The Colletotrichum boninense species complex

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Abstract: Although only recently described, Colletotrichum boninense is well established in literature as an anthracnose pathogen or endophyte of a diverse range of host plants worldwide. It is especially prominent on members of Amaryllidaceae, Orchidaceae, Proteaceae and Solanaceae. Reports from literature and preliminary studies using ITS sequence data indicated that C. boninense represents a species complex. A multilocus molecular phylogenetic analysis (ITS, ACT, TUB2, CHS-1, GAPDH, HIS3, CAL) of 86 strains previously identified as C. boninense and other related strains revealed 18 clades. These clades are recognised here as separate species, including C. boninense s. str., C. hippeastri and 12 previously undescribed species, C. annellatum, C. beeveri, C. brassicicola, C. brasiliense, C. colombiense, C. constrictum, C. cymbidiicola, C. dacyrcarpic, 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 epihytified and the name replaced with C. petchii. Typical for species of the C. boninense species complex are the conidigenous 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. Suredanrath Pal) Damm, P.F. Cannon & Crous. Name replacement - C. petchii Damm, P.F. Cannon & Crous.

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 Coffee 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 Podocarpus 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
| Species                          | Accession No. | Host/Substrate                  | GenBank No. | Country                  | ITS     | GAPDH   | CHS-1    | HIS3    | ACT      | TUB2    | CAL    |
|--------------------------------|---------------|---------------------------------|-------------|--------------------------|---------|---------|---------|---------|---------|---------|--------|
| C. annellatum                   | CBS 129826, CHB 11514* | Hevea brasiliensis, leaf   | JQ005581    | Colombia                 | JQ005579 |         |         |         |         |         |        |
| C. beeveri                      | CBS 129827, ICMP 10338 | Brachypodium sp.              | JQ005577    | New Zealand              | JQ005575 |         |         |         |         |         |        |
| C. boninense                    | CBS 129830, ICMP 10338 | Camellia sp.                  | JQ005576    | New Zealand              | JQ005574 |         |         |         |         |         |        |
| C. brasiliense                   | CBS 129831, ICMP 10338 | Leucospermum sp.              | JQ005580    | New Zealand              | JQ005578 |         |         |         |         |         |        |
| C. cymbidiicola                 | CBS 129832, ICMP 10338 | Cymbidium sp.                 | JQ005574    | New Zealand              | JQ005576 |         |         |         |         |         |        |
| C. constrictum                  | CBS 129833, ICMP 10338 | Citrus limon                   | JQ005582    | New Zealand              | JQ005580 |         |         |         |         |         |        |
| C. dappticola                   | CBS 129834, ICMP 10338 | Capsicum annuum               | JQ005584    | New Zealand              | JQ005582 |         |         |         |         |         |        |
| C. dolichocarpum                | CBS 129835, ICMP 10338 | Anthurium sp.                 | JQ005586    | New Zealand              | JQ005584 |         |         |         |         |         |        |

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1. Accession No. 1: Indicates additional accessions for the same species.
Table 1. Continued.

| Accession No. | Species | GenBank No. | Host/Substrate | Country | ITS | GAPDH | CHS-1 | HIS3 | ACT | TUB2 | CAL |
|---------------|---------|-------------|----------------|---------|-----|-------|-------|------|-----|------|-----|
| CBS 105.91    | C. karstii | CBS 106.91  | Carica papaya, fruit spots | Brazil | JQ00520 | JQ005307 | JQ005394 | JQ005481 | JQ005568 | JQ005654 | JQ005741 |
| CBS 12851.1CIP | C. mellea | CBS 12852.1CIP | Citrus sp. | New Zealand | JQ00523 | JQ00532 | JQ00541 | JQ00550 | JQ00559 | JQ00568 | JQ00577 |
| CBS 12852.1CIP | C. mellea | CBS 12853.1CIP | Citrus sp. | New Zealand | JQ00521 | JQ00530 | JQ00540 | JQ00549 | JQ00558 | JQ00567 | JQ00575 |
| CBS 12855.1CIP | C. mellea | CBS 12856.1CIP | Citrus sp. | New Zealand | JQ00524 | JQ00533 | JQ00542 | JQ00551 | JQ00560 | JQ00569 | JQ00578 |
| CBS 12857.1CIP | C. mellea | CBS 12858.1CIP | Citrus sp. | New Zealand | JQ00525 | JQ00534 | JQ00543 | JQ00552 | JQ00561 | JQ00570 | JQ00579 |
| CBS 12859.1CIP | C. mellea | CBS 12860.1CIP | Citrus sp. | New Zealand | JQ00526 | JQ00535 | JQ00544 | JQ00553 | JQ00562 | JQ00571 | JQ00580 |
| CBS 12861.1CIP | C. mellea | CBS 12862.1CIP | Citrus sp. | New Zealand | JQ00527 | JQ00536 | JQ00545 | JQ00554 | JQ00563 | JQ00572 | JQ00581 |
| CBS 12863.1CIP | C. mellea | CBS 12864.1CIP | Citrus sp. | New Zealand | JQ00528 | JQ00537 | JQ00546 | JQ00555 | JQ00564 | JQ00573 | JQ00582 |
| CBS 12865.1CIP | C. mellea | CBS 12866.1CIP | Citrus sp. | New Zealand | JQ00529 | JQ00538 | JQ00547 | JQ00556 | JQ00565 | JQ00574 | JQ00583 |
| CBS 12867.1CIP | C. mellea | CBS 12868.1CIP | Citrus sp. | New Zealand | JQ00530 | JQ00539 | JQ00548 | JQ00557 | JQ00566 | JQ00575 | JQ00584 |
| CBS 12869.1CIP | C. mellea | CBS 12870.1CIP | Citrus sp. | New Zealand | JQ00531 | JQ00540 | JQ00549 | JQ00558 | JQ00567 | JQ00576 | JQ00585 |
| CBS 12871.1CIP | C. mellea | CBS 12872.1CIP | Citrus sp. | New Zealand | JQ00532 | JQ00541 | JQ00550 | JQ00559 | JQ00568 | JQ00577 | JQ00586 |
| CBS 12873.1CIP | C. mellea | CBS 12874.1CIP | Citrus sp. | New Zealand | JQ00533 | JQ00542 | JQ00551 | JQ00560 | JQ00569 | JQ00578 | JQ00587 |
| CBS 12875.1CIP | C. mellea | CBS 12876.1CIP | Citrus sp. | New Zealand | JQ00534 | JQ00543 | JQ00552 | JQ00561 | JQ00570 | JQ00579 | JQ00588 |
| CBS 12877.1CIP | C. mellea | CBS 12878.1CIP | Citrus sp. | New Zealand | JQ00535 | JQ00544 | JQ00553 | JQ00562 | JQ00571 | JQ00580 | JQ00589 |
| CBS 12879.1CIP | C. mellea | CBS 12880.1CIP | Citrus sp. | New Zealand | JQ00536 | JQ00545 | JQ00554 | JQ00563 | JQ00572 | JQ00581 | JQ00590 |
| Species                  | Accession No. | Host/Substrate               | Country     | GenBank No. |
|-------------------------|---------------|------------------------------|-------------|-------------|
|                         |               |                              |             | ITS         | GAPDH       | CHS-1       | HIS3        | ACT         | TUB2        | CAL         |
| C. karstii              | CBS 124969, LCM 232 | Quercus salicifolia, leaf endophyte | Panama      | JQ005179   | JQ005266    | JQ005353    | JQ005440    | JQ005527    | JQ005613    | JQ005700    |
|                         | CBS 127591    | Sapum integrerrimum          | Australia    | JQ005186   | JQ005273    | JQ005360    | JQ005447    | JQ005534    | JQ005620    | JQ005707    |
|                         | CBS 12815, T.A.7 | Solanum betaceum, fruit      | Colombia     | JQ005187   | JQ005274    | JQ005361    | JQ005448    | JQ005535    | JQ005621    | JQ005708    |
|                         | CBS 128548, ICMP 18589 | Solanum lycopersicum        | New Zealand  | JQ005205   | JQ005292    | JQ005379    | JQ005466    | JQ005553    | JQ005639    | JQ005726    |
|                         | CBS 508.97, LARS 168 | Stylophanthes sympodialis   | Australia    | JQ005193   | JQ005280    | JQ005367    | JQ005454    | JQ005541    | JQ005627    | JQ005714    |
|                         | CBS 12552, ICMP 18276 | Synsepalum dulcificum, leaves | Taiwan      | JQ005188   | JQ005275    | JQ005362    | JQ005449    | JQ005536    | JQ005622    | JQ005709    |
|                         | CBS 124951    | Theobroma cacao, leaf endophyte | Panama      | JQ005180   | JQ005267    | JQ005354    | JQ005441    | JQ005528    | JQ005614    | JQ005701    |
|                         | CBS 128540, STE-U 698 | Tricium sp.             | South Africa | JQ005210   | JQ005297    | JQ005384    | JQ005471    | JQ005558    | JQ005644    | JQ005731    |
|                         | CBS 124956    | Zamia obliqua, leaf endophyte | Panama      | JQ005216   | JQ005303    | JQ005390    | JQ005477    | JQ005564    | JQ005650    | JQ005737    |
|                         | CBS 124956    | Zamia obliqua, leaf endophyte | Panama      | JQ005216   | JQ005303    | JQ005390    | JQ005477    | JQ005564    | JQ005650    | JQ005737    |
|                         | CBS 125388    | Zamia obliqua, leaf endophyte | Panama      | JQ005185   | JQ005272    | JQ005359    | JQ005446    | JQ005533    | JQ005619    | JQ005706    |
| C. novae-zelandiae      | CBS 128505, ICMP 12944* | Capsicum annuum, fruit rot | New Zealand  | JQ005228   | JQ005315    | JQ005402    | JQ005489    | JQ005576    | JQ005662    | JQ005749    |
|                         | CBS 130240, ICMP 12064 | Citrus spp. (grapefruit) | New Zealand  | JQ005229   | JQ005316    | JQ005403    | JQ005490    | JQ005577    | JQ005663    | JQ005750    |
| C. oncidii              | CBS 129828*   | Oncidium sp., leaf           | Germany      | JQ005169   | JQ005256    | JQ005343    | JQ005430    | JQ005517    | JQ005603    | JQ005690    |
|                         | CBS 130242    | Oncidium sp., leaf           | Germany      | JQ005170   | JQ005257    | JQ005344    | JQ005431    | JQ005518    | JQ005604    | JQ005691    |
| C. parsonsiae           | CBS 128525, ICMP 18590* | Passonisa capsulata, leaf endophyte | New Zealand  | JQ005233   | JQ005320    | JQ005407    | JQ005494    | JQ005581    | JQ005687    | JQ005754    |
| C. petchii              | CBS 378.94*   | Dracaena marginata, spotted leaves | Italy        | JQ005223   | JQ005310    | JQ005397    | JQ005484    | JQ005571    | JQ005657    | JQ005744    |
|                         | CBS 379.94    | Dracaena marginata, spotted leaves | Italy        | JQ005224   | JQ005311    | JQ005398    | JQ005485    | JQ005572    | JQ005658    | JQ005745    |
|                         | CBS 118193, AR 3658 | Dracaena sanderana, living leaves | China       | JQ005227   | JQ005314    | JQ005401    | JQ005488    | JQ005575    | JQ005661    | JQ005748    |
|                         | CBS 118774, AR 3751 | Dracaena sanderana, living stems | China       | JQ005225   | JQ005312    | JQ005399    | JQ005486    | JQ005573    | JQ005659    | JQ005746    |
|                         | CBS 125957, NB 145 | Dracaena, leaf spots       | Netherlands  | JQ005226   | JQ005313    | JQ005400    | JQ005487    | JQ005574    | JQ005660    | JQ005747    |
| C. phyllanthi           | CBS 175.67, MACS 271* | Phyllanthus acidus, anthracose | India        | JQ005221   | JQ005308    | JQ005395    | JQ005482    | JQ005569    | JQ005655    | JQ005742    |
| C. torulosum            | CBS 128544, ICMP 18589* | Solanum melongena        | New Zealand  | JQ005164   | JQ005251    | JQ005338    | JQ005425    | JQ005512    | JQ005638    | JQ005685    |
|                         | CBS 102667    | Passiflora edulis, leaf blotch | New Zealand  | JQ005165   | JQ005252    | JQ005339    | JQ005426    | JQ005513    | JQ005659    | JQ005686    |
| Colletotrichum sp.      | CBS 123921, MAFF 238642 | Dendrobium kinganum | Japan        | JQ005163   | JQ005250    | JQ005337    | JQ005424    | JQ005511    | JQ005597    | JQ005684    |

1 CBS: Culture collection of the Centraalbureau voor Schimmelcultures, Fungal Biodiversity Centre, Utrecht, The Netherlands; IMI: Culture collection of CABI Europe UK Centre, Egham, UK; MAFF: MAFF Genebank Project, Ministry of Agriculture, Forestry and Fisheries, Tsukuba, Japan; BRIP: Plant Pathology Herbarium, Department of Employment, Economic, Development and Innovation, Queensland, Australia; ICMP: International Collection of Microorganisms from Plants, Auckland, New Zealand; STE-U: Culture collection of the Department of Plant Pathology, University of Stellenbosch, South Africa; MACS: MACS Collection of Microorganisms, Pune, India; * ex-holotype or ex-epitype cultures.
complex were detected in blastn searches in GenBank. Yang et al. (2011) recently reported C. boninense from Pleione bulbocodioides and Oncidium flexuosum (Orchidaceae) in China and described a related species, C. karstii that occurs on several orchids in China.

Conidia of C. boninense s. lat. are similar to those of C. gloeosporioides, differing only slightly in length/width ratio and in the presence of a prominent scar at the base of the conidium (Morwaki et al. 2003). Isolates of C. boninense have often been identified as C. gloeosporioides in the past (Morwaki 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 Morwaki 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 Staatsammlung 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 (Carbon & Kohn 1999), CHS-354R + CHS-79F (Carbon & Kohn 1999), BT2Fd + BT4R (Woudenberg et al. 2009) or T1 (O’Donnell & Cigelnik 1997) + BT-2b (Glass & Donaldson 1995), CYL13F + CYL13R (Crous et al. 2004b) and CAL 228F + CAL 737R (Carbon & 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 μL 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 Woudenburg 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. phylanthi and C. annellatum, group with this big clade with a bootstrap/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-zeelandiae 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. oncidi (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. beeeri and C. brassicicola, and the C. colombiense clade (100/1.00) containing two strains. The clades representing C. hippocastri and C. brasiliense consist of three and two strains respectively, and are well supported (100/1.00). They group (100/1.00) with a single strain clade (C. parsonsiae). The C. constrictum clade (100/1.00) containing two strains and the single strain clade representing C. dacycarpi 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. beeeri 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. phylanthi, has a known telemorph and is shown here as belonging to the Colletotrichum boninense species complex. All species studied in culture are characterised below.

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

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

Teleomorph developed on Anthriscus stem. Ascomata ovoid to obpyriform, medium brown. Ascii cylindrical to clavate, 60–70
The *Colletotrichum boninense* species complex

Fig. 1. One of 958 most parsimonious trees obtained from a heuristic search of the combined ITS, GAPDH, CHS-1, ACT, HIS3, TUB2 and CAL sequences alignment of the *Colletotrichum boninense* species complex. Bootstrap support values (500 replicates) above 70% (bold) and Bayesian posterior probability values above 0.95 are shown at the nodes. *Colletotrichum gloeosporioides* CBS 112999 is used as outgroup. Numbers of ex-type and ex-epitype strains are emphasised in bold.
Fig. 2. Colletotrichum annellatum (from ex-holotype strain CBS 129826). A–B. Conidiomata. C–E. Conidiophores. F. Basis of seta and conidiophores. G. Tip of seta. H–I. Conidiophores. J–K. Conidia. L–M. Ascomata. N. Ascospores. O. Paraphyses. P–R. Asci. S. Peridium in cross section. T. Outer surface of peridium. A, C–E, J. from Anthriscus stem; B, F–I, K–T. from SNA. A–B, L. Dissecting microscope (DM), C–K, M–T. Differential interference contrast illumination (DIC), Scale bars: A, L = 100 µm, M = 50 µm, C, N = 10 µm. Scale bar of A applies to A–B. Scale bar of C applies to C–K. Scale bar of N applies to N–T.
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 *G. 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 & Chaverrí 2010, Gazis et al. 2011, Damm et al. 2012, this issue). However, one isolate from *Hevea guianensis* in Peru has an ITS sequence placing it in the *C. boninense* species complex, within *C. karstii* or *C. phyllanthi* (Gazis et al. 2011; GenBank HQ022474). The ITS sequence of *C. annelatum* differs in two bp from *C. annellatum* 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/filter paper 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. *Chlamydomspores* not observed. *Conidiodiata* absent, conidiophores and setae formed directly from vegetative hyphae or on a small cushion of hyaline to pale brown, angular cells 3–6 µm diam. *Setae* pale to medium brown, smooth to verruculose, especially towards the tip, 2–4-septate, 70–160 µm long, the base cylindrical, sometimes slightly inflated, 3.5–5.5 µm diam, the tip ± rounded. *Conidiophores* hyaline to very pale brown, smooth-walled, septate, branched, to 80 µm long. *Conidiogenous cells* hyaline to very pale brown, smooth-walled, cylindrical, sometimes extending to form new conidiogenous loci, 4–22 × 4–5 µm, opening 1–2 µm diam, collarette < 0.5 µm long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, asceptate, cylindrical, the apex and base rounded, with a prominent scar, contents granular or guttulate, often with two big walled, aseptate, cylindrical, the apex and base rounded, with a prominent scar, contents granular or guttulate, often with two big 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 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, annelations frequently observed, 7–21 × 3.5–5 µm, opening 1.5–2 µm diam, collarette 0.5–1 µm long. *Conidia* hyaline, smooth-walled, asceptate, 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 (29–29.5 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 annelatum* 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. annelatum*). *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. annelatum* frequently produces conidiogenous cells that have annellide-like proliferations on *Anthriscus* stem, while on SNA conidiogenous cells with a distinct periclinal thickening were predominant.
with two big guttules, \((11.5–)12–14(–16) \times 5.5–6.5 \, \mu m\), mean ± SD = 13.2 ± 1.0 × 6.0 ± 0.3 µm, L/W ratio = 2.2. Appressoria single, dark brown, irregular, but often elliptical to navicular in outline, the margin lobate, \((5.5–)7.5–12.5(–14.5) \times (4–)5.5–8.5(–9) \, \mu m\), mean ± SD = 10.1 ± 2.5 × 7.1 ± 1.4 µm, L/W ratio = 1.4.

Anamorph on Anthriscus stem. Conidiomata acervular, conidiophores and setae formed on a cushion of medium brown, thick-walled angular cells, 3–10 µm diam. Setae (only a few observed at the margin of acervuli) dark brown, smooth-walled, 2–3-septate, 80–95 µm long, base conical to cylindrical, 4.5–6 µm diam, tip roundish to ± acute. Conidiophores pale to medium brown, smooth-walled, septate, branched, to 20 µm long. Conidiogenous cells pale to medium brown, smooth-walled, septate, cylindrical, the apex and base rounded, with a prominent scar, contents granular or guttulate, sometimes with two big guttules, \((12.5–)12–14(–15.5) \times 5.5–6.5 \, \mu m\), mean ± SD = 14.3±0.8 × 6.0±0.4 µm, L/W ratio = 2.4.

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

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

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

No species of Colletotrichum has been previously described from Brachyglottis, and none of those species described from members of the Asteraceae originate from Australasia. According to sequence comparisons with six genes, C. beeveri (identified as C. boninense) was isolated as an endophyte of healthy roots of Pleione bulbocodioides (Orchidaceae) in China (Yang et al. 2011). Several endophytic strains from Podocarpaceae leaves from New Zealand have the same or similar ITS sequences as C. beeveri (e.g. EU482210, EU482288 and EU482283; Joshee et al. 2009).
**Colletotrichum boninense** Moriwaki, Toy. Sato & Tsukib., *Mycoscience* 44(1): 48. 2003. Fig. 4.

Teleomorph developed on OA (CBS 123756). Ascomata perithecia, variable in shape but usually subglobose to pyriform, glabrous, medium brown, 100–300 × 100–200 µm, ostiolate, periphysate, neck hyaline to pale brown, to 100 µm in length, outer wall composed of flattened angular cells 4–15 µm diam. Interascal tissue composed of rather irregular thin-walled hyaline septate paraphyses. Asci in a basal fascicle, cylindric-clavate, 45–60 × 12.5–17 µm, 8-spored, with a ± truncate apex and a small refractive apical ring. Ascospores initially hyaline and aseptate, becoming 1–3-septate, septation sometimes occurring inside the ascus, light to medium brown-p 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 anamorphs or not developed, conidiomata and setae formed directly on hyphae. Setae rare, medium brown, smooth to verruculose, 1–2-septate, 20–60 µm long, base cylindrical, conical or slightly inflated, 3–7 µm diam at the widest part, tip ± rounded. Conidiophores hyaline or pale brown, simple or septate, branched or unbranched, to 40 µm long. Conidiogenous cells hyaline or pale brown, cylindrical, 6–15 × 3–5 µm, opening 1–2 µm diam, collarette 0.5–1.5 µm long, periclinal thickening conspicuous. Conidia hyaline, smooth-walled, aseptate, straight, cylindrical, apex round, base round, with a prominent hilum, often containing two big polar guttules, (8.5–)11–14.5(–17.5) × (4–)5–6(–6.5) µm, mean ± SD = 12.8 ± 1.6 × 5.4 ± 0.4 µm, L/W ratio = 2.4. *Appressoria* solitary or in short chains, medium brown, thick-walled, entire edge or crenate, rarely lobate, smooth-walled, irregular in shape, but often bullet-shaped or navicular with an acute tip, (4.5–)7–14(–18) × (4–)5–8(–11) µm, mean ± SD = 10.5 ± 3.3 × 6.4 ± 1.5 µm, L/W ratio = 1.6.

Anamorph developed on Anthriscus stem (CBS 123755). Conidiomata acervular, conidiophores and setae formed from a cushion of pale brown, roundish to angular cells, 3–9 µm diam. Setae rare, medium brown, basal cell often paler, verruculose, 1–2-septate, 30–70 µm long, base cylindrical, conical or slightly inflated, 3.5–6.5 µm diam, tip ± round to ± acute. Conidiophores pale brown, septate, branched or unbranched, to 40 µm long. Conidiogenous cells pale brown, cylindrical to ellipsoid, 5.8–17 × 3.5–6 µm, opening 0.5–1.5 µm diam, collarette ≤ 0.5 µm long, periclinal thickening visible to conspicuous. Conidia hyaline, smooth-walled, aseptate, straight, cylindrical to clavate, apex round, base round with a prominent hilum, sometimes with two big polar guttules, (9–)12–14.5(–16.5) × (4–)5–6.5 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).

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*, *Solanaeae* 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 ellipsoid, encased in a mucous sheath, sometimes extending to form new conidiogenous loci, 7–14 × 4.5–7.5 µm, opening 1–2 µm diam, collarette visible, ≤ 0.5 µm long, periclinal thickening visible, in strain CBS 128528 conidiogenous cells longer (12–25 µm) and periclinal thickening conspicuous. Conidia hyaline, smooth-walled, aseptate, cylindrical, the apex and base rounded, with a prominent scar, contents granular or guttulate, (11.5–)13–16(–18) × 5–5.5(–6) µm, mean ± SD = 14.6 ± 1.6 × 5.4 ± 0.2 µm, L/W ratio = 2.7, conidia of strain CBS 128528 longer, measuring (13.5–)14–19(–22.5) × (4.5–)5.5–(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 ellipsoid, sometimes extending to form new conidiogenous loci, 6–12 × 3.5–7.5 µm, opening 1–2 µm diam, collarette 1 µm long, periclinal thickening visible, in strain CBS
Fig. 4. Colletotrichum boninense. A–B. Conidiomata. C–D. Conidiophores. E–F. Setae. G. Tip of seta. H–J. Conidiophores. K–P. Appressoria. Q–R. Conidia. S–T. Ascomata. U. Paraphyses. V–W. Apical regions of asc. X–Y. Asci. Z. Ascospores. AC. Outer surface of peridium. A–R. from ex-holotype strain CBS 123755. S–AC. from strain CBS 123756. A, C–E, Q. from Anthriscus stem. B, F–P, R. from SNA. A–B, S. DM. C–R, T–AC. DIC. Scale bars: A, S = 100 µm, T = 25 µm, D, U = 10 µm. Scale bar of A applies to A–B. Scale bar of D applies to C–R. Scale bar of U applies to U–AC.
The Colletotrichum boninense species complex

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

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

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

Notes: There are four species in the C. boninense species complex known to occur on Passiflora: C. brasiliense from Brazil (on fruits), C. colombiense from Colombia (on leaves), C. torulosum from New Zealand (on leaves) and C. karstii from Japan and Colombia (on leaves) and from Brazil (on fruits). According to Johnston & Jones (1997), C. gloeosporioides Group E (= C. novae-zelandiae) and C. gloeosporioides Group I (= C. constrictum) have also been isolated from Passiflora, although this has not been confirmed by molecular methods. Colletotrichum brasiliense and C. colombiense are at this stage known only from Passiflora. Colletotrichum brasiliense is known only from Brazil where it causes anthracnose of yellow passion fruit (Passiflora edulis f. flavicarpa; Tozze et al. 2010). Colletotrichum brasiliense is closely related to C. parsonsiae and C. hippeastri. Colletotrichum brasiliense is distinguished from these species with most of the genes, including ITS, although the CHS-1 sequence of one isolate was the same as that of C. parsonsii. Appressoria have a lower LW 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 Sp., described from Passiflora sp. in Argentina, forms longer conidia (20–30 × 5–6 µm) than any of the species in the C. boninense species complex known from Passiflora (Spegazzini 1899). Conidia of C. passiflorae Siemaszko, which was described on leaves of Passiflora edulis in Transcaucasia (today belonging to Armenia, Azerbaijan, and Georgia) are smaller, measuring 14–25 × 4–6 µm (Siemaszko 1923). Most of the species treated here have shorter conidia. Only conidia of C. brasiliense isolate CBS...
128528 sometimes exceed 20 µm, but their average length is 16.5 µm and their L/W ratio is 3.3 rather than 3.5–4.25 as implied by Siemaszko’s measurements.

Colletotrichum passiflorae F. Stevens & P.A. Young (Stevens 1925), described on fruits of *P. lauifolia* 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. brassicicola* are numerous, 90–225 µ in diameter. Setae brown, 50–75 by 5 µm. Conidia tend to be inaequilateral.

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

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

Teleomorph developed on *Anthriscus* stem. Ascomata globose to subglobose, pale brown, 100–250 × 90–150µm, glabrous, ostiolate, neck hyaline to pale brown, outer wall composed of flattened angular cells 8–19.5 × 5.5–15.5 µm in size. Interscalar tissue composed of paraphyses; hyaline, septate, branched, 55–100 × 4–8 µm. Ascii cylindrical, 65–105 × 12–13.5 µm, 8-spored. Ascospores (only 7 observed) arranged biseriately, hyaline and aspate, fusiform, sometimes broader towards one side, sometimes curved, smooth, (15–)17.3–21(–24) × (3.5–)4.5–5.7(–8) µm, mean ± SD = 19.1 ± 1.8 × 4.8 ± 0.8 µm, L/W ratio = 4.0. On filter paper ascospores (16.5–)18–22.5(–23.5) × 4.5–5.5(–6.5) µm, mean ± SD = 20.3 ± 2.4 × 5.1± 0.5 µm, L/W ratio = 4.0.

Anamorph developed on SNA. Vegetative hyphae 1–5 µm diam, hyaline, smooth-walled, septate, branched. Chlamydospores not observed. *Conidiomata* poorly developed, conidiophores and setae formed directly on hyphae. Setae medium brown, verruculose, 1–3-septate, 30–70 µm long, base cylindrical, conical or slightly inflated, 4–6.5 µm diam at the widest part, tip round. *Conidiophores* pale brown, septate, unbranched or branched, to 30 µm long. *Conidiogenous cells* hyaline or pale brown, smooth to verruculose, clavate, cylindrical or doliiform, sometimes lacking a basal septum and continuous with the conidiophore, 7–14 × 4–5.5 µm, opening 1.5–2 µm diam, collarette 0.5–1(–1.5) µm long, periclinal thickening conspicuous. *Conidia* hyaline, smooth-walled, aseptate, straight, 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.

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.

Vassiljevski and Karakulin (1950) described *Colletotrichum brassicaceae* on Brassica as having slightly curved, fusoid conidia that are longer (19–24 µm) than those of *C. brassicicola*. *Colletotrichum brassicaceae* 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. Ascii and paraphyses. W. Apical region of an ascus. X. Paraphyses. Y. Outer surface of peridium. Z. Peridium in cross section. A, C–E, P, R–S, U–Z. from Anthriscus stem. B, F–O, Q. from SNA. T. from filter paper. A–B, R, DM, C–Q, T–Z. DIC. Scale bars: A, R = 100 µm, S = 50 µm, D = 10 µm. Scale bar of A applies to A–B. Scale bar of D applies to C–Q. Scale bar of T applies to T–Z.
An isolate on *Passiflora* sp. from Colombia (Pass-65, Afanador-Kafuri et al. 2003) has the same ITS sequence as *C. brassicicola*, and isolates from leaves of *Podocarpus totara* and *Prumnopitys ferruginea* in New Zealand (Joshee et al. 2009) differ by only two or three substitutions in ITS sequences. We cannot be sure whether these strains belong to *C. brassicicola* or to other segregates of the *C. boninense* group.

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

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

**Teleomorph** not observed, but on OA spherical structures on the agar surface and within the medium that lack any conidia or ascospores. **Anamorph on SNA. Vegetative hyphae** 1–6 µm diam, hyaline, smooth-walled, septate, branched. **Chlamydospores** not observed. **Conidiomata** absent, conidiophores formed directly from vegetative hyphae. **Setae** not observed. **Conidiophores** hyaline, smooth-walled, septate, branched, to 50 µm long. **Conidiogenous cells** hyaline, smooth-walled, cylindrical, sometimes slightly inflated, surrounded by several mucous layers, often extending to form new conidiogenous loci, opening 1–1.5 µm diam, collarette < 0.5 µm long, pericentral thickening observed. **Conidia** hyaline, smooth-walled, aseptate, cylindrical, the apex and base rounded, with a prominent scar, contents granular or guttulate, often with two big guttules (11.5–)12–14(--15.5) × (4.5–) 5–6(--6.5) µm, mean ± SD = 13.1 ± 1.0 × 5.7 ± 0.4 µm, L/W ratio = 2.3. Appressoria single, medium to dark brown, roundish to elliptical in outline, the margin undulate to lobate, (5.5–)6–10(--12.5) × (3.5–)4.5–7.5(--10) µm, mean ± SD = 7.8 ± 2.0 × 6.0 ± 1.5 µm, L/W ratio = 1.3, appressoria of strain CBS 129817 larger, (7–) 7.5–14.5(--21.5) × (5–)6–10(--12.5) µm, mean ± SD = 11.0 ± 3.5 × 8.1 ± 1.9 µm, L/W ratio = 1.3.

**Anamorph on Anthriscus stem. Conidiomata** acervular, conidiophores and setae formed on a cushion of pale brown, angular cells, 3–8 µm diam. **Setae** medium brown, verruculose, 1–3-septate, 35–110 µm long, base cylindrical to strongly inflated, 3.5–8.5 µm diam, tip rounded. **Conidiophores** hyaline, smooth-walled, septate, branched, to 40 µm long. **Conidiogenous cells** hyaline, smooth-walled, cylindrical, sometimes surrounded by a gelatinous sheath, sometimes extending to form new conidiogenous loci, 7–26 × 3–5.5 µm, opening 1–1.5 µm diam, collarette < 0.5 µm long, pericentral thickening observed. **Conidia** hyaline, smooth-walled, aseptate, cylindrical, the apex and base rounded, with a prominent scar, contents granular or guttulate, (11–)12–14(--15) × (5–)5.5–6 µm, mean ± SD = 13.1 ± 1.1 × 5.7 ± 0.3 µm, L/W ratio = 2.3.

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

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**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–Q. Appressoria. P–Q. Conidia. A, C–G, P. from Anthriscus stem. B, H–K, Q. from SNA. A–B. DM, C–Q. DIC, Scale bars: A = 100 µm, E = 10 µm. Scale bar of A applies to A–B. Scale bar of E applies to C–Q.
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, Tiacabuy, from a leaf of Passiflora edulis, 22 Jan. 2010, D. Riascos, CBS H-20699 holotype, culture ex-type CBS 129818 = G2; Cundinamarca, Tiacabuy, 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. beeeri and C. brassicicola. It differs from C. beeeri in morphology by setae that are verrucose and rounded, and shorter conidiogenous cells. Other species isolated from Passiflora have pigmented conidiogenous cells (C. brassicicola and C. karstii on the media used here) or much more complex appressoria (C. torulosum). See under C. brassicicola 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 Dam, 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, smooth-walled, 6–10 µm thick, solitary, non-stromatic, ovoid to obpyriform, ostiolate, glabrous, smooth-walled, septate, branched.

Ascogenous hyphae

Chlamydospores conidiogenous loci, 8–20 × 3–7.5 µm, opening 1–2 µm diam, walled, cylindrical to ampulliform, often extending to form new conidiogenous loci, 7–15 × 3.5–7.5 µm, 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 × 3.5–7.5 µm, opening 1–2 µm diam, collarette < 0.5 µm long, periclinal thickening distinct. Conidia hyaline, smooth-walled, aseptate, straight, cylindrical, ampulliform, often extending to form new conidiogenous loci, 7–15 × 3.5–7.5 µm, tip acute.

Conidiomata 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. Ascii uniseriate, 8-spored, cylindrical to clavate, tapering to apex and base, 50–95 × 15–20 µm, the base broadly truncate. Ascospores biseriately arranged, aseptate, hyaline, smooth-walled, 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, verrucose, 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 × 3.5–7.5 µm, opening 1–2 µm diam, collarette < 0.5 µm long, periclinal thickening distinct. Conidial hyaline, smooth-walled, aseptate, straight, cylindrical, ampulliform, often extending to form new conidiogenous loci, 10–15 × 3.5–7.5 µm, mean ± SD = 13.3 ± 1.5 × 6.5 ± 1.1 µm, L/W ratio = 2.3.

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, with short white aerial mycelium; reverse buff, vinaceous buff to brown, yellowish brown, partly rosy buff, grey to black, covert with white mycelium; reverse 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). Colonies on OA flat with entire margin, 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 × 3.5–7.5 µm, opening 1–2 µm diam, collarette < 0.5 µm long, periclinal thickening distinct. Conidia hyaline, smooth-walled, aseptate, straight, cylindrical, ampulliform, often extending to form new conidiogenous loci, 10–15 × 3.5–7.5 µm, mean ± SD = 13.3 ± 1.5 × 6.5 ± 1.1 µm, L/W ratio = 2.3.

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

Colletotrichum constrictum was previously referred to as C. gloeosporioides group I by Johnston & Jones (1997) and is only known from New Zealand. Isolates studied here are from Citrus sp. and Solanum betaceum. According to Johnston & Jones (1997), the species also occurs on Passiflora edulis and P. mollissima, although this has not been confirmed by molecular methods.
Fig. 8. Colletotrichum constrictum (from ex-holotype strain CBS 128504). A–B. Conidiomata. C. Tip of seta. D. Basis of seta. E–F. Conidiophores. G. Tip of seta. H. Basis of seta. I–J. Conidiophores. K–P. Appressoria. Q–R. Conidia. S–T. Ascomata. U. Outer surface of peridium. V. Peridium in cross section. W. Ascospores. X–AA. Asci. AB–AC. Apical regions of asci. AD. Paraphyses. A, C–F, Q, S, Z–AC. from Anthriscus stem. B, G–P, R, T–Y, AD. from SNA. A–B, S–T. DM, C–R, U–AD. DIC. Scale bars: A = 200 µm, B, S = 100 µm, E, U = 10 µm. Scale bar of E applies to C–R. Scale bar of S applies to S–T. Scale bar of U applies to U–AD.
**Colletotrichum cymbidiicola** Damm, P.F. Cannon, Crous, P.R. Johnst. & B. Weir, *sp. nov*. MycoBank MB560740. Fig. 9.

**Etyymology:** 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, subphotospherical to ovoid, ostiolate, glabrous, medium brown, 130–160 × 170–220 µm. **Peridium** 10–12 µm thick, composed of pale to medium brown flattened angular cells 3.5–15 µm diam. **Ascogenous hyphae** hyaline, smooth-walled, delicate, rarely visible. **Interascal tissue** not observed. **Asci** unitunicate, 8-spored, cylindrical, tapering to apex and base, smooth-walled, 40–48 × 9.5–11 µm, the base truncate, apex 3.5–4 µm wide. **Ascospores** biseriately arranged, aspeseate, hyaline, smooth-walled, fusiform, slightly curved, base rounded, apex acute or rounded, (12.5–)15–18.5(–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. **Ascospores** biseriately arranged, aspeseate, 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. **Conidiophores** medium brown, verruculose, 1–4-septate, 50–150 µm long, base cylindrical to conical, 5–7 µm diam, tip ± acute to rounded, often also with a constriction. **Conidiophores** hyaline, smooth-walled, septate, branched, to 50 µm long. **Conidiogenous cells** hyaline, smooth-walled, cylindrical, often extending to form new conidiogenous loci, 7.5–17 × 3–5.5 µm, opening 1–2 µm diam, collarette ≤ 0.5 µm diam, periclinal thickening conspicuous. **Conidia** hyaline, smooth-walled, aspeseate, 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-feltly white aerial mycelium, **Anthriscus** stem and filter paper partly covered with grey to black conidiodmata partly oozing salmon to orange conidia; reverse hyaline to honey, filter paper with grey to black spots due to conidiodmata 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 conidiodmata, 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 IMI 347923). New Zealand, AK, Mangere, from leaf spot of *Cymbidium sp.*, 22 Mar. 1990, P. Broadhurst. **Cultures** CBS 128543 = ICMP 18584.

**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.

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

**Teleomorph not observed.**

**On SNA. Vegetative hyphae 1–6 µm diam, hyaline, smooth-walled, septate, branched. Chlamydospores** not observed. **Conidiomata** globose to flask-shaped, apparently opening by rupture, wall cells medium brown, angular; conidiophores formed from a cushion of medium brown, angular cells 3–7.5 µm diam. **Setae** not observed. **Conidiophores** hyaline, smooth-walled, septate, branched, to 60 µm long. **Conidiogenous cells** hyaline, smooth-walled, cylindrical to ampulliform, sometimes extending to form new conidiogenous loci, sometimes annelides observed, 11–28 × 2.5–4.5 µm, the opening 2–3 µm diam, collarette ≤ 0.5 µm, periclinal thickening distinct. **Conidia** hyaline, smooth-walled, aspeseate, 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–F, Q, U, X–AA. from Anthriscus stem. B, G–P, R, T–W, AB. from SNA. S. from filter paper. A–B, S. DM, C–R, T–AB. DIC. Scale bars: A, S = 100 µm, W = 50 µm, E, T = 10 µm. Scale bar of A applies to A–B. Scale bar of E applies to C–R. Scale bar of T applies to T–V and X–AB.
**The Colletotrichum boninense species complex**

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

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

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

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

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

Teleomorph not observed. On SNA. Vegetative hyphae 1–6 µm diam, hyaline to pale brown, usually smooth-walled, sometimes warted, septate, branched. Chlamydospores not observed. Conidiomata absent, conidiophores and setae formed directly on hyphae. Setae medium brown, verruculose, 2–7-septate, 70–200 µm long, the base cylindrical or inflated, 4–7 µm diam, the tip rounded. Conidiophores pale to medium brown, septate,
branched, to 50 µm long. Conidiogenous cells pale brown, hyaline towards the tip, smooth or verruculose, cylindrical, the upper part surrounded by a gelatinous sheath of several layers, 13–27.5 × 4–6.5 µm, the opening 1.5–2.5 µm diam, collarette and periclinal thickening not visible. Conidia hyaline, smooth-walled, aseptate, straight, cylindrical, the apex and base rounded, cytoplasm appearing granular, (14.5–)18.5–30(–39) × (5–)6–8(–9) µm, mean ± SD = 24.2 ± 5.8 × 6.9 ± 0.9 µm, L/W ratio = 3.5.

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

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

Material examined: China, Guizhou Province, Guiyang, isolated from leaf of Hippeastrum vittatum, 23 May 2009, Y.L. Yang, culture ex-holotype CBS 125376 = CSSG1. Netherlands, isolated from leaf of Hippeastrum sp., deposited in CBS from Plantenziektenkundige Dienst Wageningen in May 1978, culture CBS 241.76 = IMI 304052.

Notes: Colletotrichum hippeastri is an outlying species in the C. boninense clade and is distinguished from related species by its large conidia as well as elongate and complex appressoria. A feature that is common with others of the complex is conidiogenous cells that are covered in a gelatinous sheath (not mentioned in the original description by Yang et al. 2009). Phylogenetically
informative sequence differences were not detected in the strains studied, and the species forms a distinct cluster within all single-gene phylogenies.

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

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

Teleomorph on SNA. Ascomata perithecia, formed after 4 wk, solitary, superficial or immersed in the agar medium, non-stromatic, globose to obpyriform, ostiolate, periphytose, 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. *Ascospora* hyaline, smooth, delicate, rarely visible. *Interascal tissue* formed of paraphyses, hyaline, smooth-walled, mostly cylindrical but tapering towards the round tip, disintegrating rapidly, septate, constricted at the septa, apically free, 30–50 × 4.5–7 µm. Ascii 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. *Conidiophores* uni- or biseriately arranged, initially aseptate but often septate with age, hyaline, smooth-walled, variable in shape, fusiform to ovoid, slightly curved, (11.5–)13–16.5(--18.5) × (4–)4.5–5.5(--6.5) µm, mean ± SD = 14.7 ± 1.8 × 5.0 ± 0.7 µm, L/W ratio = 2.9. *Conidia* of ascoспорate CBS 128550 larger, measuring (14.5–)16–18–(18.5) × (3.5–)4.5–6–(6.5) µm.

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

**Anamorph on SNA.** Vegetative *hyphae* 1–5 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydosporae* not observed. *Conidiomata* absent, the conidiophores formed directly from vegetative hyphae. CBS 128333 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. *Conidigenous cells* hyaline or pale brown, smooth, cylindrical to elongate-ampulliform, sometimes extending to form new conidigenous loci, 9–20 × 3–5 µm, opening 1–1.5 µm diam, collarette < 0.5 µm diam, periclinal thickening conspicuous. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical, the apex and base rounded, with a prominent hilum ca. 1 µm diam, < 0.3 µm long, the contents appearing granular, (11.5–)12.5–14–(14.5) × (5–)5.5–6–(6.5) µm, mean ± SD = 13.1 ± 0.7 × 5.8 ± 0.4 µm, L/W ratio = 2.2, conidia of CBS 111998 sometimes longer (up to 18.5 µm, L/W ratio = 2.8). *Appressoria* single or in small groups of 2–3, pale to medium brown, often navicular to bullet-shaped, not nodose, smooth-walled to undulate, (4.5–)6–12–(16.5) × (2.5–)4–7–(10) µm, mean ± SD = 8.9 ± 2.9 × 5.4 ± 1.5 µm, L/W ratio = 1.7, appressoria of CBS 129833 larger, measuring (5.5–)7.5–13–17) × (4.5–)5.5–8–(10.5) µm, mean ± SD = 10.3 ± 2.6 × 7.1 ± 1.5 µm, L/W ratio = 1.4.

**Anamorph on Anthriscus stem.** *Conidiotrema* acervular, conidiophores and setae formed from a cushion of pale brown, angular cells, 3–10 µm diam. *Setae* rare, medium to dark brown, verruculose, 2–3-septate, 80–120 µm long, base conical to slightly inflated, 4.5–5.5 µm diam, tip rounded, setae of isolate CBS 128550 more frequent, pale to medium brown, 2–7–septate, 60–160 µm long, base cylindrical-conical to slightly inflated, 4–7 µm diam, tip acute. *Conidiophores* hyaline to pale brown, aseptate or septate, branched, to 80 µm long. *Conidiogenous cells* hyaline to pale brown, smooth-walled, cylindrical to ampulliform, sometimes extending to form new conidigenous loci, 4.5–15 × 3–6 µm, opening 1–2 µm diam, collarette < 0.5 µm long, periclinal thickening conspicuous. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical, apex round, base round with a prominent hilum, the contents appearing granular, (12–)13–15–(16.5) × 5.5–(6–6.5) µm, mean ± SD = 14.0 ± 1.1 × 5.7 ± 0.3 µm, L/W ratio = 2.4, conidia of CBS 11998 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 conidiotroma 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 conidiotroma, lacking aerial mycelium; reverse buff, rosy buff to honey, 23.0–28.5 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 conidiotroma scattered over the surface, reverse colourless to pale orange with numerous dark flecks corresponding to the ascomata. *Conidia* in mass orange.

Material examined. **Australia.** QLD, Palmwoods, latitude 26° 41′ S, longitude 152° 57′ E, from calyx necrosis of *Diospyros* australis, 1 May 2002, H. Drew, CBS H-20712, culture CBS 127597 = BRRP 29055c (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 128333; Cooitepec Harinas, from fruit *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 *Perea 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 (Morkawi 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 karatii (from strain CBS 127597). A–B. Conidiomata. C. Tip of seta. D. Basis of seta. E–I. Conidiophores. J–N. Appressoria. O–P. Conidia. Q–R. Ascomata. S. Outer surface of peridium. T. Peridium in cross section. U. Ascospores. V–X. Asci. Y. Paraphyses. A, C–F, O. from Anthriscus stem. B, G–N, P–Y. from SNA. A–B, Q. DM, C–P, R–Y. DIC. Scale bars: A = 200 µm, B, Q = 100 µm, R = 50 µm, E, S = 10 µm. Scale bar of E applies to C–P. Scale bar of S applies to S–Y.
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 2009), Maytenus ilicifolia from Brazil (Pileggi et al. 2009) and Passiflora sp. in Florida, U.S.A. (Tarnowski & Ploetz 2010) are identical or similar to those of C. karstii (and C. phyllanthi).

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

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

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

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

**Teleomorph** not observed. **Anamorph** on SNA. **Vegetative hyphae** 1.5–10 µm diam, hyaline, smooth-walled, septate, branched. **Chlamydospores** not observed. Conidiomata absent, conidiophores formed directly from vegetative hyphae or from angular to roundish, hyaline, thick-walled cells, 3–8 µm diam. Setae not observed. Conidiophores hyaline, smooth-walled, septate, branched, to 50 µm long. Conidiogenous cells hyaline, smooth-walled, cylindrical to more or less inflated, often extending to form new conidiogenous loci, making the conidiogenous cell appear catenate, sometimes polysiphidic, 4.5–20 × 4–6 µm, opening 1.5–2 µm diam, collarette
to 1 µm diam, periclinal thickening conspicuous. Conidia hyaline, smooth-walled, aseptate, cylindrical, the apex and base rounded, with a prominent scar, contents granular or guttulate, (12.5–14.5) × 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, 3.5–5–5.5 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 × 5.7–7.5 µm, mean ± SD = 10.2 ± 2.0 × 6.7 ± 0.9 µm, L/W ratio = 1.5.

Anamorph on Anthriscus stem. Conidionatum acervulatum, 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. Conidigenous cells pale brown, smooth-walled, (broadly) cylindrical, often extending to form new conidigenous 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, 24–27.5 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 annum (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 130240).

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. phylanthi. 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 “Gломерела 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. nova-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. Chlamydoospores 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, setae, branched, to 75 µm long. Conidigenous cells hyaline, smooth-walled, cylindrical, often extending to form new conidigenous 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–)5–10–(13) µm, mean ± SD = 12.2 ± 3.8 × 7.8 ± 2.2 µm, L/W ratio = 1.6.

Anamorph on Anthriscus stem. Conidionatum acervulatum, 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. Conidigenous 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 oливaceous 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 oливaceous grey aerial mycelium; reverse buff, honey, cinnamon, oливaceous gey to iron grey, 30–31.5 mm in 7 d (39–40 mm in 10 d). Conidia in mass salmon to orange.

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

Notes: Colletotrichum oncidii forms a sister group to C. cymbidiicola, also orchid pathogens but recorded from the Asia-Pacific region.
rather than Europe. The known isolates of *C. oncidii* were from
plants in greenhouses, and the ultimate origin of the species is
uncertain. It has well-developed strongly setose conidiomata in
culture, pale conidia and conidiogenous cells that extend to form
new conidiogenous loci.

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

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

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

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

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

*Anamorph* on *Anthriscus* stem. *Conidiomata* acervular,
conidiophores and setae formed from a cushion of pale brown,
Fig. 15. Colletotrichum parsonsiae (from ex-holotype strain CBS 128525). A–B. Conidiomata. C. Setae. D–J. Conidiophores. F. Tip of seta. G. Basis of seta. H–J. Conidiophores. K–N. Appressoria. O–Q. Conidia. R. Ascomata. S–T. Apical region of ascus. U. Ascospores. V–X. Asci. Y. Paraphyses. A, C–E, O, Q. from Anthriscus stem. B, F–N, P, R–Y. from SNA. A–B, Q. DM, C–P, R–Y. DIC. Scale bars: A, Q = 100 µm, D, R = 10 µm, K = 25 µm. Scale bar of A applies to A–B. Scale bar of D applies to C–J and O–P. Scale bar of K applies to K–N. Scale bar of R applies to R–Y.
angular, thick-walled cells, 4–10.5 µm diam. 

**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 24 mm in 7 d (32.5–34 mm in 10 d). Colonies on OA flat with entire to slightly undulate margin; surface hyaline with woolly white aerial mycelium on 20–25 mm in 7 d (33–35.5 mm in 10 d). **Conidia** in mass salmon to orange.

**Material examined:** New Zealand, Auckland, leaf endophyte from *Parsonsia capsularis*, 1 Dec. 2008, G. Carroll, (CBS H-20710 holotype, culture ex-type CBS 128925 = 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 all of those other species. The conidal width is the same or less, resulting in comparatively high L/W ratios, especially on **Anthriscus** stem (L/W ratio = 3.7).

**Colletotrichum petchii** Damm, P.F. Cannon & Crous, nov. nom. 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. Interscalar tissue composed of paraphyses; hyaline, septate, apparently unbranched, the basal cells strongly inflated, 45–50 × 13–15.5 µm. Ascii clavate, the apex ± truncate with a well-developed refractive apical ring, 45–85 × 12–15.5 µm, 8-spored. Ascospores arranged biseriately, hyaline to pale brown, asceptate, 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 × 6.7 ± 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. **Conidia** 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. Conidiomata pale brown, septate, branched, surrounded by a slime 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 conidiomata loci, 11–16 × 3.5–5 µm, opening 1–1.5 µm diam, collar and periclinal thickening inconspicuous. **Conidia** hyaline, smooth-walled, asceptate, straight, cylindrical, 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 = 2.7. Appressoria irregular in shape, dark brown, sometimes nodose, not formed in chains, (4.5–)8–15.5–(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 3–10 µm diam. **Conidia** 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. Conidiomata 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, collarate ≤ 0.5–1 µm long, periclinal thickening conspicuous. **Conidia** hyaline, smooth-walled, asceptate, 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, (12.3–)14.5–18–(21.1) × (5–)6.5–6.5 µm, mean ± SD = 16.1 ± 8.6 × 6.3 ± 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(KM) 125641. *holotype* of *C. dracaenae* Petch, 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 aleitifolium* (syn. *D. latifolia*), Apr. 1895, J.E. Weiss, M-0090064, *holotype* of *C. dracaenae* Allescher.

**Notes:** Conidia of *C. petchii* are larger than those of *C. boninense* and *C. brassicicola*. Conidia, ascospores and asc are usually
Fig. 16. Colletotrichum petchii (from ex-epitype strain CBS 378.94). A–B. Conidiomata. C. Tip of seta. D. Basis of seta. E–F. Conidiophores. G. Seta. H–J. Conidiophores. K–P. Appressoria. Q–R. Conidia. S. Ascomata. T. Outer surface of peridium. U. Paraphysis. V. Ascospores. W–Y. Asci. A, C–F, Q, S–T, V, Y. from Anthriscus stem. B, G–P, R, U, W–X. from SNA. A–B, S. DM, C–R, T–Y. DIC, Scale bars: A, S = 100 µm, E, T = 10 µm. Scale bar of A applies to A–B. Scale bar of E applies to C–R. Scale bar of T applies to T–Y.
also larger than those of \textit{C. karstii} and \textit{C. phylanthi}. Conidia of \textit{C. hippeastr}i are larger, while \textit{C. dracaenophilum} occurs on \textit{Dracaena} spp. as well, and is not closely related to \textit{C. petchii} as demonstrated by Farr et al. (2006). Their study included CBS 118193 and CBS 118774 (\textit{C. petchii}). Another species from \textit{Dracaena}, \textit{C. dracaenae-fragrantis}, has narrower conidia, measuring 5–12 × 2.5–3.5 µm (Saccardo 1899); its affinities are unclear.

\textit{Colletotrichum dracaenicola} (syn. \textit{C. dracaenae} Trinchieri 1909, non Allesch.) may be a synonym of \textit{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 \textit{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 \textit{C. dracaenae} Allesch. and \textit{C. dracaenae} Petch to be synonyms of \textit{C. gloeosporioides}. Farr et al. (2006) agreed with this conclusion concerning \textit{C. dracaenae} Allesch. after studying type material, although their focus was on the need to demonstrate distinctions between \textit{C. dracaenae} and their new species \textit{C. dracaenophilum}. The shape of the conidia of \textit{C. dracaenae} is similar to \textit{C. gloeosporioides}, including the overall length and the constriction in the central part. The conidia were found to be noticeably wider in \textit{C. dracaenae} compared with “typical” \textit{C. gloeosporioides}.

The original description (Allescher 1902) of the conidia of \textit{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–)13.5–15 × 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 \textit{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 \textit{C. petchii} (a diagnostic feature of the \textit{C. boninense} aggregate) we have chosen not to use Allescher’s name.

Part of the type of \textit{C. dracaenae} Petch was examined by Farr et al. (2006), who noted that the fruit bodies had a very thin subhypothecial 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 \textit{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 \textit{C. boninense} aggregate, and it is not unreasonable to suppose that it is synonymous with \textit{C. dracaenae} Allesch. Petch (1925) contrasted his species with \textit{C. cordylines} Pollacci but was evidently unaware of Allescher’s work.

In contrast to other species in the \textit{C. boninense} complex, \textit{C. dracaenae} may be host-specific to \textit{Dracaena}. The majority of \textit{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. \textit{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.

\textit{Colletotrichum phylanthi} (H. Sundrendranath Pai) Damm, P.F. Cannon & Crous, \textit{comb. nov.} MycoBank MB560746. \textit{Basionym: Glomerella phylanthi} H. Sundrendranath Pai, Mycopath. Mycol. appl. 42: 70. 1970.

\textbf{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). \textit{Anamorph and teleomorphic structures} not observed in the culture available.

\textbf{Material examined:} India, Maharashtra, Poona, from leaf anthracnose on \textit{Phyllanthus acidus}, 10 Feb. 1966, H. Sundrendranath Pai, IMI 122626, \textit{holotype:} Maharashtra, Poona, isolated from anthracnose symptoms on leaves of \textit{Phyllanthus acidus}, 10 Feb. 1966, H. Sundrendranath Pai, CBS H-7188, \textit{isotype, dried culture} (POA) of ascigerous stage, culture ex-isotype CBS 175.67 = MACS 271.

\textbf{Notes:} \textit{Glomerella phylanthi} is known only from the original collection taken from leaves of \textit{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, ooctosporous, arising in basal layers, sessile to sub sessile, 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 \textit{G. phylanthi} was the teleomorph of \textit{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 \textit{Glomerella phylanthi} are narrower than the other species within the \textit{C. boninense} complex and none formed ascomata with a long beak as reported from \textit{G. phylanthi}, though it must be recognised that culture medium and growth conditions were not the same. According to the multigene phylogeny, \textit{G. phylanthi} forms a separate lineage close to \textit{C. karstii}. This was the situation also in 5 of 7 single-gene phylogenies.

\textit{Glomerella phylanthi} causes an anthracnose disease on leaves of \textit{Phyllanthus acidus} in India (Pai 1966) but has not been reported since. Farr & Rossman (2011) list \textit{C. gloeosporioides} from \textit{Phyllanthus emblica} in China (Zhuang 2001) and \textit{P. reticulatus} in Myanmar (Thaung 2008) as well as an unidentified \textit{Colletotrichum} sp. from \textit{P. acidus} in India (Mathur 1979), of which at least the latter could be identical with \textit{G. phylanthi}.
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 × 7.5–8 µm by Petch (1906), wrongly cited by Pai (1970) as 18–24 × 5–8 µm.

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

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

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

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

**Anamorph on SNA**: Vegetative hyphae 1–7.5 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. Conidiomata absent and conidiophores and setae formed directly from hyphae. *Setae* medium brown, basal cell paler, verruculose, 2–5-septate, 65–120 µm long, sometimes branched, base cylindrical, 3.5–5.5 µm diam, tip ± acute to ±rounded. Conidiophores hyaline, smooth-walled, septate, branched, to 75 µm long. Conidiogenous cells hyaline, smooth-walled, cylindrical, 8–23 × 3.5–5.5 µm, opening 1–2 µm diam, collarette ≤ 0.5 µm diam, periclinal thickening conspicuous. Conidia hyaline, smooth-walled, aseptate, cylindrical, the apex and base rounded, with a prominent scar and an apparently verrucose vesicle attached to...
it, contents granular, (13–)14–17(–21) × 5.5–6.5(–7.5) µm, mean ± SD = 15.5 ± 1.5 × 6.0 ± 0.4 µm, L/W ratio = 2.6, conidial size 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. Appressorium 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, verrucose, 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.

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

Colletotrichum torulosum is known from two New Zealand collections, on Solanum and Passiflora. Endophytic strains from Dacrycarpus dacyrioides (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. dacyrcarp 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. nova-zelandiae and C. oncidi. Additionally, several species had an apparent gelatinous multi-layered coating around the conidiogenous cells.

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

Species of the C. boninense complex appear to be concentrated in certain regions of the world, and prefer certain host plants. Isolates treated in this paper and found by nucleotide blastn searches of GenBank originate mainly from New Zealand/Australia, South and East Asia (Japan, China, Taiwan, Thailand, Vietnam, India), South and Central America (Columbia, Brazil, Panama, Mexico, Guyana) and South and East Africa (South Africa, Zimbabwe, Kenya). A number of isolates from Europe (Italy, Netherlands, Germany and probably Hungary) have been associated with indoor/greenhouse plants (Dracaena, Hippeastrum and Gossypium species and several orchids) or air from greenhouses with orchids (Magyar et al. 2011). A few samples from Coffee arabica and Leucospemum 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 Glomerella C. boninense complex are host-specific, but the monocot clade contained isolates from different tree species in the same area, they also did not need more research, as some endophytes may be needs more research, as some endophytes may be

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 complexes can undergo meiosis, including the C. acutatum group (Guerber & Correll 2001, Guerber et al. 2003, Marcelino et al. 2008), the C. destructivum group (Armstrong-Ch & 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 Jokwok Forest Reserve in Guyana by means of ISSR-PCR, RADP 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 plant-parasite relations of the fungi belonging to this clade.

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

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REFERENCES

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

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

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

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

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

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

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

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

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

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

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

Crous PW, Groenewald JZ, Risse JD, Hywel-Jones NL (2004b). Calonectria species and their Cylindrocladium anamorphs: species with sphaeropedunculate vesicles. Studies in Mycology 50: 415–430.
Crous PW, Verkleij GMJ, Groenewald JZ, Samson RA (eds) (2009). Fungal Biodiversity. CBS Laboratory Manual Series 1. Centraalbureau voor Schimmelcultures, Utrecht, Netherlands.

Damm U, Crous PW, Fourie PH (2007). Botryosphaeriaceae as potential pathogens of Prunus species in South Africa, with descriptions of Diplocyclos africana and Lasiobotryosphaeria sp. nov. Mycologia 99: 684–680.

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

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

Damm U, Cannon PF, Woudenberg JHC, Crous PW (2012). The Colletotrichum acutatum species complex. Studies in Mycology 73: 57–113.

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

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

Di Lenna P, Montecchi L (1995). Gravi danni da antracnosis (Colletotrichum gloeosporioides) su cultore di Dracaena deremensis in serra. Informator Fitopatologico 4: 24–26.

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

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

Gazis R, Rahman M, Chavener P (2011). Species delimitation in fungal endophyte diversity studies and its implications in ecological and biogeographic inferences. Molecular Ecology 20: 3001–3013.

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

Guerber JC, Correll JC (2001). Characterization of Colletotrichum acutatum, the teleomorph of Colletotrichum acutatum. Mycologia 93: 215–229.

Guerber JC, Correll JC (2001). Characterization of Colletotrichum acutatum, the teleomorph of Colletotrichum acutatum. Mycologia 93: 215–229.

Jeune JC (1993). Relationships among Colletotrichum isolates from fruit-rotting pathogens assessed using rDNA sequences. Mycologia 85: 872–895.

Hillis DM, Bull JJ (1993). An empirical test of bootstrapping as a method for assessing phylogenetic confidence. Systematic Biology 42: 162–192.

Hoog GS de, Gerrits van den Ende AHG (1998). Molecular dissection of plant-fungal interactions. Fungal Microbiology Interactions 17: 272–282.

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

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

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

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

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

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

Pileggi SA, Vieira de Oliveira SF, Andrade CW, Vicente VA, Dalzoto Pde R, et al. (2008). Molecular and morphological markers for rapid distinction between two Colletotrichum species. Canadian Journal of Microbiology 55: 1076–1088.

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

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

Rodriguez-Guerra R, Ramirez-Rueda MT, Cabral-Enciso M, Garcia-Serrano M, Lira-Maldonado Z, et al. (2005). Heterothallic mating observed between Colletotrichum acutatum var. nov.) and Colletotrichum acutatum. Mycologia 97: 313–328.

Saccardo PA, Trotter A (1913). A Mycological Colour Chart. Schimmelcultures, Utrecht, Netherlands.

Saccardo PA (1895). Mycological Research. Botanical Research Institute of Formosa. 35: 1–10.

Saccardo PA (1895). Mycological Research. Botanical Research Institute of Formosa. 35: 1–10.

Saccardo PA (1895). Mycological Research. Botanical Research Institute of Formosa. 35: 1–10.

Saccardo PA (1895). Mycological Research. Botanical Research Institute of Formosa. 35: 1–10.

Saccardo PA (1895). Mycological Research. Botanical Research Institute of Formosa. 35: 1–10.

Saccardo PA (1895). Mycological Research. Botanical Research Institute of Formosa. 35: 1–10.

Saccardo PA (1895). Mycological Research. Botanical Research Institute of Formosa. 35: 1–10.

Saccardo PA (1895). Mycological Research. Botanical Research Institute of Formosa. 35: 1–10.

Saccardo PA (1895). Mycological Research. Botanical Research Institute of Formosa. 35: 1–10.

Saccardo PA (1895). Mycological Research. Botanical Research Institute of Formosa. 35: 1–10.

Saccardo PA (1895). Mycological Research. Botanical Research Institute of Formosa. 35: 1–10.

Saccardo PA (1895). Mycological Research. Botanical Research Institute of Formosa. 35: 1–10.
Sutton BC (1980). *The Coelomycetes: Fungi Imperfecti with Pycnidia, Acervuli and Stromata*. Commonwealth Mycological Institute, Kew, UK.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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