**Abstract**

**Background:** The Tc1/mariner superfamily might represent the most diverse and widely distributed group of DNA transposons. Several families have been identified; however, exploring the diversity of this superfamily and updating its classification is still ongoing in the life sciences.

**Results:** Here we identified a new family of Tc1/mariner transposons, named *Incomer* (IC), which is close to, but distinct from the known family DD34E/Tc1. ICs have a total length of about 1.2 kb, and harbor a single open reading frame encoding a ~346 amino acid transposase with a DD36E motif and flanked by short terminal inverted repeats (TIRs) (22–32 base pairs, bp). This family is absent from prokaryotes, and is mainly distributed among vertebrates (141 species of four classes), including Agnatha (one species of jawless fish), Actinopterygii (132 species of ray-finned fish), Amphibia (four species of frogs), and Mammalia (four species of bats), but have a restricted distribution in invertebrates (four species in Insecta and nine in Arachnida). All ICs in bats (*Myotis lucifugus*, *Eptesicus fuscus*, *Myotis davidii*, and *Myotis brandtii*) are present as truncated copies in these genomes, and most of them are flanked by relatively long TIRs (51–126 bp). High copy numbers of miniature inverted-repeat transposable elements (MITEs) derived from ICs were also identified in bat genomes. Phylogenetic analysis revealed that ICs are more closely related to DD34E/Tc1 than to other families of Tc1/mariner (e.g., DD34D/mariner and DD×D/pogo), and can be classified into four distinct clusters. The host and IC phylogenies and pairwise distance comparisons between RAG1 genes and all consensus sequences of ICs support the idea that multiple episodes of horizontal transfer (HT) of ICs have occurred in vertebrates. In addition, the discovery of intact transposases, perfect TIRs and target site duplications of ICs suggests that this family may still be active in Insecta, Arachnida, frogs, and fish.

**Conclusions:** Exploring the diversity of Tc1/mariner transposons and revealing their evolutionary profiles will help provide a better understanding of the evolution of DNA transposons and their impact on genomic evolution. Here, a newly discovered family (DD36E/Incomer) of Tc1/mariner transposons is described in animals. It displays a similar structural organization and close relationship with the known DD34E/Tc1 elements, but has a relatively narrow distribution, indicating that DD36E/IC might have originated from the DD34E/Tc1 family. Our data also support the hypothesis of horizontal transfer of IC in vertebrates, even invading one lineage of mammals (bats). This study expands our understanding of the diversity of Tc1/mariner transposons and updates the classification of this superfamily.

**Keywords:** Tc1/mariner transposons, DD36E, Horizontal transfer
Background

Fragments of DNA sequences, which can autonomously replicate and translocate between chromosomes, are called transposable elements (TEs) or transposons. The first transposon was discovered by Barbara McClintock in maize [1]. They were subsequently detected in various organisms, such as bacteria, fungi, and insects. Based on their mechanism of transposition, TEs can be divided into two major classes: class I transposons transpose by DNA (also called DNA transposons); and class II transposons transpose by RNA (also called retrotransposons). Class II transposons can be further divided into three subcategories: the classical “cut-and-paste” DNA transposons, “rolling circle” DNA transposons, and “self-synthesizing” DNA transposons [2]. For a long time, transposons were designated as “junk DNA” in the genome and ignored. However, with the completion of large-scale genome sequencing projects, transposons have been found to exist in almost all genomes. It is now believed that TEs play important roles in genomic evolution and are regarded as important factors in determining genome expansion. They can simultaneously modify gene structures, provide sources of regulatory sequences [3, 4], and have important impacts on the structure and evolution of the genes of eukaryotes [5, 6].

Tc1/mariner is an important superfamily of “cut-and-paste” transposons, which was first discovered in Drosophila mauritiana [7, 8]. Elements in this superfamily are generally 1300–2400 base pairs (bp) in size and encode a 340-amino acid (aa) transposase that is flanked by TIRs and a TA target site duplication (TSD) at each end [9]. Tc1/mariner transposases contain a DNA-binding domain (DBD), which harbors two helix–turn–helix (HTH) motifs [10], a conserved GRPR-like sequence between the two HTH motifs [11], and a conserved catalytic amino acid triad motif (DDE/D), which usually interacts with a divalent cation (Mg^{2+} or Mn^{2+}) to perform the biochemical steps of the transposition reaction [12]. The distance between the first two “D” amino acids is variable across different transposase families, while the distance between the “D” and the third “D/E” is highly conserved. Accordingly, the length of this spacer has been used to characterize this transposase family [13]. Regarding variations of the DDE/D signature motif, Tc1/mariner elements have been classified into eight distinct families: DD34E/Tc1, DD34D/mariner, DD37E/TRT, DD37D/maT, DD39D, DD × D/pogo, DD41D, and DD × E [14]. Although many Tc1/mariner transposons have been identified in nature, only a few naturally active Tc1/mariner transposons have been discovered, such as Thm3 [15], Tc1 [16], Tc3 [17], and Mos1 [18]. This is because insertion of the transposon results in instability of the genome; therefore, long-term purifying natural selection, genetic drift, and mutations can result in gradual inactivation or even disappearance of transposons within the host genome [19, 20]. In addition, studies have shown that horizontal transfer (HT) of transposons is an important way to avoid inactivation and extinction. The HT of transposons between species is considered to be an important driver of genomic variation and biological innovation [21]. Almost all kinds of eukaryotic superfamily TEs have been proved to be capable of HT [21], while the Tc1/mariner superfamily seems to be more prone to this behavior [22]. More than 1200 HT events of Tc1/mariner have been reported to date [23].

Gaining further insight into the evolutionary profile of Tc1/mariner transposons will provide a better understanding of DNA transposon evolution and their impact on genome evolution. Here, we uncovered a new family of Tc1/mariner transposons, which is closely related to the DD34E/Tc1 family, but forms a distinct clade and harbors a DD36E motif in its DDE domain. We also report the taxonomic distribution of ICs, describe the structural organization of these elements, and provide evidence to support the occurrence of HT among vertebrates, and the invasion of this family in one lineage of mammals (bats).

Results

Taxonomic distribution of ICs

Using TBLASTN searching (https://blast.ncbi.nlm.nih.gov/BLAST) with the DD34E references (Passport, Prince, Quetzal, and Sleeping Beauty) as queries, we identified an intact Tc1/mariner-like transposon in Rhinella marina, where it harbors a newly identified transposase family with a DD36E motif, which is close to, but distinct from the previously known family of DD34E/Tc1. We named this newly discovered member of the Tc1/mariner superfamily Incomer or DD36E/IC. To investigate the evolutionary profile of this family, a TBLASTN search against all the available organism genomes of prokaryotes (bacteria and archaea) and the eukaryotes (Protozoa, Animalia, Fungi, Plantae, and Chromista) deposited at the National Center for Biotechnology Information (NCBI) database (https://www.ncbi.nlm.nih.gov) was performed using the IC transposase (346 aa) of R. marina as the query term. The obtained IC transposases were in turn used as query terms to identify more IC elements. These searches revealed that this family was absent in prokaryotes, and displayed a narrow distribution in eukaryotes with a main distribution in the animal kingdom (Fig. 1 and Additional file 1: Table S1). Further analysis revealed that the IC transposons were present in invertebrate and vertebrate groups, but that IC showed a very narrow distribution in invertebrates, only present in two classes (four species of Insecta and nine species of Arachnida) among the Arthropoda. In vertebrates, IC
transposons were found in 141 species among four classes, including Agnatha (one species of jawless fish), Actinopterygii (132 species of ray-finned fish), Amphibia (four species of frogs), and Mammalia (four species of bats). This family did not undergo significant expansion in most classes of animals, but radiated in the Actinopterygii, where it displays an extensive distribution in 132 species of 38 orders compared with other classes (Additional file 2: Figure S1).

In addition, most of the \( IC \) transposons are present as truncated copies: thus, in Actinopterygii, more than half of the species (76/132) contain full-length \( IC \) elements (with two detectable TIRs), but only 33 species contain intact \( IC \) copies (with an intact transposase and two detectable TIRs). Among the Anura, four species contain full-length \( ICs \) and three of them harbor intact copies of \( ICs \). Intact \( IC \) copies were also detected in one species of Agnatha, while all \( ICs \) in the four species (\( Myotis lucifugus, Eptesicus fuscus, M. davidii, M. brandtii \)) of the Chiroptera are present as truncated copies and an intact copy was not detectable. Among the Arthropoda, four species of Insecta and seven species of Arachnida contain full-length \( IC \) copies, with four and three species harboring intact \( IC \) elements, respectively (Table 1). The discovery of intact transposases, perfect TIRs, and TSDs of \( ICs \) suggests that this family could still be active in insects, Arachnida, frogs, and fish.

In addition, the copy number of \( ICs \) in the genomes of different organisms varies dramatically, from only one copy (> 90% of identity and > 1000 bp in length) in some organisms (e.g., \( Seriola dumerili, Amphilophus citrinellus, Gadiculus argenteus, \) and \( Xenocatantops brachycerus \)) to several thousand copies in a few species including \( R. marina, Esox lucius, \) and \( Clitarchus hookeri \). \( ICs \) have undergone significant amplification in a few species (e.g., \( R. marina, E. lucius \) and \( C. hookeri \)); i.e., more than 5000 copies of \( ICs \) were detected and more than half of them are full-length copies (2949 copies). \( ICs \) are also enriched in the genomes of \( E. lucius \) (5418 copies) and \( C. hookeri \) (3,956 copies) (Additional file 1: Table S1). Previous studies revealed that both the \( R. marina \) and \( C. hookeri \) genomes contain high repeat contents, with 63.9 and 51.6% of their genomes covered by repeats, respectively [24, 25]. These data indicate that some organisms might be more susceptible to HT of transposons and tend to enrich repeated copies in their genomes.

**Structural organization of \( ICs \)**

The structural organization of \( ICs \) was found to be highly conserved across different classes of animals including insects, Arachnida, fish, frogs, and bats. Most intact \( IC \) transposons had a total length of about 1.2 kb and harbored a single open reading frame (ORF) encoding a protein of about 346 aa (range 335–382 aa) flanked by short TIRs (22–32 bp) (Table 1 and Fig. 2). The \( IC \) elements were found to be flanked by TA target site duplication (Table 1). The intact \( IC \) transposon in \( R. marina \), representing a typical structure of this family, is 1225 bp long, encoding a 346 aa transposase and flanked by 29 bp TIRs (Fig. 2). Several conserved motifs, including six predicted helices in two HTHs and GRPR in the N-terminal DBD, and a nuclear localization sequence (NLS), which are characteristic of \( Tc1/mariner \) transposases [11], were identified in most \( IC \) transposases by in silico prediction. The DDE signature and its spacing (36 aa) in the DDE domain seems to be highly conserved across the \( IC \) family (Fig. 2 and Additional file 2: Figure S2). All \( ICs \) in the four genomes of bats (\( M. lucifugus, E. fuscus, M. davidii, \) and \( M. brandtii \)) presented as truncated copies; the longest \( ICs \) in these species are 1220, 1487, 1056, and 1005 bp, respectively, and encode a truncated transposase (235 aa) containing a partial DBD and a DDE domain. Moreover, the TIR lengths of bat \( ICs \) also vary slightly in three bat species compared with the \( IC \) TIRs in the genomes of other organisms, with
126 bp in *M. lucifugus*, 51 bp in *M. davidii*, and 55 bp in *M. brandtii* (Fig. 2). We also found a high copy number of miniature inverted-repeat transposable elements (MITEs) derived from ICs in the four bat genomes and most of these have a length of about 810 bp. Some MITE copies also encode the truncated transposase (235 aa) (Fig. 2 and Table 2).

**Phylogenetic analysis and evidence for multiple HT events of ICs**

To accurately establish the evolutionary relationships of the IC elements that we identified, the conserved DDE domain of the identified IC transposases were aligned to the 28 known DNA transposases representing the eight families in the *Tc1/mariner* superfamily based on MAFFT v 7.310 [26]. The alignment was used for phylogenetic analysis using the maximum-likelihood method implemented in IQ-TREE [27], and the TP36_RB, which is an insertion element family identified in bacteria, and close to the *Tc1/mariner* transposases [28] was used as the outgroup. The polygenetic tree confirmed that all these elements identified belong to the DD36E/IC family, which is more closely related to the DD34E/Tc1 family than to other families of *Tc1/mariner* (e.g., DD34D/mariner and DD × D/pogo; Fig. 3). The deduction is also well supported by the highest transposase sequence identity between these two families (Fig. 4), and further confirmed by the phylogenetic tree generated by using the alignment of the full-length transposases (Additional file 2: Figure S3).

The above phylogeny showed that IC elements identified in this study could be classified into four major clusters: Cluster A includes five species (one frog and four bats); Cluster B includes 59 species (three frogs and 56 fishes); Cluster C includes five species (two fishes and three insects); and Cluster D includes four species (all insects; Additional file 2: Figure S4). Phylogenetic analysis also suggested that the host and IC phylogenies were incongruent (Fig. 3 and Additional file 2: Figure S5), which implied that IC elements might have been exposed to several episodes of HT. To test this, pairwise distances between recombination-activating gene 1 (*RAG1*) and all consensus sequences of ICs in vertebrate were calculated and compared, which are usually used to infer the HT events of transposons in vertebrates [29, 30]. As illustrated in Fig. 5, for almost all (177/196) pairwise comparisons, the distances computed for IC (average 0.121; standard deviation, SD ± 0.067; range 0.001–0.259) are much lower than those calculated for *RAG1* (average 0.278; SD ± 0.106; range 0.009–0.457) (Additional files 3: Table S2). TE s are known to evolve neutrally after insertion in a host genome [31]; thus, TE distances between taxa are expected to be higher than distances between orthologous genes and to evolve faster than the host genes that evolve under purifying selection because of functional constraints under vertical transmission of the TEs. The low pairwise IC distances, combining deep divergence times, with most species involved sharing a last common ancestor more than 110 million years ago (Ma), indicate multiple HT events of ICs in vertebrates.

To further illustrate the HT profiles of IC elements in animal, we compared the average sequence identities of IC elements across species and clusters, which was summarized in Fig. 6. And the sequence identity matrix showed that most ICs in cluster B represent higher sequence identities (> 78%; average 87.96 ± 5.41%) between species, indicating that the cluster B may represent a very young HT event, while high and low sequence identities of ICs between species co-exist in cluster A, C, and D, indicating that these cluster may experience young and old invasions of ICs.

**Discussion**

**Expanding the diversity of the Tc1/mariner superfamily**

Compared with other DNA transposons, the *Tc1/mariner* superfamily might not only be the most widely distributed group of transposons in nature, but also displays the highest diversity. Phylogenetic analyses based on the distinct “DDE/D” signatures of transposases from diverse organisms suggest that *Tc1/mariner* transposons comprise at least eight families in
The host of the earliest branching IC clade was the phylum Arthropoda, the next earliest branching clade included elements from Agnatha. However, here the phylogenetic trees generated by using both of the full-length transposases and the DDE domains indicated that the IC family is closest to the DD34E/Tc1 family; thus, an origin in the DD34E/Tc1 family for the entire group of ICs in metazoans is more plausible, given that several DD34E/Tc1 elements, such as Minos [34], Bari [35], S element [36], Quetzal [37], and Topi [38], were also identified in Arthropoda. To date, diverse DD34E/Tc1 elements have been identified and described [34–40]; the DD34E/Tc1 family seems to display a more extensive distribution than DD36E/IC and can be classified into several subfamilies, such as Passport-like, Frog Prince-like, SB-like, Bari-like, Minos-like [24], and Gambol [41], although the intra-group classification of DD34E/Tc1 is still ambiguous. The structural organization of ICs is very similar to some DD34E/Tc1 elements identified in the neoteleost genomes of Actinopterygii [32], Bari (Drosophila melanogaster) [35], and Topi (Anoplolepis gambei) [38] identified in Arthropoda, where these families are relatively shorter in total length (about 1200 bp) and contain a single ORF (about 340 aa) flanked by short TIRs (about 30 bp). The structural organization of transposases, including the protein motifs of six helices, GRPR, and NLS in the DDB domain, between ICs and DD34E/Tc1 is very similar as well [32, 35, 38]. Furthermore, our data also indicated that the IC family and DD34E/Tc1 have the highest transposase sequence identity compared to other families. Taken together, these data indicate that the DD36E/IC might originate from the DD34E/Tc1 family.

Table 2 Incomer in bats

| Species     | TE name   | Length | Transposase length | Copy number | % Ave. Divergence ±SE |
|-------------|-----------|--------|--------------------|-------------|-----------------------|
| M. lucifugus| IC-MITE1-Mylu | 1220   | 235                | 407         | 4.4 ± 0.08            |
|             | IC-MITE2-Mylu | 810    | 235                | 951         | 5.2 ± 0.09            |
| E. fuscus   | IC-MITE1-Epfu | 1487   | 235                | 367         | 3.9 ± 0.05            |
| M. davidii  | IC-MITE1-Myda | 1056   | 235                | 4           | NA*                  |
|             | IC-MITE2-Myda | 810    | 235                | 147         | 5.3 ± 0.06            |
| M. brandtii | IC-MITE1-Mybr | 1005   | 235                | 48          | 4.0 ± 0.15            |
|             | IC-MITE2-Mybr | 810    | 235                | 215         | 3.5 ± 0.06            |

SE standard error
* Average percent divergence could not be determined for full-length IC elements due to low copy number
Distribution and activity of ICs in animals

Compared with the DD34E/Tc1 family, which displays extensive expansion in invertebrates and vertebrates [32, 41, 42], even among fungi [43], ICs show a very relatively narrow distribution in invertebrates and are only present in 13 species of two classes (Insecta and Arachnida) of Arthropoda. In vertebrates, ICs were detected in 141 species of four classes (Agnatha, Actinopterygii, Osteichthyes, and Chondrichthyes) as well as in a few amphibians, reptiles, and birds. However, no ICs were found in mammals or birds, indicating a more restricted distribution compared to the DD34E/Tc1 family. This suggests that ICs may have been acquired or lost during evolution, or may have evolved differently to allow them to persist in a more limited set of species.
Amphibia, and Mammalia). ICs display a slight burst in the Actinopterygii with an expansion into 132 species of 38 orders and have even invaded the mammalian lineage (Chiroptera) lineage, that has been suggested to be more susceptible to HT of transposons than other groups, and have experienced HT events of most DNA transposons (hATs, piggyBacs, Tc1/mariner, and Helitron) [44]. Here we provide evidence to support another HT event from a newly discovered family of Tc1/mariner transposons in bats, suggesting that some DNA transposons tend to show recurrent invasion of some mammalian lineages. This was confirmed in the evolution of the hAT superfamily, which was also found to undergo repeated HT events in mammals [30]. These data also indicate that HT of DNA transposons has contributed significantly to shaping and diversifying the genomes of multiple mammalian species, although HT of DNA transposons is relatively rare in mammals. In addition, the taxonomic distribution of ICs revealed by this study might have been underestimated, because of inefficient sequencing.

![Fig. 4](image-url) Sequence identities between IC family and eight other families. The sequence identities were measured by pairwise comparisons of full-length transposases.

![Fig. 5](image-url) Pairwise distances of IC elements and RAG1. The distances are obtained from all possible pairwise comparisons (n = 196; labeled on the x-axis) between the four (Cluster A) and 20 (Cluster B) species in which ICs were identified and complete. The coding sequence (CDS) regions of the RAG1 gene in the NCBI database are available (Additional file 7: Text S3 and Additional file 8: Text S4).
or assembly technologies, or the unavailability of some genome sequences.

Several families of Tc1/mariner have been suggested to be active (e.g., Tc1, TRT, Tana1, and pogo) [15, 29, 32, 39, 45] and some of them have been shown to transpose experimentally, such as Passport and Thm3 in fish [15, 39]. Here, intact copies of ICs were identified in 33 species of bony fish, three species of frogs, one species of jawless fishes, and seven species of Arthropoda. They did not harbor internal stop codons or frameshift mutations and presented all expected functional domains, as well as intact TIRs, combining the narrow taxonomic distribution of this family, suggesting that IC is young and might be associated with current or recent activity in these host genomes.

**Conclusions**

Our results represent the first in silico evidence for a newly identified family (DD36E/IC) of the Tc1/mariner superfamily and uncover the evolutionary landscape of this family in nature. This family is about 1200 bp in total length, encoding a transposase of ~346 aa flanked by short TIRs (about 30 bp), and mainly distributed in vertebrates (141 species), with a restricted presence in invertebrates (13 species). This family can be subdivided into four distinct clusters based on the catalytic domain signature DD36E. Based on structural organization, protein motifs and phylogenetic analyses, the IC transposons are closely related to DD34E/Tc1 elements, indicating a recent common ancestor. Furthermore, evidence for HT events in vertebrates is well supported for this family. We have also demonstrated the presence of IC in the bat lineage of mammals. We propose an update of the classification of the Tc1/mariner superfamily and illustrate the evolutionary relationships among these distinct families.

**Methods**

**Identification and copy number determination of IC**

The IC family was first identified in R. marina by TBLASTN searching with the DD34E references (Passport, Prince, Quetzal, and Sleeping beauty), then its taxonomic distribution was investigated by a TBLASTN search against all the available organism genomes deposited at the NCBI database using the IC R. marina transposase (346 aa) as query. The IC transposon was considered to be present in one species when a unique DD36E motif of the transposon catalytic domain was detected. The obtained IC transposases were in turn used as queries to identify more IC elements. To determine...
the boundaries of these elements in each species, the best hits were extracted with a 2 kb flanking sequences, aligned using the ClustalW program within the BioEdit tool [46], and the transposon boundaries were then checked manually. In addition, copies (>10) in each species were also aligned using the ClustalW program within the BioEdit tool [46] and their consensus sequences were reconstructed using the above multiple alignments in each genome using DAMBE after gaps were removed [47]. If one genome sequence contained a low copy number (<10), the best hit was used as the representative sequence of IC in this species. Then, these consensus sequences were entered into BLASTN for each host genome to estimate copy numbers. All BLAST hits with more than 1000 bp in size and 90% identity were used to calculate copy numbers. The copy of the transposon possessing the complete TIR sequence and encoding the entire or longest transposase was used as a representative sequence for the transposon in the species for further structural organization and polygenetic analysis.

**Sequence analyses**

TIRs were manually checked by using the BioEdit tool [46]. The potential ORF of *Incomer* used in the present study was predicted by Genscan (http://hollywood.mit.edu/GENSCAN.html). Protein secondary structures of IC-encoded transposases were predicted using PSIPRED [48]. Putative NLS motifs were predicted using PSORT II Prediction as provided in the PSORT Internet server (http://psort.nibb.ac.jp/). Multiple alignments of these elements were created by MUSCLE [49]. Shading and minor manual refinements of these aligned sequences were deduced using GeneDoc [50]. The pairwise divergence between elements and the average divergence from the consensus sequence were calculated using Kimura’s 2-parameter method in MEGA software v. 7.2.06 [51]. Sequence identities between IC family and eight other families were measured with the pairwise comparisons of full-length transposases by using the BioEdit tool [46]. And sequence identities between IC elements among species were measured by pairwise comparisons of full-length IC consensus sequences, and ICs in 10 species in cluster B were selected as the representatives for this analysis.

**Phylogenetic and HT analyses**

The conserved DDE domain of the identified IC transposases and full-length transposases were aligned to the 28 known DNA transposases representing eight families from *Tc1/mariner* superfamily separately by MAFFT v 7.310 [26] (Additional file 4: Text S1 and Additional file 5: Text S2). The species that only had highly fragmented copies and incomplete DD36E motifs in their genome were not included in this analysis. Transposase sequences of DD34E/*Tc1*, DD34D/*Mariner*, DD37D/*maT*, DD39D, DD41D, DD35E, DD × D/*pogo* and DD37E/*TRT* were downloaded from GenBank. The best-suited aa substitution model for these data was the VT + G4 model according to BIC which were selected by ModelFinder embed in IQ-TREE program [27, 52]. Bootstrapped (1000 replicates) phylogenetic trees were inferred by using the maximum-likelihood method in IQ-TREE (v. 1.6.1) [27].

Coding sequence of *RAG1* genes were used in the comparison with transposon distance, with the purpose of testing HT hypothesis. Their accession numbers were listed in (Additional file 6: Table S3). Species that cannot find the complete CDS region of the *RAG1* gene in NCBI database are not included in this calculation. Multiple alignments of *RAG1* and IC were created using MUSCLE [49]. Then, comparison distances of *RAG1* and IC were calculated using MEGA software v. 7.2.06 [51] (pairwise deletion, maximum composite likelihood) based on two aligned files (Additional file 7: Text S3 and Additional file 8: Text S4).

**Supplementary information**

Supplementary information accompanies this paper at https://doi.org/10.1186/s13100-019-0188-x.

**Additional file**

**Table S1.** Taxonomic distribution of *Incomer*.  
**Additional file 2:** Figure S1–S5. **Figure S1:** Taxonomic distribution of IC elements in Actinopterygii. **Figure S2:** Alignment of domains of *Incomer* and DD34E/*Tc1* transposases. **Figure S3:** Full tree of IC elements with eight other members of the *Tc1/mariner* superfamily based on their full-length transposases. **Figure S4:** Full tree of IC elements with eight other members of the *Tc1/mariner* superfamily based on their DDE/D motifs. **Figure S5:** Time tree of species harboring IC elements.  
**Additional file 3:** Table S2. Distance of IC elements and *RAG1* genes and divergence time of each species using pairwise comparisons. (XLS 52 kb)  
**Additional file 4:** Text S1. Sequence alignment of transposase DDE/D domains used to calculate the tree.  
**Additional file 5:** Text S2. Sequence alignment of full-length transposase used to calculate the tree.  
**Additional file 6:** Table S3. Access number of *RAG1* genes. Species only with the complete CDS region of the *RAG1* gene in the NCBI database are listed.  
**Additional file 7:** Text S3. Alignment of CDS regions of *RAG1* genes.  
**Additional file 8:** Text S4. Alignment of IC elements.

**Abbreviations**

bp: base pairs; DBD: DNA-binding domain; HTH: Helix-turn-helix; Ma: Million years ago; MITEs: Miniature inverted-repeat transposable elements; NLS: Nuclear localization sequence; *RAG1*: Recombination-activating gene 1; TEs: Transposable elements; TIRs: Terminal inverted repeats.
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Author’s contributions
CS and ZI conceived the study; BG participated in its design. BG, YS, MD, WZ, CC, DS, SW, YW performed the analysis. CS and BG wrote the manuscript. All authors have read and approved the final manuscript.

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Availability of data and materials
All data generated or analysed during this study are included in this published article and its supplementary information files.

Ethics approval and consent to participate
Not applicable.

Consent for publication
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Competing interests
The authors declare that they have no competing interests.

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