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A New *Branchipolynoe* (Aphroditiformia: Polynoidae) Scale Worm from the Onnuri Deep-sea Hydrothermal Vent Field, Northern Central Indian Ridge

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Deep-sea hydrothermal vents are dynamic environments with exotic fauna, including bathymodiolin mussels and scale worm annelids that are often in close association. In this study, we found a new species of *Branchipolynoe* (Aphroditiformia: Polynoidae) living in the recently discovered mussel *Gigantidas vrijenhoeki* in deep-sea hydrothermal vents and methane seeps at 2,014–2,023 m depth. Based on the morphology and full mitochondrial genome sequences of specimens of *Branchipolynoe* from the Onnuri vent field (OVF) on the northern Central Indian Ridge, we describe them as a new species: *Branchipolynoe onnuriensis* sp. nov. This species resembles *B. longqiensis* and *B. tjiasmantoi*, but can be distinguished from these species by the shape of the notopodial acicular lobe and the tips of the subacicular neurochaetae. This identity is well-supported by genetic distance and phylogenetic analyses based on the mitochondrial *c* oxidase subunit I (*COI*) gene, with the new species being closest to the Western Pacific species *B. tjiasmantoi*. Phylogenetic analyses support close relationships between the Indian Ocean and Western Pacific hydrothermal polychaetes. Our data provide a foundation for exploring the evolutionary relationship between scale worms and bathymodiolin mussels.

Key words: Chemosynthetic environment, Full mitochondrial genome, Hydrothermal vent, Mitochondrial cytochrome *c* oxidase subunit I (*COI*), Polychaeta, Taxonomy.

BACKGROUND

Hydrothermal vents were first discovered on a sea ridge crest off the Galapagos Islands in 1977 (Lonsdale 1977). Many vents continue to be discovered along global mid-ocean ridge systems, back-arc diffusion centers, and off-axis submarine volcanoes (Beedessee et al. 2013). Deep-sea hydrothermal vents are dynamic environments with steep nutrient gradients and physicochemical conditions driven by volcanic and tectonic activities (Ryu et al. 2020). Investigations of the diversity and distribution of vent communities are critical due to their unique nature (Wu et al. 2019). Vents are commonly associated with dense communities and high biomass of organisms, and are patchily distributed on the deep-sea bottom (Van Dover 1990; Rogers et al. 2012). These communities contribute significantly to the production of chemosynthetic biomass and

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demonstrate the remarkable adaptability of life to the extreme conditions of hydrothermal ecosystems (Van Dover et al. 2001), as the organisms in these habitats are maintained by chemically synthesized energy sources, such as hydrogen sulfide and methane released from hydrothermal mineral deposits (Dubilier et al. 2008).

Since the discovery of a hydrothermal vent community at the Kairei vent field near the Rodriguez Triple Junction in the Indian Ocean in 2000 (Hashimoto et al. 2001), five hydrothermal vent ecosystems have been found along the northern Central India Ridge (CIR) and Southwest Indian Ridge (SWIR), including the Dodo, Edmond, Longqi, Solitaire, and Onnuri vent fields (Copley et al. 2016; Jang et al. 2020; Nakamura et al. 2012). As a consequence, the biogeographical connectivity of Indian Ocean vent fauna has become a focus of research (Beedessee et al. 2013). Indian Ocean mid-ocean ridges have been suggested to function as biogeographical pathways linking Western Pacific and Atlantic Ridge vent fauna (German et al. 1998). Thus, the evolutionary affinity of Western Pacific and Indian Ocean vent invertebrates has been proposed to exhibit an asymmetric assembly pattern , with a positive bias in the Western Pacific (Van Dover et al. 2001).

Polychaetes of the suborder Aphroditiformia (Annelida) are commonly referred to as scale worms due to their dorsal scales (elytra) (Rouse and Fauchald 1997). Scale worms are found throughout the tropics, polar regions, intertidal zones, and deep seas (Pettibone 1986; Wiklund et al. 2005; Glasby and Hutchings 2010; Norlinder et al. 2012; Salazar-Silva 2020). Those in the genus *Branchipolynoe* Pettibone, 1984 live within the mantle cavities of bathymodiolin mussels inhabiting hydrothermal vents and methane seeps (Desbruyères et al. 2006). Notably, they have well-developed arborescent branchiae that are larger than those of other polynoids (Hourdez and Jouin-Toulmond 1998). Unlike typical scale worms, which have large scales completely covering the dorsum, species of *Branchipolynoe* have small scales, leaving most of the dorsum uncovered (Lindgren et al. 2019), which is characteristic of symbiotic species of the polynoids (Martín and Britayev 1998 2018). In the Indian Ocean, species of *Branchipolynoe* have been reported from SWIR deep-sea hydrothermal vents (Zhou et al. 2017).

Species of *Branchipolynoe* have been described as symbionts of host mussels, with recent studies suggesting they may be parasitic (Bebianno et al. 2018). For example, *Branchipolynoe seepensis* may cause gill filament displacement and minor gill tissue damage in its host mussels (Ward et al. 2004). These scale worms eat particulate organic matter filtered by the mussels, and accidentally consume mussel tissues during the feeding process, thus being considered kleptoparasites rather than true parasites or commensals (Britayev et al. 2007). The most recent common ancestor of eastern Pacific species of *Branchipolynoe* may be a methane seep inhabiting species that later migrated to hydrothermal vents in the western Pacific and Indian Oceans (Lindgren et al. 2019).

In this study, we examined numerous specimens of *Branchipolynoe* collected during a survey of the hydrothermal vents of the Onnuri vent field (OVF) in 2019. Based on analyses of both morphological traits and the full mitochondrial genome, we describe these specimens as a new species and assess the phylogenetic associations of this species within *Branchipolynoe* based on the *c* oxidase subunit I (*COI*) gene.

MATERIALS AND METHODS

Specimen collection and preservation

Specimens of *Gigantidas vrijenhoeki* Jang et al. 2020 containing *Branchipolynoe* were collected from OVF deep-sea hydrothermal vents on the northern CIR (Fig. S1). The OVF is located along the CIR at 11°24.880'S, 66°25.420'E. All specimens were obtained at 2,014 to 2,023 m depth using a video-guided hydraulic grab (television grab) during a Korea Institute of Ocean Science and Technology research cruise in 2019, preserved onboard in 95% (v/v) ethanol solution in a freezer (-20°C) and then transported to a laboratory. The type specimens were deposited in the Library of Marine Samples of the Korea Ocean Science & Technology (KIOST).

Morphological examination

We used a Leica DMC 4500 camera mounted on a Leica M205C stereomicroscope for micrography, and the Helicon Focus v6 software (Helicon Ltd., Kharkiv, Ukraine) to incorporate images into stacks. For scanning electron microscope (SEM) observations, several parapodia were dissected, rinsed with absolute ethanol, dehydrated, coated with gold, inspected, and photographed using a Hitachi S-4300 SEM.

All known species of *Branchipolynoe* were tabulated to allow for comparison of key morphological characteristics, including the elytra, filaments, branchiae, dorsal cirri, notochaetae, and neurochaetae.

DNA extraction, amplification, and sequencing

The mitochondrial *COI* (~700 bp) was amplified via polymerase chain reaction (PCR) using the primers polyLCO and polyHCO (Carr et al. 2011)

with the D'Neasy Blood and Tissue Kit (Qiagen, Hilden, Germany) (Table S1). PCR amplification was performed in 20 μL reaction volumes containing 10 μL 2× TOPsimpe DyeMIX-Tenuto (Enzynomics, Korea), 1 μL template DNA (10 pmol/μL), 0.5 μL each primer (20 pmol/μL), and 8 μL distilled water (dH_2O) under the following conditions: 1 cycle of 95°C (2 min), followed by 35 cycles of 95°C (30 s), 60°C (1 min), and 72°C (1 min) and a final extension at 72°C (5 min). The PCR products were confirmed through 1% agarose gel electrophoresis in 1× TAE buffer.

Genome sequencing and trimming

Two libraries (insert size, 550 bp) were constructed using the TruSeq DNA Nano 550 bp kit. The libraries were sequenced using the Illumina Novaseq 6000 platform. Low-quality reads (less than Q20) were trimmed using Trim Galore (ver. 0.6.6), discarding reads shorter than 120 bp and reads with unknown nucleotides ("N"). We obtained a total of 131,865,089 reads (Choi et al. 2022).

Mitochondrial genome assembly and annotation

After the filtering process, *de novo* assembly was performed using MITOZ (Meng et al. 2019) and SPAdes (ver. 3.14.0) software (Bankevich et al. 2012). Putative mitochondrial contigs generated by both programs were identified and annotated on the MITOS web server (Bernt et al. 2013). The circular mitogenome was visualized using Circos (ver. 0.69-8) (Krzywinski et al. 2009).

Phylogenetic analyses

To reconstruct phylogenetic relationships, we used both *COI* and 13 protein coding genes (PCGs). For the *COI* dataset, we gathered sequences for 10 species of *Branchipolynoe* downloaded from the National Center for Biotechnology Information (NCBI) database and used *Branchinotogluma japonicus* as the outgroup (Table S2). Multiple sequence alignment of the coding genes was performed using MAFFT (ver. 7.475) with the default options. *COI* distance matrices were implemented in MEGA X software using the Kimura two-parameter model (Kumar et al. 2018) (Table 1). We used corrected Akaike information criterion (AICc) values to select the best model for phylogenetic tree reconstruction using IQ-TREE software (Kalyaanamoorthy et al. 2017). The combined General Time Reversible, fitness, and invariable sites (GTR+F+I) evolutionary model was the best fit for the sequences in the dataset.

For the dataset of 13 PCGs, we concatenated each gene into 12 mitochondrial genome sequences (11 from Polynoidae and one individual from Aphroditidae which was used as outgroup) (Table S5). Each sequence was aligned separately using MAFFT (ver. 7.475). The best-fit partitioning schemes and best evolutionary model for the 13 PCGs dataset were determined using the Partition Finder 2 program with the Bayesian information criterion (BIC). The GTR+I+G (G, rate of variation across sites) nucleotide substitution model was used for phylogenetic analysis.

A maximum likelihood (ML) phylogeny was reconstructed using the RAxML-NG tool (Kozlov et al. 2019). ML node support was determined from a majority-rule consensus tree constructed using 1,000 bootstrap replicates. Bayesian inference (BI) analysis was performed using MrBayes (ver. 3.2.7) (Ronquist and Huelsenbeck 2003). Markov chain Monte Carlo (MCMC) searches were performed twice for 10^6 generations with four chains, with sampling every 500

Table 1. Kimura two-parameter distance matrix of genus *Branchipolynoe* taxon *COI* sequences. (*Branchipolynoe seepensis*, *B. symmytilida*, *B. pettiboneae*, *B. longqiensis*, *B. eliseae*, *B. halliseyae*, *B. kajsae*, *B. meridae*, *B. tjiasmantoi*, *B. onnuriensis* sp. nov., and *Branchinotogluma japonicus*)

	B. seepensis	*B. symmytilida*	*B. pettiboneae*	*B. longqiensis*	*B. eliseae*	*B. halliseyae*	*B. kajsae*	*B. meridae*	*B. tjiasmantoi*	*B. onnuriensis* sp. nov.
Branchipolynoe seepensis										
B. symmytilida	0.184									
B. pettiboneae	0.156	0.194								
B. longqiensis	0.164	0.194	0.070							
B. eliseae	0.162	0.098	0.171	0.183						
B. halliseyae	0.068	0.178	0.158	0.168	0.175					
B. kajsae	0.063	0.179	0.166	0.179	0.179	0.057				
B. meridae	0.162	0.091	0.185	0.187	0.081	0.177	0.176			
B. tjiasmantoi	0.161	0.189	0.111	0.100	0.207	0.167	0.178	0.198		
B. onnuriensis sp. nov.	0.172	0.191	0.095	0.106	0.207	0.189	0.192	0.191	0.049	
Branchinotogluma japonicus	0.193	0.232	0.236	0.234	0.220	0.219	0.238	0.220	0.243	0.215

generations for each analysis. The phylogenetic tree was visualized using FigTree (ver. 1.4.4).

RESULTS

TAXONOMY

Family Polynoidae Kinberg, 1856
Subfamily Aphroditiformia Pettibone, 1984
Genus *Branchipolynoe* Pettibone, 1984

Branchipolynoe onnuriensis sp. nov.

(Figs. 1–4)

urn:lsid:zoobank.org:act:7E5DB4C2-75E2-4AD2-9BE7-A4860812BBC9

Material examined: Six specimens. Holotype (B_S_MA_0031740) and five paratypes (B_S_MS_00031741-5), collected from the OVF on the northern Central Indian Ridge (st. GTV1906 - 11°24.96'S, 66°25.397'E, 2064 m depth).

Etymology: Named in honor of the discoverer of the OVF.

Ecology: The new species is only known to occur in association with the hydrothermal vent mussel *Gigantidas vrijenhoeki* Jang et al. 2020. It lives inside the pallial cavity of the host (Fig. S1). The deep-sea OVF in the Indian Ocean is a hydrothermal system characterized by low-temperature diffuse emissions with high concentrations of dissolved methane (Jang et al. 2020).

Description: Body slightly tapered anteriorly and posteriorly, flattened ventrally and arched dorsally, with 21 segments, first segment achaetous (Fig. 1A, B). Ten pairs of elytrophores and elytra on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, and 19; elytra moderately large, smooth, oval without border papillae (Fig. 2C–F), covering the dorsum in the anterior and posterior regions, but leaving the mid-dorsum partially uncovered (Fig. 1A, B). Cirrophorous segments with short cylindrical cirrophores and short, smooth dorsal cirri with short slender tips, tapering gradually, exceeding the anterior and ventral cirri, not extending past the tips of neurochaetae (Fig. 1A).

Prostomium ellipsoidal, bilobed, with rounded anterior lobes. A pair of short conical palps and short conical median antennae between the two anterior lobes (Fig. 1C). Median antenna and palps smooth, tapering to slender tip; palps extending beyond prostomium. Prostomium lacking frontal peaks, eyes, and lateral antennae. First segment with two pairs of tentacular cirri, fused to the prostomium; tentacular cirri smooth, slightly slender, not exceeding prostomium length (Fig. 1C). Thick, muscular pharynx with five pairs of dorsal and ventral small, sac-like terminal papillae surrounding

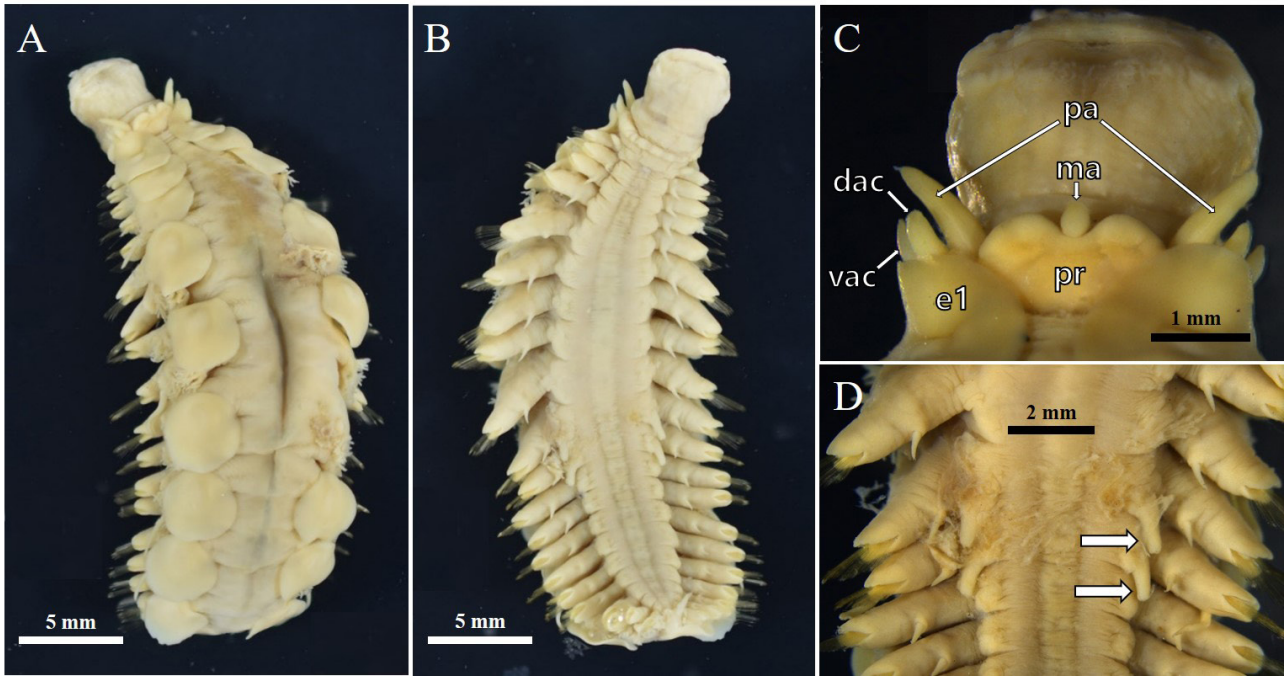

Fig. 1. *Branchipolynoe onnuriensis* sp. nov. holotype, female. (A) Dorsal view. (B) Ventral view. (C) Anterior region in dorsal view. (D) Mid-body in ventral view; arrows indicating the nephridial papillae. Pa: palps; ma: median antenna; pr: prostomim; e1: first elytron; dtc: dorsal tentacular cirrus; vtc: ventral tentacular cirrus.

the mouth (Fig. 2A).

Branchiae on segments 3–21, dense, arborescent, with short terminal filaments (Fig. 2B), not extending beyond the elytral border, gradually decreasing in size anteriorly and posteriorly, separated into two types emerging dorsally and ventrally, respectively. Dorsal tubercles non-discernible.

Parapodia subbiramous. Notopodia smaller than neuropodia, with few notochaetae projecting beyond notopodia (Fig. S2). Neuropodia large, rounded, enclosing numerous neurochaetae with rounded lobes. Notochaetae smooth; stouter and shorter than neurochaetae (Fig. 3A). Notochaetae few (up to 8 per parapodium), more numerous in middle and posterior than anterior segments, slightly tapering, with serrated distal parts, rounded unidentate tips and shafts with indistinctive serrations (Fig. 3B–D). Neurochaetae numerous, more abundant on middle than anterior and posterior segments, arranged as a lateral fan, tapering, with subdistal swelling and small spines along the edge, serrations starting at the midpoint of the expanded distal part on only one side and extending distally; supraacicular neurochaetae long, stout, with slender tips, bidentate, with hooked distal teeth, serrated distally and flattened on one side; subacicular neurochaetae similar to supraacicular but with shorter distal serrated

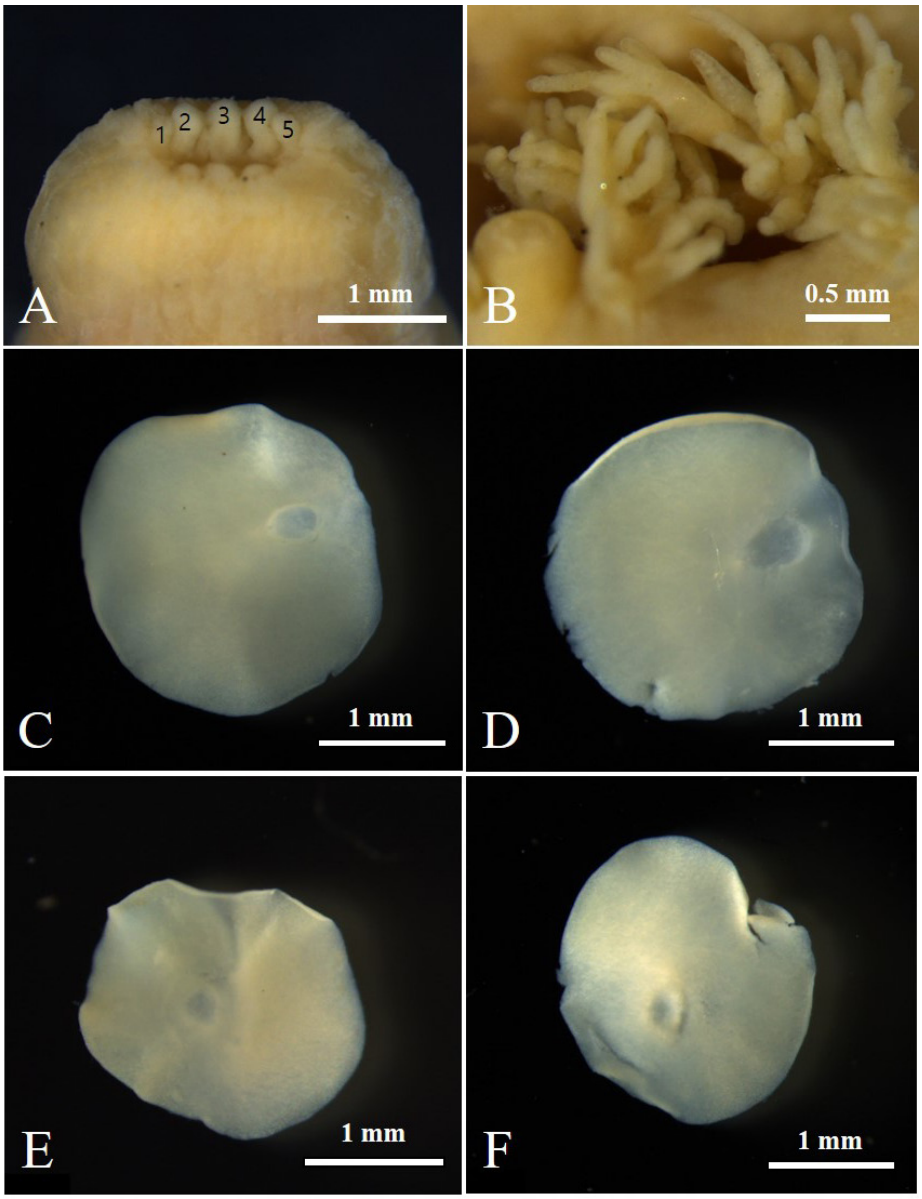

Fig. 2. *Branchipolynoe onnuriensis* sp. nov. paratype 5. (A) Frontal view of pharynx. (B) Branchia from segment 10. (C) Left 4th elytron from segment 7. (D) Left 6th elytron from segment 11. (E) Left 8th elytron from segment 15. (F) Left 9th elytron from segment 17.

parts (Fig. 4).

Ventral cirri smooth, small, lacking papillae, inserted in the middle of neuropodia; projecting anteriorly (Fig. 1D). Nephridial papillae ventral, on segments 11 and 12 in females, long, reaching the next segment, projecting posteriorly (Fig. 1D). Pygidium small, round with a pair of short, stout, tapered anal cirri, not fused (Fig. 1B).

Morphological variation: Holotype 28 mm long and 13 mm wide (including parapodia); paratypes 23–31 mm long and 8–14 mm wide (including parapodia). All specimens showing nephridial papillae on segments 11 and 12, suggesting all were females.

Remarks: Nine species of *Branchipolynoe* have been described (Pettibone 1984 1986; Miura and Hashimoto 1991; Zhou et al. 2017; Lindgren et al. 2019; Wu et al. 2019). The diagnostic characteristics of this genus were established based on *Branchipolynoe symmytilida* and amended based on *B. seepensis* to include the first position of branchiae, the presence of cephalic peaks, and the form of parapodia (Pettibone 1984 1986). Subsequently, *B. longqiensis* was described from the Indian Ocean and five additional species were described from the Pacific Ocean (Lindgren et al. 2019; Zhou et al. 2017) (Table S2). Members of this genus have 21 segments, 10 elytra partially covering the dorsal region and bilobed prostomium (except *B. kajsae*) lacking cephalic peaks (except *B. symmytilida*).

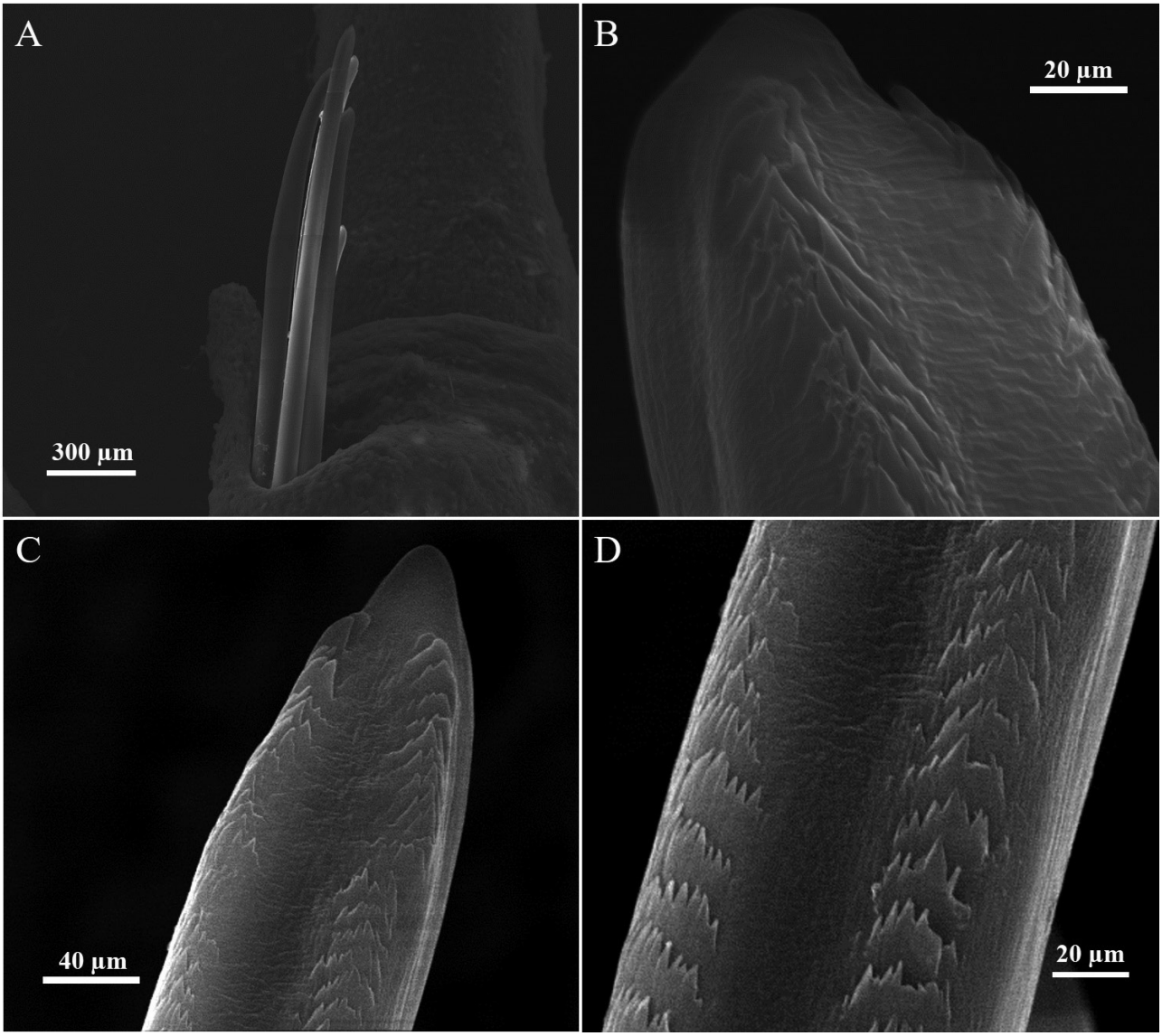

Fig. 3. *Branchipolynoe onnuriensis* sp. nov. paratype 5, female, showing left notopodium on segment 4. (A) Detail of notochaetae tip. (B) Detail of distal part of notochaetae. (C) Detail of notochaetae tip. (D) Detail of serration in distal part of notochaetae.

Branchipolynoe onnuriensis sp. nov. most closely resembles *B. longqiensis* and *B. tjiasmantoi* in having branchiae starting on the third segment and subbiramous parapodia, but differs in the two latter species have short, rounded notopodial acicular lobes, inconspicuous pharyngeal papillae, and different tip shapes of their sub-acicular neurochaetae (Table S3).

Phylogenetic analyses

The *COI* genetic distances between species of *Branchipolynoe* ranged from 0.049 to 0.207 (0.167 on average, Table 1). The closest species to *B. onnuriensis* sp. nov. was *B. tjiasmantoi* from the western Pacific, followed by *B. pettiboneae* and *B. longqiensis*, which were considered sister species due to their similar morphology (Lindgren et al. 2019), and then by *B. longqiensis* from the Indian Ocean (Table 1).

As the *COI* sequences obtained through PCR and genome assembly were identical, we used the latter dataset for reconstruction of the phylogeny tree. The ML tree and BI analyses inferred from *Branchipolynoe* mitochondrial *COI* sequences produced a single topology for each region (Fig. 5). The branch containing *B. onnuriensis* sp. nov. and *B. tjiasmantoi* had high support values (ML: 92%, BI: 1.0).

Phylogenetic relationships among Polynoidae were inferred using a concatenated 13-gene dataset, which produced similar topologies to ML and BI analyses (Fig. 6). Interestingly, the genus *Branchipolynoe* formed a clade with high support (ML: 100%, BI: 1.0) and the gene orders within this clade were identical, while the subfamily Lepidonotinae was not monophyletic.

General features of mitochondrial genomes

The complete mitochondrial genome of *B. onnuriensis* sp. nov. was 16,217 bp in length, comprising 15 protein-coding genes (PCGs) (Fig. 7), 7 NADH dehydrogenase subunits (nad1–6 and nad4L), 4

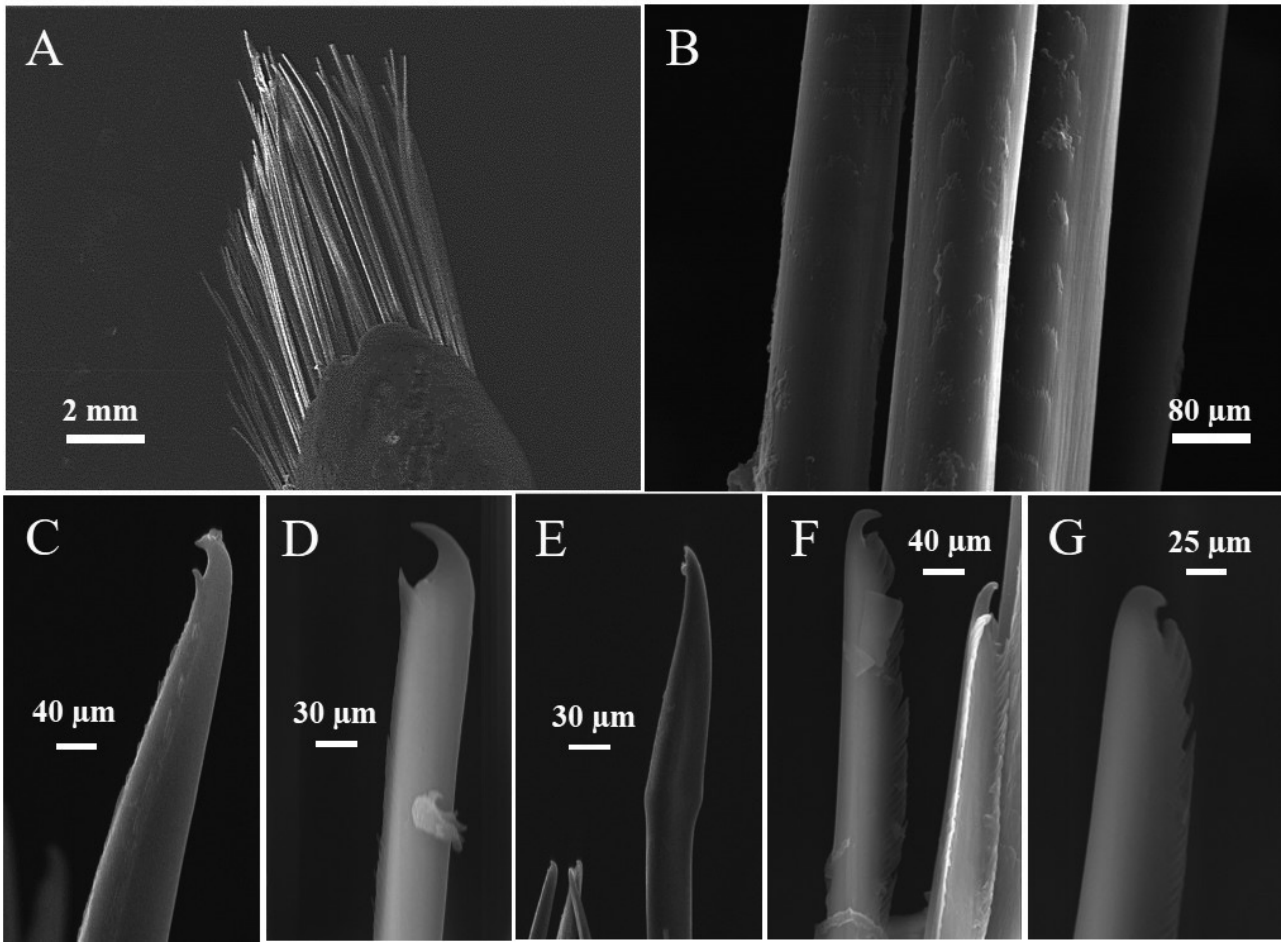

Fig. 4. *Branchipolynoe onnuriensis* sp. nov. paratype 5, female, showing left neuropodium on segment 6. (A) Neurochaetae. (B) Serration at distal part of supraaciular neurochaetae. (C–E) Detail of supraacicular neurochaeta tips. (F) Distal parts of two subacicular neurochaeta. (G) Detail of subacicular neurochaeta tip.

cytochrome oxidase subunits (cob and cox1–3), 2 ATP synthase subunits (atp6 and atp8), and 2 small and large ribosomal RNA genes (rns and rnl). We identified 22 transfer RNA genes (tRNAs) and an A+T-rich region. Among these genes, ND5 was the longest (1,525 bp) and atp8 was the shortest (160 bp). The tRNA length ranged from 64 (trnC) to 71 (trnQ), with an average length of 66.41 bp (Table 2).

The gene order was identical for all three species of *Branchipolynoe* investigated (Fig. 6). Within the subfamily Lepidonotinae, *Halosydna* sp., and *Lepidonotopodium* sp. had a different syntenic arrangement wherein ATP6, ND4L, ND5 and ND6 were translocated (Zhang et al. 2018).

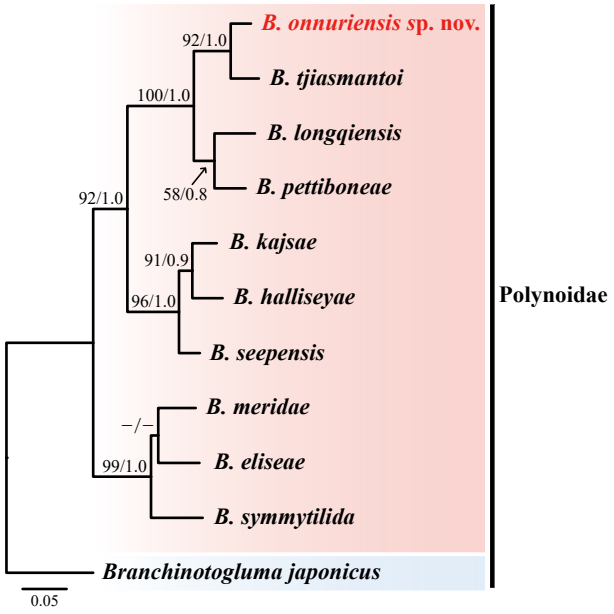

Fig. 5. Maximum likelihood (ML) tree inferred from mitochondrial cytochrome *c* oxidase I (*COI*) sequences of the species of *Branchipolynoe*. Numbers at nodes represent ML and Bayesian inference supports.

Base composition

To assess the mitochondrial genome, we calculated its nucleotide composition (A%, C%, G%, T%, A + T%, C + G%), AT skew, and GC skew. AT and GC skew were calculated as follows: AT skew = (A – T%) / (A% + T%) and GC skew = (G – C%) / (G% + C%). The overall nucleotide composition of the complete mitochondrial genome was 28.45% A, 24.44% C, 8.99% G, and 38.12% T. The proportion of AT content (66.57%) was ~1.99 times higher than that of GC content (33.43%) (Table S4). Most genes showed positive AT skew, except rns and rnl. All genes also showed negative GC skew, indicating that PCGs in *B. onnuriensis* sp. nov. contained a higher percentage of T and C than A and G, except rns and rnl.

DISCUSSION

At present, *Branchipolynoe* includes 10 species from hydrothermal vents and methane seeps worldwide, including five found in the eastern Pacific, two in the western Pacific, and two in the Indian Ocean (Lindgren

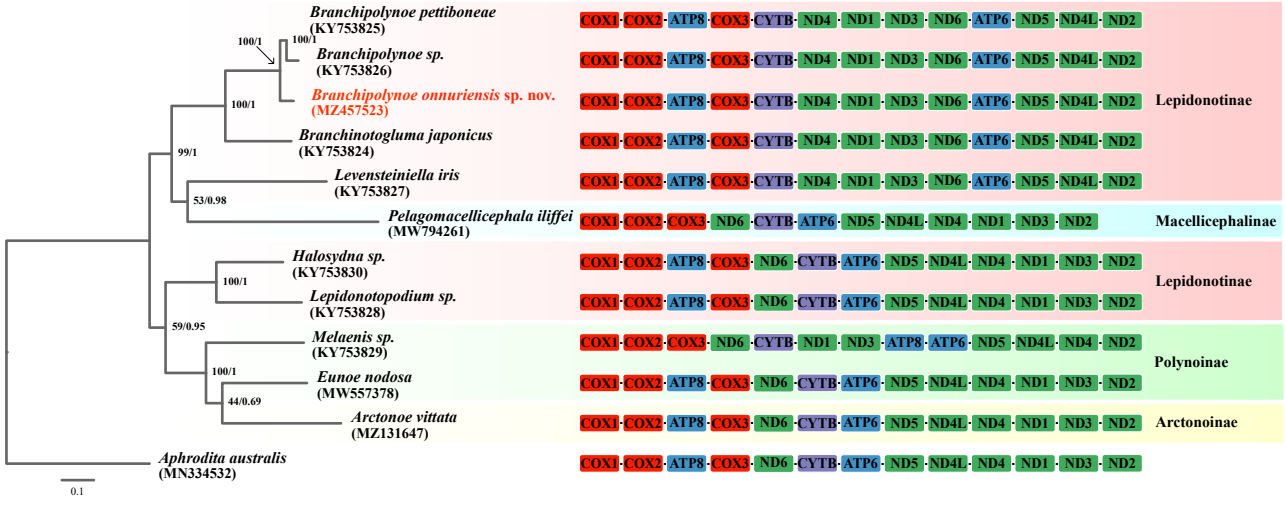

Fig. 6. Reconstruction of phylogenetic tree based on 13 protein coding genes using Maximum likelihood and Bayesian inference analysis. A total of 12 species from Phyllodocida was used (11 species from Polynoidae and one Aphroditidae). Numbers indicate Maximum likelihood bootstrap support and Bayesian posterior probability values. Mitochondrial gene arrangement of Phyllodocida superimposed on the phylogenetic tree. Whole mtDNA length and length of each coding gene were not measured in the result.

et al. 2019). *Branchipolynoe onnuriensis* sp. nov. is the second species of this genus found at Indian Ocean deep-sea hydrothermal vents. Morphologically, it resembles *B. longqiensis* from the Indian Ocean and *B. tjiasmantoi* from the western Pacific, and the latter species is phylogenetically closest. The most recent common ancestor of *Branchipolynoe* could have lived at methane seeps in the eastern Pacific, which share basic ecological conditions with western Pacific and Indian Ocean hydrothermal vents. This origin could facilitate the westward migration of *Branchipolynoe*. Migration patterns of *Branchipolynoe* to other regions in the Indian Ocean, as well as their evolutionary processes during adaptation to these harsh environments requires further investigation.

Branchipolynoe onnuriensis sp. nov. showed interspecific genetic distances sufficient to support its description as a new species. Animal species are commonly described without apparent morphological differences based on molecular data alone (Halt et al.

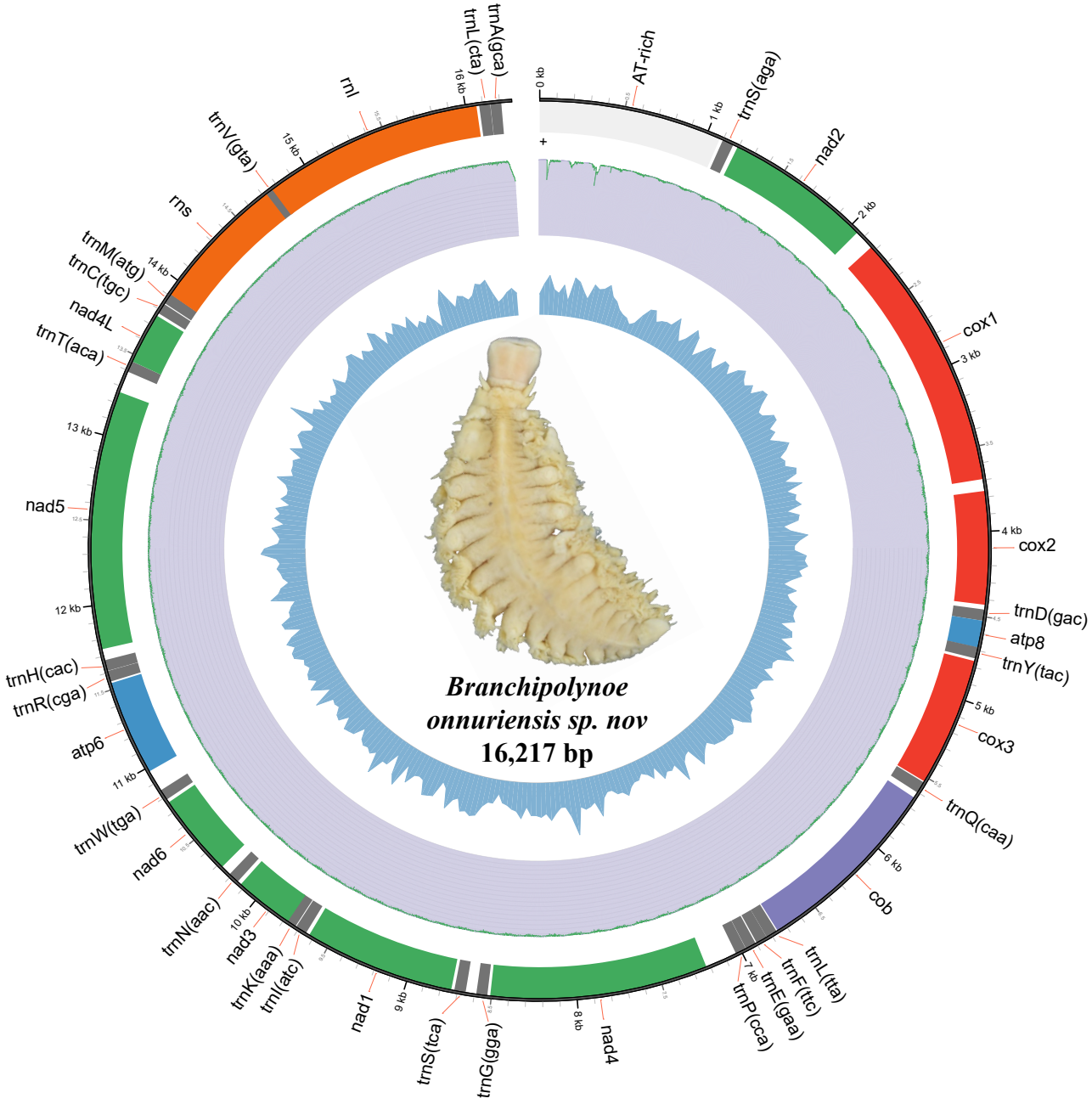

Fig. 7. Circular map of the complete mitochondrial genome of *Branchipolynoe onnuriensis* sp. nov. Outer to inner circles represent: (i) the positions of annotated genes, (ii) the sequencing depth and (iii) the GC content.

2009). Molecular tools appear sufficiently reliable to separate species of polychaetes, which may contribute to elucidation of their geographic distribution patterns (Nygren 2014). Polynoids are the most diverse and widely distributed polychaete group at hydrothermal vents and seeps, and are a good model for evaluating the biogeographic distributions of deep-sea fauna (Wu et al. 2019).

Species of *Branchipolynoe* live at either hydrothermal vents or in methane seeps, although *B. pettiboneae* occurs in both environments. Two undescribed species have been reported from hydrothermal fields on the CIR and SWIR (Copley et al. 2016). *Branchipolynoe* sp. "Dragon," a commensal scale worm found in bivalve mussels in the Longqi vent field on the SWIR, genetically resembles the other undescribed species (*Branchipolynoe* sp. "VG-2002") from the Kairei vent field on the CIR.

Minimum *COI* distances are not commonly accepted for classification of species, and each taxon appears to have a different minimum *COI* distance (Berriman et al. 2018). Therefore, a minimum interspecific distance greater than the maximum interspecies distance is often used to identify new species (Meier et al. 2008). Lindgren et al. (2019) found that the minimum *COI* distance between *Branchipolynoe* species was 3.7%, and most distances exceeded 5% (Lindgren et al. 2019). For our new species, the minimum genetic distance to another species was 0.049, representing a genetic difference of > 5% from the most closely

Table 2. Annotation of the *Branchipolynoe onnuriensis* sp. nov. mitochondrial genome

Gene	Strand	Position	Length (bp)	Initiation codon	Stop codon
trnS	+	1,099–1,167	69		
nad2	+	1,168–2,193	1026	ATG	TAA
cox1	+	2,171–3,712	1542	ATG	TAA
cox2	+	3,765–4,454	690	ATG	TAA
trnD	+	4,459–4,524	66		
atp8	+	4,525–4,680	156	ATG	TAA
trnY	+	4,682–4,748	67		
cox3	+	4,750–5,529	780	ATG	TAA
trnQ	+	5,534–5,603	70		
cob	+	5,627–6,763	1137	ATG	TAA
trnL	+	6,765–6,831	67		
trnF	+	6,832–6,898	67		
trnE	+	6,906–6,969	64		
trnP	+	6,971–7,034	64		
nad4	+	7,161–8,522	1362	ATG	TAA
trnG	+	8,525–8,589	65		
trnS	+	8,653–8,719	68		
nad1	+	8,720–9,652	67	ATG	TAG
trnI	+	9,651–9,718	933		
trnK	+	9,724–9,790	68		
nad3	+	9,792–10,145	67	ATG	TAA
trnN	+	10,150–10,213	354		
nad6	+	10,275–10,763	64	ATG	TAA
trnW	+	10,784–10,847	489		
atp6	+	10,848–11,549	64	ATG	TAG
trnR	+	11,548–11,611	702		
trnH	+	11,613–11,676	64		
nad5	+	11,677–13,374	64	ATG	TAA
trnT	+	13,395–13,459	1698		
nad4L	+	13,460–13,762	65	ATG	TAA
trnC	+	13,780–13,842	303		
trnM	+	13,849–13,912	63		
rns	+	13,911–14,728	64		
trnV	+	14,723–14,785	818		
rnl	+	14,757–16,120	63		
trnL	+	16,081–16,145	1364		
trnA	+	16,147–16,210	65		

related species, *B. tjiasmantoi*. Thus, the molecular data confirm the observed morphological differences and support the designation of a new species.

Branchipolynoe onnuriensis sp. nov. lives symbiotically with the recently discovered mussel *G. vrijenhoeki*. *Branchipolynoe* species are usually found in bivalve mussels, and are most often solitary (rarely, two are found within one mussel) (Plouviez et al. 2008). Thus, the lack of previous records of symbiotic polynoids in the OVF is may be due to the apparent rarity of *Bathymodiolus* mussels (McKiness et al. 2005). These symbiotic polynoids subsist on host chemical synthesis byproducts, and obtain protection from external risks from host shells (Company et al. 2007). Symbiont haplotypes and host species or depth ranges appear unrelated, as the populations showed no significant within-species genetic distances (Lindgren et al. 2019). Species of *Branchipolynoe* have evolved to coexist with a variety of hosts at different depths, and any mussel adapted to life around hydrothermal vents or methane seeps appears to be a suitable host.

In this investigation, only female individuals of *Branchipolynoe onnuriensis* sp. nov. were identified among the six specimens, based on the presence of nephridial papillae on segments 11 and 12. Some species (*e.g.*, *Branchipolynoe seepensis*) are sexually dimorphic in favor of larger females, with sex ratios between 1.4:1 and 2:1 (Van Dover et modified by our side 1999; Jollivet et modified by our side 2000). This result could be related to an interesting ecological or life cycle feature of the genus *Branchipolynoe*. As suggested previously, females may have reduced mobility (and thus always remain inside the host mussel), while males are more motile and can leave the host for reproductive purposes (Britaev et al. 2003). Britaev modified by our side (2003) investigated the correlation between *Branchipolynoe seepensis* and trauma in the *Bathmodiolus* mollusc host, and found no evidence to suggest that this polychaete consumed host tissue as food. *B. seepensis* could be considered parasitic rather than symbiotic with *Bathymodiolus* molluscs. The unique environment of deep-sea hydrothermal vents may lead to differences from general parasitic relationships observed in nature, and therefore additional research on the relationships between *Branchipolynoe* and their hosts is needed.

Among hydrothermal vent species, *B. symmytilida* lives with the mussel *B. thermophilus*, *B. pettiboneae* with *B. brevior*, *B. longqiensis* with *B. marisindicus* and *B. tjiasmantoi* with *B. brevior*. However, some species of this genus have recently been discovered in cold seeps, and their larvae may be capable of traveling long distances between hydrothermal vents or among vent systems, allowing for gene flow (Lindgren et al. 2019). Further studies are needed to determine whether species of *Branchipolynoe* have preferred host mussels, how they coexist, their evolutionary history, and the role they play in hydrothermal environments.

CONCLUSIONS

A new species of *Branchipolynoe* was described from the deep-sea hydrothermal OVF on the northern CIR. The identity of the new species was supported by genetic distance and phylogenetic analyses based on the *COI* gene, and the new species was most closely related to the western Pacific species *Branchipolynoe tjiasmantoi*. In addition, the full mitochondrial genome was assessed. Our data provide information about the evolutionary relationship between scale worms and bathymodiolin mussels.

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Authors’ contributions: SLK and OHY performed morphological description and molecular work. HC and SE performed the molecular analysis. All authors have read and approved the final manuscript.

Competing interests: All authors declare that they have no competing interests.

Availability of data and materials: The data presented in this study are available in the main text and associated supplementary materials. The complete mitochondrial sequence was submitted to GenBank with an accession number MZ457523.

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Supplementary materials

Fig. S1. Location of *Branchipolynoe onnuriensis* sp. nov. inside the mussel *Gigantidas vrijenhoeki.* (download)

Fig. S2. *Branchipolynoe onnuriensis* sp. nov. paratype 5, female. A, Left parapodium from segment 2, posterior view. B, Left parapodium from segment 3, posterior view. C, Left parapodium from segment 4, posterior view. D, Left parapodium from segment 5, posterior view. E, Left parapodium from segment 7, posterior view. F, Left parapodium from segment 8, posterior view. (download)

Table S1. Primer sets for the mitochondrial cytochrome *c* oxidase I (*COI*) genes used in this study. (download)

Table S2. Sampling information for species used for phylogenetic analysis in this study. (download)

Table S3. Main morphological characteristics of the ten-known species of *Branchipolynoe*. (download)

Table S4. Base composition of the mitochondrial genome of *Branchipolynoe onnuriensis* sp. nov. (download)

Table S5. Sampling information of species used for phylogenetic analysis in this study. (download)