

Article

Mt. Fuji in the Ocean—Description of a Strange New Species of Sea Anemone, *Discoactis tritentaculata* fam., gen., and sp. nov. (Cnidaria; Anthozoa; Actiniaria; Actinostoloidea) from Japan, with the Foundation of a New Family and Genus[†]

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urn:lsid:zoobank.org:act:B0E8B56E-B622-4AC7-AF85-D8F82FF15E04;
urn:lsid:zoobank.org:act:9B346F9E-E38E-4645-BE45-4D8425ECA907.

Abstract: A new species in a new family and genus of sea anemone, *Discoactis tritentaculata* fam. gen. and sp. nov., was discovered at several localities around Japan. These anemones were indicated to belong to the superfamily Actinostoloidea by phylogenetic analyses. However, the specimens have flat, disc-like bodies; triplet tentacles on the oral disc; endocoels without tentacles; 10 macrocnemes in the column; and numerous microcnemes only in the aboral end. These features are unique among not only Actinostoloidea but also sea anemones in general, and thus they could not be accommodated into any existing families and genera in Actinostoloidea. Therefore, we establish the new family Discoactinidae and the new genus *Discoactis* for this species of anemone. Our phylogenetic analyses also suggested that the family Capneidae, of which the phylogenetic position has not been certainly convinced yet, also should be a member of Actinostoloidea, and thus we revised its placement and discussed the diagnosis of the superfamily. With these results, the superfamily Actinostoloidea now accommodates eight families.

Keywords: Enthemonae; Actinostoloidea; Sagami Bay; Suruga Bay; biological dredge; beam trawl; mesenterial arrangement; imperfect mesentery; endocoel



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1. Introduction

Sea anemones, a well-known marine animal group distributed broadly in the world's oceans, belong to the order Actiniaria Hertwig, 1882 [1] of the class Anthozoa of the phylum Cnidaria. Actiniaria currently contains approximately 1100 valid species from 264 genera of 50 families [2]. All sea anemones are free-living individual polyps and are composed of only soft tissues in three layers—ectoderm, endoderm, and mesoglea; thus, their bodies are flexible and deformable by habitat effects [3]. Sea anemones have relatively few reliable taxonomic diagnostic characters, and therefore researchers have been puzzled by their taxonomy, often struggling to correctly classify them by morphology [4].

Mesenterial arrangements and sphincter muscles are two of the few effective characters for the classification of sea anemones. Mesenteries are some of the most prominent

structures in the body plan of sea anemones. They develop in the direction of the distal–proximal axis and separate the actinarian coelenteron into partitions. Mesenteries are some of the most important tissues of sea anemones and play multiple roles: supporting the actinopharynx and in the elongation and contraction of the body, digestion, and reproduction. The mesenteries of Actiniaria are distinguished into two types in their bodies: macrocnemes, which are usually distinct and develop several structures such as retractor muscles, gonads, and filaments; and microcnemes, which are small and without these structures [5,6]. The mesenteries usually form pairs with one another and develop in particular cyclic patterns, and the arrangement may differ depending on the species and genera and are thus considered as the important taxonomic characters of sea anemones [4].

Sphincter muscles form the endodermal circular musculature at the upper end of the column to tighten the oral disk. The endodermal musculature is embedded in the mesoglea (“mesogleal sphincter”) or accumulated at the branched mesoglea separate from the main mesogleal body (“endodermal sphincter”) [5]. The type of sphincter, mesogleal or endodermal, is one of most important morphological characters for higher taxon classification within Actiniaria. Although this structure is one of the most characteristic features of Actiniaria, some species have no sphincter, even sometimes at the superfamily level (e.g., Actinernoidea [7]).

In 2014, Rodríguez et al. conducted the most comprehensive molecular analyses of Actiniaria to date [8]. The study concluded that the classification system of Carlgren [5] did not accurately reflect the phylogeny, and hence thoroughly revised the classification system of the order Actiniaria. Rodríguez et al. (2014) [8] rearranged the higher taxa of Actiniaria into several superfamilies and suborders (see Table 1 in [9]). In this paper, the superfamily Actinostoloidea Carlgren, 1932 [10], was revived.

Actinostoloidea is one of the three superfamilies of the suborder Enthemonae Rodríguez and Daly, 2014. This suborder was established by Carlgren in 1932 [10] to include Actinostolidae Carlgren, 1932 [10] and Exocoelactinidae Carlgren, 1925 [11]. After that, these families of anemones were accommodated in tribe Mesomyaria [5] but re-established as one of the members of Enthemonae [4,8]. According to the definition of this superfamily, the marginal sphincter muscles of the species of Actinostoloidea are all mesogleal (a key character of Mesomyaria) and the mesenterial pairs of this taxon generally unequally develop in this suborder (“Actinostola rule”; [5] p. 77). These characters have thought to be unique to Actinostoloidea, and anemones of this superfamily have been distinguished from other anemones by the combination of unequally sized mesenterial arrangements and mesogleal sphincter muscles.

Recently, however, peculiar groups have been added into this superfamily. For example, Halcampulactidae Gusmão, Berniler, Deussen, Harris, and Rodríguez, 2019 [12], which have macrocneme–microcneme pairs in the first mesenterial cycle like Edwardsiidae Andres, 1882 [13], do not obey the Actinostola rule. Moreover, Actonostolidae, which accommodates over 20 genera, was divided into several families in 2021 [14] (see the Discussion), and thus the common features of this superfamily have become ambiguous.

In the present study, we report on unique anemone specimens collected from Japanese waters. These anemones have unique features: flat, disc-like bodies; triplet tentacles on the oral disc; endocoels without tentacles; 10 macrocnemes in the column; and numerous microcnemes only in the aboral end. These features do not correspond to any existing anemones, and we report and formally describe this species in this study via morphological and molecular analyses as a member of a new genus and family within Actinostoloidea.

Among the known anemones, based on molecular analyses, the family Capneidae Forbes, 1841 [15] was suggested to be the most related family to our undescribed species by high support rates. Among Capneidae, *Capnea geogiana* (Carlgren, 1927) was already

included in the robust analysis of Rodríguez et al. [8], who placed it within Actinostoloidea. Subsequently, Capneidae was redescribed as a family of Actinostoloidea in 2021 [16]. However, these studies did not revise the definition of Actinostoloidea, and thus the diagnosis of this superfamily still does not support the inclusion of Capneidae concerning the sphincter muscles and mesenterial arrangement. Therefore, here, along with the formal species description of our specimens, we also comprehensively revised the diagnosis of Actinostoloidea to accommodate Capneidae and another new family based on our phylogenetic analyses.

2. Materials and Methods

2.1. Sample Collection and Preservation

Nine specimens of the unique anemone were collected in this study from several localities of Japan (Figure 1A–D). Two specimens, including the holotype, were collected on 17 May 2003 at Senoumi Bank off Shizuoka Prefecture by the deep tow dredge (a box dredge, 50 cm in length, 35 cm in width, and 15 cm in height [17]) during a research cruise of *R/V Natsushima* (JAMSTEC, Cruise No. NT 03-05, DT-6C); three paratypes were collected from the west off Misaki, Kanagawa Prefecture with a 50 cm biological dredge on *R/V Rinkai-Maru* (Misaki Marine Biological Station, University of Tokyo); three more specimens were collected from the southwest off Iki Island, Nagasaki Prefecture or the west off Sukumo, Kochi Prefecture with a 50 cm biological dredge or a beam trawl during a research cruise of *R/V Toyoshio-Maru* (Hiroshima University); and the final one was collected from the southwest off Otsuchi, Iwate Prefecture by a 50 cm biological dredge on *R/V Yayoi* (AORI).

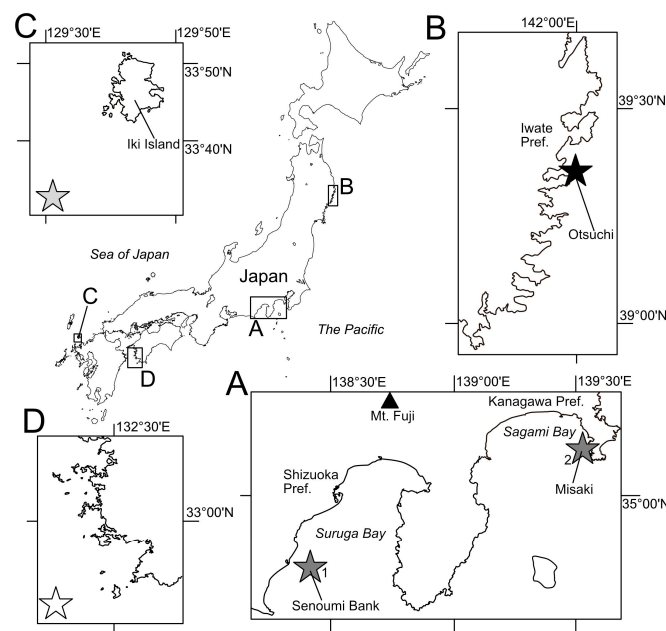


Figure 1. Sampling localities of *Discoactis tritentaculata* fam. gen. and sp. nov. in this study. A: Kanagawa and Shizuoka Prefs. A1: Senoumi Bank, Suruga Bay; A2: Misaki, Sagami Bay. B: Otsuchi, Iwate Pref. C: Iki, Nagasaki Pref. D: Sukumo, Kochi Pref.

Additionally, a specimen of a Capneidae species, identified as *Capnea japonica* (Carlgren, 1940) [18], was provided from Aquamarine Fukushima aquarium. The specimen was collected off Fukushima Prefecture.

For some specimens, *in vitro* images of living polyps were taken prior to fixation to record the external form, color, and size of the individuals. Individuals were then anesthetized using a magnesium chloride solution while they elongated their tentacles, and

we dissected their tentacle tissues (preserved in 99% ethanol for DNA extraction), which were fixed in a 10–20% (*v/v*) formalin in sea water solution. The other specimens were preserved directly in a formalin–sea water solution.

The specimens examined have been deposited at either the National Museum of Nature and Science, Tokyo (NSMT), or the Coastal Branch of Natural History Museum and Institute, Chiba (CMNH).

2.2. Preparation of Histological Sections

Histological sections were prepared following standard protocols [19]. Specimens were dissected to obtain tissues. Dissected tissues were dehydrated with ethanol, cleared in xylene, embedded in paraffin, sliced into serial sections (7–10 µm thick) using a microtome, mounted on glass slides, and stained with hematoxylin and eosin. The pictures of these sections were taken by an optical microscope at NSMT.

2.3. Observation with SEM

For *Capnea japonica*, a specimen was embedded in paraffin with three horizontally dissected parts. Then, the middle parts were dissected by a microtome to sharpen the horizontal surface, deparaffinized with xylol, substituted with butyl alcohol, dried in a t-BuOH freeze dryer, and coated with gold using an ion sputter machine. This tissue was observed using a scanning electron microscope (SEM) for the observation of the three-dimensional mesenterial arrangement.

2.4. Cnidae Observation

Cnidae were observed in the tentacles, actinopharynx, column, and filaments of four specimens (NSMT-Co 1908, 1909, CMNH-ZG 10795, and 10797), although some tissues of some specimens were not examined as they were too damaged (See the description part for the damaged tissues). We also observed the tissues of the basal disc, but no cnidae were observed. Tissues from each part were placed on slide glasses and mounted using a 50% (*v/v*) glycerin in sea water solution. Images of the cnidae were taken by differential interference contrast microscopy at NSMT. The length and width were measured using the software ImageJ ver. 1.49 [20]. The cnidae nomenclature followed Mariscal (1974) [21].

2.5. Phylogenetic Analyses

DNA was extracted from the tissues preserved in 99% EtOH from two specimens (NSMT-Co 1908 from Misaki and NSMT-Co 1909 from Sea of Japan) by a ChargeSwitch gDNA Micro Tissue Kit (Invitrogen: Minato-Ku, Tokyo, Japan). PCR amplifications were performed in 10 µL reaction volumes, consisting of 0.4 µL of 25 µM forward and reverse primers, 2.0 µL of EmeraldAmp PCR Master Mix (TaKaRa: Kusatsu, Japan), and 3.4 µL of distilled water. For PCR amplifications, three mitochondrial markers—12S, 16S rDNA, and cytochrome oxidase III (COXIII)—and two nuclear markers—18S and 28S rDNA—were used. The primers and amplification conditions are shown in Table 1; all markers were adopted from Rodriguez et al. (2014) [8], though the primer sets of 12S and 28S were different. The PCR products were processed using exonuclease I and shrimp alkaline phosphate (ExoSAP-IT; Thermo Fisher: Waltham, MA, USA) before sequencing. Sequencing reactions were performed using BigDye Terminator Cycle Sequencing Ready Reaction Kit v3.1 (Applied Biosystems: Waltham, MA, USA) and PCR primers (12S, 16S, and COXIII) or PCR primers and internal primers (four internal primers for 18S and three for 28S; Table 1). Sequencing was performed by an ABI 3500xL Genetic Analyzer (Applied Biosystems) at NSMT. Fragments were individually assembled by GeneStudio ver. 2.2.0.0 (<https://sourceforge.net/projects/genestudio/>; accessed on 15 April 2020). New sequences obtained in this study have been deposited in GenBank (Table 2).

Table 1. Primers and protocols of polymerase chain reactions of every molecular marker.

Marker	Primers	Sequences (5'-3')	PCR Protocol	References
12S	12S1a	TAAGTGCCAGCAGACGCGGT	(95 °C for 4 min) + 4 × [(94 °C for 30 s) → (50 °C for 1 min) → (72 °C for 2 min)]	[22]
	12S3r	ACGGGCAATTTGTACTAACA	+30 × [(94 °C for 30 s) → (55 °C for 1 min) → (72 °C for 2 min)] + (72 °C for 4 min)	
16S	ANEM16SA ANEM16SB	CACTGACCGTGATAATGTAGCGT CCCCATGGTAGCTTTTATTCTG	(95 °C for 4 min) + 30 × [(95 °C for 30 s) → (46 °C for 45 s) → (72 °C for 1 min)] + (72 °C for 5 min)	[23]
COXIII	COIIF COIIR	CATTTAGTTGATCCTAGGCCTTGACC CAAACCACATCTACAAAATGCCAATATC	(95 °C for 2 min) + 30 × [(95 °C for 30 s) → (46 °C for 45 s) → (72 °C for 1 min)] + (72 °C for 5 min)	[23]
18S	PCR	18SA 18SB	AACCTGGTTGATCCTGCCAGT TGATCCTTCCGCAGGTTACCT	[24,25]
		18SL 18SC 18SY 18SO	CCAACTACGAGCTTTTTAACTG CGGTAATTCCAGCTCCAATAG CAGACAAATCGCTCCACCAAC AAGGGCACCACCAGGAGTGGAG	
	Only Sequence			
28S	PCR1	F63sq R2077sq	AATAAGCGGAGGAAAAGAAAC GAGCCAATCCTTWTCCTCGARGTT	[26]
	PCR2	LSU5 LSU1600R	TAGGTCGACCCGCTGAAYTTAAGCA AGCGCCATCCATTTTCAGG	
	Only Sequence	LSU330F LSU900F ECD2S	CAAGTACCGTGAGGGAAAGTTG CCGTCTTGAAACACGGACCAAG CTTGGTCCGTGTTTCAAGACGG	[27–29]

For the phylogenetic analyses of Actiniaria, sequence data of *Capnea japonica*, a species of Capneidae, Actinostoloidea, were obtained by us [16] using the same methods as mentioned above. In addition, the sequences of sea anemones used by Rodriguez et al. (2014) [8] were also obtained from GenBank (Table 2). The dataset was aligned by MAFFT ver. 7.402 [30] under the default settings. Ambiguously aligned regions were eliminated by Gblocks ver. 0.91b [31]: the type of sequences was DNA and the parameters were the default, except for allowing small final blocks and gap positions within the final blocks. Next, the file was processed by Kakusan 4 [32] to test substitution models for analyses of both RAxML and MrBayes (alignment available from the corresponding author upon request). Maximum-likelihood (ML) analyses were performed by RAxML-VI-HPC [33], with the GTR+ Γ evolutionary model recommended by Kakusan 4 and evaluated by 100 bootstrap replicates. Bayesian inference (BI) was conducted using MrBayes ver. 3.2.6 [34] with HKY85_Gamma as the substitution parameter. Two independent runs of the Markov Chain Monte Carlo were carried out simultaneously for 5,000,000 generations, sampling trees every 100 generations and calculating the average standard deviation of split frequencies (ASDSFs) every 100,000 generations. As the ASDSF was calculated based on the last 75% of the samples, the initial 25% of the sampled trees were discarded as the burn-in.

Finally, the two resultant trees were combined by FigTree ver. 1.4.3 (<http://tree.bio.ed.ac.uk/software/figtree/>; accessed on 15 April 2020) and low bootstrap (<50) and posterior probability values (<0.50) were manually deleted on each node.

The phylogenetic analysis was at first conducted on the level of the order Actiniaria, and then, after the approximate taxonomic position of our undescribed species was confirmed, held on the superfamily level (Table 2).

Table 2. Base sequences in the phylogenetic analyses. Taxa indicated with a gray background were analyzed in this study. Sequences indicated in bold were obtained in this study and deposited in GenBank. Species of Zoanthidea and Relicanthidae were the outgroups for the phylogenetic analysis of the order Actiniaria.

Higher Taxa	Families	Genus	Species	(Remarks)	12S	16S	18S	28S	COXIII
Actiniaria									
Anenthemonae									
Actinernoidea	Actinernidae	<i>Actinernus</i>	<i>antarcticus</i>		KJ482930	KJ482966	KJ483023	KJ483126	-
		<i>Isactinernus</i>	<i>quadrolobatus</i>		KJ482932	KJ482968	KJ483024	KJ483105	KJ482998
		<i>Synhalcurias</i>	<i>laevis</i>		KJ482942	-	KJ483021	KJ483120	-
	Halcuriidae	<i>Halcurias</i>	<i>pilatus</i>		KJ482931	KJ482967	KJ483020	KJ483109	KJ482997
Edwardsioidea	Edwardsiidae	<i>Edwardsia</i>	<i>japonica</i>		GU473274	GU473288	GU473304	KJ483048	GU473359
		<i>Edwardsia</i>	<i>timida</i>		GU473281	-	GU473315	KJ483088	KJ482996
		<i>Edwardsianthus</i>	<i>gilbertensis</i>		EU190728	EU190772	EU190859	EU190817	-
		<i>Nematostella</i>	<i>vectensis</i>		EU190750	AY169370	AF254382	KJ483089	FJ489501
Enthemonae									
Actinostoloidea	Capneidae	<i>Capnea</i>	<i>japonica</i>	(CMNH-ZG 06547; off Misaki)	LC602145	LC602146	LC602147	LC602148	LC602149
		<i>Capnea</i>	<i>georgiana</i>		-	KJ482951	KJ483022	KJ483050	KJ482990
	Discoactinidae	<i>Discoactis</i>	<i>tritentaculata</i>	(NSMT-Co 1908; off Misaki)	LC874807	LC875472	LC875474	LC875477	LC876766
		<i>Discoactis</i>	<i>tritentaculata</i>	(NSMT-Co 1909; off Iki Island)	LC874806	LC875473	LC875475	-	LC876767
	Halcampulactinidae	<i>Halcampulactis</i>	<i>solamar</i>		MK279362	MK279363	MK279364	MK279365	MK279366
	Exocoelactinidae	<i>Exocoelactis</i>	<i>actinostoloides</i>	(CMNH-ZG 05926; off Misaki)	KP793003	KP793004	LC875476	LC875478	LC876768
	Actinostolidae	<i>Actinostola</i>	<i>crassicornis</i>		-	EU190753	EU190843	KJ483098	GU473332
		<i>Actinostola</i>	<i>chilensis</i>		-	GU473285	GU473302	KJ483110	GU473357
		<i>Actinostola</i>	<i>georgiana</i>		KJ482928	KJ482952	KJ483032	KJ483099	KJ482991
		<i>Antholoba</i>	<i>achates</i>		GU473269	GU473284	GU473301	KJ483128	GU473356
		<i>Stomphia</i>	<i>didemon</i>		KJ482929	EU190795	EU190875	KJ483127	GU473348
	Anthosactinidae	<i>Stomphia</i>	<i>selaginella</i>		GU473280	GU473298	GU473314	GU473331	GU473349
		<i>Anthosactis</i>	<i>janmayeni</i>		KJ482938	GU473292	GU473308	KJ483091	GU473363
		<i>Anthosactis</i>	<i>pearseae</i>		EU190751	EU190798	EU190878	EU190841	GU473365
		<i>Hormosoma</i>	<i>scotti</i>		EU190733	EU190778	EU190863	KJ483090	GU473366
		<i>Tealidium</i>	<i>konoplinorum</i>		MZ569954	MZ567264	MZ569926	MZ569979	MZ576886
	Sicyonidae	<i>Sicyonis</i>	<i>denisovi</i>		MZ569948	MZ567258	MZ569920	MZ569973	MZ576880
		<i>Ophiodiscus</i>	<i>bukini</i>		MZ569953	MZ567263	MZ569925	MZ569978	MZ576885

Table 2. Cont.

Higher Taxa	Families	Genus	Species	(Remarks)	12S	16S	18S	28S	COXIII
Actinoidea	Actiniidae	<i>Actinia</i>	<i>fragacea</i>		EU190714	EU190756	EU190845	EU190845	GU473334
		<i>Anemonia</i>	<i>viridis</i>		EU190718	EU190760	EU190849	EU190849	GU473335
		<i>Anthopleura</i>	<i>elegantissima</i>		EU190713	EU190755	EU190844	EU190844	GU473333
		<i>Anthostella</i>	<i>stephensoni</i>		JQ810719	JQ810721	JQ810723	JQ810723	JQ810726
		<i>Bolocera</i>	<i>kerguelensis</i>		KJ482925	KJ482965	KJ483029	KJ483029	KJ482985
		<i>Bunodactis</i>	<i>verrucosa</i>		EU190723	EU190766	EU190854	EU190854	-
		<i>Bunodosoma</i>	<i>grandis</i>		EU190722	EU190765	EU190853	EU190853	GU473336
		<i>Epiactis</i>	<i>lisbethae</i>		EU190727	EU190771	EU190858	EU190858	GU473360
		<i>Glyphoperidium</i>	<i>bursa</i>		KJ482923	KJ482961	KJ483033	KJ483033	KJ482982
		<i>Isotealia</i>	<i>antarctica</i>		JQ810720	JQ810722	-	-	JQ810727
		<i>Isosicyonis</i>	<i>alba</i>		-	KJ482959	KJ483030	KJ483030	KJ482981
		<i>Isosicyonis</i>	<i>striata</i>		EU190736	EU190781	EU190864	EU190864	FJ489493
		<i>Korsaranthus</i>	<i>natalinesis</i>		KJ482920	KJ482958	KJ483017	KJ483017	KJ482987
		<i>Macroductyla</i>	<i>doreenensis</i>		EU190739	EU190785	EU190867	EU190867	GU473342
		<i>Urticina</i>	<i>coriacea</i>		GU473282	EU190797	EU190877	EU190877	GU473351
	Actinodendridae	<i>Actinostephanus</i>	<i>haeckeli</i>		KJ482936	EU190762	KJ483034	KJ483034	GU473353
	Haloclavidae	<i>Haloclava</i>	<i>producta</i>		EU190734	EU190779	AF254370	AF254370	JF833008
		<i>Haloclava</i>	<i>sp.</i>		KJ482924	KJ482963	KJ483031	KJ483031	KJ482989
		<i>Harenactis</i>	<i>argentina</i>		KJ482926	KJ482964	KJ483026	KJ483026	KJ482984
		<i>Peachia</i>	<i>cylindrica</i>		EU190743	EU190789	KJ483015	KJ483015	-
		<i>Stephanthus</i>	<i>antarcticus</i>		KJ482927	KJ482960	KJ483019	KJ483019	KJ482983
	Liponematidae	<i>Liponema</i>	<i>brevicornis</i>		EU190738	EU190784	EU190866	EU190866	KJ483001
		<i>Liponema</i>	<i>multiporum</i>		KJ482922	KJ482962	-	-	-
	Phymanthidae	<i>Phymanthus</i>	<i>loligo</i>		EU190745	EU190791	EU190871	EU190871	GU473345
	Preactiidae	<i>Dactylanthus</i>	<i>antarcticus</i>		GU473272	AY345877	AF052896	AF052896	GU473358
		<i>Preactis</i>	<i>milliardae</i>		KJ482921	KJ482957	KJ483018	KJ483018	KJ482986
	Stichodactidae	<i>Heteractis</i>	<i>magnifica</i>		EU190732	EU190777	EU190862	EU190862	KJ482988
Metridioidea	Actinoscyphiidae	<i>Actinoscyphia</i>	<i>plebeia</i>		EU190712	EU190754	FJ489437	KJ483067	FJ489476
	Aiptasiidae	<i>Aiptasia</i>	<i>mutabilis</i>		JF832963	FJ489418	FJ489438	KJ483115	FJ489505
		<i>Aiptasia</i>	<i>pallida</i>		EU190715	EU190757	EU190846	EU190803	KJ482979
		<i>Bartholomea</i>	<i>annulata</i>		EU190721	EU190763	EU190851	KJ483068	FJ489483
		<i>Neoaipiasia</i>	<i>morbilla</i>		EU190742	EU190788	EU190869	KJ483075	JF833010
	Aliciidae	<i>Alicia</i>	<i>sansibarensis</i>		KJ482933	KJ482953	KJ483016	KJ483116	KJ483000
		<i>Triactis</i>	<i>producta</i>		EU490525	-	EU190876	KJ483125	GU473350
	Amphianthidae	<i>Amphianthus</i>	<i>sp.</i>		FJ489413	FJ489432	FJ489450	FJ489467	FJ489502
		<i>Peronanthus</i>	<i>sp.</i>		KJ482917	KJ482956	KJ483014	KJ483066	KJ482976
	Andvakiidae	<i>Andvakia</i>	<i>boninensis</i>		EU190717	EU190759	EU190848	KJ483053	FJ489479

Table 2. Cont.

Higher Taxa	Families	Genus	Species	(Remarks)	12S	16S	18S	28S	COXIII
		<i>Andvakia</i>	<i>discipulorum</i>		GU473273	GU473287	GU473316	KJ483051	-
		<i>Telmatactis</i>	sp.		JF832968	JF832979	KJ483013	KJ483135	-
	Antipodactinidae	<i>Antipodactis</i>	<i>awii</i>		GU473271	GU473286	GU473303	KJ483074	GU473337
	Bathypheiliidae	<i>Bathypheilia</i>	<i>australis</i>		FJ489402	FJ489422	EF589063	EF589086	FJ489482
	Boloceroiidae	<i>Boloceroidea</i>	<i>mcmurrici</i>		GU473270	-	EU190852	KJ483103	KJ483002
		<i>Bunodeopsis</i>	<i>globulifera</i>		KJ482940	KJ482949	KJ483025	KJ483122	KJ482992
	Diadumenidae	<i>Diadumene</i>	<i>cincta</i>		EU190725	EU190769	EU190856	KJ483106	FJ489490
		<i>Diadumene</i>	<i>leucolena</i>		JF832957	JF832977	JF832986	KJ483123	JF833006
		<i>Diadumene</i>	sp.		JF832960	JF832976	JF832980	KJ483130	JF833005
	Galantheanthemidae	<i>Galatheaanthemum</i>	sp.		KJ482918	KJ482955	KJ483012	KJ483065	KJ482977
		<i>Galatheaanthemum</i>	<i>profundus</i>		KJ482919	KJ482954	KJ483011	KJ483119	KJ482978
	Gonatiniidae	<i>Gonactinia</i>	<i>prolifera</i>		KJ482935	-	KJ483008	KJ483112	KJ482994
		<i>Protantea</i>	<i>simplex</i>		KJ482939	KJ482970	KJ483010	KJ483078	KJ482993
	Halcampidae	<i>Cactosoma</i>	sp. nov.		GU473279	GU473297	GU473313	GU473329	GU473346
		<i>Halcampa</i>	<i>duodecimcirrata</i>		JF832966	EU190776	AF254375	EU190820	-
		<i>Halcampoides</i>	<i>purpurea</i>		EU190735	EU190780	AF254380	KJ483100	-
	Haliplanellidae	<i>Haliplanella</i>	<i>lineata</i>		EU190730	EU190774	EU190860	KJ483108	FJ489506
	Hormathiidae	<i>Actinauge</i>	<i>richardi</i>		EU190719	EU190761	EU190850	KJ483055	FJ489480
		<i>Adamsia</i>	<i>palliat</i>		FJ489398	FJ489419	FJ489436	KJ483101	FJ489474
		<i>Allantactis</i>	<i>parasitica</i>		FJ489399	FJ489420	FJ489439	KJ483056	FJ489478
		<i>Calliactis</i>	<i>japonica</i>		FJ489403	FJ489423	FJ489441	KJ483057	FJ489486
		<i>Calliactis</i>	<i>parasitica</i>		EU190711	EU190752	EU190842	KJ483102	FJ489475
		<i>Calliactis</i>	<i>polypus</i>		FJ489407	FJ489427	FJ489445	KJ483058	FJ489485
		<i>Calliactis</i>	<i>tricolor</i>		FJ489405	FJ489425	FJ489443	KJ483059	FJ489488
		<i>Chondrophellia</i>	<i>orangina</i>		FJ489406	FJ489426	FJ489444	KJ483060	FJ489489
		<i>Hormathia</i>	<i>armata</i>		EU190731	EU190775	EU190861	KJ483062	FJ489491
		<i>Hormathia</i>	<i>lacunifera</i>		FJ489409	FJ489428	FJ489446	KJ483063	FJ489492
		<i>Hormathia</i>	<i>pectinata</i>		FJ489415	FJ489430	FJ489448	FJ489465	FJ489497
		<i>Paracalliactis</i>	<i>japonica</i>		FJ489411	FJ489429	FJ489447	KJ483061	FJ489496
		<i>Paraphelliactis</i>	sp.		FJ489412	FJ489431	FJ489449	FJ489466	FJ489498
	Isanthidae	<i>Isanthus</i>	<i>capensis</i>		JF832967	GU473291	GU473307	KJ483096	GU473362
	Kadosactinidae	<i>Alvinactis</i>	<i>chessi</i>		GU473278	GU473296	GU473312	KJ483052	GU473352
		<i>Cyananthea</i>	<i>hourdezi</i>		GU473275	GU473293	GU473309	KJ483081	GU473364
		<i>Kadosactis</i>	<i>antarctica</i>		FJ489410	EU190782	EU190865	KJ483080	FJ489504
		<i>Metridium</i>	<i>senile</i>		EU190740	EU190786	AF052889	KJ483076	FJ489494
	Nemathidae	<i>Nemanthus</i>	<i>nitidus</i>		EU190741	EU190787	EU190868	KJ483064	FJ489495
	Phelliidae	<i>Phellia</i>	<i>gausapata</i>		EU190744	EU190790	EU190870	KJ483054	FJ489473
		<i>Phellia</i>	<i>exlex</i>		JF832958	JF832978	JF832984	KJ483121	JF833004

Table 2. Cont.

Higher Taxa	Families	Genus	Species	(Remarks)	12S	16S	18S	28S	COXIII
	Sagartiidae	<i>Actinothoe</i>	<i>sphyrrodeta</i>		FJ489401	FJ489421	FJ489440	KJ483111	FJ489481
		<i>Anthothoe</i>	<i>chilensis</i>		FJ489397	FJ489416	FJ489434	FJ489453	FJ489470
		<i>Cereus</i>	<i>pedunculatus</i>		EU190724	EU190767	EU190855	EU190813	FJ489471
		<i>Cereus</i>	<i>herpetodes</i>		JF832956	JF832969	JF832983	JF832992	-
		<i>Sagartia</i>	<i>trogodytes</i>		EU190746	EU190792	EU190872	KJ483073	FJ489499
		<i>Sagartia</i>	<i>ornata</i>		JF832959	JF832975	JF832985	KJ483069	JF833011
		<i>Sagartiogeton</i>	<i>laceratus</i>		EU190748	EU190794	EU190874	KJ483071	FJ489500
		<i>Sagartiogeton</i>	<i>undatus</i>		FJ489400	FJ489417	FJ489435	KJ483070	FJ489472
		<i>Verrillactis</i>	<i>paguri</i>		FJ489414	FJ489433	FJ489440	KJ483046	FJ489503
Zoanthidea	Epizoanthidae	<i>Epizoanthus</i>	<i>illoricatus</i>		AY995901	EU591597	KC218424	KJ483036	-
	Parazoanthidae	<i>Parazoanthus</i>	<i>axinellae</i>		GQ464940	EU828754	KC218416	KJ483044	-
		<i>Savalia</i>	<i>savaglia</i>		AY995905	DQ825686	HM044299	HM044298	-
Undknown	Relicanthidae	<i>Relicanthus</i>	<i>daphneae</i>		KJ482934	KJ482971	KJ483028	KJ483131	KJ482999

3. Results and Discussions

3.1. Taxonomic Section

Order ACTINIARIA Hertwig, 1882

Suborder ENTHEMONAE Rodríguez and Daly, 2014

Superfamily ACTINOSTOLOIDEA Carlgren, 1932

(Japanese name: setomono-isoginchaku-jouka: Izumi et al., 2019a)

Family DISCOACTINIIDAE fam. nov.

(New Japanese name: enban-isoginchaku-ka)

urn:lsid:zoobank.org:act:EA2105B4-D768-40DF-991C-DBC12356B0C2

Diagnosis. See the diagnosis of the genus *Discoactis*.

Type genus. *Discoactis* gen. nov. (monotypic).

Remarks. *Discoactis tritentaculata* fam., gen., and sp. nov., collected from several localities in Japan, was the sister group of *Capnea* of family Capneidae Forbes, 1841 [15] in the present phylogenetic tree (Figure 7). However, there are several differences between *Discoactis* and *Capnea* as shown below. *Capnea* has numerous vesicle-like tentacles [5,16], in contrast to the few slender tentacles of *Discoactis* (Figure 2). Only *Discoactis* has endocoels without tentacles (Figure 2), in contrast to *Capnea*, which develops two or more tentacles in every exocoel/endocoel [5,16,18]. *Capnea* has conspicuous pinnate endodermal sphincter muscles ([16,18]), one of the characteristic features of this genus, while there is only a weak mesogleal muscle in *Discoactis* (Figure 3B). *Discoactis* has only 10 macrocnemes (two dorso-lateral macrocnemes of the first cycle mesenteries are absent; Figure 3C), while *Capnea* has at least 12 macrocnemes in first cycle. Thus, we judged that it was inappropriate to unify *Discoactis* into Capneidae even though they were sister groups in the phylogenetic tree (Figure 7). Thus, we established a new family, Discoactinidae fam. nov., for the genus *Discoactis*.

The most characteristic feature of Discoactinidae is the unequal mesenterial pair in the first cycle, and this mesenterial arrangement is particular in Actinostoloidea. In this superfamily, almost all of the existing families are developing their mesenteries in the first cycle completely [4,5,14]. The only exceptional families are Halcampulactidae Gusmão, Berniker, Deussen, Harris, and Rodriguez, 2019: *Halcampulactis solimar* has only eight macrocnemes [12]. Therefore, only Halcampulactidae and Discoactinidae have unequally developed mesenterial pairs in the first cycle. However, there is an apparent difference in dorso-lateral mesenteries: in contrast to Halcampulactidae, of which the dorso-lateral mesenterial pair develops unequally [12], Discoactinidae anemones develop the pair equally (also see Discussion). Moreover, they can be distinguished from each other by the distribution of mesenteries in distal–proximal axis. As mentioned below, the mesenteries of *D. tritentaculata* sp. nov. increase in the proximal part, in contrast to *Halcampulactis solimar*, which has more microcnemes in the distal end [12]. Additionally, concerning the marginal sphincter muscle, only *Discoactinis tritentaculata* develops a mesogleal one. *D. tritentaculata*, therefore, has too unique features to accommodate Halcampulactinidae.

In addition to morphology, we can advocate this based on phylogeny (Figure 7): though the topology around Halcampulactidae is not fixed (it might be ascribed from the long branch attraction of *Halcampulactis solimar* [12]), at least it is shown that *D. tritentaculata* is most related to Capneidae (BV/PP = 88/0.99). In conclusion, we can indicate that *D. tritentaculata* should be accommodated into a new family based on the morphological differences from Capneidae species.

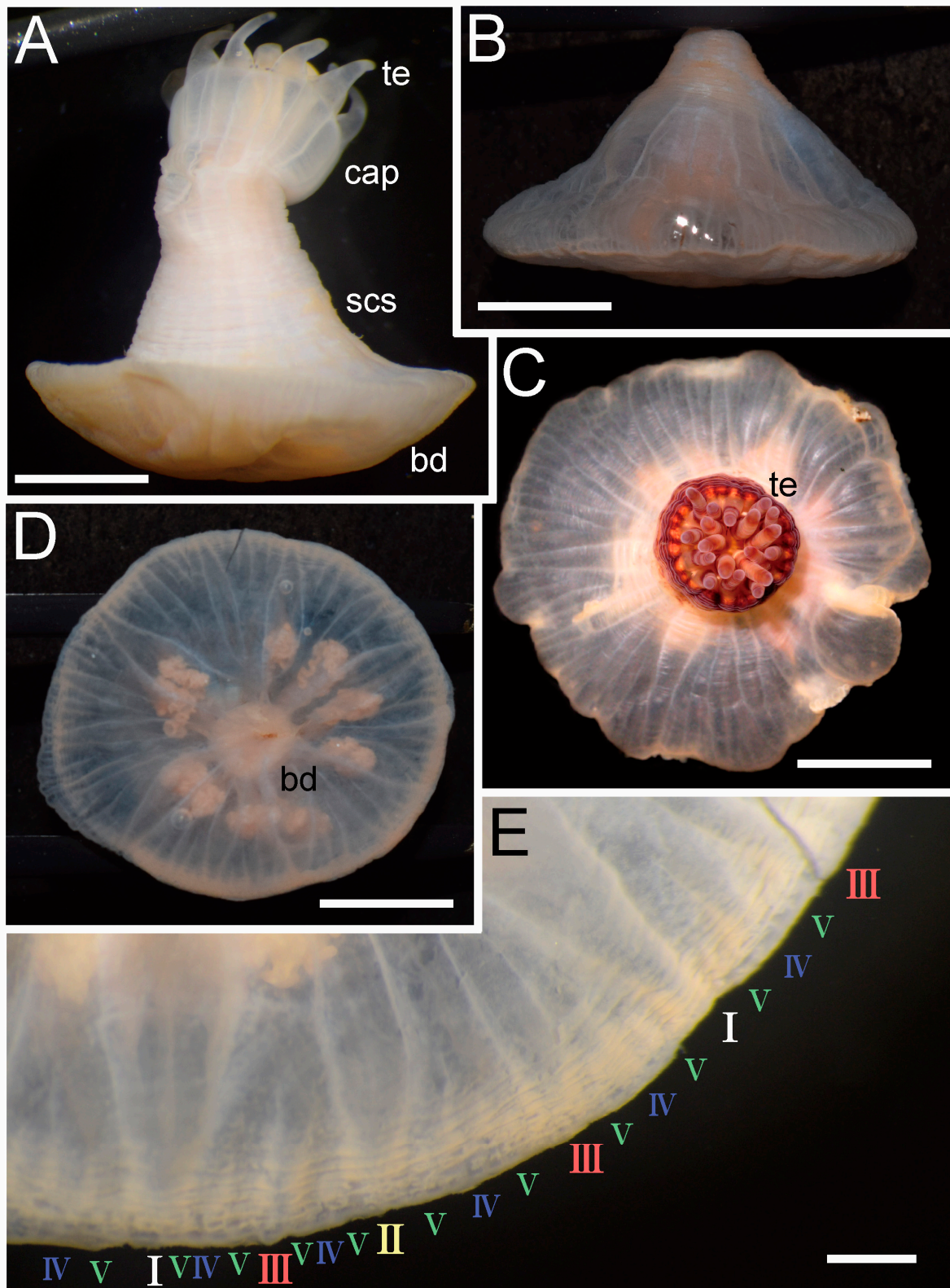


Figure 2. External morphology of *Discoactis tritentaculata*. (A,B,D,E) Views of a preserved specimen, and (C) view of living specimen. (A) Tentacles elongated (CMNH-ZG 10795). (B) Tentacles contracted (CMNH-ZG 10796). (C) Oral view of the oral disc of NSMT-Co 1908. (D) Proximal view of the basal disc (CMNH-ZG 10796). (E) Enlarged view of D (CMNH-ZG 10796). I–V indicates the number of the mesenterial cycle. Abbreviations: bd, basal disc; cap, capitulum; scs, scapus; te, tentacle. Scale bars indicate 5 mm in (A–D), 1 mm in E, 100 μ m.

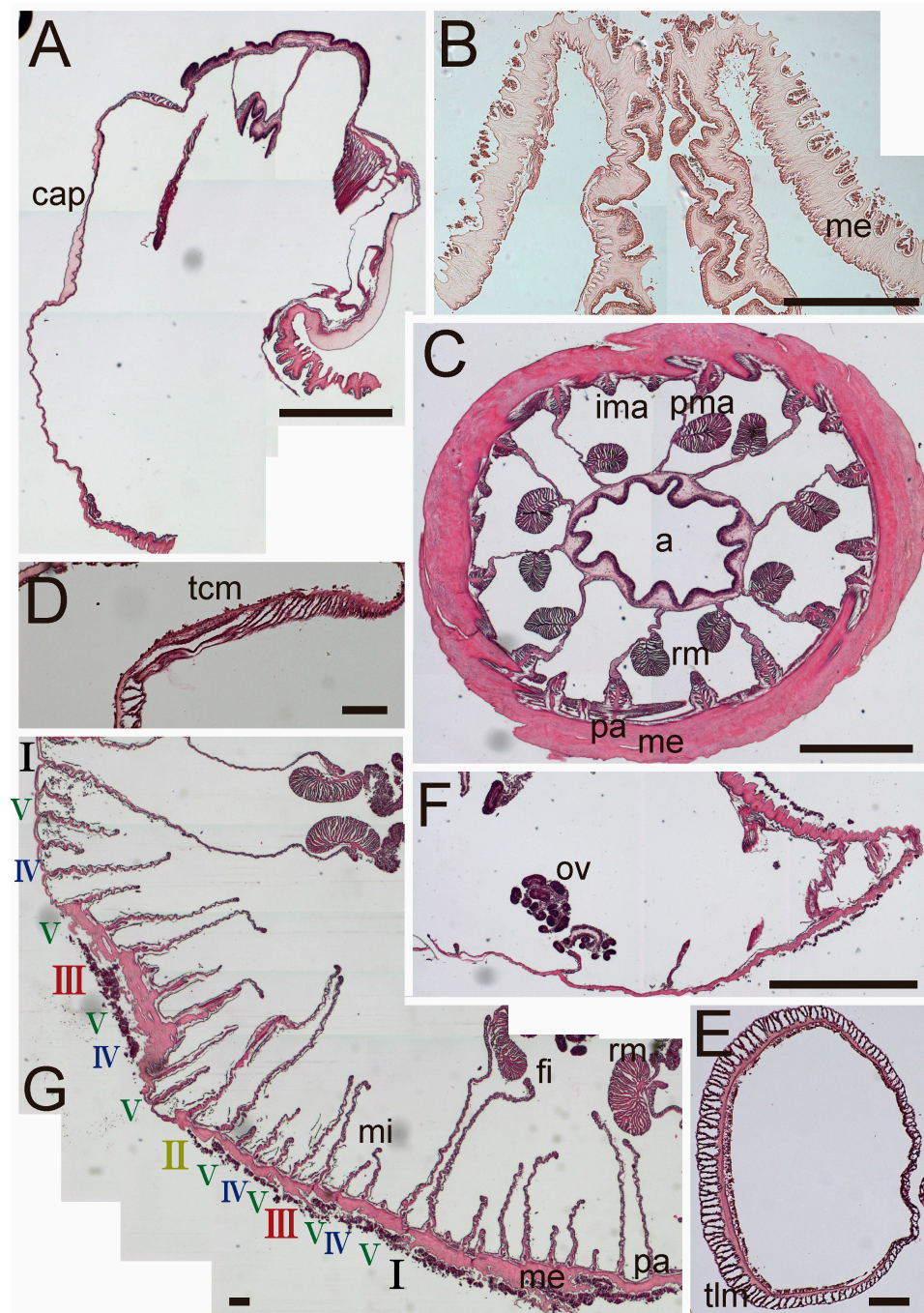


Figure 3. Internal morphology of *Discoactis tritentaculata*. (A,C–G) CMNH-ZG 10795, (B) CMNH-ZG 10796. (A,B) Longitudinal section of the distal end; (C) transverse section of the upper column; (D) longitudinal section of a tentacle; (E) transverse section of a tentacle; (F) transverse section of the proximal end (basal disc); (G) enlarged view of the transverse section of the column. I–V indicates the number of the mesenterial cycle. Abbreviations: a, actinopharynx; cap, capitulum; fi, filament; ima, imperfect macrocneme; me, mesoglea; mi, microcneme; ov, ovary; pa, parietal muscle; pma, perfect macrocneme; rm, retractor muscle; sp, sphincter muscle (mesogleal); tcm, tentacle circular muscle; tlm, tentacle longitudinal muscle. Scale bars indicate 1 mm in (A–C,F) and 100 μ m in (D,E,G).

Genus *Discoactis* gen. nov.

(New Japanese name: enban-isoginchaku-zoku)

urn:lsid:zoobank.org:act:B0E8B56E-B622-4AC7-AF85-D8F82FF15E04

Diagnosis. Actinostoloidea anemone with a very wide pedal disc. Column comparatively smooth, divisible into scapus and capitulum, the former provided with a more or less

distinct periderm. Sphincter weak, mesogleal. Tentacles 14–18, long and slender, simple, few in number, arranged in a peculiar pattern: 6 tentacles with each exocoel in first cycle. Eight–twelve tentacles in each exocoel: tentacles absent in the endocoels of the second cycle. Longitudinal muscles of tentacles and radial muscles of oral disc chiefly mesogleal. One siphonoglyph. Mesenteries far more numerous proximally than distally. Three types of mesenteries: 10 perfect macrocnemes; 10–14 imperfect macrocnemes with strong parietals in first and second cycles; and numerous tiny, weaker imperfect microcnemes younger than the third cycle, without filaments, only on the proximal side. Retractor distinct, circumscribed. Parietal muscles well developed in first/second cycles. Cnidom: spirocysts, basitrichs, and microbasic *p*-mastigophores.

Etymology. The type species of this genus, *Discoactis tritentaculata* sp. nov., has a very conspicuous basal disc that becomes disc-like in shape after preservation. “Disco-” is derived from this shape; “-actis” means radiated sunshine, and this term has been often used in the names of actiniarian genera.

Type species. *Discoactis tritentaculata* sp. nov. (monotypic).

Remarks. The most distinguishable character of this genus is existence of endocoels without tentacles on the distal end. While almost all anemones have at least one tentacle in each exocoel/endocoel in the distal end [5], this group has endocoels that bear no tentacles in the second cycle. In addition to the tentacular arrangement, it is also peculiar that two dorso-lateral mesenteries in first mesenterial cycle do not develop into perfect mesenteries. There are only a few known anemones with 10 macrocnemes (*Limnactinia* Carlgren, 1921 [35] or *Decapheilia* Bourne, 1918 [36]), and thus this character is also diagnostic of this genus.

Discoactis tritentaculata sp. nov.

(Japanese name: umi-no-fujisan)

urn:lsid:zoobank.org:act:9B346F9E-E38E-4645-BE45-4D8425ECA907

Figures 2–4; Table 3

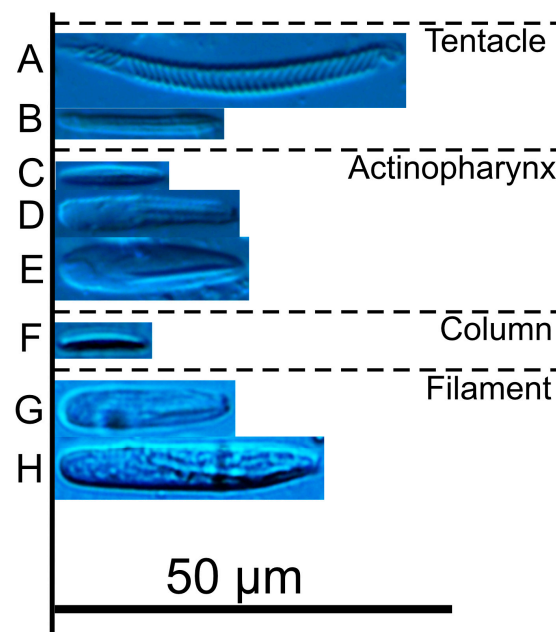


Figure 4. Cnidae of *Discoactis tritentaculata* (CMNH-ZG10795). (A) Spirocyst of the tentacle; (B) basitrichs of the tentacle; (C) basitrich of the actinopharynx; (D) gracile microbasic *p*-mastigophore in the actinopharynx; (E) robust microbasic *p*-mastigophore in the actinopharynx; (F) basitrich of the column; (G) small microbasic *p*-mastigophore in the actinopharynx; (H) large microbasic *p*-mastigophore in the actinopharynx.

Table 3. Cnidom of *Discoactis tritentaculata* fam. gen. and sp. nov.

<i>Discoactis tritentaculata</i> Izumi, Yanagi, and Kohtsuka, 202x											
CMNH-ZG 10795 (Suruga Bay)						NSMT-Co 1908 (Sagami Bay)					
		Length × Width (μm)	Mean	SD	N	Frequency	Length × Width (μm)	Mean	SD	N	Frequency
Tentacle											
	basitrichs	13.6–21.9 × 2.0–3.3	18.6 × 2.6	1.71 × 0.32	27	numerous	13.4–20.5 × 1.7–3.1	17.0 × 2.5	1.95 × 0.35	29	numerous
	spirocysts	17.5–52.0 × 2.4–4.5	32.4 × 3.3	8.28 × 0.46	88	numerous	15.3–41.4 × 2.1–4.6	25.6 × 3.3	6.99 × 0.66	48	numerous
Actinopharynx											
	basitrichs	11.7–15.4 × 1.9–2.9	13.3 × 2.4	1.07 × 0.28	13	few	11.8–14.1 × 1.8–2.6	13.4 × 2.1	0.82 × 0.28	5	rare
	microbasic	19.5–26.9 × 3.4–4.8	23.6 × 4.0	1.44 × 0.36	36	numerous	20.8–25.5 × 3.3–5.1	22.8 × 4.2	1.24 × 0.39	26	numerous
	p-mastigophores	20.9–25.6 × 5.4–7.4	23.6 × 6.4	1.15 × 0.47	34	numerous	20.0–25.3 × 5.3–6.7	22.3 × 5.8	1.62 × 0.41	11	few
Column											
	basitrichs	11.2–15.9 × 2.0–2.4	13.2 × 2.2	1.71 × 0.15	4	rare	10.0–16.2 × 1.7–2.8	13.1 × 2.3	1.88 × 0.30	4	rare
Filament											
	spirocysts	-	-	-	-	none	21.3–26.6 × 2.5–3.0	24.6 × 2.8	2.39 × 0.25	3	rare
	holotrichs	-	-	-	-	none	23.1–23.7 × 6.3–6.6	23.5 × 6.5	0.35 × 0.17	2	rare
	microbasic	18.8–21.7 × 4.1–6.2	20.6 × 4.9	0.82 × 0.51	10	few	16.2–20.8 × 3.3–5.1	18.2 × 4.2	1.50 × 0.50	9	few
	p-mastigophores	28.2–36.1 × 4.8–7.6	32.2 × 6.5	1.71 × 0.59	75	numerous	22.5–28.6 × 4.7–6.2	25.2 × 5.5	1.49 × 0.38	33	numerous
<i>Discoactis tritentaculata</i> Izumi, Yanagi, and Kohtsuka, 202x											
CMNH-ZG 10797 (Otsuchi)						NSMT-Co 1908 (Sea of Japan)					
		Length × Width (μm)	Mean	SD	N	Frequency	Length × Width (μm)	Mean	SD	N	Frequency
Tentacle											
	basitrichs	14.2–18.9 × 2.0–3.7	16.5 × 2.5	0.99 × 0.25	29	numerous	13.9–18.3 × 2.1–2.9	16.3 × 2.5	1.20 × 0.22	15	numerous
	spirocysts	15.2–30.1 × 2.1–3.8	22.6 × 3.2	4.57 × 0.46	20	numerous	14.2–42.4 × 2.1–4.1	24.8 × 2.9	6.77 × 0.51	49	numerous
Actinopharynx							Damaged				
	basitrichs	14.5–20.6 × 2.3–3.0	18.3 × 2.6	2.05 × 0.25	7	few					
	microbasic	16.6–26.3 × 3.5–6.7	23.7 × 4.8	2.04 × 0.98	24	numerous					
	p-mastigophores										
Column											
	basitrichs	10.2–15.5 × 1.9–3.3	13.1 × 2.5	1.34 × 0.35	17	numerous	10.6–20.1 × 1.9–3.3	13.2 × 2.5	3.08 × 0.45	7	few
Filament											
	basitrichs	No cnidae observed in the specimen					17.2–21.1 × 1.7–3.0	19.4 × 2.5	1.17 × 0.28	22	numerous
	spirocysts						27.1–31.2 × 2.5–3.0	29.1 × 2.7	2.02 × 0.25	2	rare
	microbasic										
	p-mastigophores						17.2–26.8 × 3.5–6.6	22.0 × 5.1	2.50 × 0.72	58	numerous

Material examined. Holotype. CMNH-ZG10795: embedded tissues in paraffin, histological sections, prepared nematocysts; collected on 17 May 2003, at Senoumi Bank off Shizuoka Prefecture, 34.587° N, 138.472° E, at 311 m in depth collected during the research cruise of *R/V Natsushima* (Cruise No. NT03-5, DT-6C) by Kensuke Yanagi. **Paratypes:** CMNH-ZG10796: dissected specimen and histological sections, same locality, date, and collector as CMNH-ZG. NSMT-Co 1908: dissected specimen, embedded tissues in paraffin, histological sections, prepared nematocysts, 17 April 2018, collected from the west off Misaki, Kanagawa Prefecture, 35°08.328' N, 139°32.568' E, at 108–198 m in depth, collected by Hisanori Kohtsuka boarding *R/V Rinkai-Maru*. NSMT-Co 1910: whole specimen, same locality, date, and collector as NSMT-Co 1908. NSMT-Co 1911: dissected specimen, embedded tissues in paraffin, histological sections, prepared nematocysts, 15 February 2017, collected from the west off Misaki, Kanagawa Prefecture, 35°08.388' N, 139°33.731' E, at 95–98 m in depth by Takato Izumi boarding *R/V Rinkai-Maru*. **Other specimens:** CMNH-ZG10797: dissected specimen, embedded tissues in paraffin, histological sections, prepared nematocysts, 24 July 2017, collected from the southwest off Otsuchi, Iwate Prefecture, 39°20.929' N, 142°02.408' E, at 117–124 m in depth by *R/V Yayoi* (St-1-4) and Kensuke Yanagi. NSMT-Co 1909: whole specimen, 25 May 2014, collected from the southwest off Iki Island, Nagasaki Prefecture, 33°03.582' N, 129°31.175' E, at 79–83 m in depth during the research cruise of *R/V Toyoshio-Maru* (St-9), collected by Takato Izumi. NSMT-Co 1912: whole specimen, same locality, date, and collector as NSMT-Co 1909. NSMT-Co 1913: whole two specimens, 24 October, 2023, collected from the west off Sukumo, Kochi Prefecture, 32°40.257' N, 132°10.056' E, at 377–401 m in depth during the research cruise of *R/V Toyoshio-Maru* (St-2), collected by Takato Izumi.

Description. External anatomy. On living specimens (NSMT-Co 1910, 1911), column white or pale yellow, semitransparent in proximal side, and distal end dark red in color. Wholly white on preserved ones. Tentacles striped with pale red and dark red (Figure 2C). Column divisible scapus and scapulus, and drastically broaden towards the proximal end (Figure 2A–D): the width of scapus is ca. 2–4 mm at the distal end but reaches to ca. 15–25 mm at the proximal end (= basal disc) of preserved specimens. The height of preserved specimen is ca. 10–15 mm. Scapus and scapulus smooth, sometimes with transversal wrinkle in preserved specimens (Figure 2A). Pedal disc adherent, semitransparent, almost circular but flexible in outline (Figure 2C). Mouth with indistinct lip. Tentacles 1.5–2.0 mm in length, long and slender, almost the same length from the center to margin (Figure 2A,C). Tentacles 14–18 in number, in a peculiar rule of arrangement: 6 tentacles in each exocoel in first cycle; 8–12 tentacles in each exocoel, with tentacles absent in endocoels of second-cycle mesenteries.

Internal anatomy. Three types of mesenteries: 10 perfect macrocnemes, fertile and with strong retractors and parietals in the first cycle; 10–14 imperfect macrocnemes (Figure 3C) with strong parietals in the first and second cycles; numerous, around 100 in number, imperfect microcnemes, weaker and tiny, between the third to fifth cycles, without filaments (Figure 3G).

Microcnemes sometimes are not equally developed within the same pair of perfect mesenteries (Figure 3G). Mesenteries at the base more numerous than at the margin: microcnemes only on proximal side (Figures 2E and 3G). Only 10 perfect macrocnemes fertile on the proximal side (Figure 3G). Retractors distinct, strong, pinnate, and consist of a main lamella with 10–16 simple branches (Figure 3C,G). Parietal muscles distinct in macrocnemes on the distal side, with 5–15 muscular processes on each side (Figure 3C), but indistinct on the proximal side. Tentacular longitudinal muscle mesogleal, distinct (Figure 3E), and circular muscle endodermal but indistinct (Figure 3D). Columnar circular muscle well-developed (Figure 3B). Sphincter muscle mesogleal and comparatively weak

(Figure 3A). Basilar and parietobasilar muscle absent (Figure 3A,B,F). Mesoglea the thickest in the column, ca. 500 µm in thickness, and thick in the actinopharynx, but very thin in the mesenteries and tentacles. Only 10 perfect mesenteries fertile with gonads, but mature gonads absent in all specimens (Figure 3F).

Cnidom. Spirocysts, basitrichs, microbasic *p*-mastigophores. See Figure 4 and Table 3 for the size and distribution.

Etymology: The species name “tritentaculata” is derived from the tentacular arrangement; that of *Discoactis tritentaculata* sp. nov. is composed six sets of three tentacles.

Japanese name: “Umi-no-Fujisan” means Mt. Fuji (Fujisan) of (no) the ocean (Umi), too. The shape of this sea anemone in living and well-fixed specimens very closely resembles the shape of Mt. Fuji. In addition, from Sagami Bay and Suruga Bay, the habitats of this sea anemone, everyone can see Mt. Fuji over the sea; actually, the authors sometimes conducted sample collection of this species while being able to see the scenery of Mt. Fuji.

Remarks. As we already mentioned in the remarks for the genus, *Discoactis tritentaculata* sp. nov. is a unique anemone that does not fit with any previously described families and genera in Actinostoloidea. However, in contrast to the singularity of its morphology, *D. tritentaculata* sp. nov. is a relatively common species and has been widely collected in Japan. Over 10 individuals of this species were collected from the Pacific Ocean, Sagami Bay (Misaki), Suruga Bay (Senoumi-Bank), Otsuchi-Bay, Bungo Strait (off Sukumo), and Sea of Japan.

Family CAPNEIDAE Gosse, 1860

(Common name: yosai-isoginchaku-ka)

Diagnosis (the arranged point from Carlgren [1949], the diagnosis of Aurelianidae, was shown in **bold**): **Actinostoloidea anemones** with a distinct, often wide pedal disc. Column smooth, or with vesicles in its upper part. Sphincter strong, circumscribed. Tentacles very short, vesicle-like, often slightly lobed, few or many communicating with each of the main exo- and endocoels. Longitudinal muscles of tentacles and radial muscles of oral disc endodermal or mesogloal. A single siphonoglyph, but two pairs of directives. All or most of the mesenteries perfect and fertile. Retractors very strong, strongly restricted, or usually circumscribed.

Remarks: Capneidae, established in Gosse 1860 [37], were previously classified as members of Endomyaria [5] because of their distinct endodermal sphincter muscle. Though the placement of this family became Actinioidea Rafinesque, 1815, as with almost all endomyarians in the thorough rearrangement of the classification of sea anemones [8], *Capnea* anemones were shown as belonging to superfamily Actinostoloidea Carlgren, 1932 recently by a phylogenetic analysis [38]. The diagnosis of this family had not changed from Carlgren (1949) [5], and thus we only have updated the classification in the diagnosis in this study.

Genus *Capnea* Gosse, 1860

Capnea japonica (Carlgren, 1940)

Figure 5

Material examined. CMNH-ZG 10798: Dissected specimens and histological sections; collected on 9 December 2020, off Iwaki, Fukushima Prefecture, at 150 m in depth during the research cruise of *R/V Iwaki-Maru* by Takashi Iwasaki, Masato Ikegawa, and the captain and crews; kept in the tank of Aquamarine Fukushima by Mai Hibino; then, preserved by Takato Izumi. CMNH-ZG 06547: see Yanagi and Izumi (2021).

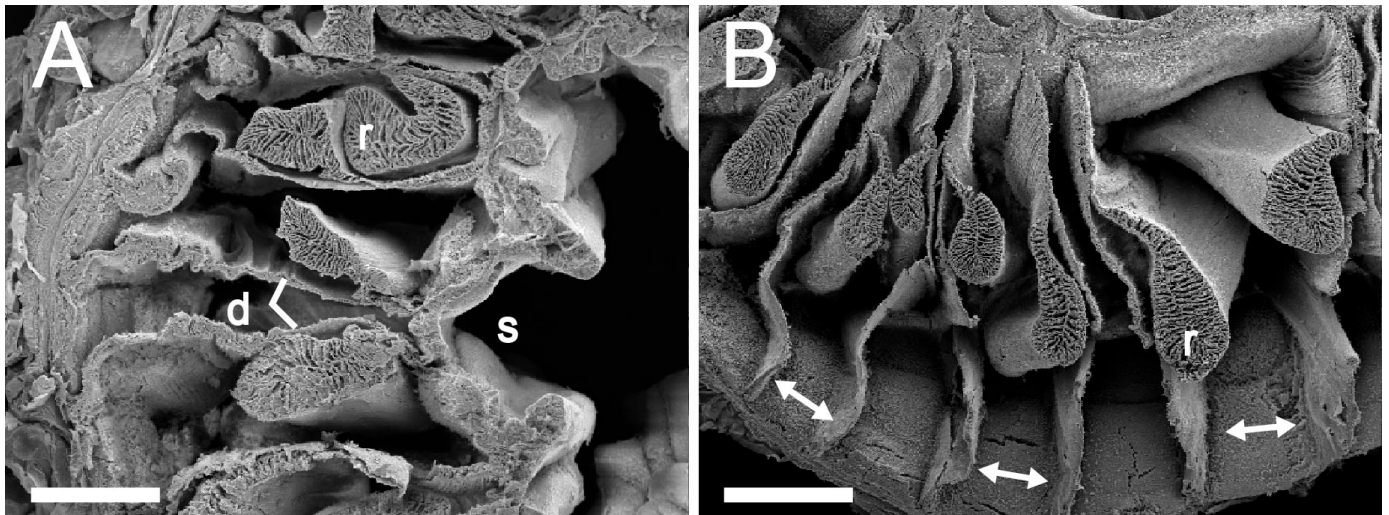


Figure 5. SEM image of a cross section of the mesenteries of *Capnea japonica* (CMNH-ZG 10798). (A) Directive mesenteries with outer side retractor muscles. (B) Three pairs of equally developed mesenteries with pinnate, circumscribed retractor muscles. Abbreviations: d, directive mesentery; r, retractor muscle; s, siphonoglyph. Left and right arrows indicate each pair of mesenteries. Scale bars indicate 500 µm.

Description. See Yanagi and Izumi (2021) [16].

Remarks. Based on an additional specimen examined in this study, we found that the pair of mesenteries was not unequally developed. Yanagi and Izumi [16] suggested that the mesenteries were unequally developed within the pair. We find that was a mistake and was caused by the poor sample condition. The retractors develop on each mesentery and are almost the same size within each pair. The retractors are pinnate and circumscribed; so, the main lamellae are completely separated from the mesentery (Figure 5).

3.2. Molecular Phylogeny

The taxonomic position in the order. In the phylogenetic tree of order Actiniaria, species were separated into two clades (Figure 6). One consisted of a clade of species of the suborder Enthemonae Rodríguez and Daly, 2014 (clade indicated by node B in Figure 6) and the other was Anenthemonae Rodríguez and Daly, 2014 (node A in Figure 6). The monophyly of each suborder clade was supported with a bootstrap value of 100% and a posterior probability of 1.00 (the nodes indicated at A and B in Figure 6).

In Enthemonae, as indicated in Rodríguez et al. (2014), there are three clades that correspond to the superfamilies Actinostoloidea Carlgren, 1932 [10], Actinioidea Rafinesque, 1815 [39], and Metridioidea Carlgren, 1893 [40]. *Discoactis tritentaculata* fam. gen. and sp. nov. (indicated by red box in Figure 6) is included in the clade of Actinostoloidea (indicated by the pale red box) and becomes a sister group with the genus *Capnea* Forbes, 1841 [15], with almost sufficient phylogenetic support late (nodes C and D).

Internal phylogeny in the superfamily. *Discoactis tritentaculata* sp. nov. (blue box in Figure 7) is the derived lineage of the superfamily Actinostoloidea and is most related to Capneidae: forming a clade with Capneidae with support of 88% and a posterior probability of 0.99 (Figure 7).



Figure 6. Maximum-likelihood tree of the order Actiniaria based on the combined dataset of mitochondrial 12S and 16S rDNA, cytochrome oxidase III (COXIII) DNA, and nuclear 18S and 28S rDNA (total 6943 bp). Two clades of suborders are indicated by bars. Numbers connected with slash characters above branches indicate ML bootstrap support values followed by BI posterior probabilities. Numbers without slash characters indicate ML bootstrap support values of the nodes (bootstrap values of $\geq 50\%$ are shown). Nodes in A and B indicate the bases of the clades of suborder Anenthemonae and Enthemonae, respectively; node C is the base of the superfamily Actinostoloidea; and node D is the node of *Discoactis tritentaculata* and the family Capneidae.

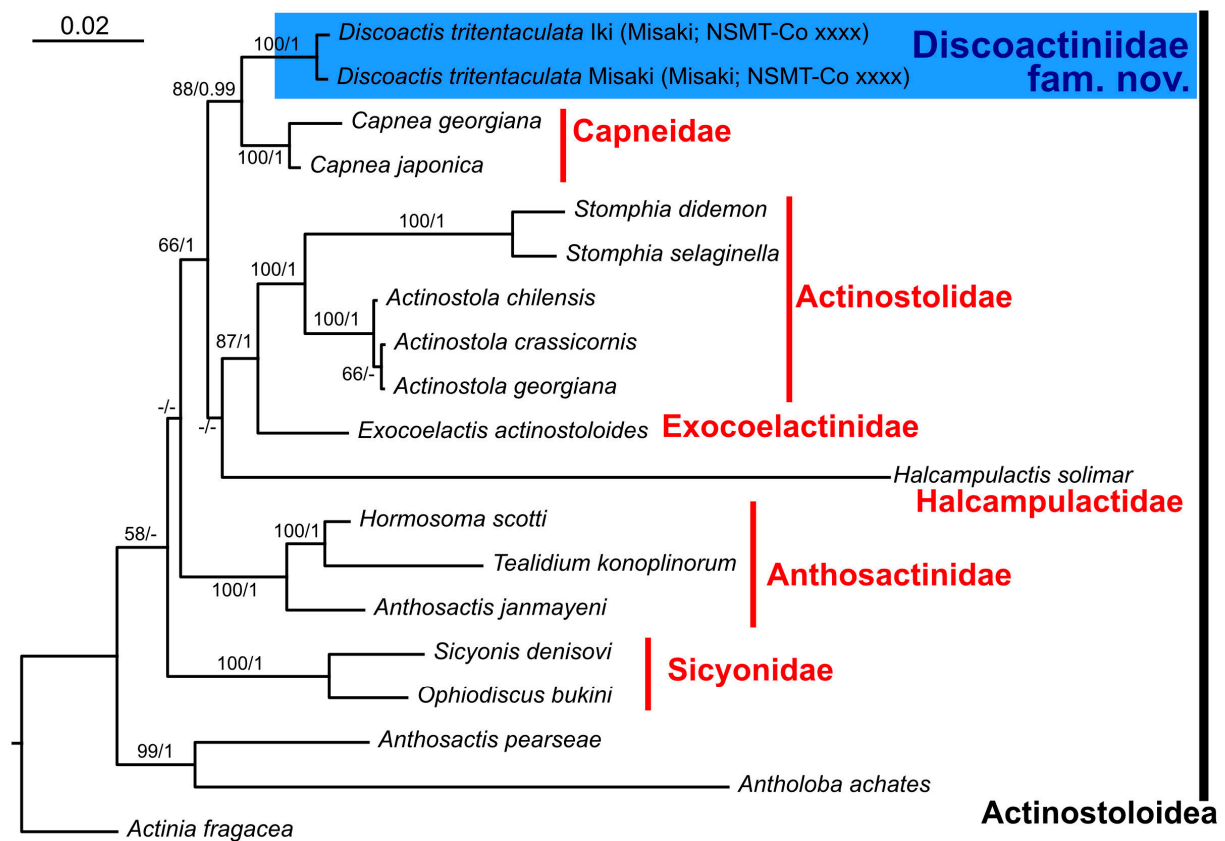


Figure 7. Maximum-likelihood tree of the order Actiniaria based on the combined dataset of mitochondrial 12S and 16S rDNA, cytochrome oxidase III (COXIII) DNA, and nuclear 18S and 28S rDNA (total 4043 bp). The clade of *Discoactis tritentaculata* is shown by the blue box, and the families are indicated nearby the OTU. Numbers connected with slash characters above branches indicate ML bootstrap support values followed by BI posterior probabilities of nodes A and B. Numbers without slash characters indicate ML bootstrap support values of the nodes (bootstrap values of $\geq 50\%$ and posterior probabilities of ≥ 0.50 are shown).

Concerning the other families, Actinostolidae (at least *Actinostola* Verrill, 1879 and *Stomphia* Gosse, 1859) is monophyletic (100/1) and Exocoelactinidae is the sister group of Actinostolidae (87/1). Halcampilactidae is the sister of these two families, but the node is not supported well. Those five families become monophyletic (66/1). Anthosactinidae (*Anthosactis* Danielssen, 1890, *Hormosoma* Stephenson, 1918, and *Antholoba* Hertwig, 1882) becomes polyphyletic in this analysis.

The clade of *Discoactis tritentaculata* is shown by the blue box, and the families are indicated nearby the OTUs. Numbers connected with slash characters above the branches indicate the ML bootstrap support values followed by the BI posterior probabilities of nodes A and B. Numbers without slash characters indicate the ML bootstrap support values of the nodes (bootstrap values $\geq 50\%$ and posterior probabilities ≥ 0.50 are shown).

The two clades of suborders are indicated by bars. Numbers connected with slash characters above the branches indicate the ML bootstrap support values followed by the BI posterior probabilities. Numbers without slash characters indicate the ML bootstrap support values of the nodes (bootstrap values $\geq 50\%$ are shown). Nodes A and B indicate the bases of the clades of suborders Anenthemonae and Enthemonae, respectively; node C is the base of the superfamily Actinostoloidea; and node D is the node of *Discoactis tritentaculata* and the family Capneidae.

4. Discussion

Recent transition of families belonging to Actinostoloidea.

After establishing Actinostoloidea Carlgren, 1932, the anemones in this group had been accommodated in the previous tribe Mesomyaria (Carlgren, 1949) because all previous families, Actinostolidae Carlgren, 1932 and Exocoelactinidae Carlgren, 1925, of Actinostoloidea have mesogleal sphincters [10,11,41]. However, recently, Rodríguez et al. (2014) [8] re-established this taxon as one of the members of Enthemonae, obeying their phylogenetic tree. According to the definition of Rodríguez et al. [8], the marginal sphincter muscles of the species of Actinostoloidea are all mesogleal (same as the characters of Mesomyaria) and the mesenterial pairs of this taxon are unequally developed in this suborder.

However, our previous research [16] suggested that there is a clade of sea anemones that have strange features (for Actinostoloidea) in the superfamily clade: Capneidae species form an internal clade of Actinostoloidea with high support. Despite *Capnea geogiana*, a species of Capneidae, already being included in the analysis by Rodríguez et al. [8] and the fact that this species is in the Actinostoloidea clade, they completely ignored this result and put *Capnea* into superfamily Actinioidea. However, the results of phylogenetic trees of the previous studies [8,12,14,42] and the present study show *Capnea* to be certainly in the superfamily of Actinostoloidea, and this result should not be neglected. This family, however, has peculiar morphological features that do not completely correspond to the main features of this superfamily: *Capnea* does not have a mesogleal sphincter but instead has an endodermal sphincter [15,16]. On the other hand, it was not certain whether Capneidae possessed unequally developed mesenterial pairs, an important feature of this superfamily in the study by Rodríguez et al. [8], or not.

Two more families of Actinostoloidea have been described after the re-establishment of this superfamily in 2024: one is Halcampilactidae Gusmão, Berniler, Deusen, Harris, and Rodríguez, 2019. According to Gusmão et al. (2019) [12], *Halcampilactis solimar* Gusmão, Berniler, Deusen, Harris, and Rodríguez, 2019, the only species of this family, has peculiar features: it has an elongated body, develops only eight macrocnemes like Edwardsiidae, lacks marginal sphincter muscles and basal discs, and lives in sand by burrowing [12]. Though these morphological features and ecologies are quite peculiar and completely different from the other families of Actinostoloidea, it was confirmed that Halcampilactidae certainly belongs to this superfamily (Figures 6 and 7; [12]). The other recently described family within Actinostoloidea is Tetracoelactinidae Sanamyan, Sanamyan, Galkin, Ivin, and Bocharova, 2021 [14] with the genus *Tetracoelactis* Sanamyan and Sanamyan, 2019, originally established as one genus of Exocoelactinidae [37] from this family.

Moreover, Sanamyan et al. (2021) [14] established one more family, Anthosactinidae Sanamyan, Sanamyan, Galkin, Ivin and Bocharova, 2021 and reinstated the family Sicyonidae Hertwig, 1882 by splitting Actinostolidae based on the phylogenetic analysis of this superfamily. Though Actinostolidae had been a huge family with containing many genera (around 20), this family was divided by moving some genera to Anthosactinidae and Sicyonidae (see Table 4).

Therefore, Discoactinidae becomes the eighth family in the present study. (Though WoRMS [43] also contains Halcampilactidae Appellöf, 1896 in this superfamily, the taxonomic position is doubted [14]).

Reconsidering of the diagnosis of superfamily Actinostoloidea.

As mentioned above, the number of families in Actinostoloidea has rapidly increased. As to the taxonomic change, discussing the diagnostic features of this superfamily is necessary.

Table 4. Comparison of Discoactinidae fam. nov., Capneidae, and the other six families of superfamily Actinostoloidea.

		Discoactinidae fam. nov.	Capneidae Gosse, 1860	Actinostolidae Carlgren, 1932	Anthosactinidae Sanamyan, Sanamyan, Galkin, Ivin, and Bocharova, 2021
Type genus		<i>Discoactis</i> gen. nov.	<i>Capnea</i> Forbes, 1841	<i>Actinostola</i> Verrill, 1879	<i>Anthosactis</i> Danielssen, 1890
The other genera		None	<i>Actinoporus</i> Duchassaing, 1850	<i>Antholoba</i> Hertwig, 1882 <i>Antiparactis</i> Verrill, 1899 <i>Bathydactylus</i> Carlgren, 1928 <i>Cnidanthus</i> Carlgren, 1927 <i>Glandulactis</i> Riemann-Zürneck, 1978 <i>Hadalanthus</i> Carlgren, 1956 <i>Ophiodiscus</i> Hertwig, 1882 <i>Paranthus</i> Andres, 1883 <i>Parasicyonis</i> Carlgren, 1921 <i>Pseudoparactis</i> Stephenson, 1920 <i>Pycnanthus</i> McMurrich, 1893 <i>Stomphia</i> Gosse, 1859 <i>Synsicyonis</i> Carlgren, 1921	Hormosoma Stephenson, 1918 Tealidium Hertwig, 1882
Characters	Number of macrocnemes in the first cycle	10	12	12	12
	Marginal sphincter muscle (origin)	Present but weak (mesogleal)	Present, strong (endodermal)	Present (mesogleal)	Present (mesogleal)
	Location of unequal mesenterial pairs	Ventrolateral mesenteries in first cycle	None	Third cycle or fourth cycle	Fourth cycle
	Remarks on a mesenterial developing rule	Original development	Following the general rule of Actiniaria	Generally following the “Actinostola rule”	
References		The present study	[5,15,16,38]	[4,5,10,14,43,44]	[14]
		Sicyonidae Hertwig, 1882	Exocoelactinidae Carlgren, 1925	Tetracoelactinidae Sanamyan, Sanamyan, Galkin, Ivin, and Bocharova, 2021	Halcampulactidae Gusmão, Berniker, Deusen, Harris, and Rodriguez, 2019
Type genus		<i>Sicyonis</i> Hertwig, 1882	<i>Exocoelactis</i> Carlgren, 1925	<i>Tetracoelactis</i> Sanamyan and Sanamyan, 2019	<i>Halcampulactis</i> Gusmão, Berniker, Deusen, Harris, and Rodríguez, 2019

Table 4. Cont.

The other genera		None	None	None	None
Characters					
	Number of macrocnemes in the first cycle	12	12	12	8
	Marginal sphincter muscle (Origin)	Absent -	Present (mesogleal)	Present (mesogleal)	Absent -
	Location of unequal mesenterial pairs	Equal	After the third cycle	Second and third cycles	Lateral mesenteries in the first cycle
	Remarks of mesenterial developing rule		Following to “Exocoelactis rule”		(same as Edwardsiidae)
References		[14]	[4,41]	[14,37]	[12]

Now, among Actinostoloidea, there is only one characteristic feature that diagnoses this superfamily: “generally having unequally developed mesenterial pairs”. This feature apparently characterizes the “Actinostola rule” in Actinostolidae and Anthosactinidae and “Exocoelactis rule” in Exocoelactinidae, which also have rarely been observed in the other families in Actinostoloidea: first cycle of *Halcampulactis* [12], one pair of perfect mesenteries in Sicyonidae, and one of the second pair of Tetracoelactinidae [14]. In the present study, the ventrolateral pairs of *Discoactis* also follow this diagnosis (Figure 3). However, based on our observations, Capneidae anemones never have this character at all, at least in the adult phase (Figure 5).

Then, it is also possible that Actinostoloidea is characterized by bilateral symmetry, as Sanamyan et al. (2021) [14] discussed. According to them, biradial symmetry may be the plesiomorphy of sea anemones and bilateral symmetry might be derived in sea anemones. The unequal mesenterial pairs which represent this superfamily can frequently clarify dorsal–ventral (D–V) axis: for example, the lateral first cycle mesenterial pairs of *Discoactis tritentaculata* and *Halcampulactis solimar* [12], which do not develop equally, can help us to distinguish the dorsal and ventral sides. In addition, anemones of Exocoelactinidae [4,41], Sicyonidae, and Tetracoelactinidae [14] can be distinguished the D–V axis. However, we cannot ensure that Capneidae, in which unequal mesenterial pairs are absent, shows bilateral symmetry or not, at least based on our materials. Moreover, there are species in which the mesenterial arrangement represents not bilateral but biradial symmetry in Actinostolidae, at least in the genus *Stomphia* [5]. Therefore, it is not favorable to define this superfamily by a bilateral symmetric mesenterial arrangement as the diagnostic character.

In conclusion, we can conclude that there is an exceptional group even the most prominent character that generally represents this superfamily. In other words, the last character by which superfamily Actinostoloidea was characterized has now disappeared. Based on those results, we now have revised the diagnosis again to accommodate those families and Discoactinidae fam. nov., as described below.

Superfamily Actinostoloidea Carlgren, 1932 [10]

Diagnosis (after Gusmão and Rodríguez (2021) [42] with editions in **bold**). Enthemonaes with **or sometimes without** basilar muscles, a mesogleal **or endodermal** marginal sphincter and no acontia or acontiods; rarely lacking basilar muscles and marginal sphincter muscle. Aboral end mostly flat and adherent; sometimes with physa. Column usually smooth; rarely with cuticles and rows of tubercles. Mesenteries **often differentiated but sometimes not differentiated** into macro- and microcnemes. Mesenteries of same pair often unequally developed: **sometimes they only existing in juvenile stage or completely absent, depending on the families**. Retractors usually diffuse weak or strong, sometimes circumscribed, **pinnate**. Cnidom: gracile spirocysts, basitrichs, holotrichs, *b*-mastigophores, and *p*-mastigophores A.

Included families. Actinostolidae; Exocoelactinidae; Halcampulactidae; Anthosactinidae; Tetracoelactinidae; Sicyonidae; **Capneidae; Discoactinidae fam. nov.**

See Table 4 for a comparison of all current families included in the suborder Actinostoloidea.

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