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Proposal for a revised taxonomy of the family *Filoviridae*: classification, names of taxa and viruses, and virus abbreviations

Jens H. Kuhn · Stephan Becker · Hideki Ebihara · Thomas W. Geisbert · Karl M. Johnson · Yoshihiro Kawaoka · W. Ian Lipkin · Ana I. Negredo · Sergey V. Netesov · Stuart T. Nichol · Gustavo Palacios · Clarence J. Peters · Antonio Tenorio · Viktor E. Volchkov · Peter B. Jahrling

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Abstract The taxonomy of the family *Filoviridae* (marburgviruses and ebolaviruses) has changed several times since the discovery of its members, resulting in a plethora of species and virus names and abbreviations. The current taxonomy has only been partially accepted by most laboratory virologists. Confusion likely arose for several reasons: species names that consist of several words or which (should) contain diacritical marks, the current orthographic identity of species and virus names, and the similar pronunciation of several virus abbreviations in the absence of guidance for the correct use of vernacular names. To rectify this problem, we suggest (1) to retain the current species names *Reston ebolavirus*, *Sudan ebolavirus*, and *Zaire ebolavirus*, but to replace the name *Cote d'Ivoire ebolavirus* [sic] with *Taï Forest ebolavirus* and *Lake Victoria marburgvirus* with *Marburg marburgvirus*; (2) to revert the virus names of the type marburgviruses and ebolaviruses to those used for decades in the field (Marburg virus instead of Lake Victoria marburgvirus and Ebola virus instead of Zaire ebolavirus); (3) to introduce names for the remaining viruses reminiscent of jargon used by laboratory virologists but nevertheless different from species names (Reston virus, Sudan virus, Taï Forest virus), and (4) to introduce distinct abbreviations for the individual viruses (RESTV for Reston virus, SUDV for Sudan virus, and TAFV for Taï Forest virus), while retaining that

J. H. Kuhn, S. Becker, H. Ebihara, T. W. Geisbert, Y. Kawaoka, S. V. Netesov, S. T. Nichol, C. J. Peters, V. E. Volchkov, P. B. Jahrling are members of the ICTV (International Committee on Taxonomy of Viruses) *Filoviridae* Study Group.

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J. H. Kuhn (✉) · P. B. Jahrling
Integrated Research Facility at Fort Detrick (IRF-Frederick), Division of Clinical Research (DCR), National Institute of Allergy and Infectious Diseases (NIAID), National Institutes of Health (NIH), National Interagency Biodefense Campus (NIBC), B-8200 Research Plaza, Fort Detrick, Frederick, MD 21702, USA
e-mail: kuhnjens@mail.nih.gov

J. H. Kuhn
Tunnell Consulting, Inc., King of Prussia, PA, USA

S. Becker
Institut für Virologie, Philipps-Universität Marburg, Marburg, Germany

H. Ebihara
Rocky Mountain Laboratories Integrated Research Facility, National Institute of Allergy and Infectious Diseases, National Institutes of Health, Hamilton, MT, USA

T. W. Geisbert
Galveston National Laboratory, University of Texas Medical Branch, Galveston, TX, USA

K. M. Johnson
University of New Mexico, Albuquerque, NM, USA

Y. Kawaoka
School of Veterinary Medicine, University of Wisconsin, Madison, WI, USA

W. I. Lipkin · G. Palacios
Center for Infection and Immunity, Columbia University Medical Center, New York, NY, USA

A. I. Negredo · A. Tenorio
Centro Nacional de Microbiología, Instituto de Salud Carlos III, Madrid, Spain

for Marburg virus (MARV) and reintroducing that used over decades for Ebola virus (EBOV). Paying tribute to developments in the field, we propose (a) to create a new ebolavirus species (*Bundibugyo ebolavirus*) for one member virus (Bundibugyo virus, BDBV); (b) to assign a second virus to the species *Marburg marburgvirus* (Ravn virus, RAVV) for better reflection of now available high-resolution phylogeny; and (c) to create a new tentative genus (*Cuevavirus*) with one tentative species (*Lloviu cuevavirus*) for the recently discovered Lloviu virus (LLOV). Furthermore, we explain the etymological derivation of individual names, their pronunciation, and their correct use, and we elaborate on demarcation criteria for each taxon and virus.

Abbreviations

adj.	*adiectivum* (adjective)
corr.	correction
emend.	emended
fam.	*familia* (family)
fem.	*femininum*
gen. nov.	*genus novum* (new genus)
gen.	*genus*
geo.	geographic
Gre.	Greek
IPA	International Phonetic Alphabet
Lat.	Latin
masc.	*masculinum*
n.	*nomen substantivum* (noun)
Neo-Lat.	Neo-Latin
neut.	*neutrum*
nom. nov.	*nomen novum* (new name)
ord.	*ordo* (order)
pl.	*numerus pluralis* (plural)
sg.	*numerus singularis* (singular)
sp.	*species*
sp. nov.	*species nova* (new species)
Spa.	Spanish
suff.	suffix
v.	*verbum* (verb)
vir.	*virus*
vir. nov.	*virus novum* (new virus)

S. V. Netesov
Novosibirsk State University, Novosibirsk, Novosibirsk Oblast, Russia

S. T. Nichol
Centers for Disease Control and Prevention, Atlanta, GA, USA

C. J. Peters
Center for Biodefense and Emerging Infectious Diseases, The University of Texas Medical Branch, Galveston, TX, USA

V. E. Volchkov
Laboratoire des Filovirus Inserm U758, Université de Lyon, UCB-Lyon-1, Ecole-Normale-Supérieure de Lyon, Lyon, France

Introduction

Virus taxonomy is the practice of describing, classifying, and naming viruses. Description involves the genetic, biological, and morphological characterization of viruses and their virions, and is typically done by laboratory virologists. Classification is the process of sorting related viruses into groups, the so-called taxa, which ideally reflect phylogeny. This is typically done by virus taxonomists of the International Committee on Taxonomy of Viruses (ICTV), the body tasked by the International Union of Microbiological Societies (IUMS) to make decisions on matters of virus classification and nomenclature, with the help of expert groups—the ICTV Study Groups. Naming involves the issuing of unique designations for taxa (names) and viruses (names and abbreviations) according to nomenclature. Nomenclature is the set of rules or process for naming as established by the ICTV in the case of taxa and the ICTV Study Groups or other expert groups in the case of taxa, viruses, strains, variants, and isolates.

The taxonomy of marburgviruses and ebolaviruses has changed several times since the discovery of the type marburgvirus in 1967 [56] and the type ebolavirus in 1976 [3, 21]. The development of their taxonomy has been reviewed in detail [25] and does not need to be repeated here. Key taxonomic changes were approved by the ICTV and published in the eight ICTV Reports [9, 13, 14, 30, 31, 37, 62, 72]. These changes over the years are summarized in Table 1 and are contrasted with the terminology used by laboratory virologists. The table emphasizes several key points addressed in this manuscript. First, laboratory virologists have been using the terms "Marburg virus" and "Ebola virus" for the type viruses of marburgviruses and ebolaviruses, respectively, for decades and have not accepted the novel names for these agents (Lake Victoria marburgvirus and Zaire ebolavirus) listed in the latest (Eighth) ICTV Report [12]. Second, laboratory virologists have embraced the fact that there are several ebolaviruses, rather than one ebolavirus with several subtypes. However, they usually do not use the names listed in the Eighth ICTV Report [12]. Third, laboratory virologists have not yet made the distinction between species (names italicized) and viruses (names not italicized) [6, 8, 26, 63–65], a fact that, as described previously by two of the authors [26], is in part due to the identical spelling of currently approved marburgvirus and ebolavirus species and virus names [26]. We address these and other problems by proposing an

Table 1 Key changes in marburgvirus and ebolavirus taxonomy

Year	ICTV-approved taxonomy/nomenclature	Nomenclature predominantly used by laboratory virologists (as judged by use in publications [25])
1967–1971	None	Marburg virus, Rhabdovirus simiae
1971–1976 [72]	Rhabdovirus monkey (Marburg) virus	Marburg virus
1976–1979 [13]	None	Marburg virus Ebola virus
1979–1982 [30]	Unclassified: Marburg (virus) Unclassified: Ebola (virus)	Marburg virus Ebola virus
1982–1991 [31]	Unclassified: Marburg virus Unclassified: Ebola virus	Marburg virus Ebola virus
1991–1995 [14]	Family *Filoviridae* Genus *Filovirus* Species Marburg virus Species Ebola virus Biotype Sudan Biotype Zaire	Family *Filoviridae* Genus *Filovirus* Virus: Marburg virus[a] Virus: Ebola virus Sudan subtype/Ebola Sudan Zaire subtype/Ebola Zaire
1995–2000 [20]	Family *Filoviridae* Genus *Filovirus* Species Marburg virus (MBGV) Species Ebola virus Reston (EBOV-R) Species Ebola virus Sudan (EBOV-S) Species Ebola virus Zaire (EBOV-Z)	Family *Filoviridae* Genus *Filovirus* Virus: Marburg virus (MBGV) Virus: Ebola virus (EBOV) Reston subtype/Ebola Reston Sudan subtype/Ebola Sudan Zaire subtype/Ebola Zaire
2000–2005 [39]	Order *Mononegavirales* Family *Filoviridae* Genus "Marburg-like viruses" Species *Marburg virus* (MARV) Genus "Ebola-like viruses" Species *Cote d'Ivoire Ebola virus* (CIEBOV) [sic] Species *Reston Ebola virus* (REBOV) Species *Sudan Ebola virus* (SEBOV) Species *Zaire Ebola virus* (ZEBOV)	Family *Filoviridae* Virus: Marburg virus (MBGV, MARV) Virus: Ebola virus (EBOV) Subtype Ivory Coast/Ebola Ivory Coast Subtype Reston/Ebola Reston Subtype Sudan/Ebola Sudan Subtype Zaire/Ebola Zaire
2005–present [12]	Order *Mononegavirales* Family *Filoviridae* Genus *Marburgvirus* Species *Lake Victoria marburgvirus* Virus: Lake Victoria marburgvirus (MARV) Genus *Ebolavirus* Species *Cote d'Ivoire ebolavirus* [sic] Virus: Cote d'Ivoire ebolavirus [sic] (CIEBOV) Species *Reston ebolavirus* Virus: Reston ebolavirus (REBOV) Species *Sudan ebolavirus* Virus: Sudan ebolavirus (SEBOV) Species *Zaire Ebola virus* Virus: Zaire ebolavirus (ZEBOV)	Order *Mononegavirales* Family *Filoviridae* Genus *Marburgvirus* Virus: Marburg virus (MARV) Genus *Ebolavirus* Virus: Ebola virus (Ivory Coast) (EBOV) Virus: Ebola virus (Reston) (EBOV) Virus: Ebola virus (Sudan) (EBOV) Virus: Ebola virus (Zaire), Zaire ebolavirus (EBOV, ZEBOV)

[a] Laboratory virologists often referred to species in their articles, but in the vast majority of cases what they meant [as judged by the authors] is viruses

improved nomenclature for the family *Filoviridae* that reflects terminology usage by laboratory scientists while upholding the rules and regulations of the ICTV. Furthermore, we suggest an updated classification based on newly obtained data.

The classification of marburgviruses and ebolaviruses has stood the test of time

The classification of marburgviruses and ebolaviruses as sister groups in a unique family related to the families *Bornaviridae*, *Paramyxoviridae*, and *Rhabdoviridae* and placed in a common order has been unchallenged since the ICTV approved it [39, 44, 45, 47]. Likewise, it is uncontroversial that there are several different ebolaviruses that obviously should be placed in different species [39, 47]. Article 3 Rule II-3.9 of the International Code for Virus Classification and Nomenclature (ICVCN) states that "[e]xisting names of taxa and viruses should be retained whenever feasible" [9]. We accept and uphold this rule for the names of the order, family, and genera harboring marburgviruses and/or ebolaviruses, as well as for three ebolavirus species. However, because of the lack of acceptance of two species names and several virus names by the laboratory virologist community (Table 1), and because of the confusion of species names with virus names [6, 8, 26, 63–65], we find the retention of several names *not feasible* and here propose changes.

Marburgviruses and ebolaviruses are mononegaviruses

Pringle et al. [45] introduced the order *Mononegavirales* in 1991 as a taxon "to embrace families of [certain] viruses with similar genomic organization and replicative strategies". These viruses, the mononegaviruses, are enveloped and contain a linear, nonsegmented, single-stranded RNA genome with the characteristic general gene order 3′-UTR —core proteins genes—envelope protein genes—polymerase gene—5′-UTR [45]. Marburgviruses and ebolaviruses fulfill these and other criteria for member inclusion [5, 10, 18, 23, 24, 36, 40, 50, 54, 68] and consequently have been assigned to this order [45].

Description of *Mononegavirales* ord. Pringle 1991 [44], Pringle et al. 1991 [45] emend. Bishop and Pringle 1995 [2], emend. Pringle 1997 [46], emend. Pringle 2000 [48], emend. Pringle 2005 [49]

Etymology of *Mononegavirales*: derived from Gre. adj. *μόνος* [*monos*]—alone or single, referring to the single-stranded [RNA] genome of order members; Lat. v. *negare*—to negate, referring to the negative polarity of the single-stranded [RNA] genomes of order members; and suff. *–virales*—ending denoting a virus order [37] → Neo-Lat. n. masc. pl. *Mononegavirales*—the order of [RNA] viruses with single-stranded genomes of negative polarity.

- Valid taxon name (fulfills ICVCN Article 3 Rule II-3.8): yes, because name is compliant with ICVCN Article 3 Rules, in particular Rules VII-3.33, VII-3.34, and IX-3.39 [9]; because it has been published [44]; and because it is associated with descriptive material.
- Accepted name (fulfills ICVCN Article 3 Rule II-3.8): yes, because name is listed in the latest (Eighth) ICTV Report [49] and the updated ICTV Master Species List 2009 (http://talk.ictvonline.org/files/ictv_documents/m/msl/1231.aspx).
- Use of the taxon (Table 2):
  - Style: capitalized, italicized, zero article.
  - Suggested pronunciation: [ˌmɒnəˌnɛgəviːˈrɑːlɨz] (IPA); m**o**-nuh-n**e**-guh-vee-r**a**h-liz (English phonetic notation).
  - Abbreviation: none.
- Use of taxon vernaculars (Table 2):
  - n. sg.: mononegavirus, or, more specific, mononegavirad (-virad: ending denoting a physical member of a virus order [66]). Suggested pronunciation: [ˌmɒnəˌnɛgəˈvɑɪrəs]/[ˌmɒnəˌnɛgəvɨˈrɑːd] (IPA); m**o**-nuh-n**e**-guh-v**ahy**-ruhs/m**o**-nuh-n**e**-guh-vi-r**a**hd (English phonetic notation).
  - n. pl.: mononegaviruses or, more specific, mononegavirads. Suggested pronunciation: [ˌmɒnəˌnɛgəˈvɑɪrəsɨz]/[ˌmɒnəˌnɛgəvɨˈrɑːdz] (IPA); m**o**-nuh-n**e**-guh-v**ahy**-ruhs-iz/m**o**-nuh-n**e**-guh-vi-r**a**hdz (English phonetic notation).
  - adj.: mononegavirus/mononegaviral/mononegavirad. Suggested pronunciation: [ˌmɒnəˌnɛgəˈvɑɪrəs]/[ˌmɒnəˌnɛgəˈvɑɪrəl]/[ˌmɒnəˌnɛgəvɨˈrɑːd] (IPA); m**o**-nuh-n**e**-guh-v**ahy**-ruhs/m**o**-nuh-n**e**-guh-v**ahy**-ruhl/m**o**-nuh-n**e**-guh-vi-r**a**hd (English phonetic notation).
  - Style: lower case, not italicized, zero article.
  - Abbreviation: none.
- Order members are characterized by [2, 44–46, 48, 49]:
  - having a linear, nonsegmented, single-stranded, noninfectious RNA genome of negative polarity with inverse-complementary 3′ and 5′ termini.
  - having an uncapped genomic RNA that is not polyadenylated and does not have a covalently linked protein.
  - replicating by synthesis of a complete antigenome.
  - frequent genetic recombination thus far demonstrated only for members of certain genera (especially genus *Avulavirus*).

Table 2 Order *Mononegavirales*

Incorrect usage	Correct usage	Explanation
Nyamanini and related viruses are novel *Mononegavirales*	Nyamanini and related viruses require the establishment of a novel taxon in the order *Mononegavirales* Nyamanini and related viruses are novel mononegaviruses Nyamanini and related viruses are novel mononegavirads	The order *Mononegavirales* is a taxon. Taxa are theoretical concepts and do not exist physically. They are defined by the properties of physical members. Viruses exist physically. A physical entity cannot be a theoretical concept. Mononegaviruses/mononegavirads are the vernacular names for (the group of) members of the order *Mononegavirales*. Hence, these vernacular names stand for physical entities
Mononegavirales matrix proteins interact with membranes	Mononegavirus matrix proteins interact with membranes Mononegavirad matrix proteins interact with membranes Mononegaviral matrix proteins interact with membranes	The order *Mononegavirales* is a taxon. Taxa are theoretical concepts and therefore do not possess matrix proteins. Mononegaviruses/mononegavirads are the physical members of the order. They have matrix proteins. "*Mononegavirales*" is a noun, whereas "mononegavirus," "mononegaviral," and "mononegavirad" are adjectives
Expression of antigenomic RNA enhances the rescue efficacies of two different members of the *Mononegavirales*	Expression of antigenomic RNA enhances the rescue efficacies of two different members of the order *Mononegavirales*	ICVCN Article 3 Rule IX-3.41 demands that "…the name of taxon [in this case "order"] shall precede the term for the taxonomic unit [in this case "*Mononegavirales*"]" [9]
Identification and characterization of a newly identified member species of the Mononegavirales	Identification and characterization of a newly identified member of the order *Mononegavirales* Identification and characterization of a novel virus requiring the establishment of a new species in the order *Mononegavirales*	The order *Mononegavirales* is a taxon. Names of taxa are italicized. Taxa are concepts, not physical entities, they cannot be identified or characterized. A new virus was identified and characterized, hence it cannot be a new species. It can, however, indicate the need for establishment of a new species

  - having a genome with the gene order 3′-UTR—core protein genes—envelope protein genes—polymerase gene—5′-UTR.
  - transcription of 5–10 mRNA species via polar sequential interrupted synthesis from a single 3′-terminal promoter.
  - having a genome that, to 93–99%, encodes proteins.
  - forming helical nucleocapsids as the functional templates for synthesis of replicative RNA and mRNAs.
  - forming infectious ribonucleoproteins.
  - encoding a virion-associated RNA-dependent RNA polymerase whose catalytic domain is highly homologous to those of other members.
  - forming virions with a molecular mass of 300–1,000 $\times$ 10^6; an S_{20W} of 550–>1,045 S; and a buoyant density in CsCl of 1.18–1.22 g/cm^3.
- Suggested type family: *Paramyxoviridae* (the ICTV currently does not endorse the status of type family. Yet, it is obvious that paramyxoviruses are the best characterized members of the order, and that the order was established after comparing characteristics of non-paramyxoviruses to those of paramyxoviruses).
- Order members: families *Bornaviridae*, *Filoviridae*, *Paramyxoviridae*, and *Rhabdoviridae* [49].
- Possible order members: a family for Nyamanini virus and Midway virus (proposed genus "*Nyavirus*") [35].

Marburgviruses and ebolaviruses are filoviruses

Marburgviruses and ebolaviruses differ from other mononegaviruses. They have longer genomes (≈19 kb) than most other members of the order: the only other mononegaviruses with similarly long genomes are assigned to the paramyxovirus genus *Henipavirus* (Hendra and Nipah viruses) [70] and the proposed paramyxovirus genus "*Jeilongvirus*" (Beilong and J viruses) [19, 28]. Marburgvirus and ebolavirus genomes encode two unusual proteins: VP30 is exceptional in that only pneumoviruses (family *Paramyxoviridae*) encode a protein with possibly similar function (M2-1) [4, 60], and VP24 is unique in that no other similar protein has yet been identified [4]. Marburgviruses and ebolaviruses are the only mammal-infecting members of the order *Mononegavirales* forming truly filamentous virions in the near absence of nonspherical forms [16, 53]. Finally, marburgviruses and ebolaviruses are the only known

mononegaviruses that cause viral hemorrhagic fever in primates [3, 21, 56]. Consequently, marburgviruses and ebolaviruses have been assigned to their own family, *Filoviridae* [22].

Description of *Filoviridae* fam. Kiley et al. 1982 [22] emend. McCormick 1991 [34], emend. Jahrling et al. 1995 [20], emend. Netesov et al. 2000 [39], emend. Feldmann et al. 2005 [12], emend. 2010

Etymology of *Filoviridae*: derived from: Lat. n. neut. sg. *filum*—thread, referring to the unique filamentous morphology of virions produced by family members; and suff. *–viridae*—ending denoting a virus family [13, 72] → Neo-Lat. n. fem. pl. *Filoviridae*—the family of thread-like viruses.

- Valid taxon name (fulfills ICVCN Article 3 Rule II-3.8): yes, because name is compliant with ICVCN Article 3 Rules, in particular Rules VI-3.31, VI-3.32, and IX-3.39 [9]; because it has been published [22]; and because it is associated with descriptive material.
- Accepted name (fulfills ICVCN Article 3 Rule II-3.8): yes, because name is listed in the latest (Eighth) ICTV Report [12] and the updated ICTV Master Species List 2009 (http://talk.ictvonline.org/files/ictv_documents/m/msl/1231.aspx).
- Use of the taxon (Table 3):
  - Style: capitalized, italicized, zero article.
  - Suggested pronunciation: [ˌfiːloʊ'viːrɨdɛ] (IPA); f**ee**-loh-**vee**-ri-d**eh** (English phonetic notation).
  - Abbreviation: none.
- Use of taxon vernaculars (Table 3):
  - n. sg.: filovirus, or, more specific, filovirid (-virid: ending denoting a physical member of a virus family [66]). Suggested pronunciation: [ˌfiːloʊ'vaɪrəs]/[ˌfiːloʊ'viːrɨd] (IPA); f**ee**-loh-**vahy**-ruhs/f**ee**-loh-**vee**-rid (English phonetic notation).
  - n. pl.: filoviruses or, more specific, filovirids. Suggested pronunciation: [ˌfiːloʊ'vaɪrəsɨz]/[ˌfiːloʊ'-viːrɨdz] (IPA); f**ee**-loh-**vahy**-ruhs-iz/f**ee**-loh-**vee**-ridz (English phonetic notation).
  - adj.: filovirus/filoviral/filovirid. Suggested pronunciation: [ˌfiːloʊ'vaɪrəs]/[ˌfiːloʊ'vaɪrəl]/[ˌfiːloʊ'viːrɨd] (IPA); f**ee**-loh-**vahy**-ruhs/f**ee**-loh-**vahy**-ruhl/f**ee**-loh-**vee**-rid (English phonetic notation).
  - Style: lower case, not italicized, zero article.
  - Abbreviation: none.
- Family members are characterized by having the properties of mononegaviruses plus [12, 20, 22, 34, 39]:
  - causing viral hemorrhagic fever in (certain) primates.
  - infecting primates, porcids (pigs) or chiroptera (bats) in nature; artificial adaptation is necessary for infection of rodents, such as mice, hamsters or guinea pigs.
  - replicating in the cytoplasm (similar to paramyxoviruses and most rhabdoviruses, but in contrast to bornaviruses and nucleorhabdoviruses).
  - having long (≈19 kb) genomes, a characteristic they only share with henipaviruses and "jeilongviruses" (other mononegaviruses: ≈8–16 kb).
  - having a genomic RNA that constitutes ≈1.1% of the virion mass, and that has a molecular weight of $\approx 4.2 \times 10^6$.
  - having a genomic RNA that contains one or more gene overlaps.
  - having a genomic RNA that encodes seven structural proteins in the order 3′-UTR-NP-VP35-VP40-GP-VP30-VP24-L-5′-UTR, one of which (VP24) is

Table 3 Family *Filoviridae*

Incorrect usage	Correct usage	Explanation
Ebola and the other filoviruses: a threat to Africa	Ebola virus and other filoviruses: a threat to Africa Ebola virus and other filovirids: a threat to Africa	Vernacular names for taxa are mass nouns, *i.e.* they are preceded by a zero article to indicate that the noun is indefinite
Infections by viruses of the *Filoviridae*	Infections by viruses of the family *Filoviridae* Infections by filoviruses Infections by filovirids	ICVCN Article 3 Rule IX-3.41 requires that "…the name of taxon [in this case "family"] shall precede the term for the taxonomic unit [in this case "*Filoviridae*"]" [9]
Filoviridae threaten the existence of the great apes in Africa	Filoviruses threaten the existence of the great apes in Africa Filovirids threaten the existence of the great apes in Africa	The family *Filoviridae* is a taxon. Taxa are theoretical concepts and do not exist physically. They are defined by the properties of physical members. Viruses exist physically. A physical entity cannot be a theoretical concept. Filoviruses/filovirids are the vernacular names for (the group of) members of the family *Filoviridae*. Hence, these vernacular names stand for physical entities

unique to family members, and one of which (VP30) is partially analogous to a protein expressed only by pneumoviruses.
- having genomes with characteristic transcription initiation and termination signals that are not found in genomes of other mononegaviruses.
- having a polar transcription mode with nonoverlapping or overlapping signals and stepwise attenuation (similar to members of the paramyxovirus subfamily *Paramyxovirinae* and members of the family *Rhabdoviridae*, but different from members of the paramyxovirus subfamily *Pneumovirinae* and members of the family *Bornaviridae*).
- forming nucleocapsids with a buoyant density in CsCl of ≈1.32 g/cm^3.
- forming nucleocapsids consisting of a central axial channel ≈10–15 nm in width surrounded by a central dark layer ≈20 nm in width and an outer helical layer composed of nucleoproteins ≈50 nm in width with cross striations featuring a periodicity of ≈5 nm.
- synthesizing spike glycoproteins ($GP_{1,2}$) that are highly glycosylated with *N*-linked glycans of the complex, hybrid, and oligomannosidic type and *O*-linked glycans of the neutral mucin type, constituting >50% of the total mass.
- synthesizing spike glycoproteins ($GP_{1,2}$) that are classical class I fusion proteins consisting of two subunits that form heterodimers, which associate as trimers.
- synthesizing spike glycoproteins ($GP_{1,2}$) that are acylated at their cytoplasmic tails.
- encoding matrix proteins (VP40) that are not glycosylated (similar to paramyxoviruses and rhabdoviruses, but in contrast to bornaviruses).
- maturing by envelopment of independently assembled nucleocapsids at membrane sites containing inserted virus proteins; budding occurs predominantly from the plasma membrane; the virion envelope is derived from the host-cell membrane and is considered to have a lipid composition similar to that of the plasma membrane.
- forming virions that are filamentous to bacilliform in shape, or U- or 6-shaped, and that can be branched.
- forming virions that can vary greatly in length (up to 14 μm) but have a uniform width of ≈80 nm.
- forming virions with an average molecular weight of ≈3.82 × 10^8; a buoyant density in potassium tartrate of ≈1.14 g/cm^3; an S_{20w} of bacilliform particles of 1.40 (but much higher for longer particles).
- forming virions that are covered with surface projections ≈7 nm in length and spaced at ≈10 nm intervals. Surface projections are trimers of the (processed) protein ($GP_{1,2}$) encoded by gene 4 (GP) and are embedded into the envelope.
- being poorly neutralized in vivo.

- Suggested type genus: *Marburgvirus* (the ICTV currently does not endorse the status of type genus. However, marburgviruses were discovered nine years prior to ebolaviruses, and ebolaviruses were recognized as relatives of marburgviruses, rather than vice versa).
- Family members: genera *Cuevavirus* (tentative, see below), *Ebolavirus*, and *Marburgvirus* [49].

Marburgviruses and ebolaviruses are distinct and belong to different genera

Marburgviruses are endemic in arid woodlands in eastern, south-central, and western Africa, whereas ebolaviruses are endemic in the humid rain forests of central and western Africa [42, 43]. Marburgviruses may be adapted to chiropteran (bat) reservoirs [59], and at least one ebolavirus may infect porcids (pigs) in nature [1]. Marburgvirus and ebolavirus genomes differ from one another by ≥50% at the nucleotide level [57]. Marburgvirus genomes differ from ebolavirus genomes in that they have only one, rather than several gene overlaps [25]. Marburgvirus gene four (GP) expresses only one protein, the spike glycoprotein $GP_{1,2}$ [74], whereas ebolavirus gene four expresses four proteins (sGP, Δ-peptide, $GP_{1,2}$, ssGP) via transcriptional editing that results in open reading frame shifts and, in the case of sGP/Δ-peptide, proteolytic processing [55, 67, 69]. Marburgvirus spike proteins are highly *N*- and *O*-glycosylated but lack sialic acids, whereas ebolavirus spike proteins are highly *N*- and *O*-glycosylated and may contain sialic acids [11, 17, 52, 73]. There is minimal to no serological cross-reactivity between marburgvirions and ebolavirions [11, 51, 71]. Marburgvirions are shorter (average of ≈665 nm in length) than ebolavirions (≈805 nm) [16]. Consequently, marburgviruses and ebolaviruses have been assigned to two different genera, *Marburgvirus* and *Ebolavirus*, respectively [12, 32, 39, 47].

Description of *Marburgvirus* gen. Netesov et al. 1998 (as "Marburg-like viruses") [39, 47] emend. nom. nov. Feldmann et al. 2002 (as *Marburgvirus*) [12, 32] emend. 2010

Etymology of *Marburgvirus*: derived from geo. *Marburg*—short form of Marburg an der Lahn, the city in Hessen [Hesse], Germany, where the type virus of this genus was first isolated; and *–virus*—ending denoting a virus genus

[72] → Neo-Lat. N. neut. sg. *Marburgvirus*—the genus of marburgviruses.

- Valid taxon name (fulfills ICVCN Article 3 Rule II-3.8): yes, because name is compliant with ICVCN Article 3 Rules, in particular Rules IV-3.26, IV-3.27, IV-3.28, and IX-3.39 [9]; because it has been published [12, 32]; and because it is associated with descriptive material.
- Accepted name (fulfills ICVCN Article 3 Rule II-3.8): yes, because name is listed in the latest (Eighth) ICTV Report [12] and the updated ICTV Master Species List 2009 (http://talk.ictvonline.org/files/ictv_documents/m/msl/1231.aspx).
- Use of the taxon (Table 4):
  - Style: capitalized, italicized, zero article.
  - Suggested pronunciation: [ˌmɑrbərg'vɑɪrəs] (IPA); **mahr**-berg-**vahy**-ruhs (English phonetic notation).
  - Abbreviation: none.
- Use of taxon vernaculars (Table 4):
  - n. sg.: marburgvirus (-virus: ending denoting a physical member of a virus genus [66]). Suggested pronunciation: [ˌmɑrbərg'vɑɪrəs] (IPA); **mahr**-berg-**vahy**-ruhs (English phonetic notation).
  - n. pl. marburgviruses. Suggested pronunciation: [ˌmɑrbərg'vɑɪrəsɨz] (IPA); **mahr**-berg-**vahy**-ruhs-iz (English phonetic notation).
  - adj.: marburgvirus/marburgviral. Suggested pronunciation: [ˌmɑrbərg'vɑɪrəs]/[ˌmɑrbərg'vɑɪrəl] (IPA); **mahr**-berg-**vahy**-ruhs/**mahr**-berg-**vahy**-ruhl (English phonetic notation).
  - Style: lower case, not italicized, one word, zero article.
  - Abbreviation: none.
- Genus members are characterized by having the properties of filoviruses plus [12, 57, 61]:
  - having a single gene overlap.
  - gene 4 (GP) encoding only the spike glycoprotein ($GP_{1,2}$), whose expression does not involve cotranscriptional editing.
  - having their peak infectivity associated with virions ≈665 nm in length.
  - having genomes that differ from that of the type virus of the type species of the type genus of the family *Filoviridae* (Marburg virus) by $<50\%$ at the nucleotide level.
  - producing virions that show almost no antigenic cross-reactivity with ebolavirions.
- Type species: *Marburg marburgvirus* (previously *Lake Victoria marburgvirus*).
- Genus members: species *Marburg marburgvirus.*

Description of *Ebolavirus* gen. Netesov et al. 1998 (as "Ebola-like viruses") [39, 47] emend. nom. nov. Feldmann et al. 2002 (as *Ebolavirus*) [12, 32] emend. 2010

Etymology of *Ebolavirus*: derived from geo. *Ebola*—name of the headstream of the Mongala River, a tributary of the Zaire River (today Congo River) in Zaire (today the

Table 4 Genera *Cuevavirus, Ebolavirus,* and *Marburgvirus*

Incorrect usage	Correct usage	Explanation
Ebolavirus VP35 suppresses the innate immune response	Ebolavirus VP35 suppresses the innate immune response VP35 of ebolaviruses suppresses the innate immune response Reston virus VP35 suppresses the innate immune response	The genus *Ebolavirus* is a taxon. Names of taxa are italicized. Taxa are concepts, not physical entities. They do not possess genes or express proteins. VP35 is a protein expressed by an ebolavirus, such as Reston virus
A model for marburgvirus based on studies using hamsters	A model for Marburg virus based on studies using hamsters A model for a marburgvirus based on studies using hamsters A model for marburgviruses based on studies using hamsters	The vernacular name for the members of the genus *Marburgvirus* is marburgviruses. Marburg virus is a marburgvirus. An animal model can either be developed for a particular marburgvirus, such as Marburg virus, or for all marburgviruses, such as Marburg virus and Ravn virus
Filoviruses include the genera *ebolavirus*, *marburgvirus*, and *cuevavirus*	The family *Filoviridae* includes the genera *Ebolavirus*, *Marburgvirus*, and *Cuevavirus* Filoviruses include ebolaviruses, marburgviruses, and cuevaviruses Filovirids include ebolaviruses, marburgviruses, and cuevaviruses	Filoviruses/filovirids is the vernacular name for the members of the family *Filoviridae*. Filoviruses/filovirids are physical entities, but the family *Filoviridae* is a taxon. Taxa, such as families, include other taxa, such as the genera *Ebolavirus*, *Marburgvirus*, and *Cuevavirus*, the names of which are always italicized and capitalized. Physical entities do not include taxa

Democratic Republic of the Congo), where the type virus of this genus was thought to be first encountered; and *–virus*—ending denoting a virus genus [72] → Neo-Lat. N. neut. sg. *Ebolavirus*—the genus of ebolaviruses.

- Valid taxon name (fulfills ICVCN Article 3 Rule II-3.8): yes, because name is compliant with ICVCN Article 3 Rules, in particular Rules IV-3.26, IV-3.27, IV-3.28, and IX-3.39 [9]; because it has been published [12, 32]; and because it is associated with descriptive material.
- Accepted name (fulfills ICVCN Article 3 Rule II-3.8): yes, because name is listed in the latest (Eighth) ICTV Report [12] and the updated ICTV Master Species List 2009 (http://talk.ictvonline.org/files/ictv_documents/m/msl/1231.aspx).
- Use of the taxon (Table 4):
  - Style: capitalized, italicized, zero article.
  - Suggested pronunciation: [iːˌboʊləˈvaɪrəs] (IPA); ee-**boh**-luh-**vahy**-ruhs (English phonetic notation).
  - Abbreviation: none.
- Use of taxon vernaculars (Table 4):
  - n. sg.: ebolavirus (-virus: ending denoting a physical member of a virus genus [66]). Suggested pronunciation: [iːˌboʊləˈvaɪrəs] (IPA); ee-**boh**-luh-**vahy**-ruhs (English phonetic notation).
  - n. pl. ebolaviruses. Suggested pronunciation: [iːˌboʊləˈvaɪrəsɪz] (IPA); ee-**boh**-luh-**vahy**-ruhs-iz (English phonetic notation).
  - adj.: ebolavirus/ebolaviral. Suggested pronunciation: [iːˌboʊləˈvaɪrəs]/[iːˌboʊləˈvaɪrəl] (IPA); ee-**boh**-luh-**vahy**-ruhs/ee-**boh**-luh-**vahy**-ruhl (English phonetic notation).
  - Style: lower case, not italicized, one word, zero article.
  - Abbreviation: none.
- Genus members are characterized by having the properties of filoviruses plus [12, 57, 61]:
  - having several gene overlaps.
  - gene 4 (GP) encoding four proteins. The soluble glycoprotein (sGP) and its cleavage product Δ-peptide are the primary expression products; the spike glycoprotein ($GP_{1,2}$) and a secondary soluble glycoprotein (ssGP) are expressed via cotranscriptional editing.
  - having their peak infectivity associated with virions ≈805 nm in length.
  - having genomes that differ from that of the type virus of the type species of the type genus of the family *Filoviridae* (Marburg virus) by ≥50% at the nucleotide level, and from the type virus of the type species of the genus *Ebolavirus* (Ebola virus) by <50% at the nucleotide level.
  - producing virions that show almost no antigenic cross-reactivity with marburgvirions.
- Type species: *Zaire ebolavirus.*
- Genus members: species *Bundibugyo ebolavirus* (new, see below), *Reston ebolavirus*, *Sudan ebolavirus*, *Taï Forest ebolavirus* (previously Cote d'Ivoire ebolavirus [sic], see below), and *Zaire ebolavirus.*

The genus *Marburgvirus* contains only one species

At least five lineages of marburgviruses exist according to the most recent phylogenetic data. Virus genomes of four of these lineages differ from each other only by 0.0–7.4%. Genomes from viruses of the fifth lineage reach 21% nucleotide difference compared to the four other lineages [57]. Representatives of all lineages are identical in gene order, number and position of gene overlaps, and other structural and organizational features. Representatives of all lineages cross-react serologically. Genomes of even the most divergent marburgvirus lineage do not reach the 30% nucleotide difference cut-off established below for differentiating members of different ebolavirus species. We suggest extrapolating the same cut-off criterion to marburgvirus species. Consequently, there is currently the need for recognition of only one marburgvirus species.

Description of *Marburg marburgvirus* sp. Netesov et al. 1998 (as *Marburg virus*) [39, 47] emend. nom. nov. Feldmann et al. 2002 (as *Lake Victoria marburgvirus*) [12, 32] emend. nom. nov. 2010 (as *Marburg marburgvirus*)

Etymology of *Marburg marburgvirus*: derived from geo. *Marburg*—short form of Marburg an der Lahn, the city in Hessen [Hesse], Germany, where the type virus of this species was first isolated; and *marburgvirus*—the genus of marburgviruses → the Marburg species of marburgviruses.

- Valid taxon name (fulfills ICVCN Article 3 Rule II-3.8): yes, because name is compliant with ICVCN Article 3 Rules, in particular Rule IX-3.40 [9]; because it has been published (this article); and because it is associated with descriptive material.
- Accepted name (fulfills ICVCN Article 3 Rule II-3.8): no, because name has yet to be accepted by the ICTV.
- Use of the taxon (Table 5):
  - Style: capitalized, italicized, zero article.

Table 5 Species *Marburg marburgvirus, Bundibugyo ebolavirus, Reston ebolavirus, Sudan ebolavirus, Taï Forest ebolavirus, Zaire ebolavirus*, and *Lloviu cuevavirus*

Incorrect usage	Correct usage	Explanation
Bats may be reservoir hosts for *Reston ebolavirus*	Bats may be reservoir hosts for Reston virus Bats may reservoir hosts for members of the species *Reston ebolavirus*	The species *Reston ebolavirus* is a taxon. Names of taxa are italicized. Taxa are concepts, not physical entities. They cannot be discovered because they are invented, rather than real. Taxa are preceded by a zero article. Members of taxa, such as Reston virus, can be discovered in animals
A novel vaccine candidate protects mice against infection with Marburg virus and against all species of Ebola Virus	A novel vaccine candidate protects mice against infection with Marburg virus and against all ebolaviruses A novel vaccine candidate protects mice against infection with Marburg virus and against members of all ebolavirus species	Species are taxa. They cannot infect an animal. Viruses infect animals. Ebola is a river. Ebola virus is a virus. There is only one Ebola virus, but there are several ebolavirus species
Several species of Ebola virus have been identified	Several species of ebolaviruses have been established	Species are taxa, *i.e.* abstract concepts. They cannot be identified, discovered, or go extinct. Viruses are physical entities. They cannot be defined. Taxa are established, whereas members are described

  - Suggested pronunciation: [‘mɑrbərg ˌmɑrbərg’vɑɪrəs] (IPA); **mahr**-berg **mahr**-berg-**vahy**-ruhs (English phonetic notation).
  - Abbreviation: none.
- Use of taxon vernaculars (Table 5):
  - n. sg.: Marburg marburgvirus. Suggested pronunciation: [‘mɑrbərg ˌmɑrbərg’vɑɪrəs] (IPA); **mahr**-berg **mahr**-berg-**vahy**-ruhs (English phonetic notation).
  - n. pl. Marburg marburgviruses. Suggested pronunciation: [‘mɑrbərg ˌmɑrbərg’vɑɪrəsɨz] (IPA); **mahr**-berg **mahr**-berg-**vahy**-ruhs-iz (English phonetic notation).
  - adj.: Marburg marburgvirus/Marburg marburgviral. Suggested pronunciation: [‘mɑrbərg ˌmɑrbərg’vɑɪrəs]/[‘mɑrbərg ˌmɑrbərg’vɑɪrəl] (IPA); **mahr**-berg **mahr**-berg-**vahy**-ruhs/**mahr**-berg **mahr**-berg-**vahy**-ruhl (English phonetic notation).
  - Style: lower case, not italicized, one word, zero article.
  - Abbreviation: none.
- Species members are characterized by having the properties of marburgviruses (because there is currently only one marburgvirus species) [12, 57, 61]. They have genomes that differ from that of the type virus of the type species of the genus *Marburgvirus* (Marburg virus) by $<30\%$ at the nucleotide level. A 30% amino acid sequence difference in the spike glycoprotein $GP_{1,2}$ may be used as a marburgvirus species demarcation cut-off criterion in the absence of full genomic data.
- Suggested type virus: Marburg virus (formerly Lake Victoria marburgvirus).
- Species members: Marburg virus and Ravn virus (formerly also Lake Victoria marburgvirus).
- Justification of name change: The name “*Lake Victoria marburgvirus*” was introduced for this species by the ICTV in 2002. This change was not accepted by the virology community, and barely has been used. The name contradicts ICVCN Article 3 Rule III-3.23 (“A species name shall consist of as few words as practicable…”) and Rule II-3.12: “…In general, short names are desirable and the number of syllables should be kept to a minimum” [9].

The genus *Ebolavirus* contains five species

The first ebolaviruses were discovered in 1976, when simultaneous viral hemorrhagic fever outbreaks occurred in Zaire (today Democratic Republic of the Congo) and Sudan [3, 21, 41]. In 1983, convincing data were published demonstrating that the viruses causing the two outbreaks were antigenically related, but not identical [7, 33, 51]. In the following years, two additional ebolaviruses were discovered that, while antigenically cross-reactive with the Zaire and Sudan viruses, were unique: the first in 1989 in the USA and the second in 1994 in the Republic of Côte d’Ivoire, [11, 15, 27]. Today, full-length genomic sequences are available for isolates of all of these viruses. Their comparison reveals that the genomes of the four viruses differ from each other by 36.7–42.3% [58]. ICVCN Article 3 Rule III-3.21 states that “[a] virus species is defined as a

polythetic class of viruses that constitutes a replicating lineage and occupies a particular ecological niche" [9]. Due to the genomic sequence diversity and the fact that the four viruses are endemic to different geographic areas and possibly different reservoir hosts, the creation of several different ebolavirus species, first accepted by the ICTV in 1995 [20], has retrospectively been justified. In 2008, a fifth ebolavirus was described whose genomic sequence differed from previously recognized viruses by 31.7–42.4% [58]. Thus, far, a formal description of a new species for this virus has not yet been forwarded to the ICTV. Here we describe all five ebolavirus species.

Description of *Bundibugyo ebolavirus* sp. nov. Towner et al. 2009 [58]

Etymology of *Bundibugyo ebolavirus*: derived from geo. *Bundibugyo*—name of the chief town of Bundibugyo District in the Republic of Uganda, where members of this species were first encountered; and *ebolavirus*—the genus of ebolaviruses → the Bundibugyo species of ebolaviruses.

- Valid taxon name (fulfills ICVCN Article 3 Rule II-3.8): yes, because name is compliant with ICVCN Article 3 Rules, in particular Rule IX-3.40 [9]; because it has been published (this article); and because it is associated with descriptive material.
- Accepted name (fulfills ICVCN Article 3 Rule II-3.8): no, because name has yet to be accepted by the ICTV.
- Use of the taxon (Table 5):
  - Style: capitalized, italicized, zero article.
  - Suggested pronunciation: [ˌbʊndiːˈbʊdʒɔː iːˌbɔʊlə'-vɑɪrəs] (IPA); **boon**-dee-**boo**-jaw ee-**boh**-luh-**vahy**-ruhs or **boon**-dee-**boo**-joh ee-**boh**-luh-**vahy**-ruhs (English phonetic notation).
  - Abbreviation: none.
- Use of taxon vernaculars (Table 5):
  - n. sg.: Bundibugyo ebolavirus. Suggested pronunciation: [ˌbʊndiːˈbʊdʒɔː iːˌbɔʊləˈvɑɪrəs] (IPA); **boon**-dee-**boo**-jaw ee-**boh**-luh-**vahy**-ruhs or **boon**-dee-**boo**-joh ee-**boh**-luh-**vahy**-ruhs (English phonetic notation).
  - n. pl. Bundibugyo ebolaviruses. Suggested pronunciation: [ˌbʊndiːˈbʊdʒɔː iːˌbɔʊləˈvɑɪrəsɪz] (IPA); **boon**-dee-**boo**-jaw ee-**boh**-luh-**vahy**-ruhs-iz or **boon**-dee-**boo**-joh ee-**boh**-luh-**vahy**-ruhs-iz (English phonetic notation).
  - adj.: Bundibugyo ebolavirus/Bundibugyo ebolaviral. Suggested pronunciation: [ˌbʊndiːˈbʊdʒɔː iːˌbɔʊlə'-vɑɪrəs]/[ˌbʊndiːˈbʊdʒɔː iːˌbɔʊləˈvɑɪrəl] (IPA); **boon**-dee-**boo**-jaw ee-**boh**-luh-**vahy**-ruhs or **boon**-dee-**boo**-joh ee-**boh**-luh-**vahy**-ruhs/**boon**-dee-**boo**-jaw ee-**boh**-luh-**vahy**-ruhl or **boon**-dee-**boo**-joh ee-**boh**-luh-**vahy**-ruhl (English phonetic notation).
  - Style: lower case, not italicized, one word, zero article.
  - Abbreviation: none.
- Species members are characterized by having the properties of ebolaviruses plus [12, 57, 61]:
  - being endemic in the Republic of Uganda.
  - having genomes with three gene overlaps (VP35/VP40, GP/VP30, VP24/L).
  - having a full-length genomic sequence different from the type virus of the type species of the genus *Ebolavirus* (Ebola virus) by ≥30% but different from the type virus of the species *Bundibugyo ebolavirus* by <30%. A 30% amino acid sequence difference in the spike glycoprotein $GP_{1,2}$ may be used as an ebolavirus species demarcation cut-off criterion in the absence of full genomic data.
- Suggested type virus: Bundibugyo virus.
- Species members: Bundibugyo virus.

Description of *Reston ebolavirus* sp. Netesov et al. 1998 (as *Reston Ebola virus*) [39, 47] emend. nom. nov. Feldmann et al. 2002 (as *Reston ebolavirus*) [12, 32]

Etymology of *Reston ebolavirus*: derived from geo. *Reston*—the town in Virginia, USA, where members of this species were first encountered; and *ebolavirus*—the genus of ebolaviruses → the Reston species of ebolaviruses.

- Valid taxon name (fulfills ICVCN Article 3 Rule II-3.8): yes, because name is compliant with ICVCN Article 3 Rules, in particular Rule IX-3.40 [9]; because it has been published [12, 32]; and because it is associated with descriptive material.
- Accepted name (fulfills ICVCN Article 3 Rule II-3.8): yes, because name is listed in the latest (Eighth) ICTV Report [12] and the updated ICTV Master Species List 2009 (http://talk.ictvonline.org/files/ictv_documents/m/msl/1231.aspx).
- Use of the taxon (Table 5):
  - Style: capitalized, italicized, zero article.
  - Suggested pronunciation: [ˈrɛstən iːˌbɔʊləˈvɑɪrəs] (IPA); **res**-tuhn ee-**boh**-luh-**vahy**-ruhs (English phonetic notation).
  - Abbreviation: none.
- Use of taxon vernaculars (Table 5):
  - n. sg.: Reston ebolavirus. Suggested pronunciation: [ˈrɛstən iːˌbɔʊləˈvɑɪrəs] (IPA); **res**-tuhn ee-**boh**-luh-**vahy**-ruhs (English phonetic notation).

  - n. pl. Reston ebolaviruses. Suggested pronunciation: [‘rɛstən iːˌboʊlə’vaɪrəsiz] (IPA); **res**-tuhn ee-**boh**-luh-**vahy**-ruhs-iz (English phonetic notation).
  - adj.: Reston ebolavirus/Reston ebolaviral. Suggested pronunciation: [‘rɛstən iːˌboʊlə’vaɪrəs]/[‘rɛstən iːˌboʊlə’vaɪrəl] (IPA); **res**-tuhn ee-**boh**-luh-**vahy**-ruhs/**res**-tuhn ee-**boh**-luh-**vahy**-ruhl (English phonetic notation).
  - Style: lower case, not italicized, one word, zero article.
  - Abbreviation: none.
- Species members are characterized by having the properties of ebolaviruses plus [12, 57, 61]:
  - being endemic in the Republic of the Philippines.
  - having genomes with two gene overlaps (VP35/VP40, VP24/L).
  - having a full-length genomic sequence different from the type virus of the type species of the genus *Ebolavirus* (Ebola virus) by ≥30% but different from the type virus of the species *Reston ebolavirus* by <30%. A 30% amino acid sequence difference in the spike glycoprotein $GP_{1,2}$ may be used as an ebolavirus species demarcation cut-off criterion in the absence of full genomic data.
- Suggested type virus: Reston virus (formerly Reston ebolavirus).
- Species members: Reston virus.

Description of *Sudan ebolavirus* sp. Netesov et al. 1998 (as *Sudan Ebola virus*) [39, 47] emend. nom. nov. Feldmann et al. 2002 (as *Sudan ebolavirus*) [12, 32]

Etymology of *Sudan ebolavirus*: derived from geo. *Sudan*—English conventional short form of the Republic of Sudan, where members of this species were first encountered; and *ebolavirus*—the genus of ebolaviruses → the Sudan species of ebolaviruses.

- Valid taxon name (fulfills ICVCN Article 3 Rule II-3.8): yes, because name is compliant with ICVCN Article 3 Rules, in particular Rule IX-3.40 [9]; because it has been published [12, 32]; and because it is associated with descriptive material.
- Accepted name (fulfills ICVCN Article 3 Rule II-3.8): yes, because name is listed in the latest (Eighth) ICTV Report [12] and the updated ICTV Master Species List 2009 (http://talk.ictvonline.org/files/ictv_documents/m/msl/1231.aspx).
- Use of the taxon (Table 5):
  - Style: capitalized, italicized, zero article.
  - Suggested pronunciation: [sʊ’dæn iːˌboʊlə’vaɪrəs] (IPA); soo-**dan** ee-**boh**-luh-**vahy**-ruhs (English phonetic notation).
  - Abbreviation: none.
- Use of taxon vernaculars (Table 5):
  - n. sg.: Sudan ebolavirus. Suggested pronunciation: [sʊ’dæn iːˌboʊlə’vaɪrəs] (IPA); soo-**dan** ee-**boh**-luh-**vahy**-ruhs (English phonetic notation).
  - n. pl. Sudan ebolaviruses. Suggested pronunciation: [sʊ’dæn iːˌboʊlə’vaɪrəsiz] (IPA); soo-**dan** ee-**boh**-luh-**vahy**-ruhs-iz (English phonetic notation).
  - adj.: Sudan ebolavirus/Sudan ebolaviral. Suggested pronunciation: [sʊ’dæn iːˌboʊlə’vaɪrəs]/[sʊ’dæn iːˌboʊlə’vaɪrəl] (IPA); soo-**dan** ee-**boh**-luh-**vahy**-ruhs/soo-**dan** ee-**boh**-luh-**vahy**-ruhl (English phonetic notation).
  - Style: lower case, not italicized, one word, zero article.
  - Abbreviation: none.
- Species members are characterized by having the properties of ebolaviruses plus [12, 57, 61]:
  - being endemic in the Republic of Sudan and the Republic of Uganda.
  - having genomes with three gene overlaps (VP35/VP40, GP/VP30, VP24/L).
  - having a full-length genomic sequence different from the type virus of the type species of the genus *Ebolavirus* (Ebola virus) by ≥30% but different from the type virus of the species *Sudan ebolavirus* by <30%. A 30% amino acid sequence difference in the spike glycoprotein $GP_{1,2}$ may be used as an ebolavirus species demarcation cut-off criterion in the absence of full genomic data.
- Suggested type virus: Sudan virus (formerly Sudan ebolavirus).
- Species members: Sudan virus.

Description of *Taï Forest ebolavirus* sp. Netesov et al. 1998 (as *Cote d’Ivoire Ebola virus* [sic]) [39, 47] emend. nom. nov. Feldmann et al. 2002 (as *Cote d’Ivoire ebolavirus* [sic]) [12, 32] nom. nov. 2010 (as *Taï Forest ebolavirus*)

Etymology of *Taï Forest ebolavirus*: derived from geo. *Parc National de Taï* [Taï National Park]—the place in the Republic of Côte d’Ivoire, where members of this species were first encountered; and *ebolavirus*—the genus of ebolaviruses → the Taï Forest species of ebolaviruses.

- Valid taxon name (fulfills ICVCN Article 3 Rule II-3.8): yes, because name is compliant with ICVCN Article 3 Rules, in particular Rule IX-3.40 [9]; because it has been published (this article); and because it is associated with descriptive material.

- Accepted name (fulfills ICVCN Article 3 Rule II-3.8): no, because name has yet to be accepted by the ICTV.
- Use of the taxon (Table 5):
  - Style: capitalized, italicized, zero article.
  - Suggested pronunciation: [tɑ:'i: 'fɔ:rɨst i:ˌboʊlə'-vɑɪrəs] (IPA); tah-**ee faw-**rist ee-**boh**-luh-**vahy**-ruhs (English phonetic notation).
  - Abbreviation: none.
- Use of taxon vernaculars (Table 5):
  - n. sg.: Taï Forest ebolavirus. Suggested pronunciation: [tɑ:'i: 'fɔ:rɨst i:ˌboʊlə'vɑɪrəs] (IPA); tah-**ee faw-**rist ee-**boh**-luh-**vahy**-ruhs (English phonetic notation).
  - n. pl. Taï Forest ebolaviruses. Suggested pronunciation: [tɑ:'i: 'fɔ:rɨst i:ˌboʊlə'vɑɪrəsɨz] (IPA); tah-**ee faw-**rist ee-**boh**-luh-**vahy**-ruhs-iz.
  - adj.: Taï Forest ebolavirus/Taï Forest ebolaviral. Suggested pronunciation: [tɑ:'i: 'fɔ:rɨst i:ˌboʊlə'-vɑɪrəs]/[tɑ:'i: 'fɔ:rɨst i:ˌboʊlə'vɑɪrəl] (IPA); tah-**ee faw-**rist ee-**boh**-luh-**vahy**-ruhs/tah-**ee faw-**rist ee-**boh**-luh-**vahy**-ruhl (English phonetic notation).
  - Style: lower case, not italicized, one word, zero article.
  - Abbreviation: none.
- Species members are characterized by having the properties of ebolaviruses plus [12, 57, 61]:
  - being endemic in the Republic of Côte d'Ivoire.
  - having genomes with three gene overlaps (VP35/VP40, GP/VP30, VP24/L).
  - having a full-length genomic sequence different from the type virus of the type species of the genus *Ebolavirus* (Ebola virus) by ≥30% but different from the type virus of the species *Taï Forest ebolavirus* by <30%. A 30% amino acid sequence difference in the spike glycoprotein $GP_{1,2}$ may be used as an ebolavirus species demarcation cut-off criterion in the absence of full genomic data.
- Suggested type virus: Taï Forest virus (formerly Cote d'Ivoire ebolavirus [sic]).
- Species members: Taï Forest virus.

Description of *Zaire ebolavirus* sp. Netesov et al. 1998 (as *Zaire Ebola virus*) [39, 47] emend. nom. nov. Feldmann et al. 2002 (as *Zaire ebolavirus*) [12, 32]

Etymology of *Zaire ebolavirus*: derived from geo. *Zaire*—English conventional short form of the Republic of Zaire (today the Democratic Republic of the Congo), where members of this species were first encountered; and *ebolavirus*—the genus of ebolaviruses → the Zaire species of ebolaviruses.

- Valid taxon name (fulfills ICVCN Article 3 Rule II-3.8): yes, because name is compliant with ICVCN Article 3 Rules, in particular Rule IX-3.40 [9]; because it has been published [12, 32]; and because it is associated with descriptive material.
- Accepted name (fulfills ICVCN Article 3 Rule II-3.8): yes, because name is listed in the latest (Eighth) ICTV Report [12] and the updated ICTV Master Species List 2009 (http://talk.ictvonline.org/files/ictv_documents/m/msl/1231.aspx).
- Use of the taxon (Table 5):
  - Style: capitalized, italicized, zero article.
  - Suggested pronunciation: [zɑ:'ɪər i:ˌboʊlə'vɑɪrəs] (IPA); zah-**eer** ee-**boh**-luh-**vahy**-ruhs (English phonetic notation).
  - Abbreviation: none.
- Use of taxon vernaculars (Table 5):
  - n. sg.: Zaire ebolavirus. Suggested pronunciation: [zɑ:'ɪər i:ˌboʊlə'vɑɪrəs] (IPA); zah-**eer** ee-**boh**-luh-**vahy**-ruhs (English phonetic notation).
  - n. pl. Zaire ebolaviruses. Suggested pronunciation: [zɑ:'ɪər i:ˌboʊlə'vɑɪrəsɨz] (IPA); zah-**eer** ee-**boh**-luh-**vahy**-ruhs-iz (English phonetic notation).
  - adj.: Zaire ebolavirus/Zaire ebolaviral. Suggested pronunciation: [zɑ:'ɪər i:ˌboʊlə'vɑɪrəs]/[zɑ:'ɪər i:ˌboʊlə'vɑɪrəl] (IPA); zah-**eer** ee-**boh**-luh-**vahy**-ruhs/zah-**eer** ee-**boh**-luh-**vahy**-ruhl (English phonetic notation).
  - Style: lower case, not italicized, one word, zero article.
  - Abbreviation: none.
- Species members are characterized by having the properties of ebolaviruses plus [12, 57, 61]:
  - being endemic in Democratic Republic of the Congo, Gabonese Republic, and Republic of the Congo.
  - having genomes with two or three gene overlaps (VP35/VP40, GP/VP30, VP24/L; VP24 and L overlap only if the second, rather than the first, transcription termination signal of VP24 is used).
  - having a full-length genomic sequence different from the type virus of the type species of the genus *Ebolavirus* (Ebola virus) by <30%. A 30% amino acid sequence difference in the spike glycoprotein $GP_{1,2}$ may be used as an ebolavirus species demarcation cut-off criterion in the absence of full genomic data.
- Suggested type virus: Ebola virus (formerly Zaire ebolavirus).
- Species members: Ebola virus.
- Comment: Note that the pronunciation of "Ebola virus" (eh-**bo**-luh **vahy**-ruhs) is different from that of

"ebolavirus/*Ebolavirus*/*ebolavirus*" (ee-**boh**-luh **vahy**-ruhs). This is because "Ebola" is the name for a river that is pronounced in French (Ébola), whereas "ebolavirus" is an artificial contraction of the words "Ebola" and "virus," to be written without a diacritical mark. The change in pronunciation is preferable over the introduction of diacritical marks ("ébolavirus/*ébolavirus*") as most databases cannot handle them and most English-speaking scientists tend to forget or ignore them.

Marburg virus and Ravn virus are distinct viruses that are members of the same species

According to ICVCN Article 3 Rule I-3.3, "[t]he ICTV is not responsible for classification and nomenclature of virus taxa below the rank of species. The classification and naming of serotypes, genotypes, strains, variants and isolates of virus species is the responsibility of acknowledged international specialist groups. It is the responsibility of ICTV Study Groups to decide if an isolate or a group of isolates should constitute a species" [9]. Traditionally, filoviruses were named by their discoverers in original publications, and these names were then accepted, and sometimes changed, by the ICTV *Filoviridae* Study Group. The names recommended and recognized by the Study Group and those used by laboratory virologists are depicted in Table 1. ICVCN Article 3 Rule I-3.3 states that "[t]he policy of the ICTV is that as far as is possible, decisions on questions of taxonomy and nomenclature should reflect *the majority view of the appropriate virological constituency*" [emphasis added by the authors] [9]. Rule II-3.19 states that "…[w]hen names are universally used by virologists in published work, these or derivatives shall be the preferred basis for creating names, irrespective of national origin" [9]. This rule was followed for most of the history of filovirology. However, in 2002/2005, the *Filoviridae* Study Group followed ICTV guidance and recommended to rename filoviruses and to create virus names that are identical in spelling to species names [12, 32], a possible violation of ICVCN Article 3 Rule III-3.24 ("A species name must provide an appropriately unambiguous identification of the species. [It] should not be in a form that could be easily confused with the names of other taxa") [9]. Five to eight years have passed since the introduction of the name Lake Victoria marburgvirus. Yet, most laboratory scientists still do not use this term either in publications or in seminars. Instead, the overwhelming majority of publications refer to "Marburg virus" (Table 6), a preference that is also followed by the public press. ICVCN Article 2.1 emphasizes that "[t]he essential principles of virus nomenclature are (1) to aim for stability; (2) to avoid or reject the use of names which might cause error or confusion; (3) to avoid the unnecessary creation of names" [9]. Introducing the name Lake Victoria marburgvirus was a mistake, as it contradicts principle (1), while the introduction of virus names identical in spelling to species names contradicts principle (2), consequently contradicting principle (3). Here, we rectify this situation by recommending that the traditional virus name ("Marburg virus") be used. Retrospectively, the virus nomenclature in most published articles will then be correct. Likewise, press articles, which almost invariably refer to "Marburg virus" will be correct retrospectively and prospectively. As the traditional name is different from the species name, confusing species and virus names will be much more difficult, even in the absence of taxonomic education.

As mentioned above, five lineages of marburgviruses are currently recognized. The genomes of representative marburgvirus variants of one of these lineages differs from all others by up to 21.3% in nucleotide sequence, whereas the genomes of variants from the other four lineages differ from each other only by as much as 0.0–7.8% [57]. To reflect the clear dichotomy of marburgvirus variants in formal classification, we suggest the existence of two distinct viruses belonging to the same species. Consequently, variants of the four related lineages continue to represent Marburg virus, the type virus of the species *Marburg marburgvirus*. We suggest the name Ravn virus and the abbreviation RAVV for a second virus in the same species to represent the divergent variants 02Uga2007, 09DRC1999, 44Bat2007, 188Bat2007, 982Bat2008, and Ravn (see [59]). Such a solution to this problem is hardly radical, since similar decisions have been made elsewhere, for instance in the case of Amur, Da Bie Shan, and Hantaan viruses (all of which are members of the species *Hantaan virus*).

Description of Marburg virus vir. Siegert et al. 1967 (as Marburg virus) [56] nom. nov. Feldmann et al. 2005 (as Lake Victoria marburgvirus]) [12, 32] nom. nov. 2010 (reverted to Marburg virus)

Etymology of Marburg virus: derived from geo. *Marburg*—short form of Marburg an der Lahn, the city in Hessen [Hesse], Germany, where this virus was first isolated; and Lat. n. neut. sg. *virus*—poison, slime, venom.

- Use of the name (Table 7):
  - Style: first word capitalized (because proper noun), not italicized, all types of articles.
  - Suggested pronunciation: [ˌmɑrbərg vaɪrəs] (IPA); **mahr**-berg **vahy**-ruhs (English phonetic notation).
  - Abbreviation: MARV.

Table 6 Use of ICTV-accepted virus names versus use of colloquial terms since the introduction of the most recent ICTV nomenclature in 2002 [32] (as of February 28, 2010)

	Occurrence in PubMed article titles	Occurrence in PubMed articles
"Lake Victoria marburgvirus" (ICTV)	1	6
"Marburg virus"	57	202
"Zaire ebolavirus" (ICTV)	7	35
"Zaire Ebola virus"	3	14
"Ebola virus Zaire"	2	5
"Ebola Zaire [virus]"	3	23
"Ebola virus"[a]	244	416
"Reston ebolavirus" (ICTV)	1	8
"Reston Ebola virus"	3	5
"Ebola virus Reston"	2	2
"Ebola Reston [virus]"	5	7
"Sudan ebolavirus" (ICTV)	0	8
"Sudan Ebola virus"	2	2
"Ebola virus Sudan"	1	2
"Ebola Sudan [virus]"	1	4
"Cote d'Ivoire ebolavirus" [sic] (ICTV)	0	3
"Côte d'Ivoire ebolavirus"	0	3
"Cote d'Ivoire Ebola virus" [sic]	0	7
"Côte d'Ivoire Ebola virus"	0	7
"Ivory Coast ebolavirus"	0	3
"Ebola Ivory Coast [virus]"	0	11
"Ebola Côte d'Ivoire [virus]"	0	7

Note that this search does not differentiate between species and viruses. However, in the vast majority of articles that refer to species names, virus names are actually meant [as judged by the authors]

[a] Ebola virus was used predominantly, but not exclusively, for "Zaire ebolavirus"—hence the correct number is slightly smaller than the one stated in this table

Table 7 Marburg virus, Ravn virus, Bundibugyo virus, Ebola virus, Reston virus, Sudan virus, Taï Forest virus, and Lloviu virus

Incorrect usage	Correct usage	Explanation
Sudan ebolavirus causes severe hemorrhagic fever	Sudan virus causes severe hemorrhagic fever	Sudan virus is a physical entity. It is not a taxon. Names of taxa are italicized, viruses are not
Ebola and the other filoviruses: a threat to Africa	Ebola virus and other filoviruses: a threat to Africa	Ebola is a river in the Democratic Republic of the Congo. Ebola does not threaten Africa, but Ebola virus may do so one day

- Virus variants are characterized by having the properties of Marburg marburgviruses plus:
  - diverging in genomic nucleotide sequence from the type variant of the type virus of the species *Marburg marburgvirus* (Musoke) by $<10\%$.
- Suggested type variant: Musoke.
- Justification for name change: "Marburg virus" is the name for this virus used by laboratory virologists since its discovery from 1967 to the present (Tables 1, 6). The ICTV agreed with this name in its First through Seventh Report [13, 20, 30, 31, 34, 39, 72]. The name was changed by the ICTV *Filoviridae* Study Group to "Lake Victoria marburgvirus" in 2002 [12]. This change was not accepted by the virology community.

Description of Ravn virus vir. nov. 2010

Etymology of Ravn virus: derived from nom. *Ravn*—last name of the Danish patient from whom this virus was first isolated; and Lat. n. neut. sg. *virus*—poison, slime, venom.

- Use of the name (Table 7):
  - Style: first word capitalized (because proper noun), not italicized, all types of articles.
  - Suggested pronunciation: [rævn vɑɪrəs] (IPA); **ra**-vuhn **vahy**-ruhs (English phonetic notation).
  - Abbreviation: RAVV.
- Virus variants are characterized by having the properties of Marburg marburgviruses plus:

  - diverging in genomic nucleotide sequence from the type variant of the type virus of the species *Marburg marburgvirus* (Musoke) by ≥10% but different from the type variant of Ravn virus by <10%.
- Suggested type variant: Ravn.

The individual members of established ebolavirus species ought to be renamed

Five to eight years have passed since the introduction of the names Cote d'Ivoire ebolavirus [sic], Reston ebolavirus, Sudan ebolavirus, and Zaire ebolavirus for the members of the four recognized ebolavirus species. Instead of using these names, the overwhelming majority of publications refer to "Ebola virus" instead of Zaire ebolavirus (Table 6), a preference that is also followed by the public press. The remainder of the viruses are usually referred to as Côte d'Ivoire/Ivory Coast/Taï Forest, Reston, and Sudan in the context of "Ebola virus." Worse, in the few cases in which the recommended names were used, they almost invariably were confused with species names (virus names italicized), an error that is understandable because discernment of the identically spelled taxa, a violation of ICVCN Article 3 Rule III-3.24, requires a thorough grasp of the difference between species and viruses [26]. Introducing the name "Zaire ebolavirus" was a mistake, as it contradicts ICVCN Article 2.1 (described above). Here, we rectify this situation by recommending that the traditional virus name ("Ebola virus") be used. Retrospectively, the virus nomenclature in most published articles will then be correct. Likewise, press articles, which almost invariably refer to "Ebola virus," and usually with that term aim at referring to the virus that is currently officially named "Zaire ebolavirus," will be correct retrospectively and prospectively. As the traditional names are different from the species names, confusing species and virus names will be much more difficult, even in the absence of taxonomic education.

Description of Bundibugyo virus vir. nov. Towner et al. 2009 [58]

Etymology of Bundibugyo virus: derived from geo. *Bundibugyo*—name of the chief town of Bundibugyo District in the Republic of Uganda, where members of this species were first encountered; and Lat. n. neut. sg. *virus*—poison, slime, venom.

- Use of the name (Table 7):
  - Style: first word capitalized (because proper noun), not italicized, all types of articles.
  - Suggested pronunciation: [ˌbʊndiːˈbʊdʒɔː vɑɪrəs] (IPA); **boon**-dee-**boo**-jaw **vahy**-ruhs or **boon**-dee-**boo**-joh **vahy**-ruhs (English phonetic notation).
  - Abbreviation: BDBV (formerly UEBOV, BEBOV).
- Virus variants are characterized by having the properties of Bundibugyo ebolaviruses plus:
  - diverging in genomic nucleotide sequence from the type variant of the type virus of the species *Bundibugyo ebolavirus* (Bundibugyo) <10%.
- Suggested type variant: Bundibugyo.

Description of Ebola virus vir. Johnson et al. 1997 (as Ebola virus) [21] and Bowen et al., and Pattyn et al. (as a possible new Marburg virus "strain") [15, 41] nom. nov. Netesov et al. 2000 (as Zaire Ebola virus) [39, 47] nom. nov. Feldmann et al. 2005 (as Zaire ebolavirus]) [12, 32] nom. nov. 2010 (reverted to Ebola virus)

Etymology of Ebola virus: derived from geo. *Ebola*—name of the headstream of the Mongala River, a tributary of the Zaire River (today Congo River), in Zaire (today the Democratic Republic of the Congo), where this virus was thought to be first encountered; and Lat. n. neut. sg. *virus*—poison, slime, venom.

- Use of the name (Table 7):
  - Style: first word capitalized (because proper noun), not italicized, all types of articles.
  - Suggested pronunciation: [ɛˈbɒlə vɑɪrəs] (IPA); eh-**bo**-luh **vahy**-ruhs (English phonetic notation).
  - Abbreviation: EBOV (formerly EBOV, then ZEBOV).
- Virus variants are characterized by having the properties of Zaire ebolaviruses plus:
  - diverging in genomic nucleotide sequence from the type variant of the type virus of the species *Zaire ebolavirus* (Mayinga) <10%.
- Suggested type variant: Mayinga.

Description of Reston virus vir. Geisbert and Jahrling 1999 (as a new "strain" of Ebola virus) [15] nom. nov. Netesov et al. 2000 (as Reston Ebola virus) [39, 47] nom. nov. Feldmann et al. 2005 (as Reston ebolavirus]) [12, 32] nom. nov. 2010 (as Reston virus)

Etymology of Reston virus: derived from geo. *Reston*—the town in Virginia, USA, where this virus was first encountered; and Lat. n. neut. sg. *virus*—poison, slime, venom.

- Use of the name (Table 7):
  - Style: first word capitalized (because proper noun), not italicized, all types of articles.
  - Suggested pronunciation: [ˈrɛstən vaɪrəs] (IPA); **res**-tuhn **vahy**-ruhs (English phonetic notation).
  - Abbreviation: RESTV (formerly REBOV).
- Virus variants are characterized by having the properties of Reston ebolaviruses plus:
  - diverging in genomic nucleotide sequence from the type variant of the type virus of the species *Reston ebolavirus* (Pennsylvania) $<10\%$.
- Suggested type variant: Pennsylvania.

Description of Sudan virus vir. Bowen et al. 1977 (as a possible new Marburg virus "strain") [15] nom. nov. Netesov et al. 2000 (as Sudan Ebola virus) [39, 47] nom. nov. Feldmann et al. 2005 (as Sudan ebolavirus]) [12, 32] nom. nov. 2010 (as Sudan virus)

Etymology of Sudan virus: derived from geo. *Sudan*—English conventional short form of the Republic of Sudan, where this virus was first encountered; and Lat. n. neut. sg. *virus*—poison, slime, venom.

- Use of the name (Table 7):
  - Style: first word capitalized (because proper noun), not italicized, all types of articles.
  - Suggested pronunciation: [sʊˈdæn vaɪrəs] (IPA); soo-**dan vahy**-ruhs (English phonetic notation).
  - Abbreviation: SUDV (formerly SEBOV).
- Virus variants are characterized by having the properties of Sudan ebolaviruses plus:
  - diverging in genomic nucleotide sequence from the type variant of the type virus of the species *Sudan ebolavirus* (Boniface) $<10\%$.
- Suggested type variant: Boniface.

Description of Taï Forest virus vir. le Guenno et al. 1995 (as a new "strain" of Ebola virus) [27] nom. nov. Netesov et al. 2000 (as Cote d'Ivoire Ebola virus [sic]) [39, 47] nom. nov. Feldmann et al. 2005 (as Cote d'Ivoire ebolavirus [sic]) [12, 32] nom. nov. 2010 (as Taï Forest virus)

Etymology of Taï Forest virus: derived from geo. *Parc National de Taï* [Taï National Park]—the place in the Republic of Côte d'Ivoire, where members of this species were first encountered; and Lat. n. neut. sg. *virus*—poison, slime, venom.

- Use of the name (Table 7):
  - Style: first word capitalized (because proper noun), not italicized, all types of articles.
  - Suggested pronunciation: [tɑːˈiː ˈfɔːrɨst vaɪrəs] (IPA); tah-**ee faw**-rist **vahy**-ruhs (English phonetic notation).
  - Abbreviation: TAFV (formerly CIEBOV).
- Virus variants are characterized by having the properties of Taï Forest ebolaviruses plus:
  - diverging in genomic nucleotide sequence from the type variant of the type virus of the species *Taï Forest ebolavirus* (Côte d'Ivoire) $<10\%$.
- Suggested type variant: Côte d'Ivoire.

Lloviu virus is a novel filovirus distinct from marburgviruses and ebolaviruses

A new virus, named Lloviu virus (LLOV), was recently detected in Schreiber's long-fingered bats (*Miniopterus schreibersii* Kuhl, 1817) in Cueva del Lloviu, Principality of Asturias, Spain. The virus has not yet been isolated in tissue culture (primarily because of the lack of maximum-containment laboratories in the region). However, RNA isolation from tissues of individual bats allowed repeated determination of the full-length genomic sequence of the virus, thereby fulfilling the prerequisites of the ICTV for classification of an uncultured virus [29]. Genomic analysis revealed that the virus fulfills the criteria characteristic for filoviruses as outlined in the Eighth ICTV Report [12] and this publication. Phylogenetic analyses using full-length genomic sequence demonstrated that LLOV is roughly equally distant from both marburgviruses and ebolaviruses ($\approx$56 and $\approx$51%, respectively, as determined by the *p*-distance method using whole-genome nucleotide sequences). Its genomic organization is more reminiscent of that of ebolaviruses than that of marburgviruses: LLOV gene four (GP) possesses three overlapping ORFs coding for sGP/Δ-peptide, $GP_{1,2}$, and ssGP analogs. However, the LLOV genome contains a rather truncated 5´-UTR compared to known ebolaviruses [38]. Together, these data justify the creation of a new tentative filovirus genus and tentative species for LLOV.

Description of *Cuevavirus* gen. nov. 2010 (tentative)

Etymology of *Cuevavirus*: derived from Spa. n. fem. sg. *la cueva*—cave, referring to the fact that members of this genus were first identified in bats located in a cave; and –*virus*—ending denoting a virus genus [72] → Neo-Lat. N. neut. sg. *Cuevavirus*—the genus of cave viruses.

- Valid taxon name (fulfills ICVCN Article 3 Rule II-3.8): yes, because name is compliant with ICVCN Article 3

Rules, in particular Rules IV-3.26, IV-3.27, IV-3.28, and IX-3.39 [9]; because it has been published ([38] and this article); and because it is associated with descriptive material.
- Accepted name (fulfills ICVCN Article 3 Rule II-3.8): no, because name has yet to be accepted by the ICTV.
- Use of the taxon (Table 4):
  - Style: capitalized, italicized, zero article.
  - Suggested pronunciation: [ˌkwɛvə'vaɪrəs] (IPA); **kwe**-vuh-**vahy**-ruhs (English phonetic notation).
  - Abbreviation: none.
- Use of taxon vernaculars (Table 4):
  - n. sg.: cuevavirus (-virus: ending denoting a physical member of a virus genus [66]). Suggested pronunciation: [ˌkwɛvə'vaɪrəs] (IPA); **kwe**-vuh-**vahy**-ruhs (English phonetic notation).
  - n. pl. cuevaviruses. Suggested pronunciation: [ˌkwɛvə'vaɪrəsɪz] (IPA); **kwe**-vuh-**vahy**-ruhs-iz (English phonetic notation).
  - adj.: cuevavirus/cuevaviral. Suggested pronunciation: [ˌkwɛvə'vaɪrəs]/[ˌkwɛvə'vaɪrəl] (IPA); **kwe**-vuh-**vahy**-ruhs/**kwe**-vuh-**vahy**-ruhl (English phonetic notation).
  - Style: lower case, not italicized, one word, zero article.
  - Abbreviation: none.
- Genus members are characterized by having the properties of filoviruses plus [12, 57, 61]:
  - being endemic in the Kingdom of Spain, and possibly other southern European countries.
  - gene 4 (GP) encoding four proteins. The soluble glycoprotein (sGP) and its cleavage product Δ-peptide are the primary expression products; the spike glycoprotein ($GP_{1,2}$) and a secondary soluble glycoprotein (ssGP) are expressed via cotranscriptional editing.
  - having genomes that differ from that of the type virus of the type species of the type genus of the family *Filoviridae* (Marburg virus) by ≥50% at the nucleotide level, and from the type virus of the type species of the genus *Cuevavirus* (Lloviu virus) by <50% at the nucleotide level.
- Type species: *Lloviu cuevavirus.*
- Genus members: species *Lloviu cuevavirus.*

Description of *Lloviu cuevavirus* sp. nov. 2010 (tentative)

Etymology of *Lloviu cuevavirus*: derived from geo. *Lloviu*, referring to the name of the cave in the Kingdom of Spain where members of this species where first encountered; and *Cuevavirus*—the genus of cave viruses → the Lloviu species of cave viruses.

- Valid taxon name (fulfills ICVCN Article 3 Rule II-3.8): yes, because name is compliant with ICVCN Article 3 Rules, in particular Rule IX-3.40 [9]; because it has been published ([38] and this article); and because it is associated with descriptive material.
- Accepted name (fulfills ICVCN Article 3 Rule II-3.8): no, because name has yet to be accepted by the ICTV.
- Use of the taxon (Table 5):
  - Style: capitalized, italicized, zero article.
  - Suggested pronunciation: [j'ɔ:vju: ˌkwɛvə'vaɪrəs] (IPA); **yaw**-vyoo **kwe**-vuh-**vahy**-ruhs (English phonetic notation).
  - Abbreviation: none.
- Use of taxon vernaculars (Table 5):
  - n. sg.: Lloviu cuevavirus. Suggested pronunciation: [j'ɔ:vju: ˌkwɛvə'vaɪrəs] (IPA); **yaw**-vyoo **kwe**-vuh-**vahy**-ruhs (English phonetic notation).
  - n. pl. Lloviu cuevaviruses. Suggested pronunciation: [j'ɔ:vju: ˌkwɛvə'vaɪrəsɪz] (IPA); **yaw**-vyoo **kwe**-vuh-**vahy**-ruhs-iz (English phonetic notation).
  - adj.: Lloviu cuevavirus/Lloviu cuevaviral. Suggested pronunciation: [j'ɔ:vju: ˌkwɛvə'vaɪrəs]/[j'ɔ:vju: ˌkwɛvə'vaɪrəl] (IPA); **yaw**-vyoo **kwe**-vuh-**vahy**-ruhs/**yaw**-vyoo **kwe**-vuh-**vahy**-ruhl (English phonetic notation).
  - Style: lower case, not italicized, one word, zero article.
  - Abbreviation: none.
- Species members are characterized by having the properties of cuevaviruses (because there is currently only one cuevavirus species). They have genomes that differ from that of the type virus (Lloviu virus) by <30% at the nucleotide level. A 30% amino acid sequence difference in the spike glycoprotein $GP_{1,2}$ may be used as a cuevavirus species demarcation cut-off criterion in the absence of full genomic data.
- Suggested type virus: Lloviu virus.
- Species members: Lloviu virus.

Description of Lloviu virus vir. nov. 2010

Etymology of Lloviu virus: derived from geo. *Cueva del Lloviu*—the cave in the Kingdom of Spain where this virus was first encountered; and Lat. n. neut. sg. *virus*—poison, slime, venom.

- Use of the name (Table 7):

  - Style: first word capitalized (because proper noun), not italicized, all types of articles.
  - Suggested pronunciation: [j'ɔ:vju: vɑɪrəs] (IPA); **yaw**-vyoo **vahy**-ruhs (English phonetic notation).
  - Abbreviation: LLOV.
- Virus variants are characterized by having the properties of Lloviu cuevaviruses plus:
  - diverging in nucleotide sequence from the type variant ≤10%.

Summary of changes

A short summary of all proposed changes contrasted with the filovirus taxonomy as described in the latest (Eighth) ICTV Report is shown in Table 8.

Table 8 Summary of changes to marburgvirus and ebolavirus classification and nomenclature

Approved taxonomy (Eighth ICTV Report)	Proposed new taxonomy
Order *Mononegavirales*	Order *Mononegavirales*
Family *Filoviridae*	Family *Filoviridae*
Genus *Marburgvirus*	Genus *Marburgvirus*
Species *Lake Victoria marburgvirus*	Species *Marburg marburgvirus*
Virus: Lake Victoria marburgvirus (MARV)	Virus 1: Marburg virus (MARV)
	Virus 2: Ravn virus (RAVV)
Genus *Ebolavirus*	Genus *Ebolavirus*
Species *Cote d'Ivoire ebolavirus* [sic]	Species *Taï Forest ebolavirus*
Virus: Cote d'Ivoire ebolavirus (CIEBOV) [sic]	Virus: Taï Forest virus (TAFV)
Species *Reston ebolavirus*	Species *Reston ebolavirus*
Virus: Reston ebolavirus (REBOV)	Virus: Reston virus (RESTV)
Species *Sudan ebolavirus*	Species *Sudan ebolavirus*
Virus: Sudan ebolavirus (SEBOV)	Virus: Sudan virus (SUDV)
Species *Zaire ebolavirus*	Species *Zaire ebolavirus*
Virus: Zaire ebolavirus (ZEBOV)	Virus: Ebola virus (EBOV)
	Species *Bundibugyo ebolavirus*
	Virus: Bundibugyo virus (BDBV)
	Genus *Cuevavirus* (tentative)
	Species *Lloviu cuevavirus* (tentative)
	Virus: Lloviu virus (LLOV)

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