Doctoral Dissertation

博士論文

Taxonomy and Phylogeny of Anenthemonae (Cnidaria: Anthozoa: Actiniaria)

（変型イソギンチャク亜目（刺胞動物門：花虫綱：イソギンチャク目）の系統分類学的研究）

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Department of Biological Sciences, Graduate School of Science,
The University of Tokyo

東京大学大学院理学系研究科生物科学専攻

Takato Izumi

泉　貴人

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Abstract

Sea anemones are a well-known group of marine animals belonging to Actiniaria, one of the largest orders of the class Anthozoa of the phylum Cnidaria with approximately 1100 species, in 264 genera within 50 families. Although there have been many species described, the taxonomy and phylogeny of sea anemones are both still in need of research because there are few morphological taxonomic characters known from their soft flexible bodies. Additionally, there is still no reliable molecular marker for phylogenetic analyses due to the slow evolutionary rates of both the mitochondrial and nuclear genomes. These numerous problems have hampered the taxonomic and phylogenetic research of sea anemones.

The first comprehensive classification system of the order Actiniaria was proposed by Oskar Carlgren in 1949. This system had been used until recently, but the latest comprehensive molecular phylogenetic analyses in 2014 suggested this classification did not reflect the actual phylogeny. Subsequently, the classification system of sea anemones was thoroughly revised, and Actiniaria was classified into two suborders, Enthemonae and Anenthemonae. The suborder Anenthemonae consisted of two superfamilies, Actinernoidea and Edwardsioidea, and the latter superfamily was composed of only one family, Edwardsiidae. Species of Edwardsiidae have particular worm-like bodies and burrow into substrates. Anatomically, Edwardsiidae are strongly characterized by having only eight perfect mesenteries in the first mesenterial cycle even as adults, whereas almost all other actiniarians have twelve perfect mesenteries in the first mesenterial cycle.

Though the family Edwardsiidae is one of the most diverse taxa in the order Actiniaria and includes approximately 85 species of 11 genera, the knowledge of the fauna of this family in Japan is still poor: only ten species of four genera have been recorded from Japan. However, no comprehensive taxonomic survey has been conducted, and hence the number of edwardsiid species and genera present in Japan could be greater than that recorded. Moreover, Edwardsiidae is also considered by taxonomic researchers to be an important group for evaluating the evolution of Anenthemonae and Actiniaria as they are considered to retain ancestral characters of sea anemones. They have one of the simplest body plans in Actiniaria: worm-like bodies, fewer numbers of tentacles, and absence of several muscles and basal discs.

Especially, the peculiar arrangement of only eight perfect mesenteries (macrocnemes) in the first mesenterial cycle has been traditionally regarded as a trace of an ancestral character among actiniarians because the development of all actiniarians involves a stage with a similar mesenterial arrangement to this family. This traditional hypothesis has been challenged recently by some taxonomists advocating that the simplified mesenterial arrangement of Edwardsiidae may be derived in the secondary adaptation to the infaunal life. However, no reliable study has been conducted to determine whether the species of Edwardsiidae retain the ancestral features of the order Actiniaria or have derived them from the secondary adaptation, because all preceding studies have examined only a few species of Anenthemonae.

In this study, I conducted comprehensive and wide sampling from Japanese waters and collected over 250 specimens of Anenthemonae. I identified 47 species, including 33 previously undescribed ones, in 15 genera. Six genera of Edwardsiidae were newly recorded in Japan.

Based on phylogenetic analyses using sequences of mitochondrial 12S and 16S rDNA, cytochrome oxidase III (COXIII) DNA, nuclear 18S, 5.8S, and 28S rDNA and internal transcribed spacers (ITS) 1and 2 DNA, I drastically revised the classification for Anenthemonae: Anenthemonae was rearranged to be monophyletic by excluding some species of the genus *Metedwardsia* (of Edwardsiidae), instead including *Halcampella maxima* and some similar species (of Halcampidae). In the suborder Anenthemonae, I classified the species into three monophyletic superfamilies, Actinernoidea, Edwardsioidea, and Halcampelloidea, the third superfamily of this suborder. In Actinernoidea, two families Actinernidae and Halcuriidae turned out to be para- and polyphyletic respectively, and thus I rearranged the inner classification of this superfamily by establishing the family Isactinernidae, into which *Isactinernus* and *Synhalcurias* were placed, and a new genus *Isohalcurias* to solve the paraphyly of Halcuriidae. In the superfamily Edwardsioidea, which included only one family Edwardsiidae, the genera *Edwardsia*, *Edwardsianthus, Paraedwardsia, Scolanthus,* and *Isoscolanthus* were included in a large monophyletic clade. Following the phylogeny, I synonymized the five genera into *Edwardsia* as species in these genera all had nemathybomes, the most characteristic features on the surfaces of edwardsiids. In addition, the genus *Tempuractis* was established in the superfamily Edwardsioidea. In the superfamily Halcampelloidea, *Halcampella maxima* and some similar species previously classified in the family Halcampidae were placed. However, the family Halcampidae was within Enthemonae; thus, I established a new family Halcampellidae for the species belonging to the new clade of Anenthemonae and two new genera *Hexactis* and *Pseudoedwardsia* in this family.

According to this study, there are now 11 species and six genera in three families of Actinernoidea, 36 species and five genera in family Edwardsioidea, and four species of three genera in family Halcampelloidea. In conclusion, my study revealed the diversity of Japanese Anenthemonae as 51 species, 14 genera, and five families in three superfamilies.

Several evolutionary trends of Anenthemonae were estimated from the constructed phylogenetic trees in the present study. Actiniarian taxa consisting of simplified worm-shaped species have evolved several times from the general columnar-shaped ancestral taxa in Actiniaria. The simple morphology of Edwardsiidae is estimated to have gradually evolved in the lineage of Anenthemonae in two steps: first, the body was transformed to the worm-like shape in the common ancestor of Edwardsioidea and Halcampelloidea, and later the basal disc and four of eight macrocnemes degenerated in the lineage of Edwardsiidae. Thus, my study indicated that the worm-like simple body of Edwardsiidae was derived by an adaptation, and thus settled the dispute concerning the morphology of edwardsiids that had continued for a century. In addition, this study showed that nemathybomes were acquired monophyletically in the lineage of the genus *Edwardsia*. The protective function of nemathybomes was suggested by this study; hence, they would be advantageous to the anemones of *Edwardsia*. The species of this genus would become more adaptive for the burrowing lifestyle by nemathybomes, and thus might have remarkably diverged and consequently occupied approximately 87% of species number in Edwardsiidae and even 70% in Anenthemonae.

Introduction

Taxonomic history of the order Actiniaria

Sea anemones are a well-known marine animal group distributed broadly in the world oceans. They belong to the order Actiniaria Hertwig, 1882 of the class Anthozoa of the phylum Cnidaria. Actiniaria currently accommodates approximately 1100 valid species from 264 genera of 50 families (Fautin, 2016).

All sea anemones are free-living individual polyps, although other anthozoans often form colonies of zooids. They are classified into diploblastic animals, and their bodies are composed of only soft tissues in three layers—ectoderm, endoderm, and mesoglea. The mesoglea consists of gelatinous substitution and works as muscles or gonads although it is not a layer of cells like the mesoderm of triploblastic animals (Yanagi, 2019). Thus, their bodies are flexible and can be deformed by habitat effects (Titus et al., 2019). Sea anemones have only a few reliable taxonomic characters in the bodies (Fig. 1; see below in detail). Therefore, researchers have been puzzled by their taxonomy and have always struggled to correctly classify them by morphology (Yanagi, 2017). Taxonomists have mainly used two characters for the classification of sea anemones.

1. **Mesenterial arrangement**. Mesenteries are one of the most prominent structures in the bodies of sea anemones (Fig. 1B, C). They develop in the direction of the distal–proximal axis and separate the actiniarian coelenteron into partitions. Mesenteries are one of the most important tissues of sea anemones and play a role in supporting the actinopharynx and in the elongation and contraction of the body, digestion, and reproduction (Carlgren, 1949; Shick, 1991). The mesenteries are distinguished into two types: macrocnemes, which are usually distinct and develop several structures such as retractor muscles, gonads, and filaments (Fig. 1C); and microcnemes, which are small and without these structures (Shick, 1991; Yanagi, 2017).

   The mesenteries usually form pairs with one another and develop in a particular cyclic pattern (Fig. 2): first, eight macrocnemes are formed (Fig. 2A) and later another four macrocnemes develop (Fig. 2B). These 12 macrocnemes (mesenteries indicated as d, ld, lv, and v in Fig. 2B) are called "mesenteries in the first cycle." Subsequently, mesenteries of the second cycle develop between the mesenteries in the first cycle (Fig. 2C, D), and younger mesenteries continue to develop. These arrangements of mesenteries differ depending on species and genera and are thus considered as the important taxonomic characters of sea anemones. In general, the thicker and larger is the column of sea anemones, the more are the macrocnemes (Carlgren, 1949).

2. The shape of the aboral end. Most sea anemones have basal discs in their aboral ends (Figs. 1A, 3A, B). Basal discs are unique structure of actiniarians in the order Anthozoa. Actiniarians can adhere to hard substrates and creep on the surface owing to the movement of the basal discs. Sea anemones are the only free-living animals among anthozoans with basal discs (Uchida and Soyama, 2001). However, several species do not have basal discs (instead, the aboral end of the species become a rounded physa; Fig. 3C, D). Thus, researchers have considered that the basal disc is a derived character obtained during the lineage of sea anemones (Carlgren, 1949).

In addition to these difficulties in taxonomic classification, sea anemones also have a serious problem in molecular phylogeny: still no reliable molecular marker that critically reflects their evolution exists because of the slow evolutionary rates of the mitochondrial and nuclear genomes of cnidarians, and thus useful molecular phylogeny methods are not yet available (Daly et al., 2010). These problems in taxonomy and phylogeny have hampered the research on sea anemones, and thus almost all taxa in the order Actiniaria can be said as problematic.

Although the taxonomy of sea anemones has been investigated since the 18th century (e.g., *Actinia equine* Linnaeus, 1766), only in the middle of the 20th century that the first comprehensive classification system of the order Actiniaria was established by Oskar Carlgren. Carlgren (1949) revised the classification for all species that had been recorded (the left side of Table 1). In this classification of Actiniaria, he regarded the two prominent characters mentioned above as the most important for classifying the higher rank of taxonomy: he classified all species of Actiniaria into three suborders by the mesenterial arrangements and tribes under the suborder on the basis of the presence basal discs (Carlgren, 1949).

This classification system has been used for over 60 years (e.g., Uchida, 1992; Sebens, 1998; Häussermann, 2009). However, recent studies of molecular phylogenetic analyses suggested that this classification did not reflect the phylogeny (Daly et al., 2008, Rodríguez and Daly, 2010; Rodríguez et al., 2012). In 2014, the group of Estefania Rodríguez conducted the most comprehensive molecular analysis of Actiniaria by including all higher taxa in the classification system of Carlgren (Rodríguez et al., 2014). This study concluded that the classification system of Carlgren did not accurately reflect the phylogeny, and hence thoroughly revised the classification system of the order Actiniaria. Rodríguez et al. (2014) rearranged the higher taxa of Actiniaria into several superfamilies and suborders (the right side of Table 1).

The two suborders suggested by Rodríguez et al. (2014), on the basis of molecular phylogeny, were supported mainly by mesenterial arrangements. First, Actiniaria was classified into two suborders, Enthemonae Rodríguez and Daly, 2014 and Anenthemonae Rodríguez and Daly, 2014. The suborder Enthemonae consisted of almost all (94%; Fautin, 2016) actiniarian families, to which species with the general mesenterial arrangement (Fig. 2D) belonged. Conversely, the suborder Anenthemonae included only three families in two superfamilies, Edwardsioidea Andres, 1881 and Actinernoidea Stephenson, 1922. They were characterized by "unique" mesenterial arrangements (Fig. 2A, C; see below for the detailed characteristics of each suborder), and the species of these superfamilies were minor in comparison to the species of Enthemonae: fewer than 100 nominal species were accommodated (Tables 2, 3).

The classification system of Rodríguez et al. (2014) is currently used in the taxonomy of sea anemones (e.g., Brandão et al., 2019). However, this classification system also has some taxonomic problems. The taxon sampling in Rodríguez et al. (2014) was still insufficient: their phylogenetic analysis lacked several families (indicated by stars in Table 1) as well as many genera. In particular, for suborder Anenthemonae, Rodríguez et al. (2014) and preceding phylogenetic studies (Daly et al., 2008, Rodríguez and Daly, 2010; Rodríguez et al., 2012) examined only a few taxa. Thus, phylogenetic studies on Anenthemonae are not sufficient yet. Hence, phylogenetic analyses with comprehensive taxon sampling in each lower taxa are required to reveal the exact phylogeny of Anenthemonae.

Classification and evolution of the suborder Anenthemonae

In this study, I mainly focused on the suborder Anenthemonae and two superfamilies Actinernoidea and Edwardsioidea.

The superfamily Actinernoidea was reestablished by Rodríguez et al. (2014). This superfamily also shares the peculiar mesenterial arrangement: mesenteries of the second and younger mesenterial cycles originate in the endocoels in the first cycle (Fig. 2C); in contrast, in all other anemones of Enthemonae, these mesenteries develop in exocoels (Fig. 2D). In addition, some species are characterized by the presence of nematocyst batteries and spirocysts on their columns. At present, Actinernoidea includes two families: Actinernidae Stephenson, 1922 and Halcuriidae Carlgren, 1918. They are distinguished by the number of siphonoglyphs attached to the actinopharynx (two for Actinernidae and one for Halcuriidae) and the number of macrocnemes (20 for Halcuriidae and more for Actinernidae). Originally, in the classification by Carlgren (1949), Actinernidae and Halcuriidae were accommodated in the suborder Endocoelantheae Carlgren, 1925 because of the peculiar mesenterial arrangement, which has been traditionally regarded as the most important characters for the classification of Actiniaria. This classification was used in the subsequent studies (Fautin and den Hartog, 2003; Uchida, 2004, 2007), until recently. However, Rodríguez et al. (2014) revealed that Endocoelantheae was closely related to the family Edwardsiidae of the suborder Anenthemonae on the basis of molecular phylogeny and concluded that Endocoelantheae was a part of the suborder Anenthemonae. Thus, they maintained the lower taxon of Anenthemonae, accommodating Actinernidae and Halcuriidae, by reviving the superfamily Actinernoidea Stephenson, 1922. At present, both families are treated as members of the superfamily Actinernoidea of the suborder Anenthemonae.

Actinernoidea had relatively rich diversity in Japan: four species of four genera of Actinernidae and three species of *Halcurias* of Halcuriidae have been reported (Table 3; Uchida, 2004; Uchida, 2007). However, a taxonomic problem still exists: two of the three species of *Halcurias* are considered invalid as nomen dubium (Fautin, 2016; Yanagi, 2017; indicated by white stars in Table 3).

The superfamily Edwardsioidea, also reestablished by Rodríguez et al. (2014), consisted of only one family, Edwardsiidae Andres, 1881. Species of Edwardsiidae are generally characterized by worm-like bodies, and the species of some genera of this family are known to have nemathybomes—the pocket-like structures that contain very large nematocysts—on their body walls (see Figs. 55A, 56A, for example; Daly, 2002a). This family has been diagnosed as having only eight macrocnemes in the first mesenterial cycle even in adults (Fig. 2A) by Carlgren (1949), whereas almost all other actiniarians have twelve macrocnemes in their first cycle (Fig. 2B–D). This family was a comparatively large group in the order Actiniaria and currently accommodates 78 nominal species (Table 2; Williams, 1981; Fautin, 2013, 2016). However, unlike Actinernoidea, the fauna of this superfamily in Japan has not been researched sufficiently: only 10 species of edwardsiids from four genera have been recorded from Japan (Table 2; Uchida, 1965; Uchida and Soyama, 2001; Yanagi, 2006; Sanamyan and Sanamyan, 2012). Of these, the morphology of only five species has been described by taxonomic studies (indicated by black stars in Table 2; Yanagi, 2006; Sanamyan and Sanamyan, 2012); however, some of those descriptions were incomplete [e.g., information about the cnidom of *Metedwardsia akkeshi* (Uchida, 1932) was absent]. Descriptions of the other five species were restricted to field guidebooks and lacked precise morphological information (white stars in Table 2; Uchida, 1965; Uchida and Soyama, 2001). Because of the difficulty of species identification owing to the scarce taxonomic characters, many species of Edwardsiidae distributed in Japan might have not yet been identified (Yanagi, 2017), and future studies were needed to understand the fauna of Japanese Edwardsiidae.

The family Edwardsiidae has been considered as the key taxon to evaluate the evolution of Actiniaria. Edwardsiid anemones have the simplest mesenterial arrangement with only eight macrocnemes even in adults (Fig. 2A), and this arrangement has long been regarded as an ancestral character among actiniarians (McMurrich, 1891; Hyman, 1940; Uchida and Soyama, 2001; reviewed in Daly, 2002a). This was because all sea anemones were known to show the same mesenterial arrangement as that in edwardsiids during their developments (Fig. 2A): this stage was named as "edwardsia-stage" (Duerden, 1899; Yanagi, 2017). However, this hypothesis has been challenged by several recent studies (Manuel, 1981a; Daly et al., 2002): they suggested that simplified mesenterial arrangement of this family may be derived from the secondary adaptation to infaunal life. Recently, Rodríguez et al. (2014) conducted a molecular phylogenetic study and suggested that the edwardsiid arrangement with eight macrocnemes was not ancestral but derived from the secondary adaptation. However, even Rodríguez et al. (2014), who has conducted the most comprehensive phylogenetic study of Edwardsiidae so far, included only five edwardsiid species of three genera; therefore, they could not address the detailed phylogeny of Anenthemonae as mentioned above. Thus, whether the peculiar morphology of Edwardsiidae was the trace of an ancestral feature or a secondly derived feature is not yet certain. Hence, the comprehensive taxonomic sampling of both superfamilies is required to discuss the phylogenetic matters.

Aims of this study

This is the first study to focus on and treat the comprehensive taxonomy and evolution of Anenthemonae, the minor and indeterminate suborder of Actiniaria. In this dissertation, the following research themes have been discussed:

1. Discovering as many species of Anenthemonae as possible and clarifying the diversity of Anenthemonae in Japan. I observed the detailed morphology of the collected specimens, specifically identified them, and provided their detailed descriptions. This study becomes the first elucidation of the Japanese fauna of Anenthemonae.
2. Establishing the systematics of Anenthemonae using molecular phylogeny with sufficient taxon sampling. I adopted a new DNA marker in addition to the traditional ones for analyzing actiniarians and inspected the detailed phylogeny of Anenthemonae.
3. Discussing about the evolution of Anenthemonae based on molecular phylogeny and morphological features. I evaluated the ancestral and derived morphological characters of the mesenterial arrangements and basal discs and estimated the evolution and diversification of Anenthemonae based on these morphological features. Finally, I tested the traditional hypothesis that the peculiar worm-like form of Edwardsiidae was the trace of an ancestral feature in Actiniaria.

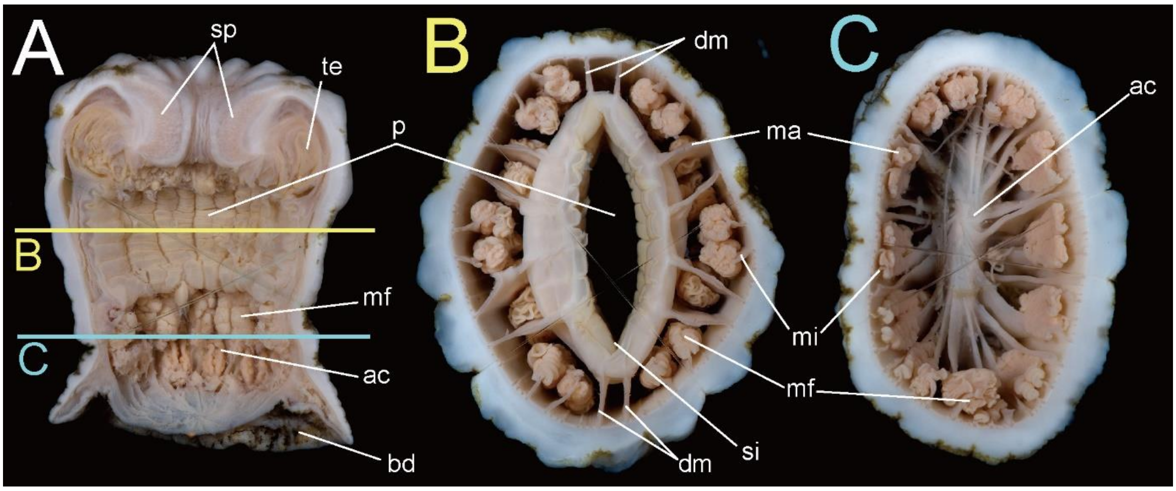


Fig. 1. The representative morphological characters of Actiniaria (gross sections of Hormathiidae sp.).

A. Longitudinal gross section. Tentacles are contracted. B. Transverse section of the upper column (the sectioning site is indicated in 1A). C. Transverse section of the lower column (the sectioning site is indicated in 1A). Abbreviations: ac, acontia; bd, basal disc; dm, directive macrocneme; ma, macrocneme; mf, filament; mi, microcneme; p, actinopharynx; si, siphonoglyph; sp, sphincter muscle; te, tentacle. Photo courtesy of Kensuke Yanagi.

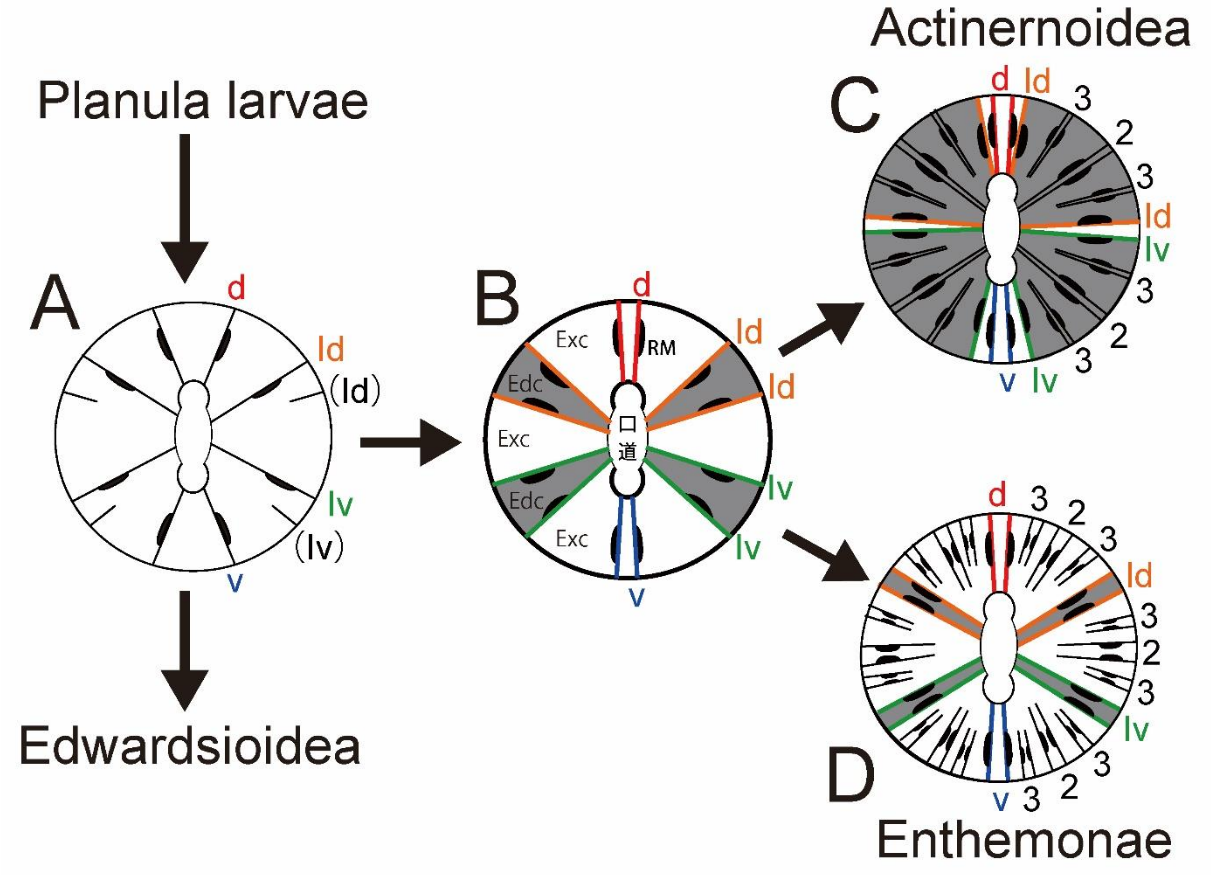


Fig. 2. Schematic diagram of the development of mesenterial arrangement.
All diagrams show the mesenterial arrangements in transversal sections. Arrows show the order of developments. A. The stage with eight macrocnemes in the first mesenterial cycle. The species of Edwardsiidae have this arrangement even in adults; B. The stage with 12 macrocnemes in six pairs. All macrocnemes of this stage are in the first mesenterial cycle; C, D: the arrangements at more developed stages. C. The arrangement of Actinernoidea. D. The arrangement of general Enthemonae. Abbreviations: d, dorsal directive (indicated in red); Edc, endocoel (in gray); Exc, exocoel (in white); ld, dorso-lateral mesentery (in orange); lv, ventro-lateral mesentery (in green); RM, retractor muscle; v, ventral directive (in blue); 2, mesenteries in the second cycle; 3, mesenteries in the third cycle. Revised from Yanagi (2017).

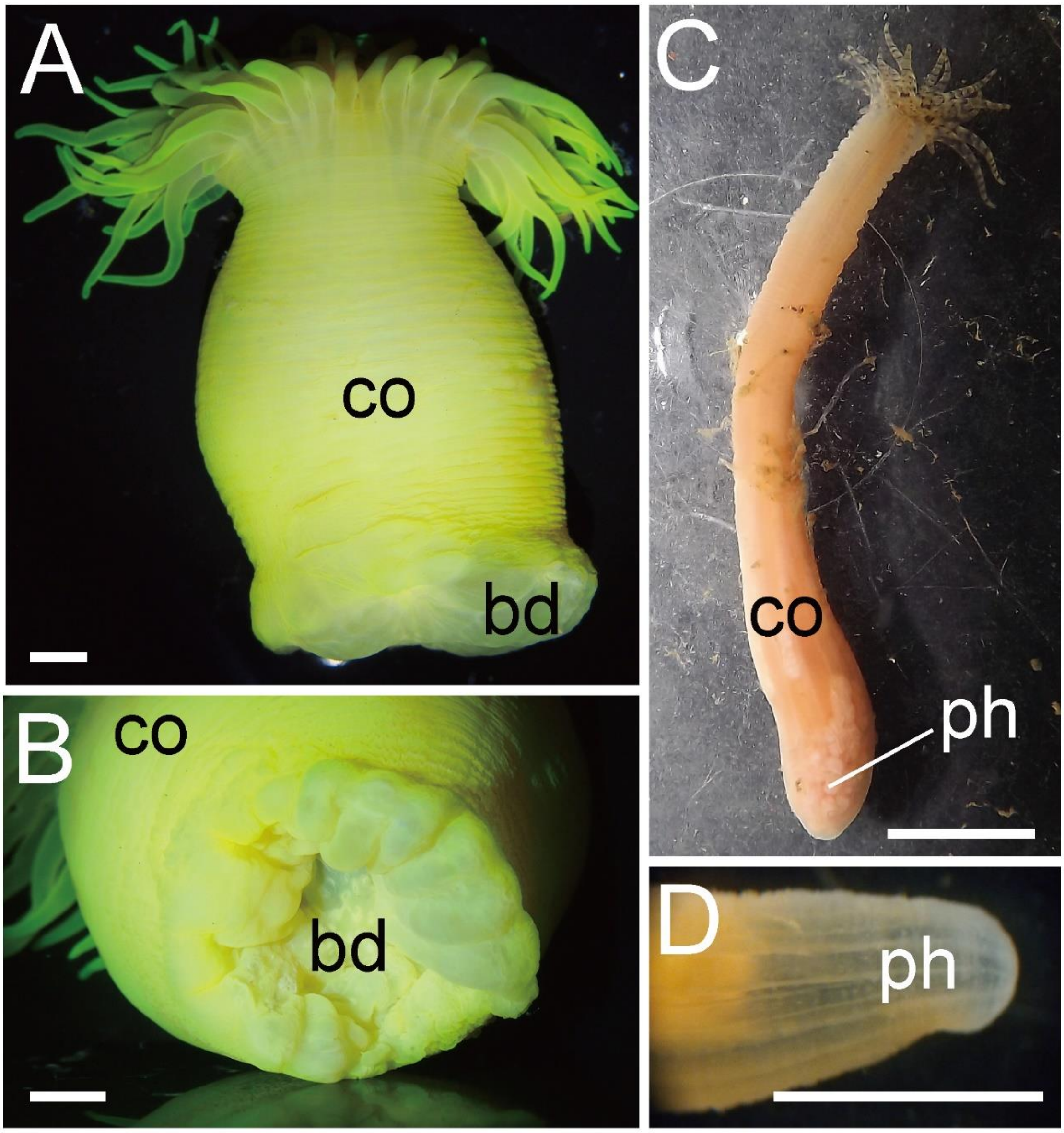
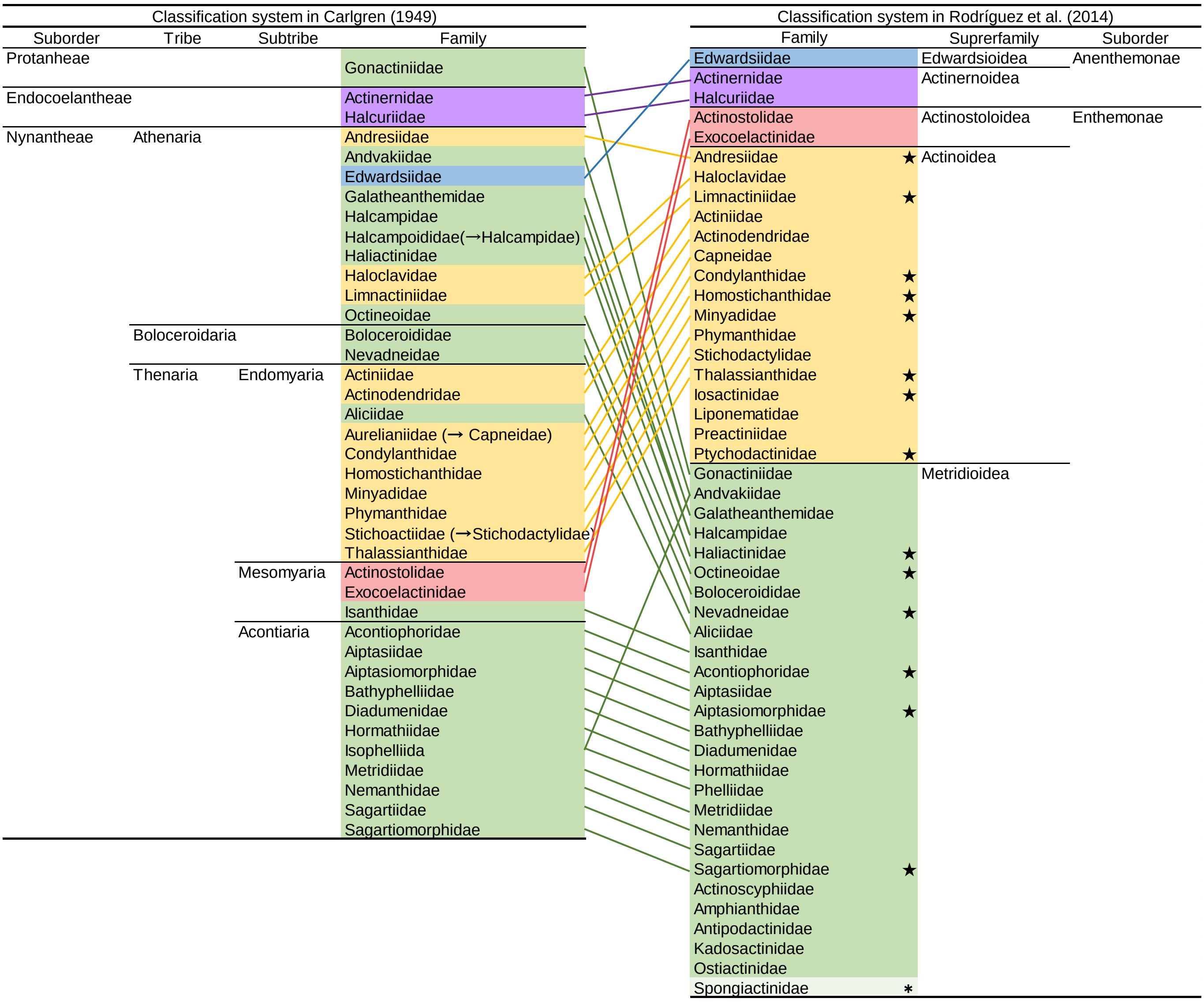


Fig. 3. The aboral ends of sea anemones.
A, B: a species with a basal disc (*Halcurias levis*). A. lateral view; B. aboral view. C, D: a species without the basal disc (*Metedwardsia akkeshi*). The aboral end becomes a rounded physa instead of the basal disc. C. lateral view; D. enlarged view of the aboral end. Abbreviations: bd, basal disc; co, column; ph, physa.

Table 1. Comparison of the classification system between Carlgren (1949) and Rodríguez et al. (2014).
Lines and colors indicate the correspondence of families between Carlgren (1949; left) and Rodríguez et al. (2014; right). Taxa indicated by stars are classified based on morphological features in Rodríguez et al. (2014) because of the absence of molecular data. This classification system reflects the changes after Rodríguez et al. (2014) eliminated four genera: Haliplanellidae Hand, 1956; Mimetridiidae Fautin, Eppard, and Mead, 1988; Oractinidae Riemann-Zürneck, 2000; Ramireziidae Fautin, Eppard, and Mead, 1988, which became invalid later (Fautin, 2016), and added Spongiactinidae, Sanamyan, Sanamyan, and Tabachnick, 2012 (Sanamyan et al., 2018; indicated by *).



Classification system in Carlgren (1949)			
Suborder	Tribe	Subtribe	Family
Protanheae			Gonactiniidae
Endocoelantheae			Actinernidae
			Halcuriidae
Nynantheae	Athenaria		Andresiidae
			Andvakiidae
			Edwardsiidae
			Galatheanthemidae
			Halcampidae
			Halcampoididae(→Halcampidae)
			Haliactinidae
			Haloclavidae
			Limnactiniidae
			Octineoidae
	Boloceroidaria		Boloceroididae
			Nevadneidae
	Thenaria	Endomyaria	Actiniidae
			Actinodendridae
			Aliciidae
			Aurelianiidae (→ Capneidae)
			Condylanthidae
			Homostichanthidae
			Minyadidae
			Phymanthidae
			Stichoactiidae (→Stichodactylidae)
			Thalassianthidae
		Mesomyaria	Actinostolidae
			Exocoelactinidae
			Isanthidae
		Acontiaria	Acontiophoridae
			Aiptasiidae
			Aiptasiomorphidae
			Bathyphelliidae
			Diadumenidae
			Hormathiidae
			Isophelliida
			Metridiidae
			Nemanthidae
			Sagartiidae
			Sagartiomorphidae

Classification system in Rodríguez et al. (2014)		
Family	Suprerfamily	Suborder
Edwardsiidae	Edwardsioidea	Anenthemonae
Actinernidae	Actinernoidea	
Halcuriidae		
Actinostolidae	Actinostoloidea	Enthemonae
Exocoelactinidae		
Andresiidae ★	Actinoidea	
Haloclavidae		
Limnactiniidae ★		
Actiniidae		
Actinodendridae		
Capneidae		
Condylanthidae ★		
Homostichanthidae ★		
Minyadidae ★		
Phymanthidae		
Stichodactylidae		
Thalassianthidae ★		
Iosactinidae ★		
Liponematidae		
Preactiniidae		
Ptychodactinidae ★		
Gonactiniidae	Metridioidea	
Andvakiidae		
Galatheanthemidae		
Halcampidae		
Haliactinidae ★		
Octineoidae ★		
Boloceroididae		
Nevadneidae ★		
Aliciidae		
Isanthidae		
Acontiophoridae ★		
Aiptasiidae		
Aiptasiomorphidae ★		
Bathyphelliidae		
Diadumenidae		
Hormathiidae		
Phelliidae		
Metridiidae		
Nemanthidae		
Sagartiidae		
Sagartiomorphidae ★		
Actinoscyphiidae		
Amphianthidae		
Antipodactinidae		
Kadosactinidae		
Ostiactinidae		
Spongiactinidae *		

Table 2. Nominal genera and species of Edwardsiidae in the world and distribution record in Japan.
Species with black stars were recorded in Japan by taxonomical literatures (Carlgren, 1931; Stimpson, 1856; Sanamyan and Sanamyan, 2012; Uchida, 1932a), and species with white stars were reported only in field guidebooks (Uchida, 1965; Uchida and Soyama, 2001).

Species	Original description	Japan	Species	Original description	Japan
Edwardsia andresi	Danielessen (1890)		*Drillactis leucomelas*	Parry (1951)	
Edwardsia annamensis	Carlgren (1943)		*Drillactis pallida*	Verrill (1880)	
Edwardsia arctica	Carlgren (1921)				
Edwardsia athalyei	England (1990)		*Edwardsianthus gilbertensis*	Carlgren (1931)	☆
Edwardsia beautempsii	de Quatrefages (1842)		*Edwardsianthus pudica*	Klunzinger (1877)	☆
Edwardsia californica	McMurrich (1913)				
Edwardsia capensis	Carlgren (1938)		*Edwardsiella andrillae*	Daly et al. (2013)	
Edwardsia carlgreni	Carlgren (1921)		*Edwardsiella carnea*	Gosse (1856)	
Edwardsia claparedii	Panceri (1869)		*Edwardsiella ignota*	Carlgren (1959)	
Edwardsia danica	Carlgren (1921)		*Edwardsiella janthina*	Andres (1881)	
Edwardsia delapiae	Carlgren and Stephenson (1928)		*Edwardsiella lineata*	Verrill (1873)	
Edwardsia duodecemtentaculata	Carlgren (1931)		*Edwardsiella loveni*	Carlgren (1892)	
Edwardsia elegans	Verrill (1869)				
Edwardsia finmarchica	Carlgren (1921)		*Isoscolanthus iemanjae*	Brandão et al. (2019)	
Edwardsia fusca	Danielessen (1890)		*Isoscolanthus janainae*	Brandão et al. (2019)	
Edwardsia handi	Daly and Ljubenkov (2008)				
Edwardsia hantuensis	England (1987)	☆	*Halcampogeton papillosus*	Carlgren (1937)	
Edwardsia islandica	Carlgren (1921)				
Edwardsia ivelli	Manuel (1975)		*Metedwardsia akkeshi*	Uchida (1932)	★
Edwardsia japonica	Carlgren (1931)	★			
Edwardsia jonesii	Seshaiya and Cuttress (1969)		*Nematostella nathorstii*	Carlgren (1921)	
Edwardsia juliae	Daly and Ljubenkov (2008)		*Nematostella polaris*	Carlgren (1921)	
Edwardsia kameruniensis	Carlgren (1927)		*Nematostella vectensis*	Stephenson (1935)	
Edwardsia longicornis	Carlgren (1921)				
Edwardsia maroccana	Carlgren (1931)		*Paraedwardsia abyssorum*	Carlgren (1951)	
Edwardsia mcmurrichi	Daly and Ljubenkov (2008)		*Paraedwardsia arenaria*	Nordgaard (1905)	
Edwardsia meridionalis	Williams (1981)		*Paraedwardsia cretata*	Stimpson (1856)	★
Edwardsia migottti	Gusmão et al. (2016)		*Paraedwardsia hadalis*	Sanamyan and Sanamyan (2018)	
Edwardsia neozelanica	Farquhar (1898)		*Paraedwardsia heia*	Daly and Ljubenkov (2008)	
Edwardsia norvegica	Carlgren (1942)	☆	*Paraedwardsia lemchei*	Carlgren (1956)	
Edwardsia octoradiata	Carlgren (1931)	★	*Paraedwardsia sarsii*	Dueben and Koren (1847)	
Edwardsia olguini	Daly and Ljubenkov (2008)				
Edwardsia profunda	Daly and Ljubenkov (2008)		*Scolanthus armatus*	Carlgren (1931)	
Edwardsia sanctaehelenae	Carlgren (1941)		*Scolanthus callimorphus*	Gosse(1853)	
Edwardsia sipunculoides	Stimpson (1853)	☆	*Scolanthus crypticus*	Brandão et al. (2019)	
Edwardsia sojabio	Sanamyan and Sanamyan (2012)	★	*Scolanthus curacaoensis*	Pax (1924)	
Edwardsia sulcata	Verrill (1864)		*Scolanthus ignotus*	Carlgren (1920)	
Edwardsia timida	de Quatrefages (1842)		*Scolanthus ingolfi*	Carlgren (1921)	
Edwardsia tinctrix	Annandale (1915)		*Scolanthus intermedius*	McMurrich (1893)	
Edwardsia tuberculata	Dueben and Koren (1847)		*Scolanthus nidarosiensis*	Carlgren (1942)	
Edwardsia vegae	Carlgren (1921)		*Scolanthus scamiti*	Daly and Ljubenkov (2008)	
Edwardsia vitrea	Danielessen (1890)		*Scolanthus triangulus*	Daly and Ljubenkov (2008)	
Edwardsia vivipara	Carlgren (1950)				
			Synhalcampella ostroumowi	Wyragévitch (1905)	

Table 3. Nominal genera and species of Actinernidae in the world and distribution record in Japan. Species with black stars have been recorded in Japan (Carlgren, 1908; Hertwig, 1882; McMurrich, 1901; Wassilieff, 1908; Uchida, 2004).

Species	Original discription	Japan	Species	Original description	Japan
Halcuriidae			Actinernidae		
Halcurias capensis	Carlgren (1928)		*Actinernus elongatus*	Hertwig (1882)	
Halcurias carlgreni	McMurrich (1901)	★	*Actinernus michaelsarsi*	Carlgren (1918)	
Halcurias endocoelactis	Stephenson (1918)		*Actinernus nobilis*	Verrill (1879)	
Halcurias mcmurrichi	Uchida (2004)		*Actinernus robustus*	Hertwig (1882)	★
Halcurias minimus	Carlgren (1928)				
Halcurias pilatus	McMurrich (1893)		*Isactinernus quadrilobatus*	Carlgren (1918)	★
Halcurias sudanensis	Riemann-Zürneck (1983)				
Halcurias levis	Uchida (2004)	★	*Synactinernus flavus*	Carlgren (1918)	★
Halcurias japonicus	Uchida (2004)	★			
			Synhalcurias elegans	Wassilieff (1908)	★
Carlgrenia desiderata	Stephenson (1918)				

Material and Methods

Sample collection and preservation

I collected approximately 250 specimens from Japanese waters (the exact number could not be determined because *Tempuractis* species were colonized and buried in host sponges and could not be accurately counted). Sampling localities of specimens are shown in Fig. 4. (Also see material examined for each species in Chapter 2). The specimens obtained in this study were collected by wading on seashore, snorkeling, scuba diving, dredging, or trawling by research vessels, fishing boats, or remotely operated vehicles (ROV). Some specimens attached to substrates were usually detached from the substrates using fingers or spatulas, but occasionally collected using pieces of substrates such as stones. Burrowing species were dug out using a shovel or sieve.

The collected specimens were generally preserved using several methods: if the specimens were sufficiently vigorous, they were kept alive in calm water in cases, aquaria, or tanks till they elongated their tentacle. Images *in vitro* were captured to record their external forms, colors, and sizes, especially of the oral disc. Subsequently, they were anesthetized using magnesium chloride solution. After they were completely anesthetized, small pieces of tissue for DNA analysis were dissected from their tentacles (of anemones in general forms) or from transversely dissected columns with filaments (in the case of worm-shaped anemones, e.g., species of Edwardsiidae) and preserved in 99% ethanol. Remaining polyps were fixed in 10%–20% (v/v) formalin sea water solution for morphological analyses. If the specimen were weakened, they were not anesthetized and immediately preserved in the same way as mentioned above. Occasionally, specimens were directly preserved in ethanol or formalin solution if they were seriously damaged or almost dead during sampling. Polyps fixed in formalin solution were immersed in 70% ethanol after they were completely preserved. For DNA analysis, I also obtained tissues of tentacles from some living polyps in several aquariums and preserved them in 99% ethanol.

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

Observation of type specimens

Some type specimens were observed in the museums in which they had been deposited: Museum of Zoology, Lund University (MZLU); Museum of Evolution Zoology, Uppsala University (UUZM); the Zoological Museum, University of Copenhagen (ZMUC); and the Natural History Museum, London (BM). The type specimens were photographed, and their external and gross internal morphological characters were examined.

Ecological observation in aquaria

Some anemones were kept in laboratory tanks of several aquariums and institutions to observe their behavior. *Antennapeachia setouchi* Izumi and Yanagi, 2016 was observed in the Seto Marine Biological Station, Kyoto University, and CMNH, Chiba; *Tempuractis rinkai* Izumi, Ise and Yanagi, 2018 was observed in Toba Aquarium; and *Synactinernus flavus* Carlgren, 1918 and *Synactinernus churaumi* Izumi and Fujii, 2019 were observed in Okinawa Churaumi Aquarium.

Morphological observation and preparation of histological sections

Morphological observations were performed on external and internal characteristics, as shown in Fig. 5A, B. (Although Fig. 5 shows Edwardsiidae as an example, the morphological characters I observed were generally common among all specimens of Actiniaria except nemathybomes.)

Preserved polyps were dissected to obtain some tissues for histological sectioning after their external morphological characters were observed. The dissected tissues were then dehydrated by ethanol and cleared in xylene, embedded in paraffin, sliced into serial sections (7–10 µm thick) by using a microtome, mounted on glass slides, and stained with hematoxylin and eosin (HE). The method of HE staining was based on Presnell and Schreibman (1997), but the staining or washing times were as those for sea anemones: the thicker was the mesoglea of the sea anemones, the longer I stained them in HE. Sections were mounted on slide glasses. Finally, anatomies of several internal features were observed using a conventional microscope.

In this study, I referred to the terminology by Carlgren (1949), Daly (2015), and Yanagi (2007) for the morphology of sea anemones.

Observation of cnidae

The cnidae of the tentacle, actinopharynx, column, and mesenterial filament were usually observed (Fig. 5C). The cnidae of acrosphere (of some species of Haloclavidae), special tentacle (of some species of *Antennapeachia*), or nemathybome (of some species of Edwardsiidae) were also observed additionally in specific anemones. Tissues from every part were placed on glass slides and mounted using 50% (v/v) glycerin–sea water. Images of the cnidae were obtained using a differential interference contrast microscope, generally following the method of Yanagi et al. (2015). The lengths and widths of the cnidae were measured using software ImageJ ver. 1.49 (Rasband, 1997–2012). I followed Mariscal (1974) for the nomenclature of the cnidom.

PCR and DNA sequences

DNA was extracted from each tissue that was preserved in 99% ethanol by using ChargeSwitch gDNA Micro Tissue Kit (Invitrogen). In addition, some tissue samples for DNA were processed following the guanidine extraction protocol (Sinniger et al., 2010). PCR amplifications were performed in 10 μL (or 25 μL) reaction volume, consisting of 0.4 (1.0) μL of 25 μM forward and reverse primers, 2.0 (5.0) μL of EmeraldAmp PCR Master Mix (TaKaRa), and 3.4 (8.5) μL of distilled water. For PCR amplifications, three mitochondrial markers—12S, 16S rDNA, and cytochrome oxidase III (COXIII)—and three nuclear markers—18S and 28S rDNA and internal transcribed spacers (ITS) 1 and 2 with 5.8S rDNA. The primers and amplification conditions are shown in Table 5. I newly adopted the ITS1/ITS2 marker with 5.8S rDNA and used the method of amplification from preceding studies for other phyla (Heath et al., 1995); I used a new set of primers of 28S rDNA during some amplifications (Littlewood et al., 2000; Williams et al., 2003; Williams and Ozawa, 2006). The other amplifications were performed using five traditional molecular markers of Actiniaria: 12S, 16S, 18S, and 28S rDNA and COXIII DNA, adopted in Rodríguez et al. (2014), following the methods of preceding phylogenetic studies on sea anemones (Meldin et al., 1988; Apakupakul et al., 1999; Geller and Walton, 2001; Medina et al., 2001; Sinniger et al., 2005). The PCR products were processed using exonuclease I and shrimp alkaline phosphate (ExoSAP-IT; Thermo Fisher) before sequencing. Sequencing reaction was performed using BigDye Terminator Cycle Sequencing Ready Reaction Kit v3.1 (Applied Biosystems) and using PCR primers (12S, 16S, COXIII, and ITS1/2) or PCR primers and internal primers (18S and 28S; Table 5). I used four internal primers (two forward and two reverse) for 18S (Apakupakul et al., 1999), and three primers (two forward and one reverse) for 28S (Williams and Ozawa, 2005). Sequencing was performed using ABI 3130xL or 3500xL Genetic Analyzer (Applied Biosystems). The sequence of each marker was individually assembled using GeneStudio ver. 2.2.0.0 (http://genestudio.com).

Phylogenetic analysis and evolutionary estimation

The base sequences used in phylogenetic analyses are shown in Table 6. Sequences data of 106 species were obtained from GenBank (registration numbers are shown in Table 6). Each dataset was aligned using MAFFT ver. 7.402 (Katoh and Standley, 2013) under the default settings. Ambiguously aligned regions were eliminated using Gblocks ver. 0.91b (Castresana, 2002) with the type of DNA sequences and in default parameters except allowing small final blocks and gap positions within the final blocks. The obtained data were processed using Kakusan 4 (Tanabe, 2011) to select the appropriate substitution models for the RAxML and MrBayes analyses (Table 7). In the combined dataset, substitution parameters were estimated separately for each gene partition (Table 8). The maximum-likelihood (ML) analysis was performed using RAxML-VI-HPC (Stamatakis, 2006), with substitution models recommended by Kakusan 4 and evaluated using 100 bootstrap replicates. Bayesian inference (BI) was conducted using MrBayes ver. 3.2.6 (Ronquist and Huelsenbeck, 2003) with substitution models recommended by Kakusan 4. Two independent runs of the Markov Chain Monte Carlo were performed simultaneously for 3,000,000–5,000,000 generations; trees were sampled every 100 generation, and the average standard deviation of split frequencies (ASDSF) every 100,000 generation were calculated. As the ASDSF was calculated on the basis of the last 75% of the samples, the initial 25% of the sampled trees were discarded as burn-in. In addition, I provisionally performed ML and BI analyses by using mitochondrial and nuclear markers, respectively, for each phylogenetic analysis.

The phylogenetic analysis was first performed following the above method at the level of the order Actiniaria (Chapter 1A). Next, after the monophyly of each lower suborder was confirmed, analyses of the suborders Enthemonae (Chapter 1B) and Anenthemonae (Chapter 1C) were performed. Similarly, the phylogenetic analyses of the superfamily Actinernoidea

(Chapter 1D), Edwardsioidea (Chapter 1F), and a newly established superfamily Halcampelloidea (Chapter 1E) were performed after monophyly was confirmed. I appropriately chose operational taxonomic units and molecular markers for each taxon (Tables 4, 6, 7).

All constructed ML and Baysian trees were rooted and combined using FigTree ver. 1.4.3 (http://tree.bio.ed.ac.uk/software/figtree/). Finally, I estimated the evolutionary trend of diagnostic morphological features based on the obtained trees from the point of view of maximum parsimony in the order Actiniaria (Chapter 3A), suborder Anenthemonae (Chapter 3B), and family Edwardsiidae (Chapter 3C).

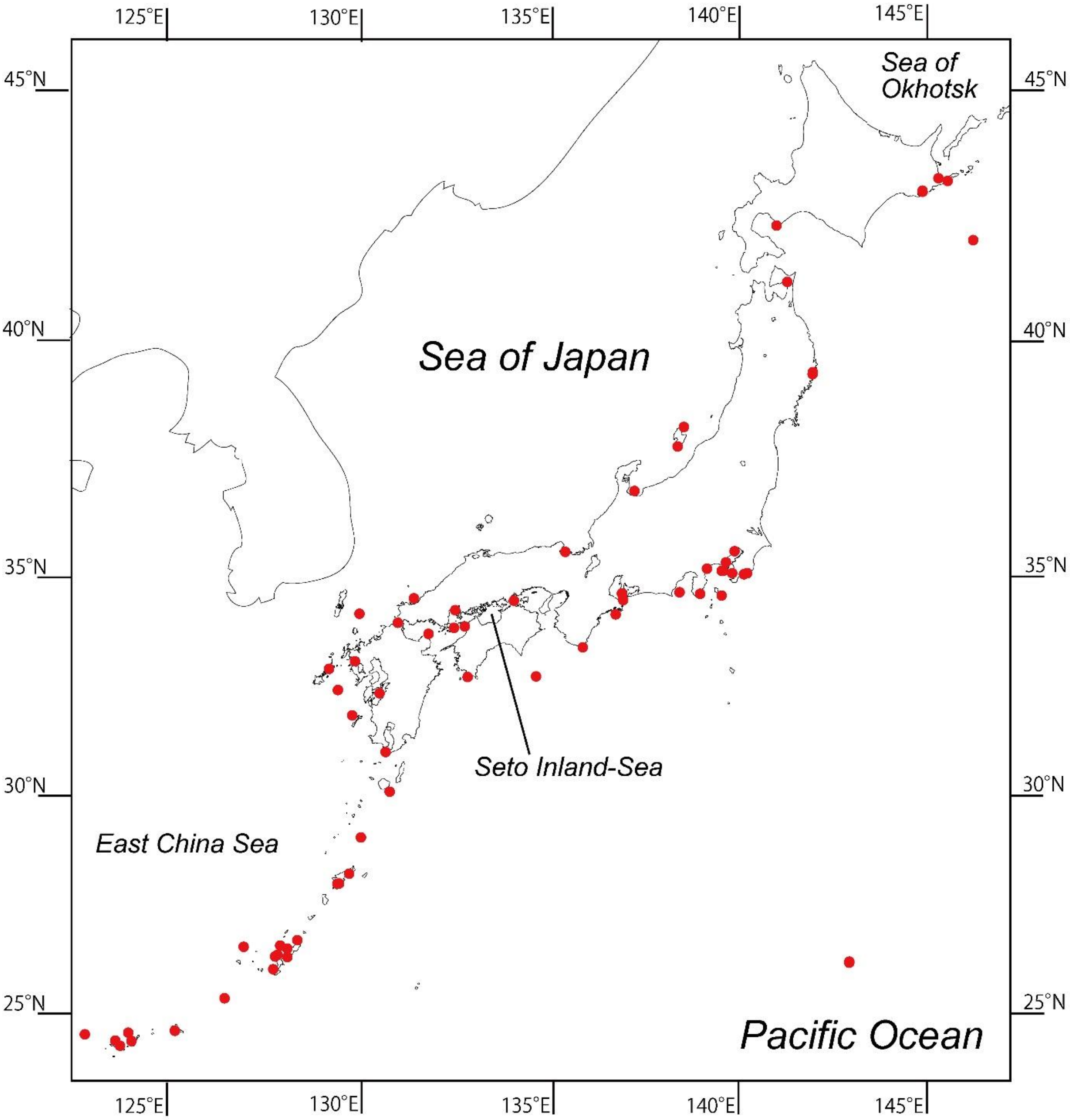


Fig. 4. Approximate localities of the sampling sites used in this study.
See each material examined in Chapter 2 for the detailed information of each locality.

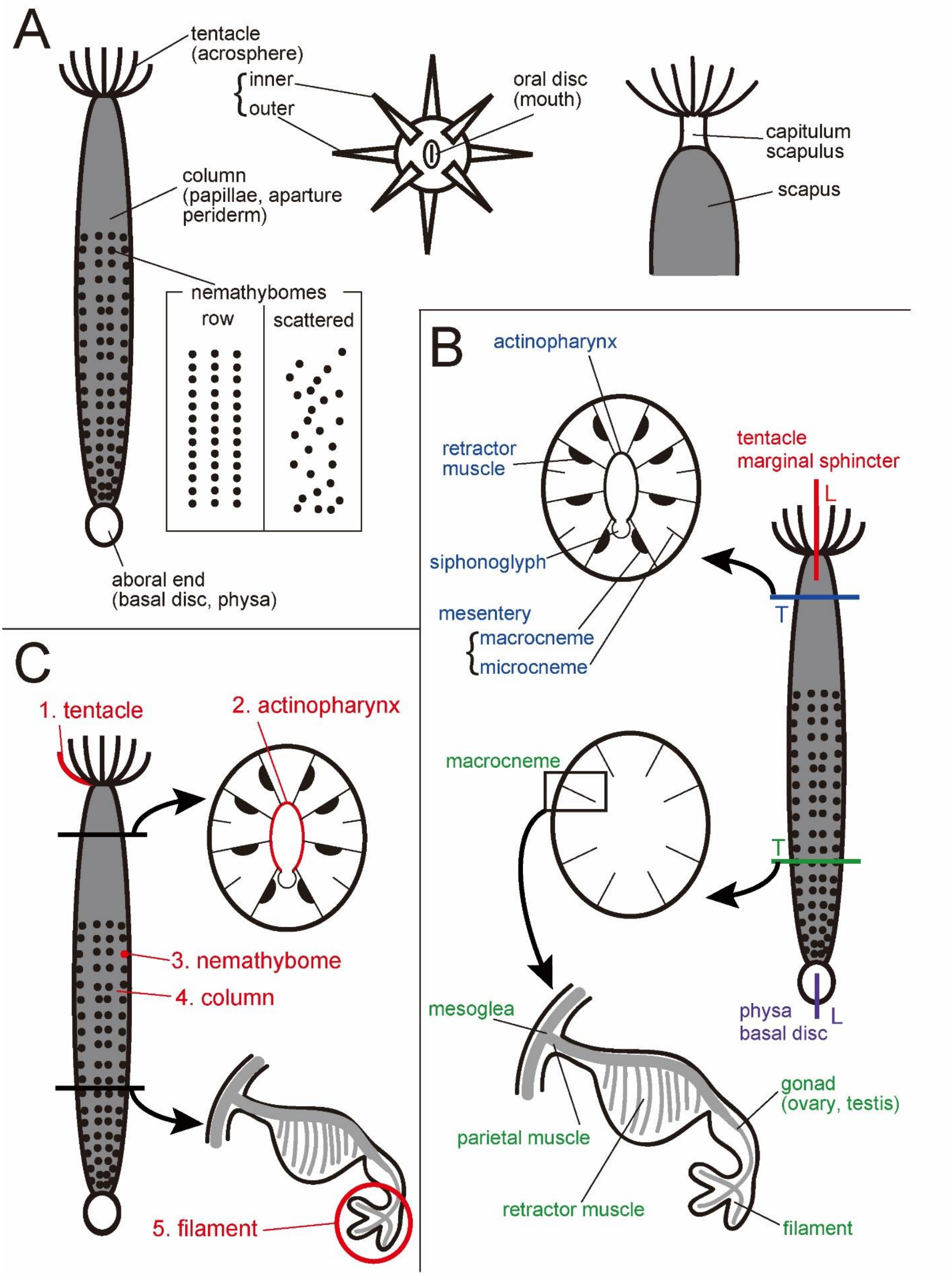


Fig. 5. Schematic view of the morphological features of Actiniaria.
A. Basic external morphology observed using stereoscopic microscopes. B. Basic internal anatomy observed using histological sections. C. Excised tissues on which cnidom was observed. The observed characters were generally common among all actiniarians except nemathybomes, characters specific to Edwardsiidae. The terminology was referred from Carlgren (1949), Daly (2015), and Yanagi (2017).

Table 4. Molecular specimens of Actiniaria used in this study.
+ means specimens included in the phylogenetic analysis of each level, and - were not included. (Blank means that the analysis of the taxon was not performed in this study.)
Base sequences indicated grey are obtained from GenBank (see Table 6).

Suborder	Superfamily	family	Genus	Species	Catalog Numbers	Including analysis			locality
						Order	Suborder	Superfamily	
Anenthemonae	Actinernoidea	Actinernidae	*Actinernus*	*robustus*	CMNH-ZG (no registration)	+	+	+	Ryukyu-Trough
			Isactinernus	*quadrilobatus*	NSMT-Co 1662	-	+	+	Kumano-nada
			Synhalcurias	*elegans*	NSMT-Co 1693	-	-	+	Mikawa-Bay
			Synhalcurias	*elegans*	NSMT-Co 1694	+	+	+	Okinawa
			Synhalcurias	sp. nov. 1	NSMT-Co 1695	+	+	+	Ogasawara
			Synactinernus	*flavus*	NSMT-Co 1660	+	+	+	Goto-nada
			Synactinernus	*flavus*	-	+	+	+	Goto-nada
			Synactinernus	*flavus*	-	+	+	+	Goto-nada
			Synactinernus	*flavus*	-	-	-	+	Goto-nada
			Synactinernus	*flavus*	-	-	-	+	Goto-nada
			Synactinernus	*flavus*	-	-	-	+	Goto-nada
			Synactinernus	*flavus*	CMNH-ZG 09732	+	+	+	Wakayama
			Synactinernus	*churaumi*	NSMT-Co 1661	+	+	+	Off Ishigaki Island
			Synactinernus	*churaumi*	-	+	+	+	Off Ishigaki Island
			Synactinernus	*churaumi*	-	-	-	+	Off Ishigaki Island
			Synactinernus	*churaumi*	-	-	-	+	Off Ishigaki Island
		Halcuriidae	*Halcurias*	*japonicus*	(Iz-001)	-	-	+	Toyama-Bay
			Halcurias	*japonicus*	(Iz-003)	-	-	+	Toyama-Bay
			Halcurias	*japonicus*	(Iz-004)	-	-	+	Toyama-Bay
			Halcurias	*japonicus*	(Iz-007)	+	+	+	Mikawa-Bay
			Halcurias	*japonicus*	(Iz-008)	+	+	+	Wakayama
			Halcurias	sp. nov. 2	(Iz-009)	+	+	+	Sado Island
			Halcurias	sp. nov. 2	(Iz-010)	+	+	+	Sado Island
			Halcurias	sp. nov. 2	(Iz-012)	+	+	+	Wakayama
			Halcurias	*carlgreni*	NSMT-Co 1697	+	+	+	Suo-Oshima
			Halcurias	*carlgreni*	NSMT-Co 1698	+	+	+	Suo-Oshima
			Halcurias	*carlgreni*	(Iz-015)	+	+	+	Kumano-nada
			Halcurias	*carlgreni*	(Iz-016)	-	-	+	Ukishima Island
			Halcurias	*carlgreni*	(Iz-017)	-	-	+	Ukishima Island
			Halcurias	*levis*	(Iz-018)	+	+	+	Kuju-kushima
			Halcurias	*levis*	-	+	+	+	Kuju-kushima
			Halcurias	*levis*	(Iz-019)	-	-	+	Off Yaku Island
			Halcurias	sp. nov. 3	NSMT-Co 1699	+	+	+	Kinko-Bay
			Halcurias	sp. nov. 3	(Iz-021)	+	+	+	Wakayama
			Actinernus	*elongatus*	-	+	+	+	(GenBank)
			Isactinernus	*quadrilobatus*	-	+	+	+	(GenBank)
			Synhalcurias	*elegans*	-	+	+	+	(GenBank)
			Halcurias	*pilatus*	-	+	+	+	(GenBank)

Edwardsioidea	Edwardsiidae	*Tempuractis*	*rinkai*	NSMT-Co 1573	+	+	+	Misaki
		Tempuractis	*rinkai*	CMNH-ZG 8974	+	+	+	Toba_Tohama
		Tempuractis	*rinkai*	CMNH-ZG 8975	+	+	+	Sado Island
		Tempuractis	sp.	(Iz-037)	+	+	+	Sado Island
		Tempuractis	sp.	(Iz-038)	+	+	+	Sado Island
		Tempuractis	sp.	(Iz-039)	+	+	+	Ie Island
		Edwardsiella	sp. nov. 6	CMNH-ZG (no registration)	+	+	+	Ogasawara
		Edwardsiella	sp. nov. 6	CMNH-ZG (no registration)	+	+	+	Ogasawara
		Halcampogeton	sp. nov. 7	(Iz-040)	+	+	+	Off Mie Pref.
		Drillactis	sp. nov. 8	(Iz-041)	+	+	+	Otsuchi
		Edwardsianthus	*pudica*	(Iz-042)	+	+	+	Amami Island
		Edwardsianthus	*gilbertensis*	CMNH-ZG 6527	+	+	+	Ishigaki Island
		Edwardsianthus	*gilbertensis*	(Iz-043)	+	+	+	Kataburu_Yonaguni
		Edwardsianthus	*gilbertensis*	(Iz-044)	+	+	+	Kataburu_Yonaguni
		Edwardsianthus	*gilbertensis*	(Iz-045)	+	+	+	Kataburu_Yonaguni
		Edwardsianthus	*gilbertensis*	(Iz-046)	-	-	+	Kataburu_Yonaguni
		Edwardsianthus	*gilbertensis*	(Iz-047)	-	-	+	Kataburu_Yonaguni
		Edwardsianthus	*gilbertensis*	(Iz-048)	-	-	+	Kataburu_Yonaguni
		Edwardsianthus	*gilbertensis*	(Iz-049)	-	-	+	Kataburu_Yonaguni
		Edwardsianthus	*gilbertensis*	(Iz-050)	-	-	+	Kataburu_Yonaguni
		Edwardsianthus	*gilbertensis*	(Iz-051)	-	-	+	Higawa_Yonaguni
		Edwardsianthus	*gilbertensis*	(Iz-052)	+	+	+	Senaga Island
		Edwardsianthus	*gilbertensis*	(Iz-053)	+	+	+	Yagaji Island
		Edwardsianthus	*gilbertensis*	(Iz-054)	-	-	+	Kikai Island
		Edwardsianthus	sp.	-	+	+	+	Iriomote Island
		Edwardsianthus	sp. nov. 9	CMNH-ZG 5954	+	+	+	Otsuki_Kochi
		Edwardsianthus	sp. nov. 10	(Iz-055)	+	+	+	Amami Island
		Edwardsianthus	sp. nov. 11	(Iz-056)	+	+	+	Oura Bay
		Edwardsianthus	sp. nov. 12	(Iz-057)	-	+	+	Oura Bay
		Edwardsianthus	sp. nov. 13	(Iz-058)	+	+	+	Yagaji Island
		Edwardsianthus	sp. nov. 14	(Iz-060)	+	+	+	Ogasawara
		Edwardsianthus	sp. nov. 14	(Iz-063)	+	+	+	Ogasawara
		Edwardsianthus	sp. nov. 15	(Iz-064)	+	+	+	Kataburu_Yonaguni
		Paraedwardsia	sp. nov. 16	(Iz-070)	+	+	+	Off Misaki
		Paraedwardsia	sp. nov. 17	(Iz-072)	+	+	+	Aburatsubo Bay
		Scolanthus	*ena*	NSMT-Co 1610	-	+	+	Ena Bay
		Scolanthus	*isei*	NSMT-Co 1611	+	+	+	Sugashima Island
		Scolanthus	*kopepe*	NSMT-Co 1613	+	+	+	Ogasawara
		Edwardsia	*alternobomen*	NSMT-Co 1657	+	+	+	Hinoshima_Amakusa
		Edwardsia	*alternobomen*	(Iz-067)	-	-	+	Manazuru
		Edwardsia	aff. *tuberculata*	NSMT-Co 1654	+	+	+	Off Ogishima
		Edwardsia	aff. *tuberculata*	(Iz-068)	+	+	+	Misaki
		Edwardsia	*japonica*	(Iz-069)	+	+	+	Otsuki_Kochi
		Edwardsia	*sipuncluloides*	NSMT-Co 1700	+	+	+	Tokyo Bay
		Edwardsia	sp. nov. 18	(Iz-073)	+	+	+	Katsuura_Chiba
		Edwardsia	sp. nov. 19	(Iz-074)	-	-	+	Hiroshima-Bay

Edwardsia	sp. nov. 20	(Iz-075)	+	+	+	Katsuura_Chiba
Edwardsia	sp. nov. 21	CMNH-ZG 4762	+	+	+	Mutsu Bay
Edwardsia	sp. nov. 22	(Iz-076)	-	+	+	Suo-Oshima
Isoscolanthus	sp. nov. 23	(Iz-078)	+	+	+	Off Mie Pref.
Isoscolanthus	sp. nov. 23	(Iz-079)	+	-	+	Off Mie Pref.
Isoscolanthus	sp. nov. 23	(Iz-080)	+	-	+	Off Mie Pref.
Edwardsia	sp.	-	+	+	+	Oura Bay
Edwardsia	sp.	-	-	-	+	Otsuki_Kochi
Edwardsia	sp.	-	+	+	+	Maizuru Bay
Edwardsia	sp.	-	+	+	+	Off Yamaguchi Pref.
Edwardsia	sp.	-	+	+	+	Aburatsubo Bay
Edwardsia	sp.	-	+	+	+	Senaga Island
Edwardsia	sp.	-	+	+	+	Senaga Island
Edwardsia	sp.	-	-	-	+	Senaga Island
Edwardsia	sp.	-	+	+	+	Higawa_Yonaguni
Edwardsia	sp.	-	+	+	+	Otsuki_Kochi
Edwardsia	sp.	-	-	-	+	Yagaji Island
Edwardsia	sp.	-	+	+	+	Otsuki_Kochi
Edwardsia	sp.	-	-	-	+	Otsuki_Kochi
Edwardsia	sp.	-	+	+	+	Otsuki_Kochi
Edwardsia	sp.	-	+	+	+	Okinawa Island
Edwardsia	sp.	-	-	-	+	Ogasawara
Edwardsia	sp.	-	+	+	+	Araihama_Misaki
Edwardsia	sp.	-	-	-	+	Araihama_Misaki
Edwardsia	sp.	-	-	-	+	Aburatsubo Bay
Edwardsia	sp.	-	+	+	+	Yokohama
Edwardsia	sp.	-	+	+	+	Misaki
Edwardsia	sp.	-	-	-	+	Off Shimoda
Edwardsia	sp.	-	+	+	+	Hinoshima_Amakusa
Edwardsia	sp.	-	+	-	+	Off Sado
Metedwardsia	*akkeshi*	NSMT-Co 1605	+	+		Lake Akkeshi
Metedwardsia	*akkeshi*	(Iz-097)	+	+		Muroran
Metedwardsia	*akkeshi*	NSMT-Co 1608	+	+		Lake Furen
Metedwardsia	*akkeshi*	(Iz-094)	+	+		Yokohama
Metedwardsia	*akkeshi*	(Iz-095)	+	+		Yokohama
Metedwardsia	sp. nov. 30	(Iz-099)	+	+		Aburatsubo Bay
Metedwardsia	sp. nov. 31	CMNH-ZG 5943	+	+		Nakajima_Ehime
Metedwardsia	sp. nov. 31	(Iz-100)	+	+		Nishidomari, Kochi
Edwardsia	*japonica*		+	+	+	(GenBank)
Edwardsia	*timida*		+	+	+	(GenBank)
Edwardsianthus	*gilbertensis*		+	+	+	(GenBank)
Nematostella	*vectensis*		+	+	+	(GenBank)

Enthemonae	Actinostoloidea	Exocoelactinidae	*Exocoelactis*	*actinostoloides*	CMNH-ZG 05926	+	+	Off Boso Peninsula
			Exocoelactis	*actinostoloides*	-	+	+	Ise Bay
		Actinostolidae	*Actinostola*	*chilensis*		+	+	(GenBank)
			Actinostola	*georgiana*		+	+	(GenBank)
			Actinostola	*crassicornis*		+	+	(GenBank)
			Antholoba	*achates*		+	+	(GenBank)
			Anthosactis	*janmayeni*		+	+	(GenBank)
			Hormosoma	*scotti*		+	+	(GenBank)
			Paranthus	*niveus*		+	+	(GenBank)
			Stomphia	*selaginella*		+	+	(GenBank)
			Stomphia	*didemon*		+	+	(GenBank)
	Actinioidea	Haloclavidae	*Peachia*	*quinquecapitata*	-	+	+	Sanriku
			Antennapeachia	*jambio*	NSMT-Co 1596	+	+	Off Misaki
			Antennapeachia	*jambio*	CMNH-ZG 6546	+	+	Off Misaki
			Anemonactis	*minuta*	NSMT-Co 1619	+	+	Misaki
			Anemonactis	*minuta*	NSMT-Co 1622	+	+	Ogasawara
			Haloclava	sp. nov. 28	(Iz-088)	+	+	Off Misaki
			Haloclava	sp. nov. 28	(Iz-089)	+	+	Off Mie Pref.
			gen.	sp.	-	+	+	Aburatsubo Bay
		Actiniidae	*Actinia*	*fragacea*		+	+	(GenBank)
			Anemonia	*viridis*		+	+	(GenBank)
			Anthopleura	*elegantissima*		+	+	(GenBank)
			Anthostella	*stephensoni*		+	+	(GenBank)
			Bolocera	*kerguelensis*		+	+	(GenBank)
			Bunodactis	*verrucosa*		+	+	(GenBank)
			Bunodosoma	*grandis*		+	+	(GenBank)
			Epiactis	*lisbethae*		+	+	(GenBank)
			Glyphoperidium	*bursa*		+	+	(GenBank)
			Isosicyonis	*alba*		+	+	(GenBank)
			Isosicyonis	*striata*		+	+	(GenBank)
			Isotealia	*antarctica*		+	+	(GenBank)
			Korsaranthus	*natalinesis*		+	+	(GenBank)
			Macrodactyla	*doreenensis*		+	+	(GenBank)
			Urticina	*coriacea*		+	+	(GenBank)
		Actinodendridae	*Actinostephanus*	*haeckeli*		+	+	(GenBank)
		Haloclavidae	*Haloclava*	*producta*		+	+	(GenBank)
			Haloclava	*sp.*		+	+	(GenBank)
			Harenactis	*argentina*		+	+	(GenBank)
			Peachia	*cylindrica*		+	+	(GenBank)
			Stephanthus	*antarcticus*		+	+	(GenBank)
		Liponematidae	*Liponema*	*brevicornis*		+	+	(GenBank)
			Liponema	*multiporum*		+	+	(GenBank)
		Phymanthidae	*Phymanthus*	*loligo*		+	+	(GenBank)
		Preactiidae	*Dactylanthus*	*antarcticus*		+	+	(GenBank)
			Preactis	*milliardae*		+	+	(GenBank)
		Stichodactidae	*Heteractis*	*magnifica*		+	+	(GenBank)

Metridioidea	Halcampidae	*Halcampa*	sp.	-	+	+		Off Misaki
		Halcampella	*maxima*	(Iz-023)	+	+	+	Off Misaki
		Halcampella	*maxima*	(Iz-024)	+	+	+	Off Misaki
		Halcampella	*cretata*	(Iz-025)	-	-	+	Off Misaki
		gen.	sp. nov. 4	(Iz-025)	+	+	+	Cape Maeda
		gen.	sp. nov. 4	(Iz-026)	+	+	+	Cape Maeda
		gen.	sp. nov. 4	(Iz-027)	+	+	+	Cape Maeda
		gen.	sp. nov. 4	(Iz-028)	+	+	+	Cape Maeda
		gen.	sp. nov. 4	-	+	+	+	Australia
		gen.	sp. nov. 5	(Iz-034)	+	+	+	Off Mie Pref.
		gen.	sp. nov. 5	(Iz-035)	-	-	+	Off Mie Pref.
		gen.	sp. nov. 5	(Iz-036)	-	-	+	Off Mie Pref.
		gen.	sp.	-	-	-	+	Off Sado
	Andvakidae	*Synandwakia*	*hozawai*	CMNH-ZG (no registration)	+	+		Lake Akkeshi
		Synandwakia	*hozawai*	CMNH-ZG (no registration)	+	+		Lake Akkeshi
	Actinoscyphiidae	*Actinoscyphia*	*plebeia*		+	+		(GenBank)
	Aiptasiidae	*Aiptasia*	*mutabilis*		+	+		(GenBank)
		Aiptasia	*pallida*		+	+		(GenBank)
		Bartholomea	*annulata*		+	+		(GenBank)
		Neoaiptasia	*morbilla*		+	+		(GenBank)
	Aliciidae	*Alicia*	*sansibarensis*		+	+		(GenBank)
		Triactis	*producta*		+	+		(GenBank)
	Amphianthidae	*Amphianthus*	*sp.*		+	+		(GenBank)
		Peronanthus	*sp.*		+	+		(GenBank)
	Andvakiidae	*Andvakia*	*boninensis*		+	+		(GenBank)
		Andvakia	*discipulorum*		+	+		(GenBank)
		Telmatactis	*sp.*		+	+		(GenBank)
	Antipodactinidae	*Antipodactis*	*awii*		+	+		(GenBank)
	Bathyphelliidae	*Bathyphellia*	*australis*		+	+		(GenBank)
	Boloceroididae	*Boloceroides*	*mcmurrichi*		+	+		(GenBank)
		Bunodeopsis	*globulifera*		+	+		(GenBank)
	Diadumenidae	*Diadumene*	*cincta*		+	+		(GenBank)
		Diadumene	*leucolena*		+	+		(GenBank)
		Diadumene	*sp.*		+	+		(GenBank)
	Galantheanthemida	*Galatheanthemum*	*sp. nov.*		+	+		(GenBank)
		Galatheanthemum	*profundus*		+	+		(GenBank)
	Gonatiniidae	*Gonactinia*	*prolifera (Chile)*		+	+		(GenBank)
		Protantea	*simplex*		+	+		(GenBank)
	Halcampidae	*Cactosoma*	*sp. nov.*		+	+		(GenBank)
		Halcampa	*duodecimcirrata*		+	+		(GenBank)
		Halcampoides	*purpurea*		+	+		(GenBank)
	Haliplanellidae	*Haliplanella*	*lineata (USA)*		+	+		(GenBank)

		Hormathiidae	*Actinauge*	*richardi*		+	+	(GenBank)
			Adamsia	*palliata*		+	+	(GenBank)
			Allantactis	*parasitica*		+	+	(GenBank)
			Calliactis	*parasitica*		+	+	(GenBank)
			Calliactis	*polypus*		+	+	(GenBank)
			Calliactis	*tricolor*		+	+	(GenBank)
			Calliactis	*japonica*		+	+	(GenBank)
			Chondrophellia	*orangina*		+	+	(GenBank)
			Hormathia	*armata*		+	+	(GenBank)
			Hormathia	*lacunifera*		+	+	(GenBank)
			Hormathia	*pectinata*		+	+	(GenBank)
			Paracalliactis	*japonica*		+	+	(GenBank)
			Paraphelliactis	*sp.*		+	+	(GenBank)
		Isanthidae	*Isanthus*	*capensis*		+	+	(GenBank)
		Kadosactinidae	*Alvinactis*	*chessi*		+	+	(GenBank)
			Cyananthea	*hourdezi*		+	+	(GenBank)
			Kadosactis	*antarctica*		+	+	(GenBank)
		Metridiidae	*Metridium*	*senile (WA)*		+	+	(GenBank)
		Nemathidae	*Nemanthus*	*nitidus*		+	+	(GenBank)
		Phelliidae	*Phellia*	*gausapata*		+	+	(GenBank)
			Phellia	*exlex*		+	+	(GenBank)
		Sagartiidae	*Actinothoe*	*sphyrodeta*		+	+	(GenBank)
			Anthothoe	*chilensis*		+	+	(GenBank)
			Cereus	*pedunculatus*		+	+	(GenBank)
			Cereus	*herpetodes*		+	+	(GenBank)
			Sagartia	*troglodytes*		+	+	(GenBank)
			Sagartia	*ornata*		+	+	(GenBank)
			Sagartiogeton	*laceratus*		+	+	(GenBank)
			Sagartiogeton	*undatus*		+	+	(GenBank)
			Verrillactis	*paguri*		+	+	(GenBank)
Unknown	Unknown	Capneidae	*Capnea*	*japonica*	CMNH-ZG 06547	+	+	Off Misaki
		Capneidae	*Capnea*	*georgiana*		+	+	(GenBank)
		fam.	gen.	sp. nov. 27	(Iz-082)	+	+	Misaki
			gen.	sp. nov. 27	(Iz-084)	+	+	Misaki
			gen.	sp. nov. 27	(Iz-086)	+	+	Off Tsushima

Table 5. Primers and protocols of polymerase chain reactions of every molecular marker.

Marker		Primer	Sequences (5'-3')	PCR protocol	Reference
12S		12S1a	TAAGTGCCAGCAGACGCGGT	(95 °C for 4 min) + 4 × [(94°C for 30 sec) → (50°C for 1 min) → (72°C for 2 min)] +30 × [(94°C for 30 sec) → (55°C for 1 min) → (72°C for 2 min)] + (72°C for 4 min)	Sinniger et al. (2005)
		12S3r	ACGGGCAATTTGTACTAACA		
16S		ANEM16SA	CACTGACCGTGATAATGTAGCGT	(95°C for 4 min) + 30 × [(95°C for 30 sec) → (46°C for 45 sec) → (72°C for 1 min)] + (72°C for 5 min)	Geller and Walton (2001)
		ANEM16SB	CCCCATGGTAGCTTTTATTCG		
		16Sant1a	GCCATGAGTATAGACGCACA	(95°C for 4 min) + 30 × [(95°C for 30 sec) → (46°C for 45 sec) → (72°C for 1 min)] + (72°C for 5 min)	Sinniger et al. (2005)
		16SbmoH	CGAACAGCCAACCCTTGG		
COXIII		COIIIF	CATTTAGTTGATCCTAGGCCTTGACC	(95°C for 2 min) + 30 × [(95°C for 30 sec) → (46°C for 45 sec) → (72°C for 1 min)] + (72°C for 5 min)	Geller and Walton (2001)
		COIIIR	CAAACCACATCTACAAAATGCCAATATC		
18S	PCR	18SA	AACCTGGTTGATCCTGCCAGT	(94°C for 4 min) + 35 × [(94°C for 20 sec) → (57°C for 20 sec) → (72°C for 1 min 45 sec)] + (72°C for 7 min)	Meldin et al. (1988) Apakupakul et al. (1999)
		18SB	TGATCCTTCCGCAGGTTCACCT		
	Only Sequence	18SL	CCAACTACGAGCTTTTTAACTG		
		18SC	CGGTAATTCCAGCTCCAATAG		
		18SY	CAGACAAATCGCTCCACCAAC		
		18SO	AAGGGCACCACCAGGAGTGGAG		
28S	PCR1	F63sq	AATAAGCGGAGGAAAAGAAAC	(94°C for 5 min) + 30 × [(94°C for 30 sec) → (45°C for 1 min) → (72°C for 3 min)] + (72°C for 10 min)	Medina et al. (2001)
		R2077sq	GAGCCAATCCTTWTCCCGARGTT		
	PCR2	LSU5	TAGGTCGACCCGCTGAAYTTAAGCA	(94°C for 5 min) + 30 × [(94°C for 30 sec) → (45°C for 1 min) → (72°C for 3 min)] + (72°C for 10 min)	Littlewood et al. (2000) Williams et al. (2003) Williams and Ozawa (2006)
		LSU1600R	AGCGCCATCCATTTTCAGG		
	Only Sequence	LSU330F	CAAGTACCGTGAGGGAAAGTTG		
		LSU900F	CCGTCTTGAAACACGGACCAAG		
		ECD2S	CTTGGTCCGTGTTTCAAGACGG		
ITS1/2		ITSF	GTTTCCGTAGGTGAACCTG	(94°C for 5 min) + 30 × [(94°C for 35 sec) → (55°C for 45 sec) → (72°C for 2 min)] + (72°C for 1 min)	Heath et al. (1995)
		ITSR	CTCGTCTGATCTGAGGTCG		

Table 6. Base sequences in the phylogenetic analyses.
Sequences indicated by accession numbers were obtained from GenBank, and those indicated by + were obtained in this study and still not deposited to GenBank. Sequences indicated by - were neither available in this study nor in GenBank. Species of Zoanthidea and Relicanthidae were for the outgroups of phylogenetic analysis of the order Actiniaria.

Higher Taxon	Family	Genus	Species	Localities	Catalog Numbers	12S	16S	18S	28S	COXIII	5.8S/ITS1/ITS2
Actiniaria											
Anenthemonae											
Actinernoidea	Actinernidae	*Actinernus*	*robustus*	Ryukyu-Trough	CMNH-ZG (no registration)	+	-	LC484632	+	-	-
		Isactinernus	*quadrilobatus*	Kumano-nada	NSMT-Co 1662	-	LC484643	LC484638	+	-	+
		Synhalcurias	*elegans*	Mikawa-Bay	NSMT-Co 1693	-	-	+	+	-	+
		Synhalcurias	*elegans*	Okinawa	NSMT-Co 1694	+	+	-	+	-	+
		Synhalcurias	sp. nov. 1	Ogasawara	NSMT-Co 1695	+	+	-	+	-	+
		Synactinernus	*flavus*	Goto-nada	NSMT-Co 1660	+	LC484639	LC484633	+	-	+
		Synactinernus	*flavus*	Goto-nada	-	+	LC484640	LC484634	+	-	+
		Synactinernus	*flavus*	Goto-nada	-	+	+	+	+	-	+
		Synactinernus	*flavus*	Goto-nada	-	+	+	+	-	-	-
		Synactinernus	*flavus*	Goto-nada	-	+	+	+	-	-	-
		Synactinernus	*flavus*	Goto-nada	-	+	+	+	-	-	-
		Synactinernus	*flavus*	Wakayama	CMNH-ZG 09732	+	+	LC484635	+	-	-
		Synactinernus	*churaumi*	Off Ishigaki Island	NSMT-Co 1661	+	LC484641	LC484636	+	-	+
		Synactinernus	*churaumi*	Off Ishigaki Island	-	+	LC484642	LC484637	+	-	+
		Synactinernus	*churaumi*	Off Ishigaki Island	-	-	+	+	-	-	-
		Synactinernus	*churaumi*	Off Ishigaki Island	-	+	+	+	-	-	-
	Actinernidae	*Actinernus*	*antarcticus*	(GenBank)		KJ482930	KJ482966	KJ483023	KJ483126	-	-
		Isactinernus	*quadrolobatus*	(GenBank)		KJ482932	KJ482968	KJ483024	KJ483105	-	-
		Synhalcurias	*laevis*	(GenBank)		KJ482942	-	KJ483021	KJ483120	-	-
	Halcuriidae	*Halcurias*	*japonicus*	Toyama-Bay	(Iz-001)	-	+	+	+	-	+
		Halcurias	*japonicus*	Toyama-Bay	(Iz-003)	-	+	+	+	-	+
		Halcurias	*japonicus*	Toyama-Bay	(Iz-004)	-	+	+	+	-	+
		Halcurias	*japonicus*	Mikawa-Bay	(Iz-007)	+	+	+	+	-	+
		Halcurias	*japonicus*	Wakayama	(Iz-008)	+	+	+	+	-	+
		Halcurias	sp. nov. 2	Sado Island	(Iz-009)	+	+	+	+	-	-
		Halcurias	sp. nov. 2	Sado Island	(Iz-010)	+	+	+	+	-	+
		Halcurias	sp. nov. 2	Wakayama	(Iz-012)	+	+	+	+	-	+
		Halcurias	*carlgreni*	Suo-Oshima	NSMT-Co 1697	+	+	+	+	-	+
		Halcurias	*carlgreni*	Suo-Oshima	NSMT-Co 1698	+	+	+	+	-	+
		Halcurias	*carlgreni*	Kumano-nada	(Iz-015)	+	+	+	+	-	-
		Halcurias	*carlgreni*	Ukishima Island	(Iz-016)	-	+	+	+	-	+
		Halcurias	*carlgreni*	Ukishima Island	(Iz-017)	-	+	-	-	-	-
		Halcurias	*levis*	Kuju-kushima	(Iz-018)	+	+	+	+	-	+
		Halcurias	*levis*	Kuju-kushima	-	+	+	+	+	-	+
		Halcurias	*levis*	Off Yaku Island	(Iz-019)	+	-	+	+	-	+
		Halcurias	sp. nov. 3	Kinko-Bay	NSMT-Co 1699	+	+	-	+	-	+
		Halcurias	sp. nov. 3	Wakayama	(Iz-022)	+	+	+	+	-	+
	Halcuriidae	*Halcurias*	*pilatus*	(GenBank)		KJ482931	KJ482967	KJ483020	KJ483109	-	-

Edwardsioidea	Edwardsiidae	*Tempuractis*	*rinkai*	Misaki	NSMT-Co 1573	+	+	+	+	-	+
		Tempuractis	*rinkai*	Toba_Tohama	CMNH-ZG 8974	+	+	+	+	-	+
		Tempuractis	*rinkai*	Sado Island	CMNH-ZG 8975	+	+	+	+	-	+
		Tempuractis	sp.	Sado Island	(Iz-037)	+	+	+	+	+	+
		Tempuractis	sp.	Sado Island	(Iz-038)	+	+	+	+	+	-
		Tempuractis	sp.	Ie Island	(Iz-039)	+	+	+	+	+	+
		Edwardsiella	sp. nov. 6	Ogasawara	CMNH-ZG (no registration)	+	+	+	+	+	-
		Edwardsiella	sp. nov. 6	Ogasawara	CMNH-ZG (no registration)	-	+	+	+	-	-
		Halcampogeton	sp. nov. 7	Off Mie Pref.	(Iz-040)	+	+	+	+	+	+
		Drillactis	sp. nov. 8	Otsuchi	(Iz-041)	+	+	+	+	+	+
		Edwardsianthus	*pudica*	Amami Island	(Iz-042)	+	+	+	+	-	+
		Edwardsianthus	*gilbertensis*	Ishigaki Island	CMNH-ZG 6527	+	+	+	+	+	+
		Edwardsianthus	*gilbertensis*	Kataburu_Yonaguni	(Iz-043)	+	+	+	+	+	-
		Edwardsianthus	*gilbertensis*	Kataburu_Yonaguni	(Iz-044)	+	+	-	-	-	-
		Edwardsianthus	*gilbertensis*	Kataburu_Yonaguni	(Iz-045)	+	+	-	-	-	-
		Edwardsianthus	*gilbertensis*	Kataburu_Yonaguni	(Iz-046)	+	+	+	+	+	+
		Edwardsianthus	*gilbertensis*	Kataburu_Yonaguni	(Iz-047)	+	+	+	+	+	+
		Edwardsianthus	*gilbertensis*	Kataburu_Yonaguni	(Iz-048)	+	+	+	+	+	+
		Edwardsianthus	*gilbertensis*	Kataburu_Yonaguni	(Iz-049)	+	+	-	+	+	+
		Edwardsianthus	*gilbertensis*	Kataburu_Yonaguni	(Iz-050)	+	+	+	+	+	+
		Edwardsianthus	*gilbertensis*	Higawa_Yonaguni	(Iz-051)	+	+	+	+	+	+
		Edwardsianthus	*gilbertensis*	Senaga Island	(Iz-052)	+	+	-	-	-	-
		Edwardsianthus	*gilbertensis*	Yagaji Island	(Iz-053)	+	+	-	-	-	-
		Edwardsianthus	*gilbertensis*	Kikai Island	(Iz-054)	+	+	+	+	+	+
		Edwardsianthus	sp.	Iriomote Island	-	+	+	+	-	+	-
		Edwardsianthus	sp. nov. 9	Otsuki_Kochi	CMNH-ZG 5954	+	+	+	+	+	+
		Edwardsianthus	sp. nov. 10	Amami Island	(Iz-055)	+	+	+	+	+	+
		Edwardsianthus	sp. nov. 11	Oura Bay	(Iz-056)	+	+	+	+	+	+
		Edwardsianthus	sp. nov. 12	Oura Bay	(Iz-057)	+	+	+	+	-	-
		Edwardsianthus	sp. nov. 13	Yagaji Island	(Iz-058)	+	+	+	+	+	+
		Edwardsianthus	sp. nov. 14	Ogasawara	(Iz-060)	+	+	+	+	+	-
		Edwardsianthus	sp. nov. 14	Ogasawara	(Iz-063)	+	+	+	+	+	+
		Edwardsianthus	sp. nov. 15	Kataburu_Yonaguni	(Iz-064)	+	+	+	+	+	+
		Paraedwardsia	sp. nov. 16	Off Misaki	(Iz-070)	+	+	+	+	+	+
		Paraedwardsia	sp. nov. 17	Aburatsubo Bay	(Iz-072)	+	+	+	+	-	+
		Scolanthus	*ena*	Ena Bay	NSMT-Co 1610	+	+	-	+	-	+
		Scolanthus	*isei*	Sugashima Island	NSMT-Co 1611	+	+	-	+	-	+
		Scolanthus	*kopepe*	Ogasawara	NSMT-Co 1613	+	+	+	+	+	+
		Edwardsia	*alternobomen*	Hinoshima_Amakusa	NSMT-Co 1657	+	+	+	+	+	-
		Edwardsia	*alternobomen*	Manazuru	(Iz-067)	+	+	+	+	+	-
		Edwardsia	aff. *tuberculata*	Off Ogishima	NSMT-Co 1654	+	+	+	+	+	+
		Edwardsia	aff. *tuberculata*	Misaki	(Iz-068)	+	+	+	+	+	+
		Edwardsia	*japonica*	Otsuki_Kochi	(Iz-069)	+	+	-	+	-	-
		Edwardsia	*sipuncluloides*	Tokyo Bay	NSMT-Co 1700	+	+	+	+	-	+
		Edwardsia	sp. nov. 18	Katsuura_Chiba	(Iz-073)	+	+	+	+	+	+
		Edwardsia	sp. nov. 19	Hiroshima-Bay	(Iz-074)	+	+	-	-	-	-
		Edwardsia	sp. nov. 20	Katsuura_Chiba	(Iz-075)	+	+	+	+	+	+
		Edwardsia	sp. nov. 21	Mutsu Bay	CMNH-ZG 4762	-	+	+	+	-	+
		Edwardsia	sp. nov. 22	Suo-Oshima	(Iz-076)	+	+	-	-	-	+

		Isoscolanthus	sp. nov. 23	Off Mie Pref.	(Iz-078)	+	+	-	+	+	+
		Isoscolanthus	sp. nov. 23	Off Mie Pref.	(Iz-079)	+	+	+	+	+	+
		Isoscolanthus	sp. nov. 23	Off Mie Pref.	(Iz-080)	+	+	+	+	+	+
		Edwardsia	sp.	Oura Bay	-	+	+	+	+	-	-
		Edwardsia	sp.	Otsuki_Kochi	-	+	+	+	+	+	+
		Edwardsia	sp.	Maizuru Bay	-	+	+	-	+	-	-
		Edwardsia	sp.	Off Yamaguchi Pref.	-	+	+	+	+	-	+
		Edwardsia	sp.	Aburatsubo Bay	-	+	+	-	-	-	-
		Edwardsia	sp.	Senaga Island	-	+	+	+	+	-	+
		Edwardsia	sp.	Senaga Island	-	+	+	+	+	-	+
		Edwardsia	sp.	Senaga Island	-	+	+	-	-	-	+
		Edwardsia	sp.	Higawa_Yonaguni	-	+	+	+	+	-	+
		Edwardsia	sp.	Otsuki_Kochi	-	+	+	+	+	+	+
		Edwardsia	sp.	Yagaji Island	-	+	+	+	+	-	-
		Edwardsia	sp.	Otsuki_Kochi	-	+	+	+	+	+	+
		Edwardsia	sp.	Otsuki_Kochi	-	+	+	-	+	+	+
		Edwardsia	sp.	Otsuki_Kochi	-	+	+	-	-	-	-
		Edwardsia	sp.	Okinawa Island	-	+	-	-	-	-	-
		Edwardsia	sp.	Ogasawara	-	+	+	-	+	+	+
		Edwardsia	sp.	Araihama_Misaki	-	+	+	+	-	+	+
		Edwardsia	sp.	Araihama_Misaki	-	+	+	+	+	+	-
		Edwardsia	sp.	Aburatsubo Bay	-	+	+	-	-	-	-
		Edwardsia	sp.	Yokohama	-	+	+	+	+	-	+
		Edwardsia	sp.	Misaki	-	+	+	+	+	-	+
		Edwardsia	sp.	Off Shimoda	-	+	-	-	-	+	+
		Edwardsia	sp.	Hinoshima_Amakusa	-	+	+	+	+	-	+
		Edwardsia	sp.	Off Sado	-	+	+	+	+	-	+
		Metedwardsia	*akkeshi*	Lake Akkeshi	NSMT-Co 1605	+	+	+	-	+	-
		Metedwardsia	*akkeshi*	Muroran	(Iz-097)	+	+	+	-	+	-
		Metedwardsia	*akkeshi*	Lake Furen	NSMT-Co 1608	+	-	+	-	+	-
		Metedwardsia	*akkeshi*	Yokohama	(Iz-094)	+	+	+	-	+	-
		Metedwardsia	*akkeshi*	Yokohama	(Iz-095)	+	+	-	-	+	-
		Metedwardsia	sp. nov. 30	Aburatsubo Bay	(Iz-099)	+	+	-	-	-	-
		Metedwardsia	sp. nov. 31	Nakajima_Ehime	CMNH-ZG 5943	+	+	+	-	+	-
		Metedwardsia	sp. nov. 31	Nishidomari, Kochi	(Iz-100)	+	+	-	-	+	-
	Edwardsiidae	*Edwardsia*	*japonica*	(GenBank)		GU473274	GU473288	GU473304	KJ483048	GU473359	-
		Edwardsia	*timida*	(GenBank)		GU473281	-	GU473315	KJ483088	KJ482996	KT852241
		Edwardsianthus	*gilbertensis*	(GenBank)		EU190728	EU190772	EU190859	EU190817	-	-
		Nematostella	*vectensis*	(GenBank)		EU190750	AY169370	AF254382	KJ483089	FJ489501	-
Enthemonae											
Actinostoloidea	Exocoelactinidae	*Exocoelactis*	*actinostoloides*	Off Boso Peninsula	CMNH-ZG 05926	+	+	-	-	-	-
		Exocoelactis	*actinostoloides*	Ise Bay	-	+	-	-	-	+	-
	Actinostolidae	*Actinostola*	*crassicornis*	(GenBank)		-	EU190753	EU190843	-	GU473332	-
		Actinostola	*chilensis*	(GenBank)		-	GU473285	GU473302	-	GU473357	-
		Actinostola	*georgiana*	(GenBank)		KJ482928	KJ482952	KJ483032	-	KJ482991	-
		Antholoba	*achates*	(GenBank)		GU473269	GU473284	GU473301	-	GU473356	-
		Anthosactis	*janmayeni*	(GenBank)		KJ482938	GU473292	GU473308	-	GU473363	-
		Hormosoma	*scotti*	(GenBank)		EU190733	EU190778	EU190863	-	GU473366	-
		Paranthus	*niveus*	(GenBank)		GU473277	GU473295	GU473311	-	GU473344	-
		Stomphia	*didemon*	(GenBank)		KJ482929	EU190795	EU190875	-	GU473348	-
		Stomphia	*selaginella*	(GenBank)		GU473280	GU473298	GU473314	-	GU473349	-

Actinoidea	Haloclavidae	*Peachia*	*quinquecapitata*	Sanriku	-	+	-	+	-	+	-
		Antennapeachia	*jambio*	Off Misaki	NSMT-Co 1596	+	+	+	-	+	-
		Antennapeachia	*jambio*	Off Misaki	CMNH-ZG 6546	+	+	+	-	+	-
		Anemonactis	*minuta*	Misaki	NSMT-Co 1619	+	+	-	-	+	-
		Anemonactis	*minuta*	Ogasawara	NSMT-Co 1622	+	+	-	-	+	-
		Haloclava	sp. nov. 28	Off Misaki	(Iz-088)	+	+	-	-	+	-
		Haloclava	sp. nov. 28	Off Mie Pref.	(Iz-089)	+	+	+	-	+	-
		gen.	sp.	Aburatsubo Bay	-	+	+	+	-	+	-
	Actiniidae	*Actinia*	*fragacea*	(GenBank)		EU190714	EU190756	EU190845	-	GU473334	-
		Anemonia	*viridis*	(GenBank)		EU190718	EU190760	EU190849	-	GU473335	-
		Anthopleura	*elegantissima*	(GenBank)		EU190713	EU190755	EU190844	-	GU473333	-
		Anthostella	*stephensoni*	(GenBank)		JQ810719	JQ810721	JQ810723	-	JQ810726	-
		Bolocera	*kerguelensis*	(GenBank)		KJ482925	KJ482965	KJ483029	-	KJ482985	-
		Bunodactis	*verrucosa*	(GenBank)		EU190723	EU190766	EU190854	-	-	-
		Bunodosoma	*grandis*	(GenBank)		EU190722	EU190765	EU190853	-	GU473336	-
		Epiactis	*lisbethae*	(GenBank)		EU190727	EU190771	EU190858	EU190816	GU473360	KT852231
		Glyphoperidium	*bursa*	(GenBank)		KJ482923	KJ482961	KJ483033	-	KJ482982	-
		Isotealia	*antarctica*	(GenBank)		JQ810720	JQ810722	-	-	JQ810727	-
		Isosicyonis	*alba*	(GenBank)		-	KJ482959	KJ483030	-	KJ482981	-
		Isosicyonis	*striata*	(GenBank)		EU190736	EU190781	EU190864	-	FJ489493	-
		Korsaranthus	*natalinesis*	(GenBank)		KJ482920	KJ482958	KJ483017	-	KJ482987	-
		Macrodactyla	*doreenensis*	(GenBank)		EU190739	EU190785	EU190867	-	GU473342	-
		Urticina	*coriacea*	(GenBank)		GU473282	EU190797	EU190877	-	GU473351	-
	Actinodendridae	*Actinostephanus*	*haeckeli*	(GenBank)		KJ482936	EU190762	KJ483034	-	GU473353	-
	Haloclavidae	*Haloclava*	*producta*	(GenBank)		EU190734	EU190779	AF254370	-	JF833008	-
		Haloclava	sp.	(GenBank)		KJ482924	KJ482963	KJ483031	-	KJ482989	-
		Harenactis	*argentina*	(GenBank)		KJ482926	KJ482964	KJ483026	-	KJ482984	-
		Peachia	*cylindrica*	(GenBank)		EU190743	EU190789	KJ483015	-	-	-
		Stephanthus	*antarcticus*	(GenBank)		KJ482927	KJ482960	KJ483019	-	KJ482983	-
	Liponematidae	*Liponema*	*brevicornis*	(GenBank)		EU190738	EU190784	EU190866	-	KJ483001	-
		Liponema	*multiporum*	(GenBank)		KJ482922	KJ482962	-	-	-	-
	Phymanthidae	*Phymanthus*	*loligo*	(GenBank)		EU190745	EU190791	EU190871	-	GU473345	-
	Preactiidae	*Dactylanthus*	*antarcticus*	(GenBank)		GU473272	AY345877	AF052896	-	GU473358	-
		Preactis	*milliardae*	(GenBank)		KJ482921	KJ482957	KJ483018	-	KJ482986	-
	Stichodactidae	*Heteractis*	*magnifica*	(GenBank)		EU190732	EU190777	EU190862	-	KJ482988	-
Metridioidea	Halcampidae	*Halcampa*	sp.	Off Misaki	-	+	+	+	-	+	-
		Halcampella	*maxima*	Off Misaki	(Iz-023)	+	+	+	+	+	-
		Halcampella	*maxima*	Off Misaki	(Iz-024)	+	+	+	-	-	-
		Halcampella	*cretata*	Off Misaki	(Iz-025)	+	+	+	+	-	-
		gen.	sp. nov. 4	Cape Maeda	(Iz-025)	+	+	+	+	+	-
		gen.	sp. nov. 4	Cape Maeda	(Iz-026)	+	+	-	+	+	-
		gen.	sp. nov. 4	Cape Maeda	(Iz-027)	+	+	+	-	-	-
		gen.	sp. nov. 4	Cape Maeda	(Iz-028)	+	+	-	-	-	-
		gen.	sp. nov. 4	Australia	-	+	+	+	+	+	-
		gen.	sp. nov. 5	Off Mie Pref.	(Iz-034)	+	+	+	+	+	-
		gen.	sp. nov. 5	Off Mie Pref.	(Iz-035)	+	+	+	+	+	-
		gen.	sp. nov. 5	Off Mie Pref.	(Iz-036)	+	-	+	-	-	-
		gen.	sp.	Off Sado	-	+	+	+	+	+	-
	Andvakidae	*Synandwakia*	*hozawai*	Lake Akkeshi	CMNH-ZG (no registration)	+	+	+	-	+	-
		Synandwakia	*hozawai*	Lake Akkeshi	CMNH-ZG (no registration)	+	+	+	-	+	-

Actinoscyphiidae	*Actinoscyphia*	*plebeia*	(GenBank)	EU190712	EU190754	FJ489437	-	FJ489476	-
Aiptasiidae	*Aiptasia*	*mutabilis*	(GenBank)	JF832963	FJ489418	FJ489438	-	FJ489505	-
	Aiptasia	*pallida*	(GenBank)	EU190715	EU190757	EU190846	-	KJ482979	-
	Bartholomea	*annulata*	(GenBank)	EU190721	EU190763	EU190851	-	FJ489483	-
	Neoaiptasia	*morbilla*	(GenBank)	EU190742	EU190788	EU190869	-	JF833010	-
Aliciidae	*Alicia*	*sansibarensis*	(GenBank)	KJ482933	KJ482953	KJ483016	-	KJ483000	-
	Triactis	*producta*	(GenBank)	EU490525	-	EU190876	-	GU473350	-
Amphianthidae	*Amphianthus*	sp.	(GenBank)	FJ489413	FJ489432	FJ489450	-	FJ489502	-
	Peronanthus	sp.	(GenBank)	KJ482917	KJ482956	KJ483014	-	KJ482976	-
Andvakiidae	*Andvakia*	*boninensis*	(GenBank)	EU190717	EU190759	EU190848	-	FJ489479	-
	Andvakia	*discipulorum*	(GenBank)	GU473273	GU473287	GU473316	-	-	-
	Telmatactis	sp.	(GenBank)	JF832968	JF832979	KJ483013	-	-	-
Antipodactinidae	*Antipodactis*	*awii*	(GenBank)	GU473271	GU473286	GU473303	-	GU473337	-
Bathyphelliidae	*Bathyphellia*	*australis*	(GenBank)	FJ489402	FJ489422	EF589063	-	FJ489482	-
Boloceroididae	*Boloceroides*	*mcmurrichi*	(GenBank)	GU473270	-	EU190852	-	KJ483002	-
	Bunodeopsis	*globulifera*	(GenBank)	KJ482940	KJ482949	KJ483025	-	KJ482992	-
Diadumenidae	*Diadumene*	*cincta*	(GenBank)	EU190725	EU190769	EU190856	-	FJ489490	-
	Diadumene	*leucolena*	(GenBank)	JF832957	JF832977	JF832986	-	JF833006	-
	Diadumene	sp.	(GenBank)	JF832960	JF832976	JF832980	-	JF833005	-
Galantheanthemidae	*Galatheanthemum*	sp.	(GenBank)	KJ482918	KJ482955	KJ483012	-	KJ482977	-
	Galatheanthemum	*profundus*	(GenBank)	KJ482919	KJ482954	KJ483011	-	KJ482978	-
Gonatiniidae	*Gonactinia*	*prolifera*	(GenBank)	KJ482935	-	KJ483008	-	KJ482994	-
	Protantea	*simplex*	(GenBank)	KJ482939	KJ482970	KJ483010	-	KJ482993	-
Halcampidae	*Cactosoma*	*sp. nov.*	(GenBank)	GU473279	GU473297	GU473313	-	GU473346	-
	Halcampa	*duodecimcirrata*	(GenBank)	JF832966	EU190776	AF254375	-	-	-
	Halcampoides	*purpurea*	(GenBank)	EU190735	EU190780	AF254380	-	-	-
Haliplanellidae	*Haliplanella*	*lineata*	(GenBank)	EU190730	EU190774	EU190860	-	FJ489506	-
Hormathiidae	*Actinauge*	*richardi*	(GenBank)	EU190719	EU190761	EU190850	-	FJ489480	-
	Adamsia	*palliata*	(GenBank)	FJ489398	FJ489419	FJ489436	-	FJ489474	-
	Allantactis	*parasitica*	(GenBank)	FJ489399	FJ489420	FJ489439	-	FJ489478	-
	Calliactis	*japonica*	(GenBank)	FJ489403	FJ489423	FJ489441	-	FJ489486	-
	Calliactis	*parasitica*	(GenBank)	EU190711	EU190752	EU190842	-	FJ489475	-
	Calliactis	*polypus*	(GenBank)	FJ489407	FJ489427	FJ489445	-	FJ489485	-
	Calliactis	*tricolor*	(GenBank)	FJ489405	FJ489425	FJ489443	-	FJ489488	-
	Chondrophellia	*orangina*	(GenBank)	FJ489406	FJ489426	FJ489444	-	FJ489489	-
	Hormathia	*armata*	(GenBank)	EU190731	EU190775	EU190861	-	FJ489491	-
	Hormathia	*lacunifera*	(GenBank)	FJ489409	FJ489428	FJ489446	-	FJ489492	-
	Hormathia	*pectinata*	(GenBank)	FJ489415	FJ489430	FJ489448	-	FJ489497	-
	Paracalliactis	*japonica*	(GenBank)	FJ489411	FJ489429	FJ489447	-	FJ489496	-
	Paraphelliactis	sp.	(GenBank)	FJ489412	FJ489431	FJ489449	-	FJ489498	-
Isanthidae	*Isanthus*	*capensis*	(GenBank)	JF832967	GU473291	GU473307	-	GU473362	-
Kadosactinidae	*Alvinactis*	*chessi*	(GenBank)	GU473278	GU473296	GU473312	-	GU473352	-
	Cyananthea	*hourdezi*	(GenBank)	GU473275	GU473293	GU473309	-	GU473364	-
	Kadosactis	*antarctica*	(GenBank)	FJ489410	EU190782	EU190865	-	FJ489504	-
	Metridium	*senile*	(GenBank)	EU190740	EU190786	AF052889	-	FJ489494	-
Nemathidae	*Nemanthus*	*nitidus*	(GenBank)	EU190741	EU190787	EU190868	-	FJ489495	-
Phelliidae	*Phellia*	*gausapata*	(GenBank)	EU190744	EU190790	EU190870	-	FJ489473	-
	Phellia	*exlex*	(GenBank)	JF832958	JF832978	JF832984	-	JF833004	-

	Sagartiidae	*Actinothoe*	*sphyrodeta*	(GenBank)		FJ489401	FJ489421	FJ489440	-	FJ489481	-
		Anthothoe	*chilensis*	(GenBank)		FJ489397	FJ489416	FJ489434	-	FJ489470	-
		Cereus	*pedunculatus*	(GenBank)		EU190724	EU190767	EU190855	-	FJ489471	-
		Cereus	*herpetodes*	(GenBank)		JF832956	JF832969	JF832983	-	-----------	-
		Sagartia	*troglodytes*	(GenBank)		EU190746	EU190792	EU190872	-	FJ489499	-
		Sagartia	*ornata*	(GenBank)		JF832959	JF832975	JF832985	-	JF833011	-
		Sagartiogeton	*laceratus*	(GenBank)		EU190748	EU190794	EU190874	-	FJ489500	-
		Sagartiogeton	*undatus*	(GenBank)		FJ489400	FJ489417	FJ489435	-	FJ489472	-
		Verrillactis	*paguri*	(GenBank)		FJ489414	FJ489433	FJ489440	-	FJ489503	-
Unknown	Capneidae	*Capnea*	*japonica*	Off Misaki	CMNH-ZG 06547	+	+	+	-	+	-
	Capneidae	*Capnea*	*georgiana*	(GenBank)		-	KJ482951	KJ483022	-	KJ482990	-
	fam.	gen.	sp. nov. 27	Misaki	(Iz-082)	+	+	+	-	+	-
		gen.	sp. nov. 27	Misaki	(Iz-084)	+	+	+	-	+	-
		gen.	sp. nov. 27	Off Tsushima	(Iz-086)	+	+	+	-	+	-
Zoanthidea											
	Epizoanthidae	*Epizoanthus*	*illoricatus*	(GenBank)		AY995901	EU591597	KC218424	-	-	-
	Parazoanthidae	*Parazoanthus*	*axinellae*	(GenBank)		GQ464940	EU828754	KC218416	-	-	-
		Savalia	*savaglia*	(GenBank)		AY995905	DQ825686	HM044299	-	-	-
Undknown	Relicanthidae	*Relicanthus*	*daphneae*	(GenBank)		KJ482934	KJ482971	KJ483028	-	-	-

Table 7. The substitution models of phylogenetic analyses on each marker. Markers indicated by (None) were not used in the analysis.

Analysis levels		Mitochondrial			Nuclear		
		12S rDNA	16S rDNA	COXIII DNA	18S rDNA	28S rDNA	5.8S rDNA/ITS1/ITS2
Order Actiniaria (Chapter 1A, Fig. 6)	ML analysis	GTR+Gamma	GTR+Gamma	(None)	GTR+Gamma	(None)	(None)
	Bayesian inference	GTR+Gamma	HKY85+Gamma		SYM+Gamma		
Suborder Anenthemonae (Chapter 1B, Fig. 7)	ML analysis	GTR+Gamma	GTR+Gamma	(None)	GTR+Gamma	GTR+Gamma	GTR+Gamma
	Bayesian inference	GTR+Gamma	GTR+Gamma		K80+Gamma	GTR+Gamma	K80+Gamma
Suborder Enthemonae (Chapter 1C, Fig. 8)	ML analysis	GTR+Gamma	GTR+Gamma	GTR+Gamma	GTR+Gamma	(None)	(None)
	Bayesian inference	GTR+Gamma	HKY85+Gamma	GTR+Gamma	SYM+Gamma		
Superfamily Actinernoidea (Chapter 1D, Figs. 9, 10)	ML analysis	GTR+Gamma	GTR+Gamma	(None)	GTR+Gamma	GTR+Gamma	GTR+Gamma
	Bayesian inference	HKY85+Gamma	K80+Gamma		K80+Gamma	GTR+Gamma	K80+Gamma
Superfamily Halcampelloidea (Chapter 1E, Fig. 11)	ML analysis	GTR+Gamma	GTR+Gamma	GTR+Gamma	GTR+Gamma	GTR+Gamma	(None)
	Bayesian inference	HKY85+Gamma	SYM+Gamma	HKY85+Gamma	SYM+Gamma	HKY85+Gamma	
Superfamily Edwardsioidea (Chapter 1F, Figs. 12, 13)	ML analysis	GTR+Gamma	GTR+Gamma	GTR+Gamma	GTR+Gamma	GTR+Gamma	GTR+Gamma
	Bayesian inference	HKY85+Gamma	HKY85+Gamma	HKY85+Gamma	K80+Gamma	GTR+Gamma	K80+Gamma

Table 8. The data partitions of each phylogenetic analysis.

	Order Actiniaria (Chapter 1A, Fig. 6)	Suborder Anenthemonae (Chapter 1B, Fig. 7)	Suborder Enthemonae (Chapter 1C, Fig. 8)	Superfamily Actinernoidea (Chapter 1D, Figs. 9, 10)	Superfamily Halcampelloidea (Chapter 1E, Fig. 11)	Superfamily Edwardsioidea (Chapter 1F, Figs. 12, 13)
Partitions	1–719 12S 720–1180 16S 1181–2910 18S	1-622 12S 623-1071 16S 1072-2831 18S 2832-4280 28S 4281-4792 ITS1/ITS2/5.8S	1-790 12S 791-1269 16S 1270-3007 18S 3008-3689 COXIII	1-440 16S 441-2148 18S 2149-3579 28S 3580-4054 ITS1/ITS2/5.8S 4055-4614 12S	1-612 12S 613-1067 16S 1068-2829 18S 2830-4284 28S 4285-4931 COXIII	1-618 12S 619-1070 16S 1071-2833 18S 2834-4272 28S 4273-4878 COXIII 4879-5406 ITS1/ITS2/5.8S

Results and Discussion

Chapter 1. Molecular Phylogeny of Actiniaria

1A. Order Actiniaria (Fig. 6)

Results. In the constructed phylogenetic tree of order Actiniaria, the species were separated into two clades (Fig. 6). One was the clade of species mainly of the suborder Enthemonae Rodríguez and Daly, 2014 (indicated by the red bar in Fig. 6), and the other was the clade of species mainly of Anenthemonae Rodríguez and Daly, 2014 (the blue bar in Fig. 6). The monophyly of each clade was supported with a bootstrap value of 100% and a posterior probability of 1 (the nodes indicated by A and B in Fig. 6). The topology was strongly supported by mitochondrial markers (with bootstrap values/posterior probabilities of 100%/1 on node A and 89%/1 on node B), but not supported well by the nuclear 18S rDNA marker (22%/0.55 on node A and 19%/0.52 on node B).

Although these two suborders established in Rodríguez et al. (2014) were shown to be almost monophyletic, there were two genera exceptionally placed in the clades of the other suborder. *Metedwardsia* Carlgren, 1947 had belonged to the family Edwardsiidae, Anenthemonae, but all three species of this genus were included in the clade of Enthemonae with high support rate (Fig. 6). As well, *Halcampella maxima* Hertwig, 1888, the type species of the genus *Halcampella* Andres, 1883 of the family Halcampidae, Enthemonae, was in the clade of Anenthemonae (Fig. 6). In addition, two unidentified halcampid species (Halcampidae gen. sp. 4 and Halcampidae gen. sp. 5) were also included in the clade of the suborder Anenthemonae.

Discussion. The traditional classification of sea anemones (Carlgren, 1949) recognized three suborders: the former suborder Protantheae Carlgren, 1891; Endocoelantheae Carlgren 1925; and Nynantheae Carlgren, 1899 within the order Actiniaria (Table 1). This classification was completely based on morphology, in particular, the sequences of mesenteries. Three families with peculiar mesenterial arrangements were accommodated in the former two suborders: Protantheae only included a family Gonactiniidae Carlgren, and Endocoelantheae included two families Halcuriidae Carlgren, 1918 and Actinernidae Stephenson, 1922 (the left side of Table 1). The remaining families were included in the suborder Nynantheae. However, Rodríguez et al. (2014) ascertained that this classification did not reflect the phylogeny of Actiniaria; hence, they instead divided Actiniaria into two suborders, Anenthemonae Rodríguez and Daly, 2014 and Enthemonae Rodríguez and Daly, 2014, according to their molecular phylogenetic analyses (the right side of Table 1).

According to my phylogenetic analysis among the entire Actiniaria (Fig. 6), the suborders established in Rodríguez et al. (2014) were almost supported (nodes A and B) except for the positioning of the two genera *Metedwardsia* and *Halcampella*. However, within each suborder, topology was not sufficiently reliable in this tree. Therefore, I separately analyzed each lower taxon by using more gene markers (see Chapter 1B–F).

1B. Suborder Anenthemonae (Fig. 7)

Results. Based on the results presented in Chapter 1A, I analyzed the species of the suborder Anenthemonae, including *Halcampella maxima* and two similar species (hereinafter called "Halcampella-like anemones") originally of Enthemonae and excluding the species of the genus *Metedwardsia*.

According to these results, Anenthemonae was divided into two clades. One was the clade of the species of superfamily Actinernoidea (indicated in the red box in Fig. 7), and the other was the clade of the species of superfamily Edwardsioidea and Halcampella-like anemones. In the latter clade, both Edwardsioidea (the blue box) and Halcampella-like anemones (the green box) became monophyletic clades, respectively. The monophyly of each clade was supported well with the bootstrap values of 85%–92% and posterior probabilities of 1 (nodes indicated in A–D in Fig. 7). The topology was strongly supported with nuclear markers (with bootstrap values/posterior probabilities of 99%/1 on node A, 89%/1 on node B, 98%/1 on node C, and 99%/1 on node D), but not supported well with mitochondrial markers (nodes A, B, and C were not supported, and node D was supported with s bootstrap value/posterior probability of 66%/1).

Discussion. The classification of Anenthemonae were established in Rodríguez et al. (2014). In the study, only two superfamilies Actinernoidea and Edwardsioidea were classified into this suborder. Superfamily Actinernoidea consisted of the species previously classified in suborder

Endocoelantheae Carlgren, 1925 in Carlgren (1949), and superfamily Edwardsioidea was a monotypic superfamily consisted of family Edwardsiidae Andres, 1881. However, as stated in Chapter 1A, several species of family Halcampidae of Enthemonae were included in the clade of Anenthemonae (Fig. 6).

According to my phylogenetic tree, three clades—Actinernoidea, Edwardsioidea, and Halcampella-like anemones—existed (indicated in different colored boxes in Fig. 7). Halcampella-like anemones were indicated as a sister group to Edwardsioidea with a high support rate (indicated at node B). However, the species of Halcampella-like anemones and species of Edwardsioidea scarcely resembled each other in morphology (see Chapter 2), thus I established a new superfamily, Halcampelloidea superfam. nov. for Halcampella-like anemones (see Table 9 for comparison of the morphology of the three superfamilies).

1C. Suborder Enthemonae (Fig. 8)

I constructed a phylogenetic tree of Enthemonae mainly using the sequences of Rodríguez et al. (2014) but included some additional sequences of the species obtained in this study, including several anemones of the genus *Metedwardsia* (Tables 4, 6). According to the constructed tree (Fig. 8), the clade of superfamily Actinostoloidea Carlgren, 1932 (indicated by the upper black bar in Fig. 8) was indicated to diverge at first, same as the results reported by Rodríguez et al. (2014). Concerning the other two superfamilies Actinioidea Rafinesque, 1815 and Metridioidea Carlgren, 1893, of which Rodríguez et al. (2014) also recognized as monophyletic, the monophyly of each superfamily was not supported in my phylogenetic analysis. Actinioidea (middle black bar in Fig. 8) was not monophyletic but paraphyletic to Metridioidea, and Metridioidea (lower black bar in Fig. 8) was not supported by the BI method.

The genus *Metedwardsia* had been accommodated in Edwardsiidae of Anenthemonae, but recently suspected as related to family Halcampidae Carlgren, 1893 (Gusmão et al., 2016). However, according to my phylogenetic analysis, the family Halcampidae (indicated in the pale green box in Fig. 8) was less related to the genus *Metedwardsia* (the green box) in Metridioidea: they formed clades at completely separated nodes, and hence, there was no possibility that *Metedwardsia* was within Halcampidae. In addition, no related species having similar morphology to *Metedwardsia* were found around the clade of *Metedwardsia* in this tree. This result suggested that an independent new family Metedwardsiidae fam. nov. should be established for the genus *Metedwardsia* in Metridioidea, Enthemonae (see Table 42 for comparison of Metedwardsiidae and the other families without basal discs in Metridioidea).

A species which could not be classified into any existing taxon (indicated in the red box in Fig. 8) formed a clade with the species of *Capnea* Forbes, 1841 (pale red box) in the clade of the superfamily Actinostoloidea. The unidentified species had quite peculiar disc-like bodies (Fig. 66) and several other peculiar characters that had been never known in the genus *Capnea*, in the family Capneidae, or even in the superfamily Actinostoloidea (see Table 35). Thus, I established a new genus *Discoactis* and a new family Discoactinidae fam. nov. for the species (see Table 35 for comparison of the morphology of the families of Actinostoloidea).

Synandwakia hozawai Uchida, 1932 (indicated in the yellow box in Fig. 8) of the family Andvakiidae was completely separated from the species of type genus *Andvakia* Danielessen, 1890 (the pale yellow box). Instead, this species was included in the clade of Diadumenidae. However, *S. hozawai* has a completely different morphology from that of the species of this family (Uchida, 1932b; Carlgren 1949). Thus, detailed morphological examination is required to clarify the taxonomic position of the genus *Synandwakia*.

Haloclavidae has been considered as a monophyletic family characterized by having one huge siphonoglyph on the ventral side of the actinopharynx (Carlgren, 1949; Barragan et al., 2018). However, Haloclavidae was paraphyletic according to my molecular analysis (indicated in the blue box in Fig. 8).

This phylogenetic tree still did not involve sufficient taxon sampling except Metedwardsiidae fam. nov. and Discoactinidae fam. nov., which I established in this study (see Chapter 2). Determination of the accurate phylogenetic relationship of Haloclavidae or the taxonomic position of *Synandwakia* and the family Andvakiidae requires further taxon samplings because the species of these taxa are distributed worldwide (e.g., Yap et al., 2014; Barragãn, 2019). Thus, in this study, the classification of Enthemonae was not rearranged except for a new genus and some new species in

Haloclavidae in addition to those two new families (see Chapter 2).

1D. Superfamily Actinernoidea (Figs. 9, 10)

Results. I analyzed the phylogeny of Actinernoidea by using 34 specimens of 11 species of all genera except *Carlgrenia* Stephenson, 1918, including both families, Actinernidae and Halcuriidae. Two large clades were formed in the phylogenetic tree (Fig. 9). One clade included three genera, *Actinernus, Isactinernus,* and *Synhalcurias* of Actinernidae, and the other included *Synactinernus* of Actinernidae and *Halcurias* of Halcuriidae. Actinernidae (the lineages indicated in pink in Fig. 9) became polyphyletic, and Halcuriidae (in orange) was paraphyletic (indicated by the orange bars in Fig. 9) to the genus *Synactinernus* (the pink bar). The monophyly of every node (A–D in Fig. 10) was supported with bootstrap values of 88%–100% and posterior probabilities of 1. The topology was strongly supported with nuclear markers (with bootstrap values/posterior probabilities of 98%/1 on node A, 100%/1 on node B, 87%/0.95 on node C, and 100%/0.99 on node D), but not supported well with mitochondrial markers (node A was not supported, and with bootstrap values/posterior probabilities of 98%/1 on node B, 51%/0.95 on node C, and 66%/0.99 on node D).

Discussion. The two families Actinernidae and Halcuriidae of the superfamily Actinernoidea have peculiar mesenterial arrangements. Only these two families develop their mesenteries of second mesenterial cycle in the endocoels of the mesenteries in the first cycle (Fig. 2C). Conversely, almost all species of actiniarians except for these two families develop mesenteries in the exocoels, out of the mesenterial pairs in the first cycle (Fig. 2D). Therefore, the previous classification system in Carlgren (1949) accommodated Actinernidae and Halcuriidae in the independent suborder Endocoelantheae and distinguished them from the other families (Table 1). Carlgren (1949) stated that these two families could be distinguished from each other by the number of cycles of mesenteries and the number of siphonoglyphs (see Introduction). This classification system of these families was still accepted until the present study. This is mainly because Actinernoidea anemones are scarcely collected owing to their rarity. Even Rodríguez et al. (2014), who conducted the most comprehensive phylogenetic analysis of Actinernoidea ever since, could contain only four species of this suborder (Table 4); hence, they only changed the taxonomic rank of actinernoidean anemones from suborder to superfamily and did not discuss regarding the inner classifications of the two families.

On the contrary, numerous specimens, 11 species covering five out of six genera of Actinernoidea, were analyzed in the molecular analysis in this study. Thus, I could show that Actinernidae was polyphyletic, and Halcuriidae was paraphyletic (Fig. 9). Based on the phylogeny, I successfully revised Actinernoidea (Fig. 10). The genus *Synactinernus* (indicated in the purple box in Fig. 10) was transferred to Halcuriidae; *Isactinernus* and *Synhalcurias* were accommodated into the newly established family Isactinernidae fam. nov. (indicated by the upper black bar) because there were few common features between *Actinernus* (in the orange box) and *Isactinernus/Synhalcurias* (in the green and yellow boxes); and some of the species of *Halcurias* were moved to the new genus *Isohalcurias* gen. nov. (in the blue box) to solve the paraphyly of the genus *Halcurias* (in the red box). This study finally showed that Japan has a very rich fauna of the superfamily Actinernoidea: six out of seven genera and over half of the species of the world were confirmed (see Table 10 for comparison of the morphology of the three families of Actinernoidea; and Table 12 for comparison of the four genera of Halcuriidae).

1E. Superfamily Halcampelloidea superfam. nov. (Fig. 11)

My phylogenetic analysis of the suborder Anenthemonae showed that Halcampella-like anemones formed the third clade of this suborder, and I recognized this clade as a new superfamily, Halcampelloidea (see Chapter 1A, 1B), thus I analyzed this superfamily independently. The obtained tree (Fig. 11) had three well-supported clades: a clade that included *Halcampella maxima* (indicated in the yellow box in Fig. 11), a clade of *Hexactis* sp. nov. 4 (in the green box), and a clade of *Pseudoedwardsia* sp. nov. 5 (in the blue box). One more specimen was included in this tree, but this specimen could not be morphologically identified because of its bad preservation (Halcampellidae gen. sp. in Fig. 11). In addition, an edwardsiid species, *Paraedwardsia cretata* (Stimpson, 1856), was included in the clade of Halcampelloidea and a sister group of *Halcampella maxima* (Fig. 11), and some morphological features were shared between these two species (see Chapter 2).

Based on these results, I established two new genera, *Hexactis* gen.

nov. and *Pseudoedwardsia* gen. nov., for *Hexactis* sp. nov. 4 and *Pseudoedwardsia* sp. nov. 5, respectively. *Paraedwardsia cretata* was moved into the genus *Halcampella*. Finally, this superfamily was composed of three genera in the new family Halcampellidae fam. nov. (see Table 15 for comparison of the morphology of the three genera of Halcampellidae).

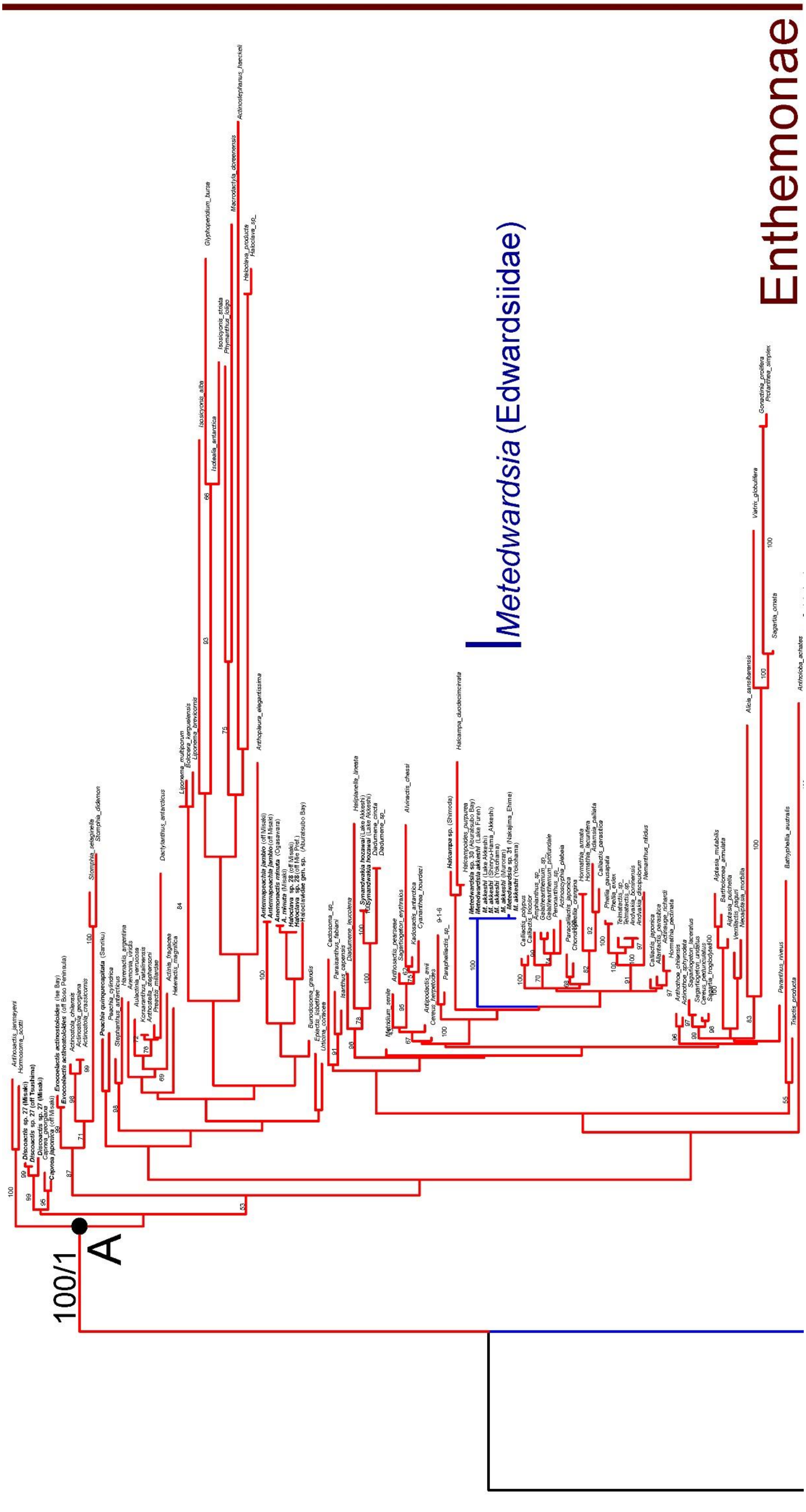
1F. Superfamily Edwardsioidea (Figs. 12, 13)

Results. According to the constructed phylogenetic tree (Figs. 12, 13), five genera, *Edwardsia* (indicated in blue in Fig. 12)*, Edwardsianthus* (green), *Scolanthus* (red), *Isoscolanthus* (gray), and *Paraedwardsia* (yellow; except for *Paraedwardsia cretata*), formed a large clade with a high support value (with a bootstrap value/posterior probability of 90%/1 on node A in Fig. 12). This node was also comparatively supported with both mitochondrial and nuclear markers (with bootstrap values/posterior probabilities of 72%/0.86 and 84%/1, respectively). In this large clade, five small subclades were recognized (Fig. 13). *Edwardsianthus* formed a monophyletic subclade out of the five, but the species of *Scolanthus, Isoscolanthus,* and *Paraedwardsia* were mingled with the species of *Edwardsia* in subclades 2–4 (Fig. 12). The other five genera, *Tempuractis* (indicated in pink in Fig. 12), *Edwardsiella* (light blue), *Nematostella* (light green), *Halcampogeton* (purple), and *Drillactis* (orange)*,* were independent from the large clade. However, except for *Drillactis,* showed that the most related genera to *Edwardsia* with reliable support rates (with 68%/0.97; Figs. 12, 13), the diverging order of these genera was not certain because of the poor support rates.

Discussion. I performed the phylogenetic analysis for Edwardsioidea (including only Edwardsiidae) by using nine out of 10 known edwardsiid genera and the genus *Tempuractis* Izumi, Ise and Yanagi, 2019 (Tables 4, 6). Only sequences on GenBank were used for *Nematostella* Stephenson, 1935, whereas the sequences for the other nine genera—*Edwardsia* de Quatrefages, 1842*, Edwardsianthus* England, 1987*, Scolanthus* Gosse, 1853*, Isoscolanthus* Brandão, Gusmão and Gomes, 2019, *Paraedwardsia* Carlgren in Nordgaard, 1905*, Drillactis* Verrill, 1922*, Halcampogeton* Carlgren, 1937*, Edwardsiella* Andres, 1883*,* and *Tempuractis*—were obtained in this study. Hence, almost all (10 of 11) genera of Edwardsiidae were included in this analysis. Only *Synhalcampella* Wyragévitch, 1905 (of which I could not obtain both specimens and DNA information) was not included. The present analysis included 60 species of 11 genera, whereas the phylogenetic study in Rodríguez et al. (2014) included only 5 species of 3 genera. Although the analysis in Daly (2002a) contained 29 species of 5 genera, their analysis was based mainly on morphological data and did not use molecular data. Thus, the number of taxa analyzed molecularly in this study was considerably larger than that analyzed in any other preceding studies, and I successfully clarified the phylogeny of Edwardsiidae (Fig. 12).

Receiving the result of the phylogenetic analysis, determining how to rearrange the five genera, *Edwardsia, Edwardsianthus, Scolanthus, Isoscolanthus*, and *Paraedwardsia*, was necessary. The result showed that the five genera that had been morphologically distinguished were included in one large clade and not well separated from each other in molecular phylogeny (Fig. 12). The five genera of this large clade just shared one prominent common morphological feature—the presence of nemathybomes. Nemathybomes are one of the specific morphological features of Edwardsiidae, but they are limited to some genera of Edwardsiidae (Carlgren, 1949; Daly, 2002a). These five genera are the only genera with nemathybomes, and the remaining six genera (including *Synhalcampella*) lacked them. Conversely, there was no apparent diagnostic morphological feature to distinguish the subclades in the large clade each other. Hence, I only settled these five subclades provisionally (Fig. 13) and did not assign genera or subgenera to them. In this study, I simply synonymized *Edwardsianthus, Scolanthus, Isoscolanthus*, and *Paraedwardsia* into *Edwardsia*, the most senior previously established genus of the five (following the International Code of Zoological Nomenclature; Ride et al., 1999).

The other six genera of Edwardsiidae need to be retained because they can be morphologically distinguished from the genus *Edwardsia* (after synonymizing the four genera) and from each other (see Table 17 for comparison of the morphology of the seven genera of Edwardsiidae).


Enthemonae
Metedwardsia (Edwardsiidae)
100/1
A
Anthosactis_janmayeni
Hormosoma_scotti
Discoactis sp. 27 (Misaki)
Discoactis sp. 27 (off Tsushima)
Discoactis sp. 27 (Misaki)
Capnea_georgiana
Caprea japonica (off Misaki)
Exocoelactis actinostoloides (Ise Bay)
Exocoelactis actinostoloides (off Boso Peninsula)
Actinostola_chilensis
Actinostola_georgiana
Actinostola_crassicornis
Peachia quinquecapitata (Sanriku)
Peachia_cylindrica
Stephanthus_antarcticus
Stomphia_selaginella
Stomphia_didemon
Hormathia_argentina
Anemonia_viridis
Aulactinia_verrucosa
Korsaranthus_natalensis
Anthopleura_stephensoni
Phlyctenactis_tuberculosa
Actinia_fragacea
Heteractis_magnifica
Dactylanthus_antarcticus
Liponema_multiporum
Bolocera_kerguelensis
Liponema_brevicornis
Isosicyonis_alba
Isoparactis_antarctica
Isosicyonis_striata
Phymanthus_loligo
Glyphoperidium_bursa
Macrodactyla_doreensis
Actinostephanus_haeckeli
Halcodava_producta
Halcodava_sp_
Anthopleura_elegantissima
Antennapeachia jamblo (off Misaki)
Antennapeachia jamblo (off Misaki)
Anemonactis minuta (Ogasawara)
A. minuta (Misaki)
Halcodava sp. 28 (off Misaki)
Halcodava sp. 28 (off Mie Pref.)
Halcodava gen. sp. (Aburatsubo Bay)
Bunodosoma_grandis
Epiactis_lisbethae
Urticina_coriacea
Cactosoma_sp_
Paranthus_fabiani
Isanthus_capensis
Diadumene_leucolena
Haliplanella_lineata
Synandwakia hozawai (Lake Akkeshi)
Synandwakia hozawai (Lake Akkeshi)
Diadumene_cincta
Diadumene_sp_
Metridium_senile
Anthosactis_pearseae
Sagartiogeton_erythraios
Alvinactis_chessi
Kadosactis_antarctica
Cyananthea_hourdezi
Antipodactis_awii
Cereus_herpetodes
Paraphelliactis_sp_
Halcampa sp. (Shimoda)
Halcampoides_purpurea
Halcampa_duodecimcirrata
Metedwardsia sp. 30 (Aburatsubo Bay)
Metedwardsia akkeshi (Lake Furen)
M. akkeshi (Lake Akkeshi)
M. akkeshi (Shinyu-Hama, Akkeshi)
M. akkeshi (Yokohama)
M. akkeshi (Muroran)
Metedwardsia sp. 31 (Nakajima, Ehime)
M. akkeshi (Yokohama)
Calliactis_polypus
Calliactis_tricolor
Amphianthus_sp_
Galatheanthemum_sp_
Galatheanthemum_profundale
Paranthus_sp_
Actinauge_plebeia
Paracalliactis_japonica
Chondrophellia_coronata
Hormathia_armata
Hormathia_lacunifera
Adamsia_palliata
Calliactis_parasitica
Phellia_gausapata
Phellia_exlex
Telmatactis_sp_
Telmatactis_sp_
Andvakia_boninensis
Andvakia_discipulorum
Nemanthus_nitidus
Calliactis_japonica
Allantactis_parasitica
Actinauge_richardi
Hormathia_pectinata
Anthothoe_chilensis
Actinothoe_sphyrodeta
Sagartiogeton_laceratus
Sagartiogeton_undatus
Cereus_pedunculatus
Sagartia_troglodytes
Aiptasia_mutabilis
Bartholomea_annulata
Aiptasia_pulchella
Verrillactis_paguri
Neoaiptasia_morbilla
Alicia_sansibarensis
Viatrix_globulifera
Gonactinia_prolifera
Protanthea_simplex
Sagartia_ornata
Antholoba_achates
Paranthus_niveus
Bathyphellia_australis
Tractis_producta
100
99
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95
87
53
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93
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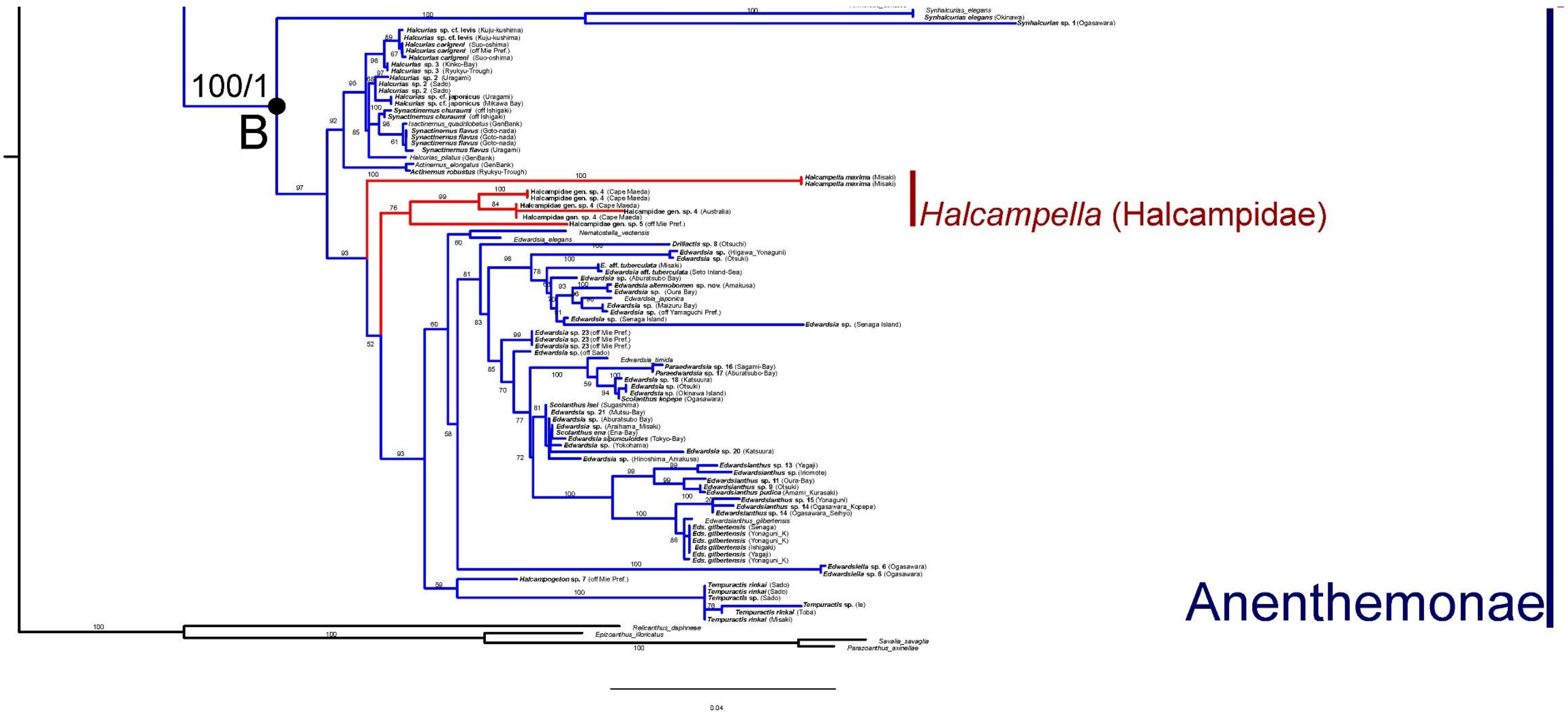

Fig. 6. Maximum-likelihood tree of the order Actiniaria based on the combined dataset of mitochondrial 12S and 16S and nuclear 18S rDNA (total 2910 bp).
The branches of the species that had been classified in the suborder Enthemonae are colored in red, and species in Anenthemonae are in blue. Two clades of suborders are indicated in red and blue bars. 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 ≥50% are shown). Nodes in A and B indicate the bases of the clades of suborder Enthemonae and Anenthemonae, respectively.

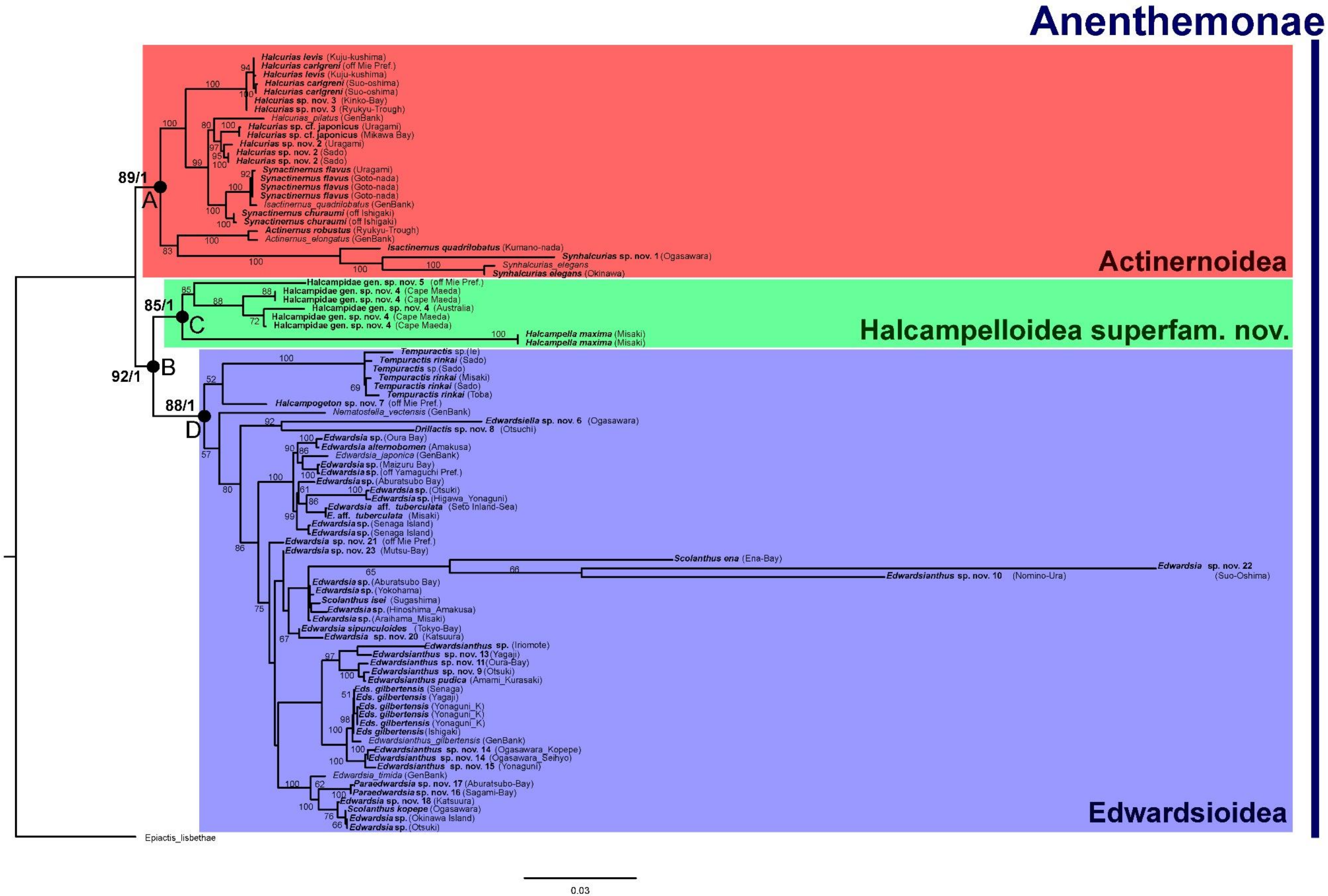

Fig. 7. Maximum-likelihood tree of the suborder Anenthemonae based on the combined dataset of mitochondrial 12S and 16S; nuclear 18S, 28S, and 5.8S rDNA; and ITS1/ITS2 (total 4792 bp).
The three clades of superfamilies are indicated in boxes in different colors. Numbers connected with slash characters above or below branches indicate ML bootstrap support values, followed by BI posterior probabilities of nodes A–D. Numbers without slash characters indicate ML bootstrap support values of the nodes (bootstrap values of ≥50% are shown). The node in A indicates the base of the clade of superfamily Actinernoidea; node B indicates that of the clade of superfamilies Edwardsioidea and Halcampelloidea superfam. nov.; node C indicates that of the clade of superfamily Halcampelloidea; and node D indicates that of superfamily Edwardsioidea.

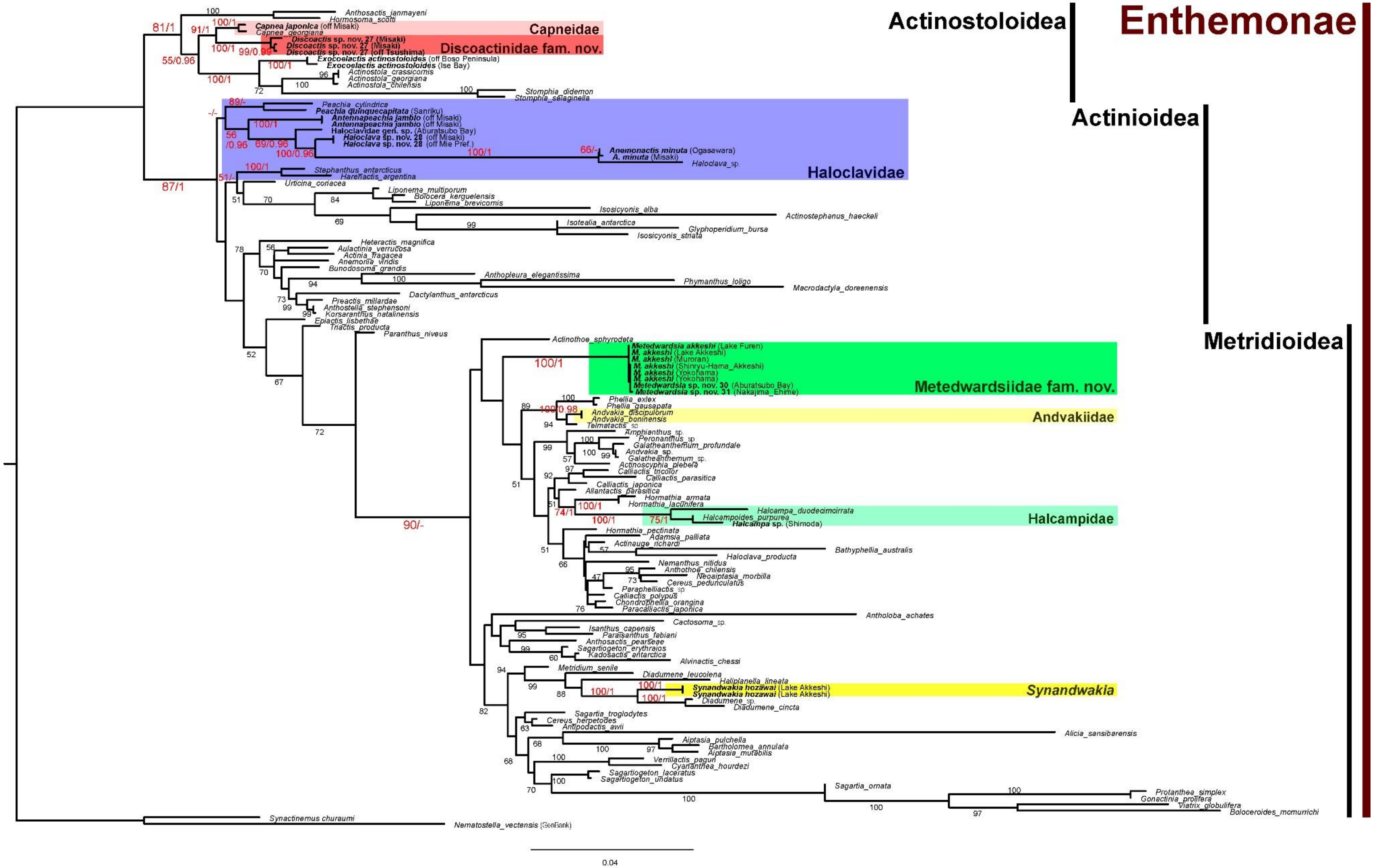

Fig. 8. Maximum-likelihood tree of the suborder Enthemonae based on the combined dataset of mitochondrial 12S and 16S rDNA and COXIII DNA as well as nuclear 18S rDNA (total 3689 bp).
The taxa mentioned in the present study are indicated in color boxes. Numbers connected with slash characters in red color above or below the branches indicate ML bootstrap support values, followed by BI posterior probabilities of the nodes (bootstrap values of ≥50% and posterior probabilities of ≥0.9 are shown). Numbers without slash characters indicate ML bootstrap support values of the nodes (bootstrap values of ≥50% are shown).

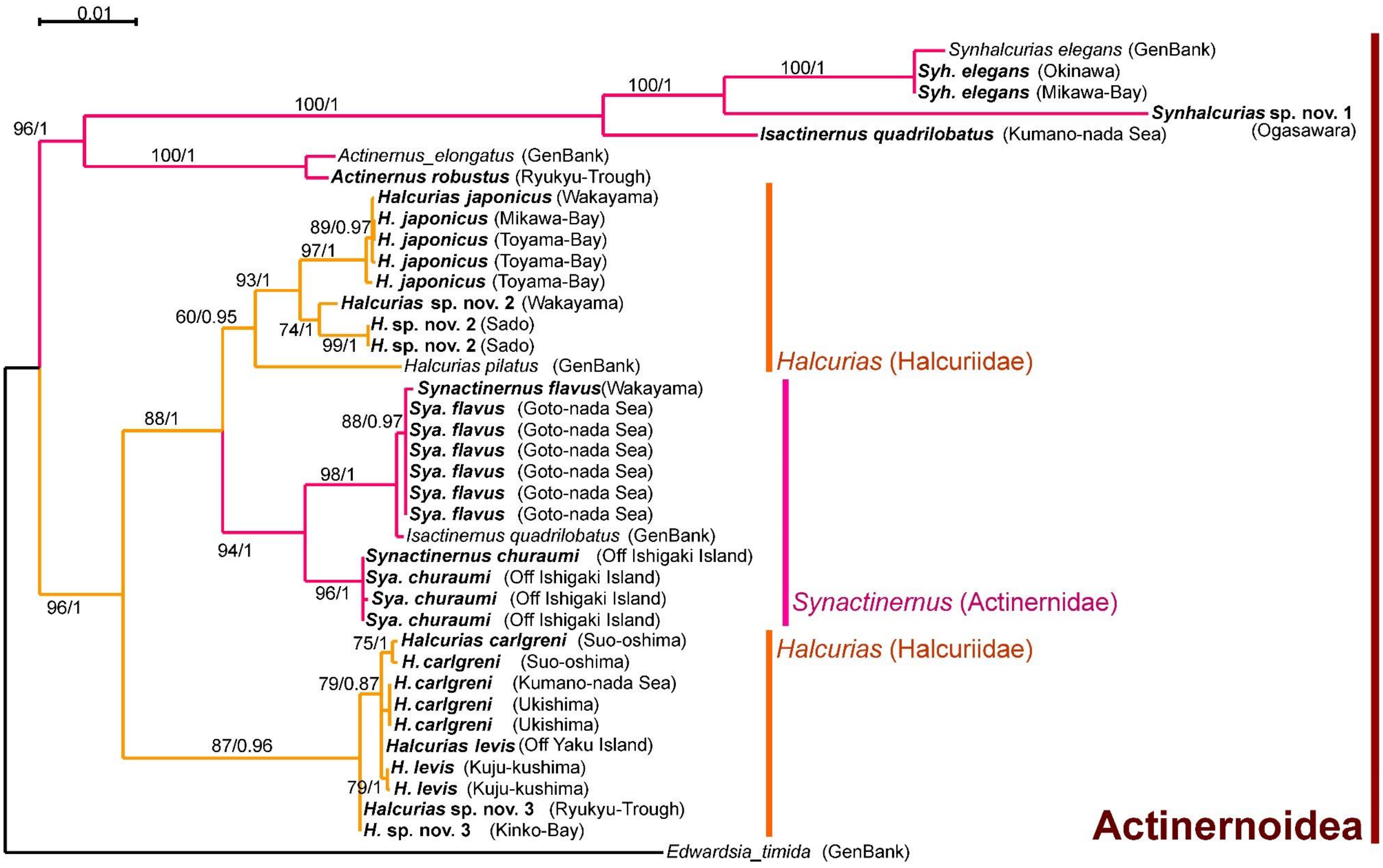

Fig. 9. Maximum-likelihood tree of the superfamily Actinernoidea based on the combined dataset of mitochondrial 12S and 16S; nuclear 18S, 28S, and 5.8S rDNA; and ITS1/ITS2 (total 4614 bp).
The lineages of the species that had been classified in the family Actinernidae are colored in pink, and lineages of species of the family Halcuriidae are in orange. The bar in pink indicates the genus *Synactinernus* (Actinernidae), and two orange bars indicate the genus *Halcurias* (Halcuriidae). Numbers above or below branches indicate ML bootstrap support values, followed by BI posterior probabilities of the nodes (bootstrap values of ≥50% and posterior probabilities of ≥0.9 are shown).

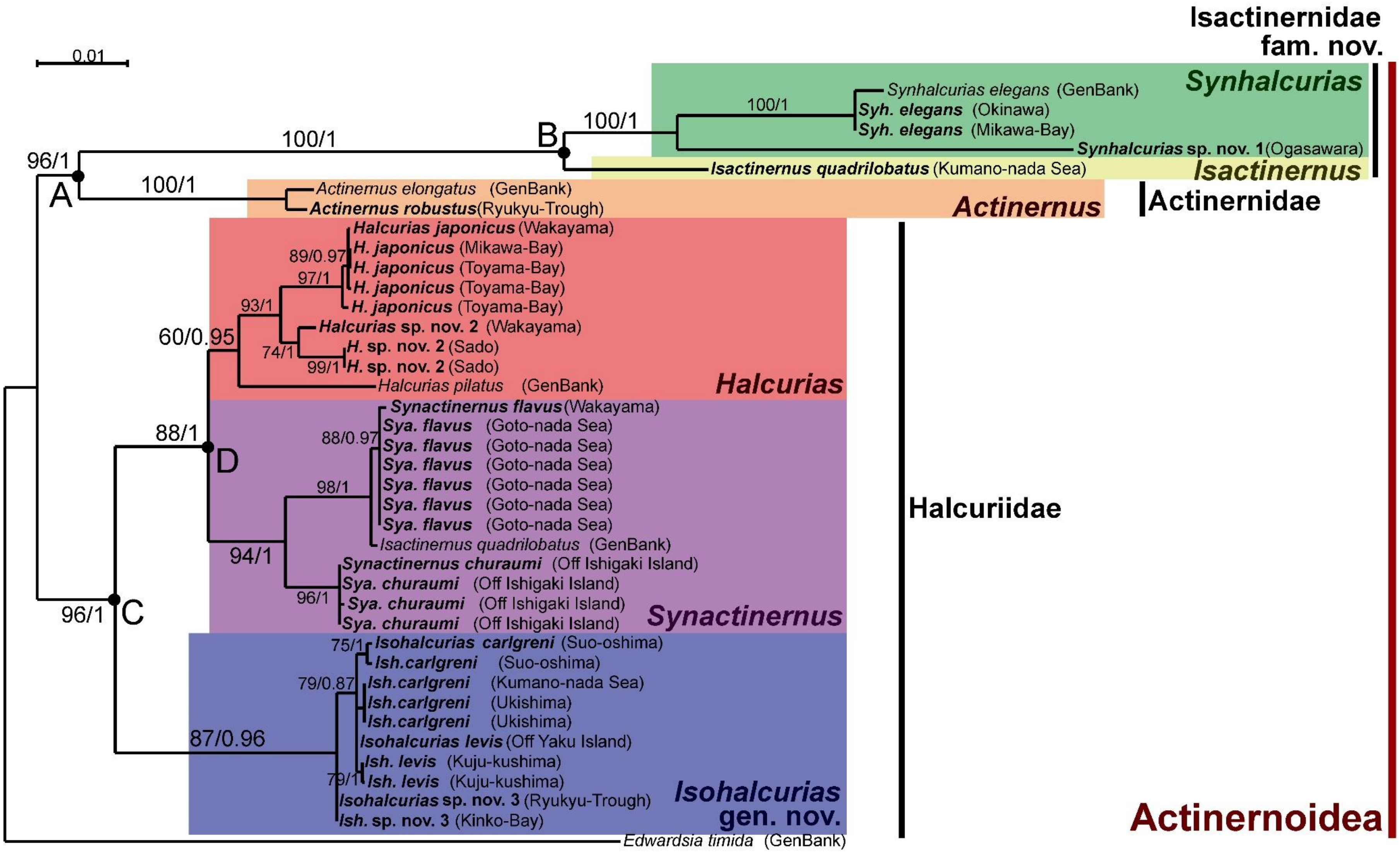

Fig. 10. Maximum-likelihood tree of the superfamily Actinernoidea based on the combined dataset of mitochondrial 12S and 16S; nuclear 18S, 28S, and 5.8S rDNA; and ITS1/ITS2 (total 4614 bp) following the new actinernoidean classification system.
Every clade of genera rearranged in the present study are indicated in boxes in different colors, and those of families are indicated by bars. Numbers above or below branches indicate ML bootstrap support values, followed by BI posterior probabilities of the nodes (bootstrap values of ≥50% and posterior probabilities of ≥0.9 are shown). The node in A indicates the base of the clade of families Actinernidae and Isactinernidae; node B indicates that of the clade of family Isactinernidae; node C indicates that of the clade of family Halcuriidae; and node D indicates that of genera *Halcurias* and *Synactinernus* in Halcuriidae.

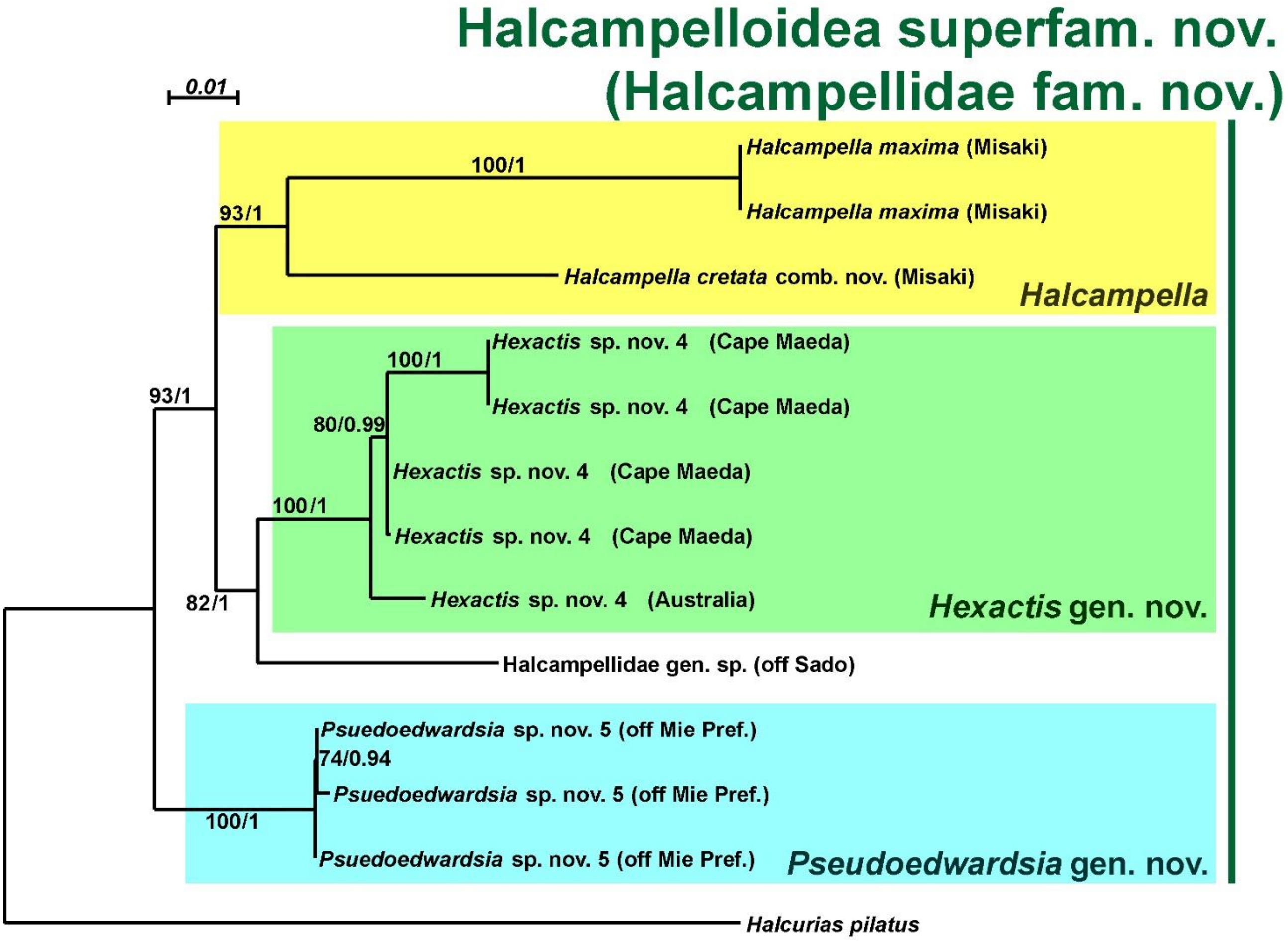

Fig. 11. Maximum-likelihood tree of the superfamily Halcampelloidea based on the combined dataset of mitochondrial 12S and 16S rDNA; COXIII DNA; and nuclear 18S and 28S rDNA (total 4931 bp) following the new halcampellid classification system.
Three clades of genera are indicated in boxes in different colors. Numbers above or below branches indicate ML bootstrap support values, followed by BI posterior probabilities of the nodes.

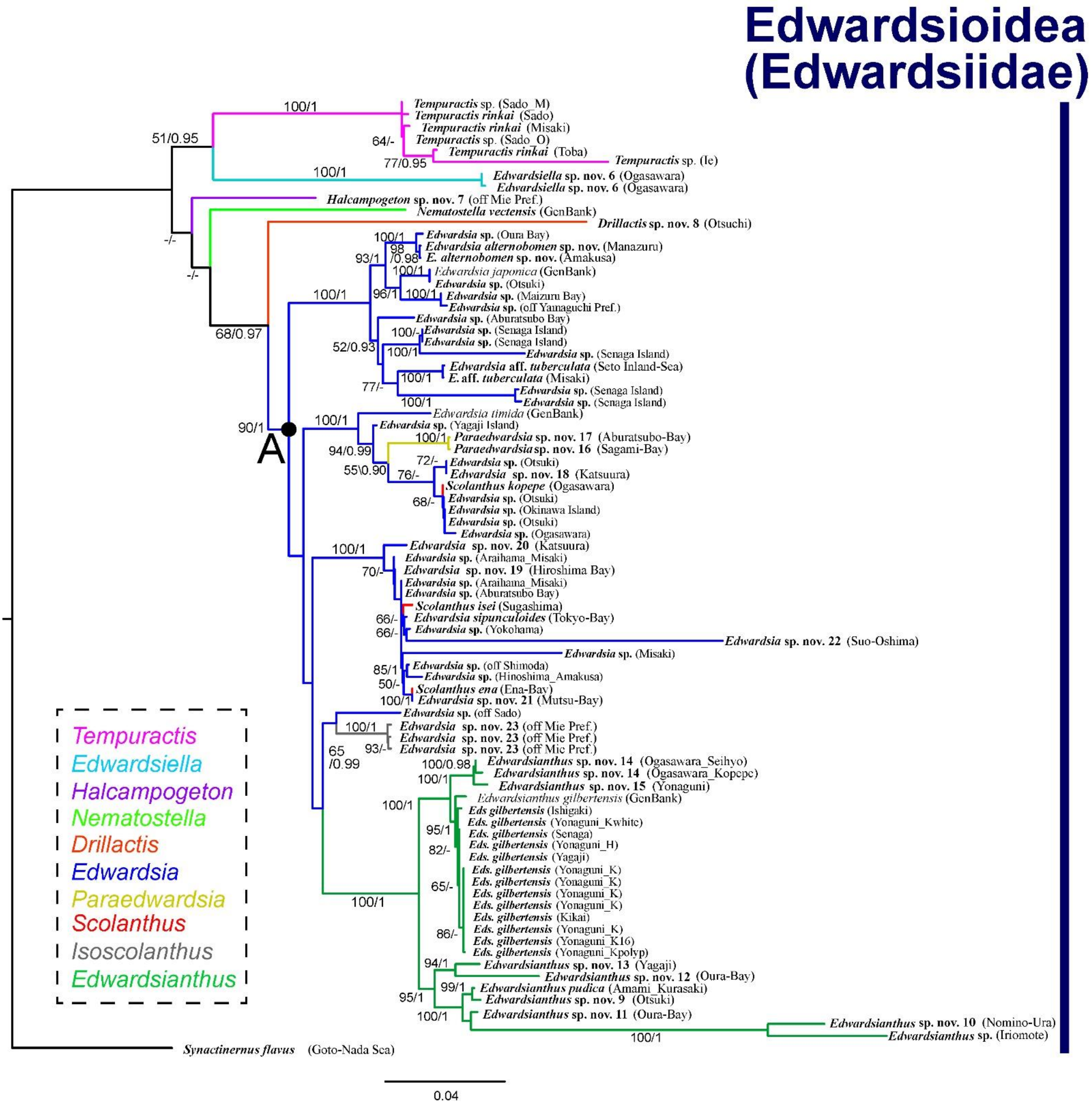

Fig. 12. Maximum-likelihood tree of the superfamily Edwardsioidea based on the combined dataset of mitochondrial 12S and 16S rDNA; COXIII DNA; nuclear 18S, 28S, and 5.8S rDNA; and ITS1/ITS2 (total 5406 bp).

The lineages of every genera are indicated in different colors (see the color pattern in this figure). Numbers above or below the branches indicate ML bootstrap support values, followed by BI posterior probabilities of the nodes (bootstrap values of ≥50% and posterior probabilities of ≥0.9 are shown). The node in A indicates the base of the clade of the genera *Edwardsia, Paraedwardsia, Scolanthus, Isoscolanthus*, and *Edwardsianthus*.

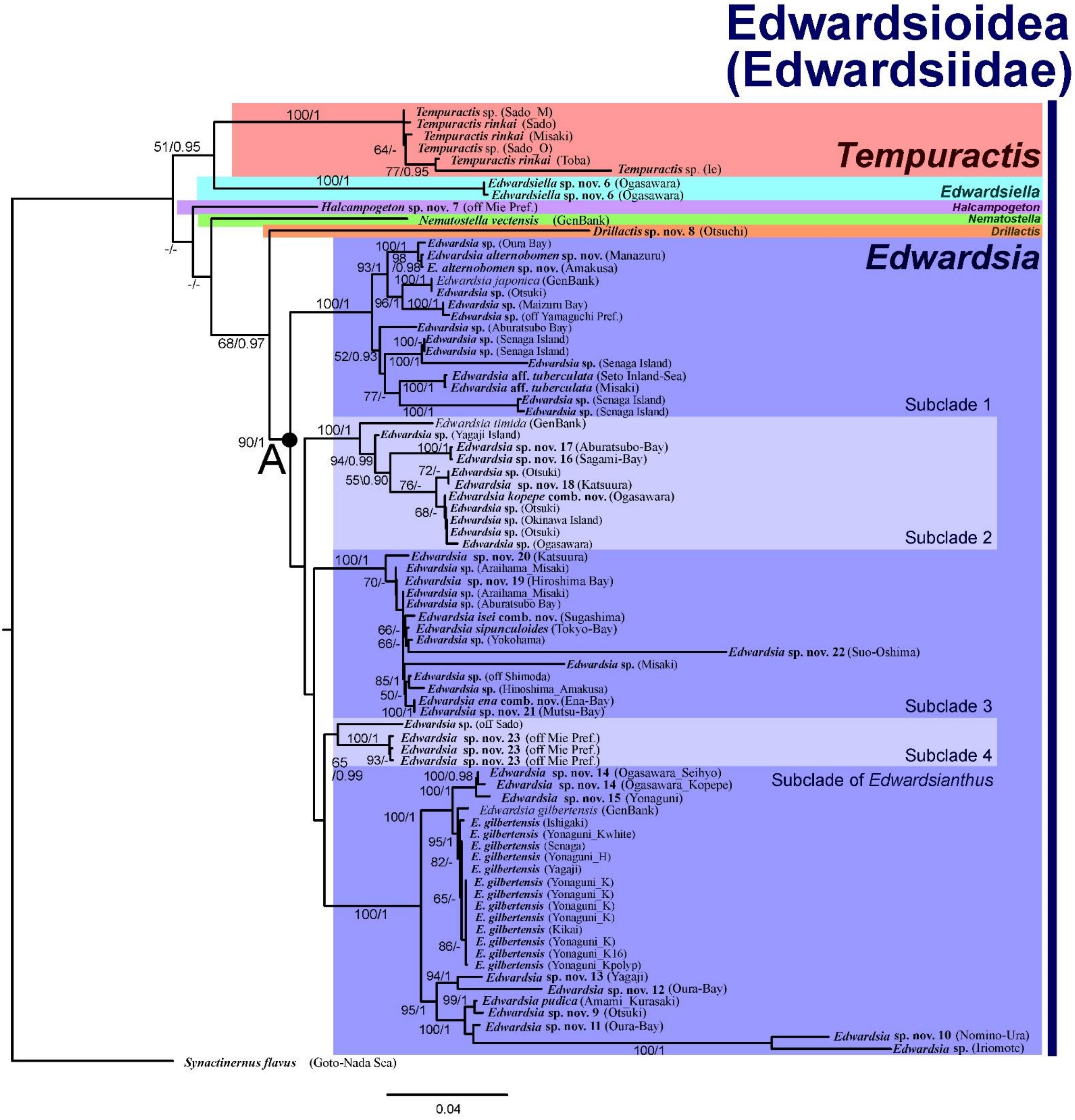

Fig. 13 Maximum-likelihood tree of the superfamily Edwardsioidea based on the combined dataset of mitochondrial 12S and 16S rDNA; COXIII DNA; nuclear 18S, 28S, and 5.8S rDNA; and ITS1/ITS2 (total 5406 bp) following the new edwardsiid classification system.
Every clade of genera rearranged in the present study are indicated in boxes of different colors. Numbers above or below the branches indicate ML bootstrap support values, followed by BI posterior probabilities of the nodes (bootstrap values of ≥50% and posterior probabilities of ≥0.9 are shown). The node in A indicates the base of the clade of the genus *Edwardsia,* after synonymizing four genera—*Paraedwardsia, Scolanthus, Isoscolanthus*, and *Edwardsianthus*—into it.

Chapter 2. Taxonomic account of Japanese Actiniaria

Order ACTINIARIA Hertwig, 1882

Suborder ANENTHEMONAE Rodríguez and Daly, 2014

(Japanese name: henkei-isoginchaku-amoku Izumi et al, 2019a)

Diagnosis. Actiniaria with proximal end either rounded, physa-like or with a more or less well-developed, flat **basal** disc; without basilar muscles. Column smooth, with nematocyst batteries or cuticle and tenaculi; divisible or not into different regions, without longitudinal ectodermal muscles. Tentacles simple, retractile or not, usually arranged hexamerously in alternating cycles or in cycles related to mesenterial arrangement. Marginal sphincter muscle usually absent, if present weak and mesogleal. Oral disc usually circular, but sometimes drawn out into lobes of varying appearance. Actinopharynx with one or two siphonoglyphs. Pairs of mesenteries distinctly arranged **in some groups**; either "only 8 macrocnemes mesenteries and at least 4 microcnemes" or "in cycles with pairs of mesenteries after first 12 mesenteries (six couples), appearing in lateral endocoels with longitudinal muscles oriented as in directives", **but the other groups have general mesenterial arrangement of Actiniaria.** Retractor muscles variable in shape, from diffuse to circumscribe. Parietobasilar muscles more or less strong; elongate forms usually with a well differentiated parietal muscle together with parietal part of longitudinal mesenterial muscles. Ciliated tracts of filaments present. Acontia absent. Cnidom: spirocysts, atrichs, basitrichs, holotrichs, microbasic *b*- and *p*-mastigophores.

(The revised points from Rodríguez et al. [2014] are indicated by **bold**)

Remarks. See Table 9 for comparison of the three superfamilies included in this suborder. Suborder Anenthemonae, established in Rodríguez et al. (2014) by their phylogenetic analysis, was defined as sea anemones having "strange mesenterial arrangements". The species of one superfamily, Actinernoidea Stephenson, 1922, develop their mesenteries in second cycle in their endocoels (while the all other anemones develop them in exocoels), and species of the other superfamily, Edwardsioidea Andres, 1881, have only eight macrocnemes (while almost all anemones have at least 12). These arrangements did not have any common point each other, thus Rodríguez et al. (2014) defined this suborder just by "unique" mesenterial arrangements (Izumi et al., 2019a). However, my phylogenetic analyses revealed that the third group, Halcampelloidea superfam. nov. was accommodates in this clade, and the group had completely general mesenterial arrangement of Actiniaria. Thus, the only common morphological feature was disappeared. Now, there is no synapomorphy among the three superfamilies, and it is expected that the common feature of this suborder will be discovered in future.

Superfamily ACTINERNOIDEA Stephenson, 1922

(Japanese name: yatsuba-kawari-ginchaku-jouka: Izumi et al., 2019a)

Diagnosis. Anenthemonae with well-developed **basal disc** but without basilar muscles. Column smooth, or with nematocyst batteries, nearly always with spirocysts. Margin tentaculate. Sphincter absent or weak mesogleal. Tentacles in variable number, with **or without** thickening aboral side, either in two alternating cycles or although usually arranged in cycles, in peculiar way related to development of mesenteries. Longitudinal muscles of tentacles and radial muscles of oral disc ectodermal, with a slight mesogleal tendency. Oral disc sometimes lobed. One or two siphonoglyphs. Usually more mesenteries than directives attached to siphonoglyphs. Unique mesenterial arrangement: after first 12 mesenteries (six couples) are developed, all subsequent pairs appear in lateral endocoels with longitudinal muscles oriented as in directives. Cnidom: spirocysts, basitrichs, holotrichs, microbasic *p*-mastigophores. (The revised points from Rodríguez et al. [2014] are indicated by **bold**)

Remarks. Actinernidae Verrill, 1879 and Halcuriidae Carlgren, 1918 have peculiar mesenterial arrangement. Despite almost all sea anemones develop their second cycle of mesenteries out of first cycle of mesenterial pairs (at exocoels), only species those two families develop them in the first cycle pairs (at endocoels). So, in the classification system of Carlgren (1949), they had been accommodated in the suborder Endocoelantheae Carlgren, 1925. However, the phylogenetic research of Rodríguez et al. (2014) revealed that species of Endocoelantheae were related to Edwardsiidae, and thus they established new suborder, Anenthemonae Rodríguez and Daly, 2014, for Actinernidae, Halcuriidae and Edwardsiidae. That was why Endocoelantheae was disappeared, and they used superfamily Actinernoidea Stephenson, 1922 instead to accommodate those two families.

There are confirmed two families and six genera of actinernoideans in Japan. According to my phylogenetic and morphological analyses (Figs. 9, 10), the monophyly was strongly supported as a superfamily, but a new family Isactinernidae and a new genus *Isohalcurias* were established.

See Table 10 for comparison of Isactinernidae fam. nov. and the other families of Actinernoidea. The new taxonomic key of this superfamily to each genera, including *Isohalcurias* gen. nov., is as below.

1A. Mesenteries distinguished macrocnemes and microcnemes.........2.
2A. Base of tentacles thickening in aboral side......*Actinernus* Verrill, 1879
2B. Tentacle simple, no thickening.........3.
3A. Edge of oral disc developed into lobes...*Synactinernus* Carlgren, 1918
3B. Edge of oral disc simple, not lobed.........4.
4A. 12 macrocnemes in column..................*Carlgrenia* Stephenson, 1918
4B. 20 macrocnemes in column.........5
5A. Spirocysts absent on column. Muscular processes simple and unified ....*Halcurias* McMurrich, 1893
5B. Spirocysts present on column. Part of retractor muscles pinnate ....***Isohalcurias* gen. nov.**
1B. All mesenteries perfect and macrocnemes............6
6A. Edge of oral disc developing into lobes.........*Isactinernus* Carlgren, 1918
6B. Edge of oral disc simple, not lobed.............*Synhalcurias* Carlgren, 1914

Family ACTINERNIDAE Stephenson, 1922
(Japanese name: yatsuba-kawari-ginchaku-ka Uchida, 1992)

Actinernidae Stephenson, 1922: 258; Carlgren, 1949: 20

Diagnosis. Actinernoidea with elongate body. Distal margin of column usually expanded and drawn into lobes, but sometimes not expanded nor lobed. Column with or without nematocyst batteries. Tentacles numerous, with basal **thickening** on their aboral side. With two siphonoglyphs. Mesenteries numerous, divisible into macro- and microcnemes**, and develop bilaterally.** Retractors rather weak. All stronger mesenteries fertile. **Cnidom: basitrichs, spirocysts, microbasic *p*-mastigophores**
(The revised points from Uchida [2007] are indicated by **bold**)

Type genus. *Actinernus* Verrill, 1879

Remarks. This family have accommodated four genera: *Actinernus* Verrill, 1879, *Synhalcurias* Carlgren, 1914, *Isactinernus* Carlgren, 1918 and *Synactinernus* Carlgren, 1918, and have been characterized by having two siphonoglyphs on their actinopharynx and lacking the deviation between macrocnemes and microcnemes (Carlgren, 1949). However, there was apparent deviation between macrocnemes and microcnemes only in *Actinernus* (see Uchida, 2007; Fig. 14) and *Synactinernus* (see Fig. 21, 23), so it had become doubtful that these four genera should be accommodated in same family.

In this study, my phylogenetic analysis (Fig. 9, 10) revealed that *Synactinernus* is not monophyletic with other three genera of Actinernidae but in the clade of Halcuriidae. So, it was necessary to eliminate this genus from Actinernidae. Moreover, there was no synapomorphy between *Actinernus* and the other two genera, and rather there were apparent differences between these genera in mesenterial arrangement and cnidom (see remarks part of Isactinernidae fam. nov.). That was why I established new family for *Isactinernus* and *Synhalcurias* and eliminated them from Actinernidae.

Finally, this family became monotypic of type genus *Actinernus*. The most characteristic feature of this genus is developing their mesenteries laterally: this arrangement is only observed on the species of *Actinernus* in Actinernoidea. In addition, the species of this family is distinguished from the species of the other two families by a combination of "lacking spirocysts in tentacle and column" and "thickening the aboral ends of tentacles".

Genus *Actinernus* Verrill, 1879
(Japanese name: Yatsuba-kawari-ginchaku-zoku)

Actinernus Verrill, 1879: 474; McMurrich, 1893: 165; Carlgren, 1914: 62; Carlgren, 1918: 31; Carlgren, 1921: 14, 184; Stephenson, 1922: 259; Carlgren, 1949: 20.

Porponia Hertwig, 1882, p. 111; Carlgren, 1914, p. 61.

Diagnosis. Column cylindrical, the upper part expanded and forms more or less distinctly 8 lobes. **Tentacles numerous, with basal thickening on their aboral side.** Mesenteries many, consist of **24–52 perfect** mesenteries and a half number of imperfect mesenteries. After formation of 10 pairs, 1st and 2nd cycles, further mesenterial formation takes place at the middle point of each 8 lateral endocoel. Then, the formation is not radial but bilateral way. Furthermore, the size in higher cycles of mesenteries is much different to its partner in each mesenterial pair. **Cnidom: basitrichs (all tissues), spirocysts (actinopharynx and filaments), microbasic *p*-mastigophores (actinopharynx**

and filaments).

(The revised points from Uchida [2007] are indicated by **bold**)

Type species. *Actinernus elongatus* (Hertwig, 1882)

Actinernus robustus (Hertwig, 1882)

(Japanese name: yatsuba-kawari-ginchaku)

Fig. 14

Porponia robusta Hertwig, 1882: 107, pl. 1 fig. 10a; Carlgren, 1914: 61.

Actinernus robustus: Carlgren, 1918: 12, 34, pl. 1 fig. 9; Stephenson, 1922: 259; Carlgren, 1949: 21

Material examined. CMNH-ZG 09735: specimen dissected, tissues embedded in paraffin, histological sections prepared, nematocysts prepared, corrected on 28 April 2002, from Okinawa Trough (27°02.34′N, 126°58.24′E; St. D-2), 1550 m in depth, during research cruise of R/V Tansei-Maru (KT02-3 reg. 2), by ORE beam trawl, by Kensuke Yanagi; CMNH-ZG 09736: specimen dissected, tissues embedded in paraffin, histological sections prepared, same collector, locality and method as CMNH-ZG 09735; CMNH-ZG 09737, 09738: whole specimens, same collector, locality and method as CMNH-ZG 09735; CMNH (no registration): specimen dissected, corrected on 23 September 2001, from Pacific off Kushiro (42°11.02′N, 146°17.02′E; St. XR-11), 5346–5473 m in depth, corrected during research cruise of R/V Hakuho-Maru (KH01-2), by ORE beam trawl, by Kensuke Yanagi. BM 89-11-25-30 (holotype): dissected specimen, collected in 1875 (date unknown), southeast off the Boso Peninsula (34°37′E, 140°32′E [collection information listed on the label]; depth unknown), in the Challenger Expedition (Fig. 22).

Diagnosis. ***External anatomy.*** Body cylindrical (Fig. 14A), up to ca. 2–6 cm in length and ca. 2.5–5 cm in width on preserved specimens. Column surface smooth, without any structures. Ectoderm of column easily peeled off, without nematocyst batteries, and nematocysts very sparsely distributed. The naked column opaque milky white in color (Fig. 14A). Basal disk in aboral end, thin and fragile, but adhesive (Fig. 14A). Upper part of column widely expanded and thrown into eight lobes, four larger and four smaller ones (Fig. 14B, C). Upper margin continued to tentacle bases, and the bases spines-like shape (Fig. 14A). Tentacles ca. 60–90 in number on oral disk, all marginal. All tentacles ca. 7–10 mm in length, pale white to brown in color, simple shape, but with strong thickenings at their aboral base. Oral disc pale brown, with radial streaks corresponding to every tentacle. Mouth at center of oral disk, apparently swelled, lip-like, brown in color.

Internal anatomy. ca. 24–52 macrocnemes (Fig. 14D) on actinopharynx; twelve, including four directives, in the first cycle; eight in the second cycle; maximum 16 in the third cycle; and maximum 16 in fourth cycle. Macrocnemes in the second cycle born in the endocoel of the first cycle mesenteries, and fourth ones in the endocoels of third ones (bilateral arrangement). Judged by the numbers of tentacles, more 20–40 microcnemes on distal end. Each tentacle either exo- or endocoelic. Tentacular longitudinal muscle and tentacular circular muscle both too weak to observe in histological sections. On aboral ends of tentacles, mesoglea apparently thickened. Retractor muscles extremely weak and diffused (Fig. 14D). Muscle processes very short, simple or a little branched, around 30–50 in each muscle pennon. Parietal muscles of macrocnemes very weak and indistinct, with a few muscle fibers. Mesoglea thickest in body wall and actinopharynx (Fig. 14D), reaching 2–2.5 mm in thickness, and far thicker than the ectoderm and endoderm. However, mesoglea thinner in mesenteries and basal disc (Fig. 14D, E), and thinnest in tentacles. Actinopharynx, with siphonoglyphs on dorsal and ventral sides (Fig. 14D), always connected to actinopharynx, and with ca. 8–12 longitudinal grooves as deep as siphonoglyphs. Sphincter muscle absent. On the aboral end, basilar muscle absent (Fig. 14E). Dioecious.

Cnidom. Basitrichs, spirocysts, and microbasic *p*-mastigophores.

Remarks. *Actinernus robustus* is the only species of this genus in Japan. My specimens were completely corresponded to the description of Hertwig (1882) and Uchida (2007). In contrast to all Japanese species of Actinernoidea which live between 20–500 m, this species inhabits in deeper than 1000 m.

Approximate morphology and cnidom of my specimens were corresponded to description of Hertwig (1882) and Uchida (2007), so these specimens can be identified as *A. robustus*. However, there were no holotrichs in filaments though Uchida (2007) observed a few ones.

Family ISACTINERNIDAE fam. nov.

(New Japanese name: yotsuba-kawari-ginchaku-ka)

Diagnosis. Actinernoidea with elongate body. Distal margin of column usually expanded and drawn into lobes, but sometimes not expanded nor lobed. Column with or without nematocyst batteries. Tentacles numerous, simple or with basal thickening or on their aboral side. With two siphonoglyphs. Mesenteries all macrocnemes, numerous, and developing cyclically. Retractors rather weak. All mesenteries fertile. Cnidom: basitrichs, spirocysts, microbasic *p*-mastigophores (each in all tissue)

Type genus. *Isactinernus* Carlgren, 1918

Etymology. Derived from the name of type genus, *Isactinernus* Carlgren, 1918.

Remarks. In this study, my phylogenetic analysis (Fig. 10) revealed that *Isactinernus* and *Synhalcurias* were the most related genera and became monophyletic with *Actinernus*. However, there was no synapomorphy between *Actinernus* and *Isactinernus/Synhalcurias* because *Synactinernus*, the polyphyletic genus of them, had almost all of general features of Actinernidae. Therefore, I could not find the accurate common feature shared with the remaining three genera. In addition, there were apparent differences between *Actinernus* and *Isactinernus/Synhalcurias* in mesenterial arrangements and cnidoms: in Actinernoidea, only latter two genera have microbasic *p*-mastigophores in tentacles and columns. In addition, only their mesenteries are all macrocnemes. That is why I establish new family for *Isactinernus* and *Synhalcurias* and eliminate them from Actinernidae (Fig. 15).

See Table 10 for comparison to the other genera of Halcuriidae. This family is characterized by possessing microbasic *p*-mastigophores in tentacles and columns and developing all mesenteries to macrocnemes.

Genus *Isactinernus* Carlgren, 1918
(Japanese name: yotsuba-kawari-ginchaku-zoku)

Isactinernus Carlgren, 1918: 29; Stephenson, 1922: 260; Carlgren, 1949: 20; Fautin and den Hartog, 2003: 107

Diagnosis. Column cylindrical, the upper part expanded, and forms 4 large lobes. With many tentacles**, thickening on aboral side**. Mesenteries ca. 34–**70** pair of large and many small ones, **all mesenteries** perfect and **almost all** fertile. After formation of 10 pairs of the oldest mesenteries, in 1st and 2nd cycles, further mesenterial formation by cyclic in each 8 lateral endocoel, just same manner as those of *Halcurias*. With two siphonoglyphs. Column ectoderm with minute nematocyst batteries. **Cnidom: basitrichs, spirocysts, microbasic *p*-mastigophores (each in all tissue).**

(The revised points from Uchida [2007] are indicated by **bold**)

Type species. *Isactinernus quadrilobatus* Carlgren, 1918

Remarks. This genus had been monotypic of *I. quadrilobatus* Carlgren, 1918 for a century. However, accompanied with Fautin and Hartog (2003), the work which synonymized *Synactinernus flavus* Carlgren, 1918 into *I. quadrilobatus,* genus *Synactinernus* became junior synonym of this genus. However, my phylogenetic analysis indicated that these genera are less related phylogenetically (Fig. 15): *I. quadrilobatus* and *S. flavus* are polyphyletic, less relative on the phylogenetic tree, and thus they should be accommodated in different family (see also remarks of *Synactinernus*).

That is why *Isactinernus* should be remained as a monotypic genus, same status as Carlgren (1918). However, this genus should not be accommodated into Actinernidae but should be included in the new family (see the remarks of the family Isactinernidae).

***Isactinernus quadrilobatus* Carlgren, 1918**

(Japanese name: yotsuba-kawari-ginchaku)

Fig. 15

Isactinernus 4-lobatus Carlgren, 1918: 7, 29, textfigs 5, 6, pl. 1 figs. 4, 5; Carlgren, 1940: 22; Carlgren, 1949: 20.

Isactinernus quadrilobatus Stephenson, 1922: 260; Fautin and den Hartog, 2003: 108–113, figs. 1–5.

Material examined. NSMT-Co 1662: specimen dissected, tissues embedded in paraffin, histological sections prepared, nematocysts prepared collected on March 8, 2016, from the Kumano-nada Sea off Hamajima Island, Mie Prefecture, around a depth of 350 m, by trawling of fishing boat *Kiei-Maru*, kept in Toba Aquarium for a while, and preserved on March 19, 2016 by Takeya Moritaki in 70 % ethanol, and re-preserved on April 19, 2016 by Takuma Fujii in 10 % formalin-seawater solution (v/v) for histological section; CMNH-ZG 09734: specimen dissected, tissues embedded in paraffin, histological sections prepared, nematocysts prepared collected on April 18, 2018, from the East China Sea off Koshikijima Island, Kagoshima Prefecture, around a depth of 380 m, by the fishing boat *Koei-Maru*, kept in Io-world Kagoshima Aquarium for a while, and preserved on 6 May 2018 by Takato

Izumi. UUZM 232 (a syntype): dissected specimen, May 5, 1914, off the Goto Islands (122°50′E [collection information listed on the label]), depth 165 m, collected by Sixten Bock (Fig. 22).

Description. ***External anatomy.*** Body cylindrical (Fig. 15A), up to ca. 4.5–7 cm in length and ca. 5 cm in width on preserved specimens. Column surface comparatively smooth, without any structures or with small tenaculi. Ectoderm of column pale white (Fig. 15A), with small nematocyst batteries. The naked column opaque milky white in color. Basal disk in aboral end, robust and adhesive (Fig. 15A). Upper part of column widely expanded and thrown into four large lobes (Fig. 15B). Upper margin continued to tentacle bases, and the bases numerous spines-like shape (Fig. 15B). Tentacles ca. 72–140 in number on oral disk, all marginal. All tentacles ca. 3–5 mm in length, pale white in color, simple shape, but with strong thickenings at their aboral base. Oral disc pale white, with radial streaks corresponding to every tentacle. Mouth at center of oral disk, apparently swelled, lip-like, cross-like shape, white in color.

Internal anatomy. ca. 72–140 macrocnemes on actinopharynx; twelve, including four directives, in the first cycle; eight in the second cycle; 16 in the third cycle; and 32 in fourth cycle. Judged by the numbers of tentacles, the mesenterial cycle reaching to sixth. Macrocnemes in the second cycle born in the endocoel of the first cycle mesenteries, same as general arrangement of Actinernoidea. Microcnemes absent (Fig. 15C). Each tentacle either exo- or endocoelic. Tentacular longitudinal muscle and tentacular circular muscle both too weak to observe in histological sections. On aboral ends of tentacles, mesoglea apparently thickened. Retractor muscles extremely weak and diffused (Fig. 15C, D). Muscle processes very short, simple or a little branched, around 40–70 in each muscle pennon. Parietal muscles of macrocnemes very weak and indistinct, with a few muscle fibers. Mesoglea thickest in body wall and actinopharynx (Fig. 15C, D), reaching 2.5–3 mm in thickness, and far thicker than the ectoderm and endoderm. Mesoglea even thick in mesenteries (Fig. 15C) and basal disc, but far thin in tentacles. Actinopharynx, with siphonoglyphs on dorsal and ventral sides, always connected to actinopharynx, and with 10 longitudinal grooves as deep as siphonoglyphs. Sphincter muscle absent. On the aboral end, basilar muscle absent. Dioecious: almost all mesenteries fertile and matured oocytes in CMNH-ZG 09734.

Cnidom. Basitrichs, spirocysts, and microbasic *p*-mastigophores.

Remarks. This species has been the only species of genus *Isactinernus* for a century. According my research, *Synactinernus flavus* Carlgren, 1918, once synonymized into *I. quadrilobatus* by Fautin and den Hartog (2003), was not only a different species but also a species in different family (see remarks of genus *Synactinernus*; Izumi et al., 2019b).

Genus *Synhalcurias* Carlgren, 1914

(Japanese name: seitaka-kawari-ginchaku-zoku)

Synhalcurias Carlgren, 1914: 53; Carlgren, 1918: 27; Stephenson, 1922: 260; Carlgren, 1949: 19.

Diagnosis. Column cylindrical, the upper part not expanded, nor forms lobes. **With many tentacles in simple shape**. Mesenteries **number 68** to ca. 100, and **all** mesenteries perfect and fertile. After formation of 10 pairs of the oldest mesenteries, in 1st and 2nd cycles, further mesenterial formation by cyclic in each 8 lateral endocoel, just same manner as those in *Halcurias*. With two siphonoglyphs. Column ectoderm with **or without** small nematocyst batteries. **Cnidom: basitrichs, spirocysts, microbasic *p*-mastigophores (each in all tissue).**

(The revised points from Uchida [2007] are indicated by **bold**)

Type species. *Synactinernus elegans* (Wassilieff, 1908)

Remarks. Differed from *Isactinernus, Synhalcurias* has been continuously monotypic since the foundation of genus. However, my research discovered a different species of *Synhalcurias*. Some individuals were apparently smaller than *S. elegans,* and there were several differences between *S. elegans* and them although their morphological features were satisfied the diagnosis of *Synhalcurias*. That was why I determined these specimens as a new species of *Synhalcurias* and described as *Synhalcurias* sp. nov. 1.

Synhalcurias has been belonging to Actinernidae so long, but it turned to be appropriate that *Synhalcurias* and *Isactinernus* shouldn't be accommodated into the family by my morphologic and phylogenetic analysis, so I established new family for these genera (see the remarks of family Isactinernidae).

Synhalcurias elegans (Wassilieff, 1908)

(Japanese name: seitaka-kawari-ginchaku)

Fig. 16

Ilyanthopsis elegans Wassilieff, 1908: 8, textfigs 2–5, pl. 1 fig. 2, pl. 3 fig. 38, pl. 4 figs. 39, 40a, 40b.

Synhalcurias elegans: Carlgren, 1914: 50–53, pl. figs. 1–4; Carlgren, 1918: 6, 27, textfigs 2-4; Stephenson, 1922: 260; Carlgren, 1940: 22; Carlgren, 1949: 20; Uchida, 1992: 129, pl. 29 fig. 5; Uchida and Soyama, 2001: 21.

Material examined. NSMT-Co 1693: specimen dissected, tissues embedded in paraffin, histological sections prepared, nematocysts prepared; originally collected from Ise-Bay, by trawling of fishing boat *Kiei-Maru*, and kept in Takeshima Aquarium, and fixed by Takato Izumi on June 1, 2016. NSMT-Co 1694: specimen dissected, tissues embedded in paraffin, histological sections prepared; originally collected in January 2018, at Uragami, Wakayama Prefecture, at 100–130 m, by Isao Hirabayashi, and fixed by Takuma Fujii and Kensuke Yanagi from the tank at the Kushimoto Marine Park on May 22, 2018.

Description. ***External anatomy.*** Body cylindrical (Fig. 16A), up to ca. 7–15 cm in length and ca. 5–10 cm in width in living, and 5–10 cm in length and 3.5–8 cm in width on preserved specimens. Column surface comparatively smooth, wrinkled but without any structures. Ectoderm of column pale orange or yellow (Fig. 16A), without nematocyst batteries. The naked column opaque milky white in color. Basal disk in aboral end, thick, robust and adhesive (Fig. 16A). Upper part of column not thrown into any lobes (Fig. 16B). Tentacles ca. 76–100 in number on oral disk, all marginal, in two rows. All tentacles ca. 5–10 mm in length, pale orange in color, simple shape and no thickening. Oral disc pale orange, with radial streaks corresponding to every tentacle. Mouth at center of oral disk, apparently swelled, lip-like, pale orange and yellow in color (Fig. 16A, B).

Internal anatomy. ca. 76–100 macrocnemes on actinopharynx; 12, including four directives, in the first cycle; eight in the second cycle; 16 in the third cycle; and 32 in fourth cycle. Judged by the numbers of tentacles, the mesenterial cycle reaching to fifth. Macrocnemes in the second cycle born in the endocoel of the first cycle mesenteries, same as general arrangement of Actinernoidea. Microcnemes absent (Fig. 16C). Each tentacle either exo- or endocoelic. Tentacular longitudinal muscle and tentacular circular muscle both too weak to observe in histological sections. On aboral ends of tentacles, mesoglea apparently thickened. Retractor muscles extremely weak and diffused (Fig. 16C–E). Muscle processes too weak to count the numbers (Fig. 16D, E). Parietal muscles of macrocnemes very weak and indistinct, with a few muscle fibers (Fig. 16D, E). Mesoglea thickest in body wall and actinopharynx (Fig. 16C), reaching 2–5 mm in thickness, and far thicker than the ectoderm and endoderm. However, mesoglea thinner in mesenteries (Fig. 16D, E) and basal disc, thinnest in tentacles. Actinopharynx, with siphonoglyphs on dorsal and ventral sides, always connected to actinopharynx, and with 18–22 longitudinal grooves (Fig. 16C). Sphincter muscle absent. On the aboral end, basilar muscle absent. Dioecious: almost all mesenteries fertile but no matured oocytes or sperms in my specimens.

Cnidom. Basitrichs, spirocysts, and microbasic *p*-mastigophores.

Remarks. This species had been the only species of *Synactinernus* since Carlgren (1914), but the second species was discovered by my research (see remarks of *Synhalcurias* sp. nov. 1 concerning the difference from the new species).

Synhalcurias sp. nov. 1

(New Japanese name: kobito-seitaka-kawari-ginchaku)

Fig. 17; Table 11

Material examined. NSMT-Co 1695: dissected specimen, embedded tissues in paraffin, histological sections, prepared nematocysts; originally collected in July 11, 2016, off northwestern Otouto-jima Island, Ogasawara Islands (27°13.13′N, 142°5.43′E), at 157 m in depth, using biological dredge, by Takato Izumi. NSMT-Co 1696: dissected specimen, embedded tissues in paraffin, histological sections, and prepared nematocysts; originally collected in May 27, 2019, off Akuseki Island, at 1106 m in depth, using beam trawl, during research cruise of RV Toyoshio-Maru, by Itaru Kobayashi.

Description. ***External anatomy.*** Body cylindrical (Fig. 17A, C), up to ca. 50 mm in height and ca. 30 mm in width in living, and 40 mm in height and 27 cm in long axis and 1.5 mm in width in preserved specimen. Column surface smooth, without tenaculi or nematocyst batteries, pale whitish orange ectoderm layer and transversal discontinuous yellow line. Aboral end of column pale yellow. Nematocysts very sparsely distributed but contains numerous spirocysts. Upper part of column a little expanded, simple and not thrown into lobes (Fig. 17B). Tentacles simple, all marginal, 8–16 mm in length, no thickenings including their aboral base, pale white to pale orange in color, and 68 in number on oral disk; inner and outer ones alternatingly bared (Fig. 17B). The tip of tentacles pointed. Basal disk in aboral end, opaque and mesenterial insertion invisible. Oral disk diameter almost same as column, pale white. Mouth at center of oral disk, highly swelled, lip-like, groove on surface, pale orange, and fluorescent yellow patch on dorsal and aboral side (Fig. 17B).

Internal anatomy. All mesenteries macrocnemes and without microcnemes; Sixty-eight (thirty-four pairs of) macrocnemes (Fig. 17H) on actinopharynx; twelve ones, including four directives, in first cycle; eight in second cycle; sixteen in third cycle; thirty-two in fourth cycle. Macrocnemes in second and younger cycle bearing in the endocoel of first cycle mesenteries, which arrangement obeying the rule of mesenterial arrangement of Actinernidae. All mesenteries perfect near the mouth, and each tentacle between either exo- or endocoelic. Tentacular longitudinal muscle and circular muscle too weak to observe in histological section (Fig. 17D–G); Retractor muscles comparatively exceedingly weak and restricted near body wall or diffused and integrated to parietal muscle (Fig. 17H, I). Muscle processes very short, simple, around 40–100 in each muscle pennon. Parietal muscles of macrocnemes too weak to observe, indistinct (Fig. 17I). Mesoglea thickest in body wall and actinopharynx (Fig. 17H), reach to 3 mm in thickness, and far thicker than ectoderm and endoderm. Mesoglea thinner than the other parts, but far thicker than endo- and ectoderm, too in tentacle (Fig. 17D–G) and in mesenteries (Fig. 17H). Actinopharynx, with siphonoglyphs on dorsal and ventral side (Figs. 24B, H), always connected to actinopharynx, and with other 12 longitudinal grooves less deep than siphonoglyphs. Sphincter muscle absent. On the aboral end, basilar muscle absent. Dioecious, immature oocyte in holotype (Fig. 17J).

Cnidom. Basitrichs, spirocysts, microbasic *p*-mastigophores, microbasic *b*-mastigophores. See Table 11 for size and distribution.

Remarks. *Synhalcurias* sp. nov. 1 is the second species of *Synhalcurias*. These sea anemones had first to third cycle of mesenteries following to mesenterial arrangement of Actinernoidea (Endocoelantheae), and they had only macrocnemes, so they were identified as a species of family Isactinernidae. In this family, many morphological features of these anemones were shared with *S. elegans*. Edges of oral discs of these specimens were never developed into lobes, which feature is observed only in *Synhalcurias* in Actinernidae, these similarities are strongly supported by phylogeny: our specimen and several specimens of *S. elegans*, including deposited on GenBank, were monophyletic.

Thus, it was undoubtful that this species was belonging to *Synhalcurias* morphologically and phylogenetically. However, this species was too separated from the clade of *S. elegans* (Fig. 10). There are several differences between *S.* sp. nov. 1 and *S. elegans* (Wassilieff, 1908) showed as below: The size of body of *S.* sp. nov. 1 (5 cm) is far smaller than *S. elegans* (around 20 cm) despite both species are adult (the gametes were matured); the number of perfect mesenteries of *S.* sp. nov. 1 is 68 (first to fourth cycle of mesenteries) while *S. elegans* has at least 76 mesenteries (our specimen and Uchida, 2007); there is no nematocyst batteries, which are apparently distribute on the column of *S. elegans*, on the smooth surface of *S.* sp. nov. 1. In addition, the diversity of nematocysts *of S.* sp. nov. 1 is poor than *S. elegans* (cnidom of *S. elegans* is detailed in fig.3 in Uchida, 2007): for example, *S.* sp. nov. 1 does not have holotrichs while *S. elegans* have (fig. 3N in Uchida, 2007). So, I determined our specimens as the second species of *Synhalcurias*.

Family HALCURIIDAE Carlgren, 1918
(Japanese name: kawari-ginchaku-ka)

Halcuriidae Carlgren, 1918: 24; Carlgren, 1921: 13; Stephenson, 1922: 257; Carlgren, 1938: 17; Carlgren, 1949: 18.

Diagnosis. (Revised parts are shown in bold). **Actinernoidea** with elongate body. Distal margin of column **lobed or** not lobed. Column with or without nematocyst batteries. Tentacles without basal **thickening** on their aboral side. With a single **or double** siphonoglyph. Mesenteries divisible into macro- and microcnemes. Macrocnemes 6 or 10 **or 18** pairs. Some of the microcnemes, however, perfect in many species. Retractors of the macrocnemes restricted. Macrocnemes fertile with filaments, but microcnemes sterile without filaments.
(The revised points from Uchida [2004] are indicated by **bold**)

Type genus. *Halcurias* McMurrich, 1893

Remarks. This family has accommodated two genera: *Halcurias*

McMurrich, 1893 and *Carlgrenia*, Stephenson, 1918 (the latter genus never confirmed from Japan including my research). However, my phylogenetic analysis revealed that *Synactinernus* Carlgren, 1918, one of the genera of Actinernidae, was in the clade of previous *Halcurias* (Fig. 10). However, species of this genus have almost same morphologies as Actinernidae, so there was no synapomorphy between *Halcurias* and *Synactinernus*. Thus, it was unnatural to accommodate synactinernid species into *Halcurias*.

That was why I divided previous *Halcurias* into "true" *Halcurias* and a new genus, *Isohalcurias* gen. nov. following the phylogeny. According to the tree, there were only two species from Japan, *Halcurias japonicus* Uchida, 2004 and *Halcurias* sp. nov. 2, in the same clade of *Halcurias pilatus* McMurrich, 1893, the type species of genus. On the other hand, the other three species of *Halcurias* were in the other clade which was paraphyletic to "true" *Halcurias* and *Synactinernus.* Thus, those three species, *Isohalcurias carlgreni* (McMurrich, 1901) comb. nov., *Isohalcurias levis* (Uchida, 2004) comb. nov., and *Isohalcurias* sp. nov. 3, turned to be accommodated in new genus, *Isohalcurias*. See Table 12 for comparison of the four genera included in the suborder Anenthemonae.

Genus *Halcurias* McMurrich, 1893

(Japanese name: kawari-ginchaku-zoku)

Halcurias McMurrich 1893: 142; McMurrich, 1901: 155, 158; Carlgren, 1914: 60; Carlgren, 1918: 25; Stephenson, 1918: 14; Carlgren 1938: 18; Carlgren, 1949: 18

Halcuriopsis Carlgren 1921: 93.

Diagnosis. Mesenteries up to 34 pairs arranged in 4 cycles, 6+4+8+16. Macrocnemes 10 pairs, fertile, filamented and with restricted retractors. Microcnemes in only upper part of the body, some of them perfect. **Retractor muscles strong and diffused. Parietal** muscles rather well developed to fairly weak. Tentacles up to 68. Dioecious. Cnidom; basitrichs **(in all tissues)**, spirocysts **(in tentacles, actinopharynx and filaments),** and microbasic *p*-mastigophores **(in actinopharynx and filaments)**.

(The revised points from Uchida [2004] are indicated by **bold**)

Type species. *Halcurias pilatus* McMurrich, 1893

Remarks. Halcuriidae Carlgren, 1918 accommodated two genera, *Halcurias* McMurrich, 1893 and *Carlgrenia* Stephenson, 1918. The latter genus has been monotypic, so almost all species of this family have been accommodated in *Halcurias*. However, according to my phylogenetic analysis, *Halcurias* became paraphyletic (Fig. 9). So, I established new genus, *Isohalcurias* gen. nov. and moved some species to that genus (Fig. 10). Compared to *Isohalcurias*, *Halcurias* is characterized by two features: lacking spirocysts in their column (compare *Halcurias* sp. nov. 2 and *Isohalcurias* sp. nov. 3 in Table 11), and retractor muscles with comparatively simple muscular processes (e.g. Figs. 18D, 19D).

The two species of Halcuriidae from Japan were remained in *Halcurias*: *Halcurias japonicus*, and *Halcurias* sp. nov. 2. In the world, *Halcurias pilatus* McMurrich, 1893 was confirmed to belong to this genus by phylogenetic analysis (Fig. 10). Concerning the other described species, classification was conjectured by cnidom of column as below.

Species possibly remained in *Halcurias*: *Halcurias mcmurrich,* Uchida, 2004 (according to Rodríguez et al. [2013], this species does not contain spirocysts in column); *Halcurias endocoelactis* Stephenson, 1918 (it was described that spirocysts were absent on body wall in Stephenson [1918]); *Halcurias capensis* Carlgren, 1928 (same as *H. endocoelactis*).

Species possibly assigned to *Isohalcurias*: *Halcurias minimus* Carlgren, 1928; *Halcurias sudanensis* Riemann-Zürneck, 1983 (They were described that spirocysts were present on body walls of both species in Carlgren [1928] and Riemann-Zürneck [1983]).

Halcurias japonicus Uchida, 2004

(Japanese name: abata-kawari-ginchaku)

Fig. 18

Halcurias japonicus Uchida, 2004: 13–15, fig. 2. pl. 1C–1E

Material examined. (Iz-001): specimen dissected, tissues embedded in paraffin, histological sections prepared, nematocysts prepared, collected on 2016 (date unknown), from Toyama-Bay, Toyama Prefecture, around a depth of 50–100 m, gill net of fishing boat *Koei-Maru*; (Iz-002): whole specimen, same date, collector and method as (Iz-001); (Iz-003): specimen dissected, tissues embedded in paraffin, histological sections prepared, nematocysts prepared, collected from Toyama-Bay, off Toyama Prefecture, by gill net (anonymous collector, and date unknown), kept in a tank of Uozu Aquarium by Tomoharu Kimura, and fixed on February 28, 2015, by Takato Izumi; (Iz-

004)–(Iz-006), same date, collector and method as (Iz-003): whole specimens; (Iz-007): whole specimen; originally collected from Ise-Bay, by trawling of fishing boat *Kiei-Maru*, and kept in Takeshima Aquarium, and fixed by Takato Izumi on June 29, 2017. (Iz-008): whole specimen; originally collected in January 2018, at Uragami, Wakayama Prefecture, at 100–130 m, by Isao Hirabayashi, and fixed by Takuma Fujii and Kensuke Yanagi from the tank at the Kushimoto Marine Park on May 22, 2018.

Description. ***External anatomy.*** Body cylindrical (Fig. 18A, B), up to ca. 40 mm in height and ca. 15 mm in width in living, and 15–30 mm in height and 5–22 mm in width in preserved specimen. Column surface comparatively rough, reddish orange ectoderm layer with white tenaculi-like nematocyst batteries. Nematocysts densely distributed, especially in nematocyst batteries. Upper part of column a little narrower, pale yellow in color, simple and not thrown into any lobes. Tentacles simple, conical, all marginal, 6–8 mm in length, no thickenings including their aboral base, pale yellow in color, and 68 in number on oral disk; inner and outer ones alternatingly bared (Fig. 18C). The tip of tentacles pointed. Basal disk in aboral end, opaque and mesenterial insertion invisible (Fig. 18A, B). Oral disk diameter as broad as column, hemi-transparent pale yellow. Mouth at center of oral disk, highly swelled, lip-like, smooth, bright yellow and orange (Fig. 18C).

Internal anatomy. 20 macrocnemes on actinopharynx (my specimens all 20); twelve, including four directives, in the first cycle; eight in the second cycle. Macrocnemes in the second cycle born in the endocoel of the first cycle mesenteries, an arrangement obeying the rule of mesenterial arrangement of Actinernidae. Mesenteries in third and fourth cycle microcnemes. Each tentacle between either exo- or endocoelic. Tentacular longitudinal muscle exocoeletic and circular muscle too weak to observe in histological section; retractor muscles restricted at the center of mesenteries, comparatively weak but distinct (Fig. 18D). Muscle processes simple, or slightly branched, around 25–41 in each muscle pennon (Fig. 18D). Parietal muscles of macrocnemes quite weak with 10–13 simple processes (Fig. 18D). Mesoglea thickest in body wall and actinopharynx, far thicker than ectoderm and endoderm (Fig. 19G). Mesoglea thinner in mesoglea (Fig. 18D, E). Actinopharynx, with siphonoglyphs on one side, always connected to actinopharynx, and with other 11 longitudinal grooves less deep than siphonoglyphs. Sphincter muscle absent. On the aboral end, basilar muscle absent. Dioecious, immature testis in my specimen (Fig. 18E). Mesenteries in second cycle fertile.

Cnidom. Basitrichs, spirocysts, microbasic *p*-mastigophores. Spirocysts are absent in the column.

Remarks. Uchida (2004) described this species as *Halcurias japonicus.* However, this species name is nomen dubium now because this article did not indicate the type specimen. Even though Uchida indicate specimen as the type belatedly in Uchida (2007), then there is no description together, so the name did not become valid. However, I provisionally report this anemones as *Halcurias japonicus* because I collected the halcuriids which were corresponded to the description of Uchida (2004). Uchida only reported this species in Japanese Sea off Hokuriku region, but I recorded this species also from the Pacific.

This halcuriid species was in the clade of *Halcurias*, and lacks spirocysts in their column, so *H. japonicus* should be remaind in this genus.

***Halcurias* sp. nov. 2**

(New Japanese name: ichigo-kawari-ginchaku)

Fig. 19; Table 11

Material examined. (Iz-009): specimen dissected, tissues embedded in paraffin, histological sections prepared, nematocysts prepared, collected by scuba diving on March 22, 2018, at Mushizaki, Sado Island, Niigata Pref., 15 m in depth, by Akihito Omori; (Iz-010)–(Iz-011): whole specimen, same date, collector and method as (Iz-009); (Iz-012): whole specimen; originally collected in January 2018, at Uragami, Wakayama Prefecture, at 100–130 m, by Isao Hirabayashi, and fixed by Takuma Fujii and Kensuke Yanagi from the tank at the Kushimoto Marine Park on May 22, 2018.

Description. ***External anatomy.*** Body cylindrical (Fig. 19A, B), up to ca. 10 mm in height and ca. 5 mm in width in living, and 9 mm in height and 4 mm in width in preserved specimen. Column surface comparatively smooth, reddish orange ectoderm layer and sometimes patchy pattern with dark red and light orange, and with white tenaculi-like nematocyst batteries. Nematocysts densely distributed, especially in nematocyst batteries. Upper part of column a little narrower, white in color, simple and not thrown into lobes. Tentacles simple, all marginal, 3–6 mm in length, no thickenings including their aboral base, bright red to orange in color and pale white in roots, and 68 in number on oral disk; inner and outer ones alternatingly bared

(Fig. 19C). The tip of tentacles pointed. Basal disk in aboral end, opaque and mesenterial insertion invisible. Oral disk diameter broader than column, hemi-transparent pale white. Mouth at center of oral disk, highly swelled, lip-like, groove on surface, bright orange (Fig. 19A).

Internal anatomy. 20 (10 pairs of) macrocnemes on actinopharynx; twelve, including four directives, in the first cycle; eight in the second cycle (Fig. 19G, H). Macrocnemes in the second cycle born in the endocoel of the first cycle mesenteries, an arrangement obeying the rule of mesenterial arrangement of Actinernidae. Mesenteries in third and fourth cycle microcnemes. Each tentacle between either exo- or endocoelic. Tentacular longitudinal muscle exocoeletic (Fig. 19F) and circular muscle too weak to observe in histological section (Fig. 19F); retractor muscles restricted near actinopharynx or filaments, obviously developed (Fig. 19D). Muscle processes simple, or slightly branched, around 15–25 in each muscle pennon (Fig. 19D). Parietal muscles of macrocnemes comparatively developed and distinct (Fig. 19D). Parietal muscle processes are simple, 4–7 in each side. Mesoglea thickest in body wall and actinopharynx, generally thicker than ectoderm and endoderm (Fig. 19G). Mesoglea thinner than the other parts, especially in tentacle: far thinner than ectoderm (Fig. 19E, F). Actinopharynx, with siphonoglyphs on one side, always connected to actinopharynx, and with other 11 longitudinal grooves less deep than siphonoglyphs (Fig. 19G). Sphincter muscle absent. On the aboral end, basilar muscle absent. Dioecious, immature testis in my specimen. Mesenteries in second cycle fertile.

Cnidom. Basitrichs, spirocysts, microbasic *p*-mastigophores. See Table 11 for size and distribution

Remarks. See Table 13 for comparison to the other species of *Halcurias*. This species can be easily distinguished from any other species of *Halcurias* by possessing two types of basitrichs in their tentacles.

This halcuriid most resembles *H. pilatus* McMurrich, 1893 in external morphology, but there is no long basitrichs in filaments of this species. The long basitrichs are strongly characterizing *H. pilatus* (Rodríguez et al., 2013). Moreover, phylogenetic analysis indicated that this halcuriid was monophyletic with *Halcurias japonicus,* and this anemones and *H. pilatus* were paraphyletic. So, I determined this sea anemone not as *H. pilatus* but as a new species and described here.

Genus *Synactinernus* Carlgren, 1918
(New Japanese name: Kuroba-kawari-ginchaku-zoku)

Synactinernus Carlgren, 1918: 30; Carlgren, 1949: 21

Diagnosis (Revised parts are shown in bold). Actinernidae with cylindrical body which distally is drawn out into 8 distinct lobes, **all 8 same size or** four larger and four smaller alternating. Column without papillae. No sphincter. Tentacles in at least 2 cycles without distinct mesogleal thickenings, **all same length or** largest at apices of the lobes, numerous. Longitudinal muscles of tentacles ectodermal, radial muscles of oral disc chiefly ectodermal, strong. Two broad siphonoglyphs **on actinopharynx. 36 macrocnemes** cyclic in arrangement, beyond them weak mesenteries of unequal size in upper part of the body. Retractors weak, **parietal** muscles **weak or** rather well developed.

Type species. *Synactinernus flavus* Carlgren, 1918.

Remarks. The genus *Synactinernus* was established in family Actinernidae by Carlgren (1918) monotypically for *Synactinernus flavus* Carlgren, 1918. Later, Carlgren (1949) transferred this genus to Family Actinernidae Stephenson, 1922 of suborder Endocoelantheae Carlgren, 1925. Recently, Fautin and den Hartog (2003) argued that *Synactinernus flavus*, the only species of *Synactinernus,* cannot be distinguished from *Isactinernus quadrilobatus* Carlgren, 1918, and so they synonymized *Synactinernus* with *Isactinernus.* However, other studies treated this genus as valid (Fautin 2007, 2016). So, the actual status of *S. flavus* and the validity of *Synactinernus* were still unclear. Additional specimens are necessary to solve this taxonomical problem, but there has been found no new specimen of *Synactinernus*. After a century since the original description of Carlgren (1918). This study becomes the first chance of revision of *Synactinernus* because our study obtained the second specimens of *S. flavus* and the second species of this genus, *Synactinernus churaumi*.

Our morphological analysis of newly collected specimens of two species of *Synactinernus* and *Isactinernus quadrilobatu*s and of the type specimens of *I. quadrilobatus* showed that tentacles of *S. flavus* and *S. churaumi* are simple in shape apparently lacking thickening of aboral side (Figs. 20, 22) while those of *Isactinernus quadrilobatus*, both our collection and type specimens, are apparently thickened at the base of aboral side (Figs. 15, 22). This clear difference suggested that the species of *Synactinernus* can be distinguished from *Isactinernus quadrilobatu*s by their tentacles. In addition, species of *Synactinernus* have a fixed number (36) of macrocnemes (Figs. 21, 23), and this prominent feature in mesentery structure should be a diagnostic character of the genus while *Isactinernus quadrilobatus* has a lot of indistinguishable mesenteries (Fig. 15). In contrast, the alternate arrangement of larger and smaller oral lobes of *Synactinernus flavus* was considered as an important morphological feature of this monotypic genus (Carlgren, 1918, 1949), turned to be not a diagnostic character because the new species *S. churaumi* has 8 lobes in same size.

Our molecular phylogeny also showed that *Synactinernus* was independent clade from any other genera of Actinernidae (Fig. 10). Moreover, two Halcuriidae clade was paraphyletic to *Synactinernus*, so this genus should not be accommodated in Actinernidae but should be in Halcuriidae.

This genus is endemic in Japan and is distributed around 300 m depth in the East China Sea and the Pacific Ocean.

Synactinernus flavus Carlgren, 1918

(Japanese name: Kuroba-kawari-ginchaku)

Figs. 20, 21; Table 11

Synactinernus flavus Carlgren, 1918: 31

Synactinernus flavus: Izumi et al., 2019b: 531–534, figs. 2, 3, 5, 6

Material examined. NSMT-Co 1660: specimen dissected, tissues embedded in paraffin, histological sections prepared, nematocysts prepared; originally collected on November 19, 2012, the Goto-nada Sea off southeastern Goto Islands, Nagasaki Prefecture (32°23.00′N, 129°03.00′E), at a depth of 304–504 m, using a biological dredge of R/V *Nagasaki-Maru* (Cruise No. 365), collected by Masanori Nonaka, and fixed by Takuma Fujii and Hiroko Takaoka from the tank at Okinawa Churaumi Aquarium on January 25, 2013. CMNH-ZG 09732: whole specimen attached to a rock; originally collected in January 2018, at Uragami, Wakayama Prefecture, at 100–130 m, by Isao Hirabayashi, and fixed by Takuma Fujii and Kensuke Yanagi from the tank at the Kushimoto Marine Park on May 22, 2018. UUZM 232 holotype: dissected specimen, May 17, 1914, off the Goto Islands (33°41′N, 128°50′E [collection information listed on the label]), depth 110 m, collected by Sixten Bock (Fig. 22).

Description. ***External anatomy.*** Body cylindrical (Fig. 20A, D), up to ca. 5–8 cm in length and ca. 2–4 cm in width when alive, and 2–4 cm in length and 1–2 cm in width on specimen. Column surface comparatively smooth, without tenaculi, with numerous discontinuous, wavy wrinkles running in a transverse direction, pale surface with pale orange ectoderm layer. Ectoderm of column without nematocyst batteries, nematocysts very sparsely distributed containing numerous spirocysts. Upper part of column widely expanded and thrown into eight lobes, four larger and four smaller ones (Fig. 20B, C). Upper margin of the lobes fluorescent yellow in color (Fig. 20A). Tentacles simple, all marginal, ca. 2–5 mm in length, no thickenings including their aboral base, pale white in color, and ca. 120–200 in number on oral disk; inner and outer ones alternatingly bared. The tip of tentacles pointed. Basal disk in aboral end, semitransparent, and mesenterial insertion visible. Oral disk diameter ca. 3–6 cm, same color as tentacles, mouth at center of oral disk, apparently swelled, lip-like.

Internal anatomy. 36 (18 pairs of) macrocnemes (Fig. 21A) on actinopharynx; twelve, including four directives, in the first cycle; eight in the second cycle; 16 in the third cycle. Macrocnemes in the second cycle born in the endocoel of the first cycle mesenteries, an arrangement obeying the rule of mesenterial arrangement of Actinernidae. Pairs of microcnemes, in the fourth cycle, observed in transverse section (Fig. 21B). Judged by the numbers of tentacles, mesenteries of *Synactinernus flavus* in the first–sixth cycles. All mesenteries perfect near the mouth, and each tentacle between either exo- or endocoelic. Tentacular longitudinal muscle ectodermal (Fig. 21C, arrowhead); tentacular circular muscle too weak to observe in histological sections (Fig. 21D). Retractor muscles comparatively weak and restricted actinopharynx or filament side (Fig. 21E). Muscle processes short, mostly simple or slightly branched, around 30–50 in each muscle pennon. Parietal muscles of macrocnemes weak, distinct with approximately 10 muscle fibers in upper part near actinopharynx (Fig. 21B), but indistinct in lower part near filaments (Fig. 21E). Mesoglea thickest in body wall and actinopharynx (Fig. 21B), reaching 2–3 mm in thickness, and far thicker than the ectoderm and endoderm. However, mesoglea thinner in mesenteries (Fig. 21B), and thinnest in tentacles (Fig. 21C, D). Actinopharynx, with siphonoglyphs on dorsal and ventral sides (Fig. 21A), always connected to actinopharynx, and with 10 longitudinal grooves as deep as siphonoglyphs. Sphincter muscle absent. On the aboral end, basilar muscle absent. Dioecious, matured eggs in gonads in NSMT-1660 (Fig. 21F). Mesenteries in the first and second cycles only fertile (Fig. 21E).

Cnidom. Basitrichs, spirocysts, and microbasic *p*-mastigophores. See Table 11 for size and distribution.

Derivation of new Japanese name. "Kuroba" means the plant clover. The oral disk with 4 large and 4 small lobes appears like the four-leaf clover, which is considered a symbol of luck.

Taxonomic remarks. I provide a detailed description of *S. flavus* based on the holotype and our new specimens in this study. I presented cnidom data of every part of the body (Table 11) and the figures of external features (Fig. 20), which were lacking in Carlgren (1918).

Almost all morphological features of the present specimen (NSMT-Co 1660) corresponded to Carlgren (1918) and the holotype (UUZM 232): cylindrical body (Figs. 20A, 22); ca. 120–200 tentacles with no thickening even on base (Figs. 20, 22); about 10 longitudinal grooves on actinopharynx (Fig. 21A); mesoglea on the actinopharynx are thick (Fig. 21B); ectodermal but weak tentacular muscle (Fig. 21C); numerous spirocysts in column (Table 11). The size of spirocysts, 20.9–47.1 μm in length and 4.1–7.6 μm in width in our specimens (Table 11), is similar to that of the syntype, 26–38 μm in length and 3–5 μm in width (Carlgren, 1918).

The number of macrocnemes is fixed to 36 in *S. flavus* (Fig. 21A), while over 100 in *I. quadrilobatus* (Fig. 15; there are the same number of mesenteries next to the actinopharynx), but it is not a strong evidence to divide the species and genus because Fautin and den Hartog (2003) reported a range in the number of mesenterial pairs among 81 specimens when the two species were synonymized (18 to 40). However, I confirmed that there are several differences between the two species other than the above-mentioned ones between the two genera; whether as mentioned in remarks of genus *Synactinernus*, thickening on the base of tentacle is only observed on *I. quadrilobatus*. At the oral disc, this species has apparently four large and four small lobes (Figs. 20B, C), but *I. quadrilobatus* has only four lobes (Fig. 15); *S. flavus* fertilizes only the first and second cycle mesenteries, total 20 in number (Fig. 21E), while *I. quadrilobatus* has many fertile mesenteries (Fig. 15D). In addition, the size of *I. quadrilobatus* is approximately twice to three times that of *S. flavus* (Fig. 15A). These several morphological differences of both species are sufficient to discuss that they are independent groups, and our molecular phylogeny analysis strongly supports the division into two species based on the several morphological differences mentioned above; *S. flavus* and *I. quadrilobatus* are not closely related on the phylogenetic tree and the difference between them is considered to be at the genus level (Fig. 15; see Chapter 1D). In conclusion, *S. flavus* is not a synonym of *I. quadrilobatus* and is different at the genus level both in morphology and molecular phylogeny. Therefore, the morphological features that Fautin and den Hartog (2003) described as intraspecific variations in *I. quadrilobatus* can also be used to distinguish *S. flavus* from *I. quadrilobatus*.

In the present study, I redescribed the species using our newly collected specimens with the addition of important features like cnidom of every part of the body (Table 11), which were lacking in Carlgren (1918), and also photographic information (Figs. 20, 21).

The locality of the holotype of *S. flavus*, UUZM 232, is described on the label as follows: “Goto Islands 28 miles N. 1/2 Ost fran Shirase fyr 128 50 O.L., 33 41 N.Br.” The locality, “Shirase”, would mean “Shiroze”, an isolated uninhabited island north off the Goto Islands (33°11'00''N, 128°48'14''E). In Japanese, the Kanji-character of “Shiroze” is sometimes pronounced as “Shirase”. Swedish “fyr” means a lighthouse. The lighthouse on Shiroze was built in December 1904, and was obviously present in 1914, when the holotype of *S. flavus* was collected. The point, 1/2 sea mile east off Shiroze, is approximately 40–45 km north from Fukue Island (the main island of the Goto Islands). These distances and directions completely match “Goto Islands 28 miles N” on the label. The depth, 110 m written on the label, is also a match. Considering the above information, the exact type locality should be here. The latitude and longitude written on the label is far away from “Shiroze”, so it may be mistaken. Our specimens would be the first topotype specimens after the collected type specimen.

Ecological remarks. It was observed that *Synactinernus flavus* reproduced by transverse fission in the tank at Okinawa Churaumi Aquarium several times. When the bodies were mechanically or thermally stimulated, for example when their basal disc was detached from the substrate, it cracked on the surface of the column, and then transverse fission of the body occurred sooner (Fig. 20D). Both halves became independent full-grown individuals. This is the first observation of transverse fission in Actinernoidea, while fission from the basal disc has been observed in Halcuriidae of Actinernoidea (Uchida, 2004).

(Description, Figs. 27–29, and part of Table 11 are revised and reprinted Izumi et al. [2019b] by courtesy of Zoological Science.)

Synactinernus churaumi Izumi and Fujii, 2019

(Japanese name: Churaumi-kawari-ginchaku)

Figs. 20, 23; Table 11

Synactinernus churaumi Izumi and Fujii, 2019: Izumi et al., 2019b: 534–537; figs. 2, 5, 7

Material examined. Holotype: NSMT-Co 1661: specimen dissected, tissues embedded in paraffin, histological sections prepared, nematocysts prepared; originally collected on February 22, 2004, off northwestern Ishigaki Island, Okinawa Prefecture, at a depth of 281–312 m, using LEO, ROV of Okinawa Churaumi Aquarium, by Takuo Higashiji, and fixed by Takuma Fujii and Hiroko Takaoka from the aquarium tank on January 25, 2013. Paratype: CMNH-ZG 09733: originally collected on September 5, 2018, off Onna Village, Okinawa Island, Okinawa Prefecture (26°34.22′N, 127°47.96′E), at a depth of 320 m, using ROV of the Okinawa Churaumi Aquarium by Takuo Higashiji, and fixed by Takato Izumi from the aquarium tank on September 10, 2018.

Description. ***External anatomy.*** Body cylindrical (Fig. 20E), up to 20–25 cm in length and 15 cm in width when alive. Regarding specimens, 12 cm in length and 10 cm in width on holotype, and 13 cm in length and 9 cm in width on paratype. Column surface smooth, without tenaculi, pale surface with orange or yellow ectoderm layer. Ectoderm of column without nematocyst batteries and nematocysts very sparsely distributed but contain numerous spirocysts. Upper part of column widely expanded and thrown into eight lobes of the same size (Fig. 20E–G). Upper margin of the lobes same as column in color (Fig. 20E). Tentacles simple, all marginal, 5–20 mm in length, no thickenings including their aboral base, pale white in color, and ca. 350–500 in number on oral disk; inner and outer ones alternatingly bared (Fig. 20F). The tip of tentacles pointed. Basal disk in aboral end, opaque and mesenterial insertion invisible. Oral disk diameter ca. 12–20 cm in living specimen, same color as tentacles or pale orange, Mouth at center of oral disk, exceedingly swollen, lip-like, pale white to yellow (Fig. 20F).

Internal anatomy. 36 (18 pairs of) macrocnemes (Fig. 23A) on actinopharynx; 12, including four directives, in the first cycle; eight in the second cycle; and 16 in the third cycle. Macrocnemes in the second cycle born in the endocoel of the first cycle mesenteries; their arrangement obeying the rule of mesenterial arrangement of Actinernidae. Mesenteries in younger than the fourth cycle microcnemes, and judged by the numbers of tentacles, mesenteries of *Synactinernus churaumi* in the first–seventh cycles. All mesenteries perfect near the mouth, and each tentacle between either exo- or endocoelic. Tentacular longitudinal muscle ectodermal (Fig. 23C, D; arrowhead); tentacular circular muscle too weak to observe in histological section; retractor muscles comparatively weak and restricted on the middle of mesenteries (Fig. 23B); or diffused and integrated to parietal muscle (Fig. 23E). Muscle processes short, mostly simple or slightly branched, around 60–90 in each muscle pennon. Parietal muscles of macrocnemes weak, distinct with approximately 10 muscle fibers in upper part near actinopharynx (Fig. 23B) but integrated to retractor muscles near filaments (Fig. 23E). Mesoglea thickest in body wall and actinopharynx (Fig. 23A, B), reaching to 8–10 mm in thickness, and far thicker than ectoderm and endoderm. However, mesoglea thinner in mesenteries (Fig. 23B, E) and thinnest in tentacle (Fig. 23C, D). Actinopharynx, with siphonoglyphs on dorsal and ventral sides (Fig. 23A), always connected to actinopharynx, and with 10 longitudinal grooves as deep as siphonoglyphs. Sphincter muscle absent. On the aboral end, basilar muscle absent. Dioecious, matured testes in NSMT-1661; a variety of stages of maturation in the same testis (Fig. 23F). Mesenteries in the first and second cycles only fertile. The release of eggs and sperm by *S. churaumi* was observed in the tank at the Okinawa Churaumi Aquarium.

Cnidom. Basitrichs, spirocysts, and microbasic *p*-mastigophores. See Table 11 for size and distribution

Etymology. The species epithet “churaumi” is named after Okinawa Churaumi Aquarium, an aquarium in Okinawa, which provided us the specimens of this species. “Chura” means beautiful in Okinawan language, and “umi” means sea in Japanese.

Derivation of new Japanese name. Same as the species epithet.

Taxonomic remarks. *Synactinernus churaumi* is the second species of this genus; this species is clearly distinguished from *S. flavus*. Comparing the two species in adult individuals which have matured gametes (Figs. 21, 23), *S. churaumi* is approximately 3–5 times larger than *S. flavus* in body length (*S. churaumi* is one of the largest species of Actinernidae), and *S. churaumi* has over 350 tentacles while *S. flavus* has around half the number. The margin of the oral disk of *S. churaumi* develops into eight same sized lobes, while that of *S. flavus* has four larger and four smaller lobes. The molecular phylogenetic tree (Fig. 9) indicated that these two species formed apparently separate clades. These evidences indicate that *S. churaumi* is not conspecific with *S. flavus* but is an independent species. In addition, there is possibly a difference in the presence of asexual fission (see Ecological remarks).

The eight-lobed oral disk of *S. churaumi* resembles that of *Actinernus* Verrill, 1879. However, *S. churaumi* does not correspond to the diagnosis of *Actinernus* of Actinernidae Stephenson, 1922. The species of *Actinernus* have mesogleal thickening at the tentacle base, and I confirmed this in both the holotype of *Actinernus robustus* Hertwig, 1882, the only species of *Actinernus* from the North Pacific, (Natural History Museum, London, BM 89-11-25-30; Fig. 22) and our specimens (CMNH-ZG 09735–09738). However, tentacles of *S. churaumi* were not thickened at any part. Moreover, mesenterial arrangement of *Actinernus* is bilateral, and the fourth cycle mesenteries is born in the endocoel of the third cycle (Carlgren, 1918), and Uchida (2007) confirmed this for *A. robustus*. The mesenterial arrangement of *S. churaumi* is completely different from that of *Actinernus*.

Ecological remarks. *Synactinernus churaumi* is distributed around depths of 320–350 m off Okinawa Island. This species forms small aggregations on the top of hill-like submarine topography as recorded by the ROV (Fig. 20H). Incidentally, no asexual fission of *S. churaumi* in the tank at the Okinawa Churaumi Aquarium was observed for 15 years, while *S. flavus* has self-divided several times over seven years (Fig. 20D).

(Description, Figs. 27, 30, and part of Table 11 are revised and reprinted Izumi et al. [2019b] by courtesy of Zoological Science.)

Genus *Isohalcurias* gen. nov.
(New Japanese name: kawari-ginntyaku-modoki-zoku)

Diagnosis. Mesenteries up to 34 pairs arranged in 4 cycles, 6+4+8+16. Macrocnemes 10 pairs, fertile, filamented and with restricted retractors. Microcnemes in only upper part of the body, some of them perfect. Retractor muscles diffused and pinnate. Parietal muscles rather well developed to fairly weak. Tentacles up to 68. Dioecious. Cnidom; spirocysts and basitrichs (in all tissues), and microbasic *p*-mastigophores (in actinopharynx and filaments).

Type species. *Isohalcurias carlgreni* (McMurrich, 1901)

Etymology. *Isohalcurias* is derived from "*Iso* (= Greek isos, equal)" + "*halcurias* (the divided genus)". The species of *Isohalcurias* so resemble species of *Halcurias* that they cannot be distinguished unless making sections or inspecting cnidae.

Remarks. According to my phylogenetic analysis (Figs. 9, 10), the species which were identified as genus *Halcurias* became paraphyletic. The outer clade, which included *H. carlgreni, H. levis,* and *H.* sp. nov. 3 (a new species), did not include the type species, *Halcurias pilatus*. Thus, this group cannot be named *Halcurias*. That was why I established new genus *Isohalcurias* gen. nov. for those three species.

See Table 12 for comparison to the other genera of Halcuriidae. This genus can be identified by having spirocysts in column (compare *Halcurias* sp. nov. 2 and *Isohalcurias* sp. nov. 3 in Table 11), and partly pinnate retractor muscles (e.g. Figs. 24D, 25D, 26C). In addition to the three species, *Halcurias minimus* Carlgren, 1928 and *Halcurias sudanensis* Riemann-Zürneck, 1983 are possibly in this new genus because these species have spirocysts in body wall (Carlgren, 1928; Riemann-Zürneck, 1928; Uchida, 2004). It is hoped to obtain molecular information of these species for phylogenetic analyses in future.

Isohalcurias carlgreni (McMurrich, 1901) comb. nov.

(Japanese name: kawari-ginchaku)

Fig. 24

Halcurias Carlgreni McMurrich 1901: 159

Halcurias carlgreni: Carlgren, 1914: 69; Uchida 2004: 9–13, fig. 1, pl. 1A, B

Material examined. NSMT-Co 1697: specimen dissected, tissues embedded in paraffin, histological sections prepared, nematocysts prepared, in September 19, 2011, collected from Suo-Oshima, Yamaguchi Pref., Japan, at 10 m in depth, by scuba diving, by Takuma Fujii; NSMT-Co 1698: specimen dissected, tissues embedded in paraffin, histological sections prepared, nematocysts prepared, same collector, locality, and method as NSMT-Co 1697; (Iz-014): whole specimen, same collector, locality, and method as NSMT-Co 1697; (Iz-015): specimen dissected, tissues embedded in paraffin, histological sections prepared, nematocysts prepared; collected by trawling of fishery boat

Shojin-Maru from Kumano-nada Sea off Mie Pref. (depth and date unknown), by Takeya Moritaki, kept in Toba Aquarium for a while, and preserved on 18 June 2017 by Takato Izumi; (Iz-016): juvenile specimen dissected, tissues embedded in paraffin, histological sections prepared, nematocysts prepared, in September 19, 2011, collected from west-off Uki-shima, Chiba Pref., Japan, at 20 m in depth, by scuba diving, by Junji Okuno; (Iz-017): whole specimen, same collector, locality, and method as (Iz-016).

Description. ***External anatomy.*** Body cylindrical (Fig. 24A, B), up to 17–70 mm in height and ca. 11–50 mm in width. Column surface comparatively smooth, with reddish orange ectoderm layer and sparse small nematocyst batteries. Nematocysts densely distributed, especially in nematocyst batteries. Tentacles simple, all marginal, 6–40 mm in length, no thickenings including their aboral base, pale white in color, and 68 in number on oral disk; inner and outer ones alternatingly bared (Fig. 24A). The tip of tentacles pointed. Basal disc distinct and adhesive (Fig. 24A), opaque and mesenterial insertion invisible. Oral disk diameter as broad as column, hemi-transparent pale white. Mouth at center of oral disk, highly swelled, lip-like, groove on surface, white in color.

Internal anatomy. 20 (10 pairs of) macrocnemes on actinopharynx; twelve, including four directives, in the first cycle; eight in the second cycle (Fig. 24C). Macrocnemes in the second cycle born in the endocoel of the first cycle mesenteries, an arrangement obeying the rule of mesenterial arrangement of Actinernidae. Mesenteries in third and fourth cycle microcnemes. Each tentacle between either exo- or endocoelic. Tentacular longitudinal muscle exocoeletic and circular muscle endocoeletic; retractor muscles restricted near parietal muscles, obviously developed and pinnate (Fig. 24D). Muscle processes well-branched, around 8–15 in each muscle pennon (Fig. 24D). Parietal muscles of macrocnemes comparatively developed and distinct with simple or slightly branched 4–11 processes in each side. Mesoglea thickest in body wall and actinopharynx, generally thicker than ectoderm and endoderm (Fig. 24D). Mesoglea thinner than the other parts, especially in tentacle: far thinner than ectoderm. Actinopharynx, with siphonoglyphs on one side, always connected to actinopharynx, and with other 15–19 longitudinal grooves less deep than siphonoglyphs (Fig. 24C). Sphincter muscle absent. On the aboral end, basilar muscle absent. Dioecious, immature testis in my specimen (Fig. 24E). Mesenteries in second cycle fertile.

Cnidom. Basitrichs, spirocysts, microbasic *p*-mastigophores. Spirocysts are numerous in the column.

Remarks. This species was described as *Halcurias Carlgreni* in McMurrich (1901) and reported from Japan in Uchida (2004). *H. carlgreni* was characterized by ectoderm of column containing numerous spirocysts (Uchida, 2004). Our specimens were corresponded these descriptions, so identified as *H. carlgreni.*

However, as mentioned in Chapter 1D, *Halcurias* became paraphyletic to *Synactinernus.* The clade including *Halcurias carlgreni, H. levis,* and *H.* sp. nov. 3 did not include the type species of the genera. Therefore, these species should be moved to new genus *Isohalcurias*, thus *H. carlgreni* became *Isohalcurias carlgreni* comb. nov.

Isohalcurias levis (Uchida, 2004) comb. nov.

(Japanese name: oo-kawari-ginchaku)

Fig. 25

Halcurias levis Uchida, 2004: 16, figs. 3, 4, pl. 1F

Material examined. CMNH (no registration): specimen dissected, tissues embedded in paraffin, histological sections prepared, nematocysts prepared; in October 7, 2008, from Aishima Island, Hagi, Yamaguchi Pref., 47 m in depth collected by scuba diving, by Kensuke Yanagi; (Iz-018): specimen dissected, tissues embedded in paraffin, histological sections prepared, nematocysts prepared, collected in January 28, 2017, from Kuju-kushima (off Kuroshima), Nagasaki Pref., 35m in depth, bycatched with fishes by gill net, kept in the tank of Saikai National Park Kuju-kushima Aquarium, and preserved on 14 April, 2017 by Takato Izumi; (Iz-019): specimen dissected, tissues embedded in paraffin, histological sections prepared, nematocysts prepared, collected in May 17, 2018, off Yaku-shima Island (30°09.39′ N, 130°38.03′ E; St. 3), at 200–255m in depth, using bean trawl, during research cruise of R/V Toyoshio-Maru, by Itaru Kobayashi.

Description. *External anatomy.* Body cylindrical (Fig. 25A, B), up to ca. 150 mm in height and ca. 100 mm in width in living, and 34–90 mm in height and 20–35 mm in width in preserved specimen. Column surface smooth and without nematocysts batteries. Whole body bright yellow in color. Nematocysts sparsely distributed on column. Upper part of column narrower, same color as column, simple and not thrown into any lobes. Tentacles simple, all marginal, 30–50 mm in length, no thickenings including their aboral base, bright yellow in color, and 68 in number; inner and outer ones alternatingly bared (Fig. 25A). The tip of tentacles pointed. Basal disk in aboral end (Fig. 25A), yellowish opaque and mesenterial insertion inapparently visible. Oral disk diameter narrower than column, hemi-transparent bright yellow. Mouth at center of oral disk, highly swelled, lip-like, groove on surface, bright yellow.

Internal anatomy. 20 (10 pairs of) macrocnemes on actinopharynx; twelve, including four directives, in the first cycle; eight in the second cycle (Fig. 25C). Macrocnemes in the second cycle born in the endocoel of the first cycle mesenteries, an arrangement obeying the rule of mesenterial arrangement of Actinernidae. Mesenteries in third and fourth cycle microcnemes. Each tentacle between either exo- or endocoelic. Tentacular longitudinal muscle and circular muscle too weak to observe in histological section (Fig. 25E); Retractor muscles diffused, weak, and pinnate (Fig. 25D, F). Muscle processes well- branched, around 9–17 in each muscle pennon (Fig. 25D). Parietal muscles of macrocnemes well-developed and distinct. Parietal muscle weak, with simple or slightly branched processes, around 10 in each side (Fig. 25D, F). Mesoglea thickest in body wall, and even thick in mesenteries and actinopharynx, far thicker than ectoderm and endoderm (Fig. 25C, D). Actinopharynx, with siphonoglyphs on one side, always connected to actinopharynx, and with other 19 longitudinal grooves, as deep as siphonoglyphs (Fig. 25C). Sphincter muscle absent. On the aboral end, basilar muscle absent. Dioecious, matured ovaries in (Iz-018) (Fig. 25F). Mesenteries in second to third cycle fertile.

Cnidom. Basitrichs, spirocysts, microbasic *p*-mastigophores, Spirocysts are sparsely present in the column.

Remarks. Uchida (2004) described this species as *Halcurias levis*. However, this species name become nomen dubium because of same reason as *H. japonicus*. The specimens I collected were corresponded to description of Uchida (2004) morphologically, so I report them as this species provisionally.

This species was accommodated in the clade of *Isohalcurias* but cannot be obviously separated from *I. carlgreni* comb. nov. on phylogenetic tree (Fig. 10). However, there were several differences between these halcuriids e.g. body sizes, presence or absence of nematocyst batteries, development of retractor muscles and so forth (see Table 14). Judged by the common view on phylogenetic analysis of sea anemones that there is still no effective molecular markers to solve intra-generic phylogeny now (Daly et al., 2010; Rodríguez et al., 2014; Titus et al., 2019), it was probable that any phylogenetic analysis method in the present day cannot distinguish *I. carlgreni* and *I. levis* on phylogenetic tree. In conclusion, this study described this species as *Isohalcurias levis* (Uchida, 2004).

This species had been discovered only from Syoga-se, off Wakayama Pref. (Uchida and Soyama, 2001; Uchida, 2004; Yamana, 2016), but I newly confirmed from Sea of Japan (CMNH-ZG [no registration]), Goto-Nada Sea ([Iz-018]), and East China Sea ([Iz-019]).

Isohalcurias sp. nov. 3

(New Japanese name: ringo-kawari-ginchaku)

Fig. 26; Table 11

Material examined. CMNH (no registration): specimen dissected, tissues embedded in paraffin, histological sections prepared, nematocysts prepared, originally collected in May 15, 2005, from Ryukyu Trough off Kume-jima Island (25°30.96′N, 126°29.21′E; St. OT-14), at 372–375 m in depth, using beam trawl, during research cruise of R/V Hakuho-Maru, by Kensuke Yanagi; NSMT-Co 1699: specimen dissected, tissues embedded in paraffin, histological sections prepared, nematocysts prepared, originally collected in May 24, 2015, west off Cape Sata (31°02.06′ N, 130°33.37′ E; St. 7), at 202 m in depth, using biological dredge, during research cruise of R/V Toyoshio-Maru, by Mikihito Arai; (Iz-020): specimen dissected, tissues embedded in paraffin, nematocysts prepared, collected in May 27, 2019, off Akuseki Island (29°08.99′ N, 129°52.18′ E; St. 5), at 1106 m in depth, using bean trawl, during research cruise of R/V Toyoshio-Maru, by Itaru Kobayashi; (Iz-021) and (Iz-022): whole specimen; originally collected in January 2018, at Uragami, Wakayama Prefecture, at 100–130 m, by Isao Hirabayashi, and fixed by Takuma Fujii and Kensuke Yanagi from the tank at the Kushimoto Marine Park on May 22, 2018.

Description. ***External anatomy.*** Body cylindrical (Fig. 26A), up to ca. 50 mm in height and ca. 30 mm in width in living, and 25–40 mm in height and 10–20 mm in width in preserved specimen. Column surface smooth and without nematocysts batteries, pale red to pale orange ectoderm layer, and sometimes fine dark red or orange patches on middle column. Aboral end of column pale yellow. Nematocysts sparsely distributed on column, but numerous spirocysts on column (Table 11). Upper part of column a little expanded, same color as column, simple and not thrown into lobes. Tentacles simple, all marginal, 10–20 mm in length, no thickenings including their aboral base, bright red to orange in color (more blight color on distal side), and 68 in number on oral disk; inner and outer ones alternatingly bared. The tip of tentacles pointed. Basal disk in aboral end (Fig. 26A), yellowish opaque and mesenterial insertion inapparently visible. Oral disk diameter broader than column, hemi-transparent pale white. Mouth at center of oral disk, highly swelled, lip-like, groove on surface, bright orange.

Internal anatomy. 20 (10 pairs of) macrocnemes on actinopharynx; twelve, including four directives, in the first cycle; eight in the second cycle (Fig. 26B). Macrocnemes in the second cycle born in the endocoel of the first cycle mesenteries, an arrangement obeying the rule of mesenterial arrangement of Actinernidae. Mesenteries in third and fourth cycle microcnemes (Fig. 26B). Each tentacle between either exo- or endocoelic. Tentacular longitudinal muscle and circular muscle too weak to observe in histological section (Fig. 26D); Retractor muscles diffused, but obviously developed and pinnate (Fig. 26C, E). Muscle processes well- branched, around 10–20 in each muscle pennon (Fig. 26C). Parietal muscles of macrocnemes well-developed and distinct. Parietal muscle processes well-branched, around 10 in each side (Fig. 26E). Mesoglea thickest in body wall and actinopharynx (Fig. 26B, E), far thicker than ectoderm and endoderm. Mesoglea a little thinner than the other parts, but generally thicker than ectoderm and endoderm (Fig. 26C, D). Actinopharynx, with siphonoglyphs on one side, always connected to actinopharynx, and with other 11 longitudinal grooves, as deep as siphonoglyphs (Fig. 26B). Sphincter muscle absent. On the aboral end, basilar muscle absent (Fig. 26G). Dioecious, matured ovaries in NSMT-Co 1699 (Fig. 26F). Mesenteries in second to third cycle fertile.

Cnidom. Basitrichs, spirocysts, microbasic *p*-mastigophores, microbasic *b*-mastigophores. See Table 11 for size and distribution

Remarks. See Table 14 for comparison to the other species of *Isohalcurias* and some species possibly assignable to this genus (since these species of *Halcurias* are possibly assignable to the genus *Isohalcurias* based on their morphological characteristics [Table 12]. However, molecular phylogenetic analyses of them have not been carried out. Thus, new combination was not proposed for these species in this study).

According to taxonomic key of Uchida (2004), these sea anemones are most similar to *Halcurias minimus* (Carlgren, 1928) because of column without longitudinal muscles, actinopharynx containing large spirocysts, column containing spirocysts (though no nematocyst batteries), and tentacles with two types of basitrichs. However, there are several differences between these anemones and *H. minimus*: there is no nematocyst batteries on this species while they sparsely distribute on column of *H. minimus* (Carlgren, 1928; Uchida, 2004); the size of *H. minimus* is 0.8 cm (Carlgren, 1928), approximate one-fourth size of our specimens. Moreover, *H. minimus* only inhabits deep sea of circum-antiboreal region, sea area which was far distant from continents or islands in southern hemisphere, so it is unnatural that same species lives in Japan, especially sea of Temperate Zone. That is why these anemones were concluded as a new species, *Isohalcurias* sp. nov. 3.

SAMMARY of Actinernoidea

My phylogenetic and taxonomic research resulted in these conclusions.

1. Superfamily Actinernoidea was monophyletic, and classified into three families, Actinernidae, Halcuriidae, and Isactinernidae fam. nov.
2. Previous Actinernidae was polyphyletic. The genus *Synactinernus* was an inner taxon of the clade of Halcuriidae, thus it was accommodated into this family. *Actinernus, Isactinernus* and *Synhalcurias* became monophyletic, but divided into two families, Actinernidae (*Actinernus*) and Isactinernidae fam. nov. (*Isactinernus* and *Synhalcurias*), because of poverty of common feature.
3. Genus *Halcurias* was divided into two clades because this genus was paraphyletic to *Synactinernus*. One taxon including type species should be remained as *Halcurias*, and the other should be a new genus, *Isohalcurias* gen. nov.. *Isohalcurias* can be distinguished from *Halcurias* by presence of spirocysts in columns and developing pinnate retractor muscles.
4. I described four new species of Actinernoidea, and thus Japanese species of Actinernoidea became 11. As a consequence of my study, over a half of the species of Actinernoidea (11/21) has been confirmed from Japan.

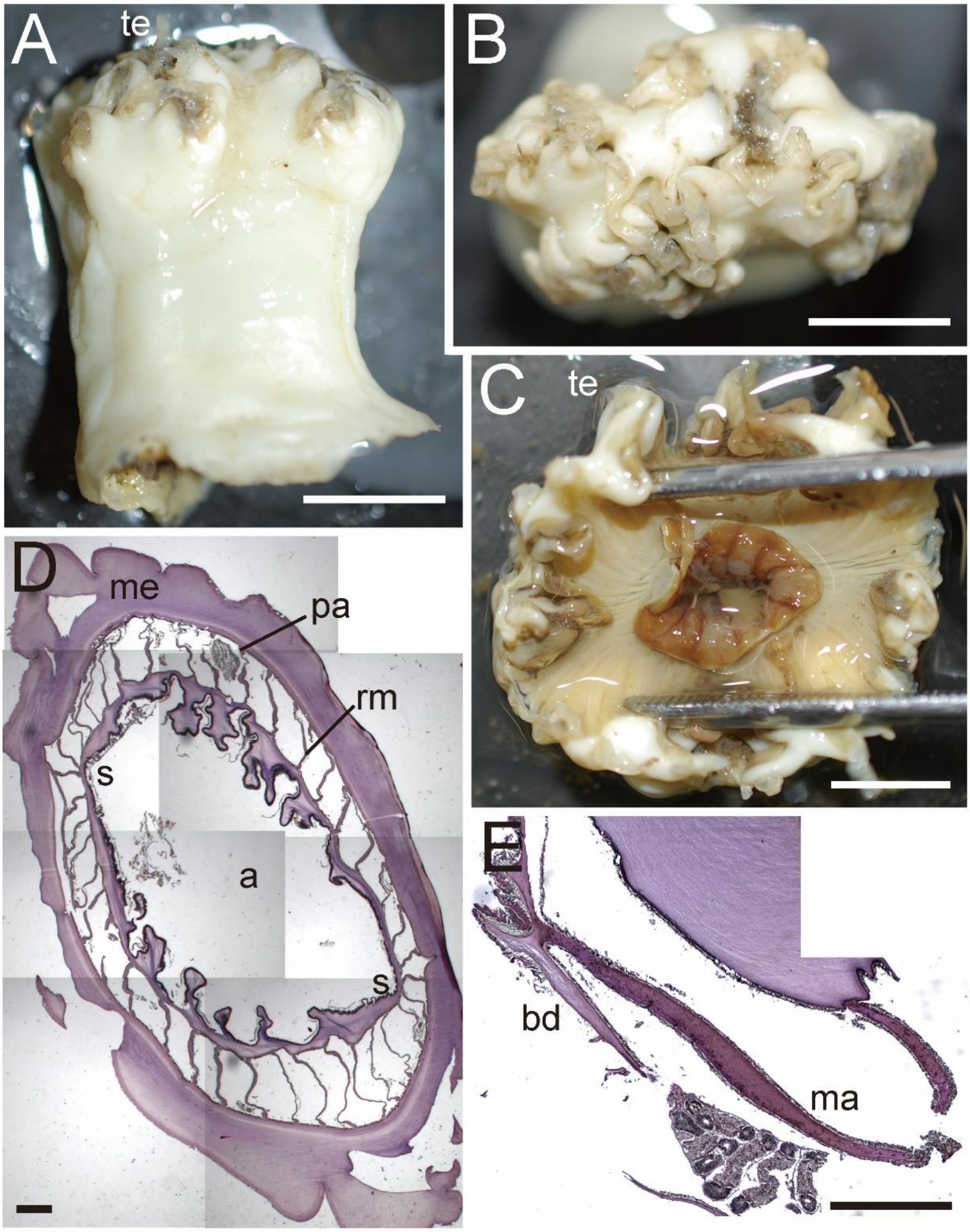

Fig. 14. External and internal morphology of *Actinernus robustus* (CMNH-ZG 9735). A. Lateral view of a fixed specimen; B. Oral view; C. Bared oral disc; D. Transverse section of column; E. Longitudinal section of basal disc. Basilar muscle absent; Abbreviations: a, actinopharynx; bd, basal disc; ma, macrocneme; me, mesoglea; pa, parietal muscle; rm, retractor muscle; s, siphonoglyph; te, tentacle. Scale bars indicate 1 cm in A and C, 1 mm in B and E, 500 μm in D and E.

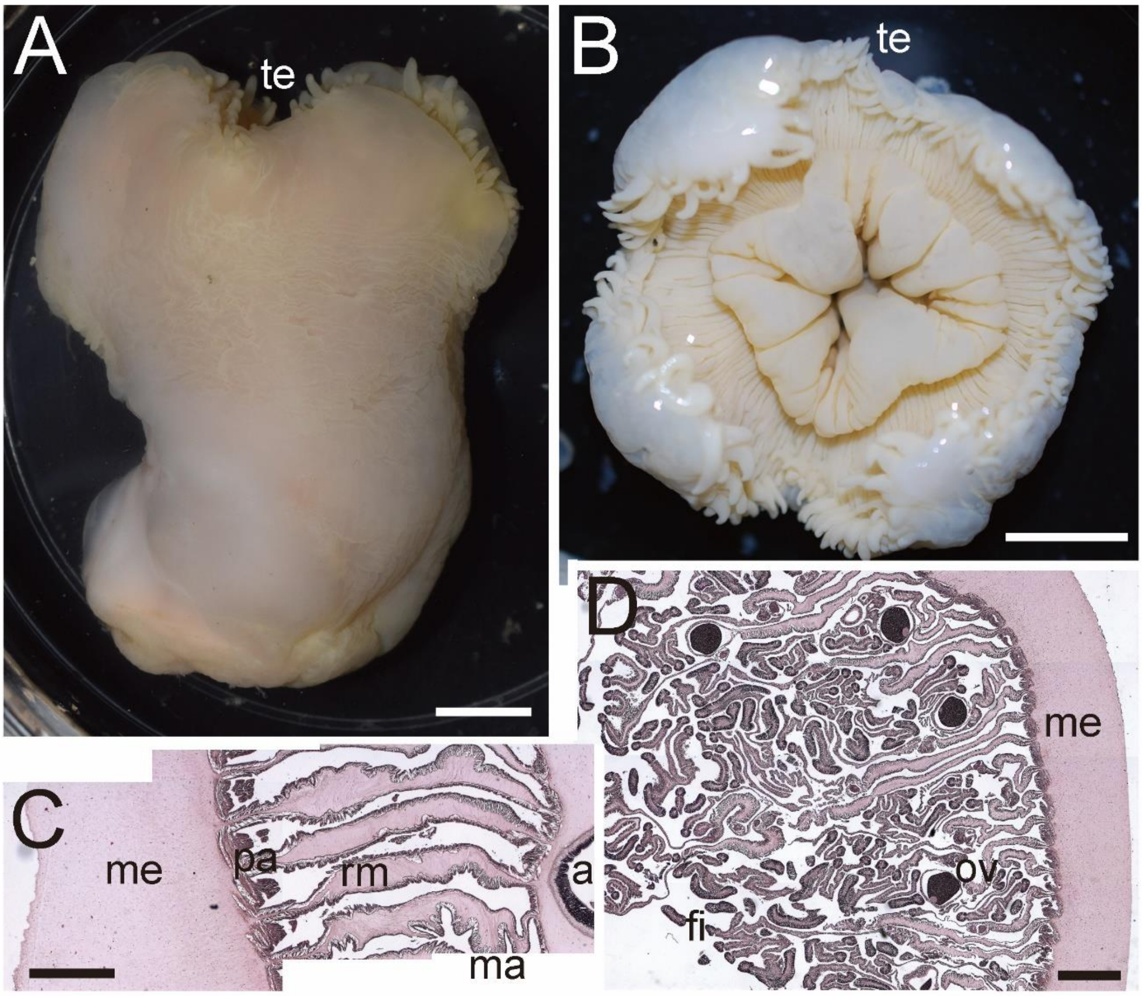

Fig. 15. External and internal morphology of *Isactinernus quadrilobatus* (CMNH-ZG 9734). A. Lateral view of a fixed specimen; B. Oral view; C. Enlarged transverse section of upper column. E. Enlarged transverse section of lower column. Abbreviations: a, actinopharynx; fi, filament; ma, macrocneme; me, mesoglea; ov, ovary; pa, parietal muscle; rm, retractor muscle; te, tentacle. Scale bars indicate 1 cm in A and B, 1 mm in C and D.

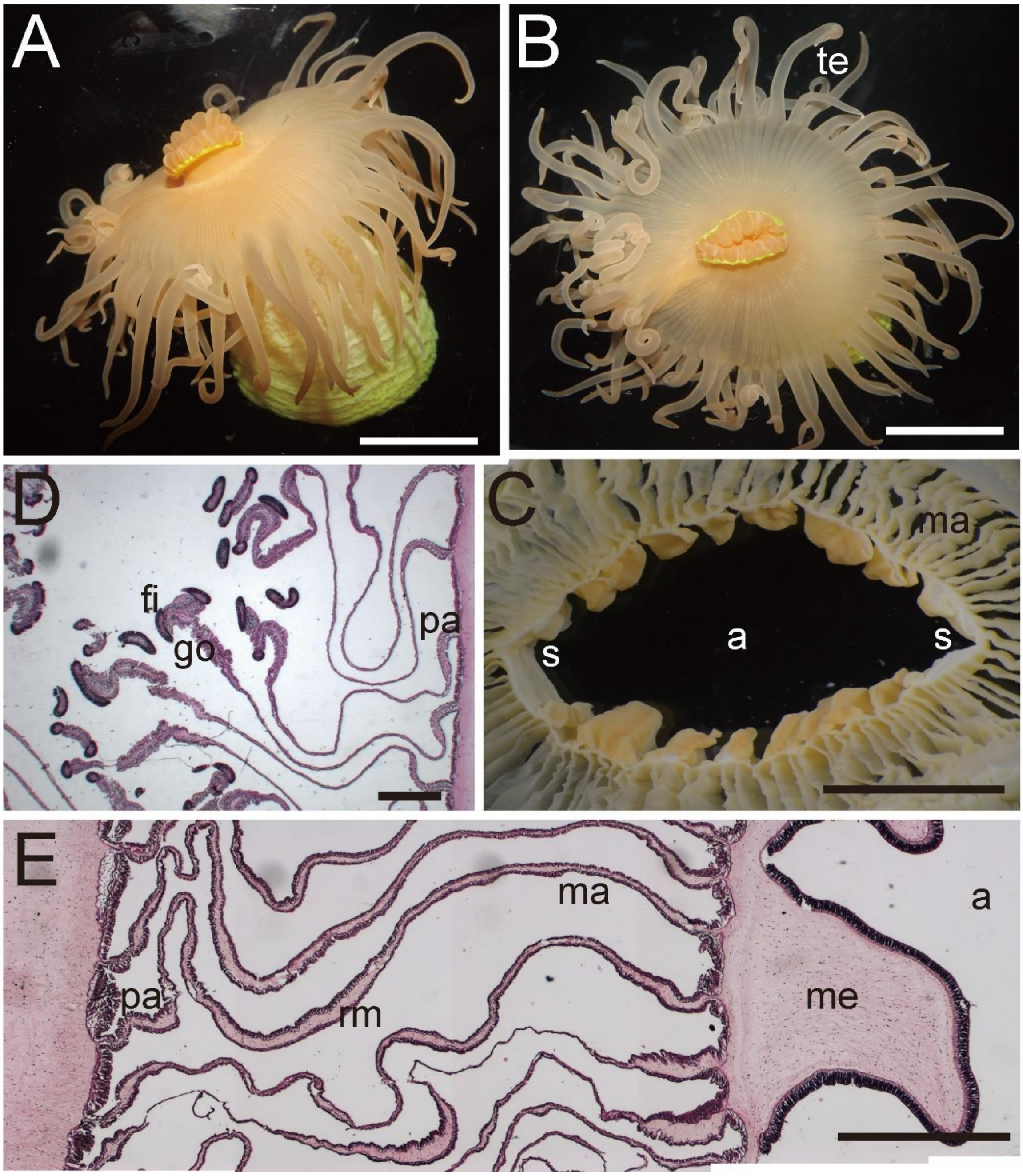

Fig. 16. External and internal morphology of *Synhalcurias elegans* (NSMT-Co 1693). A. Lateral view of a living specimen; B. Oral view; C. Enlarged view of actinopharynx in dissected specimen; D. Enlarged transverse section of lower column; E. enlarged transverse section of upper column; Abbreviations: a, actinopharynx; fi, filament; go, gonad; ma, macrocneme; me, mesoglea; pa, parietal muscle; rm, retractor muscle; s, siphonoglyph; te, tentacle. Scale bars indicate 5 cm in A and B, 1 cm in C, 1 mm in D and E.

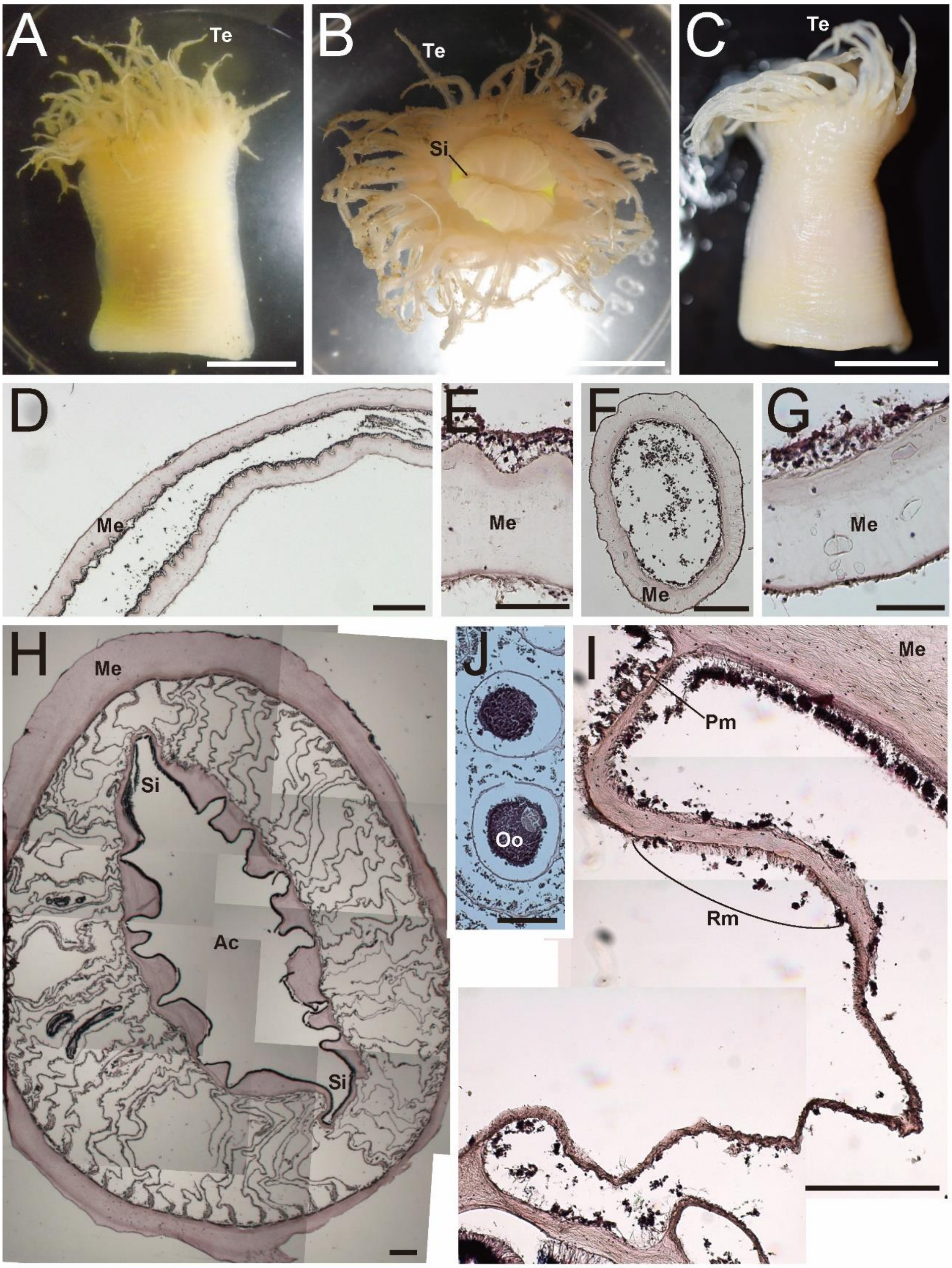

Fig. 17. External and internal morphology of *Synhalcurias* sp. nov. 1 (NSMT-Co 1695). A. Lateral view of a living specimen; B. Oral view; C. lateral view of a fixed specimen; D. Enlarged longitudinal section of tentacle. E. Enlarged view of D; F. Enlarged transverse section of tentacle. G. Enlarged view of F; H. transverse section of upper column; I. Enlarged transverse section of macrocnemes; J. Enlarged view of ovary. Abbreviations: Ac, actinopharynx; Me, mesoglea; Oo, oocytes; Pm, parietal muscle; Rm, retractor muscle; Si, siphonoglyph; Te, tentacle. Scale bars indicate 1 cm in A–C, 500 μm in H and I, 200 μm in D and F, 100 μm in E, G and J.

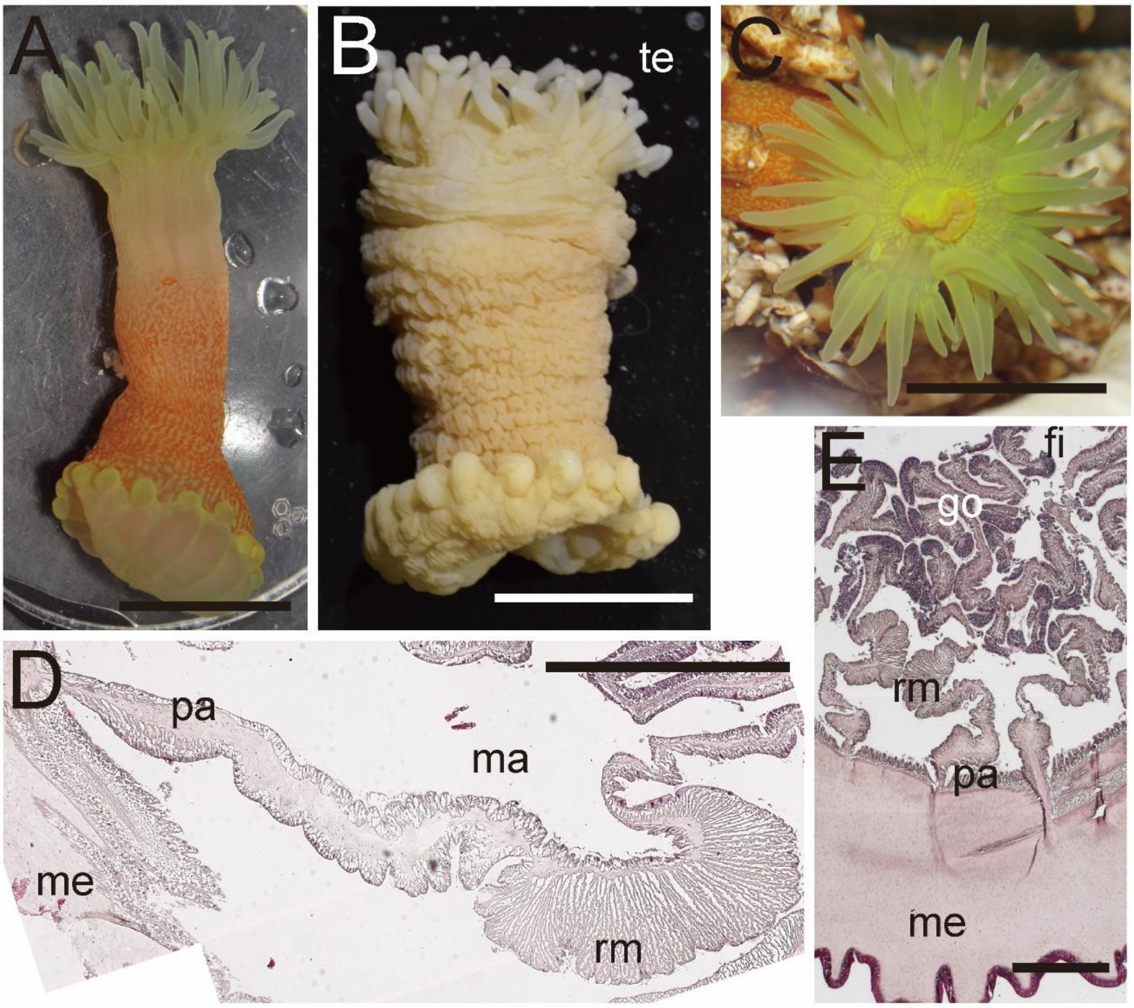

Fig. 18. External and internal morphology of *Halcurias japonicus* (Iz-001).
A. Lateral view of a living specimen; B. Lateral view of a fixed specimen; C. Oral view of a living specimen; D. Enlarged transverse section of upper column; E. Enlarged transverse section of lower column; Abbreviations: fi, filament; go, gonad; ma, macrocneme; me, mesoglea; pa, parietal muscle; rm, retractor muscle; te, tentacle. Scale bars indicate 1 cm in A–C, 500 μm in D and E.

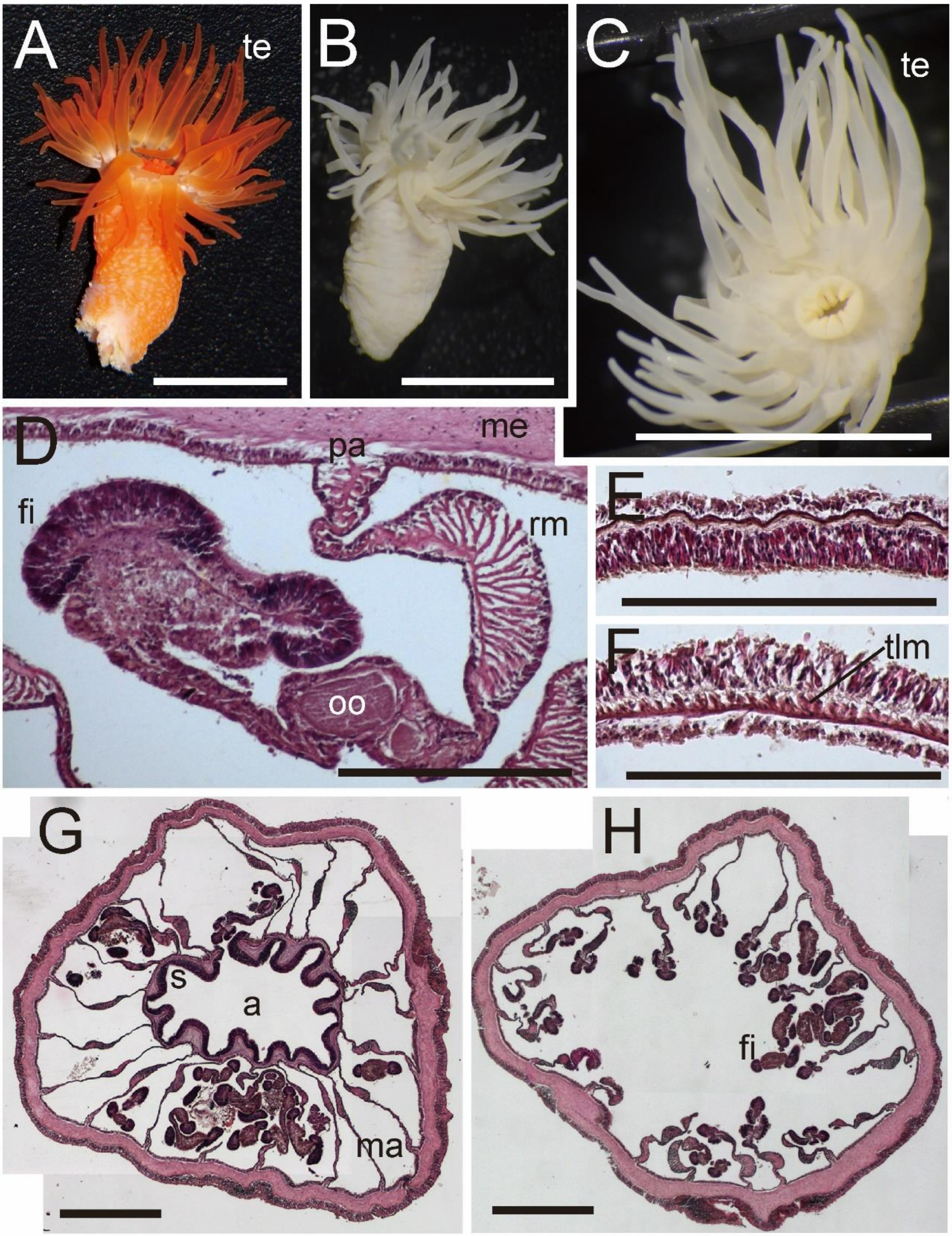

Fig. 19. External and internal morphology of *Halcurias* sp. nov. 2 (Iz-009).
A. Lateral view of a living specimen; B. Lateral view of a fixed specimen; C. Oral view of a fixed specimen; D. Enlarged transverse section of upper column; E. Enlarged longitudinal section of tentacle; F. Enlarged transverse section of tentacle; G. Enlarged transverse section of upper column; H. Enlarged transverse section of lower column. Abbreviations: a, actinopharynx; fi, filament; ma, macrocneme; me, mesoglea; oo, oocyte; pa, parietal muscle; rm, retractor muscle; s, siphonoglyph; te, tentacle. Scale bars indicate 1 cm in A–C, 1 mm in G and H, 500 µm in D, 100 µm in E and F. Picture A was taken by Akihito Omori.

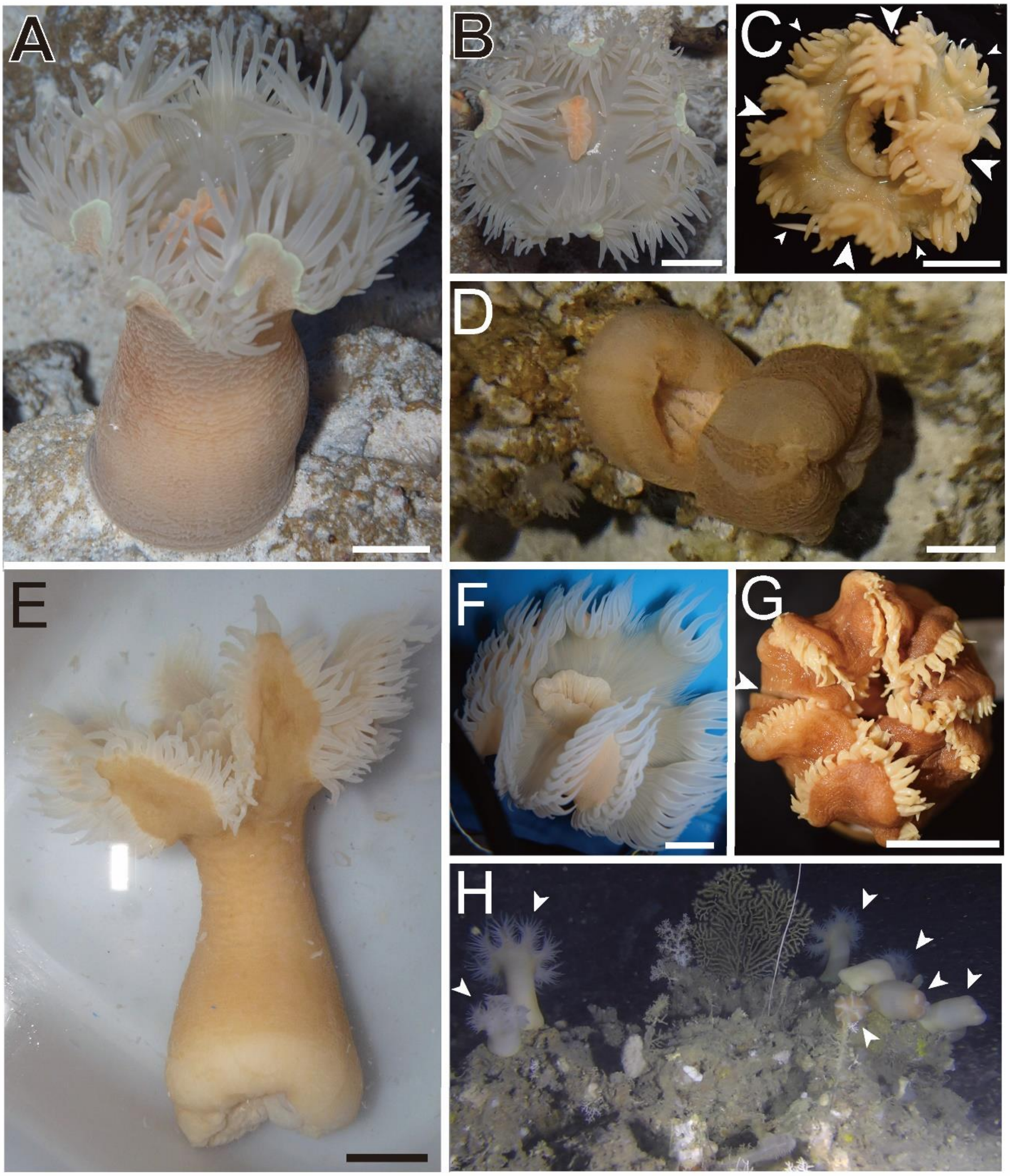

Fig. 20. External morphology and ecological observation of *Synactinernus flavus* (A–D) and *S. churaumi* (E–H).
A. Living specimen (NSMT-Co 1660) in the tank at the Okinawa Churaumi Aquarium; B. Oral view of living specimen (NSMT-Co 1660); C. Oral view of fixed specimen (NSMT-Co 1660). Large arrowheads indicate large lobes, and small arrowheads indicate small ones; D. A living individual undergoing transverse fission in the tank at the Okinawa Churaumi Aquarium (Photograph by Toshiki Higa); E. Lateral view of living specimen (NSMT-Co 1661); F. Oral view of living specimen (NSMT-Co 1661); G. Oral view of fixed specimen (NSMT-Co 1661). An arrowhead indicates a notch by our dissection; H. Underwater photograph of an aggregation of *S. churaumi* off Okinawa Island (around a depth of 320 m taken by ROV of the Okinawa Churaumi Aquarium). Each individual is indicated by arrowheads. Scale bars indicate 1 cm in A–D; 5 cm in E–G. Pictures A, B, E, F were taken by Takuma Fujii, and H is provided by Okinawa Churaumi Aquarium.

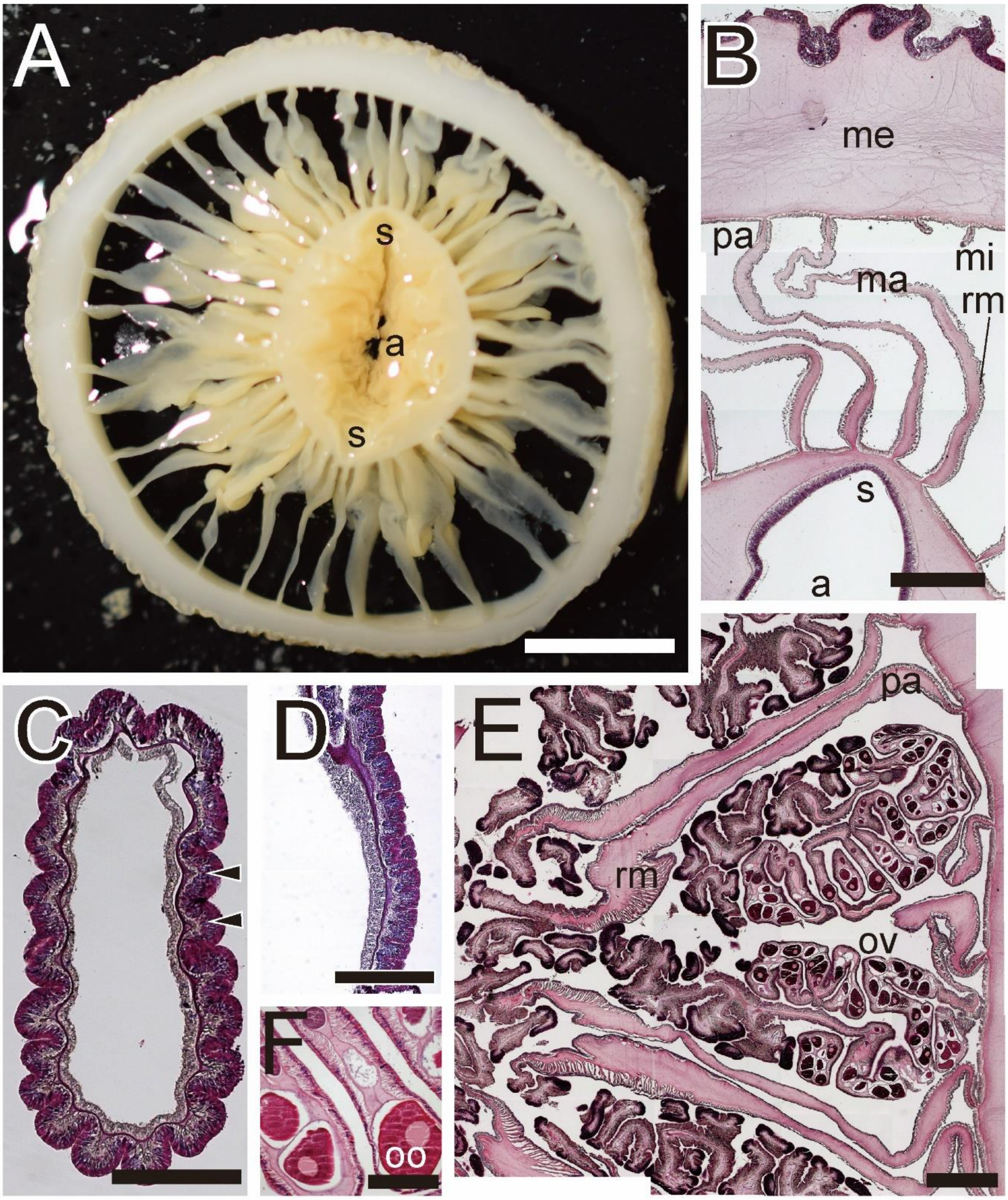

Fig. 21. Internal morphology of *Synactinernus flavus* (NSMT-Co 1660).
A. Transverse section of actinopharynx of the gross specimen; B. Transverse section of macrocnemes and microcnemes; C. Transverse section of the tentacle. Arrowheads indicate tentacular longitudinal muscle; D. Longitudinal section of the most basal part of the tentacle; E. Transverse section of filaments and gonads; F. Enlarged view of gonad. Abbreviations: a, actinopharynx; ma, macrocneme; me, mesoglea; mi, microcneme; oo, oocyte; ov, ovary; pa, parietal muscle; rm, retractor muscle; s, siphonoglyph. Scale bars indicate 5 mm in A, 1 mm in B and E, 500 µm in C and D, and 200 µm in F.

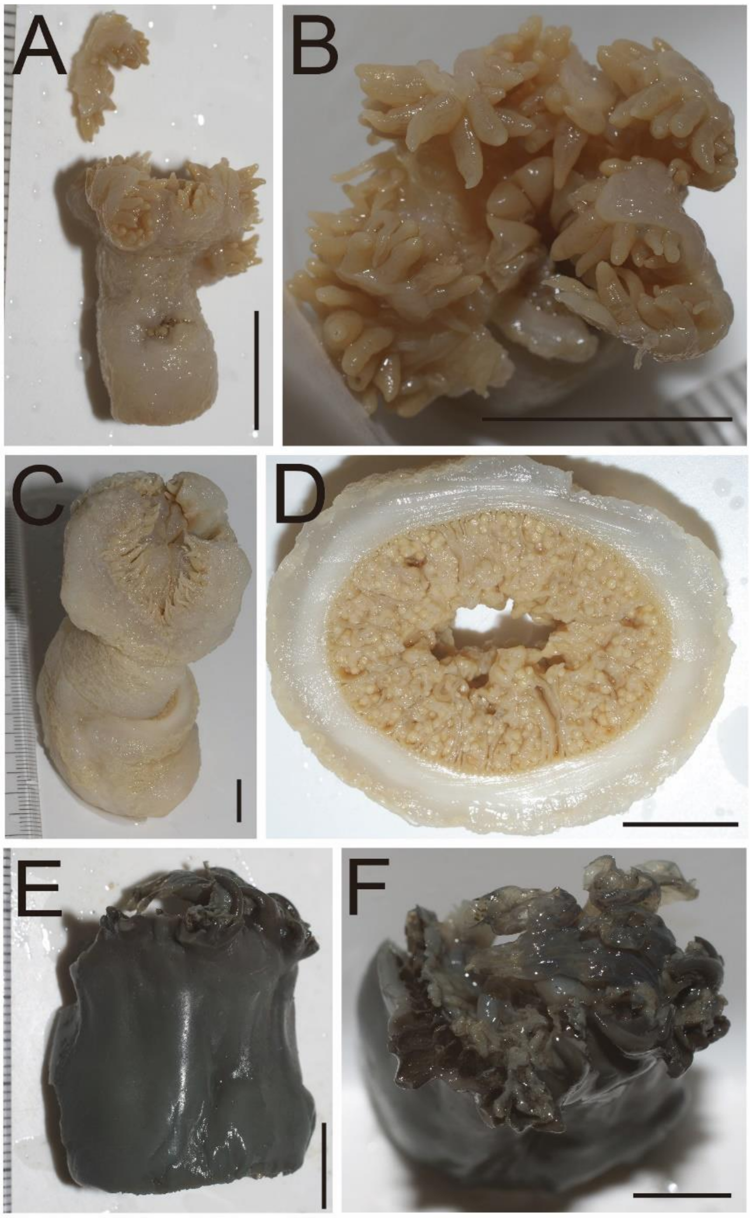

Fig. 22. The type specimens of *Synactinernus flavus* ((A, B), UUZM232, holotype), *Isactinernus quadrilobatus* ((C, D), UUZM 102a, one of the syntypes), and *Actinernus robustus* ((E, F), BM 89-11-25-30, holotype).

A. Whole aspect; B. Oral view. C. Whole aspect; D. Gross section of mesenteries of lower part; E. Whole aspect; F. Oral view. All scale bars indicate 1 cm. All pictures were taken and provided by Kensuke Yanagi.

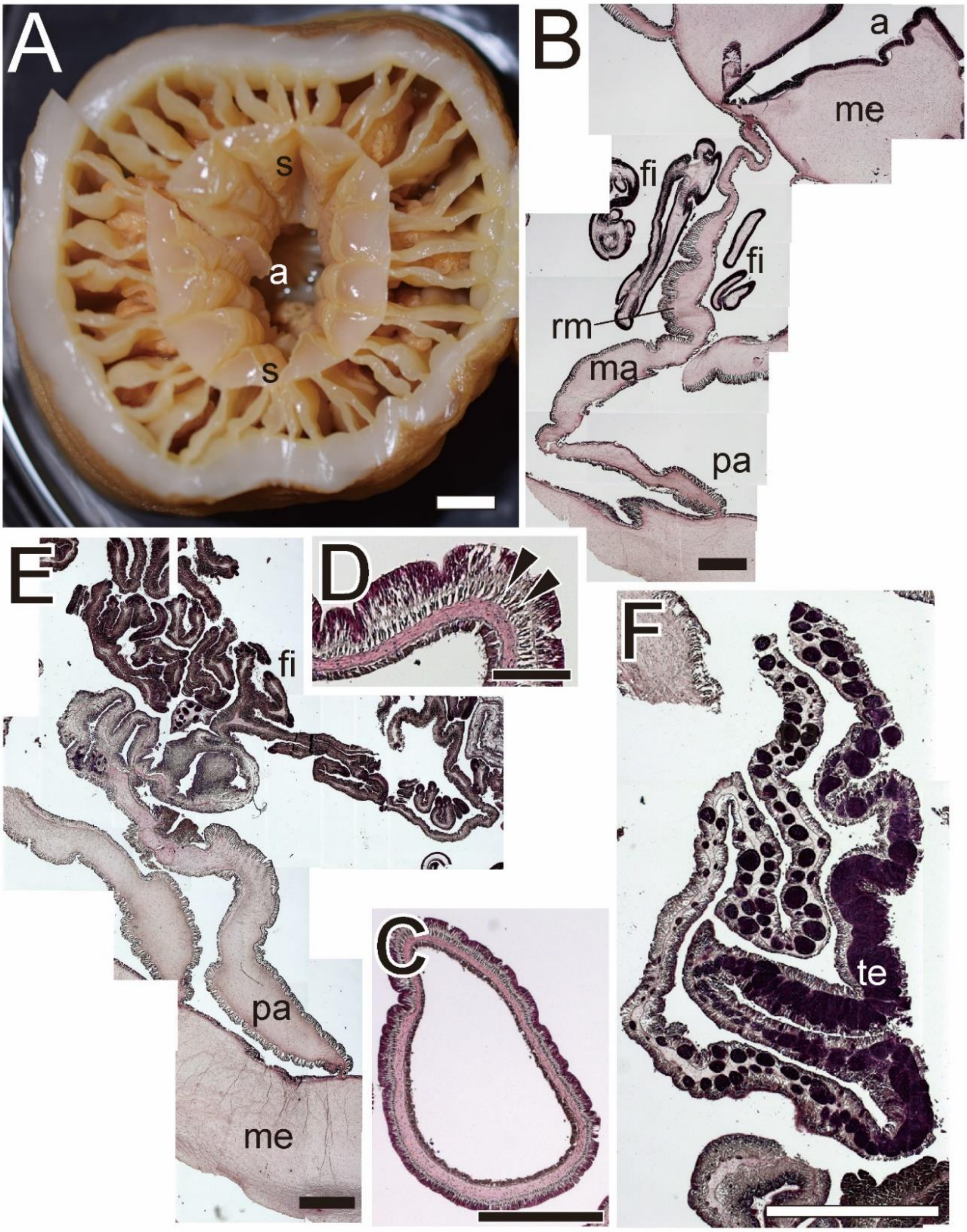

Fig. 23. Internal morphology of *Synactinernus churaumi* (NSMT-Co 1661).
A. Transverse section of actinopharynx of the gross specimen; B. Transverse section of a macrocneme; the dark purple tissues around the macrocneme are fragments of filaments; C. Transverse section of the tentacle; D. Enlarged view of transverse section of tentacle. Arrowheads indicate tentacular longitudinal muscle; E. Transverse section of filaments and gonads; F. Enlarged view of the gonad. Abbreviations: a, actinopharynx; fi, filament; ma, macrocneme; me, mesoglea; pa, parietal muscle; rm, retractor muscle; s, siphonoglyph; te, testis. Scale bars indicate 5 mm in A; 1 mm in B, C, E, and F; and 200 μm in D.

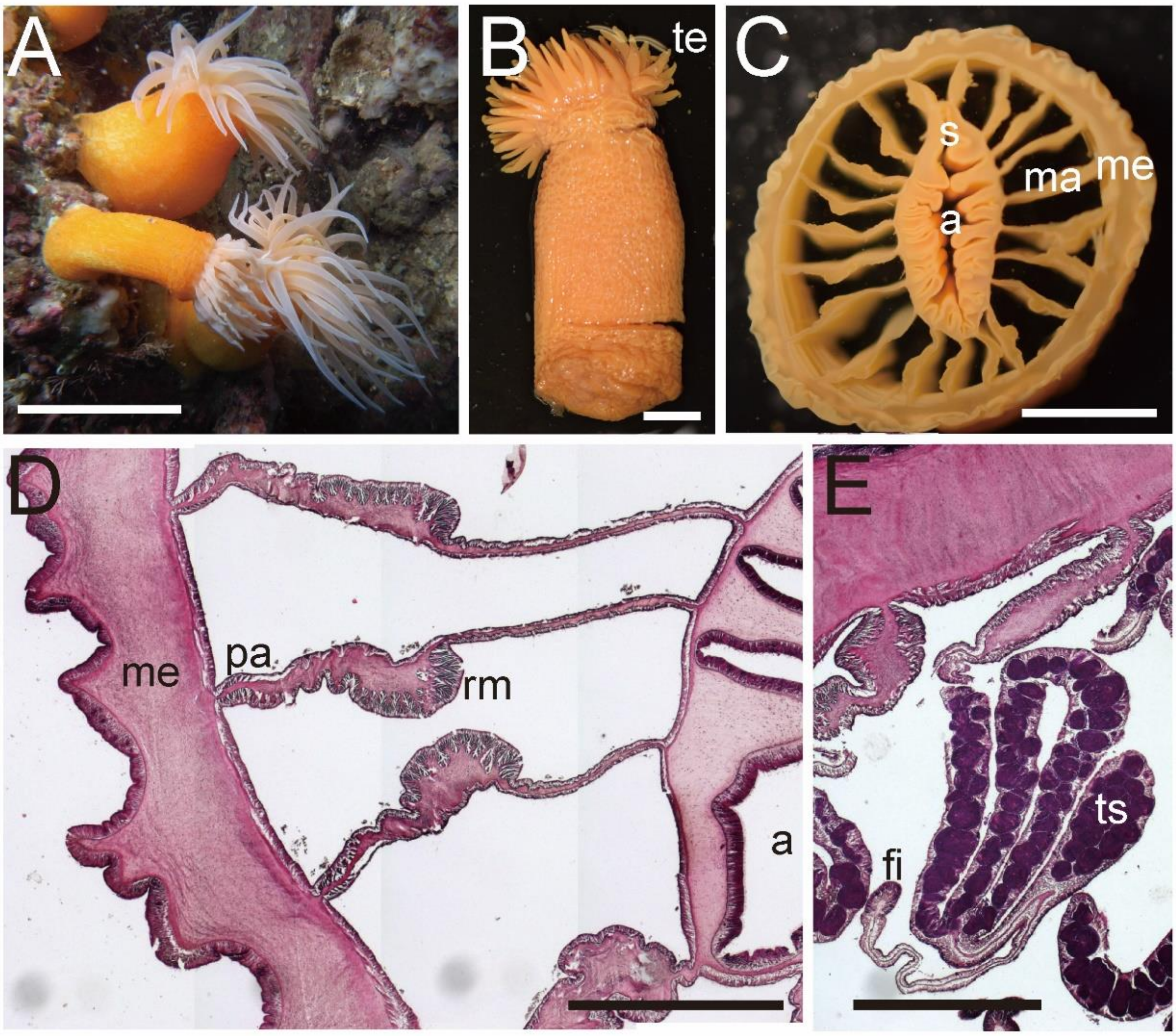

Fig. 24. External and internal morphology of *Isohalcurias carlgreni* (NSMT-Co 1697). A. Living individuals in nature; B. lateral view of a fixed specimen; C. Oral view of a fixed specimen; D. Enlarged transverse section of upper column; E. Enlarged longitudinal section of tentacle; F. Enlarged transverse section of tentacle; G. Enlarged transverse section of upper column; H. Enlarged transverse section of lower column. Abbreviations: a, actinopharynx; fi, filament; ma, macrocneme; me, mesoglea; pa, parietal muscle; rm, retractor muscle; s, siphonoglyph; te, tentacle; ts, testis. Scale bars indicate 5 cm in A, 1 cm in B and C, 1 mm in D, 500 µm in E. Picture A was taken by Takuma Fujii.

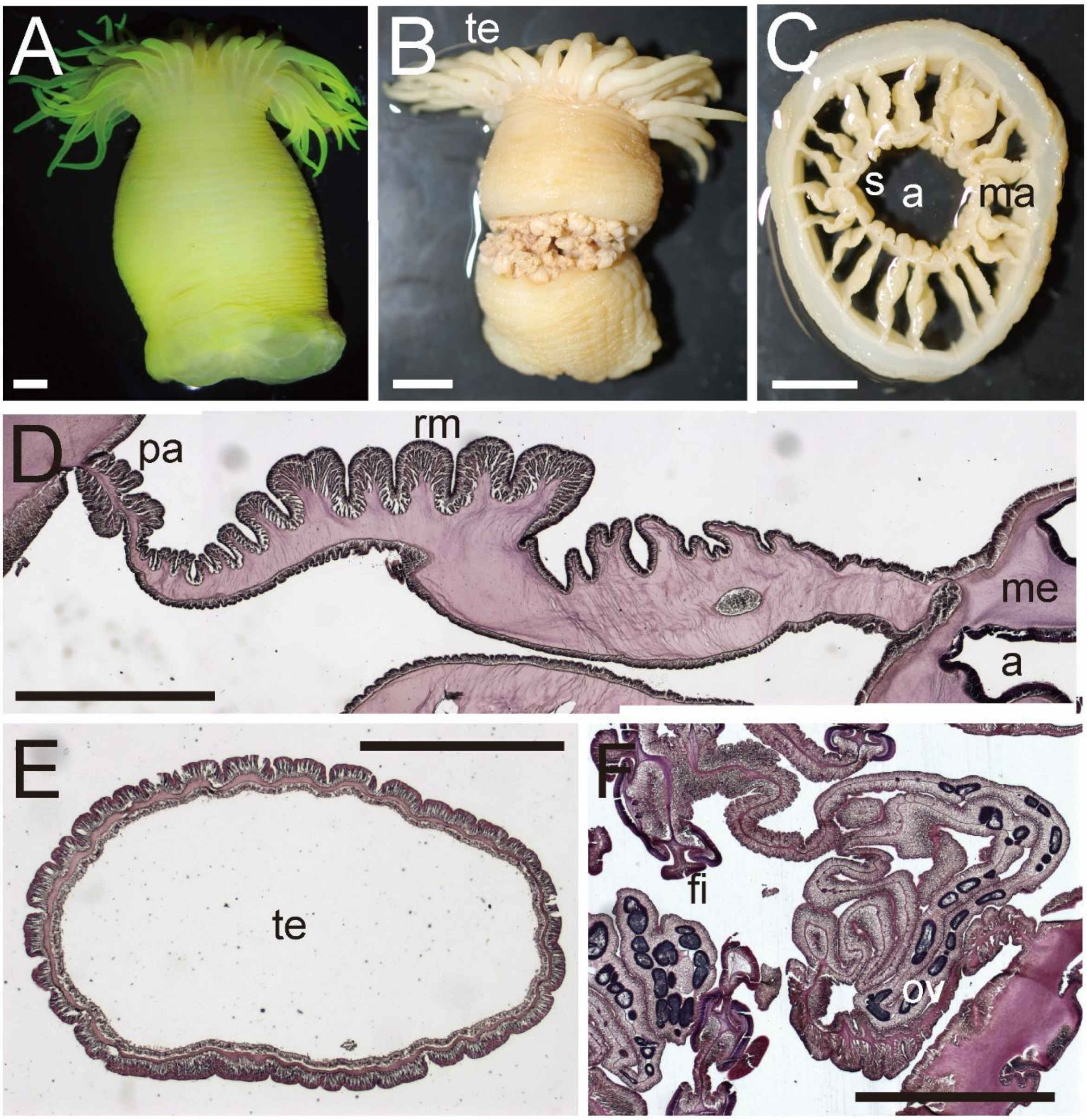

Fig. 25. External and internal morphology of *Isohalcurias levis* (Iz-018).
A. lateral view of a living specimen; B. lateral view of a fixed specimen; C. Transverse section of dissected specimen; D. Enlarged transverse section of upper column; E. Enlarged longitudinal section of lower column. Abbreviations: a, actinopharynx; fi, filament; ma, macrocneme; me, mesoglea; ov, ovary; pa, parietal muscle; rm, retractor muscle; s, siphonoglyph; te, tentacle. Scale bars indicate 1 cm in A–C, 1 mm in D and E.

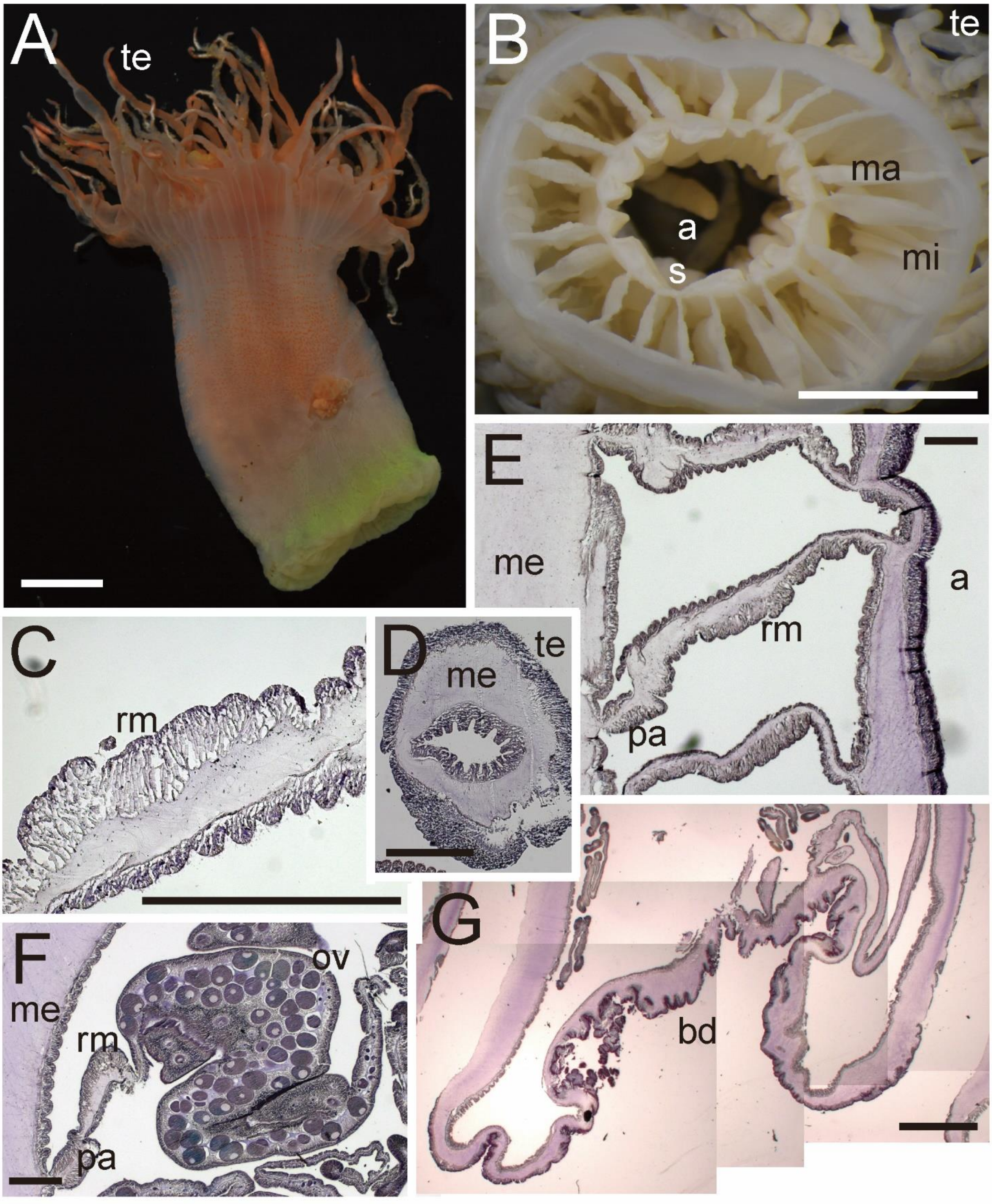

Fig. 26. External and internal morphology of *Isohalcurias* sp. nov. 3 (NSMT-Co 1699). A. lateral view of a living specimen (photographed by Mikihito Arai); B. Transverse section of dissected specimen; C. Enlarged view of retractor muscle; D. Transverse section of tentacle; E. Enlarged transverse section of upper column; F Enlarged transverse section of lower column; G. longitudinal section of basal disc. Abbreviations: a, actinopharynx; fi, filament; ma, macrocneme; me, mesoglea; mi, microcneme; ov, ovary; pa, parietal muscle; rm, retractor muscle; s, siphonoglyph; te, tentacle; te, testis. Scale bars indicate 1 cm in A and B, 1 mm in G, 500 μm in C, E, and F, 200 μm in D. Picture A was taken by Mikihito Arai.

Table 9. Comparison of Halcampelloidea superfam. nov. and the other superfamilies of suborder Anenthemonae.

	Actinernoidea Stephenson, 1922	**Halcampelloidea superfam. nov.**	Edwardsioidea Andres, 1881
Included families	Actinernidae Stephenson, 1922 Halcuriidae Carlgren, 1918 Isactinernidae fam. nov.	Halcampelloidea fam. nov.	Edwardsiidae Andres, 1881
Characters			
General form	Columnar	Worm-like	Worm-like
Main habitat	On hard substrates	In sand or mud	In sand or mud
Basal disc	Present	Present	Absent (physa)
Number of macrocnemes in the first cycle	12	12	8
References	Stephenson (1922) Carlgren (1949) Rodriguez et al. (2014)	Hertwig (1881) Carlgren (1949) **The present study**	Andres (1881) Carlgren (1949) Rodriguez et al. (2014)

Table 10. Comparison of Isactinernidae fam. nov. and the other two families in superfamily Actinernoidea.

	Isactinernidae fam. nov.	Actinernidae Stephenson, 1922	Halcuriidae Carlgren, 1918
Type genus	*Isactinernus* Carlgren, 1918	*Actinernus* Verrill, 1879	*Halcurias* McMurrich, 1893
The other genera	*Synhalcurias* Carlgren, 1914	none	*Synactinernus* Carlgren, 1918 *Carlgrenia* Stephenson, 1918 *Isohalcurias* gen. nov.
Characters			
Mesenterial arrangement	Cyclic	Bilateral	Cyclic
Microcnemes	Absent	Present	Present
Number of macrocnemes	Unfixed (more than 68)	Unfixed (more than 20)	Fixed (12, 20, or 36)
References	Carlgren (1914) Carlgren (1918) Uchida (2007) **The present study**	Stephenson (1922) Uchida (2007)	McMurrich (1893) Carlgren (1918) Stephenson (1918) Uchida (2004) Uchida (2007) **The present study**

Table 11. Cnidoms of the species of *Synhalcurias*, *Halcurias*, *Synactinernus*, and *Isohalcurias*.

		Synhalcurias sp. nov. 1 NSMT-Co 1695		*Halcurias* sp. nov. 2 Iz-009		*Synactinernus flavus* NSMT-Co 1660		*Synactinernus churaumi* NSMT-Co 1661		*Isohalcurias* sp. nov. 3 NSMT-Co 1699	
		Length × Width (µm)	frequency	Length × Width (µm)	frequency	Length × Width (µm)	frequency	Length × Width (µm)	frequency	Length × Width (µm)	frequency
Tentacle											
basitrichs	S	30.4-41.8 × 3.5-4.8	numerous	9.7-13.7 × 2.0-3.2	a few	15.3-33.4 × 2.3-4.4	numerous	30.0-42.2 × 2.1-3.3	numerous	25.7-36.2 × 3.2-4.5	rare
	L			21.1-27.5 × 2.5-4.7	numerous					25.7-36.2 × 3.2-4.6	numerous
spirocysts		25.1-45.4 × 3.8-6.8	numerous	20.8-31 × 3.5-7.1	numerous	18.5-45.7 × 3.0-9.8	numerous	17.8-56.8 × 2.6-8.3	numerous	21.8-41.2 × 4.0-7.3	numerous
microbasic *p*-mastigophores		11.9-20.9 × 3.9-4.8	a few								
microbasic *b*-mastigophores										30.1-36.3 × 3.4-6.0	a few
Actinopharynx											
basitrichs		27.5-34.9 × 2.8-4.4	numerous	22.8-32.6 × 2.4-4.0	numerous	23.8-39.6 × 2.6-4.2	numerous	26.5-42.5 × 3.2-4.6	numerous	25.7-36.2 × 3.2-4.5	numerous
spirocysts		31.4-43.4 × 5.9-9.5	numerous	19.6-27.8 × 4.2-5.3	a few	25.8-40.2 × 5.4-8.0	numerous	34.4-43.1 × 5.8-8.9	numerous	31.5-52.0 × 5.8-9.6	numerous
microbasic *p*-mastigophores	S	26.5-33.3 × 4.7-6.9	a few	20.3-29.2 × 4.5-7.7	numerous	23.0-23.9 × 4.0-5.0	rare	34.3-39.5 × 5.6-6.8	numerous	29.0-35.2 × 5.3-7.2	numerous
	L									30.1-37.1 × 5.6-7.4	a few
Column											
basitrichs		24.8-46.7 × 3.1-4.0	numerous	31.1-39.9 × 2.3-4.2	numerous	27.9-42.7 × 2.9-5.0	numerous	36.1-46.4 × 2.9-4.6	numerous	23.8-34.2 × 2.7-4.1	numerous
spirocysts		32.4-42.8 × 5.6-9.8	numerous			20.9-47.1 × 4.1-7.6	numerous	28.6-39.2 × 4.3-6.0	numerous	27.8-37.1 × 4.2-6.1	numerous
microbasic *p*-mastigophores		42.8-48.0 × 6.6-8.0	rare								
Filament											
basitrichs	S	31.0-39.7 × 3.0-4.7	numerous	23.9-33.5 × 2.4-4.3	numerous	28.5-38.5 × 2.5-4.3	numerous	21.6-36.3 × 2.4-3.7	numerous	9.9-19.8 × 1.7-4.4	numerous
	L									26.7-28.0 × 3.8-5.0	rare
spirocysts		27.2-35.0 × 5.0-7.0	numerous	24.8 × 5.3	rare	19.9-31.0 × 3.4-6.5	numerous	24.5-36.1 × 4.6-7.3	numerous	28.3-33.3 × 5.4-7.1	rare
microbasic *p*-mastigophores		26.3-34.3 × 5.0-6.5	a few	13.4-29.6 × 3.5-10.5	a few	20.5-27.5 × 4.5-6.7	numerous	28.1-39.4 × 4.8-7.1	numerous	25.2-34.8 × 5.6-9.2	numerous
microbasic *b*-mastigophores		15.9 × 4.5	rare								

Table 12. Comparison of *Isohalcurias* gen. nov. and the other genera of Halcuriidae.

	***Isohalcurias* gen. nov.**	*Halcurias* McMurrich, 1893	*Synactinernus* Carlgren, 1918	*Carlgrenia* Stephenson, 1918
Type species	*Isohalcurias carlgreni* (McMurrich, 1901) comb. nov.	*Halcurias pilatus* McMurrich, 1893	*Synactinernus flavus* Carlgren, 1918	*Carlgrenia desiderata* Stephenson, 1918
Characters				
Edge of oral disc	Simple, not forming any lobes	Simple, not forming any lobes	Forming eight lobes	Simple, not forming any lobes
Number of macrocnemes	20 (10 pairs)	20 (10 pairs)	36 (18 pairs)	12 (6 pairs)
Shape of retractor muscle	Pinnate	Simple	Simple	Strongly restricted
Spirocysts of column	Present	Absent	Present	Unknown
References	McMurrich (1901) Carlgren (1928) Uchida (2004)	McMurrich (1893) Carlgren (1949) Uchida (2004)	Carlgren (1918) Fautin and den Hartog (2003) Uchida (2007)	Stephenson (1918) Carlgren (1949)

Table 13. Comparison of *Halcurias* sp. nov. 2. and the other species of *Halcurias* including species possibly assignable to the genus.

	***Halcurias* sp. nov. 2**	*Halcurias japonicus* Uchida, 2004	*Halcurias pilatus* McMurrich, 1893	**Halcurias capensis* Carlgren, 1928	**Halcurias endocoelactis* Stephenson, 1918	**Halcurias mcmurrichi* Uchida, 2004
Characters						
Size (height)	9-10 mm	15-30 mm	14-15 mm	12-22 mm	48 mm	40 mm
Basitrichs of tentacles	2 types	1 type	1 type	1 type	1 type	1 type
Spirocysts in actinopharynx	Present	Present	Present	Absent	Absent	Present
Long basitrichs in filaments	Absent	Absent	Present	Unknown	Unknown	Absent
References	**The present study**	Uchida (2004) **The present study**	McMurrich (1893) Rodriguez et al. (2013)	Carlgren (1928) Uchida (2004)	Stephenson (1918) Uchida (2004)	Uchida (2004) Rodriguez et al. (2013)

*Species without molecular phylogenetic information

Table 14. Comparison of *Isohalcurias* sp. nov. 3. and the other species of *Isohalcurias* gen. nov. including a species possibly assignable to the genus.

	***Isohalcurias* sp. nov. 3**	*Isohalcurias carlgreni* (McMurrich, 1901) comb. nov.	*Isohalcurias levis* (Uchida, 2004) comb. nov.	**Halcurias minimus* Carlgren, 1928	**Halcurias sudanensis* Riemann-Zürneck, 1983
Characters					
Size (height)	25-40 mm	11-50 mm	34-90 mm	8 mm	30 mm
Retractor muscle	Distinct Pinnate	Distinct Strongly pinnate	Weak Strongly pinnate	Distinct Pinnate	Weak Slightly Pinnate
Parietal muscle	Distinct with well-branched muscular processes	Weak with simple muscular processes	Weak with simple muscular processes	Weak with simple muscular processes	Weak with simple muscular processes
Basitrichs of tentacles	2 types	1 type	2 types	2 types	1 type
Spirocysts in actinopharynx	Present	Present	Present	Absent	Present
Spirocysts in column	Present	Present	Present	Present (but sparse)	Present
Long basitrichs in filaments	Absent	Absent	Absent	Unknown	Absent
References	**The present study**	McMurrich (1901) Uchida (2004) **The present study**	Uchida (2004) **The present study**	Carlgren (1928) Uchida (2004)	Riemann-Zürneck (1983)

*Species without molecular phylogenetic information

Superfamily HALCAMPELLOIDEA superfam. nov.

(New Japanese name: nasubi-isoginchaku-jouka)

Diagnosis. Anenthemonae with elongate, vermiform body divisible into at least two regions, long scapus with cuticle and distal scapulus or indivisible any regions. Aboral end tapered, like physa. No marginal sphincter muscle or acontia. 10 or 12 macrocnemes in first cycle. Macrocnemes divided into two pairs of directives and six–eight lateral mesenteries. Retractors generally restricted. Parietal muscles always distinct. Cnidom: spirocysts, basitrichs, microbasic *p*-mastigophores, microbasic *b*-mastigophores.

Etymology. Derived from the family and genus name.

Remarks. There had been two superfamilies, Actinernoidea and Edwardsioidea in the suborder Anenthemonae. However, according to my analysis, an additional clade of sea anemones, include *Halcampella maxima* (Wassilieff, 1908), was formed in the Anenthemonae clade and became a sister group of Edwardsioidea (Fig. 7). So, though *H. maxima* has been belonging to Halcampidae Andres, 1893 (this family is in Enthemonae clade), these sea anemones were no longer Enthemonae. However, superfamily Edwardsioidea was too peculiar to accommodate these anemones: species of Edwardsioidea were characterized by having eight perfect mesenteries, but these species have 10–12 perfect ones. That was why I established the third superfamily, Halcampelloidea superfam. nov. in Anenthemonae.

Family HALCAMPELLIDAE fam. nov.

(New Japanese name: nasubi-isoginchaku-ka)

Diagnosis. Halcampelloidea with elongate, vermiform body divisible into at least two regions, long scapus with cuticle and distal scapulus or indivisible any regions. Aboral end tapered, like physa. No marginal sphincter muscle or acontia. At least 12 macrocnemes in first cycle. Macrocnemes divided into two pairs of directives and eight lateral mesenteries (four lateral pairs). Retractors generally restricted. Parietal muscles always distinct. Cnidom: spirocysts, basitrichs, microbasic *p*-mastigophores, microbasic *b*-mastigophores.

Type genus. *Halcampella* Andres, 1883

Etymology. Derived from the name of type genus.

Remarks. I accommodated the species in this clade into one family, Halcampellidae fam. nov.. Even though the species can be split into three families by the topology of tree (Fig. 11), there was no sufficient evidence to split these species into different families. See Table 15 for comparison of all included genera of Halcampellidae.

Genus *Halcampella* Andres, 1883
(New Japanese name: nasubi-isoginchaku-zoku)

Halcampella Andres, 1883: 315; Hertwig, 1888: 29; Carlgren, 1949: 28

Diagnosis. Halcampellidae with the elongate body divisible into physa, scapus and scapulus. **Basal disc** more or less distinct, scapus with tenaculi. No sphincter. Tentacles short, more numerous than the mesenteries in the aboral part of the body, their longitudinal muscles ectodermal. Radial muscles of oral disc ectodermal to meso-ectodermal. Siphonoglyphs weak. 6 pairs of perfect and fertile mesenteries, 2 pairs of directives. Microcnemes only in the uppermost part of the body. Retractors strong, diffuse, restricted, forming numerous high folds. Parietal muscles rather well developed.
(The revised points from Carlgren [1949] are indicated by **bold**)

Type species. *Halcampella maxima* Hertwig, 1888

Remarks. *Halcampella* had been a genus of Halcampidae and accommodated four species (Fautin, 2016). *Halcampella maxima* collected from Japan was the type species of this genus. *Halcampella* once had been included in family Halcampoididae Appellof, 1896, and later moved into Halcampidae Andres, 1883 in association with the unification of these two families (Gusmão et al., 2016). However, my research showed that *Halcampella maxima* was not in Enthemonae but a species of Anenthemonae.

However, *Halcampa*, the type genus of Halcampidae was exactly Enthemonae (Fig. 7), so it was undoubtful that *Halcampella* was no longer the member of family Halcampidae. Moreover, though it was also possible to reestablish of previous family Halcampoididae, a species of *Halcampoides*, the type genus of this family, was also in the Enthemonae clade (the sister node with *Halcampa*; Fig. 7). Thus, *Halcampella* had been wrongly accommodated into families Halcampidae or Halcampoididae because of their morphological similarity, and a new family should be established for this genus in Anenthemonae. In conclusion, *Halcampella* becomes the type genus of the new family, Halcampellidae fam. nov.

Halcampella maxima Hertwig, 1888

(Japanese name: nasubi-isoginchaku; Uchida, 1965)

Fig. 27; Table 16

Halcampella maxima Hertwig, 1888: 29–32; Wassilieff, 1908: 6–7, fig. 1.

Material examined. (Iz-023): dissected specimen, histological sections, tissues in paraffin, and prepared nematocysts, preserved from an aquarium of Misaki Marine Biological Station, collected by biological dredge of R/V Rinkai-Maru, off Misaki, Kanagawa Pref., Japan (detailed locality and date are unknown), by Mamoru Sekifuji and Hisanori Kotsuka; (Iz-024):whole specimen, 4 July 2017, by biological dredge of R/V Rinkai-Maru, off Misaki, Kanagawa Pref., Japan (St-5: 35°08.925′N, 139°34.948′E), 76–79 m depth, collected during the second Coastal Organism Joint Survey of JAMBIO, Japanese Association for Marine Biology, by Takato Izumi.

Description. ***External anatomy.*** Column of contracted specimen ca. 120 – 150 mm in whole length, and 10–20 mm in width. In living specimen, the maximum length ca. 200–250 mm. Column cylinder-like in shape, but slightly swollen on middle part (Fig. 27A). Body divided into scapulus, scapus and disc-like physa; surface of scapus covered gray periderm, rough but without any structures, attaching grinds of sand. Scapulus white or pale yellow, naked, with obvious mesenterial insertion (Fig. 27B). Aboral end differentiated from scapus, disc-like physa, naked, and more or less adherent. Tentacles 40 in number, in two cycles of 20, same length in each cycle (Fig. 27C), pale pink, and ambiguously brownish striped. Mouth apparently swelled.

Internal anatomy. 12 perfect mesenteries in first cycle macrocnemes, distributed along whole body from distal to proximal end, pairs into six pairs plus. 28 tiny microcnemes (Fig. 27D), without muscles, limited to distal-most part: 8 between dorsal directives and dorso-lateral mesenteries, 12 between dorso- and ventro-lateral mesenteries, and 8 between ventro-lateral mesenteries and ventral directives. All macrocnemic mesenteries bear retractor and parietal muscles. Each retractor muscle distinctly developed (Fig. 27G), restricted in actinopharynx side, with approximately 30–50 simple or slightly branched muscular processes (Fig. 27H) in distal side; weakly developed, restricted with 10–20 simple muscular processes in lower part (Fig.

27I). Parietal muscles of macrocnemes distinct, with 10–20 a little branched muscular processes in each side in distal part, and 20–30 processes in lower part (Fig. 27I). Actinopharynx short, 11 grooved and a distinct siphonoglyph. One tentacle in each endo- or exocoel. Tentacular longitudinal muscle ectodermal and distinct (Fig. 27F). Tentacular circular muscle endodermal but indistinct (Fig. 27E). Marginal sphincter muscle and basilar muscle absent (Fig. 27E). Mesoglea generally thin in mesenteries and tentacles, but comparatively thick next to retractor and parietal muscle and the thickest in body wall and actinopharynx (Fig. 27D, G). Gonads on mesenteries between retractor muscles and filaments; gametocytes immature (Fig. 27I).

Cnidom. Spirocysts, basitrichs, and microbasic *p*-mastigophores. See Table 16 for size and distribution.

Remarks. After the original description of Hertwig (1888), there was only one taxonomic description of *Halcampella maxima* in Wassilieff (1908). The specimens obtained in this research corresponded their description. The description of Hertwig (1888) and Wassilieff (1908) did not contained detailed pictures and cnidom, so I redescribed with adding these data.

Halcampella cretata (Stimpson, 1856) comb. nov.

(Japanese name: nise-mino-mushimodoki)

Figs. 28, 29; Table 16

Paraedwardsia cretata Stimpson, 1856: 376; Verrill, 1868: 320

Material examined. (Iz-025): dissected specimen, histological sections, tissues in paraffin, and prepared nematocysts, collected at 21 May 2015, by biological dredge of R/V Rinkai-Maru, off Jogashima Island, Misaki, Kanagawa Pref., Japan (Station-2: 35°06.929′N, 139°34.611′E), 86–88 m depth, by Takato Izumi; YPM6856 (holotype): a part of dissected specimen, collected in the US North Pacific Expedition, 1854 (date unknown), from Kagoshima Bay, by William Stimpson.

Description. ***External anatomy.*** Column of well-elongated specimen 40 mm in whole length, and 8 mm in width. Column long barrel-like in shape, slightly swollen on middle part (Fig. 28A). Body divided into scapulus, scapus and disc-like physa; surface of scapus covered brown periderm, rough but without any structures, and attaching grinds of sand densely (Fig. 28A). Scapulus white, naked, with obvious mesenterial insertion. Aboral end differentiated from scapus, disc-like physa (Fig. 28A), naked, and more or less adherent. Tentacles 24 in number, in two cycles of 12, same length in each cycle, hemitransparent, pale white with dark red patches. Mouth apparently swelled (Fig. 28C).

Internal anatomy. 12 perfect mesenteries in first cycle macrocnemes (Fig. 28D, E), distributed along whole body from distal to proximal end, pairs into six pairs plus. 12 tiny microcnemes, without muscles, limited to distal-most part: 4 between dorsal directives and dorso-lateral mesenteries, 4 between dorso- and ventro-lateral mesenteries, and 4 between ventro-lateral mesenteries and ventral directives. All macrocnemic mesenteries bear retractor and parietal muscles (Fig. 28D). Each retractor muscle distinctly developed; restricted in actinopharynx or filament side, with approximately 20–30 simple or slightly branched muscular processes (Fig. 28F, G) on both distal and proximal side. Parietal muscles of macrocnemes distinct, with 10–15 a little branched muscular processes in each side in distal part (Fig. 28F), and 4–7 processes in lower part (Fig. 28G). Actinopharynx short, 11 grooved and a distinct siphonoglyph. One tentacle in each endo- or exo- coel. Tentacular longitudinal and tentacular circular muscle both indistinct. Marginal sphincter muscle and basilar muscle absent. Mesoglea generally thin in mesenteries and tentacles, but comparatively thick next to retractor and parietal muscle and the thickest in body wall and actinopharynx (Fig, 2D, F). Gonads on mesenteries between retractor muscles and filaments; gametocytes immature.

Cnidom. Spirocysts, basitrichs, and microbasic *p*-mastigophores. See Table 16 for size and distribution.

Remarks. *Paraedwardsia cretata* (Stimpson, 1856), collected from Kagoshima Bay (Stimpson, 1856), had been classified in Edwardsiidae since this study. However, the observation of gross transversal section of the type specimen at Yale Peabody Museum (YPM 6856) revealed that this species has 12 perfect mesenteries (Fig. 29) despite Edwardsiidae has been characterized by eight mesenteries. Therefore, *Paraedwardsia cretata* is not no longer Edwardsiidae.

Now, one specimen collected from Misaki corresponded to the description of Stimpson (1856) and the morphology of the type specimen. By phylogenetic analysis using the specimen, this species was in the clade of Halcampelloidea and related with *H. maxima* in my phylogenetic tree (Fig. 11). These two species shared several similar morphological features than the other two species (*Hexactis* sp. nov. 4 and *Pseudoedwardsia* sp. nov. 5). That was why I accommodated *P. cretata* into *Halcampella* and renamed this species as *Halcampella cretata* comb. nov., with revising the diagnosis of genus.

Genus *Hexactis* gen. nov.

(New Japanese name: rokkaku-ginchaku-zoku)

Diagnosis. Halcampellidae with the elongate body indivisible into regions. Basal disc indistinct. Scapus hexagonal, with thick robust periderm, without tenaculi. No sphincter. Aboral end disc-like physa, strongly adhesive. Tentacles short, more numerous than the mesenteries in the aboral part of the body, their longitudinal muscles ectodermal. No siphonoglyphs. 6 pairs of perfect and fertile mesenteries, 2 pairs of directives. Microcnemes only in the uppermost part of the body. Retractors strong, restricted, forming numerous high folds. Parietal muscles rather well developed.

Type species. *Hexactis* sp. nov. 4 (monotypic)

Etymology. "*Hexa*" is derived apparent hexagonal shape of species in this genus. "*-actis*" is commonly used in actiniarian genus names, meaning radiation of sunshine in Greek.

Remarks. See Table 15 for comparison to the other genera of Halcampellidae. Compared to the other two genera, species of *Hexactis* are characterized by column in apparent hexagonal shape with thick robust periderm. Moreover, only *Hexactis* species have aboral ends with strong adherence. *Hexactis* sp. nov. 4 inhabited on the walls of underwater caves in contrast to the other species of this superfamily inhabited burying in stony sand, thus anemones of this species need to fix their body in the cavity of rock wall by the power of adherence.

Hexactis sp. nov. 4

(New Japanese name: rokkaku-ginchaku)

Fig. 30; Table 16

Material examined. (Iz-026): dissected specimen, histological sections, tissue in paraffin, and prepared cnidae, collected by SCUBA diving on 12 August 2012 at a depth of 1 m in underwater cave at Okinawa Island, Okinawa Pref., Japan, by Takuma Fujii; (Iz-27)–(Iz-32): dissected specimen, same locality, method and collector as (Iz-026); (Iz-33): dissected specimen, collected at underwater cave at Australia (locality in detail unknown), by James Davis Reimer.

Description. ***External anatomy.*** Column of contracted specimen ca. 30–60 mm in whole length, and ca. 7–10 mm in width. Column long cylinder-like in shape, slightly swollen on middle part, and characteristically hexagonal transversely (Fig. 30A). Body little divided into scapus and physa; surface of scapus covered very robust light brown periderm, rough but without any structures. Mesenterial insertion invisible. Aboral end a little differentiated from scapus, disc-like physa, naked, and strongly adherent. Tentacles 24–32 in number, same length in each cycle, slender, dark red in color. Mouth apparently swelled.

Internal anatomy. 12 perfect mesenteries in first cycle macrocnemes, distributed along whole body from distal to proximal end, into six pairs on both side of each angle of hexagonal shape (Fig. 30 A, F). 12–20 tiny microcnemes, without muscles, limited to distal-most part: 4–8 between dorsal directives and dorso-lateral mesenteries, 4 between dorso- and ventro-lateral mesenteries, and 4–8 between ventro-lateral mesenteries and ventral directives. All macrocnemic mesenteries bear retractor and parietal muscles. Each retractor muscle distinctly developed; restricted in actinopharynx or filament side, elongated, with approximately 30–40 simple to well-branched muscular processes (Fig. 30C) next to actinopharynx, and with 10–15 well-branched processes (Fig. 30D) in proximal side. Parietal muscles of macrocnemes distinct, with 15–24 a little branched muscular processes in each side in distal part (Fig. 30C), and 8–12 processes in lower part (Fig. 30D). Actinopharynx short, 12 grooved, with no siphonoglyph. One tentacle in each endo- or exocoel. Tentacular longitudinal muscle exocoeletic and tentacular circular muscle endocoeletic, both distinct (Fig. 30B, E). Marginal sphincter muscle and basilar muscle absent (Fig. 30G), but circular muscle of body well-developed and distinct. Mesoglea far thicker in body wall (especially thickest in angle of hexagonal shape; Fig. 30F), but comparatively thin in mesenteries, retractor and parietal muscles, or tentacles (Fig. 30E). Gonads on mesenteries between retractor muscles and filaments; matured oocytes inside (Fig. 30D).

Cnidom. Spirocysts, basitrichs, and microbasic *p*-mastigophores. See Table 16 for size and distribution.

Ecological remarks. *H.* sp. nov. 4 has been discovered only in shallow zone of underwater cave. This species adhered the hollows or cavities of rock with their strong aboral end.

Remarks. *Hexactis* sp. nov. 4 inhabited only in overhanging walls of caves in the sea. This species adhered to the hollows of overhanging rock by their disc-like aboral ends. Till now, this sea anemones were discovered only underwater caves in Okinawa and Australia. Because this species had unique morphological features in Anenthemonae (see remarks of the genus), I established a new genus, *Hexactis* gen. nov., for this species.

Genus *Pseudoedwardsia*

(New Japanese name: nise-mushimodoki-zoku)

Diagnosis. Halcampellidae with the elongate body divisible into physa-like basal disc, scapus and capitulum. Basal disc more or less distinct, scapus without tenaculi. No sphincter. Tentacles short, more numerous than the mesenteries in the aboral part of the body, their longitudinal muscles ectodermal. Siphonoglyphs weak. 10 perfect mesenteries: 4 pairs of perfect and fertile mesenteries, 2 pairs of directives, and 2 not-paired perfect mesenteries. Microcnemes only in the uppermost part of the body. Retractors strong, restricted. Parietal muscles rather well developed.

Type species. *Pseudoedwardsia* sp. nov. 5 (monotypic)

Etymology. *Pseudoedwardsia* sp. nov. 5, the only species of this genus, resembles species of Edwardsiidae at a glance (Fig. 31A). So, "*Pseudo*", meaning false, is followed by "*edwardsia*".

Remarks. See Table 15 for comparison to the other genera of Halcampellidae. The species *Pseudoedwardsia* (*P.* sp. nov. 5) was far similar to species of Edwardsiidae (especially to species of *Paraedwardsia*). However, this species had 10 perfect mesenteries, which was not like edwardsiids having eight macrocnemes. The mesenterial arrangement with 10 perfect mesenteries is so peculiar in Actiniaria: this number was observed on only a few species (see remarks part of Discoactinidae fam. nov.). According to phylogenetic analysis, it was likely that *Pseudoedwardsia* was related to anemones of Halcampellidae, thus now I established new genus *Pseudoedwardsia* for this species and accommodated in Halcampellidae.

Pseudoedwardsia sp. nov. 5

(New Japanese name: nise-mushimodoki)

Fig. 31; Table 16

Material examined. (Iz-034) :dissected specimen, histological sections, cnidae slides, by biological dredge, 9 November 2017, off Mie Pref., Japan, 190–196 m in depth, collected during the research cruise of R/V Seisui-Maru (St-5: 34°09.80′N, 136°38.20′E), by Itaru Kobayashi; (Iz-035) :whole specimen, same locality, method and collector as (Iz-034); (Iz-036): dissected specimen, 7 October 2015, by biological dredge, off Mie Pref., Japan, 155 m depth, collected during the research cruise of R/V Seisui-Maru (St-3: 34°10.8′N, 136°35.7′E), by Akito Ogawa.

Description. ***External anatomy.*** Column of contracted specimen ca. 10–20 mm in whole length, and 3–4 mm in width. Column cylinder-like in shape, but slightly swollen on proximal part (Fig. 31A). Body divided into capitulum, scapus and disc-like physa; surface of scapus dark-brown or dark-gray periderm, rough but without any structures, attaching grinds of sand. Scapulus naked, with obvious mesenterial insertion. Aboral end differentiated from scapus, disc-like physa, naked, and more or less adherent. Tentacles 16 in number, in two cycles of 8, almost same length in each cycle (Fig. 31B). Mouth apparently swelled. The color in living unknown.

Internal anatomy. 10 perfect mesenteries in first cycle macrocnemes, distributed along whole body from distal to proximal end, pairs into four pairs and two dependent macrocnemes. 6 microcnemes, without muscles, limited to distal-most part: 4 between dorsal directives and dorso-lateral mesenteries, and 2 between ventro-lateral mesenteries and ventral directives (facing to independent macrocnemes). All macrocnemic mesenteries bear retractor and parietal muscles (Fig. 31E, G). Each retractor muscle distinctly developed; restricted in the middle part of mesenteries, with approximately 8–12 simple or slightly-branched muscular processes (Fig. 31G) from distal to proximal side (Fig. 31G). Parietal muscles of macrocnemes distinct, with 3–5 a well-branched muscular processes in each side in lower part (Fig. 31G). Actinopharynx short, 10 grooved and an indistinct siphonoglyph. One tentacle in each endo- or exo- coel. Tentacular longitudinal muscle ectodermal but indistinct (Fig. 31C). Tentacular circular muscle indistinct (Fig. 31D). Marginal sphincter muscle and basilar muscle absent (Fig. 31F, H). Mesoglea generally thin in mesenteries and tentacles, but comparatively thick next to retractor and parietal muscle and the thickest in body wall and actinopharynx (Fig. 31E). Gonads on mesenteries between retractor muscles and filaments; gametocytes immature (Fig. 31G).

Cnidom. Spirocysts, basitrichs, microbasic *b*-mastigophores and microbasic *p*-mastigophores. See Table 16 for size and distribution.

Remarks. This species was similar to edwardsiids at a glance, but there were several differences. Concerning the mesenterial arrangement, the number of macrocnemes (ten) differed from not only Edwardsiidae (eight) but also any other Halcampellidae anemones (twelve). The arrangement was observed in only a few groups of anemones (e.g. Discoactinidae fam. nov.). The aboral ends of *Pseudoedwardsia* are adhesive while few edwardsiid have the ability to adhere (e.g. *Tempuractis rinkai* Izumi, Yanagi and Fujita, 2018, which apparently adhered the rock under their hosts). Moreover, this species was phylogenetically separated from other two genera of Halcampellidae (Fig. 11). That was why I concluded these anemones as belonging to new genus.

SAMMARY of Halcampelloidea superfam. nov.

1. Halcampelloidea superfam. nov. accommodates only one family, Halcampellidae fam. nov., and three genera, *Halcampella* Andres, 1883*,* *Hexactis* gen. nov., and *Pseudoedwardsia* gen. nov.
2. Genus *Halcampella* accommodates *H. cretata* (Stimpson, 1856) comb. nov., renamed from *Paraedwardsia cretata* (Stimpson, 1856), which had been accommodated in Edwardsiidae.
3. The two new genera *Hexactis* and *Pseudoedwardsia* were established. Both genera are monotypic for the time being.

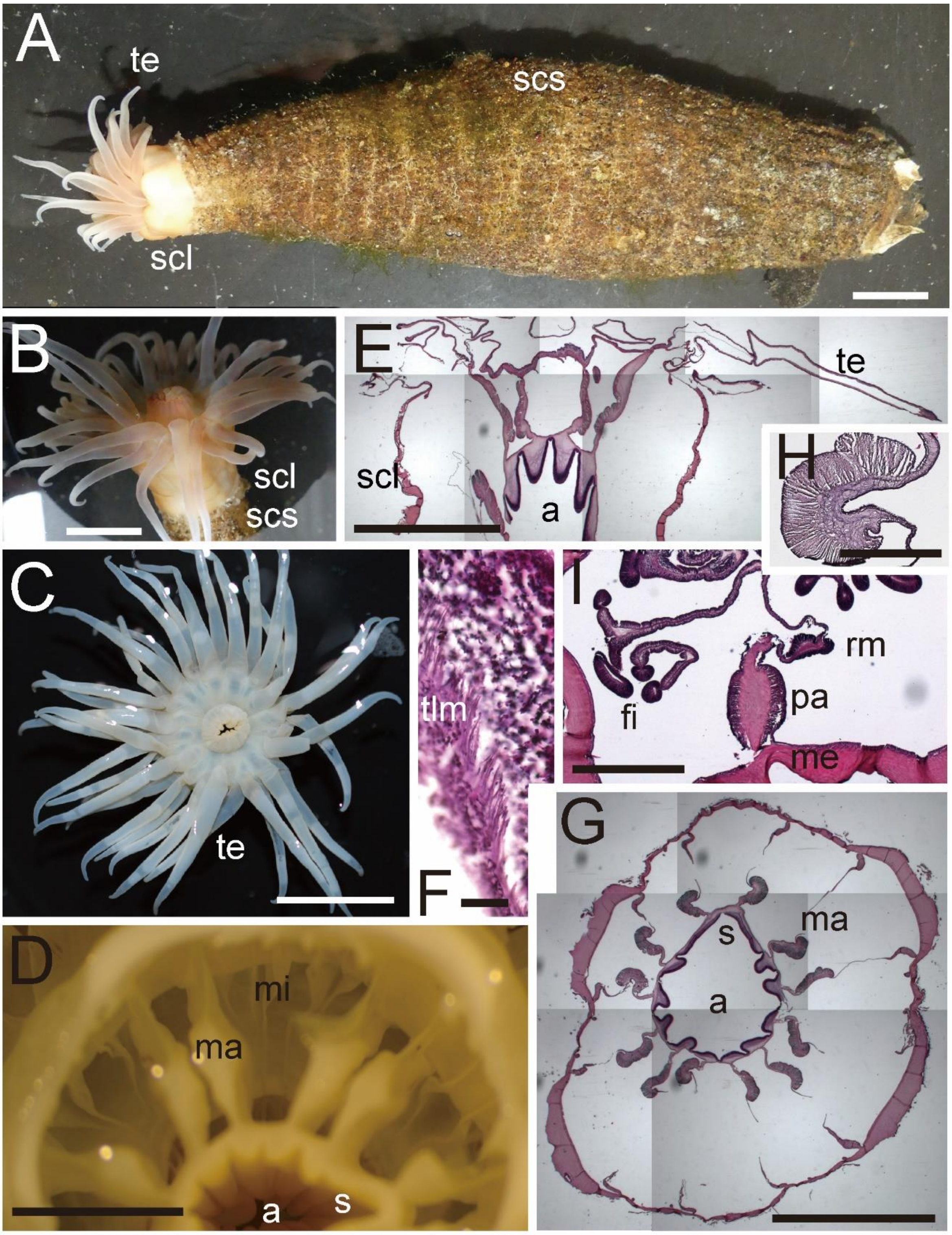

Fig. 27. External and internal morphology of *Halcampella maxima* (Iz-023).
A. lateral view of a living specimen; B. Enlarged view of oral disc; C. Oral view of a fixed specimen; D. Transverse section of dissected specimen; E. longitudinal section of oral disc; F. Enlarged view of longitudinal section of tentacle; G. Transverse section of lower column; H. Enlarged view of retractor muscle; I. Enlarged view of transverse section of lower column. Abbreviations: a, actinopharynx; fi, filament; go, gonad; ma, macrocneme; me, mesoglea; pa, parietal muscle; rm, retractor muscle; s, siphonoglyph; scl, scapulus; scs, scapus; te, tentacle. Scale bars indicate 1 cm in A, B, and C, 5 mm in D, E, and G, 1 mm in I, 500 µm in H, 100 µm in F.

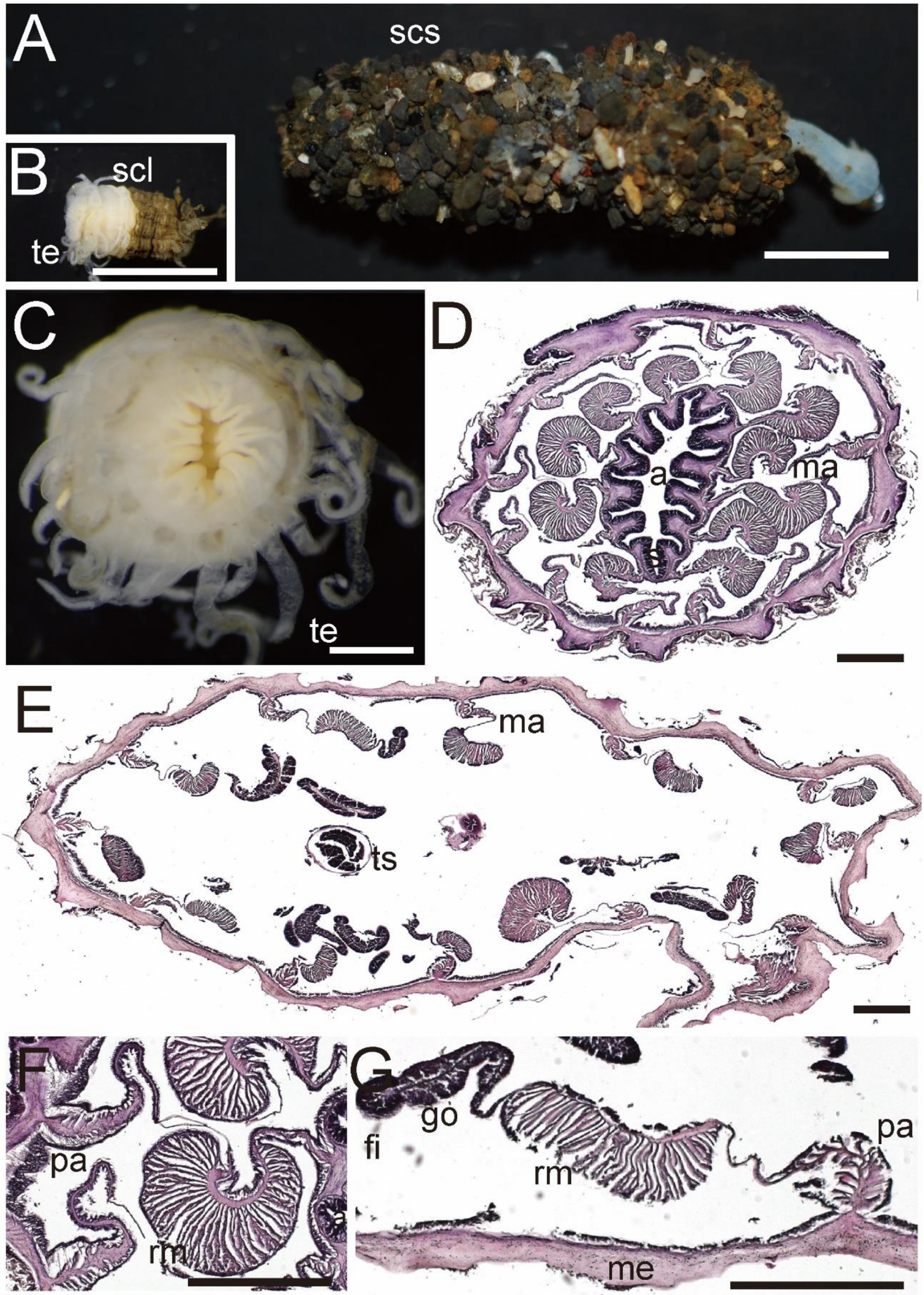

Fig. 28. External and internal morphology of *Halcampella cretata* (Iz-025).
A, B. lateral view of a preserved specimen; C. Oral view of oral disc; D. Transverse section of upper column; E. Transverse section of lower column; F Enlarged view of retractor muscle; G. Enlarged view of transverse section of lower column. Abbreviations: a, actinopharynx; fi, filament; ma, macrocneme; me, mesoglea; pa, parietal muscle; rm, retractor muscle; s, siphonoglyph; scl, scapulus; scs, scapus; te, tentacle; tlm, tentacle longitudinal muscle. Scale bars indicate 1 cm in A, B, 1 mm in C, 500 µm in D–G.

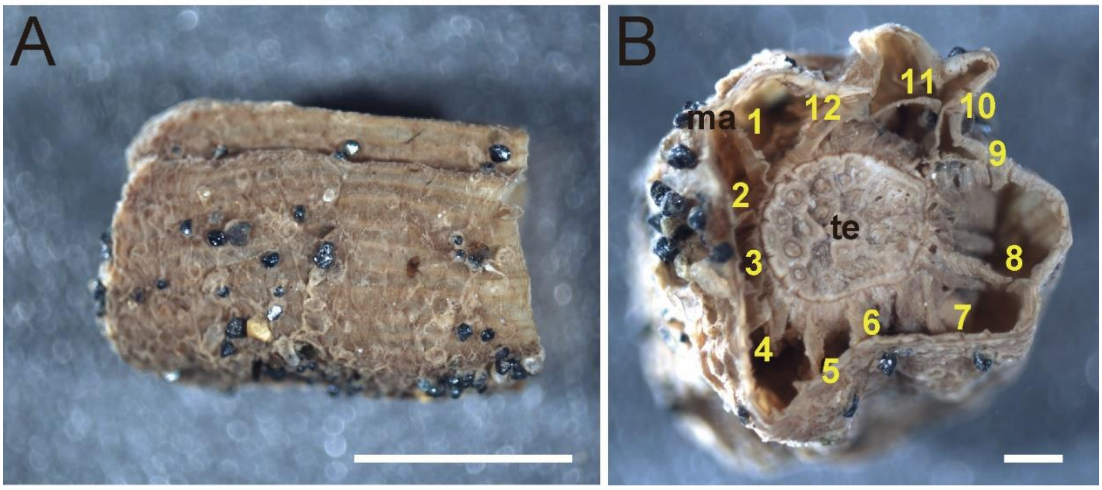

Fig. 29. The holotype of *Halcampella cretata* (YPM 6856: Yale Peabody Museum). A. Lateral view. B. Transverse section of dissected specimen. Characters indicate numbers of macrocnemes (Photo courtesy of Kensuke Yanagi).

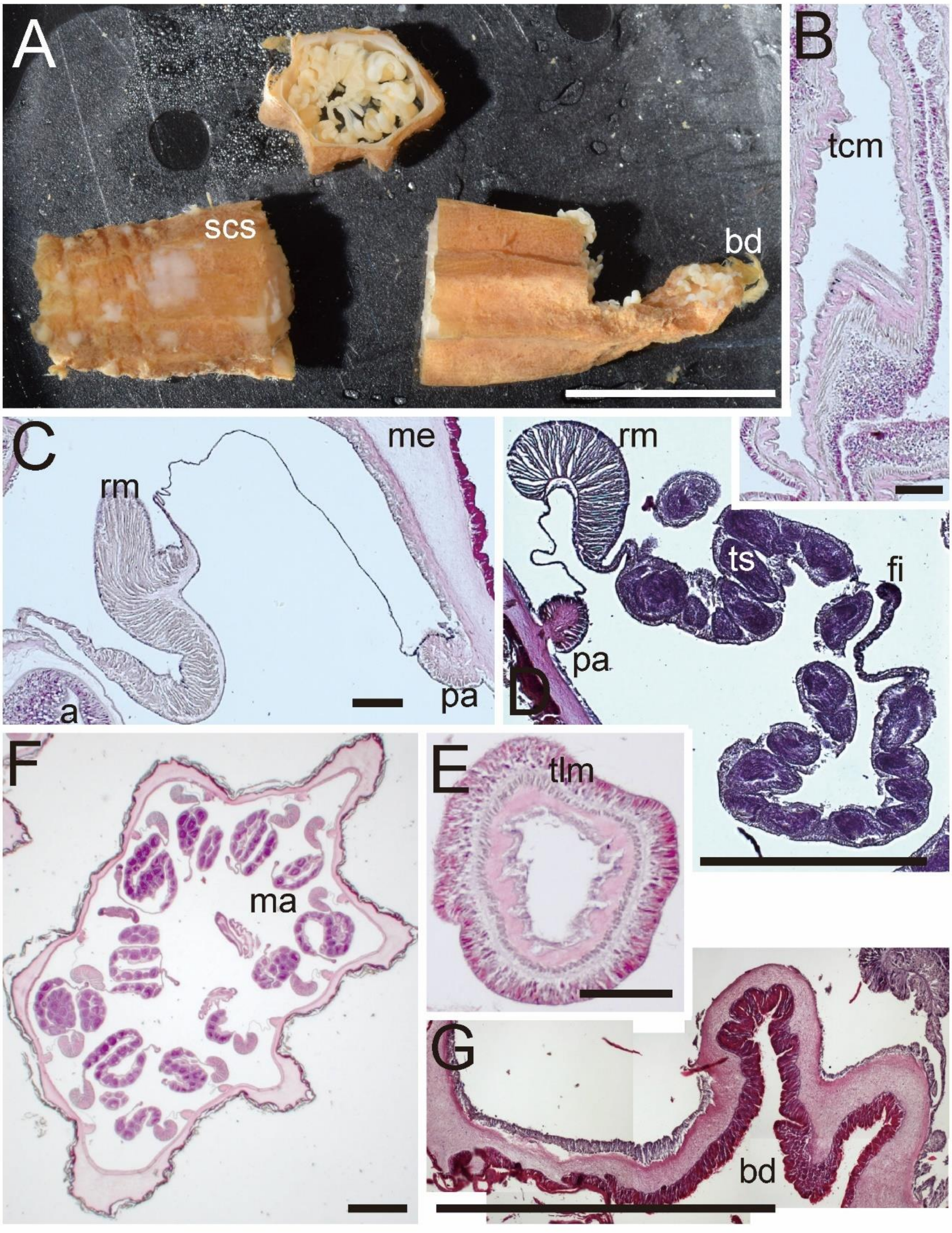

Fig. 30. External and internal morphology of *Hexactis* sp. nov. 4 (Iz-026).
A. lateral view of a preserved specimen; B. longitudinal section of tentacle; C. Enlarged transverse section of upper column; D. Enlarged transverse section of lower column; E. Transverse section of tentacle; F. Transverse section of lower column; G. Longitudinal section of proximal end. Abbreviations: a, actinopharynx; bd, basal disc; fi, filament; ma, macrocneme; me, mesoglea; mi, microcneme; pa, parietal muscle; rm, retractor muscle; scs, scapus; tcm, tentacle circular muscle; te, tentacle; tlm, tentacle longitudinal muscle; ts, testis. Scale bars indicate 1 cm in A, 1 mm in F, G, 500 μm in D, 200 μm in C, 100 μm in B, E.

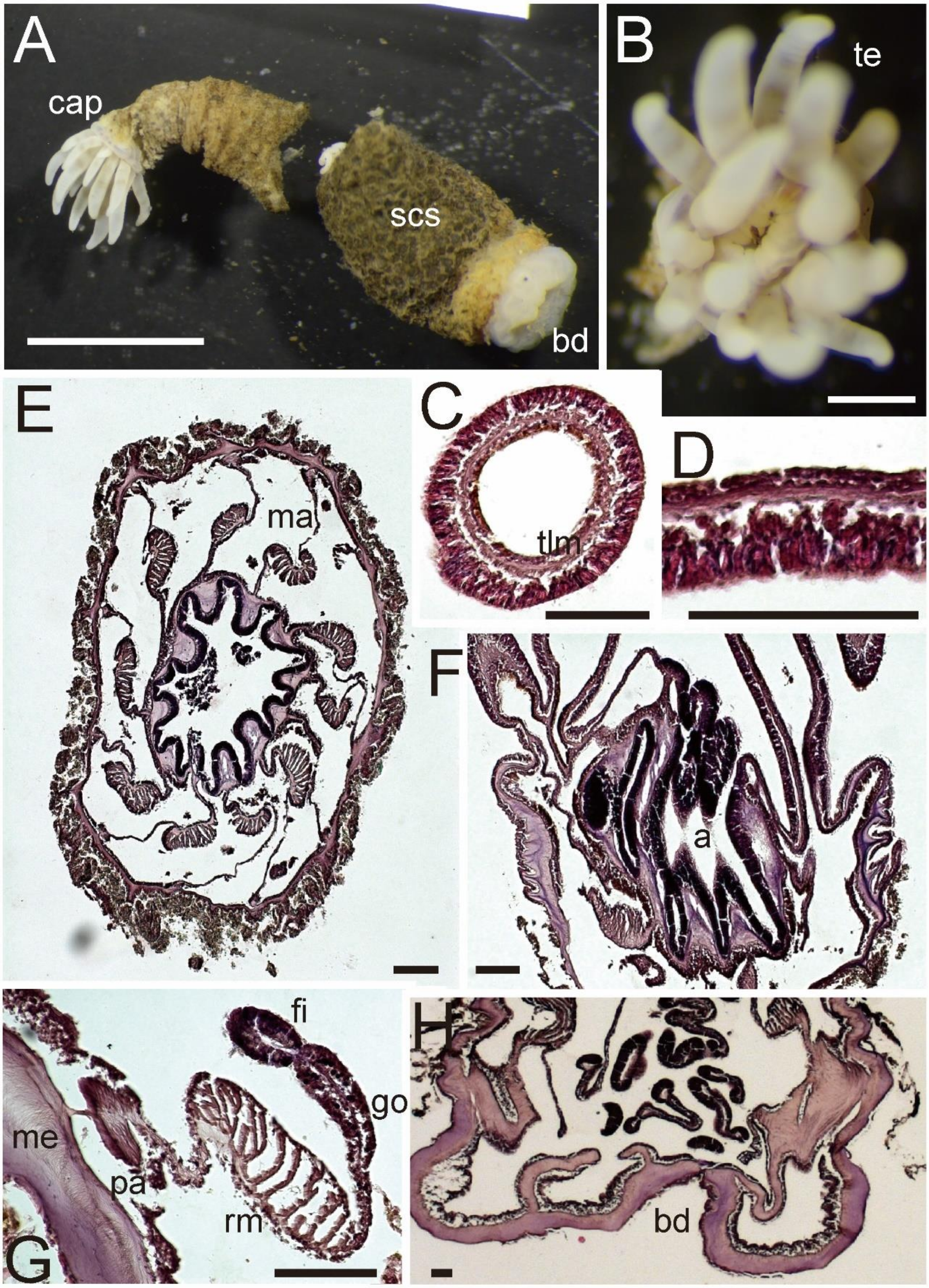

Fig. 31. External and internal morphology of *Pseudoedwardsia* sp. nov. 5 (Iz-034). A, B. lateral view of a preserved specimen; C. Oral view of oral disc; D. Transverse section of upper column; D. Transverse section of lower column; E. Enlarged view of retractor muscle; I. Enlarged view of transverse section of lower column. Abbreviations: a, actinopharynx; bd, basal disc; fi, filament; ma, macrocneme; me, mesoglea; mi, microcneme; pa, parietal muscle; rm, retractor muscle; s, siphonoglyph; scl, scapulus; scs, scapus; te, tentacle; tlm, tentacle longitudinal muscle. Scale bars indicate 1 cm in A, 1 mm in B, 100 μm in C–H.

Table 15. Comparison of two new genera and genus *Halcampella*.

	Halcampella Andres, 1883	***Hexactis* gen. nov.**	***Pseudoedwardsia* gen. nov.**
Type species	*Halcampella maxima* Hertwig, 1888	*Hexactis* sp. nov. 4	*Pseudoedwardsia* sp. nov. 5
Characters			
Main habitat	In sand or mud	On the rockwall in underwater caves	In sand or mud
Shape of the column	Rounded	Hexagonal	Rounded
Number of macrocnemes	12	12	10
References	Andres (1883) Hertwig (1888) Carlgren (1949) **The present study**	**The present study**	**The present study**

Table 16. Cnidoms of the species of *Halcampella*, *Hexactis,* and *Pseudoedwardsia*.

	Halcampella maxima		*Halcampella cretata* comb. nov.		*Hexactis* sp. nov. *4*		*Pseudoedwardsia* sp. nov. *5*	
	Iz-023		Iz-025		Iz-026		Iz-034	
	Length × Width (μm)	frequency	Length × Width (μm)	frequency	Length × Width (μm)	frequency	Length × Width (μm)	frequency
Tentacle								
basitrichs	24.8-33.6 × 2.7-4.1	numerous	16.8-37.7 × 1.9-2.9	numerous	15.5-26.7 × 2.6-4.5	numerous	23.7-32.3 × 2.7-4.1	numerous
spirocysts	19.4-47.2 × 2.6-6.8	numerous	10.9-21.2 × 2.0-3.8	numerous	13.3-33.8 × 2.6-7.4	numerous	16.2-32.5 × 3.1-7.1	numerous
Actinopharynx								
basitrichs	28.7-35.1 × 2.7-4.6	numerous	22.9-32.3 × 2.6-4.1	numerous	24.5-31.8 × 2.8-4.4	numerous		
spirocysts	26.3-38.4 × 4.0-6.0	numerous	15.3-27.5 × 2.7-5.3	numerous	17.5-26.5 × 4.1-5.8	numerous	23.1-28.3 × 4.7-7.2	numerous
microbasic *p*-mastigophores	30.1-42.2 × 4.7-6.9	numerous	22.5-27.8 × 4.2-5.7	numerous	21.9-28.2 × 5.8-7.7	numerous	19.2-21.9 × 4.5-4.8	rare
microbasic *b*-mastigophores							23.4-30.2 × 2.6-4.1	numerous
Column								
basitrichs	20.5-28.7 × 3.3-5.5	numerous			17.0-32.9 × 3.6-5.6	numerous	12.6-17.7 × 1.9-4.6	numerous
microbasic *p*-mastigophores								
Filament								
basitrichs	51.5-77.7 × 3.5-6.3	numerous	20.9-28.4 × 1.7-3.6	numerous			16.0-20.0 × 2.7-4.2	numerous
microbasic *p*-mastigophores			16.8 × 4.2	rare	15.9-25.6 × 4.5-8.8	numerous	16.4-24.1 × 4.2-6.6	numerous

Superfamily EDWARDSIOIDEA, Andres, 1881

(New Japanese name: mushimodoki-ginchaku-jouka; Izumi et al., 2019a)

Diagnosis. Anenthemonae with elongate, vermiform body usually divisible into at least two regions, long scapus with cuticle and distal scapulus but often also with thin capitulum below tentacles. Aboral end **usually** rounded, naked physa. No marginal sphincter muscle or acontia. Only 8 macrocnemes mesenteries and at least 4 microcnemes. Macrocnemes divided into two pairs of directives and four lateral mesenteries, two on each side, with retractors facing ventral directives. Retractors diffuse to strongly restricted. Parietal muscles always distinct. Cnidom: spirocysts, atrichs, basitrichs, **holotrichs,** microbasic *p*-mastigophores, **microbasic *b*-mastigophores, and macrobasic mastigophores.** (The revised points from Rodríguez et al. [2014] are indicated by **bold.**)

Remarks. Now, Edwardsioidea includes only one family Edwardsiidae. It was showed that the sister group of Edwardsioidea was Actinernoidea in Rodríguez et al., 2014, but Halcampelloidea superfam. nov. was turned to be more related to this superfamily according to the present study (Fig. 7; See Chapter 1B).

Family EDWARDSIIDAE Andres, 1881

(Japanese name: mushimodoki-ginchaku-ka)

Edwardsiidae Andres, 1881: 333; Carlgren, 1949: 22; Williams, 1981: 326; England, 1987: 215.

Diagnosis. Anenthemonae with elongate, vermiform body usually divisible into two or more regions: between long scapus provided with periderm and short capitulum may be short scapulus that lacks periderm and epidermal specializations. Proximal end rounded, without basilar muscles, may be differentiated into a physa. Single weak siphonoglyph. No sphincter muscle or acontia. Mesenteries divisible into macro- and microcnemes; always eight macrocnemes and at least **two** microcnemes. Macrocnemes comprise two pairs of directives and four lateral mesenteries, two on each side, whose retractors face ventral directives. Retractors restricted, diffuse to strongly circumscribe; parietal muscles always distinct. (Revised point from Brandão et al., 2019 is indicated in **bold**)

Type genus. *Edwardsia* de Quatrefages, 1842

Remarks. Edwardsiidae is characterized its peculiar mesenterial arrangement with 8 macrocnemes. Despite almost all sea anemones develop 12 (6 pairs of) macrocnemes in first cycle, four mesenteries in first cycle of Edwardsiidae do not develop to macrocnemes, and thus four lateral macrocnemes are not paired. Although there are some group which have only 8 perfect mesenteries in Actiniaria (see remarks part of Metedwardsiidae fam. nov.), the characteristic vermiform shape is also strongly distinguishable. That is why the outline of Edwardsiidae has been nearly untouched till recently.

My research revealed that a genus of this family, *Metedwardsia* Carlgren, 1947, was not belonging to Anenthemonae but Enthemonae, so I eliminate it from Edwardsiidae (in detail, see the remarks of Metedwardsiidae fam. nov.). However, the monophyly of Edwardsiidae in Anenthemonae was supported in this research as before (Fig. 12) though the inner phylogeny became drastically complicated: five genera which have nemathybomes or traces of those formed a monophyletic clade, but complicated in the clade of phylogenetic tree (Fig. 13; hereafter see Chapter 1F, and remarks of genus *Edwardsia*).

See Table 17 for comparison of all genera of Edwardsiidae receiving the rearrangement of this study. Though some of the other six genera, including *Synhalcampella*, were not supported their monophyly in my phylogenetic analysis (Figs. 12, 13), the morphology of them can be certainly distinguished. Thus, I retain them in this study. I had made the newest taxonomic keys in Izumi et al. (2018a), but it needs to be revised because of those drastically reorganization of classification system in the present study. So, taxonomic keys in the revised version of Edwardsiidae are here.

A1. Microcnemes are limited nearby the distal end ....B
  B1. Scapus with batteries of nematocysts (nemathybomes) or the trace of those, sunk in the mesoglea ....***Edwardsia***
  B2. Scapus without nemathybomes C
    C1. Scapus with rows of solid papillae forming nematocyst batteries ....***Halcampogeton***
    C2. Scapus covered by a strong cuticle (periderm), scapulus distinct ....***Edwardsiella***
    C3. Scapus smooth ....F
      D1. Nematosomes in the coelenteron ....***Nematostella***

D2. Nematosomes absent ....G

E1. Scapus rich in holotrichs. Inhabits in sponge symbiotically ....***Tempuractis***

E2. Scapus holotrichs absent. Inhabits ....***Drillactis***

A2. Microcnemes are along the whole body ....***Synhalcampella***

The revised points are as below: the genera *Edwardsianthus*, *Scolanthus* and *Paraedwardsia* were accommodated into *Edwardsia*; *Metedwardsia*, no longer Edwardsiidae, was eliminated from the keys.

Genus *Tempuractis* gen. nov. Izumi, Ise, and Yanagi, 2018
(Japanese name: tempura-isoginchaku-zoku)

Tempuractis Izumi, Ise and Yanagi, 2018: Izumi et al, 2018a: 190

Diagnosis. Edwardsiid with very tiny column, not differentiated into the capitulum, scapus, and physa. Surface of long column smooth, lacking nemathybomes or tenaculi. Tentacle sixteen, in two cycles, arranged octamerously, with eight axes of symmetry on the tentacular circle; inner cycle tentacles comparatively longer than outer ones. There is no siphonoglyph. Sphincter muscle not present. Aboral end tapered or rounded but not differentiated into a physa. Inhabits only in homoscleromorph sponge symbiotically and never lives independently. Cnidae: spirocysts, basitrichs, holotrichs, and microbasic *p*-mastigophores. (Izumi et al., 2018a)

Type species. *Tempuractis rinkai* Izumi, Ise, and Yanagi, 2018 (monotypic)

Etymology. *Tempura* is a deep-fried, batter-coated nugget of seafood and/or vegetables in Japanese cuisine. This word comprises the first half of the Japanese name of the type species of this genus, as the shape of the actiniarian when embedded in a sponge tissue resembles shrimp *tempura*. The siffix *-actis* is commonly used in actiniarian genus names, meaning radiation of sunshine in Greek.

Remarks. See Table 17 for comparison to the other genera of Edwardsiidae. Within the Edwardsiidae, *Tempuractis* gen. nov. morphologically resembles the valid genera *Edwardsiella* Andres, 1881, *Drillactis* Verrill, 1922, *Nematostella* Stephenson, 1935, and *Metedwardsia* Carlgren, 1947 in possessing a smooth scapus with no nemathybomes or tenaculi. The following genera are distinguishable from this new genus: *Edwardsia* de Quatrefages, 1842, *Scolanthus* Gosse, 1853, *Isoscolanthus*

Brandão, Gusmão and Gomes, 2019, and *Edwardsianthus* England, 1987 have nemathybomes (Gosse, 1853; Carlgren, 1949; England, 1987); *Paraedwardsia* Nordgaard, 1905 and *Synhalcampella* Carlgren, 1921 have tenaculi on the scapus, and the former generally adhere grains of sand on the column; and *Halcampogeton* Carlgren, 1937 has 12 longitudinal rows of solid papillae (Carlgren, 1937). The most prominent difference between *Tempuractis* and *Edwardsiella* is periderm; species in *Edwardsiella* bear periderm on the scapus, but the column in *Tempuractis rinkai* is naked and has no periderm. In addition, tentacular arrangement is useful for reference; in contrast with *Tempuractis rinkai* which has *Edwardsia*-like tentacular arrangement, *Edwardsiella* species possess three or more cycles of tentacles that are hexamerously arranged, with the innermost cycle being the longest (Daly et al., 2013). *Drillactis* species are most similar to *Tempuractis rinkai*, but there are several differences between them: holotrichs are abundant in *T. rinkai*, but are absent in *Drillactis* (Carlgren, 1949, 1954). As a reference, all *Drillactis* species are distinguishable from *Tempuractis* by the difference of characters as below; tentacles in *Drillactis* species has vertical rows of white spots (Carlgren, 1954; Verrill, 1880) while there are no patterns on tentacles of *T. rinkai*; the two *Drillactis* species have far larger bodies than *T. rinkai* (e.g., the body lengths of *T. rinkai* are even much smaller than the tentacle lengths of *Drillactis pallida*) (Verrill, 1922; Carlgren, 1954; Fautin, 2013); *T. rinkai* inhabits only in a homoscleromorph sponge, an extraordinary place for the sea anemone, with symbiotic ecology, while both *Drillactis* species live in sand, very ordinary habitat for edwardsiids, and without symbiosis (Verrill, 1922). *Nematostella* is characterized by having nematosomes, the spherical structures, 15–45 μm in diameter, and flagellated bodies containing nematocysts (Hand and Uhlinger, 1992), which are structures that are present only in this genus in Edwardsiidae (Hand, 1994) and are the origin of the name of this genus. However, there was no structure like a nematosome observed both from the outside when they were living and in their coelenteric cavity on transversal sections in *T. rinkai.* Therefore, this new species does not belong to *Nematostella*. *Metedwardsia* is monotypic for *Metedwardsia* akkeshi (Uchida, 1932a). This species, the only edwardsiid without nemathybomes in Japan, is obviously distinguished from all other edwardsiids by the distribution of microcnemes; microcnemes of M. akkeshi are elongated from distal to proximal end (Carlgren, 1947; Uchida, 1932a), while all other edwardsiids' microcnemes are limited to the distal end. This is the most unique character of *Metedwardsia*, so *T. rinkai*, in which the elongation of microcnemes is the same that in other edwardsiids, also cannot be included this genus (In the first place, it is no possibility that this species would be included into *Metedwardsia* because this genus is proven as no longer Edwardsiidae [see Chapter 1A, 1C and 2]).

Given the above, it is inappropriate to include this new species in existing genera. To begin with, this species has several peculiar morphological features for Edwardsiidae; *T. rinkai* has large holotrichs, which is one of the most recognizable characteristics of this genus; there is no description of holotrichs in any recent genus diagnosis of Edwardsiidae (e.g., Carlgren, 1949; Daly and Ljubenkov, 2008; Daly et al., 2013; Gusmão et al., 2016). *Tempuractis rinkai*, especially in the column, is rich in prominently large holotrichs, so the cnidom can be said to be a unique character of this genus. In addition, the new species also possesses a few microbasic p-mastigophores and spirocysts in its column, which is peculiar to Edwardsiidae. Moreover, the small size of this species, less than 5 mm in whole body length even for adults, is prominent in this family. Ultimately, the habitat of this species is very unique for not only edwardsiids but also for sea anemones in general; only *Spongiactis japonica* Sanamyan, Sanamyan and Tabachnick, 2012 is recorded to be symbiotic with sponges (Sanamyan et al., 2012). *Tempuractis rinkai* is quite different from *S. japonica* in morphological features and, of course, belongs to a quite different taxon at the family level. Therefore, I establish the new genus *Tempuractis* to accommodate the newly identified sea anemone, which is characterized by possessing holotrichs, a smooth body surface without nemathybomes or cuticles, s tentacular arrangement in two octamerous cycles, a quite tiny body and inhabiting symbiotically in a sponge.

Tempuractis rinkai Izumi, Ise, and Yanagi, 2018

(Japanese name: tempura-isoginchaku)

Figs. 32–34; Table 18

Tempuractis rinkai Izumi, Ise and Yanagi, 2018: Izumi et al., 2019: 193–194, fig. 2–8, table 2, 3

Material examined. *Holotype*. NSMT-Co 1573. One specimen cut into three parts and prepared for nematocyst observation, collected by wading on 7 June 2013 from the intertidal zone of Aburatsubo, Misaki, Kanagawa, Japan by Yuji Ise. *Paratypes.* CMNH-ZG 08969. Whole specimen extracted from a sponge; CMNH-ZG 08970. Whole specimen left inside a sponge; CMNH-ZG 08971. Series of histological longitudinal sections; CMNH-ZG 08972. Series of histological cross sections, all specimens collected by wading on June 7, 2013 from the intertidal zone of Aburatsubo, Misaki, Kanagawa, Japan by Yuji Ise; CMNH-ZG 08973. Histological sections. Collected by SCUBA diving on 3 October 2013 at a depth of 8 m in Shukunegi, Sado Island, Niigata, Japan by Yuji Ise; CMNH-ZG 08974. Whole specimen left in a portion of the sponge, collected by wading on August 22, 2013 from the intertidal zone of Tohama, Toba City, Mie, Japan by Takeya Moritaki; CMNH-ZG 08975. Whole specimen, collected by snorkeling on 13 October 2014 at a depth of 2 m in Sugashima, Toba City, Mie, Japan by Yuji Ise; (Iz-037). A whole specimen. Collected by SCUBA diving on 3 October 2015 at a depth of 8 m in Shukunegi, Sado Island, Niigata, Japan by Yuji Ise.

Note. Series of histological sections were prepared from a specimen from the same host sponge from which the holotype and paratypes were collected.

Description. ***External anatomy.*** Column naked, smooth, very small, ca. 3.0–5.0 mm in length (3.0 mm in the holotype) and 0.7–1.2 mm in width (0.8 mm in the holotype), and pipe-like in form (Fig. 32B). The surface of column simple, no nemathybomes or tenaculi. Epidermis adhesion with endopinacocytes of *Oscarella* sp. very tight. Aboral end tapered, not differentiated from scapus, but more or less adherent (see Ecological remarks below). Tentacles slender, without acrospheres, but bearing white patches on each tip, ca. 2.5–4.0 mm in length in living and 1.0–2.0 mm (1.2–1.8 mm in the holotype) in fixed specimens, longer than diameter of oral disk, but well contractible. Tentacles 16 in number, arranged in two concentric cycles of eight inner and eight outer ones positioned alternately, inner tentacles a little longer than outer ones. Oral disk 0.7–1.2 mm in diameter (0.8 mm in the holotype). Column and tentacles pale orange or pale pink, semitransparent so that mesenterial insertion visible in upper part when alive, no pattern or patches. Area around mouth and actinopharynx white. Body completely surrounded by the tissue of host sponge *Oscarella* sp. except tentacles and capitulum (Fig. 32A, C–F), so the color of column unidentifiable in alive.

Internal anatomy. Mesenterial arrangement as typical as that of *Edwardsia*. Eight macrocnemes, four dorsal and ventral directives, and the other four lateral mesenteries (Fig. 33G). All macrocnemes perfect, present along whole length of body (extending from oral to aboral end). Retractor muscles of lateral mesenteries all facing ventrally (Fig. 33G). Eight tiny microcnemes, without muscles, only in distal-most part of column, extending about 30 μm under the base of tentacles (Fig. 33C). Four microcnemes between dorsal directives and dorso-lateral mesenteries, two between the dorso- and ventro-lateral mesenteries and two between the ventrolateral mesenteries and ventral directives. Each tentacle between either exo- or endocoelic. Retractor muscles comparatively weak, restricted or reniform in upper part, but diffused in lower part (Fig. 33G, I, J). Muscle processes mostly simple, around 10 in each muscle pennon. Parietal muscles of macrocnemes not distinct. Actinopharynx short, without distinct siphonoglyphs (Fig. 33A). Tentacular circular muscle endodermal and longitudinal muscle ectodermal (Fig. 33B, D–F). Mesoglea in body wall, mesenteries, and actinopharynx thin, < 10 μm in thickness (Fig. 33G). Marginal sphincter muscle and basilar muscle absent. All parts of body wall, except capitulum, tightly adhered to endopinacocytes of *Oscarella* sp. (Fig. 33A, H). Many cilia from epidermis of sea anemone, invaginating into endopinacocytes of the sponge, this structure may strengthen the adhering between epidermis of *T. rinkai* and endopinacocytes of *Oscarella* sp. (Fig. 34). No mature gametes in holotype. Mature testes observed in paratype (CMNH-ZG 08973; Fig. 33K).

Cnidom. Spirocysts, basitrichs, holotrichs and microbasic *p*-mastigophores. See Table 18 for size and distribution.

Etymology. The species epithet is dedicated to marine biological stations around Japan. The first specimens of this species were collected from a rocky shore in front of the Misaki Marine Biological Station (the University of Tokyo). This station is called "Misaki rinkai jikkenjo" in Japanese ("rinkai" means seaside and "jikkennjo" means research facility). Other specimens were collected during a subsequent faunistic survey in collaboration with other marine biological stations: Sugashima Marine Biological Laboratory (Nagoya University) and Sado Marine Biological Station (Niigata University).

Ecological remarks. Colonies of *Tempuractis rinkai* were always found in the host sponge *Oscarella* sp., and no living individual was found independently outside of a sponge. The position of *T. rinkai* inside the sponge was unique, as the oscula of the sponge opens beside the oral disc of sea anemone (Fig. 32C), which means that the sea anemones do not utilize the spongicoel or central cavity of the host sponge as do other temporary visitors. Each polyp of *T. rinkai* was isolated from other polyps and was completely buried in the sponge body, exhibiting a bunch-like shape (Fig. 32A). The epidermis of *T. rinkai* was strongly adherent to the endopinacocytes of *Oscarella* sp. Although the majority of individuals were completely buried in the sponge, some sea anemones were piercing their body through *Oscarella* sp. and adhered to the substrate by their aboral end. Thus, the aboral end of this sea anemone is more or less adhesive.

Tempuractis rinkai and the host sponges were found in cryptic habitats, such as the underside of overhangs, underside of rocks, or interstices of beach rocks. This phenomenon is probably the result of the habitat preference of the host sponge, rather than that of *T. rinkai*, and allows these sea anemones to live in habitats that differ from those of other edwardsiids, which are usually buried in sandy or muddy sea bottom.

Tempuractis rinkai elongated its tentacles outside its host sponge when relaxed, and when exposed to various external stimuli, such as being touched by something, being exposed to a strong current, or when a shadow of something fell on them, they retracted their tentacles and hid themselves inside the sponge. Tentacles of *T rinkai* were sometimes observed to be in contact with those of other polyps because colonies of *T. rinkai* were densely distributed (Fig. 32A, C, F); however, they did not retract their tentacles or attack each other.

Tempuractis rinkai and its host sponge *Oscarella* sp. are likely to be involved in a symbiotic relationship. Histological sections suggested that the epidermis of *T. rinkai* and the endopinacocytes of *Oscarella* sp. were strongly adhered (Fig. 33H), in that they were difficult to separate in both live and ethanol-preserved samples. Based on TEM observation (Fig. 34), it appeared that the surface structures of both the sea anemone and the sponge are closely related. The cilia of the sea anemone are projecting to the depressions of endopinacocytes of *Oscarella* sp. and twisting each other (Fig. 34). This structure suggests that there is specific mechanism of adhesion between the sponge endopinacocytes and sea anemone epidermis. Transmission electron microscopy images suggest that the epidermis of *T. rinkai* anchors to endopinacocytes of *Oscarella* sp. by bundles of cilia. This may stabilize their position. When *T. rinkai* shrinks, its column is totally encased by sponge tissue. During this process, it seems that the *T. rinkai* epidermis pulls the endopinacocytes of *Oscarella* sp., thereby completely closing the holes that the sea anemones live in. So far, no *Tempuractis rinkai* has been found outside the host sponge *Oscarella* sp., and all of the *Oscarella* sp. sponges collected during the present study contained several *T. rinkai*, suggesting that these animals are involved in an obligate symbiotic relationship. The benefit of this symbiosis has not been precisely determined yet; however, it is expected that *T. rinkai* hide their body in the host sponge when they are attacked by unknown predators. The advantage of this symbiosis for the host sponge *Oscarella* sp. is unclear; however, the possible role of *T. rinkai* in this symbiosis can be assumed from the following observations in the field: sea slugs, *Berthella stellata* (Risso, 1826) (Pleurobranchidae, Notaspidea, Gastropoda, Mollusca), were sometimes observed to feed on *Oscarella* sp. inhabited by few polyps of *T. rinkai* in the present sampling localities, and there have been several studies showing that *Berthella* spp. feed on homoscleromorph sponges (Delaloi and Tardy, 1977; Willan, 1984; Picton, 2002; Rudman, 2005, 2007, 2010; Goddard, 2007), and thus *Berthella* species are thought to be specific predators on homoscleromorph sponge (Goddard, 2007). Therefore, *T. rinkai* might protect its host sponge from *Berthella* species using the cnidae on its tentacles, because the nudibranch may not approach the area where the tentacles of *T. rinkai* extend, protecting the sponge from being totally eaten.

Tempuractis rinkai forms aggregation in each individual of *Oscarella* sp., and recently, the extension of aggregation was observed in aquarium (Moritaki, 2019): *T. rinkai* reproduces asexually. Aboral end of anemones is pinched, and then detach worm-like individual. This worm-like anemones do not have tentacles yet so far, so they can creep out from sponge and crawls around (the ecology that edwardsiid anemone crawls is the first-ever observation). Later, worm-like individuals sneak into sponge again, and appeared their distal end by penetrating body of host sponge. Finally, surprisingly *Oscarella* sp. itself thicken their body part covering scapus of anemones. In conclusion, the “tempura-like” structure of symbiosis of anemone and sponge is formed by host side. It might be a strong evidence of obligate symbiosis of *Tempuractis rinkai* and *Oscarella* sp. However, the sexual reproduction has been observed neither *T. rinkai* nor host sponge, and thus the origin of the symbiosis is not observed yet. Because it is observed that *T. rinkai* have eggs and sperms by inspection of histological section, it is probable that this species reproduces by spawning, thus the mechanism how larvae or young anemones find and inhabit in host sponge is still in mystery.

This is the first report of symbiosis among members of the Actiniaria (and also Cnidaria) and Homoscleromorpha both ecologically and morphologically. As for *Oscarella* sponge, or the family Oscarellidae, this is undoubtedly first record of symbiosis with any other metazoans. Concerning cnidarians, symbiotic relationships between order Zoantharia and Porifera have been documented far more frequently than those between the Actiniaria and Porifera. For example, several species of *Epizoanthus* Grey, 1867, *Parazoanthus* Haddon and Shackleton, 1891, and *Umimayanthus*, Montenegro, Sinniger and Reimer, 2015 inhabit in/on sponges (Swain and Wulff, 2007; Montenegro and Acosta, 2010; Montenegro et al., 2015). Among these, species of *Epizoanthus* bury their bodies much deeper in the sponge than the other genera (Swain and Wulff, 2007; Montenegro and Acosta, 2010; Montenegro et al., 2015), like *Tempuractis rinkai*. However, there has been no report of zoanthids inhabiting in/on homoscleromorph sponges.

In contrast to the diversity of sponge-symbiotic zoanthids, only a single species of Actiniaria is known to live in sponges. The first detailed report of a symbiotic relationship between members of Actiniaria and Porifera was about an actiniarian and a hexactinellid sponge (Sanamyan et al., 2012). According to Sanamyan et al. (2012), the host sponge *Hyalonema sieboldi* Gray, 1832 forms “specific minute volcano-like rises” above the sea anemone *Spongiactis japonica*. Although these structures resemble the bunch-like parts of *Oscarella* sp. where *Tempuractis rinkai* lives, the adhesion mechanisms and lineages involved in the two symbioses are completely different. In the *S. japonica*/*H. sieboldi* symbiosis, the sea anemones adhere to the host sponge *via* the perforation of their columns by long spicules of the sponge (Sanamyan et al., 2012). However, the family Oscarellidae, including *Oscarella* spp., totally lack spicules (Muricy and Diaz, 2002; Gazave et al., 2010, 2012; Ruiz et al., 2017), thereby precluding a similar adhesion mechanism. The different adhesion mechanisms might be a consequence of the different surface structures of the host sponges because the pinacocytes of homoscleromorph sponges form an epithelium (e.g., Ereskovsky et al., 2009), whereas those of hexactinellid sponges do not (e.g., Leys et al., 2007).

In homoscleromorph sponges, the zoanthid “*Epizoanthus* sp. nov.” sensu Crocker and Reiswig (1981) was reported to live exclusively inside three species of the sponge genus *Plakortis* Schulze, 1880 (Crocker and Reiswig, 1981; Swain and Wulff, 2007), but this cnidarian species was revealed to be an edwardsiid species, Edwardsiidae sp, by molecular phylogenetic study (Swain, 2009). However, although the embedded form of Edwardsiidae sp., of which only the tentacles protrude from the sponge (Swain and Wulff, 2007; Montenegro and Acosta, 2010), resembles that of *T. rinkai*, this sea anemones were just ascertained to belong to the family Edwardsiidae only by molecular phylogeny. And there was no subsequent study showing the details of its morphological characters, and so the detailed taxonomy of this sea anemone is still unknown. I presume that "Edwardsiidae sp." in Swain (2009) is a different species from *T. rinkai* because the host sponges belong to different families; *Oscarella* sp. belongs to Oscarellidae, while the host sponges of "Edwardsiidae sp." in Swain (2009) belong to Plakinidae. Furthermore, the localities of sampling sites are very different and distant; *T. rinkai* and its host sponge *Oscarella* sp. were found from temperate rocky shores of Japan, but "Edwardsiidae sp." in Swain (2009) and its host sponges were found from coral reefs of the Caribbean (Crocker and Reiswig, 1981).

In recent, more species of Homoscleromorph sponge containing edwardsiids resembling to *T. rinkai* has been found in Japan. From Shukunegi, Sado Island, Niigata, specimens of *Tempuractis* ([Iz-038]; Fig. 35A, B) were collected with host sponge of Plakinidae, a species of sponge of different family from *Oscarella* sp. (Ise, 2013). In an underwater cave of Ie Island, Okinawa, *Tempuractis* species were confirmed to living symbiotically in gray oscarellan sponge, different species from *Oscarella* sp. in which *T. rinkai* inhabits ([Iz-039]; Fig. 35C–E). These anemones were confirmed to belong to the genus *Tempuractis* Izumi, Ise and Yanagi, 2018 morphologically, ecologically and phylogenetically. The anemones were inhabiting in host Homoscleromorph sponges (Fig. 35) and were in same clade with *T. rinkai* on phylogenetic tree (Figs. 12, 13). However, it is not certain now whether these anemones are same species as *T. rinkai* or undescribed species because these anemones were too tiny to extract sufficient morphological features.

T. rinkai should be dioecious because there were a kind of gametocytes in their gonads (Fig. 33). It is confirmed that there is only one sexuality in a colony in an individual of sponge. However, an individual of the specimen of (Iz-039) from the cave under the sea off Ie Island had both testis and ovary (Fig. 35E). So, the strategy of reproduction might be varied in this genus.

In conclusion, the present study revealed the new symbiosis between members of Actiniaria and Porifera and provided the first detailed record between an actiniarian and a homoscleromorph sponge. Moreover, this study suggests that a brand new and more diverse symbiotic relationships among members of the Cnidaria and Porifera.

(Description, Figs. 32–34, and part of Table 18 are revised and reprinted Izumi et al. [2018a] by courtesy of Zoological Science.)

Genus *Edwardsiella* Andres, 1883

(Japanese name: atsugi-mushimodoki-ginchaku-zoku)

Edwardsiella Andres, 1883: 305–306; Manuel, 1981a, 195: Daly et al., 2013: 4.

Milne-edwardsia Carlgren, 1892: 455–456.

Fagesia Delphy, 1938: 620: Carlgren, 1949: 25.

Diagnosis. Edwardsiidae with column clearly differentiated into capitulum, **or scapulus,** and scapus. **Two,** three or more cycles of tentacles. Tentacles hexamerously **or hexamerously** arranged, those of innermost cycle longest. Capitulum ridged; nematocysts concentrated on ridges. Scapus generally bears **strong** periderm, always lacks nemathybomes or tenaculi. Aboral end rounded but not differentiated into a physa. Ciliated tracts of filaments short, discontinuous.

(Revised points from Daly et al. [2014] are indicated in **bold**.)

Type species. *Edwardsiella carnea* (Gosse, 1856)

Remarks. See Table 17 for comparison to the other genera of Edwardsiidae. This genus was established by Andres (1883). However, some species of this genus had traced a little strange history: *Edwardsiella loveni* (Carlgren, 1892) and other some species were described as species of genus *Milne-Edwardsia,* Carlgren, 1892. However, *Milneedwardsia* was a junior homonym of *Milneedwardsia* Bourguignat, 1877, a genus of Mollusca (Delphy, 1838), so the genus was renamed *Fagesia* Delphy, 1838. However, this genus turned to be the homonym of *Fagesia*, Pervinquière, 1907, the genus of Mollusca. Finally, Manuel (1981a) synonymized this genus into *Edwardsiella*, and Daly (2002b) agrees this treatment and settle *Edl. loveni.* After that, this genus has not doubted for the validity till current day.

Collection of *Edl.* sp. nov. 6 also means the first discovery of the genus

Edwardsiella from the northwest Pacific.

Edwardsiella sp. nov. 6

(Japanese name: Seihyo-Atsugi-Mushimodoki)

Fig. 36; Table 18

Material examined. CMNH-ZG (no registration): One specimen cut into parts, prepared histological sections, and prepared for nematocyst observation, collected by scuba diving on 11 May 2009 at a depth of 28m off Seihyo Seashore, Chichijima Island, Tokyo Met., Japan by Sinniger Frederic; CMNH-ZG (no registration): two specimen, whole body preserved in Ethanol, same collection date and collector as above; CMNH-ZG (no registration): nine whole specimen, same collection date and collector as above;

Description. ***External anatomy.*** Column ca. 8.0–12.0 mm in length and ca. 1.0 -1.5 mm in width, and pipe-like in form (Fig. 36A, B). Column divided into scapus, capitulum. Surface of scapus covered by thick periderm, brown in proximal side and black in distal side, rough but no nemathybomes or tenaculi. Capitulum naked, hemitransparent, divisible 8 mesenterial insertions. Aboral end undeveloped into small physa, tapered or rounded, a little differentiated from scapus. Tentacles slender, simple, without acrospheres, transparent with white tiny cross line, ca. 1.0–3.0 mm in length in fixed specimens, longer than diameter of oral disk. Tentacles 16 in number, arranged in two concentric cycles of eight inner and eight outer ones positioned alternately, the typical arrangement of *Edwardsia* (Fig. 36C), inner tentacles longer than outer ones. Oral disk transparent, ca. 1.0–1.5 mm in diameter, with a little swelled mouth.

Internal anatomy. Mesenterial arrangement as typical as that of *Edwardsia*. Eight macrocnemes, four dorsal and ventral directives, and the other four lateral mesenteries (Fig. 36E). All macrocnemes perfect, present along whole length of body (extending from oral to aboral end). Retractor muscles of lateral mesenteries all facing ventrally (Fig. 36E). Eight tiny microcnemes, without muscles, only in distal-most part of column (Fig. 36D). Four microcnemes between dorsal directives and dorso-lateral mesenteries, two between the dorso- and ventro-lateral mesenteries and two between the ventrolateral mesenteries and ventral directives. Each tentacle between either exo- or endocoelic. Retractor muscles comparatively weak, restricted in actinopharynx or filament side (Fig. 36F, G). Muscle processes mostly simple, around 8–10 in each muscle pennon. Parietal muscles of macrocnemes indistinct, with a few muscular processes. Actinopharynx short, without distinct siphonoglyphs (Fig. 36E). Tentacular circular muscle and longitudinal muscle indistinct. Mesoglea in body wall, tentacle, and actinopharynx thin, <10 μm in thickness, but thicker in parietal and retractor muscles (Fig. 36F). Marginal sphincter muscle and basilar muscle absent (Fig. 36 D, H). No mature gametes in histological sections (Fig. 36G).

Cnidom. Spirocysts, basitrichs, microbasic *b*-mastigophores, microbasic *p*-mastigophores, and macrobasic mastigophores. See Table 18 for size and distribution.

Ecological remarks. This species inhabits in muddy bottom off Seihyo Seashore, around 30–40m depth, in high density.

Remarks. This is the first discovery of *Edwardsiella* species from northwest Pacific: there had been only *Edwardsiella ignota* Carlgren, 1959 reported from the Pacific, but the locality was Chili, far distant from Japan (Carlgren, 1959).

See Table 19 for comparison to the other species of *Edwardsiella. Edwardsiella* sp. nov. 6 have two rows of eight tentacles, octamerously arranged. So, it was not corresponded to this genus strictly because Daly et al. (2013), in which the most recent diagnosis of *Edwardsiella* was stated, dictated that *Edwardsiella* has three or more cycle tentacles with hexamerously arranged. However, *Edwardsiella andrillae* Daly, 2013, the species which newly described in the article, did not follow the rule because this species has same arrangement as *Edwardsiella* sp. nov. 6 (this disagreement point may be overlooked by them). So, diagnosis is now emended. Compared to *Edl. andrillae*, *Edl.* sp. nov. 6 can be easily distinguishable by its habitat: the former species lives only in ice under Ross Ice Shelf. Moreover, macrobasic *p*-mastigophores were only observed in this species, not only among *Edwardsiella* but family Edwardsiidae (Table 18). In conclusion, this edwardsiid can be determined as new seventh species of *Edwardsiella*.

It is known that *Edwardsiella lineata,* a species of this genus, uses *Mnemiopsis leidyi*, a species of comb jellyfishes, as carriers of larvae in Atlantic Ocean (Dnyansagar et al., 2018). However, there has been no record that comb jellyfishes of Japan carried larvae of edwardsiids. Perhaps the reproduction and distribution expanding system of *Edwardsiella* is different in Pacific.

Genus *Halcampogeton* Carlgren, 1937
(Japanese name: ibo-mushimodoki-ginchaku-zoku)

Halcampogeton Carlgren, 1937: 1; Carlgren, 1949: 24.

Diagnosis. Edwardsiidae with elongate body divisible into physa, scapus and scapulus (or capitulum). Scapus with 12 **or 16** longitudinal rows of solid papillae containing very large nematocysts. Tentacles more or less cylindrical, of ordinary length, **12 or 16 in number**. No distinct siphonoglyphs. Mesenteries probably never more than six pairs. 8 macrocnemes arranged as the macrocnemes in *Edwardsia* and 4 microcnemes. Not more mesenteries proximally than distally. Retractors of the **perfect** mesenteries restricted, more or less kidney-like. Parietal muscles strong. (The revised points from Carlgren [1937] are indicated by **bold**.)

Type species. *Halcampogeton papillous* Carlgren, 1937

Remarks. See Table 17 for comparison to the other genera of Edwardsiidae. This is a monotypic genus by *Halcampogeton papillous* Carlgren, 1937. This species was corrected only once from Puerto Rico (Carlgren, 1937), and the status of genus is doubtful in recent (Fautin, 2013). Now, an individual I found in my collection was almost corresponded to diagnosis of Halcampogeton, so this became the rediscovery of a species of this genus over 80 years. Moreover, I succeeded first molecular phylogenetic analysis of the species of this genus. According to it (Fig. 12), *Halcampogeton* was accommodated in Edwardsiidae certainly, and was early diverged from "nemathybomes-present" edwardsiids (Fig. 12).

Halcampogeton sp. nov. 7
(New Japanese name: seisui-ibo-mushimodoki)
Fig. 37; Table 18

Material examined. (Iz-040), histological sections, tissues in paraffin, and prepared nematocysts, 10 November 2017, by biological dredge during research cruise of R/V Seisui-Maru (No. 1722), off Shima Peninsula, Kumano-nada Sea (Station-10: 33°59.51′N, 136°56.67′E), 768–796 m depth, collected by Itaru Kobayashi.

Description. ***External anatomy.*** Column ca. 13 mm in length and ca. 5.0 mm in width in preserved, and cone-like in form (Fig. 37A). Column divided into scapus and capitulum. Surface of scapus covered by thick pale-yellow cuticle, rough, with longitudinal wrinkled cavities, with no nemathybomes, but solid papillae in 16 rows in proximal side (Fig. 37A). Scapulus naked, hemitransparent, divisible mesenterial insertion. Aboral end undifferentiated from scapus, with solid papillae (Fig. 37B). Tentacles slender, simple, without acrospheres, ca. 0.8–1.2 mm in length in living specimens. Tentacles 16 in number, in *Edwardsia* arrangement. Oral disk ca. 0.8 mm in diameter.

***Internal anatomy* (the specimen was badly preserved, so some characters not observed).** Mesenterial arrangement as typical as that of *Edwardsia*. Eight macrocnemes, four dorsal and ventral directives, and the other four lateral mesenteries (Fig. 37F). All macrocnemes perfect, present along whole length of body (extending from oral to aboral end). Retractor muscles of lateral mesenteries all facing ventrally. Eight tiny microcnemes, without muscles, only in distal-most part of column, extending about 30 µm under the base of tentacles. Four microcnemes between dorsal directives and dorso-lateral mesenteries, two between the dorso- and ventro-lateral mesenteries and two between the ventrolateral mesenteries and ventral directives. Each tentacle between either exo- or endocoelic. Retractor muscles comparatively diffused (Fig. 37G). Muscular processes slightly branched, around 20 in each muscle pennon. Parietal muscles of macrocnemes quite distinct, elongated, with simple 10–15 muscular processes (Fig. 37E). Tentacular circular muscle indistinct, and longitudinal muscle distinct and exocoeletic (Fig. 37C, D). Mesoglea in body wall exceedingly thick, especially in papillae (Fig. 37F, H), and comparatively thick in tentacle, and mesenteries (Fig. 37C–E). Marginal sphincter muscle and basilar muscle absent.

Cnidom. Spirocysts, basitrichs, microbasic *p*-mastigophores, holotrichs. See Table 18 for size and distribution.

Remarks. *Halcampogeton* sp. nov. 7 can be distinguished from *H. papillous* Carlgren, 1937 by the number of rows of solid papillae on their column: *H. papillous* has 12 rows of solid papillae on their body (Carlgren, 1937), but this specimen has 16 rows (Fig. 37A, B).

Concerning cnidom, holotrichs are rare in Edwardsiidae: only *Tempuractis rinkai* had been known as possessing the kind of nematocysts. However, the cnidom of *H. papillous* does not sure, so I postpone editing the cnidom of diagnosis of this genus. Moreover, some features were not observed in this specimen anatomically because of bad preservation, so the revision of diagnosis was minimized in this article.

Genus *Drillactis* Verrill, 1922
(Japanese name: doriru-mushimodoki-ginchaku-zoku)

Drillactis Verrill, 1922: 133; Carlgren, 1949: 26

Diagnosis. Edwardsiidae with often tapered aboral end. Body very elongate slender. No distinct division into scapus and scapulus (capitulum). Tentacles up to 24, the inner shorter than **or as same length as** the outer ones Macro- and microcnemes as in *Edwardsia.* **No** nematosomes in the coelenteron. Cnidom: spirocysts, basitrichs, microbasic *p*-mastigophores.

(The revised points from Carlgren [1949] are indicated in **bold**.)

Type species. *Drillactis pallida* (Verrill, 1879)

Remarks. See Table 17 for comparison to the other genera of Edwardsiidae. *Drillactis* Verrill, 1922 was established as a monotypic genus with establishing the type species *Drillactis* pallida (Verrill, 1879). This genus was characterized as "having no characteristic features": the surface of this genus is quite simple, and absent any structures as nemathybomes (in *Edwardsia, Edwardsianthus, Scolanthus*), strong cuticles (in *Edwardsiella*), solid papillae (in *Halcampogeton*) or attaching other structures (in *Paraedwardsia*, sand grains, or in *Tempuractis* gen. nov., sponges). Even the remaining genera, they have peculiar characters in their column: *Nematostella* have nematosomes in their coelenterons, and *Synhalcampella* have extra microcnemes in their proximal sides. However, almost all of edwardsiids ever described or collected had somewhat characteristic features on or in their columns, so this genus had included only 2 species (Table 2). Thus, the cases of discoveries of *Drillactis* edwardsiids were rare. The discovery of *Drillactis* sp. nov. 8 was the first discovery of *Drillactis* from northwest Pacific, and of course from Japan.

Drillactis sp. nov. 8
(Japanese name: Ootsuchi-doriru-mushimodoki)
Fig. 38; Table 18

Material examined. (Iz-041), histological sections, tissues in paraffin, and prepared nematocysts, 4 July 2017, by biological dredge of R/V Yayoi, north off Cape Ohakozaki, Iwate Pref. (Station-6': 39°21.95′N, 141°59.93′E), 68–85 m depth, collected by Kensuke Yanagi.

Description. ***External anatomy.*** Column ca. 14.0 mm in length and ca. 3.0 mm in width in living, well-contracted, and stick-like in form: proximal end swelled like knob (Fig. 38A, B). Column divided into scapus and capitulum. Surface of scapus naked or covered mucus-like thin periderm, light brownish hemitransparent and divisible mesenterial insertions in whole body, with no nemathybomes or tenaculi. Capitulum naked, transparent, divisible actinopharynx clearly. Aboral end undifferentiated from scapus, with mucus-like thin periderm, hemitransparent, rounded or pointed. Tentacles slender, simple, without acrospheres, transparent, with a white spot at the tip, ca. 1.0–1.5 mm in length in living specimens, longer than diameter of oral disk. Tentacles 16 in number, arranged in two concentric cycles of eight inner and eight outer ones positioned alternately, the typical arrangement of *Edwardsia*, inner tentacles a little longer than outer ones. Oral disk transparent, ca. 0.8 mm in diameter, with a little swelled mouth.

Internal anatomy. Mesenterial arrangement as typical as that of *Edwardsia*. Eight macrocnemes, four dorsal and ventral directives, and the other four lateral mesenteries (Fig. 38E). All macrocnemes perfect, present along whole length of body (extending from oral to aboral end). Retractor muscles of lateral mesenteries all facing ventrally (Fig. 38E). Eight tiny microcnemes, without muscles, only in distal-most part of column under the base of tentacles (Fig. 38A). Four microcnemes between dorsal directives and dorso-lateral mesenteries, two between the dorso- and ventro-lateral mesenteries and two between the ventrolateral mesenteries and ventral directives. Each tentacle between either exo- or endocoelic. Retractor muscles exceedingly weak, diffused (Fig. 38E). Muscle processes slightly branched, around 2–5 in each muscle pennon. Parietal muscles of macrocnemes indistinct, with a few muscular processes. Actinopharynx short, without siphonoglyphs (Fig. 38E). Tentacular circular muscle indistinct, and longitudinal muscle distinct and ectodermal (Fig. 38D). Mesoglea thin among whole body. Marginal sphincter muscle and basilar muscle absent. Gonads present, but no mature gametes in histological sections (Fig. 38C).

Cnidom. Spirocysts, basitrichs, microbasic *p*-mastigophores. See Table 18 for size and distribution.

Remarks. See Table 20 for comparison to the other species of *Drillactis*. *Drillactis* is a small genus of Edwardsiidae, only with two species, *D. pallida* and *D. leucomedia* (Fautin, 2016). *Drillactis* sp. nov. 8 can be easily distinguished from both species by its body size: *D. pallida* (Verrill, 1879) and *D. leucomedia* (Parry, 1951) reach 10 cm in length (Verrill, 1922; Parry, 1951). In addition, this species is also distinguishable from *D. leucomedia* by the number of tentacles because *D. leucomedia* has 48 tentacles (Parry, 1951), far more than *D.* sp. nov. 8 does.

Genus *Edwardsia* de Quatrefages, 1842
(Japanese name: mushimodoki-ginchaku-zoku; Uchida, 1965)

Edwardsia de Quatrefages, 1842: 68; Andres, 1881: 334; Carlgren, 1949: 22; Williams, 1981: 326; England, 1987: 215.

Scolanthus Gosse, 1853: 157; Manuel, 1981b: 266.

Edwardsioides Danielessen, 1890: 100; England, 1987: 224.

Paraedwardsia Carlgren in Nordgaard, 1905: 158; Carlgren, 1949: 24.

Isoedwardsia Carlgren, 1921: 56; Carlgren, 1949: 24 (in part).

Edwardsianthus England, 1987: 224.

Isoscolanthus Brandão, Gusmão and Gomes, 2019: Brandao et al., 2019: 1088.

Diagnosis. Edwardsiidae with body divisible into scapus, scapulus, and capitulum**, and sometimes physa in aboral end**. Physa short, ampullaceous, without nemathybomes or periderm. Nemathybomes with one or two types of nematocysts. Scapus long, with batteries of nemathybomes**, containing large nematocysts**, **or traces of those** sunk into mesoglea. Tentacles at least **10**, inner ones shortest. Eight macrocnemes and at least **two** imperfect, very weak microcnemes in distal column. Retractors relatively large, well developed, diffuse to restricted reniform; parietal muscles well developed. Cnidom: spirocysts, basitrichs, microbasic *b*-, *p*-mastigophores.

Type species. *Edwardsia beautempsii* de Quatrefages, 1842

Remarks. Almost all of Edwardsiidae previously described and specimens collected in this research were classified into five genera, *Edwardsia*, *Edwardsianthus*, *Scolanthus, Isoscolanthus,* and *Paraedwardsia*. The only common feature of these five genera was having nemathybomes or trace of them (*Paraedwardsia* has been said that they do not have nemathybomes, but my research revealed that even *Paraedwardsia* edwardsiids had trace of nemathybomes, pocket-like features [see Fig. 51G]). According to my phylogenetic analysis, all of them, including species deposited on GenBank (Table 6), were in one gigantic clade and isolated the other genera which lack nemathybomes (Fig. 12; see Chapter 1F). However, four genera except *Edwardsianthus* were complexly mingled on the large clade (Fig. 12), so the framework of genera was no longer reflecting the phylogeny.

Though they formed five small subclades in comparatively reliable rate (Fig. 13), there was no morphological feature by which these subclades were distinguished each other except the subclade of genus *Edwardsianthus* England, 1987. Moreover, I cannot gotten molecular information of the type species, *Edwardsia beautempsii* de Quatrefages, 1842 yet, so it cannot be discussed that which subclade includes the type species although this species must be accommodated into the genus *Edwardsia* morphologically because of existence of nemathybomes on its scapus (de Quatrefages, 1842; Manuel, 1981a; Table 17). That is why I synonymize these genera of "nemathybomes-present" anemones into one large genus *Edwardsia,* the most senior previously established genus of them, in the present study (Fig. 13; see Chapter 1F). See Table 17 for comparison to the other genera of Edwardsiidae.

My phylogenetic research still contained several unidentified species of *Edwardsia* because it was difficult to identify the species quickly because of many nominal species of this genus (Table 2). Therefore, after the other four genera were combined into *Edwardsia*, there is a potential that the genus *Edwardsia* will accommodate over 100 species, one of the largest number of species in one genus of Actiniaria (Fautin, 2016). Considering that anemones of Edwardsiidae are hidden in substrates (usually escaping collectors), and almost all of edwardsiids are classified into *Edwardsia* now, this genus might have potential to become the largest genus in the order Actiniaria. See Chapter 3C for evaluation and consideration of the reason why this genus is such highly diverged.

***Edwardsia pudica* Klunzinger, 1877**

(New Japanese name: manyo-mushimodoki-ginchaku)

Fig. 39

Edwardsia pudica Klunzinger, 1877: 80–81, pl. 6, fig. 3; Carlgren, 1931: 18–20, figs. 16, 17

Edwardsiella pudica Andres, 1883: 309
Edwardsia adenensis Faurot, 1895: 121, pl. 6, fig. 5, pl. 7, fig. 6
Edwardsia bocki Carlgren, 1931: 7–9, figs. 5–6.
Edwardsia stephensoni Carlgren, 1950: 128–129, figs. 1–2.
Edwardsianthus pudica: England, 1987: 224–229, fig. 10

Material examined. (Iz-042), histological sections, tissues in paraffin, and prepared nematocysts, collected by SCUBA diving on 7 November 2015 off Kurasaki seashore, Amami-Oshima Island, Kagoshima, Japan, depth unknown but shallower than 30 m, by Takuma Fujii.

Description. ***External anatomy.*** Column, ca. 120–200 mm in whole length, and ca. 12–15 mm in width in living specimen, and ca. 80–130 mm in length and ca. 8–10 mm in width in preserved specimen (Fig. 39A). cylinder-like form, and the proximal part narrower to some extent. The column consisting of capitulum, scapus, and physa. The distal-most part capitulum, translucent and visible magenta mesenteries within, short, without nemathybomes. Scapus with very thick and easily removed periderm-like cuticle, dark gray in color, and with dense nemathybomes (Fig. 39A). Nemathybomes tiny, pale white in color, scattered. Tentacles 20 in number in two cycle: inner tentacle 8 and outer 12, magenta pink or purple in color with brown obscure patches (Fig. 39B), without acrospheres. Inner tentacles short, slender, ca. 5–6 mm in length, and outer ones long and slender, 10–14 mm in length. Mouth in oral disc apparently swollen, white in color.

Internal anatomy. Eight perfect mesenteries, all macrocnemes. Four dorsal and ventral directives, and four lateral mesenteries not paired with other macrocnemes, arranged in normal *Edwardsia* pattern. All macrocnemes present along whole length of the body from oral to aboral end and bearing distinct retractor and parietal muscles. The retractor muscles of lateral mesenteries all ventrally facing. Twelve tiny microcnemes, without muscles, confined only in distal-most part. Four microcnemes between dorsal directives and dorso-lateral mesenteries, four between dorso-and ventro-lateral mesenteries, and four between ventro-lateral mesenteries and ventral directives. Each tentacle between either exo- or endocoelic. Retractor muscles strongly developed and diffused (Fig. 39F), pennon-like, configured with ca. 100 muscular processes. Processes except some basal ones simple or a little branched, and pinnate in some part. Some processes nearest to body wall extremely well-branched, secondly and thirdly (Fig. 39F; England, 1981: fig.

10). Parietal muscles not so developed, apparently elongated to direction of mesenteries, with ca. 15–20 simple or a little branched muscular processes in each side (Fig. 39E). Existence of siphonoglyph unknown because of contracting. Tentacular circular muscle indistinct (Fig. 39C), and longitudinal muscle distinct, ectodermal (Fig. 39D). Mesoglea thickest in body wall, over 200 µm in thickness in some part, and comparatively thick in physa and mesenteries, but thinner in parietal muscles and tentacles (Fig. 41C–E). Nemathybomes sunk into mesoglea. Marginal sphincter muscle and basilar muscle absent (Fig. 39G). Gonads apart from retractor muscles, distinct, but no mature gametocyte observed in my specimen (Fig. 39F).

Cnidom. Basitrichs, spirocysts, and microbasic amastigophores.

Remarks. This specimen from Amami Oshima Island quite resembled *Edwardsianthus pudica* stated in England (1987). He redescribed *Eds. pudica* in detail and set this species as the type of new genus, *Edwardsianthus* England, 1987. That study described that *Eds. pudica* had a large body reaching 200 mm in length and 15 mm in width, a thick walled scapus with easily stripped periderm, scattered small nemathybomes, long slender tapered tentacles, swelled mouth, extremely developed and diffused retractor muscles composed of 70–90 muscular processes, well-developed parietal muscle with 20–30 simple or a little branched processes, and dioecious gonads. These features almost corresponded to my specimen. The tentacles translucent purple or magenta-pink in color (England, 1987) were also similar to tentacles and capitulum of my specimen in color. Moreover, *Eds. pudica* inhabits broad area of Pacific and Indian Ocean, so it is not unnatural if this species inhabits in Japan.

This species has been the type species of *Edwardsianthus* in England, (1987). However, according to the present study, this species should be treated as a member of *Edwardsia*. *Edwardsianthus* became an ingroup of *Edwardsia* as mentioned above, thus it is no longer valid genus (see below).

Treatment of *Edwardsianthus* England, 1987. The genus *Edwardsianthus* England, 1987 was established in order to reorganizing *Edwardsia*, which had become too large genus then. *Edwardsia* de Quatrefages, 1842, the type genus of Edwardsiidae, had accommodated so many species, approximate 45 nominal species (Williams, 1981), that England (1987) allocated the species of *Edwardsia* to three genera, *Edwardsia*, *Edwardsioides* Danielessen, 1890, and new genus *Edwardsianthus* England,

1987. That study accommodated only two species in *Edwardsianthus*: *Eds. pudica* (Klunzinger, 1877) and *Eds. gilbertensis* (Carlgren, 1931). However, as mentioned remarks of genus, *Edwardsianthus* was turned to be an ingroup of *Edwardsia* in my phylogenetic analyses (Fig. 13), thus this genus should be re-accommodated into *Edwardsia*. Consequently, *Edwardsia* remained the largest genus in this family.

According to my research, 11 species which could be classified in *Edwardsianthus,* including nine new species, were collected in Japan (see Table 22). Of course, this is surprising numbers of species compared to known species number (two). Considering that *E. gilbertensis* Carlgren, 1931 and *E. pudica* Klunzinger, 1877 mainly distribute tropical and subtropical zone of Pacific and Indian Ocean (Carlgren, 1931, England, 1987; Fautin, 2013), this group is endemic and apparently diverged in this area.

Edwardsia gilbertensis **Carlgren, 1931**

(Japanese name: minami-mushimodoki-ginchaku; Uchida and Soyama, 2001)

Fig. 40

Edwardsia gilbertensis Carlgren, 1931: 10–12

Edwardsianthus gilbertensis: England, 1987: 218, 231, fig. 10

Material examined. CMNH-ZG 06527: dissected specimen, histological sections, tissues in paraffin, and prepared nematocysts, collected by wading on 7 June 2013 from the intertidal zone of Kabira-Bay, Ishigaki-Island, Okinawa Pref., Japan, by Kensuke Yanagi; NSMT-Co 1701 : dissected specimens (2 individuals), collected by wading on 26 March 2015 from the intertidal zone of Funaura-Bay, Iriomote-Island, Okinawa Pref., Japan, by Takato Izumi; [no registration]: dissected or whole specimens (3 individuals), collected by wading on 17 March 2015 from the intertidal zone of Yonaha-Bay, Miyako-Island, Okinawa Pref., Japan, by Takato Izumi; (Iz-043): histological sections, tissues in paraffin, and prepared nematocysts, collected by wading on 19 March 2014 from the intertidal zone of Kataburu-Beach, Yonaguni-Island, Okinawa Pref., Japan, by Takato Izumi; (Iz-044): histological sections, tissues in paraffin, and prepared nematocysts, collected by wading on 23 March 2015 from the intertidal zone of Kataburu-Beach, Yonaguni-Island, Okinawa Pref., Japan, by Takato Izumi; (Iz-045)–(Iz-050): whole or dissected specimens, collected by wading on 17 March 2016 from the intertidal zone of

Kataburu-Beach, Yonaguni-Island, Okinawa Pref., Japan, by Takato Izumi; (Iz-051): dissected specimens (3 individuals), collected by wading on 24 March 2015 from the intertidal zone of Higawa-Bay, Yonaguni-Island, Okinawa Pref., Japan, by Takato Izumi; (Iz-052): histological sections, tissues in paraffin, collected by wading on 23 September 2014 from the intertidal zone of Senaga-Island, Okinawa Pref., Japan, by Takato Izumi; (Iz-053): histological sections, tissues in paraffin, collected by wading on 21 September 2014 from the intertidal zone of Yagaji-Island, Okinawa Pref., Japan, by Takato Izumi; (Iz-054): histological sections, tissues in paraffin, collected by snorkeling on 9 November 2015 from Shio-michi, Kikai-Island, Kagoshima Pref., Japan, 1 m depth, by Takato Izumi.

Description. ***External anatomy.*** Column, ca. 20–40 mm in whole length, and 2.5–3.5 mm in width in preserved specimen, worm-like form, and equal width among whole body. The column consisting of capitulum, scapus, and physa. The distal-most part capitulum, translucent or opaque gray in color, short, without nemathybomes. Scapus with thick periderm-like cuticle, brownish orange in color, and with dense nemathybomes (Fig. 40A). Nemathybomes tiny, pale white in color, scattered but more or less in 8 rows. Aboral end apparent physa (Fig. 40A). Tentacles 20 in number in two cycle: inner tentacle 4–5 and outer 10–15, opaque whitish-gray in color (Fig. 40B), without acrospheres. Inner tentacles slender, ca. 1 mm in length, and outer ones long, slender, short, with sparse white spots on surface, 2–3 mm in length. Mouth in oral disc swollen.

Internal anatomy. Eight perfect mesenteries, all macrocnemes. Four dorsal and ventral directives, and four lateral mesenteries not paired with other macrocnemes, arranged in normal *Edwardsia* pattern (Fig. 40E). All macrocnemes present along whole length of the body from oral to aboral end and bearing distinct retractor and parietal muscles. The retractor muscles of lateral mesenteries all ventrally facing. Approximately seven–twelve tiny microcnemes, without muscles, confined only in distal-most part. Four microcnemes between dorsal directives and dorso-lateral mesenteries, four between dorso-and ventro-lateral mesenteries, and four between ventro-lateral mesenteries and ventral directives. Each tentacle between either exo- or endocoelic. Retractor muscles distinct and diffused (Fig. 40E, F), pennon-like, configured with ca. 15–35 simple or a little branched muscular processes (Fig. 40F). Parietal muscles developed, apparently elongated to direction of mesenteries, with ca. 10 simple to muscular processes in each side (Fig. 40F). Actinopharynx without siphonoglyph. Tentacular circular muscle indistinct, and longitudinal muscle distinct, ectodermal. Mesoglea thickest in body wall (Fig. 40E), and comparatively thick in tentacles (Fig. 40C), but thinner in mesenteries and parietal muscles (Fig. 40F). Nemathybomes protruding from mesoglea (Fig. 40D). Marginal sphincter muscle and basilar muscle absent. Gonads apart from retractor muscles, distinct, but no mature gametocyte.

Cnidom. Basitrichs, spirocysts, microbasic *b*-mastigophores, and microbasic amastigophores.

Remarks. As same as *E. pudica*, this species has been a member of *Edwardsianthus* in England, (1987). However, the present study treats this species as a member of *Edwardsia* following my phylogenetic analysis.

Ecological remarks. *Edwardsia gilbertensis* was originally described from Gilbert Islands, Kiribati (Carlgren, 1931), and there were several reports from other localities in tropical/subtropical zone in the Pacific (Fautin, 2013). However, there had been no official record of *E. gilbertensis* from Japan although Uchida and Soyama (2001) reported from Kabira Bay, Ishigaki Island. Now, my research discovered many individuals of *E. gilbertensis* living not only in intertidal zone of Kabira Bay in Ishigaki Island (Fig. 40B), but also broad area of Nansei Islands, from Kikai Island, Amami islands (Kagoshima Pref.) to Yonaguni Island, Yaeyama Islands (Okinawa Pref.).

Edwardsia **sp. nov. 9**

(New Japanese name: kougyoku-mushimodoki-ginchaku)

Fig. 41; Table 21

Material examined. CMNH-ZG 05954, histological sections, tissues in paraffin, and prepared nematocysts, collected by SCUBA diving on 10 Jury 2013, Nishidomari (in front of Kuroshio Biological Institute), Kochi Pref., Japan, 5 m depth, by Kensuke Yanagi.

Description. ***External anatomy.*** Column, ca. 60 mm in whole length, and 10–15 mm in width in preserved specimen (but distal side strongly contracted and aboral side torn off during sampling, so body length estimated over 100 mm in living), cylinder-like form, and the proximal part narrower to some extent. The column consisting of capitulum and scapus. The distal-most part capitulum, transparent and visible scarlet color of inside, short, without nemathybomes. Scapus with very thick periderm-like cuticle, dark brown in color, and with dense nemathybomes (Fig. 41A). Nemathybomes tiny, pale white in color, scattered. Aboral end unknown because of torn off (Fig. 41A). Tentacles 20 in number in two cycle: inner tentacle 5 and outer 15, vivid scarlet in color (Fig. 41B), without acrospheres. Inner tentacles short, blunt, ca. 6 mm in length, and outer ones long, slender, with sparse white spot on surface, 15–20 mm in length. Mouth in oral disc apparently swollen

Internal anatomy. Eight perfect mesenteries, all macrocnemes. Four dorsal and ventral directives, and four lateral mesenteries not paired with other macrocnemes, arranged in normal *Edwardsia* pattern (Fig. 41C, D). All macrocnemes present along whole length of the body from oral to aboral end and bearing distinct retractor and parietal muscles. Retractor muscles of lateral mesenteries all ventrally facing. Twelve tiny microcnemes, without muscles, confined only in distal-most part. Four microcnemes between dorsal directives and dorso-lateral mesenteries, four between dorso-and ventro-lateral mesenteries, and four between ventro-lateral mesenteries and ventral directives. Each tentacle between either exo- or endocoelic. Retractor muscles strongly developed and diffused (Fig. 41E), pennon-like, configured with ca. 60–90 muscular processes, simple or a little branched, and pinnated in some part. Some processes nearest to body wall extremely well-branched, secondary and thirdly (Fig. 41E). Parietal muscles not so developed, apparently elongated to direction of mesenteries, with ca. 20–30 simple to muscular processes in each side (Fig. 41E). Existence of siphonoglyph unknown because of contracting. Tentacular circular muscle indistinct, and longitudinal muscle distinct, ectodermal. Mesoglea thickest in body wall, over 200 μm in thickness in some part (Fig. 41C, D), and comparatively thick in tentacle and mesenteries (nearby retractor), but thinner in parietal muscle (Fig. 41E). Nemathybomes protruding from mesoglea (Fig. 41G). Marginal sphincter muscle and basilar muscle absent. Gonads apart from retractor muscles, distinct, in which densely immature testis (Fig. 41F).

Cnidom. Basitrichs, spirocysts, microbasic *b*-mastigophores, and microbasic amastigophores. See Table 21 for size and distribution.

Remarks. See Table 22 for comparison to the other species which have the characters of *Edwardsianthus*. The most characteristic feature of this species is vivid red tentacle. This species can be distinguished from the other species in clade Edwardsianthus by not only this color, but also by having two types of nematocysts in both actinopharynx and nemathybomes. Genus

Edwardsianthus is traditionally characterized by nemathybomes containing only one type of nematocysts, but the definition became incorrect by the discovering of this species. According to my phylogenetic analysis, the most related species of *E.* sp. nov. 9 was *Edwardsia pudica*, but they can be distinguished by cnidom of nemathybomes (Table 21; England, 1987). To sustain this conclusion, it is needed to collect additional specimens, especially which have complete proximal end. However, this species was collected only once from the locality, and there has been no additional case of observation on the field at all.

Edwardsia sp. nov. 10

(New Japanese name: suigyoku-mushimodoki-ginchaku)

Fig. 42; Table 21

Material examined. (Iz-055): histological sections, tissues in paraffin, and prepared nematocysts, collected by SCUBA diving on 31 January 2016, off Shirahama seashore, Amami-Oshima Island, Kagoshima, Japan, 15m depth, by Daisuke Uyeno.

Description. ***External anatomy.*** Column, ca. 70 mm in whole length, and ca. 15 mm in width in preserved specimen, and ca. 100 mm in living. Column cylinder-like form, and the middle part swollen to some extent (Fig. 42A, B). The column consisting of capitulum, scapus and quite small physa. The distal-most part capitulum, transparent, short, without nemathybomes. Scapus with thick periderm, brownish black in color, and with protruding scattered nemathybomes (Fig. 42A). Nemathybomes tiny, dingy gray in color. Aboral end differentiated small, tapered physa. Tentacles 20 in number in two cycle: inner tentacle 5 and outer 15, brilliant green in color and pale purple at the tips, no pattern, comparatively slender, without acrospheres. Inner tentacles ca. 7 mm and outer ones ca. 10–15 mm in length. Mouth in oral disc slightly swollen.

Internal anatomy. Eight perfect mesenteries, all macrocnemes. Four dorsal and ventral directives, and four lateral mesenteries not paired with other macrocnemes, arranged in normal *Edwardsia* pattern (Fig. 42F). All macrocnemes present along whole length of the body from oral to aboral end and bearing distinct retractor and parietal muscles. Retractor muscle of lateral mesenteries all ventrally facing. Twelve tiny microcnemes, without muscles, confined only in distal-most part. Four microcnemes between dorsal directives and dorso-lateral mesenteries, four between dorso-and ventro-lateral mesenteries, and four between ventro-lateral mesenteries and ventral directives. Each tentacle between either exo- or endocoelic. Retractor muscles weakly developed but distinct, diffused (Fig. 42C), pennon-like, configured with ca. 50–60 muscular processes, simple or a little branched. One process nearest to body wall well-branched (Fig. 42C). Parietal muscles indistinct, elongated in direction of mesenteries, consisted of short and slightly branched processes, sparsely, less than 10 in each side (Fig. 42C). Existence of siphonoglyph unknown because of contracting. Tentacular circular muscle endodermal, distinct, and longitudinal muscle ectodermal, both distinct. Mesoglea thickest in body wall and actinopharynx, maximum 400 μm in thickness (Fig. 42F), but far thinner in parietal muscle and tentacles (Fig. 42C–E), and thinnest, less than 10 μm in mesenteries. Nemathybomes protruding from mesoglea (Fig. 42H). Marginal sphincter muscle and basilar muscle absent. Gonads apart from retractor muscles, distinct (Fig. 42G), in which matured oocytes.

Cnidom. Basitrichs, spirocysts, microbasic *p*-mastigophores and microbasic amastigophores. See Table 21 for size and distribution.

Remarks. See Table 22 for comparison to the other species which have the characters of *Edwardsianthus*. Species of *Edwardsianthus* usually have strongly developed and diffused retractor and parietal muscle, but those of this species exceptionally not so developed. This character is distinct in addition to brilliant light green tentacles. Moreover, according to my phylogenetic analysis, this species was far isolated from other anemones of *Edwardsianthus* (Fig. 13).

This species has been discovered only once in nature.

Edwardsia **sp. nov. 11**

(New Japanese name: sougyoku-mushimodoki-ginchaku)

Fig. 43; Table 21

Material examined. (Iz-056): histological sections, tissues in paraffin, and prepared nematocysts, collected by SCUBA diving on 24 June 2012, in Oura-Bay, Okinawa Island, Okinawa Pref., Japan, depth unknown, by Takuma Fujii.

Description. ***External anatomy.*** Column, ca. 150 mm in whole length, and 20–35 mm in width in preserved specimen, and over 300 mm in living, one of the largest species in edwardsiid. Column cylinder-like form, and the proximal part swollen to some extent. The column consisting of capitulum, scapus and quite small physa. The distal-most part capitulum, transparently blue, short, without nemathybomes. Scapus with thin and easily stripped periderm, brown in color, and with quite numerous scattered nemathybomes (Fig. 43B). Nemathybomes tiny, pale white in color. Aboral end differentiated small, tapered physa. Tentacles 20 in number in two cycle: inner tentacle 5 and outer 15, metallic greenish blue in color with no pattern (Fig. 43A), slender, without acrospheres. Inner tentacles ca. 10 mm and outer ones ca. 15–25 mm in length. Mouth in oral disc apparently swollen.

Internal anatomy. Eight perfect mesenteries, all macrocnemes. Four dorsal and ventral directives, and four lateral mesenteries not paired with other macrocnemes, arranged in normal *Edwardsia* pattern (Fig. 43C). All macrocnemes present along whole length of the body from oral to aboral end and bearing distinct retractor and parietal muscles. Retractor muscle of lateral mesenteries all ventrally facing. Twelve tiny microcnemes, without muscles, confined only in distal-most part. Four microcnemes between dorsal directives and dorso-lateral mesenteries, four between dorso-and ventro-lateral mesenteries, and four between ventro-lateral mesenteries and ventral directives. Each tentacle between either exo- or endocoelic. Retractor muscles strongly developed and diffused (Fig. 43E), pennon-like, configured with ca. 120–150 muscular processes, simple or a little branched. One process nearest to body wall extremely well-branched, with over 100 secondly and thirdly branched processes (Fig. 43E). Parietal muscles developed peculiarly: consisted of ca. 20–30 processes in each side, and only one of them extremely developed, branched into secondly 15–25 processes, and expanded broadly. So, parietals entirely appearing characteristic shape like clubs of cards (Fig. 43D). Existence of siphonoglyph unknown because of contracting. Tentacular circular muscle endodermal, indistinct (Fig. 43G), and longitudinal muscle ectodermal, distinct and sometimes pinnated (Fig. 43H). Mesoglea thickest in body wall, sometimes reaching 1 mm in thickness (Fig. 43C), but thinner in mesenteries, parietal muscle, and tentacles (Fig. 43E–H). Nemathybomes protruding from mesoglea. Marginal sphincter muscle and basilar muscle absent. Gonads apart from retractor muscles, distinct (Fig. 43C, F), in which matured oocytes.

Cnidom. Basitrichs, spirocysts, microbasic amastigophores. See Table

21 for size and distribution.

Remarks. See Table 22 for comparison to the other species which have the characters of *Edwardsianthus*. This species is characterized by not only gigantic body and bluish metallic tentacle, but also strange club-like shape of parietal muscles. Almost all species have parietal muscle with simple or slightly branched processes, and there has been no case confirmed parietal muscles with such secondly branched muscular processes like this species. So, shape of parietal muscle of this species is conspicuous in Edwardsiidae.

There were several cases of observation of metallic blue tentacle resembling to this species reported during SCUBA diving in Amami Oshima. However, it is difficult to dig out buried large edwardsiid anemones from substrates even if the places of anemones were certain. This is because they usually quickly shrunk their tentacles and hide whole bodies into deep substrate.

Edwardsia sp. nov. 12

(New Japanese name: shigyoku-mushimodoki-ginchaku)

Fig. 44; Table 21

Material examined. (Iz-057): histological sections, tissues in paraffin, and prepared nematocysts, collected by SCUBA diving on 28 March 2013, in Oura-Bay, Okinawa Island, Okinawa Pref., Japan, 15m depth, by Takuma Fujii.

Description. ***External anatomy.*** Column, ca. 200 mm in whole length, and 7–20 mm in width in preserved specimen, and over 300 mm in living, one of the largest species in edwardsiid (Fig. 44B). Column worm-like form, and the distal part swollen to some extent (maybe because of condition during preservation). The column consisting of capitulum, scapus and quite small physa. The distal-most part short capitulum, without nemathybomes. Scapus with thin and easily stripped periderm, light brown in color, and surface of it completely smooth, with extremely small nemathybomes-like spots (Fig. 44B). Aboral end differentiated small, rounded physa. Tentacles 20 in number in two cycle: inner tentacle 5 and outer 15, pale purple in color with several dark purple spots, slender, without acrospheres but a little capitated tip (Fig. 44A). Inner tentacles ca. 10 mm and outer ones ca. 15–20 mm in length. Mouth in oral disc apparently swollen.

Internal anatomy. Eight perfect mesenteries, all macrocnemes. Four dorsal and ventral directives, and four lateral mesenteries not paired with other macrocnemes, arranged in normal *Edwardsia* pattern. All macrocnemes present along whole length of the body from oral to aboral end and bearing distinct retractor and parietal muscles. Retractor muscle of lateral mesenteries all ventrally facing. Twelve tiny microcnemes, without muscles, confined only in distal-most part. Four microcnemes between dorsal directives and dorso-lateral mesenteries, four between dorso-and ventro-lateral mesenteries, and four between ventro-lateral mesenteries and ventral directives. Each tentacle between either exo- or endocoelic. Retractor muscles strongly developed and diffused (Fig. 44E), pennon-like, configured with ca. 100–150 muscular processes, simple to well branched: processes near filament short and branched well. One process nearest to body wall extremely well-branched, with approximately 80 secondly and thirdly branched processes (Fig. 44E). Parietal muscles distinct, consisted of ca. 10–15 simple processes in each side (Fig. 44E). Existence of siphonoglyph unknown because of contracting. Tentacular circular muscle indistinct (Fig. 44C), and longitudinal muscle ectodermal, distinct (Fig. 44D). Mesoglea thickest in body wall and actinopharynx, ca. 200 μm in thickness (Fig. 44E), but far thinner in mesenteries, retractor muscles, and tentacles (Fig. 44C, D). Nemathybomes-like structures protruding from mesoglea, but without nematocysts at all (Fig. 44G). Marginal sphincter muscle and basilar muscle absent. Gonads apart from retractor muscles, distinct (Fig. 44F), in which matured oocytes.

Cnidom. Basitrichs, spirocysts, and microbasic amastigophores. There are no nematocysts in nemathybome-like structures. See Table 21 for size and distribution.

Remarks. See Table 22 for comparison to the other species which have the characters of *Edwardsianthus*. The most characteristic feature of this species is nemathybome-like features without nematocysts. This character was also observed in the species of previous *Paraedwardsia* (Fig. 51), but it was the first case in *Edwardsianthus* anemones, so *E.* sp. nov. 13. can be easily distinguished from other species of the previous genus *Edwardsianthus* by absence of cnidae in nemathybome-like structures. It is suggested that degenerating of nemathybome is occurred several times in Edwardsiidae.

Edwardsia **sp. nov. 13**

(New Japanese name: haneji-mushimodoki-ginchaku)
Fig. 45; Table 23

Material examined. (Iz-058): histological sections, tissues in paraffin, and prepared nematocysts, collected by wading on 21 September 2014, from the intertidal zone of Yagaji-Island, Okinawa Pref., Japan, by Takato Izumi; (Iz-059): whole specimen, collected by wading on 23 November 2019, from the intertidal zone of Haneji Inland-Sea, Okinawa Pref., Japan, by Masanori Taru and Gen Kanaya.

Description. ***External anatomy.*** Column, ca. 50–65 mm in whole length, and 8–10 mm in width in preserved specimen, and over 90 mm in living (Fig. 45A). Column cylinder-like form, and the middle part swollen to some extent. The column consisting of capitulum, scapus and large physa (Fig. 45B). The distal-most part short capitulum, brownish translucent with white patches, without nemathybomes. Scapus with thin periderm, light orange to light brown in color, and surface of it completely smooth, with apparent dark red nemathybomes (Fig. 45C). Aboral end rounded, transparent physa (Fig. 45B). Tentacles 20 in number in two cycle (Fig. 45G): inner tentacle 5 and outer 15. Tentacle except dorsal brownish translucent with white line-like spots, slender, without acrospheres; one dorsal tentacle whitish opaque with no pattern (Fig. 45G). Inner tentacles ca. 10 mm and outer ones ca. 15 mm in length. Mouth in oral disc a little swollen.

Internal anatomy. Eight perfect mesenteries, all macrocnemes. Four dorsal and ventral directives, and four lateral mesenteries not paired with other macrocnemes, arranged in normal *Edwardsia* pattern. All macrocnemes present along whole length of the body from oral to aboral end and bearing distinct retractor and parietal muscles. Retractor muscle of lateral mesenteries all ventrally facing (Fig. 45D). Twelve tiny microcnemes, without muscles, confined only in distal-most part. Four microcnemes between dorsal directives and dorso-lateral mesenteries, four between dorso-and ventro-lateral mesenteries, and four between ventro-lateral mesenteries and ventral directives. Each tentacle between either exo- or endocoelic. Retractor muscles strongly developed and diffused (Fig. 45D, E), pennon-like, configured with ca. 50–70 muscular processes, simple to slightly branched (Fig. 45E). One process nearest to body wall well-branched, with approximately 40 secondly and thirdly branched processes (Fig. 45E). Parietal muscles distinct, consisted of ca. 5–9 slightly branched processes in each side (Fig. 45E).

Existence of siphonoglyph unknown because of contracting. Tentacular circular muscle and longitudinal muscle indistinct. Mesoglea thickest in body wall and actinopharynx, ca. 300 µm in thickness (Fig. 45E), but far thinner in mesenteries, retractor muscles, and tentacles (Fig. 45D–E). Nemathybomes protruding or sunk into mesoglea. Marginal sphincter muscle and basilar muscle absent. Gonads apart from retractor muscles, distinct (Fig. 45F), in which immature oocytes.

Cnidom. Basitrichs, and microbasic *p*-mastigophores, and microbasic *b*-mastigophores. See Table 23 for size and distribution.

Remarks. See Table 22 for comparison to the other species which have the characters of *Edwardsianthus*. Compared from the other species of the previous genus *Edwardsianthus*, *Edwardsia* sp. nov. 13 can be easily distinguished by absence of spirocysts in tentacle. Moreover, this species had strange tentacular coloration: one opaque tentacle in dorsal side and the other 19 brownish translucent tentacles (Fig. 45G). The other species in the previous genus *Edwardsianthus* have tentacles unified in colors (see Figs. 39–44, 46, 47; Carlgren, 1931; England, 1987). This species can be distinguished from *Edwardsia* sp. nov. 12, the most related species (Fig. 13), by possessing nematocysts in their nemathybomes (Tables 21–23).

This species was only collected from Haneji Inland Sea surrounded by Okinawa and Yagaji Islands. I also collected some other species from here, so the diversity of Edwardsiidae would be rich there.

Edwardsia sp. nov. 14

(New Japanese name: ogasawara-jitte-mushimodoki)

Fig. 46; Table 23

Material examined. (Iz-060): histological sections, tissues in paraffin, and prepared nematocysts, collected by wading on 26 June 2014 from the intertidal zone of kopepe-Beach, Chichijima Island, Ogasawara, Tokyo Met., Japan, by Takato Izumi; (Iz-061): histological sections, tissues in paraffin, and prepared nematocysts, collected by SCUBA diving on 21 June 2014 from the 8 m depth of Miyanohama-Beach, Chichijima Island, Ogasawara, Tokyo Met., Japan, by Takato Izumi; (Iz-062): whole specimens. same method, collector, and date as (Iz-060); (Iz-063): whole specimens histological sections, tissues in paraffin, and prepared nematocysts, collected by SCUBA diving on 16 February 2017, off Seihyo Seashore, Chichijima Island, Ogasawara Islands, Tokyo Met., Japan, 15–25 m depth, by Yoshihisa Fujita.

Description. ***External anatomy.*** Column, ca. 20–30 mm in whole length, and 0.7–1.2 mm in width in living individuals, and ca. 12–17mm in length in preserved specimen. Column worm-like form, uniform width. The column consisting of short capitulum, scapus and quite small physa but indistinctly differentiated. The distal-most part long capitulum, hemitransparent, without nemathybomes and periderm. Scapus with quite thin hemitransparent periderm, and with scattered tiny nemathybomes (Fig. 46A). Nemathybomes quite tiny, pale white in color. Aboral end slightly differentiated small, tapered physa. Tentacles 10 in number in two cycle: inner tentacle 3 and outer 7, greenish brown in color with white lines in transverse direction, slender, without acrospheres (Fig. 46B). Inner tentacles ca. 1 mm and outer ones ca. 1.5 mm in length. Mouth in oral disc not swollen.

Internal anatomy. Eight perfect mesenteries, all macrocnemes. Four dorsal and ventral directives, and four lateral mesenteries not paired with other macrocnemes, arranged in normal *Edwardsia* pattern (Fig. 46D, F). All macrocnemes present along whole length of the body from oral to aboral end and bearing distinct retractor and parietal muscles. Retractor muscle of lateral mesenteries all ventrally facing. Two tiny microcnemes, without muscles, confined only in distal-most part, between dorso-and ventro-lateral mesenteries (Fig. 46D). Retractor muscles weakly developed and restricted to filament side (Fig. 46G), pennon-like, configured with simple or a little branched ca. 12–16 muscular processes. Parietal muscles weak, consisted of ca. 2–4 simple or a little branched processes in each side (Fig. 46G). Siphonoglyph absent in actinopharynx (Fig. 46D). Tentacular circular muscle and longitudinal muscle indistinct (Fig. 46C). Mesoglea entirely thin among whole body, especially in mesenteries (Fig. 46E, G). Nemathybomes protruding from or half sunk into mesoglea (Fig. 46F). Marginal sphincter muscle and basilar muscle absent (Fig. 46H). Gonads concatenated with retractor muscles, distinct (Fig. 46G), in which matured testis. Endocoel of tentacle and distal side of column containing dense zooxanthellae (Fig. 46E).

Cnidom. Basitrichs, spirocysts, microbasic *p*-mastigophores, and microbasic amastigophores. See Table 23 for size and distribution.

Remarks. Subclade *Edwardsianthus* included strange two species. *Edwardsia* sp. nov. 14 and *Edwardsia* sp. nov. 15 did not have the typical arrangement of *Edwardsianthus*, 20 tentacles, but had only 10 tentacles arranged as inner three and outer seven. This arrangement was with the least number of tentacles recorded in Edwardsiidae (and also in sea anemones ever known). Edwardsiidae had been diagnosed with eight macrocnemes, so it was clear that these species have only two microcnemes. This is the least number not only in the genus *Edwardsia* but also in Edwardsiidae.

See Table 22 for comparison to the other species which have the characters of *Edwardsianthus*. *Edwardsia* sp. nov. 14 can be distinguished from *E.* sp. nov. 15 by slender tentacles, hemitransparent body with quite thin periderm, weak parietal muscles, and presence of microbasic *p*-mastigophores in actinopharynx.

Edwardsia sp. nov. 15

(New Japanese name: yonaguni-jitte-mushimodoki)

Fig. 47; Table 23

Material examined. (Iz-064): dissected specimen, histological sections, tissues in paraffin, and prepared nematocysts, collected by wading on 23 March 2015 from the intertidal zone of Kataburu-Beach, Yonaguni Island, Okinawa Pref., Japan, by Takato Izumi; (Iz-065): whole specimen, collected by wading on 23 March 2015 from the intertidal zone of Kataburu-Beach, Yonaguni Island, Okinawa Pref., Japan, by Takato Izumi. (Iz-066): whole specimens, collected by wading on 17 March 2016 from the intertidal zone of Kataburu-Beach, Yonaguni Island, Okinawa Pref., Japan, by Takato Izumi.

Description. ***External anatomy.*** Column, ca. 20–25 mm in whole length, and 2–3 mm in width in living individuals, and ca. 11–16 mm in length in preserved specimen. Column cylinder-like form, swollen in proximal side. The column consisting of short scapulus, scapus and quite small physa. The distal-most part short scapulus, opaque, without nemathybomes and periderm. Scapus with thick and easily stripped periderm (Fig. 47A). Nemathybomes invisible from outside. Proximal end small physa, tapered. Tentacles 10 in number in two cycle: inner tentacle 3 and outer 7, brown with dense white patches, quite blunt like rugby ball, rugged on surface, without acrospheres (Fig. 47B). Inner tentacles ca. 1 mm and outer ones ca. 1.5–2 mm in length. Mouth in oral disc well swollen.

Internal anatomy. Eight perfect mesenteries, all macrocnemes. Four dorsal and ventral directives, and four lateral mesenteries not paired with other macrocnemes, arranged in normal *Edwardsia* pattern (Fig. 47C, E). All macrocnemes present along whole length of the body from oral to aboral end and bearing distinct retractor and parietal muscles. Retractor muscle of lateral mesenteries all ventrally facing. Two tiny microcnemes, without muscles, confined only in distal-most part, between dorso-and ventro-lateral mesenteries. Retractor muscles distinctly developed and restricted to filament side (Fig. 47F), pennon-like, configured with simple to slightly branched ca. 20–30 muscular processes. Parietal muscles strong, consisted of ca. 8–11 simple or a little branched processes in each side (Fig. 47F). Weak one siphonoglyph in actinopharynx. Tentacular circular muscle and longitudinal muscle indistinct. Mesoglea thickest in body wall (Fig. 47E), but thinner in mesenteries, both muscles, and actinopharynx (Fig. 47C–E). Nemathybomes small, protruding from mesoglea (Fig. 47E). Marginal sphincter muscle and basilar muscle absent (Fig. 47G). Gonads concatenated with retractor muscles, distinct, in which immature testis (Fig. 47F). Endocoel of tentacle and distal side of column containing zooxanthellae (Fig. 47D).

Cnidom. Basitrichs, spirocysts, microbasic *b*-mastigophores and microbasic *p*-mastigophores. See Table 23 for size and distribution.

Remarks. See Table 22 for comparison to the other species which have the characters of *Edwardsianthus*. Same as *Edwardsia* sp. nov. 14, *E.* sp. nov. 15 was one of the species with least numbers of tentacles. *Edwardsia* sp. nov. 15 can be distinguished from *E.* sp. nov. 14 by blunt opaque tentacles, thick periderm, distinctly developed parietal muscles and presence of microbasic *p*-mastigophores in actinopharynx.

Edwardsia alternobomen **Izumi and Fujita, 2019**

New Japanese name: gyorai-mushimodoki-ginchaku

Fig. 48; Table 24

Edwardsia alternobomen Izumi and Fujita, 2019: 538–543, figs. 3, 4

Material examined. The holotype: NSMT-Co 1657, dissected specimen, histological sections, and prepared cnidae, collected on 13 October, 2015, in Hokabira-coast, Hinoshima Island, Amakusa Islands, Kumamoto Prefecture (32°23′39″N, 130°25′21″E), 1 m depth by wading, collected by Takato Izumi; 3 paratypes: NSMT-Co 1656, histological sections, and prepared cnidae, collected in 24 June, 2014, same locality and method as holotype, collected by Naoto Jimi; NSMT-Co 1658, 1659, dissected specimen, same date, locality and collector as NSMT-Co 1657; the other specimen: (Iz-067), dissected specimen, histological sections, and prepared cnidae, collected on 3 April, 2016, in Kotogahama-Beach, Manazuru, Kanagawa Prefecture, 10 m depth, collected by Naoto Jimi.

External anatomy. Column cylinder-like, both in living and preserved specimens, wrinkled by huge nemathybomes,25–30 mm in whole length (30 mm in NSMT-Co 1657 [holotype]), and 2–4 mm in width (3 mm in NSMT-Co 1657) in expanded specimens, (Fig. 48A). Body divided into capitulum, scapus and physa (Fig. 48A). Scapus covered with bright orange periderm. Nemathybomes of two types: huge, up to 1.5 mm in diameter, protruding like papillae, and small, less than 300 µm in diameter, covered by periderm. Nemathybomes queued in eight-rows: four rows of larger ones and four rows of smaller ones arranged alternately: all larger nemathybomes in four rows, and never in the other four rows (Fig. 48B). Compared to *E. tuberculata*, large nemathybomes sparse in each row. Aboral physa differentiated from scapus, naked, a little rounded, without nemathybomes (Fig. 48A). Tentacles transparent with a row of white patches and two rows of wine-red tiny patches on surface, 2-4 mm in length, 12 in number, in two cycles of six tentacles each (Fig. 48C). Oral disk 1 mm in diameter, light in color, with wine red circle, and pale white rhomb only on dorsal side (Fig. 48C).

Internal anatomy. Eight perfect mesenteries, macrocnemes, distributed along whole body from distal to proximal end. Paired dorsal and ventral directives plus four lateral, unpaired mesenteries (Fig. 48F, H). Four tiny microcnemes, one of the fewest in Edwardsiidae, each without muscles, limited only to distal-most column. Two microcnemes between dorso- and ventro-lateral mesenteries and two between ventro-lateral mesenteries and ventral directives. One tentacle in each end- or exo- coel. All macrocnemic mesenteries bear retractor and parietal muscles. Retractor muscle of each lateral mesentery faces ventrally (Fig. 48F). Each retractor muscle distinctly developed as pennon, restricted to filament side; with 15–20 multiply branched muscular processes next to actinopharynx, and with 10–15 multiply branched muscular processes in lower part (Fig. 48E, G). Parietal muscles of macrocnemes comparatively distinct, semi-elliptic or triangular shape with 3–4 slightly branched muscular processes in each side (Fig. 48E, G). Actinopharynx very short, grooved, with no distinct siphonoglyph. Tentacular longitudinal muscle ectodermal but indistinct. Marginal sphincter muscle and basilar muscle absent (Fig. 48D). Mesoglea generally thin in mesenteries, and comparatively thick in body wall (Fig. 48E, F). Larger nemathybomes, however, far thicker than mesoglea, greatly protruding from the body wall and containing very large basitrichs (Fig. 48F, I). Dioecious: gonads between retractor muscles and filaments; oocytes in gonads of NSMT-Co 1656.

Cnidom. Spirocysts, basitrichs, and microbasic *p*-mastigophores, and *b*-mastigophores. See Table 24 for size and distribution.

Etymology: the specific epithet consists of alterno (alternately in Latin) and bomen (meaning nemathybome). This name is derived from the alternately arranged nemathybomes.

Remarks. See Table 25 for comparison to the other species of *Edwardsia* which have 12 tentacles. This species has two characteristic features: 12 tentacles and huge basitrichs reaching 200 µm in length. There are a few species of *Edwardsia* that have only 12 tentacles: *E. andresi* Danielessen, 1890, *E. duodecemtentaculala* Car1gren, 1931, *E. fusca* Danielessen, 1890, *E. jonesii* Seshaiya and Cuttress, 1969, and *E. juliae* Daly and Ljubenkov, 2008. *Edwardsia alternobomen* can be distinguished from the former three species by the arrangement of nemathybomes: it has rows of nemathybomes whereas the nemathybomes of *E. andresi, E. duodecemtentaculala* and *E. fusca* are scattered (see England. 1987). Concerning the other two species, *E. alternobomen* can be distinguished from *E. jonesii* in having extremely large nemathybomes and no nemathybomes in two rows: nemathybomes of *E. jonesii* are very small and sometimes become double rows in mid scapus (Seshaiya and Cuttress, 1969), and can be distinguished from *E. juliae* in having two cycle of slender tentacles, whereas the tentacles of *E. juliae* are blunt and in a single cycle (Daly and Ljubenkov, 2008). In addition, *E. alternobomen* can be distinguished from all species mentioned above by its huge basitrichs, which reach 200 µm in length. The maximum length of basitrichs in the nemathybomes of *E. alternobomen* is the longest reported for Edwardsiidae.

This new species has many basitrichs >150 µm in length. Such large basitrichs are also observed in four other species of *Edwardsia*, *E. tuberculata*, *E. californica*, *E. claparedi*, and *E. maroccana* (see Remarks of *E. tuberculata*, above). However, *E. alternobomen* can be distinguished easily by having only 12 tentacles, while the other species of *Edwardsia* here with very large basitrichs all have 16 tentacles. Because *E. alternobomen* is sexually mature, I do not think that it is a juvenile. Beyond the differences in size and arrangement of nemathybomes, *Edwardsia tuberculata* has larger and far more densely arranged nemathybomes than *E. alternobomen*. Moreover, in *E. tuberculata* the physa is flattened whereas in *E. alternobomen* it is rounded. The muscular processes of *E. tuberculata* are about as twice as numerous as those of *E. alternobomen* (Carlgren, 1921). In *Edwardsia californica, t*he mesenterial muscle has a distinctive shape (Carlgren, 1936) and far more processes than the muscles of *E. alternobomen*. The body of *Edwardsia claparedi* is approximately four times longer and broader than *E. alternobomen* (Manuel 1981a). *Edwardsia maroccana* has far more developed retractor muscles (with 30 processes: Carlgren, 1931) than does *E. alternobomen*. In addition, *E. alternobomen* has two sizes of nemathybomes alternatively arranged in eight rows (Fig. 48B), whereas any other previously described species of *Edwardsia* does not. This unusual arrangement of nemathybomes is one of the most prominent morphological features for this new species.

It is the first observed case in the world that nematocysts contained in nemathybome can discharge to outside on this species (Fig. 48I) because this species have extremely large nemathybome. This histological section became a hint to suspect the role of nemathybomes (see Chapter 3C).

(Description, Fig. 48, and part of Table 24 are revised and reprinted Izumi and Fujita [2019] by courtesy of ZOOTAXA.)

Edwardsia aff. *tuberculata* Dueben and Koren, 1847

(New Japanese name: oozutsu-mushimodoki-ginchaku)

Fig. 49; Table 24

Edwardsia tuberculata Dueben and Koren, 1847: 267; Carlgren, 1921: 29

Edwardsia aff. *tuberculata*: Izumi and Fujita, 2019: 535–537, figs. 2, 4

Material examined. NSMT-Co 1654, dissected specimen, histological sections, and prepared cnidae, collected in 6 November, 2014, east of Ogishima Island, Kagawa Pref., Seto Inland Sea (34°24′54″N, 134°05′30″E), 16 m depth, collected by Naoto Jimi; NSMT-Co 1655, histological sections of damaged individuals, same date, locality, and collector as NSMT-Co 1654; (Iz-068), dissected specimen, collected by scuba diving, in 22 December, 2017, Araihama, Misaki, Kanagawa Pref. Japan at 5 m depth, by Hisanori Kotsuka.

External anatomy. Column of contracted specimen 20–25 mm in whole length (25.0 mm in NSMT-Co 1654), and 6–7 mm in width (7 mm in NSMT-Co 1654), swelled by huge nemathybomes, cylinder-like in shape but slightly swollen proximally (Fig. 49A). Body divided into capitulum, scapus and physa; in our specimen, capitulum shrunken in column, invisible. About half of scapus occupied by nemathybomes, remaining half covered with brownish gray periderm. Nemathybomes extremely large, like papillae, up to 1.5 mm in diameter (Fig. 49B), in eight rows in proximal part, gradually becoming smaller distally (Fig. 49A). Aboral physa differentiated from scapus, naked, not rounded but tapered, without nemathybomes (Fig. 49A). Tentacles 16 in number, in two cycles of eight, relative size of each cycle unclear because tentacles contracted into scapus.

Internal anatomy. Eight perfect mesenteries, macrocnemes, distributed along whole body from distal to proximal end. These eight are the paired dorsal and ventral directives plus four unpaired lateral mesenteries. Eight tiny microcnemes, without muscles, limited to distal-most part: four between dorsal directives and dorso-lateral mesenteries, two between dorso- and ventro-lateral mesenteries, and two between ventro-lateral mesenteries and ventral directives. All macrocnemic mesenteries bear retractor and parietal muscles. Retractor muscle of each lateral mesentery faces ventrally (Fig. 49E, F). Each retractor muscle distinctly developed; diffuse, with approximately 20 simple or slightly branched muscular processes next to actinopharynx (Fig. 49D); diffuse or restricted to parietal muscle side, developed like a pennon, with 10–25 simple or slightly branched muscular processes in lower part (Fig. 49E, F). Parietal muscles of macrocnemes distinct, semi-elliptic, with 10 slightly branched muscular processes in each side (Fig. 49D–F). Actinopharynx very short, grooved but without distinct siphonoglyph. One tentacle in each endo- or exo-coel. Tentacular longitudinal muscle ectodermal and distinct. Marginal sphincter muscle and basilar muscle absent (Fig. 49C, H). Mesoglea generally thin in mesenteries, and comparatively thick in body wall (Fig. 49D, F). Nemathybomes far thicker than mesoglea, greatly protruding from body wall and containing very large basitrichs (Fig. 49F, G). Gonads on mesenteries between retractor muscles and filaments; gametocytes immature.

Cnidom. Spirocysts, basitrichs, microbasic *p*-mastigophores. See

Table 24 for size and distribution.

Remarks. *Edwardsia tuberculata* was originally described in Dueben and Koren (1847), and more detailed morphological features were described in Carlgren (1921). Morphology of the examined specimens agrees well with the description by Carlgren (1921): shrunken body size is 2 cm in length and 7 mm in width (Fig. 49A); a few outstandingly large nemathybomes look like papillae arranged in 8 rows (Fig. 49B, F, G); physa is developed but flattened or tapered (Fig. 49A, H); retractor muscles are diffused with slightly branched processes and parietal muscle is distinct with 20 processes (Fig. 49D–F). The cnidom also almost perfectly corresponds to the description of Carlgren (1921): this species is characterized by large nemathybomes that contain huge basitrichs. The larger type of basitrichs in nemathybomes of our specimen are 116–187 μm in length and 4.8–9.0 μm in width (Table 24). This matches the nematocysts of *E. tuberculata* reported by Carlgren (1921), which he measured at 110–190 μm in length and 5–7 μm in width. In filaments, Carlgren (1921) mentioned that some of nematocysts are a little broader than the others. This observation would be convincing if one assumes that the wide nematocyst of Carlgren (1921) is what I identify as microbasic *b*-mastigophores in our specimen. There were some small differences between the description and our specimens. For example, the retractor muscles of our specimen were composed of 10–25 muscular processes while Carlgren (1921) mentioned more 30 processes, and I found some spirocysts in actinopharynx, although Carlgren (1921) did not mention these.

According to England (1987), in addition to *E. tuberculata* three other species of *Edwardsia* have basitrichs over 150 μm in length; *E. californica* McMurrich, 1913, *E. maroccana* Carlgren, 1931, and *E. claparedi* (Panceri. 1869). However, they never exceed 170 μm even in maximum size (Carlgren, 1931, 1936; England, 1987; Manuel, 1977). The huge basitrichs are, however, now also reported in *Edwardsia alternobomen*, described above, which has basitrichs over 200 μm in length (Table 24).

Edwardsia tuberculata is distinguished from the other species with large basitrichs in their nemathybomes by having larger basitrichs than those other species and by some anatomical features. Between mesenteries, *E. tuberculata* consistently has a single row of nemathybomes, whereas *E. californica* has two or three rows on the proximal part (Carlgren, 1936). *Edwardsia tuberculata* has flattened physa but *E. californica* has very apparent, large, rounded physa. *Edwardsia californica* has a very characteristic restricted retractor muscles with approximately 40 muscular processes, whereas one of our specimens has diffused retractor muscles composed of about 20 processes. According to Carlgren (1931), *Edwardsia maroccana* has more developed muscles with 30 processes, and it is apparently pinnate near the column, whereas those of *E. tuberculata* do not branch so much. In addition, Carlgren (1931) showed basitrichs of 30–40 µm in length and 6.5 µm in width bearing a shimmering thread in the capsule in the actinopharynx, these are likely a kind of mastigophores, a type of nematocyst not found in actinopharynx of the examined specimen of *E. tuberculata*. The body size of *E. tuberculata* (20–25 mm in length) is completely different from *Edwardsia claparedi,* which reach to 120 mm in length (Manuel, 1981a).

Edwardsia tuberculata can also be distinguished from the other species of *Edwardsia* that have two types of basitrichs in their nemathybomes (i.e., *E. elegans* Verrill, 1869, *Edwardsia handi* Daly and Ljubenkov, 2008, *E. hantueusis* England, 1987, *E. sulcata* Verrill, 1864). However, the larger type of basitrichs in nemathybomes of those species barely exceed 100 µm and at most 117 µm for *E. handi* (Daly and Ljubenkov, 2008).

Although our specimens clearly align with the description of *E. tuberculata*, this species is distributed only in north Western Europe and there is no record from the Pacific or from the eastern Arctic Ocean. Recognizing that expanding the range so much without intermediate populations or an explanation for the long-distance dispersal is problematic, and pending comprehensive analysis through genetics, I mark our specimens as having an affinity for *E. tuberculata*, rather than assigning that name to them definitively.

(Description, Fig. 49, and part of Table 24 are revised and reprinted Izumi and Fujita [2019] by courtesy of ZOOTAXA.)

Edwardsia kopepe **(Izumi and Fujita, 2018) comb. nov.**

(Japanese name: kopepe-ashinashi-mushimodoki)

Fig. 50; Table 26

Scolanthus kopepe Izumi and Fujita, 2018: 14–19, figs. 5–7

Material examined *Holotype.* NSMT-Co 1613, histological sections, and tissue for DNA analysis, 26 June 2014, Kopepe Seashore, Chichijima

Island, Ogasawara Islands, Tokyo, Japan (27°3'52" N, 142°11'33" E), coral sand at 1 m depth, collected by snorkeling with a shovel and a sieve by Takato Izumi. *Paratypes.* NSMT-Co 1614, dissected tissues, and prepared nematocysts, at same date, place, by same method, and collector as NSMT-Co 1613.; NSMT-Co 1615, prepared nematocysts, at same date, place, by same method, and collector as NSMT-Co 1613.; NSMT-Co 1616, histological sections, and dissected tissues, at same date, place, by same method, and collector as NSMT-Co 1613 ; NSMT-Co 1617, whole specimen, at same date, place, by same method, and collector as NSMT-Co 1613; NSMT-Co 1618, histological sections 21 June 2014, Miyanohama coast, Chichijima Island, Ogasawara Islands, Tokyo, Japan (27°6'18" N, 142°11'39" E), coral sand at 7 m depth, collected by scuba diving with a shovel and a sieve by Takato Izumi.

Description ***External anatomy.*** Column comparatively smooth, ca. 15–25 mm in whole length (25.0 mm in holotype), and 1–2 mm in width (1.8 mm in holotype), naked and extremely long and narrow pipe-like form both in living (Fig. 50A) or fixed specimens. The upper part as narrow as lower part. The most proximal part capitulum, transparent and thin. The remaining part to aboral end of body scapus, with white to pale yellow periderm, and with scattered nemathybome but no papillae. Aboral end a little rounded or tapered, not differentiated from scapus, with nemathybomes (Fig. 50A, I). Tentacles slender, capitated on the tentacle tip, transparent with white patch on each tentacle tip, 1.5–2.0 mm in length, longer than oral disk diameter, but well expanded and contacted. Tentacles 16 in number, in two cycles; eight in inner and eight in outer cycle, same as *Edwardsia*'s arrangement, the inner tentacles shorter than outer ones. Oral disk ca. 1 mm in diameter, white with a brownish red stripe from ventral side to dorsal side. The mouth not swollen.

Internal anatomy. Eight perfect mesenteries, all macrocnemes. Four dorsal and ventral directives, and four lateral mesenteries not paired with other macrocnemes, arranged in normal *Edwardsia* pattern (Fig. 50E). All macrocnemes present along whole length of the body, from oral to aboral end, and bearing retractor and parietal muscles. Retractor muscle of lateral mesenteries all ventrally facing (Fig. 50E). Eight tiny microcnemes, without muscles, only in distal most part. Four microcnemes between dorsal directives and dorso-lateral mesenteries, two between dorso- and ventro-lateral mesenteries, and two between ventro-lateral mesenteries and ventral directives, common arrangement in Edwardsiidae. Each tentacle between either exo- or endocoelic. Each retractor muscle like pennon, diffused, small and weak next to actinopharynx (Fig. 5E) but restricted, comparatively developed, and limited besides gonads in lower part (Fig. 50F, G). Muscle pennons consisting of approximately 2–5 simple muscular processes (Fig. 50G). Parietal muscles of macrocnemes not very distinct (Fig. 50G). Actinopharynx very short, no distinct siphonoglyph (Fig. 50E). Tentacular circular muscle indistinct (Fig. 50C) and longitudinal muscle ectodermal and distinct (Fig. 50D). Marginal sphincter muscle and basilar muscle absent. Mesoglea generally thin in the whole body, a few micrometers even in body wall (Fig. 50E–G, I). Nemathybomes, approximately 100 μm in diameter, protrude from the body wall as their diameter far larger than the thickness of mesoglea. Gonads next the retractor muscles, but no mature gametes in specimens I observed (Fig. 50G).

Cnidom. Spirocysts, basitrichs, microbasic *b*-mastigophores. See Table 26 for size and distribution.

Etymology. Most of the specimens were collected from Kopepe Coast. “Kopepe” is the name of the native people that used to live in the Ogasawara Islands, who had emigrated from the Gilbert Islands, now the Republic of Kiribati. The word “kopepe” is a noun in apposition.

Remarks. In Izumi and Fujita (2018), this species was described as *Scolanthus kopepe*. Genus *Scolanthus* Gosse, 1853 is characterized by aboral ends which do not differentiate into physa, and with nemathybomes and periderms. This genus currently had been included 10 valid species (Table 2; Fautin, 2013; Brandão et al., 2019), including two more species once accommodated within *Isoedwardsia*, which was synonymized to *Scolanthus* in Manuel (1981b). This genus is widely distributed, from tropical (*S. armatus* [Carlgren, 1931]) to subarctic regions (*S. nidarosiensis* [Carlgren, 1942]). No *Scolanthus* species, however, had previously been collected from Japan. In my study, *Scolanthus armatus* and three new species of *Scolanthus* had been reported from Japan, representing the first records of this genus from Japan (Izumi and Fujita, 2018). Consequently, the number of *Scolanthus* species had been 13. However, my recent phylogenetic analysis revealed that *Scolanthus* was polyphyletic and inner group of *Edwardsia* (see Chapter 1F and Figs. 19, 20). So, this article treats the four species I described or re-described as the species *Edwardsia*. However, it was still useful to categorize aboral end with nemathybomes for comparison, so I will compare *E. kopepe* with previous

Scolanthus species for identification (see also description and remarks of *Edwardsia ena* comb. nov., *E. isei* comb. nov., and *E. armata*).

See Table 27 for comparison to the other species which have the characters of previous genus *Scolanthus* (though these species of *Scolanthus* are possibly assignable to the genus *Edwardsia* based on their morphological characteristics, molecular phylogenetic analyses of them have not been carried out. Thus, new combination was not proposed for these species in this study). This species resembles not only *Edwardsia armata* but also *S. scamiti* Daly & Ljubenkov, 2008, *S. triangulus* Daly & Ljubenkov, 2008, *S. curacaoensis* (Pax, 1924), *S. nidarosiensis* (Carlgren, 1942), *S. callimorphus* Gosse, 1853, and *S. cryptics* Brandão, Gusmão and Gomes, 2019 in terms of having 16 tentacles (Gosse 1853, Manuel 1981, England 1987, Daly and Ljubenkov 2008). *Edwardsia kopepe* is similar to *E. armata*, and both are found around the same island. *E. kopepe,* however, is morphologically distinguishable by several points as below: *E. kopepe* is smaller than *E. armata*, one-third to a half in length and one-fifth to one-third in width (the specimen of *E. armata* is even far larger than living *E. kopepe*); *E. kopepe* has brownish red stripe from ventral side to dorsal side on oral disk and white patch on capitated tentacle tip, both features are not present on *E. armata*; the number of muscular processes of both retractor muscles and parietal muscles of *E. kopepe* are far fewer than those of *E. armata* (Figs. 69G, H, 57E, G; England 1987); moreover, the *E. kopepe* holotype has two types of basitrichs in the tentacles, actinopharynx and nemathybomes while *E. armata* has only one type (Table 26). The body of *E. kopepe* is slender and uniform in width (both in living and preserved specimens) while that of *S. scamiti* is stout and increasing in width toward to the aboral end (Daly and Ljubenkov 2008). Besides, the basitrichs in the nemathybomes of *E. kopepe* are two types while those of *S. scamiti* are only one type (Table 26). *Edwardsia kopepe* is 15–25 mm in body length while *S. triangulus* has a maximum body length of 11 mm (Daly and Ljubenkov 2008), smaller than *E. kopepe* Furthermore, basitrichs of *S. triangulus* are over 63 µm (Daly and Ljubenkov 2008; table 3), larger than both types of basitrichs of *E. kopepe*. Basitrichs in the nemathybomes of *S. callimorphus* are of only one type and are over 60 µm in length (Manuel 1981b, p 265), while *E. kopepe* has two types of basitrichs in the nemathybomes and both of them are less than 60 µm in length. *Scolanthus curacaoensis* has far larger body, 45 mm in length (Pax 1924), and has well-developed circumscribed retractor muscles and rounded distinct parietal muscles (Pax 1924; fig. 4, 5) while *E. kopepe* has diffused and undeveloped retractor and indistinct parietal muscle. *Scolanthus nidarosiensis* lives in the deep sea of a cold region (125–150 m depth of Norway; Carlgren 1942) in contrast to *E. kopepe*, which lives in shallow waters in the subtropical region. The retractor muscles of *S. nidarosiensis* are well developed and muscle processes were obviously branching (Carlgren 1942; fig. 71) while those of *E. kopepe* are far less developed with simple processes. Moreover, nemathybomes of *S. nidarosiensis* contain longer basitrichs than the large basitrichs of *E. kopepe*, and *S. nidarosiensis* has only one type of basitrichs (Carlgren 1942) while *E. kopepe* has two types of basitrichs. Finally, *E. kopepe* with two types of basitrichs in nemathybomes can be easily distinguished from *S. kopepe* with one type of basitrichs there. (Description, Fig. 50, and part of Table 26 are revised and reprinted Izumi and Fujita [2018] by courtesy of Zookeys.)

Edwardsia sp. nov. 16

(Japanese name: mino-mushimodoki)

Fig. 51; Table 26

Material examined. (Iz-070), dissected specimen, histological sections, and prepared cnidae, 9 May 2016, off Misaki, Kanagawa Pref. (35°07.080′N, 139°037′E), 370 m depth, collected by Hiroshi Namikawa; (Iz-071), dissected specimen, histological sections, and prepared cnidae, 16 February 2017, off Misaki, Kanagawa Pref. (35°06.921′N, 139°423′E), 150–201 m depth, collected by Takato Izumi.

Description ***External anatomy.*** Column ca. 25 mm in whole length, and ca. 3 mm in distal side and 6 mm in proximal side in width in preserved. Column cylinder-like, with proximal side swollen, divided into capitulum and scapus. The most proximal part capitulum, transparent, divisible mesenterial insertion and jaggy pattern with pale white and reddish orange (Fig. 51B). The remaining part of body scapus, surface of which rough, with brown periderm and weak tenaculi, and attaching sand grains densely. Aboral end not differentiated from scapus: with periderm and sand grain and rounded (Fig. 51A). Nemathybomes invisible from outside of column. Tentacles slender, transparent with white patches, little capitated and opaque on the tip, 3–4 mm in length, longer than oral disk diameter, but well expanded and contacted. Tentacles 16 in number, in two cycles; eight in inner and eight in outer cycle, same as *Edwardsia* arrangement (Fig. 51C), the inner tentacles shorter than outer ones. Oral disk ca. 3 mm in diameter, white with jaggy brownish red stripes. The mouth a little swollen (Fig. 51A).

Internal anatomy. Eight perfect mesenteries, all macrocnemes. Four dorsal and ventral directives, and four lateral mesenteries not-paired with other macrocnemes, arranged in normal *Edwardsia* pattern. All macrocnemes present along whole length of the body, from oral to aboral end, and bearing retractor and parietal muscles. Retractor muscles of lateral mesenteries all ventrally facing (Fig. 51H). Eight tiny microcnemes, without muscles, only in distal most part. Four microcnemes between dorsal directives and dorso-lateral mesenteries, two between dorso- and ventro-lateral mesenteries, and two between ventro-lateral mesenteries and ventral directives, common arrangement in Edwardsiidae. Each tentacle between either exo- or endocoelic. Each retractor muscle like pennon, circumscribed, and distinct. Muscle pennons particular shape: composed of 15–25 slightly a little branched muscular processes, but an extremely, secondly and thirdly branched process at the middle of muscle pennon (Fig. 51I). Parietal muscles of macrocnemes distinct, rounded, with well-branched 5–9 muscular processes (Fig. 51H, I). Actinopharynx short, no distinct siphonoglyph (Fig. 51H). Tentacular circular muscle endodermal and indistinct (Fig. 51E) and longitudinal muscle ectodermal and distinct (Fig. 51D). Marginal sphincter muscle and basilar muscle absent (Fig. 51F). Mesoglea thickest in body wall and actinopharynx, but generally thin mesenteries and tentacle (Fig. 51D–I). Tiny pocket-like structures, considered as trace of nemathybomes, in mesoglea but no nematocysts observed in them (Fig. 51G). Gonads next the retractor muscles, and immature testis observed in the specimen (Fig. 51I).

Cnidom. Basitrichs, spirocysts, microbasic *p*-mastigophores. See Table 26 for size and distribution.

Remarks. Several species of edwardsiid anemones which apparently attaching sand grains on their bodies have been classified in genus *Paraedwardsia*. This genus had included seven species (Table 2; including *Halcampella cretata*, which was turned not to be edwardsiid and renamed in this research; see remarks of *H. cretata*), but I discovered two additional species which should be in this genus. However, according to my phylogenetic analysis, this genus was an inner group of the large clade of *Edwardsia* (Fig.

12). That was why I treated these two anemones as two species of *Edwardsia*, *E.* sp. nov. 16 and *E.* sp. nov. 17. The genus *Paraedwardsia* also should be synonymized into *Edwardsia*. Concurrently, I found the traces of nemathybomes on the surface of *E.* sp. nov., 16 (Fig. 51G). It was the first discovery of nemathybomes in *Paraedwardsia*, which has been said as without nemathybomes (I think that these traces just should be overlooked in the other species of *Paraedwardsia* because they were sometimes invisible from outside and too tiny to observe even on histological sections in old days). Thus, now it is natural to synonymize this genus into *Edwardsia*, which was characterized by the presence of nemathybomes.

See Table 28 for comparison to the other species which have the characters of previous genus *Paraedwardsia* (though these species of *Paraedwardsia* are possibly assignable to the genus *Edwardsia* based on their morphological characteristics, molecular phylogenetic analyses of them have not been carried out. Thus, any new combination was not proposed for these species in this study). *Edwardsia* sp. nov. 16 can be distinguished from each species of *Paraedwardsia* morphologically. *P. heia* Daly and Ljubenkov, 2008 had muscle pennons not in particular shape like *E.* sp. nov. 16. In addition, there were microbasic *p*-mastigophores in actinopharynx of *P. heia* (Daly and Ljubenkov, 2008) while they were absent in actinopharynx of *E.* sp. nov. 16 (Table 26); *P. arenaria* Carlgren, 1905 had strong tenaculi (Carlgren in Nordgaard, 1905; he wrote as “papilla”) on the body wall but *E.* sp. nov. 16 did not; *P. sarsii* (Dueben and Koren, 1847) had 20–30 tentacle in hexamerously arranged (Carlgren, 1921), while *E.* sp. nov. 16 had octamerously arranged 16 tentacles. These three species had been recorded from shallower than 2000 m depth. Other three species, *P. abyssolum* Carlgren, 1951, *P. lemchei* Carlgren, 1956, *P. hadilis* Sanamyan and Sanamyan, 2018, inhabit in completely different depth, abyssal zone (5000–8000 m depth; Carlgren, 1951, 1956, Sanamyan and Sanamyan, 2018).

In addition, traces of nemathybomes never had been discovered in all other species of *Paraedwardsia* (provided that, there is also a possibility that all previous studies could overlooked them at all).

***Edwardsia* sp. nov. 17**

(Japanese name: asaba-mino-mushimodoki)
Fig. 52; Table 26

Material examined. (Iz-072): histological sections, tissues in paraffin, and prepared nematocysts, collected by SCUBA diving on 14 March 2015, at entrance of Moroiso Bay, Misaki, Kanagawa Pref., Japan, 6 m depth, by Hisanori Kotsuka.

Description ***External anatomy.*** Column ca. 25 mm in whole length, and ca. 3 mm in distal side and 6 mm in proximal side in width in preserved. Column lightbulb-like form: proximal side distinctly swollen, divided into capitulum and scapus. The most proximal part capitulum, transparent, divisible mesenterial insertion and jaggy pattern with pale yellow and dark red. The remaining part of body scapus, surface of which rough, with brown periderm and weak tenaculi but without nemathybomes, and attaching sand grains densely. Aboral end not differentiated from scapus: with periderm and sand grain and rounded (Fig. 52A). Tentacles slender, transparent with white patches, little capitated and opaque on the tip, 3–4 mm in length, longer than oral disk diameter, but well expanded and contacted. Tentacles 16 in number, in two cycles; eight in inner and eight in outer cycle, same as *Edwardsia*'s arrangement (Fig. 52B), the inner tentacles shorter than outer ones. Oral disk ca. 3 mm in diameter, white with jaggy brownish red stripes. The mouth not swollen.

Internal anatomy. Eight perfect mesenteries, all macrocnemes. Four dorsal and ventral directives, and four lateral mesenteries not paired with other macrocnemes, arranged in normal *Edwardsia* pattern. All macrocnemes present along whole length of the body, from oral to aboral end, and bearing retractor and parietal muscles. Retractor muscles of lateral mesenteries all ventrally facing (Fig. 52C, E). Eight tiny microcnemes, without muscles, only in distal most part. Four microcnemes between dorsal directives and dorso-lateral mesenteries, two between dorso- and ventro-lateral mesenteries, and two between ventro-lateral mesenteries and ventral directives, common arrangement in Edwardsiidae. Each tentacle between either exo- or endocoelic. Each retractor muscle like pennon, distinct: diffused, comparatively weak next to actinopharynx (Fig. 52C) but strongly circumscribed, comparatively strong, and limited besides gonads in lower part (Fig. 52F). Muscle pennons consisting of approximately 7–11 simple to well-branched processes: processes at the middle of muscle pennon well-branched (Fig. 52E, F). Parietal muscles of macrocnemes indistinct, elongated in direction of mesenteries (Fig. 52F). Actinopharynx short, no distinct siphonoglyph (Fig. 52C). Tentacular longitudinal muscle only distinct in the capitated part, ectodermal, and tentacular circular muscle distinct, endodermal. Mesoglea generally thin in the whole body, thinnest in mesenteries (Fig. 52F). No sphincter and basilar muscle (Fig. 52D, G). No nemathybomes on body wall. Testis next the retractor muscles, and immature sperm there (Fig. 52F).

Cnidom. Basitrichs, microbasic *p*-mastigophores. See Table 26 for size and distribution.

Remarks. See Table 28 for comparison to the other species which have the characters of previous genus *Paraedwardsia* (though these species of *Paraedwardsia* are possibly assignable to the genus *Edwardsia* based on their morphological characteristics, molecular phylogenetic analyses of them have not been carried out. Thus, new combination was not proposed for these species in this study). This species was collected at 6 m depth, this is the shallowest record of species of previous *Paraedwardsia* ever known. Species of Paraedwardsia usually inhabit deeper than 2000 m (Carlgren, 1949, 1951, 1956; Daly and Ljubenkov 2008), and only *Paraedwardsia sarsii* (Dueben and Koren, 1847) was collected shallower than 200 m. *E.* sp. nov. 18 can be distinguished easily from *P. sarsii* by number and arrangement of tentacles: the latter species has 20–30 tentacle in hexamerously arranged (Carlgren, 1921).

Different from *E.* sp. nov. 16, traces of nemathybomes were not observed on the column of *E.* sp. nov. 17. It can be thought that nemathybomes has been completely degenerated on this lineage (see Chapter 3C).

***Edwardsia* sp. nov. 18**

(Japanese name: shihou-mushimodoki-ginchaku)

Fig. 53; Table 26

Material examined. (Iz-073), dissected specimen, histological sections, and prepared cnidae, 18 June 2015, rocky seashore in front of Coastal Branch of Natural History Museum and Institute, Chiba, Katsuura, Chiba Pref., intertidal, collected by Miori Kaneko.

Description ***External anatomy.*** Column ca. 25 mm in whole length, and ca. 1 mm in distal side and 3 mm in proximal side in width in living. Column worm-like, uniform, divided into capitulum, scapulus, scapus and physa. The most proximal part capitulum, whitish opaque, divisible mesenterial insertion. Scapulus between capitulum and scapus, dark red, hemitransparent, divisible mesenterial insertion. Aboral end physa, rounded or tapered, hemitransparent, without periderm or physa. The remaining part of body scapus, covered with flesh periderm, and with scattered tiny nemathybomes (Fig. 53A). Tentacles slender, transparent with white patches, little capitated and opaque on the tip; outer tentacles, ca. 5–7 mm in length, far longer than inner, ca. 3 mm length (Fig. 53B). Both tentacles longer than oral disk diameter, but well expanded and contacted. Tentacles 16 in number, in two cycles; four in inner and twelve in outer cycle, peculiar arrangement in *Edwardsia* (Fig. 53C). Oral disk ca. 2 mm in diameter, white with brown stripes from dorsal to ventral side. The mouth not swollen.

Internal anatomy. Eight perfect mesenteries, all macrocnemes. Four dorsal and ventral directives, and four lateral mesenteries not paired with other macrocnemes, arranged in normal *Edwardsia* pattern. All macrocnemes present along whole length of the body, from oral to aboral end, and bearing retractor and parietal muscles. Retractor muscles of lateral mesenteries all ventrally facing (Fig. 53G, H). Eight tiny microcnemes, without muscles, only in distal most part. Four microcnemes between dorsal directives and dorso-lateral mesenteries, two between dorso- and ventro-lateral mesenteries, and two between ventro-lateral mesenteries and ventral directives, common arrangement in Edwardsiidae. Each tentacle between either exo- or endocoelic. Each retractor muscles like pennon, distinct: diffused, comparatively weak next to actinopharynx (Fig. 53G) but restricted, comparatively strong, and limited besides gonads in lower part (Fig. 53D, H). Muscle pennons consisting of approximately 7–11 simple or a little branched muscular process (Fig. 53D, G). Parietal muscles of macrocnemes indistinct, elongated in direction of mesenteries (Fig. 53D). Actinopharynx short, no distinct siphonoglyph (Fig. 53G). Tentacular longitudinal muscle only distinct in the capitated part, ectodermal (Fig. 53E), and tentacular circular muscle distinct, endodermal (Fig. 53F). Mesoglea generally thin in the whole body, thinnest in mesenteries (Fig. 53D–H). Nemathybomes, far thicker than mesoglea, protruding from it (Fig. 53H). Gonads next retractor muscles, but immature (Fig. 53D).

Cnidom. Basitrichs, microbasic *b*-mastigophores. See Table 26 for size and distribution.

Remarks. There are many species in *Edwardsia* with 16 tentacles, so it is usually difficult to identify 16-tentacles edwardsiids. The 16 tentacles, however, always arranged as two cycle, inner eight and outer eight: this arrangement is so common in *Edwardsia* that it is called as "Edwardsia pattern". In other words, there has been no species which have other arrangement pattern (England, 1987). This anemone had inner 4 and outer 12 tentacle, unequally in number. Edwardsiidae with tentacular cycles of unequal number of tentacles in each cycle was minority: except *Edwardsianthus* species, which have inner five and outer 15 tentacles or inner three and outer seven (*Edwardsia* sp. nov. 14, *E.* sp. nov. 15), there were only a few species which have unequal number of 12 tentacles. So, the inequality of tentacles numbers in each tentacular cycle has been useful to distinguish species: this method was used in *Edwardsia* in 12 tentacles: there were some edwardsiids have 12 tentacles (e.g. *Edwardsia alternobomen* Izumi and Fujita, 2019; Fig. 48A, B), but most species have one cycle of 12 or two cycles of six. On the other hand, *Edwardsia* with inner three and outer nine tentacles were so peculiar that new species *Edwardsia ivelli* diagnosed by this arrangement was established (Manuel, 1981b). As same method, *Edwardsia* sp. nov. 18 with 4+12 tentacular arrangement can be strongly distinguished from the other species.

There was one more particular character in this species: existence of large basitrichs on the tentacles. According to Table 26, tentacles of this species contained nematocysts at least 40 μm in length. However, there has been no species which have basitrichs reach to 40 μm on their tentacles: I had referred all preceding studies which mentioned cnidoms of species of this family (Annandale, 1915; Carlgren, 1921, 1931, 1942, 1943, 1950; Daly and Ljubenkov, 2008; Manuel, 1977a, 1981a, 1981b; England, 1990), but no species of *Edwardsia* had such large basitrichs on tentacles. On the contrary, this species lacks spirocysts on their tentacle while all edwardsiid species had. In conclusion, the cnidom of *E.* sp. nov. 18 also should be a distinct feature of *E.* sp. nov. 18.

Edwardsia sipunculoides **(Stimpson, 1853)**

(Japanese name: hoshi-mushimodoki Uchida, 1965)

Fig. 54; Table 29

Actinia sipunculoides Stimpson, 1853: 7–8.

Edwardsia sipunculoides: Verrill, 1864: 58; Andres, 1883: 307;

Carlgren, 1931: 22–23; Uchida, 1965: 260.

Material examined. NSMT-Co 1700: histological sections, tissues in paraffin, and prepared nematocysts, collected by SCUBA diving on 27 March 2017, in Tokyo Bay off Odaiba, Tokyo Met., Japan, 2 m depth, by Masanori Taru.

Description. ***External anatomy.*** Column of contracted specimen ca. 80 mm in whole length, and ca. 7–8 mm in width in preserved specimen, and ca. 100 mm in length in living, cylinder-like in shape but slightly swollen proximally (Fig. 54A). Body divided into capitulum, scapulus, scapus and physa. Capitulum distinct, yellowish opaque with indistinct dark purple patch, divisible mesenterial insertion. Scapulus short, yellowish opaque. Scapus long, with brown to dark brown thick periderm, and divisible mesenterial insertion as hollowing 8 rows. Nemathybomes small, apparently scattered on scapus (Fig. 54A). Aboral end physa, differentiated from scapus, naked, rounded but a little tapered, without nemathybomes (Fig. 54A). Tentacles uniformly yellowish opaque, with no apparent pattern, 9–12 mm in length, 20 in number, in two cycles (inner 8 and outer 12; Fig. 54B). Oral disk 5 mm in diameter, opaque yellow in color, with discontinuous orange circle (Fig. 54B) and radiated 8 line of perfect mesenteries. Mouth apparently swelled, rugged.

Internal anatomy. Eight perfect mesenteries, macrocnemes, distributed along whole body from distal to proximal end. These eight are the paired dorsal and ventral directives plus four unpaired lateral mesenteries. Twelve tiny microcnemes, without muscles, limited to distal-most part: four between dorsal directives and dorso-lateral mesenteries, four between dorso- and ventro-lateral mesenteries, and four between ventro-lateral mesenteries and ventral directives. All macrocnemic mesenteries bear retractor and parietal muscles. Retractor muscle of each lateral mesentery faces ventrally (Fig. 54E). Each retractor muscle distinctly developed; diffused, with approximately 23–26 simple or slightly branched muscular processes next to actinopharynx (Fig. 54E); diffused muscle side, developed like a pennon, with approximately 18–25 simple or slightly branched muscular processes in lower part (Fig. 54G). Parietal muscles of macrocnemes distinct, elongated to direction of mesenteries, with 4–5 simple or a little branched muscular processes in each side (Fig. 54G). Actinopharynx short, apparently grooved but without distinct siphonoglyph. Each one tentacle in each endo- or exocoel.

Tentacular longitudinal muscle ectodermal and distinct (Fig. 54F), and circular muscle indistinct (Fig. 54C). Marginal sphincter muscle and basilar muscle absent (Fig. 54D). Mesoglea generally thin in mesenteries and tentacles, but quite thick in body wall and thickening part of actinopharynx (Fig. 54E). Nemathybomes protruding from mesoglea on scapus. Gonads on mesenteries between retractor muscles and filaments; gametocytes immature (Fig. 54G).

Cnidom. Spirocysts, basitrichs, microbasic *b*-mastigophores, microbasic *p*-mastigophores, and microbasic amastigophores. See Table 29 for size and distribution.

Remarks. *Edwardsia sipunculoides* (Stephenson, 1853), described with specimens collected from North America, was once reported in Japan (Uchida, 1965). However, this report was only in field guidebook, so this species had not been counted as Japanese Edwardsiidae formally (Yanagi, 2006).

The specimen collected from Tokyo Bay was identified as *E. sipunculoides* by characters described in those references in as below: ca. 12 cm in length and 5 mm in width; 20 yellow tentacles; column with brown periderm, scattered tiny nemathybomes, and 8 hollows on surface; tapered physa; retractor muscles around 30 muscular processes, and only the processes nearby the body wall are well-branched. Moreover, the cnidom was not contradiction from description of Stimpson (1856) and Carlgren (1931). There was a minor difference from description: Carlgren (1931) stated that tentacles were short, but tentacles of my specimen are comparatively slender. However, sea anemones can contract tentacles easily, and tentacles tend to contract during preservation. So, I identified this species as *E. sipunculoides*.

This specimen was collected at the inner place of Tokyo Bay. This species was known to distribute in Pacific coasts of America, but confirmed informally in Japan (Uchida, 1965), so it is not unnatural even if *E. sipunculoides* inhabits in Tokyo Bay. However, I think there is another possibility that this species was brought from North America with ballast water because there are many visiting ships there. Thus, it is necessary to check whether additional specimens are collected from Japan in future or not.

Edwardsia ena **(Izumi and Fujita, 2018) comb. nov.**

(Japanese name: taru-ashinashi-mushimodoki)

Fig. 55; Table 29

Scolanthus ena Izumi and Fujita, 2018: 9–12, figs. 3, 6, 7.

Material examined ***Holotype.*** NSMT-Co 1610. One specimen cut into several parts, histological sections and prepared nematocysts, 17 May 2014, Ena Bay, Kanagawa, Japan, mud in the intertidal zone, collected by wading with a shovel, by Masanori Taru.

Description ***External anatomy.*** Column rough, rugged and uneven, ca. 80 mm in whole length in holotype, and 10–15 mm in width, pipe-like in form both in living (Fig. 55A) and fixed specimen. The most upper part narrower to some extent. The most proximal part of column capitulum, dark brownish semitransparent, and the remaining part to aboral end scapus. The periderm of column orange, with no pattern in color, but thinner on the mesenteries so that the mesenterial line visible through the body wall. Scapus with scattered nemathybomes but no papillae. Aboral end rounded, not differentiated from scapus, with nemathybome (Fig. 55A, H). No pedal disk, but no physa or physa-like structure. Tentacles slender, no acrosphere, brownish, semi-transparent with white patch on each surface (Fig. 55A). Tentacles 20 in number, in two cycles; ten in inner and ten in outer cycle (Fig. 55A), 7.0–10.0 mm in length, longer than oral disk diameter and the inner tentacles shorter than outer ones. Oral disk ca. 5.0 mm in diameter. The mouth swelled and dome-like.

Internal anatomy. Eight perfect mesenteries, all macrocnemes. Four dorsal and ventral directives, and four lateral mesenteries not paired with other macrocnemes (Fig. 55E). All macrocnemes present along whole length of the body, from oral to aboral end and bearing distinct retractor and parietal muscles. Retractor muscles of lateral mesenteries all ventrally facing (Fig. 6B). Twelve tiny microcnemes, without muscles, confirmed only in distal-most part. Four microcnemes between dorsal directives and dorso-lateral mesenteries, four between dorso- and ventro-lateral mesenteries, and four between ventro-lateral mesenteries and ventral directives (Fig. 55E), an unusual arrangement for Edwardsiidae. Each tentacle between either exo- or endocoelic. Each retractor muscle like pennon, restricted throughout the whole body (Fig. 55E, F), comparatively smaller next to actinopharynx but largely developed in lower part, limited to the part next to actinopharynx or filaments of each macrocneme (Fig. 55E, F). Muscle pennons consisting of approximately 30–60 muscular processes, some of which are well-branched into 10 or more branches (Fig. 55F). Parietal muscles with approximately 15 branched muscular processes (Fig. 55F). Actinopharynx short, no distinct siphonoglyph (Fig. 55E). Tentacular circular muscle endodermal (Fig. 55D) and longitudinal muscle ectodermal (Fig. 55C), both distinct. Mesoglea thickest in the aboral end, thick in body wall, approximately 70–120μm thick (Fig. 55B, F, H). However, mesoglea far thinner in actinopharynx and thinnest in mesenteries (Fig. 55E, F). Nemathybomes, around 200 μm in diameter, half buried into mesoglea on the column including the aboral end (Fig. 55G). Marginal sphincter muscle and basilar muscle absent (Fig. 55B, H). Gonads next to retractor muscles, comparatively long (Fig. 55F). Testes in gonads of holotype, between filaments and retractor muscles.

Cnidom. Spirocysts, basitrichs, microbasic *b*-mastigophores, and microbasic *p*-mastigophores. See Table 29 for size and distribution.

Etymology. The species epithet is named after the type locality, Ena Bay. The word “ena” is a noun in apposition.

Remarks. This species was described as *Scolanthus ena* Izumi and Fujita (2019). Thus, see Table 27 for comparison to the other species which have the characters of previous genus *Scolanthus* (though these species of *Scolanthus* are possibly assignable to the genus *Edwardsia* based on their morphological characteristics, molecular phylogenetic analyses of them have not been carried out. Thus, new combination was not proposed for these species in this study). *Edwardsia ena* has 20 tentacles, as do *Scolanthus ignotus* (Carlgren, 1920) and *Edwardsia isei* comb. nov.: the other species of previous *Scolanthus* have 16 tentacles (England 1987, Daly and Ljubenkov 2008, and this study; Table 27). Small and large types of basitrichs in nemathybomes of *E. ena* are far smaller and far larger, respectively, than basitrichs in nemathybomes of *S. ignotus* (Carlgren 1920, England 1987). Moreover, *E. ena* is 80 mm in body length, approximately three to four times longer than the 20–30 mm of *S. ignotus*. *Edwardsia ena* is different from *E. isei* in its tentacular arrangement (*Edwardsia ena* has 10 inner tentacles and 10 outer ones while *E. isei* has 8 inner and 12 outer; see Figs. 62A, 63B), structure of column surface (periderm of *E. ena* does not have trichome-like structures [Fig. 56A] unlike *E. isei*; the nemathybomes of *E. ena* are far sparser than those of *E. isei*), body size (*E. ena* is far larger than *E. isei*), and Cnidom (only *E. ena* has microbasic *b*-mastigophores in their filaments) (see Table 2). In addition, *E. isei* lives in cavities of bare rocks, a different habitat compared to that of *E. ena* (see Remarks of *E. isei*).

This species was one of the largest species in the previous genus *Scolanthus*: all previously reported species of nominal *Scolanthus* have bodies less than 80 mm in length (Gosse 1853, McMurrich 1893, Carlgren 1920, Carlgren 1921, Pax 1924, Carlgren 1931, Carlgren 1942, Daly and Ljubenkov 2008, Brandão et al., 2019).

Despite several sample collection surveyed at Ena Bay, *E. ena* was collected only once, and no specimens have been collected from any other locality. It is said by local people that the environment of Ena Bay has changed from several decades ago; the bottom of bay was previously rocky, and a muddy flat has formed in recent years by inflow of sediment. Considering some *Scolanthus* live in rocky habitats compared to other edwardsiids (e.g. *E. isei*), the primary habitat of *E. ena* might be rocky, and perhaps the numbers of individuals have decreased in Ena Bay by recent rapid changes in the environment. It is difficult, however, to examine this hypothesis because Edwardsiidae sea anemones living in or between rocks often cannot be collected easily even if there are many individuals present.
Even though there is only one specimen of *E. ena*, the character differences from other (previous) *Scolanthus* species make it obvious that this specimen is not a formerly described *Scolanthus* species. Examination of additional specimens in the future may help better delineate this species.
(Description, Fig. 55, and part of Table 29 are revised and reprinted Izumi and Fujita [2018] by courtesy of Zookeys.)

Edwardsia isei **(Izumi and Fujita, 2018) comb. nov.**

(Japanese name: sugashima-gareba-ashinashi-mushimodoki)

Fig. 56; Table 29

Scolanthus isei Izumi and Fujita, 2018: 12–14, figs. 4, 6, 7

Material examined *Holotype.* NSMT-Co 1611. One specimen cut into several parts, histological sections and prepared nematocysts, on 1 August, 2014, Sugashima Island, Mie, Japan (34°29'4" N, 136°52'31" E), cavity of a rock at a depth around 50 cm at low tide, collected by snorkeling by hand, by Yuji Ise. *Paratype*. NSMT-Co 1612. Histological sections, damaged slightly when collected, on 4 August, 2014, Sugashima, Mie, Japan (34°28'51" N, 136°52'46" E), cavity of a rock at a depth around 30 cm at low tide, collected by hand, by Yuji Ise.

Description ***External anatomy.*** Column rough, rugged and uneven, ca. 30 mm in whole length in fixed holotype, and 10–12 mm in width, truncated cone-like form both in living and fixed (Fig. 56A) specimen, comparatively tubby form for edwardsiids. Paratype a little small, ca. 18 mm in length and ca. 9 mm in width. Upper part narrower than lower part. No apparent capitulum, all parts of column uniformly scapus. Periderm brownish or whitish, no pattern in color, with trichome-like structure (Fig. 56A), and easily stripped. Column with highly densely scattered nemathybome but no papillae, and the surface on the mesenteries slightly sunken (Fig. 56A). Aboral end rounded, not differentiated from scapus, with nemathybome. No pedal disk, but no physa or physa-like structure (Fig. 56A, G). Tentacles slender, no acrosphere, completely transparent and white patches or stripes on each surface. Tentacles 20 in number, in two cycles; eight in inner and twelve in outer cycle (Figs 63B), 5.0–7.0 mm in length, longer than oral disk diameter and the inner tentacles shorter than outer ones. Oral disk ca. 4.0 mm in diameter. Mouth not swollen.

Internal anatomy. Eight perfect mesenteries, all macrocnemes. Four dorsal and ventral directives, and four lateral mesenteries not paired with other macrocnemes (Fig. 56G). All macrocnemes present along whole length of the body, from oral to aboral end, and bearing distinct retractor and parietal muscles. Retractor muscle of lateral mesenteries all ventrally facing (Fig. 56G). Twelve tiny microcnemes, without muscles, confined only in distal-most part. Four microcnemes between dorsal directives and dorso-lateral mesenteries, four between dorso- and ventro-lateral mesenteries, and four between ventro-lateral mesenteries and ventral directives, in unusual arrangement for Edwardsiidae. One tentacle each between exocoels and endocoels (Fig. 6C). Retractor muscles like pennons, diffused throughout the whole body, smaller next to the actinopharynx (Fig. 56F), but largely developed and almost integrated to gonads in lower part (Fig. 56G). Each muscle pennons consisting of approximately 20–30 single or slightly branched muscular processes (Fig. 56F, G). Parietal muscles with approximately 15–20 muscular processes (Fig. 56G). Actinopharynx short, no distinct siphonoglyph (Fig. 56F). Both tentacular circular muscle and longitudinal muscle too weakly developed to observe (Fig. 56C, D). Mesoglea thickest in the body wall and aboral end, approximately 200–300 and in some parts over 500 μm thick. However, mesoglea far thinner in actinopharynx and mesenteries (Fig. 56E, F, G), and thinnest in tentacles (Fig. 56C, D). Nemathybomes, around 150 μm in diameter, protruded from body wall (Fig. 56I) in the column but a little buried into the mesoglea in the aboral end (Fig. 56G, J). Marginal sphincter muscle and basilar muscle absent (Fig. 56E, G). Gonads next to retractor muscles, short, and wide (Fig. 56G). Ovary between retractor muscles and filaments, and oocytes in gonads of holotype.

Cnidom. Spirocysts, basitrichs, microbasic *b*-mastigophores, and microbasic *p*-mastigophores. See Table 29 for size and distribution.

Etymology. The species name was named after Yuji Ise, the collector of both holotype and paratype specimens.

Remarks. Same as *E. ena*, this species is originally described as *Scolanthus isei* in Izumi and Fujita (2018), thus see Table 27 for comparison to the other species which have the characters of previous genus *Scolanthus* (though these species of *Scolanthus* are possibly assignable to the genus *Edwardsia* based on their morphological characteristics, molecular phylogenetic analyses of them have not been carried out. Thus, new combination was not proposed for these species in this study). In terms of having 20 tentacles, *Edwardsia isei* resembles *S. ignotus* and *S. ena*, while all other *Scolanthus* edwardsiid species have 16 tentacles (England 1987, Daly and Ljubenkov 2008, and this study). This species is different from *S. ignotus* in having two types of basitrichs of different sizes in nemathybomes (Carlgren 1920), and the larger type is far larger than the basitrichs of *S. ignotus*. The differences between *E. isei* and *E. ena* are principally regarding the tentacular arrangement and body size (see Remarks of *E. ena*).

(Description, Fig. 56, and part of Table 29 are revised and reprinted Izumi and Fujita [2018] by courtesy of Zookeys.)

***Edwardsia* sp. nov. 19**

(Japanese name: hiroshima-mushimodoki-ginchaku)

Fig. 57; Table 29

Material examined. (Iz-074): histological sections, tissues in paraffin, and prepared nematocysts, collected by SCUBA diving on 17 February 2017, in Hiroshima-Bay, Hiroshima Pref., Japan, 5 m depth, by Daisuke Uyeno.

Description. ***External anatomy.*** Column of preserved specimen ca. 35 mm in whole length, and ca. 4 mm in width in preserved specimen, and ca. 50 mm in length in living, worm-like in shape but slightly swollen proximally

(Fig. 57A). Body divided into capitulum, scapus and physa. Capitulum distinct, transparent, and divisible mesenterial insertion. Scapus long, with pale brown periderm, and divisible mesenterial insertion as hollowing 8 rows. Nemathybomes very small, scattered on scapus (Fig. 57A). Aboral end physa, differentiated from scapus, naked, rounded, without nemathybomes (Fig. 57A). Tentacles, 3–5 mm in length, 20 in number, all in same cycles (Fig. 57B). Color pattern of tentacles peculiar: two lateral tentacles white and opaque, but the other 18 transparent and with several transversal white lines. Oral disk ca. 2 mm in diameter, dark brown in color, with particular orange pattern: circle around mouth and two lines connected to two white tentacle (Fig. 57B). Mouth not swelled.

Internal anatomy. Eight perfect mesenteries, macrocnemes, distributed along whole body from distal to proximal end. These eight are the paired dorsal and ventral directives plus four unpaired lateral mesenteries. Twelve tiny microcnemes, without muscles, limited to distal-most part: four between dorsal directives and dorso-lateral mesenteries, four between dorso- and ventro-lateral mesenteries, and four between ventro-lateral mesenteries and ventral directives. All macrocnemic mesenteries bear retractor and parietal muscles. Retractor muscle of each lateral mesentery faces ventrally (Fig. 57F). Each retractor muscle distinctly developed, restricted to side of actinopharynx or filaments: with approximately 13–18 simple to well-branched muscular processes next to actinopharynx (Fig. 57F); muscular processes in lower part developed like a pennon, with approximately 13–16 simple or slightly branched: one process nearest body wall most well-branched (Fig. 57E). Parietal muscles of macrocnemes distinct, triangular, with 2–3 slightly branched muscular processes in each side (Fig. 57E). Actinopharynx short, apparently grooved but without distinct siphonoglyph. Each one tentacle in each endo- or exocoel: the white tentacle in endocoels of second mesenterial pair between dorso- and ventro-lateral mesenteries in first cycle. Tentacular longitudinal muscle ectodermal but indistinct, and circular muscle indistinct (Fig. 57C). Marginal sphincter muscle and basilar muscle absent (Fig. 57C). Mesoglea generally thin in mesenteries and tentacles, but quite thick in body wall and thickening part of actinopharynx (Fig. 57F). Nemathybomes protruding from mesoglea on scapus. Gonads on mesenteries between retractor muscles and filaments; gametocytes immature.

Cnidom. Spirocysts, basitrichs, microbasic *b*-mastigophores, microbasic *p*-mastigophores. See Table 29 for size and distribution.

Remarks. There were few nominal edwardsiids which have 20 tentacles: only four species of *Edwardsia* with 20 tentacles were known in the world: *E. sipunculoides*, *E. kamerunensis* Carlgren, 1927, *E. timida* de Quatrefages, 1842, and *E. finmarchica* Carlgren, 1921. Thus, it was needed to compare them if identify *Edwardsia* with 20 tentacles.

See Table 30 for comparison to the other species of *Edwardsia* with 20 tentacles. *Edwardsia* sp. nov. 19, with 20 tentacles, can be distinguished from them with the features as below: *E. sipunculoides* (12 cm in length; Carlgren, 1931) and *E. timida* (reaching 20 cm in length, and 7 cm even they contracted; Manuel 1977) are the large size species in Edwardsiidae, so *E.* sp. nov. 19 can be distinguished from them easily by its size; tentacular arrangement of *E. finmarchica* is composed of three tentacular rows (Carlgren, 1921) while that of *E.* sp. nov. 19 is of only one row (Fig. 57B). In addition, retractor muscles of *E. finmarchica* is constructed by muscular processes over 50 in number (Carlgren, 1921), so *E.* sp. nov. 19 also can be distinguished by littleness of muscular processes; *E. kamerunensis* is the most resembling described species to *E.* sp. nov. 19, but muscular processes in retractor are over than 30 in number (Carlgren, 1927), far more than this species. Moreover, *E. kamerunensis* was only discovered in tropical zone of Atlantic besides Africa, so there is very little possibility that this edwardsiids inhabits in Japan, the far distant and isolated locality. In conclusion, it is valid to identify *E.* sp. nov. 19 as a new species.

This species had peculiar color pattern in tentacles and oral disc: one tentacle in each left and right side were quite different in color from other tentacles, and an orange line from left to right on oral disc. No edwardsiid described so far has the lateral pattern like *E.* sp. nov. 19 although some anemones have dorsal-ventral pattern (e.g. *Edwardsia alternobomen* Izumi and Fujita, 2019; Fig. 48B). This pattern would be the key character of species, but it is uncertain every individual of this species have this pattern, so collections of additional specimens are expected.

***Edwardsia* sp. nov. 20**

(Japanese name: umihaku-mushimodoki-ginchaku)

Fig. 58; Table 31

Material examined. (Iz-075), dissected specimen, histological sections, and prepared cnidae, 18 June 2015, rocky seashore in front of Coastal Branch of Natural History Museum and Institute, Chiba, Katsuura, Chiba Pref., intertidal, collected by Miori Kaneko.

Description. ***External anatomy.*** Column of preserved specimen ca. 30 mm in whole length, and ca. 5 mm in width in living specimen, and ca. 20 mm in length in preserved, cylinder-like in shape but slightly swollen proximally (Fig. 58A). Body divided into scapulus, scapus and physa. Scapulus distinct, hemitransparent, and divisible mesenterial insertion. Scapus long, with pale brown periderm, and divisible mesenterial insertion as hollowing 8 rows. Nemathybomes comparatively large, in 8 row on scapus (Fig. 58A). Aboral end physa, differentiated from scapus, quite large, naked, rounded, without nemathybomes (Fig. 58A). Tentacles 20 in number, in two cycles; ten in inner and ten in outer cycle (Fig. 58B), both 3.0–4.5 mm in length, as long as oral disk diameter. All tentacles transparent with transversal white bands. Oral disk ca. 4 mm in diameter, dark brown in color, brown circle around mouth (Fig. 58B). Mouth white, not swelled.

Internal anatomy. Eight perfect mesenteries, macrocnemes, distributed along whole body from distal to proximal end. These eight are the paired dorsal and ventral directives plus four unpaired lateral mesenteries. Twelve tiny microcnemes, without muscles, limited to distal-most part: four between dorsal directives and dorso-lateral mesenteries, four between dorso- and ventro-lateral mesenteries, and four between ventro-lateral mesenteries and ventral directives. All macrocnemic mesenteries bear retractor and parietal muscles. Retractor muscle of each lateral mesentery faces ventrally (Fig. 58F). Each retractor muscle distinctly developed, diffused: with approximately 13–20 a little or slightly branched muscular processes next to actinopharynx (Fig. 58E); muscular processes in lower part developed like a pennon, with approximately 10–20 simple to slightly branched (Fig. 58F). Parietal muscles of macrocnemes distinct, triangular, with 6–8 slightly branched muscular processes in each side (Fig. 58E, F). Actinopharynx short, apparently grooved but without distinct siphonoglyph (Fig. 58E). Each one tentacle in each endo- or exo-coel: the white tentacle in endocoels of second mesenterial pair between dorso- and ventro-lateral mesenteries in first cycle. Tentacular longitudinal muscle ectodermal but indistinct, and circular muscle indistinct (Fig. 58C, D). Marginal sphincter muscle and basilar muscle absent (Fig. 58C). Mesoglea generally thin in mesenteries and tentacles, but quite thick in body wall and thickening part of actinopharynx (Fig. 58C–F). Nemathybomes protruding from mesoglea on scapus (Fig. 58E). Gonads on mesenteries between retractor muscles and filaments; matured testis there (Fig. 58G).

Cnidom. Spirocysts, basitrichs, microbasic *b*-mastigophores, microbasic *p*-mastigophores. See Table 31 for size and distribution.

Remarks. By the same logic as *Edwardsia* sp. nov. 19, *E.* sp. nov. 20 is needed to be compared *Edwardsia* with 20 tentacles for identification: *E. sipunculoides*, *E. kamerunensis*, *E. timida*, and *E. finmarchica,* and *E.* sp. nov. 19 itself.

See Table 30 for comparison to the other species of *Edwardsia* with 20 tentacles. *Edwardsia* sp. nov. 20 is distinguished from them in the features as below: *E. sipunculoides* (12 cm in length; Carlgren, 1931) and *E. timida* (reaching 20 cm in length, and 7 cm even they contracted; Manuel 1977) are large size species in Edwardsiidae, so *E.* sp. nov. 20 can be distinguished from them easily; tentacular arrangement of *E. finmarchica* is composed of three tentacular rows (Carlgren, 1921) while that of *E.* sp. nov. 20 is of two rows (Fig. 58B). Retractor muscles of *E. finmarchica* is constructed with muscular processes over 50 in number (Carlgren, 1921), thus, same as *E.* sp. nov. 19, *E.* sp. nov. 20 can be distinguished by littleness of muscular processes; physa of *E. kamerunensis* is very small and contractible (Carlgren, 1927) in contrast to distinctly developed physa of this species. *Edwardsia* sp. nov. 20 can be distinguished from *E.* sp. nov. 19 by nemathybomes in eight rows, lacking microbasic *p*-mastigophores in actinopharynx, and uniform tentacles and oral disc without peculiar pattern of coloration.

Edwardsia sp. nov. 21

(Japanese name: mutsu-mushimodoki-ginchaku)

Fig. 59; Table 31

Edwardsioides sp. Yanagi, 2007: 88, figs. 7, 8

Material examined. CMNH-ZG 04762: histological sections, tissues in paraffin, and prepared nematocysts, collected by wading on 17 June 2007, at intertidal zone of muddy flat next to estuary of Usori River, Mutsu-Bay, Aomori Pref., Japan, by Kensuke Yanagi.

Description. ***External anatomy.*** Column of contracted specimen ca. 30–50 mm in whole length, and ca. 6 mm in width in preserved specimen, and reaching to 60 mm in length in living, cylinder-like in shape (Fig. 59). Body divided into capitulum, scapus and physa. Capitulum distinct, transparent, and divisible mesenterial insertion. Scapus long, with brownish orange periderm, and slightly divisible mesenterial insertion. Nemathybomes comparatively large, opaque white, in 8 rows on scapus (Fig. 59A). Aboral end physa, differentiated from scapus, naked, rounded but a little tapered, without nemathybomes (Fig. 59A). Tentacles hemitransparent, white, with obscure white patterns, 5–7 mm in length, 16 in number, in two cycles (inner 8 and outer 8; Fig. 59B). Oral disk 4–5 mm in diameter, hemitransparent in color, with no pattern but divisible mesenterial insertion. Mouth not swelled.

Internal anatomy. Eight perfect mesenteries, macrocnemes, distributed along whole body from distal to proximal end. These eight are the paired dorsal and ventral directives plus four unpaired lateral mesenteries. Eight tiny microcnemes, without muscles, limited to distal-most part: four between dorsal directives and dorso-lateral mesenteries, two between dorso- and ventro-lateral mesenteries, and two between ventro-lateral mesenteries and ventral directives. All macrocnemic mesenteries bear retractor and parietal muscles. Retractor muscle of each lateral mesentery faces ventrally (Fig. 59D, E). The development of retractor muscles comparatively weak; restricted to actinopharynx side, with less than 10 simple or slightly branched muscular processes next to actinopharynx (Fig. 59F); restricted to filament side, developed like a pennon, with approximately 8–13 simple to well-branched muscular processes in lower part (Fig. 59E). Parietal muscles of macrocnemes distinct, elongated to direction of mesenteries, with 6–8 a little branched muscular processes in each side (Fig. 59G). Actinopharynx short, a little grooved but without distinct siphonoglyph. Each one tentacle in each endo- or exo-coel. Tentacular longitudinal muscle and circular muscle both indistinct (Fig. 59C). Marginal sphincter muscle and basilar muscle absent (Fig. 59C). Mesoglea generally thin among whole body, but comparatively thick in body wall (Fig. 59C–G). Nemathybomes sunk in mesoglea on scapus. Gonads on mesenteries between retractor muscles and filaments; gametocytes immature.

Cnidom. Spirocysts, basitrichs, and microbasic amastigophores. See Table 31 for size and distribution.

Remarks. Genus *Edwardsia* (even before my research) has so many species that identification is difficult in this genus. Yanagi (2007) noticed the possibility of this anemone as an unidentified species, but there had been no conclusion whether this species is unidentified or not.

The characteristic feature of this species is nemathybomes in eight rows with only one type of nematocysts. Nemathybomes with only one type of nematocysts are comparatively minor in Edwardsiidae, thus England (1987) had classified a part of species of *Edwardsia* with only a type of cnidae in nemathybomes into another genus, *Edwardsioides*. According to the list of species of *Edwardsioides* in England (1987), almost all of species of *Edwardsioides* with nemathybomes containing one type of nematocysts had scattered nemathybomes. So, having nemathybomes in eight rows was easily distinguished from them.

See Table 32 for comparison to the other species of *Edwardsia* with nemathybomes containing only one type of nematocysts in eight rows. Only *E. jonesii* Seshaiya and Cutress, 1969 have nemathybomes in eight lows in previous *Edwardsioides* species (England, 1987), but *E.* sp. nov. 21 is easily distinguishable because *E. jonesii* has 12 tentacles (Seshaiya and Cutress, 1956) and living in Indian Sea of tropical zone. In addition, *Edwardsia* sp. nov. 18 and *E.* sp. nov. 19 also have nemathybomes with one type of nematocysts in eight rows. *Edwardsia* sp. nov. 21 can be distinguished from them in tentacular arrangements (Table 32).

Edwardsia sp. nov. 22

(Japanese name: yashiro-mushimodoki-ginchaku)

Fig. 60; Table 31

Material examined. (Iz-076): histological sections, tissues in paraffin, and prepared nematocysts, collected by SCUBA diving on 20 September 2011, in Suo-Oshima Island, Yamaguchi Pref., Japan, 10 m depth, by Takuma Fujii. (Iz-077): dissected specimen, histological sections, and tissues in paraffin, same method, collector and date as (Iz-076).

Description. ***External anatomy.*** Column of ca. 25–35 mm in whole length, and ca. 3–3.5 mm in distal side and ca. 6 – 8 mm in proximal side in width in preserved specimen (Fig. 60A). Column cylinder-like, but distal side apparently swelling. Body divided into capitulum, scapus and physa. Capitulum distinct and divisible mesenterial insertion. Scapus long, with yellowish brown periderm, and slightly divisible mesenterial insertion. Nemathybomes comparatively small, opaque white, scattered on scapus (Fig.

60A). Aboral end physa, differentiated from scapus, naked, rounded but a little tapered, without nemathybomes (Fig. 60). Tentacles blunt, 1–2 mm in length, 20 in number, in two cycles (inner 8 and outer 12; Fig. 60B). Oral disk 3–4 mm in diameter, with no pattern but divisible mesenterial insertion. Mouth obviously swelled.

Internal anatomy. Eight perfect mesenteries, all macrocnemes. Four dorsal and ventral directives, and four lateral mesenteries not paired with other macrocnemes, arranged in normal *Edwardsia* pattern. All macrocnemes present along whole length of the body, from oral to aboral end, and bearing retractor and parietal muscles. Retractor muscle of lateral mesenteries all ventrally facing (Fig. 60E, F). Eight tiny microcnemes, without muscles, only in distal most part (Fig. 60E). Four microcnemes between dorsal directives and dorso-lateral mesenteries, two between dorso- and ventro-lateral mesenteries, and two between ventro-lateral mesenteries and ventral directives, common arrangement in Edwardsiidae. Each tentacle between either exo- or endocoelic. Each retractor muscles like pennon, restricted to filament or actinopharynx side. They indistinct near actinopharynx (Fig. 60E) but a little circumscribed and distinct in lower side (Fig. 60F, G). Muscle pennons consisting of approximately 20–25 slightly or well branched muscular processes (Fig. 60G). Parietal muscles of macrocnemes distinct, elongated in direction of mesenteries, with 8–10 muscular processes (Fig. 60G). The distal muscular processes apparently branched (Fig. 60). Actinopharynx short, a little grooved but without distinct siphonoglyph (Fig. 60E). Each one tentacle in each endo- or exo-coel. Tentacular longitudinal muscle a little distinct and ectodermal (Fig. 60D). Tentacular circular muscle indistinct (Fig. 60C). Marginal sphincter muscle and basilar muscle absent (Fig. 60H). Mesoglea generally thin among whole body, but comparatively thick in body wall (Fig. 60C–H). Nemathybomes sunk in mesoglea on scapus. Gonads ovary, on mesenteries between retractor muscles and filaments, and filled with matured oocytes (Fig. 60G).

Cnidom. Spirocysts, basitrichs, and microbasic *p*-mastigophores. See Table 31 for size and distribution.

Remarks By the same logic as *Edwardsia* sp. nov. 19 and 20, *E.* sp. nov. 22 was needed to be compared with species of *Edwardsia* with 20 tentacles for identification, thus see Table 30 for comparison to the other species of *Edwardsia* with 20 tentacles. *Edwardsia* sp. nov. 22 is far smaller than *E. timida* and *E. sipunculoides* (Carlgren, 1931; Manuel, 1977). *E.* sp. nov. 22 can be distinguished from *E. finmarchica* by tentacles in two rows (see remarks of *E.* sp. nov. 19). *Edwardsia kamerunensis* has only one type of basitrichs in their nemathybomes (Carlgren, 1927; England, 1987) while *E.* sp. nov. 22 has two types (Table 31). This difference was once a key of dividing genera (England 1987; see remarks of *Edwardsia* sp. nov. 21), and even now it should be the key of identification of species though genus *Edwardsioides* was already synonymized into *Edwardsia* (Fautin, 2007).

The most peculiar feature of this species was the arrangement of blunt tapered tentacles. There are few species which has "8+12", inner eight tentacles and outer 12, arrangement. This arrangement is rare in Edwardsiidae: only *Edwardsia pudica*, *E. sipunculoides* and *Edwardsia isei* have this peculiar arrangement (Figs. 39, 54, 56). The inequality of inner and outer tentacles of this species should be a diagnostic character of species (see remarks of *E. isei* and *E.* sp. nov. 18).

Edwardsia sp. nov. 23

(New Japanese name: nise-ashinashi-mushimodoki)

Fig. 61; Table 31

Material examined. (Iz-078): histological sections, tissues in paraffin, and prepared nematocysts, 9 November 2017, by biological dredge during research cruise of R/V Seisui-Maru (No. 1722), off Shima Peninsula, Kumano-nada Sea (Station-7: 34°10.11′N, 136°44.64′E), 130–132 m depth, collected by Itaru Kobayashi; (Iz-079): dissected specimen, 7 October 2015, by biological dredge, off Mie Pref., Japan, 108 m depth, collected during the research cruise of R/V Seisui-Maru (St-2: 34°12.4′N, 136°32.1′E), by Akito Ogawa; (Iz-080): dissected specimen, 7 October 2015, by biological dredge, off Mie Pref., Japan, 155 m depth, collected during the research cruise of R/V Seisui-Maru (St-3: 34°10.8′N, 136°35.7′E), by Akito Ogawa.

Description. ***External anatomy.*** Column of contracted specimen ca. 30–40 mm in whole length, and ca. 4 mm in width in preserved specimen, cylinder-like and uniform in shape (Fig. 61A). Body divided into scapulus, scapus and physa. Capitulum distinct, transparent, and divisible mesenterial insertion. Scapus long, with brown thin periderm in distal side and brownish orange easily stripped periderm in proximal side, and invisible mesenterial insertion. Nemathybomes comparatively small, opaque white, scattered on scapus (Fig. 61A, C). Aboral end physa-like swelled, a little differentiated from scapus, rounded, with dense nemathybomes (Fig. 61C). Tentacles simple and blunt in shape, 3–4 mm in length, 16 in number, in two cycles, coloration uncertain (inner 8 and outer 8; Fig. 61B). Oral disk ca. 3 mm in diameter, divisible mesenterial insertion. Mouth apparently swelled.

Internal anatomy. Eight perfect mesenteries, macrocnemes, distributed along whole body from distal to proximal end. These eight are the paired dorsal and ventral directives plus four unpaired lateral mesenteries (Fig. 61H). Eight tiny microcnemes, without muscles, limited to distal-most part: four between dorsal directives and dorso-lateral mesenteries, two between dorso- and ventro-lateral mesenteries, and two between ventro-lateral mesenteries and ventral directives. All macrocnemic mesenteries bear retractor and parietal muscles. Retractor muscle of each lateral mesentery faces ventrally (Fig. 61H). The development of retractor muscles distinct; restricted in the middle of macrocnemes (Fig. 61G, H), with 8–14 simple to slightly branched muscular processes: a process next to actinopharynx well-branched (Fig. 61G, H). Parietal muscles of macrocnemes distinct, elongated to direction of mesenteries, with 6–8 a little branched muscular processes in each side (Fig. 6G). Actinopharynx short, a little grooved but with distinct siphonoglyph (Fig. 61H). Each one tentacle in each endo- or exo-coel. Tentacular longitudinal muscle distinct, ectodermal (Fig. 61E) and circular muscle distinct, (Fig. 61F). Marginal sphincter muscle and basilar muscle absent (Fig. 61D, I). Mesoglea generally thin among whole body, but comparatively thick in body wall and aboral end (Fig. 61D–I). Nemathybomes sunk in mesoglea on scapus (Fig. 61I). Gonads on mesenteries between retractor muscles and filaments; gametocytes immature (Fig. 61G).

Cnidom. Spirocysts, basitrichs, microbasic *p*-mastigophores, microbasic *b*-mastigophores, and microbasic amastigophores. See Table 31 for size and distribution.

Remarks. This species has peculiar morphologies: physa-like swelled aboral endwith many nemathybomes. The former character was same as *Edwardsia*, but the latter was similar to *Scolanthus.* In 2019, Brandão et al. (2019) described genus *Isoscolanthus*. This genus was characterized by physa-like aboral ends with nemathybomes, thus this species completely corresponded to the diagnosis. In addition, the features of these anemones that one siphonoglyph and robust basitrichs (Brandão et al. [2019] called this type of nematocysts as pterotrichs) in nemathybomes were shared with *Isoscolanthus* species. So, it was needed to compare two *Isoscolanthus* species in Brandão (2019) when identifying this sea anemone.

See Table 33 for comparison to the other species which have the characters of previous genus *Isoscolanthus* (though these species of *Isoscolanthus* are possibly assignable to the genus *Edwardsia* based on their morphological characteristics, molecular phylogenetic analyses of them have not been carried out. Thus, new combination was not proposed for these species in this study). This species can be distinguished from the other species by features as below: *Edwardsia* sp. nov. 23 has 16 tentacles while two *Isoscolanthus* edwardsiids have 12 tentacles; basitrichs of nemathybomes of the two *Isoscolanthus* species are far smaller than *Edwardsia* sp. nov. 23 (the maximum size of both *Isoscolanthus* species were even smaller than the minimum size of *E.* sp. nov. 23; Brandão et al., 2019). Now *Isoscolanthus* species has been only discovered in Atlantic coast of Brazil (Brandão et al., 2019), too separated area from Japan, thus it is the first discovery of species of *Isoscolanthus* from the Pacific.

According to my phylogenetic analyses, it was revealed that *Isoscolanthus* was also an ingroup of *Edwardsia* (Fig. 12) and so should be synonymized into it (Fig. 13). So, I finally treat this species as a new species of the genus *Edwardsia*.

Edwardsia armata **Carlgren, 1931**

(Japanese name: Ogasawara-ashinashi-mushimodoki)

Fig. 62; Table 34

Edwardsia armata Carlgren, 1931: 2, figs 1–2; Carlgren 1949: 24

Scolanthus armatus: England 1987: 229, figs 13–14; Izumi and Fujita, 2018: 5–9, fig. 2

Material examined. NSMT-Co 1609, histological sections, dissected tissues, tissues embedded in paraffin, and prepared nematocysts, 27 June 2014, Seihyo Coast (Fig. 1A–2), Chichijima Island, Ogasawara Islands, Tokyo, Japan (27°09'47"N, 142°20'26"E), coral sand, 3 m depth, collected by scuba diving with a shovel and a sieve, by Takato Izumi.

Description. ***External anatomy.*** Column rough, ca. 35–40 mm in whole length, and ca. 4–8 mm in width, worm-like form, and the proximal part narrower to some extent. The column consists of capitulum, scapulus and scapus. The most proximal part of column capitulum, distinct, extremely short, whitish and semitransparent, but scapulus and scapus indistinct. The periderm-like cuticle, brownish orange with no pattern in color, covering the whole column except capitulum and tentacle but easily stripped off from epidermis (Fig. 62A). The scapus beneath periderm semitransparent, with scattered small prominent nemathybomes but no papillae (Fig. 62A). Aboral end of the column tapered or flattened, not differentiated from scapus, with scattered nemathybomes (Fig. 62A). No pedal disk, and no physa or physa-like structure. Tentacles in two cycles, 16 in number, eight in inner and eight in outer cycle. All tentacles long and slender, 1.5–2.0 mm in length (Fig. 6B), the inner tentacles as long as outer ones, transparent or semi-transparent, and capitated on their tip (Fig. 62B). Oral disk ca. 1.5 mm in diameter.

Internal anatomy. Eight perfect mesenteries, all macrocnemes. Four dorsal and ventral directives, and four lateral mesenteries not paired with other macrocnemes, arranged in normal *Edwardsia* pattern. All macrocnemes present along whole length of the body from oral to aboral end and bearing distinct retractor and parietal muscles. Retractor muscle of lateral mesenteries all ventrally facing. Eight tiny microcnemes, without muscles, confined only in distal-most part. Four microcnemes between dorsal directives and dorso-lateral mesenteries, two between dorso-and ventro-lateral mesenteries, and two between ventro-lateral mesenteries and ventral directives. Each tentacle between either exo- or endocoelic. Retractor muscles strongly developed and diffused (Fig. 62F–H), pennon-like, configured with 15–30 muscular processes, each slightly branched (Fig. 62F). Parietal muscles with approximately 10 muscular processes (Fig. 62F). Actinopharynx short, ca. 2.5 mm in length, no distinct siphonoglyph (Fig. 62C). Tentacular circular muscle indistinct (Fig. 62D) and longitudinal muscle ectodermal and distinct (Fig. 62E). Mesoglea thin in the whole body, less than 100 µm even at the thickest part of body wall (Fig. 62C–I). Nemathybomes, ca. 100 µm in diameter, protrude from mesoglea on the column including the aboral end (Fig. 62I). Marginal sphincter muscle and basilar muscle absent (Fig. 62C, H). Gonads adjacent to the retractor muscles, relatively long (Fig. 62H). Testes between filaments and retractor muscles.

Cnidom. Basitrichs, spirocysts, microbasic *b*-mastigophores. See Table 34 for size and distribution.

Remarks. *Edwardsia armata* Carlgren, 1931 had been known as

Scolanthus armatus before this research. This species was originally described by Carlgren (1931) as *Edwardsia armata* when the genus *Scolanthus* was a junior synonym of *Edwardsia* (see remarks of *Edwardsia kopepe*). After *Scolanthus* was revived by Manuel (1981), this species was transferred to *Scolanthus* by England (1987). This species had no physa-like structure but many nemathybomes in the aboral end. This is the most characteristic feature of *Scolanthus,* and this feature is not found in *Edwardsia*. The specimen from the Ogasawara (Bonin) Islands almost completely agrees with the description of *Scolanthus armatus* in England (1987); e.g. 16 tentacles which are capitated on the tip; rounded or flattened aboral end; scattered nemathybomes extending to the proximal end; strong and diffused retractor muscles (slightly branched muscular processes also correspond to England, 1987; fig. 13). The proportion and size of body is also similar to England's description. There are, however, a few differences in the cnidom; England (1987) mentioned nothing about *b*-mastigophores in the description; stating that basitrichs and microbasic *b*-mastigophores could be distinguished by both the large diameter of the capsule and the broadened shaft shape (England, 1991). However, both cnidom are still easily confused and they are difficult to delineate. Thus, microbasic *b*-mastigophores with their broadened shape were judged by England (1987) to probably be basitrichs. This probability is reinforced by England (1987: table 6): two types of "basitrichs" in filament of *S. armatus*, but one type of basitrichs with apparently broader capsules than the other type while the lengths are not different. In addition, there are very long basitrichs in our specimen, but they are few in number. If the numbers of these long basitrichs are very low, it is possible that England (1987) did not observe them. Moreover, the other cnidae size ranges resemble those of specimens of England (1987).

In conclusion, I had identified this specimen as *S. armatus* because of its similarity in almost all morphological features to the original description of the species. The slight difference observed in the Cnidom may be simply individual variation.

However, receiving phylogenetic study, I revealed that species of Edwardsiidae which had included *Scolanthus* should be synonymized into *Edwardsia*. So, this species is also reclassified to this genus, and so renamed to the original name of *Edwardsia armata*.

(Description, Fig. 62, and part of Table 34 are revised and reprinted Izumi and Fujita [2018] by courtesy of Zookeys.)

Edwardsia sp. nov. 24

(New Japanese name: juzu-mushimodoki-ginchaku)

Fig. 63; Table 34

Material examined. CMNH-ZG (no registration): histological sections, tissues in paraffin, and prepared nematocysts, collected by wading on 12 March 2012, from the intertidal zone of Nomino-Ura, Kakeroma Island, Kagoshima Pref., Japan, by Masanori Sato.

Description. ***External anatomy.*** Column comparatively smooth, ca. 70 mm in whole length, and ca. 6 mm in width, slender worm-like form, and the proximal part narrower to some extent. The column consisting of physa and scapus. The differentiation of most proximal part of column unknown because of contraction. Scapus with periderm-like cuticle, brown in color (Fig. 63A), and partly covered with tiny black glandular materials: totally appearing stripe pattern in longitudinal direction of brown and black. Nemathybomes protruding from scapus and periderm, connecting with each other in moniliform or anastomosing, appearing rosary or net-like (Fig. 63B). Aboral end physa, rounded, differentiated from scapus, without nemathybomes, no pedal disk (Fig. 63A, E). Tentacles in two cycles, 20 in number, but length and color unknown because of shrinking. Oral disk diameter unknown.

Internal anatomy. Eight perfect mesenteries, all macrocnemes. Four dorsal and ventral directives, and four lateral mesenteries not paired with other macrocnemes, arranged in normal *Edwardsia* pattern (Fig. 63C, D). All macrocnemes present along whole length of the body from oral to aboral end and bearing distinct retractor and parietal muscles. Retractor muscle of lateral mesenteries all ventrally facing. Twelve tiny microcnemes, without muscles, confined only in distal-most part. Four microcnemes between dorsal directives and dorso-lateral mesenteries, four between dorso-and ventro-lateral mesenteries, and four between ventro-lateral mesenteries and ventral directives. Each tentacle between either exo- or endocoelic. Retractor muscles strongly developed and diffused (Fig. 63C, D, G), pennon-like, configured with 70–90 muscular processes, simple to slightly branched except the well-branched process nearest to body wall (Fig. 63G). Parietal muscles rounded and elongated to direction of mesenteries, with approximately 8–10 slightly branched muscular processes (Fig. 63F). Actinopharynx short, no distinct siphonoglyph. Tentacular circular muscle and longitudinal muscle indistinct. Mesoglea thickest in body wall, over 200 µm in thickness in some part (Fig. 63E, F), but far thinner in mesenteries (Fig. 63C, D, F, G). Nemathybomes, protruding from mesoglea but also sunk into mesoglea (Fig. 63C, D). Marginal sphincter muscle and basilar muscle absent. Gonads adjacent to the retractor muscles, relatively long (Fig. 63G), in which immature gametes.

Cnidom. Basitrichs, microbasic *b*-mastigophores and microbasic *p*-mastigophores. See Table 34 for size and distribution.

Remarks. It was impossible to perform phylogenetic analysis of *Edwardsia* sp. nov. 24 and *E.* sp. nov. 25 because these specimen were wholly preserved formalin. However, these species had completely same arrangement of previous genus *Edwardsianthus*, thus it was likely that these species are related to species of previous *Edwardsianthus*.

See Table22 for comparison of *Edwardsia* sp. nov. 24 and the other species which have the characters of previous genus *Edwardsianthus*. This anemone has nemathybomes which concatenated each other and looks like moniliform or anastomosing. Nemathybomes of every species of edwardsiids are independent each other no matter how densely distributed. Thus, this exceptional arrangement of nemathybomes cannot evaluate whether “in rows” or “scattered”. That was why this character strongly became the identity of this species.

This anemone was only once collected from intertidal zone Nomino-Ura of Kakeroma Island, Amami Islands, contaminated with other species of *Edwardsia* spp. (still unidentified, but several species would be included). Masanori Sato, the collector of these anemones, said that anemones of Edwardsiidae were densely distributed in Nomino-Ura (over 100 individuals per square meter), but there was no anemone there I went Nomino-Ura for collection in 2015. Local people said that several sediment runoffs were occurred in 2014 in Kakeroma Island because of heavy rain, so perhaps the locality of this species destructed, and anemones disappeared.

Edwardsia **sp. nov. 25**

(New Japanese name: yangu-kon-isoginchaku)

Fig. 64; Table 34

Material examined. CMNH-ZG (no registration): histological sections, tissues in paraffin, and prepared nematocysts, collected by SCUBA diving on

18 March 1998, off Suzaki, Chichijima Island, Ogasawara Islands, Tokyo Met., Japan, 3 m depth, by Hiroyuki Tachikawa.

Description. ***External anatomy.*** Column, ca. 100 mm in whole length, and ca. 7 mm in width in preserved specimen, slender worm-like form, and the proximal part narrower to some extent. The column consisting of physa, scapus and scapulus. The distal-most part scapulus, very short, without nemathybomes. Scapus with periderm-like cuticle, brownish yellow in color, and with dense papillae-like protruding (Fig. 64A, B): a nemathybome at the top of which. Nemathybomes small and densely scattered (Fig. 64B). Aboral end physa, the column rounded, differentiated from scapus, without nemathybomes, no pedal disk but attaching small stones (Fig. 64A). Tentacles 20 in number in two cycle: inner tentacle 5 and outer 15, short and blunt, without acrospheres. Color of them in living unknown. Mouth in oral disc swollen, but how it swollen is unclear because actinopharynx inverting in the specimen.

Internal anatomy. Eight perfect mesenteries, all macrocnemes. Four dorsal and ventral directives, and four lateral mesenteries not paired with other macrocnemes, arranged in normal *Edwardsia* pattern (Fig. 64D). All macrocnemes present along whole length of the body from oral to aboral end and bearing distinct retractor and parietal muscles. Retractor muscle of lateral mesenteries all ventrally facing. Twelve tiny microcnemes, without muscles, confined only in distal-most part. Four microcnemes between dorsal directives and dorso-lateral mesenteries, four between dorso-and ventro-lateral mesenteries, and four between ventro-lateral mesenteries and ventral directives. Each tentacle between either exo- or endocoelic. Retractor muscles strongly developed and diffused (Fig. 64F), pennon-like, configured with 60–80 muscular processes, slightly to well, sometimes complicatedly branched. The process nearest to body wall most branched well, secondly and thirdly (Fig. 64F). Parietal muscles apparently elongated to direction of mesenteries, with approximately 20 simple to slightly branched muscular processes in each side (Fig. 64F). Existence of siphonoglyph unknown because of inverting. Tentacular circular muscle and longitudinal muscle indistinct. Mesoglea thickest in body wall, over 500 μm in thickness in some part (Fig. 64C, D), and comparatively thick in tentacles and parietal muscles (Fig. 64C), but thinner in mesenteries (Fig. 64F). Nemathybomes completely sunk into mesoglea of papillae-like protruding (Fig. 64D, E). Marginal sphincter muscle and basilar muscle absent (Fig. 64G). Gonads adjacent to the retractor muscles, relatively short (Fig. 64F), in which immature testis.

Cnidom. Basitrichs, spirocysts, microbasic *b*-mastigophores, and microbasic amastigophores. See Table 34 for size and distribution.

Remarks. *Edwardsia* sp. nov. 25 was collected from Ogasawara only once. The most characteristic feature of this anemone is apparently protruding structures like papillae on the body wall and small nemathybomes at the top of the papillae. There are several species whose nemathybomes protruding (e.g. *E.* aff. *tuberculata*), but this species is clearly distinct from them because body wall itself protrudes from column like papillae. This character is similar to genus *Halcampogeton* rather than *Edwardsia*. However, the structures of *E.* sp. nov. 25 are apparently different from *Halcampogeton* in terms of existing nemathybomes at the tips of them. So, this species can be distinguished from any other *Edwardsia* with the character of column.

See Table22 for comparison of *Edwardsia* sp. nov. 25 and the other species which have the characters of previous genus *Edwardsianthus.* This species has tentacular and mesenterial arrangement of *Edwardsianthus*. However, because the only specimen was wholly preserved in formalin, the certain clade to which this species belong is unknown.

Edwardsia sp. nov. 26

(New Japanese name: denkyu-mushimodoki-ginchaku)

Fig. 65; Table 34

Material examined. (Iz-081): dissected specimen in paraffin, histological sections, and prepared cnidae, collected on 7 September 2010, South-Tosa-Bae, off. Kochi Pref., (32°56.4′N, 134°34.9′E), 897 m depth, collected during researching voyage of R/V Soyo-Maru by Masanori Okanishi.

External anatomy. Column of contracted specimen 20 mm in whole length, and 5 mm in distal side and 10 mm in proximal side in width in preserved, cylinder-like form but exceedingly swelled in aboral side: lightbulb-like shape in whole specimen (Fig. 65A). Body divided into scapus and physa; in my specimen, capitulum shrunken in column, invisible. Scapus with thick periderm and densely scattered tiny nemathybomes, brownish yellow in color. Aboral physa differentiated from scapus, exceedingly swelled but tapered in aboral end, with thin fragile periderm, with sparse nemathybomes (Fig. 65A). Tentacles 16 in number, but shape, color or relative size of them unclear because tentacles contracted into scapus (Fig. 65B).

Internal anatomy. Eight perfect mesenteries, macrocnemes, distributed along whole body from distal to proximal end. These eight are the paired dorsal and ventral directives plus four unpaired lateral mesenteries (Fig. 65C). Eight tiny microcnemes, without muscles, limited to distal-most part: four between dorsal directives and dorso-lateral mesenteries, two between dorso- and ventro-lateral mesenteries, and two between ventro-lateral mesenteries and ventral directives. All macrocnemic mesenteries bear retractor and parietal muscles. Retractor muscle of each lateral mesentery faces ventrally (Fig. 65C, F). Each retractor muscle distinctly developed and circumscribed, with approximately 10–15 slightly branched and well folded muscular processes (Fig. 65E). Parietal muscles of macrocnemes quite distinct, spade-like shape, with 8–13 slightly branched muscular processes in each side (Fig. 65E, F). Actinopharynx very short, without distinct siphonoglyph (Fig. 65D). One tentacle in each endo- or exo-coel. Tentacular longitudinal muscle ectodermal and distinct. Marginal sphincter muscle and basilar muscle absent (Fig. 65G). Mesoglea generally thin in mesenteries and tentacles, but comparatively thick in physa (Fig. 65G), and the thickest in column (Fig. 65C, D). Nemathybomes sunk in mesoglea (Fig. 65C, D, G). Gonads on mesenteries between retractor muscles and filaments, immature testis there (Fig. 65E).

Cnidom. Basitrichs and microbasic *p*-mastigophores. See Table 34 for size and distribution.

Remarks. In 2019, Brandão et al (2019) established genus *Isoscolanthus* Brandão, Gusmão and Gomes, 2019 with two new species collected from Brazil. The characters of this specimen exactly corresponded to the diagnosis of this genus, especially a physa-like structure with nemathybomes at its proximal end. Thus, now this species may belong to previous genus *Isoscolanthus*. Following my classification, however, all edwardsiids which have nemathybomes should be classified in *Edwardsia*, so this species should be *Edwardsia* sp. nov. 26, even though DNA could not be extracted from this specimen at all because the whole body was preserved in formalin solution.

See Table 33 for comparison to the other species which have the characters of previous genus *Isoscolanthus* (though these species of

Isoscolanthus are possibly assignable to the genus *Edwardsia* based on their morphological characteristics, molecular phylogenetic analyses of them have not been carried out. Thus, new combination was not proposed for these species in this study). This species can be distinguished from two species of *Isoscolanthus* described in Brandao et al. (2019) by having 16 tentacles and from *Edwardsia* sp. 23 by the apparently swelled physa-like aboral end.

SAMMARY of Edwardsioidea

According to my phylogenetic and taxonomic researches, these conclusions were derived.

1. Edwardsiidae was monophyletic and should be remained as the only family in this superfamily.
2. Five genera, *Edwardsia, Edwardsianthus, Scolanthus, Isoscolanthus* and *Paraedwardsia* were synonymized to one gigantic genus *Edwardsia*, which is characterized by nemathybomes on the body walls (including traces of them) and accommodates almost all species of Edwardsiidae. On the other hand, six other genera can be retained because they are distinguished morphologically from *Edwardsia* and each other.
3. In *Edwardsia*, there were five small subclades. Though the genus *Edwardsianthus* formed one subclade by itself, *Scolanthus, Isoscolanthus* and *Paraedwardsia* were dispersed to several subclades and mingled with species of *Edwardsia*.
4. As a consequence of my study, the record of Japanese edwardsioidean anemones drastically increased. I discovered additional six genera (including three genera which were synonymized into *Edwardsia* in this research), two newly recorded species, and 27 new species from Japan. Taking my results of phylogenetic analysis in consideration, Japanese species of Edwardsioidea finally increased from 10 species in four genera to 36 species in five genera.

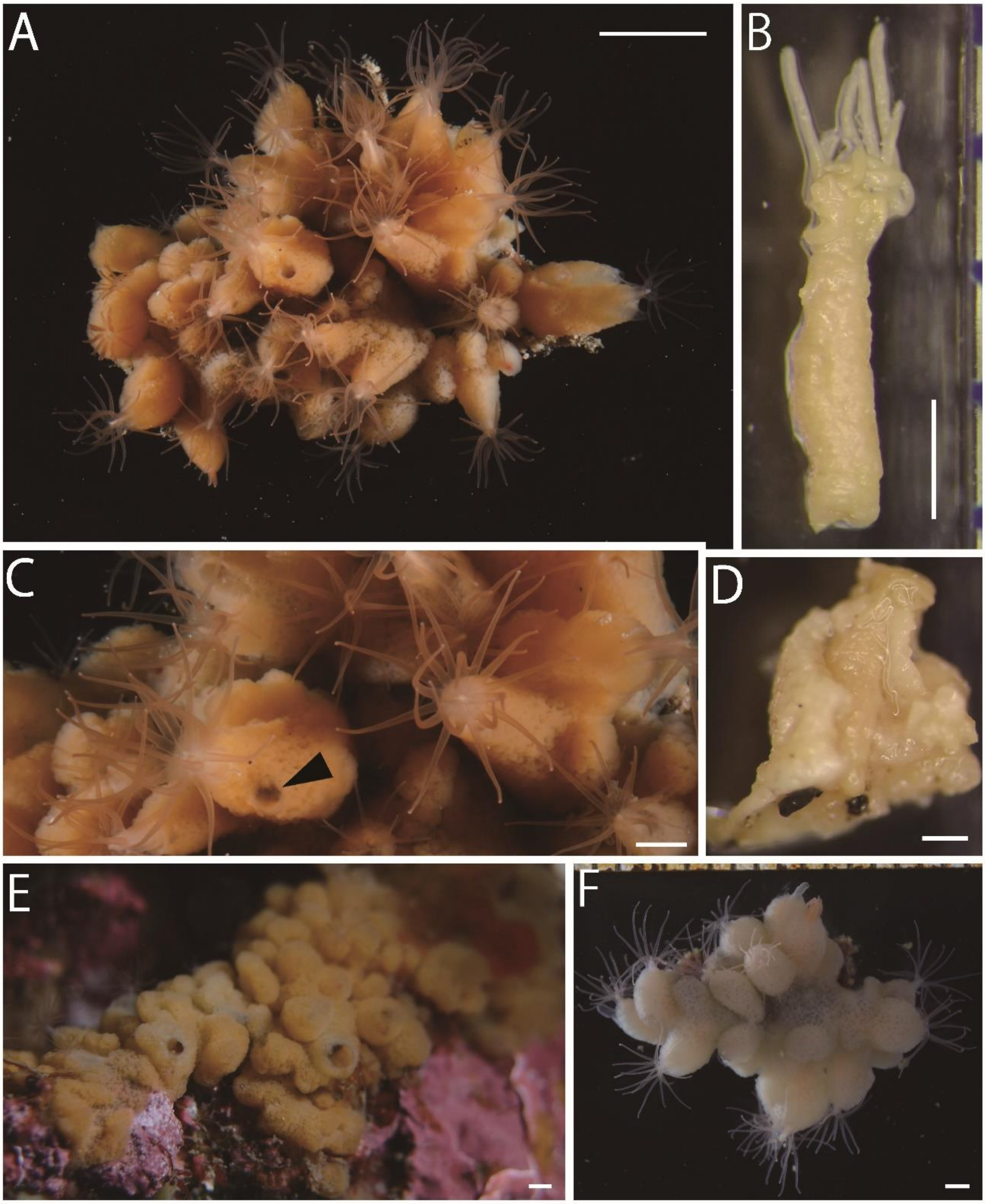

Fig. 32. External morphology of *Tempuractis rinkai* and its host sponge *Oscarella* sp. A, C, E, and F: living colony of *T. rinkai* A, B, C, and D: specimens collected from Misaki, Kanagawa. A. A living colony of *T. rinkai* with *Oscarella* sp., including a holotype (NSMT-Co 1573) and four paratypes (CMNH-ZG 08969 to 08972). B. Excised and preserved *T. rinkai* specimen (NSMT-Co 1573) with elongated tentacles. C. *T. rinkai* living in a bunch-like part of *Oscarella* sp. Arrowhead indicates the oscular opening of the host sponge. D. Dissected host sponge, showing whole body of a *T. rinkai* specimen (NSMT-Co 1573) with shrunken tentacles that was totally buried in the host sponge. E. Field image of *Oscarella* sp. collected from Shukunegi, Sado, Niigata. Numerous *T. rinkai* are buried in the sponge, including paratype CMNH-ZG 08973. F. Living colony of *T. rinkai*, including paratype CMNH-ZG 08974, collected from Tohama, Toba, Mie. All scale bars represent 1 mm. Pictures A, C, E were taken by Yuji Ise.

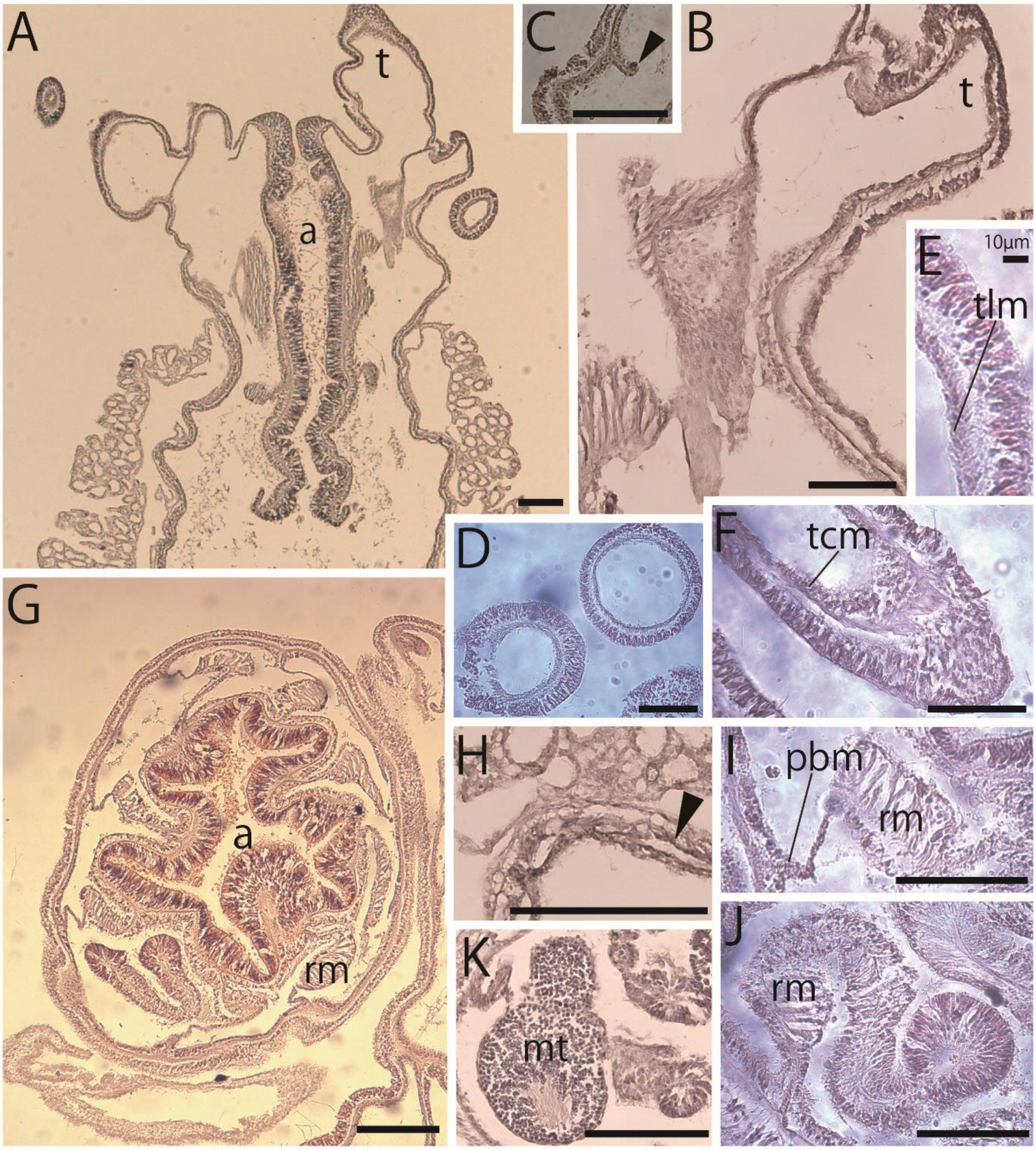

Fig. 33. Internal anatomy of *Tempuractis rinkai.*
A, B: paratype CMNH-ZG 08971. C–J: paratype CMNH-ZG 08972. K: specimen CMNH-ZG 08973. A. Longitudinal section. B. Enlarged view of the longitudinal section, showing absence of sphincter muscle. C. Transverse section of a microcneme (arrowhead). D. Transverse section of the tentacles. E. Enlarged view of the tentacle transverse section. F. Longitudinal section of a tentacle tip. G. Longitudinal section of column, showing eight macrocnemes and no microcnemes at the actinopharynx. H. Longitudinal section of *T. rinkai* adhered to the inner surface of the sponge (arrowhead). I. Macrocnemes and retractor muscle at the actinopharynx. J. Macrocnemes in the gastral cavity. K. Longitudinal section of a macrocneme, showing retractor muscle and gonad (mature testis) with mature sperm cells. Abbreviations: a, actinopharynx; mt, matured testis cyst; pbm, parietal basilar muscle; rm, retractor muscle; t, tentacle; tcm, tentacular circular muscle; tlm, tentacular longitudinal muscle. All scale bars represent 100 µm unless otherwise noted.

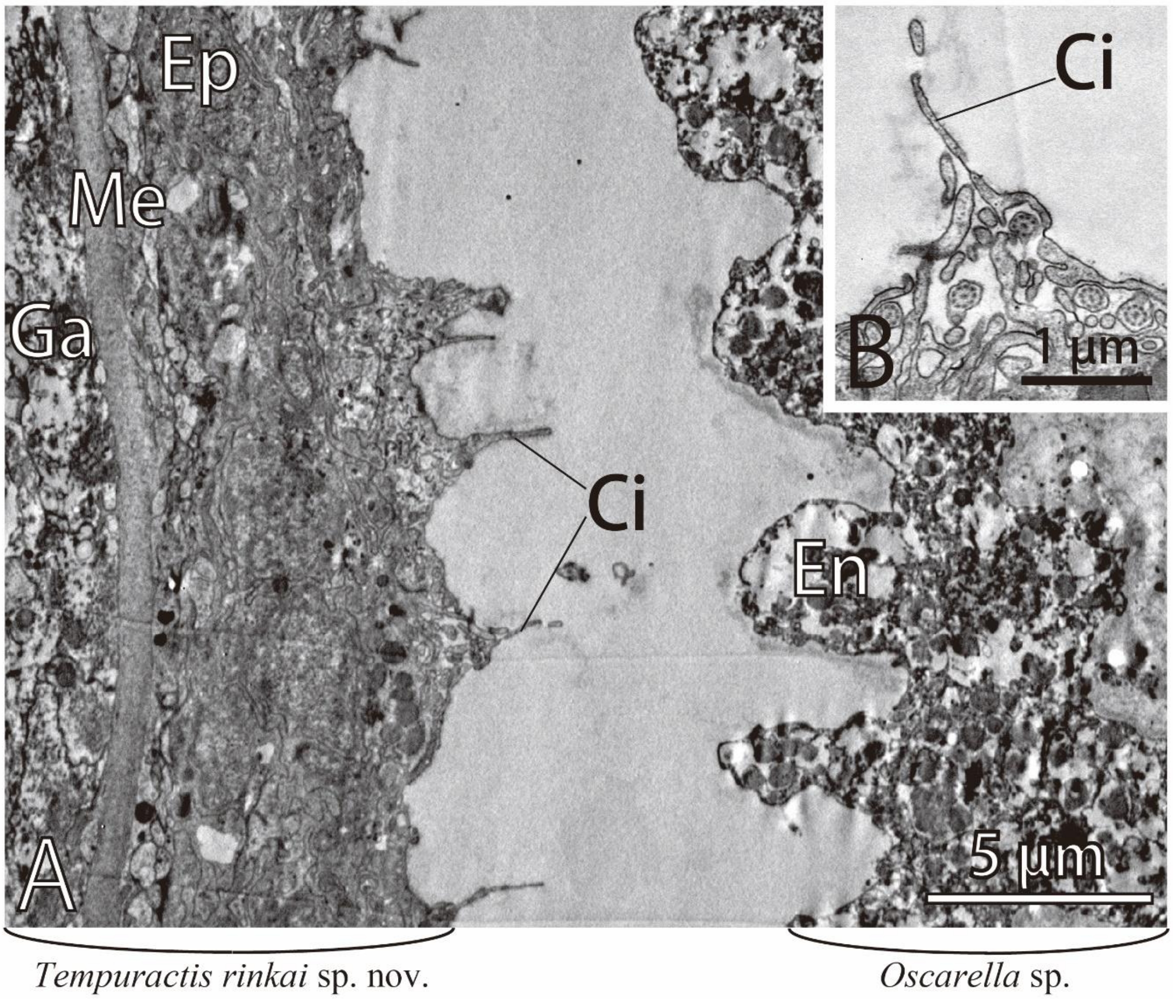

Fig. 34. The images of sections between *Tempuractis rinkai* and *Oscarella* sp. obtained by transmission electron microscope (TEM).
A. Structure between the sea anemone and the sponge. The obtruding cilia of the sea anemone are corresponding to the sites of depression of endopinacocytes of the sponge; B. Enlarged view of the obtruding cilia of sea anemone. Several cilia are twisting around each other. Abbreviations: Ci, cilia; En, endopinacocyte of *Oscarella* sp.; Ep, epidermis of *T. rinkai*; Ga, gastrodermis of *T. rinkai*; Me, mesoglea of *T. rinkai*.

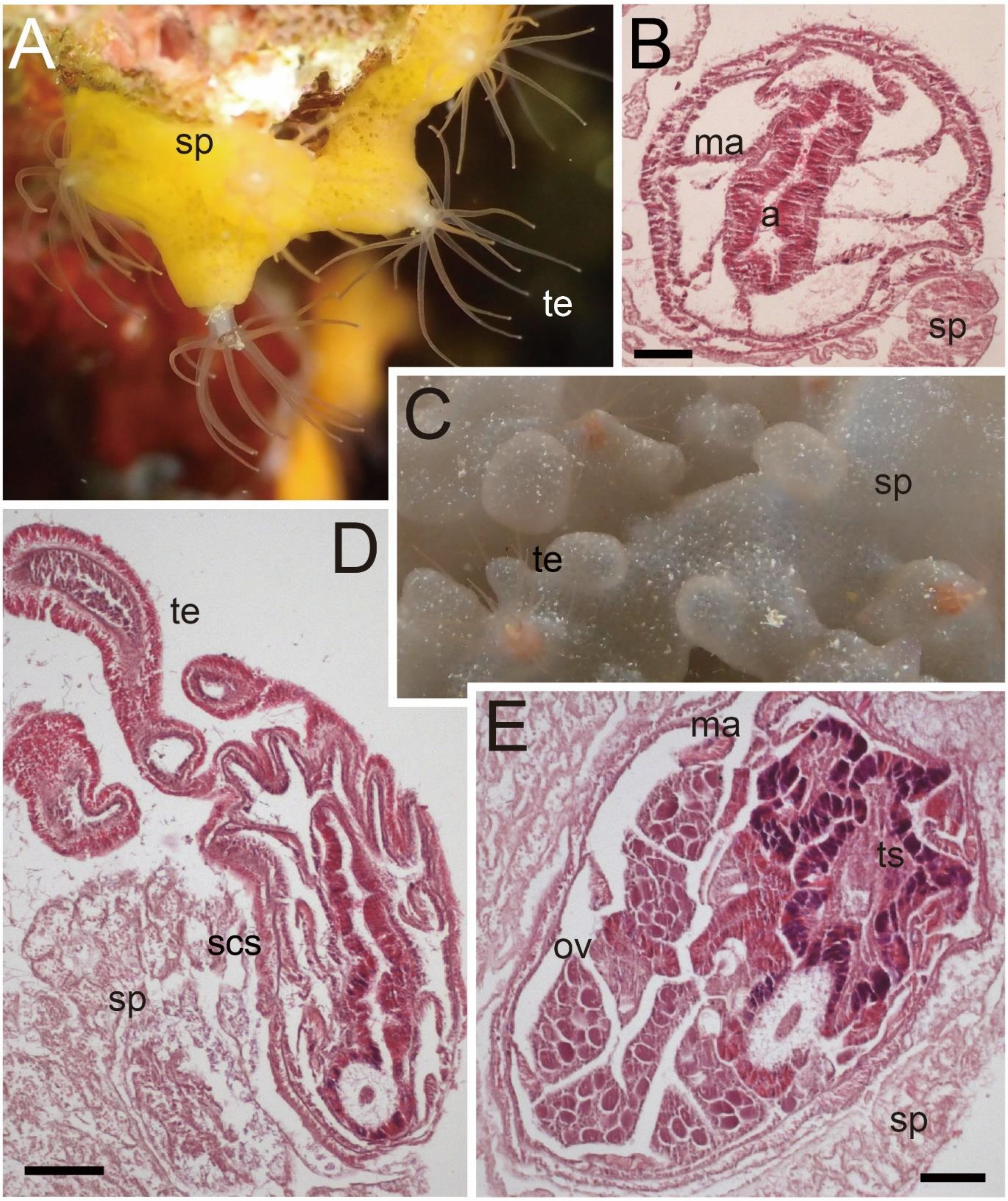

Fig. 35. External and internal morphology of *Tempuractis* spp.
A. Outer view of live specimen of *Tempuractis* sp. (Iz-038) in Plakiidae sponge (photographed by Yuji Ise); B. Transverse section of actinopharynx of (Iz-038); C. Outer view of live specimen of *Tempuractis* sp. (Iz-039) in gray *Oscarella* sponge (photographed by Yuji Ise); D. Longitudinal section of (Iz-039); E. Transverse section of filaments and gonads in both sexuality. Abbreviations: a, actinopharynx; ma, macrocneme; ov, ovary; scs, scapus; sp, sponge; te, tentacle; ts, testis. Scale: 100 μm in B, D, E. Pictures A and C were taken by Yuji Ise.

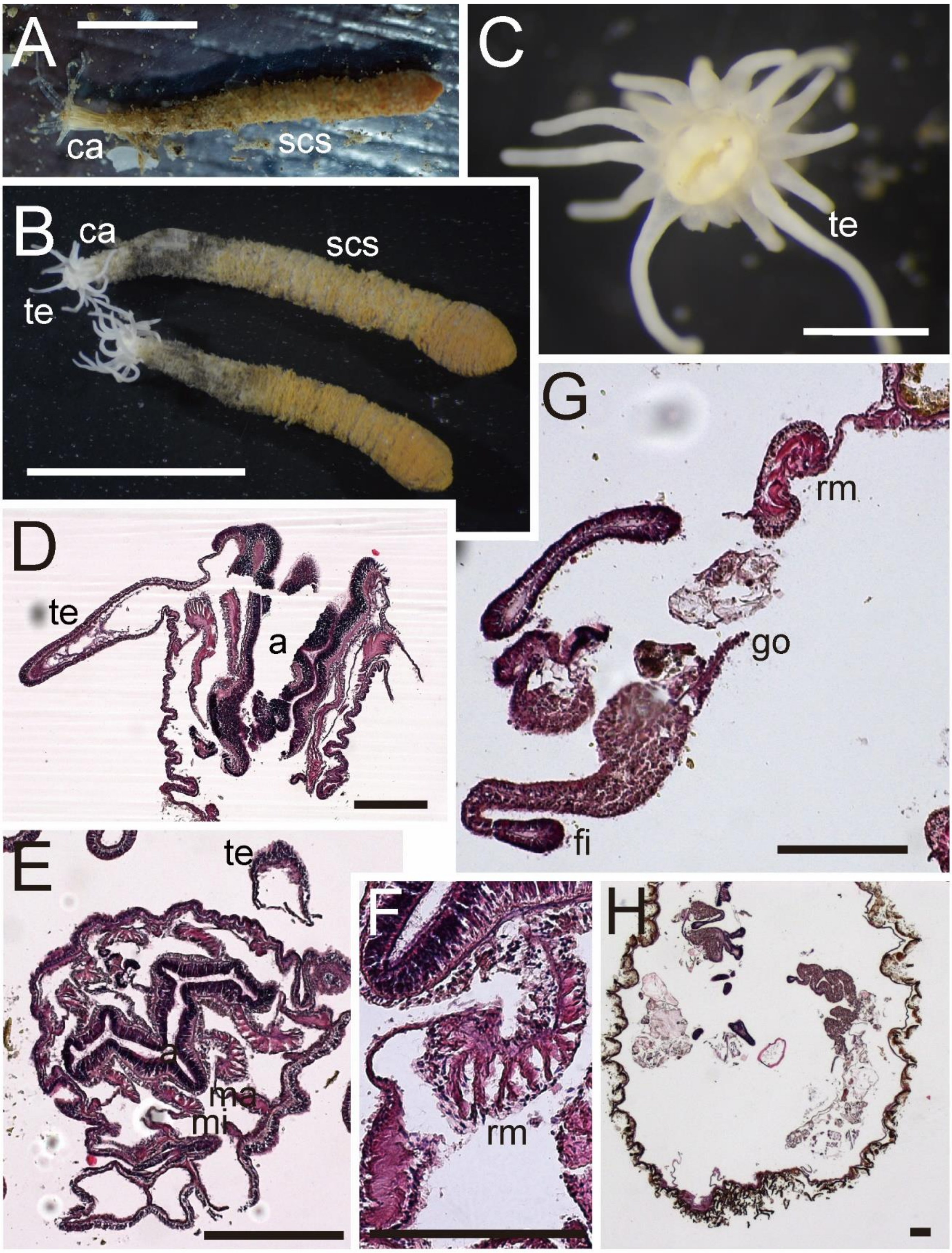

Fig. 36. External and internal morphology of *Edwardsiella* sp. nov. 6 (CMNH-ZG [no registration]).
A. Outer view of live specimen; B. Outer view of preserved specimen; C. Oral view; D. Longitudinal section of oral part; E. Transverse section of actinopharynx and column; F. Enlarged view of macrocnemes; G. Transverse section of mesenteries in lower part; H. Longitudinal section of physa. Abbreviations: a, actinopharynx; ca, capitulum; fi, filament; go, gonad; ma, macrocneme; mi, microcneme; pa, parietal muscle; rm, retractor muscle; scs, scapus; te, tentacle. Scale: 5 mm in A, B; 1 mm in C; 100 µm in C–H. Picture A was taken by Sinniger Frederic.

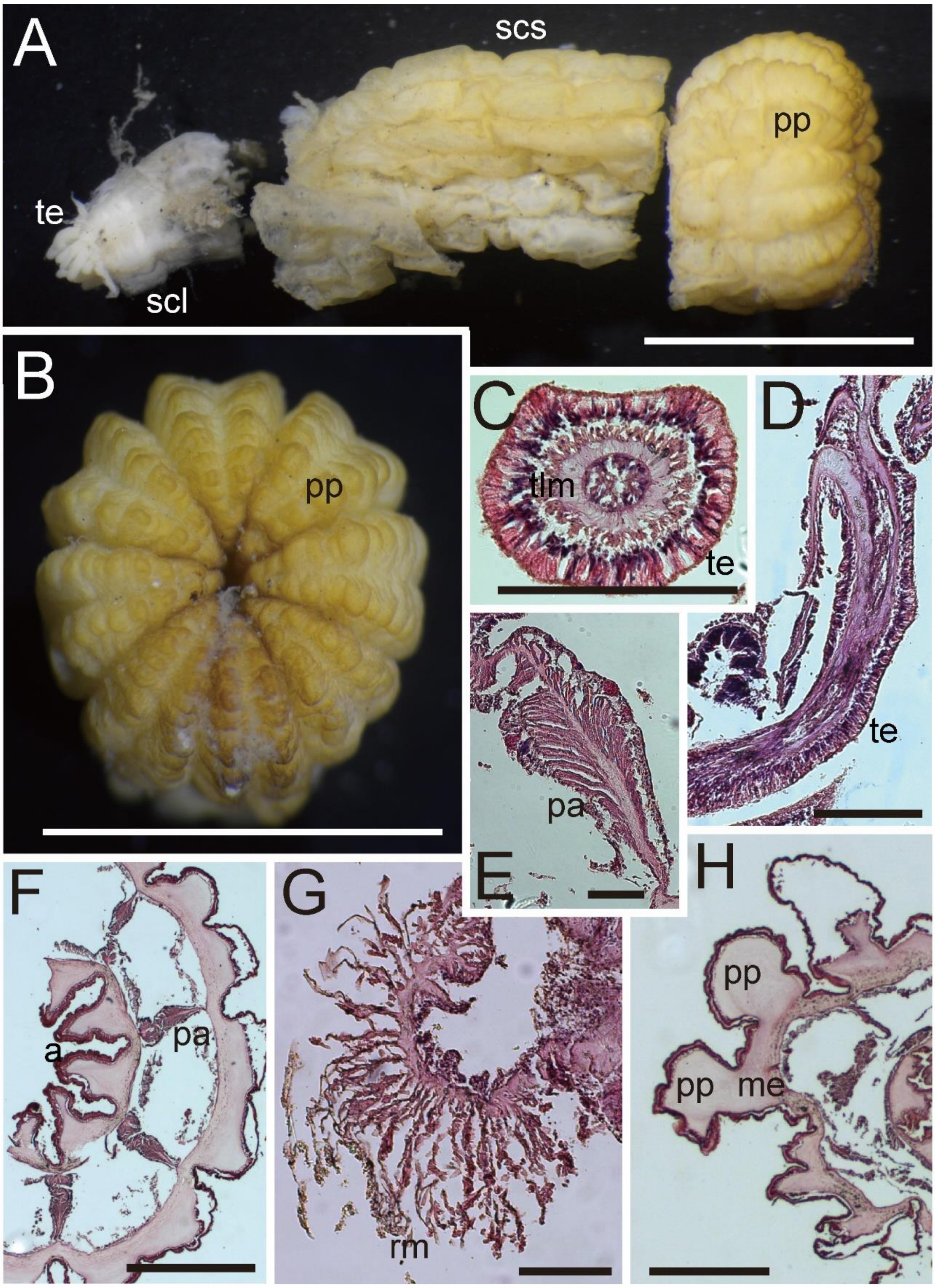

Fig. 37. External and internal morphology of *Halcampogeton* sp. nov. 7 (Iz-040). A. Outer view of preserved specimen; B. proximal view of preserved specimen; C. Oral view; D. Transverse section of tentacle E. Longitudinal section of tentacle; E. Transverse section of parietal muscle; G. Transverse section of mesenteries in lower part; F. Transverse section of lower column; H. Transverse section of lower column. Abbreviations: a, actinopharynx; me, mesoglea; pa, parietal muscle; pp, papillae; rm, retractor muscle; scl, scapulus; scs, scapus; te, tentacle. Scale; tlm, tentacular longitudinal muscle. Scales: 5 mm in A, B; 1 mm in C; 100 μm in C–H.

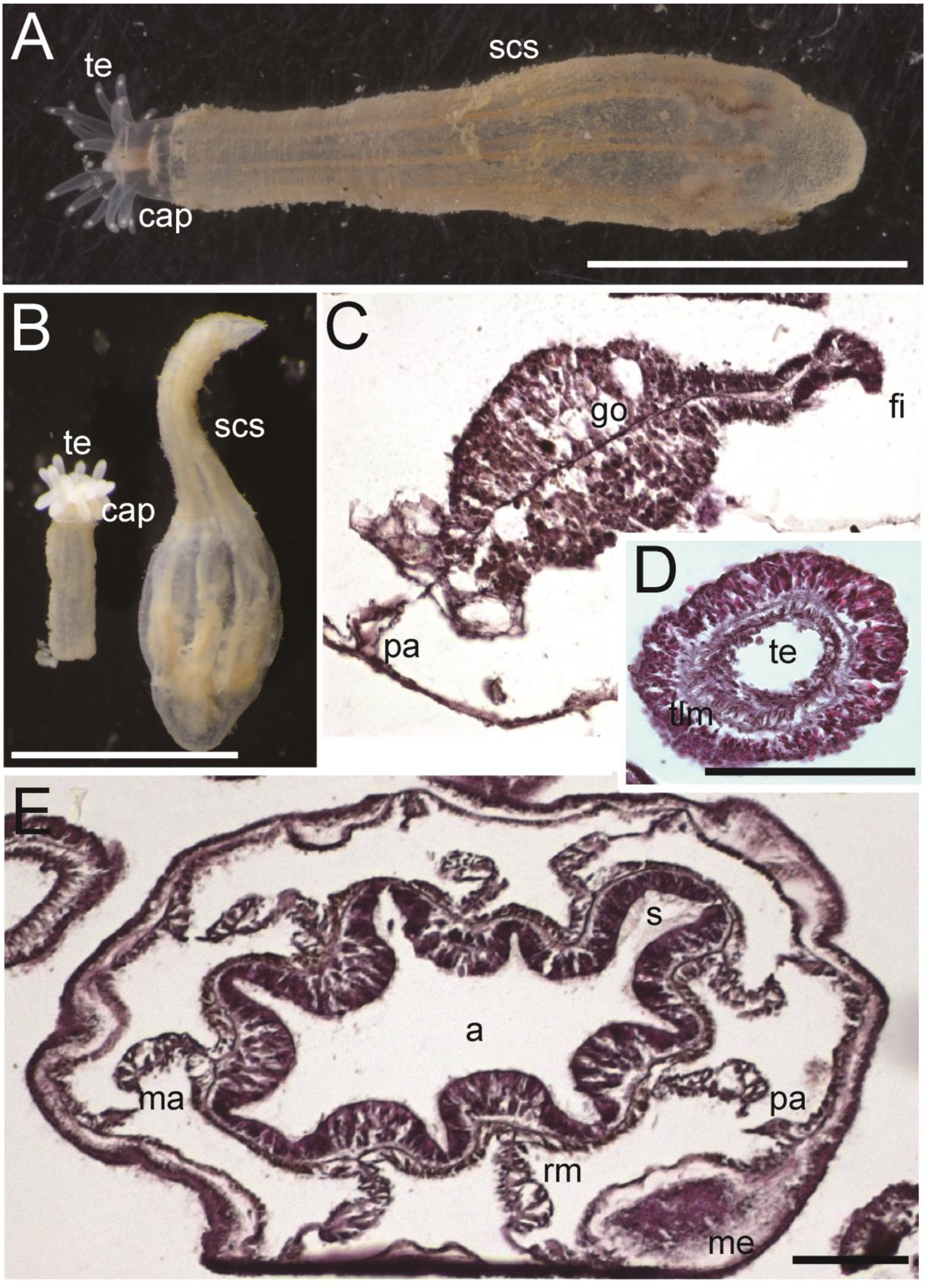

Fig. 38. External and internal morphology of *Drillactis* sp. nov. 8 (Iz-041).
A. Outer view of living specimen (photographed by Kensuke Yanagi); B. Outer view of preserved specimen; C. Transverse section of mesenteries; D. Transverse section of tentacle; E. Transverse section of column and actinopharynx in upper part. Abbreviations: a, actinopharynx; cap, capitulum; fi, filament; go, gonad; ma, macrocneme; me, mesoglea; pa, parietal muscle; rm, retractor muscle; s, siphonoglyph; scs, scapus; te, tentacle. Scale: 5 mm in A, B; 1 mm in C; 100 µm in C–E. Picture A was taken by Kensuke Yanagi.

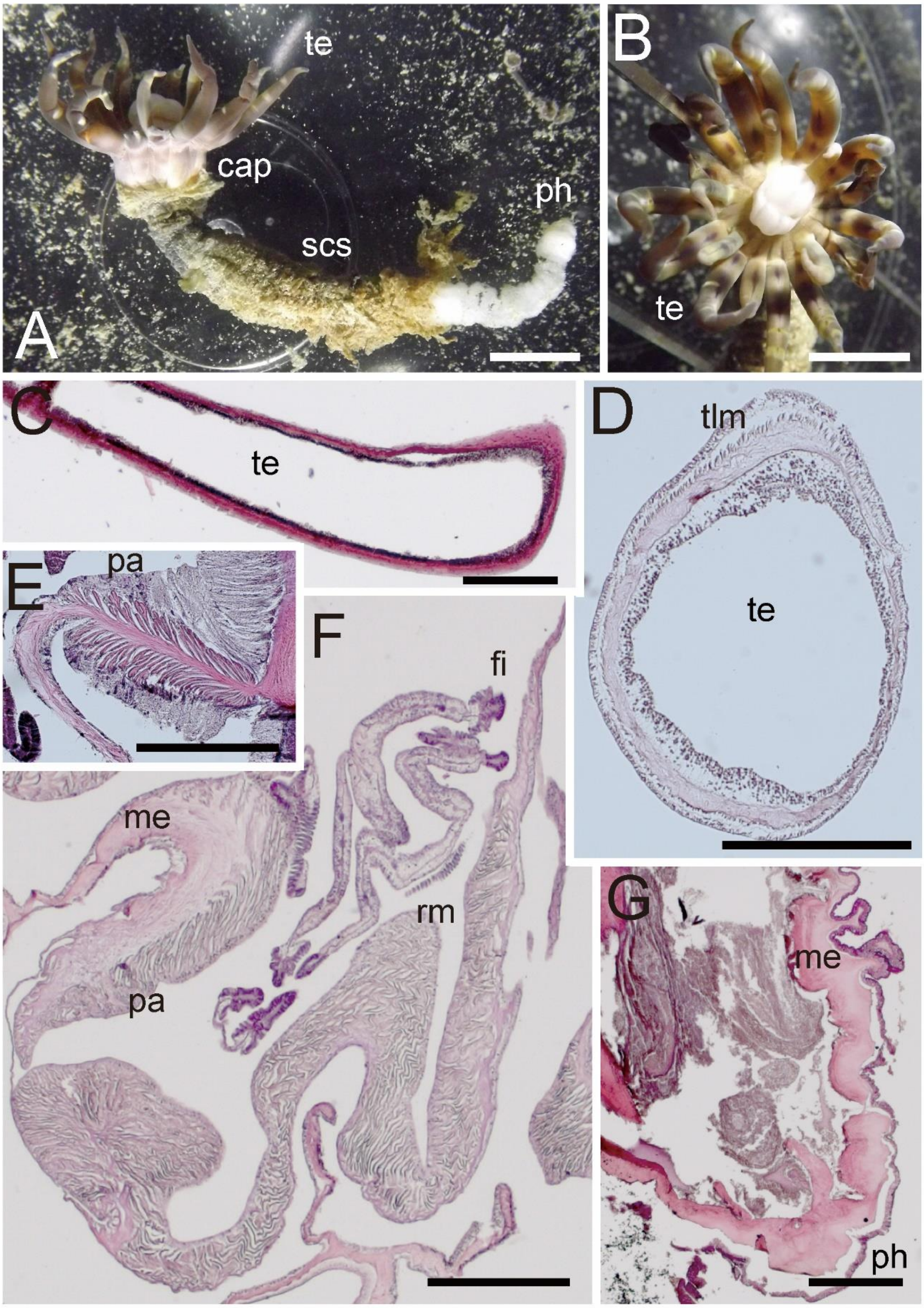

Fig. 39. External and internal morphology of *Edwardsia pudica* (Iz-042). A. Outer view of living specimen; B. Oral view of living specimen; C. Longitudinal section of tentacle; D. Transverse section of tentacle; E. Transverse section of parietal muscle; F. Transverse section of macrocnemes; G. Longitudinal section of physa. Abbreviations: cap, capitulum; fi, filament; me, mesoglea; pa, parietal muscle; ph, physa; rm, retractor muscle; scs, scapus; te, tentacle; tlm, tentacular longitudinal muscle. Scale: 5 mm in A; 1 mm in B; 1 mm in C; 500 µm in C, D, F; 100 µm in E.

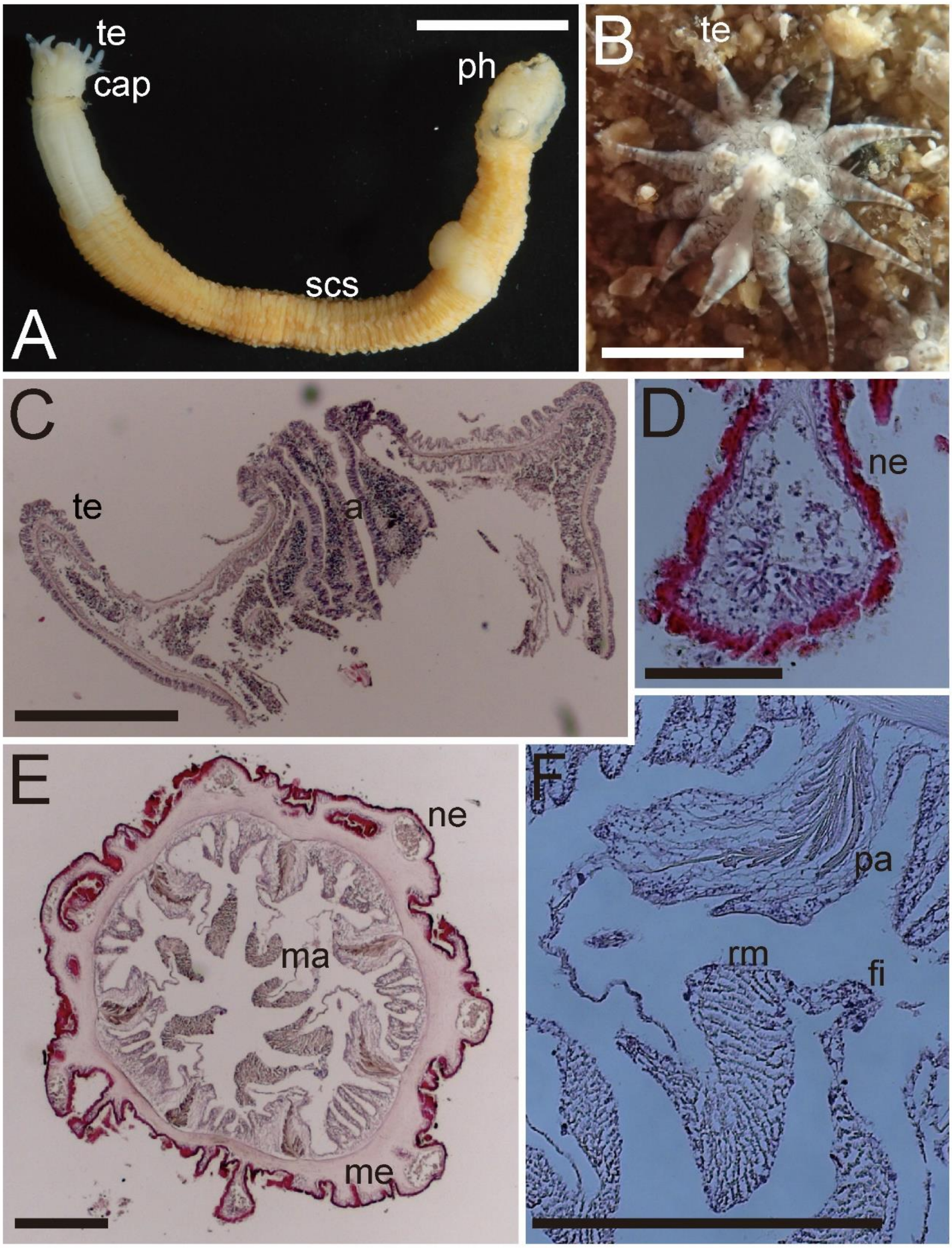

Fig. 40. External and internal morphology of *Edwardsia gilbertensis* (CMNH-ZG 06527 except for B).
A. Outer view of preserved specimen; B. Oral view of living specimen with 18 tentacles in the habitat; C. Longitudinal section of oral end; D. Transverse section of nemathybome; E. Transverse section of column in lower part; F. Enlarged view of transverse section of mesenteries. Abbreviations: a, actinopharynx; cap, capitulum; fi, filament; ma, macrocneme; ne, nemathybomes; pa, parietal muscle; ph, physa; rm, retractor muscle; scs, scapus; te, tentacle. Scale: 5 mm in A; 1 mm in B; 1 mm in C; 500 μm in C, D, F; 100 μm in E. Picture B was taken by Kensuke Yanagi.

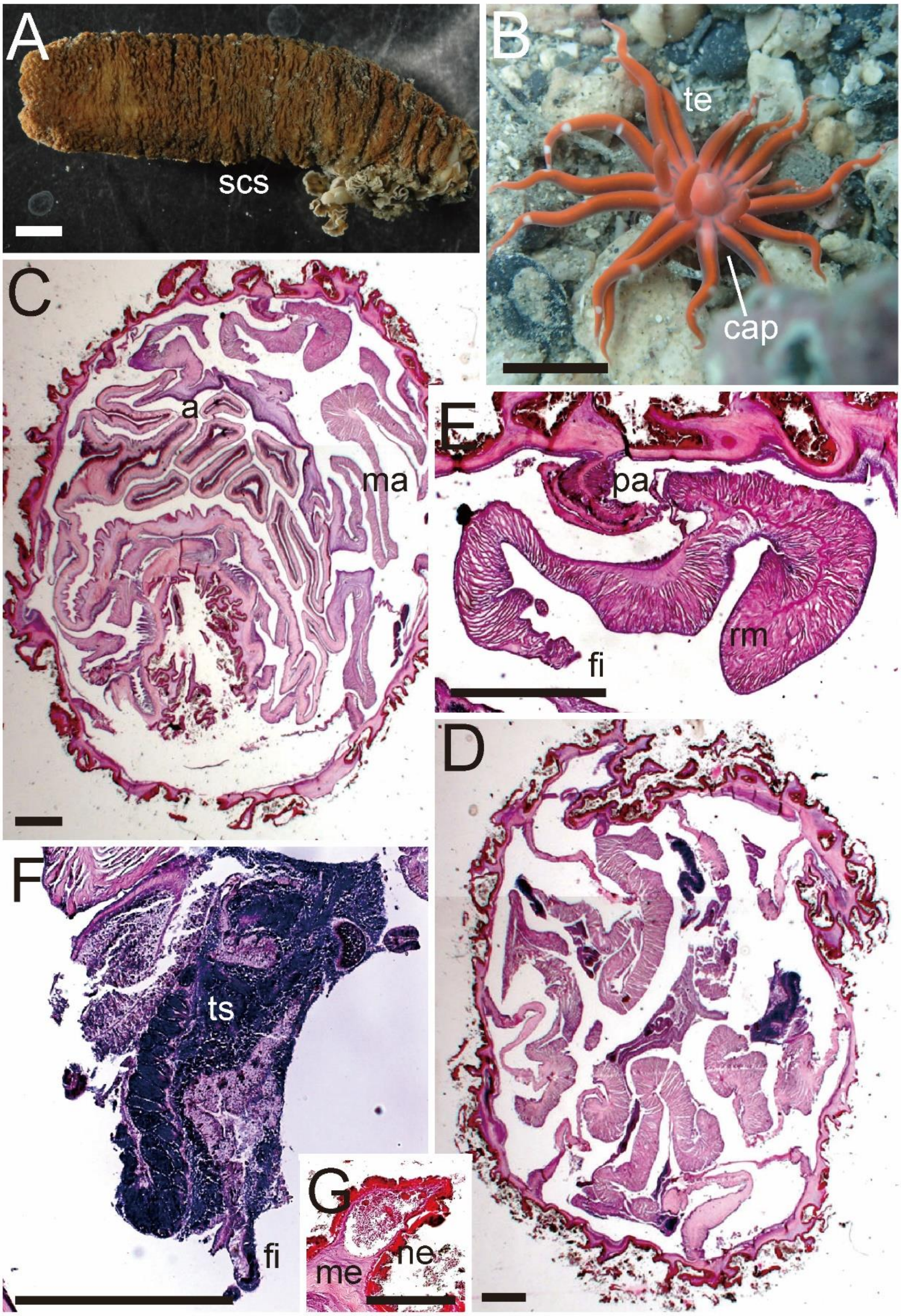

Fig. 41. External and internal morphology of *Edwardsia* sp. nov. 9 (CMNH-ZG 05954).

A. Outer view of preserved specimen (aboral end is damaged); B. Oral view of living specimen in the habitat (photographed by Kensuke Yanagi); C. Transverse section of column in upper part; D. Transverse section of lower column in lower part; E. Transverse section of the macrocneme; F. Transverse section of testis. G. Transverse section of nemathybomes. Abbreviations: a, actinopharynx; cap, capitulum; fi, filament; me, mesoglea; ne, nemathybomes; pa, parietal muscle; rm, retractor muscle; scs, scapus; te, tentacle. Scale: 5 mm in A, B; 500 µm in C–F; 100 µm in G. Picture B was taken by Kensuke Yanagi.

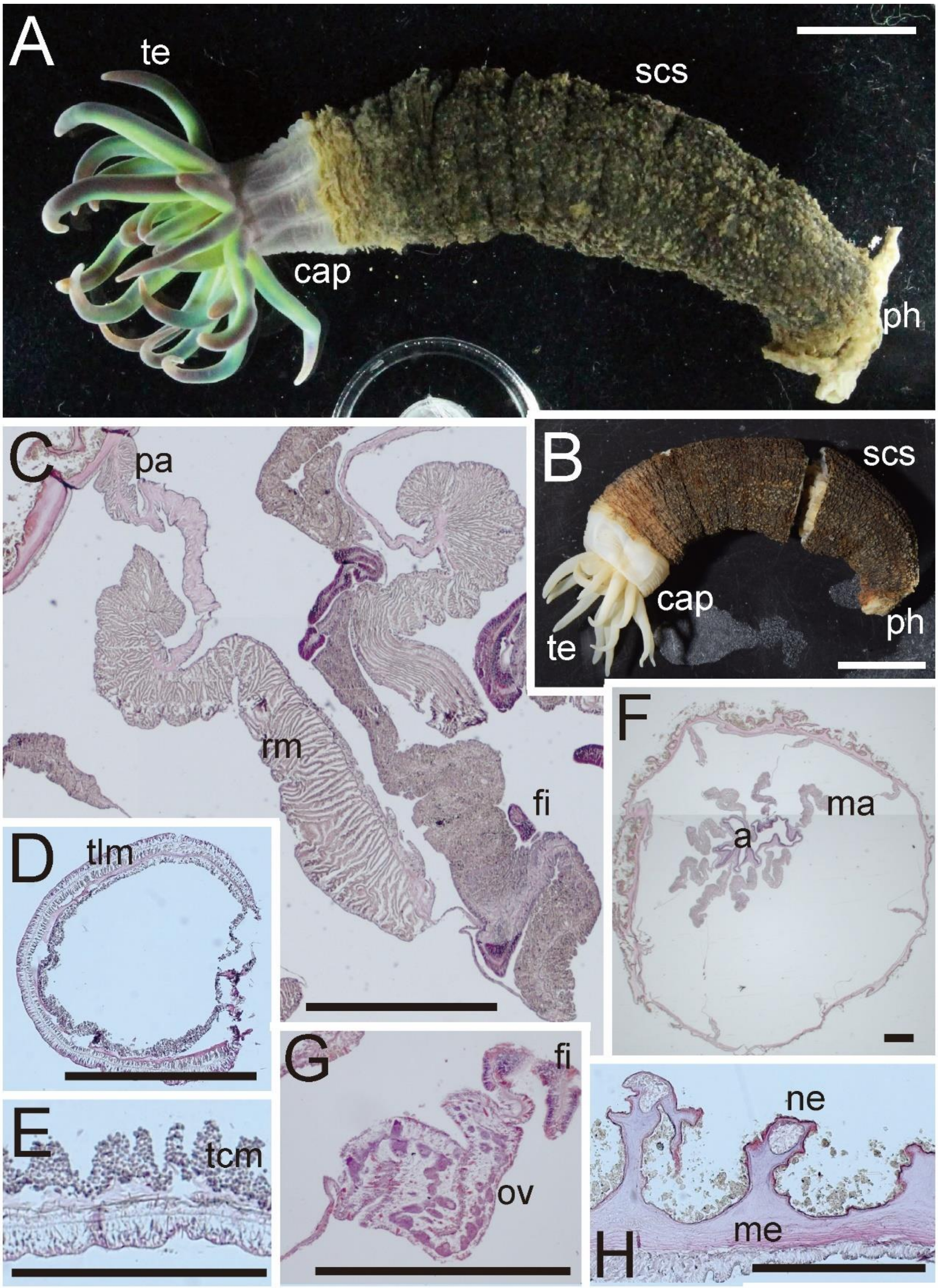

Fig. 42. External and internal morphology of *Edwardsia* sp. nov. 10 (Iz-055). A. Outer view of living specimen; B. Outer view of preserved specimen; C. Transverse section of retractor muscle; D. Transverse section of the tentacle; E. Longitudinal section of the tentacle; F. Transverse section of column. G. Enlarged view of transverse section of ovary; H. Transverse section of a nemathybome. Abbreviations: a, actinopharynx; cap, capitulum; fi, filament; ma, macrocneme; me, mesoglea; ne, nemathybomes; ov, ovary; pa, parietal muscle; ph, physa; rm, retractor muscle; scs, scapus; te, tentacle; tcm, tentacular circular muscle; tlm, tentacular longitudinal muscle. Scale: 1 cm in A, B; 500 μm in C–H. Picture A was taken by Takuma Fujii.

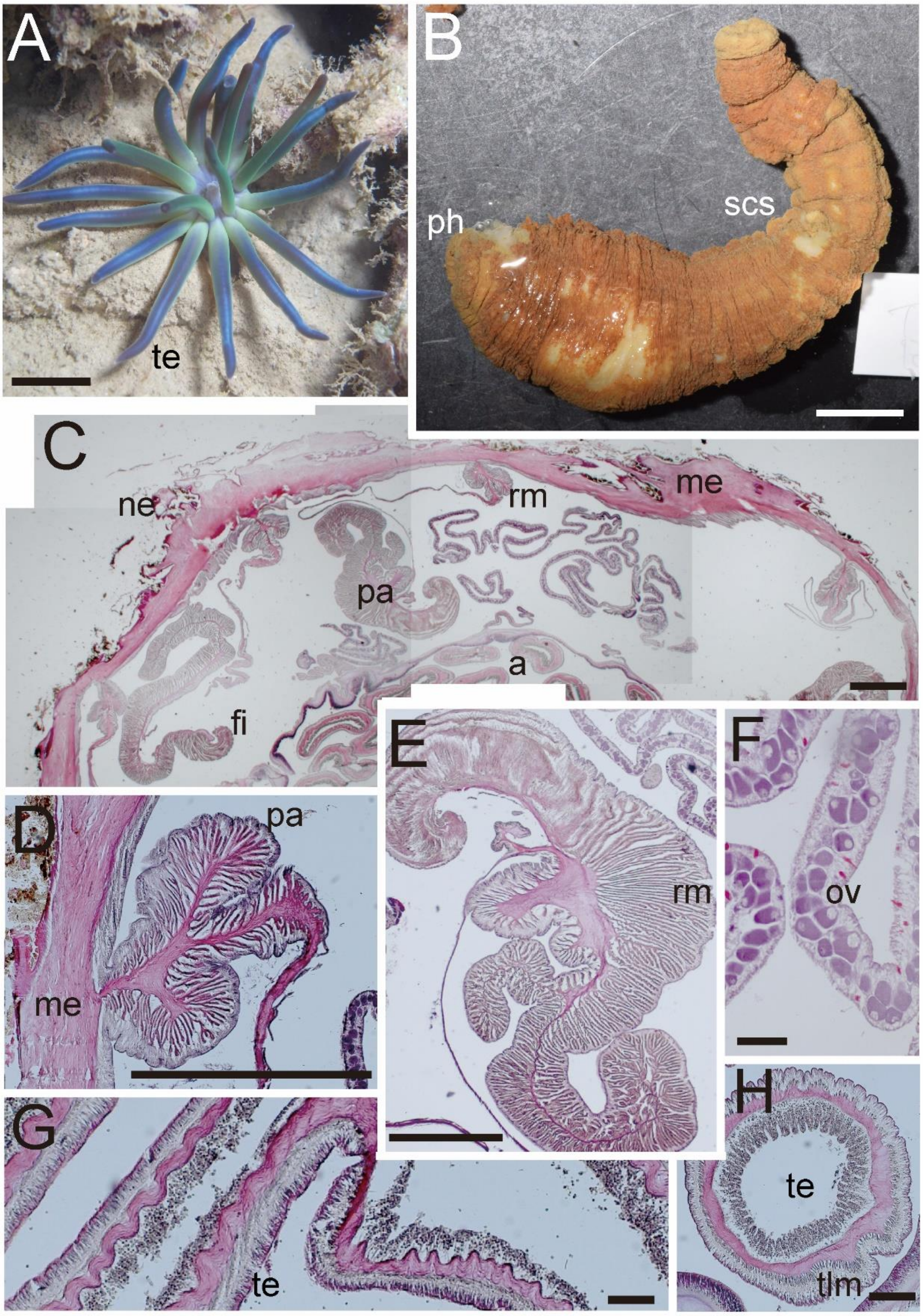

Fig. 43. External and internal morphology of *Edwardsia* sp. nov. 11 (Iz-056). A. Oral view of living specimen in the habitat; B. Outer view of preserved specimen; C. Transverse section of column in upper part; D. Enlarged view of transverse section of parietal muscle; E. Enlarged view of transverse section of retractor muscle; F. Transverse section of ovary; G. Longitudinal section of tentacle; H. Transverse section of tentacle. Abbreviations: a, actinopharynx; fi, filament; me, mesoglea; ne, nemathybome; ov, ovary; pa, parietal muscle; ph, physa; rm, retractor muscle; scs, scapus; te, tentacle; tlm, tentacular longitudinal muscle. Scale: 1 cm in A, B; 1 mm in B; 1 mm in C; 500 μm in C, D, F; 100 μm in E. Picture A was taken by Takuma Fujii.

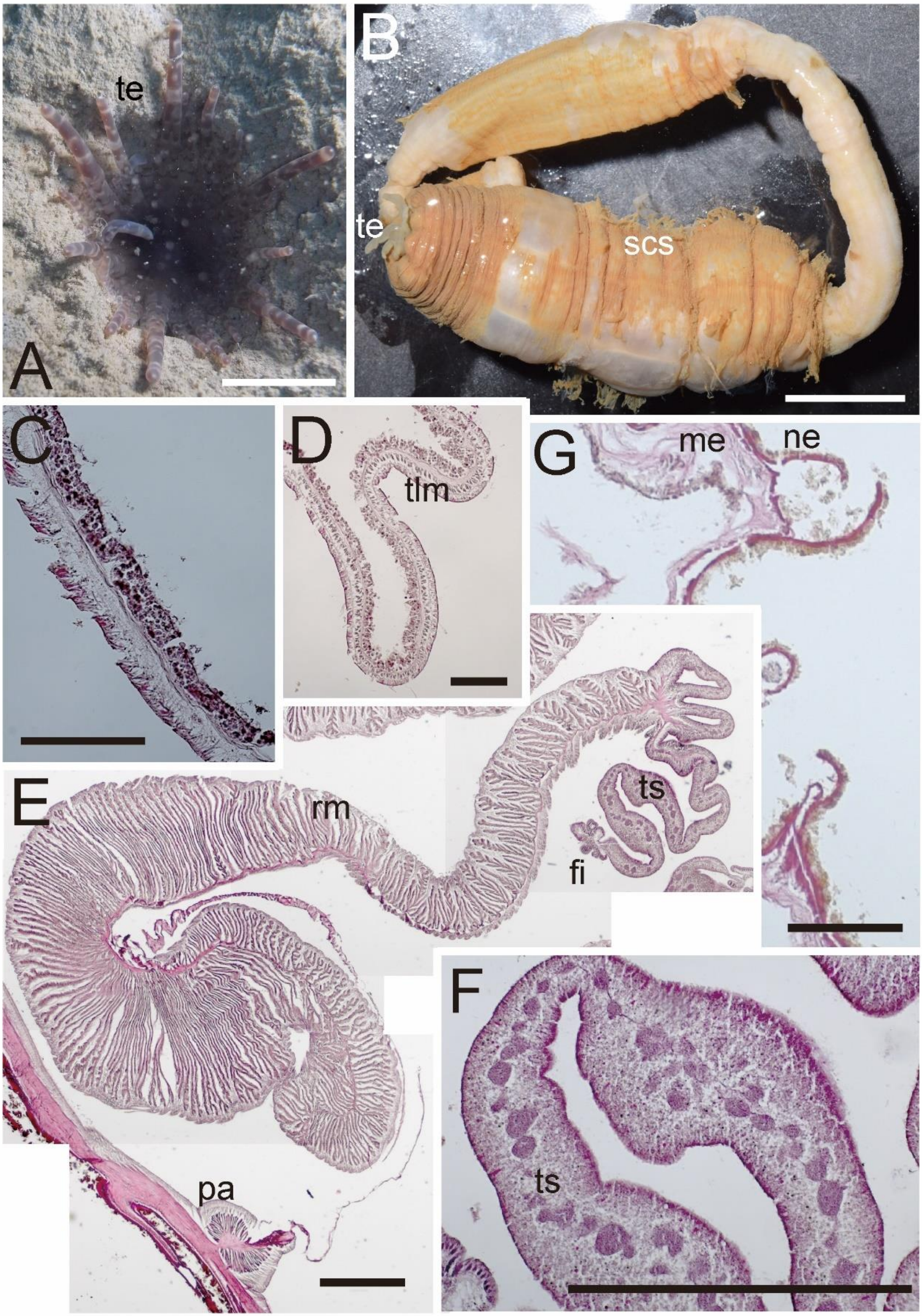

Fig. 44. External and internal morphology of *Edwardsia* sp. nov. 12 (Iz-057). A. Oral view of living specimen in the habitat; B. Outer view of preserved specimen; C. Longitudinal section of tentacle; D. Transverse section of tentacle; E. Transverse section of retractor muscle; F. Transverse section of testis; G. Transverse section of trace of nemathybome. Abbreviations: fi, filament; me, mesoglea; ne, nemathybome-like structure; pa, parietal muscle; rm, retractor muscle; scs, scapus; te, tentacle; tlm, tentacle longitudinal muscle; ts, testis. Scale: 1 cm in A, B; 1 mm in B; 1 mm in C; 500 µm in E, F; 100 µm in C, D, G. Picture A was taken by Takuma Fujii.

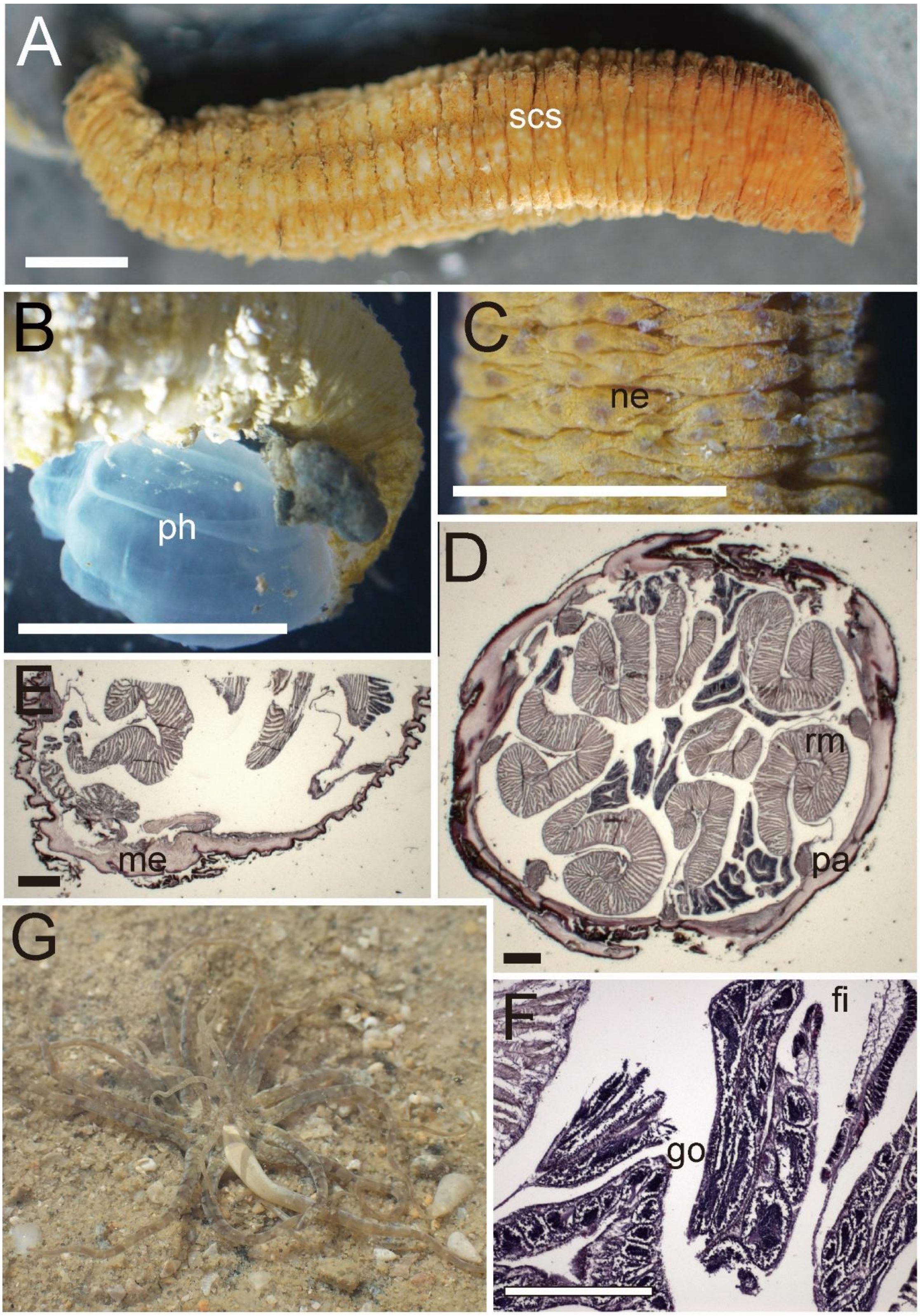

Fig. 45. External and internal morphology of *Edwardsia* sp. nov. 13.
A–F: (Iz-058), G: (Iz-059). A. Outer view of living specimen; B. Enlarged view of aboral end; C. Enlarged view of nemathybomes; D. Transverse section of column in upper part; E. Longitudinal section of aboral end; F. Transverse section of column in lower part; G. Transverse section of gonad: fi, filament; go, gonad; me, mesoglea; ne, nemathybome; pa, parietal muscle; ph, physa; rm, retractor muscle; scs, scapus. Scale: 5 mm in A–C; 500 µm in D–G. Picture G was taken by Gen Kanaya.

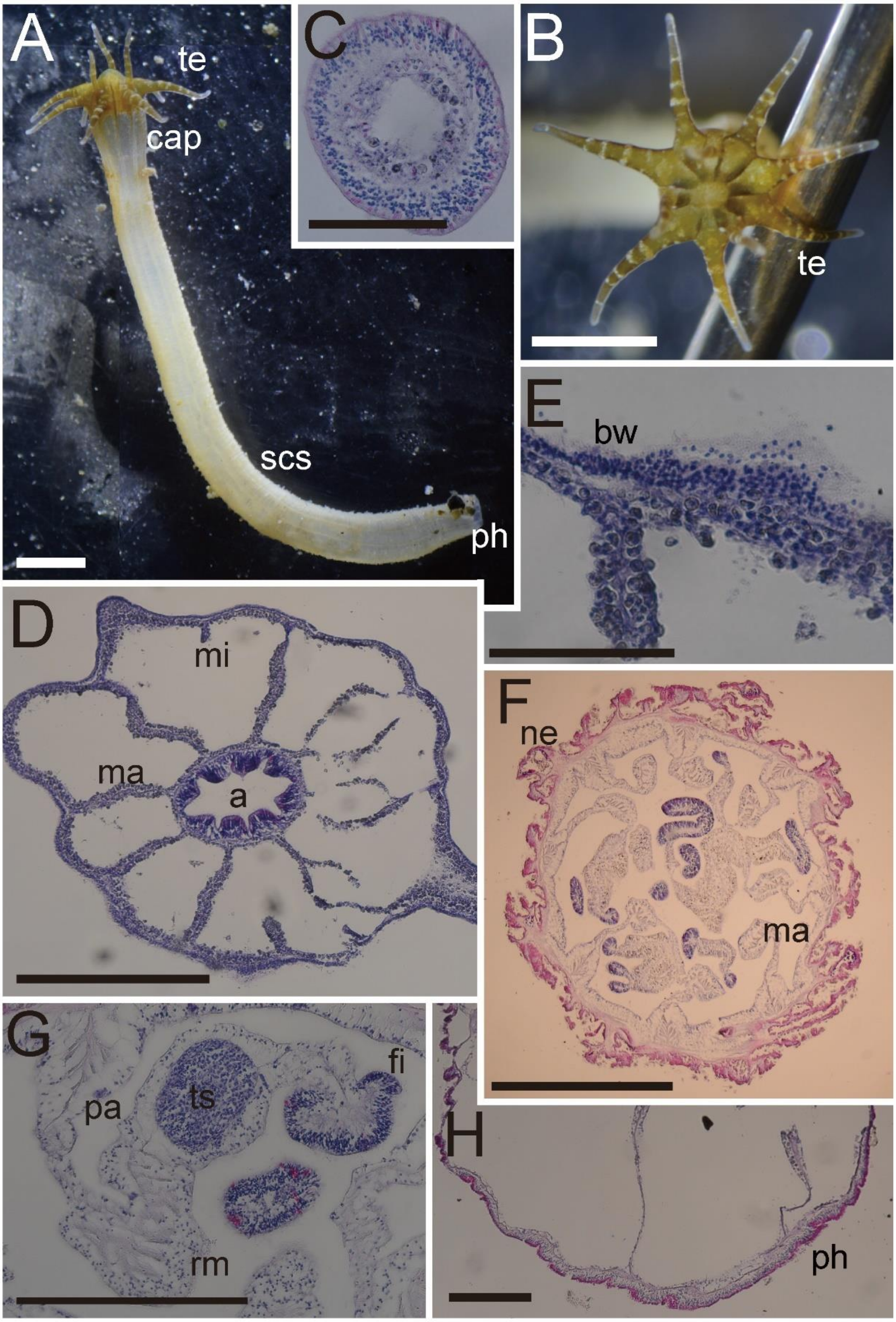

Fig. 46. External and internal morphology of *Edwardsia* sp. nov. 14 (Iz-060). A. Outer view of living specimen; B. Oral view of living specimen; C. Transverse section of tentacle; D. Transverse section of column in upper part; E. Enlarged view of body wall with zooxanthellae; F. Transverse section of column in lower part; G. Transverse section of macrocneme; H. Longitudinal section of aboral end. Abbreviations: a, actinopharynx; bw, body wall; cap, capitulum; fi, filament; ma, macrocneme; mi, microcneme; ne, nemathybome; pa, parietal muscle; ph, physa; rm, retractor muscle; scs, scapus; te, tentacle; ts, testis. Scale: 1 mm in A, B; 500 μm in D, F, H; 100 μm in C, E, G.

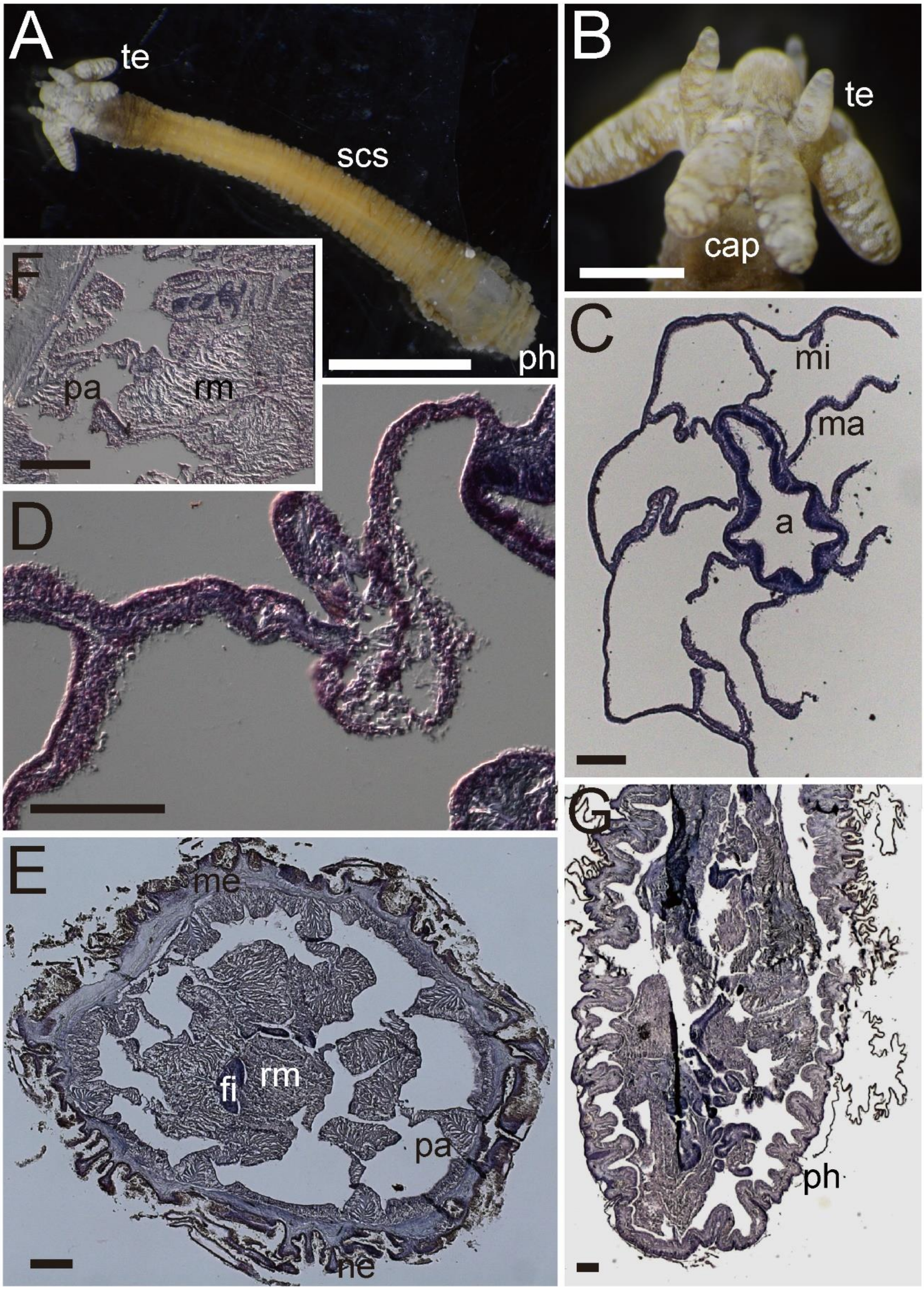

Fig. 47. External and internal morphology of *Edwardsia* sp. nov. 15 (Iz-064).
A. Outer view of living specimen; B. Enlarged view of oral end of the specimen; C. Transverse section of column in upper part; D. Enlarged view of body wall and a mesentery with zooxanthellae; E. Transverse section of column in lower part; F. Enlarged view of transverse section of retractor muscle; G. Longitudinal section of aboral end. Abbreviations: a, actinopharynx; fi, filament; ma, macrocneme; mi, microcneme; ne, nemathybome; pa, parietal muscle; ph, physa; rm, retractor muscle; scs, scapus; te, tentacle. Scale: 5 mm in A; 1 mm in B; 500 µm in C, E, F, G; 100 µm in D.

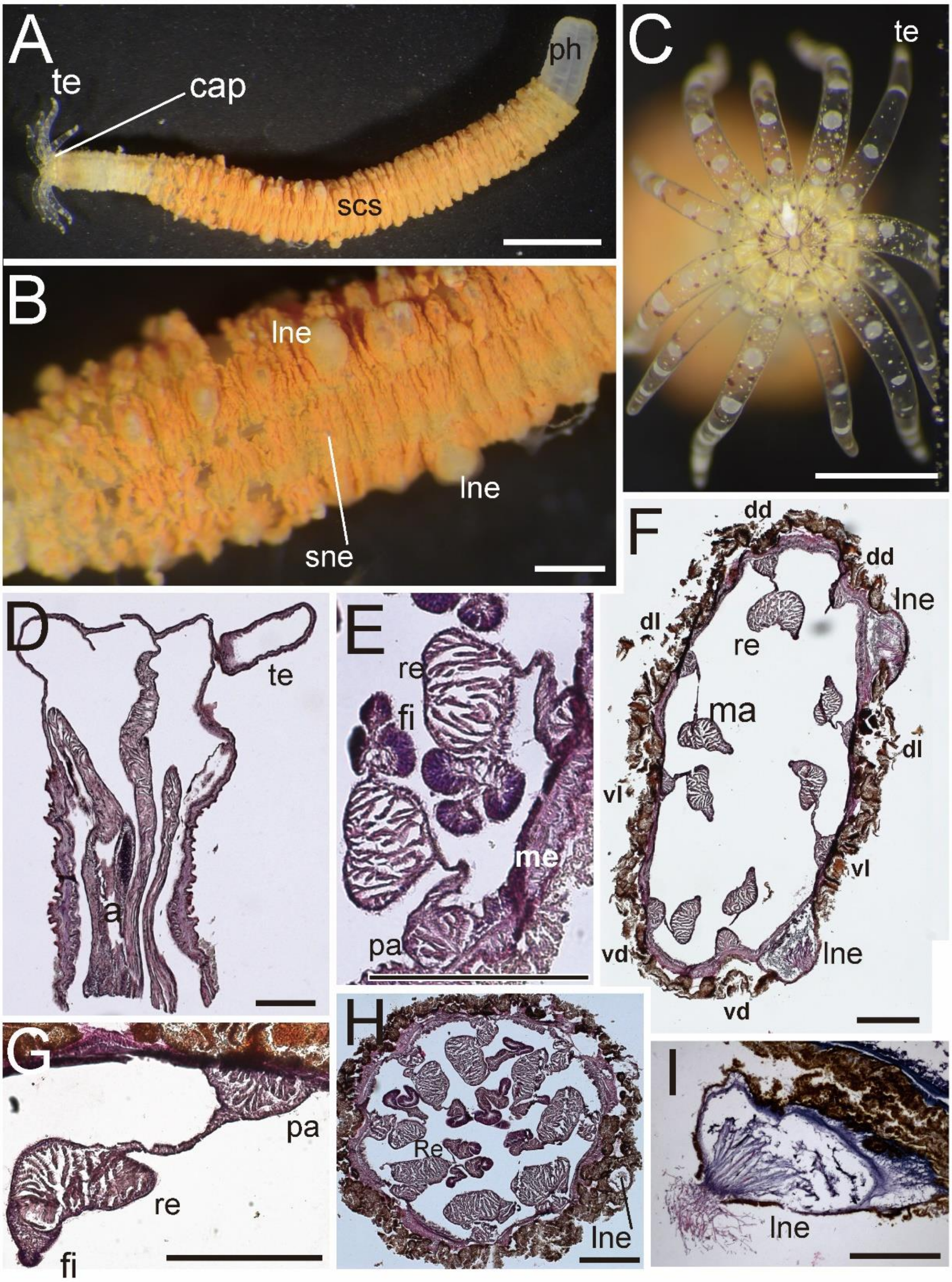

Fig. 48. External and internal morphology of *Edwardsia alternobomen* Izumi and Fujita, 2019.
A–C, External view of NSMT-Co 1657 (holotype); A. anesthetized specimen. B. Enlarged view of body wall and nemathybomes in the middle part of the body C. Oral view of the specimen. D–I, histological section. D–H, NSMT-Co 1657 and I, NSMT-Co 1656 (paratype); D. Longitudinal section of uppermost part. E. Transverse section of mesenteries. F. Transverse section of middle part of body with large nemathybomes. G. Enlarged view of a mesentery (lower part than E). H. Transverse section of lower part. I. Enlarged view of a nemathybome. Large basitrichs are indicated. Abbreviations: cap, capitulum; dd, dorsal directive; dl, dorso-lateral mesentery; lne, large nemathybome; me, mesoglea; pa, parietal muscle; ph, physa; re, retractor muscle; sc, scapus; sne, small nemathybome; te, tentacle vd, ventral directive; vl, ventro-lateral mesentery. Scale bars indicate 5 mm in A, 1 mm in B, 500 µm in C–H.

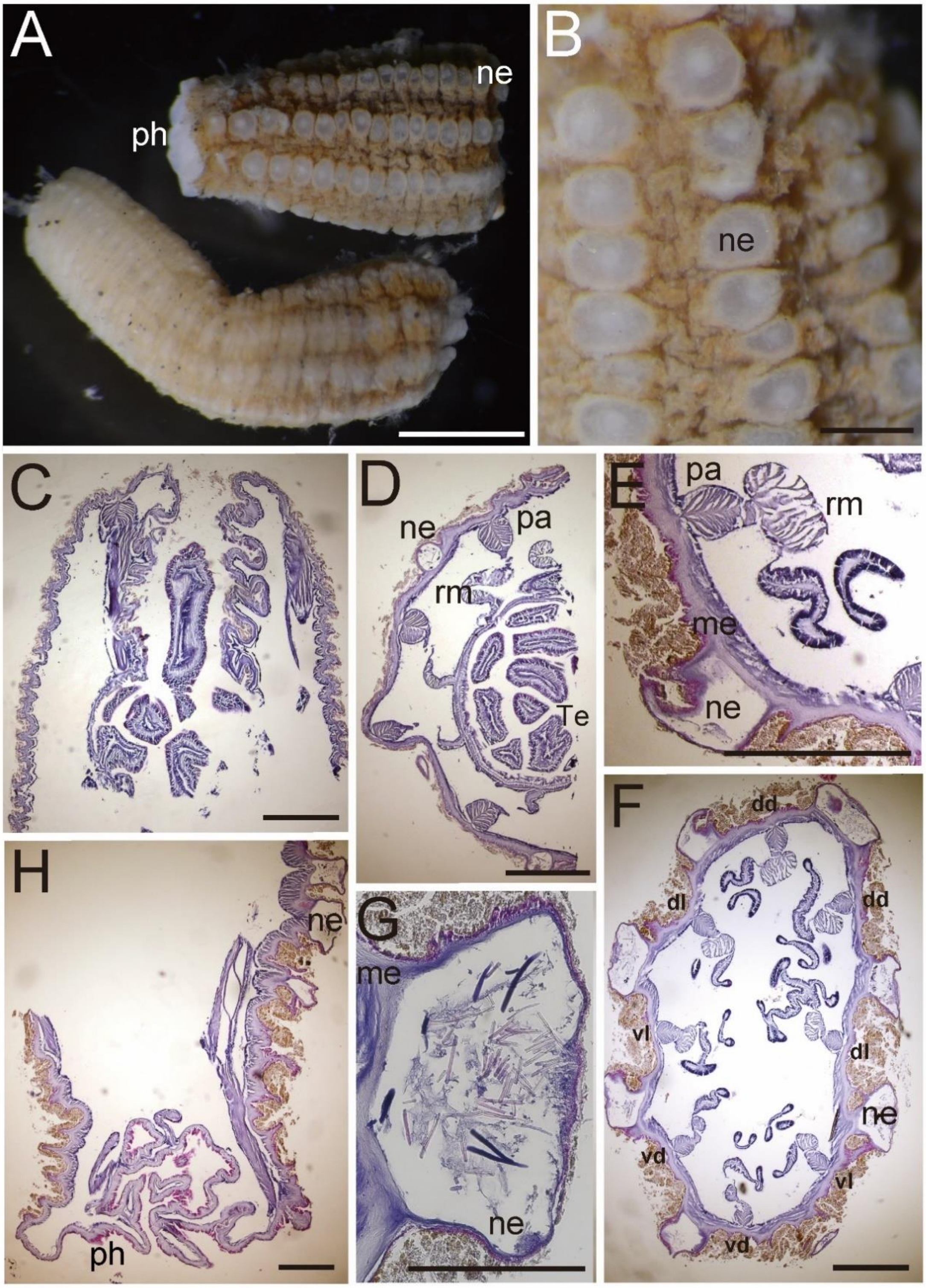

Fig. 49. External and internal morphology of *Edwardsia* aff. *tuberculata* Dueben and Koren, 1847.
A and B, External view of NSMT-Co 1654; A. Preserved specimen (dissected into two halves) B. Enlarged view of body wall and nemathybomes. C–H, histological section of NSMT-Co 1654; C. Longitudinal section of uppermost part. D. Transverse section of upper part. E. Enlarged view of a mesentery. F. Transverse section of lower part of body. G. Enlarged view of a nemathybome. Large basitrichs are indicated. H. longitudinal section of lowermost part. Abbreviations: dd, dorsal directive; dl, dorso-lateral mesentery; me, mesoglea; ne, nemathybome; pa, parietal muscle; ph, physa; re, retractor muscle; te, tentacle; vd, ventral directive; vl, ventro-lateral mesentery. Scale bars indicate 5 mm in A, 1 mm in B, 500 μm in C–H.

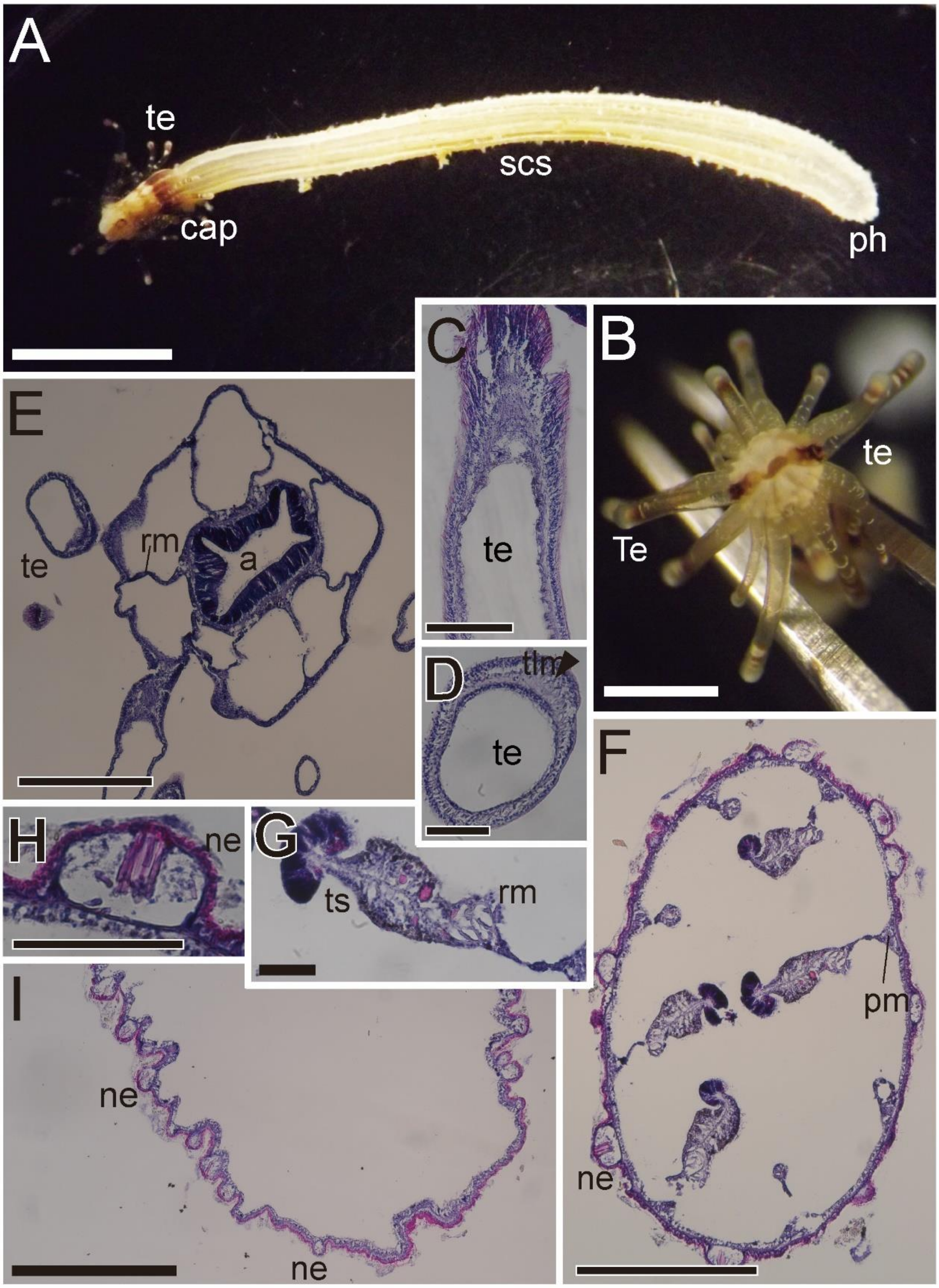

Fig. 50. External and internal views of *Edwardsia kopepe* (Izumi and Fujita, 2019) comb. nov. A, B, F–I: NSMT-Co 1613; C–E: NSMT-Co 1616.
A and B, External view; A. Whole living specimen of *E. kopepe*. B. Enlarged view of tentacular circle. C-I, Internal view (histological section); C. longitudinal section of tentacle. D. Transverse section of tentacle. E. Transverse section of actinopharynx. F. Transverse section of filaments. G. Enlarged view of mesentery. H. Transverse section of nemathybome. I. Longitudinal section of aboral end. Nemathybomes distributed up to the tip of aboral end. Abbreviations: a, actinopharynx; ne, nemathybome; pm, parietal muscle; rm, retractor muscle; te, tentacle; tlm, tentacular longitudinal muscle; ts, testis. Scale bars indicate 5 mm in A, 1 mm in B, 500 μm in E, F, G, I and 100 μm in C, D, H, J.

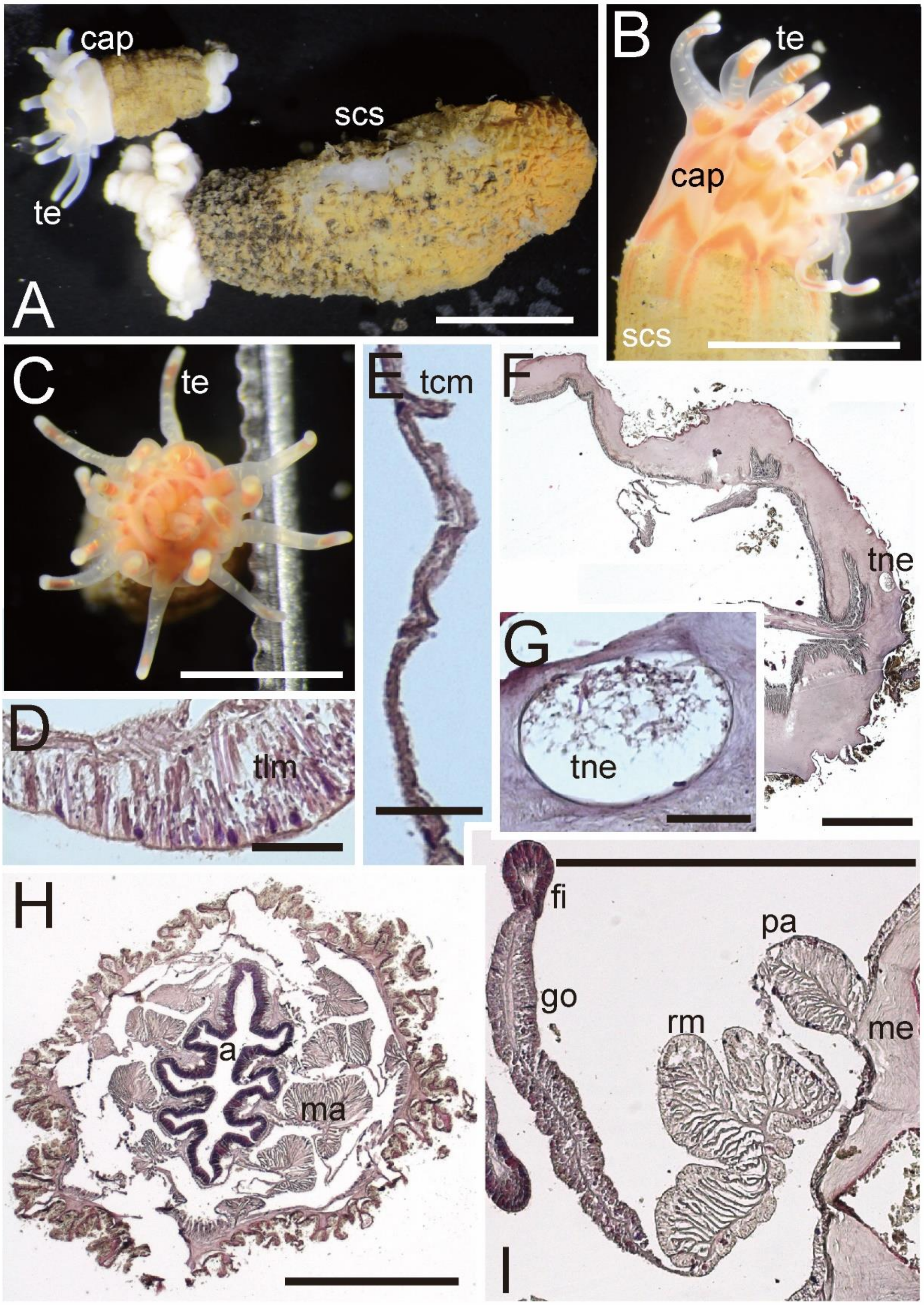

Fig. 51. External and internal views of *Edwardsia* sp. nov. 16 (Iz-070).
A. Dissected preserved specimen of *E.* sp. nov. 16. B. Enlarged view of distal end. C. Oral view. D-I, Internal view (histological section); D. Transverse section of tentacle. E. Longitudinal section of tentacle. F. Longitudinal section of aboral end. G. Enlarged view of transverse section of a nemathybome. H. Transverse section of upper column. I. Transverse section of the macrocneme of lower column. Abbreviations: a, actinopharynx; cap, capitulum; fi, filament; go, gonad; ma, macrocneme; me, mesoglea; pa, parietal muscle; rm, retractor muscle; scs, scapus; tcm, tentacular circular muscle; te, tentacle; tlm, tentacular longitudinal muscle; tne, trace of nemathybome. Scale bars indicate 5 mm in A–C, 1 mm in F, H, I, 100 μm in D, E, G.

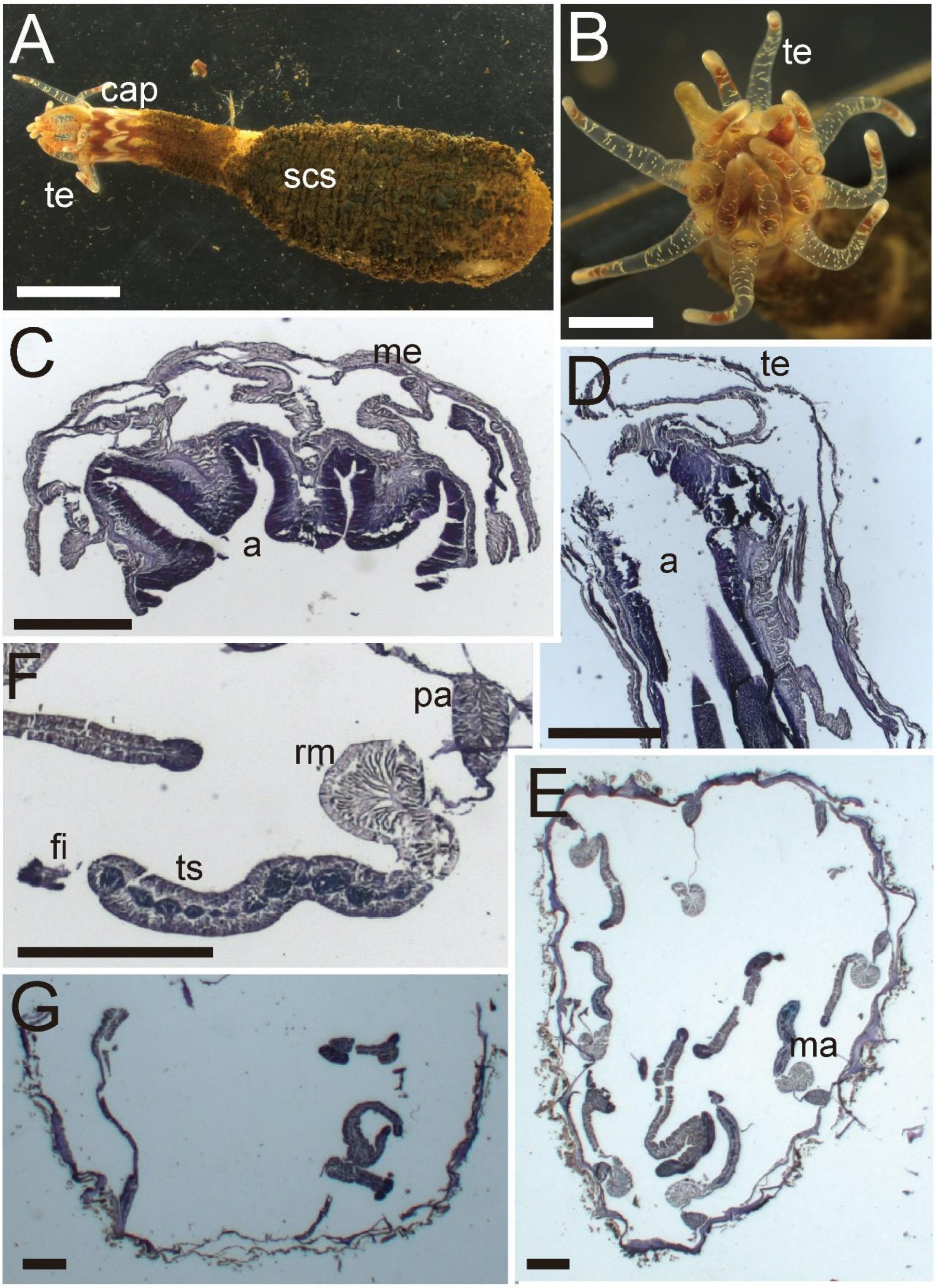

Fig. 52. External and internal views of *Edwardsia* sp. nov. 17 (Iz-072).
A. Whole living specimen of *E.* sp. nov. 17. B. Enlarged view of tentacular circle. C-G, Internal view (histological section); C. Longitudinal section of distal end. D. Transverse section of upper column. E. Transverse section of lower column. F. Transverse section of a macrocneme. G. Longitudinal section of aboral end. Abbreviations: a, actinopharynx; cap, capitulum; fi, filament; go, gonad; ma, macrocneme; me, mesoglea; pa, parietal muscle; rm, retractor muscle; scs, scapus; tcm, tentacular circular muscle; te, tentacle; tlm, tentacular longitudinal muscle; ts, testis. Scale bars indicate 5 mm in A, 1 mm in B, 500 μm in C–G.

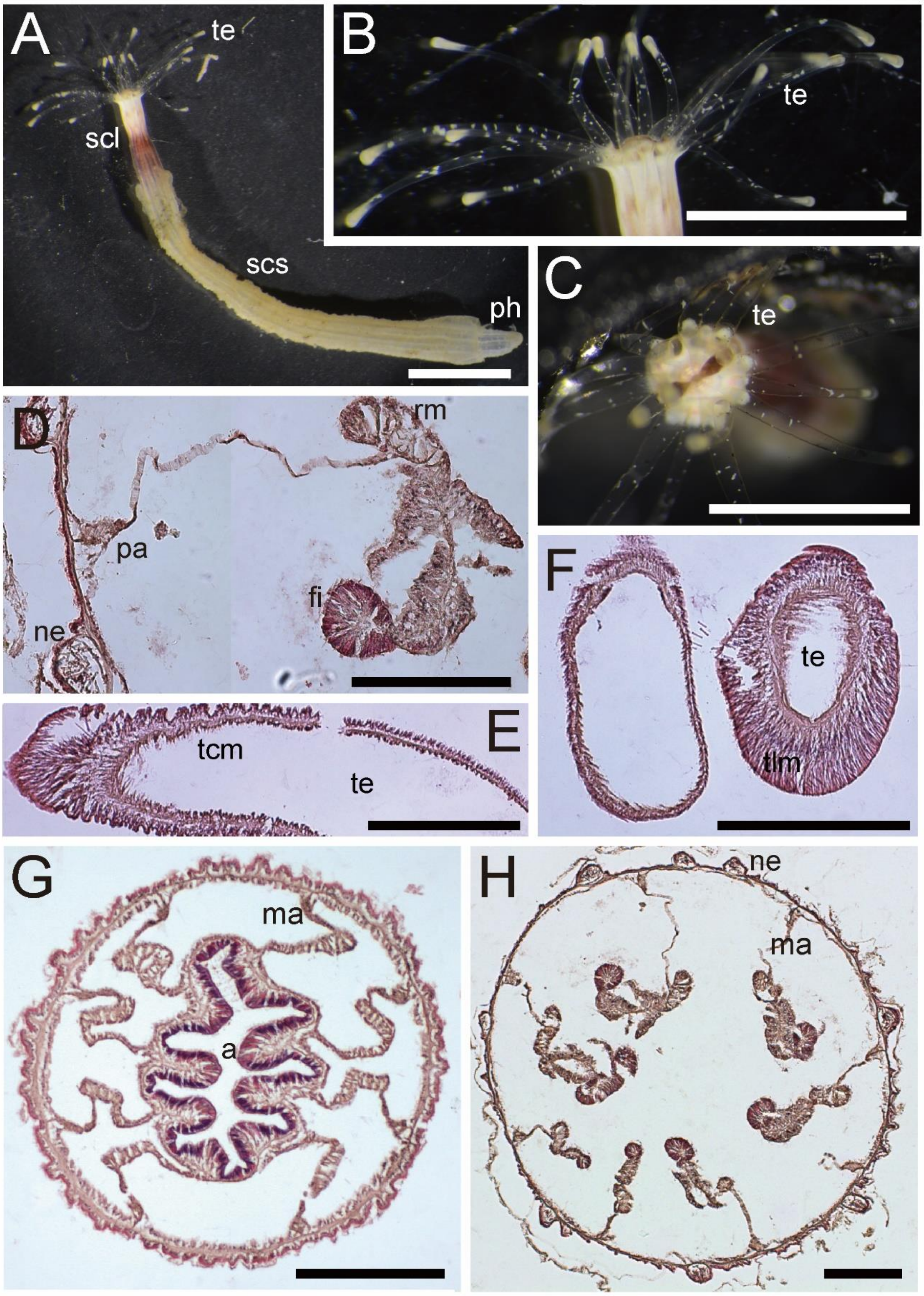

Fig. 53. External and internal views of *Edwardsia* sp. nov. 18 (Iz-073).
A. Whole living specimen. B. Enlarged view of distal end. C. Oral view of tentacular circle. D. Transverse section of macrocneme and retractor muscle. E. Longitudinal section of a tentacle. F. Transverse section of tentacles: capitated tip (right) and middle part (left). G. Transverse section of upper column. H. Transverse section of lower column. Abbreviations: a, actinopharynx; fi, filament; ma, macrocneme; ne, nemathybome; ph, physa; pa, parietal muscle; rm, retractor muscle; scl, scapulus; scs, scapus; te, tentacle. Scale bars indicate 5 mm in A–C, 1 mm in G, H, 200 μm in D–F.

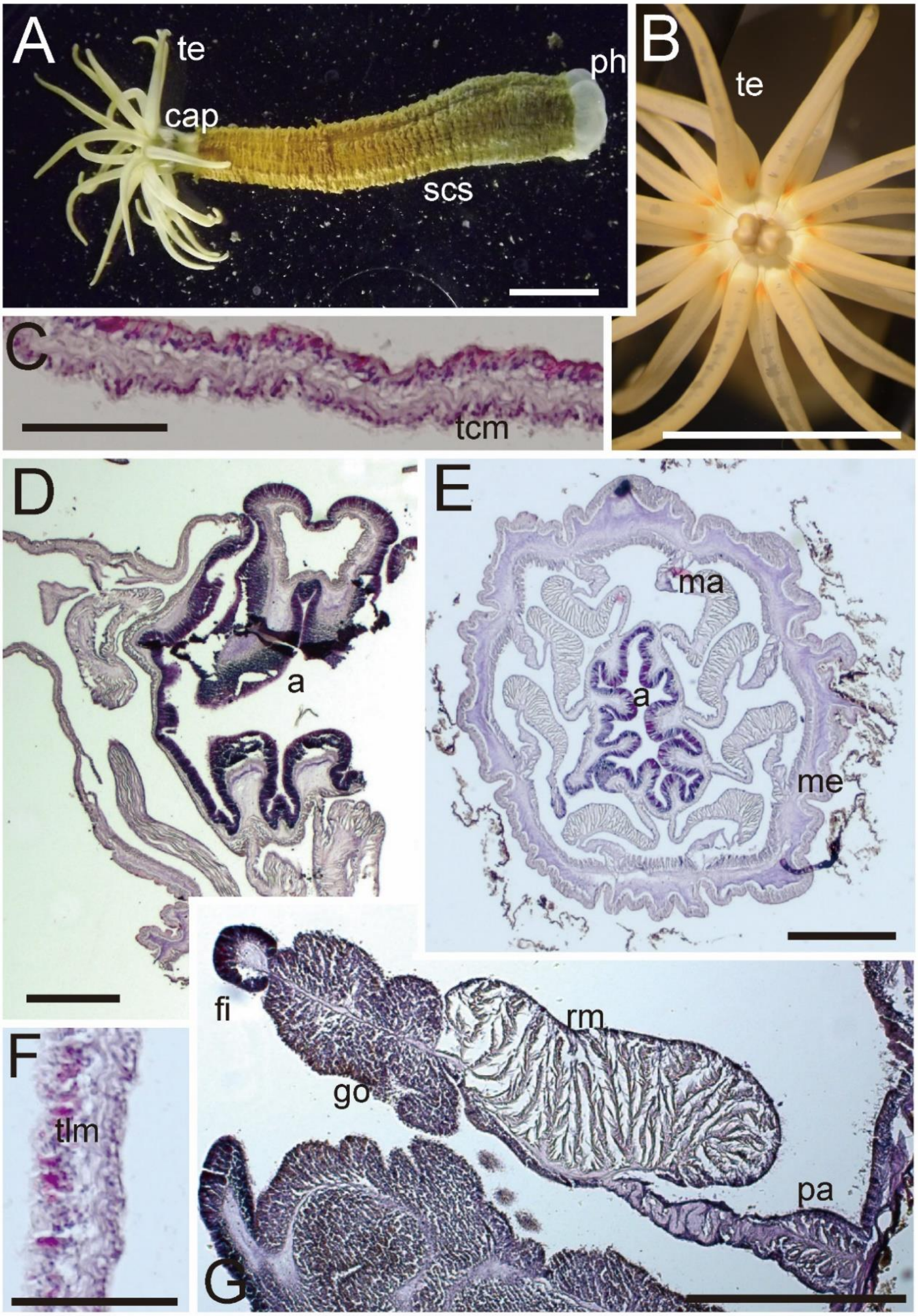

Fig. 54. External and internal views of *Edwardsia sipunculoides* (NSMT-Co 1700). A. Whole living specimen. B. Oral view of tentacular circle in living specimen. C. longitudinal section of tentacle. D. Transverse section of tentacle. E. Transverse section of column in upper part. F. Transverse section of tentacle. G. Enlarged view of transverse section of mesentery. Abbreviations: a, actinopharynx; cap, capitulum; fi, filament; go, gonad; ma, macrocneme; me, mesoglea; pa, parietal muscle; rm, retractor muscle; te, tentacle; tlm, tentacular longitudinal muscle. Scale bars indicate 1 cm in A, B, 500 μm in D, E, G, and 100 μm in C, F.

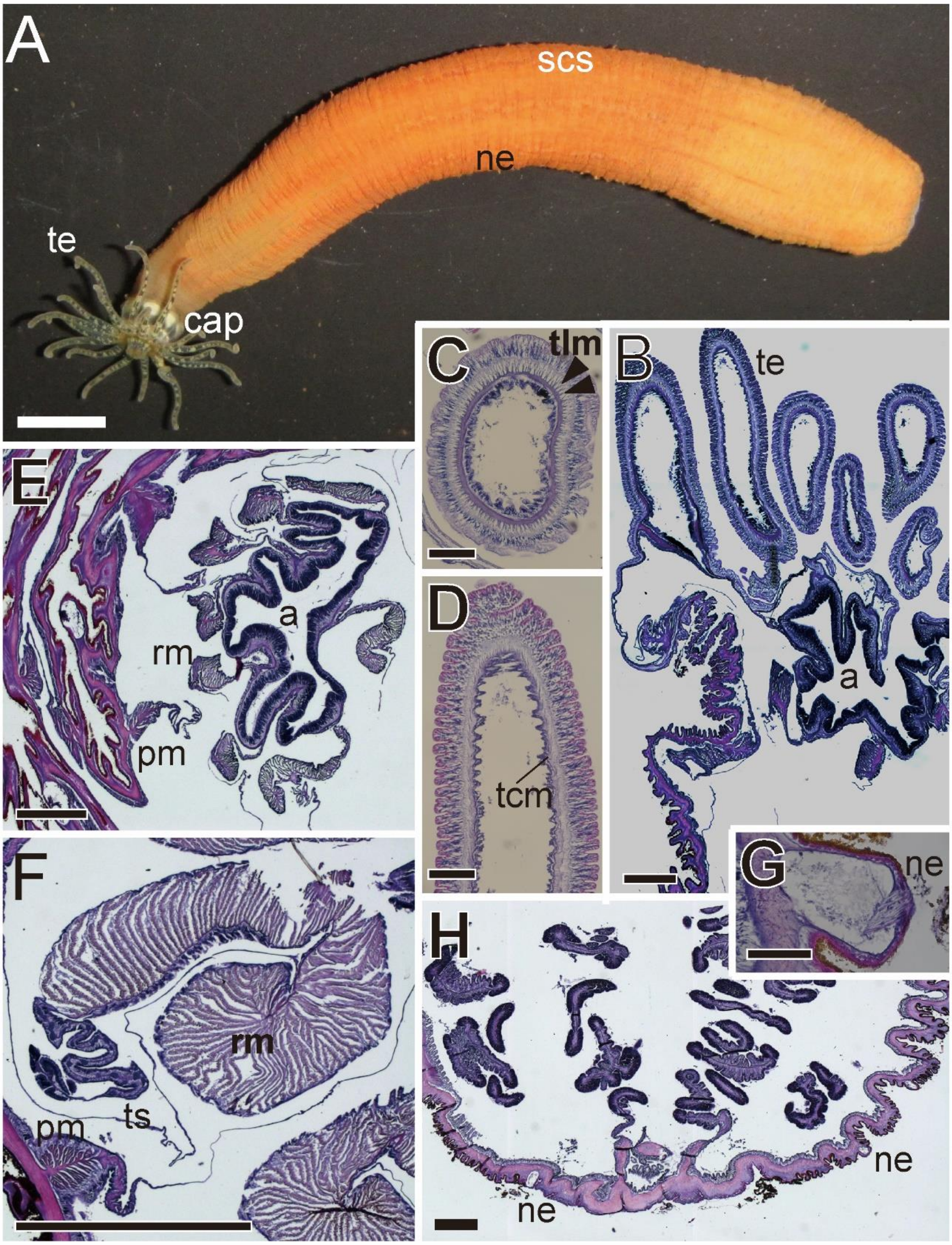

Fig. 55. External and internal views of *Edwardsia ena* (Izumi and Fujita, 2019) comb. nov., (NSMT-Co 1610).
A. External view. Whole living specimen of *S. ena*. B–H, Internal view. B. Longitudinal section of distal end. C. Transverse section of tentacle. D. Longitudinal section of tentacle. E. Transverse section of actinopharynx F. Enlarged view of mesentery. G. Transverse section of nemathybome. H. Longitudinal section of aboral end. Nemathybomes distributed up to aboral end. Abbreviations: a, actinopharynx; ne, nemathybome; pm, parietal muscle; rm, retractor muscle; tcm, tentacular circular muscle; te, tentacle; tlm, tentacular longitudinal muscle; ts, testis. Scale bars indicate 5 mm in A, 1 mm in B, 500 μm in E, F, H and 100 μm in C, D, G. Picture A was taken by Masaatsu Tanaka.

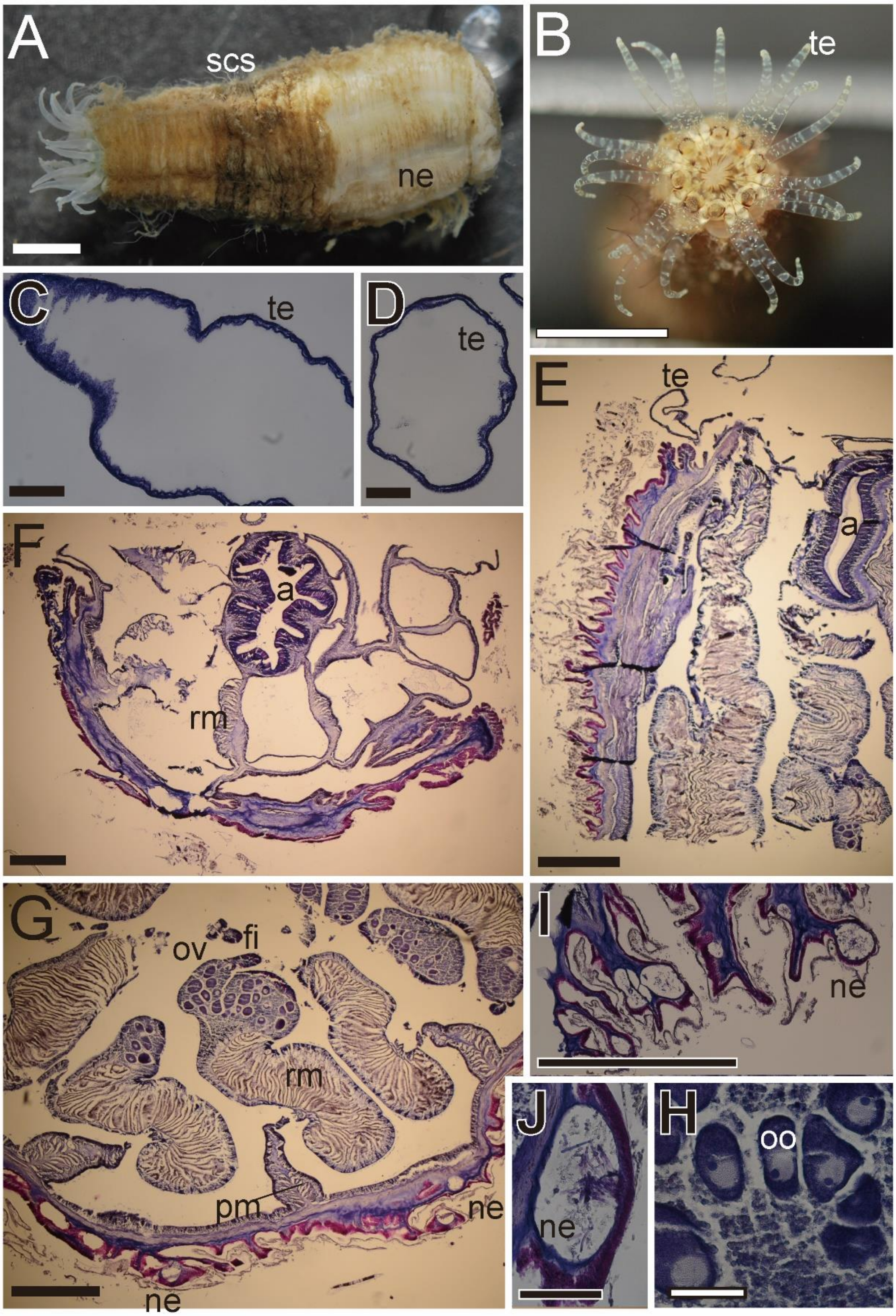

Fig. 56. External and internal views of *Edwardsia isei* (Izumi and Fujita, 2019) comb. nov., (NSMT-Co 1611).
A and B, External view; A. Whole preserved specimen of *E. isei*. B. View of tentacular circle of living specimen. C-J, Internal view (histological section); C. Longitudinal section of tentacle. D. Transverse section of tentacle. E. Longitudinal section of oral end. F. Transverse section of actinopharynx (half of body). G. Enlarged view of mesentery. H. Enlarged view of gonad. Several matured oocytes contained. I. Densely distributed nemathybomes. J. Enlarged view of transverse section of nemathybome. Abbreviations: a, actinopharynx; ne, nemathybome; oo, oocyte; ov, ovary; pm, parietal muscle; rm, retractor muscle; te, tentacle. Scale bars indicate 5 mm in A, B, 500 μm in E, F, G, I and 100 μm in C, D, H, J

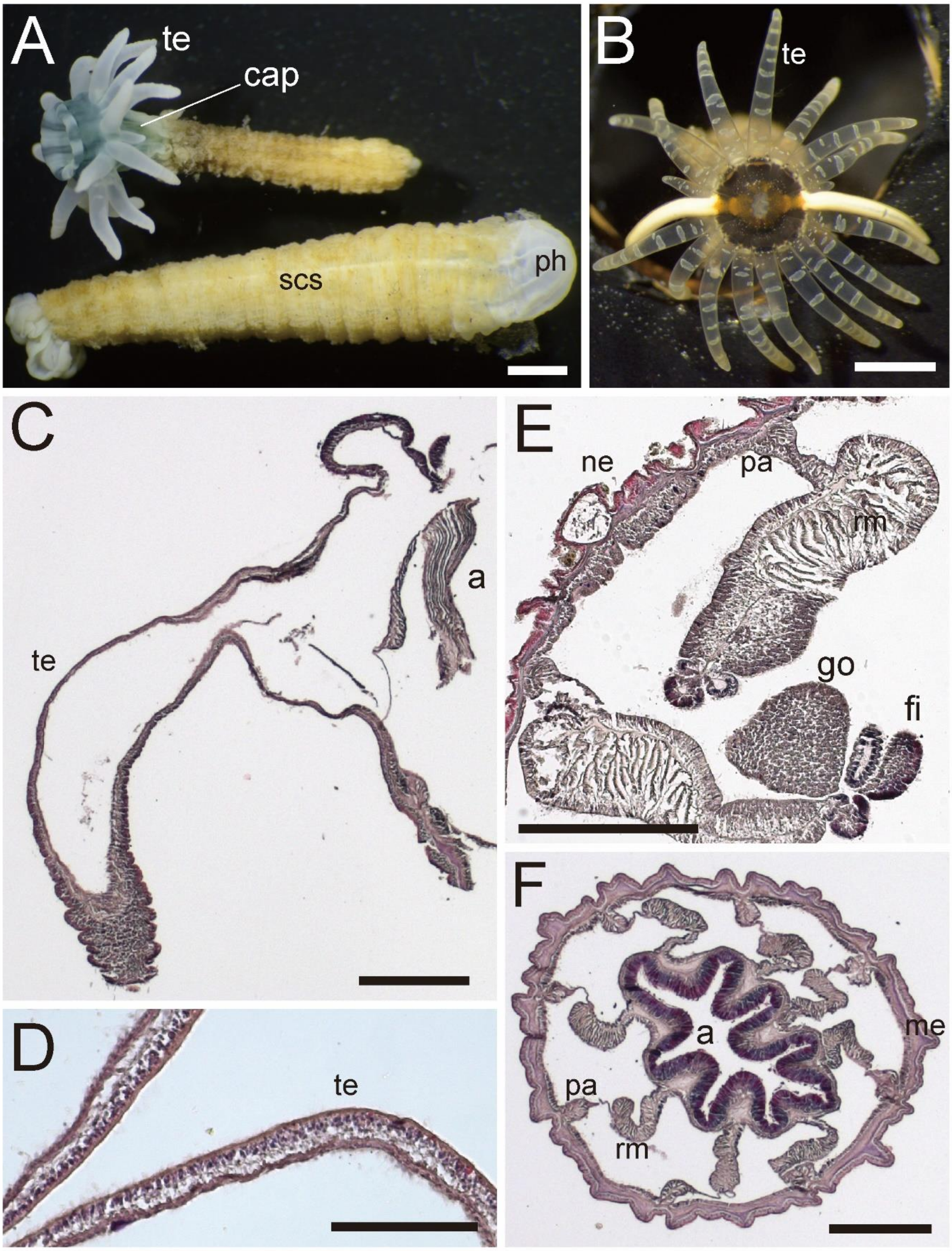

Fig. 57. External and internal views of *Edwardsia* sp. nov. 19 (Iz-074).
A. Whole preserved specimen (dissected). B. Oral view of tentacular circle in living specimen. C. longitudinal section of tentacle and distal part. D. Transverse section of tentacle. E. Transverse section of column in lower part. F. Transverse section of upper part of section. Abbreviations: a, actinopharynx; cap, capitulum; fi, filament; go, gonad; me, mesoglea; ne, nemathybome; pa, parietal muscle; ph, physa; rm, retractor muscle; te, tentacle. Scale bars indicate 1 mm in A, B, 500 μm in C, E, F, and 100 μm in D.

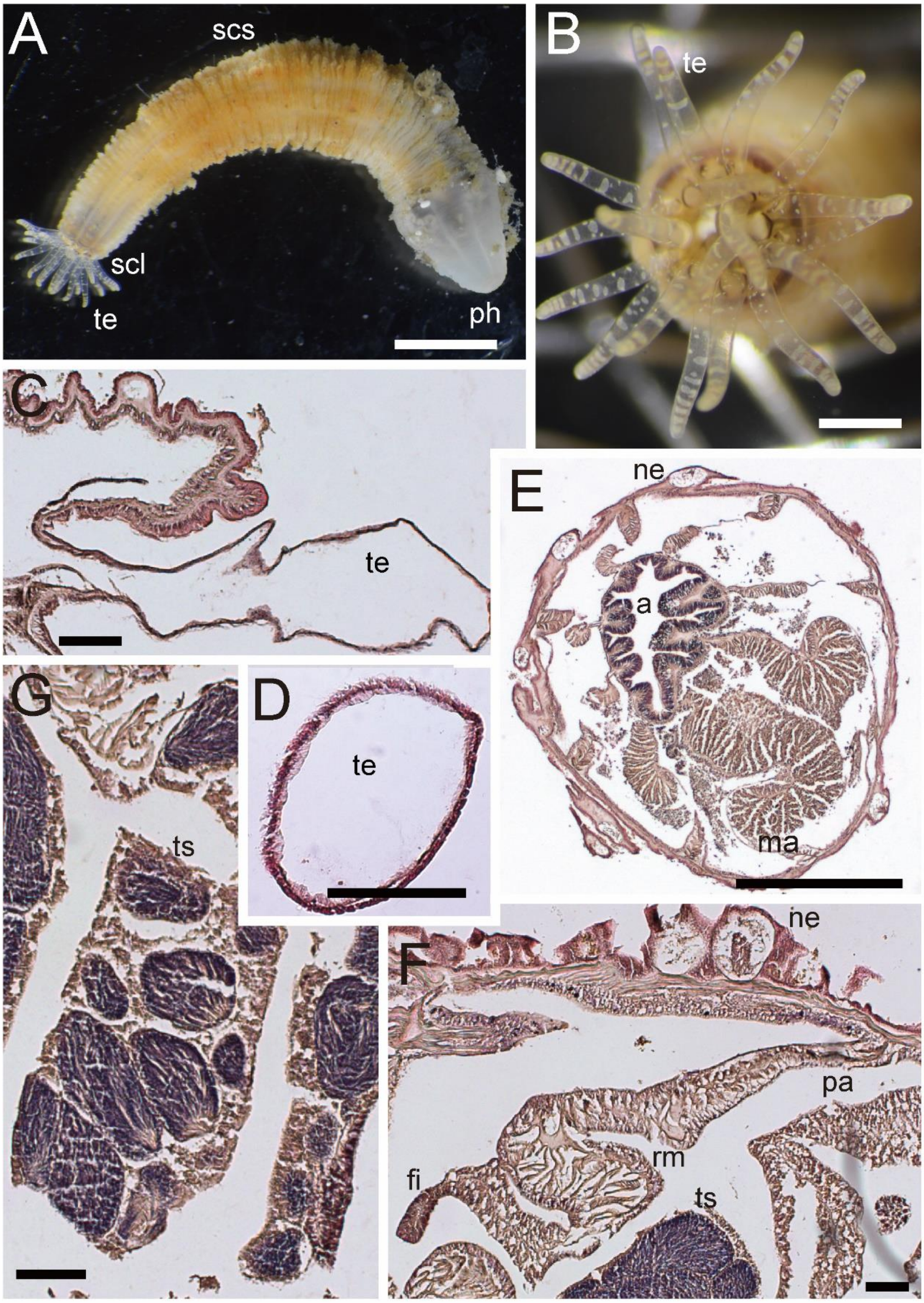

Fig. 58. External and internal views of *Edwardsia* sp. nov. 20 (Iz-075).
A. Whole living specimen. B. Oral view of tentacular circle in living specimen. C. longitudinal section of tentacle. D. Transverse section of tentacle. E. Transverse section of column in upper part. F. Enlarged view of section of testis. G. Transverse section of a macrocneme. Abbreviations: a, actinopharynx; fi, filament; ma, macrocneme; ne, nemathybome; pa, parietal muscle; rm, retractor muscle; te, tentacle; ts, testis. Scale bars indicate 5 mm in A, B, 1 mm in E, and 100 μm in C, D, F, G.

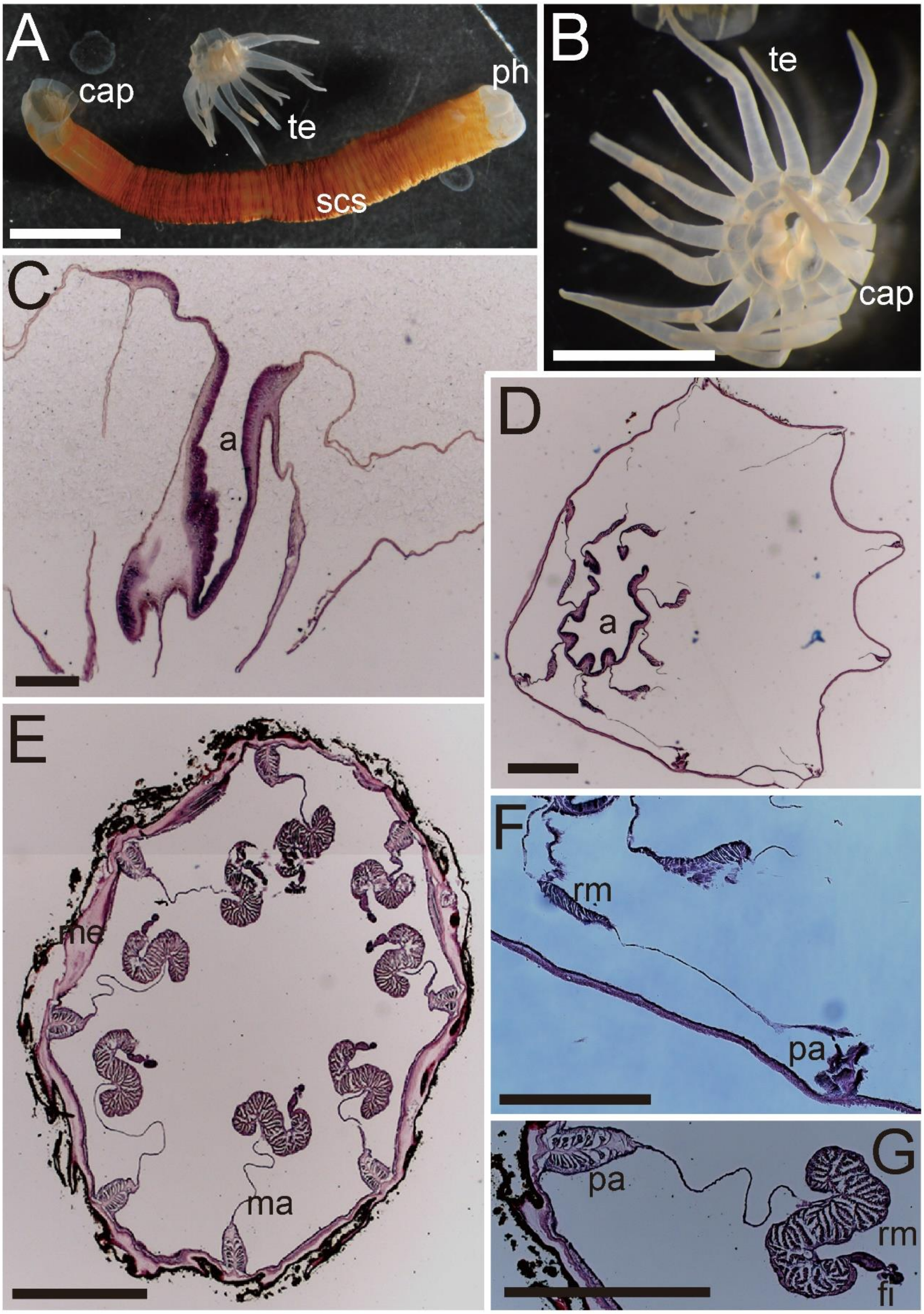

Fig. 59. External and internal views of *Edwardsia* sp. nov. 21 (CMNH-ZG 04762). A. Outer view of the preserved specimen. B. Oral view of the preserved specimen. C. Longitudinal section of distal end. D. Transverse section of column in upper part. E. Transverse section of column in lower part. F. Enlarged view of Transverse section of mesenteries with actinopharynx. G. Enlarged view of transverse section of mesentery in lower part. Abbreviations: a, actinopharynx; cap, capitulum; fi, filament; ma, macrocneme; pa, parietal muscle; ph, physa; rm, retractor muscle; te, tentacle. Scale bars indicate 5 mm in A, B, 500 µm in C–G.

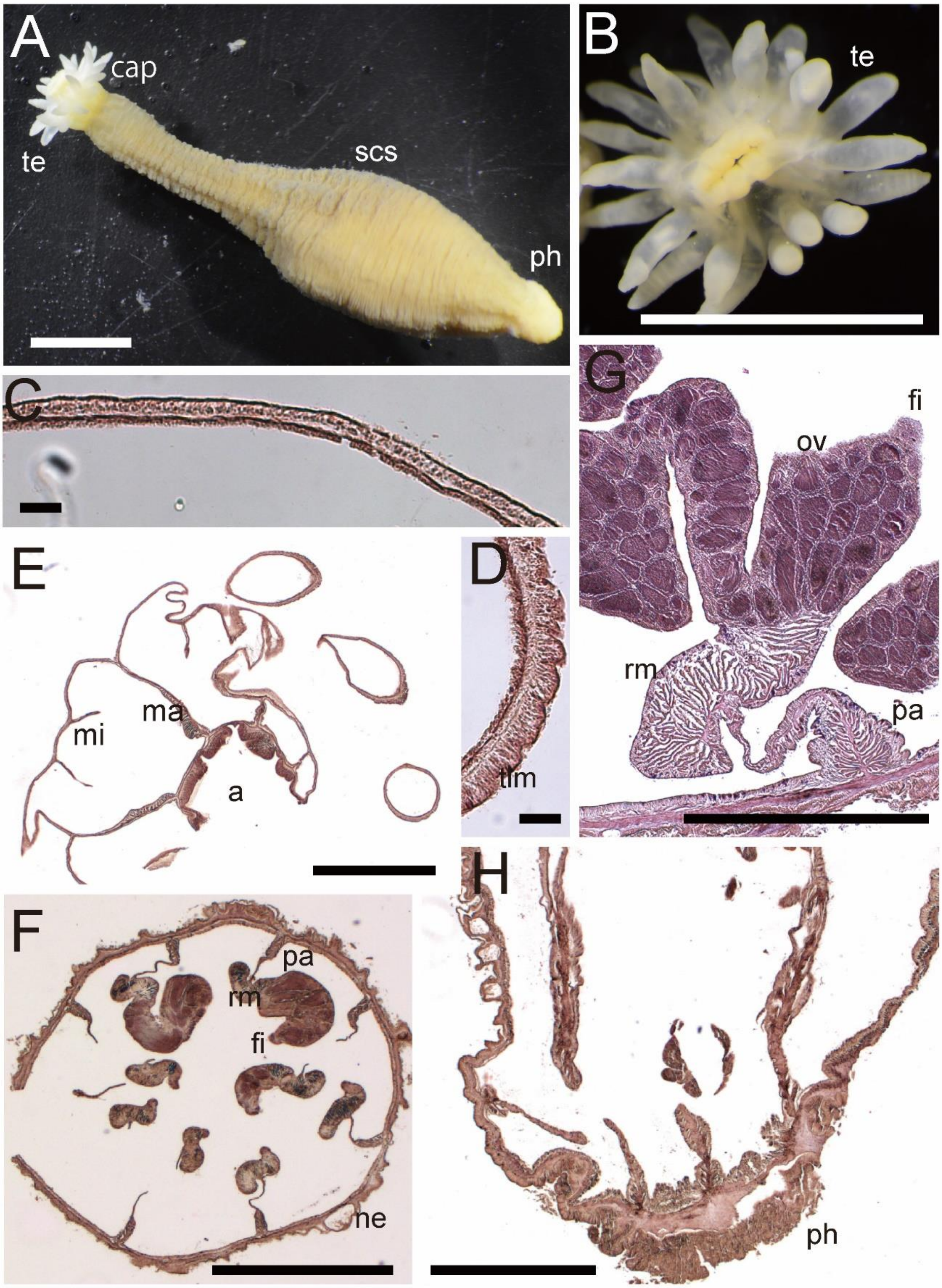

Fig. 60. External and internal views of *Edwardsia* sp. nov. 22 (Iz-076).
A. Whole preserved specimen. B. Oral view of tentacular circle in preserved specimen. C. longitudinal section of tentacle. D. Transverse section of tentacle. E. Transverse section of column in upper part. F. Transverse section of lower column. G. Enlarged view of transverse section of mesentery. H. Longitudinal section of aboral end. Abbreviations: a, actinopharynx; cap, capitulum; fi, filament; ma, macrocneme; mi, microcneme; ov, ovary; pa, parietal muscle; ph, physa; rm, retractor muscle; te, tentacle; tlm, tentacular longitudinal muscle. Scale bars indicate 5 mm in A, B, 1 mm in E–H, and 100 μm in C, D.

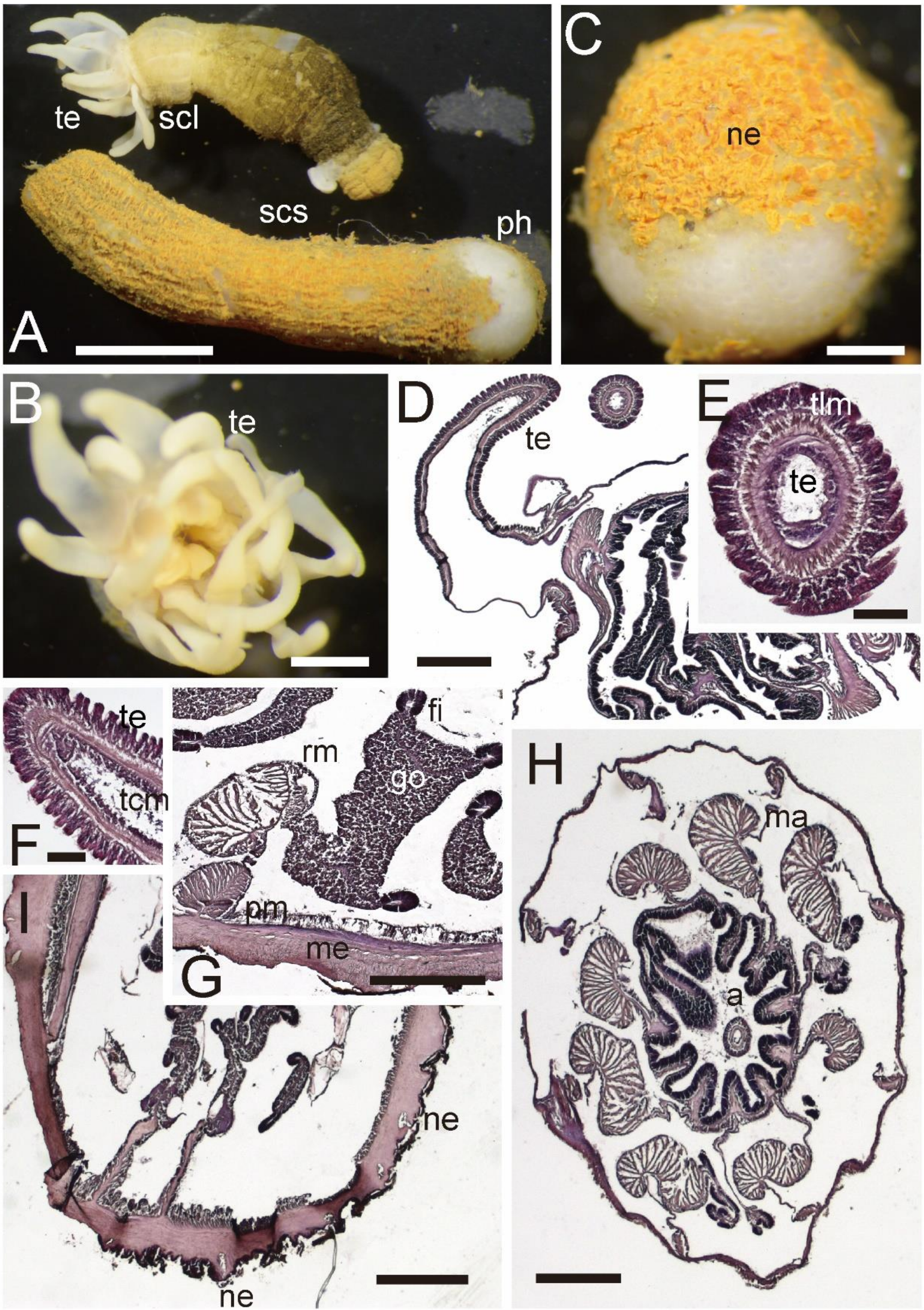

Fig. 61. External and internal views of *Edwardsia* sp. nov. 23 (Iz-078). A. Dissected preserved specimen. B. Oral view of tentacular circle in preserved specimen. C. Enlarged view of aboral end. D. Longitudinal section of distal end. E. Transverse section of tentacle. F. Longitudinal section of tentacle. G. Enlarged view of Transverse section of a macrocneme. H. Transverse section of upper column. I. Longitudinal section of aboral end. Abbreviations: a, actinopharynx; fi, filament; go, gonad; ma, macrocneme; me, mesoglea; ne, nemathybome; pa, parietal muscle; ph, physa; rm, retractor muscle; scl, scapulus; scs, scapus; tcm, tentacular circular muscle; te, tentacle; tlm, tentacular longitudinal muscle. Scale bars indicate 5 mm in A, B, 500 μm in D, G – I, and 100 μm in E, F.

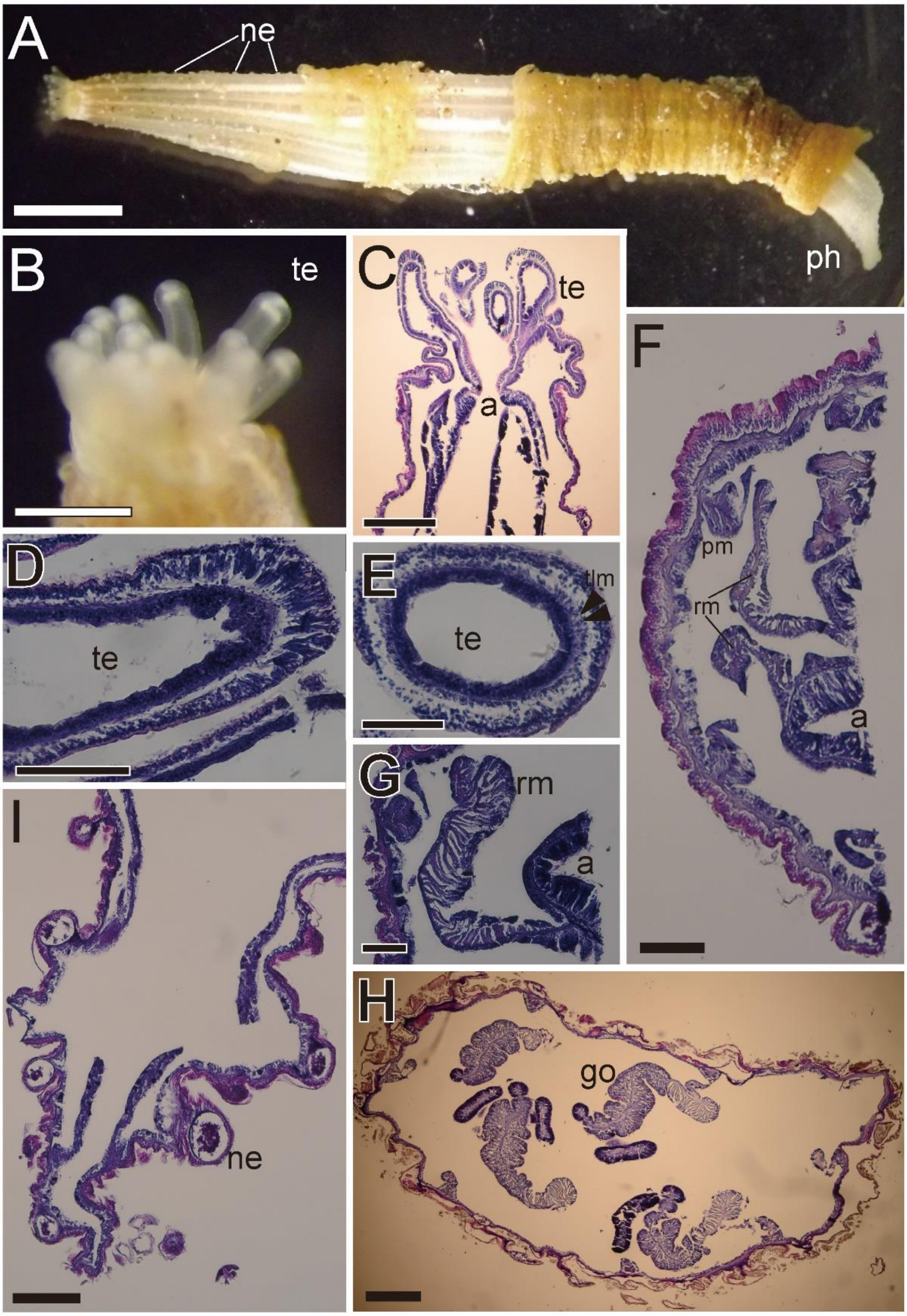

Fig. 62. External and internal views of *Edwardsia armata* (NSMT-Co 1609). External views (A, B) and internal histological sections (C–I). A. Whole living specimen of *E. armata*. The periderm of aboral end was stripped off while the sampling. B. Enlarged view of most distal part C. Longitudinal section of oral end. D. Longitudinal section of a tentacle. E. Transverse section of a tentacle. F. Transverse section of actinopharynx of the longitudinal half of body. G. Transverse section of mesentery. H. Transverse section of filaments. I. Longitudinal section of aboral end. Nemathybomes distributed up to the tip of aboral end. Abbreviations: a, actinopharynx; go, gonad; ne, nemathybome; ph, physa; pm, parietal muscle; rm, retractor muscle; te, tentacle; tlm, tentacular longitudinal muscle. Scale bars indicate 5 mm in A, 1 mm in B, 500 μm in C, F, H, I and 100 μm in D, E, G.

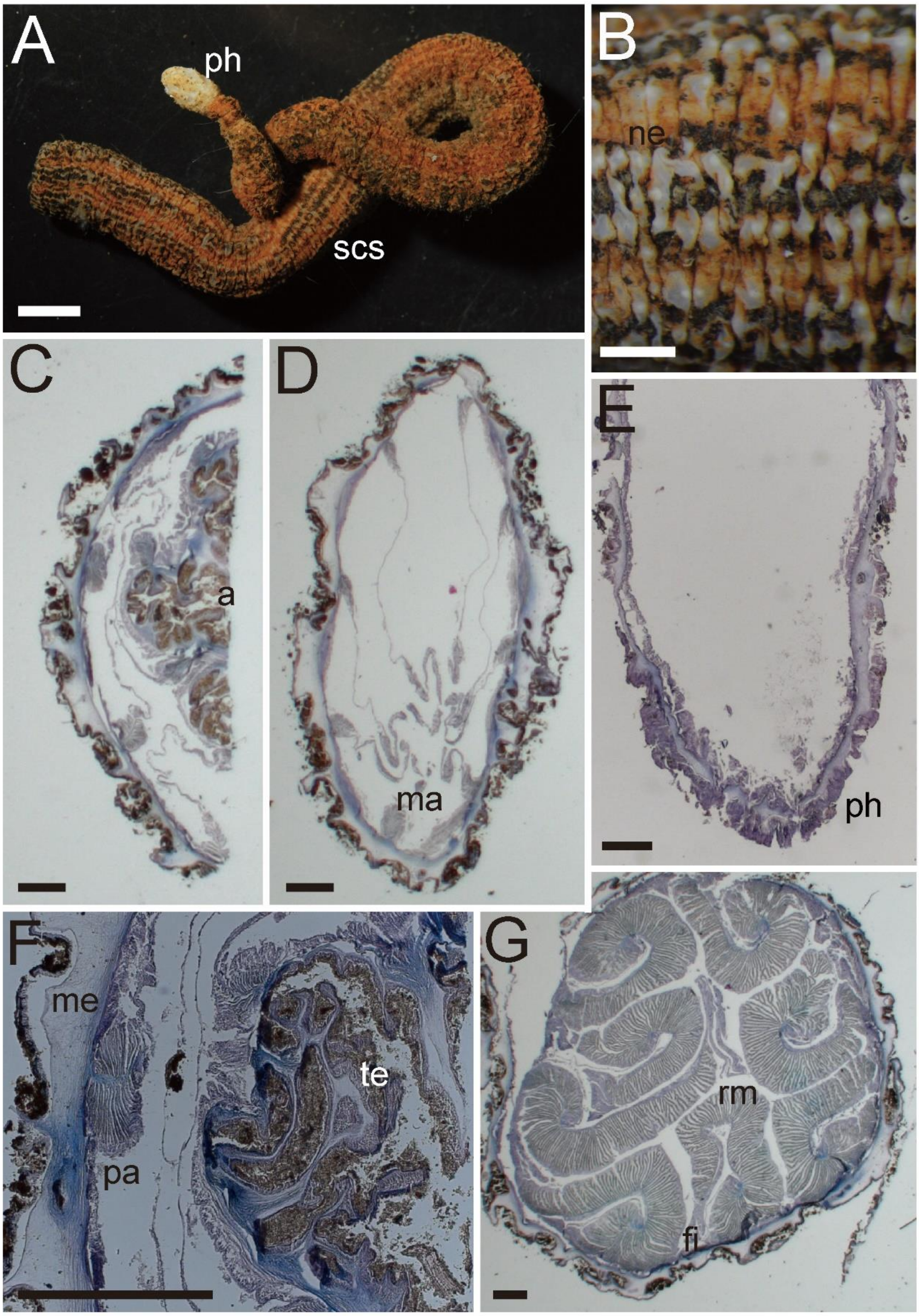

Fig. 63. External and internal morphology of *Edwardsia* sp. nov. 24 (CMNH-ZG [no registration]).
A. Outer view of preserved specimen; B. Enlarged view of nemathybomes (connected each other); C. Transverse section of column in upper part; D. Transverse section of column in middle part; E. Longitudinal section of aboral end; F. Enlarged view of transverse section of tentacle and parietal muscle; G. Transverse section of column in lower part. Abbreviations: a, actinopharynx; fi, filament; me, mesoglea; ne, nemathybome; pa, parietal muscle; ph, physa; rm, retractor muscle; scs, scapus; te, tentacle. Scale: 5 mm in A; 1 mm in B; 500 μm in C–G.

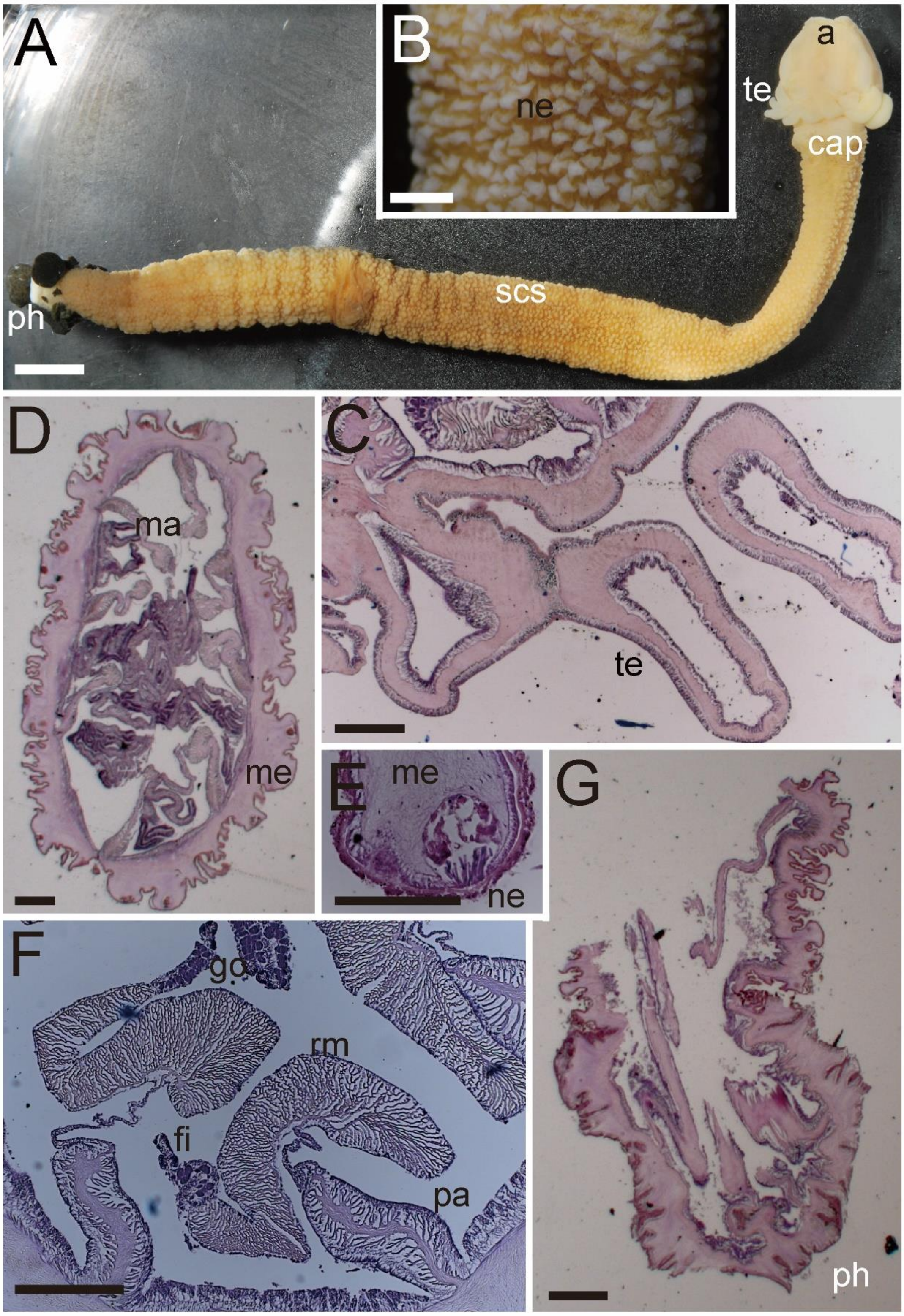

Fig. 64. External and internal morphology of *Edwardsia* sp. nov. 25 (CMNH-ZG [no registration]).
A. Oral view of preserved specimen; B. Enlarged view of nemathybomes; C. Longitudinal section of tentacle; D. Transverse section of column in lower part; E. Enlarged view of transverse section of nemathybome; F. Transverse section of a mesentery; G. Longitudinal section of aboral end. Abbreviations: a, actinopharynx; cap, capitulum; fi, filament; go, gonad; ma, macrocnemes; me, mesoglea; ne, nemathybome; pa, parietal muscle; ph, physa; rm, retractor muscle; scs, scapus; te, tentacle. Scale: 5 mm in A; 1 mm in B; 500 μm in C, D, F, G; 100 μm in E.

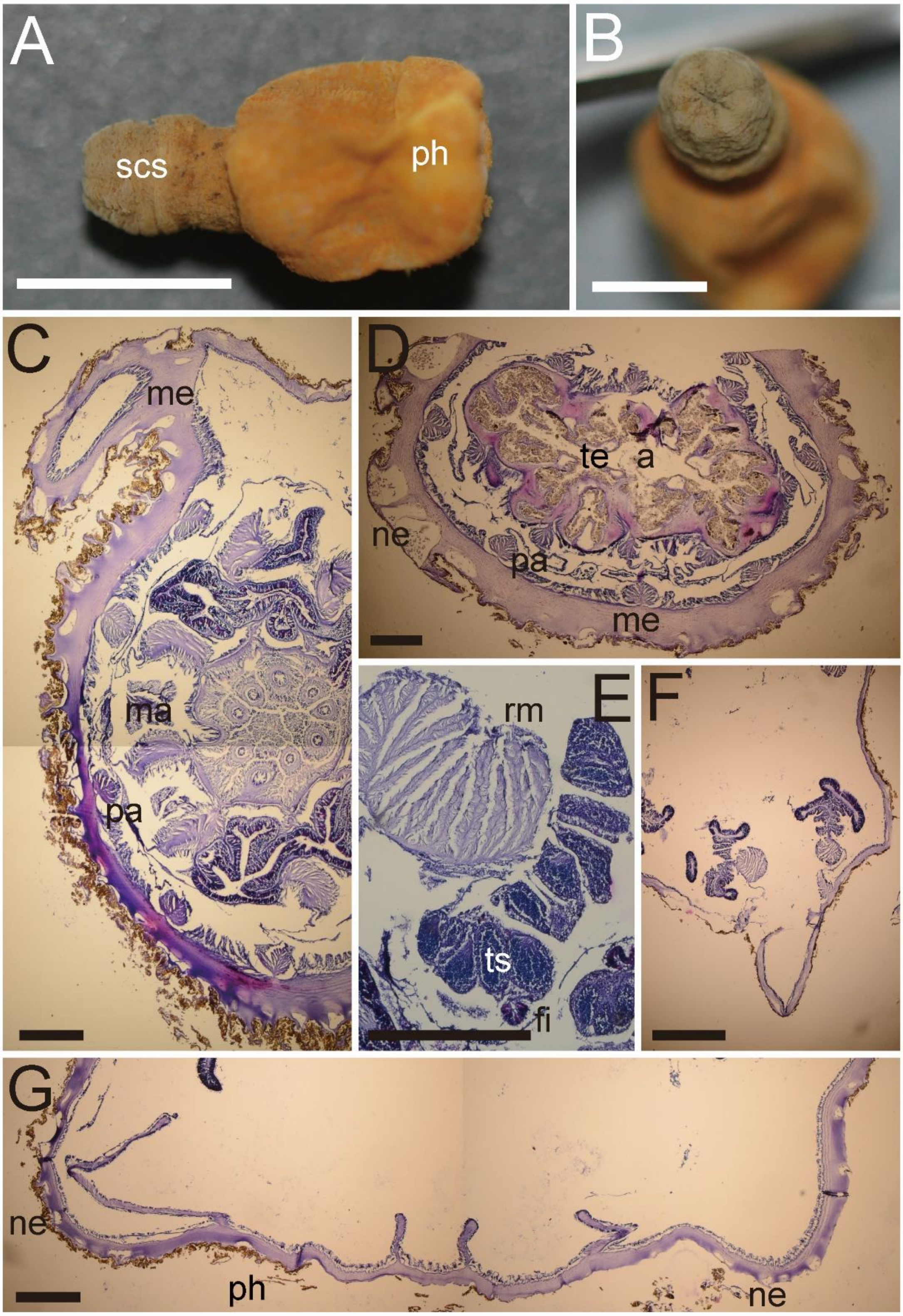

Fig. 65. External and internal morphology of *Edwardsia* sp. nov. 26 (Iz-081). A. Outer view of preserved specimen; B. Oral view of preserved specimen; C. Transverse section of column in middle part and tentacles; D. Transverse section of column in upper part; E. Enlarged view of Transverse section of retractor muscle; F. Transverse section of column in lower part; G. Longitudinal section of aboral end. Abbreviations: a, actinopharynx; fi, filament; ma, macrocneme; me, mesoglea; ne, nemathybome; pa, parietal muscle; ph, physa-like organ; rm, retractor muscle; scs, scapus; te, tentacle; ts, testis. Scale: 5 mm in A; 1 mm in B; 1 mm in C–E; 200 μm in H; 100 μm in F, G.

Table 17. Comparison of genus *Tempuractis* and all other genera of Edwardsiidae.

	Tempuractis **Izumi, Ise and Yanagi, 2018**	*Edwardsiella* Andres, 1883	*Halcampogeton* Carlgren, 1937	*Drillactis* Verrill, 1922	**Synhalcampella* Carlgren, 1921	***Edwardsia*** **de Quatrefages, 1842**
Type species	*Tempuractis rinkai* Izumi, Ise and Yanagi, 2018	*Edwardsiella carnea* (Gosse, 1856)	*Halcampogeton papillous* Carlgren, 1937	*Drillactis pallida* (Verrill, 1880)	*Synhalcampella ostroumowi* (Wyragevitch, 1905)	*Edwardsia beautempsii* de Quatrefages, 1842
Characters						
Main habitat	In Oscarella sponges	Various (In ice, rock crevices, or sand)	In sand or mud	In sand or mud	Unknown	In sand or mud
Structures on the column	None, smooth	Thick periderm	Robust papillae	None, smooth	Tenaculi	Thin periderm Nemathybomes or trace of them
Distribution of microcnemes	Only at distal end	Only at distal end	Only at distal end	Only at distal end	In whole body	Only at distal end
References	Izumi et al. (2018a) **The present study**	Andres (1883) Gosse (1856) Manuel (1981a) Daly (2002b) Daly et al. (2013) **The present study**	Carlgren (1937) **The present study**	Verrill (1880) Verrill (1922) Carlgren (1949) **The present study**	Wyragevitch (1905) Carlgren (1921) Carlgren (1949)	de Quatrefages (1842) Gosse (1853) Nordgaard (1905) Carlgren (1949) Manuel (1981) England (1987) Brandão (2019) **The present study**

*Genus without molecular phylogenetic information

Table 18. Cnidoms of the species of *Tempuractis*, *Edwardsiella, Halcampogeton* and *Drillactis*.

	Tempuractis rinkai NSMT-Co 1573		*Edwardsiella* sp. nov. 6 CMNH-ZG (no registration)		*Halcampogeton* sp. nov. 7 Iz-040		*Drillactis* sp. nov. 8 Iz-041	
	Length × Width (µm)	frequency	Length × Width (µm)	frequency	Length × Width (µm)	frequency	Length × Width (µm)	frequency
Tentacle								
basitrichs	12.1–18.0 × 2.1–3.4	numerous	12.4–17.9 × 2.5–4.0	numerous	19.5–22.5 × 4.8–6.4	numerous	11.1–14.7 × .1.5–2.5	a few
spirocysts	13.6–24.9 × 2.3–4.1	numerous	13.7–25.5 × 2.8–5.2	numerous	18.3–37.1 × 3.6–7.7	numerous	10.4–18.1 × 2.5–4.1	numerous
holotrichs	23.6–27.2 × 3.4–5.0	rare						
Actinopharynx								
basitrichs	6.7–19.6 × 1.0–4.1	numerous	15.2–22.9 × 2.4–4.1	numerous			12.6–20.3 × 1.7–3.1	numerous
holotrichs					26.0–29.5 × 5.9–7.2	a few		
microbasic *p*-mastigophores	21.9–27.7 × 3.7–5.6	numerous	17.6–23.5 × 4.1–6.4	numerous	24.5–31.6 × 5.6–7.9	numerous		
microbasic *b*-mastigophores			18.9–21.9 × 5.9–8.4	numerous				
macrobasic mastigophores			33.2–42.7 × 7.4–10.0	numerous				
Column								
basitrichs	8.2–13.6 × 1.7–2.9	numerous					14.8–41.9 × 1.1–2.3	numerous
spirocysts	17.2–20.7 × 2.6–3.8	rare						
holotrichs	13.0–30.2 × 3.1–7.0	numerous			30.6–35.2 × 6.7–7.9	rare		
microbasic *p*-mastigophores	21.0–27.0 × 4.3–5.7	rare			30.8–41.4 × 6.2–8.7	numerous		
microbasic *b*-mastigophores			21.6–33.5 × 3.2–4.6	numerous				
Filament								
basitrichs	10.1–29.8 × 2.1–7.0	numerous	15.0–25.4 × 2.6–4.1	a few			10.3–27.7 × 0.9–2.3	numerous
microbasic *p*-mastigophores	21.0–27.0 × 4.3–5.7	a few	18.0–23.4 × 4.9–5.9	a few	19.5–35.4 × 3.2–7.8	numerous	19.7–26.7 × 4.3–6.1	a few
microbasic *b*-mastigophores			19.2–24.4 × 6.7–7.9	numerous				
macrobasic mastigophores			26.4–42.2 × 7.0–10.0	numerous				

Table 19. Comparison of *Edwardsiella* sp. nov. 6 and the other species of genus *Edwardsiella*.

	***Edwardsiella* sp. nov. 6**	*Edwardsiella andrillae* Daly, Rock, and Zack, 2013	*Edwardsiella carnea* (Gosse, 1856)	*Edwardsiella ignota* (Carlgren, 1959)	*Edwardsiella janthina* (Andres, 1881)	*Edwardsiella liniata* (Verrill, 1873)	*Edwardsiella loveni* (Carlgren, 1892)
Characters							
Distribution	Pacific Sea	Antarctic Sea	Atlantic Sea	Pacific Sea	Atlantic Sea	Atlantic Sea	Pacific Sea and Atlantic Sea
Habitat	In sand	In ice shelf	In rock crevices	In sand	Unknown	In rock crevices	In rock crevices
Arrangement of tentacles	Octamerous	Octamerous	Hexamerous	Hexamerous	Hexamerous	Hexamerous	Hexamerous
Number of tentacular cycle	2	2	3	3	Unknown	2-3	3
References	**The present study**	Daly et al. (2013)	Gosse (1856) Carlgren (1949) Dnyansagar et al. (2018)	Carlgren (1959)	Andres (1881) Carlgren (1949)	Verrill (1873) Daly (2002b)	Carlgren (1892) Sanamyan et al. (2018)

Table 20. Comparison of *Drillactis* sp. nov. 8 and the other species of the genus.

	***Drillactis* sp. nov. 8**	*Drillactis pallida* (Verrill, 1879)	*Drillactis pallida* (Parry, 1951)
Characters			
Body length	14 mm	Reach to 100 mm	Reach to 100 mm
Number of tentacles	16	Often 18, maximum 24	48
Pattern of tentacles	Transparent, a white patch on the tips	Greenish or grayish white, a olive-green line in the center, with opaque white spots	Translucent, two longitudinal brack lines, and white patches
References	**The present study**	Verrill (1879) Verrill (1922)	Parry (1951)

Table 21. Cnidoms of the species of *Edwardsia* (*Edw.* sp. nov. 9-*Edw.* sp. nov. 12).

		Edwardsia sp. nov. 9 CMNH-ZG 05954		*Edwardsia* sp. nov. 10 (Iz-055)		*Edwardsia* sp. nov. 11 (Iz-056)		*Edwardsia* sp. nov. 12 (Iz-057)	
		Length × Width (µm)	frequency	Length × Width (µm)	frequency	Length × Width (µm)	frequency	Length × Width (µm)	frequency
Tentacle									
basitrichs	S	25.9-34.6 × 2.7-4.3	numerous	25.4-40.3 × 3.0-4.7	numerous	27.5-37.3 × 3.0-4.8	numerous	17.0-32.6 × 2.7-4.3	numerous
spirocysts		11.8-21.0 × 2.5-3.7	numerous	12.1-21.7 × 2.5-5.1	numerous	14.9-23.6 × 2.8-4.9	numerous	14.6-24.1 × 3.0-4.9	numerous
Actinopharynx									
basitrichs	S	14.3-16.9 × 3.5-3.9	rare	20.5-23.6 × 2.5-3.0	a few	20.2-25.9 × 2.3-3.6	numerous	12.3-18.2 × 2.7-4.7	numerous
	L	36.1-48.8 × 3.2-5.0	numerous	34.9-47.7 × 3.5-5.9	numerous	34.1-44.1 × 3.6-5.6	numerous	28.9-49.1 × 3.8-4.7	rare
microbasic *p*-mastigophores	S			35.1-42.0 × 7.2-8.5	rare				
Nemathybome									
basitrichs	S	16.6-19.9 × 3.9-4.1	rare	16.5-17.1 × 3.0-3.7	rare	16.9-20.5 × 3.2-3.9	a few		
	L	46.8-56.6 × 3.2-5.6	numerous	48.7-61.6 × 3.0-4.7	numerous	39.8-75.2 × 2.8-4.9	numerous		
Column									
basitrichs		47.9-53.8 × 3.4-4.8	numerous						
Filament									
basitrichs	S	22.4-32.2 × 3.2-5.0	numerous	18.6-32.2 × 2.5-4.1	numerous	25.2-29.8 × 2.6-3.9	rare	12.6-17.3 × 2.9-4.8	numerous
	L			39.3-52.0 × 4.6-7.1	numerous	38.4-50.5 × 4.3-6.2	numerous	27.4-46.3 × 3.6-5.2	numerous
spirocysts				15.6-18.2 × 3.0-4.2	rare			13.3-23.6 × 3.2-6.1	numerous
microbasic *b*-mastigophores		27.6-44.3 × 4.1-5.8	a few						
microbasic amastigophores		30.1-31.8 × 5.3-5.9	rare	30.9-41.2 × 6.6-8.6	a few	33.1-42.3 × 5.9-8.3	numerous	35.1 × 7.8	rare

Table 23. Cnidoms of the species of *Edwardsia* (*Edw.* sp. nov. 13-*Edw.* sp. nov. 15).

		Edwardsia sp. nov. 13 (Iz-058)		*Edwardsia* sp. nov. 14 (Iz-060)		*Edwardsia* sp. nov. 15 (Iz-064)	
		Length × Width (µm)	frequency	Length × Width (µm)	frequency	Length × Width (µm)	frequency
Tentacle							
basitrichs		10.2-22.7 × 2.7-5.0	numerous	9.7-27.3 × 2.4-4.3	numerous	11.6-35.5 × 2.5-4.4	numerous
spirocysts				9.6-13.2 × 2.1-3.5	numerous	9.6-11.3 × 2.6-3.6	rare
Actinopharynx							
basitrichs	S	16.2-26.4 × 3.8-4.4	a few	12.7-18.6 × 1.8-3.4	numerous	16.7-36.7 × 2.4-5.1	numerous
	L			25.2-33.6 × 3.2-5.5	numerous		
microbasic *p*-mastigophores				24.0-34.1 × 5.5-9.3	numerous		
Nemathybome							
basitrichs	S	24.1-49.1 × 3.0-4.4	numerous	9.6-16.0 × 2.8-4.3	numerous	10.4-16.7 × 2.3-3.5	a few
	L					32.9-42.3 × 3.3-5.2	numerous
Column							
basitrichs				11.7-33.5 × 2.9-4.9	numerous	11.2-17.8 × 2.7-4.1	numerous
Filament							
basitrichs		13.4-21.9 × 2.4-3.7	numerous	11.6-23.6 × 2.8-3.9	numerous	12.0-25.8 × 2.2-3.7	a few
spirocysts							
microbasic *p*-mastigophores		22.4-32.2 × 4.1-6.3	numerous			25.3-29.2 × 7.6-10.1	a few
microbasic *b*-mastigophores		18.0-25.3 × 4.6-7.3	numerous	24.9-32.6 × 3.8-6.2	numerous	26.3-40.6 × 3.6-6.1	numerous
microbasic amastigophores				27.0-36.3 × 6.8-10.5	numerous		

Table 22. Comparison of nine new species of genus *Edwardsia* and the other two species which had accommodated in genus *Edwardsianthus* England, 1987.

	***Edwardsia* sp. nov. 9**	***Edwardsia* sp. nov. 10**	***Edwardsia* sp. nov. 11**	***Edwardsia* sp. nov. 12**	***Edwardsia* sp. nov. 13**
Characters					
Body length (Preserved)	60 mm (a little damaged)	70 mm	150 mm	200 mm	50-65 mm
Number of tentacles	20	20	20	20	20
(Arrangement)	(5+15)	(5+15)	(5+15)	(5+15)	(5+15)
Shape of tentacles	Blunt (inner), slender (outer)	Slender	Slender	Slender, capitated on the tip	Slender
Color and pattern of tentacles	Vivid scarlet, some white patches	Brilliant green, pale purple on the tip	Meteric greenish blue	Pale purple with dark purple patches	Whitish opaque (one dorsal tentacle) Brownish translucent (the other)
Retractor muscles	Strongly developed, diffused	Comparatively weak, diffused	Strongly developed, diffused	Strongly developed, diffused	Strongly developed, diffused
Number of muscular processes	60-90	50-60	120-150	100-150	50-70
Parietal muscles	Weak	Weak	Distinct, club-like form	Distinct, simple form	Distinct, simple form
Nemathybomes	Present, scattered	Present, scattered	Present, scattered	Absent	Present, scattered
Cnidom of nemathybomes	2 types of nematocysts	2 types of nematocysts	2 types of nematocysts	-	1 type of nematocysts
References	**The present study**	**The present study**	**The present study**	**The present study**	**The present study**

	***Edwardsia* sp. nov. 14**	***Edwardsia* sp. nov. 15**	***Edwardsia* sp. nov. 24**	***Edwardsia* sp. nov. 25**	***Edwardsia pudica* Klunzinger, 1877**	***Edwardsia gilbertensis* Carlgren, 1931**
Characters						
Body length (Preserved)	20-30 mm	20-25 mm	70 mm	100 mm	80-130 mm	20-40 mm
Number of tentacles	10	10	20	20	20	14-20
(Arrangement)	(3+7)	(3+7)	(5+15)	(5+15)	(8+12)	(4-5+10-15)
Shape of tentacles	Slender	Quite blunt, like rugby ball	Uncertain	Slender	Slender	Slender
Color and pattern of tentacles	Greenish brown, with white lines	Brown, with dense white patches	Uncertain	Uncertain	Purple or magenta pink, with brown patches	Gray with white patches
Retractor muscles	Weak, restricted	Distinctly developed, restricted	Strongly developed, diffused	Strongly developed, diffused	Strongly developed, diffused	Strongly developed, diffused
Number of muscular processes	60-90	20-30	70-90	60-80	around 100	15-36
Parietal muscles	Weak	Distinct, simple form	Distinct, simple form	Distinct, simple form	Distinct, simple form	Distinct, simple form
Nemathybomes	Present (arrangement uncertain)	Present (arrangement uncertain)	Present, moniliform	Present, scattered, obtrude	Present, scattered	Present, (more or less) in rows
Cnidom of nemathybomes	1 type of nematocysts	2 types of nematocysts	1 type of nematocysts	2 types of nematocysts	1 type of nematocysts	1 type of nematocysts
References	-	**The present study**	**The present study**	**The present study**	Klunzinger (1877) England (1987) **The present study**	Carlgren (1931) England (1987) Uchida and Soyama (2001) **The present study**

Table 24. Cnidoms of the species of *Edwardsia* (*Edw. alternobomen* and *Edw. tuberculata*).

		Edwardsia aff. tuberculata		*Edwardsia alternobomen*			
		NSMT-Co 1654		NSMT-Co 1656 (paratype)		NSMT-Co 1657 (holotype)	
		Length × Width (µm)	frequency	Length × Width (µm)	frequency	Length × Width (µm)	frequency
Tentacle							
basitrichs	S	20.1-31.2 × 2.8-4.9	numerous	12.8-20.8 × 2.6-3.7	a few	13.1-19.1 × 1.9-2.9	numerous
	L			26.0-38.0 × 3.1-4.8	numerous	24.6-35.3 × 3.8-4.6	rare
spirocysts		9.1-20.8 × 1.9-3.7	numerous	9.4-17.9 × 2.3-4.8	numerous	9.5-14.3 × 2.0-3.3	numerous
Actinopharynx							
basitrichs	S	15.7-20.8 × 1.8-2.9	numerous	13.2-38.3 × 2.6-4.5	numerous	12.0-26.3 × 2.0-3.9	numerous
	L	28.5-36.8 × 2.7-5.0	numerous				
spirocysts		15.5-20.2 × 2.4-3.6	numerous				
holotrichs							
microbasic *p*-mastigophores	S	20.7-28.8 × 4.2-7.4	numerous	22.6-33.3 × 4.6-6.8	numerous	19.0-25.0 × 5.0-8.1	numerous
Nemathybome							
basitrichs	S	77.1-99.1 × 2.9-4.8	a few	19.1-30.7 × 3.7-5.5	rare	17.4-67.4 × 2.4-3.8	a few
	L	116.1-187.1 × 4.8-9.0	numerous	70.3-202.6 × 5.1-8.4	numerous	82.4-195.2 × 5.5-8.6	numerous
Filament							
basitrichs	S	31.3-43.0 × 3.5-5.4	numerous	12.0-26.3 × 2.4-4.6	numerous	15.6-25.9 × 2.8-4.5	numerous
spirocysts				12.1-15.5 × 3.2-4.5	a few		
microbasic *p*-mastigophores						17.5-24.6 × 4.1-6.9	numerous
microbasic *b*-mastigophores	S	9.1-12.2 × 2.6-3.6	numerous				
	L	21.6-32.5 × 3.6-5.3	numerous				

Table 25. Comparison of *Edwardsia alternobomen* and the other species of the genus with 12 tentacles.

	Edwardsia alternobomen **Izumi and Fujita, 2019**	***Edwardsia andresi*** **Danielessen, 1890**	***Edwardsia duodecemtentaculala*** **Carlgren, 1931**	***Edwardsia fusca*** **Danielessen, 1890**	***Edwardsia jonesii*** **Seshaiya and Cuttress, 1969**	***Edwardsia juliae*** **Daly and Ljubenkov, 2008.**
Characters						
Body length	25-30 mm	90 mm	20-50 mm	55 mm	80 mm	5-10 mm
Arrangement of nemathybomes	in 8 rows (4 rows of large + 4 rows of small)	Scattered	Scattered	Scattered	in 16 rows (Equal size)	in 8 rows (Equal size)
Cnidom of nemathybomes	2 types of nematocysts	1 type of nematocysts	1 type of nematocysts	1 type of nematocysts	1 type of nematocysts	1 type of nematocysts
The maximum length of basitrichs in nemathybomes	> 200 µm	< 100 µm	< 100 µm	< 100 µm	< 100 µm	< 100 µm
References	**The present study**	Danielessen (1890) Carlgren (1921) England (1987)	Carlgren (1931)	Danielessen (1890) Carlgren (1921) England (1987)	Seshaiya and Cuttress (1969)	Daly and Ljubenkov (2008)

Table 26. Cnidoms of species of *Edwardsia* (*Edw. kopepe* comb. nov. and *Edw.* sp. nov. 16-*Edw.* sp. nov. 18).

		Edwardsia kopepe comb. nov. NSMT-Co 1614		*Edwardsia* sp. nov. 16 (Iz-070)		*Edwardsia* sp. nov. 17 (Iz-072)		*Edwardsia* sp. nov. 18 (Iz-073)	
		Length × Width (µm)	frequency	Length × Width (µm)	frequency	Length × Width (µm)	frequency	Length × Width (µm)	frequency
Tentacle									
basitrichs	S	11.3-17.3 × 2.8-4.1	numerous	12.1-72.7 × 2.2-5.1	numerous	29.4-68.4 × 2.0-3.5	numerous	41.6-62.1 × 3.1-4.7	numerous
	L	31.9-55.2 × 2.7-4.9	numerous						
spirocysts		10.4-18.3 × 1.6-2.8	numerous	12.0-21.0 × 1.7-3.0	numerous				
Actinopharynx									
basitrichs	S	14.9-28.3 × 2.3-3.8	numerous	12.2-15.5 × 1.7-2.0	rare	27.1-39.0 × 3.0-4.6	numerous	22.5-33.9 × 2.1-3.8	numerous
	M			22.7-35.9 × 2.4-3.9	a few				
	L	33.8-46.7 × 3.1-4.6	numerous	50.7-69.2 × 4.3-5.4	a few	54.6-77.0 × 4.2-6.8	numerous	33.6-55.5 × 3.7-5.5	numerous
spirocysts									
holotrichs									
microbasic *p*-mastigophores	S								
Nemathybome									
basitrichs	S	18.9-25.0 × 2.7-4.3	numerous			(no nemathybome-like structures)		31.9-51.6 × 3.6-5.3	numerous
	L	29.8-58.0 × 2.8-5.2	numerous						
Column									
basitrichs		14.3-50.5 × 3.9-4.2		17.3-19.9 × 3.9-4.0	rare				
Filament									
basitrichs	S	19.6-29.7 × 2.7-4.3	numerous	49.2-86.6 × 3.2-5.1	numerous	56.4-75.9 × 3.6-5.7	numerous	30.6-45.7 × 2.6-4.3	numerous
spirocysts									
microbasic *p*-mastigophores				46.2-60.1 × 6.0-9.0	numerous	49.0-61.7 × 6.5-9.1	numerous		
microbasic *b*-mastigophores	S	32.3-39.6 × 5.2-7.8	numerous					35.9-43.1 × 5.7-7.7	numerous
	L								

Table 27. Comparison of two new species of genus *Edwardsia* and species of *Scolanthus* Gosse, 1853 possibly assignable to *Edwardsia*.

	Edwardsia ena **(Izumi and Fujita, 2018) comb. nov.**	***Edwardsia isei*** **(Izumi and Fujita, 2019) comb. nov.**	***Edwardsia kopepe*** **(Izumi and Fujita, 2019) comb. nov.**	***Edwardsia armata*** **Carlgren, 1931**	****Scolanthus ignotus*** **(Carlgren, 1920)**	****Scolanthus ingolfi*** **(Carlgren, 1921)**
Characters						
Body length	80 mm	30 mm	15-25 mm	35-40 mm	20-30 mm	11-21 mm
Body width	10-15 mm	10-12 mm	1-2 mm	4-8 mm	3-7 mm	5-6 mm
Number of tentacles	20	20	16	16	20	16
Tentacular arrangement	10+10	8+12	8+8	8+8	10+10	Unknown
Pattern of oral disc	Brown, hemitransparent	White with brown radial pattens	White with a brownish red stripe	Uncertain	Unknown	Unknown
The number of muscular processes of retractor muscles	30-60	20-30	2-5	ca. 10	around 100	30 (well-branched)
Development of muscle	Restricted, distinct	Diffused, distinct	Restricted, weak	Restricted, distinct	Diffused, distinct	Distinct, diffused
Size lange of basitrichs in tentacles (Length × Width; µm)	21.2-38.3 × 2.4-3.6	10.1-13.0 × 1.8-2.8 19.1-26.6 × 3.0-4.5	11.3-17.3 × 2.8-4.1 31.9-55.2 × 2.7-4.9	13.1-54.4 × 2.7-5.3	18-29 × 2-2.5	31-36 × 3
Size lange of basitrichs in actinopharynx (Length × Width; µm)	22.6-26.9 × 2.4-2.9 37.5-51.2 × 3.0-4.7	21.9-39.8 × 3.1-4.7	14.9-28.3 × 2.3-3.8 33.8-46.7 × 3.1-4.6	19.4-39.6 × 2.7-4.8	34-42 × 3.5-4.5	41-46 × 3-4
Cnidom of nemathybomes	Two types of basitrichs	Two types of basitrichs	Two types of basitrichs	One type of basitrichs	One type of basitrichs	One type of basitrichs
Size lange of basitrichs in nemathybomes (Length × Width; µm)	9.7-15.2 × 2.2-3.2 63.9-105.6 × 3.4-5.5	9.7-12.4 × 2.0-3.2 62.8-85.0 × 3.8-6.2	18.9-25.0 × 2.7-4.3 29.8-58.0 × 2.8-5.2	36.2-63.0 × 3.4-5.8	34-48 × 3-3,5	50-60 × 4-5
References	The present study	The present study	The present study	Carlgren (1931) The present study	Carlgren (1920)	Carlgren (1921) Carlgren (1950)

	Scolanthus callimorphus **Gosse, 1853**	****Scolanthus crypticus*** **Brandão, Gusmão, and Gomes, 2019**	****Scolanthus curacaoensis*** **(Pax, 1924)**	****Scolanthus intermedius*** **(McMurrich, 1893)**	****Scolanthus nidarosiensis*** **(Carlgren, 1942)**	****Scolanthus scamiti*** **Daly and Ljubenkov, 2008**	****Scolanthus triangulus*** **Daly and Ljubenkov, 2008**
Body length	120-140 mm	10-15 mm	42-45 mm	17 mm	14 mm	15 mm	11 mm
Body width	12 mm	2-4 mm	3 mm	4.5 mm	1.5(distal)-2.4(proximal) mm	1.5(distal)-2.5(proximal) mm	4 mm
Number of tentacles	16	16	16	12	15	16	16
Tentacular arrangement	5+11	Unknown, but in two rows	Unknown	Unknown	Unknown	Unknown	Unknown
Pattern of oral disc	Pale buff or cream, with a well-defined pattern of rich, often purplish brown	Unknown	Unknown	Unknown	Translucent	Translucent	Unknown
The number of muscular processes of retractor muscles	Unknown	Few (4-5)	Around 50	Unknown	15-20	Around 30	Few (4-5)
Development of muscle	Distinct	Circumscribed, weak	Diffused, distinct	Unknown	Diffused, distinct	Diffused, distinct	Small but distinct, restricted
Size lange of basitrichs in tentacles (Length × Width; µm)	Unknown	26.9–56.5 × 2.5–4.2	Unknown	Unknown	34-45 × 2.8	16.0-24.7 (26.7) × (1.7) 2.1-3.4 18.4-42.4 × 2.0-3.9	15.6-18.3 × 1.9-2.7 (19.7) 21.7-29.9 × 2.0- 3.2
Size lange of basitrichs in actinopharynx (Length × Width; µm)	21-36 × 2.5-3.5 45-70 x 4.0-5.5	24.6–29.1 × 2.1–2.9	Unknown	Unknown	26-31 × 2.5-2.8 41-49.5 × 5.6	(15.3) 17.0-20.9 × 1.7-2.6 34.1-42.2 × 2.7-4.3	27.5-40.5 × 2.2- 3.2 27.5-32. 1 × 3.9-4.5
Cnidom of nemathybomes	One type of basitrichs	One type of basitrichs	One type of basitrichs	Unknown	Two types of basitrichs	Two types of basitrichs	Two types of basitrichs
Size lange of basitrichs in nemathybomes (Length × Width; µm)	60-90 × 3.0-5.0	24.3–56.3 × 3.9–5.5	(38) 43–53 × 2.5	Unknown	62-67 × 2.5-3	19.0-22.1 × 1.7-25 9.6-44.8 × 2.9-4.3(4.8)	25.6-33.5 × 2.0-2.8 50.1- 63.8 × 3.2-4.3
References	Gosse (1853) Manuel (1981a) Manuel (1981b)	Brandão et al. (2019)	Pax (1924) Carlgren (1931)	McMurrich (1893)	Carlgren (1942)	Daly and Ljubenkov (2008)	Daly and Ljubenkov (2008)

*Species without molecular phylogenetic information

Table 28. Comparison of two new species of the genus *Edwardsia* and species of *Paraedwardsia* Carlgren in Nordgaard, 1905 possibly assignable to *Edwardsia.*

	***Edwardsia* sp. nov. 16**	***Edwardsia* sp. nov. 17**	**Paraedwardsia abyssorum* Carlgren, 1951	**Paraedwardsia arenaria* Carlgren in Nordgaard, 1905	**Paraedwardsia hadalis* Sanamyan and Sanamyan, 2018	**Paraedwardsia heia* Daly and Ljubenkov, 2008	**Paraedwardsia lemchei* Carlgren, 1956	**Paraedwardsia sarsii* (Dueben and Koren, 1847)
Characters								
Distribution	Pelagic to Mesopelagic zone (151-370 m)	Pelagic Zone (6 m)	Abyssal zone (deeper than 5000 m)	Mesopelagic zone (231-658 m)	Abyssal zone (deeper than 5000 m)	Bathyal zone (2500-3000 m)	Abyssal zone (deeper than 5000 m)	Pelagic Zone (22-183 m)
Number of tentacles	16	16	12	16	12	16	14-16	20-30
Number of tentacular cycle	2	2	2	2	2	2	2	3
Surface of the column	Attaching sand grains	Attaching sand grains	Attaching sand grains	Attaching sand grains	No attaching materials	Attaching sand grains	Attaching sand grains	Attaching sand grains
Tenaculi on the column	Present, weak	Present, weak	Present	Present, strong (like papillae)	Absent	Present	Present	Present
Traces of nemathybomes	Present	Absent	Absent	Absent	Absent	Absent	Absent	Absent
Shape of retractor muscles	Peculiar shape (trilobate)	Simple, restricted	Simple, restricted	Simple, restricted	Simple, restricted	Simple, restricted	Simple, diffused	Simple, restricted
References	**The present study**	**The present study**	Carlgren (1951)	Nordgaard (1905) Carlgren (1921) Carlgren (1949)	Sanamyan and Sanamyan (2018)	Daly and Ljuvenkov (2008)	Carlgren (1956)	Dueben and Koren (1847) Carlgren (1921) Carlgren (1949)

*Species without molecular phylogenetic information

Table 29. Cnidoms of the species of *Edwardsia* (*Edw. sipunculoides*, *Edw. ena* comb. nov., *Edw. isei* comb. nov., and *Edw.* sp. nov. 18).

		Edwardsia sipunculoides NSMT-Co 1700		*Edwardsia ena* comb. nov. NSMT-Co 1610		*Edwardsia isei* comb. nov. NSMT-Co 1611		*Edwardsia* sp. nov. 19 (Iz-074)	
		Length × Width (µm)	frequency	Length × Width (µm)	frequency	Length × Width (µm)	frequency	Length × Width (µm)	frequency
Tentacle									
basitrichs	S	31.6-40.1 × 2.4-3.7	numerous	21.2-38.3 × 2.4-3.6	numerous	10.1-13.0 × 1.8-2.8	numerous	21.2-29.7 × 2.9-4.1	numerous
	L					19.1-26.6 × 3.0-4.5	numerous		
spirocysts		14.5-25.9 × 2.3-4.0	numerous	11.2-20.9 × 2.1-3.3	numerous	11.0-16.0 × 2.4-3.8	numerous	13.4-26.4 × 3.0-5.5	numerous
Actinopharynx									
basitrichs	S	22.9-26.7 × 2.6-3.3	rare	22.6-26.9 × 2.4-2.9	rare	21.9-39.8 × 3.1-4.7	numerous	19.5-39.3 × 2.6-4.9	numerous
	L	31.4-44.1 × 2.9-4.3	numerous	37.5-51.2 × 3.0-4.7	numerous				
microbasic *p*-mastigophores		21.2-31.4 × 5.6-8.2	numerous	21.7-30.6 × 4.9-6.10	numerous	25.1-38.1 × 4.2-6.4	numerous	27.4-35.6 × 5.2-7.0	numerous
microbasic *b*-mastigophores		26.7-28.1 × 8.1-9.3	rare						
Nemathybome									
basitrichs	S	19.5-23.4 × 3.1-4.0	rare	9.7-15.2 × 2.2-3.2	numerous	9.7-12.4 × 2.0-3.2	a few	58.9-87.6 × 3.9-5.9	numerous
	L	46.2-87.0 × 3.4-5.8	numerous	63.9-105.6 × 3.4-5.5	numerous	62.8-85.0 × 3.8-6.2	numerous		
Filament									
basitrichs	S	32.7-40.4 × 2.2-3.4	numerous	33.4-45.5 × 3.7-5.7	numerous	18.2-26.6 × 2.3-3.6	numerous	22.1-33.0 × 2.1-3.6	numerous
spirocysts	L					38.7-49.8 × 4.6-6.7	numerous	14.1-19.9 × 3.0-4.3	a few
microbasic *p*-mastigophores		22.9-27.1 × 5.2-6.9	numerous	23.5-29.6 × 5.7-7.8	a few	31.9-34.0 × 5.2-6.1	a few	23.9-30.3 × 5.1-6.9	numerous
microbasic *b*-mastigophores		22.3-44.1 × 4.0-8.8	numerous	34.3-40.0 × 5.1-6.7	a few			24.1-32.9 × 4.4-5.4	numerous

Table 30. Comparison of three new species of genus *Edwardsia* and the other species of the genus with 20 tentacles.

	***Edwardsia* sp. nov. 19**	***Edwardsia* sp. nov. 20**	***Edwardsia* sp. nov. 22**	***Edwardsia sipunculoides* (Stimpson, 1853)**	***Edwardsiella kamerunensis* Carlgren, 1927**	***Edwardsiella finmarchica* Carlgren, 1921**	***Edwardsia timida* de Quatrefages, 1842**
Characters							
Body length	35 mm	30 mm	25-35 mm	80-120 mm	17 mm (damaged specimen)	32 mm	70-200 mm
Number of tentacular cycles	1	2	2	2	Unknown	3	3
(Arrangement)	(20)	(10+10)	(8+12)	(8+12)	Unknown	Unknown	(4+8+8)
Retractor muscle	Restricted, distinct	Diffused, distinct	Circumscribed, distinct	Diffused, distinct	Restricted, distinct	Diffused, distinct	Diffused, weak
Number of muscular processes	13-18	10-20	20-25	23-40	About 30	30-50	20-33
Cnidom of nemathybomes	1 type of nematocysts	1 type of nematocysts	2 types of nematocysts	2 types of nematocysts	1 type of nematocysts	1 type of nematocysts	1 type of nematocysts
References	**The present study**	**The present study**	**The present study**	Stimpson (1853) Carlgren (1931) England (1987) **The present study**	Carlgren (1927) England (1987)	Carlgren (1921) England (1987)	de Quatrefages (1842) Manuel (1977) Manuel (1981a) England (1987)

Table 31. Cnidoms of the species of *Edwardsia* (*Edw.* sp. nov. 20-*Edw.* sp. nov. 23).

		Edwardsia sp. nov. 20 (Iz-075)		*Edwardsia* sp. nov. 21 CMNH-ZG 4762		*Edwardsia* sp. nov. 22 (Iz-076)		*Edwardsia* sp. nov. 23 (Iz-078)	
		Length × Width (µm)	frequency	Length × Width (µm)	frequency	Length × Width (µm)	frequency	Length × Width (µm)	frequency
Tentacle									
basitrichs	S	16.9-24.0 × 2.3-3.5	numerous	20.5-28.3 × 2.8-4.3	numerous	9.7-14.1 × 1.8-3.1	numerous	28.3-37.5 × 3.2-5.0	numerous
	L					16.0-25.4 × 2.6-4.3	numerous		
spirocysts		8.0-16.2 × 2.2-3.5	numerous	9.1-17.3 × 2.2-3.6	numerous	10.2-16.6 × 2.3-3.8	numerous	13.5-35.6 × 2.3-5.8	numerous
Actinopharynx									
basitrichs	S	14.3-32.2 × 1.8-5.3	numerous	27.1-42.4 × 2.8-5.3	numerous	13.8-40.1 × 2.1-5.0	numerous	18.5-26.1 × 2.4-3.6	numerous
	L							34.0-50.9 × 4.3-6.2	numerous
microbasic *p*-mastigophores						19.7-26.3 × 4.3-7.0	numerous	25.6-34.8 × 5.4-7.7	numerous
microbasic amastigophores				23.1-28.6 × 2.5-3.7	numerous			28.2-28.8 × 7.3-7.6	rare
Nemathybome									
basitrichs	S	58.8-72.3 × 4.2-6.0	numerous	56.7-78.1 × 3.8-4.9	numerous	8.8-11.5 × 2.1-3.4	numerous	81.5-106.3 × 4.7-6.5	numerous
	L					51.6-74.6 × 4.0-5.9	numerous		
Column									
basitrichs						9.5-12.3 × 2.1-2.9	a few		
Filament									
basitrichs	S	20.7-29.3 × 2.4-3.4	numerous	27.3-38.1 × 4.0-6.1	numerous	23.1-32.1 × 2.3-3.8	numerous	15.8-27.2 × 2.1-3.1	numerous
	L					28.1-35.0 × 4.5-6.5	numerous	23.3-38.3 × 3.7-5.0	numerous
microbasic *p*-mastigophores		22.5-27.1 × 5.4-7.6	numerous			22.6-29.1 × 5.5-7.5	numerous	25.6-31.1 × 6.0-8.3	numerous
microbasic *b*-mastigophores		28.2-32.1 × 4.9-6.5	numerous					38.2-41.2 × 4.9-6.5	a few
microbasic amastigophores				21.8-29.7 × 5.3-7.5	numerous				

Table 32. Comparison of *Edwardsia* sp. nov. 21 and the other species of the genus with nemathybomes in eight rows and containing only one type of basitrichs.

	***Edwardsia* sp. nov. 21**	***Edwardsia jonesii* Seshaiya and Cutress, 1969**	***Edwardsia* sp. nov. 18**	***Edwardsia* sp. nov. 19**
Characters				
Body length	30-50 mm	80 mm	25 mm	35 mm
Number of tentacles	16	12	16	20
(Tentacular arrangement)	(8+8)	(6+6)	(4+12)	(20)
References	**The present study**	Seshaiya and Cutress (1969)	**The present study**	**The present study**

Table 33. Comparison of two new species of *Edwardsia* and species of *Isoscolanthus* Brandão, Gusmão, and Gomes, 2019 possibly assignable to *Edwardsia*.

	***Edwardsia* sp. nov. 23**	***Edwardsia* sp. nov. 26**	***Isoscolanthus iemanjae*** **Brandão, Gusmão, and Gomes, 2019**	***Isoscolanthus janainae*** **Brandão, Gusmão, and Gomes, 2019**
Characters				
Number of tentacles	16	16	12	12
Physa	Present but indistinct	Distinct, apparently swelled	Present but indistinct	Present but indistinct
Retractor muscles	Restricted, distinct	Circumscribed, distinct	Circumscribed, weak	Circumscribed, distinct
Number of muscular processes	8-14	10-15	15 in avarage	14-20
Size lange of basitrichs in nemathybomes (Length × Width; μm)	81.5-106.3 μm in length 4.7-6.5 μm in width	37.6-60.2 μm in length 3.2-6.9 μm in width	32.6-71.5 μm in length 2.8-4.0 μm in width	40.0-47.0 μm in length 3.2-4.0 μm in width
References	**The present study**	**The present study**	Brandão et al. (2019)	Brandão et al. (2020)

*Species without molecular phylogenetic information

Table 34. Cnidoms of the species of *Edwardsia* (*Edw. armata* and *Edw.* sp. nov. 24-*Edw.* sp. nov. 26).

		Edwardsia armata NSMT-Co 1609		*Edwardsia* sp. nov. 24 CMNH-ZG [no registration]		*Edwardsia* sp. nov. 25 CMNH-ZG [no registration]		*Edwardsia* sp. nov. 26 (Iz-081)	
		Length × Width (μm)	frequency	Length × Width (μm)	frequency	Length × Width (μm)	frequency	Length × Width (μm)	frequency
Tentacle									
basitrichs	S	13.1-54.4 × 2.7-5.3	numerous	10.2-22.7 × 2.7-5.0	numerous	19.6-25.9 × 3.4-5.2	numerous	22.7-39.8 × 3.2-4.2	a few
	L							37.1-39.8 × 3.9-4.9	rare
spirocysts		11.8-20.7 × 1.7-3.7	numerous			13.3-22.2 × 3.2-5.3	numerous		
Actinopharynx									
basitrichs		19.4-39.6 × 2.7-4.8	numerous	16.2-26.4 × 3.8-4.4	a few	21.0-27.9 × 2.5-4.0	numerous	16.9-24.5 × 2.8-4.2	numerous
microbasic *b*-mastigophores		22.2-34.5 × 3.5-5.2	numerous			34.9-43.5 × 3.4-5.5	numerous		
Nemathybome									
basitrichs	S	36.2-63.0 × 3.4-5.8	numerous	24.1-49.1 × 3.0-4.4	numerous	13.1-16.7 × 2.6-3.9	numerous	37.6-60.2 × 3.2-6.9	numerous
	L					40.8-55.7 × 3.0-4.7	numerous		
Column									
basitrichs		10.5-50.0 × 2.8-5.0	numerous						
Filament									
basitrichs	S	31.3-43.0 × 3.5-5.4	numerous	13.4-21.9 × 2.4-3.7	numerous	22.1-35.1 × 2.9-4.2	numerous	33.5-79.1 × 4.2-4.9	a few
	L	95.6-114.5 × 2.7-4.2	rare						
microbasic *p*-mastigophores				18.0-25.3 × 4.6-7.3	numerous				
microbasic *b*-mastigophores		33.8-45.7 × 5.2-7.9	numerous	22.4-32.2 × 4.1-6.3	numerous	32.9-45.0 × 4.2-5.8	numerous	44.0 × 6.9	rare
microbasic amastigophores						27.7-35.0 × 5.1-7.5	numerous		

Suborder ENTHEMONAE Rodríguez and Daly, 2014

(New Japanese name: jinjo-isoginchaku-amoku Izumi et al, 2019a)

Diagnosis. See Rodríguez et al. (2014)

Remarks. Suborder Enthemonae is the largest group of anemones: this suborder includes all sea anemones except family Actinernidae, Halcuriidae and Edwardsiidae. Thus, 47 families (94 %) and approximately 1000 species (91 %; calculated on the bases of Fautin, 2016) are belonging. This fact results in the ambiguous diagnosis of this group, and there are almost no exact common characters.

Based on the results of the phylogenetic analysis (Fig. 6), I eliminated *Halcampella* and added *Metedwardsia* from/into Enthemonae, but the diagnosis of this suborder should not be revised now because there is still needed a comprehensive taxon sampling for phylogenetic analyses to discuss the detail.

Superfamily ACTINOSTOLOIDEA Carlgren, 1932

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

Diagnosis. Enthemonae with **or without** basilar muscles, marginal sphincter **absent, endocoelic or** mesogleal and no acontia or acontioids. Aboral end flattened and adherent, and **basilar muscle absent or present**. Column usually smooth. Tentacles and mesenteries usually numerous. Mesenteries not differentiated into macro- and microcnemes. Mesenteries of same pair **often** unequally developed. Retractors usually diffuse weakly or strongly, **or** circumscribed. Cnidom: gracile spirocysts, basitrichs, holotrichs, microbasic *b*- and *p*-mastigophores.

Remarks. After establishing Actinostoloidea Carlgren, 1932, the anemones in this group had been accommodated in previous tribe Mesomyaria (Carlgren, 1949). However, in recent Rodríguez et al. (2014) re-established this taxon as one of the member of Enthemonae (Table 1). According to the definition of the article, the marginal sphincter muscles of the species of Actinostoloidea were all mesogleal (this was the characters of Mesomyaria) and the mesenterial pairs of this taxon were unequally developed in this suborder.

However, my research revealed that there was a clade of sea anemones which have strange features for Actinostoloidea in the superfamily clade: species of Capneidae and Discoactinidae fam. nov. were formed an inner clade of Actinostoloidea by high support rates (Fig. 8), but these species were not corresponding those main features of this superfamily. Despite *Capnea geogiana*, a species of *Capneidae*, was already included in the analysis of Rodríguez et al. (2014), and this species was in the clade of Actinostoloidea, they completely ignored this result and put *Capnea* into superfamily Actinioidea. However, the results of phylogenetic trees both of Rodríguez et al. (2014) and mine showed *Capnea* was certainly a family of Actinostoloidea and should not be neglected. Thus, I revised the diagnosis to accommodate Capneidae and Discoactinidae fam. nov. See Table 35 for comparison of the all families included in the suborder Actinostoloidea.

Family DISCOACTINIIDAE fam. nov.
(New Japanese name: enban-isoginchaku-ka)

Diagnosis. Actinostoloidea with very wide pedal disc. Column without vesicles, smooth, divisible into scapus and capitulum, Sphincter muscle absent. Tentacles slender, simple, comparatively few, arranged in cycles; tentacles not developed in some endocoel. Longitudinal muscles of tentacles mesogleal. One siphonoglyph. Mesenteries more numerous proximally than distally. 10 mesenteries perfect, fertile and with strong pinnate, circumscribed retractors. Parietal muscles well developed but parietal basilar and basilar muscle absent. The weaker mesenteries, in the proximal part of the body, without, filaments. Cnidom: spirocysts, basitrichs, microbasic *p*-mastigophores.

Etymology. Derived from the name of the type genus.

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

Remarks. *Discoactis* sp. nov. 27, collected several localities in Japan, was the sister group of *Capnea* of family Capneidae on the phylogenetic tree (Fig. 8). However, there are several differences between *Discoactis* and *Capnea* as below: *Capnea* has numerous vesicle-like (Carlgren, 1949) tentacles in contrast to a few slender tentacles of *Discoactis*; only *Discoactis* has endocoels without tentacles in contrast to *Capnea*, which develops two or more tentacles in every exocoel/endocoel (Carlgren, 1940, 1949); *Capnea* has conspicuous pinnate endodermal sphincter (Carlgren, 1940), one of the characteristic features of this genus, but no sphincter-like structure in *Discoactis*; *Discoactis* has only 10 macrocnemes (two dorso-lateral macrocnemes in the first cycle mesenteries are absent) while *Capnea* has at least 12 macrocnemes in first cycle perfectly. That was why I judged that it was inappropriate to unify *Discoactis* into Capneidae, thus I established a new family, Discoactinidae. See Table 35 for comparison of the family Discoactiniidae and the other families of the suborder Actinostoloidea.

Genus *Discoactis* gen. nov.
(New Japanese name: enban-isoginchaku-zoku)

Diagnosis. Discoactinidae with very wide pedal disc. Column comparatively smooth, divisible into scapus and capitulum, the former provided with a more or less distinct periderm. Sphincter absent. Tentacles 14–18, long and slender, simple, a few in number, arranged in peculiar rule: six tentacles communicating with each exocoel in first cycle; 8–12 tentacles in each exocoels: tentacles absent in endocoels of second cycle. Longitudinal muscles of tentacles and radial muscles of oral disc chiefly mesogleal. One siphonoglyph. Mesenteries far more numerous proximally than distally. 3 types of mesenteries: 10 perfect macrocnemes; 10–14 imperfect macrocnemes with strong parietals in first second cycles; numerous tiny, weaker imperfect microcnemes younger than third cycle, without filaments, only on proximal side. Parietal muscles well developed in first/second cycle. Cnidom: spirocysts, basitrichs, microbasic *p*-mastigophores.

Etymology. The type species of this genus, *Discoactis* sp. nov. 27, has very conspicuous basal disc and becomes like disc-like shape after preservation. "*Disco-*" is derived from this shape. "*-actis*" is commonly used in actiniarian genus names, meaning radiation of sunshine in Greek.

Type species. *Discoactis* sp. nov. 27 (monotypic).

Remarks. The most distinguishable character of this genus is existence of endocoels without tentacles on distal end. While almost all anemones have at least one tentacle in each exocoel/endocoel in distal end (Carlgren, 1949), this group has endocoels which bear no tentacle in second mesenterial cycle. In addition to the tentacular arrangement, it is also peculiar that two dorso-lateral mesenteries in first mesenterial cycle dose not develop to perfect mesenteries. There has been known few anemones with 10 tentacles (e.g. *Pseudoedwardsia* sp. nov. 5; Fig. 31), so this is also the diagnostic character of this genus.

Discoactis sp. nov. 27

(Japanese name: umi-no-fujisan)

Figs. 66, 67; Table 36

Material examined. CMNH (no registration 1): 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 684 m in depth collected during research cruise of R/V Natsushima, by Kensuke Yanagi; CMNH (no registration 2): dissected specimen and histological sections, same locality, date and collector as CMNH (no registration 1); (Iz-084): dissected specimen, embedded tissues in paraffin, histological sections, prepared nematocysts, 17 April, 2018, collected from west off, Misaki, Kanagawa Prefecture, 35°08.328′N, 139°32.568′E, at 108–198 m in depth, by Hisanori Kotsuka and Mamoru Sekifuji; (Iz-085): whole specimen, same locality, date and collector as (Iz-084); (Iz-086): dissected specimen, embedded tissues in paraffin, histological sections, prepared nematocysts, 15 February, 2017, collected from west off, Misaki, Kanagawa Prefecture, 35°08.388′N, 139°33.731′E, at 95–98 m in depth, by Takato Izumi; (Iz-087): dissected specimen, embedded tissues in paraffin, histological sections, prepared nematocysts, 24 July, 2017, collected from 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. (Iz-088), (Iz-089): whole two specimens, 25 May, 2014, collected from southwest off Iki Island, Nagasaki Prefecture, 33°03.582′N, 129°31.175′E, at 79–83 m in depth, during research cruise of R/V Toyoshio (St-9), collected by Takato Izumi.

Description. ***External anatomy***. On living specimens (Iz-084), 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 (Fig. 66C). Column divisible scapus and scapulus, and drastically broaden towards the proximal end (Fig. 66A–D): the width of scapus is ca. 2–4 mm in distal end but reaching to ca. 15–25 mm in proximal end (= basal disc) on preserved specimens. The height of preserved specimen ca. 10–15 mm. Scapus and scapulus smooth, sometimes with transversal wrinkle in preserved (Fig. 66A). Pedal disc adherent, semitransparent, almost circular but flexible in outline (Fig. 66C). Mouth with indistinct lip. Tentacles 1.5–2.0 mm in length, long and slender, almost same length from center to margin (Fig. 66A, C). Tentacles 14–18 in number, in peculiar rule of arrangement: six tentacles in each exocoel in first cycle; 8–12 tentacles in each exocoels: 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 first cycle; 10–14 imperfect macrocnemes (Fig. 67C) with strong parietals in first second cycles; numerous, around 100 in number, imperfect microcnemes, weaker and tiny, between third to fifth cycle, without filaments (Fig. 67G). Microcnemes sometimes not equally developed within the same pair of perfect mesenteries (Fig. 67G). Mesenteries at the base more numerous than at the margin: microcnemes only on proximal side (Figs. 66E and 67G). Only 10 perfect macrocnemes fertile in proximal (Fig. 67G). Retractors distinct, strong, circumscribed, with 10–16 well-branched muscular processes (Fig. 67C, G). Parietal muscles distinct in macrocnemes on distal side, with 5–15 muscular processes in each side (Fig. 67C), but indistinct in proximal side. Tentacular longitudinal muscle mesogleal, distinct (Fig. 67E), and circular muscle endodermal but indistinct (Fig. 67D). Columnar circular muscle well-developed (Fig. 67B). Sphincter muscle and basilar muscle absent (Fig. 67A, B, F). Mesoglea the thickest in column, ca. 500 μm in thickness, and also thick in actinopharynx, but very thin in mesenteries and tentacles. Only 10 perfect mesenteries fertile with gonads, but matured gonads absent in my specimens (Fig. 67F).

Cnidom. Spirocysts, basitrichs, microbasic *p*-mastigophores. See Table 36 for size and distribution.

Remarks. As I already mentioned in remarks of the genus, *Discoactis* sp. nov. 27 was so peculiar anemones that no existed families and genera in Actinostoloidea (even in Actiniaria) can accommodate this species. However, in contrast to the singularity of the morphology, *D.* sp. nov. 27 was relatively ordinary species and widely collected in Japan. Over 10 individuals of this species were collected from Sagami-Bay (Misaki), Suruga Bay (Senoumi-Bank), Otsuchi-Bay and Sea of Japan.

Superfamily ACTINIOIDEA Rafinesque, 1815

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

Family HALOCLAVIDAE Verrill, 1899

(Japanese name: kombo-isoginchaku-zoku)

Haloclavidae Verrill, 1899: 41; Carlgren, 1949: 29.

Type genus. *Haloclava* Verrill, 1899

Genus *Antennapeachia* Izumi and Yanagi, 2016
(Japanese name: antena-isoginchaku-zoku)

Antennapeachia Izumi and Yanagi, 2016: Izumi et al., 2016: 449

Diagnosis. Elongate haloclavid with well-developed, rounded or tapered aboral end. Column indistinctly divisible into regions, without tenaculi, but with minute adherent areas on surface. Sphincter absent. Tentacles 14–16 (two distal tentacles [or antenna tentacles] near mouth and 12 or 14 marginal tentacles), without acrospheres. Single, very deep siphonoglyph, with oral end drawn out in lobate conchula, never forming distinct tube separated from cavity of actinopharynx by ectodermal fusion. Pairs of macrocnemes six or eight; two independent microcnemes between ventral directives and ventrolateral mesenteries. All mesenteries, except two microcnemes in second cycle perfect, fertile, with filaments and strong diffuse retractors. Cnidom: spirocysts, basitrichs, microbasic *b*-mastigophores, microbasic *p*-mastigophores, microbasic amastigophores, macrobasic mastigophores. (Excerpted from Izumi et al. [2017].)

Etymology. The name *Antennapeachia* is derived from antenna tentacles, the discriminating characteristic structure of this genus (which are two irregular tentacles of *Antennapeachia setouchi* Izumi and Yanagi, 2016 and *A. jambio* Izumi, Yanagi, and Fujita, 2017 straight up and resembling antennas), and the morphologically related genus *Peachia*.

Type species. *Antennapeachia setouchi* Izumi and Yanagi, 2016

Remarks. When *Antennapeachia setouchi* Izumi and Yanagi, 2016 was discovered, the belonging genus was questioned: within Haloclavidae, *Peachia* (Gosse, 1855) had been the only genus that has both conchula and imperfect mesenteries. However, the diagnosis of *Peachia* stated "Pairs of mesenteries 10 (6+4 lateral and ventrolateral pairs of second cycle)" (Carlgren, 1949). The mesenterial arrangement of *Antennapeachia setouchi*, which comprises only six pairs of macrocnemes and two macrocneme-microcneme pairs, does not fit this diagnosis. Moreover, *A. setouchi* had irregular inner tentacles, whereas *Peachia* species have uniformly shaped and arranged tentacles. So, this species cannot be considered within genus *Peachia*, as the uniformity of tentacles and mesenterial arrangement are quite different between the two taxa. Considering that the diagnosis of mesenterial arrangement is fixed in each genus of sea anemone that has a few mesenteries such as Haloclavidae, *A. setouchi* could not be treated within the genus *Peachia*. Moreover, none of the known species from *Peachia* and the entire order Haloclavidae had irregular tentacles that were observed in this species, making *A. setouchi* unique in this character. I therefore had proposed the establishment of a new genus *Antennapeachia* Izumi and Yanagi, 2016 defined by the characteristic mesenterial arrangement, six macrocnemes pairs and two macrocneme-microcneme pairs, and the unique tentacle arrangement, to accommodate *A. setouchi* Izumi et al., 2016. *Antennapeachia jambio* Izumi, Yanagi and Fujita, 2017, however, had two additional marginal tentacles at the outer circle, and accordingly, two additional macrocnemes in its column. Each of the additional macrocnemes was located between the macrocneme and microcneme and paired with the independent macrocnemes; the eight macrocneme pairs–six pairs in the first cycle and two more pairs–were in its column, and two microcnemes were independent. As a result, the diagnosis of the genus was revised to include both types of mesentery arrangement and tentacular arrangement found in these two species of *Antennapeachia*. I also found an additional type of cnidae, microbasic *p*-mastigophores, in *A. jambio*, which was not found in *A. setouchi* (Table 38). Thus, the diagnosis of cnidom was also revised. Finally, the diagnosis of *Antennapeachia* was emended to accommodating two species.

See Table 37 for comparison of the genus *Antennapeachia* and the other haloclavid genera with conchula. Based on the taxonomic key in Yap et al. (2014), I revised the diagnostic key to the genera with conchula in the family Haloclavidae to include the new genus *Antennapeachia*.

1A. Mesenteries all complete (macrocnemes); siphonoglyph completely separated from the actinopharynx............. 2

1B. Some mesenteries complete (macrocnemes), the others incomplete (microcnemes); siphonoglyph rarely completely separated from the actinopharynx............. 3

2A. Eight pairs of macrocnemes only, 16 tentacles............. *Metapeachia*

2B. Ten pairs of macrocnemes only, 20 tentacles............. *Synpeachia*

3A. Six pairs of macrocnemes and four pairs of microcnemes; all tentacles marginal and similar in shape.............*Peachia*

3B. Six pairs of macrocnemes and two pairs of one macrocneme and one microcneme; 12 regular tentacles marginal and two irregular tentacles (antenna tentacles) inner............***Antennapeachia* gen. nov.**

Antennapeachia setouchi Izumi and Yanagi, 2016

(Japanese name: antena-isoginchaku)

Figs. 68, 69; Table 38

Antennapeachia setouchi Izumi and Yanagi, 2016: 450–451, figs. 2–5

Material examined. Holotype: NSMT-Co 1653: histological sections, tissues in paraffin, and prepared nematocysts, 28 May 2014, west of Himeshima Island, Oita Pref., Seto Inland Sea (33°44.408′N, 131°34.109′E), 30 m depth, collected by Takato Izumi. Paratypes: CMNH-ZG 05927: whole specimen, 7 November 2012, Nagasu, Okayama Pref., Seto Inland Sea, 25-26 m depth, collected by Mariko Kawamura; NSMT-Co 1654: whole specimen, November 5, 2014, east of Ogishima Island, Kagawa Pref., Seto Inland Sea (34°24.899′N, 134°05.486′E), 16 m depth, collected by Naoto Jimi.

Etymology. The species is named after Setouchi, the local Japanese name for the region around the Seto Inland Sea, where the specimens were collected.

Description. ***External anatomy.*** Column smooth, cylindrical or barrel-like, ca. 10 mm in length, 7 mm in diameter. Color of the body brownish orange (Fig. 68A). Column surface smooth, papillae absent, with discontinuous line and dense orange spots. Center of aboral end hollow, donut-like shaped (Fig. 68C). Pedal disc absent. Two circles of tentacles on oral disc; number of tentacles 14. Twelve regular tentacles in outer circle, two irregular tentacles in inner circle (Fig. 68B). Regular tentacles protruding to outside or hung along column. Irregular tentacles (= ‘antenna tentacles’) (Fig. 68A) always rising straight upward. All tentacles nearly the same length, approximately 4-5 mm when fully expanded, with no acrospheres. Coloration of regular tentacles with cross-bands or M-shaped pattern of orange and brown (Fig. 68B). Antenna tentacles with symmetric bands of orange, brown, and white. Conchula on ventral side (Fig. 68B).

Internal anatomy. Six pairs of macrocnemes and two pairs of mesenteries consisting of macrocneme and microcneme between ventro-lateral mesenteries and ventral directives (Figs. 3B, 4A). All macrocnemes perfect between oral disc and aboral end. Muscle of macrocneme paired with microcneme facing directives. No microcnemes near oral disc (Fig. 69B, C).

Antenna tentacles situated between ventro-lateral mesenteries (Fig. 69A). Five regular tentacles on ventral side. Retractor muscles circumscribed to diffused and parietal muscles of macrocnemes distinct (Fig. 69A, I). Tentacular circular muscle endodermal (Fig. 69D) and tentacular longitudinal muscle ectodermal (Fig. 69E, F). No histological differences between antenna tentacles and regular tentacles (Fig. 69E–H). Mesoglea in body wall far thicker than ectoderm and endoderm, but much thinner in actinopharynx, and the thinnest in siphonoglyph. In actinopharynx, siphonoglyph on ventral side and always connected to actinopharynx (Fig. 69A). Sphincter muscle absent. On the aboral end, basilar muscle absent (Fig. 69J, K).

Cnidom. Spirocysts, basitrichs, microbasic amastigophores, microbasic *b*-mastigophores and macrobasic mastigophores. See Table 38 for size and distribution

Aquarium observations. During the observation of the paratype specimen (CMNH-ZG 05927) in the aquarium, the antenna tentacles were always rising upward even when the other tentacles shrunk or adhered to their column. In the dark, this specimen often inflated its body significantly, like a balloon by elongating its bellows-like body wall with peristaltic motion. Eventually, the length of the body increased approximately three-fold and the diameter increased two-fold. The sea anemone then drifted with the water current and moved to another place. In our observations, the sea anemone moved to the other corner of the aquarium. As its body inflated, their regular and antenna tentacles remained extended. This behavior was observed at least six times in 10 days, always in the dark.

Remarks. Role of antenna tentacles. Some sea anemones have extraordinary, specialized tentacles called catch tentacles with specialized functions. The catch tentacles of *Metridium senile* Linnaeus, 1761 are specialized to attack other conspecific individuals (Purcell, 1977). The tip of these tentacles contains many more holotrichs than the tip of other tentacles (summarized by Fautin and Mariscal, 1991). The catch tentacles of *Haliplanella luciae* Verrill, 1898 differ from the other ordinary tentacles in distribution of cnidae and in internal anatomy (Williams, 1975; Fukui, 1986). In *Antennapeachia setouchi*, however, the cnidae distribution and internal structure of the antenna tentacles are not very different from those of regular tentacles (Figs. 4E-H, 7). This suggests that the antenna tentacles are not used for catching prey or for attacking. Antenna tentacles and regular tentacles are different only in the location and their movement. *Antennapeachia setouchi* always raise their antenna tentacles upward (Fig. 68A), even when they are drifting, and they do not contract the antenna tentacles when the other regular tentacles are contracted into their column. The function of the antenna tentacles could not be inferred from their anatomy and aquarium observations. I speculate that they may act as receptors that accept stimuli from above the animal, as they are always extended in that direction, although it is unclear what specific functions the antenna tentacles perform.

Ecological significance of the balloon-like shape. A few species of actiniarians are known to 'swim' actively. For example, *Boloceroides mcmurrichi* Kwietniewski, 1898 swim in water by paddling with their tentacles when escaping from the predatory nudibranchs (Shick, 1991). Some species of *Stomphia* detach their basal disc from the seafloor and swim with whip-like movements, migrating as much as 1.5 m to escape from asteroids, their predators (Mauzey et al., 1968). This escaping behavior is triggered by chemical substance released by the starfish or by mechanical stimulation from the starfish contact (summarized by Shick, 1991). In these cases, sea anemones detach from the seafloor after detecting stimuli from their predator (Description, Figs. 68, 69, and part of Table 38 are revised and reprinted Izumi et al. [2016] by courtesy of Zoological Science.)

Antennapeachia jambio Izumi, Yanagi and Fujita, 2017

(Japanese name: misakino-antena)

Fig. 70; Table 38

Antennapeachia jambio Izumi, Yanagi, and Fujita, 2017: Izumi et al, 2017: 110–113, figs. 2–4.

Material examined. Holotype: CMNH-ZG 06546: dissected specimen, embedded tissues in paraffin, histological sections, prepared nematocysts; February 19, 2014, off Jogashima, Kanagawa Prefecture, 35°06.082'N, 139°34.232'E, at 238-309 m in depth collected by Kensuke Yanagi. Paratype; NSMT-Co 1596: whole specimen, somewhat damaged in proximal end; February 15, 2017, off Miura Peninsula, Kanagawa Prefecture, 35°08.0383'N, 139°33.731'E, at 95-97 m in depth collected by Takato Izumi.

Etymology. This species was named, because the type specimens were collected in the second and twelfth JAMBIO Coastal Organism Joint Survey. JAMBIO stands for "Japanese Association for Marine Biology."

Description. ***External anatomy.*** Column smooth, cylindrical or barrel-like, rich in expansibility, length *ca.* 9 mm, diameter *ca.* 7 mm in alive, and length 8 mm diameter 6 mm in preserved specimens. Color of body orange (Fig. 70A, B). Column surface smooth, papillae absent, with numerous discontinuous wavy wrinkles running direction of transversal and pale white patches (Fig. 70B). Aboral end flattened or slightly concaved, like a shape of donut, with tiny hole in center, semitransparent, so that line of mesenteries visible from outer side. Pedal disc absent, but somewhat sticky so that particles of mud adhered to column or aboral end (Fig. 70B). Two circles of tentacles on oral disc; 16 tentacles. Fourteen marginal tentacles in outer circle; two antenna tentacles in inner circle (Fig. 70A). Marginal tentacles protruding outside or hanging along column. Antenna tentacles rising straight upward. Marginal tentacles approximately 4-5 mm in length when fully expanded. Antenna tentacles 1 - 2 mm in length, far shorter than marginal tentacles. Both tentacles simple, without acrospheres. Coloration of marginal tentacles brownish, obscure cross-bands of yellow and brown; surface complicatedly wrinkled. Antenna tentacles without cross-bands; surface wrinkled (Fig. 70A). Oral disc diameter *ca.* 4 mm, same color as tentacles. Mouth at center of oral disc, a little swelled, with well-extended and robed conchulaon ventral side (Fig. 70A)

Internal anatomy. Eight pairs of macrocnemes, six of first cycle and extra two pairs between ventro-lateral mesenteries and ventral directives; two independent microcnemes between ventro-lateral mesenteries and ventral directives (Fig. 70C). All macrocnemes perfect and continuing along whole length of body. Microcnemes present from proximal end to middle part of body, but absent near oral end. Antenna tentacles between ventro-lateral endocoels (Fig. 70C). Seven marginal tentacles of outer cycle on dorsal half of body; one of them raised from dorsal endocoel; two (one on each side) from dorso-lateral exocoels; two from dorso-lateral endocoels; other two from lateral exocoels. Other seven on ventral half of body; one of them raised from ventral endocoel; two from endocoel between two extra pairs of macrocnemes; the other four in ventrolateral exocoel (Fig. 70A). Tentacular circular muscle endodermal (Fig. 70D); tentacular longitudinal muscle ectodermal (Fig. 70E). Retractor muscles strongly circumscribed, limited at the center of each macrocneme (Fig. 70C, F), with approximately 15–30 a little branched muscular processes; parietal muscles of macrocnemes distinct, with around ten simple muscular processes (Fig. 70F, H). Mesoglea in body wall far thicker than ectoderm and endoderm, thinner in actinopharynx and siphonoglyph (Fig. 70F). Actinopharynx smooth, comparatively long in column, with huge siphonoglyph on ventral side, which always connected to it (Fig. 70C). Sphincter muscle absent (Fig. 70G). On aboral end, basilar muscle absent (Fig. 70I). Filaments at the tips of macrocnemes, small and limited near aboral end. Matured gametes not observed, so sexuality of specimens not clear.

Cnidom. Spirocysts in both tentacles, basitrichs in every tissue, microbasic amastigophores in actinopharynx and filament, microbasic *p*-mastigophores in actinopharynx and filament. See Table 38 for size and distribution.

Remarks. This species resembles *A. setouchi* in having antenna tentacles, forming a siphonoglyph (which is connected to conchula) beside their actinopharynx and having wrinkled orange color column. *Antennapeachia jambio*, however, has many different features from *A. setouchi*; antenna tentacles are far smaller than marginal tentacles, in contrast those of *A. setouchi* are larger and more prominent than marginal ones (Figs. 68A, B, 69A, B); *A. jambio* has a different type of cnidae from *A. setouchi*, especially the microbasic *p*-mastigophores are only in actinopharynx and filament of *A. jambio* (Table 38); the two pairs of macrocnemes between ventro-lateral mesenteries and ventral directives are only formed in the column of *A. jambio*. The last difference is most characteristic, that is why I judge that *A. jambio* is appropriate to be treated as new species, and I revised the diagnosis of genus.
(Description, Fig. 70, and part of Table 38 are revised and reprinted Izumi et al. [2017] by courtesy of Species Diversity.)

Genus *Haloclava* Verrill, 1899
(Japanese name: konbo-isoginchaku-zoku; Uchida and Soyama, 2001)
Haloclava Verrill, 1899: 41; Carlgren, 1949: 30.
Type species. *Haloclava producta* (Stephenson, 1865)

Haloclava **sp. nov. 28**

(Japanese name: konbo-isoginchaku)
Fig. 71; Table 39

Material examined. (Iz-088): dissected specimen, embedded tissues in paraffin, histological sections, prepared nematocysts; 9 May, 2017, off Jogashima, Misaki, Kanagawa Pref., 35°06.838'N, 139°34.063'E, at 272–370 m in depth, collected by Hiroshi Namikawa, kept in a tank of Misaki Marine Biological Station, and preserved by Takato Izumi; (Iz-089): dissected specimen, embedded tissues in paraffin, histological sections, prepared nematocysts; 9 November, 2017, off Mie Pref, 34°10.109'N, 136°44.644'E, at 130–132 m in depth, collected by Itaru Kobayashi.

Description. ***External anatomy.*** Column barrel or corn-like, not differentiated into parts, with high degree of expansibility, length ca. 15–20 mm, diameter ca. 7–12 mm in live specimens, and length ca. 15 mm and diameter 7–10 mm in preserved specimens. Body pale orange to brown (Fig. 71A, B), with transversal wrinkles (Fig. 71A), and divisible mesenterial insertions. Column surface smooth and no apertures (Fig. 71A). Aboral end physa-like, rounded, sometimes with a tiny hole in the center, same in color as column. Pedal disc absent, and slightly sticky to adhere to any substrates at aboral end. 20 Tentacles, in two indistinct cycles of 10, on oral disc (Fig. 71B). Outer tentacles protruding outside or hanging along the column, and inner ones protruding to distal direction. Outer tentacle far thicker, longer than inners: the former ca. 9–12 mm in length when fully expanded, but the latter ca. 5–7 mm. Tentacles apparently capitate with indistinct acrospheres on the tip, but uniform in middle part: acrospheres on outer tentacles far larger and robust than inner ones. Tentacles semitransparent orange, surface smooth (Fig. 71A, B), and acrospheres patchy pattern with dark red and white, surface rough. Oral disc diameter ca. 10 mm, uniformly orange. Mouth at the center of oral disc, not swelled, no conchula (Fig. 71B).

Internal anatomy. 20 mesenteries, all macrocnemes. 10 pairs; 6 of them first cycle and 4 alternative pairs (Fig. 71E). All macrocnemes perfect, fertile, and continuing along the whole-body length. Microcnemes absent. All tentacles arise from each endocoel and exocoel. Tentacular longitudinal muscle ectodermal (Fig. 71C); tentacular circular muscle endodermal (Fig. 71D). Acrosphere on tentacle tips with densely arranged large basitrichs (Fig. 71D, Table 39). Retractor muscles circumscribed or restricted, limited at the center of each macrocneme (Fig. 71E), with approximately 25–40 multiple-branched muscular processes (Fig. 71F); parietal muscles of macrocnemes distinct, in peculiar shape: muscle with 10 slightly branched processes on each side bared from thin mesenteries by body wall, and additional muscle with simple 10–20 processes bared from thick mesoglea between body wall and retractor muscle (Fig. 71F). Moreover, several small slightly-branched muscular process on opposite side of retractor muscle on macrocnemes. Mesoglea in the body wall far thicker than the ectoderm and remarkably thicker than the endoderm of body wall, actinopharynx and siphonoglyph (Fig. 71E). Actinopharynx smooth, grooved, approximately 2/3–3/4 the column length. Single distinct siphonoglyph on the ventral side of actinopharynx, always connected to it, and sustained by ventral directives (Fig. 71E). Sphincter muscle absent. On the aboral end, basilar muscle absent (Fig. 71H). Filaments at the tips of the macrocnemes, small and limited near the aboral end (Fig. 71F). All specimens dioecious; mature ovary contains several oocytes in the mesoglea of each mesentery as observed in (Iz-088; Fig. 71G).

Cnidom. Basitrichs, microbasic *b*-mastigophores. See Table 39 for size and distribution.

Remarks. See Table 40 for comparison of *Haloclava* sp. nov. 28 and the other species of the genus *Haloclava*. *Haloclava* sp. nov. 28 is the first-discovered species of *Haloclava* in Japan. This species was identified as this genus by two features as below: the simple mouth without conchula (Fig. 71A; for comparison, see Fig. 68B for mouth with conchula), and smooth simple surface of body without any apertures. However, this species has quite peculiar shapes of muscles not only in this genus but also in the family (Fig. 71F). Moreover, the difference of shape between inner and outer tentacles is quite apparent in this species. There is no *Haloclava* species which has such differentiated tentacles confirmed.

The other minor differences from other species of *Haloclava* are as below: *Haloclava capensis* (Verrill, 1865) has six inner tentacles (Verrill, 1865) in contrast to 10 inners of *H.* sp. nov. 28; *H. stimpsonii* (Verrill, 1868) does not develop acrospheres like this species (Verrill, 1868); *H. brevicornis* (Stephenson, 1856) has 20 uniform blunt tentacles, not resembling to tentacles of *H.* sp. nov. 28 in shape; *H. producta* Stimpson, 1865 has 20 lines of sticky papillae on its column (Pei, 1998) though surface of *H.* sp. nov. 28 is smooth, and the body of *H. producta* reaches to 70 mm, far larger than *H.* sp. nov. 28; *H. chinensis* Carlgren, 1931 most resembles *H.* sp. nov. 28, but the shapes of retractors are more circumscribed and strongly restricted (Carlgren, 1931).

The basitrichs of acrosphere of *H.* sp. nov. 28, reaching to 273 μm, were extremely large record of Actiniaria. I have not confirmed any species which have longer nematocysts than this species.

Genus *Anemonactis* Andres, 1881
(New Japanese name: kinoko-ginchaku-zoku)

Anemonactis Andres, 1881: 329; Carlgren, 1949: 30.

Eloactis Andres, 1883: 464.

Diagnosis. Haloclavidae with elongate, cylindrical column not divided into regions, and lacking sphincter. Column with **numerous** cinclides and scattered solid papillae **or smooth**; rounded aboral end perforated by numerous apertures. Capitate tentacles **12**–20, inner tentacles shorter than the outer ones. **Siphonoglyph without conchula.** Cnidom: basitrichs, **microbasic *b*-mastigophores**, and traces of spirocysts. (Revised from Fautin [1998] and Carlgren [1949]. The revised points are indicated in **bold**.)

Type species. *Anemonactis magnifica* Andres, 1881

Remarks. The diagnosis of this genus was revised to include *Anemonactis minuta* comb. nov. and *Anemonactis* sp. nov. 29. On the occasion, several important features which were lacked in previous studies were added. See Table 41 for comparison of all species of this genus.

***Anemonactis minuta* (Wassilieff, 1908) comb. nov.**

(Japanese name: chibinasu-isoginchaku; Uchida, 1965)

Figs. 72, 73; Table 39

Halcampella minuta Wassilieff, 1908: 7.

Haloclava minuta: Carlgren, 1949: 30.

Anemonactis minutus: Uchida, 1992: 131; Uchida and Soyama, 2001: 86.

Anemonactis mazeli (Jourdan): Yanagi, 2006, p. 119, Pl. 1F (in part).

Material examined. NSMT-Co 1619: dissected specimen, histological section and nematocysts; 19 January 2015, Koajiro Bay, Aburatsubo, Misaki, Kanagawa Prefecture, 35°09.950′N, 139°36.640′E, at 14–15 m depth, collected by Takato Izumi during the 5th Coastal Organism Joint Survey of the Japanese Association for Marine Biology (JAMBIO); NSMT-Co 1620:

dissected specimen, histological section and nematocysts, same date, locality, depth, and collector as NSMT-Co 1619; NSMT-Co 1621: histological sections; 16 May 2014, Koajiro Bay, Aburatsubo at 12 m depth, collected by Takato Izumi; CMNH-ZG 09203: dissected specimen, histological sections and nematocysts, 13 February 2015, Tateyama Bay off Koyatsu, Chiba Prefecture, 35°08.0383′N, 139°33.731′E, at 95–97 m depth, collected by Takato Izumi; CMNH-ZG 1938: dissected specimen and histological sections, 9 May 2002, Namajima, Kamogawa, Chiba Prefecture, at 13 m depth, collected by Kensuke Yanagi; CMNH-ZG2193 (includes two individuals): whole specimens, 9 July 2002, mouth of Funakoshi Bay, Iwate Prefecture, 39°23.60′N, 141°59.52′E, at 79.5 m depth, collected by Taiji Kurozumi, Hiroyuki Tachikawa and Kensuke Yanagi; NSMT-Co 1622: whole specimen, 18 February 2017, Omura Beach, Futami Bay, Chichijima Island, Tokyo Prefecture, collected by Yoshihisa Fujita and Akitsugu Mukai; (Iz-090), (Iz-091): whole specimens, 16 May 2018, Araihama Beach, Misaki at intertidal zone, collected by Hisanori Kotsuka.

Description. ***External anatomy.*** Column cylindrical or barrel-like, not differentiated into parts, with high degree of expansibility, length ca. 10–20 mm, diameter ca. 7–10 mm in live specimens, and length ca. 6–10 mm and diameter 5–7 mm in preserved specimens. Body white, pale pink, or pale orange (Fig. 72A, C, E), with longitudinal white lines (Fig. 72A, C) or orange lines (Fig. 72E). Column surface rough, solid papillae scattered, sometimes with numerous discontinuous fluorescent green wavy wrinkles, and perforated by numerous apertures (Fig. 72A, C, E). Aboral end physa-like, rounded to flattened, sometimes with a tiny hole in the center, semitransparent, with a line of mesenteries visible from outer side (Fig. 72A). Pedal disc absent, and slightly sticky to adhere to any substrates at aboral end. Tentacles in two indistinct cycles of 8, on oral disc (Fig. 72B, D). Tentacles protruding outside or hanging along the column. All tentacles uniformly ca. 8–15 mm long when fully expanded. Tentacles capitate, apparently swelled in middle part, and with indistinct acrospheres. Tentacles semitransparent dark red, white, or both (Fig. 72B, D, E), sometimes whitish or brownish patches on the surface (Fig. 72D), and border of tentacles sometimes with running fluorescent green lines (Fig. 72B, E); tentacle surface smooth. Oral disc diameter ca. 4 mm, usually dark red. Mouth at the center of oral disc, sometimes slightly swelled, no conchula (Fig. 72B, D).

Internal anatomy. Sixteen mesenteries, all macrocnemes. Eight pairs; six of them first cycle and two alternative pairs (Fig. 3F). All macrocnemes perfect, fertile, and continuing along the whole-body length. Microcnemes absent. All tentacles arise from each endocoel and exocoel. Tentacular longitudinal muscle ectodermal (Fig. 73B); tentacular circular muscle endodermal (Fig. 73C). Acrosphere on tentacle tips with densely arranged large basitrichs (Fig. 3D, E). Retractor muscles strongly circumscribed, limited at the center or by parietal muscles on each macrocneme (Fig. 73F, H, I), with approximately 20–40 multiple-branched muscular processes (Fig. 73G, H); parietal muscles of macrocnemes distinct, with approximately 10 simple or branched muscular processes (Fig. 73G, H). Mesoglea in the body wall as thick as or slightly thicker than the ectoderm and remarkably thicker than the endoderm (Fig. 73F, G) of the body wall, but thinner in actinopharynx and siphonoglyph (Fig. 73F, H, I). Actinopharynx smooth, extended approximately 2/3–3/4 the column length. Single distinct siphonoglyph on the ventral side of actinopharynx, always connected to it, and sustained by ventral directives (Fig. 73C). Sphincter muscle absent (Fig. 73A). On the aboral end, basilar muscle absent (Fig. 73G). Filaments at the tips of the macrocnemes, small and limited near the aboral end (Fig. 73I). All specimens dioecious; mature ovary contains several oocytes in the mesoglea of each mesentery as observed in NSMT-Co 1620.

Cnidom. Basitrichs, microbasic *b*-mastigophores. See Table 39 for size and distribution.

Distribution. They usually inhabit the muddy seafloor near the Pacific coast of Honshu (Iwate, Chiba, Kanagawa, and Shizuoka Prefectures: The present study and Uchida and Soyama, 2001, p. 86), Seto Inland-Sea (Uchida, 1965, p. 261), and Ogasawara Islands (this study).

Remarks. The vicissitude of *Anemonactis minuta* comb. nov. and *Anemonactis mazeli*. *Anemonactis mazeli* comb. nov. was established as *Halcampella minuta* Wassilieff, 1908 for its tentacular and mesenterial arrangement (Wassilieff, 1908), at that time belonging to the subfamily Halcampinae, family Ilyanthidae. The holotype had been collected from the sandy bottom at 20 m depth in Aburatsubo, Sagami Bay, Japan. Wassilieff (1908) described mesenterial arrangement to contain six pairs, two directives, and four laterals, and two extra pairs at exocoels between dorso- and ventro-lateral mesenteries, and the latter two pairs were indicated as imperfect mesenteries. However, in the second description of this species by Carlgren (1949), 40 years after the original description, *Halcampella minuta* was transferred to the family Haloclavidae because of the single siphonoglyph on the actinopharynx, which is the most important feature of this family, and listed as *Haloclava minuta*. Uchida (1965) adopted this combination and gave this species the Japanese name Chibinasu-isoginchaku.

Since Uchida (1965), there had been no study on this species until Fautin (1998), who focused on the difference in body size between *A. mazeli* and *H. minuta*. Fautin (1998) suggested that the smaller number of tentacles of *H. minuta*, 16, compared with 20 tentacles found in *A. mazeli*, can be attributed to a small specimen that was still growing. For that reason, he synonymized *H. minuta* with *A. mazeli* (Fautin, 1998).

In contrast, Uchida (1992) and Uchida and Soyama (2001) described this sea anemone as a valid species, *Anemonactis minutus*, in their field guide book and provided an underwater photograph and short diagnosis. They indicated that *Anemonactis minutus* was easily distinguished from *Anemonactis mazeli* by the octoradial body shape (Uchida and Soyama, 2001, p. 86); however, they did not conduct a detailed study.

The type specimens of both *Anemonactis mazeli* and *Halcampella minuta* have been missing. Despite examining the specimen stored in ZSM, which houses the actinian specimens described by Wassilieff (1908), I could not find the type specimen of *Halcampella minuta* Wassilieff 1908. As a result, verification of the taxonomic status of *A. minuta* was impossible without collecting fresh specimens from the type locality Aburatsubo.

In this study, I analyzed a number of specimens, including topotypes. Detailed observations revealed that individuals of *A. minuta*, despite their small size, were adults because some specimens had matured gonads (Fig. 73I). Considering that all the specimens, including the adults, had 16 tentacles, the maximum number of tentacles of this species must be 16. The analysis of these specimens revealed that they belong to Wassilieff's (1908) *H minuta*, with which they share common morphological characters: wrinkling column surface (Fig. 72A, C); rounded aboral end; semitransparent tentacles with acrospheres (Fig. 72B, D); lacking marginal sphincter (Fig. 73A); ectodermal tentacular longitudinal muscle (Fig. 73B); and eight pairs of mesenteries (Fig. 73F). Our histological sections are almost identical to three figures in Wassilieff (1908, figs. 35, 36, and 37): circumscribed (or more or less restricted) retractor muscles with 20–40 simple or slightly branched muscular processes (Fig. 73H; fig. 35 in Wassilieff, 1908); distinct parietal muscles with around 10 simple or slightly branched muscular processes (Fig. 73H; fig. 36 in Wassilieff, 1908); and outstandingly capitate tentacle tips with large basitrichs and both thickened mesoglea and thickened endoderm in transversal sections of tentacles (Fig. 73E; fig. 37 in Wassilieff, 1908) Moreover, the size of the specimen in Wassilieff (1908) was 1 cm, which corresponds to the size of our smaller specimen. The presence of a huge siphonoglyph and the absence of conchula indicate that this species belongs to the genus *Anemonactis*.

Although almost all characteristics of our specimens correspond to the description by Wassilieff (1908), there are a few differences in tentacles and mesenteries: Wassilieff (1908) reported 15 tentacles, one tentacle less than in our specimens. However, in our specimens, the tentacle size was inconsistent (Fig. 72D) and sometimes the tentacles were miniscule. It is therefore probable that Wassilieff counted one tentacle less in his specimen. Moreover, the diagram in Wassilieff (1908, text-fig. 1, p. 8) precisely depicts 16 mesenteries, which also suggests that this species should have 16 tentacles. Assessed from the schematic diagram, four lateral mesenteries in Wassilieff's specimen were separated from the actinopharynx. The 16 mesenteries in our adult specimens were all connected to the actinopharynx (Fig. 73F), but I sometimes observed that lateral mesenteries were separated from the actinopharynx in younger specimens. I suspect that four lateral mesenteries are separated in juvenile individuals and gradually connect to the actinopharynx from the proximal end as the sea anemone matures.

Wassilieff (1908) does not mention the gonads of *A. minuta* in detail. Considering the comparatively small body size and unconnected four mesenteries, it is possible that Wassilieff's specimen was more or less young and gonads were immature. However, I observed mature gametes in the gonads in some of our specimens (NSMT-Co 1620, Fig. 73I, and CMNH-ZG 09203); therefore, individuals of this species should be considered adults when they reach around 2 cm in length and having 16 tentacles. I believe that the number of tentacles is a prominent character of *A. minuta*, and therefore, this species is not the growing phase of *A. mazeli*, as suggested in Fautin (1998, p. 94), but a distinct species. The presence of several apertures and solid papillae on the column and simple mouth without conchula ascertain the placement of *A. minuta* within the genus *Anemonactis*; therefore, I adopted the species identification by Uchida (1992) and Uchida and Soyama (2001), and the name *Anemonactis minuta* comb. nov. (Wassilieff, 1908) is proposed in this study. (The previous two studies listed the species as "*Anemonactis minutus*," but *A. minuta* is the correct Latin epithet). Thus, this species becomes the fourth *Anemonactis* species (along with the three species recognized by Fautin, 2016).

There are several additional differences between *A. mazeli* and *A. minuta*: *A. minuta* is always less than 2 cm long, and thus remarkably smaller than *A. mazeli*, which sometimes reaches 12 cm (Carlgren, 1945); although both species have capitate tentacles, the tentacles of *A. minuta* are apparently swelled in the middle part, and therefore, acrospheres are not conspicuous. In contrast, in *A. mazeli*, acrospheres on the tentacles are very conspicuous (Stephenson, 1935; Pax and Müller, 1962; Wood, 2005); *A. minuta* individuals have microbasic *b*-mastigophores in their filaments, while *A. mazeli* have only basitrichs (Carlgren, 1921, 1940; Yanagi, 2006). The microbasic *b*-mastigophores are specific to *A. minuta* and *Anemonactis* sp. nov. 29 in this genus; therefore, I also revised the diagnosis of *Anemonactis* in the present article. In addition, the largest basitrichs in the filament, which are as large as those on the acrospheres, are also specific to *A. minuta*.

Incidentally, the number of tentacles is useful for distinguishing *A. minuta* from other *Anemonactis* species: *Anemonactis clavus* (Quoy and Gaimard, 1833) has 12 tentacles (Hertwig, 1882) and 12 perfect mesenteries (Pax, 1912, fig. a), which are four fewer than *A. minuta*. The species *Anemonactis australis* (Carlgren, 1931), whose taxonomic status as a synonym of *A. clavus* remains questionable (Fautin 2013), can be distinguished by the presence of 20 tentacles and body length of 4 cm. Regarding *Anemonactis* sp. nov. 29, *A. minuta* is easily distinguishable from this new species by the number of tentacles and its size: *A.* sp. nov. 29 has 20 tentacles, the same as that in *A. mazeli*, and a remarkably larger body size, approximately five times as large as *A. minuta*. *Anemonactis globulosa* (Quoy and Gaimard, 1833), which had been considered an *Eloactis* species till recently (Fautin, 2013), can be distinguished from *A. minuta* in having 14 tentacles (Quoy and Gaimard, 1833). Due to the difference in the number of tentacles in *Anemonactis*, the diagnosis of this genus should be revised to include the number of tentacles not only of *A. mazeli* but also of *A. clavus*, *A.*

globuosa, and *A. minuta*, because older genus diagnosis mentions only the number of tentacles as 20.

Anemonactis sp. nov. 29

(Japanese name: kinoko-ginchaku; Uchida, 1965)

Figs. 74, 75; Table 39

Eloactis mazelii (Jourdan): Uchida, 1938: 288; Uchida, 1941: 385.
Anemonactis mazelii (Jourdan): Uchida, 1965: 261; Pei, 1998: 81.
Anemonactis mazeli sense Uchida: Uchida and Soyama, 2001: 87.
Anemonactis mazeli (Jourdan): Yanagi, 2006: 119 (in part).
Non *Eloactis mazelii* Jourdan, 1880: 41

Material examined. Holotype. CMNH-ZG 0275: dissected specimen, histological sections, prepared cnidae; 20 August 1999, Hattone, Kamogawa, Chiba Prefecture, 12 m depth, collected during scuba diving by Kensuke Yanagi. Other specimens. NSMT-Co R334: dissected specimen, 18 February 1950, off Ajirozaki, Sagami Bay, 32 m depth; NSMT-Co R786: dissected specimen, 15 February 1960, off Hayama, Sagami Bay; NSMT-CoR907: dissected specimen, 13 February 1965, off Hayama, Sagami Bay.

Description. ***External anatomy.*** Column barrel-like, not differentiated into parts, with high degree of expansibility, height ca. 70 mm, diameter ca. 35 mm in live individuals, and height ca. 49 mm and diameter 21 mm in preserved holotype (CMNH-ZG 0275). Body pink, with white dotted longitudinal lines distally (Fig. 74A). Column surface smooth, with transversal wrinkles, small apertures but without papillae-like structures (Fig. 74B, C, D). Body wall thin and translucent; therefore, mesenterial insertions visible from outside as 20 white lines. Aboral end physa-like, rounded, and translucent, and slightly sticky for adhering to any substrate at aboral end (Fig. 74B, C). Twenty tentacles in two cycles of 10, all marginal (Yanagi, 2006; plate 1G). Outer tentacles usually protruding outside or hanging along column; inner ones pointing upwards, curving. All tentacles ca. 10–20 mm in length when fully expanded, and inner ones generally shorter than outer. Tentacles 3 mm in diameter, bold, bar-like with acrospheres at tip. Acrospheres shaped like raisins, apparently wizened (Figs. 81A, B, 82B, C) even in live individuals. Tentacles translucent dark red, with whitish patches or short lines (Yanagi, 2006; plate 1G). Oral disc diameter ca. 20 mm in live individuals and 13 mm in preserved specimens, usually dark red, with 10 radial white lines. The mouth at center of oral disc like slits, with apparently swelled lips and without conchula (Yanagi, 2006; plate 1G).

Internal anatomy. Twenty mesenteries in all macrocnemes. Ten pairs; six of them in first cycle and four additional pairs (Fig. 75A). All macrocnemes perfect, fertile, and continuing along entire body length. Microcnemes absent. One tentacle arising from each endocoel and exocoel. Longitudinal muscle of tentacle ectodermal (Fig. 75D); circular muscle of tentacle endodermal (Fig. 75E). Acrosphere on tentacle tip (Fig. 75B, C) with densely arranged large basitrichs. Retractor muscles strong and restricted (Fig. 75A, F), with approximately 15–35 multiple-branched muscular processes (Fig. 75F); parietal muscles distinct, strongly developed especially on each exocoel side, with approximately 30–60 simple or slightly branched muscular processes (Fig. 75F, G). In holotype, mesoglea in body wall ca. 80 μm, thicker than ectoderm (ca. 50 μm), and thinner than endoderm (ca. 110 μm), but thinner in actinopharynx and siphonoglyph (Fig. 75A, F). Actinopharynx with numerous folds, extended to approximately 1/2 column length. Single distinct siphonoglyph on ventral side of actinopharynx, never drawn out into a separate tube, and sustained by ventral directives (Fig. 75A). Marginal sphincter muscle absent. Basilar muscle absent. Filaments at proximal edge of macrocnemes small and limited near aboral end. All specimens dioecious, and matured oocytes in mesoglea of each mesentery of holotype (Fig. 75F).

Cnidom. Basitrichs, microbasic *b*-mastigophores. See Table 39 for size and distribution.

Distribution and habitat. Pacific coast of Honshu (Chiba and Miyagi prefectures: the present study and Uchida, 1941, p. 385). This species usually inhabits muddy sand between rocks.

Common name. Kinoko-ginchaku (Uchida, 1965)

Remarks. Differences between *Anemonactis* sp. nov. 29 and *A. mazeli*
Anemonactis mazeli (Jourdan, 1880) has been considered to be a cosmopolitan species because this species had been recorded from many localities worldwide: the Mediterranean Sea, including Marseille, the type locality (Jourdan, 1880; Andres, 1881), the Atlantic coast of Europe (Garstang, 1892; Rees, 1913; Carlgren, 1921, 1940; Stephenson, 1935; Pax and Müller, 1962; Wood, 2005), Japan and East China Sea (Uchida, 1938, 1941, 1965; Pei, 1998), and the Pacific coast of North America (Fautin, 1998). However, this wide distribution led to a debate whether the haloclavids from the Pacific are

the same species as *A. mazeli* from Europe. In particular, Carlgren (1949) speculated whether Japanese *A. mazeli* described by Uchida (1938, 1941) was the same species as the *A. mazeli* individuals from Europe. Nevertheless, the type specimens from the Mediterranean Sea are missing (Yanagi, 2006), and there is no information about new *A. mazeli* specimens from around the type locality. Therefore, I could assess the indistinguishability of these *Anemonactis* only by comparing the literature. Pax and Müller (1962) reported on the intraspecific variation of *A. mazeli.* As the Japanese species resembles "var. *rubra*" (Pax and Müller, 1962) the most in its comparatively large size and reddish color, I carefully inspected old descriptions of *A. mazeli* that mentioned their reddish color and large size to obtain morphological information about *A. mazeli* (e.g., Faurot, 1895; Carlgren, 1921; Stephenson, 1935; etc.).

In the present study, I observed two Japanese specimens which resemble *A. mazeli* and found several differences between *A. mazeli* and the Japanese specimens. Regarding the external anatomy, there is an apparent difference in the shape of acrospheres: those of *A.* sp. nov. 29 are elongated in the direction of tentacles and roughly wizened like raisins not only in preserved specimens but also in live individuals (Figs. 81A, 82B, C). These features have never been described in older literature mentioned above, but instead, the acrospheres of *A. mazeli* were depicted as smooth, spherically shaped both externally (Faurot, 1895; Stephenson, 1935, Pax and Müller, 1962, Fautin,1998) and internally (Rees, 1913). Moreover, the most recent picture of *A. mazeli* showed completely spherical acrospheres (Wood, 2005, p. 83), which affirmed the descriptions mentioned above. In addition, there is a difference in the column surface: the surface in *A.* sp. nov. 29 is completely smooth, without papillae, but always with papillae in *A. mazeli* (e.g., Stephenson [1935], p. 91 described the column as "covered with microscopic pale spots (papillae) scattered thickly over the surface and occurring both over and between the mesenterial insertions"); this character is common in the genus *Anemonactis*. As *A.* sp. nov. 29 can be distinguished from *A. mazeli* by the absence of small solid papillae on the column, the diagnosis of *Anemonactis* should be revised. The most characteristic difference of *A.* sp. nov. 29 from other *Anemonactis* species is in the cnidom; microbasic *b*-mastigophores, which are apparently distinguishable from the other two types of basitrichs not only by their size but also the inner shape of their shafts, are present in filaments of *A.* sp. nov. 29 (Table 39). This type of cnidae was never observed in *A. mazeli* (Carlgren, 1940; table 1 in Yanagi, 2006). Notably, these microbasic *b*-mastigophores are apparently different from the middle-size basitrichs present in the filaments of *A. mazeli* in Carlgren (1940) because the width of the former is twice as large as those of the latter, despite the lengths being almost the same (table 1 in Yanagi, 2006). In addition, the basitrichs types are different: *A.* sp. nov. 29 has two types but *A. mazeli* has three (Carlgren, 1940). Moreover, there are two types of basitrichs in the column of *A.* sp. nov. 29 (Table 39; table 1 and fig. 2c, d in Yanagi, 2006), in contrast with *A. mazeli*, which possesses only one type of basitrichs (Carlgren, 1940).

In addition to the morphological differences mentioned above, the geographical isolation of the Asian localities from the type locality of *A. mazeli* reinforces the distinctness of this species. In conclusion, I identified this *Anemonactis* species living in Japan as a new species, *Anemonactis* sp. nov. 29. I presume that '*Anemonactis mazeli*' individuals found in Japan (Uchida, 1941, 1965, Uchida and Soyama, 2001) are in fact *Anemonactis* sp. nov. 29. Moreover, *A.* sp. nov. 29 may be distributed in China: Pei (1998; fig. 89) depicted "*Anemonactis mazeli*" from East China Sea with apparently wizened acrospheres on its tentacle tips, which resembles those of *A.* sp. nov. 29. The article by Pei (1998) lacks detailed cnidae data, and therefore, it is currently impossible to conclude with certainty about species identity, although the geographical distribution suggests that the Chinese *Anemonactis* belong to *A.* sp. nov. 29. and not to *A. mazeli*.

See Table 41 for comparison of *Anemonactis* sp. nov. 29 and the other species of *Anemonactis*. The taxonomic keys of *Anemonactis* is as below.

1. Tentacle number 12 …*Anemonactis clavus* (Quoy and Gaimard, 1833)
  - Tentacle number 14 …*Anemonactis globulosa* (Quoy and Gaimard, 1833)
  - Tentacle number 16 … ***Anemonactis minuta* (Wassilieff, 1908) comb. nov.**
  - Tentacle number 20 … 2
  2. Acrospheres smooth and spherical. Microbasic *b*-mastigophores absent … *Anemonactis mazeli* (Jourdan, 1880)
    - Acrospheres wizened like raisins. Microbasic *b*-mastigophores present … ***Anemonactis* sp. nov. 29**

Superfamily METRIDIOIDEA Carlgren, 1893

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

Family METEDWARDSIIDAE fam. nov.

(New Japanese name: Hoso-isoginchaku-ka)

Diagnosis. Elongated anemones of Metridioidea. Body more or less divisible into physa, scapus, and scapulus. Scapus and physa slightly differentiated from each other, the former with a thin epidermis without nemathybomes. No sphincter. Tentacles comparatively short, the inner shorter than the middle and outer ones. 8 perfect and fertile mesenteries arranged as the macrocnemes in *Edwardsia*. 16 microcnemes, elongated from distal to proximal end. The number distally is always equal or less than proximally. Retractors of macrocnemes reniform to circumscribed. Parietal muscles distinct but weak. No nematosomes in the coelenteron. Cnidae; basitrichs, spirocysts, microbasic *b*-mastigophores, and microbasic amastigophores.

Etymology. Derived from the name of type genus.

Type genus. *Metedwardsia* Carlgren, 1947 (monotypic)

Remarks. *Metedwardsia*, the monotypic genus of this family now, was established by Carlgren as a member of Edwardsiidae in 1947. Although there were a few peculiar features on *M. akkeshi* e.g. microcnemes distributed on whole body, *Metedwardsia* has been consequently accommodated in Edwardsiidae because of their few mesenteries (see remarks of the genus).

However, this genus was turned to be a member of Enthemonae and no longer the member of Edwardsiidae by my phylogenetic analysis (Figs. 6, 8). The phylogenetic analysis indicated that it was not possible that *M. akkeshi* (= *Metedwardsia*) is belonging any other existed families (see Chapter 1C). That was why new family for *Metedwardsia* should be established. See Table 42 for comparison of the family Metedwardsiidae and the other families without basal discs of the suborder Metridioidea.

Genus *Metedwardsia* Carlgren, 1947

(Japanese name: hoso-isoginchaku-zoku: Izumi et al., 2018b)

Metedwardsia Carlgren, 1947: 1; Carlgren, 1949: 26.

Diagnosis. (Revised from Carlgren [1949]. Revised points are indicated in **bold.** The diagnosis of cnidom is newly added)

Metedwardsiidae, body **more or less** divisible into physa, scapus, and **scapulus**. Scapus and physa slightly differentiated from each other, the former with a thin epidermis without nemathybomes. No sphincter. Tentacles **comparatively** short, the inner shorter than the **middle and** outer ones. 8 perfect and fertile mesenteries arranged as the macrocnemes in *Edwardsia*. **16** microcnemes, **elongated from distal to proximal end**. **The number distally is always equal or less than proximally**. Retractors of macrocnemes reniform to circumscribed. Parietal muscles distinct but weak. No nematosomes in the coelenteron. **Cnidae; basitrichs, spirocysts, microbasic *b*-mastigophores, and microbasic amastigophores**.

Type species. *Metedwardsia akkeshi* (Uchida, 1932a)

Remarks. Genus *Metedwardsia* was established to accommodate *Milneedwardsia akkeshi* of Edwardsiidae because of its worm-like shape and eight macrocnemes, and because some morphological characters of this species did not correspond to the diagnosis of *Milneedwardsia* (Carlgren, 1947). Since then, the diagnosis of *Metedwardsia* had not been revised due to lack of new specimens. Based on the current re-description of *Metedwardsia akkeshi* resulting from thorough examination of the characteristics of newly collected topotypic specimens, revision of this diagnosis is required. As the cnidom of *M. akkeshi* has never been formally described, I added a description of the cnidom to the diagnosis. The microcnemes extending from the oral to the aboral end in this genus were thought as the only character among the Edwardsiidae, suborder Anenthemonae. The 16 microcnemes are easily distinguishable from the eight macrocnemes by their smaller size, absence of retractor muscles, and the trilobated filament and gonad, and they are elongated from the distal to proximal end.

Although this genus has been included in Edwardsiidae for several decades, but there were some different opinions. Gusmão et al. (2016) recently suggested placing *M. akkeshi* in the Halcampidae, a family belonging to the different suborder, Enthemonae, because *Metedwardsia* does not have microcnemes but rather imperfect macrocnemes extended along the entire body in which muscles develop, whereas the microcnemes in other Edwardsiidae genera are restricted to the distal-most column and have poorly developed musculature: which features rather resembles Halcampidae than Edwardsiidae. However, their taxonomic conclusion was based only on the reference citation of the morphological characteristics of *M. akkeshi*. Contrary, a molecular phylogenetic tree developed by Rodríguez and Daly (2010) assigned *M. akkeshi* to the Actiniidae subclade within the Endomyaria clade. Actiniid sea anemones belong to the farther clade from Halcampidae: this two families are different in superfamily level (Rodríguez et al. 2014). Accordingly, based on this phylogenetic tree, *Metedwardsia*, which is strongly related to Actiniidae, should be accommodated neither to Halcampidae nor Edwardsiidae. However, Rodríguez and Daly (2010) did not provide detailed information about the morphological features of *M. akkeshi* specimen on which their phylogenetic analysis was based. Therefore, it was still possible that the molecular data of *M. akkeshi* in Rodríguez and Daly (2010) might be based on a misidentified, or wrong specimen. As such, I had concluded *Metedwardsia* should be remained in Edwardsiidae in Izumi et al. (2018b).

In this study, *Metedwardsia akkeshi* (Uchida, 1932) and similar anemones were concluded to be the independent group from any anemones which are similar to *Metedwardsia* in morphology (see Chapter 1 and remarks of family Metedwardsiidae fam. nov.). The discussion of belonging of *Metedwardsia akkeshi* would be finished with this research.

Metedwardsia akkeshi **(Uchida, 1932)**

(Japanese name: Hoso-isoginchaku; Uchida 1965)
Figs 76, 77; Table 43

Milne-Edwardsia akkeshi Uchida, 1932: 571, figs 1–4; Uchida, 1940: 266.

Drillactis akkeshi: Uchida, 1940: p. 267.

Metedwardsia akkeshi: Carlgren, 1949: 26; Song, 2003: 288, figs 3A–F, 5C, table 2 (sic); Izumi et al., 2018: figs. 2–4, table 2

Material examined. NSMT-Co 1605: dissected specimen, histological sections, tissues in paraffin, and prepared nematocysts, 30 June 2015, Chikarakotan mud flats, Lake Akkeshi, Hokkaido (43°01.28′N, 144°52.46′E), by wading, intertidal, collected by Takato Izumi and Kensuke Yanagi; CMNH-ZG 09137, two whole specimen, same date and place as NSMT-Co 1605; NSMT-Co 1606: whole specimens, 25 June 2017, Shinryu-hama Beach, Lake Akkeshi, Hokkaido (43°05.23′N, 144°84.43′E), by wading, intertidal, collected by Naoto Jimi; CMNH-ZG 4314: dissected specimen, histological sections, tissues in paraffin, and prepared nematocysts, 31 July 2006, mud flats near the Onne-to Ohashi Bridge, Lake Onne-to, Hokkaido (43°26.50′N, 145°49.77′E), by wading, intertidal, collected by Kensuke Yanagi and Marymegan Daly; NSMT-Co 1607: whole specimen, 27 June 2015, at same lake as CMNH-ZG 4314 (43°15.56′N, 145°29.56′E), by wading, intertidal, collected by Takato Izumi and Kensuke Yanagi; NSMT-Co 1608: dissected specimen, histological sections, tissues in paraffin, and prepared nematocysts, 25 October 2014, Lake Furen, Hokkaido, by wading, intertidal, collected by Naoto Jimi; (Iz-093): whole specimens (4 individuals), same method, collector and date as NSMT-Co 1605; (Iz-094): dissected specimen, 8 November 2014, beach in Umi-no-koen Park, Yokohama, Kanagawa Pref., by snorkeling, 1 m depth, collected by Naoto Jimi; (Iz-095): whole or dissected specimens (8 individuals), 18 June 2017, beach in Umi-no-koen Park, Yokohama, Kanagawa Pref., by wading, intertidal, collected by Masako Ojima and Takato Izumi; (Iz-096): dissected specimen, histological sections, tissues in paraffin, and prepared nematocysts, 4 November 2014, Denshin-hama beach, Hokkaido, by snorkeling, 3 m depth, collected by Naoto Jimi; (Iz-097): whole specimen (damaged), 11 June 2017, Denshin-hama beach, Hokkaido, by snorkeling (depth unknown), collected by Naoto Jimi; (Iz-098): whole specimens (two individuals), 12 September 2019, Syunkuni-Tai, Lake Furen, Hokkaido, intertidal, collected by Itaru Kobayashi.

Description. ***External anatomy.*** Body elongated and worm-like in shape; little divided into physa, scapus, and scapulus (Fig. 76A, B). Surface of column smooth, without nemathybomes. Outside of scapus surrounded thin covering imbued with detritus particles, mucus-membrane secerned by mucus cells. Scapulus and physa mostly concealed in the covering when contracted. Scapulus short and provided with 24 short conical tentacles arranged in three alternating cycles (Fig. 76C). Tentacles of inner and middle cycles same length or shorter than those of the outer. Lines indicating the insertion of mesenteries observed from outside in submarginal region but gradually obscure toward proximal end owing to the presence of thick ectoderm and well-developed mesogleal ring muscle. Physa, usually small and barely distinguishable from scapus, well expanded and contractible. Length of body *ca.* 20–40 mm and breadth of oral disc ca. 3–5 mm. Scapus and physa a little narrower than tentacular cycle. General color of column pale pink, tentacles brownish white, with dark brownish cross band (Fig. 76C). Occasional white spot on marginal part of oral disc below base of each tentacle. However, patterns absent on the tentacles of specimen from Muroran (Fig.

76A).

Internal anatomy. Epidermis of scapus and scapulus containing glandular cells thicker than mesoglea, furnished with ring muscles (Fig. 76D). Gastrodermis of scapulus generally similar in structure and thickness to those of both scapus and physa. Epidermis of scapus thick with a large number of glandular cells. Mesoglea thick in scapus, actinopharynx, and physa, but thinner in mesenteries and tentacles (Fig. 76D–J). Ectoderm thicker than mesoglea in physa. No sphincter muscle in capitulum and no basilar muscle in aboral end (Fig. 76D). Actinopharynx folded, ectoderm as thick as its mesoglea, and granular cells present. Tentacular longitudinal muscle ectodermal, distinct (Fig. 76F); tentacular circular muscle indistinct.

Mesenteries 24 in number of which 8 macrocnemes and 16 microcnemes (Fig. 76E). Out of 8 macrocnemes, 4 in two directive pairs, dorsal and ventral. Other dorso- or ventro-lateral mesenteries, unpaired with other macrocnemes. Out of 16 microcnemes, 4 between dorsal directives and dorso-lateral mesenteries, 6 between dorso-lateral mesenteries and ventro-lateral ones, and the other 6 between ventro-lateral ones and ventral directives, comparatively tiny (Fig. 76E). All mesenteries including microcnemes extend from oral to aboral ends (Fig. 76E, H, J). On 8 macrocnemes, retractor muscles short and circumscribed and arranged in bilateral symmetry. Retractor muscles well developed, generally similar in form from scapulus to aboral end (Fig. 76H, I). Muscle fibers in the most developed muscle pennon about 10, each fiber highly branched (Fig. 76I) into 10 or more; 2–3 in lower part also branched into several fibers. On 16 microcnemes, muscle a little developed or not at all, rarely branched into muscle fiber. Parietal muscle folds few and radially elongated (Fig. 76G). Mesenterial filament shape trilobated leaf near upper part, consisting of a median cnidoglandular and two lateral ciliated tracts; in lower part, mesenterial filament shape broadly kidney-like, furnished with glandular cells and nematocysts (Fig. 76I). Base of ciliated tract digestive region and arranged by high density of endoderm cells. Reproductive region between muscle pennon and mesenterial filaments. Ovary or testicular saccules in a row imbedded in mesoglea, ovary in histological sections (Fig. 76I), dioecious. All microcnemes devoid of filaments and little furnished with parietal muscle similar to that of macrocnemes (Fig. 76).

Cnidom. Basitrichs, spirocysts, microbasic *b*-mastigophores, microbasic amastigophores. See Table 43 for size and distribution.

Habitat. Generally, inhabits soft mud in the brackish intertidal zone, associated with the sea grass *Zostera japonica*. Although Shinryu-hama Beach in Akkeshi Bay opens on to the sea, the water is brackish due to input from Lake Akkeshi. This species tends to live in patchy aggregations of several individuals. Habitat of Yokohama is completely in sea water exceptionally, but there are also sea grasses bearing.

Remarks. The examined specimens corresponded well to the description of Uchida in 1932, but some morphological features were found to differ slightly or were not included in the original description. For example, Uchida (1932a) noted that *M. akkeshi* has a capitulum, but I identified the part of the column near the tentacles as scapulus rather than capitulum. The cnidom, which were not included in Uchida (1932a), are here described for the first time.

After the description of Uchida (1932a), there are few study referring to *M. akkeshi* (Uchida et al., 1963; Uchida and Soyama, 2001), and none of them recorded additional specimen newly collected. So, this research should be the collection of *M. akkeshi* after a long time from description over 80 years before.

Whether this species inhabits out of Hokkaido, or not. Song (2003) reported *M. akkeshi* from Deokjeokdo Island, South Korea, which is the sole record of *M. akkeshi* from localities other than Akkeshi. Based on their description, it is probable that the Korean specimen is at least within the genus *Metedwardsia*, because it only has 8 macrocnemes and 16 microcnemes extending beyond the whole bodies, but I suspect that the Korean specimen is not *Metedwardsia akkeshi*, for the following reasons. First, several differences between the cnidoms in the specimens of Song (2003) and those of this study are apparent; for example, Song (2003) described three types of microbasic *p*-mastigophores that differed in size in the filaments. Comparison of the sizes of these microbasic *p*-mastigophores with those of our specimens suggested that the smallest microbasic *p*-mastigophores in the Korean specimens would be equivalent to the microbasic amastigophores of the Akkeshi specimens, and the medium sized Korean ones would be equivalent to the microbasic b-mastigophores of our specimens. However, large Korean microbasic *p*-mastigophores were not found in our specimens, and I did find any spirocysts in the column or the scapus. Second, Deokjeokdo Island, where the Korean specimen was collected, is over 1500 km across the Yellow Sea from Akkeshi; moreover, the distribution of *M. akkeshi* in Japan appears to be limited to southeast Hokkaido, and only Yokohama was the exceptional locality in Japan. Finally, Song (2003) reported that the Korean specimens were found in sandy mud flats, whereas *M. akkeshi* in Hokkaido always inhabits quite muddy seashore environments, which feature substantially different substratum. Thus, I thought that it was not likely that species of *Metedwardsia* in Korea was *M. akkeshi.*

However, this study collected several individuals of species of *Metedwardsia* inhabited in Hakkeijima, Yokohama, Kanagawa Prefecture (Fig. 77B). These anemones were so resembling that they cannot be distinguished from *Metedwardsia akkeshi* by both external and internal features. So, this study resulted in the conclusion that *M. akkeshi* is somehow living in Yokohama, far distant from localities in Hokkaido. I thought two possibilities: one is that this species had been carried by someone from original locality, like ballast water of ships (see remarks of *Edwardsia sipunculoides*). If this hypothesis is right, Korea species might be *M. akkeshi* introduced from Japan in recent years. The other possibility is just there are cryptic species in *M. akkeshi.*

Where is the original locality? Uchida (1932a) reported that the *Metedwardsia akkeshi* specimens used in the original description were collected in “Akkeshi Cove” but did not provide more detailed information regarding the specific location. I could not identify the exact location of the cove because there are two cove-like coastline features in Akkeshi, one along Akkeshi Bay, an inlet on the Pacific Ocean, and the other along Lake Akkeshi, a brackish lake connected to Akkeshi Bay by a narrow channel. Identifying the exact location of the original specimens is essential because many environmental factors, such as sediment type and water salinity, differ greatly between Akkeshi Bay and Lake Akkeshi. Uchida (1940) noted that *M. akkeshi* was unique to “this Bay” and that *M. akkeshi* is common in muddy flats along the shoreline of “Akkeshi Cove”. Based on these clues, I speculate that Akkeshi Cove, the type locality of this edwardsiid, is most likely located along the shoreline of Lake Akkeshi. In addition, the reference to “muddy” flats points toward the intertidal zone of Lake Akkeshi, as the intertidal sediments of the lake are generally muddier than those of Akkeshi Bay. Nevertheless, I could not assert with certitude the exact location of “Akkeshi

Cove” based on Uchida’s descriptions.

Here, I re-described *M. akkeshi* from specimens recently collected in both Lake Akkeshi and Akkeshi Bay, in Hokkaido, Japan. In both locations, *M. akkeshi* inhabited brackish intertidal zones with muddy substratum; in Akkeshi Bay, *M. akkeshi* was found solely at Shinryu-hama Beach, where the substratum is exceptionally muddy, and no *M. akkeshi* were found in other intertidal areas in the bay, which are mainly rocky or stony. Salinity levels are also likely to be lower at Shinryu-hama Beach than at other seashore sites in Akkeshi Bay, as it is located near to the junction with Lake Akkeshi and thus is exposed to brackish water flow from the lake. Given that both *M. akkeshi* specimens from Nemuro (Lake Onne-to and Furen) were collected from brackish lakes, the brackish waters and muddy substrates of Lake Akkeshi likely provide the preferred habitat of this species. Finally, I conclude that the “Akkeshi Cove” referred to by Uchida (1932a, 1940) is located along the shoreline of Lake Akkeshi.

(Description, Fig. 76, and part of Table 43 are revised and reprinted Izumi et al. [2017] by courtesy of Species Diversity.)

***Metedwardsia* sp. nov. 30**

(New Japanese name: madara-hoso-isoginchaku)

Fig. 78; Table 43

Material examined. (Iz-099): histological sections and prepared nematocysts, 16 May 2014, Muddy bottom in Aburatsubo-Bay, Misaki, Kanagawa Pref., 3–4 m in depth, collected by Takato Izumi.

Description. ***External anatomy.*** Body elongated and worm-like in shape; apparently divided into scapus and scapulus (Fig. 78A). Surface of column smooth, mucus-membrane indistinct. Scapulus concealed in the covering when contracted. Scapulus apparent and provided with 24 long slender tentacles arranged in three alternating cycles. Tentacles of inner and middle cycles same length or shorter than those of the outer. Lines indicating the insertion of mesenteries observed from outside in submarginal region, and gradually apparent toward proximal end owing to the semitransparent body. Proximal end barely distinguishable from scapus, semitransparent, well expanded and contractible. Length of body *ca.* 12 mm and breadth of body ca. 3 mm. General color pale white or semitransparent, tentacles brownish yellow, with black and white patches mingled (Fig. 78B).

Internal anatomy. Gastrodermis of scapulus generally similar in structure and thickness to those of both scapus. Distinct glandular cells absent on scapus. Mesoglea thick in actinopharynx, scapulus and distal side of scapus, but thinner in proximal side of scapus, mesenteries and tentacles (Fig. 78C, D). Ectoderm thin (Fig. 78C, D). No sphincter muscle in capitulum and no basilar muscle in aboral end. Actinopharynx folded, ectoderm thicker than mesoglea.

Mesenterial arrangement same as *M. akkeshi*. Microcnemes tiny (Fig. 78C). All mesenteries including microcnemes extend from oral to aboral end. On 8 macrocnemes, retractor muscles short and circumscribed and arranged in bilateral symmetry. Retractor muscles well developed, generally similar in form from scapulus to aboral end (Fig. 78C–E). Muscle fibers in the most developed muscle pennon about 10, each process highly branched (Fig. 78D, E), but indistinct because of insufficiently fixed. On 16 microcnemes, muscles too little developed to observing, rarely branched into muscle fiber. Parietal muscle indistinct or collapsed for bad preservation (Fig. 78E). Reproductive region between muscle pennon and mesenterial filaments, but matured gametes absent. All microcnemes devoid of filaments and little furnished with parietal muscle similar to that of macrocnemes.

Cnidom. Basitrichs, spirocysts, microbasic *b*-mastigophores, and microbasic *p*-mastigophores. See Table 43 for size and distribution.

Remarks. See Table 44 for comparison to the other species of the genus *Metedwardsia*. This species was distinguished from *M. akkeshi* by the differences as below: contrary to the *M. akkeshi* which have bodies not differentiated into scapus and scapulus, the border between scapus and scapulus of *Metedwardsia* sp. nov. 30 is quite distinct; microbasic *p*-mastigophores only exists in actinopharynx of *Metedwardsia* sp. nov. 30; body size of *M.* sp. nov. 30 is apparently smaller than *M. akkeshi*; concerning to the habitats, *Metedwardsia* sp. nov. 30 inhabits in seawater while *M. akkeshi* generally inhabits in brackish water.

Though this anemone was determined as a new species, it is expected that new specimens in good conditions are collected from Aburatsubo-Bay in future.

***Metedwardsia* sp. nov. 31**

(New Japanese name: goku-boso-isoginchaku)

Fig. 79; Table 43

Material examined. CMNH-ZG 5943: dissected specimen, histological sections, tissues in paraffin, and prepared nematocysts, 8 July 2013, Ogushi, Nakajima-Island, Ehime Pref., intertidal, collected by Kensuke Yanagi; (Iz-100): dissected specimen, histological sections, tissues in paraffin, and prepared nematocysts, 28 April 2017, muddy bottom in Nishidomari-Port, Kochi Pref., 3m depth, collected by Takato Izumi.

Description. ***External anatomy.*** Body quite elongated, slender and worm-like in shape; little divided into physa, scapus, and scapulus (Fig. 79A). Surface of column smooth, without nemathybomes. Mucus-membrane indistinct. 24 short conical tentacles arranged in three alternating cycles (Fig. 79B). Tentacles of inner and middle cycles same length or shorter than those of the outer. Lines indicating the insertion of mesenteries observed from whole body but generally obscure. Proximal end of the body barely distinguishable from scapus, well expanded and contractible. Length of body *ca.* 20 mm and breadth ca. 2 mm. Scapus equally narrow among whole body. General color of column and tentacles pale white, the latter with dark gray cross bands (Fig. 79B). Discontinuous gray circle on oral disc around mouth.

Internal anatomy. Epidermis of scapus containing glandular cells as thick as mesoglea, furnished with ring muscles (Fig. 79C). Gastrodermis thinner than mesoglea in scapus. Glandular cells indistinct. Mesoglea thick in scapus, actinopharynx, but thinner in mesenteries and tentacles (Fig. 79C–H). Ectoderm thicker than mesoglea in proximal end (Fig. 79H). No sphincter muscle in scapus and no basilar muscle in aboral end (Fig. 79C, H). Actinopharynx folded, ectoderm as thick as its mesoglea. Tentacular longitudinal and circular muscle indistinct (Fig. 79G).

Mesenterial arrangement same as *M. akkeshi*. Microcnemes tiny (Fig. 79E). Microcnemes comparatively tiny (Fig. 79F). All mesenteries including microcnemes extend from oral to aboral ends (Fig. 79 D–F). On 8 macrocnemes, retractor muscles short and circumscribed and arranged in bilateral symmetry. Retractor muscles well developed, generally similar in form from scapulus to aboral end (Fig. 79D–F). Muscle fibers in the most developed muscle pennon about 6–8, each fiber slightly branched (Fig. 79F) into 5–13 processes. On 16 microcnemes, muscle a little developed or not at all, sometimes branched into <10 muscle processes (Fig. 79F). Parietal muscle folds few and radially elongated (Fig. 79F). Mesenterial filament shape rarely trilobated, shape broadly kidney-like, furnished with glandular cells and nematocysts. Base of ciliated tract digestive region and arranged by high density of endoderm cells. Reproductive region between muscle pennon and mesenterial filaments, but matured gametes absent (Fig. 79D). Lateral four mesenteries the most fertile (Fig. 79F), and directives less furnished. All microcnemes devoid of filaments and little furnished with parietal muscle similar to that of macrocnemes.

Cnidom. Basitrichs, spirocysts, microbasic *b*-mastigophores, and microbasic *p*-mastigophores. See Table 43 for size and distribution.

Remarks. See Table 44 for comparison to the other species of the genus *Metedwardsia*. This species was distinguished from *M. akkeshi* by the differences as below: the body proportion of *Metedwardsia* sp. nov. 31 is slenderer and uniform than *M. akkeshi*; both microbasic *p*-mastigophores and *b*-mastigophores only exists in actinopharynx of *Metedwardsia* sp. nov. 31; concerning to the habitats, *Metedwardsia* sp. nov. 31 inhabits in seawater while *M. akkeshi* inhabits in brackish water. *Metedwardsia* sp. nov. 31 is distinguished from *M.* sp. nov. 30 by its column which is not strongly differentiated into scapulus and physa and the plenty of variation of cnidae in actinopharynx (Table 43).

SAMMARY of topical taxa of Enthemonae

1. The superfamily Actinostoloidea have ignored the family Capneidae. The present study diagnostically revised this superfamily to include Capneidae and a new family Discoactinidae, to which *Discoactis* sp. nov. 27 with strange mesenterial and tentacular arrangements is belonging.
2. In the superfamily Actinioidea, I have discovered four new species and one redescribed species in Haloclavidae. *Anemonactis minuta* comb. nov., which has been synonymized into another species, is reestablished in this study.
3. Species of *Metedwardsia* should be accommodated into a new family Metedwardsiidae in the superfamily Metridioidea. There are two additional species, *M.* sp. nov. 30 and *M.* sp. nov. 31, in this genera other than the type species, *M. akkeshi*.

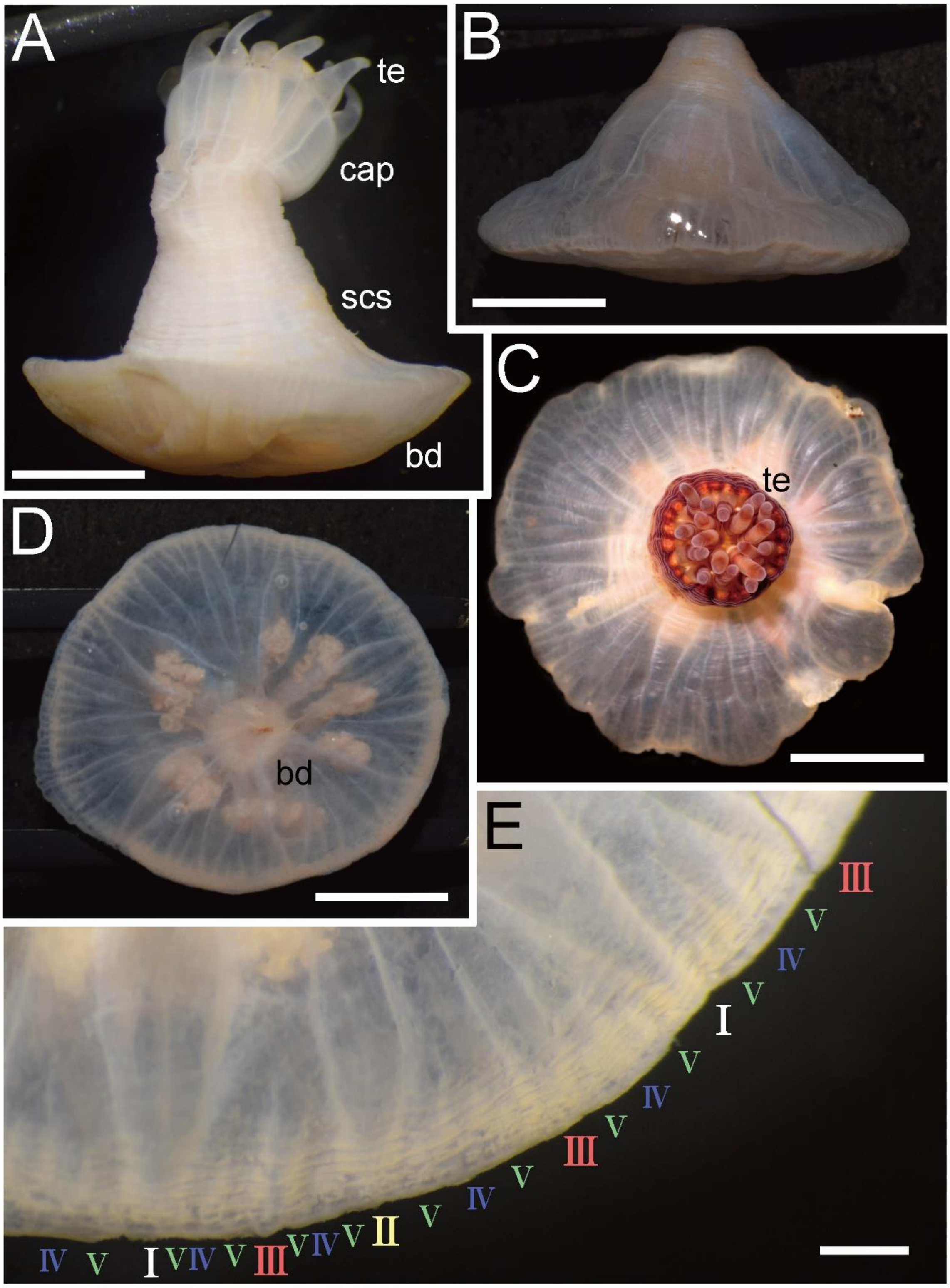

Fig. 66. External morphology of *Discoactis* sp. nov. 27.
A, B, D, and E: views of a preserved specimen, C: view of living specimen. A. tentacles elongated (CMNH-ZG [no registration 1]). B. tentacles contracted (CMNH-ZG [no registration 2]); C. Oral view of oral disc (Iz-084); D. Proximal view of basal disc (CMNH-ZG [no registration 2]); E. Enlarged view of D (CMNH-ZG [no registration 2]). I–V indicates the number of 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 μm.

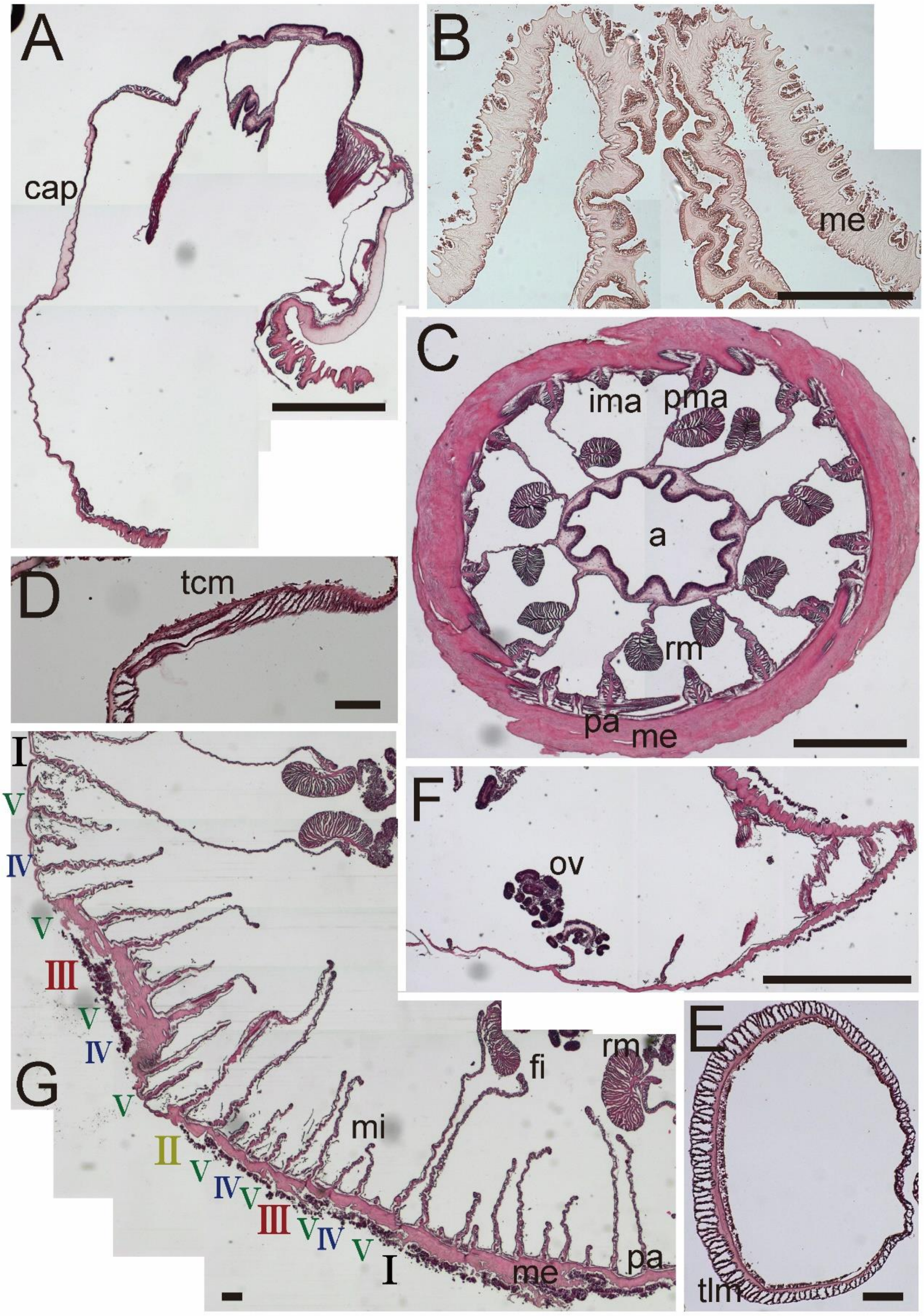

Fig. 67. Internal morphology of *Discoactis* sp. nov. 27.
A, C–G: CMNH-ZG (no registration 1), B: CMNH-ZG (no registration 2). A, B. Longitudinal section of distal end; C. Transverse section of upper column D. longitudinal section of tentacle; E. Transverse section of tentacle; F. transverse section of proximal end (basal disc); G. Enlarged view of transverse section of column. I–V indicates the number of 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; tcm, tentacle circular muscle; tlm, tentacle longitudinal muscle. Scale bars indicate 1 mm in A–C, F, 100 µm in D, E, G.

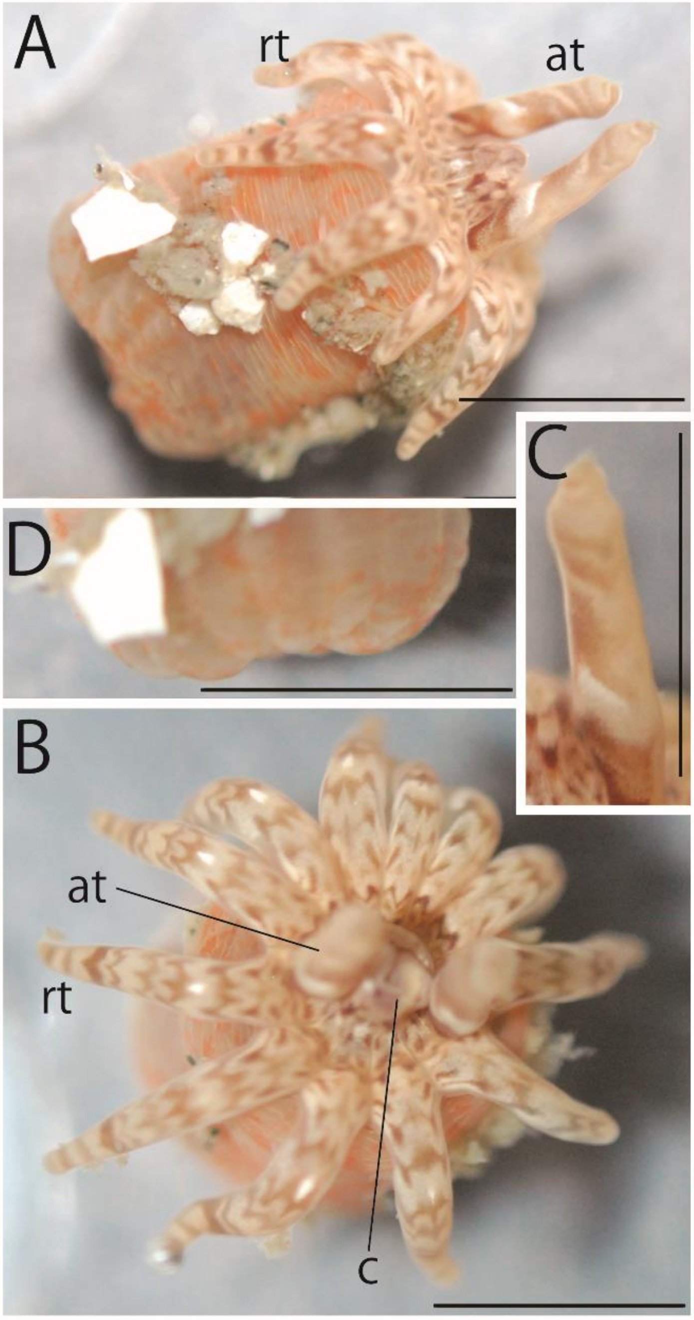

Fig. 68. External morphology of *Antennapeachia setouchi* Izumi and Yanagi, 2016, holotype, NSMT-Co1653, in living state.
A. Lateral view, with attached particles of mud and pieces of shell; two antenna tentacles are rising upward; B. Oral view; conchula is located on ventral side of mouth; C. Lateral view of aboral end. Abbreviations: at, antenna tentacles; c, conchula; rt, regular tentacle. All scale bars indicate 5 mm.

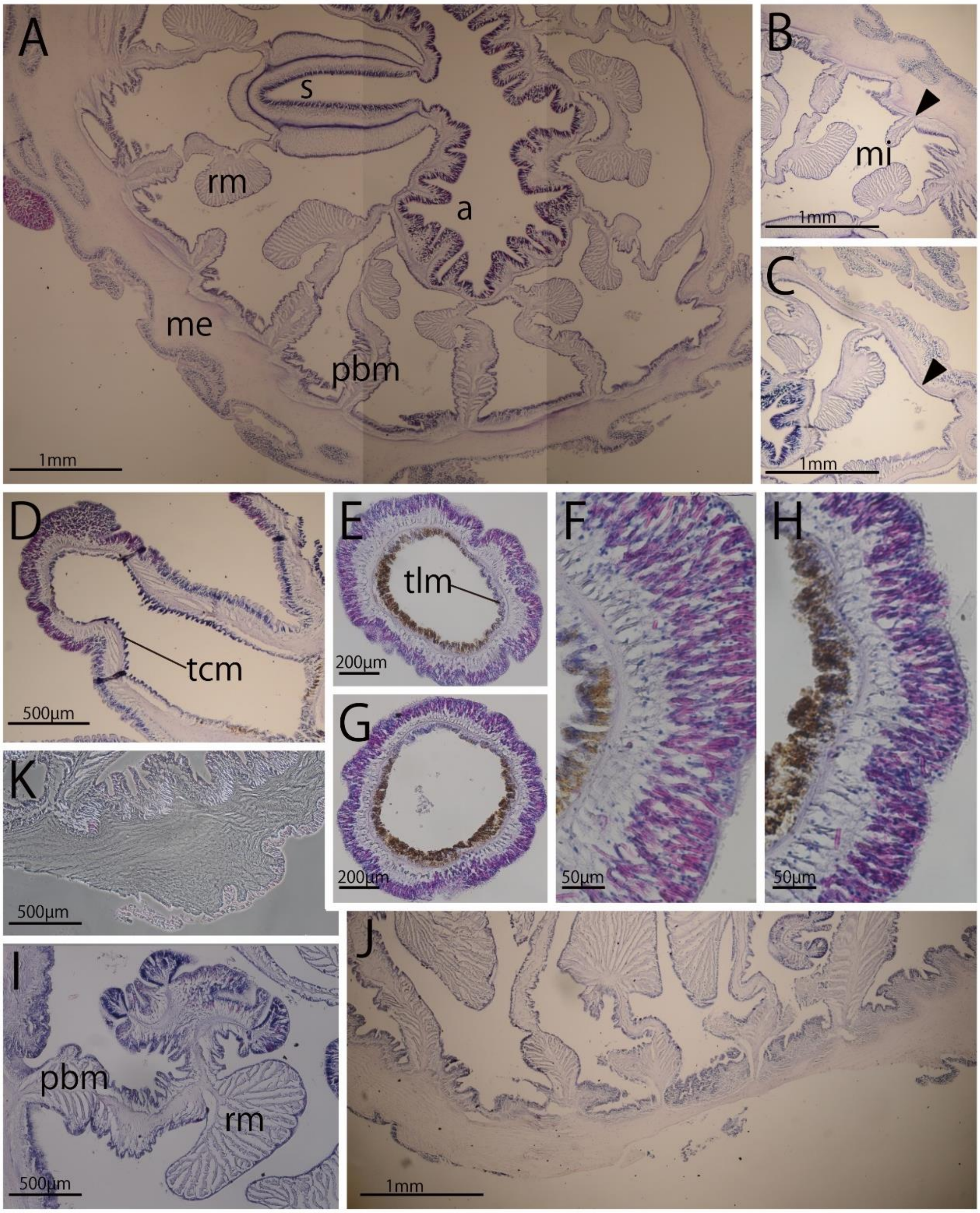

Fig.69. Internal morphology of *Antennapeachia setouchi*, holotype, NSMT-Co 1653. A. Transverse section of column, actinopharynx, and siphonoglyph; B. Transverse section of microcneme between a ventral directive and a single macrocneme (arrowhead); C. Transverse section of the upper part of the column, same direction in B, The microcneme in B is disappeared, arrowhead indicates the position of the microcneme located in B; D. Longitudinal section of regular tentacles; E. Transverse section of regular tentacle; F. Enlargement of a part of E, showing ectodermal longitudinal muscles (indicated by arrowheads); G. Transverse section of antenna tentacles; H Enlarged view of a part of G, showing ectodermal longitudinal muscles (indicated by arrowheads); I. Transverse section of a macrocneme with filament; J. Longitudinal section of the aboral end. The aboral end is somewhat hollowed without basal muscle; K. Enlarged view of a part of J. no basal muscles were observed at the base of the mesentery. Abbreviations: a, actinopharynx; f, filament; me, mesoglea; mi, microcneme, pbm, parietal basilar muscle, rm, retractor muscle, s, siphonoglyph; sma, single macrocneme; tcm, tentacular circular muscle; tlm, tentacular longitudinal muscle; vd, ventral directive.

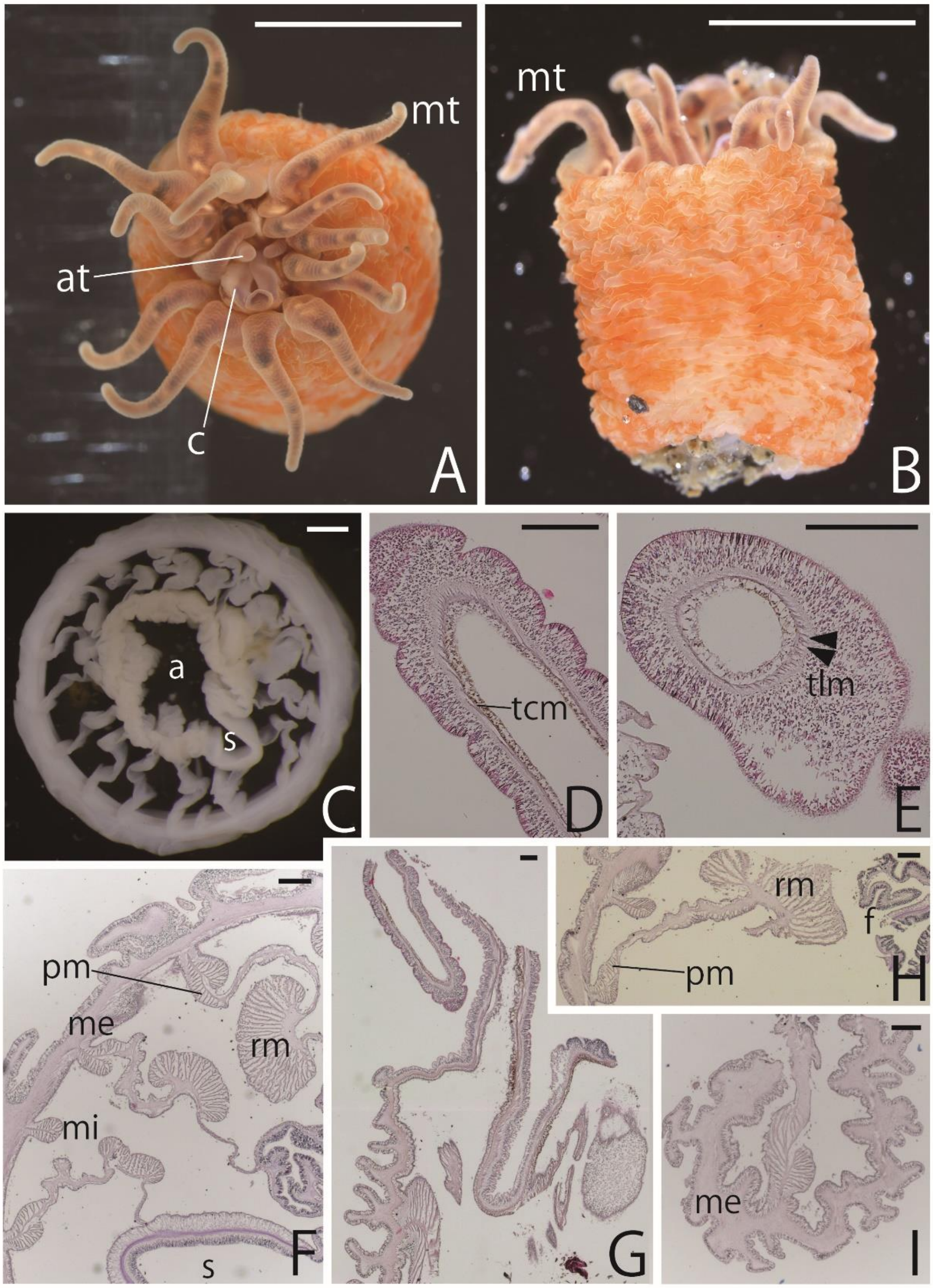

Fig. 70. *Antennapeachia jambio* Izumi, Yanagi, and Fujita, 2017, CMNH-ZG 06546 (holotype). External morphology in living state (A, B) and internal morphology of the preserved specimen (C–I).
A. Oral view; the conchula is located on the ventral side of the mouth; B. Lateral view of the whole body; C. Transverse section of the column; D. Longitudinal section of a tentacle; E. Transverse section of a tentacle showing the ectodermal longitudinal muscles (indicated by arrowheads); F. Transverse section of the column, enlargement of a part of C; G. Longitudinal section of the oral end of the column; H. Transverse section of the mesentery with filament; I. Longitudinal section of the aboral end. Abbreviations: a, actinopharynx; at, antenna tentacle; c, conchula; f, filament; me, mesoglea; mi, microcneme; mt, marginal tentacle; pm, parietal muscle; rm, retractor muscle; s, siphonoglyph; tcm, tentacular circular muscle; tlm, tentacular longitudinal muscle. Scale bars indicate 5 mm in A and B, 1 mm in C, and 100 µm in D–I. Pictures A and B were taken by Kensuke Yanagi.

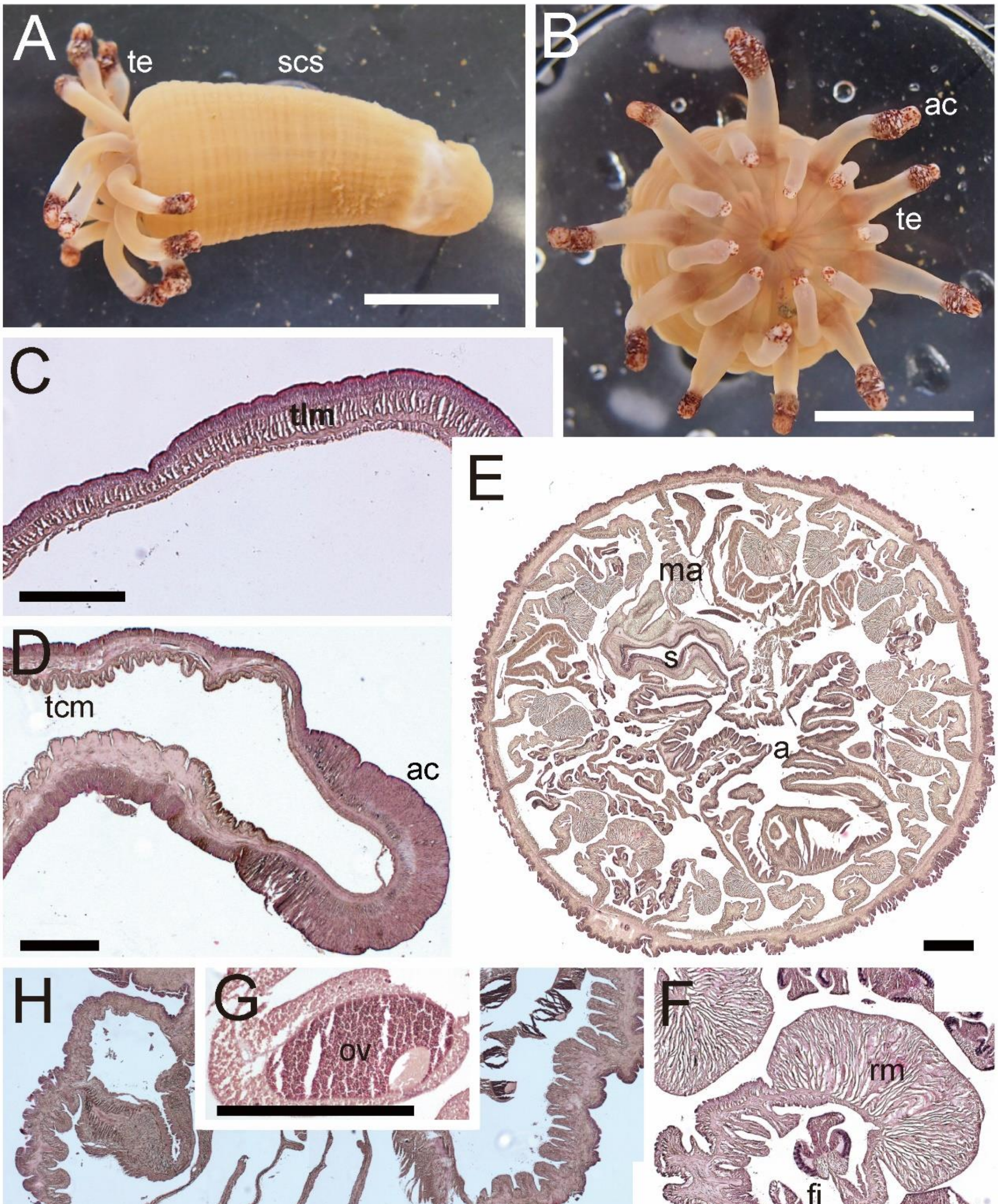

Fig. 71. External and internal morphology of *Haloclava* sp. nov. 28 (Iz-088). External morphology in living state (A, B) and internal morphology of the preserved specimen (C–H). A. Lateral view of the whole body; B. Oral view; C. Transverse section of a tentacle; D. Longitudinal section of a tentacle; E. Transverse section of middle column; F. Transverse section of the macrocneme; G. Enlarged view of transverse section of ovary; H. Longitudinal section of the aboral end. Abbreviations: a, actinopharynx; ac, acrosphere; fi, filament; ma, macrocneme; mi, microcneme; mt, marginal tentacle; ov, ovary; pa, parietal muscle; rm, retractor muscle; s, siphonoglyph; scs, scapus; tcm, tentacular circular muscle; te, tentacle; tlm, tentacular longitudinal muscle. Scale bars indicate 1 cm in A and B, 1 mm in E, and 500 μm in C, D, F–H.

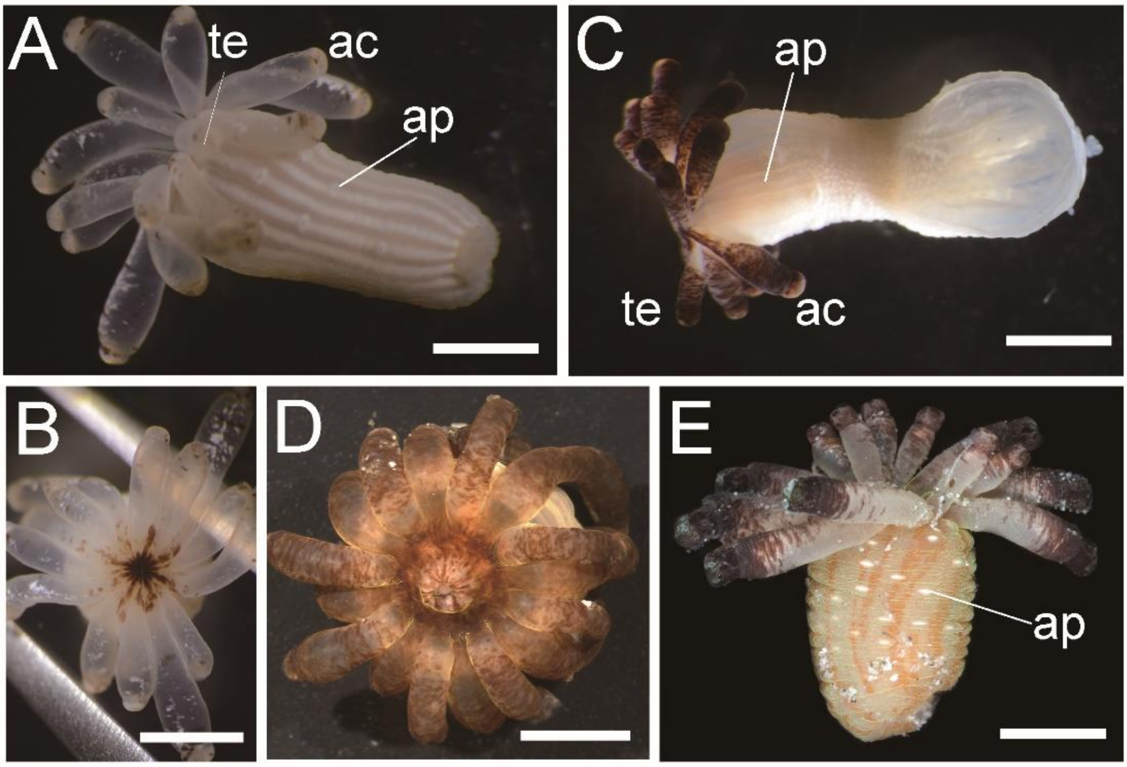

Fig. 72. External views of *Anemonactis minuta* (Wassilieff, 1908) comb. nov. A–B: CMNH-ZG 1619; A. Whole live specimen; B. View from oral direction. C. Whole live specimen of CMNH-ZG 09203; D. View from oral direction of NSMT-Co 1621. E. NSMT-Co 1622, whole live specimen (taken by Yoshihisa Fujita). Abbreviations: ac, acrosphere; ap, aperture; te, tentacle. All scale bars 5 mm.

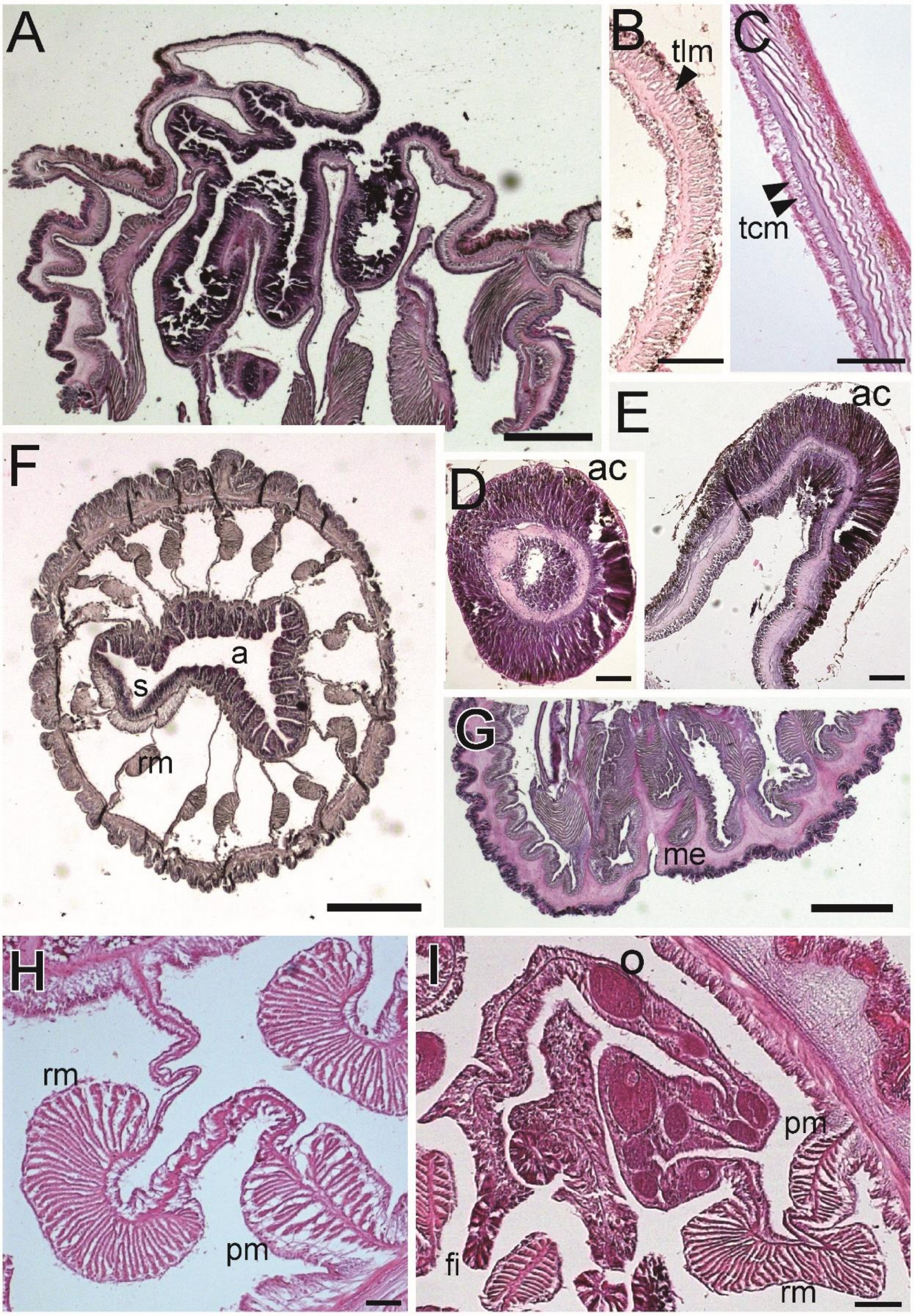

Fig. 73. Histological sections of *Anemonactis minuta* (Wassilieff, 1908) comb. nov. A, B, D, E, G: NSMT-Co 1621; C, H, I: NSMT-Co 1620; F: NSMT-Co 1619. A. Longitudinal section of proximal end. B. Transverse section of tentacle. C. Longitudinal section of tentacle. D. Transverse section of acrosphere. E. Longitudinal section of acrosphere. F. Transverse section of actinopharynx. G. Longitudinal section of aboral end. H. Transverse section of a mesentery. I. Transverse section of gonad. Abbreviations: ac, acrosphere; ap, actinopharynx; me, mesoglea; o, oocyte; pm, parietal muscle; rm, retractor muscle; s, siphonoglyph; tcm, tentacular circular muscle; tlm, tentacular longitudinal muscle. Bold scale bars 500 µm and fine scale bars 100 µm.

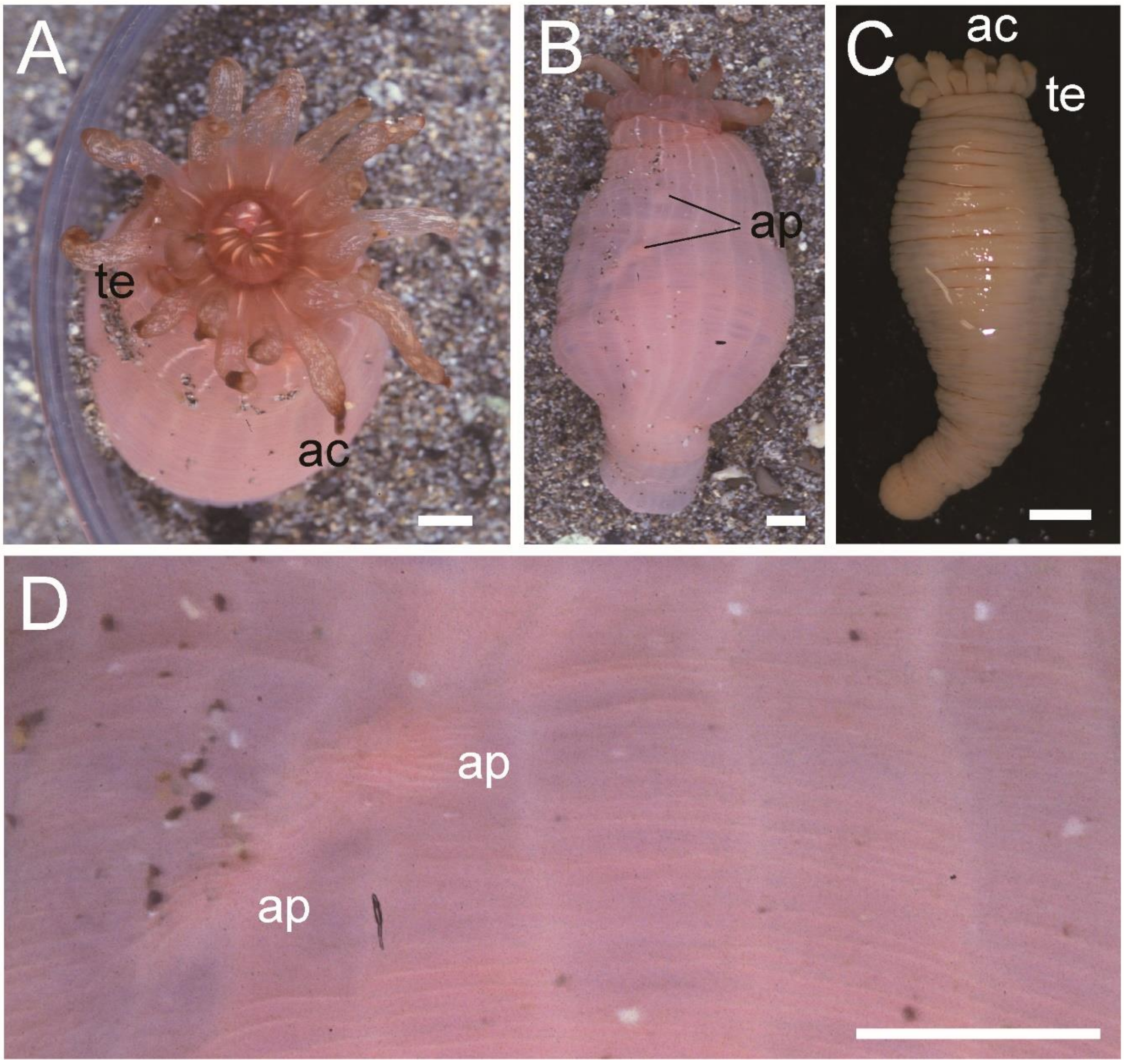

Fig. 74. External views of *Anemonactis* sp. nov. 29.
A, B, D: CMNH-ZG 0275; C: NSMT-Co R907. A. Lateral view of live specimen; B. View from oral direction. (Note that the object on the mouth is not a conchula but inversion of actinopharynx because it can be contained in the mouth completely.); C. Lateral view of fixed specimen; D. Enlarged view of column (white spots are sand grains). Abbreviations: ac, acrosphere; ap, aperture; te, tentacle. All scale bars indicate 5 mm. Photograph of (a) was reproduced from Yanagi (2006). Picture A, B, D were taken by Kensuke Yanagi.

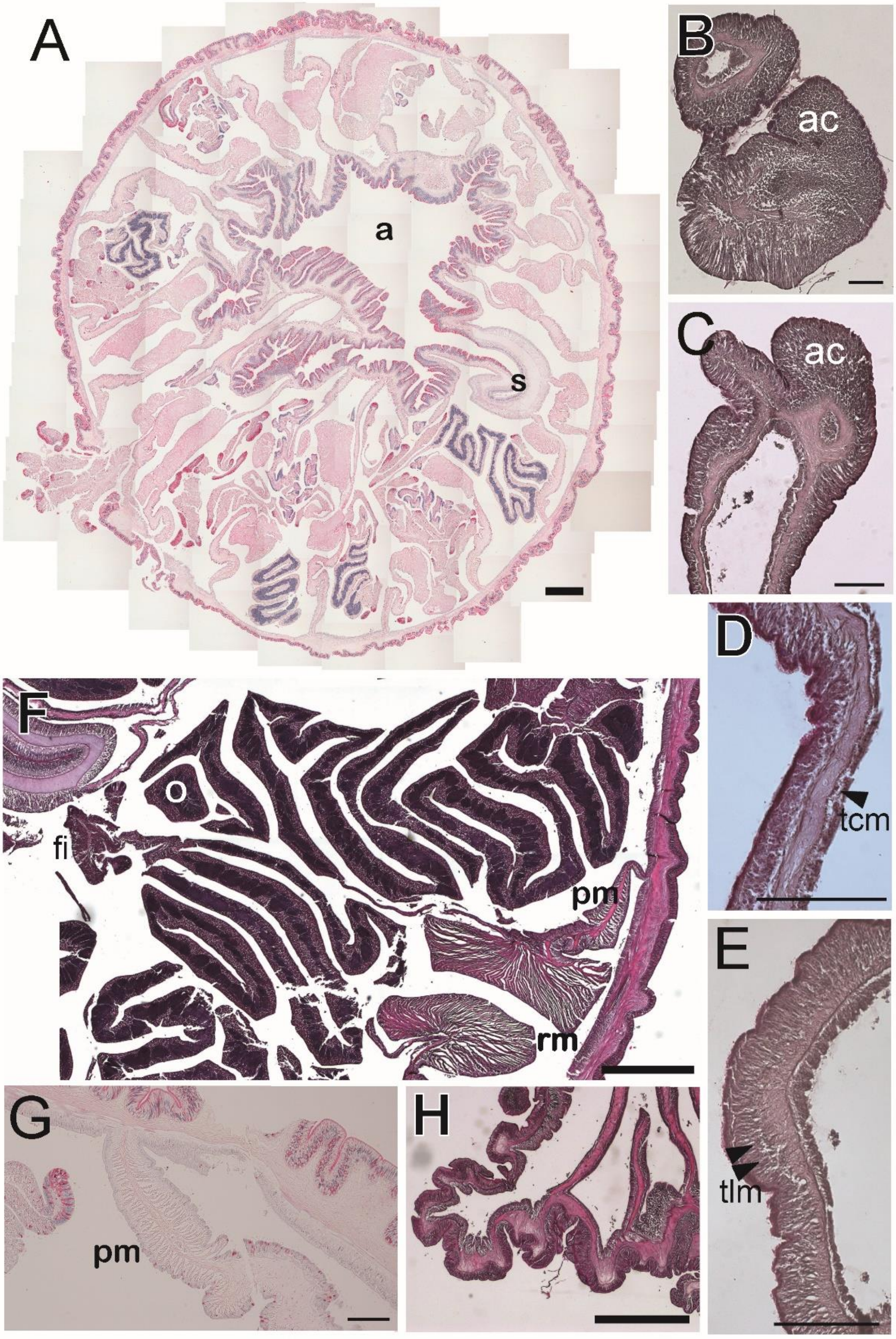

Fig. 75. Histological sections of *Anemonactis* sp. nov. 29 (CMNH-ZG 0275). A. Transverse section of actinopharynx; B. Transverse section of acrosphere; C. Longitudinal section of acrosphere; D. Longitudinal section of tentacle; E. Transverse section of tentacle; F. Transverse section of a mesentery and gonads; G. Enlarged view of transverse section of parietal muscle; H. Longitudinal section of aboral end. Abbreviations: ac, acrosphere; o, oocyte; pm, parietal muscle; rm, retractor muscle; tcm, tentacular circular muscle; tlm, tentacular longitudinal muscle. Bold scale bars in A, F, H indicates 1 mm and fine scale bars in B–E, G indicates 200 μm. Photograph A is reproduced from Yanagi (2006).

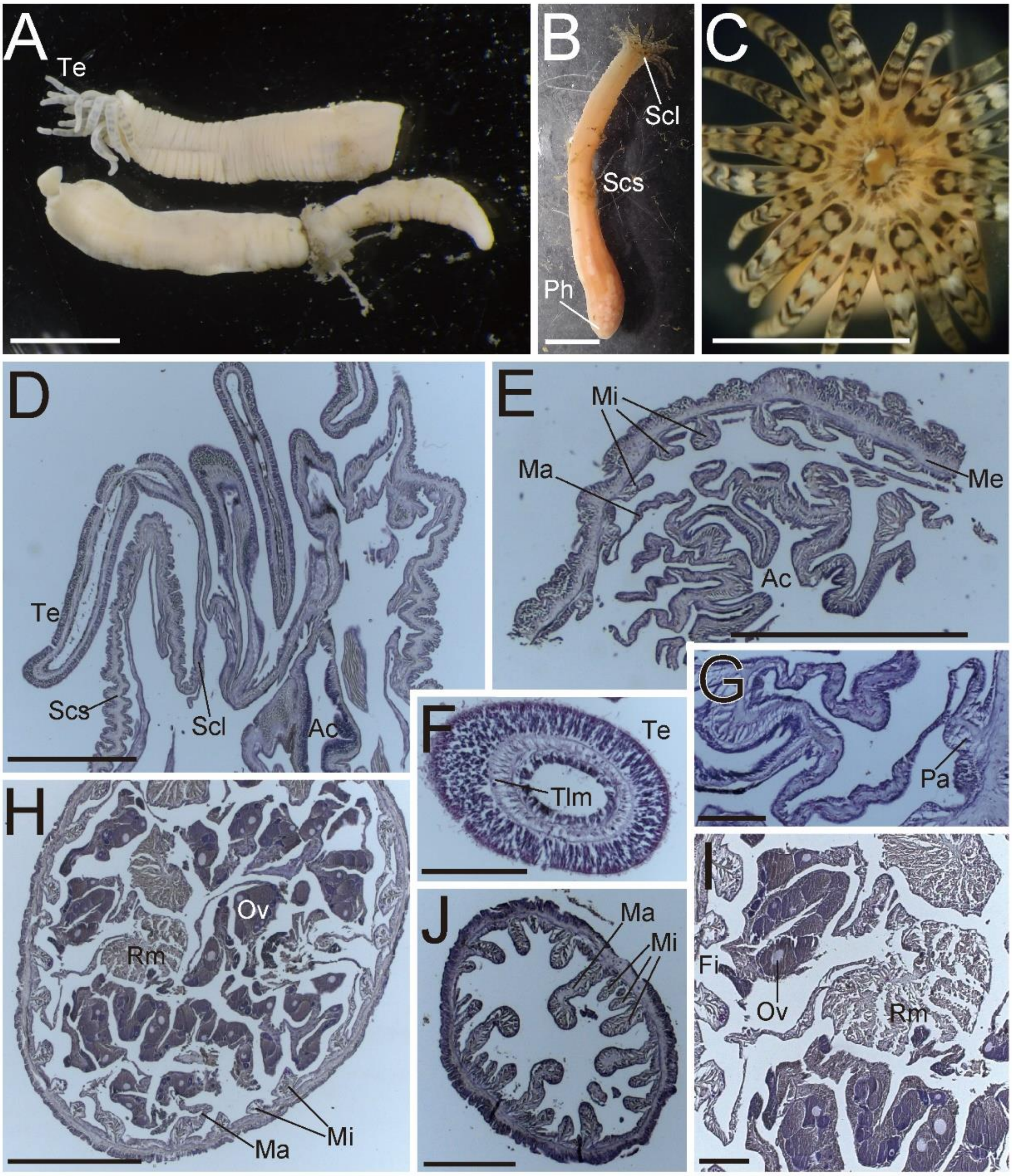

Fig. 76. External and internal morphology of *Metedwardsia akkeshi* Uchida, 1932.
A. Outer view of *Metedwardsia akkeshi* (NSMT-Co 1605); B. Outer view of live specimen (NSMT-Co 1606); C. Oral view (NSMT-Co 1606); D. Longitudinal section of oral part of *M. akkeshi* (NSMT-Co 1605, same hereafter); E. Transverse section of actinopharynx and column; F. Transverse section of tentacle; G. Transverse section of a mesentery and parietal basal muscle; H. Transverse section of mesenteries, gonads, and filaments; I. Enlarged view of mesenteries. J. Transverse section of physa. Abbreviations: Ac, actinopharynx; Fi, filament; Ma, macrocneme; Me, mesoglea; Mi, microcneme; Ov, ovary; Pa, parietal muscle; Ph, physa; Rm, retractor muscle; Scl, scapulus; Scs, scapus; Te, tentacle; Tlm, tentacular longitudinal muscle. Scale: 5 mm in A–C; 1 mm in D, E, H; 500 μm in J; 100 μm in F, G, I.

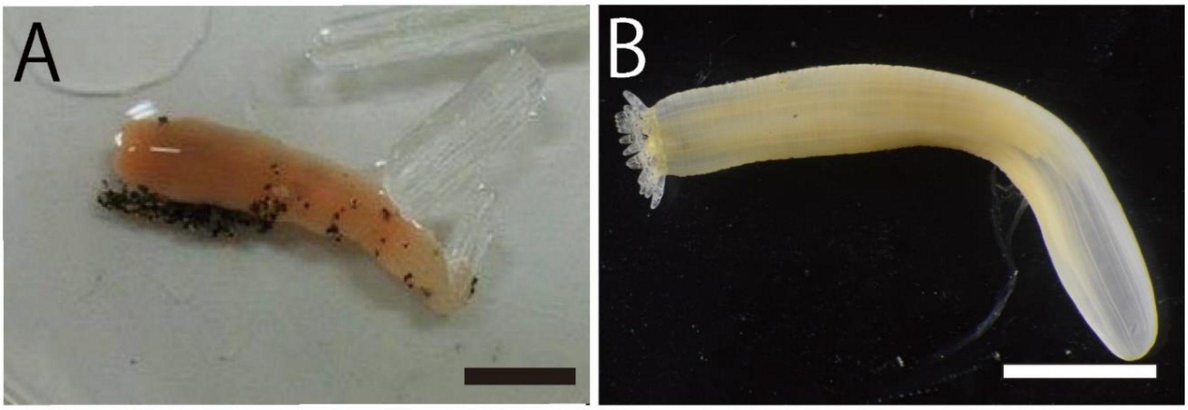

Fig. 77. Intraspecific difference of *Metedwardsia akkeshi*.
A. *M. akkeshi* from Muroran, Hokkaido. (Iz-096). B. *M. akkeshi* from Yokohama, Kanagawa Pref. (Iz-095). Picture A was taken by Naoto Jimi.

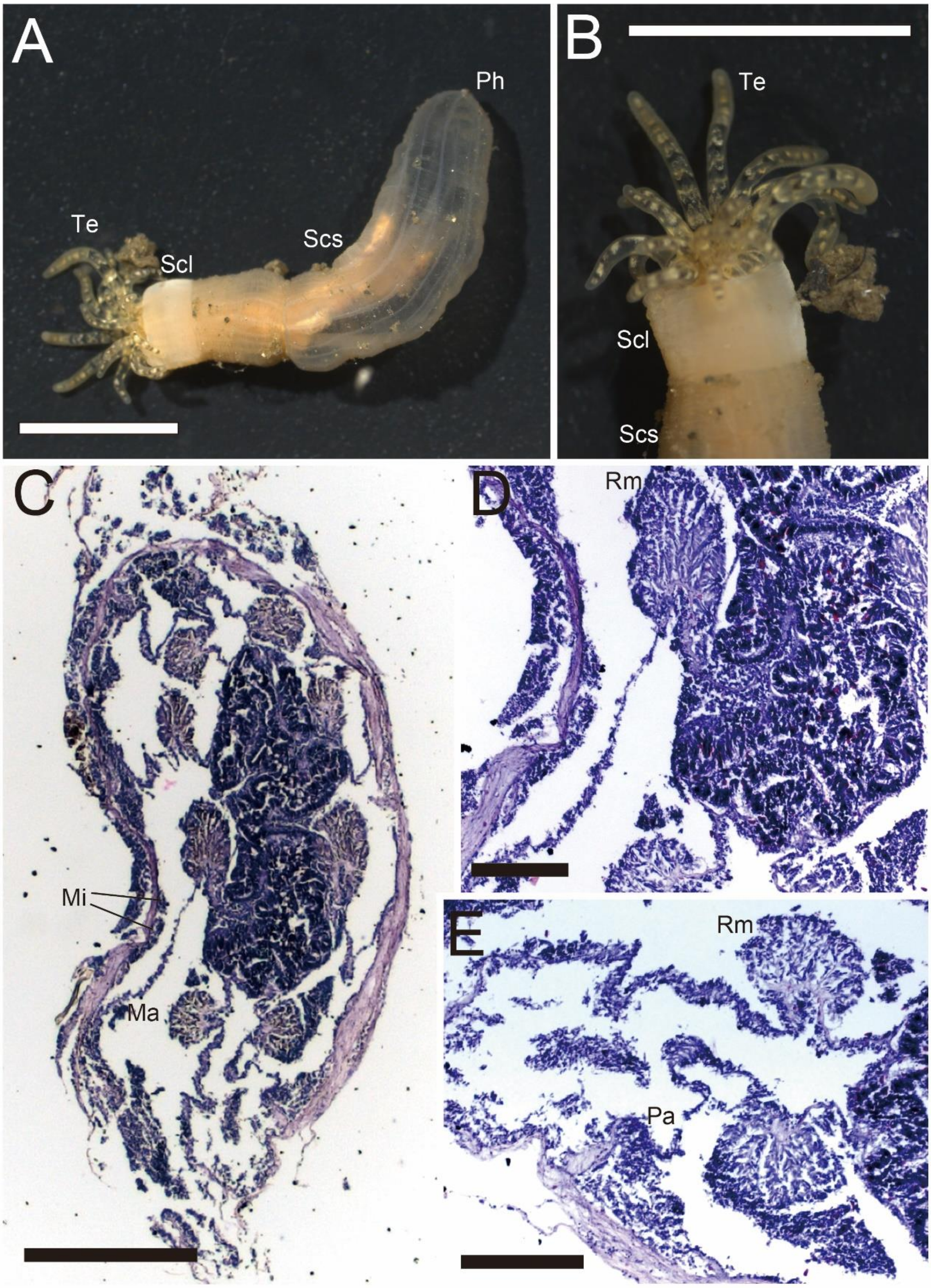

Fig. 78. External and internal morphology of *Metedwardsia* sp. nov. 30 (Iz-099). A. Outer view of *Metedwardsia* sp. nov. 30; B. Enlarged view of distal end; C. Transverse section of a mesentery and parietal muscle; D, E. Enlarged view of mesenteries and actinopharynx. Abbreviations: Ac, actinopharynx; Ma, macrocneme; Mi, microcneme; Pa, parietal muscle; Ph, physa; Rm, retractor muscle; Scl, scapulus; Scs, scapus; Te, tentacle; Tlm, tentacular longitudinal muscle. Scale: 5 mm in A, B; 500 μm in C; 100 μm in D, E.

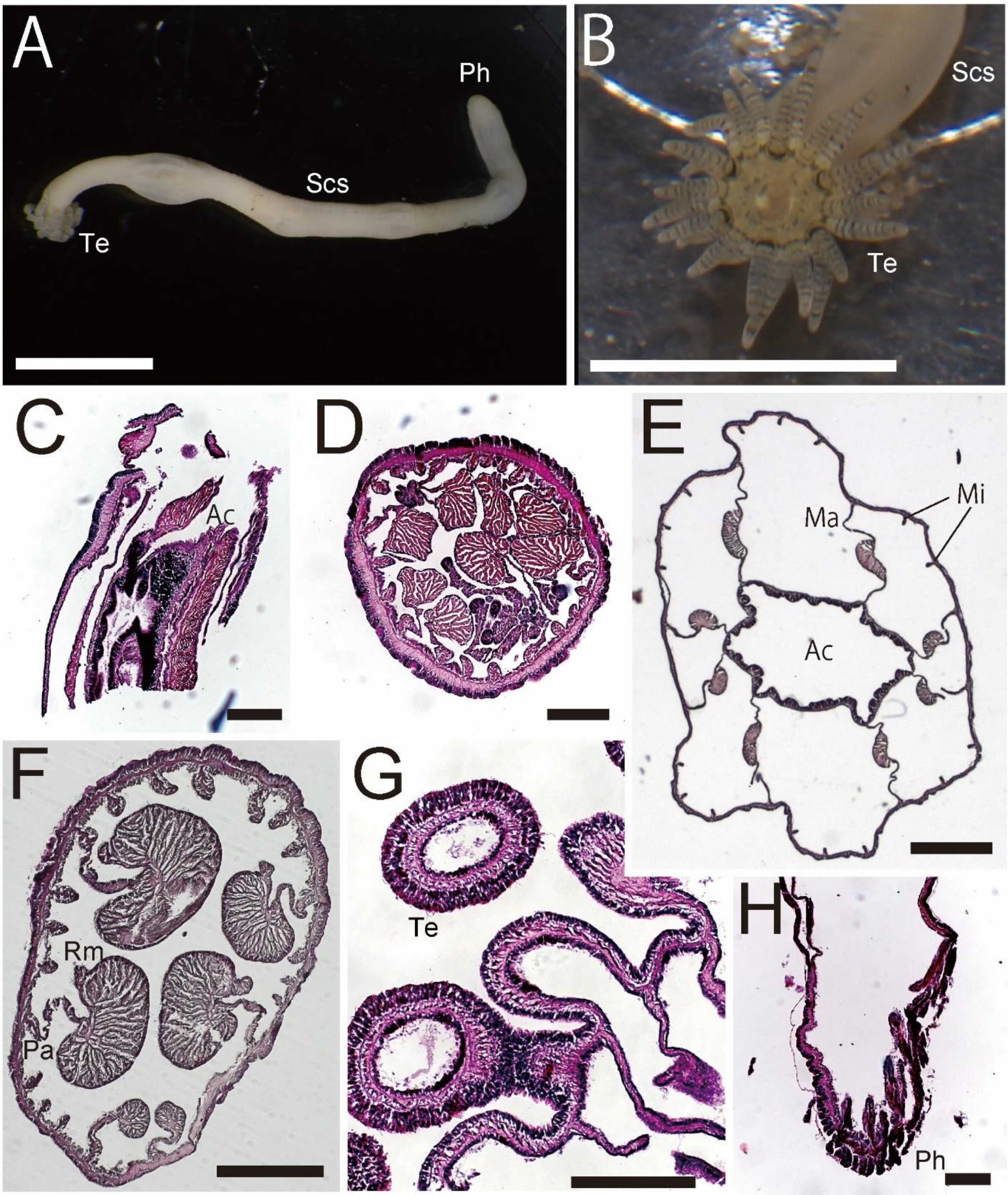

Fig. 79. External and internal morphology of *Metedwardsia* sp. nov. 31.
A–D, F–H: CMNH-ZG 5943, E: (Iz-100). A. Outer view of *Metedwardsia* sp. nov. 31 (CMNH-ZG 5943); B. Oral view of live specimen; C. Longitudinal section of oral part; D. Transverse section of mid-part of column; E. Transverse section of upper part of column and actinopharynx; F. Transverse section of lower part of column; G. Transverse and longitudinal section of tentacles; H. Longitudinal section of physa. Abbreviations: Ac, actinopharynx; Ma, macrocneme; Mi, microcneme; Pa, parietal muscle; Ph, physa; Rm, retractor muscle; Scs, scapus; Te, tentacle. Scale: 5 mm in A, B; 500 μm in C–F, H; 100 μm in G. Picture B was taken by Kensuke Yanagi.

Table 35. Comparison of Discoactinidae fam. nov. and the other three families of superfamily Actinostoloidea.

	Discoactinidae fam. nov.	Capneidae Gosse, 1860	Actinostolidae Carlgren, 1932	Exocoelactinidae Carlgren, 1925
Type genus	*Discoactis* gen. nov.	*Capnea* Forbes, 1841	*Actinostola* Verrill, 1879	*Exocoelactis* Carlgren, 1925
The other genera		*Actinoporus* Duchassaing, 1850	*Antholoba* Hertwig, 1882 *Anthosactis* Danielssen, 1890 *Antiparactis* Verrill, 1899 *Bathydactylus* Carlgren, 1928 *Cnidanthus* Carlgren, 1927 *Glandulactis* Riemann-Zürneck, 1978 *Hadalanthus* Carlgren, 1956 *Hormosoma* Stephenson, 1918 *Ophiodiscus* Hertwig, 1882 *Paranthus* Andres, 1883 *Parasicyonis* Carlgren, 1921 *Pseudoparactis* Stephenson, 1920 *Pycnanthus* McMurrich, 1893 *Sicyonis* Hertwig, 1882 *Stomphia* Gosse, 1859 *Synsicyonis* Carlgren, 1921 *Tealidium* Hertwig, 1882	
Characters				
Number of macrocnemes in the first cycle	10	12	12	12
Marginal sphincter muscle	Absent	Present	Present	Present
(Origin)	-	(Endodermal)	(Mesogleal)	(Mesogleal)
Size of mesenterial pairs	Equal	Equal	Unequal	Unequal
(Developing rule)	(General rule)	(General rule)	(Actinostola rule)	(Exocoelactis rule)
References	**The present study**	Forbes (1841) Gosse (1860) Carlgren (1949)	Verrill (1879) Carlgren (1932) Carlgren (1949) Yanagi (2017)	Carlgren (1925) Yanagi et al. (2015) Yanagi (2017)

Table 36. Cnidom of *Discoactis* sp. nov. 27

		Discoactis sp. nov. 27 CMNH-ZG (no registration 1)	
		Length × Width (μm)	frequency
Tentacle			
basitrichs		13.6-21.9 × 2.0-3.3	numerous
spirocysts		17.5-52.0 × 2.4-4.5	numerous
Actinopharynx			
basitrichs		11.7-15.4 × 1.9-2.9	numerous
microbasic *p*-mastigophores	S	19.5-26.9 × 3.4-4.8	numerous
	L	20.9-25.6 × 5.4-7.4	numerous
Column			
basitrichs		11.2-15.9 × 2.0-2.4	rare
Filament			
microbasic *p*-mastigophores	S	18.8-21.7 × 4.1-6.2	a few
	L	28.2-36.1 × 4.8-7.6	numerous

Table 38. Cnidoms of the species of *Antennapeachia*.

		Antennapeachia setouchi NSMT-Co 1653		*Antennapeachia jambio* CMNH-ZG 06546	
		Length × Width (μm)	frequency	Length × Width (μm)	frequency
Antenna tentacle					
basitrichs		12.0-31.8 × 1.4-3.9	numerous	18.6–26.9 × 2.9–4.2	numerous
spirocysts		13.7-29.9 × 2.0-4.2	numerous	16.0–37.4 × 2.5–5.3	numerous
Regular tentacle					
basitrichs		8.3-34.8 × 1.6-4.2	numerous	20.4–27.5 × 2.4–4.2	numerous
spirocysts		10.3-23.7 × 1.9-3.9	numerous	16.6–39.4 × 2.7–4.9	numerous
microbasic amastigophores				44.6–47.9 × 9.9–11.6	rare
Actinopharynx					
basitrichs		7.0-16.0 × 1.5-3.3	numerous	20.7–30.2 × 2.6–4.1	numerous
microbasic *p*-mastigophores	type-1			44.2–51.8 × 9.5–13.5	numerous
	type-2			51.9–61.7 × 11.2–14.9	rare
microbasic amastigophores				38.3–45.8 × 9.3–12.0	numerous
Column					
basitrichs		7.9-29.2 × 1.5-3.7	numerous	12.9–17.6 × 2.6–4.4	numerous
microbasic amastigophores		23.5-28.6 × 4.6-5.5	rare		
Filament					
basitrichs	S	7.5-17.9 × 1.3-2.9	numerous	10.5–13.2 × 2.6–3.2	a few
	L	24.2-31.4 × 2.2-3.6	a few	20.3–27.9 × 2.3–4.2	numerous
spirocysts		17.0-34.7 × 2.5-4.5	numerous		
microbasic *p*-mastigophores				26.1–38.9 × 5.6–9.4	numerous
microbasic *b*-mastigophores		22.6-35.6 × 4.0-5.8	numerous		
microbasic amastigophores		21.0-27.0 × 4.6-6.7	numerous	51.0–52.9 × 11.9–12.8	rare
macrobasic mastigophores		41.4-43.6 × 14.5-15.0	rare		

Table 37. Comparison of genus *Antennapeachia* and the other three genera of Haloclavidae with conchula on their mouth.

	Antennapeachia **Izumi and Yanagi, 2016**	***Peachia*** **Gosse, 1855**	***Metapeachia*** **Carlgren, 1943**	***Synpeachia*** ***Yap, Fautin, Ramos and Tan, 2014***
Type species	*Antennapeachia setouchi* Izumi and Yanagi, 2016	*Peachia hastata* Gosse, 1855	*Metapeachia tropica* (Panikkar, 1938)	*Synpeachia tamasek* Yap, Fautin, Ramos and Tan, 2014
Characters				
Antenna tentacle	Present	Absent	Absent	Absent
Mesenteries	Macrocnemes and Microcnemes	Macrocnemes and Microcnemes	All macrocnemes	All macrocnemes
Siphonoglyph	Connected to actinopharynx	Connected to actinopharynx	Completely separated	Completely separated
Number of mesenteries	14 or 16	12	16	20
References	Izumi et al. (2016)	Gosse (1855) Yap et al. (2014)	Carlgren (1943) Yap et al. (2014)	Yap et al. (2014)

Table 39. Cnidoms of the species of *Haloclava* and *Anemonactis*. The cnidom of *Anemonactis* sp. nov. 29 is reproduced from Yanagi (2006).

		Haloclava sp. nov. 28 (Iz-088)		*Anemonactis minuta* NSMT-Co 1619		*Anemonactis minuta* NSMT-Co 1620		*Anemonactis* sp. nov. 29 CMNH-ZG 275	
		Length × Width (μm)	frequency	Length × Width (μm)	frequency	Length × Width (μm)	frequency	Length × Width (μm)	frequency
Acrosphere									
basitrichs		158.9-273.8 × 3.3-7.0	numerous	70.2-133.7 × 4.1-6.4	numerous	72.7-144.6 × 3.5-6.1	numerous	75.8-186.7 × 3.0-5.7	numerous
Tentacle									
basitrichs	S	10.0-19.0 × 2.4-3.9	numerous	11.1-20.6 × 2.9-3.9	a few	10.4-14.4 × 2.7-3.6	a few	11.5-20.2 × 1.9-3.4	numerous
	L	31.1-42.4 × 4.3-6.2	numerous						
Actinopharynx									
basitrichs	S	10.2-17.9 × 2.7-3.9	numerous	11.6-14.6 × 2.5-3.2	a few	10.1-12.3 × 2.3-3.1	rare	19.0-21.0 × 2.6-3.3	rare
	M							28.1-51.6 ×3.0-5.2	numerous
	L	47.1-70.9 × 6.6-8.7	numerous	34.7-46.2 × 3.9-5.8	numerous	38.2-48.4 ×4.3-7.1	numerous	56.0-75.5 ×4.9-7.5	numerous
Column									
basitrichs	S	13.5-32.8 × 3.1-4.1	numerous	12.7-21.6 × 2.3-4.4	numerous	13.9-19.9 × 2.8-4.3	numerous	9.9-21.1 × 1.6-3.1	numerous
	L	27.7-41.5 × 5.1-6.8	a few					23.5-31.7 × 3.2-4.7	numerous
Filament									
basitrichs	S	16.2-20.6 × 2.7-4.0	numerous	11.2-18.1 × 2.4-4.0	numerous	8.5-15.9 × 2.3-3.5	a few	15.4-19.4 × 2.5-3.2	a few
	M			25.2-39.3 × 4.0-5.7	numerous	33.5-44.5 × 3.8-5.6	numerous	73.2-99.5 × 4.0-5.9	numerous
	L	73.5-94.6 × 4.8-6.6	numerous	93.2-138.2 × 3.7-5.4	rare	131.1-141.3 × 3.5-4.8	rare		
microbasic *b*-mastigophores		62.2-78.8 × 7.0-8.9	a few	33.3-43.5 × 6.9-10.4	numerous	32.5-43.4 × 6.2-8.8	numerous	53.0-78.9 × 6.9-9.1	numerous

Table 40. Comparison of *Haloclava* sp. nov. 28 and the other species of genus *Haloclava*.

	***Haloclava* sp. nov. 28**	*Haloclava producta* (Stimpson, 1856)	*Haloclava brevicornis* (Stimpson, 1856)	*Haloclava capensis* (Verrill, 1868)	*Haloclava chinensis* Carlgren, 1931	*Haloclava stimpsoni* (Verrill, 1868)
Characters						
Number of inner tentacles	10	10	10	6	10	10
Form of tentacles	Not uniform	Not uniform	Uniform	Unknown	Not uniform	Not uniform
Acrospheres	Developed	Developed	Developed	Developed	Developed	Not developed
Surface of the column	Smooth	Sticky papillae	Unknown	Unknown	Smooth	Unknown
Shape of retractor muscle	Restricted	Restricted	Unknown	Unknown	Strongly circumscribed	Unknown
Shape of parietal muscle	Separated into two parts	No peculiar shape	No peculiar shape	No peculiar shape	No peculiar shape	No peculiar shape
References	**The present study**	Stimpson (1856)	Stimpson (1856)	Verrill (1868)	Carlgren (1931)	Verrill (1868)

Table 41. Comparison of *Anemonactis* sp. nov. 29, *A. minuta* (Wassilieff, 1908), and the other species of genus *Anemonactis*.

	***Anemonactis minuta* (Wassilieff, 1908)**	***Anemonactis* sp. nov. 29**	***Anemonactis mazeli* (Jourdan, 1880)**	***Anemonactis clavus* (Quoy and Gaimard, 1833)**	***Anemonactis globulosa* (Quoy and Gaimard, 1833)**
Characters					
Number of tentacles	16	20	20	12	14
Acrospheres shape	Spherical, smooth	Wizened	Spherical, smooth	Unknown	Unknown
Microbasic *b*-mastigophores	Present	Present	Absent	Unknown	Unknown
References	Wassilieff (1908) Uchida (1992) Uchida and Soyama (2001) **The present study**	Uchida (1938) Uchida (1965) Uchida and Soyama (2001) Yanagi (2006) **The present study**	Jourdan (1880) Faurot (1895) Rees (1913) Stephenson (1935) Carlgren (1940) Pax and Müller (1962) Fautin (1998) Wood (2005)	Quoy and Gaimard, (1833) Hertwig (1882)	Quoy and Gaimard, (1833)

Table 42. Comparison of Metedwardsiidae fam. nov. and the other families without the basal disc in superfamily Metridioidea.

	Metedwardsiidae fam. nov.	Halcampidae Andres, 1883	Andvakiidae Danielessen, 1890	Galatheanthemidae Carlgren, 1956
Type genus	*Metedwardsia* Carlgren, 1947	*Halcampa* Gosse, 1858	*Andvakia* Danielessen, 1890	*Galatheanthemum* Carlgren, 1956
The other genera	none	*Cactosoma* Danielssen, 1890 *Halcampaster* Carlgren, 1938 *Halianthella* Kwietniewski, 1896 *Kodioides* Danielssen, 1890 *Mena* Stephenson, 1920 *Neohalcampa* Sanamyan, 2001 *Parahalcampa* Carlgren, 1927 *Halcampoides* Danielssen, 1890 *Acthelmis* Lütken, 1875 *Calamactinia* Carlgren, 1949 *Calamactis* Carlgren, 1951 *Pentactinia* Carlgren, 1900 *Scytophorus* Hertwig, 1882 *Siphonactinopsis* Carlgren, 1921	*Ilyactis* Andres, 1881 *Synandwakia* Carlgren, 1947	none
Characters				
Number of macrocnemes in the first cycle	8	12	12	12
Marginal sphincter muscle	Absent	Present or absent	Present	Present
References	Carlgren (1947) Carlgren (1949) **The present study**	Gosse (1858) Andres (1883) Carlgren (1949) Fautin (2016) Gusmão et al. (2016)	Danielessen (1890) Carlgren (1949)	Carlgren (1956) Rodríguez et al. (2014)

Table 43. Cnidoms of the species of *Metedwardsia*.

		Metedwardsia akkeshi				*Metedwardsia* sp. nov. 30		*Metedwardsia* sp. nov. 31	
		NSMT-Co 1605		CMNH-ZG 4314		(Iz-099)		CMNH-ZG 5943	
		Length × Width (µm)	frequency	Length × Width (µm)	frequency	Length × Width (µm)	frequency	Length × Width (µm)	frequency
Tentacle									
basitrichs		13.3-22.3 × 1.7-3.6	numerous	15.9-24.0 × 2.0-3.5	numerous	7.9-16.5 × 2.0-3.2	numerous	10.7-19.8 × 2.4-3.7	numerous
spirocysts		11.0-19.2 × 2.0-3.3	numerous	12.0-21.2 × 1.8-3.8	numerous	10.3-18.2 × 2.4-4.3	numerous	12.3-19.4 × 2.7-4.0	numerous
Actinopharynx									
basitrichs	S	12.4-28.7 × 1.6-3.4	numerous	11.4-18.8 × 2.0-3.4	numerous	10.9-24.8 × 1.9-3.3	numerous	13.9-18.5 × 2.4-3.3	numerous
	L							15.9-24.0 × 2.0-3.6	numerous
microbasic *p*-mastigophores						22.9-30.1 × 3.9-6.3	a few	23.8-29.6 × 3.6-6.1	numerous
microbasic *b*-mastigophores		21.9-27.0 × 3.5-5.4	a few					25.1-30.1 × 4.2-5.4	numerous
Column									
basitrichs		8.9-19.9 × 2.0-3.2	numerous	8.0-16.0 × 2.0-3.8	numerous	8.1-16.0 × 1.7-3.6	numerous	10.4-16.0 × 2.1-3.8	numerous
Filament									
basitrichs		15.9-37.7 × 2.3-4.7	numerous	15.0-43.6 × 2.1-4.8	numerous	10.3-15.9 × 1.8-3.3	numerous	13.3-17.9 × 2.3-3.7	numerous
microbasic *p*-mastigophores	S					8.3-11.1 × 3.1-3.9	a few	10.2-11.7 × 2.9-3.6	rare
	L							25.8-33.7 × 3.4-5.9	a few
microbasic *b*-mastigophores		22.2-30.8 × 3.5-5.0	numerous	25.3-35.5 × 3.9-6.1	numerous	21.2-28.7 × 3.7-4.6	a few	24.0-29.2 × 4.6-5.2	rare
microbasic amastigophores		8.8-12.3 × 2.9-4.2	numerous	9.6-15.4 × 2.9-4.7	numerous				

Table 44. Comparison of two new species of *Metedwardsia* and *Metedwardsia akkeshi*.

	Metedwardsia akkeshi (Uchida, 1932)	***Metedwardsia* sp. nov. 30**	***Metedwardsia* sp. nov. 31**
Characters			
Habitat	Brackish Lake (or brackish areas of the sea)	Sea	Sea
Body length	20-40 mm	12 mm	20-22 mm
Body width	3-5 mm	3 mm	2 mm
Pattern on tentacles	Dark brownish cross bands	Mingled black and white patches	Dark brownish cross bands
Cnidom of actinopharynx	Only one type of nematocysts	Two types of nematocysts	Three types of nematocysts
References	Uchida (1932) Carlgren (1947) **The present study**	**The present study**	**The present study**

Chapter 3. Evolutionary Estimation of Anenthemonae

3A. Ancestral body form of Actiniaria and evolution of the basal disc

Carlgren (1949) emphasized that the basal disc and mesenterial arrangement were the most important morphological features for the classification of the higher taxa of Actiniaria. In Actiniaria, the species of the family Edwardsiidae has a worm-like body without a basal disc and only eight perfect mesenteries in the first mesenterial cycle. Duerden (1899) suggested that these simple body plans of edwardsiids would be the ancestral characters of Actiniaria because all actiniarians develop through the “edwardsia-stage” larvae having eight perfect mesenteries same as those in edwardsiids when they are juveniles (Fig. 2). The basal disc, a unique structure to actiniarians (see Introduction), was thought to be obtained in the derived lineage of the order Actiniaria, and thus Carlgren (1949) accommodated Edwardsiidae and several families without basal discs into the independent tribe Athenaria (Table 1). Because of these two evidences, Carlgren and several other researchers (e.g., Stephenson, 1922; Hyman, 1940) especially suspected that Edwardsiidae, the family characterized by the simplest mesenterial arrangements and without any basal discs, was the taxon that retains the most ancestral features of Actiniaria. However, this hypothesis often has been questioned recently: for example, Manuel (1981a) and Daly et al. (2002) suspected that the simple morphology of Edwardsiidae secondarily degenerated by adaptation to burial habit. Most recently, Rodríguez et al. (2014) suggested that Edwardsiidae belonged to the clade of Anenthemonae, became the sister group of the superfamily Actinernoidea, and was separated from the other families classified in the previous tribe Athenaria on their phylogenetic tree. This topology of the tree suggested that the simple forms of anemones, absence of basal discs and few macrocnemes in the first cycle, could not be ancestral but derived. This was because these characters would not be their basal characters in the phylogenetic tree. However, confirming that the simplest forms of Edwardsiidae are certainly derived required specific phylogenetic studies with more species of Anenthemonae.

According to the molecular analyses performed by using the highest number of specimens of Anenthemonae in the present study, the species of Edwardsiidae were at a derivative lineage in Anenthemonae (Figs. 7, 80). The other families of the previous tribe Athenaria were also polyphyletic and at many separate derivative lineages of Actiniaria (Figs. 8, 80), as suggested by Rodríguez et al. (2014). Thus, the species in the ancestral lineages of actiniarians would have basal discs (Fig. 80, indicated in black), which would have degenerated at several lineages of Actiniaria (Fig. 80, indicated in red).

Based on these results, I suspect that the common ancestor of Actiniaria was sessile and had a columnar body with a basal disc, same as that in the general extant species of sea anemones. In Enthemonae, most species have developed basal discs and acquired basilar muscles [structure called as “pedal discs” in Carlgren (1949) and Daly (2015)], and thus they can strongly attach to and actively creep on hard substrates. However, only a small number of exceptional species of Enthemonae (the species that were classified in the previous tribe Athenaria) have derivatively lost their basal discs. In contrast, in Anenthemonae, the species of Edwardsioidea in the derivative lineage would have degenerated basal disc and a worm-like body. They could have evolved the distinct lifestyles of burrowing in soft sediment substrates (see chapter 3B).

3B. Evolutionary history of Anenthemonae: Significant morphological adaptation to sandy bottom habitats

Edwardsiid anemones have been considered to have retained the ancestral characters of sea anemones because of their simple morphological features; however, in this study, they were found to be a taxon in the derivative lineage of the suborder Anenthemonae (See Chapter 3A). According to the phylogenetic analysis in this study (Fig. 7), the superfamily Actinernoidea first diverged from the other two superfamilies in the lineage of Anenthemonae, and the family Edwardsioidea was derived later from the sister superfamily Halcampelloidea superfam. nov. (Figs. 7, 81).

The molecular phylogeny of Anenthemonae suggested the evolutionary history of edwardsiid morphology and ecology. Edwardsiids are burrowers in a broad range of substrates: most species burrow in sand or mud, some species can enter the crevices of rocks or dead coral skeletons (e.g., some species of *Edwardsiella*: Daly, 2002b; Sanamyan and Sanamyan, 2018; *Edwardsia isei* comb. nov.: the present study, see Chapter 2), and a few species exceptionally live even in ice or homoscleromorph sponges (Daly et al., 2013; Izumi et al., 2018). Their simple morphology, fewer numbers of perfect mesenteries and tentacles, worm-like slender bodies, and absence of a part of macrocnemes and basal discs, is likely to be advantageous for inhabiting such habitats. As mentioned in Chapter 3A, these morphological and ecological features had been considered to be the traces of ancestral features (McMurrich, 1891; Hyman, 1940), but some recent studies challenged this hypothesis (Manuel, 1981a; Daly, et al., 2002; see Chapter 3A): these researchers advocated that the peculiar morphology of edwardsiid anemones should be secondarily derived features resulting from the adaptation to the burial lifestyles. Therefore, settling the dispute whether simple forms of edwardsiids are ancestral or adaptively derived was necessary, but any recent preceding phylogenetic analysis could not address this issue because of poor taxon samplings. Daly (2008), Rodríguez and Daly (2010), and Rodríguez et al. (2012), who conducted comparatively comprehensive phylogenetic analyses of sea anemones, only included less than five edwardsiids and no actinernoideans. Even in Rodríguez et al. (2014), the first and only phylogenetic study including Actinernidae, only nine Anenthemonae species were included.

In contrast, my phylogenetic analysis included at least 49 (and other many unidentified) species of Anenthemonae, including four species of Halcampelloidea superfam. nov. (Fig. 7 and Tables 4, 6). Thus, I could provide the detailed phylogeny of Anenthemonae and successfully indicate that the lineage of Edwardsiidae would be derivative. Rodríguez et al. (2014) did not include species of *Halcampella* in their molecular analyses, and hence, they only recognized that two superfamilies were sister groups in the suborder Anenthemonae. My analysis showed the third superfamily, Halcampelloidea superfam. nov., in addition to the two other known superfamilies, Actinernoidea and Edwardsioidea, in the suborder Anenthemonae. The superfamily Halcampelloidea was the sister group of Edwardsioidea with high reliability (Fig. 7), and hence, Edwardsioidea was strongly suggested to be a derived superfamily in Anenthemonae.

The topology of the tree obtained in this study helps to discuss the evolution of Edwardsiidae, especially of their simple reduced form. I suggest that the simple and reduced morphology of Edwardsioidea is the adaptive feature to the burrowing habit according to this obtained phylogeny (Fig. 81). The evolutionary scenario is as follows.

1. The ancestor of Anenthemonae could have a “general form” of actiniarians

with 12 perfect mesenteries, a basal disc, and a columnar body. Ancestral anemones lived adherently to solid substrates by baring their whole bodies. Such general actiniarian forms are retained in the external morphology of Actinernoidea, but they originally changed their mesenterial arrangement after the second cycle in their lineage (Fig. 81A; see Chapter 2).

2. In the common lineage of Halcampelloidea and Edwardsioidea, the body changed from the columnar shape to a worm-like slender one. This might be an adaptation to the soft substrate: the slenderer they were, the easier it was for them to burrow into soft sediment (Fig. 81B). However, anemones of Halcampelloidea (except *Pseudoedwardsia*) still have 12 perfect mesenteries and disc-like aboral ends (Figs. 27–30). My observations of *Halcampella maxima* in aquaria showed that they buried only their aboral parts of their bodies in sand and adhered more or less strongly to solid substrates such as small stones using the disc-like aboral ends. Halcampelloidean anemones are so-called "hemi-burial" anemones: although they have the adaptive morphology for the burial lifestyle, they would tend to stabilize their bodies adhering to some solid substrates in the sediment habitats.
3. After the lineage of Edwardsioidea diverged from Halcampelloidea, their bodies completely lost the basal discs from the aboral ends (Fig. 81C) and reduced the number of macrocnemes in the first mesenterial cycle from 12 to eight. The remaining four macrocnemes degenerated to small microcnemes (Fig. 81C, indicated in blue in the diagram). The aboral end without the basal disc, called physa, could be used as an anchor in soft substrates by expanding and swelling it. Less number of bulky perfect mesenteries could deform their columns to become slenderer, and this form would be advantageous for edwardsiids to burrow into sediment. In other words, species of Edwardsioidea derivatively evolved for the completely burial lifestyle.

The preceding study proposing a similar hypothesis to this scenario was Daly et al. (2002). They suggested not only that edwardsiids are advanced sea anemones to have burrowing lifestyles in sand and mud rather than attaching, but also that edwardsiids perhaps might be derived anemones that have retained a juvenile morphology through paedomorphosis. Unfortunately, the conclusion could not be confirmed in their study because the molecular phylogeny method was not advanced then, but the possibilities they discussed have remarkable values to understand edwardsiid evolution even in the present day.

Regarding the long-standing dispute of whether the peculiar morphology of Edwardsiidae was obtained by retaining the ancestral characters or derived secondarily, I strongly suggest that the simple forms of edwardsiids are derived during the adaptation to sandy habitats. The simple mesenterial arrangements of edwardsiids are not the traces of ancestral characters in actiniarians but would be neotenically developed from the common juvenile stage of actiniarians (Fig. 2).

3C. Diversification of Edwardsiidae after obtaining nemathybomes

In this study, five genera of Edwardsiidae were combined into one genus, *Edwardsia* (see Chapter 1F and remarks of family Edwardsiidae and genus *Edwardsia* in Chapter 2). These species have a prominent synapomorphy—the presence of nemathybomes on their body wall (Fig. 83). Nemathybomes are sac-like or pocket-like structures on or inside the body wall. Many significantly large nematocysts are contained in the nemathybomes (Carlgren, 1949; England, 1987). Nemathybomes have been noted since the late 19th century in Edwardsiidae (Danielessen, 1890; McMurrich, 1893) and were already known as the specific features for the classification of Edwardsiidae since the early 20th century (Carlgren, 1920, 1921; Pax 1924; Stephenson, 1928). They were considered as the diagnostic features for some genera of Edwardsiidae by Carlgren (1949) and were long considered as important for the classification of Edwardsiidae. Even recently, the arrangement and cnidae of nemathybomes have been considered as important characters to classify edwardsiid sea anemones (Daly et al., 2015). However, their exact function was not yet known because nemathybomes were generally too tiny to observe their detailed morphology using conventional microscopes. Although many studies observed their inner structures by conducting histological analysis (e.g., England, 1987; Daly and Ljubenkov, 2008), they only reported the presence of large nematocysts "contained" there.

In contrast, I found some species of *Edwardsia* that have extraordinarily large nemathybomes (e.g., Fig. 48B, I in *Edwardsia alternobomen*; Fig. 49B, G) in this study, and thus successfully observed their structure by using a conventional microscope. The histological section of a nemathybome of *E. alternobomen* Izumi and Fujita, 2019 (Fig. 48I) shows many large nematocysts in the nemathybome that discharge their threads toward the outside of its column. In addition, some histological sections also indicated that the nematocysts of nemathybomes were apparently "charged" at the surfaces of nemathybomes (Figs. 50G, 64E). The external observation of each nemathybome also suggested that the nematocysts of them were densely concentrated at a point (Figs. 48B, 49B). These observations of nemathybomes suggest that they might be able to sting foreign materials by using the large nematocysts.

Sea anemones are known to have some kinds of countermeasures with nematocysts against enemies. For example, tentacles are well-known defensive organs of cnidarians that are used for stinging. Some groups of sea anemones are known to develop specific tentacles for defense (Purcell, 1977; Uchida and Soyama, 2001). General metridioidean anemones have another type of defensive organ called acontia—thread-like structure with dense nematocysts (Shick, 1991; Rodríguez et al., 2014). In particular, when metridioideans are stricken on their columns, they can defend their columns from their enemies by discharging acontia from cinclides on the body walls (Shick, 1991; Yanagi, 2017). Now, same as acontia, nemathybomes probably play a role in defending against outside stimuli because they would perform the common behavior of stinging external objects using the dense nematocysts on the surfaces. Burrowing edwardsiids cannot counter predators by using their tentacles because their tentacles cannot reach their buried lower column. Thus, edwardsiids would use nemathybomes distributed on their bodies instead of their tentacles to protect their columns from attacks of predators. Even in sediment, some possible infaunal predators might be present, e.g., polychaetous annelids, sipunculans, and platyhelminthes (Brusca and Brusca, 2003). Edwardsiids may have adapted to infaunal habitats by using nemathybomes to prevent themselves from predation.

Several genera of Edwardsiidae do not have nemathybomes (Fig. 82). They were indicated to have diverged from the lineage of the ancestral *Edwardsia* before obtaining nemathybomes. They may probably protect their columns by using other methods: the species of *Edwardsiella* have thick periderms (Fig. 36B, E; Daly, 2002b), or burrow into ice shelf or rock crevices

(Daly et al., 2013; Sanamyan et al., 2018); species of *Halcampogeton* have solid papillae on their columns (Fig. 37B; Carlgren, 1937). Some species may use cryptic habitats to protect themselves: in this study, I found *Tempuractis rinkai* live in the homoscleromorph sponge (Figs. 32–35; see Chapter 2 for details). Although the species of *Nematostella* does not have any structures on their body walls, nematosomes, the sphere-like structures with dense nematocysts (Carlgern, 1949), are present in their coelenterons. (There is no defensive structure on/in the bodies of the species of the genus *Drillactis*; Fig. 38.) However, the number of species without nemathybomes in these genera is far less than that of species with nemathybomes in the genus *Edwardsia*. Even *Edwardsiella*, to which most species without nemathybomes belong, accommodates less than 10 species (Table 2).

In contrast, the species with nemathybomes of the genus *Edwardsia* (Fig. 83) have diverged into over 80 species and are distributed worldwide. The diversification of *Edwardsia* suggests that nemathybomes might be adaptive for their burial lifestyles and have advantages to distribute to broad niches of sediment bottoms. Moreover, nemathybomes would have been modified secondarily in some species of *Edwardsia* (Fig. 83). The nemathybomes of general *Edwardsia* are only distributed on the lateral sides of their columns and not at the aboral ends for most of the species (e.g., Figs. 48A, 49A). However, nemathybomes are developed on the whole body, as well as on the aboral end, of the species of the previous genera *Scolanthus* and *Isoscolanthus* (e.g., Figs. 55A, 56A; Fig. 83, indicated in red and gray in Fig. 83). Conversely, nemathybomes of the species of the previous genus *Paraedwardsia* have degenerated secondarily (Figs. 51G), and these species attach sand grains to their surfaces of columns instead (Fig. 83, indicated in yellow).

Considering the characteristics of nematocysts, another possibility for the function of nemathybomes exists. Nematocysts were known to help in attaching (Thorington and Hessinger, 1996). Especially cnidarians are known to use nematocysts to attach to substrates like anchors in planula larvae or small polyps of jellyfish (Donaldson, 1974; Yamashita et al., 2003). Spirocysts have been known as the cnidae for attaching materials, but other penetrants, stinging nematocysts, including basitrichs and microbasic *p*- and *b*-mastigophores, are also known to play the same roles of attaching as spirocysts (Thorington and Hessinger, 1996; Ostman, 2000). Therefore, edwardsiids might be able to use nemathybomes to attach some substrates on their bodies. However, nemathybomes are unlikely to be mainly used to attach something according to the observations of the present study. Most species of *Edwardsia* with nemathybomes did not attach to any substrates on their columns. Moreover, *Edwardsia* sp. nov. 16, which attaches sand grains on the column, only has the trace of nemathybomes without nematocysts (Fig. 51G). These cases suggested that attaching something on nemathybomes is not advantageous, and densely concentrated nematocysts in nemathybomes would not be effective for anchoring (Figs. 48B, 49B). Thus, I suggest that nemathybomes are not mainly used for adherence but for defense.

Some burrowing anemones have no apparent defensive structure. For example, *Metedwardsia akkeshi* (Fig. 76) and the other species of this genus (Fig. 78, 79) have worm-like bodies, but no structure for defense were noted on the smooth body surfaces. They also had no acontia, although they were included in the clade of the superfamily Metridioidea. The dense and patch-like distribution of the species of *Metedwardsia* (see Chapter 2) could be the strategy for their survival, but this hypothesis needs to be investigated in the future works. The knowledge of defensive structures of sea anemones, including for the anemones without any defensive structures at a glance such as species of the genus *Drillactis* (see above), is still lacking now.

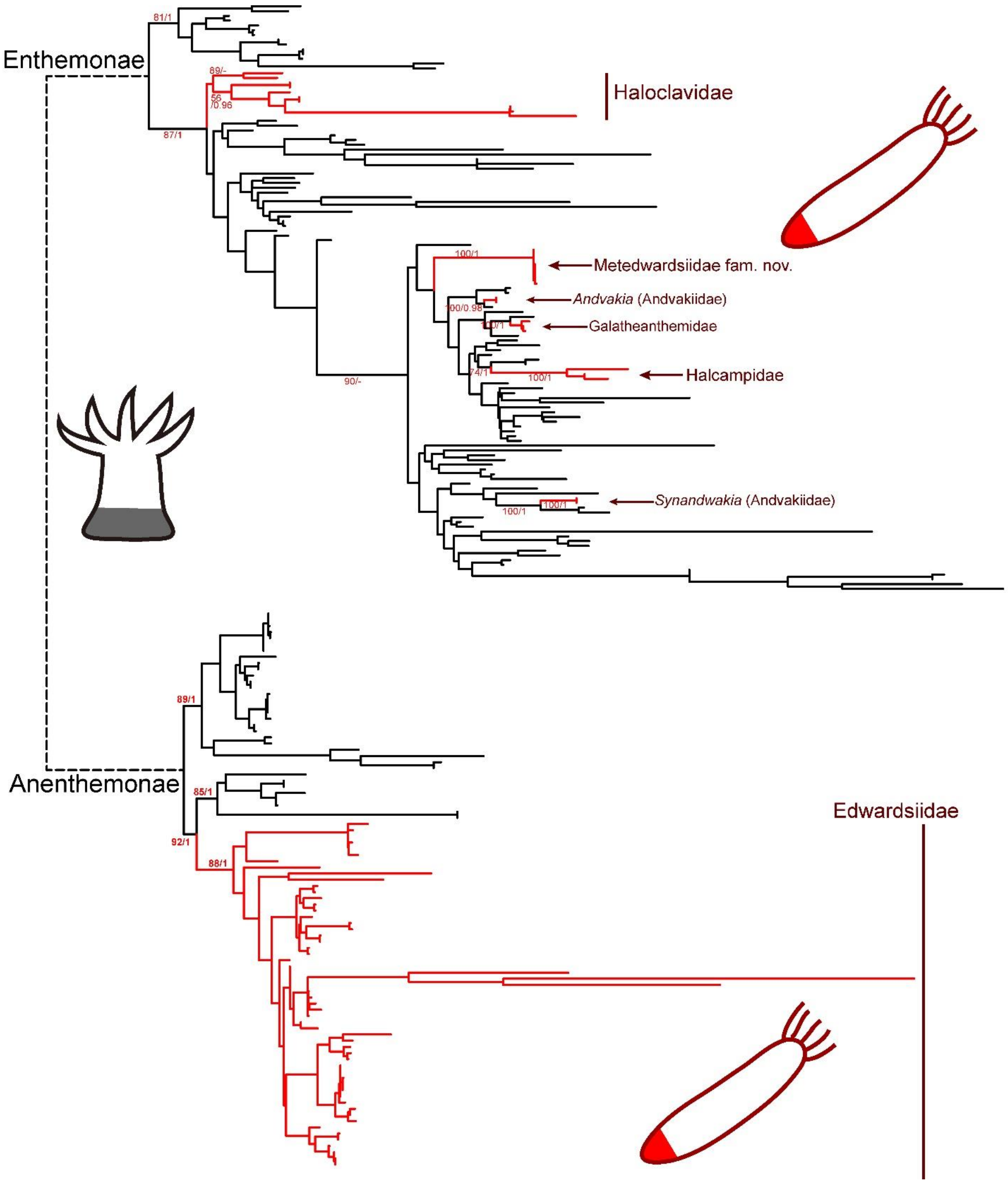

Fig. 80. Degeneration of the basal disc in the Actiniaria lineage.
The topology of this phylogenetic tree is based on phylogenetic analyses of Enthemonae and Anenthemonae in Chapter 1B and 1C (the constructed trees are shown in Fig. 7 [Anenthemonae] and Fig. 8 [Enthemonae]). Considering parsimoniously, basal discs would be present in the lineages indicated in black, including the ancestor of Actiniaria, and might have degenerated independently in the lineages in red.

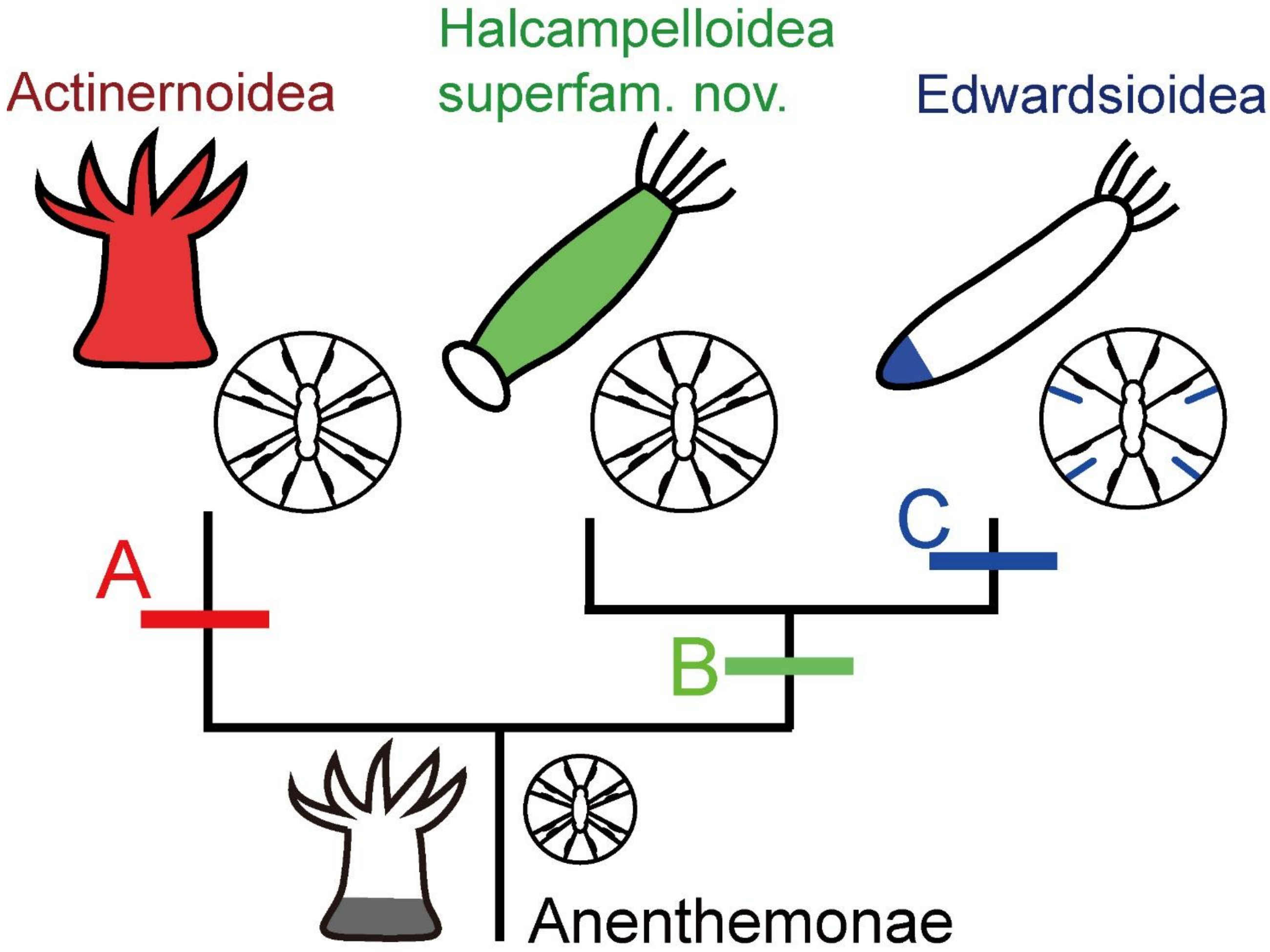

Fig. 81. Gradual evolution of Anenthemonae adapting to the burial lifestyle in sandy habitats. The ancestor of Anenthemonae was thought to have columnar body like general sea anemones, with a basal disc (indicated in gray) and 12 perfect mesenteries. Species of Actinernoidea retained the ancestral columnar external morphology of Anenthemonae (A; in red). After branching from Actinernoidea, the common ancestor of Edwardsioidea and Halcampelloidea acquired worm-like shape (B; in green). Species of Halcampelloidea should retained the basal disc and 12 perfect mesenteries even after Edwardsioidea was branched out. In contrast, in the lineage of Edwardsioidea, the basal disc would have degenerated, and the number of perfect mesenteries decreased to eight (C; in blue).

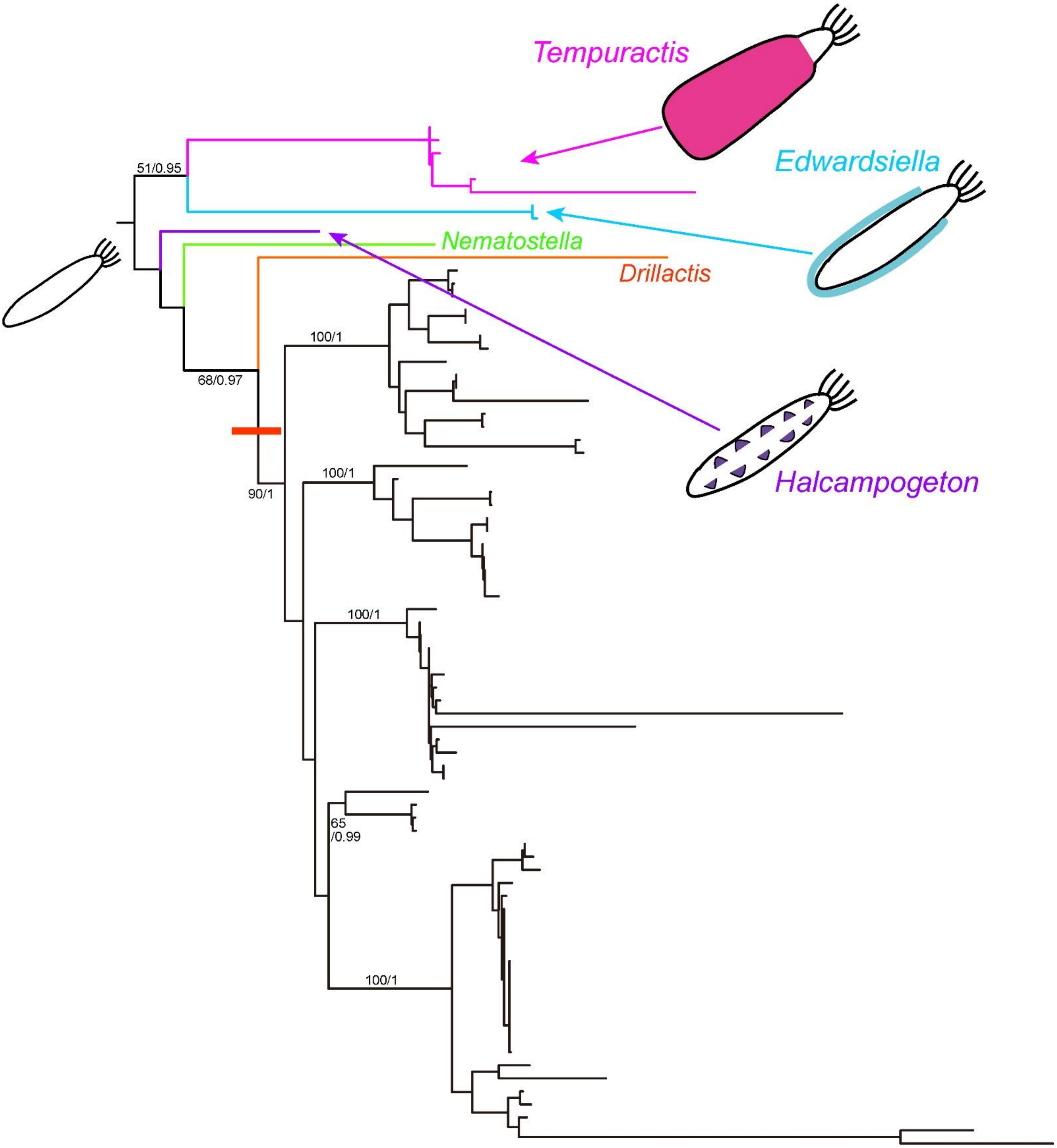

Fig. 82. Evolution of the genera without nemathybomes in Edwardsiidae.
Nemathybomes were obtained in the lineage indicated by the red bar. *Tempuractis, Edwardsiella, Halcampogeton*, *Nematostella*, and *Drillactis* have no nemathybomes, but other morphological or ecological features have evolved in several genera: species of *Tempuractis* (indicated in pink) symbiotically inhabit in sponge; *Edwardsiella* (in light blue) edwardsiids thicken their periderm; species of *Halcampogeton* (in purple) develop solid papillae on the scapus. No particular structure was noted on the surfaces of *Nematostella* (in light green) and *Drillactis* (in orange) edwardsiids.

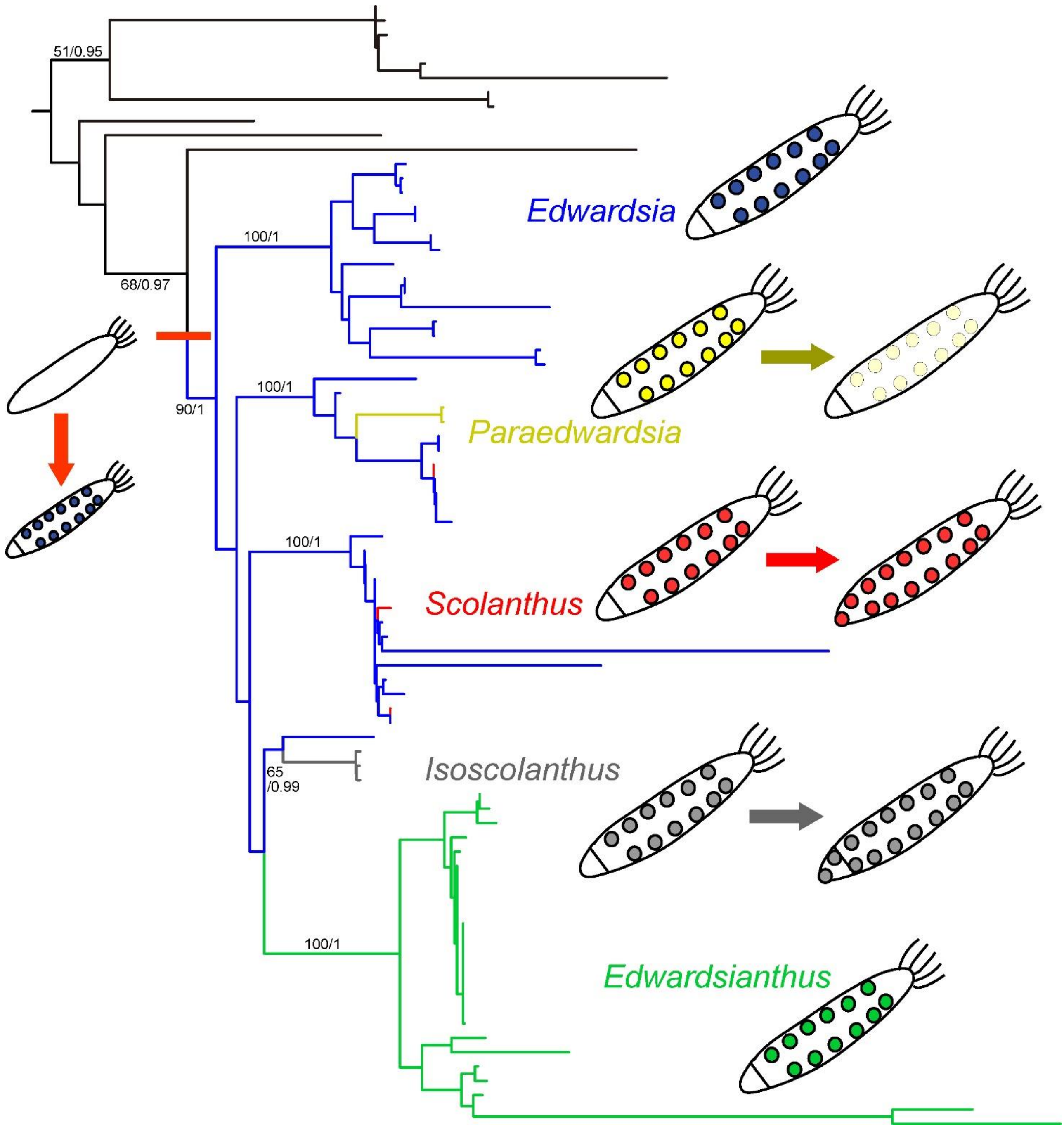

Fig. 83. Evolution of the genera with nemathybomes in Edwardsiidae.
Species of *Edwardsia*, including previous genera *Paraedwardsia, Scolanthus, Isoscolanthus*, and *Edwardsianthus,* would have monophyletically acquired nemathybomes (indicated by the orange bar). The edwardsiids on several lineages were additionally transformed: nemathybomes degenerated and became like traces in the species of previous *Paraedwardsia* (indicated in yellow). In contrast, species of previous *Scolanthus* (in red) and *Isoscolanthus* (in gray) have also developed nemathybomes in their aboral ends.

Conclusions

I conducted taxonomic, phylogenetic, and evolutionary studies on sea anemones of the suborder Anenthemonae mainly by using the specimens collected widely from Japanese waters. The classification system of Anenthemonae was comprehensively revised using molecular phylogenetic analyses. Based on the results of phylogenetic and taxonomic analyses, I evaluated the evolution of sea anemones of Anenthemonae by estimating morphological transitions along the phylogeny and reached the following conclusions.

1. The suborder Anenthemonae was revised to be monophyletic by excluding species of *Metedwardsia* and including *Halcampella maxima*, the type species of the genus *Halcampella,* and two similar species of the suborder Enthemonae. Anenthemonae now consists of three clades of superfamilies; Actinernoidea, Edwardsioidea, and Halcampelloidea—a newly established superfamily. In Actinernoidea, the family Isactinernidae and the genus *Isohalcurias* were established for solving the polyphyly of the family Actinernidae and the paraphyly of the family Halcuriidae. *Synactinernus,* formerly belonging to Actinernidae, was moved to Halcuriidae, and genus *Halcurias* was divided into two genera. In Edwardsioidea, five genera, *Edwardsia, Edwardsianthus, Paraedwardsia, Scolanthus*, and *Isoscolanthus*, complicatedly formed a large clade, and hence, they were all synonymized into the most senior previously established genus *Edwardsia.*

2. I comprehensively revised the classification system of Anenthemonae based on molecular phylogeny. Therefore, the taxonomy of Anenthemonae has changed as shown below: in the superfamily Actinernoidea, Halcuriidae accommodates *Synactinernus* and the new genus *Isohalcurias* in addition to two previously erected genera, *Halcurias* and *Carlgrenia*; the new family Isactinernidae accommodates two genera, *Isactinernus* and *Synhalcurias*; and Actinernidae became a monotypic family with *Actinernus*. The new superfamily Halcampelloidea consists of only one family Halcampellidae and three genera *Halcampella*, *Hexactis*, and *Pseudoedwardsia*. In Edwardsioidea (Edwardsiidae), the genus *Tempuractis* was established; the genus *Metedwardsia* was eliminated; and four genera—*Edwardsianthus,*

Paraedwardsia, Scolanthus, and *Isoscolanthus*—were synonymized into *Edwardsia*. Thus, there were seven genera in Edwardsiidae now.

From Japanese waters, 51 species, 14 genera, and five families in three superfamilies of Anenthemonae, including a new superfamily, two new families, and four new genera, were confirmed. In detail, Japanese Actinernoidea is composed of 11 species, including four new species, six genera, and three families. All genera except *Carlgrenia* and more than half of actinernoidean species in the world have been collected from Japanese waters. Halcampelloidea (Halcampellidae) includes four species, including two newly described ones. Edwardsioidea (Edwardsiidae) consists of 36 species with 26 new species in five genera, including a new genus *Tempuractis* and three newly discovered genera—*Edwardsiella, Halcampogeton*, and *Drillactis*—from Japan.

3. The common ancestors of Actiniaria likely did not have worm-like shapes, but columnar forms with 12 macrocnemes in the first mesenterial cycle and adhesive basal discs, which are noted in most species of extant sea anemones. The basal discs would have degenerated in several lineages in both Enthemonae and Anenthemonae. In Anenthemonae, the anemones of Edwardsiidae are strongly suggested to have acquired their peculiar shapes as follows: first, the common ancestors of Edwardsioidea and Halcampelloidea transformed their body forms to worm-like by adaptation to sandy habitats; subsequently, they lost the basal discs and four of the 12 macrocnemes in the lineage of Edwardsiidae to adapt to burrowing lifestyles. Thus, the traditional hypothesis that anemones of Edwardsiidae retain the primitive morphology of Actiniaria is improbable. The worm-like shapes of edwardsiids were derived in the edwardsiid lineage and for the adaptation to their burial lifestyles.

   In addition, the highly diverged and large clade of the genus *Edwardsia* is characterized by nemathybomes. The present study suggests that the novel function of nemathybomes is for protection from enemies by stinging using the large nematocysts contained in them. With the presence of the defensive nemathybomes, species of *Edwardsia* could expand their distribution worldwide and diverge into many species across several different niches.

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