

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

Code assigned:	2016.020a-gP		(to be completed by ICTV officers)			
Alphaendornavirus and create						
Author(s):						
Mahmoud Khalifa, mkha201@aucklanduni.ac.nz Sead Sabanadzovic, ssabanadzovic@entomology.msstate.edu (member Endornaviridae SG) Ryo Okada, r-okada.44224@hotmail.co.jp Michael Pearson, m.pearson@auckland.ac.nz Rodrigo A. Valverde, ravalve@lsu.edu (Chair Endornaviridae SG)						
Corresponding author with 6	e-mail address:					
Rodrigo A Valverde, email: r	avalve@lsu.edu	l				
List the ICTV study group(s)	) that have seen	n this proposal				
A list of study groups and contacts is provided at <a href="http://www.ictvonline.org/subcommittees.asp">http://www.ictvonline.org/subcommittees.asp</a> . If in doubt, contact the appropriate subcommittee chair (fungal, invertebrate, plant, prokaryote or vertebrate viruses)  Endornaviridae SG						
ICTV Study Group comments (if any) and response of the proposer:						
Chair and one member of the SG are among the authors of the proposal. Other members of the SG reviewed the proposal and voiced no objections.						
Date first submitted to ICTV: July 2016 Date of this revision (if different to above):						
ICTV-EC comments and response of the proposer:						

#### MODULE 3: **NEW GENUS**

creating a new genus

Ideally, a genus should be placed within a higher taxon.

Code	201	6.020aP	(assigned by ICTV officers)	
To create	a new	genus within:		Fill in all that apply
				Fill in all that apply.
Subfa	mily:			If the higher taxon has yet to be created  (in a later mandal, halon) write "(read)"
Far	mily:	Endornaviridae		(in a later module, below) write "(new)" after its proposed name.
O	rder:	Unassigned		If no family is specified, enter
				"unassigned" in the family box

naming a new genus

Code	2016.020bP	(assigned by ICTV officers)
To name the new genus: Betaendornavirus		

Assigning the type species and other species to a new genus

Code	2016.020cP	(assigned by ICTV officers)		
To design	To designate the following as the type species of the new genus			
Sclerotin	Sclerotinia sclerotiorum betaendornavirus 1  Every genus must have a type species. This should be a well characterized species although not necessarily the first to be discovered			
are being	moved from elsewhere (Module 7b).	Please	s created and assigned to it (Module 2) and any that enter here the TOTAL number of species	
(including the type species) that the genus will contain:				
	4, comprising 1 existing species and 3 species proposed in the accompanying proposal			
2016.019a,bP				

### Reasons to justify the creation of a new genus:

Additional material in support of this proposal may be presented in the Appendix, Module 11

### **Background and Justification:**

The family *Endornaviridae* includes viruses infecting plants, fungi, and oomycetes; lacking virions and, with a few exceptions, not affecting the host phenotype (Fukuhara et al., 2012; Pfeiffer 1998; Roossinck et al., 2011; Yaegashi and Kanematsu, 2016). They have been reported to infect economically important crops such as avocado, barley, bell pepper, common bean, fava bean, melon, and rice, with the exception of isolates of *Vicia faba endornavirus* (Pfeiffer, 1998) their overall effect on plants is not known. In the case of fungal endornaviruses, a role in host virulence has been reported for isolates of *Helicobasidium mompa endornavirus 1* (Osaki et al., 2006), however for all other mycoendornaviruses described to date there is no evidence of an effect to the host.

Endornaviruses have a monocistronic genome composed of linear RNA that ranges from 9.6-17.6 kb in size and codes for a large polyprotein containing several functional domains. Conserved motifs for RNA-dependent RNA polymerase (RdRp) and RNA helicase-1 (Hel-1) or Helicase-like

proteins have been universally identified among all endornaviruses. Some, but not all, endornaviruses contain motifs for UDP-glucose glycosyltransferase (UGT), methyl transferase (MTR), and capsular polysaccharide synthase (CPS) (Khalifa and Pearson, 2014; Okada et al., 2011, 2013; Roossinck et al., 2011; Sabanadzovic et al., 2016).

The 12 currently approved endornaviruses (Adams et al., 2016) are listed in **Table 1**, while their genome organization is illustrated in Fig 1. According to the current classification, all recognized species are assigned to a single genus, *Endornavirus*.

Nevertheless, it has been recently pointed out that isolates of the species *Sclerotinia sclerotiorum endornavirus 1* (Khalifa and Pearson, 2014) clearly differ from the rest of endornaviruses. In particular:

- SsEV-1 genome (10.5 kb) is shorter compared to others (ranging from 12 kb to 17.6 kb) (Fig. 1)
- SsEV-1 methyltransferase, helicase and RdRp domains (Fig. 2A-C) belong to a distinct lineage compared to counterparts in other recognized members that appear monophyletic
- SsEV-1 infects a different host.

Therefore, based upon the information provided above, and previous literature support, we propose to create a new genus *Betaendornavirus* to accommodate the divergent species *Sclerotinia* sclerotiorum endornavirus 1 (renamed *Sclerotinia sclerotiorum betaendornavirus* 1).

The need for this reorganization is strongly supported by recently acquired knowledge on a number of putative endornavirus species (for further details, please see sister proposal about creation of 10 novel species in the two genera proposed in this document).

Table 2 summarizes the current and new organization of the family.

The existing genus, *Endornavirus*, (to be renamed *Alphaendornavirus*) will continue to accommodate the other 11 of 12 existing species, but with a new type species, *Oryza sativa alphaendornavirus* (formerly *Oryza sativa endornavirus*) replacing *Vicia faba endornavirus* (see 2016.020dP, below)

# Organization of the new genus Betaendornavirus

The newly proposed genus *Betaendornavirus* contains a single species, currently assigned to the genus *Endornavirus*. Species assigned to the new genus is:

Sclerotinia sclerotiorum endornavirus 1 (type species) which is renamed to Sclerotinia sclerotiorum betaendornavirus 1.

General properties of the members of the genus *Betaendornavirus*:

- Known betaendornaviruses infect ascomycetes.
- Betaendornaviruses are characterized by shorter genomes (up to c 12 kb) than endornavirus(es) belonging to genus *Endornavirus* (proposed name *Alphaendornavirus*).
- Genomes of studied betaendornaviruses apparently lack of site-specific nick near the 5'end of their coding strand.
- Genomes of members of this genus lack a glucosyltransferase domain, present in all known alphaendornaviruses.
- Polyproteins encoded by the type isolate of the type species in the genus (as well as other possible betaendornaviruses) contain an MTR domain.

- RdRp and Helicase domains encoded by members of betaendornaviruses belong to a distinct evolutionary lineage from those encoded by alphaendornaviruses.

Species demarcation criteria for genus Betaendornavirus:

- Differences in host range
- Overal nucleotide sequence identity below 75%

Tables, figures and references are provided in Appendix (Module 11). In addition, please see cross-linked proposal for creation of 10 new species in the family (of which 3 are in the genus *Betaendornavirus*)

#### Origin of the new genus name:

The second letter of the Greek alphabet followed by "endornavirus".

### Reasons to justify the choice of type species:

Sclerotinia sclerotiorum betaendornavirus 1 (formerly Sclerotinia sclerotiorum endornavirus 1) is proposed as the type species as it is fairly well studied and the complete or near complete genome sequences of several strains have been published or made available in GenBank.

#### **Species demarcation criteria in the new genus:**

If there will be more than one species in the new genus, list the criteria being used for species demarcation and explain how the proposed members meet these criteria.

The species demarcation criteria within the genus Betaendornavirus are:

- Differences in host range.
- Overall nt identity less than 75%.

# MODULE 3: **NEW TYPE SPECIES**

Assigning the type species and other species to a new genus

Code

2016.020dP

(assigned by ICTV officers)

To designate the following as the new type species of the genus Endornavirus (proposed name Alphaendornavirus

Every genus must have a type species. This should be a well characterized species although not necessarily the first to be discovered

The new genus will also contain any other new species created and assigned to it (Module 2) and any that are being moved from elsewhere (Module 7b). Please enter here the TOTAL number of species (including the type species) that the genus will contain:

18, comprising 11 existing species (including *Vicia faba endornavirus*, the previous type species) and 7 new species proposed in an accompanying proposal, 2016.019a,bP

### Origin of the new genus name:

The first letter of the Greek alphabet followed by "endornavirus".

#### Reasons to justify the choice of type species:

Oryza sativa alphaendornavirus (formerly Oryza sativa endornavirus) is proposed to replace Vicia faba endornavirus as the type species of the renamed genus Endornavirus (proposed name, Alphaendornavirus) because:

- Endornaviruses are generally asymptomatic in their hosts. Viruses representing *Vicia faba endornavirus* (along with those assigned to *Heterobasidium mompa endornavirus 1*) are an exception to that rule as they are reported associated with cytoplasmic male sterility in the lane "447" of faba beans. Viruses assigned to *Oryza sativa alphaendornavirus* are symptomless in their host rice.
- Ten out of 11 members of alphaendornaviruses code for glycosyltransferase (See Fig. 1). Exceptions are viruses belonging to *Vicia faba endornavirus*.
- Viruses of the species *Oryza sativa alphaendornavirus* are the best studied of all endornaviruses. Most of the general knowledge on biological and molecular features of endornaviruses (alphaendornaviruses in particular) is generated using OsEV/rice as a study model.

#### **Species demarcation criteria in the new genus:**

If there will be more than one species in the new genus, list the criteria being used for species demarcation and explain how the proposed members meet these criteria.

The species demarcation criteria within the genus Alphaendornavirus are:

- Differences in host range.
- Overall nt identity less than 75%.

### MODULE 7: MOVE

Use this module whenever an existing taxon needs to be moved and re-assigned (e.g. when a species is moved from one genus to another).

moving an existing taxon

Code	201	16.020eP	(assigned by IC	CTV officers)
To mov	e the f	ollowing taxon (or taxa)	from their pr	esent position:
Scleroti	nia scl	erotiorum endornavirus	1	
The pre	sent ta	axonomic position of the	se taxon/taxa:	
C	Genus: Endornavirus (proposed name Alphaendornavirus)		ed name	
Subfa	mily:			Fill in all that apply.
Fa	mily:	Endornaviridae		
(	Order:			
Code	201	16.020fP	(assigned by IC	CTV officers)
To re-as	ssign t	he taxon (or taxa) listed	in Part (a) as	follows:
				Fill in all that apply.
G	enus:	Betaendornavirus		If the higher taxon has yet to be
Subfa	mily:			created write "(new)" after its proposed name and complete
Fa	mily:	Endornaviridae		relevant module to create it.
(	Order:			If no genus is specified, enter

## **Reasons to justify the re-assignment:**

- If it is proposed to re-assign species to an existing genus, please explain how the proposed species differ(s) from all existing species.
  - 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.
- Provide accession numbers for genomic sequences
- Further material in support of this proposal may be presented in the Appendix, Module 11

#### Please refer to 2016.020cP

#### **MODULE 9: RENAME**

Use this module to change the name of one or more existing taxa (but note that stability of nomenclature is encouraged wherever possible). Insert extra lines in the table if needed.

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Renaming one or more taxa

Code	2016.020gP	(assigned by ICTV officers)			
To rena	To rename the following taxon (or taxa):				
Curren	t genus name		Proposed genus name		
Endornavirus			Alphaendornavirus		
Curren	t species name	$\dashv$	Proposed species name		
Basella	alba endornavirus 1		Basella alba alphaendornavirus 1		
Bell pepper endornavirus			Bell pepper alphaendornavirus		
Helicobasidium mompa endornavirus 1			Helicobasidium mompa alphaendornavirus 1		
Oryza rufipogon endornavirus			Oryza rufipogon alphaendornavirus		
Oryza sativa endornavirus			Oryza sativa alphaendornavirus		
Persea americana endornavirus 1			Persea americana alphaendornavirus 1		
Phaseo	lus vulgaris endornavirus 1		Phaseolus vulgaris alphaendornavirus 1		
Phaseolus vulgaris endornavirus 2			Phaseolus vulgaris alphaendornavirus 2		
Phytophthora endornavirus 1			Phytophthora alphaendornavirus 1		
Vicia faba endornavirus			Vicia faba alphaendornavirus		
Yerba n	nate endornavirus		Yerba mate alphaendornavirus		
Sclerotinia sclerotiorum endornavirus 1		'	Sclerotinia sclerotiorum betaendornavirus 1		

### Reasons to justify the renaming:

Explain why the taxon (or taxa) should be renamed

To complement Betaendornavirus, the other genus in the family.

Names of all 12 recognized species are changed to reflect new family organization and their assignments in one of the two genera.

### Organization of the renamed genus Alphaendornavirus

The genus *Alphaendornavirus* contains 11 of 12 species assigned to the former genus *Endornavirus*." Species proposed to be assigned to the new genus *Alphaendornavirus* are:

Basella alba endornavirus 1

Bell pepper endornavirus

Helicobasidium mompa endornavirus 1

Oryza rufipogon endornavirus

Oryza sativa endornavirus (type species)

Persea americana endornavirus 1

Phaseolus vulgaris endornavirus 1

Phaseolus vulgaris endornavirus 2

Phytophthora endornavirus 1

Vicia faba endornavirus Yerba mate endornavirus

General properties of the members of the genus *Alphaendornavirus*:

- The genus includes endornaviruses from plants, fungi and the oomycete *Phytophthora*
- Members of this genus are characterized by longer genomes than endornavirus(es) belonging to genus *Betaendornavirus*.
- Genomes of studied alphaendornaviruses are characterized by the presence of site-specific nick near the 5'end of their coding strand.
- The majority of alphaendornaviruses code for a glucosyltransferase domain.
- Polyproteins encoded by the majority of alphaendornaviruses lack identifiable MTR domain. The only exceptions are BPEV and PvEV2.
- RdRp and Helicase domains encoded by isolates of all species in this genus belong to the same evolutionary lineage.

Species demarcation criteria for genus Alphaendornavirus:

- Differences in host range.
- Overal nucleotide sequence identity below 75%.

Tables, figures and references are provided in Appendix (Module 11) as support to this proposal.

In addition, please see also a cross-linked proposal concerning creation of 10 new species in the family (of which 7 are in the genus *Alphaendornavirus*).

#### MODULE 11: APPENDIX: supporting material

additional material in support of this proposal

#### **References:**

#### References

Adams MJ, Lefkowitz EJ, King AMQ, et al. (2016) Ratification vote on taxonomic proposals to the International Committee on Taxonomy of Viruses. Arch Virol. doi:10.1007/s00705-016-2977-6

Candresse T, Marais A, Sorrentino R, Faure C, Theil S, Cadot V, Rolland M, Villemot J, Rabenstein F (2015) Complete genomic sequence of barley (*Hordeum vulgare*) endornavirus (HvEV) determined by next-generation sequencing. Arch Virol 161:741-74

Chen X, Punja ZK (2014) Characterization of a novel dsRNA endornavirus in the plant pathogenic fungus *Thielaviopsis basicola*. Mycology 5:10-15.

Das S, Falloon RE, Stewart A, Pitman AR (2014). Molecular characterisation of an endornavirus from Rhizoctonia solani AG-3PT infecting potato. Fungal Biol 118:924-34. doi: 10.1016/j.funbio.2014.08.003.

Du Z, Lin W, Qiu P, Liu X, et al. (2016) Complete sequence of a double-stranded RNA from the phytopathogenic fungus *Erysiphe cichoracearum* that might represent a novel endornavirus. Arch Virol

DOI 10.1007/s00705-016-2911-y

Fukuhara T, Gibbs MJ (2012) Endornaviridae. In: King AMQ, Adams MJ, Carstens EB, Lefkowitz EJ (eds) Virus taxonomy, ninth report of the International Committee on Taxonomy of Viruses. Elsevier, San Diego, pp 519-521

Khalifa ME, Pearson MN (2014) Molecular characterization of an endornavirus infecting the phytopathogen *Sclerotinia sclerotiorum*. Virus Res 189:303-309

Kumar S, Stecher G and Tamura K (2016) MEGA7: Molecular Evolutionary Genetics Analysis Version 7.0 for Bigger Datasets. Mol Biol Evol 33:1870-1874 doi:10.1093/molbev/msw054

Kwon S-J, Tan S, Vidalakis G (2014) Complete genome sequence and genome organization of an endornavirus from bottle gourd (*Lagenaria siceraria*) in California U. S. A. Virus Genes 49:163-168

Le SQ, Gascuel O (1993) An Improved General Amino Acid Replacement Matrix. Mol Biol Evol 25:1307-1320

Li W, Zhang T, Sun H, Deng Y, Zhang A, Chen H, Wang K. (2014) Complete genome sequence of a novel endornavirus in the wheat sharp eyespot pathogen *Rhizoctonia cerealis*. Arch Virol 159: 1213-1216. doi:10.1007/s00705-013-1893-2

Okada R, Kiyota K, Moriyama H, Fukuhara T, Valverde RA (2014) A new endornavirus species infecting Malabar spinach (*Basella alba* L.). Arch Virol 159:807-809.

Okada R, Kiyota E, Sabanadzovic S, Moriyama H, Fukuhara T, Saha P, Roossinck MJ, Severin A, Valverde RA (2011) Bell pepper endornavirus: molecular and biological properties and occurrence in

additional material in support of this proposal

#### **References:**

the genus Capsicum. J Gen Virol 92:2664-2673

Okada R, Young CK, Valverde RA, Sabanadzovic S, Aoki N, Hotate S, Kiyota E, Moriyama H, Fukuhara T (2013) Molecular characterization of two evolutionally distinct endornaviruses co-infecting common bean (*Phaseolus vulgaris*). J Gen Virol 94:220-229

Osaki H, Nakamura H, Sasaki A, Matsumoto N, Yoshida K (2006) An endornavirus from a hypovirulent strain of the violet root rot fungus, *Helicobasidium mompa*. Virus Res 118:143-149.

Pfeiffer, P (1998) Nucleotide sequence, genetic organization and expression strategy of the double-stranded RNA associated with the '447' cytoplasmic male sterility trait in *Vicia faba*. J Gen Virol 79: 2349-2358

Sabanadzovic S, Wintermantel WM, Valverde RA, McCreight JD, Aboughanem-Sabanadzovic N (2016) *Cucumis melo* endornavirus: Genome organization, host range and co-divergence with the host. Virus Res 214:49-58

Shang H, Zhong J, Zhang R, Chen C-Y, Gao B-D, Zhu H-J (2015) Genome sequence of a novel endornavirus from the phytopathogenic fungus *Alternaria brassicicola*. Arch Virol 160:1827-1830 doi:10.1007/s00705-015-2426-y

Yaegashi H, Kanematsu S (2016) Natural infection of the soil-borne fungus *Rosellinia necatrix* with novel mycoviruses under greenhouse conditions. Virus Res 219:83-91

#### **Annex:**

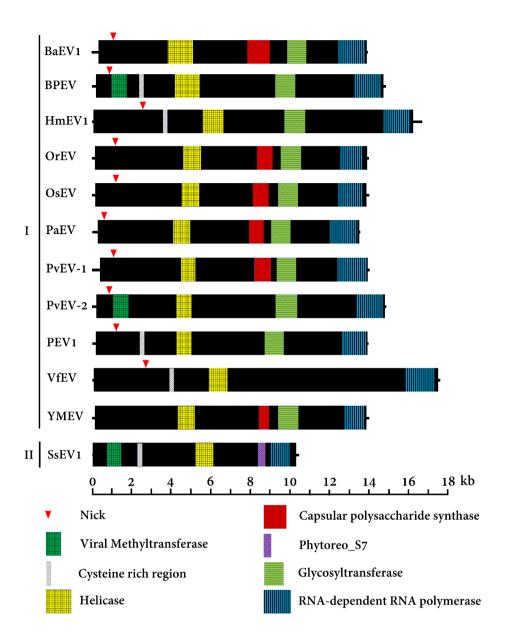
Include as much information as necessary to support the proposal, including diagrams comparing the old and new taxonomic orders. The use of Figures and Tables is strongly recommended but direct pasting of content from publications will require permission from the copyright holder together with appropriate 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.

**Table 1.** Viruses representing currently recognized species in the genus *Endornavirus*, family *Endornaviridae*.

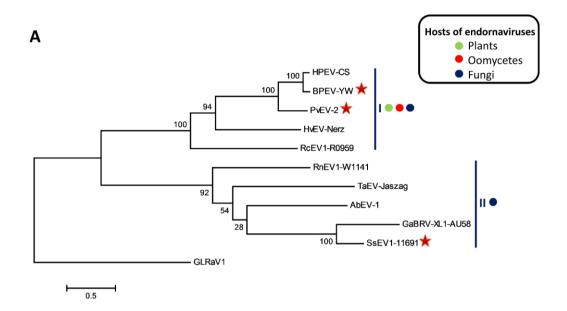
Virus	Acronym	Genome length (nt)	GenBank Accession No.
Basella alba endornavirus 1	BaEV1	14027	AB844265
bell pepper endornavirus	BPEV	14728	JN019858
Helicobasidium mompa endornavirus 1	HmEV1	16614	AB218287
Oryza rufipogon endornavirus	OrEV	13936	AB014344
Oryza sativa endornavirus	OsEV	13952	D32136
Persea americana endornavirus 1	PaEV1	13459	JN880414
Phaseolus vulgaris endornavirus 1	PvEV-1	13908	AB719397
Phaseolus vulgaris endornavirus 2	PvEV-2	14820	AB719398
Phytophthora endornavirus 1	PEV1	13883	AJ877914
Vicia faba endornavirus	VfEV	17635	AJ000929
yerba mate endornavirus	YMEV	13954	KJ634409
Sclerotinia sclerotiorum endornavirus 1	SsEV1	10513	KJ123645

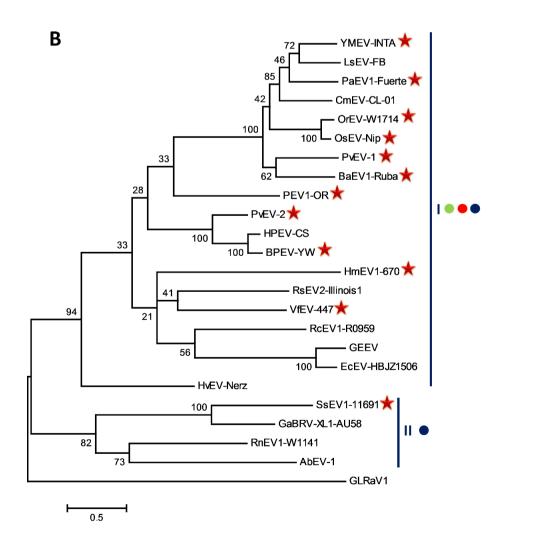
Table 2: Current structure of the family *Endornaviridae* and proposed reorganization

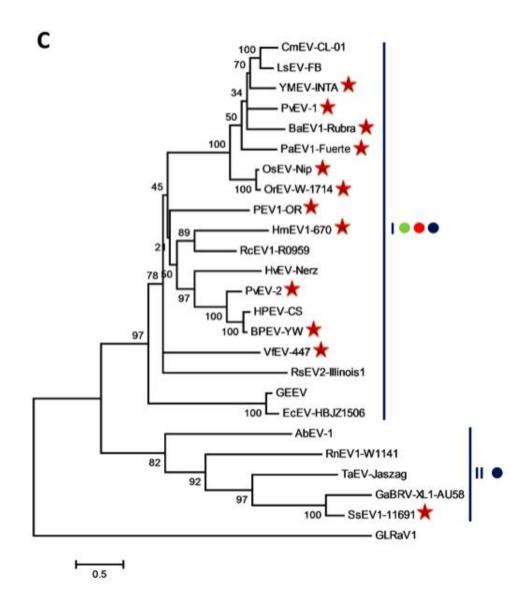
Current organization	Proposed organization
Genus Endornavirus	Genus Alphaendornavirus (previous name, Endornavirus)
Basella alba endornavirus 1	Basella alba alphaendornavirus 1
Bell pepper endornavirus	Bell pepper alphaendornavirus
Helicobasidium mompa endornavirus 1	Helicobasidium mompa alphaendornavirus 1
Oryza rufipogon endornavirus	Oryza rufipogon alphaendornavirus
Oryza sativa endornavirus	Oryza sativa alphaendornavirus (type species)
Persea americana endornavirus 1	Persea americana alphaendornavirus 1
Phaseolus vulgaris endornavirus 1	Phaseolus vulgaris alphaendornavirus 1
Phaseolus vulgaris endornavirus 2	Phaseolus vulgaris alphaendornavirus 2
Phytophthora endornavirus 1	Phytophthora alphaendornavirus 1
Sclerotinia sclerotiorum endornavirus 1	Vicia faba alphaendornavirus
Vicia faba endornavirus (type species)	Yerba mate alphaendornavirus
Yerba mate endornavirus	
	Genus Betaendornavirus
	Sclerotinia sclerotiorum betaendornavirus 1 (type species



**Figure 1.** Schematic representation of the genome organisation of currently approved members in the *Endornaviridae* family. Conserved domains are represented by colored boxes. The presence of a site-specific nick has not been studied in YMEV. Virus names are listed in **Table 1.** 







**Figure 2.** Maximum likelihood phylogenetic trees constructed with (**A**) the methyltransferase (MTR), (**B**) the helicase (Hel), and (**C**) the RNA-dependent RNA polymerase (RdRp) domains of endornaviruses. The best-fit substitution models were chosen and maximum likelihood phylogenetic trees constructed using MEGA7 software (Kumar et al., 2016). The Le and Gascuel with gamma-distributed site rates and invariant sites (LG+G+I) was used. Numbers on the nodes represent bootstrap support from 100 replicates. Names, acronyms and GenBank accession numbers for viruses used to construct trees are: Alternaria brassicicola endornavirus 1 (AbEV-1, KP239989.1), Basella alba endornavirus 1 (BaEV1, AB844264.1), bell pepper endornavirus (BPEV, JN019858.1), Cucumis melo endornavirus (CmEV, KT727022.1), Erysiphe cichoracearum endornavirus (EcEV, KT388110.1), Gremmeniella abietina type B RNA virus XL (GaBRV-XL, YP\_529670.1), grapevine endophyte endornavirus (GEEV, JX678977.1), Helicobasidium mompa endornavirus 1 (HmEV-1, AB218287.1), Hordeum vulgare endornavirus (HvEV, KT721705.1), hot pepper endornavirus (HpEV, KR080326.1), Lagenaria siceraria endornavirus (LsEV, KF562072.1), Oryza rufipogon endornavirus (OrEV, YP\_438202.1), **Oryza sativa endornavirus (OsEV**, YP\_438200.1), **Persea americana endornavirus 1 (PaEV1**,

YP\_005086952.1), Phaseolus vulgaris endornavirus 1 (PvEV-1, AB719397.1) Phaseolus vulgaris endornavirus 2 (AB719398.1), Phytophthora endornavirus 1 (PEV1, YP\_241110.1), Rhizoctonia cerealis endornavirus 1 (RcEV1, KF311065.1), Sclerotinia sclerotiorum endornavirus 1 (SsEV-1, KJ123645.1), Tuber aestivum endornavirus (TaEV, YP\_004123950.1), Vicia faba endornavirus (VfEV, YP\_438201.1), yerba mate endornavirus (YmEV, KJ634409.1). The closterovirus grapevine leafroll associated virus 1 (GLRaV-1, JQ023131.1) was used as an outgroup. Currently recognized members in the *Endornaviridae* are marked with red asterisks. These viruses are listed in Table 1. All other viruses presented in these trees represent members of putative new species in the taxon which recognition is proposed in a separate Taxonomic Proposal (please see the accompanying proposal 2016.019a,bP for creation of 10 new species in the family *Endornaviridae* submitted by the same team of authors). Roman numerals I and II indicate genera *Alphaendornavirus* and *Betaendornavirus*, respectively.