Redescription of the Sea Anemone *Capnea japonica* (Cnidaria: Anthozoa: Actiniaria)

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The sea anemone *Capnea japonica* (Carlgren, 1940) was described based on two specimens collected in 1914 off the coast of Misaki, Sagami Bay, Japan. Besides the two syntypes, no further specimens are known to have been collected. The original description of *C. japonica* is brief, and, therefore it is difficult to identify the species based on the available information. In 2014, we collected a single specimen of *Capnea* Gosse, 1860 from around the type locality of *C. japonica* and examined its morphological characters, such as the external features, cnidome, and musculature, and then compared it with the syntypes of *C. japonica*. The characteristic form of tentacles, size and distribution of cnidae, and very strong sphincter muscle in our specimen were a good match to the original description and to the results of examining the syntypes. Based on the topotype and syntypes, we redescribe *C. japonica* and show its phylogenetic position with newly obtained DNA sequencing data.

Key Words: sea anemone, *Capnea*, Enthemonae, phylogenetic analysis, Sixten Bock, Capneidae, Sagami Bay.

Introduction

During mid 19th century to early 20th century, almost 50 species of actiniarians had been collected around Japanese waters and described as new species (Stimpson 1856; Verrill 1867, 1869a, b, 1899a, b; Hertwig 1882; McMurrich 1901; Wassilieff 1908; Carlgren 1918, 1928, 1931, 1940, 1943). In many case, the descriptions of these species were not sufficient to the current taxonomy, such as internal morphology, cnidae examination, and images for them. And also, many of these species have not been reinvestigated ever since those original descriptions. The reason above, the identification for many of these species has been difficult and uncertain. But the identification of the species is very keenly needed for many scientific studies using these specimens. In recent years, some species were redescribed based on type specimens and newly collected topotypes (e.g., Yanagi et al. 2015). These studies help as to identify the species more easily. The taxonomic reinvestigations should be done to more species still remain uncertain. *Capnea japonica* (Carlgren, 1940) is one of such species based on the specimens collected in 1914 by Dr. Sixten Bock around Japanese waters and we redescribe here. Characteristic features of the genus *Capnea* Gosse, 1860 include very short vesicle-like tentacles and the presence of only a few tentacles arranged in each of the main exocoels and endocoels (Carlgren 1949). The endodermal sphincter of *Capnea* is "strong circumscribed", and thus the genus was considered to be a member of the subtribe Endomyaria (Carlgren 1949), which is under the order Actiniaria. Recently, the higher-level classification within Actiniaria was reconstructed mainly using molecular data, but also based on information on morphological characters (Rodríguez et al. 2014). In the phylogenetic tree put forth by Rodríguez et al. (2014), however, *Capnea* was not placed with the endomyarians. The authors concluded that the position of *Capnea* was not definitive, because of its low support value in the phylogenetic analysis, and temporarily placed it within the family Actiniidae based on morphological characters (presence of an endothermal sphincter). The phylogenetic position of *Capnea* is, therefore, still uncertain.

Four valid species of *Capnea* are recognized (Fautin 2013; Daly and Fautin 2021), viz., *C. georgiana* (Carlgren, 1927), from around the Antarctic waters; *C. indica* (Verrill, 1869), in the Java Sea; *C. sanguinea* Forbes, 1841, from British waters; and *C. japonica* from Misaki, Japan.

The two syntypes of *C. japonica* were collected at a depth of 210 m, off the coast of Misaki, Sagami Bay, on 6 June 1914, by Dr. Sixten Bock. The original description of *C. japonica* was just a brief description of the size and the type of cnidae of each body part (Carlgren 1940: 35). In the appendix of this article other morphological characters of *C. japonica* were briefly described (Carlgren 1940: 60, lines 16–24). He also described this species was very similar with *Aureliana* (sic.) *heterocera* (Thompson, 1853), although he mentioned the differences between these species in the number of tentacles and perfect pairs of mesenteries (both fewer in *C. japonica*). As per Yanagi (2006), there have been no further records of collection of *C. japonica* in the last several decades, after Dr. Sixten Bock collected the two specimens of *C. japonica* almost a century back. Owing to the dearth of information in the original description of the
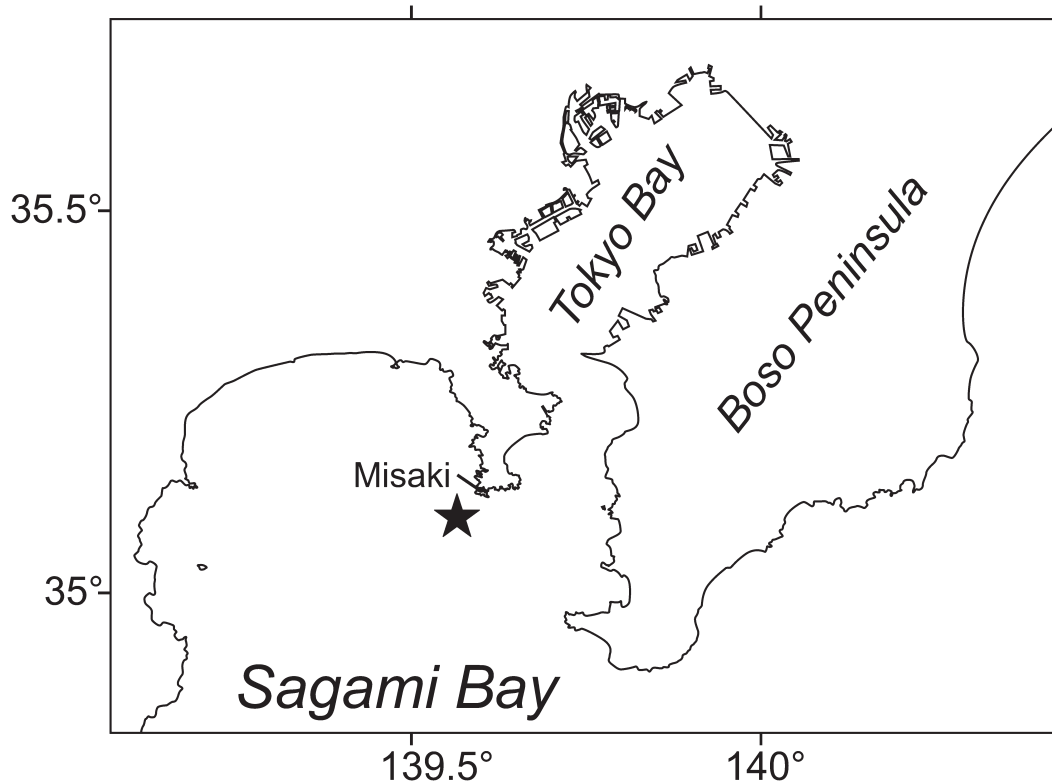
Fig. 1. Collection locality (star) of the topotype of *Capnea japonica* around Sagami Bay, Japan.

species, to identify the species correctly the type material required reexamination. Examination of a newly collected specimen, properly identified based on the type material allowed us to study details of morphological characters (colors in living specimen, details of histological characters, etc.) and obtain DNA sequencing data for phylogenetical analyses.

We collected a specimen of *C. japonica* at a depth of 238–309 m, off the coast of Misaki, Sagami Bay (the type locality of the species), in February 2014. The syntypes of *C. japonica* are preserved in the Museum of Evolution, Uppsala University, Uppsala, Sweden, and were examined in October 2014.

Herein, we re-describe *C. japonica* and analyze its phylogenetic position within Actiniaria based on mitochondrial 12S and 16S rDNA, cytochrome *c* oxidase subunit III, and nuclear 18S and 28S rDNA sequence data. These are the first molecular data reported for this species. The sequence data suggests that *Capnea* is a member of the superfamily Actinostoloidea within Actiniaria.

Materials and Methods

The single specimen in this study was collected by a dredge off the coast, southwest of Jogashima, Misaki, Sagami Bay (Fig. 1). This specimen was deposited in the zoological collection of the Coastal Branch of Natural History Museum and Institute, Chiba (CMNH-ZG 06547).

The specimen was photographed in situ, then anesthetized overnight using a solution of MgSO$_4$. A few tentacles were removed from the anesthetized specimen for DNA

analyses. The specimen was fixed in seawater with 20% formalin, then preserved in 70% EtOH. Histological sections, 6 μm thick and stained with hematoxylin and eosin (Presnell and Schreibman 1997), were made for the observation of tentacle musculature, sphincter musculature, and mesenterial arrangement. The histological sections were observed in bright field and incident-light fluorescence (using a Nikon DM510 Blue B-2A BA520 Cube filter) under the microscope Nikon Eclipse E800 with VMF Epifluorescence attachment (the incident-light fluorescence observation method was based on unpublished data of Dr. Noburu Sensui, University of the Ryukyus). The remaining embedded tissue was deparaffinization and transferred into 70% EtOH for the observation of gross anatomy of internal morphological characters. The cnidae were observed in smash preparations at 1000× using differential interference light microscopy (Nikon Eclipse E800). All observed cnidae were photographed using a Nikon DS-L1 digital camera system, and their lengths and widths were measured using digital imaging software (ImageJ 1.51j8, Wayne Rasband, National Institutes of Health, USA; http://imagej.nih.gov/ij). Terminology for the cnidae follows that reported by Mariscal (1974). The terms "basitrich" and "microbasic *b*-mastigophore" have often been incorrectly used, leading to confusion (e.g., Carlgren 1940; Östman et al. 2010; Sanamyan et al. 2012). England (1991: 696) clearly defined the differences between basitrichs and microbasic *b*-mastigophores, and we have used "basitrich" as per his definition.

DNA was extracted from the tentacles preserved in 99% EtOH using a ChargeSwitch gDNA Micro Tissue Kit (Invitrogen, Thermo Fisher Scientific). PCR amplifica-

tions were performed for the following five regions: mitochondrial 12S ribosomal DNA (12S) using primers 12S1a (5′-TAA GTG CCA GCA GAC GCG GT-3′) and 12S3r (5′-ACG GGC AAT TTG TAC TAA CA-3′), mitochondrial 16S ribosomal DNA (16S) using primers ANEM16SA (5′-CAC TGA CCG TGA TAA TGT AGC GT-3′) and ANEM16SB (5′-CCC CAT GGT AGC TTT TAT TCG-3′), mitochondrial cytochrome *c* oxidase subunit III DNA (COX III) using primers COXIIIF (5′-CAT TTA GTT GAT CCT AGG CCT TGA CC-3′) and COXIIIR (5′-CAA ACC ACA TCT ACA AAA TGC CAA TAT C-3′), nuclear 18S ribosomal DNA (18S) using primers 18SA (5′-AAC CTG GTT GAT CCT GCC AGT-3′) and 18SB (5′-TGA TCC TTC CGC AGG TT C ACC T-3′), and nuclear 28S ribosomal DNA (28S) using primers F635sq (5′-CCG TCT TGA AAC ACG GAC C-3′) and R2077sq (5′-GAG CCA ATC CTT WTC CCG ARGT T-3′). Primers were chosen based on Medlin et al. (1988), Apakupakul et al. (1999), Geller and Watson (2001), Medina et al. (2001), and Sinniger et al. (2005). The PCR amplifications were performed in 10 μL solutions consisting of 0.4 μL of forward and reverse primers (25 μM), 2.0 μL of EmeraldAmp PCR Master Mix (Takara Bio Inc.) or GoTaq Master Mix (Promega), and 3.4 μL of distilled water. The amplification conditions followed those of the respective previous studies. The positive PCR reactions were treated with Exonuclease I and shrimp alkaline phosphate (Exo-SAP) prior to sequencing. The sequencing reaction with a BigDye Terminator Cycle Sequencing Ready Reaction Kit v3.1 (Applied Biosystems) was performed using only PCR primers (12S, 16S, and COX III) or PCR and internal primers (18S and 28S): concerning 18S, we used four internal primers: two forwards, 18SC (5′-CGG TAA TTC CAG CTC CAA TAG-3′) and 18SO (5′-AAG GGC ACC ACC AGG AGT GGA G-3′), and two reverses, 18SL (5′-CCA ACT ACG AGC TTT TTA ACT G-3′) and 18SY (5′-CAG ACA AAT CGC TCC ACC AAC-3′) (Apakupakul et al. 1999); concerning 28S, we used two internal primers, F1379sq (5′-GAC AGC AGG ACG GTG GYCAT GG-3′) and R1630 (5′-CCY TTC YCC WCT CRG YCT TTC-3′) (Medina et al. 2001). Sequencing was performed by ABI 3130xL or 3500xL Genetic Analyzer (Applied Biosystems). The resulting sequences were assembled by GeneStudio ver. 2.2.0.0 (http://genestudio.com) by each marker. The new sequences obtained in this study were deposited in DNA Data Bank of Japan (accession numbers; LC602145 for 12S, LC602146 for 16S, LC602147 for 18S, LC602148 for 28S, LC602149 for COX III, respectively).

For the phylogenetic analyses, datasets generated by previous research were obtained from GenBank in 2017, referring to Rodríguez et al. (2014), and were chosen so as to include all genera except those which might cause 'long branch attraction': *Synhalcurias elegans* (Wassilieff, 1908) and *Telmatactis* sp. (see Appendix). The data were separately aligned by MAFFT ver. 7.402 (Katoh and Standley 2013) under the default settings, and then poorly aligned regions were manually corrected by eye. The five aligned files were checked for ambiguously aligned regions in Gblocks ver. 0.91b (Castresana 2002), which were duly removed: Type of sequences was DNA; the parameter was default except al

lowing small final blocks and gap positions within the final blocks. Next, the five files were combined by Kakusan4 (Tanabe 2011), with testing of the substitution models for both analyses of RAxML and MrBayes below (the alignment is available from the corresponding author upon request). The maximum-likelihood (ML) analysis was performed by RAxML-VI-HPC (Stamatakis 2006), with the GTR+Γ evolutionary model, which is recommended by Kakusan4, and then evaluated by 100 bootstrap replicates. The Bayesian tree was constructed using MrBayes ver. 3.2.6 (Ronquist et al. 2012); in the combined dataset, substitution parameters were estimated separately for each gene partition (12S: SYM+Γ; 16S: HKY85+Γ; 18S: SYM+Γ; 28S: GTR+Γ; COX III: GTR+Γ). Two independent runs of Markov chain Monte Carlo were carried out simultaneously for 5 million generations, with sampling of trees every 100 generations and calculating the average standard deviation of split frequencies (ASDSFs) every 100000 generations. As ASDSF was calculated based on the last 75% of the samples, the initial 25% of the sampled trees were discarded as burn-in.

Finally, the resulting trees were processed by the software FigTree ver. 1.4.3 (http://tree.bio.ed.ac.uk/software/figtree/), and low rates (<75 on ML tree, and <0.800 on Bayes tree) of bootstrap values or posterior probabilities were deleted on every node.

Taxonomic Accounts

Superfamily **Actinostoloidea** Carlgren, 1932
Family **Capneidae** Gosse, 1860
Genus *Capnea* Gosse, 1860
Capnea japonica (Carlgren, 1940)
[New Japanese name: Yosai Isoginchaku]
(Figs 2–7; Table 1)

Aureliana japonica Carlgren, 1940: 7, 33, 35, 60, fig. IX9–12; Carlgren 1949: 71 (misspelled).

Material examined. UUZM 101 (collection of the Zoology Section of the Museum of Evolution, Uppsala University): two syntypes, collected on 6 June 1914, off the coast of Misaki, Sagami Bay, 210 m depth, collected by Dr. Sixten Bock. CMNH-ZG 06547: one specimen, collected on 19 February 2014, off the coast SW of Jogashima, Misaki, Sagami Bay (from 35°06.086′N–139°34.232′E and 35°05.862′N–139°34.089′E) at a depth of 238–309 m, collected by R/V Rinkai-Maru using a dredge, during a marine faunal research survey conducted by the Japanese Association for Marine Biology (JAMBIO).

Description. *External anatomy* (Figs 2, 3). In freshly collected, living specimen (CMNH-ZG 06547), column orange in color, gradually paler towards the proximal end (Fig. 2A, B); tentacles pale orange with scattered dark orange spots (Fig. 2A). Expanded body, column height ca. 15 mm; oral disc diameter ca. 8 mm, pedal disc diameter ca. 12 mm; pedal disc adherent (adhered to a pebble when collected), circular in outline. In 2 syntypes (UUZM 101),
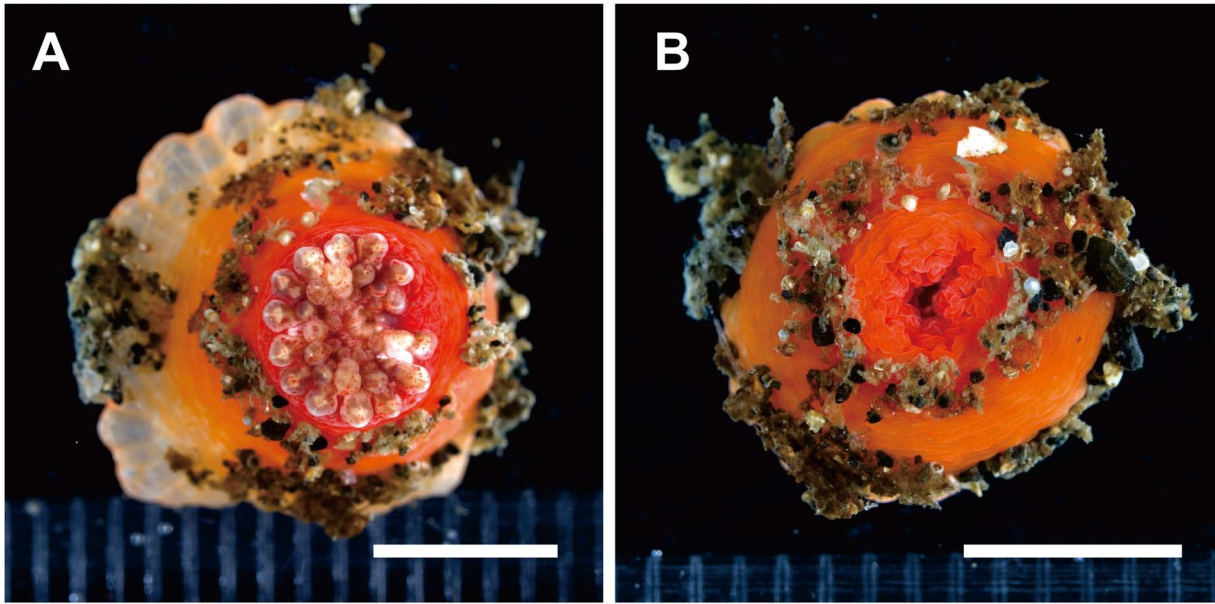
Fig. 2.   Living *Capnea japonica* from the type locality of Misaki, Sagami Bay, Japan (CMNH-ZG 06547), oral view. A, Slightly expanded state; B, contracted state. Scale bars: 5 mm.
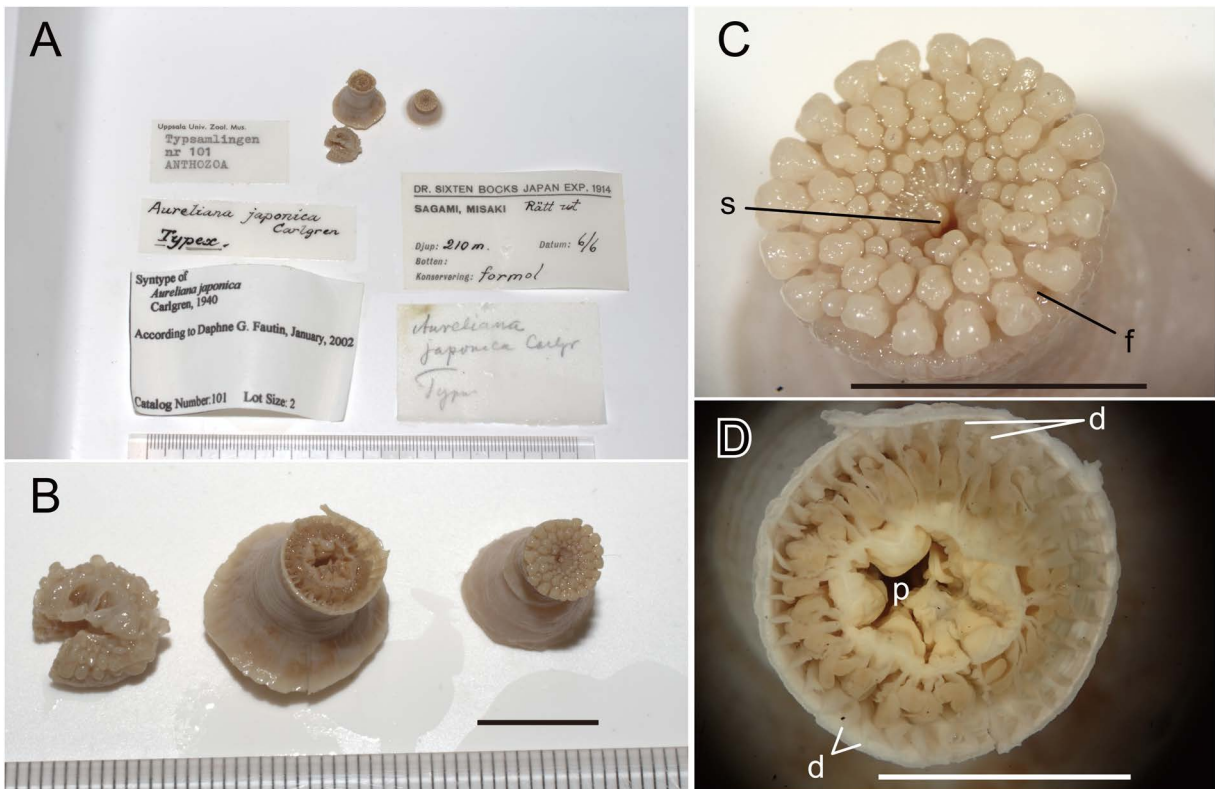

Fig. 3.   Syntypes of *Capnea japonica* (UUZM 101). A, Two syntypes with the labels of the specimen; B, oral view of two syntypes, the larger specimen (left and center ones) dissected horizontally at the level of pharynx; C, oral view of the smaller specimen; D, enlarged view of cross-sectional surface of larger specimen. Abbreviations: d, pairs of directive mesenteries; f, fosse; p, pharynx; s, siphonoglyph. Scale bars: 10 mm in B; 5 mm in C and D.

column height 13 mm (small specimen) and 18 mm (large specimen); oral disc diameter 7 mm and 10 mm; pedal disc diameter 11 mm and 15 mm, respectively. In all specimens: scapus smooth, shallow fosse at the distal end (Figs 2B, 3C). Mouth oval, with indistinct lip (Figs 2B, 3C). Tentacles very

short, knob like, smaller towards the center from margin (Figs 2B, 3B, C). Outer tentacles largest. Tentacles at least 42 in number (impossible to count all the tentacles in CMNH-ZG 06547 because of the condition of the specimen), 72 in smaller specimen of UUZM 101 (Fig. 3C), and not count-
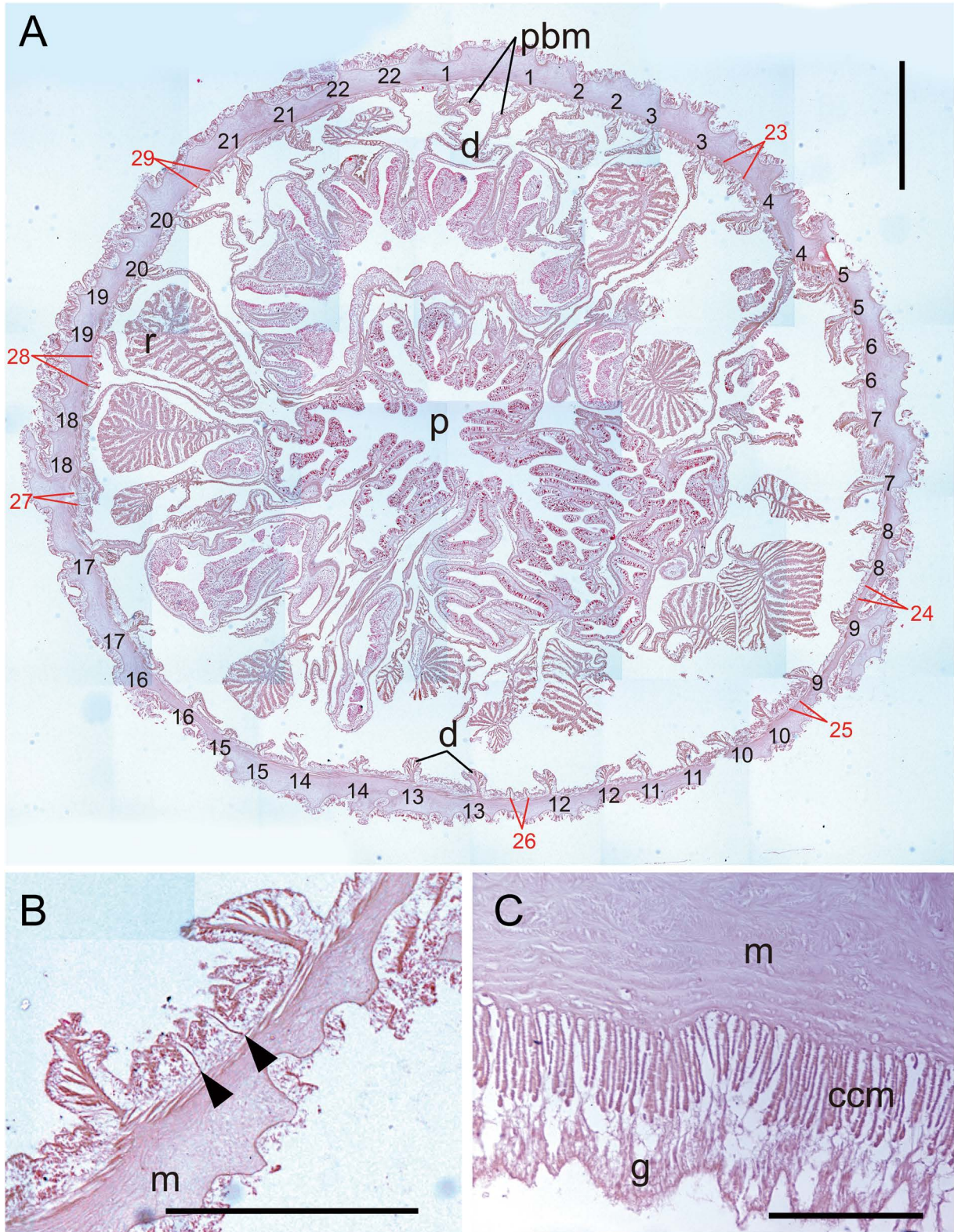
Fig. 4. Histological aspects of *Capnea japonica* (CMNH-ZG 06547). A, Transverse section, the number indicating the order of each pair of mesenteries from one directives, numbers 23 to 29 indicate the pairs of the rudimental small mesenteries; B, enlarged A showing immature small pair of mesenteries (arrow heads); C, longitudinal section of the gastrodermis of the column. Abbreviations: ccm, columnar circular muscle; d, directive mesentery; g, gastrodermis; m, mesoglea; p, pharynx; pbm, parietobasilar muscles; r, retractor muscle. Scale bars: 1 mm in A; 500 μm in B; 100 μm in C.

able in larger specimen of UUZM 101. Two tentacles in each exocoel and endocoel. The siphonoglyph less distinct from external and also internal view (Figs 2B, 3C).

Mesenteries (Figs 3D, 4A, B). 20 perfect mesenteries in CMNH 06546 and 18 in larger specimen of UUZM 101. Mesenteries not equally developed within the same pair
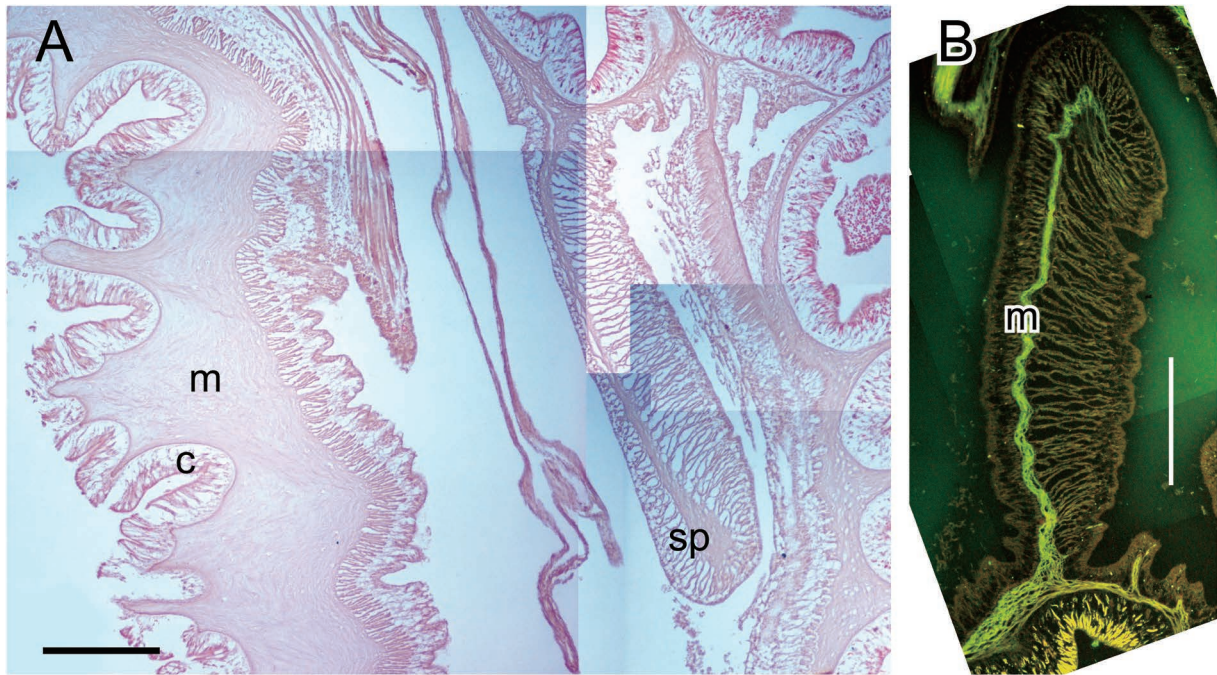
Fig. 5.   Sphincter muscle of *Capnea japonica* (CMNH-ZG 06547). A, Longitudinal section through the upper part of the column; B, same as A but under fluorescent light. Abbreviations: c, column; m, mesoglea; sp, sphincter. Scale bars: 200 μm.
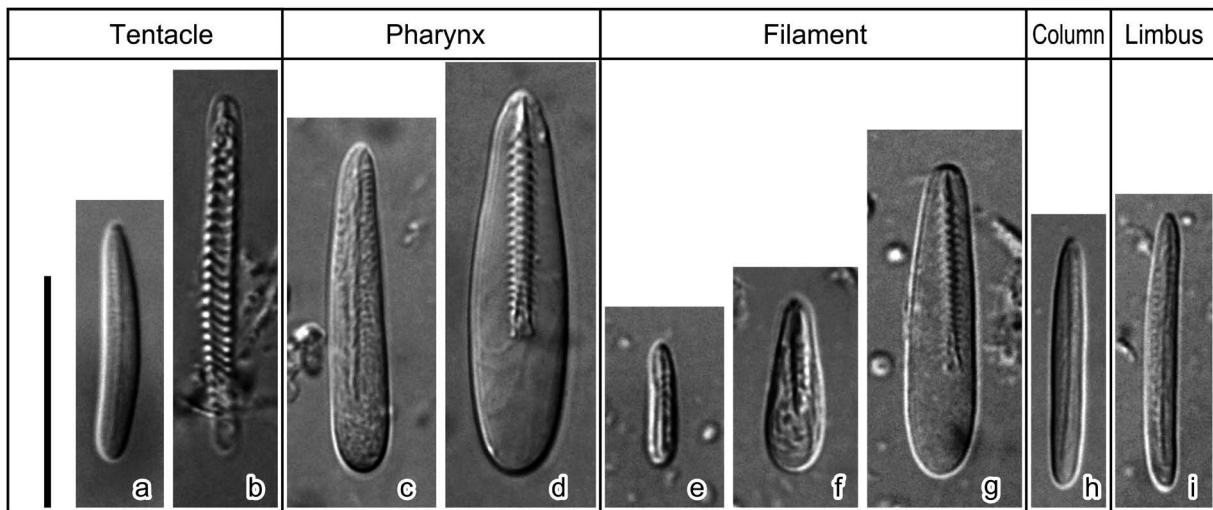

Fig. 6.   Cnidae from tentacle, pharynx, mesenterial filaments, column, and limbus of *Capnea japonica* (CMNH-ZG 06547). For letters a–i, refer to Table 1. Scale bar: 20 μm.

(Fig. 4A, see the pair numbered 19). Mesenteries at the base more numerous than at the margin. At least 7 pairs of imperfect small mesenteries in CMNH 06545 (Fig. 4A, B). Fertile mesentery not detected in examined specimens.

Musculature (Figs 4, 5). Retractors strong circumscript, distinctly restricted (Fig. 4A). Parietobasilar muscles distinct in perfect mesenteries without pennon (Fig. 4A). Columnar circular muscle well-developed (Fig. 4C). Sphincter muscle endodermal, strong pinnate circumscript, elongated, with thick mesogleal main lamella, which strongly fluoresced (Fig. 5A, B).

Cnidae (Figs 6, 7; Table 1). Spirocysts, basitrichs, microbasic *p*-mastigophores. See Table 1 and Fig. 7 for size and distribution.

Distribution. Known to occur in Misaki, Sagami Bay, Japan. Bathymetric range 210–309 m.

Phylogenetic analyses. We performed phylogenetic analyses using the concatenated sequences of five regions, resulting in a total of 4159 bp. The resulting trees of the concatenated 12S, 16S, 18S, 28S and COX III DNA are shown in Fig. 8A (maximum likelihood: ML) and Fig. 8B (Bayesian inference: Bayes). Both trees showed *Capnea japonica* and *C. georgiana* in the same clade as the suborder Enthemonae (ML=100%, Bayes=1), and it is likely that *Capnea* is included in the superfamily Actinostoloidea (ML=54%, Bayes=0.994; Fig. 8A, B).
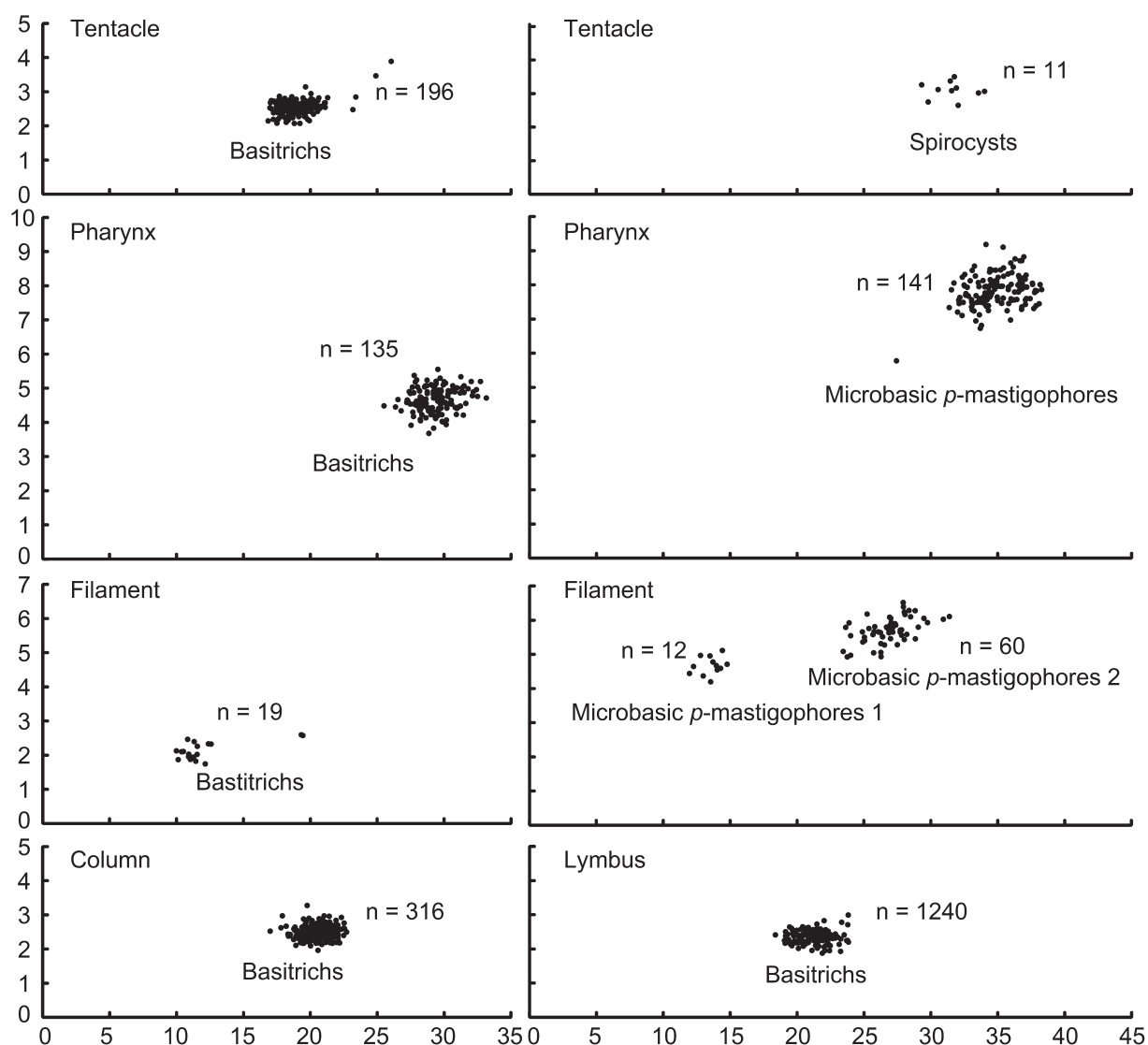
Fig. 7. Size distribution of cnidae of *Capnea japonica* (CMNH-ZG 06547). X and y axes represent the length and width of cnidae in μm, respectively. "n" is the number of capsules measured.

Table 1. Size and distribtuion of cnidae of *Capnea japonica* in CMNH-ZG 06547 (this study) and UUZM 101 (one of the syntypes). "n" is the number of capsules measured. The letter preceding each type of cnida refer to the lettered panels of Figs 6 and 7.

| Tissue | Type of cnida | CMNH-ZG 06547 | | | | | | | | | UUZM 101 (syntype) | | | | | | | | |
| | | Length (μm) | | | | Width (μm) | | | | n | Length (μm) | | | | Width (μm) | | | | n |
		min.	max.	ave.	S.D.±	min.	max.	ave.	S.D.±		min.	max.	ave.	S.D.±	min.	max.	ave.	S.D.±	
Tentacle	a) spirocysts	29.3	34.0	31.4	1.56	2.6	3.4	3.1	0.25	11									
	b) basitrichs	16.9	26.1	19.0	1.23	2.1	3.9	2.5	0.21	196									
Pharynx	c) basitrichs	25.5	33.2	29.4	1.40	3.7	5.5	4.7	0.36	135									
	d) microbasic *p*-mastigophores	27.4	38.3	34.9	1.80	5.8	9.2	7.8	0.47	141									
Filaments	e) basitrichs	10.0	19.4	12.1	2.68	1.7	2.6	2.1	0.26	19									
	f) microbasic *p*-mastigophores 1	12.0	14.8	13.5	0.87	4.2	5.1	4.7	0.27	12									
	g) microbasic *p*-mastigophores 2	23.5	31.4	26.8	1.68	4.9	6.5	5.7	0.36	60									
Column	h) basitrichs	17.0	22.7	20.5	0.90	2.0	3.3	2.5	0.17	316	12.8	23.8	18.0	4.72	2.0	2.9	2.5	0.41	5
Limbus	i) basitrichs	15.4	24.4	21.4	1.09	1.8	3.0	2.4	0.18	1240									

Remarks. The newly collected specimen (CMNH-ZG 06547) from the type locality of *Capnea japonica* possesses very characteristic knob like tentacles, a smooth column, and strong endodermal sphincters. It also has two tentacles within the exocoels and endocoels. These features could support the identification of CMNH-ZG 06547 as a species
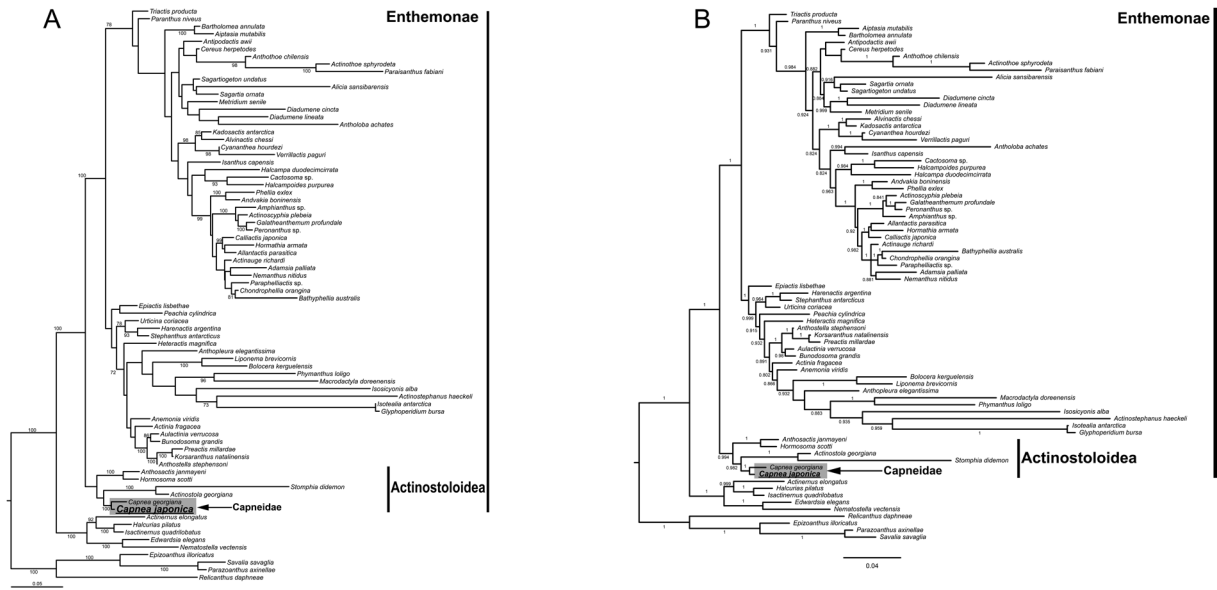
Fig. 8. Concatenated phylogenetic trees based on 12S, 16S, 18S, 28S, and COX III sequences. A, Tree inferred by Maximum likelihood (ML) analysis; B, tree inferred by using Bayesian inference (BI) method. Numbers on nodes represent bootstrap values (in ML tree) or posterior probabilities (in BI tree).

of *Capnea*. The only species known from the Pacific is *C. japonica*. Except for the syntypes, no additional specimens of *C. japonica* have been recorded. The morphological characters of the syntypes and those included in Carlgren's original description (Carlgren 1940: 35, 60) were almost the same as those observed in CMNH-ZG 06547. Based on the morphological comparison between the syntypes and CMNH-ZG 06547, we identified the latter as *C. japonica*. This is the third known specimen of *C. japonica* after the two syntypes, collected in 1914.

Carlgren (1940) described 18 pairs of perfect mesenteries in the syntypes; however, we found that the smaller specimen had not been dissected. CMNH-ZG 06547 has at least 20 pairs of perfect mesenteries, although it is not a normal arrangement in that the mesenteries within the same pair are unequally developed (Fig. 4A). In the larger specimen of the syntypes, it is difficult to identify the pairs of mesenteries because no histological sections were prepared for detailed observation, and, therefore, we could not examine them. Dunn (1983: 39) said "Up to four cycles of thin mesenteries; regularly arrayed but those of highest cycle may develop asynchronously…", in the description of *C. georgiana*. This does not mean asynchronous development of the mesenteries within the same pairs; however, this is not the "regular arrangement." The mesenterial arrangement of the other *Capnea* species has not been investigated in detail and therefore further investigation of the developing of mesenteries of *Capnea* species is needed.

Phylogeny of Capneidae. Rodríguez et al. (2014) considered Capneidae to be included in Actinioidea. This might be because *Capnea* has no characters in common with the other two superfamilies; it has neither mesenteries arranged according to the Actinostola rule, the characteristic feature of the part of Actinostoloidea; nor acontia, a characteristic feature of Metridioidea. Their phylogenetic analyses, howev-

er, indicated different results: *C. georgiana* was nested in the clade of Actinostoloidea, despite the reliability being low. By including *C. japonica*, our phylogenetic analyses reinforced the hypothesis of Capneidae belonging within Actinostoloidea. In the present study, the mesenterial arrangement of *C. japonica*. *japonica* was not the regular arrangement seen in most Actiniidae species. The unequally developed mesenteries within the pair might be because of the 'Actinostola rule' which Carlgren (1949: 77) stated as "In the younger cycles the mesenteries of each pair are usually unequally developed in such a way that the mesentery with turns its longitudinal muscle towards nearest mesentery of the preceding cycle is larger than its partner." The possession of a strong endodermal sphincter, however, still needs to be evaluated in terms of its origin and homology between the different types of endomyarian sphincters. Also, the development of mesenteries of *Capnea* species should be examined in detail to discuss the phylogenetic relationships between Capneidae and the other family, Actinostolidae, in Actinostoloidea.

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Appendix. Sequences used in this study, with individual accession numbers.

Suborder	Superfamily	Family	Genus	Species	DNA marker				
					12S	16S	COXIII	18S	28S
Anenthemonae	Actinernoidea	Actinernidae	*Actinernus*	*elongatus*	KJ482930	KJ482966	———	KJ483023	KJ483126
			Isactinernus	*quadrilobatus*	KJ482932	KJ482968	KJ482998	KJ483024	KJ483105
		Halcuriidae	*Halcurias*	*pilatus*	KJ482931	KJ482967	KJ482997	KJ483020	KJ483109
	Edwardsioidea	Edwardsiidae	*Edwardsia*	*elegans*	EU190726	EU190770	GU473338	AF254376	KJ483087
			Nematostella	*vectensis*	EU190750	AY169370	FJ489501	AF254382	KJ483089
Enthemonae	Actinioidea	Actiniidae	*Actinia*	*fragacea*	EU190714	EU190756	GU473334	EU190845	KJ483085
			Anemonia	*viridis*	EU190718	EU190760	GU473335	EU190849	KJ483095
			Anthopleura	*elegantissima*	EU190713	EU190755	GU473333	EU190844	KJ483104
			Anthostella	*stephensoni*	JQ810719	JQ810721	JQ810726	JQ810723	KJ483132
			Aulactinia	*verrucosa*	EU190723	EU190766	FJ489484	EU190854	EU190812
			Bolocera	*kerguelensis*	KJ482925	KJ482965	KJ482985	KJ483029	KJ483133
			Epiactis	*lisbethae*	EU190727	EU190771	GU473360	EU190858	EU190816
			Glyphoperidium	*bursa*	KJ482923	KJ482961	KJ482982	KJ483033	KJ483136
			Isotealia	*antarctica*	JQ810720	JQ810722	JQ810727	———	———
			Isosicyonis	*alba*	———	KJ482959	KJ482981	KJ483030	KJ483134
			Korsaranthus	*sp.*	KJ482920	KJ482958	KJ482987	KJ483017	KJ483117
			Macrodactyla	*doreenensis*	EU190739	EU190785	GU473342	EU190867	KJ483049
			Urticina	*coriacea*	GU473282	EU190797	GU473351	EU190877	KJ483094
		Actinodendridae	*Actinostephanus*	*haeckeli*	KJ482936	EU190762	GU473353	KJ483034	———
		Haloclavidae	*Harenactis*	*argentina*	KJ482926	KJ482964	KJ482984	KJ483026	KJ483047
			Peachia	*cylindrica*	EU190743	EU190789	———	KJ483015	EU190832
			Stephanthus	*antarcticus*	KJ482927	KJ482960	KJ482983	KJ483019	KJ483092
		Liponematidae	*Liponema*	*brevicornis*	EU190738	EU190784	KJ483001	EU190866	KJ483139
		Phymanthidae	*Phymanthus*	*loligo*	EU190745	EU190791	GU473345	EU190871	———
		Preactiniidae	*Preactis*	*millardae*	KJ482921	KJ482957	KJ482986	KJ483018	KJ483118
		Stichodactylidae	*Heteractis*	*magnifica*	EU190732	EU190777	KJ482988	EU190862	KJ483093
	Actinostoloidea	Actinostolidae	*Actinostola*	*georgiana*	KJ482928	KJ482952	KJ482991	KJ483032	KJ483099
			Antholoba	*achates*	GU473269	GU473284	GU473356	GU473301	KJ483128
			Anthosactis	*janmayeni*	KJ482938	GU473292	GU473363	GU473308	KJ483091
			Hormosoma	*scotti*	EU190733	EU190778	GU473366	EU190863	KJ483090
			Paranthus	*niveus*	GU473277	GU473295	GU473344	GU473311	KJ483072
			Stomphia	*didemon*	KJ482929	EU190795	GU473348	EU190875	KJ483127
		Capneidae	*Capnea*	*georgiana*	———	KJ482951	KJ482990	KJ483022	KJ483050
			Capnea	**japonica**	**LC602145**	**LC602146**	**LC602149**	**LC602147**	**LC602148**
	Metridioidea	Actinoscyphiidae	*Actinoscyphia*	*plebeia*	EU190712	EU190754	FJ489476	FJ489437	KJ483067
		Aiptasiidae	*Aiptasia*	*mutabilis*	JF832963	FJ489418	FJ489505	FJ489438	KJ483115
			Bartholomea	*annulata*	EU190721	EU190763	FJ489483	EU190851	KJ483068
			Neoaiptasia	*morbilla*	EU190742	EU190788	JF833010	EU190869	KJ483075
		Aliciidae	*Alicia*	*sansibarensis*	KJ482933	KJ482953	KJ483000	KJ483016	KJ483116
			Triactis	*producta*	EU490525	———	GU473350	EU190876	KJ483125
		Amphianthidae	*Amphianthus*	*sp.*	FJ489413	FJ489432	FJ489502	FJ489450	FJ489467
			Peronanthus	*sp.*	KJ482917	KJ482956	KJ482976	KJ483014	KJ483066
		Andvakiidae	*Andvakia*	*boninensis*	EU190717	EU190759	FJ489479	EU190848	KJ483053
		Antipodactinidae	*Antipodactis*	*awii*	GU473271	GU473286	GU473337	GU473303	KJ483074
		Bathyphelliidae	*Bathyphellia*	*australis*	FJ489402	FJ489422	FJ489482	EF589063	EF589086
		Boloceroididae	*Boloceroides*	*mcmurrichi*	GU473270	———	KJ483002	EU190852	KJ483103
		Diadumenidae	*Diadumene*	*cincta*	EU190725	EU190769	FJ489490	EU190856	KJ483106
			Diadumene	*lineata*	EU190730	EU190774	FJ489506	EU190860	KJ483108
		Galatheanthemidae	*Galatheanthemum*	*profundus*	KJ482919	KJ482954	KJ482978	KJ483011	KJ483119
		Halcampidae	*Cactosoma*	*sp.*	GU473279	GU473297	GU473346	GU473313	GU473329
			Halcampa	*duodecimcirrata*	JF832966	EU190776	———	AF254375	EU190820
			Halcampoides	*purpurea*	EU190735	EU190780	———	AF254380	KJ483100
		Hormathiidae	*Actinauge*	*richardi*	EU190719	EU190761	FJ489480	EU190850	KJ483055
			Adamsia	*palliata*	FJ489398	FJ489419	FJ489474	FJ489436	KJ483101
			Allantactis	*parasitica*	FJ489399	FJ489420	FJ489478	FJ489439	KJ483056
			Calliactis	*japonica*	FJ489403	FJ489423	FJ489486	FJ489441	KJ483057
			Chondrophellia	*sp.*	FJ489406	FJ489426	FJ489489	FJ489444	KJ483060
			Hormathia	*armata*	EU190731	EU190775	FJ489491	EU190861	KJ483062
			Paraphelliactis	*sp.*	FJ489412	FJ489431	FJ489498	FJ489449	FJ489466
		Isanthidae	*Isanthus*	*capensis*	JF832967	GU473291	GU473362	GU473307	KJ483096
			Paraisanthus	*fabiani*	JF832964	GU473283	GU473355	GU473300	GU473317
		Kadosactinidae	*Alvinactis*	*chessi*	GU473278	GU473296	GU473352	GU473312	KJ483052
			Cyananthea	*hourdezi*	GU473275	GU473293	GU473364	GU473309	KJ483081
			Kadosactis	*antarctica*	FJ489410	EU190782	FJ489504	EU190865	KJ483080
		Metridiidae	*Metridium*	*senile*	EU190740	EU190786	FJ489494	AF052889	KJ483076
		Nemanthidae	*Nemanthus*	*nitidus*	EU190741	EU190787	FJ489495	EU190868	KJ483064
		Ostiactinidae	*Ostiactis*	*pearseae*	EU190751	EU190798	GU473365	EU190878	KJ483082
		Phelliidae	*Phellia*	*exlex*	JF832958	JF832978	JF833004	JF832984	KJ483121
		Sagartiidae	*Actinothoe*	*sphyrodeta*	FJ489401	FJ489421	FJ489481	FJ489440	KJ483111
			Anthothoe	*chilensis*	FJ489397	FJ489416	FJ489470	FJ489434	FJ489453
			Cereus	*herpetodes*	JF832956	JF832969	———	JF832983	JF832992
			Sagartia	*ornata*	JF832959	JF832975	JF833011	JF832985	KJ483069
			Sagartiogeton	*undatus*	FJ489400	FJ489417	FJ489472	FJ489435	KJ483070
			Verrillactis	*paguri*	FJ489414	FJ489433	FJ489503	FJ489451	KJ483046
Zoanthidea (outgroups)		Epizoanthidae	*Epizoanthus*	*illoricatus*	AY995901	EU591597	———	KC218424	KJ483036
		Parazoanthidae	*Parazoanthus*	*axinellae*	GQ464940	EU828754	———	KC218416	KJ483044
			Savalia	*savaglia*	AY995905	DQ825686	DQ825686	HM044299	HM044298
Hexacorallia incertis ordinis (outgroup)		Relicanthidae	*Relicanthus*	*daphneae*	KJ482934	KJ482971	KJ482999	KJ483028	KJ483131