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VIROLOGY DIVISION NEWS

Past, present, and future of arenavirus taxonomy

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Abstract Until recently, members of the monogeneric family *Arenaviridae* (arenaviruses) have been known to infect only muroid rodents and, in one case, possibly phyllostomid bats. The paradigm of arenaviruses exclusively infecting small mammals shifted dramatically when several groups independently published the detection and isolation of a divergent group of arenaviruses in captive alethinophidian snakes. Preliminary phylogenetic analyses suggest that these reptilian arenaviruses constitute a sister clade to mammalian arenaviruses. Here, the members of the International Committee on Taxonomy of Viruses (ICTV) *Arenaviridae* Study Group, together with other experts, outline the taxonomic reorganization of the family *Arenaviridae* to accommodate reptilian arenaviruses and other recently discovered mammalian arenaviruses and to improve compliance with the Rules of the International Code of Virus Classification and Nomenclature (ICVCN). PAirwise Sequence Comparison (PASC) of arenavirus genomes and NP amino acid pairwise distances support the modification of the present classification. As a result, the current genus *Arenavirus* is replaced by two genera, *Mammarenavirus* and *Reptarenavirus*, which are established to accommodate mammalian and reptilian arenaviruses, respectively, in the same family. The current species landscape among mammalian arenaviruses is upheld, with two new species added for Lunk and Merino Walk viruses and minor corrections to the spelling of some names. The published snake arenaviruses are distributed among three new separate reptarenavirus species. Finally, a non-Latinized binomial species name scheme is adopted for all arenavirus species. In addition, the current virus abbreviations have been evaluated, and some changes are

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The taxonomic changes outlined here have been accepted by the International Committee on Taxonomy of Viruses (ICTV) Executive Committee at the end of 2014 and have been ratified by the Virology Division members in early 2015, thereby making these changes official.

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introduced to unequivocally identify each virus in electronic databases, manuscripts, and oral proceedings.

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Introduction

Mammalian arenavirions are enveloped and spherical to pleomorphic in shape, ranging from 50 to 300 nm in diameter (Fig. 1; reviewed in references [28, 40, 71, 98]). The particles' sandy appearance in electron microscopy sections, originally thought to be due to the incorporation of host cell ribosomes, earned these viruses their name (Latin *arena* = sand). The mammalian arenavirus genome consists of two single-stranded ambisense RNA molecules, designated L (large) and S (small). Purified arenavirion RNA is not infectious. The 5' and 3' ends of the L and S RNA segments have noncoding untranslated regions (UTRs) and contain conserved reverse complementary sequences of 19 to 30 nucleotides at each extremity [8]. These termini are predicted to form panhandle structures through base pairing [65, 120, 144]. The 3' UTR of each segment contains the arenaviral genomic promoter that directs RNA replication and gene transcription (Fig. 2) [66, 107].

Each mammalian arenaviral genomic segment encodes two different proteins in two nonoverlapping open reading frames (ORF) of opposite polarities (ambisense coding arrangement) [9]. The L segment (≈7,200 nt) encodes a viral RNA-dependent RNA polymerase (L) and a zinc-binding matrix protein (Z) [121]. The S segment (≈3,500 nt) encodes a nucleoprotein (NP) and an envelope glycoprotein precursor (GPC) [26, 79, 83]. The two ORFs in each segment are separated by an intergenic noncoding region (IGR) that could form one or more energetically stable stem-loop (hairpin) structures [9, 143]. The IGR functions in structure-dependent transcription termination [96, 97, 132] and in virus assembly and/or budding [111].

Mammalian arenavirus mRNAs are capped and not polyadenylated [96, 126, 127]. The 5' ends of viral mRNAs contain several nontemplated bases, resembling the mRNAs of influenza A viruses and bunyaviruses [62, 96, 112]. The mammalian arenaviral transcription-initiation mechanism resembles the cap-snatching mechanism of influenza A viruses and bunyaviruses and involves cleavage of the caps and associated bases by an endonuclease activity associated with the L polymerase [112]. The cap leader is subsequently used to prime transcription of the arenavirus genome.

NP is the mammalian arenaviral major structural protein. The protein is a component of nucleocapsids and is associated with viral RNA in the form of bead-like structures. NP is essential for both transcription and replication [107, 110]. Like other RNA-dependent RNA polymerases, L carries out two different processes: transcription and replication [61–63, 77, 85]. The matrix protein Z contains a zinc-binding RING motif [121–123] and is the main driving force for mammalian arenavirus budding [54, 107, 130]. Z also inhibits RNA synthesis in a dose-dependent manner [44–46, 64, 76, 87]. GP1 and GP2, the two envelope glycoproteins, are derived from posttranslational cleavage of GPC. GP1 and GP2 together with a stable

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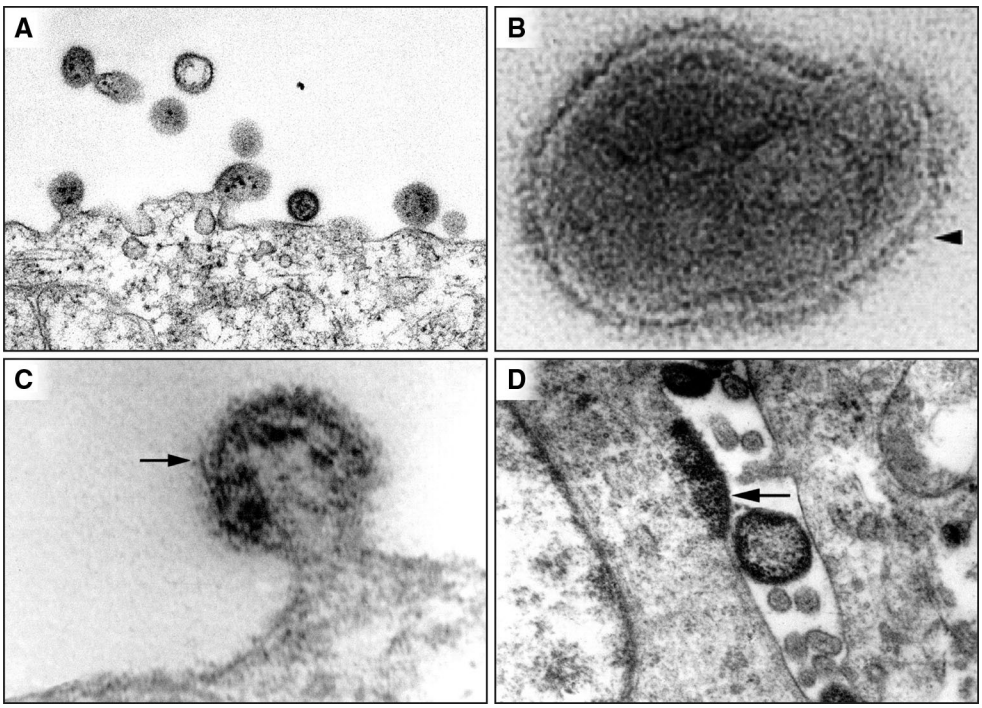

Fig. 1 (A) Electron micrographs of arenavirus particles emerging from an infected cell [125]; (B) Sucrose-gradient-purified and negatively stained arenavirus particles; (C, D) Ultrathin sections of arenavirus-infected Vero cells. Surface projections on arenavirus particles (panels B and C) and a budding membrane site within an arenavirus-infected cell (panel D) are indicated by *arrows* [88]

signal peptide (SSP), cleaved off during GPC synthesis, form the virion spike that mediates attachment and fusion with host membranes.

During infection, mammalian arenaviruses attach to cell-surface receptors and are internalized by endocytosis [16, 90, 136]. pH-dependent fusion with late endosomes releases the virus ribonucleoprotein (RNP) complex containing NP, L, and viral genomic RNA into the cytoplasm, where the RNP directs both RNA genome replication and gene transcription [98]. During replication, L reads through the IGR transcription-termination signal and generates uncapped antigenomic and genomic RNAs [84]. These RNAs contain a single nontemplated G at the 5' end [62, 112]. Consequently, replication initiation might involve a slippage mechanism of L on the nascent RNA [63]. Transcription of *GPC* and *Z* mRNAs occurs only after one round of virus replication, during which S and L antigenomes are produced. The GPC polyprotein is synthesized into the lumen of the endoplasmic reticulum (ER), where it is extensively *N*-glycosylated, and where it is thought to oligomerize prior to proteolytic processing by the subtilisin kexin-isozyme-1/site-1 protease (SKI-1/S1P). Proteolytic maturation of GPC, as well as its trafficking from the ER to the cell surface, is dependent on the SSP [112]. Virion budding occurs from the cellular plasma membrane, thereby providing the virion envelope [48, 54, 107, 130].

Past developments in arenavirus taxonomy

In 1933, Armstrong and Lillie discovered the "virus of experimental lymphocytic choriomeningitis" [7], today known as lymphocytic choriomeningitis virus (LCMV). In 1935, Traub identified the house mouse (*Mus musculus*) as LCMV's natural reservoir host [134]. Around the same time, Rivers and McNair Scott demonstrated that LCMV is the cause of an aseptic meningitis in humans that today is called lymphocytic choriomeningitis [93, 114, 115]. In 1956, a novel agent later called Tacaribe virus (TCRV) was isolated from Jamaican fruit-eating bats (*Artibeus jamaicensis trinitatis*) in Trinidad and Tobago, but the virus was not associated with overt human disease [52] (anecdotal reports suggest a single human infection that resulted in a mild febrile illness). In 1959, Junín virus (JUNV), maintained in nature by drylands lauchas (*Calomys musculinus*), was identified as the cause of Junín/Argentinian hemorrhagic fever [105, 106].

In 1963, Mettler *et al.* established the "Tacaribe antigenic group" after demonstrating a serological relationship between TCRV and JUNV using the complement fixation test and differences between the viruses using a neutralization assay [94]. Machupo virus (MACV), isolated from a patient with Machupo/Bolivian hemorrhagic fever in 1963 [72], was also found to be antigenically closely

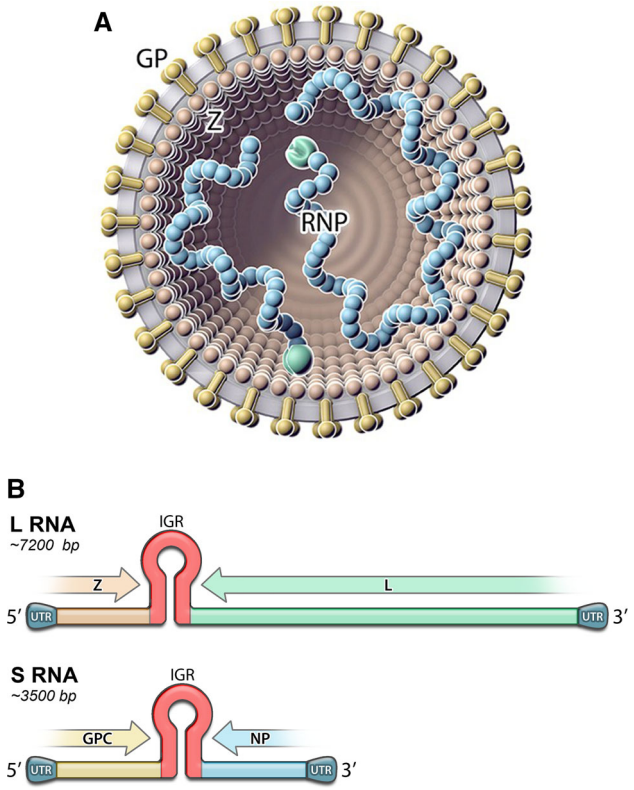

Fig. 2 Schematic diagrams of an arenavirus particle (A) and the organization of the bi-segmented arenavirus L and S RNA genome segments (B). The 5' and 3' ends of both segments are complementary at their termini, likely promoting the formation of circular RNPs within the arenavirion, as illustrated for the L RNP in panel A and in reference [144]

related to JUNV by complement fixation tests [140]. In nature, MACV was found to be carried by big lauchas (*Calomys callosus*) [73]. In the following years, the "Tacaribe antigenic group" expanded to include additional newly discovered viruses: Amaparí (AMAV) [109], Latino (LATV, first mentioned in reference [101]), Paraná (PARV) [139], Pichindé (PICV) [133], and Tamiami viruses (TAMV) [36]. None of these viruses are known to cause human disease (although there are anecdotal reports of two severe PICV infections in humans), but all of them were found to be maintained in nature by specific rodent hosts.

Next, LCMV and the Tacaribe complex viruses were proposed to constitute a new taxonomic group of viruses, tentatively named "Arenoviruses" (later corrected to "Arenaviruses") [117]. This proposal was based on the similar morphology and morphogenesis of LCMV and the Tacaribe complex viruses [100, 101] and cross-serological reactivity between them in indirect immunofluorescence assays [118]. In 1969, a novel arenavirus later named Lassa virus (LASV) was recovered from Lassa fever patients in Nigeria [58]. Soon after, in 1970, LASV was demonstrated to be antigenically related to LCMV and to some of the Tacaribe complex viruses [30], and LASV's morphology was found to resemble that observed for LCMV [128]. Taken together, the morphological, physicochemical, and serological properties of all of these viruses became the basis for a formal proposal and the definition of the "arenavirus group," with LCMV as the (proto)type virus.

In addition to the morphological and serological criteria for the grouping, several of the viruses were noted to have similar limited geographical distributions, ecological associations with specific rodent hosts (with the exception of TCRV), and abilities to induce clinically similar infectious diseases with fever and/or hemorrhagic manifestations. In 1971, the taxon Arenavirus (at the time not italicized) was approved at the genus level by the International Committee on Nomenclature of Viruses (ICNV) [141], the predecessor of the International Committee on Taxonomy of Viruses (ICTV). In 1976, the family Arenaviridae (at the time not italicized) was established to include the genus Arenavirus (not italicized) with LCMV and Tacaribe complexes recognized [56]. Further developments and highlights of arenavirus taxonomy as accepted by the ICTV throughout the years are summarized in Table 1.

Current arenavirus taxonomy

As of January 21, 2014, the family *Arenaviridae* includes a single genus, *Arenavirus*, which includes 25 approved species (Table 2) [1, 124]. Historically, based on antigenic properties and geographical distribution (with the exception of LCMV ubiquity), the 30 members of these 25 species were divided into two distinct groups. Old World arenaviruses ("Lassa–lymphocytic choriomeningitis serocomplex") include viruses indigenous to Africa, and the ubiquitous LCMV, and New World arenaviruses ("Tacaribe serocomplex") include viruses indigenous to the Americas [17, 31, 42, 118]. Subsequent phylogenetic analysis based on sequences of the NP genes of all arenaviruses has provided support for the previously defined antigenic grouping and further defines virus relationships. Sequence data derived from other regions of arenavirus genomes, if available, are largely consistent with this analysis. The 30 member viruses of the 25 species represent four to five phylogenetic groups. The Old World arenaviruses form one monophyletic group that is deeply rooted to three or four New World arenavirus groups [4, 18, 19, 138]. Among the Old World viruses, LASV, Mobala virus (MOBV), and Mopeia virus (MOPV) are monophyletic, while Ippy virus (IPPYV) and LCMV are more distantly related. The recently discovered Lujo virus (LUJV), most likely endemic in Zambia, is most closely related to Old World viruses but contains elements of New World sequences in its GP gene [25].

Table 1 History of arenavirus taxonomy (typography as used in the ICTV Reports)

Years	Highlights and developments	Newly recognized arenaviruses/ arenavirus species
Until 1971 (prior to 1st ICTV[a] Report) [117, 118]	Morphological similarities between lymphocytic choriomeningitis, Junín, and Machupo virions led to the establishment of the taxonomic "LCM group", later renamed "arenoviruses"	
1971-1976 (1st ICTV[a] Report) [141]	• Spelling of "arenoviruses" corrected to "arenaviruses," and genus Arenavirus established • Lymphocytic choriomeningitis virus or "Arenavirus m-1" selected as "type species" • Virion morphology characterized • Taxon inclusion criteria: serology-based group-specific antigen recognition by immunofluorescence/complement fixation	Amapari virus [sic] Junin virus [sic] Lassa virus Latino virus lymphocytic choriomeningitis virus Machupo virus Parana virus [sic] Pichinde virus [sic] Pistillo virus[b] Tacaribe virus Tamiani virus [sic]
1976-1979 (2nd ICTV Report) [56]	Family Arenaviridae established • Tacaribe complex recognized and separated from Lassa virus • Spelling of "Tamiani virus" corrected to Tamiami virus • "Species" Pistillo virus deleted • Nature of genomic material described • Recognition of specific rodent hosts with persistent infection for each arenavirus	None
1979-1982 (3rd ICTV Report) [91]	• Genus name now italicized (*Arenavirus*) • Description of physiochemical properties and virion properties (virus nucleic acids and proteomics) • Some information on the arenavirus lifecycle elucidated • Description of antigenic properties used for classification and definition of species and complexes • Introduction of the terms "Old World arenaviruses" (for the LCMV-LASV complex) and "New World arenaviruses" (for the Tacaribe complex) • Characterization of host range and mode of transmission	None Tentative: Mozambique virus, Flescal virus [sic]
1982-1991 (4th ICTV Report) [92]	• Family name now italicized (*Arenaviridae*) • Incorporation of further details on arenavirus lifecycle and arenavirion properties • Spelling of "Flescal virus" corrected to "Flexal virus"	None
1991-1995 (5th ICTV Report) [59]	• Clear division into two separate serogroups: LCMV-LASV complex and Tacaribe complex • Mozambique virus absorbed in "species" Mopeia virus • "Machupo virus" misspelled as "Macupo virus"	Flexal virus Ippy virus Mobala virus Mopeia virus
1995-2000 (6th ICTV Report) [27]	• "Species" name abbreviations are assigned • GenBank sequence accession numbers are included, and taxonomic structure of the genus is based on both serology- and sequence-based analyses • "Species" Latino virus is removed	Guanarito virus SPH 114202 virus Tentative: Sabio virus [sic]

New World arenaviruses are subdivided into three or four phylogenetic groups, A, B, C, and possibly D. Group A includes Allpahuayo virus (ALLV), Flexal virus (FLEV), PARV, PICV, and Pirital virus (PIRV) from South America. Group B contains the human pathogenic viruses Chapare virus (CHPV), Guanarito virus (GTOV), JUNV, MACV, and Sabiá virus (SABV), as well as the non-pathogenic AMAV, Cupixi virus (CPXV), and TCRV.

Table 1 continued

Years	Highlights and developments	Newly recognized arenaviruses/ arenavirus species
2000-2005 (7th ICTV Report) [43]	• Species names now italicized (all virus names introduced previously were copied and introduced as species names)[c] • Species (and virus name) corrections: *Junin virus*→*Junín virus*; *Parana virus*→*Paraná virus* • SPH 114202 virus and "Sabio virus" combined, and "Sabio virus" corrected to "Sabiá virus" • New World arenaviruses subdivided into Clades A-C • Virus strains and serotypes associated with genomic sequence information • Indication of natural hosts and their geographic distribution • Phylogenetic relationships within the family are based on the nucleic acid sequence of the *N* gene • Species demarcation criteria are based on association with a specific host, geographic distribution, ability to cause human disease, differences in antigenic cross-reactivity, and amino acid sequence divergence	*Latino virus* *Oliveros virus* *Pirital virus* *Sabiá virus* *Whitewater Arroyo virus* Tentative: Pampa virus
2005-2011 (8th ICTV Report) [55]	• Viruses and species now differentiated • Genome sequencing of Bear Canyon, Tamiami, and Whitewater Arroyo viruses sparks discussion whether they are recombinants of ancestral arenaviruses from different lineages	Allpaahuayo virus [sic] (species *Allpaahuayo virus* [sic]) Bear Canyon virus (species *Bear Canyon virus*) Cupixi virus (species *Cupixi virus*) Tentative: Rio Cacarana virus [sic][d]
2011-present (9th ICTV Report and ICTV updates) [1, 2, 74]	• Pampa virus absorbed in Oliveros virus (species *Oliveros virus*) • "Allpaahuayo virus" and "*Allpaahuayo virus*" corrected to "Allpahuayo virus" and "*Allpahuayo virus*," respectively • Species demarcation criterion is specified to at least 12 % in the NP amino acid sequence	Chapare virus (species *Chapare virus*) Lujo virus (species *Lujo virus*) Luna virus (species *Luna virus*) Tentative: Dandenong virus, Kodoko virus, Merino Walk virus

[a] At the time called the International Committee on Nomenclature of Viruses (ICNV)

[b] The origin of this name is unclear

[c] Note that, from that moment on, species (concepts of the mind) and viruses (physical entities) were clearly distinguished conceptually by the ICTV but not necessarily by ICTV study groups. This distinction is still not widely understood. Hence, in the 7th ICTV Report, species are listed as viruses rather than as taxa and therefore erroneously received abbreviations

[d] The sequence of the Río Carcarañá virus S RNA was determined, but virus could not be isolated and the sample was lost. Consequently, this virus was dropped from the list of classifiable arenaviruses (Victor Romanowski, personal communication)

Group C is composed of LATV and Oliveros virus (OLVV).

Recombination may have influenced the evolution of some arenaviruses. The NP and GP genes of Bear Canyon virus (BCNV), TAMV, and Whitewater Arroyo virus (WWAV) from North America have divergent phylogenetic histories. Separate analyses of full-length amino acid sequences revealed that the NPs of these three viruses are related to those of New World Group A viruses, while the GPCs are more closely related to those of New World Group B viruses [6, 38, 39, 60]. Together, these viruses are currently regarded as a tentative Group D of New World viruses.

Current family and genus inclusion criteria

Since the family *Arenaviridae* is currently monogeneric, the inclusion criteria for both family and genus are identical. According to the latest 9th ICTV Report [74], the current polythetic parameters to define an arenavirus (i.e., a member of the family *Arenaviridae* and the genus *Arenavirus*) are:

1) enveloped spherical or pleomorphic virions;
2) bisegmented single-stranded, ambisense RNA genome without polyadenylated tracts at the 3' termini;
3) 5'- and 3'-end sequence complementarity;

Table 2 Current arenavirus classification (ICTV-approved and ratified species names) [1, 2, 29, 32, 37, 40–42, 49, 71, 74, 82, 102, 119, 124]

Virus species name	Species member(s): virus (virus abbreviation)	Geographic virus distribution	Natural host reservoir (species name)
OLD WORLD ARENAVIRUSES			
Ippy virus	Ippy virus (IPPYV)	Central African Republic	**unstriped grass rats (*Arvicanthis* spp. Lesson, 1842)**[a]; soft-furred mice (*Praomys* spp. Thomas, 1915)
Lassa virus	Lassa virus (LASV)	Western Africa	Natal mastomys (*Mastomys natalensis*[b] Smith, 1834)
Lujo virus	Lujo virus (LUJV)	Zambia	unknown
Luna virus	Luna virus (LUNV)	Southern Africa, Zambia	Natal mastomys (*Mastomys natalensis*[b] Smith, 1834)
Lymphocytic choriomeningitis virus	lymphocytic choriomeningitis virus (LCMV)	worldwide	**house mice (*Mus* (*Mus*) *musculus* Linnaeus, 1758)**; long-tailed field mice (*Apodemus sylvaticus* Linnaeus, 1758)
Mobala virus	Mobala virus (MOBV)	Central African Republic	soft-furred mice (*Praomys* spp. Thomas, 1915)
Mopeia virus	Mopeia virus (MOPV)	Mozambique, Zimbabwe	Natal mastomys (*Mastomys natalensis*[b] Smith, 1834)
	Morogoro virus (MORV)	Tanzania	Natal mastomys (*Mastomys natalensis*[b] Smith, 1834)
NEW WORLD ARENAVIRUSES, CLADE A			
Allpahuayo virus	Allpahuayo virus (ALLV)	Peru	Brazilian oecomys (*Oecomys paricola* Thomas, 1904); white-bellied oecomys (*Oecomys bicolor* Tomes, 1860)
Flexal virus	Flexal virus (FLEV)	Brazil	Unidentified member of the oryzomyini
Paraná virus	Paraná virus (PARV)	Paraguay	Angouya oryzomys (*Oryzomys angouya*[c] Fischer, 1814)
Pichinde virus [sic]	Pichindé virus (PICV)	Colombia	white-throated oryzomys (*Oryzomys albigularis* Tomes, 1860)
Pirital virus	Pirital virus (PIRV)	Venezuela	**Alston's cotton rats (*Sigmodon* (*Sigmomys*) *alstoni* Thomas, 1880);** short-tailed zygodonts (*Zygodontomys brevicauda* Allen and Chapman, 1893)
NEW WORLD ARENAVIRUSES, CLADE B			
Amapari virus [sic]	Amaparí virus (AMAV)	Brazil	Guianan neacomys (*Neacomys guianae* Thomas, 1905)[d]
Chapare virus	Chapare virus (CHPV)	Bolivia	unknown
Cupixi virus	Cupixi virus (CPXV)	Brazil	Azara's broad-headed oryzomys (*Oryzomys megacephalus* Fischer, 1814)
Guanarito virus	Guanarito virus (GTOV[e])	Venezuela	**short-tailed zygodonts (*Zygodontomys brevicauda* Allen and Chapman, 1893);** Alston's cotton rats (*Sigmodon* (Sigmomys) *alstoni* Thomas, 1880);
Junín virus	Junín virus (JUNV)	Argentina	**drylands lauchas (*Calomys musculinus* Thomas, 1913)**; Azara's akodonts (*Akodon* (*Akodon*) *azarae* Fischer, 1829); little lauchas (*Calomys laucha* Fischer, 1814)
Machupo virus	Machupo virus (MACV)	Bolivia	big lauchas (*Calomys callosus* Rengger, 1830)[f]
Sabiá virus	Sabiá virus (SABV)	Brazil	?
Tacaribe virus	Tacaribe virus (TCRV[g])	Trinidad	Jamaican fruit-eating bats (*Artibeus* (*Artibeus*) *jamaicensis trinitatis* Anderson, 1906)
NEW WORLD ARENAVIRUSES, CLADE C			
Latino virus	Latino virus (LATV)	Bolivia	big lauchas (*Calomys callosus* Rengger, 1830)[h]
Oliveros virus	Oliveros virus (OLVV)	Argentina	Argentine akodonts (*Necromys benefactus* Thomas, 1919)[i]
NEW WORLD ARENAVIRUSES, TENTATIVE CLADE D			
Bear Canyon virus	Bear Canyon virus (BCNV)	California, USA	**big-eared woodrats (*Neotoma* (*Neotoma*) *macrotis* Thomas, 1893);** California deermice (*Peromyscus californicus* Gambel, 1848)
Tamiami virus	Tamiami virus (TAMV)	Florida, USA	**Alston's cotton rats (*Sigmodon* (Sigmomys) *alstoni* Thomas, 1880);** marsh oryzomys (*Oryzomys palustris* Harlan, 1837)

Table 2 continued

Virus species name	Species member(s): virus (virus abbreviation)	Geographic virus distribution	Natural host reservoir (species name)
Whitewater Arroyo virus	Big Brushy Tank virus (BBTV)	southwestern USA	white-throated woodrats (*Neotoma* (*Neotoma*) *albigula* Hartley, 1894)
	Catarina virus (CTNV)		southern plains woodrats (*Neotoma* (*Neotoma*) *micropus* Baird, 1855)
	Skinner Tank virus (SKTV)		Mexican woodrats (*Neotoma* (*Neotoma*) *mexicana* Baird, 1855)
	Tonto Creek virus (TTCV)		white-throated woodrats (*Neotoma* (*Neotoma*) *albigula* Hartley, 1894)
	Whitewater Arroyo virus (WWAV)		white-throated woodrats (*Neotoma* (*Neotoma*) *albigula* Hartley, 1894)

[a] Predominant/main hosts are in printed bold

[b] Also sometimes referred to as *Praomys natalensis*

[c] Also sometimes referred to as *Sooretamys angouya* Fischer, 1814

[d] Initial studies reported members of *Oryzomys* sp. as possible hosts [119]

[e] Previously also abbreviated GUAV [27]

[f] Members of *Calomys* cf. *callosus* have been reported to be the actual reservoir of MACV [119]. These lauchas are morphologically indistinguishable from members of *Calomys callosus* (s.s.) but may comprise a separate species

[g] Previously also abbreviated TACV [27]

[h] The proper species name for this reservoir rodent is *Calomys callosus* (*s.s.*) [119]

[i] Members of *Necromys benefactus* Waterhouse, 1837 were previously thought to be the hosts [119]

4) nucleotide sequences that could form one or more hairpin configurations within the intergenic regions of both genomic RNA molecules;
5) capped but not polyadenylated viral mRNAs;
6) induction of a persistent and frequently asymptomatic infection in reservoir hosts, in which chronic viremia and viruria occur.

Current species demarcation criteria

According to the latest 9th ICTV Report, "[t]he parameters used to define a species in the genus are:

1) an association with a specific host species [sic] or group of species [sic];
2) presence in a defined geographical area;
3) etiological agent (or not) of disease in humans;
4) significant differences in antigenic cross-reactivity, including lack of cross-neutralization activity where applicable;
5) significant amino acid sequence difference from other species [sic] in the genus (i.e., showing a divergence between species of at least 12 % in the nucleoprotein amino acid sequence)" [124].

Not all criteria need to be fulfilled for a novel virus to define a new species (polythetic principle). For example, although PIRV and GTOV are endemic in the same region of Venezuela, they have been assigned to two different species (*Pirital virus* and *Guanarito virus*, respectively) because the viruses are maintained in different rodent hosts (Table 2), their titers differ by at least 64-fold using ELISA, and partial NP sequences are less than 55 % similar at the amino acid level. In another example, LASV and MOPV share common rodent hosts (Table 2), yet are distinguished by their different geographical range, profiles of reactivity with panels of monoclonal antibodies, and by NP amino acid sequence divergence of about 26 %. Also, LASV causes viral hemorrhagic fever in humans, whereas MOPV has not been found to be associated with human disease. Consequently, these two viruses have also been assigned to two different species (*Lassa virus* and *Mopeia virus*, respectively) in the past.

Current challenges in arenavirus taxonomy

Classification: discovery of novel arenaviruses

The number of sequenced coding-complete or complete genomes (for the sequencing nomenclature used see reference [80]) of viral pathogens has increased dramatically in recent years. Newly developed "next-generation" sequencing (NGS) technologies allow the rapid and cost-effective acquisition of thousands to millions of short sequence reads from a single sample and provide unprecedented possibilities for the large-scale sequencing of virus genomes [50, 68, 89, 95]. These technological

advances promise an even richer haul of genomic data for arenaviruses in the near future, mainly due to their generally small genomes. Furthermore, NGS enables sequencing of viral genomes directly from clinical samples without the manipulation and adaptation often associated with culture prior to PCR-based methodologies.

Most virological science today is focused on the study of a relatively small number of pathogens. These viruses are studied either because of their easy propagation in the laboratory or their association with human or animal disease. However, many viruses cannot be cultured under standard laboratory conditions. The lack of knowledge of the size and characteristics of the global virome and the diversity of viral genomes are critical issues in the field of viral ecology that remain to be examined in detail [23]. Such knowledge would contribute to a better understanding of important issues, such as the origin of emerging pathogens and the extent of gene exchange among viruses.

Recently, NGS has been applied to direct whole genome sequencing of uncultured viral assemblages in a process termed "viral metagenomics," and this advance has dramatically expanded our understanding of viral diversity. Researchers are now using this approach to explore viral communities in various biological and environmental matrices, including human samples from feces [21, 24, 57, 113, 145], blood [22], and the respiratory tract [142], as well as bat [51, 53, 86] and rodent [108, 137] samples. Metagenomic approaches present a fascinating opportunity to identify previously uncultured viruses and to understand the biodiversity, function, interactions, adaptation, and evolution of these viruses in different environments [5, 13, 20, 21, 23, 50, 116].

An example of how NGS and viral metagenomics studies can bring about such advances in arenavirology can be found in a recent study by Stenglein *et al*. [129]. Three novel arenaviruses, CAS virus, Golden Gate virus, and Collierville virus were identified in sick boid snakes as possible etiological agents of snake inclusion body disease (IBD). This discovery was made possible by unbiased high-throughput metagenomic analysis of RNA extracted directly from IBD-positive and –negative snake tissues. In fact, isolation attempts using common reptile cell lines or the mammalian arenavirus-permissive grivet-derived Vero cell line failed to detect productive replication of Golden Gate virus. Only a continuous cell line generated from a female boa constrictor, the alethinophidian host of Golden Gate virus, supported efficient virus replication. Thus, this study exemplifies the potential of NGS and viral metagenomics studies in advancing discovery and characterization of novel arenaviruses, which might be difficult or impossible to culture under standard laboratory conditions.

Recently, two other studies used similar approaches and identified two additional snake viruses that have genomes with the typical organization of arenaviruses [14, 67]. All of these newly discovered snake arenaviruses differ from all other known arenaviruses in several key aspects:

- they infect alethinophidian snakes, rather than mammals [14, 67, 129];
- their genes and genomes do not cluster with either Old World or New World arenaviruses in sequence alignments but together form a monophyletic sister group to both clusters [14, 67, 129];
- their *GPC* genes encode a GP2 subunit highly reminiscent of that of Ebola virus (family *Filoviridae*) [67, 75, 129];
- their Z proteins do not possess N-terminal glycine residues but have transmembrane domains at the N-termini; they do not contain known late budding motifs [129];
- putative late budding motifs are found at the C-termini of their NP proteins [129].

At the time of writing, most published alethinophidian arenaviruses were isolated in culture. Together with the data summarized above, these snake arenaviruses will have to be classified, but they cannot be included in any of the established mammalian arenavirus species [67].

In addition to the alethinophidian arenaviruses, several novel mammalian Old and New World arenaviruses have been described in recent years. A summary list of all currently unclassified arenaviruses is presented in Table 3. Most of the unclassified mammalian arenaviruses would not be recognized as members of new species under the current species demarcation criteria. Such an example is Dandenong virus, the NP amino acid sequence of which is only 3 % different from that of LCMV, suggesting it is a member of the species *Lymphocytic choriomeningitis virus*. However, some viruses do comply with all or most of the species demarcation criteria. One example is the newly discovered Merino Walk virus, the NP amino acid sequence of which is more than 31 % different from that of MOPV, the most closely related arenavirus.

Nomenclature: spelling of arenavirus species names

Arenavirus names and arenaviral species names are traditionally derived from geographic locations, such as towns, regions, or rivers. Since many mammalian New World arenaviruses were discovered in South America, their names are derived from South American locations, which are spelled using the Spanish alphabet. The ICTV *Arenaviridae* Study Groups of the past have already corrected

Table 3 Currently unclassified arenaviruses

Suggested virus name (suggested abbreviation)	Genomic sequence availability and amino acid sequence divergence to closely related virus homologs	Serology	Isolation in culture	Natural host reservoir (species name)	Reference and GenBank accession numbers
OLD WORLD MAMMALIAN ARENAVIRUSES					
Dandenong virus (DANV)	*GP*, *NP*, *L*, *Z*. LCMV: GPC (6 %) and NP (3 %)	yes (IgG and IgM)	yes (confirmed by CPE, RT-PCR, IFA-α OWA, EM)	unknown	[103] S: EU136038 L: EU136039
Gbagroube virus (none)	complete S segment, partial L segment. LASV: GPC (9.8 %) and NP (14.1 %)	yes (α OWA IgG)	no	Peters's mice (*Mus* (*Nannomys*) *setulosus* Peters, 1876)	[47] S: GU830848
Jirandogo virus (none)	partial *GP*, *NP*, *L*. LASV: NP (18 %)	no	no	Baoule's mice (*Mus* (*Nannomys*) *baoulei* Vermeiren and Verheyen, 1980)	[78] Only partial sequencess
Kodoko virus (KODV)	partial *NP*, partial *L*. LCMV: NP (24.6 %), and L (7.2 %)	no	no	African pygmy mice (*Mus* (*Nannomys*) *minutoides* Smith, 1834)	[82] Only partial sequences
Lunk virus (LNKV)	complete S and L segments. LCMV: NP (17.7 %)	no	yes	African pygmy mice (*Mus* (*Nannomys*) *minutoides* Smith, 1834)	[70] S: AB693150 L: AB693151
Menekre virus (none)	complete S segment, partial L segment. MOPV: GPC (21.5 %), LASV: NP (24.7 %)	yes (α OWA IgG)	no	African wood mice (*Hylomyscus* sp. Thomas, 1926)	[47] S: GU830862
Merino Walk virus (MWV)	complete genome. MOPV: NP (31.4 %)	CF testing: related to MOPV, MOBV, and IPPYV, but unrelated to LCMV	yes (confirmed by EM)	Bush Ka(r)roo rats (*Myotomys unisulcatus* Cuvier, 1829)	[104] S: GU078660 L: GU078661
NEW WORLD MAMMALIAN ARENAVIRUSES					
"[New World] arenavirus 96010025"	complete S segment. AV 96010151: NP (8.2 %)	no	?	bushy-tailed woodrats (*Neotoma* (*Teonoma*) *cinerea* Ord, 1815)	Unpublished S: EU486820
"[New World] arenavirus H0380005"	complete S segment. AV 96010151: NP (6.8 %)	no	yes?	southern plains woodrats (*Neotoma* (*Neotoma*) *micropus* Baird, 1855)	Unpublished S: EU910959
"North American arenavirus 96010024"	complete S segment. AV 96010151: NP (7.3 %)	no	?	Mexican woodrats (*Neotoma* (*Neotoma*) *mexicana* Baird, 1855)	[35] S: EU123331
"North American arenavirus 96010151"	complete S segment. WWAV: NP (5.7 %)	no	?	Mexican woodrats (*Neotoma* (*Neotoma*) *mexicana* Baird, 1855)	[35] S: EU123330
"North American arenavirus D1240007"	complete S segment. AV 96010151: NP (7.3 %)	no	?	Mexican woodrats (*Neotoma* (*Neotoma*) *mexicana* Baird, 1855)	[35] S: EU123329

Table 3 continued

Suggested virus name (suggested abbreviation)	Genomic sequence availability and amino acid sequence divergence to closely related virus homologs	Serology	Isolation in culture	Natural host reservoir (species name)	Reference and GenBank accession numbers
Black Mesa virus (none)	complete *GP*, *N*, and partial *L* gene. AV 96010151: NP (7.7 % and 7.9 %)*	no	no	white-throated woodrats (*Neotoma* (*Neotoma*) *albigula* Hartley, 1894)	unpublished (FJ719106, FJ032026, FJ719107, FJ032027, EU938670)
Middle Pease River virus (MPRV)	*GP*, *NP*. CTNV: NP (11-12 %)	yes (ELISA: WWAV)	Yes (confirmed by IFA-αWWAV)	southern plains woodrats (*Neotoma* (*Neotoma*) *micropus* Baird, 1855)	[34] S: JX560798, JX560799
Ocozocoautla de Espinosa virus (OCEV)	complete S segment. JUNV: NP (16.1 %), TCRV: GPC (24.7 %)	yes	no	Mexican deermice (*Peromyscus mexicanus* Saussure, 1860)	[33] S: JN897398
Orogrande virus (none)	partial *L* gene	no	no	southern plains woodrats (*Neotoma* (*Neotoma*) *micropus* Baird, 1855)	unpublished (EU938669)
Pinhal virus (none)	partial *N* gene	no	no	delicate lauchas (*Calomys tener* Winge, 1887)	unpublished (EU280546, EU280547, EU280545, EU220740, EU329718)
Real de Catorce virus (none)	complete S segment. CTNV: NP (11.6 %), SKTV: GPC (28.3 %) WWAV: GPC (32 %), NP (13.7 %)	yes (ELISA: WWAV)	no	white-toothed woodrats (*Neotoma* (*Neotoma*) *leucodon* Merriam, 1894)	[69] S: GQ903697
REPTILIAN ARENAVIRUSES					
Boa Av NL B3 virus (none)	near-complete genome; UHV: GPC (38 %), NP (16 %), Z (11 %), L (8 %)	no	no	captive boa constrictors (*Boa constrictor* Linnaeus, 1758) and emerald tree boas (*Corallus caninus* Linnaeus, 1758) with inclusion body disease	[14, 15] S: KC508669 L: KC508670
CAS virus (CASV)	complete genome. Boa Av NL B3 virus: NP (43.9 %), GPC (41.6 %), L (48.9 %), Z (48.6 %) TCRV: NP (74.2 %), L (80.8 %)	no	no	captive annulated tree boas (*Corallus annulatus* Cope, 1875) with inclusion body disease	[129] S: JQ717262 L: JQ717261
Colliervillle virus (CVV)	no	no	no	captive boa constrictors (*Boa constrictor* Linnaeus, 1758) with inclusion body disease	[129]
Golden Gate virus (GGV)	complete genome Boa Av NL B3 virus: NP (33.7 %), GPC (15.2 %), L (20.9 %) UHV: Z (9.2 %) LASV: NP (74.9 %), TCRV: L (81.5 %)	no	yes	captive boa constrictors (*Boa constrictor* Linnaeus, 1758) with inclusion body disease	[129] S: JQ717264 L: JQ717263

Table 3 continued

Suggested virus name (suggested abbreviation)	Genomic sequence availability and amino acid sequence divergence to closely related virus homologs	Serology	Isolation in culture	Natural host reservoir (species name)	Reference and GenBank accession numbers
University of Helsinki virus (UHV)	near-coding-complete genome. Boa Av NL B3 virus: GPC (38 %), NP (16 %), L (8 %), GGV: Z (5 %)	no	yes	captive boa constrictors (*Boa constrictor* Linnaeus, 1758), annulated tree boas (*Corallus annulatus* Cope, 1875), common tree boas (*Corallus hortulanus* Linnaeus, 1758) with inclusion body disease	[67] S: KF297880 L: KF297881

CF, complement fixation; IFA, immunofluorescence assay; αOWA, anti-Old World arenavirus antibody; αWWAV, anti-WWAV antibody; EM, electron microscopy; CPE, cytopathic effect; ELISA, enzyme-linked immunosorbent assay; RT-PCR, reverse transcription polymerase chain reaction; * The two values are for the two strains of Black Mesa virus

several arenavirus and arenaviral species names by incorporating correct diacritical marks (Table 1). However, at least two species names still contain incorrectly spelled word stems (Amapari [sic] and Pichinde [sic]).

Communication among virologists and database searches are crucially dependent on virus name abbreviations being unique to avoid confusion. Several abbreviations for classified arenaviruses do not fulfill this condition:

- CHPV as the abbreviation for Chandipura virus (a vesiculovirus) and chicken parvovirus preceded the use of CHPV as the abbreviation for Chapare virus;
- CPXV as the abbreviation for cowpox virus (an orthopoxvirus) preceded the use of CPXV for Cupixi virus;
- LUNV as the abbreviation for Lundy virus (an orbivirus) preceded the use of LUNV as the abbreviation for the recently discovered Luna virus;
- PARV as the abbreviation for Paraná virus is not ideal because the abbreviations PARV4 and ParV-3 are in use for the unclassified parvovirus PARV4 virus and the unclassified potexvirus parsnip virus 3, respectively;
- PICV as the abbreviation for Pichindé virus is not ideal, as PiCV is in use for pigeon circovirus;
- SABV as the abbreviation for Sabiá virus is problematic, as SABV also stands for Saboya virus (a flavivirus); and
- TAMV as the abbreviation for Tamiami virus is not ideal, as TaMV is in use for Tulare apple mosaic virus (an ilarvirus).

Several abbreviations suggested for unclassified arenaviruses are also not unique:

- BBTV should not be used as an abbreviation for Big Brushy Tank virus, as BBTV is already in use for banana bunchy top virus (a babuvirus);
- CVV should not be used as an abbreviation for Collierville virus as it is already in use for citrus variegation virus (an ilarvirus);
- GGV as the abbreviation for Golden Gate virus is problematic as GgV is in use for Gaeumannomyces graminis virus (a partitivirus);
- MPRV as the abbreviation for Middle Pease River virus is problematic as MpRV is in use for Micromonas pusilla reovirus; and
- MWV as the abbreviation for Merino Walk virus is problematic as MwV has been suggested for the unclassified alphanodavirus Manawatu virus.

In addition, several unclassified arenavirus names do not have abbreviations: Black Mesa virus, Gbagroube virus, Jirandogo virus, Menekre virus, Orogrande virus, Pinhal virus, and Real de Catorce virus (RDCV has been

suggested in one publication [10]). Finally, "Boa Av NL B3 virus" and several North American arenaviruses lack proper virus names and abbreviations.

Problems related to the International Code of Virus Classification and Nomenclature

Classification and nomenclature of viruses are subject to Rules formalized in a Code, the International Code of Classification and Nomenclature (ICVCN) [74]. At the moment, arenavirus names and arenaviral species names are spelled identically and only differ by the absence or presence of italics (e.g., Junín virus is a member of the species *Junín virus*). This is a problem in particular for electronic databases, which often cannot differentiate between Roman and italicized text. Second, the genus name *Arenavirus* and the family name *Arenaviridae* are only differentiated by their specific suffixes ("*-virus*" vs. "*-viridae*") but contain the same word stem ("*arena*"). The members of the family are therefore called arenaviruses, while the members of the genus are also called arenaviruses. At present, this lack of precision is unproblematic, as the family currently includes only a single genus. However, the establishment of a second genus for alethinophidian arenaviruses will make "arenavirus" an ambiguous term, as it will not be clear whether, upon its use, all members of the family are meant or only those of one of the two genera. Together, current arenavirus taxonomy is therefore at odds with ICVCN

- Rule 2.1(ii): "The essential principles of virus nomenclature are…to avoid or reject the use of names which might cause error or confusion";
- Rule 3.14: "New names shall not duplicate approved names. New names shall be chosen such that they are not closely similar to names that are in use currently or have been in use in the recent past";
- Rule 3.21: "A species name shall consist of as few words as practicable but be distinct from names of other taxa"; and
- Rule 3.22: "A species name must provide an appropriately unambiguous identification of the species" [3, 74].

Solutions to current challenges in arenavirus taxonomy

New family and taxon inclusion criteria

Due to the recognition of the widely expanding diversity of arenaviruses, we base arenavirus classification on objective criteria based on coding-complete genomic segment sequences [80]. Based on consensus voting of ICTV *Arenaviridae* Study Group members, arenaviruses are now classifiable if:

1) coding-complete genomic sequences are available for both S and L segments even in the absence of a culturable isolate; or
2) a coding-complete genomic sequence is available for the S segment together with a culturable isolate.

Based on these criteria, all currently classified arenaviruses (Table 2) should remain classified. Boa AV NL B3, CAS virus, Dandenong virus, Golden Gate virus, Lunk virus, Merino Walk virus, Middle Pease River virus, Tonto Creek virus, and University of Helsinki virus should be classified. Black Mesa virus, Collierville virus, Gbagroube virus, Jirandogo virus, Kodoko virus, Ocozocoautla de Espinosa virus, Orogrande virus, Pinhal virus, Real de Catorce virus, and the unnamed North American arenaviruses (Table 3) should be considered tentative members of the family until more data become available.

The PAirwise Sequence Comparison (PASC) tool, accessible at the National Center for Biotechnology Information (NCBI) website (http://www.ncbi.nlm.nih.gov/sutils/pasc/viridty.cgi?textpage=overview) and/or alternatives such as DivErsity pArtitioning by hieRarchical Clustering (DeMARC) [81] or the Species Demarcation Tool (SDT) [99] should be used for preliminary classification of novel, classifiable arenaviruses. PASC analysis creates histograms to visualize the distances between pairs of virus sequences, resulting in peaks that may represent different taxon levels. The percentages of the lowest points of the valleys between the peaks can guide taxon demarcation criteria (for more information on PASC, see references [11, 12]). Ideally, these percentages cutoffs are concordant with the arenavirus diversity deduced from other phylogenetic analyses and are not contradicted by known biological characteristics of individual arenaviruses. Such characteristics include: differences in host specificity and thereby geographic distribution, serological cross-reactions between virions, and the ability to cause human disease. If individual analyses do not come to the same conclusions in regard to classification, the ICTV *Arenaviridae* Study Group will have to resolve them by criterion weighing and establishment of compromises.

The results of the arenavirus PASC analysis can be accessed on the PASC webpage (S segments: http://www.ncbi.nlm.nih.gov/sutils/pasc/viridty.cgi?cmdresult=main&id=448; L segment: http://www.ncbi.nlm.nih.gov/sutils/pasc/viridty.cgi?cmdresult=main&id=446).

PASC analysis and determination of NP amino acid pairwise distances (Fig. 3) were therefore performed to evaluate whether the various possible outcomes would match the current arenavirus classification and possibly accommodate novel viruses that are thought to require the

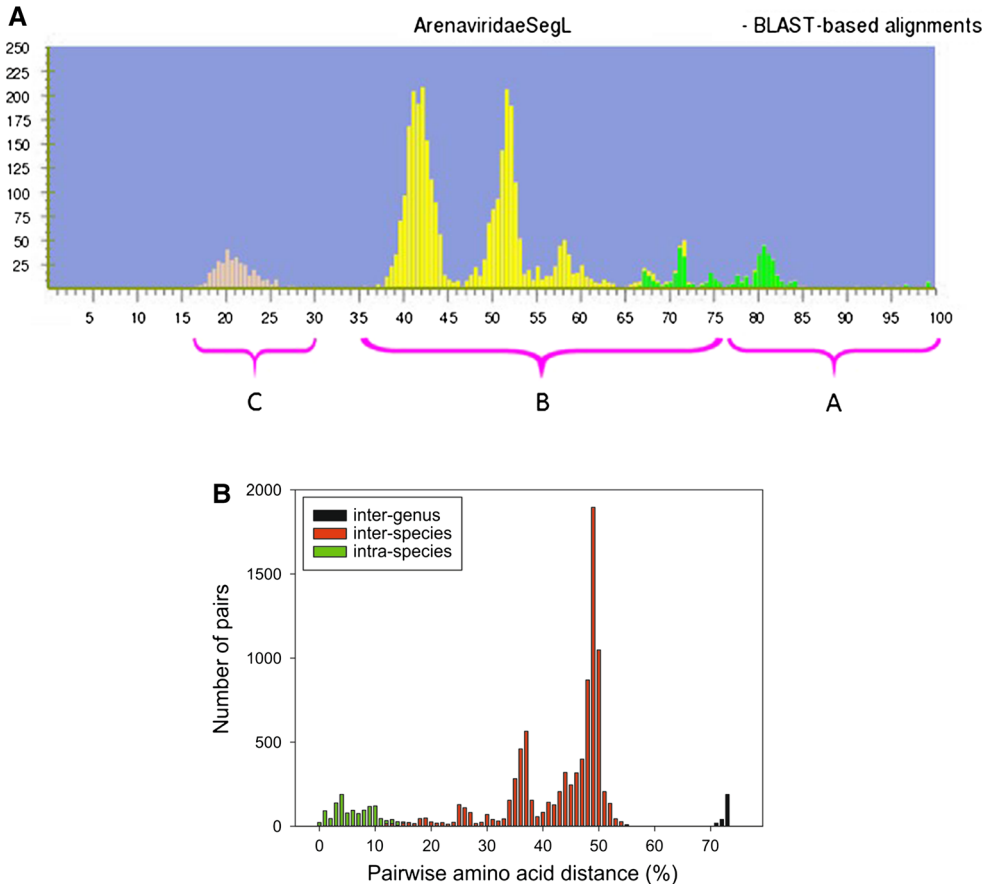

Fig. 3 Pairwise Sequence Comparison (PASC) analysis of L segment sequences and amino acid distance analysis of NP sequences. (A) Distribution of pairwise identities among 87 complete sequences of the L segments of members of the family *Arenaviridae*. Regions A, B and C represent virus pairs from the same species (100 %-76 %), different species but the same genus (76 %-35 %), and different genera (16 %-30 %), respectively, based on the proposed identity values indicated in parentheses. The x-axis shows percent identity, and the y-axis shows the number of L segment sequence pairs. (B) Amino acid sequence distances were compared using the pairwise-distance algorithm in the MEGA 6 software package and shown as frequency histograms. This analysis was done based on a multiple alignment generated using the ClustalW algorithm implemented in MEGA 6 [131]

establishment of novel taxa. Indeed, both analyses substantiate that the family *Arenaviridae* contains at least two genera, one for mammalian and one for reptilian arenaviruses. For the S segment, the pairwise nucleotide sequence identities within the same proposed genus are higher than 40 %, while those from different proposed genera are lower than 29 %. The genus separation cutoff in PASC was therefore set to 29-40 % for the S segment, and to 30-35 % for the L segment.

Depending on the various valleys-between-peaks in PASC, several alternative sequence cutoffs could be chosen for arenavirus species demarcation. The members of the ICTV *Arenaviridae* Study Group agreed that the most conservative approach be taken, i.e. that these values should be chosen in a way that introduces the fewest changes and causes the least disruption of the current arenavirus classification scheme. Accordingly, >80 % nucleotide sequence identity in the S segment and >76 % identity in the L segment were chosen as values for arenaviruses that should belong to the same species. The ICTV *Arenaviridae* Study Group agreed that PASC or similar methods alone cannot necessarily justify species classification and that, whenever possible, other criteria should be considered to confirm or reject analysis outcomes. These species classification criteria include:

1) association of the arenavirus with a main host or a group of sympatric hosts;
2) dispersion of the arenavirus in a defined geographical area;
3) significant differences in antigenic cross-reactivity, including lack of cross-neutralization activity;
4) significant protein amino acid sequence differences compared to the homologous proteins of viruses from other species in the same genus (e.g., showing a divergence between members of different species of at least 12 % in the nucleoprotein amino acid sequence);
5) association (or not) with human disease.

Revised classification of previously classified arenaviruses and inclusion of newly discovered classifiable arenaviruses

The results obtained by PASC analyses for preliminary arenavirus classification are outlined in Table 4. This classification is largely in accordance with the current classification of mammalian arenaviruses, which was largely based on biological criteria. The only modification that PASC analyses suggests to the current

Table 4 Preliminary classification of arenaviruses based on PASC results[a]

Family	Genus	Species	Virus	Notes and GenBank accession numbers
Arenaviridae (members: arenaviruses)				
	Genus 1 (members: mammalian arenaviruses)			
OLD WORLD ARENAVIRUSES				
		Species 1	Dandenong virus	also includes "LCMV M2" (AB261990), "LCMV BRC" (AB627953)
		Species 2	Ippy virus	
		Species 3	Lassa virus	"LASV Josiah" (J04324)
		Species 4	"Lassa virus"	"LASV 11620" (AF181853), "LASV Pinneo" (AY628207)
		Species 5	"Lassa virus"	"LASV 803213" (AF181854), Nig08-04 (GU481068), Nig08-A47 (GU481078), Nig08-A37 (GU481074), Nig08-A41 (GU481076)
		Species 6	"Lassa virus"	"LASV GA391" (X52400), "LASV Weller" (AY628206), Nig08-A18 (GU481070), Nig08-A19 (GU481072)
		Species 7	"Lassa virus"	"LASV CSF" (AF333969)
		Species 8	"Lassa virus"	"LASV AV" (AF246121, FR832711), "LASV Soromba-R" (KF478765), "LASV Bamba-R114" (KF478766), "LASV Komina-R16" (KF478767), "LASV Ouoma-R123" (KF478768), "LASV Soromba-R30" (KF478769)
		Species 9	Lujo virus	
		Species 10	Luna virus	
		Species 11	Lunk virus	
		Species 12	lymphocytic choriomeningitis virus	"LCMV Armstrong 53b" (M20869)
		Species 13	"lymphocytic choriomeningitis virus"	"LCMV Bulgaria" (GQ862982)
		Species 14	"lymphocytic choriomeningitis virus"	"LCMV GR01" (FJ895883)
		Species 15	"lymphocytic choriomeningitis virus"	"LCMV CABN" (FJ895882), "LCMV SN05" FJ895884)
		Species 16	"lymphocytic choriomeningitis virus"	"LCMV 810935" (FJ607029)
		Species 17	Merino Walk virus	
		Species 18	Mobala virus	
		Species 19	Mopeia virus	"MOPV AN 21366" (M33879)
		Species 20	"Mopeia virus"	"MOPV" (DQ328874) (= Mozambique virus)
		Species 21	Morogoro virus	
NEW WORLD ARENAVIRUSES				
		Species 22	Allpahuayo virus	
		Species 23	Flexal virus	
		Species 24	Paraná virus	

Table 4 continued

Family	Genus	Species	Virus	Notes and GenBank accession numbers
		Species 25	Pichindé virus	
		Species 26	Pirital virus 1	"PIRV VAV-488" (AF485262)
		Species 27	Pirital virus 2	"PIRV VAV-1743" (AY575850)
		Species 28	Pirital virus 3	"PIRV 1645" (AY573921)
		Species 29	Pirital virus 4	"PIRV 97021016" (AY573923), "PIRV 97020912" (AY574571)
		Species 30	Amaparí virus	
		Species 31	Chapare virus	
		Species 32	Cupixi virus	
		Species 33	Guanarito virus	
		Species 34	Junín virus	
		Species 35	Machupo virus	
		Species 36	Sabiá virus	
		Species 37	Tacaribe virus	
		Species 38	Latino virus	
		Species 39	Oliveros virus	
		Species 40	Bear Canyon virus	
		Species 41	Big Brushy Tank virus	
		Species 42	Middle Pease River virus	
		Species 43	Catarina virus	
		Species 44	Skinner Tank virus	
		Species 45	Tamiami virus	
		Species 46	Tonto Creek virus	
		Species 47	Whitewater Arroyo virus	Includes "North American arenaviruses" deposited under EU123330, EU123331
		Species 48	"[New World] arenavirus H0380005"	EU910959
		Species 49	"North American arenavirus D1240007"	EU123329
		Species 50	"[New World] arenavirus 96010025"	EU486820
	Genus 2 (members: reptilian arenaviruses)			
		Species 1	Golden Gate virus	
		Species 2	University of Helsinki virus, Boa AV NLB3	
		Species 3	CAS virus	

[a] This table summarizes the combined results of PASC analysis of arenaviral S segments. The classification is consistent with that for L segments for almost all viruses for which coding-complete S and L segments are available. Viruses were deemed suitable for analysis if a) the complete sequence of the S segment and an isolate in culture were available or b) if the complete S and L segment sequences were available

arenavirus classification is the establishment of nine new species (for Big Brushy Tank virus, Catarina virus, Dandenong virus, Lunk virus, Merino Walk virus, Middle Pease River virus, Morogoro virus, Skinner Tank virus, and Tonto Creek virus) and that the current species for LASV, LCMV, MOPV, PIRV, and WWAV have to be split.

The ICTV *Arenaviridae* Study Group determines the taxonomic status of individual arenaviruses using the current ICTV definition of species (ICVCN Rule 3.20: "A species is the lowest taxonomic level in the hierarchy approved by the ICTV. A species is a monophyletic group of viruses whose properties can be distinguished from those of other species by multiple criteria") [3, 74]. The set of six

Table 5 Updated and corrected taxonomy of the family *Arenaviridae*

Family	Genus	Species	Virus (Abbreviation)
Arenaviridae (members: arenaviruses)			
	Mammarenavirus (members: mammarenaviruses)		
OLD WORLD ARENAVIRUSES			
		Ippy mammarenavirus	Ippy virus (IPPYV)
		Lassa mammarenavirus	Lassa virus (LASV)
		Lujo mammarenavirus	Lujo virus (LUJV)
		Luna mammarenavirus	Luna virus (LUAV)
		Lunk mammarenavirus	Lunk virus (LNKV)
		Lymphocytic choriomeningitis mammarenavirus	lymphocytic choriomeningitis virus (LCMV)
		Merino Walk mammarenavirus	Merino Walk virus (MRWV)
		Mobala mammarenavirus	Mobala virus (MOBV)
		Mopeia mammarenavirus	Mopeia virus (MPOV), Morogoro virus (MORV)
NEW WORLD ARENAVIRUSES			
		Allpahuayo mammarenavirus	Allpahuayo virus (ALLV)
		Flexal mammarenavirus	Flexal virus (FLEV)
		Paraná mammarenavirus	Paraná virus (PRAV)
		Pichindé mammarenavirus	Pichindé virus (PICHV)
		Pirital mammarenavirus	Pirital virus (PIRV)
		Amaparí mammarenavirus	Amaparí virus (AMAV)
		Chapare mammarenavirus	Chapare virus CHAPV)
		Cupixi mammarenavirus	Cupixi virus (CUPXV)
		Guanarito mammarenavirus	Guanarito virus (GTOV)
		Junín mammarenavirus	Junín virus (JUNV)
		Machupo mammarenavirus	Machupo virus (MACV)
		Sabiá mammarenavirus	Sabiá virus (SBAV)
		Tacaribe mammarenavirus	Tacaribe virus (TCRV)
		Latino mammarenavirus	Latino virus (LATV)
		Oliveros mammarenavirus	Oliveros virus (OLVV)

Table 5 continued

Family	Genus	Species	Virus (Abbreviation)
		Bear Canyon mammarenavirus	Bear Canyon virus (BCNV)
		Tamiami mammarenavirus	Tamiami virus (TMMV)
		Whitewater Arroyo mammarenavirus	Catarina virus (CTNV), Big Brushy Tank virus (BBRTV), Skinner Tank virus (SKTV), Tonto Creek virus (TTCV), Whitewater Arroyo virus (WWAV)
	Reptarenavirus (members: reptarenaviruses)		
		Alethinophid 1 reptarenavirus	Golden Gate virus (GOGV)
		Alethinophid 2 reptarenavirus	ROUT virus (ROUTV), University of Helsinki virus (UHV)
		Alethinophid 3 reptarenavirus	CAS virus (CASV)

polythetic criteria outlined in this article is sufficient to determine the taxonomic status of an arenavirus isolate; however, each criterion by itself is not necessarily sufficient for accurate classification. Several species criteria are directly or distantly related to phylogenetic relationships, and by extension, to monophyly. The genetic proximity of viruses is determined either by PASC analysis or by NP amino acid differences. Even differences in antigenic cross-reactivity could be related to the genetic proximity of the NP and GPC amino acid sequences of the viruses. Other criteria are related to the relationships between the virus and its environment (i.e., the "ecological niche"), such as the association with a host, the geographic area, and the ability to cause human disease.

As mentioned above, based solely on PASC analysis, several arenavirus species would have to be "split" even if the most conservative cutoffs are chosen. However, such a "split" would be in contradiction to the polythetic nature of virus species (i.e., in contradiction to the other biological demarcation criteria described above). Furthermore, in some cases, PASC analysis alone may not provide consistent results for the S and L segments (e.g., the S segment of LCMV isolate 810366 [FJ607028] shares >80 % sequence identity with those of other LCMV isolates, whereas its L segment [FJ607019] shares less than 76 % identity with others). This inconsistency is not surprising considering that members of virus species constantly replicate and evolve and, therefore, form fuzzy sets with hazy boundaries.

In general, virus species can be viewed as biological continua, with members from both extremes differing significantly from each other when considering one or several parameters but are still related through multiple members with intermediate variance values. This concept is especially true for genetic distances: divergence of two isolates could be higher than the cutoff value, but these isolates could still be linked together through other intermediate isolates. For example, the NP amino acid distance between Skinner Tank virus and "arenavirus AV 96010025" is 15.65 %, i.e., above the chosen 12 % criterion. However, they form a biological continuum with Big Brushy Tank virus and "North American arenavirus AV 96010151" with inter-NP distances below 11 %.

After discussing these issues, the ICTV *Arenaviridae* Study Group decided (i) not to address the species splits suggested by PASC analysis at this point and (ii) to postpone the possibly necessary establishment of novel species for Big Brushy Tank virus, Catarina virus, Dandenong virus, Middle Pease River virus, Morogoro virus, Skinner Tank virus, and Tonto Creek virus until further biological data are reviewed and additional comparative sequence analyses are performed. However, the group has decided to establish new species for Lunk virus and Merino Walk virus as suggested by PASC. Also, until further analyses are performed, the group considers Morogoro virus a member of the species already established for MOPV, and Big Brushy Tank virus, Catarina virus, Skinner Tank virus, and Tonto Creek virus members of the species already established for WWAV. The group decided to postpone any decisions on the taxonomic status of Dandenong virus and Middle Pease River virus until further phylogenetic and biological analyses are performed and isolates are obtained. These viruses are therefore considered unclassified mammalian arenaviruses at the time of writing.

Table 6 Pronunciation of arenavirus names and taxon names

Arenavirus name[a]	International Phonetic Alphabet (IPA)	English phonetic notation[b]
Allpahuayo virus	[ˌɑlpɑ'wɑjɔ ˈvaɪrəs] or [ˌælpæ'wæjoʊ ˈvaɪrəs][c]	ahl-pah-**wah**-yaw (al-pa-**wa**-yoh) **vahy**-r*uh*s[d]
Alethinophid reptarenavirus	[ˌæləθinˈoʊfɪd rɛptəˈrinəˌvaɪrəs] or [ˌæləθinˈoʊfɪd rɛpt ˌerənəˈvaɪrəs]	al-*uh*-theen-**oh**-phid rept-*uh*-**ree**-n*uh*-vahy-r*uh*s (rept-**er**-*uh*-n*uh*-vahy-r*uh*s)
Amaparí virus	[ˌɑmɑpɑ'ri ˈvaɪrəs] or [ˌæmæpə'ri ˈvaɪrəs]	ah-mah-pah-**ree** (a-ma-p*uh*-**ree**) **vahy**-r*uh*s
arenavirid	[əˈrinəˌvɪrɪd] or [ˌerənəˈvɪrɪd]	*uh*-**ree**-n*uh*-vee-rid (er-*uh*-n*uh*-**vee**-rid)
Arenaviridae	[əˈrinəˌvɪrɪdi or [ˌerənəˈvɪrɪdi]	*uh*-**ree**-n*uh*-vee-ri-dee (er-*uh*-n*uh*-**vee**-ri-dee)
arenavirus	[əˈrinəˌvaɪrəs] or [ˌerənəˈvaɪrəs]	*uh*-**ree**-n*uh*-vahy-ruhs (er-*uh*-n*uh*-**vahy**-r*uh*s)
Bear Canyon virus	[bɛər ˈkænyən ˈvaɪrəs]	bair **kan**-y*uh*n **vahy**-r*uh*s
Big Brushy Tank virus	[bɪg ˈbrʌʃi tæŋk ˈvaɪrəs]	big **bruhsh**-ee tangk **vahy**-r*uh*s
Black Mesa virus	[ˈblæk ˈmeɪsə ˈvaɪrəs]	blak **mey**-s*uh* **vahy**-r*uh*s
CAS virus	[kæs ˈvaɪrəs]	kas **vahy**-r*uh*s
Catarina virus	[ˌkætəˈrinə ˈvaɪrəs]	ka-t*uh*-**ree**-n*uh* **vahy**-r*uh*s
Chapare virus	[tʃɑˈpɑrɛ ˈvaɪrəs] or [tʃɑˈpɑreɪ ˈvaɪrəs]	chah-**pahr**-eh (chah-**pahr-**ey) **vahy**-r*uh*s
Collierville virus	[ˈkɒlyərˌvɪl ˈvaɪrəs]	**kol-**yer-vil **vahy**-r*uh*s
Cupixi virus	[kʊˈpiʃ ˈvaɪrəs]	k*oo*-**peesh** **vahy**-r*uh*s
Dandenong virus	[ˈdændiˌnoŋ ˈvaɪrəs]	**dan**-dee-nong **vahy**-r*uh*s
Flexal virus	[flɛˈʃɑl ˈvaɪrəs] or [flɛˈʃɑʊ ˈvaɪrəs]	fle-**shahl** (fle-**show**) **vahy**-r*uh*s
Gbagroube virus	[bɑˈrʊbɛ ˈvaɪrəs] or [bɑˈrʊbeɪ ˈvaɪrəs]	bah-**roo**-beh (bah-**roo**-bey) **vahy**-r*uh*s
Golden Gate virus	[ˈgoʊldən geɪt ˈvaɪrəs]	**gohl**-d*uh*n geyt **vahy**-r*uh*s
Guanarito virus	[ˌgwɑnɑˈritɔ ˈvaɪrəs] or [ˌgwænəˈritoʊ ˈvaɪrəs]	gwah-nah-**ree**-taw (gwa-n*uh*-**ree-**toh) **vahy**-r*uh*s
Ippy virus	[ˈɪpi ˈvaɪrəs]	**ip**-ee **vahy**-r*uh*s
Jirandogo virus	[ˌdʒirənˈdɔgɔ ˈvaɪrəs] or [ˌdʒirənˈdɒgoʊ ˈvaɪrəs]	jee-r*uh*n-**daw**-gaw (jee-r*uh*n-**dog**-oh) **vahy**-r*uh*s
Junín virus	[hʊˈnin ˈvaɪrəs]	h*oo*-**nin** **vahy**-r*uh*s
Kodoko virus	[kɔˈdɔkɔ ˈvaɪrəs] or [kəˈdoʊkoʊ ˈvaɪrəs]	kaw-**daw**-kaw (k*uh*-**doh**-koh) **vahy**-r*uh*s
Lassa virus	[ˈlɑsɑ ˈvaɪrəs] or [ˈlɑsə ˈvaɪrəs]	**lah**-sah (**lah**-s*uh*) **vahy**-r*uh*s
Latino virus	[ləˈtinoʊ ˈvaɪrəs] or [læˈtinoʊ ˈvaɪrəs]	l*uh*-**tee**-noh (la-**tee**-noh) **vahy**-r*uh*s
Lujo virus	[ˈlʊdʒoʊ ˈvaɪrəs]	**l*oo***-joh **vahy**-r*uh*s
Luna virus	[ˈlʊnə ˈvaɪrəs]	**loo**-n*uh* **vahy**-r*uh*s
Lunk virus	[ˈlʊŋk ˈvaɪrəs]	loongk **vahy**-r*uh*s
lymphocytic choriomeningitis virus	[ˌlɪmfəˈsɪtɪk ˈkɔrioʊˌmɛnɪnˈdʒaɪtɪs ˈvaɪrəs]	lim-f*uh*-**sit**-ik **kawr**-ee-oh-men-in-**jahy**-tis **vahy**-r*uh*s
Machupo virus	[mɑˈtʃʊpɔ ˈvaɪrəs] or [məˈtʃʊpoʊ ˈvaɪrəs]	mah-**ch*oo***-paw (m*uh*-**ch*oo***-poh) **vahy**-r*uh*s
mammarenavirus	[mæməˈrinəˌvaɪrəs] or [mæmˌerənəˈvaɪrəs]	mam-*uh*-**ree**-n*uh*-vahy-r*uh*s (mam-**er**-*uh*-n*uh*-vahy-r*uh*s)
Menekre virus	[mɛˈnɛkrɛ ˈvaɪrəs] or [məˈnɛkreɪ ˈvaɪrəs]	meh-**nek**-reh (m*uh*-**nek-**rey) **vahy**-r*uh*s
Merino Walk virus	[məˈrinoʊ wɔk ˈvaɪrəs]	m*uh*-**ree**-noh wawk **vahy**-r*uh*s
Middle Pease River virus	[ˈmɪdl piz ˈrivər ˈvaɪrəs]	**mid**-l peez **riv**-er **vahy**-r*uh*s
Mobala virus	[mɔˈbɑlɑ ˈvaɪrəs] or [məˈbɑlə ˈvaɪrəs]	maw-**bah**-lah (m*uh*-**bah**-l*uh*) **vahy**-r*uh*s
Mopeia virus	[mɔˈpeɪɑ ˈvaɪrəs] or [məˈpeɪə ˈvaɪrəs]	maw-**pey-**ah (m*uh*-**pey**-*uh*) **vahy**-r*uh*s
Morogoro virus	[mɔrɔˈgɔrɔ ˈvaɪrəs] or [mərəˈgoʊroʊ ˈvaɪrəs]	maw-raw-**gaw**-raw (m*uh*-r*uh*-**goh**-roh) **vahy**-r*uh*s
Ocozocoautla de Espinosa virus	[ɔˌkɔsɔkɔˈaʊtlɑ dɛ ˌɛspəˈnɔsɑ ˈvaɪrəs] or [ɔˌkɔsɔkɔˈaʊtlɑ ˌdiəspəˈnoʊzə ˈvaɪrəs]	aw-kaw-saw-kaw-**out**-lah deh es-p*uh*-**naw**-sah (dee-*uh*s-p*uh*-**noh**-z*uh*) **vahy**-r*uh*s
Oliveros virus	[ɔliˈvɛrɔs ˈvaɪrəs] or [ɒliˈvɛəroʊz ˈvaɪrəs]	aw-lee-**veh**-raws (o-lee-**vair**-ohz) **vahy**-r*uh*s
Orogrande virus	[ˌɔrɔˈgrændi ˈvaɪrəs] or [ˌɔrɔˈgrɑndeɪ ˈvaɪrəs]	aw-raw-**gran**-dee (aw-raw-**grahn**-dey) **vahy**-r*uh*s
Paraná virus	[ˌpærəˈnɑ ˈvaɪrəs]	par-*uh*-**nah** **vahy**-r*uh*s
Pichindé virus	[ˌpitʃinˈdɛ ˈvaɪrəs] or [ˌpitʃinˈdeɪ ˈvaɪrəs]	pee-cheen-**deh** (pee-cheen-**dey**) **vahy**-r*uh*s
Pinhal virus	[pinˈyɑl ˈvaɪrəs] or [piˈnyɑʊ ˈvaɪrəs]	peen-**yahl** (pee-**nyow**) **vahy**-r*uh*s
Pirital virus	[piriˈtɑl ˈvaɪrəs]	pee-ree-**tahl** **vahy**-r*uh*s
Real de Catorce virus	[rɛˈɑl dɛ kəˈtɔrsə ˈvaɪrəs] or [reɪˈɑl deɪ kəˈtɔrzeɪ ˈvaɪrəs]	reh-**ahl** deh k*uh*-**tawrs**-*uh* (rey-ahl dey k*uh*-**tawrz**-ey) **vahy**-r*uh*s

Table 6 continued

Arenavirus name[a]	International Phonetic Alphabet (IPA)	English phonetic notation[b]
reptarenavirus	[rɛptəˈrinəˌvaɪrəs] or [rɛptˌerənəˈvaɪrəs]	rept-*uh*-**ree**-n*uh*-vahy-r*uh*s (rept-**er**-*uh*-n*uh*-vahy-r*uh*s)
Río Carcarañá virus	[ˈrioʊ ˌkɑrkɑranˈyɑ ˈvaɪrəs]	**ree**-oh kahr-kahr-ahn-**yah** **vahy**-r*uh*s
ROUT virus	[raʊt ˈvaɪrəs]	rout **vahy**-r*uh*s
Sabiá virus	[ˌsɑbiˈjɑ ˈvaɪrəs] or [ˌsəbiˈja ˈvaɪrəs]	sah-bee-**yah** (s*uh*-bee-**yah**) **vahy**-r*uh*s
Skinner Tank virus	[ˈskɪnər tæŋk ˈvaɪrəs]	**skin**-er tangk **vahy**-r*uh*s
Tacaribe virus	[ˌtɑkɑˈribɛ ˈvaɪrəs] or [ˌtəkəˈribɪ ˈvaɪrəs]	tah-kah-**ree**-beh (t*uh*-k*uh*-**ree**-bey) **vahy**-r*uh*s
Tamiami virus	[ˈtæmiˌæmi ˈvaɪrəs]	**ta**-mee-a-mee **vahy**-r*uh*s
Tonto Creek virus	[ˈtɔntoʊ krik ˈvaɪrəs] or [ˈtɒntoʊ ˈvaɪrəs]	**tawn**-toh (**ton**-toh) kreek **vahy**-r*uh*s
University of Helsinki virus	[ˌyunəˈvɜrsɪti ʌv ˈhɛlsɪŋkɪ ˈvaɪrəs]	yoo-n*uh*-**vur**-si-tee *uh*v **hel**-sing-kee **vahy**-r*uh*s
Whitewater Arroyo virus	[ˈʰwaɪtˌwɒtər əˈrɔɪoʊ ˈvaɪrəs]	**hwahyt**-wot-er *uh*-**roi**-oh **vahy**-r*uh*s

[a] The pronunciations of the word stems depicted here for virus names are to be used for species names as well

[b] Conventions of http://dictionary.reference.com/

[c] Two variants are included for words of foreign origin that do not have an established pronunciation in English. The first variant is closer to the pronunciation in the original language, and the second one is more anglicized

[d] In the English respelling system, the italics signify a slightly different vowel, e.g., *uh* vs. uh is equivalent to [ə], as in **virus** vs. [ʌ] as in **brush**; oo vs. *oo* is equivalent to [uː] as in **boot** vs. [ʊ] as in **put**

Changes of genus and species names to correct spelling mistakes and to comply with ICVCN Rules

The ICTV *Arenaviridae* Study Group voted to name the genus for mammalian arenaviruses *Mammarenavirus*, and that for reptilian arenaviruses *Reptarenavirus*. To bring arenavirus taxonomy in compliance with the ICVCN, non-Latinized binomial species names [135] are introduced for species of both genera. Since most virologists work with actual viruses, do not need to address species frequently, and are accustomed to the established virus names, it is unlikely that the non-Latinized binomial species names would still be used accidentally for viruses. Furthermore, the species name parts "*Pichinde*" and "*Amapari*" are corrected to "*Pichindé*" and "*Amaparí*," respectively. Unique abbreviations are assigned to all viruses (as judged by screening of the 9th ICTV Report [74]). After communication with the discoverers, "Boa AV NL B3" was renamed ROUT virus (ROUTV) (Rogier Bodewes *et al.*, personal communication). A summary of all currently changes can be found in Table 5.

Pronunciation guidelines for arenavirus and arenavirus taxon names

Arenavirus names and arenavirus taxon names are traditionally derived from geographic locations. Table 6 provides guidance for their correct pronunciation using the International Phonetic Alphabet (IPA) and an English phonetic notation.

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