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; 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 (Rodriguez et al. 2014). In the phylogenetic tree put forth by Rodriguez 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
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 MgSO₄. 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., Carl-gren 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-
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Superfamily *Actinostoloidea* Carlgren, 1932
Family *Capneidae* Gosse, 1860
Genus *Capnea* Gosse, 1860

*Capnea japonica* (Carlgren, 1940)

[A 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 (JAMBO).

**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); 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), alowing small final blocks and gap positions within the final blocks. Next, the five files were combined by Kakusan4 (Tateane 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 (<0.75 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)

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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-
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. 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.
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 Entemonae (ML=100%, Bayes=1), and it is likely that Capnea is included in the superfamily Actinostoloidea (ML=54%, Bayes=0.994; Fig. 8A, B).
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**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.

Table 1. Size and distribution 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. ± | n   | min. | max. | ave. | S.D. ± | n   |
| Tentacle | a) spirocysts                  | 29.3 | 34.0 | 31.4 | 1.56 | 2.6  | 3.4  | 3.1  | 0.25 | 11   | 12.8 | 23.8 | 18.0 | 4.72 | 2.0 | 2.9 | 2.5 | 0.41 | 5   |
|         | b) basitrichs                  | 16.9 | 26.1 | 19.0 | 1.23 | 2.1  | 3.9  | 2.5  | 0.21 | 196  | 12.8 | 23.8 | 18.0 | 4.72 | 2.0 | 2.9 | 2.5 | 0.41 | 5   |
| Pharynx  | c) basitrichs                  | 25.5 | 33.2 | 29.4 | 1.40 | 3.7  | 5.5  | 4.7  | 0.36 | 135  | 12.8 | 23.8 | 18.0 | 4.72 | 2.0 | 2.9 | 2.5 | 0.41 | 5   |
|         | d) microbasic p-mastigophores  | 27.4 | 38.3 | 33.9 | 1.80 | 5.8  | 9.2  | 7.8  | 0.47 | 141  | 12.8 | 23.8 | 18.0 | 4.72 | 2.0 | 2.9 | 2.5 | 0.41 | 5   |
| Filaments | e) basitrichs                  | 10.0 | 19.4 | 12.1 | 2.68 | 1.7  | 2.6  | 2.1  | 0.26 | 19   | 12.8 | 23.8 | 18.0 | 4.72 | 2.0 | 2.9 | 2.5 | 0.41 | 5   |
|         | f) microbasic p-mastigophores 1| 12.0 | 14.8 | 13.5 | 0.87 | 4.2  | 5.1  | 4.7  | 0.27 | 12   | 12.8 | 23.8 | 18.0 | 4.72 | 2.0 | 2.9 | 2.5 | 0.41 | 5   |
|         | g) microbasic p-mastigophores 2| 23.5 | 31.4 | 26.8 | 1.68 | 4.9  | 6.5  | 5.7  | 0.36 | 60   | 12.8 | 23.8 | 18.0 | 4.72 | 2.0 | 2.9 | 2.5 | 0.41 | 5   |
| 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 | 12.8 | 23.8 | 18.0 | 4.72 | 2.0 | 2.9 | 2.5 | 0.41 | 5   |

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.
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, however, 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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fluorescence observation methods that he is currently testing for histological sections stained with eosin. The editor, Dr. Keiichi Kaku, and the reviewers, Dr. Karen Sanamyan and Dr. James Reimer gave us insightful comments to improve the manuscript. This study was supported by JSPS KAKENHI, grants JP25440221 to KY and JP1703267 to TI.

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| Suborder | Superfamily | Family | Genus | Species | DNA marker |
|----------|-------------|--------|-------|---------|------------|
| Actinideidae | Actinostoloidea | Actinostola | Actinostola | georgiana | KJ482921 |
| Actinideidae | Actinostoloidea | Actinostola | Actinostoloidea | Actinostolidae | KJ482936 |
| Actinideidae | Actinostoloidea | Actinostola | Actinostoloidea | Capneidae | KJ482929 |
| Actinideidae | Actinostoloidea | Actinostola | Actinostoloidea | Boloceroides | KJ482929 |
| Actinideidae | Actinostoloidea | Actinostola | Actinostoloidea | Antipodactinidae | KJ482945 |
| Actinideidae | Actinostoloidea | Actinostola | Actinostoloidea | Cactosoma | KJ482952 |
| Actinideidae | Actinostoloidea | Actinostola | Actinostoloidea | Aiptasiidae | KJ482952 |
| Actinideidae | Actinostoloidea | Actinostola | Actinostoloidea | Heteractis | KJ482921 |
| Actinideidae | Actinostoloidea | Actinostola | Actinostoloidea | Parathus | KJ482923 |
| Actinideidae | Actinostoloidea | Actinostola | Actinostoloidea | Paraphelliactis | KJ482952 |
| Actinideidae | Actinostoloidea | Actinostola | Actinostoloidea | Capnea | KJ482924 |
| Actinoidae | Actinoidae | Actinoidae | Actinoidae | Actinuruus | KJ482936 |
| Actinoidae | Actinoidae | Actinoidae | Actinoidae | Parazoonathidae | KJ482937 |
| Actinoidae | Actinoidae | Actinoidae | Actinoidae | Paraisanthus | KJ482940 |
| Actinoidae | Actinoidae | Actinoidae | Actinoidae | Kadosactis | KJ482940 |
| Actinoidae | Actinoidae | Actinoidae | Actinoidae | Epiactis | KJ482937 |
| Actinoidae | Actinoidae | Actinoidae | Actinoidae | Halcurias | KJ482937 |
| Actinoidae | Actinoidae | Actinoidae | Actinoidae | Allantactis | KJ482937 |
| Actinoidae | Actinoidae | Actinoidae | Actinoidae | Parazoanthidae | KJ482937 |
| Actinoidae | Actinoidae | Actinoidae | Actinoidae | Parazoanthus | KJ482937 |
| Actinoidae | Actinoidae | Actinoidae | Actinoidae | Verrillactis | KJ482937 |
| Actinoidae | Actinoidae | Actinoidae | Actinoidae | Sagartia | KJ482937 |
| Actinoidae | Actinoidae | Actinoidae | Actinoidae | Sagartia | KJ482937 |
| Actinoidae | Actinoidae | Actinoidae | Actinoidae | Hexacorallia | KJ482937 |
| Actinoidae | Actinoidae | Actinoidae | Actinoidae | Relicanthus | KJ482937 |