

Family of Tc1-like elements from fish genomes and horizontal transfer

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Abstract

The involvement of horizontal transfer (HT) in the evolution of vertebrate transposable elements (TEs) is a matter of an ongoing debate. The phylogenetic relationships between Tc1 TEs, based on limited dataset have been previously used to infer a case of Tc1 HT between the genomes of fish and frogs. Here this hypothesis has been critically evaluated by the experimental approach including comparative data on the range of fish species available today. The distribution of a Tc1 subfamily of TE in selected fish species was investigated by PCR with a single primer complementary to ITRs and showed that they are widespread in the studied 17 fish species. They belong to five different subfamilies of Tc1 TEs, as revealed by the comparison with current genomic data for fish and amphibians. The original hypothesis would get much weaker support from the current data, although at least one novel potential and more convincing case of HT was identified between genomes of Perciformes fish. An interesting case of recombination-driven mobilisation of a degenerated TE by distantly related TE from different subfamily was discovered in the genome of pike. The occurrence of such cases widens the range of TE elements identifiable with the employed experimental approach. Further similar studies would help to explain the evolution of the multiple Tc1 lineages including species for which full genome sequences will not be available soon.

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1. Introduction

Transposable elements (TE) are mobile genetic elements, widely distributed in prokaryotic and eukaryotic genomes. TE can accelerate rate of the genome evolution by generating mutations, e.g. frameshifts, point mutations, duplications or deletions and increase genetic plasticity (Kidwell and Lisch, 2000). Transposons utilise a cut-and-paste mechanism (Plasterk et al., 1999). They are characterized by inverted terminal repeats (ITRs) flanking gene encoding a transposase.

The superfamily of DNA transposons Tc1 mariners appears to be the most widespread family of transposons and occurs in

such groups as fungi, plants, ciliates and animals, including nematodes, arthropods, fish, frogs and human. Tc1-like element consists of 54 bp ITRs flanking the transposase gene. It is present in the genomes of various species but seems to be particularly spread in the fish and amphibian species (Radice et al., 1994). Predominant majority of these transposons are defective in their transposase gene because of deletions, insertions or base substitutions leading to in-frame termination within this gene. It causes inactivity of the transposon and since the mutation event the transposon becomes a permanent component of the genome, a genetic fossil accumulating mutations.

Distribution and diversity of active and inactive transposons may be explained by appropriate model of their evolution. A general model assumes that transposable element invades the germline of an organism, through some vectors like viruses (Lohe et al., 1995; Miskey et al., 2005; Sinzelle et al., 2006). The transposons increase copy number within a genome during transposition events and afterwards spread through the

Abbreviations: bp, base pair; PCR, polymerase chain reaction; RFLP, restriction-fragment length polymorphism; SDS, sodium dodecyl sulfate; SSC, 0.15 M NaCl/0.015 M Na₃* citrate pH 7.6; U, unit; MYA, million years ago; ME, minimum evolution; MP, maximum parsimony; NJ, neighbour joining.

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populations in processes of sexual reproduction. Thus inherited transposons are then donated to the progeny (vertical transmission). They are continuously subjected to an influence of accumulating random mutations (vertical inactivation). However, the transposase produced by other functional elements may mobilise in trans the mutated copies of TE in the same genome. Eventually, mutations inactivate all the copies present in the genome. Therefore, with time, the rate of propagation slows down, and finally, due to random genetic drift, active or inactive transposons can be eliminated from the host genome in the process named a stochastic loss.

Some transposons may undergo a horizontal transfer or transmission (HT) from a host species to a different, reproductively isolated species. In this way they start their life cycle over again. HTs are thought to be selection events because only active copies can establish a new lineage in new populations and species. The phenomenon of HT has been well documented for P transposable element, first detected in *Drosophila melanogaster*. It is suggested that P elements rapidly spread through natural populations of *D. melanogaster* within several last decades and entered the genome of this species by horizontal transmission from *Drosophila willistoni* (Daniels et al., 1990). HT is also documented as a major mechanism for the dissemination of mariner-like elements (MLE) among species, particularly within insects. For instance, it was found that *Drosophila erecta* contains copies of MLE from mellifera subfamily that is 97% identical in nucleotide sequence to an element from the cat flea *Ctenocephalis felis*. This relationship suggests a horizontal transmission between the ancestors of *C.*

felis and *D. erecta* (Lohe et al., 1995). Elements from the same subfamily were found in the genomes of insects representing four different orders: the earwig *Forficula auricularia*, the honey bee *Apis mellifera*, the Mediterranean fruit fly *Ceratitis capitata* and the blister beetle *Epicauta funebris* (Lampe et al., 2003). Phylogenetic analysis revealed that these full-length transposons were closely related and underwent a recent HT into four orders of insects. It has been argued that recent HT of MLE occurred in lineages of distantly related insects: the fruit fly *Drosophila ananassae*, the horn fly *Haematobia irritans*, the African mosquito *Anopheles gambiae* and the green lacewing *Chrysoperla plorabunda*, also on the basis of significant sequence similarity (Robertson and Lampe, 1995). MLE present in two distantly related hydrothermal crustaceans — Amphipod and Decapod genomes exhibited 99.5% similarity, which suggests a HT between them (Casse et al., 2006). HT of mariner elements between distant phyla (platyhelminthe and arthropods) has been postulated based on the 73% sequence similarity (Garcia-Fernandez et al., 1995). It was found that mariner elements from irritans subfamily are present in chordate genomes, including most craniates (Sinzelle et al., 2006). It has been shown that these elements rarely undergo HT during the vertebrate evolution and are maintained in genomes via vertical transmission. Ancestral irritans subfamily was vertically inherited during chordate evolution 750 MYA while observed phylogenetic distortions may be explained by differing rates of evolution, depending on the host species, stochastic loss and the presence of polymorphism in ancestor genomes.

Table 1
Numbers of examined specimens (*n*), their sampling sites and the results of PCR with primer I (PCR1) and PCR with primers APK1/APK2 (PCR2)

Family	Species	<i>n</i>	Sampling site	PCR1 (%)	PCR2 (%)
Pleuronectidae	<i>Platichthys flesus</i> (flounder)	142	97 from the Baltic Sea	100	100
			39 from the North Sea	100	100
			6 from the Liverpool Bay of the Irish Sea	100	100
	<i>Pleuronectes platessa</i> (plaice)	25	From the Baltic Sea	100	100
	<i>Reinhardtius hippoglossoides</i> (halibut)	3	From the Norwegian Sea	0	0
Scophthalmidae	<i>Scophthalmus maximus</i> (turbot)	82	37 from the Baltic Sea	71	45
			45 from the North Sea	98	8
Esocidae	<i>Esox lucius</i> (pike)	15	From the Zarnowieckie Lake (North Poland)	93	36
Salmonidae	<i>Salmo salar</i> (salmon)	7	From the Norwegian Sea	100	86
	<i>Oncorhynchus nerka</i> (red salmon)	6	From the Pacific Ocean	33	0
	<i>Salmo trutta</i> (trout)	19	16 from aquaculture, Goscicino (North Poland)	100	100
			3 from Ochrid Lake (Macedonia)	100	100
Percidae	<i>Perca fluviatilis</i> (perch)	33	27 from the Baltic Sea	85	0
			6 from the Zarnowieckie Lake (North Poland)	100	0
	<i>Stizostedion lucioperca</i> (zander)	11	3 from the Baltic Sea	100	0
			8 from the Lebskie Lake (North Poland)	100	12
Gobiidae	<i>Neogobius melanostomus</i> (round goby)	5	From the Baltic Sea	100	0
Merlucciidae	<i>Merluccius merluccius</i> (hake)	2	The Atlantic Ocean	50	0
Cyprinidae	<i>Cyprinus carpio</i> (carp)	2	From aquaculture, Goscicino (North Poland)	0	0
	<i>Rutilus rutilus</i> (roach)	5	From the Zarnowieckie Lake	20	0
	<i>Abramis brama</i> (bream)	11	3 from the Straszynskie Lake (North Poland)	0	0
			8 from Wyspowo Lake (North Poland)	100	0
	<i>Blicca bjoerkna</i> (white bream)	1	From the Zarnowieckie Lake	100	0
Clupeidae	<i>Clupea harengus</i> (herring)	4	From the Baltic Sea	100	0
Belonidae	<i>Belone belone</i> (garpike)	8	From the Baltic Sea	100	0

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