AIMS Animal Science, 1 (1): 181–195.
DOI: 10.3934/aas.2025009
Received: 17 September 2025
Revised: 19 November 2025
Accepted: 28 November 2025
Published: 25 December 2025

https://www.aimspress.com/journal/aas

Perspective

Amdoparvoviruses. Part 1. Phylogenetic analysis of complete VP2 protein sequences provided support for a global taxonomic analysis of the Aleutian mink disease virus

Irina Zyrianova*

Department of Biotechnology, FSBSI V.A. Afanasyev RI for Fur and Rabbit Farming, Moscow region, Ramenki district, Rodniki, 140143 Russian Federation

* **Correspondence:** Email: mirsimzyrianova@mail.ru.

Abstract: Aleutian mink disease virus (AMDV) is a highly contagious parvovirus that is a causative agent of Aleutian mink disease (AMD). AMD is a commercially important infectious disease because it causes great economic losses to mink farmers worldwide. AMDVs represent themselves as a highly variable group of the *Parvoviridae* family. The AMDV group is quickly filled out with various representatives. Only about 10 years have passed since this group included only two species. Today, there are 11 species in this group. AMDV is the typical representative of this group, and all AMDV-like parvoviruses are now integrated into the *Amdoparvovirus* genus. In this study, a global phylogenetic analysis of the full VP2 protein sequences of the *Amdoparvovirus* genus was performed. This analysis more fully assessed the phylogenetic relationships of amdoparvoviruses. It showed that about one-third of *Amdoparvovirus* strains and isolates classified to date, as *Amdoparvovirus carnivoran1* could probably be considered not as *Amdoparvovirus carnivoran1* species but as new independent species in perspective or joined already introduced species, different from *Amdoparvovirus carnivoran1*. It had also been shown that the primary host of the representatives should be an important feature for the classification of *Amdoparvovirus* species. Moreover, the analysis showed that bats play a significant role in transmission from protoparvoviruses to amdoparvoviruses.

Keywords: Aleutian mink disease virus*; Amdoparvovirus*; *Parvovirinae*; *Parvoviridae*; VP2 protein sequence phylogeny

1. Introduction

Aleutian mink disease virus (AMDV) remains one of the most problematic viruses for mink farming because it is the causative agent of Aleutian mink disease (AMD) affecting minks. AMD manifests as enlarged kidneys, spleen, and lymph nodes, commonly known as deadly plasmocytosis and hyperglobulinemia in mink, which could also lead to spontaneous abortions. On the molecular level, the reason for such manifestations is immunocomplexes, which are formed as a result of AMDV pathogenesis [1–3].

AMD is a very contagious disease with more than 90% seroprevalence [1,4], with virus DNA detection up to 100% [4]. There are no effective ways to combat the disease. There are no effective vaccines [2]. Eradication of mink herds may not lead to satisfactory results [1,2]. Therefore, AMD continues to cause great economic losses to mink farmers worldwide for over 70 years [1,2].

AMDV is a member of the *Parvoviridae* family, and it was the sole member of its genus until 2013. The genus was named *Parvovirus*, and it was renamed *Amdovirus* in 2004. In 2013, according to the ICTV proposal, the *Amdovirus* genus was renamed *Amdoparvovirus.* AMDV was renamed *Carnivore amdoparvovirus 1. Aleutian mink disease virus-G* (GenBank accession number M20036) was the first representative. The second member of this genus was *Carnivore amdoparvovirus 2: Gray fox amdovirus* (GenBank accession number JN202450) [5]. Subsequently, many other species were introduced into the *Amdoparvovirus* genus [6]. However, according to the International Committee on Taxonomy of Viruses (ICTV), a mega-taxonomic rank was determined only in 2019. For today, *Amdoparvovirus* genus belongs to *Parvovirinae* subfamily, *Parvoviridae* family, *Piccovirales* order, *Quintoviricetes* class, *Cossaviricota* phylum, *Shotokuvirae* kingdom, and *Monodnaviria* realm [6,7]. Only about 10 years have passed since this genus included only the two species mentioned above. Today, there are 11 species in this genus [6]. Due to the accumulated data about the high variability of the AMDVs [3,4,8–11] and about AMDV prevalence among different species of *Mustelidae* family [3,4,8,9] and other animals [3,4,9,12], it seems like this is a sequential event.

Like other members of *Parvoviridae* family, the virus is non-enveloped, small, and has a single-stranded DNA [13]. The reference genome of the AMDV has 4,801 bp (AMDV-G, GenBank accession number M20036). However, shorter specimens are also represented in GenBank. For example, mink-f strains with a genome size of 4,369 bp (GenBank accession numbers KU856560.1− KU856568.1) and more [14].

The AMDV genome contains two large open reading frames (ORFs), left and right (L-ORF and R-ORF), two middle ORFs (M-ORF1 and M-ORF2), and one small ORF (S-ORF) (Figure 1) [15]. R-ORF is found to be involved in coding of VP1 and VP2 capsid proteins, and this ORF is found on the 3d reading frame (RF3). VP2 is fully encoded by R-ORF, but VP1 is not. Ten amino acids from the N-end of VP1 are not found in R-ORF (on RF3). These amino acids are found on the 2nd reading frame (RF2). However, the authors do not notice the independent ORF for these amino acids (Figure 1) [15].

The rest of the ORFs encode three non-structural proteins (NS1, NS2, and NS3). L-ORF (on RF2) encodes most of the N-parts of all three NS proteins. C-ends of NS proteins are coded by the different ORFs. S-ORF and M-ORF1 are located on RF1 and code C-ends of NS3 and NS1 proteins, respectively. M-ORF2 is located on RF3 and codes the C-end of NS2 protein [15].

Ends of a negative, single-stranded DNA of the AMDV form hairpins (Figure 1) [15,16]. The 3'-hairpin could prime to synthesize the complementary positive strand, as it happens in other *Parvoviridae* viruses [13]. Continuous duplex intermediates are formed during 'rolling hairpin'

replication, from which NS1, with its endonuclease activity, excises single strands [13].

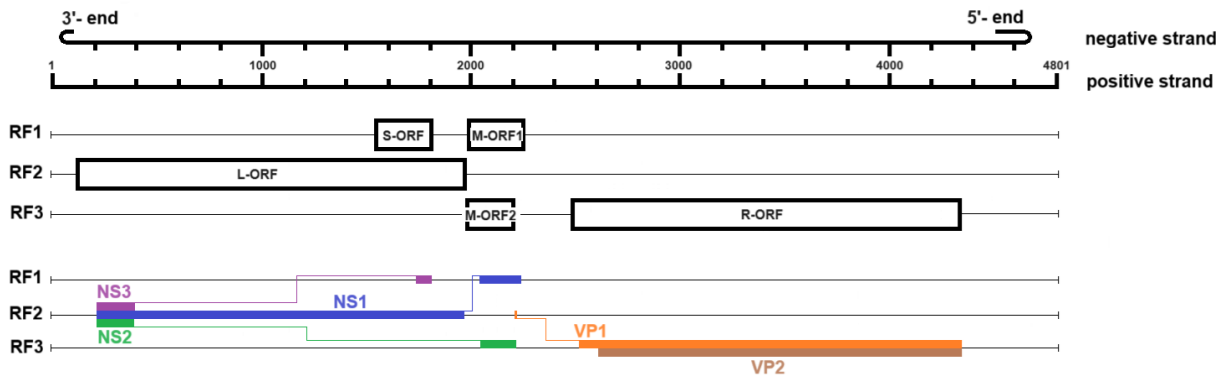

Figure 1. The AMDV schematic map according to Hagberg et al., 2016 [15].

The AMDV capsid has an icosahedral form, which is assembled via two-, three- and five-fold symmetry [17,18]. It has a maximum diameter of ~300 Å [17]. VP2 is the major protein of the AMDV's capsid with immunogenic properties [19]. B-cell epitopes were found in the VP2 protein of AMDV [20,21].

VP2 is smaller than VP1 at the N-end. This part of VP1 (VP1u) can be up to more than 300 amino acids in *Parvovirinae* viruses, but not in AMDV [17]. The long VP1u part is important for viral functionality and contains a phospholipase A_2 (PLA_2) domain, which is mostly presented in *Parvovirinae* viruses but not in the AMDV [22]. VP1u of AMDV has only 43 amino acids and does not have PLA_2. Instead of this, VP2 of AMDV is the largest among orthologs of other *Parvovirinae* viruses. There are some insertions and deletions in VP2 of AMDV found in comparison with orthologs, the composition of which results in a greater length. Most insertions are localized on the surface of the capsid. This fact led the authors to speculate that the missing functions of VP1u are performed by the full VP2 due to these additional insertions compared to orthologs of other *Parvovirinae* viruses [17]. In addition, the N-end of AMDV's VP2 has the longest glycine-rich region among orthologs of other Parvovirinae viruses [22].

One more feature of VP2 of AMDVs has become widely known among researchers. This is a hypervariable region between amino acids 232–242, according to VP2 of the AMDV-G strain (GenBank accession number M20036) [18,23–26]. This region is considered suitable for the phylogenetic analysis of AMDV strains [23,26,27].

The purpose of this study was to conduct the phylogenetic analysis of full VP2 proteins of AMDVs available to date and to suggest a new view on the classification grouping of them. The next article in the *Amdoparvovirus* series (Amdoparvovirus. Part 2.) proposes to describe the structural features of VP2 protein orthologs in accordance with this phylogenetic analysis.

2. Materials and methods

A total of 425 full-length VP2 protein sequences of *Parvovirinae* viruses were used in this study. From them, 345 sequences were for the *Amdoparvovirus* genus, which were available from GenBank and from the literature on June 3, 2024. Some VP2 sequences from articles were not found in

GenBank [18,28–31]. Many sequences of AMDVs were not included in the analysis due to the uncertainty of one or more amino acids, except for one sequence for *Amdoparvovirus carnivoran8* identified so far [32]. *Amdoparvovirus carnivoran8* (GenBank accession number ON375541.1) has three unidentified positions (232, 235, and 344), according to the AMDV-G strain (GenBank accession number M20036). It was proposed eight variants of VP2 for this sequence using combinatorics.

The phylogenetic analysis was performed with the help of the MEGA X (Version 10.0.5) program [33] using the Maximum Likelihood method and the JTT matrix-based model [34]. The bootstrap analysis with 1,000 replicates was used to assess a confidence level of tree branches as an option of the MEGA X program. The option for uniform rates among sites was used. The analysis was performed twice.

Ethics approval of this research is not required because all data were taken from the GenBank database and literature.

3. Results and discussion

Parvovirinae subfamily has 11 genera [6]. The phylogenetic analysis in this study was limited to *Amdoparvovirus, Protoparvovirus*, *Tetraparvovirus*, *Erythroparvovirus*, *Aveparvovirus*, *Bocaparvovirus,* and *Dependoparvovirus* genera, as the remaining genera had not yet had full VP2 protein sequences determined by the time of data collection from GenBank. Dependoparvoviruses had been defined as having three structural proteins in the capsid (VP1, VP2, and VP3) with the VP3 protein as the major of them [35]. Therefore, it was considered to include VP3 in the analysis instead of VP2. Moreover, the alignment showed that the VP3 had more homology with other parvovirus VP2 protein sequences (data not shown). There were only up to two VP2 (or VP3) sequences used for each species for genera noted, except for the *Amdoparvovirus* genus. For the last one, as many full-length sequences of the VP2 protein were used as were found in GenBank and in the literature to date noted.

Tracing the phylogenetic relationships between representatives of the genus *Amdoparvovirus* and the *Parvovirinae* genera in general, based on phylogenetic analysis of complete VP2 protein sequences, it was revealed that the genus *Protoparvovirus* is considered ancestral genus of *Amdoparvovirus*. The same results were found earlier for the partial NS1 phylogeny [32]. However, there was some difference in the topology of the tree (Figure 2, Supplementary Figure 1). The difference appears to be explainable because different sequences were analyzed. This is the first explanation. The second explanation is that it was used a different program (RAxML), not MEGA X [32]. The third explanation is that the uniform rate among sites was used for the analysis in this study instead of gamma distribution, which was used in the mentioned results [32]. The uniform rate among sites was used in this study because of the following thoughts. The analysis of the phylogenetic history of parvoviruses had been conducted since the 1960s [36]. This is only for 70 years. This is close to the present time in terms of millions of years. The mathematical plot of the time-dependent pattern of molecular rates among sites (substitutions per site per million years) and deviation from real node age shows that it makes almost no difference whether the gamma distribution is used or not in times close to the present [37]. Therefore, uniform rates (or linear dependence) among sites are suitable for analysis within the time that can be estimated as ‘the recent time’, as a definition in the context of the evolutionary time.

Thus, the results of this study showed that the amino acid sequences of VP2 could be applied to the detailed classification of the genus *Amdoparvovirus*, as well as the entire subfamily *Parvovirinae.* However, some authors believe that the amino acid sequences of VP2 cannot be applied to the classification [38].

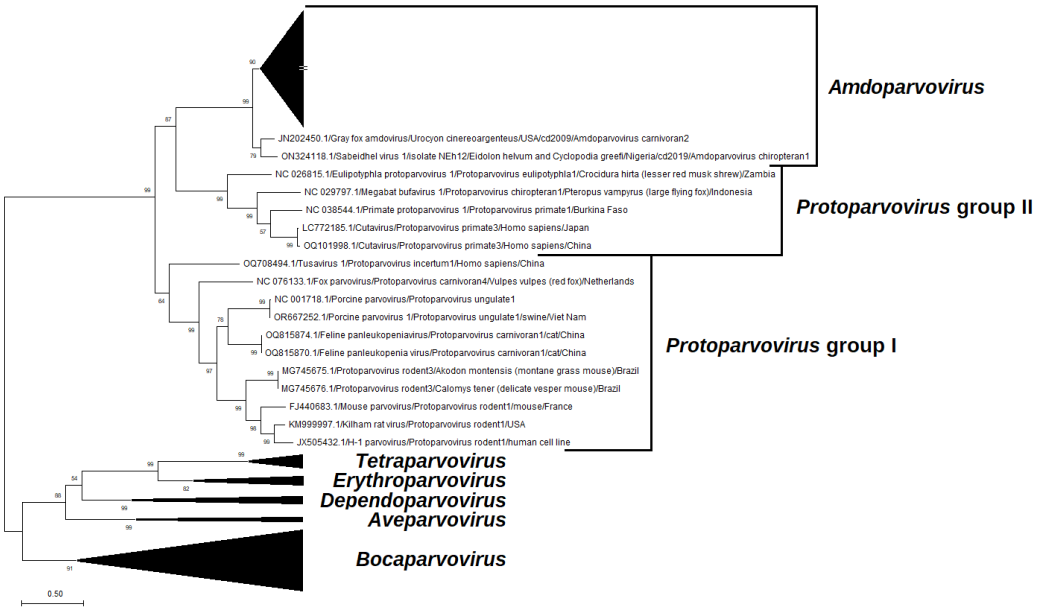

Figure 2. The simplified evolutionary tree of VP2 protein sequences of *Parvovirinae* representatives with the highest log likelihood (-67518.55). Numbers are the percentage of trees in which the associated taxa are clustered together (shown next to the branches).

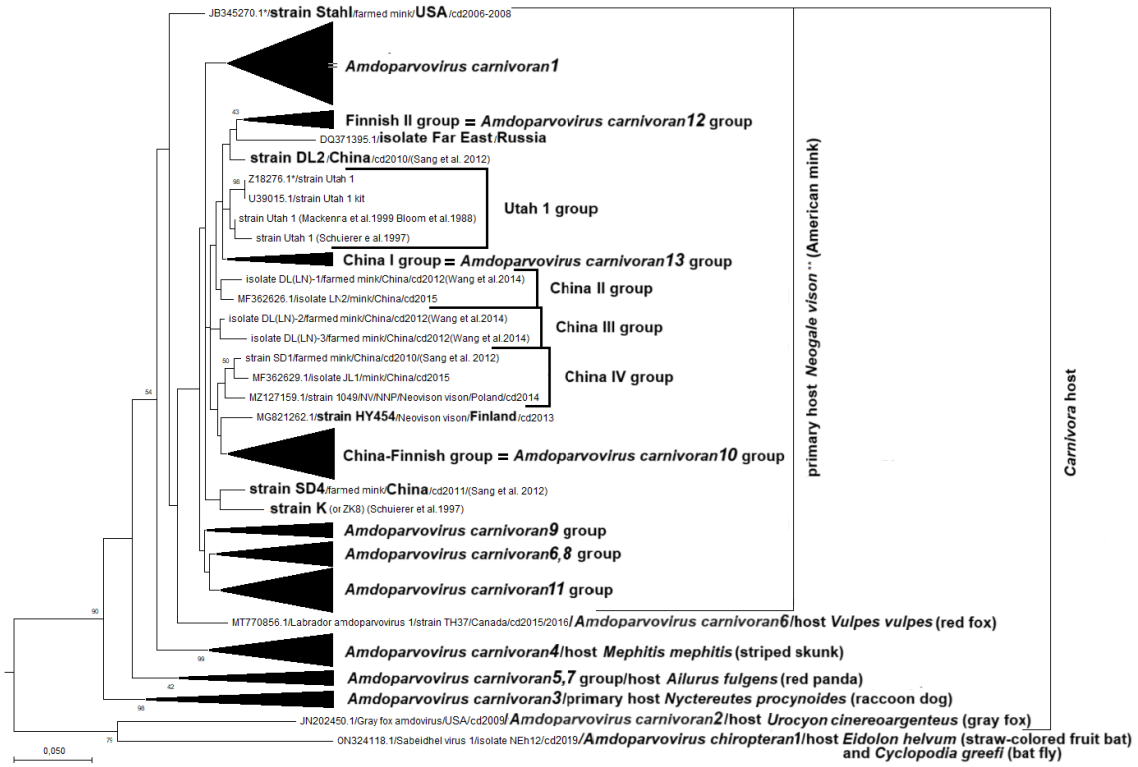

Figure 3. The simplified *Amdoparvovirus* subtree. Numbers are as in Figure 2; cd—the collection date; *—VP2 sequences predicted in this work from genome virus DNA sequences available from GenBank; **—*Neogale vison* has synonyms such as *Neovison vison* and *Mustela vison*.

Amdoparvovirus genus was analyzed in this study as fully as was found in the GenBank and in the literature: a total of 345 VP2 sequences, some of which were deduced from genome nucleotide sequences. It is mentioned above that ten years ago the *Amdoparvovirus* genus had only two species. Today, there are already 11 species in this genus [6], which are fully represented in this study (Figure 3). The full history of the introduction and renaming of all species can be seen on the website of the ICTV [6].

The analysis of this study showed that about two-thirds of strains and isolates known so far as *Amdoparvovirus carnivoran1* could actually be considered as *Amdoparvovirus carnivoran1*. This group of *Amdoparvovirus carnivoran1* representatives is clustered into a large phylogenetic branch with minor substitutions per site (Figure 3, 4). Some groups can be highlighted among them: Danish I-III, Finnish I, Canadian I-III, Russian, G, and LN1-TR groups, which can probably be considered as subspecies of *Amdoparvovirus carnivoran1.* Individually branched HB-5/China and Utah/USA isolates may also be the basis for new subspecies of *Amdoparvovirus carnivoran1* in the future (Figure 4).

About one-third of the remaining *Amdoparvovirus* strains and isolates classified to date as *Amdoparvovirus carnivoran1* can probably be considered as not *Amdoparvovirus carnivoran1* species. To further emphasize that their classification needs to be revised, these strains and isolates are not labeled as *Amdoparvovirus carnivoran1* in Figures 3 and further. It will be described below which of these representatives are allocated to independent groups with the perspective of isolating them into independent species and which have joined already existing species, different from *Amdoparvovirus carnivoran1*.

Onwards, on Figure 5(A), it can be seen that only MAPT17 and BCWM-1 strains, also known as *Labrador amdoparvovirus 1* and *British Columbia amdoparvovirus*, respectively, are currently classified as *Amdoparvovirus carnivoran6* and *Amdoparvovirus carnivoran8* species, respectively. The other six representatives are classified as the *Amdoparvovirus carnivoran1* according to ICTV. However, phylogenetic analysis showed that these six strains and isolates were clustered together with *Amdoparvovirus carnivoran6* and *Amdoparvovirus carnivoran8* in one clade (Figure 3, 5(A)). (See "Materials and Methods" about variants of *Amdoparvovirus carnivoran8*.) Therefore, all these strains and isolates, together with MAPT17 and BCWM-1, classified as *Amdoparvovirus carnivoran6* and the *Amdoparvovirus carnivoran8*, respectively, are designated in this study as one *Amdoparvovirus carnivoran6*,*8* group (Figure 3, 5(A)). Another point of the debate in this regard is the TH37/Canada strain, or *Labrador amdoparvovirus 1*, classified as *Amdoparvovirus carnivoran6* too, according to ICTV, together with the mentioned MART17/Canada strain. However, in this study, these strains branched off separately from each other (Figure 3, 5(A)). Moreover, these two strains (TH37 and MART17) have different hosts: red fox (*Vulpes vulpes*, *Canidae*) and American marten (*Martes americana*, *Mustelidae*), respectively (Figure 3, 5(A)). Therefore, although these two strains (TH37/Canada and MART17/Canada) are both classified so far as *Amdoparvovirus carnivoran6*, they should be classified as different species. One of them (the mentioned MART17/Canada strain) united in this study in one *Amdoparvovirus carnivoran6*,*8* group. Another one (the TH37/Canada strain) can probably stay as *Amdoparvovirus carnivoran6.*

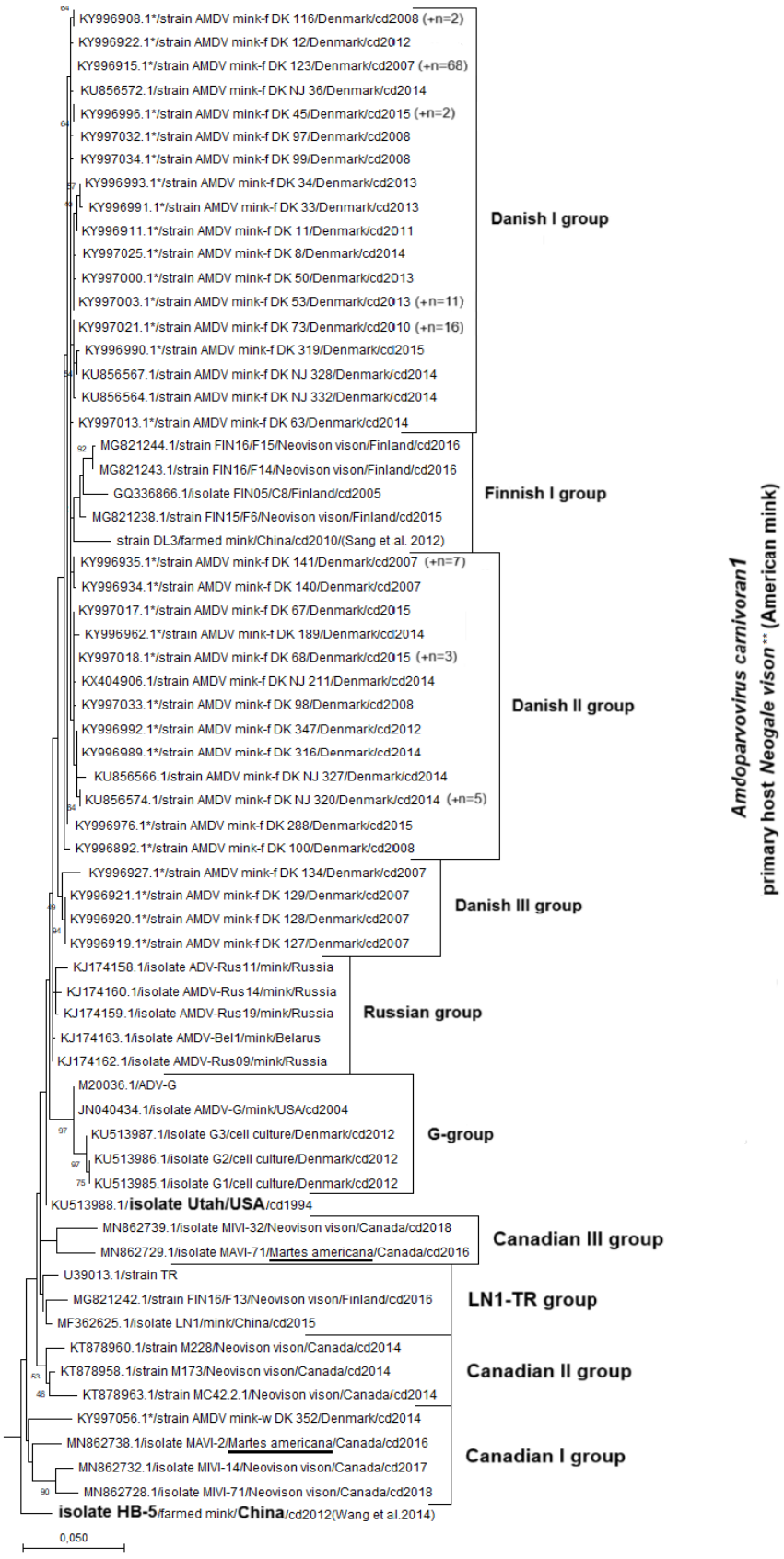

Figure 4. The *Amdoparvovirus carnivoran1* subtree. Numbers, cd, * and ** as in Figures 2,3. Underlines indicate non-primary hosts.

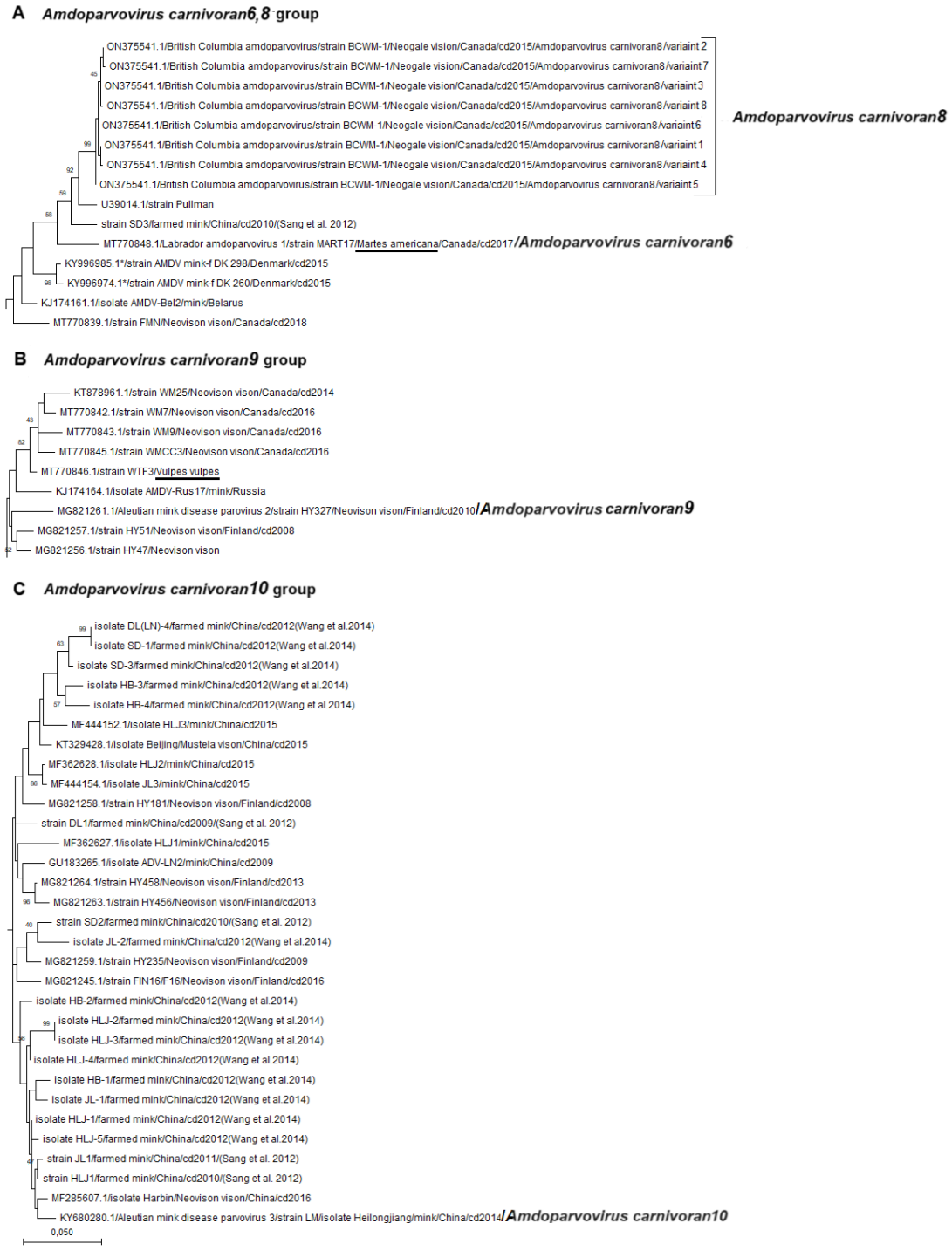

Figure 5. Subtrees of *Amdoparvovirus carnivoran6*,*8* (A), *Amdoparvovirus carnivoran9* (B), and *Amdoparvovirus carnivoran10* (C) groups. Numbers, cd, *, ** and underlines as in Figures 2–4.

Further about *Amdoparvovirus carnivoran9* and *Amdoparvovirus carnivoran10* groups. There are *Aleutian mink disease parvovirus 2* and *Aleutian mink disease parvovirus 3* species (or HY327 and LM strains, respectively) within them, which are renamed according to ICTV *Amdoparvovirus*

carnivoran9 and *Amdoparvovirus carnivoran10*, respectively. However, the other eight and thirty strains, respectively, that branched off with them are still classified by ICTV as *Amdoparvovirus carnivoran1* (Figure 3, 5(B, C)). Therefore, their classification should also be revised, and these representatives should be considered as *Amdoparvovirus carnivoran9* and *Amdoparvovirus carnivoran10*, respectively.

The next groups of strains, Dutch-Polish (14 strains) and Danish IV (13 strains) groups, which are also classified as the *Amdoparvovirus carnivoran1* to date, emerged as the big paraphyletic group manifesting separately from the actually considered *Amdoparvovirus carnivoran1* representatives in this study (Figure 3, 6(A)). This group certainly cannot be classified as *Amdoparvovirus carnivoran1*. It is proposed herein to unite them as the *Amdoparvovirus carnivoran11* group.

The same situation exists with the Finnish II (11 strains) group, which is named herein as the *Amdoparvovirus carnivoran12* group (Figure 3, 6(B)). The other smaller clade of the China I (8 isolates) group is named as the *Amdoparvovirus carnivoran13* group (Figure 3, 6(C)). In addition, Utah I (4 strains), China II (2 isolates), China III (2 strains), and China IV (2 strains and 1 isolate) groups branch out separately. All these groups can probably also be considered new species of the *Amdoparvovirus* genus, as well as single representatives of their branches: K (or ZK8), SD4/China, HY454/Finland, DL2/China, Far East/Russia, and Stahl/USA (Figure 3).

The remarkable discovery was made about the Stahl/USA strain classified as *Amdoparvovirus carnivoran1* to date. This strain manifests itself as the ancestor for all species and groups of amdoparvoviruses, which have American mink (*Neogale vison*, *Mustelidae* family) as the primary host (Figure 3). The Stahl/USA strain also appears to be the ancestral strain for the TH37/Canada strain (known also as *Labrador amdoparvovirus1* and *Amdoparvovirus carnivoran6*), which already has the red fox (*Vulpes vulpes*, *Canidae* family) as the host and branches off in the second branch after the Stahl/USA strain. Further, the Stahl/USA strain itself has *Amdoparvovirus carnivoran4* as the ancestral species, which has the striped skunk (*Mephitis mephitis*, *Mephitidae* family) as the host (Figure 3, 7(A)). Such position of the Stahl/USA strain in the tree leads to some conclusions. It looks like this strain is the turning point in the evolution of the *Amdoparvovirus* genus and in the transmission of amdoparvoviruses from one of the *Mustelidae* hosts (striped skunk) to another (American mink). TH37/Canada strain with the canid host (red fox) branches off among branches that have mustelid hosts (striped skunk and mink). It says that the inclusion of switching to the host of different families here in the tree indicates easy adaptation of the virus to the hosts during close contacts between host species in natural habitats. Host switching inclusions also appear at other points of the tree (Figure 4, 5(A, B), 7(B)).

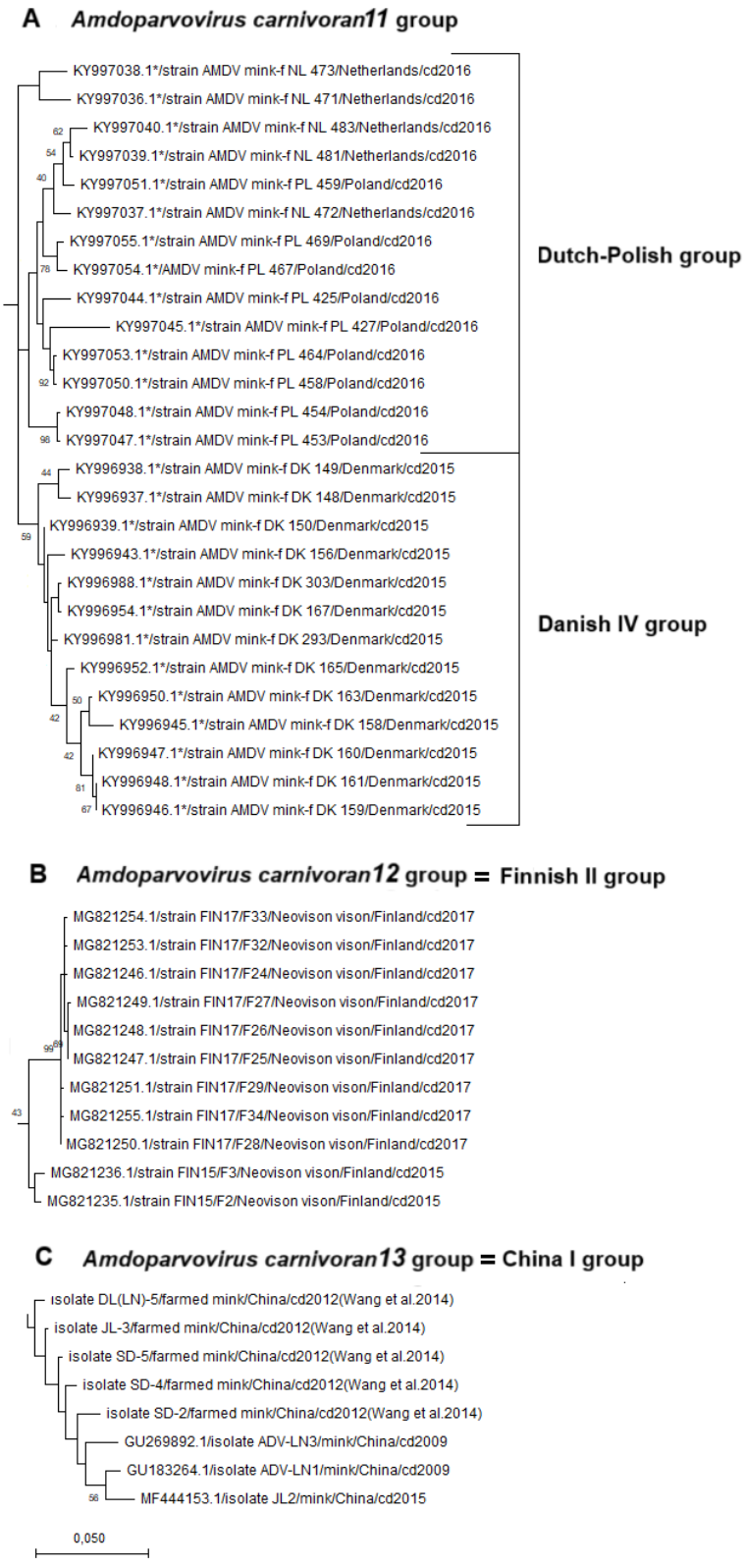

Figure 6. Subtrees of *Amdoparvovirus carnivoran11* (A), *Amdoparvovirus carnivoran12* (B), and *Amdoparvovirus carnivoran13* (C) groups. Numbers, cd, * and ** as in Figures 2, 3.

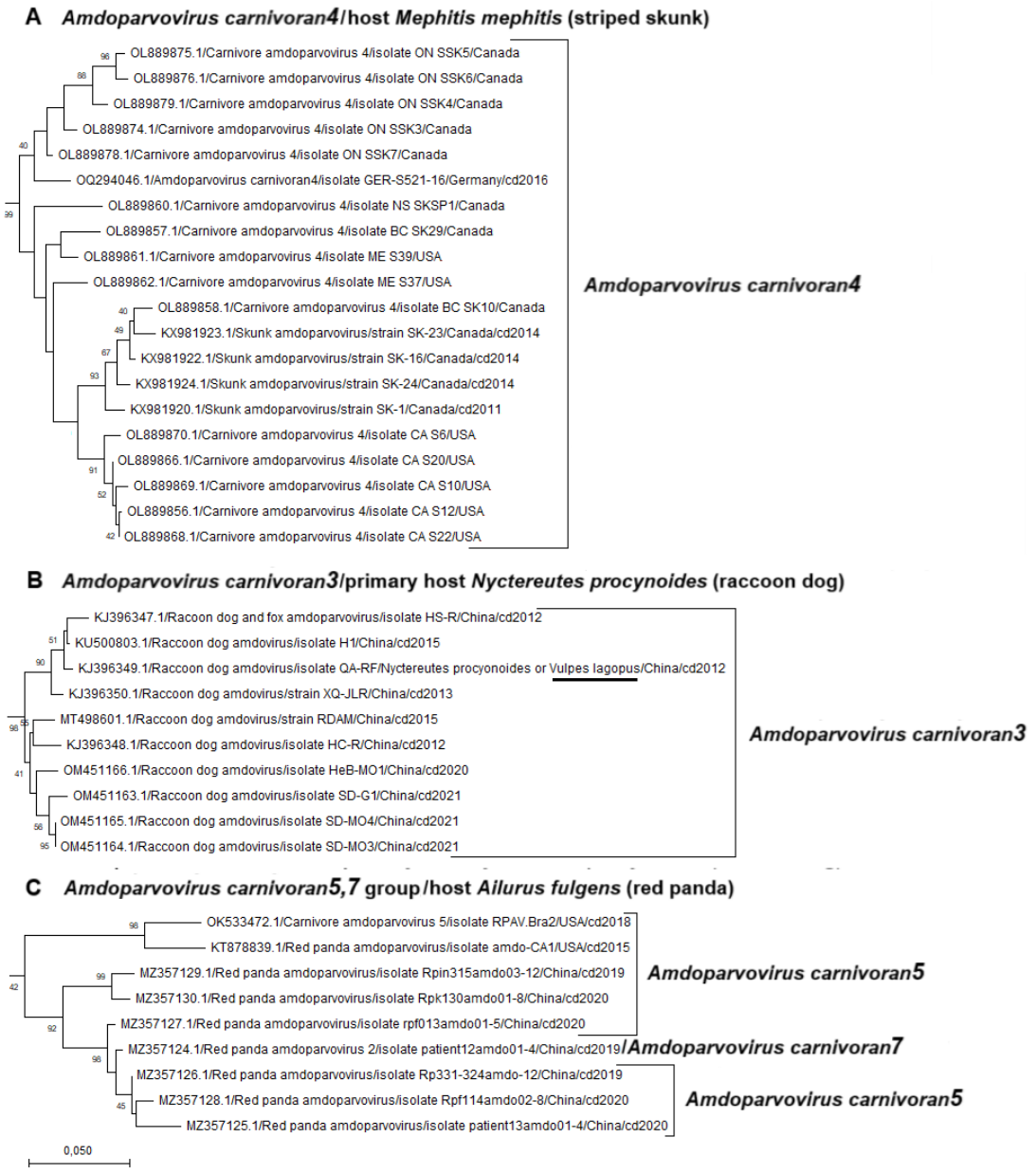

Figure 7. Subtrees of *Amdoparvovirus carnivoran4* (A), *Amdoparvovirus carnivoran3* (B), and *Amdoparvovirus carnivoran5,7* (C). Numbers, cd, *, ** and underlines as in Figures 2–4.

Further along the tree. It can be seen that *Amdoparvovirus carnivoran5* and *Amdoparvovirus carnivoran7* are clustered together (Figure 3, 7(C)), and they have one host: red panda (*Ailurus fulgens, Ailuridae*). Therefore, these two species should probably be considered as one species. They are united as the *Amdoparvovirus carnivoran5,7* group in this work.

Representatives of *Amdoparvovirus carnivoran4, Amdoparvovirus carnivoran3*, and *Amdoparvovirus carnivoran2* branch off without unexpectedly appearing in different branches of the tree (Figure 3, 7(A, B)). Their branch structure of the tree supports the new species predictions made in this study.

The remarkable discovery of *Amdoparvovirus chiropteran1* and introducing this species into the *Amdoparvovirus* genus that has the bat host (the straw-colored fruit bat, *Eidolon helvum, Pteropodidae* family) [39] is the evidence that bats play not the least role in the evolution of amdoparvoviruses. The analysis in this study reveals that all hosts of the *Amdoparvovirus* genus are carnivoran mammals, except for *Amdoparvovirus chiropteran1*, which has the chiropteran mammal as the host (the straw-colored fruit bat). This species is the first branch in the evolutionary tree after protoparvovirus species (Figure 2, 3, Supplementary Figure 1). So that, the *Amdoparvovirus chiropteran1* can be considered as one of the main ancestral species for all amdoparvoviruses. It is known that several important viruses, including protoparvoviruses, cause disease outbreaks associated with bats [40–42]. Because of this, the discovery of *Amdoparvovirus chiropteran1* can be considered a sequential event for amdoparvoviruses, and bats can be considered as playing a significant role in transmission of the virus from protoparvoviruses to amdoparvoviruses.

Furthermore, all phylogenetic groups proposed in this study as separate *Amdoparvovirus* species have only one primary host. Three species (*Amdoparvovirus carnivoran4, Amdoparvovirus carnivoran3*, and *Amdoparvovirus carnivoran2*), which have no addition suggestions about their classification in this study, have one host each too. Therefore, the primary host for *Amdoparvovirus* species should be considered as the important feature for their classification.

4. Conclusions

First, the global phylogenetic analysis of the full VP2 protein sequences of the *Amdoparvovirus* genus in this study more fully assessed the phylogenetic relationships of amdoparvoviruses. The analysis showed that about two-thirds of strains and isolates known so far as *Amdoparvovirus carnivoran1* could actually be considered as *Amdoparvovirus carnivoran1*. Some groups among them should be highlighted, which could probably be considered subspecies of *Amdoparvovirus carnivoran1.* Second, the analysis showed that about one-third of *Amdoparvovirus* strains and isolates currently classified as *Amdoparvovirus carnivoran1* should probably not be considered *Amdoparvovirus carnivoran1*, but rather new, distinct species or joined already existing species, different from *Amdoparvovirus carnivoran1.* Third, the primary host is the important feature during the classification of *Amdoparvovirus* species. Fourth, bats play the significant role in the transmission to the *Amdoparvoviruses* genus.

Use of AI tools declaration

The author declares she has not used Artificial Intelligence (AI) tools in the creation of this article.

Acknowledgments

This work was supported by the Ministry of Science and Higher Education of the Russian Federation, assignment number FGGR-2024-0002.

Conflict of interest

The author declares that there are no conflicts of interest.

References

1. Vahedi SM, SalekArdestani S, Banabazi MH, et al. (2023) Epidemiology, pathogenesis, and diagnosis of Aleutian disease caused by Aleutian mink disease virus: A literature review with a perspective of genomic breeding for disease control in American mink (Neogale vison). *Virus Res* 336: 99208. https://doi.org/10.1016/j.virusres.2023.199208
2. Markarian NM, Abahamyan L (2021) AMDV Vaccine: Challenges and perspectives. *Viruses* 13: 833. https://doi.org/10.3390/v13091833
3. Canuti M, Whitney HG, Lang AS. (2015) Amdoparvoviruses in small mammals: Expanding our understanding of parvovirus diversity, distribution, and pathology. *Front Microbiol* 6: 119. https://doi.org/10.3389/fmicb.2015.01119
4. Zaleska-Wawro M, Szczerba-Turek A, Szweda W, et al. (2021) Seroprevalence and molecular epidemiology of Aleutian Disease in various countries during 1972–2021: A review and Meta-analysis. *Animals* 11: 975. https://doi.org/10.3390/ani11102975
5. Cotmore SF, Agbandje-McKenna M, Chiorini JA, et al. (2013) Rationalization and extension of the taxonomy of the family Parvoviridae. Report number: ICTV [International Committee for Taxonomy of Viruses] Proposal (Taxoprop) No.2013.001a-aaaV.A.v4.Parvoviridae.
6. Current ICTV Virus Taxonomy Release. Available from: https://ictv.global/taxonomy
7. Koonin EV, Dolja VV, Krupovic M, et al. (2019) Create a megataxonomic framework, filling all principal taxonomic ranks, for ssDNA viruses. Report number: ICTV [International Committee for Taxonomy of Viruses] Proposal (Taxoprop) No. 2019.005G. https://doi.org/10.13140/RG.2.2.36696.85760
8. Virtanen J, Zalewski A, Kołodziej-Sobocińska M, et al. (2021) Diversity and transmission of Aleutian mink disease virus in feral and farmed American mink and native mustelids. *Virus Evol* 7: eab075. https://doi.org/10.1093/ve/veab075
9. Canuti M, McDonald E, Graham SM, et al. (2020) Multi-host dispersal of known and novel carnivore amdoparvoviruses. *Virus Evol* 6: eaa072. https://doi.org/10.1093/ve/veaa072
10. Kowalczyk M, Horecka B, Jakubczak A (2019) Aleutian Mink Disease Virus in the breeding environment in Poland and its place in the global epidemiology of AMDV. *Virus Res* 270: 97665. https://doi.org/10.1016/j.virusres.2019.197665
11. Virtanen J, Smura T, Aaltonen K, et al. (2019) Co-circulation of highly diverse Aleutian mink disease virus strains in Finland. *J Gen Virol* 100: 27–236. https://doi.org/10.1099/jgv.0.001187
12. Canuti M, Doyle HE, Britton AP, et al. (2017) Full genetic characterization and epidemiology of a novel amdoparvovirus in striped skunk (Mephitis mephitis). *Emerg Microbes Infect* 6: 30. https://doi.org/10.1038/emi.2017.13
13. Cotmore SF, Agbandje-McKenna M, Canuti M, et al. (2019) ICTV Virus Taxonomy Profile: Parvoviridae. *J Gen Virol* 100: 67–368. https://doi.org/10.1099/jgv.0.001212
14. Hagberg EE, Pedersen AG, Larsen LE, et al. (2017) Evolutionary analysis of whole-genome sequences confirms inter-farm transmission of Aleutian mink disease virus. *J Gen Virol* 98: 360–1371. https://doi.org/10.1099/jgv.0.000777
15. Hagberg EE, Krarup A, Fahnøe U, et al. (2016) A fast and robust method for whole genome sequencing of the Aleutian mink disease virus (AMDV) genome. *J Virol Methods* 234: 3–51. https://doi.org/10.1016/j.jviromet.2016.03.010

16. Xi J, Wang J, Yu Y, et al. (2016) Genetic characterization of the complete genome of an Aleutian mink disease virus isolated in north China. *Virus Genes* 52: 63–473. https://doi.org/10.1007/s11262-016-1320-3
17. Lakshmanan R, Mietzsch M, Ybargollin AJ, et al. (2022) Capsid structure of Aleutian mink disease virus and Human Parvovirus 4: New faces in the. *Viruses* 14: 219. https://doi.org/10.3390/v14102219
18. McKenna R, Olson NH, Chipman PR, et al. (1999) Three-dimensional structure of Aleutian mink disease parvovirus: Implications for disease pathogenicity. *J Virol* 73: 882–6891. https://doi.org/10.1128/JVI.73.8.6882-6891.1999
19. Clemens DL, Wolfinbarger JB, Mori S, et al. (1992) Expression of Aleutian mink disease parvovirus capsid proteins by a recombinant vaccinia virus: Self-assembly of capsid proteins into particles. *J Virol* 66: 077–3085. https://doi.org/10.1128/JVI.66.5.3077-3085.1992
20. Yi L, Cheng Y, Zhang M, et al. (2016) Identification of a novel Aleutian mink disease virus B-cell epitope using a monoclonal antibody against VP2 protein. *Virus Res* 223: 9–42. https://doi.org/10.1016/j.virusres.2016.06.014
21. Lu T, Wang Y, Ge J, et al. (2018) Identification and characterization of a novel B-cell epitope on Aleutian Mink Disease virus capsid protein VP2 using a monoclonal antibody. *Virus Res* 248: 4–79. https://doi.org/10.1016/j.virusres.2017.12.008
22. Mietzsch M, Pénzes JJ, Agbandje-McKenna M (2019) Twenty-Five Years of Structural Parvovirology. *Viruses* 11: 62. https://doi.org/10.3390/v11040362
23. Jahns H, Daly P, McElroy MC, et al. (2010) Neuropathologic features of Aleutian disease in farmed mink in Ireland and molecular characterization of Aleutian mink disease virus detected in brain tissues. *J Vet Diag Invest* 22: 101–105. https://doi.org/10.1177/104063871002200120
24. Tong M, Sun N, Cao Z, et al. (2020) Molecular epidemiology of Aleutian mink disease virus from fecal swab of mink in northeast China. *BMC Microbiol* 20: 234. https://doi.org/10.1186/s12866-020-01910-8
25. Leng X, Liu D, Li J, et al. (2018) Genetic diversity and phylogenetic analysis of Aleutian mink disease virus isolates in north-east China. *Arch Virol* 163: 1241–1251. https://doi.org/10.1007/s00705-018-3754-5
26. Jakubczak A, Kowalczyk M, Kostro K, et al. (2016) High molecular polymorphism of the hypervariable region in the VP2 gene of Aleutian mink disease virus. *Acta Virol* 60: 354–360. https://doi.org/10.4149/av_2016_04_354
27. Prieto A, Fernández-Antonio R, López-Lorenzo G, et al. (2020) Molecular epidemiology of Aleutian mink disease virus causing outbreaks in mink farms from Southwestern Europe: A retrospective study from 2012 to 2019. *J Vet Sci* 21: e65. https://doi.org/10.4142/jvs.2020.21.e65
28. Bloom ME, Alexandersen S, Perryman S, et al. (1988) Nucleotide sequence and genomic organization of Aleutian mink disease parvovirus (ADV): Sequence comparisons between a nonpathogenic and a pathogenic strain of ADV. *J Virol* 62: 2903–2915. https://doi.org/10.1128/JVI.62.8.2903-2915.1988
29. Schuierer S, Bloom ME, Kaaden OR, et al. (1997) Sequence analysis of the lymphotropic Aleutian disease parvovirus ADV-SL3. *Arch Virol* 142: 157–166. https://doi.org/10.1007/s007050050066
30. Sang Y, Ma J, Hou Z, et al. (2012) Phylogenetic analysis of the VP2 gene of Aleutian mink disease parvoviruses isolated from 2009 to 2011 in China. *Virus Genes* 45: 31–37. https://doi.org/10.1007/s11262-012-0734-9

31. Wang Z, Wu W, Hu B, et al. (2014) Molecular epidemiology of Aleutian mink disease virus in China. *Virus Res* 184: 14–19. https://doi.org/10.1016/j.virusres.2014.02.007
32. Penzes JJ, Canuti M, Francois S, et al. (2023) Creating 13 new species in family *Parvoviridae.* ICTV/Approved proposals.2023, Code assigned: 2023.007D.
33. Kumar S, Stecher G, Li M, et al. (2018) MEGA X: molecular evolutionary genetics analysis across computing platforms. *Mol Biol Evol* 35: 1547–1549. https://doi.org/10.1093/molbev/msy096
34. Jones DT, Taylor WR, Thornton JM (1992) The rapid generation of mutation data matrices from protein sequences. Comput *Appl Biosci* 8: 275–282. https://doi.org/10.1093/bioinformatics/8.3.275
35. Snijder J, van de Waterbeemd M, Damoc E, et al. (2014) Defining the stoichiometry and cargo load of viral and bacterial nanoparticles by Orbitrap mass spectrometry. *J Am Chem Soc* 136: 7295–7299. https://doi.org/10.1021/ja502616y
36. Shackelton LA, Parrish CR, Truyen U, et al. (2005) High rate of viral evolution associated with the emergence of carnivore parvovirus. *Proc Natl Acad Sci USA* 102: 379–384. https://doi.org/10.1073pnas.0406765102
37. Soubrier J, Steel M, Lee MSY, et al. (2012) The influence of rate heterogeneity among sites on the time dependence of molecular rates. *Mol Biol Evol* 29: 3345–3358. https://doi.org/10.1093/molbev/mss140
38. Canuti M, Pénzes JJ, Lang AS (2022) A new perspective on the evolution and diversity of the genus Amdoparvovirus (family Parvoviridae) through genetic characterization, structural homology modeling, and phylogenetics. *Virus Evol* 8: veac056. https://doi.org/10.1093/ve/veac056
39. Kamani J, González-Miguel J, Msheliza EG, et al. (2022) Straw-Colored Fruit Bats (*Eidolon helvum*) and Their Bat Flies (*Cyclopodia greefi*) in Nigeria Host Viruses with Multivarious Modes of Transmission. *Vector Borne Zoonotic Dis* 22: 45–552. https://doi.org/10.1089/vbz.2022.0025
40. Moratelli R, Calisher CH (2015) Bats and zoonotic viruses: can we confidently link bats with emerging deadly viruses? *Mem Inst Oswaldo Cruz* 110: 1–22. https://doi.org/10.1590/0074-02760150048
41. Zhou P, Yang XL, Wang XG, et al. (2020) A pneumonia outbreak associated with a new coronavirus of probable bat origin. *Nature* 579: 70–273. https://doi.org/10.1038/s41586-020-2012-7
42. El-Sayed A, Kamel M (2021) Coronaviruses in humans and animals: The role of bats in viral evolution. *Environ Sci Pollut Res Int* 28: 9589–19600. https://doi.org/10.1007/s11356-021-12553-1