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Letter

Genomic characterization of three unclassified rhabdoviruses from mosquitoes in Malaysia and Central Africa

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Dear Editor,

Viruses transmitted by arthropods (arboviruses) are highly diverse, both genetically and in terms of host insect species. They are widely distributed across the virosphere, with significant representation in the family *Rhabdoviridae*, which encompasses a total of 580 different species divided into 4 sub-families and 62 genera (ICTV: https://talk.ictvonline.org/) (Kuhn et al., 2023; Walker et al., 2022). Among them, 45 (73%) of the different genera are associated with invertebrates, mostly insects. Some of them have been demonstrated to be transmitted by arthropods, such viruses infecting plants, or vertebrates (*i.e.* arboviruses). Most other insect rhabdoviruses can also be considered arboviruses, as they are found both in biting arthropods feeding on vertebrates, and in different vertebrates, such as birds in the genera *Hapavirus* and *Sunrhavirus*. Finally, the role of arboviruses has yet to be confirmed for some other insect rhabdoviruses, as the presence or exposure of vertebrates to these viruses remains sporadic, or only indirectly observed (seroprevalence). The rhabdovirus virion usually contains a single or segmented molecule of linear negative-strand RNA of size approximately 10–16 kb, with five canonical genes encoding the nucleoprotein (N), the phosphoprotein (P), the matrix protein (M), the glycoprotein (G), and the RNA-dependent RNA polymerase (L) (Longdon et al., 2015; Walker et al., 2015). These canonical genes are typically found in separate transcriptional units that are flanked by conserved transcription initiation (TI) and transcription termination/polyadenylation (TTP) signals. In addition, various putative accessory genes have been identified in rhabdoviruses, located in overlapping, alternative or additional open reading frames (ORFs) (Walker et al., 2011). Next-generation sequencing (NGS) and metagenomic approaches applied to the animal kingdom have extended our knowledge of the virosphere, particularly of rhabdoviruses present in invertebrates such as arthropods (Li et al., 2015; Zhang et al., 2019). These results represent an important step towards a better assessment of the global diversity of rhabdoviruses, in particular by enriching sequence databases and identifying new species which help to retrace the evolutionary history of these viruses. In this study, we characterized three recently classified rhabdoviruses—Porton virus (PORV), Bangoran virus (BGNV), and Boteke virus (BOTV)—at the coding-complete genome level using NGS. These viruses were originally isolated in the 1960s from mosquitoes: PORV from Malaysia, and BGNV and BOTV from the Central African Republic (Calisher et al., 1989; Mekki et al., 1981) (Fig. 1A).

Nearly complete genome sequences (without the 3′ leader and 5′ trailer sequences) were obtained for the three viruses. Average coverage for each sequence varied from 200 × to 2200 × (Fig. 1B, Supplementary Fig. S1). The genome sequences exhibit a classical rhabdovirus organization, with the five canonical genes encoding N, P, M, G, and L proteins, in addition to several other accessory genes (additional ORFs) (Fig. 1C).

BOTV, which was most closely related to the genus *Sunrhavirus* after BLASTn analysis, had a partial genome size of 12,432 nt (Fig. 1B). The length of each canonical gene was comparable between BOTV and the other sunrhavirus members, and each presented a highly conserved TI signal, with the AACA consensus sequence. Similarly, the consensus sequence for TTP was also conserved, with the TG$(A)_7$ motif (Fig. 1D).

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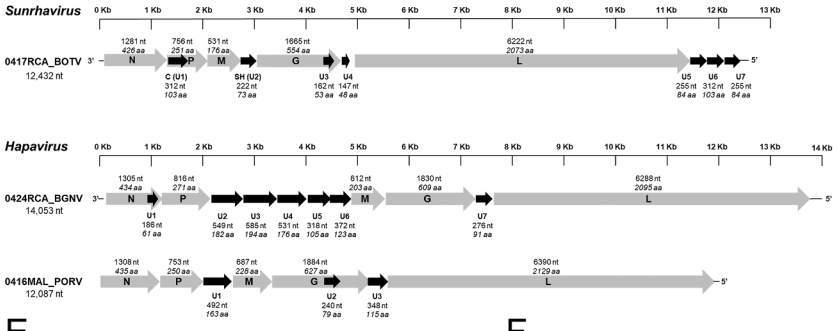
A

Isolate (reference)	Name	Acronym	City	Country	Date of collection	Host (species)	Original sample	Tested sample
0417RCA (ArB1077)	Boteke virus	BOTV	Boteke	Central African Republic	16/09/1968	Dipteran *(Coquillettidia maculipennis)*	Batch of adult females	Mouse brain
0424RCA (ArB2053)	Bangoran virus	BGNV	Bangoran	Central African Republic	26/07/1969	Dipteran *(Culex perfuscus)*	Batch of adult females	Mouse brain
0416MAL (1643)	Porton virus	PORV	Unknow	Malaysia (Sarawak)	Unknow	Dipteran *(Mansonia uniformis)*	Unknow	Mouse brain

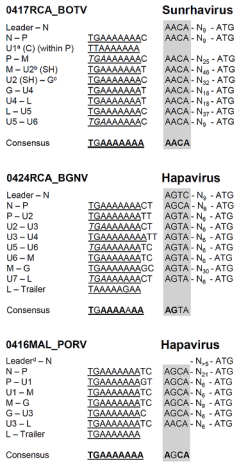
B

Isolate	Virus	Contig size (nt)	Raw reads (No)	Reads cleaned (No)	Mapped reads (No)	Average coverage depth (x)	GenBank accession number
0417RCA	BOTV	12,432	4,129,592	3,502,922	16,460	194.48	MW491753
0424RCA	BGNV	14,053	11,668,352	9,538,284	28,347	296.34	MW491752
0416MAL	PORV	12,087	3,789,354	3,247,292	176,959	2179.65	MW491751

C



D



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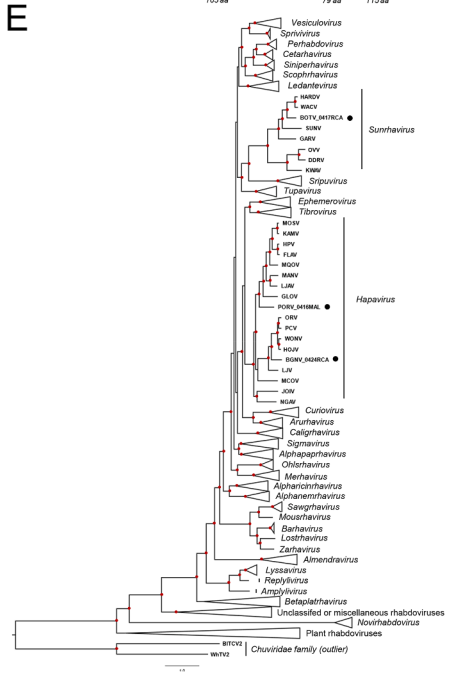
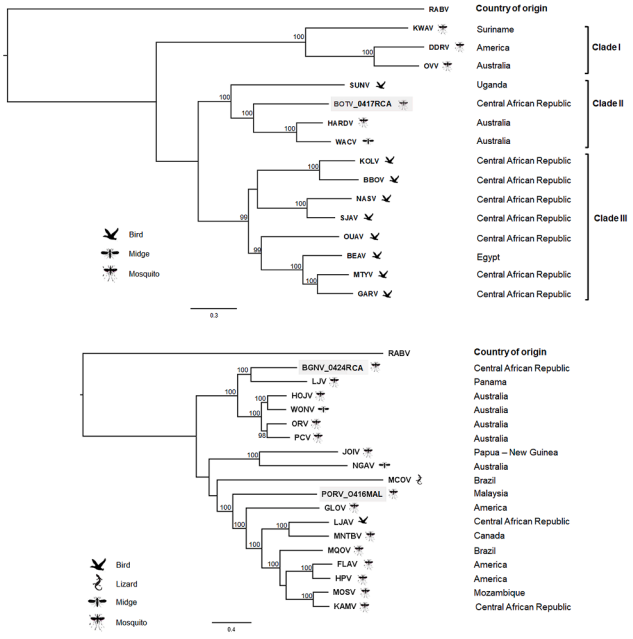


F



G

	BOTV	HARDV	WCV	SUNV	GARV	DDV	OVRV	KWAV
BOTV	100							
HARDV	60.5	100						
WACV	59.4	74.8	100					
SUNV	53.1	54	53.5	100				
GARV	52.2	52.3	51.5	48.8	100			
DDRV	43.9	44.4	43.1	42.5	42.5	100		
OVV	42.3	43.2	42.6	41.4	41.9	65.2	100	
KWAV	42.9	43.6	42.8	42.1	42.2	52.3	51.8	100

H

	PORV	BGNV	ORV	PCV	HJV	WONV	LJV	FLAV	HPV	KAMV	MOSV	MQOV	LJAV	MANV	GLOV	JOIV	NGAV	MCOV
PORV	100																	
BGNV	47.8	100																
ORV	49.5	60.8	100															
PCV	49	60.5	74.9	100														
HJV	49.2	61.2	74.1	73.2	100													
WONV	49	60.3	74.3	73	77	100												
LJV	47.5	59.2	58.2	58.1	58.2	58.4	100											
FLAV	51.9	49.1	50.2	50	50	50.2	48.8	100										
HPV	52.1	48.5	49.9	50.1	49.7	49.7	48.2	76.4	100									
KAMV	51.5	48.1	48.8	48.7	49.1	49.2	47.9	63.5	63.4	100								
MOSV	51.3	48.5	49	49.2	49.4	49.4	48.1	63	63.2	78.3	100							
MQOV	51.4	48.3	49.4	49.5	49	49.3	48.2	62.2	61.8	62.4	62.4	100						
LJAV	52	48.8	49.7	49.5	49.2	49.2	47.8	57.2	57.9	56.3	56.3	56.8	100					
MANV	51.7	49.2	50.3	50.5	51.1	50.3	48.3	57.9	58.4	56.8	56.7	56.8	64.1	100				
GLOV	50.7	48.2	49.4	49.3	48.7	49	47.5	54.4	54.2	54.3	54.6	53.9	52.9	53.3	100			
JOIV	46.3	46.5	47.5	48	47.5	47.9	45.7	47.5	47.4	46.3	46.4	47.1	46.9	47.7	46.8	100		
NGAV	45.7	46.9	46.9	47.3	46.4	46.6	45.7	47	46.8	46.5	46.4	46.2	45.9	46.5	45.9	52.8	100	
MCOV	45.1	46.3	46.3	46	46.4	45.9	44.7	45.3	45.2	45.1	45.8	44.8	45.3	45.5	44.2	44.9	43.4	100

(caption on next page)

Numerous accessory genes were identified in the BOTV genome, with seven ORFs ranging in length from 147 nt to 312 nt, accounting for the longest genome size in the genus *Sunrhavirus* (Supplementary Table S1). As with other sunrhaviruses, the C protein (U1) was found overlapping the *P* gene (Fig. 1C). This protein presented similar characteristics and profiles to other C proteins from representative sunrhaviruses (Supplementary Fig. S2 and Table S2), and was most closely related to the one from Kolongo virus (KOLV) and Bimbo virus (BBOV) with 85.1% and 81.6% amino acid identity, respectively (Supplementary Table S3). A putative modified TTP signal was observed for U1, with T instead of G in the consensus sequence $TG(A)_7$ (Fig. 1D). The small hydrophobic (SH) protein U2 of BOTV was localized at the junction between the *M* and *G* genes. This protein was similar to most of the other SH-related transmembrane proteins commonly found for sunrhaviruses but also for some viruses belonging to the genus *Tupavirus* (Supplementary Fig. S3 and Table S4). The strongest identity was observed with KLOV, Klamath virus (KLAV) and BBOV virus with 80.8%, 79.6% and 79.5% identity, respectively (Supplementary Table S3). Interestingly, three additional accessory ORFs were arranged in tandem at the end of the BOTV genome (U5, U6 and U7), and differed from other rhabdovirus genomic structures, including other sunrhaviruses. U5 and U6 are predicted to be non-cytoplasmic proteins, unlike U7, and no signal peptide was associated with these three proteins (Supplementary Table S1). In addition, classical TI and TTP sequence signals were identified for U5, and only a classical TI signal was observed for U6 (Fig. 1D). The amino acid sequence alignments of U5 and U7 demonstrated the presence of various conserved regions and/or residues, which strongly suggested that these duplicated genes could share a common ancestor (Supplementary Fig. S4). Conversely, fewer conserved patterns were observed between U6 and U5 or between U6 and U7 proteins, despite higher amino-acid identities between U5 and U6 (81.3%) or between U6 and U7 (85.9%) than between U5 and U7 (75.3%) (Supplementary Table S5). However, PSI-Search conducted on UniProtKB Viruses database confirmed the similarity between U5 and U7 proteins (Supplementary Table S1). No other similarity was observed after BLASTp (on non-redundant protein sequences) and PSI-Search analysis for the other additional ORFs, with default parameters (Supplementary Table S1).

BGNV was related to the genus *Hapavirus* by BLASTn analysis, which was subsequently confirmed by the presence of similar genomic organization. The TI and TTP signal sequences in the canonical genes of this virus were conserved, with the AGTA and $TG(A)_7$ motifs, respectively (Fig. 1D). BGNV presented numerous accessory ORFs, with one putative accessory gene (U1) in the *N* gene, five arranged in tandem (U2–U6) between the *P* and *M* genes (also identified as coding P-M intergenic region proteins or PMIPs), and one (U7) between the *G* and *L* genes (Fig. 1C and Supplementary Table S1). Regarding PMIPs, classical TI and TTP signals were also observed for U2, U3 and U6 (Fig. 1D). Both U4 and U5 appeared to share the same transcription signals, with a TI upstream of the initiation codon of U4, and a TTP after the stop codon of U5. These two proteins may be synthesised from a single ORF by a reading frameshift mechanism, as the ATG codon of U5 was partly the stop codon of U4. It is also possible that another reading frameshift could occur in the U5 sequence, at the end of the U4 sequence, to give a putative U5′ that extends the U5 protein by six amino acids. These five PMIPs were all considered as non-cytoplasmic proteins and exhibited a range of isoelectric point (pI) values (Supplementary Table S1). Amino acid sequence alignments of these five PMIPs demonstrated some degree of identity, which suggested that these duplicated genes could share a common ancestor, as previously observed with other hapaviruses (Supplementary Fig. S5) (Walker et al., 2015). The amino-acid identities for these PMIPs ranged between 74.4% and 90.1% (Supplementary Table S6). U7 of BGNV, localized between the *G* and the *L* genes, corresponded to a transmembrane protein with no similarity to other proteins found after PSI-Search or BLASTp analysis (Supplementary Table S1). However, this protein presented similar structural characteristics of viroporin-like proteins which can be found at the same genomic location in almost all other members of the genus *Hapavirus* (Supplementary Fig. S6). U7 could share the same TI and TTP signals with the *G* gene, the latter's stop codon being separated by one nucleotide from the initiation codon of U7. For the other additional ORFs of BGNV, the U1 ORF, encompassed within the *N* gene, did not exhibit any TI or TTP sequences. Only the U2 and U3 ORFs of BGNV showed similarity to ORFs in the corresponding genomic region of other hapaviruses after BLASTp or PSI-Search. U2 exhibited similarity in BLASTp analysis

Fig. 1. Genomic characterization of the three insect (dipteran) related rhabdoviruses BOTV (0417RCA isolate), BGNV (isolate 0424RCA) and PORV (isolate 0416MAL). **A** Description of these three rhabdoviruses and their associated epidemiological data. All were initially collected from dipterans originating in the Central Africa Republic (BOTV and BGNV) or Malaysia (PORV). **B** Illumina sequencing-based results. Average coverage for each nucleotide (nt) sequence varied from 200 × to 2200 × , and was obtained after the last mapping round. **C** Schematic organization of genomic sequences. Grey and black arrows represent the five canonical open reading frames (ORFs) (N, P, M, G and L), and the putative additional ORFs (≥180 nt, except for U3 and U4 from BOTV), respectively. The length (nucleotide and amino acid) of each ORF is indicated. **D** Description of the transcription initiation (TI) and transcription termination/polyadenylation (TTP) signal sequences. The TI and the TTP signal sequences are indicated in grey or underlined, respectively. The position of the TI sequences related to the ATG of the associated ORF is shown. Consensus sequences are displayed, with all unchanged positions shown in bold. The TGA motif in italics in some TTP signal sequences indicates the presence of the stop codon of the corresponding ORF. A putative TTP signal sequence was found for U1 from BOTV (a), another potential TI signal sequence (AACA) for U2 from BOTV was present 19 nt after this first TI sequence (b), another potential TI signal sequence (AACA) for G from BOTV was present 6 nt after the first TI sequence (c) and the leader sequence and the beginning of the *N* gene (including the TI signal sequence) were missing for PORV (d). **E** Phylogenetic analysis based on the complete sequence of the L protein. A maximum likelihood phylogenetic tree was performed using MEGA7.0 and the LG + G + I + F model with 1000 bootstrap, including also 235 other rhabdoviruses previously reported on GenBank (Supplementary Table S7). All rhabdovirus genera used are indicated (see Supplementary Fig. S9 for more details) and members of the same genus are collapsed, except for the genera *Sunrhavirus* and *Hapavirus*. Insect rhabdoviruses described in this study are indicated by black dots. All bootstrap proportion (BSP) values ≥ 90% are indicated by red dots. The scale bar indicates amino acid substitutions per site. The two members BlTCV2 and WhTV2 of the family *Chuviridae* were used as outliers. **F** Phylogenetic analysis based on concatenated ORF nucleotide sequences (N-P-M-G-L). A maximum likelihood phylogenetic tree was constructed using PhyML3.0 with the GTR + G + I model with 100 bootstrap, including representative members of the genera *Sunrhavirus* (top) and *Hapavirus* (bottom). The main animal reservoirs for each virus are indicated by specific illustrations, and the three insect-related rhabdoviruses described in this study are indicated in grey. The country of origin for each virus is indicated to the right of the illustration. All bootstrap proportion (BSP) values ≥ 90% are indicated. The scale bar indicates nucleotide substitutions per site. The classical rabies virus (RABV, genus *Lyssavirus*) was included as an outlier. **G** Nucleotide identities of concatenated canonical ORFs (N, P, M, G, and L) of members of the genus *Sunrhavirus*. Identities were calculated by pairwise deletion (%) using MEGA (version 11.0.13), with the following virus acronyms: BOTV: Boteke virus, DDRV: Dillard's Draw virus, GARV: Garba virus, HARDV: Harrison Dam virus, KWAV: Kwatta virus, OVV: Oak Vale virus, SUNV: Sunguru virus, WACV: Walkabout Creek virus. **H** Nucleotide identities of concatenated canonical ORFs (N, P, M, G, and L) of members of the genus *Hapavirus*. Identities were calculated through pairwise deletion (%) using MEGA (version 11.0.13) with the following virus acronyms: BGNV: Bangoran virus, FLAV: Flanders virus, GLOV: Grey Lodge virus, HPV: Hart Park virus, HJV: Holmes Jungle virus, JOIV: Joinjakaka virus, KAMV: Kamese virus, LJV: La Joya virus, LJAV: Landjia virus, MANV: Manitoba virus, MCOV: Marco virus, MQOV: Mosqueiro virus, MOSV: Mossuril virus, NGAV: Ngaingan virus, ORV: Ord River virus, PCV: Parry Creek virus, PORV: Porton virus, WONV: Wongabel virus.

on non-redundant protein sequences to the U1 proteins of Parry Creek virus (PCV), Wongabel virus (WONV), Holmes Jungle virus (HJV) and Ord River virus (ORV), which was confirmed by pairwise alignment (Supplementary Fig. S7 and Table S1). Similarly, the U3 protein also presented BLASTp and pairwise alignment similarity with U2 of WONV (Supplementary Fig. S7 and Table S1).

PORV was also related to the genus *Hapavirus* by BLASTn analysis, and subsequently confirmed by a similar genomic organization. The consensus sequences of the TI and TTP signal motifs for the canonical genes were AGTA and $TG(A)_7$, respectively (Fig. 1D). Only three putative accessory genes were observed, with U1 between the *P* and *M* genes, U2 within the *G* gene and U3 between the *G* and *L* genes (Fig. 1C). Classical TI and TTP signals were observed for U1 and U3, but none of them was found for U2 (Fig. 1D). None of these three additional ORFs exhibited similarities with other known proteins after BLASTp. However, the unique U1 PMIP, even if expected to be a transmembrane protein, demonstrated similarity to U3 PMIP of some other hapaviruses such as Flanders virus (FLAV), Hart Park virus (HPV), Kamese virus (KAMV) and Mossuril virus (MOSV) after PSI-Search, or after alignment and genetic comparison (Supplementary Fig. S8 and Table S1). In addition, U3 also demonstrated similarities to U5 of WONV and U5 of PCV in PSI-Search analysis. This putative transmembrane protein, containing a peptide signal, exhibited the same characteristics as viroporin-like proteins commonly found in hapaviruses, including BGNV (Supplementary Fig. S6).

Phylogenetic analysis, based on the complete L proteins of the three insect rhabdoviruses, with sequences of 235 other representative rhabdoviruses available on GenBank (Supplementary Table S7), confirmed that BOTV clustered within the genus *Sunrhavirus*, and that BGNV and PORV were new members of the genus *Hapavirus* (Fig. 1E). The analysis based on the nucleotide sequences of concatenated canonical ORFs also clarified the phylogenetic relationships within each of the two genera of interest (Fig. 1F). The genus *Sunrhavirus* encompassed insect- and bird-related viruses distributed among three potential major phylogroups with clades I, II and III. BOTV was clustered in the clade II and was found closely related to Harrison Dam virus (HARDV) and Walkabout Creek virus (WACV), both isolated from Australian mosquitoes in 1975 and 1981, respectively (Fig. 1F). BOTV was also genetically close to Sunguru virus (SUNV), which was the only virus in this clade isolated from birds (Luo et al., 2021; McAllister et al., 2014). Analysis of the concatenated ORF nucleotide sequences showed strong divergence between the BOTV isolate and other sunrhaviruses from clades I and II, with nucleotide identities ranging from 42.3% to 60.5% (Fig. 1G). N and L proteins of BOTV were the most conserved compared with the other sunrhaviruses (Supplementary Table S8).

Within the genus *Hapavirus*, BGNV formed a distinct phylogroup and was more specifically associated with La Joya virus (LJV), which was discovered in mosquitoes from Panama in 1958 (Fig. 1F) (Walker et al., 2015). PORV exhibited a greater genetic divergence compared to the other insect-related hapaviruses and also represented the only hapavirus found in an Asian country so far (Fig. 1F). For PORV and BGNV, concatenated canonical ORF sequences demonstrated low nucleotide identities compared with the other hapaviruses, with nucleotide identities ranging from 45.1% to 52.1%, and from 46.3% to 61.2% for PORV and BGNV, respectively (Fig. 1H). At the level of individual canonical proteins, analysis of amino acid identity also showed that the N and L proteins were more conserved among members of the genus *Hapavirus* (Supplementary Table S9).

In summary, we confirmed that BOTV and both PORV and BGNV represent new species in the genera *Sunrhavirus* and *Hapavirus*, respectively, fulfilling the International Committee on Taxonomy of Viruses (ICTV) criteria for species demarcation. These three new species were ratified by the ICTV in March 2022, with the binomial names *Sunrhavirus boteke, Hapavirus porton* and *Hapavirus bangoran* for BOTV, PORV and BGNV, respectively. Based on only three genomes, our study also confirmed the extreme diversity and complexity of the genomic organization of rhabdoviruses. This complexity results from different mechanisms of genetic evolution and offers rhabdoviruses great flexibility and adaptability (Walker et al., 2015). However, the structure and function of these additional proteins remains to be determined. In addition, these three viruses have been identified from dipterans, after virus isolation on mouse brain. So far, more than half of rhabdoviruses have been identified in invertebrates, mostly from the class Insecta. This is especially true for the genus *Hapavirus*, which has been isolated primarily from passerine birds and culicine mosquitoes, with a mosquito-bird transmission and circulation mode (Allison et al., 2014). Further studies are needed to assess the possibility of BOTV, BGNV and PORV acting as arboviruses in mammals, including humans.

FOOTNOTE

We thank the sequencing facilities of the “Plate-forme de microbiologie mutalisée (P2M)” of Institut Pasteur, Paris, France for technical assistance with NGS sequencing. We would also thank Corinne Maufrais for her continuous assistance in NGS analysis. Lastly, we would like to thank Peter Walker for his advice with the binomial nomenclature selection of the insect-related rhabdoviruses and their submission to the ICTV.

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The nearly complete genome sequences of BOTV, PORV and BGNV viruses were deposited in GenBank under accession number MW491753, MW491751 and MW491752, respectively.

Other detailed materials, methods and supplemented data were attached in supplementary files.

APPENDIX A. SUPPLEMENTARY DATA

Supplementary data to this article can be found online at https://doi.org/10.1016/j.virs.2025.11.003.

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