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SHORT COMMUNICATION

The Northern Brown Hagfish, *Eptatretus walkeri* (McMillan and Wisner, 2004) (Myxiniformes: Myxinidae), is Widely Distributed in Japanese Coastal Waters

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Abstract

The hagfish species found in the Sea of Japan has commonly and erroneously been identified as *Eptatretus atami* (Dean, 1904). In this study, hagfish specimens were collected from four locations in the coastal area of Choshi, Awa-Katsuyama, Enoshima and Noshiro in Japan for morphological and molecular analyses. Part of the cytochrome oxidase subunit 1 gene (COX1) in the mitochondrial DNA of hagfish specimens were sequenced to reconstructed a phylogenetic tree. Both morphological and molecular data suggest that the hagfish species from the Sea of Japan is not *E. atami*, but *Eptatretus walkeri* (McMillan and Wisner, 2004). The present study also indicates that *E. walkeri* is widely distributed not only on the Pacific coast of Honshu Island but also in the Sea of Japan.

Keywords: COX1, distribution, genetic divergence

Introduction

The brown hagfish, *Eptatretus atami* (Dean, 1904), was first described by Dean (1904) from a specimen obtained from Sagami Bay, on the Pacific coast of Honshu Island, Japan. In 1962, Honma reported that *E. atami* is distributed not only along the Pacific coast of Honshu Island but also in the Sea of Japan (Honma, 1962). However, Fernholm (1998) noted that the species has in the past been confused with one or two similar undescribed taxa that are commonly and erroneously identified as *E. atami*. In 2004, McMillan and Wisner described two new species, *E. moki* (McMillan and Wisner, 2004) and *E. walkeri* (McMillan and Wisner, 2004), based on differences in morphology. They noted that *E. atami* had 3/3 fused cusps (anterior/posterior multicusps), whereas *E. moki* and *E. walkeri* had 3/2 fused cusps, and *E. moki* is distinguished from *E. walkeri* by its well-developed ventral finfold (VFF) with pale margin. They also reported that *E. moki* is only found at Misaki near Sagami Bay on the Pacific coast of Honshu Island, Japan. In contrast, *E. walkeri* is found both off Choshi, on the Pacific coast of Honshu Island, and along the northwest coast in the Sea of Japan from

Izumozaki to Niigata. This suggests that previous identification of hagfish in the Sea of Japan as *E. atami* was erroneous. In 2017, Kase et al. (2017) showed genetic variations between the two *E. atami* populations off Honshu Island from Suruga Bay on the Pacific coast and from the Sea of Japan off Akita on the northwest coast using a part of the cytochrome oxidase subunit 1 (COX1) gene from the mitochondrial genome and three G protein-coupled receptor (GPR) genes from the nuclear genome. They suggested that the brown hagfish from the Sea of Japan constitutes a distinct species from *E. atami*, and might be *E. walkeri*. Since the holotype of *E. walkeri* was collected off Choshi on the Pacific coast of Honshu Island (McMillan and Wisner, 2004), a genetic divergence may occur between *E. walkeri* from the Pacific coast of Honshu Island and hagfish in the Sea of Japan. Due to the uncertainty of the identification, Kase et al. (2017) tentatively named the species *Eptatretus* sp. Akita. Thus, further study is necessary to investigate the correct identity of hagfish. Hence, this study was conducted to confirm the identity of the hagfish by doing morphological and molecular analyses on

samples collected from coastal areas of Honshu Island, Japan.

Materials and Methods

Hagfish specimens were collected from three locations from the Pacific coast of Honshu Island and from Noshiro in the Sea of Japan (Fig. 1). Specimens were caught by trawl fishery in off Choshi and by conger tube fishery in off Awa-Katsuyama, off Enoshima, and off Noshiro. Information on individuals and their morphological characteristics is summarized in Table 1. Detailed individual data are provided in Supplementary Table S1.

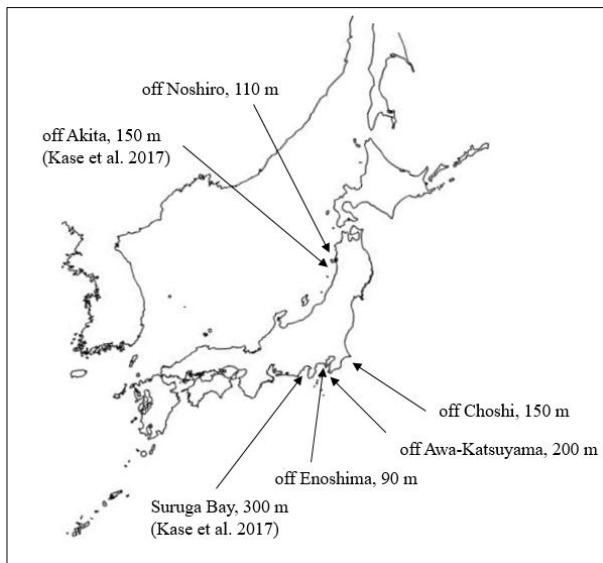


Fig. 1. Locations and capture depth of specimens used in this study and in Kase et al. (2017).

DNA extraction and PCR strategies used followed the methods of Kase et al. (2017). Four primers, pat-23 (5'-AACTCACCATTACTCTAACCTA-3'), pat-30 (5'-CATAATTAGTTCTGGTGCAG-3'), pat-73 (5'-CCAACTGTGAATATGTGATG-3'), and pat-74 (5'-TAAACAGTTCACCCAGTTCC-3') were used for sequencing. The fragment of *COX1* used in this study was shorter than the one used by Kase et al. (2017), but sufficiently long to be compared with other sequences belonging to the genus from the GenBank database (Supplementary Table S2). A multiple alignment was performed using the MUSCLE program (Edgar, 2004), and a phylogenetic tree was constructed by the neighbour-joining method (Saitou and Nei, 1987) with the Tamura and Nei (1993) model implemented in the MEGA7 software (Kumar et al., 2016).

Results and Discussion

In terms of morphology, all individuals from off Choshi, two individuals from off Enoshima, and four individuals from off Noshiro were differentiated as *E. walkeri* (Table 1). They have 3/2 fused cusps (Fig. 2a),

and their six-gill pouches arrangement is closely spaced in a slightly irregular (Fig. 2b). All individuals from off Awa-Katsuyama were differentiated as *E. atami*. They have 3/3 fused cusps (Fig. 2c), and their six-gill pouches arrangement is closely spaced in a slightly irregular (Fig. 2d). Nine individuals from off Enoshima and an individual from off Noshiro were differentiated as *E. burgeri* (Girard, 1855). They have 3/2 fused cusps (Fig. 2e), and their six-gill pouches arrangement is well spaced in a linear pattern (Fig. 2f).

We obtained 35 nucleotide sequences (ten from specimens off Choshi, nine from off Awa-Katsuyama, 11 from off Enoshima, and five from off Noshiro) of a 706 bp section of *COX1*. Nucleotide sequence data were deposited into the DDBJ/EMBL/GenBank International Nucleotide Sequence Database (accession numbers: LC378949–LC378983). Details on haplotypes are provided in Supplementary Table S1. Two different haplotypes (c1 and c2) were found from off Choshi, four (ak1, ak2, ak3 and ak4) from off Awa-Katsuyama, two (e1 and e2) from off Enoshima, and three (n1, n2 and n3) from off Noshiro. A phylogenetic tree based on these *COX1* data was constructed (Fig. 3) using a dataset including the haplotypes found in this study along with further sequences of the genus from the international nucleotide sequence databases (Supplementary Table S2). All four haplotypes from off Awa-Katsuyama clustered with *E. atami* from Suruga Bay with a bootstrap value of 95 %.

Furthermore, a well-supported cluster (100 % bootstrap value) include haplotypes belonging to individuals that were morphologically differentiated from *E. walkeri*. Haplotypes c2 from off Choshi, e2 from off Enoshima and n1 from off Noshiro were identical to haplotype a1 from off Akita (*Eptatretus* sp. Akita) (Kase et al. 2017). Haplotype n2 from off Noshiro was identical with haplotype a2 from off Akita (*Eptatretus* sp. Akita) (Kase et al. 2017). Results from the present study suggests that *E. walkeri* is widely distributed both on the Pacific coast of Honshu Island and along the northwest coast in the Sea of Japan.

Haplotypes n3 from off Noshiro and e1 from off Enoshima formed a cluster with *E. burgeri* suggest that *E. burgeri* lives in sympatry with *E. walkeri* off Noshiro and Enoshima. All the phylogenetic relationships evidenced for *COX1* haplotypes were consistent with morphological data (Table 1).

The present study indicates that the hagfish from the Sea of Japan is not *E. atami* (brown hagfish, Kuro-nutaunagi) but identified as *E. walkeri* (northern brown hagfish, Kita Kuro-nutaunagi). Furthermore, according to McMillan and Wisner (2004), the present results also suggested that *E. walkeri* is widely distributed not only on the Pacific coast of Honshu Island but also in the Sea of Japan.

Table 1. Gill pouches and numbers of cusps in selected hagfish (*Eptatretus* spp.).

	McMillan and Wisner (2004)				Kase et al. (2017)				This study			
	<i>E. burgeri</i> (Girard, 1855)	<i>E. atami</i> (Dean, 1904)	<i>E. moki</i> (McMillan and Wisner, 2004)	<i>E. walkeri</i> (McMillan and Wisner, 2004)	Suruga Bay	off Akita	off Choshi	off Awa-Katsuyama	off Enoshima	off Noshiro		
Capture depth (m)	10-270	300-536	100	75-120	300	90-150	150	200	90	90-110	90-110	
Maximum TL (mm)	690	610	470	518	-	500	515	575	514	479	563	
No. of individuals	-	-	-	-	14	16	10	9	2	4	1	
VFF	w/VFF	w/oVFF	w/VFF	w/VFF	w/oVFF	w/VFF	w/VFF	w/oVFF	w/VFF	w/VFF	w/VFF	
DF	w/DF	w/oDF	-	w/oDF	w/oDF	w/oDF	w/oDF	w/oDF	w/oDF	w/oDF	w/DF	
Gill pouches	6	6	6	6	6	6	6	6	6	6	6	
AGP	w/AGP	ci/AGP	ci/AGP	ci/AGP	ci/AGP	ci/AGP	ci/AGP	ci/AGP	ci/AGP	ci/AGP	w/AGP	
Fused cusps	3/2	3/3	3/2	3/2	3/3	3/2	3/2	3/3	3/2	3/2	3/2	
AUC (Right)	6-8	9-10	6-8	6-8	8-9	6-8	7-9	8-10	8	7-8	8	
AUC (Left)					8-9	7-8	7-8	7-10	7-9	7-8	8	
PUC (Right)	7-9	8-10	7-9	6-9	7-9	7-9	8-9	7-9	8-9	8-9	9	
PUC (Left)					5-9	7-9	8-9	7-10	8-9	8-9	8	
Total cusps	35-42	47-52	38-42	38-44	42-47	37-42	40-45	41-51	36-40	40-44	43	

TL, total length; AUC, anterior unicusps; PUC, posterior unicusps; VFF, ventral finfold; w/VFF, with ventral finfold; w/oVFF, without ventral finfold; DF, Dorsal finfold; w/DF, with dorsal finfold; w/oDF, without dorsal finfold; AGP, arrangement of gill pouches; ci/AGP, closely spaced in a slightly irregular pattern; w/AGP, well spaced in a linear pattern; w/oAGP, closely spaced in a nearly straight line.
See also Supplementary Table S1.

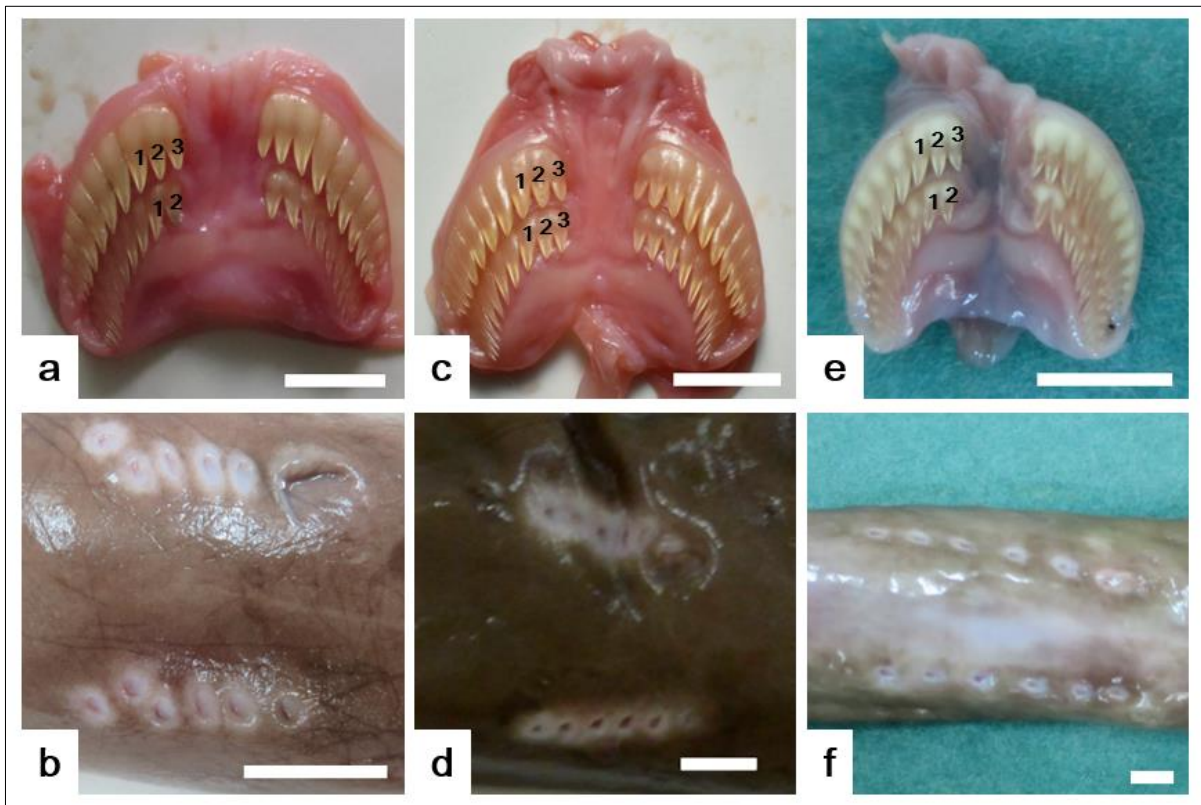


Fig. 2. Cusps and gill pouches in selected hagfish (*Eptatretus* spp.). 3/2 fused cusps (a) and six closely spaced gill pouches in a slightly irregular pattern (b), from *E. walkeri* off Choshi. 3/3 fused cusps (c) and six closely spaced gill pouches in a slightly irregular pattern (d), from *E. atami* off Awa-Katsuyama. 3/2 fused cusps (e) and six well-spaced gill pouches in a linear pattern (f), from *E. burgeri* off Enoshima. Left anterior (outer) and posterior (inner) fused cusps are numbered. Scale bars = 5.0 mm.

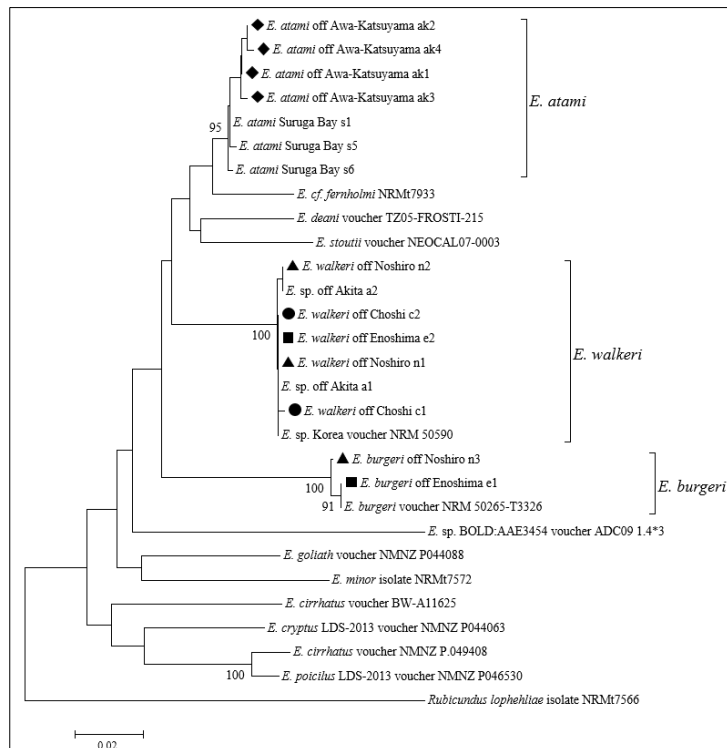


Fig. 3. Phylogenetic tree of nucleotide sequence data for *COX1* in hagfish species, constructed using the neighbor-joining method (Saitou and Nei 1987) and the Tamura and Nei (1993) model. Nucleotide sequence data are listed in Supplementary Table S2. A sequence from *Rubicundus lopheliae* (Fernholm & Quattrini, 2008) was used as the outgroup. Scale bar: 0.02 nucleotide substitutions per site. The nodes of the trees with bootstrap values lower than 75 % were considered not well-supported and thus collapsed. Haplotypes sequenced in the study were marked as follows: black circle, off Choshi; black diamond, off Awa-Katsuyama; black square, off Enoshima; black triangle, off Noshiro.

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Supplementary Table S1A. Gill pouches, numbers of cusps, and COX1 haplotypes from specimens collected off Chishi (150 m; 27 September 2017).

Individual ID	TL (mm)	BL (mm)	Body color	Gill pouches			Cusps						COX1 haplotype	Note					
				DFF	VFF	AGP	Right cusps			Left cusps					Total cusps				
							Fused cusps	Unicusps	Anterior	Fused cusps	Unicusps	Anterior				Fused cusps	Unicusps	Total cusps	
oC01	479	473	Dark brown	w/oDFF	w/VFF	ci/AGP	2	8	3	7	20	2	8	3	7	20	40	c1	
oC02	512	504	Dark brown	w/oDFF	w/VFF	ci/AGP	2	9	3	7	21	2	9	3	8	22	43	c2	
oC03	414	407	Dark brown	w/oDFF	w/VFF	ci/AGP	2	8	3	7	20	2	8	3	8	21	41	c2	
oC04	411	407	Dark brown	w/oDFF	w/VFF	ci/AGP	2	8	3	7	20	2	8	3	7	20	40	c2	
oC05	455	444	Dark brown	w/oDFF	w/VFF	ci/AGP	2	8	3	7	20	2	8	3	7	20	40	c2	
oC06	463	457	Dark brown	w/oDFF	w/VFF	ci/AGP	2	9	3	9	23	2	9	3	8	22	45	c2	
oC07	463	454	Dark brown	w/oDFF	w/VFF	ci/AGP	2	9	3	8	22	2	8	3	7	20	42	c2	
oC08	459	451	Dark brown	w/oDFF	w/VFF	ci/AGP	2	9	3	8	22	2	9	3	8	22	44	c2	
oC09	515	506	Dark brown	w/oDFF	w/VFF	ci/AGP	2	8	3	7	20	2	8	3	8	21	41	c2	
oC10	461	453	Dark brown	w/oDFF	w/VFF	ci/AGP	2	8	3	7	20	2	8	3	7	20	40	c2	

TL, total length; BL, body length; VFF, ventral finfold; w/VFF, with ventral finfold; w/oVFF, without ventral finfold; DFF, dorsal finfold; w/DFF, with dorsal finfold; w/oDFF, without dorsal finfold; AGP, arrangement of gill pouches; ci/AGP, closely spaced in a slightly irregular pattern; w/AGP, well-spaced in a linear pattern.

Supplementary Table S1B: Gill pouches, numbers of cusps, and COX1 haplotypes from specimens collected off Awa-Katsuyama (200 m; 23 July 2017).

Individual ID	TL (mm)	BL (mm)	Body color	VFF	DFF	Gill pouches		Right cusps						Left cusps						COX1 haplotype	Note						
						Number	AGP	Posterior		Anterior		Posterior		Anterior		Posterior		Anterior									
								Fused cusps	Unicusps	Fused cusps	Unicusps	Fused cusps	Unicusps	Fused cusps	Unicusps	Fused cusps	Unicusps	Fused cusps	Unicusps			Fused cusps	Unicusps				
oAK01	484	478	Black	w/oVFF	w/oDFF	6	ci/AGP	3	9	3	9	3	9	3	9	3	9	3	9	3	9	3	9	24	48	ak1	lack 1 left posterior fused cusps
oAK02	394	385	Black	w/oVFF	w/oDFF	6	ci/AGP	3	9	3	9	3	9	3	9	3	9	3	9	3	9	3	9	24	48	ak1	
oAK03	488	480	Black	w/oVFF	w/oDFF	6	ci/AGP	3	9	3	9	3	9	3	9	3	9	3	9	3	9	3	9	24	48	ak1	51 eggs
oAK04	536	529	Black	w/oVFF	w/oDFF	6	ci/AGP	3	9	3	9	3	9	3	9	3	9	3	9	3	9	3	9	23	47	ak2	
oAK05	575	566	Black	w/oVFF	w/oDFF	6	ci/AGP	3	9	3	10	3	10	3	9	3	9	3	10	3	10	3	10	25	50	ak1	
oAK06	377	372	Black	w/oVFF	w/oDFF	6	ci/AGP	3	9	3	10	3	10	3	10	3	10	3	10	3	10	3	10	26	51	ak3	
oAK07	394	391	Black	w/oVFF	w/oDFF	6	ci/AGP	3	8	3	8	3	8	3	8	3	8	3	8	3	8	3	8	22	44	ak2	
oAK08	542	533	Black	w/oVFF	w/oDFF	6	ci/AGP	3	8	3	8	3	8	3	8	3	8	3	8	3	8	3	8	22	44	ak1	52 eggs
oAK09	341	336	Black	w/oVFF	w/oDFF	6	ci/AGP	3	7	3	8	3	8	3	7	3	8	3	7	3	7	3	7	20	41	ak4	

TL, total length; BL, body length; VFF, ventral finfold; w/VFF, with ventral finfold; w/oVFF, without ventral finfold; DFF, dorsal finfold; w/DFF, with dorsal finfold; w/oDFF, without dorsal finfold; AGP, arrangement of gill pouches; ci/AGP, closely spaced in a slightly irregular pattern; wl/AGP, well-spaced in a linear pattern.

Supplementary Table S1C. Gill pouches, numbers of cusps, and COX1 haplotypes from specimens collected off Enoshima (90 m; 11 June 2017).

Individual ID	TL (mm)	BL (mm)	Body color	VFF	DFF	Gill pouches		Right cusps						Left cusps			COX1 haplotype	Total cusps	Note		
						Number	AGP	Posterior		Anterior		Posterior		Anterior		Fused cusps				Unicusps	Total cusps
								Fused cusps	Unicusps	Fused cusps	Unicusps	Fused cusps	Unicusps	Fused cusps	Unicusps						
oE01	518	510	Light brown	w/VFF	w/DFF	6	w/AGP	2	7	3	7	2	7	3	7	3	7	19	38	e1	
oE02	474	466	Light brown	w/VFF	w/DFF	6	w/AGP	2	7	3	6	2	7	3	6	3	6	18	36	e1	
oE03	464	455	Light brown	w/VFF	w/DFF	6	w/AGP	2	7	3	6	2	7	3	7	3	7	19	37	e1	
oE04	514	503	Black	w/VFF	w/oDFF	6	ci/AGP	2	8	3	8	2	8	3	7	3	7	20	41	e2	
oE05	434	425	Light brown	w/VFF	w/DFF	6	w/AGP	2	8	3	7	2	8	3	7	3	7	20	40	e1	
oE06	497	489	Light brown	w/VFF	w/DFF	6	w/AGP	2	8	3	7	2	7	3	7	3	7	19	39	e1	
oE07	342	334	White	w/oVFF	w/oDFF	6	ci/AGP	2	9	3	8	2	9	3	9	3	9	23	45	e2	
oE08	479	474	Light brown	w/VFF	w/DFF	6	w/AGP	2	7	3	7	2	7	3	6	3	6	18	37	e1	
oE09	453	446	Light brown	w/VFF	w/DFF	6	w/AGP	2	7	3	6	2	7	3	6	3	6	18	36	e1	
oE10	423	415	Light brown	w/VFF	w/DFF	6	w/AGP	2	7	3	6	2	7	3	6	3	6	18	36	e1	
oE11	427	422	Light brown	w/VFF	w/DFF	6	w/AGP	2	7	3	6	2	7	3	6	3	6	18	36	e1	

TL, total length; BL, body length; VFF, ventral finfold; w/VFF, with ventral finfold; w/oVFF, without ventral finfold; DFF, dorsal finfold; w/DFF, with dorsal finfold; w/oDFF, without dorsal finfold; AGP, arrangement of gill pouches; ci/AGP, closely spaced in a slightly irregular pattern; w/AGP, well-spaced in a linear pattern.

Supplementary Table S1D. Gill pouches, numbers of cusps, and COX1 haplotypes from specimens collected off Noshiro (110 m; 11 July 2016).

Individual ID	TL (mm)	BL (mm)	Body color	Gill pouches			Right cusps						Left cusps						COX1 haplotype	Total cusps	Note			
				VFF	DFF	Number	Posterior		Anterior		Posterior		Anterior		Posterior		Anterior							
							Fused cusps	Unicusps	Fused cusps	Unicusps	Fused cusps	Unicusps	Fused cusps	Unicusps	Fused cusps	Unicusps	Fused cusps	Unicusps						
oN01	236	233	Dark brown	w/VFF	wo/DFF	6	2	9	3	8	22	2	9	3	8	22	2	9	3	8	22	44	n1	
oN02	347	342	Dark brown	w/VFF	wo/DFF	6	2	8	3	8	21	2	8	3	8	21	2	8	3	8	21	42	n2	
oN03	563	551	Light brown	w/VFF	w/DFF	6	2	9	3	8	22	2	8	3	8	21	2	8	3	8	21	43	n3	
oN04	171	163	Dark brown	w/VFF	wo/DFF	6	2	8	3	8	21	2	8	3	8	21	2	8	3	8	21	42	n1	
oN05	189	183	Dark brown	w/VFF	wo/DFF	6	2	8	3	7	20	2	8	3	7	20	2	8	3	7	20	40	n1	

TL, total length; BL, body length; VFF, ventral finfold; w/VFF, with ventral finfold; wo/VFF, without ventral finfold; DFF, dorsal finfold; w/DFF, with dorsal finfold; wo/DFF, without dorsal finfold; AGP, arrangement of gill pouches; ci/AGP, closely spaced in a slightly irregular pattern; wi/AGP, well-spaced in a linear pattern.

Supplementary Table S2. List of species and sequences deposited in the DDBJ/EMBL/GenBank International Nucleotide Sequence Database.

Species	Accession No.	Note	Reference
<i>Eptatretus atami</i> (Dean, 1904)	LC178903	Suruga Bay COX1-s1	Kase et al. 2017
<i>Eptatretus atami</i> (Dean, 1904)	LC178907	Suruga Bay COX1-s5	Kase et al. 2017
<i>Eptatretus atami</i> (Dean, 1904)	LC178912	Suruga Bay COX1-s6	Kase et al. 2017
<i>Eptatretus</i> sp. Akita	LC178916	Akita COX1-a1	Kase et al. 2017
<i>Eptatretus</i> sp. Akita	LC178920	Akita COX1-a2	Kase et al. 2017
<i>Eptatretus burgeri</i> (Girard, 1855)	KC807320.1	voucher NRM 50265-T3326	Fernholm et al. 2013
<i>Eptatretus</i> cf. <i>fernholmi</i>	KC807333.1	NRMt7933	Fernholm et al. 2013
<i>Eptatretus cirrhatus</i> (Forster, 1801)	KC807345.1	voucher NMNZ P.049408	Fernholm et al. 2013
<i>Eptatretus cirrhatus</i> (Forster, 1801)	JX050996.1	voucher BW-A11625	Smith et al. unpublished
<i>Eptatretus deani</i> (Evermann & Goldsborough, 1907)	FJ164598.1	voucher TZ05-FROSTI-215	Steinke et al. 2009
<i>Eptatretus goliath</i> Mincarone & Stewart, 2006	KF144301.1	voucher NMNZ P044088	Zintzen et al. 2015
<i>Eptatretus minor</i> Fernholm & Hubbs, 1981	KC807329.1	isolate NRMt7572	Fernholm et al. 2013
<i>Eptatretus stoutii</i> (Lockington, 1878)	FJ164600.1	voucher NEOCAL07-0003	Steinke et al. 2009
<i>Eptatretus cryptus</i> LDS-2013	KF144287.1	voucher NMNZ P044063	Zintzen et al. 2015
<i>Eptatretus poicilus</i> LDS-2013	KF696684.1	voucher NMNZ P046530	Zintzen et al. 2015
<i>Eptatretus</i> sp. BOLD:AAE3454	JF493945.1	voucher ADC09 1.4*3	Steinke et al. unpublished
<i>Eptatretus</i> sp. 'Korea'	KC807324.1	voucher NRM 50590	Fernholm et al. 2013
<i>Rubicundus lopheliae</i> (Fernholm & Quattrini, 2008)	KC807325.1	isolate NRMt7566	Fernholm et al. 2013