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THE COMPLETE MITOCHONDRIAL GENOME OF SILVER CROAKER *Argyrosomus argentatus* (Perciforems; Sciaenidae): GENOME CHARACTERIZATION AND PHYLOGENETIC CONSIDERATION

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The complete mitochondrial genome sequence of the silver croaker, *Argyrosomus argentatus*, was obtained by using LA-PCR and sequencing. The mitogenome is 16485 bp in length, consists of 13 protein-coding genes, two ribosomal RNAs, 22 transfer RNAs, and a non-coding control region like those found in other vertebrates, with the gene order similar to that of typical teleosts. Most of the genes of *A. argentatus* were encoded on the H-strand, while the *ND6* and eight tRNA (Gln, Ala, Asn, Cys, Tyr, Ser (UCN), Glu and Pro)) genes were encoded on the L-strand. The reading frames of two pairs of genes overlapped: *ATPase8* and *6* and *ND4L* and *ND4* by ten and seven nucleotides, respectively. The origin of L-strand replication in *A. argentatus* was in a cluster of five tRNA genes (WANCY) and was 46 nucleotides in length. The conserved motif (5'-GCGGG-3') was found at the base of the stem within the tRNA^{Cys} gene. Within the control region, we identified all of the conserved motifs except for CSB-F.

***Keywords*: *Argyrosomus argentatus*, complete mitochondrial genome, sciaenidae, control region.**

The mitochondrial DNA (mtDNA) of vertebrates is a self-replicating, approximately 15–20 kb long, circular duplex molecule. It usually encodes 13 proteins, 22 transfer RNAs, and two ribosomal RNAs. Additionally, most of the determined vertebrate mtDNAs have a large non-coding region, highly variable in size and structure among same or different lineages, which contains signals for its replication and transcription [1, 2]. Mainly because of its maternal inheritance, lack of recombination and an accelerated mutation rate compared to that of the nuclear DNA, the use of mtDNA has become popular in phylogenetics studies, comparative and evolutionary genomics, population genetics and molecular evolution among various animal taxa [3, 4].

The silver croaker, *Argyrosomus argentatus*, is a benthonic oceanodromous fish that inhabits sandy or muddy bottoms in coastal inlets to a depth of 140 m. It is mainly distributed from Japan to the East China Sea, the Yellow Sea, the Bohai Sea and the Indo Pacific [5, 6]. The silver croaker is one of the major components of benthonic fish assemblages in coastal waters of China, supporting an important commercial fishery, thus several programs for investigation of the silver croaker have been launched with the aim of rational utilization and resource management. Intensive studies have been performed in the areas of population dynamics, feeding habits, artificial incubation and reproductive cycle [7–9]. However, only a few studies concerning the genetic structure or phylogeny have been conducted on the silver croaker, and to date, there are no detailed studies on the characteristics of the complete mitochondrial genome of this species.

In this study, we present the complete nucleotide sequence for the mitochondrial genome of the silver croaker and determine its mitochondrial genomic structure. We also report on the organization, gene arrangement, and codon usage of silver croaker mitochondrial DNA and compare it to those of other Perciformes species. We expect that the present result will facilitate the further investigations of the molecular evolution of the Sciaenidae.

EXPRERIMENTAL

Sample collection and DNA isolation. Specimens of the silver croaker captured from the wild were obtained from a local fish market in China, and the whole tail fin was immediately preserved in 100% ethanol. Mitochondrial DNA was extracted using the high-concentration-salt precipitation method [10] and kept at –20°C.

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Table 1. Primers used in the amplifications

Primer	Sequence (5'-3')
Dloop-F	CACCCYTRRCTCCCAAAGCYA
Dloop-R	GGTGCGGRKACTTGCATGTRTAA
COI-F	AGTATAAGCGTCTGGGTAGTC
COI-R	CCTGCAGGAGGAGGAGAYCC
LA-1F	AAATCAAATAAGTGGTGACAGGCGAGAC
LA-1R	GTAAATAGTGGGAATCAATGAACGAAGC
LA-2F	GTGGGCGGACTGACAGGAATCGTATTAGC
LA-2R	TGGGCTGTAGTTGTTCAAGTTGACGAGATG

Amplification and sequencing. Two pairs of universal primers (D-loop-F/R and COI-F/R) were used to amplify the segments of the control region and COI, respectively [11, 12]. 50 μL of the PCR mixture contained 0.2 μM of each primers, 5.0 μL of 10×Taq Plus polymerase buffer, 0.2 mM dNTPs, 2 unit of *Taq* Plus DNA polymerase with proof-reading characteristic ("TIANGEN"), and 1 μL of the DNA template. PCR was performed on a PTC-200. The PCR conditions were as follows: predenaturation at 94°C for 4 min; 35 cycles of denaturation at 94°C for 50 s, annealing at 60°C for 60 s, extension at 72°C for 1 min; and a final extension at 72°C for 10 min. The PCR products were electrophoresed on a 1% agarose gel in order to check the integrity and visualized by the Molecular Imager Gel Doc XR system ("BioRad", USA). The PCR products were purified using a QIAE II Gel Extraction Kit ("Qiagen"). The purified fragments were ligated into PMD18-T vectors ("Takara") and transformed into TOP10 cells ("TIANGEN") according to the standard protocol. Positive clones were screened via PCR with M13(+/–)-primers. Amplicons were sequenced using an ABI 3730 automated sequencer with M13(+/–)-primers. To amplify the complete mitochondrial genome, two Pairs of LA-PCR primers (LA-1F/1R and LA-2F/2R), designed basing on the sequence of control region and the COI segments were used (Table 1). The amplified products were purified and then sequenced directly. All of the obtained sequence fragments were edited in Sequencher™ (Gene Code, Ann Arbor, MI, USA) for a contig assembly to make the complete mitochondrial genome.

Sequence analysis. Annotation of protein-coding and ribosomal RNA (rRNA) genes and determination of their gene boundaries were carried out using reference sequences of the Sciaenidae available in the GenBank. Most tRNA genes and their secondary cloverleaf structures were identified in tRNAscan-SE1.21 [13]. The remaining tRNA genes, which could not be found by tRNAscan-SE, were identified by sequence homology, secondary structures and specific anticodons. Nucleotide base frequencies and codon usage of protein-coding genes were determined using MEGA 4 [14]. The complete mitochondrial genome (mitogenome) sequence of the silver croaker was deposited in the public database GenBank under accession number NC_015202.

RESULTS AND DISCUSSION

Genome organization and structure

The complete nucleotide sequence of the L-strand of the silver croaker mtDNA was determined to be 16485 bp long, which is within the range of other teleost mitogenomes, and consisted of 13 protein-coding genes, two ribosomal RNA genes (rRNAs), 22 transfer RNA genes (tRNA), and a putative control region (Table 2, Fig. 1). The mitochondrial genome structure of the silver croaker is very similar to those found in other vertebrates; both the protein-coding gene lengths and gene order in the mitogenomes are identical to previously reported patterns [15–21]. Specifically, the genes are similar in length to those found in other fish [22]. Also as in other vertebrates, most of the genes are encoded on the H-strand, and only the NADH dehydrogenase gene subunit (*ND*) 6 and eight tRNA genes ($tRNA^{Gln}$, $tRNA^{Ala}$, $tRNA^{Asn}$, $tRNA^{Cys}$, $tRNA^{Tyr}$, $tRNA^{Ser(UCN)}$, $tRNA^{Glu}$, and $tRNA^{Pro}$) are encoded on the L-strand. The silver croaker mitochondrial genes overlapped by a total of 38 bp in seven different locations with one to 20 bp long ovelaps. The mtDNA genome of the silver croaker also includes 13 intergenic spacers, ranging from 1 to 35 bp in length (69 bp in total), only one of which spans longer than 10 bp. Compared to the genes, the extent of the overlaps and spacers differs in the various fish mitochondrial genomes [23–25]. Analysis of the overall base composition (T: 26.3%; C: 30.2%; A:

Table 2. Characterizations of the mitochondrial genome of silver croaker, *Argyrosomus argentatus*

Gene	Position		Size, bp		Codon		Intergenic nucleotide**	Strand
	from	to	nucleotide	amino acid	initiation	stop*		
$tRNA^{Phe}$	1	68	68				0	H
12S rRNA	69	1018	947				2	H
$tRNA^{Val}$	1022	1094	73				1	H
16S rRNA	1096	2805	1710				0	H
$tRNA^{Leu(UUR)}$	2806	2879	74				0	H
ND1	2880	3851	972	323	ATG	TAA	4	H
$tRNA^{Ile}$	3856	3925	70				0	H
$tRNA^{Gln}$	3926	3996	71				–1	L
$tRNA^{Met}$	3996	4064	69				0	H
ND2	4065	5110	1046	348	ATG	TA-	0	H
$tRNA^{Trp}$	5111	5181	71				0	H
$tRNA^{Ala}$	5182	5250	69				3	L
$tRNA^{Asn}$	5254	5326	73				35	L
$tRNA^{Cys}$	5362	5427	66				0	L
$tRNA^{Tyr}$	5428	5497	70				1	L
CO1	5499	7055	1557	518	ATG	AGA	–5	H
$tRNA^{Ser(UCN)}$	7051	7121	71				3	L
$tRNA^{Asp}$	7125	7193	69				7	H
CO2	7201	7891	691	230	ATG	T–	0	H
$tRNA^{Lys}$	7892	7966	75				1	H
ATPase8	7968	8135	168	55	ATG	TAA	–1	H
ATPase6	8126	8809	684	227	ATG	TAA	0	H
CO3	8809	9593	785	261	ATG	TA-	0	H
$tRNA^{Gly}$	9594	9664	71				0	H
ND3	9665	10013	349	116	ATG	T–	0	H
$tRNA^{Arg}$	10014	10082	69				0	H
ND4L	10083	10379	297	98	ATG	TAA	–7	H
ND4	10373	11753	1381	460	ATG	T–	0	H
$tRNA^{His}$	11754	11822	69				0	H
$tRNA^{Ser(AGY)}$	11823	11889	67				6	H
$tRNA^{Leu(CUN)}$	11896	11967	72				–20	H
ND5	11948	13789	1842	613	GTG	TAA	–4	H
ND6	13786	14307	522	172	ATG	TAA	1	L
$tRNA^{Glu}$	14309	14376	68				1	L
Cytb	14378	15518	1141	380	ATG	T–	0	H
$tRNA^{Thr}$	15519	15590	72				4	H
$tRNA^{Pro}$	15595	15663	69				–15	L
Control region	15649	16485	836					H

* – TA- and T– represent incomplete stop codons.
** – Numbers correspond to the nucleotides separating adjacent genes. Negative numbers indicate overlapping nucleotides.

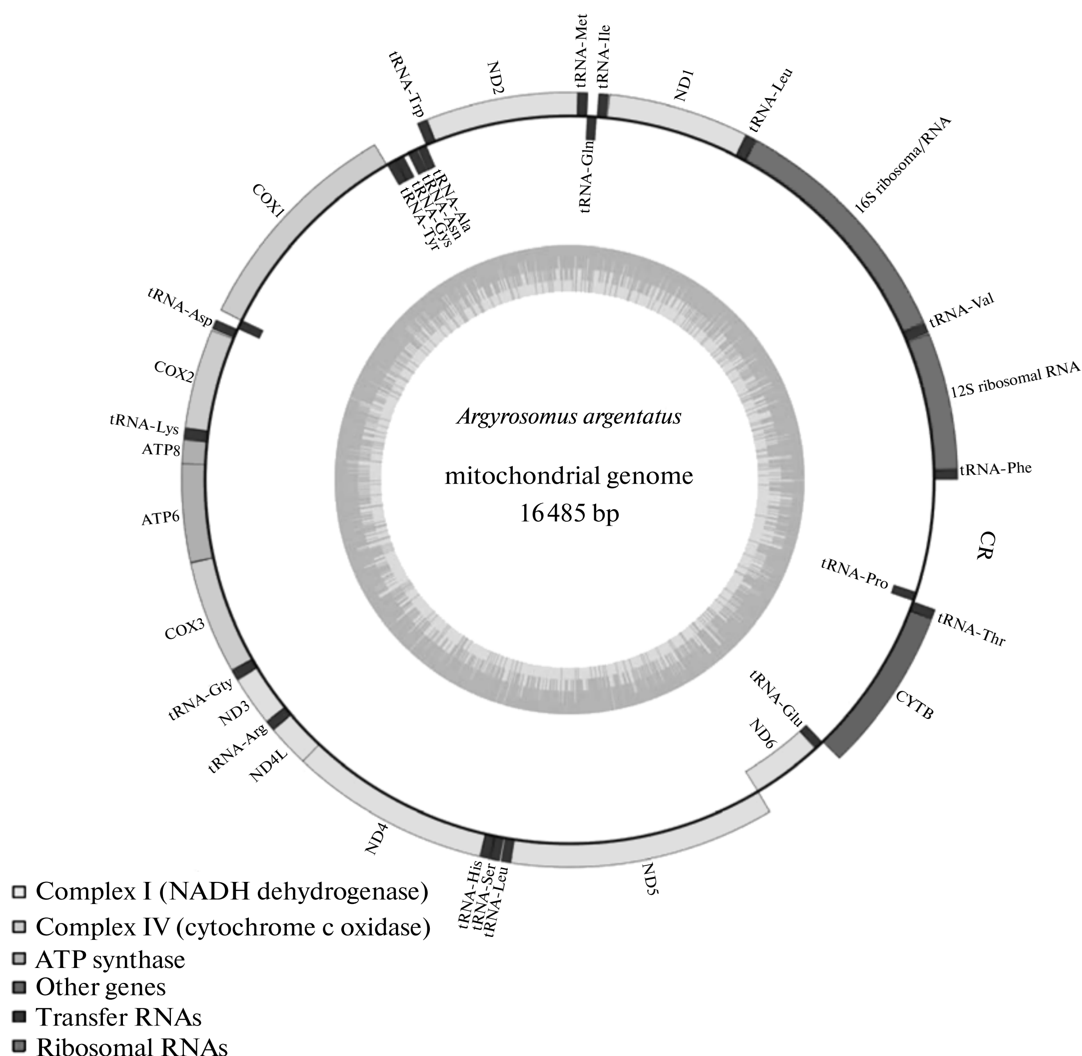

Fig. 1. Gene map of the *Argyrosomus argentatus* mitochondrial genome. Genes encoded on the heavy or light strands are shown outside or inside the circular gene map, respectively. The inner ring indicates the GC content. The figure was initially generated with OrganellarGenomeDRAW and modified manually.

27.5%; G: 16.0%) (Table 3) reflected the usual for vertebrates G-skew on the L-strand, which is due to a strong bias against the use of G residues in the third codon position [26, 27]. The A+T content is 53.8%, similar to that of other teleosts [28, 29].

Protein-coding gene

Three pairs of overlapping protein-coding genes – *ATPase8* and *ATPase6*, *ND4L* and *ND4*, *ND5* and *ND6* – were observed, and they share 1, 7, 4 bp, respectively, as in other bony fishes [30, 31]. Thirteen protein-coding genes of the silver croaker mitogenome were from 55 amino acid residues (*ATPase8*) to 613 residues (*ND5*) long. All of the protein-coding genes use the canonical ATG initiation codon with the exception of *ND5*, which uses GTG as an alternative start codon. In most vertebrate mitogenomes the GTG start codon is used by *COI*, rather than *ND5*. Variance in the termination codons seems to be a common tendency in fish mitogenomes [32, 33]. Seven protein-coding genes terminated with the stop codon TAA or AGA, while *ND2*, *COII*, *COIII*, *ND3*, *ND4* and *Cytb* ended with an incomplete T or TA, which is completed by addition of 3' A residue(s) to the mRNA by post-transcriptional polyadenylation [34]. The T : A: C : G base composition of the mitochondrial 13 protein-coding gene sequences is 28.3 : 31.3 : 24.7 : 15.6 and is summarized in Table 3. The A+T composition at the first codon position is 45.7%. The values for the second and third codon positions are 59.3 and 54.0% respectively. As with reported Sciaenidae fishes, the A+T composition of the second codon position is the highest, and is also higher than that of most of Percoi-

Table 3. Base composition of silver croaker mitochondrial genome

Gene/region	Base composition, %				
	T	C	A	G	A+T
Protein coding					
1st	21	28.3	24.7	25.6	45.7
2nd	41	27.8	18.3	13.2	59.3
3rd	23	37.9	31.0	8.1	54.0
Total	28.3	31.3	24.7	15.6	53.0
tRNA	27.4	21.7	27.9	23.0	55.3
sRNA	21.1	26.5	32.7	19.7	53.8
Control region	30.7	21.9	32.4	15.1	63.1
Overall	26.3	30.2	27.5	16.0	53.8

dei fishes (data not shown). The codon usage of 13 protein genes was analyzed (Table 4). Of the protein-coding genes, the H-strand sequence was used for the *ND6* gene. The total number of codons used is 3801. Of the 3801 codons, the portion of leucine codons is 18% (683/3801, the most often found codon), while cysteine is 0.7% (25/3801, the rarest codon). Among amino acids with fourfold degenerate third codon position, codons ending in C are most often observed, followed by codons ending in A and T. Among twofold degenerate codon position, C appears to be used more than T in pirimidine codon families except for isoleucine, whereas the purine codon families end mostly with A. Third positions of fourfold and twofold degenerate codons end mostly with C, what reflects the average base composition of all protein coding genes in the silver croaker. This pattern is common for codon usage in other fish species [25, 35, 36].

Ribosomal and transfer RNA genes

The 12S and 16S rRNA genes of the silver croaker are 947 bp and 1710 bp long, respectively (Table 2). As for other mitochondrial genomes, both rRNA genes exhibited the typical location between the $tRNA^{Phe}$ and $tRNA^{Leu\text{-}UUR}$, separated by $tRNA^{Val}$. The T : C : A : G base composition of the two rRNAs gene sequence is 21.1 : 26.5 : 32.7 : 19.7. The A+T content of the silver croaker rRNA genes was 53.8%, which is the highest among the Sciaenidae fishes [17–21], and is also slightly A+T-rich compared to other bony fishes [16, 37, 38].

The mitogenome of the silver croaker contains 22 tRNA genes, which are interspersed between the rRNA and protein-coding genes. Of these tRNAs, two forms of $tRNA^{Leu\ (UUR\ and\ CUN)}$ and $tRNA^{Ser\ (UCN\text{-}AGY)}$ were identified (Table 2). The three tRNA clusters (IQM, WANCY and HSL) were well conserved in the silver croaker as those of typical vertebrate mitochondrial genomes. The size of tRNA genes ranged from 66 bp ($tRNA^{Cys}$) to 75 bp ($tRNA^{Lys}$) (Table 2). All of them possess a complete clover leaf secondary structure, except the $tRNA^{Ser(AGN)}$, which lacks the DHU stem. In general, lack of the DHU stem in $tRNA^{Ser}$ is a common feature in vertebrate mitogenomes [22, 39]. The tRNA acceptor stems are 7 bp whereas the DHU loops (2–4 bp) and TΨC loops (4–5 bp) are more variable. 22 tRNAs show 42 pair mismatches in their stems, including nine pairs in the DHU stems, 15 pairs in the amino acid acceptor stems, 9 pairs in the TΨC stems and nine pairs in the anticodon stems. The mismatched bases are mainly G-U, U-G or U-U, additionally, A-A, A-C and A-G mismatches were also observed (Fig. 2). These mutations appear to accumulate in mitochondrial genes, in part because mitochondrial DNA is not subjected to the recombination process, which may facilitate the elimination of deleterious mutations [40].

Non-coding regions

As reported for most of the vertebrates, the silver croaker light strand replication origin is located in a cluster of five tRNA genes (the WANCY region). This region has the potential to fold into a stable stem-loop secondary structure containing 12 bp in the stem and 13 bp in the loop. The motif 5'-GCCGG-3' was found at the base of the stem within the $tRNA^{Cys}$ gene. This motif has been demonstrated to be involved in the transition from RNA to DNA synthesis in humans [41].

The mitogenome of the silver croaker contains a non-coding control region of up to 836 bp, longer than those of *Larimichthys* fishes, *Collichthys* fishes and *Nibea albiflora* [17, 19, 20], but shorter than that of *Miichthys miiuy* [18] (Fig. 3). The control region has a higher A+T content (63.1%) than the average value of the whole genome (53.8%) of the silver croaker, a fea-

Table 4. Codon usage in silver croaker mitochondrial protein-coding genes

Amino acid	Codon	Number	Amino acid	Codon	Number
Phe	TTT	106	Tyr	TAT	41
	TTC	133		TAC	72
Leu	TTA	90	Cys	TGT	5
	TTG	19		TGC	20
	CTT	156	His	CAT	30
	CTC	186		CAC	76
	CTA	174	Gln	CAA	85
	CTG	58		CAG	14
Ile	ATT	171	Asn	AAT	27
	ATC	107		AAC	87
Met	ATA	86	Lys	AAA	64
	ATG	53		AAG	12
Val	GTT	53	Asp	GAT	19
	GTC	70		GAC	57
	GTA	65	Glu	GAA	79
	GTG	21		GAG	25
Ser	TCT	37	Trp	TGA	109
	TCC	87		TGG	10
	TCA	64	Ser	AGT	19
	TCG	9		AGC	29
Pro	CCT	56	Gly	GGT	36
	CCC	109		GGC	96
	CCA	53		GGA	63
	CCG	7		GGG	41
Thr	ACT	52	Arg	CGT	12
	ACC	126		CGC	17
	ACA	98		CGA	36
	ACG	11		CGG	11
Ala	GCT	61	Stop*	TAA	6
	GCC	172		TAG	0
	GCA	103		AGA	1
	GCG	17			

* The incomplete T or TA of the termination codon is not included.

ture that has been reported in vertebrates. This major non-coding region exhibited the typical tripartite structure with ETAS, central, and CSB domains [42]. ETAS contains the TACAT motif and a corresponding palindrome sequence ATGTA, as found in other Sciaenidae fishes. These sequence motifs can form a stable hairpin structure that acts as a synthesis termination signal for the D-loop strand [43, 44]. In the central domain of the control region, only two central conserved sequence blocks (CSB-E and CSB-D) were identified. As a matter of fact, absence of such conserved blocks is also observed in most of the reported

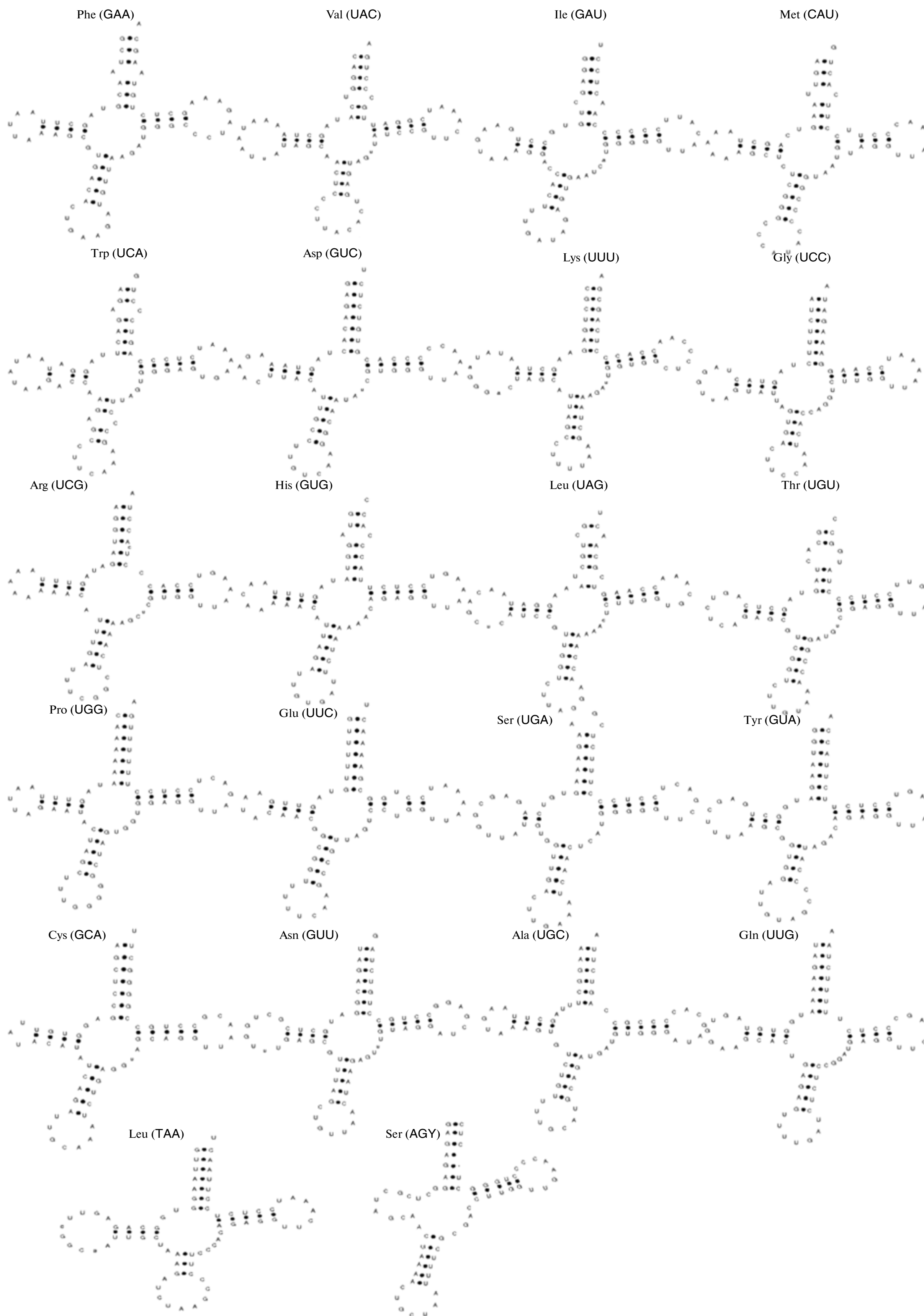

Fig. 2. Sequences of the *A. argentatus* mitochondrial tRNA genes represented in the clover-leaf form.

ETAS

TTAAACTATTTTTTGTACATATATGTATATACACCATACATTTATATTAACCATATCAATATTATGCAAGTACATACAT

GTATTATCAACATCACTTGATATTCCCCATTCATATACCACCATAACAATAAGATTTTCATAAACCATATATAGATGAA

ATCCAAAATCAAATAAGTGGTGACAGGCGAGACTTAAGATTTTAACAGCTCCGTCCATAAGTCAAGATATACCACGAAC

TCAACATCTCGTCAACTTGAACAACTACAGCCCAATAAGAACCGACCATCAGTTGATATCTTAATGCATACGGTTATTG

CSB-E CSB-D

AAGGTGAGGGACAAATATTGTGGGGGTTTCACAACATGCACTATTCCTGGCATTTGGTTCCTATTTCAGGGCCATTAAT

TGGTATCATTCCTCACACTTTCATCGACGCTTGCATAAGTTAATGGTGGTAATACATAAGCGGGAGCACCCCCCATGCC

GAGCGTTCTTTCTAGAGGGTCACTGGTATTTTTTTTCTCTTTTTCCTTTCACTTTGCATTTCACAGTGCACACTAAATT

GAAATAATAAGGTCGTACATACACTTTGAATTCATGGAAATAGTATTAATGATAAAAGATATTATTTAAGAACCACATA

CSB-1

TTAGGATATCATGTGCATAATATATGACTTATTACCTGAGAGATACCTAAGAGTGCCCCTGGGTTTTTGCGCGTAAACC

CSB-3

CCCCCTACCCCCCCACACTCCTGGGATCTCTAACACTCCTGTAAACCCCCCCGTAAACAGGAAAACCCCTGGTAGCATG

CSB-2

ATTTAGGTCCAAAATGTATCTATTTACATTATTAAAATAATGCGCAT

Fig. 3. Complete sequence of the control region of *A. argentatus*. The sequence is presented as the L-strand sequence from the 5'- to the 3'-end. In the control region, the putative conserved elements (ETAS, CSB-E, CSB-D, CSB-1, CSB-2, and CSB-3) are shadowed and marked.

Sciaenidae fishes [17, 19, 20] and several Percoidei fishes (AP004445; AP006007), although they are generally conserved in all fish mitogenomes. The function of these blocks remains unclear but may play a role in the regulation of the H-strand replication and initiation of the D-loop structure [42]. Conserved sequences blocks CSB-1, CSB-2 and CSB-3, which are thought to be involved in the positioning of the RNA polymerase both for transcription and for priming replication [45, 46], were found in the CSB domain. All these features suggest that the asymmetrical replication mechanism revealed for mammalian mtDNA also operates in the silver croaker.

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