Indian Phytopathology (2023) 76:215–221
https://doi.org/10.1007/s42360-022-00573-x

RESEARCH ARTICLE

# Characterization of tomato leaf curl Palampur virus naturally infecting wild melon in Oman

**Muhammad Shafiq Shahid**[1]

Received: 9 June 2022 / Revised: 19 August 2022 / Accepted: 17 November 2022 / Published online: 3 December 2022
© Indian Phytopathological Society 2022

**Abstract**
Weeds plants serve as a reservoir of begomoviruses Begomovirus and play a vital role in the diversity of single stranded DNA viruses. Wild melon (*Cucumis melo*) plants showing leaf curling and color breaking symptoms were collected and used in for Begomovirus amplification. Cloning, sequencing and bioinformatics analysis revealed the association of a bipartite Begomovirus isolate with the diseased *C. melo* host. The complete genome of DNA-A (2756 bp) of a bipartite Begomovirus isolate exhibited 99.5% nucleotide similarity with DNA-A of tomato leaf curl Palampur virus (ToLCPalV) reported from Iran ([IR: Jir8:T58P:08] FJ660431). Further pairwise identity derived implemented in sequence demarcation tool identified that the DNA-B (2719 bp) showed maximum 98.7% sequence identity to the corresponding DNA-B of ToLCPalV ([IR: Jir-T65X:08] JF501720). The phylogenetic dendrogram of DNA-A and DNA-B genome components grouped respectively with ToLCPalV DNA-A and DNA-B of Iran isolates and far from Pakistan and India clade. This study provides the first identification of a bipartite Begomovirus ToLCPalV from *C. melo* in Oman and also indicates the requirement for more investigation of ToLCPalV, as ToLCPalV is a major threat particularly to tomato crops in India and Pakistan and recently introduced in Iran.

**Keywords** Bipartite begomovirus · Diversity · Whitefly · *Cucumis melo*

## Introduction

Plant infecting arthropod- transmitted circular single-stranded DNA (ssDNA) viruses belong to the family of monophyletic group of viruses recognized as *Geminiviridae*. Geminiviruses causes huge losses to both mono-and dicotyledonous crops (Rojas et al. 2005). Based on the genome orientation, nature of transmitting vector and host range, the *Geminiviridae* comprises 520 virus species that are divided into 14 genera (Walker et al. 2021). Among them Begomovirus genus contains 445 documented virus species, spread globally through a complex of cryptic (with 44 known) whitefly (*Bemisia tabaci*) species and causes enormous economic damages to crops (Walker et al. 2021). They can cause disease to dicotyledonous and all economically significant host plant species. The viruses of Begomovirus genus are subdivided into monopartite (containing DNA-A molecule) and bipartite (having DNA-A and DNA-B molecules), whereas monopartite Begomoviruses are also accompanied with DNA satellites (known as alphasatellite, betasatellite, and/or deltasatellite). Monopartite Begomoviruses predominantly occur in the Old World (consisting of Australia, Asia, Middle East, Africa and Europe), whereas bipartite Begomoviruses mostly originate in the New World (America). In bipartite Begomoviruses, the DNA-A component is homologous to the monopartite Begomovirus genome which encodes Rep protein; required for Begomoviruses replication, REn protein; required for optimal replication of viral ssDNA, TrAp protein; a transactivator protein, a symptom determinant protein (C4), coat protein (CP) and pre-coat protein (V2) which is lacking in the NW Begomoviruses (Fondong 2013). The DNA-B of bipartite Begomovirus encodes proteins for cell-to-cell movement as movement protein (MP) and for long distance movement identified as nuclear shuttle protein (NSP). Both DNA-A and DNA-B genome molecules share a generic region located between noncoding intergenic region (IR), holding an adequate level

✉ Muhammad Shafiq Shahid
mshahid@squ.edu.om

[1] Department of Plant Sciences, College of Agricultural and Marine Sciences, Sultan Qaboos University, Al-Khod, 123 Muscat, Oman

of identity to let the Rep protein of DNA-A in replication of cognate DNA components.

Weeds have been considered as main reservoirs of Begomoviruses epidemics, where different susceptible weeds have been shown to be significant in the introduction and spread of diverse Begomoviruses (Mubin et al. 2010; Al-Mabsli et al. 2021). The main aim of this study was to identified the Begomovirus infecting wild melon grown as an alternate host species occurring with a view to understand the role of this weed in Begomovirus epidemiology.

## Materials and methods

### Sample collection of tomato leaf curl Palampur virus

In 2018, wild melon (*Cucumis melo*) plants expressing leaf curling, vein thickening and stunted growth suspected to be a Begomovirus infection were collected adjacent to Khasab, Oman (26.1657°N 56.2428°E) (Fig. 1a). In order to identify the casual organism, two symptomatic (Ka1-Ka4) and two asymptomatic (Kb1-Kb2) samples collected from two locations were proceeded for genomic DNA isolation by CTAB protocols as described by Doyle (1991), with slight modifications. The quality of DNA was measured by NanoDrop 2000/2000c sepctrophotometer, afterwards, DNA dilutions were prepared for use in downstream reactions.

### Identification of tomato leaf curl Palampur virus

Initial Begomovirus detection was done by PCR employing Taq DNA polymerase (Thermo Fisher Scientific) with thermal cycler C1000 TouchTm (Bio-Rad, USA). The degenerate primers AV494/AC1048 designed for begomovirus detection were used to amplified ~ 550 bp coat protein (CP) core region of genome DNA fragments (Wyatt and Brown 1996). The PCR mixture consists of 31.5 µl of $dH_2O$, 0.5 µl of Taq DNA Polymerase (5 U/µl), 5 µL of 10xbuffer, 4 µl (2.5 mM) of dNTPs, 5 µl (150 ng) of DNA Template, and 2 µl (10 uM) each of Forward and Reverse primer. PCR amplification program was as follows: denaturation at 93 °C for 1 min followed by 35 cycles of 93 °C for 30 s, 54 °C for 30 s, 72 °C for 45 s, and a final extension at 72 °C for 10 min. The PCR products were visualized by agarose gel (1%) electrophoresis. The amplified PCR products were purified for sanger dideoxy sequenced through Macrogen Inc. (South Korea). These sequences were compared to reference sequences in a GenBank by running online BLASTn search option (https://blast.ncbi.nlm.nih.gov). Begomovirus.

### Cloning of full-length tomato leaf curl Palampur virus

To acquire full-length genome (DNA-A and DNA-B) of the Begomovirus, DNA extracts were used in rolling circle amplification (RCA) employing Phi-29 DNA polymerase in TempliPhi 100 Amplification Kit (GE Healthcare, USA) as per the manufacturer instructions. Briefly, 5 ul (20 ng) of DNA template was dissolved in 5 ul of sample buffer, denatured at 95 °C for 3 min at and cooled down at the room temperature. Later 5ul reaction buffer and 0.2 ul enzyme ø29 DNA polymerase were added to the mixture and incubated at 30 °C. After 18–20 h of incubation reaction was terminated by heating at 65 °C for 10 min to stop the reaction. The RCA reaction produced a high molecular weight concatemer products, which were used in restriction fragment length polymorphism (RFLP) utilizing diverse restriction endonucleases such as *BamH*I, *Hind*III, *EcoR*I, *Kpn*I, *Nco*I, *Nde*I, *Sac*I, *Sal*I, *Pst*I, *Xba*I, *Xho*I. After RFLP analysis, *Nco*I and *Nde*I enzymes yielded ~ 2.7 kb linear molecules on the 1% agarose gel, which were gel purified using gel isolation kit (Thermo Fisher Scientific), reconfirmed by simply running

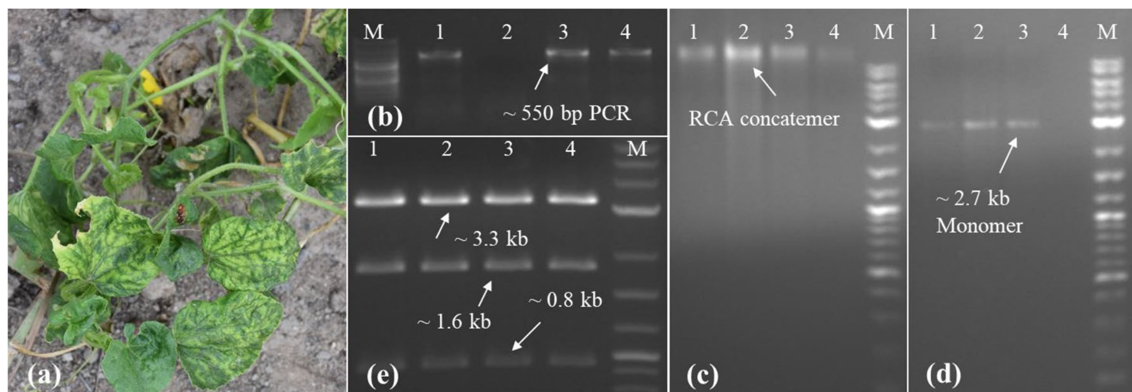


**Fig. 1** Wild melon plant naturally infected by ToLCPalV showing yellow, mosaic and color breaking symptoms (**a**), amplification of virus by PCR (**b**), RCA amplification (**c**), yielded monomer molecule of ToLCPalV by restriction digestion (**d**), and virus recombinant molecule production (**e**)

on 1.5% agarose gel and subsequently cloned into pGEM-T Easy vector systems (Promega) at the compatible restriction sites. Full-length clones were produced by either *NdeI* (DNA-A) or through *NcoI* (DNA-B) restricted RCA product, reconfirmed in RFLP by digesting DNA-A and DNA-B clones with two restriction enzymes in double digestion and sequenced them completely through chain termination method by Macrogen Inc. (South Korea). None of the DNA satellites (alphasatellite, betasatellite or deltasatellite) were detected from the tested samples using universal detection primers for DNA satellites.

### Sequence analysis

Multiple sequence contigs (each consisting of approximately 750–1000 bp) were received which were assembled and computed to produce full-length monomer molecules for both DNA-A and DNA-Bwith Lasergene package DNAStar Inc. (Madison, WI, USA). The open reading frames (ORFs) were investigated through ORF finder run online at NCBI page https://www.ncbi.nlm.nih.gov/orffinder/. To proceed multiple sequence alignments complete genome (DNA-A and DNA-B) of identified Begomovirus were compared to the submitted sequences in BLASTn search and highly similar sequences were retrieved from GenBank and used in pairwise nt analysis through sequence demarcation tool (SDT V1.2) (Table 1). Further, nucleotide variability in identified Begomovirus (DNA-A and DNA-B) sequences was analyzed to the extracted representative sequences from GenBank andphylogenetic dendrogram were produced in MEGAX software with Maximum-Likelihood (ML) method and with selected parameters including anticipated best-fit Kimura-2 paradigm and 1000 bootstrap values.

## Results

### Characterization of tomato leaf curl Palampur virus

Four full-length DNA-A genomes of bipartite Begomovirus isolates (wed14-1 to wed14-4) were determined from a symptomatic *C. melo* plant (Fig. 1b–d) and each of them was to be 2756 nucleotides (nt) in length. After sequencing analysis, it was identified that all the isolates were identical and for this reason isolate wed14-3 was submitted to GenBank database (Accession number ON366387). The wed14-3 isolate showed genome structure characteristic of DNA-A of bipartite Begomovirus reported from the Old World, including six ORFs, TrAp, REn and AC4 on the complementary and CP and MP on the virion strand (Table 2). In pairwise sequence analysis with SDT the wed14-3 isolate showed highest 98.8% nucleotide identity with the DNA-A isolate of ToLCPalV reported from Iran ([IR: Jir8:T58P:08] FJ660431) [6], followed by 96–98% and 92–97% from Pakistan and India, respectively (Fig. 2A) (Heydarnejad et al. 2013; Shafiq et al. 2019; Dhkal et al. 2020). According to the International Committee on Taxonomy of Viruses (ICTV) demarcation rules for Begomoviruses species set at $\geq$91%, the virus isolates identified here from *C. melo* are isolates of previously reported ToLCPalV species from Iran (Suppl Table 1). In phylogenetic analysis the evolutionary relationships of DNA-A sequences of ToLCPalV indicate a degree of geographical clustering among ToLCPalV DNA-A isolates (Fig. 3A). It can be seen from the tree that wed14-3 isolate discovered in this study cluster with most closely related to the ToLCPalV Iran relatives. None of the recombinant event was identified for ToLCPalV in RDP 4.1 program by means of different algorithms (viz. RDP, GENECONV, BootScan, MaxChi, SiScan, Chimaera and 3SEQ) (Martin et al. 2015). Three DNA-B clones (wed14-7 to wed14-9) were also identified and each of them had 2719 nt in length. Further sequence analysis exhibited that these (wed14-7 to wed14-9) DNA-B isolates were identical, and wed14-8 isolate was submitted into GenBank accession number ON366387. The cognate DNA-B components have genome arrangement similar to DNA-B of all bipartite Begomoviruses genomes, comprising of a nuclear shuttle protein and movement protein into complimentary and virion sense, respectively (Table 2). The pairwise sequence analysis using SDT revealed that DNA-B exhibited 98% pairwise nt identity to the cognate DNA-B component of ToLCPalV ([IR: Jir6:T3P:07] FJ660427) (Fig. 2B). In phylogenetic analysis DNA-B of ToLCPalV from Oman group with cognate DNA-B of ToLCPalV reported from Iran but clustering away from India or Pakistan isolates (Fig. 3B).

**Table 1** Identification of ToLCPalV from different countries (single/multiple) and citation index

| Country | Articles | SCP | MCP | Total citations | Average article citations |
|---|---|---|---|---|---|
| India | 19 | 19 | 0 | 178 | 9.37 |
| Pakistan | 3 | 3 | 0 | 34 | 11.33 |
| Iran | 2 | 0 | 2 | 23 | 11.50 |
| Iraq | 1 | 1 | 0 | 1 | 1.00 |

*SCP* Single author country publication, *MCP* multiple author country publication

### Geographical distribution of tomato leaf curl Palampur virus

The first detection of ToLCPalV was done from India infecting tomato (*Solanum lycopersicum*) in 2008 (Kumar et al. 2008). After the first report of ToLCPalV infection, the distribution of ToLCPalV to infect different plant species into different geographical areas have been increased. For

**Table 2** Features of DNA-A and DNA-B of ToLCPalV naturally infecting wild melon plants

| Tomato leaf curl Palampur virus (DNA-A) | | | | | | | | | DNA-B | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Position of genes (coordinates)/no. of amino acids [predicted coding capacity in kDa] | | | | | | | | | Position of gene (coordinates)/no. of amino acids [predicted coding capacity in kDa] | | | | |
| Isolate | Acc.# no | Size (nt) | CP | V2 | Rep | TrAP | REn | C4 | Isolate | Acc. # no | Size (nt) | BV1 | BC1 |
| Wed14-3 | MZ423187 | 2756 | 280–1050/256 (28.42) | 120–467/115 (12.77) | 1499–2602/367 (40.74) | 1177–1596/139 (15.43) | 1047–1457/136 (15.1) | 2269–2445/58 (6.44) | Wed14-8 | | 2719 | 426–1232/268 (29.75) | 1298–2143/281 (31.19) |

instance, in 2009 ToLCPalV was reported from Iran infecting tomato plants, later on several other species of vegetable crops (cucumber, melon, squash, watermelon and bean) were also reported to be infect by this virus (Heydarnejad et al. 2009). Likewise, in 2010 first article was online claiming the occurrence of ToLCPalV infecting Bitter gourd (*Momordica charantia* L.) from Pakistan (Ali et al. 2010). Recently, co-infection of ToLCPalV with squash leaf curl China virus (SLCuCNV) and squash leaf curl virus (SLCuV) have been studied to infect pumpkin (*Cucurbita moschata*) and zucchini squash plants, respectively in India and Iraq (Jaiswal et al. 2012; Mohammed et al. 2021). Similarly, few diverse betasatellites such as cotton leaf curl Multan betasatellite (CLCuMuB) and Pepper leaf curl betasatellite (PepLCB) were also associated with this bipartite Begomovirus complex (Namrata et al. 2010; Kumar et al. 2011).

## Discussion

Wild melon (*Cucumis melo*) is an important weed commonly grown as volunteer on the Arabian Peninsula. Due to severe summer (high temperature) season, *C. melo* can frequently be seen during winter months, a time when open crops are cultivated widely and the high density of whitefly (*Bemisia tabaci*) population can be seenBegomovirus. The results of this study showed that *C. melo* is harboring a bipartite begomovirus infection. The PCR, RCA, cloning and bioinformatics analysis revealed that disease symptoms observed in *C. melo* in Oman is caused by a bipartite ToLCPalV. ToLCPalV has previously been identified in numerous distinct hosts including the bean, cucurbit, cucumber, melon, muskmelon, watermelon, zucchini and significantly tomato crop (Kumar et al. 2008; Heydarnejad et al. 2009, 2013; Ali et al. 2010; Tiwari et al. 2012; Khanna et al. 2019; Shafiq et al. 2019; Dhkal et al. 2020; Venkataravanappa et al. 2020; Hanamasagar et al. 2021). This indicates that ToLCPalV likely has a host range that extends to other host plant including *C. melo* as confirmed in this study. Co-infection amongst Begomoviruses and Begomovirus-associated satellites is a frequent phenomenon. The earlier reports indicate that there has previously been a co-infection between ToLCPalV with SLCuV and SLCuCNV (Jaiswal et al. 2012) (Esmaeili et al. 2015). Since SLCuV has also been identified in Oman (Shahid et al. 2020), there is likely possibility that ToLCPalV could interact with SLCuV resulting into evolution of novel Begomoviruses. On the other hand, another study described that ToLCPalV has previously been associated with cotton leaf curl Multan betasatellite and pepper leaf curl betasatellite infecting Nepal dock (*Rumex nepalensis*) and pumpkin (*Cucurbita moschata*), respectively in India (Namrata et al. 2010;

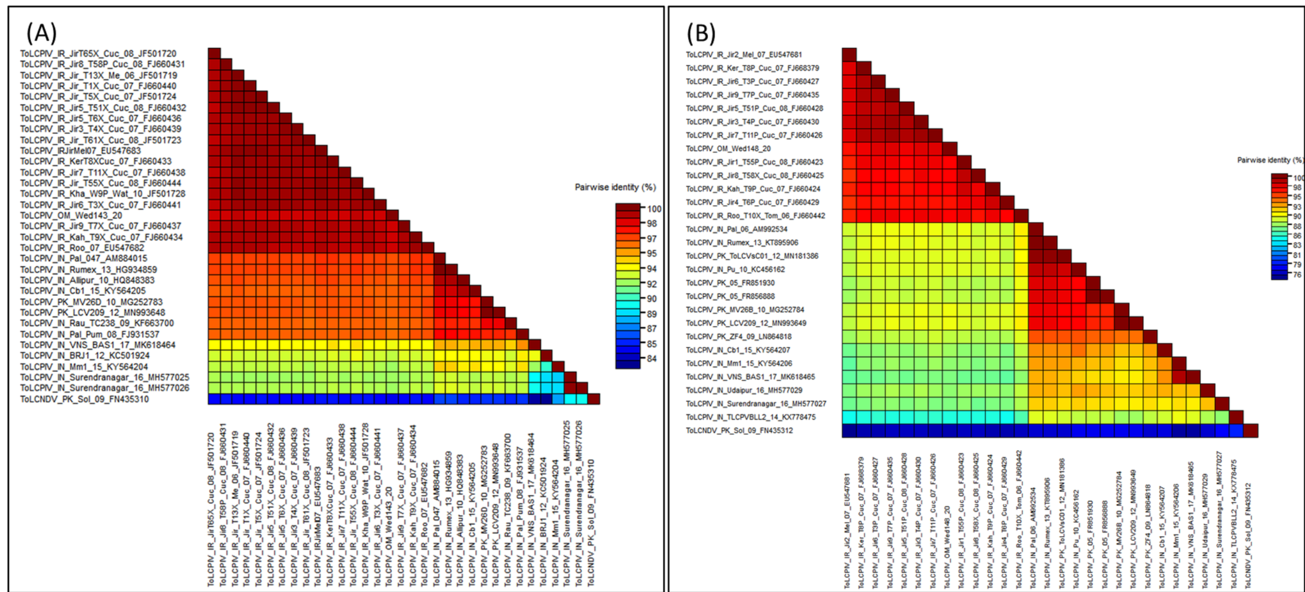


**Fig. 2** Pairwise sequence analysis using sequence demarcation tool (SDT V1.2), DNA-A (**A**) and DNA-B (**B**)

Sharma et al. 2019). Two betasatellites, tomato leaf curl betasatellite (ToLCB), frequently associated with all Begomoviruses and okra leaf curl betasatellite (OLCB), so far only associated with cotton leaf curl Gezira virus (CLCGeV) reported in Oman) (Akhtar et al. 2014; Shafiq et al. 2021), the fear is that ToLCPalV could interact with either of these betasatellites and develop a virus complex that will not only extend its host range but also have a strong synergistic effect on Oman agricultural crop production.

The geographical clustering reflected that the wed14-3 and Iran isolates were evolved at similar time and are closer to each other to that which has been reported from India and Pakistan. Furthermore, the highest nt identity and close clustering of Oman isolates with Iran isolates reflects that the introduction of ToLCPalV into Khasab happened quite recently, possibly through agriculture trade between both countries. Since, Iran is very close to the Khasab, and has a close relation for trade between both sides of the countries. There is possibility that ToLCPalV transfer to Oman via trade of infected materials (vegetables, ornamental or fruit plants) or might be somehow infected whitefly vector could transport to this area, nevertheless, such opinions need to be verified at genome level.

Oman has not been extensively surveyed for the presence of Begomoviruses. Some Begomoviruses including chilli leaf curl virus, CLCGeV, squash leaf curl virus, mungbean yellow mosaic virus, tomato yellow leaf curl virus and watermelon leaf curl virus have been identified there (Khan et al. 2012, 2013, 2014; Al Shihi et al. 2018; Shahid et al. 2019, 2020), but this known diversity does not match the diversity of Begomoviruses identified in India, Pakistan and Iran. The amplification here of an earlier undiscovered bipartite Begomovirus supports the idea that there is a far greater diversity of Begomoviruses yet to be known in the Arabian Peninsula.

This is the first identification of a bipartite Begomovirus ToLCPalV from ornamental *C. melo* in Oman. The host-switching of a tomato infecting Begomovirus may possibly increase host range of this virus in the Sultanate of Oman. Nevertheless, this is too early to conclude and requires an extensive exploration to discover the virus epidemiology and host range. However, due to limited agricultural land in the Sultanate of Oman intercropping of different crops particularly tomato (a natural host for ToLCPalV) is a routine in the farmer's fields, the fear is that the whitefly vector may transmit the virus to the tomato plants. To prevent very likely outbreak of ToLCPalV epidemics in tomato fields, therefore, the removal of *C. melo* plants form fields and development resistant cultivars and other sustainable and eco-friendly components of integrated pest management are recommended. Further studies will be essential to determine the geographic distribution of ToLCPalV and the significance of this virus to Oman agricultural crops production.

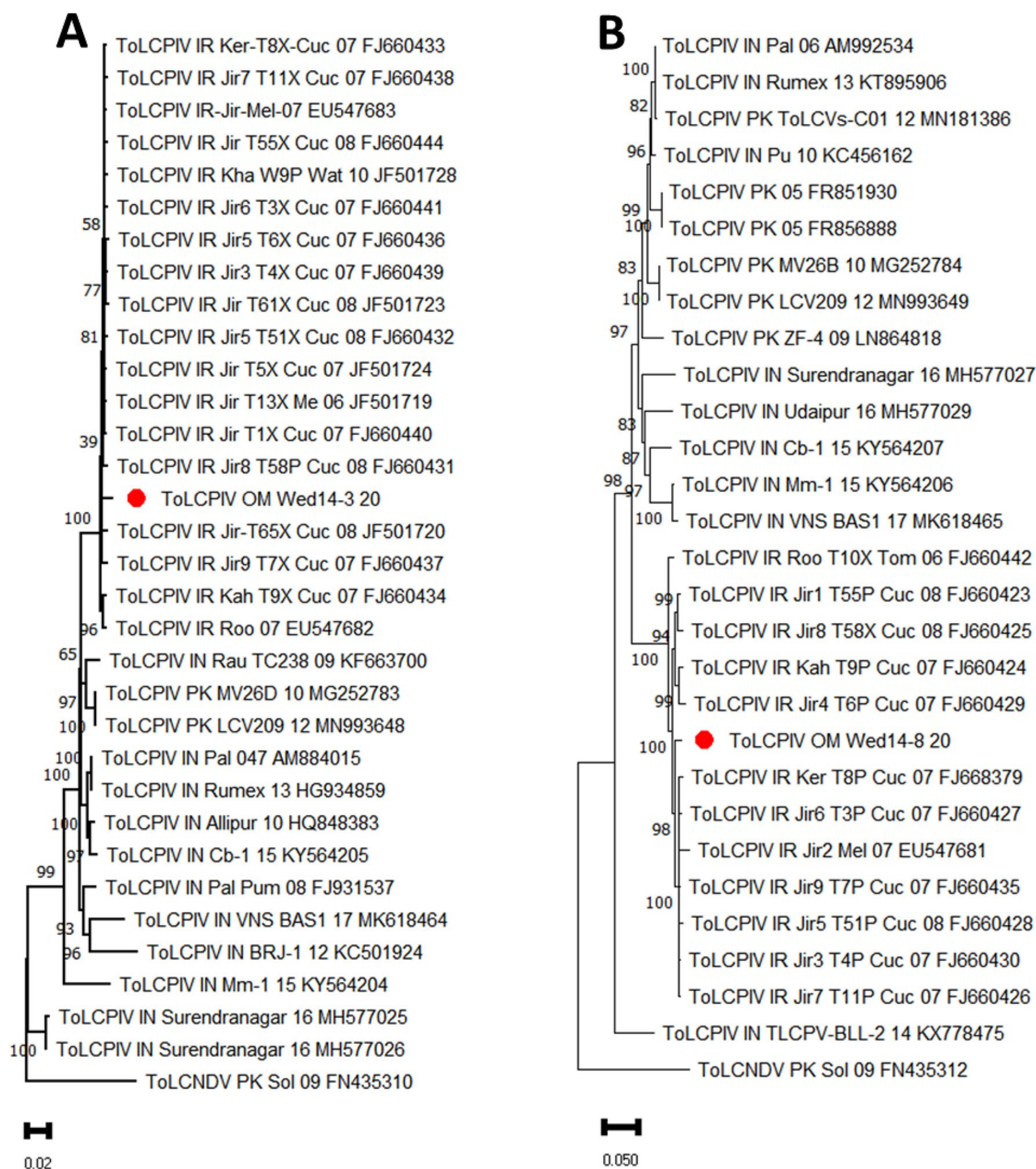


**Fig. 3** Phylogenetic dendrograms based on complete nucleotide sequences of DNA-A (**A**) and DNA-B (**B**) genome components. To calculate mutation distances, vertical and horizontal branches are arbitrary and proportional, respectively. Both trees were arbitrarily rooted on the sequence of tomato leaf curl New Dehli virus DNA-A and DNA-B, respectively

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1007/s42360-022-00573-x.

**Acknowledgements** The author is grateful to Sultan Qaboos University for financial support under IG/AGR/CROP/20/02 project.

**Data availability** Tha data related to this article is available on request from the author.

## Declarations

**Conflict of interest** None to declare.

**Ethical approval** This study does not involve any human/animals related activities by any of the authors.

## References

Akhtar S, Khan AJ, Singh AS, Briddon RW (2014) Identification of a disease complex involving a novel monopartite begomovirus with beta-and alphasatellites associated with okra leaf curl disease in Oman. Arch Virol 159:1199–1205

Al Shihi AA, Al Sadi AM, Deadman M, Briddon RW, Shahid MS (2018) Identification of a distinct strain of Cotton leaf curl Gezira virus infecting tomato in Oman. J Phytopathol 166:199–205
Ali I, Malik AH, Mansoor S (2010) First report of tomato leaf curl Palampur virus on bitter gourd in Pakistan. Plant Dis 94:276
Al-Mabsli SS, Al-Wahaibi AK, Al-Sadi AM, Shahid MS (2021) Association of a monopartite begomovirus and associated betasatellite with yellow vein disease of a weed host Senna Italica Mill in Oman. Virusdisease 32:378–380
Dhkal M, Sharma A, Kaur G (2020) First report of tomato leaf curl Palampur virus infecting muskmelon in India. J Plant Pathol 102:1367
Doyle J (1991) DNA protocols for plants. Molecular techniques in taxonomy. Springer, Berlin, pp 283–293
Esmaeili M, Heydarnejad J, Massumi H, Varsani A (2015) Analysis of watermelon chlorotic stunt virus and tomato leaf curl Palampur virus mixed and pseudo-recombination infections. Virus Genes 51:408–416
Fondong VN (2013) Geminivirus protein structure and function. Mol Plant Pathol 14(6):635–649
Hanamasagar Y, Naganur P, Shankarappa KS, Venkataravanappa V, Lakshminarayana Reddy CN (2021) Characterization of Tomato leaf curl Palampur virus associated with leaf curl and yellowing disease of watermelon from India. Indian Phytopathol 74:1075–1088
Heydarnejad J, Mozaffari A, Massumi H, Fazeli R, Gray AJA, Meredith S, Lakay F, Shepherd DN, Martin DP, Varsani A (2009) Complete sequences of tomato leaf curl Palampur virus isolates infecting cucurbits in Iran. Arch Virol 154:1015–1018
Heydarnejad J, Hesari M, Massumi H, Varsani A (2013) Incidence and natural hosts of Tomato leaf curl Palampur virus in Iran. Australas Plant Pathol 42:195–203
Jaiswal N, Saritha RK, Datta D, Singh M, Dubey RS, Rai AB, Rai M (2012) Mixed infections of begomoviruses in pumpkins with yellow vein mosaic disease in North India. Arch Phytopathol Plant Protect 45:938–941
Khan AJ, Akhtar S, Briddon RW, Ammara U, Al-Matrooshi AM, Mansoor S (2012) Complete nucleotide sequence of watermelon chlorotic stunt virus originating from Oman. Viruses 4:1169–1181
Khan AJ, Akhtar S, Al-Matrushi AM, Fauquet CM, Briddon RW (2013) Introduction of East African cassava mosaic Zanzibar virus to Oman harks back to "Zanzibar, the capital of Oman." Virus Genes 46:195–198
Khan AJ, Akhtar S, Singh AK, Al-Shehi AA, Al-Matrushi AM, Ammara U, Briddon RW (2014) Recent evolution of a novel begomovirus causing tomato leaf curl disease in the Al-Batinah region of Oman. Arch Virol 159:445–455
Khanna S, Rana S, Singh J, Goyal M, Kumar P, Singh N, Pant RP, Baranwal VK (2019) First report of association of begomovirus in yellow mosaic disease of bur cucumber in India. Indian Phytopathol 72:181–184
Kumar Y, Hallan V, Zaidi AA (2008) Molecular characterization of a distinct bipartite begomovirus species infecting tomato in India. Virus Genes 37:425–431
Kumar Y, Hallan V, Zaidi AA (2011) Chilli leaf curl Palampur virus is a distinct begomovirus species associated with a betasatellite. Plant Pathol 60:1040–1047
Martin DP, Murrell B, Golden M, Khoosal A, Muhire B (2015) RDP4: detection and analysis of recombination patterns in virus genomes. Virus Evol. https://doi.org/10.1093/ve/vev003
Mohammed D, Adhab M, Al-Kuwaiti N (2021) Molecular characterization of viruses associated to leaf curl disease complex on zucchini squash in iraq reveals deng primer set could distinguish between new and old world begomoviruses. Anais Acad Bras Cienc. https://doi.org/10.1590/0001-3765202120210050
Mubin M, Shahid MS, Tahir MN, Briddon RW, Mansoor S (2010) Characterization of begomovirus components from a weed suggests that begomoviruses may associate with multiple distinct DNA satellites. Virus Genes 40:452–457
Namrata J, Saritha RK, Datta D, Singh M, Dubey RS, Rai AB, Rai M (2010) Molecular characterization of tomato leaf curl palampur virus and pepper leaf curl betasatellite naturally infecting pumpkin (Cucurbita moschata) in India. Indian J Virol 21:128–132
Rojas MR, Hagen C, Lucas WJ, Gilbertson RL (2005) Exploiting chinks in the plant's armor: evolution and emergence of geminiviruses. Annu Rev Phytopathol 43:361–394
Shafiq M, Ahmad M, Nisar A, Manzoor MT, Abid A, Mushtaq S, Riaz A, Ilyas M, Sarwar W, Nawaz-Ul-Rehman MS, Haider S, Younus A, Mubin M (2019) Molecular characterization and phylogenetic analysis of tomato leaf curl Palampur virus, a bipartite begomovirus, associated with Cucumis sativus L. in Pakistan. 3 Biotech 9:204
Shafiq M, Sattar MN, Shahid MS, Al-Sadi AM, Briddon RW (2021) Interaction of watermelon chlorotic stunt virus with satellites. Australas Plant Pathol 50:117–128
Shahid MS, Shafiq M, Ilyas M, Raza A, Al-Sadrani MN, Al-Sadi AM, Briddon RW (2019) Frequent occurrence of Mungbean yellow mosaic India virus in tomato leaf curl disease affected tomato in Oman. Sci Rep 9:16634
Shahid M, Al-Sulaimani H, Al-Sadi A (2020) Squash leaf curl virus: a new world bipartite Begomovirus threatening squash production in Oman. Plant Dis 104:2533–2533
Sharma D, Kulshreshtha A, Roshan P, Hallan V (2019) Molecular characterization and infectivity analysis of a bipartite begomovirus associated with cotton leaf curl Multan betasatellite naturally infecting Rumex nepalensis in northern India. J Plant Pathol 101:935–941
Tiwari AK, Snehi SK, Singh R, Raj SK, Rao GP, Sharma PK (2012) Molecular identification and genetic diversity among six Begomovirus isolates affecting cultivation of cucurbitaceous crops in Uttar Pradesh, India. Arch Phytopathol Plant Protect 45:62–72
Venkataravanappa V, Ashwathappa KV, Reddy CNL, Shankarappa KS, Reddy MK (2020) Characterization of tomato leaf curl New Delhi virus associated with leaf curl and yellowing disease of watermelon and development of LAMP assay for its detection. 3 Biotech 10:1–2
Walker PJ, Siddell SG, Lefkowitz EJ, Mushegian AR, Adriaenssens EM, Alfenas-Zerbini P, Davison AJ, Dempsey DM, Dutilh BE, García ML, Harrach B, Harrison RL, Hendrickson RC, Junglen S, Knowles NJ, Krupovic M, Kuhn JH, Lambert AJ, Łobocka M, Nibert ML, Oksanen HM, Orton RJ, Robertson DL, Rubino L, Sabanadzovic S, Simmonds P, Smith DB, Suzuki N, Van Doorslaer K, Vandamme A-M, Varsani A, Zerbini FM (2021) Changes to virus taxonomy and to the international code of virus classification and nomenclature ratified by the international committee on taxonomy of viruses (2021). Arch Virol 166:2633–2648
Wyatt S, Brown J (1996) Detection of subgroup III geminivirus isolates in leaf extracts by degenerate primers and polymerase chain reaction. Phytopathology 86:1288–1293

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.