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Holothuroidea of the Emperor Seamount Chain: Taxonomy, Morphology and Molecular Data

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The present paper provides first data on the fauna of Holothuroidea of the Emperor Seamount Chain (ESC, northwestern Pacific). Samples were collected using ROV *Comanche 18* from four guyots, Kinmei, Koko, Nintoku and Ojin, in 2019 and 2021 at depths from 750 to 2240 m during two cruises of RV *Akademik M.A. Lavrentyev*. Sixteen species were recognized. Orders Elasipodida and Synallactida were the most diverse. Here we provide morphological descriptions and molecular data on *COI* and *16S* rRNA for nine species belonging to eight genera and also for three taxa identified to the family level. One genus and two species are described as new: *Parvathuria dautovae* gen. et sp. nov. and *Peniagone koko* sp. nov. Two representatives were assigned to the genus *Hansenothuria*; we discuss the phylogenetic position of this genus based on molecular data. Only one of the recorded taxa is known outside the Pacific Ocean. More than a half of the examined species has the closest genetic affinity to holothuroids from the Pacific, indicating predominantly local origin of the ESC holothuroid fauna.

Keywords: Bathyal fauna, Distribution, DNA barcoding, Echinodermata, Molecular phylogeny, North Pacific, Sea cucumbers, Taxonomy

BACKGROUND

The Emperor Seamount Chain (ESC) is an undersea range of mostly flat-topped mountains (guyots) stretching over 2400 km from Kamchatka peninsula to the Hawaiian ridge. Data on ESC benthic fauna is extremely scarce, although this area has been used for commercial benthic fishery for a long time (Baco et al. 2020). As many other seamounts in the ocean, ESC is characterized by enhanced biological productivity of benthic and pelagic communities (Samadi et al. 2007; Dautova et al. 2019). Most of faunistic studies on ESC were focused on fish (Baytalyuk et al. 2010; Zolotov et al. 2014; Somov et al. 2019). Limited data are also available on selected invertebrate taxa, including Ophiuroidea and Echinoidea (Sirenko and Smirnov 1989; Volkova et al. 2025), Hydrozoa (Calder and Watling 2021), Octocorallia (Miyamoto et al. 2017; Cairns et al. 2018; Dautova et al. 2019), Porifera (Dautova et al. 2019), Nemertea (Chernyshev and Kuznetsov 2024), Crustacea (Egorova and Dautova 2025; Kolbasov and Savchenko 2025) and Kinoryncha (Adrianov and Maiorova 2024). Data on Holothuroidea of ESC are almost lacking. Preliminary studies on the ESC benthic fauna obtained by the RV *Akademik M.A. Lavrentyev* LV86 cruise in 2019 showed that holothuroids were abundant on Koko and Nintoku guyots, both on rocky and soft substrates (Dautova et al. 2019). In this study we provide the first detailed account on the composition and distribution of ESC Holothuroidea, one of the dominant groups of ESC benthic communities. We describe one new genus and two new species based on morphology and genetics and provide descriptions and molecular data on all other

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recorded taxa except *Orphnurgus* sp., *Pannychia* spp. and *Psolus* sp.

MATERIALS AND METHODS

Sampling

Holothuroids were obtained using the ROV *Comanche* 18 during the LV86 and LV94 cruises of RV *Akademik M.A. Lavrentyev* in 2019 and 2021 on four guyots Kinmei, Koko, Nintoku and Ojin (Table S1, Fig. 1). Two other guyots, Jingu and Yuryaku, were also explored but no holothuroids were sampled. Specimens were collected at depths of 750–2240 m using manipulator of ROV or a slurp gun. A unique ID number was assigned to each collected specimen or a group of specimens assumed to belong to the same species. Specimens were preserved in 96% ethanol. Tissue samples for genetic studies were taken from some specimens and kept separately at -18°C. The voucher specimens also received a unique Voucher code. Specimens are stored at the Museum (MIMB) of A.V. Zhirmunsky National Scientific Center of Marine Biology, Far Eastern Branch, Russian Academy of Sciences (NSCMB FEB RAS). Ossicle, SEM preparations and tissue samples are deposited at the P.P. Shirshov Institute of Oceanology, Russian Academy of Sciences (IORAS).

Morphological studies

Specimens were examined and photographed using Leica M205C stereomicroscope equipped with a Leica FLEXACAM C1 digital camera. Ossicles were examined and photographed using the light microscope Olympus BX43 with a ToupCam U3CMOS08500KPA digital camera and scanning electron microscope (SEM) KYKY EM6900LV. Ossicles were extracted using domestic bleach solution with subsequent rinsing in the distilled water. For light microscopy, ossicles were transferred onto a glass slide, dried using a heating stage and mounted in Canada balsam. For SEM, ossicles were dehydrated in 96% ethanol, mounted on aluminium stubs, and sputter-coated with gold. Coating was performed using a GVC-1000 Ion Sputter Coater for 42–62 seconds at 10 mA under an argon atmosphere to achieve a layer 10–15 nm thick. SEM was operating at 20 kV, under high vacuum conditions, with secondary electron detector imaging.

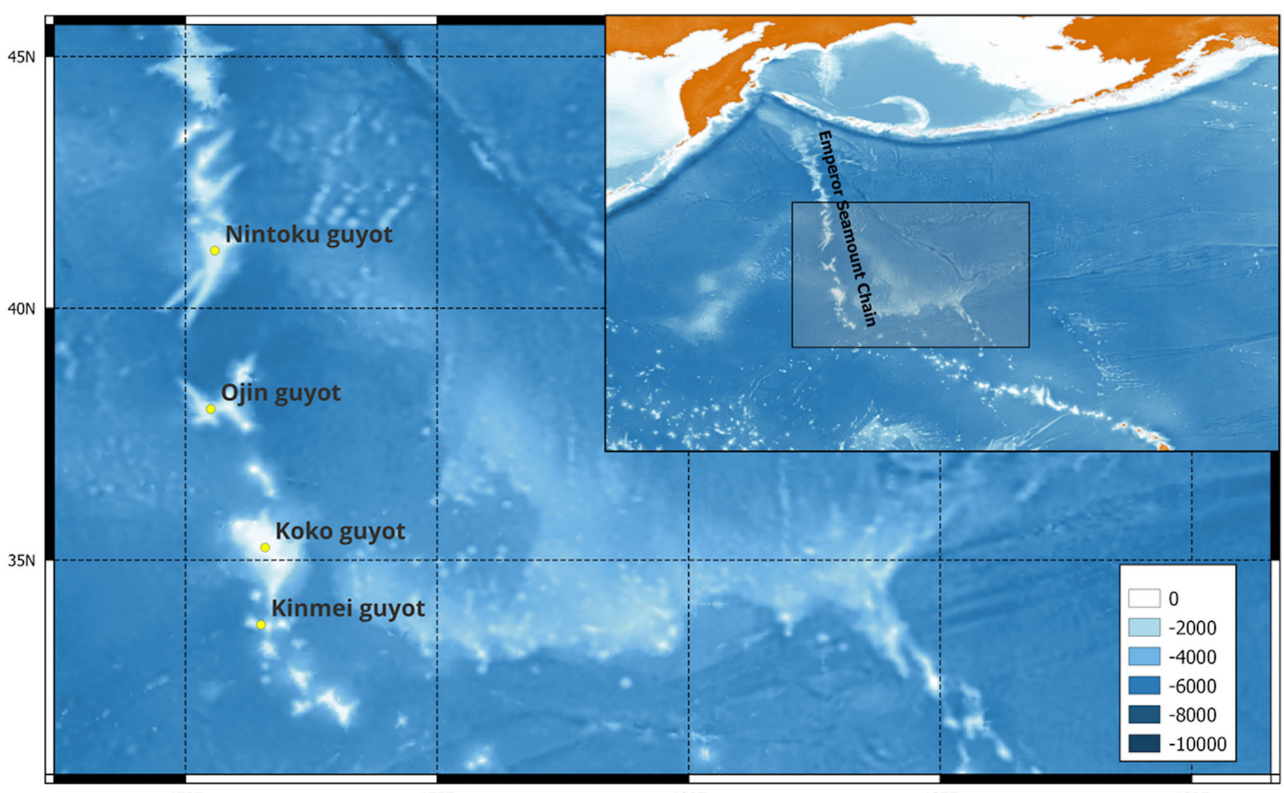

Fig. 1. Sampling area. Map generated using QGIS 3.28 *Firenze*.

Molecular methods

Partial sequences of the mitochondrial genes, cytochrome *c* oxidase subunit I (*COI*) and *16S* rRNA (*16S*) were obtained (Table S1). For *Parvathuria dautovae* gen. et sp. nov. partial *COI* sequences as well as nuclear *18S* rRNA (*18S*) were obtained. For evaluation of the phylogenetic position of *Hansenothuria* Miller and Pawson, 1989, sequences of nuclear *18S* and *H3* histone (*H3*) were generated. Additional specimen of *Hansenothuria* sp. from the Bering Sea (MIMB 48717, Table S1) was sequenced to enhance the taxonomic representation in our phylogenetic analysis.

The genomic DNA was extracted using QuickExtract™ DNA Extraction Solution (Lucigen) with modified manufacturer protocol: incubation at 65°C for 60 min and then at 98°C for 2 min. PCR amplification was conducted using Encyclo Plus PCR kit (Evrogen) according to the manufacturer protocol and primers listed in the table S2, with annealing temperature set at 48–52°C; amplicons were visualized in a 1.5% agarose gel stained with SYBR Safe (Lumiprobe). PCR products were purified from agarose gel using either Clean Up Mini kit (Evrogen) or by enzymatic purification using Exogen (Genterra); the purified samples were sequenced using the Sanger method on Applied Biosystems ABI 3900 by Evrogen company (Moscow, Russia) with the same primers used for PCR amplification.

Contigs were assembled from forward and reverse electropherograms using the MUSCLE algorithm implemented in Geneious 10.0.9 and then manually edited. Sequences of *COI* and *H3* were aligned in MEGA7 (Kumar et al. 2016) with MUSCLE algorithm. Sequences of *16S* and *18S* were aligned using MAFFT implemented in Geneious 10.0.9 with E-INS-i algorithm. *COI* and *H3* alignments were checked for stop-codon presence. Poorly aligned regions were removed using Gblocks ver. 0.91b (Castresana 2000) with less stringent options. Phylogenetic analysis was performed using the maximum likelihood (ML) and Bayesian inference (BI) approaches. PartitionFinder 2 (Lanfear et al. 2016) was used for selecting best-fit partitioning schemes and models of nucleotide evolution. ML tree search and bootstrapping was conducted in RAxML-NG (Kozlov et al. 2019) using auto MRE bootstrapping convergence option with cutoff = 0.03. BI analysis was performed using MrBayes 3.2 (Ronquist et al. 2012). The analysis was conducted in two runs, four chains (one cold and three heated) with trees and parameters sampled every 500 generations. Run convergence was evaluated by analyzing output parameters in MrBayes log and by using Tracer v1.7.1; average standard deviation of split frequencies < 0.01, Potential Scale Reduction Factor approaching 1, minimum and average Estimated Sample Size > 200, and chain swap 0.1–0.7 indicated sufficient convergence. First 25% of the trees were discarded as burn-in. Clade supports were assessed using Bayesian posterior probabilities (PP) and Felsenstein bootstrap scores (BS) generated in BI and ML analyses, respectively. PopArt (Leigh and Bryant 2015) was used to construct a haplotype network. Genetic uncorrected *p*-distances were calculated in MEGA7, with transitions and transversions included and uniform rates among sites.

Additional data on sequences obtained in this study and voucher specimens are also available at the Barcode of Life database (BOLD) website (https://boldsystems.org) using the BOLD process ID code listed in table S1. Each *COI* sequence was assigned to the Barcode Index Number (BIN) in the BOLD database. Data on sequences used in the phylogenetic analysis obtained from GenBank and BOLD is given in table S3.

RESULTS

Sixteen species of holothuroids were recognized in the material from two cruises of RV *Akademik M.A. Lavrentyev*. The species belong to five orders and seven families. Six taxa were identified to the species level including three new species, seven taxa were identified to a genus and three to a family. 32 sequences of *COI* and 35 sequences of *16S* were obtained for examined specimens. Also, six *18S* sequences were generated for *Parvathuria dautovae* gen. et sp. nov. and three sequences of *H3* for *Hansenothuria* sp. The obtained *COI* sequences were assigned to 13 BINs (Tables 1 and S1), of which eight were new to the BOLD database. Below are descriptions of species except for *Orphnurgus* sp., *Psolus* sp. and *Pannychia* sp., which will be described separately, and *Pannychia henrici* Ludwig, 1894 described by Ogawa et al. (2022).

Order Apodida
Family Chiridotidae
Chiridota sp.
(Fig. 2)

Material: MIMB 47795 (1 ex.) (Table S1).

Description: Body length ca. 50 mm in preserved state. Skin transparent *in vivo* (Fig. 2a), whitish and semi-transparent in ethanol. Tentacles 12, tentacle discs with six digits (Fig. 2b), inner digits slightly larger. Ossicles wheels (Fig. 2c–e), located in wheel-papillae; wheel-papillae arranged in a single row on mid-dorsal interradius from anterior to posterior end, few wheel-

Table 1. List of the ESC holothuroids and their distribution

Order	Family	Species	BIN	Geographic distribution		Nearest BIN and its geographic distribution[1]
				ESC depth (m)	Other areas depth (m)	
Apodida	Chiridotidae	*Chiridota* sp.	BOLD:AEU4983*	Nintoku 1154–1162		BOLD:ADU4046 Chukchi Sea
Dendrochirotida	Psolidae	*Psolus* sp.[2]	BOLD:AFP5848	Ojin 1281		BOLD:AAC9852 amphiboreal
Elasipodida	Elpidiidae	Elpidiidae gen. et sp. indet.	BOLD:AEP5721*	Koko 1368–1372		BOLD:AAG4363 Antarctic
Elasipodida	Elpidiidae	*Parvathuria dautovae* gen. et sp. nov.	BOLD:AEP5715*	Koko, Nintoku 750–1161		BOLD:ABA2135 Antarctic
Elasipodida	Elpidiidae	*Peniagone koko* sp. nov.	BOLD:AER8429	Koko 1993–2231		BOLD:ADM0802 Southwest Atlantic
Elasipodida	Laetmogonidae	*Laetmogone* cf. *wyvillethomsoni*	BOLD:AES2585	Koko 1983–2240	CCFZ, South China Sea 3132–3568	BOLD:AAJ2967 Antarctic
Elasipodida	Laetmogonidae	Laetmogonidae gen. et sp. indet. 1	BOLD:AEO8803*	Kinmei 1894		BOLD:AFT2165 East Pacific
Elasipodida	Laetmogonidae	Laetmogonidae gen. et sp. indet. 2	BOLD:AFI9967*	Kinmei 1852		BOLD:AFT2165 East Pacific
Elasipodida	Laetmogonidae	*Pannychia henrici*[4]	BOLD:AEO7632	Koko, Kinmei, Ojin 1419–1894	Northwest Pacific 433–2600[4]	BOLD:AAI5301 North Pacific
Elasipodida	Laetmogonidae	*Pannychia* sp.	NA	Koko 1419		NA
Holothuriida	Mesothuriidae	*Mesothuria carnosa*	BOLD:AEO8167	Koko 2135	Hawaii islands 406–858 Australian IOT 2189–2264	BOLD:AGY0676 Indian Ocean
Synallactida	Deimatidae	*Orphnurgus* sp.	BOLD:AET0539*	Koko 1993–2231		BOLD:AGD9287 South China Sea
Synallactida	Synallactidae	*Bathyplotes* sp.	BOLD:AEO6442*	Koko, Kinmei 1363–1881		BOLD:AGY0647 Australian IOT
Synallactida	Synallactidae	*Hansenothuria* sp. 1	BOLD:AET3377	Koko 1372–1422		BOLD:ABA6534 French Polynesia
Synallactida	Synallactidae	*Hansenothuria* sp. 2	BOLD:AET3378*	Koko 1880–1881		BOLD:AEX6305 Pacific (CCFZ)
Synallactida	Synallactidae	*Synallactes* sp.	BOLD:ABA2309	Nintoku, Ojin 1110–1161[3]	off Australia, depth unknown	BOLD:ADM0329 East Pacific

[1] based on BOLD *COI* database. [2] see Panina et al. 2026. [3] range known only for ESC. [4] see Ogawa et al. 2022. *new BIN to BOLD database.

papillae present in right and left ventrolateral interradii anteriorly.

Remarks: Several *Chiridota* species from temperate Pacific waters, *C. discolor* Eschscholtz, 1829, *C. laevis* (O. Fabricius, 1780), and *C. tauiensis* Saveljeva, 1941, have semi-transparent, light-coloured, or colourless skin. *Chiridota* sp. from the ESC is distinguished from them by its wheel-papillae arrangement. Furthermore, it differs from other North Pacific species (*C. albatrossi* Edwards, 1907; *C. hawaiiensis* Fisher, 1907; *C. impatiens* Yamana and Tanaka, 2017; *C. nanaimensis* Heding, 1928 and *C. pacifica* Heding, 1928) in lack of rod-shaped ossicles, wheel-papillae arrangement and colouration. Finally, it can be differentiated from the North Pacific species *C. orientalis* Smirnov, 1981 and *C. ochotensis* Saveljeva, 1941 by its colour and wheel papillae arrangement.

According to BOLD database, the closest species is a record from the Chukchi Sea (BIN BOLD:ADU4046, *p*-distance 6.88%).

Distribution: Single record at Nintoku guyot, depth 1162–1154 m.

Order Elasipodida
Family Elpidiidae
Parvathuria gen. nov. Kremenetskaia et Gebruk

(Figs. 3–7)
urn:lsid:zoobank.org:act:617DAD54-A19F-496A-B6BC-015F01638598

Type species: *Parvathuria dautovae* sp. nov., by present designation.

Etymology: The genus name refers to the small size of the type species, *P. dautovae* sp. nov., which is among the smallest elpidiids. Such a small size is also known for *Kolga nana* (Théel, 1879) (Billett and Hansen 1982).

Diagnosis: Body length up to 12 mm in preserved state. Skin transparent, colourless *in vivo*. Body elongated. Tentacles 10, tentacle discs with finger-like processes. Velum of two pairs of papillae fused at base, dorsal free papillae two–three pairs on mid- and posterior dorsum. Tube feet 8–12 pairs, with some gap between the first pair and tentacle crown, tube feet decreasing in size and arranged closely posteriorly. Calcareous ring consisting of five isolated pieces; each

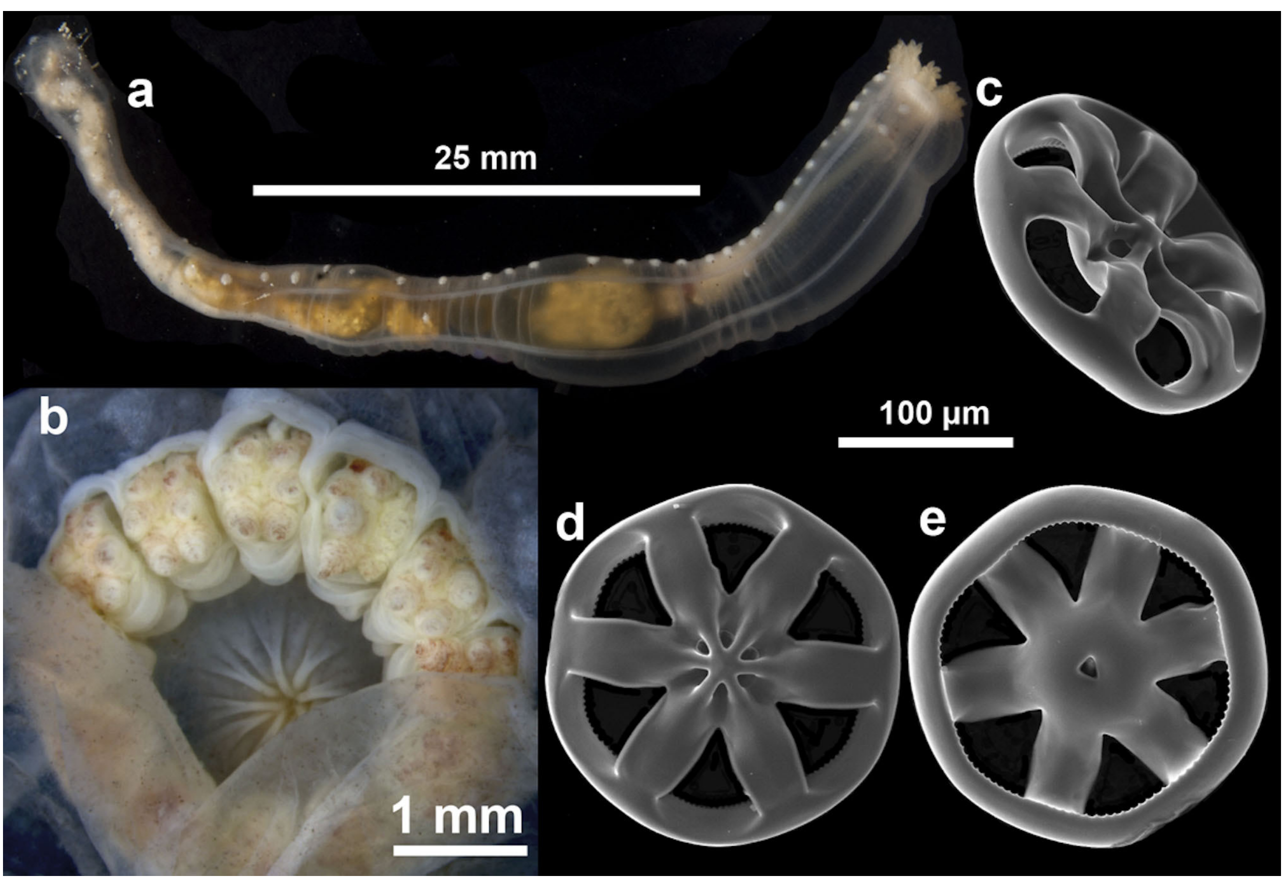

Fig. 2. *Chiridota* sp.: a, specimen MIMB 47795 before preservation; b, tentacles in preserved specimens; c–e, wheel ossicles from wheel-papilla. Image courtesy: a, Kirill Minin.

piece with four pairs of arms, inner arms branching.

Remarks: The new genus *Parvathuria* gen. nov. is assigned to Elpidiidae based on the following diagnostic characters: (i) tube feet arranged along ventrolateral radii and absent on the mid-ventral radius (Fig. 3a, b); (ii) presence of a velum, a dorsal ambulacral appendage composed of two pairs of papillae (Fig. 3a, b, f, g); (iii) ossicles exclusively in the form of rods, plates absent (Fig. 4); and (iv) a distinctive elpidiid-type calcareous ring consisting of five delicate, star-shaped segments (Fig. 5a–e). According to phylogenetic analysis of *COI* + *18S* dataset (Fig. 7), *Parvathuria dautovae* gen. et sp. nov. is sister to *Rhipidothuria racovitzai* Hérouard, 1901 MNHNP IE-2009-4932 (PP = 1; BS = 99). The genera

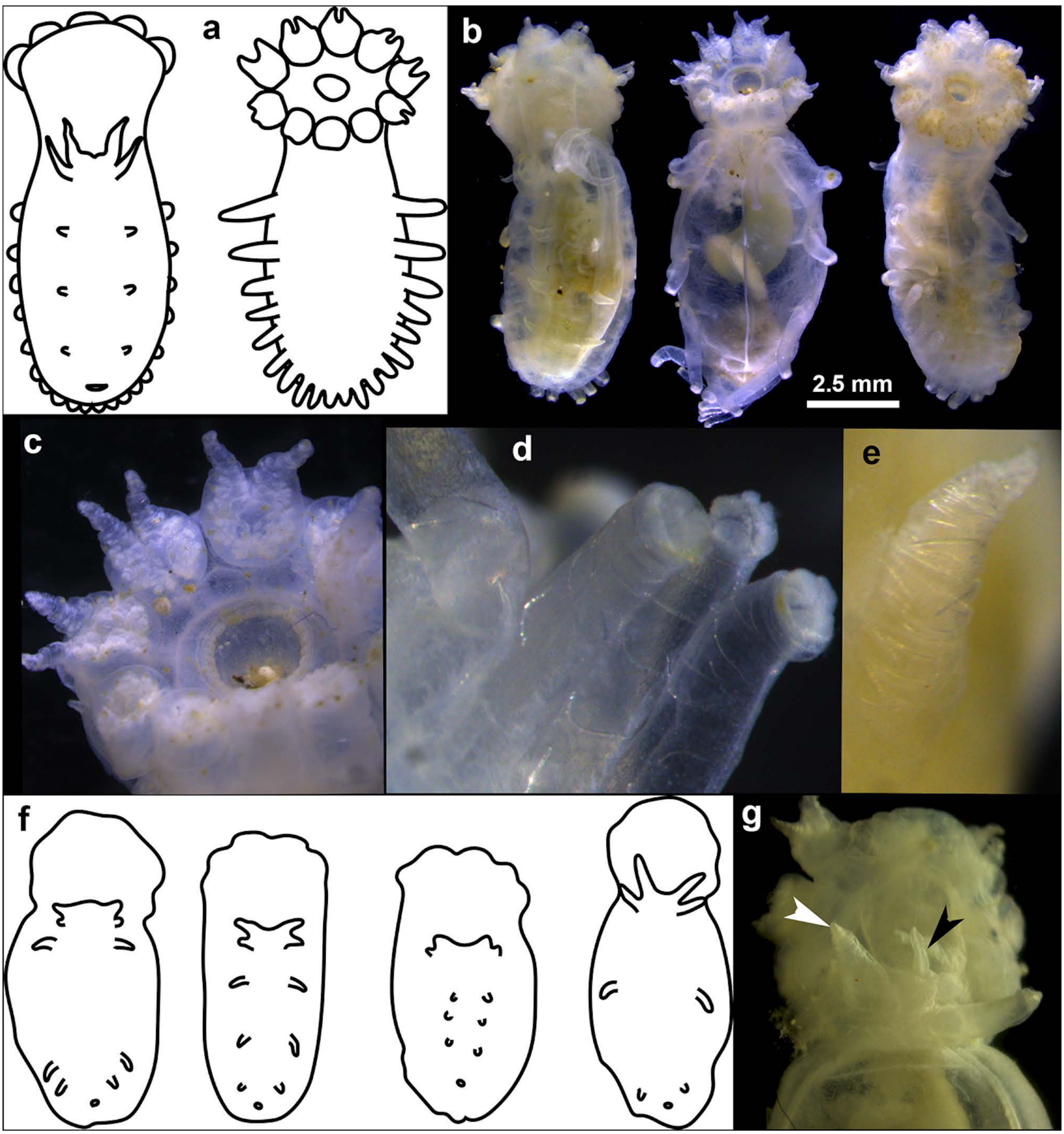

Fig. 3. *Parvathuria dautovae* gen. et sp. nov.: a, schematic external morphology; b, holotype (left) and two paratypes preserved in ethanol; c, tentacles, d, tube feet; e, dorsal papilla; f, variation in velum shape and papillae arrangement in preserved paratypes; g, velum papillae (white arrow) and genital papilla (black arrow).

Parvathuria gen. nov. and *Rhipidothuria* Hérouard, 1901 share the following morphological characters: presence of velum, serial pairs of dorsal papillae and presence of tube feet in anterior body half. *Parvathuria* gen. nov. differs by (i) lower number of serial papillae against 5–7 pairs in *Rhipidothuria*; (ii) colourless skin, whereas in *Rhipidothuria* tentacle discs and mouth area are slightly purple; (iii) smaller size of *Parvathuria* gen. nov. (maximum body length in preserved state 12 mm in *P. dautovae* gen. et sp. nov. vs 70 mm in *R. racovitzai*); and (iv) more gracile calcareous ring pieces. From other genera of the family, *Parvathuria* gen. nov. differs in presence of velum and serial papillae on mid- and posterior dorsum.

We have compared *Parvathuria dautovae* gen. et sp. nov. with *Rhipidothuria racovitzai* from the IORAS collection (Cat. ECH02855, Table S1). Similarly to *P. dautovae* gen. et sp. nov., *R. racovitzai* ECH02855 has single Polian vesicle, calcareous ring pieces with four arm pairs and it lacks terminal plates in tube feet. In contrast to *P. dautovae* gen. et sp. nov., *R. racovitzai* has 6–7 pairs of free papillae along the dorsum, purple tint of tentacle discs and mouth area, lacks body wall ossicles, and has more robust and branched calcareous ring pieces (Fig. 5f–h).

Parvathuria dautovae **gen. et sp. nov.** **Kremenetskaia et Gebruk**

(Figs. 3–7)
urn:lsid:zoobank.org:act:D2E5AFB6-EA70-4B73-823D-099CC8BE5D24

Type Material: *Holotype*: MIMB 47806, Sampling ID 1653, body length 11 mm in preserved state, 96% ethanol, coll. 07-Aug-2019, cruise LV86, St. LV86-21, ROV *Comanche 18*; locality Nintoku guyot, ca.

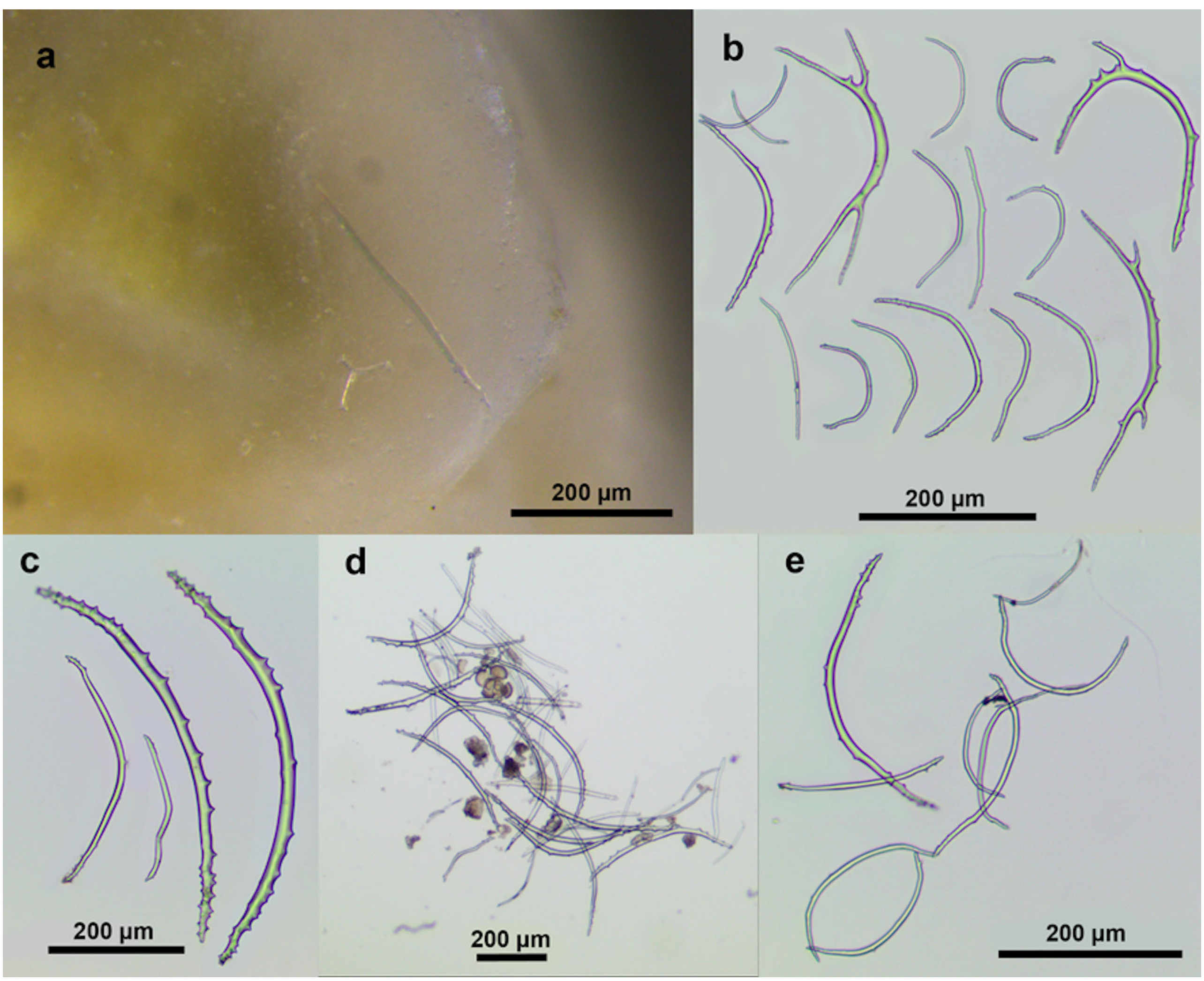

Fig. 4. *Parvathuria dautovae* gen. et sp. nov., ossicles: a, fragment of dorsal skin with rod-shaped ossicle; b, rod-shaped ossicles of various shape from tentacles; c, d, rods from tube feet; e, papilla rods.

41.00°N, ca. 170.00°E (exact locality unknown because of technical problems with ROV during St. LV86-21), depth 1161 m.

Paratypes: 67 specimens, 96% ethanol; MIMB 47802 (1 ex.), MIMB 47803 (23 ex.), MIMB 47804 (1 ex.), MIMB 47805 (7 ex.), MIMB 47806 (1 ex.) and MIMB 48125 (1 ex.) collected at same station and locality as holotype; MIMB 47800 (1 ex.) and MIMB 47801 (1 ex.), coll. 20-Jul-2019, cruise LV86, St. LV86-5, ROV *Comanche 18*; locality Koko guyot, 35.603°N, 171.223°E, depth 776 m; MIMB 48126 (26 ex.), MIMB 48127 (1 ex.), MIMB 48128 (1 ex.), MIMB 48129 (1 ex.), coll. 29-Jul-2021, cruise LV94, St. LV94-2, ROV *Comanche 18*; locality Koko guyot, 35.602°N–35.603°N, 171.225°E, depth 750–752 m (see Table S1 for further details).

Type locality: The North Pacific Ocean, Nintoku guyot, depth 1161 m.

Etymology: The species is named after Tatiana Nikolayevna Dautova (NSCMB FEB RAS), chief scientist of two research cruises to ESC onboard RV *Akademik M.A. Lavrentyev*, for her exceptional contribution to the knowledge of ESC biodiversity.

Diagnosis: As for the genus.

Description: Body length up to 12 mm in ethanol. Skin colourless, transparent *in situ*, semi-transparent in ethanol (Fig. 3b), very soft, easily damaged. Dorsal side convex with its anterior part more flat; ventral side flatten. Tentacles 10, anterior 7 tentacles with finger-like processes on outer margin that can be strongly contracted after preservation in ethanol; posterior tentacles with short processes (Fig. 3c). Velum small (Fig. 3g), consisting of two pairs of papillae; in specimens preserved in 96% ethanol velum could be almost fully contracted. Three (rarely two) pairs of conspicuous free papillae on dorsum of similar length, or posterior pair slightly shorter: first pair in anterior half of dorsum; second pair on mid-dorsum or in posterior one-third of dorsum; third pair in posterior one-third of dorsum (Fig. 3f). Tube feet 8–12 pairs, slightly decreasing in size and arranged closely posteriorly, anteriormost one or two pairs in the anterior body half (Fig. 3a, b); tube feet with tuberculous surface on extremities, supporting rods not numerous (Fig. 3d); terminal plates absent. Ossicles rods (Fig. 4); rods in body wall few or even absent, straight or slightly curved in shape, spinous at ends, length up to 350 µm (Fig. 4a); in tube feet curved rods, 100–650 µm

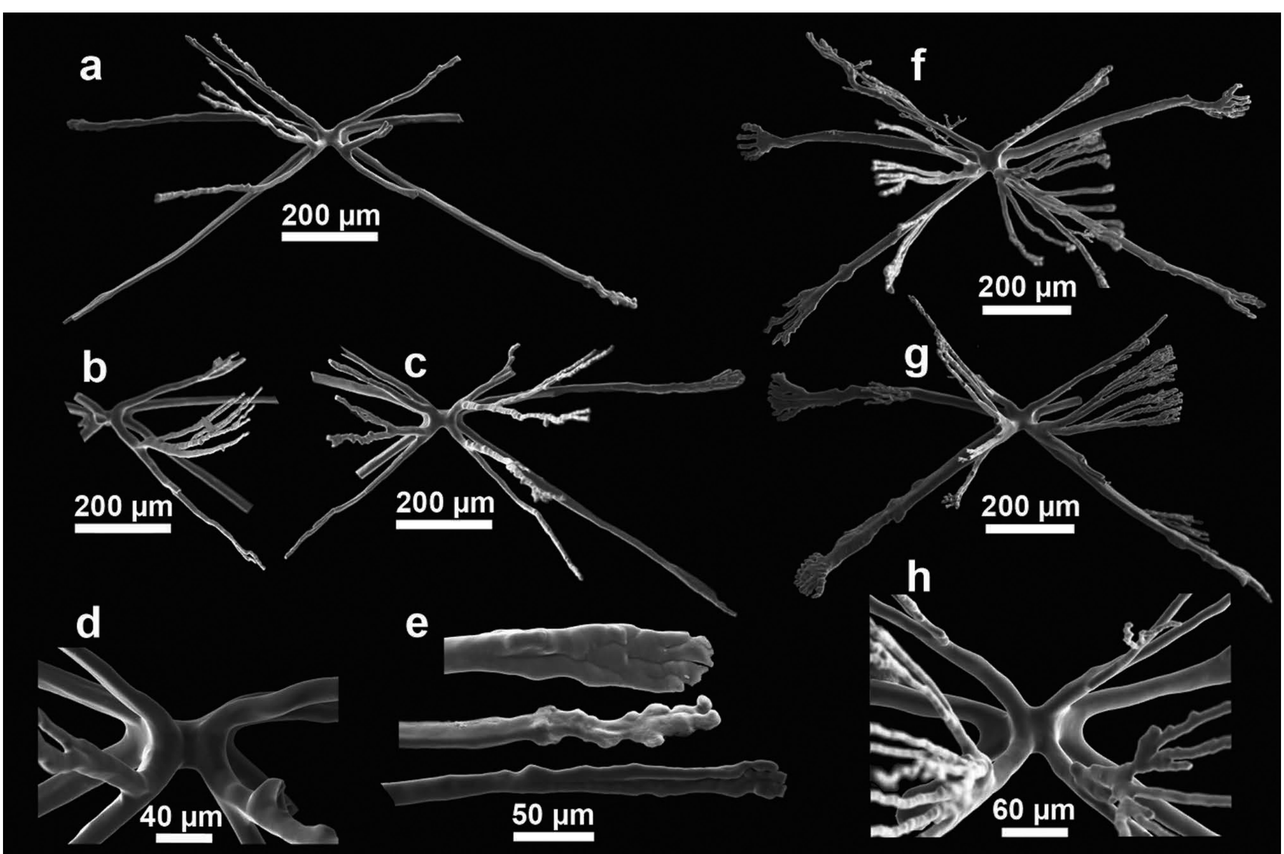

Fig. 5. Calcareous ring pieces: a–e, *Parvathuria dautovae* gen. et sp. nov., MIMB 47803; f–h, *Rhipidothuria racovitzai*, IORAS ECH02855.

long, from slender and mostly smooth to more robust and spinous (Fig. 4c, d); tentacle rods most variable in length and shape, slightly or strongly curved, from almost smooth to spinous, bigger rods sometime with additional processes, length up to 450 µm (Fig. 4b); ossicles in papillae similar in shape to those in tube feet, but generally smaller, up to 400 µm in length (Fig. 4e). Gonad well-developed even in smallest specimens; located on left dorsal side; in some specimens tubules expand into posterior third of dorsum; in males long dichotomously branched tubules with constrictions at the ends. Gonopore located on top of well-developed genital papilla located anteriorly of velum; genital papilla can reach 0.75 mm in length (Fig. 3g). Calcareous ring made of five isolated pieces; each piece with four arm pairs (Fig. 5a–e), two inner and two outer, inner arms branched in basal part or more distally; arms with enlarged, branched or even comb-like ends. Polian vesicle single.

Distribution: The North Pacific Ocean, Koko (depth 750–776 m) and Nintoku (depth 1161–1158 m) guyots.

Ecology: Found in aggregations in sedimented areas together with ophiuroids (Fig. 6). This species was repeatedly observed swimming.

Elpidiidae gen. et sp. indet.

(Fig. 8)

Material: MIMB 47796 (1 ex.); MIMB 47797 (1 ex.); MIMB 47798 (1 ex.); MIMB 47799 (1 ex.) (Table S1).

Description: Body length *in situ* up to 60 mm, in ethanol up to 45 mm; specimens very damaged. Colour *in vivo* from slightly violet in bigger specimens to almost transparent (Fig. 8a), colourless in smaller specimens; colour in ethanol greyish, skin semi-transparent. Tentacles were not possible to count due to preservation conditions; tentacle discs with short lobes. Velum consists of two pairs of papillae fused at

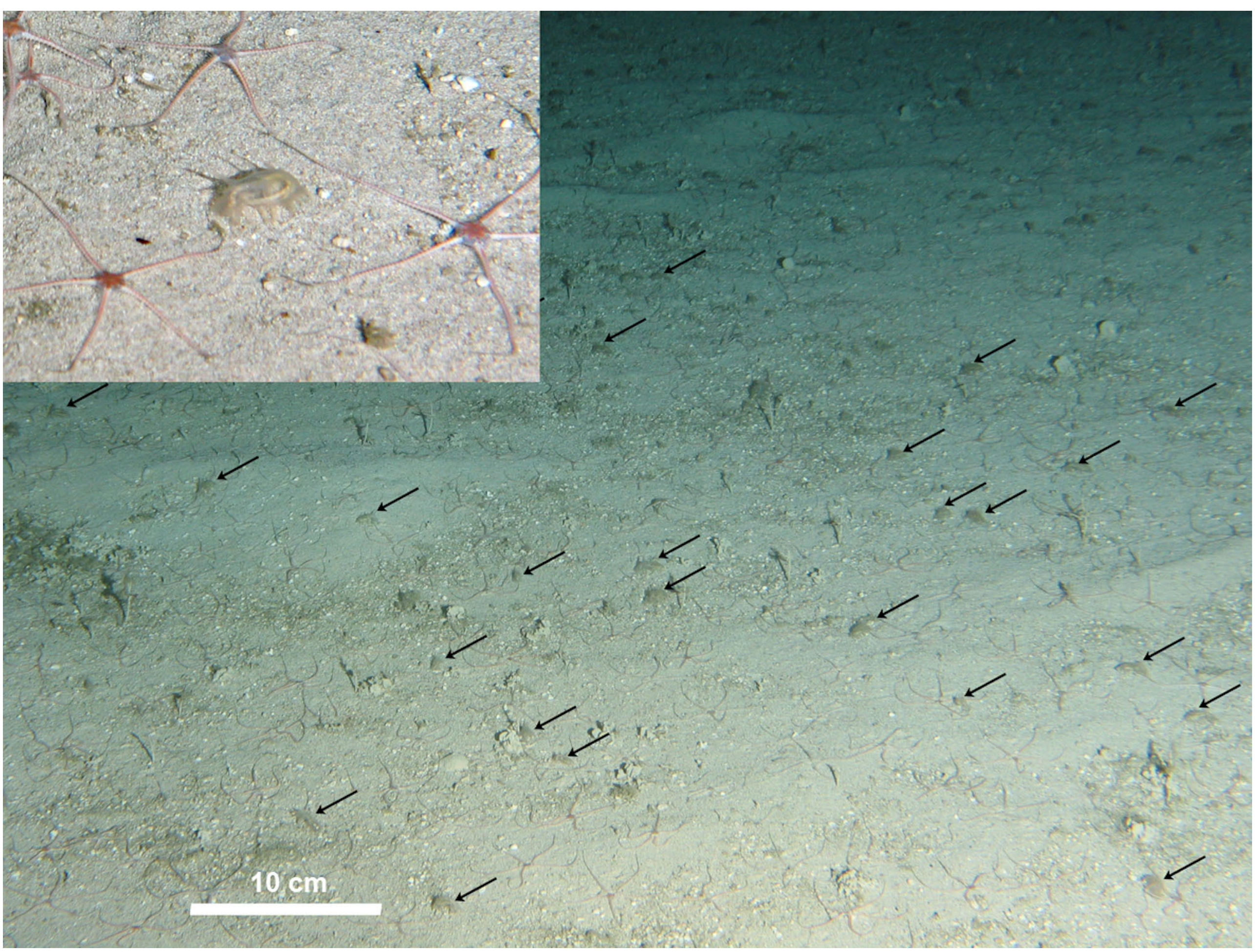

Fig. 6. Aggregation of *Parvathuria dautovae* gen. et sp. nov. (black arrows) and ophiuroids at Koko guyot (St. LV94-2). Image courtesy: NSCMB FEB RAS.

the basis. Free pair of long dorsal papillae in posterior half or one-third of dorsum (Fig. 8a, b). Tube feet ca. 12 pairs, with well-developed terminal plate, anteriormost tube feet located just behind velum, posteriormost tube feet partly fused into a brim. Ossicles rods (Fig. 8c), very scarcely arranged, almost absent on dorsum, on ventrum more numerous slender rods, up to 130 µm long, slightly bent or rarely straight, with pointed ends with several spines and small swallow in the middle. Gonad single, tubules arranged in a dense cluster. Madreporite located near gonopore, anteriorly of velum.

Remarks: Scarcely arranged ossicles and single free pair of papillae in posterior dorsal half are also known in *Penilpidia ludwigi* (von Marenzeller, 1893) and *P. desbarresi* Gebruk, Rogacheva et Pawson in Gebruk et al., 2013, from which Elpidiidae gen. et sp. indet. differs by rod ossicle morphology. Very few morphological characters distinguish these three species, therefore their relationships should be clarified using molecular data.

No closely related species was found based on molecular data: the closest match to *COI* was Elpidiidae (BIN BOLD:AAG4363, *p*-distance 10.14%), for *16S* sequence – *Amperima robusta* (Théel, 1882) GenBank KX856728 (87.65% similarity).

Distribution: The North Pacific Ocean, Koko guyot, depth 1368–1372 m, on rocks.

***Peniagone koko* sp. nov. Kremenetskaia et Gebruk**

(Fig. 9)
urn:lsid:zoobank.org:act:837EAFB5-BF07-4D46-93FA-4780057EAEEF

Type Material: *Holotype*: MIMB 48711, voucher ID LV1_1180, ca. 70 mm in length in the preserved state, 96% ethanol, coll. 21-Jul-2019, cruise LV86, St. LV86-6, ROV *Comanche 18*; locality Koko guyot, 35.7841°N, 171.0656°E, depth 1993–1983 m.

Paratype 1: MIMB 48712; voucher ID LV6_2348, in two fragments 55 mm and 40 mm in length in the preserved state; 96% ethanol; coll. 25-Aug-2021, cruise LV94, St. LV94-12, ROV *Comanche 18*; locality Koko guyot, 35.7891°N, 171.0489°E, depth 2231 m.

Paratype 2: MIMB 48710, voucher ID LV1_1175, 38 mm in length in the preserved state, 96% ethanol, coll. 21-Jul-2019, cruise LV86, St. LV86-6, ROV *Comanche 18*; locality Koko guyot, 35.7841°N, 171.0645°E, depth 2004 m.

Type locality: The North Pacific Ocean, Koko guyot, depth 1993–1983 m.

Etymology: The species name (a noun in apposition) refers to its type locality, Koko guyot.

Diagnosis: Body length up to 100 mm *in vivo*. Colour *in vivo* from reddish to pinkish. Skin thin, semi-

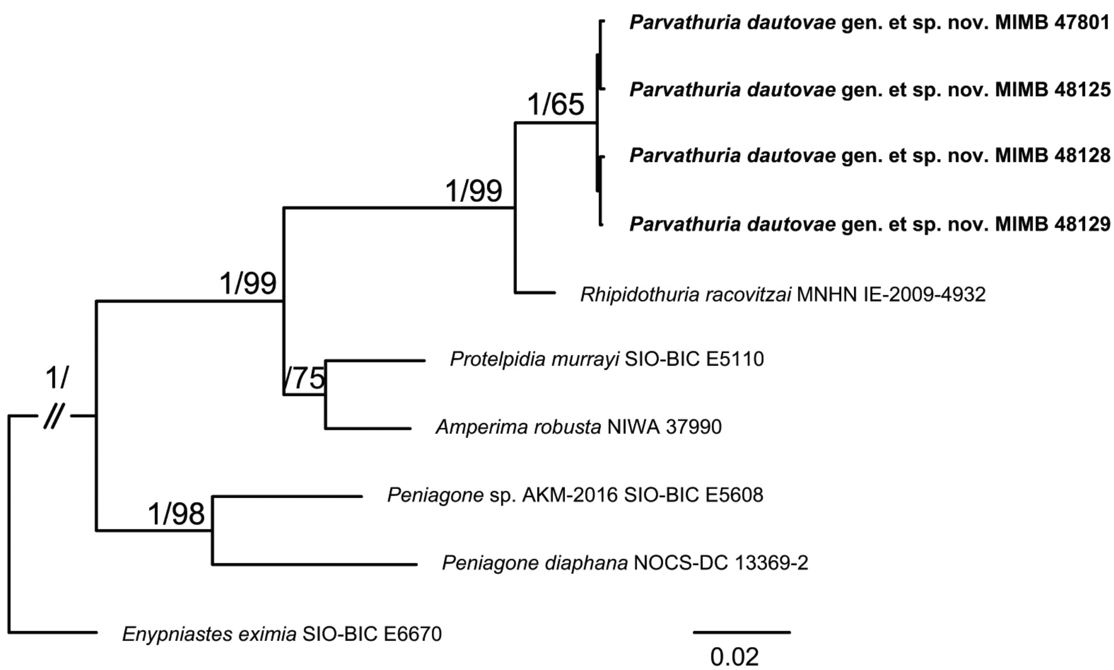

Fig. 7. BI tree inferred from concatenated *COI* and *18S* data (2664 positions). The analysis applied the following models: in BI GTR+G for *COI* position 1 and 2, GTR for *COI* position 3 and GTR+I for *18S*; in ML TIM1+G model for *COI* position 1 and 2, K81uf for *COI* position 3, and GTR+I for *18S*. Outgroup: *Enypniastes eximia*. Support values: PP ≥ 0.95/ BS ≥ 65. Vouchers, for which sequences were obtained in this study, are in bold. BI and ML were conducted for 10,000,000 generations and 300 replicates, respectively.

transparent, soft, with dense ossicle layer. Tentacles 10. Velum wide, consisting of two pairs of papillae; velum papillae fused along most their length; two pairs of very small free papillae behind velum. Tube feet 9–10 pairs in posterior body half; anterior three pairs of tube feet arranged more spaciously than others; posterior five-six pairs form narrow brim. Ossicles on dorsum gracile, *Peniagone*-type with four arms and four apophyses; arms slightly longer than apophyses, arms usually shorter than 200 µm in length; arms and apophyses with small spines. Ventral ossicles flatten *Peniagone*-type; arms spinous, almost horizontal; apophyses four, short, spinous.

Description: Body length up to 100 mm before preservation, 38–70 mm after preservation. Holotype (Fig. 9e) and both paratypes damaged: holotype with ruptured and extruded intestine; paratype MIMB 48712 in two fragments; paratype MIMB 48710 with damaged anterior part. Colour from reddish to pinkish (Fig. 9a–e); tentacle discs and anus area brightly coloured; colouration was also observed in some internal structures: ambulacral canals of velum and tentacles, water-vascular ring and radial canals; specimens preserved in ethanol were uniformly whitish or greyish. Skin thin, semi-transparent, soft, with dense ossicles layer. Body elongated, slightly swallowed in the middle (Fig. 9a). Tentacles 10, conspicuous in size; tentacle discs with two long lobes up to 3 mm in preserved state, the processes more developed on anteriormost tentacles (Fig. 9f). Velum up to 1/2 of body length, wider than body, consisting of two pairs of papillae fused at most their length; free papillae two pairs, little, behind velum, almost not visible in preserved state. Tube feet 9–10 pairs (10 pairs in holotype, 9 pairs in both paratypes), absent in anterior body half, tube feet size and space between them decrease towards posterior end, anterior first pair remarkably bigger than the second and other pairs; posterior five-six pairs of tube feet fused forming narrow brim. Dorsal ossicles gracile, central stem slender, 6–10 µm in diameter in big ossicles, arms and apophyses slightly spinous, arms rarely exceed 200 µm in length (Fig. 9g, h, i); arms strongly curved downward; apophyses four, up to 170 µm in length, slightly curved inward or almost straight, in some ossicles arms widely spaced (Fig. 9g, right). Ventral ossicles smaller than dorsal; arms up to 110 µm almost horizontal with four apophyses; apophyses short, 30–40 µm in length, spinous, spines spirally arranged (Fig. 9k); central stem up to 10 µm in diameter in big ossicles, with very small spines along its entire length (Fig. 9j). Tube foot ossicles rods, flat crosses and *Peniagone*-type ossicles (Fig. 9m); terminal plates absent; rods curved, not numerous, up to 700 µm in length, flat crosses smooth or with apophyses, arms slightly spinous, arms up to 220 µm; *Peniagone*-type ossicles with arms from almost horizontal to strongly downwardly curved up to 150 µm, four apophyses up to 110 µm; arms and apophyses spinous. Ossicles in tentacle stem of *Peniagone*-type with downwardly curved arms up to 150 µm in length, with four apophyses slightly curved inward or outward; arms and apophyses slightly spinous (Fig. 9l). Tentacle disc ossicles thin curved rods, up to 1.6 mm long, and flat crosses, often irregular in shape, with 0–4 apophyses, with arms usually not exceeding 150 µm; sometime crosses bigger, with arms up to 350 µm (Fig. 9n).

Gonad in female (paratype 1) grape-shaped, dichotomously branched; paratype 2 was probably also female with reduced gonad consisting of four very small branches, this reduction could indicate post-spawning reproduction stage. Calcareous ring pieces with 8–9 arm pairs. Stone canal solid, whitish, madreporite opens closely to gonopore. Polian vesicle single. Statocysts

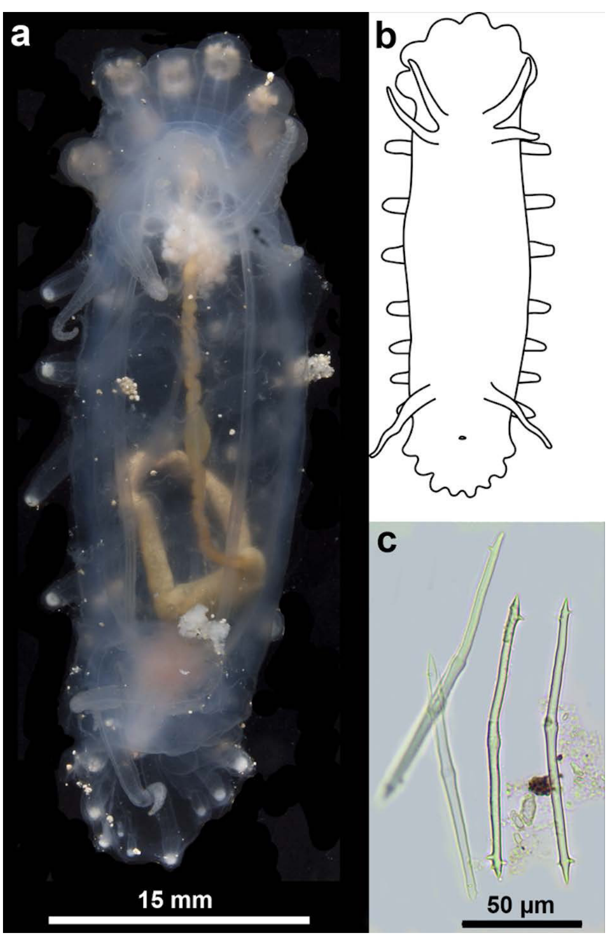

Fig. 8. Elpidiidae gen. et sp. indet.: a, specimen before preservation; b, schematic morphology from dorsal side showing arrangement of appendages; c, ventral rod-shaped ossicles (specimen MIMB 47799). Image courtesy: a, Kirill Minin.

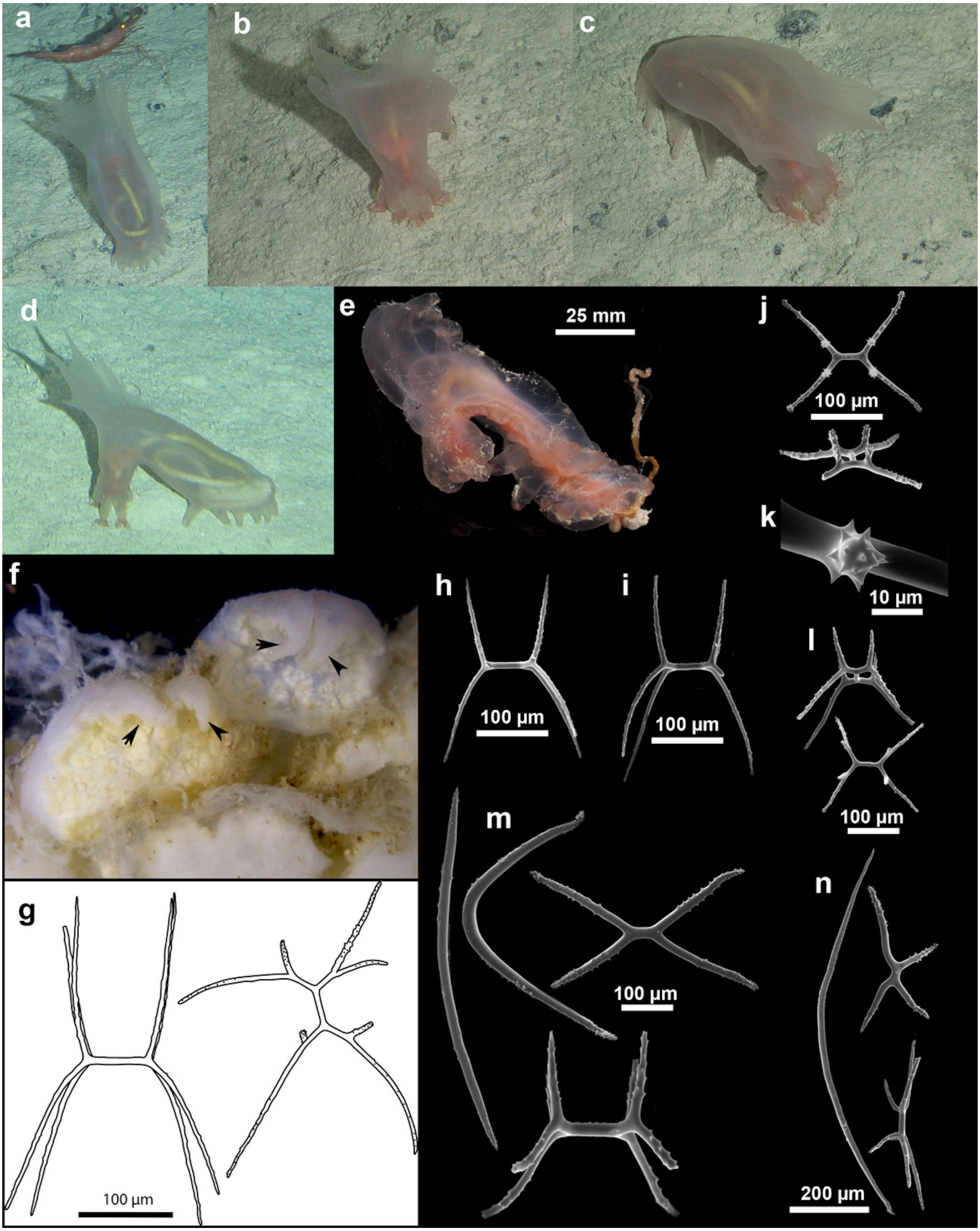

Fig. 9. *Peniagone koko* sp. nov.: a–d, *in situ* on Koko guyot (St. LV94-12); e, holotype before preservation; f, tentacle discs (arrows show long lobes); g–i, – dorsal ossicles of *Peniagone*-type, apophyses partly broken; j–k, *Peniagone*-type ventral ossicles; l, tentacle stem ossicles of *Peniagone*-type; m, tube foot ossicles rods, cross and of *Peniagone*-type; n, tentacle disc ossicles: rod, cross and of *Peniagone*-type. Image courtesy: a–d, NSCMB FEB RAS; e, Kirill Minin.

not found.

Remarks: Similar morphotype including a relatively short body, big tentacles and velum, bright colour and absence of tube feet in anterior body half, is known for *P. coccinea* Rogacheva et Gebruk in Rogacheva et al., 2013, *P. lugubris* Théel, 1882 and *P. purpurea* (Théel, 1882), from which *P. koko* sp. nov. differs by velum shape, colour (from *P. lugubris* and *P. purpurea* that are purple or dark violet) and ossicle size and morphology. Reddish colour is also known for *P. leander* Pawson and Foell, 1986 that differs from *P. koko* sp. nov. by shorter velum, reduction of anterior tube feet and bigger ossicles. Slender, gracile ossicles are known for *P. gracilis* (Ludwig, 1893), but in the latter arms in body wall ossicles are remarkably shorter than apophyses.

Peniagone koko sp. nov. is clearly morphologically distinct from all other North Pacific species of the genus. The new species differs from:

- *Peniagone dubia* (Djakonov et Saveljeva in Djakonov et al., 1958) by larger dorsal ossicles with four vertical apophyses;
- *P. minuta* Kremenetskaia et Gebruk in Kremenetskaia et al., 2021 by well-developed tube feet and larger velum;
- *P. mus* Djakonov, 1952 and *P. saveljevae* Kremenetskaia et Gebruk in Kremenetskaia et al., 2021 by less elongated body, larger velum, the presence of tube feet restricted to the posterior body half, and its distinct dorsal ossicle morphology (specifically, the ossicles of *P. mus* bear 1–4 closely spaced apophyses, while those of *P. saveljevae* are more robust);
- *P. vitrea* Théel, 1882 by less elongated body, larger velum and much smaller dorsal ossicles;
- *P. japonica* Ohshima, 1915 and all other northwest Pacific species except *P. purpurea* and *P. vitrea* by distinctive colouration, ranging from whitish to light orange in the compared species.

Based on phylogenetic analysis of the *COI* dataset (Fig. 10), *P. koko* sp. nov. is sister to a clade (*P. azorica* NMVF 308267 + (*P. coccinea* NMVF 296857 + *P. coccinea* NMVF 308188)) from the Australian Indian Ocean Territories (Australian IOT; Mackenzie et al. 2024). According to BOLD database the closest match is undescribed species from the South Atlantic off Argentina (BIN BOLD:ADM0802, *p*-distance 4.33%).

Distribution: The North Pacific Ocean, Koko guyot, depth 1993–2231 m.

Ecology: *Peniagone koko* sp. nov. was recorded on soft sediments and observed swimming. This species has conspicuous tentacles that are characteristic of actively swimming forms in this genus.

Family Laetmogonidae

Laetmogone cf. *wyvillethomsoni* Théel, 1879

(Fig. 11)

Laetmogone cf. *wyvillethomsoni* Théel, 1979 – Bribiesca-Contreras et al. 2022: 78–79, fig. 49.

Material: MIMB 48702 (1 ex.); MIMB 48703 (1 ex.); MIMB 48704 (1 ex.) (Table S1).

Description: Body length up to 300 mm on *in situ* photographs, 74–90 mm in preserved state. Skin semi-transparent, purple *in situ* (Fig. 11a), rough owing to dense ossicle layer. Tentacles 15, tentacle disc rounded, flattened, with small knobs; anterior tentacles have two bigger knobs on outer margin of tentacle disc (Fig. 11e). Anus terminal, on dorsal side. Papillae 7–10 pairs, conspicuous, arranged in two rows along dorsal radii, up to 80 mm long *in situ*, sometimes unpaired papillae present (Fig. 11b). Ventrolateral tube feet 16–19 pairs, conspicuous, narrowed towards extremities, with sucking discs at tips. Mid-ventral tube feet absent (Fig. 11c). Dorsal ossicles (Fig. 11f, g, m) wheels of a single type, up to 250 µm in diameter, largest wheels with 5–9 central rays (usually 6–7 rays), sometime rays irregularly branched; spokes 10–14 (usually 12–13), rim smooth, sometime not developed; smallest wheels 50 – 70 µm, usually with 4–5 central rays, 12–15 spokes. Ventral ossicles (Fig. 11i, j, k, n) wheels and rods, wheels up to 150 µm in diameter, usually 30–60 µm in diameter, with 4–5 central rays, with 13–16 spokes, rim smooth; rods numerous, up to 350 µm in length (most rods not exceed 220 µm in length), rods thick, smooth, curved, straight or slightly bent, with blunt ends. Ossicles in tube feet wheels, rods and terminal plates (Fig. 11h, l). Ossicles in tentacle stems wheels; smaller wheels numerous, 50–70 µm in diameter, with 5 central rays; bigger wheels reached 220 µm in diameter, of the same morphology as smaller wheels, but with fewer spokes, central rays 4–7 (mainly 5–6), spokes 9–11. Ossicles in tentacle disc rods and wheels; wheels 20–140 µm in diameter, with 4–7 central rays (usually 5–6), bigger wheels with 8–11 spokes; rods from thin to thick, thick rods often with blunt end, thin rods usually with pointed, slightly spinous ends.

Remarks: The phylogenetic *COI*-based analysis of all available data for the *Laetmogone wyvillethomsoni* species complex (Fig. 12) placed ESC specimens within a well-supported clade with *L.* cf. *wyvillethomsoni* CCZ_062 from Clarion-Clipperton Fracture Zone area (CCFZ), IDSSE-EEB-HS48 and IDSSE-EEB-HS49 from the South China Sea (PP = 0.99, ML = 91). The *COI* haplotype network supported the well-defined groupings for Pacific, Antarctic I and Antarctic II localities. The Pacific haplogroup includes two haplotypes. Specimens MIMB 48702, CCZ_062, IDSSE-EEB-HS48 and IDSSE-EEB-HS49 belong to the same haplotype. The average between group *p*-distances, based on *COI* sequence data, were as follows: 4.67% (between Pacific and Antarctic I haplogroups), 3.84% (Pacific and Antarctic II) and 5.69% (Antarctic I and Antarctic II). These values support the hypothesis that *L. wyvillethomsoni* constitutes a species complex (O'Loughlin et al. 2011; Bribiesca-Contreras et al. 2022; Xiao and Zhang 2025). However, it is currently unclear whether any of the identified haplogroups corresponds to *L. wyvillethomsoni* s. str. Revision of *L. wyvillethomsoni* complex requires re-examination of the syntypes of *L. wyvillethomsoni.*

Distribution: The Pacific Ocean, Koko guyot, depth 1969–2240 m, South China Sea (depth 3566–3568 m) and a seamount in the CCFZ (APEI 7) area, depth 3132 m.

Ecology: Found mainly on soft sediments, sometime with pebbles. Colonies of hydroids were observed on all three examined specimens, mainly on tentacles, anterior body part and anterior papillae (Fig. 11d).

Laetmogonidae gen. et sp. indet. 1

(Fig. 13)

Material: MIMB 48705 (1 ex.) (Table S1).

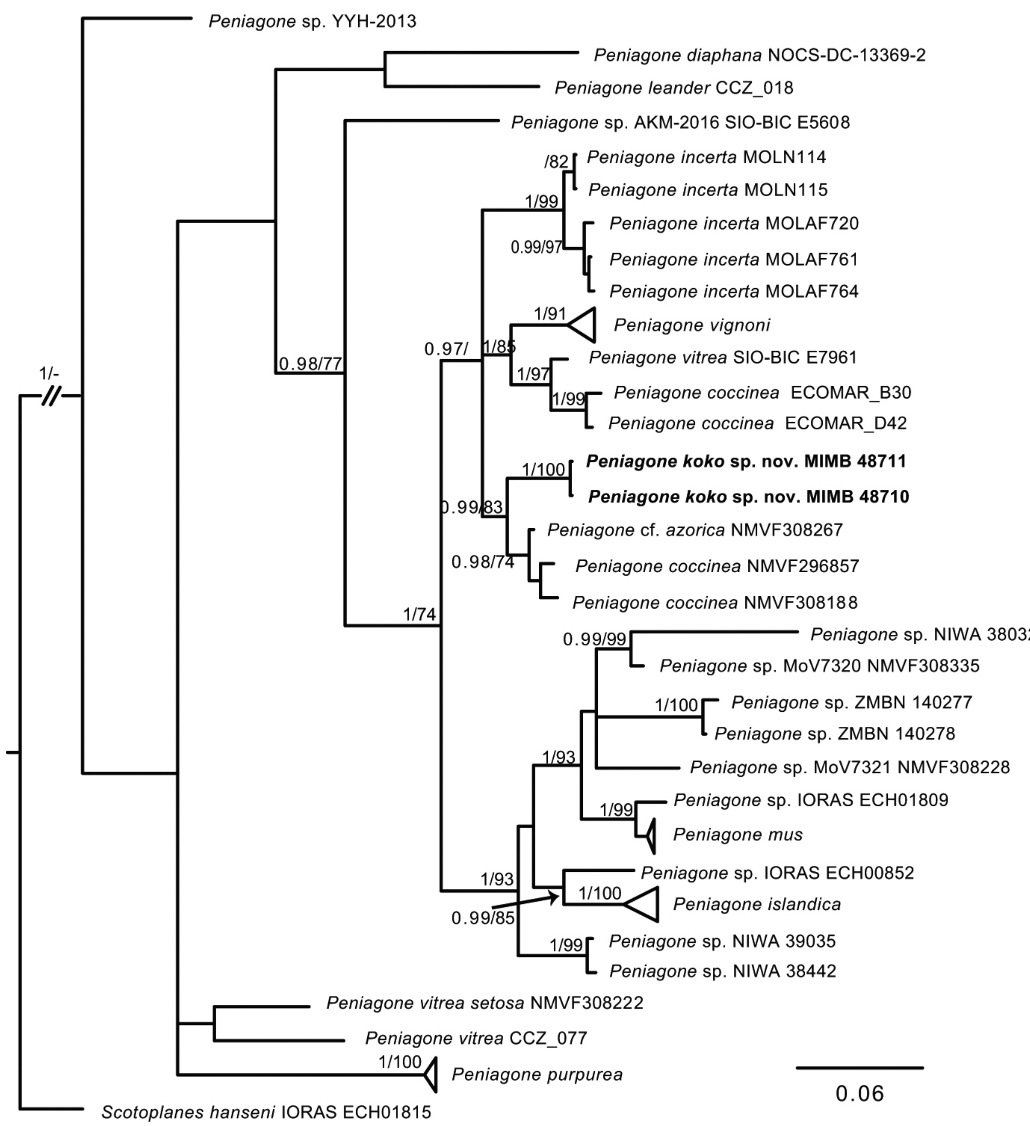

Fig. 10. BI tree of *Peniagone* inferred from *COI* data (840 positions) using GTR+I+G model for all the partitions in BI; in ML analysis TN93+I+G model for *COI* positions 1 and 2, and K81UF+I+G for *COI* position 3. Outgroup: *Scotoplanes hanseni*. Support values: PP ≥ 0.95/ BS ≥ 75. Sequences obtained in this study are in bold. BI and ML were conducted for 20,000,000 generations and 15,000 replicates, respectively.

Description: Body length approximately 60 mm in ethanol; specimen strongly damaged. Skin *in situ* transparent (Fig. 13), light violet, tentacle discs reddish, in ethanol skin whitish. Dorsal papillae several pairs, long. Anterior end framed by papillae. Ventrolateral tube feet small, numerous. Mid-ventral tube feet absent. Ossicles exclusively small wheels, with central primary cross, usually less than 100 µm in diameter (Fig. 13).

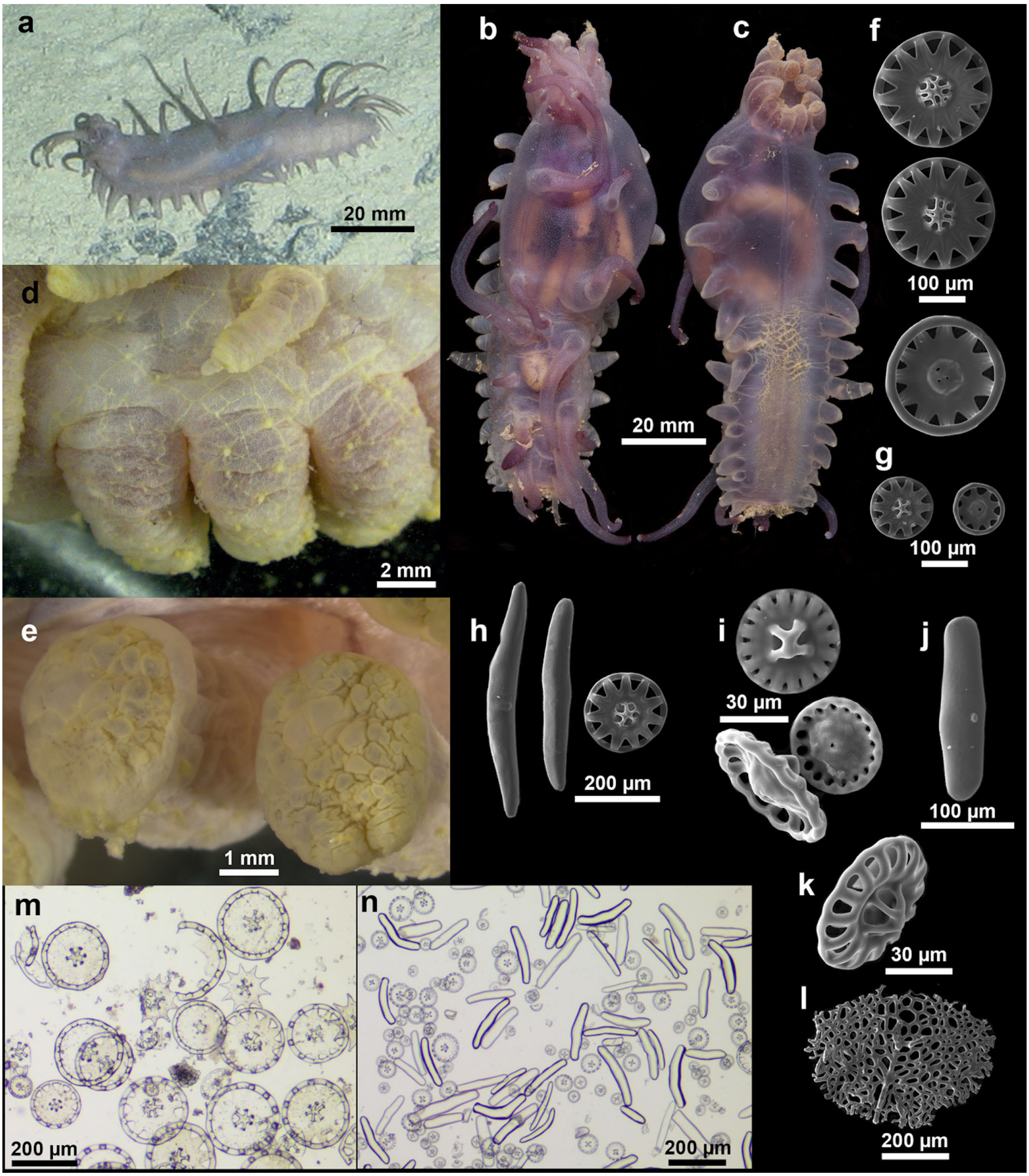

Fig. 11. *Laetmogone* cf. *wyvillethomsoni*: a, *in situ* on Koko guyot (St. LV94-12); b–n, specimen MIMB 48704: b, c, dorsal and ventral view, *in vivo*; d, anterior body part with hydroid colonies on tentacles, body wall skin and papillae; e, tentacle discs; f, g, m, dorsal wheel ossicles; h, tube feet ossicles rods and wheel; i, j, k, n, rod and wheel ossicles from ventrum; l, tube foot terminal plate. Image courtesy: a, NSCMB FEB RAS; b, c, Kirill Minin.

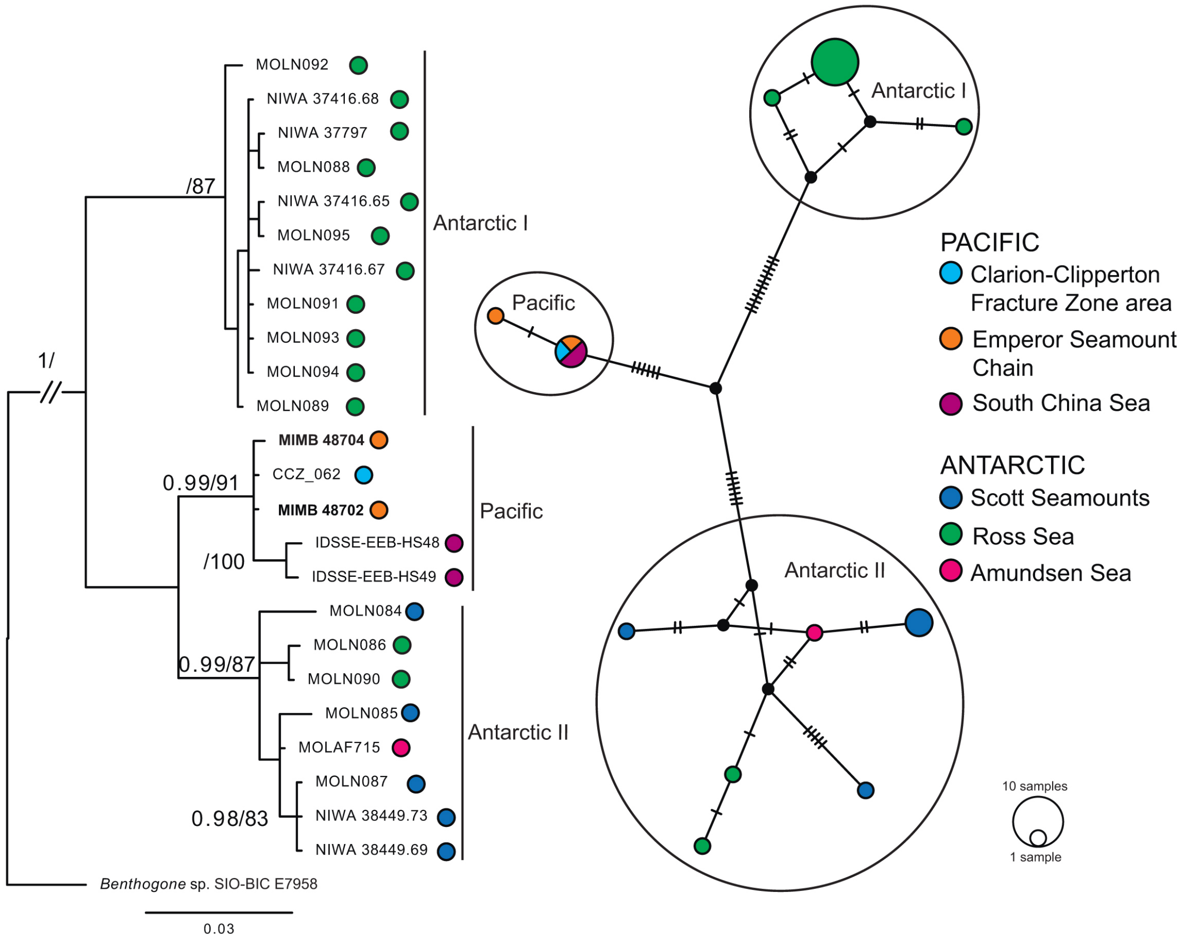

Fig. 12. BI tree (left) and TCS haplotype network of *Laetmogone wyvillethomsoni* species complex inferred from *COI* data (840 and 435 positions, respectively). Vouchers, for which sequences were generated in this study, are in bold. Outgroup: *Benthogone* sp. Support values: PP ≥ 0.95/ BS ≥ 75. BI and ML were conducted for 10,000,000 generations and 512 replicates, respectively, using HKY model for *COI* position 1 and 2, and TIM1+G (ML) or GTR+G (BI) for *COI* position 3.

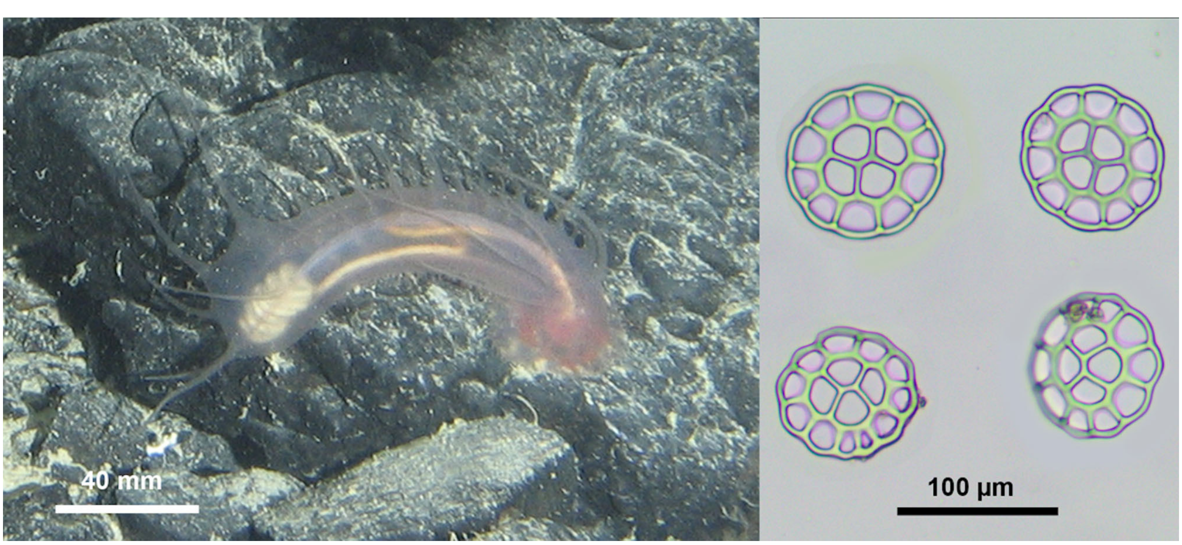

Fig. 13. Laetmogonidae gen. et sp. indet. 1: specimen MIMB 48705, *in situ* (left); dorsal small wheel ossicles (right). Image courtesy: left, NSCMB FEB RAS.

Remarks: According to BOLD database, the closest match for *COI* data is *Benthogone* sp. from the East Pacific (BIN BOLD:AFT2165, *p*-distance 7.53%).

Distribution: Single record in the North Pacific Ocean, Kinmei guyot, depth 1894 m, rocky substrate.

Laetmogonidae gen. et sp. indet. 2

Material: MIMB 48706 (1 ex.) (Table S1).

Remarks: Single specimen is represented by poorly preserved fragments. Identification is based on *COI* and *16S* sequence data. Closest match in the BOLD database is *Benthogone* sp. from the East Pacific (BIN BOLD:AFT2165, *p*-distance 11.95%).

Distribution: Single record on in the North Pacific Ocean, Kinmei guyot, depth 1852 m.

Order Holothuriida
Family Mesothuriidae
Mesothuria carnosa Fisher, 1907
Mesothuria carnosa Fisher, 1907: 679–683, pl. LXX(4a–f), LXXI(4a)
(Fig. 14)

Material: MIMB 48707 (1 ex.) (Table S1). Another specimen was observed at the same station.

Description: Body length approximately 20 cm in ethanol. Colour whitish *in situ* (Fig. 14a–b), brownish in preserved state. Skin rough with dense ossicle layer. Body form cylindrical, ventral side slightly flattened. Mouth ventral, anus subventral. Tentacles fully retracted into oral cavity. Tube feet with sucking discs, arranged scarcely on dorsum, more abundant in posterior dorsal half, numerous on ventrum especially its posterior 1/5; biggest tube feet located in bands along ventrolateral radii. Dorsal ossicles tables (Fig. 14c), table disc of irregular shape, with one crown of perforations, with 7–8 bigger perforations and additional smaller perforations, sometime smaller perforations absent and table disc round; spire low, shorter or equal to disc diameter in height, built up of four apophyses, one transverse beam in the middle and four beams on the top, spire ends with four short, smooth teeth, each tooth with few small spines on top. Ventral ossicles of the same type and size as on dorsum; some tables with spire with few spines on teeth. Gonad in a single tuft. Polian vesicle single.

Remarks: According to *COI*, *Mesothuria* sp. was recovered in the same BIN (BOLD:AEO8167) with the specimen NMV-F296863 identified as *Mesothuria gargantua* Deichmann, 1930 from the Australian IOT (Mackenzie et al. 2024; *p*-distance 1.06%).

Distribution: The North Pacific Ocean, Hawaii Islands, depth 406–858 m and Koko guyot, depth 2135 m; Australian IOT, depth 2189–2264 m.

Ecology: Observed on soft sediments.

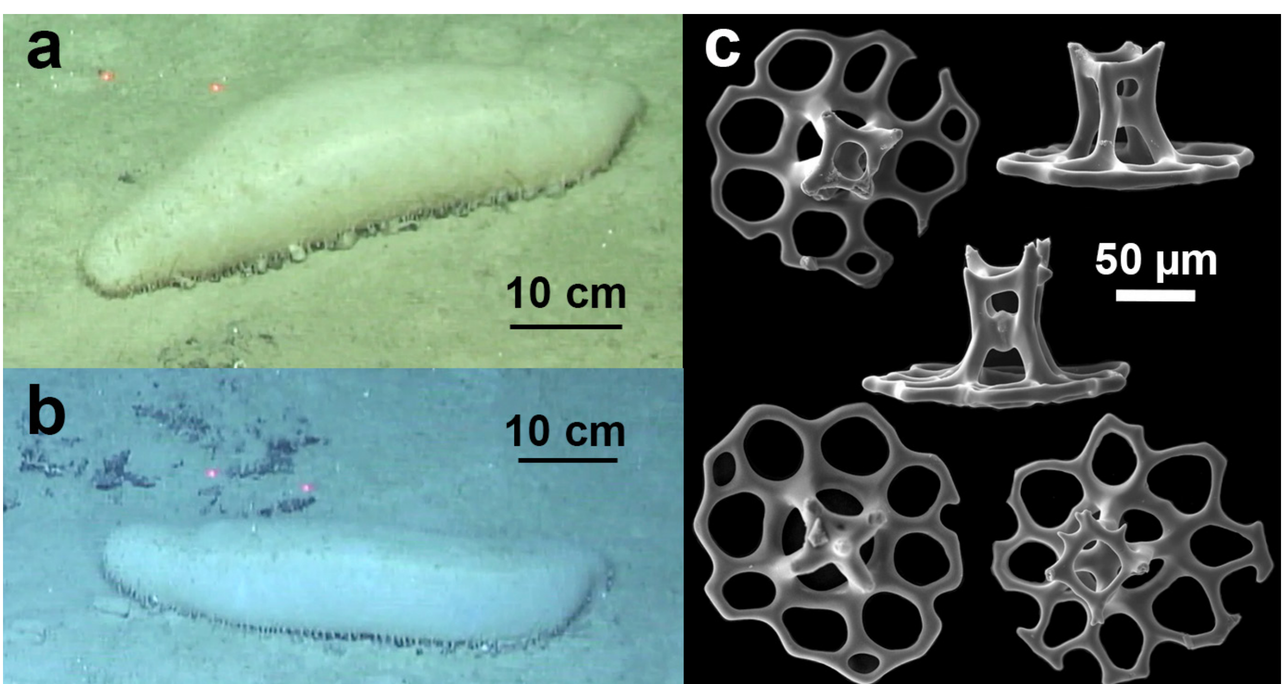

Fig. 14. *Mesothuria carnosa* Fisher, 1907: a, *in situ* (specimen MIMB 48707); b, *in situ* (not examined specimen from the same locality); c, dorsal table ossicles. Image courtesy: a–b NSCMB FEB RAS.

Order Synallactida
Family Synallactidae
Bathyplotes sp.
(Figs. 15, 19b, S1a)

Material: MIMB 47789 (1 ex.); MIMB 47790 (1 ex.); MIMB 47791 (1 ex.); MIMB 47792 (1 ex.); MIMB 47793 (1 ex.); MIMB 4774 (1 ex.) (Table S1).

Description: Body length 100–120 mm before preservation, 70–90 mm in ethanol. Colour from reddish to pinkish in live or freshly caught specimens (Fig. 15a), from whitish to greyish in ethanol. Body surrounded by narrow ventrolateral brim contracted in ethanol preserved specimens. Skin tight. Tentacles 15–19. Dorsal papillae in two rows along dorsal radii, most of papillae short, several papillae remarkably longer than others (2–3 pairs, sometime can be unpaired); few anteriormost pairs of dorsal papillae slightly longer than other short papillae. Tube feet along both ventrolateral radii in 1–2 rows, slender; mid-ventral tube feet absent. Dorsal ossicles four-armed tables; arms usually not exceed 150 µm in length, perforated at the ends, sometime arm ends connected by lateral processes; spire made of four processes (Fig. 15b, c). Ventral tables smaller, with disc 40–60 µm in diameter and spire up to 90 µm long (Fig. 15d). Papillae tables and table-crosses with higher spire than on dorsum and ventrum (Fig. 15e, f).

Remarks: The examined specimens probably represent a new species. It is distinct by combination of the following characters: three pairs of papillae longer than others, naked mid-ventral radius, pinkish colour and absence of C-shaped ossicles.

Six sequences of *COI* and six of *16S* were obtained. *COI* sequences were identical and assigned to the BIN BOLD:AEO6442. According to BOLD, the closest species is *Bathyplotes* sp. MoV7341 from Australian IOT (Mackenzie et al. 2024; BIN BOLD:AGY0647, *p*-distance 2.12%). This Australian species formed a sister clade to the clade of *Bathyplotes* sp. from the ESC, though this sister relationship received poor support in both BI and ML analyses (Fig. S1a).

Distribution: The North Pacific Ocean, Koko and Kinmei guyots, depth 1363–1881 m.

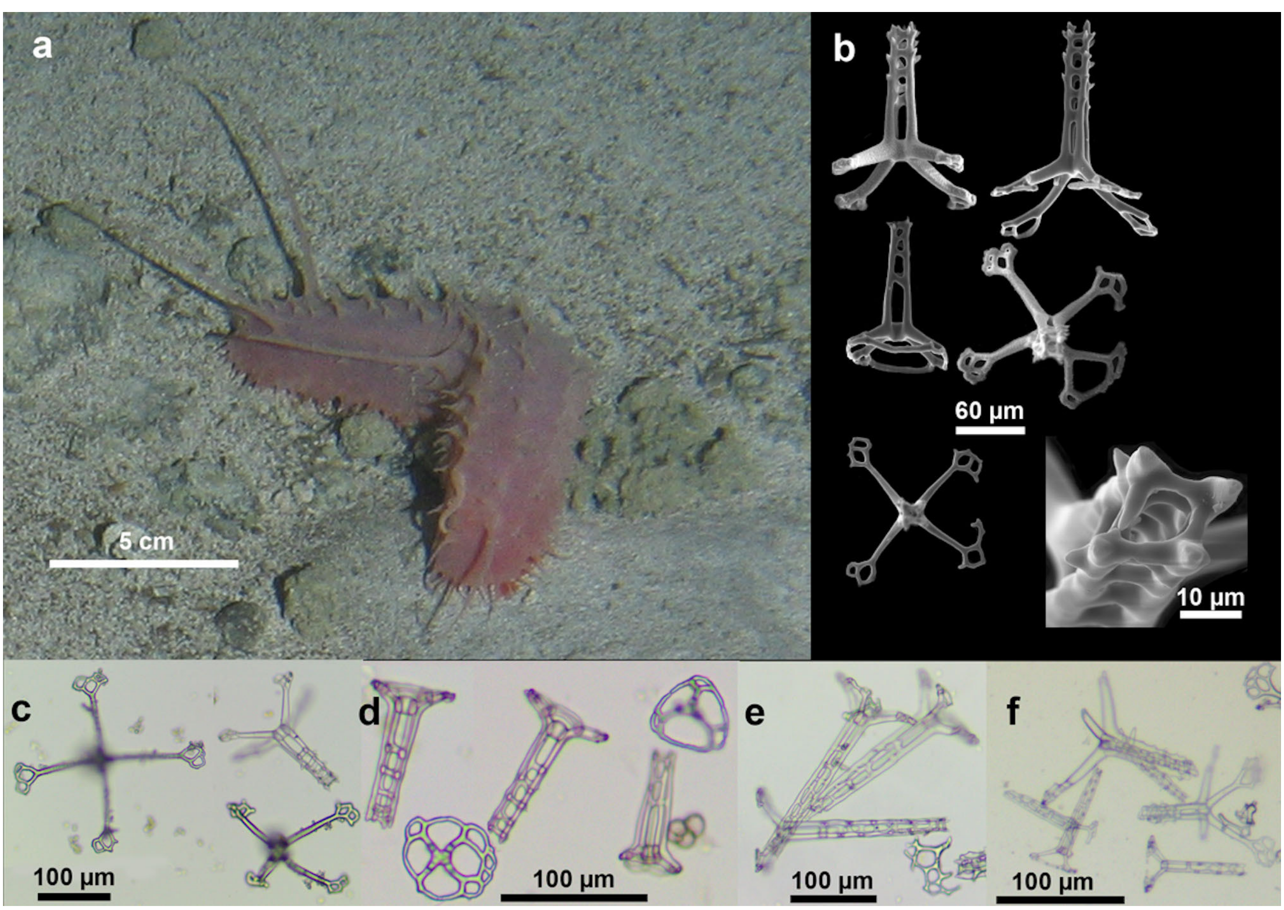

Fig. 15. *Bathyplotes* sp.: a, *in situ* (MIMB 47789); b, c, dorsal ossicles tables and table-crosses (b, MIMB 47789; c, MIMB 47793); d, ventral tables (MIMB 47793); e, f, papilla tables and table-cross ossicles. Image courtesy: a, NSCMB FEB RAS.

Ecology: Commonly occurred on Koko guyot both on soft and rocky substrates.

***Hansenothuria* sp. 1**
(Figs. 16, S1b, c)

Material: MIMB 48130 (1 ex.); MIMB 48131 (1 ex.); MIMB 48693 (fragments of 2 ex.); MIMB 48694 (1 ex.); MIMB 48695 (1 ex. and fragments); MIMB 48696 (1 ex.); MIMB 48697 (1 ex.); MIMB 48698 (1 ex.); MIMB 48699 (1 ex.); MIMB 48700 (1 ex.) (Table S1).

Description: Body length up to 150 mm, usually ca. 100 mm *in situ*, and up to 46 mm in ethanol. Colour from light purple to light pinkish (Fig. 16a–c); in ethanol whitish, tentacles yellowish. Body covers gelatinous, semi-transparent. Body slightly concave dorsally and flattened ventrally, surrounded by ventrolateral brim with short free tips of papillae. Dorsal papillae short, slender, in 1–2 rows along each dorsal radius. Tentacles 18, retracted in some specimens. Anus ventral. Mid-ventral tube feet absent. Body wall ossicles spinous rods, up to 200 µm in length, scarcely distributed (Fig. 16e–f), shape from straight to curved, sometime irregularly branched. Tentacle ossicles rods curved and knobbed, up to 300 µm in length. Tube feet lack or lost ossicles except for terminal plates (Fig. 16d).

Remarks: Examined specimens were assigned to *Hansenothuria* based on presence of the following characters: body arched dorsally and flattened ventrally, gelatinous fragile skin, dorsal papillae short, slender and numerous in a single row along each dorsal radius, naked mid-ventral radius, ossicles rod-shaped, curved and tuberculous. *Hansenothuria* sp. 1 differs from *Hansenothuria benti* Miller and Pawson, 1989, the type species of this monotypic genus, by smaller size, reaching 230 mm in *H. benti*, more transparent skin and lighter papilla colour. No molecular data is available for *H. benti* therefore the affinity of this species cannot be clarified using the phylogenetic analysis.

Eight and four sequences were obtained of *16S* and *COI*, respectively. The latter were assigned to the BIN BOLD:AET3377 (within BIN maximum *p*-distance 0.64%). According to BOLD, the closest neighbour was a specimen from French Polynesia designated as Elasipodida (BIN BOLD:ABA6534, *p*-distance 3.29%); the latter identification was probably a result of contamination or misidentification.

According to phylogenetic analysis (Fig. S1b), the clade of *Hansenothuria* sp. 1 was sister to the clade containing *Hansenothuria* sp. 2 MIMB 48717 from the Bering Sea and Synallactidae CCZ_061 from the CCFZ area. The latter species probably also belongs to *Hansenothuria* as it is characterized by the convex dorsum with two rows of short, slender papillae, tapered posterior part, and robust curved rod ossicles.

Distribution: The North Pacific Ocean, Koko guyot, depth 1372–1422 m.

Ecology: This species was repeatedly observed swimming at St. LV86-17 and St. LV94-11. Swimming achieved through the powerful strokes of the anterior and posterior ends of the body, in S-shaped manner. Commonly occurred on Koko guyot on rocky substrates.

***Hansenothuria* sp. 2**
(Figs. 17, S1b)

Material: MIMB 48701 (1 ex., strongly damaged) (Table S1).

Description: Specimen was preserved in a very bad condition and probably lost most of its skin, therefore the external morphology cannot be revealed with confidence. Ossicles tuberculous, curved rods, found only in tentacles (Fig. 17c). Body wall, papillae and tube feet ossicles absent or lost.

Remarks: Two morphospecies of *Hansenothuria* sp. were observed and collected from this locality (Fig. 17a, b), and it is not clear which morphotype corresponds to the specimen MIMB 48701 because of preservation condition.

Remarks: Two sequences (*COI* and *16S*) were obtained. Closest match in BOLD database was Synallactidae stet. CCZ_061 (GenBank Acc. ON400688) from a seamount in CCFZ area (*p*-distance 6.17%). The phylogenetic *COI*-based analysis recovered *Hansenothuria* sp. 2 in an averagely supported clade (PP = 0.96, BS = 78) with Synallactidae stet. CCZ_061 ON400688 and *Hansenothuria* sp. MIMB 48717 from the Bering Sea (Fig. S1b). *COI*-based *p*-distance between *Hansenothuria* sp. 2 and *Hansenothuria* sp. MIMB 48717 was 7.15% suggesting they represent separate species. Sea also *Remarks* for *Hansenothuria* sp. 1.

Distribution: The North Pacific Ocean, Koko guyot, depth 1880–1881 m.

Ecology: Occurred on soft substrate.

***Synallactes* sp.**
(Figs. 18, 19c)

Material: MIMB 48713 (1 ex.); MIMB 48714 (1 ex.); MIMB 48715 (1 ex.); MIMB 48716 (1 ex.) (Table S1).

Description: Body length 60–120 mm *in vivo*. Colour from whitish (in smaller specimen, see Fig. 18d, e) to brownish (Fig. 18a, b). Body subcylindrical, with flat ventral side. Tentacles 18. Dorsal papillae conspicuous, in double rows along each dorsal radius,

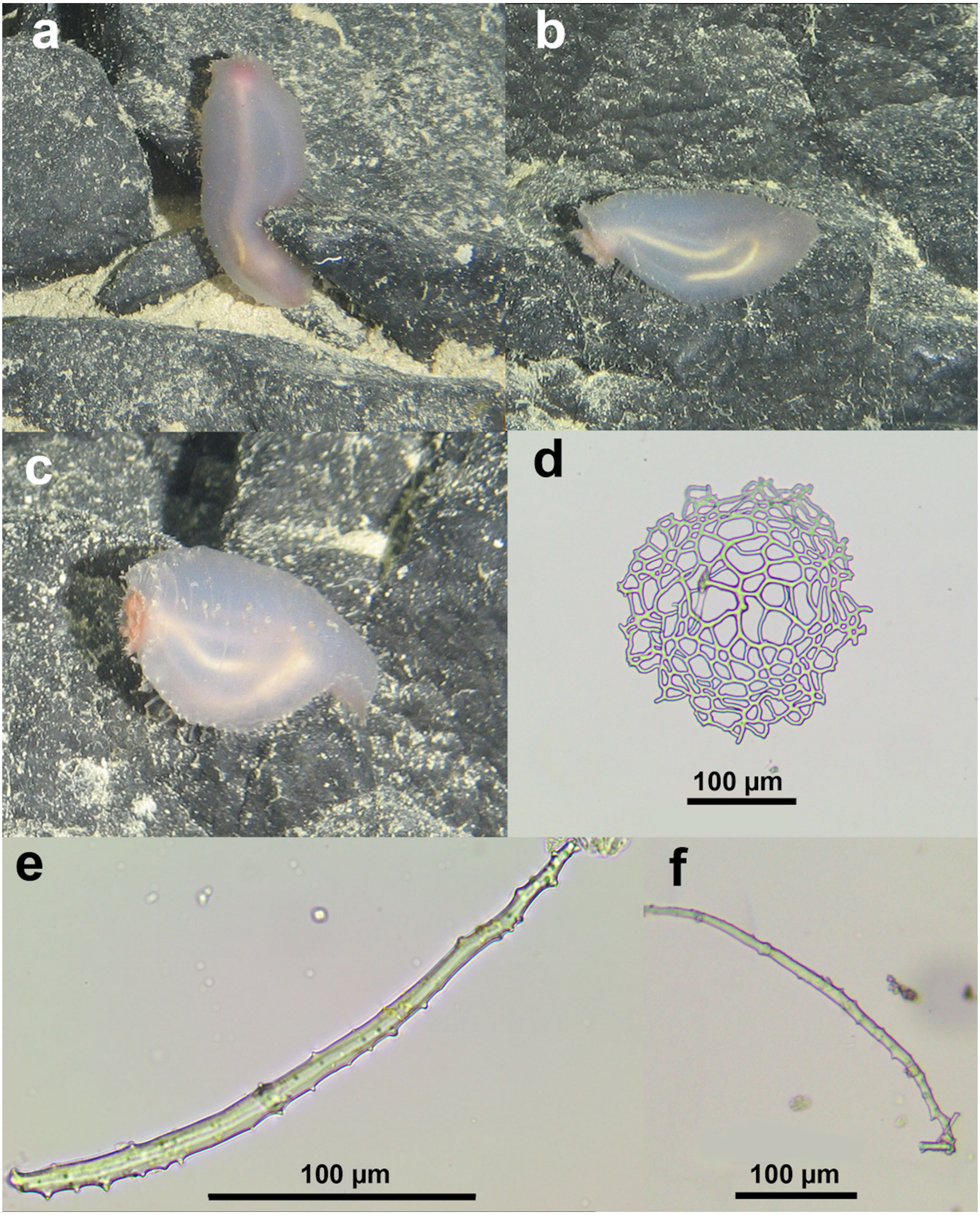

Fig. 16. *Hansenothuria* sp. 1: a–c, *in situ* at St. LV94-4; d, terminal plate from tube foot; e–f, tentacle rod ossicles. Image courtesy: a–c, NSCMB FEB RAS.

and in a single row along ventrolateral radii. Tube feet located in 2–4 rows along both ventrolateral radii; mid-ventral tube feet conspicuous, arranged in 2–3 rows. Dorsal ossicles (Fig. 18f–k) four- or three-armed tables, with perforations on distal parts of arms; sometime arms with dichotomous branches, rarely arms branch irregularly; arms up to 200 µm in length; spire up to 140 µm divided into three spiny processes, which can be subdivided; in some tables branches joint at the top of spire by cross beams. Ventral ossicles tables, smaller than dorsal, with 3–4 arms additionally branching and perforated distally. Papillae ossicles tables and rods; tables bigger and more perforated than on dorsum, arms up to 250 µm; rods curved, 35–40 µm in length, with spines or small perforated processes. Internal anatomy (examined in MIMB48716) features (i) a single Polian vesicle; (ii) gonads arranged in two tufts at both sides of dorsal mesentery consisting of long thin constricted tubules and (iii) a stone canal attached to the dorsal mesentery.

Remarks: Ventral side of the specimen MIMB 48715 was covered by dense colony of hydroids (Fig. 18c). Based on papillae and tube feet arrangement, the ESC specimens resemble *Synallactes nozawai* Mitsukuri, 1912 in presence of 6 rows of dorsal papillae and 3- and 4-armed dorsal ossicle, but differ in body colour (*S. nozawai* has violet tint on dorsum) and by absence of big rods on papillae and more numerous tube feet.

Three sequences of *COI* and three of *16S* were obtained; *COI* sequences were assigned to BIN BOLD:ABA2309 (within BIN maximum *p*-distance 0.86%). This BIN also includes 21 private records from off Australia identified as *Synallactes challengeri* (Théel, 1886). The latter differs from ESC specimens in having 2–5 Polian vesicles and smaller body wall ossicles with relatively long spire: tables ca. 60 µm in diameter and spire ca. 80 µm long. According to BOLD, the closely related species is *Synallactes* sp. from the East Pacific (BIN BOLD:ADM0329, *p*-distance 2.04%).

Distribution: Nintoku and Ojin guyots, 1110–1161 m and off Australia (depth unknown).

Ecology: On ESC this species was recorded on rocky substrates (Fig. 19c).

DISCUSSION

Faunistic composition

Overall, 16 species of Holothuroidea were identified from four ESC guyots, Kinmei, Koko, Nintoku and Ojin, at depths of 750–2240 m (Table 1). Among them only three were assigned to the known species and three more described as new to science. Other species either are tentatively new to science or their identification requires revision of other related species. The most diverse were Elasipodida (8 species) and Synallactida (5 species). The family Laetmogonidae was the most speciose among Elasipodida, including two species of *Pannychia* Théel, 1882, one species of the *Laetmogone wyvillethomsoni* complex and two unidentified species. Interestingly, the two latter were found at same station on Kinmei guyot and both occurred on rocky substrate.

Among all found species, only four are known outside the ESC area; all are found in the Pacific Ocean, and one of these is also present in the Indian Ocean

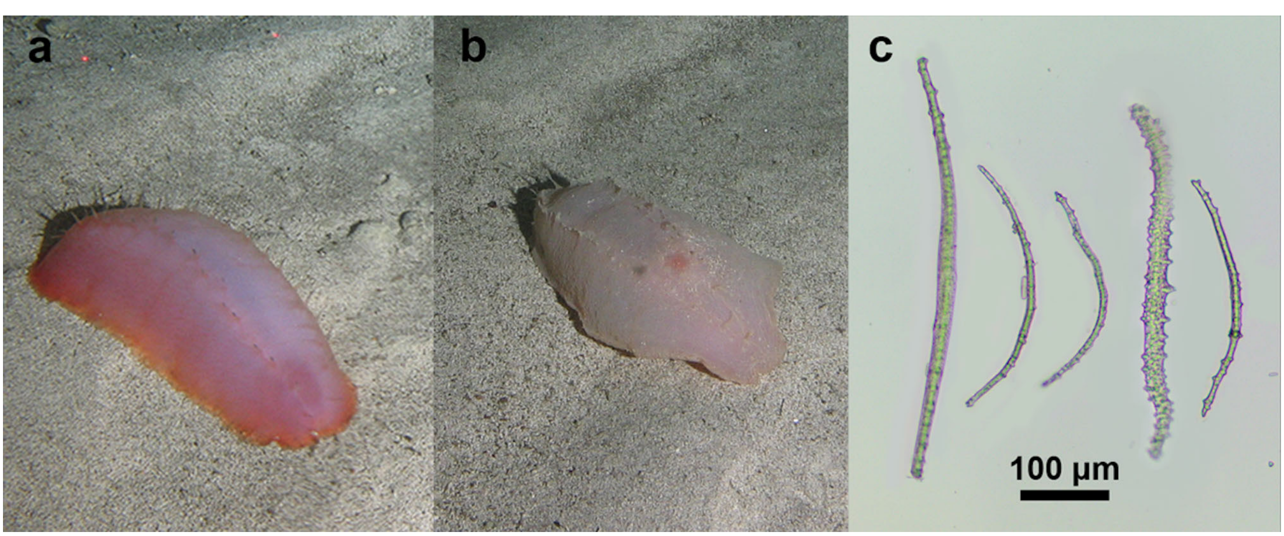

Fig. 17. Two morphospecies of *Hansenothuria* observed at St. LV86-11 (a, b); c, *Hansenothuria* sp. 2, tentacle rod ossicles. Image courtesy: a, b, NSCMB FEB RAS.

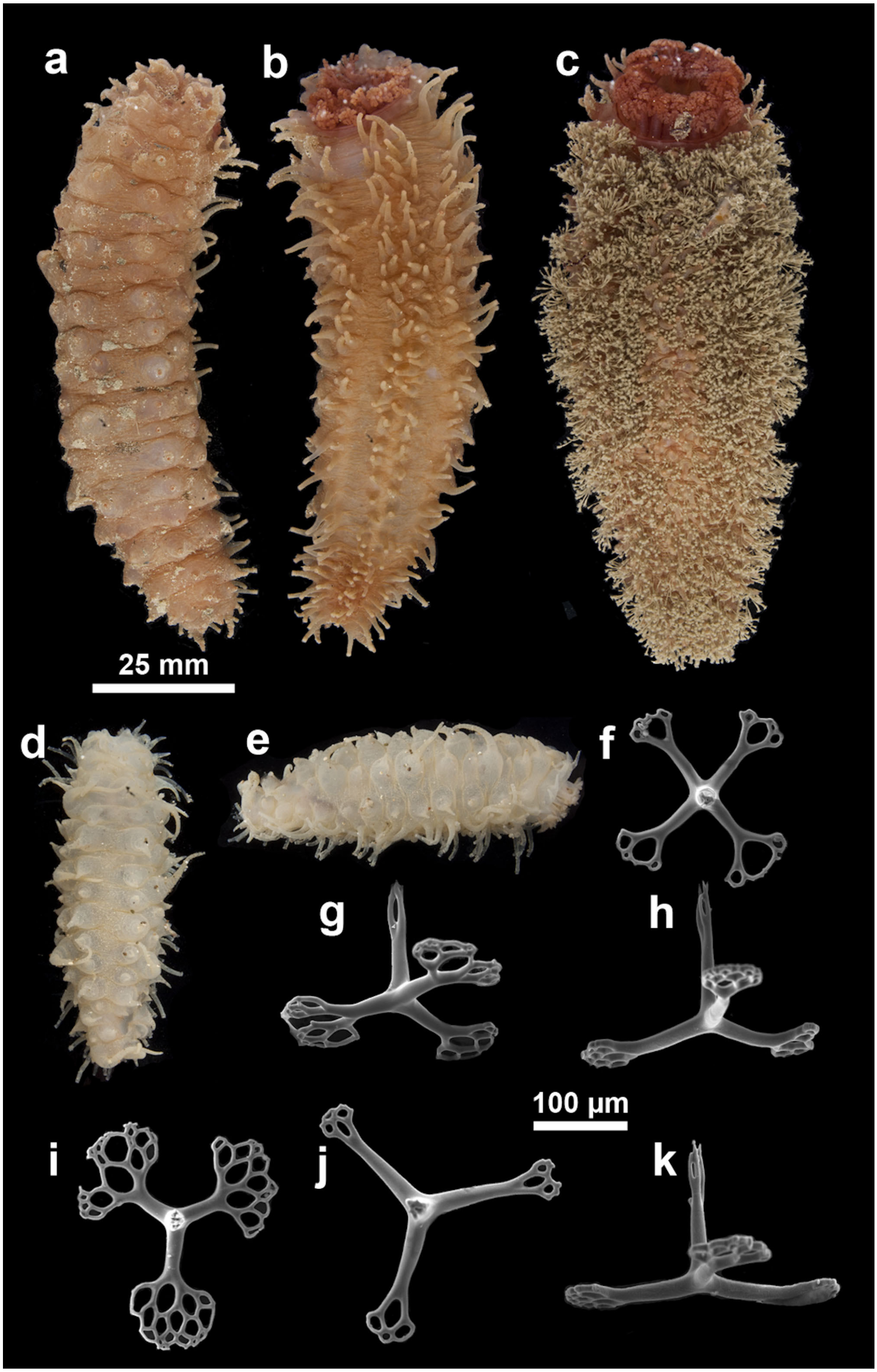

Fig. 18. *Synallactes* sp.: a, b, MIMB 48716, dorsal and ventral side, *in vivo*; c, MIMB 48715, ventral side covered by dense hydroid colonies, *in vivo*; d, e, MIMB 48713, dorsal and side view, *in vivo*; f–k, dorsal three- and four-armed table ossicles (MIMB 48714). a–e, scale 25 mm; f–k, scale 100 µm. Image courtesy: a–e, Kirill Minin.

(Table 1). Relatively high endemicity at the species level unlikely is true, it is rather related to the poor knowledge of the Pacific bathyal holothuroids. Analysis of distribution patterns of nearest BINs (Table 1) shows that more than a half of them (57%) are limited to the Pacific (56%) suggesting predominantly Pacific origin of the ESC fauna.

The most diverse holothuroid fauna with 11 species occurred on Koko guyot. On other seamounts the number of species was the following: four species on Kinmei and three each on Nintoku and Ojin. Apart from more extensive sampling on Koko guyot (16 stations versus 4 on Ojin, 2 on Kinmei and 2 on Nintoku), the variation in the number of taxa and their composition may be attributed to different habitats on different guyots. In particular, it is known that the substrate diversity is higher on Koko than on other studied seamounts (Galkin et al. 2020); this diversity includes soft sediments, soft sediments with pebbles and rocky substrates covered with sediments to a different degree. Also, the ESC extends from north to south over 2400 km (Roden et al. 1982) through different latitude zones with different environmental conditions. It can be expected that productivity and sedimentation – key factors responsible for quality and quantity of sediment organic matter controlling the distribution of holothuroids, vary at different seamounts of ESC. Indeed, a biogeographic boundary located north of the Koko guyot was proposed for the bathyal benthic fauna (Sirenko and Smirnov 1989). The effect of this boundary on the distribution of holothuroid species is very likely, however more biogeographic data are required to prove it.

Hansenothuria: taxonomy, phylogeny and distribution

Hansenothuria is a monotypic poorly known genus with unclear phylogenetic position. The single species *H. benti* was described from bathyal on the slope of Bahama Islands in the West Atlantic (Miller and Pawson 1989). Holothuroids of this genus vary in size from small to medium, they are pinkish or purple, gelatinous, with concave dorsum bearing two rows of short and slender dorsal papillae, with ventrolateral brim and naked mid-ventral radius. Ossicles in *Hansenothuria* are irregularly curved, tuberculous and spinous rods, present in tentacles, tube feet and papillae. Because of the gelatinous consistency, these holothuroids are difficult to sample: they disintegrate in trawl catches, and even when sampled using ROV they rarely remain intact. As a result, *Hansenothuria* only few times was reported since the original description: in the Atlantic (Rogacheva et al. 2013) and in the Pacific, CCFZ (Bribiesca-Contreras et al. 2022 as Synallactidae stet. CCZ_061 and Synallactidae stet. CCZ_066). In all cases specimens of *Hansenothuria* were obtained using ROV. Rare findings of this genus emphasize the importance of new samples of the *Hansenothuria* at ESC, where two unidentified species were found on the Koko guyot. The ESC specimens of *Hansenothuria*, except for several small ones from St. LV94-11, were represented by poorly preserved fragments without ambulacral appendages, ossicles and internal organs.

The phylogenetic position of the genus, including the family assignment, is not yet clear. In the molecular analysis of extant holothuroids by Miller et al. (2017) the genus *Hansenothuria* was not included, but the authors suggested that *Hansenothuria* belongs to the order Persiculida based on absence of ossicles in body wall skin. Here we provided the first data on the phylogenetic position of this genus. According to *18S*, *H3*, *16S* and *COI* data (Fig. S1c) the proposed clade of *Hansenothuria* was sister to the clade of *Paelopatides* SIO-BIC E4365 and SIO-BIC E5609 (PP = 1, BS = 99) and appeared within the Synallactida clade defined by Miller et al. (2017). *Hansenothuria* resembles *Paelopatides* Théel, 1886 in the benthopelagic lifestyle,

Fig. 19. Holothuroids on rocky substrates: a, *Pannychia henrici* (Koko guyot, St. LV94-4); b, *Bathyplotes* sp. (Koko guyot, St. LV94-4), c, *Synallactes* sp. (Nintoku guyot, St. LV86-21). Scale bar = 10 cm. Image courtesy: NSCMB FEB RAS.

flattened body, gelatinous covers and ventrolateral brim. Similar morphology and swimming ability are also characteristic for *Benthothuria* Perrier R., 1898 also assigned by Miller et al. (2017) to Persiculida based on the lack of ossicles. Relationships of this genus require verification using molecular data. The family assignment of *Hansenothuria* remains unclear. According to Smirnov (2012) and Miller et al. (2017) the family Synallactidae requires revision. Here we consider the genus *Hansenothuria* in the family Synallactidae until new data for the revision of this group become available.

Apparently *Hansenothuria* is widely distributed in the Pacific. Many records of this genus were reported from the North and South Pacific Ocean by *Okeanos Explorer* (Benthic Deepwater Animal Identification Guide https://www.ncei.noaa.gov/maps/benthic-animal-guide/, accessed 21.02.2024): Chamorro, Malulu, Musicians, and Polo Seamounts, off Johnston and Rose Atolls (some records were identified as *Paelopatides* sp. or Synallactidae).

Ecology

Holothuroids were one of the common components of benthic fauna of ESC. They were especially numerous on soft sediments, although some were found exclusively or predominantly on rocky substrates: among the latter were *Bathyplotes* sp., Elpidiidae gen. et sp. indet., Laetmogonidae gen. et sp. indet. 1 and 2, *Hansenothuria* sp. 1 and *Synallactes* sp. (Fig. 19). Some species were mentioned among benthic community dominants (Dautova et al. 2019 and unpublished cruise reports): Elpidiidae gen. et sp. indet. (Koko guyot, west slope with massive lava rocks, depth ca. 1370 m), *Parvathuria dautovae* gen. et sp. nov. (Koko guyot, soft sediment slope, depth ca. 770 m and on east plateau of Nintoku, soft sediments, depth ca. 1160 m), *Hansenothuria* sp. 1 (southwest slope of Koko guyot, basalt rocks, depth ca. 1400 m), *Peniagone koko* sp. nov. (Koko guyot, north slope, sedimented areas, depth ca. 2000–2200 m) and *Psolus* sp. (Ojin guyot, calcareous rocks and tuff-sandstone with an iron-manganese crust, depth ca. 1200 m). These facts demonstrate that holothuroids can be abundant in the deep sea not only on soft sediments but also on variety of other substrates.

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Competing interests: The authors declare no conflict of interest.

Availability of data and materials: Species occurrences are published in GBIF (Kremenetskaia et al. 2024). DNA sequences are available in GenBank and BOLD. The specimens are deposited at the Museum of A.V. Zhirmunsky National Scientific Center of Marine Biology (MIMB), Far Eastern Branch, Russian Academy of Sciences (Vladivostok, Russia).

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Supplementary materials

Table S1. List of examined material on Holothuroidea. (download)

Table S2. Primers for PCR amplification and sequencing. (download)

Table S3. Data on sequences used in the analysis obtained from GenBank and BOLD. (download)

Fig. S1. Phylogenetic relationships of *Bathyplotes* sp. (a) and *Hansenothuria* ssp. (b–c) from ESC inferred from *COI* 840 position datasets (a–b) and from 3264 position concatenated dataset of *COI*, *16S*, *18S* and *H3* (c); shown are rooted BI (a, c) and ML trees (b). The substitution models were: a, TRN+I+G model (GTR+I+G in BI) for *COI* codon positions 1 and 2 and HKY+I+G for *COI* position 3; b, TRNEF+G (GTR+G in BI), F81, GTR+G for *COI* positions 1–3, respectively; c, GTR+I+G for *COI* (all positions), *16S* and *18S*, and TVM+I+G for H3 (GTR+I+G in BI for all positions). Outgroups: *Paelopatides* sp. (a), *Paroriza prouhoi* (b), and an echinoid *Echinosigra phiale* (c). Support values: PP ≥ 0.95/ BS ≥ 75, nodes with PP ≥ 0.99 and BS ≥ 90 indicated with circles. Vouchers, for which sequences were obtained in this study, are in bold; sequences from GenBank and BOLD are given in the table S3. BI was conducted for 5,000,000 (a), 10,000,000 (b) and 50,000,000 generations (c); ML analysis was conducted for 1000 (a, b) and 1900 (c) replicates. The orange rectangle shows proposed clade of *Hansenothuria* (b). (download)