Two new species of *Parahesione* (Annelida: Hesionidae) associated with ghost shrimps (Crustacea: Decapoda) and their phylogenetic relationships

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Abstract

Two new species of Hesionidae, *Parahesione pulvinata* sp. nov. and *Parahesione apiculata* sp. nov. are described based on materials collected at tidal flats in Okinawa (Japan) from burrows of the ghost shrimps *Neocallichirus jousseaumei* and *Glypturus armatus*. The two new species ~~*Parahesione pulvinata* sp. nov. and *Parahesione apiculata* sp. nov.~~ are characterized by~~: *i)*~~ having eight enlarged cirri~~,~~ ~~*; ii)* having~~ flattened dorsal cirrophores and biramous parapodia~~;~~ , and by~~*iii)*~~ lacking median antenna~~; and *iv)* having biramous parapodia~~. *Parahesione apiculata* sp. nov. ~~is distinguished from *P. pulvinata* sp. nov. by~~ ha~~s~~ving digitate lobes on the posterior margin of

the dorsal cirrophores (absent in *P. pulvinata* sp. nov.) and ~~having~~ large dorsal cirrophores from chaetiger 1 (from ~~chaetiger~~ 6 in *P. pulvinata* sp. nov.). The two new species were never found outside ~~of~~ the ghost shrimp burrows, suggesting ~~that~~ they are obligate symbionts. Phylogenetic analyses based on four concatenated genes suggest that ~~a~~ the symbiotic lifestyle ~~in hesionids~~ has evolved several times in Hesionidae.

Introduction

The narrow ~~Decapod~~ burrows excavated by decapods in tidal flats are frequently ~~serve as habitats for~~occupied by different symbionts (Campos et al. 2009; Pillay and Branch 2011). ~~These~~ However, these ~~narrow burrows provide~~ safe ~~environments~~habitats~~, but~~ must be shared with decapod hosts, often under hypoxic conditions (Atkinson & Taylor 2005) to which ~~.~~ ~~Nevertheless,~~ some symbionts become~~are~~ adapted ~~to this mode of life~~ (Pillay & Branch 2011). These~~;~~ includ~~ing~~e polynoid and hesionid polychaetes living in burrows of callianassid ghost shrimps and upogebiid mud shrimps (Martin and Britayev 1998).

~~—~~Hesionidae includes more than ~~180~~ 199 species (~~Rouse et al. 2018, 2022~~Read & Fauchald, 2023[DM1]), with about 30 being considered obligate or facultative invertebrate ~~symbionts (mainly echinoderms)~~symbionts, mainly living in association with echinoderms, but also with ~~. Several species inhabit~~ burrow~~ing~~s ~~of~~ sipunculids, hemichordates and ~~burrowing~~ polychaetes, among others ~~or are otherwise symbiotic with other animals~~ (Martin and Britayev 1998, 2018; Martin et al. 2017; Rouse et al. 2018). However, ~~but~~ only ~~*two species,*~~ *Parahesione luteola* (Webster, 1879) and *Parahesione* sp. ~~were found in~~are known from mud shrimp burrows (Pettibone 1956; Britayev & Antokhina 2012).

The phylogenetic relationships among hesionids are well known, providing an excellent base to assess the evolution of morphological characters (Ruta et al. 2007; Martin et al. 2015; Bonifacio et al. 2018; Rouse et al. 2018). However, additional studies are required to understand (1) the nature of their adaptations to a symbiotic mode of life and (2) the evolutionary consequences of their symbiotic relationships with burrowing decapods~~ and their burrows, which may help~~to try to elucidate their ~~ability to be~~ adapt~~ability~~ed to different environmental condition~~s~~.

In this ~~study~~paper, we are describing two new species of Hesionidae ~~based on the specimens collected from~~living inside burrows of callianassid ghost shrimps~~.~~ and ~~W~~we ~~also~~ analyze the phylogenetic relationships within the family, based on four concatenated genes, ~~in order~~ to ~~understand~~ assess the evolution of ~~both~~ both ~~the~~ symbiotic species and their adaptations to living inside decapod burrows.

Materials & Methods

~~Hesionid~~ The specimens were collected with a yabby pump from inside of the burrows of *Neocallichirus jousseaumei* (Nobili, 1904) (Axiidea: Eucalliacidae) and *Glypturus armatus* (A. Milne-Edwards, 1870) (Gebiidea: Upogebiidae), ~~which~~ living~~es~~ in tidal flats throughout the

Ryukyu Islands, Japan (Fig. 1). All specimens were fixed and preserved in 70% ethanol. Additional studied specimens were reported as: (1) *Parahesione* sp. ~~used in (~~Britayev & Antokhina ~~(~~2012)~~,;~~ (2) *Parahesione* sp. ~~used in (~~Ruta et al. ~~(~~2007, first paragraph, page 101), reported as *P. luteola* in GenBank; (3) *Parahesione* ~~collected~~ from Papua New Guinea, collected by GW~~reg~~ R~~ouse,~~ likely from ~~the~~ burrow of *Calliaxina bulimba* (Poore & Griffin, 1979) (Axiidea: Eucalliacidae)~~,;~~ and (4) *P~~arahesione~~. luteola* ~~used in (~~Pettibone, ~~(~~1956) (No. USNM 430 and 28175)~~ were also studied. On GenBank, the Ruta et al (2007)'s sequence is called *Parahesione luteola*. However, in the paper, they concluded it was undescribed species *Parahesione* sp. (Ruta et al. 2007, the first paragraph of pp. 101). The Genbank name is therefore incorrect and is treated as *Parahesione* sp. in this study~~.

The Japanese specimens were observed using a Nikon SMZ1500 dissecting microscope and a Nikon ECLIPSE Ni-U compound light microscope. Photographs were taken with an Olympus OM-D5 digital camera. The Papua New Guinea specimen was ~~studied~~ observed with a Leica MZ9.5 stereomicroscope and photographed with a Canon Rebel T3i camera.

T~~he t~~ype specimens ~~were~~ are deposited in the National Museum of Nature and Science, Tsukuba, Japan (NSMT) and the Scripps Institution of Oceanography Benthic Invertebrate Collection, La Jolla, California, USA (SIO-BIC). The following abbreviations are used ~~I~~in the 'Material examined' section: CS~~,~~ (complete specimens)~~ are indicated by 'CS'.~~, ~~The length (~~L~~)~~ (length, ~~i~~s measured from the anterior margin of the prostomium to the posterior border of the last segment), W~~, while the~~ ~~width~~ (~~W)~~ width ~~is taken~~ at the widest segment, including parapodia but excluding chaetae).

The total DNA of~~For~~ the Japanese holotype ~~specimens, total DNA~~ was extracted from a dissected parapodium using a DNeasy Tissue Kit (Qiagen) ~~from a parapodium of holotype~~. The reaction mixture [0.2 μL TaKaRa Ex Taq (Takara, Japan), 2 μl of 10 × Ex Taq Buffer (Takara, Japan), 1.8 μL dNTP mixture (Takara, Japan), 1 μL of each primer pair (10 μM), 1 μL of extracted DNA, and 14 μL of distilled water] was used for PCR amplification, which~~. PCR amplification~~ was performed with the primer pairs: (1) polyLCO (5'-GAYTATWTTCAACAAATCATAAAGATATTGG-3') and polyHCO (5'-TAMACTTCWGGGTGACCAAARAATCA-3') for part of mitochondrial cytochrome *c* oxidase subunit I gene (*COI*) (Carr et al. 2011), (2) 16SarL (CGCCGTTTATCAAAAACAT) and 16SbrH (CCGGTCTGAACTCAGATCACGT) for the part of mitochondrial 16S rRNA gene (*16S*) (Palumbi et al. 1991), (3) 1F (TACCTGGTTGATCCTGCCAGTAG) and 9R (GATCCTTCCGCAGGTTCACCTAC) (Giribet et al. 1996) for the part of nuclear 18S rRNA gene (*18S*), and (4) LSU5 (TAGGTCGACCCGCTGAAYTTAAGCA) and rd5b (CCACAGCGCCAGTTCTGCTTAC) (Littlewood 1994; Schwendinger & Giribet 2005) for the part of nuclear 28S rRNA gene (*28S*) gene. We~~,~~ used~~ing~~ an Applied Systems 2720 thermal cycler following the protocol: (a) for *COI* and *16S*, preheating at 94°C for 2 min; 35 cycles at 94°C for 40 s, 50°C for 60 s, and 72°C for 60 s; and a final extension at 72°C for 7 min; (b) for *18S* and *28S* preheating at 94°C for 2 min; for 18S and 28S, 35 cycles at 94°C for 40 s, 52°C for 75 s, and 72°C for 60 s; and a final extension at 72°C for 7 min. Nucleotide sequencing was

performed using internal primers in addition to the same primer pairs with an ABI BigDye Terminator ver. 3.1 Cycle Sequencing Kit and an ABI 3100 Avant Genetic Analyser (Applied Biosystems). The internal primers were: (1) 3F (GTTCGATTCCGGAGAGGGA) and 5R (CTTGGCAAATGCTTTCGC) (Giribet et al. 1996) and 18Sbi (GAGTCTCGTTCGTTATCGGA) and a2.0 (ATGGTTGCAAAGCTGAAAC) (Whiting et al. 1997) for *18S*, and (2) D2F (CTTGAAGAGAGAGTTC) and D3R (ATAGTTCACATCTTTCGG) (Littlewood 1994) for *28S*. ~~For t~~The *Parahesione* ~~collected~~ from Papua New Guinea were extracted~~ion protocols were~~ following~~ed from~~ Rouse et al. (2018) and *COI* was generated for the specimen. ~~The~~ All newly obtained sequences *COI* (625 bp), *16S* (552 bp), *18S* (1677 bp), *28S* (987 bp) were deposited in GenBank.

~~A total of 200~~Two-hundred sequences (59 species) were used for molecular analyses, including~~. A total of~~ 190 ~~sequences were~~ downloaded from GenBank (https://www.ncbi.nlm.nih.gov/genbank)~~, and the remaining sequences were from this study~~. All ~~sequences~~ them were aligned using MAFFT ver. 7.205 according to the E-INS-i strategy (Katoh & Standley 2013). Alignment-ambiguous positions were removed using trimAL with the gappyout method (Capella-Gutiérrez et al. 2009). The trimmed sequences of the four genes, *COI* (657 bp), *16S* (513 bp), *18S* (1654 bp), and *28S* (947 bp), were concatenated using the program Kakusan (Tanabe 2007), which recommended a GTR+G evolutionary model for each of the genes. A phylogenetic tree was constructed using the maximum likelihood (ML) method in the RAxML-VI-HPC program (Stamatakis 2006). The robustness of the ML tree was evaluated by 1,000 bootstrap pseudo-replicates (F option) and the bootstrap support (BS) is indicated as %. Bayesian Inference (BI) analysis was conducted using MrBayes 3.2.2 (Ronquist et al. 2012), with Markov chains of 10 million generations. The model choice for each partition was also based on the Kakusan results. Run convergence was analyzed using Tracer v1.6 (Rambaut et al. 2018); the first one million generations were discarded as burn-in. *Dysponetus caecus* (Langerhans, 1880) was used as the outgroup following Rouse et al. 2018 and Tillic et al. (2022). Additionally, four species were used for calculating K2P genetic distances using MEGAX (Stecher et al. 2020). The hesionids were classified into three groups: obligate and facultative symbionts, according to Martin et al. (2017), and free-living based on previously published data (Table 2).[DM2]

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Results

Systematics

Ophiodrominae Pleijel, 1998

Amphidurini Pleijel et al., 2012

***Parahesione* Pettibone, 1956**

Diagnosis (emended). Body flattened, reddish when alive. Prostomium with two lateral antennae, without median antenna, two pairs of eyes. Palps with or without palpophores. Six or eight pairs ~~Anterior enlarged~~of tentacular cirri ~~as six or eight pairs~~. Cirrophores of ~~D~~dorsal cirri ~~cirrophores~~ cylindrical or flat. Parapodia biramous. Notopodia with numerous capillary chaetae. Neuropodia with numerous compound chaetae.

Remarks. [DM3]*Parahesione* ressembles in having enlarged dorsal cirri on segments 1–5, but differs in lacking median antenna (having a short one in *Amphiduros* and *Amphiduropsis*).

Parahesione pulvinata sp. nov.

[New Japanese name: ana-yadori-otohime]

(Figs. 2–5)

LSID: urn:lsid:zoobank.org:act:2E42DB94-DF8C-447A-A7F8-8C2FDA9FF4CA

Parahesione sp.: Britayev and Antokhina (2012): 33, Pl. 9 C, D

~~Zoobank LSID: urn:lsid:zoobank.org:act:2E42DB94-DF8C-447A-A7F8-8C2FDA9FF4CA~~

Material examined. Holotype: NMST-Pol H-893 (museum numbers will be provided by NSMT after accepting this manuscript), Genbank No.: COI OP404166, 16S OP407585, 18S OP407566, 28S OP407536, CS, L18 mm, W 4 mm for 45 chaetigers, East China Sea, Iriomote Island, Uehara, intertidal area, ~~burrow of~~associated to *N.~~eocallichirus~~ jousseaumei*, 5 September 2020, collected by HN. Paratypes: NSMT-Pol P-894, CS, L 20 mm, W 5 mm for 45 chaetigers, same collection data ~~same~~ as holotype, but ~~(~~from another burrow of *N. jousseaumei*~~)~~. Paratypes: NSMT-Pol P-895, CS, L 17 mm, W 4 mm for 39 chaetigers, East China Sea, Iriomote Island, Uehara, Todomari Beach, 1–2 m in depth, associated to a ~~burrow of~~ unknown crustacean~~s~~, 24 January 2021, collected by TS. Paratypes: NSMT-Pol P-896, CS, L 18 mm, W 4 mm for 36 chaetigers, East China Sea, Okinawa Island, Sunabe, intertidal, associated to a ~~burrow of~~ unknown crustacean~~s~~, 20 September 2021, collected by TS. Paratypes: NSMT-Pol P-897, CS, L 12 mm, W 3 mm for 24 chaetigers, East China Sea, Okinawa Island, Kouri, intertidal, associated to a ~~burrow of~~ unknown crustacean~~s~~, 27 February 2021, collected by HN. SIO-BIC A13742, 1 specimen, Madang Lagoon, Tab Island, Madang Province, Papua New Guinea, 5.17° S; 145.84° E, likely ~~in burrow of~~associated to *C.~~alliaxina~~ bulimba,* 13 December 2012, collected by Art Anker and ~~Greg Rouse~~GWR.

Additional material: IPEE RAS – Pol. 2004/01, 1 specimen in four fragments, L 19.5 mm, W 4.4 mm for 48 chaetigers, South China Sea, Nhatrang Bay, River Be estuary, intertidal, sandy silt, ~~burrows of~~associated to *Upogebia* sp., 18 April 2004, collected by Ivan Marin.

~~——~~**Description of holotype**[DM4]**.** Body flat, tapered in posterior region, reddish when alive (Fig. 2), pinkish after fixation (Fig~~s~~. ~~2~~[DM5]~~,~~–3). Prostomium rectangular, wider than long (Figs. 3E, 4A). Lateral a~~A~~ntennae cylindrical, distally tapering[DM6]. Palpophores cylindrical, shorter than antennae[DM7]. Palpostyles cylindrical, thinner than [DM8]palpophores, ~~shorter than antennae (~~2/3 of antennae length~~)~~. Two pairs of eyes, inconspicuous when alive (Fig. 3A, 3E), brownish after fixation[DM9]~~., inconspicuous~~ [DM10]~~when alive (Fig. 3E).~~

Cirrophores of tentacular cirri cylindrical, basally fused; ~~Dorsal enlarged~~ tentacular cirri on segments 1–5 (dorsal, longest one reachinged chaetiger 8)~~,~~ and ~~ventral enlarged cirri on segments~~ 1–4 (ventral)[DM11]. Chaetae absent from segments 1–4. ~~Cirrophores of enlarged cirri segments cylindrical, basally fused.~~

~~Parapodia with chaetal lobes cylindrical, truncate, longer~~ [DM12]~~than wide. Chaetiger 1 uniramous. Chaetiger 2 and following chaetigers biramous.~~ Dorsal cirrophores of chaetigers 1–5 cylindrical~~, normal hesionid shape~~ (Fig. 4B)~~:.~~ F~~f~~rom chaetiger 6~~, dorsal cirrophores~~ large, pillow shaped, extremely flattened, partially covering subsequent segment (Fig. 3C[DM13])~~:.~~ all ~~D~~dorsal cirrostyles long, conical, smooth[DM14]. Ventral cirrophores ~~not developed,~~ fused to parapodia~~:.~~ ~~V~~ventral cirrostyles short, conical, smooth (Fig. 3D). Noto- and neuro aciculae brownish, tip of aciculae not seen in vivo, reddish after fixation[DM15]~~, unknown in alive~~.

All chaetigers biramous except chaetiger 1 (uniramous). Parapodia with chaetal lobes cylindrical, truncate, longer [DM16]than wide; ~~N~~notopodia small, conical, with about 40 simple capillary notochaetae~~.~~; ~~N~~neuropodia large, truncated, with prechaetal lobes and a postero-dorsal digitiform projection [DM17](Fig. 4C) and about 30 compound neurochaetae with unidentate serrated blades; blades ~~of~~ in most ventral chaetae shorter [DM18]than in most dorsal (Fig. 4D, 4E). Pygidium with two long [DM19]smooth anal cirri~~, smooth~~.

~~——~~**Etymology.** The specific name "*pulvinata*", derived from the Latin *pulvinus* (meaning cushion, pillow)~~ and~~, referring to the shape of dorsal cirrophores. The specific name is an adjective in the nominative case.

~~——~~**Remarks.** *Parahesione pulvinata* sp. nov. resemble *P. luteola*, the type species of the genus and the single previously known, in lacking the median antenna while having a flattened body and living symbiotically with ghost shrimps. However it differs in having flattened dorsal cirrophores and eight tentacular anterior cirri (cylindrical and six in *P. luteola*). *Parahesione* sp. from Vietnam and Papua New Gui~~e~~ni~~c~~a (Fig. 5) are morphologically identical to the Japanese materials, therefore confirming that they belong to *P. pulvinata* sp. nov. The COI sequences for the Japanese and Papua New Guinea were only slightly divergent ~~and the haplotype network is shown in (~~Figure 9~~)~~.[DM20]

~~——~~**Distribution and habitat.** Ryukyu Islands (Japan, East China Sea), Nhatrang Bay (Vietnam, South China Sea), and Madang Lagoon, Papua New Guinea (Southwestern Pacific

Ocean), in intertidal mud flats, living inside burrows of *N. jousseaumei* ~~(Axiidea: Eucalliacidae)~~ (Japan) and *Upogebia* sp. ~~(Gebiidea: Upogebiidae)~~ (Vietnam), or at 1–5 m inside burrows of ~~*Calliaxina*~~ *C. bulimba* ~~(Axiidea: Eucalliacidae)~~.

Parahesione apiculata sp. nov.
[New Japanese name: toge-ana-yadori-otohime]
(Figs. 6–8)
Zoobank LSID: urn:lsid:zoobank.org:act:1AB8DAA4-2268-445D-A3A6-9AE9C085A856

Material examined. Holotype: NSMT-Pol H-898, Genbank No.: COI OP404167, 16S OP407586, 28S OP407537, specimen with posterior part lost, L 12 mm, W 4 mm for 28 chaetigers, Philippine Sea, Okinawa Island, Shikenbaru beach, 1–2 m in depth, burrow of ~~*Glypturus*~~ *G. armatus*, 23 December 2019, collected by TS. Paratype: NSMT-Pol P-899, specimen with posterior part lost, L 8 mm, W 4 mm for 20 chaetigers, Philippine Sea, Okinawa Island, Nanjo, Ou beach, intertidal, burrow of *G. armatus*, 20 August 2021, collected by HN. Paratype: NSMT-Pol P-900, specimen with posterior part lost, L 9 mm, W 3 mm for 24 chaetigers, East China Sea, Okinawa Island, Kujyuzaki, intertidal, burrow of *G. armatus*, 22 August 2021, collected by TS.

Description of holotype[DM21]**.** Body flat, tapering in posterior region, reddish when alive (Fig. 6), pale orange ~~after fixation~~when preserved (Figs~~. 6,~~ 7).

Prostomium rectangular, wider [DM22]than long (Fig. 8A). Lateral a~~A~~ntennae cylindrical, tapering distally[DM23]. Palpophores cylindrical~~.~~; ~~P~~palpostyles cylindrical, thinner [DM24]than palpophores, ~~shorter than antennae (~~5/7 of antennae length~~)~~. ~~Eyes present, t~~Two pairs of eyes, ~~brownish after fixation, unknown~~ not seen in vivo (Fig. 6 D)~~, alive~~ [DM25]brownish after fixation (Fig. 7E).

Cirrophores of tentacular cirri cylindrical, basally fused; ~~Dorsal enlarged~~ tentacular cirri on segments 1–5 (dorsal) ~~,~~ and~~ventral enlarged cirri on segments~~ 1–4 (ventral), longest [DM26]one reaching chaetiger 8~~ in holotype~~. Chaetae absent on segments 1–4.~~ Cirrophores of enlarged cirri segments cylindrical, basally fused~~.

~~Parapodia with chaetal lobes cylindrical, truncate, longer than wide. Chaetiger 1 uniramous. Chaetiger 2 and following chaetigers biramous. From chaetiger 1,~~All dorsal cirrophores ~~of chaetiger 1 and following chaetigers~~ large, extremely flattened, partially covering subsequent segment, with a digitate lobe on posterior ~~side~~ margin (Figs. 7C, 8B~~). .~~); ~~D~~dorsal cirrostyle long, conical, smooth (Fig. 7C[DM27]). Ventral cirrophore fused with parapodia~~.~~; ~~Ventral~~ ventral cirrostyle short[DM28], conical, smooth. Noto- and neuroaciculae not seen in vivo, brownish~~,~~ with reddish tips ~~after fixation~~when preserved~~, unknown in alive~~.

All chaetigers biramous except chaetiger 1 (uniramous). Parapodia with chaetal lobes cylindrical, truncate, longer than wide. Notopodia small, conical, with about 40 simple capillary notochaetae. Neuropodia large, truncated, with pre- and post-chaetal lobes and a digitiform projection present on postero-dorsal part [DM29](Fig. 7C, 8B). About 30 compound neurochaetae

with unidentate serrated blades, those; blades in most ventral chaetae shorter [DM30]than in most dorsal side chaetae (Fig. 8C, 8D). Pygidium with two long anal cirri, smooth.

Etymology. The specific name "*apiculata*", derived derives from the Latin *apiculatus* (meaning short pointed) and referring to the digitate lobe on posterior side margin of dorsal cirrophores, is as an adjective in the nominative case.

Remarks. Like *P. pulvinata* sp. nov., *P. apiculata* sp. nov. resemble *P. luteola* in lacking the median antenna, having a flattened body and living symbiotically with ghost shrimps, while differing in having flattened dorsal cirrophores and eight tentacular anterior cirri (cylindrical and six in *P. luteola*). *Parahesione apiculata* sp. nov. differs from *P. pulvinata* sp. nov. is characterized by the following features: i) in having digitate lobes on posterior margin of dorsal cirrophores (absent in *P. pulvinata* sp. nov.) and, ii) having large dorsal cirrophores from the firstfrom chaetiger 8 (from chaetiger 6 in *P. pulvinata* sp. nov.), as well as in iii) living in association with the burrows of *G. armatus* (compared to *N. jousseaumei, C. bulima* and *Upogebia* sp. in *P. pulvinata* sp. nov.).

Distribution and habitat. Ryukyu Islands (Japan, Philippine Sea and East China Sea), in intertidal mud flats, living inside burrows of *G. armatus*.

Molecular analyses

Parahesione apiculata sp. nov. and *Parahesione* sp. from Papua New Guinea form a clade, sister to *P. pulvinata* sp. nov with 69% of BS in ML and 0.99 of PP in BI (Fig. 9A[DM31]). *Parahesione pulvinata* sp. nov. forms a sister clade to the *P. apiculata Parahesione* sp. clade, with 95% of BS in ML and 1.00 PP[DM32]. . Alltogether, they constitute tThe *Parahesione* clade which, in turn, is sister to the clade *Amphiduros–Amphiduropsis* clade (Fig. 9[DM33])with 95% of BS in ML and 1.00 PP in BI. COI K2P genetic distance for the COI sequences between the two new species is 11.0%. (Uncorrected genetic distance is 10.1% uncorrected).[DM34]

Discussion

Phylogenetic position of two new species and its relationships with *Parahesione* species and other hesionids

The two new species resemble *Parahesione luteola*, which is type species of *Parahesione*, in lacking a median antenna while having a flattened body and living symbiotically with ghost shrimps, while differing by having flattened dorsal cirrophores and eight enlarged anterior cirri, instead of cylindrical dorsal cirrophores and six enlarged anterior cirri. *Parahesione luteola* has beenwas reported from oyster shells and burrows of *Upogebia affinis* (Say, 1818) in the Atlantic coast of the United States of America (Pettibone 1963) and is regarded as a facultative symbiontic species (Martin and Britayev 1998). Unidentified species of *Parahesione* species have beenwere known from several areas, includingreported from: the Arctic Sea (Atkinson and Percy 1991), Australia (Gunton et al. 2021), Costa Rica (Maurer, Vargas, and Dean 1988), New

Caledonia (Ruta et al. 2007) and Vietnam (Britayev and Antokhina 2012). The Vietnamese specimen is here considered as belonging to *P. pulvinata* sp. nov., as suggested by Britayev and Antokhina (2012) and discussed above in the corresponding Remarks section. The specimen of *Parahesione* sp. collected by Ruta et al. (2007) in Papua New Guinea (Pacific Ocean) and form the *Parahesione* clade together with our the two new species fall into the same clade. However, our observations confirm the it has six enlarged cirri and non-flattened dorsal cirrophores (Fig. 10A, B), like *P. luteola* (Fig. 10C, D). Our molecular results, together with the large geographical distance between them (Pacific vs. specimen identified by Ruta et al. (2007) as *Parahesione* sp. was collected in New Caledonia (Pacific Ocean), far from the type locality of the single known species of the genus, the eastern Atlantic, respectively coast of the United States (Pettibone1956). We) suggest that the reexamined the specimen from Papua New Guinea could belong to an undescribed used in Ruta et al. (2007) and confirmed that the specimen has six enlarged cirri and non-flattened dorsal cirrophores (Fig. 10A, B) and is likely another new species, whose formal description would require new morphological and molecular data based on newly collected materialsbut is not described here. In fact, there is a single partial sequence of 28S (381 bp) available for the specimen from Papua New Guinea, while we could not obtain sequences from other genes because the specimen we received as a loan was preserved in formalin. Additionally, we observed the specimens of *P. luteola* in the USNM (Fig. 10C, D). The specimens showed *P. luteola* has six enlarged cirri and non-flattened dorsal cirrophores in according with Pettibone (1956)'s description.

——— Nevertheless, the inclusion of our new species in In this situation, we assign these species to the same genus *Parahesione*, led us to amend and modify the genus diagnosis of the genus. However, we could not discard further distinguishing However, the DNA repository data for *Parahesione* sp. used in Ruta et al. (2007) is very limited, with only a single partial sequence of 28S (381 bp). We could not determine the other gene sequences because the specimen was preserved in formalin. Given the situation described above, it is possible that the two morpho-types of *Parahesione* (i.e., six vs. eight vs. enlarged cirri & and non-flattened vs. flattened dorsal cirrophores vs. six enlarged cirri & non-flattened dorsal cirrophores) could be distinguished on a molecular phylogenetic tree if they areonce re-examined with additional specimens and, thus, gene sequences, could be examined. Overall our phylogenetic results (Fig. 9) showed thatplace *Parahesione* as closest to thesister to the *Amphiduros-Amphiduropsis* clade, in agreement consistent with Ruta et al. (2007), andthus supporting its inclusion in Amphidurini as suggested by Pleijel et al. (2012). *Amphiduros* and *Amphiduropsis* also have enlarged dorsal cirri on segments 1–5, but bear a short median antenna, distinguishing them from *Parahesione*.

Despite their obvious morphological and molecular differences, *P. apiculata* sp. nov. and *P. pulvinata* sp. nov. have always been found inside ghost shrimp burrows,[DM35] suggesting they are obligate symbionts. Moreover, they have always been found in association with *G. armatus* and with *N. jousseaumei* (Axiidea: Eucalliacidae) and *Upogebia* spp. (Gebiidea: Upogebiidae), (however, the identification of the latter host was rough andstill requiring a more precise identification, needs to be confirmedJimi pers. obs.), thus suggesting a high degree of host

specificity. Moreover, like many other symbiotic polychaetes (Martin, and Britayev 1998, 2018), both species show morphological adaptations to symbiosis. These include flat bodies, which may facilitate the worm movement between the host body and the walls of the narrow burrows[DM36]. Flat bodies have been reported for symbiotic polynoids living in association with tube dwelling chaetopterids, which also have to move between the host body and the tube walls (Britayev et al. 2017; Britayev and Martin 2021). Another interesting adaptation is the extreme flatness of their dorsal cirrophores, which is not found in the non-symbiotic species of the *Amphiduropsis-Amphiduros* sister clade. We suggest this flat cirrophores may help the worms to increase the body surface either to be in contact with the host or with the burrow walls. Body expansions in symbiotic polychaetes have been only previously reported for *Gastrolepidia clavigera* Schmarda, 1861, which shows ventral sucker-like lobes increasing the body surface in contact with the slippery holothurian host body and, combined with body arching, probably have a sucker-like function (Gibbs 1971[DM37], Martin and Britayev 1998).

The bodies of the two new species also have bright red-color when alive. Agai, this contrasts with the free-living species of the *Amphiduropsis-Amphiduros* clade, suggesting this trait was newly acquired in *Parahesione*. A bright red color was also reported for the species of *Hesperonoe* (Polynoidae), which also live in association with mud shrimps (Sato et al. 2001; Hong et al. 2017), while some crustacean-associated mollusks have red blood cells that are considered as an adaptation to thrive in the burrow hypoxic conditions (Goto et al. 2018). Therefore, we agree with Martin and Britayev (2018), who suggested that red bodies (likely associated to the presence of dissolved pigment) in *Hesperonoe* may be an adaptation to live in the burrows' hypoxic environment. Further observations based on living specimens and histological sections are thus required to confirm the presence of these red coelomocytes[DM38], and thus, to assess whether the red color in *Parahesione* is also an adaptation to live in hypoxic conditins.

Conclusions

The genus *Parahesione*, belonging to Hesionidae, is a rare group with poorly understood ecology[DM39]. We have discovered two new *Parahesione* species associated with ghost shrimps from the northwest Pacific. Through morphological observations and phylogenetic tree reconstruction using four genes, we have revealed how their symbiotic relationship with ghost shrimp has evolved[DM40] and what morphological characteristics have been acquired as a result. This is the first record of the genus *Parahesione* from Japan.

Acknowledgements

We thank Philippe Bouchet (Muséum national d'Histoire naturelle, Paris), who organized the Madang field trip (Papua New Guinea Revisited) and James Thomas (Nova Southeastern University) for support for Madang collecting by GWR, and to Art Anker who collected the specimen. Thanks also to Charlotte Seid (SIO-BIC) for cataloguing, and to Avery Hiley for DNA sequencing, the PNG material.

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FIGURE[DM41] AND TABLE LEGENDS

Figure 1. Sampling locations for type specimens
Red stars: *Parahesione pulvinata* sp. nov.; ~~(Red star) and~~ Blue dot: *Parahesione apiculata* sp. nov. ~~(Blue dot)"~~

Figure 2. [DM42]~~Observations of~~ *Parahesione pulvinata* sp. nov. *In situ* observations, ~~and its hosts~~host (*Neocallichirus jousseaumei*) and symbiont specimens ~~in situ~~
A, sampling at the sandy tidal fat of Uehara; B, a host ~~and the new species~~with one symbiont on the filtration sieve; C, detail of the host ~~*Neocallichirus jousseaumei*~~; D, another host with its symbiont (inside a plastic tube); E, dorsal view ~~of the new species~~ of a living specimen of the new species (NSMT-Pol H-893); F, dorsal view of ~~a preserved~~ the same specimen, a preserved ~~(NSMT-Pol H-893)~~.

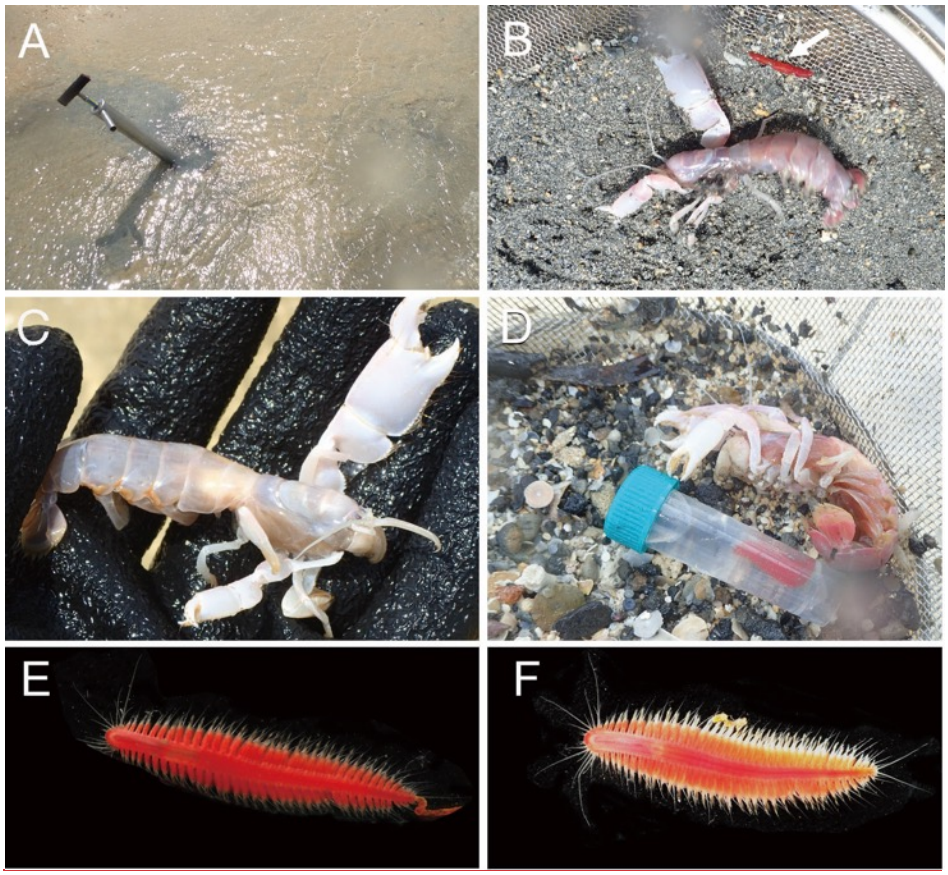

Figure 3. [DM43]*Parahesione pulvinata* sp. nov. (NSMT-Pol H-893)
A, whole specimen, dorsal view; B, whole specimen, ventral view; C, middle segments, dorsal view (white triangles pointing on pillow-shaped dorsal cirrophores); D, middle segments, ventral view; E, anterior end, dorsal view; F, anterior end, ventral view. ~~White arrows indicate pillow-shaped dorsal cirrophore without digitate lobes~~.
Abbreviations: la, lateral antenna; p, palp; ec, enlarged cirrus. Scale bars: A3B, 5 mm; C3D, 2 mm; E3F, 1 mm.

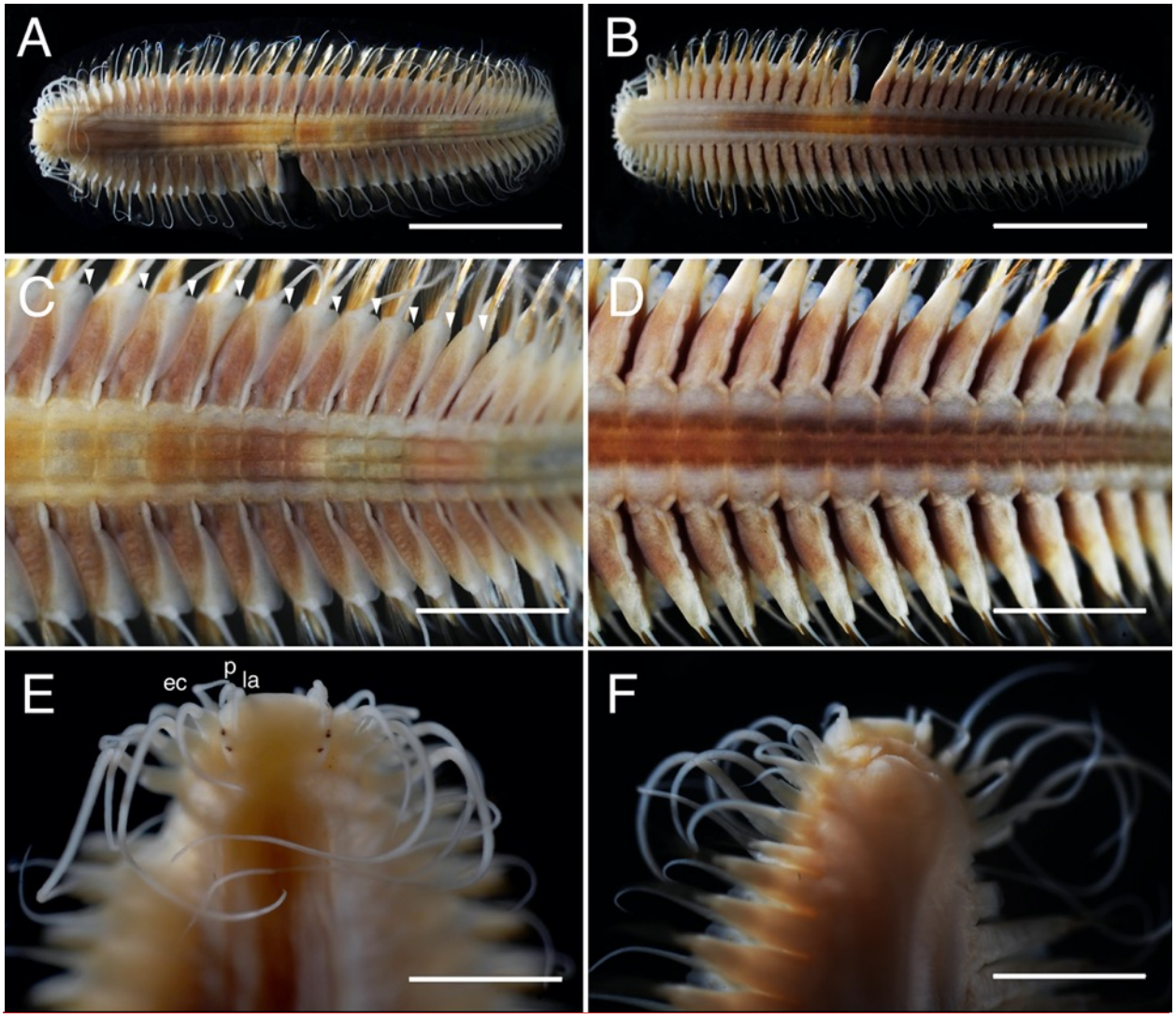

Figure 4. *Parahesione pulvinata* sp. nov. (NSMT-Pol H-893)
A, anterior end, dorsal view; B, parapodium of chaetiger 1, rear view; C, parapodium of chaetiger 17, frontal view;[DM44] D, neurochaeta, upper side, chaetiger 17; E, neurochaeta, lower side, chaetiger 17. Scale bars: A, 1 mm; B, 100 μm; C, 500 μm; E3F, 100 mm. Abbreviation: la, lateral antenna; p, palp; ec, enlarged cirrus.

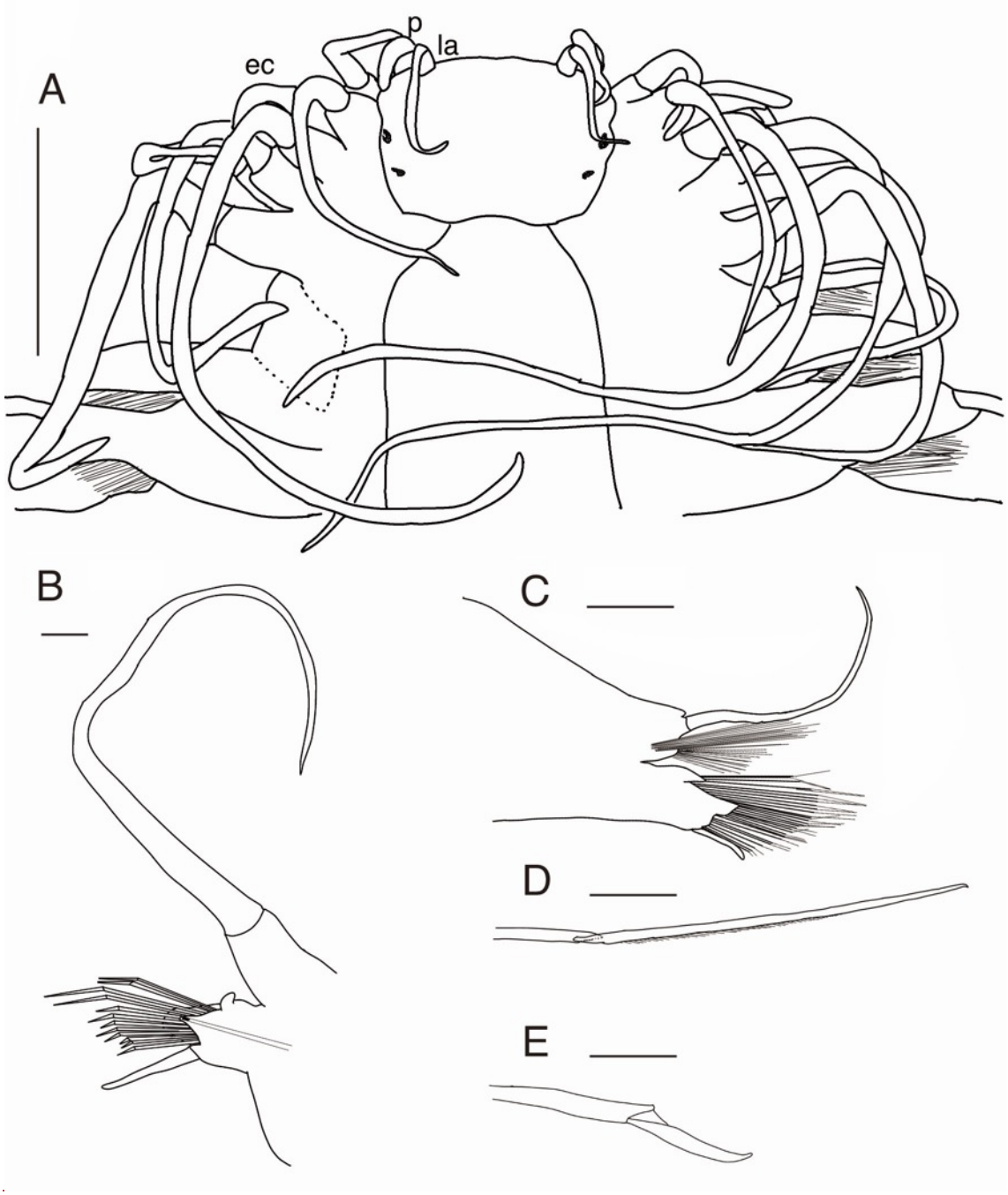

Figure 5. [DM45]*Parahesione pulvinata* sp. nov., living~~e~~ specimen (SIO-BIC A13742, Papua New Guinea)
A, anterior end, dorsal view; B, enlarged view of anterior end, dorsal view; C, middle segments, dorsal view; D, posterior segments, dorsal view. Scale bars: A3B, 5 mm; C3D, 2 mm; E3F, 1 mm."

Figure 6. *Parahesione apiculata* sp. nov. and hosts (*Glypturus armatus*) *in situ*
A, sampling location at the Nanjo sandy tidal ûat; B, living ~~specimen of the~~ symbiont (NSMT-Pol P-899); C, living ~~specimen of the *Glypturus armatus* (~~host~~)~~; D, dorsal view of ~~a~~same living ~~specimen~~symbiont as in B, lacking posterior most segments ~~(same individual with Fig. 6B, NSMT-Pol P-899)~~.

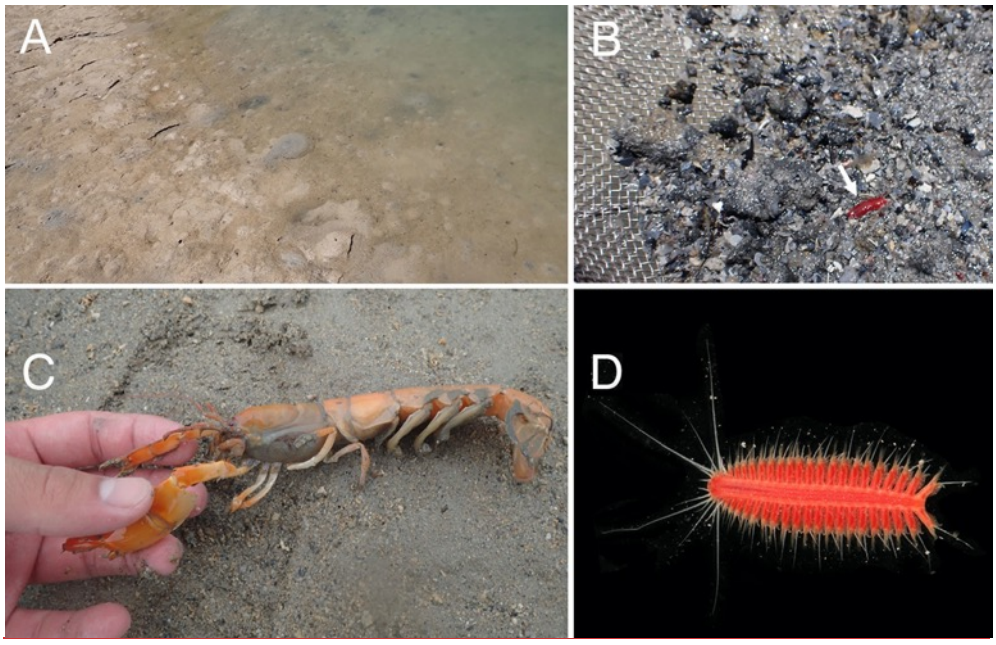

Figure 7. [DM46]*Parahesione apiculata* sp. nov. (NSMT-Pol H-898)
A, whole specimen, dorsal view; B, whole specimen, ventral view; C, middle segments, dorsal view (white arrows pointing on digitate lobes); D, middle segments, ventral view; E, anterior end, dorsal view; F, anterior end, ventral view~~. White arrows indicate digitate lobes~~.
Abbreviations: la, lateral antenna; p, palp; ec, enlarged cirrus. Scale bars: A3B, 3 mm; C3D, 1 mm; E3F, 1 mm.

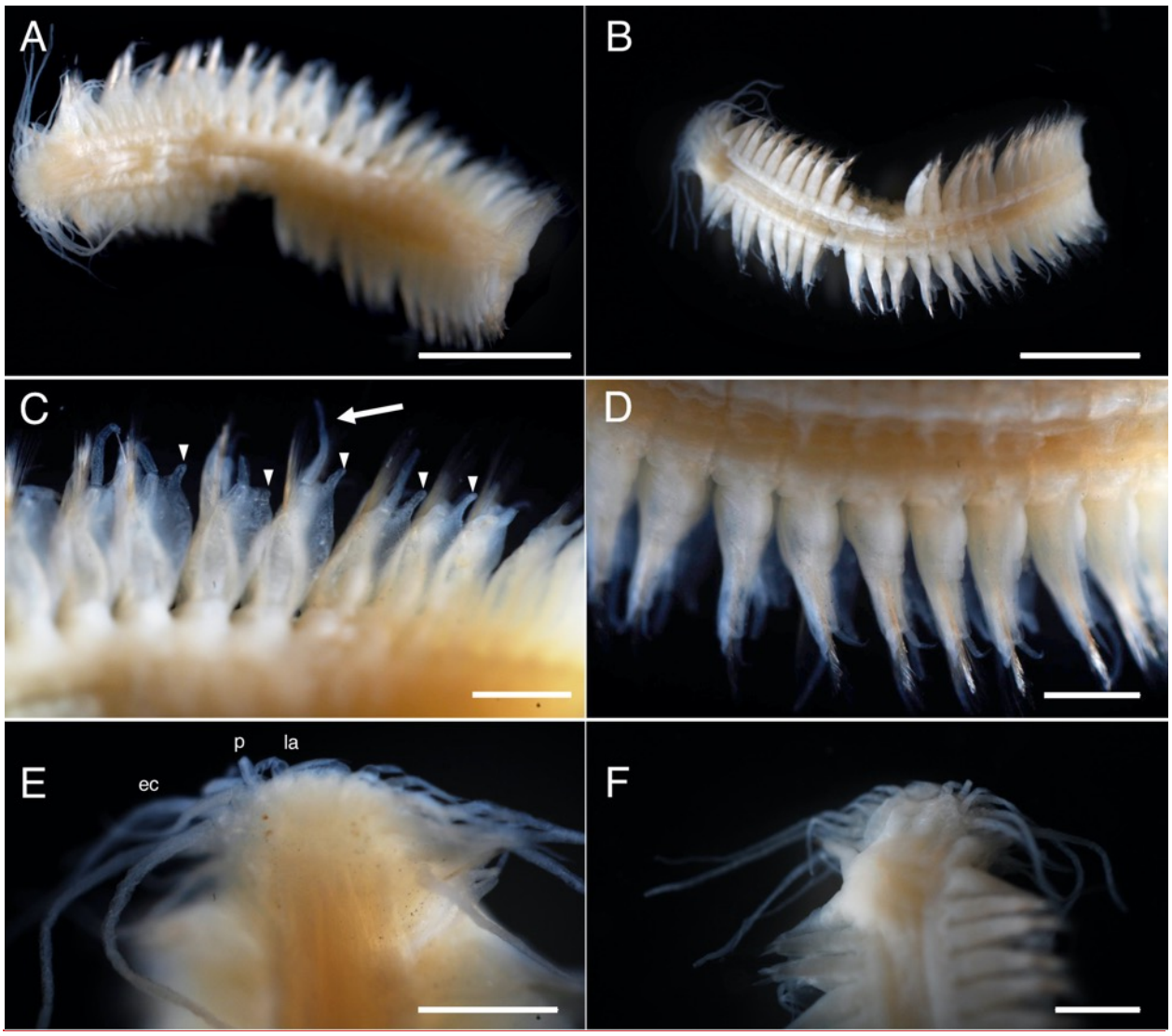

Figure 8. *Parahesione apiculata* sp. nov. (NSMT-Pol H-898)
A, anterior end, dorsal view; B, parapodium of chaetiger 17, frontal view (black arrow pointing on the digitate lobe)[DM47]; D, neurochaeta, upper side, chaetiger 17; D, neurochaeta, lower side, chaetiger 17~~. Black arrow indicates a digitate lobe~~.
Abbreviations: la, lateral antenna; p, palp; ec, enlarged cirrus. Scale bars: A, 1 mm; B, 500 μm; C3D, 100 mm.

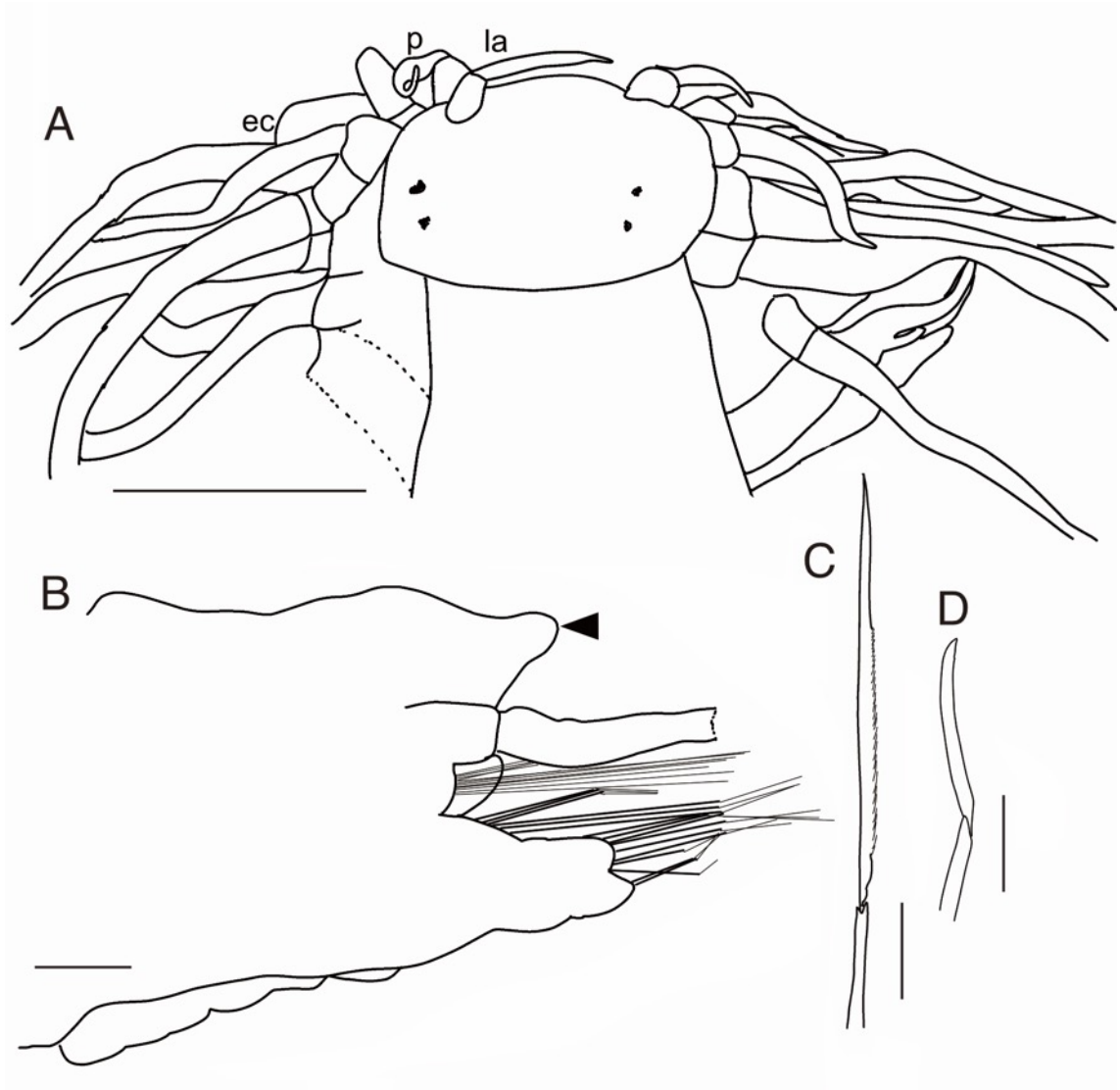

Figure 9 A. Maximum-likelihood phylogenetic tree of Hesionidae based on COI, 16S, 18S and 28S sequences

Numbers on branches: ~~N~~nodal bootstrap support (BS) ~~values higher than~~> 50% ~~are indicated for each branch~~ / ~~. P~~posterior probability (PP)~~; of each branch is also shown behind the bootstrap value.~~ *, BS = ~~=~~100, PP = ~~in BS and~~ 1~~.00 in PP;~~ -, ~~=~~ node absent in the Bayesian tree~~:~~. ~~R~~red circles, ~~indicate~~ symbiotic species.

Figure 10. *Parahesione* sp. (A/B) ~~used in Ruta et al. (2007)~~ and *Parahesione luteola* (C/D) ~~used in Pettibone (1956)~~

From Ruta et al. (2007): A, anterior end, dorsal view; B, anterior end, ventral view. From~~;~~ Pettibone (1956): C, anterior end, lateral view; D, anterior end, ventral view.

Table 1(on next page)

List of hesionids included in the phylogenetic analysis and their Genbank accession numbers

Table 2(on next page)

Life style of hesionids (and host taxa in case of symbionts) included in the phylogenetic analysis~~, indicating the mode of life and the host taxa in case of symbionts~~

Main document changes and comments

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Parahesione pulvinata sp. nov. and *Parahesione apiculata* sp. nov.

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were also studied. On GenBank, the Ruta et al (2007)'s sequence is called *Parahesione luteola*. However, in the paper, they concluded it was undescribed species *Parahesione* sp. (Ruta et al. 2007, the first paragraph of pp. 101). The Genbank name is therefore incorrect and is treated as *Parahesione* sp. in this study

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Remarks. *Parahesione* ressembles in having enlarged dorsal cirri on segments 1–5, but differs in lacking median antenna (having a short one in *Amphiduros* and *Amphiduropsis*).

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It ssems you are just describing the holotype. So, what happens with the paratypes? Is there any variability? Whether there is or not, this has to be indicated and, if there is any, then described, either in the remarks or in a specific section.

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inconspicuous when alive (Fig. 3A, 3E),

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it seems more logical to report the information on the specimen when alive before than when preserved.

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, inconspicuous when alive (Fig. 3E).

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what do yo mean with inconspicuous? This means they are not clearly visible because they are reddish, like othe overall colour of the prostomium? Do you have a photo of a living specimen in a close view to illustrate this?

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Cirrophores of tentacular cirri cylindrical, basally fused;

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Dorsal enlarged

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tentacular

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(dorsal

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ventral enlarged cirri on segments

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no information on length here?

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(ventral)

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Cirrophores of enlarged cirri segments cylindrical, basally fused.

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Parapodia with chaetal lobes cylindrical, truncate, longer than wide. Chaetiger 1 uniramous. Chaetiger 2 and following chaetigers biramous.

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please be more precise

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normal hesionid shape

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, dorsal cirrophores

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d

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This is a very relevant structure, giving the name to the species. So, why it is not seen in figure 4C? The Dorsal cirrophre here illustrated looks normal, without any expansion.

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Not illustrated?

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not developed,

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not seen in vivo,

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Is it possible to have a photo od a dissected parapodia?

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, unknown in alive

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All chaetigers biramous except chaetiger 1 (uniramous). Parapodia with chaetal lobes cylindrical, truncate, longer than wide;

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These sentences seem to be contradictory. Please clarify. also it is not clear what you mean with small and large when refering to noto and neuropodia. What are you describing is also not clear in the figure. Mabe the lobes have to be also indicated with labels.

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of

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please be more precise

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please be more precise, e.g., compare the leght with that of dorsal cirri.

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smooth

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, smooth

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meaning

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and

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Parahesione pulvinata sp. nov. resemble *P. luteola*, the type species of the genus and the single previously known, in lacking the median antenna while having a flattened body and living symbiotically with ghost shrimps. However it differs in having flattened dorsal cirrophores and eight tentacular anterior cirri (cylindrical and six in *P. luteola*).

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and the haplotype network is shown in

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Figure 9 represents the phylogenetic tree, not the haplotype network. From the phylogenetic tree there seems to be also differences between the japanese and the Papua New Guinea specimen. Why BS and PP are not shown for this node? You mention they are slightly divergent, but this is subjective. I think it merits to estimate the genetic distances between these sequences. Also with the information contained in Figure 5 it is not enugh to judge if this specimen is morphilogically similar to the Japanese ones, so more information is required, either as a brief description and as illustrations of the different morphlogical characters..

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(Axiidea: Eucalliacidae)

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(Gebiidea: Upogebiidae)

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Calliaxina

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C.

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(Axiidea: Eucalliacidae)

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Glypturus

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Same comment as in previous description

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(Fig. 6)

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after fixation

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when preserved

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Lateral a

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A

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what about antenophoes?

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p

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shorter than antennae (

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Eyes present, t

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T

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of eyes

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brownish after fixation, unknown

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not seen

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vivo (Fig. 6 D),

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alive

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It will be nice to have a photo of the anterior end at higher magnification. The sitution is the same as in the previous species? Then, why not using the same term or the same words in both descriptions?

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brownish after fixation

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Cirrophores of tentacular cirri cylindrical, basally fused;

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Dorsal enlarged

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tentacular

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(dorsal)

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and

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ventral enlarged cirri on segments

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(ventral)

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dorsal or ventral? See previous description.

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in holotype

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Cirrophores of enlarged cirri segments cylindrical, basally fused

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Parapodia with chaetal lobes cylindrical, truncate, longer than wide. Chaetiger 1 uniramous. Chaetiger 2 and following chaetigers biramous. From chaetiger 1,

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All

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of chaetiger 1 and following chaetigers

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(Fig. 7C)

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Mark the dorsal cirrostyle with an rrow.

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Ventral

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ventral

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please indicate what you mean with long and short.

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not seen in vivo,

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,

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after fixation

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when preserved

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All chaetigers biramous except chaetiger 1 (uniramous). Parapodia with chaetal lobes cylindrical, truncate, longer than wide.

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But you mentioned in previous paragraph that the digitifor projection belonged to the dorsal cirrophores. Or do you mean there are two digitiform expansions? Is fso, both have to be identifiable somway in the figures. Please clarify.

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, those

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Like *P. pulvinata* sp. nov., *P. apiculata* sp. nov. resemble *P. luteola* in lacking the median antenna, having a flattened body and living symbiotically with ghost shrimps, while differing in having flattened dorsal cirrophores and eight tentacular anterior cirri (cylindrical and six in *P. luteola*).

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differs from *P. pulvinata* sp. nov.

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is characterized by the following features: i)

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in

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and

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, ii) having

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from the first

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from

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from chaetiger

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as well as in

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iii)

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association with

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the burrows of

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compared to

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from Papua New Guinea

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, sister to *P. pulvinata* sp. nov

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with 69% of BS in ML and 0.99 of PP in BI (Fig. 9A). *Parahesione pulvinata* sp. nov. forms a sister clade to the *P. apiculata–Parahesione* sp. clade, with 95% of BS in ML and 1.00 PP

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there is a single illustration, so whi 9A?

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The data are already included in Fig. 9, so it is npt necessary to repear them here

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. Alltogether, they constitute t

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which, in turn,

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clade

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clade (Fig. 9)

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there is a single illustration, so whi 9A?

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with 95% of BS in ML and 1.00 PP in BI

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COI

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for the COI sequences

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Uncorrected genetic distance is

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uncorrected)

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What about the genetic distance between the two new species and the Parahesione sp. from Papua New Guinea?

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Phylogenetic position of two new species and its relationships with *Parahesione* species and other hesionids

The two new species resemble *Parahesione luteola*, which is type species of *Parahesione*, in lacking a median antenna while having a flattened body and living symbiotically with ghost shrimps, while differing by having flattened dorsal cirrophores and eight enlarged anterior cirri, instead of cylindrical dorsal cirrophores and six enlarged anterior cirri.

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has been

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species have been

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known from several areas, including

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s suggested by Britayev and Antokhina (2012) and discussed above in the corresponding

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form the *Parahesione* clade together with our

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the

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fall into the same clade

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our observations confirm

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it has six enlarged cirri and non-flattened dorsal cirrophores (Fig. 10A, B), like *P. luteola* (Fig. 10C, D). Our molecular results, together with the large geographical distance between them (Pacific vs.

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specimen identified by Ruta et al. (2007) as *Parahesione* sp. was collected in New Caledonia (Pacific Ocean), far from the type locality of the single known species of the genus, the

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, respectively

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coast of the United States (Pettibone1956). We

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) suggest that the

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reexamined the

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from Papua New Guinea could belong to an undescribed

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used in Ruta et al. (2007) and confirmed that the specimen has six enlarged cirri and non-flattened dorsal cirrophores (Fig. 10A, B) and is likely another new

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, whose formal description would require new morphological and molecular data based on newly collected materials

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but is not described here

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In fact, there is a single partial sequence of 28S (381 bp) available for the specimen from Papua New Guinea, while we could not obtain sequences from other genes because the specimen we received as a loan was preserved in formalin.

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Additionally, we observed the specimens of *P. luteola* in the USNM (Fig. 10C, D). The specimens showed *P. luteola* has six enlarged cirri and non-flattened dorsal cirrophores in according with Pettibone (1956)'s description.

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he inclusion of our new species in

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In this situation, we assign these species to the same genus

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, led us to amend

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and modify

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genus

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of the genus

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However, we could not discard further distinguishing

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However, the DNA repository data for *Parahesione* sp. used in Ruta et al. (2007) is very limited, with only a single partial sequence of 28S (381 bp). We could not determine the other gene sequences because the specimen was preserved in formalin. Given the situation described above, it is possible that

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of

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i.e., six vs.

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vs.

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&

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and non-

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vs. flattened

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vs. six enlarged cirri & non-flattened dorsal cirrophores

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could be distinguished on a molecular phylogenetic tree if they are

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once

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re-examined with

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, thus,

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, could be examined

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(Fig. 9) showed that

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place

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closest to the

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sister to the

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, in agreement

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consistent

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thus

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Amphiduros and *Amphiduropsis* also have enlarged dorsal cirri on segments 1–5, but bear a short median antenna, distinguishing them from *Parahesione*.

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obvious. Not necessary

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(Axiidea: Eucalliacidae)

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(Gebiidea: Upogebiidae),

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however, the identification of

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host was rough and

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still requiring a more precise identification

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needs to be confirmed

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,

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and

Page 8: Commented [DM36] **Daniel Martin** **2/27/23 2:23:00 PM**

This could be true is you were talking about body flattness, but you are not. Which is flatten in your species are the dorsal cirrophores.

Page 8: Commented [DM37] **Daniel Martin** **2/27/23 2:41:00 PM**

Gibbs, P.E., 1971. The polychaete fauna of the Solomon Islands. Bulletin of the British Museum of Natural History, 21 (5), 101-211.

Page 8: Commented [DM38] **Daniel Martin** **2/27/23 2:54:00 PM**

You have not mentionned these celle before, juts dissoved pigment. Please clarify.

Page 9: Commented [DM39] **Daniel Martin** **2/27/23 2:55:00 PM**

In do not agree with this sentence. According to what is written in this paper. It is clear that the worm s in this genus are crustacean symbionts. Which is not wel-known are the details

of the association and the behaviour of the partners.

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re

Page 9: Commented [DM40] Daniel Martin 2/27/23 2:57:00 PM

I think this statment is not correct. There is no demonstrations on how the symbiotic mode of life has evolved, juts that the genus seems to be closer to a non-symbiotic clade. I cannot see here any evolutive demonstration.

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the genus

Page 15: Commented [DM41] Daniel Martin 2/28/23 9:21:00 AM

Most figures can be improved, basically by eliminating non-informative parts and empti spaces. also, the bars and labels in some of them are too small/thin, and some interesting structures require to be marked with arrows. Also, some photos could be imrpoved to allow better distinguish relevant structures. I have modified them based on the available JPGs, so that the authors can use them to improve their origunals.

Page 15: Inserted Daniel Martin 2/28/23 9:26:00 AM

Red stars:

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;

Page 15: Deleted Daniel Martin 2/28/23 9:27:00 AM

(Red star) and

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Blue dot:

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(Blue dot)"

Page 15: Commented [DM42] Daniel Martin 2/28/23 9:47:00 AM

scales are required

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Observations of

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In situ observations,

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and its hosts

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host (*Neocallichirus jousseaumei*) and symbiont specimens

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in situ

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a

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and the new species

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with one symbiont on the filtration sieve

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Neocallichirus jousseaumei

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inside a plastic

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of the new species

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of the new species

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a preserved

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the same

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(NSMT-Pol H-893)

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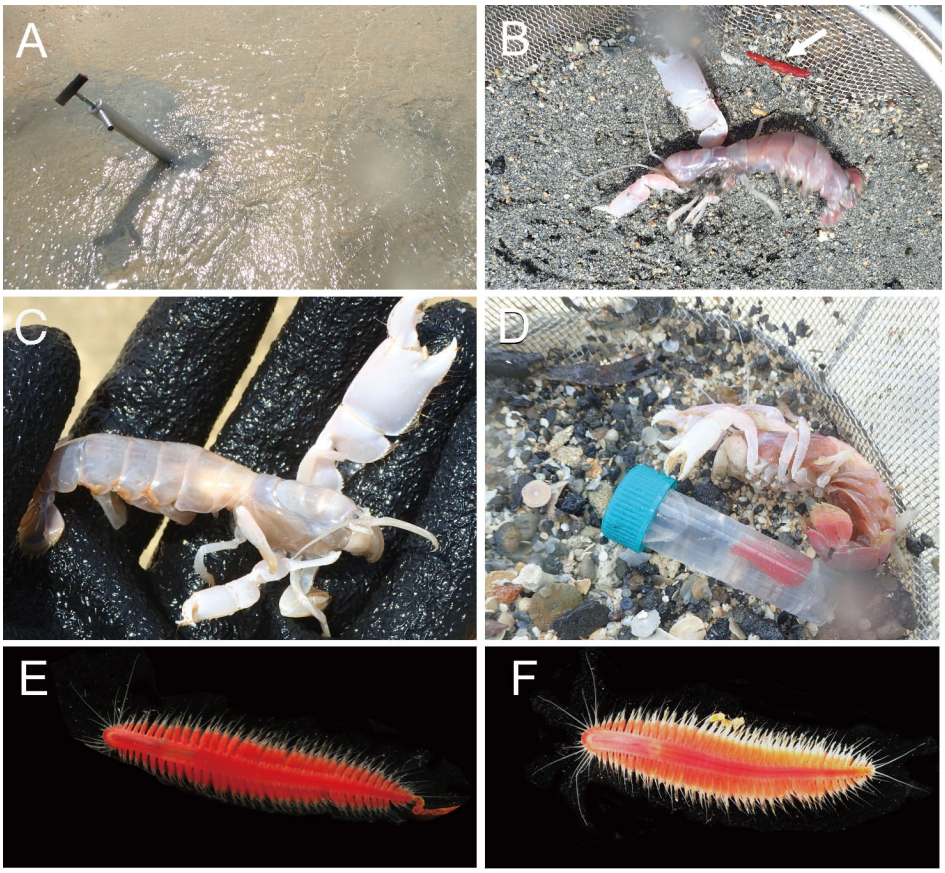

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Please explain in the text why some parapodia are lacking in theis specimen.

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(white triangles pointing on pillow-shaped dorsal cirrophores)

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White arrows indicate pillow-shaped dorsal cirrophore without digitate lobes

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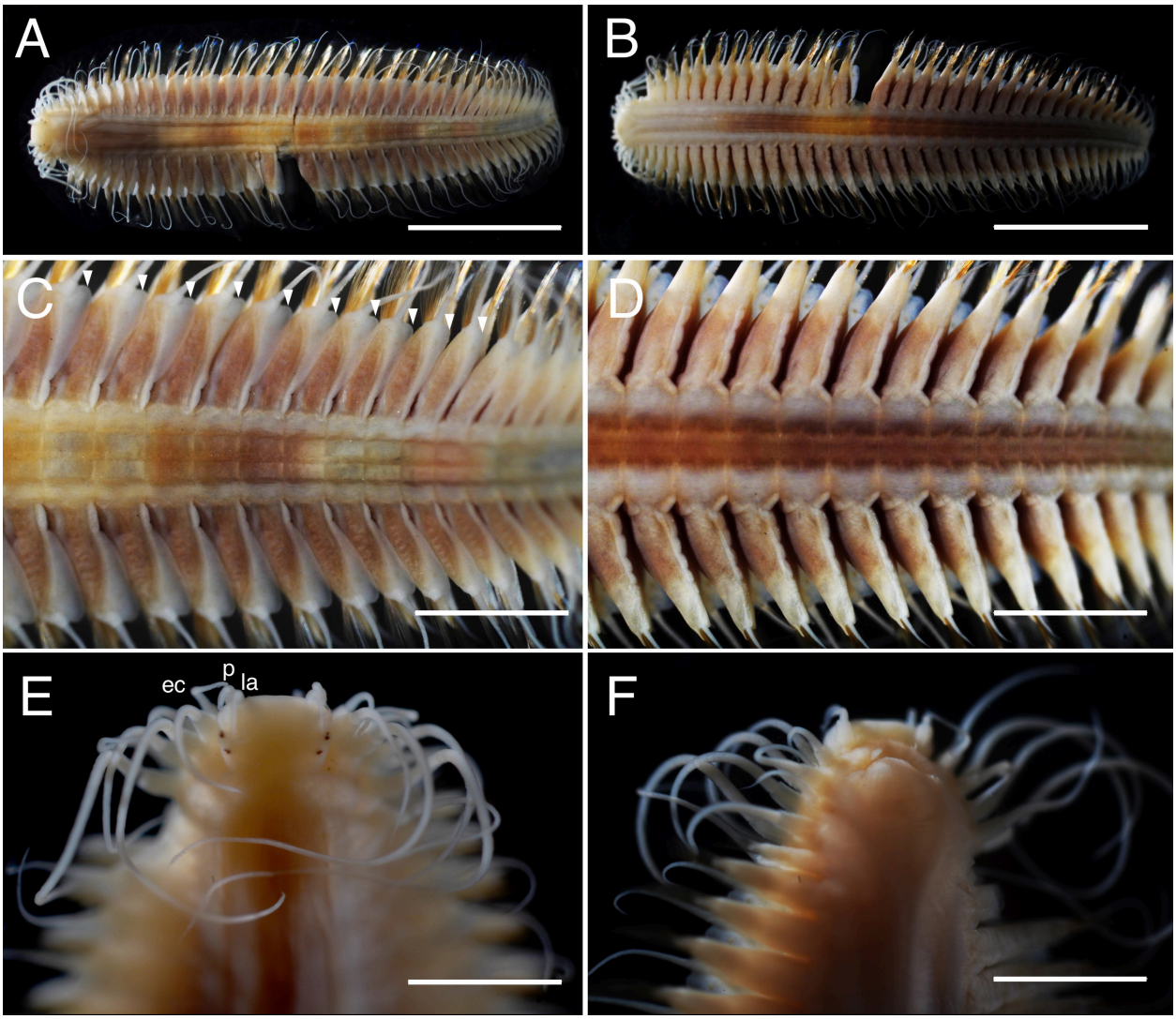
Page 16: Inserted	Daniel Martin	2/28/23 2:59:00 PM



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Page 17: Commented [DM44] Daniel Martin 2/28/23 9:48:00 AM

please indicate where the pillow-like expansion are located

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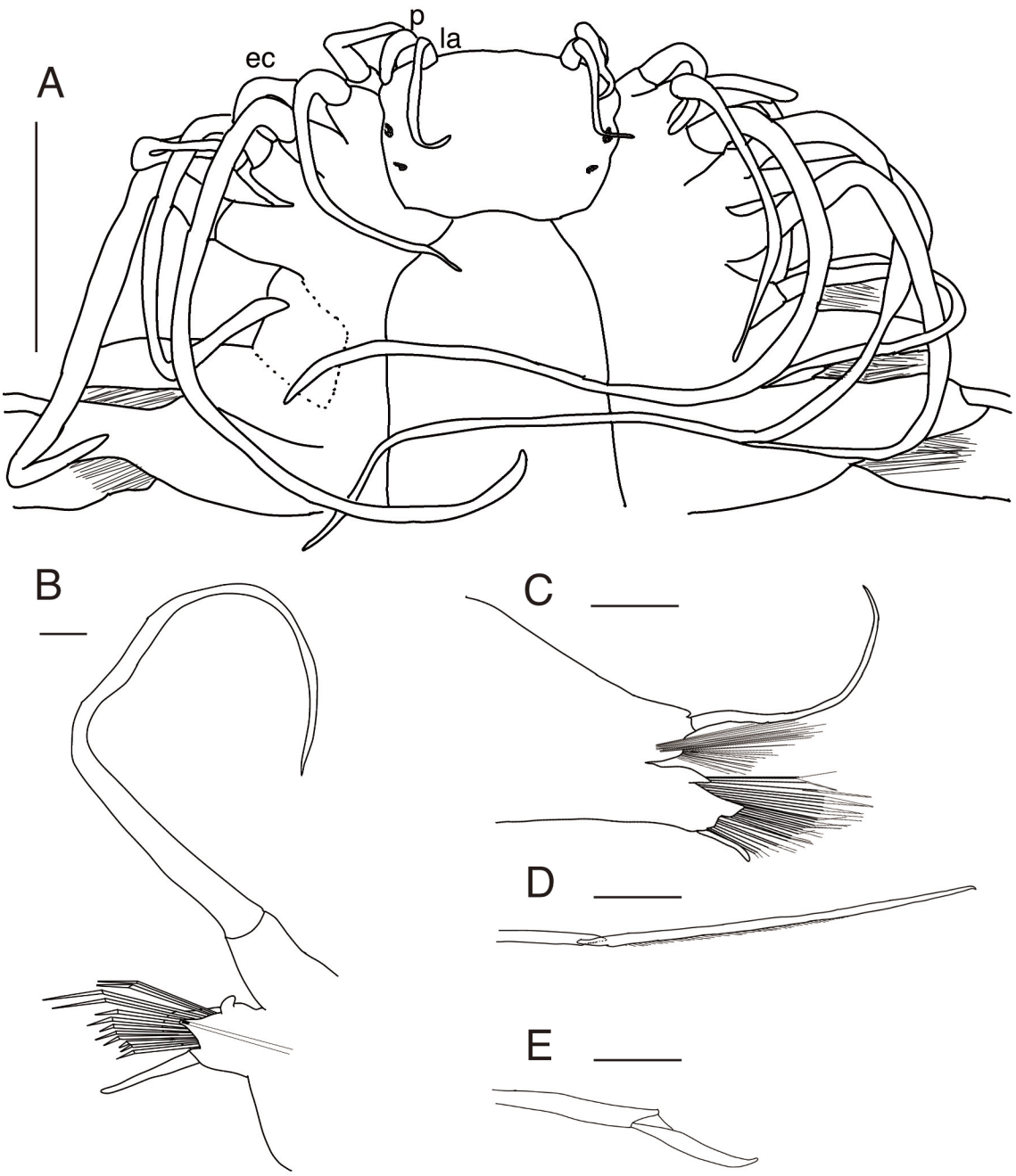

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indicate the pillow -like expansions as in the other figure.

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(*Glypturus armatus*)

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specimen of the

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(NSMT-Pol P-899)

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specimen of the *Glypturus armatus* (

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)

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a

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same

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specimen

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symbiont as in B

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(same individual with Fig. 6B, NSMT-Pol P-899)

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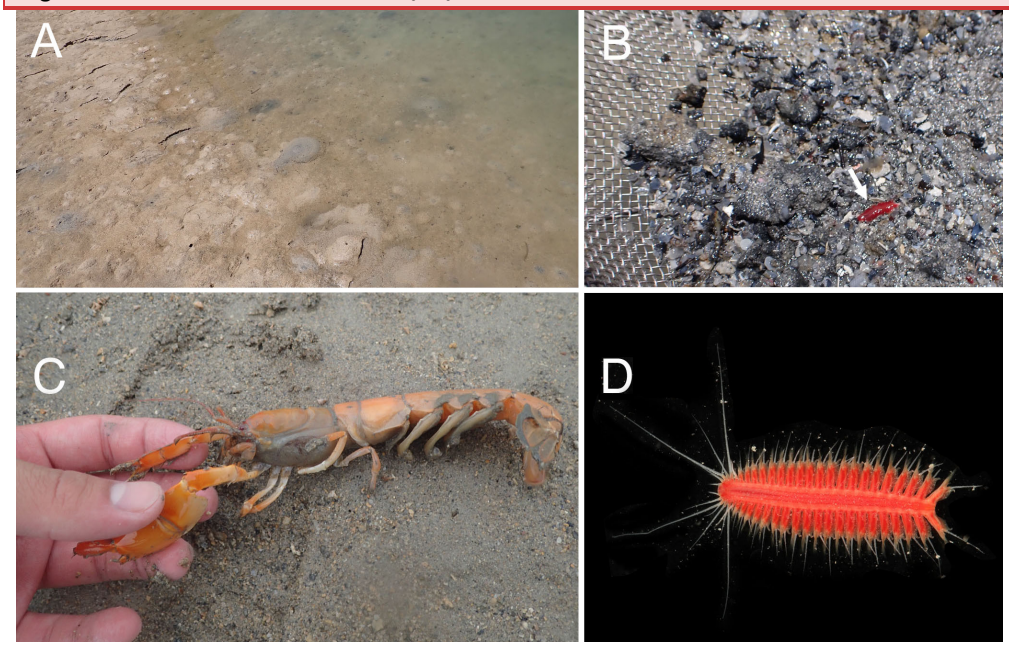

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please explain in text why som parapodia are lacking in this specimen.

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(white arrows pointing on digitate lobes)

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. White arrows indicate digitate lobes

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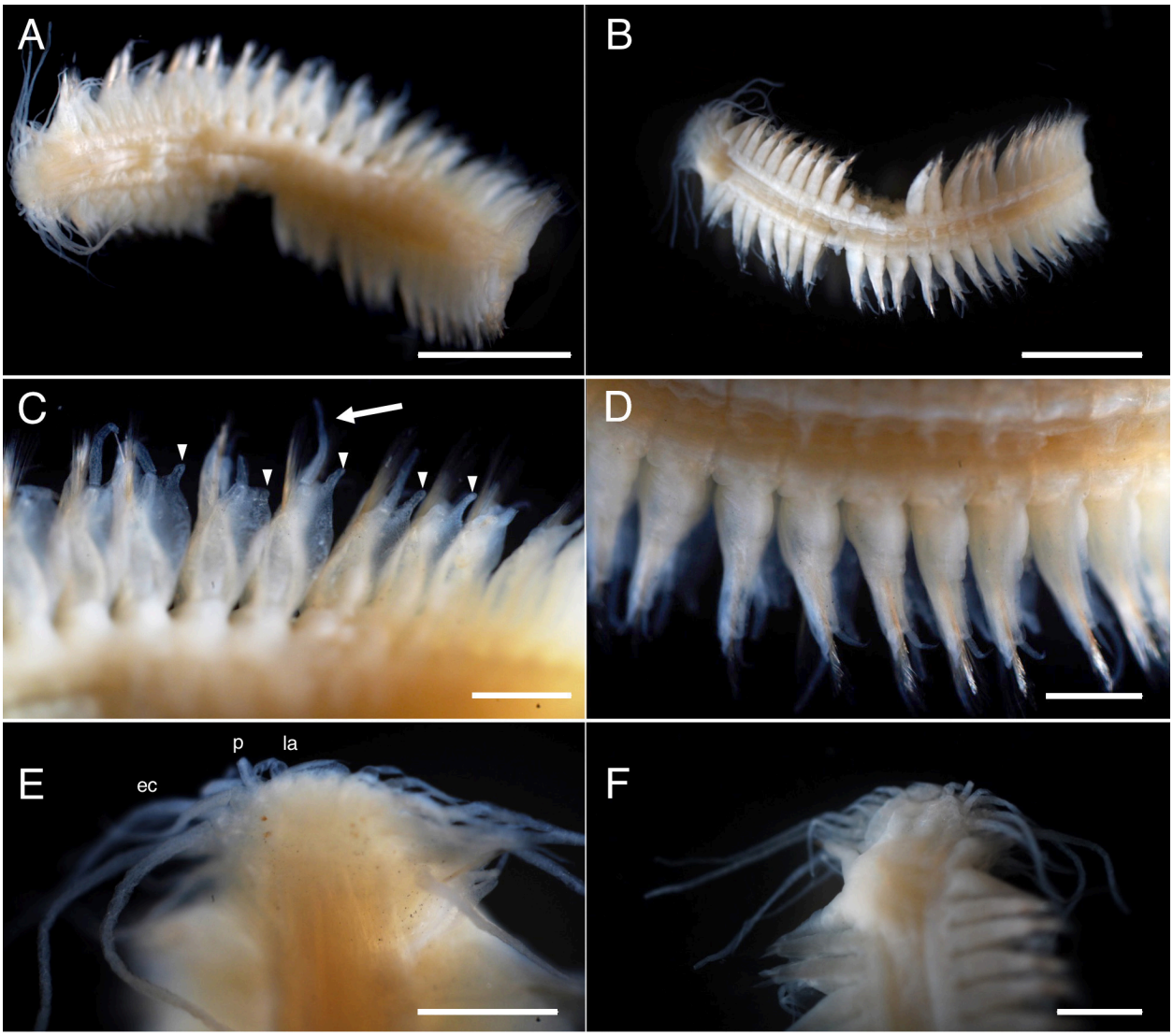

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(black arrow pointing on the digitate lobe)

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from this image it is not clear that the diitate lobe belongs to an expanded cirrophore.

Please clarify.

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. Black arrow indicates a digitate lobe

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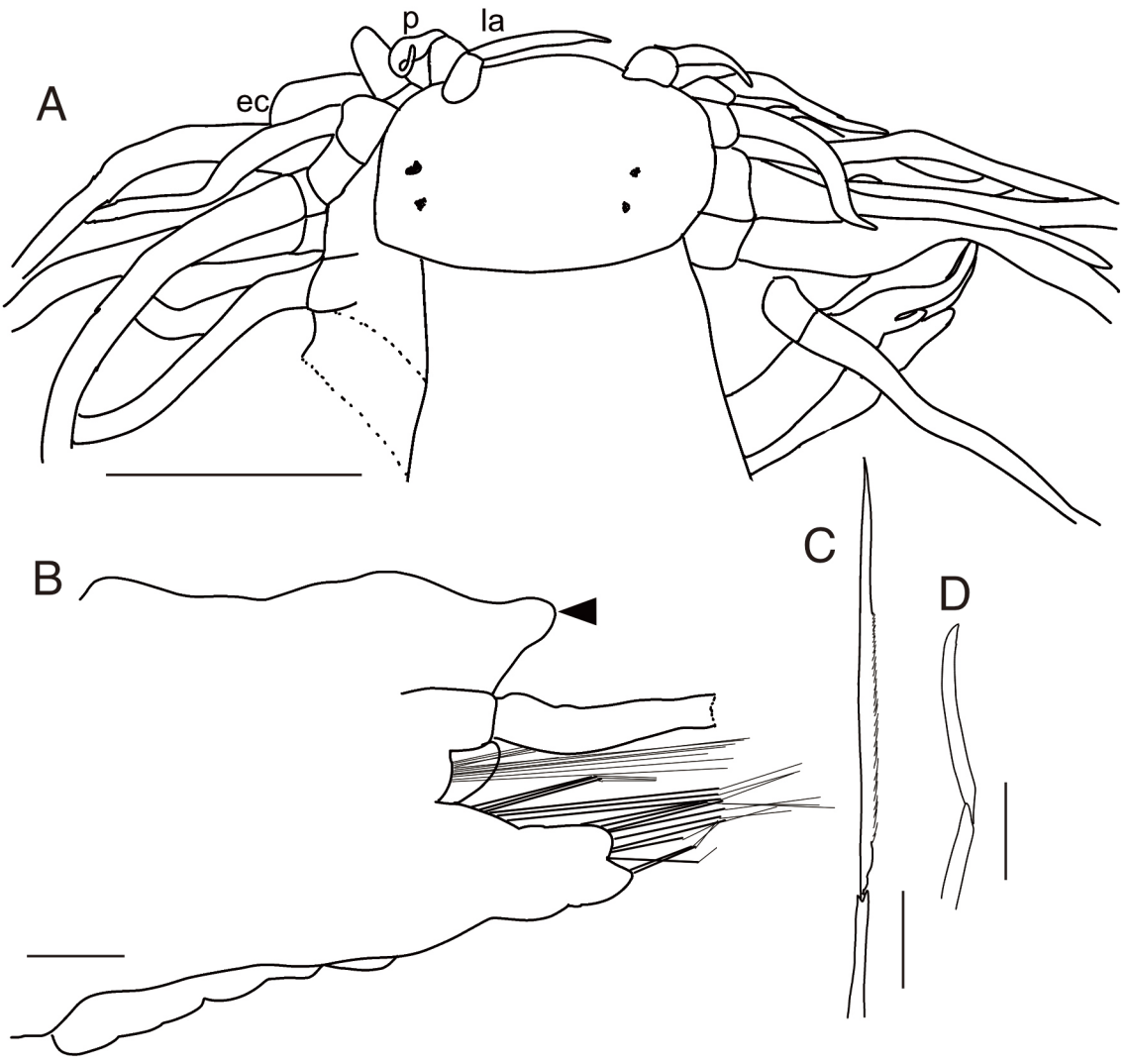

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Numbers on branches:

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values higher than

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are indicated for each branch

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of each branch is also shown behind the bootstrap value.

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indicate

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used in Ruta et al. (2007)

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used in Pettibone (1956)

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From Ruta et al. (2007):

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Pettibone (1956):

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(and host taxa in case of symbionts)

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, indicating the mode of life and the host taxa in case of symbionts

Header and footer changes

Text Box changes

Header and footer text box changes

Footnote changes

Endnote changes