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FULL PAPER

Adult form of a giant anguilliform leptocephalus *Thalassenchelys coheni* Castle and Raju 1975 is *Congriscus megastomus* (Günther 1877)

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Abstract Anguilliform leptocephali of the genus *Thalassenchelys* Castle and Raju 1975 are remarkably large and peculiarly shaped eel larvae, whose adult form has been unknown since the discovery of the larvae in the 1950s. We found bigmouth conger *Congriscus megastomus* (Günther 1877) collected off the Pacific coasts of Japan to have mitochondrial DNA sequences (16S rDNA and COI) nearly identical to those of *Thalassenchelys coheni* Castle and Raju 1975 published to date and collected recently in the north Pacific. Vertebrae counts of *C. megastomus* were consistent with the myomere counts of *T. coheni*. We conclude that *T. coheni*, so-called larval species described by Castle and Raju (1975), is a junior synonym of *C. megastomus*. Therefore, the family to which the leptocephali belong must be Congridae.

Keywords Anguilliformes · Giant leptocephalus · DNA barcoding · *Thalassenchelys coheni* · *Congriscus megastomus*

Introduction

Anguilliform leptocephali of the genus *Thalassenchelys* Castle and Raju 1975 are remarkably large and peculiarly shaped eel larvae. This is a so-called larval genus created by Castle and Raju (1975). The giant leptocephali were first reported by Aron (1958) who collected two individuals

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in 1957 using a shallow plankton tow (< 30 m) operated in the northeast Pacific (49°N, 144°W). The third specimen was reported from a plankton sample collected by a shallow water trawl operated off the coast of Washington in 1956 (Cohen 1959). Castle and Raju (1975) further searched archived specimens in museums and institutes and found 43 leptocephali of *Thalassenchelys*, including the specimens of Aron (1958) and Cohen (1959), in which they noticed that two groups amongst these leptocephali of *Thalassenchelys* from tropical to subtropical areas in the Indo-western Pacific were smaller (maximum size 228 mm) and had lower myomere counts ranging from 142 to 153. The other group from the central to northeast Pacific was larger (maximum size 304 mm) and had higher myomere counts ranging from 152 to 163. The former and the latter were then described as *Thalassenchelys foliaceus* Castle and Raju 1975 and *Thalassenchelys coheni* Castle and Raju 1975, respectively (Castle and Raju 1975). Further additional specimens from more recent research indicated a wider distribution of *T. coheni* throughout the North Pacific (Shimokawa et al. 1995; Takahashi et al. 2008; Hanke et al. 2014; Shubin and Koinov 2014). The adult form of *Thalassenchelys* has not been identified, and the family to which the giant leptocephali belong has been controversial amongst researchers. Castle and Raju (1975) reported remarkable agreements in vertebrae (= myomere) counts between leptocephali of *Thalassenchelys* (*T. foliaceus* and *T. coheni*) and two species of the genus *Congriscus* Jordan and Hubbs 1925: *Congriscus megastomus* (Günther 1877) and *Congriscus maldivensis* (Norman 1939). Nevertheless, Castle and Raju (1975) considered the similarity to be coincidental and finally disqualified *Congriscus* as a candidate for the adult form of *Thalassenchelys*, since Asano (1962) described leptocephali of *C. megastomus* to have a much lower body height. After eliminating many anguilliform families, Castle and Raju (1975) assigned Chlopsidae (formerly Xenocongridae) as the most probable candidate family for *Thalassenchelys* on the basis of its deep body and relatively short intestine. But Smith (1979) considered the assumption by Castle and Raju (1975) to be unlikely, and molecular phylogenetic analysis did not support the chlopsid affinity of *Thalassenchelys* (Obermiller and Pfeiler 2003; López et al. 2007; Inoue et al. 2010; Santini et al. 2013; Tang and Fielitz 2013; Chen et al. 2014). Obermiller and Pfeiler (2003) using mitochondrial ribosomal DNA sequence analysis suggested a close taxonomic position of *T. coheni* with the family Serrivomeridae. On the other hand, López et al. (2007) proposed that *Thalassenchelys* may be included in the family Colocongridae. This is because López et al. (2007) observed that *Thalassenchelys coheni* and *Coloconger cadenati* Kanazawa 1961 formed a distinct clade in the phylogenetic trees and the mitochondrial ribosomal DNA sequence divergence between these species was comparable with those between the other congeneric anguilliform species. However, in the phylogenetic trees presented by López et al. (2007), several species such as *Anguilla reinhardtii* Steindachner 1867 plus *Serrivomer sector* Garman 1899 and *Rhynchoconger flavus* (Goode and Bean 1896) plus *Saurenchelys fieraster* (Jordan and Snyder 1901) from different families also formed distinct clades. Furthermore, phylogenetic analysis by Inoue et al. (2010) using whole mitogenome sequences of 56 anguilliforms did not support the inclusion of *Thalassenchelys* in the family Colocongridae. Thus, the family to which *Thalassenchelys* belongs remained *incertae sedis* as suggested by Lavenberg (1988).

In our periodical field surveys followed by occasional molecular species identification, we encountered a congrid eel species sharing a nearly identical mitochondrial DNA sequences with *T. coheni*. Here, we present molecular and morphological evidence that *T. coheni* is a larval form of a deep sea conger eel species *C. megastomus*, resolving decades of uncertainty concerning the true identity of *T. coheni* leptocephali.

Materials and methods

Materials examined. Collection information on the fish samples used in this study is presented in Table 1. Twenty-two eel leptocephali having considerably large (> 200 mm) and deep bodies were extracted from the mid-water trawl samples of RV *Kaiyo-maru* (Fisheries Agency of Japan), operated at central North Pacific in June 2012. Unfortunately, after DNA extraction, these leptocephali had rotted due to fixation failure and were discarded, but the morphological peculiarity strongly suggested these to be species of the genus *Thalassenchelys*. Twenty leptocephali collected in the western North Pacific were initially identified to be *T. coheni* according to the collection locality, the large and deep body with rounded tail, short head, and no pigmentation (Fig. 1). Nineteen of these were caught in May to June 2013 by the RV *Soyo-maru* (Fisheries Research Agency of Japan) and one in May 2009 by the TS *Hokuho-maru* (Hokkaido Board of Education Management), both using a mid-water trawl net. These leptocephali were frozen on board and transferred to the laboratory. Seven bigmouth conger *Congriscus megastomus* (Fig. 2)

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Table 1 Collection information for *Thalassenchelys* leptocephali and bigmouth conger *Congriscus megastomus*

Species	Voucher	TL (mm)	Collection date	Ship (landing site)	Depth (m)	Latitude	Longitude
Thalassenchelys							
Thalassenchelys sp.	(22 individuals)	>200	June 20, 23, 2012	*Kaiyo-maru*	0–30	42°18′–43°30′N	159°56′–165°08′W
T. coheni	SNFR20565	177	May 31, 2013	*Soyo-maru*	0–26	34°52′–34°54′N	158°08′–158°09′E
T. coheni	SNFR20566–20571	145–212	June 1, 2013	*Soyo-maru*	0–25	37°27′–37°28′N	159°46′–159°47′E
T. coheni	SNFR20576	273	June 4, 2013	*Soyo-maru*	0–25	39°34′–39°35′N	155°48′–155°50′E
T. coheni	KYUM-PI4639	142	June 4, 2013	*Soyo-maru*	0–25	39°34′–39°35′N	155°48′–155°50′E
T. coheni	KYUM-PI4640	143	June 5, 2013	*Soyo-maru*	0–25	39°37′N	154°53′E
T. coheni	KYUM-PI4641–4646	106–134	June 3, 2013	*Soyo-maru*	0–25	38°38′N	159°29′E
T. coheni	KYUM-PI4647	108	June 2, 2013	*Soyo-maru*	0–25	38°41′N	159°45′E
T. coheni	KYUM-PI4648, 4649	117, 146	June 4, 2013	*Soyo-maru*	0–25	39°34′–39°35′N	155°48′–155°50′E
T. coheni	KYUM-PI4650	115	May 19, 2009	*Hokuho-maru*	-	38°33′N	155°29′E
Congriscus							
C. megastomus	SNFR20558	290	Oct 8, 2014	*Hinode-maru*	222–460	34°37′–34°43′N	138°40′–138°42′E
C. megastomus	SNFR20559–20564	272–348	Mar 18, 2015	*Hinode-maru*	147–405	34°42′–34°53′N	138°27′–138°29′E
C. megastomus	KYUM-PI4580–4582	210–228	May 19, 2014	*Tosa Kaiyo-maru*	303–305	33°23′N	133°64′E
C. megastomus	KYUM-PI4583, 4584	274, 283	April 28, 2014	(Katahara Port)	-	Off Gamagori, Aichi	
C. megastomus	KYUM-PI4585	196	May 19, 2014	*Tosa Kaiyo-maru*	303–305	33°23′N	133°64′E

(one in October 2014 and six in March 2015) were caught by the *Hinode-maru* using a Danish seine (bottom trawl) at Suruga Bay, Shizuoka, Japan. Four *C. megastomus* were caught in May 2014 by the *Tosa Kaiyo-maru* (Kochi Prefecture), using a bottom trawl operated off of the Niyodo River. Two *C. megastomus* were obtained at Katahara Port in April 2014, which were caught using a bottom trawl off Gamagori, Aichi Prefecture. The leptocephali and bigmouth conger were deposited in the Seikai National Research Institute, Fish Specimens Collection (SNFR), National Fisheries Research Agency, Nagasaki, Japan, and in the Kyushu University Museum (KYUM), Fukuoka, Japan.

After collecting a small piece of muscle tissue for DNA analysis, leptocephali were fixed in 8 % neutralized formaldehyde in seawater, while conger eels were fixed in 10 % neutralized formaldehyde solution for several weeks and transferred to 50 % isopropanol. Total and preanal myomere counts and myomere counts at the last vertical blood vessel (LVBV) were examined in the leptocephali, since these may be the most diagnostic characteristics to identify and separate *T. coheni* from *T. foliaceus* (see Castle and Raju 1975; Shimokawa et al. 1995). Pectoral-fin ray and vertebrae counts (total and trunk) were examined in *C. megastomus*, since these characteristics are known to differ among the three *Congriscus* species (Karmovskaya 2004). Total myomere counts in leptocephali are known to correspond to total vertebrae number in adults (Jespersen 1942; Smith 1979). Trunk or precaudal vertebrae counts in adults and LVBV in leptocephali are not equal, but can be used to compare between species of *Congriscus* and leptocephali of *Thalassenchelys* (see Castle and Raju 1975).

DNA analysis. Crude DNA was extracted from muscle tissue. Primers used to amplify partial sequences of the mitochondrial 16S rRNA and COI genes are presented in Table 2. PCR amplification was performed in a 12 μL final volume containing 1 μL of template DNA, 1.2 μL 10× buffer, 1 mM each dNTPs, 0.4 μM each primer, and 0.5 units of EX Taq polymerase (TaKaRa, Japan). The same reaction condition was applied for two primer pairs, in which the reaction mixtures were preheated at 94 °C for 4 min, followed by 35 amplification cycles (94 °C for 30 sec, 53 °C for 30 sec, and 72 °C for 50 sec), with a final extension at 72 °C for 7 min. Direct nucleotide sequencing was performed using PCR primers. Mitochondrial 16S rRNA sequences of *T. coheni* were obtained from Obermiller and Pfeiler (2003), López et al. (2007) and Tang and Fielitz (2013) and that of *Thalassenchelys* sp. was from Inoue et al. (2010). COI sequences of *Thalassenchelys* sp. were obtained from Inoue et al. (2010) and Chen et al. (2014). Sequence divergence was estimated by Kimura's two-parameter distance (K2P) using MEGA v6 (Tamura et al. 2013).

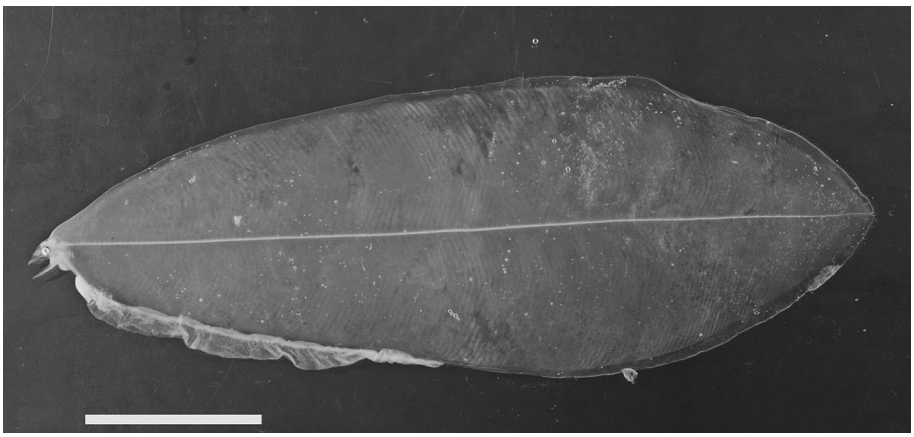

Fig. 1 Lateral view of *Thalassenchelys coheni*, SNFR20567, 210 mm TL. *Bar* 50 mm. Photograph by Koichi Hoshino

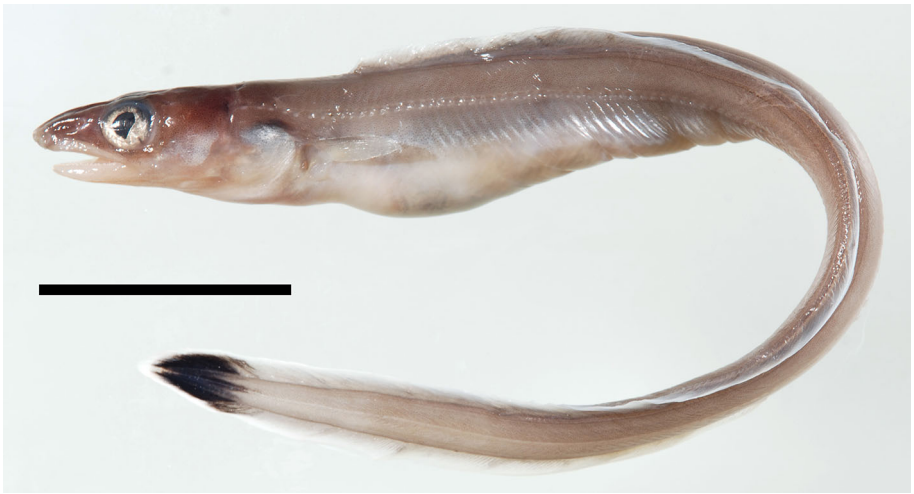

Fig. 2 Lateral view of *Congriscus megastomus*, SNFR20562, 272 mm TL. *Bar* 50 mm. Photograph by Koichi Hoshino

Table 2 Four primer sequences used to amplify two partial mitochondrial DNA regions

Region	Primer	Sequence (5′-3′)	Source
16S rRNA	16Sar-L	CGCCTGTTTATCAAAAACAT	Palumbi et al. 1991
	16Sbr-H	GGTCTGAACTCAGATCACGT	Palumbi et al. 1991 (modified)
COI	LCOm	ACRAATCAYAARGATATTGG	Folmer et al. 1994 (modified)
	FishR2m	GGGTGACCGAAGAATCAGAA	Ward et al. 2005 (modified)

Results

Morphological analysis. The results of a meristic comparison among *Thalassenchelys* and *Congriscus* are shown in Table 3. Twenty *T. coheni* collected and examined in this study had total myomeres ranging from 152 to 158, 19 individuals had preanal myomeres from 64 to 69, and 16 individuals had LVBV from 59 to 63. These counts corresponded closely to those of *T. coheni* in the original and subsequent descriptions (Castle and Raju 1975; Shimokawa et al. 1995; Shubin and Koinov 2014) and were distinct from *T. foliaceus* in the original description (Castle and Raju 1975). Of 13 *C. megastomus* collected and examined in this study, nine individuals had pectoral-fin ray count ranging from 17 to 19, and 13 individuals had total vertebrae from 153 to 162 and trunk vertebrae from 55 to 60, all corresponding to those of *C. megastomus* as previously described (Asano 1962; Castle and Raju 1975; Karmovskaya 2004). *Congriscus maldivensis* had the least number of total and trunk vertebrae, and *C. marquesaensis* Kamovskaya 2004 had the largest number of pectoral-fin rays (see Karmovskaya 2004).

Molecular analysis. Nucleotide sequences of all individuals examined in the present study are available in

Table 3 Meristic comparison among leptocephali of *Thalassenchelys* and eels of *Congriscus*

Species	Reference	*n*	TL	Pectoral-fin	Myomere or vertebrae counts			
			(mm)	ray	total	trunk	LVBV[d]	preanal
Thalassenchelys								
T. foliaceus	Castle and Raju (1975)	25	34.5–228.0	15, 18[b]	142–153		50–58	55–62
T. coheni	Castle and Raju (1975)	18	147.0–304.0	-	152–163		55–67	67–74
T. coheni	Shimokawa et al. (1995)	4	121.5–250.0	-	153–157		61–64	69–71
T. coheni	Shubin and Koinov (2014)	4	190.0–270.0	-	152–160		61–64	66–72
T. coheni	present study	20	106.0–273.0	-	152–158		59–63[e]	64–69[f]
Congriscus								
C. maldivensis	Castle and Raju (1975)	1	?	19	148	47		
C. maldivensis	Karmovskaya (2004)	41	175.0–370.0	15–20	137–152	47–52		
C. marquesaensis	Karmovskaya (2004)	4	222.0-273.0	22	158–164	55–57		
C. megastomus	Asano (1962)	71	221.0–345.5	16–20	150–159	54–59		
C. megastomus	Asano (1962)[a]	32	209.0–246.0	17–19				
C. megastomus	Castle and Raju (1975)	?	?	-	150–159	54-59		
C. megastomus	Karmovskaya (2004)	10	208.0-485.0	19–20	153–157	58–60		
C. megastomus	present study	13	196.0–348.0	17–19[c]	153–162	55–60		

[a] Asano (1962) described these 32 to be larval forms, but probably metamorphosing individuals

[b] Fifteen indistinct rays from a leptocephalus and 18 rays from a metamorphic individual

[c] Pectoral-fin ray count was based on nine individuals

[d] LVBV = last vertical blood vessel

[e] Based on 16 leptocephali

[f] Based on 19 leptocephali

DDBJ/EMBL/GenBank (accession no. LC056713 to LC056741, LC061534 to LC061578, and LC073316 to LC073333).

Partial 16S rRNA sequences of 22 *Thalassenchelys* sp., 20 *T. coheni*, and 13 *C. megastomus* were determined. We obtained the 476 bp region from 16S rRNA for 59 individuals including four from the database (three *T. coheni* and one *Thalassenchelys* sp.), and the sequence alignment revealed 11 variable sites including two indels. Average nucleotide sequence divergences between individuals within *Thalassenchelys* sp., *T. coheni*, and *C. megastomus* collected in the present study were 0.10 ± 0.04 %, 0.06 ± 0.04 %, and 0.15 ± 0.09 %, respectively, and overall average for the 55 samples was 0.10 ± 0.04 %. Average nucleotide sequence divergence between all 55 samples (42 *Thalassenchelys* leptocephali plus 13 *C. megastomus*) and four sequences from the database (three *T. coheni* plus one *Thalassenchelys* sp.) was 0.05 ± 0.02 %. These values were well within the range of intraspecific divergence in fish 16S rRNA (Kochzius et al. 2010).

Partial COI sequences of 22 *Thalassenchelys* sp., eight *T. coheni*, and seven *C. megastomus* were also determined. We obtained the 636 bp region from the COI gene for 39 individuals including two from the database. Sequence alignment revealed no indel and all substitutions observed at 22 sites were silent. The average nucleotide sequence divergence between individuals within *Thalassenchelys* sp., *T. coheni*, and *C. megastomus* collected in the present study were 0.36 ± 0.11 %, 0.30 ± 0.14 %, and 0.39 ± 0.13 %, respectively, and the overall average of 37 samples was 0.35 ± 0.10 %. Average nucleotide sequence divergence between all 37 samples (30 leptocephali of *Thalassenchelys* plus seven *C. megastomus*) and two *Thalassenchelys* sp. sequences from the database was 0.35 ± 0.16 %. These values were well within the range of intraspecific divergence in fish COI (Ward et al. 2005; Kochzius et al. 2010).

Discussion

The results obtained indicate that all specimens of *Thalassenchelys* collected and analyzed in the present study are *T. coheni*, and that *T. coheni* is a larval form of *Congriscus megastomus*. Therefore, *T. coheni* appears to be a junior synonym of *C. megastomus*.

Asano (1962) reported that *C. megastomus* leptocephali were abundantly captured together with the adult form in deep sea trawl. On the other hand, almost all leptocephali of *Thalassenchelys* have been caught by mid to near surface trawling (Aron 1958; Cohen 1959; Shimokawa et al.

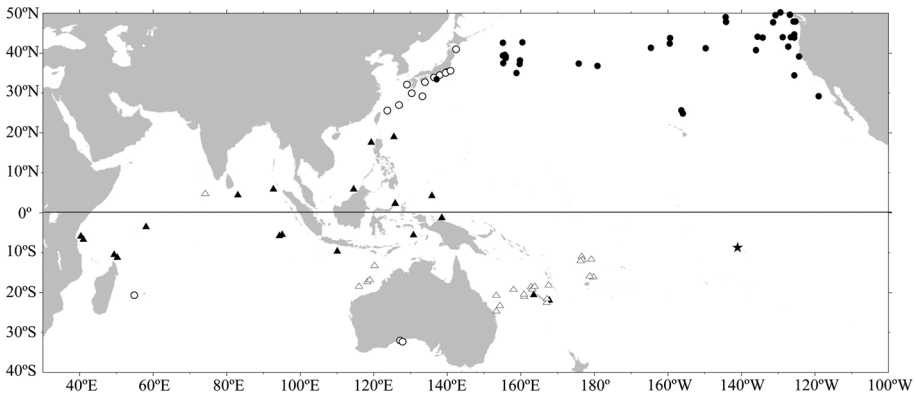

Fig. 3 Map showing the collection locality records for larval and adult forms of three species of *Congriscus*. *Closed circle*: *C. megastomus* leptocephali (= *T. coheni*); *open circle*: *C. megastomus* adult; *closed triangle*: *C. maldivensis* leptocephali (= *T. foliaceus*); *open triangle*: *C. maldivensis* adult; *closed star*: *C. marquesaensis* adult. Data were obtained from Asano (1962), Castle and Raju (1975), Shimokawa et al. (1995), Shinohara and Matsuura (1997), Shinohara et al. (2001), Meckelenburg et al. (2002), Karmovskaya (2004), Hanke et al. (2014), Yamada et al. (2007), and Shubin and Koinov (2014)

1995; Takahashi et al. 2008; Hanke et al. 2014; Shubin and Koinov 2014; present study). Therefore, the *C. megastomus* leptocephali described by Asano (1962) must be the final stage of metamorphosis having considerably reduced body height, which consequently misled Castle and Raju (1975).

There are currently three recognized species in the genus *Congriscus*: *C. megastomus* distributed in the Indo-western North Pacific, *C. maldivensis* distributed in the Indo-western tropical Pacific, and the recently described *C. marquesaensis* found in the Marquesas Islands (Karmovskaya 2004). Surprisingly, none of them has been subjected to DNA analysis. *Congriscus megastomus* specimens had a distinctive dark-colored area stretching along their body and vertical fins near the end of their tail (Asano 1962; Masuda et al. 1984) (see Fig. 2). *Congriscus marquesaensis* had a black spot in front of the pectoral fin, while *C. maldivensis* had neither such a dark-colored area nor a black spot (Karmovskaya 2004). Meristic characteristics can also discriminate these three species as shown in Table 3. *Thalassenchelys foliaceus* had the least number of total myomere and LVBV. These meristic characteristics together with distribution records of the larval and adult forms strongly suggest that *T. foliaceus* is the larval form of *C. maldivensis* and that the larval form of *C. marquesaensis* is not yet known. In this study, we revealed the adult form of leptocephali of *Thalassenchelys* to be a species of the genus *Congriscus*; thus the family to which leptocephali of *Thalassenchelys* belong must be Congridae.

Collection localities of adult and larval forms of species of *Congriscus* reported to date are shown in Fig. 3. The distribution of *C. megastomus* leptocephali (= *T. coheni*) is throughout the North Pacific, and no striking size difference of the leptocephali was observed among areas, ranging from 106 to 273 mm ($n = 60$) in the western North Pacific (Asano 1962; Shimokawa et al. 1995; Shubin and Koinov 2014; present study), larger than 200 mm ($n = 22$) in the central North Pacific (present study), and from 147 to 304 mm ($n = 22$) in the eastern North Pacific (Castle and Raju 1975; Meckelenburg et al. 2002; Hanke et al. 2014). The adults of *C. megastomus* have been reported in the Indo-western North Pacific (Asano 1962; Masuda et al. 1984; Karmovskaya 2004; Garilao and Reyes 2015), while no capture was reported in the bottom trawl surveys performed around seamounts in the central (163°E–174°W) and eastern North Pacific (130°W–141°W) (Anonymous 1974, 1981). The distribution of *C. megastomus* in Japanese waters has been reported from north of Honshu to the Okinawa Trough and the Kyushu-Palau Ridge (Asano 1962; Machida 1984; Shinohara and Matsuura 1997; Shinohara et al. 2001; Yamada et al. 2007), and this species is commonly encountered as shown in FishPix (Senou and Matsuura 1998). Asano (1962) reported that 32 *C. megastomus* leptocephali (209–246 mm body length) captured by deep sea trawls together with the adult form in Japan had considerably reduced body height, indicating these to be in a metamorphic state. On the other hand, none of leptocephali captured in the central and eastern North Pacific were metamorphic (Castle and Raju 1975; Meckelenburg et al. 2002; Hanke et al. 2014; present study). These suggest that *C. megastomus* leptocephali in the North Pacific metamorphose and settle only in the western North Pacific.

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