

The *Colletotrichum boninense* species complex

U. Damm^{1*}, P.F. Cannon², J.H.C. Woudenberg¹, P.R. Johnston³, B.S. Weir³, Y.P. Tan⁴, R.G. Shivas⁴, and P.W. Crous^{1,5,6}

¹CBS-KNAW Fungal Biodiversity Centre, Uppsalalaan 8, 3584 CT Utrecht, The Netherlands; ²CABI Europe-UK, Bakeham Lane, Egham, Surrey TW20 9TY, UK and Royal Botanic Gardens, Kew, Richmond TW9 3AB, UK; ³Landcare Research, Private Bag 92170 Auckland, New Zealand; ⁴Plant Biosecurity Science, Ecosciences Precinct, Dutton Park, Queensland 4102, Australia; ⁵Utrecht University, Department of Biology, Microbiology, Padualaan 8, 3584 CH Utrecht, The Netherlands; ⁶Wageningen University and Research Centre (WUR), Laboratory of Phytopathology, Droevendaalsesteeg 1, 6708 PB Wageningen, The Netherlands

*Correspondence: Ulrike Damm, u.damm@cbs.knaw.nl

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.

Species	Accession No.1	Host/Substrate	Country	GenBank No.									
				ITS	GAPDH	CHS-1	HIS3	ACT	TUB2	CAL			
<i>C. annellatum</i>	CBS 129826, CH1*	<i>Hevea brasiliensis</i> , leaf	Colombia	JQ005222	JQ005309	JQ005396	JQ005483	JQ005570	JQ005656	JQ005743			
<i>C. beeveri</i>	CBS 128527, ICMP 18594*	<i>Brachyglottis repanda</i>	New Zealand	JQ005171	JQ005258	JQ005345	JQ005432	JQ005519	JQ005605	JQ005692			
<i>C. boninense</i>	CBS 128547, ICMP 10338	<i>Camellia</i> sp.	New Zealand	JQ005159	JQ005246	JQ005333	JQ005420	JQ005507	JQ005593	JQ005680			
	CBS 123756, MAFF 306094	<i>Crinum asiaticum</i> var. <i>sinicum</i>	Japan	JQ005154	JQ005241	JQ005328	JQ005415	JQ005502	JQ005589	JQ005675			
	CBS 123755, MAFF 305972*	<i>Crinum asiaticum</i> var. <i>sinicum</i>	Japan	JQ005153	JQ005240	JQ005327	JQ005414	JQ005501	JQ005588	JQ005674			
	MAFF 306162, ICMP 18596	<i>Crinum asiaticum</i> var. <i>sinicum</i> , leaf	Japan	JQ005155	JQ005242	JQ005329	JQ005416	JQ005503	-	JQ005676			
	CBS 128526, ICMP 18591	<i>Dacrycarpus dacrydioides</i> , leaf endophyte	New Zealand	JQ005162	JQ005249	JQ005336	JQ005423	JQ005510	JQ005596	JQ005683			
	CBS 112115, STE-U 2966	<i>Leucospermum</i> sp.	Australia	JQ005160	JQ005247	JQ005334	JQ005421	JQ005508	JQ005594	JQ005681			
	CBS 129831, STE-U 2965	<i>Leucospermum</i> sp.	Australia	JQ005161	JQ005248	JQ005335	JQ005422	JQ005509	JQ005595	JQ005682			
	CBS 128549, ICMP 15444	<i>Solanum betaceum</i> , flowers	New Zealand	JQ005156	JQ005243	JQ005330	JQ005417	JQ005504	JQ005590	JQ005677			
	CBS 128506, ICMP 12950	<i>Solanum lycopersicum</i> , fruit rot	New Zealand	JQ005157	JQ005244	JQ005331	JQ005418	JQ005505	JQ005591	JQ005678			
<i>C. brasiliense</i>	CBS 128546, ICMP 18595	<i>Tecomaria speciosa</i>	New Zealand	JQ005158	JQ005245	JQ005332	JQ005419	JQ005506	JQ005592	JQ005679			
	CBS 128501, ICMP 18607, PAS12*	<i>Passiflora edulis</i> , fruit anthracnose	Brazil	JQ005235	JQ005322	JQ005409	JQ005496	JQ005583	JQ005669	JQ005756			
	CBS 128528, ICMP 18606, PAS10	<i>Passiflora edulis</i> , fruit	Brazil	JQ005234	JQ005321	JQ005408	JQ005495	JQ005582	JQ005668	JQ005755			
<i>C. brassicicola</i>	CBS 101059, LYN 16331*	<i>Brassica oleracea</i> var. <i>gemmifera</i> , leaf spot	New Zealand	JQ005172	JQ005259	JQ005346	JQ005433	JQ005520	JQ005606	JQ005693			
<i>C. colombiense</i>	CBS 129817, G1	<i>Passiflora edulis</i> , leaf	Colombia	JQ005173	JQ005260	JQ005347	JQ005434	JQ005521	JQ005607	JQ005694			
	CBS 129818, G2*	<i>Passiflora edulis</i> , leaf	Colombia	JQ005174	JQ005261	JQ005348	JQ005435	JQ005522	JQ005608	JQ005695			
<i>C. constrictum</i>	CBS 128504, ICMP 12941*	<i>Citrus limon</i> , fruit rot	New Zealand	JQ005238	JQ005325	JQ005412	JQ005499	JQ005586	JQ005672	JQ005759			
	CBS 128503, ICMP 12936	<i>Solanum betaceum</i> , fruit rot	New Zealand	JQ005237	JQ005324	JQ005411	JQ005498	JQ005585	JQ005671	JQ005758			
<i>C. cymbidicola</i>	CBS 123757, MAFF 306100	<i>Cymbidium</i> sp.	Japan	JQ005168	JQ005255	JQ005342	JQ005429	JQ005516	JQ005602	JQ005689			
	IMI 347923*	<i>Cymbidium</i> sp., leaf lesion	Australia	JQ005166	JQ005253	JQ005340	JQ005427	JQ005514	JQ005600	JQ005687			
	CBS 128543, ICMP 18584	<i>Cymbidium</i> sp., leaf spot	New Zealand	JQ005167	JQ005254	JQ005341	JQ005428	JQ005515	JQ005601	JQ005688			
<i>C. dacrycarpi</i>	CBS 130241, ICMP 19107*	<i>Dacrycarpus dacrydioides</i> , leaf endophyte	New Zealand	JQ005236	JQ005323	JQ005410	JQ005497	JQ005584	JQ005670	JQ005757			
<i>C. gloeosporioides</i>	CBS 112999, STE-U 4295*	<i>Citrus sinensis</i>	Italy	JQ005152	JQ005239	JQ005326	JQ005413	JQ005500	JQ005587	JQ005673			
<i>C. hippeastrii</i>	CBS 241.78, IMI 304052	<i>Hippeastrum</i> sp.	Netherlands	JQ005232	JQ005319	JQ005406	JQ005493	JQ005580	JQ005666	JQ005753			
	CBS 125377, CSSK4	<i>Hippeastrum vittatum</i>	China	JQ005230	JQ005317	JQ005404	JQ005491	JQ005578	JQ005664	JQ005751			
<i>C. karstii</i>	CBS 125376, CSSG1*	<i>Hippeastrum vittatum</i> , leaf	China	JQ005231	JQ005318	JQ005405	JQ005492	JQ005579	JQ005665	JQ005752			
	CBS 128500, ICMP 18585	<i>Annona cherimola</i> , fruit	New Zealand	JQ005202	JQ005289	JQ005376	JQ005463	JQ005550	JQ005636	JQ005723			
	CBS 128550, ICMP 17896	<i>Annona cherimola</i> , fruit anthracnose	Mexico	JQ005219	JQ005306	JQ005393	JQ005480	JQ005567	JQ005653	JQ005740			
	CBS 129927	<i>Anthurium</i> sp.	Thailand	JQ005206	JQ005293	JQ005380	JQ005467	JQ005554	JQ005640	JQ005727			
	CBS 861.72	<i>Bombax aquaticum</i>	Brazil	JQ005184	JQ005271	JQ005358	JQ005445	JQ005532	JQ005618	JQ005705			
	CBS 128545, ICMP 18587	<i>Capsicum annuum</i>	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
<i>C. karstii</i>	CBS 106.91	<i>Carica papaya</i> , fruit spots	Brazil	JQ005220	JQ005307	JQ005394	JQ005481	JQ005568	JQ005654	JQ005741
	CBS 128524, ICMP 18588	<i>Citrus lanatus</i> , rotten fruit	New Zealand	JQ005195	JQ005282	JQ005369	JQ005456	JQ005543	JQ005629	JQ005716
	CBS 126532, STE-U 6830	<i>Citrus</i> sp.	South Africa	JQ005209	JQ005296	JQ005383	JQ005470	JQ005557	JQ005643	JQ005730
	CBS 128551, ICMP 12065	<i>Citrus</i> sp.	New Zealand	JQ005208	JQ005295	JQ005382	JQ005469	JQ005556	JQ005642	JQ005729
	MAFF 306204, ICMP 18597	<i>Clivia miniata</i> , leaf	Japan	JQ005196	JQ005283	JQ005370	JQ005457	JQ005544	JQ005630	JQ005717
	CBS 125468	<i>Coffea</i> sp., berry tissue	Vietnam	JQ005197	JQ005284	JQ005371	JQ005458	JQ005545	JQ005631	JQ005718
	MAFF 305998, ICMP 18599	<i>Cucumis melo</i>	Japan	JQ005191	JQ005278	JQ005365	JQ005452	JQ005539	JQ005625	JQ005712
	CBS 127597, BRIP 29085a	<i>Diospyros australis</i> , calyx necrosis	Australia	JQ005204	JQ005291	JQ005378	JQ005465	JQ005552	JQ005638	JQ005725
	CBS 110779	<i>Eucalyptus grandis</i>	South Africa	JQ005198	JQ005285	JQ005372	JQ005459	JQ005546	JQ005632	JQ005719
	CBS 127535, STE-U 193	<i>Eucalyptus grandis</i>	South Africa	JQ005199	JQ005286	JQ005373	JQ005460	JQ005547	JQ005633	JQ005720
	CBS 129830, STE-U 195B	<i>Eucalyptus grandis</i>	South Africa	JQ005200	JQ005287	JQ005374	JQ005461	JQ005548	JQ005634	JQ005721
	CBS 127536, STE-U 196	<i>Eucalyptus grandis</i>	South Africa	JQ005201	JQ005288	JQ005375	JQ005462	JQ005549	JQ005635	JQ005722
	CBS 127552	<i>Eugenia uniflora</i>	Brazil	JQ005217	JQ005304	JQ005391	JQ005478	JQ005565	JQ005651	JQ005738
	CBS 129829	<i>Gossypium hirsutum</i>	Germany	JQ005189	JQ005276	JQ005363	JQ005450	JQ005537	JQ005623	JQ005710
	CBS 130235	<i>Gossypium hirsutum</i>	Germany	JQ005190	JQ005277	JQ005364	JQ005451	JQ005538	JQ005624	JQ005711
	CBS 111860, STE-U 2193	<i>Leucospermum</i> sp.	USA, Hawaii	JQ005211	JQ005298	JQ005385	JQ005472	JQ005559	JQ005645	JQ005732
	CBS 111998, STE-U 2999	<i>Leucospermum</i> sp.	Australia	JQ005212	JQ005299	JQ005386	JQ005473	JQ005560	JQ005646	JQ005733
	CBS 112762, STE-U 3000	<i>Leucospermum</i> sp.	Australia	JQ005213	JQ005300	JQ005387	JQ005474	JQ005561	JQ005647	JQ005734
	CBS 486.97	<i>Lupinus albus</i> , cv. Lu Blanc	Germany	JQ005182	JQ005269	JQ005356	JQ005443	JQ005530	JQ005616	JQ005703
	CBS 113087, STE-U 5288	<i>Malus</i> sp.	USA	JQ005181	JQ005268	JQ005355	JQ005442	JQ005529	JQ005615	JQ005702
	CBS 127596, BRIP 28443a	<i>Mangifera indica</i> , stem, endophyte	Australia	JQ005203	JQ005290	JQ005377	JQ005464	JQ005551	JQ005637	JQ005724
	CBS 129832	<i>Musa</i> sp.	Mexico	JQ005177	JQ005264	JQ005351	JQ005438	JQ005525	JQ005611	JQ005698
	CBS 129833	<i>Musa</i> sp.	Mexico	JQ005175	JQ005262	JQ005349	JQ005436	JQ005523	JQ005609	JQ005696
	CBS 129834	<i>Musa</i> sp.	Mexico	JQ005176	JQ005263	JQ005350	JQ005437	JQ005524	JQ005610	JQ005697
	CBS 129824, B1	<i>Musa</i> AAA, fruit	Colombia	JQ005215	JQ005302	JQ005389	JQ005476	JQ005563	JQ005649	JQ005736
	CBS 127595	<i>Musa banksii</i>	Australia	JQ005178	JQ005265	JQ005352	JQ005439	JQ005526	JQ005612	JQ005699
	CBS 118401	<i>Pachira</i> sp., living leaves	China	JQ005192	JQ005279	JQ005366	JQ005453	JQ005540	JQ005626	JQ005713
	MAFF 305973, ICMP 18598	<i>Passiflora edulis</i>	Japan	JQ005194	JQ005281	JQ005368	JQ005455	JQ005542	JQ005628	JQ005715
	CBS 129822, G7	<i>Passiflora edulis</i> , leaf	Colombia	JQ005218	JQ005305	JQ005392	JQ005479	JQ005566	JQ005652	JQ005739
	CBS 112982, STE-U 2289	<i>Protea cynaroides</i>	Zimbabwe	JQ005183	JQ005270	JQ005357	JQ005444	JQ005531	JQ005617	JQ005704
	CBS 115535, STE-U 5210	<i>Protea obtusifolia</i>	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
<i>C. karsii</i>	CBS 124989, LCM 232	<i>Quercus salicifolia</i> , leaf endophyte	Panama	JQ005179	JQ005266	JQ005353	JQ005440	JQ005527	JQ005613	JQ005700
	CBS 127591	<i>Sapium integerrimum</i>	Australia	JQ005186	JQ005273	JQ005360	JQ005447	JQ005534	JQ005620	JQ005707
	CBS 129815, T.A.7	<i>Solanum betaceum</i> , fruit	Colombia	JQ005187	JQ005274	JQ005361	JQ005448	JQ005535	JQ005621	JQ005708
	CBS 128548, ICMP 18589	<i>Solanum lycopersicum</i>	New Zealand	JQ005205	JQ005292	JQ005379	JQ005466	JQ005553	JQ005639	JQ005726
	CBS 508.97, LARS 168	<i>Stylosanthes sympodialis</i>	Australia	JQ005193	JQ005280	JQ005367	JQ005454	JQ005541	JQ005627	JQ005714
	CBS 128552, ICMP 18276	<i>Synsepalum dulcificum</i> , leaves	Taiwan	JQ005188	JQ005275	JQ005362	JQ005449	JQ005536	JQ005622	JQ005709
	CBS 124951	<i>Theobroma cacao</i> , leaf endophyte	Panama	JQ005180	JQ005267	JQ005354	JQ005441	JQ005528	JQ005614	JQ005701
	CBS 128540, STE-U 698	<i>Triticum</i> sp.	South Africa	JQ005210	JQ005297	JQ005384	JQ005471	JQ005558	JQ005644	JQ005731
	CBS 124956	<i>Zamia obliqua</i> , leaf endophyte	Panama	JQ005216	JQ005303	JQ005390	JQ005477	JQ005564	JQ005650	JQ005737
	CBS 124956	<i>Zamia obliqua</i> , leaf endophyte	Panama	JQ005216	JQ005303	JQ005390	JQ005477	JQ005564	JQ005650	JQ005737
<i>C. novae-zelandiae</i>	CBS 125388	<i>Zamia obliqua</i> , leaf endophyte	Panama	JQ005185	JQ005272	JQ005359	JQ005446	JQ005533	JQ005619	JQ005706
	CBS 128505, ICMP 12944*	<i>Capsicum annuum</i> , fruit rot	New Zealand	JQ005228	JQ005315	JQ005402	JQ005489	JQ005576	JQ005662	JQ005749
<i>C. oncidii</i>	CBS 130240, ICMP 12064	<i>Citrus</i> sp. (grapefruit)	New Zealand	JQ005229	JQ005316	JQ005403	JQ005490	JQ005577	JQ005663	JQ005750
	CBS 129828*	<i>Oncidium</i> sp., leaf	Germany	JQ005169	JQ005256	JQ005343	JQ005430	JQ005517	JQ005603	JQ005690
<i>C. parsonisiae</i>	CBS 130242	<i>Oncidium</i> sp., leaf	Germany	JQ005170	JQ005257	JQ005344	JQ005431	JQ005518	JQ005604	JQ005691
	CBS 128525, ICMP 18590*	<i>Parsonsia capsularis</i> , leaf endophyte	New Zealand	JQ005233	JQ005320	JQ005407	JQ005494	JQ005581	JQ005667	JQ005754
<i>C. petchii</i>	CBS 378.94*	<i>Dracaena marginata</i> , spotted leaves	Italy	JQ005223	JQ005310	JQ005397	JQ005484	JQ005571	JQ005657	JQ005744
	CBS 379.94	<i>Dracaena marginata</i> , spotted leaves	Italy	JQ005224	JQ005311	JQ005398	JQ005485	JQ005572	JQ005658	JQ005745
<i>C. phyllanthi</i>	CBS 118193, AR 3658	<i>Dracaena sanderana</i> , living leaves	China	JQ005227	JQ005314	JQ005401	JQ005488	JQ005575	JQ005661	JQ005748
	CBS 118774, AR 3751	<i>Dracaena sanderana</i> , living stems	China	JQ005225	JQ005312	JQ005399	JQ005486	JQ005573	JQ005659	JQ005746
<i>C. torulosum</i>	CBS 125957, NB 145	<i>Dracaena</i> , leaf spots	Netherlands	JQ005226	JQ005313	JQ005400	JQ005487	JQ005574	JQ005660	JQ005747
	CBS 175.67, MACS 271*	<i>Phyllanthus acidus</i> , anthracnose	India	JQ005221	JQ005308	JQ005395	JQ005482	JQ005569	JQ005655	JQ005742
<i>Colletotrichum</i> sp.	CBS 128544, ICMP 18586*	<i>Solanum melongena</i>	New Zealand	JQ005164	JQ005251	JQ005338	JQ005425	JQ005512	JQ005598	JQ005685
	CBS 102667	<i>Passiflora edulis</i> , leaf blotch	New Zealand	JQ005165	JQ005252	JQ005339	JQ005426	JQ005513	JQ005599	JQ005686
	CBS 123921, MAFF 238642	<i>Dendrobium kingianum</i>	Japan	JQ005163	JQ005250	JQ005337	JQ005424	JQ005511	JQ005597	JQ005684

¹CBS: Culture collection of the Centraalbureau voor Schimmelcultures, Fungal Biodiversity Centre, Utrecht, The Netherlands; IMI: Culture collection of CAB International, 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 transferred 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 MgCl₂, 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. cymbidicola* (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. parsonsi*). 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 teleomorph 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. Ascospores 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 biserially, 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. Ascospores ovoid to obpyriform, medium brown. *Asci* cylindrical to clavate, 60–70

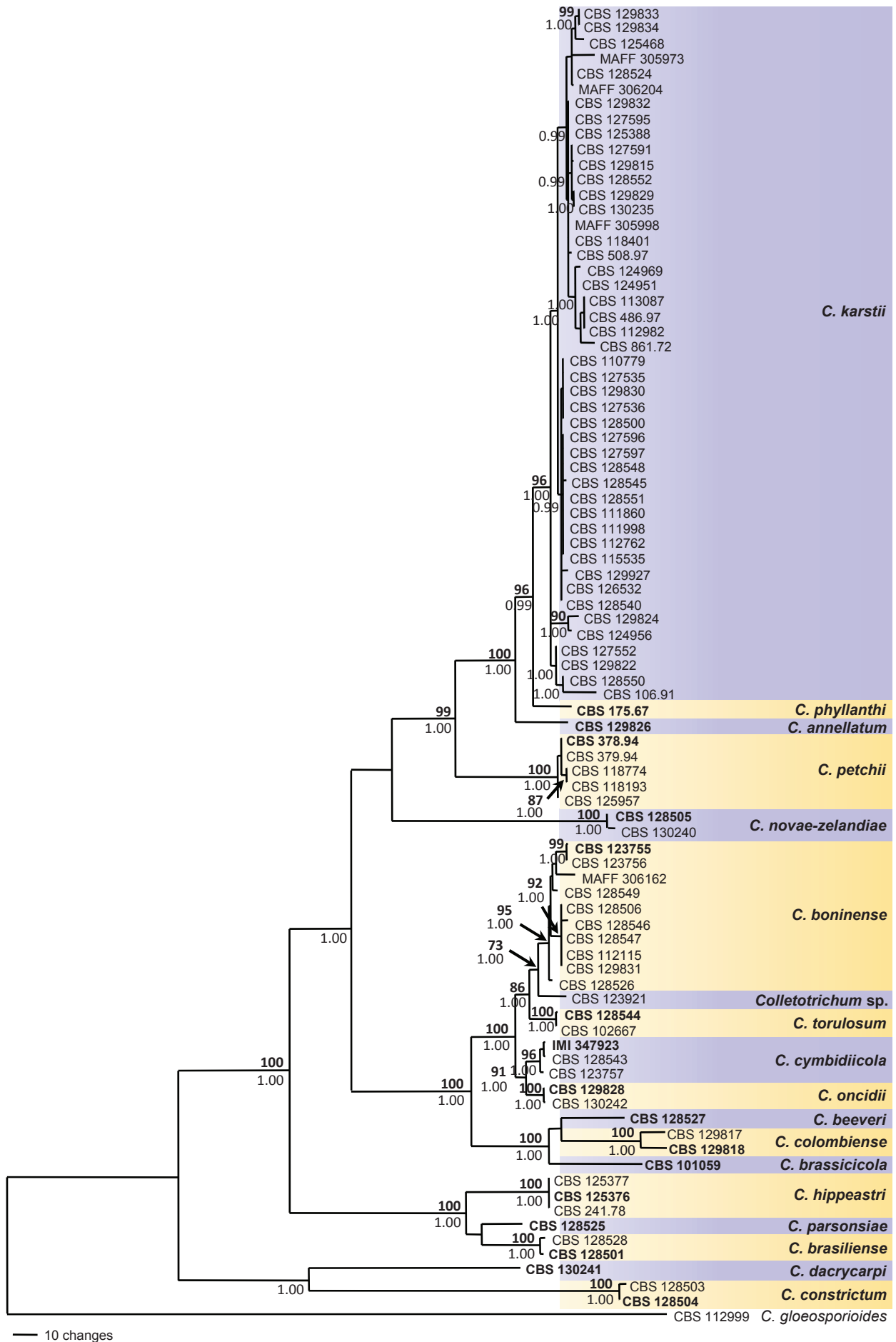


Fig. 1. One of 958 most parsimonious trees obtained from a heuristic search of the combined ITS, GAPDH, CHS-1, ACT, HIS3, TUB2 and CAL sequences alignment of the *Colletotrichum boninense* species complex. Bootstrap support values (500 replicates) above 70 % (bold) and Bayesian posterior probability 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.

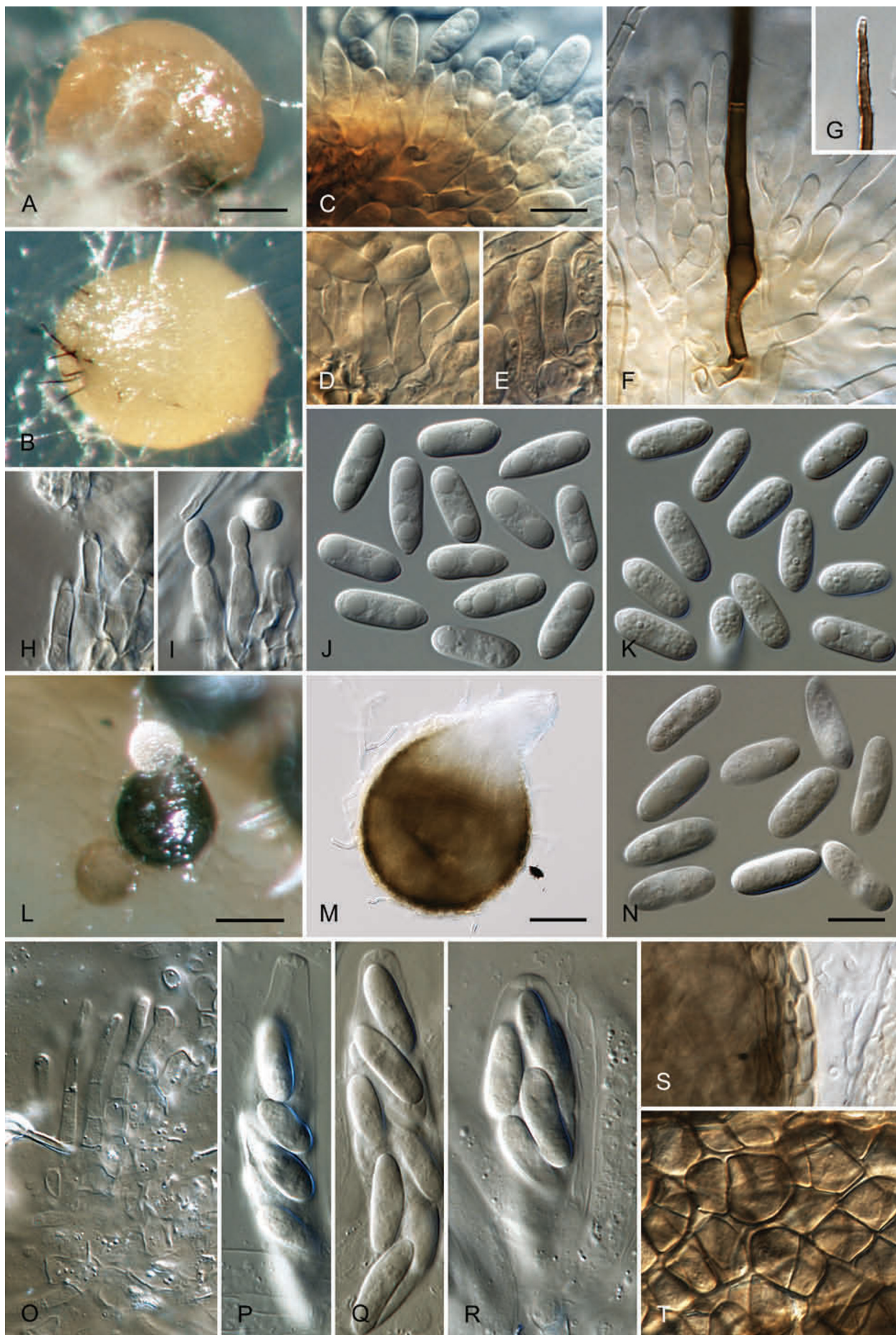


Fig. 2. *Colletotrichum annellatum* (from ex-holotype strain CBS 129826). A–B. Conidiomata. C–E. Conidiophores. F. Basis of seta and conidiophores. G. Tip of seta. H–I. Conidiophores. J–K. Conidia. L–M. Ascomata. N. Ascospores. O. Paraphyses. P–R. Asci. S. Peridium in cross section. T. Outer surface 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 μ m, M = 50 μ m, C, N = 10 μ m. 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 biserially, 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, collarete < 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, collarete 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. annellatum* 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 × 0.5–6.5 µm, opening 1–1.5 µm diam, collarete ≤ 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 μ m, E = 10 μ m. Scale bar of A applies to A–B. Scale bar of E applies to C–R.

with two big guttules, $(11.5\text{--}12\text{--}14\text{--}(16) \times 5.5\text{--}6.5 \mu\text{m}$, mean \pm SD = $13.2 \pm 1.0 \times 6.0 \pm 0.3 \mu\text{m}$, L/W ratio = 2.2. *Appressoria* single, dark brown, irregular, but often elliptical to navicular in outline, the margin lobate, $(5.5\text{--}7.5\text{--}12.5\text{--}(14.5) \times (4\text{--})5.5\text{--}8.5\text{--}(9) \mu\text{m}$, mean \pm SD = $10.1 \pm 2.5 \times 7.1 \pm 1.4 \mu\text{m}$, 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 \pm 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, $9\text{--}15 \times 4.5\text{--}5.5 \mu\text{m}$, 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, $(12.5\text{--}12\text{--}14\text{--}(15.5) \times 5.5\text{--}6.5 \mu\text{m}$, mean \pm SD = $14.3 \pm 0.8 \times 6.0 \pm 0.4 \mu\text{m}$, 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. Beaver, 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, \pm 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, cylindrical-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, collarete 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, collarete ≤ 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, collarete 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, collarete 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 μ m, T = 25 μ m, D, U = 10 μ m. 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 μ m, E = 10 μ m. 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) \times (4.5–)5–5.5(–6) μ m, mean \pm SD = 14.8 \pm 1.3 \times 5.3 \pm 0.3 μ m, L/W ratio = 2.8, conidia of strain CBS 128528 longer, measuring (13–)14–19(–22.5) \times (4–)4.5–5.5(–6), mean \pm SD = 16.7 \pm 2.5 \times 5.1 \pm 0.5 μ m, 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. parsoniae* 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. parsoniae*. 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 \times 5–6 μ m) 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 \times 4–6 μ m (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. Ascumata globose to subglobose, pale brown, 100–250 × 90–150 µm, 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 biserially, 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 doliform, sometimes lacking a basal septum and continuous with the conidiophore, 7–14 × 4–5.5 µm, opening 1.5–2 µm diam, collarete 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, collarete 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/ascumata on filter paper; reverse filter paper rosy buff to hazel with black sclerotia/ascumata 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.

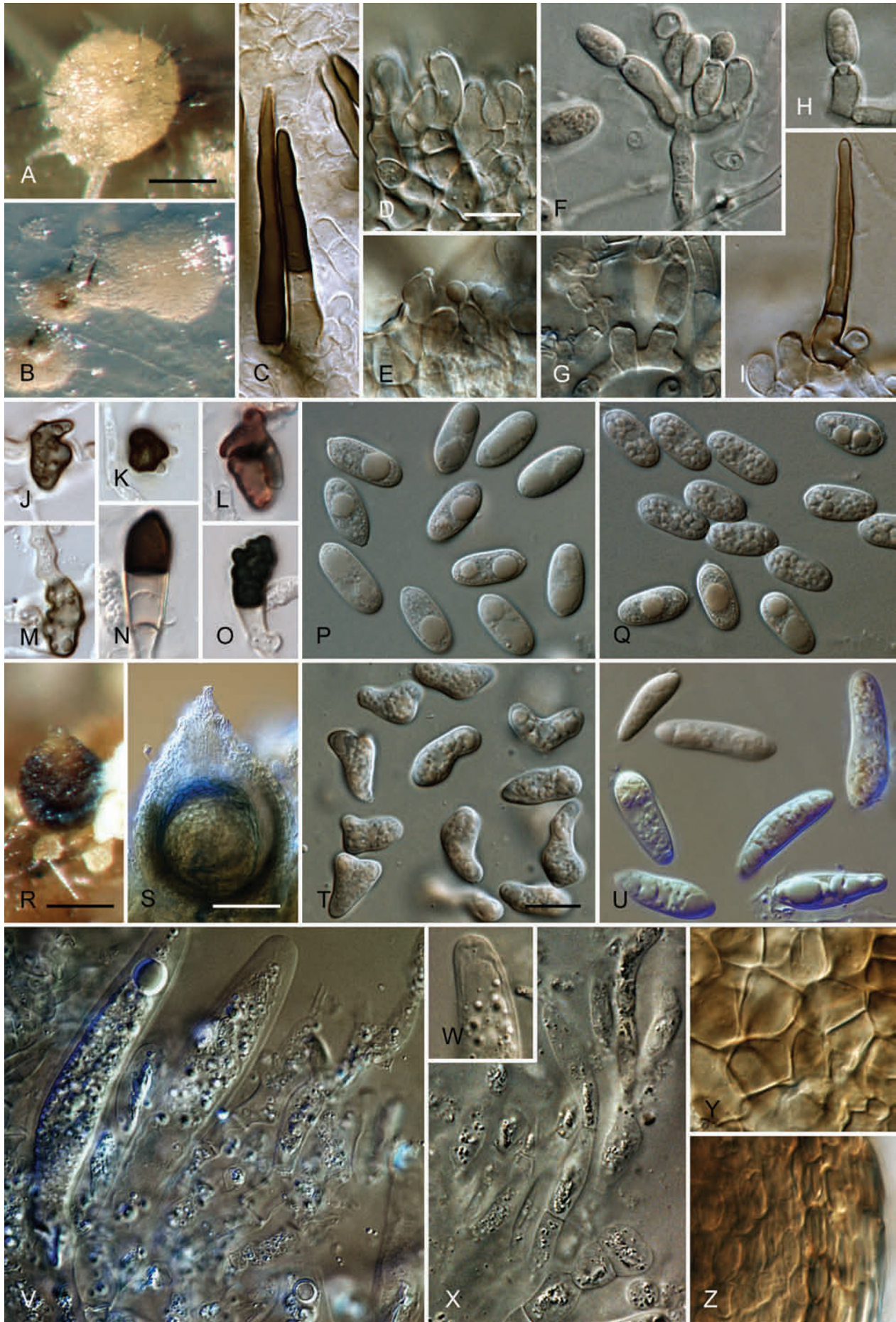


Fig. 6. *Colletotrichum brassicicola* (from ex-holotype strain CBS 101059). A–B. Conidiomata. C. Setae. D–H. Conidiophores. I. Seta and conidiophores. J–O. Appressoria. P–Q. Conidia. R–S. Ascomata. T. Conidia formed in closed conidiomata. U. Ascospores. V. Asci and paraphyses. W. Apical region of an 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 μ m, S = 50 μ m, D, T = 10 μ m. Scale bar of A applies to A–B. Scale bar of D applies to C–Q. Scale bar of T applies to T–Z.

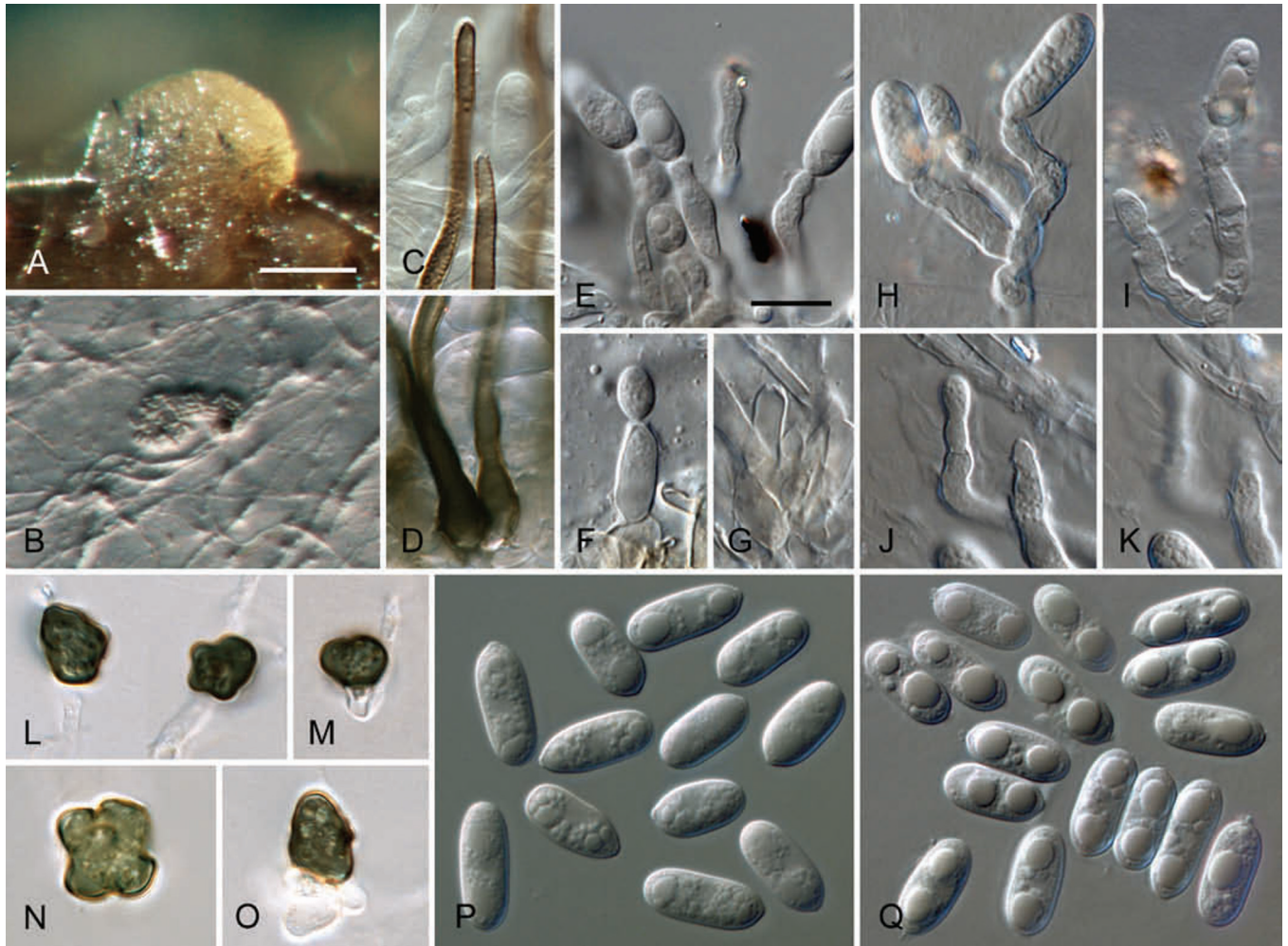


Fig. 7. *Colletotrichum colombiense* (from ex-holotype strain CBS 129818). A–B. Conidiomata. C. Tips of setae. D. Bases of setae. E–K. Conidiophores. L–O. Appressoria. P–Q. Conidia. A, C–G, P. from *Anthriscus* stem. B, H–K, Q. from SNA. A–B. DM, C–Q. DIC, Scale bars: A = 100 μ m, E = 10 μ m. Scale bar 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 μ m 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 μ m long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical, sometimes slightly inflated, surrounded by several mucous layers, often extending to form new conidiogenous loci, 7–18 \times 3.5–5 μ m, opening 1–1.5 μ m 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) \times (4.5–) 5–6(–6.5) μ m, mean \pm SD = 13.1 \pm 1.0 \times 5.7 \pm 0.4 μ m, 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) \times (3.5–)4.5–7.5(–10) μ m, mean \pm SD = 7.8 \pm 2.0 \times 6.0 \pm 1.5 μ m, L/W ratio = 1.3, appressoria of strain CBS 129817 larger, (7–) 7.5–14.5(–21.5) \times (5–)6–10(–12.5) μ m, mean \pm SD = 11.0 \pm 3.5 \times 8.1 \pm 1.9 μ m, 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 μ m diam. *Setae* medium brown, verruculose, 1–3-septate, 35–110 μ m long, base cylindrical to strongly inflated, 3.5–8.5 μ m diam, tip rounded. *Conidiophores* hyaline, smooth-walled, septate, branched, to 40 μ m long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical, sometimes surrounded by a gelatinous sheath, sometimes extending to form new conidiogenous loci, 7–26 \times 3–5.5 μ m, opening 1–1.5 μ m diam, collarette < 0.5 μ m 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) \times (5–)5.5–6 μ m, mean \pm SD = 13.1 \pm 1.1 \times 5.7 \pm 0.3 μ m, 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* biserially 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* biserially 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, collarete ≤ 0.5 µm, periclinal thickening distinct. *Conidia* hyaline,

smooth-walled, aseptate, straight, cylindrical, the apex and base rounded, with a prominent scar, contents 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 occasionally 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, collarete < 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 μ m, B, S = 100 μ m, E, U = 10 μ m. 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* biserially 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* biserially 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 appearance, (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, collarete ≤ 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, collarete ≤ 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 teleomorph 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, collarete ≤ 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.

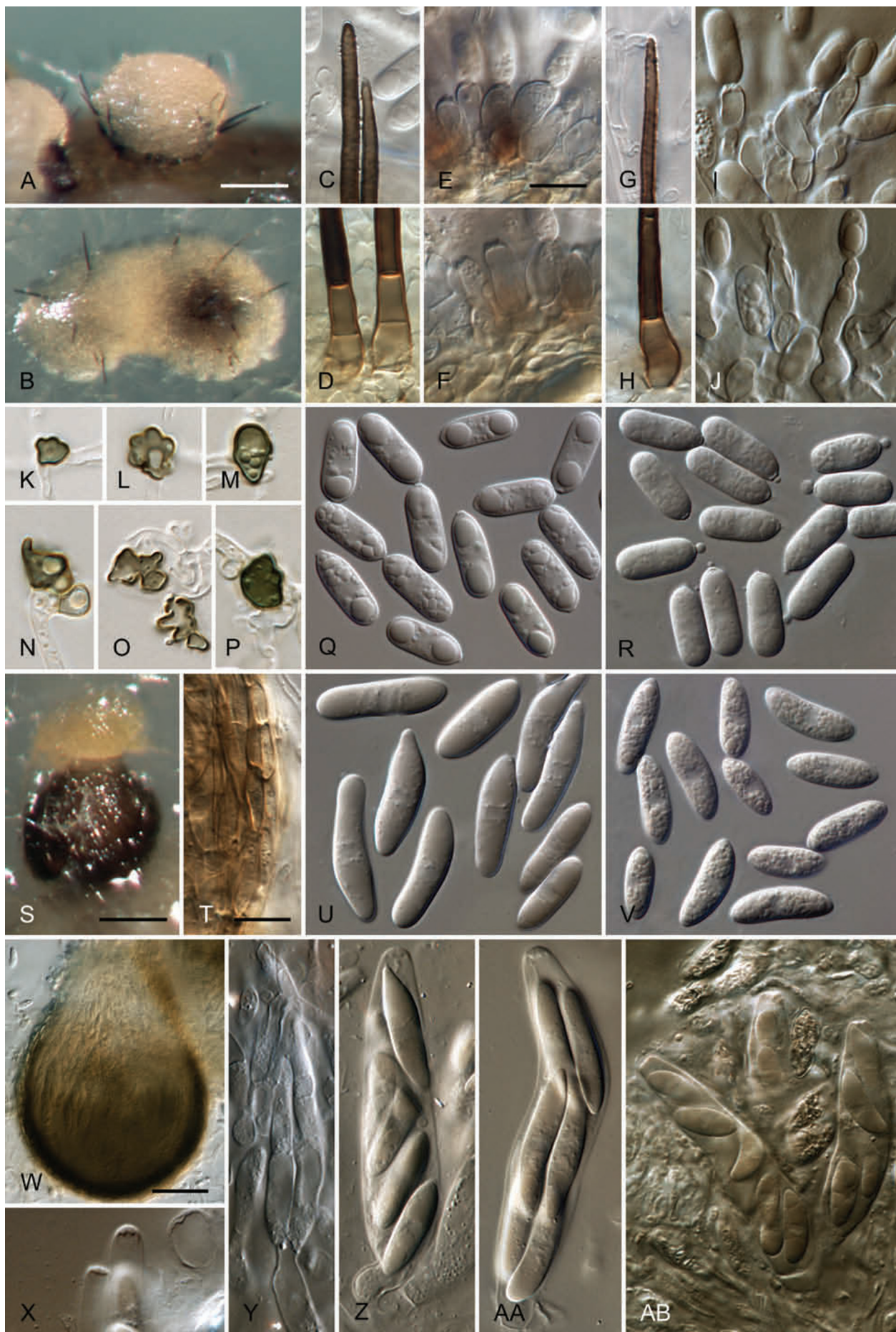


Fig. 9. *Colletotrichum cymbidiicola* (from ex-holotype strain IMI 347923). A–B. Conidiomata. C. Tips of setae. D. Bases of setae. E–F. Conidiophores. G. Tip of seta. H. Basis of seta. I–J. Conidiophores. K–P. Appressoria. Q–R. Conidia. S, W. Ascomata. T. Peridium in cross section. U–V. Ascospores. X. 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 μ m, W = 50 μ m, E, T = 10 μ m. 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.

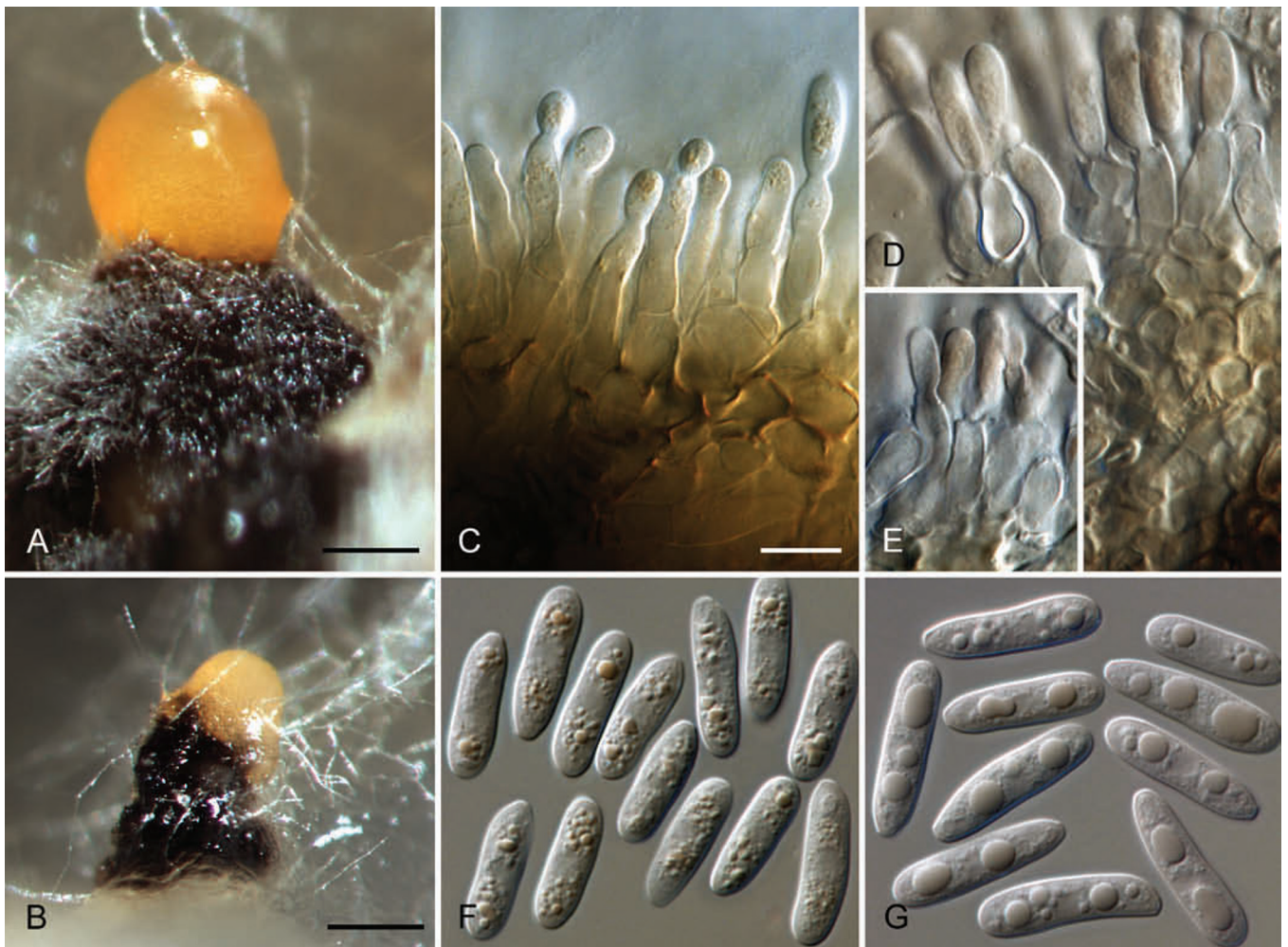


Fig. 10. *Colletotrichum dacrycarpi* (from ex-holotype strain CBS 130241). A–B. Conidiomata. C–E. Conidiophores. F–G. Conidia. A, C, F. from *Anthriscus* stem. B, D–E, G. from SNA. A–B. DM, C–G. DIC. Scale bars: A = 100 μ m, B = 200 μ m, C = 10 μ m. Scale bar of C applies to C–Q.

On Anthriscus stem. Conidiomata globose, apparently opening by rupture, wall cells medium brown, angular, 7–20 μ m diam. Setae not observed. Conidiophores hyaline, smooth-walled, septate, branched, to 50 μ m long, developing from a cushion of medium brown, angular to rounded cells, 3.5–12 μ m 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 \times 3–5 μ m, the opening 1.5–2.5 μ m 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) \times 5–6(–6.5) μ m, mean \pm SD = 17.3 \pm 2.0 \times 5.5 \pm 0.3 μ m, 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 μ m 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 μ m long, the base cylindrical or inflated, 4–7 μ m diam, the tip rounded. Conidiophores pale to medium brown, septate,

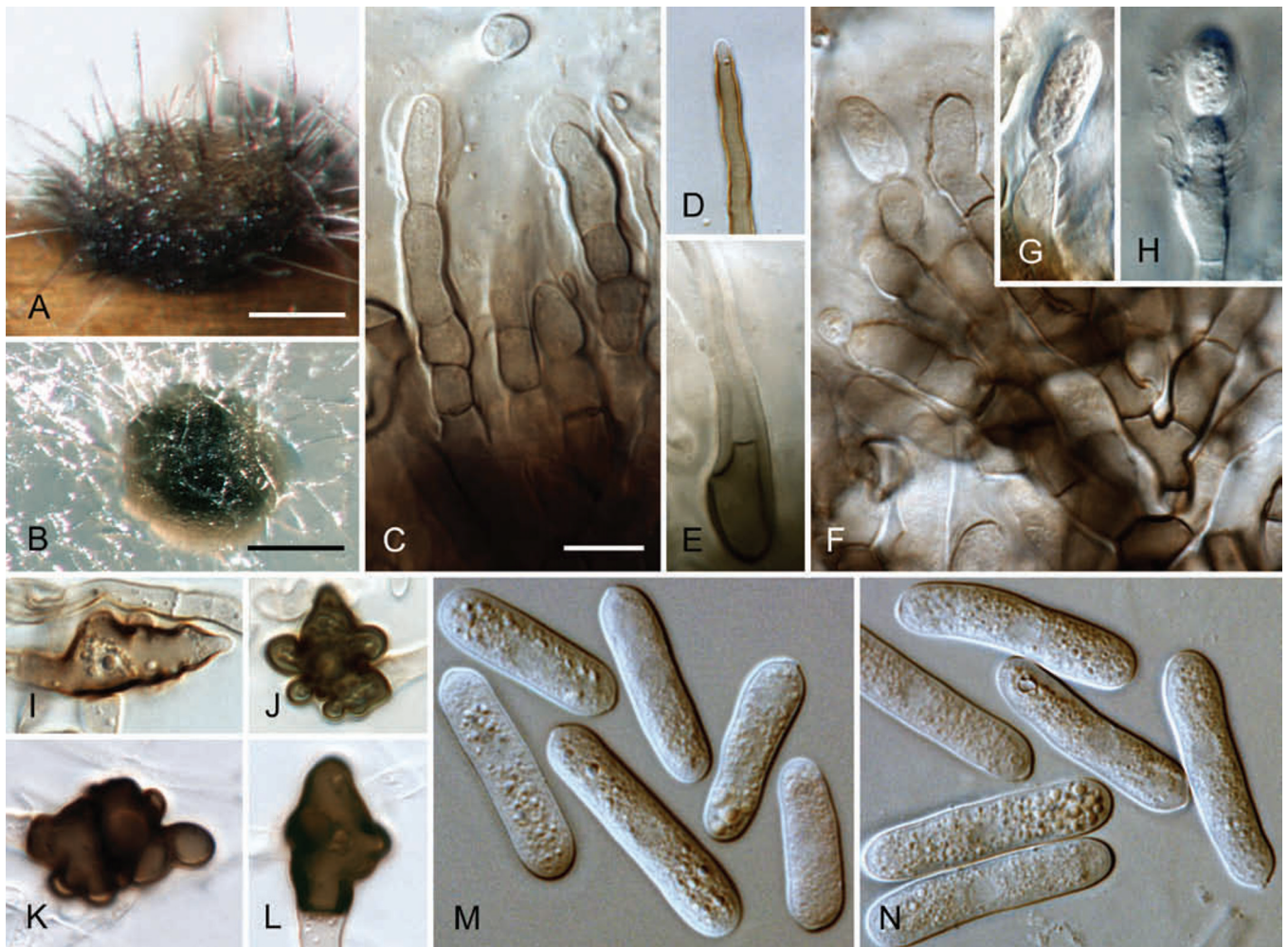


Fig. 11. *Colletotrichum hippeastrii* (from ex-holotype strain CBS 125377). A–B. Conidiomata. C. Conidiophores. D. Tip of seta. E. Basis of seta. F–H. Conidiophores. I–L. Appressoria. M–N. Conidia. A, C–F, M. from *Anthriscus* stem. B, F–L, N. from SNA. A–B. DM, C–N. DIC, Scale bars: A = 100 μ m, B =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

branched, to 50 μ m 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 \times 4–6.5 μ m, the opening 1.5–2.5 μ m 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) \times (5.5–)6–7.5(–8.5) μ m, mean \pm SD = 28.5 \pm 4.1 \times 6.8 \pm 0.6 μ m, L/W ratio = 4.2. Strain CBS 241.78 differs in forming shorter and broader conidia, measuring (10.5–)17–31.5(–40) \times (6–)6.5–8(–8.5) μ m, mean \pm SD = 24.4 \pm 7.3 \times 7.2 \pm 0.7 μ m, L/W ratio = 3.4. *Appressoria* dark brown, irregular in shape and strongly nodose, (8.5–)10–20(–32) \times (5.5–)7.5–12.5(–15) μ m, mean \pm SD = 14.9 \pm 5.0 \times 10.0 \pm 2.5 μ m, 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 μ m diam. *Setae* pale brown, darker towards the base, smooth and very thick-walled, 1–6-septate, the septa concentrated towards the base, 50–150 μ m long, the base cylindrical, conical or inflated, 5.5–10 μ m diam, the tip rounded. *Conidiophores* pale to medium brown, septate, branched, to 70 μ m 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 \times 4.5–5.5 μ m, the opening 1.5–2 μ m 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) \times (5–)6–8(–9) μ m, mean \pm SD = 24.2 \pm 5.8 \times 6.9 \pm 0.9 μ m, 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 ascogonia?) 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 hippeastrii* 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. hippeastrii* 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. hippeastrii* 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. Ascumata 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 biserially 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. Ascumata ± 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 biserially.

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, collarete < 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, verrucose, 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, collarete < 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 ascumata. *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

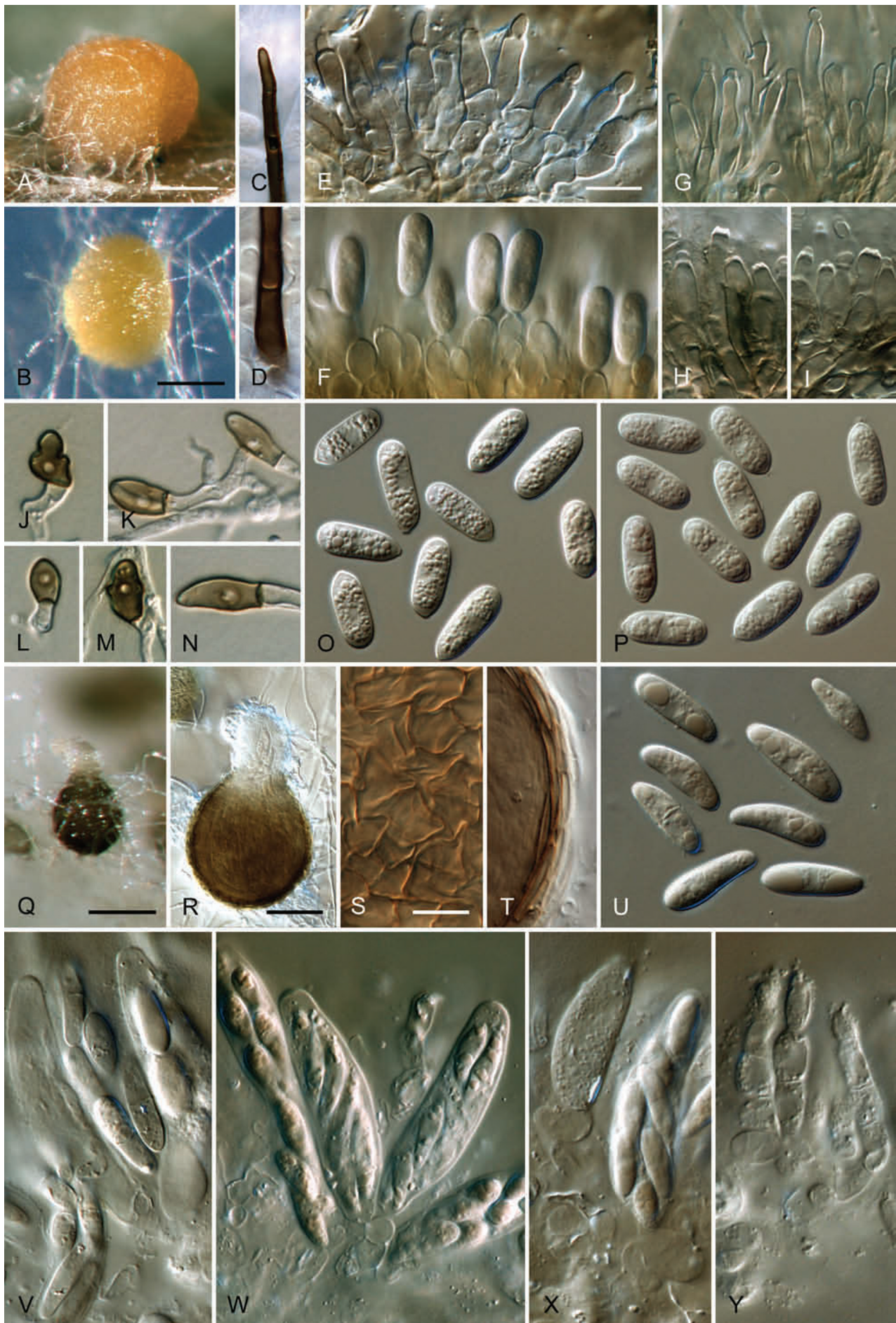


Fig. 12. *Colletotrichum karstii* (from strain CBS 127597). A–B. Conidiomata. C. Tip of seta. D. Basis of seta. E–I. Conidiophores. J–N. Appressoria. O–P. Conidia. Q–R. Ascomata. S. Outer surface of peridium. T. Peridium in cross section. U. Ascospores. V–X. Asci. Y. Paraphyses. A, C–F, O. from *Anthriscus* stem. B, G–N, P–Y. from SNA. A–B, Q. DM, C–P, R–Y. DIC. Scale bars: A = 200 μ m, B, Q = 100 μ m, R = 50 μ m, E, S = 10 μ m. 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 μ m, C = 10 μ m, L = 25 μ m. 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 \times 140–170 μ m) and brown, roundish closed conidiomata that open by irregular rupture, and covered with brown, verrucose to warted hairs/hyphae, 3–3.5 μ m wide. In addition, the setae are more frequent, shorter (40–80 μ m long) and broader at the base (5–7.5 μ m diam). The appressoria are larger, measuring (5.5–)7.5–13(–17) \times (4.5–

5.5–8.5(–10.5) μ m, mean \pm SD = 10.3 \pm 2.6 \times 7.1 \pm 1.5 μ m, 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 μ m 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 μ m diam. *Setae* not observed. *Conidiophores* hyaline, smooth-walled, septate, branched, to 50 μ m 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 \times 4–6 μ m, opening 1.5–2 μ m 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 covered 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 almond 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 grey 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 oncidi* (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 μ m, E = 10 μ m, J = 25 μ m. 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. oncidi* 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 oncidi 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 oncidi* 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 μ m long, and 1–2-septate. No teleomorph is known.

Colletotrichum parsoniae 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 \times 120–220 μ m. *Peridium* composed of pale to medium brown, flattened *textura angularis* with cells 5–16 μ m diam. *Interascal tissue* formed of paraphyses, hyaline, smooth-walled, mostly cylindrical but tapering towards the rounded tip, disintegrating quickly, septate, apically free, 50–70 \times 3–4 μ m. *Asci* unitunicate, 8-spored, cylindrical to clavate, tapering

to apex and base, smooth-walled, 70–80 \times 10–13 μ m. *Ascospores* biserially arranged, aseptate, hyaline, smooth-walled, broadly allantoid with rounded ends, (12.5–)14–17(–18) \times (5–)5.5–6(–6.5) μ m, mean \pm SD = 15.7 \pm 1.4 \times 5.8 \pm 0.4 μ m, L/W ratio = 2.7.

Anamorph on SNA. *Vegetative hyphae* 1–7 μ m 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 μ m diam. *Setae* pale to medium brown, basal cell often paler, smooth-walled, 2–4-septate, 50–150 μ m long, base cylindrical to conical, 4–6 μ m diam, tip \pm acute to rounded. *Conidiophores* hyaline to pale brown, smooth-walled, septate, branched, to 45 μ m 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 \times 3–5.5 μ m, opening 1–2 μ m diam, collarete \leq 0.5 μ m 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) \times 5–6(–6.5) μ m, mean \pm SD = 18.5 \pm 1.8 \times 5.4 \pm 0.3 μ m, 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) \times (4.5–)5.5–8(–10.5) μ m, mean \pm SD = 13.2 \pm 3.3 \times 6.6 \pm 1.3 μ m, L/W ratio = 2.0.

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



Fig. 15. *Colletotrichum parsonsiiae* (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. Ascogonium. 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 μ m, D, R = 10 μ m, K = 25 μ m. 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, collarete ≤ 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 patchii 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 biserially, 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, collarete 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, collarete ≤ 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 alettriformis* (syn. *D. latifolia*), Apr. 1895, J.E. Weiss, M-0090064, **holotype** of *C. dracaenae* Allescher.

Notes: Conidia of *C. patchii* 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. Ascogonium. 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 μ m, E, T = 10 μ m. 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. hippaeatri* 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 (Allscher 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 μ m, D = 10 μ m. 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 teleomorph 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 \times 7.5–8 μ m by Petch (1906), wrongly cited by Pai (1970) as 18–24 \times 5–8 μ m.

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 \pm cylindrical conidia with rounded ends that are mostly 14.5–16 \times 4–6 μ m 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 μ m 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 μ m long, sometimes branched, base cylindrical, 3.5–5.5 μ m diam, tip \pm acute to \pm rounded. *Conidiophores* hyaline, smooth-walled, septate, branched, to 75 μ m long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical, 8–23 \times 3.5–5.5 μ m, opening 1–2 μ m diam, collarette \leq 0.5 μ m 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 blight 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 *Dacrydium 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 Moriwaki *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 blast 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. Morikawa *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 occurring 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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