



Colletotrichum species causing anthracnose disease of chili in China

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Key words

DNA phylogeny
multi-gene analysis
plant pathogen
systematics

Abstract Anthracnose caused by *Colletotrichum* species is a serious disease of more than 30 plant genera. Several *Colletotrichum* species have been reported to infect chili in different countries. Although China is the largest chili-producing country, little is known about the species that have been infecting chili locally. Therefore, we collected samples of diseased chili from 29 provinces of China, from which 1285 strains were isolated. The morphological characters of all strains were observed and compared, and multi-locus phylogenetic analyses (ITS, *ACT*, *CAL*, *CHS-1*, *GAPDH*, *TUB2*, and *HIS3*) were performed on selected representative strains. Fifteen *Colletotrichum* species were identified, with *C. fioriniae*, *C. fructicola*, *C. gloeosporioides*, *C. scovillei*, and *C. truncatum* being prevalent. Three new species, *C. conoides*, *C. grossum*, and *C. liaoningense*, were recognised and described in this paper. *Colletotrichum aenigma*, *C. cliviae*, *C. endophytica*, *C. hymenocallidis*, *C. incanum*, *C. karstii*, and *C. viniferum* were reported for the first time from chili. Pathogenicity of all species isolated from chili was confirmed, except for *C. endophytica*. The current study improves the understanding of species causing anthracnose on chili and provides useful information for the effective control of the disease in China.

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INTRODUCTION

Chili (*Capsicum* spp.) is an important vegetable crop worldwide. China maintains the largest planted area of chili, producing more than 28 M tons per year for domestic consumption and export (Li et al. 2009). One of the most destructive diseases restricting chili production is anthracnose, caused by *Colletotrichum* spp. (Bailey & Jeger 1992, Poonpolgul & Kumphai 2007, Than et al. 2008), resulting in up to 40 % yield loss in China (Lin et al. 2004).

Colletotrichum species can infect more than 30 plant genera (Perfect et al. 1999, Dean et al. 2012, Farr & Rossman 2016). More than 10 *Colletotrichum* species have been reported from chili, with different distributions among countries (Than et al. 2008, Liao et al. 2012, Kanto et al. 2014, Sharma et al. 2014, Diao et al. 2015). For example, anthracnose on chili is caused by *C. coccodes*, *C. fructicola*, *C. siamense*, and *C. truncatum* in India (Sharma & Shenoy 2014); by *C. acutatum*, *C. coccodes*, and *C. gloeosporioides* in the USA; by *C. acutatum*, *C. dematium*, *C. gloeosporioides*, and *C. truncatum* in Australia; by *C. acutatum*, *C. coccodes*, *C. dematium*, *C. gloeosporioides*, and *C. panacicola* in Korea (Than et al. 2008); and by *C. acutatum*, *C. gloeosporioides*, *C. truncatum*, and *C. coccodes* in China (Shin et al. 1999, Liao et al. 2012). Most of these reports, however, were based on morphology and ITS sequences or a combination of ITS and *TUB2* sequences, which have been shown to be insufficient in distinguishing closely related taxa in several species complexes. In addition, these records were mostly based on a small sampling from restricted areas, and, thus, may underestimate the species diversity.

The current study aimed to investigate the *Colletotrichum* species causing anthracnose on chili in China, by employing large-scale sampling and isolation, and via morphological characterisation and multi-locus phylogeny of the obtained strains.

MATERIALS AND METHODS

Sample collection and isolation

From 2008 to 2014, fruits and leaves of chili (*Capsicum* spp.) with anthracnose symptoms were collected from 50 locations in 29 provinces of China (Fig. 1). In each location, a hierarchical sampling method was used as previously described (Kohli et al. 1995). Five fields were chosen at each sampling location, and 25 chili fruits and also leaves in some cases were collected from each field along a diagonal transect. *Colletotrichum* species were isolated as described by Cai et al. (2009). All isolates were grown at 28 °C for further study. Type specimens of new species from this study were deposited in the Mycological Herbarium, Institute of Microbiology, Chinese Academy of Sciences, Beijing, China (HMAS), and ex-type living cultures were deposited in the China General Microbiological Culture Collection Centre (CGMCC), Beijing, China.

Morphological characterisation

Mycelial plugs (5 mm) were transferred from the edge of actively growing cultures to fresh potato dextrose agar (PDA, 1.5 %, Difco) plates. Cultures were kept at 28 °C with a 12/12 h fluorescent light/dark cycle. The morphological characters for all isolates, including colony and conidial characteristics, were observed. Microscopic characters were examined with the Carl Zeiss Imager A2 microscope after 1 mo of cultivation. Among the 1 285 obtained isolates (Table 1), 121 representative isolates were selected for further multilocus phylogenetic analyses based on geographical location, morphology (colony shape and colour and characteristics of aerial mycelia and conidia), and

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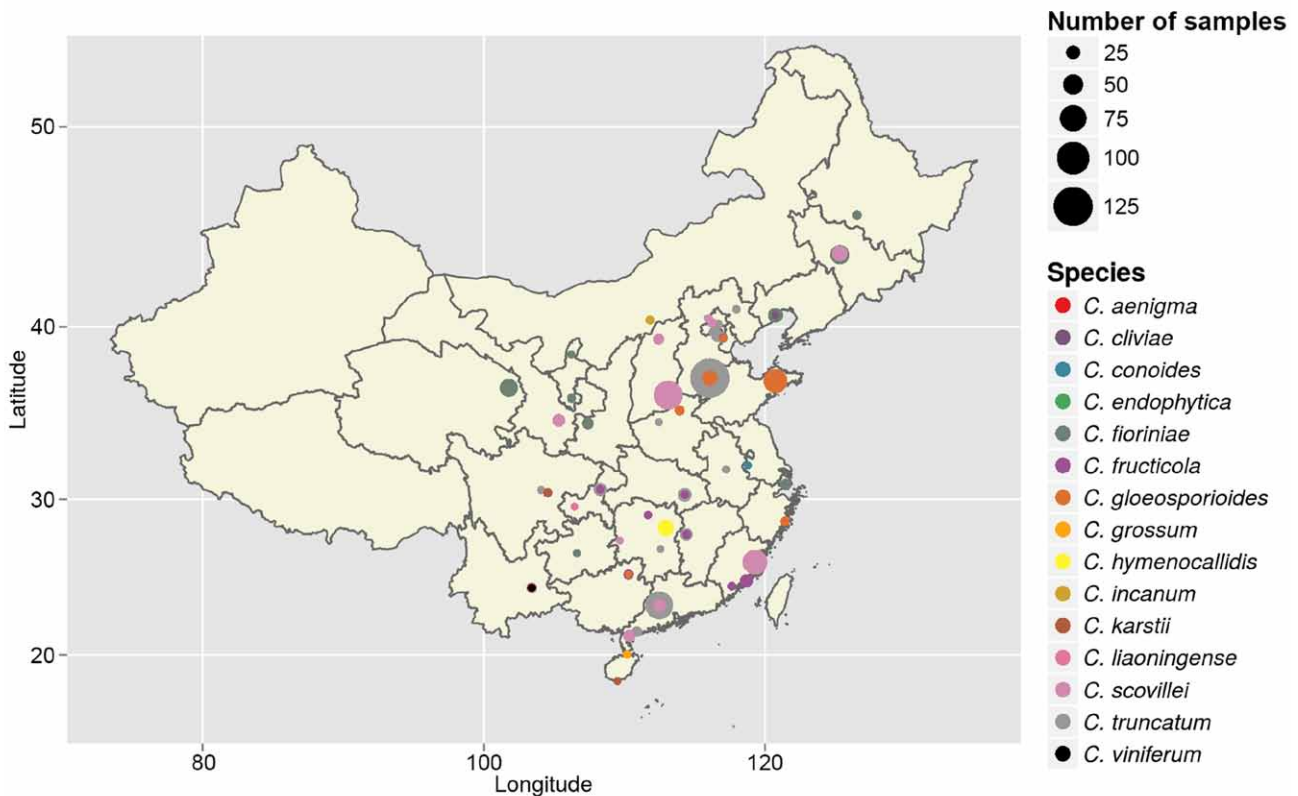


Fig. 1 Map showing locations in China where chili was sampled for *Colletotrichum* species. Each coloured circle represents one species by preliminary identification, and the size of the circle indicates the number of isolates collected from that location.

ITS sequences. Different morphological types were selected from each location, and the number of representative isolates selected depended on the number of isolates with different morphologies. Furthermore, if the number of isolates with high morphological and ITS sequence similarities was less than 10 in one location, then one isolate was randomly selected as a representative. If the number was more than 10, on the other hand, then an additional isolate (one from each of the 10 isolates) was selected for multi-locus phylogenetic analyses. The length and width of 30 conidia for each isolate were measured in lactic acid, and mean values calculated. The formation of appressoria was induced as described by Cai et al. (2009).

DNA extraction, PCR amplification, and sequencing

Genomic DNA was extracted from 121 representative isolates as previously described (Murray & Thompson 1980, Diao et al. 2015). The following loci were amplified with the indicated primers: the internal transcribed spacer regions and intervening 5.8S nrRNA gene (ITS) with primers ITS4/ITS5 (White et al. 1990); partial sequences of the glyceraldehyde-3-phosphate dehydrogenase (*GAPDH*) with primers GDF1/GDR1 (Templeton et al. 1992); actin gene (*ACT*) with primers ACT512F/ACT783R (Carbone & Kohn 1999); beta-tubulin (*TUB2*) with primers T1/Bt2b (Glass & Donaldson 1995, O'Donnell & Cigelnik 1997); calmodulin (*CAL*) with primers CL1/CL2A (O'Donnell et al. 2000); chitin synthase 1 (*CHS-1*) with primers CHS-79F/CHS-345R (Carbone & Kohn 1999); and histone3 (*HIS3*) with primers CYLH3F/CYLH3R (Crous et al. 2004b). PCR reactions were performed as described by Damm et al. (2009). DNA sequencing was conducted by Sunbiotech, Beijing, China with a 3730 DNA Analyzer (Applied Biosystems, USA). The sequences obtained from forward and reverse primers were used to obtain consensus sequences with DNAMAN v. 6.0 (Lynnon Biosoft, USA). Sequences were aligned using MAFFT v. 6 (Katoh & Toh 2010).

Phylogenetic analysis

All sequences of the 121 representative isolates were blasted in GenBank. Sequences with high similarities were selected and included in the analyses (Table 2a–c). Concatenated analyses of ITS, *GAPDH*, *CHS-1*, *HIS3*, *ACT*, and *TUB2* were conducted for the *C. acutatum* species complex and *Colletotrichum* species with curved conidia, while ITS, *GAPDH*, *CAL*, *ACT*, *CHS-1*, and *TUB2* were concatenated for the analysis of the *C. gloeosporioides* species complex and other species. Maximum parsimony (MP) analyses based on the combined datasets were conducted using PAUP v. 4.0b10 (Swofford 2002). Phylogenetic trees were generated using the heuristic search option with TBR branch swapping and 1 000 random sequence additions. Maxtrees were unlimited, with branches of zero length collapsed, and all multiple parsimonious trees were saved. Clade stability was assessed using a bootstrap analysis with 1 000 replicates. Afterward, tree length (TL), consistency index (CI), retention index (RI), rescaled consistency index (RC), and homoplasy index (HI) were calculated. Bayesian inference (BI) was used to reconstruct the phylogenetic tree using MrBayes v. 3.2.1 (Ronquist & Huelsenbeck 2003). Best-fit models of nucleotide substitution were selected using MrModelTest v. 2.3 (Nylander 2004). Two analyses of four MCMC chains were run from random trees for 1 000 000 generations, and trees were sampled every 100 generations resulting in 20 000 total trees. The first 25 % of the trees were discarded as the burn-in phase of each analysis, and the remaining trees were used to calculate posterior probabilities (Cai et al. 2006, Liu et al. 2012, 2013). An additional Maximum likelihood (ML) analysis was implemented in the *C. gloeosporioides* species complex using the CIPRES Science Gateway v. 3.3 (www.phylo.org), and the RAxML-HPC BlackBox was selected with default parameters. Sequences derived in this study were deposited in GenBank (Table 2), and the concatenated alignments were deposited in TreeBASE (<http://treebase.org/treebase-web/home.html>; study

Table 1 A list of all *Colletotrichum* isolates collected from chili in China based on preliminary identification.

| Species | Location | Host tissue | Year | Number of isolates | Longitude | Latitude |
|---------------------------|---------------------------|---------------------|-------|--------------------|-----------|----------|
| <i>C. aenigma</i> | Yangliuqing, Tianjin | Fruit | 2012 | 1 | 39.4 | 117.01 |
| <i>C. cliviae</i> | Xingcheng, Liaoning | Fruit | 2012 | 1 | 40.63 | 120.74 |
| <i>C. conoides</i> | Nanjing, Jiangsu | Fruit | 2010 | 3 | 32.06 | 118.79 |
| <i>C. endophytica</i> | Mile, Yunnan | Fruit | 2011 | 1 | 24.41 | 103.41 |
| <i>C. fioriniae</i> | Fengxiang, Shanxi | Fruit | 2011 | 17 | 34.55 | 107.4 |
| | Changchun | Fruit | 2011 | 47 | 43.81 | 125.32 |
| | Xining, Qinghai | Fruit | 2011 | 42 | 36.61 | 101.78 |
| | Sanya, Hainan | Fruit | 2012 | 2 | 18.25 | 109.51 |
| | Guiyang, Guizhou | Fruit | 2012 | 3 | 26.64 | 106.63 |
| | Xingcheng, Liaoning | Fruit | 2012 | 29 | 40.63 | 120.74 |
| | Yinchuan, Ningxia | Fruit | 2012 | 4 | 38.48 | 106.23 |
| | Guyuan, Ningxia | Fruit | 2012 | 8 | 36.01 | 106.24 |
| | Fengxian, Shanghai | Fruit | 2012 | 16 | 30.91 | 121.47 |
| | Harbin, Heilongjiang | Fruit | 2012 | 9 | 45.8 | 126.53 |
| <i>C. fructicola</i> | Fuzhou, Fujian | Fruit | 2011 | 2 | 26.07 | 119.29 |
| | Guilin, Guangxi | Fruit | 2011 | 10 | 25.27 | 110.29 |
| | Hengyang, Hunan | Fruit | 2012 | 4 | 29.03 | 111.69 |
| | Changsha, Hunan | Fruit | 2012 | 20 | 28.23 | 112.94 |
| | Laiyang, Shandong | Fruit | 2011 | 32 | 36.99 | 120.74 |
| | Wucheng, Shandong | Fruit | 2012 | 15 | 37.16 | 116.08 |
| | Zhangzhou, Fujian | Fruit | 2008 | 5 | 24.51 | 117.64 |
| | Quanzhou, Fujian | Fruit | 2009 | 23 | 24.87 | 118.67 |
| | Fengxiang, Shanxi | Fruit | 2011 | 5 | 34.55 | 107.4 |
| | Xinxiang, Henan | Fruit | 2011 | 5 | 35.3 | 113.93 |
| | Yichun, Jiangxi | Fruit | 2011 | 6 | 27.81 | 114.41 |
| | Jiayang, Sichuan | Fruit | 2011 | 8 | 30.41 | 104.55 |
| | Mile, Yunnan | Fruit | 2011 | 10 | 24.41 | 103.41 |
| | Yangliuqing, Tianjin | Fruit | 2012 | 4 | 39.4 | 117.01 |
| | Wuhan, Hubei | Fruit | 2012 | 4 | 30.28 | 114.29 |
| | Xingcheng, Liaoning | Fruit | 2012 | 4 | 40.63 | 120.74 |
| Shizhu, Chongqing | Fruit | 2013 | 4 | 30.6 | 108.29 | |
| <i>C. gloeosporioides</i> | Guilin, Guangxi | Fruit | 2011 | 1 | 25.27 | 110.29 |
| | Qingyuan, Guangdong | Fruit | 2013 | 21 | 23.28 | 112.48 |
| | Qingyuan, Guangdong | Fruit | 2014 | 1 | 23.28 | 112.48 |
| | Laiyang, Shandong | Fruit | 2011 | 64 | 36.99 | 120.74 |
| | Wucheng, Shandong | Fruit | 2011 | 30 | 37.16 | 116.08 |
| | Fengxiang, Shanxi | Fruit | 2011 | 10 | 34.55 | 107.4 |
| | Xinxiang, Henan | Fruit | 2011 | 10 | 35.3 | 113.93 |
| | Taizhou, Zhejiang | Fruit | 2011 | 8 | 28.65 | 121.42 |
| | Changsha, Hunan | Fruit | 2012 | 20 | 28.23 | 112.94 |
| | Mile, Yunnan | Fruit | 2011 | 5 | 24.41 | 103.41 |
| | Jiayang, Sichuan | Fruit | 2011 | 4 | 30.41 | 104.55 |
| | Guyuan, Ningxia | Fruit | 2012 | 2 | 36.01 | 106.24 |
| | Wuqing, Tianjin | Fruit | 2012 | 1 | 39.38 | 117.04 |
| | Xingcheng, Liaoning | Fruit | 2012 | 4 | 40.63 | 120.74 |
| <i>C. grossum</i> | Haikou, Hainan | Fruit | 2011 | 3 | 20.04 | 110.19 |
| <i>C. hymenocallidis</i> | Changsha, Hunan | Fruit | 2012 | 35 | 28.23 | 112.94 |
| <i>C. incanum</i> | Helingeer, Inner Mongolia | Fruit | 2012 | 6 | 40.37 | 111.82 |
| <i>C. karstii</i> | Sanya, Hainan | Fruit | 2012 | 3 | 18.25 | 109.51 |
| | Jiayang, Sichuan | Fruit | 2011 | 5 | 30.41 | 104.55 |
| | Mile, Yunnan | Fruit | 2011 | 1 | 24.41 | 103.41 |
| <i>C. liaoningense</i> | Xingcheng, Liaoning | Fruit | 2012 | 11 | 40.63 | 120.74 |
| | Shapingba, Chongqing | Fruit | 2012 | 1 | 29.54 | 106.46 |
| <i>C. scovillei</i> | Yanqing, Beijing | Fruit | 2011 | 4 | 40.45 | 115.97 |
| | Changping, Beijing | Fruit | 2013 | 8 | 40.22 | 116.23 |
| | Fuzhou, Fujian | Fruit | 2011 | 68 | 26.07 | 119.29 |
| | Gangu, Gansu | Fruit | 2012 | 21 | 34.73 | 105.33 |
| | Jida, Jilin | Fruit | 2013 | 33 | 43.88 | 125.31 |
| | Changzhi, Shanxi | Fruit | 2011 | 84 | 36.19 | 113.11 |
| | Shuozhou, Shanxi | Fruit | 2012 | 14 | 39.33 | 112.43 |
| | Sanya, Hainan | Fruit | 2012 | 1 | 18.25 | 109.51 |
| | Zhijiang, Hunan | Fruit | 2011 | 1 | 27.44 | 109.68 |
| | Zhanjiang, Guangdong | Fruit | 2011 | 18 | 21.27 | 110.35 |
| | Qingyuan, Guangdong | Fruit | 2012 | 20 | 23.28 | 112.48 |
| | <i>C. truncatum</i> | Qingyuan, Guangdong | Fruit | 2013 | 80 | 23.28 |
| Qingyuan, Guangdong | | Fruit | 2014 | 10 | 23.28 | 112.48 |
| Maoming, Guangdong | | Fruit | 2013 | 13 | 21.55 | 110.88 |
| Yichun, Jiangxi | | Leave | 2011 | 20 | 27.81 | 114.41 |
| Shizhu, Chongqing | | Fruit | 2013 | 23 | 30.6 | 108.29 |
| Wuhan, Hubei | | Fruit | 2013 | 25 | 30.28 | 114.29 |
| Fengxiang, Shanxi | | Fruit | 2011 | 12 | 34.55 | 107.4 |
| Wucheng, Shandong | | Fruit | 2011 | 125 | 37.16 | 116.08 |
| Laiyang, Shandong | | Fruit | 2011 | 10 | 36.99 | 120.74 |
| Yangliuqing, Tianjin | | Fruit | 2012 | 11 | 39.4 | 117.01 |

Table 1 (cont.)

| Species | Location | Host tissue | Year | Number of isolates | Longitude | Latitude |
|-----------------------------|----------------------|--------------|-------|--------------------|-----------|----------|
| <i>C. truncatum</i> (cont.) | Langfang, Hebei | Fruit | 2011 | 20 | 39.52 | 116.61 |
| | Chengde, Hebei | Fruit | 2013 | 5 | 40.95 | 117.96 |
| | Daxing, Beijing | Fruit | 2011 | 9 | 39.73 | 116.34 |
| | Shunyi, Beijing | Fruit | 2011 | 10 | 40.13 | 116.65 |
| | Xingcheng, Liaoning | Fruit | 2012 | 16 | 40.63 | 120.74 |
| | Changchun, Jilin | Fruit | 2012 | 7 | 43.71 | 125.54 |
| | Chengdu, Sichuan | Fruit | 2011 | 3 | 30.57 | 104.07 |
| | Hefei, Anhui | Fruit | 2011 | 2 | 31.82 | 117.23 |
| | Fuzhou, Fujian | Fruit | 2011 | 2 | 26.07 | 119.29 |
| | Luoyang, Henan | Fruit | 2011 | 1 | 34.62 | 112.45 |
| | Xinxiang, Henan | Fruit | 2011 | 2 | 35.3 | 113.93 |
| | Changsha, Hunan | Fruit | 2012 | 1 | 28.23 | 112.94 |
| | Hengyang, Hunan | Fruit | 2012 | 1 | 26.89 | 112.57 |
| | Changde, Hunan | Fruit | 2012 | 3 | 29.03 | 111.69 |
| | Mile, Yunnan | Fruit | 2011 | 4 | 24.41 | 103.41 |
| | Zhanjiang, Guangdong | Fruit | 2011 | 5 | 21.27 | 110.36 |
| | Xining, Qinghai | Fruit | 2011 | 1 | 36.61 | 101.78 |
| | Shuozhou, Shanxi | Fruit | 2012 | 1 | 39.33 | 112.43 |
| | <i>C. viniferum</i> | Mile, Yunnan | Fruit | 2011 | 1 | 24.41 |
| Total | | | | 1285 | | |

S17061), and the descriptions and nomenclature in MycoBank (Crous et al. 2004a).

Genealogical concordance phylogenetic species recognition analysis

New species and their most closely related neighbours were analysed using the Genealogical Concordance Phylogenetic Species Recognition (GCPSR) model with a pairwise homoplasy index (PHI) test as described by Quaedvlieg et al. (2014). The PHI tests were performed in SplitsTree4 (Huson 1998, Huson & Bryant 2006) to determine the recombination level within phylogenetically closely related species using a six-locus concatenated dataset (*ACT*, *CAL*, *CHS*, *GAPDH*, *ITS*, and *TUB2*) for *C. conoides*, *C. grossum*, and *C. liaoningense* and their respective related species. A pairwise homoplasy index below a 0.05 threshold ($\Phi_w < 0.05$) indicated the presence of significant recombination in the dataset. The relationship between closely related species was visualised by constructing a split graph.

Pathogenicity assay

Seven chili cultivars, *Capsicum annuum* cv. Chaotianjiao, Denglongjiao, Sanyingjiao, Zidantou, *C. frutescens* cv. Shuangla, Xiaomila and *C. chinense* cv. Huangdijiao, were inoculated with representative strains of 15 *Colletotrichum* species respectively (Table 3, 4). Pathogenicity tests were conducted on chili following the methods described by Montri et al. (2009) and Mongkolporn et al. (2010). Healthy, ripe red and green chili fruits were surface sterilised in 1 % NaClO for 5 min separately, washed twice with sterile-distilled water, and air dried on sterile filter paper. Each fruit was inoculated with 1 μ L of a conidial suspension (1×10^6 conidial/mL), which was injected onto the non-wounded fruit surface using a microsyringe (Shanghai, China). Control fruits were treated with 1 μ L of distilled water. Each isolate was inoculated to five replicate fruits. The inoculated fruits were incubated in a moist chamber at 28 °C and were examined for symptoms daily for 9 d. The virulence and pathotypes were evaluated as described by Montri et al. (2009). The experiment was conducted twice.

RESULTS

Disease survey and strain isolation

Symptoms of anthracnose were circular or angular sunken lesions on chili fruits and irregularly shaped brown spots with dark brown edges on leaves. A total of 1 285 isolates of *Colletotrichum* spp. were obtained from 29 provinces in China (Fig. 1, Table 1). Attempts were made to collect samples from multiple locations in Tibet and Xinjiang provinces for several years but failed to locate symptomatic plants. All strains were isolated from fruits except those from Jiangxi province, where serious damage was found on chili leaves rather than on fruits.

Group assessment

Based on megablast searches in GenBank using ITS sequences and the colony morphologies on PDA, all strains were assigned to four groups, i.e., those that produce cylindrical conidia with round ends were assigned to the *C. gloeosporioides* species complex; those that produce acute ends or \pm cylindrical conidia with only one acute end were assigned to the *C. acutatum* species complex; those that produce dark setae and curved conidia were assigned to the *Colletotrichum* species with curved conidia; and the remaining strains were assigned to a fourth group. Among the 121 isolates, 31 belonged to the *C. gloeosporioides* complex; 48 belonged to the *C. acutatum* complex; 34 belonged to the *Colletotrichum* species with curved conidia, and eight belonged to the fourth group (Damm et al. 2012a, b, 2013, 2014, Weir et al. 2012, Crouch 2014).

Multi-locus phylogenetic analyses

The 121 representative isolates from chili were subjected to multi-locus phylogenetic analyses (Table 2a–c). The trees generated from the Bayesian and RaxML analyses were essentially similar to that from the MP analysis (Fig. 2) and are therefore not shown. In Fig. 2, the 31 isolates in the *C. gloeosporioides* complex clustered in eight clades, eight with *C. fruticola*, 13 with *C. gloeosporioides*, and four with *C. aenigma*, *C. endophytica*, *C. hymenocallidis*, and *C. viniferum*, respectively. In addition, two distinct lineages, which clustered distantly from any known species in the complex, were recognised as new species and herein described as *C. conoides* and *C. grossum* (Fig. 2). In Fig. 3, the isolates of the *C. acutatum* complex clustered in two clades, 31 with *C. scovillei* and 17 with *C. fioriniae*. In the *Colletotrichum* species with curved conidia, 33 isolates

Table 2a Strains used for the phylogenetic analysis of the *Colletotrichum gloeosporioides* species complex and other species with details about host, location, and GenBank accession numbers.

| Species | Isolate | Host | Location | GenBank accessions | | | | | | |
|---------------------------|---------------|---|-------------|--------------------|----------|----------|----------|----------|----------|--|
| | | | | ITS | GAPDH | CAL | ACT | CHS-1 | TUB2 | |
| <i>C. aenigma</i> | ICMP 18686 | <i>Pyrus pyrifolia</i> | Japan | JX010243 | JX009913 | JX009684 | JX009519 | JX009789 | JX010390 | |
| | ICMP 18608* | <i>Persea americana</i> | Israel | JX010244 | JX010044 | JX009683 | JX009443 | JX009774 | JX010389 | |
| <i>C. aeschynomenes</i> | ICMP 17673* | <i>Aeschynomene virginica</i> | USA | JX010176 | JX009930 | JX009721 | JX009483 | JX009799 | JX010392 | |
| | CBS 304.67* | <i>Dioscorea alata</i> | India | JX010190 | JX009990 | JX009738 | JX009470 | JX009837 | JX010383 | |
| <i>C. alatae</i> | ICMP 18122 | <i>Dioscorea alata</i> | Nigeria | JX010191 | JX010011 | JX009739 | JX009470 | JX009846 | JX010449 | |
| | ICMP 12071* | <i>Malus domestica</i> | New Zealand | JX010251 | JX010028 | JX009654 | JX009572 | JX009882 | JX010411 | |
| <i>C. aotearoa</i> | ICMP 18621 | <i>Persea americana</i> | New Zealand | JX010246 | JX009959 | JX009657 | JX009552 | JX009755 | JX010386 | |
| | ICMP 18537* | <i>Coprosma</i> sp. | New Zealand | JX010205 | JX010005 | JX009611 | JX009584 | JX009853 | JX010420 | |
| <i>C. asianum</i> | ICMP 18580* | <i>Coffea arabica</i> | Thailand | FJ972612 | JX010053 | FJ917506 | JX009584 | JX009867 | JX010406 | |
| | ICMP 18696 | <i>Mangifera indica</i> | Australia | JX010192 | JX009915 | JX009723 | JX009576 | JX009753 | JX010384 | |
| <i>C. boninense</i> | MAFF 305972* | <i>Crinum asiaticum</i> var. <i>sinicum</i> | Japan | JX010292 | JX009905 | JQ005674 | JX009583 | JX009827 | JQ005588 | |
| | CBS 128547 | <i>Carnellia</i> sp. | New Zealand | JQ005159 | JQ005246 | JQ005680 | JQ005507 | JQ005333 | JQ005593 | |
| <i>C. brevisporum</i> | BCC 38876* | <i>Neoregalia</i> sp. | Thailand | JN050238 | JN050228 | JN050222 | JN050216 | KF687760 | JN050244 | |
| | MFLUCC100182 | <i>Pandanus pygmaeus</i> | Thailand | JN050239 | JN050228 | JN050222 | JN050217 | JN050245 | JN050245 | |
| <i>C. clidemiae</i> | ICMP 18706 | <i>Clidemia hirta</i> | USA | JX010274 | JX009909 | JX009639 | JX009476 | JX009777 | JX010439 | |
| | CBS 125375* | <i>Clivia miniata</i> | China | JX519223 | JX546611 | JX519240 | JX519240 | JX519232 | JX519249 | |
| <i>C. cliviae</i> | CSSS1 | <i>Clivia miniata</i> | China | GU109479 | GU085867 | GU085861 | GU085861 | GU085869 | GU085870 | |
| | CSSS2 | <i>Clivia miniata</i> | China | GU109480 | GU085868 | GU085862 | GU085862 | GU085870 | GU085870 | |
| <i>C. conoides</i> | CAUO6 | <i>Capsicum annuum</i> | China | KP890168 | KP890162 | KP890123 | KP890100 | KP890131 | KP890115 | |
| | CAUG17* | <i>Capsicum annuum</i> | China | KP890169 | KP890163 | KP890150 | KP890144 | KP890156 | KP890174 | |
| <i>C. conoides</i> | CAUG3 | <i>Capsicum annuum</i> | China | KP890170 | KP890164 | KP890151 | KP890145 | KP890157 | KP890175 | |
| | CAUG34 | <i>Capsicum annuum</i> | China | KP890170 | KP890164 | KP890152 | KP890146 | KP890158 | KP890176 | |
| <i>C. cordylincola</i> | ICMP 18579 | <i>Cordylone fruticosa</i> | Thailand | JX010226 | JX009975 | HM470238 | HM470235 | JX009864 | JX010440 | |
| | CBS 118199* | <i>Draacaena</i> sp. | China | JX519222 | JX546707 | JX519238 | JX519238 | JX519230 | JX519247 | |
| <i>C. endophytica</i> | CAUG28 | <i>Capsicum annuum</i> | China | KP145441 | KP145413 | KP145357 | KP145329 | KP145385 | KP145469 | |
| | LC0324* | <i>Pennisetum purpureum</i> | Thailand | KC633854 | KC832854 | KC810018 | KF306258 | | | |
| <i>C. fructicola</i> | MFLUCC 100676 | <i>Pennisetum purpureum</i> | Thailand | KF242123 | KF254846 | KF254846 | KF157827 | | | |
| | CAUG1 | <i>Capsicum</i> sp. | China | KP145416 | KP145388 | KP145332 | KP145304 | KP145360 | KP145444 | |
| <i>C. fructicola</i> | CAUG5 | <i>Capsicum</i> sp. | China | KP145420 | KP145392 | KP145336 | KP145308 | KP145364 | KP145448 | |
| | CAUG6 | <i>Capsicum</i> sp. | China | KP145421 | KP145393 | KP145337 | KP145309 | KP145365 | KP145449 | |
| <i>C. fructicola</i> | CAUG8 | <i>Capsicum</i> sp. | China | KP145422 | KP145394 | KP145338 | KP145310 | KP145366 | KP145450 | |
| | CAUG10 | <i>Capsicum</i> sp. | China | KP145424 | KP145396 | KP145340 | KP145312 | KP145368 | KP145452 | |
| <i>C. fructicola</i> | CAUG11 | <i>Capsicum</i> sp. | China | KP145425 | KP145397 | KP145341 | KP145313 | KP145369 | KP145453 | |
| | CAUG16 | <i>Capsicum</i> sp. | China | KP145430 | KP145402 | KP145346 | KP145318 | KP145374 | KP145458 | |
| <i>C. fructicola</i> | CAUG18 | <i>Capsicum</i> sp. | China | KP145431 | KP145403 | KP145347 | KP145319 | KP145375 | KP145459 | |
| | CBS 125395 | <i>Theobroma cacao</i> | Panama | JX010172 | JX009992 | JX009666 | JX009543 | JX009873 | JX010408 | |
| <i>C. fructicola</i> | ICMP 17789 | <i>Malus domestica</i> | USA | JX010178 | JX009914 | JX009665 | JX009451 | JX009809 | | |
| | ICMP 12568 | <i>Persea americana</i> | Australia | JX010166 | JX009946 | JX009680 | JX009529 | JX009762 | JX010405 | |
| <i>C. fructicola</i> | ICMP 18581* | <i>Coffea arabica</i> | Thailand | JX010165 | JX010033 | FJ917508 | FJ907426 | JX009866 | JX010388 | |
| | ICMP 18613 | <i>Limonium sinuatum</i> | Israel | JX010167 | JX009998 | JX009675 | JX009491 | JX009772 | JX010394 | |
| <i>C. fructicola</i> | ICMP 18727 | <i>Fragaria ananassa</i> | USA | JX010179 | JX010035 | JX009682 | JX009565 | JX009812 | JX010394 | |
| | CBS 238.49* | <i>Ficus edulis</i> | Germany | JX010181 | JX009923 | JX009671 | JX009495 | JX009839 | JX010400 | |
| <i>C. gloeosporioides</i> | CBS 125397* | <i>Tetragastris panamensis</i> | Panama | JX010173 | JX010032 | JX009674 | JX009581 | JX009874 | JX010409 | |
| | CAUG2 | <i>Capsicum</i> sp. | China | KP145417 | KP145389 | KP145333 | KP145305 | KP145361 | KP145445 | |
| <i>C. gloeosporioides</i> | CAUG3 | <i>Capsicum</i> sp. | China | KP145418 | KP145390 | KP145334 | KP145306 | KP145362 | KP145446 | |
| | CAUG12 | <i>Capsicum</i> sp. | China | KP145426 | KP145398 | KP145342 | KP145314 | KP145370 | KP145454 | |
| <i>C. gloeosporioides</i> | CAUG13 | <i>Capsicum</i> sp. | China | KP145427 | KP145399 | KP145343 | KP145315 | KP145371 | KP145455 | |
| | CAUG14 | <i>Capsicum</i> sp. | China | KP145428 | KP145400 | KP145344 | KP145316 | KP145372 | KP145456 | |
| <i>C. gloeosporioides</i> | CAUG15 | <i>Capsicum</i> sp. | China | KP145429 | KP145401 | KP145345 | KP145317 | KP145373 | KP145457 | |
| | CAUG19 | <i>Capsicum</i> sp. | China | KP145432 | KP145404 | KP145348 | KP145320 | KP145376 | KP145460 | |
| <i>C. gloeosporioides</i> | CAUG20 | <i>Capsicum</i> sp. | China | KP145433 | KP145405 | KP145349 | KP145321 | KP145377 | KP145461 | |

| | | | | | | | | |
|---|----------------|--|--------------|----------|----------|----------|----------|----------|
| C. gloeosporioides (cont.) | CAUG22 | <i>Capsicum</i> sp. | China | KP145435 | KP145407 | KP145323 | KP145379 | KP145463 |
| | CAUG23 | <i>Capsicum</i> sp. | China | KP145436 | KP145408 | KP145324 | KP145380 | KP145464 |
| | CAUG24 | <i>Capsicum</i> sp. | China | KP145437 | KP145409 | KP145325 | KP145381 | KP145465 |
| | CAUG25 | <i>Capsicum</i> sp. | China | KP145438 | KP145410 | KP145326 | KP145382 | KP145466 |
| | CAUG26 | <i>Capsicum</i> sp. | China | KP145439 | KP145411 | KP145327 | KP145383 | KP145467 |
| | CAUG29 | <i>Capsicum</i> sp. | China | KP145442 | KP145414 | KP145330 | KP145386 | KP145470 |
| | IMI 356878* | <i>Citrus sinensis</i> | Italy | JX010152 | JX010056 | JX009731 | JX009818 | JX010445 |
| | CORCG4 | <i>Vanda</i> sp. | Thailand | HM034808 | HM034806 | HM034800 | | |
| | CORCG5 | <i>Vanda</i> sp. | Thailand | HM034809 | HM034807 | HM034801 | HM034805 | HM034811 |
| <i>C. grevillea</i> | CBS 132879* | <i>Grevillea</i> sp. | Italy | KC297078 | KC297010 | KC296941 | KC296987 | KC297102 |
| C. grossum | CAUG7* | <i>Capsicum</i> sp. | China | KP890165 | KP890159 | KP890141 | KP890163 | KP890171 |
| | CAU31 | <i>Capsicum</i> sp. | China | KP890166 | KP890160 | KP890142 | KP890154 | KP890172 |
| | CAUG32 | <i>Capsicum</i> sp. | China | KP890167 | KP890161 | KP890143 | KP890155 | KP890173 |
| <i>C. hebeense</i> | JZB330024 | <i>Vitis vinifera</i> cv. Cabernet Sauvignon | China | KF156873 | KF377505 | KF377542 | KF289008 | KF289875 |
| | JZB330028* | <i>Vitis vinifera</i> cv. Cabernet Sauvignon | China | KF156863 | KF377495 | KF377532 | KF145367 | KP145451 |
| C. hymenocallidis | CAUG9 | <i>Hymenocallis americana</i> | China | KP145423 | KP145395 | KP145311 | GQ856730 | JX010410 |
| <i>C. kahawae</i> subsp. <i>ciggaro</i> | ICMP 12952 | <i>Persea americana</i> | China | JX010278 | JX010019 | JX009709 | GQ856775 | JX010426 |
| | ICMP 18539* | <i>Olea europaea</i> | China | JX010230 | JX009966 | JX009635 | JX009757 | JX010426 |
| <i>C. karstii</i> | CGMCC 3.14194* | <i>Vanda</i> sp. | Australia | HM585409 | HM585391 | HM581995 | JX009800 | JX010434 |
| | CAUOS1 | <i>Capsicum</i> sp. | China | KP890103 | KP890134 | KP890096 | KP890126 | KP890110 |
| | CAUOS7 | <i>Capsicum</i> sp. | China | KP890108 | KP890139 | KP890118 | KP890132 | KP890116 |
| | CAUOS8 | <i>Capsicum</i> sp. | China | KP890109 | KP890140 | KP890125 | KP890133 | KP890117 |
| | CAUOS2* | <i>Capsicum</i> sp. | China | KP890104 | KP890135 | KP890097 | KP890127 | KP890111 |
| C. liaoningense | CAUOS3 | <i>Capsicum</i> sp. | China | KP890105 | KP890136 | KP890098 | KP890128 | KP890112 |
| | CAUOS4 | <i>Capsicum</i> sp. | China | KP890106 | KP890137 | KP890120 | KP890129 | KP890113 |
| | CAUOS5 | <i>Capsicum</i> sp. | China | KP890107 | KP890138 | KP890122 | KP890130 | KP890114 |
| <i>C. musae</i> | ICMP 19119* | <i>Musa</i> sp. | USA | JX010146 | JX010050 | JX009742 | JX009896 | HQ596280 |
| | IMI 52264 | <i>Musa sapientum</i> | USA | JX010142 | JX010015 | JX009689 | JX009815 | JX010395 |
| <i>C. nupharicola</i> | ICMP 17938 | <i>Nuphar lutea</i> subsp. <i>polysepala</i> | Kenya | JX010189 | JX009936 | JX009661 | JX009834 | JX010397 |
| | ICMP 17940 | <i>Nymphaea odorata</i> | USA | JX010188 | JX010031 | JX009662 | JX009836 | JX010399 |
| | ICMP 18187* | <i>Nuphar lutea</i> subsp. <i>polysepala</i> | USA | JX010187 | JX009972 | JX009663 | JX009835 | JX010398 |
| | ICMP 19120* | <i>Psidium</i> sp. | Italy | JX010219 | JX009967 | JX009743 | JX009901 | JX010443 |
| <i>C. queenslandicum</i> | ICMP 1778* | <i>Carica papaya</i> | Australia | JX010276 | JX009934 | JX009691 | JX009899 | JX010414 |
| <i>C. salsae</i> | ICMP 19051 | <i>Salsola tragus</i> | Hungary | JX010242 | JX009916 | JX009696 | JX009863 | JX010403 |
| <i>C. siamense</i> | CBS 130420 | <i>Jasminum sambac</i> | Vietnam | HM131511 | HM131497 | JX009713 | JX009895 | JX010415 |
| <i>C. thailandicum</i> | BCC 38879* | <i>Hibiscus rosa-sinensis</i> | Thailand | JN050242 | JN050231 | JN050220 | JN050248 | JN050248 |
| | MFLUCC10092 | <i>Alocasia</i> sp. | Thailand | JN050243 | JN050232 | JN050221 | JN050249 | JN050249 |
| <i>C. theobromicola</i> | CBS 124945* | <i>Theobroma cacao</i> | Panama | JX010294 | JX010006 | JX009591 | JX009869 | JX010447 |
| | ICMP 17814 | <i>Fragaria vesca</i> | USA | JX010288 | JX010003 | JX009589 | JX009819 | JX010379 |
| | ICMP 17957 | <i>Stylosanthes viscosa</i> | Australia | JX010289 | JX009962 | JX009597 | JX009821 | JX010380 |
| <i>C. ti</i> | ICMP 4832* | <i>Cordylone</i> sp. | New Zealand | JX010269 | JX009952 | JX009649 | JX009898 | JX010442 |
| | ICMP 5285 | <i>Cordylone australis</i> | New Zealand | JX010267 | JX009910 | JX009553 | JX009897 | JX010441 |
| <i>C. tropicale</i> | CBS 124949* | <i>Theobroma cacao</i> | Panama | JX010264 | JX010007 | JX009719 | JX009870 | JX010407 |
| | ICMP 18672 | <i>Litchi chinensis</i> | Japan | JX010275 | JX010020 | JX009722 | JX009826 | JX010396 |
| <i>C. tropicicola</i> | BCC 38877* | <i>Citrus maxima</i> | Thailand | JN050240 | JN050229 | JN050218 | JN050246 | JN050246 |
| | MFLUCC100167 | <i>Paphiopedilum bellatolum</i> | Thailand | JN050241 | JN050230 | JN050219 | JN050247 | JN050247 |
| C. viniferum | CAUG27 | <i>Capsicum</i> sp. | China | KP145440 | KP145412 | KP145356 | KP145384 | KP145468 |
| | GZAAS 5.08601* | <i>Vitis vinifera</i> , cv. 'Shuijing' | China | JN412804 | JN412798 | JQ309639 | | JN412813 |
| | GZSSS 5.08608 | <i>Vitis vinifera</i> , cv. 'Hongji' | China | JN412802 | JN412800 | JQ412782 | | JN412811 |
| <i>C. xanthorrhoeae</i> | ICMP 17903* | <i>Xanthorrhoea preissii</i> | Australia | JX010261 | JX009927 | JX009653 | JX009823 | JX010448 |
| <i>C. yunnanense</i> | CBS 132135* | <i>Buxus</i> sp. | China | JX546804 | JX519248 | JX519239 | JX519231 | |
| <i>Glomella circinata</i> | ICMP 10643 | <i>Carnellia williamsii</i> | UK | JX010224 | JX009908 | JX009630 | JX009891 | JX010436 |
| <i>Monilochaetes infuscans</i> | CBS 869.96* | <i>Ipomoea batatas</i> | South Africa | JQ005780 | JX546612 | JQ005843 | JQ005801 | JQ005864 |

* = Ex-type culture. Strains studied in this paper are in bold font.

Table 2b Strains used for the phylogenetic analysis of the *Colletotrichum acutatum* species complex with details about host, location, and GenBank accession numbers.

| Species | Isolate | Host | Location | GenBank accessions | | | | | | |
|---------------------------|-------------|---------------------------------|-------------|--------------------|----------|----------|----------|----------|----------|--|
| | | | | ITS | GAPDH | CHS-1 | HIS3 | ACT | TUB2 | |
| <i>C. acutatum</i> | CBS 112996* | <i>Carica papaya</i> | Australia | JQ005776 | JQ948677 | JQ005797 | JQ005818 | JQ005839 | JQ005860 | |
| | CBS 144.29 | <i>Capsicum annuum</i> | Sri Lanka | JQ948401 | JQ948732 | JQ949062 | JQ949392 | JQ949722 | JQ950052 | |
| | CBS 126518 | <i>Carthamus</i> sp. | Netherlands | JQ948271 | JQ948601 | JQ948932 | JQ949262 | JQ949592 | JQ949922 | |
| <i>C. chrysanthemi</i> | IMI 364540 | <i>Chrysanthemum coronarium</i> | China | JQ948272 | JQ948602 | JQ948933 | JQ949263 | JQ949593 | JQ949923 | |
| | CAUA18 | <i>Capsicum annuum</i> | China | KP145016 | KP145096 | KP145048 | KP145064 | KP145032 | KP145080 | |
| | CAUA20 | <i>Capsicum annuum</i> | China | KP145226 | KP145162 | KP145290 | KP145194 | KP145130 | KP145258 | |
| <i>C. fioriniae</i> | CAUA24 | <i>Capsicum annuum</i> | China | KP145017 | KP145097 | KP145049 | KP145065 | KP145033 | KP145081 | |
| | CAUA25 | <i>Capsicum annuum</i> | China | KP145018 | KP145098 | KP145050 | KP145066 | KP145034 | KP145082 | |
| | CAUA26 | <i>Capsicum annuum</i> | China | KP145019 | KP145099 | KP145051 | KP145067 | KP145035 | KP145083 | |
| <i>C. gloeosporioides</i> | CAUA27 | <i>Capsicum annuum</i> | China | KP145020 | KP145100 | KP145052 | KP145068 | KP145036 | KP145084 | |
| | CAUA28 | <i>Capsicum annuum</i> | China | KP145021 | KP145101 | KP145053 | KP145069 | KP145037 | KP145085 | |
| | CAUA29 | <i>Capsicum annuum</i> | China | KP145022 | KP145102 | KP145054 | KP145071 | KP145038 | KP145086 | |
| <i>C. godetiae</i> | CAUA30 | <i>Capsicum annuum</i> | China | KP145023 | KP145103 | KP145055 | KP145072 | KP145039 | KP145087 | |
| | CAUA31 | <i>Capsicum annuum</i> | China | KP145024 | KP145104 | KP145056 | KP145077 | KP145040 | KP145088 | |
| | CAUA32 | <i>Capsicum annuum</i> | China | KP145025 | KP145105 | KP145057 | KP145073 | KP145041 | KP145089 | |
| <i>C. guajavae</i> | CAUA33 | <i>Capsicum annuum</i> | China | KP145026 | KP145106 | KP145058 | KP145074 | KP145042 | KP145090 | |
| | CAUA34 | <i>Capsicum annuum</i> | China | KP145027 | KP145107 | KP145059 | KP145075 | KP145043 | KP145091 | |
| | CAUA35 | <i>Capsicum annuum</i> | China | KP145028 | KP145108 | KP145060 | KP145076 | KP145044 | KP145092 | |
| <i>C. latiphilum</i> | CAUA36 | <i>Capsicum annuum</i> | China | KP145029 | KP145109 | KP145061 | KP145077 | KP145045 | KP145093 | |
| | CAUA37 | <i>Capsicum annuum</i> | China | KP145030 | KP145110 | KP145062 | KP145078 | KP145046 | KP145094 | |
| | CAUA38 | <i>Capsicum annuum</i> | China | KP145031 | KP145111 | KP145063 | KP145079 | KP145047 | KP145095 | |
| <i>C. nympheae</i> | CAUA39 | <i>Capsicum annuum</i> | USA | JQ948299 | JQ948629 | JQ948960 | JQ949290 | JQ949620 | JQ949950 | |
| | CAUA40 | <i>Malus domestica</i> | USA | JQ948317 | JQ948647 | JQ948978 | JQ949308 | JQ949638 | JQ949968 | |
| | CAUA41 | <i>Vaccinium</i> sp. | USA | JQ948292 | JQ948622 | JQ948953 | JQ949283 | JQ949613 | JQ949943 | |
| <i>C. orchidophilum</i> | CBS 125396 | <i>Vaccinium</i> sp. | USA | JQ948317 | JQ948647 | JQ948978 | JQ949308 | JQ949638 | JQ949968 | |
| | CBS 127537 | <i>Florinia</i> sp. | USA | JQ948292 | JQ948622 | JQ948953 | JQ949283 | JQ949613 | JQ949943 | |
| | CBS 128517* | <i>Vaccinium</i> sp. | USA | JQ948317 | JQ948647 | JQ948978 | JQ949308 | JQ949638 | JQ949968 | |
| <i>C. scovillei</i> | CBS 129916 | <i>Persea</i> sp. | Australia | JQ948310 | JQ948640 | JQ948971 | JQ949301 | JQ949631 | JQ949961 | |
| | CBS 293.67 | <i>Mangifera</i> sp. | Australia | JQ948311 | JQ948641 | JQ948972 | JQ949302 | JQ949632 | JQ949962 | |
| | CBS 127601 | <i>Vitis</i> sp. | Portugal | JQ948343 | JQ948673 | JQ949004 | JQ949334 | JQ949664 | JQ949994 | |
| <i>C. salicis</i> | CBS 200.35 | <i>Rubus</i> sp. | USA | JQ948293 | JQ948623 | JQ948954 | JQ949284 | JQ949614 | JQ949944 | |
| | IMI 356878* | <i>Citrus sinensis</i> | Italy | JX010152 | JX010056 | JX009818 | | JX009531 | JX010445 | |
| | CBS 133.44* | <i>Godetia</i> sp. | Denmark | JQ948402 | JQ948733 | JQ949063 | JQ949393 | JQ949723 | JQ950053 | |
| <i>C. scovillei</i> | IMI 350839* | <i>Psidium</i> sp. | India | JQ948270 | JQ948600 | JQ948931 | JQ949261 | JQ949591 | JQ949921 | |
| | CBS 112989* | <i>Hevea</i> sp. | India | JQ948289 | JQ948619 | JQ948950 | JQ949280 | JQ949610 | JQ949940 | |
| | CBS 515.78* | <i>Nymphaea</i> sp. | Netherlands | JQ948197 | JQ948527 | JQ948858 | JQ949188 | JQ949518 | JQ949848 | |
| <i>C. scovillei</i> | CBS 632.80* | <i>Dendrobium</i> sp. | USA | JQ948151 | JQ948481 | JQ948812 | JQ949142 | JQ949472 | JQ949802 | |
| | CBS 607.94* | <i>Salix</i> sp. | Netherlands | JQ948460 | JQ948791 | JQ949121 | JQ949451 | JQ949781 | JQ950111 | |
| | CAUA1 | <i>Capsicum annuum</i> | China | KP145208 | KP145144 | KP145272 | KP145176 | KP145112 | KP145240 | |
| <i>C. scovillei</i> | CAUA2 | <i>Capsicum annuum</i> | China | KP145209 | KP145145 | KP145273 | KP145177 | KP145113 | KP145241 | |
| | CAUA3 | <i>Capsicum annuum</i> | China | KP145210 | KP145146 | KP145274 | KP145178 | KP145114 | KP145242 | |
| | CAUA4 | <i>Capsicum annuum</i> | China | KP145211 | KP145147 | KP145275 | KP145179 | KP145115 | KP145243 | |
| <i>C. scovillei</i> | CAUA5 | <i>Capsicum annuum</i> | China | KP145212 | KP145148 | KP145276 | KP145180 | KP145116 | KP145244 | |
| | CAUA6 | <i>Capsicum annuum</i> | China | KP145213 | KP145149 | KP145277 | KP145181 | KP145117 | KP145245 | |
| | CAUA7 | <i>Capsicum annuum</i> | China | KP145214 | KP145150 | KP145278 | KP145182 | KP145118 | KP145246 | |
| <i>C. scovillei</i> | CAUA8 | <i>Capsicum annuum</i> | China | KP145215 | KP145151 | KP145279 | KP145183 | KP145119 | KP145247 | |
| | CAUA9 | <i>Capsicum annuum</i> | China | KP145216 | KP145152 | KP145280 | KP145184 | KP145120 | KP145248 | |
| | CAUA10 | <i>Capsicum annuum</i> | China | KP145217 | KP145153 | KP145281 | KP145185 | KP145121 | KP145249 | |
| <i>C. scovillei</i> | CAUA11 | <i>Capsicum annuum</i> | China | KP145218 | KP145154 | KP145282 | KP145186 | KP145122 | KP145250 | |

| | | | | | | | | |
|-------------|------------------------|-----------|----------|----------|----------|----------|----------|----------|
| CAUA12 | <i>Capsicum annuum</i> | China | KP145219 | KP145155 | KP145283 | KP145187 | KP145123 | KP145251 |
| CAUA13 | <i>Capsicum annuum</i> | China | KP145220 | KP145156 | KP145284 | KP145188 | KP145124 | KP145252 |
| CAUA14 | <i>Capsicum annuum</i> | China | KP145221 | KP145157 | KP145285 | KP145189 | KP145125 | KP145253 |
| CAUA15 | <i>Capsicum annuum</i> | China | KP145222 | KP145158 | KP145286 | KP145190 | KP145126 | KP145254 |
| CAUA16 | <i>Capsicum annuum</i> | China | KP145223 | KP145159 | KP145287 | KP145191 | KP145127 | KP145255 |
| CAUA17 | <i>Capsicum annuum</i> | China | KP145224 | KP145160 | KP145288 | KP145192 | KP145128 | KP145256 |
| CAUA19 | <i>Capsicum annuum</i> | China | KP145225 | KP145161 | KP145289 | KP145193 | KP145129 | KP145257 |
| CAUA21 | <i>Capsicum annuum</i> | China | KP145227 | KP145163 | KP145291 | KP145195 | KP145131 | KP145259 |
| CAUA22 | <i>Capsicum annuum</i> | China | KP145228 | KP145164 | KP145292 | KP145196 | KP145132 | KP145260 |
| CAUA23 | <i>Capsicum annuum</i> | China | KP145229 | KP145165 | KP145293 | KP145197 | KP145133 | KP145261 |
| CAUA33 | <i>Capsicum annuum</i> | China | KP145230 | KP145166 | KP145294 | KP145198 | KP145134 | KP145262 |
| CAUA34 | <i>Capsicum annuum</i> | China | KP145231 | KP145167 | KP145295 | KP145199 | KP145135 | KP145263 |
| CAUA35 | <i>Capsicum annuum</i> | China | KP145232 | KP145168 | KP145296 | KP145200 | KP145136 | KP145264 |
| CAUA36 | <i>Capsicum</i> sp. | China | KP145233 | KP145169 | KP145297 | KP145201 | KP145137 | KP145265 |
| CAUA42 | <i>Capsicum</i> sp. | China | KP145234 | KP145170 | KP145298 | KP145202 | KP145138 | KP145266 |
| CAUA43 | <i>Capsicum</i> sp. | China | KP145235 | KP145171 | KP145299 | KP145203 | KP145139 | KP145267 |
| CAUA44 | <i>Capsicum</i> sp. | China | KP145236 | KP145172 | KP145300 | KP145204 | KP145140 | KP145268 |
| CAUA45 | <i>Capsicum</i> sp. | China | KP145237 | KP145173 | KP145301 | KP145205 | KP145141 | KP145269 |
| CAUA46 | <i>Capsicum</i> sp. | China | KP145238 | KP145174 | KP145302 | KP145206 | KP145142 | KP145270 |
| CAUA47 | <i>Capsicum</i> sp. | China | KP145239 | KP145175 | KP145303 | KP145207 | KP145143 | KP145271 |
| CBS 120708 | <i>Capsicum</i> sp. | Thailand | JQ948269 | JQ948599 | JQ948930 | JQ949260 | JQ949590 | JQ949920 |
| CBS 126529* | <i>Capsicum</i> sp. | Indonesia | JQ948267 | JQ948597 | JQ948928 | JQ949258 | JQ949588 | JQ949918 |
| CBS 126530 | <i>Capsicum</i> sp. | Indonesia | JQ948268 | JQ948598 | JQ948929 | JQ949259 | JQ949589 | JQ949919 |
| CBS 122122* | <i>Carica</i> sp. | Australia | JQ948276 | JQ948606 | JQ948937 | JQ949267 | JQ949597 | JQ949927 |

C. simmondsii

* = Ex-type culture. Strains studied in this paper are in bold font.

clustered with *C. truncatum*, and one clustered with *C. incanum* (Fig. 4). The remaining isolates were assigned to *C. cliviae* and *C. karstii*. A new lineage belonging to the fourth group, distinct from all known species, is herein described as a new species, *C. liaoningense* (Fig. 6).

Pathogenicity

All tested isolates except that of *C. endophytica* were pathogenic to most of the detached ripe red chili fruits (Table 3). All *Capsicum annuum* and *Ca. frutescens* cultivars were susceptible to all tested *Colletotrichum* species (except *C. endophytica*), with disease scores from 5 to 9. *Capsicum chinense* was susceptible to most of the *Colletotrichum* species, except *C. cliviae* CAUOS5, *C. endophytica* CAUG28, and *C. hymenocallidis* CAUG9. *Capsicum annuum* and *Ca. frutescens* were the most susceptible, with average scores of 7. Three pathotypes (PC1-R, PC2-R, and PC3-R) were identified (Table 3) based on three differential reactions of tested strains with *Capsicum chinense* cv. Huangdijiao, *Ca. annuum* and *Ca. frutescens*. Host reactions of the mature green fruit were similar to those of the ripe fruit (Table 4). Similar to the ripe fruit, all three cultivars of the mature green fruit of *Capsicum annuum*, Zidantou, Denglongjiao, and Sanyingjiao were susceptible to all tested *Colletotrichum* species, except *C. endophytica*, with average scores from 5 to 6. Most of the *Capsicum frutescens* cultivars and *Ca. chinense* cv. Huangdijiao at the green fruit stage were susceptible to most isolates, except *C. aenigma* CAUG26, *C. conoides* CAUG17, *C. gloeosporioides* CAUG2, *C. grossum* CAUG7, *C. fructicola* CAUG1 and *C. karstii* CAUOS1. Five pathotypes were identified based on the differential reactions with Xiaomila, Shuangla, and Huangdijiao (Table 4). All of the pathogenic isolates formed sunken, brown to dark lesions on the fruits. No symptoms developed on the negative controls.

Prevalence of *Colletotrichum* species

To determine the prevalence of the *Colletotrichum* species associated with chili in China, the sample locations and the number of isolates were assessed for each species. Isolates with highly similar morphology and ITS sequences to those of the ex-type of *C. truncatum* appear to be most common (N = 422), representing 33 % of all isolates, and presenting in 56 % of all sampling locations (Fig. 5). All 34 isolates chosen from this group for multi-locus phylogenetic analysis were confirmed to be *C. truncatum* (Fig. 4). It therefore appears that *C. truncatum* is the most prevalent species of *Colletotrichum* on chili in China. The next most prevalent species included *C. scovillei*, *C. gloeosporioides*, *C. fioriniae*, and *C. fructicola*, which accounted for 21, 14, 14, and 13 % of all the isolates, respectively. The remaining species were detected in less than 3 % of the sampling locations.

TAXONOMY

Based on the morphology and the multi-locus phylogeny, the 121 isolates were assigned to 15 species. Seven species (*C. aenigma*, *C. cliviae*, *C. endophytica*, *C. hymenocallidis*, *C. incanum*, *C. karstii*, and *C. viniferum*) were reported from chili for the first time. Three other species (*C. fioriniae*, *C. fructicola*, and *C. scovillei*) were reported for the first time in China, and a further three species newly described.

Colletotrichum conoides Y.Z. Diao, C. Zhang, L. Cai & X.L. Liu, *sp. nov.* — MycoBank MB812003; Fig. 7

Etymology. Referring to the host variety (*Capsicum annuum* var. *conoides*) from which the fungus was first collected.

Colonies on PDA attaining 53–55 mm diam in 4 d at 28 °C; aerial mycelia greyish white; reverse light grey to medium grey

Table 2c Strains used for the phylogenetic analysis of *Colletotrichum* species with curved conidia with details on host, location, and GenBank accession numbers.

| Species | Isolate | Host | Location | GenBank accession numbers | | | | | |
|--------------------------|----------------|--|----------------|---------------------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| | | | | ITS | ACT | TUB2 | CHS-1 | GAPDH | HIS3 |
| <i>C. anthrisci</i> | CBS 125335 | <i>Anthriscus sylvestris</i> | Netherlands | GU227846 | GU227944 | GU228140 | GU228336 | GU228238 | GU228042 |
| <i>C. chlorophyti</i> | IMI 103806* | <i>Chlorophytum</i> sp. | India | GU227894 | GU227992 | GU228188 | GU228384 | GU228236 | GU228090 |
| | CBS 142.79 | <i>Stylosanthes hamata</i> | Australia | GU227895 | GU227993 | GU228189 | GU228385 | GU228287 | GU228091 |
| <i>C. circinans</i> | CBS 111.21 | <i>Allium cepa</i> | USA | GU227854 | GU227952 | GU228148 | GU228344 | GU228246 | GU228050 |
| | CBS 221.81* | <i>Allium cepa</i> | Serbia | GU227855 | GU227953 | GU228149 | GU228345 | GU228247 | GU228051 |
| <i>C. dematium</i> | CBS 125.25* | <i>Eryngium campestre</i> | France | GU227819 | GU227917 | GU228113 | GU228309 | GU228211 | GU228015 |
| | CBS 125340 | Apiaceae | Czech Republic | GU227820 | GU227918 | GU228114 | GU228310 | GU228212 | GU228016 |
| <i>C. fructi</i> | CBS 346.37* | <i>Malus sylvestris</i> | USA | GU227844 | GU227942 | GU228138 | GU228334 | GU228236 | GU228040 |
| <i>C. incanum</i> | ATCC 64682* | <i>Glycine max</i> | USA | KC110789 | KC110825 | KC110816 | | KC110807 | KC110798 |
| | IL6A | <i>Glycine max</i> | USA | KC110787 | KC110823 | KC110814 | | KC110805 | KC110796 |
| | IL9A | <i>Glycine max</i> | USA | KC110788 | KC110824 | KC110815 | | KC110806 | KC110797 |
| | CAUCT34 | Capsicum sp. | China | KP145641 | KP145505 | KP145675 | KP145539 | KP145573 | KP145607 |
| <i>C. lilii</i> | CBS 109214 | <i>Lilium</i> sp. | Japan | GU227810 | GU227908 | GU228104 | GU228300 | GU228202 | GU228006 |
| <i>C. lindemuthianum</i> | CBS 151.28 | <i>Lilium</i> sp. | Netherlands | GU227800 | GU227898 | GU228094 | GU228290 | GU228192 | GU227996 |
| <i>C. lineola</i> | CBS 125337* | Apiaceae sp. | Czech Republic | GU227829 | GU227927 | GU228123 | GU228319 | GU228221 | GU228025 |
| | CBS 125339 | Apiaceae sp. | Czech Republic | GU227830 | GU227928 | GU228124 | GU228320 | GU228222 | GU228026 |
| <i>C. liriopes</i> | CBS 119444* | <i>Liriope muscari</i> | Mexico | GU227804 | GU227902 | GU228098 | GU228294 | GU228196 | GU228000 |
| | CBS 122747 | <i>Liriope muscari</i> | Mexico | GU227805 | GU227903 | GU228099 | GU228295 | GU228197 | GU228001 |
| <i>C. phaseolorum</i> 1 | CBS 157.36 | <i>Phaseolus radiatus</i> var. <i>aureus</i> | Japan | GU227896 | GU227994 | GU228190 | GU228386 | GU228288 | GU228092 |
| <i>C. phaseolorum</i> 2 | CBS 158.36 | <i>Vigna sinensis</i> | Japan | GU227897 | GU227995 | GU228191 | GU228387 | GU228289 | GU228093 |
| <i>C. rusci</i> | CBS 119206* | <i>Ruscus</i> sp. | Italy | GU227818 | GU227916 | GU228112 | GU228308 | GU228210 | GU228014 |
| | CBS 167.49* | <i>Hosta sieboldiana</i> | Germany | GU227807 | GU227905 | GU228101 | GU228297 | GU228199 | GU228003 |
| <i>C. spaethianum</i> | CBS 100063 | <i>Lilium</i> sp. | South Korea | GU227808 | GU227906 | GU228102 | GU228298 | GU228200 | GU228004 |
| | CBS 101631 | <i>Hemerocallis</i> sp. | New Zealand | GU227809 | GU227907 | GU228103 | GU228299 | GU228201 | GU228005 |
| <i>C. spinaciae</i> | CBS 128.57 | <i>Spinacia oleracea</i> | Netherlands | GU227847 | GU227945 | GU228141 | GU228337 | GU228239 | GU228043 |
| | IMI 104607 | <i>Spinacia</i> sp. | Italy | GU227850 | GU227948 | GU228144 | GU228340 | GU228242 | GU228046 |
| <i>C. tofieldiae</i> | CBS 168.49 | <i>Lupinus polyphyllus</i> | Germany | GU227802 | GU227900 | GU228096 | GU228292 | GU228194 | GU227998 |
| | CBS 495.85 | <i>Tofieldia calyculata</i> | Switzerland | GU227801 | GU227899 | GU228095 | GU228291 | GU228193 | GU227997 |
| <i>C. trichellum</i> | CBS 118198 | <i>Hedera</i> sp. | Guatemala | GU227813 | GU227911 | GU228107 | GU228303 | GU228205 | GU228009 |
| | CBS 217.64 | <i>Hedera helix</i> | UK | GU227812 | GU227910 | GU228106 | GU228302 | GU228204 | GU228008 |
| <i>C. truncatum</i> | CBS 182.52 | <i>Glycine max</i> | USA | GU227866 | GU227964 | GU228160 | GU228356 | GU228258 | GU228062 |
| | CBS195.32 | <i>Glycine max</i> | USA | GU227865 | GU227963 | GU228159 | GU228355 | GU228257 | GU228061 |
| | CBS 345.70 | <i>Glycine max</i> | Denmark | GU227867 | GU227965 | GU228161 | GU228357 | GU228259 | GU228063 |
| | CBS 151.35* | <i>Phaseolus lunatus</i> | USA | GU227862 | GU227960 | GU228156 | GU228352 | GU228254 | GU228058 |
| | CAUCT1 | Capsicum annuum | China | KP145608 | KP145472 | KP145642 | KP145506 | KP145540 | KP145574 |
| | CAUCT2 | Capsicum annuum | China | KP145609 | KP145473 | KP145643 | KP145507 | KP145541 | KP145575 |
| | CAUCT3 | Capsicum annuum | China | KP145610 | KP145474 | KP145644 | KP145508 | KP145542 | KP145576 |
| | CAUCT4 | Capsicum annuum | China | KP145611 | KP145475 | KP145645 | KP145509 | KP145543 | KP145577 |
| | CAUCT5 | Capsicum annuum | China | KP145612 | KP145476 | KP145646 | KP145510 | KP145544 | KP145578 |
| | CAUCT6 | Capsicum annuum | China | KP145613 | KP145477 | KP145647 | KP145511 | KP145545 | KP145579 |
| | CAUCT7 | Capsicum sp. | China | KP145614 | KP145478 | KP145648 | KP145512 | KP145546 | KP145580 |
| | CAUCT8 | Capsicum sp. | China | KP145615 | KP145479 | KP145649 | KP145513 | KP145547 | KP145581 |
| | CAUCT9 | Capsicum sp. | China | KP145616 | KP145480 | KP145650 | KP145514 | KP145548 | KP145582 |
| | CAUCT10 | Capsicum sp. | China | KP145617 | KP145481 | KP145651 | KP145515 | KP145549 | KP145583 |
| | CAUCT11 | Capsicum sp. | China | KP145618 | KP145482 | KP145652 | KP145516 | KP145550 | KP145584 |

| | | | | | | | | |
|---------|---------------------|-------|----------|----------|----------|----------|----------|----------|
| CAUCT12 | <i>Capsicum</i> sp. | China | KP145619 | KP145483 | KP145653 | KP145517 | KP145551 | KP145585 |
| CAUCT13 | <i>Capsicum</i> sp. | China | KP145620 | KP145484 | KP145654 | KP145518 | KP145552 | KP145586 |
| CAUCT14 | <i>Capsicum</i> sp. | China | KP145621 | KP145485 | KP145655 | KP145519 | KP145553 | KP145587 |
| CAUCT15 | <i>Capsicum</i> sp. | China | KP145622 | KP145486 | KP145656 | KP145520 | KP145554 | KP145588 |
| CAUCT16 | <i>Capsicum</i> sp. | China | KP145623 | KP145487 | KP145657 | KP145521 | KP145555 | KP145589 |
| CAUCT17 | <i>Capsicum</i> sp. | China | KP145624 | KP145488 | KP145658 | KP145522 | KP145556 | KP145590 |
| CAUCT18 | <i>Capsicum</i> sp. | China | KP145625 | KP145489 | KP145659 | KP145523 | KP145557 | KP145591 |
| CAUCT19 | <i>Capsicum</i> sp. | China | KP145626 | KP145490 | KP145660 | KP145524 | KP145558 | KP145592 |
| CAUCT20 | <i>Capsicum</i> sp. | China | KP145627 | KP145491 | KP145661 | KP145525 | KP145559 | KP145593 |
| CAUCT21 | <i>Capsicum</i> sp. | China | KP145628 | KP145492 | KP145662 | KP145526 | KP145560 | KP145594 |
| CAUCT22 | <i>Capsicum</i> sp. | China | KP145629 | KP145493 | KP145663 | KP145527 | KP145561 | KP145595 |
| CAUCT23 | <i>Capsicum</i> sp. | China | KP145630 | KP145494 | KP145664 | KP145528 | KP145562 | KP145596 |
| CAUCT24 | <i>Capsicum</i> sp. | China | KP145631 | KP145495 | KP145665 | KP145529 | KP145563 | KP145597 |
| CAUCT25 | <i>Capsicum</i> sp. | China | KP145632 | KP145496 | KP145666 | KP145530 | KP145564 | KP145598 |
| CAUCT26 | <i>Capsicum</i> sp. | China | KP145633 | KP145497 | KP145667 | KP145531 | KP145565 | KP145599 |
| CAUCT27 | <i>Capsicum</i> sp. | China | KP145634 | KP145498 | KP145668 | KP145532 | KP145566 | KP145600 |
| CAUCT28 | <i>Capsicum</i> sp. | China | KP145635 | KP145499 | KP145669 | KP145533 | KP145567 | KP145601 |
| CAUCT29 | <i>Capsicum</i> sp. | China | KP145636 | KP145500 | KP145670 | KP145534 | KP145568 | KP145602 |
| CAUCT30 | <i>Capsicum</i> sp. | China | KP145637 | KP145501 | KP145671 | KP145535 | KP145569 | KP145603 |
| CAUCT31 | <i>Capsicum</i> sp. | China | KP145638 | KP145502 | KP145672 | KP145536 | KP145570 | KP145604 |
| CAUCT32 | <i>Capsicum</i> sp. | China | KP145639 | KP145503 | KP145673 | KP145537 | KP145571 | KP145605 |
| CAUCT33 | <i>Capsicum</i> sp. | China | KP145640 | KP145504 | KP145674 | KP145538 | KP145572 | KP145606 |
| CAUCT33 | <i>Capsicum</i> sp. | China | KP145640 | KP145504 | KP145674 | KP145538 | KP145572 | KP145606 |

* = Ex-type culture. Strains studied in this paper are in bold

with white margin. *Chlamydospores* not observed. *Vegetative hyphae* hyaline, smooth-walled, septate, branched. *Conidiomata* and *setae* not observed. *Conidiophores* formed directly on aerial mycelium, hyaline, aseptate. *Conidiogenous cells* hyaline, cylindrical to clavate, 22–30 × 3.5–5 µm, opening 2.5–3 µm. *Conidia* hyaline, aseptate, smooth-walled, cylindrical to clavate, both ends obtusely rounded, contents granular and mostly equally distributed, 13–17.5 × 5–6.5 µm (av. = 15.9 × 5.9 µm), L/W ratio = 2.7. *Appressoria* single or in small groups, medium to dark brown, aseptate, mostly ellipsoidal to irregular in outline, and crenate or deeply lobed at margin, 4–11.5 × 6–10.5 µm (av. = 8.35 × 7.1 µm), L/W ratio = 1.2. Sexual morph not observed after 8 wk.

Specimen examined. CHINA, Jiangsu Province, Nanjing City, on fruits of *Capsicum annuum* var. *conoides*, Sept. 2010, Y.Z. Diao (holotype HMAS 246481, ex-type living culture CGMCC 3.17615 = CAUG17 = LC6226); *ibid.*, NJ26, living culture CAUG33; *ibid.*, NJ27, living culture CAUG34.

Notes — *Colletotrichum conoides* is phylogenetically most closely related to *C. hebeiense* (Fig. 2). Sequence data from ITS and *CHS-1* could not separate the two species, but they can be distinguished by *GAPDH* (12 bp), *ACT* (4 bp), or *TUB* (3 bp). The two species also differ in the following characteristics: the granules are uniformly distributed in the conidia of *C. conoides* but mostly present at the polar ends in the conidia of *C. hebeiense*; most appressoria of *C. conoides* are ovoid ellipsoidal with crenate or deeply lobed margin, while those of *C. hebeiense* are clavate to subglobose; conidia of *C. conoides* are slightly larger than those of *C. hebeiense* (13–17.5 × 5–6.5 µm vs 11.6–15.3 × 4.47–6.88 µm). In addition, *C. conoides* was described from *Capsicum annuum* var. *conoides*, while *C. hebeiense* was described from *Vitis vinifera* (Yan et al. 2015). A PHI test revealed no significant recombination event between *C. conoides* and *C. hebeiense* (Fig. 8).

Colletotrichum grossum Y.Z. Diao, C. Zhang, L. Cai & X.L. Liu, *sp. nov.* — MycoBank MB812006; Fig. 9

Etymology. Referring to the host variety (*Capsicum annuum* var. *grossum*) from which the fungus was first collected.

Colonies on PDA attaining 49–52 mm diam in 4 d at 28 °C; aerial mycelia white, reverse light grey with white margin. *Chlamydospores* not observed. *Vegetative hyphae* hyaline, smooth-walled, septate, branched. *Conidiomata* and *setae* not observed. *Conidiophores* formed directly on aerial mycelium, hyaline, aseptate. *Conidiogenous cells* hyaline, cylindrical to clavate, 22–32 × 3–3.5 µm, opening 2–2.5 µm. *Conidia* hyaline, aseptate, smooth-walled, cylindrical to clavate, both ends rounded or one end acute, contents granular and mostly present at the polar ends, 14.5–20.5 × 5–7.5 µm (av. = 16.8 × 6.3 µm), L/W ratio = 2.7. *Appressoria* single, medium brown, aseptate, mostly ovoid or ellipsoidal to irregular in outline, and crenate in margin. 5.5–11.5 × 4–10.5 µm (av. = 8.65 × 6.1 µm), L/W ratio = 1.4. Sexual morph not observed after 8 wk.

Specimen examined. CHINA, Hainan Province, Haikou city, on chili fruits (*Capsicum annuum* var. *grossum*), Oct. 2010, Y.Z. Diao (holotype HMAS 246480, ex-type living culture CGMCC3.17614 = CAUG7 = LC6227); *ibid.*, HN2, living culture CAUG31; *ibid.*, HN3, living culture CAUG32.

Notes — *Colletotrichum grossum* is phylogenetically most closely related to *C. theobromicola* (Fig. 2). The sequence data of ITS and *CAL* do not separate the two species, but they can be distinguished by *GAPDH* (3 bp), *ACT* (5 bp), and *TUB* (8 bp). In morphology, *C. grossum* differs from *C. theobromicola* by having wider conidia (14.5–20.5 × 5–7.5 µm vs 14.5–18.7 × 4.5–5.5 µm) and colonies that are flat white rather than black as in *C. theobromicola* (Rojas et al. 2010). A PHI test revealed no significant recombination event between *C. grossum* and *C. theobromicola* (Fig. 8).

Fig. 2 Maximum parsimony tree of isolates in the *Colletotrichum gloeosporioides* species complex obtained from a heuristic search of combined *ACT*, *CAL*, *CHS-1*, *GAPDH*, *ITS*, and *TUB2* gene sequences. *Colletotrichum boninense* was used as the outgroup. Bootstrap support values $\geq 50\%$, Bayesian posterior probability values ≥ 0.95 and RAxML bootstrap support values (ML $\geq 50\%$) are shown at the nodes. Tree length = 1665, CI = 0.672, RI = 0.889, RC = 0.597, HI = 0.328. Ex-type strains are emphasised in **bold**.

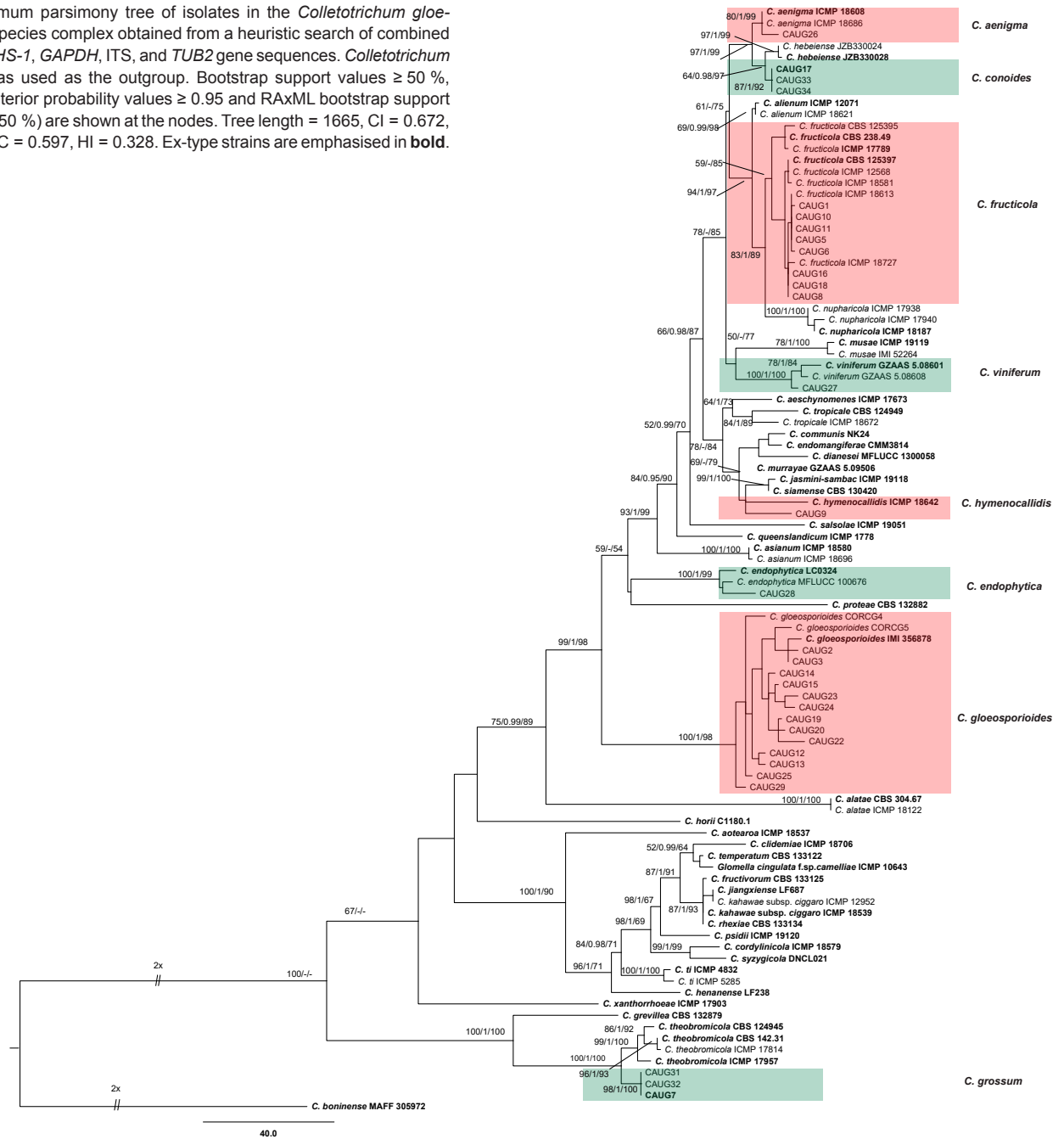


Table 3 Anthracnose severity scores on a 0–9 scale and pathotypes of 15 *Colletotrichum* species isolates at the ripe red fruit stage of seven chili cultivars.

| Isolate | <i>Capsicum annuum</i> | | | | <i>C. frutescens</i> | | <i>C. chinense</i> | Mean | Pathotype |
|---------------------------------|------------------------|--------------|-------------|----------|----------------------|----------|--------------------|------|-----------|
| | Chaotianjiao | Denglongjiao | Sanyingjiao | Zidantou | Shuanla | Xiaomila | Huangdijiao | | |
| <i>C. aenigma</i> CAUG26 | 5 | 5 | 7 | 5 | 5 | 7 | 5 | 6 | PC1-R |
| <i>C. cliviae</i> CAUOS5 | 7 | 7 | 5 | 7 | 7 | 5 | 0 | 5 | PC2-R |
| <i>C. conoides</i> CAUG17 | 7 | 7 | 7 | 7 | 7 | 5 | 5 | 6 | PC1-R |
| <i>C. endophytica</i> CAUG28 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | PC3-R |
| <i>C. fiorinae</i> CAUT34 | 7 | 7 | 9 | 9 | 9 | 9 | 7 | 8 | PC1-R |
| <i>C. fruticola</i> CAUG1 | 7 | 7 | 9 | 9 | 9 | 9 | 7 | 8 | PC1-R |
| <i>C. gloeosporioides</i> CAUG2 | 7 | 7 | 9 | 9 | 7 | 7 | 5 | 7 | PC1-R |
| <i>C. grossum</i> CAUG7 | 7 | 7 | 7 | 7 | 5 | 5 | 7 | 6 | PC1-R |
| <i>C. hymenocallidis</i> CAUG9 | 5 | 7 | 9 | 9 | 7 | 7 | 0 | 6 | PC2-R |
| <i>C. incanum</i> CAUT34 | 5 | 7 | 7 | 5 | 7 | 5 | 5 | 6 | PC1-R |
| <i>C. karstii</i> CAUOS1 | 7 | 5 | 7 | 7 | 9 | 9 | 7 | 7 | PC1-R |
| <i>C. liaoningense</i> CAUOS2 | 9 | 7 | 9 | 9 | 5 | 9 | 5 | 8 | PC1-R |
| <i>C. scovillei</i> CAUA1 | 7 | 9 | 9 | 9 | 9 | 7 | 9 | 8 | PC1-R |
| <i>C. truncatum</i> CAUT1 | 7 | 7 | 9 | 7 | 9 | 9 | 7 | 8 | PC1-R |
| <i>C. viniferum</i> CAUG27 | 5 | 7 | 9 | 9 | 9 | 9 | 5 | 8 | PC1-R |
| Mean | 6 | 6 | 7 | 7 | 7 | 7 | 5 | 6 | – |

Fig. 3 Maximum parsimony tree of isolates in the *Colletotrichum acutatum* species complex obtained from a heuristic search of combined *ACT*, *CHS-1*, *GAPDH*, *HIS3*, *ITS*, and *TUB2* gene sequences. *Colletotrichum gloeosporioides* was used as the outgroup. Bootstrap support values $\geq 50\%$ and Bayesian posterior probability values ≥ 0.95 are shown at the nodes. Tree length = 943, CI = 0.757, RI = 0.912, RC = 0.691, HI = 0.243. Ex-type strains are emphasised in **bold**.



Table 4 Anthracnose severity scores on a 0–9 scale and pathotypes of 15 *Colletotrichum* species isolates at the mature green fruit stage of seven chili cultivars.

| Isolate | <i>Capsicum annuum</i> | | | | <i>C. frutescens</i> | | <i>C. chinense</i> | Mean | Pathotype |
|---------------------------------|------------------------|--------------|-------------|----------|----------------------|----------|--------------------|------|-----------|
| | Chaotianjiao | Denglongjiao | Sanyingjiao | Zidantou | Shuanla | Xiaomila | Huangdijiao | | |
| <i>C. aenigma</i> CAUG26 | 5 | 5 | 5 | 5 | 0 | 0 | 0 | 3 | PC1-G |
| <i>C. cliviae</i> CAUOS5 | 7 | 9 | 5 | 7 | 7 | 5 | 7 | 7 | PC2-G |
| <i>C. conoides</i> CAUG17 | 7 | 5 | 0 | 5 | 7 | 5 | 0 | 4 | PC3-G |
| <i>C. endophytica</i> CAUG28 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | PC4-G |
| <i>C. fioriniae</i> CAUT34 | 9 | 9 | 7 | 7 | 9 | 9 | 7 | 8 | PC2-G |
| <i>C. fruticola</i> CAUG1 | 7 | 9 | 9 | 5 | 0 | 7 | 7 | 6 | PC5-G |
| <i>C. gloeosporioides</i> CAUG2 | 5 | 9 | 7 | 5 | 0 | 7 | 7 | 6 | PC5-G |
| <i>C. grossum</i> CAUG7 | 3 | 3 | 0 | 5 | 5 | 5 | 0 | 3 | PC3-G |
| <i>C. hymenocallidis</i> CAUG9 | 5 | 5 | 5 | 5 | 7 | 7 | 7 | 6 | PC2-G |
| <i>C. incanum</i> CAUT34 | 5 | 5 | 5 | 3 | 7 | 5 | 5 | 5 | PC2-G |
| <i>C. karstii</i> CAUOS1 | 5 | 7 | 7 | 7 | 0 | 0 | 0 | 4 | PC1-G |
| <i>C. liaoningense</i> CAUOS2 | 5 | 5 | 9 | 7 | 5 | 3 | 7 | 6 | PC2-G |
| <i>C. scovillei</i> CAUA1 | 7 | 7 | 7 | 7 | 9 | 9 | 7 | 7 | PC2-G |
| <i>C. truncatum</i> CAUT1 | 7 | 5 | 5 | 7 | 7 | 7 | 5 | 6 | PC2-G |
| <i>C. viniferum</i> CAUG27 | 5 | 5 | 5 | 7 | 9 | 9 | 7 | 7 | PC2-G |
| Mean | 5 | 6 | 5 | 5 | 5 | 5 | 4 | 5 | – |

Fig. 4 Maximum parsimony tree of *Colletotrichum* species with curved conidia obtained from a heuristic search of combined *ACT*, *CHS-1*, *GAPDH*, *HIS3*, ITS, and *TUB2* gene sequences. *Colletotrichum lindemuthianum* was used as the outgroup. Bootstrap support values $\geq 50\%$ and Bayesian posterior probability values ≥ 0.95 are shown at the nodes. Tree length = 2853, CI = 0.467, RI = 0.859, RC = 0.401, HI = 0.533. Ex-type strains are emphasised in **bold**.

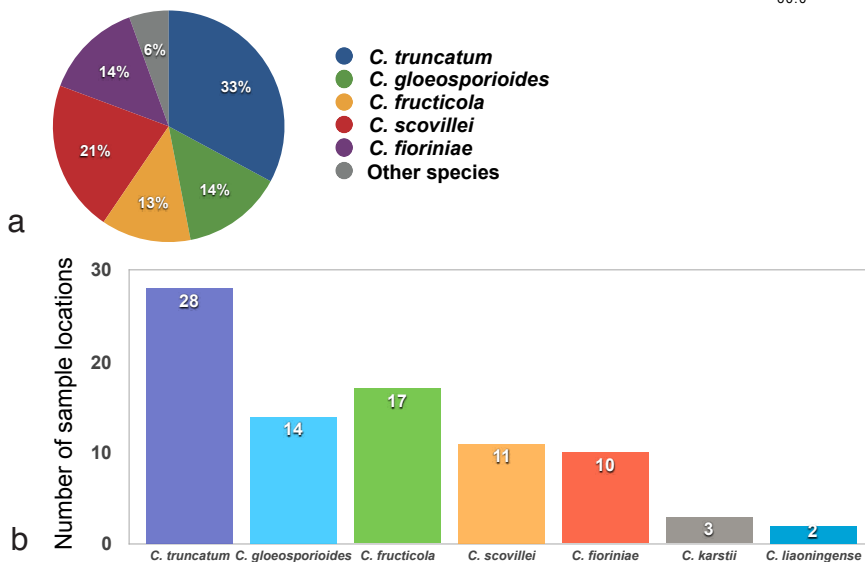
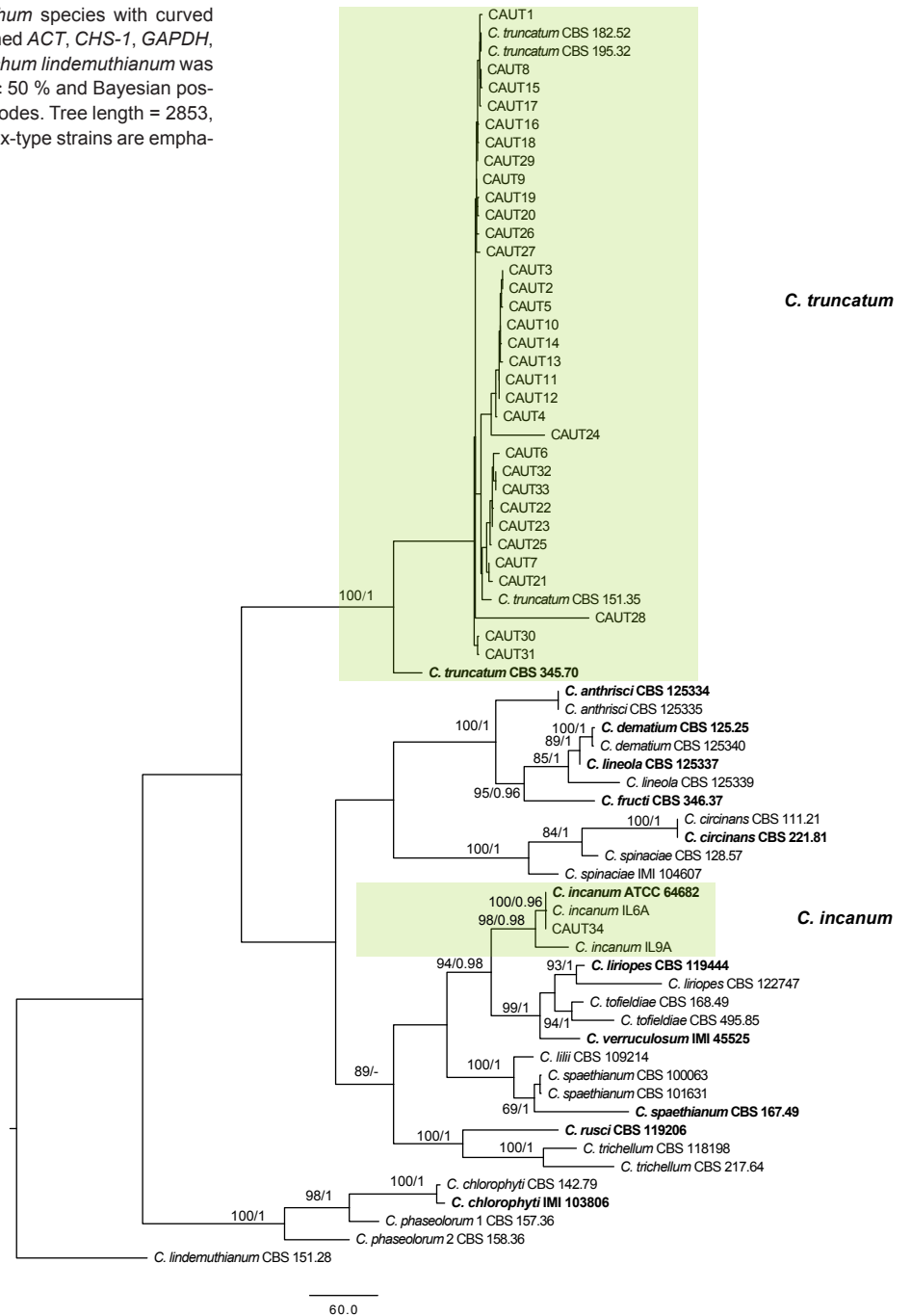


Fig. 5 Prevalence of *Colletotrichum* species on chili in China based on preliminary identifications. a. The percentage of isolates represented by the indicated *Colletotrichum* species on chili; b. number of sampling locations where the seven most prevalent species were isolated.

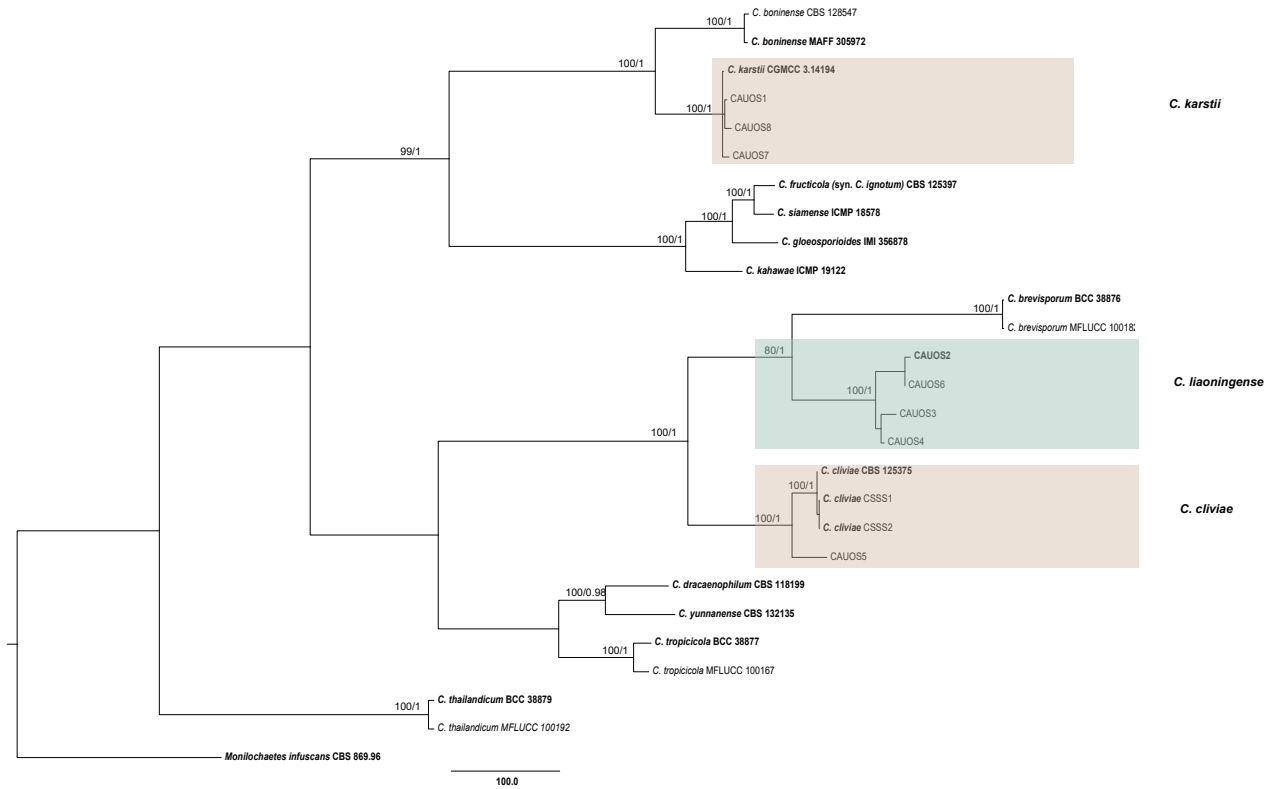


Fig. 6 Maximum parsimony tree of isolates of *Colletotrichum* species in the fourth group obtained from a heuristic search of combined *ACT*, *CAL*, *CHS-1*, *GAPDH*, *ITS*, and *TUB2* gene sequences. *Monilochaetes infuscans* was used as the outgroup. Bootstrap support values $\geq 50\%$ and Bayesian posterior probability values ≥ 0.95 are shown at the nodes. Tree length = 2913, CI = 0.717, RI = 0.870, RC = 0.624, HI = 0.283. Ex-type strains are emphasised in **bold**.



Fig. 7 *Colletotrichum conoides* (CAUG17). a–b. Colonies on PDA above and below; c. conidiophores; d–e, g–h: appressoria; f. conidia. — Scale bars: c–h = 10 μm .

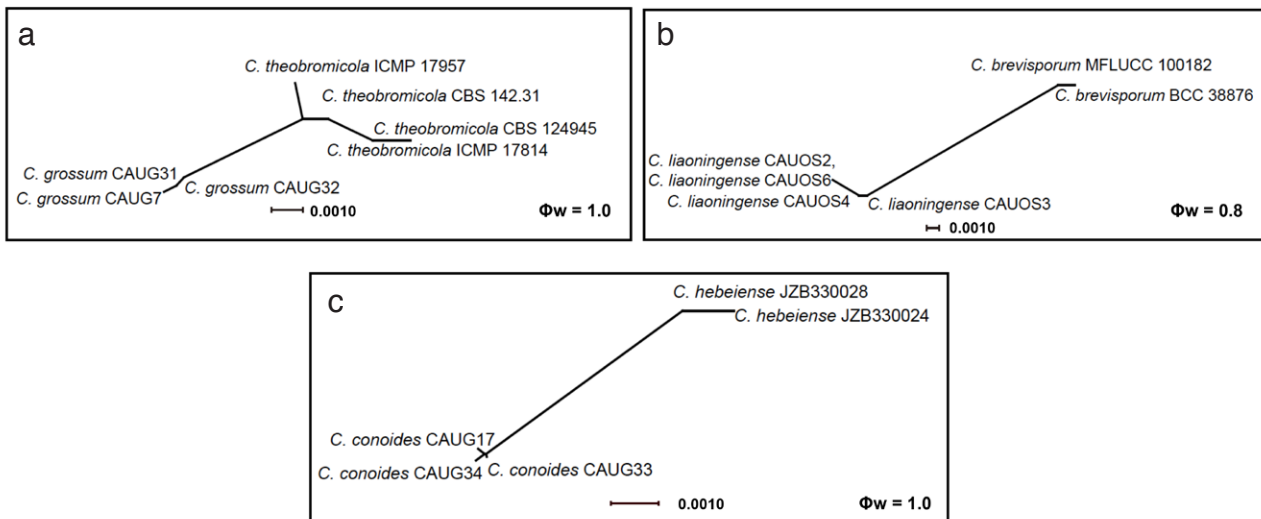


Fig. 8 The results of the pairwise homoplasies (PHI) test of closely related species using both LogDet transformation and splits decomposition. PHI test results (Φ_w) < 0.05 indicate significant recombination within the dataset.

Colletotrichum liaoningense Y.Z. Diao, C. Zhang, L. Cai & X.L. Liu, *sp. nov.* — MycoBank MB812007; Fig. 10

Etymology. Referring to the province in China where the fungus was first collected.

Colonies on PDA attaining 48–51 mm diam in 4 d at 28 °C; aerial mycelia light grey, reverse medium to dark brown with white margin. **Chlamydospores** not observed. **Vegetative hyphae** hyaline, smooth-walled, septate, branched. **Conidiomata** acervular. **Setae** medium grey, smooth-walled to verruculose, 3–6-septate, 46–68 µm long, base cylindrical, conical, or slightly inflated, 4.5–6.5 µm diam at the widest part, tip rounded. **Conidiophores** formed directly on aerial mycelium, hyaline, aseptate. **Conidiogenous cells** hyaline, cylindrical to clavate, 27–30 × 3.5–4.5 µm, opening 2–4 µm. **Conidia** cylindrical to clavate, both ends rounded or one end acute, contents granular and mostly present at the polar ends, hyaline, aseptate, smooth-walled, 14–18.5 µm × 5–7.5 µm (av. = 16.3 × 6.1 µm), L/W ratio = 2.7. **Appressoria** single, medium to dark brown, aseptate, mostly ellipsoidal to irregular in outline, and crenate at margin, 3.5–5 × 2.5–4.5 µm (av. = 4.1 × 2.9 µm), L/W ratio = 1.4. Sexual morph not observed after 8 wk.

Specimen examined. CHINA, Xingcheng city, Liaoning Province on chili fruits (*Capsicum annuum* var. *conoides*), Oct. 2012, Y.Z. Diao (holotype HMAS 246479, ex-type living culture CGMCC3.17616 = CAUOS2 = LC6228); *ibid.*, LN3, living culture CAUOS3; *ibid.*, LN4, living culture CAUOS4; *ibid.*, LN6, living culture CAUOS6.

Notes — *Colletotrichum liaoningense* is phylogenetically most closely related to *C. brevisporum* (Fig. 6). The sequence data from ITS and *ACT* could not separate the two species; however, they can be distinguished from each other via *GAPDH* (10 bp) or *TUB* (12 bp). The granules are equally distributed in the conidia of *C. liaoningense* but mostly present at the polar ends in conidia of *C. brevisporum*. The appressoria of *C. liaoningense* are smaller than those of *C. brevisporum* (3.5–5 × 2.5–4.5 µm vs 10–13 × 8–11 µm) (Noireung et al. 2012). A PHI test revealed no significant recombination event between *C. liaoningense* and *C. brevisporum* (Fig. 8).

DISCUSSION

Colletotrichum truncatum, the most frequently isolated species in this study, has been reported from more than 460 plant species (Farr & Rossman 2016). This taxon has also been shown

to cause serious damage to chili production in Australia, China, India, Thailand, and other countries (Poonpolgul & Kumphai 2007, Than et al. 2008, Sharma et al. 2014, Diao et al. 2015). In China, *C. truncatum* has been reported from tomato, dragon fruit, pumpkin, and other crops (Chai et al. 2014, Cheng et al. 2014, Diao et al. 2014, Guo et al. 2014). Geographic populations of *C. truncatum* in China exhibit significant genetic differentiation and recombination abilities, which can probably be attributed to the prevalence of this species (Diao et al. 2015).

Colletotrichum gloeosporioides has been reported to infect chili in Australia, China, India, Korea, Thailand, the USA, and other countries (Shin et al. 1999, Kim et al. 2008, Than et al. 2008). However, a recent study revealed this taxon to be a species complex comprising many morphologically similar taxa (Weir et al. 2012). Therefore, this new classification system necessitates a re-investigation of species in the *C. gloeosporioides* species complex on chili, as species in this complex exhibit biological and physiological differences. In the current study, *C. gloeosporioides* s.str. and *C. fructicola* were revealed to be most prevalent in this complex, representing 47 % and 42 % of the isolates, respectively (Fig. 2). *Colletotrichum fructicola* was originally isolated from coffee berries (Prihastuti et al. 2009), and has since been found on a wide range of host plants (Weir et al. 2012). However, this is the first report of *C. fructicola* infecting chili. In previous studies, *C. gloeosporioides* s.str. was shown to be an uncommon pathogen on chili and other fruits in the tropics (Phoulivong et al. 2010). Additionally, we failed to isolate *C. gloeosporioides* s.str. from chili in the tropical regions of China, e.g. Hainan, south of Guangdong, and Yunnan provinces (Table 1), which suggested a significant effect of climate on the distribution of these pathogens. Pathogenicity of all obtained species from chili in this study was confirmed by inoculation tests, except for that of *C. endophytica*. *Colletotrichum endophytica*, which was originally reported as an endophytic fungus in tropical grasses (Manamgoda et al. 2013), did not show pathogenicity to any chili cultivars in our test, further underlining the possible endophytic nature of this species.

Colletotrichum acutatum is a commonly reported species, and causes anthracnose on numerous plants worldwide (Damm et al. 2012a). It was originally described from *Carica papaya*, *Capsicum frutescens*, and *Delphinium ajacis* in Australia (Simmonds 1965), but has subsequently been reported to infect chili in almost all pepper-growing countries, such as Australia, China, India, Korea, New Zealand, Thailand, and the USA (Than et



Fig. 9 *Colletotrichum grossum* (CAUG7). a–b. Colonies on PDA above and below; c–e: conidiophores; f: conidia; g–k: appressoria. — Scale bars: c–f, j–k = 10 μ m (j applied to g–j).

al. 2008). Like *C. gloeosporioides*, *C. acutatum* has also been shown to represent a species complex (Damm et al. 2012a). Interestingly, *C. acutatum* s.str. was not found on chili in China (Fig. 3). Only *C. scovillei* and *C. fioriniae* were identified from this complex (Fig. 3).

No *Colletotrichum* species were detected on chili in Tibet and Xinjiang, despite the fact that several field trips have been made to these provinces, and attempts have been made for to isolate these fungi. The failure to detect *Colletotrichum* species from these regions might be explained by the high latitude,

small growing area, dry climate, and high day/night variation in temperature. *Colletotrichum fructicola* and *C. truncatum* were isolated from leaves in the Jiangxi province, and were also found from fruits in other sampling regions. In previous studies, these two species were primarily isolated from fruits from various plants (Poonpolgul & Kumphai 2007, Than et al. 2008, Alaniz et al. 2015, Diao et al. 2015).

In summary, the current study represents the hitherto most intensive investigation of *Colletotrichum* species on chili in China, which revealed 15 species, with the dominant species



Fig. 10 *Colletotrichum liaoningense* (CAUOS2). a–b. Colonies on PDA above and below; c–e: conidiophores; f: conidia; g–k: appressoria. — Scale bars: d–k = 10 µm (d applies to c–d).

being *C. fioriniae*, *C. fructicola*, *C. gloeosporioides*, *C. scovillei*, and *C. truncatum*. The information provided here could prove useful for the control of anthracnose on chili, as well as for the screening of new chili cultivars against anthracnose.

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