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RESEARCH PAPER

Metatranscriptomic analysis reveals two new viruses and highly expressed endogenous elements in pepper in Iraq

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ABSTRACT

Pepper plants exhibiting severe leaf curling and deformation in open fields in Iraq were investigated to characterize their associated virome using metatranscriptomic sequencing. High-throughput sequencing (HTS) revealed the presence of bell pepper alphaendornavirus (BPEV) and pepper cryptic virus 2 (PCV-2), together with fragmented sequences related to tobacco vein clearing virus (TVCV). A nearly complete genome of the Iraqi BPEV isolate (14,700 bp) and both genomic segments of PCV-2 (1,623 bp and 1,513 bp) were assembled and deposited in GenBank. Phylogenetic analysis showed that the BPEV isolate clustered closely with isolates from South Korea, Jamaica, and the Dominican Republic, whereas both PCV-2 genomic segments were most closely related to Turkish isolates, indicating high genetic conservation among geographically distant populations. In addition, transcriptome mapping revealed abundant expression of ten endogenous pararetroviral elements integrated within the pepper genome, with most transcripts corresponding to reverse transcriptase (RT-LTR) and RNase H domains. This study represents the first comprehensive metatranscriptomic characterization of the pepper virome in Iraq, documenting the first detection of BPEV and PCV-2 in the country while revealing extensive expression of endogenous viral elements. These findings expand current knowledge of pepper-associated viruses in the Middle East and demonstrate the value of metatranscriptomic sequencing for detecting both exogenous viruses and endogenous viral components.

Keywords: Bell pepper alphaendornavirus, endogenous pararetroviruses, metatranscriptomics, pepper cryptic virus 2, virome

INTRODUCTION

Pepper is a fruiting plant belonging to the genus Capsicum and the family *Solanaceae* (nightshades). It is one of the world's most important vegetable crops but is susceptible to nearly 70 viruses belonging to diverse taxonomic groups (Arogundade et al., 2020). Recent advances in high-throughput sequencing (HTS), particularly metatranscriptomic approaches, have revolutionized plant virology by enabling the simultaneous detection of known viruses, discovery of novel viruses, characterization of complete plant viromes, and analysis of viral diversity without prior knowledge of the infecting agents (Hadidi et al., 2016; Villamor et al., 2019). Metatranscriptomic sequencing has become particularly valuable for discovering previously uncharacterized viruses and expanding knowledge of plant viromes in regions where virus diversity remains poorly documented. Consequently, HTS has become an indispensable tool for virus surveillance, diagnostics, epidemiological studies, and the identification of emerging plant viruses (Hadidi et al., 2016; Villamor et al., 2019).

Among the persistent viruses infecting pepper, bell pepper alphaendornavirus (*Alphaendornavirus capsici*; family *Endornaviridae*) is a capsidless double-stranded RNA virus transmitted vertically through seeds and pollen. Endornaviruses generally establish persistent infections, occur at low copy numbers, and do not induce obvious disease symptoms (Roossinck et al., 2011; Escalante & Valverde, 2024). Bell pepper alphaendornavirus was first recognized as large double-stranded RNA molecules in *C. annuum* and was subsequently classified within the family *Endornaviridae* based on molecular and phylogenetic evidence (Valverde et al., 1990; Valverde & Gutiérrez, 2007).

Another group of persistent viruses associated with pepper belongs to the family *Partitiviridae*, including pepper cryptic virus 2 (PCV-2). Members of this family possess bipartite or multipartite double-stranded RNA genomes encapsidated in separate virus particles and are transmitted primarily through seeds and pollen (Nibert et al., 2014; Zhang et al., 2023). Pepper cryptic virus 2 has been reported in the United States, China, India, Turkey, and Slovakia (Sabanadzovic & Valverde, 2011; Sun et al., 2017; Tomašechová et al.,

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2020; Paslay & Ali, 2025), indicating its widespread distribution in pepper-growing regions.

In addition to exogenous viruses, pepper genomes harbor abundant endogenous pararetrovirus sequences (EPRVs), which originated from ancient integrations of pararetroviral genomes into the host genome. Although many EPRVs remain transcriptionally silent, some may become activated under environmental or genomic stress and potentially influence host physiology, antiviral defense, or virus evolution (Matzke et al., 2004).

Despite the economic importance of pepper cultivation in Iraq, information regarding the pepper virome remains extremely limited. To date, tobacco mosaic virus is the only virus reported infecting pepper in the country (Adhab et al., 2021), and no comprehensive metatranscriptomic survey has been conducted. Because HTS enables the unbiased detection of both known and previously undescribed viruses, as well as endogenous viral elements, it provides an ideal approach for comprehensive characterization of the pepper virome (Hadidi et al., 2016; Villamor et al., 2019). Therefore, this study employed metatranscriptomic analysis to identify viruses associated with pepper in Iraq, characterize their genomic features, and investigate the expression of endogenous pararetroviral elements.

MATERIALS AND METHODS

Research Site. This research was conducted at the Molecular biology Laboratory, Faculty of Agriculture, University of Kufa, Najaf-Iraq, from February to December 2023.

Sample Collection. Leaf samples were collected from open-field pepper (*Capsicum annuum* cv. California Wonder) plants in the Abbasiya district, Najaf Province, Iraq, between 15 April and 15 May 2023. Ten symptomatic leaf samples showing mosaic, leaf distortion, and stunting were collected, placed individually in sterile plastic bags, and transported on ice to the Molecular Plant Virus Laboratory, Department of Plant Protection, Faculty of Agriculture, University of Kufa, for further analyses.

Sap Inoculation. Leaf tissues from symptomatic plants were homogenized in sterile phosphate buffer (0.01 M, pH 7.0) at a ratio of 1:2 (w/v). The homogenate was filtered through double-layer cheesecloth and stored at −20 ºC until use. Mechanical inoculation was performed by injecting the crude sap into the midrib of healthy pepper (*C. annuum* cv. California Wonder) leaves using a sterile syringe and needle. Plants inoculated with sterile distilled water served as negative controls. Inoculated plants were maintained under greenhouse conditions and monitored regularly for symptom development.

RNA Extraction. Total RNA was extracted from a symptomatic leaf sample using the RNeasy Plant Mini Kit (Qiagen, Hilden, Germany) according to the manufacturer's instructions. Briefly, approximately 0.5 × 0.5 cm of infected leaf tissue was excised, placed in an RNAlater® solution (Thermo Fisher Scientific), and shipped to JS-Link Co., Republic of Korea, for RNA extraction and sequencing. RNA quality and concentration were evaluated using a NanoDrop spectrophotometer and an Agilent 2100 Bioanalyzer before library preparation.

Metatranscriptomic Analysis. RNA sequencing libraries were prepared using the TruSeq Total RNA Library Preparation Kit (Illumina, San Diego, CA, USA) following the manufacturer's protocol. Library quality was assessed using an Agilent 2100 Bioanalyzer prior to paired-end sequencing (2 × 101 bp) on an Illumina NovaSeq 6000 platform. The raw sequencing data were deposited in the NCBI Sequence Read Archive (SRA) under accession number SRR21032823 (Figure 1). Ribosomal RNA sequences were computationally removed during the bioinformatic analysis by mapping sequence reads to reference rRNA databases.

Mapping Analysis and Virus Identification. Raw sequence reads were analyzed using Geneious Prime v11 (Kearse et al., 2012). Reads were initially mapped at low-to-medium sensitivity against reference genomes of 30 viruses previously reported to infect pepper. Consensus sequences were generated from assembled reads. Subsequently, all RNA-seq reads were compared with viral sequences available in GenBank (5,040 reference sequences comprising 76,145,671 nucleotides) to identify both known and previously undescribed viruses.

To investigate endogenous viral elements, RNA-seq reads were also mapped against previously reported endogenous pararetrovirus (EPRV) sequences from pepper (Caulimovirus-1_CAn, Caulimovirus-2_CAn, Caulimovirus-2B_CAn, Caulimovirus-3_CAn, Caulimovirus-4_CAn, Caulimovirus-4B_CAn, and Caulimovirus-5_CAn), the tomato endogenous pararetrovirus LycEPRV, and two eggplant EPRVs (Caulimovirus-SMe and SmelV) obtained from the

Repbase database (Jurka et al., 2005). Relative copy numbers were estimated as the product of assembled read numbers and read length divided by the corresponding reference sequence length (Mustafa et al., 2018).

Phylogenetic Analysis. Phylogenetic analyses were performed using MEGA version 11 (Tamura et al., 2021). Viral nucleotide sequences obtained in this study and representative sequences retrieved from GenBank were aligned using the ClustalW algorithm implemented in Geneious Prime v11 (Kearse et al., 2012; http://www.geneious.com). Phylogenetic trees were reconstructed using the Neighbor-Joining method under the General Time Reversible (GTR) substitution model. Tree robustness was evaluated using Bayesian inference implemented in MrBayes version 3.2.6 (Huelsenbeck & Ronquist, 2001). *Capsicum frutescens* endornavirus 1 isolate LA-C (GenBank accession MT013202) was used as the outgroup for bell pepper alphaendornavirus analyses, whereas vitis cryptic virus 2 served as the outgroup for phylogenetic analyses of pepper cryptic virus 2.

RESULTS AND DISCUSSION

Metatranscriptomic Analysis. Sap extracted from symptomatic pepper leaves induced severe leaf curling and deformation following mechanical inoculation onto healthy pepper plants, confirming the infectious nature of the causal agents (Figure 1). Total RNA extracted from symptomatic leaves had a concentration of 68.6 ng/µL, an A260/A280 ratio of 2.0, and an RNA Integrity Number (RIN) of 2.9. Despite the relatively low RIN value, high-throughput sequencing (HTS) generated 55,353,498 high-quality paired-end reads, demonstrating that metatranscriptomic sequencing remained suitable for comprehensive virus detection.

Mapping of the sequencing reads against reference viral genomes identified three major viral components. The highest number of assembled reads (1,359,356) corresponded to bell pepper alphaendornavirus (BPEV), from which a nearly complete genome of 14,700 nt was reconstructed and deposited in GenBank under accession number OR589768. The genome contains a single open reading frame encoding a large polyprotein with conserved methyltransferase (MTR), RNA helicase (Hel-1), UDP-glucose glycosyltransferase (UGT), and RNA-dependent RNA polymerase (RdRp) domains (Figure 2A). Pairwise comparison revealed 99.8% nucleotide identity with the Jamaica-Clarendon isolate (ON260927).

Two genomic segments of pepper cryptic virus 2 (PCV-2) were also detected. RNA1 (1,623 nt; accession OR589769) contained the RdRp coding region and showed 99.9% nucleotide identity with the Turkish isolate (LC325817), whereas RNA2 (1,513 nt; accession OR589770) encoded the putative coat protein and exhibited 100% identity with the Turkish isolate (LC325818) (Figure 2B). Detection of both genomic segments confirms the presence of a complete PCV-2 genome rather than fragmented viral RNA, indicating active maintenance of this persistent virus in the infected pepper plants.

In addition, fragmented sequences of tobacco vein clearing virus (TVCV) were detected, with 206,727 assembled reads covering approximately

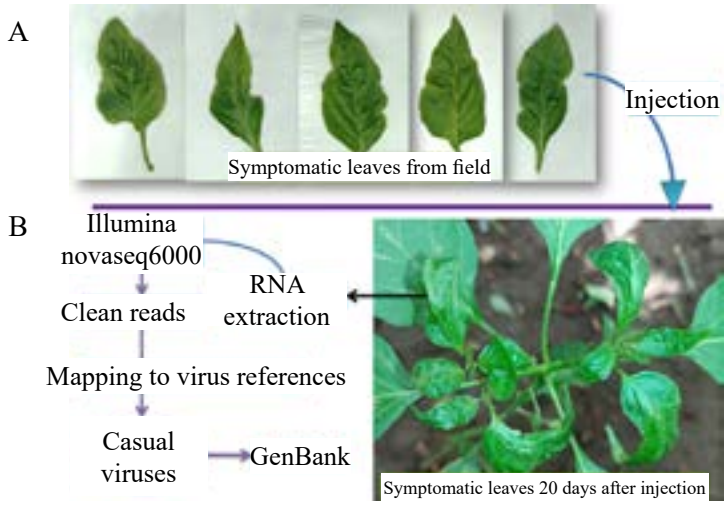

Figure 1. Symptoms observed on pepper leaves. A. Severe leaf curling and deformation in naturally infected pepper plants. B. Representative symptomatic leaf selected for RNA sequencing and metatranscriptomic analysis.

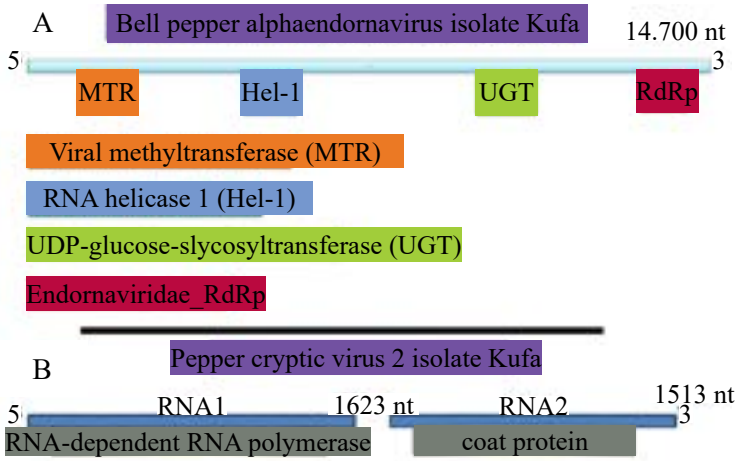

Figure 2. Genome organization of the viruses identified by metatranscriptomic sequencing. A.Genome organization of bell pepper alphaendornavirus (BPEV) isolate Kufa showing the conserved methyltransferase (MTR), RNA helicase (Hel-1), UDP-glucose glycosyltransferase (UGT), and RNA-dependent RNA polymerase (RdRp) domains. B. Genome organization of pepper cryptic virus 2 (PCV-2) isolate Kufa, consisting of two genomic segments: RNA1 encoding the RNA-dependent RNA polymerase (RdRp) and RNA2 encoding the putative coat protein (CP).

44.4% of the reference genome and exhibiting 96.4% nucleotide identity. Most reads mapped to genomic regions encoding the protease, peptidase A3, reverse transcriptase (RT-LTR), and RNase H domains. Because only partial genome coverage was obtained, the biological significance of TVCV in symptom development remains uncertain and requires confirmation using virus-specific molecular assays.

Phylogenetic Analysis. Phylogenetic analysis confirmed the taxonomic identity of the detected viruses. The Iraqi bell pepper alphaendornavirus (BPEV) isolate clustered closely with isolates from the Dominican Republic (KX525267), South Korea (ON759517), Jamaica, and the United States, sharing more than 99.9% nucleotide identity with these isolates (Figure 3). Similar phylogenetic relationships have also been reported between bell pepper alphaendornavirus and winged bean endornavirus 1 (WBEV-1), suggesting that endornaviruses infecting solanaceous and leguminous hosts share a common evolutionary origin within the family *Endornaviridae* (Okada et al., 2017). The high level of sequence conservation observed among geographically distant isolates is consistent with the biology of endornaviruses, which are transmitted predominantly through seeds and pollen, thereby limiting opportunities for horizontal transmission and rapid genetic diversification (Roossinck et al., 2011; Escalante & Valverde, 2024).

Similarly, both genomic segments of pepper cryptic virus 2 (PCV-2) clustered closely with Turkish isolates (Figures 4 and 5), suggesting either a common ancestral origin or the movement of infected pepper germplasm among neighboring regions. Comparable genetic conservation has been reported for PCV-2 isolates from geographically distant countries, reflecting the predominantly vertical transmission and long-term evolutionary stability of members of the family *Partitiviridae* (Sabanadzovic & Valverde, 2011; Paslay & Ali, 2025).

Expression of Endogenous Pararetroviral Elements (EPRVs). Because bell pepper alphaendornavirus is a persistent virus that is vertically transmitted and generally establishes symptomless infections (Escalante & Valverde, 2024; Paudel et al., 2024), we further investigated whether endogenous viral elements were transcriptionally active in the infected pepper plants.

Mapping analysis revealed abundant transcription of endogenous pararetroviral elements (EPRVs) integrated within the pepper genome. Among the detected elements, Caulimovirus-4B_CAn exhibited the highest number of mapped reads, whereas Caulimovirus-2_CAn showed the lowest abundance. Complete genome coverage was obtained for Caulimovirus-3_CAn, while Caulimovirus-5_CAn shared 100% nucleotide identity with its reference sequence. In contrast, LycEPRV, Caulimovirus-SMe, and SmelV were only partially represented despite exhibiting high nucleotide identities. Most expressed regions corresponded to the reverse transcriptase (RT-LTR) and RNase H domains, whereas movement protein transcripts were additionally detected in

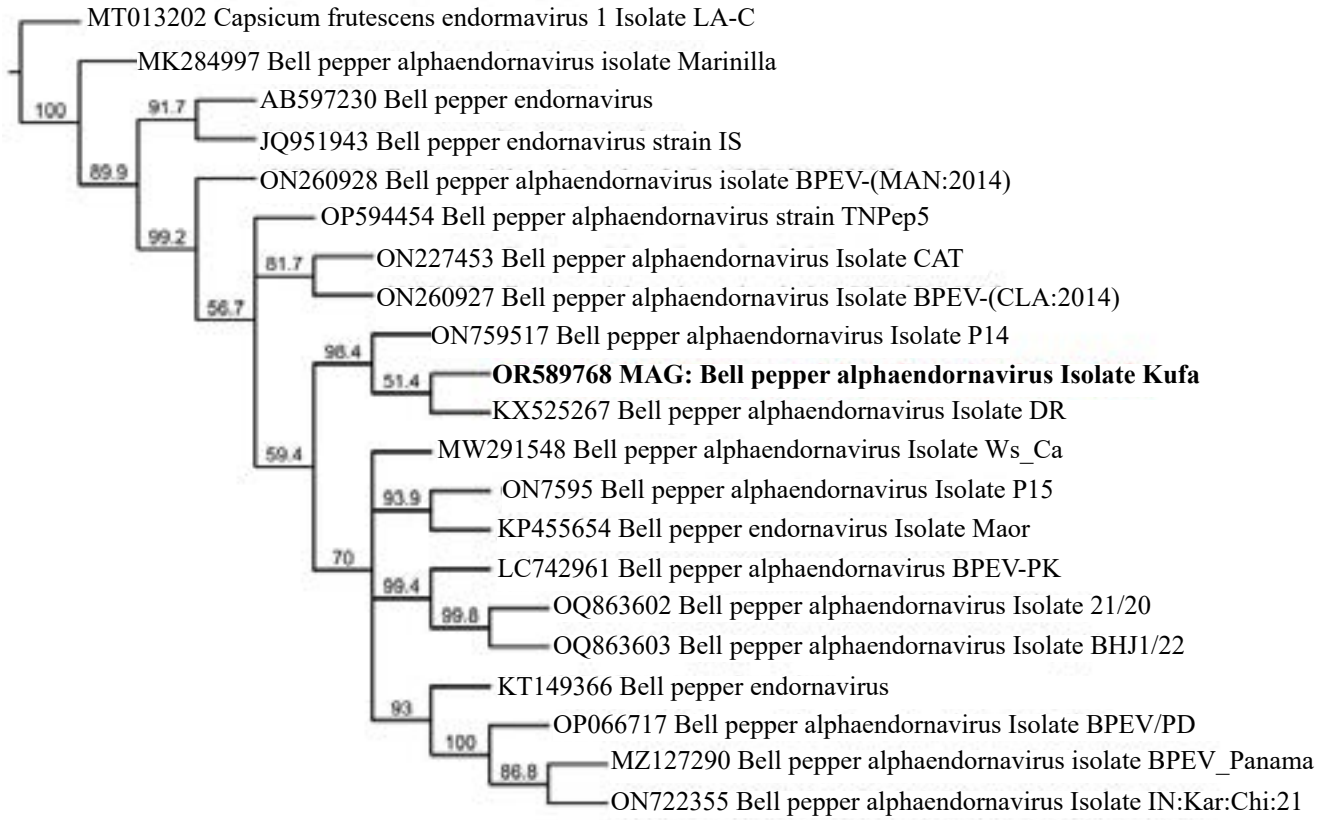

Figure 3. Neighbor-joining phylogenetic tree of bell pepper alphaendornavirus (BPEV) isolate Kufa inferred from complete genome sequences of 19 representative *Bell pepper alphaendornavirus* isolates retrieved from the GenBank database. *Capsicum frutescens* endornavirus 1 isolate LA-C (GenBank accession no. MT013202) was used as the outgroup.

Caulimovirus-1_CAn and Caulimovirus-2B_CAn (Table 1).

Although endogenous pararetroviral elements are generally regarded as transcriptionally inactive genomic relics, increasing evidence indicates that they may become transcriptionally activated under biotic or abiotic stress conditions. The extensive expression observed in the present study may therefore reflect host responses to mixed viral infections rather than active replication of endogenous viruses. Interestingly, previous studies conducted in Iraq reported relatively low transcriptional activity of endogenous viral elements in eggplant, fig, and alfalfa (Alisawi, 2019; Khaffajah et al., 2022; Al-Kaeath et al., 2024; Ali et al., 2024). In contrast, the abundant expression detected in pepper suggests that transcriptional activation of EPRVs may vary considerably among host species and could be influenced by host genetic background, viral co-infections, or environmental conditions. Whether these expressed endogenous viral elements contribute to antiviral defense, genome regulation, or symptom development remains unclear and warrants further investigation.

Biological Significance of the Pepper Virome. The metatranscriptomic approach revealed that symptomatic pepper plants in Iraq harbor a considerably more complex virome than previously recognized. The successful recovery of nearly complete viral genomes demonstrates the high sensitivity of HTS for detecting persistent viruses directly from infected tissues. Unlike conventional PCR-based diagnostics, which require prior knowledge of the target virus, metatranscriptomic sequencing enables the simultaneous detection of known viruses, novel viruses, and endogenous viral elements, making it a powerful tool for comprehensive plant virus surveillance and virome characterization (Hadidi et al., 2016; Villamor et al., 2019).

This study represents the first comprehensive metatranscriptomic characterization of the pepper virome in Iraq. The simultaneous detection of bell pepper alphaendornavirus (BPEV), pepper cryptic virus 2 (PCV-2), fragmented tobacco vein clearing virus sequences, and actively expressed endogenous pararetroviral elements demonstrates that symptomatic pepper plants harbor a considerably more complex viral community than previously recognized.

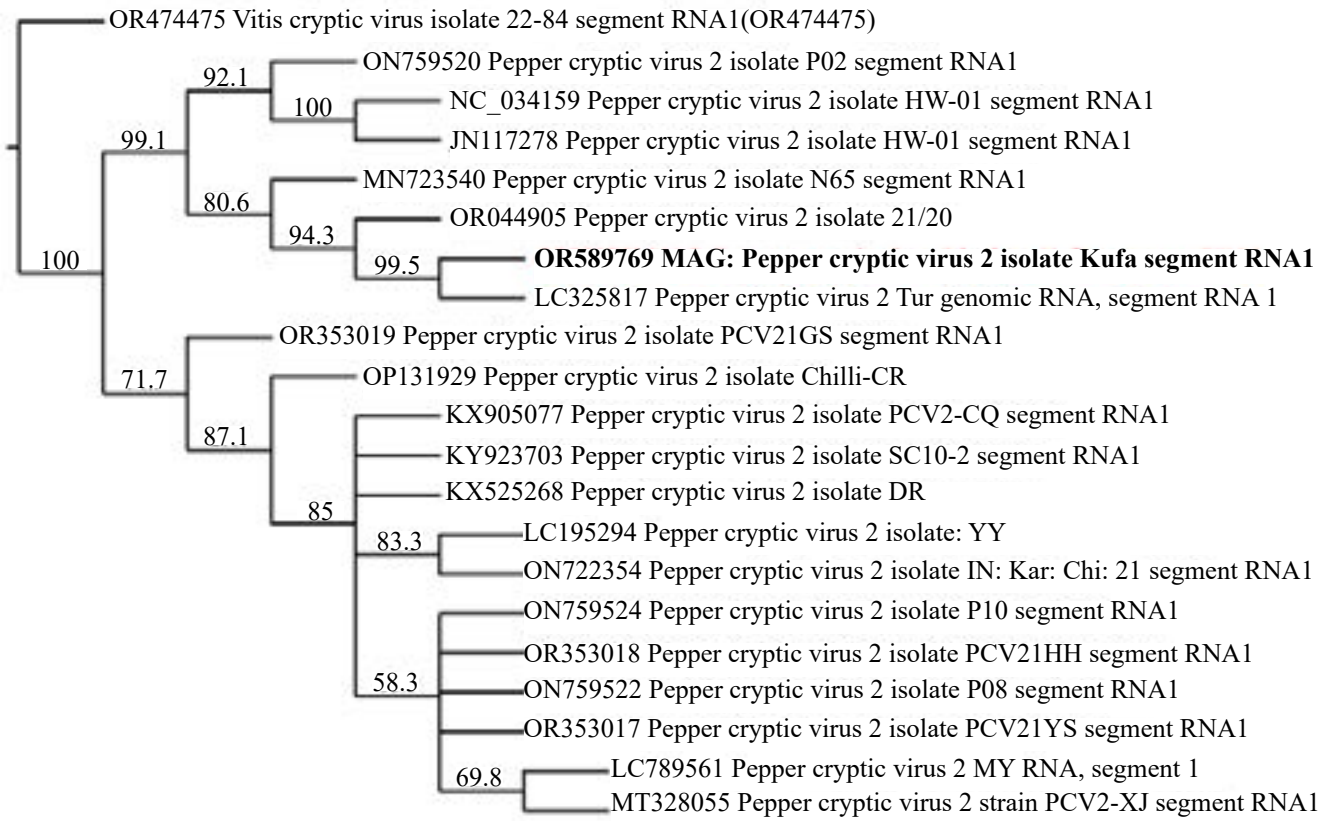

Figure 4. Neighbor-joining phylogenetic tree of pepper cryptic virus 2 (PCV-2) RNA1 inferred from complete RNA1 genome sequences of 19 representative PCV-2 isolates retrieved from the GenBank database. vitis cryptic virus isolate 22-84 RNA1 (GenBank accession no. OR474475) was used as the outgroup.

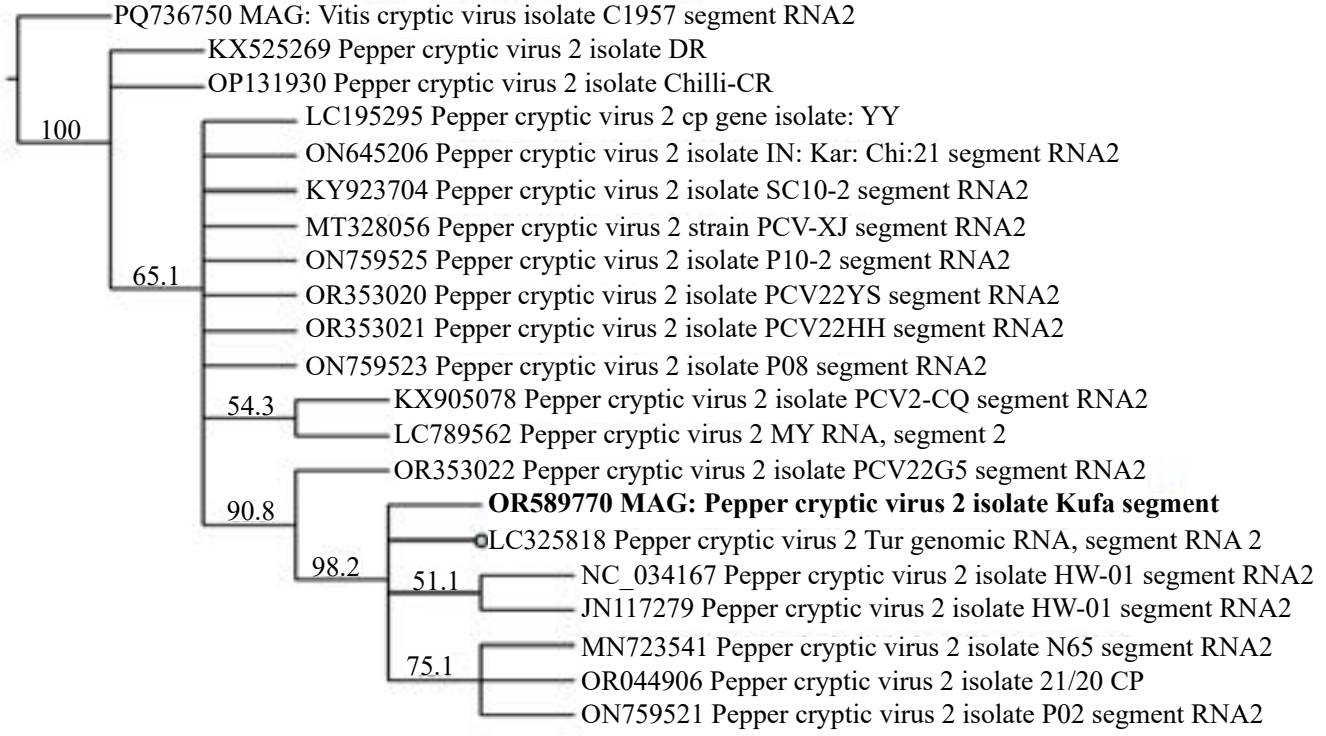

Figure 5. Neighbor-joining phylogenetic tree of pepper cryptic virus 2 (PCV-2) RNA2 inferred from complete RNA2 genome sequences of 19 representative PCV-2 isolates retrieved from the GenBank database. vitis cryptic virus isolate C1957 RNA2 (GenBank accession no. PQ736750) was used as the outgroup.

Table 1. Expression of endogenous pararetroviral elements (EPRVs) detected in pepper, showing assembled reads, genome coverage, pairwise nucleotide identity, and major expressed protein domains

EPRV	Assembled reads	Coverage (%)	Pairwise identity (%)	Major expressed protein domains
Caulimovirus-1_CAn	474,699	95.6	92.9	MP, RT_LTR, RNase_HI_RT_Ty3
Caulimovirus-2_CAn	48,209	75.1	90.6	RNase_HI_RT_Ty3, RT_RNaseH
Caulimovirus-2B_CAn	48,957	67.5	89.9	MP, RT_LTR, RNase_HI_RT_Ty3
Caulimovirus-3_CAn	184,872	100	97.8	retropepsin_like, RT_LTR, RNase_HI_RT_Ty3
Caulimovirus-4_CAn	1,088,515	97.0	89.0	RT_LTR, RNase_HI_RT_Ty3
Caulimovirus-4B_CAn	1,774,356	90.6	99.7	RT_LTR, RNase_HI_RT_Ty3
Caulimovirus-5_CAn	555,592	91.6	100	RT_LTR, RNase_HI_RT_Ty3
LycEPRV	204,048	43.7	96.3	RT_LTR, RNase_HI_RT_Ty3
Caulimovirus-SMe	11,030	29.6	92.6	RT_LTR, RNase_HI_RT_Ty3
SmelV	58,865	38.8	92.0	RT_LTR, RNase_HI_RT_Ty3

Bell pepper alphaendornavirus has previously been reported from the United States, Jamaica, South Korea, Slovakia, China, and several other pepper-producing countries (Tomašechová et al., 2019; Zhang et al., 2020; Jo et al., 2022). Although traditionally regarded as a symptomless persistent virus, increasing evidence indicates that endornaviruses can influence host gene expression, redox metabolism, and responses to both biotic and abiotic stresses (Escalante & Valverde, 2024). Comparative studies using near-isogenic pepper lines further demonstrated that BPEV infection reduced fruit weight and dry matter accumulation, suggesting that persistent viruses may subtly affect plant performance despite the absence of conspicuous disease symptoms.

Consistent with the findings for BPEV, pepper cryptic virus 2 has also been reported from the United States, China, India, Turkey, Slovakia, and Poland (Sabanadzovic & Valverde, 2011; Sun et al., 2017; Tomašechová et al., 2020; Minicka et al., 2024; Paslay & Ali, 2025). Members of the family Partitiviridae are likewise persistent viruses that are transmitted predominantly through seeds and pollen, which explains their remarkable genetic conservation and widespread occurrence in cultivated pepper germplasm.

One of the most important findings of the present study is the demonstration of a complex viral community within symptomatic pepper plants. The simultaneous presence of BPEV, PCV-2, fragmented TVCV sequences, and transcriptionally active endogenous viral elements indicates that symptom development cannot be confidently attributed to a single virus. Instead, the observed leaf curling and deformation are more likely to result from complex virus–virus and virus–host interactions. Mixed viral infections are known to alter virus accumulation, symptom expression, host physiology, and antiviral defense through both synergistic and antagonistic interactions among co-infecting viruses.

Overall, the first detection of bell pepper alphaendornavirus and pepper cryptic virus 2 in Iraq substantially expands the known geographical distribution of these persistent viruses and provides the first comprehensive overview of the Iraqi pepper virome. Beyond documenting new virus records, this study demonstrates the value of metatranscriptomic sequencing for uncovering complex viral communities and endogenous viral elements that are difficult to detect using conventional diagnostic approaches. These findings provide an important foundation for future epidemiological studies, virus surveillance programs, and investigations into the biological roles of persistent viruses and endogenous viral elements in pepper health and productivity.

CONCLUSION

This study provides the first comprehensive metatranscriptomic characterization of the pepper virome in Iraq. High-throughput sequencing successfully identified the presence of bell pepper alphaendornavirus (BPEV), pepper cryptic virus 2 (PCV-2), fragmented tobacco vein clearing virus (TVCV) sequences, and abundant transcription of endogenous pararetroviral elements (EPRVs) in symptomatic pepper plants. Phylogenetic analyses demonstrated that the Iraqi BPEV isolate is closely related to isolates from the Dominican Republic, South Korea, Jamaica, and the United States, whereas both genomic segments of PCV-2 clustered

with Turkish isolates, indicating a high degree of genetic conservation among geographically distant populations. The extensive expression of endogenous pararetroviral elements further suggests that mixed viral infections may influence host transcriptional responses and highlights the complexity of the pepper virome. Overall, these findings considerably expand current knowledge of virus diversity in Iraqi pepper crops and demonstrate the value of metatranscriptomic sequencing for comprehensive virus surveillance, early detection of emerging viruses, and future investigations into the biological significance of persistent viruses and endogenous viral elements in pepper.

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AUTHORS' CONTRIBUTIONS

SZ and OA conceived the study, conducted sample collection, virus isolation, inoculation experiments, and molecular analyses. FA and WA performed the metatranscriptomic data analysis, interpreted the results, and prepared the manuscript. All authors critically revised the manuscript, approved the final version, and agreed to be accountable for all aspects of the work.

COMPETING INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this study.

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