taxonomy

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Communication

Resolving the *Orthoflavivirus encephalitidis* Paraphyly by Species Splitting

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Abstract

Our communication summarizes the recent changes in the paraphyletic species *Orthoflavivirus encephalitidis*. The paraphyly arises due to louping-ill virus (LIV), which is genetically closer to the European subtype of tick-borne encephalitis virus (TBEV). To maintain a concept of monophyly, we have split *Orthoflavivirus encephalitidis* into two monophyletic species: *Orthoflavivirus zilberi* (after Lev A. Zilber—the head of the expedition that identified and characterized TBEV in the Soviet Far East in 1937) and *Orthoflavivirus neudoerflense*, named after Neudörfl, a town in Austria where the reference strain Neudoerfl was first isolated. Also, to remove the resulting ambiguity in the virus name "tick-borne encephalitis virus", we have proposed new names—Asian TBEV (TBEV-AS) for *Orthoflavivirus zilberi*, and European TBEV (TBEV-EU) for *Orthoflavivirus neudoerflense*.

Keywords: tick-borne encephalitis virus; TBEV; phylogenetics; taxonomic proposal; delimitation; *Orthoflavivirus zilberi*; *Orthoflavivirus neudoerflense*; looping-ill virus; LIV

1. Introduction

Tick-borne encephalitis virus (TBEV) (*Flaviviridae*: *Orthoflavivirus*) was discovered in 1937, making it a virus with a nearly 90-year research history [1]. The virus genome comprises a positive-sense single-strand RNA (ssRNA+) with a length of about 11,000 nucleotides. The genome contains one open reading frame (ORF) coding three structural and seven non-structural proteins which is flanked by untranslated (non-coding) regions (UTRs). The ORF is co- and post-translationally cleaved by viral and host proteases [2].

TBEV is one of the twelve tick-borne flaviviruses (TBFVs), and along with four closely related human pathogenic TBFVs, forms the so-called "Tick-borne encephalitis serocomplex" [3]. The virus circulates between its principal vectors, hard ticks (Ixodidae: mainly of the genus *Ixodes*), and small mammals (reservoir hosts) [4]. TBEV is a causative agent of tick-borne encephalitis with approximately 5000–10,000 human cases registered annually [5].

Intraspecific genetic diversity of TBEV is represented by five subtypes whose names reflect the areas where the viruses are found (listed chronologically by the date of the first complete genome sequence):

- European (TBEV-EU)—Mandl et al. (1989) [6];
- Far-Eastern (TBEV-FE)—Pletnev et al. (1990) [7];
- Siberian (TBEV-Sib)—Gritsun et al. (1997) [8];
- Baikalian (TBEV-Bkl)—Demina et al. (2010) [9];

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- Himalayan (TBEV-Him)—Dai et al. (2018) [10].

Prior to the discovery of tick-borne encephalitis virus, louping-ill virus (LIV) was identified in 1931 [11]. LIV is the closest relative of TBEV, particularly of TBEV-EU (Figure 1), which has a similar genome composition in terms of length and the number of structural (3) and non-structural (7) proteins. Despite being RNA viruses, TBEV and LIV have relatively slow evolutionary rate with the same order of magnitude (10^{-5} nucleotide substitutions per site per year) [12,13]. The complete genome of LIV was sequenced and submitted to GenBank in 1997 [8]. Since then, phylogenies encompassing both TBEV and LIV clearly demonstrate their paraphyletic relationships (Figure 1) [13,14].

In April 2023, the taxonomic proposal to rename the genus *Flavivirus* to *Orthoflavivirus* was approved by the ICTV [15]. In addition, to adhere to a Latinized binomial format, the species names were also changed: *Tick-borne encephalitis virus* was renamed to *Orthoflavivirus encephalitidis*, and *Louping-ill virus* was modified to *Orthoflavivirus loupingi*. However, despite all changes, the phylogenetic relationships and, as a consequence, the paraphyly of TBEV and LIV, remained intact. Meanwhile, according to the ICTV Code, a species is "a monophyletic group of viruses whose properties can be distinguished from the properties of other species by multiple criteria" [16].

There were two main ways to resolve the paraphyly of TBEV and LIV and make them monophyletic: (1) to merge two viruses into a single species, or (2) to delimit the European subtype of TBEV as a separate species [17] (Figure 1).

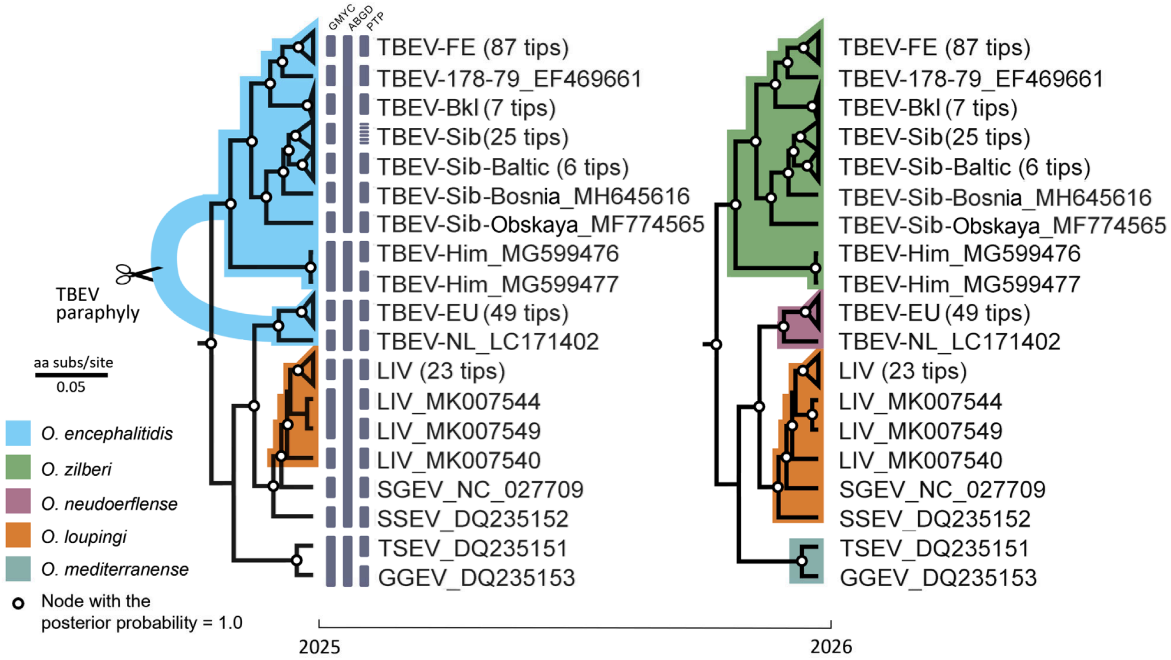

Figure 1. Schematic representation of tick-borne encephalitis virus (TBEV) taxonomy alteration that occurred in 2026. The phylogeny was reconstructed in BEAST v1.10.4 [18] using 211 amino acid (aa) sequences of a viral polyprotein with a length of 3414 aa. The nodes marked with white circles have a posterior probability of 1.0. The abbreviations used in tip names: TBEV-FE—Far-Eastern TBEV subtype; -178-79—178-79 lineage; -Bkl—Baikalian subtype; -Sib—Siberian subtype and its lineages: Baltic, Bosnia, Obskaya; -Him—Himalayan subtype; -EU—European subtype; -NL—the Netherlands strain; LIV—louping-ill virus; SGEV—Spanish goat encephalitis virus; SSEV—Spanish sheep encephalitis virus; TSEV—Turkish sheep encephalitis virus; GGEV—Greek goat encephalitis virus. The dark gray vertical bars in the left tree display delimited species entities according to delimitation analysis performed by three methods: Generalized Mixed Yule Coalescent (GMYC) method with 16 species, Automatic Barcode Gap Discovery (ABGD) with 5 species, and Poisson tree processes (PTP) model with 24 species.

The first approach implementing the merge of TBEV and LIV was proposed several times [19–21]. However, the supporting analyses either relied on a very limited number of sequences, or contradicted the species demarcation criteria for the genus *Orthoflavivirus* (https://ictv.global/report/chapter/flaviviridae/flaviviridae/orthoflavivirus (accessed on 15 August 2026)). The criteria include nucleotide and amino acid sequence data (i), antigenic characteristics (ii), geographic association (iii), vector association (iv), host association (v), disease association (vi) and ecological characteristics (vii).

In our taxonomic proposal, we followed the second approach of splitting TBEV-EU from the common TBEV clade and took into account all of the criteria listed above. In March 2026, the ICTV ratified our taxonomic proposal (https://ictv.global/ictv/proposals/2025.007S.Orthoflavivirus_2nsp_1spren.zip (accessed on 15 August 2026)) [22]. In the current communication, we aim to describe the reason for our proposal and outline its main taxonomic and virologic features.

2. Bioinformatic Analysis

In our species delimitation analysis, we scrutinized 211 complete amino acid sequences of a viral polyprotein to delineate species entities within the TBEV + LIV group. We applied three methods: Generalized Mixed Yule Coalescent (GMYC) method [23], Automatic Barcode Gap Discovery (ABGD) [24], and Poisson tree processes (PTP) model [25]. Briefly, GMYC detects the point on an ultrametric tree where branching shifts from a Yule (speciation) process to a coalescent (intraspecific) process. ABGD groups sequences by finding a significant gap between intra- and interspecific pairwise distances, without requiring a tree. PTP models speciation and coalescence as two Poisson processes on a tree and places species boundaries at the shift between them. Although the methods were not in concordance on the number of detected species (Figure 1), all of them rejected the null hypothesis that all TBEV subtypes and LIV form a single species. Furthermore, all three methods delineated TBEV-EU as a separate species entity (Figure 1).

The ABGD method was the most conservative and agreed almost completely with our taxonomic proposal for dividing the TBEV + LIV clade into four species (Figure 1). The only point of disagreement was that ABGD separated TBEV-Him as a distinct species. This may well be correct, but more data are needed to assess this against all the criteria established for the genus *Orthoflavivirus*.

3. Ecology, Antigenicity, and Disease Association

For genetically closely related species, the demarcation criteria of the genus *Orthoflavivirus*—such as host and vector associations, antigenic properties, and pathogenicity—can be particularly useful (Table 1).

For example, LIV is primarily found in red grouse and sheep, where it induces encephalitis with a high mortality rate (78% in red grouse [26], 5–60% in sheep [27]), whereas TBEV mainly persists asymptomatically in small rodents, which act as its primary reservoir. Although rodents such as field voles (*Microtus agrestis*), bank voles (*M. glareolus*) and wood mice (*Apodemus sylvaticus*) raised an antibody response to LIV infection, they could not produce substantial viremia and did not support non-viraemic transmission between co-feeding ticks [28].

The existence of Eastern and Western geographic and antigenic variants of TBEV has been recognized for four decades [29]. Initial characterization of the virus's antigenic properties identified two distinct subtypes—Eastern and Western [30]—which were also designated as 'Persulcatus' and 'Ricinus' variants based on their ecological characteristics [31].

Table 1. Comparative characteristics of tick-borne encephalitis virus and louping-ill virus.

Virus [1]	Delimitation Analysis with ABGD [2]	Primary Host (Mortality Rate)	Vector	Ecology	Primary CNS [3] Target	Disease Course (in Most Cases)	Severity in Children	CFR [4] in Humans
LIV	Distinct species	Red grouse (78%), sheep (5–60%)	*Ixodes ricinus*	Moorland	No data	Biphasic	No data	1 fatal case registered
TBEV-EU	Distinct species	Small rodents (asymptomatically)		Woodland	Glia		Less severe than in adults	1–2%
TBEV-FE and TBEV-Sib	Distinct species		*Ixodes persulcatus*		Neurons	Monophasic	More severe than in adults	20–60%

[1] Virus abbreviations: LIV—louping-ill virus; TBEV—tick-borne encephalitis virus; TBEV-EU—European subtype; TBEV-FE—Far-Eastern subtype; TBEV-Sib—Siberian subtype. [2] ABGD—Automatic Barcode Gap Discovery, a delimitation method for finding interspecies threshold using genetic and genomic data. [3] CNS—central nervous system. [4] CFR—case fatality rate.

Hubálek et al. (1995) [32] employed an indirect immunofluorescence assay (IIFT) with a panel of 17 monoclonal antibodies (MoAbs) to determine the reactivity patterns of flavivirus isolates. To compare these reactivity patterns, the authors used the unweighted pair group method with arithmetic mean (UPGMA), a hierarchical clustering method that groups objects by average linkage, which placed TBEV-EU, LIV, Turkish sheep encephalitis virus (TSEV), and Spanish sheep encephalitis virus (SSEV) in a single clade, with similarity values ranging from 84.0% (TBEV-EU vs. TSEV) to 96.6% (TBEV-EU vs. SSEV). In contrast, TBEV-FE (strain Sofjin) formed an outgroup with only 73% similarity, reflecting a distinct MoAbs reactivity profile. We reproduced their UPGMA dendrogram from the original data using R; the resulting tree (Figure S1), the data, and the R script is provided as the Supplementary Materials.

TBEV subtypes also have different clinical features. TBEV-EU has a clear biphasic course in about 74% of cases [33] (Gritsun et al. (2003) [34] reported a rate of 20–30%), whereas TBEV-FE and -Sib infections are mostly monophasic, with only a small fraction of cases demonstrating a biphasic pattern [35]. TBEV-FE's fatality rate reaches 20–60% [36] and the disease in children is more severe than in adults. Conversely, TBEV-EU infection demonstrates a low case fatality rate of 1–2% and children tend to develop less severe disease than adults [34]. For LIV, the only one fatal case was documented [37].

Votiakov et al. (2002) [38] documented prominent clinical observations in laboratory-acquired TBE cases that occurred in Belarus (n = 9), Slovakia (n = 11), and the Russian Far East (n = 10). All five lethal cases were registered in the Far East, whereas in Belarus and Slovakia, the disease mostly manifested in a meningeal form. These outcomes, however, may reflect not only the virus subtype but also age, vaccination status, preexisting illnesses, infectious dose, route of exposure, and the timing and quality of medical care. Experiments on monkeys and sheep showed that TBEV-EU did not initially replicate in neuronal cells or damage them, even after intracerebral infection occurred [39]. Instead, the primary target of TBEV-EU was lymphoid tissue, and the virus later appeared in the brains of animals that developed encephalitis, predominantly in the cerebellum, 6–9 days after inoculation. In contrast, TBEV-FE directly infected and damaged brain neurons, causing severe encephalitis. These findings strongly indicate that TBEV-FE is more neurotropic than TBEV-EU (see also Gritsun, et al. (2003) [34]).

Votiakov, et al. (2002) [38] inoculated sheep subcutaneously or intracerebrally with TBEV-EU and TBEV-FE. Subcutaneous inoculation with TBEV-EU caused meningitis alone, while intracerebral TBEV-EU produced a biphasic illness with 12.5% mortality, lower CNS viral titres than in blood, and moderate glial pathology (glial nodules 14.6% FOV)

with secondary neuronal damage. In contrast, intracerebral inoculation with TBEV-FE, by contrast, led to a monophasic, 100% fatal disease, with viral loads in the CNS exceeding those in blood and extensive primary degenerative changes (neuronophagia 37.5% FOV, glial nodules 56.1% FOV). These findings demonstrate that the two TBEV subtypes clearly differ in neurotropism, at least in the sheep model.

4. New Virus Names Proposed

The previous name "TBEV" is now paraphyletic as it refers to two distinct species. For now, this conflict is resolved by assigning temporary virus names: TBEV1 for *Orthoflavivirus zilberi*, and TBEV2 for *Orthoflavivirus neudoerflense*. In turn, we propose the following geographically derived names: Asian TBEV (TBEV-AS) for *Orthoflavivirus zilberi* and European TBEV (TBEV-EU) for *Orthoflavivirus neudoerflense* (Table 2). It should be noted that TBEV-EU is no longer considered a subtype but rather a distinct virus that represents the species *Orthoflavivirus neudoerflense*; the term now denotes this separate viral species, not a lineage.

Table 2. Taxonomic reassignment of TBEV and LIV.

Old Species Name	New Species Name	Virus Name	Subtype
Orthoflavivirus encephalitidis	*Orthoflavivirus neudoerflense*	European tick-borne encephalitis virus (TBEV-EU)	European (formerly a subtype of TBEV; now a distinct virus)
	Orthoflavivirus zilberi	Asian tick-borne encephalitis virus (TBEV-AS)	Far-Eastern (TBEV-FE) Siberian (TBEV-Sib) Baikalian (TBEV-Bkl) Himalayan (TBEV-Him)
Orthoflavivirus loupingi	*Orthoflavivirus loupingi*	Louping-ill virus (LIV)	LIV genotypes 1–4 Spanish sheep encephalitis virus (SSEV) Spanish goat encephalitis virus (SGEV)
Unclassified	*Orthoflavivirus mediterranense*	Mediterranea virus (MEDV)	Turkish sheep encephalitis virus (TSEV) Greek goat encephalitis virus (GGEV)

5. Conclusions

We have outlined the major points of our taxonomic proposal on splitting the paraphyletic species *Orthoflavivirus encephalitidis* into two monophyletic species. Further details are available in the proposal (2025.007S.Orthoflavivirus_2nsp_1spren) on the ICTV website (https://ictv.global/ictv/proposals/2025.007S.Orthoflavivirus_2nsp_1spren.zip (accessed on 15 August 2026)).

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/taxonomy6030052/s1, Figure S1: UPGMA tree reconstructed using the similarity matrix (pairwise dice coefficients) derived from comparison of monoclonal antibody reactivity patterns of flaviviruses.

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