



Mitochondrial genome of the shorthead catfish (*Pelteobagrus eupogon*): structure, phylogeny, and intraspecific variation

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Genet. Mol. Res. 15 (2): gmr.15028634

Received March 23, 2016

Accepted April 11, 2016

Published May 13, 2016

DOI <http://dx.doi.org/10.4238/gmr.15028634>

ABSTRACT. The complete 16,532-nucleotide sequence of the mitochondrial genome of the shorthead catfish (*Pelteobagrus eupogon*) was determined using the long and accurate polymerase chain reaction method, and compared with the mitochondrial genome sequences of 49 other catfish species belonging to the order Siluriformes. The locations of protein-coding genes and ribosomal ribonucleic acids (RNAs) were identified by comparison with known sequences of other catfishes, including *P. fulvidraco* and *P. nitidus*. The *P. eupogon* mitochondrial genome was composed of 13 protein-coding genes, two ribosomal RNAs, 22 transfer RNA genes, and a non-coding control region. The gene order was identical to that of other Siluriformes. Phylogenetic analyses based on mitochondrial 12S ribosomal RNA, 16S ribosomal RNA, and 13 protein-coding gene sequence data sets were carried out to further clarify the relative phylogenetic position of *P. eupogon*, and identify phylogenetic relationships among 24 families of Siluriformes. Phylogenetic analyses Randomized Axelerated Maximum Likelihood (RAXML) 8.0.X were congruent with a basal split of the order into Clupeiformes, Characiformes, Cypriniformes, and Siluriformes, and

supported a closer relationship of *P. eupogon* with Amblycipitidae than Siluridae. We therefore concluded that this species appears to be closely related to the Amblycipitidae. In the phylogenetic tree, the Amblycipitidae appeared as the most basal extant lineage within the Siluriformes, while the Bagridae appeared as the sister group of Cranoglanididae and Pangasiidae. The mitochondrial genome sequence of *P. eupogon* has been deposited in GenBank (accession No. KJ001784).

Key words: Intraspecific variation; Mitochondrial genome; Phylogeny; Shorthead catfish

INTRODUCTION

Mitochondrial DNA is commonly used in population and phylogenetic studies due to its maternal mode of inheritance and relatively low recombination rate (Cuore and Kocher, 1999). The mitochondrial DNA (mtDNA) of most animals is a self-replicating, circular DNA molecule, approximately 16 kb long, that codes for 13 mitochondrial proteins, 22 mitochondrial tRNAs, and two mitochondrial specific ribosomal RNAs (12S and 16S rRNA). It also contains DNA regions that control its replication and transcription (control region). From an evolutionary viewpoint, mtDNAs are “small genomes” that co-evolve at their own rate within the organism in which they reside (Peng et al., 2006).

Catfishes (Siluriformes) are widely distributed across all continents of the globe. In China, Siluriformes are composed of 11 families (Chen, 1977), the most widely distributed of which is the Bagridae family that includes the shorthead catfish (*Pelteobagrus eupogon*). Many Bagridae species are economically important in China, and the genetic diversity of wild populations is crucial for artificial culture. However, wild populations of these species have rapidly declined in recent years due to overfishing, pollution, and human other disturbances. Therefore, it is important to assess the genetic diversity of wild populations, to understand the impact that such rapid declines in populations have had. With the recent improvement of molecular techniques, it has become comparatively easier to obtain complete sequences of mitochondrial genomes.

In this study, we analyzed the complete DNA sequence and structure of the mitochondrial genome of shorthead catfish from the Hokiang, a tributary of the Yangtze River. We also assessed phylogenetic relationships within the order Siluriformes in combination using the mitochondrial genomes of other fishes (Table 1). To date, five mitochondrial genomes from four species in the genus *Pelteobagrus* have been reported to GenBank, including two from *P. eupogon* (Table 1). Thus, genetic variation can be analyzed across different geographical populations. Our findings provide a strong basis for evaluating the genetic diversity of catfish species in natural populations.

MATERIAL AND METHODS

Fish samples and DNA extraction

A shorthead catfish (*P. eupogon*) specimen was collected from the Hokiang in Sichuan

Province, China, and identified from morphology as described previously (Wu, 1989). The nuclear and mitochondrial DNA as extracted from muscle tissues using a 3S Spin Genomic DNA Miniprep Kit (Shanghai, China) following the manufacturer's protocol.

Table 1. Mitochondrial genome information for fishes in Siluriformes and other related orders.

Species	GenBank ID	Source
Siluriformes		
<i>Amphilius</i> sp NM-2010	AP012002	Nakatani et al. (2011)
<i>Amblydoras gonzalezi</i>	AP012001	Nakatani et al. (2011)
<i>Auchenoglanis occidentalis</i>	AP012005	Nakatani et al. (2011)
<i>Astroblepus</i> sp NM-2010	AP012004	Nakatani et al. (2011)
<i>Bunocephalus coracoideus</i>	AP012006	Nakatani et al. (2011)
<i>Chaca bankanensis</i>	AP012008	Nakatani et al. (2011)
<i>Centromochlus perugiae</i>	AP012024	Nakatani et al. (2011)
<i>Cetopsidium</i> sp NM-2010	AP012007	Nakatani et al. (2011)
<i>Chrysiichthys</i> sp NM-2010	AP012009	Nakatani et al. (2011)
<i>Clarias</i> sp NM-2010	AP012010	Nakatani et al. (2011)
<i>Corydoras rabauti</i>	AB054128	Saitoh et al. (2003)
<i>Cranoglanis boudierius</i>	AY898626	Peng et al. (2006)
<i>Diplomystes nahuelbutaensis</i>	AP012011	Nakatani et al. (2011)
<i>Glyptothorax fokiensis</i>	JQ917224	Zhou et al. (2012)
<i>Hara jerdoni</i>	AP012012	Nakatani et al. (2011)
<i>Hemibagrus macropterus</i>	JF834542	Zeng et al. (2012)
<i>Helogenes marmoratus</i>	AP012014	Nakatani et al. (2011)
<i>Heteropneustes fossilis</i>	AP012013	Nakatani et al. (2011)
<i>Ictalurus punctatus</i>	AF482987	Waldbieser et al. (2003)
<i>Leiocassis crassilabris</i>	JX867257	Liang et al. (2013)
<i>Leiocassis longirostris</i>	GU596454	Wang et al. (2011)
<i>Liobagrus kingi</i>	Kc193779	Jia et al. (2013a)
<i>Liobagrus marginatoides</i>	Kc473938	Jia et al. (2013b)
<i>Liobagrus nigricauda</i>	KC316116	Jia et al. (2013c)
<i>Liobagrus obesus</i>	DQ321752	Kartavtsev et al. (2007)
<i>Liobagrus reini</i>	AP012015	Nakatani et al. (2011)
<i>Malapterurus electricus</i>	AP012016	Nakatani et al. (2011)
<i>Pangasianodon gigas</i>	AY762971	Jondeung et al. (2007)
<i>Pangasius larnaudii</i>	AP012018	Nakatani et al. (2011)
<i>Pareutropius debauwi</i>	AP012017	Nakatani et al. (2011)
<i>Pelteobagrus eupogon</i>	JQ734476	Wang et al. (2013)
<i>Pelteobagrus eupogon</i>	KJ001784	Wang et al. (this study)
<i>Pelteobagrus fulvidraco</i>	HM641815	Liang et al. (2012a)
<i>Pelteobagrus nitidus</i>	HM746659	Liang et al. (2012b)
<i>Pelteobagrus vachellii</i>	HM746660	Liang et al. (2011)
<i>Pimelodus pictus</i>	AP012019	Nakatani et al. (2011)
<i>Plotosus japonicas</i>	AP012020	Nakatani et al. (2011)
<i>Pseudobagrus brevicaudatus</i>	JX867256	Liang et al. (2014a)
<i>Pseudobagrus brevicorpus</i>	HM355585	Kim et al. (2011)
<i>Pseudobagrus tokiensis</i>	AB054127	Saitoh et al. (2003)
<i>Pseudobagrus truncatus</i>	JX867259	Liang et al. (2014b)
<i>Pseudobagrus ussuriensis</i>	KC188782	Wan et al. (2013)
<i>Pterygoplichthys disjunctivus</i>	AP012021	Nakatani et al. (2011)
<i>Sciades seemanni</i>	AP012003	Nakatani et al. (2011)
<i>Silurus asotus</i>	JX087351	Wang et al. (2015)
<i>Silurus glanis</i>	AM398425	Vittas et al. (2011)
<i>Silurus lanzhouensis</i>	JF895472	Wang et al. (2012)
<i>Silurus meridionalis</i>	JX087350	Wang et al. (2015)
<i>Synodontis schoutedeni</i>	AP012023	Nakatani et al. (2011)
<i>Trichomycterus areolatus</i>	AP012026	Nakatani et al. (2011)
<i>Tetranemachthys quadrifilis</i>	AP012025	Nakatani et al. (2011)
Outgroup		
Cypriniformes		
<i>Crossostoma lacustre</i>	M91245	Tzeng et al. (1992)
Clupeiformes		
<i>Sardinops melanostictus</i>	AB032554	Inoue et al. (2000)
Characiformes		
<i>Phenacogrammus interruptus</i>	AB054129	Saitoh et al. (2003)

PCR amplification and sequencing

A total of seven long and accurate polymerase chain reaction (LA-PCR) primer pairs were designed by primer premier 5.0 (Table 2), based on the complete mitochondrial genome of *P. fulvidraco* (GenBank ID HM641815). Two short fragments were amplified to link the long fragments based on their sequences.

Table 2. PCR primers for *Pelteobagrus eupogon* mtDNA amplification.

Forward	Sequence (5'-3')	Reverse	Sequence (5'-3')	Size (bp)
Phe-ND2 F	AATCAAAGCATAACACTG	Phe-ND2 R	GCTTATGAATGTGAGGGT	4100
ND1-Trp F	AAACTTCCTGCCCTGAC	ND1-Trp R	GAATGCTCGCTGGCTTGA	2500
ND2-CO2 F	CAGCGAGCATTTCATCTAC	ND2-CO2 R	GAACGGCTTCTACAACAA	2600
Ser-ND3 F	TTACCACCAAACCTACCA	Ser-ND3 R	GAAGAATCGTAGGGAAAA	2500
CO3-ND5 F	TGCTGATATTGACACTT	CO3-ND5 R	GCAGACTTCCAGTAGCG	3000
ND5-Cytb F	TCGGCTGAGAAGGAGTAGGA	ND5-Cytb R	TAGGGATGCGAGGGCTGT	2600
Cytb-12S F	CTACAAAGACATTCTAGGGTTC	Cytb-12S R	ATGGCTAAGCATAGTGGG	2000

Long and accurate PCR (LA-PCR) was carried out in 50 μ L reactions containing 5 μ L 10X LA PCR buffer II, 8 μ L 1.5 mM mix dNTPs, 2 μ L each primer at 10 μ M, 0.5 U LA Taq polymerase (Takara, Dalian China), and approximately 50 ng template DNA. The thermal cycle profile was: pre-denaturation at 94°C for 4 min; 40 cycles of denaturation at 94°C for 60 s; annealing at 50°C for 60 s; extension at 72°C for 5 min; final extension at 72°C for 10 min. The PCR mixture for short fragments was the same as in LA-PCR, with the exception that the first extension time was changed to 1 min in the PCR program. PCR products were sent to Biosune Biotech Company (Beijing) for sequencing with primer walking.

Data analysis

DNA sequences were analyzed using the Sequencing Analysis software v 3.4.1 (Applied Biosystems, USA) and SeqMan v 5.05 (DNASTAR Inc., USA). The locations of protein-coding genes and rRNAs were identified by comparison with known sequences of other catfishes, including *P. fulvidraco* (GenBank ID: HM641815), (Liang et al., 2012a) and *P. nitidus* (GenBank ID: HM746659), (Liang et al., 2012b). Transfer RNA genes were identified by tRNA scan-SE 1.21 (Lowe and Eddy, 1997). Alignment of DNA sequences was performed using ClustalX version 1.81 (Thompson et al., 1997). Phylogenetic relationships were generated from the nucleotide sequences of the mitochondrial genes (including 12S and 16S rRNA genes), and the deduced amino acid sequences of each of the 13 complete mitochondrial protein-coding genes, using RAxML 8.0.X Inference (Stamatakis, 2006). The locations of the protein-coding genes and rRNAs were identified based on known sequences of other catfish species, including *P. fulvidraco* (GenBank ID HM641815) and *P. vachelli* (GenBank ID HM746660) (Liang et al., 2011). The DNA sequences of the 13 mitochondrial protein-coding genes used for analysis of *P. eupogon* are listed in Table 3.

RESULTS AND DISCUSSION

Structure of the mitochondrial genome

The complete mitochondrial genome of *P. eupogon*, with a total length of 16,532 bp,

was sequenced and deposited in GenBank (GenBank ID KJ001784). The gene order and gene-coding strands in *P. eupogon*: two rRNAs, 22 tRNAs, 13 protein-coding genes, and a control region (Table 3 and Figure 1), were identical to those of the Atlantic cod, Javeline goby, and Japanese flying fish (Johansen and Bakke, 1996; Nagase et al., 2005; Kim et al., 2011). The overall base composition of H-strand in *P. eupogon* was as follows: A, 30.3%; C, 28.7%; G, 16.0%; and T, 25.0%.

Table 3. Organization of the *Pelteobagrus eupogon* mitochondrial genome.

Gene	Abbreviation	Strand	Position	Size	Start codon	Stop codon
tRNA ^{Phe}	F	H	1-72	72		
12S ribosomal RNA	12S	H	73-1026	953		
tRNA ^{Val}	V	H	1027-1098	72		
16S ribosomal RNA	16S	H	1099-2776	1678		
tRNA ^{Leu}	L	H	2777-2851	75		
NADH dehydrogenase subunit 1	ND1	H	2852-3826	975	ATG	TAA
tRNA ^{Ile}	I	H	3831-3902	72		
tRNA ^{Gln}	Q	L	3903-3973	71		
tRNA ^{Met}	M	H	3973-4041	69		
NADH dehydrogenase subunit 2	ND2	H	4042-5088	1047	ATG	TAG
tRNA ^{Tyr}	W	H	5087-5157	71		
tRNA ^{Ala}	A	L	5160-5228	69		
tRNA ^{Asn}	N	L	5230-5302	73		
tRNA ^{Cys}	C	L	5334-5400	66		
tRNA ^{Tyr}	Y	L	5401-5471	71		
Cytochrome c oxidase subunit 1	COI	H	5473-7023	1551	GTG	TAA
tRNA ^{Ser}	S	L	7024-7094	71		
tRNA ^{Asp}	D	H	7099-7171	73		
Cytochrome c oxidase subunit 2	COII	H	7186-7876	691	ATG	T-
tRNA ^{Lys}	K	H	7877-7950	74		
ATP synthase F0 subunit 8	ATP8	H	7952-8119	168	ATG	TAA
ATP synthase F0 subunit 6	ATP6	H	8110-8793	684	ATG	TAA
Cytochrome c oxidase subunit 3	COIII	H	8793-9576	784	ATG	T-
tRNA ^{Gly}	G	H	9577-9650	74		
NADH dehydrogenase subunit 3	ND3	H	9651-10001	351	ATG	TAG
tRNA ^{Arg}	R	H	10000-10070	71		
NADH dehydrogenase subunit 4L	ND4L	H	10071-10367	297	ATG	TAA
NADH dehydrogenase subunit 4	ND4	H	10361-11741	1381	ATG	T-
tRNA ^{His}	H	H	11742-11811	70		
tRNA ^{Ser}	S	H	11812-11882	71		
tRNA ^{Leu}	L	H	11883-11955	73		
NADH	ND5	H	11956-13782	1827	ATG	TAA
NADH	ND6	L	13779-14294	516	ATG	TAA
tRNA ^{Glu}	E	L	14295-14363	69		
Cytochrome	Cyt B	H	14366-15503	1138	ATG	T-
tRNA ^{Thr}	T	H	15504-15576	73		
tRNA ^{Pro}	P	L	15575-15644	70		
Displacement loop (control region)	D-loop	H	15645-16532	888		

The protein-coding genes in the *P. eupogon* mitochondrial genome utilize ATG as a start codon, except for COI that initiated with GTG (Table 3). These findings are similar to the dogfish, Chinese longsnout catfish, and Yellow River catfish (Delarbre et al., 1998; Wang et al., 2011; Wang et al., 2012). Nine open reading frames ended with TAA or TAG, and the remaining genes had an incomplete stop codon T (Table 3). In *P. eupogon*, overlaps were found in ATP8-ATP6 (10 bp) and ND4-ND4L (7 bp), which occurred on the same strand, and in ND5-ND6 (5 bp) located on different strands.

The mitochondrial genome of *P. eupogon* contained 22 tRNA genes, ranging from 66 to 75 bp in size. All tRNA genes, except for tRNA^{Ser} (AGY), were predicted to display the typical cloverleaf secondary structure with normal base pairing. Among these tRNA genes, nine

were encoded on L-strand, and the remaining on H-strand. The 12S and 16S rRNA genes in *P. eupogon* had 953 and 1678 bp, respectively. 12S and 16S rRNA genes were located between the tRNA^{Phe} and tRNA^{Leu} genes and separated by the tRNA^{Val} gene, as in *S. meridionalis* and *S. asotus* (Wang et al., 2015) (Figure 1).

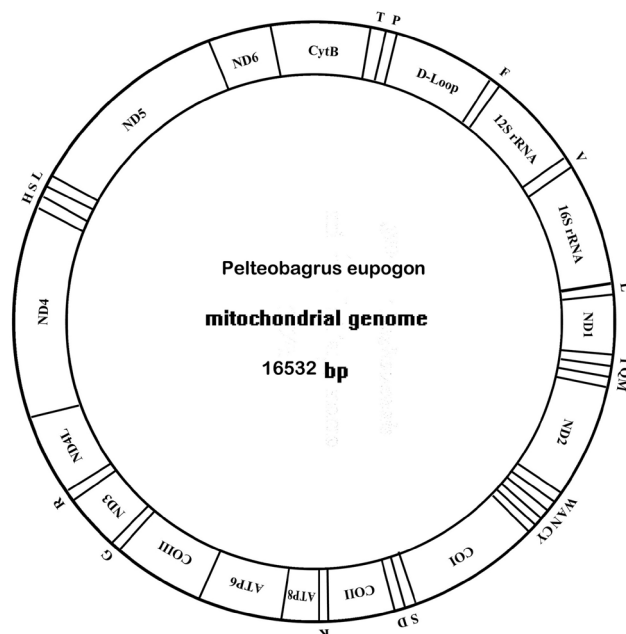


Figure 1. Gene organization of the *Pelteobagrus eupogon* mitochondrial genome. Gene names and abbreviations are listed in Table 3.

The major non-coding segment of the mitochondrial genome is the control region, which regulates replication and transcription (Inoue et al., 2000; Jondeung et al., 2007). The control region in *P. eupogon* was 888 bp long. Similar to other fish species (Kim et al., 2005; Xu et al., 2011), there are three candidates for promoters containing the TATA box conserved sequence block 5'-GTATATATACA-3' (CSB) domains that were found in the control region of *P. eupogon*: CSB-1 at the 5' end, and CSB-2 and CSB-3 at the 3' end (see annotation in GenBank ID KJ001784).

Phylogenetic analysis

Phylogenetic relationships of *P. eupogon* within the order Siluriformes are shown in Figure 2. Twelve species of catfish in the family Bagridae formed a distinct clade with high bootstrap values (100). This is consistent with the previously determined morphological classification of Bagridae, and its significant differentiation from other families within Siluriformes (Chen, 1977). As expected, the monophyly of Siluriformes, and the inclusion of *P. eupogon* within this order, were highly supported (bootstrap value of 100).

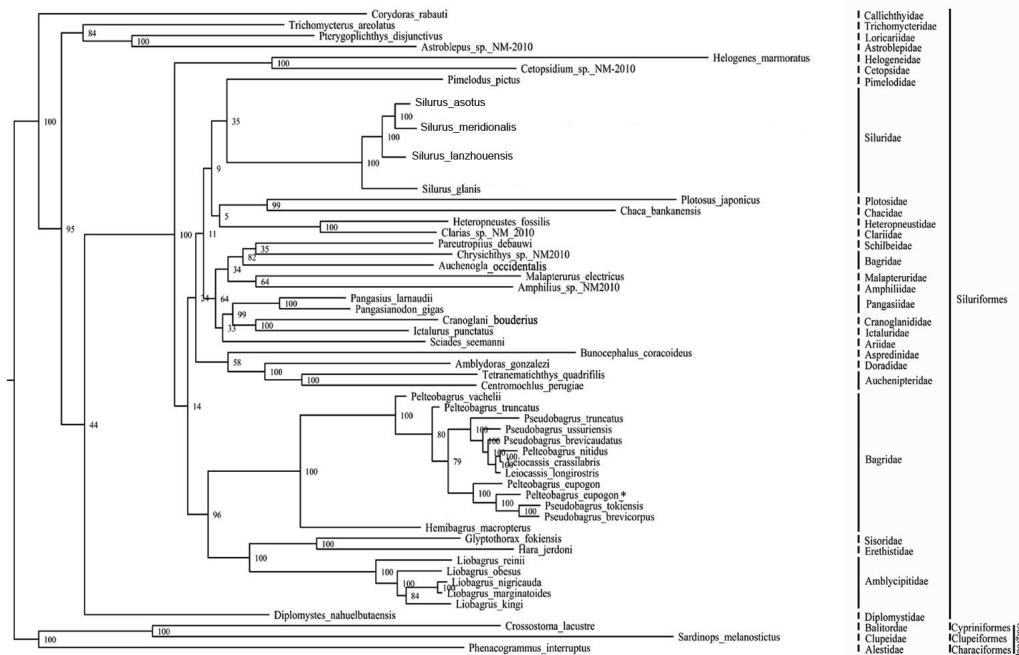


Figure 2. Phylogenetic relationships among Siluriformes as determined by RAxML. Majority rule consensus of maximum likelihood bootstrap measure trees from RAxML inference analysis based on rRNA and protein code data set under the GTR+I+G (General Time Reversible; I: invariable sites; G: gamma distribution) model is shown. Branch lengths are mean estimates. Asterisks indicate specimens used in the present study. Numbers in the nodes are from highest to lowest bootstrap value. The scale in the left lower corner indicates relative branch lengths.

The family of Bagridae and a sister group comprising Amblycipitidae, Sisoridae, and Erethistidae were strongly supported (bootstrap value of 96). These findings are consistent with the previously determined morphological classification that Bagridae is significantly differentiated from other families within Siluriformes. Bagridae was recovered with maximal support (bootstrap value of 100) as a sister group of Amblycipitidae. The Sisoridae and Erethistidae families were recovered as other sister groups. The Bagridae and Amblycipitidae families were closely related, however, *Chrysiichthys* sp NM 2010 (Nakatani et al., 2011) and *Auchenoglanis occidentalis* are excluded from Bagridae.

In other branches, the Schilbeidae, Malapteruridae, Amphiliidae, Cranoglanididae, Pangasiidae, Ariidae, and Ictaluridae families formed a distinct group (bootstrap value of 100). Four catfish species in the family Siluridae formed a distinct clade with high bootstrap support (100), in agreement with the previously determined morphological classification, indicating that the family Siluridae is significantly differentiated from other families within Siluriformes. Siluridae was recovered with maximal support as a sister group of *Pimelodus pictus* (Pimelodidae), which is consistent with the previous report (Nakatani et al., 2011). The families of Plotosidae, Chacidae, Heteropneustidae, and Clariidae were also recovered as sister groups, however, these relationships were not as well supported (bootstrap value of 9).

Even though phylogenetic interrelationships of highly diversified families of the order Siluriformes are well studied at the molecular level, the main phylogenetic interrelationships

of families, such as Loricariidae, Trichomycteridae, Astroblepidae, and Callichthyidae, remain largely unresolved. *Corydoras rabauti* (Callichthyidae), which is assigned to the suborder Loricarioidei, was placed as a sister group to all other analyzed Siluriformes. The family Callichthyidae is an independent clade in the Siluriformes. The phylogenetic relationship of the Siluriformes families obtained in this study were similar to another study based on the entire mitochondrial genome, excluding the control region (Delarbre et al., 1998). At a higher taxonomic level, the monophyly of Otophysi (Cypriniformes, Gymnotiformes, Characiformes, and Siluriformes) was highly supported (bootstrap value of 100) by all methods of phylogenetic inference. We inferred therefore that Siluriformes originate from Characiformes. The monophyly of the different orders within Ostariophysi is well supported on morphological grounds.

Nucleotide variation

When the mitochondrial genome of *P. eupogon* obtained in the present study was compared with two others submitted to GenBank (Table 4), among the 16589 bp aligned sequences, 9.9% of the sites were variable. The rRNA genes showed 11.3% variable sites, and tRNAs were fairly conserved with 3.2% variable sites. Meanwhile, the control region was more variable at 15.4%. The percentages of variable sites in all 13 protein-coding genes ranged from 2.3% (COXII) to 19.1% (ND1), with an average of 10.1% (Table 4). The specimen of *P. eupogon* in this study was sampled from the Hokiang, the upstream branch of the Yangtze River in Sichuan Province (China), whereas the precise location of the specimen used for comparison was not available from GenBank (GenBank ID JQ733476). However, the intraspecific variation between the two specimens is considerable, and may even suggest that the two specimens are different species.

Table 4. Intraspecific variation of mitochondrial genomes of two *Pelteobagrus eupogon* individuals (GenBank ID KJ001784 and JQ734476).

	Length of aligned sequence	Number of variable sites	Percentage of variable sites (%)
<i>All sites</i>	16,589	1,640	9.9
rRNAs	1,570	51	3.2
tRNAs	2,647	298	11.3
Control region	928	143	15.4
Protein-coding genes	11,384	1,149	10.1
ND1	975	186	19.1
ND2	1,047	126	12.0
COX1	1,551	51	3.3
COX2	691	15	2.3
ATP8	168	5	2.9
ATP6	684	19	2.8
COX3I	784	75	9.6
ND3	351	17	4.8
ND4L	297	38	9.4
ND4	1,381	199	14.4
ND5	1,827	223	12.2
ND6	516	64	12.4
CytB	1,138	141	12.4

ACKNOWLEDGMENTS

We thank Ms. Zeng Yanling for collecting field sample. Research supported by the key project of Science & Technology Department of Guizhou Province [Qiankehe #NZ

(2013)3027], the important scientific project in the “125” Program of Guizhou Province [Qianjiaohe #(2013)025], and the Joint Research Program of Guizhou [#LKZS (2012)20 and #LKZS (2012)17].

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