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Morphological and molecular characterization of *Wilsoniana amaranthi* (*Albuginales, Oomycota*) on *Amaranthus retroflexus* in Iran

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Abstract: White blister rust causal agents, previously assigned to the genus *Albugo*, are obligate plant pathogens affecting numerous plant families. The genus *Wilsoniana* has been erected from the genus *Albugo* to accommodate species infecting hosts in the *Caryophyllales*. Starting from spring 2018, we observed symptoms resembling white blister rust disease on leaves of *Amaranthus retroflexus* L. in the northern Iran. The specimens were subjected to molecular study by analyzing *cox2*, LSU and ITS rDNA sequences and morphological data sets. The results confirmed that the specimens belong to *Wilsoniana amaranthi* (Schwein.) Y.J. Choi, Thines & H.D. Shin (*Albuginales, Oomycota*). To our knowledge, this is the first confirmed and documented record of *W. amaranthi* (ex *Amaranthus retroflexus*) from both Iran and West Asia. The results of this study will provide a reference for further resolution of *W. amaranthi* species concept.

Key words: *Albuginales*, *Caryophyllales*, Phylogeny, Ultrastructure

INTRODUCTION

Amaranthus L. is a genus of approximately 95 species of annual herbaceous plants from the family *Amaranthaceae* and the subfamily Amaranthoideae, distributed worldwide (Nejad Falatouri 2020; Sheidai & Mohammadzadeh 2008; Wolosik & Markowska 2019).

Several species of this genus are often considered weeds, some ornamentals and a number have an ecological role or serve as a source of food and medicine. *Amaranthus* species occur in various habitats, including cultivated areas, flood plains, roadsides, wastelands, deserts, and marine environments in tropical, subtropical, and temperate climates (Ehleringer 1983; Keinath et al. 2003; Grubben 2004; Mahklouf et al. 2016; Manyelo et al 2020; Sheikh & Babakhani 2020).

A broad range of biotrophic pathogens as the causal agents of rust, smut, downy mildew, and white blister rust diseases have been reported on *Amaranthus* spp. worldwide (Farr & Rossman 2021).

The causal agents of white rust disease on *Caryophyllales* previously assigned to the genus, *Albugo*, are now placed in the genus *Wilsoniana* based on morphological and molecular phylogenetic studies (Thines & Spring 2005; Ploch et al. 2010).

The genus *Wilsoniana* comprises the species combinations including *W. achyranthis* (Henn.) Thines, *W. amaranthi* (Schwein) Y.J. Choi, Thines & H.D. Shin, *W. bliti* (Biv.) Thines, *W. platensis* (Speg.) Thines and *W. portulacae* (DC. Ex Duby) Thines (Thines & Spring 2005, Choi et al. 2007). Two distinctive species of *Wilsoniana* on *Amaranthus* spp. hosts involving *W. bliti* and *W. amaranthi* have been identified (Voglmayr & Riethmuller 2006).

From Asia, *W. amaranthi* has been reported on *A. hybridus*, *A. dubius* and *W. bliti* on *A. blitum* in South Korea (Kim et al. 2019; Lee et al. 2019; Lee et al. 2020).

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The first reports of this pathogen on *Amaranthus retroflexus* in Iran were in 1948 and 1952 under the name *A. bliti* (cited in Ershad 2009). The existence of *W. portulacae* on *Portulaca* in Iran has already briefly noted by Poladi et al., 2017. Very recently, detailed descriptions and illustrations along with phylogenetic placement were provided for *W. portulacae* on *Portulaca* sp. (Mirzaee et al. 2021a).

Wilsoniana species on *Amaranthus* spp. have not been confirmed or documented yet in the Middle East; hence, this study is the first documented record of a member of this genus on *Amaranthus* in the region.

MATERIALS AND METHODS

Sampling and morphological investigations

In May 2018, samples of redroot pigweed (*Amaranthus retroflexus* L.) exhibiting typical symptoms of white rust were collected from Golestan province in the north of Iran. Handmade cross-sections were prepared from leaves bearing pustules and thoroughly crushed with standard razor blades. The slides for microscopic observations and measurements were prepared using lactophenol solution (equal parts of lactic acid, phenol, glycerol and distilled water). Measurements are presented as mean ± standard deviation following the minima and maxima within parentheses and mean values marked as underlying (Mirzaee et al. 2021b). Voucher specimens have been lodged at the Iranian Fungal Culture Collection, Iranian Research Institute of Plant Protection, Tehran.

Photographs were taken using an Olympus DP25 digital camera connected to an Olympus BX51 light microscope. A scanning electron microscopy (SEM) study was performed using a VEGA/TESCAN SEM (Czech Republic) as mentioned by Salimi Moghadam et al. (2015).

Phylogenetic analysis

DNA was extracted from individual sori excised from infected plant tissue according to the method described in Walsh et al., 1991; Hirata & Takamatsu, 1996. Polymerase chain reaction (PCR) amplifications were performed using WizPure 2X PCR MasterMix containing 0.5% DMSO in an MJ Mini thermal cycler (Bio-Rad, Hercules, USA), with an initial denaturation step (98˚C, 30 s), followed by 36 cycles of denaturation (98˚C, 10 s), annealing (53˚C, 30 s), extension (72˚C, 1 min) and final extension (72˚C, 10 min). The primers *cox*2-F/*cox*2-R, LR0R-O/LR6-O and ITS1-O/LR0 were used for the analysis of *cox2* (cytochrome c oxidase subunit 2), LSU (large ribosomal subunit) and ITS (internal transcribed spacer of rDNA) regions, respectively (Ploch et al. 2018).

The newly determined *cox2* and LSU sequences and related sequences retrieved from GenBank were aligned using the G-INS-i model of MAFFT (Katoh and Stadley 2013) implemented in Trease (http://thineslab.senckenberg.de/trease) (Mishra et al. on-line). Also, Maximum Likelihood (ML) inference was performed by RAxML (Stamatakis 2014) using the GTRGAMMA model with 1000 bootstrap replicates. Minimum Evolution analysis using the Tamura-Nei evolution model with 1,000 bootstrap replicates, was conducted in MEGA 5 software (Tamura et al. 2011).

RESULTS AND DISCUSSION

Starting from spring 2018, we observed symptoms of white blister rust (WBR) disease on leaves of *Amaranthus retroflexus* in Gorgan, Golestan province of Iran. Infected leaves exhibited characteristic circular to irregular ellipsoidal sori, 1-6 mm in diameter forming along the lower surfaces.

Microscopic observations showed organs of a WBR pathogen resembling a *Wilsoniana* species characterized by distinct morphology of sporangia as mentioned by Thines & Spring (2005).

Sporogenous hyphae were colorless, aseptate, unbranched, mostly grouped, clavate to cylindrical (close to a straight shape or slightly curved), producing sporangia in chains, (25-)25.2-37-49(-55) × (12.5-) 12.6-13.9-15.2(-16) µm in diameter (n = 35). The primary sporangia were hyaline with overall thickened wall, globose to subglobose or sometimes triangular, (11.5-) 13.6-15.7-17.8(-20) µm in diameter (n = 90), with a wall thickness of (1.25-) 2.3-3.5-4.7(-5) µm. Secondary sporangia were hyaline, ovoid to pyriform, (12.5-) 14-15.5-17(-20) × (15-)15.9-18-20.3(22.5) µm in diameter (n = 95) (Fig. 1; Table 2). Oospores were not found.

Specimens examined. Iran, Golestan province, Gorgan, on *Amaranthus retroflexus*, 13 May 2018, leg. & det. M.R. Mirzaee (IRAN 17918 F). – Ibid., 14 May 2018, leg. & det. M.R. Mirzaee (IRAN 18092F).

The morphological comparison of literature data for *Wilsoniana amaranthi* and *W. bliti* with representative specimen of *W. amaranthi* (IRAN17918F) and sequences generated in this study are shown in Tables 2 and 1, respectively.

Under SEM, the primary sporangial wall showed irregular, short linear striate ornamentation, sometimes microverrucose pattern with thickness variation *(*Fig. 1). Secondary sporangia in SEM exhibited the same overall characteristics of the previous study (Thines & Spring 2005), in which irregularly striate pattern sometimes consisting of verrucose lines was reported.

The mean size of the *W. amaranthi* sporogenous hyphae on *A. retroflexus* in Iran, was larger in comparison to that of *W. amaranthi* specimen recorded on *A. hybridus* (Kim et al. 2019) but similar to the specimen infecting *A. dubius* (Lee et al. 2020) and has a larger length (55 µm) compared with *A. dubius* (44 µm) and *A. hybridus* (38 µm). However, the size of the sporogenous hyphae has not been a taxonomic trait in white blister rust pathogens (Table 2). Primary and secondary sporangia

measurements of the species in this study, did not show markedly difference from those of other studied specimens. However, primary sporangia were thicker reaching even up to 5 µm in diameter (Table 2).

The ITS BLAST search against NCBI indicated closest sequence similarity of 97.5 % followed by 86.2% (89% query cover) to *W. amaranthi* specimens and *W. bliti* (KSNUH520), respectively, indicating limited available information in the sequence GenBank for ITS. The ITS sequence-based phylogeny analysis was ruled out due to the low availability of the ITS region sequences for *W. amatanthi*.

To further resolve the taxonomic position, phylogenetic trees were generated using Minimum Evolution and Maximum Likelihood analyses from sequences of *cox2* and LSU genes. The LSU sequences (accession nos. MW605161 and MW605162) yielded from this study formed a well-supported clade (ME = 99; ML = 89) with four more specimens of *W. amaranthi* indigenous to South America and different locations in Europe (Fig. 2).

Table 1. Specimens investigated in this study and their GenBank accession numbers.

Taxon	Host plant	Specimen no.	Origin	GeneBank accession numbers		
				cox2	ITS	LSU
Albugo amaranthi	*Amaranthus spinosus*	SMK19835	South Korea	AY913805	AY929824	
A. amaranthi	*A. powellii*	HV441	Austria	-		AY035543
A. amaranthi	*A. hybridus*	AR290	Germany	-		DQ007509
A. achyranthis	*Achyranthes japonicus*	SMK19955	-	AY913807	DQ643905	
A. gomphrenae	*Gomphrena martiana*	HV2139	Argentinia			DQ007501
A. aff. gomphrenae	*Iresine diffusa*	AR 166	Costa Rica	EU826093		AY035545
A. caryophyllacearum	*Spergularia salina*	HV2131	Austria			DQ007499
A.Ipomoeae-paduratae	*Ipomoea hederacea*	SMK 19628	?	AY913804		
A. occidentalis	*Spinacia oleracea*	AR362	USA	-	-	DQ007500
Wilsoniana amaranthi	*Amaranthus* sp.	HNC 40	Colombia	EU826091		EU826107
W. amaranthi	*A. dubius*	KSNUH401	South Korea	MN533957	MN526483	
W. amaranthi	*A. hybridus*	KNUH292	South Korea	MK335465	MK333400	
W. amaranthi	*A. powellii*	GLM-F073357		KJ654158		
W. amaranthi	*Amaranthus* sp.	MG 10-03	France	EU826090		EU826106
W. amaranthi	*A. chlorostachys*	FR0046016	Iran	JN849486	JN849470	
W. amaranthi	*A. chlorostachys*	FR0046015	Iran	JN849487	JN849471	
W. amaranthi *	*A. retroflexus*	IRAN 17918 F	Iran	MW605163	MW605160	MW605161
W. amaranthi *	*A. retroflexus*	IRAN 18092 F	Iran	MW605164	-	MW605162
W. bliti	*A. blitum*	KSNUH520	South Korea	MT006231	MT000644	
W. bliti	*A. viridis*	A165	Australia	GU292161		
W. portulacae	*Portulaca oleracea*	SMK18991	-	AY913806	DQ643921	
W. portulacae	*P. oleracea*	AR 164	Costa Rica	EU826105		
W. portulacae	*P. oleracea*	Ram-Por-15	Iran			MG825650
W. portulacae	*P. oleracea*	HUH 640	China	-		EU826120
W. platensis	*Boerhavia deserticola*	AR375	Namibia			DQ007502
W. bliti	*Amaranthus blitum*	HV2137	Austria			DQ007504
W. bliti	*A. blitum*	AR291	Taiwan			DQ007503
W. portulacae,	*Portulaca oleracea*	8Ham	Iran			MF171162
W. portulacae,	*Portulaca* sp.	AR 305	Re´union			DQ007505
W. portulacae,	*P. oleracea*	AR374	Namibia	-		DQ007506
W. portulacae,	*P. oleracea*	HV 374	Namibia			AY035544
W. achyranthis,	*Achyranthes sicula*	AR384	Namibia			DQ007508
W. achyranthis,	*A. aspera*	AR383	Namibia			DQ007507
W. amaranthi	*A. hybridus*	AR290	Germany			DQ007509
Air samples	Uncultured *Wilsoniana*	MZO006			MF095131	
Phytopythium vexans		STE-U6729		GU133541		
Pythium middletonii		CBS528.74				AF119608

*Specimens sequenced in this study

The *cox2* tree provided further resolution for the relationships among *W. amaranthi* specimens. Based on the *cox2* analysis, the sequences representing *W. amaranthi* in this study were placed in a branching clade composed of *W. amaranthi* specimens (ME=100; ML=80), within which it formed a subclade with eight GenBank accessions from *Amaranthus* sp., *A. chlorostachys*, *A. spinosus*, *A. dubius*, *A. hybridus* and *A. powellii* distributed across Asia, Europe and South America. Two specimens of *Wilsonian amaranthi* (EU826090, KJ654158), infecting *Amaranthus* sp. and *A. powelli,* clustered together with a high bootstrap value, but their relationship to the current specimens was not well supported (Fig. 3).

Although, two *cox2* and ITS sequences for *W. amaranthi* infecting *A. chlorostachys* in Iran are available in NCBI (Mirzaee et al. 2013), with 97.4% (query cover = 100%) and 99% (query cover = 96%) similarity to the ITS (accession no. MW605160) and *cox2* sequences of this study, there is no documented report on this taxon from Iran. Also, both specimens did not form a cluster with GenBank accession numbers MW605163 (Herbarium no. IRAN17918F) and MW605164 (Herbarium no. IRAN18092F) of this study using the *cox2* gene fragments. Specimen

IRAN17918F can be differentiated by its ITS data from other *W. amaranthi* sequences available in Genbank with 97.5% identity (12 nucleotides different). Regarding the missing oospore data for the specimens of this study, besides lacking sporangial SEM features of hitherto reported *W. amaranthi*, specimens indigenous to Iran would be restricted to the clade containing all sequenced *W. amaranthi* until more collections and morphological data are provided.

Data outlined from this study, together with the further morphological and molecular investigations and more specimen collections on various hosts with worldwide geographical distribution are expected to aid the future elucidation of *W. amaranthi* species concept. From Asia, *W. amaranthi* on *A. hybridus, A. dubius* and *W. bliti* on *A. blitum* have been reported in South Korea (Kim et al. 2019; Lee et al. 2019; Lee et al. 2020). In Iran, the white blister rust pathogen on *A. retroflexus* was first noted as *Albugo bliti* in the 1940s (Ershad 2009). However, due to the insufficient morphological records and lack of molecular data for these specimens, their identity is considered obscure. This study is the first documented and illustrated record along with its molecular assessment of a member of this genus on an amaranth host in Iran

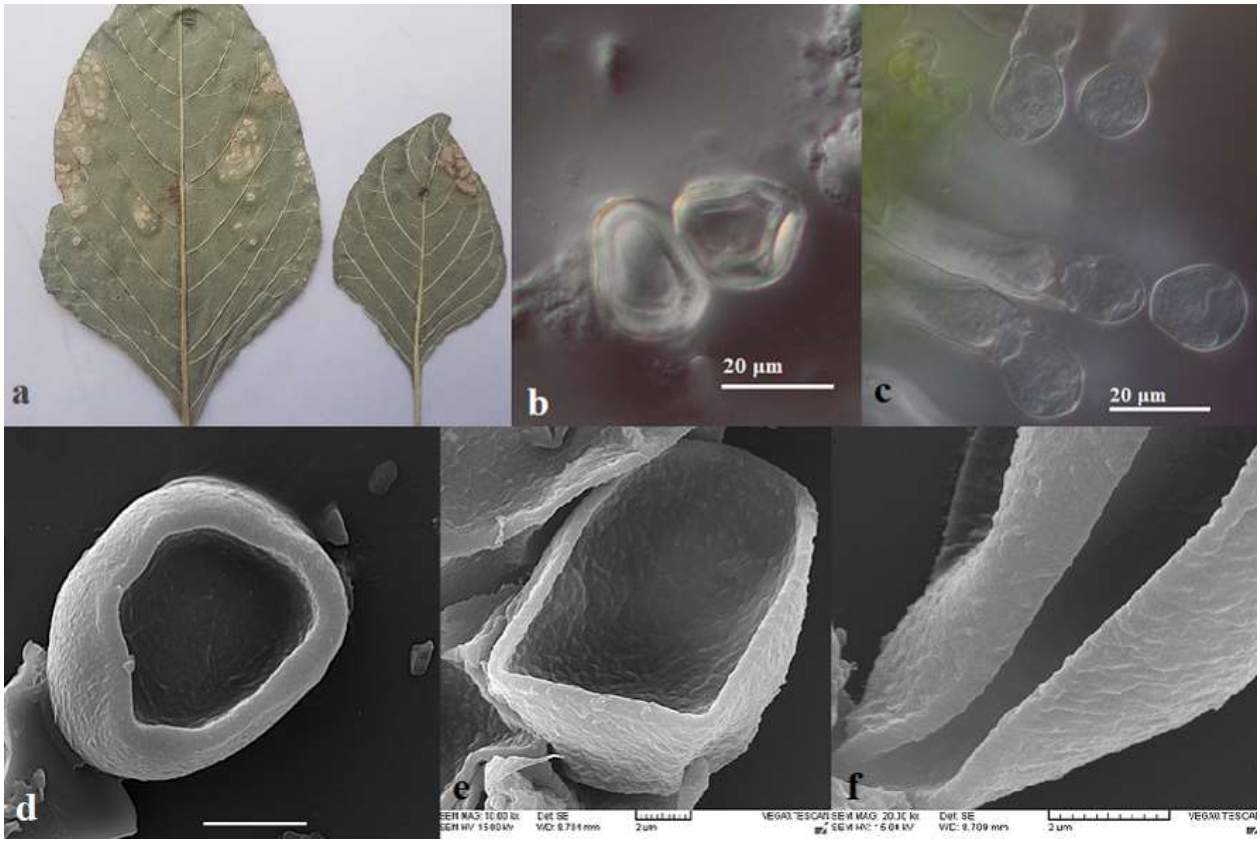

Fig 1. *Wilsoniana amaranthi* on *Amaranthus retroflexus*: (a) Symptoms; micromorphological features including (b) Primary sporangia (prs), (c) Sporogenous hyphae and secondary sporangia (ssp), (d) Primary sporangia (SEM). Bar= 5 µm, (e) Secondary sporangia (SEM), (f) Majority of primary sporangia appear deformation under mutual pressure (as mentioned by Constantinescu & Thines 2006).

Table 2. Morphological comparison of literature data for *Wilsoniana amaranthi* and *W. bliti* with specimens of the present study. An asterisk (*) indicates representative specimen of W. amaranthi (IRAN17918F) examined in this study.

Taxon	Host	Sporogenous hyphae (µm)	Primary sporangia (µm)	Secondary sporangia (µm)	Oospore (µm)	Wall thickness of prs (µm)	References
Wilsoniana amaranthi	***Amaranthus dubius***	(24-) 32 × 42 (-44) (av. 37.2)	(12-) 14.9 × 16.6 (-18) (av. 15.26)	(15-) 16.7 - 19.4 (- 21) (av. 18.09) × (12-) 14.0 × 16.5 (-19) (av. 15.27)	(34-) 39.6 × 50.8 (- 56) (av. 45.2)	1.5- 2.5	Lee et al. 2020
W. amaranthi	***A. hybridus***	(17–) 24.6 × 34.1 (–38) (av. 29.3)	(11–) 12.6 × 15.6 (–17) (av. 14.1)	(13–) 17.4 - 20.4 (–22) (avg. 18.9) × (10–) 13.3 - 16.5 (–19) (avg. 14.9)	(31–) 38.5 × 48.9 (–56) (av. 43.7)	-	Kim et al. 2019
W. amaranthi*	***A. retroflexus***	(25-)25.2-49(-55) (av. 37)	(11.5-)13.6-17.8(-20) (av. 15.7)	(12.5-)14-17(-20), av. 15.5 × (15-)15.9-20.3(22.5), av. 18.1	-	(1.25-)2.3 × 4.5(5-), av. 3.5	This study
W. bliti	***A. blitum***	(33-) 39 × 55 (-58) (av. 47.5)	(10-) 13.5 × 16.9 (-18) (av. 15.2)	(17-) 18.2 - 22 (- 24) (av. 20.11) × (13-) 14.5 - 17.5 (- 20) (av. 16.01)	(42-) 48.3 × 58 (-61) (av. 53.6)	1-3	Lee et al. 2019

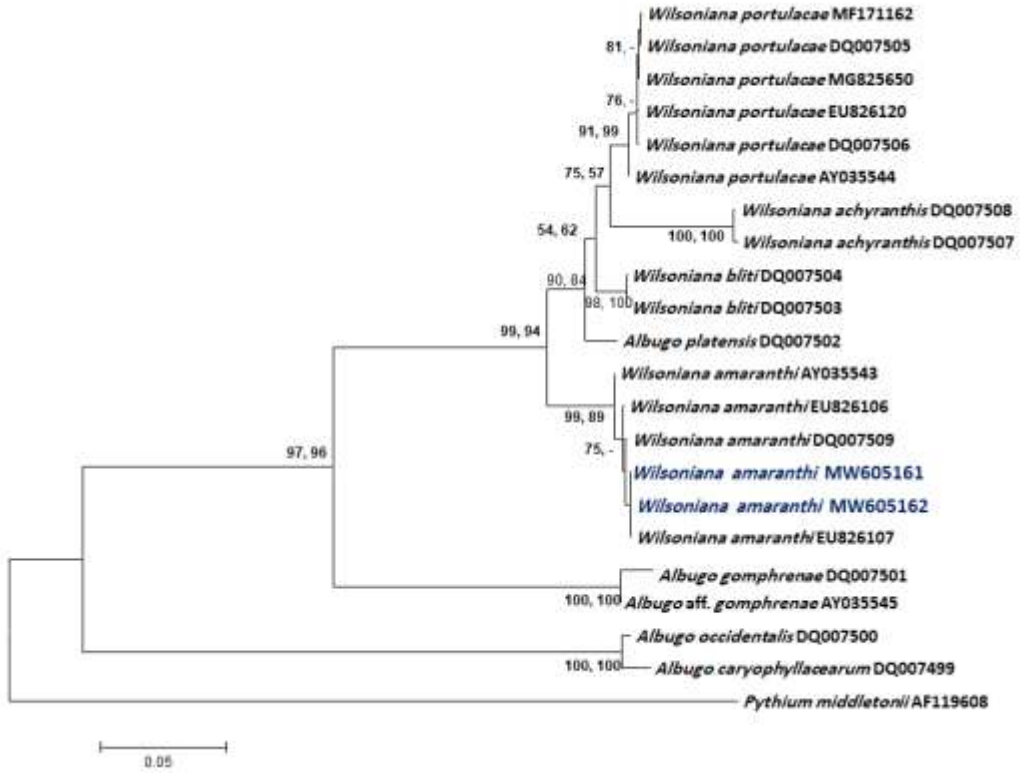

Fig 2. Phylogenetic tree based on LSU-rDNA gene sequences of *Wilsoniana* species using Minimum Evolution (ME) analysis. Support values (Minimum Evolution/Maximum Likelihood bootstraps) are shown around the branch.

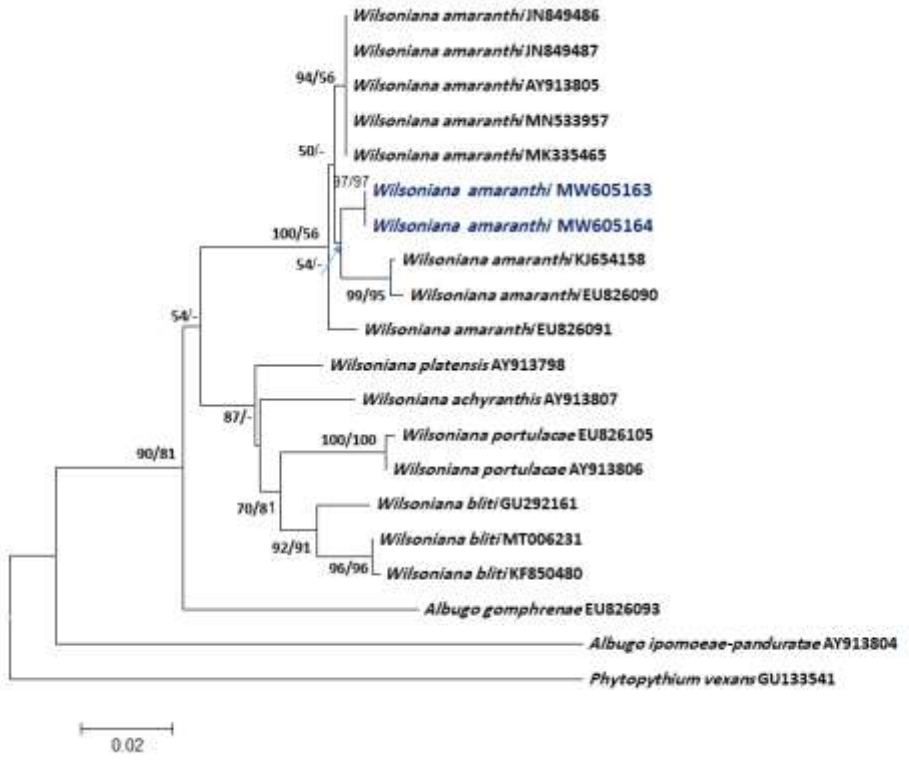

Fig 3. Phylogenetic tree based on *cox2* gene sequences of *Wilsoniana* species using Minimum Evolution analysis. Support values (Minimum Evolution/Maximum Likelihood bootstraps) are shown around the branch.

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ویژگی‌های ریخت‌شناختی و مولکولی *Wilsoniana amaranthi* (*Albuginales, Oomycota*) روی میزبان *Amaranthus retroflexus* از ایران

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چکیده: عوامل بیماری زنگ سفید، که قبلا به جنس *Albugo* منسوب شده بودند، بیمارگرهای اجباری هستند که چندین تیره گیاهی را آلوده می کنند. جنس *Wilsoniana*، شامل بیمارگرهای عامل بیماری زنگ سفید راسته *Caryophyllales*، از جنس *Albugo* جدا و توصیف شده است. در بهار ۱۳۹۷، علائم بیماری زنگ‌سفید روی برگ‌های تاج‌خروس (*Amaranthus retroflexus* L.)در شمال ایران مشاهده شد. نمونه‌های جمع‌آوری شده بر اساس ویژگی‌های ریخت‌شناختی و تبارشناختی مبتنی بر توالی‌یابی نواحی *cox2*، LSU و ITS-rDNA مورد بررسی قرار گرفتند. بر اساس نتایج، نمونه‌ها به آرایه *Wilsoniana amaranthi* (Schwein.) Y.J. Choi, Thines & H.D. Shin تعلق داشتند. بر اساس اطلاعات ما، این نخستین گزارش تایید شده و مستند از *W. amaranthi* روی گونه *A. retroflexus* بر اساس ترکیب ویژگی‌های مولکولی و ریخت شناختی از ایران و غرب آسیا است. نتایج این مطالعه، اطلاعاتی برای درک بهتر مفهوم گونه مرکب *Wilsoniana amaranthi* فراهم خواهد نمود.

کلمات کلیدی: آلبوجیناسه، تبارشناختی، راسته *Caryophyllales*، فراساختاری

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