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 are characterized by having eight enlarged cirri, dorsal cirrophores with dorsal foliose lobe and biramous parapodia, and by lacking median antenna. *Parahesione apiculata* sp. nov. has digitate lobes on the posterior margin of the dorsal foliose lobe (absent in *P. pulvinata* sp. nov.). The two new species were never found outside the ghost shrimp burrows, suggesting they are obligate symbionts. Phylogenetic analyses based on four concatenated genes suggest that the symbiotic lifestyle has evolved several times in Hesionidae.

INTRODUCTION

The narrow burrows excavated by decapods in tidal flats are frequently occupied by different symbionts (*Campos, Campos & Manriquez, 2009*; *Pillay & Branch, 2011*). However, these secure habitats often exist under hypoxic conditions (*Atkinson & Taylor, 2005*), leading to the adaptation of certain symbionts (*Pillay & Branch, 2011*). These include polynoid and hesionid polychaetes living in burrows of callianassid ghost shrimps and upogebiid mud shrimps (*Martin & Britayev, 1998*).

Hesionidae includes more than 199 species (*Rouse, Carvajal & Pleijel, 2018*; *Rouse, Pleijel & Tilic, 2022*; *Read & Fauchald, 2023*), with about 30 being considered obligate or facultative invertebrate symbionts, mainly living in association with echinoderms, but also with burrowing sipunculids, hemichordates and polychaetes, among others (*Martin & Britayev, 1998*, *2018*; *Martin et al., 2017*; *Rouse, Carvajal & Pleijel, 2018*). However, only

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Parahesione luteola (*Webster, 1879*) and *Parahesione* sp. are known from mud shrimp burrows (*Pettibone, 1956*; *Britayev & Antokhina, 2012*). *Parahesione* was proposed by *Pettibone (1956)* for *Podarke luteola Webster, 1879* (type species), whose type material was lost, and *Hesione agilis* Webster & Benedict, 1884. The former was found on an oyster bank in Great Egg Harbor, New Jersey, whereas the latter was found living commensally with *Upogebia affinis* (*Say, 1818*). These two species were regarded by *Pettibone (1963)* as synonyms and have been considered as facultative symbionts (*Martin & Britayev, 1998*).

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*; *Bonifácio, Lelièvre & Omnes, 2018*; *Rouse, Carvajal & Pleijel, 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 to try to elucidate their adaptability to differential environmental conditions.

In this article, we describe two new species of Hesionidae living inside burrows of callianassid ghost shrimps and analyze the phylogenetic relationships within the family, based on four concatenated genes, to assess the evolution of both symbiotic species and their adaptations to living inside host burrows.

MATERIALS AND METHODS

The specimens were collected with a yabby pump from inside of the burrows of *Neocallichirus jousseaumei* (*Nobili, 1904*) (Axiidea: Callichiridae) and *Glypturus armatus* (*Milne-Edwards, 1870*) (Axiidea: Callichiridae), living 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. (*Britayev & Antokhina, 2012*), (2) *Parahesione* sp. (*Ruta et al., 2007*, first paragraph, page 101), reported as *P. luteola* in Genbank, (3) *Parahesione* from Papua New Guinea, collected by GR likely from burrow of *Calliaxina bulimba* (*Poore & Griffin, 1979*) (Axiidea: Eucalliacidae), and (4) *P. luteola* (*Pettibone, 1956*) (No. USNM 430 and 28175).

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 observed with a Leica MZ9.5 stereomicroscope and photographed with a Canon Rebel T3i camera.

Type specimens 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 in the 'Material examined' section: CS (complete specimens), L (length, measured from the anterior margin of the prostomium to the posterior border of the last segment), W (width the widest segment, including parapodia but excluding chaetae).

The total DNA of the Japanese holotype was extracted from a dissected parapodium using a DNeasy Tissue Kit (Qiagen, Hilden, Germany). DNA extraction, sequencing,
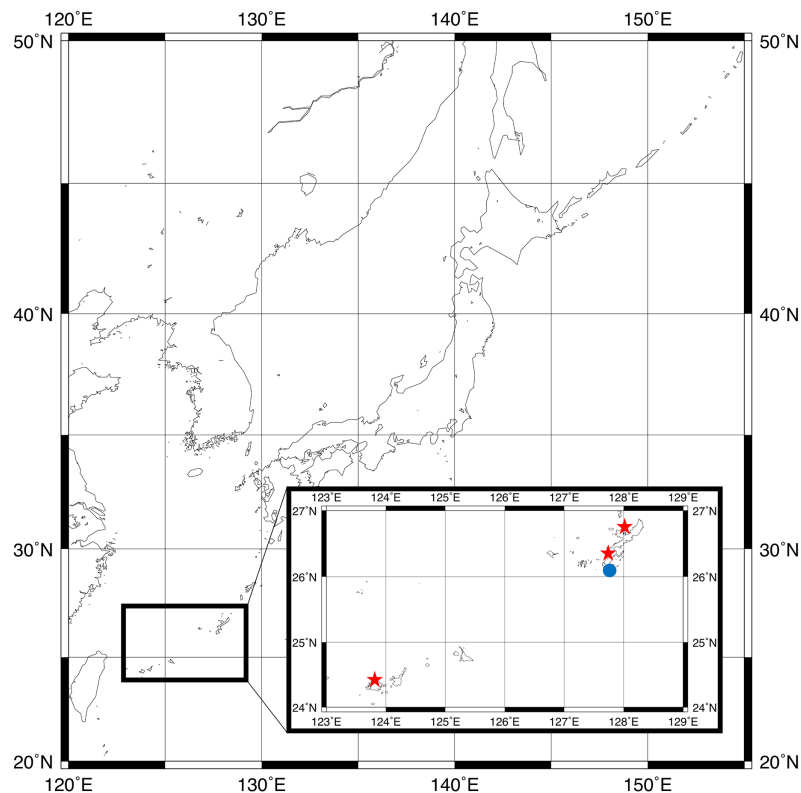
Figure 1 Sampling locations for type specimens. *Parahesione pulvinata* sp. nov. (Red star) and *Parahesione apiculata* sp. nov. (Blue dot). The map was generated using GMT 6 (*Wessel et al., 2019*; https://www.generic-mapping-tools.org/).

alignment, and removing ambiguous positions were carried out for the method of *Jimi et al. (2021)*. The *Parahesione* from Papua New Guinea were extracted following from *Rouse, Carvajal & Pleijel (2018)* and *COI* was generated for the specimen. All newly obtained sequences *COI* (625 bp), *16S* (552 bp), *18S* (1,677 bp), *28S* (987 bp) were deposited in GenBank. 198 sequences (59 species) were used for molecular analyses, including 191 downloaded from GenBank (https://www.ncbi.nlm.nih.gov/genbank) (Table 1). Phylogenetic analyses were also carried out for the method of *Jimi et al. (2021)*. *Dysponetus caecus* (*Langerhans, 1880*) was used as the outgroup following *Rouse, Carvajal & Pleijel (2018)* and *Tilic et al. (2022)*. Additionally, four species were used for calculating K2P genetic distances using MEGAX (*Stecher, Tamura & Kumar, 2020*). To understand the evolution of symbiosis in the family Hesionidae, we divided them into the following three groups: obligate and facultative symbionts, according to *Martin et al. (2017)*, and free-living based on previously published data (Table 2). In the molecular phylogenetic tree, we mapped species with symbiotic ecology based on this table.

The map of Fig. 1 was generated by using GMT 6 (*Wessel et al., 2019*).

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Table 1 List of hesionids included in the phylogenetic analysis and the Genbank accession numbers.

Species	18S	16S	28S	COI	References
Dysponetus caecus (Langerhans, 1880)	AY839568	EU555047	EU555028	AF221568	*Wiklund et al. (2009), Dahlgren et al. (2000)*
Amphiduros fuscescens (Marenzeller, 1875)	DQ442584	DQ442569	DQ442598	DQ442561	*Ruta et al. (2007)*
Amphiduropsis cf. *axialensis sensu Rouse, Carvajal & Pleijel (2018)*	MG649239	MG523356	MG649243	MG517505	*Rouse, Carvajal & Pleijel (2018)*
Amphiduros pacificus Hartman (1961)	JN631334	JN631324	JN631345	JN631312	*Pleijel et al. (2012)*
Elisesione imajimai Jimi, Eibye-Jacobsen & Salazar-Vallejo, 2018	LC361352	–	LC361353	LC361354	*Jimi, Eibye-Jacobsen & Salazar-Vallejo, 2018*
Gyptis brunnea (Hartman, 1961)	JN631335	JN631323	JN631346	JN631313	*Pleijel et al. (2012)*
Gyptis golikovi (Averincev, 1990)	JN631336	JN631321	JN631347	–	*Pleijel et al. (2012)*
Gyptis hians Fauchald & Hancock, 1981	JN571891	JN571880	JN571900	JX503009	*Summers, Pleijel & Rouse (2015)*
Gyptis pacificus (Hessle, 1925)	JN631337	JN631322	JN631348	JN631314	*Pleijel et al. (2012)*
Gyptis paucilineata Pleijel, Rouse & Nygren (2009)	–	–	–	EU498243	*Pleijel, Rouse & Nygren (2009)*
Gyptis polymorpha Pleijel, Rouse & Nygren, 2009	–	–	–	EU498247	*Pleijel et al. (2012)*
Gyptis propinqua Marion & Bobretzky, 1875	–	DQ442573	DQ442602	EU498229	*Pleijel, Rouse & Nygren (2009)*
Gyptis robertscrippsi Rouse, Carvajal & Pleijel, 2018	MG649238	MG523360	MG649247	MG517513	*Rouse, Carvajal & Pleijel (2018)*
Gyptis simpsonorum Pleijel, Rouse & Nygren, 2009	–	–	–	KU738203	*Pleijel, Rouse & Nygren (2009)*
Gyptis shannonae Summers, Pleijel & Rouse, 2015	KP745537	KP745534	KP745540	–	*Summers, Pleijel & Rouse (2015)*
Hesiolyra bergi Blake, 1985	AM159577	MG523359	–	MG517521	*Rouse, Carvajal & Pleijel (2018)*
Hesione sp. *sensu Ruta et al. (2007)*	DQ442617	DQ442615	DQ442619	–	*Ruta et al. (2007)*
Hesiospina aurantiaca (Sars, 1862)	JN852829	JN631319	JN852897	–	*Pleijel et al. (2012)*
Hesiospina vestimentifera Blake, 1985	JN631330	JN852860	JN631343	JN631310	*Pleijel et al. (2012)*
Heteropodarke formalis Perkins, 1984	–	KJ855065	KJ855076	–	*Martin et al. (2015)*
Heteropodarke pleijeli Muona, 2006	–	KY823464	KY823481	–	*Martin et al. (2015)*
Leocrates chinensis Kinberg, 1866	DQ442589	DQ442575	DQ442605	DQ442565	*Ruta et al. (2007)*
Leocratides kimuraorum Jimi, Tanaka & Kajihara, 2017	LC480516	LC480518	LC480517	LC258082	*Jimi, Tanaka & Kajihara (2017), Goto, Hirabayashi & Palmer (2019)*
Micropodarke dubia (Hessle, 1925)	JN571888	DQ442576	JN571899	JN571825	*Summers, Pleijel & Rouse (2015)*
Neogyptis carriebowcayi Pleijel et al., 2012	JN631338	JN631325	JN631349	JN631315	*Pleijel et al. (2012)*
Neogyptis fauchaldi Pleijel et al., 2012	JN631339	JN631326	–	JN631316	*Pleijel et al. (2012)*
Neogyptis hinehina Pleijel, et al., 2012	JN631340	JN631328	JN631350	JN631317	*Pleijel et al. (2012)*
Neogyptis jeffruoccoi Rouse, Carvajal & Pleijel, 2018	JN852831	–	MG649244	MG517514	*Rouse, Carvajal & Pleijel (2018)*
Neogyptis mediterranea (Pleijel, 1993)	–	DQ442572	DQ442601	DQ442563	*Ruta et al. (2007)*
Neogyptis rosea (Malm, 1874)	JN571890	DQ442574	DQ442603	JN571826	*Ruta et al. (2007), Summers, Pleijel & Rouse (2015)*
Neogyptis julii Summers, Pleijel & Rouse, 2015	KP745538	KP745535	KP745541	KP745532	*Summers, Pleijel & Rouse (2015)*
Neogyptis sp. A *sensu Pleijel et al. (2012)*	JN631341	JN631327	JN631351	JN631318	*Pleijel et al. (2012)*
Nereimyra aphroditoides (Fabricius, 1780)	–	JF317211	JF317204	JF317198	*Pleijel et al. (2012)*
Nereimyra punctata (Müller, 1788)	DQ442591	DQ442577	DQ442606	DQ442566	*Ruta et al. (2007)*

Species	18S	16S	28S	COI	References
Nereimyra woodsholea (Hartman, 1965)	–	–	JF317207	AY644802	Nygren, Pleijel & Sundberg (2005)
Oxydromus fauveli (Uchida, 2004)	–	–	KJ855078	KJ855071	Martin et al. (2015)
Oxydromus flexuosus (Delle Chiaje, 1825)	DQ442592	DQ442578	DQ442607	DQ442567	Ruta et al. (2007)
Oxydromus okupa (Martin et al., 2017)	KJ855075	KJ855070	KJ855082	–	Martin et al. (2015, 2017), Meca, Drake & Martin (2019)
Oxydromus microantennatus (Hutchings & Murray, 1984)	–	KJ855067	KJ855079	KJ855072	Martin et al. (2015)
Oxydromus obscurus (Verrill, 1873)	–	KJ855068	KJ855080	KJ855073	Martin et al. (2015)
Oxydromus pallidus Claparède, 1864	DQ442593	DQ442579	DQ442608	–	Ruta et al. (2007)
Oxydromus pugettensis (Johnson, 1901)	DQ790086	KJ855069	KJ855081	KJ855074	Martin et al. (2015)
Parahesione apiculata sp. nov.	–	OP407586	OP407537	OP404167	This study
Parahesione pulvinata sp. nov.	OP407566	OP407585	OP407536	OP404166	This study
Parahesione sp.	–	–	DQ442613	–	Ruta et al. (2007)
Podarkeopsis arenicolus (La Greca, 1946)	JN571889	JN571879	DQ442609	JN571827	Summers, Pleijel & Rouse (2015)
Podarkeopsis helgolandicus (Hilbig & Dittmer, 1979)	JN631331	–	JN631344	JN631311	Pleijel et al. (2012)
Psamathe fusca Johnston, 1836	DQ442595	DQ442581	DQ442610	DQ513294	Ruta et al. (2007)
Sirsoe dalailamai Rouse, Carvajal & Pleijel, 2018	MG649240	MG523357	MG649245	MG517498	Rouse, Carvajal & Pleijel (2018)
Sirsoe methanicola (Desbruyères & Toulmond, 1998)	JN631332	DQ442582	DQ442611	DQ513295	Ruta et al. (2007)
Sirsoe munki Rouse, Carvajal & Pleijel, 2018	MG649241	MG523358	MG649246	MG517510	Rouse, Carvajal & Pleijel (2018)
Sirsoe sirikos Summers, Pleijel & Rouse, 2015	JN571893	JN571882	JN571902	JN571829	Summers, Pleijel & Rouse (2015)
Syllidia armata Quatrefages, 1866	DQ442596	DQ442583	DQ442612	DQ442568	Ruta et al. (2007)
Vrijenhoekia balaenophila Pleijel et al., 2008	JN631333	DQ513301	DQ513306	DQ513296	Pleijel et al. (2008)
Vrijenhoekia ahabi Summers, Pleijel & Rouse, 2015	JN571898	JN571887	JN571907	JN571876	Summers, Pleijel & Rouse (2015)
Vrijenhoekia falenothiras Summers, Pleijel & Rouse, 2015	JN571897	JN571886	JN571906	JN571875	Summers, Pleijel & Rouse (2015)
Vrijenhoekia ketea Summers, Pleijel & Rouse, 2015	JN571896	JN571885	JN571905	JN571838	Summers, Pleijel & Rouse (2015)
Vrijenhoekia sp. A sensu Summers, Pleijel & Rouse, 2015	KP745539	KP745536	KP745542	KP745533	Summers, Pleijel & Rouse (2015)

Table 2 Life style of hesionids included in the phylogenetic analysis, indicating the mode of life and the host taxa in case of symbionts.

Species	Mode of life	Host	References
Dysponetus caecus (Langerhans, 1880)	Free-living	–	Watson et al. (2014)
Amphiduros fuscescens (Marenzeller, 1875)	Free-living	–	Pleijel (2001)
Amphiduropsis cf. axialensis sensu Rouse, Carvajal & Pleijel (2018)	Free-living	–	Rouse, Carvajal & Pleijel (2018)
Amphiduros pacificus Hartman, 1961	Free-living	–	Pleijel (2001)
Elisesione imajimai Jimi, Eibye-Jacobsen & Salazar-Vallejo, 2018	Free-living	–	Jimi, Eibye-Jacobsen & Salazar-Vallejo (2018)

(Continued)

Species	Mode of life	Host	References
Gyptis brunnea (*Hartman, 1961*)	Free-living	–	*Hartman (1961)*
Gyptis golikovi (*Averincev, 1990*)	Free-living	–	*Averincev (1990)*
Gyptis hians *Fauchald & Hancock, 1981*	Free-living	–	*Banse & Hobson (1968)*
Gyptis pacificus (*Hessle, 1925*)	Free-living	–	*Hessle (1925)*
Gyptis paucilineata *Pleijel, Rouse & Nygren, 2009*	Free-living	–	*Pleijel, Rouse & Nygren (2009)*
Gyptis polymorpha *Pleijel, Rouse & Nygren, 2009*	Free-living	–	*Pleijel, Rouse & Nygren (2009)*
Gyptis propinqua *Marion & Bobretzky, 1875*	Free-living	–	*Parapar, Besteiro & Moreira (2005)*
Gyptis robertscrippsi *Rouse, Carvajal & Pleijel, 2018*	Free-living	–	*Rouse, Carvajal & Pleijel (2018)*
Gyptis simpsonorum *Pleijel, Rouse & Nygren, 2009*	Free-living	–	*Pleijel, Rouse & Nygren (2009)*
Gyptis shannonae *Summers, Pleijel & Rouse, 2015*	Free-living	–	*Summers, Pleijel & Rouse (2015)*
Hesiolyra bergi *Blake, 1985*	Free-living	–	*Blake (1985)*
Hesione sp. *sensu* *Ruta et al. (2007)*	Free-living	–	*Ruta et al. (2007)*
Hesiospina aurantiaca (*Sars, 1862*)	Free-living	–	*Pleijel (2004)*
Hesiospina vestimentifera *Blake, 1985*	Facultative symbiont	Annelids	*Pleijel (2004)*
Heteropodarke formalis *Perkins, 1984*	Free-living	–	*Perkins (1984)*
Heteropodarke pleijeli *Muona, 2006*	Free-living	–	*Pleijel (1999)*, *Muona (2006)*
Leocrates chinensis *Kinberg, 1866*	Facultative symbiont	Corals	*Martin et al. (2017)*, *Wang, Qiu & Salazar-Vallejo (2018)*
Leocratides kimuraorum *Jimi, Tanaka & Kajihara, 2017*	Obligate-symbiont	Sponges	*Jimi, Tanaka & Kajihara (2017)*
Micropodarke dubia *Hessle (1925)*	Free-living	–	*Hessle (1925)*
Neogyptis carriebowcayi *Pleijel et al., 2012*	Free-living	–	*Pleijel et al. (2012)*
Neogyptis fauchaldi *Pleijel et al., 2012*	Free-living	–	*Pleijel et al. (2012)*
Neogyptis hinehina *Pleijel et al. (2012)*	Free-living	–	*Pleijel et al. (2012)*
Neogyptis jeffruoccoi *Rouse, Carvajal & Pleijel, 2018*	Facultative symbiont	Bivalves	*Rouse, Carvajal & Pleijel (2018)*
Neogyptis mediterranea (*Pleijel, 1993*)	Free-living	–	*Pleijel et al. (2012)*
Neogyptis rosea (*Malm, 1874*)	Free-living	–	*Pleijel et al. (2012)*
Neogyptis julii *Summers, Pleijel & Rouse, 2015*	Free-living	–	*Summers, Pleijel & Rouse, 2015*
Neogyptis sp. A *sensu* *Pleijel et al. (2012)*	Free-living	–	*Pleijel et al. (2012)*
Nereimyra aphroditoides (*Fabricius, 1780*)	Free-living	–	*Pleijel, Rouse & Nygren (2011)*
Nereimyra punctata (*Müller, 1788*)	Free-living	–	*Pleijel, Rouse & Nygren (2011)*
Nereimyra woodsholea (*Hartman, 1965*)	Free-living	–	*Pleijel, Rouse & Nygren (2011)*
Oxydromus fauveli *Uchida, Lopez & Sato, 2019*	Free-living	–	*Uchida, Lopez & Sato (2019)*
Oxydromus flexuosus (*Delle Chiaje, 1825*)	Facultative symbiont	Starfish, holothuroids, annelids	*Martin et al. (2017)*
Oxydromus humesi (*Pettibone, 1961*)	Obligate symbiont	Bivalves	*Pettibone (1961)*, *Martin et al. (2012, 2017)*
Oxydromus okupa (*Martin et al., 2017*)	Obligate symbiont	Bivalves	*Martin et al. (2012, 2017)*, *Meca, Drake & Martin (2019)*

Species	Mode of life	Host	References
Oxydromus microantennatus (*Hutchings & Murray, 1984*)	Free-living	–	*Hutchings & Murray (1984)*
Oxydromus obscurus (*Verrill, 1873*)	Facultative symbiont	Annelids, holothuroids	*Martin & Britayev (1998)*
Oxydromus pallidus Claparède, 1864	Facultative symbiont	Annelids	*Martin et al. (2017)*
Oxydromus pugettensis (*Johnson, 1901*)	Facultative symbiont	Echinoderms, decapods, gastropods, bivalves	*Martin & Britayev (1998)*
Parahesione apiculata sp. nov.	Obligate symbiont	Decapods	This study
Parahesione pulvinata sp. nov.	Obligate symbiont	Decapods	This study
Parahesione sp.	Facultative symbiont?	Decapods	*Ruta et al. (2007)*
Podarkeopsis arenicolus (*La Greca, 1946*)	Free-living	–	*La Greca (1946)*
Podarkeopsis helgolandicus (*Hilbig & Dittmer, 1979*)	Free-living	–	*Hilbig & Dittmer (1979)*
Psamathe fusca Johnston, 1836	Free-living	–	*Parapar, Besteiro & Moreira (2005)*
Sirsoe dalailamai Rouse, Carvajal & Pleijel, 2018	Free-living	–	*Rouse, Carvajal & Pleijel (2018)*
Sirsoe methanicola (*Desbruyères & Toulmond, 1998*)	Free-living	–	*Desbruyères & Toulmond (1998)*
Sirsoe munki Rouse, Carvajal & Pleijel, 2018	Free-living	–	*Rouse, Carvajal & Pleijel (2018)*
Sirsoe sirikos Summers, Pleijel & Rouse, 2015	Free-living	–	*Summers, Pleijel & Rouse (2015)*
Syllidia armata Quatrefages, 1866	Free-living	–	*Ruta & Pleijel (2006)*
Vrijenhoekia balaenophila Pleijel et al., 2008	Free-living	–	*Pleijel et al. (2008)*
Vrijenhoekia ahabi Summers, Pleijel & Rouse, 2015	Free-living	–	*Summers, Pleijel & Rouse (2015)*
Vrijenhoekia falenothiras Summers, Pleijel & Rouse, 2015	Free-living	–	*Summers, Pleijel & Rouse (2015)*
Vrijenhoekia ketea Summers, Pleijel & Rouse, 2015	Free-living	–	*Summers, Pleijel & Rouse (2015)*
Vrijenhoekia sp. A *sensu Summers, Pleijel & Rouse (2015)*	Free-living	–	*Summers, Pleijel & Rouse (2015)*

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RESULTS

Systematics

Ophiodrominae *Pleijel, 1998*

Amphidurini *Pleijel et al., 2012*

Parahesione Pettibone, 1956

Diagnosis (emended). Body depressed, reddish when alive. Prostomium with two lateral antennae, without median antenna, two pairs of eyes. Palps simple or biarticulate. Six or eight pairs of tentacular cirri. Dorsal cirrophores fused with or without dorsal foliose lobe extending to base of parapodia. Parapodia biramous. Notopodia with numerous capillary chaetae. Neuropodia with numerous compound chaetae: homogomph and/or heterogomph falcigers, and heterogomph spingers (after *Pettibone, 1956*).

Remarks. *Parahesione* resembles *Amphiduros* and *Amphiduropsis* in having enlarged dorsal cirri on segments 1–5, but differs in lacking median antenna (having a short one in *Amphiduros* and *Amphiduropsis*). Two species of the genus, type species *P. luteola* and *Parahesione* sp. from New Caledonia (*Ruta et al., 2007*) have six enlarged tentacular cirri and cilindrical dorsal cirrophores, while two new species, *P. pulvinata* and *P. apiculata* have eight pairs of tentacular cirri and dorsal cirrophores fused with dorsal foliose lobe extending to base of parapodia. We assign these species to the same genus *Parahesione* and modify the diagnosis of the genus. However, since the DNA repository data for *Parahesione* sp. used in *Ruta et al. (2007)* is very limited, and for the type species *P. luteola* is unavailable (formaldehyde fixation), it is possible that the two morpho-types *Parahesione* (eight enlarged cirri & dorsal cirrophores with dorsal foliose lobe *vs.* six enlarged cirri & dorsal cirrophores without dorsal foliose lobe) would be assigned to different genera if molecular sequences for additional specimens of first morpho-type would be obtained.

Parahesione pulvinata Jimi, Gonzalez, Rouse and Britayev sp. nov.
[New Japanese name: ana-yadori-otohime]
(Figs. 2–5, Fig. S1)
Zoobank LSID: urn:lsid:zoobank.org:act:2E42DB94-DF8C-447A-A7F8-8C2FDA9FF4CA
Parahesione sp.: *Britayev & Antokhina (2012)*: 33, Pl. 9 C, D

Diagnosis. *Parahesione* with dorsal foliose lobe, without dorso-lateral digitate extension, and eight tentacular anterior cirri.

Material examined. Holotype: NMST-Pol H-893, 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, associated to *N. 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 as holotype, but from another burrow of
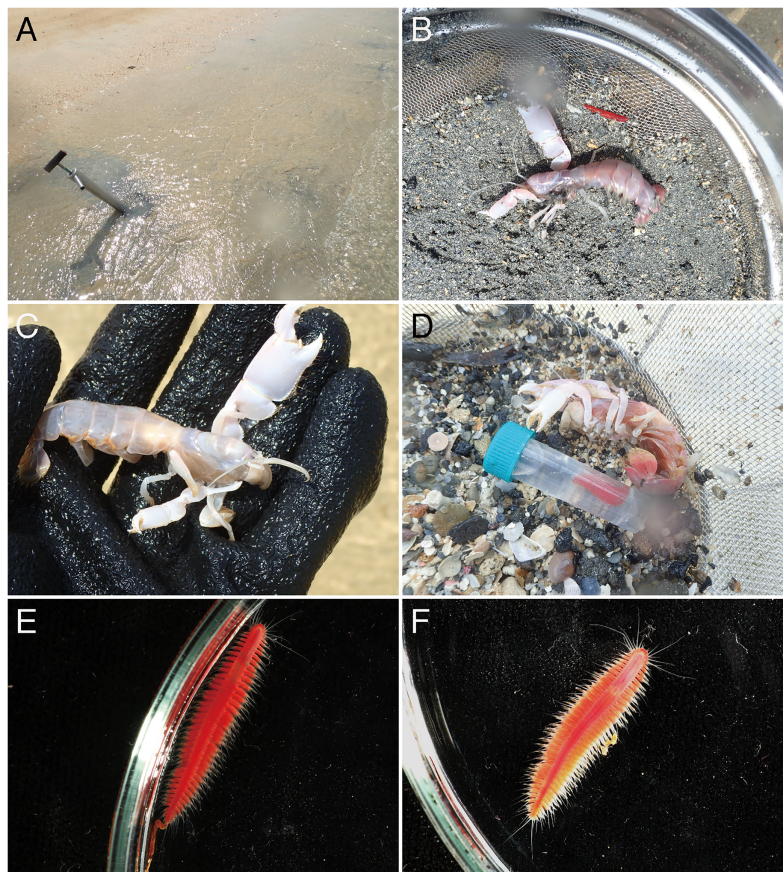
Figure 2 **Observations of *Parahesione pulvinata* sp. nov. and its hosts *in situ*.** (A) Sampling at the sandy tidal flat of Uehara; (B) host and the new species; (C) detail of the host *Neocallichirus jousseaumei*; (D) another host with its symbiont (tube); (E) dorsal view of the new species of a living specimen (NSMT-Pol H-893); (F) dorsal view of a preserved specimen (NSMT-Pol H-893).

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 an unknown crustacean, 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 an unknown crustacean, 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 an unknown crustacean, 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 associated to *C. bulimba*, 13 December 2012, collected by Art Anker and GR. 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, associated to *Upogebia* sp., 18 April 2004, collected by Ivan Marin.
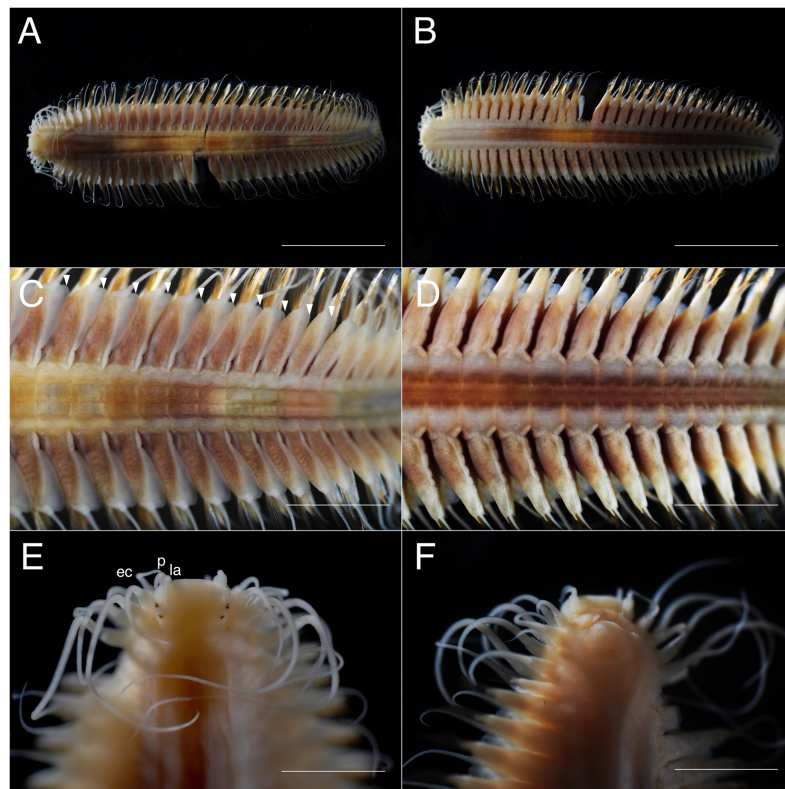
Figure 3 *Parahesione pulvinata* **sp. nov. (NSMT-Pol H-893).** (A) Whole specimen, dorsal view; (B) whole specimen, ventral view; (C) middle segments, dorsal view; (D) middle segments, ventral view; (E) anterior end, dorsal view; (F) anterior end, ventral view. White arrows indicate pillow-shaped dorsal cirrophore without digitate lobes. Abbreviation: la, lateral antenna; p, palp; ec, enlarged cirrus. Scale bars: A and B, 5 mm; C and D, 2 mm; E and F, 1 mm.
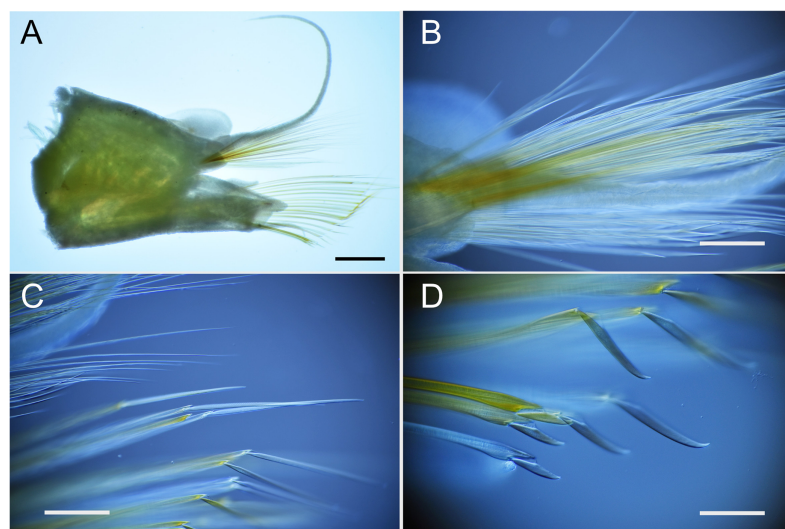
Figure 4 *Parahesione pulvinata* **sp. nov. (NSMT-Pol H-893).** (A) Parapodium of chaetiger 12, rear view; (B) notochaetae, chaetiger 12; (C) upper side of neurochaetae, chaetiger 12; (D) lower side of neurochaetae. Scale bars: A, 200 μm; B–D, 100 μm.
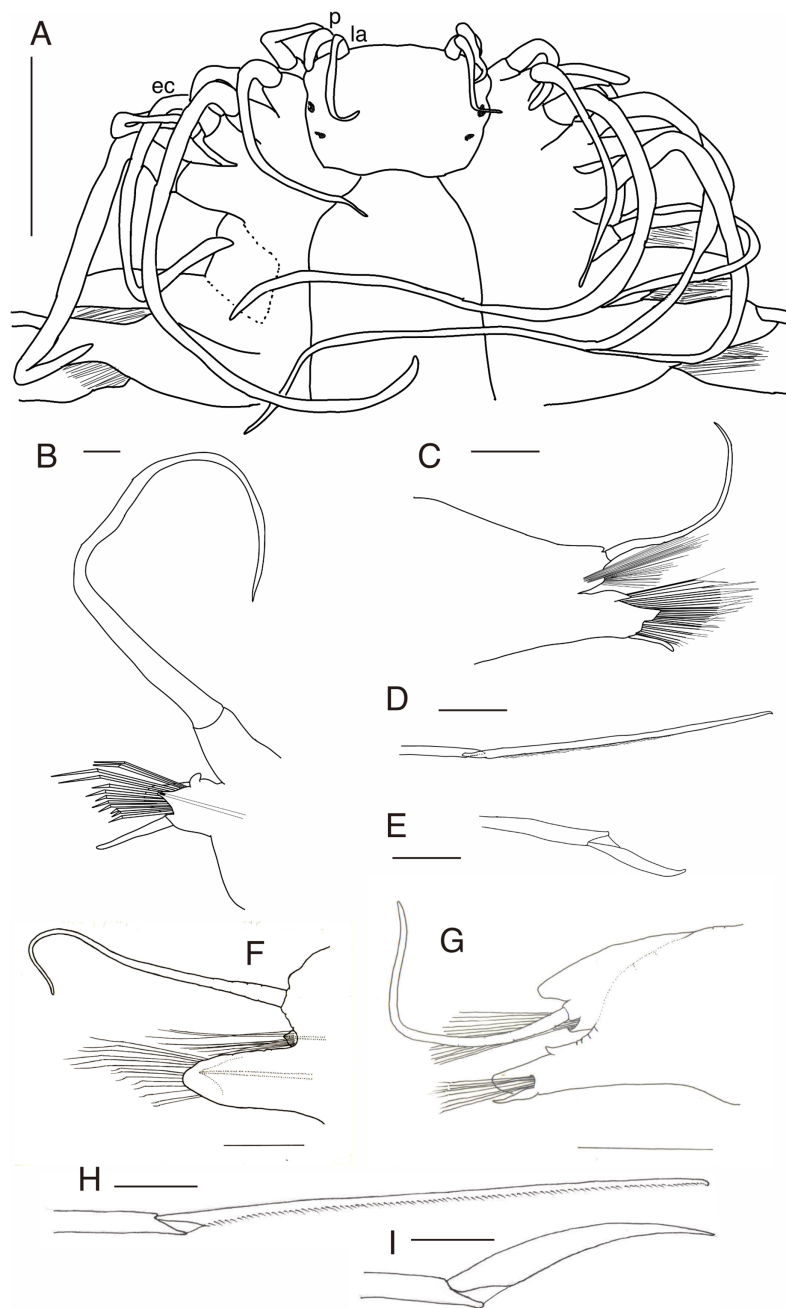
Figure 5 *Parahesione pulvinata* **sp. nov. (NSMT-Pol H-893: A–E, IPEE RAS – Pol. 2004/01: E–I).** (A) Anterior end, dorsal view; (B) parapodium of chaetiger 1, rear view; (C) parapodium of chaetiger 17, frontal view; (D) neurochaeta, upper side, chaetiger 17; (E) neurochaeta, lower side, chaetiger 17; (F) parapodium of chaetiger 18, frontal view; (G) parapodium of chaetiger 23, rear view; (H) supreacicular spiniger; (I) uppermost falciger. Scale bars: A, 1 mm; B, 100 µm; C, 500 µm; D and E, 100 mm; F and G, 500 µm; H and I, 100 µm. Abbreviation: la, lateral antenna; p, palp; ec, enlarged cirrus.

Description of holotype. Body depressed, tapered in posterior region, reddish when alive (Fig. 2), pinkish after fixation (Fig. 3). Prostomium rectangular, wider than long (Figs. 3E and 5A). Lateral antennae slightly shorter than head length, cylindrical, with distally

tapering style and short cylindrical ceratophores. Palps 2/3 antennae length, with cylindrical distally tapering palpostyles and short cylindrical palpophores. Two pairs of eyes, dark reddish in alive, brownish after fixation.

Elongated dorsal cirri on segments 1–5; tentacular cirri eight pairs, on segments 1–4, cirrophores of tentacular cirri cylindrical, basally fused; longest dorsal cirri reaching chaetiger 8, longest ventral cirri reaching chaetiger 5. Chaetae absent from segments 1–4.

Dorsal cirrophores from segment 6 (= chaetiger 2) fused with dorsal foliose lobe extending to base of parapodia, partially covering subsequent segment (Fig. 3C); all dorsal cirrostyles long, twice as long or longer than neuropodial lobe with chaetae, conical, smooth (Fig. 5C). Ventral cirrophores fused to parapodia; ventral cirrostyles short, slightly extending beyond neuropodial lobe, conical, smooth (Figs. 3D and 5C). Noto- and neuro aciculae brownish, tip of aciculae not seen *in vivo*, reddish after fixation.

All chaetigers biramous (Fig. 4A) except chaetiger 1 (uniramous notopodia small, conical, pointed, with about 40 simple capillary very fine notochaetae Fig. 4B); neuropodia large, truncated, longer than wide, with prechaetal lobes and a postero-dorsal digitiform projections (Fig. 5C) and about 30 compound heterogomph chaetae, supraacicular spinigers (Fig. 4C) and subacicular falcigers (Fig. 4D) with unidentate blades faintly serrated in spinigers and superior falcigers (Figs. 5H and 5I); smooth in most inferior falcigers; length of blades in bundle decreases from superior to inferior neurochaetae (Figs. 5D and 5E). Pygidium with two smooth anal cirri twice as long as dorsal cirri.

Variation. Body length 12.0–19.5 mm; number of chaetigers 24–48. Morphology of paratypes corresponds to description of holotype; anterior pair of dark red eyes was visible in specimen from Nhatrang when alive.

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

Remarks. *Parahesione pulvinata* sp. nov. resembles *P. luteola*, the type species of the genus and the single previously known species, in lacking the median antenna while having a flattened body and living symbiotically with ghost shrimps. However, it differs in having flattened dorsal parapodial extension and eight tentacular anterior cirri (without extension and and six tentacular cirri in *P. luteola*). *Parahesione* sp. from Vietnam (Figs. 5F–5I) and Papua New Guinea (Fig. S1) 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.

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* (Japan) and *Upogebia* sp. (Vietnam), or at 1–5 m inside burrows of *C. bulimba*.

Parahesione apiculata Jimi, Gonzalez, Rouse and Britayev sp. nov.
[New Japanese name: toge-ana-yadori-otohime]
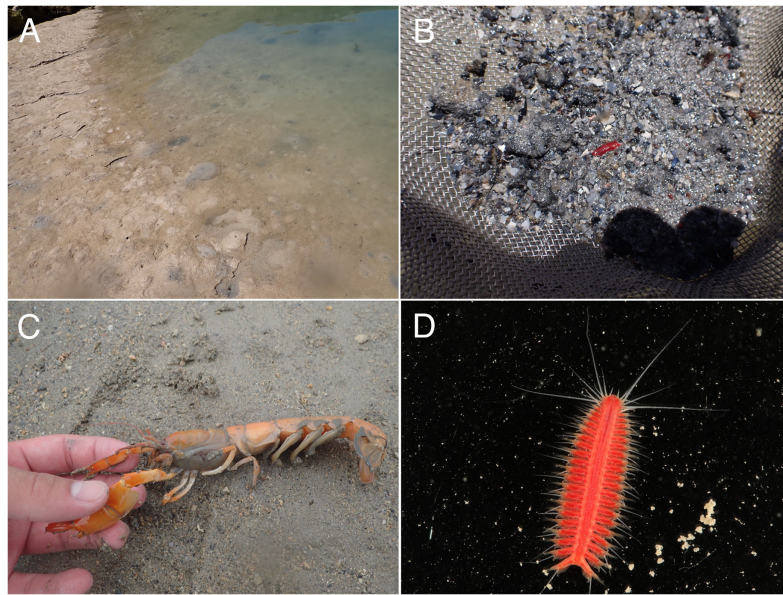
Figure 6 *Parahesione apiculata* sp. nov. and hosts *in situ* (A) Sampling location at the Nanjo sandy tidal flat; (B) living specimen of the symbiont; (C) living specimen of the *Glypturus armatus* (host); (D) dorsal view of a living specimen, lacking posterior most segments (same individual with Fig. 6B, NSMT-Pol P-899).

(Figs. 6–9)

Zoobank LSID: urn:lsid:zoobank.org:act:1AB8DAA4-2268-445D-A3A6-9AE9C085A856

Diagnosis. *Parahesione* with dorsal foliose lobe, dorso-lateral digitate extension, and eight tentacular anterior cirri.

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 *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, Kujuzaki, intertidal, burrow of *G. armatus*, 22 August 2021, collected by TS.

Description of holotype. Body depressed, tapering in posterior region, reddish when alive, pale orange after fixation (Figs. 6 and 7).

Prostomium rectangular, wider than long (Fig. 9A). Lateral antennae as long as head length, cylindrical, with distally tapering style and short cylindrical ceratophores. Palps 5/7 antennae length, with cylindrical distally tapering palpostyles and short cylindrical palpophores. Two pairs of eyes (Figs. 7E and 9A), inconspicuous when alive (Fig. 6D), brownish after fixation (Fig. 7E).
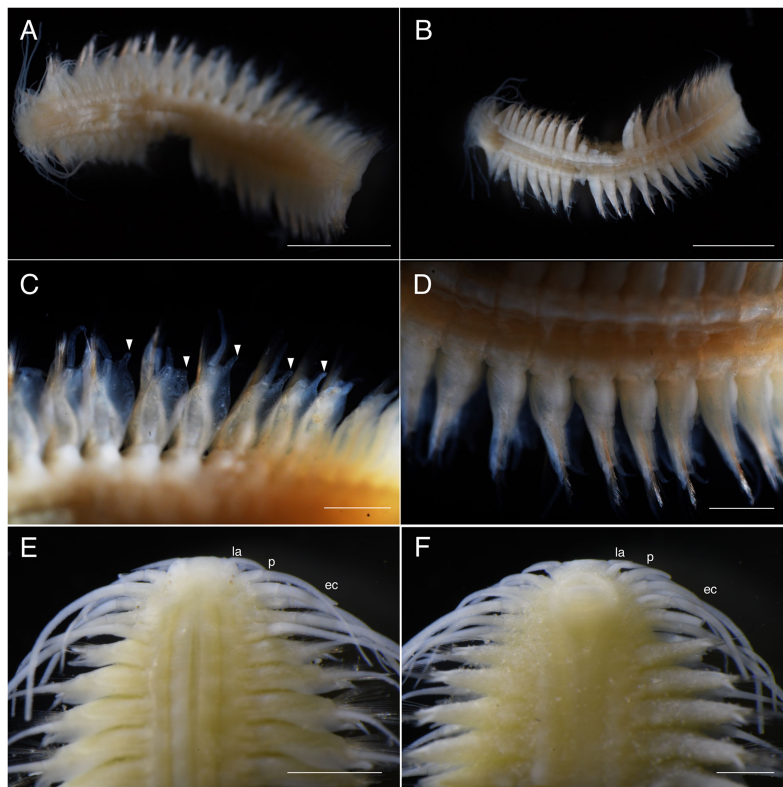
Figure 7 *Parahesione apiculata* sp. nov. (NSMT-Pol H-898). (A) Whole specimen, dorsal view; (B) whole specimen, ventral view; (C) middle segments, dorsal view; (D) middle segments, ventral view; (E) anterior end, dorsal view; (F) anterior end, ventral view. White arrows indicate digitate lobes. Abbreviation: la, lateral antenna; p, palp; ec, enlarged cirrus. Scale bars: A and B, 3 mm; C and D, 1 mm; E and F, 1 mm.
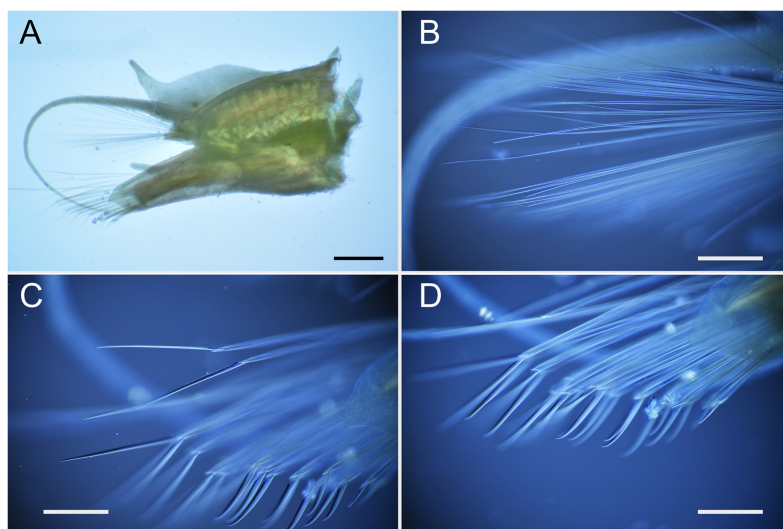
Figure 8 *Parahesione apiculata* sp. nov. (NSMT-Pol H-898). (A) Parapodium of chaetiger 12, frontal view; (B) notochaetae, chaetiger 12; (C) upper side of neurochaetae, chaetiger 12; (D) lower side of neurochaetae. Scale bars: A, 200 μm; B–D, 100 μm.
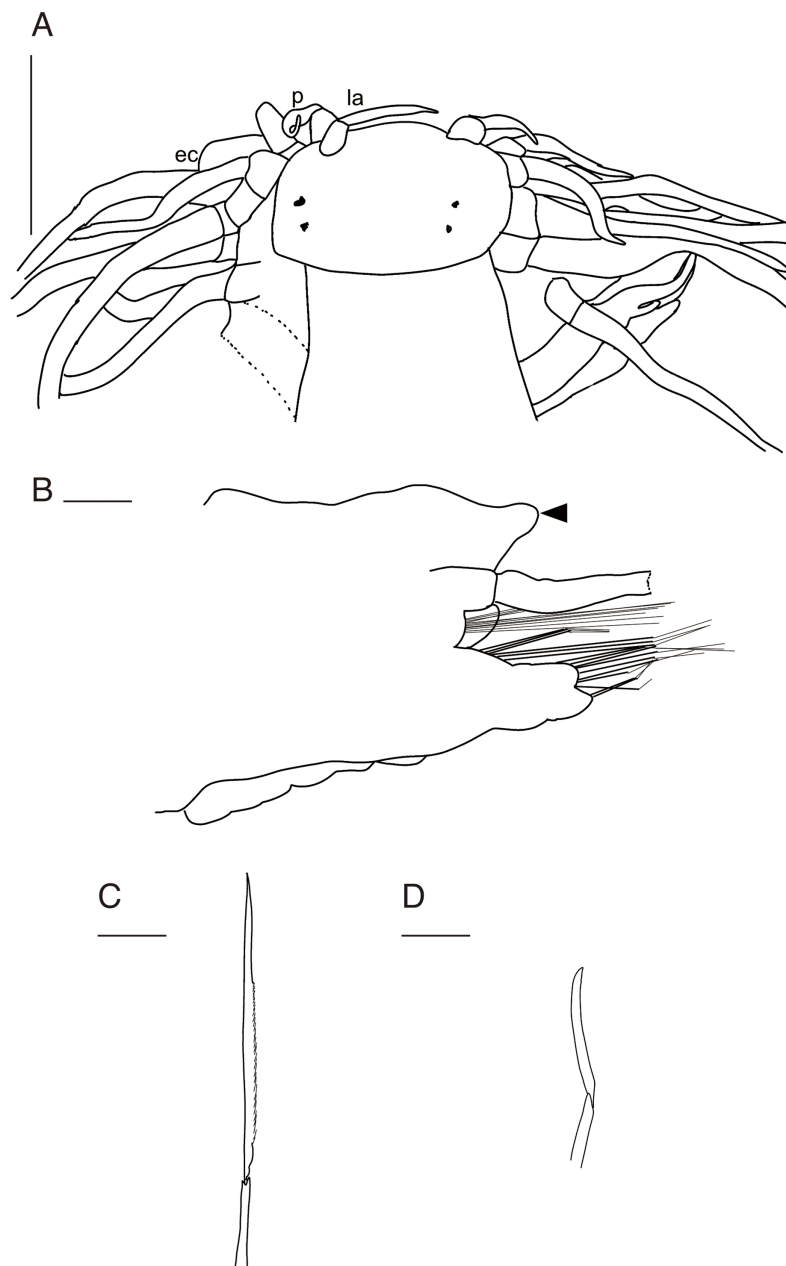
Figure 9 *Parahesione apiculata* sp. nov. (NSMT-Pol H-898). (A) Anterior end, dorsal view; (B) parapodium of chaetiger 17, frontal view; (D) neurochaeta, upper side, chaetiger 17; (D) neurochaeta, lower side, chaetiger 17. Black arrow indicates a digitate lobe. Abbreviation: la, lateral antenna; p, palp; ec, enlarged cirrus. Scale bars: A, 1 mm; B, 500 μm; C and D, 100 mm.

Elongated dorsal cirri on segments 1–5; tentacular cirri eight pairs, on segments 1–4, cirrophores of tentacular cirri cylindrical, basally fused; longest dorsal cirri reaching chaetiger 8, longest ventral cirri reaching chaetiger 7. Chaetae absent from segments 1–4.

All dorsal cirrophores cylindrical; from segment 6 (= chaetiger 2) fused with dorsal foliose lobe extending to base of parapodia, partially covering subsequent segment (Figs.

7C, 8A and 9B); dorsal foliose lobe with dorso-lateral digitate extension; dorsal cirrostyle long, equal, or slightly longer than neuropodia with chaetae, conical, smooth (Fig. 7C). Ventral cirrophore fused with parapodia; ventral cirrostyle short, slightly extending beyond neuropodial lobe, conical, smooth. Noto- and neuroaciculae not seen *in vivo*, brownish with reddish tips when preserved.

All chaetigers biramous except chaetiger 1 (uniramous). Notopodia small, conical, with about 40 simple capillary notochaetae (Fig. 8B), faintly serrated. Neuropodia large, truncated, longer than wide, with pre- and post-chaetal lobes and a digitiform projection present on postero-dorsal part (Figs. 7C and 9B). About 30 heterogomph chaetae, supraacicular spinigers (Fig. 8C) and subacicular falcigers (Fig. 8D) with unidentate blades; faintly serrated in spinigers and superior falcigers; smooth in most inferior falcigers; length of blades in bundle decreases from superior to inferior neurochaetae (Figs. 9C and 9D). Pygidium with two long anal cirri, smooth.

Etymology. The specific name "*apiculata*", derives from the Latin *apiculatus* (meaning short pointed) and referring to the digitate extension on dorso-lateral margin of dorsal foliose lobe, 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 dorsal foliose lobe and eight tentacular anterior cirri (absent and six in *P. luteola*). *Parahesione apiculata* sp. nov. differs from *P. pulvinata* sp. nov. in having digitate extension on posterior margin of dorsal foliose lobe (digitate extension absent in *P. pulvinata* sp. nov.), as well as in living in association with *G. armatus* (*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*.

Key to species of *Parahesione*

1. Parapodia with dorsal foliose lobe ……………………………………………………
2 – Parapodia without dorsal foliose lobe ………………… *P. luteola* (*Webster, 1879*)
2. Dorsal foliose lobe with digitate extension in opposite side of body ……………………
………………………… ………………………… *P. apiculata* sp. nov. This study
3. Dorsal foliose lobe without digitate extension in opposite side of body ………………
………………………………………………… *P. pulvinata* sp. nov. This study

Molecular analyses

Parahesione apiculata sp. nov. and *Parahesione* sp. from Papua New Guinea form a clade, sister to *P. pulvinata* sp. nov. All together, they consitute the *Parahesione* clade which, in turn, is sister to the *Amphiduros–Amphiduropsis* clade (Fig. 10). K2P genetic distance between the two new species is 11.0% (10.1% uncorrected).
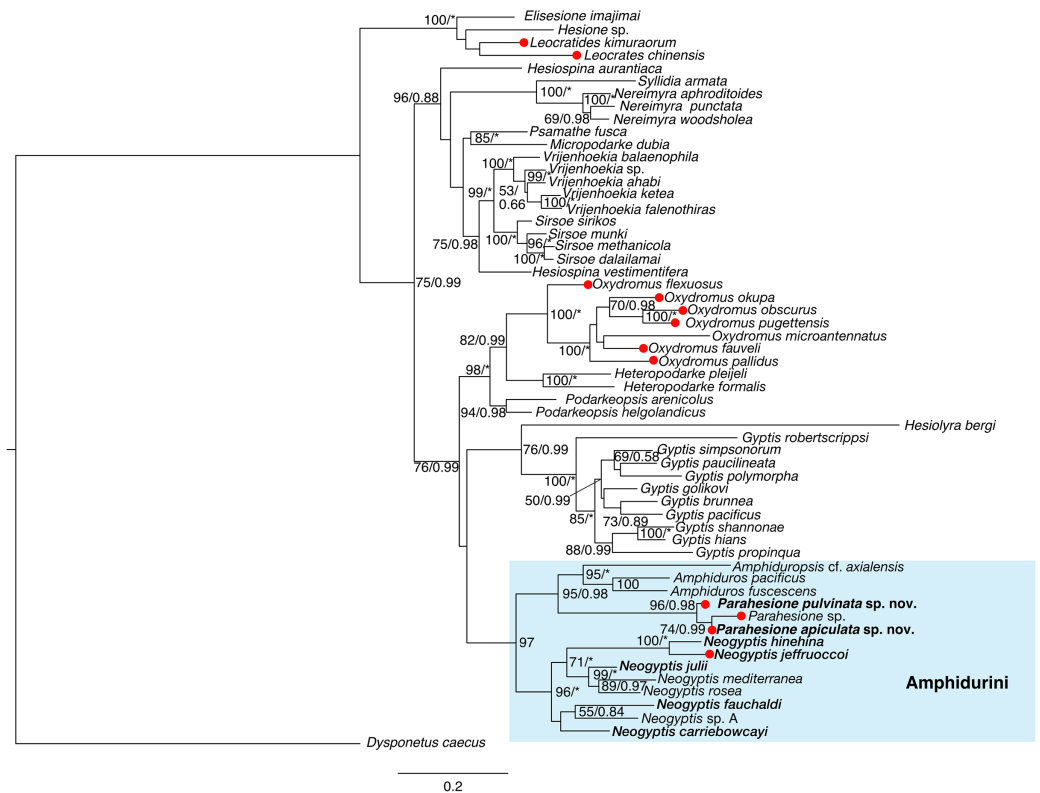
Figure 10 Maximum-likelihood phylogenetic tree of Hesionidae based on *COI*, *16S*, *18S* and *28S* sequences. Nodal bootstrap support (BS) values higher than 50% are indicated for each branch. Posterior probability (PP) of each branch is also shown behind the bootstrap value. * = 100 in BS and 1.00 in PP; - = node absent in the Bayesian tree. Red circles indicate symbiotic species.

DISCUSSION

Parahesione luteola was reported from oyster shell 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 symbiont (*Martin & Britayev, 1998*). Unidentified species of *Parahesione* were reported from the Arctic Sea (*Atkinson & Percy, 1991*), Australia (*Gunton et al., 2021*), Costa Rica (*Maurer, Vargas & Dean, 1988*), New Caledonia (*Ruta et al., 2007*) and Vietnam (*Britayev & Antokhina, 2012*). The Vietnamese specimen is here considered as belonging to *P. pulvinata* sp. nov. as suggested by *Britayev & Antokhina (2012)* and discussed above in the corresponding *Remarks* section. The specimen of *Parahesione* sp. collected by *Ruta et al. (2007)* in New Caledonia (Pacific Ocean), is far from the type locality of the single known species of the genus, the eastern Atlantic coast of the United States (*Pettibone, 1956*). We reexamined the specimen used in *Ruta et al. (2007)* and confirmed that the specimen has six enlarged cirri and dorsal cirri without dorsal foliose lobe (Figs. S2A and S2B) and is likely another new species but is not described here. Additionally, we examined the specimens of *P. luteola* in the USNM (Figs. S2C and S2D) and they have six enlarged cirri and dorsal cirri without dorsal foliose lobe agreeing with *Pettibone (1956)*'s description.

In this situation, we assign these two new species to the same genus *Parahesione* and modify the diagnosis of the genus. However, the DNA repository data for *Parahesione* sp. used in *Ruta et al. (2007)* is very limited, with only a single partial sequence of 28 S (381 bp). We could not determine the other gene sequences because the specimen was preserved in formalin. Given the situation described above, there exists a possibility that the two morpho-types *Parahesione* (eight enlarged cirri, rectangle prostomium, dorsal cirri with dorsal foliose lobe *vs.* six enlarged cirri, trapezoidal prostomium, dorsal cirri without dorsal foliose lobe) could be distinguished on a molecular phylogenetic tree if they are re-examined with additional specimens and gene sequences. To validate whether these characteristics are indicative of phylogenetic affiliations, the necessity for further additional sampling is unequivocal.

Our phylogenetic results (Fig. 10) showed that *Parahesione* as closest to the *Amphiduros-Amphiduropsis* clade consistent with *Ruta et al. (2007)*, and 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, *Parahesione apiculata* sp. nov. and *P. pulvinata* have always been found inside ghost shrimp burrows, suggesting they are obligate symbionts. Moreover, they have always been found in association with *G. armatus* and with *N. jousseaumei* and *Upogebia* sp. (the latter still requiring a more precise identification, N. Jimi, 2022, personal observation), thus suggesting a high degree of host specificity. Moreover, like many other symbiotic polychaetes (*Martin & Britayev, 1998*, *2018*), both species show morphological adaptations to symbiosis. These include flat bodies and dorsal foliose lobes, which is not found in the non-symbiotic species of the *Amphiduropsis-Amphiduros* sister clade. 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 & Martin, 2021*). Another interesting adaptation is the extreme flatness of body and dorsal foliose lobe. We suggest these features may facilitate the worm movement between the host body and the walls of the narrow burrowsand 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* Schamarda, 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*; *Britayev & Zamyshliak, 1996*). The other possible function of the the dorsal foliose lobes may also be related to the efficiency of gas exchange under conditions of hypoxia in host burrows.

The bodies of the two new species also have bright red-colour when alive. Again, this contrasts with the free-living species of *Amphiduropsis-Amphiduros* clade, suggesting this trait was newly acquired in *Parahesione*. A bright red color was also reported for *Hesperonoe* (Polynoidae), which also live in association with mud shrimps (*Sato et al., 2001*; *Hong, Lee & Sato, 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 & 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. Thus, further anatomical and histological studies are needed to confirm the gas exchange function of the foliose lobes and the presence of red bodies and thus assess whether they are adaptations of *Parahesione* to life under hypoxic conditions.

CONCLUSIONS

The genus *Parahesione*, belonging to Hesionidae, is a rare group of symbiotic polychaetes living in ghost shrimp burrows with two different sets of tentacular cirri; in one species there are only six whereas in the other there are eight. Interestingly, the prostomium have different shape being trapezoidal in those species with six pairs of tentacular cirri, and rectangular for those having eight pairs of tentacular cirri. Further, the dorsal parapodial modifications involving a foliose dorsal projection has been only reported in those species with eight pairs of tentacular cirri, whereas it has not been recorded in the only species having six pairs of tentacular cirri. We have discovered two new *Parahesione* species associated with ghost shrimps from the northwest Pacific. Both species are characterized by a flattened body, expanded foliose bases of cirrophores, and a bright red color. We consider these features as adaptations to thrive in the burrow hypoxic conditions. Reconstruction of the phylogenetic tree using four genes revealed their close relationship with non-symbiotic species of the sister clade *Amphiduropsis-Amphiduros*, suggested the independent establishment of symbiosis in various clades of the family Hesionidae.

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Competing Interests

The authors declare that they have no competing interests.

Author Contributions

- Naoto Jimi conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.
- Hiroki Nakajima performed the experiments, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.
- Taigi Sato performed the experiments, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.
- Brett C. Gonzalez performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.
- Sau Pinn Woo performed the experiments, analyzed the data, authored or reviewed drafts of the article, and approved the final draft.
- Greg W. Rouse performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.
- Temir Britayev conceived and designed the experiments, performed the experiments, analyzed the data, authored or reviewed drafts of the article, and approved the final draft.

DNA Deposition

The following information was supplied regarding the deposition of DNA sequences:

The sequences of Parahesione apiculata and *P. pulvinata* are available at GenBank: OP404166, OP404167, OP407536, OP407537, OP407566, OP407585, and OP407586.

Data Availability

The gene sequences are available at GenBank: OP404166, OP404167, OP407536, OP407537, OP407566, OP407585, and OP407586.

New Species Registration

The following information was supplied regarding the registration of a newly described species:

Publication LSID: urn:lsid:zoobank.org:pub:6D64D9F4-0E29-4F67-B941-300E1888108C

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

Parahesione apiculata LSID: urn:lsid:zoobank.org:act:1AB8DAA4-2268-445D-A3A6-9AE9C085A856
Supplemental Information

Supplemental information for this article can be found online at http://dx.doi.org/10.7717/peerj.16346#supplemental-information.

REFERENCES

Atkinson EG, Percy JA. 1991. Stomach content analysis of marine benthic fish from Arctic Canada. *Canadian Data Report of Fisheries and Aquatic Sciences* **840**:1–31.

Atkinson RJA, Taylor AC. 2005. Aspects of the physiology, biology and ecology of thalassinidean shrimps in relation to their burrow environment. *Oceanography and Marine Biology* **43**:1–600.

Averincev VG. 1990. The polychaete fauna of the Laptev Sea. *Issledovaniya Fauny Morei* **37**:147–186.

Banse K, Hobson D. 1968. Benthic polychaetes from Puget Sound, Washington, with remarks on four other species. *Proceedings of the United States National Museum* **125(3667)**:1–53 DOI 10.5479/si.00963801.125-3667.1.

Blake JA. 1985. Polychaeta from the vicinity of deep-sea geothermal vents in the eastern Pacific. I: Euphrosinidae, Phyllodocidae, Hesionidae, Nereididae, Glyceridae, Dorvilleidae, Orbiniidae and Maldanidae. *Bulletin of the Biological Society of Washington* **6**:67–101.

Bonifácio P, Lelièvre Y, Omnes E. 2018. A new species and phylogenetic insights in *Hesiospina* (Annelida, Hesionidae). *Zootaxa* **4441**:59–75 DOI 10.11646/zootaxa.4441.1.3.

Britayev TA, Antokhina TI. 2012. Symbiotic polychaetes from Nhatrang Bay, Vietnam. In: Britayev TA, Pavlov DS, eds. *Benthic Fauna of the Bay of Nhatrang, Southern Vietnam.* Vol. 2, 11–44.

Britayev TA, Martin D. 2021. Behavioral traits and territoriality in the symbiotic scaleworm *Ophthalmonoe pettiboneae. Scientific Reports* **11**:12408 DOI 10.1038/s41598-021-91810-2.

Britayev TA, Mekhova E, Deart Y, Martin D. 2017. Do syntopic host species harbour similar symbiotic communities? The case of *Chaetopterus* spp. (Annelida: Chaetopteridae). *PeerJ* **5**: e2930 DOI 10.7717/peerj.2930.

Britayev TA, Zamyshliak EA. 1996. Association of the commensal scaleworm *Gastrolepidia clavigera* (Polychaeta: Polynoidae) with holothurians near the coast of South Vietnam. *Ophelia* **45**:175–190 DOI 10.1080/00785326.1996.10432470.

Campos E, Campos A, Manriquez I. 2009. Intertidal thalassinidean shrimps (Thalassinidea, Callianassidae and Upogebiidae) of the West cost of Baja California, Mexico: annotated checklist, key for identification, and symbionts. *Crustaceana* **82**:1249–1263 DOI 10.1163/001121609X12481627024454.

Claparède É. 1864. Glanures zootomiques parmi les annélides de Port-Vendres (Pyrénées Orientales). *Mémoires de la Société de Physique et d'Histoire Naturelle de Genéve* **17**:463–600.

Dahlgren TG, Lundberg J, Pleijel F, Sundberg P. 2000. Morphological and molecular evidence of the phylogeny of Nereidiform polychaetes (Annelida). *Journal of Zoosystematics and Evolutionary Research* **38**:249–253 DOI 10.1046/j.1439-0469.2000.384150.x.

Delle Chiaje S. 1825. POLYCHAETA context. *Memorie sulla storia e notomia degli animali senza vertebre del Regno di Napoli* **2**:185–444.

Desbruyères D, Toulmond A. 1998. A new species of hesionid worm, *Hesiocaeca methanicola* sp. nov. (Polychaeta: Hesionidae), living in ice-like methane hydrates in the deep Gulf of Mexico. *CBM—Cahiers de Biologie Marine* **39**:93–98 DOI 10.21411/CBM.A.BA5D76AF.

Fabricius O. 1780. Fauna groenlandica, systematice sistens animalia groenlandiae occidentalis hactenus indagata, quoad nomen specificium, triviale, vernaculumque, synonyma auctorum

plurimum, descriptionem, locum, victum, generationem, mores, usum capturamque singuli, pro ut detegendi occasio fuit, maximaque parte secundum proprias observationes. *Hafniae [= Copenhagen] & Lipsiae [= Leipzig], Ioannis Gottlob Rothe*. xvi+452.

Fauchald K, Hancock DR. 1981. Deep-water polychaetes from a transect off central Oregon. *Allan Hancock Monographs in Marine Biology* **11**:1–73.

Gibbs PE. 1971. The polychaete fauna of the Solomon Islands. *Bulletin of the British Museum (Natural History) Zoology* **21**:99–211.

Goto R, Fukumori H, Kano Y, Kato M. 2018. Evolutionary gain of red blood cells in a commensal bivalve (Galeommatoidea) as an adaptation to a hypoxic. *Biological Journal of the Linnean Society* **125**:368–376 DOI 10.1093/biolinnean/bly104.

Goto R, Hirabayashi I, Palmer AR. 2019. Remarkably loud snaps during mouth-fighting by a sponge-dwelling worm. *Current Biology* **29**:368–376 DOI 10.1016/j.cub.2019.05.047.

Gunton LM, Kupriyanova EK, Alvestad T, Avery L, Blake JA, Biriukova O, Böggemann M, Borisova P, Budaeva N, Burghardt I, Capa M, Georgieva MN, Glasby CJ, Hsueh P-W, Hutchings P, Jimi N, Kongsrud JA, Langeneck J, Meißner K, Murray A, Nikolic M, Paxton H, Ramos D, Schulze A, Sobczyk R, Watson C, Wiklund H, Wilson RS, Zhadan A, Zhang J. 2021. Annelids of the eastern Australian abyss collected by the 2017 RV 'Investigator' voyage. *ZooKeys* **1020**:1–198 DOI 10.3897/zookeys.1020.57921.

Hartman O. 1961. Polychaetous annelids from California. *Allan Hancock Pacific Expeditions* **25**:1–226.

Hartman O. 1965. Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas. *Occasional Papers of the Allan Hancock Foundation* **28**:1–384.

Hessle C. 1925. Einiges über die Hesioniden und die Stellung der Gattung *Ancistrosyllis*. *Arkiv för Zoologi* **17a**:1–36.

Hilbig B, Dittmer J-D. 1979. *Gyptis helgolandica* sp. n. (Hesionidae, Annelida), eine neue Polychaetenart aus dem sublitoral der deutschen bucht. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven* **18**:101–110.

Hong J-S, Lee C-L, Sato M. 2017. A review of three species of *Hesperonoe* (Annelida: Polynoidae) in Asia, with descriptions of two new species and a new record of *Hesperonoe hwanghaiensis* from Korea. *Journal of Natural History* **51**:2925–2945 DOI 10.1080/00222933.2017.1397225.

Hutchings P, Murray A. 1984. Taxonomy of polychaetes from the Hawkesbury River and the Southern Estuaries of New South Wales, Australia. *Records of the Australian Museum Supplement* **3**:1–118 DOI 10.3853/j.0812-7387.3.1984.101.

Jimi N, Eibye-Jacobsen D, Salazar-Vallejo SI. 2018. Description of *Elisesione imajimai* sp. nov. from Japan (Annelida: Hesionidae) and a redescription of *E. problematica* (Wesenberg-Lund, 1950) and its confirmation within Hesionini. *Zoological Studies* **57**:8 DOI 10.6620/ZS.2018.57-08.

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 shells. *Journal of Zoological Systematics and Evolutionary Research* **59**:801–818 DOI 10.1111/jzs.12463.

Jimi N, Tanaka M, Kajihara H. 2017. *Leocratides* (Annelida: Hesionidae) from the Pacific coast of middle Honshu, Japan, with a description of *Leocratides kimuraorum* sp. nov. *Species Diversity* **22**:133–141.

Johnson HP. 1901. The Polychaeta of the Puget Sound region. *Proceedings of the Boston Society for Natural History* **29**:381–437.

Kinberg JGH. 1866. Annulata nova. Continuatio. [various errantia & sedentaria]. *Öfversigt af Königlich Vetenskapsakademiens förhandlingar, Stockholm* **22**:239–258.

La Greca M. 1946. Studii sui Policheti del Golfo di Napoli. *Pubblicazioni della Stazione Zoologica di Napoli* **20**:270–280.

Langerhans P. 1880. Die wurmfauna Madeiras. II. *Zeitschrift für Wissenschaftliche Zoologie* **33**:271–316.

Malm AW. 1874. Annulata i hafvet utmed Sveriges westkust och omkring Göteborg. Göteborgs Königlich vetenskaps-och vitterhetssamhälles handlingar. [Zoologiska observationer. VII.]. *Göteborgs Königlich vetenskaps-och vitterhetssamhälles handlingar* **14**:67–105.

Marenzeller E. 1875. Zur Kenntniss der adriatischen Anneliden. Zweiter Beitrag. (Polynoinen, Hesioneen, Syllideen). *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Wien, Mathematisch-Naturwissenschaftliche Classe* **72**:129–171.

Marion AF, Bobretzky N. 1875. Étude des Annélides du golfe de Marseille. *Annales des Sciences naturelles, Paris* **6**:1–106.

Martin D, Britayev TA. 1998. Symbiotic polychaetes: review of known species. *Oceanography and Marine Biology: 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**:371–447.

Martin D, Cuesta JA, Drake P, Gil J, Nygren A, Pleijel F. 2012. The symbiotic hesionid *Parasyllidea humesi* Pettibone, 1961 (Annelida: Polychaeta) hosted by *Scrobicularia plana* (da Costa, 1778) (Mollusca: Bivalvia: Semelidae) in European waters. *Organisms Diversity & Evolution* **12**:145–153 DOI 10.1007/s13127-012-0086-2.

Martin D, Meca MA, Gil J, Drake P, Nygren A. 2017. Another brick in the wall: population dynamics of a symbiotic species of *Oxydromus* (Annelida, Hesionidae), described as new based on morphometry. *Contributions to Zoology* **86**:181–211 DOI 10.1163/18759866-08603001.

Martin D, Nygren A, Hjelmstedt P, Drake P, Gil J. 2015. On the enigmatic symbiotic polychaete 'Parasyllidea' humesi Pettibone, 1961 (Hesionidae): taxonomy, phylogeny and behaviour. *Zoological Journal of Linnean Society* **174**:429–446 DOI 10.1111/zoj.12249.

Maurer D, Vargas J, Dean H. 1988. Polychaetous annelids from the Gulf of Nicoya, Costa Rica. *Internationale Revue der gesamten Hydrobiologie und Hydrographie* **73**:43–59 DOI 10.1002/iroh.19880730105.

Meca MA, Drake P, Martin D. 2019. Does polyxenous symbiosis promote sympatric divergence? A morphometric and phylogeographic approach based on *Oxydromus okupa* (Annelida, Polychaeta, Hesionidae). *Contributions to Zoology* **88**:173–200 DOI 10.1163/18759866-20191403.

Milne-Edwards A. 1870. Révision du genre *Callianassa* (Leach) et description de plusieurs espèces nouvelles de ce groupe faisant partie de la collection du Muséum. *Nouvelles Archives du Muséum d'Histoire Naturelle de Paris* **6**:75–102.

Müller OF. 1788. Zoologia Danica seu animalium Daniae et Norvegiae rariorum ac minus notorum descriptiones et historia. Volumen secundum, 1–56.

Muona J. 2006. To be named or not to be named—*Heteropodarke pleijeli* sp. n. (Annelida, Polychaeta). *Cladistics* **22**:634–635 DOI 10.1111/j.1096-0031.2006.00123.x.

Nobili G. 1904. Diagnoses préliminaires de vingt-huit espèces nouvelles de stomatopodes et décapodes macroures de la Mer Rouge. *Bulletin du Muséum d'Histoire Naturelle* **10**:228–238.

Nygren A, Pleijel F, Sundberg P. 2005. Genetic relationships between *Nereimyra punctata* and *N. woodsholea* (Hesionidae, Polychaeta). *Journal of Zoological Systematics and Evolutionary Research* **43**:273–276 DOI 10.1111/j.1439-0469.2005.00321.x.

Parapar J, Besteiro C, Moreira J. 2005. Fauna Ibérica-Annelida Polychaeta I: Familia Hesionidae. In: *Annelida Polychaeta I.* Vol. 25. Spain: CSIC, 210–267.

Perkins TH. 1984. New species of Phyllodocidae and Hesionidae (Polychaeta), principally from Florida. *Proceedings of the Biological Society of Washington* **97**:555–582.

Pettibone MH. 1956. Some polychaete worms of the families Hesionidae, Syllidae, and Nereidae from the east coast of North America, West Indies, and Gulf of Mexico. *Journal of the Washington Academy of Sciences* **46**:281–293.

Pettibone MH. 1961. New species of polychaete worms from the Atlantic Ocean, with a revision of the dorvilleidae. *Proceedings of the Biological Society of Washington* **74**:167–186.

Pettibone MH. 1963. *Marine polychaete worms of the New England region. 1. Families Aphroditidae through Trochochaetidae.* Washington: Smithsonian Institution.

Pillay D, Branch GM. 2011. Bioengineering effects of burrowing thalassinidean shrimps on marine soft-bottom ecosystems. *Oceanography and Marine Biology: An Annual Review* **49**:137–192 DOI 10.1201/b11009-5.

Pleijel F. 1993. Taxonomy of European species of *Amphiduros* and *Gyptis* (Polychaeta: Hesionidae). *Proceedings of the Biological Society of Washington* **106**:158–181.

Pleijel F. 1998. Phylogeny and classification of Hesionidae (Polychaeta). *Zoologica Scripta* **27**:89–163 DOI 10.1111/j.1463-6409.1998.tb00433.x.

Pleijel F. 1999. Phylogenetic taxonomy, a farewell to species, and a revision of *Heteropodarke* (Hesionidae, Polychaeta, Annelida). *Systematic Biology* **48**:755–789 DOI 10.1080/106351599260003.

Pleijel F. 2001. Revision of *Amphiduros* Hartman, 1959 (Polychaeta, Hesionidae, Gyptini). *Ophelia* **54**:15–27 DOI 10.1080/00785326.2001.10409453.

Pleijel F. 2004. A revision of *Hesiospina* (Psamathini, Hesionidae, Polychaeta). *Journal of Natural History* **38**:2547–2566 DOI 10.1080/00222930310001647433.

Pleijel F, Rouse GW, Nygren A. 2009. Five colour morphs and three new species of *Gyptis* (Hesionidae, Annelida) under a jetty in Edithburgh, South Australia. *Zoologica Scripta* **38**:89–99 DOI 10.1111/j.1463-6409.2008.00356.x.

Pleijel F, Rouse GW, Nygren A. 2011. A revision of *Nereimyra* (Psamathini, Hesionidae, Aciculata, Annelida). *Zoological Journal of the Linnean Society* **164**:36–51 DOI 10.1111/j.1096-3642.2011.00756.x.

Pleijel F, Rouse GW, Ruta C, Wiklund H, Nygren A. 2008. *Vrijenhoekia balaenophila*, a new hesionid polychaete from a whale fall off California. *Zoological Journal of the Linnean Society* **152**:625–634 DOI 10.1111/j.1096-3642.2007.00360.x.

Pleijel F, Rouse GW, Sundkvist T, Nygren A. 2012. A partial revision of *Gyptis* (Gyptini, Ophiodrominae, Hesionidae, Aciculata, Annelida), with descriptions of a new tribe, a new genus and five new species. *Zoological Journal of the Linnean Society* **165**:471–494 DOI 10.1111/j.1096-3642.2012.00819.x.

Poore GCB, Griffin DJG. 1979. The Thalassinidea (Crustacea: Decapoda) of Australia. *Records of the Australian Museum* **32**:217–321 DOI 10.3853/j.0067-1975.32.1979.457.

Quatrefages A. 1866. Histoire naturelle des Annelés marins et d'eau douce. *Annélides et Géphyriens* **2**:1–794.

Read G, Fauchald K. 2023. World Polychaeta database. *Available at https://www.marinespecies.org/polychaeta/*.

Rouse GW, Carvajal JI, Pleijel F. 2018. Phylogeny of Hesionidae (Aciculata, Annelida), with four new species from deep-sea eastern methane seeps, and resolution of the affinity of *Hesiolyra*. *Invertebrate Systematics* **32**:1050–1068 DOI 10.1071/IS17092.

Rouse GW, Pleijel F, Tilic E. 2022. *Annelida.* London/New York: Oxford University Press, 418.

Ruta C, Nygren A, Rousset V, Sundberg P, Tiller A, Wiklund H. 2007. Phylogeny of Hesionidae (Aciculata, Polychaeta), assessed from morphology, 18S rDNA, 28S rDNA, 16S rDNA and COI. *Zoologica Scripta* **36**:99–107 DOI 10.1111/j.1463-6409.2006.00255.x.

Ruta C, Pleijel F. 2006. A revision of *Syllidia* (Psamathini, Hesionidae, Polychaeta). *Journal of Natural History* **40**:503–521 DOI 10.1080/00222930600727291.

Sars M. 1862. Uddrag af en af detaillerede Afbildninger ledsaget udf rlig Beskrivelse over f lgende norske Annelider. *Forhandlinger fra Videnskabs-Selskabet i Christiania* **1861**:87–95.

Sato M, Uchida H, Itani G, Yamashita H. 2001. Taxonomy and life history of the scale worm *Hesperonoe hwanghaiensis* (Polychaeta: Polynoidae), newly recorded in Japan, with special reference to commensalism to a burrowing shrimp, *Upogebia major. Zoological Science* **18**:981–991 DOI 10.2108/zsj.18.981.

Say T. 1818. An account of the Crustacea of the United States. *Journal of the Academy of Natural Sciences of Philadelphia* **1**:57–63.

Stecher G, Tamura K, Kumar S. 2020. Molecular evolutionary genetics analysis (MEGA) for macOS. *Molecular Biology and Evolution* **37**:1237–1239 DOI 10.1093/molbev/msz312.

Summers M, Pleijel F, Rouse GW. 2015. Whale falls, multiple colonisations of the deep, and the phylogeny of Hesionidae (Annelida). *Invertebrate Systematics* **29**:105–123 DOI 10.1071/IS14055.

Tilic E, Stiller J, Campos E, Pleijel F, Rouse GW. 2022. Phylogenomics resolves ambiguous relationships within Aciculata (Errantia, Annelida). *Molecular Phylogenetics and Evolution* **166**:107339 DOI 10.1016/j.ympev.2021.107339.

Uchida H. 2004. Hesionidae (Annelida, Polichaeta [sic]) from Japan. I. *Kuroshio Biosphere* **1**:27–92.

Uchida H, Lopez E, Sato M. 2019. Unavailable names introduced by Uchida, 2004 revisited, with reestablishment of their availability. *Species Diversity* **24**:69–95 DOI 10.12782/specdiv.24.69.

Verrill AE. 1873. XVIII. Report upon the invertebrate animals of vineyard sound and the adjacent waters, with an account of the physical characters of the region. *Report on the Condition of the Sea Fisheries of the South Coast of New England [later becomes Reports of the United States Commissioner of Fisheries]* **1**:295–778.

Wang Z, Qiu J-W, Salazar-Vallejo SI. 2018. Redescription of *Leocrates chinensis* Kinberg, 1866 (Annelida, Hesionidae). *Zoological Studies* **57**:5 DOI 10.6620/ZS.2018.57-05.

Watson C, Chivers AJ, Narayanaswamy BE, Lamont P, Turnewttsch R. 2014. Chrysopetalidae (Annelida: Phyllodocida) from the senghor seamount, north-east Atlantic: taxa with deep-sea affinities and morphological adaptations. *Memoirs of Museum Victoria* **71**:311–325 DOI 10.24199/j.mmv.2014.71.24.

Webster HE. 1879. The Annelida Chaetopoda of New Jersey. *Annual Report of the New York State Museum of Natural History* **32**:101–128.

Wessel P, Luis JF, Uieda L, Scharroo R, Wobbe F, Smith WH, Tian D. 2019. The generic mapping tools version 6. *Geochemistry, Geophysics, Geosystems* **20(11)**:5556–5564 DOI 10.1029/2019GC008515.

Wiklund H, Glover AG, Johannessen PJ, Dahlgren TG. 2009. Cryptic speciation at organic-rich marine habitats: a new bacteriovore annelid from whale-fall and fish farms in the North-East Atlantic. *Zoological Journal of the Linnean Society* **155(4)**:774–785 DOI 10.1111/j.1096-3642.2008.00469.x.