



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:	2012.005a-dV	(to be completed by ICTV officers)				
Short title: Create genus <i>Cuevavirus</i> in the family <i>Filoviridae</i> (e.g. 6 new species in the genus <i>Zetavirus</i>)						
Modules attached (modules 1 and 9 are required)	1 <input checked="" type="checkbox"/>	2 <input checked="" type="checkbox"/>	3 <input checked="" type="checkbox"/>	4 <input type="checkbox"/>	5 <input type="checkbox"/>	
	6 <input type="checkbox"/>	7 <input type="checkbox"/>	8 <input type="checkbox"/>	9 <input checked="" type="checkbox"/>		

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List the ICTV study group(s) that have seen this proposal:

A list of study groups and contacts is provided at http://www.ictvonline.org/subcommittees.asp . If in doubt, contact the appropriate subcommittee chair (fungal, invertebrate, plant, prokaryote or vertebrate viruses)	ICTV <i>Filoviridae</i> Study Group
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ICTV-EC or Study Group comments and response of the proposer:

1) The statement that LLOV is "almost equally distant (>56% and 51%, respectively) to those of marburgviruses (genus Marburgvirus) and ebolaviruses (genus Ebolavirus)" should be put into context. Ebolaviruses can differ from each other by 41%, so on this scale, LLOV is

appreciably more similar to ebolaviruses.

We apologize for being unclear in our writing. Whole genome sequence comparisons (Table 1 in the revised version of this TaxoProp) reveal that LLOV is ≈50% different from BDBV, ≈50% different from EBOV, ≈50% different from RESTV, ≈50% different from SUDV, ≈50% different from TAFV, ≈56% different from MARV, and ≈56% different from RAVV. LLOV is therefore in our opinion not appreciably more similar to ebolaviruses than to marburgviruses on a nt comparison basis alone (except if you consider 6% dramatic). We have now made this clearer in the text of the TaxoProp and added a legend to Table 1.

LLOV is, however, somewhat more similar to ebolaviruses based on genomic organization (editing of GP gene, number of gene overlaps).

Two independent studies of filovirus phylogeny have confirmed the considerable divergence of LLOV from both marburgviruses and ebolaviruses. Bao *et al.* 2012 (forwarded with this proposal to the ICTV EC) used PASC analysis, and Lauber *et al.* 2012 (forwarded with this proposal to the ICTV EC) used DEmARC analysis. Lauber *et al.*'s analysis is particularly useful, as it demonstrated that even if sequence-based taxon demarcation criteria (see comment 4) were to be changed up or down, the separation of LLOV from the ebolaviruses and marburgviruses would remain (Lauber *et al.* 2012, Figure 2). Lauber *et al.* suggest that on a higher level, LLOV and ebolaviruses cluster together, and could be classified as two different genera in one subfamily different from a subfamily that would contain marburgviruses (Lauber *et al.* 2012, Figure 2). At the moment, the ICTV *Filoviridae* Study Group does not feel that the establishment of subfamilies would solve an existing problem in the field and therefore voted against it (0:17 in favor), whereas the group remains in total agreement that LLOV should be classified in a genus separate from *Marburgvirus* and *Ebolavirus* (17:0 in favor), thereby confirming the consensus result of the previous ICTV *Filoviridae* Study Group (Kuhn *et al.* 2010; forwarded with this proposal to the ICTV EC).

2) There seems no reference to amino acid sequence distances between members of the three putative species (either for longest gene, or concatenated sequences from all seven genes). Given the substantial nucleotide sequence divergence between and within species, these may be helpful in further demonstrating underlying genetic relationships. What are the relative distances between LLOV, ebolaviruses and marburgviruses at the amino acid level, and how do these compare to intra-species distances?

We are unclear what the EC means with “three putative species”. There is currently only one putative species, the one proposed here for LLOV (species *Lloviu cuevavirus*). There are six established filovirus species, one in the genus *Marburgvirus* (species *Marburg marburgvirus*), and five in the genus *Ebolavirus* (species *Bundibugyo ebolavirus*, *Reston ebolavirus*, *Sudan ebolavirus*, *Tai Forest ebolavirus*, and *Zaire ebolavirus*).

In the past (9th ICTV Report and before), only the glycoprotein (GP_{1,2}) amino acid sequences were considered to be useful for filovirus classification. A Lasergene Clustal W alignment of LLOV GP_{1,2} versus GP_{1,2} of other filoviruses yields the following similarity values:

LLOV vs MARV: 28.0%
LLOV vs RAVV: 27.8%
LLOV vs BDBV: 36.1%
LLOV vs EBOV: 36.7%
LLOV vs RESTV: 36.7%
LLOV vs SUDV: 39.8%
LLOV vs TAFV: 39.2%

[This analysis emphasizes the considerable divergence of LLOV GP_{1,2} compared to the GP_{1,2}s of marburgviruses and ebolaviruses \(while also showing that LLOV is somewhat closer related to ebolaviruses than to marburgviruses\).](#)

3) The argument that LLOV falls outside the size range of ebolaviruses (and thus supports its assignment as a separate species) seems at odds with the current GenBank entry for LLOV (JF828358) which states a genome length of 18.9 kb. This puts it into the ebolavirus size range and negates the argument. The true length of LLOV should be clarified and this statement updated.

The EC is right. This was a mistake on our side and the statement has now been deleted.

4) The Filoviridae chapter in the ICTV 9th Report does not specify a nucleotide (or amino acid) distance threshold that might be used to assign species. Is this actually being proposed here? Is there any independent justification for this level?

[The ICTV *Filoviridae* Study Group has established taxon demarcation criteria in 2010 based on genome sequence divergence of all then-available filovirus genome sequences in GenBank \(Kuhn et al. 2010\). This paper is also cited in the 9th ICTV Report chapter.](#)

Accordingly, a virus is a marburgvirus (member of the genus *Marburgvirus*) if it has the characteristics of a filovirus (member of the family *Filoviridae*) and its genome sequence differs from that of the “type virus” of the type species of the “type genus” of the family *Filoviridae* by <50% at the nucleotide level. The Study Group then established the genus *Marburgvirus* as the “type genus”, the species *Marburg marburgvirus* as the type species of this genus, and Marburg virus (MARV), as the “type virus” of this species.

A virus was defined as an ebolavirus (member of the genus *Ebolavirus*) if it has the characteristics of a filovirus (member of the family *Filoviridae*) and its genome sequence differs from that of the “type virus” of the type species of the “type genus” of the family *Filoviridae* (i.e., MARV) by $\geq 50\%$ at the nucleotide level, and from the “type virus” of the type species of the genus *Ebolavirus* by <50% at the nucleotide level. The Study Group then established the species *Zaire ebolavirus* as the type species of this genus, and Ebola virus (EBOV), as the “type virus” of this species.

A virus was defined as a Marburg marburgvirus (member of the species *Marburg marburgvirus*) if has the properties of marburgviruses and a genome that differs from that of the “type virus” of the type species of the genus *Marburgvirus* (i.e., MARV) by <30% at the nucleotide level (if it is >30% but <50% a new species would have to be established).

A virus was defined as a Bundibugyo ebolavirus (member of the species *Bundibugyo ebolavirus*) if has the properties of ebolaviruses and a genome different from the “type virus” of the type species of the genus *Ebolavirus* (i.e., EBOV) by $\geq 30\%$ but different from the “type virus” of the species *Bundibugyo ebolavirus* by <30%. The Study Group then designated Bundibugyo virus (BDBV) as the “type virus” of this species.

A virus was defined as a Reston ebolavirus (member of the species *Reston ebolavirus*) if has the properties of ebolaviruses and a genome different from the “type virus” of the type species of the genus *Ebolavirus* (i.e., EBOV) by $\geq 30\%$ but different from the “type virus” of the species *Reston ebolavirus* by <30%. The Study Group then designated Reston virus (RESTV) as the “type virus” of this species.

A virus was defined as a Sudan ebolavirus (member of the species *Sudan ebolavirus*) if has the properties of ebolaviruses and a genome different from the “type virus” of the type species of the

genus *Ebolavirus* (i.e., EBOV) by $\geq 30\%$ but different from the “type virus” of the species *Sudan ebolavirus* by $< 30\%$. The Study Group then designated Sudan virus (SUDV) as the “type virus” of this species.

A virus was defined as a Taï Forest ebolavirus (member of the species *Taï Forest ebolavirus*) if has the properties of ebolaviruses and a genome different from the “type virus” of the type species of the genus *Ebolavirus* (i.e., EBOV) by $\geq 30\%$ but different from the “type virus” of the species *Taï Forest ebolavirus* by $< 30\%$. The Study Group then designated Taï Forest virus (TAFV) as the “type virus” of this species.

A virus was defined as a Zaire ebolavirus (member of the species *Zaire ebolavirus*) if has the properties of ebolaviruses and a genome different from the “type virus” of the type species of the genus *Ebolavirus* (i.e., EBOV) by $< 30\%$. The Study Group then designated Ebola virus (EBOV) as the “type virus” of this species.

These demarcation criteria have indeed been independently verified. Bao *et al.* 2012 (attached) used PASC analysis, and Lauber *et al.* 2012 (attached) used DEmARC analysis. Both came to the conclusion that these demarcation criteria are not wrong.

5) The points about differences in glycoprotein expression seem to refer to differences between ebolaviruses and marburgviruses. It isn't made clear which of these characteristics are unique to LLOV and which support the species proposal.

We apologize for being unclear in our writing. We have now made clear in the proposal that LLOV in this regard resembles ebolaviruses, and not marburgviruses, because (theoretically) LLOV encodes four, rather than one, protein from its GP gene.

6) The transcription initiation signal (CUUCUU(A/G)UAAUU) differs from other ebolaviruses (and marburgviruses) at only two sites, one of which (position 3) is also polymorphic within ebolaviruses. We are not sure this really contributes greatly to the concept that LLOV represents a separate species.

We agree with the EC and have changed the statement to “slightly different...signals”.

7) There are considerable uncertainties about the host range for ebolaviruses and serology surveys have demonstrated high exposure frequencies in a large number of different bat species throughout Africa and Asia. Finding LLOV in Schreiber's long-fingered bats is not *prima facie* evidence for the existence of a new virus species until more is known about the distribution and genetic relationships of filoviruses in European bat species (should more be found).

We disagree with this statement. The results of most serologic surveys are not believed in the filovirus community, as according to such surveys filoviruses can be found pretty much everywhere, including the Arctic, in the complete absence of other supporting data. If one demands more stringent support, such as simultaneous IFA/ELISA detection of antibodies PLUS western blot confirmation or antibody detection plus genome detection in the same sample, then the number of more convincing surveys shrinks to a handful – and those support what we know about filovirus endemicity, i.e. the results confirm the presence of filoviruses in Equatorial Africa and the Philippines. It is important to note here that a) live marburgviruses (both MARV and RAVV) have been isolated from apparently healthy Egyptian rousettes (fruit bats of the species *Rousettus aegyptiacus*) in Uganda but not from any other healthy animal anywhere else, whereas none of the five ebolaviruses has ever been isolated from any healthy animal. Antibodies against and/or genomic sequence fragments, but never complete genomes, of marburgviruses and ebolaviruses have been detected in bats of several species in Equatorial Africa and the Philippines, but thus far never in a European bat and never in a bat belonging to the genus *Miniopterus*. Finally, all bats implicated in exposure to marburgviruses or filoviruses thus far have been

without obvious clinical signs, whereas all bats found to be infected with LLOV have been found dead due to a severe disease. [Therefore, the Study Group finds the detection of a complete and strongly divergent filovirus genome in sick/dead *Miniopterus* bats in Spain highly significant and important for filovirus classification.](#)

Comments on Figures / Tables:

Tree on Page 6. No information on what sequences were compared or how the tree was constructed is provided. It should ideally include an outgroup so that potential bootstrap support for the LLOV / Ebolavirus branch can be shown.

Second tree on Page 7. Branch lengths are not to scale and its appearance is misleading. The long branches corresponding to Marburg and Ravn viruses are out of scale to their actual divergence (21%), much less than between ebolaviruses (up to 41%). Bootstrap support for ebolaviruses is marginal (71%) although 100% in the tree shown in Fig. 6. Can these differences be resolved?

[We deleted both trees and replaced them with a single new tree with an appropriate figure legend outlining the method. See also Figure 5 in a recent paper by Carroll *et al.* 2013 \(forwarded with this proposal to the ICTV EC\).](#)

Table on Page 8. As far as we can tell this table was not in the original paper and as such does not provide information on what genes were compared, nucleotide or amino acid sequences etc. More information required.

[This has been corrected and a legend has been added.](#)

Date first submitted to ICTV:	June 06, 2012
Date of this revision (if different to above):	June 24, 2013

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	2012.005aV	(assigned by ICTV officers)
To create new species within:		
Genus:	<i>Cuevavirus</i>	Fill in all that apply. • If the higher taxon has yet to be created (in a later module, below) write “ (new) ” after its proposed name. • If no genus is specified, enter “ unassigned ” in the genus box.
Subfamily:		
Family:	<i>Filoviridae</i>	
Order:	<i>Mononegavirales</i>	
And name the new species:		GenBank sequence accession number(s) of reference isolate:
<i>Lloviu cuevavirus</i>		JF828358.1 = NC_016144.1 (complete genome of Lloviu virus prototype Bat86)

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

- 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.**
 - 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](#)

A new virus, named Lloviu virus (LLOV) by its discoverers, was identified in Schreiber’s long-fingered bats (*Miniopterus schreibersii*) in Spain after lethal epizootics among these cave bats in 2002 (Negredo et al. 2011). LLOV has biological and molecular features consistent with members of the order *Mononegavirales*, family *Filoviridae*, as outlined in the 9th ICTV Report (Easton et al. 2011; Kuhn et al. 2011). Within the family *Filoviridae*, LLOV should be assigned to a new species and a new genus because its full-length genomic sequence is almost equally distantly related ($\approx 56\%$ and $\approx 51\%$, respectively) to those of each marburgvirus (genus *Marburgvirus*: MARV and RAVV) and to those of each ebolavirus (genus *Ebolavirus*: BDBV, EBOV, RESTV, SUDV, and TAFV) (Table 1; Kuhn et al. 2010, 2011, Negredo et al. 2011).

Fulfilling the criteria for new filovirus taxa outlined in a 2010 ICTV *Filoviridae* Study Group article (Kuhn et al. 2010) and in the 9th ICTV Report (Kuhn et al. 2011), LLOV has the properties of a filovirus in that

a) it infects bats in nature (just like proven for marburgviruses and hypothesized for ebolaviruses)

b) it has a ≈ 19 kb RNA genome that contains gene overlaps (just like marburgviruses and ebolaviruses)

c) its genome contains at least seven genes in the order 3'-UTR-NP-VP35-VP40-GP-VP30-VP24-L-5'-UTR (just like marburgviruses and ebolaviruses)

d) its *VP24* gene is not homologous to genes of other mononegaviruses

e) its genome contains transcription initiation and termination signals not found in genomes of other mononegaviruses (just like marburgviruses and ebolaviruses)

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plus

- it has a genome organization reminiscent of ebolaviruses in that it contains more than one gene overlap and in that its *GP* gene encodes four proteins (GP_{1,2}, sGP, ssGP, and Δ-peptide) compared to marburgvirus genomes, which contain only 1 gene overlap and encode only one protein (GP_{1,2}) from the *GP* gene

- it has a genome that differs from that of the “type virus” of the type species of the “type genus” of the family *Filoviridae* (Marburg virus) by $\geq 50\%$ at the nucleotide level, as well as of the “type virus” of the type species of the genus *Ebolavirus* by $\geq 50\%$ at the nucleotide level (taxon demarcation criteria used as established in Kuhn et al. 2010)

- it is being found in a geographic area (Europe) in which filoviruses have not known to be endemic; and it is being found in members of a bat species (*Miniopterus schreibersii*) that has not previously been implicated as a potential filovirus host

In addition, LLOV differs from other filoviruses (marburgviruses and ebolaviruses)

- in that its seven predicted structural proteins are most likely transcribed from only six, rather than seven, mRNAs

- in that it has transcription initiation signals slightly different from those of filoviruses assigned to other species

The divergence of LLOV from both marburgviruses and ebolaviruses has been independently verified using PASC (Bao et al. 2012), DEmARC (Lauber et al. 2012), and Bayesian coalescent analysis (Carroll et al. 2013). The respective publications have been made available to the ICTV Executive Committee.

MODULE 3: **NEW GENUS**

creating a new genus

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

Code	2012.005bV	(assigned by ICTV officers)
To create a new genus within:		
Subfamily:		Fill in all that apply. • If the higher taxon has yet to be created (in a later module, below) write “ (new) ” after its proposed name. • If no family is specified, enter “ unassigned ” in the family box
Family:	Filoviridae	
Order:	Mononegavirales	

naming a new genus

Code	2012.005cV	(assigned by ICTV officers)
To name the new genus: <i>Cuevavirus</i>		

Assigning the type species and other species to a new genus

Code	2012.005dV	(assigned by ICTV officers)
To designate the following as the type species of the new genus		
<i>Lloviu cuevavirus</i>	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:		
1		

Reasons to justify the creation of a new genus:

Additional material in support of this proposal may be presented in the Appendix, Module 9

See criteria listed for new species <i>Lloviu cuevavirus</i>
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Origin of the new genus name:

Derived from Spanish <i>la cueva</i> , meaning cave, referring to Cueva de Lloviu, where Lloviu virus was first encountered (Kuhn et al. 2010)
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Reasons to justify the choice of type species:

Currently only one species in this genus.

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.

See criteria listed for new species <i>Lloviu cuevavirus</i>
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MODULE 9: **APPENDIX**: supporting material

additional material in support of this proposal

References:

Bao Y., Chetvernin V., Tatusova T. (2012) PAirwise Sequence Comparison (PASC) and Its Application in the Classification of Filoviruses. *Viruses* 4(8): 1318-27.

Carroll S. A., Towner J. S., Sealy T. K., McMullan L. K., Khristova M. L., Burt F. J., Swanepoel R., Rollin P. E., Nichol S. T. (2013) Molecular evolution of viruses of the family *Filoviridae* based on 97 whole-genome sequences. *J Virol* 87(5): 2608-16.

Easton A. J., Pringle C. R. (2011) Order *Mononegavirales*. In King Andrew M. Q., Adams Michael J., Carstens Eric B., Lefkowitz Elliot J.: *Virus Taxonomy - Ninth Report of the International Committee on Taxonomy of Viruses*. Elsevier/Academic Press, London, United Kingdom, pp 653-657.

Felsenstein J. (1985). Confidence limits on phylogenies: An approach using the bootstrap. *Evolution* 39:783-791

Kuhn J. H., Becker S., Ebihara H., Geisbert T. W., Jahrling P. B., Kawaoka Y., Netesov S. V., Nichol S. T., Peters C. J., Volchkov V. E., Ksiazek T. G. (2011) Family *Filoviridae*. In King Andrew M. Q., Adams Michael J., Carstens Eric B., Lefkowitz Elliot J.: *Virus Taxonomy - Ninth Report of the International Committee on Taxonomy of Viruses*. Elsevier/Academic Press, London, United Kingdom, pp 665-671.

Kuhn J. H., Becker S., Ebihara H., Geisbert T. W., Johnson K. M., Kawaoka Y., Lipkin W. I., Negrodo A. I., Netesov S. V., Nichol S. T., Palacios G., Peters C. J., Tenorio A., Volchkov V. E., Jahrling P. B. (2010) Proposal for a revised taxonomy of the family *Filoviridae*: classification, names of taxa and viruses, and virus abbreviations. *Archives of virology* 155(12): 2083-103.

Lauber C., Gorbalenya A. E. (2012) Genetics-based classification of filoviruses calls for expanded sampling of genomic sequences. *Viruses* 4(9): 1425-37.

Negrodo A., Palacios G., Vazquez-Moron S., Gonzalez F., Dopazo H., Molero F., Juste J., Quetglas J., Savji N., de la Cruz Martinez M., Herrera J. E., Pizarro M., Hutchison S. K., Echevarria J. E., Lipkin W. I., Tenorio A. (2011) Discovery of an ebolavirus-like filovirus in Europe. *PLoS Pathog* 7(10): e1002304.

Saitou N. and Nei M. (1987). The neighbor-joining method: A new method for reconstructing phylogenetic trees. *Mol Biol Evol* 4:406-425.

Tamura K. and Nei M. (1993). Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. *Mol Biol Evol* 10:512-526.

Tamura K., Peterson D., Peterson N., Stecher G., Nei M., and Kumar S. (2011). MEGA5: Molecular Evolutionary Genetics Analysis using Maximum Likelihood, Evolutionary

additional material in support of this proposal

References:

Distance, and Maximum Parsimony Methods. Mol Biol Evol 28(10):2731-2739.
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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. Estimates of evolutionary divergence between the genomic sequence of LLOV compared to ebolaviruses (BDBV, EBOV, RESTV, SUDV, TAFV) and marburgviruses (MARV, RAVV).

	Lloviu virus (LLOV)	Tai Forest virus (TAFV)	Bundibugyo virus (BDBV)	Sudan virus (SUDV)	Ebola virus (EBOV)	Reston virus (RESTV)	Marburg virus (MARV)	Ravn virus (RAVV)
Lloviu virus (LLOV)								
Tai Forest virus (TAFV)	0.500							
Bundibugyo virus (BDBV)	0.502	0.322						
Sudan virus (SUDV)	0.510	0.414	0.420					
Ebola virus (EBOV)	0.509	0.376	0.375	0.409				
Reston virus (RESTV)	0.509	0.411	0.415	0.417	0.402			
Marburg virus (MARV)	0.566	0.555	0.557	0.545	0.547	0.547		
Ravn virus (RAVV)	0.564	0.558	0.558	0.546	0.548	0.550	0.212	

The number of base differences per site from between sequences are shown. The analysis involved eight representative complete genome nucleotide sequences. All positions were included. All ambiguous positions were removed for each sequence pair. There were a total of 15,715 positions in the final dataset. Evolutionary analyses were conducted in MEGA5 (Tamura et al. 2011).

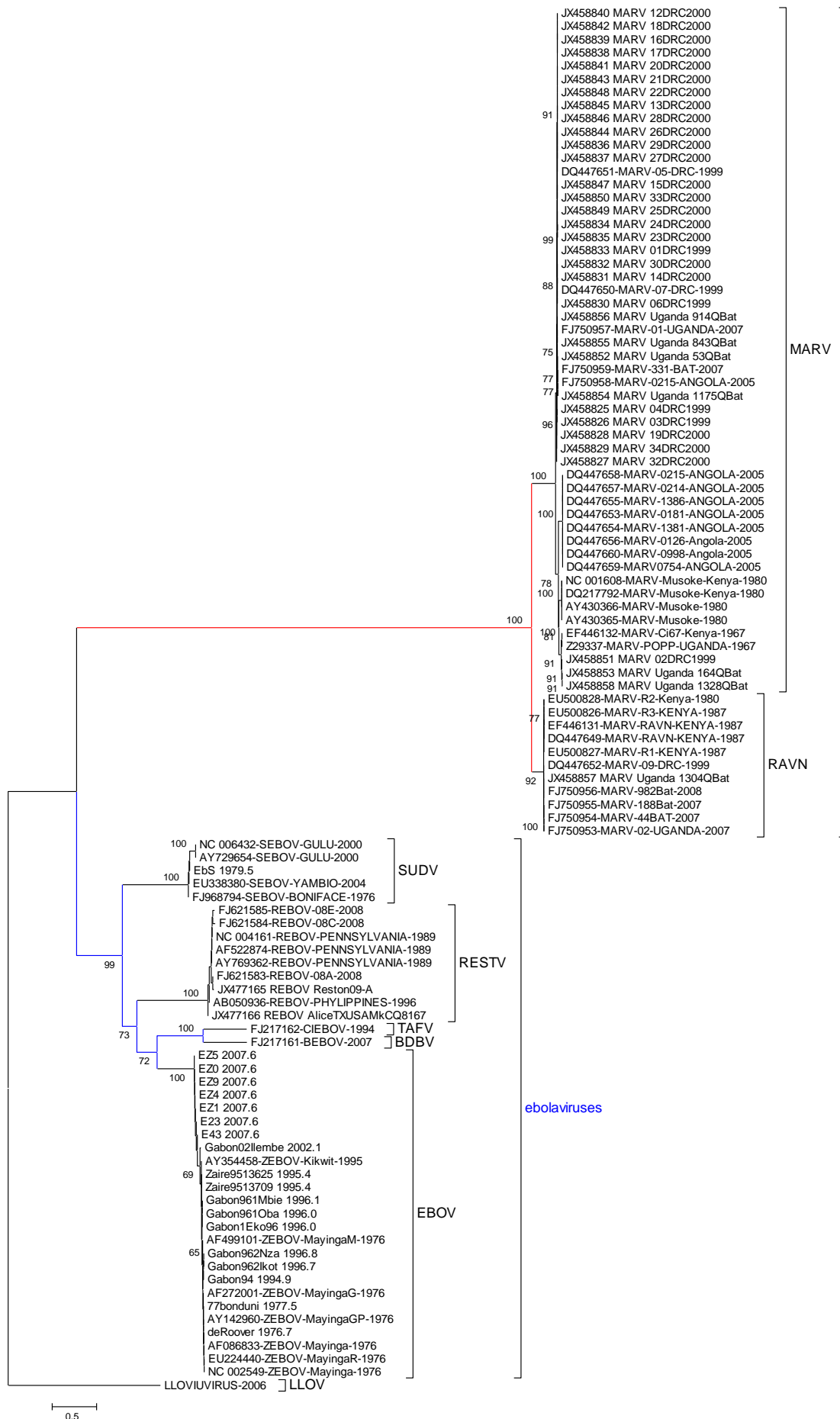


Figure 1. Evolutionary relationships of filovirus taxa

The evolutionary history was inferred using the Neighbor-Joining method (Saitou & Nei 1987). The optimal tree is shown. The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (500 replicates) are shown next to the branches (Felsenstein, 1985). The tree is drawn to scale, with branch lengths in the same units as those of the evolutionary distances used to infer the phylogenetic tree. The evolutionary distances were computed using the Tamura-Nei method (Tamura and Nei, 1993) and are in the units of the number of base substitutions per site. The rate variation among sites was modeled with a gamma distribution (shape parameter = 0.51). The analysis involved 105 nucleotide sequences (all available filoviral complete genomes). All ambiguous positions were removed for each sequence pair. There were a total of 21,596 positions in the final dataset. Evolutionary analyses were conducted in MEGA5 (Tamura *et al.*, 2011). The model of substitution was selected by using a Modeltest selection process to find the best-fit selection model. Models with the lowest BIC scores (Bayesian Information Criterion) are considered to describe the substitution pattern the best. For each model, AICc value (Akaike Information Criterion, corrected), Maximum Likelihood value (lnL), and the number of parameters (including branch lengths) were calculated. The Tamura-Nei model including gamma distribution was considered the best-fit.

Summary of proposed taxonomy changes

Approved Taxonomy (Ninth ICTV Report and 2012 ICTV Ratifications)	Proposed New Taxonomy
Order <i>Mononegavirales</i> Family <i>Filoviridae</i> Genus <i>Marburgvirus</i> Species <i>Marburg marburgvirus</i> Genus <i>Ebolavirus</i> Species <i>Tai Forest ebolavirus</i> Species <i>Reston ebolavirus</i> Species <i>Sudan ebolavirus</i> Species <i>Zaire ebolavirus</i> Species <i>Bundibugyo ebolavirus</i>	Order <i>Mononegavirales</i> Family <i>Filoviridae</i> Genus <i>Marburgvirus</i> Species <i>Marburg marburgvirus</i> Genus <i>Ebolavirus</i> Species <i>Tai Forest ebolavirus</i> Species <i>Reston ebolavirus</i> Species <i>Sudan ebolavirus</i> Species <i>Zaire ebolavirus</i> Species <i>Bundibugyo ebolavirus</i> Genus <i>Cuevavirus</i> (new) Species <i>Lloviu cuevavirus</i> (new)