

Doctoral Dissertation (Censored)

博士論文（要約）

Systematic study of the order Elasipodida

(Echinodermata, Holothuroidea) in Japanese waters

（日本近海における板足目（棘皮動物門，ナマコ綱）

の系統分類学的研究）

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Abstract

The order Elasipodida Théel, 1882 (Echinodermata: Holothuroidea) inhabits the worldwide deep sea floor ranging from 70 to above 10000 m in depth, including the polar region and hadal trench areas. Elasipodida is easily recognized by their gelatinous and often translucent body walls, conspicuous dorsal papillae or their derivatives, and large tube feet or fused into brims on ventrolateral edge. The order contains 171 extant species of 24 genera of 4 families, but the taxonomy is not well studied. The taxonomic research of Elasipodida prevented by their remote habitats with great water depths and the difficulty collecting specimen in good condition due to their easily damaged gelatinous body. Moreover, molecular analysis has been poorly applied to them. The purpose of the present study is the taxonomical revision of the order Elasipodida by molecular and morphological data mainly on the Japanese species. Based on the new taxonomic knowledge and phylogenetic relationships obtained, I discussed about the species richness of Elasipodida in the northwest Pacific Ocean, the categorization of body ossicles, and actual conditions of widely distributed elasipodid species.

In Chapter 2, I examined the detailed morphology of approximately 500 specimens and compared them with type specimens of 11 species to revise the species from Japanese waters based on the new systematics proposed by molecular phylogeny in the later chapters. I recognized a total of 42 species of 13 genera from 6 families in Japanese waters, including 3 new species and 6 newly recorded species. I also clearly defined terms of body ossicles of each family, which had been confusingly used in previous taxonomic literatures. Detailed description including clear photographs were given for taxonomically revised species.

For body ossicle observation, I used not only differences of shapes based on numbers and presence or absence of specific ultrastructure that have been conventionally accepted, but also made a quantitative comparison of their shapes by SEM especially for genera *Benthogone*, *Laetmogone* and *Pannychia*. In particular in these genera, intraspecific variation in wheel ossicle morphology is very large, and they were successfully diagnosed by body ossicle characteristics observing maximum diameter of ossicles and the ratio of diameter of central connecting portion and entire ossicle diameter.

In Chapter 3, to evaluate the family and generic classification of the order Elasipodida, I carried out molecular phylogenetic analyses using a protein coding gene, cytochrome c oxidase subunit 1 (COI), and two ribosomal genes, 16S and 18S rDNA, gene for 97 holothurian taxa covering 35 species, 15 genera, 4 families in Elasipodida collected from the Pacific, Atlantic, and Antarctic Oceans. The monophyly of the current Elasipodida was highly supported in both maximum likelihood and Bayesian trees. Elasipodida was the second basal group after Apodida was firstly divided in the class Holothuroidea. The trees suggested that the paraphyly of Laetmogonidae, and the existence of six clades in Elasipodida. However, detected several clades and their relationships within Elasipodida

were not obtained enough statistical supports. These trees confirmed the monophyly of four genera, *Laetmogone*, *Pannychia*, *Eynpniastes*, and *Psychropotes*, and showed the polyphyly of *Amperima* and *Ellipinion*, and the paraphyly of *Benthodytes* and *Peniagone*. The validity of monophyletic four genera were phylogenetically supported, but it was suggested that polyphyletic two genera and paraphyletic two genera need future taxonomic revisions.

To improve the basal resolution, family-rank relationships were analyzed using relatively conservative two ribosomal genes, 18S and 28S rDNA, of 15 representative species, which were selected two or three species from each clade of indicated six clades in the COI+16S+18S analyses. This concentrated analysis showed six distinct clades within Elasipodida. Among four current families, Elpidiidae, Pelagothuriidae, and Psychropotidae were monophyletic, while Laetmogonidae was paraphyletic with two separate clades. The monophyletic Elpidiidae contained two clades separated by large genetic distance. All six clades, including two of Laetmogonidae and two of Elpidiidae, were clearly distinguished by diagnostic morphological characters: arrangements of dorsal papillae, structure of calcareous ring, and type of body wall ossicles. I concluded that the six clades in Elasipodida should be treated as family rank taxa based on genetic distance between clades and morphological differences. Therefore, I established one new family and promoted one subfamily to family and classified the Elasipodida into six families to accord with the phylogenetic trees.

In Chapter 4, to evaluate the species diversity of the genus *Pannychia*, I sequenced COI gene and genome wide single-nucleotide polymorphism (SNP) sites using Multiplexed inter simple sequence repeat genotyping by sequencing (MIG-seq) for 221 individuals from the eastern and western Pacific, south Indian, and Antarctic Oceans. The phylogenetic analyses detected ten distinct clades within genus *Pannychia*. These ten clades were genetically divergent from each other. Currently only two species, *P. moseleyi* and *P. taylorae*, were valid in the genus, but I concluded that these ten clades should be treated as species rank taxa of *Pannychia*. Based on the morphological observations of the specimens, five clades were identified to the two valid species, three synonyms of *P. moseleyi*, and other two Japanese clades were described as new species. The other two southwest Pacific and an Antarctic clades still need more morphological observations for taxonomic treatments because of sample conditions. Two clades had geographically isolated distributions from the other clades to the eastern Pacific and Antarctic Oceans, and five and three clades occurred in northwest and southwest Pacific Ocean, respectively. The western Pacific eight species had locally overlapping distributions each other, but show different geographical and bathymetrical distribution ranges.

In Chapter 5, I discussed about species diversity of Elasipodida in the northwest Pacific Ocean, the categorization of body ossicles in Elasipodida based on revealed phylogenetic relationships, and actual conditions of widely distributed elasipodid species, such as cosmopolitan species.

Out of 178 valid species in Elasipodida recognized in this study, 42 species distributed to Japanese waters. In the northwestern Pacific containing Japanese waters, 49 species was distributed

and it surpassed 36 species in the North Atlantic Ocean, which is the most investigated region in the world. The habitats of elasipodid species spread a wide depth ranges from the continental shelf to the bottom of trench, and the northwest Pacific region including Japanese waters also contains various deep-sea environment from the upper bathyal to hadal zones. It is presumed that the diversity of the deep-sea benthic environments in this region provides suited habitats for various elasipodid species, and makes a high species diversity in this region.

Body ossicles have been used as the most important taxonomic character in Elasipodida likewise other holothurians. I reevaluated their categorization based on new family rank systematics. Body ossicles of Elasipodida were categorized into four types: rod, wheel, C-shaped and four-armed ossicles. Three types of ossicles, rod, wheel and four-armed ossicles, were shared by multiple families scattered in Elasipodida, and it was presumed that these three ossicles types might already differentiated before Elasipodida branched into six elasipodid families. In contrast, since C-shaped type ossicles occurred only in Elpidiidae, and it might be acquired in Elpidiidae after separated from other elasipodid families.

My molecular phylogenetic analyses revealed that *Pannychia moseleyi*, a typical widely distributed species regarded as a single species over the Pacific Ocean, was not a single species, but contained at least nine species. That suggested species diversity of *Pannychia* has been underestimated due to missing the species boundaries of closely similar species having partly overlapped distributions.

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DISCLAIMER: The present study is not issued for permanent scientific record and no part of it is to be considered published within the meaning of the International Code of Zoological Nomenclature (see Code, Art. 8b).

Chapter 1. General introduction

Holothuroidea Blainville, 1834 is a unique class of echinoderms with a soft, bilaterally symmetrical and elongated body bearing characteristic microscopic calcareous ossicles embedded in tissue. Unlike the other echinoderm classes having the pentaradial symmetry with vertical axis, sea cucumber has that with horizontal axis (Smirnov 2014). The five ambulacral radii which run longitudinally across the oral to anus area are two dorsal radii and three ventral radii. Littoral sea cucumbers are known as one of the precious marine fishery resources. It contains approximately 1700 valid species (WoRMS 2020) distributed to the worldwide sea floor from shallow to deep waters, including tropical brackish beaches (Semper 1867), deep-sea hydrothermal vents (Smirnov *et al.* 2000), and trenches (Hansen 1956).

The order Elasipodida (= Elasipoda) Théel, 1882 is easily recognized by their gelatinous and often translucent body walls, conspicuous dorsal papillae or their derivatives, and large tube feet or fused brims on ventrolateral edge. Elasipodida contains 171 extant species of 24 genera of 4 families (WoRMS 2020), of which there are known 33 species and 12 genera in 4 families in Japanese waters in present (*e.g.* Mitsukuri 1912; Ohshima 1915; explained in chapter 2). The elasipodid holothurians primarily inhabit the worldwide deep-sea floor ranging from 70 to above 10000 m in depth (Théel 1876; Hansen 1956), and several species show benthopelagic life forms (*e.g.* Ohta, 1985; Miller & Pawson, 1990). Elasipodid species sometimes becomes one of the dominant megafauna in the deep-sea floor (*e.g.* Caney & Caney 1976; Belyaev 1971; Rybakova *et al.* 2020). In particular, elasipodid holothurians are one of the most important species in the hadal depth trench area for diversity and density (Jamieson 2015).

The oldest record of Elasipodida, which inhabits only deep waters, is newer than other shallow water holothurians, and Théel (1876) described the first species, *Elpidia glacialis* Théel, 1876, from the Kara Sea in the Arctic Ocean. Subsequently, the second and third species, *Irpa abyssicola* Danielssen & Koren, 1878 and *Kolga hyaline* Danielssen & Koren, 1879, were reported from the Norwegian Sea (Danielssen & Koren 1878, 1879). Based on collections of the H.M.S. Challenger expedition, Théel (1879, 1882) presented 55 species/subspecies and 19 genera from worldwide oceans at a stroke, and divided the order into three families as the first systematic classification of Elasipodida: Deimatidae Théel, 1882, Elpidiidae Théel 1882 and Psychropotidae Théel, 1882. Since then, many authors conducted elasipodid taxonomic studies using collections of deep-sea expeditions operated by European countries and the United States in 19th century or early 20th century (Ludwig 1893, 1894; Koehler 1896; Perrier 1896, 1902; Mitsukuri 1897, 1912; Sluiter 1901a, 1901b; Koehler & Vaney 1905; Fisher 1907; Herouard 1901, 1902, 1906, 1923; Ohshima 1915; H.L. Clark 1913, 1920). During this time, two elasipodid families Pelagothuriidae Ludwig, 1893 and Laetmogonidae Ekman, 1926 were isolated and erected from Elpidiidae and Deimatidae, respectively, and Ekman (1926) proposed

two subfamilies Elpidiinae and Peniagoninae in Elpidiidae. The first comprehensive revision of the present order was provided by Hansen (1975), in which he reviewed 165 known species in that time (except for Pelagothuriidae) and revised to 106 species including 11 new species and 18 junior synonymizations. He divided the five elasipodid families into two suborders, Deimatina and Psychropotina. Basically, while his classification system is the most common used to date, Gebruk (1989, 1990) presented revised classification for Pelagothuriidae and Elpidiidae.

Early phylogenetic studies based on morphological characters (Kerr & Kim 2001) and molecular data of a single locus (Lacey *et al.* 2005) showed that after Apodida Brandt, 1835 derived from the other holothurians, Elasipodida secondary branched from the remaining Holothuroidea. Solís-Marín (2003) and Miller *et al.* (2017) demonstrated polyphyly of traditional Elasipodida by their molecular phylogenetic analyses, and Deimatidae was removed from Elasipodida (Smirnov 2012; Miller *et al.* 2017). Miller *et al.* (2017) performed analysis contained 14 elasipodid species, 9 genera, 5 families, and also suggested paraphyly of Laetmogonidae with poorly statistical supports. However, these studies used still a few species and genera for their analysis, and did not resolve robust relationships among basal branches.

The morphology and composition of calcareous ossicles buried in the body walls have been used as an important character in the classification of Elasipodida as well as the other holothurians (*e.g.* Théel 1882). Type classification based on the similarity of ossicle morphology has been carried out in taxonomic studies of extant Elasipodida (*e.g.* Hansen 1975; Gebruk 1990) and fossil holothurians (*e.g.* Gilliland 1993; Boczarowski 2001). Their homology and morphological evolution have been discussed along with the early evolution of Elasipodida (Gebruk 1990; Reich 2010). However, no studies have so far assessed the homology and evolution of body wall ossicles based on molecular data.

There are known many cosmopolitan and/or eurybathic species in order Elasipodida (Hansen 1956, 1967), but various studies of other marine invertebrates have consistently recognized the existence of multi species within putative cosmopolitan species (*e.g.* Addamo *et al.* 2020). There is only one previous work focusing population structure of elasipodid cosmopolitan species, *Psychropotes longicauda* Théel, 1882 (Gubili *et al.* 2016), which revealed the genetic divergence in this species. However, no study has examined the actual conditions of cosmopolitan distribution of elasipodid species based on both molecular data and morphological characters.

I conducted the revision of the systematics in order Elasipodida mainly based on the species in Japanese waters. In Chapter 2, based on the results of molecular phylogenetic analyses performed in the latter chapters, I proposed a new family-level systematics of the order Elasipodida. I examined approximately 500 specimens collected from around the world, mainly Japanese waters including type species, and revised Japanese species according to the new systematics. In Chapter 3, I examined the phylogenetic relationships of elasipodid taxa especially focusing on its family and generic ranks, using

new molecular data. In Chapter 4, I reevaluated species taxonomy of the genus *Pannychia* based on mt DNA COI gene and single-nucleotide polymorphism data. In Chapter 5, I additionally discussed about species richness of Elasipodida in the northwest Pacific Ocean, about reevaluation of the categorization of body ossicles based on phylogenetic relationships, and about cosmopolitan and eurybathic species resulting from taxonomic confusion in Elasipodida.

Chapter 2: Taxonomy of the order Elasipodida from Japanese waters

2.1 Introduction

The oldest records of the order Elasipodida in Japanese waters are *Laetmogone sponiosa* Théel, 1879 (= *Laetmogone violacea* Théel, 1879) and *Laetmogone wyvillethomsoni* Théel, 1879 based on the collection of the H.M.S. *Challenger* voyage by Théel (1879, 1882). Following Kishinouye (1894) reported *Pannychia moseleyi* Théel, 1882 from Sagami Bay, Mitsukuri (1897, 1912) and Ohshima (1915, 1916, 1917a, 1917b, 1917c, 1919) recorded 18 species/subspecies and 10 genera including 11 new species/subspecies from Japanese waters. Savel'eva (1933) and D'yakonov *et al.* (1958) reported 4 species/subspecies and 4 genera including 2 new species/subspecies from the Okhotsk Sea and the Sea of Japan. Belyaev (1971, 1975) investigated trench areas, the Kuril-Kamchatka, Japan, and Izu-Ogasawa Trenches, and described 7 species in the genus *Elpidia* Théel, 1876. Many of these Japanese elasipodid species had been reported only once with a simple description and sketches.

Hansen (1975) conducted a comprehensive revision of order Elasipodida, and proposed a new classification system, and his classification has been commonly used for a long time. In his revision, Japanese species were also reviewed with junior synonymizations of 9 species/subspecies. He presented many cosmopolitan and eurybathic species with junior synonymizations, but some of synonymized species were re-separated to be valid species by Gebruk (1983, 1988) and Gebruk *et al.* (2020). Totally, there are 33 species and 12 genera in 4 families in Japanese waters in present.

Taxonomy of elasipodid holothurians has been behind that of remaining Holothuroidea. Elasipodid species usually inhabits remote deep-sea bottom (*e.g.* Théel 1882; Hansen 1975), so special sampling gears, *e.g.* bottom trawls and remote operated vehicles (ROV), conducted by a research vessel are necessary and essential for collecting deep-sea benthic animals, such as elasipodids (Jimi *et al.* 2020). Traditionally, the morphology of external appendages (tentacles, papillae and tube feet) and of micro ossicles in body walls has been used for the taxonomy of elasipodid species as well as other holothurians (*e.g.* Théel 1882; Hansen 1975), but these taxonomic characters are easily damaged or lost during such a sampling event because of their thin and gelatinous skin. Holothurian's micro ossicles have been very important for the taxonomy, but the morphology contains large variation between individuals, between body parts, and even within the same body part. Although several authors attempted to assess the variation quantitatively (*e.g.* Hansen 1975; Imaoka 1977), it is insufficient and very difficult to describe the entire variations including multiple patterns and parameters from a limited number of samples. To exactly describe the elasipodid species, it is essential to develop a methodology for quantitative observation of ossicle structures.

In Japanese waters, the number of *in situ* observations of elasipodid species has increased with the recent development of deep-sea research techniques (*e.g.* Fujikura *et al.* 2012). However, they

have been reported without accurate identification or detailed description because specimens were rarely obtained and no taxonomists has been studying deep-sea holothurians for a long time in Japan.

第 2 章

本章の一部については，5年以内に学術雑誌に投稿予定のため，非公開.

2.3 Results

2.3.1 Taxonomic account

Class Holothuroidea Blainville, 1834

Order Elasipodida Théel, 1882

Family Elpidiidae Théel, 1882

[Japanese name: kuma-namako-ka]

Genus *Elpidia* Théel, 1876¹

[New Japanese name: Kuma-namako-zoku]

(Table 2-27)

Elpidia Théel, 1876: 1–7; 1877: 1–30; Belyaev, 1971: 329–330; Hansen, 1975: 172–173; Rogacheva, 2007: 368–372.

Tutela R. Perrier, 1896: 901.

Diagnosis [modified from Hansen (1975) and Rogacheva (2007)]. Tentacles 10, having discs with long and slender, retractile processes. Tube feet 4 pairs (5 pairs for *E. decapoda*), cylindrical, prominent, well spaced and equal in size. Papillae conical, separate, present along the entire dorsal radii, sometimes divided into an anterior and posterior groups. *Elpidia*-type ossicles (= rods with two paired horizontal arms and one paired vertical apophyses; Gebruk 1990) present; wheels occasionally present; C-shape ossicles absent. Calcareous ring strong and continuous, each piece with four pairs of arms.

Type species. *Elpidia glacialis* Théel, 1876.

Remarks. The remarkable morphological characters of genus *Elpidia* are four paired tube feet and mainly *Elpidia*-type ossicles (Gebruk 1990) in dorsal and ventral body walls. Although *E. decapoda* has five paired tube feet as an exception, *E. decapoda* has only *Elpidia*-type ossicles and shares the other diagnostic characters. *Elpidia*-type ossicles were also founded in the genera *Penilpidia* Gebruk, 1988 and *Protelpidia* Gebruk, 1983, but *Elpidia* differs from these two genera in the combination with other type ossicles (Rogacheva 2007): *Penilpidia* and *Protelpidia* have C-shape ossicles, while they do not occur in *Elpidia*. Therefore, the diagnosis of genus *Elpidia* was modified and written clearly the exceptional number of papillae for *E. decapoda*, and the absence of C-shape ossicles.

Twenty-four nominal species and subspecies have been described in this genus (*e.g.*, Belyaev 1971, 1975; Hansen 1975; Rogacheva 2007). In the genus *Elpidia*, two morphologically distinct species groups, based upon axis diameter of dorsal *Elpidia*-type ossicles, have been recognized (Belyaev 1971; Hansen 1975). The axis diameter is less than 40 μm in the so-called slender axis group and more than 40 μm in the robust axis group. The slender axis group includes six nominal species:

¹ The contents of the description of this genus have been partly published in:

Ogawa, A., Morita, T. and Fujita, T., *Elpidia soyoae*, a New Species of Deep-sea Holothurian (Echinodermata) from the Japan Trench Area, *Species diversity*, **25**, 153–162, 2020.

E. adenensis Belyaev, 1971, *E. antarctica* Belyaev, 1971, *E. chilensis* Belyaev, 1971, *E. gracilis* Belyaev, 1975, *E. minutissima* Belyaev, 1971, and *E. theeli* Hansen, 1956 (Belyaev 1971, 1975; Hansen 1975). Although Hansen (1975) had synonymized *E. antarctica* into *E. theeli*, *E. antarctica* is treated a valid species in this study because it is distinguishable from *E. theeli* in having cross ossicles in its both dorsal and ventral body wall (Belyaev 1971). In the robust axis group, 17 nominal species and subspecies has been reported: *E. belyaevi* Rogacheva, 2007, *E. kermadecensis* Hansen, 1956, *E. atakama* Belyaev, 1971, *E. birsteini* Belyaev, 1971, *E. decapoda* Belyaev, 1975, *E. glacialis* Théel, 1876, *E. hanseni hanseni* Belyaev, 1971, *E. hanseni idzubonensis* Belyaev, 1971, *E. heckeri* Baranova, 1989, *E. javanica* Belyaev, 1971, *E. kurilensis* Baranova and Belyaev in Belyaev, 1971, *E. lata* Belyaev, 1975, *E. longicirrata* Belyaev, 1971, *E. ninae* Belyaev, 1975, *E. solomonensis* Belyaev, 1971, *E. sundensis* Hansen, 1956, and *E. uschakovi* Belyaev, 1971 (Théel 1877; Belyaev 1971, 1975; Hansen 1975; Rogacheva 2007). *Elpidia echinata* (Perrier, 1896) has not been allocated to either group because Perrier (1896) did not describe its external or ossicle morphology in details. These two groups have different bathymetrical distributions with the exception of the Arctic and Antarctic species: the slender axis group occurs in abyssal depths, 2710–5740 m, and the robust axis group is found in hadal depths of 6156–9735 m (Hansen 1956; Belyaev 1971, 1975).

In Japanese waters, Seven species and subspecies of *Elpidia* distributed to the Izu-Ogasawara, Japan, and Kurile-Kamchatka Trench areas: *E. birsteini*, *E. hanseni hanseni*, *E. hanseni idzubonensis*, *E. kurilensis*, *E. longicirrata*, *E. minutissima*, and *E. soyoae* sp. nov. (Belyaev 1971, 1975; Mironov *et al.* 2019; present study). The former five species and subspecies belong to the robust axis group, and the later two species belong to the slender axis group.

***Elpidia soyoae* sp. nov.**

[New Japanese name: Soyo-kuma-namako]

(Figs 2-21–2-26; Tables 2-26, 2-27)

Type materials examined. Holotype. The Japan Trench area, east of Iwate Prefecture, northern Japan, Northwest Pacific Ocean, 39°4.914'N to 39 ° 10.312'N, 143°39.570'E to 143°42.027'E, depth 3570–4145 m RV Soyo-maru (Japan Fisheries Research and Education Agency: FRA) St. Iwate 4200 Kago, NSMT E-12638 (BL 18 mm; BW 11 mm).

10–11 Jul 2018. Paratypes (four individuals): NSMT E-12635 (BL 25 mm; BW 13 mm); NSMT E-12636 (BL 21 mm; BW 12 mm); NSMT E-12637 (BL 19 mm; BW 12 mm); NSMT E-12639 (BL 12 mm; BW 8 mm). All paratypes were also collected from the same sampling station of holotype.

Other materials examined. JAMSTEC 1110025849.

Diagnosis. Body length up to 25 mm. Dorsal papillae up to five pairs along the entire dorsal radii; second pairs widely separated from third ones. Purple pigmentation spots on dorsal and ventral body walls, tentacles, and tube feet. Ossicles in dorsal body wall mainly rods, *Elpidia* type, with two pairs of horizontal arms and one pair of vertical apophyses, rod axis up to 1336 μm long, 8.1–33 μm in diameter, length of apophyses 5.1–47% of axis length; tentacle rods with arched axis, and short arms and/or apophyses.

Description. Body semi-ellipsoidal with flat ventrum, 12–25 mm long (5 individuals), 1.5–1.9 times as long as wide (Fig. 2-21). Mouth anteroventral. Anus at posterior end of body. Dorsal papillae conical, 0.2–5.0 mm long (N=49 from 5 individuals, Table 2-26), four or five paired and 0–3 unpaired papillae present on two dorsal radii (four to seven papillae on each radius, Fig. 2-22). Paired large papillae 0.3–5.0 mm long (N=42 from 5 individuals), anterior two pairs widely separated from third paired ones. Unpaired minute papillae 0.2–2.7 mm long (N=7 from 3 individuals), between second and third paired papillae on holotype and one paratype (NSMT E-12639), and on the posterior dorsum of holotype and one paratype (NSMT E-12635). Ventrolateral radii without conical papillae. Tube feet cylindrical, four on each ventrolateral radius. Mid-ventral radius without tube feet. Tentacles ten, with cylindrical stems, and four conical digits on terminal discs. Papillae, tube feet, and tentacles nonretractile. Calcareous ring comprising five pieces surrounding pharynx (Fig. 2-23A), each piece with four pairs of straight arms (Fig. 2-23B): inside anterior pair (495–1131 μm long, N=10 in holotype), inside posterior pair (266–907 μm long, N=8 in holotype), outside anterior pair (1092–2075 μm long, N=7 in holotype), and outside posterior pair (968–1972 μm long, N=9 in holotype). Tips of inside arm pairs branched or broadened in holotype (Fig. 2-23C). Gonad white unpaired tuft, comprising central genital ducts and surrounding genital vesicles. Polian vesicle single, fusiform, transparent, whitish in holotype. Body skin whitish, occasionally with purple pigmentation spots composed of small purple particles on dorsal and ventral surfaces. Discs of tube feet and tentacles light yellow, sometimes with purple pigmentation spots composed of small purple particles.

Ossicles (Table 2-26). Ossicles in dorsal body wall mostly rods, *Elpidia*-type, and rarely wheels (Fig. 2-24). Rod axis 193–1336 μm in length (DOL, N=104 from 5 individuals), straight, with two paired horizontal arms, and one pair of vertical apophyses. Axis 8.1–33 μm in diameter (N=192 from 5 individuals), with conical tips at both ends. The height of apophyses 17–232 μm (DAH, N=236 from 5 individuals). DAH/DOL ratio between 0.051–0.47 (N=150 from 5 individuals). Wheels rare, 30–33 μm in diameter (N=3 from 3 individuals), central connecting portion 18–21 μm in diameter (N=3 from 3 individuals), with nine spokes (N=3 from 3 individuals), three central rays (N=2 from 2 individuals), and triangular brim teeth (N=3 from 3 individuals) (Fig. 2-24B). Ossicles in ventral body wall only rods, *Elpidia*-type ossicles (Fig. 2-25). Rod axis 73–557 μm in length (VOL, N=200 from 5 individuals), straight, with two paired horizontal arms, and one pair of vertical apophyses, sometimes

shortened. Axis in diameter 4–24 μm (N=274 from 5 individuals). The height of apophyses 10–142 μm (VAH, N=438 from 5 individuals), VAH/VOL ratio between 0.071–0.70 (N=332 from 5 individuals). Ossicles in tentacles only rods, *Elpidia*-type ossicles (Fig. 2-26). Rods 77–776 μm in length (TOL, N=223 from 5 individuals), with one arched axis, shortened arms and/or shortened apophyses sometimes completely lacking arms and apophyses. Axis in diameter 4.2–39 μm (N=243 from 5 individuals). The height of apophyses 2.7–227 μm (TAH, N=380 from 5 individuals), TAH/TOL ratio between 0.0077–0.58 (N=380 from 5 individuals).

Distribution. NORTH PACIFIC OCEAN. Japan Trench area, deep 3229–4145 m (present study).

Etymology. The species is named after the R/V *Soyo-maru*, which collected these specimens.

Remarks. Morphological features of examined specimens were well coincident with five diagnostic characters of the genus *Elpidia* (see the Diagnosis section for the genus above). The dorsal rods of the examined specimens ranged from 8.1 to 33 μm in axis diameter, indicating *Elpidia soyoae* sp. nov. belong to the slender axis group. A morphological comparison of *E. soyoae* sp. nov. with six species of the slender axis group is provided in Table 2-27. *Elpidia soyoae* sp. nov. is distinguished from other species by the following four features: i) dorsal papillae on two dorsal radii, four or five paired papillae and unpaired papillae present along the entire dorsal radii (four to seven papillae on each radius), with wide separation between second and third paired papillae, ii) maximum length of dorsal rods exceeds 1000 μm , iii) tentacle rods with arched axis and shortened or occasionally completely reduced arms and apophyses, and iv) purple pigmentation spots composed of small purple particles on dorsal and ventral body walls. In addition, this species is easily distinguished from non-grouped species, *E. echinata*, which has 3 papillae on each dorsal radius (Perrier 1896).

Chapter 3. Molecular phylogeny of order Elasipodida

第3章

本章については、5年以内に学術雑誌に投稿予定のため、非公開。

Chapter 4. Reevaluation of species of the genus *Pannychia* based on mt DNA COI gene and single-nucleotide polymorphism data

第4章

本章については、5年以内に学術雑誌に投稿予定のため、非公開.

Chapter 5. General discussion

第5章

本章については、5年以内に学術雑誌に投稿予定の内容を含むため、非公開.

Chapter 6. Conclusion

第 6 章

本章については, 5 年以内に学術雑誌に投稿予定の内容を含むため, 非公開.

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Tables

Table 2-26. Morphological counts and measurements of type specimens of *Elpidia soyoae* sp. nov.

Morphological characters	Catalogue Number/ Type status				
	NSMT E-12638 Holotype	NSMT E-12635 Paratype	NSMT E-12636 Paratype	NSMT E-12637 Paratype	NSMT E-12639 Paratype
Body length (BL, mm)	18	25	21	19	12
Body width (BW, mm)	11	13	12	12	8
BL/BW ratio	1.6	1.9	1.8	1.5	1.5
Right papillae number	7	6	4	4	4
Left papillae number	5	6	4	4	5
Maximum papillae length (mm)	3.4	5	3.2	3.6	0.8
Minimum papillae length (mm)	0.2	0.7	1.6	1.3	0.3
Tube feet pair number	4	4	4	4	4
Tentacle number	10	10	10	10	10
Rods, <i>Elpidia</i> -type ossicles, from dorsal body wall:					
Length (DOL, μm)	259–673 (N = 16)	317–1336 (N = 21)	256–956 (N = 24)	265–1065 (N = 29)	193–952 (N = 14)
Maximum axis diameters (μm)	10–30 (N = 36)	9.4–29 (N = 34)	10–26 (N = 44)	10–33 (N = 42)	8.1–28 (N = 36)
Axis shape	Straight	Straight	Straight	Straight	Straight
Apophyses height (DAH, μm)	25–219 (N = 56)	32–174 (N = 32)	17–145 (N = 55)	44–232 (N = 67)	28–167 (N = 26)
DAH/DOL ratio	0.12–0.33 (N = 25)	0.083–0.34 (N = 24)	0.051–0.23 (N = 36)	0.13–0.47 (N = 50)	0.12–0.27 (N = 15)
Wheel ossicles from dorsal body wall:					
Diameter (μm)	33 (N = 1)	31 (N = 1)	NA	NA	30 (N = 1)
Diameter of central connecting portion (μm)	21 (N = 1)	20 (N = 1)	NA	NA	18 (N = 1)
Spokes number	9	9	NA	NA	9
No. of central rays	NA	3	NA	NA	3
Rods, <i>Elpidia</i> -type ossicles, ossicles from ventral body wall:					
Length (VOL, μm)	150–532 (N = 54)	91–557 (N = 32)	73–495 (N = 37)	161–521 (N = 44)	178–539 (N = 33)
Maximum axis diameters (μm)	7–24 (N = 55)	7–19 (N = 54)	4–18 (N = 63)	8–18 (N = 52)	6.7–19 (N = 50)
Axis shape	Straight	Straight	Straight	Straight	Straight
Apophyses height (VAH, μm)	22–119 (N = 95)	27–140 (N = 90)	10–115 (N = 103)	27–125 (N = 83)	36–142 (N = 67)
VAH/VOL ratio	0.078–0.35 (N = 93)	0.12–0.70 (N = 53)	0.071–0.51 (N = 68)	0.11–0.37 (N = 71)	0.082–0.36 (N = 47)
Rod, <i>Elpidia</i> -type ossicles, ossicles from tentacles:					
Length (TOL, μm)	160–580 (N = 51)	234–776 (N = 44)	211–588 (N = 47)	151–535 (N = 38)	77–408 (N = 43)
Maximum axis diameters (μm)	6.3–30 (N = 53)	4.2–39 (N = 44)	8.6–31 (N = 50)	11–35 (N = 47)	11–25 (N = 49)
Axis shape	Arched	Arched	Arched	Arched	Arched
Apophyses height (TAH, μm)	2.4–177 (N = 91)	9.0–227 (N = 76)	3.4–162 (N = 73)	6.9–151 (N = 67)	4.7–93 (N = 73)
TAH/TOL ratio	0.0097–0.57 (N = 91)	0.012–0.47 (N = 76)	0.0077–0.45 (N = 73)	0.020–0.36 (N = 67)	0.021–0.58 (N = 73)

Table 2-27. Morphological comparison of *Elpidia soyoae* sp. nov. with *Elpidia* species in the slender axis group. DAH and DOL indicate apophyses height and ossicle length of rods in dorsal body wall, respectively.

Morphological characteristics	<i>E. soyoae</i> sp. nov.	<i>E. theeli</i> Hansen, 1956	<i>E. minutissima</i> Belyaev, 1971	<i>E. antarctica</i> Belyaev, 1971	<i>E. adenensis</i> Belyaev, 1971	<i>E. chilensis</i> Belyaev, 1971	<i>E. gracilis</i> Belyaev, 1975
Maximum body length (mm)	25	12	13	33	11	22	23
Number of papillae along each dorsal radius	4–7	5–7	3	4–6	4	2	3
Papillae distribution	Entirely from anterior to posterior; large 4 or 5 paired papillae and 0–3 unpaired papillae; 2nd and 3rd pairs widely separated	Entirely from anterior to posterior, regular intervals	Anterior to 3rd tube feet	1st and 2nd pairs widely separated	Anterior to 3rd tube feet	Anterior half	Anterior to 2nd tube feet
Skin pigmentation	Purple spots composed of small particles	Purple particles	Scattered purple particles	Unknown	Without pigmentation	Unknown	Unknown
Rods, <i>Elpidia</i> -type ossicles, of dorsal body wall							
Maximum length (µm)	1336	700	850	570	1200	1250	1200
DAH/DOL ratio	0.12–0.33	ca. 0.40	0.25–0.35	0.20–0.50	0.07–0.15	0.10–0.14	0.20–0.70
Axis diameters (µm)	9–30	35	< 40	< 20	35	35	20–30
Additional ossicles in dorsal body wall	Wheels	Wheels	Unknown	Cruciform ossicles	Unknown	Unknown	Unknown
Rods, <i>Elpidia</i> -type ossicles, of tentacles							
Axis shape	Arched	Arched	Arched	Arched	Arched	Unknown	Arched
Arms	Shortened, sometimes completely reduced	Unknown	Shortened, sometimes completely reduced	Shortened, sometimes completely reduced	Shortened, sometimes completely reduced	Unknown	Shortened
Apophyses	Shortened, sometimes completely reduced	Unknown	Shortened, sometimes completely reduced	Shortened, sometimes completely reduced	Shortened, sometimes completely reduced	Unknown	Well developed
Distribution	Japan Trench area, depth 3570–4145 m	Tasman Sea, depth 4510 m	Aleutian Trench; Bering Sea; Japan Trench area: depth 4100–5740 m	Ross Sea, depth 650–700 m	Gulf of Aden, depth 3070 m	Peru–Chile Trench area, depth 2710–4600 m	Scotia Sea, depth 5450–5480 m
References	This study	Hansen (1956, 1967, 1975); Belyaev (1971)	Belyaev (1971, 1975)	Belyaev (1971)	Belyaev (1971)	Belyaev (1971)	Belyaev (1975); Rogacheva (2007)

Figures

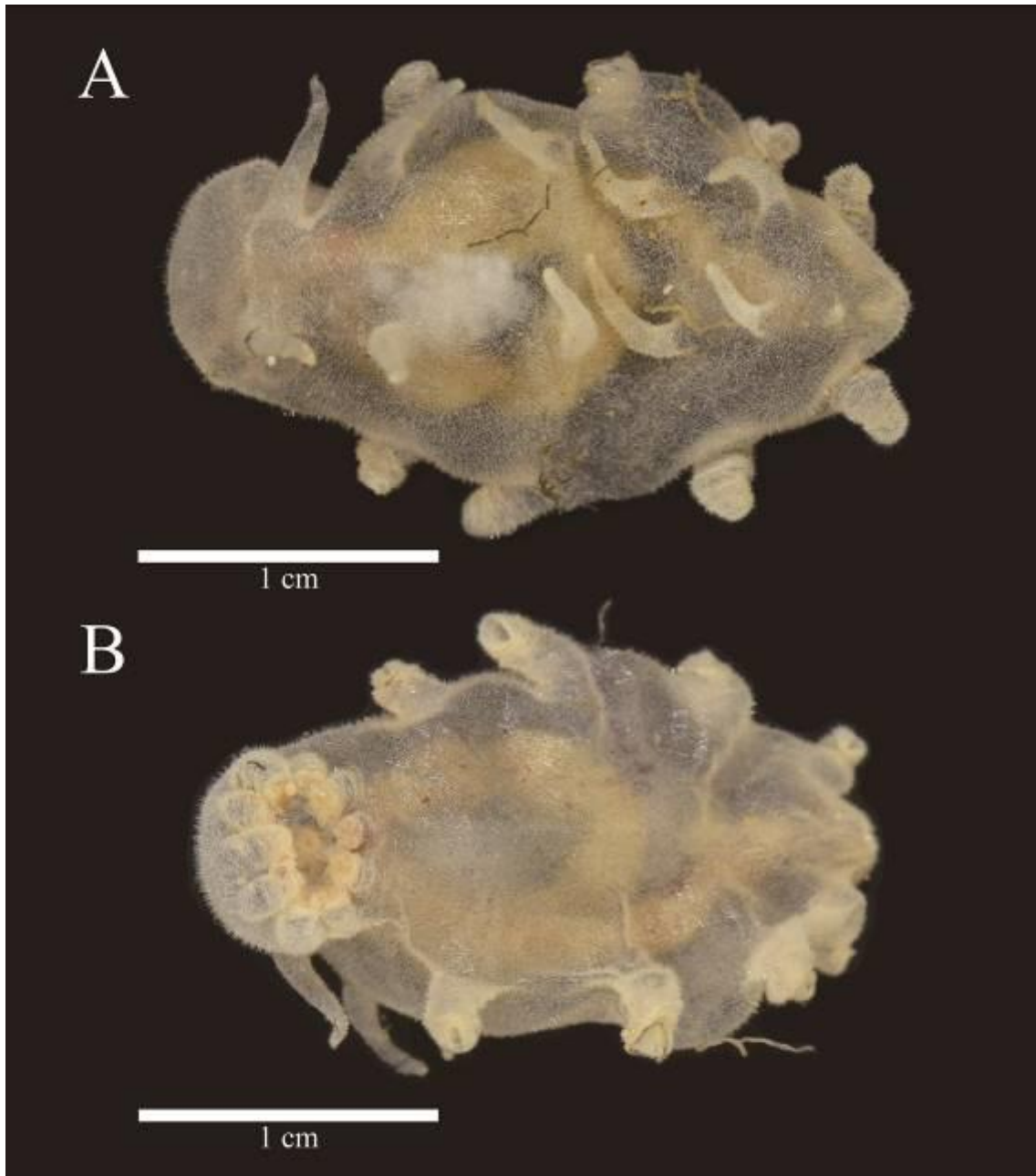


Fig. 2-21 Fresh specimen of *Elpidia soyocae* sp. nov. (NSMT E-12635: paratype). A, dorsal view; B, ventral view.

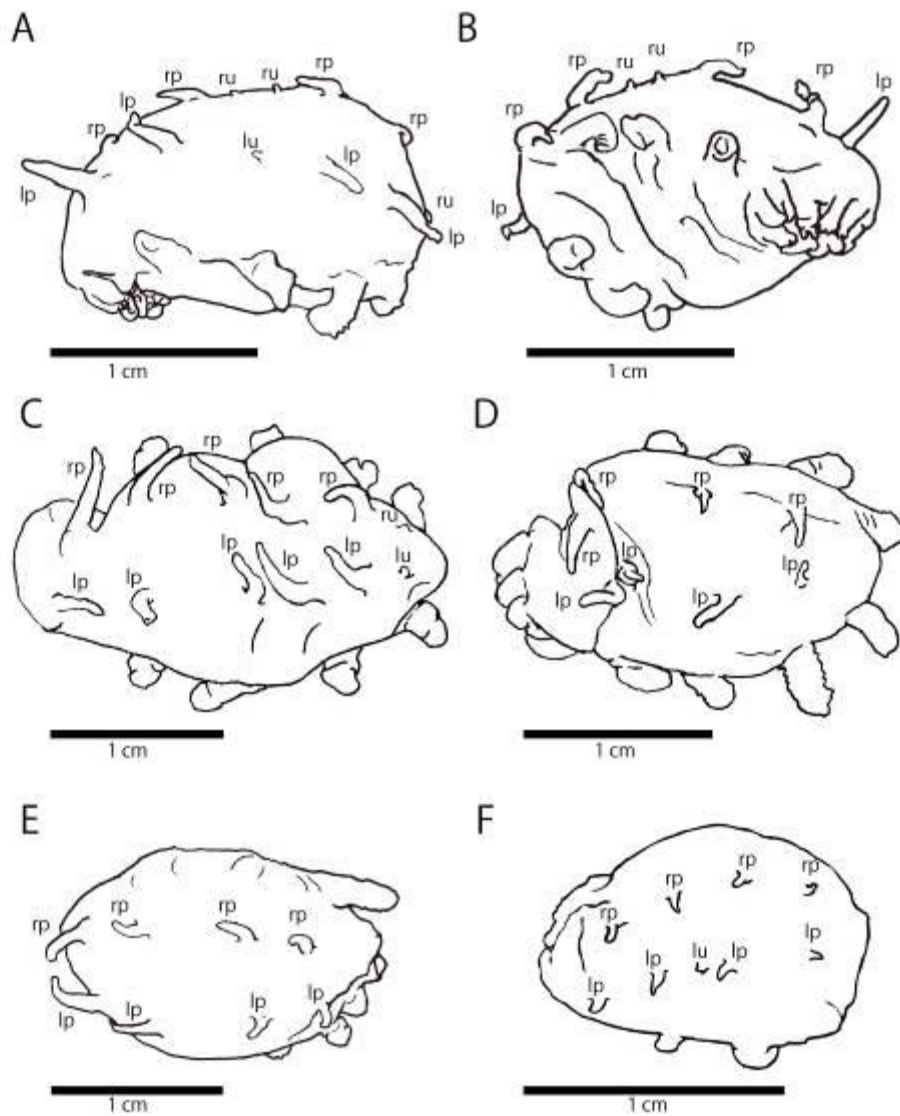


Fig. 2-22 Papillae arrangements of *Elpidia soyoae* sp. nov. A, left side view; B, right side view; C–F, dorsal side. A–B, holotype; C, NSMT E-12635: paratype; D, NSMT E-12636: paratype; E, NSMT E-12637: paratype; F, NSMT E-12639: paratype. Abbreviations: lp, paired papillae on dorsal left radius; lu, unpaired papillae on dorsal left radius; rp, paired papillae on dorsal right radius; ru, unpaired papillae on dorsal right radius.

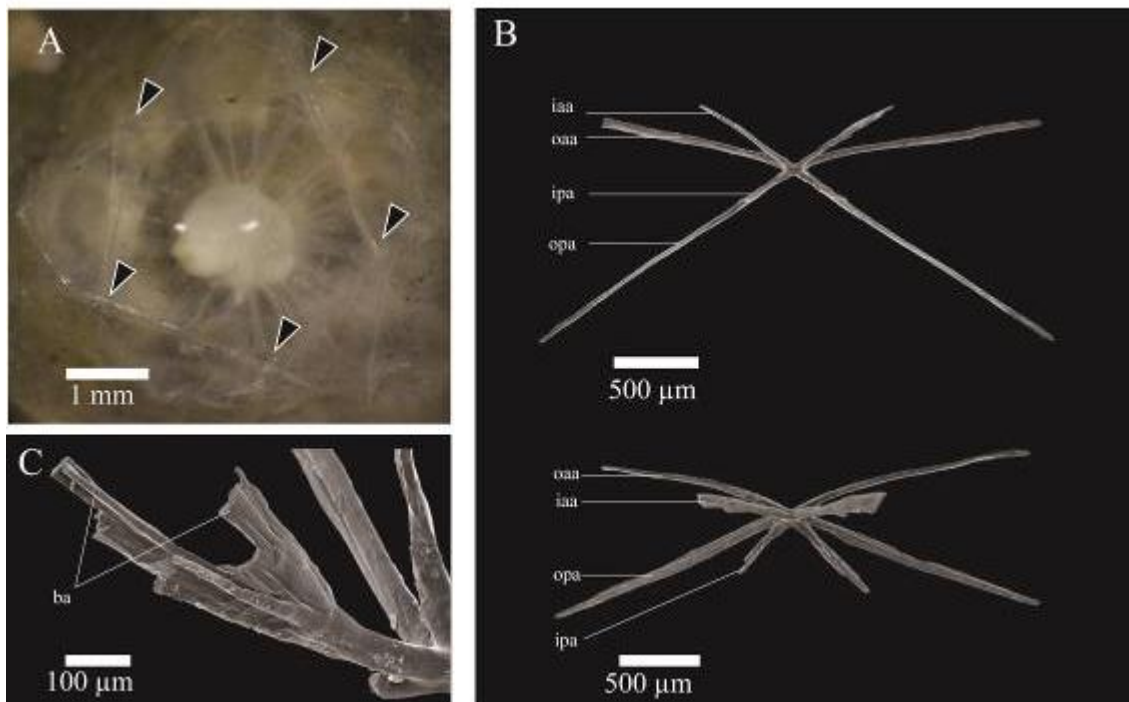


Fig. 2-23 Calcareous ring of *Elpidia soyuae* sp. nov. (NSMT E-12638: holotype). A, entire ring in dorsal view; B, variation of isolated pieces; C, branched inside posterior arm. Black arrowheads show five pieces surrounding pharynx. Abbreviations: ba, branched arm of inside posterior arms; iaa, inside anterior arms; ipa, inside posterior arms; oaa, outside anterior arms; opa, outside posterior arms.

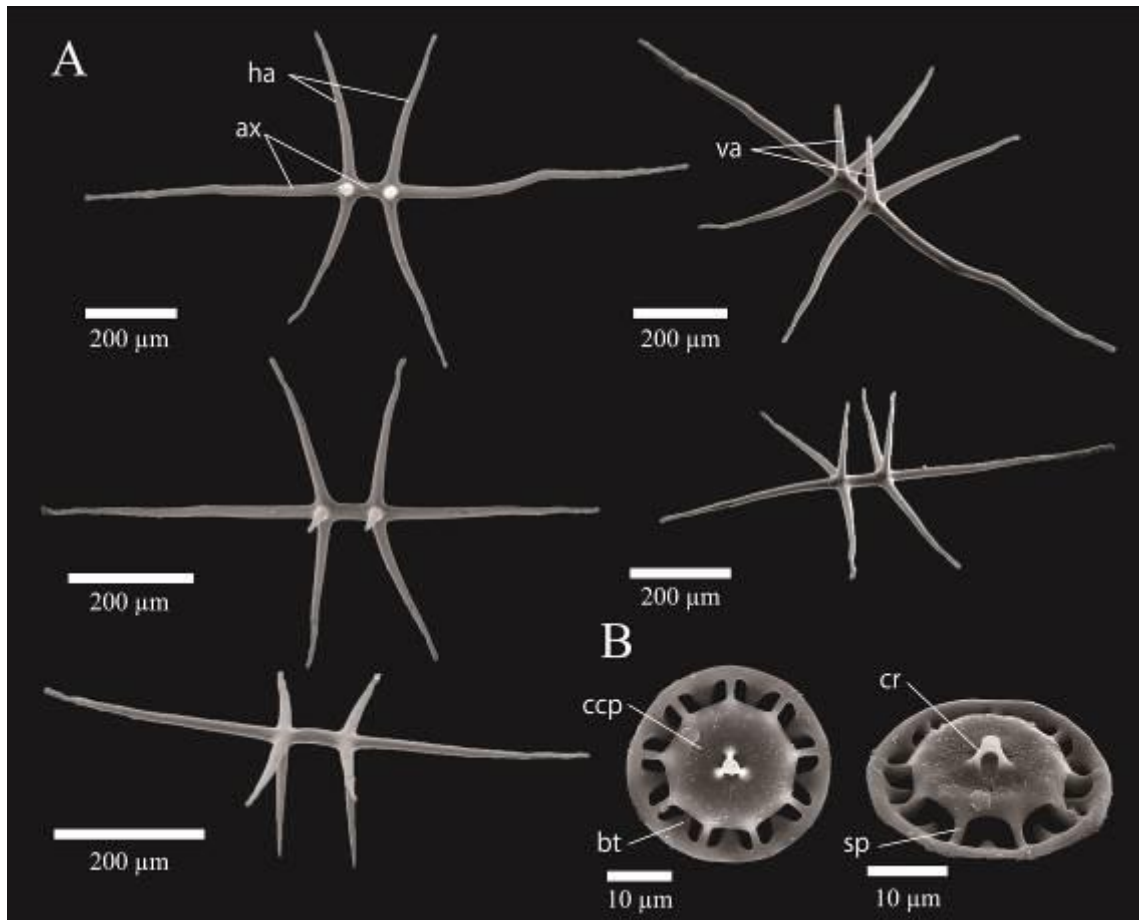


Fig. 2-24 SEM images of ossicles from dorsal body wall of *Elpidia soyoae* sp. nov. (NSMT E-12635: paratype). A, rods with straight axis, well developed horizontal arms, and vertical apophyses; B, wheel from convex side and obliquely lateral side. Abbreviations: ax, axis; bt, brim teeth; ccp, central

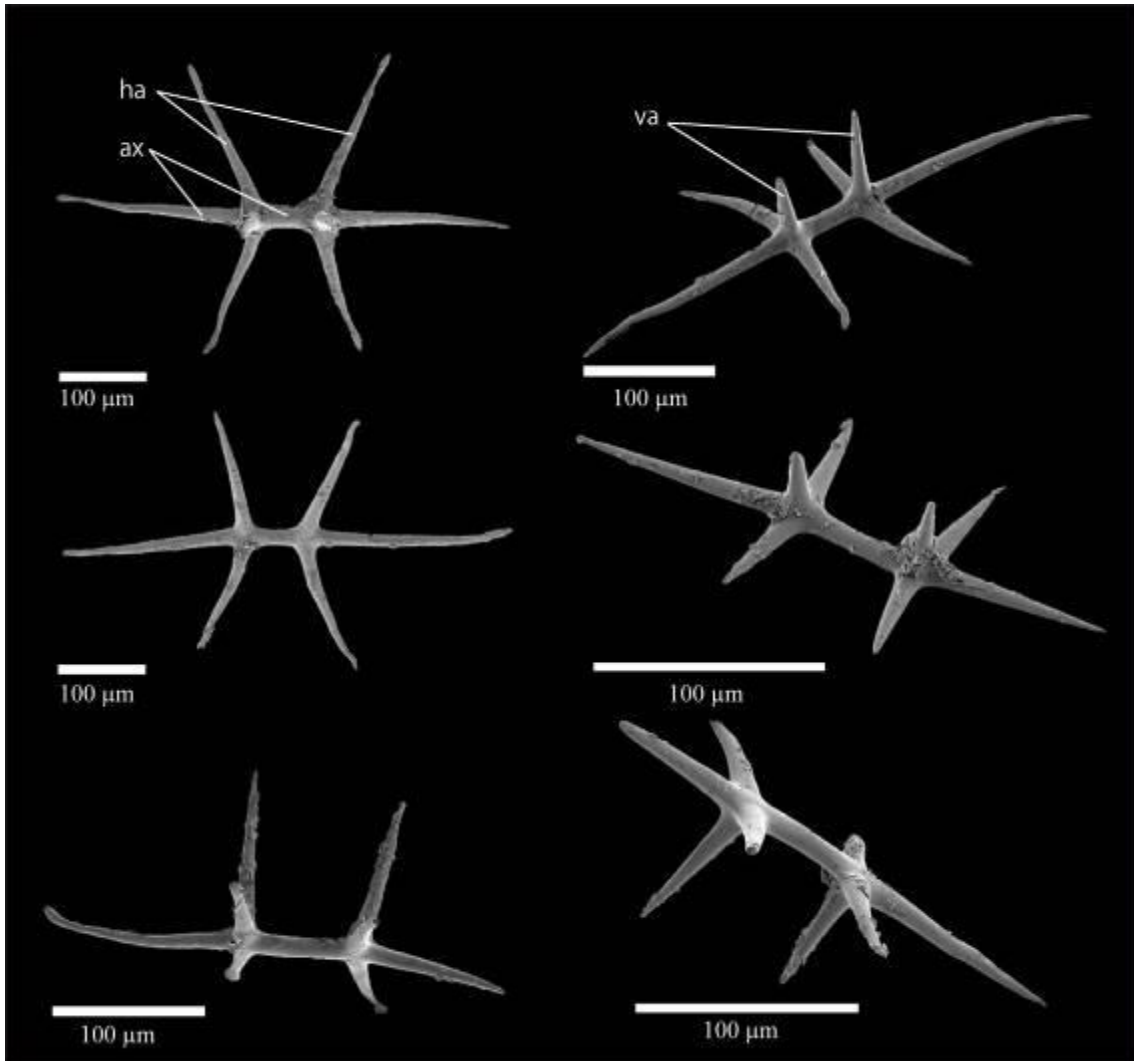


Fig. 2-25 SEM images of ossicles from ventral body wall of *Elpidia soyoae* sp. nov. (NSMT E-12639: holotype). Rods with straight axis, well developed horizontal arms, and vertical apophyses. Abbreviations: ax, axis; ha, horizontal arms; va, vertical apophyses.

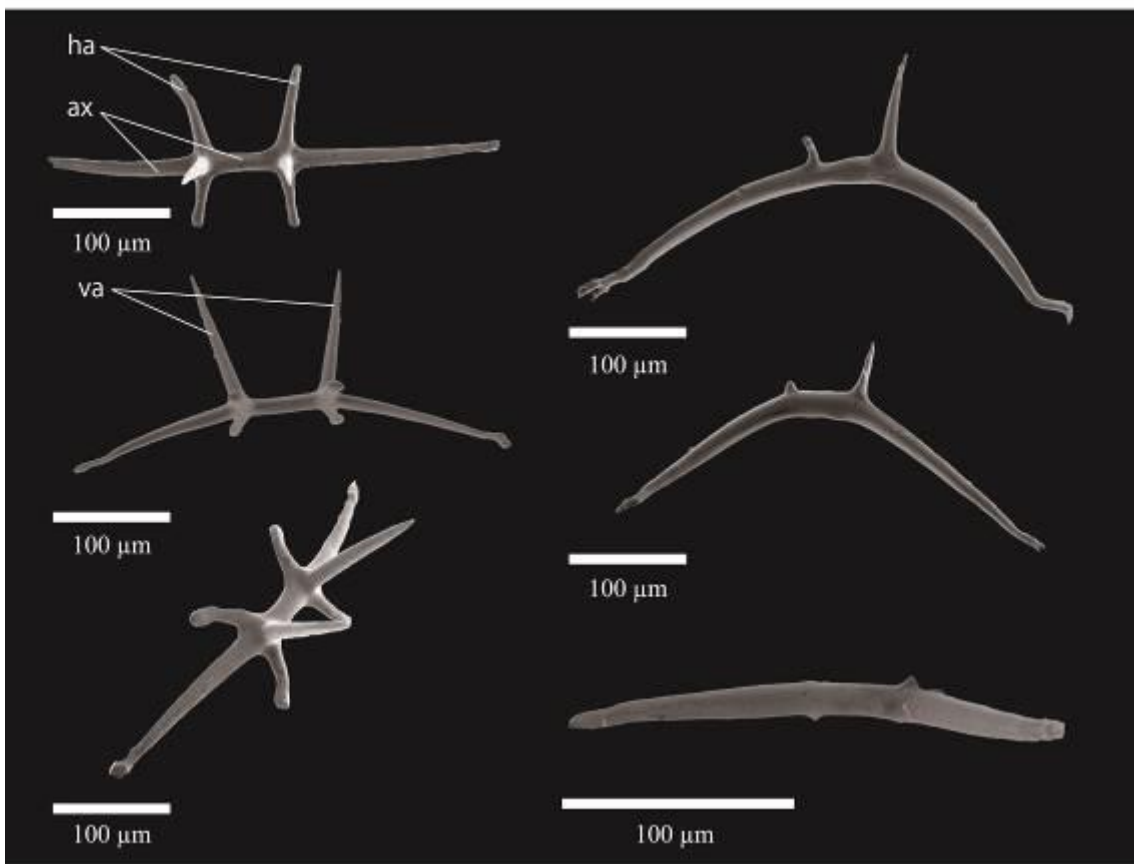


Fig. 2-26 SEM images of rods from tentacles of *Elpidia soyoae* sp. nov. (NSMT E-12635: paratype). Rods with arched axis, especially shortened horizontal arms, and vertical apophyses. Abbreviations: ax, axis; ha, horizontal arms; va, vertical apophyses.