

# The *Colletotrichum acutatum* species complex

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

**Key words:** anthracnose, Ascomycota, *Colletotrichum acutatum*, *Gloeosporium*, *Glomerella*, phylogeny, systematics.

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

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## INTRODUCTION

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

On strawberry, *C. acutatum* mainly causes black spot of fruit but can also attack crowns, roots and leaves (Freeman & Katan 1997), and is one of the most serious diseases in commercial fruit production. Largely due to its economic importance as a strawberry

pathogen, *C. acutatum* was treated for many years as a regulated plant quarantine pest by the European and Mediterranean Plant Protection Organization (EPPO), though it is absent from the current list (EPPO 2011) – presumably due to its now widespread distribution in Europe. Inoculum sources are frequently transplant material, mostly with quiescent infections (Rahman & Louws 2008), infected plants, weeds and other hosts (McInnes *et al.* 1992, Parikka *et al.* 2006), while the survival rate of conidia in natural field soil is low (Freeman *et al.* 2002).

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

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

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

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

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

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

## MATERIALS AND METHODS

### Isolates

A total of 331 strains have been studied, mostly previously identified as *C. acutatum*, as well as other related strains from the CBS, IMI and other culture collections. Type material (holotypes and epitypes) of the species studied are located in the Herbarium of the Centraalbureau voor Schimmelcultures (CBS), Utrecht, The Netherlands, in the IMI Fungarium, which is based in the Royal Botanic Gardens, Kew (IMI and K(M)), UK, US National Fungus Collections (BPI), Beltsville, Maryland, USA, the Botanic Garden and Botanical Museum Berlin-Dahlem, Freie Universität Berlin (B), Germany and in the dried collection of the Botanische Staatssammlung München (M), Germany. All descriptions are based on the ex-type, ex-epitype or ex-neotype culture as appropriate. Features of other strains are added if deviant. Subcultures of the types, epitypes and neotypes, respectively, as well as all other isolates used for morphological and sequence analyses are maintained in the culture collections of CBS and IMI (Table 1).

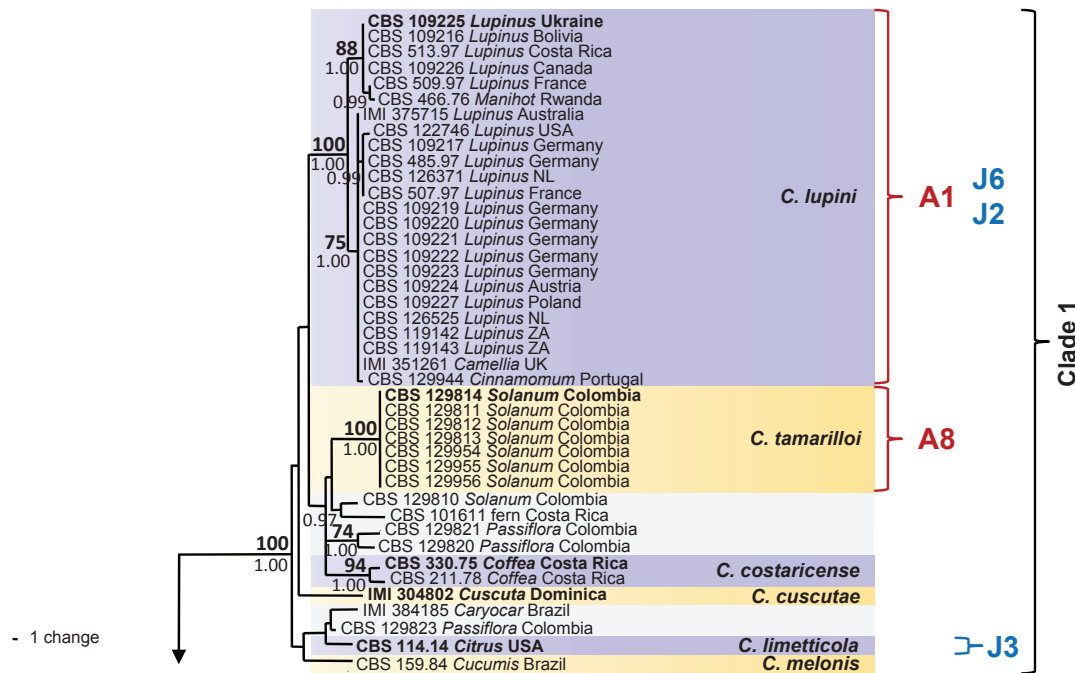
### Morphological analysis

To enhance sporulation, autoclaved filter paper and double-autoclaved stems of *Anthriscus sylvestris* were placed onto the surface of synthetic nutrient-poor agar medium (SNA; Nirenberg 1976). SNA and oatmeal agar (OA; Crous *et al.* 2009) cultures were incubated at 20 °C under near UV light with 12 h photoperiod for 10 d. Measurements and photographs of characteristic structures were made according to Damm *et al.* (2007). Appressoria on hyphae were observed on the reverse side of SNA plates. Microscopic preparations were made in clear lactic acid, with 30 measurements per structure and observed with a Nikon SMZ1000 dissecting microscope (DM) or with a Nikon Eclipse 80i microscope using differential interference contrast (DIC) illumination. In the *C. acutatum* species complex, conidia are usually formed in acervular conidiomata and additionally in the aerial mycelium. Unless mentioned otherwise, only conidia from conidiomata were used in this study for morphological examination.

Colony characters and pigment production on SNA and OA cultures incubated at 20 °C under near UV light with 12 h photoperiod were noted after 10 d. Colony colours were rated according to Rayner (1970). Growth rates were measured after 7 and 10 d.

### Phylogenetic analysis

Genomic DNA of the isolates was extracted using the method of Damm *et al.* (2008). The 5.8S nuclear ribosomal gene with the two flanking internal transcribed spacers (ITS), a 200-bp intron of the glyceraldehyde-3-phosphate dehydrogenase (GAPDH), and partial



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

sequences of the chitin synthase 1 (CHS-1), histone3 (HIS3), actin (ACT) and beta-tubulin (TUB2) genes were amplified and sequenced using the primer pairs ITS-1F (Gardes & Bruns 1993) + ITS-4 (White *et al.* 1990) or V9G (de Hoog & Gerrits van den Ende 1998) + ITS-4, GDF1 + GDR1 (Guerber *et al.* 2003), CHS-354R + CHS-79F (Carbone & Kohn 1999), CYLH3F + CYLH3R (Crous *et al.* 2004b), ACT-512F + ACT-783R (Carbone & Kohn 1999) and BT2Fd + BT4R (Woudenberg *et al.* 2009) or T1 (O'Donnell & Cigelnik 1997) + Bt-2b (Glass & Donaldson 1995), respectively. The PCRs were performed in a 2720 Thermal Cycler (Applied Biosystems, Foster City, California) in a total volume of 12.5  $\mu$ L. The GAPDH, CHS-1, HIS3, ACT and TUB2 PCR mixture contained 1  $\mu$ L 20x diluted genomic DNA, 0.2  $\mu$ M of each primer, 1x PCR buffer (Bioline, Luckenwalde, Germany), 2 mM  $MgCl_2$ , 20  $\mu$ M of each dNTP, 0.7  $\mu$ L DMSO and 0.25 U Taq DNA polymerase (Bioline). Conditions for PCR of these genes constituted an initial denaturation step of 5 min at 94  $^{\circ}$ C, followed by 40 cycles of 30 s at 94  $^{\circ}$ C, 30 s at 52  $^{\circ}$ C and 30 s at 72  $^{\circ}$ C, and a final denaturation step of 7 min at 72  $^{\circ}$ C, while the ITS PCR was performed as described by Woudenberg *et al.* (2009). The DNA sequences generated with forward and reverse primers were used to obtain consensus sequences using Bionumerics v. 4.60 (Applied Maths, St-Marthens-Lathem, Belgium), and the alignment assembled and manually adjusted using Sequence Alignment Editor v. 2.0a11 (Rambaut 2002).

To determine whether the six sequence datasets were congruent and combinable, tree topologies of 70 % reciprocal Neighbour-Joining bootstrap with Maximum Likelihood distances (10 000 replicates) with substitution models determined separately for each partition using MrModeltest v. 2.3 (Nylander 2004) were compared visually (Mason-Gamer & Kellogg 1996). A maximum parsimony analysis was performed on the multilocus alignment (ITS, GAPDH, CHS-1, HIS3, ACT, TUB2) as well as for each gene separately with PAUP (Phylogenetic Analysis Using Parsimony) v. 4.0b10 (Swofford 2000) using the heuristic search option with 100

random sequence additions and tree bisection and reconstruction (TBR) as the branch-swapping algorithm. Alignment gaps were treated as missing and all characters were unordered and of equal weight. No more than 10 trees of score (length) greater than or equal to 10 were saved in each replicate. The robustness of the trees obtained was evaluated by 10 000 bootstrap replications using the Fast-stepwise addition algorithm (Hillis & Bull 1993). Tree length, consistency index (CI), retention index (RI), rescaled consistency index (RC) and homoplasy index (HI) were calculated for the resulting tree. A Markov Chain Monte Carlo (MCMC) algorithm was used to generate phylogenetic trees with Bayesian probabilities using MrBayes v. 3.1.1 (Ronquist & Huelsenbeck 2003) for the combined sequence datasets. Models of nucleotide substitution for each gene determined by MrModeltest v. 2.3 were included for each gene partition. The analyses of two MCMC chains were run from random trees for 1000 000 generations and sampled every 100 generations. The likelihood score of the two runs were 2 500 and 2 200 and therefore, the first 2 350 (the average of both) trees were discarded as the burn-in phase of the analysis and posterior probabilities determined from the remaining trees. For additional comparison, a Neighbour-Joining analysis was performed on the multigene alignment using PAUP and 1000 bootstrap replications. Sequences derived in this study have been lodged at GenBank, the alignment in TreeBASE ([www.treebase.org/treebase-web/home.html](http://www.treebase.org/treebase-web/home.html)), and taxonomic novelties in MycoBank (Crous *et al.* 2004a).

## RESULTS

### Phylogeny

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

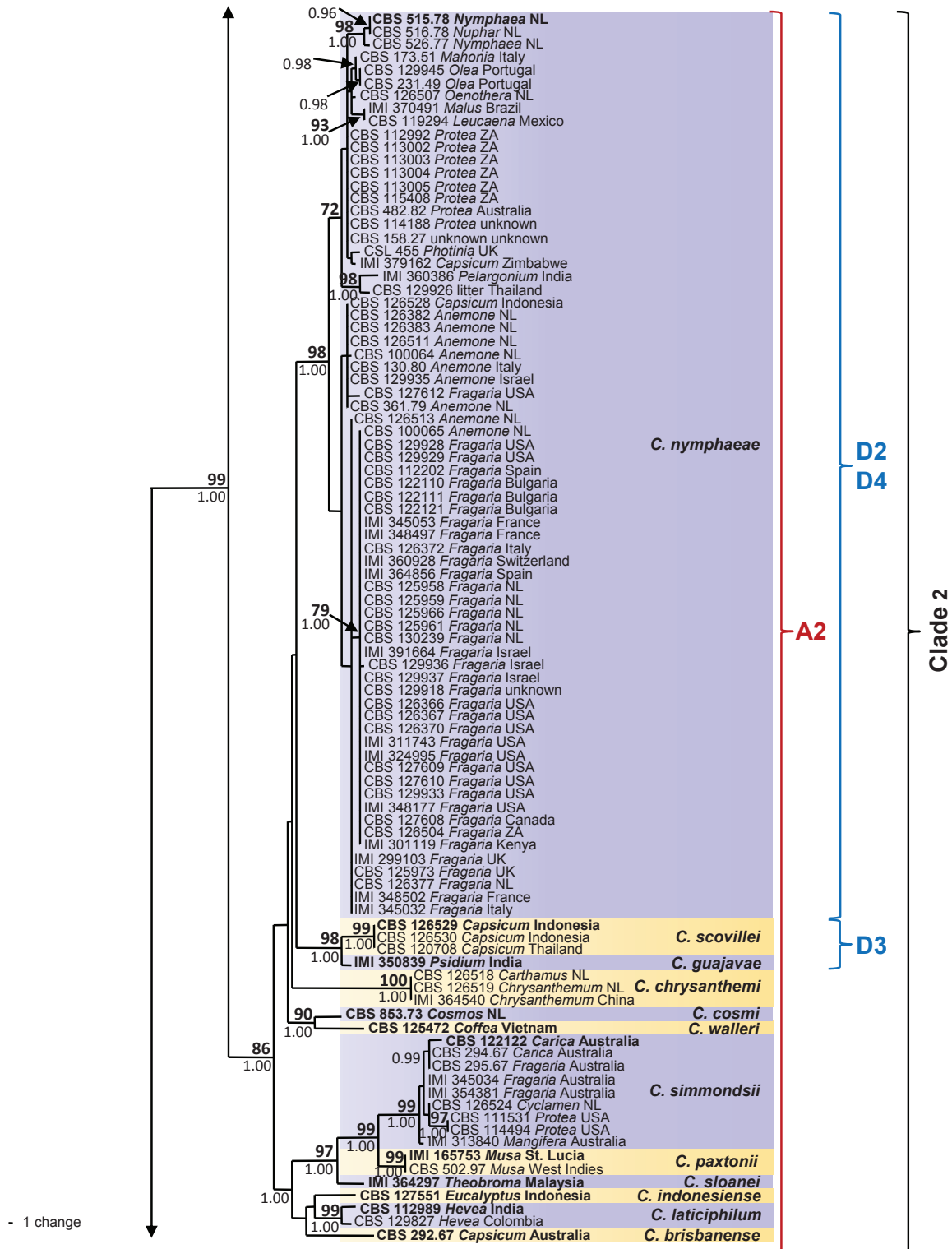


Fig. 1. (Continued).

to combine them. In the multigene analyses (gene boundaries of ITS: 1–546, GAPDH: 557–829, CHS-1: 840–1121, HIS3: 1131–1519, ACT: 1530–1786, TUB2: 1797–2290) of 330 isolates of *C. acutatum* and related *Colletotrichum* species including the outgroup (*C. orchidophilum* strains CBS 631.80, CBS 632.80, CBS 119291, IMI 309357), 2290 characters including the alignment gaps were processed, of which 468 characters were parsimony-informative, 65 parsimony-uninformative and 1757 constant. One strain that was revealed as not belonging to the *C. acutatum* species complex (CBS 436.77, *C. pseudoacutatum*) was not included in the analysis presented in Fig. 1. After a heuristic search using PAUP, 830 most

parsimonious trees were retained (length = 1008 steps, CI = 0.643, RI = 0.981, RC = 0.681, HI = 0.357) of which one is shown in Fig. 1. The topology of the 830 trees was similar, which was verified for a large selection of trees. They differed only in the position of taxa within the subclades. For Bayesian analysis, a HKY+I model was selected for ITS, a HKY+G model for GAPDH and TUB2, a K80+I+G model for CHS-1, a HKY+I+G model for HIS3, a GTR+G model for ACT, and incorporated in the analysis. The consensus tree obtained from Bayesian analyses and the NJ tree (not shown) confirmed the tree topology obtained with parsimony. Bayesian posterior probability values agreed with bootstrap supports (Fig. 1).

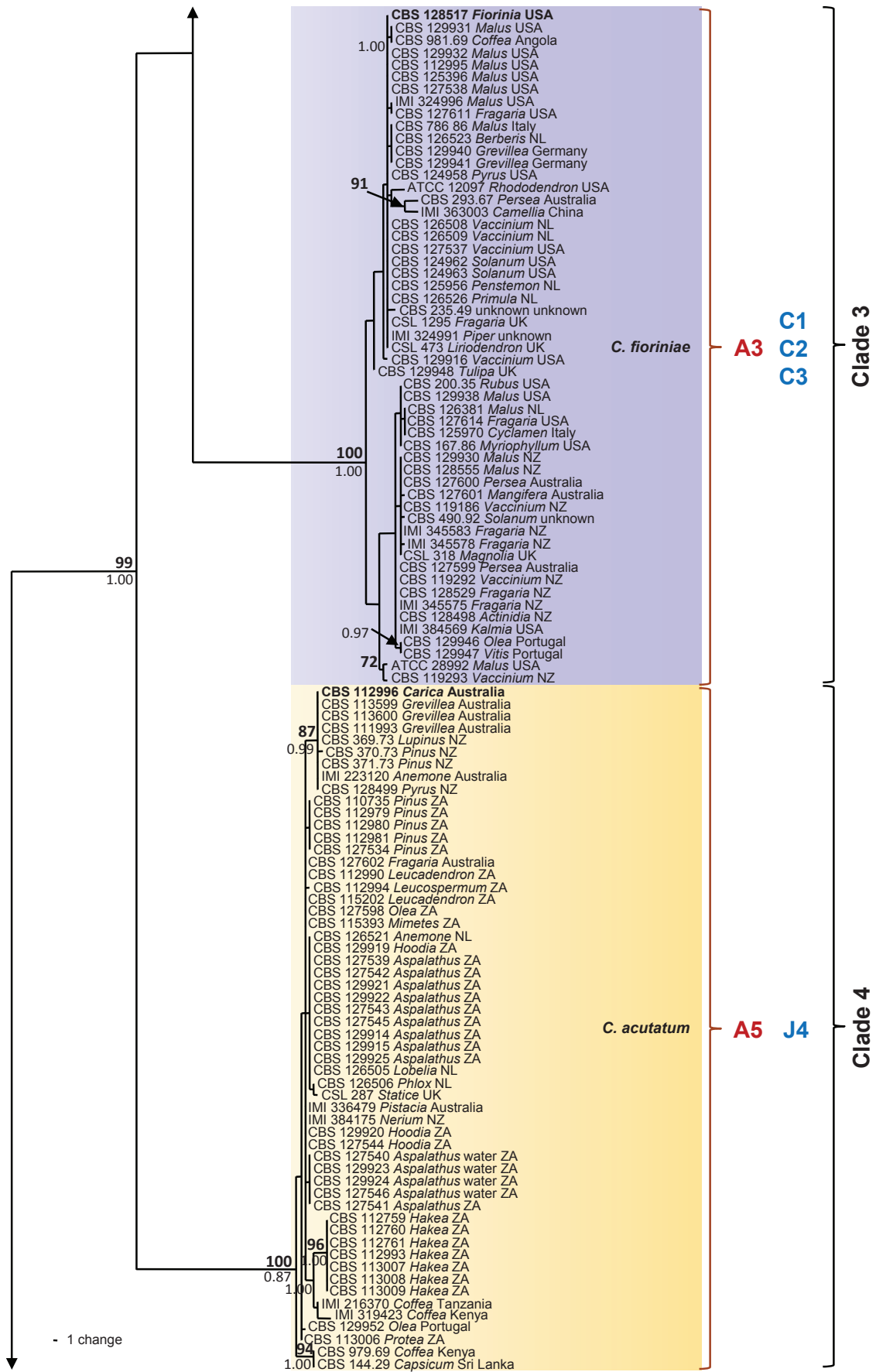


Fig. 1. (Continued).

The analyses resulted in detection of five main clades and 29 subclades within *C. acutatum* s. lat., which we accept as representing different *Colletotrichum* species. The corresponding groups according to Sreenivasaprasad & Talhinhas (2005,

numbers beginning with A) and Guerber *et al.* (2003, mtDNA RFLP haplotypes, numbers beginning with C...K), which are the most differential and comparable studies, are listed in brackets below and are indicated in the phylogenetic tree (Fig. 1). The

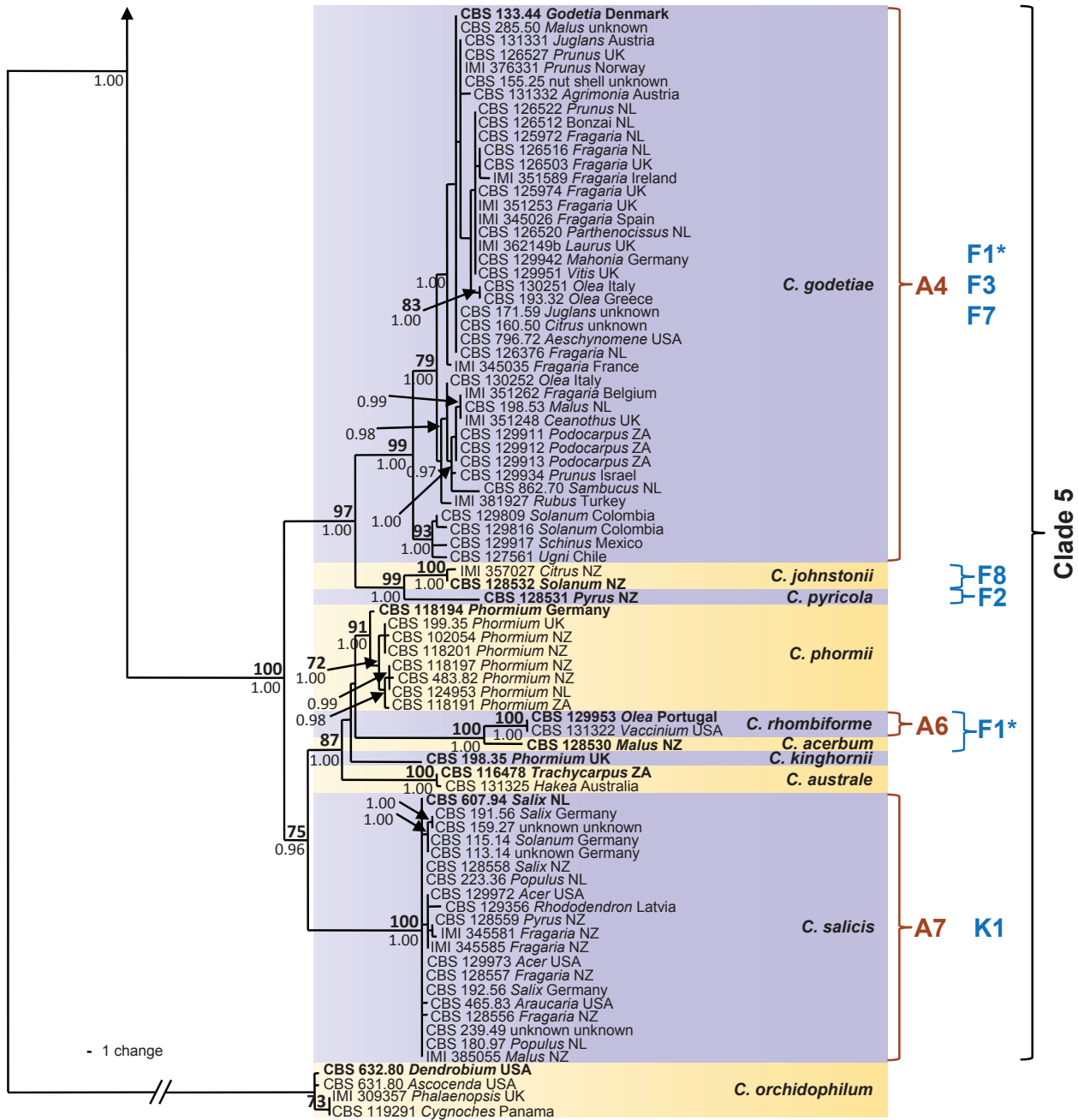
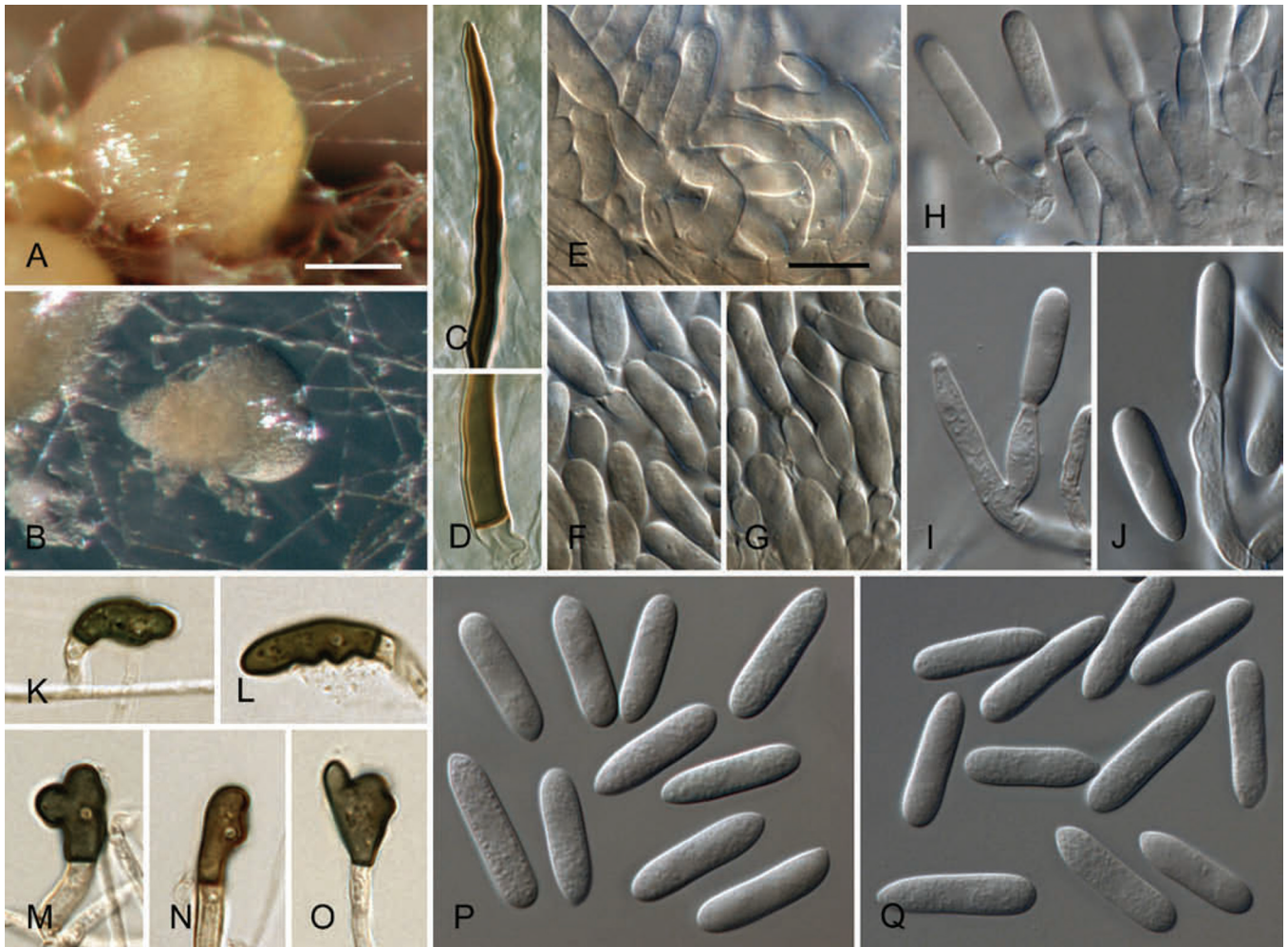


Fig. 1. (Continued).

first clade is well supported with a bootstrap support of 100 % and a Bayesian posterior probability value of 1.00. It consists of two frequently isolated, well-supported clades (bootstrap support/Bayesian posterior probability value of both 100/1.00) comprising several strains each, representing *C. lupini* (A1, J2/J6) and *C. tamarilloi* (A8). Other less frequently encountered subclades in the first clade include *C. costaricense* (94/1.00) with two strains, *C. cuscutae* and *C. melonis* both represented by single-strain clades on long branches, and several short-branched single-strain clades, including the known species *C. limetticola* (J3) and six further unnamed strains. The majority of strains in clade 2 (A2, 86/1.00) belong to *C. nymphaeae* (98/1.00, D2/D4), while most of the other 11 subclades of this clade are occupied by only one or few strains. The clade representing *C. scovillei* (99/1.00) consists of three strains and groups (98/1.00) with a single-strain clade formed by *C. guajavae*. These two adjacent clades probably correspond to clade D3 in Guerber *et al.* (2003). The other sister clades represent *C. simmondsii* (99/1.00), *C. chrysanthemi* (100/1.00), *C. paxtonii*

(99/1.00), *C. laticiphilum* (99/1.00), *C. cosmi*, *C. walleri*, *C. sloanei*, *C. indonesiense* and *C. brisbanense*, the last five of which consist of single-strain clades. Clades 3 and 4 are well-supported (100/1.00 and 100/0.87) and on long branches; they represent *C. fiorinae* (A3, C1/C2/C3) and *C. acutatum* (A5, J4). Clade 5 consists of two sister clades. *Colletotrichum godetiae* (A4, F1\*, 99/1.00), formed by a large number of strains, belongs to the first sister clade and groups (97/1.00) with *C. johnstonii* (F8, 100/1.00) and a single-strain clade representing *C. pyricola* (F2). The other sister clade (75/1.00) consists of six subclades: a large, long-branched and almost homogenous subclade representing *C. salicis* (A7, K1, 100/1.00); a short-branched subclade representing *C. phormii* (91/1.00); *C. rhombiforme* (A6, 100/1.00), which groups with a single-strain clade representing *C. acerbum* on a long branch (F1\*, 100/1.00); plus *C. australe* (100/1.00) and *C. kinghornii* on long branches. Strains named F1 appear in the phylogeny of Guerber *et al.* (2003) in different subclades, corresponding to *C. acerbum*, *C. godetiae* and probably also *C. rhombiforme*. *Colletotrichum pseudoacutatum*



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

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

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

## Taxonomy

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

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

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

*Sexual morph* not observed. *Asexual morph on SNA.* Vegetative hyphae 1–6  $\mu$ m diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* absent, conidiophores formed directly on hyphae. *Setae* not observed. *Conidiophores* hyaline, smooth-walled, septate, branched, to 30  $\mu$ m long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical to ampulliform, sometimes lacking a basal septum and continuous with the conidiophore, sometimes extending to form new conidiogenous loci, polyphialides sometimes observed, discrete phialides measure 7–18  $\times$  3–4.5  $\mu$ m, opening 1.5–2  $\mu$ m diam, collarette 0.5–1.5  $\mu$ m long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical to clavate with one end round and one end slightly acute or both ends round, 15.5–20.5(–29)  $\times$  (4–) 4.5–5  $\mu$ m, mean  $\pm$  SD = 17.9  $\pm$  2.4  $\times$  4.7  $\pm$  0.2  $\mu$ m, L/W ratio = 3.8. *Appressoria* single or in loose groups, medium to dark brown, smooth-walled, clavate, ovate or irregular outline, the edge entire or undulate, sometimes lobate, (8–)9–14(–16.5)  $\times$  (4–)5–7.5(–9.5)  $\mu$ m, mean  $\pm$  SD = 11.3  $\pm$  2.4  $\times$  6.2  $\pm$  1.2  $\mu$ m, L/W ratio = 1.8.

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

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

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



Table 1. (Continued).

Species	Accession No. <sup>1</sup>	Host/Substrate	Country	GenBank No.						
				ITS	GAPDH	CHS-1	HIS3	ACT	TUB2	
<b>C. acutatum</b>	CBS 113007, STE-U 4462	<i>Hakea sericea</i>	South Africa	JQ948395	JQ948726	JQ949056	JQ949386	JQ949716	JQ950046	
	CBS 113009, STE-U 4467	<i>Hakea sericea</i>	South Africa	JQ948397	JQ948728	JQ949058	JQ949388	JQ949718	JQ950048	
	CBS 113008, STE-U 4463	<i>Hakea sericea</i>	South Africa	JQ948396	JQ948727	JQ949057	JQ949387	JQ949717	JQ950047	
	CBS 112761, STE-U 4461	<i>Hakea sericea</i>	South Africa	JQ948393	JQ948724	JQ949054	JQ949384	JQ949714	JQ950044	
	CBS 129919, CPC 13876	<i>Hoodia</i> sp.	South Africa	JQ948370	JQ948701	JQ949031	JQ949361	JQ949691	JQ950021	
	CBS 129920, CPC 13877	<i>Hoodia</i> sp.	South Africa	JQ948371	JQ948702	JQ949032	JQ949362	JQ949692	JQ950022	
	CBS 127644, CPC 13945	<i>Hoodia</i> sp.	South Africa	JQ948372	JQ948703	JQ949033	JQ949363	JQ949693	JQ950023	
	CBS 112990, STE-U 4448	<i>Leucadendron</i> sp., cv. Safari Sunset	South Africa	JQ948360	JQ948691	JQ949021	JQ949351	JQ949681	JQ950011	
	CBS 115202, STE-U 5233	<i>Leucadendron</i> sp., cv. Safari Sunset	South Africa	JQ948362	JQ948693	JQ949023	JQ949353	JQ949683	JQ950013	
	CBS 112994, STE-U 5122	<i>Leucospermum</i> sp.	South Africa	JQ948361	JQ948692	JQ949022	JQ949352	JQ949682	JQ950012	
	CBS 126505, PD 97/4384	<i>Lobelia</i> sp., cv. Blue Moon, leaf spots	Netherlands	JQ948387	JQ948718	JQ949048	JQ949378	JQ949708	JQ950038	
	CBS 369.73, NRCC 10081	<i>Lupinus angustifolius</i>	New Zealand	JQ948350	JQ948681	JQ949011	JQ949341	JQ949671	JQ950001	
	CBS 115393, STE-U 5433	<i>Mimetes</i> sp.	South Africa	JQ948365	JQ948696	JQ949026	JQ949356	JQ949686	JQ950016	
	IMI 384.175, CPC 18936	<i>Nerium oleander</i> , leaf	New Zealand	JQ948369	JQ948700	JQ949030	JQ949360	JQ949690	JQ950020	
	CBS 127598, 223/09	<i>Olea europaea</i>	South Africa	JQ948363	JQ948694	JQ949024	JQ949354	JQ949684	JQ950014	
	CBS 129952, PT227, RB015	<i>Olea europaea</i>	Portugal	JQ948364	JQ948695	JQ949025	JQ949355	JQ949685	JQ950015	
	CBS 126506, PD 90/443	<i>Phlox</i> sp., leaf spots	Netherlands	JQ948388	JQ948719	JQ949049	JQ949379	JQ949709	JQ950039	
	CBS 110735, Lundquist 256, STE-U 163	<i>Pinus radiata</i>	South Africa	JQ948354	JQ948685	JQ949015	JQ949345	JQ949675	JQ950005	
	CBS 112979, Lundquist 258, STE-U 160	<i>Pinus radiata</i>	South Africa	JQ948355	JQ948686	JQ949016	JQ949346	JQ949676	JQ950006	
	CBS 112980, STE-U 164	<i>Pinus radiata</i>	South Africa	JQ948356	JQ948687	JQ949017	JQ949347	JQ949677	JQ950007	
CBS 112981, Lundquist 253, STE-U 162	<i>Pinus radiata</i>	South Africa	JQ948357	JQ948688	JQ949018	JQ949348	JQ949678	JQ950008		
CBS 127634, Lundquist 257, STE-U 161	<i>Pinus radiata</i>	South Africa	JQ948358	JQ948689	JQ949019	JQ949349	JQ949679	JQ950009		
CBS 370.73, NRCC 10088	<i>Pinus radiata</i>	New Zealand	JQ948351	JQ948682	JQ949012	JQ949342	JQ949672	JQ950002		
CBS 371.73, NRCC 10086	<i>Pinus radiata</i>	New Zealand	JQ948352	JQ948683	JQ949013	JQ949343	JQ949673	JQ950003		
IMI 336479, CPC 18881	<i>Pistacia vera</i> , pericarp	Australia	JQ948367	JQ948698	JQ949028	JQ949358	JQ949688	JQ950018		
CBS 113006, STE-U 4460	<i>Protea cynaroides</i>	South Africa	JQ948390	JQ948721	JQ949051	JQ949381	JQ949711	JQ950041		
CBS 128499, ICMP 17992, PRJ 10.208	<i>Pyrus pyrifolia</i> , black spot on fallen, immature fruit	New Zealand	JQ948368	JQ948699	JQ949029	JQ949359	JQ949689	JQ950019		
CSL 287, RB117	<i>Statice</i> sp.	UK	JQ948389	JQ948720	JQ949050	JQ949380	JQ949710	JQ950040		
CBS 116478, HKUCC 2616*	<i>Trachycarpus fortunei</i>	South Africa	JQ948455	JQ948786	JQ949116	JQ949446	JQ949776	JQ950106		
CBS 131325, CPC 19820	<i>Hakea</i> sp.	Australia	JQ948456	JQ948787	JQ949117	JQ949447	JQ949777	JQ950107		
CBS 292.67, DPI 11711*	<i>Capsicum annuum</i>	Australia	JQ948291	JQ948621	JQ948952	JQ949282	JQ949612	JQ949942		
IMI 364540, CPC 18930	<i>Chrysanthemum coronarium</i> , leaf spot	China	JQ948273	JQ948603	JQ948934	JQ949264	JQ949594	JQ949924		
CBS 126518, PD 84/520	<i>Carthamus</i> sp., twisted stem	Netherlands	JQ948271	JQ948601	JQ948932	JQ949262	JQ949592	JQ949922		

**C. australe****C. brisbanense****C. chrysanthemi**

Table 1. (Continued).

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

Table 1. (Continued).

Species	Accession No. <sup>1</sup>	Host/Substrate	Country	GenBank No.						
				ITS	GAPDH	CHS-1	HIS3	ACT	TUB2	
<b>C. fiorinae</b>	CBS 125396, GJS 08-140A	<i>Malus domestica</i> , fruit lesion	USA	JQ948299	JQ948629	JQ948960	JQ949290	JQ949620	JQ949950	
	IMI 324996, CPC 18880	<i>Malus pumila</i>	USA	JQ948301	JQ948631	JQ948962	JQ949292	JQ949622	JQ949952	
	CBS 235.49	<i>Malus</i> sp.	USA	JQ948325	JQ948655	JQ948986	JQ949316	JQ949646	JQ949976	
	CBS 127601, BRIP 28761a	<i>Mangifera indica</i> , stem endophyte	Australia	JQ948311	JQ948641	JQ948972	JQ949302	JQ949632	JQ949962	
	CBS 167.86	<i>Myriophyllum spicatum</i> , submerged stem	USA	JQ948324	JQ948654	JQ948985	JQ949315	JQ949645	JQ949975	
	CBS 129946, PT1170, RB021	<i>Olea europaea</i>	Portugal	JQ948342	JQ948672	JQ949003	JQ949333	JQ949663	JQ949993	
	CBS 126509, PD 92/1060	<i>Parthenocissus</i> sp., cv. Disci, soft rot	Netherlands	JQ948316	JQ948646	JQ948977	JQ949307	JQ949637	JQ949967	
	CBS 125956, NB 112	<i>Penstemon</i> sp., symptoms in the bottom part of the plant	Netherlands	JQ948321	JQ948651	JQ948982	JQ949312	JQ949642	JQ949972	
	CBS 293.67, DPI 13120	<i>Persea americana</i>	Australia	JQ948310	JQ948640	JQ948971	JQ949301	JQ949631	JQ949961	
	CBS 127600, BRIP 20127a	<i>Persea americana</i> , fruit rot	Australia	JQ948308	JQ948638	JQ948969	JQ949299	JQ949629	JQ949959	
	CBS 127599, BRIP 29284a	<i>Persea americana</i> , fruit rot	Australia	JQ948309	JQ948639	JQ948970	JQ949300	JQ949630	JQ949960	
	IMI 324991, CPC 18878	<i>Piper nigrum</i>	Unknown	JQ948338	JQ948668	JQ948999	JQ949329	JQ949659	JQ949989	
	CBS 126526, PD 93/1373, BBA 70343	<i>Primula</i> sp., leaf spots	Netherlands	JQ948323	JQ948653	JQ948984	JQ949314	JQ949644	JQ949974	
	CBS 124958	<i>Pyrus</i> sp., fruit rot	USA	JQ948306	JQ948636	JQ948967	JQ949297	JQ949627	JQ949957	
	ATCC 12097, CPC 19392	<i>Rhododendron</i> sp.	USA	JQ948307	JQ948637	JQ948968	JQ949298	JQ949628	JQ949958	
	CBS 200.35	<i>Rubus</i> sp.	USA	JQ948293	JQ948623	JQ948954	JQ949284	JQ949614	JQ949944	
	CBS 490.92, ATCC 60260	<i>Solanum lycopersicum</i>	New Zealand	JQ948326	JQ948656	JQ948987	JQ949317	JQ949647	JQ949977	
	CBS 124962	<i>Solanum lycopersicum</i> , fruit rot	USA	JQ948319	JQ948649	JQ948980	JQ949310	JQ949640	JQ949970	
	CBS 124963	<i>Solanum lycopersicum</i> , fruit rot	USA	JQ948320	JQ948650	JQ948981	JQ949311	JQ949641	JQ949971	
	CBS 129948, RB128	<i>Tulipa</i> sp.	UK	JQ948344	JQ948674	JQ949005	JQ949335	JQ949665	JQ949995	
CBS 126508, PD 92/906, BBA 70339	<i>Vaccinium corymbosum</i> (blueberry), fruit rot	Netherlands	JQ948315	JQ948645	JQ948976	JQ949306	JQ949636	JQ949966		
CBS 119293, MEP 1322	<i>Vaccinium corymbosum</i> (blueberry), fruit	New Zealand	JQ948314	JQ948644	JQ948975	JQ949305	JQ949635	JQ949965		
CBS 119186, MEP 1325	<i>Vaccinium</i> sp., fruit	New Zealand	JQ948312	JQ948642	JQ948973	JQ949303	JQ949633	JQ949963		
CBS 119292, MEP 1323	<i>Vaccinium</i> sp., fruit	New Zealand	JQ948313	JQ948643	JQ948974	JQ949304	JQ949634	JQ949964		
CBS 127537, STE-UJ 5289	<i>Vaccinium</i> sp. (blueberry)	USA	JQ948318	JQ948648	JQ948979	JQ949309	JQ949639	JQ949969		
CBS 129916, CPC 16823	<i>Vaccinium</i> sp. (blueberry)	USA	JQ948317	JQ948647	JQ948978	JQ949308	JQ949638	JQ949968		
CBS 129947, CR46, RB022	<i>Vitis vinifera</i>	Portugal	JQ948343	JQ948673	JQ949004	JQ949334	JQ949664	JQ949994		
CBS 796.72	<i>Aeschynomene virginica</i>	USA	JQ948407	JQ948738	JQ949068	JQ949398	JQ949728	JQ950058		
CBS 131332	<i>Agrimonia eupatoria</i> , leaf spot	Austria	JQ948429	JQ948760	JQ949090	JQ949420	JQ949750	JQ950080		
CBS 126512, PD 889958	Bonzai, sunken brown spots on fruit	Netherlands	JQ948412	JQ948743	JQ949073	JQ949403	JQ949733	JQ950063		
IMI 351248, CPC 18894	<i>Ceanothus</i> sp.	UK	JQ948433	JQ948764	JQ949094	JQ949424	JQ949754	JQ950084		
CBS 160.50	<i>Citrus aurantium</i> , fruit rot	Unknown	JQ948406	JQ948737	JQ949067	JQ949397	JQ949727	JQ950057		
CBS 133.44*	<i>Clarkia hybrida</i> , cv. Kelvon Glory, seed	Denmark	JQ948402	JQ948733	JQ949063	JQ949393	JQ949723	JQ950053		

Table 1. (Continued).

Species	Accession No. <sup>1</sup>	Host/Substrate	Country	GenBank No.						
				ITS	GAPDH	CHS-1	HIS3	ACT	TUB2	
<i>C. godetiae</i>	IMI 351262, CPC 18897	<i>Fragaria × ananassa</i>	Belgium	JQ948422	JQ948753	JQ949083	JQ949413	JQ949743	JQ950073	
	IMI 345035, CPC 18885	<i>Fragaria vesca</i>	France	JQ948425	JQ948756	JQ949086	JQ949416	JQ949746	JQ950076	
	IMI 351589, CPC 18921	<i>Fragaria × ananassa</i>	Ireland	JQ948423	JQ948754	JQ949084	JQ949414	JQ949744	JQ950074	
	CBS 125972, PD 85/456	<i>Fragaria × ananassa</i>	Netherlands	JQ948416	JQ948747	JQ949077	JQ949407	JQ949737	JQ950067	
	CBS 126376, PD 95/5903	<i>Fragaria × ananassa</i>	Netherlands	JQ948417	JQ948748	JQ949078	JQ949408	JQ949738	JQ950068	
	CBS 126516, PD 88/548	<i>Fragaria × ananassa</i> , fruit rot	Netherlands	JQ948418	JQ948749	JQ949079	JQ949409	JQ949739	JQ950069	
	IMI 345026, CPC 18882	<i>Fragaria × ananassa</i>	Spain	JQ948424	JQ948755	JQ949085	JQ949415	JQ949745	JQ950075	
	CBS 125974, PD 88/858	<i>Fragaria × ananassa</i>	UK	JQ948419	JQ948750	JQ949080	JQ949410	JQ949740	JQ950070	
	CBS 126503, PD 88/859, BBA 70342	<i>Fragaria × ananassa</i>	UK	JQ948420	JQ948751	JQ949081	JQ949411	JQ949741	JQ950071	
	IMI 351253, CPC 18895	<i>Fragaria × ananassa</i>	UK	JQ948421	JQ948752	JQ949082	JQ949412	JQ949742	JQ950072	
	CBS 171-59	<i>Juglans regia</i>	Unknown	JQ948405	JQ948736	JQ949066	JQ949396	JQ949726	JQ950056	
	CBS 131331	<i>Juglans regia</i> , leaf spot	Austria	JQ948404	JQ948735	JQ949065	JQ949395	JQ949725	JQ950055	
	IMI 362149b, CPC 18927	<i>Laurus nobilis</i> , dead fallen leaf	UK	JQ948427	JQ948758	JQ949088	JQ949418	JQ949748	JQ950078	
	CBS 129942	<i>Mahonia aquifolium</i> , leaf spots	Germany	JQ948428	JQ948759	JQ949089	JQ949419	JQ949749	JQ950079	
	CBS 198-53	<i>Malus sylvestris</i> , fruit	Netherlands	JQ948432	JQ948763	JQ949093	JQ949423	JQ949753	JQ950083	
	CBS 285-50	<i>Malus sylvestris</i> , fruit	Unknown	JQ948403	JQ948734	JQ949064	JQ949394	JQ949724	JQ950054	
	CBS 155-25	Nut shell	Unknown	JQ948410	JQ948741	JQ949071	JQ949401	JQ949731	JQ950061	
	CBS 193-32	<i>Olea europaea</i>	Greece	JQ948415	JQ948746	JQ949076	JQ949406	JQ949736	JQ950066	
	CBS 130251, OL 10, IMI 398854	<i>Olea europaea</i>	Italy	JQ948413	JQ948744	JQ949074	JQ949404	JQ949734	JQ950064	
	CBS 130252, IMI 398855, OL 20	<i>Olea europaea</i>	Italy	JQ948414	JQ948745	JQ949075	JQ949405	JQ949735	JQ950065	
	CBS 126520, PD 87/383	<i>Parthenocissus</i> sp., leaf and stem spots	Netherlands	JQ948426	JQ948757	JQ949087	JQ949417	JQ949747	JQ950077	
	CBS 129911, CPC 15124	<i>Podocarpus</i> sp.	South Africa	JQ948434	JQ948765	JQ949095	JQ949425	JQ949755	JQ950085	
	CBS 129912, CPC 15125	<i>Podocarpus</i> sp.	South Africa	JQ948435	JQ948766	JQ949096	JQ949426	JQ949756	JQ950086	
	CBS 129913, CPC 15126	<i>Podocarpus</i> sp.	South Africa	JQ948436	JQ948767	JQ949097	JQ949427	JQ949757	JQ950087	
	CBS 126527, PD 93/1748	<i>Prunus avium</i>	UK	JQ948408	JQ948739	JQ949069	JQ949399	JQ949729	JQ950059	
	CBS 126522, PD 88/472, BBA 70345	<i>Prunus cerasus</i> , fruit, die-back	Netherlands	JQ948411	JQ948742	JQ949072	JQ949402	JQ949732	JQ950062	
	CBS 129934, ALM-IKS-7Q	<i>Prunus dulcis</i>	Israel	JQ948431	JQ948762	JQ949092	JQ949422	JQ949752	JQ950082	
	IMI 376331, CPC 18933	<i>Prunus</i> sp., fruit	Norway	JQ948409	JQ948740	JQ949070	JQ949400	JQ949730	JQ950060	
	IMI 381927, CPC 18935	<i>Rubus idaeus</i> , cane	Turkey	JQ948438	JQ948769	JQ949099	JQ949429	JQ949759	JQ950089	
	CBS 862-70	<i>Sambucus nigra</i> , fruit	Netherlands	JQ948437	JQ948768	JQ949098	JQ949428	JQ949758	JQ950088	
	CBS 129951, RB118	<i>Vitis</i> sp.	UK	JQ948430	JQ948761	JQ949091	JQ949421	JQ949751	JQ950081	
	CBS 129917, CPC 16002	<i>Schinus molle</i>	Mexico	JQ948441	JQ948772	JQ949102	JQ949432	JQ949762	JQ950092	
	CBS 129809, T.A.1	<i>Solanum betaceum</i> , fruit, anthracnose	Colombia	JQ948439	JQ948770	JQ949100	JQ949430	JQ949760	JQ950090	

Table 1. (Continued).

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

Table 1. (Continued).

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

Table 1. (Continued).

Species	Accession No. <sup>1</sup>	Host/Substrate	Country	GenBank No.						
				ITS	GAPDH	CHS-1	HIS3	ACT	TUB2	
<i>C. nymphaeae</i>	CBS 126504, C 105	<i>Fragaria</i> × <i>ananassa</i>	South Africa	JQ948265	JQ948595	JQ948926	JQ949256	JQ949586	JQ949916	
	CBS 112202	<i>Fragaria</i> sp., fruit lesions	Spain	JQ948234	JQ948564	JQ948895	JQ949225	JQ949555	JQ949885	
	IMI 364856, CPC 18931	<i>Fragaria</i> × <i>ananassa</i> , crown	Spain	JQ948244	JQ948574	JQ948905	JQ949235	JQ949565	JQ949895	
	IMI 360928, CPC 18926	<i>Fragaria</i> × <i>ananassa</i> , fruit lesion	Switzerland	JQ948243	JQ948573	JQ948904	JQ949234	JQ949564	JQ949894	
	IMI 299103, CPC 18871	<i>Fragaria vesca</i>	UK	JQ948231	JQ948561	JQ948892	JQ949222	JQ949552	JQ949882	
	CBS 125973, PD 88/857	<i>Fragaria</i> × <i>ananassa</i>	UK	JQ948232	JQ948562	JQ948893	JQ949223	JQ949553	JQ949883	
	CBS 129918, MUCL 44838	<i>Fragaria</i> sp.	Unknown	JQ948254	JQ948584	JQ948915	JQ949245	JQ949575	JQ949905	
	IMI 311743, CPC 18874	<i>Fragaria</i> sp., fruit lesion	USA	JQ948258	JQ948588	JQ948919	JQ949249	JQ949579	JQ949909	
	CBS 127612, DAOM 213709, H-1984	<i>Fragaria</i> × <i>ananassa</i>	USA	JQ948230	JQ948560	JQ948891	JQ949221	JQ949551	JQ949881	
	CBS 129928, 216	<i>Fragaria</i> × <i>ananassa</i>	USA	JQ948228	JQ948558	JQ948889	JQ949219	JQ949549	JQ949879	
	CBS 129929, 2.6.23	<i>Fragaria</i> × <i>ananassa</i>	USA	JQ948229	JQ948559	JQ948890	JQ949220	JQ949550	JQ949880	
	CBS 126366, PD 92/785	<i>Fragaria</i> × <i>ananassa</i>	USA	JQ948255	JQ948585	JQ948916	JQ949246	JQ949576	JQ949906	
	CBS 126367, PD 92/786	<i>Fragaria</i> × <i>ananassa</i>	USA	JQ948256	JQ948586	JQ948917	JQ949247	JQ949577	JQ949907	
	CBS 126370, PD 92/790	<i>Fragaria</i> × <i>ananassa</i>	USA	JQ948257	JQ948587	JQ948918	JQ949248	JQ949578	JQ949908	
	IMI 324995, CPC 18879	<i>Fragaria</i> × <i>ananassa</i>	USA	JQ948259	JQ948589	JQ948920	JQ949250	JQ949580	JQ949910	
	CBS 127609, DAOM 213394, CA-37-2-2	<i>Fragaria</i> × <i>ananassa</i>	USA	JQ948260	JQ948590	JQ948921	JQ949251	JQ949581	JQ949911	
	CBS 127610, DAOM 213395, CA-37-2-4	<i>Fragaria</i> × <i>ananassa</i>	USA	JQ948261	JQ948591	JQ948922	JQ949252	JQ949582	JQ949912	
	CBS 129933, Goff99	<i>Fragaria</i> × <i>ananassa</i>	USA	JQ948262	JQ948592	JQ948923	JQ949253	JQ949583	JQ949913	
	IMI 348177, CPC 18890	<i>Fragaria</i> × <i>ananassa</i> , crown	USA	JQ948263	JQ948593	JQ948924	JQ949254	JQ949584	JQ949914	
	CBS 119294, MEP 1534	<i>Leucaena</i> sp., fruit	Mexico	JQ948205	JQ948535	JQ948866	JQ949196	JQ949526	JQ949856	
	CBS 129926, CPC 18719	Litter	Thailand	JQ948216	JQ948546	JQ948877	JQ949207	JQ949537	JQ949867	
	CBS 17351	<i>Mahonia aquifolium</i> , leaf	Italy	JQ948200	JQ948530	JQ948861	JQ949191	JQ949521	JQ949851	
	IMI 370491, CPC 18932	<i>Malus pumila</i> , fruit	Brazil	JQ948204	JQ948534	JQ948865	JQ949195	JQ949525	JQ949855	
	CBS 516.78, IAM 14670	<i>Nuphar luteum</i> , leaf spot	Netherlands	JQ948198	JQ948528	JQ948859	JQ949189	JQ949519	JQ949849	
	CBS 526.77	<i>Nymphaea alba</i> , leaf	Netherlands	JQ948199	JQ948529	JQ948860	JQ949190	JQ949520	JQ949850	
	CBS 515.78*	<i>Nymphaea alba</i> , leaf spot	Netherlands	JQ948197	JQ948527	JQ948858	JQ949188	JQ949518	JQ949848	
	CBS 126507, PD 91/1392	<i>Oenothera</i> sp., black staining of stem	Netherlands	JQ948203	JQ948533	JQ948864	JQ949194	JQ949524	JQ949854	
	CBS 129945, PT135, RB012	<i>Olea europaea</i>	Portugal	JQ948201	JQ948531	JQ948862	JQ949192	JQ949522	JQ949852	
	CBS 231.49	<i>Olea europaea</i>	Portugal	JQ948202	JQ948532	JQ948863	JQ949193	JQ949523	JQ949853	
	IMI 360386, CPC 18925	<i>Pelargonium graveolens</i> , petiole, leaf and twig	India	JQ948206	JQ948536	JQ948867	JQ949197	JQ949527	JQ949857	
	CSL 455, RB126	<i>Phytinia</i> sp.	UK	JQ948217	JQ948547	JQ948878	JQ949208	JQ949538	JQ949868	
	CBS 482.82	<i>Protea</i> sp.	Australia	JQ948213	JQ948543	JQ948874	JQ949204	JQ949534	JQ949864	
	CBS 115408, STE-U 5357	<i>Protea cynaroides</i>	South Africa	JQ948212	JQ948542	JQ948873	JQ949203	JQ949533	JQ949863	

Table 1. (Continued).

Species	Accession No. <sup>1</sup>	Host/Substrate	Country	GenBank No.						
				ITS	GAPDH	CHS-1	HIS3	ACT	TUB2	
<b>C. nymphaeae</b>	CBS 112992, STE-U 4452	<i>Protea magnifica</i>	South Africa	JQ948207	JQ948637	JQ948868	JQ949198	JQ949528	JQ949858	
	CBS 113002, STE-U 4456	<i>Protea repens</i>	South Africa	JQ948208	JQ948638	JQ948869	JQ949199	JQ949529	JQ949859	
	CBS 113003, STE-U 4457	<i>Protea</i> sp.	South Africa	JQ948209	JQ948639	JQ948870	JQ949200	JQ949530	JQ949860	
	CBS 113004, STE-U 4458	<i>Protea</i> sp.	South Africa	JQ948210	JQ948640	JQ948871	JQ949201	JQ949531	JQ949861	
	CBS 113005, STE-U 4459	<i>Protea</i> sp.	South Africa	JQ948211	JQ948641	JQ948872	JQ949202	JQ949532	JQ949862	
	CBS 114188, STE-U 2971	<i>Protea</i> sp., cv. Pink Ice	Unknown	JQ948214	JQ948644	JQ948875	JQ949205	JQ949535	JQ949865	
<b>C. orchidophilum</b>	CBS 158.27	<i>Phaseolus</i> sp.	Netherlands	JQ948215	JQ948645	JQ948876	JQ949206	JQ949536	JQ949866	
	CBS 631.80	<i>Ascoendia</i> sp.	USA	JQ948152	JQ948482	JQ948813	JQ949143	JQ949473	JQ949803	
	CBS 119291, MEP 1545	<i>Cynoches aureum</i>	Panama	JQ948154	JQ948484	JQ948815	JQ949145	JQ949475	JQ949805	
	CBS 632.80*	<i>Dendrobium</i> sp.	USA	JQ948151	JQ948481	JQ948812	JQ949142	JQ949472	JQ949802	
	IMI 309357, CPC 18815	<i>Phalaenopsis</i> sp.	UK	JQ948153	JQ948483	JQ948814	JQ949144	JQ949474	JQ949804	
	CBS 502.97, LARS 58	<i>Musa nana</i>	"West Indies"	JQ948286	JQ948616	JQ948947	JQ949277	JQ949607	JQ949937	
<b>C. paxtonii</b>	IMI 165753, CPC 18868*	<i>Musa</i> sp.	Saint Lucia	JQ948285	JQ948615	JQ948946	JQ949276	JQ949606	JQ949936	
	CBS 102054	<i>Phormium</i> sp., leaf spot	New Zealand	JQ948448	JQ948779	JQ949109	JQ949439	JQ949769	JQ950099	
	CBS 118201, MEP 1334	<i>Phormium</i> sp., leaf	New Zealand	JQ948449	JQ948780	JQ949110	JQ949440	JQ949770	JQ950100	
	CBS 199.35, DSM 1168	<i>Phormium</i> sp.	UK	JQ948447	JQ948778	JQ949108	JQ949438	JQ949768	JQ950098	
	CBS 118191, AR 3787	<i>Phormium</i> sp., leaf	South Africa	JQ948453	JQ948784	JQ949114	JQ949444	JQ949774	JQ950104	
	CBS 118197, AR 3389	<i>Phormium</i> sp.	New Zealand	JQ948450	JQ948781	JQ949111	JQ949441	JQ949771	JQ950101	
<b>C. pseudoacutatum</b>	CBS 124953	<i>Phormium</i> sp., leaf	Netherlands	JQ948452	JQ948783	JQ949113	JQ949443	JQ949773	JQ950103	
	CBS 483.82	<i>Phormium tenax</i>	New Zealand	JQ948451	JQ948782	JQ949112	JQ949442	JQ949772	JQ950102	
	CBS 118194, AR 3546*	<i>Phormium</i> sp.	Germany	JQ948446	JQ948777	JQ949107	JQ949437	JQ949767	JQ950097	
	CBS 436.77*	<i>Pinus radiata</i>	Chile	JQ948480	JQ948811	JQ949141	JQ949471	JQ949801	JQ950131	
	CBS 128531, ICMP 12924, PRJ 977.1*	<i>Pyrus communis</i> , fruit rot	New Zealand	JQ948445	JQ948776	JQ949106	JQ949436	JQ949766	JQ950096	
	CBS 129953, PT250, RB011*	<i>Olea europaea</i>	Portugal	JQ948457	JQ948788	JQ949118	JQ949448	JQ949778	JQ950108	
<b>C. salicis</b>	CBS 131322, DAOM 233253, C10, MS1L34	<i>Vaccinium macrocarpum</i>	USA	JQ948458	JQ948789	JQ949119	JQ949449	JQ949779	JQ950109	
	CBS 129972, MP1, RB096	<i>Acer platanoides</i> , symptomatic leaves	USA	JQ948466	JQ948797	JQ949127	JQ949457	JQ949787	JQ950117	
	CBS 129973, MP2, RB097	<i>Acer platanoides</i> , symptomatic leaves	USA	JQ948467	JQ948798	JQ949128	JQ949458	JQ949788	JQ950118	
	CBS 465.83	<i>Araucaria excelsa</i> , anthracnose and dieback	USA	JQ948468	JQ948799	JQ949129	JQ949459	JQ949789	JQ950119	
	IMI 345585, CPC 19376	<i>Fragaria x ananassa</i> , petiole spot	New Zealand	JQ948476	JQ948807	JQ949137	JQ949467	JQ949797	JQ950127	
	CBS 128556, ICMP 12954, PRJ 11071	<i>Fragaria x ananassa</i> , fruit rot	New Zealand	JQ948473	JQ948804	JQ949134	JQ949464	JQ949794	JQ950124	
<b>C. paxtonii</b>	CBS 128557, ICMP 12955, PRJ 1115.1	<i>Fragaria x ananassa</i> , fruit rot	New Zealand	JQ948474	JQ948805	JQ949135	JQ949465	JQ949795	JQ950125	
	IMI 345581, CPC 19377	<i>Fragaria x ananassa</i> , lesion	New Zealand	JQ948475	JQ948806	JQ949136	JQ949466	JQ949796	JQ950126	
	CBS 113.14	<i>Malus domestica</i> , cv. Manks Küchenapfel, fruit	Germany	JQ948478	JQ948809	JQ949139	JQ949469	JQ949799	JQ950129	



Table 1. (Continued).

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

Table 1. (Continued).

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

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

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

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

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

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

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

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

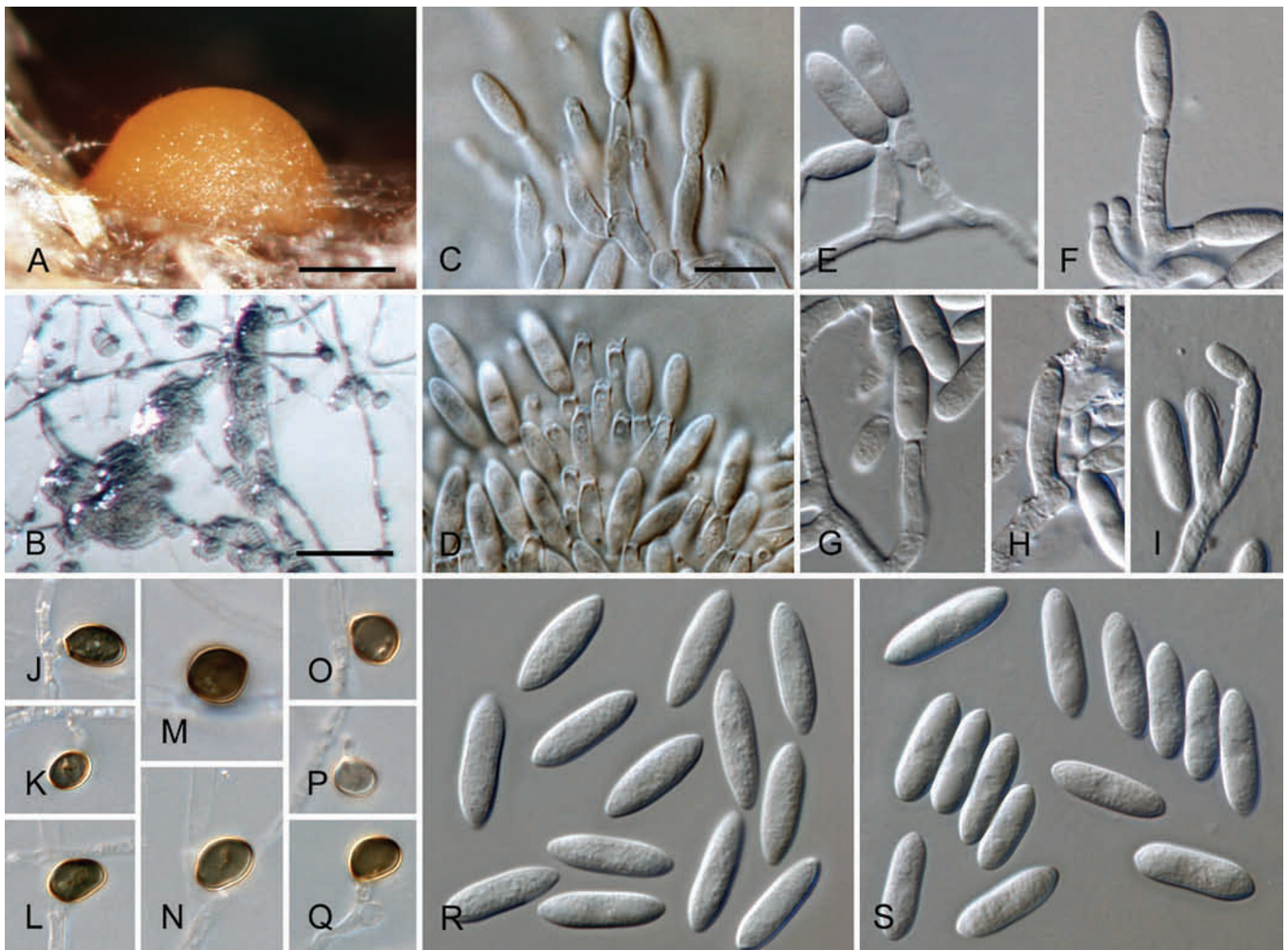


Fig. 3. *Colletotrichum acutatum* (from ex-epitype strain CBS 112996). A–B. Conidiomata. C–I. Conidiophores. J–Q. Appressoria. R–S. Conidia. A, C–D, R. from *Anthriscus* stem. B, E–Q, S. from SNA. A–B. DM, C–S. DIC, Scale bars: A = 200  $\mu$ m, B = 100  $\mu$ m, C = 10  $\mu$ m. Scale bar of C applies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

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

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

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

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

to obovate, entire edge, sometimes undulate, (4–)5.5–9(–13)  $\times$  (3–)4–6.5(–9.5)  $\mu$ m, mean  $\pm$  SD = 7.3  $\pm$  2.0  $\times$  5.4  $\pm$  1.2  $\mu$ m, L/W ratio = 1.3.

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

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

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

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

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

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

*Colletotrichum acutatum* s. str. causes diseases of a wide range of unrelated plants, some of which are economically significant, including papaya (*Carica papaya*), strawberry (*Fragaria* × *ananassa*), pine (*Pinus* spp.), *Hakea* spp. and rooibos (*Aspalathus linearis*). Two of these are associated with recognition of *formae speciales*. These are not accepted as a taxonomic rank in the

International Code of Nomenclature for Algae, Fungi and Plants (ICN) as they are based on fungus/plant interactions rather than single species, and formal ICN-compliant taxa cannot use *formae speciales* as basionyms for new combinations.

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

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

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

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

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

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

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

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

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

Apart from *C. acutatum* and *C. simmondsii*, there have been other *Colletotrichum* and *Gloeosporium* species described on *Carica papaya*, all from Brazil. Conidia of *C. papayae* Henn. described from branches and petioles of papaya in Sao Paulo, are larger and differ in shape from *C. acutatum* s. str.; they are cylindrical, straight to curved, hyaline, and measure 12–20 × 5–7 µm (Saccardo *et al.* 1931), while those of *C. acutatum* measure on average 8.8–15.5 × 3.2–4.5 µm, depending on strain and medium. *Gloeosporium papayae* Henn., described from stems of papaya in Uberaba, Minas Gerais, forms cylindrical-oblong to subclavate, obtuse, straight, hyaline to pale yellowish conidia that measure 11–14 × 5–6 µm (Hennings 1895); conidia of *C. acutatum* are hyaline and broader. A presumed isotype in K(M) of *G. papayae*, “E. Ule n. 1947”, collected in June 1892, is actually a species of *Phomopsis*. *Gloeosporium fructus-caricae* Henn. forms conidia that overlap in size with those of *C. acutatum*, however their shape is described as oblong-cylindrical with both ends rounded, while conidia of *C. acutatum* usually have both ends acute. Even if the description matches completely with that of *C. acutatum* we could not be sure they are the same species; the morphology of most

species in the *C. acutatum* species complex is highly variable and overlapping. There is no strain from papaya in Brazil included in this study, and there is no report of *C. acutatum* s. lat. from Brazil listed in Farr & Rossman (2012). We have tried to draw a reasonable balance between respect for the rules of priority and the need for nomenclatural stability, and in this case we feel that Simmonds' name should be conserved if such a synonymy is established.

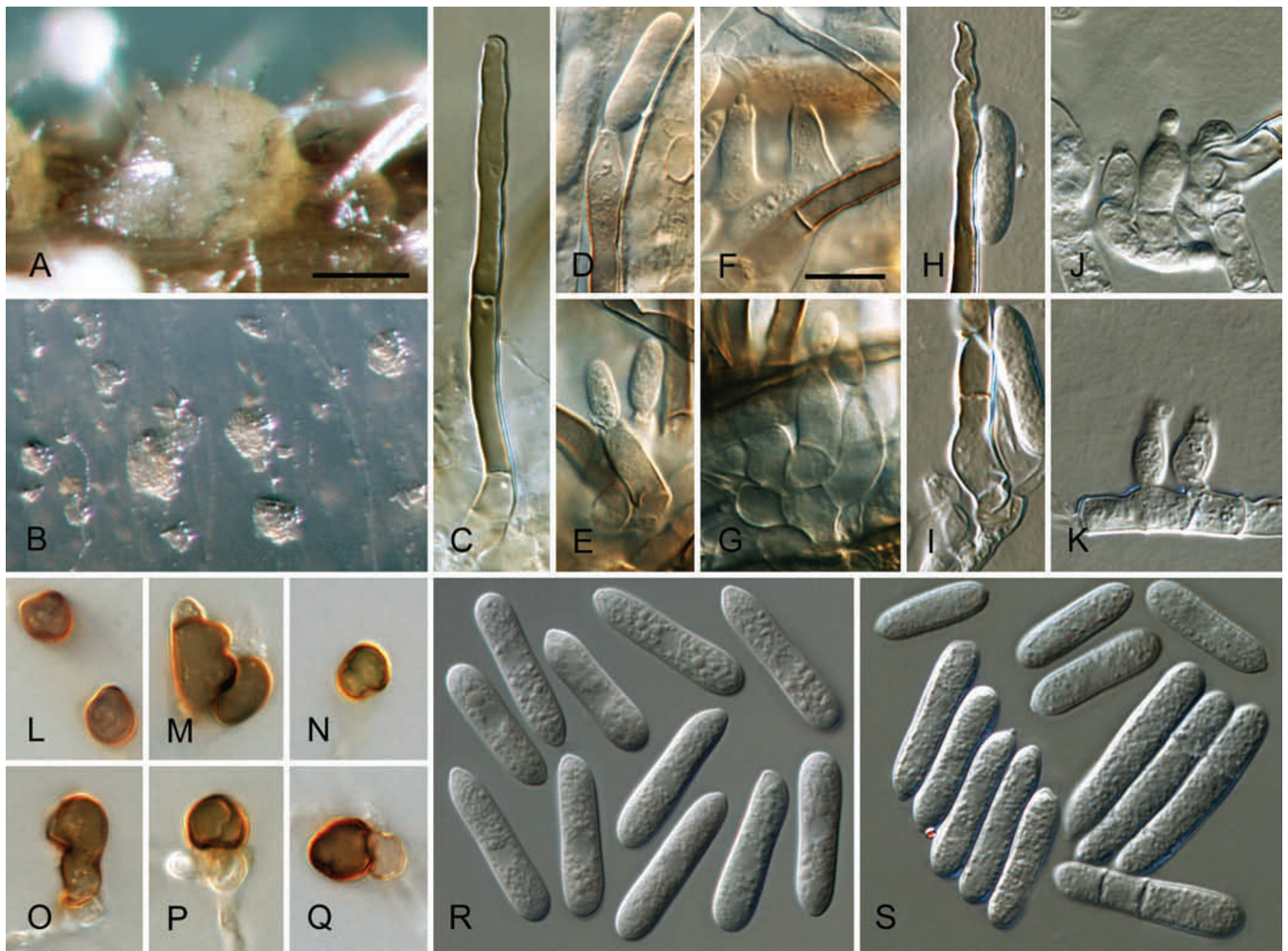
*Colletotrichum acutatum* is separated from other species by all genes. Closest matches in a blastn search with the TUB2 sequence of strain CBS 112996, with 100 % identity, were GU183307–GU183309 and GU183311–GU183314, from *Boronia*, *Anemone*, *Fragaria*, *Pistacia*, *Anemone*, *Olea*, *Ranunculus*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

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

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

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

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



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

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

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

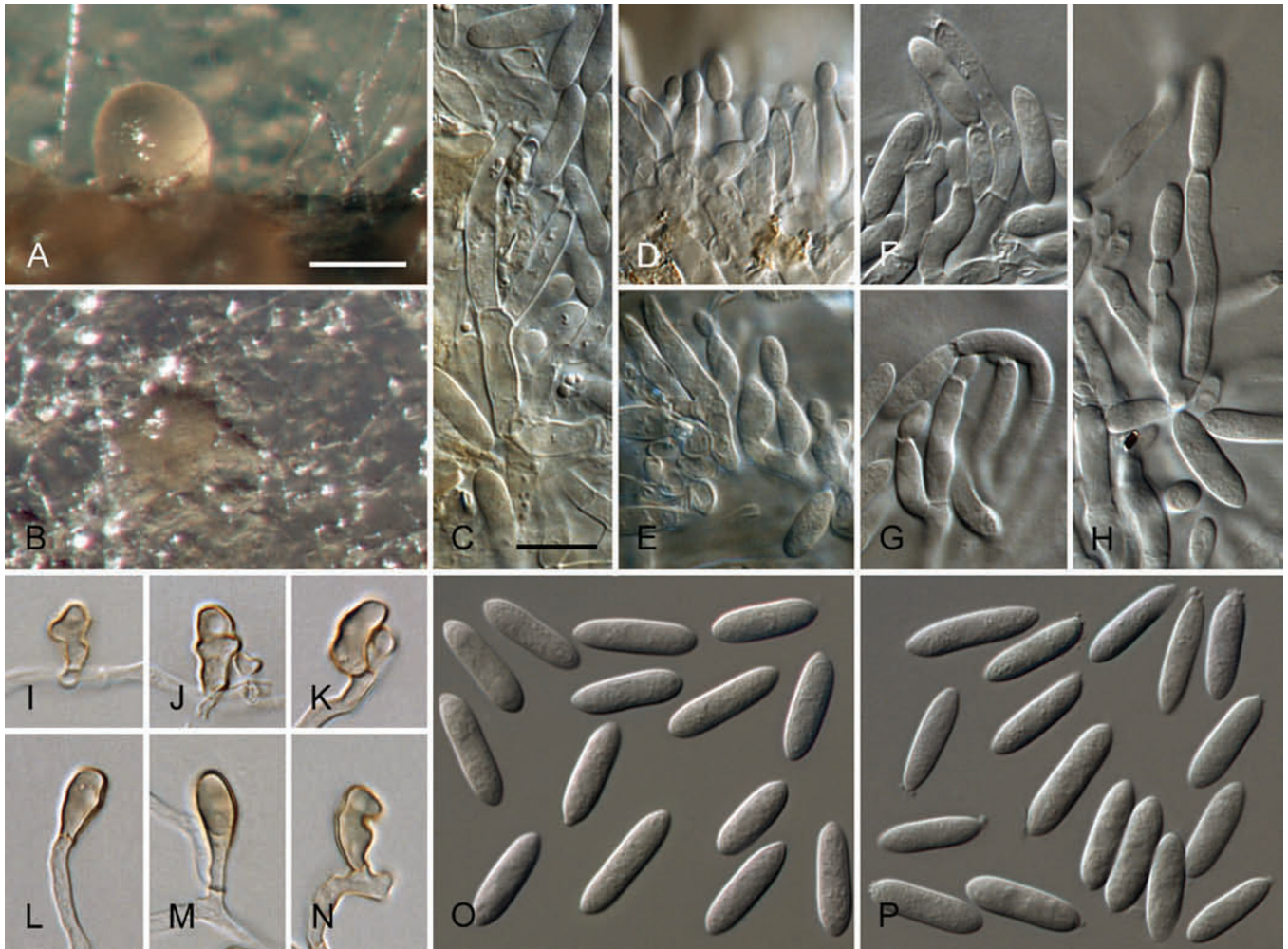
**Material examined:** **South Africa**, Stellenbosch, university campus, from *Trachycarpus fortunei*, 2 Jan. 1998, J.E. Taylor, (CBS-H 20721 **holotype**, culture ex-type CBS 116478 = HKUCC2616). **Australia**, Western Australia, Alcoa, from *Hakea* sp., 12 Jul. 2011, W. Gams, culture CBS 131325.

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

while those of *C. australe* are cylindrical. Additionally, appressoria of *C. australe* are shorter than those of *C. phormii*. Conidia of *C. rhombiforme* are shorter, while those of *C. kinghornii* are narrower.

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

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



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

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

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

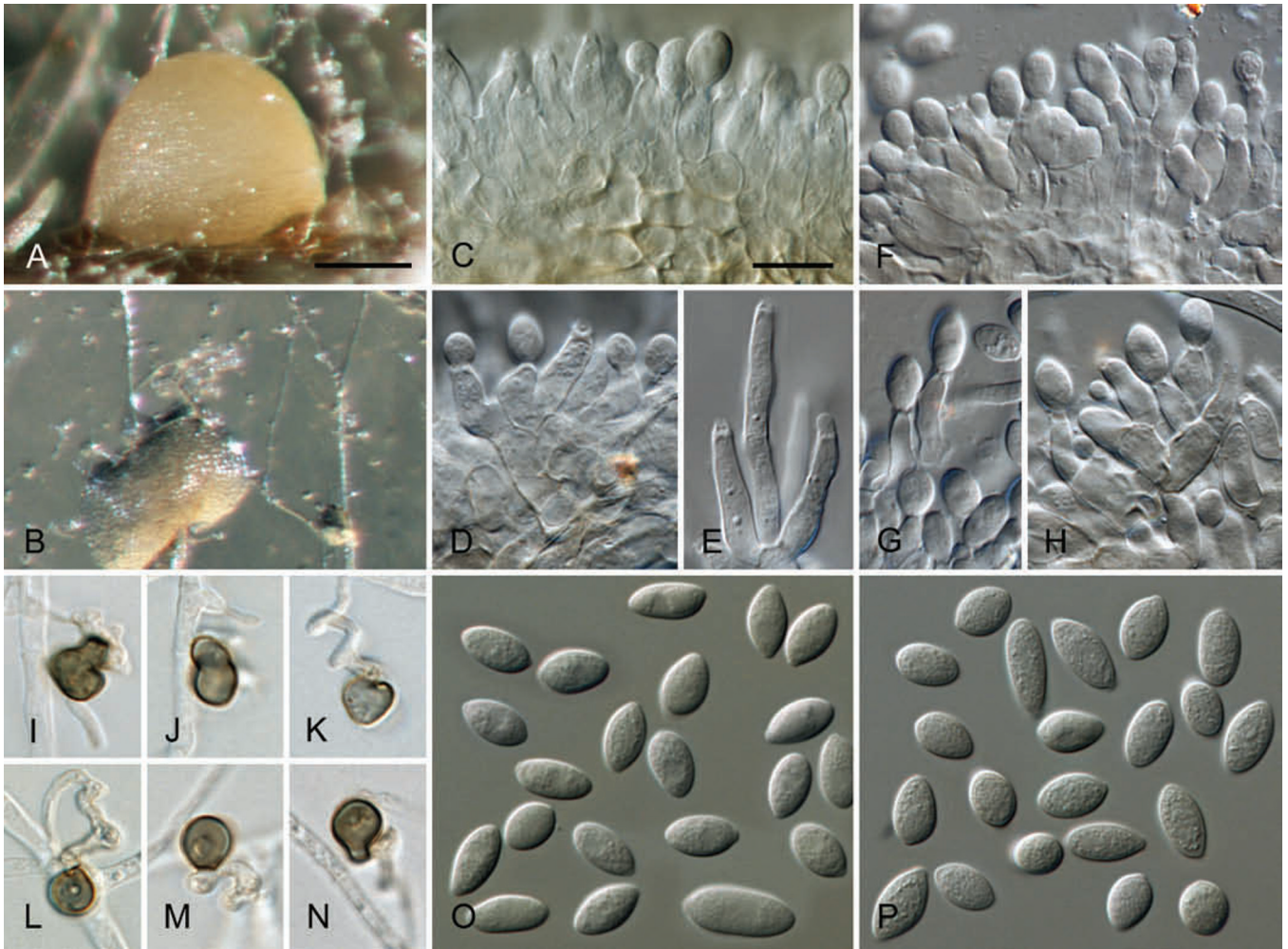
**Etymology:** Named after Brisbane, the city in Queensland, Australia where the species was collected.

**Sexual morph** not observed. **Asexual morph on SNA.** **Vegetative hyphae** 1–8 µm diam, hyaline, smooth-walled, septate, branched. **Chlamydospores** not observed. **Conidiomata** not developed, conidiophores formed directly on hyphae. **Setae** not observed. **Conidiophores** hyaline, smooth-walled, septate, branched, to 30

µm long. **Conidiogenous cells** hyaline, smooth-walled, cylindrical to slightly inflated, sometimes lacking a basal septum and continuous with the conidiophore, sometimes proliferating and extending to form a new conidiogenous locus, discrete phialides measure 8.5–21 × 2.5–4 µm, opening 1–1.5 µm diam, collarette 1–1.5 µm long, periclinal thickening distinct. **Conidia** hyaline, smooth-walled, aseptate, straight, cylindrical with both ends slightly acute or one end round and one end slightly acute, (12–)12–17.5(–25) × (3–) 3.5–4(–5) µm, mean ± SD = 14.8 ± 2.8 × 3.8 ± 0.5 µm, L/W ratio = 3.9. **Appressoria** single or in loose groups, pale brown, smooth-walled, mostly clavate, the edge entire to undulate, (5–)7.5–14.5(–18) × (2.5–)3.5–5(–6) µm, mean ± SD = 11.1 ± 3.4 × 4.3 ± 0.9 µm, L/W ratio = 2.6.

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

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



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

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

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

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

A blastn search with the TUB2 sequence of strain CBS 292.67 resulted in a 100 % match with GU183275, the sequence of the

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

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

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

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



subglobose, elliptical or irregular in outline, with entire, undulate or lobate margin,  $(5-5.5-9.5(-11.3) \times (3-4.5-6.5(-7.5)) \mu\text{m}$ , mean  $\pm$  SD =  $7.5 \pm 1.8 \times 5.4 \pm 1.1 \mu\text{m}$ , L/W ratio = 1.4.

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

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

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

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

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

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

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

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

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

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

*Asexual morph on Anthriscus stem*. *Conidiomata* either not developed, conidiophores formed directly on hyphae, or acervular, conidiophores formed on pale brown, angular, basal cells, 3–9  $\mu\text{m}$  diam. *Setae* not observed. *Conidiophores* hyaline to pale brown, smooth-walled, septate, branched, to 40  $\mu\text{m}$  long. *Conidiogenous cells* hyaline to pale brown, smooth-walled, cylindrical, 9–24  $\times$  3–3.5  $\mu\text{m}$ , opening 1–1.5  $\mu\text{m}$  diam, collarette 1–1.5  $\mu\text{m}$  long, periclinal thickening conspicuous. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical to fusiform with both ends  $\pm$  acute,  $(12-14-16.5(-18)) \times (3.5-4-4.5) \mu\text{m}$ , mean  $\pm$  SD =  $15.3 \pm 1.4 \times 4.0 \pm 0.3 \mu\text{m}$ , L/W ratio = 3.8.



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

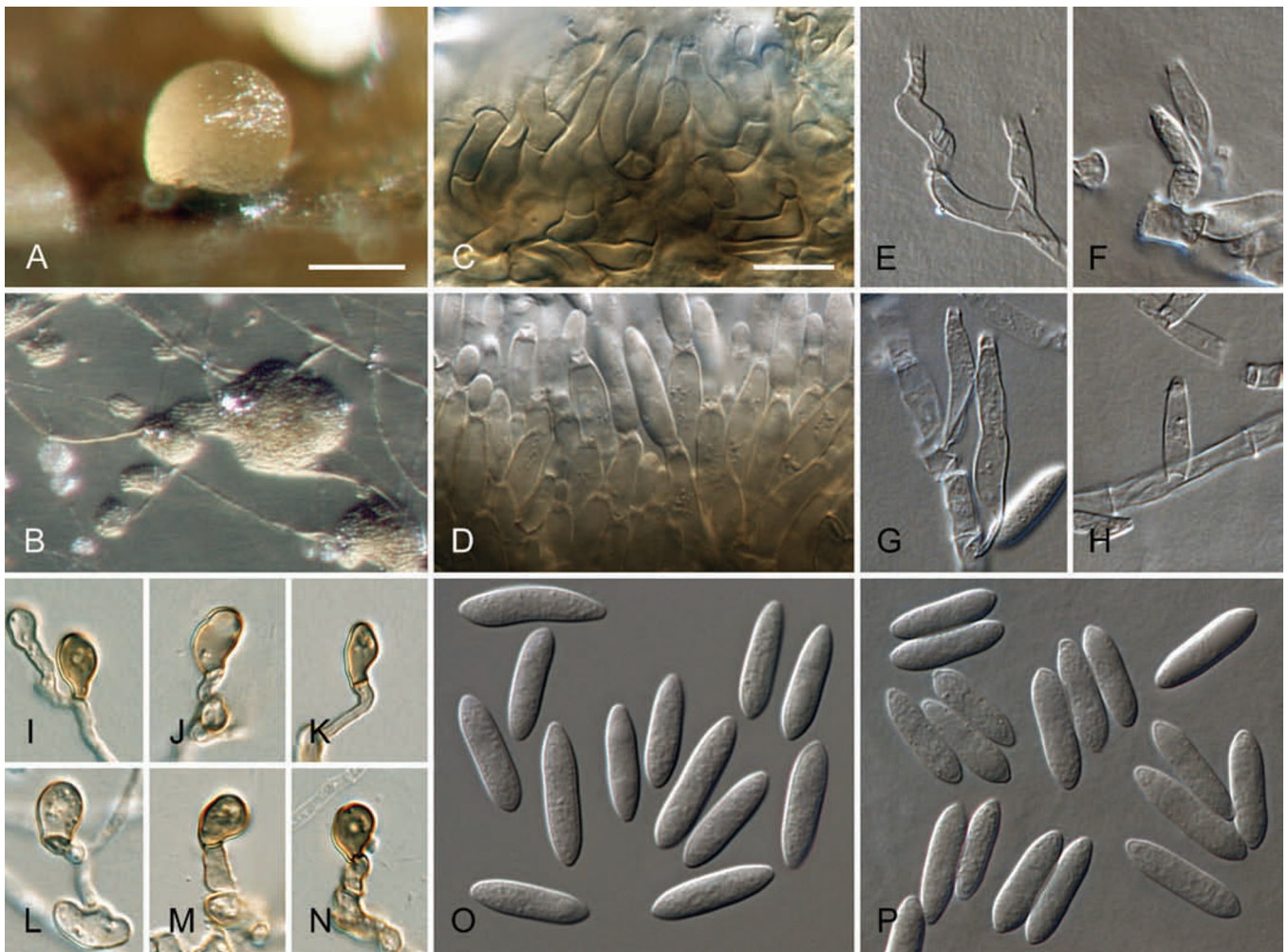
**Culture characteristics:** Colonies on SNA flat with entire margin, hyaline, buff to pale honey, on filter paper partly pale olivaceous grey, the medium, filter paper and *Anthriscus* stem partly covered with floccose-felty whitish to pale olivaceous grey aerial mycelium and orange acervuli, reverse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

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

**Notes:** Kwon *et al.* (1999) report *C. acutatum* (*s. lat.*) to cause sunken brownish spots on stems, as well as symptoms on leaves, flowers and floral axes of *Cosmos bipinnatus* in Korea. Morphological characters (conidia, appressoria) are similar to those of strain CBS 853.73, except for setae, which our strain did not develop in our standard culture conditions. It is therefore possible that the collection from Korea represents *C. cosmi*. *Colletotrichum acutatum* (*s. lat.*) is also known as an anthracnose pathogen of flowers and flower buds of *Cosmos bipinnatus* in Japan (Yaguchi *et al.* 1996). The shape of conidia and appressoria of the Japanese fungus are similar to our strain, but the conidia are smaller, measuring 11–14  $\times$  2.8–3.5  $\mu$ m.

Two other species are reported from *Cosmos bipinnatus* in India, *C. truncatum* (as *C. capsici*) associated with seeds and causing seed and seedling rot (Srivastava *et al.* 1981) and *C. gloeosporioides* associated with leaves (Kumari *et al.* 1981). When strain CBS 853.73 was first accessed into CBS, von Arx identified it as *C. gloeosporioides*, but with the remark “deviating by longer, slender conidia”. Molecular data do not support this identification; the strain belongs to the *C. acutatum* complex, but it is possible that reports of *C. gloeosporioides* refer to this species.

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



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

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

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

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

*Asexual morph on Anthriscus stem.* Conidiomata not developed, conidiophores and setae formed directly on hyphae. Setae medium to dark brown, smooth-walled to finely verruculose, 0–2-septate, 50–60  $\mu$ m long, base cylindrical, 3.5–4.5  $\mu$ m diam, the tip  $\pm$  acute. Conidiophores hyaline to pale brown, smooth-walled,

septate, branched, to 40  $\mu$ m long. Conidiogenous cells hyaline to pale brown, smooth-walled, cylindrical to ampulliform, 8–22  $\times$  3–5  $\mu$ m, opening 1–1.5  $\mu$ m diam, collarette 1–1.5  $\mu$ m long, periclinal thickening distinct. Conidia hyaline, smooth-walled, aseptate, straight, cylindrical with both ends acute, (12.5–)13.5–16(–18)  $\times$  3.5–4  $\mu$ m, mean  $\pm$  SD = 14.8  $\pm$  1.4  $\times$  3.8  $\pm$  0.3  $\mu$ m, L/W ratio = 3.9.

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

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

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

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

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

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

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

*Sexual morph* not observed. *Asexual morph* on SNA. *Vegetative hyphae* 1–5.5 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* not developed, conidiophores formed directly on hyphae. *Setae* not observed. *Conidiophores* hyaline, smooth-walled, simple or septate and branched, to 35 µm long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical to ampulliform, often integrated, polyphialides

occasionally observed, discrete phialides measuring 4–14.5 × 2.5–4.5 µm, opening 1.5–2 µm diam, collarete 0.5–1.5 µm long, periclinal thickening conspicuous. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical with both ends acute, (15.5–)17.5–21(–27) × (3–)3.5–4.5 µm, mean ± SD = 19.2 ± 1.7 × 4.0 ± 0.3 µm, L/W ratio = 4.8. *Appressoria* single or in loose clusters, pale brown, smooth-walled, elliptical to clavate, entire edge (3.5–)5.5–11.5(–15.5) × (2–)3.5–5.5(–6.5) µm, mean ± SD = 8.5 ± 3.2 × 4.6 ± 0.9 µm, L/W ratio = 1.8.

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

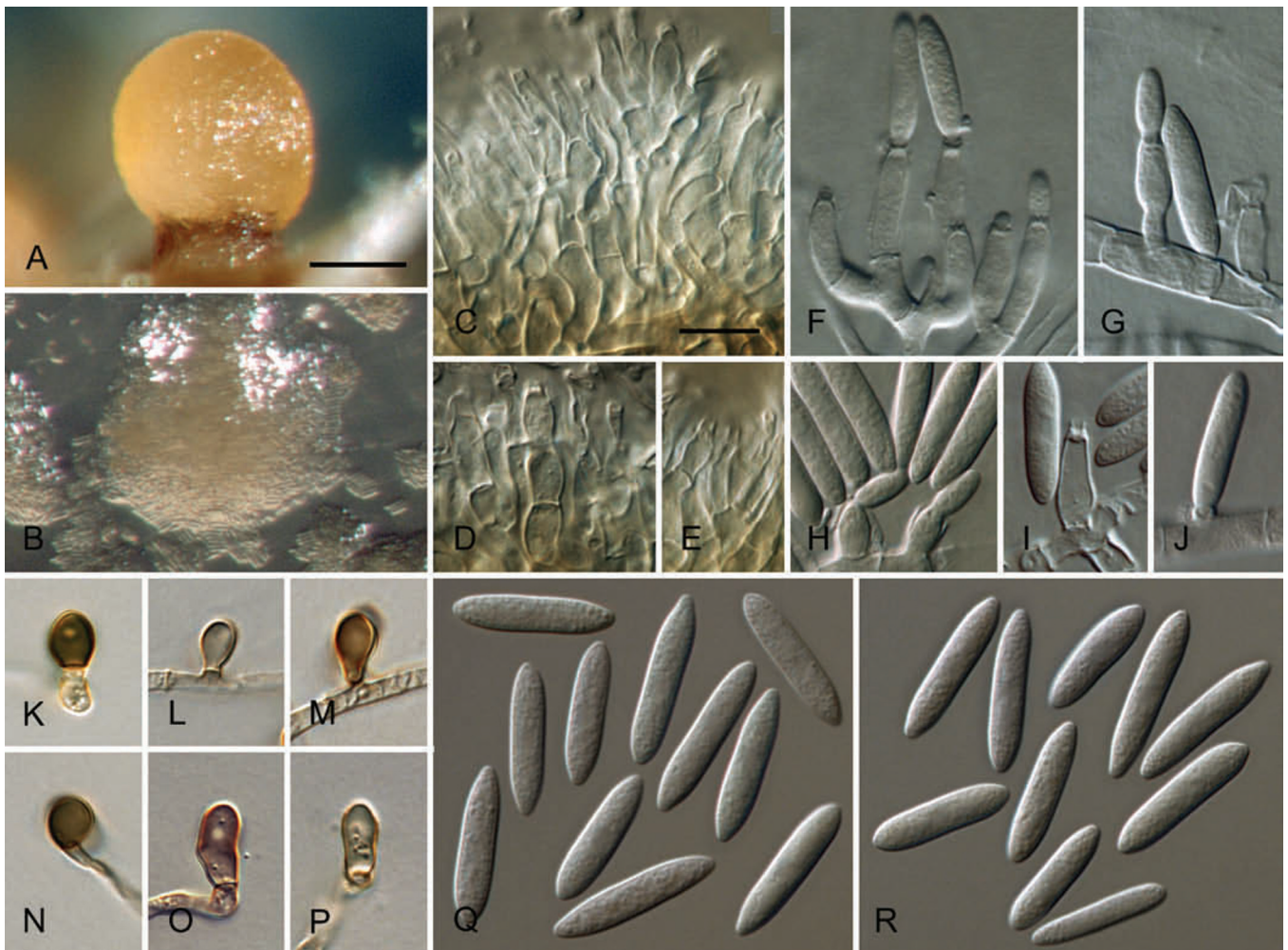
*Culture characteristics:* Colonies on SNA flat with entire margin, hyaline to buff, on filter paper and *Anthriscus* stem partly covered with woolly to felty white to pale grey aerial mycelium and orange acervuli, reverse hyaline to buff, under filter paper pale olivaceous grey; growth 20 mm in 7 d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

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

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

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

Guerber *et al.* (2003) studied isolates from *Cuscuta* in the USA and China that belong to two different species, neither of which is conspecific with *C. cuscutae*. Based on GAPDH sequences



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

(Guerber *et al.* 2003), isolates FRC2 and FRC7 from dodder in the USA are *C. fioriniae*, while strain 783 from China (apparently identical with strain Lu Bao no. 1) belongs to a subclade of clade 2 that is not included in this study. Strain 783 was found to have a haplotype of *Msp1* mtDNA identical to those of two Australian strains causing terminal crook disease of pine, and distinct from those of other *Cuscuta* strains.

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

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

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

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

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

$\equiv$  *Glomerella acutata* var. *fioriniae* Marcelino & Gouli, Mycologia 100: 362. 2008.

*Sexual morph* not observed. *Asexual morph on SNA.* Vegetative hyphae 1.5–7.5  $\mu$ m diam, hyaline to pale brown, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* conidiophores formed directly on hyphae. *Setae* not observed. *Conidiophores* hyaline to pale brown, smooth-walled, septate, branched, up to 35  $\mu$ m long. *Conidiogenous cells* hyaline to pale brown, smooth-walled, cylindrical to ampulliform, sometimes lacking a basal septum and continuous with the conidiophore, sometimes covert with a mucous coating, discrete phialides measure 4–12  $\times$  2.5–3.5  $\mu$ m, opening 1–2  $\mu$ m diam, collarette 1  $\mu$ m long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, fusiform to cylindrical with both ends acute, (10.5–)13.5–16.5(–19.5)  $\times$  4–5(–5.5)  $\mu$ m, mean  $\pm$  SD = 15.0  $\pm$  1.6  $\times$  4.5  $\pm$  0.3  $\mu$ m, L/W ratio = 3.3  $\mu$ m, conidia of strain CBS 129947 are smaller, measuring (10.5–)12–15(–17)  $\times$  3.5–5(–6)  $\mu$ m, mean  $\pm$  SD = 13.5  $\pm$  1.7  $\times$  4.1  $\pm$  0.8  $\mu$ m, L/W ratio = 3.3  $\mu$ m. *Appressoria* solitary or in loose groups, pale to medium brown, smooth-walled, ellipsoidal, clavate to irregular outline, entire edge or undulate, (4.5–)7–11.5(–



**Fig. 10.** *Colletotrichum fioriniae* (from ex-holotype strain CBS 128517). A–B. Conidiomata. C–L. Conidiophores. M–R. Appressoria. S–T. Conidia. A, C–G, S, from *Anthriscus* stem. B, H–R, T, from SNA. A–B, DM, C–T, DIC, Scale bars: A = 200  $\mu$ m, B = 100  $\mu$ m, C = 10  $\mu$ m. Scale bar of C applies to C–T.

15.5)  $\times$  (4–)4.5–7(–10.5)  $\mu$ m, mean  $\pm$  SD =  $9.2 \pm 2.2 \times 5.6 \pm 1.2$   $\mu$ m, L/W ratio = 1.6.

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

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

**Material examined:** **USA**, New York, Ward Pound Ridge Reserve, on mummified adult *Fiorinia externa* (elongate hemlock scale, insect), 2005, J.A.P. Marcelino and S. Gouli, **culture ex-holotype** of *C. fioriniae* CBS 128517 = EHS<sub>88</sub> = ARSE 10222; Michigan, from *Vaccinium* sp. (blueberry), collection date and collector unknown (isolated by A. Schilder), culture CBS 129916 = CPC 16823; **Unknown country (probably USA)**, from *Rubus* sp., collection date and collector unknown (deposited in CBS collection Apr. 1935 by K.J. Kadow as *Glomerella rubicola*), culture CBS 200.35. **Australia**, Queensland, Mount Tamborine, from fruit rot of *Persea americana*, 4 Sep. 2002, K.G. Pegg, culture CBS 127599 = BRIP 29284a; Queensland, Brisbane, from *Persea americana*, collection date and collector unknown (isolated J.H. Simmonds, No. 13120, 25 Jun 1958) culture CBS 293.67 = DPI 13120; Queensland, Yarwun, endophytic from stem of *Mangifera indica*, 16 Feb. 1994, G.I. Johnson, culture CBS 127601 = BRIP 28761a. **Portugal**, Lisbon, from *Vitis vinifera*, 2000, collector unknown, culture CBS 129947.

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

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

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

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

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

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

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

made. The name *C. rubicola* was cited on herbarium labels by Ellis & Everhart but only as an asexual name for *Glomerella rubicola*; apparently it was never accompanied by a description.

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

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

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

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

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

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



**Fig. 11.** *Colletotrichum godetiae* (F–G, L–M, T–U from ex-holotype strain CBS 133.44. A–E, H–K, N–S from strain CBS 125972). A–B. Conidiomata. C. Tip of a seta. D. Basis of a seta. E–M. Conidiophores. N–S. Appressoria. T–U. Conidia. A, C–H, T. from *Anthriscus* stem. B, I–S, U. from SNA. A–B. DM, C–U. DIC, Scale bars: A = 100 µm, E = 10 µm. Scale bar of A applies to A–B. Scale bar of E applies to C–U.

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

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

**Material examined:** **Denmark**, from seed of *Clarkia* (syn. *Godetia*) hybrida cv. Kelvedon Glory 463 C in seed disinfection experiment, 17 Jun. 1943, P. Neergaard, **culture ex-holotype** of *C. godetiae* CBS 133.44. **Italy**, Calabria, Rizziconi, from rotten fruit of *Olea europaea*, Oct. 1992, G.E. Agosteo and G. Magnano di San Lio, **culture ex-holotype** of *C. clavatum* CBS 130251 = OL10 = IMI 398854. **Greece**, from *Olea europaea*, collection date and collector unknown (deposited in CBS collection Jan. 1932 by L. Petri), culture CBS 193.32. **Netherlands**, Tilburg, from

*Fragaria × ananassa*, collection date and collector unknown, culture CBS 125972 = PD 85/456; near Meerssen, from fruit of *Sambucus nigra*, collection date and collector unknown (deposited in CBS collection Oct. 1970), culture CBS 862.70. **South Africa**, from *Podocarpus* sp., collection date unknown, A. Wood, culture CBS 129911. **Colombia**, Cundinamarca, from fruit anthracnose of *Solanum betaceum*, 13 Aug. 2010, J. Molina, culture CBS 129809 = T.A.1; Cundinamarca, from fruit anthracnose of *Solanum betaceum*, 13 Aug. 2010, J. Molina, culture CBS 129816 = T.A.8. **Chile**, Puerto Saavedra, from tip necrosis on twig of *Ugni molinae*, 1 Oct. 2008, A. Schilder, culture CBS 127561. **Mexico**, Montecillo, from *Schinus molle*, unknown collection date, M. de Jesus Yarez-Morales, culture CBS 129917. **USA**, Arkansas, Fayetteville, from *Aeschynomene virginica* (but see notes), collection date and collector unknown (deposited in CBS collection Aug. 1972 by G.E. Templeton as *C. gloeosporioides* f. sp. *aeschynomenes*), G.E. Templeton, culture CBS 796.72.

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



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

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

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

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

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

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

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

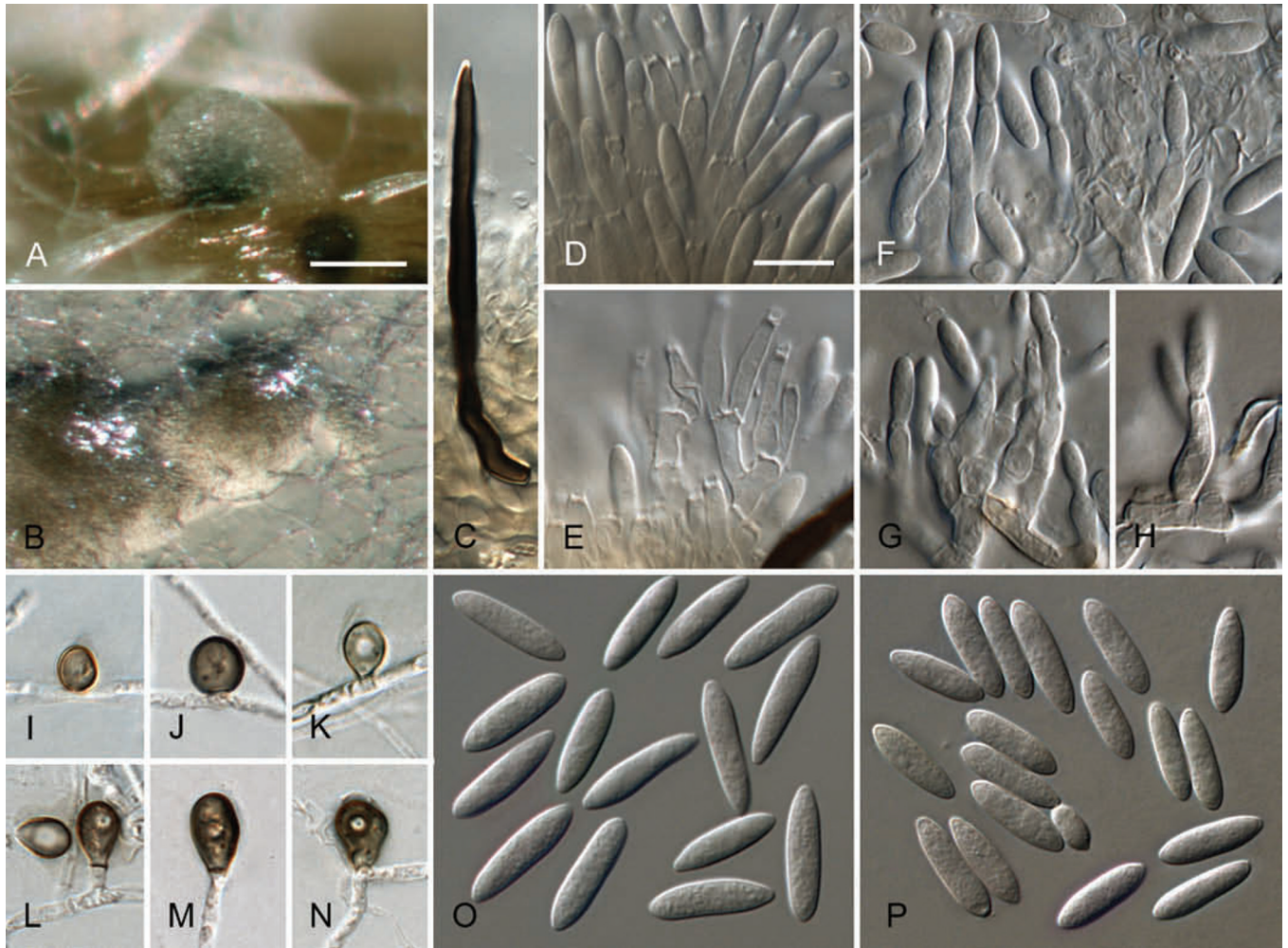
*Sexual morph* not observed. *Asexual morph on SNA.* Vegetative hyphae 1–6 µm diam, hyaline to pale brown, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* not developed, conidiophores formed directly on hyphae. *Setae* not observed. *Conidiophores* hyaline to pale brown,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

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

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

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

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



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

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

Peres *et al.* (2002) isolated *C. acutatum* (*s. lat.*) from a guava fruit in Brazil. It caused lesions on guava fruits that were slightly larger than those caused by a *C. acutatum* (*s. lat.*) isolate from strawberry. Based on the ITS sequences they generated, the isolates from guava and strawberry from Brazil belong to the same major clade as *C. guajavae*; the ITS sequence is in fact identical to that of *C. guajavae*, but also the same as a number of other species in this complex, making an identification to species level impossible without additional information. Based on a phylogeny from combined GAPDH and GS sequences in the study by Guerber *et al.* (2003), both strains belong to clade D (= clade 2 in this study), but not to the same subclade. The GAPDH sequence generated in Guerber *et al.* (2003) differs in 5 bp from that of *C. guajavae* ex-holotype strain IMI 350839. A strain from guava from New Zealand, included in the same study,

belongs to clade J3 *sensu* Guerber *et al.* (2003) (= *C. acutatum* *s. str.*). Apart from *C. acutatum* *s. lat.* and *C. psidii*, Farr & Rossman (2012) list reports from *Psidium* for *C. coccodes* in Myanmar, *C. gloeosporioides* in Brazil, China, Cuba, India, Mexico, Puerto Rico, South Africa, USA, Virgin Islands and Mexico, and *Colletotrichum* sp. in Brazil, Jamaica and Mexico; it is possible that some of these reports should be referred to *C. guajavae*.

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

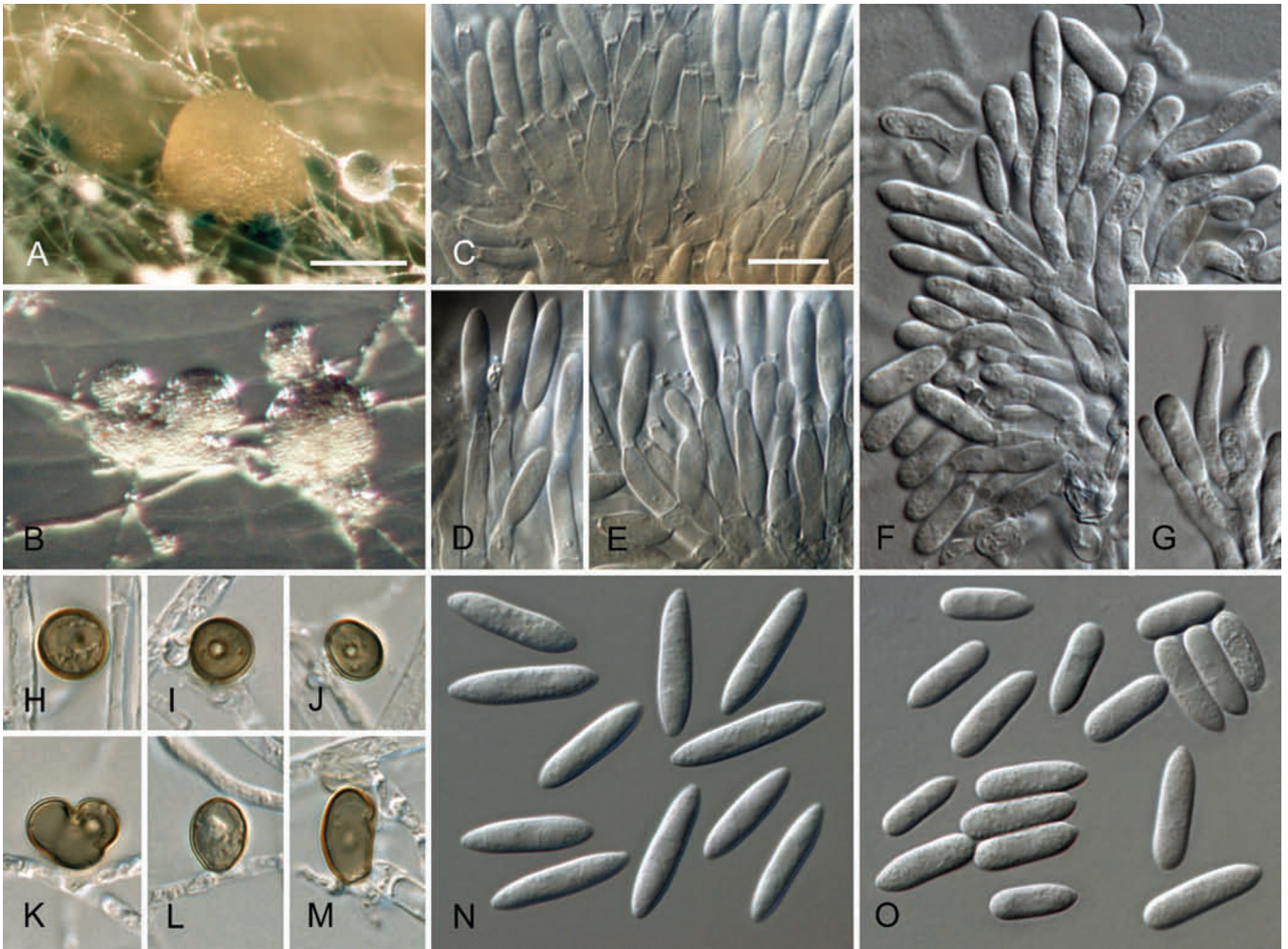


Fig. 13. *Colletotrichum indonesiense* (from ex-holotype strain CBS 127551). A–B. Conidiomata. C–G. Conidiophores. H–M. Appressoria. N–O. Conidia. A, C–E, N. from *Anthriscus* stem. B, F–M, O. from SNA. A–B. DM, C–O. DIC, Scale bars: A = 100  $\mu$ m, C = 10  $\mu$ m. Scale bar of A applies to A–B. Scale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

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

*Etymology*: Named after the country of origin, Indonesia.

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

*Asexual morph on Anthriscus stem*. *Conidiomata* acervular, conidiophores formed on pale brown, angular, basal cells 2.5–6  $\mu$ m diam. *Setae* not observed. *Conidiophores* hyaline to pale brown, smooth-walled, septate, branched, to 60  $\mu$ m long. *Conidiogenous cells* hyaline to pale brown, smooth-walled, cylindrical, sometimes  $\pm$  inflated, 9–25  $\times$  2–4  $\mu$ m, opening 1–1.5  $\mu$ m diam, collarette

1–1.5  $\mu$ m long, periclinal thickening visible. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical to fusiform with both ends acute, (10.5–)13–17.5(–19)  $\times$  (3–)3.5–4  $\mu$ m, mean  $\pm$  SD = 15.4  $\pm$  2.2  $\times$  3.7  $\pm$  0.2  $\mu$ m, L/W ratio = 4.1.

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

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

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

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

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

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

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

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

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

*Sexual morph* not observed. *Asexual morph* on SNA. *Vegetative hyphae* 1–7 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* not developed, conidiophores formed directly on hyphae. *Setae* not observed in

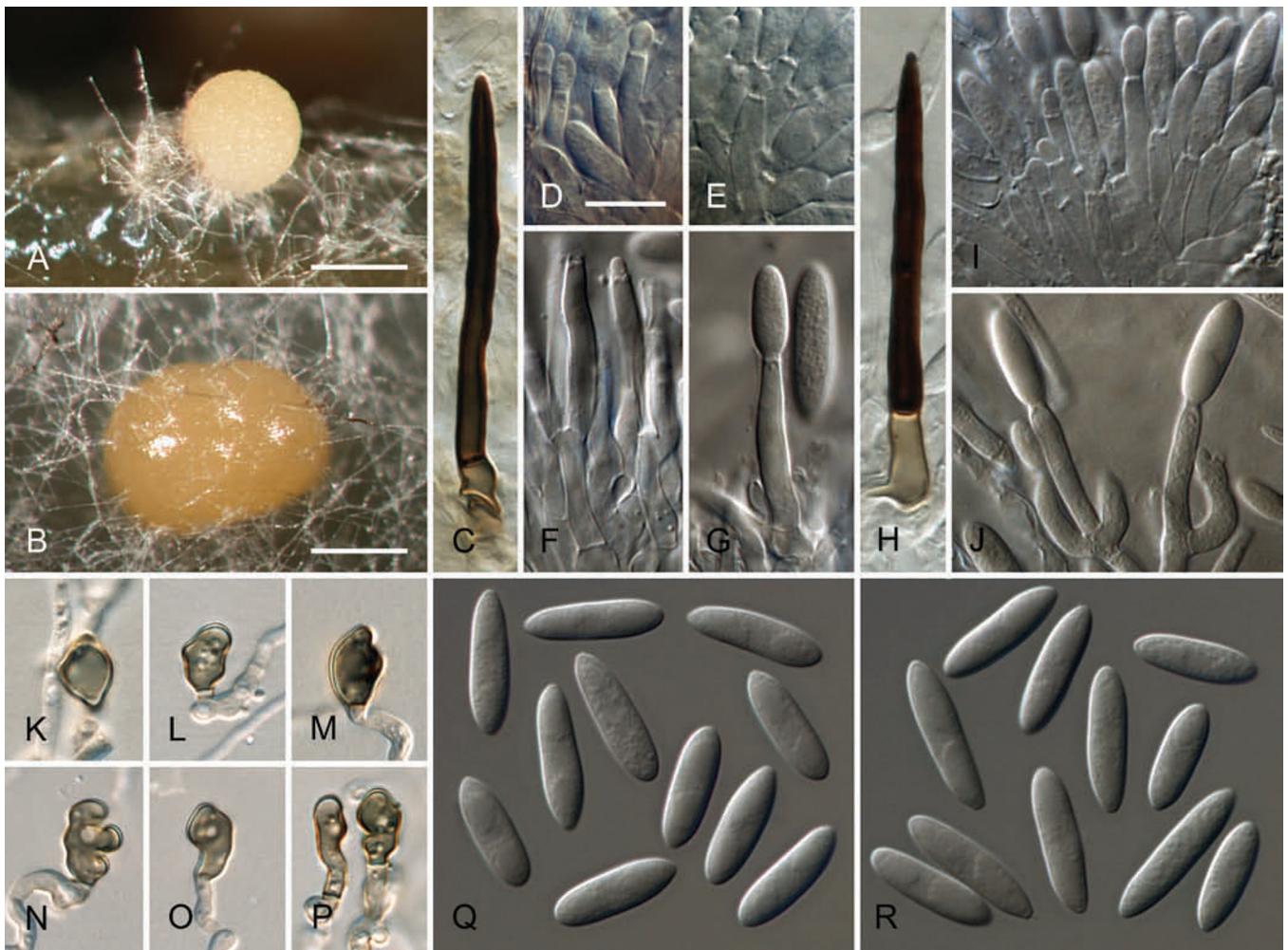
type, but present in strain IMI 357027, medium brown, basal cell sometimes pale brown, smooth-walled, 0–1-septate, 35–55 µm long, base cylindrical-conical, often constricted at septum, 3.5–4 µm diam, the tip ± acute. *Conidiophores* hyaline, smooth-walled, septate, branched. *Conidiogenous cells* hyaline smooth-walled, cylindrical, sometimes slightly inflated, sometimes lacking a basal septum and continuous with the conidiophore, some polyphialides observed, discrete phialides measure 6–27 × 2.5–4 µm, opening 1–2 µm diam, collarette 1–1.5 µm long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical to fusiform with one end slightly acute and one end round or slightly acute, (13.5–)14.5–19(–21.5) × (3.5–)4.5–5(–6) µm, mean ± SD = 16.7 ± 2.1 × 4.7 ± 0.4 µm, L/W ratio = 3.6. *Appressoria* sparse, single or in loose groups, pale to medium brown, smooth-walled, elliptical to clavate or irregular, the outline undulate or entire, (6–)8–11.5(–14) × (2–)4–7.5(–10.5) µm, mean ± SD = 9.6 ± 1.7 × 5.8 ± 1.9 µm, L/W ratio = 1.7.

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

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

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

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



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

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

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

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

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

**Sexual morph** not observed. **Asexual morph on SNA.** *Vegetative hyphae* hyaline, smooth-walled, septate, branched, 1–6  $\mu$ m diam. *Chlamydospores* not observed. *Conidiomata* absent, conidiophores formed directly on hyphae. *Setae* not observed. *Conidiophores* hyaline, smooth-walled, simple or septate and branched, up to 45

$\mu$ m long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical, conical or  $\pm$  inflated, 5.5–18  $\times$  2–3.5  $\mu$ m, opening 1–1.5  $\mu$ m diam, collarette 0.5–1.5, periclinal thickening visible. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical to fusiform with one round and one truncate end, (11–)15.5–21(–22.5)  $\times$  (3–)3.5–4(–4.5)  $\mu$ m, mean  $\pm$  SD = 18.3  $\pm$  2.9  $\times$  3.8  $\pm$  0.4  $\mu$ m, L/W ratio = 4.9. *Appressoria* not observed.

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

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

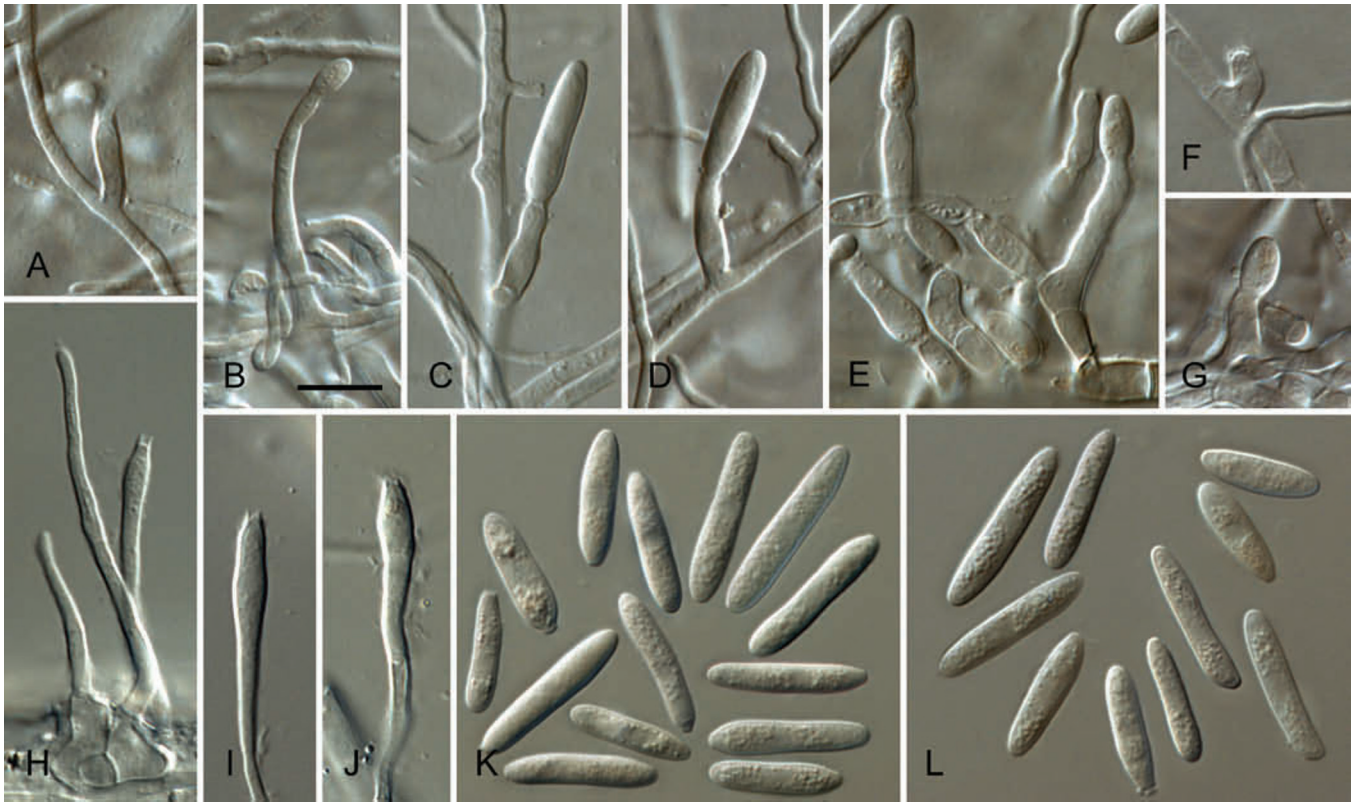


Fig. 15. *Colletotrichum kinghornii* (from ex-holotype strain CBS 198.35). A–J. Conidiophores. K–L. Conidia. H–K. from *Anthriscus* stem. A–G, L. from SNA. A–L. DIC, Scale bars: B = 10  $\mu$ m. Scale bar of B applies to A–L.

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

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

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

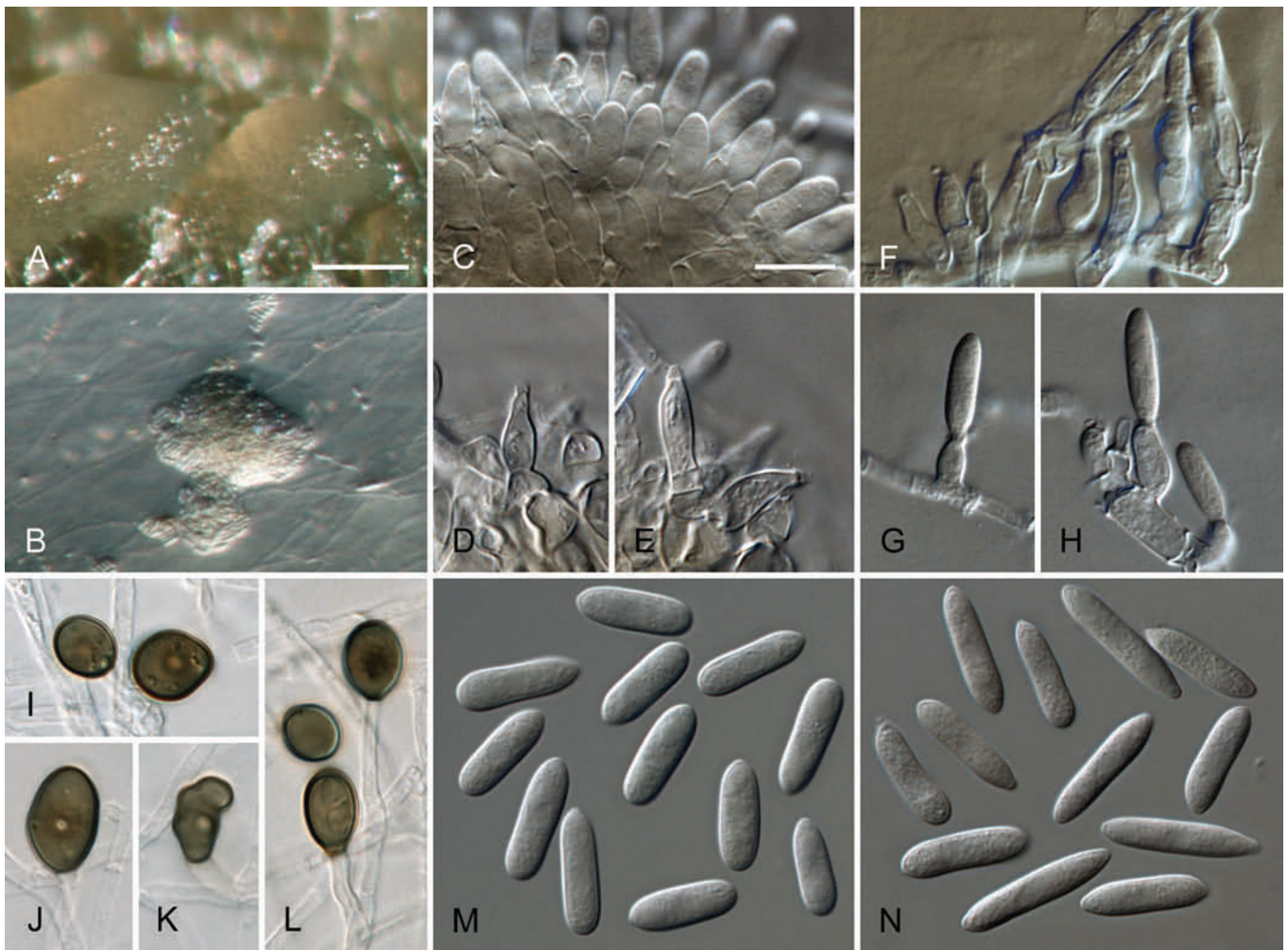
Closest match in blastn searches with the TUB2 sequence of strain CBS 198.35 (with 98 % identity, 7 bp differences) was *Glomerella acutata* isolate PCF 459 (EU635504) from strawberry in Belgium (Debode *et al.* 2009) and with 98 % identity (8 bp differences) isolate PT250 (= CBS 129953) AJ748624 from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

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

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

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

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



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

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

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

**Material examined:** **India**, Kerala, Kottayam, Rubber Research Institute campus, from raised spots on leaf of *Hevea brasiliensis*, 1999, unknown collector, (CBS H-20799 **holotype**, culture ex-type CBS 112989 = IMI 383015 = STE-U 5303 = CG<sub>3</sub>). **Colombia**, Meta, Villavicencio, from leaf, anthracnose of *Hevea brasiliensis*, 14 Aug. 2010, O. Castro, culture CBS 129827 = CH2.

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

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

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

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

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

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

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

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

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

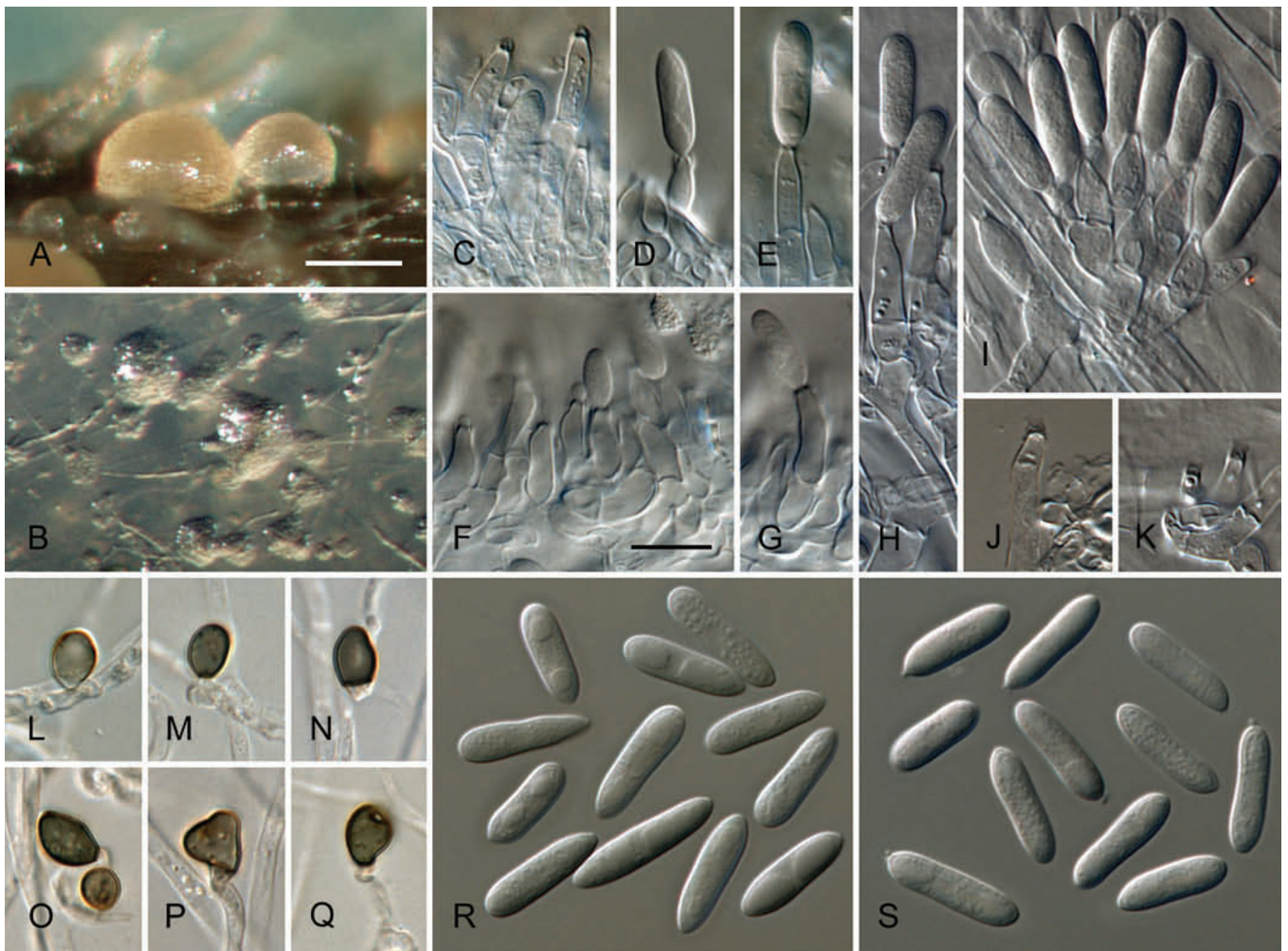
***Colletotrichum limetticola*** (R.E. Clausen) Damm, P.F. Cannon & Crous, **comb. nov.** MycoBank MB455483. Fig. 17. *Basionym*: *Gloeosporium limetticola* [as *Gm. limetticolum*] R.E. Clausen, *Phytopathology* 2: 231. 1912.

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

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

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





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

slightly) acute or both ends acute, (12–)13–18(–24)  $\times$  (3.5–)4–4.5(–5.5)  $\mu$ m, mean  $\pm$  SD = 15.5  $\pm$  2.3  $\times$  4.3  $\pm$  0.4  $\mu$ m, L/W ratio = 3.6.

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

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

**Notes:** *Gloeosporium limetticola* was described by Clausen (1912) following pathogenicity trials in California on young sour lime (*Citrus medica* var. *acida* = *Citrus aurantifolia*, Key lime) trees inoculated with strains from sour lime from Cuba and with strains from orange, lemon, pomelo and tangerine from Cuba, California, and Florida. The Cuban sour lime strain from Herradura consistently caused wither tip disease symptoms on tester plants from that species, and

another Cuban strain (from Santiago de las Vegas) caused broadly similar symptoms on both sour lime and lemon (*Citrus limon*) trees. Clausen stated that a virulent form of wither tip occurred in Florida also, but this author was unable to access diseased material to compare with the Cuban pathogen.

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

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

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

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

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

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

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

Chen *et al.* (2005) identified a gene (*KLAP1* gene) that was required for causing KLA, particularly for the infection of Key lime leaves, but not for the infection of flower petals.

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

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

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

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

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

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

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

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



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

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

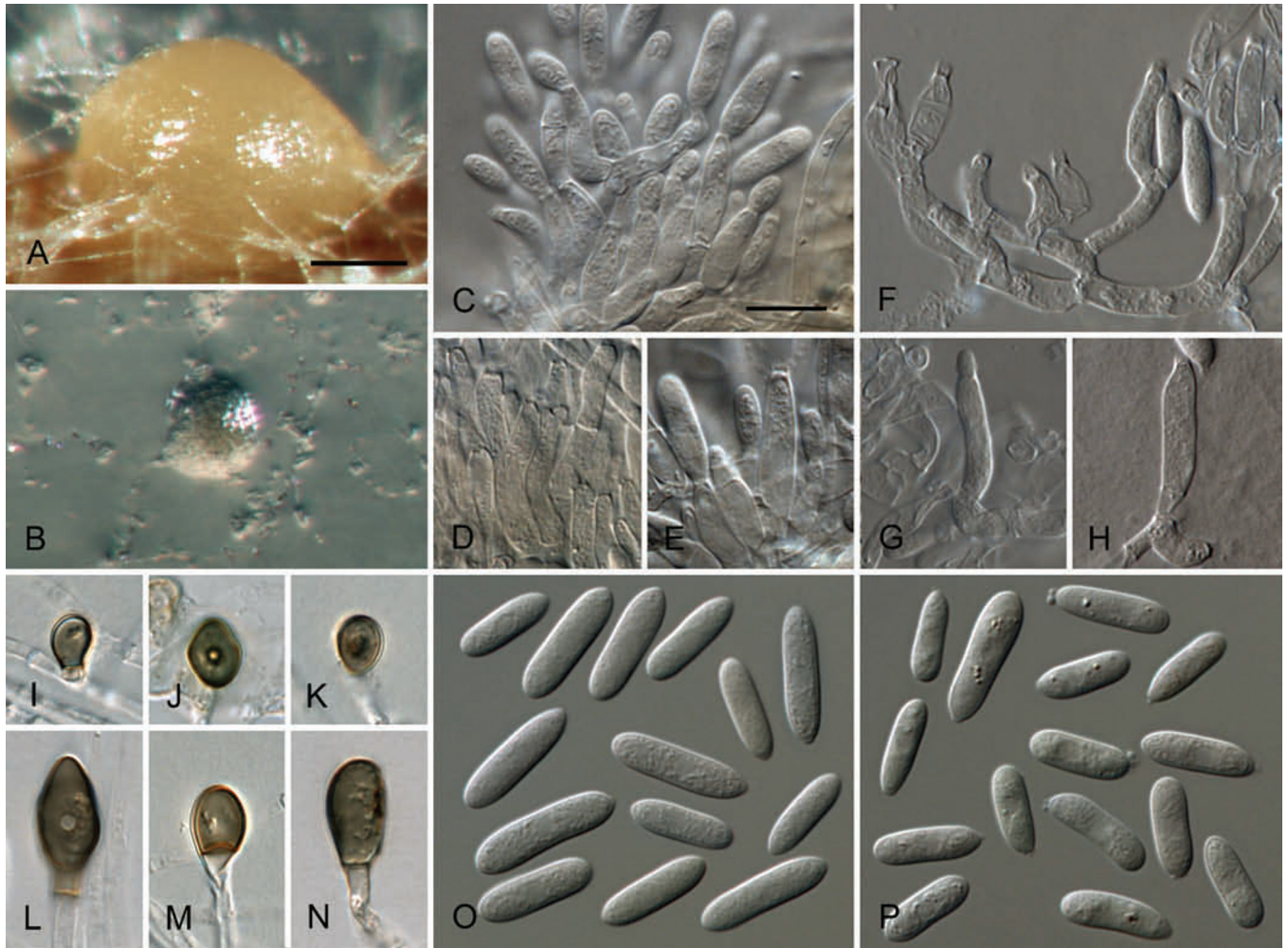
**Notes:** Two studies on the causal agent of lupin anthracnose published in 2002 arrived at different results: while Talhinas *et al.* (2002) regarded the causal agent of lupin anthracnose as *C. acutatum*, Nirenberg *et al.* (2002) concluded that the causal isolates belonged to a separate species,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

Nirenberg *et al.* (2002) additionally described a variety of the lupin pathogen, *C. lupini* var. *setosum*. They noted few morphological and physiological differences between the two varieties: strains of var. *lupini* were observed to produce more conidia than var. *setosum* in the aerial mycelium, as well as to grow slightly slower on PDA and to have a lower optimum growth temperature. In addition, var. *lupini* isolates usually formed concentric growth rings in culture, while var. *setosum* did not. The authors rarely observed setae in var. *lupini*, but these were regularly seen in var. *setosum*. In our study, the ex-holotype strain of *C. lupini* var. *setosum* formed a few setae.

Nirenberg and colleagues indicated that the ITS sequences of the two varieties differ in only one base. Our study, based on analysis of six genes, showed few other bp differences, blurring the distinction between the two varieties. The name *C. lupini* var. *setosum* was also invalidly published (Art. 43.1). As the species name *C. lupini* was invalid itself at the time, and as we do not accept the variety as a distinct taxon, we do not validate the name here.

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

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



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

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

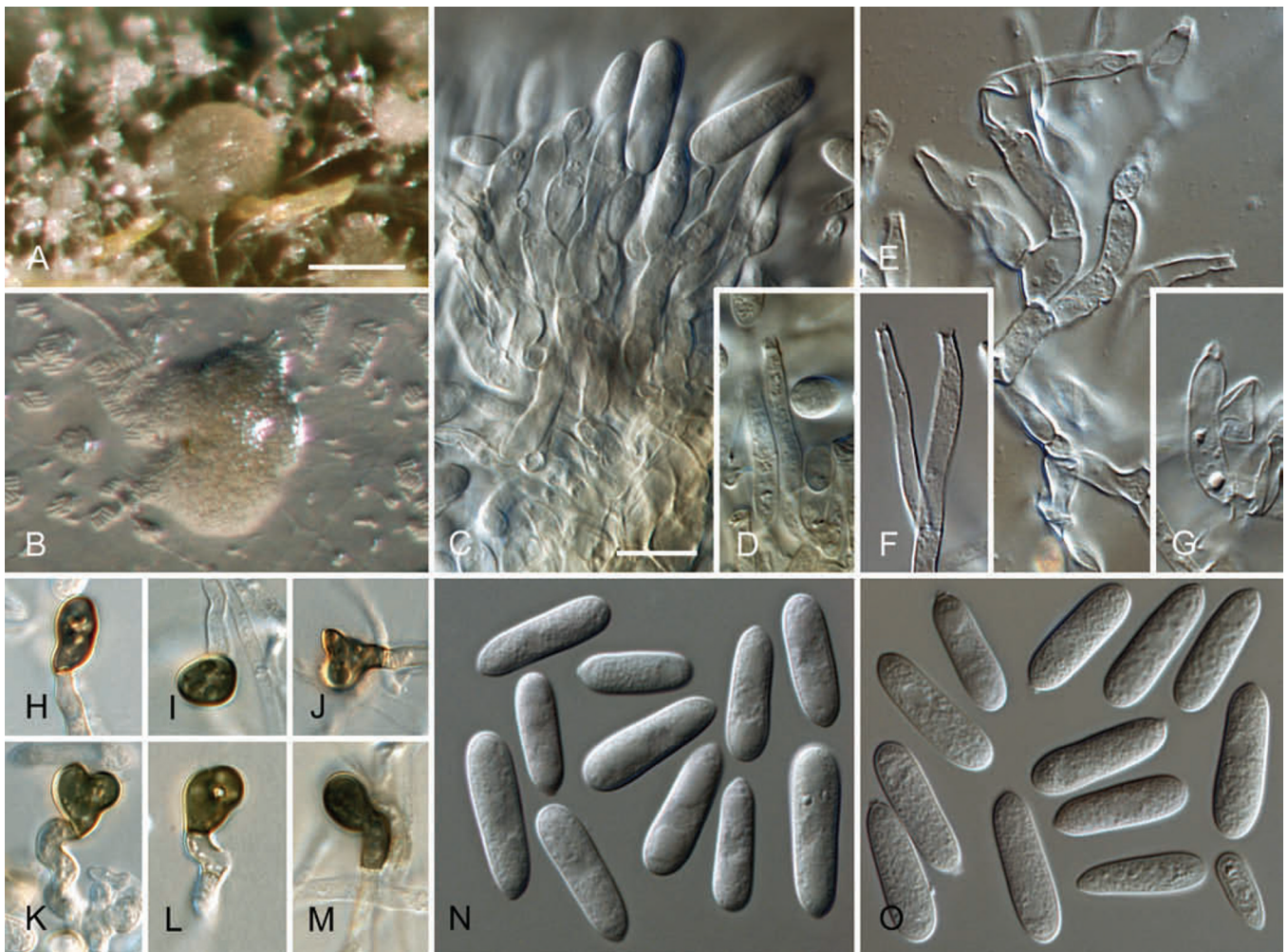
Our phylogeny clearly supports *C. lupini* as a distinct species within the *C. acutatum* species complex. *Colletotrichum lupini* is separated from other species by all genes included, except for ACT, with TUB2 providing the best differential test.

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

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

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

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



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

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

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

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

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

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

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

***Colletotrichum nymphaeae*** (Pass.) Aa, Netherlands J. Pl. Pathol., Supplement 1 84: 110. 1978. Fig. 20.

**Basionym:** *Ascochyta nymphaeae* Pass., in Rabenh., Fungi Europaei edn 2: 2251 (1876, in sched.); Hedwigia 16: 120. 1877.

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

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

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

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

**Material examined:** **Italy**, Parma, in horto botanico, from leaf of *Nymphaea alba*, summer 1875, G. Passerini, in Rabenhorst, *Fungi Europaei exsiccati* edn 2: 2251 (holotype not selected by the original author and location uncertain; K(M) 176820 isotype, here designated as **lectotype**; K(M) 99741 isolectotype; CBS H-00769 isolectotype). **Netherlands**, Oude Waal near Nijmegen, Gem. Ubbergen, from leaf spots of *Nymphaea alba*, 7 Aug. 1978, G. van der Velde, (CBS H-20787 **epitype**, here designated, culture ex-epitype CBS 515.78 = van der Aa No. 6573); Kortenhoefse Plassen from leaf of *Nymphaea alba*, collection date and collector unknown (isolated Aug. 1977 by H.A. van der Aa), culture CBS 526.77; from curl disease of *Anemone coronaria* De Caen, collection date and collector unknown, CBS 126382 = PD 79/648. **Italy**, Rome, from leaf of *Mahonia aquifolium*, collection

date and collector unknown (deposited in CBS collection Jun. 1951 by R. Ciferri), culture CBS 173.51; Rome, from *Fragaria x ananassa*, cv. Idea, collection date and collector unknown (send to Plantenziektenkundige Dienst Wageningen by L. Corazza), culture CBS 126372 = PD 93/1666A. **South Africa** Western Cape, Stellenbosch, Elsberg Farm, from *Protea magnifica*, 1 Apr. 2001, K. Lubbe, culture CBS 112992 = STE-U 4452. **Spain**, from fruit lesions of *Fragaria* sp., Mar. 2002, H.A. van der Aa, culture CBS 112202.

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

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

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

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

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



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

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

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

*Colletotrichum nymphaeae* is well separated from other species with TUB2, but not in its ITS. With all other genes the intraspecific variability is very high. The closest matches (100 % identity) in a blastn search using the TUB2 sequence of the ex-epitype strain were AB618090 from *Apium* in Japan (Fujinaga *et al.* 2011); AY376551–AY376555 from *Protea* (Lubbe *et al.* 2004); AJ409296, AJ314716, AJ314718 from *Fragaria* in USA, Portugal and Australia; AJ314722, AJ409300, AJ748636 from *Lupinus* and *Anemone* (Talhinhas *et al.* 2002, 2005); and DQ454063, DQ454064 from *Fragaria* in Thailand (Than *et al.* 2008a). With 99 % identity reflecting 1 bp difference,

the search yielded AJ748605, AJ748607, AJ748608, AJ748611, AJ748615 from olive; AM992148, AM992147 probably also from olive; AJ748633 from *Photinia* (Talhinhas *et al.* 2005, 2009); and GQ369612 from a strain identified as *C. caudatum* (Chen H, Feng Y and Hyde KD, unpubl. data). With 99 % identity reflecting 2 bp differences, we got EF593327 and EF593328 from strains ARSEF4360 and EMA26, respectively, from *Orthezia praelonga* in Brazil (Marcelino *et al.* 2008). These two strains were identified as *C. gloeosporioides* f. sp. *ortheziidae* and have entomopathogenic activity to the scale insect *Orthezia praelonga*. They are apparently being used effectively as a biological control agent against this insect in Brazil (Cesnik *et al.* 1996, Cesnik & Ferraz 2000). Several of these strains listed above are included in this study.

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

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

*Sexual morph* not observed. *Asexual morph* on SNA. *Vegetative hyphae* 1.5–7  $\mu$ m diam, hyaline to pale brown, smooth-walled, septate, branched. *Chlamydo-spores* not observed. *Conidiomata* not developed, conidiophores and setae formed directly on hyphae. *Setae* abundant, medium brown, basal cell often paler, smooth-

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

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

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

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

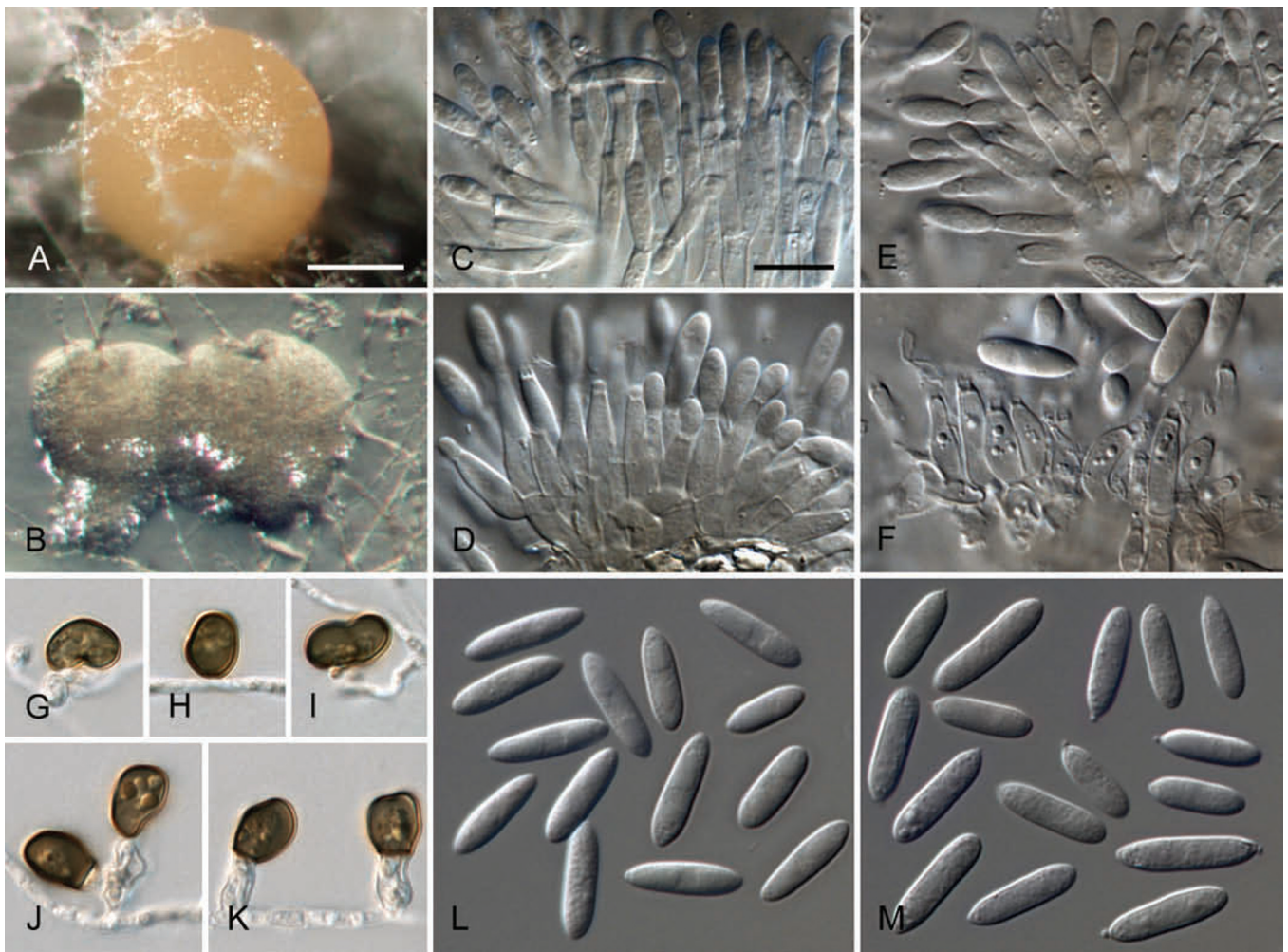
**Notes:** Diagnostic features for *C. orchidophilum* include its very narrow (usually 3–3.5 µm wide) cylindrical conidia, abundantly formed setae and dark brown, uniformly shaped, pyriform to spatulate appressoria. *Colletotrichum orchidophilum* is basal to the *C. acutatum* species complex (fig. 1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

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

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

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





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

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

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

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

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

*Sexual morph* not observed. *Asexual morph on SNA.* Vegetative hyphae 1–8  $\mu$ m diam, hyaline to pale brown, smooth-walled, septate, branched. *Chlamydo-spores* not observed. *Conidiomata* not developed, conidiophores formed directly on hyphae. *Setae* not observed. *Conidiophores* hyaline, smooth-walled, septate, branched, to 30  $\mu$ m long. *Conidiogenous cells* hyaline, smooth-walled, cylindrical to  $\pm$  inflated, 5–10  $\times$  2–4  $\mu$ m, opening 1–1.5  $\mu$ m diam, collarette 1–1.5  $\mu$ m long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical with one end round and one end slightly acute both ends slightly acute, (5–)10.5–15.5(–19.5)  $\times$  (2.5–)3.5–4(–4.5)  $\mu$ m, mean  $\pm$  SD = 13.0  $\pm$  2.6  $\times$  3.7  $\pm$  0.3  $\mu$ m, L/W ratio = 3.5. *Appressoria* single or in loose groups, medium brown, smooth-walled, subglobose, elliptical or clavate, the edge undulate or entire, (5–)6–11.5(–16.5)  $\times$  (3.5–)5.5–7.5(–8.5)  $\mu$ m, mean  $\pm$  SD = 8.8  $\pm$  2.7  $\times$  6.5  $\pm$  1.1  $\mu$ m, L/W ratio = 1.4, strain CBS 502.97 forms smaller appressoria, measuring (3.5–)4.5–7.5(–10.5)  $\times$  (3–)3.5–5(–5.5)  $\mu$ m, mean  $\pm$  SD = 6.0  $\pm$  1.7  $\times$  4.2  $\pm$  0.7  $\mu$ m, L/W ratio = 1.4.

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

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

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

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

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

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

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

Additional species on *Musa* have been described in *Gloeosporium*. *Gloeosporium musarum* Cooke & Massee has elongate-ellipsoidal conidia with both ends rounded, measuring 12

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

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

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

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

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

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

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

$\equiv$  *Gloeosporidium rhodocyclum* (Mont. ex Almeida & Souza da Camara) Höhn., Anns mycol. 18(1/3): 92. 1920.

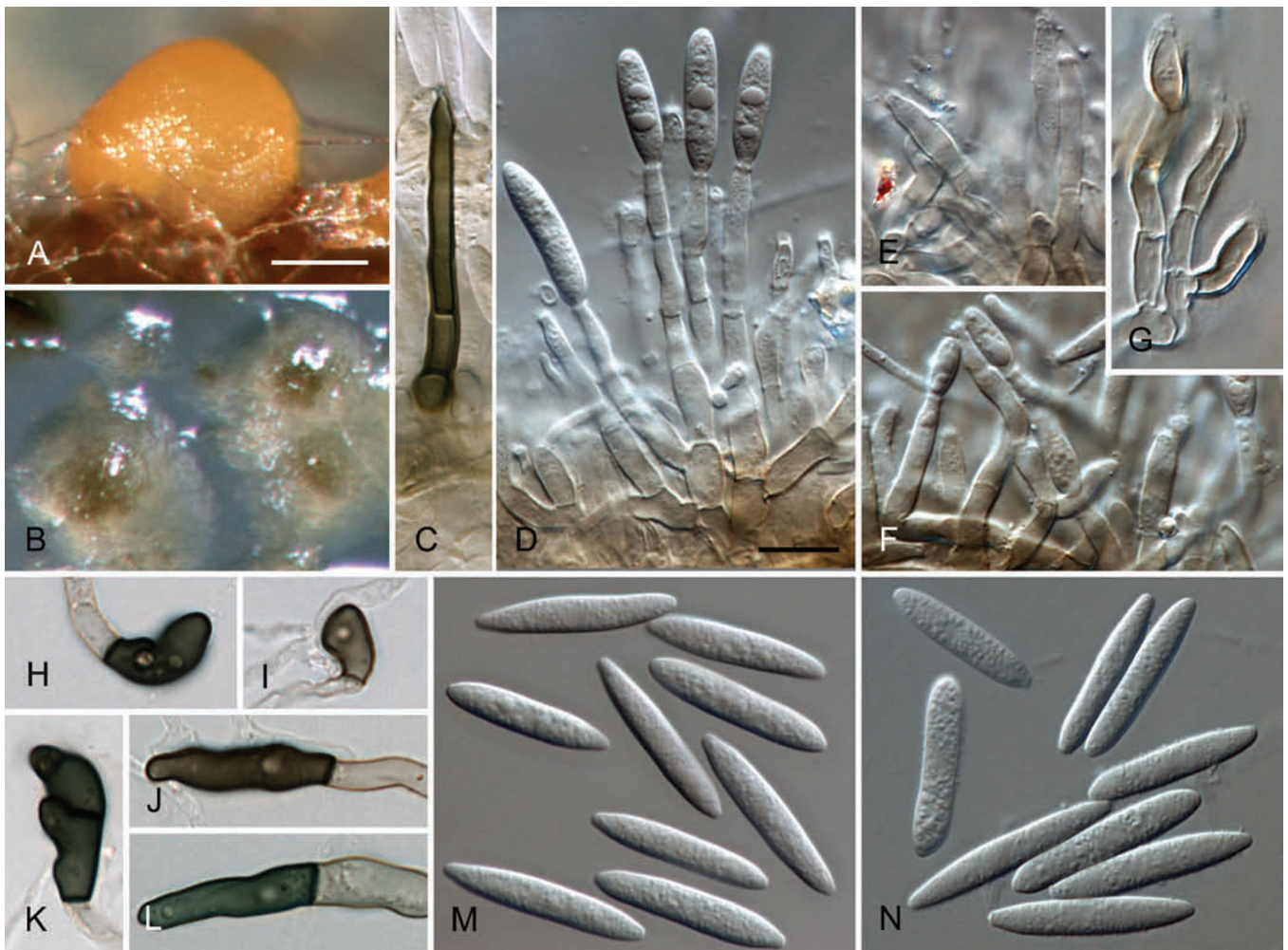
$\equiv$  *Colletotrichum rhodocyclum* (Mont. ex Almeida & Souza da Camara) Petr., Anns mycol. 25(3/4): 251. 1927.

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

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

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

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



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

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

*Asexual morph on Anthriscus stem.* *Conidiomata* acervular, conidiophores and setae formed on a cushion of pale brown roundish to angular cells, 2.5–10  $\mu$ m diam. *Setae* few, hyaline to medium brown, smooth-walled, 0–1-septate, 25–70  $\mu$ m long, base cylindrical, to 5  $\mu$ m diam, tip  $\pm$  roundish to  $\pm$  acute. *Conidiophores* pale brown, smooth-walled, septate, branched, to 50  $\mu$ m long. *Conidiogenous cells* pale brown, smooth-walled, usually cylindrical, sometimes elongate ampulliform to ampulliform, 8–25  $\times$  2.5–3.5(–5.5)  $\mu$ m, opening 1–1.5  $\mu$ m diam, collarette 1  $\mu$ m long, periclinal thickening visible. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical to fusiform with both ends acute, (14–)20–24.5(–25.5)  $\times$  4–4.5(–5)  $\mu$ m (one conidium measured 47  $\times$  5  $\mu$ m), mean  $\pm$  SD = 22.3  $\pm$  2.3  $\times$  4.3  $\pm$  0.2  $\mu$ m, L/W ratio = 5.2,

conidia of most other strains are slightly broader and those of strain CBS 118191 are additionally shorter than conidia of the ex-epitype strain, measuring (14–)18.5–22(–24)  $\times$  (4–)4.5–5(–5.5)  $\mu$ m, mean  $\pm$  SD = 20.3  $\pm$  1.9  $\times$  4.9  $\pm$  0.4  $\mu$ m, L/W ratio = 4.1.

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

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

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

Species	Accession No.	Conidia on SNA			Conidia on <i>Anthriscus</i> stem		
		length × width (µm) <sup>2</sup>	length × width (µm) mean ± stdev	L/W ratio	length × width (µm) <sup>2</sup>	length × width (µm) mean ± stdev	L/W ratio
<i>C. acerbum</i>	CBS 128530*	15.5–20.5(–29) × (4–)4.5–5	17.9 ± 2.4 × 4.7 ± 0.2	3.8	(12.5–)15–18.5(–20.5) × (4–)4.5–5	16.8 ± 1.7 × 4.7 ± 0.3	3.6
	CBS 112996*	(7.5–)11–14.5(–19) × 3.5–4(–4.5)	12.6 ± 1.8 × 3.9 ± 0.3	3.2	(8.5–)12–16.5(–17.5) × (3–)3.5–4.5(–5)	14.3 ± 2.1 × 4.1 ± 0.4	3.5
<i>C. acutatum</i>	CBS 111993	(10.5–)12–16(–20) × (3–)3.5–4.5(–5)	14.0 ± 1.8 × 4.0 ± 0.5	3.5	(12.5–)14–17(–18) × (3.5–)4–4.5(–5)	15.5 ± 1.3 × 4.2 ± 0.3	3.7
	CBS 127602	(8–)11.5–14.5(–15) × (2.5–)3.5–4	13.0 ± 1.5 × 3.8 ± 0.4	3.5	(8–)12.5–18.5(–22) × 4–4.5	15.5 ± 2.9 × 4.2 ± 0.3	3.7
<i>CBS 112990</i>	(8.5–)12.5–15.5(–17.5) × (2.5–)4–5	14.1 ± 1.6 × 4.3 ± 0.5	3.3	(8.5–)11.5–15.5(–17) × (3.5–)4–4.5(–5)	13.5 ± 1.8 × 4.2 ± 0.3	3.2	
<i>CBS 129915</i>	(7–)12–15.5(–16.5) × (3.5–)4–4.5(–5)	13.8 ± 1.9 × 4.1 ± 0.3	3.3	(6.5–)11–14.5(–15.5) × (3.5–)4–4.5(–5)	12.8 ± 2.0 × 4.3 ± 0.3	2.9	
<i>CBS 112759</i>	(6.5–)8.5–12(–13) × (2.5–)3–4	10.3 ± 1.9 × 3.4 ± 0.5	3.1	(8–)11–15(–19) × (3–)4–5	12.9 ± 1.9 × 4.5 ± 0.4	2.9	
<i>CBS 112761</i>	(7.5–)10–15.5(–20.5) × (3–)3.5–4.5(–6)	12.7 ± 2.7 × 4.1 ± 0.5	3.1				
<i>CBS 37073</i>							
<i>CBS 79772</i>	(6–)8.5–13(–18) × 3.5–4.5(–5)	10.8 ± 2.3 × 4.0 ± 0.3	2.7	(5–)6.5–11(–12.5) × (2–)2.5–3.5(–4.5)	8.8 ± 2.1 × 3.2 ± 0.5	2.7	
<i>CBS 110735</i>	(7.5–)11–16.5(–21) × (3–)3.5–4(–4.5)	13.7 ± 2.5 × 3.8 ± 0.4	3.6	(5.5–)10–14(–15.5) × (3–)4–5	12.0 ± 2.2 × 4.4 ± 0.5	2.7	
<i>CBS 112979</i>	(7.5–)9–13(–15) × (2–)3–3.5(–4)	11 ± 2.0 × 3.3 ± 0.4	3.3	(12.5–)14–17(–17.5) × (3.5–)4–4.5(–5)	15.5 ± 1.5 × 4.4 ± 0.3	3.5	
<i>CBS 97969</i>	(5–)8.5–14.5(–16.5) × (2.5–)3–4(–4.5)	11.5 ± 3.1 × 3.5 ± 0.4	3.3	(9–)10.5–15.5(–16.5) × (3–)3.5–4.5(–5)	13.1 ± 2.4 × 4.2 ± 0.5	3.1	
<i>IMI 319423</i>	(8–)11.5–14.5(–16) × (3–)3.5–4.5	13.2 ± 1.5 × 4.0 ± 0.3	3.3	(12–)13–15.5(–17) × (3.5–)4–4.5(–5)	14.1 ± 1.3 × 4.1 ± 0.3	3.4	
<i>CBS 116478*</i>	(10–)14.5–19.5(–25) × (3.5–)4–5(–6)	17.0 ± 2.4 × 4.4 ± 0.5	3.9	(7.5–)11.5–15.5(–19.5) × (3–)3.5–4.5	13.6 ± 2.0 × 4.0 ± 0.4	3.4	
<i>CBS 131320</i>	(14–)15–19(–26) × (3.5–)4–5(–5.5)	17.0 ± 2.0 × 4.5 ± 0.3	3.8	(16–)17–20(–22) × (4–)4.5–5(–5.5)	18.6 ± 1.6 × 4.7 ± 0.4	4.0	
<i>CBS 29267*</i>	(12–)12–17.5(–25) × (3–)3.5–4(–5)	14.8 ± 2.8 × 3.8 ± 0.5	3.9	(13.5–)15–17.5(–18) × (3.5–)4–5(–5.5)	16.3 ± 1.1 × 4.4 ± 0.4	3.7	
<i>CBS 126518</i>	(6–)7–9.5(–12) × (3–)4–5(–6)	8.3 ± 1.3 × 4.8 ± 0.6	1.7	(9.5–)12–15(–17) × (3–)3.5–4	13.5 ± 1.4 × 3.9 ± 0.3	3.5	
<i>CBS 126518'</i>	(3.5–)4.5–9(–15) × 3–5(–6.5)	6.7 ± 2.3 × 4.1 ± 0.8	1.6	(3.5–)6.5–10.5(–13.5) × (3.5–)4–5(–5.5)	8.5 ± 1.8 × 4.5 ± 0.5	1.9	
<i>CBS 126519'</i>	(4–)5–10(–14) × (3–)3.5–5(–6)	7.4 ± 2.6 × 4.1 ± 0.6	1.8	(6.5–)8–10.5(–14.5) × (3–)4–5(–5.5)	9.2 ± 1.4 × 4.5 ± 0.4	2.0	
<i>IMI 364540</i>	(4.5–)6.5–13(–26) × (3–)3.5–5(–11)	9.8 ± 3.2 × 4.3 ± 0.9	2.3	(5–)6.5–12.5(–21) × (2–)3.5–5(–6)	9.4 ± 2.9 × 4.3 ± 0.7	2.2	
<i>CBS 853.73*</i>	(7–)13–18.5(–19.5) × (3–)3.5–4.5	15.8 ± 2.5 × 4.0 ± 0.4	4.0	(12–)14–16.5(–18) × (3.5–)4–4.5	15.3 ± 1.4 × 4.0 ± 0.3	3.8	
<i>CBS 330.75*</i>	(9–)11.5–18(–28) × (3–)3.5–4(–4.5)	14.6 ± 3.1 × 3.7 ± 0.3	4.0	12.5–)13.5–16(–18) × 3.5–4	14.8 ± 1.4 × 3.8 ± 0.3	3.9	
<i>CBS 211.78</i>	(11.5–)12–16(–20) × (3.5–)4–4.5	13.9 ± 1.9 × 4.3 ± 0.2	3.2	(12–)14–16.5(18.5) × (3.5–)4–4.5	15.2 ± 1.4 × 4.2 ± 0.2	3.6	
<i>IMI 304802*</i>	(15.5–)17.5–21(–22.5) × (3–)3.5–4.5	19.2 ± 1.7 × 4.0 ± 0.3	4.8	(15–)17–20(–21) × (3.5–)4–4.5	18.6 ± 1.5 × 4.2 ± 0.2	4.5	
<i>CBS 128517*</i>	(10–)13.5–16.5(–19.5) × 4–5(–5.5)	15.0 ± 1.6 × 4.5 ± 0.3	3.3	(12.5–)14–18.5(–24.5) × 4–5	16.1 ± 2.2 × 4.4 ± 0.4	3.6	
<i>CBS 200.35</i>	(8–)10.5–17.5(–30.5) × 3.5–5(–6.5)	14.1 ± 3.4 × 4.3 ± 0.6	3.3	(9–)12.5–17.5(–23) × (3.5–)4–5	15.0 ± 2.3 × 4.4 ± 0.4	3.4	
<i>CBS 127599</i>	(7.5–)12–16.5(–17) × (2.5–)4–5(–5.5)	14.4 ± 2.4 × 4.5 ± 0.6	3.2	(10.5–)13.5–17(–17.5) × (3.5–)4–5	15.1 ± 1.7 × 4.4 ± 0.4	3.4	
<i>CBS 129916</i>	(6.5–)11.5–16 × (3–)3.5–4.5(–5)	13.8 ± 2.2 × 3.9 ± 0.4	3.5	(10–)13–16.5(–18) × (4–)4.5–5(–5.5)	14.8 ± 1.7 × 4.7 ± 0.3	3.2	
<i>CBS 127601</i>	(4.5–)10.5–18(–20) × (3.5–)4–5(–5.5)	14.2 ± 4.0 × 4.5 ± 0.4	3.2	(7–)13.5–18.5(–19) × (3.5–)4–4.5(–5)	15.9 ± 2.3 × 4.4 ± 0.4	3.6	
<i>CBS 129947</i>	(10.5–)12–15(–17) × 3.5–5(–6)	13.5 ± 1.7 × 4.1 ± 0.8	3.3	(13–)14–16(–17) × (3.5–)4–4.5(–5)	15.0 ± 1.0 × 4.3 ± 0.4	3.5	
<i>CBS 29367</i>	(8.5–)12.5–16(–17.5) × (3–)3.5–4.5(–5)	14.4 ± 1.7 × 4.0 ± 0.5	3.6	(13–)14–16.5(–18) × (4–)4.5–5(–5.5)	15.2 ± 1.3 × 4.7 ± 0.3	3.2	
<i>CBS 133.44*</i>	(7–)10.5–14.5(–15.5) × (3.5–)4–5(–5.5)	12.4 ± 2.0 × 4.3 ± 0.5	2.9	(9.5–)10.5–15(–20.5) × 4–5	12.8 ± 2.3 × 4.5 ± 0.4	2.8	
<i>CBS 125972</i>	(5.5–)12–16.5(–17) × (3.5–)4–4.5(–5)	14.2 ± 2.2 × 4.3 ± 0.4	3.3	(13.5–)14–16(–17) × (4–)4.5–5	15.1 ± 0.9 × 4.7 ± 0.3	3.2	

Table 2. (Continued).

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

Table 2. (Continued).

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

\*ex-type strain

<sup>1</sup>aerial mycelium<sup>2</sup>(min-)min-stdev-max-stdev(-max)

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

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

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

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

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

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

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

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

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

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

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

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

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



Table 3. (Continued).

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

\* ex-type strain

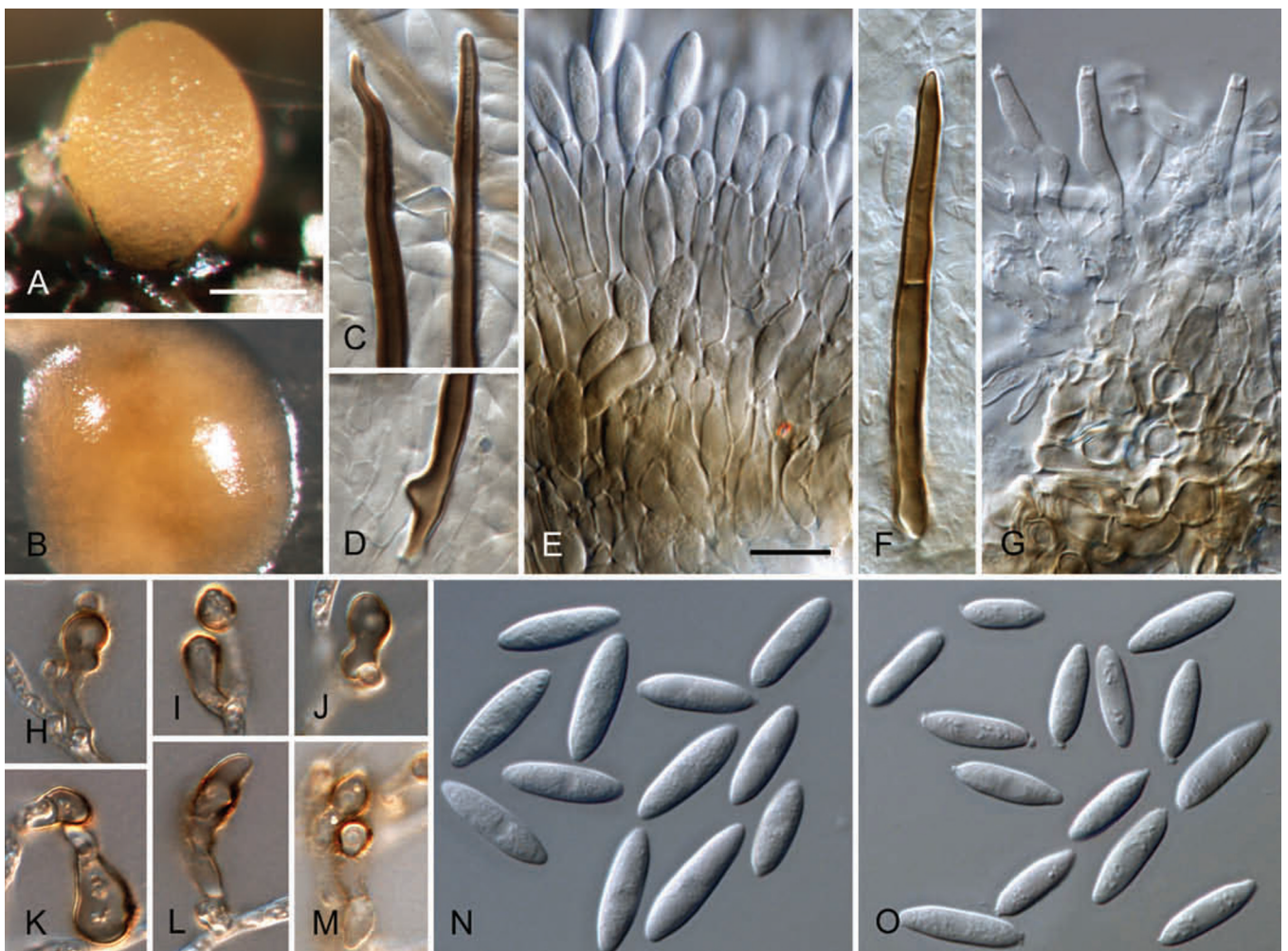
<sup>1</sup>(min–)min–stdev–max–stdev(–max)

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



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

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

Strain CBS 436.77 turns out not to be closely related to *C. acutatum* f. *pineum*, which belongs to *C. acutatum* s. str. (Fig. 1). *Colletotrichum pseudoacutatum* is at best basal to the *C. acutatum* species complex and forms a sister group to a clade containing the *C. acutatum* complex and *C. orchidophilum* (fig. 2 in Cannon *et al.* 2012, this issue). The closest matches in a blastn search on the ITS sequence of strain CBS 436.77 (with only 94 % identity) are unidentified *Colletotrichum* isolates, e.g. from *Podocarpaceae* in New Zealand (Joshee *et al.* 2009), plus several *C. coccodes* strains including the ex-epitype strain CBS 164.49 (HM171678, Liu *et al.* 2011), *C. trichellum* strains MEP1535 (= CBS 118198, DQ286152, Farr *et al.* 2006) and DAOM 188792 (= CBS 125343, EU400142, wrongly identified as *C. dematium*, Chen YY, Conner R, Babcock C, Penner W, unpubl. data) and “*C. gloeosporioides*” strains DAOM

183087 (EU400145, probably *C. coccodes*, Chen YY, Conner R, Babcock C, Penner W, unpubl. data) and BBA 71369 from *Pleione* (AJ301980, probably *C. orchidophilum*, Nirenberg *et al.* 2002). The closest matches with the TUB2 sequence showed only 82 % identity, including *C. trichellum* strains HKUCC 10378, CBS 217.64 and CBS 118198 (GQ849447, Yang *et al.* 2009, GU228106, GU228107, Damm *et al.* 2009). There is no match over the whole span of the GAPDH sequence of this species.

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

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

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

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

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

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

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

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

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

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

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

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

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

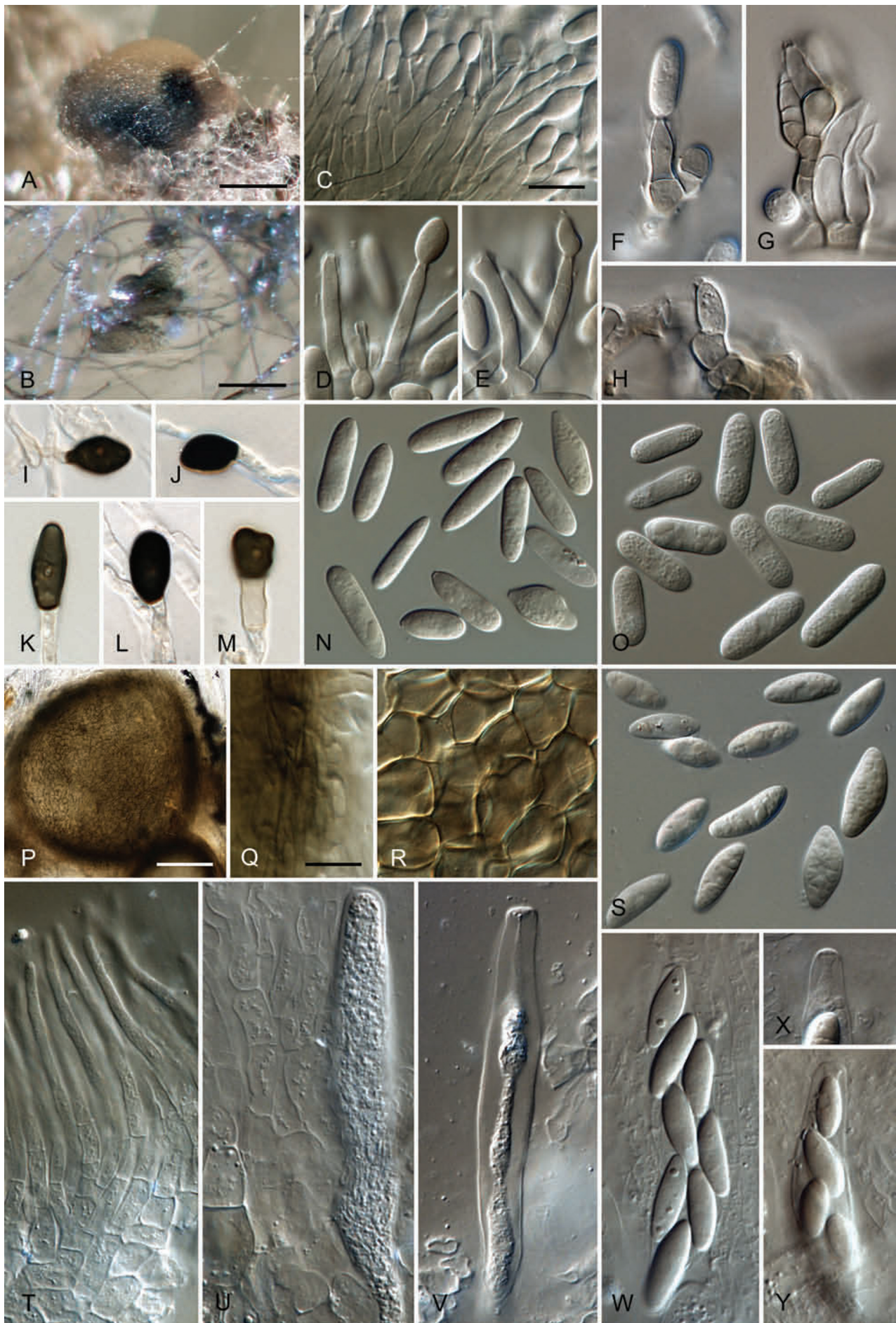
*Etymology:* Named after the shape of the ascospores, which can be rhomboidal.

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

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

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

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



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

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

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

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

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

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

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

CBS 131322, the other isolate of *C. rhombiforme* included in this study) (Robideau *et al.* 2008).

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

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

- ≡ *Sphaeria salicis* Auersw., in Fuckel, Fungi Rhen. no. 913, in sched. 1864, nom. nud.
- ≡ *Physalospora salicis* (Fuckel) Sacc., Syll. fung. (Abellini) 1: 439. 1882.
- ≡ *Physosporella salicis* (Fuckel) Höhn., Annl. mycol. 16: 58. 1918.
- ≡ *Anisostomula salicis* (Fuckel) Petr., Hedwigia 65: 198. 1925.
- ≡ *Plectosphaera salicis* (Fuckel) Arx & E. Müll., Beitr. Kryptfl. Schweiz 11 (no. 1): 204. 1954.
- ≡ *Glomerella salicis* (Fuckel) L. Holm, in Holm & Ryman, Thunbergia 30: 6. 2000.
- = *Phyllachora amenti* Rostr., Skr. Christiana Vidensk.-Selsk. Forhandl. 9: 5. 1891.
- ≡ *Haplothecium amenti* (Rostr.) Theiss. & Syd., Annl. Mycol. 13: 615. 1915.
- ≡ *Glomerella amenti* (Rostr.) Arx & E. Müll., Beitr. Kryptfl. Schweiz 11 (no. 1): 197. 1954.
- = *Glomerella lycopersici* F. Krüger, Arbeiten Kaiserl. Biol. Anst. Land-Forstw. 9: 308. 1913.
- ≡ *Gloeosporium lycopersici* F. Krüger, Arbeiten Kaiserl. Biol. Anst. Land-Forstw. 9: 308. 1913.
- ≡ *Colletotrichum kruegerianum* Vassiljevsky, Fungi Imperfecti Parasitici 2: 321. 1950 [non *C. lycopersici* Chester 1891].
- = *Physalospora miyabeana* Fukushi, Annl. phytopath. Soc. Japan 1 (no. 4): 7. 1921.
- ≡ *Glomerella miyabeana* (Fukushi) Arx, Phytopath. Z. 29: 448. 1957.

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

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



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

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

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

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

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

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

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

*Phyllachora amenti* was described from *Salix reticulata* in Dovre, Norway by Rostrup (1891). Von Arx & Müller (1954) transferred the species to *Glomerella* (apparently not noticing the similarities with *Plectosphaera salicis*). We have not seen Rostrup's type, but his description and that of von Arx & Müller are highly reminiscent of *C. salicis* and we are confident of the synonymy. Rostrup also described a putative asexual morph of *Phyllachora*

*amenti* with filiform septate conidia, 35–45 × 1 µm in size, formed in pycnidia. This is most likely to be an accompanying species rather than a genetically linked morph. It may be *Septoria didyma*.

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

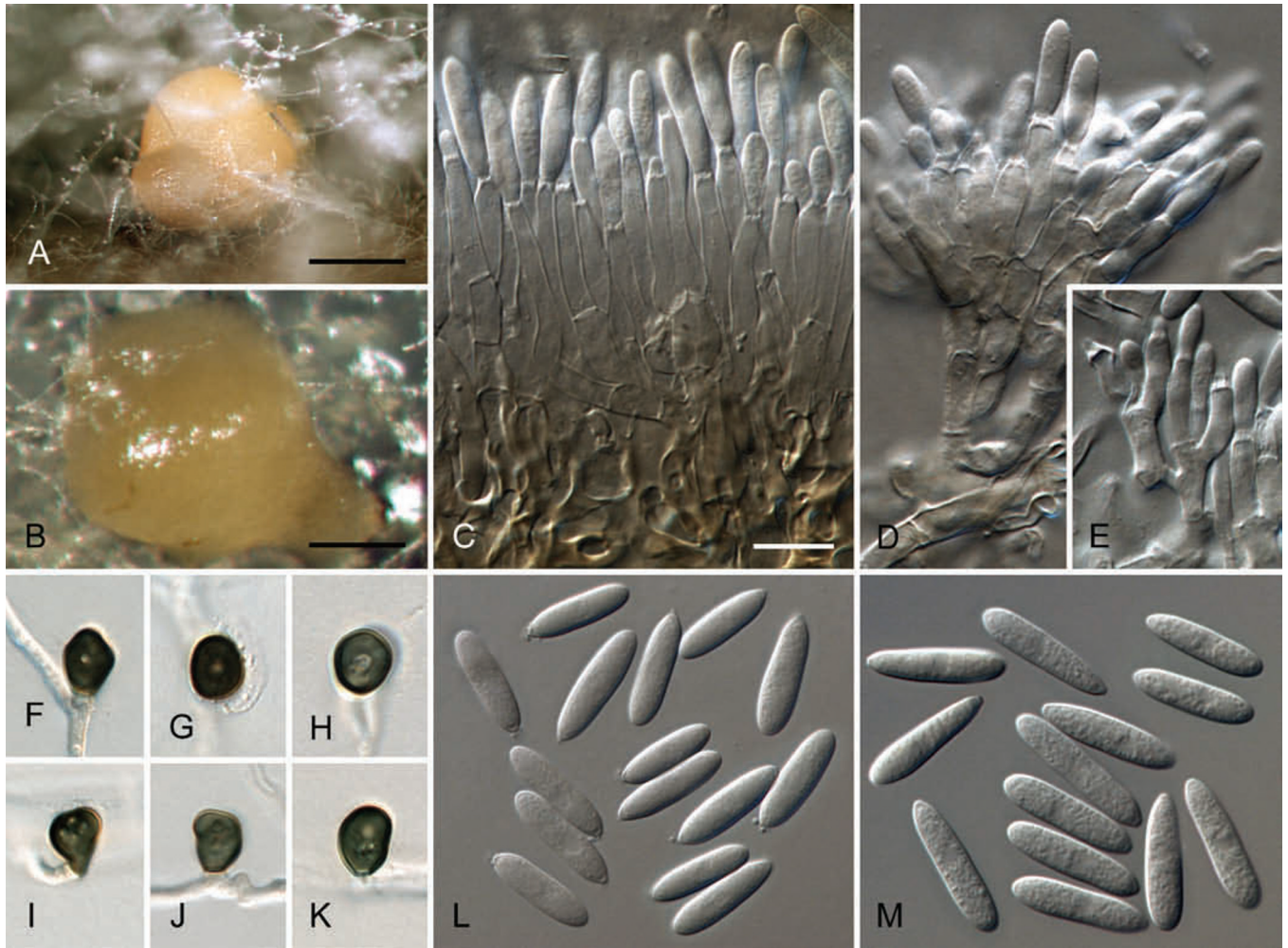
*Glomerella lycopersici* was described from a mummified fruit of *Solanum lycopersicum* (= *Lycopersicon esculentum*) in Germany. The ex-syntype strain CBS 115.14 hardly sporulates and did not form a sexual morph in culture, but molecular data confirm the synonymy. The ascospore measurements (15–17.3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

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

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

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

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



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

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

*Colletotrichum salicis* is separated from other species by all genes, except for ITS; it forms a well-supported clade (bootstrap support 98–99 %) with little sequence variation in HIS3, TUB2, GAPDH and ACT. The closest match in a blastn search with the TUB2 sequence of CBS 607.94 (with 97 % identity, 13 bp differences) was *Ga. acutata* isolate PCF 459 (EU635504) from

strawberry in Belgium (Debode *et al.* 2009). With the GAPDH sequence of CBS 607.94 no match closer than 87 % identity was found. In blastn searches with the ITS sequence, numerous matches with 100 % identity were found, some of which we know to belong to distinct species.

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

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

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



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

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

*Culture characteristics:* Colonies on SNA flat with entire margin, hyaline, on filter paper pale olivaceous grey, on medium, filter paper and *Anthriscus* stem partly covered with floccose whitish to pale olivaceous grey aerial mycelium and on *Anthriscus* stem with few orange acervuli, reverse hyaline, rosy buff to greyish sepia, on filter paper and *Anthriscus* stem partly fuscous black; growth rate 22–22.5 mm in 7 d (33.5–35 mm in 10 d). Colonies on OA flat with entire margin; surface covered with short floccose whitish to pale olivaceous grey aerial mycelium, margin rosy buff, reverse rosy buff, olivaceous grey to iron grey in the centre; growth rate 19–20 mm in 7 d (33–35 mm in 10 d). *Conidia* in mass salmon.

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

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

The ex-type strain was included in the study of Nirenberg *et al.* (2002) as *C. acutatum*, and one of the strains studied (CBS 120708) was included in a paper on *Colletotrichum* diseases of chilli in Thailand (Than *et al.* 2008a), in which ITS and TUB2 sequences were generated. The strain was identified there as *C. acutatum*, a representative of one of two clades of that species complex associated with chilli. In drop inoculation tests, strains from that clade were found to cause typical anthracnose symptoms on chilli fruits. Two other species (or species complexes) were reported to cause disease of chilli by Than *et al.* (2008a), with isolates identified also as *C. gloeosporioides* and *C. capsici*. The latter taxon was found to be a synonym of *C. truncatum* by Damm *et al.* (2009). Other *Colletotrichum* species were also reported from the *C. boninense* species complex, namely *C. novae-zelandiae* and *C. karstii* in New Zealand, both

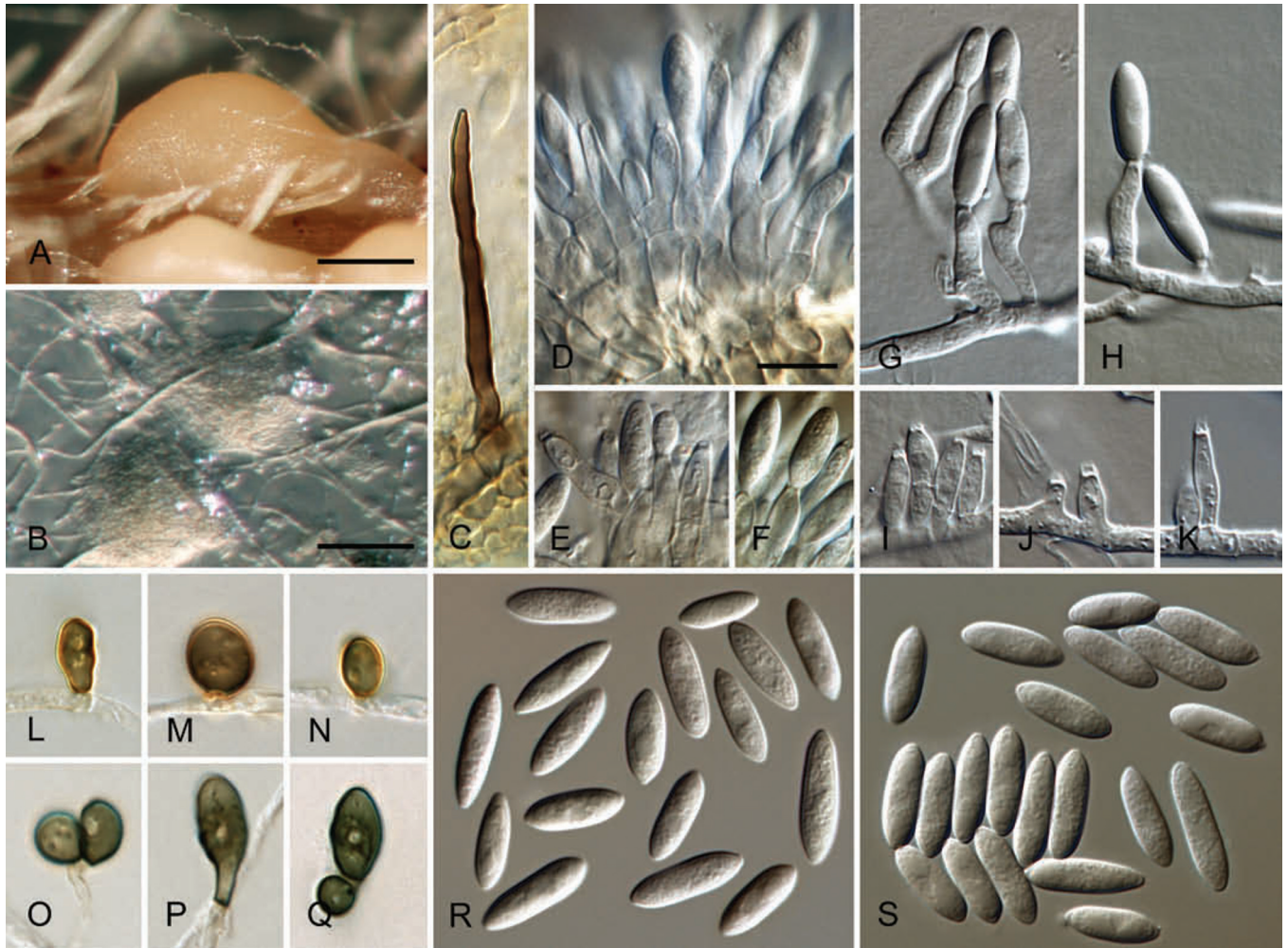
occurring also on other host plants (Damm *et al.* 2012, this issue). There are several reports of *C. coccodes*, inclusive of its synonym *C. atramentarium* and of *C. nigrum*, on *Capsicum* in different countries (Farr & Rossman 2012). These species do not belong to the *C. acutatum* complex. *Colletotrichum coccodes* is more closely related to some of the curved-spored species (fig. 1 in Cannon *et al.* 2012, this issue). The identity of *C. nigrum* has not been studied recently, and it is most probably either a further synonym of *C. coccodes* or a member of the *C. gloeosporioides* complex. Another species on *Capsicum annuum* from Australia belonging to the *C. acutatum* species complex, *C. brisbanense*, is described above. Apart from earlier reports of the strains included in this study, *C. acutatum* (*s. lat.*) has also been reported on *Capsicum* in Bulgaria (Jelevev *et al.* 2008), India (Kaur & Singh 1990), Korea (Cho & Shin 2004) and Taiwan (Liao *et al.* 2012).

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

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

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

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



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

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

**Culture characteristics:** Colonies on SNA flat with entire margin, hyaline to to pale isabelline, on filter paper and on *Anthriscus* stem partly covered with short white to pale grey felty aerial mycelium, reverse of filter paper white to olivaceous grey, growth 10–16 mm in 7 d (16–26 mm in 10 d), other strains differ from the type strain by growing faster, e.g. CBS 294.67 grows 20.5–31 mm in 7 d (34–40 mm in 10 d). Colonies on OA flat with entire margin;

surface covered with felty white aerial mycelium, becoming pale olivaceous grey towards the centre, margin white or rosy buff, reverse dark olivaceous grey or salmon and purplish to iron-grey towards the margin, growth 10–16 mm in 7 d (14–24 mm in 10 d), other strains differ from the type strain by growing faster, e.g. CBS 294.67 grows 21–27 mm in 7 d (32.5–40 mm in 10 d). *Conidia in mass* not observed in the ex-type strain, those of other strains are salmon-orange.

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

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

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

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

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

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

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

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

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

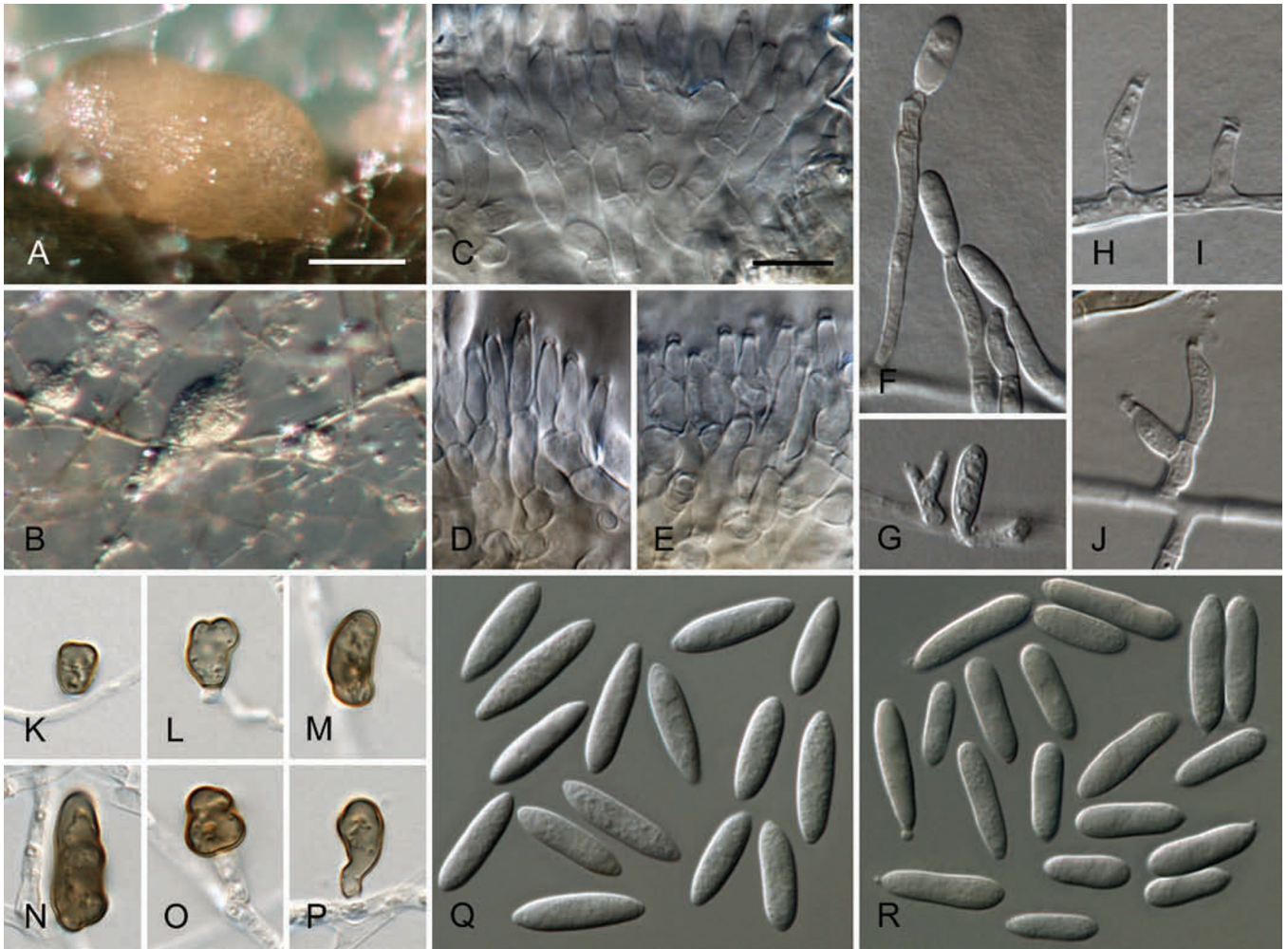
*Sexual morph* not observed. *Asexual morph on SNA.* Vegetative hyphae 1–8.5 µm diam, hyaline to pale brown, smooth-walled, septate, branched. *Chlamydoconidia* not observed. *Conidiomata* not developed, conidiophores formed directly on hyphae. *Setae* not observed. *Conidiophores* hyaline to pale brown,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

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

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

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

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



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

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

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

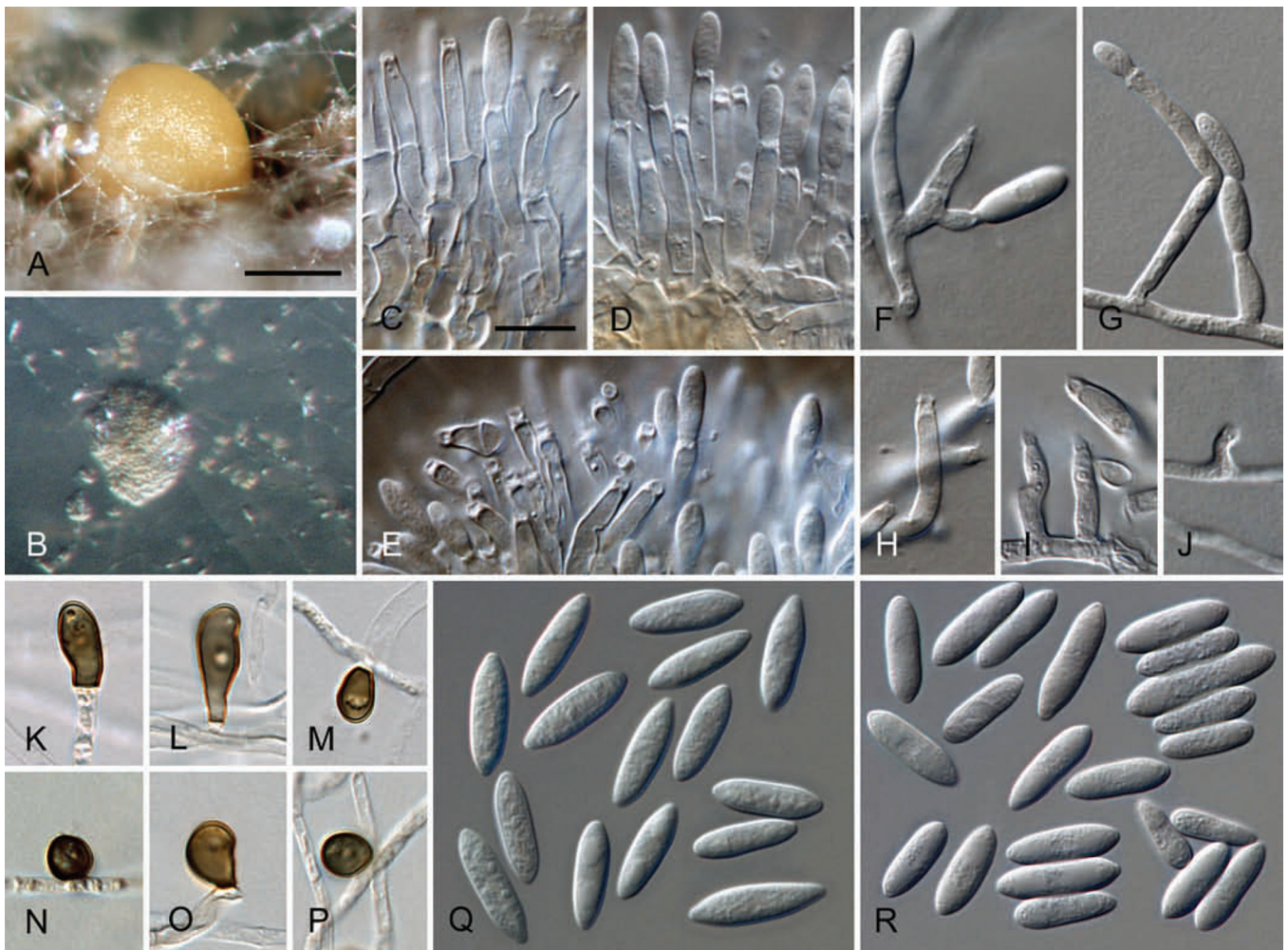
*Colletotrichum cradwickii*, described from branches of *T. cacao* in Jamaica, forms conidia that are hyaline (red in mass), elongate, constricted in the middle, and 14–17  $\times$  5  $\mu$ m, with setae that are straight, rigid, acute, 2–3-septate, purplish and 70–100  $\times$  4–6  $\mu$ m in size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

setae described for these two species is reminiscent of species in the *C. gloeosporioides* complex.

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

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

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



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

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

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

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

*Sexual morph* not observed (structures that are possibly immature ascomata were seen on *Anthriscus* stem). *Asexual morph on SNA.* Vegetative hyphae 1–5.5  $\mu$ m diam, hyaline to pale brown, smooth-walled, septate, branched. *Chlamydospores* not observed. *Conidiomata* not developed, conidiophores formed directly on hyphae. *Setae* not observed. *Conidiophores* hyaline, smooth-walled, septate, branched, to 30  $\mu$ m long. *Conidiogenous cells* hyaline smooth-walled, cylindrical to  $\pm$  inflated, often integrated,

discrete phialides measure 8–18  $\times$  2.5–3.5  $\mu$ m, opening 1–1.5  $\mu$ m diam, collarette distinct, 1–1.5  $\mu$ m long, periclinal thickening conspicuous. *Conidia* hyaline, smooth-walled, aseptate, straight, cylindrical to fusiform with both ends acute, sometimes clavate with one round and one acute end, (8.5–)11.5–14.5(–15)  $\times$  (2.5–)3–4(–4.5)  $\mu$ m, mean  $\pm$  SD = 13.0  $\pm$  1.4  $\times$  3.5  $\pm$  0.4  $\mu$ m, L/W ratio = 3.7. *Appressoria* single, medium brown, smooth-walled, subglobose, elliptical or clavate, the edge entire, rarely slightly undulate, (4–)5–10.5(–16)  $\times$  (3.5–)4.5–6.5(–8)  $\mu$ m, mean  $\pm$  SD = 7.8  $\pm$  2.6  $\times$  5.5  $\pm$  0.9  $\mu$ m, L/W ratio = 1.4.

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

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

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

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

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

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

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

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

Falconi & van Heusden (2011) studied *Colletotrichum* isolates collected from *Lupinus mutabilis* and tamarillo in the Ecuadorian

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

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

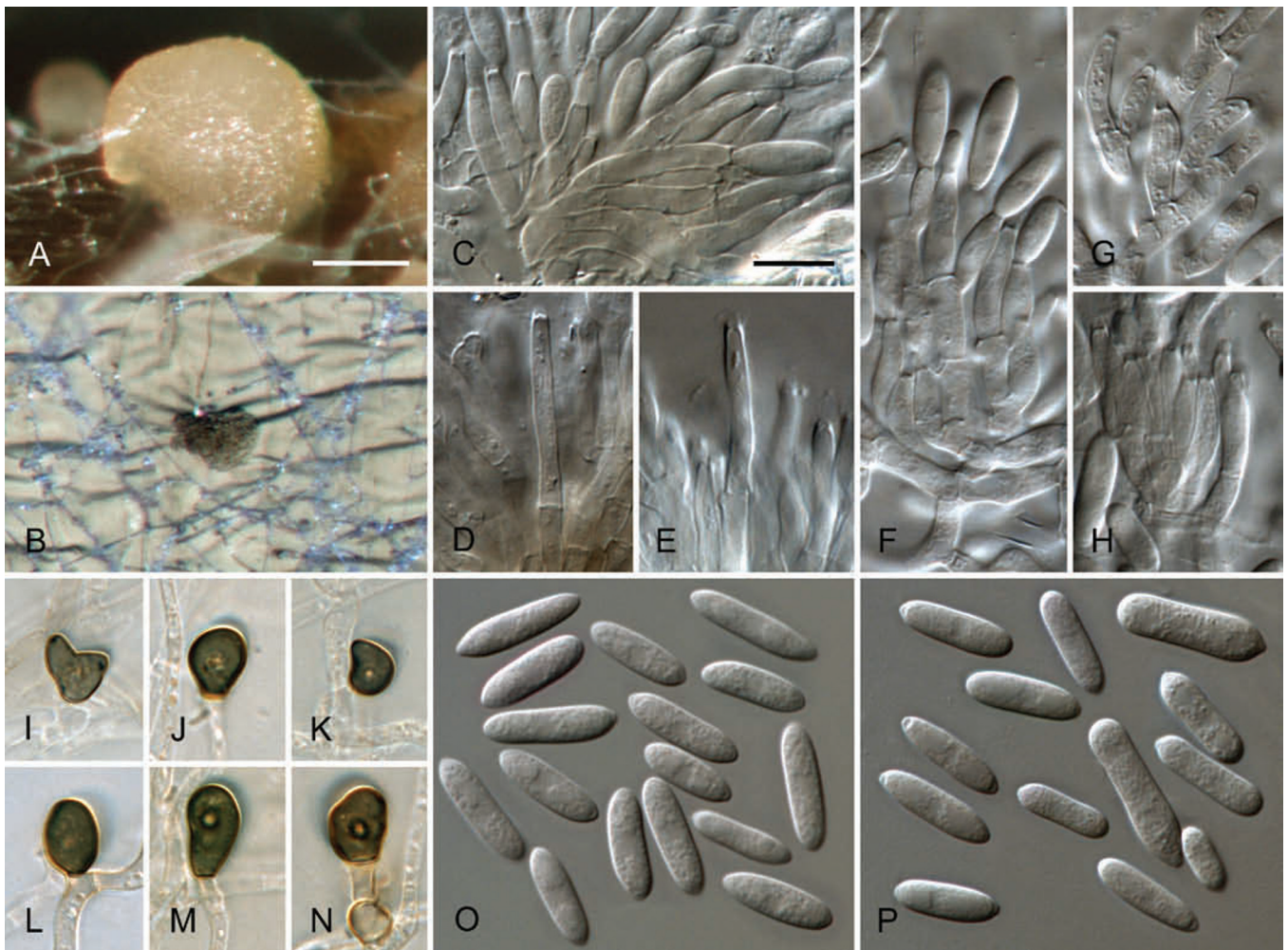
***Colletotrichum walleri* Damm, P.F. Cannon & Crous, sp. nov.** MycoBank MB800517. Fig. 32.

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

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

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

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



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

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

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

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

*Colletotrichum walleri* is separated from other species by almost all genes. It is most easily distinguished using HIS3 and ITS

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

## DISCUSSION

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

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

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

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

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

Sreenivasaprasad & Talhinhas (2005) distinguished eight distinct molecular groups within *C. acutatum*, A1–A8 (based on ITS

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

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

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

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



There is limited evidence of restricted geographical range for some of the species we accept here. For most species, the number of strains available is too small to allow us to draw definite conclusions. For example, except for *C. lupini*, all isolates of clade 1 (some of which are not recognised as separate species) appear to have an origin restricted to Central and South America and the southern USA. The globalisation of agriculture has in all probability led to frequent unrecognised introductions to new regions. The baseline information we have on native versus exotic taxa is inadequate to allow introductions to be mapped. However, some of the apparently specific host-fungus connections could be supported further by tracing more strains from the respective hosts in future blast searches, e.g. for *C. scovillei* and *C. limetticola*.

*Colletotrichum acutatum* has been regarded as a pathogen of countless host plant species, and also as occurring everywhere. Sreenivasaprasad & Talhinhos (2005) discovered that *C. acutatum* group A5, here accepted as *C. acutatum* s. str., occurs only on certain hosts, mostly in the southern hemisphere. This study confirms that *C. acutatum* s. str. does in fact have multiple hosts, but the known host spectrum is much smaller than previously accepted.

Some host plants appear to be particularly susceptible to infection by multiple *Colletotrichum* taxa. Occurrence of species on strawberry has been particularly well researched due to the former status of *C. acutatum* as a regulated quarantine pathogen. We have found that strains from this host belong to six different clades within the *C. acutatum* species complex, namely *C. simmondsii* (three strains from Australia), *C. nymphaeae* (38 strains, mostly from Europe and the USA), *C. fioriniae* (seven strains from New Zealand, UK and USA), *C. godetiae* (10 strains, all from Europe), *C. acutatum* s. str. (one strain from Australia) and *C. salicis* (four strains from New Zealand). In a study by MacKenzie *et al.* (2009), strains from strawberry were shown to be more aggressive to strawberry than strains from *Vaccinium*. Based on TUB2 sequences generated by those authors, the strains from strawberry were assigned to *C. nymphaeae*, and the strains from *Vaccinium* to *C. fioriniae*. Possibly the reason for apparent differences in pathogenicity, lie not in the different hosts, but in the fact that the strains studied belong to different species. To our knowledge, *C. acutatum* s. str. has rarely been found in Europe, and then mostly on ornamental plants. So far, it has been isolated from strawberry only in Australia. In pathogenicity tests by Talhinhos *et al.* (2005), an isolate of *C. acutatum* s. str. from olive caused anthracnose symptoms on strawberry fruits; the virulence of this isolate was not different from that of of group A2 (*C. nymphaeae* and related species), A3 (*C. fioriniae*) or A4 (*C. godetiae*). If further quarantine regulation is to take place, other than generalised prohibition of contamination by any and all members of the *C. acutatum* species complex, then more rigorous diagnostic methods will be needed.

Other hosts that are attacked by more than one species of the *C. acutatum* species complex include apple, citrus, olive, cranberry and blueberry. For example the causal organisms of bitter rot of apple in Korea belong to *C. acutatum* clades 2 (*C. nymphaeae* and related species) and 3 (*C. fioriniae*) (Lee *et al.* 2007). In our study there are strains from *Malus* belonging to five species, namely *C. acerbum* (one strain), *C. fioriniae* (13 strains), *C. godetiae* (two strains), *C. nymphaeae* (one strain) and *C. salicis* (two strains). Talhinhos *et al.* (2005) found five groups, now recognised as species, within *C. acutatum* s. lat. occurring on olives in Portugal: A2 (actually *C. nymphaeae*), A3 (*C. fioriniae*), A4 (*C. godetiae*), A5 (*C. acutatum*) and A6 (*C. rhombiforme*).

Our study emphasises the complex nature of the evolutionary pathways that have been traversed within the *C. acutatum* species

complex. Speciation has taken place much more prolifically than has been suspected so far. It seems likely that the *C. acutatum* species complex is still evolving rapidly. The emergence of new species is doubtless encouraged by the opportunities for mixing of gene pools that are provided by modern global agricultural practices combined with imperfect phytosanitary regulation.

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