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Continent-wide Multi-Segment Phylogenomic Study of Host and Geographic Structuring of African Hantaviruses.

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Abstract

Background:

African hantaviruses remain among the least characterized members of the family *Hantaviridae*, with fragmented genomic data limiting our understanding of their evolutionary relationships, host associations, and geographic structuring. Here, we investigated the integrated continent-wide phylogenomic structure of African hantaviruses using all three coding genomic segments.

Methods:

We compiled and curated 281 full-length and partial coding sequences representing the L segment (n = 166), M segment (n = 48), and S segment (n = 67) from 13 African countries, alongside representative global reference strains. Temporal signal was evaluated using root-to-tip regression analysis. Segment-specific phylogenetic reconstructions were performed to characterize host-associated and geographic structuring. Additionally, pairwise tanglegram comparisons of the L, M, and S phylogenies were constructed to evaluate topological congruence and identify potential signals of genetic reassortment.

Results: Root-to-tip regressions revealed weak temporal signal across the L (R^2 = 0.069), M (R^2 = 0.021), and S (R^2 = 0.046) datasets, precluding reliable molecular-clock inference. Phylogenetic analyses demonstrated pronounced host-associated and geographic structuring across all three segments. Rodent, shrew, and bat-associated hantaviruses formed distinct evolutionary clades, with bat and shrew-borne lineages occupying basal, divergent positions relative to rodent-associated viruses. Endemic African hantaviruses exhibited marked regional clustering, forming distinct Malagasy, East African, and West African assemblages, whereas Senegalese, Beninese, and Malian sequences clustered within globally distributed, *Rattus*-associated Seoul orthohantavirus lineages. Comparative analyses highlighted complementary phylogenetic signals: the L segment provided a robust framework for resolving deep evolutionary relationships, the M segment offered clear discrimination among closely related host and geographic groups, and the S segment consistently recovered primary lineage boundaries. Pairwise tanglegrams demonstrated substantial topological concordance among segments highest between L and M with localized incongruences primarily in the L–S comparison restricted to closely related terminal taxa, consistent with but not definitive evidence of reassortment

Conclusions: African hantaviruses display strong host-associated and geographic structuring, with major evolutionary relationships broadly conserved across all three genomic segments. These findings provide an integrated continent-wide phylogenomic framework, establishing a foundation for future genomic surveillance, evolutionary studies, and One Health strategies across Africa.

Keywords: African hantaviruses, Phylogenomics, Orthohantavirus, One Health, Virus-host co-divergence, Zoonotic surveillance

Introduction

Emerging zoonotic viruses, including hantaviruses, continue to pose significant threats to global public health [1,2]. Africa is recognized as a hotspot for pathogen emergence because of its exceptional biodiversity, rapid environmental change, and increasing human–wildlife interactions [3]. Although considerable attention has focused on high-profile viral haemorrhagic fevers such as Ebola virus disease and Lassa fever, the diversity, ecology, and evolutionary history of many other zoonotic viruses remain poorly understood. Among these neglected pathogens are hantaviruses (family *Hantaviridae*), which were historically regarded as rodent-borne viruses distributed predominantly across Europe, Asia, and the Americas [1].. However, increasing molecular surveillance over the past two decades has demonstrated that hantaviruses are also widely distributed throughout Africa and circulate in diverse mammalian hosts, revealing substantially broader evolutionary and ecological diversity than previously recognized [4,5].

Members of the family *Hantaviridae* are enveloped viruses with a tripartite, negative-sense, single-stranded RNA genome comprising the Small (S), Medium (M), and Large (L) segments, which encode the nucleocapsid protein, glycoprotein precursor, and RNA-dependent RNA polymerase, respectively [6]. Hantaviruses were traditionally considered highly host-associated viruses that evolved predominantly in rodents through long-term virus–host associations [7,8]. However, the discovery of genetically divergent hantaviruses in shrews, moles, and bats substantially expanded this paradigm and demonstrated that the evolutionary diversity of the family extends across multiple mammalian orders [5,9]. These discoveries are particularly relevant to

Africa, which represents an important but underexplored reservoir of hantavirus diversity, harbouring diverse ecosystems and mammalian hosts that remain incompletely characterized [10,11].

The discovery of Sangassou virus in the African wood mouse (*Hylomyscus simus*) in Guinea provided the first molecular evidence of an indigenous African rodent-associated hantavirus and established that African rodents harbour evolutionarily distinct viral lineages [6,12]. Subsequent investigations expanded the known diversity through the identification of Tanganya virus and Bowe virus in *Crocidura* shrews in Guinea [9], Azagny virus in the West African pygmy shrew (*Crocidura obscurior*) in Côte d'Ivoire [13], and highly divergent hantaviruses in banana pipistrelle bats (*Neoromicia nanus*) from Côte d'Ivoire [14]. Rodent-, shrew-, and bat-associated hantaviruses have subsequently been reported from Gabon, Sierra Leone, Kenya, Ethiopia, Tanzania, the Democratic Republic of Congo, Madagascar, Egypt, Senegal, Benin, and, more recently, Mali, highlighting the substantial host and geographic diversity of African hantaviruses [15,16,17,18].

The increasing availability of viral genomic sequences has revealed pronounced host-associated and geographic structuring among African hantaviruses [19,20]. Previous phylogenetic investigations indicate that indigenous African hantaviruses comprise several deeply divergent evolutionary lineages associated with rodents, shrews, and bats, whereas Seoul orthohantavirus (SEOV), primarily associated with commensal *Rattus* species, exhibits broader phylogenetic relationships with globally distributed lineages [17]. These observations suggest that African hantavirus diversity comprises geographically structured endemic lineages alongside widely distributed commensal-rodent-associated viruses. Nevertheless, the evolutionary relationships among these lineages and the extent to which host association and geographic structure are

conserved across genomic segments remain incompletely resolved because most previous studies have focused on individual virus species, single genomic segments, or restricted geographic regions.

Understanding the evolutionary ecology of African hantaviruses is increasingly important because ecological disturbance, urbanization, agricultural intensification, climate variability, and habitat fragmentation are altering wildlife communities and potentially increasing opportunities for zoonotic spillover [3]. Human infection occurs predominantly through inhalation of aerosolized excreta from infected reservoir hosts, and retrospective serological investigations have provided evidence of human exposure in several African countries [4,6]. However, hantavirus infections remain poorly recognized in routine clinical practice because their nonspecific manifestations overlap with those of malaria, typhoid fever, Lassa fever, leptospirosis, and other endemic febrile illnesses [21]. Consequently, the burden of hantavirus infection in Africa is likely underestimated, particularly in countries such as Nigeria, where hantavirus diversity and human infection remain poorly characterized. The recent 2026 Andes virus outbreak associated with the *M/V Hondius* cruise ship further demonstrates the potential for hantaviruses to generate cross-border public-health events requiring multinational surveillance, laboratory investigation, contact tracing, and coordinated international responses [22]. These observations emphasize the need to strengthen hantavirus surveillance within broader One Health frameworks for emerging zoonotic disease detection and preparedness.

The segmented genome of hantaviruses provides an important basis for investigating whether evolutionary patterns are consistently represented across different genomic regions. Because the L, M, and S segments encode proteins with distinct biological functions, they may experience different evolutionary constraints, rates of sequence

change, and selective pressures [23,24]. The L segment encodes the RNA-dependent RNA polymerase and contains relatively conserved regions that can provide phylogenetic information across divergent lineages, whereas the M segment encodes the viral glycoprotein precursor involved in virus–host cell interactions and may exhibit substantial sequence variation among viral lineages. The S segment encodes the nucleocapsid protein and provides an additional functionally distinct marker for resolving evolutionary relationships. Consequently, phylogenies reconstructed from individual genomic segments may differ in their ability to resolve deep and shallow evolutionary relationships, including geographic and host-associated lineages [11,23,24].

In addition, comparison of segment-specific phylogenies enables assessment of whether viral lineages share a common evolutionary history. Strong topological concordance among segment phylogenies supports a broadly shared evolutionary history, whereas phylogenetic incongruence may reflect genetic reassortment or other segment-specific evolutionary processes [25,26]. Reassortment can occur following co-infection of a host with genetically distinct viruses and may generate discordant evolutionary histories among genomic segments [6,26]. Comparative analysis across all three genomic segments is therefore important for distinguishing robust host- and geographic-associated evolutionary patterns from signals specific to individual genomic regions.

Despite the increasing discovery of genetically diverse hantaviruses in Africa, a continent-wide comparative framework integrating evolutionary relationships, host associations, geographic structure, and genomic congruence remains limited [11,17,27]. In particular, the extent to which host- and geographic-associated phylogenetic patterns are concordantly recovered across the L, M, and S genomic

segments remains poorly characterized at the continental scale. Addressing these gaps is important for understanding the evolutionary organization of African hantavirus diversity and for identifying genomic and ecological priorities for One Health surveillance.

In the present study, we performed a continent-wide comparative phylogenomic analysis of African hantaviruses using the L, M, and S genomic segments. We analysed 281 full-length and partial coding sequences from 13 African countries together with representative global reference sequences to characterize host-associated and geographic structuring and assess phylogenetic congruence among genomic segments. Pairwise tanglegram analyses were used to assess topological congruence among the L, M, and S phylogenies and identify discordant relationships potentially consistent with reassortment. By integrating multi-segment phylogenetic evidence with reservoir-host and geographic information, this study establishes a continent-wide framework for understanding the evolutionary structure of African hantaviruses and provides a foundation for future genomic surveillance, One Health preparedness, and global health security.

Materials and Methods

Sequence dataset

A total of 281 hantavirus nucleotide sequences representing the three genomic segments were analyzed: 48 M-segment, 67 S-segment, and 166 L-segment sequences (Supplementary Table 1). All sequences from Africa (Egypt, Senegal, Benin, Mali, Guinea, Côte d'Ivoire, Sierra Leone, Gabon, the Democratic Republic of the Congo, Ethiopia, Kenya, Tanzania, and Madagascar) were retrieved from National Center for Biotechnology Information (NCBI) GenBank and represent isolates collected between

2004 and 2024 with no isolates from 2025 together with selected reference strains from Asia, Europe, and the Americas to provide global phylogenetic context.

Sequence alignment

Nucleotide sequences for each genomic segment (L, M, and S) were aligned independently using MAFFT v7 [28] with the --auto algorithm and otherwise default parameters. Alignments were inspected and manually edited in AliView v1.01 [29] to ensure positional homology. Ambiguously aligned regions and sites with excessive gaps were removed prior to phylogenetic inference.

Phylogenetic inference

Maximum-likelihood (ML) phylogenies for each segment were inferred using IQ-TREE v2.1.3 [30]. For each alignment the best-fit nucleotide substitution model was selected by ModelFinder [31] implemented within IQ-TREE. Node support was assessed with 1,000 ultrafast bootstrap replicates [32]. The ML trees files were exported in Newick format with branch lengths in substitutions/site and visualized in interactive Tree Of Life version 7.6 iTOL [33].

Assessment of temporal signal

Temporal signal of each segment dataset was evaluated using Clockor2 v1.9.1 [34] (https://clockor2.github.io). ML trees with branch lengths in substitutions/site (Newick format) and sampling dates (from sequence metadata or CSV file) were used as inputs. Root-to-tip regression was performed independently for the L, M, and S datasets. The temporal signal was judged insufficient to support reliable molecular clock dating. Therefore, time-calibrated Bayesian phylogenetic analyses and molecular clock dating were not performed.

Comparative phylogenetic analysis and detection of reassortment

To ensure consistent taxon labels across segment datasets, isolates were assigned unique identifiers (HTV001–HTV198) and a mapping file linking identifiers to accession numbers and metadata is provided in Supplementary Table 1. Trees were rooted consistently by midpoint rooting in FigTree v1.4.4 [35].

Congruence among the L, M, and S genomic segments, ML trees were compared using Dendroscope v3.5.7 [36]. Pairwise tanglegrams (L–M, L–S, and M–S) were generated using the Tanglegram module; the built-in untangling algorithm was applied to minimize edge crossings while preserving topology. Trees used for tanglegrams were exported in NEXUS format. Putative reassortment events were identified by examining isolates that occupied incongruent phylogenetic positions between paired segment trees. Particular attention was given to taxa that clustered within different evolutionary lineages while maintaining strong branch support in the original phylogenetic analyses. Given that topological discordance may also arise from incomplete phylogenetic resolution, stochastic error, or differences in evolutionary histories among genomic segments, putative reassortment events were interpreted conservatively by integrating tanglegram patterns with branch support, host species, geographic origin, and the broader phylogenetic context.

Results

Dataset Characteristics

We compiled and curated 281 full-length and partial coding sequences representing the three hantavirus genomic segments: L, encoding the RNA-dependent RNA polymerase (n = 166), M, encoding the glycoprotein precursor (n = 48), and S, encoding the nucleocapsid protein (n = 67) (Supplementary Table 1). The dataset comprised sequences from 13 African countries spanning West n= 70, Central n=2, East n=46, and North Africa n= 16 and Madagascar n=91, together with

representative global reference strains (supplementary table 1). African sequences were derived from diverse mammalian hosts, including rodents, shrews, and bats, allowing comparative assessment of host-associated and geographic phylogenetic structure.

Assessment of Temporal Signal

Root-to-tip regression showed weak temporal structure for the L, M and S datasets (R^2 = 0.069, 0.021 and 0.046, respectively), indicating insufficient temporal signal for reliable molecular-clock inference. Consequently, time-calibrated phylogenetic and phylogeographic analyses were not undertaken. Subsequent evolutionary comparisons were therefore based on phylogenetic topology, branch support, host association, and geographic distribution rather than divergence-time estimates.

Host-Associated Evolutionary Relationships

Phylogenetic analyses consistently identified strong host-associated structuring across the L, M, and S genomic segments (Figures 1–4, Table 1). Rodent-associated hantaviruses formed distinct evolutionary groups, with viruses associated with *Hylomyscus simus* in Guinea clustering separately from those associated with *Hylomyscus endorobae* in Kenya. These patterns were broadly consistent across the three genomic segments. Shrew-associated hantaviruses formed distinct lineages separated from rodent-associated viruses. West African viruses associated with *Crocidura douceti* and *Crocidura obscurior* clustered together, whereas Tanzanian viruses associated with *Myosorex zinki* and *Myosorex geata* formed a distinct East African lineage. Bat-associated hantaviruses from East and Central Africa consistently occupied deep-branching positions relative to rodent-associated viruses

across the three genomic segments, supporting pronounced evolutionary divergence between bat-associated and rodent-associated lineages.

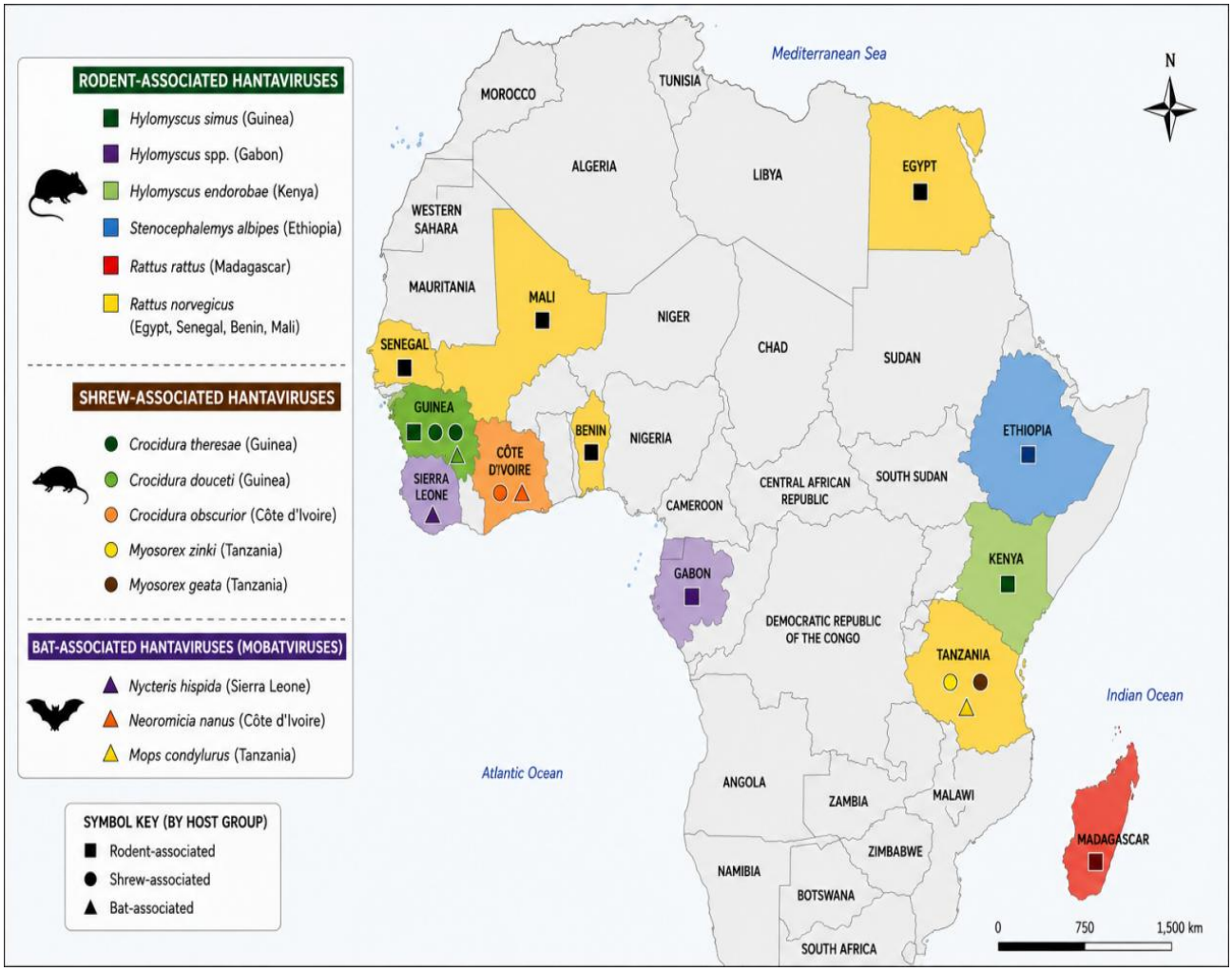


Figure 1. Geographic distribution and host diversity of African hantaviruses. Map of Africa showing the documented locations of rodent-, shrew-, and bat-associated hantaviruses alongside their respective mammalian reservoir host species. Symbology highlights host groups (squares = rodents, circles = shrews, triangles = bats) across endemic countries in West, East, North, and Insular Africa. Geographic distribution maps were generated using QGIS [37].

Table 1. Reported hantaviruses in Africa, their reservoir hosts, and year of first detection

Country	Hantavirus	Reservoir host	Scientific name	Host group	Year of first detection	Key reference
Guinea	Sangassou virus (SANGV)	African wood mouse	*Hylomyscus simus*	Rodent	2004	[12]
Guinea	Tanganya virus (TANGV)	Therese's shrew	*Crocidura theresae*	Shrew	2004	[38]
Guinea	Bowe virus (BOWV)	Doucet's musk shrew	*Crocidura douceti*	Shrew	2012	[9]
Côte d'Ivoire	Azagny virus (AZGV)	West African pygmy shrew	*Crocidura obscurior*	Shrew	2009	[13]
Côte d'Ivoire	Mouyassu virus (MOUV)	Banana pipistrelle	*Neoromicia nanus*	Bat	2011	[14]
Sierra Leone	Magboi virus (MGBV)	Hairy slit-faced bat	*Nycteris hispida*	Bat	2009	[39]
Senegal	Seoul orthohantavirus (SEOV)	Brown rat	*Rattus norvegicus*	Rodent	2013	[17]

Country	Hantavirus	Reservoir host	Scientific name	Host group	Year of first detection	Key reference
Benin	Seoul orthohantavirus (SEOV)	Brown rat	*Rattus norvegicus*	Rodent	2018	[17]
Mali	Seoul orthohantavirus (SEOV)	Brown rat	*Rattus norvegicus*	Rodent	2023	[18]
Gabon	Makokou virus (MAKV)	African wood mouse	*Hylomyscus* spp.	Rodent	2009	[16]
DRC	Kiwira virus-related hantavirus	Angolan free-tailed bat	*Mops condylurus*	Bat	2013	[40]
Tanzania	Kiwira virus	Angolan free-tailed bat	*Mops condylurus*	Bat	2017	[40]
Tanzania	Kilimanjaro virus (KILV)	Kilimanjaro mouse shrew	*Myosorex zinki*	Shrew	2017	[20]
Tanzania	Uluguru virus (ULUV)	Geata mouse shrew	*Myosorex geata*	Shrew	2017	[20]

Country	Hantavirus	Reservoir host	Scientific name	Host group	Year of first detection	Key reference
Ethiopia	Tigray virus (TIGV)	Ethiopian white-footed mouse	*Stenocephalemys albipes*	Rodent	2010	[41]
Kenya	Novel hantavirus	African wood mouse	*Hylomyscus endorobae*	Rodent	2014	[42]
Kenya	Novel shrew-associated hantavirus	Somali shrew	Crocidura somalica	Shrew	2020	[43]
Madagascar	Anjozorobe virus (ANJZV)	Black rat	*Rattus rattus*	Rodent	2008	[15]
Madagascar	Thailand ortho-hantavirus (THAIV)	Black rat	*Rattus rattus*	Rodent	2019-2021	[44]
Egypt	Seoul orthohantavirus (SEOV)	Brown rat	*Rattus norvegicus*	Rodent	1992	[45]

Geographic Structure of African Hantaviruses

The phylogenetic analyses revealed pronounced geographic structuring among endemic African hantaviruses (Figures 2–4, Table 2). West African viruses comprised geographically associated endemic lineages as well as globally distributed *Rattus*-associated SEOV lineages. Guinean viruses, including Sangassou virus-related strains, formed a distinct endemic lineage, whereas Côte d'Ivoire sequences included deeply divergent shrew-associated lineages. Viruses from Senegal, Benin, and Mali clustered within globally distributed *Rattus*-associated SEOV lineages including human associated isolates from Europe and Asia. Central African viruses from the Democratic Republic of the Congo were distributed among sub-Saharan Murinae-associated lineages rather than forming a single geographically exclusive clade. East African viruses from Kenya, Tanzania, and Ethiopia formed a distinct regional assemblage characterized by substantial genetic diversity among countries. North African viruses from Egypt clustered with Western Palearctic and Eurasian Murinae-associated hantaviruses rather than with the principal sub-Saharan endemic lineages. Viruses from Madagascar formed a distinct, well-supported monophyletic lineage, indicating pronounced genetic differentiation from mainland African viruses.

Table 2. Hantaviruses strains in Africa and their locations

Hantavirus strain	Country	Reference
Sangassou virus (SANGV)	Guinea	[12]
Tanganya virus (TANGV)	Guinea	[38]
Bowe virus (BOWV)	Guinea	[9]
Azagny virus (AZGV)	Côte d'Ivoire	[13]
Mouyassu virus (MOUV)	Côte d'Ivoire	[14]
Magboi virus (MGBV)	Sierra Leone	[39]
Seoul orthohantavirus (SEOV)	Senegal	[17]
Seoul orthohantavirus (SEOV)	Benin	[17]
Seoul orthohantavirus (SEOV)	Mali	[18]
Makokou virus (MAKV)	Gabon	[16]
Kiwira virus-related hantavirus	DRC	[40]
Kiwira virus	Tanzania	[40]
Kilimanjaro virus (KILV)	Tanzania	[20]
Uluguru virus (ULUV)	Tanzania	[20]
Tigray virus (TIGV)	Ethiopia	[41]
Novel hantavirus	Kenya	[42]
Novel shrew-associated hantavirus	Kenya	[43]
Anjozorobe virus (ANJZV)	Madagascar	[15]
Thailand orthohanta-virus (THAIV)	Madagascar	[44]
Seoul orthohantavirus (SEOV)	Egypt	[45]

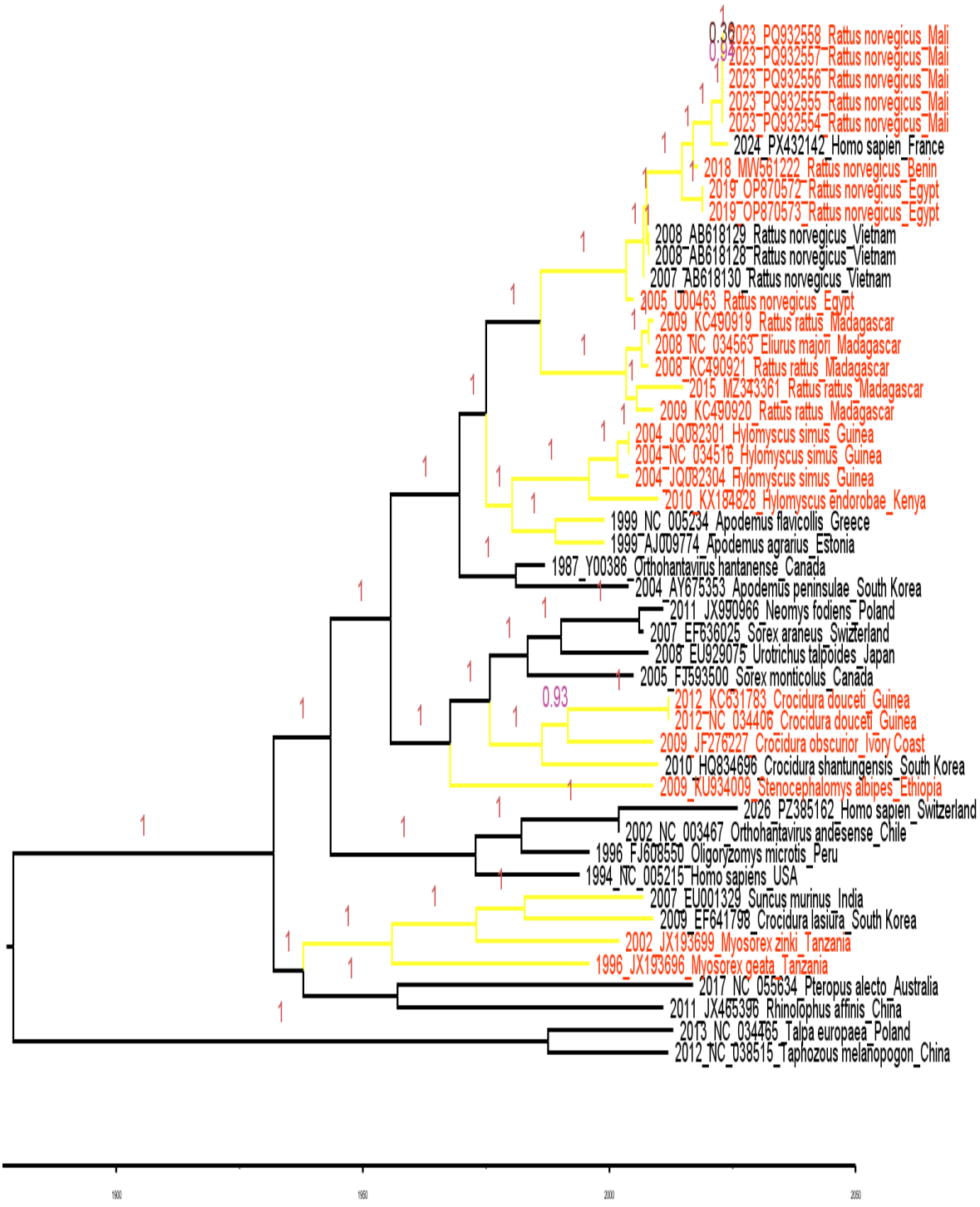


Figure 2. Geographic structuring of African hantaviruses based on maximum-likelihood phylogenetic analysis of the M segment. African evolutionary lineages are highlighted in yellow, with African sequences indicated by red tip labels. Non-African lineages and sequences are shown in black. The phylogeny illustrates the relationships between African hantaviruses and representative global reference strains.

Conversely, *Rattus*-associated Seoul orthohantavirus (SEOV) sequences exhibited broader geographic connectivity, clustering with globally distributed lineages, in contrast to the more geographically structured endemic African hantaviruses. The Madagascan viruses lineage formed a distinct monophyletic clade, whereas Senegalese, Beninese, and Malian sequences clustered with globally distributed SEOV strains (including human isolates from Europe and Asia).

Complementary Phylogenetic Resolution Across Genomic Segments

Comparative analysis of the L, M, and S phylogenies revealed broadly concordant host-associated and geographic relationships, while demonstrating complementary differences in phylogenetic resolution (Figures 3–5). The L segment, which encodes the conserved RNA-dependent RNA polymerase, provided a strong framework for resolving relationships among the major evolutionary lineages, including the separation of divergent host-associated groups (Madagascan, East African, and West African assemblages) (Figure 3). The M segment, encoding the host-interacting glycoproteins, provided particularly clear discrimination among several closely related lineages, with major geographic and host-associated groups (Madagascar, Ethiopia/Guinea, Senegal, Tanzania, and Mali/Benin/Egypt-associated assemblages) (Figure 4) being readily resolved. The S segment, encoding the nucleocapsid protein, consistently recovered the principal host-and geographic-associated lineages, although several deeper relationships were less well resolved (Figure 5). Overall, the major evolutionary groupings were consistently recovered across the three genomic segments.

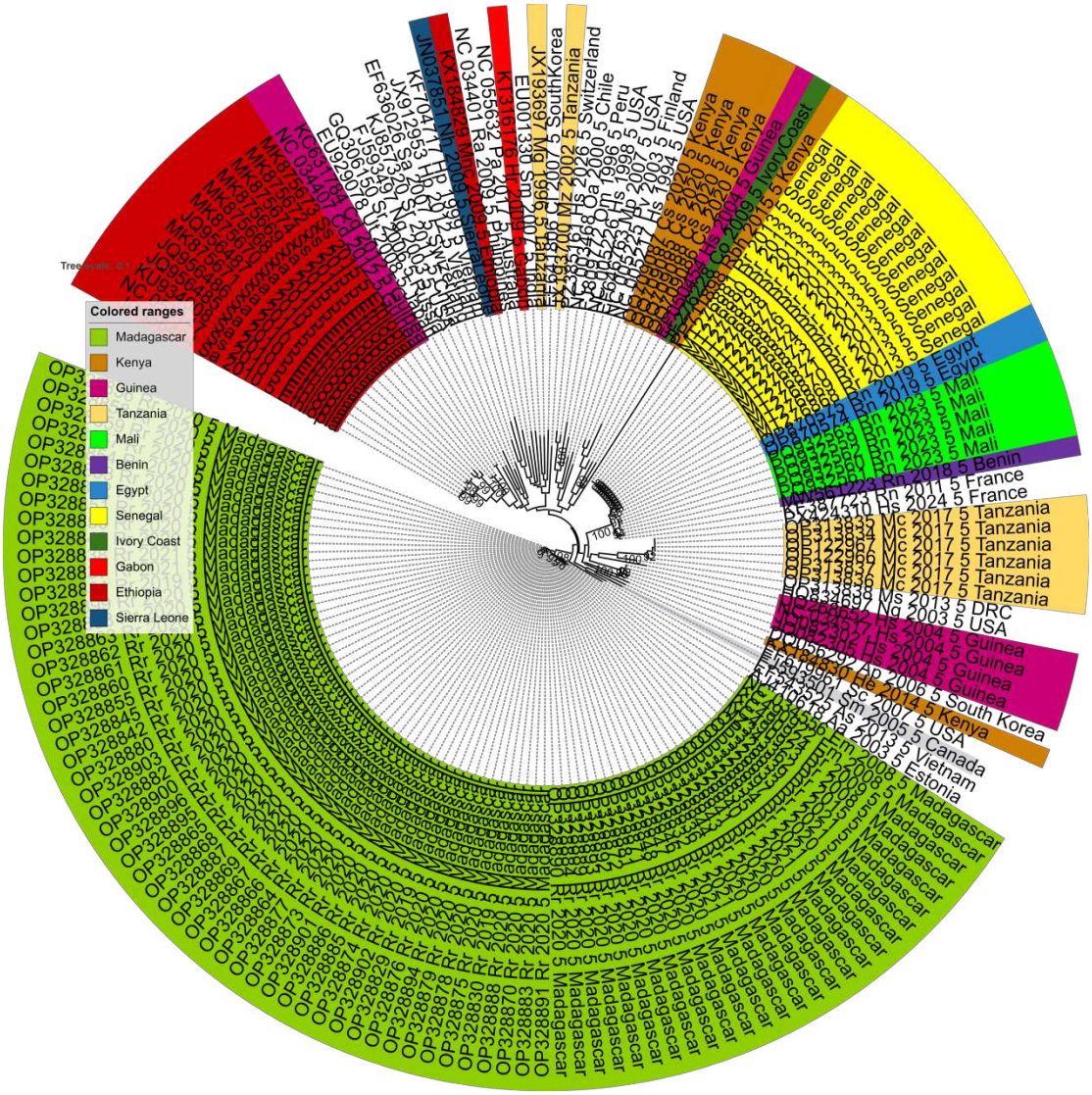


Figure 3. Circular Maximum Likelihood phylogenetic tree of hantavirus L segment sequences annotated by geographic origin. Phylogenetic tree rendered in iTOL showing the evolutionary relationships among African hantavirus isolates across different sampling years and host taxa. Colored outer metadata ranges correspond to the country of origin for each sequence to illustrate geographic representation across clades. Bootstrap support values are indicated at internal nodes.

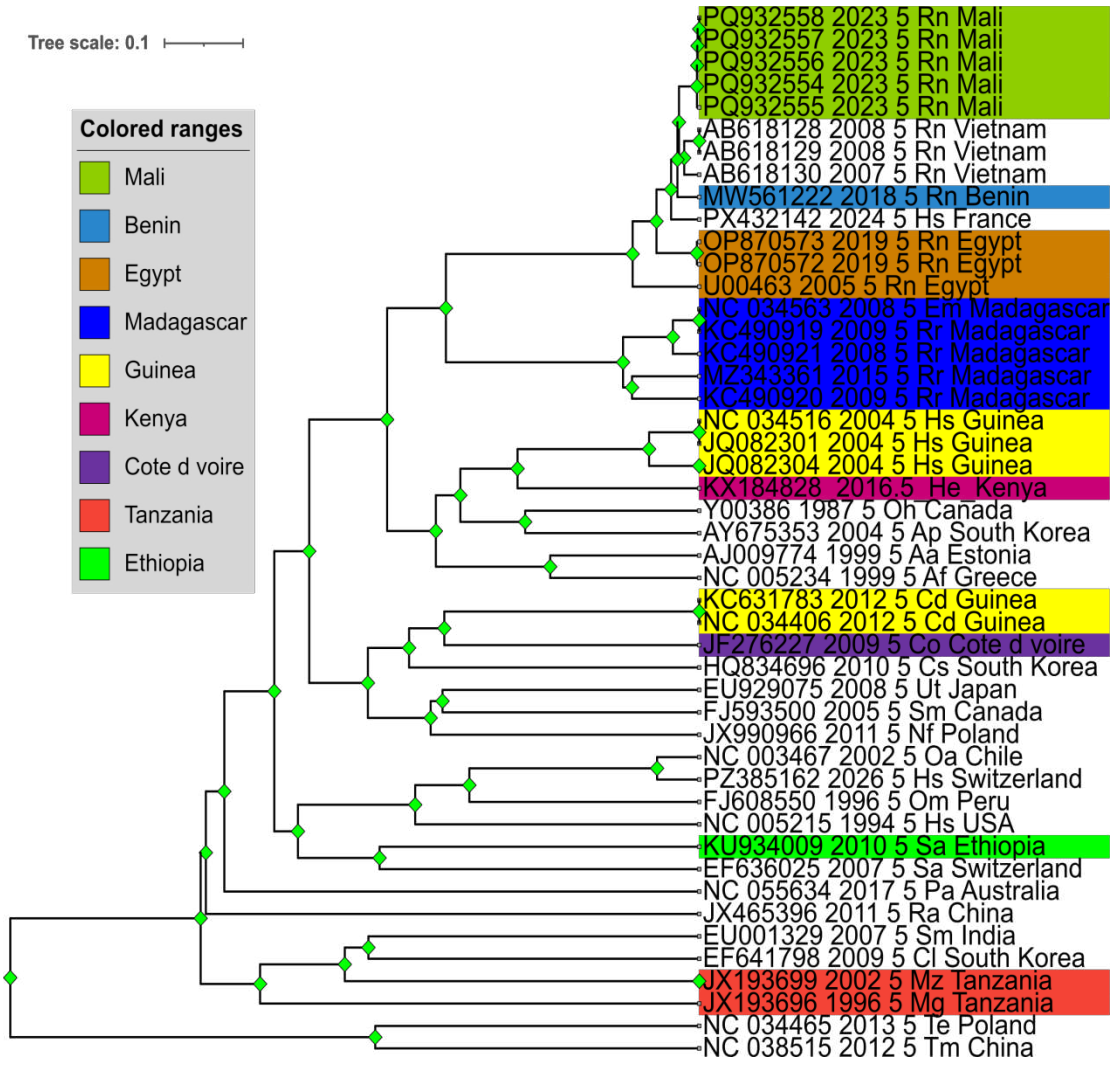


Figure 4. Maximum likelihood phylogenetic tree of African hantavirus sequences annotated by geographic origin. Phylogenetic tree rendered in iTOL showing the evolutionary relationships among African hantavirus isolates across different sampling years and host taxa. Taxa are highlighted using color-coded range strips corresponding to geographic collection locations: Mali (lime green), Benin (sky blue), Egypt (orange), Madagascar (dark blue), Guinea (yellow), Kenya (magenta), Côte d'Ivoire (purple), Tanzania (coral red), and Ethiopia (bright green). Node symbols (green diamonds) denote clade bootstrap support values.

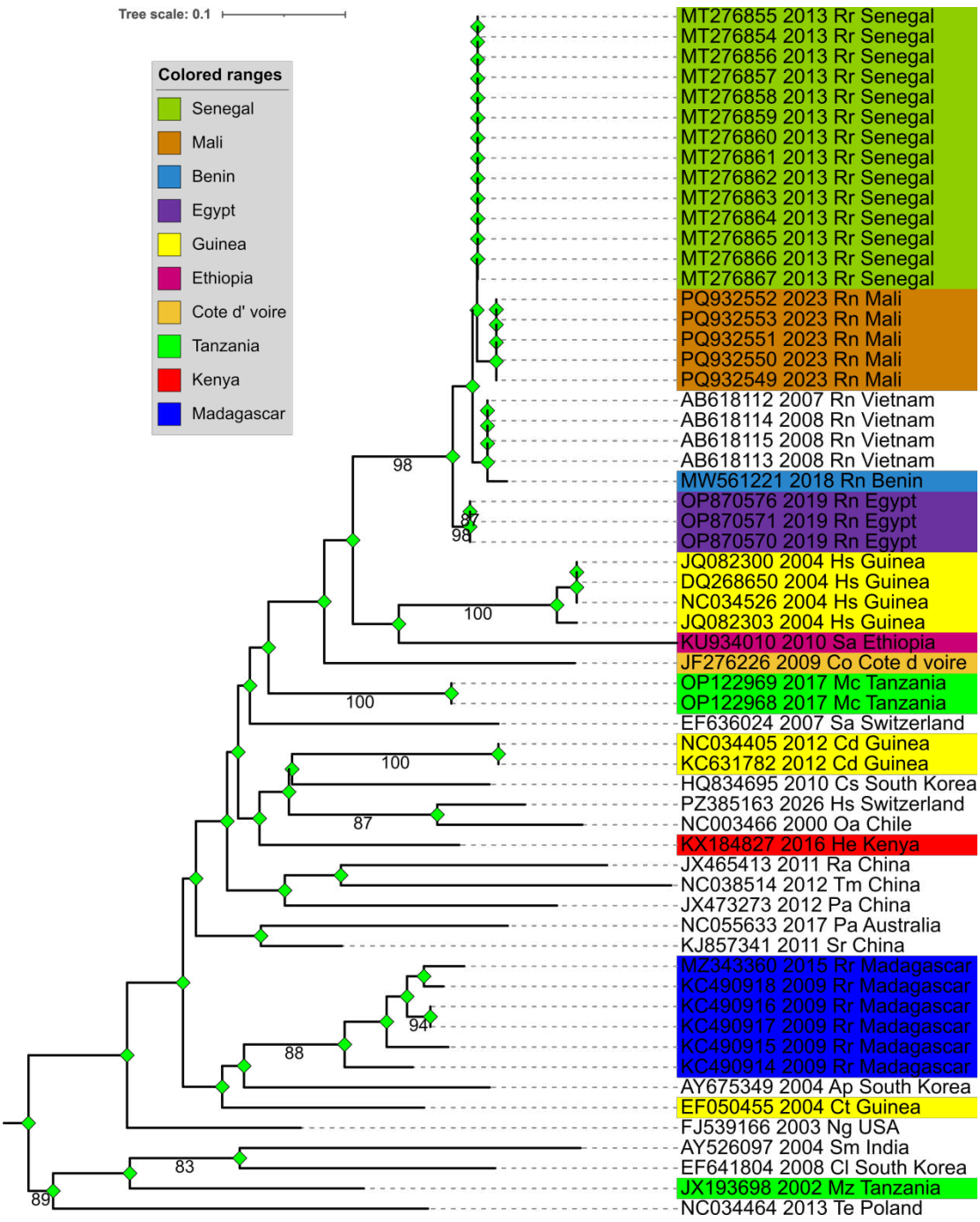


Figure 5. Maximum likelihood phylogenetic tree of African hantaviruses highlighting geographic origin and sampling locations. Phylogenetic tree rendered in iTOL showing the evolutionary

relationships among African hantavirus isolates across different host species and collection years. Taxa background ranges are color-coded by country of origin: Senegal (light green), Mali (brown/orange), Benin (light blue), Egypt (purple), Guinea (yellow), Ethiopia (dark pink), Côte d'Ivoire (beige), Tanzania (bright green), Kenya (red), and Madagascar (dark blue). Node symbols (green diamonds) represent statistical clade support values.

Topological Congruence and Evidence of Reassortment

Pairwise tanglegram comparisons were used to assess topological congruence among the L, M, and S phylogenies (Figures 6–8). The L–M comparison showed the greatest overall topological congruence, with corresponding isolates occupying highly similar positions in the two phylogenies (Figure 6). The M–S comparison also showed substantial concordance, with only minor rearrangements among closely related taxa (Figure 7). The greatest topological discordance was observed in the L–S comparison (Figure 8). However, the major host and geographic-associated clades remained conserved between the two phylogenies, and the observed incongruences were largely restricted to terminal branches involving closely related isolates. These localized topological differences provide signals consistent with, but not definitive evidence of, reassortment among the sampled African hantaviruses. Nevertheless, localized discordance may also arise from differences in phylogenetic resolution, stochastic uncertainty, or segment-specific evolutionary processes; therefore, the observed incongruences were interpreted as signals consistent with, but not definitive evidence of reassortment.

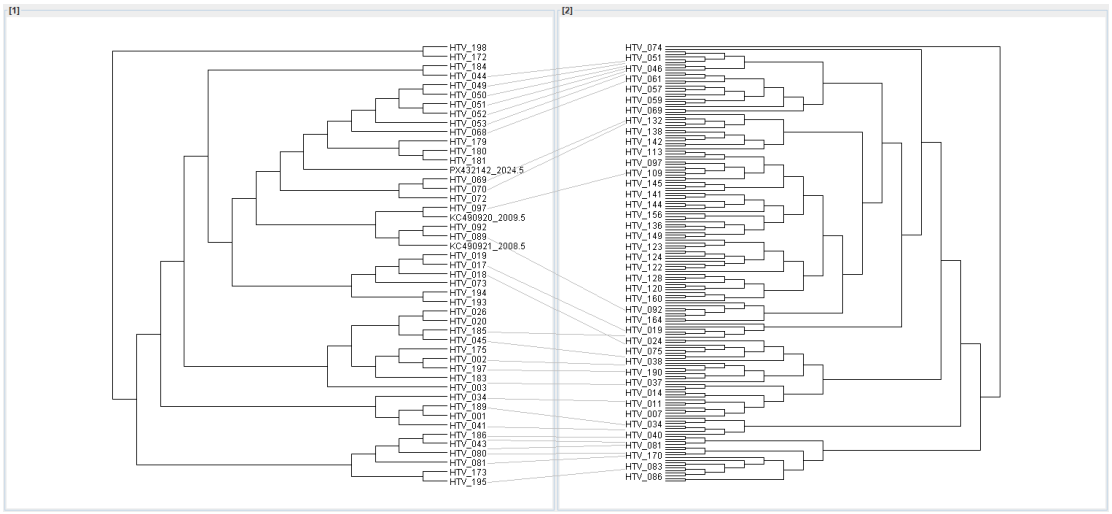


Figure 6. Tanglegram comparing the maximum likelihood phylogenies inferred from the L and M genomic segments of hantaviruses. Corresponding isolates are linked by connecting lines. Parallel connections indicate congruent phylogenetic placement, whereas crossing lines indicate topological incongruence between genomic segments.

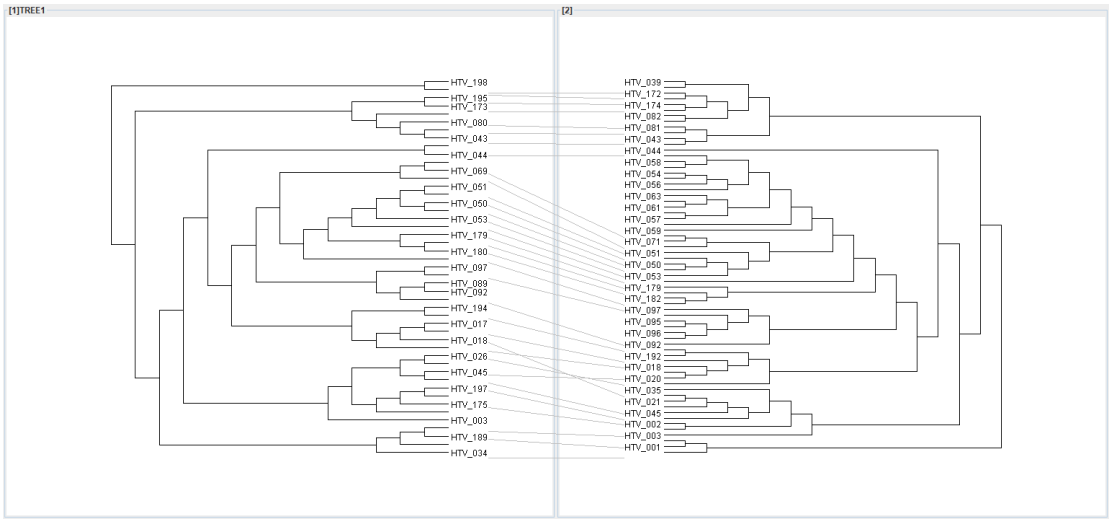


Figure 7. Tanglegram comparing the M and S genomic segment phylogenies. Corresponding isolates are connected by lines between trees. Crossing connections indicate discordant phylogenetic relationships among genomic segments and were evaluated as evidence of possible genome segment reassortment.

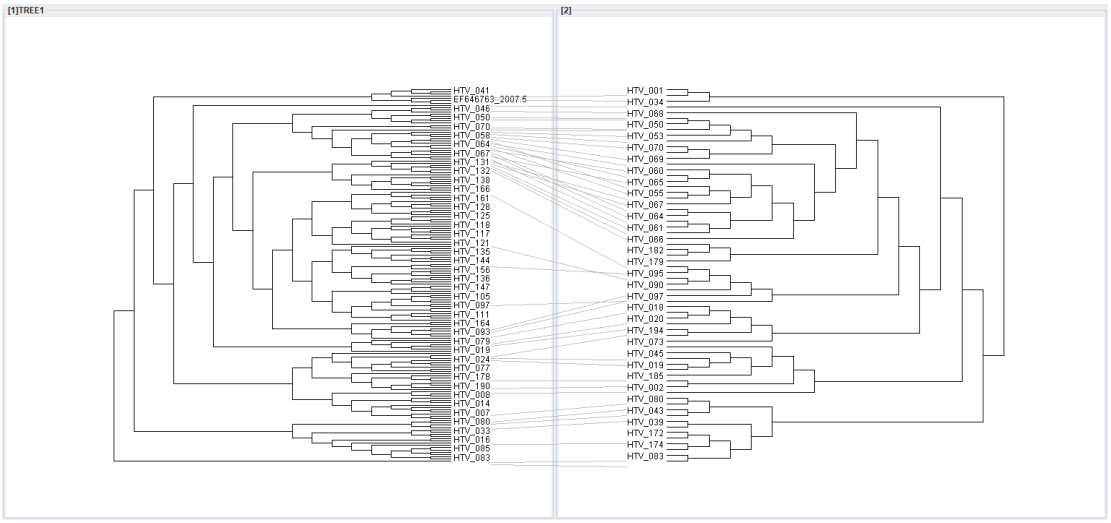


Figure 8. Tanglegram comparing the L and S genomic segment phylogenies.
Corresponding isolates are connected by lines between trees. Crossing connections indicate discordant phylogenetic relationships among genomic segments and were evaluated as evidence of possible genome segment reassortment.

Discussion

This study provides a continent-wide comparative phylogenetic assessment of African hantaviruses using sequences from the L, M, and S genomic segments. The principal finding is that African hantavirus diversity is strongly structured by both reservoir host association and geography, with broadly concordant evolutionary patterns across the three genomic segments. Unlike previous investigations focused on individual viral species, single genomic segments, or geographically restricted regions [11,12,15], the present multi-segment approach provides an integrated perspective on hantavirus diversity and evolutionary relationships across Africa. The results indicate that endemic lineages have diversified within geographically and ecologically structured reservoir populations, whereas cosmopolitan *Rattus*-associated viruses, particularly SEOV, exhibit broader relationships with globally distributed lineages [17].

The inclusion of viruses associated with rodents, shrews, and bats further highlights the remarkable host diversity of African hantaviruses. Although rodents remain the principal reservoirs of orthohantaviruses, the recognition of genetically divergent viruses in insectivorous mammals and bats has substantially expanded current understanding of hantavirus evolution and taxonomy [10,46,47]. Africa therefore represents an important reservoir of hantavirus diversity, while remaining one of the least intensively sampled continents (Figure 1, Table 1).

Across all three genomic segments, the phylogenetic analyses resolved major host-associated evolutionary groups corresponding broadly to rodent-, shrew-, and bat-associated hantaviruses. The deep positions occupied by several shrew- and bat-associated viruses relative to rodent-associated lineages are consistent with hypotheses proposing early hantavirus diversification among insectivorous mammals followed by extensive diversification within rodents [9,46,48]. The placement of divergent viruses such as Kiwira and Azagny viruses further supports a complex evolutionary history involving long-term virus-host associations and historical host-switching events [9,11,46].

Within the rodent-associated lineage, phylogenetic relationships broadly reflected both host identity and geographic origin. For example, viruses associated with *Hylomyscus simus* in Guinea were differentiated from those associated with *Hylomyscus endorobae* in Kenya, illustrating the combined influence of host specificity and geographic isolation. Similarly, West African shrew-associated viruses detected in *Crocidura douceti* and *Crocidura obscurior* were distinct from East African lineages associated with *Myosorex zinki* and *Myosorex geata*. These patterns are consistent with previous evidence that hantaviruses often exhibit strong host fidelity, with ecological specialization and restricted connectivity among reservoir populations contributing to lineage diversification [1,2,16]. Although historical host-switching has

undoubtedly contributed to hantavirus evolution, the overall correspondence between phylogeny and reservoir taxonomy observed here suggests that long-term host association remains an important driver of African hantavirus diversification (Table 2).

Geographic structure was also evident across the continent (Figure 2). West Africa showed substantial phylogenetic diversity, containing both endemic lineages and globally distributed SEOV associated with commensal *Rattus* species. Guinean viruses, including Sangassou virus-related strains, were genetically differentiated from related Gabonese viruses, whereas shrew-associated viruses from Côte d'Ivoire occupied distinct deep-branching positions. In contrast, viruses from Senegal, Benin, and Mali clustered within globally distributed *Rattus*-associated SEOV lineages. This pattern is consistent with the widespread dissemination of SEOV through commensal rodents transported through international trade and human-mediated movement [17,24,49,50]. The coexistence of geographically restricted endemic viruses and cosmopolitan *Rattus*-associated lineages therefore illustrates the contrasting influence of local reservoir evolution and anthropogenic dispersal on hantavirus diversity in Africa.

East African viruses from Kenya, Tanzania, and Ethiopia also formed geographically structured assemblages, although considerable differentiation was evident among countries. The ecological and topographic heterogeneity of East Africa, including the East African Rift System, may contribute to restricted connectivity among small-mammal populations and consequently promote localized viral diversification. Similar relationships between environmental barriers, host population structure, and viral genetic differentiation have been proposed previously [11,41]. However, because the present study did not directly test associations among viral divergence, host population structure, or landscape connectivity, these ecological features should

be regarded as plausible contributors rather than demonstrated drivers of hantavirus diversification.

Elsewhere, Central African sequences showed relationships spanning lineages represented in other parts of sub-Saharan Africa, although limited sampling prevented the identification of a clearly distinct regional assemblage **(**Figure 2). North African viruses from Egypt clustered with Western Palearctic and Eurasian Murinae-associated lineages, consistent with the historical role of the Mediterranean region as an interface for rodent-mediated viral exchange. Madagascar represented the most geographically distinct assemblage, with Madagascan viruses forming a monophyletic group separated from mainland African lineages. This pattern is consistent with previous evidence suggesting introduction through commensal rodents followed by diversification under insular ecological conditions [15,50,51]. The observed relationships are also consistent with reports of Anjozorobe virus, a variant of Thailand orthohantavirus, circulating among rodent populations in Madagascar and evidence of human exposure to hantaviruses on the island [52].

Comparison of the L, M, and S genomic segments demonstrated that each region provides complementary phylogenetic information while preserving the principal evolutionary structure (Figures 3–5). Although the major phylogenetic architectures were broadly congruent, the three segments differed in their ability to resolve particular evolutionary relationships. Such differences are biologically plausible because the L, M, and S segments encode proteins with distinct functional roles and may consequently experience different evolutionary constraints. The L segment provided a strong framework for resolving relationships among the major evolutionary lineages, including the separation of divergent host-associated groups (Figure 3). As the largest and most conserved genomic segment, encoding the viral RNA-dependent RNA

polymerase, the L segment is subjected to strong functional constraints that reduce sequence variability while preserving ancestral phylogenetic signal. In our dataset, the L phylogeny clearly separated several geographically and host-associated groups, including distinct Madagascar, East African, West African, and other African lineages. Conserved genomic regions have similarly been shown to improve inference of deep evolutionary relationships in other negative-sense RNA viruses by minimizing homoplasy associated with rapidly evolving loci. In contrast, the M segment provided greater discrimination among several closely related geographic lineages (Figure 4), potentially reflecting evolutionary constraints associated with the viral glycoprotein precursor and its role in virus-host interactions [23,24]. However, the present analysis does not directly estimate evolutionary rates or selection, and therefore the mechanistic basis of the observed difference in resolution remains to be established.

The S segment showed comparatively lower resolution at some deeper nodes but consistently identified the principal host-associated and geographic groupings (Figure 5). Together, these findings demonstrate that the evolutionary history inferred from African hantaviruses is not dependent on a single genomic region and highlight the value of multi-segment analyses for resolving both deep and recent evolutionary relationships.

The broad congruence among segment-specific phylogenies was reinforced by the tanglegram analyses (Figures 6–8). Corresponding isolates generally occupied similar phylogenetic positions across the L, M, and S trees, with the strongest agreement observed between the L and M segments (Figure 6), followed closely by the M and S comparison, where corresponding isolates generally occupied similar phylogenetic positions (Figure 7). The greatest discordance occurred between the L and S segment phylogenies (Figure 8), but these inconsistencies were largely confined to terminal branches, whereas the major host-associated and geographic clades

remained stable. Such localized incongruence may reflect limited reassortment among sympatric viruses, but could also result from stochastic variation in phylogenetic reconstruction or differences in evolutionary rates among genomic segments. Similar patterns have been reported in comparative hantavirus genomic studies, where reassortment appears to occur predominantly among closely related viruses sharing compatible hosts and ecological niches rather than between deeply divergent lineages [53,54]. Overall, the preservation of the principal phylogenetic architecture across genomic segments provides limited evidence for extensive reassortment among the sampled African hantaviruses and suggests that long-term host association and geographic isolation may have played more prominent roles in maintaining evolutionary structure.

These findings have important implications for One Health surveillance and diagnostic preparedness in Africa. The considerable genetic divergence among endemic African hantavirus lineages raises concerns about the sensitivity and specificity of molecular and serological assays developed primarily against European or American viruses. Regionally adapted diagnostic approaches may therefore be necessary to improve detection of divergent African lineages such as Sangassou, Kiwira, and Azagny viruses [47]. In addition, the widespread distribution of commensal *Rattus*-associated SEOV highlights the potential role of urbanization, trade, and human-mediated rodent dispersal in facilitating zoonotic risk. Given that SEOV causes haemorrhagic fever with renal syndrome in humans, targeted hantavirus testing may be valuable in investigations of unexplained febrile illness, particularly in settings with frequent exposure to commensal rodents [18].

The detection of divergent hantaviruses in shrews and bats further emphasizes the need to expand surveillance beyond traditional rodent reservoirs. Integrated One Health approaches

combining wildlife, environmental, and clinical surveillance will be important for identifying previously unrecognized hantavirus diversity and understanding potential pathways for zoonotic emergence [47,55].

Several limitations should be considered when interpreting these findings. First, weak temporal signal precluded reliable molecular clock inference; consequently, the present analyses describe phylogenetic relationships rather than evolutionary rates or divergence times. Second, geographic and host sampling remains uneven, particularly in Central, Southern, and parts of North Africa, and the current dataset likely represents only a fraction of African hantavirus diversity [56,57]. Third, publicly available sequences were heterogeneous in length and completeness, limiting the number of isolates available for direct comparison across all three genomic segments. These limitations may influence phylogenetic resolution and the apparent strength of host-associated patterns.

Future studies incorporating systematic wildlife sampling in underrepresented regions, broader host surveillance, and increased availability of complete genomes will be essential for resolving the full evolutionary diversity and geographic distribution of African hantaviruses [55]. Nevertheless, the present findings complement recent global evidence that hantavirus evolution is shaped by the interaction of long-term virus-host association, ecological specialization, geographic isolation, anthropogenic dispersal, and localized reassortment [47]. By integrating evidence across all three genomic segments, this study provides a consolidated evolutionary framework for understanding hantavirus diversity in Africa and establishes a foundation for future genomic surveillance and One Health preparedness.

Conclusion

This study provides a continent-wide phylogenomic framework for African hantaviruses and demonstrates strong host-associated and geographic structuring across the L, M, and S genomic segments. Rodent, shrew, and bat-associated viruses formed distinct evolutionary groups, while endemic African lineages exhibited pronounced regional clustering and *Rattus*-associated Seoul orthohantavirus showed broader phylogenetic relationships with globally distributed lineages. Comparative analysis of the three genomic segments revealed complementary phylogenetic signals, with the L segment providing strong resolution of deeper relationships, the M segment offering greater discrimination among closely related lineages, and the S segment consistently identified the principal host- and geographic-associated patterns. The high topological concordance among genomic segments, together with only localized incongruence, provides limited evidence for extensive reassortment among the sampled viruses. Although uneven geographic and genomic sampling limits the completeness of the inferred diversity, these findings establish a robust baseline for future multi-segment genomic surveillance and evolutionary studies of African hantaviruses. Expanded sampling of underrepresented regions and mammalian hosts, coupled with increased availability of complete genomes, will be essential for resolving the broader diversity, host associations, and geographic structure of hantaviruses across Africa and strengthening One Health preparedness for emerging zoonotic infections and global health security.

List of abbreviations

S Small

M Medium

L Large

SEOV Seoul orthohantavirus

DRC Democratric Republic of Congo

Declarations

Ethics approval and consent to participate: Not applicable. This study used publicly available nucleotide sequence data and did not involve experimental procedures on animals.

Consent for publication: Not applicable

Competing interests: No conflict of interest.

Originality/non-duplicate-submission statement. We confirm that this manuscript has not been published previously and is not currently under consideration for publication elsewhere.

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