pigmented isolates caused CBD (unpubl. data, D. Silva, Centro de Investigação das Ferrugens do Cafeeiro). Rodriguez *et al.* (1991) reported further variation in cultural appearance amongst CBD causing isolates.

Waller *et al.* 1993 stated that *C. kahawae* was not known to form ascospores. However, Gielink & Vermeulen (1983) observed the production of perithecia on coffee berries that had been inoculated with CBD-causing isolates, many months after inoculation and death of the berries. At least one of the isolates that they cited with this biology, CBS 135.30, has the GS sequence typical of *C. kahawae* subsp. *kahawae*. Vermeulen *et al.* (1984) grew cultures from the perithecia that developed on the previously inoculated berries, and found that none were pathogenic to coffee. It is possible that the perithecia developing on inoculated berries reported by Gielink & Vermeulen (1983) were from other *Colletotrichum* spp. present on the berries before they were inoculated, and represented species distinct from *C. kahawae* subsp. *kahawae*. A similar situation has been noted with some of our inoculations, where species present on tissues prior to inoculation, either endophytic or latent, started to sporulate on the dead tissue following inoculation (unpubl. data, B.S. Weir).

Based on ITS sequences, most of the accessions in GenBank identified as *C. kahawae* and isolated from coffee, match our concept of *C. kahawae* subsp. *kahawae*. There are two exceptions, AF534468 (from Malawi) and AY376540 (STE-U 5295 = IMI 319424 = CBS 112985, from Kenya). The Kenyan isolate was cited as *C. kahawae* in Lubbe *et al.* (2004). Based on the ITS sequences, and the TUB2 sequence from isolate STE-U 5295 (AY376588), these isolates represent *C. siamense*.

Specimens examined: **Angola**, Ganada, on *Coffea arabica* berry, coll. J.N.M. Pedro 16/65, 2 Jun. 1965 (IMI 310524 = CBS 982.69 = ICMP 17915). **Cameroon**, on *Coffea arabica* (IMI 361501 = ICMP 17905). **Kenya**, Ruiru, Kakuzi Estate, on *Coffea arabica* young shoots, coll. D.M. Masaba 22/87, 29 Jan. 1987 (**ex-holotype culture** of *C. kahawae* – IMI 319418 = ICMP 17816); on *Coffea* sp., coll. E.C. Edwards, May 1930 (CBS 135.30 = ICMP 17982). **Malawi**, on *Coffea arabica* (IMI 301220 = ICMP 17811).

*** *Colletotrichum kahawae* subsp. *ciggaro*** B. Weir & P.R. Johnst., **subsp. nov.** MycoBank MB563758. Figs 26, 27.

= *Glomerella cingulata* var. *migrans* Wollenw., Z. Parasitenk. (Berlin) 14: 262. 1949.

= *Glomerella rufomaculans* var. *vaccinii* Shear, Bull. Torrey Bot. Club. 34: 314. 1907.

Etymology: Based on the title of the Jim Jarmusch movie "Coffee and Cigarettes", referring to the close genetic relationship between *C. kahawae* subsp. *ciggaro* and the coffee pathogen *C. kahawae* subsp. *kahawae*; ciggaro is Portuguese for cigarette.

Holotype: **Australia**, on *Olea europaea*, coll. V. Sergeeva UWS124, 1989, PDD 102232; ex-type culture ICMP 18539.

Colonies grown from single conidia on Difco PDA 75–85 mm diam after 10 d for most isolates, the ex-holotype culture of *G. cingulata* var. *migrans* 48–49 mm diam. Aerial mycelium cottony, grey, dense, or in some isolates with dark stromatic masses and associated orange conidial ooze showing through mycelium from agar surface; in reverse agar with pinkish-orange pigments (6B4–7B4), irregular scattered black spots, and variable levels of development of overlying dark grey to green-grey pigments (4C2–5D4), these sometimes in discrete sectors. See notes below about a divergent growth form single ascospore cultures from perithecia in culture. *Conidia* form on dark-based acervuli, (12–)16–19.5(–29) × (4.5–)5(–8) µm (av. 17.8 × 5.1 µm, n = 214), cylindric, straight, apex rounded, often tapering slightly towards the base. *Appressoria* typically cylindric to fusoid in shape, deeply lobed. *Perithecia* numerous, forming tightly packed clumps, individual perithecia globose, small, about 250 µm diam, with a short ostiolar neck. *Asci* 55–100 × 10–12 µm, 8–spored. *Ascospores* (13.5–)17.5–20(–24) × (4–)4.5–5(–6.5) µm (av. 18.8 × 4.8 µm, n = 121), gently curved, tapering to quite narrow, rounded ends, widest point usually towards one end of the spore.

Geographic distribution and host range: Known from Australia, Germany, New Zealand, and South Africa. Both host and geographic range of the isolates we accept in *C. kahawae* subsp. *ciggaro* are broad. *Genetic identification*: ACT, CAL, CHS-1, GAPDH, TUB2, SOD2, and ITS sequences match those from *C. kahawae* subsp. *kahawae*. The two subspecies can be distinguished by GS sequences. Collectively, the two subspecies can be distinguished from all other species using ITS sequences alone.

Notes: The authentic isolate of *G. cingulata* var. *migrans* (CBS 237.49) differed from all other isolates we accept in *C. kahawae* subsp. *ciggaro* by its slower growth rate. Wollenweber & Hochapfel (1949) distinguished *Glomerella cingulata* var. *migrans* from *G. cingulata* var. *cingulata* on the basis of pathogenicity (*G. cingulata* var. *migrans* was pathogenic to *Hypericum* and not to apple) and because of its slightly longer ascospores and shorter conidia — ascospores average 21 × 4.2 µm versus 18 × 4.6 µm, conidia average 14 × 5.2 µm versus 18 × 5 µm (Wollenweber & Hochapfel 1949). We were unable to produce ascospores from CBS 237.49, the conidia were similar in size to that reported by Wollenweber & Hochapfel (1949), averaging 16.6 × 5.3 µm. However, the average ascospore and conidial lengths of our *C. kahawae* subsp. *ciggaro* isolates varied across the range cited by Wollenweber & Hochapfel (1949) for both *G. cingulata* var. *cingulata* and *G. cingulata* var. *migrans*, the average ascospore length from individual isolates ranging from 16.6 to 20 µm, the average conidial length ranging from 14.9 to 21.2 µm.

Glomerella rufomaculans var. *vaccinii* was described by Shear (1907) for a fungus isolated from cranberry that was morphologically identical to isolates from apple and other hosts but which appeared to be biologically distinct (Shear 1907, Shear & Wood 1913). A putatively authentic isolate of this species, deposited by Shear in CBS in 1922, matches *C. kahawae* subsp. *ciggaro* genetically. Polashock *et al.* (2009) discussed the diversity of *Colletotrichum*

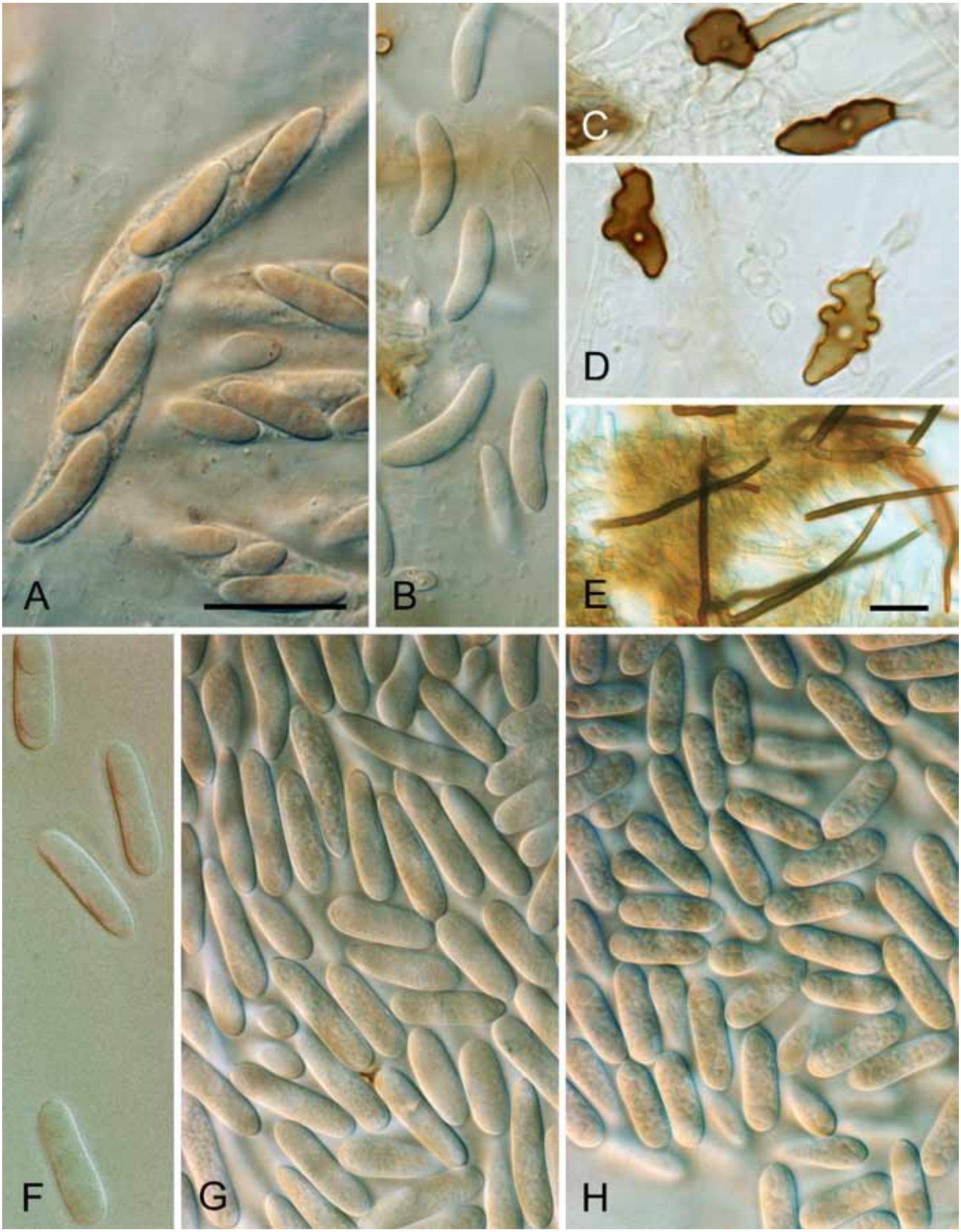


Fig. 26. *Colletotrichum kahawae* subsp. *ciggaro*. A. ICMP 12952. B, D. ICMP 17932 (ex CBS 112984). E, H. ICMP 17931 (ex IMI 359911). C, F. ICMP 18539 – ex-holotype culture. G. ICMP 18531. A–B. Asci and ascospores. C–D. Appressoria. E. Setae. F–H. Conidia. Scale bars A, E = 20 µm. Scale bar of A applies to A–D, F–H.

spp. associated with North American cranberry fruit rots, reporting a close match between their isolates and *C. kahawae*. Incorporation of their ITS sequences into our alignment confirms this. Whether or not there is a genetically distinct, cranberry specialised taxon within *C. kahawae* requires additional genes to be sequenced from the cranberry-associated isolates.

Colletotrichum kahawae subsp. *ciggaro* was referred to as *C. gloeosporioides* Group B by Johnston & Jones (1997) and Johnston

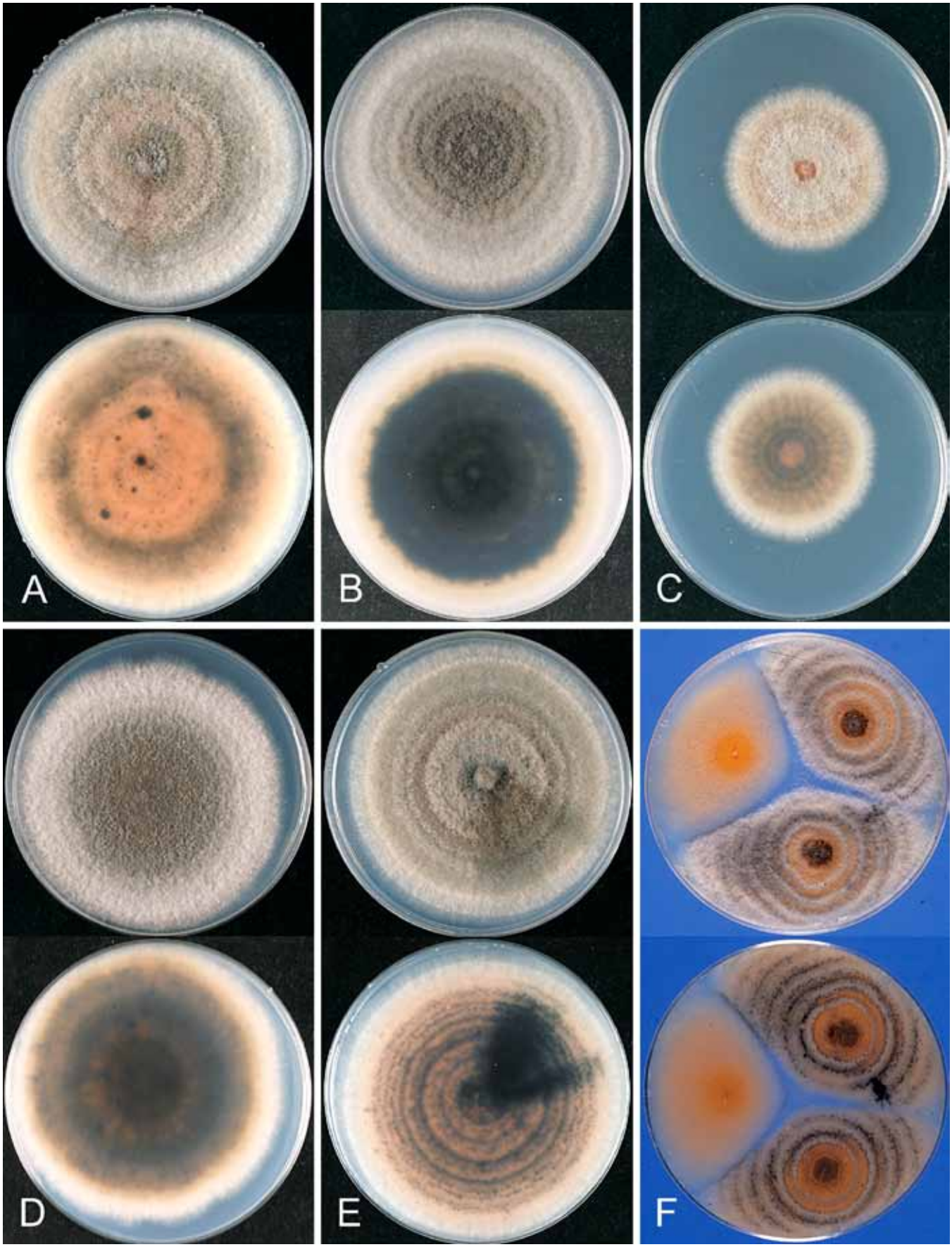


Fig. 27. *Colletotrichum kahawae* subsp. *ciggaro*. A. ICMP 12953. B. ICMP 18534. C. ICMP 17922 (ex CBS 237.49 – ex-holotype culture of *Glomerella cingulata* var. *migrans*). D. ICMP 17932 (ex CBS 112984). E. ICMP 18539 – ex-holotype culture of *C. kahawae* subsp. *ciggaro*. F. ICMP 12952 – single ascospore cultures from single conidial isolate. Cultures on PDA, 10 d growth from single conidia, from above and below.

et al. (2005), and as Undescribed Group 1 by Silva et al. (2012b).

Single ascospore isolates derived from perithecia forming in single conidial cultures of the avocado-associated isolates of *C. kahawae* subsp. *ciggaro* from New Zealand showed two highly divergent growth forms (Fig. 27F). One typical of the "wild type" (cottony, grey to dark grey aerial mycelium with dark-based acervuli

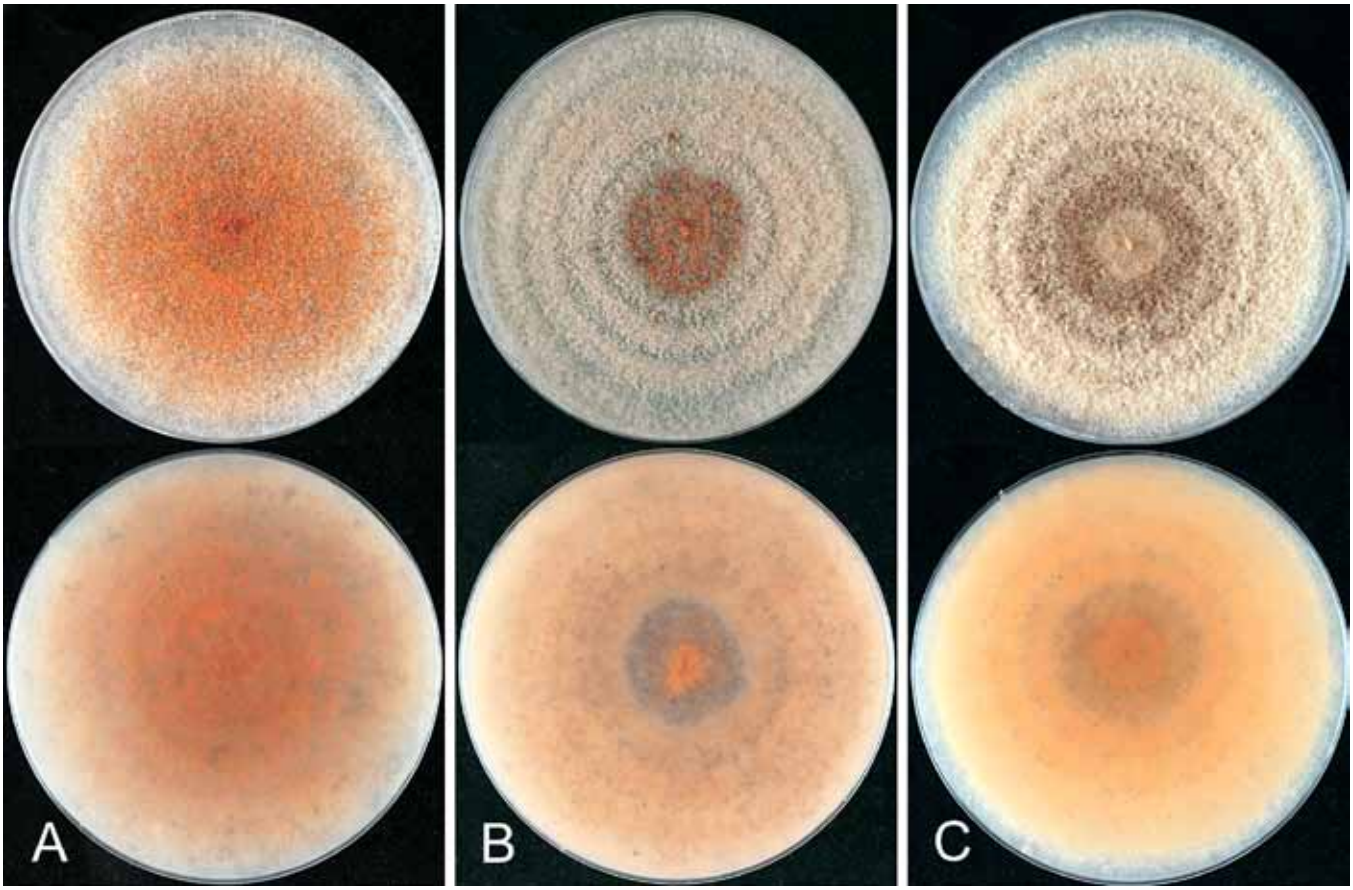


Fig. 28. *Colletotrichum musae*. A. ICMP 12930. B. ICMP 18600. C. ICMP 17817 (ex IMI 52264). Cultures on PDA, 10 d growth from single conidia, from above and below.

and orange conidial masses visible through the mycelium, in reverse with pinkish-orange pigmentation, in places this masked by irregular patches or sectors of dark grey pigmentation), the other more or less lacking aerial mycelium, the surface of the colony covered with small, pale-based acervuli with bright orange conidial ooze, in reverse bright orange from the conidial ooze. Although common from single ascospores, the bright, conidial cultural type is rarely formed by isolates from nature (unpubl. data). Similar dimorphic cultural types have been observed also from single ascospore isolates from a member of the *C. boninense* complex, *C. constrictum* (unpubl. data, P.R. Johnston).

Other specimens examined: **Brazil**, on leaves of *Miconia* sp., coll. R. Barreto RWB1054, 2009 (ICMP 18728). **Germany**, Berlin-Dahlem, on stem of *Hypericum perforatum*, Jun. 1937 (**ex-holotype culture** of *Glomerella cingulata* var. *migrans* – CBS 237.49 = ICMP 17922). **New Zealand**, Auckland, Waitakere Ranges, on leaves of *Kunzea ericoides*, coll. S. Joshee 5Kun3.10 (ICMP 18741); Auckland, Waitakere Ranges, on leaves of *K. ericoides*, coll. S. Joshee 7Kun5.2 (ICMP 18534); Auckland, Waitakere Ranges, on leaves of *Toronia toru*, coll. G. Carroll TOROTO3 (ICMP 18544); Te Puke, on *Persea americana* fruit rot, coll. W.F.T. Hartill, 19 Jan. 1989 (ICMP 18531); Te Puke, on *P. americana* fruit rot, coll. W.F.T. Hartill, 8 Feb. 1988 (ICMP 12952); Te Puke, on *P. americana* fruit rot, coll. W.F.T. Hartill, 28 Sep. 1991 (ICMP 12953). **South Africa**, Madeira, on *Dryandra* sp., coll. J.E. Taylor, 1 Apr. 2001 (CBS 112984, as *C. crassipes* = ICMP 17932). **Switzerland**, on *Dryas octopetala*, coll. P. Cannon (IMI 359911 = CBS 12988 = ICMP 17931). **USA**, on *Vaccinium macrocarpum* leaves, coll. C.L. Shear, Apr. 1922 (**authentic culture** of *G. rufomaculans* var. *vaccinii* – CBS 124.22 = ICMP 19122).

Colletotrichum manihotis Henn., Hedwigia 43: 94. 1904.

Notes: Anthracnose is an important disease of cassava (*e.g.* Chevaugeon 1956, Makambila 1994, Fokunang *et al.* 2000, Owolade *et al.* 2008), variously referred to *Colletotrichum manihotis*, *Gloeosporium manihotis* Henn., *Glomerella manihotis* (Sacc.) Petr., *Glomerella cingulata* "f. sp. *manihotis*", or *C. gloeosporioides* "f. sp. *manihotis*". The original descriptions of both *C. manihotis* and *Gloeosporium manihotis* are of species with short, broad conidia (8–15 × 4–6 µm), and Chevaugeon (1956) regarded all of these cassava-associated fungi as con-specific. However, based on Fokunang *et al.* (2000), a morphologically highly diverse set of *Colletotrichum* isolates are associated with diseased plants. There are three GenBank accessions of *Colletotrichum* from cassava, all from China, and although only ITS sequences are available for these isolates, they appear to represent a single, distinct species within the *C. gloeosporioides* complex. How these Chinese isolates relate to cassava-associated isolates from other parts of the world is not known.

**** Colletotrichum musae*** (Berk. & M.A. Curtis) Arx, Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Sect. 2 51(3): 107. 1957. Fig. 28.
Basionym: *Myxosporium musae* Berk. & M.A. Curtis, Grevillea 3: 13. 1874.

Su *et al.* (2011) provide a description.

Geographic distribution and host range: Found in association with fruit lesions of *Musa* spp. in many regions.

Genetic identification: ITS sequences separate *C. musae* from all other species.

Notes: *Colletotrichum musae* was originally described from North Carolina (Berkeley 1874), and the name was recently epitypified by Su *et al.* (2011) on the basis of a specimen collected in Florida

(ex-epitype culture CBS 116870). Su *et al.* (2011) cite several strains from Thailand that match their concept of *C. musae*, and isolates from anthracnose symptoms on banana fruit from several parts of the world are the same based on our study. These isolates form a well-supported clade within the *C. gloeosporioides* species complex, show low levels of genetic differentiation, and based on ITS sequences are consistent with *C. musae sensu* Sreenivasaprasad *et al.* (1996), Nirenberg *et al.* (2002) and Shenoy *et al.* (2007). The morphology in culture agrees with the description of Sutton & Waterston (1970).

We have not seen a *Glomerella* state in culture and none was mentioned by Su *et al.* (2011). However, Rodriguez & Owen (1992) reported rare production of perithecia from crosses between two of 14 isolates identified as *C. musae*. It is not known whether the isolates studied by Rodriguez & Owen (1992) match our concept of *C. musae* genetically, but it is possible that this species behaves in a similar way to some species in the *C. acutatum* complex, where the sexual morph can be generated in culture under suitable conditions (Guerber & Correll 2001). The name "*Glomerella musae*", used by Rodriguez & Owen (1992) and Krauss *et al.* (2001), has never been validly published.

More than one species of *Colletotrichum* has been found in association with rotting banana fruit. From isolates with well characterised sequence data these include a species belonging to *C. acutatum s. lat.* (Sherriff *et al.* 1994, Johnston & Jones 1997) that is described as *C. paxtonii* (Damm *et al.* 2012a, this issue), and *C. karstii* that belongs to the *C. boninense* species complex (Damm *et al.* 2012b, this issue). The latter forms a sexual stage in culture and is known from *Musa* in South America and Australia, as well as from many other hosts worldwide, often as an endophyte. Species in the *C. boninense* species complex have been previously confused with *C. gloeosporioides s. lat.* Greene (1967) referred isolates pathogenic to banana that were not associated with a teleomorph to *C. musae*, and a second non-pathogenic species that formed fertile ascospores, to *C. gloeosporioides*. Whether *Glomerella musarum* Petch, described from leaves of banana and cited as the teleomorph of *C. musae* by Sutton (1992) and Hyde *et al.* (2009), is a synonym of *C. musae* in the sense we use the name here is not known, but seems unlikely given the rare production of perithecia by this species.

Specimens examined: **Indonesia**, on *Musa* sp., coll. G. von Becze, Jan. 1931 (CBS 192.31 = ICMP 17923). **Kenya**, on *Musa sapientum*, coll. R.M. Nattrass 1850, 1 Jan. 1953 (IMI 52264 = ICMP 17817). **New Zealand**, Auckland (imported fruit), on *Musa* sp., coll. P.R. Johnston C1197.1, 24 May 1991 (ICMP 12931; PDD 59100); Auckland (fruit imported from the Phillipines), on *Musa* sp., coll. S. Bellgard, 5 May 2009 (ICMP 18600); Auckland, Mt Albert Research Centre, *Musa* sp. spots on green fruit, coll. P.R. Johnston C809.2, 12 Aug. 1987 (ICMP 12930; PDD 46160); Auckland (fruit imported from the Phillipines), on *Musa* sp., coll. B. Weir, 17 May 2009 (ICMP 18701; PDD 97438). **USA**, Florida, on *Musa* sp., coll. M. Arzanlou A-1 (**ex-epitype culture** of *C. musae* – CBS 116870 = ICMP 19119).

Glomerella musarum Petch, Ann. Roy. Bot. Gard. Peradeniya 6(3): 223. 1917.

Notes: See notes under *C. musae*.

*** *Colletotrichum nupharicola*** D.A. Johnson, Carris & J.D. Rogers, Mycol. Res. 101: 647. 1997. Fig. 29.

Johnson *et al.* (1997) provide a description.

Geographic distribution and host range: Known only from the USA, on the aquatic plants *Nuphar* and *Nymphaea* spp.

Genetic identification: One of the two ITS haplotypes of *C. nupharicola* is identical with *C. queenslandicum*. All other genes distinguish this species well from other species in the *C. gloeosporioides* complex.

Notes: Sequence data from the ex-holotype culture of *C. nupharicola* places it within the *C. gloeosporioides* complex, genetically close to *C. fructicola* and *C. alienum* in the Musae clade. This apparently host-specific species and has a distinctive, slow growth in culture and massive conidia (Johnson *et al.* 1997).

Johnson *et al.* (1997) compare *C. nupharicola* with another water plant pathogen, *C. nymphaeae*, that is epitypified and shown to belong to the *C. acutatum* species complex by Damm *et al.* (2012a, this issue).

Specimens examined: **USA**, Washington, King Co., on *Nuphar lutea* subsp. *polysepala*, coll. D.A. Johnson A-7, Oct. 1993 (CBS 469.96 = ICMP 17938); Washington, Yakima Co., on *N. lutea* subsp. *polysepala*, coll. D.A. Johnson A-2, Oct. 1993 (**ex-holotype culture** − CBS 470.96 = ICMP 17939); Rhode Island, on *Nymphaea ordorata*, coll. R.D. Goos RDG-291, 1979 (CBS 472.96 = ICMP 18187).

Gloeosporium pedemontanum Pupillo, Ann. Sperim. Agrar. n.s. 6: 57. 1952.

Notes: Placed here in synonymy with *C. gloeosporioides*. See notes under *C. gloeosporioides*.

Specimen examined: **Italy**, on *Citrus limon* juice, coll. G. Goidánich, 1951 (**ex-holotype culture** of *G. pedemontanum* – CBS 273.51 = ICMP 19121).

*** *Colletotrichum psidii*** Curzi, Atti dell'Istituto Botanico dell'Università di Pavia, ser. 3, 3: 207. 1927. Fig. 30.

Colonies grown from single conidia on Difco PDA 58–63 mm diam after 10 d, aerial mycelium dense, cottony to felted, uniform in height, white to off-white; in reverse uniformly pale creamy yellow (2A2–2A3) or in some cultures becoming dull greyish yellow (2D2–2E2) towards the centre. No *conidiogenous cells* or *conidia* seen.

Geographic distribution and host range: Known from a single isolate, from *Psidium* from Italy.

Genetic identification: Although known from only one isolate, ITS sequences separate *C. psidii* from all other taxa.

Notes: A putatively authentic isolate of this species, deposited in CBS by Curzi shortly after publication of *C. psidii*, represents a genetically distinct species within the Kahawae clade. The only available culture is stale, no longer forming conidia. Curzi (1927) describes the conidia as 12–15 × 3.5–4.5 µm, cylindric with rounded ends, straight or rarely slightly curved.

Anthracnose diseases have been noted for *Psidium* spp. (guava) from several tropical regions of the world (*e.g.* MacCaughey 1917, Venkatakrishniah 1952, Liu 1972, Misra 2004). It is likely that several *Colletotrichum* spp. are associated with guava fruit rots. Whether the fungus described by Curzi from an Italian botanical garden represents one of the species causing a guava disease in the tropics is not known. All other members of the Kahawae clade are predominantly tropical, so perhaps this fungus was introduced to Italy along with its host plant. Misra (2004) uses *C. psidii* to refer to a *Colletotrichum* species with curved conidia.

One other species has been described from this host, *Glomerella psidii* (basionym *Gloeosporium psidii*), the relationship

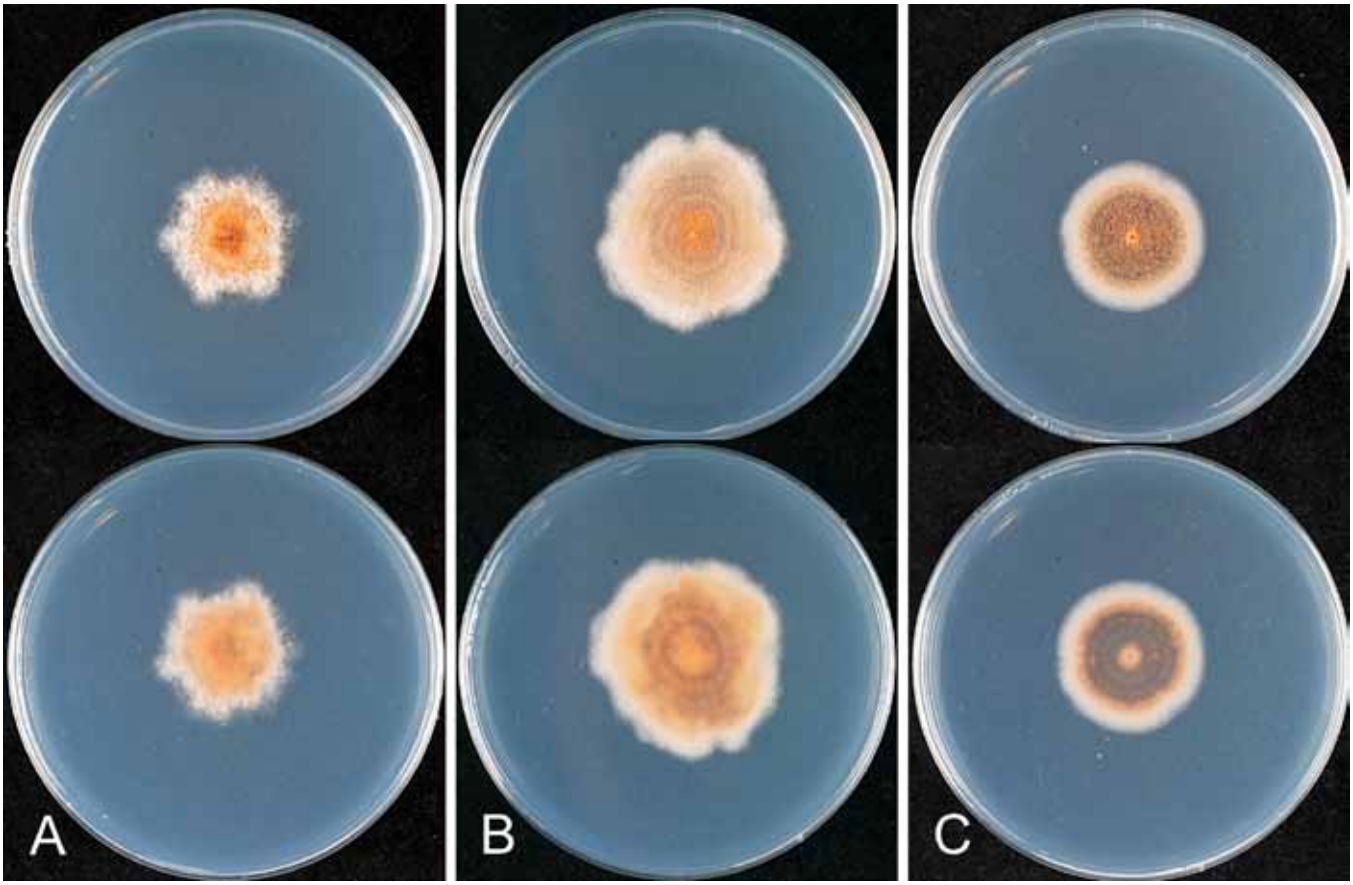


Fig. 29. *Colletotrichum nupharicola*. A. ICMP 17939 (ex CBS 470.96 – ex-holotype culture). B. ICMP 17938 (ex CBS 469.96). C. ICMP 18187 (ex CBS 472.96). Cultures on PDA, 10 d growth from single conidia, from above and below.

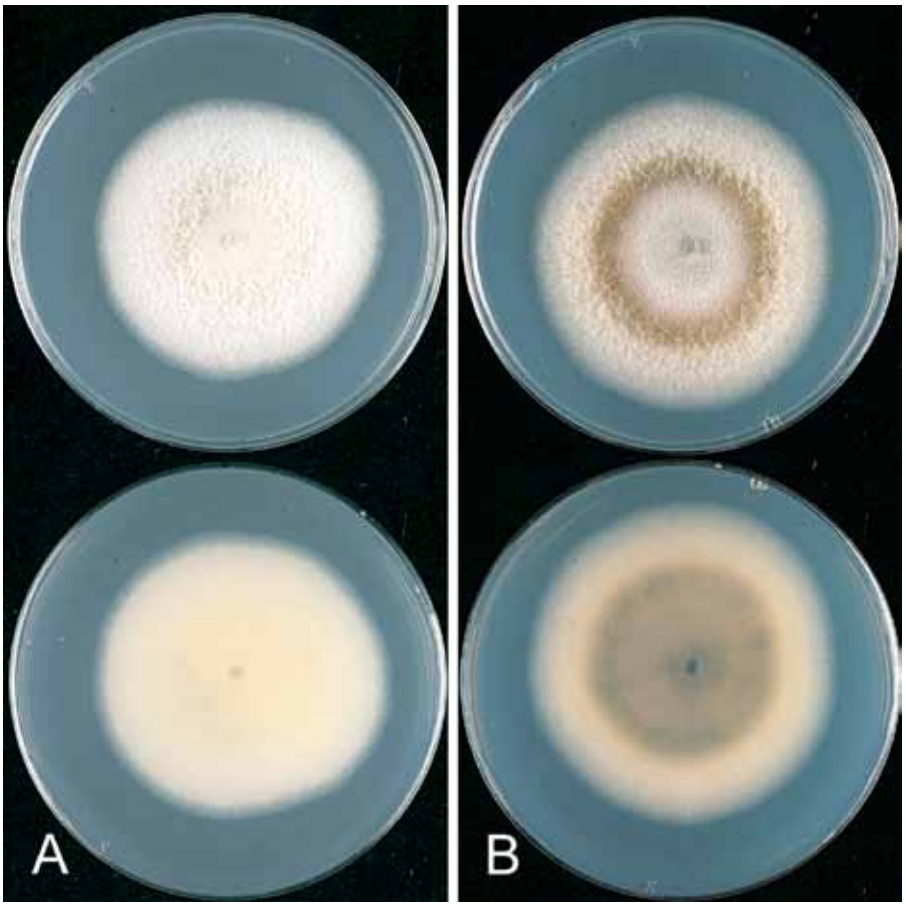


Fig. 30. *Colletotrichum psidii* (ICMP 19120, ex CBS 145.29 – authentic culture). Cultures on PDA, 10 d growth from single hyphal tips, from above and below.

of this species to *C. psidii* remains unknown. A new species on *Psidium guajava*, *C. guajavae*, belonging to the *C. acutatum* species complex, is described elsewhere in this volume (Damm *et al.* 2012a).

Specimen examined: **Italy**, Rome, on *Psidium* sp., coll. M. Curzi (**authentic culture** of *C. psidii* – CBS 145.29 = ICMP 19120).

Glomerella psidii (Delacr.) J. Sheld., Bull. West Virginia Agric. Exp. Sta. 104: 311. 1906.
Basionym: *Gloeosporium psidii* Delacr., Bull. Soc. Mycol. France. 19: 144. 1903.

Notes: Sheldon (1906) produced perithecia in culture from isolates he considered typical of *Gloeosporium psidii* and on this basis recombined the species described by Delacroix (1903) in *Glomerella*. The relationship of *G. psidii* to *Colletotrichum psidii*, also described from guava, is not known. See notes under *C. psidii*.

*** *Colletotrichum queenslandicum*** B. Weir & P.R. Johnst., **nom. nov. et stat. nov.** MycoBank MB563593. Fig. 31.
Basionym: *Colletotrichum gloeosporioides* var. *minus* Simmonds, Queensland J. Agric. Anim. Sci. 25: 178A. 1968. [as var. *minor*]

Etymology: based on the region from which the type specimen of this species was collected.

Holotype: Australia, Queensland, Ormiston, on *Carica papaya*, coll. J.H. Simmonds, Oct. 1965, IMI 117612.

Epitype: **Australia**, Queensland, Brisbane, on *Carica papaya*, coll. J.H. Simmonds 11663C, Sep. 1965, **epitype** here designated PDD 28797; ex-epitype culture ICMP 1778.

Colonies grown from single conidia on Difco PDA 62–74 mm diam after 10 d, aerial mycelium either dense, cottony, uniform, grey, or with aerial mycelium lacking, towards centre of colony with numerous, small acervuli with dark bases and orange conidial ooze; in reverse cultures with copious aerial mycelium uniformly dark grey (1F2), those with little aerial mycelium having a pinkish brown (8B4) pigment within the agar, the dark bases of the acervuli and the colour of the conidial ooze visible through the agar. *Conidia* (12–)14.5–16.5(–21.5) × (3.5–)4.5–5(–6) µm (av. 15.5 × 4.8 µm, n = 96), cylindric, straight, sometimes slightly constricted near centre, ends broadly rounded. *Appressoria* about 6–12 µm diam., globose to short-cylindric, rarely lobed. *Perithecia* not seen.

Geographic distribution and host range: Known from *Carica papaya* and *Persea americana* from Queensland, Australia, and from *Coffea* berries from Fiji. Simmonds (1965) reported from Australia what he considered to be the same fungus also from *Mangifera indica*, *Malus sylvestris*, and "many other hosts".

Genetic identification: ITS sequences do not separate *C. queenslandicum* from some *C. fructicola*, some *C. siamense*, and some *C. tropicale* isolates. It is best distinguished from these taxa using TUB2, GAPDH, or GS.

Notes: The ex-type cultures cited by Simmonds (1968) are no longer in storage at BRIP in Queensland (R. Shivas, pers. comm.) and presumably lost. However, we do have two cultures identified as *C. gloeosporioides* var. *minus* by Simmonds and isolated from the same host from the same locality as the holotype (Simmonds isolates 16633C and 1647A2), that had been sent to Joan Dingley in 1965 and subsequently stored in the ICMP culture collection. The culture selected here as epitype (Simmonds 11663C = ICMP 1778) matches the Simmonds (1965) description of this fungus as having "an abundance of aerial mycelium in culture". Our conidial measurements from ICMP 1778 and 1780 are broader than those given by Simmonds (1965), but he does note that "Confusion can occur between narrower strains of *C. gloeosporioides* and broader strains of *C. gloeosporioides* var. *minus* …". Simmonds (1965) also notes that perithecia may rarely be seen in cultures of some isolates.

The isolates accepted here as *C. queenslandicum* are genetically distinct within the Musae clade of *C. gloeosporioides s. lat*. *Colletotrichum minus* Zimm. (1901) requires that we propose a *nom. nov.* for this fungus at species rank.

Simmonds (1965) considered *C. gloeosporioides* var. *minus* to be the conidial state of *Glomerella cingulata* var. *minor* Wollenw. Wollenweber & Hochapfel (1949) used the name *Gloeosporium elasticae* Cooke & Massee for the conidial state of *G. cingulata* var. *minor*, the type specimens for both names being from *Ficus*. Simmonds (1965) noted that it was not possible to transfer *G. elasticae* to *Colletotrichum* because *Colletotrichum elasticae* had already been published for a different fungus. However, rather than proposing a nom. nov. for *Gloeosporium elasticae*, he described *C. gloeosporioides* var. *minus* as a new variety, with a different type specimen. *Glomerella cingulata* var. *minor* is genetically distinct from the specimen Simmonds chose as the type of *C. gloeosporioides* var. *minus*, see notes under *G. cingulata* var. *minor*.

Other specimens examined: **Australia**, Queensland, Brisbane, on *Carica* sp., coll. J.H. Simmonds 16347A2 (ICMP 1780, dried culture stored as PDD 28797); Queensland, Home Hill, on *Persea americana*, coll. L. Coates 22516, Feb. 1983 (ICMP 12564). **Fiji**, on *Coffea* sp. berry, coll. R. Gounder, Apr. 1988 (ICMP 18705).

Glomerella rufomaculans* var. *vaccinii Shear, Bull. Torrey Bot. Club. 34: 314. 1907.

Notes: Placed here in synonymy with *Colletotrichum kahawae* subsp. *ciggaro*. See notes under *C. kahawae* subsp. *ciggaro*. Note that Saccardo & Trotter (1913) place Shear's variety in *Glomerella fructigena* (Clint.) Sacc., a rarely used species name, placed in synonymy with *G. cingulata* by von Arx & Müller (1954).

Specimen examined: **USA**, on *Vaccinium macrocarpum* leaves, coll. C.L. Shear, Apr. 1922 (authentic isolate of *G. rufomaculans* var. *vaccinii* – CBS 124.22 = ICMP 19122).

*** *Colletotrichum salsolae*** B. Weir & P.R. Johnst., **sp. nov.** MycoBank MB563589. Fig. 32.
= *Colletotrichum gloeosporioides* "f. sp. *salsolae*" (Berner *et al.* 2009).

Etymology: Based on *C. gloeosporioides* "f. sp. *salsolae*", referring to the host from which this fungus was originally collected.

Holotype: **Hungary**, on *Salsola tragus*, coll. D. Berner [specimen from plants inoculated with strain 96-067, originally collected I. Schwarczinger & L. Vajna on *Salsola tragus* from Bugac, near Kiskunsag National Park, 1996], BPI 878740; ex-holotype culture ICMP 19051.

Colonies grown from single conidia on Difco PDA 38–42 mm diam after 10 d, aerial mycelium sparse, cottony, pale grey, surface of

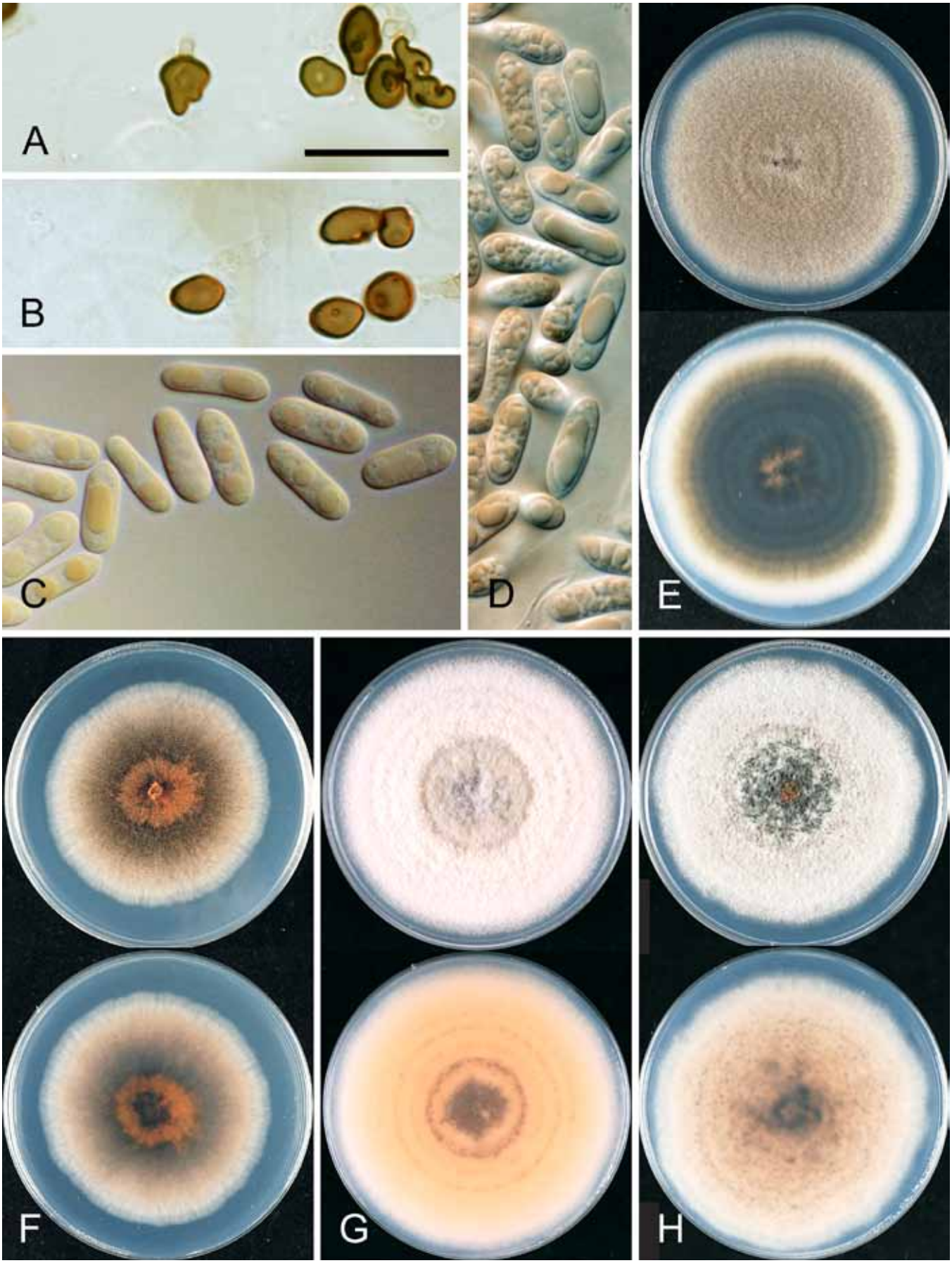


Fig. 31. *Colletotrichum queenslandicum*. A, C, E. ICMP 1778 – ex-epitype culture. B, F. ICMP 1780. D, G. ICMP 12564. H. ICMP 18705. A–B. Appressoria. C–D. Conidia. E–H. Cultures on PDA, 10 d growth from single conidia, from above and below. Scale bar A = 20 µm. Scale bar of A applies to A–D.

colony dark, a more or less continuous layer of acervulus-like structure with deep orange brown conidial masses and numerous setae; in reverse dark purplish-black near centre of colony, dark olivaceous near the margin. *Conidia* (10–)14–16.5(–20.5) × (4.5–)5.5–6(–7.5) µm (av. 15.3 × 5.8 µm, n = 24), highly variable in size and shape, subglobose to long-cylindric, apex usually broadly

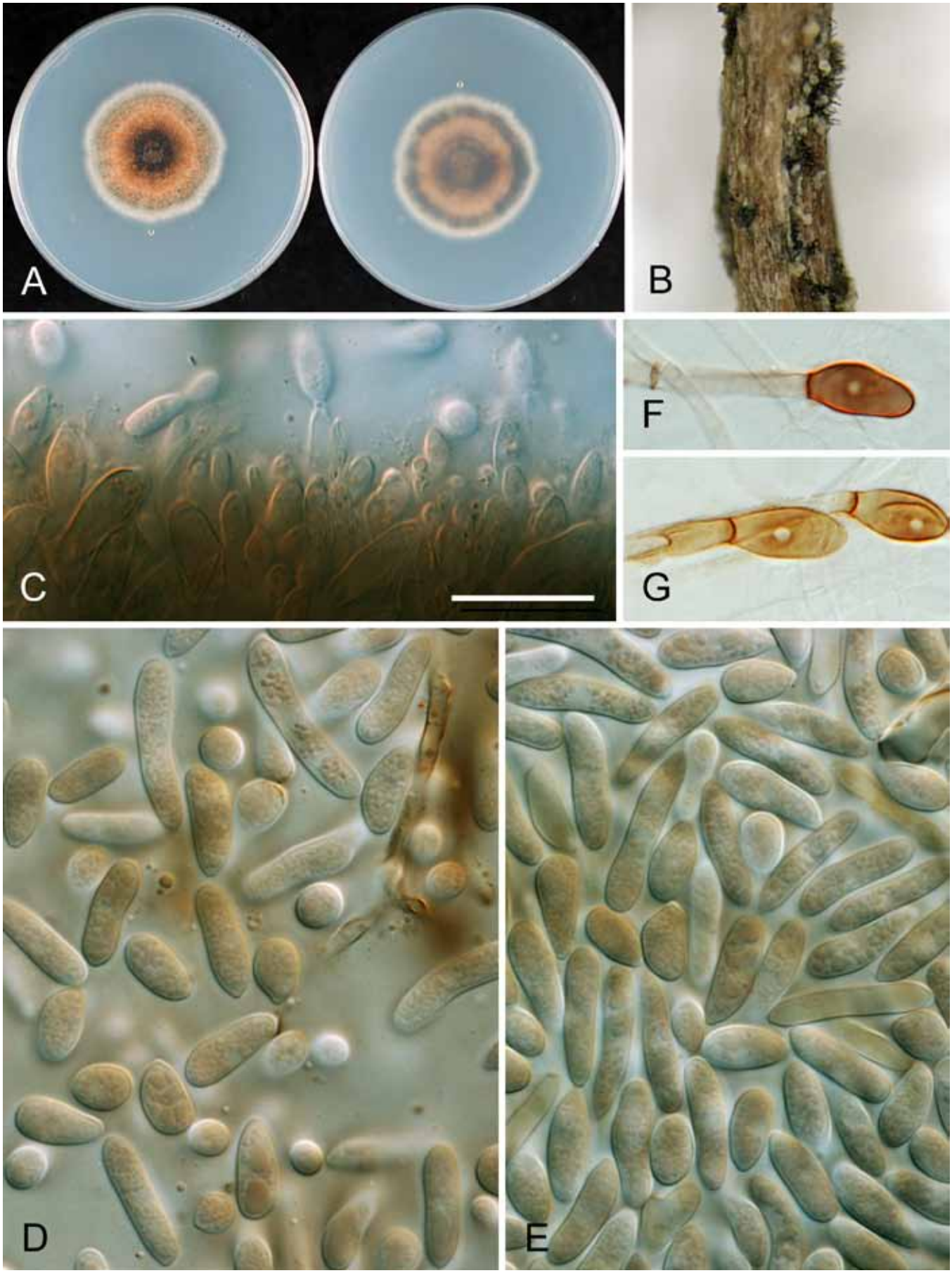


Fig. 32. *Colletotrichum salsolae*. A, C–H. ICMP 19051 – ex-holotype culture. B. BPI 878740 – holotype. A. Cultures on PDA, 10 d growth from single conidia, from above and below. B. Lesion on stem, dried type specimen. C. Conidiogenous cells. D–E. Conidia. F–G. Appressoria. Scale bars B = 1 mm, C = 20 µm. Scale bar of C applies to C–G.

rounded, small truncate scar at base. *Conidiogenous cells* 13–18 × 4–6.5 µm, cylindric to flask-shaped, tapering at apex to narrow, phialidic conidiogenous locus, wall at base often encrusted with dark brown material. *Appressoria* sparsely developed, cylindric to

elliptic, simple; many putatively partially developed appressoria, similar in shape to those with dark and thick walls and also with an appressorial pore, but the wall remains thin and only slightly pigmented. *Perithecia* not seen.

Geographic distribution and host range: Known from throughout the geographic range of *Salsola tragus* (Berner *et al.* 2009), reported in nature only from *Salsola* spp.

Genetic identification: ITS sequences of *C. salsolae* are very close to *C. alienum* and some *C. siamense* isolates. These species can be distinguished using TUB2 or GAPDH.

Notes: Isolates of *C. gloeosporioides* pathogenic to *Salsola tragus* were reported by Schwarczinger *et al.* (1998) and referred to as *C. gloeosporioides* "f. sp. *salsolae*" by Berner *et al.* (2009). Although mildly pathogenic to a wide range of hosts in glasshouse pathogenicity tests, this fungus causes severe disease only on *Salsola* spp. with the exception of *S. orientalis*, *S. soda*, and *S. vermiculata* (Berner *et al.* 2009).

Colletotrichum salsolae belongs to the Musae clade, and although genetically close to several other species, it is biologically and morphologically distinctive.

Other specimen examined: **Hungary**, additional isolate of strain selected as the holotype, recovered from inoculated *Glycine max* plants (MCA 2498 = CBS 119296 = ICMP 18693).

*** *Colletotrichum siamense*** Prihastuti, L. Cai & K.D. Hyde, Fungal Diversity 39: 98. 2009. Fig. 33.

= *Colletotrichum jasmini-sambac* Wikee, K.D. Hyde, L. Cai & McKenzie, Fungal Diversity 46: 174. 2011.

= *Colletotrichum hymenocallidis* Yan L. Yang, Zuo Y. Liu, K.D. Hyde & L. Cai, Fungal Diversity 39: 138. 2009.

Descriptions of this species are provided by Prihastuti *et al.* (2009), Wikee *et al.* (2011), and Yang *et al.* (2009).

Geographic distribution and host range: *Colletotrichum siamense* was originally described from coffee from Thailand, but our concept of this species is biologically and geographically diverse, found on many hosts across several tropical and subtropical regions.

Genetic identification: ITS sequences do not reliably separate *C. siamense* from *C. alienum*, *C. fructicola*, or *C. tropicale*. These species are best distinguished using CAL or TUB2.

Notes: Yang *et al.* (2009) and Wikee *et al.* (2011) discussed genetic and morphological differences between *C. siamense*, *C. jasmini-sambac*, and *C. hymenocallidis*. However, both studies used a limited set of isolates within the *C. gloeosporioides* complex, making interpretation of the genetic differences difficult. The morphological differences they described are commonly seen as within-species variation in other *Colletotrichum* spp. In our analysis, *C. siamense* is represented by 30 isolates from a wide range of hosts from several tropical regions, and forms a monophyletic clade that cannot be further subdivided genetically. Variation in cultural appearance is broad but in part this probably reflects the different conditions under which the isolates had been stored. Shape and size of appressoria, and the characteristically small conidia are similar in all isolates.

Based on matching translation elongation factor (TEF) and TUB2 sequences, isolates referred by Rojas *et al.* (2010) to *Colletotrichum* sp. indet. 2 also represent *C. siamense*. Note that TEF data was excluded from our phylogenetic analyses because the TEF gene tree was often incongruent with the trees from the other genes that we sequenced. For example, compare our isolate ICMP 17797 (GenBank GU174571) with isolates Rojas *et al.* (2010) cite as *Colletotrichum* sp. indet. 2, V1H1_1 (GenBank GU994297) and 7767 (GenBank GU994298).

The *C. siamense* protologue designates the holotype as MFLU 090230, but the culture derived from holotype as "BCC" with no specimen number. The ex-holotype culture is listed as BDP-I2 in Table 1 of Prihastuti *et al.* (2009) but not in the description of the species. Strain BDP-I2 was obtained from the authors (Prihastuti *et al.* 2009) for this study and deposited as ICMP 18578.

Specimens examined: **Australia**, New South Wales, Murwillumbah, on *Persea americana* fruit rot, coll. L. Coates 23695, 1 Apr. 1990 (ICMP 12567); New South Wales, Muswellbrook, on *Pistacia vera* (DAR 76934 = ICMP 18574); Queensland, Mt Tamborine, on *Persea americana* fruit rot, coll. L. Coates T10-1, 1 Sep. 1993 (ICMP 12565). **China**, Guangxi, Nanning, on *Hymenocallis americana* leaf spot, coll. Y.L. Yang CSSN2, 19 Jun. 2008 (**ex-holotype culture** of *C. hymenocallidis* − CBS 125378 = ICMP 18642); Guangxi Province, Nanning, on *H. americana* leaf, coll. Y.L. Yang CSSN3 (CBS 125379 = ICMP 18643). **Nigeria**, Ibadan, on *Dioscorea rotundata* seed, coll. M. Abang CgS2 (ICMP 18121); Ibadan, on *D. rotundata* seed, coll. M. Abang CgS6 (ICMP 18117); Ibadan, on *Commelina* sp. leaf, coll. M. Abang Cg29 (ICMP 18118). **South Africa**, on *Carica papaya* fruit, coll. L. Korsten PMS 1 (ICMP 18739). on *Persea americana*, coll. L. Korsten Cg227 (ICMP 18570); on *Persea americana*, coll. L. Korsten Cg231 (ICMP 18569). **Thailand**, Chiang Mai, Mae Lod Village, on *Coffea arabica* berries, coll. H. Prihastuti BPD-I2, 12 Dec. 2007 (**ex-holotype culture** of *C. siamense* – MFLU 090230 = ICMP 18578). Kanchanaburi, on *Capsicum annuum*, P.P. Than Ku4 (HKUCC 10884 = ICMP 18575); Nakhonpathon, on *C. annuum*, coll. P.P. Than Ku8 (HKUCC 10881 = ICMP 18618). **USA**, Florida, on *Vitis vinifera* leaf, coll. N. Peres ssgrape 10 (ICMP 18572); Florida, on *Fragaria* × *ananassa* crown, coll. N. Peres strawberry 6 (ICMP 18571); Florida, on *V. vinifera* leaf, coll. N. Peres DI-grape-6 (ICMP 18573); North Carolina, Wilkes County, on *Malus domestica* fruit, coll. T. Sutton LD Cg12 2001 (ICMP 17795); North Carolina, Johnston County, on *M. domestica* fruit, coll. T. Sutton GD 8 2002 (ICMP 17791); North Carolina, Johnston County, on *M. domestica* fruit, coll. T. Sutton GD 7 2002 (ICMP 17797); Alabama, on *M. domestica* fruit, coll. T. Sutton AL 1 2001 (ICMP 17785). **Vietnam**, Cu Chi District, Trung An Ward, on living leaves of *Jasminium sambac*, Jan. 2009, coll. Hoa Nguyen Thi LLTA–01 (**ex-holotype culture** of *C. jasmini-sambac* – CBS 130420 = ICMP 19118).

*** *Colletotrichum theobromicola*** Delacr., Bull. Soc. Mycol. France. 31: 191. 1905. Fig. 34.

= *Colletotrichum fragariae* A.N. Brooks, Phytopathology 21: 113. 1931.

= *Colletotrichum gloeosporioides* f. *stylosanthis* Munaut, Mycol. Res. 106: 591. 2002.

= *Colletotrichum gloeosporioides* f. *stylosanthis* "f. sp. *stylosanthis*" (Munaut *et al.* 2002).

= *Colletotrichum gloeosporioides* f. *stylosanthis* "f. sp. *guianensis*" (Munaut *et al.* 2002).

A modern description of this species is provided by Rojas *et al.* (2010).

Geographic distribution and host range: Broadly distributed in tropical and subtropical regions on a wide range of hosts.

Genetic identification: ITS sequences distinguish *C. theobromicola* from all other species.

Notes: The ex-epitype culture of *Colletotrichum fragariae*, the ex-neotype culture of *C. theobromicola*, and the ex-holotype culture of *C. gloeosporioides* f. *stylosanthis*, selected by Buddie *et al.* (1999), Rojas *et al.* (2010), and Munaut *et al.* (2002) respectively, belong in a clade that we accept genetically as a single species. Also in this clade are authentic isolates of C. *gloeosporioides* f. *stylosanthis* "f. sp. *stylosanthis*" and *C. gloeosporioides* f. *stylosanthis* "f. sp. *guianensis*" (but see notes under *C. gloeosporioides* f. *stylosanthis*).

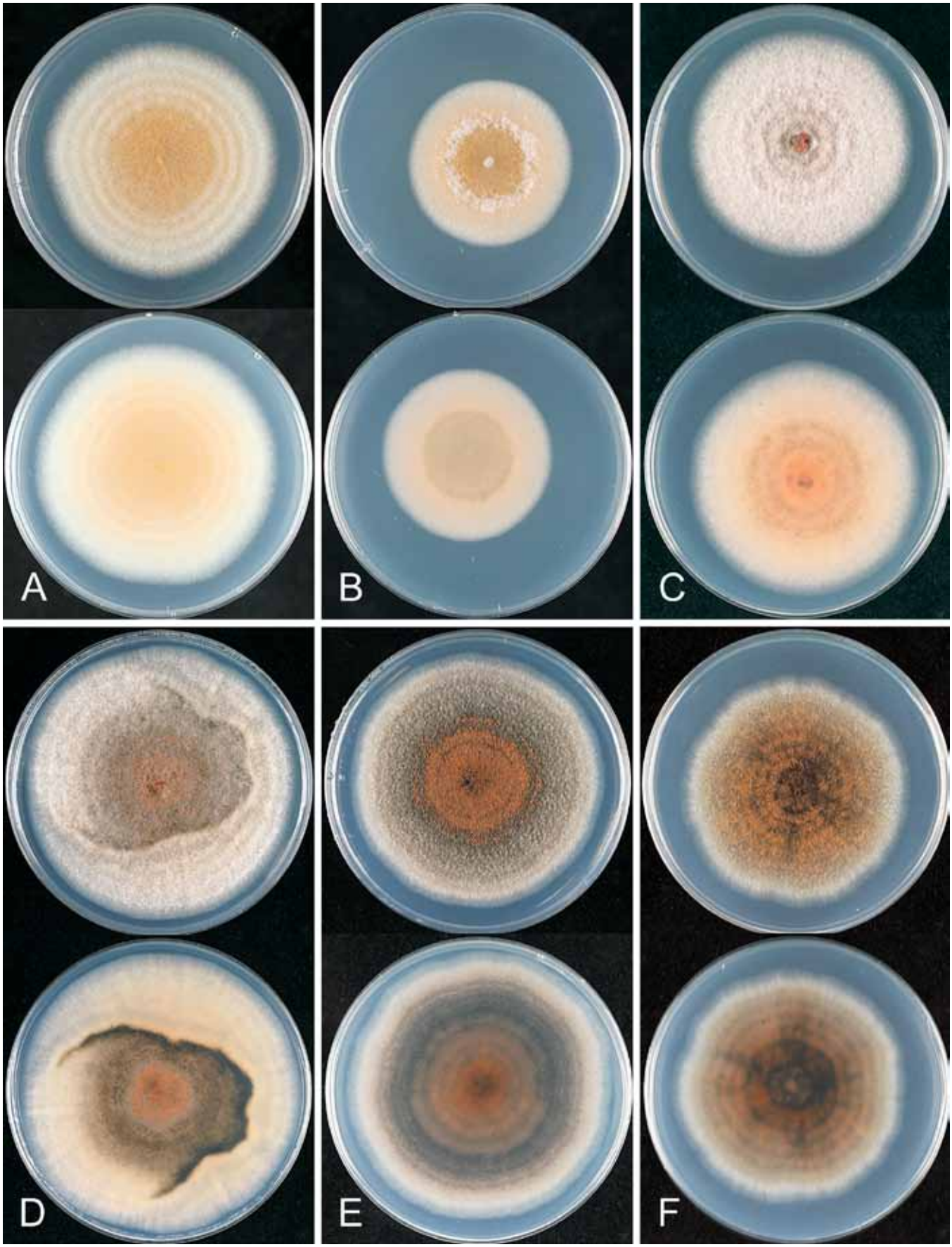


Fig. 33. *Colletotrichum siamense*. A. ICMP 18642 (ex CBS 125378 – ex-holotype culture of *C. hymenocallidis*). B. ICMP 18578 (ex MFLU 090230 – ex-holotype culture of *C. siamense*). C. ICMP 12565. D. ICMP 18574 (ex DAR 76934). E. ICMP 18618 (ex HKUCC 10881). F. ICMP 18121. Cultures on PDA, 10 d growth from single conidia, from above and below.

Colletotrichum theobromicola as accepted here contains several putatively specialised pathogens, including the pathogen of strawberry runners described by Brooks (1931) as *C. fragariae*, and the pathogens of *Stylosanthes* referred to as *C. gloeosporioides* f. *stylosanthis* (Munaut *et al.* 2002). Future studies may show that the species should be segregated based on their pathogenicity

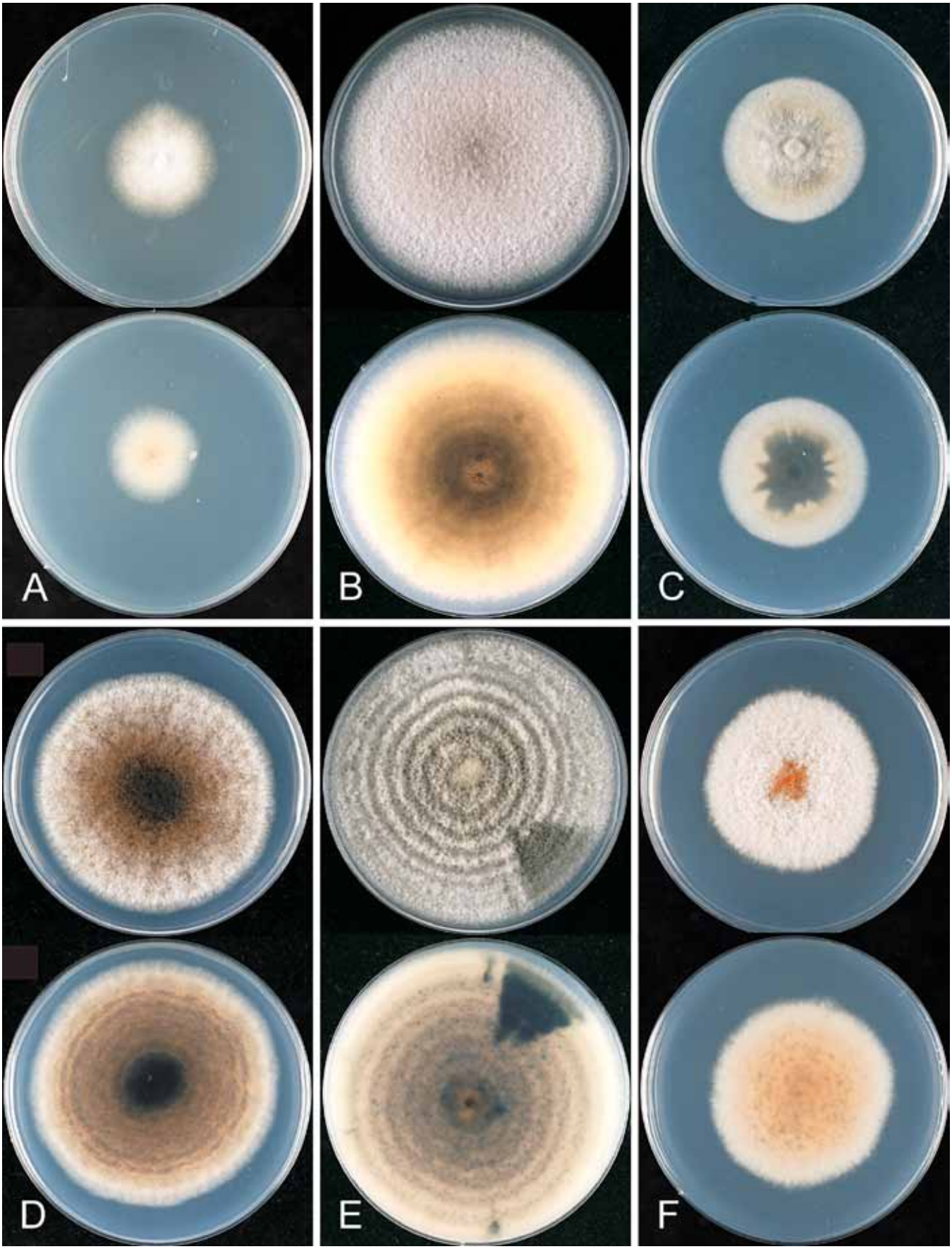


Fig. 34. *Colletotrichum theobromicola*. A. ICMP 17957 (ex MUCL 42294 – ex-holotype culture of *C. gloeosporioides* f. *stylosanthis*). B. ICMP 17927 (ex CBS 142.31 – ex-epitype culture of *C. fragariae*). C. ICMP 17958 (ex MUCL 42295). D. ICMP 17895. E. ICMP 18567. F. ICMP 18566. Cultures on PDA, 10 d growth from single conidia, from above and below.

to specific hosts. See also notes under *C. fragariae* and *C. gloeosporioides* f. *stylosanthis.*

Munaut *et al.* (2002) distinguished *C. gloeosporioides* f. *stylosanthis* from isolates they considered to represent *C.*

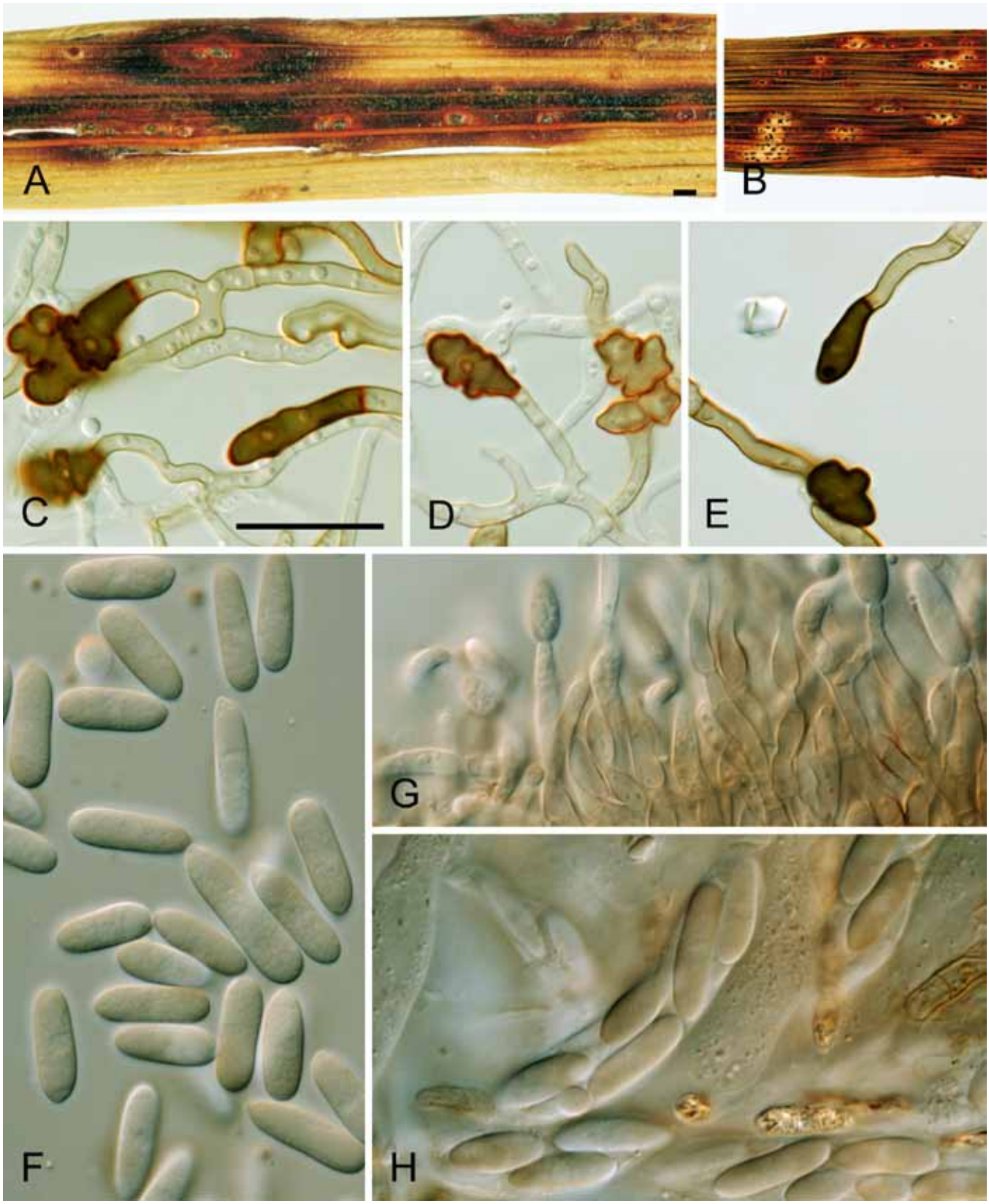


Fig. 35. *Colletotrichum ti*. A. PDD 24881 – holotype. B. PDD 30206. C, D, F, H. ICMP 4832 – ex-holotype culture. E, G. ICMP 19444. A–B. Lesions on dried herbarium specimens. C–E. Appressoria. F. Conidia. G. Conidiogenous cells. H. Ascospores. Scale bars A = 1 mm, C = 20 µm. Scale bar of A applies to A–B, scale bar of C applies to C–H.

gloeosporioides f. *gloeosporioides* because of 2 additional C's at positions 93 and 94 in the ITS1 region, giving a string of 7 C's at this position. This characteristic feature of the ITS-1 is found also in the ex-neotype isolate of *C. theobromicola*, the ex-epitype isolate of *C. fragariae* and all other isolates of *C. theobromicola*, although a few isolates have 3 additional C's rather than 2. None of the other isolates that we sampled from the *C. gloeosporioides* species complex have this characteristic string of C's.

Rojas *et al.* (2010) provide a description for their concept of *C. theobromicola*, MacKenzie *et al.* (2008) for *C. fragariae*, and Irwin & Cameron (1978) for C. *gloeosporioides* f. *stylosanthis* "f. sp. *stylosanthis*" (as *C. gloeosporioides* Type A) and *C. gloeosporioides*

f. *stylosanthis* "f. sp. *guianensis*" (as *C. gloeosporioides* Type B). In cultural appearance the isolates we accept in this species are variable, from the very dark ex-neotype isolate of *C. theobromicola* to the slow-growing, pale coloured *C. gloeosporioides* f. *stylosanthis* "f. sp. *guianensis*". None of the isolates that we examined formed perithecia in culture. All had conidia tapering slightly towards each end, this more pronounced towards the base, matching the description of *C. fragariae* by Gunnell & Gubler (1992), who regarded the conidial shape as distinctive for the species. Some of the isolates studied by Gunnell & Gubler (1992) were included in the study of MacKenzie *et al.* (2008), their genetic concept of *C. fragariae* matching ours.

See also notes under *C. fragariae* and *C. gloeosporioides* f. *stylosanthis*.

Specimens examined: **Australia**, Queensland, Townsville, on *Stylosanthes viscosa*, coll. J.A.G. Irwin 21365 (HM335), 1976 (**ex-holotype** culture of *C. gloeosporioides* f. *stylosanthis* − MUCL 42294 = ICMP 17957); Samford, on *Stylosanthes guianensis*, coll. J.A.G. Irwin 21398 (HM336), 1979 (MUCL 42295 = ICMP 17958); New South Wales, *Olea europaea* fruit, coll. V. Sergeeva UWS 128, 21 Apr. 2008 (ICMP 18566); New South Wales, *O. europaea* fruit, coll. V. Sergeeva UWS 130, 21 Apr. 2008 (ICMP 18565); New South Wales, *O. europaea* fruit, coll. V. Sergeeva UWS 98, 8 Apr. 2008 (ICMP 18567). **Israel**, on *Limonium* sp. leaf lesion, coll. S. Freeman P1 (cited in Maymon *et al.* 2006) (ICMP 18576). **Mexico**, on *Annona diversifolia*, coll. R. Villanueva-Aroe Gro-7, Jul. 2003 (ICMP 17895). **New Zealand**, Kerikeri, on *Acca sellowiana*, coll. M.A. Manning MM317, 1 Feb. 2004 (ICMP 15445). **Panama**, Chiriqui Province, San Vicente, on *Theobroma cacao* pod lesion, coll. E.J. Rojas ER08-9, Jan. 2008 (CBS 125393 = ICMP 18650); Chiriqui Province, Escobal, on *T. cacao* leaf spot, coll. E.J. Rojas GJS 08-50, Jan. 2008 (**ex-neotype culture** of *C. theobromicola* − CBS 124945 = ICMP 18649). **USA**, Florida, Dover, Plant City, on *Fragaria* × *ananassa*, coll. S. MacKenzie 326-1, 1988 (ICMP 17099); Florida, Lake Alfred, on *Quercus* sp. leaf, coll. S. MacKenzie LA-oak-13, 2002 (ICMP 17100); Louisiana, on *F. vesca*, 1985 (IMI 348152 = ICMP 17814); Florida, on *F.* × *ananassa*, coll. A.N. Brooks, 1931 (**ex-epitype culture** of *C. fragariae* − CBS 142.31 = ICMP 17927).

*** *Colletotrichum ti*** B. Weir & P.R. Johnst., **sp. nov.** MycoBank MB563594. Figs 35, 36.

Etymology: Based on the Maori name for *Cordyline australis*, tī.

Holotype: **New Zealand**, Taupo, on *Cordyline* sp., coll. J.M. Dingley 65187, Sep. 1965, PDD 24881; ex-holotype culture ICMP 4832.

Leaf spots oblong to elliptic in shape, up to about 1 × 2 mm, sometimes coalescing when close together on a leaf, pale grey and necrotic in the centre with a reddish margin; acervuli numerous, base pale to dark grey, with scattered, dark brown setae about 50–80 µm long. *Perithecia* not seen on infected leaves. Freshly isolated colonies on Difco PDA 50–55 mm diam after 10 d, margin slightly irregular and feathery, aerial mycelium lacking from ex-holotype culture, when present fine, cottony, pale grey, surface of colony dark towards the centre, pale pinkish orange (7A6) towards margin, conidia forming over all parts of culture, mostly not associated with well differentiated acervuli, setae not observed; in reverse purple (12E3) near centre, orange outside, sometimes with concentric rings of grey pigment. *Conidiogenous cells* cylindric, mostly 15–25 × 3.5–4.5 µm, towards centre of colony arranged in closely packed palisade, towards margin the conidiophores with a much looser structure, irregularly branched, conidiogenous loci at apex and often also at septa. *Conidia* (11.5–)14–17.5(–23.5) × (4–)5–5.5(–7.5) µm (av. 16 × 5.2 µm, n = 53), cylindric, ends broadly rounded, sometimes tapering towards basal end. *Appressoria* often narrow-cylindric, often tapering towards apex, sometimes irregularly lobed. *Perithecia* developing in small numbers in culture after about 4 wk, solitary, scattered across plate, dark-walled, globose with well-developed, tapering ostiolar neck. *Asci* (60–)65–75(–78) × (10–) 11(–12) µm (av. 69.6 × 11 µm, n = 5), cylindric to subfusoid, 8–spored. *Ascospores* (14.5–)15.5–16.5(–19) × (4.5–)5–5.5(–6) µm (av. 15.9 × 5.2 µm, n=18), broad-cylindric, ends broadly rounded, not tapering to the ends, in side view mostly flat on one side, often slightly curved.

Geographic distribution and host range: Known only from *Cordyline* spp. from New Zealand.

Genetic identification: ITS sequences do not distinguish *C. ti* from *C. aotearoa*. The two species can be distinguished using TUB2 or GAPDH.

Notes: A member of the Kahawae clade, this fungus causes a leaf spot of *Cordyline* spp. in New Zealand. It is genetically distinct from *C. cordylinicola*, described from *Cordyline fruticosa* from Thailand. Based on the published description of *C. cordylinicola* (Phoulivong *et al.* 2011) the two fungi are morphologically similar. Inoculation tests using culture ICMP 5285 when freshly isolated (J.M. Dingley, unpublished data), showed it to be pathogenic to *Cordyline australis*, forming spots on leaves 2 wk after inoculation, but causing no symptoms on apple, even after wounding.

Although only four of the specimens examined have been compared genetically, all of the cited specimens examined match in terms of associated symptoms and conidial size and shape. A specimen from *Cordyline banksii* (PDD 78360) has narrower conidia, forms perithecia on the infected leaves, and perhaps represents a different species. Specimens accepted here as *C. ti* were referred to *Glomerella cingulata* by Laundon (1972).

The appearance in culture varies between isolates. The J.M. Dingley cultures, first isolated in the mid-1960's, have dense, felted aerial mycelium and limited conidial production; one has a much slower growth rate than the more recent collections.

Other specimens examined: **New Zealand**, Auckland, on *Cordyline australis*, coll. J.M. Dingley 6653, Mar. 1966 (PDD 30206; ICMP 5285); Taranaki, New Plymouth, Duncan and Davies Nursery, on *C. australis* × *C. banksii* leaf spots, coll. G.F. Laundon LEV 3343, 26 May 1969 (PDD 50634); Taranaki, New Plymouth, Duncan and Davies Nursery, on *C australis* × *C. banksii* leaf spots, coll. G.F. Laundon, 26 May 1969 (PDD 26775); Waikato, Cambridge, Anton Nursery, on *C. australis* leaf spots, coll. L.A. Houghton, 23 Jul. 1992 (PDD 61219; ICMP 19444).

*** *Colletotrichum tropicale*** E.I. Rojas, S.A. Rehner & Samuels, Mycologia 102: 1331. 2010. Fig. 37.

Rojas *et al.* (2010) provide a description.

Geographic distribution and host range: Rojas *et al.* (2010) noted that *C. tropicale* has been isolated from a wide range of hosts in forests in tropical America, from rotting fruit as well as leaf endophytes. We include also an isolate from tropical Japan, from *Litchi chinensis* leaves.

Genetic identification: ITS sequences do not separate *C. tropicale* from some *C. siamense* or some *C. queenslandicum* isolates. *Colletotrichum tropicale* is best distinguished using TUB2, CHS-1, GS, or SOD2.

Notes: *Colletotrichum tropicale* is genetically close to *C. siamense* and the two species share a number of morphological features; slow growth in culture, short and broad conidia with broadly rounded ends and often slightly constricted near the centre, and simple appressoria.

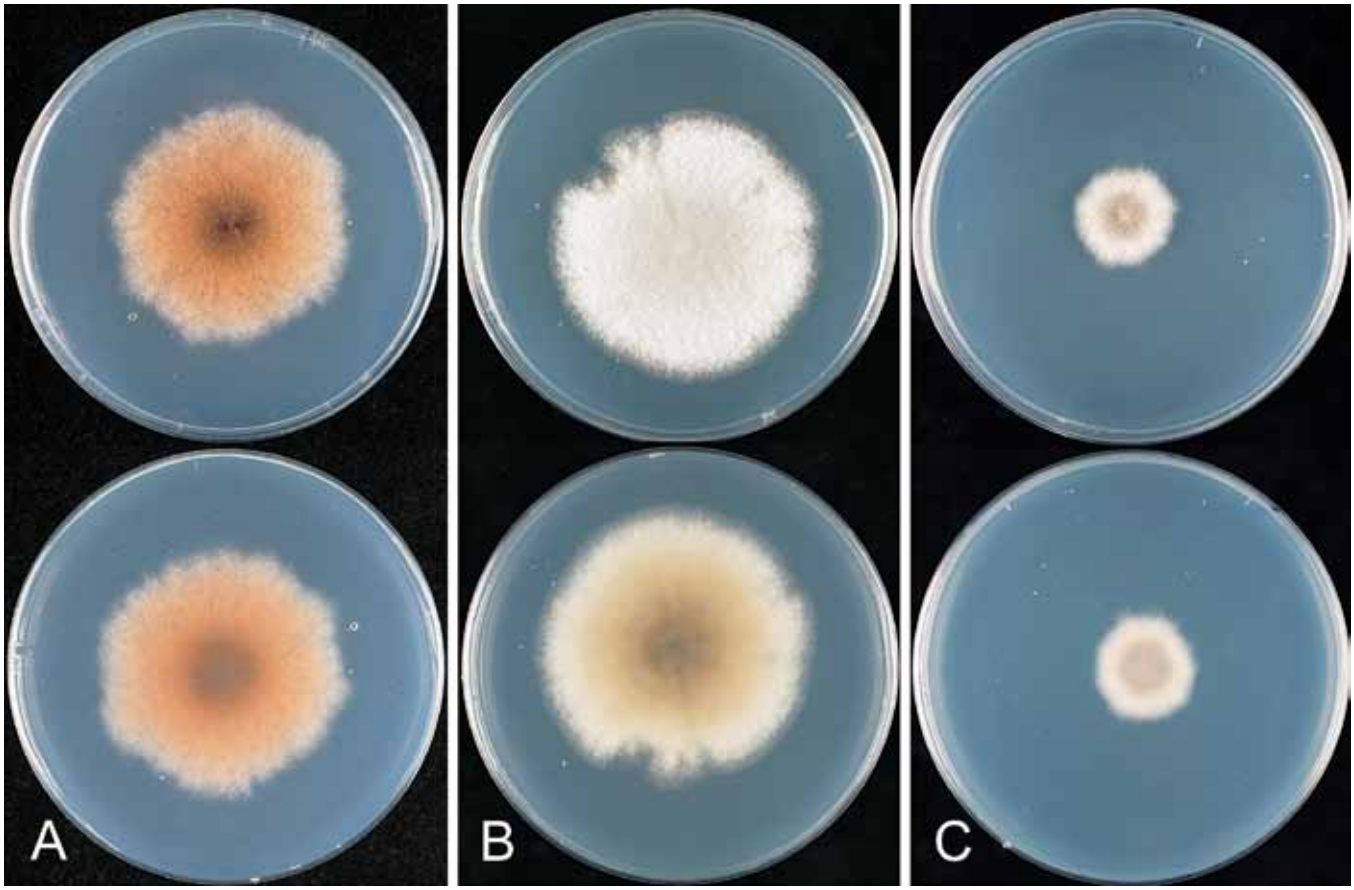


Fig. 36. *Colletotrichum ti*. A. ICMP 19444. B. ICMP 4832 – ex-holotype culture. C. ICMP 5285. Cultures on PDA, 10 d growth from single conidia, from above and below.

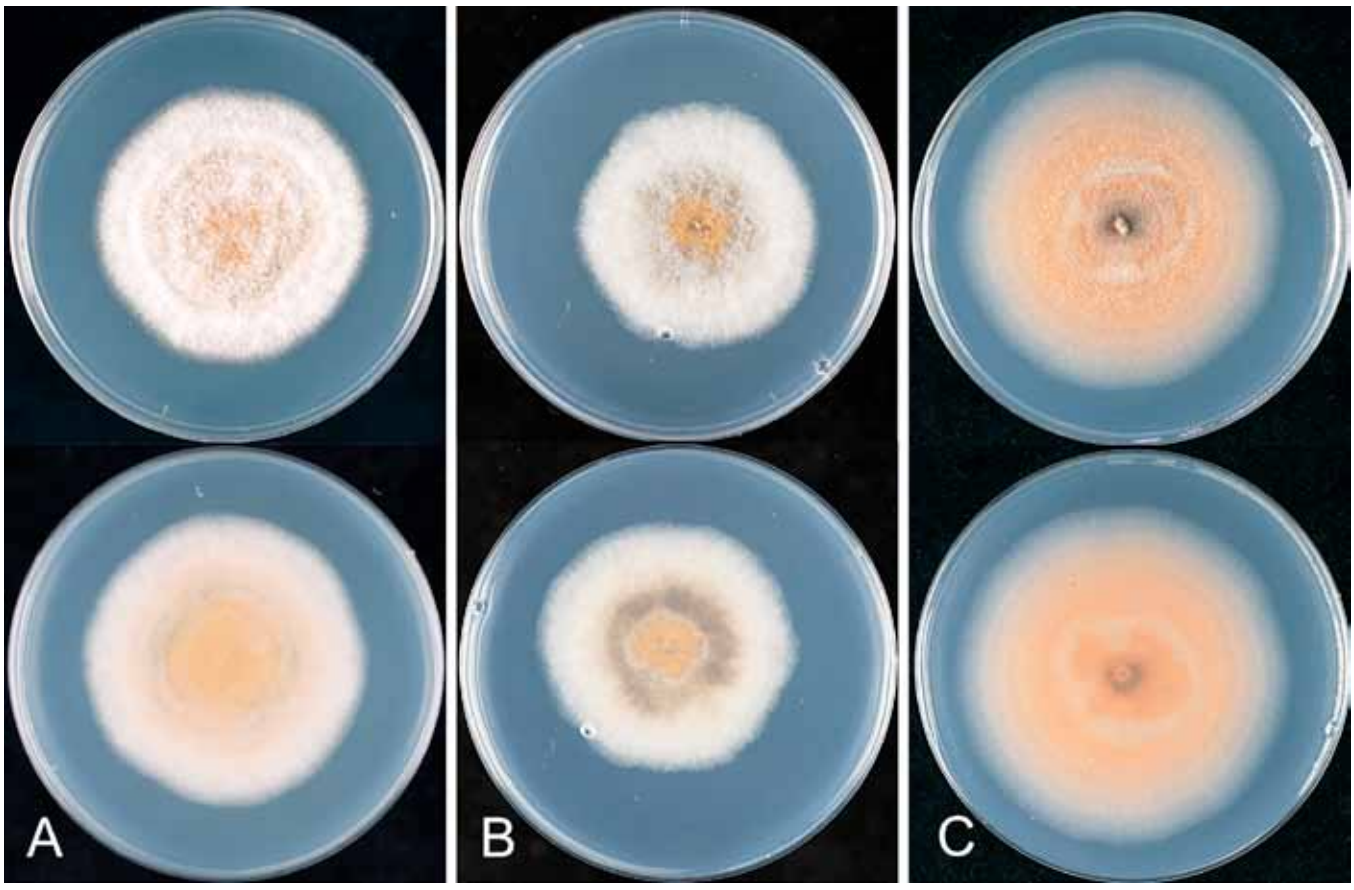


Fig. 37. *Colletotrichum tropicale*. A. ICMP 18653 (ex CBS 124949 – ex-holotype culture). B. ICMP 18651 (ex CBS 124943). C. ICMP 18672 (ex MAFF 239933). Cultures on PDA, 10 d growth from single conidia, from above and below.

Specimens examined: **Japan**, Okinawa, on *Litchi chinensis* leaf (MAFF 239933 = ICMP 18672). **Panama**, Barro Colardo Monument, on *Theobroma cacao* leaf, coll. E.I. Rojas, L.C. Mejía, Z. Maynard 5101, 2008 (**ex-holotype culture** – CBS 124949 = ICMP 18653); Escobal, Chiriqui, on *Annona muricata* fruit rot, coll. E.I. Rojas GJS 08-42 (CBS 124943 = ICMP 18651).

*** *Colletotrichum xanthorrhoeae*** R.G. Shivas, Bathgate & Podger, Mycol. Res. 102: 280. 1998. Fig. 38.

Shivas *et al.* (1998) provide a description. One of the isolates we examined (ICMP 17820) formed fertile perithecia in culture, a feature not mentioned in the original description. *Perithecia* are dark-walled, globose with a prominent, narrow neck, wall comprising several layers of pseudoparenchymatous cells 8–15 µm diam, with several layers of densely packed hyphae outside this. *Asci* 75–100 × 10–12 µm, 8-spored. *Ascospores* (17–)18.5–20(–22) × (5–)5.5–6 µm (av. 19.4 × 5.6 µm, n = 24), more or less elliptic, tapering to narrow, rounded ends, in side view flattened on one side, but generally not curved.

Genetic identification: ITS sequences distinguish *C. xanthorrhoeae* from all other species.

Notes: This pathogen of *Xanthorrhoea* has a distinctive morphology, with a very slow growth rate in culture and large conidia which taper towards the basal end. The ascospore shape is distinct to that of most taxa within the *C. gloeosporioides* group, which typically have bent or curved ascospores.

Specimens examined: **Australia**, Western Australia, Melville, on *Xanthorrhoea preissii* leaf spots, coll. F.D. Podger, Jan. 1994 (**ex-holotype culture** − BRIP 45094 = ICMP 17903 = CBS 127831); Queensland, Cunningham's Gap, Main Ranges National Park, on *Xanthorrhoea* sp. leaf spot (IMI 350817a = ICMP 17820).

DISCUSSION

The species that we accept in the *Colletotrichum gloeosporioides* species complex together form a strongly supported clade in the *Colletotrichum* ITS gene tree (fig. 1 in Cannon *et al.* 2012, this issue). All species are micro-morphologically typical of *C. gloeosporioides sensu* von Arx (1970) and Sutton (1992). However, morphology alone cannot unequivocally place an isolate in this complex, making the ITS particularly important for identification at the species complex level in *Colletotrichum*. For example, members of the *C. boninense* species complex (Damm *et al.* 2012b, this issue) and *C. cliviae* (Yang *et al.* 2009) are micro-morphologically similar to species in the *C. gloeosporioides* complex but genetically distinct (Cannon *et al.* 2012, this issue). The utility of ITS sequences is enhanced by their strong representation in GenBank, but this can also be a problem. Nilsson *et al.* (2006) summarised the frequency of inaccurately annotated data in GenBank. The diversity of taxonomic concepts around the name *C. gloeosporioides* makes this a particular problem. This is illustrated by the phylogeny presented by Hyde *et al.* (2010), based on GenBank accessions of ITS sequences identified as *C. gloeosporioides* and *Glomerella cingulata*, that shows the taxa represented belong to many species in different *Colletotrichum* species complexes. See notes under *C. boehmeriae*, *C. crassipes*, and *C. kahawae* subsp. *kahawae* for specific examples of misidentified GenBank accessions.

The species we accept are based on a phylogenetic species concept, all species forming strongly supported, monophyletic clades within our multigene phylogenies. However, not all terminal clades are recognised as named species. In most cases any well supported, within-species phylogenetic structure evident in the multi-gene phylogeny is not resolved consistently in all gene trees. This lack of congruence between gene trees is a signal that the diversity being sampled is below the species level, according to the logic of the genealogical concordance phylogenetic species recognition (GCPSR) concept (Taylor *et al*. 2000). Although the concatenation of gene sequences is a convenient way to present multigene data, it masks discordance between individual gene phylogenies. An alternative method, using a species-tree approach (Figs 3, 4B, 5B) combines multi-gene data from multiple isolates hypothesised to represent a single species, so that the evolutionary history of the species rather than that of individual isolates is estimated. Fig. 3, shows the results of such an analysis for the *C. gloeosporioides* complex, Figs 4B and 5B show relationships within the Musae and Kahawae clades respectively, at an expanded scale. Posterior probabilities for some of the speciation events are low, particularly within the Musae and Kahawae clades. This may be because although the species-trees algorithms account for incomplete lineage sorting (Heled & Drummond 2010, Chung & Ané 2011), most do not compensate for horizontal gene transfer, reassortment, or introgression. Hybridisation could also result in discordant gene phylogenies. Hybrids are known in the *C. acutatum* complex, *e.g. Glomerella acutata*, a hybrid formed by crossing *C. acutatum* and *C. fioriniae* strains in the laboratory, and a putative hybrid strain between the same two species that had been collected from terminal crook disease on *Pinus* in New Zealand, where both species occur in nature (Damm *et al*. 2012a, this issue). Hybrids also form in the *C. gloeosporioides* complex, *e.g.* the *Carya* and *Aeschynomene* populations discussed by Cisar *et al.* (1994), more or less genetically equivalent to our species within the *C. gloeosporioides* complex.

Our taxonomic conclusions are based, of necessity, on the limited set of genes sampled. Potentially more powerful genes, such as ApMAT and Apn25L (Silva *et al*. 2012a) may provide finer resolution within the species-level clades that we recognise. However, even with these potentially more informative genes, the low levels of genetic divergence across the *C. gloeosporioides* complex may always provide a technical challenge (Silva *et al*. 2012a). The low level of diversity within this species complex is reflected by the branch lengths in fig. 2, Cannon *et al*. (2012, this volume), and is especially true across the Musae clade, where average pairwise identity between all isolates treated in our 5 gene alignment is 98.6 %. Pairwise identity between isolates of *C. siamense* and *C. theobromicola*, two species showing strong within-species phylogenetic structure, are 99.4 % and 99.6% respectively. This suggests that the species recognised within the *C. gloeosporioides* complex are very recently evolved and Silva *et al*. (2012b) provide data supporting this. Their hypothesis of recent evolution of host-specialised *Colletotrichum* populations from more generalist fungi was also invoked in relation to the *C. acutatum* complex by Lardner *et al*. (1999) using the "episodic selection" framework of Brasier (1995).

Several of the species we accept contain isolates with divergent lifestyles, for example *C. aotearoa*, *C. clidemiae*, *C. kahawae*, and *C. theobromicola*. Each of these species includes isolates capable of causing specific diseases. In the case of *C. kahawae*, recent pathogenicity tests have shown that only some isolates are able to cause coffee berry disease (Silva *et al.* 2012a, Silva & Weir, unpubl. data) and that these isolates can be distinguished using GS sequences (this study), Apn25L and MAT1-2-1 (Silva *et al*. 2012b). Because of the well understood pathogenicity of isolates within

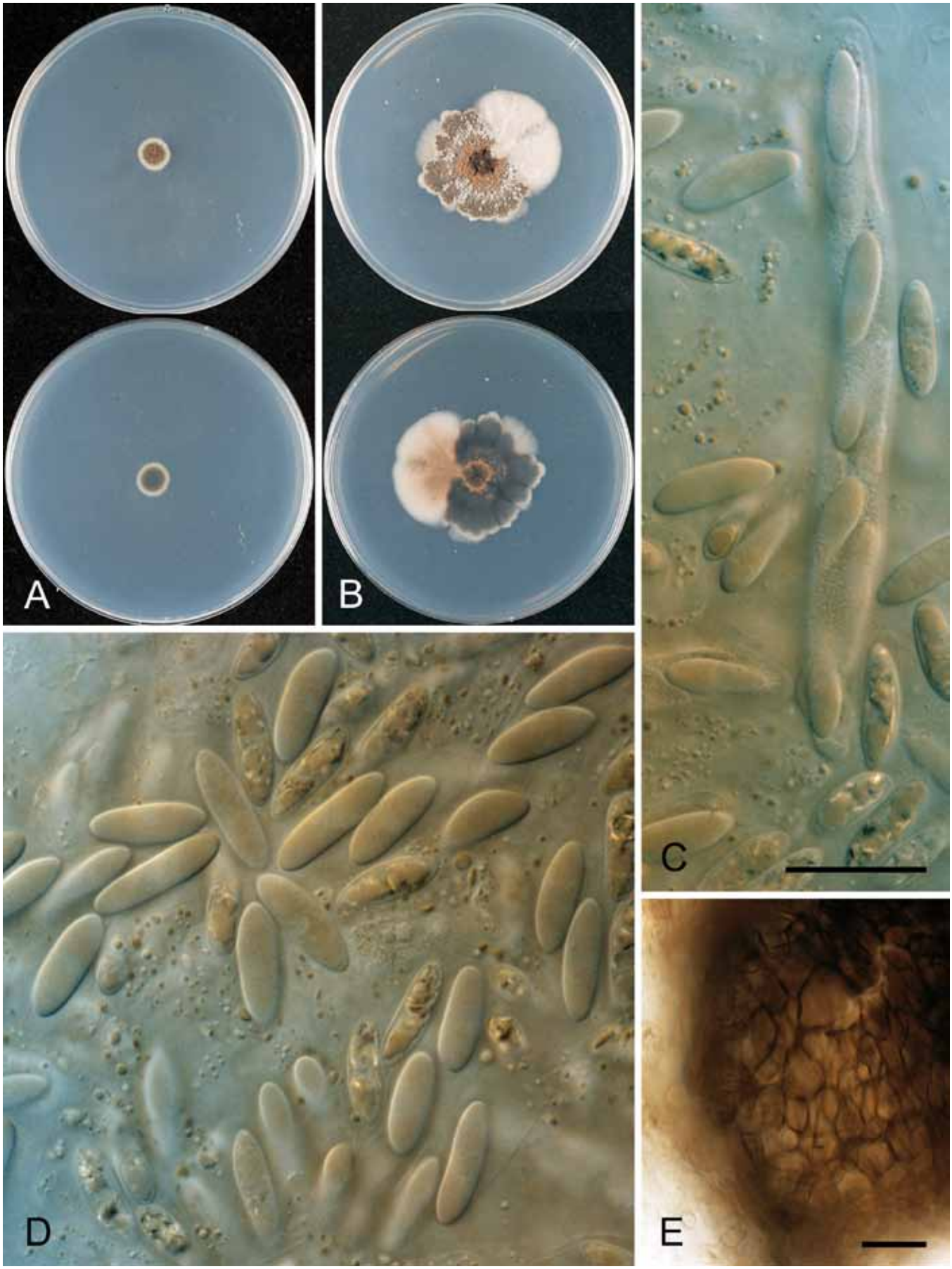


Fig. 38. *Colletotrichum xanthorrhoeae*. ICMP 17903 (ex BRIP 45094 – ex-holotype culture). A. Cultures on PDA, 10 d growth from single conidia, from above and below. B. Culture on PDA at 4 wk showing sectoring with variation in pigmentation and growth form. C–D. Asci and ascospores. E. Perithecial wall in squash mount. Scale bar C = 20 µm. Scale bar of C applies to C–E.

C. kahawae, the biosecurity importance of coffee berry disease, and the ability to distinguish the disease-causing isolates using carefully selected genetic markers, we recognise the disease-causing isolates taxonomically at the subspecific level. Future study of the comparative pathogenicity of isolates within *C. aotearoa*, *C. clidemiae*, and *C. theobromicola* may reveal genetically distinct, host-specialised pathogenic populations within these species that future workers may also choose to recognise taxonomically.

The classification we accept here is deliberately taxonomically conservative, minimising nomenclatural changes. This reflects continuing uncertainty about sensible species limits within the *C. gloeosporioides* complex that relate to low levels of genetic divergence across the complex, gene selection, isolate selection, and a lack of understanding of the mechanisms driving species and population divergence amongst these fungi. For example, the two haplotype subgroups of *C. fructicola* are not distinguished taxonomically because collectively they form a monophyletic clade, both subgroups include sets of isolates with similar geographic and host diversity, and there is no practical need to distinguish them taxonomically.

Molecular tools are increasingly being used for day-to-day identification by biosecurity officers and plant pathology researchers, providing a need for both a taxonomy that closely reflects groups that are resolved genetically, as well as simple and reliable protocols for identifying those taxa. The internal transcribed spacer region (ITS) has been proposed as the official fungal barcoding gene (Schoch *et al.* 2012). Although ITS is useful at the species complex level, it does a poor job of resolving species within the *C. gloeosporioides* complex, resolving only 10 of 22 accepted species. This reflects the low number of base changes in the ITS region across the *C. gloeosporioides* complex; species often distinguished by only one or two base changes. In some cases, chance variation in the ITS sequence within or between species means that some species cannot be distinguished (Fig. 6). Examples of taxa with identical ITS sequences include *C. clidemiae, C. tropicale*, *C. ti* and some *C. siamense* isolates; *C. fructicola* and some *C. siamense* isolates; and *C. alienum*, *C. aenigma* and some *C. siamense* isolates.

Protein-coding genes and their introns often have more variation than ITS, and the need for secondary barcodes based on these kinds of genes has been discussed in relation to some groups of fungi (Fitzpatrick *et al*. 2006, Aguileta *et al*. 2008, Weir & Johnston 2011). Ideally, one of the seven protein coding genes that were used in this study could be proposed as a secondary barcode to obtain an accurate identification of species within the *C. gloeosporioides* complex. A preliminary analysis of the genes performance as barcodes was conducted as part of Cai *et al*. (2009) with GAPDH, CAL, and ACT performing well, but CHS-1, ITS, and TEF (EF1α) poorly. However, the analysis (Cai *et al*. 2009) included only five species within the *C. gloeosporioides* complex, the Musae and Kahawae clades being treated at the level of species. With the final classification presented here, none of the genes we analysed provides an effective barcode ont its own across the entire complex. Of the single genes, TUB2, GS, and GAPDH are amongst the most effective at distinguishing species. However, *C. clidemiae* is polyphyletic in the TUB2 gene tree and GS sequences are needed to distinguish *C. fructicola* and *C. alienum*. With GS, *C. aotearoa*, *C. kahawae* subsp. *ciggaro*, and *C. siamense* are paraphyletic. GAPDH is the easiest of all the genes tested to amplify and sequence, however when using this gene GS sequences are needed to distinguish *C. fructicola* from *C. alienum* and *C. aeschynomenes* from *C. siamense*, and *C. tropicale* is paraphyletic. In the species descriptions we provide notes on which genes are the best for genetic identifications, and in Table 4 these are summarised for all species and genes. For species represented by a single or only a few isolates the species boundaries may not be accurate, we recommend two protein-coding genes in addition to ITS for sequence-based identifications. A meta-analysis of DNA barcodes across the whole genus will be required to find the combination of genes that are effective for all species of the genus that distinguish all *Colletotrichum* species.

Several studies have shown that cultural morphology can be useful for grouping isolates when they are sampled at a local or regional level (*e.g.* Johnston & Jones 1997, Prihastuti *et al.* 2009). However, our experience is that such groups often break down when the geographic sample within a clade is extended to a global scale. Many of the species we accept have few or no diagnostic morphological or cultural features that can be consistently and reliably used to identify them. Our morphological examinations were confined to cultures on Difco PDA agar plates, and we will have missed any features that develop solely in association with plant material. In addition, the cultures we used have been sourced from different labs and collections from around the world, many with no information on storage history. Storage history and method has a major impact on the appearance of *Colletotrichum* in culture. Cultures can become "stale" during storage, losing the ability to produce pigments, the aerial mycelium often becoming very dense and felted, and losing the ability to form well-differentiated acervuli, conidia, or perithecia. In some clades, even freshly isolated cultures are highly variable, forming distinct sectors with differences in the production of pigment, aerial mycelium, acervuli, and conidia. Some isolates form two very different cultural types from single conidia or ascospores derived from colonies themselves started from single ascospores. Figure 27F shows single ascospore cultures from an isolate of *C. kahawae* subsp. *ciggaro*. One has the typical appearance of cultures of this fungus isolated from the field. The other, with a uniform, dense layer of conidia across the colony surface without well differentiated acervuli and more or less no aerial mycelium, is common from single ascospore isolates in culture, but rarely found in cultures isolated directly from the field. This kind of variation, and that revealed from sectoring during colony growth, makes morphological variation difficult to interpret for accurate identification.

Many of the species recognised in this work remain poorly understood in terms of their pathogenicity and host preference. This in part reflects a lack of certainty about the biological relationship between the fungi and the plants from which they were isolated. Species that are pathogenic on one host can also be isolated from others following opportunistic colonisation of senescing tissue, such as the *C. salicis* example discussed by Johnston (2000, as *Glomerella miyabeana*). The multiple *Colletotrichum* spp. associated with a single host are likely to have a variety of life styles: primary pathogens of healthy tissue, species with the ability to invade and cause minor disease when the host plant is under stress, species that develop latent infections and fruit only following senescence of the host tissue or ripening of host fruit and endophytic species that sporulate only following host tissue death. The combination of this range of distinct life styles, the fact that several *Colletotrichum* spp. may become established on a single host, and the ability of most of these species to also establish on a range of other hosts, has been a large part of the confusion surrounding species limits within *Colletotrichum*.

In some cases, apparently clear differences in pathogenicity of isolates in the *C. gloeosporioides* complex are not reflected

Table 4. Performance of individual genes at resolving species within the *Colletotrichum gloeosporioides* species complex. Y – species distinguished from all others. N – species not distinguished from all others. N* – distinguishes at the subspecies level.

Species	ITS	GAPDH	CAL	TUB2	ACT	CHS-1	GS	SOD
C. fructicola	N	N	Y	N	N	Y	Y	Y
C. nupharicola	N	Y	Y	Y	Y	Y	Y	Y
C. alienum	N	N	Y	N	N	Y	Y	Y
C. musae	Y	Y	Y	Y	Y	Y	Y	Y
C. aenigma	N	Y	Y	Y	N	Y	Y	Y
C. siamense	N	N	Y	Y	N	N	N	N
C. aeschynomenes	N	N	N	Y	N	Y	Y	Y
C. tropicale	N	N	N	Y	Y	N	Y	Y
C. queenslandicum	N	Y	Y	Y	N	N	Y	N
C. salsolae	N	Y	Y	Y	Y	Y	N	Y
C. asianum	Y	Y	Y	Y	Y	Y	Y	Y
C. gloeosporioides	Y	Y	Y	Y	Y	Y	Y	Y
C. alatae	Y	Y	Y	Y	Y	Y	Y	Y
C. theobromicola	Y	Y	Y	Y	Y	Y	Y	Y
C. xanthorrhoeae	Y	Y	Y	Y	Y	Y	Y	Y
C. horii	Y	Y	Y	Y	Y	Y	Y	Y
C. aotearoa	N	N	Y	Y	N	Y	Y	N
C. ti	N	Y	Y	Y	N	Y	Y	Y
C. kahawae	N	Y	N	Y	Y	N	N*	N
G. cingulata "f. sp. *camelliae*"	Y	N	Y	Y	Y	N	Y	Y
C. clidemiae	N	N	N	N	Y	Y	Y	N
C. psidii	Y	Y	Y	Y	N	Y	Y	Y
C. cordylinicola	Y	Y	Y	Y	N	Y	Y	Y

genetically. For example, the fungi referred to as *C. gloeosporioides* f. *stylosanthis* "f. sp. *guianensis*" and *C. gloeosporioides* f. *stylosanthis* "f. sp. *stylosanthis*", are reportedly associated with two distinct diseases of *Stylosanthes* (Irwin & Cameron 1978; Munaut *et al.* 2002), but both taxa genetically match *C. theobromicola* and are here placed in synonymy with *C. theobromicola*. It is possible that screening additional genes across a set of isolates from *Stylosanthes* with known pathogenicity will reveal one or more genes that generate a phylogeny that correlates with pathogenicity. This is the case with another specialised pathogen, *C. kahawae*. Originally described as a pathogen of green coffee berries, almost genetically identical isolates have subsequently been found on a wide range of hosts (see notes under *C. kahawae*). The isolates from other hosts are not pathogenic to coffee berries (Silva *et al.* 2012b). The difference in pathogenicity correlates with a genetic difference in the GS gene, and we taxonomically recognise this biologically specialised population at the subspecies level. A similar approach could potentially be taken for other biologically distinct populations within a genetically strongly supported species.

Despite the epitypification of *C. gloeosporioides* in 2008, web search hits on the name *C. gloeosporioides* from papers published over the past 12 mo show that many authors will continue to use the name in the sense of the *C. gloeosporioides* species complex, presumably regarding this level of identification as sufficient for their research. All of the isolates that we accept in the *C. gloeosporioides* complex share the string 5'–GGGCGGGT–3' about 139–142 bases after the ITS1F primer binding site. Based on a comparison with GenBank data, this string appears to be specific to isolates that we would accept as members of the *C. gloeosporioides* complex.

Several authors have developed PCR-based, rapid identification tools for distinguishing members of the *C. gloeosporioides* complex from members of the *C. acutatum* species complex. This has been prompted because some members of the *C. acutatum* complex have conidia without the acute ends characteristic of this species as described by Simmonds (1965), and have at times been confused with *C. gloeosporioides* (Damm *et al.* 2012, this issue). Primers reportedly specific to *C. gloeosporioides* include the CgInt primer for ITS (Mills *et al.* 1992). In our data set this primer sequence is found in *C. gloeosporioides s. str.*, *C. fructicola*, and *C. siamense* but all of the other taxa that we recognise within the *C. gloeosporioides* complex have one or more bases not matching the CgInt primer. The practical impact of these differences will depend in part on the position of the mismatch and stringency of the PCR reaction. Talhinas *et al.* (2005) discussed the TBCG primer for β-tubulin, and this is found within all of our taxa within the *C. gloeosporioides* group except *C. musae* and *C. asianum*. Liu *et al.* (2011) describe characteristic RFLP bands from glutamine synthetase using the restriction enzyme Pst1. Based on our sequences, this method will generate the characteristic *C. gloeosporioides* bands reported by Liu *et al.* (2011) for *C. aenigma*, *C. alienum*, *C. aotearoa*, *C. asianum*, *C. clidemiae*, *C. cordylinicola*, *C. fructicola*, *C. gloeosporioides s. str.*, *C. horii*, *C. queenslandicum*, *C. salsolae*, *C. siamense*, *C. ti*, and *C. tropicale*. Different banding patterns will be produced by *C. aeschynomenes* (band sizes 253, 316, 388), the two *C. kahawae* subspp. (band sizes 112, 388, 457), *G. cingulata* "f. sp. *camelliae*" (band sizes 51, 112, 337, 457), and *C. musae* (band sizes 388, 552), but none match the bands reported for *C. acutatum* by these authors.

Comparison of our data with gene sequences reported as *C. gloeosporioides* in recent papers allows most to be placed with confidence in one of the species that we accept. There are exceptions, such as the pecan-associated isolates from Liu *et al.* (2011), and the pistachio-associated isolates reported by Yang *et al.* (2011), both of which appear to represent undescribed species within the *C. gloeosporioides* complex. Clearly, more species remain to be described within the *C. gloeosporioides* complex. In addition, taxonomic issues still to be resolved amongst the species discussed in this paper include the relationship between *G. cingulata* "f. sp. *camelliae*" and *C. camelliae*, the identity of the cotton pathogens referred to *C. gossypii*, the identity of the cassava pathogens referred to *C. manihotis*, the relationship between *C. aeschynomenes* and *C. gloeosporioides* "f. sp. *jussiaeae*", whether the various yam diseases discussed in the literature are all caused by *C. alatae*, and whether the isolates of *C. aotearoa* from *Meryta* leaf spots form a biologically distinct population. A more general question relates to better understanding the frequency of hybrids within the *C. gloeosporioides* complex and the impact of this on the interpretation of the phylogenies within the complex. The impact of hybridisation on the evolution of disease specialised populations has barely been explored.

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REFERENCES

Aa HA van der (1978). A leaf spot of *Nymphaea alba* in the Netherlands. *Netherlands Journal of Plant Pathology* **84**: 109–115.

Abang MM, Winter S, Green KR, Hoffmann P, Mignouna HD, Wolf GA (2002). Molecular identification of *Colletotrichum gloeosporioides* causing anthracnose of yam in Nigeria. *Plant Pathology* **51**: 63–71.

Abang MM, Winter S, Mignouna HD, Green KR, Asiedu R (2003). Molecular taxonomic, epidemiological and population genetic approaches to understanding yam anthracnose disease. *African Journal of Biotechnology* **2**: 486–496.

Afanador-Kafuri L, Minz D, Maymon M, Freeman S (2003). Characterisation of *Colletotrichum* isolates from tamarillo, passiflora, and mango in Colombia and identification of a unique species from the genus. *Phytopathology* **93**: 579–587.

Aguileta G, Marthey S, Chiapello H, Lebrun MH, Rodolphe F, *et al.* (2008). Assessing the Performance of Single-Copy Genes for Recovering Robust Phylogenies *Systematic Biology* **57**: 613–627.

Alahakoon PW, Brown AE, Sreenivasaprasad S (1994). Genetic characterisation of *Colletotrichum gloeosporioides* isolates obtained from mango. *International Journal of Pest Management* **40**: 225–229.

Alfieri Jr SA, Langdon KR, Wehlburg C, Kimbrough JW (1984). Index of Plant Diseases in Florida (Revised). *Florida Department of Agriculture and Consumer Services, Division of Plant Industries Bulletin* **11**: 1–389.

Archibald JK, Mort ME, Crawford DJ (2003). Bayesian inference of phylogeny: a non-technical primer. *Taxon* **52**: 187–191

Arx JA von (1957). Die Arten der Gattung *Colletotrichum* Cda. *Phytopathologische Zeitschrift* **29**: 413–468.

Arx JA von (1970). A revision of the fungi classified as *Gloeosporium*. *Bibliotheca Mycologica* **24**: 1–203.

Arx JA von, Müller E (1954). Die Gattung der amerosporen Pyrenomyceten. *Beiträge zur Kryptogamenflora der Schweiz* **11(1)**: 1–434.

Bailey JA, Nash C, Morgan LW, O'Connell RJ, TeBeest DO (1996). Molecular taxonomy of *Colletotrichum* species causing anthracnose on the *Malvaceae*. *Phytopathology* **86**: 1076–1083.

Beever RE (1984). Observations on puka (*Meryta sinclairii*) on the Chickens Islands, with an assessment of the hypothesis that it was transferred there by the Maori. *Tane* **30**: 77–92.

Berkeley MJ (1874). Notices of North American fungi. *Grevillea* **3**: 1–17.

Berner DK, Bruckart WL, Cavin CA, Michael JL, Carter ML, Luster DG (2009). Best linear unbiased prediction of host-range of the facultative parasite *Colletotrichum gloeosporioides* f. sp. *salsolae*, a potential biological control agent of Russian thistle. *Biological Control* **51**: 158–168.

Bogo A, Casa RT, Rufato L, Gonçalves MJ (2012). The effect of hail protection nets on *Glomerella* leaf spot in 'royal Gala' apple. *Crop Protection* **31**: 40–44

Boyette CD, Templeton GE, Smith JR (1979). Control of waterprimrose (*Jussiaea decurrens*) and northern jointvetch (*Aeschynomene virginica*) with fungal pathogens. *Weed Science* **27**: 497–501.

Brasier CM (1995). Episodic selection as a force in fungal microevolution, with special reference to clonal speciation and hybrid introgression. *Canadian Journal of Botany* **73** (Supplement 1): S1213–S1221.

Brooks AN (1931). Anthracnose of strawberry caused by *Colletotrichum fragariae* n. sp. *Phytopathology* **21**: 739–744.

Buddie AG, Martínez-Culebras P, Bridge PD, García MD, Querol A, *et al.* (1999). Molecular characterisation of *Colletotrichum* strains derived from strawberry. *Mycological Research* **103**: 385–394.

Cai L, Hyde KD, Taylor PWJ, Weir BS, Waller J, *et al.* (2009). A polyphasic approach for studying *Colletotrichum*. *Fungal Diversity* 39: 183–204.

Cannon PF, Buddie AG, Bridge PD (2008). The typification of *Colletotrichum gloeosporioides*. *Mycotaxon* **104**: 189–204.

Cannon PF, Damm U, Johnston PR, Weir BS (2012). *Colletotrichum* – current status and future directions. *Studies in Mycology* **73**: 181–213.

Carbone I, Kohn LM (1999). A method for designing primer sets for speciation studies in filamentous ascomycetes. *Mycologia* **91**: 553–556.

Carpenter JB, Stevenson JA (1954). A secondary leaf spot of the *Hevea* rubber tree caused by *Glomerella cingulata*. *Plant Disease Reporter* **38**: 494–499.

Castro RA, Mendes-Costa MC, Souza EA (2006). Dimorfismo de ascósporos em *Glomerella cingulata* f. sp. *phaseoli*. *Fitopatologia Brasileira* **31**: 598–600.

Chevaugeon J (1956). Les maladies cryptogamiques du manioc en Afrique Occidentale. *Encyclopédie Mycologique* **28**: 1–205.

Chung WS, Ishii H, Nishimura K, Fukaya M, Yano K, Kajitani Y (2006). Fungicide sensitivity and phylogenetic relationship of anthracnose fungi isolated from various fruit crops in Japan. *Plant Disease* **90**: 506–512.

Chung Y, Ané C (2011). Comparing Two Bayesian Methods for Gene Tree/Species Tree Reconstruction: Simulations with Incomplete Lineage Sorting and Horizontal Gene Transfer. *Systematic Biology* **60**: 261–275

Cisar CR, Spiegel FW, TeBeest DO, Trout C (1994). Evidence for mating between isolates of Colleto*trichum gloeosporioides* with different host specificities. *Current Genetics* **25**: 330–335.

Correll JC, Rhoads DD, Guerber JC (1993). Examination of mitochondrial DNA restriction fragment length polymophisms, DNA fingerprints, and randomly amplified polymorphic DNA of *Colletotrichum orbiculare*. *Phytopathology* **83**: 1199–1204.

Crouch JA, Clarke BB, Hillman BI (2006). Unravelling evolutionary relationships amongst divergent lineages of *Colletotrichum* causing anthracnose disease in turfgrass and corn. *Phytopathology* **96**: 46–60.

Crous PW, Gams W, Stalpers JA, Robert V, Stegehuis G (2004). MycoBank: an online initiative to launch mycology into the 21st century. *Studies in Mycology* **50**: 19–22.

Curzi M (1927). De novis Eumycetibus. *Atti dell'Istituto Botanico della Università e Laboratorio Crittogamico di Pavia* **3 (3)**: 203–208.

Damm U, Cannon PF, Woudenberg JHC, Crous PW (2012a). The *Colletotrichum acutatum* species complex. *Studies in Mycology* **73**: 37–113.

Damm U, Cannon PF, Woudenberg JHC, Johnston PR, Weir BS, *et al*. (2012b). The *Colletotrichum boninense* species complex. *Studies in Mycology* **73**: 1–36.

Daniel JT, Templeton GE, Smith RJ, Fox WT (1973). Biological control of northern jointvetch in rice with an endemic fungal disease. *Weed Science* **21**: 303–307.

Delacroix G (1903). De la tavelure goyaves produite par le *Gloeosporium psidii* nov. sp. G. Del. *Bulletin de la Société Mycologique de France* **19**: 143–145.

Deng Y, Zhang M, Luo H (2012). Identification and antimicrobial activity of two alkaloids from traditional Chinese medicinal plant *Tinospora capillipes*. *Industrial Crops and Products* **37**: 298–302.

Dickens JSW, Cook RTA (1989). *Glomerella cingulata* on *Camellia*. *Plant Pathology* **38**: 75–85.

Ditmore M, Moore JW, TeBeest DO (2008). Interactions of two selected field isolates of *Colletotrichum gloeosporioides* f. sp. *aeschynomene* on *Aeschynomene virginica*. *Biological Control* **47**: 298–308.

Drummond AJ, Ashton B, Buxton S, Cheung M, Cooper A, *et al.* (2011). Geneious v5.4, Available from http://www.geneious.com/

Drummond AJ, Suchard MA, Xie D, Rambaut A (2012). Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution* **29**: 1969–1973.

Du M, Schardl CL, Nuckles EM, Vaillancourt L (2005). Using mating-type gene sequences for improved phylogenetic resolution of *Colletotrichum* species complexes. *Mycologia* **97**: 641–658.

Edgerton CW (1909). The perfect stage of the cotton anthracnose. *Mycologia* **1**: 115–120.

Farr DF, Aime MC, Rossman AY, Palm ME (2006). Species of *Colletotrichum* on Agavaceae. *Mycological Research* **110**: 1395–1408.

Fitzpatrick DA, Logue ME, Stajich JE, Butler G (2006). A fungal phylogeny based on 42 complete genomes derived from supertree and combined gene analysis. *BMC Evolutionary Biology* **6**: 99.

Fokunang CN, Dixon AGO, Akem CN, Ikotun T (2000). Cutural, morphological and pathogenic variability in *Colletotrichum gloeosporioides* f. sp. *manihotis* isolates from cassava (*Manihot esculenta*) in Nigeria. *Pakistan Journal of Biological Sciences* **3**: 542–546.

Gardes M, Bruns TD (1993). ITS primers with enhanced specificity for basidiomycetes – application to the identification of mycorrhizae and rusts. *Molecular Ecology* **2**: 113–118.

Glass NL, Donaldson GC (1995). Development of primer sets designed for use with the PCR to amplify conserved genes from filamentous ascomycetes. *Applied and Environmental Microbiology.* **61**: 1323–1330.

Gielink AJ, Vermeulen H (1983). The ability of American and African *Colletotrichum* isolates to cause coffee berry disease symptoms and the association of some isolates with *Glomerella cingulata*. *Netherlands Journal of Plant Pathology* **89**: 188–190.

Gorter GJMA (1956). Anthracnose fungi of olives. *Nature* **178**: 1129–1130.

Green KR, Simons SA (1994). 'Dead skin' on yams (*Dioscorea alata*) caused by *Colletotrichum gloeosporioides*. *Plant Pathology* **43**: 1062–1065.

Greene GL (1967). Effect of 2-dehydroxy-D-glocose on the respiration of tropical anthracnose fungi. *Physiologia Plantarum* **20**: 580–586.

Guerber JC, Correll JC (2001). Characterisation of *Glomerella acutata*, the teleomorph of *Colletotrichum acutatum*. *Mycologia* **93**: 216–229.

Guerber JC, Liu B, Correll, JC, Johnston PR (2003). Characterization of diversity in *Colletotrichum acutatum sensu lato* by sequence analysis of two gene introns, mtDNA and intron RFLPs, and mating compatibility. *Mycologia* **95**: 872–895.

Gunnell PS, Gubler WD (1992). Taxonomy and morphology of *Colletotrichum* species pathogenic to strawberry. *Mycologia* **84**: 157–165.

Harris P (1993). Effects, constraints and the future of weed biocontrol. *Agriculture, Ecosystems and Environment* **46**: 289–303.

Heled J, Drummond AJ (2010). Bayesian Inference of Species Trees from Multilocus Data. *Molecular Biology and Evolution* **27:** 570–580.

Higgins BB (1926). Anthracnose of pepper (*Capsicum anuum* L.). *Phytopathology* **16**: 333–345.

Hildebrand PD, Jensen KIN (1991). Potential for the biological control of St Johns's-wort (*Hypericum perforatum*) with an endemic strain of *Colletotrichum gloeosporioides*. *Canadian Journal of Plant Pathology* **13**: 60–70.

Hindorf H (1973). *Colletotrichum*-Population auf *Coffea arabica* L. in Kenia II. Qualitative und quantitative Unterschiede in der *Colletotrichum*-Population. *Phytopathologische Zeitschrift* **77***:* 216–234

Hosdson A, Mills PR, Brown AE (1993). Ribosomal and mitochondrial DNA polymorphisms in *Colletotrichum gloeosporioides* isolated from tropical fruits. *Mycological Research* **97**: 329–335.

Hsiang T, Goodwin PH (2001). Ribosomal DNA sequence comparisons of *Colletotrichum graminicola* from turfgrasses and other hosts. *European Journal of Plant Pathology* **107**: 593–599.

Hyde KD, Cai L, Cannon PF, Crouch JA, Crous PW, *et al*. (2009). *Colletotrichum* – names in current use. *Fungal Diversity* **39**: 147–182.

Hyde KD, Chomnunti P, Crous PW, Groenewald JZ, Damm U, *et al.* (2010). A case for re-inventory of Australia's plant pathogens. *Persoonia* **25**: 50–60.

Irwin JAG, Cameron DF (1978). Two diseases in *Stylosanthes* caused by *Colletotrichum gloeosporioides* in Australia, and pathogenic specialisation within one of the causal organisms. *Australian Journal of Agricultural Research* **29**: 3015–317.

Johnson DA, Carris LM, Rogers JD (1997). Morphological and molecular characterization of *Colletotrichum nymphaeae* and *C. nupharicola* sp. nov. on water-lilies (*Nymphaea* and *Nuphar*). *Mycological Research* **101**: 641–649.

Johnston PR (2000). The importance of phylogeny in understanding host relationships within *Colletotrichum*. In: *Colletotrichum: host specificity, pathogenicity, and host-pathogen interactions* (Prusky D, Dickman MB, Freeman S eds). APS Press, St Paul, Minnesota: 21–28.

Johnston PR, Jones D (1997). Relationships among *Colletotrichum* isolates from fruit rots assessed using rDNA sequences. *Mycologia* **89**: 420–430.

Johnston PR, Pennycook SR, Manning MA (2005). Taxonomy of fruit-rotting fungal pathogens: what's really out there? *New Zealand Plant Protection* **58**: 42–46.

Kaan F (1973). A study on inheritance of eggplant (*Solanum melongena* L.) resistance to fruit anthracnose (*Colletotrichum gloeosporioides* f. sp. *melongenae* Penzig Fournet). *Annales De l'Amelioration des Plantes* **23**:127–151.

Kenny MK, Galea VJ, Price TV (2012). Germination and growth of *Colletotrichum acutatum* and *Colletotrichum gloeosporioides* isolates from coffee in Papua New Guinea and their pathogenicity. *Australasian Plant Pathology* (online, doi:10.1007/s13313-012-0117-7).

Killgore EM, Sugiyama LS, Barreto RW, Gardner DE (1999). Evaluation of *Colletotrichum gloeosporioides* for Biological Control of *Miconia calvescens* in Hawaii. *Plant Disease* **83**: 964.

Kornerup A, Wanscher JH (1963). *Methuen handbook of colour*. Methuen and Co. London.

Krauss U, Matthews P, Bidwell R, Hocart M, Anthony F (2001). Strain discrimination by fungal antagonists of *Colletotrichum musae*: implications for biocontrol of crown rot of banana. *Mycological Research* **105**: 67–76.

Lardner R, Johnston PR, Plummer KM, Pearson MN (1999). Morphological and molecular analysis of *Colletotrichum acutatum sensu lato*. *Mycological Research* **103**: 275–285.

Larkin MA, Blackshields G, Brown NP, Chenna R, McGettigan PA, *et al*. (2007). Clustal W and Clustal X v. 2.0. *Bioinformatics* **23**: 2947–2948.

Laundon GF (1972) [1971]. Records of fungal plant diseases in New Zealand – 2. *New Zealand Journal of Botany* **9**: 610–624.

Li R, Ma H (1993). Studies in the occurrence and control of ramie anthracnose. Acta *Phytophylacica Sinica* **20**: 83–89. [in Chinese]

Liu LJ (1972). Identification and occurrence of perfect stage and cultural and morpholoical variants of *Colletotrichum gloeosporioides* from guava in Puerto Rico. *Journal of Agriculture of the University of Puerto Rico* **56**: 171–180.

Liu B, Louws FJ, Sutton TB, Correll JC (2011). A rapid qualitative molecular method for the identification of *Colletotrichum acutatum* and *C. gloeosporioides*. *European Journal of Plant Pathology* **132**: 593–607.

Lubbe CM, Denman S, Cannon PF, Groenewald JZ, Lamprecht SC, Crous PW (2004). Characterisation of *Colletotrichum* species associated with *Proteaceae*. *Mycologia* **96**: 1268–1279.

MacCaughey V (1917). The guavas of the Hawaiian Islands. *Bulletin of the Torrey Botanical Club* **44**: 513–524.

Mackenzie SJ, Seijo TE, Legard DE, Timmer LW, Peres NA (2007). Selection for pathogenicity to strawberry in populations of *Colletotrichum gloeosporioides* from native plants. *Phytopathology* **97**: 1130–1140.

Mackenzie SJ, Mertely JC, Seijo TE, Peres NA (2008). *Colletotrichum fragariae* is a pathogen on hosts other than strawberry. *Plant Disease* **92**: 1432–1438.

McNeill J, Barrie FR, Burdet HM, Demoulin V, Hawksworth DL, *et al*. (2006). *International Code of Botanical Nomenclature (Vienna Code). Adopted by the Seventeenth International Botanical Congress, Vienna, Austria, July 2005*. Regnum Vegetabile 146. 568 p.

Makambila C (1994). The fungal diseases of cassava in the Republic of Congo, Central Africa. *African Crop Science Journal* **2**: 511–517.

Makowski RMD, Mortensen K (1989). *Colletotrichum gloeosporioides* f. sp. *malvae* as a bioherbicide for round-leafed mallow (*Malva pusilla*): conditions for successful control in the field. In: *Proceedings of the 7th International Symposium for the Biological Control of Weeds*. (Delfosse ES ed.). *Istituto Sperimentale per la Patalogia Vegetale, Rome*: 513–522.

Marcelino J, Giordano R, Gouli S, Gouli V, Parker BL, *et al.* (2008). *Colletotrichum acutatum* var. *fioriniae* (teleomorph: *Glomerella acutata* var. *fioriniae* var. nov.) infection of a scale insect. *Mycologia* **100**: 353–374.

Martínez-Culebras PV, Barrio E, García MD, Querol A (2000). Identification of *Colletotrichum* species responsible for anthracnose of strawberry based on the internal transcribed spacers of the ribosomal region. *FEMS Microbiology Letters* **189**: 97–101.

Martinez-Culebras PV, Querol A, Suarez-Fernandez MB, Garcia-Lopez MD, Barrio E (2003). Phylogenetic relationships among *Colletotrichum* pathogens of strawberry and design of PCR primers for their identification. *Journal of Phytopathology* **151**: 135–143.

Maymon M, Zveibil A, Pivonia S, Minz D, Freeman S (2006). Identification and characterisation of benomyl-resistant and sensitive- populations of *Colletotrichum gloeosporioides* from statice (*Limonium* spp.). *Phytopathology* **96**: 542–548.

Menten JOM, Kimati H, Costa CP (1980). Reação de populações de pepino (*Cucumis sativus* L.) a *Colletotrichum gloeosporioides* f. sp. *cucurbitae* (Berk. et Mont.) N. Comb. *Summa Phytopathologica* **5**: 127–133.

Mills PR, Sreenivasaprasad S, Brown AE (1992). Detection and differentiation of *Colletotrichum gl* Maymon *oeosporioides* isolates using PCR. *FEMS Microbiological Letters* **98**: 137–144.

Misra AK (2004). Guava diseases – their symptoms, causes and management. In: *Diseases of fruits and vegetables. Diagnosis and management Volume 2*. (Naqvi SAMH. ed.). Kluwer Academic Publishers, Dordrecht: 81–119.

Mordue JEM (1971). *Glomerella cingulata*. CMI Desriptions of Plant Pathogenic Fungi No. 315. Commonwealth Mycological Institute, Kew.

Moriwaki J, Sato T, Tsukiboshi T (2003). Morphological and molecular characterisation of *Colletotrichum boninense* sp. nov. from Japan. *Mycoscience* **44**: 47–53.

Moriwaki J, Sato T (2009). A new combination for the causal agent of tea anthracnose: *Discula theae-sinensis* (I. Miyake) Moriwaki & Toy. Sato, comb. nov. *Journal of General Plant Pathology* **75**: 359–361.

Moriwaki J, Tsukiboshi T (2009). *Colletotrichum echinochloae*, a new species on Japanese barnyard millet (*Echinochloa utilis*). *Mycoscience* **50**: 273–280.

Munaut F, Hamaide N, Maraite H (2002). Genomic and pathogenic diversity in *Colletotrichum gloeosporioides* from wild native Mexican *Stylosanthes* spp., and taxonomic implications. *Mycological Research* **106**: 579–593.

Munaut F, Hamaide N, Vander Stappen J, Maraite H (1998). Genetic relationships among isolates of *Colletotrichum gloeosporioides* from *Stylosanthes* spp. in Africa and Australia using RAPD and ribosomal DNA markers. *Plant Pathology* **47**: 641–648.

Muraleedharan N, Baby UI (2007). Tea disease: ecology and control. In: *Encyclopedia of Pest Management Vol. 2* (Pimentel D, ed.) [electronic resource]. CRC Press, Boca Raton: 668–671.

Nilsson RH, Ryberg M, Kristiansson E, Abarenkov K, Larsson KH, Kõljalg U (2006). Taxonomic reliability of DNA sequences in public sequence databases: a fungal perspective. *PLoS ONE* **1(1)**: e59.

Nirenberg HI, Feiler U, Hagedorn G (2002). Description of *Colletotrichum lupini* comb. nov. in modern terms. *Mycologia* **94**: 307–320.

Noak F (1901). Die Krankheiten des Kaffeebaumes in Brasilien. *Zeitschrift für Pflanzenkrankheiten* **11**: 196–203.

Ocfemia, GO, Agati JA (1925). The cause of anthracnose of avocado, mango and upo in the Philippine Islands. *Philippine Agriculturalist* **14**: 199–216.

O'Donnell K, Cigelnik E (1997). Two divergent intragenomic rDNA ITS2 types within a monophyletic lineage of the fungus *Fusarium* are nonorthologous. *Molecular Phylogenetics and Evolution* **7**:103–116.

O'Donnell K, Nirenberg HI, Aoki T, Cigelnik E (2000). A Multigene phylogeny of the *Gibberella fujikuroi* species complex: Detection of additional phylogenetically distinct species. *Mycoscience* **41**: 61–78.

Owolade OF, Dixon AGO, Alabi BS, Akande SR, Olakojo SA (2008). A combining ability analysis of cassava *Manihot esculenta* Crantz genotypes to anthracnose disease. *Electronic Journal of Environmental, Agricultural and Food Chemistry* **7**: 2959–2968.

Parvin S, Lee OR, Sathiyaraj G, Khorolragchaa A, Kim YJ, *et al.* (2012). Interrelationship between calmodulin (CaM) and H2O2 in abscisic acid-induced antioxidant defense in the seedlings of *Panax ginseng*. *Molecular Biology Reports* **39**: 7327–7338.

Penzig AGO (1882). Fungi agrumicoli. Contribuzione allo studio dei funghi parassiti degli agrumi. *Michelia* **2**: 385–508.

Phoulivong S, Cai L, Parinn N, Chen H, Abd-Elsalam K, *et al.* (2011). A new species of *Colletotrichum* from *Cordyline fruticosa* and *Eugenia javanica* causing anthracnose disease. *Mycotaxon* **114**: 247–257.

Polashock JJ, Caruso FL, Oudemans PV, McManus PS, Crouch JA (2009). The North American cranberry fruit rot fungal community: a systematic overview using morphological and phylogenetic affinities. *Plant Pathology* **58**: 1116–1127.

Pollacci G (1899). Contribuzione alla micologia ligustica. *Atti dell' Istituto Botanico dell' Università di Pavia, Serie 2* **5**: 29–46.

Posada D. (2008). jModelTest: Phylogenetic Model Averaging. *Molecular Biology and Evolution* **25**: 1253–1256

Prasad N, Singh RD (1960). Anthracnose disease of *Dioscorea alata* L. (Yam, Eng., Ratalu, Hind.). *Current Science* **29**: 66–67.

Prihastuti H, Cai L, Chen H, McKenzie EHC, Hyde KD (2009). Characterisation of *Colletotrichum* species associated with coffee berries in northern Thailand. *Fungal Diversity* **39**: 89–109.

R Development Core Team (2011). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rambaut A, Drummond AJ (2007). Tracer v. 1.4, Available from http://beast.bio.ed.ac.uk/Tracer

Rodrigues CJ, Varzea VMP, Hindorf H, Medeiros EF (1991). Strains of *Colletotrichum coffeanum* Noack causing coffee berry disease in Angola and Malawi with characteristics different to the Kenya strain. *Journal of Phytopathology* **131**: 205–209.

Rodriguez RJ, Owen JL (1992). Isolation of *Glomerella musae* [teleomorph of *Colletotrichum musae* (Berk. & Curt.) Arx] and segregation analysis of ascospore progeny. *Experimental Mycology* **16**: 291–301.

Rodríguez-Guerra R, Ramírez-Rueda M, Cabral-Enciso M, García-Serrano M, Lira-Maldonado Z, *et al.* (2005). Heterothallic mating observed between Mexican isolates of *Glomerella lindemuthiana*. *Mycologia* **97**: 793–803.

Rojas EI, Rehner SA, Samuels GJ, Van Bael SA, Herre EA, *et al.* (2010). *Colletotrichum gloeosporioides* s.l. associated with *Theobroma cacao* and other plants in Panamá: multilocus phylogenies distinguish host-associated pathogens from asymptomatic endophytes. *Mycologia* **102**: 1318–1338.

Ronquist F, Teslenko M, van der Mark P, Ayres D, Darling A, *et al.* (2012). MrBayes v. 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* **61**: 539–542.

Saccardo PA, Trotter A (1913). Supplementum Universale Pars. IX. Ascomycetae-Deuteromycetae. *Sylloge Fungorum* **22**: 1–1612.

Sanders GM, Korsten L (2003). Comparison of cross inoculation potential of South African avocado and mango isolates of *Colletotrichum gloeosporioides*. *Microbiological Research* **158**: 143–150.

Sawada T (1922). New Japanese fungi notes and translations – XI. *Mycologia* **14**: 81–89.

Schoch CL, Seifert KA, Huhndorf S, Robert V, Spouge JL, *et al.* (2012). Nuclear ribosomal internal transcribed spacer (ITS) region as a universal DNA barcode marker for Fungi. *Proceedings of the National Academy of Sciences* **109**: 6241–6246.

Schwarczinger I, Vajna L, Bruckart WL (1998). First report of *Colletotrichum gloeosporioides* on Russian thistle. *Plant Disease* **82**: 1405.

Seifert KA (2009). Progress towards DNA barcoding of fungi. *Molecular Ecology Resources* **9** (Suppl. 1): 83–89.

Shear CL (1907). New species of fungi. *Bulletin of the Torrey Botanical Club* **34**: 305–317.

Shear CL, Wood AK (1907). Ascogenous forms of *Gloeosporium* and *Colletotrichum*. *Botanical Gazette* **43**: 259–266.

Shear CL, Wood AK (1913). Studies of fungus parasites belonging to the genus *Glomerella*. *USDA Bureau of Plant Industry Bulletin* **252**: 1–110.

Sheldon JL (1906). The ripe rot or mummy disease of guavas. *Bulletin of the West Virginia University Experimental Station* **104**: 299–315.

Shenoy BD, Jeewon R, Lam WH, Bhat DJ, Than PP, *et al.* (2007). Morpho-molecular characterisation and epitypification of *Colletotrichum capsici* (*Glomerellaceae, Sordariomycetes*), the causative agent of anthracnose on chilli. *Fungal Diversity* **27**: 197–211.

Sherf AF, MacNab AA (1986). *Vegetable diseases and their control*. John Wiley and Sons. USA.

Sherriff C, Whelan MJ, Arnold GM, Lafay JF, Brygoo Y, Bailey JA (1994). Ribosomal DNA sequence analysis reveals new species groupings in the genus *Colletotrichum*. *Experimental Mycology* **18**: 121–138.

Shivas RG, Bathgate J, Podger FD (1998). *Colletotrichum xanthorrhoeae* sp. nov. on *Xanthorrhoea* in Western Australia. *Mycological Research* **102**: 280–282.

Silva DN, Talhinas P, Várzea V, Cai L, Paulo OS, Batista D (2012a). Application of the Apn2/MAT locus to improve the systematics of the *Colletotrichum gloeosporioides* complex: an example from coffee (*Coffea* spp.) hosts. *Mycologia* **104**: 396–409.

Silva DN, Talhinhas P, Cai L, Manuel L, Gichuru EK, *et al.* (2012b). Host-jump drives rapid and recent ecological speciation of the emergent fungal pathogen *Colletotrichum kahawae*. *Molecular Ecology* **21**: 2655–2670.

Silva VN da, Guzzo SD, Mantovanello-Lucon CM, Harakava R (2011). Promoção de crescimento e inducção de resistência à antracnose por *Trichoderma* spp. em pepineiro. *Pesquisa Agropecuária Brasileira* **46**: 1609–1618.

Silva-Mann R, Carvalho Vieira MGG, Machado JC, Bernandino Filho JR, Salgado KCC, Stevens MR (2005). AFLP markers differentiate isolates of *Colletotrichum gossypii* from *C. gossypii* var. *cephalosporioides*. *Fitopatologia Brasileira* **30**: 169–172.

Simmonds JH (1965). A study of the species of *Colletotrichum* causing ripe fruit rots in Queensland. *Queensland Journal of Agricultural and Animal Sciences* **22**: 437–459.

Simmonds JH (1968). Type specimens of *Colletotrichum gloeosporioides* var. *minor* and *Colletotrichum acutatum*. *Queensland Journal of Agricultural and Animal Sciences* **25**: 178A.

Singh UP (1974). A new forma specialis of *Colletotrichum gloeosporioides* Penz. from India. *Beihefte zur Nova Hedwigia* **47**: 451–452.

Singh UP (1975). *Colletotrichum gloeosporioides* Penzig - A mycoparasite on *Ravenelia sessilis* Berkeley. *Current Science* **44**: 623–624.

Singh RD, Prasad N, Mathur RL (1966). On the taxonomy of the fungus causing anthracnose of *Dioscorea alata* L. *Indian Phytopathology* **19**: 65–71.

Small W (1926). On the occurrences of a species of *Colletotrichum*. *Transactions of the British Mycological Society* **11**: 112–137.

Snowdon AL 1991. *A colour atlas of post-harvest diseases and disorders of fruit and vegetables. Volume 2. Vegetables*. Wolfe Scientific.

Sosa de Castro NT, Cabrera de Alvarez MG, Alvarez RE (2001). Primera información de *Colletotrichum camelliae* como patógeno de *Camellia japonica*, en Corrientes. Retrieved 6 Oct 2010 from www1.unne.edu.ar/cyt/2001/5-Agrarias/A-056.pdf.

Southworth EA (1891). Antracnose of cotton. *Journal of Mycology* **6**: 100–105.

Spaulding P (1958). *Diseases of foreign trees growing in the United States, an annotated list*. USDA Agriculture Handbook 139.

Spegazzini CL (1878). Ampelomiceti Italici, ossia enumerazione, diagnosi e storia dei principali parassiti della vite. *Rivista Viticoltura ed Enologia* **2**: 405–411.

Sreenivasaprasad S, Mills PR, Meehan B M, Brown AE (1996). Phylogeny and systematics of 18 *Colletotrichum* species based on ribosomal DNA spacer sequences. *Genome* **39**: 499–512.

Stephenson SA, Green JR, Manners JM, Maclean DJ (1997). Cloning and characterisation of glutamine synthetase from *Colletotrichum gloeosporioides* and demonstration of elevated expression during pathogenesis on *Stylosanthes guianensis*. *Current Genetics* **31**: 447–454.

Stevens FL, Hall JG (1909). Eine neue Feigen-Anthraknose (Colletotrichose). *Zeitschrift für Pflanzenkrankheiten* **19**: 65–68.

Stoneman B (1898). A comparative study of the development of some anthracnoses. *Botanical Gazette* **26**: 69–120.

Su YY, Noireung P, Liu F, Hyde KD, Moslem MA, *et al.* (2011). Epitypification of *Colletotrichum musae*, the causative agent of banana anthracnose. *Mycoscience* **52**: 376–382.

Sutton BC, Waterston JM (1970). *Colletotrichum musae*. *CMI Descriptions of Plant Pathogenic Fungi and Bacteria* No. 222.

Sutton BC (1980). *The Coelomycetes*. Commonwealth Mycological Institite. Kew.

Sutton BC (1992). The genus *Glomerella* and its anamorph *Colletotrichum*. In: *Colletotrichum Biology, Pathology and Control*. (Bailey JA, Jeger MJ, eds). CAB International, Wallingford: 1–26.

Talhinas P, Sreenivasaprasad S, Neves-Martins J, Oliviera H (2005). Molecular and phenotypic analyses reveal association of diverse *Colletotrichum acutatum* groups and a low level of *C. gloeosporioides* with olive anthracnose. *Applied and Environmental Microbiology* **71**: 2987–2998.

Taylor JW, Jacobson DJ, Kroken S, Kasuga T, Geiser DM, *et al.* (2000). Phylogenetic species recognition and species concepts in fungi. *Fungal Genetics and Biology* **31**: 21–32.

Taylor JW, Berbee ML (2006). Dating divergences in the Fungal Tree of Life: review and new analyses. *Mycologia* **98**: 838–849.

TeBeest DO (1988). Additions to host range of *Colletotrichum gloeosporioides* f. sp. *aeschynomene*. *Plant Disease* **72**: 16–18.

Templeton MD, Rikkerink EHA, Solon SL, Crowhurst RN. (1992). Cloning and molecular characterization of the glyceraldehyde-3-phosphate dehydrogenase-encoding gene and cDNA from the plant pathogenic fungus *Glomerella cingulata*. *Gene* **122**: 225–230.

Than PP, Jeewon R, Hyde KD, Pongsupasamit S, Mongkolporn O, Taylor PWJ (2008). Characterisation and pathogenicity of *Colletotrichum* species asscoaited with anthracnose on chilli (*Capsicum* spp.) in Thailand. *Plant Pathology* **57**: 562–572.

Thang MM (2008). Biodiversity survey of coelomycetes in Burma. *Australasian Mycologist* **27**: 74–110.

Trujillo EE, Latterell FM, Rossi AE (1986). *Colletotrichum gloeosporioides*, a possible biological control agent for *Clidemia hirta* in Hawaiian forests. *Plant Disease* **70**: 974–976.

Tsurushima T, Ueno T, Fukami H, Irie H, Inoue M (1995). Germination of self-inhibitors from *Colletotrichum gloeosporioides* f. sp. *jussiaea*. *Molecular Plant-Microbe Interactions* **8**: 652–657.

Vajna L, Bagyinka T (2002). Occurrence of privet anthracnose in Hungary caused by Glomerella cingulata. *Plant Disease* **51**: 403.

Varzea VMP, Rodrigues Junior CJ, Lewis BG (2002). Distinguishing characteristics and vegetative compatibility of *Colletotrichum kahawae* in comparison with other related species from coffee. *Plant Pathology* **51**: 202–207.

Venkatakrishniah NS (1952). *Glomerella psidii* (Del.) Sheld. and *Pestalotia psidii* Pat. associated with a cankerous disease of guava. *Proceedings of the Indian Academy of Plant Sciences* **36**: 129–134.

Vermeulen H, De Ferrante B, Gielink AJ (1984). Genetic and morphological diversity of mono-spore isolates of *Glomerella cingulata* associated with coffee berry disease. *Netherlands Journal of Plant Pathology* **90**: 213–223.

Vinijsanun T, Irwin JAG, Cameron DF (1987). Host range of three strains of *Colletotrichum gloeosporioides* from tropical pasture legumes, and comparative histological studies of interactions between Type B disease-producing strains and *Stylosanthes scabra* (non-host) and *S. guianensis* (host). *Australian Journal of Botany* **35**: 665–677.

Waller JM, Bridge PD, Black R, Hakiza G (1993). Characterisation of the coffee berry disease pathogen, *Colletotrichum kahawae* sp. nov. *Mycological Research* **97**: 989–994.

Wang XX, Wang B, Liu JL, Chen J, Cui XP, *et al.* (2010). First reports of anthracnose caused by *Colletotrichum gloesporioides* on ramie in China. *Plant Disease* **94**: 1508.

Weir BS, Johnston PR (2009). Defining and delimiting genetic species in *Colletotrichum*. Asian Mycologyical Congress 2009. Taichung Taiwan November 15–19. pg O-128.

Weir BS, Johnston PR (2010). Characterisation and neotypification of *Gloeosporium kaki* Hori as *Colletotrichum horii* nom. nov. *Mycotaxon* **111**: 209–219.

Weir BS, Johnston PR (2011). Towards a secondary fungal barcode for Colletotrichum [Sordariomycetes, Ascomycota]. Forth international barcode of life conference, Adelaide Australia, 28 November – 3 December 2011.

White TJ, Bruns T, Lee S, Taylor JW. (1990). Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: *PCR Protocols: A Guide to Methods and Applications*. (Innis MA, Gelfand DH, Sninsky JJ, White TJ eds). Academic Press: New York: 315–322.

Wickham H (2009). *ggplot2: elegant graphics for data analysis*. Springer New York.

Wikee S, Cai L, Pairin N, McKenzie EHC, Su YY, *et al.* (2011). *Colletotrichum* species from Jasmine (*Jasminum sambac*). *Fungal Diversity* **46**: 171–182.

Willis JC (1899). DCLII - Tea and coffee diseases. *Bulletin of Miscellaneous Information Royal Botanical Gardens Kew* **1899**: 89–94.

Winch JE, Newhook FJ, Jackson GVH, Cole JS (1984). Studies of *Colletotrichum gloeosporioides* disease on yam, *Dioscorea alata*, in Solomon Islands. *Plant Pathology* **33**: 467–477.

Wollenweber HW, Hochapfel H (1949). Beiträge zur Kenntnis parasitärer und saprophytischer Pilze. VI. *Vermicularia*, *Colletotrichum*, *Gloeosporium*, *Glomerella* und ihre Beziehung zur Fruchtfäule. *Zeitschrift für Parasitenkunde* **14**: 181–268.

Xie L, Zhang JZ, Cai L, Hyde KD (2010a). Biology of *Colletotrichum horii*, the causal agent of persimmon anthracnose. *Mycology* **1**: 242–253.

Xie L, Zhang JZ, Wan Y, Hu DW (2010b). Identification of *Colletotrichum* spp. isolated from strawberry in Zhejiang Province and Shanghai City, China. Journa*l of Zhejiang University Science B (Biomedicine & Biotechnology)* **11**: 61–70.

Yamamoto W (1960). A revision of the genus and species names of anthracnose fungi in Japan. *Plant Protection* **14**: 49–52. [in Japanese]

Yan J, Wu PS, Du HZ, Zhang QE (2011). First report of black spot caused by *Colletotrichum gloeosporioides* on paper mulberry in China. *Plant Disease* **95**: 880.

Yang SY, Su SC, Liu T, Fan G, Wang J (2011). First report of anthracnose caused by *Colletotrichum gloeosporioides* on pistachio (*Pistacia vera*) in China. *Plant Disease* **95**: 1314.

Yang YL, Liu ZY, Cai L, Hyde KD, Yu ZN, McKenzie EHC (2009). *Colletotrichum* anthracnose of Amaryllidaceae. *Fungal Diversity* **39**: 123–146.

Zhang TY (1985). A forma specialis of *Colletotrichum gloeosporioides* on *Cuscuta* sp. *Acta Mycologica Sinica* **4**: 223–239. [In Chinese]

Zhang X, Yang G, Yang J, Shu Q (2012). Physiological mechanism of resistance to anthracnose of different *Camellia* varieties. *African Journal of Biotechnology* **11**: 2026–2031.

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Colletotrichum – current status and future directions

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Abstract: A review is provided of the current state of understanding of *Colletotrichum* systematics, focusing on species-level data and the major clades. The taxonomic placement of the genus is discussed, and the evolution of our approach to species concepts and anamorph-teleomorph relationships is described. The application of multilocus technologies to phylogenetic analysis of *Colletotrichum* is reviewed, and selection of potential genes/loci for barcoding purposes is discussed. Host specificity and its relation to speciation and taxonomy is briefly addressed. A short review is presented of the current status of classification of the species clusters that are currently without comprehensive multilocus analyses, emphasising the orbiculare and destructivum aggregates. The future for *Colletotrichum* biology will be reliant on consensus classification and robust identification tools. In support of these goals, a Subcommission on *Colletotrichum* has been formed under the auspices of the International Commission on Taxonomy of Fungi, which will administer a carefully curated barcode database for sequence-based identification of species within the BioloMICS web environment.

Key words: anamorph-teleomorph linkages, barcoding, *Colletotrichum*, database, *Glomerella*, host specialisation, phylogeny, systematics, species concepts.

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INTRODUCTION

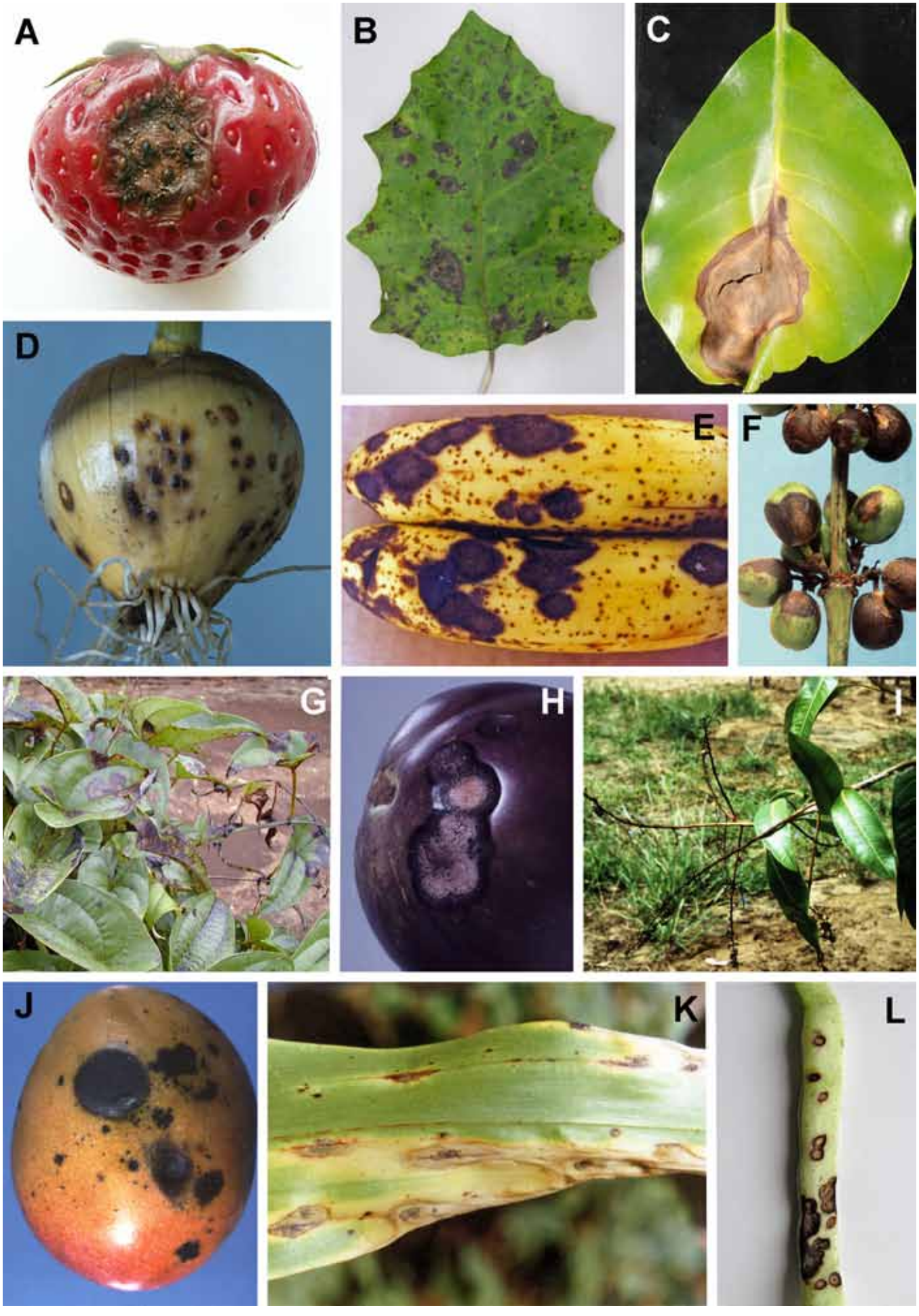
The genus *Colletotrichum* includes a number of plant pathogens of major importance, causing diseases of a wide variety of woody and herbaceous plants. It has a primarily tropical and subtropical distribution, although there are some high-profile species affecting temperate crops. Fruit production is especially affected, both high-value crops in temperate markets such as strawberry, mango, citrus and avocado, and staple crops such as banana. *Colletotrichum* species cause devastating disease of coffee berries in Africa, and seriously affect cereals including maize, sugar cane and sorghum. The genus was recently voted the eighth most important group of plant pathogenic fungi in the world, based on perceived scientific and economic importance (Dean *et al*. 2012).

As plant pathogens, *Colletotrichum* species are primarily described as causing anthracnose diseases, although other maladies are also reported such as red rot of sugar cane, coffee berry disease, crown rot of strawberry and banana, and brown blotch of cowpea (Lenné 2002). Anthracnose disease symptoms include limited, often sunken necrotic lesions on leaves, stems, flowers and fruit, as well as crown and stem rots, seedling blight etc. (Waller *et al.* 2002, Agrios 2005). A range of disease symptoms is illustrated in Fig. 1. Many species may be seed-borne and can survive well in soil by growing saprobically on dead plant fragments, and may be spread via water-splash dispersal of conidia and air transmission of ascospores from the sexual morph (Nicholson & Moraes 1980). Infection occurs via an appressorium that develops from the germinating spore on the plant surface, followed by turgor-driven penetration of the cuticle (Deising *et al*. 2000) and in some cases also of epidermal cells by infective hyphae (Bailey *et al.* 1992). Establishment within plant tissues is aided via production by the fungus of host-induced virulence effectors (Kleeman *et al.* 2012, O'Connell *et al.* 2012). Nascent colonies in most cases then enter a biotrophic phase with infected tissues remaining externally symptomless and which may be short (1–3 d; O'Connell *et al.* 2000) or extended and presumably involving dormancy (Prusky & Plumbley 1992). Then, the fungus enters a necrotrophic phase that results in significant death of plant cells and the emergence of pathogenic lesions. This delayed onset of disease symptoms may lead to significant post-harvest losses, with apparently healthy crops degenerating in storage (Prusky & Plumbley 1992). The biotrophic life strategies adopted by *Colletotrichum* species may also contribute to their prominence as symptomless endophytes of living plant tissues (Lu *et al.* 2004, Joshee *et al.* 2009, Rojas *et al.* 2010, Yuan *et al.* 2011). There are no comprehensive modern reviews of the biology, pathology and host/parasite interactions of *Colletotrichum* species, but useful information can be found in Bailey & Jeger (1992) and Prusky *et al.* (2000).

Colletotrichum species are also extensively studied as model organisms for research into genetics. This work has a long history; the first investigation into mating types in *Glomerella* was published a century ago (Edgerton 1912, 1914), and genetic mechanisms in *G. cingulata* were extensively studied in the 1940's and 50's (*e.g.* Andes 1941, Lucas *et al.* 1944, Wheeler 1950, 1954, Olive 1951).

Research into host/parasite systems has had almost as long a history, originating with work on the *C. lindemuthianum*/*Phaseolus vulgaris* interaction by Barrus (1918). Mechanisms of infection and disease development in the same model system were extensively studied in the 1980's (*e.g.* Bell *et al.* 1984, O'Connell *et al.* 1985, 1986).

Maize anthracnose caused by *Colletotrichum graminicola* is an economically important disease on a global level, stimulating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a further body of research into *Colletotrichum* genetics, pathology and host-parasite interactions. It has been reviewed by Nicholson (1992), Bergstrom & Nicholson (1999), Vaillancourt *et al.* (2000) and Crouch & Beirn (2009).

The relationship between *Colletotrichum higginsianum* and its *Brassica hosts* has also been the subject of much recent research (Perfect *et al.* 1999, O'Connell *et al.* 2004). Huser *et al.* (2009) discovered pathogenicity genes in *C. higginsianum* by random insertional mutagenesis. Jaulneau *et al.* (2010) compared the defence reactions of resistant or susceptible lines *of Medicago truncatula* to the alfalfa pathogen *C. trifolii* with reactions of the nonadapted pathogens *C. lindemuthianum* and *C. higginsianum*. O'Connell *et al.* (2012) studied the genomes and transcriptomes of two species, *C. higginsianum* and *C. graminicola* with different infection strategies.

Work on the genetics of pathogenicity in the *C. orbiculare* species aggregate (*e.g.* Pain *et al.* 1994, Rodriguez & Redman 2000) led to transformation of pathogenic strains to endophytic forms. These were shown to exhibit mutualistic activity by protection against virulent strains of the same species, and also to *Fusarium* pathogens. Gene manipulation techniques such as *Agrobacterium tumefaciens*-mediated transformation or protoplast transformation are established (Tsuji *et al.* 2003) and for host parasite interaction studies with *C. orbiculare*, a model plant *Nicotiana benthamiana* is being used. Several genes involved in signal transduction pathways essential for the formation of infection structures were identified (Takano *et al.* 1997, Tanaka *et al.* 2009) and two peroxisome biogenesis genes, PEX6 and PEX13 that are essential for pathogenesis were functionally analysed (Kimura *et al.* 2001, Fujihara *et al.* 2010). Asakura *et al.* (2009) discovered the importance of the pexophagy factor ATG26 for appressorium function.

Whole-genome sequences of *C. graminicola* and *C. higginsianum* have been completed (O'Connell *et al*. 2012) – the latter genome from a pathogen of the model plant organism *Arabidopsis thaliana* – and projects to sequence several other species are in progress or preparation (Damm *et al.* 2010). The research to date is already demonstrating step changes in our understanding of host-parasite interactions in *Colletotrichum.*

Colletotrichum is traditionally recognised as an asexual genus of fungi, with a number of species linked to sexual morphs assigned to the genus *Glomerella* (*Glomerellaceae*, *Glomerellales*; Zhang *et al.* 2006, Réblová *et al.* 2011). In the light of recent moves towards a unified nomenclatural system for the *Fungi*, we will for the most part refer to species using asexual names, which not only have date priority in all cases we have identified, but are much better known in the applied sciences.

HOST RELATIONS AND SPECIFICITY

For many years, *Colletotrichum* species were assumed to be specific to the plants they infected, leading to large numbers of taxa described with little in the way of distinctive features apart from the identity of their plant partners.

Our current understanding of the extent that *Colletotrichum* species exhibit host specificity is imperfect. This is due to a number of factors, including incomplete sampling, restriction of data largely to populations affecting crop or ornamental plants, and poor knowledge of pathogenic effects. Information on most strains in culture collections indicates an association with a particular plant species, but rarely provides details of the interaction. Many studies on *Colletotrichum* are restricted to strains affecting single crop species (*e.g.* Buddie *et al*. 1999, González *et al*. 2006, Gazis *et al*. 2011), significantly reducing the extent of the gene pool being sampled. Mackenzie *et al.* (2007) demonstrated gene flow between populations of *C. acutatum* from native plants and those from adjacent strawberry crops, demonstrating the limitations of host-restricted studies.

The ability of many *Colletotrichum* species to exist as endophytes adds extra complication to our understanding of host specificity (Lu *et al.* 2004, Liu *et al.* 2007, Rojas *et al.* 2010). Isolation from living plant tissue does not necessarily imply that the species is a latent pathogen with a hemibiotrophic phase (Latunde-Dada 2001, Peres *et al.* 2005, Münch *et al.* 2008), and distinguishing between the two life strategies is problematic. Freeman & Rodriguez (1993) and Redman *et al.* (1999) demonstrated that a single disruption event of a pathogenicity gene transformed a pathogenic strain of *Glomerella magna* from *Citrullus lanatus* into an endophyte that conferred protection for the host plant against wild type strains and other pathogens. Similar single gene effects on pathogencity are documented from the interaction between *C. graminicola* and maize (Thon *et al*. 2000, 2002). Research into the molecular basis of host-parasite interactions in *Colletotrichum* is currently highly active (see O'Connell *et al*. 2012), and such approaches will dominate research in the future into the extent of host specificity exhibited by *Colletotrichum* species.

We are not aware of any major group of angiosperms that does not harbour endophytic *Colletotrichum* colonies. There are also well-documented cases of *Colletotrichum* living as endophytes and disease agents of conifers (Dingley & Gilmour 1972, Wang *et al.* 2008, Joshee *et al.* 2009, Damm *et al*. 2012a) and ferns (Leahy *et al.* 1995, MacKenzie *et al.* 2009). Species are associated widely with both herbaceous and woody plants, though the latter appear mainly to contain colonies in fruits, leaves and other non-lignified tissues.

There are isolated accounts of *Colletotrichum* species causing infections of insects, including *C. fioriniae* on hemlock scale insects in New England and a claimed member of the *C. gloeosporioides* aggregate on citrus scale insects in Brazil (Marcelino *et al.* 2008). Infection mechanisms are not fully understood; under experimental conditions the insects became infected after being sprayed with a conidial suspension (Marcelino *et al.* 2009). In the field it seems possible that endophytic colonies of the fungus are ingested via the insect mouth-parts, the reverse of a process that has been shown in members of the *Clavicipitaceae* to infect plants via the stylets of sap-sucking insects (Torres *et al.* 2007, Tadych *et al.* 2009).

Fig. 1A-L. (see page 182). Disease symptoms caused by *Colletotrichum* species. The causal organisms have in most cases been identified to species complex level only. A. Anthracnose on strawberry fruit caused by *C. nymphaeae* (acutatum clade). B. Leaf spot of *Brachyglottis repanda* caused by *C. beeveri* (boninense clade). C. Anthracnose symptoms on leaves of *Tecomanthe speciosa* caused by *C. boninense* agg. D. Anthracnose of onion bulb caused by *C. circinans* (dematium clade). E. Anthracnose of banana caused by *C. musae* (gloeosporioides clade). F. Coffee berry disease caused by *C. kahawae* subsp. *kahawae* (gloeosporioides clade). G. Leaf anthracnose of yam caused by *C. gloeosporioides* agg. H. Anthracnose of aubergine (eggplant) fruit caused by *C. gloeosporioides* agg. I. Blossom blight of mango caused by an undetermined *Colletotrichum* sp. J. Anthracnose of mango caused by *C. gloeosporioides* agg. K. Leaf blight of maize caused by *C. graminicola* (graminicola clade). L. Anthracnose of bean pod caused by *C. lindemuthianum* (orbiculare agg.). A, © Ulrike Damm/CBS. B, C, D, H © Landcare Research, New Zealand. E, F, K © Jim Waller/CABI. G © Paul Cannon/CABI. I, J © Barbara Ritchie/CABI. L © Lu Guo-zhong, Dalian, China.

In rare instances, *Colletotrichum* species have been implicated in human disease, causing keratitis and subcutaneous infections (*e.g.* Ritterband *et al*. 1997, Guarro *et al*. 1998, Shiraishi *et al.* 2011, Shivaprakash *et al*. 2011). A single occurrence of disseminated mycotic infection of a sea turtle has also been recorded (Manire *et al*. 2002). Cano *et al*. (2004) reviewed the identification procedures for *Colletotrichum* species of clinical interest.

Some *Colletotrichum* clades appear to contain species that show at least a degree of host specificity, though these data may be linked to incomplete sampling and/or species concepts that assume specificity. The orbiculare clade is a case in point; here species seem to be restricted to individual host genera (Liu *et al.* 2007). That clade is a basal group (see Fig. 2), which might suggest that the extraordinary flexibility in host preference demonstrated by most other clades evolved subsequent to appearance of the genus itself. The graminicola group contains several species that are limited to host genera within the *Poaceae* (Crouch *et al.* 2009a). *Colletotrichum cereale*, a grass-inhabiting taxon which occupies a separate clade from the graminicola aggregate, does not appear to show genus-level specificity, though all strains to date derive from the same family (Crouch *et al.* 2009c). Here, population-level specificity is found in some cases, though the basal lineage is plurivorous, suggesting that host specialisation is in the process of development.

At a finer scale, several *Colletotrichum* species have been shown to exhibit substantial pathogenic variation at race level, although in most cases the precise phylogenetic position and diversity of the strains studied has not been established. In a large-scale project on strains identified as *C. lindemuthianum* from South, Central and North America, Balardin *et al*. (1997) characterised 41 races from a total of 138 isolates, based on virulence to 12 cultivars of *Phaseolus vulgaris*. No coevolutionary pattern between fungus and plant was detected, but greatest pathogen diversity occurred in Central America, which is the centre of origin of the host plant. In a similar study, 90 pathotypes were detected by Mahuku & Riascos (2004) from 200 isolates collected in Central and South America. Greater diversity was detected in the Mesoamerican region compared with Andean populations. Sharma *et al.* (2007) conducted a similar study in north-west India, detecting substantial further diversity with 29 pathogenic races from a pool of 90 isolates, of which 17 had not been reported by Mahuku & Riascos (2004). On a smaller scale, six different races of *C. lindemuthianum* were reported from two counties in the state of Minas Geraes, Brazil (Pinto *et al*. 2012), demonstrating complex population structure within a small area. Heterothallic mating and teleomorph formation were demonstrated for *C. lindemuthianum* by Rodriguez-Guerra *et al*. (2005). This body of research provides indications that the taxon concerned is undergoing rapid evolutionary change.

Variability and evolution at population level have been investigated for other species and species clusters in *Colletotrichum* including *C. acutatum* (*e.g.* Freeman *et al*. 2000, 2001, Denoyes-Rothan *et al.* 2003, Peres *et al*. 2008), *C. cereale* (Crouch *et al*. 2008, 2009d), *C. coccodes* (Ben-Daniel *et al.* 2010), *C. gloeosporioides* (Cisar *et al*. 1994, Cisar & TeBeest 1999), *C. graminicola* (*e.g.* Vaillancourt *et al*. 2000, Chen *et al*. 2002, Valèrio *et al*. 2005), *C. sublineola* (Rosewich *et al*. 1998), *C.* "*truncatum*" (actually a member of the *C. destructivum* clade; Menat *et al.* 2012). This is by no means a comprehensive list of research papers on this topic – a full assessment would justify a further major review.

HISTORY OF CLASSIFICATION

The generic name *Colletotrichum* was introduced by Corda (1831) for *C. lineola*, a species found associated with a member of the *Apiaceae* in the Czech Republic. *Colletotrichum lineola* was long considered a synonym of the older taxon *C. dematium*, but was recently re-established as an independent species (Damm *et al.* 2009). That work included the acquisition and culture of a recent collection of *C. lineola* from a similar host and locality, and designation of an epitype for the name.

The genus *Vermicularia* (Tode 1790) could be regarded as an earlier name for *Colletotrichum* according to some interpretations of the Code of Nomenclature for Algae, Fungi and Plants. The nomenclatural details have been outlined successively in the light of the then current rules by Duke (1928), Sutton (1992) and Damm *et al.* (2009), and will not be repeated here. Any move to establish *Vermicularia* as a replacement name for *Colletotrichum* would have disastrous consequences for scientific communication, and would certainly trigger a conservation proposal. *Vermicularia* was adopted quite widely for curved-spored species in the early years of *Colletotrichum* systematics, even though the type species of *Colletotrichum* also has curved conidia. The genus *Gloeosporium* (Montagne 1849) was also frequently confused with *Colletotrichum* in the late 19th and early 20th centuries. It was used for taxa of *Colletotrichum* without conidiomatal setae (their development in many species is variable) but also included quite unrelated fungi. The type of *Gloeosporium*, *Gl. castagnei* is not congeneric with *Colletotrichum* and is currently included in *Marssonina*, technically providing an earlier name for that genus (von Arx 1957a, 1970). A further 10 generic synonyms for *Colletotrichum* were listed by Sutton (1980); none has been in recent use.

Two further species (both currently of uncertain application) were added to *Colletotrichum* by Corda in the years following the original publication of the genus name (Corda 1837, 1840), but the group only came to prominence in the late 19th century with publication of Saccardo's *Sylloge Fungorum* compilations. Fifty new taxa at species level or below were described between 1880 and 1900, and this trend of new species recognition accelerated well into the 20th century. At the time of the first formal monographic treatment of *Colletotrichum*, by von Arx (1957b), around 750 names were in existence. This explosion of what might now be regarded as largely futile taxonomic activity seems to have been driven largely by uncritical assumptions that *Colletotrichum* species are strongly host-specific. The result was that in many instances a new taxon was erected each time an infection caused by a *Colletotrichum* species was discovered on a plant genus for which no disease had previously been reported, even in the absence of unique morphological diagnostic characters.

The impact of von Arx's monograph (von Arx 1957b) was considerable, and it set the stage for a new era in *Colletotrichum* taxonomy. His approach was based on morphological characteristics with little or no emphasis on placed on pathological features, which led to a reduction in accepted species from around 750 to 11 (within a total of 23 accepted specific and infraspecific taxa). Many taxa were evaluated based on descriptions from the literature rather than evaluation of type specimens. Such a drastic reduction in numbers of taxa provided a new foundation on which to develop subsequent systematic treatments, but it is clear that even von Arx himself regarded the 11 accepted species as broadly circumscribed aggregates rather than individual taxa. In particular, the account of *C. gloeosporioides* (itself with around 600 synonyms) incorporated

a series of nine "abweichende Formen" [variant forms], including five taxa combined into *Colletotrichum* by von Arx in this work or the companion volume on *Gloeosporium* (von Arx 1957a). These variant forms were considered to be host-specific variants that could not reliably be distinguished on a morphological basis from the main bulk of *C. gloeosporioides*. Included were species now treated within the *C. orbiculare*, *C. acutatum* and *C. gloeosporioides* aggregates, as well as other taxa that are currently of uncertain affiliation. Von Arx's approach to *Colletotrichum* classification now appears crude even in purely morphological terms, and as Sutton (1992) and Cannon *et al.* (2000) both noted, more attention to matters of typification would have been valuable. Nonetheless, this seminal work of von Arx laid the foundation for all subsequent morphological taxonomic work on the genus *Colletotrichum*.

Subsequent taxonomic treatments primarily focused on species groups, or taxa associated with particular crop plants. Important contributions were made in the 1960s by Simmonds (1965; recognition of *Colletotrichum acutatum*), and by Sutton (1966, 1968; taxonomy of the *C. graminicola* complex and the value of appressorial morphology in classification). The next comprehensive treatment of *Colletotrichum* was by Sutton (1980), who accepted 22 species, and a study of 11 South African species was contributed by Baxter *et al.* (1983). Both of these accounts focused primarily on morphological and cultural characteristics, and most of the taxa were considered to be plurivorous. Similar approaches were adopted by Smith & Black (1990) for species on strawberry, and Walker *et al.* (1991) for those associated with *Xanthium*, but with increased emphasis on integration of taxonomic and pathological data.

The first International Workshop on *Colletotrichum* was held in late 1990 at the University of Bath, UK (Bailey & Jeger 1992), bringing together experts on taxonomy, molecular biology, host/parasite interactions and pathology. This marked the advent of the wide-scale application of molecular methods in *Colletotrichum* studies, which has revolutionised research in that genus as with many other fungal groups. Initially, work focused on infraspecific variation; DNA polymorphisms were detected in *C. gloeosporioides* by Dale *et al.* (1988), Braithwaite & Manners (1989) and Braithwaite *et al.* (1990a, b), and strains of that species (as then circumscribed) were found to have variable numbers of chromosomes (Masel *et al.* 1990).

The first applications of DNA sequence data to distinguish between *Colletotrichum* species were published by Mills *et al.* (1992) and Sreenivasaprasad *et al.* (1992), who identified sequence variation in the ITS1 region of nrDNA between six species of *Colletotrichum*, as well as detecting polymorphisms in the same region between strains of *C. gloeosporioides* from different hosts. More comprehensive studies followed rapidly; Sherriff *et al.* (1994) presented the first bootstrapped NJ trees for *Colletotrichum*, using ITS2 and LSU sequences of 27 strains indicated as belonging to 13 species. This study recognised the *C. orbiculare* aggregate as a distinct taxonomic unit, and detected genetic congruence between the four curved-spored species studied. In a portent of things to come, Sherriff *et al*. showed that not all of the strains examined were correctly identified using morphological characteristics, with one strain each of *C. gloeosporioides* and *C. lindemuthianum* clustering separately from the others. A second phylogenetic study of the genus was published by Sreenivasaprasad *et al.* (1996) using parsimony analysis of ITS 1 and 2 sequences from 18 species of *Colletotrichum*, and the authors were able to identify six infrageneric groups. Sreenivasaprasad *et al.* also used infra- and interspecific nucleotide identity in the ITS region as indicators of the taxonomic rank at which strains should be differentiated, as an early forerunner of the DNA barcoding initiatives.

The number of papers using molecular methods to elucidate relationships in *Colletotrichum* increased rapidly after the early 1990s. Most of these studies focused on small groups within the genus, usually associated with a particular crop (see Table 1). More wide-ranging studies were presented by Johnston & Jones (1997), who used LSU rDNA sequences to analyse strains from diseased fruit crops in New Zealand, and Moriwaki *et al.* (2002) who studied ITS-2/LSU rDNA of *Colletotrichum* species from Japan. The first multilocus phylogenetic analyses of *Colletotrichum* species were published by Talhinhas *et al*. (2002), a study of the *C. acutatum* aggregate associated with lupins using ITS, TUB2 and HIS4 sequences, and Vinnere *et al.* (2002) using ITS, TUB2 and mtSSU in a study on the same species cluster associated with *Rhododendron* in Sweden and Latvia. Talhinhas *et al*. (2002) found that the three loci they studied displayed broadly similar levels of phylogenetic resolution. Guerber *et al.* (2003) used glyceraldehyde-3-phosphate dehydrogenase (GAPDH) and glutamine synthetase (GS) nucleotide sequences in a further study of the *C. acutatum* group, and the HMG-box section of the mating-type genes MAT-1 was found to be a valuable evolutionary marker by Du *et al.* (2005). From around this time, multilocus analyses became the norm as sequencing costs reduced, with sequence data generated from loci such as actin (ACT), calmodulin (CAL), chitin synthase I (CHS-1), DNA lyase (APN2), manganese superoxide dismutase (SOD2), the large subunit of RNA polymerase II (RPB1) and the translation elongation factor 1-α (EF1α) (see Table 1 for references).

A further milestone in *Colletotrichum* systematics was reached with publication of a special issue of the journal *Fungal Diversity* in late 2009, containing a group of papers presenting taxonomic revisions and review articles relevant to the genus. This includes an introductory paper focusing on the need for correct identification (Hyde *et al.* 2009b), a review of the cereal-inhabiting species (Crouch & Beirn 2009), a revision of the species with curved conidia from herbaceous hosts (Damm *et al.* 2009), a study of the species affecting coffee berries in Thailand (Prihastuti *et al.* 2009), a partial revision of the *C. acutatum* group (Shivas & Tan 2009) and research on the species associated with *Amaryllidaceae* (Yang *et al.* 2009). The issue concludes with a review of the status of *Colletotrichum* names in current use (Hyde *et al.* 2009a) and recommendations for polyphasic methods (Cai *et al.* 2009).

The list of *Colletotrichum* names in current use (Hyde *et al.* 2009a) accepted a total of 66 species, with an additional 20 recently used names considered as doubtful. This assessment represented a substantial increase in the number of recognised species compared with the 23 taxa recognised by von Arx (1957) and the 39 species accepted by Sutton (1992), and reflected the increasing reliance on molecular methods for species definition. With publication of the current volume of Studies in Mycology, a further 41 species are introduced, bringing the current number of accepted *Colletotrichum* species to over 100. It is likely that further *Colletotrichum* taxa remain to be recognised in the major clades that have not yet been the subject of comprehensive multilocus studies.

Colletotrichum species from non-cultivated plants in natural and semi-natural habitats are much less commonly studied than those associated with cultivated plant hosts, with most studies being of endophytic strains. A study on leaf endophytes of native forest trees by Lu *et al.* (2004) examined diversity within the *C. gloeosporioides* and *C. boninense* species clusters, and Xiao *et al.* (2004) and Mackenzie *et al*. (2007) compared strains of the *C. gloeosporioides*

Table 1. Summary of principal phylogenetic research papers on *Colletotrichum* species based on DNA sequence data.

Publication	Clade	Host taxa	Geographical limits	Loci used
Mills *et al.* (1992)	genus-wide	Tropical fruits		ITS
Sreenivasaprasad *et al.* (1992)	acutatum, gloeosporioides	Strawberry		ITS
Sreenivasaprasad *et al.* (1993)	gloeosporioides	Coffee		ITS
Sherriff *et al.* (1994)	genus-wide			ITS-2, LSU
Sherriff *et al.* (1995)	graminicola	*Poaceae*		LSU
Bailey *et al.* (1996)	orbiculare	*Malvaceae*		ITS, LSU
Sreenivasaprasad *et al.* (1996)	genus-wide			ITS
Johnston & Jones (1997)	genus-wide	Fruit crops	New Zealand	LSU
Munaut *et al.* (1998)	gloeosporioides	*Stylosanthes*	Africa, Australia	ITS
Balardin *et al.* (1999)	orbiculare	*Phaseolus*		ITS
Martin & García-Figueres (1999)	acutatum, gloeosporioides	Olive	Spain	ITS
Freeman *et al.* (2000)	acutatum, gloeosporioides	Almond, avocado, strawberry	Israel, USA	ITS, LSU
Freeman *et al.* (2001)	acutatum	Mostly fruit crops		ITS
Hsiang & Goodwin (2001)	graminicola	*Poaceae*		ITS
Abang *et al.* (2002)	gloeosporioides	Yam	Nigeria	ITS
Chen *et al*. (2002)	graminicola	*Agrostis*	Canada	MAT2
Moriwaki *et al.* (2002)	genus-wide		Japan	ITS-2, LSU
Munaut *et al.* (2002)	gloeosporioides	*Stylosanthes*	Mexico	ITS
Nirenberg *et al.* (2002)	acutatum	Lupin		ITS
Talhinhas *et al.* (2002)	acutatum	Lupin		ITS, TUB2, HIS4
Vinnere *et al.* (2002)	acutatum	*Rhododendron*	Sweden, Latvia	ITS, TUB2, mtSSU
Afanador-Kafuri *et al.* (2003)	acutatum, gloeosporioides	Mango, passion-fruit, tamarillo	Colombia	ITS
Denoyes-Rothan *et al.* (2003)	acutatum, gloeosporioides	Strawberry		ITS
Guerber *et al.* (2003)	acutatum		USA, New Zealand	GAPDH, GS
Martínez-Culebras *et al.* (2003)	acutatum, gloeosporioides	Strawberry		ITS
Moriwaki *et al.* (2003)	boninense		Japan	ITS
Sanders & Korsten (2003)	gloeosporioides	Avocado, mango	South Africa	ITS
Ford *et al*. (2004)	destructivum	Legumes		ITS
Lu *et al.* (2004)	boninense, gloeosporioides	Endophytes of tropical trees	Guyana	ITS
Lubbe *et al.* (2004)	Genus-wide	*Proteaceae*	primarily Africa	ITS, TUB2
O'Connell *et al.* (2004)	destructivum			ITS
Du *et al.* (2005)	acutatum, graminicola, gloeosporioides			ITS, MAT1-2 (HMG marker)
Lee *et al.* (2005)	boninense	*Euonymus japonicus*	Korea	ITS
Lotter & Berger (2005)	acutatum	Lupin	South Africa	ITS, TUB1, TUB2
Photita *et al.* (2005)	genus-wide		Thailand	ITS
Talhinhas *et al.* (2005)	acutatum, gloeosporioides	Olive	Portugal	ITS, TUB2
Chung *et al.* (2006)	acutatum, gloeosporioides	Fruit crops	Japan	ITS
Crouch *et al.* (2006)	graminicola	*Poaceae*	USA	ITS, MAT1-2 (HMG marker), SOD2
Farr *et al.* (2006)	genus-wide	*Agavaceae*		ITS, LSU
González *et al.* (2006)	acutatum, gloeosporioides	Apple	USA, Brazil	GAPDH
Ramos *et al.* (2006)	acutatum, gloeosporioides	*Citrus*	Portugal	ITS, TUB2
Latunde-Dada & Lucas (2007)	destructivum, truncatum, graminicola			ITS, LSU
Lee *at al.* (2007)	acutatum, gloeosporioides	Apple	Korea	ITS, TUB2
Liu *et al.* (2007a)	orbiculare			GAPDH, GS
Liu *et al.* (2007b)	dracaenophilum	*Buxus*	China	ITS
Shenoy *et al.* (2007)	truncatum	*Solanaceae*		ITS, TUB2
Whitelaw-Weckert *et al.* (2007)	acutatum	Grape	Australia	ITS, TUB2
Cannon *et al.* (2008)	gloeosporioides			ITS

Table 1. (Continued).

Publication	Clade	Host taxa	Geographical limits	Loci used
Crouch *et al.* (2008)	graminicola	*Poaceae*		Ccret2
LoBuglio & Pfister (2008)	acutatum	*Acer platanoides*	USA	ITS, LSU
Marcelino *et al.* (2008)	acutatum	Insects	USA	ITS, LSU, TUB2, GAPDH, GS, MAT1-2
Peres *et al.* (2008)	acutatum	*Citrus*	N and S America	ITS, GAPDH
Than *et al.* (2008a)	acutatum, truncatum, gloeosporioides			ITS, TUB2
Than *et al.* (2008b)	acutatum			ITS, TUB2
Crouch *et al.* (2009c)	graminicola	*Poaceae*		ITS, APN2/IGS/MAT1-2, SOD2
Crouch *et al.* (2009d)	graminicola	*Poaceae*		ITS, APN2/IGS/MAT1-2, SOD2
Damm *et al.* (2009)	dematium, spaethianum, truncatum			ITS, ACT, GAPDH, CHS-1, TUB2, HIS3
Garrido *et al.* (2009)	acutatum	Strawberry	Spain	ITS
MacKenzie *et al.* (2009)	acutatum		USA, Costa Rica	ITS, GAPDH, GS
McKay *et al.* (2009)	acutatum, boninense, gloeosporioides	Almond	Australia	ITS
Moriwaki & Tsukiboshi (2009)	graminicola	*Echinochloa*	Japan	ITS, MAT1-2 (HMG marker), SOD2
Pileggi *et al.* (2009)	boninense, gloeosporioides	*Maytenus ilicifolia*	Brazil	ITS
Polashock *et al.* (2009)	acutatum, gloeosporioides	Cranberry	N America	ITS, LSU
Prihastuti *et al.* (2009)	gloeosporioides	Coffee	Thailand	ITS, ACT, TUB2, CAL, GS, GAPDH
Shivas & Tan (2009)	acutatum			ITS, TUB2
Sun & Zhang (2009)	destructivum			ITS
Talhinhas *et al.* (2009)	acutatum, gloeosporioides	Olive	Portugal	ITS, TUB2
Yang *et al.* (2009)	genus-wide	*Amaryllidaceae*	China, Thailand	ITS, ACT, TUB2, CAL, CHS-1, GAPDH
Giaretta *et al.* (2010)	acutatum, gloeosporioides	Apple	Brazil	ITS
Hemelrijk *et al.* (2010)	acutatum	Strawberry	Belgium	ITS
Lopez & Lucas (2010)	gloeosporioides	Cashew	Brazil	LSU
Manuel *et al.* (2010)	gloeosporioides	Coffee	Angola	ITS
Nguyen *et al.* (2010)	genus-wide	Coffee	Vietnam	ITS, mtSSU
Phoulivong *et al.* (2010)	gloeosporioides	Tropical fruits	Laos, Thailand	ITS, TUB1, TUB2, ACT, GAPDH
Phuong *et al.* (2010)	genus-wide	Coffee	Vietnam	ITS, mtSSU
Prihastuti *et al.* (2010)	graminicola	*Poaceae*		ITS, APN2/IGS/MAT1
Rojas *et al.* (2010)	gloeosporioides	Cacao	S America, China	ITS, EF1α, TUB2, RPB1, APN2, MAT1-2
Weir & Johnston (2010)	gloeosporioides	Persimmon		ITS, GAPDH, EF1α
Wikee *et al.* 2010	gloeosporioides, truncatum	Jasmine	Vietnam	ITS, ACT, TUB2, CAL, GS, GAPDH
Xie *et al.* (2010)	acutatum, gloeosporioides	Strawberry	China	ITS
Choi *et al.* (2011)	destructivum		Korea	ITS, ACT, EF1α, GS
Faedda *et al.* (2011)	acutatum	Olive	Italy	ITS, TUB2
Gazis *et al.* (2011)	gloeosporioides	*Hevea* species	Peru	ITS, TEF, GPD
Liu *et al.* (2011)	coccodes	Potato		ITS, ACT, GAPDH, TUB2
Rampersad (2011)	gloeosporioides, truncatum	Papaya	Trinidad	ITS, TUB2
Silva-Rojas & Ávila-Quezada (2011)	acutatum, boninense, gloeosporioides	Avocado	Mexico	ITS, LSU
Yang *et al.* (2011)	genus-wide	Orchidaceae	China	ITS, ACT, TUB2, CAL, CHS-1, GAPDH
Crouch & Tomaso-Peterson (2012)	graminicola	Centipedegrass, sorghum		ITS, APN2/IGS/MAT1-2, SOD2

Table 1. (Continued).

Publication	Clade	Host taxa	Geographical limits	Loci used
Damm *et al.* (2012a)	acutatum			ITS, ACT, GAPDH, CHS-1, TUB2, HIS3
Damm *et al.* (2012b)	boninense			ITS, ACT, GAPDH, CHS-1, TUB2, HIS3, CAL
Silva *et al.* (2012a,b)	gloeosporioides	Coffee		ITS, ApMAT, Apn15L, MAT1-2, MAT5L, Apn1Ex3, Apn13L, TUB2, GS
Weir *et al.* (2012)	gloeosporioides			ITS, ACT, GAPDH, CHS-1, TUB2, CAL, GS, SOD2
Yang *et al.* (2012)	genus-wide	*Hemerocallis*	China	ITS, ACT, GAPDH, CHS-1, TUB2

cluster from strawberry and non-crop species. Crouch *et al*. (2006, 2009d) distinguished clades within the *C. cereale* cluster that correlated with pathogenicity, with some causing disease of turfgrasses and others isolated from asymptomatic prairie grasses. Gazis *et al*. (2011) compared Amazonian populations of endophytic taxa belonging to the *C. gloeosporioides* cluster associated with two species of *Hevea*, the cultivated *H. brasiliensis* and the non-cultivated *H. guianensis*. Higgins *et al*. (2011) studied *Colletotrichum* endophytes from grass and non-grass hosts in tropical forest in Panama, recovering some genetically distinct taxa via direct sequence from surface-sterilised grass tissue that were not detected using cultural methods. They also observed that many taxa were detected from more than one grass host genus, corroborating observations by Lu *et al*. (2004) and Arnold & Lutzoni (2007) that the commonest tropical endophytes appear to be host generalists. However, the ITS sequences used to define OTUs in all these studies are too conservative to reflect all speciation events (Crouch *et al*. 2009b, Gazis *et al*. 2011). Several endophyte taxa isolated from cacao in Panama by Rojas *et al*. (2010) were thought to comprise part of the background endophytic community in the Panamanian forest ecosystem, but most strains studied came from crop plants and their status as native species needs further investigation.

All of the studies of *Colletotrichum* associated with non-crop plants detailed above demonstrate considerable diversity of taxa. Despite preliminary evidence that host specificity is less in native tropical forest ecosystems compared with managed environments, the sheer number of habitats (in the form of leaves, fruits etc.) that remain unsampled indicate the likelihood that overall species-level diversity of the genus is still significantly under-represented.

PHYLOGENETIC POSITION

Colletotrichum, as an asexual fungal genus, was included in morphological classifications of the *Ascomycota* as its sexual genus *Glomerella*. Successive editions of the *Dictionary of the Fungi* until edn 6 (Ainsworth, 1971) listed *Glomerella* as a member of the *Phyllachoraceae* in the order *Sphaeriales*. The *Phyllachoraceae* was originally described by Theissen & Sydow (1915) as part of the *Dothideales*. Petrak (1924) concluded that *Phyllachora*, *Polystigma* and *Physalosporina* (= *Stigmatula*; see Cannon 1996) constituted a natural family that did not belong to the *Dothideales*. Chadefaud (1960) introduced (but did not validly publish) the ordinal name *Glomerellales*, including *Glomerella*, *Phyllachora* and two other genera in a non-ranked group "Eu-Glomérellales". Barr (1976) introduced (but again did not validly publish) the ordinal name *Phyllachorales*, in which was included a disparate set of families with the *Phyllachoraceae* subsumed into the *Melogrammataceae*. *Glomerella* was accepted as part of that assemblage. Seven years later, Barr (1983) validated the ordinal name *Phyllachorales* but did not explicitly alter its composition. The same year, Hawksworth *et al.* (1983) placed *Glomerella* in its traditional position in the *Phyllachoraceae*, but treated the family as the only representative of the *Polystigmatales*, yet another name that appears not to have been validly published. Edition 8 of the *Dictionary of the Fungi* (Hawksworth *et al*. 1995) adopted a similar classification, though the ordinal name *Polystigmatales* was replaced by *Phyllachorales.*

Glomerella had long been considered to be an outlier within the *Phyllachoraceae* due to its non-stromatic nature (Cannon 1991). The family name *Glomerellaceae* was first published (invalidly) by Locquin (1984), in a general account of the fungi in which no fewer than 278 new families were introduced. Locquin's work was generally ignored, until preliminary sequence-based studies along with ontogenetic research (Uecker 1994) confirmed that *Glomerella* and *Phyllachora* did not belong to the same order of fungi. The *Glomerellaceae* was adopted in the 9th edition of the *Dictionary of the Fungi* with an uncertain position within the *Sordariomycetidae* (Kirk *et al.* 2001), and in the 10th edition as an unplaced taxon within the *Hypocreomycetidae* (Kirk *et al.* 2008).

The first attempts to place *Glomerella*/*Colletotrichum* within a molecular phylogenetic system were published by Illingworth *et al.* (1991) and Berbee & Taylor (1992), using 18S rDNA sequences. Although the number of taxa sampled was insufficient to provide reliable placement, the samples of *C. gloeosporioides* included in these studies were shown to cluster with members of the *Hypocreales*. Most subsequent phylogenetic studies included *Glomerella/Colletotrichum* only as outgroups, or to provide an overall framework for the phylogeny of unrelated groups (*e.g.* Zhang & Blackwell 2002, Castlebury *et al.* 2004, Huhndorf *et al.* 2004).

There is very little information available on sequences from the *Phyllachoraceae sensu stricto*. Winka & Eriksson (2000) found that two 18S rDNA sequences from *Phyllachora* species clustered in the *Sordariomycetidae* clade, while *Glomerella cingulata* was considered to be more closely related to the *Hypocreomycetidae*. Wanderlei-Silva *et al.* (2003) also published a study based on 18S rDNA, that claimed that the *Phyllachoraceae* was polyphyletic. In this work, core taxa clustered with the *Sordariales*, *Ophiodothella vaccinii* clustered within the *Xylariales*, and *Glomerella/Colletotrichum* was shown as a sister group to the *Hypocreales.*

Zhang *et al.* (2006) confirmed the phylogenetic position of *Glomerella* within the *Hypocreomycetidae*, and provided a Latin

diagnosis for the *Glomerellaceae*. A sister taxon relationship with *Verticillium* was recovered (Zhang *et al.* 2006), but this clustering appears to be an artefact of limited taxa sampling. Subsequent investigations assigned *Verticillium* to the *Plectosphaerellaceae* (Zare *et al.* 2007, Cannon *et al.* 2012), following the conclusions of Zare *et al.* (2000). The phylogenetic position of the *Glomerellaceae* was further elucidated by Réblová *et al.* (2011) in a study using ITS, LSU, SSU and rpb2 genes. In this work, the *Glomerellaceae* occupied a common clade with two newly recognised families, the *Australiascaceae* and *Reticulascaceae*. They accordingly validated the order *Glomerellales* (first introduced by Chadefaud 1960 but without a Latin diagnosis) for the three families. Based on SSU data, Réblová *et al.* (2011) showed that the *Glomerellales* occupied a well-supported clade that included the *Hypocreales*, *Microascales* and the *Plectosphaerellaceae*, equivalent to the *Hypocreomycetidae* as delimited by Zhang *et al.* (2006). Similar results were obtained with LSU sequence data, although the separation of the *Hypocreomycetidae* was not supported by bootstrap analysis or posterior probability measures (Réblová *et al.* 2011). This is probably not the final word in elucidation of the phylogenetic position of *Colletotrichum*, but the *Glomerellales* clade is well supported despite significant morphological differences between the three families included.

SEXUAL MORPHS AND SEXUAL-ASEXUAL CONNECTIONS

In common with many other fungal pathogens, the *Colletotrichum* asexual morph is most commonly associated with disease symptoms, with the sexual morph tending to develop on moribund or dead host tissues (Sutton 1992). *Colletotrichum* sexual morphs are therefore under-studied in comparison with the asexual stages. This lack of attention to the sexual morphs is compounded by the need to identify species from cultures, the preparation of which may keep compatible strains separate. This makes it difficult to assess the prominence of the *Glomerella* stages in nature compared with their asexual morphs.

Colletotrichum sexual morphs were first described by Stoneman (1898) in the genus *Gnomoniopsis* Stoneman, in a comprehensive and well-illustrated account of the development of anthracnose diseases in the USA. Four species were described in full, all of which were linked to previously described asexual morphs; *Gn. cingulata* (anamorph *Gloeosporium cingulatum*, from *Ligustrum vulgare*), *Gn. piperata* (asexual *Gl. piperatum*, from *Capsicum annuum*), *Gn. cincta* (asexual *Colletotrichum cinctum*, from the orchids *Maxillaria picta* and *Oncidium* sp.) and *Gn. rubicola* (asexual *C. rubicola*, from *Rubus strigosus*). A fifth species, given the name *Gnomoniopsis*? *vanillae* (asexual *Colletotrichum* sp., from *Vanilla*) was also described in a preliminary manner. All of the species accepted were linked to their asexual morphs by cultural methods in the laboratory.

Von Schrenk & Spaulding (1903) pointed out that Stoneman's genus was a later homonym of *Gnomoniopsis* Berl. (Berlese 1893; type *Gn. chamaemori*), which is not closely related to the anthracnose pathogens. *Gnomoniopsis* Berl. has recently been confirmed as a genus of the *Gnomoniaceae* (*Diaporthales*) rather than the *Glomerellaceae* (Sogonov *et al.* 2008). Von Schrenk and Spaulding (1903) accordingly proposed the name *Glomerella* for the anthracnose-causing species, making new combinations for the four species definitely accepted by Stoneman in her genus and adding a fifth, *Glomerella rufomaculans*, considered to be the causal agent of bitter rot of apple (see also Du *et al.* 2005). The type of *Gnomoniopsis* Stonem. was not originally specified, and nor was that of *Glomerella*. The earliest lectotypification of *Glomerella* appears to be by Clements & Shear (1931), who designated *Ga. cingulata* as type. This choice has been accepted by subsequent authors, most notably by von Arx & Müller (1954) and von Arx (1987).

A comprehensive monograph for *Glomerella* has never been published. The broadest treatment to date is by von Arx & Müller (1954), at a similar level of detail to the revision of *Colletotrichum* three years later by von Arx (1957b). Von Arx & Müller recognised only five species, two of which are poorly known and cannot be confirmed as belonging to *Glomerella*.

Those excluded by us from von Arx & Müller's concept of *Glomerella* include *Ga. guevinae* (syn. *Chiloëlla guevinae*), which has ascospores that are covered in a gelatinous sheath and are much smaller than those of typical *Glomerella* species. No asexual morph has been seen. Sydow (1928) suggested that *Chiloëlla* has affinities with *Physalospora* (*Hyponectriaceae*) or *Plagiostoma* (*Gnomoniaceae*). Type material has not been traced, and so *Chiloëlla* remains of uncertain affinity. *Ga. montana* (syn. *Physalospora montana*, *Phyllachora montana*) was considered by Parbery (1964) to have affinities with a small group of *Phyllachora* species on montane grasses with sexual morphs that mature on dead plant tissues. Authentic material of the species in K conforms with this interpretation. Von Arx & Müller (1954) did find the type material to be in association with old *Colletotrichum* fruit-bodies, but there is no demonstrated connection between the morphs.

The three species treated by von Arx & Müller (1954) that definitely belong to *Glomerella* are the type *Ga. cingulata*, *Ga. tucumanensis* and *Ga. amenti*. *Glomerella tucumanensis* is widely accepted as the sexual morph of *Colletotrichum falcatum*, the cause of red rot of sugarcane. Work by Sutton (1968) and Crouch *et al*. (2009c) confirm this species as a distinct and apparently host-specific pathogen using both morphological and molecular criteria. *Glomerella amenti* (syn. *Phyllachora amenti*, *Haplothecium amenti*) was described from flower stalks and bracts of the arctic-alpine species *Salix reticulata*, an unexpected habitat for a species of *Glomerella*, but its phylogenetic position has been reassessed (Damm *et al.* 2012a), and confirmed as a synonym of *C. salicis*, a member of the *C. acutatum* clade.

Glomerella cingulata is now widely recognised as a species aggregate and the sexual counterpart to the *C. gloeosporioides* aggregate, although the connection has not been explicitly proved, and the link at species level may well be incorrect. As far as we are aware, type material of *Ga. cingulata* has not been examined in modern times (though a possible authentic specimen is preserved in BPI). Similarly, the identity of *Gloeosporium cingulatum* Atk., with which *Ga. cingulata* was linked by Stoneman (1898), has not been critically reassessed, and the conidia of *Gloeo. cingulatum* as illustrated by Stoneman could also belong to the *C. acutatum* clade.

Shear & Wood (1907) and Edgerton (1908) considered that at least several of the putatively host-specific taxa described by Stoneman (1898) as species of *Gnomoniopsis* were conspecific, although they did not include material ascribed to *Ga. cingulata* in their studies. The equation of the name *Ga. cingulata* with the species aggregate rather than the fungus causing disease of *Ligustrum* was further established in works by Dastur (1920) and Small (1921, 1926), which focused on cross-inoculation experiments.

Since the name *Glomerella cingulata* was originally published, unnecessary or poorly justified taxa proliferated for the same reason

Table 2. *Colletotrichum* species with reported *Glomerella* sexual morphs.

***Colletotrichum* species**	***Glomerella* species**	**Reference**	**Method**	**Teleomorph placement (von Arx & Müller 1954)**	**Current clade**	**Notes**
C. "acutatum"	*Ga. acutata*	Guerber & Correll (2001), Damm *et al.* (2012a)	Laboratory crossing	NA	acutatum	Teleomorph type a hybrid between *C. acutatum* and *C. fioriniae*
C. annellatum	Unnamed	Damm *et al.* (2012b)	Developed on SNA medium and sterile plant stem in culture	NA	boninense	
C. boninense	Unnamed	Damm *et al.* (2012b)	Developed on SNA and OA medium	NA	boninense	
C. brassicicola	Unnamed	Damm *et al.* (2012b)	Developed on sterile plant stem in culture	NA	boninense	
C. cinctum	*Ga. cincta*	Stoneman (1898)	Laboratory culture	*Ga. cingulata*		Connection doubtful (see Damm *et al.* 2012b), modern revision needed
Gloeosporium cingulatum	*Ga. cingulata*	Stoneman (1898)	Laboratory culture of sterilised bean stem, single-ascospore cultures	*Ga. cingulata*	gloeosporioides ?	Identity and placement uncertain, modern revision needed
C. cliviae	Unnamed	Yang *et al.* (2011)	Developed on PDA medium	NA		Not closely related to any established clade
C. constrictum	Unnamed	Damm *et al.* (2012b)	Developed on SNA medium and sterile plant stem in culture	NA	boninense	
C. cymbidiicola	Unnamed	Damm *et al.* (2012b)	Developed on SNA medium and sterile plant stem in culture	NA	boninense	
C. destructivum	*Ga. glycines*	Manandhar *et al.* (1986)	Laboratory culture	*Ga. cingulata*	destructivum	Identification of both morphs doubtful, modern revision needed
C. falcatum	*Ga. tucumanensis*	Carvajal & Edgerton (1944), Politis (1975)	Laboratory culture	*Ga. tucumanensis*	graminicola	
C. fioriniae	*Ga. fioriniae*	Marcelino *et al.* (2008), Shivas & Tan (2009)	Laboratory mating study	NA	acutatum	
C. fructicola	Unnamed	Prihastuti *et al.* (2009)	Laboratory culture	NA	gloeosporioides	
C. gloeosporioides	*Ga. cingulata*	*e.g.* Cisar *et al.* (1994), Cisar & TeBeest (1999)	Co-occurrence on host, laboratory mating study	*Ga. cingulata*	gloeosporioides	Connection unlikely to be correct, placement uncertain
C. glycines	*Ga. glycines*	Lehman & Wolf (1926)	Culture of both morphs	*Ga. cingulata*	truncatum	Treated as an independent species by von Arx (1987). Connection doubtful, modern revision needed
C. gossypii	*Ga. gossypii*	Edgerton (1909)	Laboratory culture	*Ga. cingulata*	gloeosporioides	Modern revision needed
C. graminicola	*Ga. graminicola*	Politis (1975), Vaillancourt & Hanau (1991, 1992)	Laboratory mating study	NA	graminicola	
C. "heveae"	*Ga. phyllanthi*	Pai *et al.* (1970)	Developed on PDA medium	NA	boninense	Connection based on wrong identification of the anamorph, see *C. phyllanthi*
C. ignotum	Unnamed	Rojas *et al.* (2010)	Laboratory culture	NA	gloeosporioides	
C. karstii	Unnamed	Yang *et al.* (2011), Damm *et al.* (2012b)	Developed on SNA and PDA medium	NA	boninense	
C. lagenarium	*Ga. lagenaria*	Stevens (1931)	CMA culture with UV irradiation	*Ga. cingulata*	orbiculare ?	Modern revision needed

Table 2. (Continued).

Colletotrichum species	*Glomerella* species	Reference	Method	Teleomorph placement (von Arx & Müller 1954)	Current clade	Notes
C. lindemuthianum	*Ga. lindemuthiana*	Shear & Wood (1913), Rodríguez-Guerra *et al.* (2005)	Laboratory culture or laboratory crossing	*Ga. cingulata*	orbiculare	Modern revision needed
Gloeosporium lycopersici	*Ga. lycopersici*	Krüger (1913)	Laboratory culture, inoculated tomato fruits	*Ga. cingulata*	acutatum	Synonym of *C. salicis*
C. mume	*Ga. mume*	Hemmi (1920)	Laboratory culture	*Ga. cingulata*		Modern revision needed
C. musae	*Ga. musarum*	Petch (1917)	present on same piece of host tissue	*Ga. cingulata*	gloeosporioides	Connection needs further research: see Weir *et al.* (2012)
C. orchidearum	Unnamed	Yang *et al.* (2011)	Developed on PDA medium	*Ga. cingulata*	Not closely related to any established clade	Identity of this fungus is not completely clarified
C. parsonsii	Unnamed	Damm *et al.* (2012b)	Developed on SNA medium	NA	boninense	
C. petchii	Unnamed	Damm *et al.* (2012b)	Developed on sterile plant stem in culture	NA	boninense	
C. phomoides	*Ga. phomoides*	Swank (1953)	both morphs developing from single-conidium isolate	*Ga. cingulata*	dematium ?	Modern revision needed
C. phormii	*Ga. phormii*	Hennings (1898), Farr *et al.* (2006), Damm *et al.* (2012a)	Developed on leaves	*Ga. phacidiomorpha* and *Ga. cingulata*	acutatum	Also see Kinghorn (1936) and von Arx (1987), misapplied as *Ga. phacidiomorpha*
C. phyllanthi	*Ga. phyllanthi*	Pai *et al.* (1970), Damm *et al.* (2012b)	based on type specimen (dried culture) and description (living culture sterile)	NA	boninense	Anamorph and teleomorph based on same type
C. piperatum	*Ga. piperata*	Stoneman (1898)	Laboratory culture	*Ga. cingulata*	gloeosporioides ?	Modern revision needed
C. rhodocyclum	*Ga. phacidiomorpha*	Kinghorn (1936)	Developed on the surface of living leaves, not in culture	*Ga. cingulata*	acutatum	Synonym of *C. phormii*, name *Ga. phacidiomorpha* misapplied (Farr *et al.* 2006)
C. rhombiforme	Unnamed	Damm *et al.* (2012a)	Developed on sterile plant stem in culture	NA	acutatum	
C. rubicola	*Ga. rubicola*	Stoneman (1898)	Single-conidium isolations produced both morphs	*Ga. cingulata*	acutatum ?	Modern revision needed
C. salicis	*Ga. salicis*	Damm *et al.* (2012a)	Developed on sterile plant stem in culture	*Ga. amenti, Ga. cingulata*	acutata	*Ga. amenti* forms no anamorph according to Arx and Müller (1954)
C. sublineolum	Unnamed	Vaillancourt & Hanau (1992)	Laboratory mating study	NA	graminicola	
C. taiwanense	*Ga. septospora*	Sivanesan & Hsieh (1993)	Single-ascospore isolations produced both morphs	NA		Perhaps does not belong to *Colletotrichum*, modern revision needed
Unnamed	*Ga. magna*	Jenkins & Winstead (1964)	Laboratory crossing	NA	Not closely related to any established clade	The anamorph has been referred to as "*C. magna*" (*e.g.* Redman *et al.* 1999) but the name does not appear to have been formally published. Modern revision needed
Unnamed	*Ga. miyabeana*	Fukushi (1921), Johnston & Jones (1997)	Found on stems and leaves of *Salix purpurea* var. *angustifolia* and on sterilised pieces of willow stem in culture	*Ga. cingulata*	acutatum	Synonym of *C. salicis*, treated as *Ga. miyabeana* by von Arx (1957b, 1987)
Unnamed	*Ga. truncata*	Armstrong-Cho & Banniza (2006)	Pairing of anamorph isolates	NA	destructivum	Anamorph misidentified as *C. truncatum* (Latunde-Dada & Lucas 2007, Damm *et al.* 2009)

as did those for *Colletotrichum gloeosporioides*, i.e. assumed host specificity. Von Arx & Müller provided a long list of 117 synonyms belonging to at least 42 independent taxa (they did not distinguish between homotypic synonyms and taxa in different genera with the same epithet). As with previous work on *C. gloeosporioides*, the contribution of Von Arx & Müller provided a valuable foundation for later investigations. Subsequent research has identified further distinct *Glomerella* taxa, and currently around 30 species of *Colletotrichum* are known to have (or have at least been claimed to have) *Glomerella* sexual morphs. They are listed in Table 2.

There has been little morphology-based comparison of the sexual taxa, and differential characters cited by researchers seem restricted to ascospore shape and size, with individual taxa showing wide variation and exhibiting overlapping ranges. For example, Lehman & Wolf (1926) described the ascospores of *Glomerella glycines* as ranging between 13 and 43 µm (though chiefly 19–28 µm) in length. Elsewhere, von Arx & Müller (1954) gave measurements for *Ga. cingulata* of 9–30 × 3–8 µm (mostly 12–24 × 4–7 µm). Comparative study has certainly been compromised by the excessively wide species concept for *Ga. cingulata*. However, the ascospores of *Ga. tucumanensis* were described as larger than the norm for *Ga. cingulata* by von Arx & Müller (1954). Guerber & Correll (2001) established that ascospores of *Ga. acutata* were smaller and somewhat less strongly pointed than those of *Ga. cingulata*, but qualified their conclusions as the strains studied of the latter species were too few to establish clear boundaries between the two taxa based on these criteria. Future study may identify further diagnostic morphology-based characters for the sexual morph of *Colletotrichum*, particularly when viewed in light of modern phylogenetic species concepts.

Assessment of historical asexual-sexual connections in *Colletotrichum* is very problematic. Many of the claimed links are not based on authentic material, thereby casting doubt on the identities of both morphs. Some are based on little more than juxtaposition on diseased plant samples. Even when the connections are well-researched and use correctly identified material (for the time), the identity of the holomorph may not be easy to establish using modern phylogenetic methods. Some of the information in Table 2 must therefore be considered as more of historic than scientific value.

The substantial changes in *Colletotrichum* species delimitation made possible by molecular systematic analysis mean that many asexual-sexual connections need further study, and in most cases the sexual names are not typified according to modern practice. From a nomenclatural perspective, the need for this work is now less critical as the requirement for separate naming of asexual and sexual taxa has been abolished (Hawksworth 2011). Nevertheless, the need to understand sexual recombination and production in terms of biological strategy (and potentially also economic significance) at species and population level remains clear.

Although currently available data are incomplete, it does appear that some *Colletotrichum* clades have species that form sexual morphs more readily than others. Those where sexual morphs are generated frequently, measured in terms of the proportion of consituent species with known meiotic morphs, include the gloeosporioides and boninense clades. To our knowledge, in contrast, there are no reliable reports of a sexual morph from any taxon within the truncatum clade. In other groups, such as the graminicola clade, individual species are well known to produce sexual morphs (*e.g. C. falcatum, C. graminicola*), but others seem to form them rarely or not at all (Crouch and Beirn 2009). Mating seems to be rare in the orbiculare clade, with only a small proportion of crosses between *C. lindemuthianum* strains producing fertile progeny (Rodríguez-Guerra *et al.* 2005).

The mechanisms of recombination and sexual production in *Colletotrichum* are still inadequately understood. Classical genetic research on mating systems in strains identified as *Glomerella cingulata* (*e.g.* Olive 1951, Wheeler 1954) indicated that both homothallic and heterothallic isolates exist, although their modern taxonomic placement within the gloeosporioides clade is not known. Despite documented heterothallic behaviour, only one mating type idiomorph has been recovered from population-level screening in a number of studies (*e.g.* Chen *et al*. 2002, Du *et al*. 2005, Crouch *et al.* 2008).

In a number of species, sexual production has only been documented in laboratory crosses (see Table 2), and the role of mating in natural populations is unclear. Fertile sexual morphs were produced resulting from what is now considered to be interspecific hybridisation of strains within the *C. acutatum* clade (Guerber & Correll 2001, Damm *et al*. 2012a), and this phenomenon may be widespread. Hybridisation between taxa within infrageneric clades of fungi has been demonstrated before, *e.g.* by O'Donnell *et al*. (2000) in the *Fusarium graminearum* complex, by Stukenbrock *et al*. (2012) in *Zymoseptoria* and by Turner *et al*. (2010, 2011) in *Neurospora*. In the *Neurospora* example, fertile progeny were produced from geographically isolated strains but not from sympatric isolates, suggesting that reproductive barriers evolve at a local level and can be overcome following long-distance dispersal of conidia. Not all of the strains used to produce sexual morphs in the acutatum clade (Guerber & Correll 2001) have been analysed using multilocus sequence technology, so we cannot say whether similar mechanisms are operating in *Colletotrichum*.

Mating-type gene sequences have been shown to be good markers for phylogenetic analysis. To date, they have been studied in the acutatum, graminicola, gloeosporioides and orbiculare clades (*e.g.* Du *et al.* 2005, García-Serrano *et al.* 2008, Marcelino *et al.* 2008, Crouch *et al.* 2009, Moriwaki & Tsukiboshi 2009, Rojas *et al.* 2010).

TYPIFICATION

Communication of information relating to *Colletotrichum* species has been seriously compromised in the past by misidentification, misapplication of names and grossly differing species concepts. Many of these problems were caused by uncritical use of species names on the assumptions that (a) all species are host-specific and (b) that only one species of *Colletotrichum* (or at least only one species with similar gross morphology) parasitises each host genus. Many older *Colletotrichum* names lack type specimens that are suitable for molecular analysis, and do not have authentic living strains preserved in culture collections. Because the nomenclatural Code (now entitled the *International Code of Nomenclature for Algae, Fungi and Plants*; Hawksworth 2011) now allows for the designation of epitypes, modern sequenceable collections can be used as substitutes for the original material. An epitype should have morphological, cultural and pathological characteristics similar to those described in the original publication, originate from the same geographical region and host, and preserve (where at all possible) application of the name in concord with modern usage (Cannon *et al.* 2008). Many currently used names of *Colletotrichum* now have epitypes designated (*e.g.* Cannon *et al*. 2008, Than *et al*. 2008, Damm *et al*. 2009, 2012a, b, Su *et al*. 2011, Weir *et al*. 2012).

Table 3 summarises the nucleotide sequences associated with type or other representative strains of *Colletotrichum* species, which we recommend as reference data to aid researchers and plant health practitioners in species identification. Some widely used species names included in Table 3 are of uncertain taxonomic application, as they have not been recently revised or their typification is in doubt. In some of these cases, strains and/or sequences are included in Table 3 that represent the species as generally accepted by modern authors (not necessarily taxonomists), and might thus be appropriate material on which to base epitypes or neotypes in order to preserve current application of the names. We cite these also in Table 3, but stress strongly that they do not have formal nomenclatural status and they should not be taken to be endorsed as authentic. These exceptions are indicated by the marker "none" in the column labelled "status of source material".

These data form the framework for an online identification system for *Colletotrichum* species, hosted by the Centraalbureau voor Schimmelcultures but administered by the recently formed *Colletotrichum* subcommission of the International Commission on Taxonomy of Fungi (ICTF; http://www.fungaltaxonomy.org/), which is in turn a body under the auspices of both the International Mycological Association (http://www.ima-mycology.org/) and the International Union of Microbiological Societies (http://www.iums.org/). This database can be accessed at http://www.cbs.knaw.nl/Colletotrichum/. The database will be updated periodically to include reference sequences for novel taxa and for species that have been subjected to modern phylogeny-based revision.

SPECIES CONCEPTS AND BARCODING

Our understanding of *Colletotrichum* species and the processes by which they have evolved has undergone several step changes over the years. The first part of this review focuses on the unreliability of host-based diagnosis, and the lack of resolution of taxonomic systems based firstly on morphological features, and latterly by ITS rDNA sequences. Here, we concentrate on the changes of the last 10 years, with rapid moves to species definition based on multilocus analysis, knowledge gains from molecular plant/fungus interaction studies, and the synergies with wider genetic research.

At the beginning of the century, concern was expressed at the wide constituent genetic variation between taxa of *Colletotrichum* recognised at the species level, and the varying utility of species concepts in the eyes of pathologists (Cannon *et al.* 2000). Some species, such as *C. gloeosporioides*, were defined partially by ITS sequence, but were primarily considered to represent morphological taxa. These were known to encompass extensive genetic variation, but were maintained for utilitarian reasons. *Colletotrichum kahawae* on the other hand was thought at the time to represent a single clonal population causing a specific, devastating disease of coffee berries. That species has recently been redefined with a broader circumscription (Weir *et al.* 2012).

In *Colletotrichum*, species definition based on ITS sequence has proved unsatisfactory, that gene fragment being too evolutionarily conservative to distinguish between taxa that can be recognised using other genes and gene combinations (*e.g.* Du *et al*. 2005, Crouch *et al.* 2009b, Gazis *et al*. 2009). This is of some concern, as the ITS region is widely used for species definition in the *Fungi* (*e.g.* Begerow *et al.* 2010, Druzhinina *et al.* 2005, Eberhardt 2010, Kelly *et al*. 2011), and has recently been proposed as a universal barcode sequence (Schoch *et al.* 2011, 2012).

ITS was proposed as the primary fungal barcode marker for various reasons, including pragmatism – the number of existing fungal ITS sequences is far greater than that for any other gene. Many other genes/gene fragments have been used for diagnostic purposes in the *Fungi*, especially beta-tubulin (TUB2) and calmodulin (*e.g.* for *Aspergillus* and *Penicillium*; Samson *et al.* 2007, Peterson 2008, Houbraken *et al.* 2011), TEF1 (for *Fusarium*; Geiser *et al.* 2004, O'Donnell *et al.* 2009) and COX1 (for *Penicillium*; Seifert *et al.* 2007).

Many other molecular markers have wide diagnostic potential for the *Fungi*, including most of those currently used for phylogenetic analysis in *Colletotrichum* (see Table 3). Further candidates are being considered. Aguileta *et al*. (2008) identified no fewer than 246 single-copy orthologous gene clusters in an optimally performing gene set, from analysis of 21 fungal genomes. Several widely used markers, including TUB2 and TEF1, were not included within their list of best-performing genes, and are probably unsuitable as universal fungal markers due to the presence of paralogs (James *et al.* 2006, Walker *et al*. 2012). Building on this work, Schmitt *et al.* (2009) developed primer sets for MCM7 and Tsr1, two of the most phylogenetically informative sequences identified by Aguileta *et al*. (2008). MCM7 has been shown to work effectively in widely divergent fungal groups within the *Ascomycota* (Schmitt *et al*. 2009, Raja *et al*. 2011). Walker *et al*. (2012) evaluated two further single-copy protein-encoding genes, FG1093 and MS204 that also have potential in fungal diagnostics.

The prospect of a single short universally amplifiable DNA sequence being diagnostic for all organisms (or even all species within a major taxonomic group) is enticing, but unrealistic. This does not mean that data from single loci such as ITS do not have wide application, for example in environmental sequencing (*e.g.* Buée *et al*. 2009) or analysis of historical specimens (*e.g.* Brock *et al*. 2009, Dentinger *et al*. 2010b). There is also evidence that ITS sequences alone can constitute useful barcode markers for some groups of the *Basidiomycota* (*e.g.* Kõljalg *et al*. 2005, Dentinger *et al*. 2011). It is not clear whether this apparent difference in utility of ITS-based diagnostics between ascomycetous and basidiomycetous fungi reflects different speciation patterns or variation in species concepts.

Comparison of a phylogenetic tree of *Colletotrichum* species derived from ITS sequences alone and one generated from multilocus data (Figs 2, 3) confirms that ITS resolves major clades well, though does not reflect their higher-order topology accurately in all cases. However, posterior probability support is lacking within many of the major clades, especially those containing *C. acutatum* and *C. gloeosporioides* and their respective relatives. A robust sequence-based identification system for *Colletotrichum* species must therefore use an alternative molecular marker, or a combination of markers.

Performance analysis of the genes used in a multilocus analysis of the *C. acutatum* clade (Damm *et al*. 2012a) indicates that the two most diagnostic markers are TUB2 and GAPDH, which resolved all 29 subclades. These were equated by those authors to species. In contrast, ITS sequences could only resolve 11 of the 29 taxa within the clade. TUB2 performed marginally better than GAPDH due to a larger overall number of bp differences, but even so, some clades differed only by one bp in the TUB2 sequence. An identification system based on this gene alone would therefore be vulnerable to sequencing error, suggesting that data from multiple loci should be used.

Table 3. Authentic sequences for accepted *Colletotrichum* species.

Species	Clade	Source material [1]	Status of source material	GenBank accession number(s)	Reference
C. acerbum	acutatum	CBS 128530, ICMP 12921	Culture from holotype	ITS: JQ948459; TUB2: JQ950110; ACT: JQ949780; CHS-1: JQ949120; GAPDH: JQ948790; HIS3: JQ949450	Damm *et al.* (2012a)
C. acutatum	acutatum	IMI 117617	Holotype	ITS: AF411700	Vinnere *et al.* (2002)
		CBS 112996, ATCC 56816	Culture from epitype	ITS: JQ005776; TUB2: JQ005860; ACT: JQ005839; CHS-1: JQ005797; GAPDH: JQ948677; HIS3: JQ005818	Damm *et al.* (2012a)
C. aenigma	gloeosporioides	ICMP 18608	Culture from holotype	ITS: JX010244; TUB2: JX010389; ACT: JX009443; CHS-1: JX009774; GAPDH: JX010044; CAL: JX009683; GS: JX010078; SOD2: JX010311	Weir *et al.* (2012)
C. aeschynomenes	gloeosporioides	ICMP 17673, ATCC 201874	Culture from holotype	ITS: JX010176; TUB2: JX010392; ACT: JX009483; CHS-1: JX009799; GAPDH: JX009930; CAL: JX009721; GS: JX010081; SOD2: JX010314	Weir *et al.* (2012)
C. agaves		CBS 118190	Morphology congruent with the type	ITS: DQ286221; LSU: DQ286222	Farr *et al.* (2006)
C. alatae	gloeosporioides	CBS 304.67, ICMP 17919	Culture from holotype	ITS: JX010190; TUB2: JX010383; ACT: JX009471; CHS-1: JX009837; GAPDH: JX009990; CAL: JX009738; GS: JX010065; SOD2: JX010305	Weir *et al.* (2012)
C. alienum	gloeosporioides	ICMP 12071	Culture from holotype	ITS: JX010251; TUB2: JX010411; ACT: JX009572; CHS-1: JX009882; GAPDH: JX010028; CAL: JX009654; GS: JX010101; SOD2: JX010333	Weir *et al.* (2012)
C. annellatum	boninense	CBS 129826	Culture from holotype	ITS: JQ005222; TUB2: JQ005656; ACT: JQ005570; CHS-1: JQ005396; GAPDH: JQ005309; HIS3: JQ005483; CAL: JQ005743	Damm *et al.* (2012b)
C. anthrisci	dematium	CBS 125334	Culture from holotype	ITS: GU227845; TUB2: GU228139; ACT: GU227943; CHS-1: GU228335; GAPDH: GU228237; HIS3: GU228041	Damm *et al.* (2009)
C. aotearoa	gloeosporioides	ICMP 18537	Culture from holotype	ITS: JX010205; TUB2: JX010420; ACT: JX009564; CHS-1: JX009853; GAPDH: JX010005; CAL: JX009611; GS: JX010113; SOD2: JX010345	Weir *et al.* (2012)
C. asianum	gloeosporioides	MFU 090233, ICMP 18580, CBS 130418	Culture from holotype	ITS: FJ972612; TUB2: JX010406; ACT: JX009584; CHS-1: JX009867; GAPDH: JX010053; CAL: FJ917506; GS: JX010096; SOD2: JX010328	Prihastuti *et al.* (2009), Weir *et al.* (2012)
C. australe	acutatum	CBS 116478, HKUCC 2616	Culture from holotype	ITS: JQ948455; TUB2: JQ950106; ACT: JQ949776; CHS-1: JQ949116; GAPDH: JQ948786; HIS3: JQ949446	Damm *et al.* (2012a)
C. axonopodi	graminicola?	IMI 279189	Culture from holotype	ITS: EU554086; Mat1/APN2: FJ377907; APN2: EU364993	Crouch *et al.* (2009c, d)
C. beeveri	boninense	CBS 128527, ICMP 18594	Culture from holotype	ITS: JQ005171; TUB2: JQ005605; ACT: JQ005519; CHS-1: JQ005345; GAPDH: JQ005258; HIS3: JQ005432; CAL: JQ005692	Damm *et al.* (2012b)
C. boninense	boninense	MAFF 305972, CBS 123755	Culture from holotype	ITS: AB051400, JQ005153; TUB2: JQ005588; ACT: JQ005501; CHS-1: JQ005327; GAPDH: GQ221769, JQ005240; HIS3: JQ005414; CAL: JQ005674	Moriwaki *et al.* (2003), Damm *et al.* (2012b)
C. brasiliense	boninense	CBS 128501, ICMP 18607	Culture from holotype	ITS: JQ005235; TUB2: JQ005669; ACT: JQ005583; CHS-1: JQ005409; GAPDH: JQ005322; HIS3: JQ005496; CAL: JQ005756	Damm *et al.* (2012b)
C. brassicicola	boninense	CBS 101059	Culture from holotype	ITS: JQ005172; TUB2: JQ005606; ACT: JQ005520; CHS-1: JQ005346; GAPDH: JQ005259; HIS3: JQ005433; CAL: JQ005693	Damm *et al.* (2012b)
C. brisbaniense	acutatum	CBS 292.67	Culture from holotype	ITS: JQ948291; TUB2: JQ949942; ACT: JQ949612; CHS-1: JQ948952; GAPDH: JQ948621; HIS3: JQ949282	Damm *et al.* (2012a)
C. carthami	acutatum	SAPA100011	Epitype	ITS: AB696998; TUB2: AB696992	Uematsu *et al.* (2012)
C. cereale **[2]**	graminicola	CBS 129663, KS20BIG	None	ITS: DQ126177, JQ005774; TUB2: JQ005858; ACT: JQ005837; CHS-1: JQ005795; HIS3: JQ005816; SOD2: DQ133277; MAT1-2: DQ131946	Crouch *et al.* (2006). O'Connell *et al.* (2012)

Table 3. (Continued).

Species	Clade	Source material [1]	Status of source material	GenBank accession number(s)	Reference
C. chlorophyti		IMI 103806	Culture from holotype	ITS: GU227894; TUB2: GU228188; ACT: GU227992; CHS-1: GU228384; GAPDH: GU228286; HIS3: GU228090	Damm *et al.* (2009)
C. chrysanthemi **[3]**	acutatum	SAPA 100010	Authentic specimen	ITS: AB696999; TUB2: AB696993	Uematsu *et al.* (2012)
		IMI 364540	None	ITS: JQ948273; TUB2: JQ949924; ACT: JQ949594; CHS-1: JQ948934; GAPDH: JQ948603; HIS3: JQ949264	Damm *et al.* (2012a)
C. circinans	dematium	CBS 221.81	Culture from epitype	ITS: GU227855; TUB2: GU228149; ACT: GU227953; CHS-1: GU228345; GAPDH: GU228247; HIS3: GU228051; LSU: JN940807	Damm *et al.* (2009), Schoch *et al.* (2012)
C. clidemiae	gloeosporioides	ICMP 18658	Culture from holotype	ITS: JX010265; TUB2: JX010438; ACT: JX009537; CHS-1: JX009877; GAPDH: JX009989; CAL: JX009645; GS: JX010129; SOD2: JX010356	Weir *et al.* (2012)
C. cliviae		CBS 125375	Culture from holotype	ITS: GQ485607, JX519223; TUB2: GQ849440, JX519249; ACT: GQ856777, JX519240; CHS-1: GQ856722, JX519232; GAPDH: GQ856756; CAL: GQ849464	Yang *et al.* (2009), this study
C. coccodes		CBS 369.75	Culture from neotype	ITS: HM171679, JQ005775; TUB2: JQ005859; ACT: HM171667, JQ005838; CHS-1: JQ005796; GAPDH: HM171673; HIS3: JQ005817; CAL: HM171670; GS: HM171676	Liu *et al.* (2011), O'Connell *et al.* (2012)
C. colombiense	boninense	CBS 129818	Culture from holotype	ITS: JQ005174; TUB2: JQ005608; ACT: JQ005522; CHS-1: JQ005348; GAPDH: JQ005261; HIS3: JQ005435; CAL: JQ005695	Damm *et al.* (2012b)
C. constrictum	boninense	CBS 128504, ICMP 12941	Culture from holotype	ITS: JQ005238; TUB2: JQ005672; ACT: JQ005586; CHS-1: JQ005412; GAPDH: JQ005325; HIS3: JQ005499; CAL: JQ005759	Damm *et al.* (2012b)
C. cordylinicola	gloeosporioides	MFU090551, ICMP 18579	Culture from holotype	ITS: HM470246, JX010226; TUB2: HM470249, JX010440; ACT: HM470234; CHS-1: JX009864; GAPDH: HM470240, JX009975; CAL: HM470237; GS: HM470243, JX010122; SOD2: JX010361	Phoulivong *et al.* (2010), Weir *et al.* (2012)
C. cosmi	acutatum	CBS 853.73	Culture from holotype	ITS: JQ948274; TUB2: JQ949925; ACT: JQ949595; CHS-1: JQ948935; GAPDH: JQ948604; HIS3: JQ949265	Damm *et al.* (2012a)
C. costaricense	acutatum	CBS 330.75	Culture from holotype	ITS: JQ948180; TUB2: JQ949831; ACT: JQ949501; CHS-1: JQ948841; GAPDH: JQ948510; HIS3: JQ949171	Damm *et al.* (2012a)
C. curcumae	truncatum	IMI 288937	Culture from epitype	ITS: GU227893; TUB2: GU228187; ACT: GU227991; CHS-1: GU228383; GAPDH: GU228285; HIS3: GU228089	Damm et al. (2009)
C. cuscutae	acutatum	IMI 304802	Culture from holotype	ITS: JQ948195; TUB2: JQ949846; ACT: JQ949516; CHS-1: JQ948856; GAPDH: JQ948525; HIS3: JQ949186	Damm *et al.* (2012a)
C. cymbidiicola	boninense	IMI 347923	Culture from holotype	ITS: JQ005166; TUB2: JQ005600; ACT: JQ005514; CHS-1: JQ005340; GAPDH: JQ005253; HIS3: JQ005427; CAL: JQ005687	Damm *et al.* (2012b)
C. dacrycarpi	boninense	CBS 130241, ICMP 19107	Culture from holotype	ITS: JQ005236; TUB2: JQ005670; ACT: JQ005584; CHS-1: JQ005410; GAPDH: JQ005323; HIS3: JQ005497; CAL: JQ005757	Damm *et al.* (2012b)
C. dematium	dematium	CBS 125.25	Culture from epitype	ITS: GU227819; TUB2: GU228113; ACT: GU227917; CHS-1: GU228309; GAPDH: GU228211; HIS3: GU228015; LSU: JN940809	Damm *et al.* (2009), Schoch *et al.* (2012)
C. destructivum	destructivum	CBS 149.34	None	ITS: AJ301942; TUB2: JQ005848; ACT: JQ005827; CHS-1: JQ005785; HIS3: JQ005806	O'Connell *et al.* (2012)
C. dracaenophilum		CBS 118199	Culture from holotype	ITS: DQ286209, JX519222; TUB2: JX519247; ACT: JX519238; CHS-1: JX519230; LSU: DQ286210	Farr *et al.* (2006), this study
C. echinochloae	graminicola	MAFF 511473	Culture from holotype	ITS: AB439811; SOD2: AB440153; MAT1-2: AB439820	Moriwaki & Tsukiboshi (2009), Crouch *et al.* (2009c, d)

Table 3. (Continued).

Species	Clade	Source material [1]	Status of source material	GenBank accession number(s)	Reference
C. eleusines	graminicola	MAFF 511155	Culture from epitype	ITS: EU554131, JX519218; TUB2: JX519243; ACT: JX519234; CHS-1: JX519226; SOD2: EU554234; APN2: EU365038	Crouch *et al.* (2009c, d), this study
C. eremochloae	graminicola	CBS 129661	Culture from holotype	ITS: JQ478447, JX519220; TUB2: JX519245; ACT: JX519236; CHS-1: JX519228; SOD2: JQ478449; Mat1/APN2: JQ478462; APN2: JQ478476	Crouch & Tomaso-Peterson (2012), this study
C. falcatum	graminicola	CGMCC 3.14187, CBS 147945	Culture from neotype	ITS: HM171677, JQ005772; TUB2: JQ005856; ACT: JQ005835; CHS-1: JQ005793; HIS3: JQ005814; Mat1/APN2: HM569769; APN2: HM569770	Prihastuti *et al.* 2010, O'Connell *et al.* (2012)
C. fioriniae	acutatum	EHS 58, CBS 128517, ARSEF 10222	Culture from holotype	ITS: EF464594, JQ948292; TUB2: EF593325, JQ949943; ACT: JQ949613; CHS-1: JQ948953; GAPDH: EF593344, JQ948622; HIS3: JQ949283; GS: EF593353; MAT1-2: EF593362; LSU: EF464581	Marcelino *et al.* (2008), Shivas & Tan (2009), Damm *et al.* (2012a)
C. fructi	dematium	CBS 346.37	Culture from epitype	ITS: GU227844; TUB2: GU228138; ACT: GU227942; CHS-1: GU228334; GAPDH: GU228236; HIS3: GU228040	Damm *et al.* (2009)
C. fructicola	gloeosporioides	MFU090228, ICMP 18581*, CBS 130416	Culture from holotype	ITS: FJ972603, JX010165; TUB2: FJ907441, JX010405; ACT: FJ907426; CHS-1: JX009866; GAPDH: FJ972578, JX010033; CAL: FJ917508; GS: FJ972593, JX010095; SOD2: JX010327	Prihastuti *et al.* (2009), Weir *et al.* (2012)
C. fuscum	destructivum	CBS 130.57	None	ITS: JQ005762; TUB2: JQ005846; ACT: JQ005825; CHS-1: JQ005783; HIS3: JQ005804	O'Connell *et al.* (2012)
C. gloeosporioides	gloeosporioides	IMI 356878, CBS 112999, ICMP17821	Culture from epitype	ITS: EU371022, JQ005152, JX010152; TUB2: FJ907445, JQ005587, JX010445; ACT: FJ907430, JQ005500, JX009531; CHS-1: JQ005326, JX009818; GAPDH: FJ972582, JQ005239, JX010056; HIS3: JQ005413; CAL: FJ917512, JQ005673, JX009731; GS: FJ972589, JX010085; SOD2: JX010365	Damm *et al.* (2012b), Weir et al. (2012)
C. godetiae	acutatum	CBS 133.44	Culture from holotype	ITS: JQ948402; TUB2: JQ950053; ACT: JQ949723; CHS-1: JQ949063; GAPDH: JQ948733; HIS3: JQ949393	Damm *et al.* (2012a)
C. graminicola	graminicola	CBS 130836, M 1.001	Culture from epitype	ITS: DQ003110, JQ005767; TUB2: JQ005851; ACT: JQ005830; CHS-1: JQ005788; HIS3: HQ005809; Mat1/APN2: FJ377994; MAT1-2: EU365081	Du *et al.* (2005), Crouch *et al.* (2009 d), O'Connell *et al.* (2012)
C. guajavae	acutatum	IMI 350839	Culture from holotype	ITS: JQ948270; TUB2: JQ949921; ACT: JQ949591; CHS-1: JQ948931; GAPDH: JQ948600; HIS3: JQ949261	Damm *et al.* (2012a)
C. hanaui	graminicola	MAFF 305404	Culture from holotype	ITS: EU554101, JX519217; TUB2: JX519242; CHS-1: JX519225; SOD2: EU554205; Mat1/APN2: FJ377922; APN2: EU365008	Crouch *et al.* (2009c, d), this study
C. hemerocallidis	dematium	CDLG5	Culture from holotype	ITS: JQ400005; TUB2: JQ400019; ACT: JQ399991; CHS-1: Q399998; GAPDH: JQ400012	Yang *et al.* 2012
C. higginsianum	destructivum	IMI 349063	None	ITS: JQ005760; TUB2: JQ005844; ACT: JQ005823; CHS-1: JQ005781; HIS3: JQ005802	O'Connell *et al.* (2012)
C. hippeastri	boninense	CBS 125376	Culture from holotype	ITS: GQ485599, JQ005231; TUB2: GQ849446, JQ005665; ACT: GQ856788, JQ005579; CHS-1: GQ856725, JQ005405; GAPDH: GQ856764, JQ005318; HIS3: JQ005492; CAL: GQ849469, JQ005752	Yang *et al.* (2009), Damm *et al.* (2012b)
C. horii	gloeosporioides	NBRC 7478, ICMP 10492	Culture from neotype	ITS: GQ329690; TUB2: JX010450; ACT: JX009438; CHS-1: JX009752; GAPDH: GQ329681; CAL: JX009604; GS: JX010137; SOD2: JX010370; TEF1: GQ329693	Weir & Johnston (2010), Weir *et al.* (2012)
C. indonesiense	acutatum	CBS 127551	Culture from holotype	ITS: JQ948288; TUB2: JQ949939; ACT: JQ949609; CHS-1: JQ948949; GAPDH: JQ948618; HIS3: JQ949279	Damm *et al.* (2012a)
C. jacksonii	graminicola	MAFF 305460	Culture from holotype	ITS: EU554108, JX519216; TUB2: JX519241; ACT: JX519233; CHS-1: JX519224; SOD2: EU554212	Crouch *et al.* (2009c, d), this study

Table 3. (Continued).

Species	Clade	Source material [1]	Status of source material	GenBank accession number(s)	Reference
C. jasminigenum	truncatum	CGMCC LLTX–01, MFU 10–0273	Culture from type	ITS: HM131513; TUB2: HM153770; ACT: HM131508; GAPDH: HM131499; CAL: HM131494; GS: HM131504	Wikee *et al.* 2010
C. johnstonii	acutatum	CBS 128532, ICMP 12926	Culture from holotype	ITS: JQ948444; TUB2: JQ950095; ACT: JQ949765; CHS-1: JQ949105; GAPDH: JQ948775; HIS3: JQ949435	Damm *et al.* (2012a)
C. kahawae* subsp. *ciggaro	gloeosporioides	ICMP 18539	Culture from holotype	ITS: JX010230; TUB2: JX010434; ACT: JX009523; CHS-1: JX009800; GAPDH: JX009966; CAL: JX009635; GS: JX010132; SOD2: JX010346	Weir *et al.* (2012)
C. kahawae* subsp. *kahawae	gloeosporioides	IMI 319418, ICMP17816	Culture from holotype	ITS: GU174550, JX010231; TUB2: JX010444; ACT: JX009452; CHS-1: JX009813; GAPDH: GU174562, JX010012; CAL: JX009642; GS: JX010130; SOD2: JX010130	Weir *et al.* (2012)
C. karstii	boninense	CBS 132134, CORCG6, CGMCC3.14194	Culture from holotype	ITS: HM585409; TUB2: HM585428; ACT: HM581995; CHS-1: HM582023; GAPDH: HM585391; CAL: HM582013	Yang *et al.* (2011)
C. kinghornii	acutatum	CBS 198.35	Culture from holotype	ITS: JQ948454; TUB2: JQ950105; ACT: JQ949775; CHS-1: JQ949115; GAPDH: JQ948785; HIS3: JQ949445	Damm *et al.* (2012a)
C. laticiphilum	acutatum	CBS 112989, IMI 383015, STE-U 5303	Culture from holotype	ITS: JQ948289; TUB2: JQ949940; ACT: JQ949610; CHS-1: JQ948950; GAPDH: JQ948619; HIS3: JQ949280	Damm *et al.* (2012a)
C. lilii	spaethianum	CBS 109214	Morphology congruent with original description	ITS: GU227810; TUB2: GU228104; ACT: GU227908; CHS-1: GU228300; GAPDH: GU228202; HIS3: GU228006	Damm *et al.* (2009)
C. limetticola	acutatum	CBS 114.14	Culture from epitype	ITS: JQ948193; TUB2: JQ949844; ACT: JQ949514; CHS-1: JQ948854; GAPDH: JQ948523; HIS3: JQ949184	Damm *et al.* (2012a)
C. lindemuthianum	orbiculare	CBS 144.31	None	ITS: JQ005779; TUB2: JQ005863; ACT: JQ005842; CHS-1: JQ005800; HIS3: JQ005821	O'Connell *et al.* (2012)
C. lineola	dematium	CBS 125337	Culture from epitype	ITS: GU227829; TUB2: GU228123; ACT: GU227927; CHS-1: GU228319; GAPDH: GU228221; HIS3: GU228025	Damm *et al.* (2009)
C. linicola	destructivum	CBS 172.51	None	ITS: JQ005765; TUB2: JQ005849; ACT: JQ005828; CHS-1: JQ005786; HIS3: JQ005807	O'Connell *et al.* (2012)
C. liriopes	spaethianum	CBS 119444	Culture from holotype	ITS: GU227804; TUB2: GU228098; ACT: GU227902; CHS-1: GU228294; GAPDH: GU228196; HIS3: GU228000	Damm *et al.* (2009)
C. lupini	acutatum	BBA 70884, CBS 109225	Culture from neotype	ITS: DQ286119, JQ948155; TUB2: JQ949806; ACT: JQ949476; CHS-1: JQ948816; GAPDH: JQ948485; HIS3: JQ949146; Mat1/APN2: DQ174704; TUB1: AJ301948	Nirenberg *et al.* (2002), Damm *et al.* (2012a)
C. malvarum	orbiculare	LW1	None	GAPDH: DQ792860	Liu *et al.* (2007a)
C. melonis	acutatum	CBS 159.84	Culture from holotype	ITS: JQ948194; TUB2: JQ949845; ACT: JQ949515; CHS-1: JQ948855; GAPDH: JQ948524; HIS3: JQ949185	Damm *et al.* (2012a)
C. miscanthi	graminicola	MAFF 510857	Culture from holotype	ITS: EU554121, JX519221; TUB2: JX519246; ACT: JX519237; CHS-1: JX519229; SOD2: EU554224; APN2: EU365028	Crouch *et al.* (2009c, d), this study
C. musae	gloeosporioides	CBS 116870, ICMP19119	Culture from epitype	ITS: HQ596292, JX010146; TUB2: HQ596280; ACT: HQ596284, JX009433; CHS-1: JX009896; GAPDH: HQ596299, JX010050; CAL: JX009742; GS: HQ596288, JX010103; SOD2: JX010335	Su *et al.* (2011), Weir *et al.* (2012)
C. navitas	graminicola	CBS 125086	Culture from holotype	ITS: GQ919067, JQ005769; TUB2: JQ005853; ACT: JQ005832; CHS-1: JQ005790; HIS3: JQ005811; SOD2: GQ919073; Mat1/APN2: GQ919071; APN2: GQ919069	Crouch *et al.* (2009a), O'Connell *et al.* (2012)
C. nicholsonii	graminicola	MAFF 511115	Culture from holotype	ITS: EU554126, JQ005770; TUB2: JQ005854; ACT: JQ005833; CHS-1: JQ005791; HIS3: JQ005812; SOD2: EU554229; Mat1/APN2: FJ377946; APN2: EU365033	Crouch *et al.* (2009c, d), O'Connell *et al.* (2012)

Table 3. (Continued).

Species	Clade	Source material [1]	Status of source material	GenBank accession number(s)	Reference
C. novae-zelandiae	boninense	CBS 128505, ICMP 12944	Culture from holotype	ITS: JQ005228; TUB2: JQ005662; ACT: JQ005576; CHS-1: JQ005402; GAPDH: JQ005315; HIS3: JQ005489; CAL: JQ005749	Damm *et al.* (2012b)
C. nupharicola	gloeosporioides	CBS 470.96, ICMP 18187	Culture from holotype	ITS: JX010187; TUB2: JX010398; ACT: JX009437; CHS-1: JX009835; GAPDH: JX009972; CAL: JX009663; GS: JX010088; SOD2: JX010320	Weir *et al.* (2012)
C. nymphaeae	acutatum	CBS 515.78	Culture from epitype	ITS: JQ948197; TUB2: JQ949848; ACT: JQ949518; CHS-1: JQ948858; GAPDH: JQ948527; HIS3: JQ949188	Damm *et al.* (2012a)
C. oncidii	boninense	CBS 129828	Culture from holotype	ITS: JQ005169; TUB2: JQ005603; ACT: JQ005517; CHS-1: JQ005343; GAPDH: JQ005256; HIS3: JQ005430; CAL: JQ005690	Damm *et al.* (2012b)
C. orbiculare	orbiculare	LARS 414, 104T, CBS 514.97	None	ITS: JQ005778; TUB2: JQ005862; ACT: JQ005841; CHS-1: JQ005799; HIS3: JQ005820	O'Connell *et al.* (2012)
C. orchidophilum		CBS 632.80	Culture from holotype	ITS: JQ948151; TUB2: JQ949802; ACT: JQ949472; CHS-1: JQ948812; GAPDH: JQ948481; HIS3: JQ949142	Damm *et al.* (2012a)
C. parsonsiae	boninense	CBS 128525, ICMP 18590	Culture from holotype	ITS: JQ005233; TUB2: JQ005667; ACT: JQ005581; CHS-1: JQ005407; GAPDH: JQ005320; HIS3: JQ005494; CAL: JQ005754	Damm *et al.* (2012b)
C. paspali	graminicola	MAFF 305403	Culture from holotype	ITS: EU554100, JX519219; TUB2: JX519244; ACT: JX519235; CHS-1: JX519227; SOD2: EU554204; Mat1/APN2: FJ377921; APN2: EU365007	Crouch *et al.* (2009c, d), this study
C. paxtonii	acutatum	IMI 165753	Culture from holotype	ITS: JQ948285; TUB2: JQ949936; ACT: JQ949606; CHS-1: JQ948946; GAPDH: JQ948615; HIS3: JQ949276	Damm *et al.* (2012a)
C. petchii	boninense	CBS 378.94	Culture from epitype	ITS: JQ005223; TUB2: JQ005657; ACT: JQ005571; CHS-1: JQ005397; GAPDH: JQ005310; HIS3: JQ005484; CAL: JQ005744	Damm *et al.* (2012b)
C. phaseolorum **[4]**	dematium	CBS 157.36	Authentic strain	ITS: GU227896; TUB2: GU228190; ACT: GU227994; CHS-1: GU228386; GAPDH: GU228288; HIS3: GU228092	Damm *et al.* (2009)
C. phormii	acutatum	CBS 118194	Culture from epitype	ITS: DQ286136, JQ948446; TUB2: JQ950097; ACT: JQ949767; CHS-1: JQ949107; GAPDH: JQ948777; HIS3: JQ949437; LSU: DQ286137	Farr *et al.* (2006), Damm *et al.* (2012a)
C. phyllanthi	boninense	CBS 175.67	Culture from holotype	ITS: JQ005221; TUB2: JQ005655; ACT: JQ005569; CHS-1: JQ005395; GAPDH: JQ005308; HIS3: JQ005482; CAL: JQ005742	Damm *et al.* (2012b)
C. pseudoacutatum		CBS 436.77	Culture from holotype	ITS: JQ948480; TUB2: JQ950131; ACT: JQ949801; CHS-1: JQ949141; GAPDH: JQ948811; HIS3: JQ949471	Damm *et al.* (2012a)
C. psidii	gloeosporioides	CBS 145.29*, ICMP 19120	Authentic strain	ITS: JX010219; TUB2: JX010443; ACT: JX009515; CHS-1: JX009901; GAPDH: JX009967; CAL: JX009743; GS: JX010133; SOD2: JX010366	Weir *et al.* (2012)
C. pyricola	acutatum	CBS 128531, ICMP 12924	Culture from holotype	ITS: JQ948445; TUB2: JQ950096; ACT: JQ949766; CHS-1: JQ949106; GAPDH: JQ948776; HIS3: JQ949436	Damm *et al.* (2012a)
C. queenslandicum	gloeosporioides	ICMP 1778	Culture from epitype	ITS: JX010276; TUB2: JX010414; ACT: JX009447; CHS-1: JX009899; GAPDH: JX009934; CAL: JX009691; GS: JX010104; SOD2: JX010336	Weir *et al.* (2012)
C. rhombiforme	acutatum	CBS 129953	Culture from holotype	ITS: JQ948457; TUB2: JQ950108; ACT: JQ949778; CHS-1: JQ949118; GAPDH: JQ948788; HIS3: JQ949448	Damm *et al.* (2012a)
C. rusci		CBS 119206	Culture from holotype	ITS: GU227818; TUB2: GU228112; ACT: GU227916; CHS-1: GU228308; GAPDH: GU228210; HIS3: GU228014	Damm *et al.* (2009)
C. salicis	acutatum	CBS 607.94	Culture from epitype	ITS: JQ948460; TUB2: JQ950111; ACT: JQ949781; CHS-1: JQ949121; GAPDH: JQ948791; HIS3: JQ949451	Damm *et al.* (2012a)

Table 3. (Continued).

Species	Clade	Source material [1]	Status of source material	GenBank accession number(s)	Reference
C. salsolae	gloeosporioides	ICMP 19051	Culture from holotype	ITS: JX010242; TUB2: JX010403; ACT: JX009562; CHS-1: JX009863; GAPDH: JX009916; CAL: JX009696; GS: JX010093; SOD2: JX010325	Weir *et al.* (2012)
C. scovillei	acutatum	CBS 126529, BBA 70349	Culture from holotype	ITS: JQ948267; TUB2: JQ949918; ACT: JQ949588; CHS-1: JQ948928; GAPDH: JQ948597; HIS3: JQ949258	Damm *et al.* (2012a)
C. sansevieriae		MAFF 239721	Culture from holotype	ITS: AB212991	Nakamura *et al.* (2006)
C. siamense	gloeosporioides	MFU 090230, ICMP 18578, CBS 130417	Culture from holotype	ITS: FJ972613, JX010171; TUB2: FJ907438, JX010404; ACT: FJ907423; CHS-1: JX009865; GAPDH: FJ972575, JX009924; CAL: FJ917505; GS: FJ972596, JX010094; SOD2: JX010326	Prihastuti *et al.* (2009), Weir *et al.* (2012)
C. simmondsii	acutatum	BRIP 28519, CBS 122122	Culture from holotype	ITS: FJ972601, JQ948276; TUB2: FJ907443, JQ949927; ACT: FJ907428, JQ949597; CHS-1: JQ948937; GAPDH: FJ972580, JQ948606; HIS3: JQ949267; CAL: FJ917510; GS: FJ972591	Shivas & Tan (2009), Damm *et al.* (2012a)
C. sloanei	acutatum	IMI 364297	Culture from holotype	ITS: JQ948287; TUB2: JQ949938; ACT: JQ949608; CHS-1: JQ948948; GAPDH: JQ948617; HIS3: JQ949278	Damm *et al.* (2012a)
C. spaethianum	spaethianum	CBS 167.49	Culture from epitype	ITS: GU227807; TUB2: GU228101; ACT: GU227905; CHS-1: GU228297; GAPDH: GU228199; HIS3: GU228003; LSU: JN940813	Damm *et al.* (2009), Schoch et al. (2012)
C. spinaciae	dematium	CBS 128.57	Morphology congruent with original description	ITS: GU227847; TUB2: GU228141; ACT: GU227945; CHS-1: GU228337; GAPDH: GU228239; HIS3: GU228043	Damm *et al.* (2009),
C. sublineola **[5]**	graminicola	BPI399463	Lectotype	ITS: JQ478437; HIS3: JQ005813; SOD2: JQ478453; Mat1/APN2: JQ478466; APN2: JQ478477	Crouch & Tomaso-Peterson (2012),
		CBS 131301, S3.001	Culture from epitype	ITS: DQ003114, JQ005771; TUB2: JQ005855; ACT: JQ005834; CHS-1: JQ005792; HIS3: JQ005813; SOD2: DO132051; Mat1/APN2: FJ378029; APN2: EU365121; MAT1-2: DQ002865	Crouch & Tomaso-Peterson (2012), Crouch *et al.* (2006), O'Connell *et al.* (2012)
C. tabacum	destructivum	CBS 161.53	None	ITS: JQ005763; TUB2: JQ005847; ACT: JQ005826; CHS-1: JQ005784; HIS3: JQ005805	O'Connell *et al.* (2012)
C. tamarilloi	acutatum	CBS 129814	Culture from holotype	ITS: JQ948184; TUB2: JQ949835; ACT: JQ949505; CHS-1: JQ948845; GAPDH: JQ948514; HIS3: JQ949175	Damm *et al.* (2012a)
C. theobromicola	gloeosporioides	ICMP 18649, CBS 124945	Culture from neotype	ITS: GU994360, JX010294; TUB2: GU994477, JX010447; ACT: JX009444; CHS-1: JX009869; GAPDH: JX010006; CAL: JX009591; GS: JX010139; SOD2: JX010372; Mat1/APN2: GU994448; APN2: GU994419; TEF1: GU994506	Rojas *et al.* (2010), Weir *et al.* (2012)
C. ti	gloeosporioides	ICMP 4832	Culture from holotype	ITS: JX010269; TUB2: JX010442; ACT: JX009520; CHS-1: JX009898; GAPDH: JX009952; CAL: JX009649; GS: JX010123; SOD2: JX010362	Weir *et al.* (2012)
C. tofieldiae	spaethianum	CBS 495.85	Morphology congruent with original description	ITS: GU227801; TUB2: GU228095; ACT: GU227899; CHS-1: GU228291; GAPDH: GU228193; HIS3: GU227997; LSU: JN940815	Damm *et al.* (2009), Schoch *et al.* (2012)
C. torulosum	boninense	CBS 128544, ICMP 18586	Culture from holotype	ITS: JQ005164; TUB2: JQ005598; ACT: JQ005512; CHS-1: JQ005338; GAPDH: JQ005251; HIS3: JQ005425; CAL: JQ005685	Damm *et al.* (2012b)
C. trichellum		CBS 217.64	Morphology congruent with original description	ITS: GU227812; TUB2: GU228106; ACT: GU227910; CHS-1: GU228302; GAPDH: GU228204; HIS3: GU228008	Damm *et al.* (2009)
C. tropicale	gloeosporioides	CBS 124949, ICMP18653	Culture from holotype	ITS: GU994331, JX010264; TUB2: GU994454, JX010407; ACT: JX009489; CHS-1: JX009870; GAPDH: JX010007; CAL: JX009719; GS: JX010097; SOD2: JX010329; Mat1/APN2: GU994425; APN2: GU994396; TEF1: GU994483	Rojas *et al.* (2010), Weir *et al.* (2012)

Table 3. (Continued).

Species	Clade	Source material [1]	Status of source material	GenBank accession number(s)	Reference
C. truncatum	truncatum	CBS 151.35	Culture from epitype	ITS: GU227862; TUB2: GU228156; ACT: GU227960; CHS-1: GU228352; GAPDH: GU228254; HIS3: GU228058; LSU: JN940819	Damm *et al.* (2009), Schoch *et al.* (2012)
C. verruculosum	spaethianum	IMI 45525	Culture from holotype	ITS: GU227806; TUB2: GU228100; ACT: GU227904; CHS-1: GU228296; GAPDH: GU228198; HIS3: GU228002	Damm *et al.* (2009)
C. walleri	acutatum	CBS 125472	Culture from holotype	ITS: JQ948275; TUB2: JQ949926; ACT: JQ949596; CHS-1: JQ948936; GAPDH: JQ948605; HIS3: JQ949266	Damm *et al.* (2012a)
C. xanthorrhoeae	gloeosporioides	BRIP 45094, ICMP 17903, CBS127831	Culture from holotype	ITS: GU048667, GU174551, JX010261; TUB2: JX010448; ACT: JX009478; CHS-1: JX009823; GAPDH: GU174563, JX009927; CAL: JX009653; GS: JX010138; SOD2: JX010369; TEF1: GU174575	Hyde *et al.* (2009), Weir & Johnston (2010), Weir *et al.* (2012)
C. yunnanense		CGMCC AS3.9167, CBS 132135	Culture from holotype	ITS: EF369490 ; TUB2: JX519248; ACT: JX519239; CHS-1: JX519231	Liu *et al.* (2007b), this study

ARSEF: ARS Collection of Entomopathogenic Fungal Cultures, Ithaca, NY, USA.

BBA: Culture collection of the Biologische Bundesanstalt für Land- und Forstwirtschaft, *Berlin*, Germany.

BPI: Systematic Mycology and Microbiology Laboratory, USDA Agricultural Research Service, Beltsville, MD, USA.

BRIP: Culture Collection of the DPI&F Plant Pathology Herbarium, Indooroopilly, Queensland, Australia.

CBS: Culture collection of the Centraalbureau voor Schimmelcultures, Fungal Biodiversity Centre, Utrecht, The Netherlands.

CGMCC: China General Microbiological Culture Collection Center, Beijing, China.

ICMP: International Collection of Microorganisms from Plants, Landcare Research, Auckland, New Zealand.

IMI: Culture collection of CABI Europe UK Centre, Egham, UK.

M1.001: sourced from Lisa Vaillancourt, University of Kentucky.

MAFF: NIAS Genebank, Microorganism Section, Tsukuba, Japan.

MFU: fungarium of Mae Fah Luang University, Thailand (cultures in BCC (BIOTEC Culture Collection, Thailand).

NBRC: NITE Biological Resource Center, Chiba, Japan.

STE-U: Culture collection of the Department of Plant Pathology, University of Stellenbosch, South Africa.

[1] Where possible, all taxa are represented by sequences from type or other authentic material. For some however, the necessary research to identify such cultures and/or to designate epitype material is not complete, especially for species within the destructivum and orbiculare clades. To be able to generate robust phylogenetic trees for the entire genus (Figs 2, 3) that include all of the major clades, we have used sequences from some strains that have been used to represent the relevant species (mostly in recent literature) but which do not currently have any special nomenclatural status. Their details are included in Table 3 for reference, and can be recognised with "none" in the type status column. It may be that some or all of these strains will be designated as epitypes in the future, but for the present it should not be assumed that they represent the species as originally circumscribed.

[2] KS20BIG was one of four epitypes designated by Crouch *et al*. (2006) for *C. cereale*; the application of the name needs to be more precisely established.

[3] Preliminary multilocus analysis suggests that *C. chrysanthemi* may not be a synonym of *C. carthami* as stated by Uematsu *et al*. (2012).

[4] These sequences derive from one of two authentic but not genetically identical strains; the species was not epitypified as neither of them are now fertile.

[5] A further collection from which a culture was obtained (CBS 131301) was designated as an epitype by Crouch *et al*. (2006) and recognised as representative of the species also by Du *et al*. (2005) and Crouch *et al*. (2009d). It was subsequently confirmed as closely similar to the lectotype based on multilocus DNA sequence analysis (Crouch & Tomaso-Peterson 2012).

Multilocus phylogenies are now typically used as the primary basis on which to describe new species of *Colletotrichum* (see Table 1) and the trend is to include more and more sequences into the analyses. One might conclude that phylogenetic signal is strongly correlated with the number of characters (in this case base pairs) included in the analysis, a position first advanced nearly 250 years ago (Adanson 1763), but genes are differential at varying positions in the hierachy of taxa. Inclusion of multiple genes that resolve at similar positions in the hierarchy can therefore increase the size (not to mention the cost) of the data set without clarifying the phylogenetic signal. This is highly relevant to species diagnosis, as was observed by Min & Hickey (2007) in a study of mitochondrial genes from 31 fungi of widely varying taxonomic position to determine the optimum sequence length for robust identification. Research by Dentinger *et al*. (2010a) showed that both bootstrap support and Bayesian posterior probability values were eroded in a multilocus ATP6/LSU/RPB1 analysis of *Boletus* species compared with an analysis based on RPB1 alone. Similar results were obtained by Walker *et al*. (2012) in a study on two genera of the *Diaporthales*. They found in an analysis of *Ophiognomonia* species that adding TEF1 sequence data to any combination of three of the other loci used (ITS, Tub2, FG1093 and MS204) decreased support and increased the number of tree topologies recovered. Our own preliminary studies on *Colletotrichum* (data not shown) also indicate that in some circumstances, increasing the number of loci may decrease phylogenetic performance, although the effect is minor. Taken together, these data suggest that the recent fungal phylogenetic "arms race", whereby a steadily increasing number of loci are analysed in concert, may add complexity but not improve insight.

MAJOR CLADES

Phylogenetic analysis of the genus *Colletotrichum* reveals that it comprises nine major clades, as well as a number of small clusters and isolated species (Figs 2, 3).

There is currently no universally accepted process for naming clades and reconciling them with the traditional taxonomic categories of the International Code of Nomenclature for Algae, Fungi and Plants (ICNAFP), although the draft *PhyloCode* (http://www.ohio.edu/phylocode/) represents a major step in this direction. Formal recognition of infrageneric categories within *Colletotrichum* is highly desirable. This is for phylogenetic reasons, in that the genus contains many monophyletic subunits with common characteristics (not least in spore morphology). There are also pragmatic reasons for defining such categories, for example to allow linkage to the immense historical body of pathological literature in which the fungal subjects are not assignable to currently accepted species.

Use of the strictly hierarchical infrageneric nomenclature system in the ICNAFP is a possible way to assign formal names to species groups within *Colletotrichum.* However, although the *Code* allows for extra categories to be interspersed between the three formal ranks (subgenus, section and series), their adoption implies an equality of taxa at the same rank that is not reconcilable with evolutionary processes. We therefore favour a formal (or at least semi-formal) clade-based nomenclature system.

In this paper, we refer to 119 *Colletotrichum* species (Table 3) that collectively encompass almost all of the known phylogenetic variety within the genus, most of them belonging to one of the nine major clades. Additionally, there is a number of small clusters and isolated species, which we believe to represent independent evolutionary units, but which are insufficiently well known to justify formal nomenclatural recognition. Throughout this paper, we refer to these clades using the specific epithet of the first-recognised (or historically most prominent) of their constituent species – for example the acutatum clade is the monophyletic unit containing *C. acutatum* and its close relatives (see Fig. 3). An obvious shortcoming of this system is that there is no objective method of deciding which is the basal node of the named clade. In the case of the acutatum clade, we have decided that the clade has *C. orchidophilum* as its sister taxon, because the ingroup taxa are much more closely related to each other than to *C. orchidophilum* or *C. pseudoacutatum*, but there are arguments for extending the clade to include this species, and indeed also *C. pseudoacutatum*. The species in the graminicola clade are much less closely related than those of the *C. acutatum* clade; the decision for combining them was made rather on the basis of common morphology and host family. The process is to some extent subjective, so while we commend adoption of the nine clades detailed below as formal entities, we hope that clade definition and recognition will be taken on as a task by the new ICTF Subcommission on *Colletotrichum*.

In this paper, reference to the term clade indicates that we are confident that the associated information can be referred to our formal clades (or to species within the clades). We also refer on occasion to informal groupings of taxa, generally as species clusters. In these circumstances, we may know that the knowledge is associated with a particular species group, but are unsure as to its constituent taxa, or to the phylogenetic extent it represents. This frequently occurs when attempting to relate information from pathology papers to our new phylogeny.

Several of the clades indicated in Fig. 3 represent the species complexes as defined by Crouch *et al.* (2009c, d), Damm *et al.* (2012a, b, this issue), and Weir *et al.* (2012, this issue). While these four complexes can be confirmed as monophyletic, the assemblage of curved-spored species from herbaceous hosts studied by Damm *et al.* (2009) can be seen to be polyphyletic; the species included in that research are placed in three of the formal clades we recognise here, with additional outliers.

In this section, we provide an overview of the nine *Colletotrichum* clades that we recognise. Several additional individual species and small clusters are recognised that do not fall into clear clades (see Fig. 3). The phylogenetic tree presented as Fig. 3 provides a comprehensive visual overview of phylogenetic diversity within *Colletotrichum* as treated in the current literature, but it seems likely that there are further outlying taxa that have not yet been sampled, or for which phylogenetic positions have not been fixed effectively. For example, the tea pathogen *C. theae-sinensis* (Moriwaki *et al*. 2002, Yoshida & Takeda 2006) has unusually small conidia and may well fall outside of *Colletotrichum* as outlined in Fig. 3. Although Moriwaki *et al.* (2002) included a strain of *C. theae-sinensis* in phylogenies derived from rDNA datasets, the relevant sequence data from that study are not found in public sequence repositories. Based on these rDNA sequence data, Moriwaki and colleagues suggested that *C. theae-sinensis* might constitute a sister group to the genus, a prediction that needs to be tested further.

Acutatum clade

The acutatum clade is defined as a collective of *Colletotrichum acutatum* and 29 closely related species (see Fig. 3), with *C.*

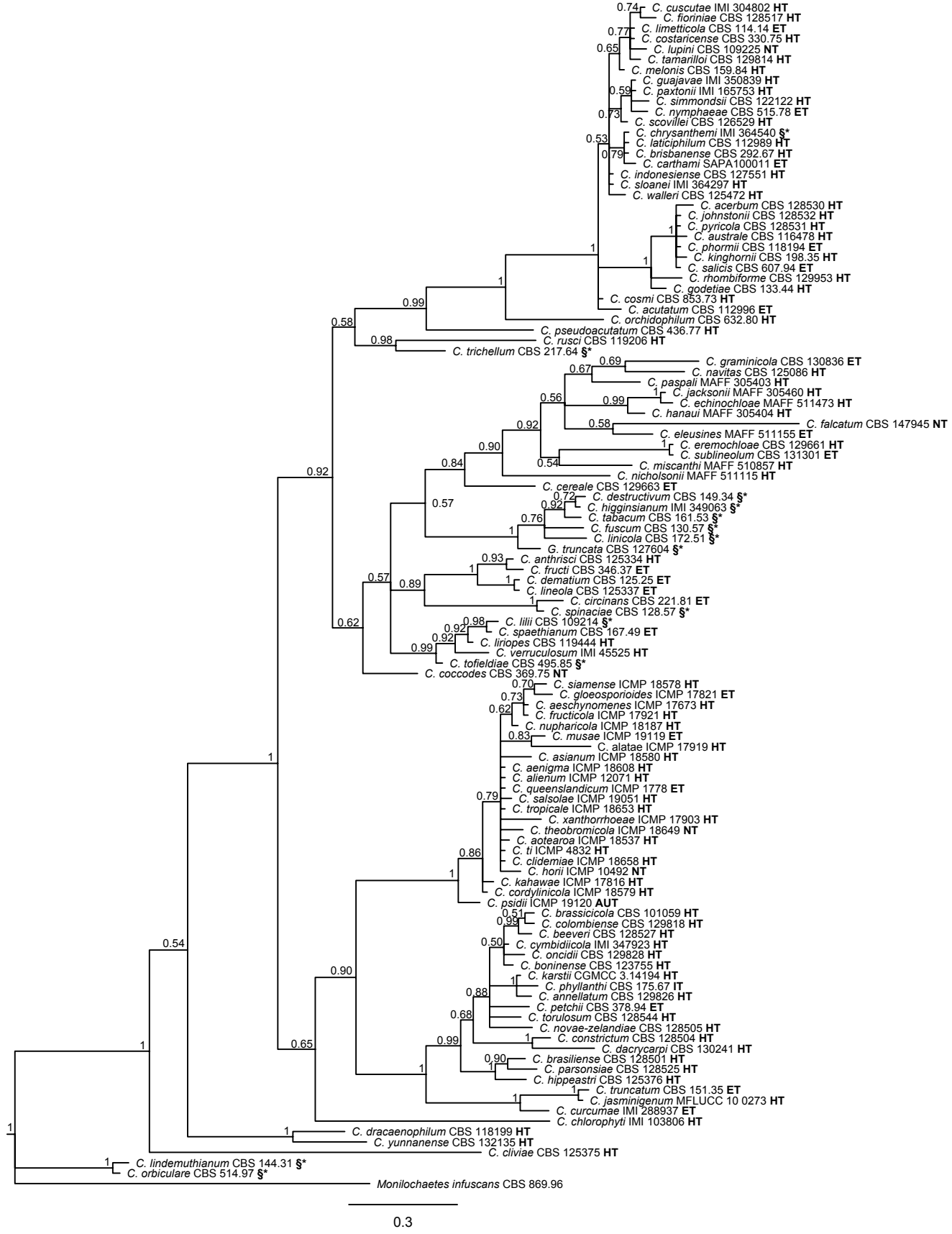

Fig. 2. Phylogenetic tree derived from a Bayesian analysis of an alignment of ITS (599 bp) sequences, run for 1×10^7 generations with a GTR+I+Γ model of DNA evolution. Species names are followed by culture number, and status of the culture, where HT = ex-holotype, ET = epitype, NT = ex-neotype, IT = ex-isotype, AUT = authentic culture. Sequences from a number of non-validated cultures have been included in order to represent clades that have not yet been subject to revision based on multilocus data. These are indicated by the symbol §*.

orchidophilum as sister taxon. The clade, along with a small number of outlying taxa, forms a sister taxon to a combination of the destructivum, graminicola and spaethianum clades and *C. coccodes*. Two principal subclades may be detected within the acutatum clade, containing 19 and nine species respectively, and *C. acutatum sensu stricto* is resolved as an outlier of a

Fig. 3. Phylogenetic tree derived from a Bayesian analysis of a partitioned, concatenated alignment of CHS-1 (251 bp), ACT (305 bp), TUB2 (545 bp) and ITS (599 bp) sequences, run for 1×10^7 generations with a GTR+I+Γ model of DNA evolution for each partition. The major clades recognised in this paper are indicated. Other details as per Fig. 2.

clade consisting of the larger of the two subclades along with *C. fioriniae*. The acutatum clade can be effectively resolved using ITS sequence data alone (Fig. 2). The major subclades are also distinguishable using ITS alone, but the analysis reveals little or no internal structure within the subclades. A comprehensive account of its constituent species can be found as Damm *et al.* (2012a).

Boninense clade

The boninense clade contains 17 species as defined here (see Fig. 3). It forms a sister taxon to the gloeosporioides clade, and our multilocus analysis reveals three subclades containing 12, three and two species respectively. *Colletotrichum boninense sensu stricto* falls within the largest subclade. The nodal structure is complex and we do not see good reason to name the subclades formally. The ITS tree (Fig. 2) shows that the boninense clade can be detected effectively using this single locus, but it is resolved as a sister clade to the truncatum rather than the gloeosporioides clade. The clade has been revised in detail by Damm *et al*. (2012b).

Dematium clade

The dematium clade contains the type species of the genus, *Colletotrichum lineola*, and was investigated by Damm *et al.* (2009), as part of a study of *Colletotrichum* species with curved conidia. As defined by ourselves, the dematium clade contains six species (Fig. 3) and forms a sister clade to a superclade consisting of the acutatum, destructivum, graminicola and spaethianum clades, along with five further outlying taxa. In the ITS tree (Fig. 2) the clade is fairly well resolved with a Bayesian posterior probability value of 0.89, but the structure of the superclade referred to above is less well defined. An additional species, *C. hemerocallidis*, closely related to *C. dematium*, was described just before finishing this review (Yang *et al.* 2012).

Colletotrichum dematium and *C. truncatum* (often referred to under its synonym *C. capsici*) have been confused historically (Sutton 1981), but are found to occupy distinct clades, with the latter species belonging to a small clade near the base of the multilocus phylogeny (Fig. 3). Strains of the six species included in the dematium clade appear to be characteristic of temperate environments, though the sample size for several of the species is inadequate to allow definite conclusions as to their climatic range. In general, members of the dematium clade are not significant in economic terms, but *C. spinaciae* (a pathogen of *Beta* and *Spinacia*; Gourley 1966, Washington *et al.* 2006) and *C. circinans* (attacking *Allium* species; Hall *et al.* 2007, Kim *et al.* 2008) both cause substantial crop losses under some circumstances. These two plant pathogenic species occupy a well-defined subclade distinct from a separate subclade made up of the putatively saprobic species *C. dematium*, *C. lineola*, *C. fructi* and *C. anthrisci* (Damm *et al.* 2009; Fig. 3). The type species of *Colletotrichum*, *C. lineola*, belongs to the dematium clade; it was described by Corda (1831) but treated as a synonym of *C. dematium* by von Arx (1957) and Sutton (1981). However, research based on newly collected strains from the region of the original collection showed that *C. lineola* and *C. dematium* are separable based on DNA sequence data (Damm *et al*. 2009).

Destructivum clade

The destructivum clade contains several important plant pathogens, but to date has not been studied in depth using molecular methods. Economically significant constituent taxa include *Colletotrichum destructivum*, *C. fuscum*, *C. higginsianum* and *C. linicola*. *Colletotrichum destructivum* is considered to be pathogenic on lucerne (alfalfa; *Medicago sativa*) and soybean (*Glycine max*) (Manandhar *et al.* 1986, Latunde-Dada *et al.* 1999), and has also been reported to parasitise a range of unrelated plants including species in the *Brassicaceae*, *Cuscutaceae*, *Lamiaceae* and *Solanaceae* (reviewed in Hyde *et al.* 2009a). *Colletotrichum higginsianum* is known as a pathogen of *Brassicaceae* (Huser *et al.* 2009) that is responsible for crop losses in northern temperate climates, and was found to be related to *C. destructivum* by O'Connell *et al.* (2004). The fungus is of particular significance as the subject of a whole-genome analysis project, and is increasingly studied as a model for host/pathogen interactions because of its pathogenicity to the model plant *Arabidopsis thaliana* (Birker *et al*. 2009, Huser *et al*. 2009, Kleeman *et al*. 2012, O'Connell *et al*. 2012). *Colletotrichum higginsianum* was reported to be synonymous with *C. destructivum* by Sun & Zhang (2009) based on ITS sequence similarity, but multilocus phylogenies of strains provisionally accepted as representative of *C. higginsianum* and *C. destructivum* indicate that these two species are distinct entities (O'Connell *et al*. 2012 and Fig. 3 of this study). Thus, although formal taxonomic work with authentic types is still pending, it appears that as with other *Colletotrichum* groups, the ITS sequence is not sufficiently differential within the destructivum clade to act as a species-level marker in isolation.

Colletotrichum fuscum is a pathogen of *Digitalis* and *Nemesia* (*Scrophulariaceae*; Tomioka *et al.* 2001). ITS and multilocus data place this species within the destructivum clade (Moriwaki *et al.* 2002, Cannon *et al.* 2008; Figs 2, 3), but more detailed information on its taxonomy and phylogenetic relationships is needed. Similarly, *C. linicola* was shown to belong in this clade based on ITS2/D2 rDNA sequences (Latunde-Dada & Lucas 2007), and preliminary multilocus studies indicate that the species is clearly distinct from others belonging to the destructivum clade (O'Connell *et al.* 2012; Fig 2).

Glomerella truncata was described as the teleomorph of *C. truncatum* (Armstrong-Cho & Banniza 2006, Menat *et al*. 2012), but the strains studied (from lentil (*Lens culinaris*) in Canada) belong to the destructivum rather than the truncatum clade (Damm *et al.* 2009; O'Connell *et al.* 2012; Figs 2, 3). The name *G. truncata* remains valid and legitimate to represent a taxon within the destructivum clade despite the misidentification of its anamorph, but assuming that no earlier synonyms are discovered, it will require a new name now that separate binomials for teleomorph and anamorph are prohibited (Hawksworth 2011) to avoid homonymy with *C. truncatum*.

An outline whole-genus multilocus phylogeny (O'Connell *et al*. 2012) shows that the destructivum clade is monophyletic and distinct from other clades within *Colletotrichum*. This is confirmed by our present multilocus study (Fig. 3), with the destructivum clade being resolved as a sister taxon to the combined graminicola and spaethianum clades, and it is also clearly resolved using ITS data alone (Fig. 2). However, none of the strains sequenced in these studies is derived from type or authentic material for the names used, and further research is required to elucidate species concepts and correct nomenclature.

Gloeosporioides clade

The *C. gloeosporioides* species complex has been studied by Weir *et al*. (2012, this issue). It is a well-supported clade (Bayesian posterior probability value 1) on a very long branch and shows few differences in the gene loci studied between most of the 22 species included. However it is a diverse clade in terms of morphology and includes a number of important plant pathogens. Weir *et al.* (2012) recognised two subclades within the species complex based on an

eight-locus analysis, both of which were supported by Bayesian posterior probability values of 1. They were named as the kahawae and musae clades. Only one of these, the kahawae clade, can be detected unequivocally in our multigene phylogeny (Fig. 3), while the musae clade as recognised by Weir *et al*. (2012) has a Bayesian posterior probability value of only 0.59. This is a result of the limited number of loci that could be included in the genus-wide alignment. The subclades cannot be effectively distinguished using ITS sequence data alone (see Fig. 2).

Graminicola clade

The *Colletotrichum* species associated with grasses form a well-defined monophyletic clade, the species of which possess characteristic widely falcate conidia. It is the only major clade that appears to be composed (at least largely) of host-specific taxa (Crouch & Beirn 2009), although further research may confirm that the orbiculare clade shares this characteristic. Multilocus analyses (Fig. 3) revealed two major subclades within the graminicola clade, in agreement with studies published by Crouch *et al*. (2009c, d). One, represented only by a single strain in Fig. 3, contains the plurivorous taxon *Colletotrichum cereale*. This is a diverse taxon in phylogenetic terms and there is evidence of significant gene flow between the various constituent populations (Crouch, *in litt*. Aug. 2012). *Colletotrichum cereale* is associated with grasses with C3 (cool-season) photosynthetic pathways as either pathogens or endophytes (Crouch *et al*. 2009d). The second subclade affects C4 (warm-season) grasses including several economically important cereal crops (Crouch *et al*. 2009a) and comprises a number of apparently host-specific species, not all of which have been described to date (Crouch *et al*. 2009c, Prihastuti *et al.* 2010). Several of the species included in the graminicola clade are of major importance, including *C. falcatum* on sugarcane (*Saccharum*), *C. graminicola* on maize (*Zea*) and *C. sublineola* on *Sorghum* species. *Colletotrichum cereale* and *C. eremochloae* are pathogens of cultivated turfgrasses (Crouch & Beirn 2009). Research has demonstrated the inadequacy of ITS sequences to differentiate between species within this group (Crouch *et al.* 2009b), and multigene analyses to date do not clearly resolve relationships within the major subclade (Crouch *et al*. 2009c, Fig. 3). The biology and evolution of the clade was reviewed by Crouch & Beirn (2009), focusing on the genetics, biology and epidemiology of the three best-researched species, *C. falcatum, C. graminicola* and *C. sublineola*. The first two of these species are essentially homothallic, while *C. sublineola* may be strictly heterothallic (Vaillancourt & Hanau 1992, Vaillancourt *et al*. 2000). With the exception of *C. falcatum*, the teleomorphs of these species have never been encountered in nature (Crouch & Beirn 2009). A whole-genome analysis of a strain of *C. graminicola* has recently been completed (O'Connell *et al*. 2012) and this work is now being extended to include further strains from grass hosts (http://www.ars.usda.gov/pandp/docs.htm?docid=22211).

Orbiculare clade

The orbiculare clade contains several important pathogen assemblages. It has been studied in a preliminary fashion from a molecular phylogenetic perspective, but has not been the subject of a recent formal revision. The orbiculare clade is thought to include the species *Colletotrichum lindemuthianum*, *C. malvarum*, *C. orbiculare* and *C. trifolii* (Liu *et al*. 2007). Multilocus phylogenies using provisionally identified strains of *C. lindemuthianum* and *C. orbiculare* (Fig. 3) show that the orbiculare group occupies a basal clade of *Colletotrichum*, and that separation of these taxa from *Colletotrichum* at generic level cannot at present be ruled out. Members of the orbiculare clade as it is currently understood share some morphological features including conidia that are not curved and are relatively short and broad, and small appressoria with simple outlines (Sutton 1980). It must be pointed out that none of these taxa has been adequately typified and linked to authentic sequences. There are in fact separate concepts in the literature for three of the species currently placed within the orbiculare clade (see below), which contributes in no small way to confusion over their identity.

As pointed out by Cannon *et al.* (2000), Mordue (1971) considered *C. lindemuthianum* to have relatively long narrow conidia with a very large size range. Mordue's illustration shows a species that would be placed in the gloeosporioides cluster based on morphological data by most authors. Sutton (1980) described and illustrated *C. lindemuthianum* with short, broad and rounded conidia – typical of those here included in the orbiculare clade (Fig. 3). The confusion presumably arose due to the frequent occurrence of fungi from the gloeosporioides cluster on host plants belonging to the *Fabaceae*. A similar confusion seems to exist for *C. orbiculare*; the species as described and illustrated by Baxter *et al.* (1983) has much longer conidia than those of the taxon as defined by other authors, and again it seems possible that strains of the gloeosporioides clade parasitising cucurbits were misidentified. Until both species names are properly typified using modern methods, confusion is likely to continue. As far as we can tell, all of the sequence-based research (bar a single sequence derived from a Taiwanese strain that is certainly misidentified; see Fig. 4) and probably a large majority of pathology reports using the names *C. lindemuthianum* and *C. orbiculare* refer to the short-spored taxa belonging to the orbiculare clade. As such, it would be highly appropriate to fix application of these species names to allow their continued use in this manner. Approximately half of the ITS sequences of strains identified as *C. trifolii* are placed in the destructivum rather than the orbiculare clade (see Fig. 4). Further research is needed before the most appropriate typification can be made; however the original description (Bain & Essary 1906) gives conidial dimensions and shape that are typical of the orbiculare clade.

The orbiculare clade was recognised as a monophyletic unit by Sherriff *et al.* (1994) and Johnston & Jones (1997) using LSU sequence analysis, Sreenivasaprasad *et al.* (1996) using ITS data, and Farr *et al.* (2006) using both gene sequences. A preliminary phylogenetic analysis based only on existing ITS sequences curated by GenBank (Fig. 4) demonstrates that the orbiculare clade is a sister taxon to the whole of the rest of the genus *Colletotrichum*. This result is consistent with previous research findings. For example, an ITS tree constructed by Yang *et al.* (2009) showed the orbiculare clade as a sister to *C. cliviae*, with the combined clade sister to *C. yunnanense* and *C. dracaenophilum*, but the clade comprising all three taxa was supported by bootstrap values below 50. Liu *et al.* (2007) published a phylogenetic analysis of the orbiculare clade, based on GAPDH and GS sequences; this also indicated that the orbiculare group is monophyletic, and that *C. lindemuthianum*, *C. malvarum* and *C. trifolii* form separate clades from a paraphyletic *C. orbiculare*.

As with other *Colletotrichum* clades, ITS data do not appear to be sufficiently variable for species level diagnostics within the orbiculare assemblage. However, ITS data do indicate (Fig. 4)

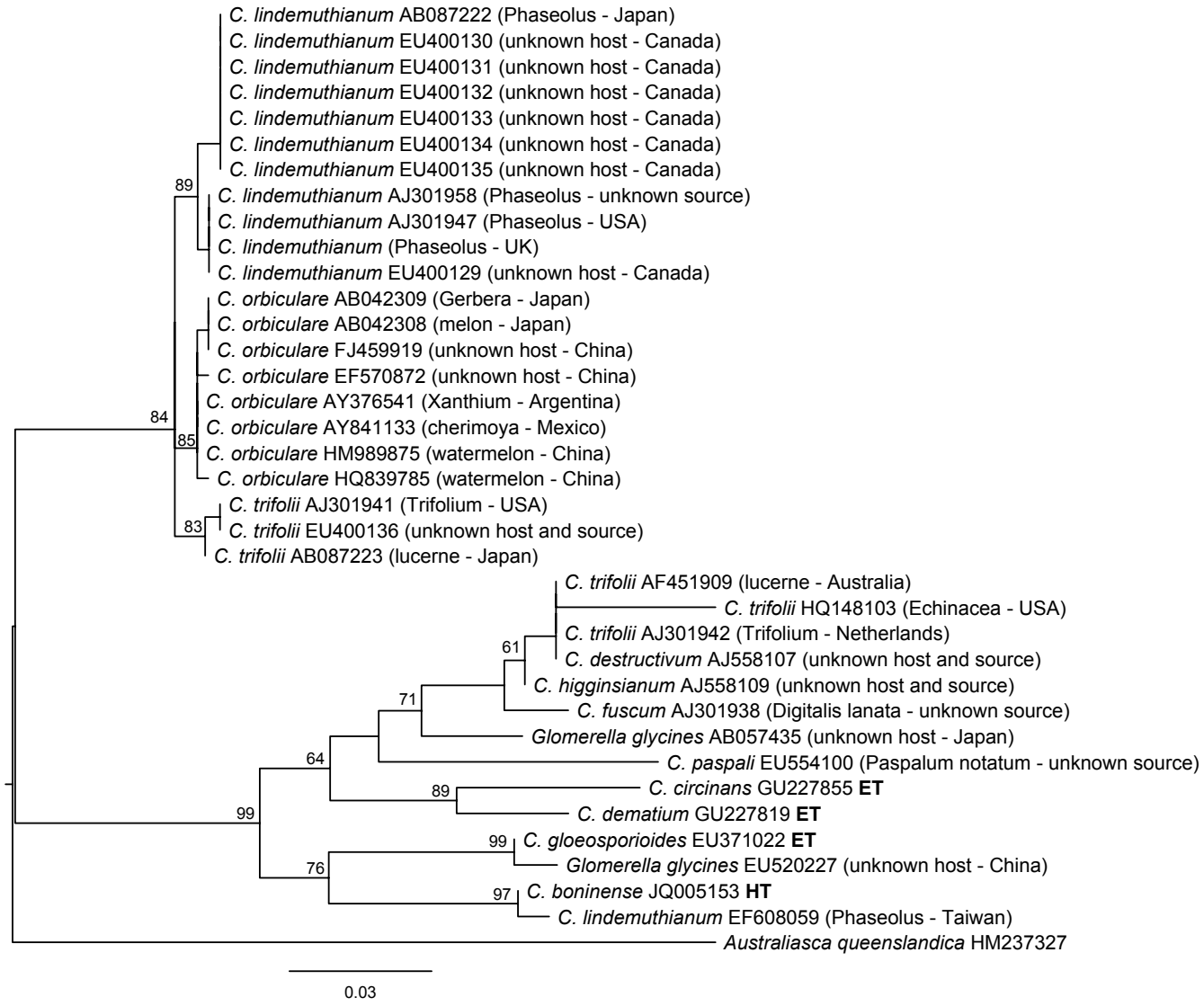

Fig. 4. Maximum likelihood phylogeny based on an ITS alignment of GenBank accessions of the *C. lindemuthianum*, *C. orbiculare*, *C. trifolii* and *C. destructivum* species complexes (alignment with ClustalX, 1000 bootstrap replicates, PhyML package).

that *C. lindemuthianum* is a separate lineage from *C. orbiculare* and *C. trifolii*, and that it might comprise more than one taxon. An analysis of *C. lindemuthianum* rDNA data by Balardin *et al.* (1999) showed that *Phaseolus* pathogens may occur in numerous subordinate clades within the lindemuthianum subclade. The number of sequences available is too small for confidence, but it does appear that *C. lindemuthianum* is specific to *Phaseolus*. However, none of the sequence data or strains used by Balardin *et al.* (1999) is available through public databases or collections; therefore these conclusions require further evaluation. There are no full ITS sequences from *Colletotrichum malvarum* available from public databanks, but a study using ITS2/LSU (Bailey *et al.* 1996) indicated that *Colletotrichum* species from *Malvaceae* occupy at least three subclades within the overall orbiculare clade.

Spaethianum clade

The spaethianum clade receives strong support in both the multilocus and ITS-only analyses (Figs 2, 3). It contains only five species as currently circumscribed, four of which are associated with petaloid monocot plants, and none appears to have economic importance. Its phylogenetic significance is as a sister group to the graminicola clade. The spaethianum clade was recognised as a distinct assemblage by Damm *et al.* (2009) in their work on the non-grass associated species of *Colletotrichum* with curved conidia. Four of the five species in this assemblage have complex appressoria, but the clade does not otherwise have diagnostic characteristics in morphological terms.

Truncatum clade

The truncatum clade includes only one major species, *C. truncatum* (also frequently referred to as *C. capsici*; Damm *et al.* 2009), which is reported as an economically destructive pathogen of many tropical crops including legumes and solanaceous plants. The truncatum clade occupies a sister position to the combined *C. gloeosporioides* and *C. boninense* clade according to our multilocus analysis (Fig. 3), but to the boninense clade only in the ITS-only analysis (Fig. 2). Conidial morphology in the truncatum group is quite different to that found in the gloeosporioides and boninense clades (Damm *et al.* 2012b, Weir *et al.* 2012), providing evidence to support the old hypothesis (Sreenivasaprasad *et al.* 1996) that the evolution of conidial form followed a complex pattern in *Colletotrichum*.

Colletotrichum curcumae also belongs to this clade, a poorly-known species considered to be the causal agent of turmeric leaf spot disease (*Curcuma longa, Zingiberaceae*; Palarpawar &

Ghurde 1988). The third member of the clade is *C. jasminigenum*, which was described as a new species causing leaf and blossom anthracnose disease on *Jasminum sambac* in Vietnam (Wikee *et al.* 2011).

Other taxa

Our multilocus tree (Fig. 3) includes various species that are isolated in phylogenetic terms, or form small clusters that do not justify recognition as major clades.

The most important of these species in economic terms is *Colletotrichum coccodes*. This is primarily a pathogen of *Solanaceae* (potato and tomato), but also survives well in soil and is reported as an associate of a wide range of crops including strawberry (Buddie *et al.* 1999, Heilmann *et al.* 2006). *Colletotrichum coccodes* was recently epitypified (Liu *et al.* 2011). The species is known to be variable in genetic terms (Ben-Daniel *et al.* 2010). It has been researched into as a potential biocontrol agent for *Abutilon theophrasti* (Dauch *et al.* 2006). *Colletotrichum coccodes* has distinctive conidia that are straight, have acute ends and are often slightly constricted in the mid portion. Our multilocus analysis (Fig. 3) places it as a sister taxon to the destructivum/spaethianum/graminicola clade. In our ITS-only tree (Fig. 2) it occupies the same position, although the posterior probability values are inadequate to confirm its phylogeny from this gene fragment alone.

Colletotrichum trichellum was placed into synonymy with *C. dematium* by von Arx (1957), though it was treated as a separate, apparently host-limited species by Sutton (1962, 1981) based on the degree of curvature of the conidia. ITS-only and multilocus phylogenetic analyses (Figs 2, 3) indicate that this species does not belong to the dematium clade, but forms a sister clade (along with *C. rusci*) with the acutatum clade.

Three poorly-known species occupy basal positions in the ITS-only and multilocus phylogenetic trees (Figs 2, 3). *Colletotrichum cliviae* (from anthracnose of *Clivia miniata*, *Amaryllidaceae*; Yang *et al*. 2009) appears to constitute a monophyletic lineage that is a sister clade to the entire genus apart from the orbiculare clade. *Colletotrichum yunnanense* and *C. dracaenophilum* together form a small clade that is basal to the entire genus apart from the combined orbiculare and *C. cliviae* clade. *Colletotrichum dracaenophilum* is a stem pathogen of *Dracaena* species (*Asparagaceae*; Farr *et al.* 2006), while *C. yunnanense* was isolated as an endophyte of *Buxus* (*Buxaceae*; Liu *et al*. 2007b). According to their publishing authors, all three species have unusually large conidia. *Colletotrichum yunnanense* and *C. cliviae* have complex appressoria; those of *C. dracaenophilum* were not recorded by the describing authors.

WHERE DO WE GO FROM HERE?

What more can we learn about *Colletotrichum* systematics? Several of the major clades have not yet been analysed comprehensively using multilocus technologies. The phylogenetic position of a large part of the species described is still unknown; these species would have to be recollected and epitypified. However, linking new strains to old species is difficult and there are hundreds of "forgotten species" with little information among them. We should therefore focus on clarifying the identity of well-known species that are commonly used and of *Glomerella* species in order to synonymise them in *Colletotrichum*. New species have been discovered regularly over the last five years (including some that are highly distinct in phylogenetic terms) and novel taxa will doubtless continue to appear. Studies of *Colletotrichum* from wild plants would be likely to be particularly fruitful, and provide insights into the taxa currently known from crops and ornamentals. It would be presumptuous even to speculate that the overall systematic framework for the genus cannot be improved.

Future innovations are likely to focus increasingly on understanding populations and host/parasite relationships, and on using increasingly sophisticated analyses of whole genomes. It is only then that we are likely to begin to understand *Colletotrichum* species in their evolutionary context, rather than as cultures in collections. The first major output in this new era of *Colletotrichum* research has now been published (O'Connell *et al*. 2012), devoted to a comparison of the genomes and transcriptomes of two individual strains of *Colletotrichum*, one each from *C. graminicola* (from *Zea mays*, *Poaceae*) and *C. higginsianum* (from *Brassica capestris*, *Brassicaceae*). Overall genome size and chromosome number was found to be broadly similar, but substantial differences were noted between the two taxa in intrachromosomal organisation and in their suites of pathogenicity-related genes, These last were shown to be a reflection of differing host cell wall characteristics; cell walls of *Poaceae* contain higher quantities of hemicellulose and phenolic compounds, while those of *Brassicaceae* are richer in pectins. The two species were estimated as diverging aound 47 M years ago, well after the divergence of their host clades.

Recent changes to the newly renamed *International Code of Nomenclature for Algae, Fungi and Plants* (Hawksworth 2011), especially those Articles relating to registration of names and the abolition of the dual nomenclature system for *Fungi*, mark a further step away from the inflexible application of the rules of date priority towards a consensus approach for choosing between competing names. In response to these historic changes, the International Subcommission on *Colletotrichum* Taxonomy has been set up within the framework of the International Commission on the Taxonomy of Fungi (http://www.fungaltaxonomy.org/). Its remit will be to promote nomenclatural stability for the genus, develop consensus phylogenies, and develop a list of protected names for key taxa that cannot be overturned by the rediscovery of obscure earlier names within the historical literature. An important part of this work is to ensure that all currently accepted species of *Colletotrichum* are adequately typified, with epitypes or neotypes linked to cultures where original type material is lost or inadequate for modern phylogenetic placement, or where no authentic original cultures have been preserved.

In the context of moving to a single name system for these fungi, probably few would argue for the retention of *Glomerella* (the later, sexual genus name with priority until the Melbourne nomenclatural congress in 2011) over *Colletotrichum* (the earlier, asexual name), but it will be the responsibility of the Subcommission to weigh the arguments for each and to recommend one or the other. Technically, we are aware that our publication prejudges this issue, but the transfer of such a large number of the names of multiple well-known economically important species currently accepted as *Colletotrichum* to *Glomerella* would cause chaos amongst the user community. The issues of synonymy between anamorph and teleomorph at the species level are complex (as exemplified by our knowledge of the identities of *Glomerella acutata* (Damm *et al*. 2012a) and *Ga. cingulata* (Weir *et al*. 2012), and it will in most cases be more practical to assign protected status to the asexual species names rather than go through the formal nomenclatural conservation procedures.

A further important activity for the *Colletotrichum* community is to establish a robust phylogeny-based online identification system with barcode reference sequences from ex-type or other verified material that can be queried using Blast tools, as a rigorous alternative to the uncurated data set accessible in GenBank. A preliminary system has already been set up by the CBS-KNAW Fungal Biodiversity Centre based on the multilocus sequence data listed in Table 3 (http://www.cbs.knaw.nl/colletotrichum). In addition to sequences, it will also include morphological and cultural characters and pictures of each species facilitating comprehensive polyphasic identification. Methods used to collect the data are explained, and cultures are listed along with ecological data available. This database will be updated as new taxa are discovered and typifications completed by members of the Subcommission on *Colletotrichum*.

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REFERENCES

Abang MM, Winter S, Green KR, Hoffmann P, Mignouna HD, *et al.* (2002). Molecular identification of *Colletotrichum gloeosporioides* causing yam anthracnose in Nigeria. *Plant Pathology* **51**: 63–71.

Adanson M (1763). *Familles des Plantes*. Vincent, Paris.

Afanador-Kafuri L, Minz D, Maymon M, Freeman S (2003). Characterization of *Colletotrichum* isolates from tamarillo, *Passiflora* and mango in Colombia and identification of a unique species from the genus. *Phytopathology* **93**: 579–587.

Agrios GN (2005). *Plant Pathology*. 5th edn. Academic Press, New York.

Aguileta G, Marthey S, Chiapello H, Lebrun M-H, Rodolphe F, *et al.* (2008). Assessing the performance of single-copy genes for recovering robust phylogenies. *Systematics and Biology* **57**: 613–627.

Ainsworth GC (ed.) (1971). *Ainsworth & Bisby's Dictionary of the Fungi*. 6th edn. CABI, Kew.

Andes JO (1941). Experiments on the inheritance of the "plus" and "minus" characters in *Glomerella cingulata*. *Bulletin of the Torrey Botanical Club* **68**: 609–614.

Armstrong-Cho CL, Banniza S (2006). *Glomerella truncata* sp. nov., the teleomorph of *Colletotrichum truncatum*. *Mycological Research* **110**: 951–956.

Arnold AE, Lutzoni F (2007). Diversity and host range of foliar fungal endophytes: are tropical leaves biodiversity hotspots? *Ecology* **88**: 541–549.

Arx JA von (1957a). Revision der zu *Gloeosporium* gestellten Pilze. *Verhandligen des Koninklijke Nederlandse Akadademie van Wetenschappen, Afd. Natuurkunde*, 2, **51**(3): 153 pp.

Arx JA von (1957b). Die Arten der Gattung *Colletotrichum* Cda. *Phytopathologische Zeitschrift* **29**: 413–468.

Arx JA von (1970). A revision of the fungi classified as *Gloeosporium*. *Bibliotheca Mycologica* **24**: 203 pp.

Arx JA von (1987). Plant Pathogenic Fungi. *Beihefte zur Nova Hedwigia* **87**: 288 pp.

Arx JA von, Müller E (1954). Die Gattungen von amerosporen Pyrenomyceten. *Beiträge zur Kryptogamenflora der Schweiz* **11**(1): 434 pp.

Asakura M, Ninomiya S, Sugimoto M, Oku M, Yamashita S, *et al.* (2009). Atg26-mediated pexophagy is required for host invasion by the plant pathogenic fungus *Colletotrichum orbiculare*. *Plant Cell* **21**: 1291–1304.

Bailey JA, Nash C, Morgan LW, O'Connell RJ, TeBeest DO (1996). Molecular taxonomy of *Colletotrichum* species causing anthracnose on the *Malvaceae*. *Phytopathology* **86**: 1076–1083.

Bailey JA, O'Connell RJ, Pring RJ, Nash C (1992). Infection strategies of *Colletotrichum* species. In *Colletotrichum. Biology, Pathology and Control* (Bailey JA, Jeger MJ, eds). CABI, Wallingford, UK: 88–120

Bailey JA, Jeger MJ (1992). *Colletotrichum. Biology, Pathology and Control*. CABI, Wallingford, UK.

Bain SM, Essary SH (1906). A new anthracnose of alfalfa and red clover. *Journal of Mycology* **12**: 192–193.

Balardin RS, Jarosz AM, Kelly JD (1997). Virulence and molecular diversity in *Colletotrichum lindemuthianum* from South, Central and North America. *Phytopathology* **87**: 1184–1191.

Balardin RS, Smith JJ, Kelly JD (1999). Ribosomal DNA polymorphism in *Colletotrichum lindemuthianum*. *Mycological Research* **103**: 841–848.

Barr ME (1976). *Buergenerula* and the *Physosporellaceae*. *Mycologia* **68**: 611–621.

Barr ME (1983). The ascomycete connection. *Mycologia* **75**: 1–13.

Barrus MF (1918). Varietal susceptability of beans to strains of *Colletotrichum lindemuthianum* (Sacc. & Magn.) B. & C. *Phytopathology* **8**: 589–605.

Baxter AP, Westhuizen GCA van der, Eicker A (1983). Morphology and taxonomy of South African isolates of *Colletotrichum*. *South African Journal of Botany* **2**: 259–289.

Begerow D, Nilsson H, Unterseher M, Maier W (2010). Current state and perspectives of fungal DNA barcoding and rapid identification procedures. *Applications in Microbiology and Biotechnology* **87**: 99–108.

Bell JN, Dixon RA, Bailey JA, Rowell PM, Lamb CJ (1984). Differential induction of chalcone synthase mRNA activity at the onset of phytoalexin accumulation in compatible and incompatible plant pathogen interactions. *Proceedings of the National Academy of Sciences of the USA* **81**: 3384–3388.

Ben-Daniel B, Bar-Zvi D, Johnson D, Harding R, Hazanovsky M, *et al.* (2010). Vegetative compatibility groups in *Colletotrichum coccodes* subpopulations from Australia and genetic links with subpopulations from Europe/Israel and North America. *Phyopathology* **100**: 271–278.

Berbee ML, Taylor JW (1992). Detecting morphological convergence in true fungi, using 18S rRNA gene sequence data. *BioSystems* **28**: 117–125.

Bergstrom GC, Nicholson RL (1999). The biology of corn anthracnose. *Plant Disease* **83**: 596–608.

Berlese AN (1893). *Icones Fungorum Omnium hucusque Cognitorum*. Pergola, Avellino vol. **1**: 91–118.

Birker D, Heidrich K, Takahara, H, Narusaka M. Deslandes L, *et al.* (2009). A locus conferring recessive resistance to *Colletotrichum higginsianum* is shared by four geographically distinct *Arabidopsis* accessions. *Plant Journal* **60**: 602–613.

Braithwaite KS, Irwin JAG, Manners JM (1990a). Ribosomal DNA as a molecular taxonomic marker for the group species *Colletotrichum gloeosporioides*. *Australian Systematic Botany* **3**: 733–738.

Braithwaite KS, Irwin JAG, Manners JM (1990b). Restriction fragment length polymorphisms in *Colletotrichum gloeosporioides* infecting *Stylosanthes* spp. in Australia. *Mycological Research* **94**: 1129–1137.

Braithwaite KS, Manners JM (1989). Human hypervariable minisatellite probes detect DNA polymorphisms in the fungus *Colletotrichum gloeosporioides*. *Current Genetics* **16**: 473–475.

Brock PM, Döring H, Bidartondo MI (2009). How to know unknown fungi: the role of a herbarium. *New Phytologist* **181**: 719–724.

Buddie AG, Martinez-Culebras P, Bridge PD, Garcia MD, Querol A, *et al.* (1999). Molecular characterization of *Colletotrichum* strains derived from strawberry. *Mycological Research* **103**: 385–394.

Buée M, Reich M, Murat C, Morin E, Nilsson RH, *et al.* (2009). 454 pyrosequencing analyses of forest soils reveal an unexpectedly high fungal diversity. *New Phytologist* **184**: 449–456.

Cai L, Hyde KD, Taylor PWJ, Weir BS, Waller J, *et al.* (2009). A polyphasic approach for studying *Colletotrichum*. *Fungal Diversity* **39**: 183–204.

Cannon PF (1991). A revision of *Phyllachora* and some similar genera on the host family *Leguminosae*. *Mycological Papers* **163**: 302 pp.

Cannon PF (1996). Systematics and diversity of the *Phyllachoraceae* associated with *Rosaceae*, with a monograph of *Polystigma*. *Mycological Research* **100**: 1409–1427.

Cannon PF, Bridge PD, Monte E (2000). Linking the past, present, and future of *Colletotrichum* systematics. In: *Colletotrichum: Host specificity, Pathology, and Host-pathogen interaction*. (Prusky D, Freeman S, Dickman, M, eds). APS Press, St Paul, USA: 1–20.

Cannon PF, Buddie AG, Bridge PD (2008). The typification of *Colletotrichum gloeosporioides*. *Mycotaxon* **104**: 189–204.

Cannon PF, Buddie AG, Bridge PD, de Neergard E, Lübeck M, *et al.* (2012). *Lectera*, a new genus of the *Plectosphaerellaceae* for the legume pathogen *Volutella colletotrichoides*. *Mycokeys* **3**: 23–36.

Cano J, Guarro J, Gené J (2004). Molecular and morphological identification of *Colletotrichum* species of clinical interest. *Journal of Clinical Microbiology* **42**: 2450–2454.

Carvajal F, Edgerton CW (1944). The perfect stage of *Colletotrichum falcatum*. *Phytopathology* **34**: 206–213.

Castlebury LA, Rossman AY, Sung GH, Hyten AS, Spatafora JW (2004). Multigene phylogeny reveals new lineage for *Stachybotrys chartarum*, the indoor air fungus. *Mycological Research* **108**: 864–872.

Chadefaud M (1960). Les Végétaux non Vasculaires. Cryptogamie. In: *Traité de Botanique Systématique* (Chadefaud M, Emberger L, eds). Masson, Paris vol.**1**: 1018 pp.

Chen F, Goodwin PH, Khan A, Hsiang T (2002). Population structure and mating-type genes of *Colletotrichum graminicola* from *Agrostis palustris*. *Canadian Journal of Microbiology* **48**: 427–436.

Choi KJ, Kim WG, Kim HG, Choi HW, Lee YK, *et al.* (2011). Morphology, molecular phylogeny and pathogenicity of *Colletotrichum panacicola* causing anthracnose of Korean ginseng. *Plant Pathology Journal* **27**: 1–7.

Chung W-H, Ishii, H, Nishimura K, Fukaya M, Yano K, *et al.* (2006). Fungicide sensitivity and phylogenetic relationship of anthracnose fungi isolated from various fruit crops in Japan. *Plant Disease* **90**: 506–512.

Cisar CR, Spiegel FW, TeBeest DO, Trout C (1994). Evidence for mating between isolates of *Colletotrichum gloeosporioides* with different host specificities. *Current Genetics* **25**: 220–335.

Cisar CR, TeBeest TO (1999). Mating system of the filamentous ascomycete *Glomerella cingulata*. *Current Genetics* **35**: 127–133.

Clements FE, Shear CL (1931). *The Genera of Fungi*. Wilson, New York.

Corda ACI (1831). Die Pilze Deutschlands. In: *Deutschlands Flora in Abbildungen nach der Natur mit Beschreibungen* (Sturm, J, ed.). Sturm, Nürnberg vol. **3**, Abt. 12: 33–64, tab. 21–32.

Corda ACI (1837). *Icones Fungorum hucusque cognitorum* vol. **1**. Calve, Prague.

Corda ACI (1840). *Icones Fungorum hucusque cognitorum* vol. **4**. Calve, Prague.

Crouch JA, Beirn LA (2009). Anthracnose of cereals and grasses. *Fungal Diversity* **39**: 19–44.

Crouch JA, Beirn LA, Cortese LM, Bonos SA, Clarke BB (2009a). Anthracnose disease of switchgrass caused by the novel fungal species *Colletotrichum navitas*. *Mycological Research* **113**: 1411–1421.

Crouch JA, Clarke BB, Hillman BI (2006). Unraveling evolutionary relationships among the divergent lineages of *Colletotrichum* causing anthracnose disease in turfgrass and maize. *Phytopathology* **96**: 46–60.

Crouch JA, Clarke BB, Hillman BI (2009b). What is the value of ITS sequence data in Colletotrichum systematics and species diagnosis? A case study using the falcate-spored graminicolous Colletotrichum group. *Mycologia* **101**: 648–656.

Crouch JA, Clarke BB, White JF, Hillman BI (2009c). Systematic analysis of the falcate-spored graminicolous *Colletotrichum* and a description of six new species from warm season grasses. *Mycologia* **101**: 717–732.

Crouch JA, Glasheen BM, Giunta MA, Clarke BB, Hillman BI (2008). The evolution of transposon repeat-induced point mutation in the genome of *Colletotrichum cereale*: reconciling sex, recombination and homoplasy in an ''asexual" pathogen. *Fungal Genetics and Biology* **45**: 190–206.

Crouch JA, Tomaso-Peterson M (2012). Anthracnose disease of centipedegrass turf caused by *Colletotrichum eremochloae*, a new fungal species closely related to *Colletotrichum sublineola*. *Mycologia*, doi: 10.3852/11-317.

Crouch JA, Tredway LP, Clarke BB, Hillman BI (2009d). Phylogenetic and population genetic divergence correspond with habitat for the pathogen *Colletotrichum cereale* and allied taxa across diverse grass communities. *Molecular Ecology* **18**: 123–135.

Dale JL, Manners JM, Irwin JAG (1988). *Colletotrichum gloeosporioides* isolates causing different anthracnose diseases on *Stylosanthes* in Australia carry distinct double-stranded RNAs. *Transactions of the British Mycological Society* **91**: 671–676.

Damm U, Barroncelli R, Cai L, Kubo Y, O'Connell R, Weir B, Yoshino K, Cannon PF (2010). *Colletotrichum*: species, ecology and interactions. *IMA Fungus* **1**: 161-165.

Damm U, Cannon PF, Woudenberg JHC, Crous PW (2012a). The *Colletotrichum acutatum* species complex. *Studies in Mycology* **73**: 37–113.

Damm U, Cannon PF, Woudenberg JHC, Johnston PR, Weir B, *et al.* (2012b). The *Colletotrichum boninense* species complex. *Studies in Mycology* **73**: 1–36.

Damm U, Woudenberg JHC, Cannon PF, Crous PW (2009). *Colletotrichum* species with curved conidia from herbaceous hosts. *Fungal Diversity* **39**: 45–87.

Dastur JF (1920). *Glomerella cingulata* (Stoneman) Spauld. & v. Sch. and its conidial forms, *Gloeosporium piperatum* E and E. and *Colletotrichum nigrum* E. and Hals., on chillies and *Carica papaya*. *Annals of Applied Biology* **6**: 245–268.

Dauch AL, Watson AK, Seguin P, Jabaji-Hare SH (2006). Real-time PCR quantification of *Colletotrichum coccodes* DNA in soils from bioherbicide field-release assays, with normalization for PCR inhibition. *Canadian Journal of Plant Pathology* **28**: 42–51.

Dean R, Van Kan JAL, Pretorius ZA, Hammond-Kosack KE, Di Pietro A, *et al.* (2012). The Top 10 fungal pathogens in molecular plant pathology. *Molecular Plant Pathology* **13**: 414–430.

Deising HB, Werner S, Wernitz M (2000). The role of fungal appressoria in plant infection. *Microbes and Infection* **2**: 1631–1641.

Denoyes-Rothan B, Guerin G, Délye C, Smith B, Minz D, *et al.* (2003). Genetic diversity and pathogenic variability among isolates of *Colletotrichum* species from strawberry. *Phytopathology* **93**: 219–228.

Dentinger BTM, Ammirati JF, Both EE, Desjardin DE, Halling RE, *et al.* (2010a). Molecular phylogenetics of porcini mushrooms (*Boletus* section *Boletus*). *Molecular Phylogenetics and Evolution* **57**: 1276–1292.

Dentinger BTM, Margaritescu S, Moncalvo J-M (2010b). Rapid and reliable high-throughput methods of DNA extraction for use in barcoding and molecular systematics of mushrooms. *Molecular Ecology Resources* **10**: 628–633.

Dentinger BTM, Didukh MY, Moncalvo J-M (2011). Comparing COI and ITS as DNA barcode markers for mushrooms and allies (*Agaricomycotina*). *PLoS ONE* **6**(9): e25081. doi:10.1371/journal.pone.0025081

Dingley JM, Gilmour JW (1972). *Colletotrichum acutatum* f.sp. *pinea* associated with terminal crook disease of *Pinus* spp. *New Zealand Journal of Forestry Science* **2**: 192–201.

Druzhinina IS, Kopchinskiy AG, Komoj M, Bissett J, Szakacs G, *et al.* (2005). An oligonucleotide barcode for species identification in *Trichoderma* and *Hypocrea*. *Fungal Genetics and Biology* **42**: 813–828.

Du M, Schardl CL, Nuckles EM, Vaillancourt LJ (2005). Using mating-type gene sequences for improved phylogenetic resolution of *Colletotrichum* species complexes. *Mycologia* **97**: 641–658.

Duke MM (1928). The genera *Vermicularia* Fr. and *Colletotrichum* Cda. *Transactions of the British Mycological Society* **13**:156–184.

Eberhardt U (2010). A constructive step towards selecting a DNA barcode for fungi. *New Phytologist* **187**: 265–268.

Edgerton CW (1908). The physiology and development of some anthracnoses. *Botanical Gazette* Chicago **45**: 367–408.

Edgerton CW (1909). The perfect stage of the cotton anthracnose. *Mycologia* **1**: 115–120.

Edgerton CW (1912). Plus and minus strains in an ascomycete. *Science* **35**: 151.

Edgerton CW (1914). Plus and minus strains in the genus *Glomerella*. *American Journal of Botany* **1**: 244–254.

Faedda R, Agosteo GE, Schena L, Mosca S, Frisullo S, *et al.* (2011). *Colletotrichum clavatum* sp. nov. identified as the causal agent of olive anthracnose in Italy. *Phytopathologia Mediterranea* **50**: 283–302.

Farr DF, Aime MC, Rossman AY, Palm ME (2006). Species of *Colletotrichum* on *Agavaceae*. *Mycological Research* **110**: 1395–1408.

Ford R, Banniza S, Photita W, Taylor PWJ (2004) Morphological and molecular discrimination of *Colletotrichum truncatum* causing anthracnose on lentil in Canada. *Australasian Plant Pathology* **33**: 559–569

Freeman S, Minz D, Jurkevitch E, Maymon M, Shabi E. (2000). Molecular analyses of *Colletotrichum* species from almond and other fruits. *Phytopathology* **90**: 608–614.

Freeman S, Minz D, Maymon M, Zveibil A (2001). Genetic diversity within *Colletotrichum acutatum sensu* Simmonds. *Phytopathology* **91**: 586–592.

Freeman S, Rodriguez RJ (1993). Genetic conversion of a fungal plant pathogen to a non-pathogenic endophytic mutualist. *Science* **260**: 75–78.

Fujihara N, Sakaguchi A, Tanaka S, Fujii S, Tsuji G, *et al.* (2010) Peroxisome biogenesis factor PEX13 is required for appressorium-mediated plant infection by the anthracnose fungus *Colletotrichum orbiculare*. *Molecular Plant-Microbe Interactions* **23**: 436–445.

Fukushi T (1921). A willow-canker disease caused by *Physalospora miyabeana* and its conidial form *Gloeosporium*. *Annals of the Phytopathological Society of Japan* **1**: 1–11.

García-Serrano M, Alfaro Laguna E, Rodríguez-Guerra R, Simpson J (2008). Analysis of the *MAT1-2-1* gene of *Colletotrichum lindemuthianum*. *Mycoscience* **49**: 312–317.

Garrido C, Carbú M, Fernández-Acero FJ, Vallejo I, Cantoral JM (2009). Phylogenetic relationships and genome organisation of *Colletotrichum acutatum* causing anthracnose in strawberry. *European Journal of Plant Pathology* **125**: 397–411.

Gazis R, Rehner S, Chaverri P (2011). Species delimitation in fungal endophyte diversity studies and its implications in ecological and biogeographic inferences. *Molecular Ecology* **20**: 3001–3013.

Geiser DM, Jiménez-Gasco M, Kang S, Makalowska I, Veeraraghavan N, *et al.* (2004). FUSARIUM-ID v.1.0: A DNA sequence database for identifying *Fusarium*. *European Journal of Plant Pathology* **110**: 473–479.

Giaretta DR, Bogo A, Coelho CMM, Guidolin AF, Dantas ACM, *et al.* (2010). ITS-rDNA phylogeny of *Colletotrichum* spp. causal agent of apple glomerella leaf spot. *Ciência Rural* **40**: 806–812.

González E, Sutton TB, Correll JC (2006). Clarification of the etiology of *Glomerella* leaf spot and bitter rot of apple caused by *Colletotrichum* spp. based on morphology and genetic, molecular and pathogenicity tests. *Phytopathology* **96**: 982–992.

Gourley CO (1966). The pathogenicity of *Colletotrichum dematium* to table beets and other hosts. *Canadian Journal of Plant Science* **46**: 531–536.

Guarro J, Svidzinski TE, Zaror L, Forjaz MH, Gené F, *et al.* (1998). Subcutaneous hyalohyphomycosis caused by *Colletotrichum gloeosporioides*. *Journal of Clinical Microbiology* **36**: 3060–3065.

Guerber JC, Correll JC (2001). Characterization of *Glomerella acutata*, the teleomorph of *Colletotrichum acutatum*. *Mycologia* **93**: 216–229.

Guerber JC, Liu B, Correll JC, Johnston PR (2003). Characterization of diversity in *Colletotrichum acutatum* sensu lato by sequence analysis of two gene introns, mtDNA and intron RFLPs, and mating compatibility. *Mycologia* **95**: 872–895.

Hall BH, Hitch CJ, Oxspring EA, Wicks TJ (2007). Leek diseases in Australia. *Australasian Plant Pathology* **36**: 383–388.

Hawksworth DL (2011). A new dawn for the naming of fungi: impacts of decisions made in Melbourne in July 2011 on the future publication and regulation of fungal names. *Mycokeys* **1**: 7–20.

Hawksworth DL, Kirk PM, Sutton BC, Pegler DN (1995). *Ainsworth & Bisby's Dictionary of the Fungi*. 8th edn. CABI, Kew.

Hawksworth DL, Sutton BC, Ainsworth GC (eds) (1983). *Ainsworth & Bisby's Dictionary of the Fungi*.7th edn. CABI, Kew.

Heilmann LJ, Nitzan N, Johnson DA, Pasche JS, Doetkott C, *et al.* (2006). Genetic variability in the potato pathogen *Colletotrichum coccodes* as determined by amplified fragment length polymorphism and vegetative compatibility group analyses. *Phytopathology* **96**: 1097–1107.

Hemelrijk W van, Debode J, Heungens K, Maes M, Creemers P (2010). Phenotypic and genetic characterization of *Colletotrichum* isolates from Belgian strawberry fields. *Plant Pathology* **59**: 853–861.

Hemmi T (1920). Beiträge zur Kenntnis der Morphologie und Physiologie der Japanischen Gloeosporien. *Journal of the College of Agriculture, Hokkaido Imperial University* **9**: 1–159.

Hennings P (1898). Die in den Gewächshäusern des Berliner Botanischen Gartens beobachteten Pilze. *Verhandlungen des Botanischen Vereins der Provinz Brandenburg* **40**: 109–177.

Higgins KL, Coley PD, Kursar TA, Arnold AE (2011). Culturing and direct PCR suggest prevalent host generalism among diverse fungal endophytes of tropical forest grasses. *Mycologia* **103**: 247–260.

Houbraken J, Frisvad JC, Samson RA (2011). Fleming's penicillin producing strain is not *P. chrysogenum* but *P. rubens*. *IMA Fungus* **2**: 87–95.

Hsiang T, Goodwin PH (2001). Ribosomal DNA sequence comparisons of *Colletotrichum graminicola* from turf-grasses and other hosts. *European Journal of Plant Pathology* **107**: 593–599.

Huhndorf SM, Miller AN, Fernández FA (2004). Molecular systematics of the *Sordariales*: the order and the family *Lasiosphaeriaceae* redefined. *Mycologia* **96**: 368–387.

Huser A, Takahara H, Schmalenbach W, O'Connell R (2009). Discovery of pathogenicity genes in the crucifer anthracnose fungus, *Colletotrichum higginsianum*, using random insertional mutagenesis. *Molecular Plant-Microbe Interactions* **22**: 143–156.

Hyde KD, Cai L, Cannon PF, Crouch JA, Crous PW, *et al.* (2009a). *Colletotrichum* – names in current use. *Fungal Diversity* **39**: 147–182.

Hyde KD, Cai L, McKenzie EHC, Yang YL, Zhang JZ, *et al.* (2009b). *Colletotrichum*: a catalogue of confusion. *Fungal Diversity* **39**: 1–17.

Illingworth CA, Andrews JH, Bibeau C, Sogin ML (1991). Phylogenetic placement of *Athelia bombacina, Aureobasidium pullulans* and *Colletotrichum gloeosporioides* inferred from sequence compansons of small subunit ribosomal RNAs. *Experimental Mycology* **15**: 65–75.

James TY, Kauff F, Schoch CL, Matheny PB, Hofstetter V, *et al.* (2006). Reconstructing the early evolution of fungi using a six-gene phylogeny. *Nature* **443**: 818–822.

Jaulneau V, Cazaux M, Hoi JWS, Fournier S, Esquerre-Tugaye MT (2010). Host and nonhost resistance in *Medicago-Colletotrichum* interactions. *Molecular Plant-Microbe Interactions* **23**: 1107–1117.

Jenkins SF, Winstead NN (1964). *Glomerella magna*, cause of a new anthracnose of cucurbits. *Phytopathology* **54**: 452–454.

Johnston PR, Jones D (1997). Relationships among *Colletotrichum* isolates from fruit-rots assessed using rDNA sequences. *Mycologia* **89**: 420–430.

Joshee S, Paulus BC, Park D, Johnston PR (2009). Diversity and distribution of fungal foliar endophytes in New Zealand *Podocarpaceae*. *Mycological Research* **113**: 1003–1015.

Kelly LJ, Hollingsworth PM, Coppins BJ, Ellis CJ, Harrold P, *et al.* (2011). DNA barccoding of lichenized fungi demonstrates high identification success in a floristic context. *New Phytologist* **191**: 288–300.

Kim WG, Hong SK, Kim JH (2008). Occurrence of anthracnose on welsh onion caused by *Colletotrichum circinans*. *Mycobiology* **36**: 274–276.

Kimura A, Takano Y, Furusawa I, Okuno T (2001) Peroxisomal metabolic function is required for appressorium-mediated plant infection by *Colletotrichum lagenarium*. *Plant Cell* **13**: 1945–1957.

Kinghorn WO (1936). *Glomerella phacidiomorpha* (Ces.) Pet. on *Phormium tenax* in Britain. *Annals of Applied Biology* **23**: 30–44.

Kirk PM, Cannon PF, David JC, Stalpers JA (2001). *Ainsworth & Bisby's Dictionary of the Fungi*. 9th edn. CABI, Egham, UK.

Kirk PM, Cannon PF, Minter DW, Stalpers JA (2008). *Ainsworth & Bisby's Dictionary of the Fungi*. 10th edn. CABI, Wallingford, UK.

Kleemann J, Rincon-Rivera LJ, Takahara H, Neumann U, van Themaat EVL, *et al.* (2012). Sequential delivery of host-induced virulence effectors by appressoria and intracellular hyphae of the phytopathogen *Colletotrichum higginsianum*. *PLoS Pathogens* **8**(4): e1002643. doi:10.1371/journal.ppat.1002643.

Kõljalg U, Larsson KH, Abarenkov K, Nilsson RH, Alexander IJ, *et al.* (2005). UNITE: a database providing web-based methods for the molecular identification of ectomycorrhizal fungi. *New Phytologist* **166**: 1063–1068.

Krüger F (1913). Beiträge zur Kenntnis einiger Gloeosporien. *Arbeiten aus der Kaiserlichen Biologischen Anstalt für Land- und Forstwirtschaft*. **9**: 233–323.

Kruger J, Hoffman FM, Hubbeling N (1977). The kappa race of *Colletotrichum lindemuthianum* and sources of resistance to anthracnose in *Phaseolus* beans. *Euphytica* **26**: 23–25.

Latunde-Dada AO (2001). *Colletotrichum*: tales of forcible entry, stealth, transient confinement and breakout. *Molecular Plant Pathology* **2**: 187–198.

Latunde-Dada AO, Lucas JA (2007). Localized hemibiotrophy in *Colletotrichum*: cytological and molecular taxonomical similarities among *C. destructivum*, *C. linicola* and *C. truncatum*. *Plant Pathology* **56**: 437–447.

Leahy R, Schubert T, Strandberg J, Stamps B, Norman D (1995). Anthracnose of leatherleaf fern. *Plant Pathology Circular* **372**: 4 pp.

Lee DH, Kim DH, Jeon YA, Uhm JY, Hong SB (2007). Molecular and cultural characterization of *Colletotrichum* spp. causing bitter rot of apples in Korea. *Plant Pathology Journal* **23**: 37–44.

Lee HB, Park JY, Jung HS (2005). Identification, growth and pathogenicity of *Colletotrichum boninense* causing leaf anthracnose on spindle tree. *Plant Pathology Journal* **21**: 27–32.

Lehman SG, Wolf FA (1926). Soybean anthracnose. *Journal of Agricultural Research* Washington **33**: 381–390.

Lenné JM (2002). Some major plant diseases. In: *Plant Pathologist's Pocketbook* (Waller JM, Lenné JM, Waller SJ, eds). 3rd edn. CABI, Wallingford, UK: 4–18.

Liu B, Wasilwa LA, Morelock TE, O'Neill NR, Correll JC (2007a). Comparison of *Colletotrichum orbiculare* and several allied *Colletotrichum* spp. for mtDNA RFLPs, intron RFLP and sequence variation, vegetative compatibility and host specificity. *Phytopathology* **97**: 1305–1314.

Liu F, Hyde KD, Cai L (2011). Neotypification of *Colletotrichum coccodes*, the causal agent of potato black dot disease and tomato anthracnose. *Mycology* **2**: 248–254.

Liu X, Xie X, Duan J (2007b). *Colletotrichum yunnanense* sp. nov., a new endophytic species from *Buxus* sp. *Mycotaxon* **100**: 137–144.

LoBuglio KF, Pfister DH (2008). A *Glomerella* species phylogenetically related to *Colletotrichum acutatum* on Norway maple in Massachusetts. *Mycologia* **100**: 710–715.

Locquin M (1984). *Mycologie Générale et Structurale*. Masson, Paris.

Lopez AMQ, Lucas JA (2010). *Colletotrichum* isolates related to anthracnose of cashew trees in Brazil: morphological and molecular description using LSU rDNA sequences. *Brazilian Archives of Biology and Technology* **53**: 741–752.

Lotter HC, Berger DK (2005). Anthracnose of lupins in South Africa is caused by *Colletotrichum lupini* var. *setosum*. *Australasian Plant Pathology* **34**: 385–392.

Lu G, Cannon PF, Reid A, Simmons CM (2004). Diversity and molecular relationships of endophytic *Colletotrichum* isolates from the Iwokrama Forest Reserve, Guyana. *Mycological Research* **108**: 53–63.

Lubbe CM, Denman S, Cannon PF, Groenewald JZ, Lamprecht SC, *et al.* (2004). Characterization of *Colletotrichum gloeosporioides* and similar species associated with anthracnose and dieback of *Proteaceae*. *Mycologia* **96**: 1268–1279.

Lucas GB, Chilton SJP, Edgerton CW (1944). Genetics of *Glomerella*. I. Studies on the behavior of certain strains. *American Journal of Botany* **31**: 233–239.

Mackenzie SJ, Seijo TE, Legard DE, Timmer LW, Peres NA (2007). Selection for pathogenicity to strawberry in populations of *Colletotrichum gloeosporioides* from native plants. *Phytopathology* **97**:1130–1140.

Mackenzie SJ, Peres NA, Barquero MP, Arauz LF, Timmer LW (2009). Host range and genetic relatedness of *Colletotrichum acutatum* isolates from fruit crops and leatherleaf fern in Florida. *Phytopathology* **99**: 620–631.

Mahuku GS, Riascos JJ (2004). Virulence and molecular diversity within *Colletotrichum lindemuthianum* isolates from Andean and Mesoamerican bean varieties and regions. *European Journal of Plant Pathology* **110**: 253–263.

Manandhar JB, Hartman GL, Sinclair JB (1986). *Colletotrichum destructivum*, the anamorph of *Glomerella glycines*. *Phytopathology* **76**: 282–285.

Manuel L, Talhinhas P, Várzea V, Neves-Martins J (2010). Characterization of *Colletotrichum kahawae* isolates causing coffee berry disease in Angola. *Journal of Phytopathology* **158**: 310–313.

Manire CA, Rhinehart HL, Sutton DA, Thompson EH, Rinaldi MG, *et al.* (2002). *Journal of Clinical Microbiology* **40**: 4273–4280.

Marcelino J, Giordano R, Gouli S, Gouli V, Parker BL, *et al.* (2008). *Colletotrichum acutatum* var. *fioriniae* (teleomorph: *Glomerella acutata* var. *fioriniae* var. nov. infection of a scale insect. *Mycologia* **100**: 353–374.

Marcelino J, Gouli S, Parker BL, Skinner M, Giordano R (2009). Entomopathogenic activity of a variety of the fungus, *Colletotrichum acutatum,* recovered from the elongate hemlock scale, *Fiorinia externa*. 11 pp. *Journal of Insect Science* **9**: article 13.

Martín MP, Garcia Figueres F (1999). *Colletotrichum acutatum* and *C. gloeosporioides* cause anthracnose on olives. *European Journal of Plant Pathology* **105**: 733–741.

Martínez-Culebras PV, Querol A, Suarez-Fernandez MB, García-Lopez MD, Barrio E (2003). *Journal of Phytopathology* **151**: 135–143.

Masel A, Braithwaite K, Irwin J, Manners J (1990). Highly variable molecular karyotypes in the plant pathogen *Colletotrichum gloeosporioides*. *Current Genetics* **18**: 81–86.

McKay SF, Freeman S, Minz D, Maymon M, Sedgley M, *et al.* (2009). Morphological, genetic, and pathogenic characterization of *Colletotrichum acutatum*, the cause of anthracnose of almond in Australia. *Phytopathology* **99**: 985–995.

Menat J, Cabral AL, Perumal V, Wei Y, Banniza S (2012). Mating system of *Glomerella truncata*: another *Glomerella* species with an atypical mating system. *Mycologia* **104**: 641–649.

Mills PR, Hodson A, Brown AE (1992). Molecular differentiation of *Colletotrichum gloeosporioides* isolates infecting tropical fruits. In: *Colletotrichum:* Biology, Pathology and Control (Bailey JA, Jeger MJ, eds). CABI, Wallingford, UK: 269–288.

Min XJ, Hickey DA (2007). Assessing the effect of varying sequence length on DNA barcoding of fungi. *Molecular Ecology Notes* **7**: 365–373.

Montagne C (1849). Sixième centurie des plantes cellulaires nouvelles tant indigènes qu'exotiques. *Annales des Sciences Naturelles*. Botanique Série 3, **12**: 285–320.

Mordue JEM (1971). *Colletotrichum lindemuthianum. CMI Descriptions of Pathogenic Fungi and Bacteria* no. 316. CMI, Kew.

Moriwaki J, Tsukiboshi T (2009). *Colletotrichum echinochloae*, a new species on Japanese barnyard millet (*Echinochloa utilis*). *Mycoscience* **50**: 273–280.

Moriwaki J, Sato T, Tsukiboshi T (2003). Morphological and molecular characterization of *Colletotrichum boninense* sp. nov. from Japan. *Mycoscience* **44**: 47–53.

Moriwaki J, Tsukiboshi T, Sato T (2002). Grouping of *Colletotrichum* species in Japan based on rDNA sequences. *Journal of General Plant Pathology* **68**: 307–320.

Munaut F, Hamaide N, Stappen J van der, Maraite H (1998). Genetic relationships among isolates of *Colletotrichum gloeosporioides* from *Stylosanthes* spp. in Africa and Australia using RAPD and ribosomal DNA markers. *Plant Pathology* **47**: 641–648.

Munaut F, Hamaide N, Maraite H (2002). Genomic and pathogenic diversity in *Colletotrichum gloeosporioides* from wild native Mexican *Stylosanthes* spp., and taxonomic implications. *Mycological Research* **106**: 579–593.

Münch S, Lingne U, Floss DS, Ludwig N, Sauer N, *et al.* (2008). The hemibiotrophic lifestyle of *Colletotrichum* species. *Journal of Plant Physiology* **165**: 41–51.

Nakamura M, Ohzono M, Iwai H, Arai K (2006). Anthracnose of *Sansevieria trifasciata* caused by *Colletotrichum sansevieriae* sp. nov. *Journal of General Plant Pathology* **72**: 253–256.

Nguyen PTH, Vinnere Pettersson O, Olsson P, Liljeroth E (2010). Identification of *Colletotrichum* species associated with anthracnose disease of coffee in Vietnam. *European Journal of Plant Pathology* **127**: 73–87.

Nicholson RL (1992). *Colletotrichum graminicola* and the anthracnose diseases of maize and sorghum. In: *Colletotrichum. Biology, Pathology and Control* (Bailey JA, Jeger MJ eds). CABI, Wallingford, UK: 186–202.

Nicholson RL, Moraes WBC (1980). Survival of *Colletotrichum graminicola*: importance of the spore matrix. *Phytopathology* **70**: 255–261.

Nirenberg HI, Feiler U, Hagedorn G (2002). Description of *Colletotrichum lupini* comb. nov. in modern terms. *Mycologia* **94**: 307–320.

O'Connell RJ, Bailey JA, Richmond DV (1985). Cytology and physiology of infection of *Phaseolus vulgaris* by *Colletotrichum lindemuthianum*. *Physiological Plant Pathology* **27**: 75–93.

O'Connell RJ, Bailey JA, Vose IR, Lamb CJ (1986). Immunogold labelling of fungal antigens in cells of *Phaseolus vulgaris* infected by *Colletotrichum lindemuthianum*. *Physiological and Molecular Plant Pathology* **28**: 99–105.

O'Connell R, Herbert C, Sreenivasaprasad S, Khatib M, Esquerré-Dugayé M-T, *et al.* (2004). A novel *Arabidopsis-Colletotrichum* pathosystem for the molecular dissection of plant-fungal interactions. *Molecular Plant-Microbe Interactions* **17**: 272–282.

O'Connell RJ, Perfect S, Hughes B, Carzaniga R, Bailey JA, *et al.* (2000). Dissecting the cell biology of *Colletotrichum* infection processes. In: *Colletotrichum. Host Specificity, Pathology and Host-Pathogen Interaction* (Prusky D, Freeman S, Dickman MB, eds). APS Press, St Paul, USA: 57–77.

O'Connell RJ, Thon MR, Hacquard S, Amyotte SG, Kleemann J, *et al.* (2012). Life-style transitions in plant pathogenic *Colletotrichum* fungi deciphered by genome and transcriptome analyses. *Nature Genetics* doi:10.1038/ng.2372.

O'Donnell K, Gueidan C, Sink S, Johnston PR, Crous PW, *et al.* (2009). A two-locus DNA sequence database for typing plant and human pathogens within the *Fusarium oxysporum* species complex. *Fungal Genetics and Biology* **46**: 936–948.

O'Donnell K, Kistler HC, Tacke BK, Casper HH (2000). Gene genealogies reveal global phylogeographic structure and reproductive isolation among lineages of *Fusarium graminearum*, the fungus causing wheat scab. *Proceedings of the National Academy of Sciences of the USA* **97**: 7905–7910.

Olive LS (1951). Homothallism and heterothallism in *Glomerella*. *Transactions of the New York Academy of Science* **13**: 238–242.

Pai HS (1970). Life cycle of *Colletotrichum heveae* inciting spot anthracnose of *Phyllanthus acidus*. *Mycopathologia et Mycologia applicata* **42**: 65–72.

Pain NA, Green JR, Gammie F, O'Connell RJ (1994). Immunomagnetic isolation of viable intracellular hyphae of *Colletotrichum lindemuthianum* (Sacc. & Magn.) Briosi & Cav. from infected bean leaves using a monoclonal antibody. *New Phytologist* **127**: 223–232.

Palarpawar MY, Ghurde VR (1988). Some new hosts of *Colletotrichum curcumae*. *Indian Journal of Mycology and Plant Pathology* **18**: 220–221.

Parbery DG (1964). Studies on graminicolous species of *Phyllachora* Fckl. IV. Evaluation of the criteria of species. *Australian Journal of Botany* **12**: 265–281.

Pastor-Corrales MA, Otoya MM, Molina A (1995). Resistance to *Colletotrichum lindemuthianum* isolates from Middle America and Andean South America in different common bean races. *Plant Disease* **79**: 63–67.

Peres NA, Timmer LW, Adaskaveg JE, Correll JC (2005). Life styles of *Colletotrichum acutatum*. *Plant Disease* **89**: 784–796.

Peres NA, MacKenzie SJ, Peever TL, Timmer LW (2008). Postbloom fruit drop of citrus and Key lime anthracnose are caused by distinct phylogenetic lineages of *Colletotrichum acutatum. Phytopathology* **98**: 345–352.

Perfect SE, Hughes HB, O'Connell RJ, Green JR (1999) *Colletotrichum*: a model genus for studies on pathology and fungal–plant interactions. *Fungal Genetics and Biology* **27**:186–198.

Petch T (1917). Additions to Ceylon fungi. *Annals of the Royal Botanic Garden, Peradeniya* **6**: 195–256.

Peterson SW (2008). Phylogenetic analysis of *Aspergillus* species using DNA sequences from four loci. *Mycologia* **100**: 205–226.

Petrak F (1924). Über die phylogenetischen Beziehungen der Gattung *Phyllachora* und ihre Bedeutung für das System der dothidealean Pilze. *Annales Mycologici* **22**: 1–10.

Photita W, Taylor PWJ, Ford R, Lumyong P, McKenzie HC, *et al.* (2005). Morphological and molecular characterization of *Colletotrichum* species from herbaceous plants in Thailand. *Fungal Diversity* **18**: 117–133.

Phoulivong S, Cai L, Chen H, McKenzie EHC, Abdelsalam K, *et al.* (2010). *Colletotrichum gloeosporioides* is not a common pathogen on tropical fruits. *Fungal Diversity* **44**: 33–43.

Phuong THN, Pettersson OV, Olsson P, Nguyen PTH (2010). Identification of *Colletotrichum* species associated with anthracnose disease of coffee in Vietnam. *European Journal of Plant Pathology* **127**: 73–87.

Pileggi SA, Vieira de Oliveira SF, Andrade CW, Vicente VA, Dalzoto P do R, *et al.* (2009). Molecular and morphological markers for rapid distinction between two *Colletotrichum* species. *Canadian Journal of Microbiology* **55**: 1076–88.

Pinto JM, Pereira R, Mota SF, Ishikawa FH, Souza EA (2012). Investigating phenotypic variability in *Colletotrichum lindemuthianum* populations. *Phytopathology* **102**: 490–497.

Polashock JJ, Caruso FL, Oudemans PV, McManus PS, Crouch JA (2009). The North American cranberry fruit rot fungal community: a systematic overview using morphological and phylogenetic affinities. *Plant Pathology* **58**: 1116–1127.

Politis DJ (1975). The identity and perfect state of *Colletotrichum graminicola*. *Mycologia* **67**: 56–62.

Prihastuti H, Cai L, Chen H, McKenzie EHC, Hyde KD (2009). Characterization of *Colletotrichum* species associated with coffee berries in northern Thailand. *Fungal Diversity* **39**: 89–109.

Prihastuti H, Cai L, Crouch JA, Phoulivong S, Moslem MA, *et al.* (2010). Neotypification of *Colletotrichum falcatum*, the causative agent of red-rot disease in sugarcane. *Sydowia* **62**: 283–293.

Prusky D, Freeman S, Dickman MB (eds) (2000). *Colletotrichum. Host Specificity, Pathology and Host-Pathogen Interaction*. APS Press, St Paul, USA.

Prusky D, Plumbley RA (1992). Quiescent infections of *Colletotrichum* in tropical and subtropical fruit. In: *Colletotrichum. Biology, Pathology and Control* (Bailey JA, Jeger MJ, eds). CABI, Wallingford, UK: 289–307.

Raja H, Schoch C, Hustad V, Shearer C, Miller A (2011). Testing the phylogenetic utility of MCM7 in the Ascomycota. *MycoKeys* **1**: 63–94.

Ramos AP, Merali Z, Talhinhas P, Sreenivasaprasad S, Oliveira H (2006). Molecular and morphological characterisation of *Colletotrichum* species involved in citrus anthracnose in Portugal. *Bulletin OILB/SROP* **29**: 317–326.

Rampersad SN (2011). Molecular and phenotypic characterization of *Colletotrichum* species associated with anthracnose disease of papya in Trinidad. *Plant Disease* **95**: 1244–1254.

Réblová M, Gams W, Seifert KA (2011). *Monilochaetes* and allied genera of the *Glomerellales*, and a reconsideration of families in the *Microascales*. *Studies in Mycology* **68**: 163–191.

Redman RS, Ranson JC, Rodriguez RJ (1999). Conversion of the pathogenic fungus *Colletotrichum magna* to a nonpathogenic, endophytic mutualist by gene disruption. *Molecular Plant-Microbe Interactions* **12**: 969–975.

Ritterband DC, Shah M, Seedor JA (1997). *Colletotrichum graminicola*: a new corneal pathogen. *Cornea* **16**: 362–364.

Rodriguez RJ, Redman RS (2000). *Colletotrichum* as a model system for defining the genetic basis of fungal symbiotic lifestyles. In: *Colletotrichum. Host Specificity, Pathology and Host-Pathogen Interaction* (Prusky D, Freeman S, Dickman MB, eds). APS Press, St Paul, USA: 114–130.

Rodríguez-Guerra R, Ramírez-Rueda MT, Cabral-Enciso M, García-Serrano M, Liro-Maldonado Z, *et al.* (2005). Heterothallic mating observed between Mexican isolates of *Glomerella lindemuthiana*. *Mycologia* **97**: 793–803.

Rojas EI, Rehner SA, Samuels GJ, Van Bael SA, Herre EA, *et al.* (2010). *Colletotrichum gloeosporioides* s.l. associated with *Theobroma cacao* and other plants in Panama: multilocus phylogenies distinguish pathogen and endophyte clades. *Mycologia* **102**: 1318–1338.

Rosewich UL, Pettway RE, McDonald BA, Duncan RR, Frederiksen RA (1998). Genetic structure and temporal dynamics of a *Colletotrichum graminicola* population in a sorghum disease nursery. *Phytopathology* **88**: 1087–1093.

Samson RA, Noonim P, Meijer M, Houbraken J, Frisvad JC, *et al.* (2007). Diagnostic tools to identify black aspergilli. *Studies in Mycology* **59**: 129–145.

Sanders GM, Korsten L (2003). Comparison of cross inoculation potential of South African avocado and mango isolates of *Colletotrichum gloeosporioides*. *Microbiological Research* **158**: 143–150.

Schmitt I, Crespo A, Divakar PK, Fankhauser JD, Herman-Sackett E, *et al.* (2009). New primers for promising single-copy genes in fungal phylogenetics and systematics. *Persoonia* **23** 35–40.

Schoch C, Seifert K, Crous P (2011). Progress on DNA barcoding of *Fungi. IMA Fungus* **2**: (5).

Schoch CL, Seifert KA, Huhndorf S, Robert V, Spouge JL, *et al.* (2012). Nuclear ribosomal internal transcribed spacer (ITS) region as a universal DNA barcode marker for fungi. *Proceedings of the National Academy of Sciences of the USA* **109**: 6241–6246.

Schrenk H von, Spaulding P (1903). The bitter-rot fungus. *Science* n.s. **17**: 750–751.

Seifert KA, Samson RA, deWaard JR, Houbraken J, Levesque CA, *et al.* (2007). Prospects for fungus identification using CO1 DNA barcodes, with *Penicillium* as a test case. *Proceedings of the National Academy of Sciences of the USA* **104**: 3901–3906.

Sharma PN, Padder BA, Sharma OP, Pathania A, Sharma P (2007). Pathological and molecular diversity in *Colletotrichum lindemuthianum* (bean anthracnose) across Himachal Pradesh, a north-western Himalayan state of India. *Australasian Plant Pathology* **36**: 191–197.

Shear CL, Wood AK (1907). Ascogenous forms of *Gloeosporium* and *Colletotrichum*. *Botanical Gazette* Chicago **43**: 259–266.

Shear CL, Wood AK (1913). Studies of fungus parasites belonging to the genus *Glomerella*. *Bulletin, Bureau of Plant Industry, US Department of Agriculture* **252**: 110 pp.

Shenoy BD, Jeewon R, Lam WH, Bhat DJ, Than PP, *et al.* (2007). Morpho-molecular characterisation and epitypification of *Colletotrichum capsici* (*Glomerellaceae*, *Sordariomycetes*), the causative agent of anthracnose in chilli. *Fungal Diversity* **27**: 197–211.

Sherriff C, Whelan MJ, Arnold GM, Bailey JA (1995). rDNA sequence analysis confirms the distinction between *Colletotrichum graminicola* and *C. sublineolum*. *Mycological Research* **99**: 475–478.

Sherriff C, Whelan MJ, Arnold GM, Lafay J-F, Brygoo Y, *et al.* (1994). Ribosomal DNA sequence analysis reveals new species groupings in the genus *Colletotrichum*. *Experimental Mycology* **18**: 121–138.

Shiraishi A, Araki-Sasaki A, Mitani A, Miyamoto H, Sunada A, *et al.* (2011). Clinical characteristics of keratitis due to *Colletotrichum gloeosporioides*. *Journal of Ocular Pharmacology and Therapeutics* **27**: 487–491.

Shivaprakash MR, Appannanavar SB, Dhaliwal M, Gupta A, Gupta S, *et al.* (2011). *Colletotrichum truncatum*: an unusual pathogen causing mycotic keratitis and endophthalmitis. *Journal of Clinical Microbiology* **49**: 2894–2898.

Shivas RG, Tan YP (2009). A taxonomic reassessment of *Colletotrichum acututum*, introducing *C. fioriniae* comb. et stat. nov. and *C. simmondsii* sp. nov. *Fungal Diversity* **39**: 111–122.

Sicard D, Michalakis Y, Dron M, Neema C (1997). Genetic diversity and pathogenic variation of *Colletotrichum lindemuthianum* in the three centers of diversity of its host, *Phaseolus vulgaris*. *Phytopathology* **87**: 807–813.

Silva DN, Talhinas P, Várzea V, Cai L, Paulo OS, Batista D (2012a). Application of the Apn2/MAT locus to improve the systematics of the *Colletotrichum gloeosporioides* complex: an example from coffee (*Coffea* spp.) hosts. *Mycologia* **104**: 396–409.

Silva DN, Talhinhas P, Cai L, Manuel L, Gichuru EK, Loureiro A, Várzea V, Paulo OS, Batista D (2012b). Host-jump drives rapid and recent ecological speciation of the emergent fungal pathogen *Colletotrichum kahawae*. *Molecular Ecology* **21**: 2655–2670.

Silva-Rojas HV, Ávila-Quezada GD (2011). Phylogenetic and morphological identification of *Colletotrichum boninense*: a novel causal agent of anthracnose in avocado. *Plant Pathology* **60**: 899–908.

Simmonds JH (1965). A study of the species of *Colletotrichum* causing ripe fruit rots in Queensland. *Queensland Journal of Agriculture and Animal Science* **22**: 437–459.

Sivanesan A, Hsieh WH (1993). A new ascomycete, *Glomerella septospora* sp. nov. and its coelomycete anamorph, *Colletotrichum taiwanense* sp. nov. from Taiwan. *Mycological Research* **97**: 1523–1529.

Small W (1921). Notes on species of *Colletotrichum* and *Phoma* in Uganda. *Bulletin of Miscellaneous Information*. Royal Botanic Gardens, Kew **1921**: 57–67

Small W (1926). On the occurrences of a species of *Colletotrichum*. *Transactions of the British Mycological Society* **11**: 112–137.

Smith BJ, Black LL (1990). Morphological, cultural and pathogenic variation among *Colletotrichum* species isolated from strawberry. *Plant Disease* **74**: 69–76.

Sogonov MV, Castlebury LA, Rossman AY, Mejía LC, White JF (2008). Leaf-inhabiting genera of the *Gnomoniaceae*, *Diaporthales*. *Studies in Mycology* **62**: 1–79.

Sousa EA, Camargo OA, Pinto JM (2010). Sexual recombination in *Colletotrichum lindemuthianum* occurs on a fine scale. *Genetics and Molecular Research* **8**: 1759–1769.

Sreenivasaprasad S, Brown AE, Mills PR (1992). DNA sequence variation and interrelationship among *Colletotrichum* species causing strawberry anthracnose. *Physiological and Molecular Plant Pathology* **41**: 265–281.

Sreenivasaprasad S, Brown AE, Mills PR (1993). Coffee berry disease pathogen in Africa: genetic structure and relationship to the group species *Colletotrichum gloeosporioides*. *Mycological Research* **97**: 995–1000.

Sreenivasaprasad S, Mills PR, Meehan BM, Brown AE (1996). Phylogeny and systematics of 18 *Colletotrichum* species based on ribosomal DNA spacer sequences. *Genome* **39**: 499–512.

Stevens FL (1931). The ascigerous stage of *Colletotrichum lagenarium* induced by ulta-violet radiation. *Mycologia* **23**: 134–139.

Stoneman B (1898). A comparative study of the development of some anthracnoses. *Botanical Gazette* Chicago **26**: 69–120.

Stukenbrock EH, Christiansen FB, Hansen TT, Dutheil JY, Schierup MH (2012). Fusion of two divergent fungal individuals led to the recent emergence of a unique widespread pathogen species. *Proceedings of the National Academy of Sciences of the USA* doi: 10.1073/pnas.1201403109.

Su YY, Noireung P, Liu F, Hyde KD, Moslem MA, *et al.* (2011). Epitypification of *Colletotrichum musae*, the causative agent of banana anthracnose. *Mycoscience* **52**: 376–382.

Sun H, Zhang JZ (2009). *Colletotrichum destructivum* from cowpea infecting *Arabidopsis thaliana* and its identity to *C. higginsianum*. *European Journal of Plant Pathology* **125**: 459–469.

Sutton BC (1962). *Colletotrichum dematium* (Pers. ex Fr.) Grove and *C. trichellum* (Fr. ex Fr.) Duke. *Transactions of the British Mycological Society* **45**: 222–232.

Sutton BC (1966). Development of fructifications in *Colletotrichum graminicola* (Ces.) Wils. and related species. *Canadian Journal of Botany* **44**: 887–897.

Sutton BC (1968). The appressoria of *Colletotrichum graminicola* and *C. falcatum*. *Canadian Journal of Botany* **46**: 873–876

Sutton BC (1980). *The Coelomycetes. Fungi Imperfecti with Pycnidia, Acervuli and Stromata*. CABI, Kew, UK.

Sutton BC (1992). The genus *Glomerella* and its anamorph *Colletotrichum*. In: *Colletotrichum: Biology, Pathology and Control* (Bailey JA, Jeger MJ, eds). CABI, Wallingford, UK: 1–26.

Swank G (1953). The perfect stage of *Colletotrichum phomoides* on tomato. *Phytopathology* **43**: 285–287.

Sydow H (1928). Fungi Chilenses a cl. E. Werdermann lecti. Pars prima. *Annales Mycologici* **26**: 100–126.

Tadych M, Chaverri P, Bergen M, White JF (2009). *Moelleriella zhongdongii*: stroma development and identification of hirsutella-like and *Aschersonia* synanamorphs. *Mycological Research* **113**: 611–615.

Takano Y, Kubo Y, Kuroda I, Furusawa I (1997). Temporal transcriptional pattern of three melanin biosynthesis genes, PKS1, SCD1, and THR1, in appressorium-differentiating and nondifferentiating conidia of *Colletotrichum lagenarium*. *Applied and Environmental Microbiology* **63**: 351–354.

Talhinhas P, Neves-Martins J, Oliveira H, Sreenivasaprasad S (2009). The distinctive population structure of *Colletotrichum* species associated with olive anthracnose in the Algarve region of Portugal reflects a host-pathogen diversity hot spot. *FEMS Microbiology Letters* **296**: 31–38.

Talhinhas P, Sreenivasaprasad S, Neves-Martins J, Oliveira H (2002). Genetic and morphological characterization of *Colletotrichum acutatum* causing anthracnose of lupins. *Phytopathology* **92**: 986–996.

Talhinhas P, Sreenivasaprasad, S, Neves-Martins J, Oliveira H (2005). Molecular and phenotypic analyses reveal association of diverse *Colletotrichum acutatum* groups and a low level of *C. gloeosporioides* with olive anthracnose. *Applied and Environmental Microbiology* **71**: 2987–2998.

Tanaka S, Ishihama N, Yoshioka H, Huser A, O'Connell R, *et al.* (2009). *Colletotrichum orbiculare* ssd1 mutant enhances plant basal resistance through activation of a mitogenactivated protein kinase pathway. *Plant Cell* **21**: 2517–2526.

Than PP, Jeewon R, Hyde KD, Pongsupasamit S, Mongkolporn O, Taylor PWJ (2008a). Characterization and pathogenicity of *Colletotrichum* species associated with anthracnose on chilli (*Capsicum* spp.) in Thailand. *Plant Pathology* **57**: 562–572.

Than PP, Shivas RG, Jeewon R, Pongsupasamit S, Marney TS, *et al.* (2008b). Epitypification and phylogeny of *Colletotrichum acutatum* J.H. Simmonds. *Fungal Diversity* **28**: 97–108.

Theissen F, Sydow H (1915). Die Dothideales. Kritische-systematische Originaluntersuchungen. *Annales Mycologici* **13**: 147–746.

Thon MR, Nuckles EM, Vaillancourt LJ (2000). Restriction enzyme-mediated integration used to produce pathogenicity mutants of *Colletotrichum graminicola*. *Molecular Plant-Microbe Interactions* **13**: 1356–1365.

Thon MR, Nuckles EM, Takach JE, Vaillancourt LJ (2002). CPR1: a gene encoding a putative signal peptidase that functions in pathogenicity of *Colletotrichum graminicola* to maize. *Molecular Plant-Microbe Interactions* **15**: 120–128.

Tomioka K, Sato T, Koganezawa H (2001). Anthracnose of *Nemesia strumosa* caused by *Colletotrichum fuscum*. *Journal of General Plant Pathology* **67**: 111–115.

Torres MS, Bischoff JF, White JF (2007). *Hypocrella panamensis* sp. nov. (*Clavicipitaceae, Hypocreales*): a new species infecting scale insects on *Piper carrilloanum* in Panama. *Mycological Research* **111**: 317–323.

Tsuji G, Fujii S, Fujihara N, Hirose C, Tsuge S, *et al.* (2003). *Agrobacterium tumefaciens*-mediated transformation for random insertional mutagenesis in *Colletotrichum lagenarium*. *Journal of General Plant Pathology* **69**: 230–239.

Turner E, Jacobson DJ, Taylor JW (2010). Biogeography of postmating reproductive isolation barriers is consistent with reinforcement selection in *Neurospora*, a model microbial eukaryote. *Journal of Evolutionary Biology* **23**: 1642–1656.

Turner E, Jacobson DJ, Taylor JW (2011). Genetic architecture of a reinforced, postmating, reproductive isolation barrier between *Neurospora* species indicates evolution via natural selection. *PLoS Genetics* **7**: e1002204. doi:10.1371/journal.pgen.1002204.

Uecker FA (1994). On the ontogeny of the ascoma of *Glomerella cingulata*. *Mycologia* **86**: 82–88.

Uematsu S, Kageyama K, Moriwaki J, Sato T (2012). *Colletotrichum carthami* comb. nov., an anthracnose pathogen of safflower, garland chrysanthemum and pot marigold, revived by molecular phylogeny with authentic herbarium specimens. *Journal of General Plant Pathology* doi10.1007/s10327-012-0397-3.

Vaillancourt LJ, Hanau RM (1991). A method for genetic analysis of *Glomerella graminicola* (*Colletotrichum graminicola*) from maize. *Phytopathology* **81**: 530–534.

Vaillancourt LJ, Hanau RM (1992). Genetic and morphological comparisons of *Glomerella* (*Colletotrichum*) isolates from maize and from sorghum. *Experimental Mycology* **16**: 219–229.

Vaillancourt L, Wang J, Hanau R (2000). Genetic regulation of sexual compatibility in *Glomerella graminicola*. In: *Colletotrichum. Host Specificity, Pathology and Host-Pathogen Interaction* (Prusky D, Freeman S, Dickman MB, eds). APS Press, St Paul, USA: 29–44.

Valèrio HM, Rèsende MA, Weikert-Oliveira RC, Casela CR (2007). Virulence and molecular diversity in *Colletotrichum graminicola* from Brazil. *Mycopathologia* **159**: 449–459.

Vinnere O, Fatehi J, Wright SAI, Gerhardson B (2002). The causal agent of anthracnose of *Rhododendron* in Sweden and Latvia. *Mycological Research* **106**: 60–69.

Walker DM, Castlebury LA, Rossman AY, White JF (2012). New molecular markers for fungal phylogenetics: Two genes for species-level systematics in the *Sordariomycetes* (*Ascomycota*). *Molecular Phylogenetics and Evolution* **64**: 500–512.

Walker J, Nikandrow A, Millar GD (1991). Species of *Colletotrichum* on *Xanthium* (*Asteraceae*) with comments on some taxonomic and nomenclatural problems in the genus *Colletotrichum*. *Mycological Research* **95**: 1175–1193.

Waller JM, Lenné JM, Waller SJ (2002). *Plant Pathologists's Pocketbook*. CABI, Wallingford, UK.

Wanderlei-Silva D, Neto ER, Hanlin R (2003). Molecular systematics of the *Phyllachorales* (*Ascomycota*, *Fungi*) based on 18S ribosomal DNA sequences. *Brazilian Archives of Biology and Technology* **46**: 315–322.

Wang YT, Lo HS, Wang PH (2008). Endophytic fungi from *Taxus mairei* in Taiwan: first report of *Colletotrichum gloeosporioides* as an endophyte of *Taxus mairei*. *Botanical Studies* **49**: 39–43.

Washington WS, Irvine G, Aldaoud R, DeAlwis S, Edwards J, Pascoe IG (2006). First record of anthracnose of spinach caused by *Colletotrichum dematium* in Australia. *Australasian Plant Pathology* **35**: 89–91.

Weir BS, Johnston PR (2010). Characterisation and neotypification of *Gloeosporium kaki* Hori as *Colletotrichum horii* nom. nov. *Mycotaxon* **111**: 209–219.

Weir B, Johnston PR, Damm U (2012). The *Colletotrichum gloeosporioides* species complex. *Studies in Mycology* **73**: 115–180.

Wheeler HE (1950). Genetics of *Glomerella*. VIII. A genetic basis for the occurrence of minus mutants. *American Journal of Botany* **37**: 304–312.

Wheeler HE (1954). Genetics and evolution of heterothallism in *Glomerella*. *Phytopathology* **44**: 342–345.

Whitelaw-Weckert MA, Curtin SJ, Huang R, Steel CC, Blanchard CL, Roffey PE (2007). Phylogenetic relationships and pathogenicity of *Colletotrichum acutatum* isolates from grape in subtropical Australia. *Plant Pathology* **56**: 448–463.

Wikee S, Cai L, Pairin N, McKenzie EHC, Su Y-Y, *et al.* (2011). *Colletotrichum* species from Jasmine (*Jasminum sambac*). *Fungal Diversity* **46**: 171–182.

Winka K, Eriksson OE (2000). *Papulosa amerospora* accommodated in a new family (*Papulosaceae*, *Sordariomycetes*, *Ascomycota*) inferred from morphological and molecular data. *Mycoscience* **41**: 96–104.

Xiao CL, MacKenzie SJ, Legard DE (2004). Genetic and pathogenic analyses of *Colletotrichum gloeosporioides* isolates from strawberry and non-cultivated hosts. *Phytopathology* **94**: 446–453.

Xie L, Zhang J, Wang Y, Hu D (2010). Identification of Colletotrichum spp. isolated from strawberry in Zhejiang Province and Shanghai City, China. *Journal of Zhejiang University-Science B* **11**: 61–70.

Yang Y, Liu Z, Cai L, Hyde KD (2012). New species and notes of *Colletotrichum* on daylilies (*Hemerocallis* spp.). *Tropical Plant Pathology* **37**: 165–174.

Yang YL, Liu ZY, Cai L, Hyde KD, Zu ZN, McKenzie EHC (2009). *Colletotrichum* anthracnose of *Amaryllidaceae*. *Fungal Diversity* **39**: 123–146.

Yang YL, Cai L, Yu ZN, Liu ZY, Hyde KD (2011). *Colletotrichum* species on orchids in southwest China. *Cryptogamie Mycologie* **32**: 229–253.

Yoshida K, Takeda Y (2006). Evaluation of anthracnose resistance among tea genetic resources by wound-inoculation assay. *JARQ* **40**: 379–386.

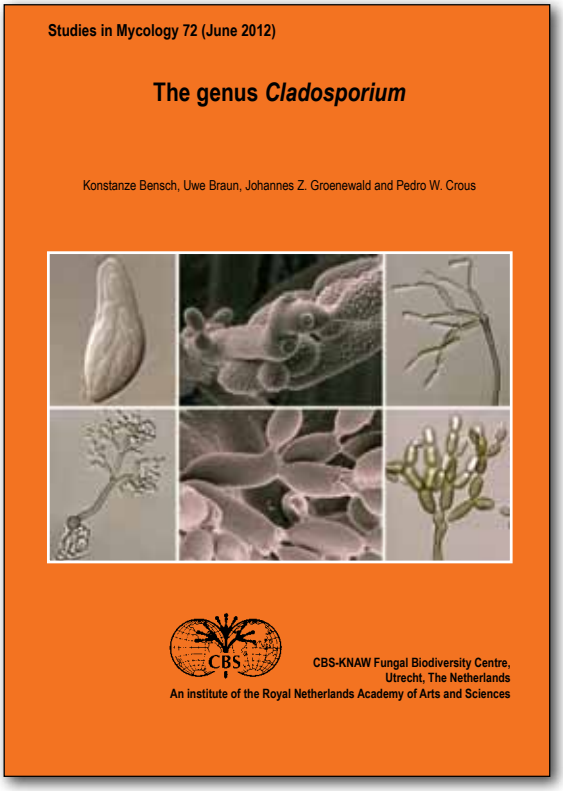
Yuan ZL, Su ZZ, Mao LJ, Peng YQ, Yang GM, *et al.* (2011). Distinctive endophytic fungal assemblage in stems of wild rice (*Oryza granulata*) in China with special reference to two species of *Muscodor* (*Xylariaceae*). *Journal of Microbiology* **49**:15–23.

Zare R, Gams W, Culham A (2000). A revision of *Verticillium* sect. *Prostrata*. I. Phylogenetic studies using ITS sequences. *Nova Hedwigia* **71**: 465–480.

Zare R, Gams W, Starink-Willemse M, Summerbell RC (2007). *Gibellulopsis*, a suitable genus for *Verticillium nigrescens*, and *Musicillium*, a new genus for *V. theobromae*. *Nova Hedwigia* **85**: 463–489.

Zhang N, Blackwell M (2002). Molecular phylogeny of *Melanospora* and similar pyrenomycetous fungi. *Mycological Research* **106**: 148–155.

Zhang N, Castlebury LA, Miller AN, Huhndorf SM, Schoch CL, *et al.* (2006). An overview of the systematics of the *Sordariomycetes* based on a four-gene phylogeny. *Mycologia* **98**: 1076–1087.



Studies in Mycology 72: The genus *Cladosporium*

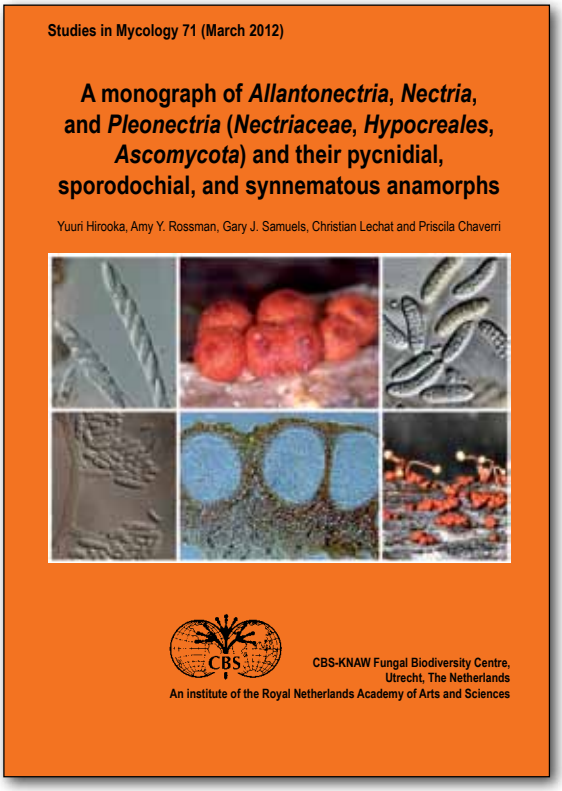
K. Bensch, U. Braun, J.Z. Groenewald and P.W. Crous

A monographic revision of the hyphomycete genus *Cladosporium s. lat.* (*Cladosporiaceae*, *Capnodiales*) is presented. It includes a detailed historic overview of *Cladosporium* and allied genera, with notes on their phylogeny, systematics and ecology. True species of *Cladosporium s. str.* (anamorphs of *Davidiella*), are characterised by having coronate conidiogenous loci and conidial hila, i.e., with a convex central dome surrounded by a raised periclinal rim. Recognised species are treated and illustrated with line drawings and photomicrographs (light as well as scanning electron microscopy). Species known from culture are described *in vivo* as well as *in vitro* on standardised media and under controlled conditions. Details on host range/substrates and the geographic distribution are given based on published accounts, and a re-examination of numerous herbarium specimens. Various keys are provided to support the identification of *Cladosporium* species *in vivo and in vitro*. Morphological datasets are supplemented by DNA barcodes (nuclear ribosomal RNA gene operon, including the internal transcribed spacer regions ITS1 and ITS2, the 5.8S nrDNA, as well as partial actin and translation elongation factor 1-α gene sequences) diagnostic for individual species. In total 993 names assigned to *Cladosporium s. lat.*, including *Heterosporium* (854 in *Cladosporium* and 139 in *Heterosporium*), are treated, of which 169 are recognised in *Cladosporium s. str.* The other taxa are doubtful, insufficiently known or have been excluded from *Cladosporium* in its current circumscription and re-allocated to other genera by the authors of this monograph or previous authors.

401 pp., fully illustrated with colour pictures (A4 format), paperback, 2012. € 70

Studies in Mycology 71: A monograph of *Allantonectria*, *Nectria*, and *Pleonectria* (*Nectriaceae*, *Hypocreales*, *Ascomycota*) and their pycnidial, sporodochial, and synnematous anamorphs.

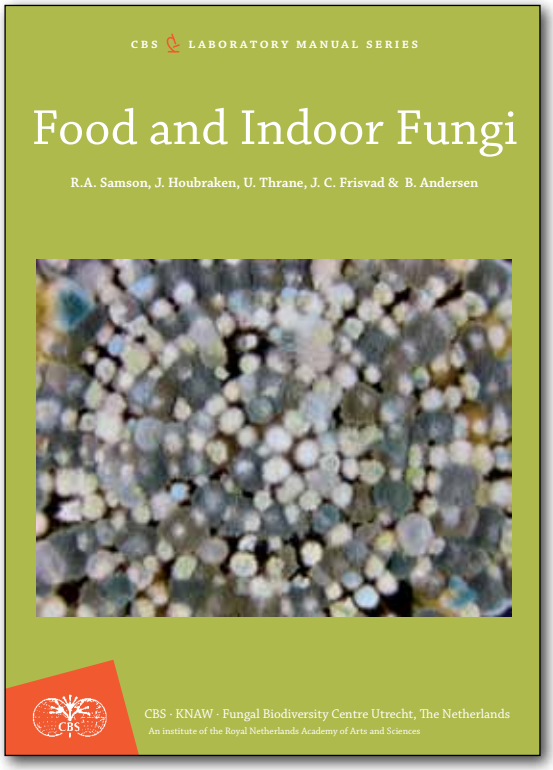
Y. Hirooka, A.Y. Rossman, G.J. Samuels, C. Lechat and P. Chaverri



Although *Nectria* is the type genus of *Nectriaceae* (*Hypocreales*, *Sordariomycetes*, *Pezizomycotina*, *Ascomycota*), the systematics of the teleomorphic and anamorphic state of *Nectria sensu* Rossman has not been studied in detail. The objectives of this study are to 1) provide a phylogenetic overview to determine if species of *Nectria* with *Gyrostroma*, *Tubercularia*, and *Zythiostroma* anamorphs form a monophyletic group; 2) define *Nectria*, segregate genera, and their species using morphologically informative characters of teleomorphic and anamorphic states; and 3) provide descriptions and illustrations of these genera and species. To accomplish these objectives, results of phylogenetic analyses of DNA sequence data from six loci (act, ITS, LSU, rpb1, tef1 and tub), were integrated with morphological characterisations of anamorphs and teleomorphs. Results from the phylogenetic analyses demonstrate that species previously regarded as the genus *Nectria* having *Gyrostroma*, *Tubercularia*, and *Zythiostroma* anamorphs belong in two major paraphyletic clades. The first major clade regarded as the genus *Pleonectria* contains 26 species with ascoconidia produced by ascospores in asci, perithecial walls having bright yellow scurf, and immersed or superficial pycnidial anamorphs (*Zythiostroma* = *Gyrostroma*). A lineage basal to the *Pleonectria* clade includes *Nectria miltina* having very small, aseptate ascospores, and trichoderma-like conidiophores and occurring on monocotyledonous plants. These characteristics are unusual in *Pleonectria*, thus we recognise the monotypic genus *Allantonectria* with *Allantonectria miltina*. The second major clade comprises the genus *Nectria sensu stricto* including the type species, *N. cinnabarina*, and 28 additional species. Within the genus *Nectria*, four subclades exist. One subclade includes species with sporodochial anamorphs and another with synnematous anamorphs. The other two paraphyletic subclades include species that produce abundant stromata in which the large perithecia are immersed, large ascospores, and peculiar anamorphs that form pycnidia or sporodochia either on their natural substrate or in culture. In this study the evolution of species, morphology, and ecology of the three genera, *Allantonectria*, *Nectria*, and *Pleonectria*, are discussed based on the phylogenetic analyses. In addition, descriptions, illustrations, and keys for identification are presented for the 56 species in *Allantonectria*, *Nectria*, and *Pleonectria*.

210 pp., fully illustrated with colour pictures (A4 format), paperback, 2012. € 65

CBS Laboratory Manual Series



CBS Laboratory Manual Series 2: Food and Indoor Fungi

R.A. Samson, J. Houbraken, U. Thrane, J.C. Frisvad and B. Andersen

This book is the second in the new CBS Laboratory Manual Series and is based on the seventh edition of INTRODUCTION TO FOOD AND AIRBORNE FUNGI. This new version, FOOD AND INDOOR FUNGI, has been transformed into a practical user's manual to the most common micro-fungi found in our immediate environment – on our food and in our houses. The layout of the book starts at the beginning with the detection and isolation of food borne fungi and indoor fungi in chapters 1 and 2, describing the different sampling techniques required in the different habitats. Chapter 3 deals with the three different approaches to identification: morphology, genetics and chemistry. It lists cultivation media used for the different genera and describes step by step how to make microscope slides and tape preparations for morphological identification. The chapter also describes how to do molecular and chemical identification from scratch, how to evaluate the results and warns about pitfalls. Chapter 4 gives all the identification keys, first for the major phyla (*Ascomycetes*, *Basidiomycetes* and *Zygomycetes*) common on food and indoors, then to the different genera in the *Zygomycetes* and the *Ascomycetes*, with a large section on the anamorphic fungi and a section for yeasts. The section on anamorphic fungi contains two keys to the different genera: a dichotomous key and a synoptic key. For each genus a key to the species treated is provided, followed by entries on the different species. For each species colour plates are accompanied by macro- and a micro-morphological descriptions, information on molecular and chemical identification markers, production of mycotoxins, habitats and physiological and ecological characteristics. The book is concluded with an extensive reference list and appendices on the associated mycobiota on different food types and indoor environments, mycotoxins and other secondary metabolites, a glossary on the mycological terms used in the book and lastly a detailed appendix on the media used for detection and identification.

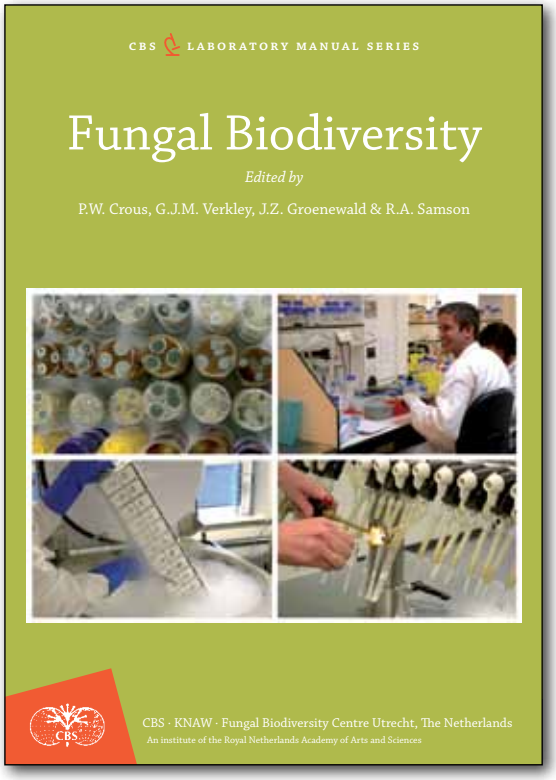
390 pp., fully illustrated with colour pictures (A4 format). Hardbound, 2010. € 70

CBS Laboratory Manual Series 1: Fungal Biodiversity

P.W. Crous, G.J.M. Verkley, J.Z. Groenewald and R.A. Samson (eds)

This book is the first in the new "CBS Laboratory Manual Series", and focuses on techniques for isolation, cultivation, molecular and morphological study of fungi and yeasts. It has been developed as a general text, which is based on the annual mycology course given at the CBS-KNAW Fungal Biodiversity Centre (Centraalbureau voor Schimmelcultures). It provides an introductory text to systematic mycology, starting with a concise treatise of *Hyphochytridiomycota* and *Oomycota*, which have long been subject of study by mycologists, but are now classified in the Kingdom *Chromista*. These are followed by sections on the groups of "true fungi": *Chytridiomycota*, *Zygomycota*, *Ascomycota* and *Basidiomycota*. This descriptive part is illustrated by figures of life-cycles and schematic line-drawings as well as photoplates depicting most of the structures essential for the study and identification of these fungi. Special attention is given to basic principles of working with axenic cultures, good morphological analysis, and complicated issues for beginners such as conidiogenesis and the understanding of life-cycles. Exemplar taxa for each of these fungal groups, in total 37 mostly common species in various economically important genera, are described and illustrated in detail. In a chapter on general methods a number of basic techniques such as the preparation and choice of media, microscopic examination, the use of stains and preparation of permanent slides, and herbarium techniques are explained. Further chapters deal with commonly used molecular and phylogenetic methods and related identification tools such as BLAST and DNA Barcoding, fungal nomenclature, ecological groups of fungi such as soil-borne and root-inhabiting fungi, water moulds, and fungi on plants and of quarantine importance. Some topics of applied mycology are also treated, including fungi in the air- and indoor environment and fungi of medical importance. Common mycological terminology is explained in a glossary, with reference to illustrations in the book. A chapter providing more than 60 mycological media for fungal cultivation, and a comprehensive list of cited references are also provided. The book is concluded with an index, and dendrograms reflecting our current understanding of the evolutionary relationships within the *Fungi*.

270 pp., fully illustrated with colour pictures (A4 format). Concealed wiro, 2009. € 50



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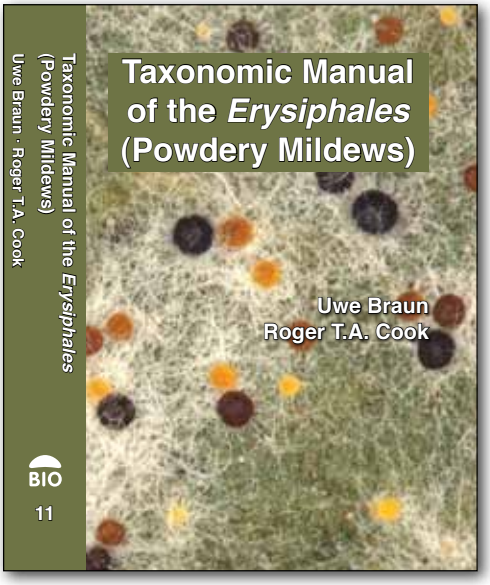


No. 11:Taxonomic Manual of the *Erysiphales* (Powdery Mildews)

Uwe Braun and Roger T.A. Cook

The "Taxonomic Manual of the *Erysiphales* (Powdery Mildews)" is a fully revised, expanded new version of U. Braun's former monograph from 1987, which is out of print. The present book covers the taxonomy of all powdery mildew fungi. New chapters have been prepared
for phylogenetic relationships, conidial germination, conidia as viewed by Scanning Electron Microscopy, fossil powdery mildews, and holomorph classification. The treatment of the *Erysiphales*, its tribes and genera are based on recent molecular phylogenetic classifications. A key to the genera (and sections), based on teleomorph and anamorph characters is provided, supplemented by a key solely using anamorph features. Keys to the species are to be found under the particular genera. A special tabular key to species based on host families and genera completes the tools for identification of powdery mildew taxa. In total, 873 powdery mildew species are described and illustrated in 853 figures (plates). The following data are given for the particular species and subspecific taxa: bibliographic data, synonyms, references to descriptions and illustrations in literature, full descriptions, type details, host range, distribution and notes. A further 236 taxonomic novelties are introduced, comprising the new genus *Takamatsuella*, 55 new species, four new varieties, six new names and 170 new combinations. A list of excluded and doubtful taxa with notes and their current status is attached, followed by a list of references and a glossary. This manual deals with the taxonomy of the *Erysiphales* worldwide, and provides an up-todate basis for the identification of taxa, as well as comprehensive supplementary information on their biology, morphology, distribution and host range. This monograph is aimed at biologists, mycologists and phytopathologists that encounter or study powdery mildew diseases.

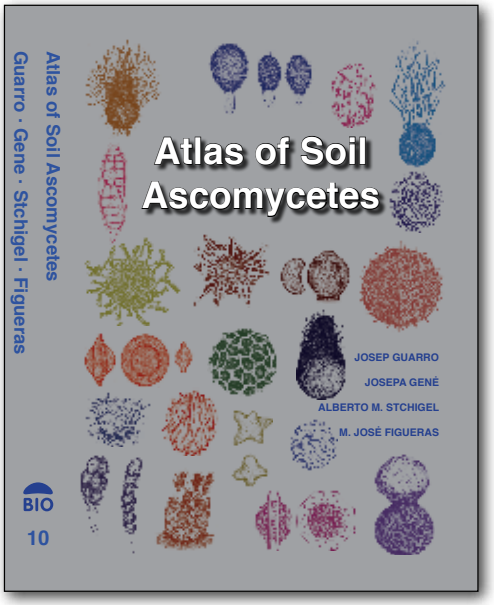
707 pp., fully illustrated with 853 pictures and line drawings (A4 format). Hardbound, 2012. € 80

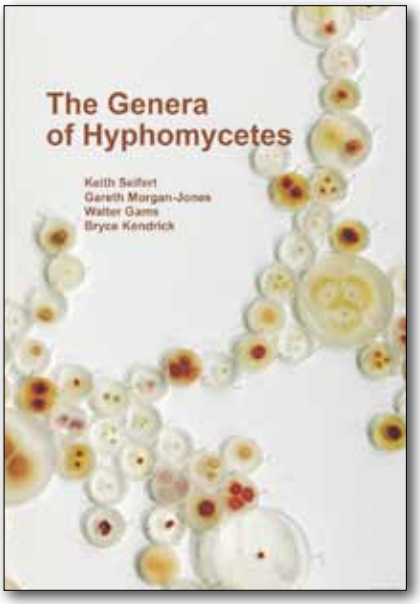
No. 10: Atlas of Soil Ascomycetes

Josep Guarro, Josepa Gené, Alberto M. Stchigel and M. José Figueras

This compendium includes almost all presently known species of ascomycetes that have been reported in soil and which sporulate in culture. They constitute a very broad spectrum of genera belonging to very diverse orders, but mainly to the Onygenales, Sordariales, Eurotiales, Thelebolales, Pezizales, Melanosporales, Pleosporales, Xylariales, Coniochaetales and Microascales. The goal of this book is to provide sufficient data for users to recognise and identify these species. It includes the description of 146 genera and 698 species. For each genus a dichotomous key to facilitate species identification is provided and for each genus and species the salient morphological features are described. These descriptions are accompanied by line drawings illustrating the most representative structures. Light micrographs, supplemented by scanning electron micrographs and Nomarski interference contrast micrographs of most of the species treated in the book are also included. In addition, numerous species not found in soil but related to those included in this book are referenced or described. This book will be of value not only to soil microbiologists and plant pathologists concerned with the soilborne fungi and diseases, but also to anyone interested in identifying fungi in general, because many of the genera included here are not confined to soil. Since most of the fungi of biotechnological or clinical interest (dermatophytes, dimorphic fungi and opportunists) are soil-borne ascomycetes, the content of this book is of interest for a wide range of scientists.

486 pp., fully illustrated with 322 pictures and line drawings (A4 format). Hardbound, 2012. € 70





No. 9: The Genera of Hyphomycetes

Keith Seifert, Gareth Morgan-Jones, Walter Gams and Bryce Kendrick

The Genera of Hyphomycetes is the essential reference for the identification of moulds to all those who work with these fungi, including plant pathologists, industrial microbiologists, mycologists and indoor environment specialists, whether they be professionals or students. The book compiles information on about 1480 accepted genera of hyphomycetes, and about 1420 genera that are synonyms or names of uncertain identity. Each accepted genus is described using a standardized set of key words, connections with sexual stages (teleomorphs) and synanamorphs are listed, along with known substrates or hosts, and continental distribution. When available, accession numbers for representative DNA barcodes are listed for each genus. A complete bibliography is provided for each genus, giving the reader access to the literature necessary to identify species. Most accepted genera are illustrated by newly prepared line drawings, including many genera that have never been comprehensively illustrated before, arranged as a visual synoptic key. More than 200 colour photographs supplement the line drawings. Diagnostic keys are provided for some taxonomic and ecological groups. Appendices include an integrated classification of hyphomycete genera in the phylogenetic fungal system, a list of teleomorph-anamorph connections, and a glossary of technical terms. With its combination of information on classical morphological taxonomy, molecular phylogeny and DNA diagnostics, this book is an effective modern resource for researchers working on microfungi.

997 pp., fully illustrated with colour pictures and line drawings (A4 format). Hardbound, 2011. € 80

CBS Biodiversity Series

No. 8: The genera of the *Parmulariaceae*

Carlos Antonio Inácio and Paul F. Cannon

The morphologically variable family *Parmulariaceae* (*Fungi*, *Ascomycota*, *Dothideomycetes*) is widespread in the tropics. The family now includes 34 accepted genera, with 24 further synonyms, and more than 100 species. The study was organised using a suite of computer databases, focusing on nomenclatural, geographical (floristic) and bibliographic information. More than 1000 scientific names were considered, and more than 1100 records of individual observations of these fungi have been gathered. All genera are fully redescribed and illustrated with drawings and microphotographs. A new key for identification of genera was constructed. A new formal taxonomic concept of the *Parmulariaceae* is introduced and two new genera *Mintera* and *Viegasella* have been re-described, *Parmulariella* is now included in the *Parmulariaceae*. *Kentingia* and *Chaetaspis* are now considered of uncertain family in the *Dothideomycetes*. The genus *Apoa*, previously placed as a synonym of *Pachypatella*, was found to be a distinct genus.

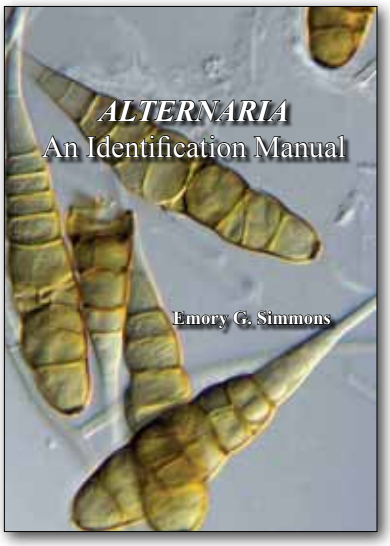
196 pp., illustrated with 111 pictures including 15 colour plates (A4 format). Hardbound, 2008. € 55

No. 6: *Alternaria* An Identification Manual

Emory G. Simmons

This book will fill a very large void in the scientific literature and it is quite certain that the volume will become the standard reference for those needing to have critical access to *Alternaria* literature and taxonomic information. There are many scientists, both research and regulatory, who are in desperate need of resources like this book to facilitate routine identification. More than 1 100 published names are associated with taxa that must be considered in the *Alternaria* context. Of these, 276 species with validly published names are maintained here as currently identifiable; these are keyed in the main text of the volume. An additional 16 named taxa, although requiring expanded information and comparison, also are accepted. A few species that have been associated with the genus for years but which now are considered anomolous in the genus have been removed to other genera. Chapters of species and genus characterisations are followed by a comprehensive list of all the nearly 1 200 names involved historically with *Alternaria* taxonomy in the period 1796-2007. Each name is listed with its source, type, and an opinion on its validity and taxonomic disposition. A host index to all accepted species is followed by a comprehensive list of literature cited and a general index. Within the context of the manual, 88 names are assigned to newly described species and genera and to taxa whose epithets appear in new combinations.

775 pp., with more than 288 line drawings (A4 format). Hardbound, 2007. € 100



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Atlas of Clinical Fungi CD-ROM version 3.1

G.S. de Hoog, J. Guarro, J. Gené and M.J. Figueras (eds)

A new electronic version of the 3rd edition is available since November 2011. It will allows fast and very comfortable search through the entire Atlas text the engine is fully equiped for simple as well as advanced search. Items are strongly linked enabling direct use of the electronic version as a benchtool for identification and comparison. Text boxes with concise definitions appear explaining all terminology while reading. Illustrations are of highest quality and viewers are provided for detailed observation. The Atlas is interactive in allowing personal annotation which will be maintained when later versions will be downloaded.

The electronic version has been developed by T. Weniger. The third edition will contain about 530 clinically relevant species, following all major developments in fungal diagnostics. Regular electronic updates of the Atlas are planned, which should include numerous references to case reports, as well as full data on antifungals. Future features will include links to extended databases with verified molecular information. Note: The Atlas runs on Windows only! Not compatible with Mac

Atlas of Clinical Fungi version 3.1, interactive CD-ROM, 2011. € 105

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