

Virus nomenclature below the species level: a standardized nomenclature for laboratory animal-adapted strains and variants of viruses assigned to the family *Filoviridae*

Jens H. Kuhn · Yiming Bao · Sina Bavari · Stephan Becker · Steven Bradfute · J. Rodney Brister · Alexander A. Bukreyev · Yíngyún Cai · Kartik Chandran · Robert A. Davey · Olga Dolnik · John M. Dye · Sven Enterlein · Jean-Paul Gonzalez · Pierre Formenty · Alexander N. Freiberg · Lisa E. Hensley · Anna N. Honko · Georgy M. Ignatyev · Peter B. Jahrling · Karl M. Johnson · Hans-Dieter Klenk · Gary Kobinger · Matthew G. Lackemeyer · Eric M. Leroy · Mark S. Lever · Loreen L. Lofts · Elke Mühlberger · Sergey V. Netesov · Gene G. Olinger · Gustavo Palacios · Jean L. Patterson · Janusz T. Paweska · Louise Pitt · Sheli R. Radoshitzky · Elena I. Ryabchikova · Erica Ollmann Saphire · Aleksandr M. Shestopalov · Sophie J. Smither · Nancy J. Sullivan · Robert Swanepoel · Ayato Takada · Jonathan S. Towner · Guido van der Groen · Viktor E. Volchkov · Victoria Wahl-Jensen · Travis K. Warren · Kelly L. Warfield · Manfred Weidmann · Stuart T. Nichol

Received: 17 December 2012 / Accepted: 21 December 2012 / Published online: 29 January 2013
© Springer-Verlag Wien (outside the USA) 2013

Abstract The International Committee on Taxonomy of Viruses (ICTV) organizes the classification of viruses into taxa, but is not responsible for the nomenclature for taxa members. International experts groups, such as the ICTV Study Groups, recommend the classification and naming of viruses and their strains, variants, and isolates. The ICTV

Filoviridae Study Group has recently introduced an updated classification and nomenclature for filoviruses. Subsequently, and together with numerous other filovirus experts, a consistent nomenclature for their natural genetic variants and isolates was developed that aims at simplifying the retrieval of sequence data from electronic databases. This is a first important step toward a viral genome annotation standard as sought by the US National Center for Biotechnology Information (NCBI). Here, this work is extended to include filoviruses obtained in the laboratory by artificial selection through passage in laboratory hosts. The previously developed template for natural filovirus

Jens H. Kuhn, Alexander A. Bukreyev, Kartik Chandran, Olga Dolnik, John M. Dye, Eric M. Leroy, Elke Mühlberger, Sergey V. Netesov, Jean L. Patterson, Janusz T. Paweska, Erica Ollmann Saphire, Sophie J. Smither, Ayato Takada, Jonathan S. Towner, Viktor E. Volchkov, and Travis K. Warren are members of the International Committee on Taxonomy of Viruses (ICTV) *Filoviridae* Study Group.

J. H. Kuhn (✉) · Y. Cai · P. B. Jahrling · M. G. Lackemeyer · V. Wahl-Jensen
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), B-8200 Research Plaza, Fort Detrick,
Frederick, MD 21702, USA
e-mail: kuhnjens@mail.nih.gov

Y. Bao · J. R. Brister
Information Engineering Branch, National Center for
Biotechnology Information, National Library of Medicine,
National Institutes of Health, Bethesda, MD, USA

S. Bavari · J. M. Dye · A. N. Honko · L. L. Lofts ·
G. G. Olinger · G. Palacios · L. Pitt · S. R. Radoshitzky ·
T. K. Warren
United States Army Medical Research Institute of Infectious
Diseases, Fort Detrick, Frederick, MD, USA

S. Becker · O. Dolnik · H.-D. Klenk
Institut für Virologie, Philipps-Universität Marburg,
Marburg, Germany

S. Bradfute
University of New Mexico, Albuquerque, NM, USA

A. A. Bukreyev · A. N. Freiberg
Department of Pathology and Galveston National Laboratory,
University of Texas Medical Branch, Galveston, TX, USA

K. Chandran
Department of Microbiology and Immunology,
Albert Einstein College of Medicine, Bronx, NY, USA

R. A. Davey · J. L. Patterson
Department of Virology and Immunology,
Texas Biomedical Research Institute, San Antonio, TX, USA

genetic variant naming (<virus name> <isolation host-suffix>/<country of sampling>/<year of sampling>/<genetic variant designation>-<isolate designation>) is retained, but it is proposed to adapt the type of information added to each field for laboratory animal-adapted variants. For instance, the full-length designation of an Ebola virus Mayinga variant adapted at the State Research Center for Virology and Biotechnology “Vector” to cause disease in guinea pigs after seven passages would be akin to “Ebola virus VECTOR/C.porcullus-lab/COD/1976/Mayinga-GPA-P7”. As was proposed for the names of natural filovirus variants, we suggest using the full-length designation in databases, as well as in the method section of publications. Shortened designations (such as “EBOV VECTOR/C.por/COD/76/May-GPA-P7”) and abbreviations (such as “EBOV/May-GPA-P7”) could be used in the remainder of the text depending on how critical it is to convey information contained in the full-length name. “EBOV” would suffice if only one EBOV strain/variant/isolate is addressed.

Introduction

Modern molecular virology, medical countermeasure development, and epidemiology are increasingly dependent on electronic databases that make exponentially increasing datasets, such as genomic sequence information, accessible and easy to interpret. Efforts to improve

databases such as GenBank or efforts to develop novel databases (which in turn often are dependent on GenBank information) are often hindered due to lack of standardized nomenclature and classification systems for particular datasets. This is especially true for virology. The International Committee on Taxonomy of Viruses (ICTV, <http://www.ictvonline.org>) was tasked by the International Union of Microbiological Societies (IUMS) to make decisions on matters of virus classification and nomenclature for increased efficiency and consistency in the assignment of individual viruses to taxa (orders, families, subfamilies, genera, and species). However, the ICTV is currently not responsible for the nomenclature of viruses and their strains, variants, and isolates. This task is usually designated to the ICTV Study Groups, which serve as advisory committees. Fauquet observed correctly that it “is *de facto* accepted by the virologists that there is no homogeneity in the demarcation criteria, nomenclature and classification below the species level, and each specialty group is establishing an appropriate system for its respective family” [9]. Unfortunately, this also means that the naming of viruses and of their strains, variants, and isolates is more or less arbitrary and differs for viruses of one family to those of another. Recently, several ICTV Study Groups and other experts, including those of the US National Center for Biotechnology Information (NCBI), have begun to develop more consistent naming schemes for virus strains, variants, and isolates in

S. Enterlein · K. L. Warfield
Integrated BioTherapeutics, Inc., Gaithersburg, MD, USA

J.-P. Gonzalez
Health Department, Institut de Recherche pour le Développement, Marseille, France

J.-P. Gonzalez
Metabiota, Inc., San Francisco, CA, USA

P. Formenty
World Health Organization, Geneva, Switzerland

L. E. Hensley
Medical Countermeasure Initiative, Food and Drug Administration, Silver Spring, MD, USA

G. M. Ignatyev
Federal State Unitary Company “Microgen Scientific Industrial Company for Immunobiological Medicines”, Ministry of Health and Social Department of the Russian Federation, Moscow, Russia

K. M. Johnson
Bozeman, MT, USA

G. Kobinger
Special Pathogens Program, National Microbiology Laboratory, Public Health Agency of Canada, Winnipeg, MB, Canada

E. M. Leroy
Centre International de Recherches Médicales de Franceville, Franceville, Gabon

M. S. Lever · S. J. Smither
Biomedical Sciences Department, Dstl, Porton Down, Salisbury, Wiltshire, UK

E. Mühlberger
Department of Microbiology and National Emerging Infectious Diseases Laboratory, Boston University School of Medicine, Boston, MA, USA

S. V. Netesov · A. M. Shestopalov
Novosibirsk State University, Novosibirsk, Novosibirsk Oblast, Russia

J. T. Paweska
Center for Emerging and Zoonotic Diseases, National Institute for Communicable Diseases of the National Health Laboratory Service, Sandringham-Johannesburg, Gauteng, South Africa

E. I. Ryabchikova
Institute of Chemical Biology and Fundamental Medicine, Siberian Branch of the Russian Academy of Sciences, Novosibirsk, Novosibirsk Oblast, Russia

anticipation of increased submissions of population genomic sequences of viruses to databases resulting from increased availability of deep-sequencing technologies. The most notable naming scheme was developed by the Rotavirus Classification Working Group (RCWG) for rotaviruses in conjunction with the development of a new electronic database [30]. Members of the ICTV *Filoviridae* Study Group and many other filovirus experts have adopted most of the RCWG's suggestions and have recently published a similar scheme for natural (aka, wild-type or naturally-occurring) filoviruses [25]. Here, it is proposed to expand this naming scheme to filoviruses generated by artificial selection through serial passages in laboratory hosts.

Summary of nomenclature below the species level for natural filoviruses

The current, ICTV-accepted, taxonomy for filoviruses is summarized in Table 1 [1, 23, 24]. In terms of natural filoviruses, it was agreed that the term “strain” is currently not applicable [25]. Natural filovirus variants were defined as follows:

“A natural genetic filovirus variant is a natural filovirus that differs in its genomic consensus sequence from that of a reference filovirus (the type virus of a particular filovirus species) by $\leq 10\%$ but is not identical to the reference filovirus and does not cause an observable different phenotype of disease (filovirus strains would be genetic filovirus variants, but most genetic filovirus variants would not be filovirus strains if a strain definition would be brought forward)” [25].

E. O. Saphire

Department of Immunology and Microbial Science and The Skaggs Institute for Chemical Biology, The Scripps Research Institute, La Jolla, CA, USA

A. M. Shestopalov

State Research Center of Virology and Biotechnology “Vector”, Koltsovo, Novosibirsk Oblast, Russia

N. J. Sullivan

Vaccine Research Center, National Institute of Allergy and Infectious Diseases, National Institutes of Health, Bethesda, MD, USA

R. Swanepoel

Zoonoses Research Unit, University of Pretoria, Pretoria, South Africa

A. Takada

Division of Global Epidemiology, Hokkaido University Research Center for Zoonosis Control, Sapporo, Japan

The definition for natural filovirus isolates is:

“A natural filovirus isolate is an instance of a particular natural filovirus or of a particular genetic variant. Isolates can be identical or slightly different in consensus or individual sequence from each other” [25].

Templates were proposed for naming individual natural filovirus variants and isolates for a) Materials and Methods sections of manuscripts (full-length designations); b) alignment and phylogram figures (shortened designations); and c) flow-text (abbreviations) [25]. These templates are generally organized in the order <virus name> <isolation host-suffix>/<country of sampling>/<year of sampling>/<genetic variant designation>-<isolate designation>. Suffixes were proposed to be used for natural filoviruses sequenced directly from the matrix of the initially infected organism in the absence of *in vitro* propagation (“-wt”), for filoviruses sequenced from cell or tissue cultures (“-tc”), for filoviruses sequenced only partially (“-frag”), or for unsequenced filoviruses not available for study anymore due to loss or destruction (“-hist”).

Nomenclature below the species level for laboratory filoviruses

There are several non-natural filoviruses. For instance, Marburg virus (MARV), Ravn virus (RAVV), and Ebola virus (EBOV) have been passaged through adult rodents, such as laboratory mice and guinea pigs (*Cavia porcellus* Linnaeus, 1758), which do not develop disease upon exposure to natural (wild-type) filoviruses and which are not known to be infected by filoviruses in nature. Serial passaging in these rodents, however, culminated in

J. S. Towner · S. T. Nichol (✉)

Viral Special Pathogens Branch (VSPB), Division of High-Consequence Pathogens Pathology (DHCPP), National Center for Emerging and Zoonotic Infectious Diseases (NCEZID), Centers for Disease Control and Prevention (CDC), 1600 Clifton Road, Atlanta, GA 30333, USA
e-mail: stn1@cdc.gov

G. van der Groen

Prins Leopold Instituut voor Tropische Geneeskunde, Antwerp, Belgium

V. E. Volchkov

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

M. Weidmann

Universitätsmedizin Göttingen, Abteilung Virologie, Göttingen, Germany

Table 1 Summary of the current filovirus taxonomy as endorsed by the ICTV *Filoviridae* Study Group and accepted by the ICTV

Current taxonomy and nomenclature (Ninth ICTV Report and updates) [1, 23, 24]	Previous taxonomy and nomenclature (Eighth ICTV Report) [10]
Order <i>Mononegavirales</i>	Order <i>Mononegavirales</i>
Family <i>Filoviridae</i>	Family <i>Filoviridae</i>
Genus <i>Marburgvirus</i>	Genus <i>Marburgvirus</i>
Species <i>Marburg marburgvirus</i>	Species <i>Lake Victoria marburgvirus</i>
Virus 1: Marburg virus (MARV)	Virus: Lake Victoria marburgvirus (MARV)
Virus 2: Ravn virus (RAVV)	
Genus <i>Ebolavirus</i>	Genus <i>Ebolavirus</i>
Species <i>Tai Forest ebolavirus</i>	Species <i>Cote d'Ivoire ebolavirus</i> [sic]
Virus: Tai Forest virus (TAFV)	Virus: Cote d'Ivoire ebolavirus [sic] (CIEBOV)
Species <i>Reston ebolavirus</i>	Species <i>Reston ebolavirus</i>
Virus: Reston virus (RESTV)	Virus: Reston ebolavirus (REBOV)
Species <i>Sudan ebolavirus</i>	Species <i>Sudan ebolavirus</i>
Virus: Sudan virus (SUDV)	Virus: Sudan ebolavirus (SEBOV)
Species <i>Zaire ebolavirus</i>	Species <i>Zaire ebolavirus</i>
Virus: Ebola virus (EBOV)	Virus: Zaire ebolavirus (ZEBOV)
Species <i>Bundibugyo ebolavirus</i>	
Virus: Bundibugyo virus (BDBV)	
Genus <i>Cuevavirus*</i>	
Species <i>Lloviu cuevavirus*</i>	
Virus: Lloviu virus (LLOV)	

* Taxa proposed to and provisionally approved by the ICTV Executive Committee

filoviruses that cause disease and death (for studies on adaptation see, for instance, [2, 5–8, 11–18, 20–22, 26–29, 31–39, 41, 42]), and recent studies correlated this evolution with specific changes in the genomes of these viruses [3, 28, 29, 39, 40]. Artificial selection results in filovirus laboratory variants that need to be distinguished from naturally occurring variants. Since natural filoviruses do not cause disease in standard adult laboratory rodents, rodent-adapted virus variants that do cause disease are clearly phenotypically different and therefore warrant designation as laboratory strains (for a more thorough discussion on the term “strain” see [25]), whereas those that do not cause disease but are characterized by genomic mutations brought on by artificial selection should be classified as laboratory variants.

Definition of “filovirus laboratory strain”:

A filovirus laboratory strain is a genetically stable filovirus laboratory variant that evolved via artificial selection

through serial passaging of a natural filovirus and causes disease in an animal that does not develop disease upon infection with the natural (wild-type) virus. The extent of genomic sequence variation is irrelevant for the classification of a variant as a strain. “Genetically stable” means that a genomic area associated with strain characteristics needs to be maintained by the virus over several rounds of replication in the laboratory host, rather than being a random mutation that occurs and disappears over time.

The definitions for filovirus laboratory variants and isolates follow those proposed for natural filoviruses:

Definition of “filovirus laboratory variant”:

A filovirus laboratory variant is a mutant natural genetic filovirus variant that

- evolved through serial passaging of a reference filovirus in a laboratory host;
- is $\leq 10\%$ different but is not identical in sequence with the natural reference filovirus; and
- does not necessarily differ from the natural reference filovirus in infection phenotype.

Definition of “filovirus laboratory isolate”:

A filovirus laboratory isolate is an instance of a particular filovirus laboratory strain or variant. Isolates can be identical or slightly different in consensus or individual sequence from each other.

We propose to designate full-length and shortened designations and abbreviations for filovirus laboratory strains/variants/isolates according to the templates published for natural filovirus variants/isolates [25]. The suffix field should be “-lab” (for “laboratory-adapted”) or a combination of “-lab” and other prefixes established in [25] if necessary (for instance, “-lab_hist”, “-lab_seq”):

Full-length designation

<virus name> <strain>/<isolation host-suffix>/<country of sampling>/<year of sampling>/<genetic variant designation>-<isolate designation>

- the **virus name** should be given in full, as outlined recently [23, 24]. For instance: “Marburg virus,” “Ebola virus,” “Sudan virus”
- the **strain** field should contain the abbreviation of the institute at which the strain was developed (Table 2)
- the **isolation host** should be provided in one word in the format “First letter of genus name.full name of species descriptor” of the laboratory host, but remain unitalized to denote the fact that the virus was isolated from an entity and not from a taxon [4]. For instance: “C.porcellus” (member of the species *Cavia porcellus*). Laboratory mice and some other laboratory animals

Table 2 Proposed abbreviations for BSL-4 institutes with filovirus research programs for the <strain> field in names of laboratory animal-adapted filovirus strains*

Institute	Proposed <strain> field abbreviation
Australian Animal Health Laboratory (AAHL), Geelong, Victoria, Australia	AAHL
Bernhard Nocht Institute for Tropical Medicine (BNI), Hamburg, Germany	BNI
Centers for Disease Control and Prevention (CDC), Atlanta, Georgia, USA	CDC
Centre International de Recherches Médicales de Franceville (CIRMF), Franceville, Gabon	CIRMF
Defence Science and Technology Laboratory (DSTL), Porton Down, Salisbury, UK	DSTL ¹
Galveston National Laboratory (GNL), National Biocontainment Facility and Robert E. Shope Laboratory, University of Texas Medical Branch (UTMB), Galveston, Texas, USA	UTMB
Health Protection Agency (HPA) Centre for Emergency Preparedness and Response, Porton Down, Salisbury, UK	CEPR ¹
Integrated Research Facility at Fort Detrick (IRF-Frederick), Fort Detrick, Frederick, Maryland, USA	IRF-F
Laboratoire P4 Jean Mérieux INSERM	INSERM
National Biodefense Analysis and Countermeasures Center (NBACC), Fort Detrick, Frederick, Maryland, USA	NBACC
National Emerging Infectious Diseases Laboratory (NEIDL), Boston University, Boston, Massachusetts, USA	NEIDL
National Institute for Communicable Diseases of the National Health Laboratory Service (NICD), Sandringham-Johannesburg, Gauteng, South Africa	NICD ¹
National Microbiology Laboratory—Public Health Agency of Canada (NML), Winnipeg, Manitoba, Canada	NML
Institut für Virologie—Philipps-Universität Marburg, Marburg, Hesse, Germany	UMR
Republican Research and Practical Center for Epidemiology and Microbiology (RRPCEM), Minsk, Republic of Belarus	RRPCEM ¹
Rocky Mountain Laboratory Integrated Research Facility (RML-IRF), Hamilton, Montana, USA	RML-IRF
State Research Center for Virology and Biotechnology “Vector” (SRCVB “Vector”), Koltsovo, Nobosibirsk Oblast, Russia	VECTOR
Texas Biomedical Research Institute, San Antonio, Texas, USA	TBRI ¹
United States Army Medical Research Institute of Infectious Diseases (USAMRIID), Fort Detrick, Frederick, Maryland, USA	USAMRIID

Table 2 continued

Institute	Proposed <strain> field abbreviation
Virological Center of the Research Institute of Microbiology, Sergiev Posad, Moscow Oblast, Russia	VC

* Only institutes that have been, are, or will be majorly involved with filovirus research are listed here. Abbreviations for other institutes can be suggested by their investigators when a name for a filovirus strain needs to be created

¹ These institutes have undergone name changes over the years. We recommend that researchers use the abbreviations in use at a particular time for filovirus strain/variant/isolate names created at that time. For instance, MRE and DERA were previous abbreviations for the laboratories now referred to as DSTL; CAMR preceded CEPR; SRIEM preceded RRPCEM etc.

cannot be assigned to a species. Consequently, this field should be filled with the official strain designation of the animal used for the experiments – in the case of laboratory mice and laboratory rats in accordance with the most recent “Guidelines for Nomenclature of Mouse and Rat Strains”, e.g. “C57BL/6” or “BALB/c” [19]

- the **country of sampling** field should contain the same information provided as in the field for the natural (wild-type) virus
- the **year of sampling** field should contain the same information provided as in the field for the natural (wild-type) virus
- the **genetic variant designation-isolate designation** field should contain the same information provided in the same field for the natural (wild-type) virus connected by a hyphen to a laboratory isolate descriptor. For instance: “Mayinga-GPA-P7”

Example for the full-length designation of an isolate in the method section of a manuscript:

“Ebola virus VECTOR/C.porcellus-lab/COD/1976/Mayinga-GPA-P7”.

Shortened designation

<virus name abbreviation> <strain>/<isolation host-suffix>/<country of sampling>/<year of sampling>/<genetic variant designation>-<isolate designation>

- the **virus name** abbreviation should be accepted by the ICTV *Filoviridae* Study Group, as outlined recently [23, 24]. For instance: “MARV,” “EBOV,” “SUDV”
- the **strain** field should contain the abbreviation of the institute at which the strain was developed (Table 2)
- the **isolation host** should be provided in a four-letter format “First letter of genus name.first three letters of species descriptor” of the laboratory host. For instance: “C.por” (member of the species *Cavia porcellus*).

Laboratory mice and some other laboratory animals cannot be assigned to a species. Consequently, this field should be filled with the official strain designation abbreviation of the animal used for the experiments – in the case of laboratory mice and laboratory rats in accordance with the most recent “Guidelines for Nomenclature of Mouse and Rat Strains”. For instance, “B6” for C57BL/6 mouse strains or “C” for “BALB/c” mouse strains [19]

- the **country of sampling** field should contain the same information provided as in the field for the natural (wild-type) virus
- the **year of sampling** field should contain the same information provided as in the field for the natural (wild-type) virus
- the **genetic variant designation-isolate designation** should contain the same information as provided in the field for the natural (wild-type) virus connected by a hyphen to an isolate abbreviation, e.g. “May-GPA-P7.”

Example for the shortened designation of an isolate in figures (alignments, phylograms) of a manuscript: “EBOV VECTOR/C.por/COD/76/May-GPA-P7.”

Abbreviation

<virus abbreviation>/<genetic variant designation-isolate designation>

- the **virus abbreviation** should be one accepted by the ICTV *Filoviridae* Study Group, as outlined recently [23, 24]. For instance: “MARV,” “EBOV,” “SUDV”
- the **genetic variant designation-isolate designation** should contain the same information as provided in the field for the natural (wild-type) virus connected by a hyphen to an isolate abbreviation, e.g. “May-GPA-P7”

Example for abbreviation in the text of a manuscript: “EBOV/May-GPA-P7” (if other isolates of the same genetic strain/variant/isolate are addressed in the same article); or simply EBOV (if the article only addresses work with one particular genetic strain/variant/isolate).

Usage of designations

As outlined in [25], we recommend that the full-length isolate designations always be used once in the Materials and Methods section of manuscripts. For example:

“HeLa cells in 96-well plates were infected for 1 h with Ebola virus VECTOR/C.porcellus-lab/COD/1976/Mayinga-GPA-P7 (derived from an Ebola virus, family *Filoviridae*, species *Zaire ebolavirus*, GenBank accession No. EU224440) at MOIs of 0.5, 1, or 5. Virus was obtained from the State Research Center for Virology and Biotechnology “Vector”,

Koltsovo, Russia, and had been passaged twice through grivet (species *Chlorocebus aethiops*) kidney epithelial (Vero E6) cells before use.”

or

“Ebola virus VECTOR/C.porcellus-lab/COD/1976/Mayinga-GPA-P7 was obtained after i.m. serial passaging of Ebola virus H.sapiens-tc/COD/1976/Mayinga-ME718 in guinea pigs (*Cavia porcellus*), a laboratory host that is susceptible to fatal infection only after adaptation.”

As for natural filoviruses, we recommend using only the virus abbreviation in the remainder of the manuscript text (in the example above: “EBOV”) after proper introduction. Abbreviated designations should be used if several variants or isolates of one filovirus are addressed. For instance:

“Here we demonstrate that infection of guinea pigs with EBOV/May-GPA-P7 protects from subsequent infection with EBOV/May-8ms-N4”.

Creating new designations

Ideally, it is up to the investigators who developed a novel laboratory filovirus to create an appropriate isolate designation according to the scheme proposed here. A framework for creating such designations is presented in [25].

Acknowledgment The content of this publication does not necessarily reflect the views or policies of the US Department of the Army, the US Department of Defense or the US Department of Health and Human Services or of the institutions and companies affiliated with the authors. This work was funded in part by the Joint Science and Technology Office for Chem Bio Defense (proposal #TMTI0048_09_RD_T to SB). YC, JHK, and VWJ performed this work as employees of Tunnell Consulting, Inc., and MGL as an employee of Lovelace Respiratory Research Institute, both subcontractors to Battelle Memorial Institute under its prime contract with NIAID, under Contract No. HHSN272200200016I. This research was also supported in part by the Intramural Research Program of the NIH, National Library of Medicine (YB and JRB).

References

1. Adams MJ, Carstens EB (2012) Ratification vote on taxonomic proposals to the International Committee on Taxonomy of Viruses (2012). *Arch Virol* 157:1411–1422
2. Bowen ETW, Platt GS, Lloyd G, Raymond RT, Simpson DIH (1980) A comparative study of strains of Ebola virus isolated from southern Sudan and northern Zaire in 1976. *J Med Virol* 6:129–138
3. Bray M, Davis K, Geisbert T, Schmaljohn C, Huggins J (1999) A mouse model for evaluation of prophylaxis and therapy of Ebola hemorrhagic fever. *J Infect Dis* 179(suppl. 1):S248–S258
4. Calisher CH, van Regenmortel MHV (2009) Should all other biologists follow the lead of virologists and stop italicizing the names of living organisms? *Zootaxa* 2113:63–68

5. Chepurinov AA, Zubavichene NM, Dadaeva AA (2001) Influence of selective passages on the change in Ebola virus properties. *Infect Dis Rev* 3:183–189
6. Chepurinov AA, Zubavichene NM, Dadaeva AA (2003) Elaboration of laboratory strains of Ebola virus and study of pathophysiological reactions of animals inoculated with these strains. *Acta Trop* 87:321–329
7. Ellis DS, Stamford S, Lloyd G, Bowen ETW, Platt GS, Way H, Simpson DIH (1979) Ebola and Marburg viruses: I. Some ultrastructural differences between strains when grown in Vero cells. *J Med Virol* 4:201–211
8. Ellis DS, Stamford S, Tvoey DG, Lloyd G, Bowen ET, Platt GS, Way H, Simpson DI (1979) Ebola and Marburg viruses: II. Their development within Vero cells and the extra-cellular formation of branched and torus forms. *J Med Virol* 4:213–225
9. Fauquet CM, Bridson RW, Brown JK, Moriones E, Stanley J, Zerbini M, Zhou X (2008) Geminivirus strain demarcation and nomenclature. *Arch Virol* 153:783–821
10. Feldmann H, Geisbert TW, Jahrling PB, Klenk H-D, Netesov SV, Peters CJ, Sanchez A, Swanepoel R, Volchkov VE (2005) Family *Filoviridae*. In: Fauquet CM, Mayo MA, Maniloff J, Desselberger U, Ball LA (eds) *Virus taxonomy—Eighth report of the International Committee on Taxonomy of Viruses*. Academic Press, USA, pp 645–653
11. Hart MK (2003) Vaccine research efforts for filoviruses. *Int J Parasitol* 33:583–595
12. Hevey M, Negley D, Geisbert J, Jahrling P, Schmaljohn A (1997) Antigenicity and vaccine potential of Marburg virus glycoprotein expressed by baculovirus recombinants. *Virology* 239:206–216
13. Hofmann H, Kunz C (1968) Das Verhalten des sogenannten “Marburg-Virus” in einigen Gewebekulturen. *Zentralbl Bakteriol Orig* 208:344–347 (German)
14. Hofmann H, Kunz C (1969) Interferonbildung im Gehirn weißer Säuglingsmäuse nach Infektion mit einigen Rhabdoviren. *Zentralbl Bakteriol Orig* 211:5–9 (German)
15. Hofmann H, Kunz C, Aspöck H, Radda A (1969) Zur Ökologie des sogenannten “Marburg-Virus” (Rhabdovirus simiae). *Zentralbl Bakteriol Orig* 212:168–173 (German)
16. Hofmann H, Kunz C (1970) Ein mauspathogener Stamm des “Marburg-Virus” (Rhabdovirus simiae). *Arch Gesamte Virusforsch* 32:244–248 (German)
17. Institut Pasteur de Dakar (1967a) Résultats des investigations sur la matériel reçu de Frankfurt et Marburg. Dakar, Senegal (December) (French)
18. Institut Pasteur de Dakar (1967b) Résultats des investigations sur la matériel reçu de Frankfurt et Marburg. Dakar, Senegal (November) (French)
19. International Committee on Standardized Genetic Nomenclature for Mice (2011) Guidelines for Nomenclature of Mouse and Rat Strains. <http://www.informatics.jax.org/mgihome/nomen/strains.shtml>
20. Kissling RE, Robinson RQ, Murphy FA, Whitfield SG (1968) Agent of disease contracted from green monkeys. *Science* 160:888–890
21. Kissling RE, Murphy FA, Henderson BE (1970) Marburg virus. *Ann NY Acad Sci* 174:932–945
22. Kuhn JH (2008) Filoviruses—A compendium of 40 years of epidemiological, clinical, and laboratory studies. *Arch Virol Suppl*, vol 20. Springer, Vienna
23. Kuhn JH, Becker S, Ebihara H, Geisbert TW, Johnson KM, Lipkin WI, Negredo A, Netesov SV, Nichol ST, Palacios G, Peters CJ, Tenorio A, Volchkov VE, Jahrling PB (2010) Proposal for a revised taxonomy of the family *Filoviridae*: classification, names of taxa and viruses, and virus abbreviations. *Arch Virol* 155:2083–2103
24. Kuhn JH, Becker S, Ebihara H, Geisbert TW, Jahrling PB, Kawaka Y, Netesov SV, Nichol ST, Peters CJ, Volchkov VE, Ksiazek TG (2011) Family *Filoviridae*. In: King AMQ, Adams MJ, Carstens EB, Lefkowitz EJ (eds) *Virus taxonomy—Ninth report of the International Committee on Taxonomy of Viruses*. Academic Press, UK, pp 665–671
25. Kuhn JH, Bao Y, Bavari S, Becker S, Bradfute S, Brister JR, Bukreyev AA, Chandran K, Davey RA, Dolnik O, Dye JM, Enterlein S, Hensley LE, Honko AN, Jahrling PB, Johnson KM, Kobinger G, Leroy EM, Lever MS, Muhlberger E, Netesov SV, Olinger GG, Palacios G, Patterson JL, Paweska JT, Pitt L, Radoshitzky SR, Saphire EO, Smither SJ, Swanepoel R, Towner JS, van der Groen G, Volchkov VE, Wahl-Jensen V, Warren TK, Weidmann M, Nichol ST (2013) Virus nomenclature below the species level: a standardized nomenclature for natural variants of viruses assigned to the family *Filoviridae*. *Arch Virol* 158:301–311
26. Kunz C, Hofmann H, Aspöck H (1968) Die Vermehrung des “Marburg-Virus” in *Aedes aegypti*. *Zentralbl Bakteriol Parasitenkd Infektionskrankh Hyg I Abt Medizin-Hyg Bakteriol, Virusforsch Parasitol Orig* 208:347–349
27. Kunz C, Hofmann H, Kovac W, Stockinger L (1968) Biologische und morphologische Charakteristika des Virus des in Deutschland aufgetretenen “Hämorrhagischen Fiebers”. *Wien Klin Wochenschr* 80:161–162, 169–170 (German)
28. Lofts LL, Ibrahim MS, Negley DL, Hevey MC, Schmaljohn AL (2007) Genomic differences between guinea pig lethal and non-lethal Marburg virus variants. *J Infect Dis* 196(suppl. 2):S305–S312
29. Lofts LL, Wells JB, Bavari S, Warfield KL (2011) Key genomic changes necessary for an *in vivo* lethal mouse marburgvirus variant selection process. *J Virol* 85:3905–3917
30. Matthijnsens J, Ciarlet M, McDonald SM, Attoui H, Banyai K, Brister JR, Buesa J, Esona MD, Estes MK, Gentsch JR, Iturriza-Gomara M, Johne R, Kirkwood CD, Martella V, Mertens PP, Nakagomi O, Parreno V, Rahman M, Ruggeri FM, Saif LJ, Santos N, Steyer A, Taniguchi K, Patton JT, Desselberger U, Van Ranst M (2011) Uniformity of rotavirus strain nomenclature proposed by the Rotavirus Classification Working Group (RCWG). *Arch Virol* 156:1397–1413
31. May G, Knothe H (1968) Bakteriologisch-virologische Untersuchungen über die in Frankfurt/M. aufgetretenen menschlichen Infektionen durch Meerkatzen. *Dtsch Med Wochenschr* 93:620–622, 624 (German)
32. Robin Y, Brès P, Camain R (1971) Passage of Marburg virus in guinea pigs. In: Martini GA, Siegert R (eds) *Marburg virus disease*. Springer, Berlin, pp 117–122
33. Siegert R, Shu H-L, Slenczka W, Peters D, Müller G (1967) Zur Ätiologie einer unbekanntenen, von Affen ausgegangenen menschlichen Infektionskrankheit. *Dtsch Med Wochenschr* 92:2341–2343 (German)
34. Siegert R (1968) Zur Isolierung, Identifizierung und Diagnostik des “Marburg-Virus”. *Med Welt* 19:1542–1543 (German)
35. Siegert R, Shu HL, Slenczka W (1968) Isolierung und Identifizierung des “Marburg-Virus”. *Dtsch Med Wochenschr* 93:604–612 (German)
36. Simpson DIH (1969) Vervet monkey disease—transmission to the hamster. *Br J Exp Pathol* 50:389–392
37. Slenczka W, Shu H-L, Piepenburg G, Siegert R (1968) Antigen-Nachweis des “Marburg-Virus” in den Organen infizierter Meerschweinchen durch Immunofluoreszenz. *Dtsch Med Wochenschr* 93:612–616 (German)
38. Slenczka W, Siegert R, Wolff G (1970) Nachweis komplementbindender Antikörper des Marburg-Virus bei 22 Patienten mit einem Zellkultur-Antigen. *Archiv Ges Virusforsch* 31:71–80 (German)

39. Subbotina E, Dadaeva A, Kachko A, Chepurnov A (2010) Genetic factors of Ebola virus virulence in guinea pigs. *Virus Res* 153:121–133
40. Volchkov VE, Chepurnov AA, Volchkova VA, Ternovoj VA, Klenk HD (2000) Molecular characterization of guinea pig-adapted variants of Ebola virus. *Virology* 277:147–155
41. Warfield KL, Alves DA, Bradfute SB, Reed DK, VanTongeren S, Kalina WV, Olinger GG, Bavari S (2007) Development of a model for Marburg virus based on severe-combined immunodeficiency mice. *Virology* 361:107–115
42. Warfield KL, Bradfute SB, Wells J, Lofts L, Cooper MT, Alves DA, Reed DK, VanTongeren SA, Mech CA, Bavari S (2009) Development and characterization of a mouse model for Marburg hemorrhagic fever. *J Virol* 83:6404–6415