

# Novel Paramyxoviruses in Bats from Sub-Saharan Africa, 2007–2012

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As part of a larger survey for detection of pathogens among wildlife in sub-Saharan Africa conducted during 2007–2012, multiple diverse paramyxovirus sequences were detected in renal tissues of bats. Phylogenetic analysis supports the presence of at least 2 major viral lineages and suggests that paramyxoviruses are strongly associated with several bat genera.

Members of the *Paramyxoviridae* family are enveloped negative-sense RNA viruses, further classified into either the *Pneumovirinae* or *Paramyxovirinae* subfamily (1). The *Paramyxovirinae* subfamily has increasingly been associated with bat species across the globe. The *Henipavirus* genus is 1 of 7 genera in this subfamily and contains the first recorded zoonotic paramyxoviruses, Hendra virus and Nipah virus. These 2 viruses are associated with severe respiratory and neurologic syndromes, and regular spillover from *Pteropus* spp. bats causes infections in humans and domestic animals (2).

Enhanced surveillance for bat-associated pathogens has led to the discovery of numerous novel paramyxoviruses (3–5). *Henipavirus*-related viruses were identified in another pteropodid species, *Eidolon helvum*, sampled in Ghana, West Africa. This finding suggests an extension of the geographic and host ranges of the members of this virus genus (6). Subsequent studies demonstrated a high diversity of paramyxoviruses in *E. helvum* bat population in Africa, as well as in other bat species from different continents. This finding suggests that bats may have a global

role as potential paramyxovirus reservoirs (3,4). To contribute toward the knowledge of bat-associated paramyxovirus diversity and distribution, we sampled multiple bat species from several sub-Saharan African countries.

## The Study

During 2007–2012, we sampled 1,220 bats representing at least 48 species from multiple locations in selected countries in Africa (Table 1). Bats were anesthetized with the use of ketamine (0.05–0.1 mg/g body mass) and exsanguinated by cardiac puncture. Voucher specimens were identified through morphologic characterization (7) or, alternatively, through genetic barcoding. Approximately 30–100 mg of renal tissue was used for RNA extraction. A heminested primer set targeting the conserved polymerase (large) gene of *Respirovirus*, *Morbillivirus*, and *Henipavirus* was used for sample screening through reverse transcription PCR (8). A total of 103 samples (8.4%) tested positive, and the obtained amplicons of ~490 bp were sequenced (online Technical Appendix Table 1, <http://wwwnc.cdc.gov/EID/article/20/10/14-0368-Techapp1.pdf>). For phylogenetic analysis, representative paramyxovirus sequences available from GenBank were included (online Technical Appendix Table 2), and Bayesian analysis was performed by using BEAST version 1.7.4 software (<http://beast.bio.ed.ac.uk/>) (Figure; <http://wwwnc.cdc.gov/EID/article/21/10/14-1368-F1.htm>).

Several samples from bat species not previously implicated as paramyxovirus reservoirs tested positive in our study. Some of these implicated species are known to roost in peridomestic environments. Sequence analysis of paramyxovirus sequences showed a clear bifurcation of the phylogenetic tree, segregating paramyxoviruses detected in pteropodid bats (*Pteropodidae*) from paramyxoviruses detected in bats of other families (Figure). The former contained henipaviruses and related viruses. Two viral sequences detected in *Rousettus aegyptiacus* bats grouped within this cluster as part of a sister clade to the henipaviruses. The second cluster contained sequences derived from nonpteropodid bats. Some of these sequences grouped with the sequences from the *Morbillivirus* and proposed *Jeilongvirus* genera, whereas others could not be included in any of the other paramyxovirus genera.

We observed a strong association of several viral lineages to particular bat genera for paramyxoviruses identified in *Hipposideros*, *Miniopterus*, *Coleura*, *Myotis*, and *Pipistrellus* bats, although the bats were sampled from geographically distant locations. In contrast to the sequences of

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**Table 1.** African bat species sampled and the number of paramyxovirus sequences detected in sub-Saharan Africa, by country, 2007–2012\*

Southern Africa		
South Africa		
<i>Chaerephon ansorgei</i> (2/0)	<b>Neoromicia nana</b> (7/2)	<i>Rhinolophus</i> sp. (1/0)
<i>Chaerephon pumilus</i> (8/0)	<i>Neoromicia rueppellii</i> (1/0)	<i>Rousettus aegyptiacus</i> (18/0)
<i>Epomophorus gambianus</i> (2/0)	<i>Neoromicia zuluensis</i> (1/0)	<i>Sauromys petrophilus</i> (1/0)
<i>Epomophorus wahlbergi</i> (15/0)	<b>Nycteris thebaica</b> (12/1)	<i>Scotophilus</i> sp. (12/0)
<b>Eptesicus hottentotus</b> (2/1)	<i>Nycticeinops schlieffeni</i> (9/0)	<i>Scotophilus dinganii</i> (26/0)
<i>Glauconycteris variegata</i> (5/0)	<i>Pipistrellus hesperidus</i> (5/0)	<i>Scotophilus leucogaster</i> (2/0)
<b>Hipposideros caffer</b> (6/2)	<i>Pipistrellus rusticus</i> (5/0)	<i>Scotophilus nigrita</i> (1/0)
<b>Kerivoula argentata</b> (1/1)	<i>Pipistrellus</i> sp. (5/0)	<i>Scotophilus viridis</i> (3/0)
<i>Miniopterus natalensis</i> (5/0)	<i>Rhinolophus darlingi</i> (5/0)	<i>Tadarida aegyptiaca</i> (5/0)
<i>Miniopterus</i> sp. (37/0)	<b>Rhinolophus denti</b> (3/2)	<i>Taphozous mauritanus</i> (2/0)
<i>Mops condylurus</i> (7/0)	<i>Rhinolophus fumigatus</i> (2/0)	
<i>Neoromicia capensis</i> (16/0)	<b>Rhinolophus landeri</b> (1/1)	
<i>Neoromicia helios</i> (6/0)	<i>Rhinolophus simulator</i> (2/0)	
Swaziland		
<i>Nycteris thebaica</i> (4/0)		
Eastern Africa		
Kenya		
<i>Coleura afra</i> (27/10)	<i>Miniopterus natalensis</i> (15/0)	<b>Rousettus aegyptiacus</b> (84/2)
<i>Eidolon helvum</i> (15/0)	<b>Miniopterus</b> sp. (77/13)	<i>Scotoecus</i> sp. (2/0)
<i>Epomophorus labiatus</i> (6/0)	<i>Neoromicia</i> sp. (25/0)	<i>Scotophilus dinganii</i> (2/0)
<i>Epomophorus wahlbergi</i> (2/0)	<b>Nycteris</b> sp. (2/1)	<i>Taphozous</i> sp. (1/0)
<i>Hipposideros vittatus</i> (71/0)	<b>Otomops martiensseni</b> (40/9)	<b>Trienops afer</b> (16/12)
<b>Hipposideros</b> sp. (8/1)	<i>Rhinolophus landeri</i> (12/0)	
<b>Miniopterus minor</b> (151/14)	<i>Rhinolophus</i> sp. (14/0)	
Central Africa		
Cameroon		
<i>Chaerephon</i> sp. (32/0)	<b>Hipposideros</b> sp. (39/1)	<b>Taphozous</b> sp. (12/3)
<i>Eidolon helvum</i> (15/0)	<b>Rhinolophus</b> sp. (9/1)	
<i>Epomophorus</i> sp. (1/0)	<i>Scotophilus dinganii</i> (1/0)	
Democratic Republic of the Congo		
<i>Chaerephon pumilus</i> (25/0)	<i>Hypsignathus monstrosus</i> (2/0)	<i>Myonycteris torquata</i> (8/0)
<i>Chaerephon</i> sp. (22/0)	<i>Megaloglossus woermanni</i> (10/0)	<i>Myotis</i> sp. (3/0)
<i>Eidolon helvum</i> (22/0)	<i>Micropteropus pusillus</i> (1/0)	<i>Neoromicia</i> sp. (1/0)
<i>Glauconycteris argentata</i> (1/0)	<i>Mimetillus moloneyi</i> (1/0)	<b>Pipistrellus</b> sp. (40/20)
<b>Hipposideros fuliginosus</b> (21/3)	<b>Miniopterus</b> sp. (41/2)	<i>Rhinolophus</i> sp. (1/0)
<i>Hipposideros gigas</i> (2/0)	<i>Mops condylurus</i> (33/0)	<i>Scotophilus dinganii</i> (2/0)
Western Africa		
Nigeria		
<i>Eidolon helvum</i> (20/0)	<b>Hipposideros</b> sp. (3/1)	<i>Rousettus aegyptiacus</i> (21/0)
<i>Hipposideros vittatus</i> (8/0)	<i>Lissonycteris angolensis</i> (8/0)	

\*Values are no. samples (no. positive). Boldface indicates implicated species. The sampling protocol was approved by the Institutional Animal Care and Use Committee of the Centers for Disease Control and Prevention; protocol 2096FRAMULX-A3 and The University of Pretoria Animal Ethics Committee (EC054–14).

European and South American origin, for which geographic clustering was observed, no such clustering was found among the sequences from African bats.

The incidence and diversity of viral sequences varied according to bat species. For example, nearly identical sequences were detected in 50% of *Pipistrellus* spp. sampled from a single colony in the Democratic Republic of the Congo (n = 40). In other cases, several distinct viral sequences were detected in different individual bats of 1 species, such as *Miniopterus minor* bats sampled from a single colony in Kenya (n = 53), which harbored 6 distinct viral sequences. Some of the sequences were found more frequently than others. In contrast to a previous study which did not identify paramyxoviruses in *Coleura afra* bats sampled in Ghana (n = 71) (4), we detected a substantial

paramyxovirus incidence (37%, n = 27) in the same bat species sampled in Kenya (Table 2).

## Conclusions

The henipaviruses were the first bat paramyxoviruses directly linked to human disease; however, most aspects of pathogenicity and the host ranges of the increasingly detected novel bat paramyxoviruses remain to be investigated. Here we report information regarding paramyxovirus distribution through molecular evidence of bat-associated paramyxoviruses in Cameroon, Nigeria, and South Africa, as well as evidence of paramyxoviruses in nonpteropodid bats from the Democratic Republic of the Congo. Our results suggest that 2 separate lineages were established during the evolution of bat-associated paramyxoviruses:

**Table 2.** Paramyxovirus incidence in selected bat species from various African countries\*

Species	Country	Tissue type†	No. sampled	No. positive	Incidence, %	Reference
<i>Coleura afro</i>	Ghana	‡	71	0	0.0	(4)
	Kenya	Kidney	27	10	37.0	§
	Central Africa¶	Spleen	25	1	4.0	(4)
<i>Eidolon helvum</i>	Cameroon	Kidney	15	0	0.0	§
	DRC	Kidney	22	0	0.0	§
	Ghana	All solid organs, blood	673	67	10.0	(4)
	Kenya	Kidney	15	0	0.0	§
	Central Africa	Spleen	49	17	34.5	(4)
	Nigeria	Kidney	20	0	0.0	§
	Republic of Congo	All solid organs, blood, salivary gland, throat swab, feces, urine	42	11	26.2	(9)
<i>Epomophorus gambianus</i>	Central Africa	Spleen	48	3	6.3	(4)
	South Africa	Kidney	2	0	0.0	§
	Ghana	‡	20	1	5.0	(4)
<i>Hipposideros caffer</i>	Central Africa	Spleen	337	3	0.9	(4)
	South Africa	Kidney	6	2	33.3	§
	DRC	Kidney	2	0	0.0	§
<i>Hipposideros gigas</i>	Gabon	Spleen	196	3	1.5	(4)
	DRC	Kidney	2	0	0.0	§
<i>Hypsignathus monstrosus</i>	Central Africa	Spleen	53	4	7.5	(4)
	DRC	Kidney	10	0	0.0	§
<i>Megaloglossus woermanni</i>	Central Africa	Spleen	34	1	2.9	(4)
	DRC	Kidney	8	0	0.0	§
<i>Myonycteris torquata</i>	Central Africa	Spleen	111	3	2.7	(4)
	Ghana	‡	1	0	0.0	(4)
<i>Rhinolophus landeri</i>	Kenya	Kidney	12	0	0.0	§
	South Africa	Kidney	1	1	100.0	§
	Ghana	‡	30	0	0.0	(4)
<i>Rousettus aegyptiacus</i>	Kenya	Kidney	84	2	2.4	§
	Central Africa	Spleen	183	18	9.8	(4)
	Nigeria	Kidney	21	0	0.0	§
	South Africa	Kidney	18	0	0.0	§

\*DRC, Democratic Republic of the Congo.

†Tissue type stated for positive samples only and may not indicate all tissues sampled.

‡Information not available.

§Species and countries sampled during this study.

¶Central Africa refers to Gabon/Republic of Congo/DRC/Republic of Central Africa.

the pteropodid bats potentially harbor 1 lineage, and the nonpteropodid bats potentially harbor the other. In contrast to the proposed chiropteran classification, which supports a sister-taxon relationship between Rhinolophidae and Pteropodidae on the suborder level, paramyxovirus divergence appears to correlate with traditional bat taxonomy. The evolution behind this divergence might be a result of multiple evolutionary origins or a single origin with subsequent divergence. As with the evolution of echolocation, this question remains to be answered (11). More extensive bat sampling and molecular dating of the paramyxovirus phylogeny may help resolve this question.

Intensified anthropogenic transformations have facilitated closer contact between humans, domestic animal populations, and wildlife. Our study demonstrates that some bat species, adapted to peridomestic roosting, can have a substantial incidence of diverse paramyxoviruses. The variation in incidence and viral diversity observed in several bat species may suggest that some species are the true reservoirs, whereas others are mere incidental hosts. Given

the observed virus diversity, implications for public health and veterinary medicine should be taken into account, especially considering the known likelihood of direct bat-to-human and human-to-human transmission of Nipah virus (12). Enhanced surveillance in bats and other animals will be useful for detecting possible spillover events and host shifts. Clearly, systematic longitudinal studies are needed to elucidate critical factors of paramyxovirus circulation within bat communities (13), and further research is needed to clarify the pathobiology, tissue tropism, and excretion pathways of these novel paramyxoviruses because these factors can be directly related to their zoonotic potential.

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Mrs. Mortlock is a doctoral student at the University of Pretoria, Pretoria, South Africa. Her research interests include molecular virology and bat-associated viral zoonoses.

## References

- King AMQ, Adams MJ, Carstens EB, Lefkowitz EJ, Carstens EB, editors. *Virus taxonomy: classification and nomenclature of viruses: ninth report of the International Committee on Taxonomy of Viruses*. San Diego: Academic Press, Elsevier; 2011.
- Hooper P, Zaki S, Daniels P, Middleton D. Comparative pathology of the diseases caused by Hendra and Nipah viruses. *Microbes Infect*. 2001;3:315–22. [http://dx.doi.org/10.1016/S1286-4579\(01\)01385-5](http://dx.doi.org/10.1016/S1286-4579(01)01385-5)
- Baker KS, Todd S, Marsh G, Fernandez-Loras A, Suu-Ire R, Wood JLN, et al. Co-circulation of diverse paramyxoviruses in an urban African fruit bat population. *J Gen Virol*. 2012;93:850–6. <http://dx.doi.org/10.1099/vir.0.039339-0>
- Drexler JF, Corman VM, Müller MA, Maganga GD, Vallo P, Binger T, et al. Bats host major mammalian paramyxoviruses. *Nat Commun*. 2012;3:796. <http://dx.doi.org/10.1038/ncomms1796>
- Wilkinson DA, Temmam S, Lebarbenchon C, Lagadec E, Chotte J, Guillebaud J, et al. Identification of novel paramyxoviruses in insectivorous bats of the Southwest Indian ocean. *Virus Res*. 2012;170:159–63. <http://dx.doi.org/10.1016/j.virusres.2012.08.022>
- Drexler JF, Corman VM, Gloza-Rausch F, Seebens A, Annan A, Ipsen A, et al. Henipavirus RNA in African bats. *PLoS ONE*. 2009;4:e6367. <http://dx.doi.org/10.1371/journal.pone.0006367>
- Monadjem A, Taylor PJ, Cotterill FPD, Schoeman MC. *Bats of southern and central Africa*. Johannesburg (South Africa): Wits University Press; 2010.
- Tong S, Wang Chern S-W, Li W, Pallansch MA, Anderson LJ. Sensitive and broadly reactive reverse transcription-PCR assay to detect novel paramyxoviruses. *J Clin Microbiol*. 2008;46:2652–8. <http://dx.doi.org/10.1128/JCM.00192-08>
- Weiss S, Nowak K, Fahr J, Wibbelt G, Mombouli J-V, Parra HJ, et al. Henipavirus-related sequences in fruit bat bushmeat, Republic of Congo. *Emerg Infect Dis*. 2012;18:1536–7. <http://dx.doi.org/10.3201/eid1809.111607>
- Posada D. jModelTest: phylogenetic model averaging. *Mol Biol Evol*. 2008;25:1253–6. <http://dx.doi.org/10.1093/molbev/msn083>
- Teeling EC, Springer MS, Madsen O, Bates P, O'Brien J, Murphy WJ. A molecular phylogeny for bats illuminates biogeography and the fossil record. *Science*. 2005;307:580–4. <http://dx.doi.org/10.1126/science.1105113>
- Luby SP, Gurley ES, Hossain MJ. Transmission of human infection with Nipah virus. *Clin Infect Dis*. 2009;49:1743–8. <http://dx.doi.org/10.1086/647951>
- Wood JLN, Leach M, Waldman L, MacGregor H, Fooks AR, Jones KE, et al. Framework for the study of zoonotic disease emergence and its drivers: spillover of bat pathogens as a case study. *Philos Trans R Soc Lond B Biol Sci*. 2012;367:2881–92. <http://dx.doi.org/10.1098/rstb.2012.0228>

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## Technical Appendix

**Technical Appendix Table 1.** Paramyxovirus sequences detected in this study

Sample	Country	Year	Bat species	GenBank sequence name	Accession number
Cam-45	Cameroon	2010	<i>Rhinolophus</i> sp.	BatPV/Rhi_sp./Cam-45/2010	KC578678
Cam-49	Cameroon	2010	<i>Taphozous</i> sp.	BatPV/Tap_sp./Cam-49/2010	KC578679
Cam-84	Cameroon	2010	<i>Taphozous</i> sp.	BatPV/Tap_sp./Cam-84/2010	KC578680
Cam-88	Cameroon	2010	<i>Hipposideros</i> sp.	BatPV/Hip_sp./Cam-88/2010	KC578681
Cam-99	Cameroon	2010	<i>Taphozous</i> sp.	BatPV/Tap_sp./Cam-99/2010	KC578682
DRC-04	DRC	2011	<i>Pipistrellus</i> sp.	BatPV/Pip_sp./DRC-04/2011	KC578653
DRC-08	DRC	2011	<i>Pipistrellus</i> sp.	BatPV/Pip_sp./DRC-08/2011	KC578654
DRC-09	DRC	2011	<i>Pipistrellus</i> sp.	BatPV/Pip_sp./DRC-09/2011	KC578655
DRC-10	DRC	2011	<i>Pipistrellus</i> sp.	BatPV/Pip_sp./DRC-10/2011	KC578656
DRC-11	DRC	2011	<i>Pipistrellus</i> sp.	BatPV/Pip_sp./DRC-11/2011	KC578657
DRC-51	DRC	2011	<i>Pipistrellus</i> sp.	BatPV/Pip_sp./DRC-51/2011	KC578658
DRC-54	DRC	2011	<i>Pipistrellus</i> sp.	BatPV/Pip_sp./DRC-54/2011	KC578659
DRC-72	DRC	2011	<i>Pipistrellus</i> sp.	BatPV/Pip_sp./DRC-72/2011	KC578660
DRC-75	DRC	2011	<i>Pipistrellus</i> sp.	BatPV/Pip_sp./DRC75/2011	KC578661
DRC-77	DRC	2011	<i>Pipistrellus</i> sp.	BatPV/Pip_sp./DRC77/2011	KC578662
DRC-79	DRC	2011	<i>Pipistrellus</i> sp.	BatPV/Pip_sp./DRC-79/2011	KC578663
DRC-82	DRC	2011	<i>Pipistrellus</i> sp.	BatPV/Pip_sp./DRC-82/2011	KC578664
DRC-83	DRC	2011	<i>Pipistrellus</i> sp.	BatPV/Pip_sp./DRC-83/2011	KC578665
DRC-85	DRC	2011	<i>Pipistrellus</i> sp.	BatPV/Pip_sp./DRC-85/2011	KC578666
DRC-86	DRC	2011	<i>Pipistrellus</i> sp.	BatPV/Pip_sp./DRC-86/2011	KC578667
DRC-90	DRC	2011	<i>Pipistrellus</i> sp.	BatPV/Pip_sp./DRC-90/2011	KC578668
DRC-92	DRC	2011	<i>Pipistrellus</i> sp.	BatPV/Pip_sp./DRC-92/2011	KC578669
DRC-94	DRC	2011	<i>Pipistrellus</i> sp.	BatPV/Pip_sp./DRC-94/2011	KC578670
DRC-112	DRC	2011	<i>Pipistrellus</i> sp.	BatPV/Pip_sp./DRC-112/2011	KC578671
DRC-113	DRC	2011	<i>Pipistrellus</i> sp.	BatPV/Pip_sp./DRC-113/2011	KC578672
DRC-216	DRC	2011	<i>Miniopterus</i> sp.	BatPV/Min_sp./DRC-216/2011	KC578673
DRC-231	DRC	2011	<i>Miniopterus</i> sp.	BatPV/Min_sp./DRC-231/2011	KC578674
DRC-328	DRC	2011	<i>Hipposideros fuliginosus</i>	BatPV/Hip_ful/DRC-328/2011	KC578675
DRC-388	DRC	2011	<i>Hipposideros fuliginosus</i>	BatPV/Hip_ful/DRC-388/2011	KC578676
DRC-399	DRC	2011	<i>Hipposideros fuliginosus</i>	BatPV/Hip_ful/DRC-399/2011	KC578677
Ken-170	Kenya	2010	<i>Triaenops afer</i>	BatPV/Tri_per/Ken-170/2010	KC578640
Ken-181	Kenya	2010	<i>Triaenops afer</i>	BatPV/Tri_per/Ken-181/2010	KC578641
Ken-217	Kenya	2010	<i>Hipposideros</i> sp.	BatPV/Hip_sp./Ken-217/2010	KC578642
Ken-219	Kenya	2010	<i>Coleura afra</i>	BatPV/Col_afr/Ken-219/2010	KC578643
Ken-221	Kenya	2010	<i>Coleura afra</i>	BatPV/Col_afr/Ken-221/2010	KC578644
Ken-241	Kenya	2010	<i>Triaenops afer</i>	BatPV/Tri_per/Ken-241/2010	KC578645
Ken-243	Kenya	2010	<i>Triaenops afer</i>	BatPV/Tri_per/Ken-243/2010	KC578646
Ken-279	Kenya	2010	<i>Coleura afra</i>	BatPV/Col_afr/Ken-279/2010	KC578647
Ken-292	Kenya	2010	<i>Triaenops afer</i>	BatPV/Tri_per/Ken-292/2010	KC578648
Ken-298	Kenya	2010	<i>Coleura afra</i>	BatPV/Col_afr/Ken-298/2010	KC578649
Ken-300	Kenya	2010	<i>Triaenops afer</i>	BatPV/Tri_per/Ken-300/2010	KC578650
Ken-345	Kenya	2011	<i>Miniopterus minor</i>	BatPV/Min_min/Ken-345/2011	KC578591
Ken-355	Kenya	2011	<i>Otomops martiensseni</i>	BatPV/Oto_mar/Ken-355/2011	KC578592
Ken-402	Kenya	2011	<i>Coleura afra</i>	BatPV/Col_afr/Ken-402/2011	KC578593
Ken-412	Kenya	2011	<i>Miniopterus minor</i>	BatPV/Min_min/Ken-412/2011	KC578594
Ken-414	Kenya	2011	<i>Miniopterus minor</i>	BatPV/Min_min/Ken-414/2011	KC578595
Ken-415	Kenya	2011	<i>Miniopterus minor</i>	BatPV/Min_min/Ken-415/2011	KC578596
Ken-434	Kenya	2011	<i>Miniopterus minor</i>	BatPV/Min_min/Ken-434/2011	KC578597
Ken-435	Kenya	2011	<i>Miniopterus minor</i>	BatPV/Min_min/Ken-435/2011	KC578598
Ken-438	Kenya	2011	<i>Otomops martiensseni</i>	BatPV/Oto_mar/Ken-438/2011	KC578599
Ken-439	Kenya	2011	<i>Otomops martiensseni</i>	BatPV/Oto_mar/Ken-439/2011	KC578600
Ken-462	Kenya	2011	<i>Otomops martiensseni</i>	BatPV/Oto_mar/Ken-462/2011	KC578601
Ken-474	Kenya	2011	<i>Triaenops afer</i>	BatPV/Tri_per/Ken-474/2011	KC578602

Sample	Country	Year	Bat species	GenBank sequence name	Accession number
Ken-484	Kenya	2011	<i>Coleura afra</i>	BatPV/Col_afr/Ken-484/2011	KC578603
Ken-490	Kenya	2011	<i>Otomops martiensseni</i>	BatPV/Oto_mar/Ken-490/2011	KC578604
Ken-491	Kenya	2011	<i>Otomops martiensseni</i>	BatPV/Oto_mar/Ken-491/2011	KC578605
Ken-492	Kenya	2011	<i>Otomops martiensseni</i>	BatPV/Oto_mar/Ken-492/2011	KC578606
Ken-514	Kenya	2010	<i>Otomops martiensseni</i>	BatPV/Oto_mar/Ken-514/2010	KC578651
Ken-534	Kenya	2010	<i>Otomops martiensseni</i>	BatPV/Oto_mar/Ken-534/2010	KC578652
Ken-678	Kenya	2011	<i>Miniopterus minor</i>	BatPV/Min_min/Ken-678/2011	KC578607
Ken-681	Kenya	2011	<i>Triaenops afer</i>	BatPV/Tri_per/Ken-681/2011	KC578608
Ken-708	Kenya	2011	<i>Miniopterus minor</i>	BatPV/Min_min/Ken-708/2011	KC578609
Ken-709	Kenya	2011	<i>Triaenops afer</i>	BatPV/Tri_per/Ken-709/2011	KC578610
Ken-712	Kenya	2011	<i>Nycteris sp.</i>	BatPV/Nyc_sp./Ken-712/2011	KC578611
Ken-718	Kenya	2011	<i>Triaenops afer</i>	BatPV/Tri_per/Ken-718/2011	KC578612
Ken-721	Kenya	2011	<i>Coleura afra</i>	BatPV/Col_afr/Ken-721/2011	KC578613
Ken-740	Kenya	2011	<i>Miniopterus sp.</i>	BatPV/Min_sp./Ken-740/2011	KC578614
Ken-747	Kenya	2011	<i>Miniopterus sp.</i>	BatPV/Min_sp./Ken-747/2011	KC578615
Ken-756	Kenya	2011	<i>Miniopterus sp.</i>	BatPV/Min_sp./Ken-756/2011	KC578616
Ken-757	Kenya	2011	<i>Miniopterus sp.</i>	BatPV/Min_sp./Ken-757/2011	KC578617
Ken-765	Kenya	2011	<i>Miniopterus sp.</i>	BatPV/Min_sp./Ken-765/2011	KC578618
Ken-766	Kenya	2011	<i>Miniopterus sp.</i>	BatPV/Min_sp./Ken-766/2011	KC578619
Ken-769	Kenya	2011	<i>Miniopterus sp.</i>	BatPV/Min_sp./Ken-769/2011	KC578620
Ken-776	Kenya	2011	<i>Miniopterus sp.</i>	BatPV/Min_sp./Ken-776/2011	KC578621
Ken-787	Kenya	2011	<i>Miniopterus sp.</i>	BatPV/Min_sp./Ken-787/2011	KC578622
Ken-789	Kenya	2011	<i>Miniopterus sp.</i>	BatPV/Min_sp./Ken-789/2011	KC578623
Ken-793	Kenya	2011	<i>Miniopterus sp.</i>	BatPV/Min_sp./Ken-793/2011	KC578624
Ken-794	Kenya	2011	<i>Miniopterus sp.</i>	BatPV/Min_sp./Ken-794/2011	KC578625
Ken-795	Kenya	2011	<i>Miniopterus sp.</i>	BatPV/Min_sp./Ken-795/2011	KC578626
Ken-803	Kenya	2011	<i>Miniopterus minor</i>	BatPV/Min_min/Ken-803/2011	KC578627
Ken-804	Kenya	2011	<i>Miniopterus minor</i>	BatPV/Min_min/Ken-804/2011	KC578628
Ken-808	Kenya	2011	<i>Triaenops afer</i>	BatPV/Tri_per/Ken-808/2011	KC578629
Ken-809	Kenya	2011	<i>Triaenops afer</i>	BatPV/Tri_per/Ken-809/2011	KC578630
Ken-814	Kenya	2011	<i>Coleura afra</i>	BatPV/Col_afr/Ken-814/2011	KC578631
Ken-815	Kenya	2011	<i>Coleura afra</i>	BatPV/Col_afr/Ken-815/2011	KC578632
Ken-839	Kenya	2011	<i>Rousettus aegyptiacus</i>	BatPV/Rou_aeg/Ken-839/2011	KC578633
Ken-841	Kenya	2011	<i>Rousettus aegyptiacus</i>	BatPV/Rou_aeg/Ken-841/2011	KC578634
Ken-856	Kenya	2011	<i>Coleura afra</i>	BatPV/Col_afr/Ken-856/2011	KC578635
Ken-857	Kenya	2011	<i>Miniopterus minor</i>	BatPV/Min_min/Ken-857/2011	KC578636
Ken-877	Kenya	2011	<i>Miniopterus minor</i>	BatPV/Min_min/Ken-877/2011	KC578637
Ken-887	Kenya	2011	<i>Miniopterus minor</i>	BatPV/Min_min/Ken-887/2011	KC578638
Ken-898	Kenya	2011	<i>Miniopterus minor</i>	BatPV/Min_min/Ken-898/2011	KC578639
Nig-955	Nigeria	2010	<i>Hipposideros sp.</i>	BatPV/Hip_sp./Nig-955/2010	KC538903
SA-163	South Africa	2007	<i>Rhinolophus denti</i>	BatPV/Rhi_den/RSA-163b/2007	KC578571
SA-170	South Africa	2007	<i>Eptesicus hottentotus</i>	BatPV/Ept_hot/RSA-170b/2007	KC578573
SA-172	South Africa	2007	<i>Rhinolophus denti</i>	BatPV/Rhi_den/RSA-172/2007	KC578574
SA-724	South Africa	2010	<i>Neoromicia nana</i>	BatPV/Neo_nan/RSA-724/2010	KC578578
SA-844	South Africa	2010	<i>Kerivoula argentata</i>	BatPV/Ker_age/RSA-844b/2010	KC578580
SA-855	South Africa	2010	<i>Nycteris thebaica</i>	BatPV/Nyc_the/RSA-855/2010	KC578581
SA-922	South Africa	2010	<i>Neoromicia nana</i>	BatPV/Neo_nan/RSA-922/2010	KC578582
SA-947	South Africa	2010	<i>Rhinolophus landeri</i>	BatPV/Rhi_lan/RSA-947/2010	KC578583
SA-1485	South Africa	2012	<i>Hipposideros caffer</i>	BatPV/Hip_caf/RSA-1485b/2012	KC578585
SA-1486	South Africa	2012	<i>Hipposideros caffer</i>	BatPV/Hip_caf/RSA-1486b/2012	KC578587

**Technical Appendix Table 2.** Additional paramyxovirus sequences used in phylogenetic analysis

Sequence	Host	Accession number
<b>General</b>		
Avian paramyxovirus 6	Birds	NC_003043
Goose paramyxovirus SF02	Geese	NC_005036
Newcastle disease virus	Birds	NC_002617
Canine distemper virus	Dogs	NC_001921
Feline morbillivirus	Cats	JQ411014
Measles virus	Humans	NC_001498
Peste-des-petits-ruminants virus	Sheep, goats	NC_006383
Rinderpest virus	Cattle	NC_006296
Bovine parainfluenza virus 3	Cattle	NC_002161
Human parainfluenza virus 1	Humans	NC_003461
Sendai virus	Mice, hamsters, rats	NC_001552
Mumps virus	Humans	NC_002200
Porcine rubulavirus	Pigs	NC_009640
Simian virus 41	Monkeys, apes	NC_006428
Fer-de-Lance virus	Reptiles	NC_005084
Beilong virus	Rats	NC_007803
J-virus	Rats	NC_007454
Mossman virus	Rats	NC_005339
Nariva virus	Rats	FJ362497
Tupaia paramyxovirus	Shrews	NC_002199
<b>Bat associated</b>		
Hendra virus	<i>Pteropus</i> spp.	NC_001906
Nipah virus	<i>Pteropus</i> spp.	NC_002728
Cedar virus	<i>Pteropus</i> sp.	JQ001776
Mapuera virus	<i>Sturnira lilium</i>	NC_009489
Menangle virus	<i>Pteropus alecto</i>	NC_007620
Tioman virus	<i>Pteropus</i> spp.	NC_004074
Tuhoko virus 1	<i>Rousettus leschenaultii</i>	GU128080
Tuhoko virus 2	<i>Rousettus leschenaultii</i>	GU128081
Tuhoko virus 3	<i>Rousettus leschenaultii</i>	GU128082
BatPV Hyp_mon/CO2569/CON/2006	<i>Hypsignathus monstrosus</i>	HQ660119
BatPMV Pte_par/KCR245M/CR/2010	<i>Pteronotus parnellii</i>	JF828295
BatPMV Pte_par/KCR370/CR/2010	<i>Pteronotus parnellii</i>	JF828296
BatPV Car_bre/BR100/BRA/2009	<i>Carollia brevicauda</i>	HQ660192
BatPV Car_bre/BR102/BRA/2009	<i>Carollia brevicauda</i>	HQ660193
BatPV Car_bre/BR96/BRA/2009	<i>Carollia brevicauda</i>	HQ660191
BatPV Car_per/BR310/BRA/2009	<i>Carollia perspicillata</i>	HQ660194
BatPV Des_rot/BR21/BRA/2008	<i>Desmodus rotundus</i>	HQ660187
BatPV Des_rot/BR22/BRA/2008	<i>Desmodus rotundus</i>	HQ660188
BatPV Des_rot/BR222/BRA/2009	<i>Desmodus rotundus</i>	HQ660189
BatPV Glo_sor/BR190/BRA/2009	<i>Glossophaga soricina</i>	HQ660190
BatPV Myo_alc/3-320/BGR/2009	<i>Myotis alcaethoe</i>	HQ660163
BatPV Myo_bec/NM98-46/GER/2008	<i>Myotis bechsteinii</i>	HQ660170
BatPV Myo_dau/NMS09-48/GER/2009	<i>Myotis daubentonii</i>	HQ660165
BatPV Myo_myo/N78-14/GER/2008	<i>Myotis myotis</i>	HQ660166
BatPV Myo_myo/N78-16/GER/2008	<i>Myotis myotis</i>	HQ660167
BatPV Myo_mys/NM98-140/GER/2008	<i>Myotis mystacinus</i>	HQ660168
BatPV Myo_mys/NM98-44/GER/2008	<i>Myotis mystacinus</i>	HQ660169
BatPV Myo_mys/NM98-47/GER/2008	<i>Myotis mystacinus</i>	HQ660171
BatPV Pte_par/KCR245H/CR/2010	<i>Pteronotus parnellii</i>	JF828297
BatPV/Col_af/GB09478/GAB/2009	<i>Coleura afra</i>	HQ660155
BatPV/Eid_hel/CD287/DRC/2009	<i>Eidolon helvum</i>	HQ660123
BatPV/Eid_hel/CD291/DRC/2009	<i>Eidolon helvum</i>	HQ660124
BatPV/Eid_hel/CD297/DRC/2009	<i>Eidolon helvum</i>	HQ660125
BatPV/Eid_hel/GB1237/GAB/2005	<i>Eidolon helvum</i>	HQ660140
BatPV/Eid_hel/GB1535/GAB/2005	<i>Eidolon helvum</i>	HQ660141
BatPV/Eid_hel/GB1659/GAB/2005	<i>Eidolon helvum</i>	HQ660142
BatPV/Eid_hel/GB1661-RMH/GAB/2005	<i>Eidolon helvum</i>	HQ660143
BatPV/Eid_hel/GB1678/GAB/2005	<i>Eidolon helvum</i>	HQ660144
BatPV/Eid_hel/GB3384/GAB/2006	<i>Eidolon helvum</i>	HQ660146
BatPV/Eid_hel/GH48/GHA/2008	<i>Eidolon helvum</i>	FJ609194
BatPV/Eid_hel/GH-M2/GHA/2009	<i>Eidolon helvum</i>	FJ971936
BatPV/Eid_hel/GH-M28/GHA/2009	<i>Eidolon helvum</i>	HQ660147
BatPV/Eid_hel/GH-M3/GHA/2009	<i>Eidolon helvum</i>	FJ971937
BatPV/Eid_hel/GH-M33/GHA/2009	<i>Eidolon helvum</i>	HQ660148
BatPV/Eid_hel/GH-M43/GHA/2010	<i>Eidolon helvum</i>	HQ660127
BatPV/Eid_hel/GH-M51a/GHA/2009	<i>Eidolon helvum</i>	HQ660132
BatPV/Eid_hel/GH-M6/2009	<i>Eidolon helvum</i>	FJ971938
BatPV/Eid_hel/GH-M61a/GHA/2009	<i>Eidolon helvum</i>	HQ660133
BatPV/Eid_hel/GH-M63a/GHA/2009	<i>Eidolon helvum</i>	HQ660136

Sequence	Host	Accession number
BatPV/Eid_hel/GH-M67a/GHA/2009	<i>Eidolon helvum</i>	HQ660131
BatPV/Eid_hel/GH-M69a/GHA/2009	<i>Eidolon helvum</i>	HQ660135
BatPV/Eid_hel/GH-M74a/GHA/2009	<i>Eidolon helvum</i>	HQ660129
BatPV/Eid_hel/GH-M77/GHA/2009	<i>Eidolon helvum</i>	HQ660130
BatPV/Eid_hel/GH-M90a/GHA/2009	<i>Eidolon helvum</i>	HQ660134
BatPV/Eid_hel/RCA-P05/RCA/2008	<i>Eidolon helvum</i>	HQ660150
BatPV/Eid_hel/RCA-P09/RCA/2008	<i>Eidolon helvum</i>	HQ660151
BatPV/Eid_hel/RCA-P10/RCA/2008	<i>Eidolon helvum</i>	HQ660149
BatPV/Epo_gam/CD078/DRC/2009	<i>Epomophorus gambianus</i>	HQ660128
BatPV/Epo_gam/CD255/DRC/2009	<i>Epomophorus gambianus</i>	HQ660120
BatPV/Epo_gam/CD273/DRC/2009	<i>Epomophorus gambianus</i>	HQ660122
BatPV/Epo_spe/CD256/DRC/2009	<i>Epomophorus</i> sp.	HQ660121
BatPV/Hip_aba/GB59-59/GHA/2009	<i>Hipposideros abae</i>	HQ660162
BatPV/Hip_caf/GB09670/GAB/2009	<i>Hipposideros caffer</i>	HQ660156
BatPV/Hip_caf/GB09790/GAB/2009	<i>Hipposideros caffer</i>	HQ660158
BatPV/Hip_caf/GB59-30/GHA/2009	<i>Hipposideros caffer</i>	HQ660161
BatPV/Hip_gig/GB09682/GAB/2009	<i>Hipposideros gigas</i>	HQ660157
BatPV/Hip_gig/GB09898/GAB/2009	<i>Hipposideros gigas</i>	HQ660159
BatPV/Hip_rub/GB19-S/GHA/2009	<i>Hipposideros ruber</i>	HQ660160
BatPV/Hip_rub/GH19-140/GHA/2009	<i>Hipposideros ruber</i>	HQ660153
BatPV/Hip_spec/GH19-T/GHA/2009	<i>Hipposideros</i> sp.	HQ660154
BatPV/Hyp_mon/RCA-P18/RCA/2008	<i>Hypsognathus monstrosus</i>	HQ660152
BatPV/Myo.mys/E20b/09	<i>Myotis mystacinus</i>	JN086953
BatPV/Myo_tor/CD356/DRC/2009	<i>Myonycteris torquata</i>	HQ660126
BatPV/Myo_tor/CO2225/CON/2005	<i>Myonycteris torquata</i>	HQ660118
BatPV/Myo_tor/GB1386/GAB/2005	<i>Myonycteris torquata</i>	HQ660137
BatPV/Pip.pip/E95b/09	<i>Pipistrellus pipistrellus</i>	JN086954
BatPV/Pip_nan/GH36/GHA/2008	<i>Pipistrellus nanus</i>	FJ609192
BatPV/Rou_aeg/GB1583/GAB/2005	<i>Rousettus aegyptiacus</i>	HQ660138
BatPV/Rou_aeg/GB1590/GAB/2005	<i>Rousettus aegyptiacus</i>	HQ660139
BatPV/Rou_aeg/GB2009/GAB/2005	<i>Rousettus aegyptiacus</i>	HQ660145
Eidolon helvum PMV U32A	<i>Eidolon helvum</i>	JN862594
Eidolon helvum PMV U42A	<i>Eidolon helvum</i>	JN862566
Eidolon helvum PMV U42B	<i>Eidolon helvum</i>	JN862577
Eidolon helvum PMV U45A	<i>Eidolon helvum</i>	JN862582
Eidolon helvum PMV U45B	<i>Eidolon helvum</i>	JN862587
Eidolon helvum PMV U49B	<i>Eidolon helvum</i>	JN862572
Eidolon helvum PMV U50B	<i>Eidolon helvum</i>	JN862580
Eidolon helvum PMV U50C	<i>Eidolon helvum</i>	JN862588
Eidolon helvum PMV U51A	<i>Eidolon helvum</i>	JN862564
Eidolon helvum PMV U51B	<i>Eidolon helvum</i>	JN862573
Eidolon helvum PMV U53A	<i>Eidolon helvum</i>	JN862568
Eidolon helvum PMV U53B	<i>Eidolon helvum</i>	JN862569
Eidolon helvum PMV U54A	<i>Eidolon helvum</i>	JN862563
Eidolon helvum PMV U54B	<i>Eidolon helvum</i>	JN862571
Eidolon helvum PMV U58B	<i>Eidolon helvum</i>	JN862583
Eidolon helvum PMV U59A	<i>Eidolon helvum</i>	JN862570
Eidolon helvum PMV U59B	<i>Eidolon helvum</i>	JN862579
Eidolon helvum PMV U5A	<i>Eidolon helvum</i>	JN862592
Eidolon helvum PMV U5B	<i>Eidolon helvum</i>	JN862591
Eidolon helvum PMV U5C	<i>Eidolon helvum</i>	JN862593
Eidolon helvum PMV U61A	<i>Eidolon helvum</i>	JN862578
Eidolon helvum PMV U62A	<i>Eidolon helvum</i>	JN862567
Eidolon helvum PMV U63A	<i>Eidolon helvum</i>	JN862574
Eidolon helvum PMV U64A	<i>Eidolon helvum</i>	JN862575
Eidolon helvum PMV U66A	<i>Eidolon helvum</i>	JN862581
Eidolon helvum PMV U66B	<i>Eidolon helvum</i>	JN862589
Eidolon helvum PMV U68A	<i>Eidolon helvum</i>	JN862584
Eidolon helvum PMV U68B	<i>Eidolon helvum</i>	JN862590
Eidolon helvum PMV U6A	<i>Eidolon helvum</i>	JN862565
Eidolon helvum PMV U6B	<i>Eidolon helvum</i>	JN862562
Eidolon helvum PMV U71A	<i>Eidolon helvum</i>	JN862585
Eidolon helvum PMV U71B	<i>Eidolon helvum</i>	JN862586
Eidolon helvum PMV U72A	<i>Eidolon helvum</i>	JN862576
Eidolon PMV_RC09_216s	<i>Eidolon helvum</i>	HE647824
Eidolon PMV_RC09_222k	<i>Eidolon helvum</i>	HE647825
Eidolon PMV_RC09_236s2	<i>Eidolon helvum</i>	HE801056
Miniopterus griveaudi PMV SMG16723 1	<i>Miniopterus griveaudi</i>	JQ886099
Miniopterus griveaudi PMV SMG16723 2	<i>Miniopterus griveaudi</i>	JQ886100
Miniopterus griveaudi PMV SMG16753 1	<i>Miniopterus griveaudi</i>	JQ886101
Miniopterus griveaudi PMV SMG16753 2	<i>Miniopterus griveaudi</i>	JQ886102
Miniopterus griveaudi PMV SMG16756	<i>Miniopterus griveaudi</i>	JQ886103
Miniopterus sororculus PMV SMG16797	<i>Miniopterus sororculus</i>	JQ886104



Sequence	Host	Accession number
Mormopterus acetabulosus PMV SMG17000	<i>Mormopterus acetabulosus</i>	JQ886105
Paramyxovirus bat/GH10/GHA/2008	<i>Eidolon helvum</i>	FJ609191
Paramyxovirus bat/GH15/GHA/2009	<i>Eidolon helvum</i>	FJ971935
Paramyxovirus bat/GH21a/GHA/2009	<i>Eidolon helvum</i>	FJ971939
Paramyxovirus bat/GH27a/GHA/2009	<i>Eidolon helvum</i>	FJ971940
Paramyxovirus IFBPV01/2010	<i>Pteropus vampyrus</i>	AB748561
Paramyxovirus IFBPV32/2011	<i>Pteropus</i> sp.	AB748559
Paramyxovirus IFBPV46/2011	<i>Pteropus</i> sp.	AB748560
Triadenops menamena PMV SMG16462	<i>Triadenops menamena</i>	JQ886096
Triadenops menamena PMV SMG16505	<i>Triadenops menamena</i>	JQ886098