Analysis of public domain plant transcriptomes expands the phylogenetic diversity of the family Secoviridae

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Abstract
Secoviruses are mono-/bipartite plant-infecting, icosahedral RNA viruses that incite economically important diseases in plants. In the present study, nine secoviruses tentatively named as Ananas comosus secovirus (AcSV), Artocarpus altillis secovirus (AaSV), Boehmeria nivea secovirus (BnSV), Gynostemma pentaphyllum secovirus (GpSV), Orobanche cernua secovirus (OcSV), Paris polyphylla secovirus 1 (PpSV1), Paris polyphylla secovirus 2 (PpSV2), Rhododendron delavayi secovirus (RdSV), and Yucca gloriosa secovirus (YgSV) were identified by probing publicly available transcriptomes of eight plant species. Coding-complete genome/genome segments of all the identified viruses encoding a polyprotein were recovered. Two of the nine identified viruses—AcSV and GpSV were discovered in few of the small RNA libraries of respective plant species. Putative cleavage sites were predicted in polyproteins encoded by AcSV, GpSV, PpSV2 and YgSV genome segments. Phylogenetic and sequence identity analyses revealed that AcSV, GpSV and YgSV, PpSV1 and RdSV putatively belong to the genera- Sadwavirus (sub genus: Cholivirus), Fabavirus, Nepovirus and Waikavirus, respectively, while AaSV, BnSV, and PpSV2 may represent a distinct group of viruses within the family Secoviridae as they could not conclusively be assigned to a single genus.

Keywords Secovirus · Novel · Public domain · Database

Secoviridae is a family of non-enveloped icosahedral viruses that cause economically important diseases in plants [1]. The positive-sense single-stranded RNA genomes of secovirids are either monopartite or bipartite and are typically 9–13.7 kb in size (size of combined RNAs in case of bipartite viruses). Mostly, the genome or genome segment contains a single large open reading frame (ORF) encoding for a polyprotein that will be cleaved into individual proteins by 3C-like proteinases encoded by the virus. In general, secoviruses are transmitted by insects or nematodes, while few members are also transmitted by seeds [1]. Currently, the family Secoviridae includes nine genera—Comovirus, Fabavirus, Nepovirus, Cheravirus, Sadwavirus, Torradovirus, Sequivirus, Waikavirus, and Stralarivirus [1, 2] with the genus Sadwavirus comprising three subgenera—Satsumavirus, Stramovirus, and Cholivirus [3].

Owing to the steady increase in transcriptome sequencing projects, substantial quantum of data is being generated and deposited in public domain Sequence Read Archive (SRA) and Transcriptome Shotgun Assembly (TSA) databases of National Centre for Biotechnology Information (NCBI). Besides plant sequences, the plant transcriptome data can also contain viral sequences, if they were infected with viruses during the time of sample collection. Thus, these databases serve as valuable resources for comprehensive discovery of known/novel viral sequences from a wide range of hosts that would otherwise require costlier viromic studies [4, 5]. Such viruses that are discovered from metagenomic datasets can be considered as bona fide ones and be included in International Committee on Taxonomy of Viruses (ICTV) taxonomy [6]. Public domain plant transcriptomes are speculated to contain secoviral sequences, whose discovery, if made, can broaden the phylogenetic diversity of the

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family Secoviridae. Thus, in the present study, eight putative novel viruses have been identified through mining of public domain plant transcriptomes for secovirial sequences.

For identification of seco viral RNA1 sequences in plant transcriptomes (Viridiplantae, taxid: 33090), tBLASTn analysis (word size: 6; e value: 0.05; matrix: BLOSUM62) was performed using RNA1-encoded polyprotein sequences of cowpea mosaic virus (NP613283.1) and rice tungro spherical virus (NP042507.1) as queries against TSA database (accessed on March, 2022). Resulting contigs of more than 5 kb were considered and manually examined. If more than one redundant contig was obtained from the same sample, the longest intact contig was considered as the putative RNA1 segment of the identified virus. Genome segments of same viruses identified from different samples/study were deemed as different isolates of the same virus. To obtain the second genomic segment of each putative novel virus, RNA2-encoded polyprotein sequence of the respective closely related virus was used as query in tBLASTn searches, and the longest intact non-redundant contig was regarded as the putative RNA2 segment. In cases where the obtained viral contigs were partial/truncated, coding-complete genome/genome segments were obtained by rnarival-SPAdes (v 3.15.4) assembly [7] of datasets from where the truncated/partial contigs were derived, after trimming using Trimmomatic (v 0.36) [8]. Further, the assembled contigs were subjected to BLASTn (v 2.10.1) [9] analysis against the recovered partial/truncated viral contigs. The bioinformatic analyses were carried out in Galaxy Australia server (https://usegalaxy.org.au/) [10]. ORFs in putative genome segments of identified viruses were predicted using NCBI ORF finder (https://www.ncbi.nlm.nih.gov/orffinder/). Molecular mass (MM) prediction and motif searches were performed as described in [11]. To identify maximum sequence identity of protein sequences encoded by the recovered viral genome segments with the existing viral sequences at maximum query coverage, BLASTp analysis against NCBI ‘non-redundant (nr)’ database was performed. Putative cleavage sites in the polyprotein sequence encoded by identified viral genome segments were predicted by multiple sequence alignment with the polyprotein sequences of related viruses. For phylogenetic investigation, the conserved protease-polymerase (Pro-Pol) amino acid (aa) sequences of seco viruses retrieved from NCBI virus database (https://www.ncbi.nlm.nih.gov/labs/virus/vssi/#), along with the corresponding sequences of identified viruses were subjected to MUSCLE alignment and phylogenetic tree construction using neighborhood-joining (NJ) method with Poisson model and 1000 bootstrap replicates. Conserved protein domains in the identified viral sequences were visualized using WebLogo (v 3.7) (https://weblogo.berkeley.edu/) [12]. To identify virus-positive small RNA (sRNA) libraries, BLASTn analysis (word size: 28; e-value: 0.05) of recovered viral genome sequences was carried out against the available sRNA libraries of respective plant species and libraries containing at least 10 reads were considered virus-positive.

A total of nine viruses tentatively named as Ananas comosus secovirus (AcSV), Arto cercus allitidis secovirus (AaSV), Boehmeria nivea secovirus (BnSV), Gynostemma pentaphyllum secovirus (GpSV), Orobanche cernua seco virus (OcSV), Paris poly phylla secovirus 1 (PpSV1), Paris poly phylla secovirus 2 (PpSV2), Rhododendron delavayi secovirus (RdSV), and Yucca gloriosa secovirus (YgSV) were identified in transcriptomes of Ananas comosus, Arto cercus allitidis, Boehmeria nivea, Gynostemma pentaphyllum, Orobanche cernua var. cumana, Paris poly phylla var. yunnanensis, Rhododendron delavayi, and Yucca gloriosa, respectively, through tBLASTn searches. Of the identified viruses, except for RdSV that contained a single genome segment, two genome segments were recovered from the respective transcriptome libraries of the same plant sample. In total, nineteen genomic segments of the identified viruses were recovered including those of two different isolates of PpSV2 (Table 1). Genome/genome segments of all the identified viruses contained a single large ORF encoding for a polyprotein (Table S1).

RNA1 of GpSV (5.7 kb) and YgSV (6.3 kb), respectively, encode for putative polyprotein 1 of MM 205 kDa and 221 kDa, that contains the RNA helicase (HEL), 3C cysteine protease (picornain 3C), and viral RNA-dependent RNA polymerase (RdRp) motifs, while polyprotein 2 encoded by RNA2 of GpSV (3.1 kb) and YgSV (5.5 kb) with MM 112 kDa and 183 kDa, respectively, contains large and small coat protein (CP) motifs. In addition to the CP motifs, a movement protein (MP) motif was predicted in polyprotein 2 of GpSV (Fig. 1, Table S1). Putative cleavage sites of GpSV polyprotein 1 are Q(297)/F, Q(887)/S, Q(913)/S, and Q(1122)/S, while those of polyprotein 2 are Q(401)/A and Q(803)/S. Cleavage sites predicted for YgSV polyprotein 1 are Q(301)/F, Q(892)/S, Q(921)/N, and Q(1122)/N, while those of polyprotein 2 are Q(401)/A and Q(803)/S. Cleavage sites predicted for YgSV polyprotein 1 are Q(301)/F, Q(892)/N, Q(921)/N, and Q(1125)/N and YgSV polyprotein 2 are Q(1021)/N and Q(1432)/G (Fig. 1). BLAST analysis of polyprotein sequences encoded by the genomic segments showed that GpSV shared maximum amino acid sequence identities (75.97% at 99% query coverage and 67.23% at 98% query coverage for polyprotein 1 and 2, respectively) with cucurbit mild mosaic virus (CuMMV), while YgSV shared maximum sequence identities (36.27% at 89% query coverage and 24.92% at 37% query coverage for polyprotein 1 and 2, respectively) with broad bean wilt virus 2 (BBWV2) (Table S1). Phylogenetic analysis grouped GpSV with CuMMV and YgSV with Prunus virus F (PrVF) (Fig. 2).

AcSV RNA1 (6.4 kb) and RNA2 (3.9 kb) encode polyprotein 1 and 2 of MM 215 kDa and 127 kDa, respectively. Polyprotein 1 contained HEL, picornain 3C, and RdRp domains, while polyprotein 2 contained nepovirus CP
domain (Fig. 1, Table S1). Proteolytic cleavage sites predicted in polyprotein 1 are Q(419)/G, Q(929)/A, Q(953)/S, and Q(1179)/S, while a cleavage site S(319)/G was predicted in polyprotein 2 (Fig. 1). AcSV polyprotein 1 and 2 shared a maximum of 47.70% (97% query coverage) and 27.23% (99% query coverage) amino acid sequence identities with dioscorea mosaic-associated virus (DMaV) and chocolate lily virus A (CLVA), respectively, in BLAST analysis (Table S1). AcSV polyproteins 1 and 2 shared 29.9% and 22.4% amino acid sequence identities, respectively, with the corresponding sequences of pineapple secovirus A (PSVA), a putative novel sadwavirus [13]. Based on the conserved Pro-Pol region, AcSV and PSVA shared only 50% amino acid sequence identity suggesting that both these viruses are distinct. Phylogenetic analysis grouped AcSV along with CLVA and DMaV (Fig. 2).

OcSV RNA1 (6.9 kb) encodes for a 255 kDa polyprotein 1 with HEL and RdRp domains, while the OcSV RNA2 (3.5 kb) encodes for a 117 kDa polyprotein 2 with viral MP domain (Fig. 1, Table S1). BLAST analysis revealed the maximum amino acid sequence identities of polyproteins 1 and 2 (76.61% at 99% query coverage and 72.72% at 100% query coverage, respectively) with Trillium govanianum cheravirus (TgCV) (Table S1). In phylogenetic analysis, OcSV and TgCV were clustered in a single sub-clade that fell apart from other cheraviruses (Fig. 2).

RNA1 (6.5 kb) and RNA2 (6.6 kb) of PpSV1 encode for 232 kDa polyprotein 1 and 186 kDa polyprotein 2 with HEL, RdRp, and nepovirus CP N-terminal, central, C-terminal domains, respectively (Fig. 1, Table S1). PpSV1 polyprotein 1 shared a maximum of 66.16% (99% query coverage) amino acid sequence identity with blackcurrant reversion virus (BRV), while polyprotein 2 shared 41.11% (65% query coverage) sequence identity with tomato ringspot virus (Table S1). Phylogenetic analysis grouped PpSV1 with BRV (Fig. 2).

The single large genomic segment of RdSV (12.4 kb) encodes for a 422 kDa polyprotein with Waikavirus CP1.
HEL, tungro spherical virus-type peptidase, and RdRp domains (Fig. 1, Table S1). BLAST analysis of polyprotein sequence of RdSV showed its maximum amino acid sequence identity of 34.71% (89% query coverage) with poaceae liege virus 1 (Table S1). Phylogenetic analysis placed RdSV in a distinct sub-clade to other waikaviruses (Fig. 2).

RNA 1 of AaSV and BnSV were of length 5.8 kb and 5.9 kb, respectively, while RNA 2 of AaSV and BnSV were 4.9 kb and 3.2 kb long, respectively. Genome segments of two PpSV2 isolates (designated as fruit and seed) were recovered in the present study. RNA 1 and 2 of PpSV2 isolate fruit were of length 5.6 kb and 3.2 kb, respectively, while RNA 1 and 2 of PpSV2 isolate seed were 5.7 kb and 3.3 kb, respectively. RNA1-encoded polyprotein 1 of AaSV with MM 204 kDa contains HEL and RdRp motifs, while that of BnSV and PpSV2 isolates with MM 213 kDa and 204 kDa, respectively, contain HEL, picornain 3C and RdRp motifs. RNA2-encoded polyprotein 2 of AaSV with MM 168 kDa contains large CP domain, while that of BnSV and PpSV2 isolates with MM 213 kDa and 204 kDa, respectively, contain large and small CP domains (Fig. 1, Table S1). Cleavage sites predicted in polyprotein 1 of PpSV2 isolate fruit are Q(300)/W, Q(875)/S, Q(903)/Y, and Q(1126)/C, while those predicted in polyprotein 2 are Q(442)/A and Q(814)/T. Similarly, the predicted cleavage sites in polyprotein 1 of PpSV2 isolate seed are Q(301)/W, Q(876)/S, Q(904)/Y, and Q(1127)/H and in polyprotein 2 are Q(445)/A and Q(817)/T (Fig. 1). BLAST analysis revealed that AaSV-encoded polyproteins shared 27.48% to 32.57% (at 62% to 97% query coverage) amino acid sequence identities with the corresponding sequences of Capsicum annuum fabavirus and a comoviral sequence, BnSV-encoded proteins shared 23.98% to 32.94% (at 96% to 99% query coverage) amino acid sequence identities with bean rugose mosaic virus, and BBWV2 and PpSV2-encoded proteins of both the isolates shared 26.57% to 40.69% (at 95% to 99% query coverage) amino acid sequence identities with PrVF and a comoviral sequence (Table S1). Phylogenetic analysis grouped PpSV2 isolates with BnSV and both these viruses fell in a distinct clade from other comoviruses and fabaviruses, while AaSV formed a distinct clade among the members of the family Secoviridae (Fig. 2).

The conserved GxxGxGKS motif found in plant picorna-like virus NTP-binding proteins and three conserved domains found in picorna-like virus RdRps [14] were
Fig. 2  Phylogenetic tree showing the relationship of secoviruses identified in the present study with other secoviruses based on the conserved Pro-Pol region. Phylogenetic tree was constructed using Neighbor-Joining (NJ) method and Poisson model with 1000 bootstrap replicates. Bootstrap values > 50% are only indicated. Identified viruses of the present study are shown in bold and indicated by blue circles. Enteroviral sequences were used as outgroups during phylogenetic tree construction.
identified in the polyprotein of RdWV and in polyprotein 1 of all the identified bipartite viruses (Fig. S1). Plants produce small RNA (sRNA) from viral replicative forms/intermediates in response to viral infection as part of their antiviral defense strategy [15]. Interestingly, AcSV and GpSV reads were identified in few of the sRNA libraries of respective plant species in which the viruses were originally identified (Table S2). Also, BLASTp analysis showed that PpSV1 RNA1-encoded polyprotein sequence shared 95.80% amino acid sequence identity (87% query coverage) with one of the partial secoviral sequences available in GenBank with accession number MZ79335.1 suggesting that the sequence is of PpSV1. Further, family-level assignment of the identified viral sequences was confirmed through the GRAVIty pipeline (http://gravity.cvr.gla.ac.uk) [16].

Based on species demarcation criteria for the family Secoviridae (<80% and <75% amino acid sequence identities for the conserved Pro-Pol and CP, respectively) [1], genome organization, predicted motifs, sequence identities and phylogeny, GpSV and YgSV can be regarded as novel members of the genus Fabavirus, AcSV as a novel sadwavirus (subgenus: Chollivirus), RdsV as a novel walkavirus, PpSV1 as a novel nepovirus, and AaSV, BnSV, PpSV2 as novel members of the family Secoviridae. It is worthy of note that two diverse secoviruses PpSV1 and PpSV2 were identified in the same host- *P. polyphylla* var. *yunnanensis* wherein a stralarivirus, cnidium vein yellowing virus 2, was also identified (data not shown). On the other hand, YgSV was identified in the same sample where a novel potexvirus- Yucca gloriosa virus 1 was identified [17]. Similarly, RdsV was identified in the sample wherein a novel betanucleorhabdovirus (Rhododendron delavayi virus 1) and a novel betaflexivirus (Rhododendron delavayi virus 2) were earlier identified [4, 17].

Though OcSV and TgCV shared 89.2% amino acid sequence identity based on the conserved Pro-Pol sequence, both the viruses were divergent enough (>25% amino acid sequence divergence) based on the CP polyprotein sequence. Moreover, TgCV was identified in *Trillium govanianum* [5], while OcSV was identified in *O. cernua* var. *cumana* in the present study. Thus, further studies on biological properties of both these viruses are needed to ascertain OcSV as a novel member of the genus Cheravirus. The present report will serve as a prelude for researches directed at exploring the biological properties of the identified viruses.

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**Author contributions** VKS: conceptualization, methodology, formal analysis and investigation, writing- original draft preparation; VR: formal analysis and investigation, writing- review and editing; VKB: conceptualization, resources, supervision, writing- review and editing.

**Data availability** The viral genome sequences described in the study are available at NCBI Third Party Annotation database with accession numbers BK061318-BK061336.

**Declarations**

**Conflict of interest** The authors declare that they have no conflict of interest.

**Research involving human participants and/or animals** This work does not contain any animal or human participants.

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