

BEYOND THE CLASSIC RABIES VIRUS: EMERGING LYSSAVIRUSES AND FUTURE CHALLENGES FOR ONE HEALTH

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Abstract

Rabies is discussed as though one virus caused it. It does not. The genus *Lyssavirus* now contains eighteen ratified species and a lengthening queue of candidates, most of them maintained quietly in bats across five continents, and every one of them capable of producing the same fatal encephalitis. This review maps that hidden diversity and asks what it means for prevention. We summarise reservoir hosts, geographical range and documented human infections for the principal emerging lyssaviruses; explain how phylogroup structure in the viral glycoprotein decides whether a rabies vaccine will work; and appraise cross-neutralisation data, monoclonal antibody products and pan-lyssavirus vaccine candidates. We then test the diagnostic toolkit, from the direct fluorescent antibody test to portable nanopore sequencing, against the specific problem of detecting a virus nobody expected. Current biologicals reliably cover phylogroup I and little else. Closing that gap is a veterinary problem long before it becomes a medical one.

Keywords: lyssavirus; rabies; bat surveillance; phylogroup; pan-lyssavirus vaccine; genomic surveillance; One Health

When Rabies Is Not Just Rabies

In October 2024 a man in his fifties was bitten by a bat in northern New South Wales. He did what public health guidance asks. He sought care, and he received post-exposure prophylaxis according to national protocol. In July 2025 he died of acute encephalitis.

The agent was not rabies virus. It was Australian bat lyssavirus: Australia's fourth recorded human case, the first ever in New South Wales. The patient received post-exposure prophylaxis according to national guidelines, but later died of acute encephalitis; the case remains under investigation to determine whether other exposures or factors contributed.¹ Australia has never had classical rabies. That reassuring fact, repeated for decades in textbooks and travel advisories, conceals something important. Rabies is a clinical syndrome, not a single pathogen.² The disease is caused by any member of the genus *Lyssavirus*, and rabies virus is simply the member that learned to live in dogs and then colonised the world.³ The others stayed in bats, and most have

never been searched for systematically.⁴ For veterinarians and public health workers, this leaves one uncomfortable question. If the vaccines, immunoglobulins and diagnostic conjugates in our freezers were all built around a single virus, how much of the genus can they actually see, and how much can they stop?

The Expanding Lyssavirus Family

The International Committee on Taxonomy of Viruses places *Lyssavirus* in the family *Rhabdoviridae*, subfamily *Alpharhabdovirinae*, alongside the vesiculoviruses and ephemeroviruses.⁵ Since 2021 every species carries a binomial name, so classical rabies virus is now *Lyssavirus rabies*, Mokola virus is *Lyssavirus mokola*, and Australian bat lyssavirus is *Lyssavirus australis*.⁵ Eighteen species are ratified. Matlo and Phala bat lyssaviruses from South Africa, a second Taiwan bat lyssavirus and Divaca bat lyssavirus wait in the queue, and the queue keeps lengthening.^{5,6} Eleven

of the eighteen were described after 2000, almost all through bat surveillance rather than clinical investigation.⁴

Structurally the genus is austere. A bullet-shaped particle carries a genome of roughly 12 kilobases encoding only five proteins, in the order nucleoprotein, phosphoprotein, matrix, glycoprotein and polymerase.⁵ That simplicity matters clinically, because the glycoprotein is the sole target of neutralising antibody, and it is the least conserved of the five.^{5,7}

Species boundaries are drawn at roughly 78 to 80 per cent nucleotide identity across the

nucleoprotein gene, supported by phylogenetic position, serological distinction and ecological niche.⁵ Bats are the ancestral and principal reservoirs for nearly every species.⁴ Rabies virus is the exception that proves the rule: it jumped from bats into carnivores, established self-sustaining transmission in dogs, foxes, raccoons and mongooses, and became a global killer while its relatives stayed local.^{3,8} Understanding why one lineage crossed and the others have not is the central evolutionary puzzle of the genus, and the reason the others cannot be dismissed.

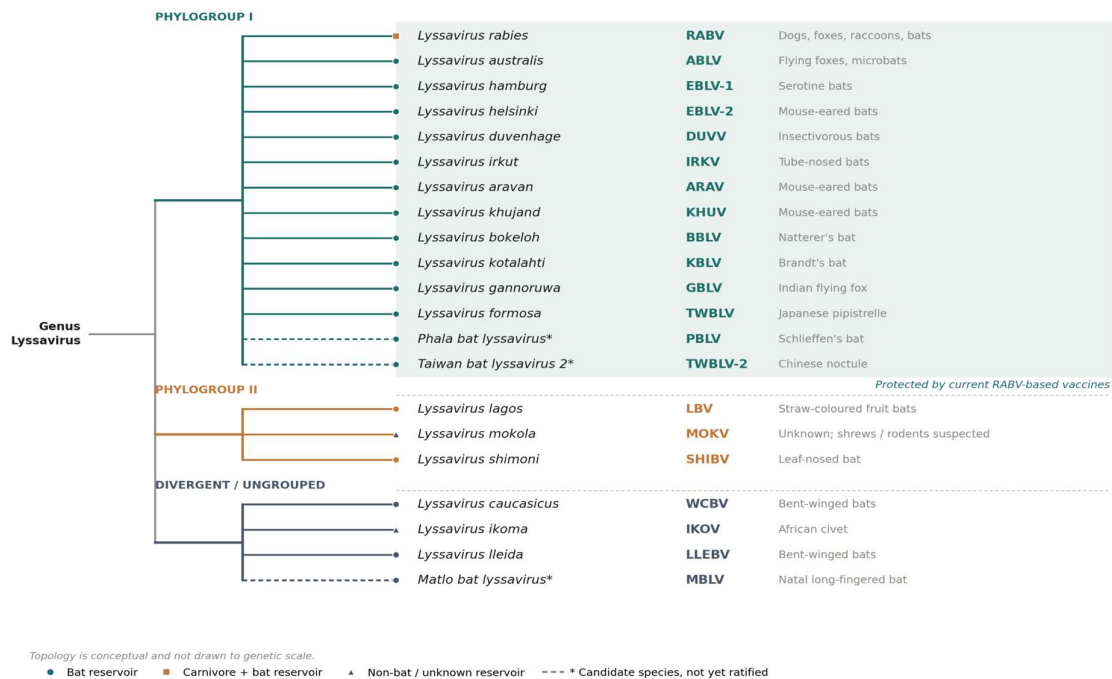


Fig. 1: Mapping the family tree. Schematic phylogeny of the genus *Lyssavirus*, showing the eighteen ICTV-ratified species arranged into phylogroup I, phylogroup II and the divergent, ungrouped viruses, with three candidate species (dashed branches) awaiting ratification. Marker shape denotes reservoir order, and the shaded band marks the approximate limit of protection conferred by current rabies virus-based vaccines. Topology is conceptual and is not drawn to genetic scale.

Original figure prepared by the authors; taxonomy, phylogroup assignment and reservoir data compiled from refs 4, 5, 6, 17 and 19.

The Emerging Players

Africa holds the deepest branches. Lagos bat virus, recovered from a fruit bat near Lagos in 1956, circulates in *Eidolon helvum* and related pteropodids and has killed cats, dogs and a water mongoose, although no human case is confirmed.⁹ Mokola virus is the outlier of the genus: the only species never isolated from a bat, recovered repeatedly from domestic cats, several of them vaccinated, with shrews and small rodents suspected as the true reservoir.¹⁰ Two human infections, one fatal, are on record.¹⁰ Duvenhage

virus, harboured by African insectivorous bats, has caused three fatal human infections, one of them in a traveller bitten in Kenya who died in the Netherlands, which makes it the clearest example of a bat lyssavirus crossing borders inside a patient.⁴ Shimoni bat virus from a Kenyan leaf-nosed bat¹¹ and Ikoma lyssavirus from an African civet in the Serengeti¹² complete the picture of a continent sampled far too thinly.

Europe is better documented because its bat surveillance is systematic. European bat

lyssavirus 1 predominates, almost entirely in serotine bats, with documented spillover into sheep, cats and a stone marten.¹³ European bat lyssavirus 2 is rarer, largely restricted to Daubenton's bats, and killed a Scottish bat conservationist in 2002.¹³ Bokeloh bat lyssavirus in Natterer's bats, Lleida bat lyssavirus in bent-winged bats and Kotalahti bat lyssavirus in a Finnish Brandt's bat have each appeared in only a handful of animals,^{13,14} a reminder that detection effort, not prevalence, usually sets the ceiling.

Across Eurasia, Aravan, Khujand, Irkut and West Caucasian bat viruses were each isolated from a few insectivorous bats between 1991 and 2002.⁵ Irkut virus deserves particular attention. It has now been implicated in several fatal human encephalitides in the Russian Far East, including cases in 2019 and 2021, in regions long regarded as rabies-free.^{15,16} West Caucasian bat virus, from

bent-winged bats in the Caucasus, is the most genetically distant member of the genus and is neutralised by essentially nothing in current clinical use.^{5,17}

In the Asia-Pacific, Australian bat lyssavirus is carried by both flying foxes and insectivorous microbats and has caused four human deaths since 1996, every one of them fatal.¹ Gannoruwa bat lyssavirus was identified in Sri Lankan flying foxes in 2016¹⁸ and Taiwan bat lyssavirus in Japanese pipistrelles.⁵ Neither has a documented human case, which, given how recently either was looked for, says more about surveillance than about risk. Read as a set, these viruses share three features that should concern any clinician: a bat reservoir, a fatal clinical course indistinguishable from rabies, and a diagnostic history that usually begins by accident.

Table 1. The emerging lyssaviruses at a glance

Virus (abbreviation)	Principal reservoir	Region	Human cases	Vaccine protection
PHYLOGROUP I — rabies virus and its close relatives				
Rabies virus (RABV)	Dogs, foxes, raccoons, skunks, mongooses, bats	Worldwide except a few island states	~59,000 deaths annually	Full
Australian bat lyssavirus (ABLV)	Flying foxes; insectivorous microbats	Australia	4, all fatal (1996, 1998, 2013, 2025)	Demonstrated
European bat lyssavirus 1 (EBLV-1)	Serotine bats (<i>Eptesicus serotinus</i>)	Europe; North Africa	3 (Ukraine 1977, presumptive; Russia 1985; France 2019)	Demonstrated
European bat lyssavirus 2 (EBLV-2)	<i>Myotis daubentonii</i> , <i>M. dasycneme</i>	Northern Europe, UK	2 (Finland 1985; Scotland 2002)	Demonstrated
Duvenhage virus (DUVV)	Insectivorous bats	Southern and East Africa	3, all fatal	Presumed
Irkut virus (IRKV)	<i>Murina</i> spp. and other insectivorous bats	Siberia, Russian Far East, NE China	Several fatal (2007, 2019, 2021)	Reduced
Aravan (ARAV); Khujand (KHUV)	<i>Myotis</i> spp.	Central Asia	None reported	Reduced
Bokeloh bat lyssavirus (BBLV)	Natterer's bat (<i>Myotis nattereri</i>)	Germany, France, Poland	None reported	Presumed; not tested <i>in vivo</i>
Kotalahti bat lyssavirus (KBLV)	Brandt's bat (<i>Myotis brandtii</i>)	Finland	None reported	Presumed

Gannoruwa bat lyssavirus (GBLV)	Indian flying fox (<i>Pteropus medius</i>)	Sri Lanka	None reported	Presumed
Taiwan bat lyssavirus (TWBLV)	Japanese pipistrelle (<i>Pipistrellus abramus</i>)	Taiwan	None reported	Presumed
PHYLOGROUP II — the African divergents				
Lagos bat virus (LBV)	<i>Eidolon helvum</i> , other pteropodids	Sub-Saharan Africa	None confirmed	None
Mokola virus (MOKV)	Unknown; shrews / rodents suspected. Never isolated from bats	Sub-Saharan Africa	2 (1 fatal)	None — recovered from vaccinated cats
Shimoni bat virus (SHIBV)	Commerson's leaf-nosed bat (<i>Hipposideros commersoni</i>)	Kenya	None reported	None
DIVERGENT / UNGROUPED — outside both phylogroups				
West Caucasian bat virus (WCBV)	Bent-winged bats (<i>Miniopterus schreibersii</i>)	Caucasus; serological signal in East Africa	None reported	None demonstrated
Ikoma lyssavirus (IKOV)	African civet (single detection)	Tanzania	None reported	None demonstrated
Lleida bat lyssavirus (LLEBV)	Bent-winged bats	Spain, France	None reported	None demonstrated

Compiled by the authors from refs 1, 4, 5, 9–22. Candidate species awaiting ICTV ratification: Matlo bat lyssavirus and Phala bat lyssavirus (South Africa), Taiwan bat lyssavirus 2, Divaea bat lyssavirus. “Presumed” denotes phylogenetic and limited serological inference rather than challenge data.

Why Current Vaccines May Not Be Enough

Antigenically the genus splits along a fault line first described in 2001.¹⁹ Phylogroup I contains rabies virus together with the Australian, European, Duvenhage, Aravan, Khujand, Irkut, Bokeloh, Kotalahti, Gannoruwa and Taiwan viruses. Phylogroup II contains Mokola, Lagos bat and Shimoni bat viruses. West Caucasian bat virus, Ikoma and Lleida sit outside both, sometimes informally grouped as phylogroup III.^{5,17}

The Nucleoprotein antigens cross-react across the entire genus, which is why one diagnostic conjugate can stain nearly all of them.⁵ Glycoprotein ectodomains are a different matter: above 75 per cent conserved within a phylogroup, below 65 per cent between phylogroups.⁵ Since neutralising antibody targets the glycoprotein alone, that difference translates directly into protection or its absence.¹⁹

Every licensed human and veterinary rabies vaccine, and every rabies immunoglobulin, is built on rabies virus.²⁰ They protect well across

phylogroup I, and human diploid cell vaccine elicits cross-neutralising responses against European and Australian bat lyssaviruses.²¹ Against phylogroup II and the divergent species they do not work.^{17,22} Mokola virus recovered from correctly vaccinated cats is the field demonstration.¹⁰ Even inside phylogroup I, coverage thins with genetic distance: neutralisation of Irkut, Aravan and Khujand viruses is measurably reduced,^{22,23} and the Australian breakthrough case is a sobering reminder that phylogenetic proximity is not a guarantee.¹

Monoclonal antibodies inherit the same limitation. The products now aligned with WHO recommendations, including the two-antibody cocktail of docaravimab and miromavimab, were selected against rabies virus glycoprotein.^{20,24} More encouraging are broadly reactive candidates such as RVC20 and RVC58, which together neutralised 35 rabies virus isolates and 25 non-

rabies lyssaviruses *in vitro* by targeting conserved epitopes in antigenic sites I and III.²⁴

Vaccine design is moving in the same direction. LyssaVax, a structurally engineered chimeric glycoprotein combining rabies and Mokola domains, elicited sera neutralising wild-type viruses across the major phylogroups.²⁵ A related construct replacing antigenic site I extended protection to Irkut virus and gave partial protection against Mokola without sacrificing rabies coverage.²⁶ Neither yet covers the divergent viruses, and neither has left the laboratory.

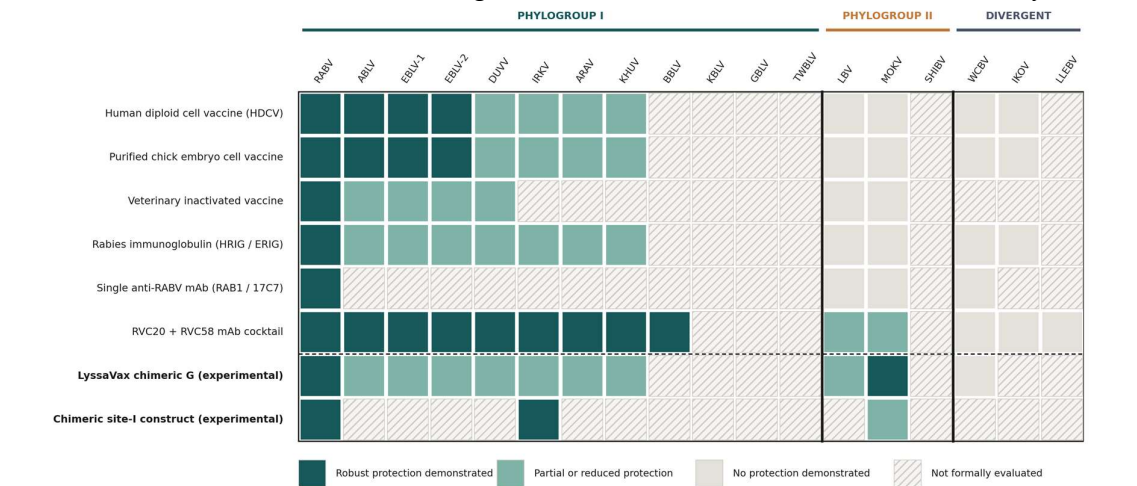


Fig. 2: Where protection stops. Cross-protection matrix for licensed rabies biologicals and two experimental pan-lyssavirus candidates, tested against the eighteen ratified lyssavirus species and ordered by phylogroup. Shading denotes robust protection, partial or reduced protection, or no protection demonstrated; hatching marks combinations that have never been formally evaluated. Heavy vertical rules mark the phylogroup boundaries, where the cliff edge in coverage becomes visible. Original figure prepared by the authors; cell assignments derived from the experimental and field evidence in refs 1, 5, 10, 17 and 19–26.

Closing the Diagnostic Gap

The direct fluorescent antibody test remains the reference method endorsed by WHO and WOA, and its strength against emerging lyssaviruses lies in a quirk of biology: because nucleoprotein antigens are conserved genus-wide, polyclonal conjugates detect nearly every species.⁵ Conjugates built on narrow monoclonal panels may not, and a negative result on a divergent virus is easy to misread as an absence of disease. The test also needs a fluorescence microscope, cold chain and an experienced reader.²⁸

Lateral flow devices push simplicity further still and are attractive for remote settings, but their sensitivity varies between manufacturers and their performance against non-rabies lyssaviruses is largely unknown.²⁷ The direct rapid immunohistochemical test removes the microscope. Validated in Tanzanian field conditions at sensitivity and specificity approaching those of the reference test, and readable by light microscopy in under an hour, it

has become the practical backbone of decentralised animal surveillance.²⁹

Molecular methods changed the picture again. The LN34 pan-lyssavirus real-time RT-PCR, designed against the conserved leader and nucleoprotein region,³⁰ achieved 99.9 per cent sensitivity and 99.7 per cent specificity across fourteen laboratories and works on decomposed and formalin-fixed tissue.³¹ Its limits are instructive: the original primers performed poorly against some rare lyssaviruses and required revision,³² which is exactly the failure mode a novel species would exploit.

Sequencing closes the remaining gap. In 2019 a French patient died of encephalitis after living beside a bat colony; antigen detection, immunohistochemistry and virus isolation were all negative, and only meta transcriptomic sequencing of brain tissue identified European bat lyssavirus 1.³³ Portable nanopore platforms have since put that capability into public health laboratories in Guatemala, India, Kenya and Vietnam that had no prior sequencing capacity.³⁴

Table 2. The diagnostic toolkit against an unexpected lyssavirus

Test	Detects	Advantages	Limitations
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Direct fluorescent antibody test (DFA / FAT)	Nucleoprotein antigen in fresh brain impressions	Reference standard (WHO / WOA); polyclonal conjugates cross-react genus-wide; result in ~2 hours	Requires fluorescence microscope, cold chain, skilled reader; monoclonal-based conjugates may miss divergent species; unusable on decomposed tissue
Direct rapid immunohistochemical test (dRIT)	Nucleoprotein antigen; light-microscope readout	Field-deployable; no fluorescence microscope; under 1 hour; validated against DFA in African field conditions	Still needs fresh brain tissue and a trained reader; conjugate supply limited; inter-operator variability in proficiency testing
Pan-lyssavirus real-time RT-PCR (e.g. LN34)	Conserved leader–nucleoprotein RNA across the genus	Very high sensitivity and specificity; resolves inconclusive antigen results; works on degraded, archived and formalin-fixed tissue	Primer / probe coverage of rare and novel species must be revalidated continually; needs thermocycler and contamination control
Conventional RT-PCR with Sanger sequencing	Partial N or G gene	Cheap; gives species identification and lineage; widely available	Lower sensitivity than real-time formats; degenerate primers may fail on divergent viruses; slower turnaround
Targeted whole-genome / amplicon NGS	Complete or near-complete viral genome	Full resolution for taxonomy, phylogroup assignment and outbreak reconstruction	Requires intact RNA, bioinformatics capacity and reference-guided primer schemes that assume prior knowledge of the virus
Metagenomic (unbiased) sequencing	Any pathogen sequence present, without prior hypothesis	The only method that reliably finds a species nobody suspected; diagnostic where all targeted tests are negative	Costly; high host background; needs specialist analysis; rarely available outside reference centres
Portable nanopore sequencing	Amplicon or whole-genome sequence, in-country	Low capital cost; real-time output; deployable in laboratories without prior sequencing capability; supports outbreak tracing	Higher raw error rate requiring consensus depth; reagent cold chain and supply continuity remain practical constraints
Lateral flow antigen devices	Nucleoprotein antigen	Minimal equipment; usable at point of collection; supports surveillance where no laboratory exists	Sensitivity varies markedly between products; performance against non-rabies lyssaviruses largely unvalidated; confirmatory testing always required

Compiled by the authors from refs 5 and 27–34.

One Health Before the Next Spillover

Preparedness for the next lyssavirus will be built in three places, and none of them is a hospital.

The first is the roost. Passive surveillance, testing sick and dead bats submitted by rehabilitators and the public, is how almost every novel lyssavirus has been found, including Matlo and Phala bat lyssaviruses during targeted work in Limpopo.⁶ Active work in bat colonies provides the ecological context that passive testing cannot: seroprevalence dynamics, seasonal birth pulses, and the crucial observation that infected bats often appear entirely healthy.^{4,13} Bat conservation and lyssavirus surveillance are not opposing interests, and framing them as such costs both.

The second is the bite. Integrated bite case management in Tanzania, in which a patient's account of an animal bite triggers investigation and testing of that animal, substantially increased detection of rabid animals and links the clinic to

the laboratory in real time.³⁵ In Romblon Province in the Philippines, genomic surveillance combined with field epidemiology showed that an outbreak in a previously rabies-free island province had been imported from Luzon, and identified exactly where control had lapsed.³⁶

The third is the network. WOA's *Terrestrial Manual* now recognises the fluorescent antibody test, the rapid immunohistochemical test and pan-lyssavirus RT-PCR as primary diagnostic methods,²⁷ and transparent international reporting turns isolated detections into a usable map. Veterinarians sit at every node: certifying vaccination, submitting brains, advising bat handlers on pre-exposure prophylaxis and antibody monitoring, and translating findings for physicians who may never have considered a bat.³³ Three countries have now been validated by WHO for eliminating dog-mediated human rabies, and those same systems are the ones that will detect whatever comes next.²

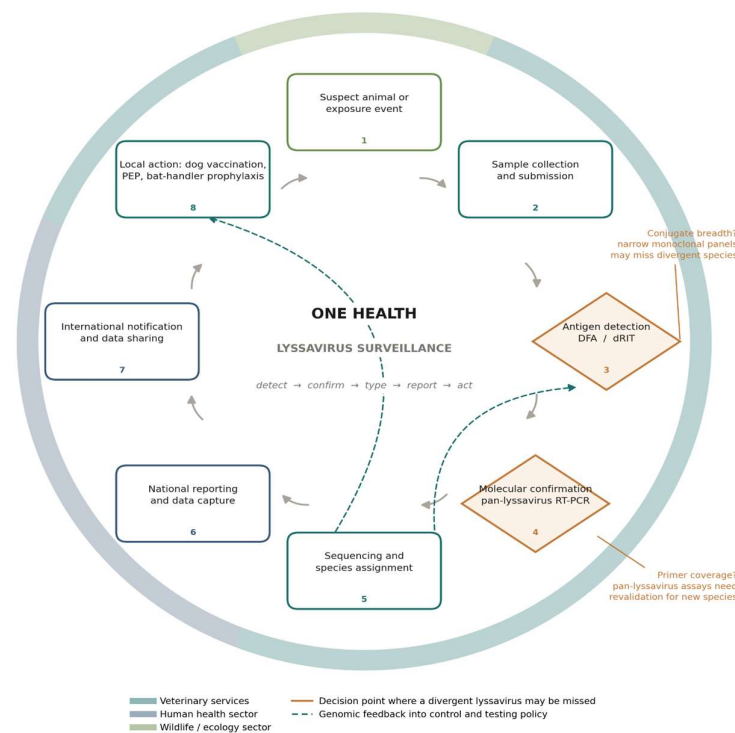


Fig. 3: One Health surveillance in practice. Circular workflow tracing a suspect case from field detection through sample submission, tiered laboratory testing, sequencing and international reporting, and back into local action. The outer ring assigns responsibility across the veterinary, human health and wildlife sectors. Amber diamonds mark the two points at which a divergent lyssavirus is most likely to be missed, and dashed arrows return genomic findings to vaccination planning and to the choice of diagnostic conjugate. *Original figure prepared by the authors; workflow and decision points informed by refs 4, 6, 27, 33, 35 and 36.*

Future Research Priorities

Four priorities would change the picture within a decade. Sustained genomic surveillance in bat populations across Africa, South and Southeast Asia and the Pacific, where sampling remains thinnest and the deepest branches sit. A pan-lyssavirus vaccine that reaches beyond phylogroup I into Mokola, Lagos bat and the ungrouped viruses, carried through the preclinical work that current chimeric candidates have only begun. Field-deployable molecular and sequencing platforms with validated coverage of the whole genus, revalidated as each new species is described. Finally, sample-sharing and reporting agreements that let a bat lyssavirus found in one country inform vaccination policy in another within weeks rather than years. None of this requires new science. It requires that the work be

funded and coordinated before the next case, not after it.

Conclusion

The man who died in New South Wales in July 2025 was bitten by an animal that looked unremarkable, in a country that considers itself rabies-free, and he received the correct treatment. That combination should unsettle us more than any exotic virus name. Our defences against rabies are excellent, narrow, and built on the assumption that the virus we meet will be the one we designed them for. Eighteen species say otherwise, and the queue is lengthening. The laboratory that identifies a virus, the veterinarian who submits the sample, the ecologist who knows the roost and the physician who asks about a bat are performing one task, not four. Rabies was never a single virus, and it will never be defeated by a single discipline.

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