ORIGINAL RESEARCH

The first complete mitochondrial genome of the Mariana Trench *Freyastera benthophila* (Asteroidea: Brisingida: Brisingidae) allows insights into the deep-sea adaptive evolution of Brisingida

Wendan Mu[1,2] | Jun Liu[1] | Haibin Zhang[1]

[1]Institute of Deep-Sea Science and Engineering, Chinese Academy of Sciences, Sanya, China

[2]University of Chinese Academy of Sciences, Beijing, China

Correspondence
Haibin Zhang, Institute of Deep-Sea Science and Engineering, Chinese Academy of Sciences, Sanya, China.
Email: hzhang@idsse.ac.cn

Abstract

Starfish (phylum Echinodermata) are ecologically important and diverse members of marine ecosystems in all of the world's oceans, from the shallow water to the hadal zone. The deep sea is recognized as an extremely harsh environment on earth. In this study, we present the mitochondrial genome sequence of Mariana Trench starfish *Freyastera benthophila*, and this study is the first to explore in detail the mitochondrial genome of a deep-sea member of the order Brisingida. Similar to other starfish, it contained 13 protein-coding genes, two ribosomal RNA genes, and 22 transfer RNA genes (duplication of two tRNAs: *trnL* and *trnS*). Twenty-two of these genes are encoded on the positive strand, while the other 15 are encoded on the negative strand. The gene arrangement was identical to those of sequenced starfish. Phylogenetic analysis showed the deep-sea Brisingida as a sister taxon to the traditional members of the Asteriidae. Positive selection analysis indicated that five residues (8 N and 16 I in *atp8*, 47 D and 196 V in *nad2*, 599 N in *nad5*) were positively selected sites with high posterior probabilities. Compared these features with shallow sea starfish, we predict that variation specifically in *atp8*, *nad2*, and *nad5* may play an important role in *F. benthophila*'s adaptation to deep-sea environment.

KEYWORDS
adaptive evolution, Brisingida, deep sea, *Freyastera benthophila*, mitochondrial genome

1 | INTRODUCTION

The class Asteroidea (sea stars and starfish) is one of the most familiar and diverse groups of the phylum Echinodermata with a long paleontological history, including nearly 1,800 species grouped into 35 families (Clark & Downey, 1992; Matsubara, Komatsu, & Wada, 2004). They are present in all of the world's oceans and occur from intertidal to abyssal, and they are most diverse in the Indo-Pacific and tropical Atlantic regions (Mah & Blake, 2012). To date, the phylogenetic relationships of these starfish have not yet been fully resolved (Knott & Wray, 2000).

Because of its maternal inheritance, and low frequency of gene recombination, mitochondrial genes (e.g., COI) are widely used for phylogenetic analysis (Boore, 1999). Compared to one gene, complete mitogenomes include more genetic information and usually could obtain more accurate phylogenetic

Name	Sequence (5′–3′)	Region	Location
W1-F	CCGCAAGAGTCGAAAGAG	cox1	3473–3490
W1-R	TCAAGGAGTCGTGGCATT	cox2	5448–5465
W2-F	TAGCTCTTTCCCGAACAC	nad4L	4993–5010
W2-R	GAACCGTAAACACTATCTGCT	cox3	7233–7253
W3-F	GACTCGCAGCTAATCTTACA	atp6	6466–6485
W3-R	CAAGACCGTATCCACCTAAC	nad4	8630–8649
W4-F	CCCTCCTTCCAACCCTCATC	nad4	8287–8306
W4-R	CACCCATCTTTCGTAGGTCTTGT	nad5	10735–10757
W5-F	CCACCGCTACTTCTCAACAT	nad5	10545–10564
W5-R	TAGAGCGAAGGATTGCATAG	cob	12860–12879
W6-F	CCACCTATTCTTCCTTCACC	cob	12614–12633
W6-R	GCATAATCATTTGCCTCTTA	16S	15183–15202
W7-F	AGCTCGATAGGGTCTTCTCGTC	16S	15063–15084
W7-R	GCAGTGGCATTGTTGACTTTGA	nad1	2040–2061
W8-F	AGCTAACGGCTGAAACAATC	nad1	1957–1976
W8-R	TTCCTGCGTAATGGGCTA	cox1	3902–3919

TABLE 1 Primers used for amplifying and sequencing the mitogenome of _Freyastera benthophila_

relationship and therefore have become more popular in recent years (Fan, Hu, Wen, & Zhang, 2011; Shen, Ma, Ren, & Zhao, 2009; Shen et al., 2017). Up to now, the complete mitochondrial genomes have been reported in many marine organisms, such as sea cucumber (Fan et al., 2011; Perseke et al., 2010; Scouras, Beckenbach, Arndt, & Smith, 2004; Sun, Qi, & Kong, 2010), sea urchin (Cantatore, Roberti, Rainaldi, Gadaleta, & Saccone, 1989; De Giorgi, Martiradonna, Lanave, & Saccone, 1996; Qureshi & Jacobs, 1993), brittle star (Perseke et al., 2008, 2010; Scouras et al., 2004; Smith, Arndt, Gorski, & Fajber, 1993), sea lily (Perseke et al., 2008; Scouras & Smith, 2006), shellfish (Plazzi, Ribani, & Passamonti, 2013; Ren, Liu, Jiang, Guo, & Liu, 2010), and crab (Liu & Cui, 2010; Yang & Yang, 2008).

Animal mitogenome is typically always circular molecule, except for some classes of cnidarians (Bridge, Cunningham, Schierwater, Desalle, & Buss, 1992). It contains 37 genes in general: 13 protein-coding genes (PCGs) (cytochrome _c_ oxidase subunits I–III [_cox1-cox3_], NADH dehydrogenase subunits 1–6 and 4L [_nad1-6, nad4L_], ATP synthase subunits 6 and 8 [_atp6, atp8_], apocytochrome _b_ [_cob_]), two ribosomal RNAs (_12S_ and _16S_), and 22 transfer RNAs (tRNAs). All 13 protein-coding genes play key roles in oxygen usage and energy metabolism (Boore, 1999; Xu et al., 2007). Because variation in mitochondrial protein-coding genes that involved in oxidative phosphorylation can directly influence metabolic performance, an increasing number of researches related to adaptive evolution of these genes have been reported (Maliarchuk, 2011; Xu et al., 2007; Yu, Wang, Ting, & Zhang, 2011; Zhou, Shen, Irwin, Shen, & Zhang, 2014). Despite strong functional constraints, mitochondrial DNA may be subject to positive directional selection in response to pressures from extreme harsh environment (Tomasco & Lessa, 2011). Indeed, mtDNA analyses have demonstrated the existence of adaptive evolution in the ATP synthase genes of the sea anemones, alvinocaridid

shrimp, and galliform birds (Sun, Hui, Wang, & Sha, 2018; Zhang, Zhang, Wang, Zhang, & Lin, 2017; Zhou et al., 2014); the NADH dehydrogenase genes of sea anemones, alvinocaridid shrimp, Tibetan horses, and Chinese snub-nosed monkeys (Sun et al., 2018; Xu et al., 2007; Yu et al., 2011; Zhang et al., 2017); the cytochrome _b_ gene of cetaceans and alpacas (da Fonseca, Johnson, O'Brien, Ramos, & Antunes, 2008); and the cytochrome _c_ oxidase genes of Tibetan antelope and anthropoids (Adkins & Honeycutt, 1994; Luo et al., 2008).

Here, we report the complete mitogenome of the starfish _Freyastera benthophila_, which collected from Mariana Trench at 5,463 m depth. _Freyastera benthophila_ exist in abyssal and is mainly distributed in the southern Pacific, eastern Pacific off California, mid-Atlantic (between Azores and Spain), the Bay of Bengal, and Biscay, ranging from 4,250 to 5,000 m depth (Downey, 1986). The mitogenome features, organization, codon usage, and gene arrangement information were presented. The phylogenetic relationships between _F. benthophila_ and 19 other species from Echinodermata were analyzed. To infer the deep-sea adaptive evolution, positive selection analysis of mitochondrial genes was also performed.

2 | MATERIALS AND METHODS

2.1 | Sample collection and DNA extraction

The specimen was collected at Mariana Trench, in June 2016 (10°51.0971′N, 141°57.2705′E, at 5,463 m depth). The collection was accomplished by deep-sea human occupied vehicle (HOV) "Jiao Long" during an expedition. The specimen was preserved in 95% ethanol. Total genomic DNA was extracted from ethanol-fixed tissue with tissue DNA kit (Omega Bio-Tek) and stored at −20°C.

TABLE 2 List of taxa used in the phylogenetic analysis

Taxon	Classification	Accession number	References
Crinoidea			
Antedom mediterranea	Crinoidea; Articulata; Comatulida; Antedonidae	NC_010692	Perseke et al. (2008)
Ophiuroidea			
Ophiocomina nigra	Ophiuroidea; Ophiuridea; Ophiurida; Ophiurina; Gnathophiurina; Ophiocomidae	NC_013874	Perseke et al. (2010)
Astrospartus mediterraneus	Ophiuroidea; Ophiuridea; Euryalida; Gorgonocephalidae	NC_013878	Perseke et al. (2010)
Echinoidea			
Strongylocentrotus purpuratus	Echinoidea; Euechinoidea; Echinacea; Echinoida; Strongylocentrotidae	NC_001453	Qureshi and Jacobs (1993)
Echinocardium cordatum	Echinoidea; Euechinoidea; Atelostomata; Spatangoida; Loveniidae	NC_013881	Perseke et al. (Unpublished)
Paracentrotus lividus	Echinoidea; Euechinoidea; Echinacea; Echinoida; Echinidae	NC_001572	Cantatore et al. (1989)
Holothuroidea			
Cucumaria miniata	Holothuroidea; Dendrochirotacea; Dendrochirotida; Cucumariidae	NC_005929	Scouras et al. (2004)
Apostichopus japonicus	Holothuroidea; Aspidochirotacea; Aspidochirotida; Stichopodidae	NC_012616	Sun et al. (2010)
Holothuria forskali	Holothuroidea; Aspidochirotacea; Aspidochirotida; Holothuriidae	NC_013884	Perseke et al. (2010)
Parastichopus nigripunctatus	Holothuroidea; Aspidochirotacea; Aspidochirotida; Stichopodidae	NC_013432	Sasaki and Hamaguchi (Unpublished)
Stichopus horrens	Holothuroidea; Aspidochirotacea; Aspidochirotida; Stichopodidae	NC_014454	Fan et al. (2011)
Asteroidea			
Freyastera benthophila	Asteroidea; Forcipulatacea; Brisingida; Brisingidae	MG563681	This study
Aphelasterias japonica	Asteroidea; Forcipulatacea; Forcipulatida; Asteriidae	NC_025766	Tang et al. (2014)
Pisaster ochraceus	Asteroidea; Forcipulatacea; Forcipulatida; Asteriidae	X55514	Smith, Banfield, Doteval, Gorski, and Kowbel (1990)
Asterias amurensis	Asteroidea; Forcipulatacea; Forcipulatida; Asteriidae	NC_006665	Matsubara et al. (2005)
Astropecten polyacanthus	Asteroidea; Valvatacea; Paxillosida; Astropectinidae	NC_006666	Matsubara et al. (2005)
Luidia quinaria	Asteroidea; Valvatacea; Paxillosida; Luidiidae	NC_006664	Matsubara et al. (2005)
Acanthaster brevispinus	Asteroidea; Valvatacea; Valvatida; Acanthasteridae	NC_007789	Yasuda et al. (2006)
Acanthaster planci	Asteroidea; Valvatacea; Valvatida; Acanthasteridae	NC_007788	Yasuda et al. (2006)
Patiria pectinifera	Asteroidea; Valvatacea; Valvatida; Asterinidae	NC_001627	Asakawa et al. (1995)

2.2 | PCR amplification and DNA sequencing

The universal metazoan primers for mtDNA were used in PCR. Three fragments *cox3*, *cob*, and *16S* were successfully amplified with the primers cox3F + cox3R (Boore, Macey, & Medina, 2005), cobF424 + cobR876 (Boore & Brown, 2000), and 16SarL + 16SbrH (Boore et al., 2005). In addition, partial sequences of *cox1*, *cox2*, *nad4L*, *atp6*, *nad4*, and *nad5* were amplified with the degenerate primers from conserved regions of other starfish in GenBank. The remaining gaps were amplified with the species-specific primers designed according to the obtained sequences. Finally, the whole mitogenome was amplified based on eight pairs of primers (Table 1).

PCRs were performed with a gradient machine (Applied Biosystems Inc.). The cycling was set up with an initial denature step at 94°C for 5 min, followed by 35 cycles (94°C for 30 s, 45–55°C for 1 min, 72°C 1–3 min), and a final extension was executed at 72°C for 10 min. LA-PCR was carried out in a 20 µl reaction volume containing 12.6 µl ddH$_2$O, 2 µl 10 × LA-PCR buffer (Mg^{2+} plus, Takara), 3.2 µl dNTP mix (2.5 mM each), 0.5 µl each primer (10 µM), 0.2 µl LA Taq DNA polymerase (5 U/µl, Takara), and 1 µl DNA template (50 ng/µl). PCR products were electrophoresed on a 1.0% agarose gel and purified with gel extraction kit (Omega Bio-Tek) and sequenced with ABI 3730x1 DNA analyzer (Applied Biosystems Inc.).
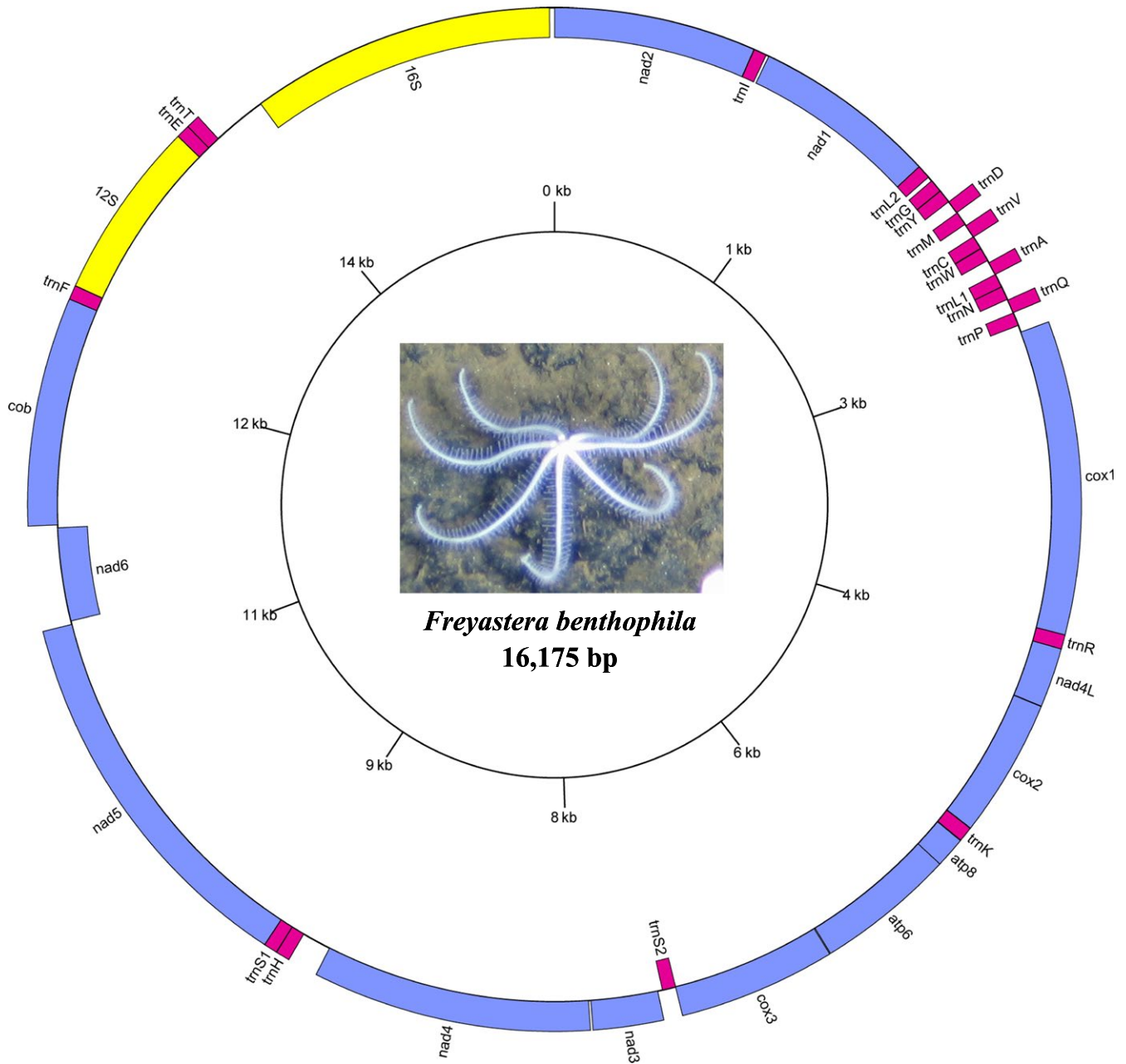
FIGURE 1 Mitochondrial gene map of *Freyastera benthophila*. All of 37 genes are encoded on the both strands. Genes for proteins and rRNAs are shown with standard abbreviation. Genes for tRNAs are designated by a single letter for the corresponding amino acid with two leucine tRNAs and two serine tRNAs differentiated by numerals

2.3 | Gene annotation and Sequence analysis

Raw sequencing reads were first processed using Phred with the quality score 20 and assembled in Phrap with default parameters (Ewing & Green, 1998; Ewing, Hillier, Wendl, & Green, 1998). Then, all assemblies and sequence quality were verified manually in Consed (Gordon, Abajian, & Green, 1998). DOGMA (Wyman, Jansen, & Boore, 2004), ORFfinder (http://www.ncbi.nlm.nih.gov/projects/gorf/orfig.cgi), and BLAST (http://blast.ncbi.nlm.nih.gov/Blast.cgi) were used to identify protein-encoding genes and rRNA genes. The tRNA genes were identified by tRNAscan-SE 1.21 (Lowe & Eddy, 1997) and ARWEN 1.2.3.c

(Laslett & Canbäck, 2008). Secondary structures for tRNAs were drawn using MITOS Web server (Bernt et al., 2013). Codon usage analysis was estimated with CodonW 1.4.4 (Peden, 1999). The mitochondrial gene map was drawn with GenomeVx (Conant & Wolfe, 2008).

2.4 | Phylogenetic analysis

Twenty echinoderm mt genomes including the one obtained in this study were used for phylogenetic analysis. All complete mtDNA sequences available in GenBank are listed in Table 2. Crinoidea is generally considered as the earliest diverged group of echinoderms (Scouras & Smith, 2006). In

TABLE 3 Genomic characteristics of Asteroidea mtDNAs

	Freyastera benthophila	*Asterias amurensis*	*Astropecten polyacanthus*	*Luidia quinaria*	*Aphelasterias japonica*	*Acanthaster brevispinus*	*Acanthaster planci*	*Patiria pectinifera*
Entire genome length (bp)	16,175	16,427	16,304	16,524	16,215	16,254	16,234	16,260
Entire genome A + T%	68.23	65.45	64.00	62.98	64.32	56.37	56.34	61.27
Protein-coding gene length (bp)	11,506	11,488	11,539	11,506	11,504	11,488	11,491	11,501
Protein-coding gene A + T%	67.15	64.45	62.48	61.02	62.95	55.95	55.64	60.12
12S gene length (bp)	891	893	901	884	900	928	929	897
12S gene A + T%	65.66	61.70	62.04	59.16	62.22	53.45	54.04	58.86
16S gene length (bp)	1,602	1,620	1,629	1,751	1,602	1,545	1,549	1,531
16S gene A + T%	72.28	70.19	69.12	69.67	69.66	55.34	56.04	66.49
tRNA length (bp)	1,557	1,580	1,561	1,563	1,566	1,546	1,550	1,585
tRNA A + T%	60.65	67.22	67.01	66.54	66.99	61.45	61.35	64.35
Largest NCR length (bp)	284	483	395	402	281	551	531	445
Largest NCR A + T%	67.25	63.98	64.56	70.15	62.63	53.90	54.99	59.78
nad2	1062 (ATG/TAG)	1062 (GTG/TAA)	1068 (GTG/TAA)	1068 (GTG/TAA)	1062 (ATG/TAG)	1065 (ATG/TAG)	1065 (ATG/TAG)	1065 (ATG/TAA)
nad1	972 (ATG/TAG)	978 (GTG/TAA)	976 (ATG/T-)	978 (GTG/TAG)	978 (GTG/TAA)	981 (GTG/TAG)	981 (GTG/TAG)	981 (GTG/TAG)
cox1	1557 (ATG/TAA)	1551 (ATG/TAA)	1554 (ATG/TAA)	1554 (ATG/TAA)	1552 (ATG/T-)	1553 (ATG/TA-)	1553 (ATG/TA-)	1554 (ATG/TAA)
nad4L	297 (ATG/TAA)	288 (ATG/TAA)	297 (ATT/TAA)	297 (ATT/TAA)	297 (ATC/TAA)	297 (ATT/TAA)	297 (ATT/TAA)	297 (ATT/TAA)
cox2	690 (ATG/TAA)	690 (ATG/TAA)	688 (ATG/T-)	693 (ATG/TAG)	690 (ATG/TAA)	688 (ATG/T-)	688 (ATG/T-)	688 (ATG/T-)
atp8	168 (ATG/TAA)	168 (ATG/TAA)	168 (ATG/TAA)	168 (ATG/TAA)	168 (ATG/TAA)	165 (ATG/TAA)	165 (ATG/TAA)	165 (ATG/TAA)
atp6	693 (ATG/TAA)	693 (ATG/TAA)	693 (ATG/TAA)	693 (ATG/TAA)	693 (ATG/TAA)	693 (ATG/TAA)	693 (ATG/TAA)	693 (ATG/TAA)
cox3	783 (TAG/TAA)	780 (ATG/TAA)	783 (ATG/TAA)	783 (ATG/TAA)	783 (ATG/TAA)	783 (ATG/TAA)	783 (ATG/TAA)	783 (ATG/TAA)
nad3	351 (ATG/TAA)	351 (ATG/TAA)	351 (ATT/TAA)	351 (ATT/TAG)	351 (ATG/TAA)	351 (ATT/TAA)	351 (ATT/TAA)	333 (ATT/TAG)
nad4	1386 (ATG/TAA)	1383 (ATG/TAA)	1380 (ATG/TAA)	1380 (ATG/TAA)	1383 (ATG/TAA)	1383 (ATG/TAG)	1383 (ATG/TAA)	1383 (ATG/TAA)
nad5	1920 (ATG/TAA)	1917 (ATG/TAA)	1905 (ATG/TAA)	1911 (ATG/TAA)	1920 (ATG/TAA)	1902 (ATG/TAA)	1902 (ATG/TAA)	1932 (GTG/TAA)
nad6	489 (ATG/TAG)	489 (ATG/TAG)	492 (ATG/TAA)	492 (ATG/TAA)	489 (ATG/TAG)	489 (ATG/TAG)	489 (ATG/TAG)	489 (ATG/TAA)
cob	1138 (ATG/T-)	1138 (ATG/T-)	1138 (ATG/T-)	1138 (ATG/T-)	1138 (ATG/T-)	1138 (ATG/T-)	1138 (ATG/T-)	1138 (ATG/T-)
Reference	This study	Matsubara et al. (2005)	Matsubara et al. (2005)	Matsubara et al. (2005)	Tang et al. (2014)	Yasuda et al. (2006)	Yasuda et al. (2006)	Asakawa et al. (1995)
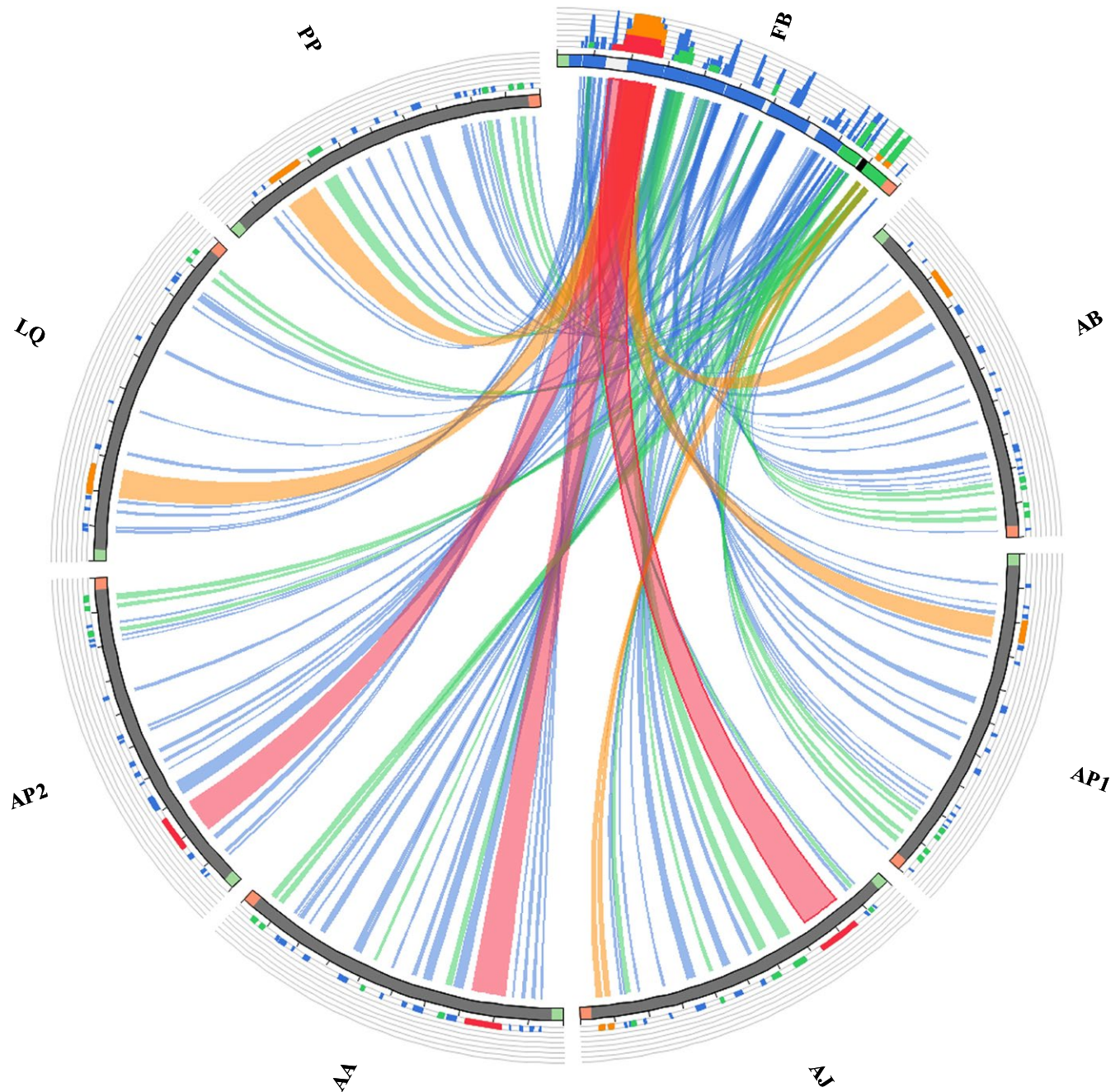
FIGURE 2 The synteny and identity level of *Freyastera benthophila* mitogenome against each of the other seven starfish mitogenomes. Ideograms and ribbons represent the similarity pairwise blastn searches. In *F. benthophila* ideogram, the 13 coding genes are colored in blue, control regions are colored in black, and rRNAs are colored in green. The figure was produced using Circoletto (Darzentas, 2010). FB (*F. benthophila*), AB (*Acanthaster brevispinus*), AP1 (*Acanthaster planci*), AJ (*Aphelasterias japonica*), AA (*Asterias amurensis*), AP2 (*Astropecten polyacanthus*), LQ (*Luidia quinaria*), PP (*Patiria pectinifera*)

this study, *Antedon mediterranea* (Crinoidea) was rooted as the out-group. The amino acid sequence from each of 13 protein-coding genes was aligned separately using Clustal ×2.0 (Larkin et al., 2007), and then, the relatively poor homologous sequence was eliminated. The aligned amino acid sequences were concatenated into a single dataset. The phylogenetic reconstruction approach was performed using neighbor joining (NJ) and maximum likelihood (ML) with MEGA 5.0 (Tamura et al., 2011). The assessment of node reliability was performed using 1,000 bootstrap replicates.

2.5 | Positive selection analysis

To evaluate the variation in selective pressure between deep-sea *F. benthophila* and other eight shallow sea starfish, we used a codon-based likelihood approach implemented in the CODEML program of the pamlX package (Xu & Yang, 2013; Yang, 2007). All models correct the transition/transversion rate and codon usage biases (F3 × 4). The branch model tests were used to analyze the difference of selective

**TABLE 4** Gene content of the *Freyastera benthophila* mitogenome

Gene	Location		Size		Codon		Intergenic	Strand
	Start	End	Nucleotide (bp)	Amino acid	Start	Stop	nucleotide (bp)	
nad2	1	1062	1,062	353	ATG	TAG	0	L
trnI	1064	1132	69				1	L
nad1	1147	2118	972	323	ATG	TAG	14	L
trnL$_2$	2119	2191	73				0	L
trnG	2216	2284	69				24	L
trnY	2286	2356	71				1	L
trnD	2357	2426	70				0	H
trnM	2428	2500	73				1	L
trnV	2509	2579	71				8	H
trnC	2578	2648	71				−2	L
trnW	2651	2721	71				2	L
trnA	2735	2804	70				13	H
trnL$_1$	2804	2875	72				−1	L
trnN	2876	2947	72				0	L
trnQ	2951	3022	72				3	H
trnP	3023	3093	71				0	L
cox1	3130	4686	1,557	518	ATG	TAA	36	H
trnR	4687	4757	71				0	H
nad4L	4758	5054	297	98	ATG	TAA	0	H
cox2	5056	5745	690	229	ATG	TAA	1	H
trnK	5747	5821	75				1	H
atp8	5824	5991	168	55	ATG	TAA	2	H
atp6	5976	6668	693	230	ATG	TAA	−16	H
cox3	6673	7455	783	260	ATG	TAA	4	H
trnS$_2$	7454	7524	71				−2	L
nad3	7549	7899	351	116	ATG	TAA	24	H
nad4	7911	9296	1,386	461	ATG	TAA	11	H
trnH	9448	9517	70				151	H
trnS$_1$	9519	9586	68				1	H
nad5	9587	11506	1,920	639	ATG	TAA	0	H
nad6	11524	12012	489	162	ATG	TAG	17	L
cob	12027	13164	1,138	379	ATG	T-	14	H
trnF	13165	13235	71				0	H
12S	13236	14126	891				0	H
trnE	14127	14194	68				0	H
trnT	14195	14263	69				0	H
16S	14548	16149	1,602				284	L

pressure between the deep-sea and shallow sea starfish. The "one-ratio" model (model 0), "free-ratio" model (model 1), and "two-ratio" model were used in the combined dataset of 13 protein-coding genes. Considering that positive selection may occur in some amino acids during the evolution of a protein, we used two branch site models (A and A null). Bayes empirical Bayes (Yang, Wong, & Nielsen, 2005) analysis was used to calculate the posterior probabilities of a specific codon site.

3 | RESULTS AND DISCUSSION

3.1 | General features

The mitogenome of the *F. benthophila* is a 16,175-bp circular molecule (Figure 1) with a nucleotide composition of 34.70% A, 21.13% C, 10.65% G, and 33.53% T bases. The genome has an overall A + T
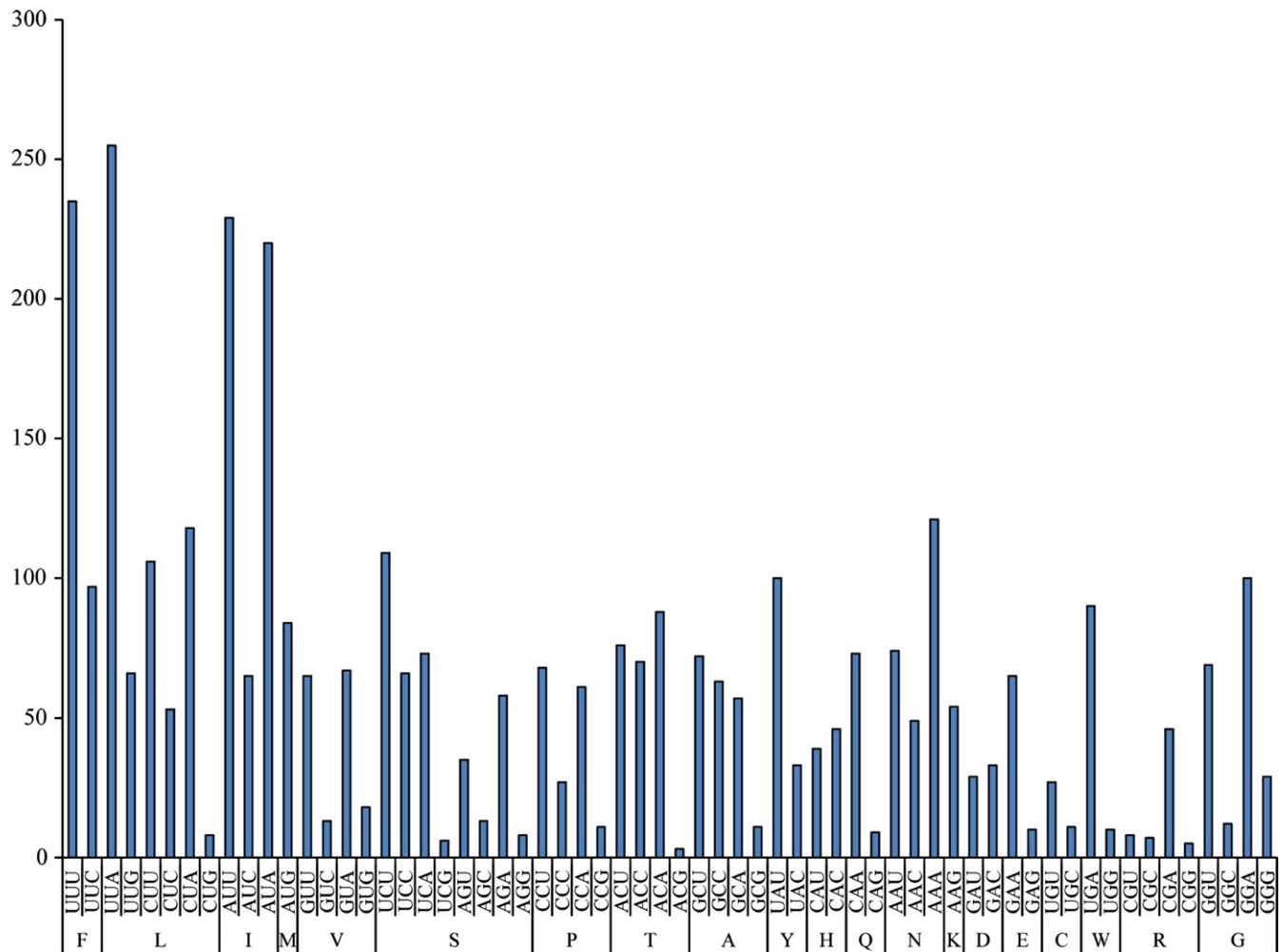
FIGURE 3 Codon usage in *Freyastera benthophila*. All codons for amino acids have been classified. Each amino acid is designated by a single letter for the corresponding codon. *x*-axis and *y*-axis represent the used times of each codon

content of 68.23%, which appears to be high for Asteroidea. Among the eight species in Asteroidea, the lowest A + T content is 56.34% in *Acanthaster planci* (Table 3). *Freyastera benthophila* has the smallest complete mitogenome found in Asteroidea thus far. The size of Asteroidea mitogenomes ranged from 16,524 bp in *Luidia quinaria* to 16,175 bp in *F. benthophila* (Table 3). The synteny and identity level between *F. benthophila* and each of the other seven starfish mitogenomes is shown in Figure 2. The lack of similarity between *F. benthophila* and *L. quinaria* is the most obvious feature in the plot.

The genome encodes 37 genes including 13 protein-coding genes (PCGs), two rRNA genes, and 22 tRNA genes (duplication of two tRNAs: *trnL* and *trnS*) on both strands. Fifteen of the genes are encoded on the negative strand, while the other 22 are encoded on the positive strand. A total of 22 noncoding regions were found, with the largest continuous region (284 bp, A + T = 67.25%) located between *trnT* and *16S*. Due to its AT richness, we predict that this part is mitochondrial control region. Furthermore, we found four overlaps: *trnC/trnV*, *trnA/trnL₁*, *atp8/atp6*, and *cox3/trnS₂*. Table 4 presents a summary of the organization of *F. benthophila* mitogenome. The complete mitochondrial DNA sequence has been deposited in GenBank (Accession Number: MG563681).

3.2 | Protein-coding genes

With regard to PCGs, nine (*cox1-cox3*, *nad3-nad5*, *nad4L*, *cob*, *atp6*, and *atp8*) are encoded by the positive strand, and the remaining three (*nad1*, *nad2*, and *nad6*) are encoded by the negative strand. These features have been observed in all Asteroidea mitogenomes published so far. Thirteen PCGs initiate with the standard start codon ATG. Most of PCGs terminate with the stop codon TAA (9 of 13), and three genes terminate with the stop codon TAG. Incomplete termination codon T is used by *cob*. However, mitogenomes often use a variety of nonstandard initiation codons (Wolstenholme, 1992). Nonstandard initiation codon GTG and incomplete termination codon TA are also used in other starfish (Table 3). The lengths of PCGs are 11,506 bp, and the A + T content is 67.15% higher than that of other Asteroidea species (Table 3).

The codon usage of *F. benthophila* is shown in Figure 3. Among PCGs, leucine (15.85%) and cysteine (0.99%) are the most and the least frequently used amino acids, respectively. Codons, UUA (leucine 6.67%) and ACG (threonine 0.08%), are the most and the least frequently used, respectively. We predict that the richness of A and
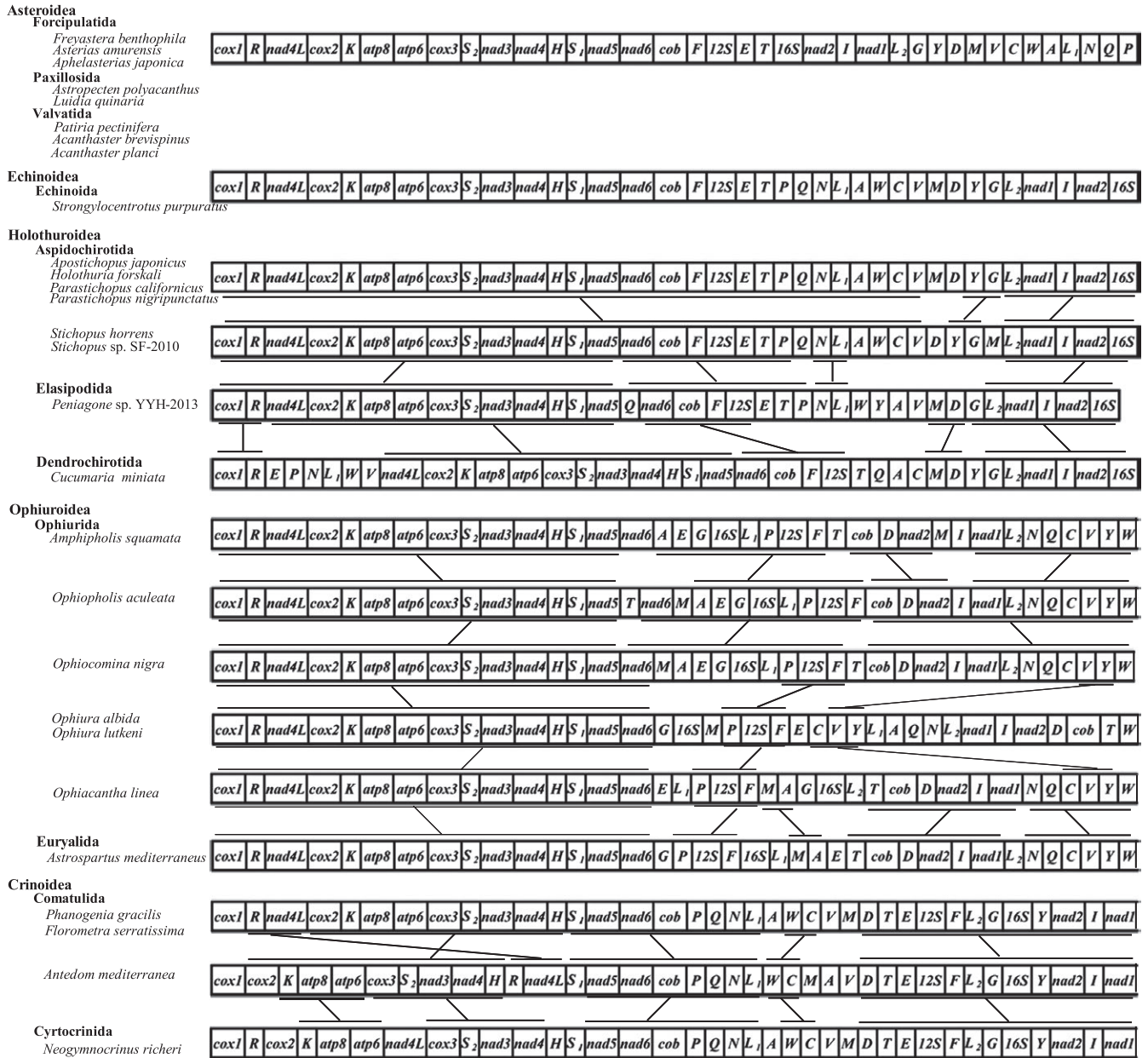
FIGURE 4 Comparison of mitochondrial gene arrangement in Echinodermata. The bars show identical gene blocks. The noncoding regions are not presented, and gene segments are not drawn to scale

T occurrence frequency of the mitogenome caused the corresponding amino acid bias to some extent. It is obvious that the A + T content of the third codon position (74.10%) is higher than that of the first (63.43%) and second positions (63.67%).

3.3 | Ribosomal RNA and transfer RNA genes

Boundaries of both the small and the large ribosomal genes were determined by BLAST and DOGMA. The *16S* and *12S* genes of *F. benthophila* are 1,602 bp (A + T = 72.28%) and 891 bp (A + T = 65.66%) in length, respectively. These lengths are typical for Asteroidea, whereas the AT contents are higher than those of other starfish (Table 3).

We analyzed the entire mitogenome sequence of *F. benthophila* and successfully identified 22 tRNA genes based on their potential secondary structures using the tRNAscan-SE, ARWEN, and MITOS Web server (Table 4, Supporting Information Figure S1). The length of these tRNA genes ranged from 68 bp (*trnS$_1$* and *trnE*) to 75 bp (*trnK*). Twenty-one of these genes displayed a common cloverleaf secondary structure, and the remaining one lacked a DHU arm from *trnS$_1$*. The D-stem absence has been found in many other starfish, such as *Acanthaster brevispinus*, *Acanthaster planci*, *Aphelasterias japonica*, *Asterias amurensis*, *L. quinaria*, and *Patiria pectinifera* (Asakawa, Himeno, Miura, & Watanabe, 1995; Matsubara et al., 2005; Tang et al., 2014; Yasuda et al., 2006).
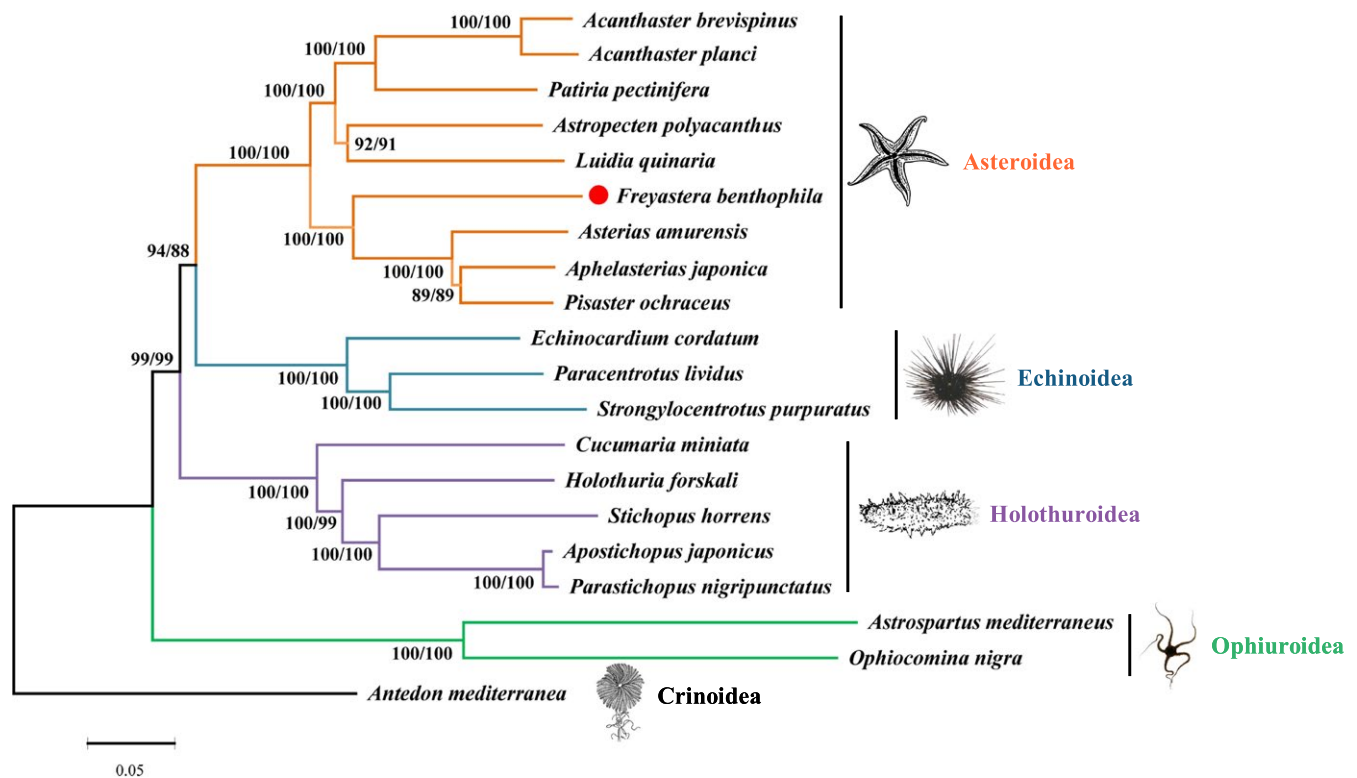
FIGURE 5 Phylogenetic trees based on the concatenated amino acids of 13 protein-coding genes. The branch length is determined with NJ analysis. _Antedon mediterranea_ was used as out-group. NJ (left number) and ML (right number) bootstrap values are given for each branch. The red dot highlights the species sequenced in this study

3.4 | Gene arrangement

Mitochondrial gene arrangement has been demonstrated to be an effective means to solve the deep phylogenetic studies (Boore, 1999; Boore & Brown, 1998). In recent years, some research on mt gene arrangement of echinoderms has been reported (Arndt & Smith, 1998; Perseke et al., 2008, 2010; Scouras et al., 2004).

In this study, mitochondrial gene order of echinoderm was compared among species within classes Asteroidea, Echinoidea, Holothuroidea, Ophiuroidea, and Crinoidea (Figure 4). We expected that the mt gene order of starfish may reveal some phylogenetically information. However, the gene component and gene order of eight species of Asteroidea are completely identical to each other. This phenomenon also happened in the class Echinoidea. We obtained 27 complete mt genomes of Echinoidea from NCBI genebank, and the gene component and gene order of 27 species of Echinoidea are also completely identical to each other. Because _Strongylocentrotus purpuratus_ has been considered as a model for developmental and systems biology, we took _S. purpuratus_ as a representative for Echinoidea in Figure 4 (Sodergren et al., 2006). However, mitochondrial gene order has undergone significant changes in the classes of Holothuroidea, Ophiuroidea, and Crinoidea. Scouras et al. (2004) suggested that it is difficult to resolve the echinoderm phylogeny using the mitochondrial gene rearrangement.

It is interesting that mt gene order of the species in the classes of Asteroidea and Echinoidea is completely identical to each other.

If the tRNA is not considered, gene order of PCGs in species within the class Holothuroidea is also the same. This raises the questions: As these species are distributed throughout the world's oceans, why had the mt gene order not been changed and how do they evolve over time. More studies of mt genome species are needed to further investigate whether this pattern is common among starfish, sea urchins, and sea cucumbers.

3.5 | Phylogenetic analysis

The gene order and transcriptional orientation of the eight Asteroidea species are completely identical to each other, so the mt genome structures would not provide the phylogenetic information. Thus, we performed the phylogenetic analysis using all amino acids of mt protein-coding genes (Figure 5). Almost all the phylogenetic relationships are supported with high values (NJ/ML bootstraps 99–100). _Acanthaster brevispinus_ is first clustered with _A. planci_ and then united with _P. pectinifera_; meanwhile, _Astropecten polyacanthus_ and _L. quinaria_ formed a clade. And these five starfish formed the Valvatacea clade. Then, _A. japonica_ is first clustered with _Pisaster ochraceus_ and then united with _A. amurensis_. Finally, _F. benthophila_ with these three species formed a Forcipulatacea clade. Blake (1987) recognized that Brisingida and Forcipulatida are the two orders within the Forcipulatacea and suggested that they were the most primitive asteroids (Blake, 1987, 1988). Mah and Foltz (2011) described that the largest clade within the Forcipulatacea is formed

TABLE 5 Selective pressure analyses of the mitochondrial genes of starfish

Branch model

Trees	Model	lnL	Estimates of parameters	Model compared	2ΔlnL	LRT p-value
NJ/ML	Model 1	−77,922.08746		Model 1 versus Model 0	127.22418	0.00000
	Two ratio	−77,985.69322	$\omega 0 = 0.06446$ $\omega 1 = 0.06371$	Two ratio versus Model 0	0.01266	0.91027
	Model 0	−77,985.69955	$\omega = 0.06438$			

Branch site model (BSM)

Gene	Model	lnL	Estimates of parameters					Model compared	2ΔlnL	LRT p-value	Positive sites
			Site class	0	1	2a	2b				
atp8	Model A	−1,269.41181	Proportion	0.53865	0.21395	0.17707	0.07033	Model A versus Model A null	1.82842	0.17632	8 N 0.996**
			Background ω	0.08240	1.00000	0.08240	1.00000				
			Foreground ω	0.08240	1.00000	151.29990	151.29990				
	Model A null	−1,270.32602									16 I 0.971*
nad2	Model A	−7,398.27984	Proportion	0.83756	0.10993	0.04641	0.00609	Model A versus Model A null	2.54316	0.11077	47 D 0.969*
			Background ω	0.04253	1.00000	0.04253	1.00000				
			Foreground ω	0.04253	1.00000	127.13451	127.13451				196 V 0.959*
	Model A null	−7,399.55142									
nad5	Model A	−12,858.89872	Proportion	0.76189	0.18603	0.04185	0.01022	Model A versus Model A null	0.34180	0.55879	599 N 0.961*
			Background ω	0.04324	1.00000	0.04324	1.00000				
			Foreground ω	0.04324	1.00000	1.52724	1.52724				
	Model A null	−12,859.06962									

*Posterior probability >95%; **Posterior probability >99%.

by the Brisingida and Asteriidae, which forms a clade of deep-sea and Southern Hemisphere taxa. In the present study, the results supported the deep-sea Brisingida as a sister taxon to the traditional members of the Asteriidae, and the branch support values are higher than those in previous studies (Glover et al., 2016; Mah & Foltz, 2011). However, the number of Brisingida species with complete mitogenome is still limited, and more mitogenomes and analysis are necessary to determine the phylogenetic relationship among members of Brisingida.

3.6 | Positive selection analysis

We examined the potential positive selection in Brisingida lineage because of the colonization of deep-sea environments which may affect the function of mitochondrial genes. The results of selective pressure analyses are shown in Table 5. When the ω ratios for the 13 concatenated mitochondrial protein-coding genes were tested between the deep-sea *F. benthophila* and other eight shallow sea starfish, we failed to find a significant difference in their ω ratios, which may be due to the large bias of sample sizes ($p > 0.05$) (Table 5). In addition, in the analyses of individual genes, we found five residues with high posterior probabilities in the *atp8* (8 N, 16 I), *nad2* (47 D, 196 V), and *nad5* (599 N), respectively (Table 5). Similar results have been observed in deep-sea animals, and the authors concluded that it may be related to the adaptation to environment (Sun et al., 2018; Zhang et al., 2017). Under the deep-sea extreme environment, survival may require a modified and adapted energy metabolism (Sun et al., 2018).

Because ATP synthase directly produces ATP, variation in ATPase protein sequence should influence ATP production (Mishmar et al., 2003; Wallace, 2007). Amino acid variations have been widely reported in the ATPase proteins (da Fonseca et al., 2008; Mishmar et al., 2003; Zhang et al., 2017; Zhou et al., 2014). *Nad2*, *nad4*, and *nad5* are suggested to act as proton-pumping devices (Brandt, 2006; da Fonseca et al., 2008); thus, mutations in these proteins should influence metabolic efficiency (da Fonseca et al., 2008; Hassanin, Ropiquet, Couloux, & Cruaud, 2009; Zhang et al., 2017). Therefore, we predict that mitochondrial protein-coding genes, specifically *atp8*, *nad2*, and *nad5*, may play an important role in *F. benthophila*'s adaptation to deep-sea environment.

4 | CONCLUSIONS

In this study, we determined the mitogenome of the deep-sea member *F. benthophila*, which is 16,175 bp in length and encodes 37 genes including 13 PCGs, two rRNA genes, and 22 tRNA genes on the both strands. We described the mitogenome features, codon usage, gene arrangement, phylogenetic analysis, and positive selection of the starfish *F. benthophila*. This study is the first determination of the mitogenome of a deep-sea member of the order Brisingida and may shed light on the adaptive evolution of Brisingida species to the deep-sea environment.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Haibin Zhang and Wendan Mu designed the study. Haibin Zhang contributed to the project coordination and collected the samples. Wendan Mu conducted the sequence analyses and drafted the manuscript. Haibin Zhang and Jun Liu helped to draft the manuscript. All authors read and approved the final manuscript.

DATA ACCESSIBILITY

The complete mitochondrial DNA sequence has been deposited in GenBank (Accession Number: MG563681).

ORCID

Haibin Zhang iD http://orcid.org/0000-0001-5429-9851

REFERENCES

Adkins, R., & Honeycutt, R. (1994). Evolution of the primate cytochrome *c* oxidase subunit II gene. *Journal of Molecular Evolution*, *38*, 215–231.

Arndt, A., & Smith, M. J. (1998). Mitochondrial gene rearrangement in the sea cucumber genus *Cucumaria*. *Molecular Biology and Evolution*, *15*, 1009–1016. https://doi.org/10.1093/oxfordjournals.molbev.a025999

Asakawa, S., Himeno, H., Miura, K., & Watanabe, K. (1995). Nucleotide sequence and gene organization of the starfish *Asterina Pectinifera* mitochondrial genome. *Genetics*, *140*, 1047–1060.

Bernt, M., Donath, A., Jühling, F., Externbrink, F., Florentz, C., Fritzsch, G., … Stadler, P. F. (2013). MITOS: Improved *de novo* metazoan mitochondrial genome annotation. *Molecular Phylogenetics and Evolution*, *69*(2), 313–319. https://doi.org/10.1016/j.ympev.2012.08.023

Blake, D. B. (1987). A classification and phylogeny of post-Palaeozoic sea stars (Asteroidea: Echinodermata). *Journal of Natural History*, *21*(2), 481–528. https://doi.org/10.1080/00222938700771141

Blake, D. B. (1988). Paxillosidans are not primitive asteroids: A hypothesis based on functional considerations. In R. D. Burke (Ed.), *Echinoderm biology* (pp. 309–314). Rotterdam, The Netherlands: Balkema.

Boore, J. L. (1999). Animal mitochondrial genomes. *Nucleic Acids Research*, *27*(8), 1767–1780. https://doi.org/10.1093/nar/27.8.1767

Boore, J. L., & Brown, W. M. (1998). Big trees from little genomes: Mitochondrial gene order as a phylogenetic tool. _Current Opinion in Genetics & Development_, _8_, 668–674. https://doi.org/10.1016/S0959-437X(98)80035-X

Boore, J. L., & Brown, W. M. (2000). Mitochondrial genomes of _Galathealinum_, _Helobdella_, and _Platynereis_: Sequence and gene arrangement comparisons indicate that Pogonophora is not a phylum and Annelida and Arthropoda are not sister taxa. _Molecular Biology and Evolution_, _17_(1), 87–106. https://doi.org/10.1093/oxfordjournals.molbev.a026241

Boore, J. L., Macey, J. R., & Medina, M. (2005). Sequencing and comparing whole mitochondrial genomes of animals. _Methods in Enzymology_, _395_, 311–348. https://doi.org/10.1016/S0076-6879(05)95019-2

Brandt, U. (2006). Energy converting NADH: Quinone oxidoreductase (complex I). _Annual Review of Biochemistry_, _75_, 69–92. https://doi.org/10.1146/annurev.biochem.75.103004.142539

Bridge, D., Cunningham, C. W., Schierwater, B., Desalle, R., & Buss, L. W. (1992). Class-level relationships in the phylum Cnidaria: Evidence from mitochondrial genome structure. _Proceedings of the National Academy of Sciences of the United States of America_, _89_(18), 8750–8753. https://doi.org/10.1073/pnas.89.18.8750

Cantatore, P., Roberti, M., Rainaldi, G., Gadaleta, M. N., & Saccone, C. (1989). The complete nucleotide sequence, gene organization, and genetic code of the mitochondrial genome of _Paracentrotus lividus_. _Journal of Biological Chemistry_, _264_(19), 10965–10975.

Clark, A. M., & Downey, M. E. (1992). _Starfishes of the Atlantic_. London, UK: Chapman and Hall.

Conant, G. C., & Wolfe, K. H. (2008). GenomeVx: Simple web-based creation of editable circular chromosome maps. _Bioinformatics_, _24_(6), 861–862. https://doi.org/10.1093/bioinformatics/btm598

da Fonseca, R. R., Johnson, W. E., O'Brien, S. J., Ramos, M. J., & Antunes, A. (2008). The adaptive evolution of the mammalian mitochondrial genome. _BMC Genomics_, _9_, 119. https://doi.org/10.1186/1471-2164-9-119

Darzentas, N. (2010). Circoletto: Visualizing sequence similarity with Circos. _Bioinformatics_, _26_(20), 2620–2621. https://doi.org/10.1093/bioinformatics/btq484

De Giorgi, C., Martiradonna, A., Lanave, C., & Saccone, C. (1996). Complete sequence of the mitochondrial DNA in the sea urchin _Arbacia lixula_: Conserved features of the echinoid mitochondrial genome. _Molecular Phylogenetics and Evolution_, _5_(2), 323–332.

Downey, M. E. (1986). _Revision of the Atlantic Brisingida (Echinodermata: Asteroidea), with description of a new genus and family_. Washington, DC: Smithsonian Institution Press.

Ewing, B., & Green, P. (1998). Base-calling of automated sequencer traces using _phred_. II. Error probabilities. _Genome Research_, _8_(3), 186–194. https://doi.org/10.1101/gr.8.3.186

Ewing, B., Hillier, L. D., Wendl, M. C., & Green, P. (1998). Base-calling of automated sequencer traces using _phred_. I. Accuracy assessment. _Genome Research_, _8_, 175–185. https://doi.org/10.1101/gr.8.3.175

Fan, S. G., Hu, C. Q., Wen, J., & Zhang, L. P. (2011). Characterization of mitochondrial genome of sea cucumber _Stichopus horrens_: A novel gene arrangement in Holothuroidea. _Science China Life Sciences_, _54_(5), 434–441. https://doi.org/10.1007/s11427-011-4168-8

Glover, A. G., Wiklund, H., Rabone, M., Amon, D. J., Smith, C. R., O'Hare, T., ... Dahlgren, T. G. (2016). Abyssal fauna of the UK-1 polymetallic nodule exploration claim, Clarion-Clipperton Zone, central Pacific Ocean: Echinodermata. _Biodiversity Data Journal_, _4_, e9277.

Gordon, D., Abajian, C., & Green, P. (1998). _Consed_: A graphical tool for sequence finishing. _Genome Research_, _8_, 195–202. https://doi.org/10.1101/gr.8.3.195

Hassanin, A., Ropiquet, A., Couloux, A., & Cruaud, C. (2009). Evolution of the mitochondrial genome in mammals living at high altitude: New insights from a study of the tribe Caprini (Bovidae, Antilopinae). _Journal of Molecular Evolution_, _68_, 293–310. https://doi.org/10.1007/s00239-009-9208-7

Knott, K. E., & Wray, G. A. (2000). Controversy and consensus in asteroid systematics: New insights to ordinal and familial relationships. _American Zoologist_, _40_, 382–392.

Larkin, M. A., Blackshields, G., Brown, N. P., Chenna, R., Mcgettigan, P. A., Mcwilliam, H., ... Lopez, R. (2007). Clustal W and Clustal X version 2.0. _Bioinformatics_, _23_(21), 2947–2948. https://doi.org/10.1093/bioinformatics/btm404

Laslett, D., & Canbäck, B. (2008). ARWEN: A program to detect tRNA genes in metazoan mitochondrial nucleotide sequences. _Bioinformatics_, _24_(2), 172–175. https://doi.org/10.1093/bioinformatics/btm573

Liu, Y., & Cui, Z. (2010). Complete mitochondrial genome of the Asian paddle crab _Charybdis japonica_ (Crustacea: Decapoda: Portunidae): Gene rearrangement of the marine brachyurans and phylogenetic considerations of the decapods. _Molecular Biology Reports_, _37_, 2559–2569. https://doi.org/10.1007/s11033-009-9773-2

Lowe, T. M., & Eddy, S. R. (1997). tRNAscan-SE: A program for improved detection of transfer RNA genes in genomic sequence. _Nucleic Acids Research_, _25_(5), 955–964. https://doi.org/10.1093/nar/25.5.0955

Luo, Y., Gao, W., Gao, Y., Tang, S., Huang, Q., Tan, X., ... Huang, T. (2008). Mitochondrial genome analysis of _Ochotona curzoniae_ and implication of cytochrome _c_ oxidase in hypoxic adaptation. _Mitochondrion_, _8_(5–6), 352–357. https://doi.org/10.1016/j.mito.2008.07.005

Mah, C. L., & Blake, D. B. (2012). Global diversity and phylogeny of the Asteroidea (Echinodermata). _PLoS ONE_, _7_(4), e35644. https://doi.org/10.1371/journal.pone.0035644

Mah, C., & Foltz, D. (2011). Molecular phylogeny of the Forcipulatacea (Asteroidea: Echinodermata): Systematics and biogeography. _Zoological Journal of the Linnean Society_, _162_, 646–660. https://doi.org/10.1111/j.1096-3642.2010.00688.x

Maliarchuk, B. A. (2011). Adaptive evolution of the _Homo_ mitochondrial genome. _Molecular Biology_, _45_(5), 845–850.

Matsubara, M., Komatsu, M., Araki, T., Asakawa, S., Yokobori, S., Watanabe, K., & Wada, H. (2005). The phylogenetic status of Paxillosida (Asteroidea) based on complete mitochondrial DNA sequences. _Molecular Phylogenetics and Evolution_, _36_(3), 598–605. https://doi.org/10.1016/j.ympev.2005.03.018

Matsubara, M., Komatsu, M., & Wada, H. (2004). Close relationship between _Asterina_ and Solasteridae (Asteroidea) supported by both nuclear and mitochondrial gene molecular phylogenies. _Zoological Science_, _21_(7), 785–793. https://doi.org/10.2108/zsj.21.785

Mishmar, D., Ruiz-Pesini, E., Golik, P., Macaulay, V., Clark, A. G., Hosseini, S., ... Wallace, D. C. (2003). Natural selection shaped regional mtDNA variation in humans. _Proceedings of the National Academy of Sciences of the United States of America_, _100_(1), 171–176. https://doi.org/10.1073/pnas.0136972100

Peden, J. F. (1999). Analysis of codon usage. Ph.D. Thesis, University of Nottingham.

Perseke, M., Bernhard, D., Fritzsch, G., Brümmer, F., Stadler, P. F., & Schlegel, M. (2010). Mitochondrial genome evolution in Ophiuroidea, Echinoidea, and Holothuroidea: Insights in phylogenetic relationships of Echinodermata. _Molecular Phylogenetics and Evolution_, _56_(1), 201–211. https://doi.org/10.1016/j.ympev.2010.01.035

Perseke, M., Fritzsch, G., Ramsch, K., Bernt, M., Merkle, D., Middendorf, M., ... Schlegel, M. (2008). Evolution of mitochondrial gene orders in echinoderms. _Molecular Phylogenetics and Evolution_, _47_(2), 855–864. https://doi.org/10.1016/j.ympev.2007.11.034

Plazzi, F., Ribani, A., & Passamonti, M. (2013). The complete mitochondrial genome of _Solemya velum_ (Mollusca: Bivalvia) and its relationships with Conchifera. _BMC Genomics_, _14_, 409. https://doi.org/10.1186/1471-2164-14-409

Qureshi, S. A., & Jacobs, H. T. (1993). Two distinct, sequence-specific DNA-binding proteins interact independently with the major replication pause region of sea urchin mtDNA. _Nucleic Acids Research_, _21_(12), 2801–2808. https://doi.org/10.1093/nar/21.12.2801

Ren, J., Liu, X., Jiang, F., Guo, X., & Liu, B. (2010). Unusual conservation of mitochondrial gene order in *Crassostrea* oysters: Evidence for recent speciation in Asia. *BMC Evolutionary Biology*, *10*, 394. https://doi.org/10.1186/1471-2148-10-394

Scouras, A., Beckenbach, K., Arndt, A., & Smith, M. J. (2004). Complete mitochondrial genome DNA sequence for two ophiuroids and a holothuroid: The utility of protein gene sequence and gene maps in the analyses of deep deuterostome phylogeny. *Molecular Phylogenetics and Evolution*, *31*(1), 50–65. https://doi.org/10.1016/j.ympev.2003.07.005

Scouras, A., & Smith, M. J. (2006). The complete mitochondrial genomes of the sea lily *Gymnocrinus richeri* and the feather star *Phanogenia gracilis*: Signature nucleotide bias and unique *nad4L* gene rearrangement within crinoids. *Molecular Phylogenetics and Evolution*, *39*(2), 323–334. https://doi.org/10.1016/j.ympev.2005.11.004

Shen, Y., Kou, Q., Zhong, Z., Li, X., He, L., He, S., & Gan, X. (2017). The first complete mitogenome of the South China deep-sea giant isopod *Bathynomus* sp. (Crustacea: Isopoda: Cirolanidae) allows insights into the early mitogenomic evolution of isopods. *Ecology and Evolution*, *7*(6), 1869–1881. https://doi.org/10.1002/ece3.2737

Shen, X., Ma, X., Ren, J., & Zhao, F. (2009). A close phylogenetic relationship between Sipuncula and Annelida evidenced from the complete mitochondrial genome sequence of *Phascolosoma esculenta*. *BMC Genomics*, *10*, 136. https://doi.org/10.1186/1471-2164-10-136

Smith, M. J., Arndt, A., Gorski, S., & Fajber, E. (1993). The phylogeny of echinoderm classes based on mitochondrial gene arrangements. *Journal of Molecular Evolution*, *36*(6), 545–554. https://doi.org/10.1007/BF00556359

Smith, M. J., Banfield, D. K., Doteval, K., Gorski, S., & Kowbel, D. J. (1990). Nucleotide sequence of nine protein-coding genes and 22 tRNAs in the mitochondrial DNA of the sea star *Pisaster ochraceus*. *Journal of Molecular Evolution*, *31*(3), 195–204. https://doi.org/10.1007/BF02109496

Sodergren, E., Weinstock, G. M., Davidson, E. H., Cameron, R. A., Gibbs, R. A., Angerer, R. C., ... Wright, R. (2006). The Genome of the Sea Urchin *Strongylocentrotus purpuratus*. *Science*, *314*(5801), 941–952.

Sun, S., Hui, M., Wang, M., & Sha, Z. (2018). The complete mitochondrial genome of the alvinocaridid shrimp *Shinkaicaris leurokolos* (Decapoda, Caridea): Insight into the mitochondrial genetic basis of deep-sea hydrothermal vent adaptation in the shrimp. *Comparative Biochemistry and Physiology Part D Genomics Proteomics*, *25*, 42–52. https://doi.org/10.1016/j.cbd.2017.11.002

Sun, X. J., Qi, L., & Kong, L. F. (2010). Comparative mitochondrial genomics within sea cucumber (*Apostichopus japonicus*): Provide new insights into relationships among color variants. *Aquaculture*, *309*(1–4), 280–285. https://doi.org/10.1016/j.aquaculture.2010.08.001

Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M., & Kumar, S. (2011). MEGA5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology and Evolution*, *28*(10), 2731–2739. https://doi.org/10.1093/molbev/msr121

Tang, M., Tan, M., Meng, G., Yang, S., Su, X., Liu, S., ... Zhang, A. (2014). Multiplex sequencing of pooled mitochondrial genomes-a crucial step toward biodiversity analysis using mito-metagenomics. *Nucleic Acids Research*, *42*(22), e166. https://doi.org/10.1093/nar/gku917

Tomasco, I. H., & Lessa, E. P. (2011). The evolution of mitochondrial genomes in subterranean caviomorph rodents: Adaptation against a background of purifying selection. *Molecular Phylogenetics and Evolution*, *61*, 64–70. https://doi.org/10.1016/j.ympev.2011.06.014

Wallace, D. C. (2007). Why do we still have a maternally inherited mitochondrial DNA? Insights from evolutionary medicine. *Annual Review of Biochemistry*, *76*, 781–821. https://doi.org/10.1146/annurev.biochem.76.081205.150955

Wolstenholme, D. R. (1992). Animal mitochondrial DNA: Structure and evolution. *International Review of Cytology*, *141*(6), 173–216. https://doi.org/10.1016/S0074-7696(08)62066-5

Wyman, S. K., Jansen, R. K., & Boore, J. L. (2004). Automatic annotation of organellar genomes with DOGMA. *Bioinformatics*, *20*(17), 3252–3255. https://doi.org/10.1093/bioinformatics/bth352

Xu, S., Luosang, J., Hua, S., He, J., Ciren, A., Wang, W., ... Zheng, X. (2007). High altitude adaptation and phylogenetic analysis of Tibetan horse based on the mitochondrial genome. *Journal of Genetics and Genomics*, *34*(8), 720–729. https://doi.org/10.1016/S1673-8527(07)60081-2

Xu, B., & Yang, Z. (2013). PAMLX: A graphical user interface for PAML. *Molecular Biology and Evolution*, *30*(12), 2723–2724. https://doi.org/10.1093/molbev/mst179

Yang, Z. (2007). PAML 4: Phylogenetic analysis by maximum likelihood. *Molecular Biology and Evolution*, *24*(8), 1586–1591. https://doi.org/10.1093/molbev/msm088

Yang, Z., Wong, W. S., & Nielsen, R. (2005). Bayes empirical Bayes inference of amino acid sites under positive selection. *Molecular Biology and Evolution*, *22*(4), 1107–1118. https://doi.org/10.1093/molbev/msi097

Yang, J.-S., & Yang, W.-J. (2008). The complete mitochondrial genome sequence of the hydrothermal vent galatheid crab *Shinkaia crosnieri* (Crustacea: Decapoda: Anomura): A novel arrangement and incomplete tRNA suite. *BMC Genomics*, *9*, 257. https://doi.org/10.1186/1471-2164-9-257

Yasuda, N., Hamaguchi, M., Sasaki, M., Nagai, S., Saba, M., & Nadaoka, K. (2006). Complete mitochondrial genome sequences for Crown-of-thorns starfish *Acanthaster planci* and *Acanthaster brevispinus*. *BMC Genomics*, *7*(1), 17. https://doi.org/10.1186/1471-2164-7-17

Yu, L., Wang, X., Ting, N., & Zhang, Y. (2011). Mitogenomic analysis of Chinese snub-nosed monkeys: Evidence of positive selection in NADH dehydrogenase genes in high-altitude adaptation. *Mitochondrion*, *11*(3), 497–503. https://doi.org/10.1016/j.mito.2011.01.004

Zhang, B., Zhang, Y. H., Wang, X., Zhang, H. X., & Lin, Q. (2017). The mitochondrial genome of a sea anemone *Bolocera* sp. exhibits novel genetic structures potentially involved in adaptation to the deep-sea environment. *Ecology and Evolution*, *7*(13), 4951–4962. https://doi.org/10.1002/ece3.3067

Zhou, T., Shen, X., Irwin, D. M., Shen, Y., & Zhang, Y. (2014). Mitogenomic analyses propose positive selection in mitochondrial genes for high-altitude adaptation in galliform birds. *Mitochondrion*, *18*, 70–75. https://doi.org/10.1016/j.mito.2014.07.012

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Mu W, Liu J, Zhang H. The first complete mitochondrial genome of the Mariana Trench *Freyastera benthophila* (Asteroidea: Brisingida: Brisingidae) allows insights into the deep-sea adaptive evolution of Brisingida. *Ecol Evol.* 2018;8:10673–10686. https://doi.org/10.1002/ece3.4427