Revisiting the Tigger Transposon Evolution Revealing Extensive Involvement in the Shaping of Mammal Genomes

Mohamed Diaby 1, Zhongxia Guan 1, Shasha Shi 1, Yatong Sang 2, Saisai Wang 1, Yali Wang 1, Wencheng Zong 3, Numan Ullah 1, Bo Gao 1 and Chengyi Song 1,*

1 College of Animal Science & Technology, Yangzhou University, Yangzhou 225009, China; dh18035@yzu.edu.cn (M.D.); mx12019065@yzu.edu.cn (Z.G.); mx12019066@yzu.edu.cn (S.S.); dx12017008@yzu.edu.cn (S.W.); dx12018009@yzu.edu.cn (Y.W.); numanhashmi@aup.edu.pk (N.U.); bgaoyzu.edu.cn (B.G.)
2 School of Life Sciences, Sun Yat-sen University, Guangzhou 510275, China; sangyt@mail2.sysu.edu.cn
3 Institute of Animal Sciences, Chinese Academy of Agricultural Sciences, Beijing 100193, China; 8210121107@caas.cn
* Correspondence: cysong@yzu.edu.cn; Tel.: +86-514-8797-9034

Simple Summary: Despite the discovery of the Tigger family of pogo transposons in the mammalian genome, the evolution profile of this family is still incomplete. Here, we conducted a systematic evolution analysis for Tigger in nature. The data revealed that Tigger was found in a broad variety of animals, and extensive invasion of Tigger was observed in mammal genomes. Common horizontal transfer events of Tigger elements were observed across different lineages of animals, including mammals, that may have led to their widespread distribution, while parasites and invasive species may have promoted Tigger HT events. Our results also indicate that the activity of Tigger transposons tends to be low in vertebrates; only one mammalian genome and fish genome may harbor active Tigger.

Abstract: The data of this study revealed that Tigger was found in a wide variety of animal genomes, including 180 species from 36 orders of invertebrates and 145 species from 29 orders of vertebrates. An extensive invasion of Tigger was observed in mammals, with a high copy number. Almost 61% of these species contain more than 50 copies of Tigger; however, 46% harbor intact Tigger elements, although the number of these intact elements is very low. Common HT events of Tigger elements were discovered across different lineages of animals, including mammals, that may have led to their widespread distribution, whereas Helogale parvula and arthropods may have aided Tigger HT incidences. The activity of Tigger seems to be low in the kingdom of animals, most copies were truncated in the mammal genomes and lost their transposition activity, and Tigger transposons only display signs of recent and current activities in a few species of animals. The findings suggest that the Tigger family is important in structuring mammal genomes.

Keywords: transposons; pogo; Tigger; evolution; horizontal transfer

1. Introduction

The movement of genetic material among reproductively separated species is known as horizontal transfer (HT). This form of transmission is ubiquitous in prokaryotes, where it is frequently used to generate genetic innovation [1,2]. HT is also becoming acknowledged as a major evolutionary driver altering eukaryotic genomes. So far, most HT events identified in eukaryotes are organelle-to-nucleus prokaryote-to-eukaryote gene transfers [3–6]. In fact, just a few occurrences of gene transfers across multicellular eukaryotes have been reported [7–9], while the vast majority of detected HTs within metazoans relate to transposable element (TE) transfers [10]. TEs are DNA pieces that can move across genomic regions, frequently replicating themselves throughout the process [11]. Due to their two distinct features, TE elements might serve as a means of interspecies gene transfer: they
are capable of mobility, and they often represent the single most abundant component of eukaryotic genomes; for example, TEs make up 45% and 85% of the human and maize genomes, respectively [10,12].

One type of transposition mechanism of TEs is DNA-mediated, thus named DNA transposons (or class II transposons); most DNA transposons move using a cut-and-paste model facilitated by transposases. They are distinguished by the presence of terminal inverted repeats (TIRs) and target site duplication (TSD) [13]. DNA transposons are categorized into distinct superfamilies based on their transposases, including pogo, Tc1/mariner, piggyBac, hAT, Zator, P, PI/F/Harbinger, PHIS, etc. [14–16].

The TEs, particularly DNA transposons, are the best-documented examples of HT between the nuclear genomes of multicellular eukaryotes [17,18]. Thus far, notable examples of HT of DNA transposons have been detected in diverse species such as insects [17,19–21], fish [22], nematodes [23], and plants in one case [24]. Retroviruses have invaded the germlines of various mammals [25–28], and there is accumulating evidence supporting the horizontal transmission of a snake retrotransposon in ruminants [29,30]. In summary, three criteria are employed to infer HT events: (1) significantly higher similarity of TEs, compared with non-mobile sequences; (2) non-congruent phylogeny between TE and host; and (3) spotty TE prevalence inside one group of taxa [17,31].

The IS630-Tc1-mariner ITm is one of the most common types of cut-and-paste DNA transposons. Elements of this group may be found in practically every part of the tree of life [32]. ITm transposons can be divided into different groups depending on the DDE/D signature. Recently, a novel ITm superfamily known as Sailor (DD82E) was discovered [33], which constitutes a unique superfamily with a discrete DDE domain (DD78-111E) and different evolutionary positions than prior superfamilies (Tc1/mariner, DD34E/Gambol, DxD/pogo, TP36, and Zator) [34–38]. Tc1/mariner, a cut-and-paste transposon superfamily, is considered to be the most ubiquitous category of DNA transposons, with many different families, including DD34D/mariner, DD37D/maT, DD39D/GT, DD41D/VS, DD34E/Tc1, DD35E/TR, DD36E/IC, and DD37E/TRT [39–46].

The pogo element was first discovered in flies [47], followed by the discovery of a variety of related transposons, such as Tigger in bees and humans [48,49], Aft1, Flipper, Pot1, Pot2, Tam1, and Fot transposons in fungi [50–55], and Lemi in plants [56], which were phylogenetically close to pogo transposase [34,57,58]. For a long time, it was thought to be a member of the Tc1/mariner superfamily [34,35], and it was known as DD×D/pogo [34]. However, recent evolutionary analyses have revealed that pogo is a distinct superfamily [14]. Gao et al. (2020) found that pogo, Gambol, and Tc1/mariner constitute well-supported monophyletic clades, implying that they are distinct superfamilies that may have evolved separately from different clades of bacterial IS630 TEs. They also highlighted that pogo transposons may have the broadest taxonomic distribution, compared with other Tc1/mariner and DNA transposon superfamilies [14]. pogo transposons were divided into six families: Passer, Mover, Tigger, Fot/Fot-like, pogoR, and Lemi [14]. The major pogo superfamily also includes a well-supported collection of numerous subclades [14].

In this paper, we analyzed the evolutionary connections, taxonomic distribution, and HT events of Tigger transposons in eukaryote genomes. The data we present show the complete evolutionary landscape of Tigger transposons and their invasion of different eukaryotes species genomes. These findings have major implications for determining the evolution of Tigger transposons and their influence on genome evolution.

2. Material and Methods

2.1. Mining of Tigger Transposons

Tc1/mariner transposons from the RepBase database were merged with reference sequences of Tigger transposons identified in previous research [14,48,59] to produce transposases sequences, to identify the distributions of Tigger transposons in the genomes. The Tigger transposase sequences were then used as queries in a TBlastN (with an E-value of 1e-100) search at the National Center for Biotechnology Information (NCBI) against the acces-
sible organism genomes of prokaryotes and eukaryotes. The newly discovered sequences were then utilized as queries to find additional elements. The top 10 non-overlapping matches and 2 kb of flanking sequences were retrieved and manually aligned using the MAFFT v. 7.310 software [60] to determine transposon boundaries (TIR and TSD). Subsequently, a consensus or representative sequence of the discovered Tigger transposon was employed for further investigation. Following that, all obtained BLAST hits (with >1000 bp in length, >40% coverage, and >80% identity) were utilized to determine copy numbers. Furthermore, elements with many copies (>5) in the genomes were aligned using DAMBE to create consensus sequences [61].

2.2. Structure and Phylogenetic Analysis of Tigger

Protein domains were detected using the online hmmscan website’s profile hidden Markov processes (https://www.ebi.ac.uk/Tools/hmmer/search/hmmscan, accessed on 13 December 2020). Pairwise comparisons of full-length consensus or representative sequences were used to determine the sequence identities of Tigger transposons across species. To correctly identify the phylogenetic relationship of Tigger transposons, relevant open reading frame (ORF) sequences were obtained and translated into protein using Bioedit software. The sequences of the conserved DDE/DDD domains of Tigger transposases and other reference pogo families [14,59] were extracted and aligned with the MAFFT software [60]. Then, using the maximum likelihood approach in IQ-TREE [62], these DDE/DDD domain sequences were used to interpret the phylogenetic tree. ModelFinder integrated into IQ-TREE [63] chose the best-fit model, and the accuracy of maximum likelihood trees was evaluated using the ultrafast bootstrap technique with 1000 repetitions.

2.3. Evidence of HT for Tigger across the Animal Kingdom

Horizontal transfer events of Tigger transposons were detected using pairwise distances between the host genes and the transposons. To determine possible Tigger HT events, the pairwise distances between Tigger transposase-coding sequences and host gene-coding sequences were determined. Ribosomal protein genes are known to be globally conserved [64]. Therefore, we selected two highly conserved ribosomal proteins (RPL3 and RPL4) as the host genes, which also have a wide taxonomic prevalence in eukaryotes with one genomic copy, according to information in the orthologs database (OrthoDB), and were applied in our previous survey [33].

By introducing four critical filters, we employed a strict stand to avoid potentially false-positive estimates of Tigger’s HT events. The first approach was based on Tigger transposon sequence identity—only transposon sequence identity of pairwise species higher than 70% was selected for HT analysis. The second standard was based on the genetic distance of transposons between species: Only if the species had genetic distance 1.2 times smaller than host genes was kept for further HT analysis. Third, two host genes (RPL3 and RPL4) were employed for late HT deducing; HT events were recognized only if the genetic distance among species was significantly less ($p < 0.01$) for transposons than for all host genes.

Two 60S ribosomal proteins RPL3 and RPL4 reported as universally conserved host genes [64] were analyzed for conservation and length and the taxonomic spread of the sole genomic copy among domains to pick the suitable host genes for the HT assumption analysis (Supplementary data S1, S3 and S4). The taxonomic distribution of host genes across eukaryote genomes was assessed using the OrthoDB web database (https://www.orthodb.org/, accessed on 25 December 2020). NCBI was used to retrieve all accessible gene annotations (coding sequences (CDS)) for host genes (RPL3 and RPL4) of species invaded by Tigger. The CDS of these genes was manually annotated by screening against the WGS via TBLASTN for those species whose host genes were not annotated. All acquired RPL3 and RPL4 sequences were collected, and sequences with considerable length deviations were excluded. Multiple alignments of RPL3 and RPL4 and Tigger were constructed, using the MAFFT software to detect HT events. Lastly, using MEGA (pairwise deletion, maximum composite likelihood) [65], the pairwise distances between
the various species were computed for the Tigger and host gene (RPL3 and RPL4) coding sequences, respectively.

Furthermore, regarding HT events of Tigger among the species, two additional genes (non-ribosomal gene) were used. Recombination-activating gene 1 (RAG1) [41,66] was used only for confirming the HT events in vertebrate species that were previously tested by RPL3 and RPL4 genes. However, the tubulin beta-3 (tub3) gene [67] was used for confirming the HT events in invertebrate species that were tested by using RPL3 and RPL4 genes. Statistical differences in genetic distances were examined using a one-factor ANOVA test in SPSS Statistics program v.25 (IBM Corp., Armonk, NY, USA).

3. Results

3.1. Taxonomic Distribution and Structure Organization of Tigger

The known Tigger transposase sequence [14,48,59] was applied as a query to explore against all available prokaryotic and eukaryotic genomes stored in the NCBI database in order to establish the taxonomic distribution of Tigger transposon. Overall, 383 Tigger homologous elements representing 325 species were collected (Supplementary data S1 and Figure S1) and submitted for phylogenetic analysis in the IQ-Tree software using the maximum-likelihood approach. Maximum-likelihood evaluation of the ORF protein sequences of the Tigger transposons, and known DNA transposases from pogo indicated that Tigger transposases constituted a major well-supported clade, with a 95% bootstrap value (Figure 1). Based on the phylogenetic tree, Tigger transposases were subsequently classified into five different intraclusters (Clusters A–E) (Figure 2). Cluster A had 12 vertebrate species (including Fishes, 2 species, and Reptiles, 10 species), and 60 invertebrates (Echinodermata, 1 species; Arthropod, 56 species; Mollusca, 1 species; Porifera, 1 species; and Cnidaria, 1 species). Cluster B had 48 vertebrates (Mammals, 33 species; Reptiles, 4 species; Fishes, 10 species; and Amphibians, 1 species), and 10 invertebrates (Arthropod, 5 species; Mollusca, 2 species; Platyhelminthes, 1 species; Annelida, 2 species; and Unrochordata, 1 species), while Cluster C had only 1 vertebrate (Reptiles, 1 species) and 23 invertebrates (Arthropod, 21 species; Nematoda, 1 species; and Platyhelminthes, 1 species). Moreover, Cluster D contained 18 vertebrates (Mammals, 7 species; Fishes, 3 species; and Reptiles, 8 species) and 22 invertebrates (Arthropod, 20 species, and Platyhelminthes, 2 species). However, Cluster E had only 1 arthropod species, and the other 60 species were mammals (Figure 2).

Tigger was first reported in humans, and also observed in invertebrates [48]. Our data revealed that the Tigger family’s distribution is restricted in animals but with extensive transmissions in both vertebrates and invertebrates; particularly, a wide expansion of Tigger was observed in mammals, where retrotransposons dominate the genomes, and DNA transposons are rare [68]. Overall, 169 Tigger elements were identified in 145 species from 29 orders of vertebrates, and 214 Tigger elements were found in 180 species from 36 orders of invertebrates (Figure 3 and Supplementary Table S1). Tigger was found in nearly all lineages of vertebrates; particularly, extensive expansion of Tigger was detected in mammals (103 species)—namely, Metatheria (3 species), Afrotheria (1 species), Carnivora (40 species), Cetartiodactyla (2 species), Chiroptera (14 species), Dermoptera (1 species), Insectivora (1 species), Lagomorpha (1 species), Perissodactyla (3 species), Pholidota (3 species), Primates (23 species), Rodents (9 species), and Xenarthra (2 species) (Figure 3 and Supplementary Table S1). Furthermore, Tigger was also found in Reptiles (20 species), Amphibians (3 species), and Birds (1 species). In comparison, in fish, which represents a great diversity of species and the major reservoir hosts of DNA transposons [69,70], only 20 species were found to harbor Tigger (Figure 3 and Supplementary Table S1). Tigger elements invaded nearly all invertebrate species as well, including Annelida (1 species of 1 order), Cnidaria (5 species of 2 orders), Cephalochordata (1 species of 1 order), Echinodermata (2 species of 1 order), Mollusca (8 species of 6 orders), Porifera (2 species of 2 order), Platyhelminthes (2 species of 1 order), Urochordata (1 species of 1 order), Nematoda (2 species of 1 order), and arthropod (155 species of 19 orders) (Supplementary Table S1).
Figure 1. Phylogenetic tree of Tigger elements detected in this analysis with five other members of the pogo superfamily (Passer, Mover, Fot/Fot-like, pogoR, and Lemi) based on transposases. In IQ-TREE, bootstrapped (1000 repetitions) phylogenetic trees were inferred using the maximum-likelihood approach.
Figure 2. Intrafamily diversity of Tigger elements in the animal kingdom; each colored branch represents a phylogenetic tree cluster.

Tigger element copy numbers (>80% identity and 40% coverage) differed dramatically among these genomes, ranging from 1 to 2324 in each (Supplementary Table S1). In mammals and reptiles, most Tigger were short truncated copies, although some long copies were found; numerous long copies of Tigger were found in Cetartiodactyla, Perissodactyla, Fishes, and even invertebrates (Supplementary Table S1). More than the majority of the species (231/325) had at least one intact Tigger element, including 87% of Arthropod species (159/183), 83% of Fishes (15/18), and 45% of Mammals (45/120). In addition, intact Tigger elements were found in almost all vertebrate and invertebrate classes detected in this study (Figure 3 and Supplementary Table S1). The distribution of Tigger elements in different eukaryotic phyla revealed that this family is still active in these organisms.

The structure of the pogo protein, as well as the transposons, has been proven to be substantially conserved in previous research [14,49]. As shown in Figure 4, Tigger’s transposase consists of a CENP-B DNA-binding domain with a helix–turn–helix (HTH) motif at the N-terminus and a catalytic domain in the C-terminus (Figure 4) [14,48,49,71]. Tigger structure was discovered to be preserved throughout a variety of eukaryote species, including insects, fish, frogs, and bats. Most complete Tigger transposons were around 2.8 kb (range 1018–4525 bp) in length and contained a single ORF encoding a protein of about 492 aa (range 300–685 aa) flanked by short 20 bp (8–33 bp) TIRs (Figure 4). Tigger
elements were discovered to be flanked by TA target site duplication (Table 1). The intact Tigger transposon in the Insecta Cryptotermes secundus is 2485 bp long, encoding a 537 aa transposase and flanked by 23 bp TIRs, and represents a common structure of this family (Figure 4).

**Figure 3.** Distribution of Tigger transposons in eukaryotes. Blue stars show Tigger elements detected in the branches, and the numbers indicate the number of species possessing Tigger elements in each branch.

**Figure 4.** Tigger’s structural organization. TIRs are shown by black arrows, CENP-B-N motifs by blue rectangles, HTH sequences by yellow rectangles, catalytic domains (D: aspartic acid) by green rectangles, and TA is the target site of duplication.
Table 1. Tigger distribution in all eukaryotes examined in this study.

| Distribution | Number of Species Containing Tigger | Number of Species Containing Full Tigger (%) a | Number of Species Containing Intact Tigger | Length of the Full Tigger (bp) b | Length of the Intact Tigger (bp) c | Transposase Length of the Intact Tigger | TIR Length of the Intact Tigger (bp) | TSD |
|--------------|------------------------------------|---------------------------------------------|---------------------------------------------|---------------------------------|---------------------------------|---------------------------------|---------------------------------|-----|
| Porifera     | 3                                  | 2/66.6                                      | 2                                           | 2288–3872                      | 2288–3872                      | 334–685                        | 20–741                         | TA  |
| Cnidaria     | 5                                  | 4/80                                        | 3                                           | 1385–3309                      | 1385–3210                      | 374–538                        | 17–25                          | TA  |
| Platyhelminthes | 3                               | 3/100                                       | 2                                           | 2049–2762                      | 2049–2762                      | 360–598                        | 17–25                          | TA  |
| Mollusca     | 8                                  | 7/87.5                                      | 6                                           | 1609–3452                      | 1609–2851                      | 332–575                        | 15–25                          | TA  |
| Nematoda     | 2                                  | 1/50                                        | 1                                           | 2399–3400                      | 3400                           | 355                            | 23–24                          | TA  |
| Echinodermata| 1                                  | 1/100                                       | 1                                           | 2988–3088                      | 3068                           | 540                            | 21–23                          | TA  |
| Loricordata  | 1                                  | 1/100                                       | 1                                           | 2381                          | 2381                           | 319                            | 22                             | TA  |
| Arthropods   | 183                                | 159/87                                      | 147                                         | 1018–4225                      | 1428–4225                      | 301–607                        | 12–33                          | TA  |
| Annelida     | 1                                  | 1/100                                       | 1                                           | 1969                          | 1969                           | 396                            | 24                             | TA  |
| Cephalochordata | 1                           | 1/100                                       | 1                                           | 2872                          | 2872                           | 305                            | 18                             | TA  |
| Actinopterygii| 11                                | 10/91                                       | 9                                           | 1385–2821                      | 1385–2821                      | 301–438                        | 13–23                          | TA  |
| Agnatha      | 1                                  | 1/100                                       | 1                                           | 2906                          | 2906                           | 580                            | 21                             | TA  |
| Sarcopterygium| 1                                | 1/100                                       | 1                                           | 2099–2418                      | 2099–2418                      | 457–582                        | 23                             | TA  |
| Chondrichthyes| 5                                 | 4/80                                        | 4                                           | 2094–4525                      | 2094–4525                      | 306–585                        | 18–23                          | TA  |
| Anura        | 3                                  | 2/66.6                                      | 2                                           | 1620–2277                      | 1620–2277                      | 340–597                        | 13–29                          | TA  |
| Squamata     | 3                                  | 4/30                                        | 4                                           | 2336–3988                      | 2336–3988                      | 532–615                        | 17–26                          | TA  |
| Crocodylata  | 6                                  | 3/50                                        | 3                                           | 2329–2516                      | 2345–2360                      | 587–640                        | 11–24                          | TA  |
| Aves         | 1                                  | ND                                         | ND                                          | 3808                          | ND                            | 584                           | 20                             | TA  |
| Testudines   | 24                                 | 21/87.5                                     | 21                                          | 1370–2740                      | 1370–2740                      | 323–601                        | 10–27                          | TA  |
| Metatheria   | 3                                  | 3/100                                       | 3                                           | 2245–2379                      | 2245–2379                      | 341–546                        | 20–24                          | TA  |
| Eutheria     | 100                                | 46/46                                       | 46                                          | 1605–2962                      | 1605–2962                      | 300–636                        | 9–27                           | TA  |

a The percentage of positive species. b Tigger elements flanked with TIRs were designated as full transposons. c The full transposons encoding intact transposases (>300 aa) were designated as intact transposons. ND: not detected; bp: base pair; TIR: terminal inverted repeats; TSD: target site duplication.
3.2. Tigger Evolutionary Dynamics in Vertebrate Genomes

Our data revealed that the recent and current activities of Tigger tend to be low in vertebrates; only a few species contain high intact copies (around eight copies) of Tigger, such as Dermochelys coriacea and Chiloscyllium punctatum (Supplementary Table S1). Particularly in mammals, about 61% of those species contain more than 50 copies of Tigger; however, 46% harbor intact Tigger elements, but the copy number of these intact elements is low (Table 1 and Supplementary Table S1), indicating that the substantial expansion of the Tigger experienced in these species and mutation accumulation resulting in activity loss would occur in these copies. To further highlight the evolution patterns of Tigger elements in vertebrates, we used a Kimura divergence to evaluate the evolutionary dynamics of Tigger elements among the species containing more than three intact Tigger copies, the findings of which are described in Figure 5. Generally, young transposons represent low Kimura divergences [72], which reflects the activity of a transposon on a relative time scale per genome [73]. The data suggested the current activities of Tigger may only exist in one species of mammal (Hipposideros armiger) and one species of fish (Latimeria chalumnae), where some copies of Tigger displayed low Kimura divergences (<2%), while most Tigger copies in most species represent high Kimura divergences (more than 10%). This stated that Tigger old transposons invaded these species and may have lost their activities and become fossils (Figure 5). Some species (including Euschistus heros, Clitarchus hookeri, Harmonia axyridis, Latrodectus hesperus, Girardia tigrina, and Schmidtea mediterranea) experienced several waves of Tigger invasion, while several other species (such as Colobus angolensis, Helogale parvula, Trichechus manatus, and Equus asinus) underwent Tiggers’ solitary wave amplification. However, Tigger may still be active in some species of invertebrates— notably, arthropods and platyhelminthes, such as Dysdera silvatica, Latrodectus Hesperus, Mesobuthus martensi, Girardia tigrina, and Schmidtea mediterranea, where we discovered that many copies were intact in certain species with numerous Tigger copies (>5) and very high transposon sequence identities (Table 1 and Supplementary Table S1).
Figure 5. Evolutionary dynamics of Tigger in animals. RepeatMasker utility scripts were used to calculate the Kimura divergence from consensus sequences or the representative sequence (Tarailo-Graovac and Chen 2009). The y-axis represents the coverage (kb) of each Tigger element in the genome and the x-axis indicates the Kimura divergence estimate. Each color in the three orders (Mammal, Reptile, and Fish) represents species from different classes of the animal kingdom.

3.3. Evidence of HT Events for Tigger across Animals

The possible Tigger HT events were determined based on the strict stands described in Methods. Overall, 121 species involved in 13 HT events (Figure 6 and Supplementary Tables S2 and S3) were recognized, with the genetic distance among species being significantly less (p < 0.01) for transposons than for the host genes (RPL3 and RPL4) (Figure 6A and Supplementary Figure S2; Tables S2 and S3). Eventually, two non-ribosomal genes RAG1 and Tub3 were used to confirm Tigger HT events obtained from RPL3 and RPL4 ribosomal genes (Supplementary Figures S5 and S6, and Table S4).
Figure 6. (A) Pairwise distance comparisons of Tigger transposons. The graph illustrates the pairwise distances of Tiggers and two organelle ribosomal proteins (L3 and L4) between the species included in this study, the red color represents Tigger transposon, the green color represents RPL3, and the blue color represents RPL4. The distances were obtained from all possible pairwise comparisons ($N_{L3} = 572$, $N_{L4} = 572$, labeled on the x-axis); (B) HT events measured among species contained Tigger elements. Sequence identities between Tigger elements among species. The sequence identities were measured via pairwise comparisons of Tigger CDS sequences (for species abbreviations, refer to Supplementary Table S1).
Using genetic distance comparison, Tigger HTs were detected in animals across many classes and orders. In detail, Tigger HT events were found in nine classes, with Eutheria being halfway between the other classes in Tigger HT events (Supplementary Tables S2 and S3, and Figure S2). In this study, most HT events were between species from the same phylum, specifically Chordata. However, some HT events were observed between different, including arthropods and Chordata (mammals, specifically Eutheria) (Supplementary Figure S2). In detail, HT events of Tigger were detected between Eutheria (26 species) and Metatheria (2 species), Actinopterygii (7 species), Chondrichthyes (2 species), Agnatha (1 species), Sarcopterygii (1 species), Crocodilia (2 species), and Testudines (3 species), respectively (Supplementary Tables S3 and S4). However, the HTs between Eutheria and arthropod (31 species) were the only between two different phyla detected in this study (Figures 6 and 7A, and Supplementary Figure S4).

Moreover, HT events between fishes, specifically Agnatha (1 species L. camtschaticum) and Eutheria (26 species from 3 orders—namely, Carnivora, Chiroptera, and Rodents) were confirmed via phylogenetic relation, which is supported by Cluster B (Figures 2 and 7B, Supplementary Figures S1 and S2). This relation highlights the role of L. camtschaticum in highlighting Tigger transposon between Agnatha and Eutheria. Similarly, the HT events between Actinopterygii (seven species, including Astatotilapia calliptera, Maylandia zebra, Oreochromis spilurus, Pandamilia nyererei, Takifugu flavidus, Takifugu rubripes, and Trophus moorii) and Carnivora (Helogale parvula) occurred across three clusters (Cluster B, Cluster E, and Cluster D) and Helogale parvula played the key role in those events. Additionally, Helogale parvula has played an important role in Tigger transposon HT between Carnivora and Sarcopterygii (one species, Latimeria chalumnae), as well as Chondrichthyes (two species—namely, Carcharodon carcharias and Scyliorhinus torazame), which were detected throughout three clusters (Cluster A, Cluster C, and Cluster E). We may infer that Helogale parvula was the essential factor of Tigger transposons HT events between Eutheria and Fishes (including Agnatha, Chondrichthyes, Actinopterygii, and Sarcopterygii) since it was the only Eutheria species that intermediated all HT events with fish. Additionally, HT events were de-
ected between two orders of mammals including Eutheria (one species—Helogale parvula and Metatheria (two species, including Gymnobelideus leadbeateri and Trichosurus vulpecula), which were confirmed phylogenetically in Cluster D and are summarized in Supplementary Tables S2 and S3.

Furthermore, *H. parvula* also intermediated the HT events of Tigger transposons between carnivores (Eutheria) and arthropods (22 species, including *Drosophila athabasca, Drosophila azteca, Drosophila truncata, Dufourea novaengliae, Delias pasithoe, Eufriesea mexicana, Glossosoma conforme, Hypothemenus hampei, Latrodectus hesperus, Marronus borbonicus, Megalopta genalis, Oryctes borbonicus, Osmia bicornis, Osmia lignaria, Schizaphis graminum, Scaptomyza flava, Tetragonula davenporti, Tetragonula hockingsi, and Tuta absoluta*), which were confirmed in three clusters (Cluster A, Cluster B, and Cluster C) (Supplementary Tables S2 and S3). However, HT events were detected between Reptiles—namely, Testudines (three species, including *Malaclemys terrapin, Pelusios castaneus,* and *Pelodiscus sinensis*)—and Eutheria, specifically Carnivora (two species, including *Helogale parvula* and *M. lucifugus*), and those species belonged to different three clusters (Cluster B, and Cluster D, Cluster E) (Supplementary Tables S2 and S3). Additionally, the HT event between reptiles, specifically Crocodilia (two species, including *Alligator sinensis* and *Cavialis gangeticus*) and Eutheria, specifically Carnivora (*Helogale parvula*) were confirmed phylogenetically and found to occur among three clusters (Cluster A, Cluster B, and Cluster E) (Supplementary Tables S2 and S3).

4. Discussion

*Tigger*1 and *Tigger*2 were the first *Tigger* elements identified from mammalian genomes and defined in terms of their resemblance to pogo and CENP-B elements in general [47,74]. *Tigger*1 has been designated as a mammalian *pogo* [47]. Despite the fact that the transposase sequences of *Tigger*1 and *Tigger*2 are similar, they are very distantly linked in a larger evolutionary perspective [59]. *Tigger* elements are polyphyletic, meaning they do not belong to a single monophyletic group. Furthermore, the use of sequence similarity to categorize elements has resulted in the annotation of new *Tigger* elements throughout a wide range of *pogo* elements diversity over time. *Tigger* transposons belong to the *pogo* superfamily of transposons on the evolutionary tree. The analysis of the structural organization of the *Tigger* family enabled us to determine some notable distinctions between them and the members of the *pogo* superfamily. The most noticeable distinction was the DDE signature—the *Tigger* family was shown to include the DD29-36D catalytic domain [14,49,59].

In this analysis, we used the available BLASTN and BLAST tools to scan the NCBI Whole-Genome Shotgun (WGS) library for *Tigger* transposons and generated their evolutionary profiles. Our findings show that *Tigger* transposons are broadly and unevenly dispersed in eukaryotes, invading 325 species across most invertebrate (excluding Ctenophora) and vertebrate groups (except for Caudata and Monotremata). Our research also found that arthropods and mammals are important reservoir lineages of *Tigger*, with 155 (19 orders) and 105 (in 12 orders) species invaded, respectively (Figures 2 and 3). This prevalence of *Tigger* elements in mammalian genomes might suggest a distinct evolutionary profile of DNA transposons in mammals. However, the *Tigger* family’s taxonomic spread was underestimated due to the omission of shortened elements from older copies. Furthermore, mammals show distinct evolutionary profiles for the TE landscape than reptiles, amphibians, and fishes, with less diversity and activity of DNA transposons [70,75,76]. Despite the fact that certain DNA transposon families have invaded mammals’ genomes, many have restricted distribution, with just a few lineages entering mammalian genomes, such as DD41D/VS and DD36E/IC, two different *Tc1/mariner* transposon families [43,44]. Our findings indicate that *Tigger* represents a distinct phylogenetic landscape in mammals, with a broader expansion range than the other DNA transposon families investigated.

As TEs exhibit radically distinct evolutionary dynamics throughout vertebrate groups, reportedly active DNA transposons tend to be highly prevalent in Actinopterygii genomes than in Aves or mammalian genomes [36,70]. Although DNA transposons have invaded
numerous mammalian lineages, most of them exist as incomplete copies in such genomes and have lost transposition activity, except piggyBac elements in Chiroptera, which have been characterized to have active copies [77]. In this study, the analysis of the evolutionary dynamics of Tigger elements revealed that mammalian species have high copies of Tigger elements, but their intact copies were low, which indicates that they appear as truncated copies in these genomes and have lost transposition activities. On the other hand, Tigger seems to be active in Arthropoda, Platyhelminthes, reptiles, and fish, which had high intact copies >5 in the genome, indicating that they are very young insertions in genomes, with most Tigger copies represented by very low Kimura divergences (Figure 5).

According to the current investigation, Tigger elements appear to be characterized by a high incidence of HT among animals. Uneven distribution of the Tigger transposon indicates the presence of putative HTs of Tigger elements in the animal genomes. Tigger transposons were found in numerous animal (vertebrates and invertebrates) lineages (mammals, fishes, reptiles, and arthropods) and displayed recurrent HT events (Figures 2 and 3). HT events of Tigger between vertebrates and invertebrates were also observed (Figures 2, 6 and 7, and Supplementary Figure S3). HT events of Tigger between vertebrates (Eutheria) and invertebrates (arthropods) were also observed (Figures 2, 6 and 7).

Overall, HTs were confirmed by 124 species pairings depending on the genetic distance assessments among transposons and the 2 host genes. In addition, a higher incidence of HT was found in Eutheria, which may indicate why Tigger elements are more abundant in mammals. The Tc1/mariner and pogo superfamilies retain the highest for confirmed HT instances among TEs [71,78]. Tigger likely inherits the capacity to endure frequent HT. Many publications have been written after the discovery of HT, detailing this activity in numerous orders of animals, including arthropods, mammals, reptiles, etc. It has been demonstrated that these events can occur across lineage and distant taxa [71,79–83]. Many HT events have been identified to date, with approximately one-third of them being related to elements of the Tc1/mariner superfamily [78]. Considering the availability of information on HT transposons and the significant number of reported examples, the mechanism behind this phenomenon remains unknown. Issues regarding the likelihood of responsive insertions being generated in the recipient’s genome and their contribution to genome evolution and speciation remain unanswered. Furthermore, the discovery of new cases of HT will contribute to our understanding of the phenomenon and come closer to resolving the difficulties raised earlier. The detection of HT instances across eukaryotes illustrates the potential of genetic information being exchanged between two distinct species.

Although most Tigger elements were retrieved from practically all animal host genomes, the host range typically differs across families. The processes underlying host range in TEs are poorly understood, and so are the trends we see for Tigger elements. For instance, if the host range is predominantly controlled via encounter or through compatibility criteria, the sensu hypothesis from host–parasite relations [84] is still an ongoing research subject. Our data displays a common horizontal transfer of Tigger elements across a wide range of hosts (Figures 6 and 7). The most likely interpretation for the reported pattern is that each Tigger family was extant in the eukaryotic ancestor lineage and that active components representing each Tigger family were preferentially maintained in only a particular host lineage (Supplementary Figures S1 and S3). Nevertheless, this would need inducing a significant range of loss events throughout the eukaryote evolution. As a result, given the improbability of the alternate explanation and recent studies illustrating the occurrence in which HT can emerge, we propose that a history of HT is the most probable answer for the identified host spread of Tigger elements. The current study of horizontal transmission in eukaryote genomes revealed that Tigger elements were the most commonly horizontally transferred. Despite their extremely careful analysis, the authors discovered multiple possible HT events involving Tigger elements between sixteen arthropod species (Anopheles coluzzii, Anopheles merus, Cataglyphis niger, Dufourea novaangliae, Eufriesea mexicana, Glossosoma conforme, Hypthenemus hampei, Latrodectus hesperus, Marronus borbonicus, Oryctes borbonicus, Osmia bicorns, Osmia lignaria, Schizaphis graminum, Sipha flava, Tetragonula daven-
porti, and Tetragonula hockingsi) and one mammal species (Helogale parvula). In addition, we also discovered that all HT events for Tigger transposons occurred between mammals and all other animal lineages, emphasizing the importance of mammals in Tigger evolution. A further surprising feature of Tigger's horizontally transferred transposons is the substantial participation of a mammal species (the common dwarf mongoose, Helogale parvula) in Tigger's HT occurrences across eukaryotes classes, which may be relative to the specific ecosystem of this species involved, where the distribution of the common dwarf mongoose is very extensive and ranges from the East to southern Central Africa. At the same time, their diet is extremely diverse and consists of insects (mainly beetle larvae, termites, grasshoppers, and crickets), spiders, scorpions, small lizards, snakes, small birds, and rodents [85]. Therefore, we speculated that the wide distribution of Helogale parvula and diversification of its diets might facilitate HT events of Tigger across mammals.

Tigger displays a unique evolution dynamics in animal genomes, where this family represent low recent and current activities, and active copies are limited in a few animal species; most copies in mammals tend to be fossils, which is different from several well-defined families of Tc1/mariner, such as DD38D/IT, DD35E/TR, DD36E/IC, DD41D, and DD37E/TRT [36,39,41,43,44]. These families display relatively high recent and current activities in some vertebrate and invertebrate lineages, particularly in ray-finned fishes; multiple intact copies and low divergences across copies in many genomes were detected, indicating that they are young invaders and represent high current activities in this lineage, and some may be still active, for example, DD38E/IT, which has been proven to be able to transpose in human HeLa cells [36]. Although limited distribution (18 species) was observed for Tigger in fish genomes, the activity tended to be low, with few species containing fewer intact copies (<8), and only 2 vertebrate species (Dermochelys coriacea and Chiloscyllium punctatum) containing 8 intact copies of Tigger, indicating the overall activity of Tigger in animals is low.

5. Conclusions

This is the first study to thoroughly show the evolutionary profiles of Tigger transposons, which exhibit a very extensive taxonomic distribution in animals and have been horizontally transferred across diverse lineages of animals. However, low activities of Tigger were observed for most species. Importantly, we showed evidence that this family was extensively involved in mammal genomes’ evolution. This research adds to our knowledge of evolution, and its findings imply that the Tigger family plays an important role in shaping mammal genomes.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/biology11060921/s1, Supplementary Figure S1: Phylogenetic tree of TEs based on the alignment of the DDE domains, Supplementary Figure S2: Sequence identities between Tigger elements among mammalian species, Supplementary Figure S3: Sequence identities between Tigger elements among Arthropoda species, Supplementary Table S1: Genome assembly information for all species, Supplementary Table S2: Distance of Tigger, L3, and L4 Ribosomal proteins, Supplementary Table S3: Distance of Tigger, L3, and L4 Ribosomal proteins classified based on phyla, classes, and orders, Supplementary Data S1: Tigger transposases protein sequences, Supplementary Data S2: Tigger CDS used for the pairwise distance identities, Supplementary Data S3: L3 ribosomal proteins CDS used for the pairwise distance identities, Supplementary Data S4: L3 ribosomal proteins CDS used for the pairwise distance identities.

Author Contributions: C.S. and B.G. conceived and designed the study. M.D., Z.G., S.S., Y.S., S.W., Y.W., W.Z. and N.U. mined transposons, collected data, and performed the data analysis. M.D. and C.S. wrote the manuscript. All authors have read and agreed to the published version of the manuscript.
23. Palazzo, A.; Escuder, E.; D’Addabbo, P.; Lovero, D.; Marsano, R.M. A Genomic Survey of Tc1-Mariner Transposons in Nematodes Suggests Extensive Horizontal Transposon Transfer Events. *Mol. Phylogenet. Evol.* 2021, 158, 107090. [CrossRef] [PubMed]

24. Diao, X.; Freeling, M.; Lisch, D. Horizontal Transfer of a Plant Transposon. *PLoS Biol.* 2006, 4, e5. [CrossRef] [PubMed]

25. Han, K.; Konkel, M.K.; Xing, J.; Wang, H.; Lee, J.; Meyer, T.J.; Huang, C.T.; Sandifer, E.; Hebert, K.; Barnes, E.W.; et al. Mobile DNA in Old World Monkeys: A Glimpse through the Rhesus Macaque Genome. *Science 2007*, 316, 238–240. [CrossRef] [PubMed]

26. Gifford, R.; Tristem, M. The Evolution, Distribution and Diversity of Endogenous Retroviruses. *Virus Genes* 2003, 26, 291–315. [CrossRef] [PubMed]

27. Shi, S.; Puzakov, M.; Guan, Z.; Xiang, K.; Diaby, M.; Wang, Y.; Wang, S.; Song, C.; Gao, B. Prokaryotic and Eukaryotic Horizontal Transfer of Pogo and Tc1/mariner Transposons in the Human Genome. *PLoS Biol.* 2005, 3, e110. [CrossRef] [PubMed]

28. Tarlinton, R.E.; Meers, J.; Young, P.R. Retroviral Invasion of the Koala Genome. *Nature 2006*, 442, 79–81. [CrossRef] [PubMed]

29. Tarlinton, R.E.; Meers, J.; Young, P.R. Retroviral Invasion of the Koala Genome. *Nature 2006*, 442, 79–81. [CrossRef] [PubMed]

30. Piskurek, O.; Okada, N. Poxviruses as Possible Vectors for Horizontal Transfer of Retroelements from Reptiles to Mammals. *Proc. Natl. Acad. Sci. USA* 2007, 104, 12046–12051. [CrossRef] [PubMed]

31. Kidwell, M.G. Horizontal Transfer of P Elements and Other Short Inverted Repeat Transposons. In *Transposable Elements and Evolution*; Springer: Berlin/Heidelberg, Germany, 1993; pp. 158–172.

32. Yuan, Y.-W.; Wessler, S.R. The Catalytic Domain of All Eukaryotic Cut-and-Paste Transposase Superfamilies. *Proc. Natl. Acad. Sci. USA* 2011, 108, 7884–7889. [CrossRef]

33. Kordis, D.; Gubensek, F. Unusual Horizontal Transfer of a Long Interspersed Nuclear Element between Distant Vertebrate Classes. *Proc. Natl. Acad. Sci. USA* 1998, 95, 10704–10709. [CrossRef]

34. Shao, H.; Tu, Z. Expanding the Diversity of the IS630-Tc1-Mariner Superfamily: Discovery of a Unique DD37E Transposon and Expansion of the Pogo-like Transposable Elements. *Genetics 2001*, 159, 1109–1115. [CrossRef] [PubMed]

35. Tellier, M.; Bouuaert, C.C.; Chalmers, R. Mariner and the ITm Superfamily of Transposons. In *Mariner Transposons: Diversity and Evolution*; ASM Press: Washington, DC, USA, 2015; pp. 753–772.

36. Coy, M.R.; Tu, Z. Gambol and Tc1 Are Two Distinct Families of DD34E Transposons: Analysis of the Anopheles Gambiae Genome. *Genes Genom.* 2016, 8, 1098–1117. [CrossRef] [PubMed]

37. Zhang, H.-H.; Shen, Y.-H.; Xiong, X.-M.; Han, M.-J.; Zhang, X.-G. Identification and Evolutionary History of the DD41D Sibling Family of DD34E/Tc1 Transposons in Animals. *Mol. Biol. Evol.* 2020, 37, 102–117. [CrossRef] [PubMed]

38. Zhang, H.H.; Li, G.Y.; Xiong, X.M.; Han, M.J.; Zhang, X.G.; Dai, F.Y. TRT, a Vertebrate and Protozoan Tc1-like Transposon: Current Activity and Horizontal Transfer. *Genome Biol. Evol.* 2016, 8, 2994–3005. [CrossRef] [PubMed]

39. Coy, M.R.; Tu, Z. Gambol and Tc1 Are Two Distinct Families of DD34E Transposons: Analysis of the Anopheles Gambiae Genome. *Genes Genom.* 2016, 8, 1098–1117. [CrossRef] [PubMed]

40. Zhang, H.-H.; Shen, Y.-H.; Xiong, X.-M.; Han, M.-J.; Zhang, X.-G. Identification and Evolutionary History of the DD41D Transposons in Insects. *Genes Genom.* 2016, 38, 109–117. [CrossRef] [PubMed]

41. Zhang, H.H.; Li, G.Y.; Xiong, X.M.; Han, M.J.; Zhang, X.G.; Dai, F.Y. TRT, a Vertebrate and Protozoan Tc1-like Transposon: Current Activity and Horizontal Transfer. *Genome Biol. Evol.* 2016, 8, 2994–3005. [CrossRef] [PubMed]

42. Sang, Y.; Gao, B.; Diaby, M.; Chen, C.; Wang, X.; Ivics, Z.; Song, C. Incomer, a DD36E Family of Tc1/mariner Transposons, Invaded Vertebrates Very Recently. *Genome Biol. Evol.* 2020, 12, 66–76. [CrossRef] [PubMed]

43. Zhang, H.-H.; Shen, Y.-H.; Xiong, X.-M.; Han, M.-J.; Zhang, X.-G. Identification and Evolutionary History of the DD41D Transposons in Vertebrates. *Genome Biol. Evol.* 2021, 13, 107143. [CrossRef] [PubMed]

44. Wang, S.; Diaby, M.; Puzakov, M.; Ullah, N.; Wang, Y.; Danley, P.; Chen, C.; Wang, X.; Gao, B.; Song, C. Divergent Evolution Profiles of Tc1/mariner Transposons in Eukaryotes. *Mol. Phylogenet. Evol.* 2021, 161, 107143. [CrossRef] [PubMed]

45. Shen, D.; Gao, B.; Miskev, C.; Chen, C.; Sang, Y.; Zong, W.; Wang, S.; Wang, Y.; Wang, X.; Ivics, Z.; et al. Multiple Invasions of Visitor, a DD41D Family of Tc1/mariner Transposons, throughout the Evolution of Vertebrates. *Genome Biol. Evol.* 2020, 12, 1060–1073. [CrossRef] [PubMed]

46. Sang, Y.; Gao, B.; Diaby, M.; Zong, W.; Chen, C.; Shen, D.; Wang, S.; Wang, Y.; Ivics, Z.; Song, C. Incomer, a DD36E Family of Tc1/mariner Transposons Newly Discovered in Animals. *Mol. DNA* 2019, 10, 45. [CrossRef] [PubMed]

47. Muñoz-López, M.; García-Pérez, J.L. DNA Transposons: Nature and Applications in Genomics. *Curr. Genom.* 2010, 11, 115–128. [CrossRef] [PubMed]

48. Nguyen, D.H.; Hermann, D.; Caruso, A.; Tastard, E.; Marchand, J.; Rouault, J.D.; Denis, F.; Thiriet-Rupert, S.; Casse, N.; Morant-Manceau, A. First Evidence of Mariner-like Transposons in the Genome of the Marine Microalgam Amphora Auctuiscula (Bacillariophyta). *Protis* 2014, 165, 730–744. [CrossRef] [PubMed]

49. Todor, M.; Lobocka, M.; Goodell, M.; Pettitt, J.; O’Hare, K. The Pogo Transposable Element Family of Drosophila Melanogaster. *MGG Mol. Genet. Genet.* 1992, 126–134. [CrossRef] [PubMed]

50. Smit, A.F.; Riggs, A.D. Tiggers and DNA Transposon Fossils in the Human Genome. *Proc. Natl. Acad. Sci. USA* 1996, 93, 1443–1448. [CrossRef] [PubMed]

51. Liu, Y.; Zong, W.; Diaby, M.; Lin, Z.; Wang, S.; Gao, B.; Ji, T.; Song, C. Diversity and Evolution of Pogo and Tc1/mariner Transposons in the Apoidea Genomes. *Biologia 2021*, 10, 940. [CrossRef] [PubMed]

52. Dufresne, M.; Lespinet, O.; Daboussi, M.J.; Hua-Van, A. Genome-Wide Comparative Analysis of Pogo-like Transposable Elements in Different Fusarium Species. *J. Mol. Evol.* 2011, 73, 230–243. [CrossRef] [PubMed]
51. Hey, P.; Robson, G.; Birch, M.; Bromley, M. Characterisation of Aft1 a Fot1/Pogo Type Transposon of Aspergillus Fumigatus. *Fungal Genet. Biol.* 2008, 45, 117–126. [CrossRef]

52. Nyyssonen, E.; Amutan, M.; Enfield, L.; Stubbs, J.; Dunn-Coleman, N.S. The Transposable Element Tan1 of Aspergillus Niger Var. Awamori, a New Member of the Fot1 Family. *Mol. Gen. Genet.* 1996, 253, 50–56. [CrossRef]

53. Levis, C.; Fortini, D.; Bryggo, Y. Flipper, a Mobile Fot1-like Transposable Element in Botrytis Cinerea. *Mol. Gen. Genet.* 1997, 254, 674–680. [CrossRef]

54. Kachroo, P.; Leong, S.A.; Chattoo, B.B. Pot2, an Inverted Repeat Transposon from the Rice Blast Fungus Magnaporthe Grisea. *MGG Mol. Gen. Genet.* 1994, 245, 339–348. [CrossRef]

55. Daboussi, M.-J.; Langin, T.; Bryggo, Y. Fot1, a New Family of Fungal Transposable Elements. *Mol. Gen. Genet.* 1997, 254, 674–680. [CrossRef]

56. Feschotte, C.; Mouches, G.; Robson, G. Evidence That a Family of Miniature Inverted-Repeat Transposable Elements (MITEs) from the Arabidopsis Thaliana Genome Has Arisen from a Pogo-like DNA Transposon. *Mol. Biol. Evol.* 2000, 17, 730–737. [CrossRef] [PubMed]

57. Gao, B.; Chen, W.; Shen, D.; Wang, S.; Chen, C.; Zhang, L.; Wang, W.; Song, C. Characterization of Autonomous Families of Tc1/mariner Transposons in Neoteleost Genomes. *Mar. Genom.* 2017, 34, 67–77. [CrossRef]

58. Gao, B.; Shen, D.; Xue, S.; Chen, C.; Cui, H.; Song, C. The Contribution of Transposable Elements to Size Variations between Four Teleost Genomes. *Mol. DNA* 2016, 7, 4. [CrossRef] [PubMed]

59. Dupeyrion, M.; Baril, T.; Bass, C.; Hayward, A. Phylogenetic Analysis of the Tc1/mariner Superfamily Reveals the Unexplored Diversity of Pogo-like Elements. *Mol. DNA* 2020, 11, 21. [CrossRef] [PubMed]

60. Yamada, K.D.; Tomii, K.; Katoh, K. Application of the MAFFT Sequence Alignment Program to Large Data—reexamination of the Usefulness of Chained Guide Trees. *Bioinformatics* 2016, 32, 3246–3251. [CrossRef] [PubMed]

61. Xia, X. DAMBE7: New and Improved Tools for Data Analysis in Molecular Biology and Evolution. *Mol. Biol. Evol.* 2018, 35, 1550–1552. [CrossRef]

62. Nguyen, L.T.; Schmidt, H.A.; Von Haeseler, A.; Minh, B.Q. IQ-TREE: A Fast and Effective Stochastic Algorithm for Estimating Maximum-Likelihood Phylogenies. *Mol. Biol. Evol.* 2015, 32, 268–274. [CrossRef]

63. Kalyaanamoorthy, S.; Minh, B.Q.; Wong, T.K.F.; von Haeseler, A.; Jermiin, L.S. ModelFinder: Fast Model Selection for Accurate Phylogenetic Estimates. *Nat. Methods* 2017, 14, 587–589. [CrossRef]

64. Harris, J.K.; Kelley, S.T.; Spiegelman, G.B.; Pace, N.R. The Genetic Core of the Universal Ancestor. *Genome Res.* 2003, 13, 407–412. [CrossRef]

65. Kachroo, P.; Leong, S.A.; Chattoo, B.B. Pot2, an Inverted Repeat Transposon from the Rice Blast Fungus Magnaporthe Grisea. *Mol. Biol. Evol.* 2000, 17, 730–737. [CrossRef] [PubMed]

66. Gilbert, C.; Cordaux, R. Horizontal Transfer and Evolution of Prokaryote Transposable Elements in Eukaryotes. *Genome Biol. Evol.* 2013, 5, 822–832. [CrossRef]

67. Zhang, H.-H.; Li, G.-Y.; Xiong, X.-M.; Han, M.-J.; Dai, F.-Y. Horizontal Transfer of a Novel Heterol in Insects. *Mol. Genet. Genomics* 2017, 292, 243–250. [CrossRef]

68. Platt, R.N.; Vandewege, M.W.; Ray, D.A. Mammalian Transposable Elements and Their Impacts on Genome Evolution. *Chromosom. Res.* 2017, 25, 24–43. [CrossRef]

69. Chalopin, D.; Naville, M.; Plard, F.; Galiana, D.; Volff, J.N. Comparative Analysis of Transposable Elements Highlights Mobilome Diversity and Evolution in Vertebrates. *Genome Biol. Evol.* 2015, 7, 567–580. [CrossRef]

70. Sotero-Caio, C.G.; Platt, R.N.; Suh, A.; Ray, D.A. Evolution and Diversity of Transposable Elements in Vertebrate Genomes. *Genome Biol. Evol.* 2017, 9, 161–177. [CrossRef]

71. Dupeyrion, M.; Leclercq, S.; Cerveau, N.; Bouchon, D.; Gilbert, C. Horizontal Transfer of Transposons between and within Crustaceans and Insects. *Mob. DNA* 2014, 5, 4. [CrossRef]

72. Dunemann, S.M.; Wasmuth, J.D. Horizontal Transfer of a Retrotransposon between Parasitic Nematodes and the Common Shrew. *Mob. DNA* 2019, 10, 24. [CrossRef]

73. Kimura, M. A Simple Method for Estimating Evolutionary Rates of Base Substitutions through Comparative Studies of Nucleotide Sequences. *J. Mol. Evol.* 1980, 16, 111–120. [CrossRef]

74. Kipling, D.; Warburton, P.E. Centromeres, CENP-B and Tigger Too. *Trends Genet.* 1997, 13, 141–145. [CrossRef]

75. Bourgeois, Y.; Boissinot, S. On the Population Dynamics of Junk: A Review on the Population Genomics of Transposable Elements. *Genes* 2019, 10, 419. [CrossRef] [PubMed]

76. Klein, S.J.; O’Neill, R.J. Transposable Elements: Genome Innovation, Chromosome Diversity, and Centromere Conflict. *Chromosom. Res.* 2018, 26, 5–23. [CrossRef] [PubMed]

77. Mitra, R.; Li, X.; Kapusta, A.; Mayhew, D.; Mitra, R.D.; Feschotte, C.; Craig, N.L. Functional Characterization of piggyBat from the Bat Myotis Lucifugus Unveils an Active Mammalian DNA Transposon. *Proc. Natl. Acad. Sci. USA* 2013, 110, 234–239. [CrossRef] [PubMed]

78. Wallau, G.L.; Vieira, C.; Loreto, É.L.S. Genetic Exchange in Eukaryotes through Horizontal Transfer: Connected by the Mobilome. *Mob. DNA* 2018, 9, 6. [CrossRef]

79. Tang, Z.; Zhang, H.-H.; Huang, K.; Zhang, X.-G.; Han, M.-J.; Zhang, Z. Repeated Horizontal Transfers of Four DNA Transposons in Invertebrates and Bats. *Mob. DNA* 2015, 6, 3. [CrossRef]
80. Novick, P.; Smith, J.; Ray, D.; Boissinot, S. Independent and Parallel Lateral Transfer of DNA Transposons in Tetrapod Genomes. *Gene* 2010, 449, 85–94. [CrossRef]

81. Oliveira, S.G.; Bao, W.; Martins, C.; Jurka, J. Horizontal Transfers of Mariner Transposons between Mammals and Insects. *Mob. DNA* 2012, 3, 14. [CrossRef]

82. Lin, X.; Faridi, N.; Casola, C. An Ancient Transkingdom Horizontal Transfer of Penelope-like Retroelements from Arthropods to Conifers. *Genome Biol. Evol.* 2016, 8, 1252–1266.

83. Suh, A.; Witt, C.C.; Menger, J.; Sadanandan, K.R.; Podsiadlowski, L.; Gertb, M.; Weigert, A.; McGuire, J.A.; Mudge, J.; Edwards, S.V.; et al. Ancient Horizontal Transfers of Retrotransposons between Birds and Ancestors of Human Pathogenic Nematodes. *Nat. Commun.* 2016, 7, 11396. [CrossRef]

84. Combes, C. *Parasitism: The Ecology and Evolution of Intimate Interactions*; University of Chicago Press: Chicago, IL, USA, 2001.

85. Manser, M.B.; Jansen, D.A.; Graw, B.; Hollén, L.I.; Bousquet, C.A.H.; Furrer, R.D.; Le Roux, A. Vocal Complexity in Meerkats and Other Mongoose Species. In *Advances in the Study of Behavior*; Elsevier: Amsterdam, The Netherlands, 2014; Volume 46, pp. 281–310.