



First report of *Colletotrichum godetiae* causing anthracnose on wild blackberry (*Rubus adenotrichos* Schltdl.) in Mexico

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Abstract

Wild plants showed potential to serve as a reservoir of plant pathogens. Sampling was conducted in the state of Michoacan, Mexico, collecting leaves and stems from *Rubus adenotrichos* exhibiting anthracnose symptoms, such as circular necrotic lesions and the presence of acervuli. Morphological and molecular characterization were performed using the *actin*, *histone 3*, and *glyceraldehyde 3-phosphate dehydrogenase* genes. Phylogenetic reconstruction analyses confirmed that the isolate clustered with *Colletotrichum godetiae*. This is the first report of this species on *Rubus adenotrichos* in Mexico.

Keywords *Colletotrichum acutatum* complex · *Rubus adenotrichos* · Anthracnose on blackberry plants

Introduction

The genus *Rubus* L. comprises approximately 700 species, 36 of which occur in Mexico and 9 in the state of Michoacan. Blackberries are shrubby plants characterized by the production of fleshy fruits in the form of small, juicy drupes (Rzedowski 2021). Mexico is the world leader in blackberry cultivation, with Michoacan as the main producer and exporter of the fruit (SIAP 2024). In 2022, anthracnose symptoms were observed on *R. adenotrichos* growing along roadsides and in transitional zones between forested

and agricultural areas in Huecorio, Michoacan, Mexico (19°31'25.5"N 101°37'23.5"W). Affected plants exhibited dark brown, sunken lesions on the surface of leaves surfaces (Fig. 1a). The objective of this study was to identify the causal agent of anthracnose affecting the wild blackberries and to confirm its pathogenicity through Koch's postulates.

Materials and methods

In September 2022, symptomatic leaves with anthracnose disease were collected from *R. adenotrichos* for pathogen isolation. Leaf fragments (0.5 cm) taken from the margins of the lesions were disinfected with 2% sodium hypochlorite for 1 min, rinsed twice with sterile distilled water, dried on sterile paper towlettes, and plated on potato dextrose agar (PDA) medium. Petri dishes were incubated at 28 °C in the dark. Mycelia from the colony margins were transferred to fresh PDA medium and incubated at 27–30 °C to obtain pure isolates.

Morphological characterization was performed by examining spores, appressoria, and hyphae under a Leica Galen III series optical microscope (Buffalo, USA). Micrographs were taken using an Axio Cam ERc 5s camera and Zeiss Zen Model 2012 (Göttingen, Alemania).

For molecular identification, total genomic DNA was extracted from fresh mycelium using the Wizard® Genomic

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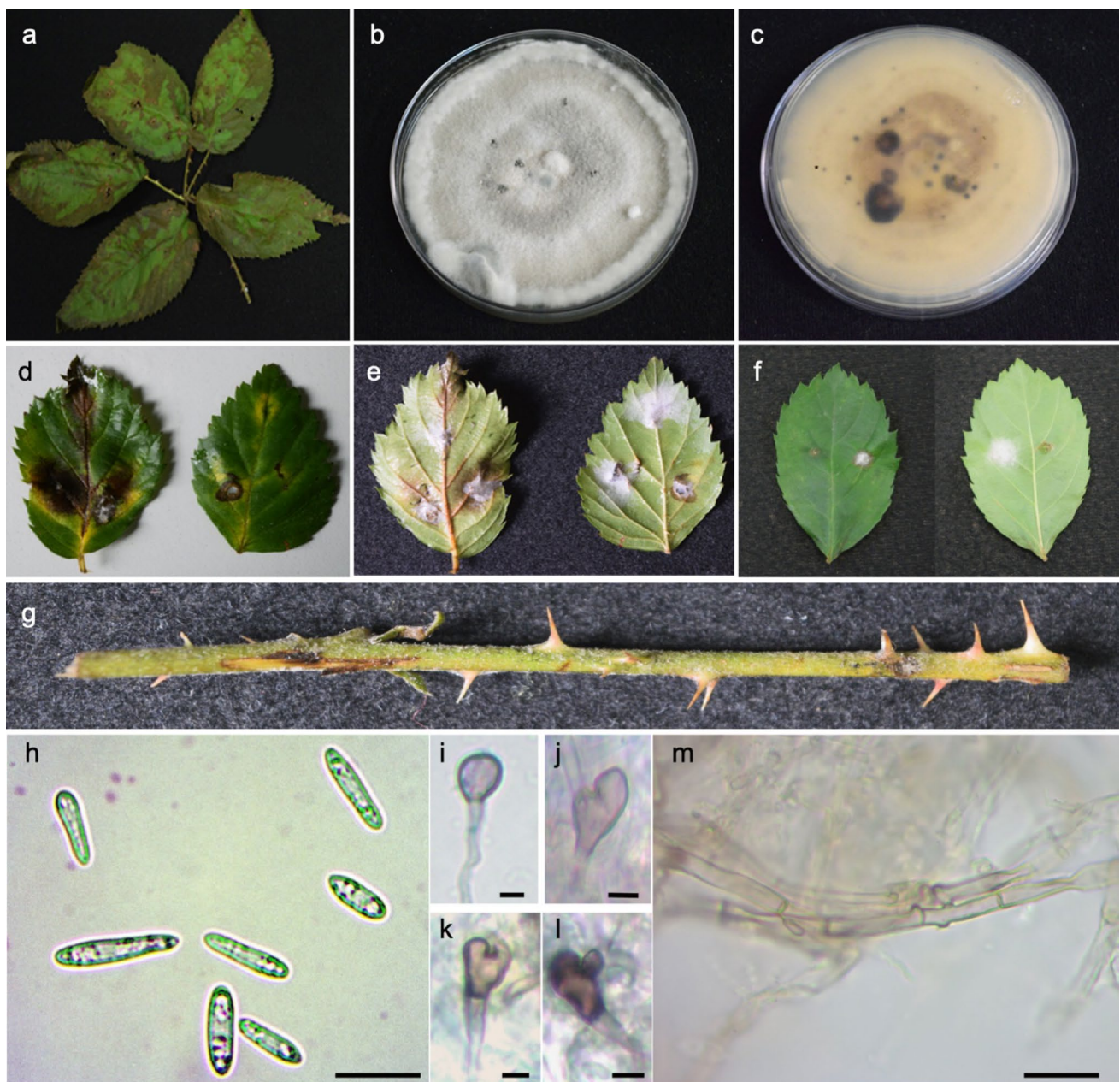


Fig. 1 Symptoms of anthracnose on *Rubus adenotrichos* leaves (a). Colony of *Colletotrichum godetiae* growing on potato dextrose agar (PDA) (b). Reverse side of the colony (c). Pathogenicity tests (d-g).

Conidia (h). Appressoria (i-l). Melanized brown hyphae (m). Scale in h, m = 10 μ m. Scale in i-l = 5 μ m

DNA Purification Kit (Promega) according to the manufacturer's instructions. Subsequently, the *actin* (*act*), *histone 3* (*his3*), and *glyceraldehyde-3-phosphate dehydrogenase* (*gapdh*) genes were amplified with the primers ACT512F/ACT783R (Carbone and Kohn 1999), CYLH3F/CYLH3R (Crous et al. 2004), and GDF1/GDR1 (Templeton et al. 1992), respectively. PCR program for amplification followed the protocols described by Fuentes-Aragón et al.

(2018) for *act*, Crous et al. (2004) for *his3*, and Templeton et al. (1992) for *gapdh*. PCR products were purified and sequenced by Macrogen Biotechnology in Seoul, South Korea. The resulting sequences were assembled and visualized using BioEdit v. 7.2.5 (Hall 1999) and compared with GenBank accessions using BLAST analysis, revealing that the isolate belonged to the *Colletotrichum acutatum* species complex, closely related to *C. godetiae*. All sequences

Table 1 Isolates and accession numbers used in phylogenetic analysis with species from the *Colletotrichum acutatum* complex

Species	Isolated	Host	Country	GenBank accession numbers			References
				act	gapdh	his3	
<i>C. abscissum</i>	COAD 1877*	<i>Citrus sinensis</i>	Brazil	KP843141	KP843129	KP843138	Crous et al. (2015)
<i>C. acerbum</i>	CBS 128,530*	<i>Malus domestica</i>	New Zealand	JQ949780	JQ948790	JQ949450	Damm et al. (2012a)
<i>C. acutatum</i>	CBS 112,996*	<i>Carica papaya</i>	Australia	JQ005839	JQ948677	JQ005818	Damm et al. (2012a)
<i>C. acutatum</i>	CBS 979.69	<i>Coffea arabica</i>	Kenya	JQ949721	JQ948731	JQ949391	Damm et al. (2012a)
<i>C. arboricola</i>	RGM 3379	<i>Nothofagus dombeyi</i>	Chile	OR645078	OR644972	OR659702	Zapata et al. (2024)
<i>C. australe</i>	CBS 116,478*	<i>Trachycarpus fortunei</i>	South Africa	JQ949776	JQ948786	JQ949446	Damm et al. (2012a)
<i>C. australe</i>	CBS 131,325	<i>Hakea sp.</i>	Australia	JQ949777	JQ948787	JQ949447	Damm et al. (2012a)
<i>C. boninense</i>	CBS 123,755*	<i>Crinum asiaticum</i>	Japan	JQ005501	JQ005240	JQ005414	Damm et al. (2012b)
<i>C. brisbanense</i>	CBS 292.67*	<i>Capsicum annuum</i>	Australia	JQ949612	JQ948621	JQ949282	Damm et al. (2012a)
<i>C. cairnsense</i>	BRIP 63,641	<i>Capsicum annuum</i>	Australia	KU923715	KU923703	KU923721	De Silva et al. (2017)
<i>C. cairnsense</i>	BRIP 63,646	<i>Capsicum annuum</i>	Australia	KU923720	KU923708	KU923726	De Silva et al. (2017)
<i>C. chrysanthemi</i>	IMI 364,540	<i>Chrysanthemum coronarium</i>	China	JQ949594	JQ948603	JQ949264	Damm et al. (2012a)
<i>C. cosmi</i>	CBS 853.73*	<i>Cosmos sp.</i>	Netherlands	JQ949595	JQ948604	JQ949265	Damm et al. (2012a)
<i>C. costaricense</i>	CBS 330.75*	<i>Coffea arabica</i>	Costa Rica	JQ949501	JQ948510	JQ949171	Damm et al. (2012a)
<i>C. cuscuteae</i>	IMI 304,802*	<i>Cuscuta sp.</i>	Dominica	JQ949516	JQ948525	JQ949186	Damm et al. (2012a)
<i>C. citri</i>	CBS 134,233*	<i>Citrus aurantiifolia</i>	China	KY855973	KC293741	KY856309	Huang et al. (2013)
<i>C. eriobotryae</i>	Cer013	<i>Eriobotrya japonica</i>	Taiwan	MN206750	MN206738	MN206762	Damm et al. (2020)
<i>C. fiorinae</i>	CBS 293.67	<i>Persea americana</i>	Australia	JQ949631	JQ948640	JQ949301	Damm et al. (2012a)
<i>C. fiorinae</i>	CBS 129,916	<i>Vaccinium sp.</i>	United States	JQ949638	JQ948647	JQ949308	Damm et al. (2012a)
<i>C. godetiae</i>	CBS 133.44*	<i>Clarkia hybrida</i>	Denmark	JQ949723	JQ948733	JQ949393	Damm et al. (2012a)
<i>C. godetiae</i>	CBS 796.72	<i>Aeschynomene virginica</i>	United States	JQ949728	JQ948738	JQ949398	Damm et al. (2012a)
<i>C. godetiae</i>	CBS 129,917	<i>Schinus molle</i>	Mexico	JQ949762	JQ948772	JQ949432	Damm et al. (2012a)
<i>C. godetiae</i>	CBS 129,934	<i>Prunus dulcis</i>	Israel	JQ949752	JQ948762	JQ949422	Damm et al. (2012a)
<i>C. godetiae</i>	CBS 129,951	<i>Vitis sp.</i>	United Kingdom	JQ949751	JQ948761	JQ949421	Damm et al. (2012a)
<i>C. godetiae</i>	IMI 351,262	<i>Fragaria × ananassa</i>	Belgium	JQ949743	JQ948753	JQ949413	Damm et al. (2012a)
<i>C. godetiae</i>	IMI 345,035	<i>Fragaria vesca</i>	France	JQ949746	JQ948756	JQ949416	Damm et al. (2012a)
<i>C. godetiae</i>	CBS 125,972	<i>Fragaria × ananassa</i>	Netherlands	JQ949737	JQ948747	JQ949407	Damm et al. (2012a)
<i>C. godetiae</i>	CBS 129,911	<i>Podocarpus sp.</i>	South Africa	JQ949755	JQ948765	JQ949425	Damm et al. (2012a)
<i>C. godetiae</i>	CBS 131,331	<i>Juglans regia</i>	Austria	JQ949725	JQ948735	JQ949395	Damm et al. (2012a)
<i>C. godetiae</i>	IMI 381,927	<i>Rubus idaeus</i>	Turkey	JQ949759	JQ948769	JQ949429	Damm et al. (2012a)
<i>C. godetiae</i>	RGM 3336	<i>Drimys winteri</i>	Chile	OR645093	OR644987	OR659718	Zapata et al. (2024)
<i>C. godetiae</i>	CBS 127,561	<i>Ugni molinae</i>	Chile	JQ949763	JQ948773	JQ949433	Damm et al. (2012a)
<i>C. godetiae</i>	CPO 27.863	<i>Persea americana</i>	Mexico	MN746507A	MN737332G	MN848380H	Fuentes-Aragon et al. (2020)
<i>C. godetiae</i>	CPO 27.907	<i>Persea americana</i>	Mexico	MN746508	MN737333	MN848381	Fuentes-Aragon et al. (2020)
<i>C. godetiae</i>	CPO 27.921	<i>Persea americana</i>	Mexico	MN746509	MN737334	MN848382	Fuentes-Aragon et al. (2020)
<i>C. godetiae</i>	IPN 10.0213	<i>Rubus sp.</i>	Mexico	PV543638	PV543641	PV543644	Nava-Delgado et al. (2025)
<i>C. godetiae</i>	IPN 10.0214	<i>Rubus sp.</i>	Mexico	PV543639	PV543642	PV543645	Nava-Delgado et al. (2025)
<i>C. godetiae</i>	IPN 10.0215	<i>Rubus sp.</i>	Mexico	PV543640	PV543643	PV543646	Nava-Delgado et al. (2025)
<i>C. godetiae</i>	MxMic_187C	<i>Rubus sp.</i>	Mexico	PX309550	PX234439	PX309549	This study
<i>C. guajavae</i>	IMI 350,839*	<i>Psidium guajava</i>	India	JQ949591	JQ948600	JQ949261	Damm et al. (2012a)
<i>C. indonesiense</i>	CBS 127,551*	<i>Eucalyptus sp.</i>	Indonesia	JQ949609	JQ948618	JQ949279	Damm et al. (2012a)
<i>C. javanense</i>	CBS 144,963	<i>Capsicum annuum</i>	Indonesia	MH846575	MH846572	MH846571	De Silva et al. (2019)
<i>C. johnstonii</i>	IMI 357,027	<i>Citrus sp.</i>	New Zealand	JQ949764	JQ948774	JQ949434	Damm et al. (2012a)

Table 1 (continued)

Species	Isolated	Host	Country	GenBank accession numbers			References
				act	gapdh	his3	
<i>C. johnstonii</i>	CBS 128,532*	<i>Solanum lycopersicum</i>	New Zealand	JQ949765	JQ948775	JQ949435	Damm et al. (2012a)
<i>C. kinghornii</i>	CBS 198.35*	<i>Phormium</i> sp.	United Kingdom	JQ949775	JQ948785	JQ949445	Damm et al. (2012a)
<i>C. laticipillum</i>	CBS 129,827	<i>Hevea brasiliensis</i>	Colombia	JQ949611	JQ948620	JQ949281	Damm et al. (2012a)
<i>C. limetticola</i>	CBS 114.14*	<i>Citrus aurantifolia</i>	United States	JQ949514	JQ948523	JQ949184	Damm et al. (2012a)
<i>C. lupini</i>	CBS 109,225*	<i>Lupinus</i> sp.	Netherlands	JQ949476	JQ948485	JQ949146	Damm et al. (2012a)
<i>C. melonis</i>	CBS 159.84*	<i>Cucumis melo</i>	Brazil	JQ949515	JQ948524	JQ949185	Damm et al. (2012a)
<i>C. nymphaeae</i>	CBS 515.78*	<i>Nymphaea alba</i>	Netherlands	JQ949518	JQ948527	JQ949188	Damm et al. (2012a)
<i>C. nymphaeae</i>	CBS 119,294	<i>Leucaena</i> sp.	Mexico	JQ949526	JQ948535	JQ949196	Damm et al. (2012a)
<i>C. paranaense</i>	CPC 20,901*	<i>Malus domestica</i>	Brazil	KC205077	KC205026	KC205004	Bragança et al. (2016)
<i>C. perseicola</i>	RGM 3376, CCCT 23.27	<i>Persea lingue</i>	Chile	OR645098	OR644992	OR659723	Zapata et al. (2024)
<i>C. paxtonii</i>	IMI 165,753*	<i>Musa</i> sp.	Saint Lucia	JQ949606	JQ948615	JQ949276	Damm et al. (2012a)
<i>C. phormii</i>	CBS 118,194*	<i>Phormium</i> sp.	Netherlands	JQ949767	JQ948777	JQ949437	Damm et al. (2012a)
<i>C. pyricola</i>	CBS 128,531*	<i>Pyrus communis</i>	New Zealand	JQ949766	JQ948776	JQ949436	Damm et al. (2012a)
<i>C. pyricola</i>	RGM 3083	<i>Cryptocarya alba</i>	Chile	OR645103	OR644997	OR659728	Zapata et al. (2024)
<i>C. rhombiforme</i>	CBS 129,953*	<i>Olea europea</i>	Portugal	JQ949778	JQ948788	JQ949448	Damm et al. (2012a)
<i>C. rhombiforme</i>	RGM 3293	<i>Gomortega keule</i>	Chile	OR645109	OR645003	OR659734	Zapata et al. (2024)
<i>C. roseum</i>	RGM 2685, CBS 145,754*	<i>Lapageria rosea</i>	Chile	MK903604	MK903603	OR659735	Zapata et al. (2019)
<i>C. salicis</i>	CBS 607.94*	<i>Salix</i> sp.	Netherlands	JQ949781	JQ948791	JQ949451	Damm et al. (2012a)
<i>C. salicis</i>	CBS 115.14	<i>Solanum lycopersicum</i>	Germany	JQ949798	JQ948808	JQ949468	Damm et al. (2012a)
<i>C. scovillei</i>	CBS 126,529*	<i>Capsicum</i> sp.	Brazil	JQ949588	JQ948597	JQ949258	Bragança et al. (2016)
<i>C. simmondsii</i>	CBS 122,122*	<i>Carica papaya</i>	Australia	JQ949597	JQ948606	JQ949267	Damm et al. (2012a)
<i>C. simmondsii</i>	CBS 111,531	<i>Protea cynaroides</i>	United States	JQ949603	JQ948612	JQ949273	Damm et al. (2012a)
<i>C. sloanei</i>	MT27-4-b	<i>Mangifera indica</i>	Taiwan	MN820667	MN820683	MN820691	Lin et al. (2023)
<i>C. tamarilloi</i>	CBS 129,814*	<i>Solanum betaceum</i>	Colombia	JQ949505	JQ948514	JQ949175	Damm et al. (2012a)

* Type, epitype, holotype, neotype species

generated in this study were deposited in GenBank under accession numbers PX309549, PX309550, and PX23443.

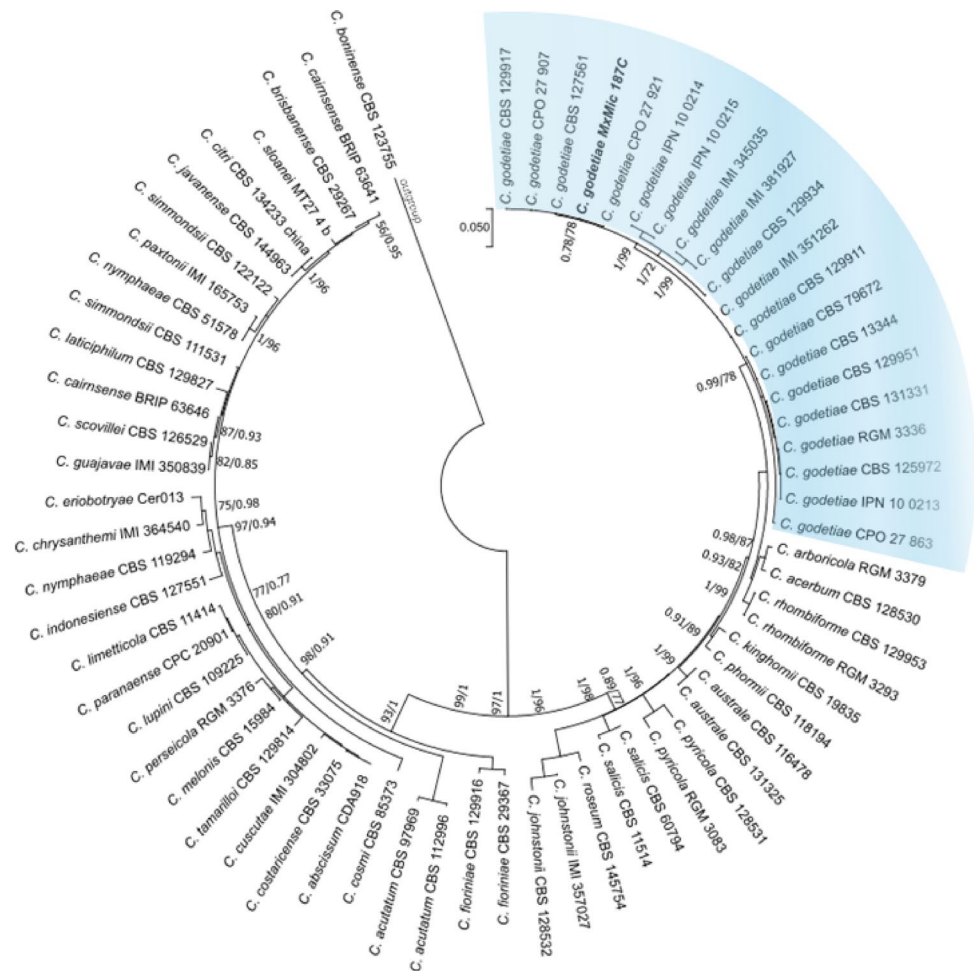
For the multilocus phylogenetic analysis, datasets were assembled for each locus (*act*, *his3*, and *gapdh*) using sequences from *Colletotrichum godetiae* and related species within the *C. acutatum* complex. GenBank sequences from the type/ holotype of different *Colletotrichum* species were selected based on previous phylogenetic studies (Afanador et al. 2014; Talhinas and Baroncelli 2021) (Table 1).

Alignments were generated using the online server MAFFT v.7 (<https://mafft.cbrc.jp/alignment/server/>), and the best-fit substitution models were determined with jModel test v. 0.1.1 (Posada 2008): TIM2+I for *act*, TPM1uf+G for *gapdh*, and TrN+G for *his3*. Phylogenetic trees were performed for individual gene-matrix and concatenated dataset (*act*, *his3*, *gapdh*), and designated to *Colletotrichum boninense* as the outgroup, with Maximum Likelihood

(ML) analysis in MEGA 7 (Kumar et al. 2016) with 1000 iterations of bootstrap, and Bayesian inference (BI) in Mr. Bayes v.3.2.7a (Ronquist et al. 2012) with 1,500,000 replicates. The phylogenetic Bayesian inference (BI) analyses were visualized using FigTree. 1.4.3 (Rambaut 2016).

Pathogenicity tests were carried out by inoculating the fresh mycelium of isolate MxMic_187C isolate onto detached healthy leaves and stems of *Rubus* cv. 'Tupy'. Three leaves and three 12-cm stems of healthy blackberry were disinfected as follows, washed with tap water, disinfected with 2% sodium hypochlorite for 1 min, rinsed three times with sterile distilled water, then sprayed with 70% alcohol for 1 min, and dried with sterile towels. Each tissue was inoculated by placing a 5 mm square of young mycelium plugs on wounds made in the leaves and stems with a sterile dissecting needle. For the control, a 5 mm square of agar without mycelia was placed on the wounded leaves and

Fig. 2 Phylogenetic tree inferred from maximum likelihood (ML) for species inside the *Colletotrichum acutatum* complex, based on concatenated *act*, *his3*, and *gapdh* sequences. *Colletotrichum* species are followed by strain IDs. The isolate of this study is highlighted in **bold**. Bayesian posterior probability (BPP>0.5) and bootstrap values (>70%) are shown at the nodes



stems. The experiment was conducted in triplicate and incubated in a humidity chamber at 30 °C for eight days. Fungal re-isolation from symptomatic tissues was performed to fulfill Koch's postulates.

Results

When processing all *Rubus adenotrichos* samples that showed anthracnose symptoms, (dark sunken circular lesions on leaves and stems, Fig. 1a) under a magnifying glass, acervuli (asexual reproductive structures) were visible. Three isolates of *Colletotrichum* sp. were obtained from the infected leaves and stems.

The molecular identification of isolate MxMic_187C was assessed after the analysis of a multi-locus dataset of *Colletotrichum acutatum* complex species, which comprised 67 sequences with an alignment length of 653 characters: *act*: 1–222, *his3*: 223–361, *gapdh*: 362–653). In the phylogenetic analyses (Fig. 2), the isolate MxMic_187C was grouped in the same clade as *C. godetiae* holotype CBS 133.44 and other members of this species from Mexico (CBS 129917,

CPO 27.907, CPO 27.921) and Chile (CBS 127561) with strong Bayesian posterior probability (0.99) and 78% bootstrap support.

Colonies of *C. godetiae* MxMic_187C on PDA were velvety and zoned, white to grayish, becoming white toward the periphery (Fig. 1b). On the reverse side of the Petri dish, it was brown in the center and light brown at the edges (Fig. 1c). Conidia were hyaline, subcylindrical with pointed or rounded ends, measuring (10.5–) 12–16 (–19) × (3.0–) 3.5–5 (–5.5) μm, average, 12.0 × 4.0 μm (Fig. 1h). Appressoria were brown, melanized, smooth-walled, clavate to irregular and lobated, sometimes bifurcated toward the apex (Fig. 1i–l). Smooth-walled, septate hyphae, both hyaline and melanized, ampulliform. Brown, melanized and hyaline, smooth-walled, septate (Fig. 1m). Black conidiomata present. Chlamydospores and setae were absent.

In the pathogenicity test, isolate MxMic_187C produced characteristic anthracnose symptoms on inoculated leaves and stems, forming brown, sunken lesions surrounded by chlorotic halos, in contrast to the control, where a small brown tissue ringed the wound (Fig. 1d–g). The fungus was

successfully re-isolated from symptomatic tissues, confirming *C. godetiae* as the causal agent.

Discussion

The isolate MxMic_187C isolate detected in *Rubus adenotrichos* samples was identified as *Colletotrichum godetiae*, based on the fact that it was grouped in the multilocus phylogenetic analyses (*act*, *his3*, and *gapdh*) in the same clade with *C. godetiae* holotype CBS 133.44 and members of the same species from Mexico (CBS 129917, CPO 27.907, CPO 27.921) and Chile (CBS 127561). The conidia measurements obtained in this study, $12.0 \times 4.0 \mu\text{m}$, were consistent with those reported for the holotype CBS 133.44, described by Damm et al. in 2012, who described conidia measuring $12.4 \times 4.3 \mu\text{m}$. The *C. acutatum* species complex consists of around 41 species reported to cause anthracnose on a wide range of hosts (Talhinhas and Baroncelli et al. 2021). *Colletotrichum godetiae* has been reported as a polyphagous species due to its wide distribution and association with various hosts, including almond, *Papaver rhoeas*, *Sinapsis arvensis*, *Fumaria officinalis*, and *Sanguisorba verrucosa* of the Rosaceae family being the most prevalent (Farr and Rossman 2025; Ramos et al. 2025; Talhinhas and Baroncelli et al. 2021). In Colombia, Afanador et al. (2014) reported the presence of *C. godetiae* affecting the *Rubus glaucus* crop, causing damage to up to 40% of the harvest. In Mexico, *C. godetiae* has been recorded to cause anthracnose on economically important crops such as *Persea americana* (Fuentes-Aragón et al. 2020; Hernández-Lauzardo et al. 2015) and cultivated blackberry, *Rubus* sp. cv. 'Tupy' (Nava-Delgado et al. 2025). Additionally, this pathogenic fungi has been reported on wild perennial hosts including *Schinus molle* (Damm et al. 2012a) and *Eriobotrya japonica* (Juárez-Vázquez et al. 2019). To date, only two species of *Colletotrichum* have been reported infecting blackberry *Rubus* spp. in Mexico: *C. gloeosporioides* (Horst 2013; Garay-Serrano et al. 2021) and *C. godetiae* (Nava-Delgado et al. 2025; this study).

Globally, the state of Michoacan is the main producer of blackberries, supplying international markets, with the United States as its primary importer (SIAP, 2024). Pathogenicity tests revealed that *C. godetiae* (MxMic_187C) isolated from wild blackberry is able to infect cultivated blackberry leaves and stems of *Rubus* cv. 'Tupy'. Our finding of the species *C. godetiae* on *Rubus adenotrichos* leaves in Michoacan, Mexico, and the presence on wild hosts, suggests that it could act as a reservoir for this fungal pathogen, as previously reported for other wild plants harboring *Colletotrichum* species (Alizadeh et al. 2022; Oliveira et al. 2016; Ramos et al. 2025).

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Author contributions ERO research, formal analysis, original draft writing, and methodology; YS, ARA, NFE. MLO review and editing; JCNC review, editing, and supervision; EGS conceptualization, editing, resources, and supervision. All authors approved the final manuscript.

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Declarations

Conflict of interest All authors declare they have no conflict of interest in any part of the research.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

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