

Comparative studies on genome organization and evolution of some fish and crustacean species

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Cellular functions are carried out by complexes of coordinately functioning proteins. Understanding genome organization and gene functions in diverse organisms can reveal new insights into the evolution of the coordinated gene expression mechanisms. It is suggested that gene sets of different species may be mostly similar, while regulatory mechanisms of the gene expression are expected to be evolved in the species-specific manner. In this work, the genome-wide peculiarities of organization, transcription and evolution of 5 fish and 4 crustacean species were explored. The interspecies BLAST comparison of annotated protein sets revealed that inter-species protein diversity of crustaceans varies in much wider range. Moreover, in some cases, comparing with the crustaceans-crustaceans homology, the crustaceans-fish protein conservation seems to be higher. A search for possible traces of the mitochondrial DNA (mtDNA) in the nuclear genome of 8 crustacean and fish species discovered that only one crustacean and one fish species (*Armadillidium vulgare* and *Carassius auratus*) have quite long (≥ 500 bp) insertions of mtDNA in the nuclear genome, including the almost complete insertion of the organelle DNA in the *C. auratus* nuclear genome. Exploring the promoter architecture of 8 crustacean and fish nuclear genes revealed that (1) most of protein genes have, at least, one putative bidirectional promoter, and (2) hundreds of genes in these genomes are organized closely in the Head-to-Head manner with a potential BDP between them. It is concluded that BDPs may play a key role in the coordinated transcription of the crustacean and fish genes involved in the same cellular processes.

Keywords: Fish, crustaceans, mtDNA, bidirectional promoter, Head-to-Head genes

INTRODUCTION

Our current knowledge suggests that the aquatic vertebrates have been evolved from heavy benthic microphages to floating, mobile, and omnivorous. Vertebrates including the first fishes were probably originated about 530 million years ago during the Cambrian explosion. The evolution of fishes seems to occur in freshwater, while crustaceans mostly evolved in marine habitats (Wagele, 1992). The bony fish species (*Osteichthyes*) with about 27 000 living species represent more than 50% of all known vertebrate species

(Spaink et al., 2013). Crustaceans (crabs, lobsters, crayfish, shrimps, prawns, krill, woodlice and barnacles) diversified over the 455 million years ago form a large, diverse arthropod taxon. To date, 67,000 crustacean species have been described. Decapods (crabs, shrimp and lobsters), the most definitely recognizable crustaceans, include over 15 000 living and 3000 fossil species from 233 families (Wolfe et al., 2019; Stillman et al., 2008).

Cellular functions are carried out by complexes of coordinately functioning proteins. Therefore, the evolution of closely related species could involve the coordinately gains or losses of such gene groups.

Therefore, understanding genome organization and gene functions via comparative genomic and proteomic studies in extremely diverse organisms can reveal new insights into the evolution of the coordinated gene expression mechanisms (Martin and Fraser, 2018). In particular, it is supposed that gene (protein and non-coding RNA) sets of different species may be mostly similar, while regulatory mechanisms of the gene expression are expected to be evolved in the species-specific manner. The comparative genomic studies are very important for both fundamental science and practical use (the development of new medicines, sustainable aquaculture strategies, etc). In the last years, the great advances in genomic studies of bony fish species and some crustaceans were achieved (Spaink et al., 2013; Martin and Fraser, 2018). To date, the nuclear genomes of about 300 fish and over 10 crustacean species have been sequenced (<https://www.ncbi.nlm.nih.gov/genome/?term=animals>).

In general, all known eukaryotic genetic systems consist of the nuclear genome and semi-autonomous mitochondrial genome; plants have also the plastid genome. Mitochondrial functions were conserved almost in all eukaryotes studied and it is supposed that these organelles are of the endosymbiotic α -proteobacterial origin. The mitochondrial genome encodes only about 10% its proteins and most of mitochondrial functions are encoded in the nuclear genome, synthesized in the cytosole and transported to the organelles. In comparison with plants, animals have smaller mitochondrial genome (Adams et al., 2002; Burger et al., 2003; Herrmann et al., 2003). The current findings suggest that during the evolution most of the organellar genes were transferred to the nucleus and, to date, such a transfer process was discovered mostly in plants (Shahmuradov et al., 2003; Barbrook et al., 2006; Noutsos et al., 2007). Moreover, the organelle-to-nucleus gene transfer seems to be presently continued. Presently (Sheppard et al 2008).

Transcription is the first, decisive phase of the genome expression. Genome transcription (when, where and how) is regulated by RNA polymerases, transcription factors and promoters. Protein coding

genes are transcribed by RNA Polymerase II (Pol II; Solovyev et al., 2010; Danino et al., 2015). Previously, it was thought that promoters are unidirectional: they can initiate transcription only on a single strand of DNA. But, recently it was revealed that a single promoter can initiate transcription in both directions (Wei et al., 2011; Duttke et al., 2015; Bagchi and Iyer, 2016; Weingarten-Gabbay et al., 2019). Moreover, it was found that most genes are transcribed from alternative promoters. Using alternative promoters is regulated in a cell/tissue-specific manner, depending on the development stage and/or environmental signals. The alternative transcription initiation seems to be one of main principles of the RNA metabolism (Chen et al., 2016).

In this work, the genome-wide peculiarities of organization, transcription and evolution of some fish and crustacean species were explored. Results of these studies are presented below.

MATERIALS AND METHODS

For the inter-species comparison of protein sets, promoter studies and search for possible splinters of mitochondrial DNA (mtDNA) in the nucleus 4 crustacean (*Armadillidium vulgare*, *Eurytemora affinis*, *Hyalella azteca* and *Daphnia pulex*) and 5 fish species (*Carassius auratus*, *Neolamprologus brichardi*, *Oryzias latipes*, *Salmo salar* and *Cyprinus carpio*) with sequenced and annotated nuclear genome were selected (<https://www.ncbi.nlm.nih.gov/genome/browse#!/overview/>).

The pairwise comparison of DNA and protein sequences was performed by **BLAST** package (Altschul et al., 1997) and **BLAN** computer program (I.Shahmuradov, unpublished). To search for the nuclear copies of the mtDNA sequences based on the BLAST comparison of nuclear and mitochondrial genomes, we applied the **TRANSFER** computer program (I.Shahmuradov, unpublished).

Search for bi-directional Pol II promoters (BDPs) and exploration of the mutual location of neighbor protein genes in a genome was done by **TSShm** and **BDPGfinder** computer programs (I. Shahmuradov, unpublished).

Table 1. Summary of the reciprocal interspecies BLAST comparisons of all annotated proteins from 4 crustacean and 5 fish species

	Avu ^{Cr}	Eaf ^{Cr}	Haz ^{Cr}	Dpu ^{Cr}	Cca ^{Fish}	Cau ^{Fish}	Nbr ^{Fish}	Ola ^{Fish}	Ssa ^{Fish}
Avu^{Cr}, 19051*		199/246	430/437	326/356	224/652	221/990	212/332	193/399	230/857
Eaf^{Cr}, 30425*	246/199		277/229	492/400	342/733	269/1341	242/388	226/532	291/1037
Haz^{Cr}, 22749*	437/430	229/277		415/407	248/693	217/1211	215/365	198/503	249/890
Dpu^{Cr}, 30611*	356/326	400/492	407/415		418/1257	392/2225	372/750	350/997	403/2166
Cca^{Fish}, 63928*	652/224	733/342	693/248	1257/418		43432/69140	11469/8768	11115/12174	1578/29117
Cau^{Fish}, 96703*	990/221	1341/269	1211/217	2225/392	69140/43432		17985/7352	16930/9402	22184/15784
Nbr^{Fish}, 31372*	332/212	388/242	365/215	750/372	8768/11469	7352/17985		12284/15342	9884/21312
Ola^{Fish}, 44766*	399/193	532/226	503/198	997/350	12174/11115	9402/16930	15342/12284		12664/19639
Ssa^{Fish}, 97555*	857/230	1037/1037	890/249	2166/403	29117/15782	15784/22184	21312/9884	19639/12664	

Species selected for pairwise BLAST comparison: **Avu** – *A. vulgare*, **Eaf** – *E. affinis*, **Haz** – *H. azteca*, **Dpu** – *D. pulex*, **Cca** – *C. carpio*, **Cau** – *C. auratus*, **Nbr** – *N. brichardi*, **Ola** – *O. latipes*, **Ssa** – *S. salar*. **Cr**: crustaceans. Full-length homology level: $\geq 80\%$. * – number of analyzed protein sequences for every species

The **TSShm** program searches for CpG, non-CpG /TATA and non-CpG/TATA-less promoters in animal DNA sequences. Depending on the promoter class, the TSShm has the highest prediction accuracy among analogous methods (90-98%). The **BDPGfinder** program identifies the close H2H gene pairs that may be associated with BDP(s) by analyzing the genome-wide TSShm results and genome annotation files in the GenBank format. Hereinafter, a DNA region with a pair of TSSs on the opposite strands of DNA and at distance less than 300 bp is termed as BDP.

RESULTS AND DISCUSSION

To study trends in evolution of fishes and crustaceans, we performed the pairwise interspecies BLAST comparison of all annotated to date proteins from 4 crustacean and 5 fish species, including crustaceans *A. vulgare* (19051 proteins), *E. affinis* (30425), *H. azteca* (22749) and *D. pulex* (30611), fishes *C. auratus* (96703), *C. carpio* (63928), *N. brichardi* (31372), *O. latipes* (44766) and *S. salar* (97555). Results of the analysis are summarized in the Table 1. Although thousands of proteins from 5 fish species show the full-length high ($\geq 80\%$) level evolutionary conservation, the inter-species protein diversity of crustaceans seems to be high. Moreover, in some cases, comparing with the crustaceans-crustaceans homology, the crustaceans-fish protein conservation seems to be higher (see Table 1: marked

in grey). The biological relevance of these findings remains to be further investigated.

Further, we performed a search for possible traces of the mtDNA in the nuclear genome of 4 crustacean (*A. vulgare*, *E. affinis*, *H. azteca* and *D. pulex*) and 4 fish species (*C. auratus*, *N. brichardi*, *S. salar* and *C. carpio*). For this purpose, an intra-species **BLAST** comparison of the DNA sequences of the nuclear and mitochondrial genomes for each species was performed, and the obtained BLAST results were analyzed using **BLAN** and **transfer** programs. Contrary to the previously discovered facts on higher plants (Adams et al. 2002; Shahmuradov et al. 2003; Shahmuradov et al., 2010), it was revealed that only one crustacean (*A. vulgare*) and one fish (*C. auratus*) species have long (≥ 500 bp) insertions of mtDNA in the nuclear genome (Table 2).

Table 2. mtDNA insertions in the nuclear genomes of analyzed crustacean and fish species

Organism	Length of mitochondrial genome, bp	Length of the mtDNA insertion, bp
<i>A. vulgare</i>	13939	2545
		1168
<i>C. auratus</i>	16580	15658

In particular, for the first time, almost complete insertion of the mtDNA was found in the fish nuclear genome. The results of this study and previous studies on the existence of the striking differences in the number and total length of DNA sequences of mitochondrial origin in the nuclear genomes suggest

that the Mitochondrion-to-Nucleus transfer in crustacean and fish species occurred after these species separated from a common ancestor.

In any genome, the neighbor genes may be organized in Tail-to-Head (T2H) or Tail-to-Tail (T2T) or Head-to-Head (H2H) manner (Fig. 1). In particular, the non-stop transcription of the closely located T2H neighbor genes may produce chimeric transcripts (proteins). The closely located H2H genes might coordinately transcribed from the BDP between them. The H2H fashion of location of close gene pairs seems to be very important in a sense of the coordinated transcription (expression) of genes via the BDP(s).

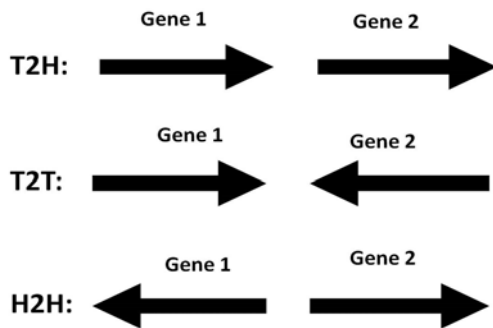


Figure 1. Schematic presentation of the T2H, T2T and H2H genes.

In this study, for 3 crustacean (*A. vulgare*, *E. affinis* and *H. azteca*) and 5 fish (*C. carpio*, *C. auratus*, *N. brichardi*, *O. latipes* and *S. salar*) species, we performed (1) the genome-wide analysis of the mutual location of the neighbor genes, (2) a search for putative BDPs for all annotated protein genes

and (3) an identification of potential H2H gene pairs with BDP between them. Results of these studies are summarized in Table 3. Initially, using the **TSShm** tool, we performed search for CpG, non-CpG/TATA and non-CpG/TATA-less promoters in [-1000:+100] regions (+1 corresponds to the gene start) of these genes. Then, applying the **BDPfinder** tool, we explored the putative BDPs for every gene analyzed. At least, 1 putative BDP was identified for 73-83% of the protein genes in 8 species (see Table 3) where most of these promoters belong to the CpG class (data not shown).

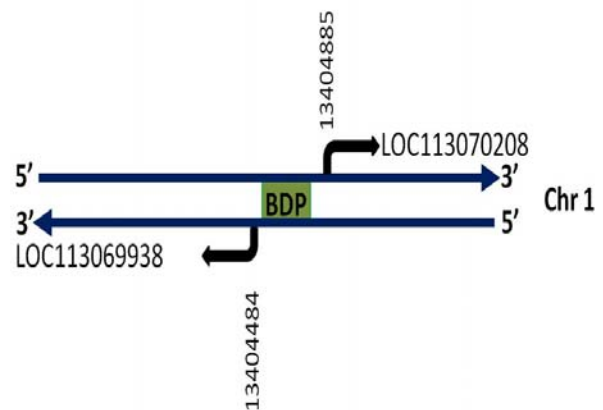


Figure 2. Bi-directional CpG-island promoter between neighbor genes LOC113069938 and LOC113070208 located on the opposite strands of the chromosome 1 of *C. auratus* (gold fish). These genes encode succinate-CoA ligase [ADP/GDP-forming] subunit alpha (mitochondrial; protein ID: XP_026098902.1) and CDGSH iron-sulfur domain-containing protein 2-like (protein ID: XP_026099249.1), respectively. Inter-genes distance – 401 bp, inter-TSSs distance - 196 bp.

Table 3. Some peculiarities of the genomic organization and promoter architecture of protein coding genes in 3 crustacean and 5 fish species

	T2H	T2T	H2H	BDPs	BDPGs
<i>Avu^{Cr}</i> , 6152*	1975/55 ^a /0 ^b	1073/20 ^a /58 ^b	739/18 ^a /66 ^b	5121; 83%	13
<i>Eaf^{Cr}</i> , 19743*	11504/615 ^a /676 ^b	3337/105 ^a /206 ^b	3339/341 ^a /555 ^b	14935; 76%	300
<i>Haz^{Cr}</i> , 17842*	7890/408 ^a /179 ^b	3510/397 ^a /238 ^b	3003/309 ^a /140 ^b	14425; 81%	303
<i>Cca^{Fish}</i> , 24424*	12986/272 ^a /507 ^b	5720/161 ^a /279 ^b	5718/637 ^a /592 ^b	18785; 77%	550
<i>Cau^{Fish}</i> , 39645*	21063/700 ^a /375 ^b	9311/701 ^a /755 ^b	9293/1671 ^a /960 ^b	3096; 78%	1416
<i>Nbr^{Fish}</i> , 18486*	9298/157 ^a /148 ^b	4310/328 ^a /195 ^b	4315/717 ^a /312 ^b	14117; 76%	599
<i>Ola^{Fish}</i> , 22040*	11390/496/204 ^b	5284/405 ^a /613 ^b	5340/997 ^a /831 ^b	17331; 79%	883
<i>Ssa^{Fish}</i> , 6719*	3517/124 ^a /78 ^b	1610/91 ^a /121 ^b	1606/224 ^a /230 ^b	4904; 73%	175

* – number of analyzed protein genes for every species. ^a – pairs of genes located at distance of ≤1000 bp and ≥50 bp; ^b – number of overlapping gene pairs. The designation of the species is the same as in table 1.

At last, H2H pairs of the neighbor and non-overlapping genes at distance from 50 bp to 1000 bp were investigated for an existence of putative BDP(s) between them. It was found that the number of H2H genes with shared BDP varies in quite diapason in the crustacean and fish species explored (Table 3).

In particular, excepting the *S. salar*, all fish species are significantly enriched in H2H pairs with putative BDP. An example of the adjacent H2H pair with a putative BDP between them is illustrated in Fig. 2. Summarizing these results, it can be concluded that BDPs may play a key role of in the coordinated transcription of genes involved in the same cellular processes.

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Bəzi balıq və xərçəng növlərinin genomlarının təşkili və təkamülünün müqayisəli tədqiqi

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Hüceyrə funksiyaları razılaşıdırılmış şəkildə işləyən zülal kompleksləri tərəfindən həyata keçirilir. Müxtəlif orqanizmlərdə genomun təşkilini və gen funksiyalarını aydınlaşdırılmaqla genlərin razılaşıdırılmış ekspresiyası mexanizmlərinin təkamülündə yeni məqamları aşkar etməyə imkan verə bilər. Güman olunur ki, müxtəlif növlərdə gen dəstlərinin çoxu oxşar ola bilər, lakin gen ekspressiyasının tənzimlənmə mexanizmləri növ-spesifik yönümdə təkamül edir. Bu işdə 5 balıq və 4 xərçəng növündə genomun təşkili, transkripsiyası və təkamül xüsusiyyətləri araşdırılmışdır. Tədqiq olunmuş xərçəngkimilər və balıqların annotasiya olunmuş zülal dəstlərinin növlərarası BLAST müqayisəsi xərçənglərdə zülalların müxtəlifliyinin daha geniş diapazonda dəyişdiyini aşkar etmişdir. Üstəlik, bəzi hallarda, xərçəng-xərçəng oxşarlığı ilə müqayisədə, xərçəng-balıq zülallarının konservativlik dərəcəsi daha yüksəkdir. 8 xərçəngkimilər və balıq növlərinin nüvə genomunda mitoxondri DNT-sinin (mtDNT) izlərinin axtarışı göstərmişdir ki, yalnız bir xərçəng və bir balıq növünün (*Armadillidium vulgare* və *Carassius auratus*) nüvə genomunda mtDNT-sinin uzun (≥ 500 nc) insersiyaları mövcuddur. O cümlədən, *C. auratus* növünün nüvə genomunda organella DNT-sinin, demək olar ki, bütöv insersiyası vardır. 8 xərçəng və balıq növünün nüvə genlərinin promotor arxitekturasını araşdırarkən, (1) zülal genlərinin çoxunun, ən azı, bir ikiistiqamətli promotorunun (İİP) olduğu və (2) bu genomlarda yüzlərlə cüt genlərin yaxın qonşuluqda Baş-Başa yerləşmişləri və onların arasında potensial İİP mövcuddur. Belə bir nəticəyə gəlinmişdir ki, İİP-lar xərçəng və balıqlarda eyni hüceyrə prosesində iştirak edən genlərinin razılaşıdırılmış transkripsiyasında mühüm rol oynaya bilər.

Açar sözlər: Balıq, xərçəngkimilər, mtDNT, ikitərəfli promotor, baş-baş genlər

Сравнительные исследования организации генома и эволюции некоторых видов рыб и ракообразных

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Функции клетки осуществляются благодаря согласованной работе комплексов функционирующих белков. Уточнение организации генома и функций генов у различных организмов создаст возможность для выявления новых аспектов в понимании эволюции механизмов скоординированной экспрессии генов. Предполагается, что наборы генов разных видов могут быть в основном похожими, в то время как, механизмы регуляции экспрессии генов, как ожидается, будут развиваться видоспецифичным образом. В данной работе исследованы полногеномные особенности организации, транскрипции и эволюции 5 видов рыб и 4 видов ракообразных. Межвидовое сравнение аннотированных наборов белков с помощью BLAST показало, что межвидовое белковое разнообразие ракообразных варьирует в гораздо более широком диапазоне. Более того, в некоторых случаях, по сравнению с гомологией ракообразные-ракообразные, консервация белка ракообразные-рыба оказывается более высокой. Поиск возможных следов митохондриальной ДНК (мтДНК) в ядерном геноме 8 видов ракообразных и рыб показал, что только у одного вида ракообразных и одного вида рыб (*Armadillidium vulgare* и *Carassius auratus*) довольно длинные (≥ 500 п.н.) вставки мтДНК в ядерный геном, включая почти полную вставку ДНК органелл в ядерный геном *C. auratus*. Изучение промоторной архитектуры 8 ядерных генов ракообразных и рыб показало, что (1) большинство генов белков имеют, по крайней мере, один предполагаемый двунаправленный промотор, (2) сотни генов в этих геномах организованы близко друг к другу в манере «голова к голове» с потенциальным двунаправленным промотором (ДНП) между ними. Сделано заключение, что ДНП могут играть ключевую роль в координированной транскрипции генов ракообразных и рыб, участвующих в одних и тех же клеточных процессах.

Ключевые слова: Рыба, ракообразные, мтДНК, двунаправленный промотор, голова-к-голове гены