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Two New Genera and Species of Polynoidae (Annelida: Polychaeta) Associated with Sea Urchins

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Symbiotic relationships between polychaetes and marine invertebrates are well-documented, with echinoderms—primary starfish and sea cucumbers—as common hosts and sea urchins being more rarely involved. Although many sea urchins possess venomous spines that are effective defenses and make them suitable hosts for symbionts, the dense packing of these spines difficult hosting symbiotic polychaetes. In this study, we describe two new genera and species of polynoid polychaetes found in association with two different species of sea urchins, collected through dredging from Sagami Bay, Japan. *Echinophilia* gen. nov. is characterized by an elongated body, 12 pairs of elytra, subdistally inflated antennae and dorsal cirri. *Paraechinophilia* gen. nov., in contrast, has a non-elongated body, 12 pairs of elytra, not inflated antennae and dorsal cirri. Additionally, we provide insights into their phylogenetic relationships based on four gene sequences (*COI*, 16S, 18S, and 28S).

Key words: Polychaetes, Symbiosis, Taxonomy, Echinodermata, Japan

BACKGROUND

Echinoderms play a crucial role in marine biodiversity as hosts for a wide array of symbiotic and parasitic organisms (Jangoux 1987), including over 200 species of polychaetes (Martin and Britayev 1998 2018). While Asteroidea (starfish) are the most common echinoderm hosts for symbiotic polychaetes, Echinoidea (sea urchins) harbor far fewer symbiotic species (Martin and Britayev 2018). Nevertheless, sea urchins are not devoid of polychaete associations, which include representatives of five families (Clark 1956; Stroch and Niggermann 1967; Martin and Britayev 1998). This relatively low number underscores the need for further unexploration to better understand the diversity of polychaetes are associated with sea urchins.

Sea urchins, with their entire body covered by spines, often armed with venom, possess well-defined structures for defense against predators. This makes them highly suitable hosts for symbiotic organisms, providing a secure refuge in the interstices between their spines where symbionts are less likely to be attacked by predators. Symbiotic relationships with sea urchins have been reported across a diverse array of taxa, including ctenophores, flatworms, arthropods, mollusks, annelids, echinoderms, and fish (Jangoux 1987a b; Britayev et al. 2013). However, much remains unknown about the biology and diversity of organisms symbiotic with sea urchins, highlighting the need for further research to clarify their species composition (Britayev et al. 2013).

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Polynoidae—commonly known as scale worms—is diverse family comprising over 900 species globally distributed across habitats ranging from shallow waters to deep sea (Bonifácio and Menot 2019; Hourdez 2022; Gonzalez et al. 2023). Around 45% of these species are symbiotic, associating with a wide spectrum of hosts including Echinodermata, Mollusca, Cnidaria, Porifera, Annelida, Crustacea, and other Polychaeta, and showing highly specialized adaptations (Taboada et al. 2021; Marin and Antokhnia 2022; Maxwell et al. 2022; Núñez et al. 2022; Sato et al. 2023). This emphasizes the need for further studying the diversity, taxonomy, and evolutionary history of scale worms (Jimi et al. 2021). Despite they are associated with a wide range of echinoderms, only ten species have been reported from sea urchins, with most found in shallow waters (Martin and Britayev 1998).

During a dredge survey conducted in Sagami Bay, Japan, we collected two species of symbiotic scale worms from two different species of sea urchins. Using morphology and molecular phylogenetics based on four genes (*COI*, 16S, 18S, and 28S), this study describes these scale worms as two new genera and two new species, discussing their phylogenetic relationships and the evolutionary implications of their symbiotic interactions with their hosts.

MATERIALS AND METHODS

The sea urchins *Araeosoma owstoni* Mortensen, 1904 and *Clypeaster virescens* Döderlein, 1885 were collected from Sagami Bay, Japan by dredging (Figs. 1A, 4A). The worms were removed from their hosts and one parapodium from holotype (NSMT-Pol H-1001 and 9001) was cut off and fixed in 99.5% ethanol for DNA extraction prior to fixed and preserve the specimen in 70% ethanol. The preserved specimens were observed under stereomicroscopes MZ 16F (LEICA, Germany) and E600 (Nikon, Japan) and then deposited in the National Museum of Nature and Science, Tsukuba (NSMT). The body width of specimens was measured as the distance between the ends of the parapodia, excluding the chaetae.

Genomic DNA was extracted from a small piece of the parapodium of the holotype (NSMT-Pol H-1001 and 9001) using the DNeasy Blood & Tissue Kit (Qiagen, USA) following the manufacturer's protocol. Partial cytochrome *c* oxidase subunit I (*COI*), 16S ribosomal RNA (16S), 18S ribosomal RNA (18S), 28S ribosomal RNA (28S) gene sequences were amplified in the polymerase chain reaction (PCR) with the primer sets of polyLCO (5'-GAYTATWTTCAACAAATCATAAAGATATTGG-3') and polyHCO (5'-TAMACTTCWGGGTGACCAAARAATCA-3') (Carr et al. 2011), 16SarL (CGCCGTTTATCAAAAACAT) and 16SbrH (CCGGTCTGAACTCAGATCACGT) (Palumbi et al. 1991), mitchA (CAACCTGGTTGATCCTGCCAGT) and mitchB (TGATCCTTCCGCAGGTTCACCTAC) (Medlin et al. 1988), and LsudiF (ACCCGCTGAATTTAAGCATA) and D3aR (ACGAACGATTTGCACGTCAG) (Lenaers et al. 1989), respectively. The reaction mixture [0.25 µl TaKaRa Ex Taq (Takara, Japan), 5 µl of 10 × Ex Taq Buffer (Takara, Japan), 4.0 µl dNTP mixture (Takara, Japan), 5 µl of each primer pair (10 µM), 0.75 µl of extracted DNA, and 35 µl of distilled water] was used for amplification. To confirm successful amplification, PCR products were visualized using 1.2% Agarose S (Nippon Gene, Japan) gel electrophoresis. Direct sequencing reaction of the PCR products was performed using the BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems, USA) and the 3130xl Genetic Analyzer (Applied Biosystems, USA). Sequencing reactions utilized the same 1-µM primers that were used for PCR amplification.

Additional sequences of other polynoids were obtained from GenBank (Table 1). All sequences were aligned using MAFFT ver. 7.205 under the E-INS-i strategy (Katoh and Standley 2013). after removing the ambiguous positions by trimAL following the gappyout strategy (Capella-Gutiérrez et al. 2009). The trimmed sequences for *COI* (517 bp), 16S (312 bp), 18S (1627 bp), and 28S (908 bp) were concatenated by using Kakusan (Tanabe 2007), following the recommended GTR+G evolutionary models. A phylogenetic tree was constructed using maximum likelihood (ML) method in RAxML-VI-HPC (Stamatakis 2006) and the robustness of the ML tree was evaluated by 1,000 bootstrap pseudo-replicates (-f option). K2P genetic distances were calculated by MEGA11 (Tamura et al. 2021).

Newly obtained sequences have been deposited in the GenBank (Table 1).

RESULTS

SYSTEMATICS

Polynoidae Kinberg, 1856

Echinophilia gen. nov.

[New Japanese name: Uni-kakure-urokomushi-zoku]
urn:lsid:zoobank.org:act:D268D40B-193F-44F5-BAE0-4D20B670176A

Type species: *Echinophilia araeosomai* gen. et sp. nov.

Diagnosis: Body flat, elongated, with 12 pairs of elytra on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 24, absent from posterior chaetigers. Prostomium lacking distinct cephalic peaks, with two pairs of eyes, two conical, elongated palps, and three antennae subdistally inflated, with filiform tip; median antenna with ceratophores inserted in anterior notch, lateral antennae with ceratophores inserted termino-ventrally on distal end of prostomium. Tentaculophores lateral to prostomium, achaetous, tentacular cirri subdistally inflated, with filiform tip. Parapodia biramous, notopodia small, neuropodia larger. Neuropodial prechaetal lobes subconical, with rounded tips; post chaetal lobes shorter, rounded. Dorsal cirri long,

Table 1. List of polynoids included in the phylogenetic analysis, together with accession numbers in GenBank

Species	18S	28S	16S	*COI*	References
Acholoe squamosa (Delle Chiaje, 1827)	AY839567	JN852850	JN852888	AY839576	Norlinder et al. (2012)
Antarctinoe ferox (Baird, 1865)	MG905039	–	MG905033	KJ676611	Neal et al. (2018)
***Asterophilia culcitae* Britayev & Fauchald, 2005**	**PQ441976**	**PQ441985**	**PQ443350**	**PQ426599**	**This study**
Branchinotogluma sagamiensis Jimi, Chen & Fujiwara, 2022	ON244618	ON244614	ON244617	ON255503	Jimi et al. (2022)
Bylgides elegans (Théel, 1879)	JN852822	JN852852	JN852890	JN852924	Norlinder et al. (2012)
Bylgides sarsi (Kinberg in Malmgren, 1866)	JN852823	JN852853	JN852891	JN852925	Norlinder et al. (2012)
***Echinophilia owstoni* gen. et sp. nov.**	**PQ441974**	**PQ441983**	**PQ443348**	**PQ431392**	**This study**
Eunoe oerstedi Malmgren, 1865	–	–	–	HQ024019	Carr et al. (2011)
Eunoe shirikishinai Imajima & Hartman, 1964	MW444683	MW444692	MW444675	MW429800	Jimi et al. (2021)
*Eunoe shirikishinai*_Korea	–	–	–	JX503009	Kim et al. (unpublished)
Eunoe spinicirris Annenkova, 1937	–	–	–	HM473744	Carr et al. (2011)
Eunoe uniseriata Banse & Hobson, 1968	–	–	–	MK390764	Carr et al. (2011)
Gastrolepidia clavigera Schmarda, 1861	JN852825	JN852855	JN852893	JN852927	Norlinder et al. (2012)
Gattyana cirrhosa (Pallas, 1766)	JN852826	JN852856	JN852894	JN852928	Norlinder et al. (2012)
Gorgoniapolynoe caeciliae (Fauvel, 1913)	KU738170	KU738185	KU738150	KU738203	Serpetti et al. (2017)
Gorgoniapolynoe corralophilia (Day, 1960)	KU738173	KU738189	KU738154	KU738206	Serpetti et al. (2017)
Harmothoe glabra (Malmgren, 1865)	JN852828	JN852858	JN852896	JN852929	Norlinder et al. (2012)
Harmothoe imbricata (Linnaeus, 1767)	AY340434	AY340400	AY340463	AY839580	Rousset et al. (2007)
Harmothoe impar (Johnston, 1839)	JN852829	JN852859	JN852897	JN852930	Norlinder et al. (2012)
Harmothoe oculinarum (Storm, 1879)	–	JN852860	JN852898	–	Norlinder et al. (2012)
Harmothoe rarispina (M. Sars, 1861)	KY823451	KY823465	KY823482	KY823497	Gonzalez et al. (2017)
Harmothoe cf. *imbricata*	KY823450	KY823464	KY823481	KY823496	Gonzalez et al. (2017)
Harmothoe sp._Norway (*Eunoe nodosa* mis ident.)	JN852824	JN852854	JN852892	JN852926	Norlinder et al. (2012)
Harmothoe sp._P1	MW444678	MW444685	MW444669	MW429795	Jimi et al. (2021)
Harmothoe sp._P3	MW444679	MW444686	MW444670	MW429796	Jimi et al. (2021)
Harmothoe sp._P5	MW444681	MW444689	MW444672	MW429798	Jimi et al. (2021)
Harmothoe sp._P6	MW444682	MW444690	MW444673	MW429799	Jimi et al. (2021)
Halosydna brevisetosa Kinberg, 1856 (outgroup)	JN852827	JN852857	JN852895	HM473394	Norlinder et al. (2012)
Hyperhalosydna striata (Kinberg, 1856) (outgroup)	JN852831	JN852862	JN852900	JN852932	Norlinder et al. (2012)
Lepidasthenia elegans (Grube, 1840)	JN852832	JN852863	JN852901	JN852933	Norlinder et al. (2012)
Malmgrenia mcintoshi (Tebble & Chambers, 1982)	JN852834	JN852866	JN852904	JN852935	Norlinder et al. (2012)
Melaenis loveni Malmgren, 1865	JN852835	JN852867	JN852905	JN852936	Norlinder et al. (2012)
Neopolynoe acanellae (Verrill, 1882)	MN653050	MN653123	MN653064	MN656076	Taboada et al. (2019)
Neopolynoe chondrocladiae (Fauvel, 1943)	MN653051	MN653124	MN653092	MN656104	Taboada et al. (2019)
Neopolynoe paradoxa (Anon, 1888)	JN852836	JN852868	JN852906	JN852937	Norlinder et al. (2012)
***Ophthlamonoe* sp.**	**–**	**–**	**PQ885508**	**PQ889565**	**This study**
Paradyte crinoidicola (Potts, 1910)	JN852837	JN852869	JN852907	JN852938	Norlinder et al. (2012)
***Paraechinophilia clypeasteri* gen. et sp. nov.**	**PQ441975**	**PQ441984**	**PQ443349**	**PQ431393**	**This study**
Paralepidonotus ampulliferus (Grube, 1878) (out group)	JN852838	–	JN852908	JN852939	Norlinder et al. (2012)
Polynoe scolopendrina Savigny, 1822	JN852839	JN852870	JN852909	JN852940	Norlinder et al. (2012)
Polynoe? sp._P7	–	MW444691	MW444674	–	Jimi et al. (2021)
Polynoe? sp._P9	MW444684	MW444693	MW444676	MW429801	Jimi et al. (2021)
Polyeunoa laevis McIntosh, 1885	KU738176	KU738193	KU738160	KU738212	Serpetti et al. (2017)
*Polyeunoa laevis*_2	–	–	–	MK593134	Bogantes et al. (2020)
Robertianella synophthalma McIntosh, 1885	MN653053	MN653126	MN653122	MN656132	Taboada et al. (2020)
Polynoidae sp.	MW444680	MW444688	MW444671	MW429797	Jimi et al. (2021)
Eunoe issunboushi	MW444677	MW444685	MW444668	MW429794	Jimi et al. (2021)

subdistally inflated, with filiform tips, throughout body. Noto- and neurochaetae with rows of serrations, semi-lunar pockets, and notched tips. Ventral cirri short, inflated subdistally and filiform tips at segment 2, conical from segment 3 till body end. Elytra with hemisphere microtubercles; macrotubercles and fringing papillae at outer or posterior margin absent. Symbiont of echinoids.

Etymology: The new genus name, masculine in gender, is composed by *Echino*, referring to the host Echinoidea, and *philia* (meaning affinity towards) in Latin, referring to the symbiotic nature of its association with sea urchins.

Remarks: *Echinophilia* gen. nov. closely resembles the echinoderm symbiont genera *Asterophilia*, *Gastrolepidia*, and *Paraechinophilia* gen. nov. in having inflated antennae and dorsal or ventral cirri. However, they differ in body shape, number of elytra pairs, presence of inflated antennae and dorsal and ventral cirri, and host (see Table 2).

***Echinophilia araeosomai* gen. et sp. nov.**

[New Japanese name: Fukuro-uni-kakure-urokomushi]
(Figs. 1–3)
urn:lsid:zoobank.org:act:053A9E76-9600-4D36-8F09-76FE9709B43A

Material examined: *Holotype*: NSMT-Pol H-982: complete specimen, 30 mm long, 3 mm width, 55 chaetigers, collected by dredging from outside body of *Araeosoma owstoni* at off Jogashima (35°08.856'N, 139°34.687'E), 80–81 m depth, 18 Nov. 2020.

Paratype: NSMT-Pol P-983: complete specimen, 25 mm long, 3 mm width, 45 chaetigers, collected during the same dredging operation as the holotype, from another individual of *Araeosoma owstoni*, used for DNA extraction and SEM observation.

Type locality: Sagami Bay, the North Western Pacific, 80–81 m depth.

Sequences: Determined from the holotype (NSMT-Pol H-982): *COI*, 653 bp, PQ431392; 16S, 492 bp, PQ443348; 18S, 1792 bp, PQ441974; 28S, 1021 bp, PQ441983.

Description: Body flat, elongated (Fig. 1), with 12 pairs of elytra on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, and 24, then absent until posterior end (Figs. 1C, 2C), whitish in vivo (Fig. 1B–D) and preserved (Fig. 2A–D), with a dorsal ciliated area between cirrophores/erytrophores (Fig. 3A–B). Mid-dorsal surface covered by elytra. Dorsal side of base of dorsal cirrophore, tentaculorphore, ceratophore, elytrophore, notopodia, and tip of neuropodial prechaetal/postchaetal lobes with brownish pigmentation (Figs. 1B–D, 2A–B). Dorsal tubercles and ventral (nephridial) papillae absent. Pharynx not seen.

Prostomium bilobed, without distinct cephalic peaks, with three antennae subdistally inflated with filiform tips, median antenna twice longer than lateral, with ceratophores inserted in anterior notch, lateral antennae with ceratophores inserted terminoventrally on distal end of prostomium (Fig. 2A). Tentaculophores lateral to prostomium, achaetous. Tentacular cirri inflated subdistally, with filiform tips, slightly longer than lateral antennae (Fig. 2A). Palps conical (Fig. 2B), not inflated, as long as lateral antennae. Two pairs of brownish eyes, anterior pair slightly larger than posterior one, present at dorsal lateral side of prostomium (Fig. 2A).

Parapodia biramous (Figs. 3, 4), with notopodia shorter than neuropodia (Figs. 3A, 3B, 4A, 4C), without branchiae. Dorsal cirri inflated subdistally throughout body, with filiform tips, three times longer than lateral antennae (Figs. 1C, 3A, 3C). About 10 notochaetae in each parapodium, ranging from 150 to 300 µm. Notochaetae short to long, with about 15 rows of serrations, semi-lunar pockets, and unidentate or bidentate tips (Figs. 3D, 4C–D). Neuropodial prechaetal lobes subconical, with rounded tips (Figs. 3F, 4C); post chaetal lobes shorter, rounded. About 15 neurochaetae in each parapodium, with about 20 rows of serrations,

Table 2. Comparison of *Asterophilia*, *Gastrolepidia*, *Echinophilia* gen. nov., and *Paraechinophilia* gen. nov.

Characters	*Asterophilia* Hanley, 1989	*Gastrolepidia* Schmarda, 1861	*Echinophilia* gen. nov.	*Paraechinophilia* gen. nov.
Body	flat, not elongated	flat, elongated	flat, elongated	flat, not elongated
Elytra	15 pairs	variable, 15–31 pairs	12 pairs	12 pairs
Antennae	inflated subdistally	inflated subdistally	inflated subdistally	not inflated subdistally
Dorsal cirri	inflated subdistally in all segments	inflated subdistally in all segments	inflated subdistally in all segments	not inflated subdistally in all segments
Ventral cirri	not inflated subdistally in all segments	not inflated subdistally in all segments	inflated subdistally in segment 2; not in following segments	inflated subdistally in all segments
Host	asteroids or holothuroids	holothuroids	echinoids	echinoids

semi-lunar pockets, and bidentate tips (Figs. 3E, 4C, 4E). Ventral cirri inflated subdistally at segment 2, with filiform tips, conical from segment 3 till body end (Figs. 2C, 2D, 3F, 4F), short, 0.5 times longer than lateral antennae. Robust acicula in each ramum (Fig. 3B), acicula tip sharp.

Pygidium with a pair of pygidial cirri, slightly inflated, with filiform tips (Fig. 2C, 2D).

Elytra trapezoidal in segment 2, oval in following elytrophorous segments, transparent, with white and brownish bands on posterior margin and hemisphere microtubercles; macrotubercles and fringing papillae at outer or posterior margin absent (Figs. 2E, 2F, 3G, 3H).

Etymology: The new specific name refers to the specific name of the host, *Araeosoma*, and is a noun in the genitive case.

Habitat and distribution: specimens of *E. owstoni* gen. et sp. nov. were found among the spines of *A. owstoni* (Fig. 1) in Sagami Bay, in the North Western Pacific coast of Japan at 80–81 m depth. The host *A. owstoni* has been recorded at 70–210 m depth (Mortensen 1935), but the presence of the symbiont at shallower or deeper waters than those explored in this study cannot be confirmed.

***Paraechinophilia* gen. nov.**

[New Japanese name: Nise-uni-kakure-urokomushi-zoku]
urn:lsid:zoobank.org:act:8B5DBECE-D4AA-404F-BFBF-E5C681F4B5E5

Type species: *Paraechinophilia clypeasteri* gen. et sp. nov.

Diagnosis: Body flat, short, with 12 pairs of elytra on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23. Prostomium without distinct cephalic peaks, with two pairs of eyes, with conical palps not inflated, with

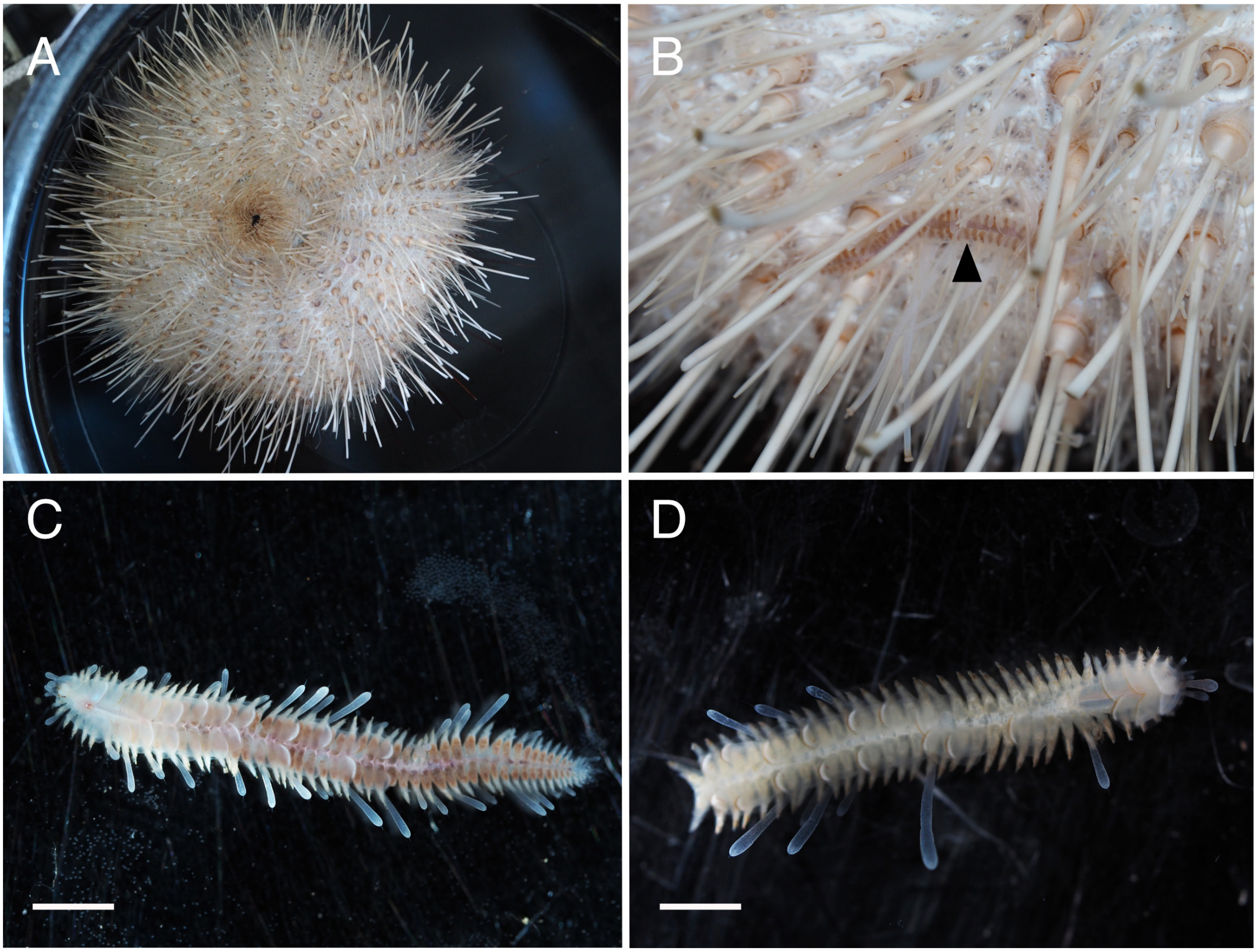

Fig. 1. Live specimens of *Echinophilia araeosomai* gen. et sp. nov. B–C, holotype (NSMT-Pol H-982), D, paratype (NSMT-Pol P-983). A, an overview of host (*Araeosoma owstoni*). B, enlarged view, in life. Black arrow indicates the worm. C–D, whole view, dorsal side. Scale bars: C–D = 5 mm.

three antennae not inflated subdistally, conical; median one with ceratophores inserted in anterior notch, lateral ones with ceratophores inserted terminoventrally on distal end of prostomium. Tentaculophores lateral to prostomium, achaetous, with tentacular cirri not inflated subdistally, conical. Parapodia biramous, notopodia small, neuropodia larger. Neuropodia with subconical prechaetal lobes subconical, with rounded tips and post chaetal lobes shorter, rounded. Dorsal cirri not inflated subdistally, conical, long. Noto- and neurochaetae with rows of serrations, semi-lunar pockets, and unidentate or bidentate tips. Ventral cirri inflated subdistally throughout body, long. Elytra without microtubercles, macrotubercles, and fringing papillae at outer or posterior margin. Symbiont of echinoids.

Etymology: The new genus-group name, masculine in gender, refers to close similarity of the symbiotic association with echinoids of both genera, so that it

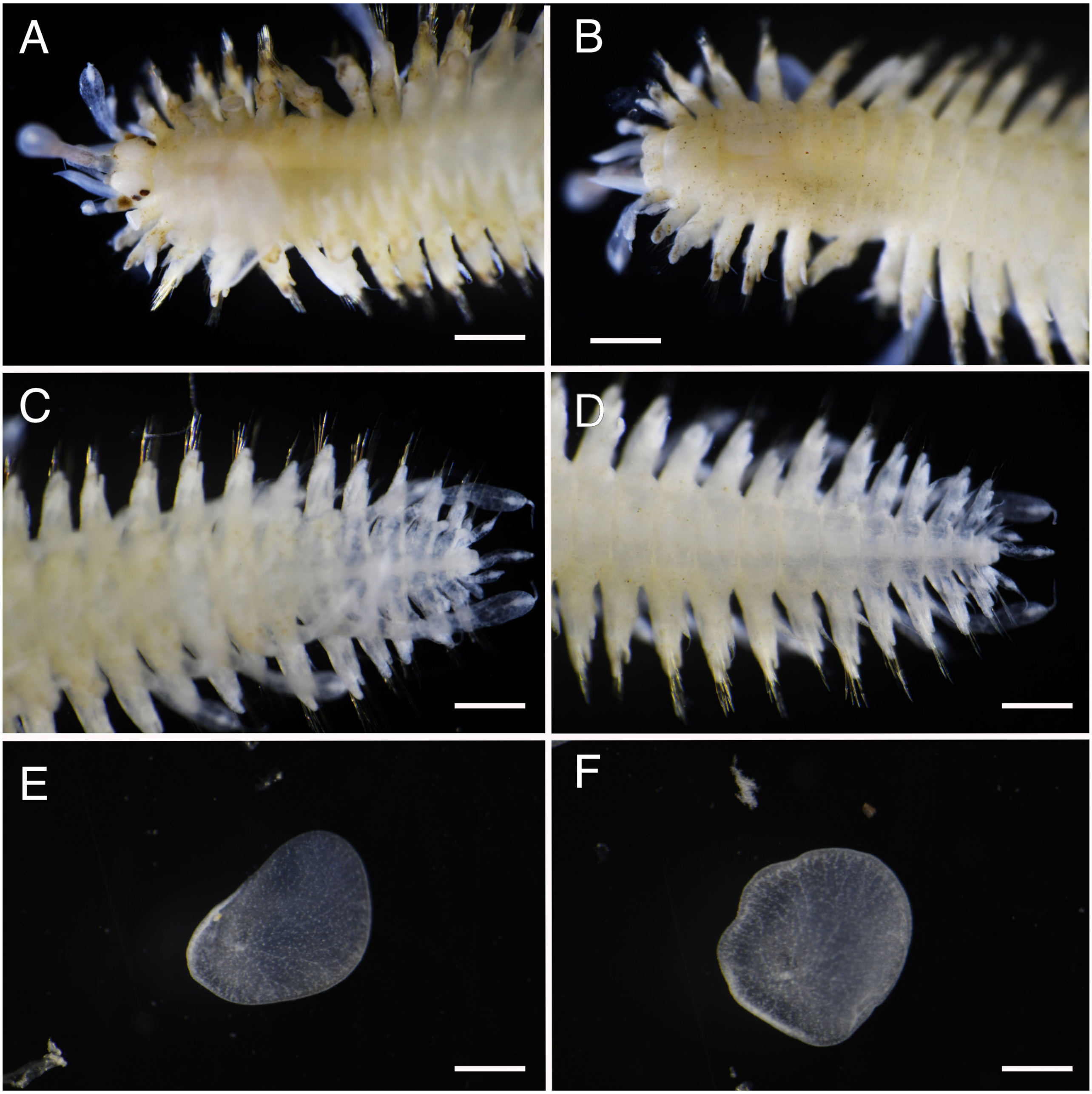

Fig. 2. *Echinophilia araeosomai* gen. et sp. nov., holotype (NSMT-Pol H-982). A, anterior end, dorsal view. B, anterior end, ventral view. C, posterior end, dorsal view. D, posterior end, ventral view. E, elytra, segment 2. F, elytra, segment 11. Scale bars: A–D = 2 mm; D–E = 1 mm.

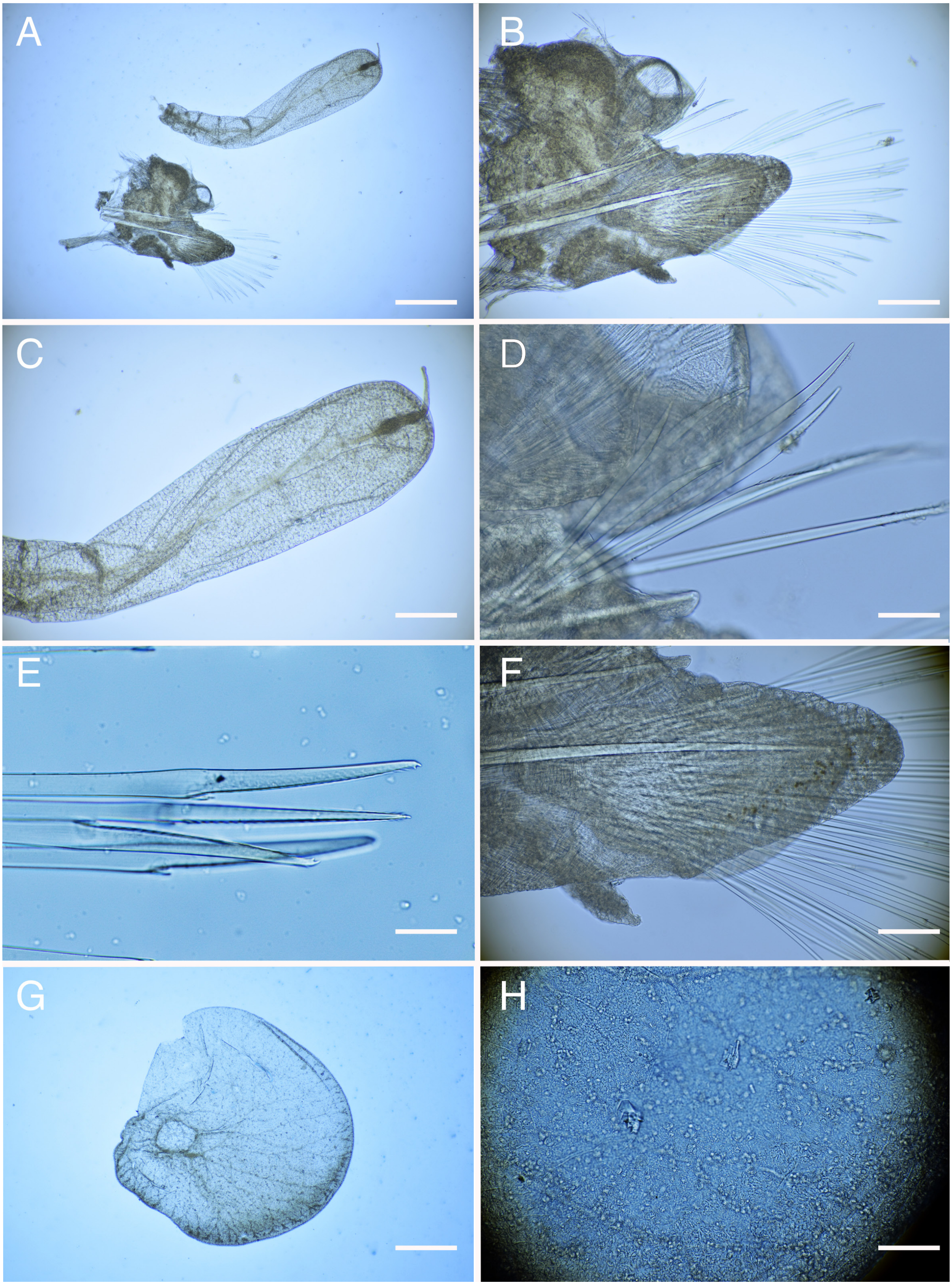

Fig. 3. *Echinophilia araeosomai* gen. et sp. nov., holotype (NSMT-Pol H-982). A, left parapodium, frontal view, chaetiger 28. B, enlarged view. C, dorsal cirrus. D, notochaetae. E, neurochaetae. F, acicula and ventral cirrus. G, elytrum, chaetiger 17. H, enlarged view of elytrum. Scale bars: A = 100 μm; B–C = 50 μm; G = 100 μm; H = 50 μm.

is formed by adding the Greek prefix *para*- (meaning proximity or close relationships) to *Echinophilia*.

Remarks: See remarks of *Echinophilia* gen. nov. and table 2. Furthermore, this genus differs from *Echinophilia* in its body coloration, featuring a white base with green transverse bands. This pattern is reminiscent of the polynoid genus *Ophthalmonoe* Petersen and Britayev, 1997. While *Paraechinophilia* has 12 pairs of elytra, subdistally inflated ventral cirri, and is symbiotic with sea urchins, *Ophthalmonoe* has

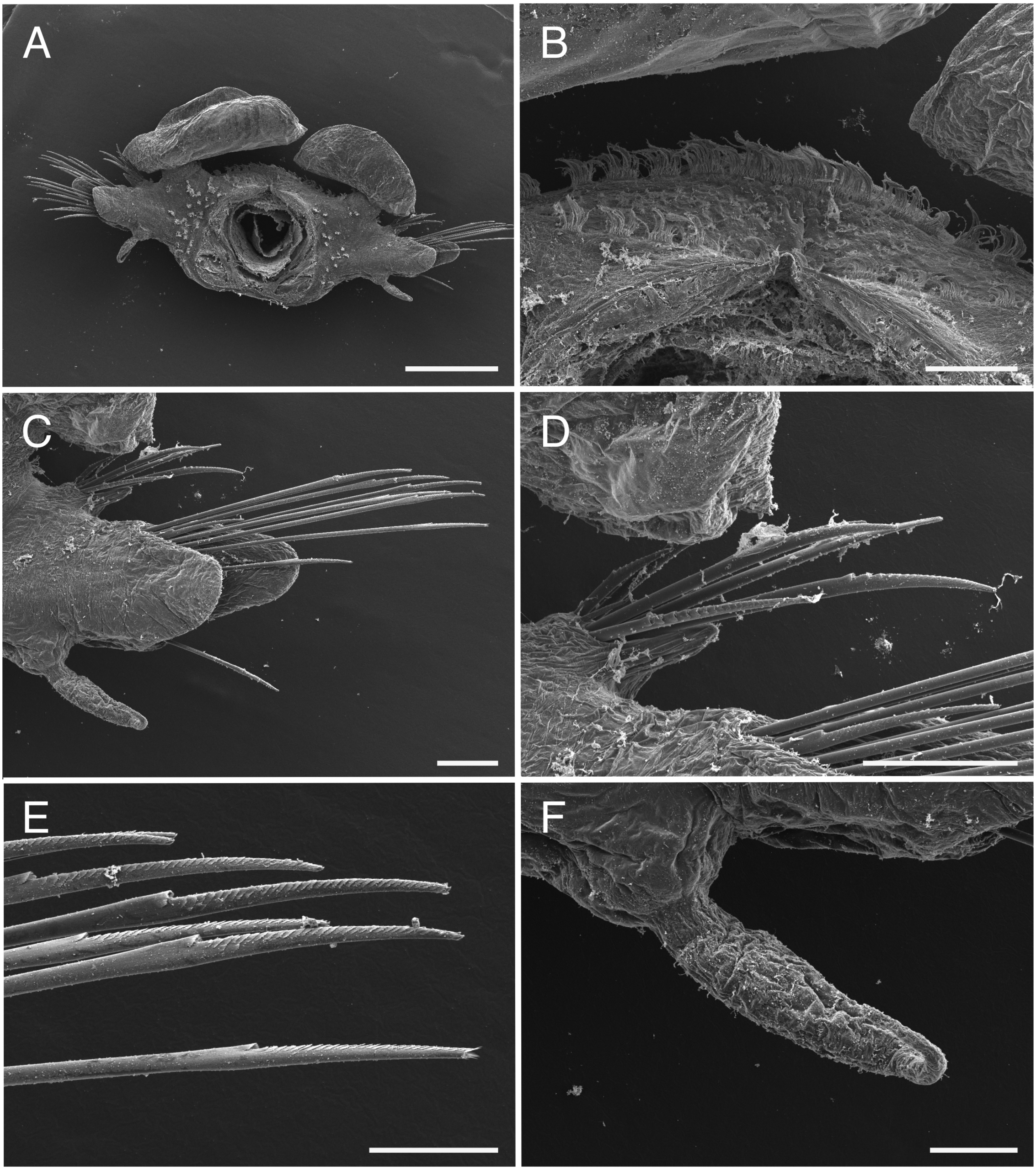

Fig. 4. *Echinophilia araeosomai* gen. et sp. nov., paratype (NSMT-Pol P-983), segment 11. A, segment 11, frontal view. B, dorsal side of body, frontal view. C, left parapodia, frontal view. D, notochaetae. E, neurochaetae. F, ventral cirri. Scale bars: A = 500 µm; B–C = 100 µm; E = 50 µm.

15–17 pairs of elytra, non-inflated ventral cirri, and is symbiotic with members of Chaetopteridae (Annelida) (Petersen and Britayev 1997).

Paraechinophilia clypeasteri **gen. et sp. nov.**

[New Japanese name: Yamataka-kakure-urokomushi]
urn:lsid:zoobank.org:act:9621F276-B94C-428A-8FF4-CF118FAF9886

Material examined: *Holotype*: NSMT-Pol H-984: complete specimen, 14 mm long, 5 mm width, 23 chaetigers, collected by dredging from outside body of *C. virescens* at off Jogashima (35°07.426'N, 139°34.016'E), 147–244 m depth,12 March 2021.

Paratype: NSMT-Pol P-985: complete specimen, 11 mm long, 5 mm width, 23 chaetigers, collected during the same dredging operation as the holotype, from another individual of *C. virescens*, used for DNA extraction and SEM observation.

Type locality: Sagami Bay, the North Western Pacific, 147–244 m depth.

Sequences. Determined from the holotype (NSMT-Pol H-984): COI, 578 bp, PQ431393; 16S, 497 bp, PQ443349; 18S, 1783 bp, PQ441975; 28S, 954 bp, PQ441984.

Description: Body flat, whitish with dorsal green transverse band both in vivo (Fig. 5B) and preserved (Fig. 5E), with 12 pairs of elytra on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, and 23, transparent, with brackish posterior margin, without microtubercles, macrotubercles, and fringing papillae at outer or posterior margin, trapezoid in segment 2, oval from segment 4 to body end (Figs. 5B, 5D, 6G, 6H). Mid-dorsal surface covered by elytra. Dorsal tubercles and ventral (nephridial) papillae absent. Prostomium bilobed (Fig. 5F), lacking distinct cephalic peak, with two palps (1.5 times longer than lateral antennae) and three antennae conical, not subdistally inflated; antennophores inserted in anterior notch (median) and terminoventrally on distal end of prostomium (lateral); median style, 0.5 times longer than lateral style (Fig. 5E). Two pairs of brownish eyes, anterior pair slightly larger than posterior one, present at dorsal lateral side of prostomium (Fig. 5E). Tentaculophores lateral to prostomium, achaetous, with tentacular cirri not inflated subdistally, conical, as long as lateral antennae (Fig. 5B, 5C). Parapodia biramous, with notopodia shorter than neuropodia, without branchiae (Figs. 6A, 7A). Dorsal cirri not inflated subdistally, conical, long, twice longer than lateral antennae (Figs. 5B, 6A, 6C). About 15 notochaetae in each parapodium, with about 10 rows of serrations, semi-lunar pockets, and unidentate or bidentate tips (Figs. 6B, 6D, 7B–C). Neuropodia with subconical prechaetal lobes subconical, with rounded tips and post chaetal lobes shorter, rounded. About 40 neurochaetae in each parapodium, with about 25 rows of serrations, semi-lunar pockets, and unidentate or bidentate tips (Figs. 6D, 6E, 7D, 7E, 7F). Ventral cirri subdistally inflated throughout body, as long as lateral antennae (Fig. 5C, 6F). Robust acicula in each ramum, acicula tip sharp (Fig. 6A, 6B).

Pygidium with one pair of pygidial cirri, not inflated, conical (Fig. 5H).

Etymology: The new specific name refers to the genus name of the host, *Clypeaster*, and is a noun in the genitive case.

Habitat and distribution: Specimens of *P. clypeasteri* gen. et sp. nov. were found among the spines on the external surface of *C. virescens*. The host echinoderms were collected in Sagami Bay, Japan, in the North Western Pacific at 144–244 m depth. *Clypeaster virescens* has been recorded at depths of 100–350 meters (Mortensen 1948), but the presence of the symbiont at shallower or deeper waters than explored in this study cannot be confirmed.

Molecular analysis

The genera *Paradyte*, *Paraechinophilia*, *Echinophilia*, *Gastrolepidia*, and *Asterophilia* formed a clade with strong support (BS = 100%) (Fig. 8). Within this clade, *Gastrolepidia* and *Asterophilia* formed a sister group relationship (BS = 98%). *Echinophilia* was resolved as the sister taxon to the *Gastrolepidia–Asterophilia* clade (BS = 70%), while *Paraechinophilia* was found to be the sister taxon to the *Echinophilia–Gastrolepidia–Asterophilia* clade (BS = 93%) (Fig. 8).

The K2P distance of nucleotide sequences between *Echinophilia* and *Paraechinophilia* was 19.9% (*COI*) and 14.3% (16S), which is comparable to the distance observed between *Asterophilia* and *Gastrolepidia* at 20.5% (*COI*) and 10.1% (16S), supporting the establishment of the new genera.

In the Remarks section for *Paraechinophilia*, we discussed the morphological similarities and differences with *Ophthalmonoe*. Additionally, we included an undescribed Japanese species of *Ophthalmonoe* in the molecular phylogenetic analysis. The results indicate that *Ophthalmonoe* sp. is not nested within the echinoderm-symbiont clade. Although we could not determine the 18S and 28S sequences, leaving the phylogenetic position somewhat ambiguous, the establishment of the new genus described in this paper and its distinction from *Ophthalmonoe* are supported by the molecular phylogenetic tree.

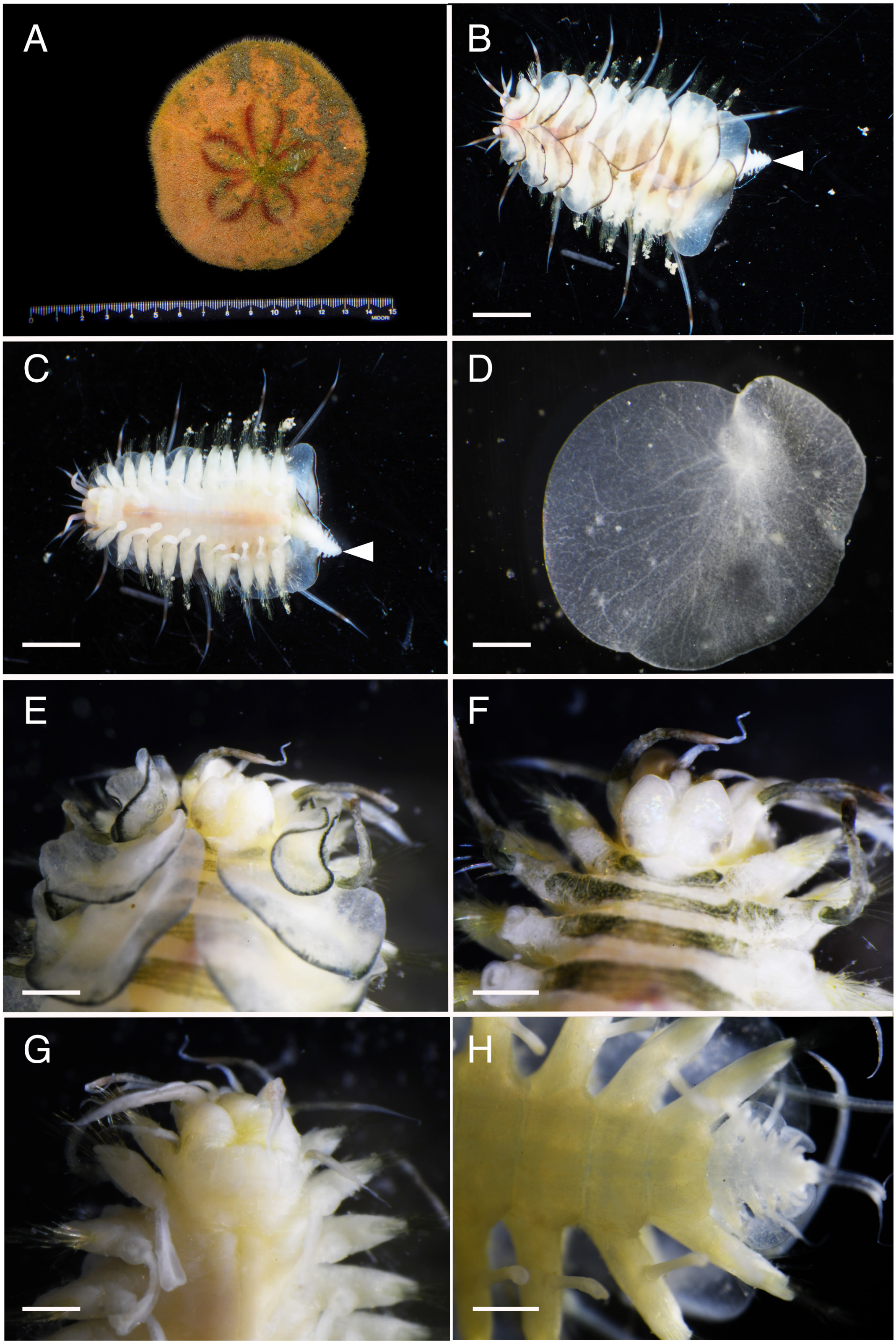

Fig. 5. *Paraechinophilia clypeasteri* gen. et sp. nov., holotype (NSMT-Pol H-984), B–C, live specimen; D–F, fixed specimen. A, an overview of host (*Clypeaster virescens*). B, anterior body, dorsal view. C, anterior body, ventral view. D, elytra, segment 11. E, anterior end, dorsal view. F, anterior end, after removing elytra. G, anterior end, ventral view. H, posterior end, ventral view. Scale bars = A–D, 3 mm; E–H = 1.5 mm. Arrows indicate *Endovermis* sp.

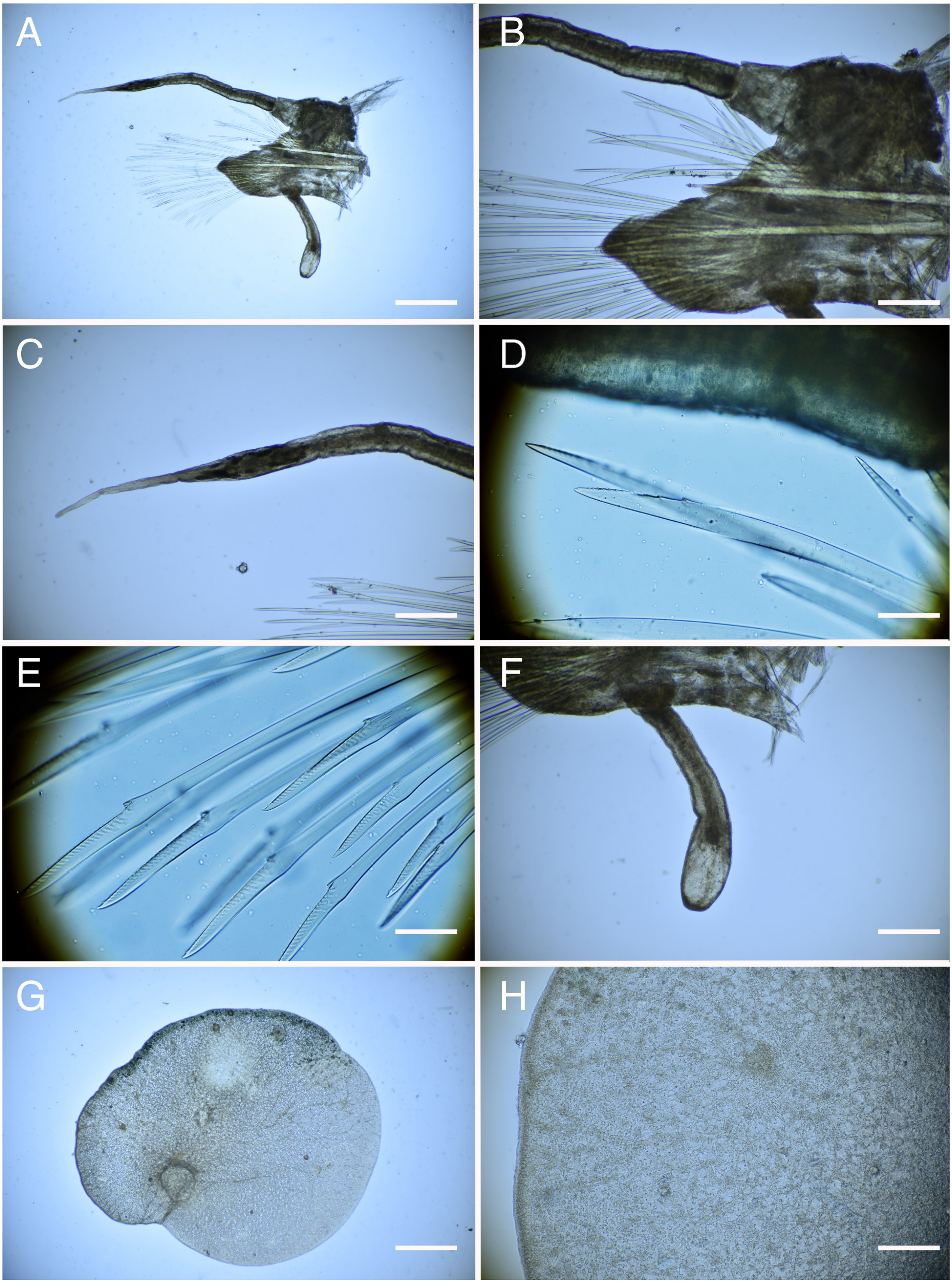

Fig. 6. *Paraechinophilia clypeasteri* gen. et sp. nov., holotype (NSMT-Pol H-984). A, left parapodium, frontal view, chaetiger 28. B, enlarged view. C, dorsal cirrus. D, notochaetae. E, neurochaetae. F, acicula and ventral cirrus. G, elytrum, chaetiger 17. H, enlarged view of elytrum. Scale bars: A = 100 µm; B–C = 50 µm; G = 100 µm; H = 50 µm.

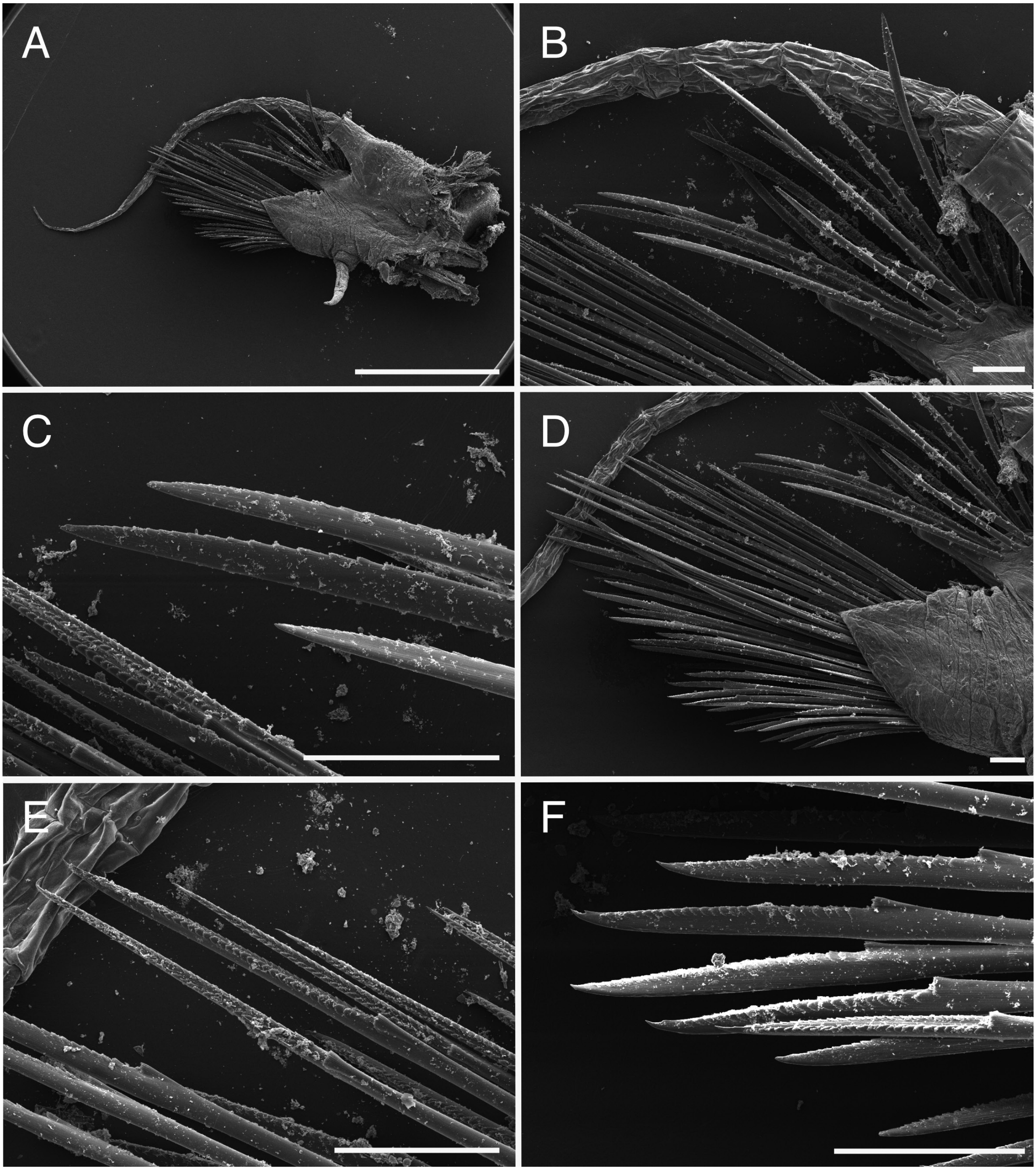

Fig. 7. *Paraechinophilia clypeasteri* gen. et sp. nov., paratype (NSMT-Pol P-985), segment 10. A, whole view of parapodium, rear view. B, notochaetae. C, enlarged view of notochaetae. D, neurochaetae. E, enlarged view of neurochaetae, upper side. F, enlarged view of neurochaetae, lower side. Scale bars: A = 1 mm; B–C = 100 μm; E = 50 μm.

DISCUSSION

In this study, the two new genera are included in a large clade alongside other echinoderm symbiotic polynoids such as *Asterophilia*, *Gastrolepidia*, and *Paradyte*, with crinoid associates apparently being the ancestral members and subsequent adaptations allowing colonization of sea urchins, starfish, and sea cucumbers. This phylogenetic framework for scale worms aligns with the broader evolutionary history of echinoderms (Reich et al. 2015; Rahman and Zamora 2024). As echinoderms diversified, it is plausible that scale worms underwent host-switching events accompanied by a significant morphological divergence, ultimately giving rise to distinct genera.

Interestingly, while another group of annelids, the Myzostomida, is well-known for co-evolving with echinoderms –primarily crinoids– (Summers and Rouse 2014), their co-evolutionary history markedly differs from that of scale worms, as myzostomids associated with ophiuroids and asteroids are considered to have derived evolved secondarily from crinoid-symbiotic ancestors (Jimi et al. 2017). Therefore, the host-switching and trait divergence proposed for scale worms, which align with the broader echinoderm phylogeny, appear unique of this group, underscoring its evolutionary significance.

Although polychaetes include over 300 symbiotic species, only about 20 have been documented as sea urchins associates, highlighting the relative rarity of this type of relationships (Martin and Britayev 1998 2021). Sea urchins having venomous spines might appear as ideal hosts. However, successful symbionts requires body adaptations that allow fitting into the confined spaces between these spines, rendering them particularly difficult to detect. Notably, the narrow, hazardous spaces between the long, venomous spines of *A. owstoni* may have significantly delayed the discovery of its relationships with the scale worm.

The two species of scale worms described in this study show distinct morphological traits that warrant their classification into separate genera, despite sharing a symbiotic lifestyle with sea urchins and forming a single clade. However, all genus in the broader echinoderm symbiotic scale worm clade is currently represented by single species or sequence. Therefore, to gain a deeper understanding of their taxonomic boundaries and phylogenetic relationships, it is essential to discover and sequencing additional species across these genera, including *Echinophilia* and *Paraechinophilia*.

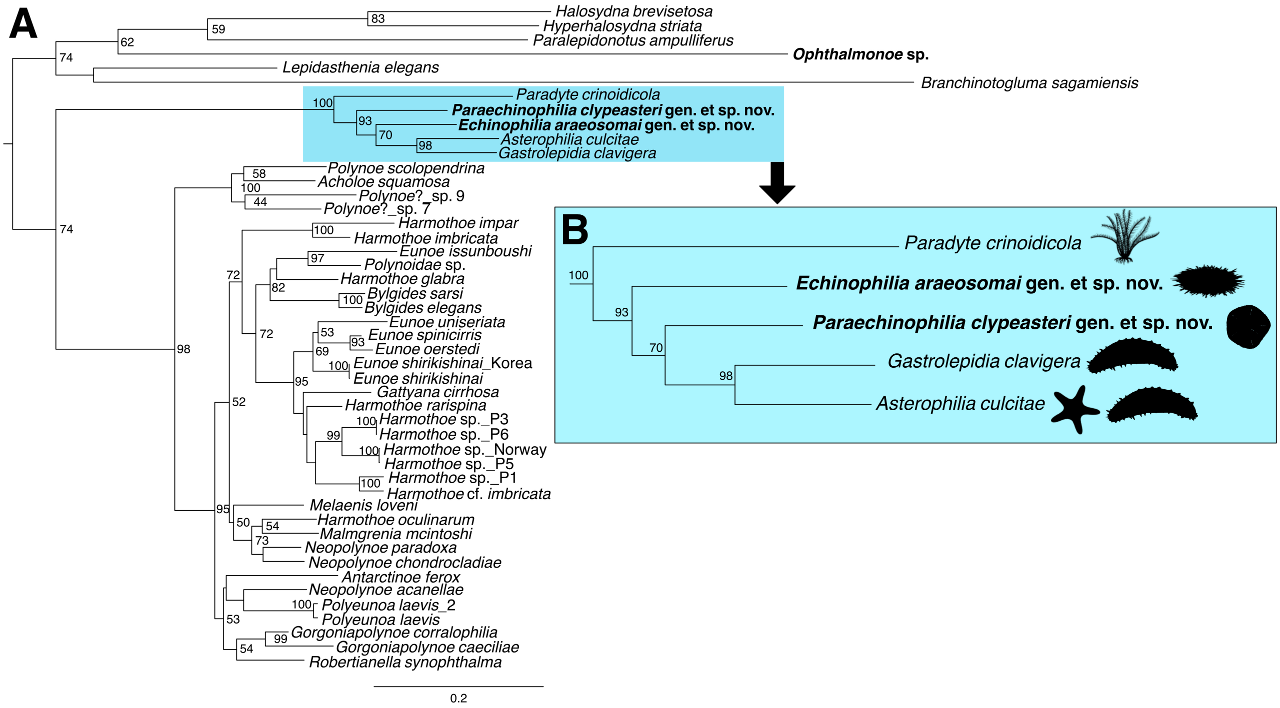

Fig. 8. Maximum-likelihood (ML) phylogenetic tree of Polynoidae based on *COI*, 16S, 18S, and 28S sequences. Nodal support values (bootstrap support [BS] value) higher than 50% are indicated on each branch.

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Authors' contributions: NJ initiated the study, NJ, NH, and HK conducted sampling, SPW and HK identified host specimens, NJ performed morphological and molecular analysis as well as drafted the manuscript. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Competing interests: We declare we have no competing interests.

Availability of data and materials: The accession numbers of specimens have been deposited in the GenBank. The examined specimens are deposited at the National Museum of Nature and Science, Tsukuba, Japan.

Consent for publication: All of the authors agreed to publish the paper.

Ethics approval consent to participate: Not applicable.

REFERENCES

Bogantes VE, Whelan NV, Webster K, Mahon AR, Halanych KM. 2020. Unrecognized diversity of a scale worm, *Polyeunoa laevis* (Annelida: Polynoidae), that feeds on soft coral. Zool Scr **49:**236–249. doi:10.1111/zsc.12400.

Bonifácio P, Menot L. 2019. New genera and species from the Equatorial Pacific provide phylogenetic insights into deep-sea Polynoidae (Annelida). Zool J Linn Soc **185:**555–635. doi:10.1093/zoolinnean/zly063.

Britayev TA, Bratova OA, Dgebuadze PY. 2013. Symbiotic assemblage associated with the tropical sea urchin, *Salmacis bicolor* (Echinoidea: Temnopleuridae) in the An Thoi archipelago, Vietnam. Symbiosis **61:**155–161. doi:10.1007/s13199-013-0263-x.

Capella-Gutiérrez S, Silla-Martínez JM, Gabaldón T. 2009. trimAL: a tool for automated alignment trimming in large-scale phylogenetic analysis. Bioinformatics **25:**1972–1973. doi:10.1093/bioinformatics/btp348.

Carr CM, Hardy SM, Brown TM, Macdonald TA, Hebert PDN. 2011. A tri-oceanic perspective: DNA barcoding reveals geographic structure and cryptic diversity in Canadian polychaetes. PLoS ONE **6:**e22232. doi:10.1371/journal.pone.0022232.

Clark RB. 1956. *Capitella capitata* as a commensal, with a bibliography of parasitism and commensalism in the polychaetes. Annals and Magazine of Natural History 12 th Series **9:**433–448.

Gonzalez BC, González VL, Martínez A, Worsaae KW, Osborn KJ. 2023. A transcriptome-based phylogeny for Polynoidae (Annelida: Aphroditiformia). Mol Phylogenet Evol **185:**107811. doi:10.1016/j.ympev.2023.107811.

Gonzalez BC, Martinez A, Borda E, Iliffe TM, Eibye-Jacobsen D, Worsaae K. 2017. Phylogeny and systematics of Aphroditiformia. Cladistics **34:**225–259. doi:10.1111/cla.12202.

Hourdez S. 2022. Polynoidae Kinberg, 1856. *In*: Purschke G, Böggemann M, Westheide W (Eds) Handbook of Zoology 4. Pleistoannelida, Errantia II, Phyllodocida. de Gruyter GmbH & Company KG, pp. 93–113.

Jangoux M. 1987a. Diseases of Echinodermata. II. Agents metazoans (Mesozoa to Bryozoa). Diseases in Aquatic Organisms **2:**205–234.

Jangoux M. 1987b. Diseases of Echinodermata. III. Agents metazoans (Annelida to Pisces). Diseases in Aquatic Organisms **3:**59–83.

Jimi N, Moritaki T, Kajihara H. 2017. Rare endoparasitic *Asteriormyzostomum* (Annelida: Asteriomyzostomidae) from Japan, including three new species descriptions and their phylogenetic position within Myzsotomida. Parasitol Int **66:**841–847. doi:10.1111/jzs.12463.

Jimi N, Hookabe N, Moritaki T, Kimura T, Imura S. 2021. First evidence of male dwarfism in scale worms: a new species of Polynoidae (Annelida) from hermit crab and molluscan shell. J Zool Syst Evol Res **59:**801–818. doi:10.1111/jzs.12463.

Katoh K, Standley DM. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Mol Biol Evol **30:**772–780. doi:10.1093/molbev/mst010.

Lenaers G, Maroteaux L, Michot B, Herzog M. 1989. Dinoflagellates in evolution. A molecular phylogenetic analysis of large subunit ribosomal RNA. J Mol Evol **29:**40–51. doi:10.1007/BF02106180.

Marin IN, Antokhina TI. 2022. A new symbiotic scale worm (Polychaeta: Polynoidae) living in association with burrowing callianassid shrimps in the Black Sea. Zoosystematica Rossica **31:**272–285. doi:10.31610/zsr/2022.31.2.272.

Martin D, Britayev TA. 1998. Symbiotic polychaetes: review of known species. Oceanogr Mar Biol: An Annual Review **36:**217–340.

Martin D, Britayev TA. 2018. Symbiotic polychaetes revisited: an update of the known species and relationships (1998–2017). Oceanography and Marine Biology: An Annual Review **56:**371–448.

Maxwell J, Taboada S, Taylor ML. 2022. *Gorgoniapolynoe caeciliae* revisited: the discovery of new species and molecular connectivity in deep-sea commensal polynoids from the Central Atlantic. Deep Sea Research Part I: Oceanographic Research Papers **185:**103804. doi:10.1016/j.dsr.2022.103804.

Medlin L, Elwood HJ, Stickel S, Sogin ML. 1988. The characterization of enzymatically amplified eukaryotic 16S-like rRNA-coding regions. Gene **71:**491–499. doi:10.1016/0378-1119(88)90066-2.

Mortensen T. 1935. A Monograph of the Echinoidea. II. Bothriocidaroida, Melonechinoida, Lepidocentroida, and Stirodonta. C. A. Reitzel & Oxford University Press, Copenhagen & London, 647 pp.

Mortensen T. 1948. A Monograph of the Echinoidea. IV, 2. Clypeasteroida. Clypeasteridæ, Arachnoidæ, Fibulariidæ, Laganidæ and Scutellidæ. C. A. Reitzel, Copenhagen, 471 pp.

Norlinder E, Nygren A, Wiklund H, Pleijel F. 2012. Phylogeny of scale-worms (Aphroditiformia, Annelida), assessed from 18SrRNA, 28SrRNA, 16SrRNA, mitochondrial cytochrome *c* oxidase subunit I (*COI*), and morphology. Mol Phyl Evol **65:**490–500. doi:10.1016/j.ympev.2012.07.002.

Núñez J, Barnich R, Monterroso Ó. 2022. A new genus and species of Polynoidae (Annelida: Polychaeta) from the Canary Islands, and update on taxa present in the Northeast Atlantic. Eur J Taxon **846:**55–74. doi:10.5852/ejt.2022.846.1965.

Palumbi SR, Martin A, Romano S, McMillan WO, Stice L, Grabowski G. 1991. A Simple Fool's Guide to PCR. Honolulu, HI: University of Hawaii Press.

Petersen ME, Britayev TA. 1997. A new genus and species of polynoid scaleworm commensal with *Chaetopterus appendiculatus* Grube from the Banda Sea (Annelida: Polychaeta), with a review of commensal of Chaetopteridae. B Mar Sci **60:**261–276.

Rahman IA, Zamora S. 2024. Origin and early evolution of echinoderms. Ann Rev Earth PL Sc **52:**295–320. doi:10.1146/annurev-earth-031621-113343.

Reich A, Dunn C, Akasak K, Wessel G. 2015. Phylogenomic analyses of Echinodermata support the sister groups of Asterozoa and Echinozoa. PLoS ONE **10:**e0119627. doi:10.1371/journal.pone.0119627.

Serpetti N, Taylor ML, Brennan D, Green DH, Rogers DH, Paterson GLJ, Narayanaswamy BE. 2017. Ecological adaptations and commensal evolution of the Polynoidae (Polychaeta) in the Southwest Indian Ocean Ridge: A phylogenetic approach. Deep-Sea Res II **137:**273–281.

Stamatakis A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics **22:**2688–2690. doi:10.1093/bioinformatics/btl446.

Stroch V, Niggemann R. 1967. Auf Echinodermen lebende Polychaeten. Kieler Meeresforschungen **23:**156–164.

Summers M, Rouse G. 2014. Phylogeny of Myzostomida (Annelida) and their relationships with echinoderm hosts. BMC Evol Biol **14:**170. doi:10.1186/s12862-014-0170-7.

Taboada S, Silva AS, Díez-Vives C, Neal L, Cristobo J et al. 2021. Sleeping with the enemy: unravelling the symbiotic relationships between the scale worm *Neopolynoe chondrocladiae* (Annelida: Polynoidae) and its carnivorous sponge hosts. Zool J Linn Soc **193:**295–318. doi:10.1093/zoolinnean/zlaa146.

Taboada S, Silva AS, Neal L, Cristobo J, Ríos P et al. 2020. Insights into the symbiotic relationship between scale worms and carnivorous sponges (Cladorhizidae, Chondrocladia). Deep Sea Res Part I **156:**103191. doi:10.1016/j.dsr.2019.103191.

Tanabe AS. 2007. KAKUSAN: a computer program to automate the selection of a nucleotide substitution model and the configuration of a mixed model on multilocus data. Mol Ecol Notes **7:**962–964. doi:10.1111/j.1471-8286.2007.01807.x.

Tamura K, Stecher G, Kumar S. 2021. MEGA11: Molecular Evolutionary Genetics Analysis version 11. Mol Biol Evol **38:**3022–3027. doi:10.1093/molbev/msab120.