

This form should be used for all taxonomic proposals. Please complete all those modules that are applicable (and then delete the unwanted sections). For guidance, see the notes written in blue and the separate document "Help with completing a taxonomic proposal"

Please try to keep related proposals within a single document; you can copy the modules to create more than one genus within a new family, for example.

MODULE 1: TITLE, AUTHORS, etc

	2015 02 4	D		(to be cor	mpleted by	ICTV	
Code assigned:	2015.024a-cP (to be completed by ICTV officers)						
Short title: Five new species in (e.g. 6 new species in the genus Modules attached (modules 1 and 10 are required)		osterovirio 1 🔀 6 🗌	lae 2 🔲 7 🔲	3 <u> </u>	4	5 □ 10 ⊠	
Author(s):	<u> </u>						
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Marc Fuchs mf13@cornell.edu							
List the ICTV study group(s) that have seen this proposal:							
A list of study groups and contact http://www.ictvonline.org/subcom in doubt, contact the appropriate chair (fungal, invertebrate, plant, vertebrate viruses)	Closteroviridae						
ICTV Study Group comments (if any) and response of the proposer:							
Date first submitted to ICTV: Date of this revision (if differe	Date first submitted to ICTV: Date of this revision (if different to above): June 2015						

ICTV-EC comments and response of the proposer:

EC Comments: Remove the three proposed species where only small sequence fragments are available (FLMaV-1, FLMaV-2 and FMMaV). All other species can be approved.

Response: FLMaV-1, FLMaV-2 and FMMaV were removed in the revised proposal.

MODULE 2: NEW SPECIES

creating and naming one or more new species.

If more than one, they should be a group of related species belonging to the same genus. All new species must be placed in a higher taxon. This is usually a genus although it is also permissible for species to be "unassigned" within a subfamily or family. Wherever possible, provide sequence accession number(s) for **one** isolate of each new species proposed.

Code	201	5.024aP	(assigned by IC	CTV offic	V officers)		
To cre	To create one new species within:						
					in all that apply.		
(Genus: Ampelovirus			 If the higher taxon has yet to be created (in a later module, below) write "(new)" after its proposed name. 			
Subf	bfamily: <i>Unassigned</i>						
F	amily:	mily: Closteroviridae			If no genus is specified, enter "unassigned" in the genus box.		
	Order:	: Unassigned					
Name of new species:		Representative isolate: (only 1 per species please)		GenBank sequence accession number(s)			
Blackberry vein banding-associated virus		Mississippi1		Full genomic RNA (KC904540)			

Reasons to justify the creation and assignment of the new species:

- Explain how the proposed species differ(s) from all existing species.
 - o If species demarcation criteria (see module 3) have previously been defined for the genus, **explain how the new species meet these criteria**.
 - o If criteria for demarcating species need to be defined (because there will now be more than one species in the genus), please state the proposed criteria.
- Further material in support of this proposal may be presented in the Appendix, Module 9

Species of the family *Closteroviridae* have filamentous particles (650-2,200nm in length) and monopartite or bipartite single-stranded RNA genomes with size varying from 12,000 to nearly 19,000 nucleotides in length. They are divided into four genera: *Closterovirus* (monopartite genome), *Ampelovirus* (monopartite genome), *Velarivirus* (monopartite genome) and *Crinivirus* (bipartite or tripartite genome). Ampeloviruses are transmitted by pseudococcid mealybugs and soft scale insects, closteroviruses are transmitted by aphids, and criniviruses are transmitted by whiteflies. No vectors are known for velariviruses. Species demarcation criteria used for all genera in the family *Closteroviridae* are particle size, size of the coat protein and coat protein minor, genome structure and organization (number and relative location of the ORFs), vector species and specificity, cytopathological features, host range, as well as amino acid sequence of relevant gene products, i.e. RNA-dependent RNA polymerase, coat protein (CP), heat shock protein 70 homolog (HSP70h), differing by more than 25%.

Blackberry vein banding-associated virus (BVBaV)

Double-stranded RNA from infected blackberry was extracted and used as template for cDNA synthesis by RT-PCR using random and specific primers, and next generation sequencing using Illumina (Thekke-Veetil et al. 2013). The 5' end of the genome was obtained using 5' RACE. The 3' end was determined by RT-PCR using cDNAs obtained from artificially polyadenylated dsRNAs. The single-stranded RNA genome of blackberry vein banding-associated virus (BVBaV) isolate Mississippi 1 consists of 18,643 nt (GenBank accession number KC904540) and

shows a similar organization than members of subgroup I of the genus Ampelovirus with a 781-nt-long 5' untranslated region (UTR), a 335 nt long 3' UTR, and 10 putative open reading frames (ORF) (Thekke-Veetil et al. 2013). ORF1a (nt 782-7936) encodes a replicationassociated protein with hallmark domains for a papain-like protease, a methyltransferase, a DNA alkylation domain, and a helicase. ORF1b has conserved motifs of an RNA-dependent RNA polymerase (RdRp), which is putatively expressed as a fusion protein with a +1 ribosomal frameshift. The central region of the genome is characterized by a 1,079 nt long intergenic region and two small ORFs coding for protein p6 (ORF2, nt 10,646-10,798) and protein p5 (ORF3, nt 10,882-11,016) with transmembrane domains. ORF4 (nt 11,054-12,673) codes for a putative heat shock protein 70 homolog (HSP70h) protein and ORF5 (nt 12,683-14,122) codes for a putative coat protein (CP) homolog. ORFs 6 and 7 code for the putative coat protein (34 kDa) and CPm (56 kDa), respectively. ORFs 8-10 code for proteins of unknown function. High amino acid identity with grapevine leafroll-associated virus 3, the type member of subgroup I ampeloviruses, was identified in the CP (53%), HSP90h (27%), CPm (34%) and RdRp (62%). Phylogenetic analyses confirm the clustering of BVBaV with subgroup I members of the genus Ampelovirus (Fig. 1). Diagnostic primers were designed and BVBaV was found in cultivated and wild blackberry in Arkansas, Georgia, Mississippi, North Carolina and South Carolina in the United States (Thekke-Veetil et al. 2013). No information is available on the vector of BVBaV. In considering the demarcation criteria for species in the family Closteroviridae, BVBaV complies with a threshold of 75% amino acid identity for the CP (11.1-53.0%), RdRp (6.3-65.0%) identity) and HSP70h (20.6-56.2% identity). Therefore, BVBaV is proposed as a new species (within subgroup I) in the genus Ampelovirus.

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40003310	accession number(s) for one isolate of each new species proposed.					
Code	Code 2015.024bP			(assigned by ICTV officers)		
To crea	To create three new species within:					
					in all that apply.	
G	enus:	Velarivirus			the higher taxon has yet to be	
Subfa	mily:	Unassigned		created (in a later module, below) write "(new)" after its proposed name. • If no genus is specified, enter		
Fa	mily:	y: Closteroviridae				
(Order:	Unassigned		"unassigned" in the genus box.		
<u> </u>		Representative iso (only 1 per species p		GenBank sequence accession number(s)		
Cordyline virus 2 SJ1		SJ1		Partial genomic RNA (JQ599282)		
Cordyline	virus 3		SJ1	•	Partial genomic RNA (JQ599283)	
Cordyline	virus 4		SJ1		Partial genomic RNA (JQ599284)	

Reasons to justify the creation and assignment of the new species:

- Explain how the proposed species differ(s) from all existing species.
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 - o If criteria for demarcating species need to be defined (because there will now be more than one species in the genus), please state the proposed criteria.
- Further material in support of this proposal may be presented in the Appendix, Module 9

Species of the family *Closteroviridae* have filamentous particles (650-2,200nm in length) and monopartite or bipartite single-stranded RNA genomes with size varying from 12,000 to nearly 19,000 nucleotides in length. They are divided into four genera: *Closterovirus* (monopartite genome), *Ampelovirus* (monopartite genome), *Velarivirus* (monopartite genome) and *Crinivirus* (bipartite or tripartite genome). Ampeloviruses are transmitted by pseudococcid mealybugs and soft scale insects, closteroviruses are transmitted by aphids, and criniviruses are transmitted by whiteflies. No vectors are known for velariviruses. Species demarcation criteria used for all genera in the family *Closteroviridae* are particle size, size of the coat protein and coat protein minor, genome structure and organization (number and relative location of the ORFs), vector species and specificity, cytopathological features, host range, as well as amino acid sequence of relevant gene products, i.e. RNA-dependent RNA polymerase, coat protein (CP), heat shock protein 70 homolog (HSP70h), differing by more than 25%.

Cordyline virus 2 (CoV-2)

Double-stranded RNA isolated from *Cordyline fruticosa* served as a template for high-throughput sequencing using a 454 GS FLX Titanium platform. Reads were assembled using Geneious Pro software and sequence gaps or low coverage regions were validated by conventional RT-PCR and sequencing. The 3' terminus was determined by polyadenylation followed by RT-PCR using an oligo dT primer and a virus specific primer near the 3' end of

available sequence. A total of 15,107 nt were determined (GenBank accession number JQ599282), with the genome incomplete at the 5' terminal region (Melzer et al 2013). Overall, the genome organization of CoV-2 is very similar to the CoV-1 from the genus Velarivirus, and shares a 63.7% nucleotide identity. The RNA-dependent RNA polymerase (RdRp), heat shock protein 70 homolog (HSP70), and coat protein (CP) of CoV-2 are 22, 31, and 33% divergent from the corresponding proteins of cordyline virus 1 (CoV-1), respectively. Although the sequence divergence between the CoV-1 and CoV-2 RdRp does not exceed the 25% threshold for species demarcation within the family Closteroviridae, the average sequence divergence for these three phylogenetically informative proteins is 29% (Melzer et al. 2013). We therefore contend that CoV-1 and CoV-2 should represent two distinct species. Phylogenetic analyses consistently place CoV-2 within the velarivirus clade of the family Closteroviridae (Fig. 1). The vector of CoV-2 is currently unknown, although since this virus can be commonly found in C. fruticosa plants grown from seed, transmission by an insect vector may occur in nature. An RT-PCR assay distinguishing CoV-2 from other closteroviruses infecting C. fruticosa has been developed (Melzer et al. 2013). Based on this evidence, CoV-2 is proposed as a new species in the genus Velarivirus.

Cordyline virus 3 (CoV-3)

Double-stranded RNA isolated from Cordyline fruticosa served as a template for highthroughput sequencing using a 454 GS FLX Titanium platform. Reads were assembled using Geneious Pro software and sequence gaps or low coverage regions were validated by conventional RT-PCR and sequencing. The 3' terminus was determined by polyadenylation followed by RT-PCR using an oligo dT primer and a virus specific primer near the 3' end of available sequence. A total of 16,274 nt were determined (GenBank accession number JQ599283), with the genome incomplete at the 5' terminal region (Melzer et al. 2013). Overall, the genome organization of CoV-3 is similar to cordyline virus 1 (CoV-1). The RNAdependent RNA polymerase (RdRp), heat shock protein 70 homolog (HSP70), and coat protein (CP) of CoV-3 are 38, 50, and 56% divergent from the corresponding proteins of CoV-1, and 38, 49, and 59% divergent from the corresponding sequences of CoV-2, respectively. These values exceed the 25% divergence threshold for species demarcation within the family Closteroviridae for these three phylogenetically informative proteins (Melzer et al. 2013). Phylogenetic analyses consistently place CoV-3 within the velarivirus clade of the family Closteroviridae (Fig. 1). The vector of CoV-3 is currently unknown, although since this virus can be commonly found in C. fruticosa plants grown from seed, transmission by an insect vector may occur in nature. An RT-PCR assay distinguishing CoV-3 from other closterovirids infecting C. fruticosa has been developed (Melzer et al. 2013). Using this assay, CoV-3 was detected in a herbarium specimen of C. fruticosa housed at the Bishop Museum in Honolulu, HI. Based on this evidence, CoV-3 is proposed as a new species in the genus Velarivirus.

Cordyline virus 4 (CoV-4)

Double-stranded RNA isolated from *Cordyline fruticosa* served as a template for high-throughput sequencing using a 454 GS FLX Titanium platform. Reads were assembled using Geneious Pro software and sequence gaps or low coverage regions were validated by conventional RT-PCR and sequencing. The 3' terminus was determined by polyadenylation followed by RT-PCR using an oligo dT primer and a virus specific primer near the 3' end of available sequence. A total of 14,619 nt were determined (GenBank accession number

JQ599284), with the genome incomplete at the 5' terminal region (Melzer et al. 2013). Overall, the genome organization of CoV-4 is similar to CoV-1, although the small hydrophobic protein situated between the RdRp and HSP70 open reading frames (ORF) that is common to all known closteroviruses appears to be absent in this location in CoV-4. This finding was consistent in the high-throughput sequence data as well as sequence obtained from RT-PCR experiments specifically targeting this region (Melzer et al. 2013). An ORF that putatively encodes a small (4 kDa) hydrophobic protein was identified within HSP70 of CoV-4, although it is unknown if this ORF is expressed. The RdRp, HSP70, and CP of CoV-4 are 41, 47, and 61% divergent from the corresponding proteins of CoV-1, 43, 49, and 60% divergent from the corresponding sequences of CoV-2, and 45, 45, and 61% divergent from the corresponding sequences of CoV-3, respectively. These values exceed the 25% divergence threshold for species demarcation within the family Closteroviridae for these three phylogenetically informative proteins. Phylogenetic analyses consistently place CoV-4 within the velarivirus clade of the family Closteroviridae (Fig. 1). The vector of CoV-4 is currently unknown, although since this virus can be commonly found in C. fruticosa plants grown from seed, transmission by an insect vector may occur in nature. An RT-PCR assay distinguishing CoV-4 from other closterovirids infecting C. fruticosa has been developed (Melzer et al. 2013). Using this assay, CoV-4 was detected in a herbarium specimen of C. fruticosa housed at the Bishop Museum in Honolulu, HI. Together, based on this evidence, CoV-4 is proposed as a new species in the genus Velarivirus.

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Code 20	15.024cP (assigned by ICTV officers)			cers)	
To create one new species within:					
				in all that apply.	
Genus	S: Unassigned	If the higher taxon has yet to be			
Subfamily	: Unassigned		created (in a later module, below) write "(new)" after its proposed name.		
Family	: Closteroviridae		If no genus is specified, enter		
Orde	r: Unassigned		"unassigned" in the genus box.		
Name of new species:		Representative iso (only 1 per species p		GenBank sequence accession number(s)	
Blueberry virus	: A	lwate-2012		Full genomic RNA (AB733585)	

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Blueberry virus A (BVA)

The complete nucleotide sequence of blueberry virus A (BVA) was determined from cDNA synthesized by RT-PCR using double-stranded RNA isolated from highbush blueberry (*Vaccinium corymbosum*) cultivar Spartan in Japan (Isogai et al., 2013). The 5' and 3' termini were determined by the 5' and 3' RACE technology. The complete nucleotide sequence is 17,798 nt long with a genome organization similar to that of closteroviruses with 10 putative ORFs (GenBank accession number AB733585). The complete nucleotide sequence of two other BVA isolates (Brandner 2 and Elliot) from Canada was determined by deep sequencing

(GenBank accession numbers KF007211 and KF007212). The 5' and 3' untranslated regions of the BVA genome are 115 nt and 117 nt long, respectively. ORF1a (nt positions 116-9,268) encodes a 328 kDa protein with motifs of two papain-like proteases (L-Pro) containing conserved His and Cys at aa positions 402 and 465 for L1-Pro, and 122 and 201 for L2-Pro, respectively. Putative autocleavage of the two proteases releases a 261.1 kDa protein with methyltransferase motifs at the N-terminus (between residues 800-981) and RNA helicases motifs at the C-terminus (between residues 2,666-2,933). The methyltransferase and helicase motifs showed the highest identities (35.6% and 46.4%, respectively) with those of carrot yellow leaf virus (CYLV) and mint virus-1 (MV-1) from the genus Closterovirus. ORF1b (nt positions 9,267-10,847) is probably expressed via a +1 ribosomal frameshift at an opal stop codon (nt positions 9,264-9,270). ORF1b contains motifs of RNA-dependent RNA polymerase with the highest aa sequence identify with that of raspberry leaf mottle virus (RLMV) from the genus Closterovirus. ORF2 (nt positions 10,962-11,135) encodes a p6 protein with a transmembrane domain between residues 13-32. ORF3 (nt positions 11,132-12,952) encodes the heat shock 70 homolog (HSP70h) protein with five ATPase motifs between residues 9-374 and the highest as sequence identify with that of MV-1 (27.6%) from the genus Closterovirus. ORF4 (nt positions 12,989-14,530) encodes a p60 protein with 34% and 36% with the orthologue in raspberry leaf mottle virus (RLMV) and CYLV from the genus Closterovirus, respectively, and conserved Arg and Asp in aa positions 473 and 477, respectively. ORF5 (nt positions 14,474-15,321) codes for the coat protein of molecular mass 23 kDa with 20.9% aa sequence identity with grapevine leafroll-associated virus 2 from the genus Closterovirus, and conserved Ser, Arg and Asp in aa positions 76, 125 and 164, respectively. ORF6 (nt positions 15,380-15,997) codes for protein p23, ORF7 (nt positions 16,424-17,170) codes for protein p28, ORF8 (nt positions 17.161-17,337) codes for protein p7 and ORF9 (nt position 17,346-17,621) codes for protein p11 (Figure 2); none of these proteins have any significant similarity with other plant virus proteins. Interestingly, no CPm was identified in the BVA genome (Figure 2); and the CP and p23 have only 12.7% identity. Phylogenetic analyses indicate that BVA does not group with any genus in the family *Closteroviridae* (Fig. 1). Diagnostic primers were designed in ORF7 (p28 protein) and used in RT-PCR for the detection of BVA. The virus was detected in asymptomatic highbush blueberry plants of several cultivars and in symptomatic Spartan plants showing leaf yellowing, suggesting that BVA causes a latent infection and is not associated with leaf yellowing (Isogai et al., 2013). Attempts to purify BVA from infected blueberry tissue were unsuccessful; so was mechanical inoculation to herbaceous hosts and blueberry seedlings. However, BVA is graft-transmissible in blueberry (Isogai et al., 2013). Attempts to transmit BVA to blueberry seedlings with Aphis gossypii from a blueberry field were unsuccessful (Isogai et al., 2013). In considering the demarcation criteria for species in the family Closteroviridae, BVA complies with a less than 75% identity for the CP (11.0-21.8%), RdRp (5.2-10.4% identity) and HSP70h (18.8-25.2% identity). Based on these criteria and the fact that BVA does not cluster with any member of recognized genera, BVA is proposed as a new unassigned species in the family Closteroviridae.

MODULE 10: APPENDIX: supporting material

additional material in support of this proposal

References:

- -Isogai, M., Muramatu, S., Watanabe, M. & Yoshikawa, N. (2013) Complete nucleotide sequence and latency of a novel blueberry-infecting closterovirus. Journal of General Plant Pathology 79:123-127.
- -Martelli, G.P., Abou Ghanem-Sabanadzovic, N., Agranowsky, A.A, Al Rawhanih, M., Dolja, V.V., Dovas, C.I., Fuchs, M., Gugerli, P., Hu, J.S., Jelkmann, W., Katis, N., Maliogka, V.I., Melzer, M.J., Menzel, W., Minafra, A., Rott, M.E., Rowhani, A., Sabanadzovic, S. and Saldarelli, P. (2012) Taxonomic revision of the family *Closteroviridae* with special reference to the grapevine leafroll-associated members of the genus *Ampelovirus* and the putative species unassigned to the family. Journal of Plant Pathology, 94:7-19.
- -Martelli, G.P., Agranowski, A.A., Bar-Joseph, M., Boscia, D., Candresse, T., Couts, R.H.A., Dolja, V.V., Hu, J.S., Jelkmann, W., Karasev, A.V., Martin R.R., Minafra, A., Namba, S., Vetten H.J. (2012). Family *Closteroviridae*. In: King A., Adams, M.J., Carstens, E.B., Lefkowitz, E. (Eds.). Virus Taxonomy: Ninth report of the International Committee on Taxonomy of Viruses. Elsevier-Academic Press, San Diego, pp. 987-1001.
- -Melzer, M.J., Sugano, J.S., Uchida, J.Y., Borth, W.B., Kawate, M.K., and Hu, J.S. (2013) Molecular characterization of closteroviruses infecting *Cordyline fruticosa* L. in Hawaii. Frontiers in Microbiology, 4:1-6.
- -Thekke-Veetil, T., Aboughanem-Sabanadzovic, N., Keller, K.E., Martin R.R., Sabanadzovic, S & Tzanetakis, I.E. (2013). Molecular characterization and population structure of blackberry vein banding associated virus, a new ampelovirus associated with yellow vein disease. Virus Research 179:234-240.
- -Thompson, J. D., Gibson, T. J., Plewniak, F., Jeanmougin, F. & Higgins, D. G. (1997). The CLUSTAL_X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acids Res 25, 4876-4882.

Annex:

Include as much information as necessary to support the proposal, including diagrams comparing the old and new taxonomic orders. The use of Figures and Tables is strongly recommended but direct pasting of content from publications will require permission from the copyright holder together with appropriate acknowledgement as this proposal will be placed on a public web site. For phylogenetic analysis, try to provide a tree where branch length is related to genetic distance.

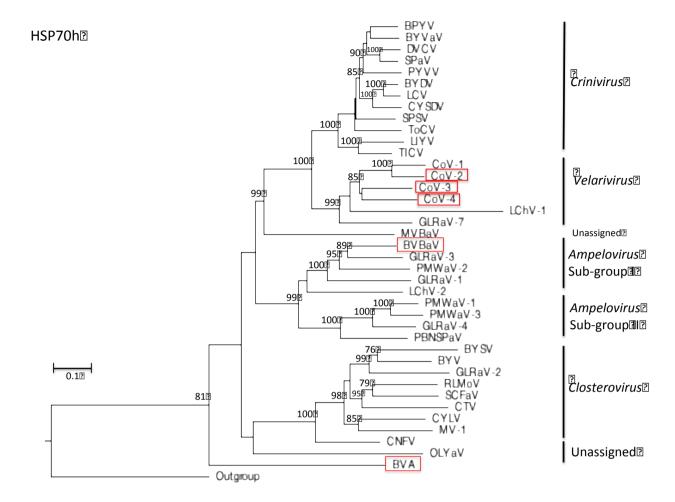


Fig. 1. Phylogenetic tree showing the relationships between the species and genera of the family Closteroviridae based on the complete amino acid sequence of the heat shock protein 70 homolog. The neighbour-joining tree was produced and boostraped using CLUSTAL W (Thompson et al., 1997). Distances are proportional to branch lengths. Boostrap values (1,000 replicates) above 75% are indicated at main branch nodes. The heat shock protein 70 from Arabidopsis thaliana (AEE75218) was used as outgroup. Newly proposed species in the genera Ampelovirus, Closterovirus and Velarivirus, and the newly proposed unassigned species in the family Closteroviridae are boxed in solid and dashed red line, respectively. The GenBank accession numbers used for each virus are as follows: Bean yellow disorder virus (BYDV, EU191904), Beet pseudoyellows virus (BPYV, AY330918), Beet yellow stunt virus (BYSV, U51931), Beet yellows virus (BYV, AF056575), Blackberry vein banding-associated virus (BVBaV, KC904540), Blueberry virus A (BVA, AB733585), Carnation necrotic fleck virus (CVFV, GU234166), Carrot yellow leaf virus (CYLV, FJ869862), Citrus tristeza virus (CTV, U16304), Cordyline virus 1 (CoV-1, HM588723), Cordyline virus 2 (CoV-2, JQ599282), Cordyline virus 3 (CoV-3, JQ599283), Cordyline virus 4 (CoV-4, JQ599284), Cucurbit yellow stunting disorder virus (CYSDV, AY242077), Diodia vein chlorosis virus (DVCV, GQ225585), Grapevine leafroll-associated virus 1 (GLRaV-1, JQ023131), Grapevine leafroll-associated virus 2 (GLRaV-2, JX513891), Grapevine leafrollassociated virus 3 (GLRaV-3, EU259806), Grapevine leafroll-associated virus 4 (GLRaV-4, FJ467503), Grapevine leafroll-associated virus 7 (GLRaV-7, HE588185), Lettuce chlorosis virus (LCV, FJ380118), Lettuce infectious yellows virus (LIYV, U15440), Little cherry virus 1 (LChV-1, EU715989), Little cherry virus 2 (LChV-2, AF531505), Mint vein banding-associated virus (MVBaV, KJ572575), Mint virus 1 (MV-1, AY792620), Olive leaf yellowing-associated virus (OLYaV,

AJ440010), Pineapple mealybug wilt-associated 1 (PMWaV-1, AF414119), Pineapple mealybug wilt-associated 2 (PMWaV-2, AF283103), Pineapple mealybug wilt-associated 3 (PMWaV-3, DQ399259), Plum bark necrosis stem pitting-associated virus (PMNSPaV, EF546442), Raspberry leaf mottle virus (RLMoV, DQ357218), Strawberry chlorotic fleck-associated virus (SCFaV, DQ860839), Potato yellow vein virus (PYVV, AJ557128), Strawberry pallidosis-associated virus (SPaV, AY488137), Sweet potato chlorotic stunt virus (SPCSV, AJ428554), Tomato chlorosis virus (ToCV, AY903447), and Tomato infectious chlorosis virus (TICV, FJ815440).

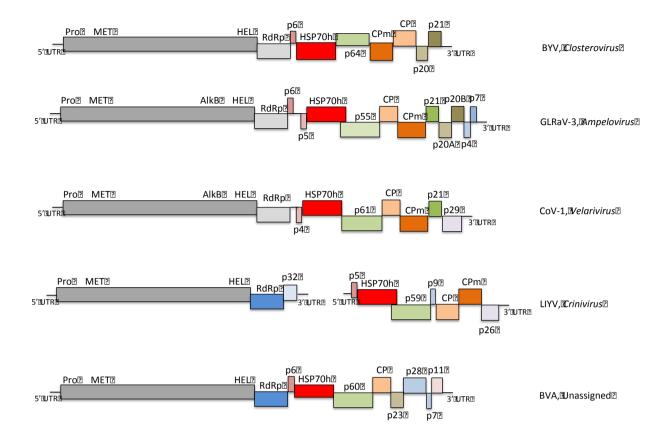


Fig. 2. Schematic representation of the genome organization for the type species of four genera (beet yellows virus from the genus *Closterovirus*, grapevine leafroll-associated virus 3 from the genus *Ampelovirus*, cordyline virus 1 from the genus *Velarivirus*, and lettuce infectious yellows virus from the genus *Crinivirus*) within the family *Closteroviridae* and for blueberry virus A, a proposed new unassigned species. Blocks represent predicted open reading frames (ORFs). The replicase proteins are shown in grey with the papain-like protease (Pro), methyltransferase (Met), alkB domain (AlkB) helicase (HEL), and RNA-dependent RNA polymerase (RdRp). Small transmembrane proteins (p4, p5 and/or p6) are shown in pink, the heat shock protein 70 homolog (HSP70h) in red, the coat protein (CP) in salmon, and the minor coat protein (CPm) in orange.