



Out of the Pacific: A New Alvinellid Worm (Annelida: Terebellida) From the Northern Indian Ocean Hydrothermal Vents

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Alvinellids have long been considered to be endemic to Pacific vents until recent discovery of their presence in the Indian Ocean. Here, a new alvinellid is characterized and formally named from recently discovered vents, Wocan, and Daxi, in the northern Indian Ocean. Both morphological and molecular evidences support its placement in the genus *Paralvinella*, representing the first characterized alvinellid species out of the Pacific. The new species, formally described as *Paralvinella mira* n. sp. herein, is morphologically most similar to *Paralvinella hessleri* from the northwest Pacific, but the two species differ in three aspects: (1), the first three chaetigers are not fused in *P. mira* n. sp., whereas fused in *P. hessleri*; (2), paired buccal tentacles short and pointed in *P. mira* but large and strongly pointed in *P. hessleri*; (3), numerous slender oral tentacles ungrouped in *P. mira* but two groups in *P. hessleri*. Phylogenetic inference using the concatenated alignments of the cytochrome c oxidase I (COI), 16S rRNA and 18S rRNA genes strongly supports the clustering of *P. mira* with two West Pacific congeners, *P. hessleri* and an undescribed species (*Paralvinella* sp. ZMBN). The resulting Indian/West Pacific lineage suggests a possible invasion into the Indian Ocean from the West Pacific. This is the third polychaete reported from Wocan hydrothermal field. Among the three species, two including *P. mira* and *Hesiohyra heteropoda* (Annelida:Hesionidae) are present in high abundance, forming an alvinellids/hesionids-dominated polychaete assemblage distinct from that at all other Central Indian Ridge and Southwest Indian Ridge vents. Thus, this study expands our understanding of alvinellid biogeography beyond the Pacific, and adds to the unique biodiversity of the northern Indian Ocean vents, with implications for biogeographic subdivision across the Indian Ocean ridges.

Keywords: *Paralvinella*, northern Indian Ocean, deep sea, hydrothermal vent, new species

INTRODUCTION

Deep-sea hydrothermal vents are extreme habitats rich in energy and reduced matters, which support flourished chemosynthesis-based ecosystems and form biodiversity hotspots along the global spreading ridge systems (Van Dover, 2000). One of the most notable features of these vent communities is that they mainly comprise vent endemic fauna, which are not in any other

habitats (Wolff, 2005). One of such typical examples is the vent endemic Alvinellidae (Annelida) Desbruyères and Laubier (1982), whose members are notable for their proximity to the fluid sources in hydrothermal vents and excellent adaptations to an extremely high temperature gradient (Jollivet and Hourdez, 2020).

A total of 12 alvinellid species have so far been described and assigned to two genera, *Alvinella* and *Paralvinella*. All of them are only known from Pacific hydrothermal vent fields, with the two *Alvinella* species (*Alvinella pompejana* Desbruyères and Laubier, 1980 and *Alvinella caudata* Desbruyères and Laubier, 1986) and three *Paralvinella* species (*Paralvinella grasslei* Desbruyères and Laubier, 1982, *Paralvinella bactericola* Desbruyères and Laubier, 1991 and *Paralvinella pandorae irlandei* Desbruyères and Laubier, 1986) reported from the East Pacific Rise (EPR) and Guaymas vent fields, four from the northeast Pacific (*Paralvinella palmiformis* Desbruyères and Laubier, 1986, *Paralvinella pandorae pandorae* Desbruyères and Laubier, 1986, *Paralvinella dela* Detinova, 1988 and *Paralvinella sulfincola* Desbruyères and Laubier, 1993), two from the southwest Pacific vent ecosystems (*Paralvinella fijiensis* Desbruyères and Laubier, 1993 and *Paralvinella unidentata* Desbruyères and Laubier, 1993), and one from the Marianas back-arc spreading center and the Okinawa Trough (*Paralvinella hessleri* Desbruyères and Laubier, 1989). These worms usually form dense aggregations on varied hard substrata, including chimney walls, basaltic cracks with venting fluids and siboglinid tubes (Tunnicliffe et al., 1993; Desbruyères et al., 1994; Hurtado et al., 2004). Although hydrothermal vent organisms usually show a high degree of regional endemism (Rogers et al., 2012), a family endemic to the Pacific vents is still rare. However, the view on this alvinellid biogeographic pattern is challenged by recent discovery of alvinellids in Indian Ocean vents.

Early investigations at Kairei and Edmond vent fields on the Central Indian Ridge (CIR) reported “notable absence” of alvinellids as one of the features that distinguish them from their Pacific counterparts (Van Dover et al., 2001). Investigations in vent fields on the Southwest Indian Ridge (SWIR) (e.g., Longqi and Tiancheng vent fields) and Southeast Indian Ridge (SEIR) (Plegia vent field) also found no signs of such worms (Copley et al., 2016; Zhou et al., 2018; Gerdes et al., 2019). However, at the Solitaire field over 800 km north of Kairei hydrothermal field, a deep-seabed image captured by the Human-Occupied Vehicle (HOV) *Shinkai 6500* surprisingly revealed a small patch of alvinellid worms (taxonomically unresolved at general level) associated with the scaly foot snail, *Chrysomallon squamiferum* Chen et al. (2015), representing the first report of such worms outside the Pacific (Nakamura et al., 2012). In 2017, we collected alvinellid specimens from two vent sites, Daxi and Wocan on the Carlsberg Ridge (CR) in the northwest Indian Ocean. These alvinellids were abundant in the Wocan field, but were not commonly seen in the Daxi field (Wang et al., 2021). Due to the very late discovery of the first active deep-sea hydrothermal vent on the Carlsberg Ridge (almost 15 years after locating the first vent in the Indian Ocean) (Wang et al., 2017), little is known about the diversity of macrobenthos inhabiting the northern Indian

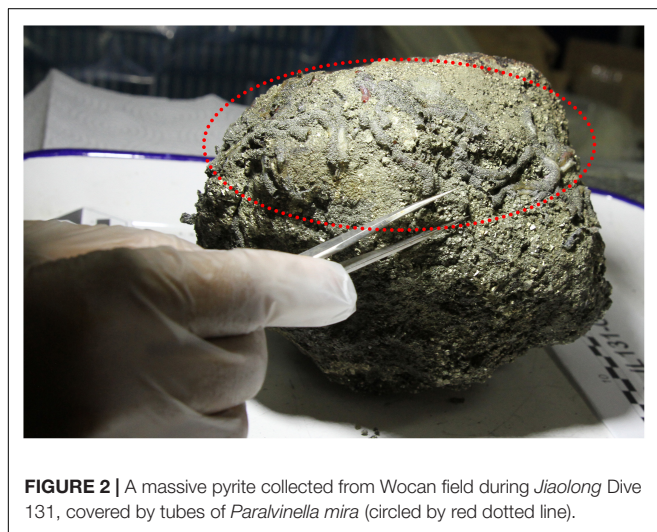
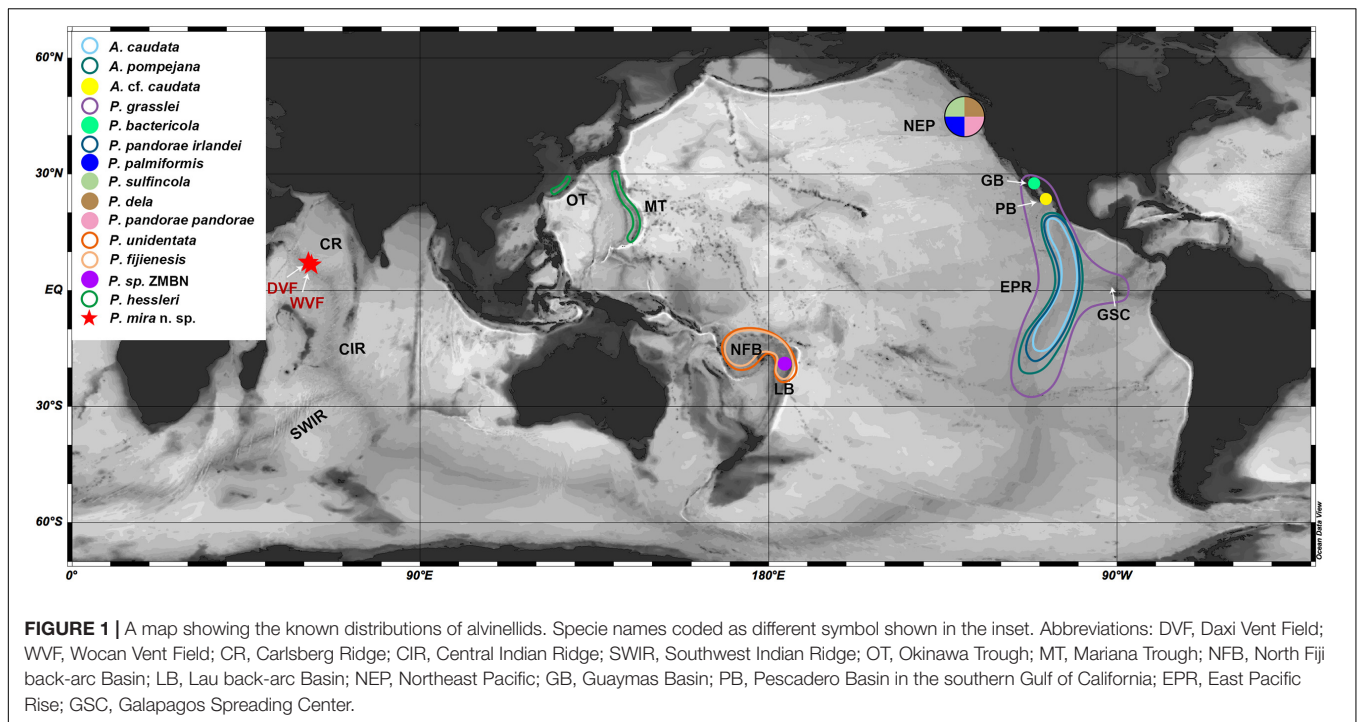
Ocean vents, with only a rough description of Daxi vent community at around 6°48'N (Wang et al., 2021). Most of the taxa are undescribed, except for three new species of polychaetes (Zhou et al., 2019; Wang et al., 2020). Since the alvinellid-dominated polychaete assemblage might be unique to the northwest Indian Ocean vents, identifying these alvinellid species and determining their phylogenetic relationships with their Pacific Ocean relatives will enhance our understanding of the divergence history and diversity of this family of vent endemic polychaetes.

An early study using allozyme recovered *Alvinella* and *Paralvinella* as two monophyletic groups (Jollivet et al., 1995). Based on DNA data, recent molecular phylogenetic studies recovered Alvinellidae as a monophyletic clade, while *Paralvinella* is a paraphyletic genus with the sequenced species split into two lineages (Vrijenhoek, 2013; Stiller et al., 2020). One *Paralvinella* lineage is composed of a pair of sibling geographic species, *P. pandorae irlandei* in the northeast Pacific and *P. pandorae pandorae* on the EPR; The other, comprising *P. fijiensis* (southwest Pacific), *P. sulfincola* (northeast Pacific), *P. grasslei* (EPR) and *P. palmiformis* (northeast Pacific), forms a clade with the *Alvinella* lineage, and this clade is sister to the *P. pandorae* lineage (Stiller et al., 2020). To address the issue of paraphyletic status of *Paralvinella*, Stiller et al. (2020) referred the *P. pandorae* lineage to *Nautalvinella* Desbruyères and Laubier, 1993 based on a combined multigene and morphological dataset, which was originally a subgenus in *Paralvinella* (Desbruyères and Laubier, 1993). Although there are three pairs of sibling geographic species (*P. palmiformis*/*P. grasslei*, *P. pandorae pandorae*/*P. pandorae irlandei*, and *P. dela/bactericola*), no sequences from the remaining four *Paralvinella* species to fully resolve the within-familial phylogeny and biogeographic pattern in the Pacific (Jollivet and Hourdez, 2020). The discovery of alvinellids in the Indian Ocean has raised questions on alvinellid phylogeny and biogeography beyond the Pacific: (1) are the Indian Ocean alvinellids new to science?, (2) do they represent a distinct lineage or not?, and (3) how may this Indian lineage contribute to a better understanding of the biogeography of alvinellids. Aiming to answer these questions, we characterize these alvinellids with a combined morphological and genetic approach.

MATERIALS AND METHODS

Collection and Preservation

During the DY38 cruise in March 2017, alvinellid materials were collected from Wocan and Daxi vent fields on the Carlsberg Ridge in the northwest Indian Ocean (Figure 1). The samples were collected at venting sites by HOV *Jiaolong* equipped with a 7-function manipulator. Over 50 alvinellid specimens from Wocan field were picked out from membranous tubes covered by coarse mineral grains and cemented to the surface of massive pyrites (Figure 2). In addition, two individuals were picked out from residues retained on a sieve after washing chimney fragments. After collection, samples were preserved in 95–100% (v/v) ethanol. Type specimens were deposited in the Repository



of the Second Institute of Oceanography, Ministry of Natural Resources (MNR), China (RSIO).

Morphology

All specimens were observed, dissected and photographed under a Zeiss Discovery V.16 stereomicroscope mounted with a CCD camera. Scanning electron microscopic (SEM) images were taken for selected notochaetae and uncini. Samples for SEM were immersed sequentially in a series of mixture of ethanol and Hexamethyldisilazane (HMDS) (1:0, 3:1, 2:2, 1:3, and 0:1 for 30 min at each step), and then coated in a magnetron sputter

(MSP-1S, Japan) after the HMDS evaporated. Prepared samples were observed using a Hitachi TM-1000 SEM.

Molecular Phylogenetic Analysis

Genomic DNA extraction of alvinellid tissues (sample ID provided in **Table 1**) was performed using the DNeasy blood and tissue kit (Qiagen, San Diego, CA, United States) according to a protocol supplied by the manufacturer. Partial gene sequences were amplified using the primer pairs, HCO2198/LCO1490 for *c* oxidase I (COI) (Folmer et al., 1994), 16Sar/16Sbr for 16S rRNA (Palumbi, 1996), and 18S1.2f/18S9R for 18S rRNA (Giribet et al., 1996). Procedures for Polymerase Chain Reaction (PCR), purification and sequencing are as detailed in Zhou et al. (2019). The COI sequences were aligned with the MUSCLE algorithm (Edgar, 2004), and 16S and 18S with MAFFT 7 (Kato and Standley, 2013) independently. Pairwise K2P distances based on COI sequences were calculated using MEGA7 (Kumar et al., 2016). The ambiguously aligned regions in each rRNA gene alignment were removed using the online server version of Gblocks under a relaxed condition (Castresana, 2002). SequenceMatrix 1.8 (Vaidya et al., 2011) was used to make a concatenated alignment of the three loci.

Phylogenetic reconstruction of alvinellids was performed on four datasets (each individual gene and their concatenated alignment) using both Bayesian Inference (BI) and Maximum Likelihood (ML) analyses. The substitution models for each of the data partitions were estimated by jModelTest 2.1.10 (Darriba et al., 2012) based on the BIC criteria before phylogenetic analyses, and TIM2 + I + G was selected for COI, TIM2 + G for 16S and TIM2ef + I + G for 18S. As TIM2 was not supported in MrBayes, GTR was used instead in both BI and ML analyses.

TABLE 1 | Sample and sequence information for taxa used in this study.

Species	Origin	Sample ID	COI	16S	18S	References
<i>Alvinella caudata</i>	East Pacific Rise	A1092	JX423737	JX423669	JX423641	Stiller et al., 2013
<i>Alvinella pompejana</i>	East Pacific Rise	A9429	AY645983	MT166794	MT166855	Stiller et al., 2020
<i>Alvinella cf. caudata</i>	Gulf of Southern California	–	KY581532	–	–	Goffredi et al., 2017
<i>Paralvinella grasslei</i>	East Pacific Rise, Guaymas Basin, Galapagos Spreading Center	A1093A	MT167009	MT166824	AY577886	Stiller et al., 2020
<i>Paralvinella palmiformis</i>	Gorda Ridge, Explorer Ridge, Juan de Fuca Ridge, Northeast Pacific	A1104	MT167010	MT166825	AF168747	Stiller et al., 2020
<i>Paralvinella sulfincola</i>	Gorda Ridge, Explorer Ridge, Juan de Fuca Ridge, Northeast Pacific	–	FJ976042	FJ976042	JN936461	Zhong et al., 2011
<i>Paralvinella hessleri</i>	Okinawa Trough, Mariana Trough, Northwest Pacific	–	MK192098	MK192098	–	Wang et al., 2019
<i>Paralvinella fijiensis</i>	North Fiji and Lau Back-Arc Basins, Southwest Pacific	ZMBN 106600	MG270110	MG253099	MG253145	Eilertsen et al., 2017
<i>Paralvinella pandorae pandorae</i>	Juan de Fuca Ridge, Northeast Pacific	A1105	DQ270466	MT166826	MT166884	Stiller et al., 2020
<i>Paralvinella</i> sp. ZMBN 106599	Lau Back-Arc Basin, Southwest Pacific	ZMBN 106599	MG270111	MG253100	MG253146	Eilertsen et al., 2017
<i>Paralvinella</i> sp. ZMBN 116035	Lau Back-Arc Basin, Southwest Pacific	ZMBN 116035	MG270112	MG253101	–	Eilertsen et al., 2017
<i>Paralvinella pandorae irlandei</i>	East Pacific Rise	–	–	–	AM159576	Pradillon et al., 2007
<i>Paralvinella mira</i>	Wocan, Carlsberg Ridge	RSIO38012	MW649793	MW653274	MW653276	This study
	Wocan, Carlsberg Ridge	RSIO38101	MW649801	MW653275	MW653277	This study
	Wocan, Carlsberg Ridge	RSIO38104	MW649794	–	–	This study
	Wocan, Carlsberg Ridge	RSIO38089	MW649795	–	–	This study
	Wocan, Carlsberg Ridge	RSIO38096	MW649796	–	–	This study
	Wocan, Carlsberg Ridge	RSIO38088	MW649797	–	–	This study
	Wocan, Carlsberg Ridge	RSIO38094	MW649798	–	–	This study
	Wocan, Carlsberg Ridge	RSIO38098	MW649799	–	–	This study
	Daxi, Carlsberg Ridge	RSIO38201	MW649800	–	–	This study
Outgroup						
<i>Amage auricula</i>		ZMBN 99281	–	MG253079	MG253131	Eilertsen et al., 2017
<i>Grubianella klugei</i>		ZMBN 95455	MG270108	–	MG253173	Eilertsen et al., 2017
<i>Amphisamytha marisindica</i>		RSIO3513	MN397204	MN397220	MN397231	Zhou et al., 2019
<i>Amphisamytha collaris</i>		RSIO3520	MN397209	MN397225	MN397233	Zhou et al., 2019
<i>Amphisamytha jacksoni</i>		SS15	JX423758	JX423675	JX423646	Stiller et al., 2013

BI analyses were carried out using MrBayes v3.2 (Ronquist et al., 2011). Four Metropolis-coupled Monte Carlo Markov chains were run for at least 2,000,000 generations until they converged with the Potential Scale Reduction Factor (PSRF) close to 1 (Ronquist et al., 2011). Trees were sampled at every 1000th generation. After discarding the first 25% initial genealogies, a majority-rule consensus tree was generated for each dataset with the remaining trees. ML analyses were carried out using IQ-TREE 1.6.10 (Trifinopoulos et al., 2016). For each dataset, three replicate runs were performed with the substitution models previously selected by jModelTest, and bootstrap support values determined by the ultrafast bootstrap algorithm for 100,000 replicates. GenBank accession numbers of the sequences used in molecular analyses are provided in **Table 1**.

RESULTS

Systematics

Order Terebellida

Family Alvinellidae Desbruyères and Laubier (1986).

Genus *Paralvinella* Desbruyères and Laubier (1982).

Paralvinella mira n. sp. (**Figures 3, 4**).

ZooBank registration number: urn:lsid:zoobank.org:act:D2A0F8FC-12B3-4157-A6E9-4ABD665D8333.

Diagnosis

First three chaetigers not fused; buccal apparatus with a pair of short, strong and acutely pointed tentacles, together with ungrouped slender oral tentacles; notopodia on chaetigers 5 to about 15 (except for chaetiger 7) bearing dorsal digitiform lobe; notochaetae consisting of one long and one short group of chaetae; uncini starting on chaetigers 15–20; Currently only known from northwest Indian Ocean vents.

Type Locality

Wocan hydrothermal vent field, Carlsberg Ridge, 60.53°E/6.36°N, depth 2920 m.

Type Materials

Holotype (RSIO38206), Wocan hydrothermal vent field (60.53°E/6.36°N, 2920 m deep), Carlsberg Ridge, *Jiaolong* Dive 129, R/V *Xiangyanghong* 9 cruise DY38-I, March 14, 2017; Paratypes (RSIO38107–38116, 38207, 38208), same for holotype; Paratype (RSIO38204), Wocan field (60.53°E/6.36°N, 2920 m deep), Carlsberg Ridge, *Jiaolong* Dive 125, R/V *Xiangyanghong* 9 cruise DY38-I, March 4, 2017; Paratypes (RSIO38087–38106), Wocan field (60.53°E/6.36°N, 2920 m deep), Carlsberg Ridge, *Jiaolong* Dive 131, R/V *Xiangyanghong* 9 cruise DY38-I, March 19, 2017; Paratypes (RSIO38200–38201), Daxi field (60.18°E/6.80°N, 3450 m deep), Carlsberg Ridge, *Jiaolong* Dive 128, R/V *Xiangyanghong* 9 cruise DY38-I, March 11, 2017. Holotype and all paratypes are deposited in the Repository of the Second Institute of Oceanography, MNR, China (RSIO).

Description

Body 9.2–20.2 mm in length (holotype 17.2 mm), 0.7–2.5 mm in width (holotype 2.0 mm), with 46–62 segments (holotype

60). Body slightly tapered posteriorly (**Figures 3A,B**). Newly collected specimens reddish, ethanol preserved specimens pale white (**Figures 3A,B**).

Prostomium with two well developed lateral lobes separated by a deep median incision and enclosing peristomium ventrally (**Figures 3C,D**). Buccal apparatus complex, bearing a pair of strong and short tapering tentacles; numerous slender grooved oral tentacles inserted on a buccal membrane between the paired strong tentacles; median oral tentacles longer than lateral ones (**Figures 3G,H**).

First two segment achaetous, fused, clearly discernible ventrally from the next three segments (chaetigers I, II, and III) (**Figure 3E**). Chaetigers I, II, and III not fused laterally and ventrally, clearly separated from each other (**Figure 3E**). Anterior chaetigers (first 14–19) with notopodia only.

Branchial region formed by four segments (segment II and chaetigers I, II, and III) (**Figure 3D**). Branchiae four pairs, in two groups, all similar, pinnate, inflated at base and gradually attenuated (**Figures 3A–E,I**). Branchial stem strong, tapering distally; secondary filaments numerous, slender, cylindrical, inserted in opposite rows along stem; distal part of stem devoid of gill filaments (**Figures 3B,I**). Chaetiger 4 with a median dorsal expansion protruding forward and separating the posterior pair of branchiae (**Figures 3C,D,F**).

Notopodia (except for chaetiger 7), short and cylindrical. First three pairs elevated dorsally, arranged in laterodorsal row, lateral to outermost branchiae (**Figures 3C–E**); the following notopodia stronger and located more laterally, bearing dorsal digitiform lobe on chaetigers 5 to about 15 (except for chaetiger 7) with the maximum size on chaetiger 8 (**Figures 3A,C–E,J; Figures 4A,B**). Chaetiger 7 strongly modified, with only a pair of small notopodial expansion bearing 4–6 strong acicular hooks directed posteriorly (**Figure 3J**). Notochaetae consisting of one long and one short group, both capillary (**Figures 4A–C**); notochaetae hirsute at distal 1/2 part (**Figures 4D–F**).

Uncinigerous neuropodial tori present on chaetigers from chaetiger 15–20 to the end of body. Uncini numerous, arranged in single rows, with two major teeth in single row above row, seldom with a small tooth duplicated laterally (**Figures 4G,H**). Pygidium blunt, smooth, without appendages (**Figure 4I**).

Tubes whitish, membranous, and covered with mineral granules (**Figure 2**).

Distribution

Abundantly found at Wocan hydrothermal vent field on the Carlsberg Ridge, and associated with the “scaly foot” *C. squamiferum* and *Alviniconcha* snails at Wocan. Only two specimens were found while washing chimney fragments collected from Daxi.

Etymology

“Mira” (Latin), wonderful, surprising, named for its unexpected presence at Wocan field in high abundance.

Remarks

The assignment of *P. mira* n. sp. in *Paralvinella* is supported by its morphological concordance with the diagnosis of the subgenus

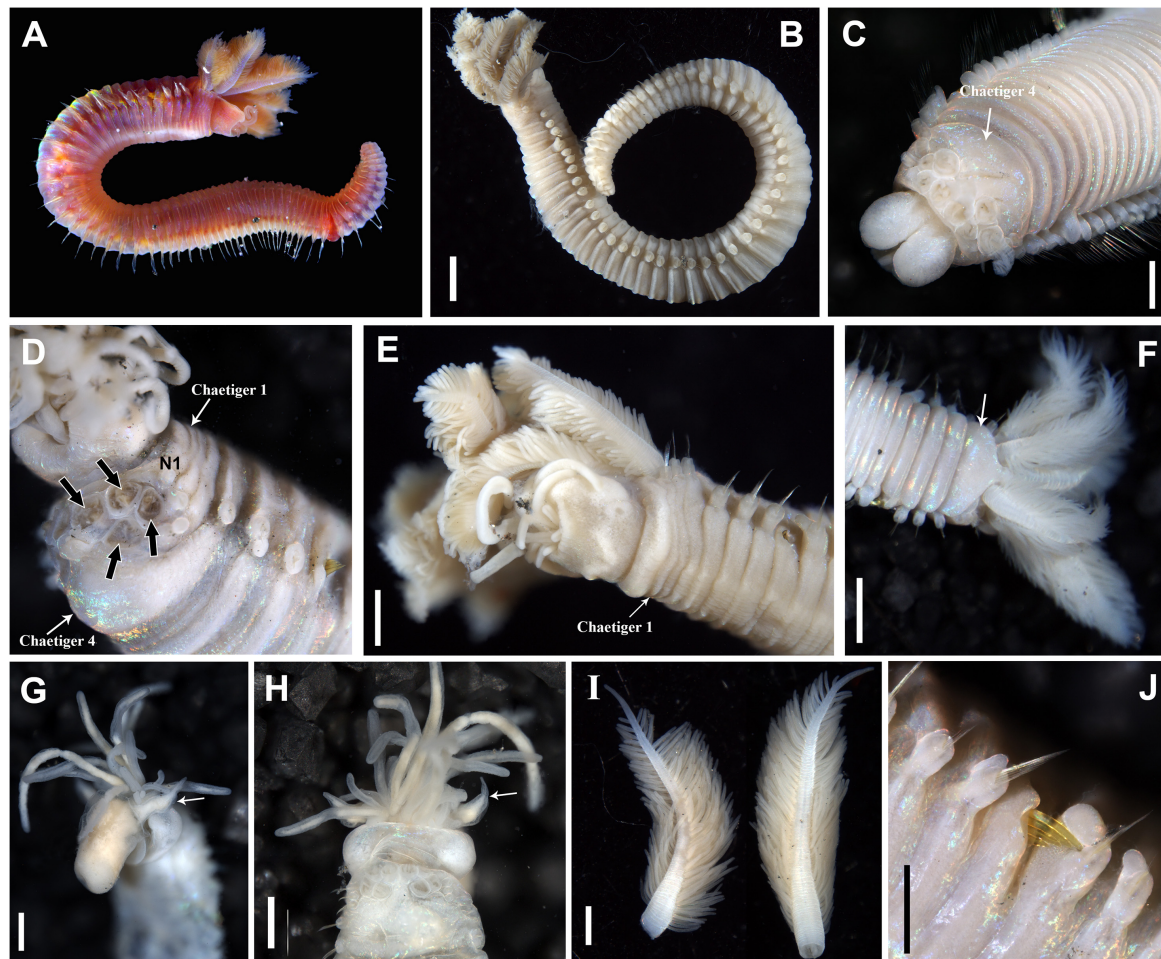


FIGURE 3 | *Paralvinella mira* n. sp. (A) Paratype (RSIO38207) before fixation, lateral view; (B) Holotype (RSIO38206), lateral view; (C) Paratype (RSIO38087), anterior part, dorsal view, with branchiae removed; (D) Paratype (38204), anterior part, dorsal lateral view, showing arrangement of branchiae (black arrows bordered by white) in relation to the first several segments, N1, notopodium on chaetiger 1; (E) Holotype (RSIO38206), anterior part, ventral lateral view; (F) Paratype (RSIO38087), anterior part, dorsal view; (G) Paratype (RSIO38106), buccal apparatus everted, showing the short, strong and pointed tentacle (white arrow), anterior view; (H) Paratype (RSIO38106), buccal apparatus everted, showing the short, strong and pointed tentacle (white arrow), dorsal view; (I) Branchiae with distal parts devoid of filaments; (J) Notopodia on chaetigers 5–9, showing modified notopodia on chaetiger 7. Scale bar: (B,D,F), 1 mm; (C,E,G–J), 0.5 mm.

Miralvinella: (1) complex buccal apparatus with paired large tentacles in males and numerous grooved oral tentacles inserted on the buccal membrane; (2) four pairs of pinnate branchiae with cylindrical filaments located on opposite areas along the stem; (3) notopodia on some anterior chaetigers (except for chaetiger 7) bearing digitiform notopodial lobes; (4) uncini starting on segments well after chaetiger 7 (Desbruyères and Laubier, 1993; Jollivet and Hourdez, 2020).

Three species have been placed in *Miralvinella*, *Paralvinella* (*Miralvinella*) *dela* Detinova (1988), *Paralvinella* (*Miralvinella*) *bactericola* Desbruyères and Laubier and *Paralvinella* (*Miralvinella*) *hessleri* Desbruyères and Laubier (1989), with *P. hessleri* being most similar to *P. mira* n. sp. according to the morphology of the branchiae and buccal apparatus. However, the new species can be distinguished from these three *Miralvinella* species in that its first three chaetigers are not fused, which can be easily examined from lateral and ventral view under a

stereomicroscope. The new species is further different from *P. hessleri* in locating oral tentacles directly on the buccal membrane instead of paired quadrilobed upper lips in the latter (Desbruyères and Laubier, 1989), and from *P. bactericola* and *P. dela* in the position of the first uncigerous neuropodial tori (chaetiger 16 vs. 32) (Desbruyères and Laubier, 1991; Detinova, 1988).

Molecular Analyses

Paralvinella mira forms a distinct lineage based either on pairwise COI distance or phylogenetic inference using the four sequence datasets (Supplementary Table 1, Figure 5, and Supplementary Figures 1–3). The new species showed lowest genetic distance with *Paralvinella* sp. ZMBN (sensu Eilertsen et al., 2017) from southwest Pacific (pairwise COI K2P distance 12.3%), falling within the range of pairwise divergence between other alvinellid

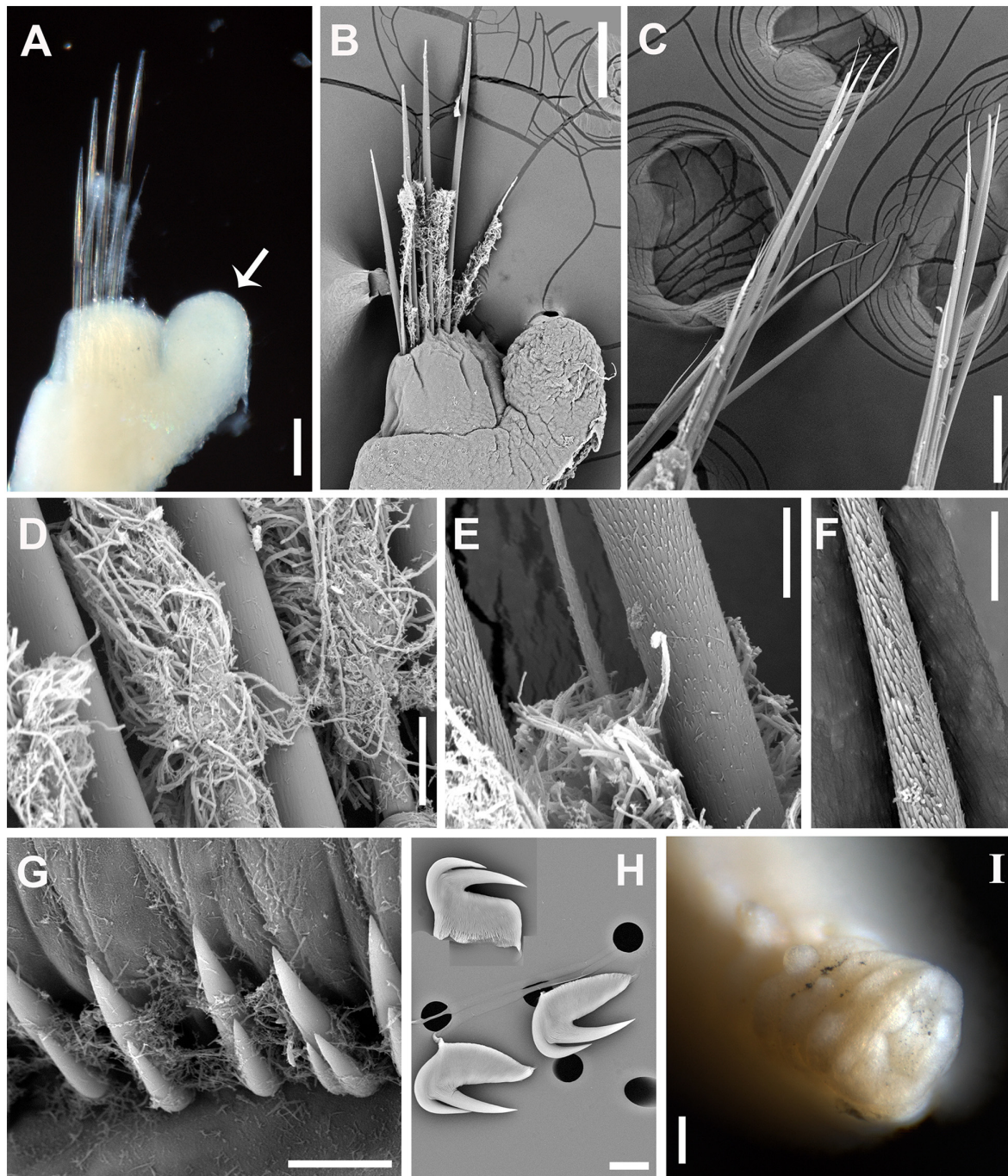
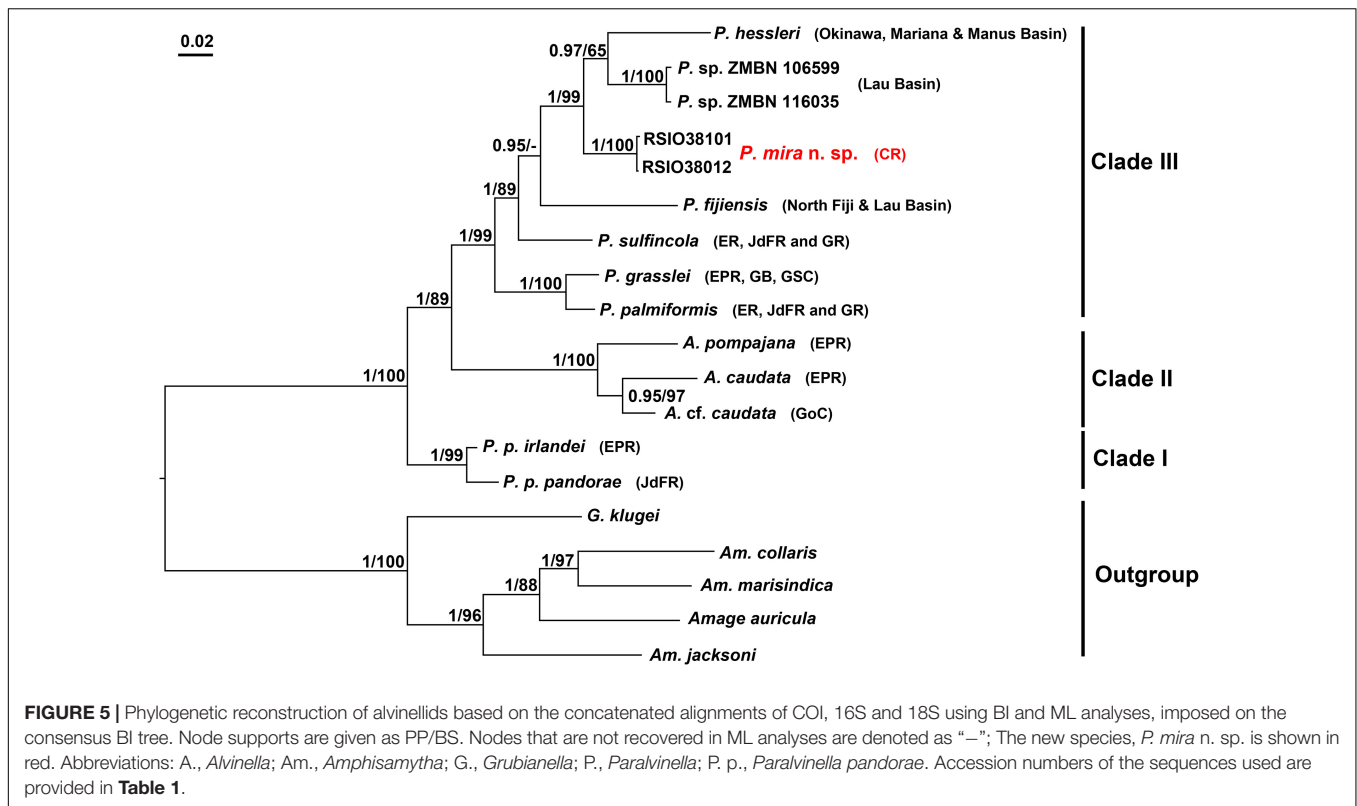


FIGURE 4 | *Paralvinella mira* n. sp. (A) Notopodia on segment 9, white arrow indicating the digitiform notopodial lobe, anterior view; (B) SEM. Notopodia on segment 9, anterior view; (C) SEM. Notochaetae on segments chaetigers 35–37; (D) SEM. Basal part of notochaetae; (E) SEM. Middle part of notochaetae; (F) SEM. Distal part of notochaetae; (G) SEM. Uncingerous torus; (H) SEM. Three uncini in details; (I) Pygidium. Scale bar: (A–C,I), 100 μ m; (D–H), 10 μ m.

species (range 6.2–26.6%) but much higher than the intra-specific values (\sim 0.2%, **Supplementary Table 1**). No genetic divergence was found between the Daxi (RSIO38201) and the Wocan individuals (range 0–0.6%).

Based on concatenated alignments of the three genes, both BI and ML analyses reconstruct trees with topology similar to

that of a previous study (**Figure 5**; Stiller et al., 2020). The Alvinellidae forms a monophyletic group with high support (Bayesian posterior probabilities, PP/ML bootstrap value, BP: 1/100), with *P. pandorae* species complex (clade I, PP/BP: 1/98) being sister to a larger clade comprising a monophyletic *Alvinella* clade (clade II, PP/BP: 1/100) and its sister clade of the remaining



Paralvinella species (clade III, PP/BP: 1/99). *P. grasslei* and *P. palmiformis* form a well-supported subclade within clade III (PP/BP: 1/100) (**Figure 5**). Each gene tree reveals topology similar to the above-mentioned pattern, but with lower supports (**Figure 5** and **Supplementary Figures 1–3**).

The Indian Ocean species, *P. mira* falls into clade III with strong support (PP/BP: 1/98) and grouped with the West Pacific species (*P. hessleri* from northwest Pacific and *Paralvinella* sp. ZMBN from southwest Pacific vents), resulting in an Indian/West Pacific subclade (**Figure 5**). The clustering of the Indian and West Pacific species is recovered in 16S and 18S gene trees with lower supports, and the topology within clade III is poorly resolved in the COI gene tree (**Figure 5** and **Supplementary Figures 1–3**).

DISCUSSION

In the present study, we described a new species of Alvinellidae from northern Indian Ocean hydrothermal vent field and confirmed its placement in the genus *Paralvinella* using both morphological and genetic evidences. The concatenated phylogeny revealed a branch pattern of three clades (clades I, II, and III in **Figure 5**) similar to other gene trees, but with higher supports. This three-clades pattern is also largely the same with that recovered in Stiller et al. (2020) except for the positions of *P. sulfincola* and *P. fijiensis* in relation to other species in clade III. The subdivision of *Paralvinella* into three subgenera was proposed by Desbruyères and Laubier (1993) based on traits of branchiae filaments, buccal apparatus, and distributions of the

notopodial lobes and the uncinigerous tori (Jollivet and Hourdez, 2020). The subgenus *Nautalvinella* matches well with Clade I and was referred to *Nautalvinella* Desbruyères and Laubier (1993) (Stiller et al., 2020), but *Paralvinella* (*Nautalvinella*) *unidentata* is not clustered with this clade in an ultrametric phylogenomic tree recently reconstructed by Jollivet and Hourdez (2020). Similarly, monophyletic cluster of the four *Paralvinella* (*Paralvinella*) species (as revealed in Stiller et al., 2020 and Jollivet and Hourdez, 2020) in clade III is likely to be unstable with the addition of the Indian and West Pacific species in the present study. It is currently not possible to determine if the Indian/West Pacific subclade (formed by *P. hessleri*, *Paralvinella* sp. ZMBN and *P. mira*) corresponds to the subgenus *Miralvinella* due to the lack of morphological data from *Paralvinella* sp. ZMBN, on one hand, and DNA data from *P. bactericola* and *P. dela*, on the other hand. Thus, a wider sampling effort on either taxa or DNA markers is needed to validate the delineation of these species at subgenus level.

The Indian Ocean alvinellids appear to be genetically closer to the West Pacific rather than to the East Pacific counterparts based on either genetic distance calculation or phylogeny inference. Genetic affiliations between Indian and West Pacific counterparts have been shown in a variety of taxa for the vent fauna, such as *Bathymodiolus* mussels (Breusing et al., 2015), *Alviniconcha* snails (Johnson et al., 2015), *Amphisamytha* (Zhou et al., 2019), *Archinome jasoni* (Borda et al., 2013), resulting in a hypothesis of historical connection between the two regions (Watanabe and Beedessee, 2015). By contrast, two other Wocan polychaetes, *Amphisamytha wocanensis* (Ampharetidae)

and *Hesiohyra heteropoda* (Hesionidae), temporally exhibit closer genetic relationships with their East Pacific congeners (Zhou et al., 2019; Wang et al., 2020). Although the phylogenetic inference may be modified with the addition of either more DNA markers or more sampling taxa in future, the current results indicate invasion of *Paralvinella* into northern Indian Ocean from the West Pacific. According to the current phylogeny, the emergence of the West Pacific alvinellid lineages appears to be more recently than their East Pacific relatives, and the latter also exhibit highest phylogenetic diversity (Jollivet and Hourdez, 2020; Stiller et al., 2020). This pattern is closer to the scenario proposed by Bachraty et al. (2009), in which EPR played a central role in the dissemination of vent fauna, although Moalic et al. (2012) tended to put the West Pacific in the central position connecting the other vent fauna provinces. In addition, due to the lack of information on the alvinellid worms collected at the Solitaire vent field on the CIR, we still do not know whether the colonization of the Indian ridge by the Western Pacific alvinellids occurred once or via two independent events.

Whatever the route taken by the ancestors of *P. mira* to invade the Indian Ocean, this invasion event has undoubtedly changed our view of vent polychaete biogeography in the Indian Ocean. The discovery of *P. mira* adds to the unique polychaete diversity at northern Indian Ocean hydrothermal vents. Together with the observation of alvinellid worms at the Solitaire vent field, this worm family appears to be absent from all well-characterized hydrothermal vents south of Solitaire, including Edmond, Kairei, Tiancheng, and Longqi (Watanabe and Beedsee, 2015; Copley et al., 2016; Zhou et al., 2018; Gerdes et al., 2019). Notably, distinct dominant polychaete assemblages are recovered at vents across the Indian Ocean Ridges: dorvillids/ampharetids/hesionids at Longqi (on the SWIR, Zhang et al., 2017; Zhou et al., 2018; Wang et al., 2020), amphinomids at Kairei (on the CIR, Watanabe and Beedsee, 2015), and alvinellids/hesionids at Wocan (on the CR, Wang et al., 2020; this study). These differences together with the observed variations of faunal composition on crustaceans and mollusks (the other two dominant taxa in deep-sea hydrothermal vents), result in a high faunal dissimilarity between the SWIR and CIR vent communities and indicate two potential sub-bioregions (Zhou et al., 2018; Sun et al., 2020). As one of the three dominant taxa, the specific polychaete assemblage at the Wocan field reinforces such dissimilarities between CR and CIR/SWIR vent communities and strengthens the point of view that the northern Indian hydrothermal vents may hold a unique biodiversity. This provides new insights toward biogeographic subdivision in the Indian Ocean.

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DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article.

AUTHOR CONTRIBUTIONS

YZ and CW designed the project. YZ collected and preserved the samples. YH and YZ performed the morphological examination and molecular analyses. All authors drafted the manuscript and contributed to the final version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2021.669918/full#supplementary-material>

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The handling editor declared a past co-authorship with several of the authors DZ, CW, and YZ.

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