This form should be used for all taxonomic proposals. Please complete all those modules that are applicable.

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Please try to keep related proposals within a single document.

Part 1: **TITLE, AUTHORS, etc**

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| --- | --- | --- |
| **Code assigned:** | ***2019.003M*** | (to be completed by ICTV officers) |
| **Short title:** Create one new species in the genus *Hapavirus,* family *Rhabdoviridae* |
| **Modules attached**  |  **1** **[x]  2 [x]  3 [ ]  4 [x]**  |
| **Author(s):** |
| Peter J. WalkerKim R. Blasdell Ralf G. DietzgenJuliana Freitas-AstúaHideki KondoGael KurathIvan V. KuzminDavid M. StoneRobert B. TeshNoel TordoNikos VasilakisAnna E. Whitfield |
| **Corresponding author with e-mail address:** |
| peter.walker@uq.edu.au |
| **List the ICTV study group(s) that have seen this proposal:** |
| A list of study groups and contacts is provided at <http://www.ictvonline.org/subcommittees.asp> . If in doubt, contact the appropriate subcommittee chair (there are six virus subcommittees: animal DNA and retroviruses, animal ssRNA-, animal ssRNA+, fungal and protist, plant, bacterial and archaeal) | *Rhabdoviridae* Study Group |
| **ICTV Study Group comments (if any) and response of the proposer:** |
| Supported by 11 of 13 SG members. There were two non-responders. Initially, several SG members expressed concern about the high level of sequence identity (96.2%) between the N proteins of HOJV and WONV, which is assigned to an existing species, *Wongabel hapavirus*. However, after discussion, all responding members supported the proposal in consideration of a detailed explanation which is now provided in the Annex as “additional comments”.  |
|  |
| Date first submitted to ICTV: |       |
| Date of this revision (if different to above): |       |

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| **ICTV-EC comments and response of the proposer:** |
|       |

**Part 2**: **PROPOSED TAXONOMY**

|  |
| --- |
| Present the proposed new taxonomy on accompanying spreadsheet |
| **Name of accompanying spreadsheet:**2019.003M.A.v1.Hapavirus.xlsx |

**Part 4:** **APPENDIX**: supporting material

| **References:** |
| --- |
| 1. **Gubala A, Walsh S, McAllister J, Weir R, Davis S, Melville L, Mitchell I, Bulach D, Gauci P, Skvortsov A, Boyle D.** 2017. Identification of very small open reading frames in the genomes of Holmes Jungle virus, Ord River virus, and Wongabel virus of the genus *Hapavirus*, family *Rhabdoviridae*. Evolutionary Bioinformatics **13:**1176934317713484.2. **Walker PJ, Firth C, Widen SG, Blasdell KR, Guzman H, Wood TG, Paradkar PN, Holmes EC, Tesh RB, Vasilakis N.** 2015. Evolution of genome size and complexity in the *Rhabdoviridae*. PLoS Pathogens **11:**e1004664.3. **Gubala A, Davis S, Weir R, Melville L, Cowled C, Walker P, Boyle D.** 2010. Ngaingan virus, a macropod-associated rhabdovirus, contains a second glycoprotein gene and seven novel open reading frames. Virology **399:**98-108.4. **Gubala AJ, Proll DF, Barnard RT, Cowled CJ, Crameri SG, Hyatt AD, Boyle DB.** 2008. Genomic characterisation of Wongabel virus reveals novel genes within the *Rhabdoviridae*. Virology **376:**13-23.5. **Humphrey-Smith I, Cybinski DH, Byrne KA, St George TD.** 1991. Seroepidemiology of arboviruses among seabirds and island residents of the Great Barrier Reef and Coral Sea. Epidemiology and Infection **107:**435-440. |

|  |
| --- |
| **Annex:** Holmes Jungle virus (HOJV) was isolated from mosquitoes (*Culex annulirostris*) collected near Darwin in the Northern Territory, Australia, in 1987 (1). There is evidence that antibodies to HOJV occur in cattle in Australia (1). The complete genome sequence (13,168 nt) has been determined (1). In a well-supported Maximum Likelihood tree inferred from complete L protein sequences of currently classified and recently proposed animal rhabdoviruses, HOJV falls with the hapaviruses in a unique monophyletic clade; it is most closely related to Wongabel virus (WONV; *Wongabel hapavirus*), Ord River virus (ORV; *Ord River hapavirus*) and Parry Creek virus (PCV; *Parry Creek hapavirus*) (**Figure 1**).The HOJV genome organization is complex and similar to those of WONV, ORV and PCV (**Figure 2**). In addition to the five canonical rhabdovirus structural protein genes (*N*, *P*, *M*, *G*, and *L*) The HOJV genome includes: i) multiple genes between the *P* gene and *M* gene encoding proteins that share low levels of sequence identity (P-M intergenic proteins; PMIPs; and ii) a gene between the *G* and *L* genes encoding a small class 1a viroporin-like protein (**Figure 3**). These genome elements are common characteristics of hapaviruses (2). The HOJV genome differs from those of WONV, ORV and PCV in that it contains an alternative ORF in the G gene that encodes a potential protein of 114 amino acids (estimated size 13.3 kDa) with a predicted central transmembrane domain and possible N-terminal signal sequence (**Figure 4**). It is not known if this protein is expressed.Amino acid sequence identities indicate that HOJV is most closely related to WONV (96.2 % in the N protein; 84.8% in the G protein; and 88.6% in the L protein) (**Tables 1–3**).Two other hapaviruses (ORV and PCV) have also been isolated from *Culex annulirostris* mosquitoes collected in the northern region of Western Australia but their vertebrate hosts are not known (2). Joinjakaka virus (JOIV; *Joinjakaka hapavirus*), isolated from unidentified culicine mosquitoes in Papua New Guinea, and Ngaingan virus (NGAV; *Ngaingan hapavirus*), isolated from biting midges (*Culicoides* spp.) in northern Australia, also appear to infect cattle (2, 3). WONV, which is most closely related to HOJV, was isolated from biting midges (*Culicoides austropalpalis*) in northern Australia and appears to infect birds (4, 5).**Species demarcation criteria**Viruses assigned to different species within the genus *Hapavirus* display several of the following characteristics: A) minimum amino acid sequence divergence of 5% in N; B) minimum sequence divergence of 10% in L; C) minimum amino acid sequence divergence of 15% G; D) significant differences in genome organisation as evidenced by numbers and locations of ORFs; E) can be distinguished in virus neutralisation tests; and F) occupy different ecological niches as evidenced by differences in hosts and/or arthropod vectors.HOJV meets demarcation criteria B, C, D and F. Although amino acid sequence divergence in the N protein between HOJV and WONV (3.8%) does not demarcation criterion A, it does exceed the level of divergence (1%) between the N proteins of Kamese virus (KAMV; *Kamese hapavirus*) and Mossuril virus (MOSV; *Mossuril hapavirus*) (**Table 1**). No data are yet available on cross-neutralisation tests between HOJV and other hapaviruses.**Additional comments:**Here in detail is the reasoning behind the conclusion that HOJV should be assigned to a new species:1. Sequence divergence between HOJV and WONV G proteins is 15.2%. That meets demarcation criterion C and exceeds that between two other viruses that are already assigned to separate species (HPV and FLAV - 14.4%).
2. Sequence divergence between HOJV and WONV L proteins is 11.4%. That meets demarcation criterion B and exceeds that between KAMV and MOSV (8.5%) and between HPV and FLAV (9.5%), all of which are already assigned to separate species.
3. Sequence divergence between HOJV and WONV N proteins is 3.8%. That falls below the 5% level set in demarcation criterion A but is much higher than between KAMV and MOSV (0.8%) which are already assigned to separate species.
4. On what basis were KAMV and MOSV approved as separate species? The following is extracted from the approved taxonomic proposal (2016) to establish the genus*Hapavirus*: *KAMV and MOSV cross-react only weakly in neutralisation tests. Although amino acid sequence identity between KAMV and MOSV is very high in the N protein (99.2%), it is relatively low in the G protein (80.4%), possibly explaining the neutralisation test data. They have similar genome organisations, differing only in small ORFs in the G and L genes that may not be expressed. They appear to have similar ecology (transmitted by culicine mosquitoes and infecting humans) and each occurs in sub-Saharan Africa.  Based on neutralisation test data and relatively low identity of G protein sequences, we propose that MOSV and KAMV should be assigned to different species.*
5. Neutralisation tests are traditionally used to distinguish viruses as neutralising antibody will cause interference between circulating viruses, drive evolution and often has practical implications for vaccination. KAMV and MOSV cross-react only weakly in neutralisation tests and have relatively high sequence identity in the G proteins (19.6%). Yet their N proteins are almost identical. This shows that (quite unexpectedly), hapaviruses that are relatively divergent in L and G proteins and are distinguishable in neutralisation tests can indeed have very low sequence divergence in the N proteins. The reason is not known. There may be severe structural constraints on N or perhaps it may be due to rare recombination events.
6. For HOJV and WONV, we do not have neutralisation test data (and we are unlikely to get the data because it would require the production of antisera which no-one is likely to do for lack of funding). However, the divergence in the G protein sequences exceeds that between HPV and FLAV (see above) which can also be distinguished in neutralisation tests.
7. The overlapping long ORF in the HOJV G protein is predicted to encode a protein of significant size (114 aa; 13.3 kDa) and with a strong structural prediction as a transmembrane protein. Although we don't know if it is expressed, it is very unusual to find an alternative ORF with such a strong structural prediction. The initiation codon is also in moderately strong Kozak context (**A**A**G**ATGT..). Significantly, this long ORF does not occur in WONV, reflecting the extent of sequence divergence.
8. Ecologically, HOJV was isolated from mosquitoes near Darwin in the Northern Territory. WONV was isolated from biting midges near Atherton in Queensland (over 1600 km to the south-east). The ecology of these two environments is very different, subtropical tableland and tropical savannah, respectively. WONV infects birds (antibodies detected) and the biting midge from which it was isolated has a feeding preference for birds. HOJV infects cattle (antibodies detected) and was isolated from mosquitoes in the vicinity of cattle. These are obviously not mutually exclusive.
9. Overall, HJOV clearly meets two of the six demarcation criteria (B and C) and arguably meets two more (D and F) as well as many other viruses that have already been classified. It does not meet one (A) and there are no data for another (E).
10. If the SG decided not to recommend HOJV assignment to a new species, it would be *de facto* a decision to assign it to the same species as WONV (*Wongabel hapavirus*). However, the only clear piece of evidence to support that position is the limited sequence divergence of N proteins. However, this runs in the face of evidence that divergence of N protein sequences of other hapaviruses can be extremely low, even when the viruses can be distinguished in neutralisation tests and have already been assigned to separate species. The accumulated evidence in favor of new species assignment far outweighs the evidence against. We could say we need more data to decide but regrettably that is unlikely to happen.

**Figure 1.** The evolutionary history was inferred from a Clustal W alignment of complete L protein sequences of Holmes Jungle virus and 112 other animal rhabdoviruses currently assigned or recently proposed for assignment to species. Phylogenetically informative sites were selected from the alignment using Gblocks resulting in 1072 positions in the final dataset. The tree was inferred in MEGA7 by using the Maximum Likelihood method based on the Whelan and Goldman + Freq. model. The tree with the highest log likelihood (-104695.9075) is shown. The percentage of trees in which the associated taxa clustered together is shown next to the branches. Initial tree(s) for the heuristic search were obtained automatically by applying Neighbor-Join and BioNJ algorithms to a matrix of pairwise distances estimated using a JTT model, and then selecting the topology with superior log likelihood value. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. Bootstrap values (100 iterations) are shown for each node.  |

**Figure 2.** Genome organisations of hapaviruses, including HOJV.  N, P, M, G and L represent ORFs encoding the structural proteins. ORFs are indicated as block arrows. P-M intergenic region protein (PMIP) ORFs are coloured in red; class 1a viroporin-like protein ORFs are coloured in yellow; other colours indicate ORFs encoding homologous proteins. Other alternative ORFs occur in some genes; only ORFs (≥180 nt) that appear likely to be expressed are shown.

HOJV MG**F**SIN**F**DPIIDK**F**RE**F**QNNINHNVNEQLDKLKMI**W**INFGSQIKYWFLVIISILIMLFIVFVLIKVT**R**LILNC**KK**IFSCCC**K**FCC**R**N**K**N**R**N**R**D**KR**ED**K**I**K**VFSITP

WONV MG**F**SIN**F**DPIINK**F**RE**F**QTNINHNINEQLDKLKMV**W**INLGSHIKYWFIIIISILTILFILFLLIKIT**K**LILNC**KK**IFSCCCNVCC**KKR**P**K**VDI**R**S**K**E**K**V**K**VFSILP

ORV MG**F**SIN**F**DPIIDG**F**RE**F**QQNINGDIDDQLDKIKII**W**TNLGTHIKYWFILIISILIVLAILFLLIKIT**R**LILNC**KK**IFSCCCDLCC**K**E**K**TS**K**Q**RR**ED**K**I**K**VFSILP

PCV MG**F**SIN**F**DPIINK**F**RE**F**QTNINNNINEQLDKIKII**W**ANLGTHIKYWFILIISILIILAVLFLLIKIT**R**LILNC**KK**IFSCCCSWCC**KK**Q**K**TQ**RRK**DD**K**V**K**IFSITP

HPV MG**F**DIGGDIGKPLKDA**F**DK**F**GADIKMT**F**LTVLN**W**MKWISIGILIVISVILICKIIKVLFQCG**K**CLLSCFGFC**KK**CV**K**GN**H**S**H**MN**K**T**RKKH**QF**R**G**K**V**KK**MTVPVI**RKK**V**K**I**RK**DPSLVELV

FLAV MG**F**DIGKDIGKPLKEA**F**DK**F**GSDIKIT**F**LTVLN**W**MKWISIGILIVISIILICKIIKVLFQFG**K**CLWSGF**K**CC**KK**CF**K**SS**K**T**R**A**K**SS**K**E**K**I**K**L**KR**AT**K**II**H**NPL**RR**NNS**R**I**KK**VPSVI**K**LI

MOSV MG**F**N**F**DVDVAKPIQNA**F**KNL**W**NDITR**FF**EP**F**LS**W**MS**Y**IGKWALIILLIIVSIKVIIIIYKIG**K**CVW**R**SGLCL**K**NCI**KR**V**KK**T**R**I**KKK**VVM**K**L**RHKR**P**RK**Q**R**IP

KAMV MG**F**N**F**DVDVAKPIQGA**F**KNLWNDITR**FF**EP**F**LT**W**ISDIGKWALIILLVIVSIKILIVIYKIG**K**CLW**K**SGLCL**KR**CF**RR**I**KK**T**K**I**RKK**VSL**K**L**R**S**KR**I**KKKR**IL

MQOV MVLKDIEK**F**GNNIKNAIVGA**F**HETKNV**F**NVIGN**Y**LKLGGYVIIIILSMIVIIKVVKTLIAIG**K**CV**K**SCFCST**RK**LI**KK**V**KK**AP**RK**A**K**IL**KR**ISG**H**TN**RHR**F**K**

LJAV MKLDLD**F**D**F**KGKIIDPLGKALVDGINKGLS**F**D**F**KGKI**F**DPITK**WF**TNT**F**NNIKDAGEPIL**YY**LKVVGIVFLSILAIIIIIKFF**K**LFELLG**K**TF**K**FIG**K**GLIIFL**KK**L**KR**IPL**K**DCC**KRR**P**K**P**KR**Q**K**PQISTISEQTGEDFRTV**K**LNPIFSNLP

LJV MV**F**PGLDLGN**F**KNDISG**FF**DKLGKD**F**KSG**F**VSLGQNINNMGDGIVNKIDKVGTDVKD**FW**AG**F**SSV**F**V**YY**GKLISLIILVLIVFTVAMKIMS**K**IFSCIAGC**R**ACWIGFTQT**R**T**KK**L**K**EEPPI**H**SIQID

GLOV MGIDLKIN**W**TELWNSITRGLREGLD**F**LRV**WF**EN**FY**NDARKWGIIVFIIIITIIIVMIIMKIL**K**CVLLI**KK**LC**K**SCD**K**TSPT**R**G**K**PV**RK**I**RK**WW**RKK**VP**KR**IQ**K**L**K**

MANV MK**W**N**F**DNKIVEPLANSIKRAIEKGLDIK**Y**D**F**NKNI**F**QPISNSIRMI**W**MDIQEQ**W**MKIIKGLEIIGIIFLIVLFCIIAFKIV**K**VLAISF**K**SC**K**QCIEYI**K**I**KKR**CN**K**PLTTINT

NGAV MVA**WW**TIIILLS**F**KIMD**F**PGVIATPTL**F**RSMINETDLDITSRIMN**Y**NIGP**F**LEK**F**KK**F**QEDLKSI**W**SKIKDKIEIIKSYIIILIIIAVIVVITLVTLKCFS**R**MITCY**K**SLTS

JOIV MGMLTGVSLEM**F**DIRDR**F**DQLINI**F**KE**F**KEKLEV**Y**VNMLSSI**F**KQILFYILVIVAVMVILKLIIIVFKTAILVI**K**CY**R**VC**K**C**KK**N**K**SV**H**V**KRKK**TSIIS**R**I**R**QA**R**LQ**RK**T**R**L**K**T**K**LDL

**Figure 3.** Hapavirus class 1a viroporin-like proteins. Predicted transmembrane domains (grey shade) and clusters of basic residues in the C-terminal domain (shaded black) are shown.

# HOJV\_Gx Length: 114

# HOJV\_Gx Number of predicted TMHs: 1

# HOJV\_Gx Exp number of AAs in TMHs: 26.27752

# HOJV\_Gx Exp number, first 60 AAs: 21.87224

# HOJV\_Gx Total prob of N-in: 0.72039

# HOJV\_Gx POSSIBLE N-term signal sequence

HOJV\_Gx TMHMM2.0 inside 1 12

HOJV\_Gx TMHMM2.0 TMhelix 13 35

HOJV\_Gx TMHMM2.0 outside 36 114

**Figure 4.** TMHMM prediction of the membrane topology of the HOJV Gx protein.

**Table 1.** Percentage amino acid sequence identities (p-distance) of a CLUSTAL W alignment of hapavirus N proteins.

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | HOJV | ORV | PCV | WONV | LJV | JOIV | NGAV | MCOV | GLOV | LJAV | MANV | MQOV | FLAV | HPV | KAMV | MOSV |
| HOJV |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| ORV | 93.1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| PCV | 90.1 | 91.3 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| WONV | 96.2 | 94.4 | 90.8 |  |  |  |  |  |  |  |  |  |  |  |  |  |
| LJV | 64.8 | 64.8 | 64.0 | 64.8 |  |  |  |  |  |  |  |  |  |  |  |  |
| JOIV | 45.4 | 45.7 | 46.9 | 45.2 | 45.4 |  |  |  |  |  |  |  |  |  |  |  |
| NGAV | 41.3 | 41.6 | 42.1 | 41.3 | 42.1 | 45.4 |  |  |  |  |  |  |  |  |  |  |
| MCOV | 32.4 | 33.2 | 32.1 | 32.7 | 33.4 | 36.2 | 31.1 |  |  |  |  |  |  |  |  |  |
| GLOV | 49.7 | 50.5 | 50.5 | 50.3 | 48.2 | 49.7 | 43.9 | 35.7 |  |  |  |  |  |  |  |  |
| LJAV | 42.3 | 42.6 | 43.1 | 41.8 | 44.9 | 45.9 | 40.8 | 34.2 | 52.8 |  |  |  |  |  |  |  |
| MANV | 42.6 | 42.9 | 43.9 | 42.6 | 42.6 | 44.4 | 40.1 | 33.7 | 55.6 | 72.4 |  |  |  |  |  |  |
| MQOV | 45.9 | 46.2 | 45.7 | 46.4 | 45.7 | 47.2 | 41.8 | 35.5 | 57.1 | 56.1 | 54.6 |  |  |  |  |  |
| FLAV | 44.4 | 44.6 | 44.1 | 44.4 | 44.4 | 45.9 | 41.1 | 34.7 | 54.1 | 53.6 | 54.6 | 72.7 |  |  |  |  |
| HPV | 44.9 | 45.2 | 44.1 | 44.4 | 43.1 | 45.2 | 41.3 | 34.9 | 54.1 | 53.1 | 54.8 | 71.7 | 95.4 |  |  |  |
| KAMV | 43.6 | 44.4 | 43.9 | 44.1 | 45.2 | 43.9 | 40.6 | 34.4 | 54.6 | 53.1 | 56.4 | 75.5 | 74.0 | 74.0 |  |  |
| MOSV | 43.9 | 44.6 | 44.1 | 44.4 | 44.9 | 43.9 | 40.6 | 34.4 | 54.3 | 52.8 | 55.9 | 75.5 | 74.0 | 74.0 | 99.2 |  |

**Table 2.** Percentage amino acid sequence identities (p-distance) of a CLUSTAL W alignment of hapavirus G proteins.

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | HOJV | ORV | PCV | WONV | LJV | JOIV | NGAV | MCOV | GLOV | LJAV | MANV | MQOV | FLAV | HPV | KAMV | MOSV |
| HOJV |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| ORV | 72.2 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| PCV | 72.2 | 75.8 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| WONV | 84.8 | 73.2 | 72.2 |  |  |  |  |  |  |  |  |  |  |  |  |  |
| LJV | 42.0 | 41.8 | 43.6 | 43.6 |  |  |  |  |  |  |  |  |  |  |  |  |
| JOIV | 29.8 | 30.8 | 31.0 | 30.2 | 26.8 |  |  |  |  |  |  |  |  |  |  |  |
| NGAV | 26.6 | 28.0 | 27.6 | 27.4 | 28.4 | 34.6 |  |  |  |  |  |  |  |  |  |  |
| MCOV | 25.8 | 25.2 | 24.8 | 25.0 | 26.2 | 23.4 | 24.4 |  |  |  |  |  |  |  |  |  |
| GLOV | 32.0 | 33.8 | 33.4 | 33.6 | 30.4 | 25.4 | 26.4 | 25.0 |  |  |  |  |  |  |  |  |
| LJAV | 28.8 | 30.8 | 28.8 | 29.0 | 30.0 | 26.6 | 27.2 | 26.4 | 39.2 |  |  |  |  |  |  |  |
| MANV | 28.6 | 31.4 | 29.8 | 29.6 | 28.8 | 28.4 | 29.2 | 25.2 | 41.2 | 54.6 |  |  |  |  |  |  |
| MQOV | 29.2 | 28.6 | 29.4 | 29.4 | 28.4 | 28.6 | 27.0 | 24.6 | 39.6 | 44.8 | 42.4 |  |  |  |  |  |
| FLAV | 30.6 | 30.0 | 30.6 | 30.2 | 30.2 | 27.4 | 26.8 | 24.4 | 37.6 | 46.0 | 44.2 | 50.8 |  |  |  |  |
| HPV | 30.6 | 30.0 | 29.4 | 30.2 | 30.0 | 28.0 | 27.0 | 25.8 | 37.4 | 47.0 | 46.0 | 52.2 | 85.6 |  |  |  |
| KAMV | 28.2 | 29.2 | 28.4 | 28.0 | 26.6 | 28.4 | 26.4 | 25.4 | 38.0 | 43.0 | 39.4 | 51.8 | 56.0 | 56.4 |  |  |
| MOSV | 28.0 | 29.4 | 28.2 | 28.8 | 29.0 | 26.2 | 27.0 | 24.8 | 39.6 | 42.4 | 40.0 | 50.2 | 55.0 | 56.2 | 80.8 |  |

**Table 3.** Percentage amino acid sequence identities (p-distance) of a CLUSTAL W alignment of hapavirus L proteins.

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | HOJV | ORV | PCV | WONV | LJV | JOIV | NGAV | MCOV | GLOV | LJAV | MANV | MQOV | FLAV | HPV | KAMV | MOSV |
| HOJV |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| ORV | 84.0 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| PCV | 84.5 | 86.4 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| WONV | 88.6 | 84.2 | 83.9 |  |  |  |  |  |  |  |  |  |  |  |  |  |
| LJV | 66.1 | 65.6 | 66.6 | 67.1 |  |  |  |  |  |  |  |  |  |  |  |  |
| JOIV | 49.7 | 50.2 | 49.5 | 50.0 | 49.2 |  |  |  |  |  |  |  |  |  |  |  |
| NGAV | 49.5 | 49.4 | 48.8 | 48.9 | 48.9 | 49.8 |  |  |  |  |  |  |  |  |  |  |
| MCOV | 51.9 | 52.0 | 52.3 | 52.3 | 52.1 | 48.8 | 49.3 |  |  |  |  |  |  |  |  |  |
| GLOV | 50.8 | 51.7 | 51.6 | 52.0 | 51.3 | 50.3 | 49.5 | 51.2 |  |  |  |  |  |  |  |  |
| LJAV | 51.2 | 51.1 | 51.6 | 51.7 | 52.0 | 51.3 | 50.6 | 52.5 | 59.8 |  |  |  |  |  |  |  |
| MANV | 52.1 | 52.6 | 52.7 | 52.9 | 52.5 | 51.5 | 51.8 | 52.8 | 59.6 | 71.4 |  |  |  |  |  |  |
| MQOV | 52.7 | 52.6 | 52.8 | 53.1 | 52.4 | 50.8 | 50.8 | 52.7 | 60.1 | 64.5 | 64.4 |  |  |  |  |  |
| FLAV | 52.1 | 52.1 | 51.7 | 52.4 | 51.8 | 50.1 | 50.8 | 51.9 | 59.8 | 64.8 | 65.1 | 70.0 |  |  |  |  |
| HPV | 52.1 | 51.9 | 51.4 | 52.5 | 51.1 | 50.3 | 50.6 | 51.5 | 60.3 | 65.1 | 65.5 | 69.7 | 90.5 |  |  |  |
| KAMV | 52.5 | 51.8 | 52.3 | 53.0 | 51.4 | 49.8 | 50.7 | 53.5 | 60.7 | 65.5 | 65.1 | 70.1 | 73.5 | 73.9 |  |  |
| MOSV | 52.2 | 52.0 | 52.5 | 53.4 | 51.5 | 50.4 | 51.3 | 53.5 | 60.9 | 65.7 | 65.7 | 70.4 | 73.3 | 73.8 | 91.5 |  |