



Re-identification of *Colletotrichum acutatum* Species Complex in Korea and Their Host Plants

Le Dinh Thao^{1,2}, Hyorim Choi¹, Yunhee Choi¹, Anbazhagan Mageswari¹, Daseul Lee¹, and Seung-Beom Hong^{1*}

¹Korean Agricultural Culture Collection, Agricultural Microbiology Division, National Institute of Agricultural Sciences, Rural Development Administration, Wanju 55365, Korea

²Plant Protection Research Institute, Duc Thang, Bac Tu Liem, Ha Noi, Vietnam

(Received on May 26, 2023; Revised on June 30, 2023; Accepted on July 3, 2023)

Colletotrichum acutatum species complex is one of the most important groups in the genus *Colletotrichum* with a high species diversity and a wide range of host plants. *C. acutatum* and related species have been collected from different plants and locations in Korea and deposited into the Korean Agricultural Culture Collection (KACC), National Institute of Agricultural Sciences since the 1990s. These fungal isolates were previously identified based mainly on morphological characteristics, and a limitation of molecular data was provided. To confirm the identification of species, 64 *C. acutatum* species complex isolates in KACC were used in this study for DNA sequence analyses of six loci: nuclear ribosomal internal transcribed spacers (ITS), beta-tubulin 2 (TUB2), histone-3 (HIS3), glyceraldehyde-3-phosphate dehydrogenase (GAPDH), chitin synthase 1 (CHS-1), and actin (ACT). The molecular analysis revealed that they were identified in six different species of *C. fiorinae* (24 isolates), *C. nymphaeae* (21 isolates), *C. scovillei* (12 isolates), *C. chrysanthemi* (three isolates), *C. lupini* (two isolates), and *C. godeliae* (one isolate), and a novel species candidate. We compared the hosts of KACC isolates with “The List of Plant Diseases in Korea”, previous reports in Korea and global reports and

found that 23 combinations between hosts and pathogens could be newly reported in Korea after pathogenicity tests, and 12 of these have not been recorded in the world.

Keywords : *Colletotrichum acutatum* species complex, host plant, identification

The fungal family *Glomerellaceae* contains only one genus *Colletotrichum* which consists of many phytopathogenic species with a wide range of hosts. *Colletotrichum* species were commonly reported as causal agents of anthracnose diseases and infected economically important crops such as apple, strawberry, pepper, citrus, peach, mango, avocado, banana, coffee and cereals (Cannon et al., 2012; Crouch and Beirn, 2009; González et al., 2006; Kim et al., 2008; Lenné, 2002; Nguyen et al., 2010; Oo et al., 2018; Peres et al., 2008; Sanders and Korsten, 2003; Tan et al., 2022).

The identification of *Colletotrichum* species was primarily based on morphological characteristics with 11 species recognized by von Arx (1957), 22 species by Sutton (1980), and 39 species by Sutton (1992). Later, 66 species were accepted by Hyde et al. (2009) based on the morphology and/or molecular analysis. However, morphological characteristics and the lack of molecular data cannot be used to identify *Colletotrichum* species accurately (Cai et al., 2011; Sato and Moriwaki, 2013). Therefore, Jayawardena et al. (2016) divided the genus *Colletotrichum* (189 species) into 11 species complexes and 23 single species, then Liu et al. (2022) updated to 280 accepted species with 16 species complexes and 15 singleton species, based on multi-locus phylogeny. The nuclear ribosomal internal transcribed spacer (ITS) region was used to determine *Colletotrichum* species complexes (Cannon et al., 2012).

*Corresponding author.
Phone) +82-31-299-1866
E-mail) funguy@korea.kr

Handling Editor : Sook-Young Park

© This is an Open Access article distributed under the terms of the Creative Commons Attribution Non-Commercial License (<http://creativecommons.org/licenses/by-nc/4.0>) which permits unrestricted noncommercial use, distribution, and reproduction in any medium, provided the original work is properly cited.

While, most members of the *C. acutatum*, *C. dematium*, *C. destructivum*, *C. orchidearum*, *C. spaethianum*, *C. dra-caenophilum*, *C. magnum*, and *C. truncatum* species complexes were identified at species level by the combination of six loci: ITS, beta-tubulin 2 (TUB2), histone-3 (HIS3), glyceraldehyde-3-phosphate dehydrogenase (GAPDH), chitin synthase 1 (CHS-1), and actin (ACT) (Damm et al., 2009, 2012, 2014, 2019; Jayawardena et al., 2016; Liu et al., 2022).

Species in the *C. acutatum* species complex are known as destructive plant pathogens worldwide, including Korea (Baroncelli et al., 2015; Cho et al., 2021; Garrido et al., 2009; Kim et al., 2022; Kwon and Kim, 2011; Lee et al., 2007; Oh, 1995; Peres et al., 2008; Talhinhas et al., 2011). To date, this complex was one of the biggest groups in the genus *Colletotrichum* with 43 accepted species and contained species with a wide or narrow range of host plants (Jayawardena et al., 2021; Liu et al., 2022). The variation in the conidial shape of many species in the complex often led to incorrectly identify based on morphology. For example, 39 *Colletotrichum* isolates, morphologically identified as *C. gloeosporioides* or *Glomerella cingulata*, were re-identified as 14 species in or closely related to the *C. acutatum* species complex based on the multi-locus analysis (Damm et al., 2012).

Isolates of *C. acutatum* and related species have been deposited into the Korean Agricultural Culture Collection (KACC), National Institute of Agricultural Sciences since the 1990s. These species were originally identified mainly based on morphological characteristics. In earlier studies, several KACC isolates in the *C. acutatum* species complex

were re-identified using a single locus or the multi-locus combination. Nevertheless, some of these were ambiguous species because of insufficient molecular data (Han et al., 2014; Kim and Kim, 2020; Kim et al., 2006, 2008, 2020; Noh et al., 2014; Park et al., 2020; Xu et al., 2018). Accurate species identification within *C. acutatum* species complex plays an important role to understand species diversity and the host plants of this complex in Korea. Hence, this study aims to: (1) re-identify the isolates of *C. acutatum* species complex in KACC using the combined analysis of six loci (ITS, TUB2, HIS3, GAPDH, CHS-1, and ACT); (2) rearrange combination between host plants and re-identified species under *C. acutatum* species complex in Korea.

Materials and Methods

Fungal isolates. Sixty-four cultures of *Colletotrichum* from many host plants and different locations in Korea have been deposited and preserved in liquid nitrogen at the KACC. Details of these isolates such as sources, locations, collected date and previous re-identifications were documented. Fresh cultures were recovered on potato dextrose agar (PDA) and used in this study.

DNA extraction, polymerase chain reaction amplification, and sequencing. Fungal mycelia were scraped from 7-day-old cultures on PDA plates. Around 50 mg of fresh mycelia was used for DNA extraction using the DNeasy plant mini kit (Qiagen, Hilden, Germany), following the manufacturer's instructions. DNA templates were checked

Table 1. Primer pairs used for PCR amplification and sequencing in this study

Locus	Primer	Direction	Sequence (5'-3')	Reference
ITS	ITS1	Forward	TCCGTAGGTGAACCTGCGG	White et al. (1990)
	ITS4	Reverse	TCCTCCGCTTATTGATATGC	
TUB2	T1	Forward	AACATGCGTGAGATTGTAAGT	O'Donnell and Cigelnik (1997)
	Bt2b	Reverse	ACCCTCAGTGTAGTGACCCTTGGC	
GAPDH	GDF1	Forward	GCCGTCAACGACCCCTTCATTGA	Guerber et al. (2003)
	GDR1	Reverse	GGGTGGAGTCGTACTIONTGGAGCATGT	
HIS3	CYLH3F	Forward	AGGTCCACTGGTGGCAAG	Crous et al. (2004)
	CYLH3R	Reverse	AGCTGGATGTCCTTGGACTG	
CHS-1	CHS-79F	Forward	TGGGGCAAGGATGCTTGGGAAGAAG	Carbone and Kohn (1999)
	CHS-345R	Reverse	TGGAAGAACCATCTGTGAGAGTTG	
ACT	ACT-512F	Forward	ATGTGCAAGCCGGTTTCGC	Carbone and Kohn (1999)
	ACT-783R	Reverse	TACGAGTCCTTCTGGCCCAT	

PCR, polymerase chain reaction; ITS, internal transcribed spacer; TUB2, β -tubulin 2; GAPDH, glyceraldehyde-3-phosphate dehydrogenase; HIS3, histone3; CHS-1, chitin synthase; ACT, actin.

by a NanoDrop Spectrophotometer (Thermo Scientific, Waltham, MA, USA).

The primer pairs, including ITS1/ITS4 (White et al., 1990), T1/BT2b (Glass and Donaldson, 1995; O'Donnell and Cigelnik, 1997), GDF1/GDR1 (Guerber et al., 2003), CYLH3F/CYLH3R (Crous et al., 2004), CHS-79F/CHS-345R (Carbone and Kohn, 1999), and ACT-512F/ACT-783R (Carbone and Kohn, 1999), were used for the amplification of ITS, TUB2, GAPDH, HIS3, CHS-1, and ACT, respectively (Table 1). Each polymerase chain reaction (PCR) volume (25 µl) consisted of 12.5 µl MyTaq HS Mix, 1 µl (4.5 pMol) of each primer, 8.5 µl nuclease-free water and 2 µl DNA template (100 ng/µl). PCR reactions were performed in a MJ Research PTC-200 Thermal Cycler (MJ Research, Ramsey, MN, USA) with an initial denaturation step at 94°C for 5 min, followed by 30 cycles: denaturation at 94°C for 30 s; annealing at 58°C (ITS), 61°C (TUB2 and GAPDH) and 61.5°C (HIS3, CHS-1, and ACT) for 30 s, extension at 72°C for 1 min and final extension at 72°C for 10 min. PCR products were checked by gel electrophoresis before sending to the Macrogen (Seoul, Korea) for sequencing with the amplifying primer pairs.

Phylogenetic analysis. Raw sequences obtained in this study were assembled by MEGA 11 (Tamura et al., 2021) and deposited to RDA-GeneBank (<http://genebank.rda.go.kr>) with accession numbers in Table 2. The sequence datasets contained sequences of 64 KACC isolates, 43 reference species (Supplementary Table 1) in the *C. acutatum* species complex, and *C. orchidophilum* (outgroup) (Liu et al., 2022). The multiple sequence alignment of each locus was separately performed using the ClustalW program in MEGA 11 and concatenated afterward. A maximum likelihood (ML) phylogenetic tree of six loci was inferred using IQ-TREE with the best-fit model “TIM2+F+I+G4”, and 1,000 ultrafast bootstrap replicates. The phylogenetic tree was viewed in MEGA11 and depicted in Adobe Illustrator.

Results

Multi-locus phylogeny. The ITS, TUB2, GAPDH, HIS3, CHS-1, and ACT alignments contained 545, 497, 247, 378, 251, and 234 characters including gaps, respectively. Concatenated alignment of six loci included the members in the *C. acutatum* species complex in this study and references (43 accepted species, and *C. orchidophilum* as an outgroup). A combined phylogenetic tree (Fig. 1) showed that 64 KACC isolates were composed of six different species and a novel species candidate. Of these, 24 KACC

isolates were grouped with the ex-type strain of *C. fioriniae* (CBS 128517), supported by a 100% ML bootstrap value. Twenty-one KACC isolates were clustered together with the ex-type strain of *C. nymphaeae* (CBS 515.78) with a 100% ML bootstrap value. Twelve KACC isolates and the ex-type strain of *C. scovillei* (CBS 126529) formed a single clade with a 99% ML bootstrap value. Three KACC isolates (KACC 40700, KACC 40801, and KACC 47036) were segregated into a separate group with *C. chrysanthemi* (IMI 364540, authentic strain), well supported by a 100% ML bootstrap value. KACC 47255 and KACC 47254 were in a group with the ex-type strain of *C. lupini* (CBS 109225) with a 97% ML bootstrap value. A single clade was generated by KACC 42911 and the ex-type strain of *C. godetiae* (CBS 133.44), well supported with a bootstrap value of 98%. The isolate KACC 40014 formed a single clade and had a distant genetic relationship with others. The GAPDH sequence of KACC 40014 had highest similarities with *C. sloanei* (IMI 364297, ex-type strain, 97.37%), *C. paxtonii* (IMI 165753, ex-type strain, 96.93%) and had 93.86% similarity with *C. simmondsii* (CBS 122122, ex-type strain). The loci of KACC 40014 were lower than 99% similarity with the closely related species such as ACT (98.7% with *C. simmondsii* and *C. paxtonii*), HIS3 (98.66% with *C. simmondsii* and *C. sloanei*), TUB2 (98.98% with *C. paxtonii* and 98.57% with *C. sloanei*), and ITS (98.9% with *C. simmondsii*). The data suggested that *Colletotrichum* sp. (KACC 40014) could be considered as a novel species candidate of the genus *Colletotrichum*.

Host plants of *C. acutatum* species complex in this study. *C. fioriniae* (24 KACC isolates) were collected from 15 different plant species belonging to 15 genera and 11 families with an abundance of Rosaceae (six isolates) and Solanaceae (six isolates). Ten host species (*Actinidia chinensis*, *Capsicum annuum*, *Camellia sinensis*, *Cayratia japonica*, *Chaenomeles sinensis*, *Machilus thunbergii*, *Pinus koraiensis*, *Schizonepeta tenuifolia* var. *japonica*, *Spiraea prunifolia* var. *simpliciflora*, and *Xylosma congesta*) have not been reported in Korea and six of which, including *C. japonica*, *C. sinensis*, *P. koraiensis*, *S. tenuifolia* var. *japonica*, *S. prunifolia* var. *simpliciflora* and *X. congesta*, have not been reported in the world. Five species (*Cucurbita* sp., *Lycium chinense*, *Malus domestica*, *Paeonia lactiflora*, and *Solanum melongena*) were previously reported in Korea. *C. nymphaeae* (21 KACC isolates) were isolated from 10 different host species, from nine genera and seven families. Most of them are from the family Rosaceae (10 isolates) and Solanaceae (four isolates). Eight host species (*Abies holophylla*, *Capsicum annuum*, *Humulus japonicas*,

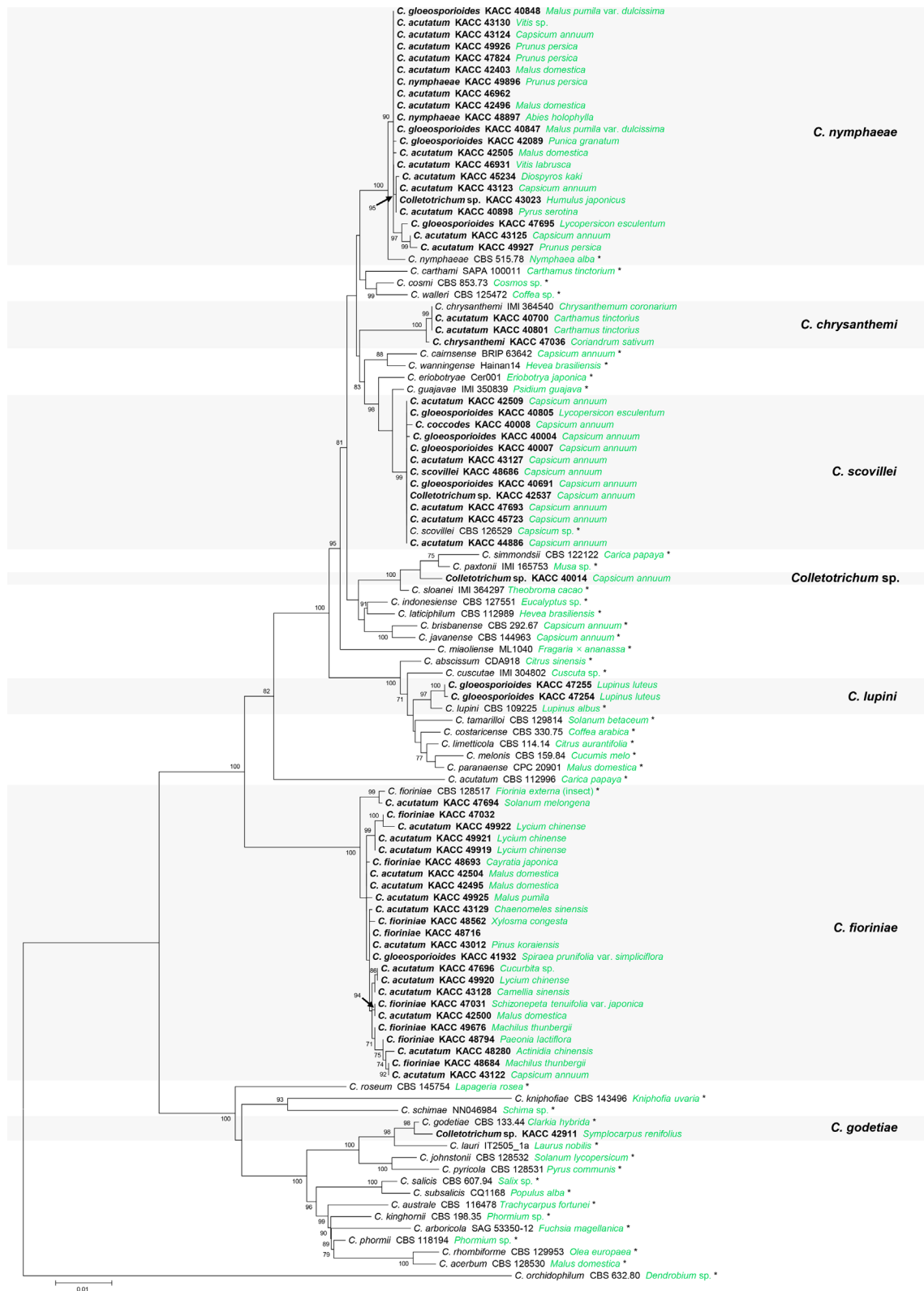


Fig. 1. A maximum likelihood tree was generated based on the analysis of multi-locus sequences of internal transcribed spacers (ITS), beta-tubulin 2 (TUB2), histone-3 (HIS3), glyceraldehyde-3-phosphate dehydrogenase (GAPDH), chitin synthase 1 (CHS-1), and actin (ACT). Species names are followed by isolate numbers and their hosts (green). Isolates in this study are in bold (original species names and isolate numbers). Ex-type strains are noted by *. *Colletotrichum orchidophilum* was used as the outgroup.

Table 2. KACC isolates under *Colletotrichum acutatum* species complex used in this study

Re-identified species	Isolate no.	Location	Collected date	Host	Species name by depositor	Previous identification	ITS	TUB2	GAPDH	HIS3	CHS-1	ACT
<i>C. chrysanthemi</i>	KACC 40700	Jecheon	1998 Jun	<i>Carthamus tinctorius</i>	<i>C. acutatum</i>	<i>C. acutatum</i> (Kim et al., 2006; 2008)	RDA0061920	RDA0062143	RDA0062355	RDA0065775	RDA0065725	RDA0065685
	KACC 40801	Uiseong	1998 Jun	<i>Carthamus tinctorius</i>	<i>C. acutatum</i>	<i>C. acutatum</i> (Kim et al., 2006)	RDA0061919	RDA0062144	RDA0062356	RDA0065780	RDA0065720	RDA0065684
<i>C. fioriniae</i>	KACC 47036	Eumseong	2012 Sep	<i>Coriandrum sativum</i>	<i>C. chrysanthemi</i>		RDA0061949	RDA0062247	RDA0062452	RDA0065759	RDA0065741	RDA00656531
	KACC 47032	Cheongyang	2012 Sep	-	<i>C. fioriniae</i>		RDA0061948	RDA0062243	RDA0062448	RDA0065763	RDA0065737	RDA00656535
	KACC 48716	Gangneung	2013 Nov	-	<i>C. fioriniae</i>		RDA0061964	RDA0062307	RDA0062501	RDA0065766	RDA0065734	RDA0065638
	KACC 48280	Jeju	2015 Sep	<i>Actinidia chinensis</i>	<i>C. acutatum</i>		RDA0061958	RDA0062281	RDA0062476	RDA0065799	RDA0065700	RDA0065665
	KACC 43128	Boseong	2006 Aug	<i>Camellia sinensis</i>	<i>C. acutatum</i>		RDA0061938	-	RDA0062418	RDA0065812	RDA0065687	RDA0065677
	KACC 43122	Jeungpyeong	2004 Jan	<i>Capsicum annuum</i>	<i>C. acutatum</i>		RDA0061932	RDA0062207	RDA0062412	RDA0065811	RDA0065688	RDA0065676
	KACC 48693	Jeju	2018 Oct	<i>Cayratia japonica</i>	<i>C. fioriniae</i>		RDA0061963	RDA0062299	RDA0062494	RDA0065768	RDA0065732	RDA0065639
	KACC 43129	Cheongju	2007 Mar	<i>Chaenomeles sinensis</i>	<i>C. acutatum</i>		RDA0061939	RDA0062214	RDA0062419	RDA0065777	RDA0065723	RDA0065646
	KACC 47696	Gangneung	2013 Nov	<i>Cucurbita</i> sp.	<i>C. acutatum</i>	<i>C. fioriniae</i> (Kim and Kim, 2020)	RDA0061955	RDA0062268	RDA0062462	RDA0065785	RDA0065715	RDA0065651
	KACC 49919	Cheongyang	-	<i>Lycium chinense</i>	<i>C. acutatum</i>		RDA0061969	RDA0062321	RDA0062517	RDA0065808	RDA0065691	RDA0065673
	KACC 49920	Cheongyang	-	<i>Lycium chinense</i>	<i>C. acutatum</i>		RDA0061970	RDA0062322	RDA0062518	RDA0065805	RDA0065694	RDA0065670
	KACC 49921	Cheongyang	-	<i>Lycium chinense</i>	<i>C. acutatum</i>		RDA0061971	RDA0062323	RDA0062519	RDA0065794	RDA0065705	RDA0065660
KACC 49922	Cheongyang	-	<i>Lycium chinense</i>	<i>C. acutatum</i>		RDA0061972	RDA0062324	RDA0062520	RDA0065752	RDA0065748	RDA0065667	
KACC 48684	Busan	2017 Aug	<i>Machilus thunbergii</i>	<i>C. fioriniae</i>		RDA0061961	RDA0062296	RDA0062490	RDA0065804	RDA0065695	RDA0065637	
KACC 42495	Bonghwa	2006 Sep	<i>Malus domestica</i>	<i>C. acutatum</i>		RDA0061910	RDA0062184	RDA0062389	RDA0065781	RDA0065719	RDA0065648	
KACC 42500	Yongin	2006 Aug	<i>Malus domestica</i>	<i>C. acutatum</i>		RDA0061908	RDA0062189	RDA0062394	RDA0065788	RDA0065712	RDA0065654	
KACC 42504	Jangsu	2006 Aug	<i>Malus domestica</i>	<i>C. acutatum</i>		RDA0061907	RDA0062193	RDA0062398	RDA0065776	RDA0065724	RDA0065645	
KACC 49925	Yeongdon	-	<i>Malus pumila</i>	<i>C. acutatum</i>		RDA0061973	RDA0062327	RDA0062523	RDA0065797	RDA0065702	RDA0065663	
KACC 48794	Gangjin	2019 Jul	<i>Paeonia lactiflora</i>	<i>C. fioriniae</i>		RDA0061965	RDA0062308	RDA0062503	RDA0065798	RDA0065701	RDA0065664	
KACC 43012	Daejeon	2006 May	<i>Pinus koraiensis</i>	<i>C. acutatum</i>		RDA0061931	RDA0062201	RDA0062407	RDA0065813	RDA0065710	RDA0065655	
KACC 47031	Eumseong	2012 Jul	<i>Schizonepeta tenuifolia</i> var. <i>japonica</i>	<i>C. fioriniae</i>		RDA0061947	RDA0062242	RDA0062447	RDA0065770	RDA0065730	RDA0065641	
KACC 47694	Gangneung	2011 Nov	<i>Solanum melongena</i>	<i>C. acutatum</i>	<i>C. fioriniae</i> (Xu et al., 2018)	RDA0061953	RDA0062266	RDA0062460	RDA0065795	RDA0065704	RDA0065661	

(Continued)

Table 2. Continued

Re-identified species	Isolate no.	Location	Collected date	Host	Species name by depositor	Previous identification	ITS	TUB2	GAPDH	HIS3	CHS-1	ACT
<i>C. fiorinia</i>	KACC 41932	Geoje	2002 May	<i>Spiraea prunifolia</i> var. <i>simpliciflora</i>	<i>C. gloeosporioides</i>	<i>C. acutatum</i> (Kim et al., 2006)	RDA0061913	RDA0062171	RDA0062375	RDA0065772	RDA0065728	RDA0065643
<i>C. fiorinia</i>	KACC 48562	Seogwipo	2018 Apr	<i>Xylosma congesta</i>	<i>C. fiorinia</i>		RDA0061960	RDA0062287	RDA0062481	RDA0065790	RDA0065709	RDA0065656
	KACC 49676	Jeju	-	<i>Machilus thunbergii</i>	<i>C. fiorinia</i>		RDA0061967	RDA0065814	-	RDA0065796	RDA0065703	RDA0065662
<i>C. godetiae</i>	KACC 42911	Hongcheon	2007 Jun	<i>Symplocarpus renifolius</i>	<i>Colletotrichum</i> sp.		RDA0061930	RDA0062200	RDA0062406	RDA0065787	RDA0065713	RDA0065653
<i>C. lupini</i>	KACC 47254	Seoul	2009 May	<i>Lupinus luteus</i>	<i>C. gloeosporioides</i>	<i>C. lupini</i> (Han et al., 2014)	RDA0061950	RDA0062249	RDA0065816	RDA0065782	RDA0065718	RDA0065649
	KACC 47255	Yongin	2013 Apr	<i>Lupinus luteus</i>	<i>C. gloeosporioides</i>		RDA0061951	RDA0062250	RDA0062454	RDA0065760	RDA0065740	RDA0065632
<i>C. nymphphaeae</i>	KACC 46962	Mungyeong	2012 Sep	-	<i>C. acutatum</i>		RDA0061946	RDA0062237	RDA0062442	RDA0065771	RDA0065729	RDA0065642
	KACC 47824	Cheongdo	2014 Aug	<i>Prunus persica</i>	<i>C. acutatum</i>		RDA0061956	RDA0062270	RDA0062464	RDA0065784	RDA0065716	RDA0065650
	KACC 48897	Tongyeong	-	<i>Abies holophylla</i>	<i>C. nymphphaeae</i>		RDA0061966	RDA0062310	RDA0062505	RDA0065806	RDA0065693	RDA0065671
	KACC 43123	Chungbuk	2002 Jan	<i>Capsicum annuum</i>	<i>C. acutatum</i>		RDA0061933	RDA0062208	RDA0062413	RDA0065778	RDA0065722	RDA0065647
	KACC 43124	Boeun	2004 Jan	<i>Capsicum annuum</i>	<i>C. acutatum</i>		RDA0061934	RDA0062209	RDA0062414	RDA0065758	RDA0065742	RDA0065629
	KACC 43125	Cheongju	2004 Jan	<i>Capsicum annuum</i>	<i>C. acutatum</i>		RDA0061935	RDA0062210	RDA0062415	RDA0065761	RDA0065739	RDA0065633
	KACC 45234	Changwon	2008 Oct	<i>Diospyros kaki</i>	<i>C. acutatum</i>		RDA0061943	RDA0062226	RDA0062433	RDA0065765	RDA0065735	RDA0065636
	KACC 47695	Gangneung	2013 Jun	<i>Lycopersicon esculentum</i>	<i>C. gloeosporioides</i>		RDA0061954	RDA0062267	RDA0062461	RDA0065773	RDA0065727	RDA0065644
	KACC 42403	Andong	2006 Sep	<i>Malus domestica</i>	<i>C. acutatum</i>	<i>C. nymphphaeae</i> (Kim et al., 2020)	RDA0061911	RDA0062178	RDA0062383	RDA0065792	RDA0065707	RDA0065658
	KACC 42496	Gunwi	2006 Sep	<i>Malus domestica</i>	<i>C. acutatum</i>		RDA0061909	RDA0062185	RDA0062390	RDA0065810	RDA0065689	RDA0065675
	KACC 42505	Gunwi	2004 Aug	<i>Malus domestica</i>	<i>C. acutatum</i>		RDA0061927	RDA0062194	RDA0062399	RDA0065786	RDA0065714	RDA0065652
	KACC 40847	Andong	1999 Oct	<i>Malus pumila</i> var. <i>dulcissima</i>	<i>C. gloeosporioides</i>	<i>C. acutatum</i> (Kim et al., 2006)	RDA0061916	RDA0062147	RDA0062365	RDA0065756	RDA0065744	RDA0065627
	KACC 40848	Yeongju	1999 Oct	<i>Malus pumila</i> var. <i>dulcissima</i>	<i>C. gloeosporioides</i>	<i>C. acutatum</i> (Kim et al., 2006)	RDA0061915	RDA0062148	RDA0062366	RDA0065753	RDA0065747	RDA0065624
	KACC 49896	Jeonju	2021 Oct	<i>Prunus persica</i>	<i>C. nymphphaeae</i>	<i>C. nymphphaeae</i> (Kim et al., 2020)	RDA0061968	RDA0062320	RDA0062516	RDA0065762	RDA0065738	RDA0065634
	KACC 49926	Sejong	-	<i>Prunus persica</i>	<i>C. acutatum</i>		RDA0061974	RDA0062328	RDA0062524	RDA0065802	RDA0065697	RDA0065668

(Continued)

Table 2. Continued

Re-identified species	Isolate no.	Location	Collected date	Host	Species name by depositor	Previous identification	RDA-GeneBank accession no.					
							ITS	TUB2	GAPDH	HIS3	CHS-1	ACT
<i>C. nymphaeae</i>	KACC 42089	Hapcheon	2004 Aug	<i>Punica granatum</i>	<i>C. gloeosporioides</i>	<i>C. acutatum</i> (Kim et al., 2006)	RDA0061912	RDA0062172	RDA0062376	RDA0065751	RDA0065750	RDA0065623
	KACC 40898	Naju	2000 Oct	<i>Pyrus serotina</i>	<i>C. acutatum</i>		RDA0061914	RDA0062167	RDA0062371	RDA0065809	RDA0065690	RDA0065674
	KACC 43130	Cheongju	2006 Jun	<i>Vitis</i> sp.	<i>C. acutatum</i>		RDA0061940	RDA0062215	RDA0062420	RDA0065807	RDA0065692	RDA0065672
<i>C. nymphaeae</i>	KACC 46931	Yeongdong	2011 Nov	<i>Vitis labrusca</i>	<i>C. acutatum</i>	<i>C. acutatum</i> (Noh et al., 2014)	RDA0061945	RDA0062235	RDA0065817	RDA0065793	RDA0065706	RDA0065659
	KACC 43023	Hongcheon	2007 Jul	<i>Humulus japonicus</i>	<i>Colletotrichum</i> sp.		RDA0061979	RDA0062203	RDA0062409	RDA0065764	RDA0065736	RDA0065622
	KACC 49927	Sejong	-	<i>Prunus persica</i>	<i>C. acutatum</i>		RDA0061975	-	RDA0065815	-	RDA0065749	-
<i>C. scovillei</i>	KACC 40004	Daejeon	-	<i>Capsicum annuum</i>	<i>C. gloeosporioides</i>	<i>C. acutatum</i> (Kim et al., 2006)	RDA0060929	RDA0062124	RDA0062331	RDA0065800	RDA0065699	RDA0065686
	KACC 40007	Daejeon	-	<i>Capsicum annuum</i>	<i>C. gloeosporioides</i>	<i>C. acutatum</i> (Kim et al., 2006)	RDA0060924	RDA0062126	RDA0062334	RDA0065755	RDA0065745	RDA0065626
	KACC 40008	Daejeon	-	<i>Capsicum annuum</i>	<i>C. coccodes</i>		RDA0060925	RDA0062127	RDA0062335	RDA0065791	RDA0065708	RDA0065657
	KACC 40691	Hoengseong	1998 Aug	<i>Capsicum annuum</i>	<i>C. gloeosporioides</i>	<i>C. acutatum</i> (Kim et al., 2006)	RDA0060937	RDA0062140	RDA0062348	RDA0065757	RDA0065743	RDA0065628
	KACC 42509	Gunwi	2005 Jul	<i>Capsicum annuum</i>	<i>C. acutatum</i>		RDA0061929	RDA0062198	RDA0062403	RDA0065767	RDA0065733	RDA0065682
	KACC 43127	Jeonbuk	2002 Jan	<i>Capsicum annuum</i>	<i>C. acutatum</i>		RDA0061937	RDA0062212	RDA0062417	RDA0065779	RDA0065721	RDA0065680
	KACC 44886	Daejeon	2008 May	<i>Capsicum annuum</i>	<i>C. acutatum</i>		RDA0061941	RDA0062224	RDA0062431	RDA0065754	RDA0065746	RDA0065679
	KACC 45723	Hwaseong	2008 Feb	<i>Capsicum annuum</i>	<i>C. acutatum</i>		RDA0061944	RDA0062229	RDA0062436	RDA0065769	RDA0065731	RDA0065640
	KACC 47693	Pyeongchang	2012 Sep	<i>Capsicum annuum</i>	<i>C. acutatum</i>		RDA0061952	RDA0062265	RDA0062459	RDA0065783	RDA0065717	RDA0065678
	KACC 48686	Gimje	2018 Sep	<i>Capsicum annuum</i>	<i>C. scovillei</i>		RDA0061962	RDA0062297	RDA0062492	RDA0065803	RDA0065696	RDA0065669
	KACC 40805	Yangpyeong	1996 Sep	<i>Lycopersicon esculentum</i>	<i>C. gloeosporioides</i>	<i>C. acutatum</i> (Kim et al., 2006)	RDA0061917	RDA0062146	RDA0065818	RDA0065774	RDA0065726	RDA0065683
	KACC 42537	Chuncheon	2006 Sep	<i>Capsicum annuum</i>	<i>Colletotrichum</i> sp.		RDA0061978	RDA0062199	RDA0062404	RDA0065789	RDA0065711	RDA0065681
<i>Colletotrichum</i> sp.	KACC 40014	Daejeon	-	<i>Capsicum annuum</i>	<i>Colletotrichum</i> sp.		RDA0061976	RDA0062132	RDA0062340	RDA0065801	RDA0065698	RDA0065666

ITS, internal transcribed spacer; TUB2, β -tubulin 2; GAPDH, glyceraldehyde-3-phosphate dehydrogenase; HIS3, histone3; CHS-1, chitin synthase; ACT, actin; RDA, Rural Development Administration; KACC, Korean Agricultural Culture Collection.

Table 3. Comparison of host plants between KACC isolates and previous reports

Species	Host				
	KACC	The List of Plant Diseases	Previous reports in Korea	Global reports	References
<i>C. chrysanthemi</i>	<i>Carthamus tinctorius</i>	-	-	<i>Carthamus tinctorius</i>	Baroncelli et al. (2015)
	<i>Coriandrum sativum</i> *	-	-	-	-
	-	<i>Chrysanthemum coronarium</i>	<i>Chrysanthemum coronarium</i>	<i>Chrysanthemum coronarium</i>	Sato and Moriwaki (2013)
<i>C. fioriniae</i>	<i>Actinidia chinensis</i>	-	-	<i>Actinidia chinensis</i>	Shivas and Tan (2009)
	<i>Capsicum annuum</i>	-	-	<i>Capsicum annuum</i>	Noor and Zakaria (2018)
	<i>Camellia sinensis</i>	-	-	<i>Camellia sinensis</i>	Wang et al. (2016)
	<i>Cayratia japonica</i> *	-	-	-	-
	<i>Chaenomeles sinensis</i> *	-	-	-	-
	<i>Cucurbita</i> sp.	<i>Cucurbita moschata</i>	<i>Cucurbita moschata</i>	<i>Cucurbita moschata</i>	Kim and Kim (2020)
	<i>Lycium chinense</i>	<i>Lycium chinense</i>	<i>Lycium chinense</i>	<i>Lycium chinense</i>	Oo et al. (2016)
	<i>Machilus thunbergii</i>	-	-	<i>Machilus thunbergii</i>	Sato et al. (2013)
	<i>Malus domestica</i>	-	<i>Malus domestica</i>	<i>Malus domestica</i>	Oo et al. (2018)
	<i>Paeonia lactiflora</i>	<i>Paeonia lactiflora</i>	<i>Paeonia lactiflora</i>	<i>Paeonia lactiflora</i>	Park et al. (2020)
	<i>Pinus koraiensis</i> *	-	-	-	-
	<i>Schizonepeta tenuifolia</i> var. <i>japonica</i> *	-	-	-	-
	<i>Solanum melongena</i>	<i>Solanum melongena</i>	<i>Solanum melongena</i>	<i>Solanum melongena</i>	Xu et al. (2018)
	<i>Spiraea prunifolia</i> var. <i>simpliciflora</i> *	-	-	-	-
	<i>Xylosma congesta</i> *	-	-	-	-
	-	<i>Ilex integra</i>	<i>Ilex integra</i>	<i>Ilex integra</i>	Woo et al. (2021)
	-	<i>Prunus persica</i>	<i>Prunus persica</i>	<i>Prunus persica</i>	Lee et al. (2020)
-	-	<i>Prunus salicina</i>	<i>Prunus salicina</i>	Hassan et al. (2019b)	
-	-	<i>Schisandra chinensis</i>	<i>Schisandra chinensis</i>	Kim et al. (2022)	
-	-	<i>Vaccinium</i> sect. <i>Cyanococcus</i>	<i>Vaccinium</i> sect. <i>Cyanococcus</i>	Cho et al. (2021)	
<i>C. godetiae</i>	<i>Symplocarpus renifolius</i> *	-	-	-	-
	-	-	-	(Continued)	-
<i>C. lupini</i>	<i>Lupinus luteus</i>	<i>Lupinus luteus</i>	<i>Lupinus luteus</i>	-	Han et al. (2014)
	-	-	-	(Continued)	-
<i>C. nymphaeae</i>	<i>Abies holophylla</i> *	-	-	-	-
	<i>Capsicum annuum</i>	-	-	<i>Capsicum annuum</i>	Nasehi et al. (2016)
	<i>Diospyros kaki</i>	<i>Diospyros kaki</i>	<i>Diospyros kaki</i>	<i>Diospyros kaki</i>	Hassan et al. (2019a)
	<i>Humulus japonicus</i> *	-	-	-	-
	<i>Lycopersicon esculentum</i> (syn. <i>Solanum lycopersicum</i>)	-	-	<i>Solanum lycopersicum</i>	Santos et al. (2018)
	<i>Malus domestica</i> (syn. <i>Malus pumila</i>)	-	<i>Malus domestica</i>	<i>Malus domestica</i>	Oo et al. (2018)

(Continued)

Table 3. Continued

Species	Host				
	KACC	The List of Plant Diseases	Previous reports in Korea	Global reports	References
<i>C. nymphaeae</i>	<i>Prunus persica</i>	-	-	<i>Prunus persica</i>	Tan et al. (2022)
	<i>Punica granatum</i>	-	-	<i>Punica granatum</i>	Xavier et al. (2019)
	<i>Pyrus serotina</i> (syn. <i>P. pyrifolia</i>)	-	-	<i>Pyrus pyrifolia</i>	Moreira et al. (2019)
	<i>Vitis labrusca</i>	-	-	<i>Vitis labrusca</i>	Chechi et al. (2019)
	-	<i>Actinidia argute</i>	<i>Actinidia argute</i>	<i>Actinidia argute</i>	Kim et al. (2018)
	-	<i>Prunus salicina</i>	<i>Prunus salicina</i>	<i>Prunus salicina</i>	Chang et al. (2018)
	-	-	<i>Vaccinium</i> sect. <i>Cyanococcus</i>	<i>Vaccinium</i> sect. <i>Cyanococcus</i>	Cho et al. (2021)
<i>C. scovillei</i>	<i>Capsicum annuum</i>	<i>Capsicum annuum</i>	<i>Capsicum annuum</i>	<i>Capsicum annuum</i>	Oo et al. (2017)
	<i>Lycopersicon esculentum</i>*	-	-	-	-
<i>Colletotrichum</i> sp. (novel species candidate)	<i>Capsicum annuum</i>*	-	-	-	-
				(Continued)	

Hosts in “bold” and followed by “*” are unreported in Korea and in the world, respectively.

Lycopersicon esculentum, *Prunus persica*, *Punica granatum*, *Pyrus serotina*, and *Vitis labrusca*) have not been reported in Korea, of which two species (*A. holophylla* and *H. japonicus*) have not been recorded in the world. Two other species (*Diospyros kaki* and *Malus domestica*) were previously reported in Korea. *C. scovillei* (12 KACC isolates) were obtained from only the family Solanaceae, including 11 isolates from *Capsicum annuum* (reported in Korea) and one isolate from *Lycopersicon esculentum* (unreported in the world). *C. chrysanthemi* (three KACC isolates) was isolated from *Coriandrum sativum* (unreported in the world) and *Carthamus tinctorius* (unreported in Korea). *C. lupini* (two KACC isolates) was found on *Lupinus luteus* (reported in Korea). *C. godetiae* (one KACC isolate) was from *Symplocarpus renifolius* (unreported in the world). A novel species candidate (KACC 40014) was collected from *Capsicum annuum* (Tables 2 and 3).

Discussion

Sixty-four Korean isolates in *C. acutatum* species complex were accurately identified into six different species (*C. fiorinae*, *C. nymphaeae*, *C. scovillei*, *C. chrysanthemi*, *C. lupini*, and *C. godetiae*) and a novel species candidate,

based on the combination of multi-locus sequences of ITS, TUB2, HIS3, GAPDH, CHS-1, and ACT. Forty-eight isolates changed their species names from the original names given by depositors. The present results also demonstrated that the identifications of the species in the *C. acutatum* species complex using a single ITS region and/or TUB2 gene in the previous publications (Han et al., 2014; Kim et al., 2006, 2008; Noh et al., 2014) were insufficient.

C. fiorinae has been reported as an entomopathogenic, endophytic and phytopathogenic fungus (Damm et al., 2012; Marcelino et al., 2008). This species has been reported as the causal agent of anthracnose diseases on *Cucurbita moschata*, *Lycium chinense*, *Malus domestica*, *Paeonia lactiflora*, *Solana melongena*, *Ilex integra*, *Prunus persica*, *Prunus salicina*, *Schisandra chinensis*, and *Vaccinium* sect. *Cyanococcus* in Korea. Six of them (*M. domestica*, *P. salicina*, *S. chinensis*, and *V. sect. Cyanococcus*) were not listed in The List of Plant Diseases in Korea (<http://genebank.rda.go.kr/english/plntDissInfo.do>), and five species (*I. integra*, *P. persica*, *P. salicina*, *S. chinensis*, and *V. sect. Cyanococcus*) were not found in this work. Meanwhile, ten host species of *C. fiorinae* in this study have not been recorded in Korea or in the world. *C. nymphaeae* was associated with serious anthracnose diseases in a wide range

of host plants, especially strawberries (*Fragaria* × *ananassa*) (Damm et al., 2012; Jayawardena et al., 2016). In the previous research, six host species of *C. nymphaeae* (*Diospyros kaki*, *Malus domestica*, *Actinidia argute*, *Prunus salicina*, *Vaccinium* sect. *Cyanococcus*, and *Ziziphus jujube*) were reported in Korea, three of that plant (*M. domestica*, *V. sect. Cyanococcus*, and *Z. jujube*) have not been updated in The List of Plant Diseases in Korea, and four species (*A. argute*, *P. salicina*, *V. sect. Cyanococcus*, and *Z. jujube*) were not recorded in this study. However, eight host species in the present study were not introduced in relationship with this fungal species before in Korea or in the world. *C. scovillei* has a narrow host range and was commonly reported as one of the highly aggressive diseases of *Capsicum* spp. in many countries such as Brazil (Giacomin et al., 2021), Korea (Oo et al., 2017) and Asia (de Silva et al., 2019). *C. scovillei* also infected *Clausena lansium* (Lin et al., 2020), *Mangifera indica* (Qin et al., 2019), *Musa* sp. (Zhou et al., 2017), and *Pseudodracontium lacourii* (Liu et al., 2022). In our findings, *C. scovillei* was isolated from *Lycopersicon esculentum* and this has not been reported in the world.

C. chrysanthemi was only reported in the family Asteraceae, including *Carthamus tinctorius* in Italy (Baroncelli et al., 2015), *Glebionis carinata* (vascular discoloration) in the Netherlands, *Glebionis coronaria* (leaf spot) in China (Damm et al., 2012), *Chrysanthemum coronarium* in Korea and *Calendula officinalis* in Japan (Sato and Moriwaki, 2013). In this study, *C. chrysanthemi* was not only collected from the Asteraceae (*Carthamus tinctorius*) but also obtained from an unrecorded family Apiaceae (*Coriandrum sativum*).

C. lupini was first reported to cause anthracnose on yellow lupin (*Lupinus luteus*) in Korea and Asia in 2013 (Han et al., 2014). This species has a narrow range of host plants, but it showed high virulence and globally widespread disease on some host species of the genus *Lupinus* (Alkemade et al., 2021). This fungal species was also found on *Camellia* sp., *Cinnamomum verum*, *Manihot utilissima*, and *Olea europaea* (Alkemade et al., 2021; Damm et al., 2012). *C. godetiae* was infected economically important crops and had a wide host range and global distribution (Alizadeh et al., 2015; Liu et al., 2022; Shivas et al., 2016; Tan et al., 2022; Tóth et al., 2017). However, this species was not commonly associated with valuable crops in Korea. In our study, this fungal species could be a new finding on Asian skunk cabbage (*Symplocarpus renifolius*).

On the other hand, considering species under *C. acutatum* species complex according to economic host plants in

this study, *C. scovillei* ($n = 11$) was dominant on *Capsicum annuum* (pepper) and *C. nymphaeae* ($n = 3$), *C. fioriniae* ($n = 1$) followed. Five *C. nymphaeae* and four *C. fioriniae* isolates were identified from *Malus* spp. including apple. Only four and two isolates of *C. nymphaeae* were isolated from peach (*Prunus persica*) and grape (*Vitis labrusca*), respectively.

The most important finding in this study is that 23 new combinations could be suggested in Korea and 12 of these have not been reported in the world. Of which, *C. fioriniae* on pepper (*Capsicum annuum*) and kiwi (*Actinidia chinensis*), *C. nymphaeae* on peach (*Prunus persica*), pear (*Pyrus serotina*) and grape (*Vitis labrusca*), and *C. scovillei* on tomato (*Lycopersicon esculentum*), are meaningful information in the agricultural field of Korea. However, the pathogenicity of KACC isolates on hosts is not clear. KACC did not confirm the pathogenicity of deposited *Colletotrichum* isolates on host plants, but depended on only the depositor's information. Therefore, new combinations suggested in this study need to be clarified via the pathogenicity tests in further studies.

Conflicts of Interest

No potential conflict of interest relevant to this article was reported.

Acknowledgments

This study was supported by a grant (PJ017286) from the National Institute of Agricultural Sciences and was a part of the “2023 KoRAA Long-term Training Program”, Rural Development Administration, Republic of Korea.

Electronic Supplementary Material

Supplementary materials are available at The Plant Pathology Journal website (<http://www.ppjonline.org/>).

References

- Alizadeh, A., Javan-Nikkhah, M., Zare, R., Fotouhifar, K. B., Damm, U. and Stukenbrock, E. H. 2015. New records of *Colletotrichum* species for the mycobiota of Iran. *Mycol. Iran.* 2:95-109.
- Alkemade, J. A., Messmer, M. M., Voegelé, R. T., Finckh, M. R. and Hohmann, P. 2021. Genetic diversity of *Colletotrichum lupini* and its virulence on white and Andean lupin. *Sci. Rep.* 11:13547.
- Baroncelli, R., Sarrocco, S., Zapparata, A., Tavarini, S., Angelini, L. G. and Vannacci, G. 2015. Characterization and epidemiol-

- ogy of *Colletotrichum acutatum sensu lato* (*C. chrysanthemi*) causing *Carthamus tinctorius* anthracnose. *Plant Pathol.* 64:375-384.
- Cai, L., Giraud, T., Zhang, N., Begerow, D., Cai, G. and Shivas, R. G. 2011. The evolution of species concepts and species recognition criteria in plant pathogenic fungi. *Fungal Divers.* 50:121-133.
- Cannon, P. F., Damm, U., Johnston, P. R. and Weir, B. S. 2012. *Colletotrichum* - current status and future directions. *Stud. Mycol.* 73:181-213.
- Carbone, I. and Kohn, L. M. 1999. A method for designing primer sets for speciation studies in filamentous ascomycetes. *Mycologia* 91:553-556.
- Chang, T. H., Hassan, O. and Lee, Y. S. 2018. First report of anthracnose of Japanese plum (*Prunus salicina*) caused by *Colletotrichum nymphaeae* in Korea. *Plant Dis.* 102:1461.
- Chechi, A., Stahlecker, J., Zhang, M., Luo, C. X. and Schnabel, G. 2019. First report of *Colletotrichum fioriniae* and *C. nymphaeae* causing anthracnose on cherry tomatoes in South Carolina. *Plant Dis.* 103:1042.
- Cho, B.-J., Choi, H.-W., Kim, D. and Lee, J. 2021. *Colletotrichum* spp. agents of anthracnose on blueberry leaves in Gangwon province, Korea. *J. For. Environ. Sci.* 37:154-162.
- Crouch, J. A. and Beirn, L. A. 2009. Anthracnose of cereals and grasses. *Fungal Divers.* 39:19-44.
- Crous, P. W., Groenewald, J. Z., Risede, J.-M. and Simoneau, P. and Hywel-Jones, N. L. 2004. *Calonectria* species and their *Cylindrocladium anamorphs*: species with sphaeropedunculate vesicles. *Stud. Mycol.* 50:415-430.
- Damm, U., Cannon, P. F., Woudenberg, J. H. C. and Crous, P. W. 2012. The *Colletotrichum acutatum* species complex. *Stud. Mycol.* 73:37-113.
- Damm, U., O'Connell, R. J., Groenewald, J. Z. and Crous, P. W. 2014. The *Colletotrichum destructivum* species complex - hemibiotrophic pathogens of forage and field crops. *Stud. Mycol.* 79:49-84.
- Damm, U., Sato, T., Alizadeh, A., Groenewald, J. Z. and Crous, P. W. 2019. The *Colletotrichum dracaenophilum*, *C. magnum* and *C. orchidearum* species complexes. *Stud. Mycol.* 92:1-46.
- Damm, U., Woudenberg, J. H. C., Cannon, P. F. and Crous, P. W. 2009. *Colletotrichum* species with curved conidia from herbaceous hosts. *Fungal Divers.* 39:45-87.
- de Silva, D. D., Groenewald, J. Z., Crous, P. W., Ades, P. K., Nasraddin, A., Mongkolporn, O. and Taylor, P. W. J. 2019. Identification, prevalence and pathogenicity of *Colletotrichum* species causing anthracnose of *Capsicum annuum* in Asia. *IMA Fungus* 10:8.
- Garrido, C., Carbú, M., Fernández-Acero, F. J., Vallejo, I. and Cantoral, J. M. 2009. Phylogenetic relationships and genome organisation of *Colletotrichum acutatum* causing anthracnose in strawberry. *Eur. J. Plant Pathol.* 125:397-411.
- Giacomin, R. M., de Fátima Ruas, C., Baba, V. Y., De Godoy, S. M., Sudré, C. P., dos Santos Bento, C., Da Cunha, M., Da Costa Geronimo, I. G., Rodrigues, R. and Gonçalves, L. S. 2021. Phenotypic, molecular and pathogenic characterization of *Colletotrichum scovillei* infecting *Capsicum* species in Rio de Janeiro, Brazil. *PeerJ* 9:e10782.
- Glass, N. L. and Donaldson, G. C. 1995. Development of primer sets designed for use with the PCR to amplify conserved genes from filamentous ascomycetes. *Appl. Environ. Microbiol.* 61:1323-1330.
- González, E., Sutton, T. B. and Correll, J. C. 2006. Clarification of the etiology of Glomerella leaf spot and bitter rot of apple caused by *Colletotrichum* spp. based on morphology and genetic, molecular and pathogenicity tests. *Phytopathology* 96:982-992.
- Guerber, J. C., Liu, B., Correll, J. C. and Johnston, P. R. 2003. Characterization of diversity in *Colletotrichum acutatum sensu lato* by sequence analysis of two gene introns, mtDNA and intron RFLPs, and mating compatibility. *Mycologia* 95:872-895.
- Han, K. S., Kim, B. S., Choi, I. Y., Park, J. H. and Shin H. D. 2014. First report of anthracnose caused by *Colletotrichum lupini* on yellow lupin in Korea. *Plant Dis.* 98:1158.
- Hassan, O., Lee, D. W. and Chang, T. 2019a. First report of anthracnose of persimmon caused by *Colletotrichum nymphaeae* in Korea. *Plant Dis.* 103:1772.
- Hassan, O., Lee, Y. S. and Chang, T. 2019b. *Colletotrichum* species associated with Japanese plum (*Prunus salicina*) anthracnose in South Korea. *Sci. Rep.* 9:12089.
- Hyde, K. D., Cai, L., Cannon, P. F., Crouch, J. A., Crous, P. W., Damm, U., Goodwin, P. H., Chen, H., Johnston, P. R., Jones, E. B. G., Liu, Z. Y., McKenzie, E. H. C., Moriwaki, J., Noireung, P., Pennycook, S. R., Pfenning, L. H., Prihastuti, H., Sato, T., Shivas, R. G., Tan, Y. P., Taylor, P. W. J., Weir, B. S., Yang, Y. L. and Zhang, J. Z. 2009. *Colletotrichum* - names in current use. *Fungal Divers.* 39:147-182.
- Jayawardena, R. S., Bhunjun, C. S., Hyde, K. D., Gentekaki, E. and Itthayakorn, P. 2021. *Colletotrichum*: lifestyles, biology, morpho-species, species complexes and accepted species. *Mycosphere* 12:519-669.
- Jayawardena, R. S., Hyde, K. D., Damm, U., Cai, L., Liu, M., Li, X. H., Zhang, W., Zhao, W. S. and Yan, J. Y. 2016. Notes on currently accepted species of *Colletotrichum*. *Mycosphere* 7:1192-1260.
- Kang, E. C., Hassan, O., Kim, K.-M. and Chang, T. 2023. Molecular characterization and fungicide sensitivity of jujube pathogens *Colletotrichum gloeosporioides sensu stricto* and *Colletotrichum nymphaeae* in South Korea. *Plant Dis.* 107:861-869.
- Kim, C. H., Hassan, O. and Chang, T. 2020. Diversity, pathogenicity, and fungicide sensitivity of *Colletotrichum* species associated with apple anthracnose in South Korea. *Plant Dis.* 104:2866-2874.
- Kim, D.-H., Jeon, Y.-A., Go, S.-J., Lee, J.-K. and Hong, S.-B. 2006. Reidentification of *Colletotrichum gloeosporioides* and *C. acutatum* isolates stored in Korean Agricultural Culture

- Collection (KACC). *Res. Plant Dis.* 12:168-177 (in Korean).
- Kim, G. H., Choi, D. H., Park, S. Y. and Koh, Y. J. 2018. First report of anthracnose caused by *Colletotrichum nymphaeae* on kiwiberry in Korea. *Plant Dis.* 102:1455.
- Kim, J., Hassan, O., Kim, K.-M. and Chang, T. 2022. First report of *Colletotrichum fioriniae* causing anthracnose on the fruit of omija (schisandra) in South Korea. *Plant Dis.* 106:2991.
- Kim, J. T., Park, S.-Y., Choi, W., Lee, Y.-H. and Kim, H. T. 2008. Characterization of *Colletotrichum* isolates causing anthracnose of pepper in Korea. *Plant Pathol. J.* 24:17-23.
- Kim, J.-Y. and Kim, B.-S. 2020. First report of *Colletotrichum fioriniae* causing anthracnose on fruit of pumpkin (*Cucurbita moschata*) in Korea. *Res. Plant Dis.* 26:190-193 (in Korean)
- Kwon, J.-H. and Kim, J. 2011. First report of fruit black spot of *Diospyros kaki* caused by *Colletotrichum acutatum* in Korea. *Plant Pathol. J.* 27:100.
- Lee, D. H., Kim, D.-H., Jeon, Y.-A., Uhm, J. Y. and Hong, S.-B. 2007. Molecular and cultural characterization of *Colletotrichum* spp. causing bitter rot of apples in Korea. *Plant Pathol. J.* 23:37-44.
- Lee, D. M., Hassan, O. and Chang, T. 2020. Identification, characterization, and pathogenicity of *Colletotrichum* species causing anthracnose of peach in Korea. *Mycobiology* 48:210-218.
- Lenné, J. M. 2002. Some major plant diseases. In: *Plant pathologist's pocketbook*, eds. by J. M. Waller, J. M. Lenné and S. J. Waller, 3rd ed., pp. 4-18. CAB International, Wallingford, UK.
- Lin, C.-H., Long, X.-P., Li, Z.-P., Zhang, Y., He, J.-J., Liu, W.-B. and Miao, W.-G. 2020. First report of anthracnose of *Clauena lansium* caused by *Colletotrichum scovillei* in China. *Plant Dis.* 104:1557.
- Liu, F., Ma, Z. Y., Hou, L. W., Diao, Y. Z., Wu, W. P., Damm, U., Song, S. and Cai, L. 2022. Updating species diversity of *Colletotrichum*, with a phylogenomic overview. *Stud. Mycol.* 101:1-56.
- Marcelino, J., Giordano, R., Gouli, S., Gouli, V., Parker, B. L., Skinner, M., TeBeest, D. and Cesnik, R. 2008. *Colletotrichum acutatum* var. *fioriniae* (teleomorph: *Glomerella acutata* var. *fioriniae* var. nov.) infection of a scale insect. *Mycologia* 100:353-374.
- Moreira, R. R., Peres, N. A. and May De Mio, L. L. 2019. *Colletotrichum acutatum* and *C. gloeosporioides* species complexes associated with apple in Brazil. *Plant Dis.* 103:268-275.
- Nasehi, A., Kadir, J., Rashid, T. S., Awla, H. K., Golkhandan, E. and Mahmodi, F. 2016. Occurrence of anthracnose fruit rot caused by *Colletotrichum nymphaeae* on pepper (*Capsicum annuum*) in Malaysia. *Plant Dis.* 100:1244.
- Nguyen, P. T. H., Vinnere Pettersson, O., Olsson, P. and Liljeroth, E. 2010. Identification of *Colletotrichum* species associated with anthracnose disease of coffee in Vietnam. *Eur. J. Plant Pathol.* 127:73-87.
- Noh, Y.-H., Kim, Y.-E., Song, M.-J., An, J.-H., Jeong, M.-J., Hong, S.-B., Kim, S.-H., Lee, H.-I. and Cha, J.-S. 2014. Post-harvest decay of 'Campbell early' grape. *Res. Plant Dis.* 20:275-282 (in Korean).
- Noor, N. M. and Zakaria, L. 2018. Identification and characterization of *Colletotrichum* spp. associated with chili anthracnose in peninsular Malaysia. *Eur. J. Plant Pathol.* 151:961-973.
- O'Donnell, K. and Cigelnik, E. 1997. Two divergent intragenomic rDNA ITS2 types within a monophyletic lineage of the fungus *Fusarium* are nonorthologous. *Mol. Phylogenet. Evol.* 7:103-116.
- Oh, I.-S. 1995. Taxonomy and pathogenicity of *Colletotrichum* spp. from red pepper (*Capsicum annuum*). Ph.D. thesis. Chungnam National University, Daejeon, Korea.
- Oo, M. M., Lim, G., Jang, H. A. and Oh, S.-K. 2017. Characterization and pathogenicity of new record of anthracnose on various chili varieties caused by *Colletotrichum scovillei* in Korea. *Mycobiology* 45:184-191.
- Oo, M. M., Tweneboah, S. and Oh, S.-K. 2016. First report of anthracnose caused by *Colletotrichum fioriniae* on Chinese matrimony vine in Korea. *Mycobiology* 44:325-329.
- Oo, M. M., Yoon, H.-Y., Jang, H. A. and Oh, S.-K. 2018. Identification and characterization of *Colletotrichum* species associated with bitter rot disease of apple in South Korea. *Plant Pathol. J.* 34:480-489.
- Park, M.-J., Lee, J.-H., Back, C.-G. and Park, J.-H. 2020. First report of *Colletotrichum fioriniae* causing anthracnose on *Paeonia lactiflora* in Korea. *Plant Dis.* 104:3259.
- Peres, N. A., Mackenzie, S. J., Peever, T. L. and Timmer, L. W. 2008. Postbloom fruit drop of citrus and key lime anthracnose are caused by distinct phylogenetic lineages of *Colletotrichum acutatum*. *Phytopathology* 98:345-352.
- Qin, L. P., Zhang, Y., Su, Q., Chen, Y. L., Nong, Q., Xie, L., Yu, G. M. and Huang, S. L. 2019. First report of anthracnose of *Mangifera indica* caused by *Colletotrichum scovillei* in China. *Plant Dis.* 103:1043.
- Sanders, G. M. and Korsten, L. 2003. Comparison of cross inoculation potential of South African avocado and mango isolates of *Colletotrichum gloeosporioides*. *Microbiol. Res.* 158:143-150.
- Santos, R. F., Ciampi-Guillard, M., Amorim, L., Massola Júnior, N. S. and Spósito, M. B. 2018. Aetiology of anthracnose on grapevine shoots in Brazil. *Plant Pathol.* 67:692-706.
- Sato, T. and Moriwaki, J. 2013. Molecular re-identification of strains in NIAS Genebank belonging to phylogenetic groups A2 and A4 of the *Colletotrichum acutatum* species complex. *Microbiol. Cult. Coll.* 29:13-23.
- Sato, T., Moriwaki, J. and Misawa, T. 2013. Molecular re-identification of strains of the *Colletotrichum acutatum* species complex deposited in the NIAS Genebank and morphological characteristics of its member species. *Jpn. Agric. Res. Q.* 47:295-305.
- Shivas, R. G. and Tan, Y. P. 2009. A taxonomic re-assessment of *Colletotrichum acutatum*, introducing *C. fioriniae* comb. et stat. nov. and *C. simmondsii* sp. nov. *Fungal Divers.* 39:111-122.

- Shivas, R. G., Tan, Y. P., Edwards, J., Dinh, Q., Maxwell, A., Andjic, V., Liberato, J. R., Anderson, C., Beasley, D. R., Bransgrove, K., Coates, L. M., Cowan, K., Daniel, R., Dean, J. R., Lomavatu, M. F., Mercado-Escueta, D., Mitchell, R. W., Thangavel, R., Tran-Nguyen, L. T. T. and Weir, B. S. 2016. *Colletotrichum* species in Australia. *Australas. Plant Pathol.* 45:447-464.
- Sutton, B. C. 1980. The Coelomycetes. Fungi imperfecti with pycnidia, acervuli and stromata. Commonwealth Mycological Institute, Kew, UK. 696 pp.
- Sutton, B. C. 1992. The genus *Glomerella* and its anamorph *Colletotrichum*. In: *Colletotrichum: biology, pathology and control*, eds. by J. A. Bailey and M. J. Jeger, pp. 1-26. CAB International, Wallingford, UK.
- Talhinhas, P., Mota-Capitão, C., Martins, S., Ramos, A. P., Neves-Martins, J., Guerra Guimarães, L., Várzea, V., Silva, M. C., Sreenivasaprasad, S. and Oliveira, H. 2011. Epidemiology, histopathology and aetiology of olive anthracnose caused by *Colletotrichum acutatum* and *C. gloeosporioides* in Portugal. *Plant Pathol.* 60:483-495.
- Tamura, K., Stecher, G. and Kumar, S. 2021. MEGA11: molecular evolutionary genetics analysis version 11. *Mol. Biol. Evol.* 38:3022-3027.
- Tan, Q., Schnabel, G., Chaisiri, C., Yin, L. F., Yin, W. X. and Luo, C. X. 2022. *Colletotrichum* species associated with peaches in China. *J. Fungi (Basel)* 8:313.
- Tóth, A., Petróczy, M. and Palkovics, L. 2017. First report of *Colletotrichum acutatum sensu lato* through the occurrence of *C. godetiae* on cornelian cherry (*Cornus mas*) in Europe. *Plant Dis.* 101:841.
- von Arx, J. A. 1957. Die arten der gattung *Colletotrichum* cda. *Phytopathol. J.* 29:413-468 (in German).
- Wang, Y.-C., Hao, X.-Y., Wang, L., Xiao, B., Wang, X.-C. and Yang, Y.-J. 2016. Diverse *Colletotrichum* species cause anthracnose of tea plants (*Camellia sinensis* (L.) O. Kuntze) in China. *Sci. Rep.* 6:35287.
- White, T. J., Bruns, T., Lee, S. and Taylor, J. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: *PCR protocols: a guide to methods and applications*, eds. by M. A. Innis, D. H. Gelfand, J. J. Sninsky and T. J. White, pp. 315-322. Academic Press, New York, USA.
- Woo, J., Kim, J.-E., Kim, M. and Cha, B. 2021. First report of mochi tree (*Ilex integra*) anthracnose caused by *Colletotrichum fioriniae* in Korea. *Plant Dis.* 105:1218.
- Xavier, K. V., Kc, A. N., Peres, N. A., Deng, Z., Castle, W., Lovett, W. and Vallad, G. E. 2019. Characterization of *Colletotrichum* species causing anthracnose of pomegranate in Southeastern United States. *Plant Dis.* 103:2771-2780.
- Xu, S. J., Aktaruzzaman, M., Kim, B. S., Kim, J. Y. and Shin, H. D. 2018. First report of anthracnose caused by *Colletotrichum fioriniae* on eggplant fruits in Korea. *Plant Dis.* 102:2642.
- Zhou, Y., Huang, J. S., Yang, L. Y., Wang, G. F. and Li, J. Q. 2017. First report of banana anthracnose caused by *Colletotrichum scovillei* in China. *Plant Dis.* 101:381.