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The complete mitochondrial genome of the pink shrimp *Farfantepenaeus duorarum* (Burkenroad, 1939) (Decapoda: Dendrobranchiata: Penaeidae)

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ABSTRACT

Farfantepenaeus duorarum (Burkenroad, 1939) is a commercially harvested decapod shrimp that ranges from the eastern coast of the United States, through the Gulf of Mexico, and as far south as Isla Mujeres, Mexico. We report for the first time the complete mitochondrial genome of *F. duorarum*. The mitochondrial genome is 15,971 base pairs in length and is comprised of 13 protein-coding genes (PCGs), 2 ribosomal RNA genes, and 22 transfer RNA genes. An intergenic space 982 bp in length located between the rrnS (12S) and trnI (Isoleucine) genes is presumed to be the D-loop. The mitochondrial gene order in *F. duorarum* is identical to that reported for congeners. To assess selection pressures within the mitochondrial genome, K_A/K_S ratios were calculated for all PCGs, and show values < 1, indicating that all genes are evolving under purifying selection. This work contributes one more mitochondrial genome to the penaeid shrimps, an economically targeted group.

Key Words: Crustacea, crustacean fisheries, mtDNA, next-generation sequencing, penaeid shrimps, protein-coding genes, selective pressure

SPECIAL SECTION: CRUSTACEAN MITOCHONDRIAL GENOMICS

INTRODUCTION

Decapod shrimps within Dendrobranchiata consists of the superfamilies Sergestoidea and Penaeoidea, and is comprised of over 500 described species (Pérez Farfante & Kensley, 1997). Dendrobranchiate shrimps play an important role in the planktonic, mesopelagic, bathypelagic, and benthic habitats throughout the world's oceans (Pérez Farfante & Kensley, 1997). Penaeid shrimps are among the most fishery-targeted crustaceans and are captured worldwide, mostly in shallow waters as these shrimps are abundant in both littoral and estuarine habitats (Pérez Farfante, 1988). Due to their economic and ecological value, these shrimps have been the focus of many biological and genetic studies (McMillen-Jackson & Bert, 2004; Chan *et al.*, 2008; Cheng *et al.*, 2018; Guo *et al.*, 2021).

In 2020, 605 t of *Farfantepenaeus* shrimps were harvested in the Gulf of Mexico, totaling $5.8 million in commercial revenue (NMFS Landings Query, 25 October 2021; https://www.fisheries.noaa.gov/national/sustainable-fisheries/commercial-fisheries-landings). *Farfantepenaeus* Burukovsky, 1997 is not currently recognized, as a previous study suggested that *Penaeus* Fabricius, 1798 *sensu lato* should be reinstated, refuting the previous six-genera classification (Ma *et al.*, 2011). We nevertheless use the name *Farfantepenaeus* even if there is still debate regarding the systematics of the family. *Farfantepenaeus duorarum* (Burkenroad, 1939) is very abundant throughout the Gulf of Mexico and the southwestern coast of Florida, USA, and is often commercially harvested for both seafood consumption and fishing bait (Holthuis, 1980). The species is found in the Atlantic Ocean from Chesapeake Bay to southern Florida, extending into the Gulf of Mexico, and as far south as Isla Mujeres, Mexico (Pérez Farfante, 1969). It is most abundant in shallow waters, with a vertical distribution range of 0–329 m (Huff & Cobb, 1979). Though its color is variable, *F. duorarum* is colloquially known as the "pink shrimp," and can often be easily identified by a dark-colored spot located between the third and fourth abdominal somite in addition to other characters such as the shape of the rostrum and reproductive organs (Pérez Farfante, 1969).

Farfantepenaeus duorarum was divided into two subspecies by Pérez Farfante (1967): *Penaeus duorarum duorarum* and *Penaeus duorarum*

notialis. These two subspecies were later recognized as two separate species, but a more recent molecular phylogeny (Timm *et al.*, 2019) revealed that *F. duorarum* and *F. notialis* (Pérez Farfante, 1967) were nestled within the same clade and have a very low (1.2%) genetic distance. Based on these findings, Timm *et al.* (2019) suggested that *F. duorarum* and *F. notialis* may not actually be two separate species. Previous molecular phylogenies relied on only one mitochondrial sequence from *F. notialis*, whereas Timm *et al.* (2019) also included five sequences from *F.* "nr" *notialis*. These individuals were collected outside of their documented distributional range but grouped with *F. notialis* in the phylogeny. These results indicate that further studies should sample multiple specimens from both *F. duorarum* and *F. notialis* across their distributional ranges as well as including the respective type specimens to better understand the true relationship between these two species. More data are needed to resolve this relationship, and understanding the characteristics of the mitochondrial genome for each species may also help to provide insight.

Although many molecular phylogenies have been published for Penaeidae (Maggioni *et al.*, 2001; Chan *et al.*, 2008; Voloch *et al.*, 2009; Ma *et al.*, 2011; Timm *et al.*, 2019; Hurzaid *et al.*, 2020), no mitochondrial genomes have been assembled and characterized for *F. duorarum* to date.

We aimed to describe in detail the complete mitochondrial genome of *F. duorarum* for the first time. We assessed the gene order and nucleotide composition across the entire mitogenome, and the codon usage profiles for all protein-coding genes (PCGs). Selective pressure constraints were analyzed for all PCGs, including those that are commonly used for phylogenetic inference. The secondary structure of all tRNA genes and the putative control region, otherwise known as the D-loop, are described in detail.

MATERIAL AND METHODS

The raw sequence data used to compile the complete mitochondrial genome were obtained from the dataset generated by Wolfe *et al.* (2019), which was composed of 5,505,501 paired reads with 27× coverage (Sequence Read Archive; accession SRX5571147) (see Supplementary material Table S3 and Wolfe *et al.* (2019) for additional details). The mitochondrial genome of *F. duorarum* was assembled de-novo using the software NOVOPlasty v. 1.2.3 (Dierckxsens *et al.*, 2016). NOVOPlasty assembled the mitochondrial genome with an average coverage of 106× per nucleotide. The reads were not quality-trimmed prior to assembly following the developer's guidelines. NOVOPlasty uses a seed-and-extend algorithm that assembles mitochondrial genomes from whole genome sequencing (WGS) data, starting from a related or distant single "seed" sequence and an optional "bait" reference mitochondrial genome (Dierckxsens *et al.*, 2016). NOVOPlasty was run using a 533 bp fragment of the cox1 gene (MG001131) as a seed and a k-mer size of 39.

Annotation and analysis of the mitochondrial genome

The assembled mitochondrial genome of *F. duorarum* was annotated using the MITOS and MITOS2 web servers (Bernt *et al.*, 2013b) specifying the invertebrate mitochondrial code. These programs predict the location and length of each tRNA and protein-coding gene (PCG). Each gene annotation was then manually curated using the software MEGAX (Kumar *et al.*, 2018) and the EXPASY Web translator tool (https://web.expasy.org/translate/). Our manually corrected annotations were also compared to the annotated mitochondrial genome of the congener *Farfantepenaeus californiensis* (Holmes, 1900) (Genbank EU497054; Peregrino-Uriarte *et al.*, 2009) as well as other closely related species of penaeid shrimps.

A visual depiction of the mitochondrial genome was rendered using GenomeVx (http://wolfe.ucd.ie/GenomeVx/) (Conant & Wolfe, 2008). We used MEGAX to calculate nucleotide composition and codon usage for the complete mitochondrial genome. A similar analysis was performed using the Sequence Manipulation Suite's Codon Usage tool (http://www.bioinformatics.org/sms2/codon_usage.html) (Stothard, 2000), specifying the invertebrate mitochondrial code to determine codon usage of all PCGs. For both analyses, the results were compared to that of *F. californiensis*.

The putative control region was examined for microsatellites using the default settings of BioPHP Microsatellite Repeats Finder (http://insilico.ehu.es/mini_tools/microsatellites/) and for tandem repeats using the basic default parameters of Tandem Repeats Finder (https://tandem.bu.edu/trf/trf.html) (Benson, 1999). The secondary structure of each tRNA was visualized using the Vienna RNA Web Services tool (http://rna.tbi.univie.ac.at/forna/) (Kerpedjiev *et al.*, 2015) by inputting the nucleotide and dot-bracketed sequences obtained from MiTFi (Jühling *et al.*, 2012) as implemented in MITOS. We then analyzed the control region for hair-pin structures using the RNA structure web server (https://rna.urmc.rochester.edu/RNAstructureWeb/Servers/Predict1/Predict1.html).

We performed a selective pressure analysis for each PCG. The values of nonsynonymous substitutions per nonsynonymous site ($K_A = d_N = S_A/L_A$), synonymous substitutions per synonymous substitution site ($K_S = d_S = S_S/L_S$), and ω (K_A/K_S ratio) were calculated using KaKs Calculator 2.0 (Wang *et al.*, 2010). The calculated values were based on a comparison between *F. duorarum* and the closely related *F. californiensis* (Genbank EU497054; Peregrino-Uriarte *et al.*, 2009). The Gγ-MYN model was used to account for variable mutation rates across sequence sites during the calculations. If the PCGs are under purifying selection (negative selection), diversifying selection (positive selection), or neutral selection, the resulting ω value (K_A/K_S ratio) is expected to be less than 1, greater than 1, or equal to 1, respectively.

RESULTS AND DISCUSSION

The mitochondrial genome of *F. duorarum* (Genbank OM364079) is 15,971 bp in length and consists of 13 PCGs, 22 tRNAs, the 12S ribosomal RNA (rrnS) gene, the 16S ribosomal RNA (rrnL) gene, and the putative control region (Fig. 1). Nine of the 13 PCGs and 14 of the 22 tRNAs are encoded on the positive strand, leaving four PCGs (nad5, nad4, nad4l, nad1), eight tRNAs (trnQ, trnC, trnY, trnF, trnH, trnP, trnL1, trnV), and both ribosomal rRNAs (12S and 16S) on the negative strand. The mitochondrial gene order (Table 1) of *F. duorarum* is identical to that of the congener *F. californiensis* and other confamilial species except that Peregrino-Uriarte *et al.* (2009) reported tRNA L1 and tRNA L2 in an opposite order (Peregrino-Uriarte *et al.*, 2009; Guo *et al.*, 2021). After re-annotating their genome in the MITOS2 webserver, however, we found that the tRNA L1 and tRNA L2 loci locations for *F. californiensis* were congruent with the findings for *F. duorarum*. This difference may be due to an increasing amount of reference data through the MITOS2 server. The mitochondrial genome of *F. duorarum* contains few intergenic spaces and is well compacted. An uninterrupted intergenic space ranging from 14,990–15,971 bp is assumed to be the putative control region, otherwise known as the D-loop.

The complete mitochondrial genome of *F. duorarum* is composed of the following nucleotide compositions: 34.81% thymine, 19.11% cytosine, 32.42% adenine, and 13.66% guanine. The combined A+T content is 67.23% and the combined C+G content is 32.77%. The mitochondrial genome of the congener *F. californiensis* has an A+T content of 67.06% and a C+G content of 32.94%, which is very similar to, however, slightly more C+G than that of *F. duorarum*. The mitochondrial genome of another confamilial species, *Litopenaeus stylirostris* (Stimpson, 1871) has an A+T content of 68.59%, thereby, reaffirming that the A+T content appears to be consistently higher than the C+G

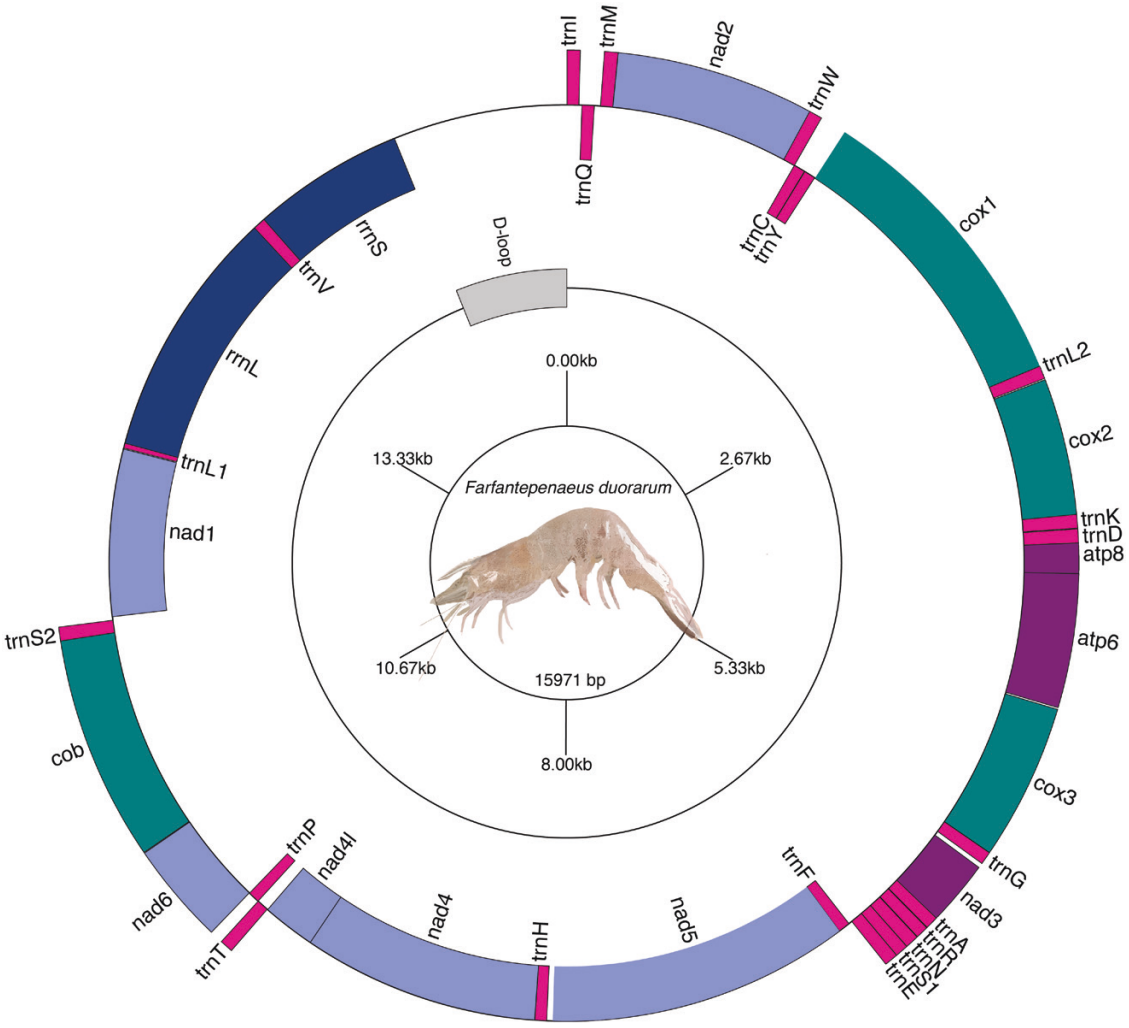

Figure 1. Circular genome depiction of the mitochondrial genome of *Farfantepenaeus duorarum*. The map is annotated and depicts 13 protein-coding genes (PCGs), 2 ribosomal RNA genes (rrnS (otherwise known as 12S ribosomal RNA) and rrnL (otherwise known as 16S ribosomal RNA)), 22 transfer RNA (tRNA) genes, and the D-loop (otherwise known as the putative control region). Illustration by SBC.

content in penaeid shrimps (Peregrino-Uriarte *et al.*, 2009; Zhong *et al.*, 2018b (*Penaeus latisulcatus* Kishinouye, 1896, as *Melicertus latisulcatus*); Zhong *et al.*, 2018a (*Penaeus japonicus* Spence Bate, 1888, as *Marsupenaeus japonicus*); Zhong *et al.*, 2018c (*Alcockpenaeopsis hungerfordii* (Alcock, 1905), as *Parapenaeopsis hungerfordii*); Zhong *et al.*, 2019a (*Metapenaeopsis mogiensis* Rathbun, 1902); Sektiana *et al.*, 2018; Zhong *et al.*, 2019b (*Metapenaeus affinis* (H. Milne Edwards, 1837)); Guo *et al.*, 2021). These findings are also consistent with the nucleotide usage analysis, as the least used codons are those composed mainly of C and G.

Seven of the 13 PCGs in the mitochondrial genome of *F. duorarum* begin with the traditional ATG start codon. Two PCGs (nad2 and nad6) begin with ATT, two PCGs (nad3 and nad1) begin with ATA, one PCG (atp8) begins with ATC, and one PCG (cox1) begins with ACG. Ten of the 13 PCGs end with the traditional stop codon TAA, one PCG (atp6) ends in TAG, and the remaining two PCGs (cox3 and nad3) end with an incomplete stop codon T. The congener *F. californiensis* has similar start codons (ATG, ATA, ATT, ACG); however, is lacking ATC and has an additional start codon GTG (nad5) (Peregrino-Uriarte *et al.*, 2009). Incomplete stop codons are seen in nad3, cox3, and cox2 in *F. californiensis*, but are only seen in cox3 and nad3 for *F. duorarum*. The confamilial species *Mierspenaeopsis hardwickii* (Miers, 1878) shows incomplete stop codons in six PCGs (nad1, nad3, nad5, nad6, cox2, and cox3) (Mao *et al.*, 2016), whereas *Penaeus simplex* Chan, Muchlisin & Hurzaid, 2021 (*Penaeus acehensis* in Sektiana *et al.*, 2018) shows incomplete stop codons in five PCGs (cox2, cox3, nad5, nad4, nad4l) (Sektiana *et al.*, 2018). Other species within the family Penaeidae (*Trachysalambria curvirostris* (Stimpson, 1860), *Parapenaeus fissuroides* Crosnier, 1986) show no incomplete stop codons (Guo *et al.*, 2021). It has recently been suggested that truncated stop codons are completed via post-translational polyadenylation processes (Baeza, 2018 and references therein).

The most frequently used codons found in the PCGs of *F. duorarum* include GTA (Val, used 134 times), GCT (Ala, 138 times), ATA (Ile, 156 times), TTT (Phe, 183 times), ATT (Ile, 217 times), and TTA (Leu, 268 times). The least used codons (excluding stop codons) include AGG (Arg, not used), TGC (Cys, 8 times), GGC (Gly, 8 times), CGG (Arg, 9 times), CCG (Pro, 10 times), and TCG (Ser, 10 times).

The K_A/K_S ratios in all PCGs found within the mitochondrial genome of *F. duorarum* shows values < 1, indicating that all mitochondrial PCGs are evolving under purifying, or negative, selection (Table 2). The cox1 gene has the lowest K_A/K_S ratio, with a value of 0.000996304, suggesting that this gene is under the greatest amount of selective pressure. This finding is particularly noteworthy because the cox1 gene is the most used mitochondrial gene to resolve evolutionary relationships, as it has long been

Table 1. Mitochondrial genome of *Farfantepenaeus duorarum*. Arrangement and annotation.

Name	Type	Start	Stop	Strand	Length (bp)	Start	Stop
trnI(atc)	tRNA	1	67	+	67		
trnQ(caa)	tRNA	84	153	–	70		
trnM(atg)	tRNA	187	255	+	69		
nad2	PCG	256	1,257	+	1,002	ATT	TAA
trnW(tga)	tRNA	1,256	1,323	+	68		
trnC(tgc)	tRNA	1,323	1,388	–	66		
trnY(tac)	tRNA	1,390	1,455	–	66		
cox1	PCG	1,458	2,996	+	1,539	ACG	TAA
trnL2(tta)	tRNA	2,992	3,057	+	66		
cox2	PCG	3,064	3,771	+	708	ATG	TAA
trnK(aaa)	tRNA	3,752	3,820	+	69		
trnD(gac)	tRNA	3,824	3,893	+	70		
atp8	PCG	3,894	4,052	+	159	ATC	TAA
atp6	PCG	4,046	4,720	+	675	ATG	TAG
cox3	PCG	4,729	5,518	+	790	ATG	T(gc)
trnG(gga)	tRNA	5,519	5,584	+	66		
nad3	PCG	5,609	5,960	+	352	ATA	T(tg)
trnA(gac)	tRNA	5,937	6,001	+	65		
trnR(cga)	tRNA	6,004	6,068	+	65		
trnN(aac)	tRNA	6,071	6,139	+	69		
trnS1(agc)	tRNA	6,140	6,206	+	67		
trnE(gaa)	tRNA	6,207	6,276	+	70		
trnF(ttc)	tRNA	6,296	6,363	–	68		
nad5	PCG	6,363	8,063	–	1,701	ATG	TAA
trnH(cac)	tRNA	8,097	8,163	–	67		
nad4	PCG	8,164	9,504	–	1,341	ATG	TAA
nad4l	PCG	9,498	9,797	–	300	ATG	TAA
trnT(aca)	tRNA	9,800	9,867	+	68		
trnP(cca)	tRNA	9,868	9,933	–	66		
nad6	PCG	9,935	10,450	+	516	ATT	TAA
cytb	PCG	10,454	11,590	+	1,137	ATG	TAA
trnS2(tca)	tRNA	11,590	11,659	+	70		
nad1	PCG	11,679	12,617	–	939	ATA	TAA
trnL1(cta)	tRNA	12,623	12,689	–	67		
rrnL	rRNA	12,650	14,066	–	1,417		
trnV(gta)	tRNA	14,062	14,133	–	72		
rrnS	rRNA	14,133	14,989	–	857		
D–loop	–	14,990	15,971		982		

thought to be under neutral pressure (Galtier *et al.*, 2009). Our findings suggest that cox1 is not under neutral pressure, which agrees with the findings from other recent studies (Galtier *et al.*, 2009; Tan *et al.*, 2019). Genes that are known to be under selection pressure are not recommended to be used for phylogenetic inferences as substitution models typically do not account for selection pressure (Roje, 2014). Based on these findings, cox1 may not be sufficient to resolve phylogenetic relationships and should be used in conjunction with other mitochondrial and/or nuclear genes. We nevertheless suggest that cox1 may still be adequate when used for barcoding studies, as selection pressures are less likely to influence species identification. Studies examining the effect of purifying selection when using cox1 and other PCGs to resolve phylogenetic relationships are warranted. The genes atp8, cox2, cox3, cytB, nad1, nad3, and nad4l all have K_A/K_S ratios one magnitude higher than that of cox1 (0.0727529, 0.00122297, 0.00488662, 0.00269692, 0.00333647, 0.00730202, and 0.00418178, respectively). The highest K_A/K_S ratios are found in nad2, nad4, nad5, and atp8 (0.0150851, 0.021288, 0.0219931, and 0.0727529, respectively), suggesting that these genes are under the weakest selective pressure. Selective pressure analyses within the mitochondrial PCGs have not yet been performed for other penaeid species (Peregrino-Uriarte *et al.*, 2009; Sektiana *et al.*, 2018 (*Penaeus simplex*, as *P. acehensis*); Zhong *et al.*, 2018c (*Alcockpenaeopsis hungerfordii*, as *Parapenaeopsis hungerfordii*); Zhong *et al.*, 2018a (*Penaeus japonicus*, as *Marsupenaeus japonicus*); Mao *et al.*, 2016 (*Mierspenaeopsis hardwickii*); Zhong *et al.*, 2019b (*Metapenaeus affinis*); Zhong *et al.*, 2019a (*Metapenaeopsis mogiensis*)). We suggest that future studies can focus on the relationship between habitat and selective pressure regimes in these shrimps.

tRNA genes found within the mitochondrial genome of *F. duorarum* range in length from 65 to 70 bp. Of the 22 tRNAs, 21 are consistent with the classical "cloverleaf" shape (Fig. 2). The only tRNA differing from this shape is trnS1 (serine 1). This finding is consistent in the congener *F. californiensis*. The asparagine and phenylalanine tRNAs of *F. duorarum* exhibit an extra loop in the secondary structure when compared to that of *F. californiensis*. Stem and/or loop tRNA arm deletions (complete/partial) are in known occurrence among other decapod crustaceans (Baeza, 2018 and references therein). An additional elongation factor Tu (EF-Tu) supports interactions with tRNAs that lack the T-arm during translation (i.e., in other invertebrates and vertebrates;

Table 2. Selective pressure analysis for all mitochonodrial protein-coding genes of *Farfantepenaeus duorarum*. K_A, K_S, and K_A/K_S values calculated using the Gγ-MYN model.

Farfantepenaeus duorarum/ F. californiensis PCG selective pressure analysis (Ka/Ks)				
PCG	**Ka Value**	**Ks Value**	**Ka/Ks Value**	**P Value**
atp6	0.0156629	2.04239	0.00766892	8.97E-53
atp8	0.0678478	0.932578	0.0727529	2.47E-07
cox1	0.00164386	1.64996	0.000996304	1.60E-132
cox2	0.00186024	1.52109	0.00122297	1.01E-52
cox3	0.00493476	1.00985	0.00488662	1.88E-53
cytB	0.00349002	1.29407	0.00269692	2.85E-96
nad1	0.00581935	1.74416	0.00333647	4.81E-83
nad2	0.0312482	2.07146	0.0150851	6.69E-73
nad3	0.00831706	1.13901	0.00730202	2.87E-25
nad4	0.0214603	1.00809	0.021288	3.67E-85
nad4L	0.00414576	0.991386	0.00418178	3.97E-19
nad5	0.0249031	1.13232	0.0219931	1.19E-110
nad6	0.0155685	1.35864	0.0114589	3.29E-39

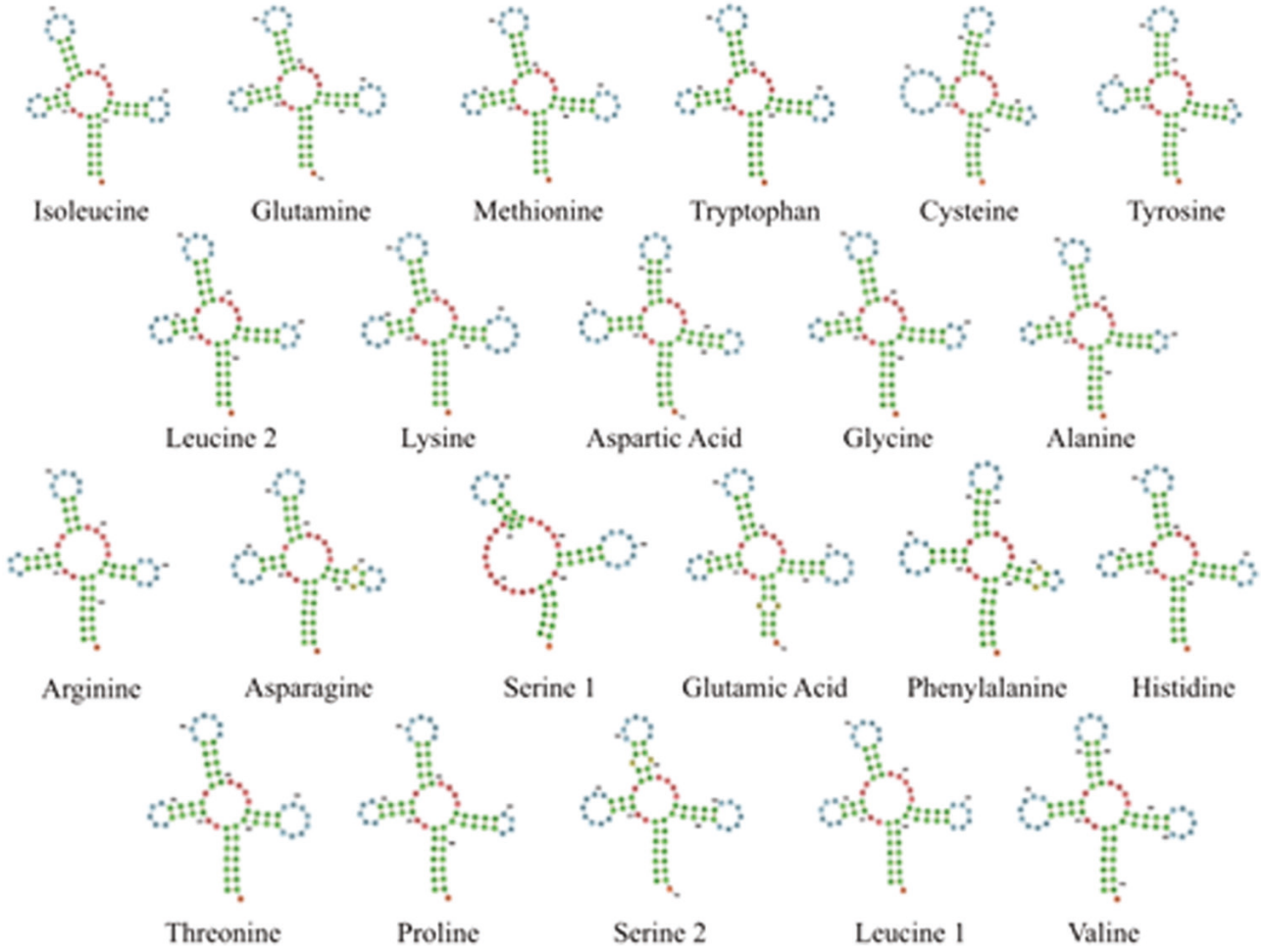

Figure 2. Secondary structures of all tRNAs in the mitochondrial genome of *Farfantepenaeus duorarum* as predicted by MITFI.

Watanabe *et al.*, 2014). The interaction between truncated tRNAs and other molecular factors during transcription remains unknown in crustaceans.

The rrnS (12S) and rrnL (16S) mitochondrial genes of *F. duorarum* are 857 and 1,417 bp in length, respectively. Both genes present an A+T bias. The nucleotide composition for rrnL (16S) is A = 33.45%, T = 37.33%, C = 18.21%, and G = 11.01%. The nucleotide composition for rrnS (12S) is A = 31.86%, T = 25.36%, C = 20.30%, and G = 12.49%. The rrnL gene is located between the trnL1 and trnV genes. The rrnS gene is located between the trnV gene and the putative control region.

The D-loop, or control region (CR), of *F. duorarum* is 982 bp in length and is located between the rrnS (12S) and trnI (Ile) genes. This region is A+T rich with the following nucleotide

compositions: A = 37.47%, T = 41.14%, C = 11.30%, and G = 10.08%. Upon analysis, 15 microsatellite repeats were found within the d-loop, all of which were A+T rich. No tandem repeats were found within the d-loop. The secondary structure prediction analysis using the Vienna RNA Web Services tool resulted in 20 possible structures found within this region with associated Gibbs free energy (ΔG) values ranging from –111.1 to –110.2 Kcal mol^{-1}. All 20 predicted secondary structures contain stem-loop structures in variable lengths and locations. Structural analyses of the putative control region have not yet been performed for any other penaeid species to date (Peregrino-Uriarte *et al.*, 2009; Mao *et al.*, 2016; Zhong *et al.*, 2018b (*Penaeus latisulcatus*, as *Melicertus latisulcatus*), Zhong *et al.*, 2018a (*Penaeus japonicus*, as *Marsupenaeus japonicus*), Zhong *et al.*, 2018c (*Alcockpenaeopsis hungerfordii*, as *Parapenaeopsis hungerfordii*); Zhong *et al.*, 2019a (*Metapenaeopsis mogiensis*); Zhong *et al.*, 2019b (*Metapenaeus affinis*); Guo *et al.*, 2021). This region contains similar features to other D-loops and is thought to be involved in the replication initiation process of the mitochondrial genome (Bernt *et al.*, 2013a). Previous studies have found high levels of genetic diversity within the mitochondrial control region of *F. duorarum* and suggest that further analyses of the control region may be useful as a genetic marker for phylogeographic purposes (McMillen-Jackson & Bert, 2004).

Our results contribute one more mitochondrial genome to family Penaeidae, a group heavily targeted by the fishing industry globally (Pérez Farfante, 1988; McMillen-Jackson & Bert, 2004).

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