European Journal of Taxonomy 864: 167–194
https://doi.org/10.5852/ejt.2023.864.2101

ISSN 2118-9773
www.europeanjournaloftaxonomy.eu
2023 · Zhang D. *et al.*

**Research article**

urn:lsid:zoobank.org:pub:326759FD-35B4-44C5-B3EF-9E89B6B91106

# *Ophryotrocha* (Dorvilleidae, Polychaeta, Annelida) from deep-sea hydrothermal vents, with the description of five new species

Dongsheng ZHANG[1,#], Yadong ZHOU[2,#], Nicole YEN[3], Avery S. HILEY[4] &
Greg W. ROUSE[5,*]

[1,2]Key Laboratory of Marine Ecosystem Dynamics, Second Institute of Oceanography, Ministry of Natural Resources, Hangzhou, 310012, China.
[3,4,5]Scripps Oceanography, University of California San Diego, La Jolla, CA 92093-0202, USA.

[*] Corresponding author: grouse@ucsd.edu
[1] Email: dszhang@sio.org.cn
[2] Email: yadong_zhou@sio.org.cn
[3] Email: nyen@ucsd.edu
[4] Email: ahiley@ucsd.edu
[#]These authors contributed equally to this work

[1]urn:lsid:zoobank.org:author:43C40412-F966-4F97-860F-0D27D3AA214C
[2]urn:lsid:zoobank.org:author:E0F2089D-29B9-48A6-9761-73AB8D09D2A8
[3]urn:lsid:zoobank.org:author:36958F99-FAE8-4FC8-A849-C011D0B4D26D
[4]urn:lsid:zoobank.org:author:B39BA63A-DA66-4512-88E9-4A564D1BEB80
[5]urn:lsid:zoobank.org:author:F4AAFAE4-85D9-44CA-8290-E0FC614E1983

**Abstract.** Dorvilleids belonging to *Ophryotrocha* Claparède & Mecznikow, 1869 are known from deep-sea hydrothermal vents in the Pacific, Atlantic, Indian and Southern Oceans. However, how they colonized and diversified in these ecosystems has not been assessed in detail. Here, a collection of Pacific hydrothermal vent *Ophryotrocha* was examined using morphology and DNA markers (COI, 16S and H3). Five new species were revealed, largely expanding the diversity of the group at this habitat type. They are *Ophryotrocha charlottae* sp. nov., *O. kailae* sp. nov., *O. marinae* sp. nov., *O. pruittae* sp. nov. from eastern Pacific, and *O. bohnorum* sp. nov. from the western Pacific. Phylogenetic analyses based on the concatenated alignments of all three genes suggest vent habitants have been colonized several times independently within *Ophryotrocha*. One clade of six vent species was recovered, indicative of diversification following a colonization of hydrothermal vents, likely in the eastern Pacific. An Indian Ocean species, *O. jiaolongi*, was nested inside this clade and was closely related to one of the new species from the Gulf of California, diverging from it by less than 4% on COI.

**Keywords.** Polychaete, deep sea, annelids, biogeography, chemosynthetic.

Zhang D., Zhou Y., Yen N., Hiley A.S. & Rouse G.W. 2023. *Ophryotrocha* (Dorvilleidae, Polychaeta, Annelida) from deep-sea hydrothermal vents, with the description of five new species. *European Journal of Taxonomy* 864: 167–194. https://doi.org/10.5852/ejt.2023.864.2101

## Introduction

*Ophryotrocha* Claparède & Mecznikow, 1869 is one of more than 30 currently accepted genera of Dorvilleidae Chamberlin, 1919 (Read & Fauchald 2022). With more than 75 accepted species described to date it comprises more than a third of the species diversity of dorvilleids. *Ophryotrocha* has a complicated systematic history, which has seen it moved in and out of Dorvilleidae (Orensanz 1990; Eibye-Jacobsen & Kristensen 1994) based on morphological characters and it is clearly a non-monophyletic assemblage (Ravara *et al.* 2021), but is now an accepted member of Dorvilleidae (Rouse *et al.* 2022).

Species of *Ophryotrocha* are distributed worldwide in diversified habitats from shallow water to deep-sea (Thornhill *et al.* 2009). While the best known *Ophryotrocha* are model organisms (Åkesson 1974; Premoli & Sella 1995), many species in this genus can reach high abundance and diversity in reducing environments, such as hydrothermal vents and cold seeps, as well as whale and wood fall ecosystems (Blake 1985; Desbruyères *et al.* 2006; Wiklund *et al.* 2009, 2012; Taboada *et al.* 2013). These opportunists have been suggested to feed mainly on filamentous *Beggiatoa*-like bacteria (Taboada *et al.* 2016). Pleijel & Eide (1996) used a dataset of morphological characters to assess cladistic relationships among a selection of species of *Ophryotrocha* for the first time. Later, DNA sequences of initially mitochondrial 16S rRNA (Dahlgren *et al.* 2001), and then cytochrome c oxidase subunit I (COI) sequences (Heggøy *et al.* 2007), were added for most of the terminals in the Pleijel & Eide (1996) study. Subsequently, DNA sequence data has become available for a range of *Ophryotrocha* and representatives of closely related taxa, such as *Exallopus* Jumars, 1974, *Iphitime* Marenzeller, 1902, *Palpiphitime* Orensanz, 1990 and *Pseudophryotrocha* Blake & Hilbig, 1991 (Wiklund *et al.* 2009, 2012; Thornhill *et al.* 2012; Taboada *et al.* 2013; Salvo *et al.* 2014; Ravara *et al.* 2021). Many of the taxa sequenced to date have been from deep-sea habitats and about half of the accepted species of *Ophryotrocha* have some sequence data available (Ravara *et al.* 2021). Thornhill *et al.* (2012) found numerous species of dorvilleids occurring at eastern Pacific seeps and their phylogenetic results suggested four independent colonizations to these habitats. Unfortunately, most of the terminals they published data for were unnamed species. Yen & Rouse (2020) resolved the status of some of these unnamed taxa with respect to the genus *Parougia* Wolf, 1986, but the terminals identified as *Ophryotrocha* and near relatives in Thornhill *et al.* (2012) remain unresolved. The remarkable diversity of dorvilleids at chemosynthetic environments has been attributed to the trophic partitioning (Levin *et al.* 2003), but the processes underlying this have yet to be fully explored.

To date, six species of *Ophryotrocha* from hydrothermal vents have been formally described, including *O. akessoni* Blake, 1985 from the Galapagos Rift, *O. platykephale* Blake, 1985 from the Guaymas Basin (Gulf of California), *O. globopalpata* Blake & Hilbig, 1990 from the Juan de Fuca Ridge, *O. wubaolingi* Miura, 1997 from Kagoshima Bay, *O. fabriae* Paxton & Morineaux, 2009 from the Mid-Atlantic Ridge and *O. jiaolongi* Zhang, Zhou, Wang & Rouse, 2017 from the Southwest and Central Indian Ridges (Blake 1985; Blake & Hilbig 1990; Solis Weiss & Hilbig 1992; Miura 1997; Paxton & Morineaux 2009; Zhang *et al.* 2017; Zhou *et al.* 2022). Also, several undescribed species of *Ophryotrocha* have been reported from hydrothermal vents in the western Pacific, southern Gulf of California (Watanabe & Kojima 2015; Goffredi *et al.* 2017). This distribution pattern makes *Ophryotrocha* of some interest from a biogeographical perspective and raises questions as to how many colonization events may have occurred at vents. To date, only two species (*O. globopalpata* and *O. jiaolongi*) have been included in phylogenetic studies, and these were placed into two distantly separated lineages of *Ophryotrocha* (Zhang *et al.* 2017).

Here, we investigate the phylogenetic position and formally describe five new species of *Ophryotrocha* from hydrothermal vents of the Pacific Ocean. The updated phylogeny of *Ophryotrocha* is based on mitochondrial cytochrome c oxidase subunit I (COI), 16S rRNA (16S), and nuclear histone H3 (H3) genes.

## Material and methods

### Sample collection and morphological analysis

Specimens of *Ophryotrocha* from hydrothermal vents were collected during several cruises from 2005–2021 utilizing the Human Occupied Vehicle (HOV) Alvin and Remotely Operated Vehicles (ROVs) Jason II, Doc Ricketts and SuBastian. Specimens from Mexico were collected under permits PPFE/DGOPA-200/18 and PPFE/DGOPA-090/21. Morphological voucher specimens were relaxed with isotonic magnesium chloride, fixed in 8–10% formaldehyde in seawater (stock "formalin" diluted 4–5 ×), rinsed with fresh water, and transferred to 50% ethanol for long-term archival. Additional specimens or tissue subsamples were preserved in 95% ethanol for genetic analysis. Some specimens were preserved in glutaraldehyde, paraformaldehyde, or RNA*later* (Ambion). Prior to preservation, specimens were examined and photographed using a Canon digital camera mounted on Leica MZ9.5 or Leica S8Apo stereo microscopes. Images of parapodia and jaws were acquired using a Leica DMR microscope with differential interference contrast. Jaws were obtained after digesting anterior ends with a dilute bleach solution at room temperature. Once the tissue was digested, the jaw elements were cleaned with distilled water. Jaws and parapodial mounts were made in Aqua-Mount® (Lerner) mounting medium. Images of jaws, parapodia and chaetae, were compiled from 'stacked' pictures merged using Helicon Focus ver. 4.2.7 (Helicon Soft Ltd.).

### DNA extraction, amplification, and sequencing

Depending on the size of available tissue, DNA extraction was done with either the Zymo Research Quick-DNA Microprep Plus Kit or the Zymo Research Quick-DNA Miniprep Plus Kit, following the protocols supplied by the manufacturer. PCR mixtures contained 12.5 µl Apex 2.0x Taq Red DNA Polymerase Master Mix (Genesee Scientific) or Conquest PCR 2.0x Master Mix 1 (Lamda Biotech) when amplification failed with the former reagent, 1 µl each primer (10 µM), 8.5 µl $ddH_2O$, and 2 µl template DNA in a mixture of 25µl total. PCR products were purified with ExoSAP-IT (USB Affymetrix, Ohio, USA), following the thermal cycler profile supplied by the manufacturer. Up to 705 base pairs (bp) of COI were amplified using the primer set LCO1490/HCO2198 (Folmer *et al.* 1994) with the reaction protocol 94°C/180 s – (94°C/30 s – 47°C/45 s – 72°C/60 s) × 5 cycles – (94°C/30 s – 52°C/45 s – 72°C/60 s) × 30 cycles – 72°C/300 s or the primer set polyLCO/polyHCO (Carr *et al.* 2011) with the reaction protocol 95°C/180 s – (95°C/40 s – 42°C/45 s – 72°C/50 s) × 40 cycles – 72°C/300 s. Up to 459 bp of 16S were amplified using the primer set 16SarL/16SbrH (Palumbi 1996) with the reaction protocol 95°C/180 s – (95°C/40 s – 50°C/40 s – 72°C/50 s) × 35 cycles – 72°C/300 s. Up to 348 bp of H3 were amplified using the primer set (Colgan *et al.* 1998) H3F/H3R with the reaction protocol 95 °C/180 s – (95°C/30 s – 53°C/45 s – 72°C/45 s) × 40 cycles – 72°C/300 s. Overlapping fragments were merged into consensus sequences using Geneious® ver. 11.1.5 (Biomatters Ltd). All new sequences obtained in this study used for phylogenetic analysis have been deposited in NCBI GenBank (Table 1).

### DNA analyses

Molecular phylogenetic analyses of *Ophryotrocha* were conducted for concatenated COI, 16S and H3 data using sequences available from GenBank, and newly generated sequences obtained in this study (Table 1). As well as available *Ophryotrocha* and relatives, we also included sequences for a range of other dorvilleids such as *Dorvillea* and *Parougia*. The eunicid *Eunice pennata* (Müller, 1776) was used as the outgroup in the analyses. Alignments of COI and H3 were performed using Muscle (Edgar 2004), while 16S was aligned using MAFFT (Katoh & Standley 2013). Phylogenetic trees were obtained using maximum likelihood (ML) and Bayesian inference (BI) analyses based on the concatenated dataset. The ML analysis was conducted using RAxML-NG (Kozlov *et al.* 2019) and ModelTest (Darriba *et al.*

**Table 1 (continued on next page).** Taxa and NCBI GenBank accession numbers. Bold indicates new sequences. * = specimen was sequenced from a whalefall in California (Wiklund *et al.* 2012) rather than the vent type locality in Mexico and is likely another species; # = *Ophryotrocha obscura* is regarded as a nomen nudum in Paxton & Åkesson 2010 and is the same taxon as *O. vellae*; % = incorrectly listed on GenBank as *O. permanni*.

| Taxa | COI | 16S | H3 |
|---|---|---|---|
| *Eunice pennata* (Müller, 1776) | AY838870 | AF321418 | DQ779731 |
| *Dorvillea erucaeformis* (Malmgran, 1865) | AY838868 | AY838827 | – |
| *Dorvillea rubrovittata* (Grube, 1855) | JQ310754 | GQ415457 | GQ415490 |
| *Dorvillea similis* (Crossland, 1924) | DQ317857 | DQ317915 | – |
| *Exallopus jumarsi** Blake, 1985 | JQ310755 | JQ310744 | – |
| *Exallopus* Jumars, 1974 seep | – | JX536712 | – |
| *Iphitime hartmanae* Kirkegaard, 1977 | GQ415472 | GQ415458 | GQ415491 |
| *Iphitime paguri* Fage & Legendre, 1934 | EF464549 | – | – |
| ***Ophryotrocha marinae*** sp. nov. | **OP311749–60,**<br>**OP561817** | KY701727 | **OP311651** |
| ***Ophryotrocha pruittae*** sp. nov. | **OP311761** | KY701728 | **OP311652** |
| ***Ophryotrocha charlottae*** sp. nov. | **OP311738–41** | **OP304893** | **OP311648** |
| ***Ophryotrocha kailae*** sp. nov. | **OP311745–748** | **OP304894** | **OP311650** |
| ***Ophryotrocha bohnorum*** sp. nov. | **OP311742–44** | **OP304895** | **OP311649** |
| ***Ophryotrocha* cf. *akessoni*** Blake, 1985 | **OP311735–37** | **OP304892** | **OP311647** |
| *Ophryotrocha adherens* Paavo, Bailey-Brock & Akesson, 2000 | JQ310756 | AF321421 | JQ310768 |
| *Ophryotrocha alborana* Paxton & Åkesson, 2011 | GQ415473 | AF321422 | GQ415492 |
| *Ophryotrocha batillus* Wiklund, Altamira, Glover, Smith, Baco & Dahlgren, 2012 | – | JQ310745 | JQ310769 |
| *Ophryotrocha birgittae* Paxton & Åkesson, 2011 | EF464539 | AF321426 | – |
| *Ophryotrocha cantabrica* Núñez, Riera & Maggio, 2014 | MW464902 | MW464897 | MW464905 |
| *Ophryotrocha chemecoli* Ravara, Wiklund & Cunha, 2021 | – | MW464898 | MW464907 |
| *Ophryotrocha clava* Taboada, Wiklund, Glover, Dahlgren, Cristobo & Avila, 2013 | KC123177 | KC123175 | KC123179 |
| *Ophryotrocha costlowi* Paxton & Åkesson, 2010 | JQ310757 | JQ310746 | JQ310770 |
| *Ophryotrocha craigsmithi* Wiklund, Glover & Dahlgren, 2009 | GQ415474 | GQ415459 | GQ415493 |
| *Ophryotrocha cyclops* Salvo, Wiklund, Dufour, Hamoutene, Pohle & Worsaae, 2014 | KM979519 | KM979517 | KM979518 |
| *Ophryotrocha diadema* Åkesson, 1976 | EF464534 | AF321425 | JQ310771 |
| *Ophryotrocha eutrophila* Wiklund, Glover & Dahlgren, 2009 | GQ415475 | GQ415460 | GQ415494 |
| *Ophryotrocha flabella* Wiklund, Altamira, Glover, Smith, Baco & Dahlgren, 2012 | JQ310759 | JQ310747 | JQ310772 |
| *Ophryotrocha geryonicola* (Esmark, 1874) | GQ415476 | GQ415461 | GQ415495 |
| *Ophryotrocha globopalpata* Blake & Hilbig, 1990 | GQ415477 | GQ415462 | GQ415496 |
| *Ophryotrocha geoffreadi* Ravara, Wiklund & Cunha, 2021 | – | MW464909 | MW464909 |
| *Ophryotrocha gracilis* Huth, 1933 | EF464545 | AF321424 | GQ415497 |
| *Ophryotrocha hartmanni* Huth, 1933 | EF464546 | AF321419 | JQ310773 |
| *Ophryotrocha japonica* Paxton & Åkesson, 2010 | GQ415478 | GQ415463 | GQ415498 |
| *Ophryotrocha jiaolongi* Zhang, Zhou, Wang & Rouse, 2017 | KY906961 | MF398963 | MF398968 |
| *Ophryotrocha labronica* La Greca & Bacci, 1962 | GQ415479 | AF321429 | GQ415499 |
| *Ophryotrocha langstrumpae* Wiklund, Altamira, Glover, Smith, Baco & Dahlgren, 2012 | JQ310760 | JQ310748 | JQ310774 |
| *Ophryotrocha lipovskyae* (Paxton, 2009) | GQ415480 | – | – |
| *Ophryotrocha lobifera* Oug, 1978 | GQ415481 | GQ415464 | GQ415500 |
| *Ophryotrocha longicollaris* Wiklund, Altamira, Glover, Smith, Baco & Dahlgren, 2012 | JQ310761 | JQ310749 | JQ310775 |
| *Ophryotrocha longidentata* Josefson, 1975 | GQ415482 | GQ415471 | GQ415501 |
| *Ophryotrocha lusa* Ravara, Marçal, Wiklund & Hilário, 2015 | – | – | KP731508 |
| *Ophryotrocha macrovifera* Paxton & Åkesson, 2010 | JQ310762 | AF321430 | JQ310776 |

**Table 1** (continued).

| **Taxa** | **COI** | **16S** | **H3** |
|---|---|---|---|
| *Ophryotrocha maculata* Åkesson, 1973 | GQ415483 | GQ415465 | JQ310777 |
| *Ophryotrocha magnadentata* Wiklund, Altamira, Glover, Smith, Baco & Dahlgren, 2012 | JQ310763 | JQ310750 | JQ310778 |
| *Ophryotrocha mammillata* Ravara, Marçal, Wiklund & Hilário, 2015 | – | – | KP731527 |
| *Ophryotrocha mediterranea* Martin, Abello & Cartes, 1991 | KR00479 | – | – |
| *Ophryotrocha nauarchus* Wiklund, Altamira, Glover, Smith, Baco & Dahlgren, 2012 | JQ310764 | JQ310751 | JQ310779 |
| *Ophryotrocha notoglandulata* Pfannenstiel, 1972 | EF464542 | AF321431 | JQ310780 |
| *Ophryotrocha nunezi* Ravara, Wiklund & Cunha, 2021 | – | MW464900 | MW464911 |
| *Ophryotrocha obscura* nom. nud.# | – | AF321435 | – |
| *Ophryotrocha orensanzi* Taboada, Wiklund, Glover, Dahlgren, Cristobo & Avila, 2013 | KC123178 | KC123176 | KC123180 |
| *Ophryotrocha permanae*% Paxton & Åkesson, 2010 | GQ415484 | AF321432 | GQ415502 |
| *Ophryotrocha puerilis puerilis* Claparède & Mecznikov, 1869 | GQ415485 | GQ415466 | GQ415503 |
| *Ophryotrocha puerilis siberti* (McIntosh, 1885) | GQ415486 | GQ415467 | GQ415504 |
| *Ophryotrocha robusta* Paxton & Åkesson, 2010 | EF464547 | AF321433 | JQ310781 |
| *Ophryotrocha rubra* Paxton & Åkesson, 2010 | GQ415487 | GQ415468 | GQ415505 |
| *Ophryotrocha sadina* Ravara, Marçal, Wiklund & Hilário, 2015 | – | – | KP731535 |
| *Ophryotrocha* seep 1a–c | – | JX536698,<br>JX536696,<br>JX536697 | – |
| *Ophryotrocha* seep 2d–e | – | JX536700,<br>JX536699 | – |
| *Ophryotrocha* seep 3f | – | JX536701 | – |
| *Ophryotrocha* seep 4g–i | – | JX536704,<br>JX536703,<br>JX536702 | – |
| *Ophryotrocha* seep 5p | – | JX536711 | – |
| *Ophryotrocha scutellus* Wiklund, Glover & Dahlgren, 2009 | GQ415488 | GQ415469 | GQ415506 |
| *Ophryotrocha shieldsi* Paxton & Davey, 2010 | HM181931 | HM181932 | JQ310782 |
| *Ophryotrocha socialis* Ockelmann & Akesson, 1990 | JQ310765 | AF321420 | JQ310783 |
| *Ophryotrocha urbis* Jimi, Taru & Imura, 2019 | LC504277 | – | – |
| *Ophryotrocha vellae*# Paxton & Åkesson, 2010 | EF464537 | AF321434 | – |
| *Ophryotrocha vivipara* Banse, 1963 | JQ310766 | JQ310752 | – |
| *Parougia albomaculata* (Åkesson & Rice, 1992) | EF464550 | AF380115 | JQ310784 |
| *Parougia batia* (Jumars, 1974) | MF176704 | MF176757 | MF279089 |
| *Parougia bermudensis* (Åkesson & Rice, 1992) | JQ310767 | JQ310753 | JQ310785 |
| *Parougia billiemiroae* Yen & Rouse, 2020 | MF176727 | MF176768 | MF198422 |
| *Parougia ceruleibohnorum* Yen & Rouse, 2020 | MF176697 | MF176764 | – |
| *Parougia chutsaoi* Yen & Rouse, 2020 | MF176732 | MF176766 | MF279077 |
| *Parougia diapason* Taboada, Bas & Avila, 2015 | KX555633 | KX555630 | KX555633 |
| *Parougia eliasoni* (Oug, 1978) | GQ415489 | GQ415470 | GQ415507 |
| *Parougia indiareinhardtae* Yen & Rouse, 2020 | MF176734 | MF176772 | MF279081 |
| *Parougia jessieae* Yen & Rouse, 2020 | MF176700 | MF176761 | MF279090 |
| *Parougia oregonensis* Hilbig & Fiege, 2001 | MF176694 | MF176754 | MF279078 |
| *Parougia ougi* Ravara, Wiklund & Cunha, 2021 | MW464904 | MW464901 | MW464913 |
| *Parougia sulleyi* Yen & Rouse, 2020 | MF176672 | MF176748 | MF279087 |
| *Parougia theloniousblueski* Yen & Rouse, 2020 | MF176728 | MF176769 | MF279084 |
| *Parougia zairahae* Yen & Rouse, 2020 | MF176696 | MF176763 | MF279085 |
| *Protodorvillea gracilis* (Hartman, 1938) | HM473654 | – | – |
| *Protodorvillea kefersteini* (McIntosh, 1869) | KF808171 | DQ779634 | DQ779759 |
| *Pseudophryotrocha* Hilbig & Blake, 1991 seep r | – | JX536713 | – |
| *Schistomeringos longicornis* (Ehlers, 1901) | HM473665 | – | – |

2020) in the raxmlGUI 2.0 interface (Edler *et al.* 2021). BI analyses were run twice using MrBayes ver. 3.2.7a (Ronquist *et al.* 2012), with four chains for 10 million generations sampling a tree every 1000 generations. The models used for each partition were the closest to those chosen in ModelTest-NG. Burn-in was determined to be 10% using Tracer ver.1.7 (Rambaut *et al.* 2018). Trees from the ML and BI analyses were visualized with FigTree ver. 1.4.4 (Rambaut & Drummond 2003). To aid in species delimitation, uncorrected pairwise distances were calculated for COI sequence divergence using PAUP ver. 4.0a168 (Swofford 2002). Haplotype networks using COI data were generated with PopART ver. 1.7 (Leigh & Bryant 2015) using the TCS algorithm (Templeton *et al.* 1992; Clement *et al.* 2000) for *O.* cf. *akessoni* and the three new species that showed haplotype variation.

### Institutional abbreviations

SIO-BIC = Scripps Institution of Oceanography Benthic Invertebrate Collection, La Jolla, California, USA
ICML-UNAM = Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Mazatlán, Sinaloa, Mexico

## Results

### Phylogeny

The concatenated dataset comprised of three aligned gene fragments was 1631 bp. Both the ML and BI analyses recovered *Ophryotrocha* as paraphyletic, though it formed a well-supported clade when including the *Exallopus*, *Iphitime* and *Pseudophryotrocha* terminals (Fig. 1). The other terminals of Dorvilleidae formed a grade, with *Parougia* as the well-supported sister group to the *Ophryotrocha*/*Exallopus*/*Iphitime*/*Pseudophryotrocha* clade. Two major clades (clades A–B) have been labelled here, along with some subclades that have been variously identified in previous studies (Fig. 1).

A total of 12 vent dorvilleid species with DNA data available were included in this analysis, with three of them belonging within *Parougia*. The other nine can arguably be placed within *Ophryotrocha*: eight of them collected from the Pacific and one from the Indian Ocean (Fig. 1). Six of these vent *Ophryotrocha* have molecular data reported for the first time, with five recognized as new to science and one as possibly being an already known species, *O.* cf. *akessoni*. The vent species of *Ophryotrocha* fell into the two main clades of *Ophryotrocha* and form four distinct lineages. Within Clade A, the vent *Exallopus jumarsi* Blake, 1985, originally described from Guaymas Basin vents, formed a relatively isolated clade with *O. nunezi* Ravara, Wiklund & Cunha, 2021 from Atlantic seeps and wood falls. It should be noted that the GenBank sequences for *E. jumarsi* are actually from a California whalefall (Wiklund *et al.* 2012), and Fig. 1 shows it as very closely related to an unnamed *Exallopus* from northeast Pacific methane seeps (Thornhill *et al.* 2012). Also, within Clade A, *O. globopalpata*, found at vents of the Juan de Fuca Ridge, clustered as a well-supported clade with a whale-fall species (*O. flabella* Wiklund *et al.*, 2012) and a seep species (*O.* seep3f). One of the new species, *Ophryotrocha bohnorum* sp. nov., from the Lau Back-Arc Basin vents, formed a clade with unnamed seep terminals (*Ophryotrocha* spp. seep4) from the northeast Pacific.

Within Clade B shown in Fig. 1, six species formed a well-supported monophyletic vent-endemic lineage, five from the eastern Pacific and one from the Indian Ocean. This vent clade was the sister group to *O. clava* Taboada, Wiklund, Glover, Dahlgren, Cristobo & Avila, 2013, which was described from whale bones in Antarctica. A clade comprised of the three *Iphitime* terminals then formed the well-supported sister group to the vent vent-endemic plus *O. clava* clade (Fig. 1). Clade B otherwise was comprised of non-vent *Ophryotrocha* terminals referred to in Figure 1 as the *labronica* clade, *lobifera* clade, *gracilis*/*hartmanni* clade and *puerilis* clade.

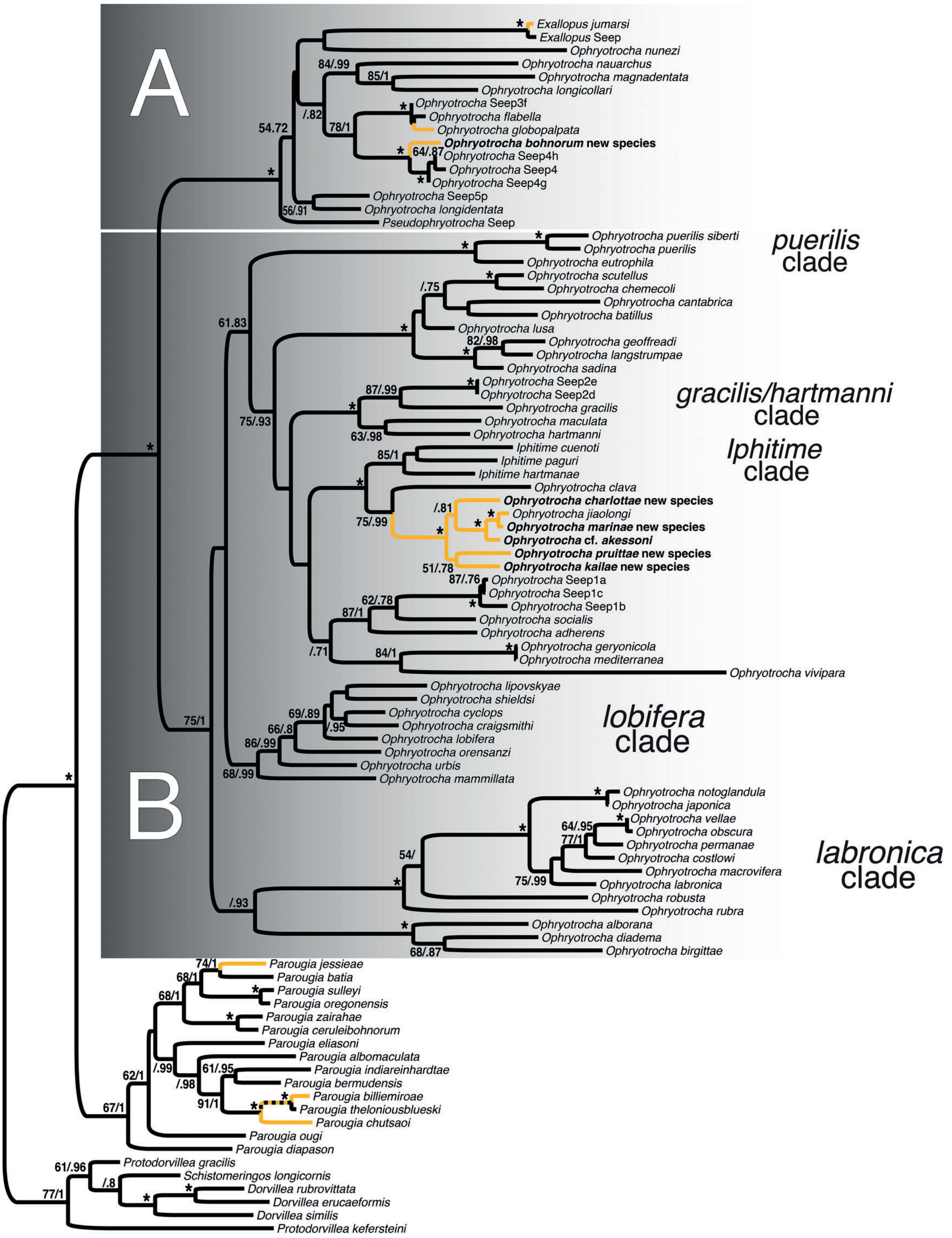

**Fig. 1.** Phylogenetic tree of Dorvilleidae *Ophryotrocha* Chamberlin, 1919 based on the Maximum Likelihood and Bayesian Inference analysis of the concatenated dataset of three genes. The outgroup, *Eunice pennata* (Müller, 1776) is not shown. Numbers on the nodes represent bootstrap support (BS) values followed by posterior probability (PP) values. Blank values indicate BS score of less than 50 or PP of less than 0.7. The * symbol indicated BS support was 95% or greater and PP was 1. Orange branches indicate hydrothermal vent lineages showing that vents have been colonized at least 5 × by Dorvilleidae, 3 × within *Ophryotrocha* Claparède & Mecznikow, 1869. The letters A and B refer to the two main clades of *Ophryotrocha* .

**Table 2.** Minimum pairwise distances of COI sequences using uncorrected p-distances for 3 eastern Pacific new vent species of *Ophryotrocha* Claparède & Mecznikow, 1869, *O.* cf. *akessoni* Blake, 1985 and the closely related vent species *O. jiaolongi* Zhang, Zhou, Wang & Rouse, 2017. Bold values represent maximum intraspecific variation when known. Values for *O. jiaolongi* based on GenBank data reported in Zhou *et al.* (2022). The smallest interspecific distance found was between *O. jiaolongi* (Indian Ocean vents) and *O. marinae* sp. nov. (Gulf of California vents) with a minimum distance of 3.73% (and a maximum of 5.2% (underlined)).

| | 1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|---|
| 1 *O. jiaolongi* Zhang, Zhou, Wang & Rouse, 2017 | **0.011** | | | | | |
| 2 *O.* cf. *akessoni* Blake, 1985 | 0.0924 | **0.0100** | | | | |
| 3 *O. charlottae* sp. nov. | 0.1559 | 0.1147 | **0.0194** | | | |
| 4 *O. kailae* sp. nov. | 0.1541 | 0.1507 | 0.1642 | **0.0029** | | |
| 5 *O. marinae* sp. nov. | <u>0.0373</u> | 0.0940 | 0.1435 | 0.1450 | **0.0088** | |
| 6 *O. pruittae* sp. nov. | 0.1861 | 0.1922 | 0.1777 | 0.1648 | 0.1959 | – |

Three members (*O.* cf. *akessoni, O. charlottae* sp. nov. and *O. kailae* sp. nov.) of the vent-endemic clade in Clade B were collected at vent fields on the southern part of the East Pacific Rise. Two of the new species, *O. marinae* sp. nov. and *O. pruittae* sp. nov., were collected at different vent systems in the southern Gulf of California, while *O. jiaolongi* has been recorded from several Indian Ocean vent systems. The eastern Pacific terminals did not cluster together based on geographical proximity. The internal topology was poorly resolved for two nodes, one where *O. kailae* sp. nov. and *O. pruittae* sp. nov. formed a clade that was the sister group to the other four taxa (Fig. 1) and another where *O. charlottae* sp. nov. was the poorly-supported sister group to *O. marinae* sp. nov., *O. jiaolongi* and

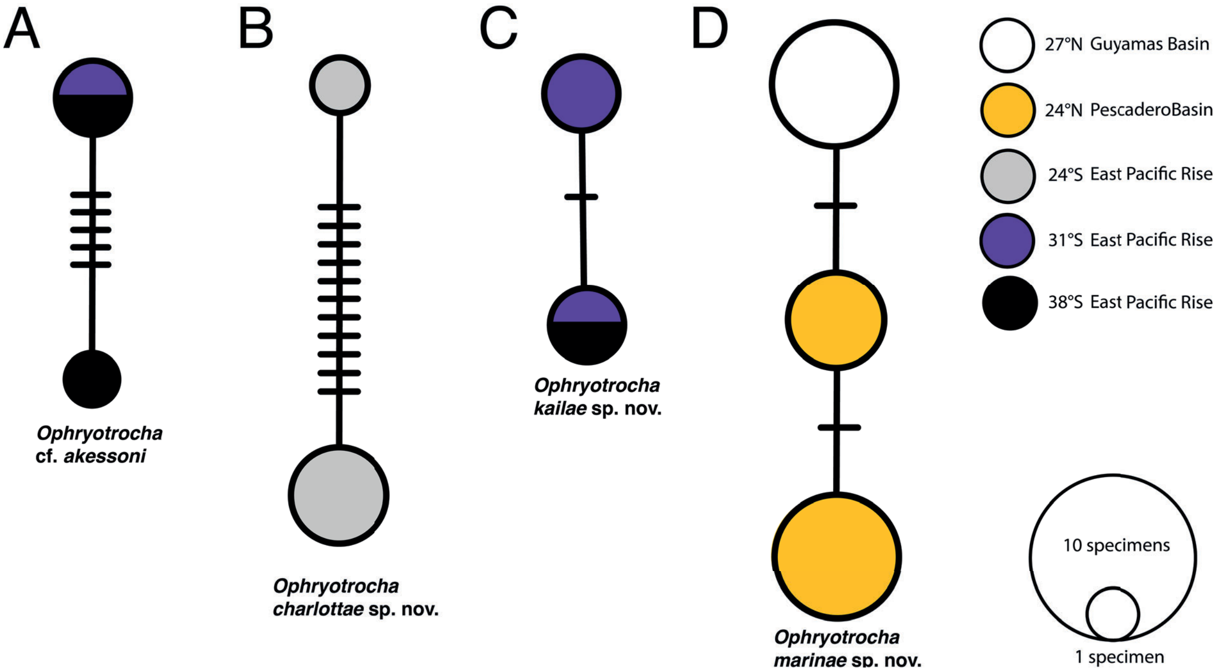

**Fig. 2.** Haplotype networks from COI data with geographic locality (°NS) coding. **A**. *Ophryotrocha* cf. *akessoni* Blake, 1985. **B**. *O. charlottae* sp. nov. **C**. *O. kailae* sp. nov. **D**. *O. marinae* sp. nov.

*O.* cf. *akessoni*. *Ophryotrocha marinae* sp. nov. and *O. jiaolongi* formed a well-supported clade that was in turn the well-supported sister group to *O.* cf. *akessoni*.

### Uncorrected distances and haplotype networks

The analysis of uncorrected pairwise distances for the COI sequences (Table 2) for the vent-endemic clade in main Clade B showed distances among the six species of *Ophryotrocha* ranging from 3.73% to 19.59%, with most distances well over 10%. The smallest distance was between members of *O. jiaolongi* (Indian Ocean) and *O. marinae* sp. nov. (Gulf of California). *Ophryotrocha* cf. *akessoni* was the only other taxon to show less than 10% divergence from other *Ophryotrocha* taxa and this was for both *O. jiaolongi* and *O. marinae* sp. nov. (Table 2). The intraspecific variation (based on untrimmed COI sequences) was maximally 1% for *Ophryotrocha* cf. *akessoni*, 1.94% for *O. charlottae* sp. nov., 0.29% for *O. kailae* sp. nov., and 0.88% for *O. marinae* sp. nov. Only one COI sequence for *O. pruittae* sp. nov. was obtained.

Sequences for specimens of *O.* cf. *akessoni* from 700 km along the southern East Pacific Rise (~38° S to ~31° S) were included in a COI haplotype network (Fig. 2A), which displayed two haplotypes, varying by five bases. One haplotype occurred in both sampled locations. *Ophryotrocha charlottae* sp. nov. specimens were only collected from a single site on the southern East Pacific Rise (~24° S). Four specimens were sequenced, with three showing the same haplotype while one was notably divergent (Fig. 2B). As with *O.* cf. *akessoni, O. kailae* sp. nov. was only found along a section of the southern East Pacific Rise (~38° S to ~31° S) and showed two haplotypes. These varied by only one base, and one haplotype occurred in both sampled locations (Fig. 2C). The 13 specimens of *O. marinae* sp. nov. included in the haplotype network displayed three haplotypes (Fig. 2D), with none shared across sites, and in the trimmed COI dataset there were only at most two base pairs different. These were collected from two localities in the Gulf of California that differed markedly in depth from ~3600 m (Pescadero Basin) to ~2000 m (Guaymas Basin).

## *Taxonomy*

Polychaeta Grube, 1850
Eunicida Dales, 1963
Dorvilleidae Chamberlin, 1919
*Ophryotrocha* Claparède & Mecznikow, 1869

### ***Ophryotrocha*** cf. ***akessoni*** Blake, 1985
Fig. 3

### Material examined

EAST PACIFIC OCEAN • 6 specs (5 fixed in formalin, 1 fixed in ethanol and the posterior end used for DNA extraction); Southern East Pacific Rise, German Flats Vent Field, active hydrothermal vents; 37.793° S, 110.916° W; depth 2216 m; 22 Mar. 2005; Greg Rouse, Nerida Wilson and Robert Vrijenhoek leg.; collecting event: HOV Alvin dive 4088; GenBank: OP311735 (COI); SIO-BIC A14105 • 2 specs (1 fixed in formalin, 1 fixed in ethanol and the posterior end used for DNA extraction); same collection data as for preceding; GenBank: OP311736 (COI); SIO-BIC A14106 • 1 spec. (fixed in ethanol and the posterior end used for DNA extraction); Southern East Pacific Rise, active hydrothermal vents; 31.151° S, 111.932° W; depth 2237 m; 29 Mar. 2005; Greg Rouse, Nerida Wilson and Robert Vrijenhoek leg.; collecting event: HOV Alvin dive 4094; GenBank: OP311737 (COI), OP304892 (16S), OP311647 (H3); SIO-BIC A14107.

### Description

Body about 7.5 mm in length and ~ 30 segments (Fig. 3A). Prostomium rounded, wider than long, slightly rise medio-posteriorly, with paired digitiform antennae inserted dorsally, paired digitiform palps similar in length with antennae, inserted ventral-laterally (Fig. 3A). Peristomium with two rings, sub-equal in length to the following segments, with ciliary band on each ring (Fig. 3A). Mandibles heavily sclerotized, with rod-like shafts, curved shape cutting plates, with single blunt peak, lateral wings weakly sclerotized (Fig. 3B). Maxillae P-type, forceps comb-like, with large main fang. Two rows of 7 free denticles, posterior most denticles (D1) comb-like, with smaller main fang. The other six denticles (D2–D7) small, shovel-shaped, with fine teeth (Fig. 3C). Parapodia uniramous, with long dorsal cirri and short stubby ventral cirri, acicular lobes sub-triangular distally (Fig. 3D). Supra-acicular chaetae simple, distally serrated, tapering into a main fang (Fig. 3D–E). Sub-acicular chaetae compound, with serrated blades (Fig. 3F–G). Sub-acicular chaetal lobe holds one simple chaeta (Fig. 3D, G). Pygidium with two short nub-like papillae laterally (Fig. 3A).

### Remarks

The specimens were collected from two sites of hydrothermal vents on the southern East Pacific Rise, also known as the Pacific Antarctic Ridge. Though collected well south of the type locality, they agree with *Ophryotrocha akessoni* described from Galapagos Rift vents in most characters, though there are differences in jaw structure. Blake (1985) described a replacement of mandibles in *O. akessoni* from serrated cutting plates in juveniles to curved cutting plates in adults. In our specimens (Fig. 3B), mandibles with curved cutting plates resemble the adult mandibles in *O. akessoni.* Paxton (2004) and

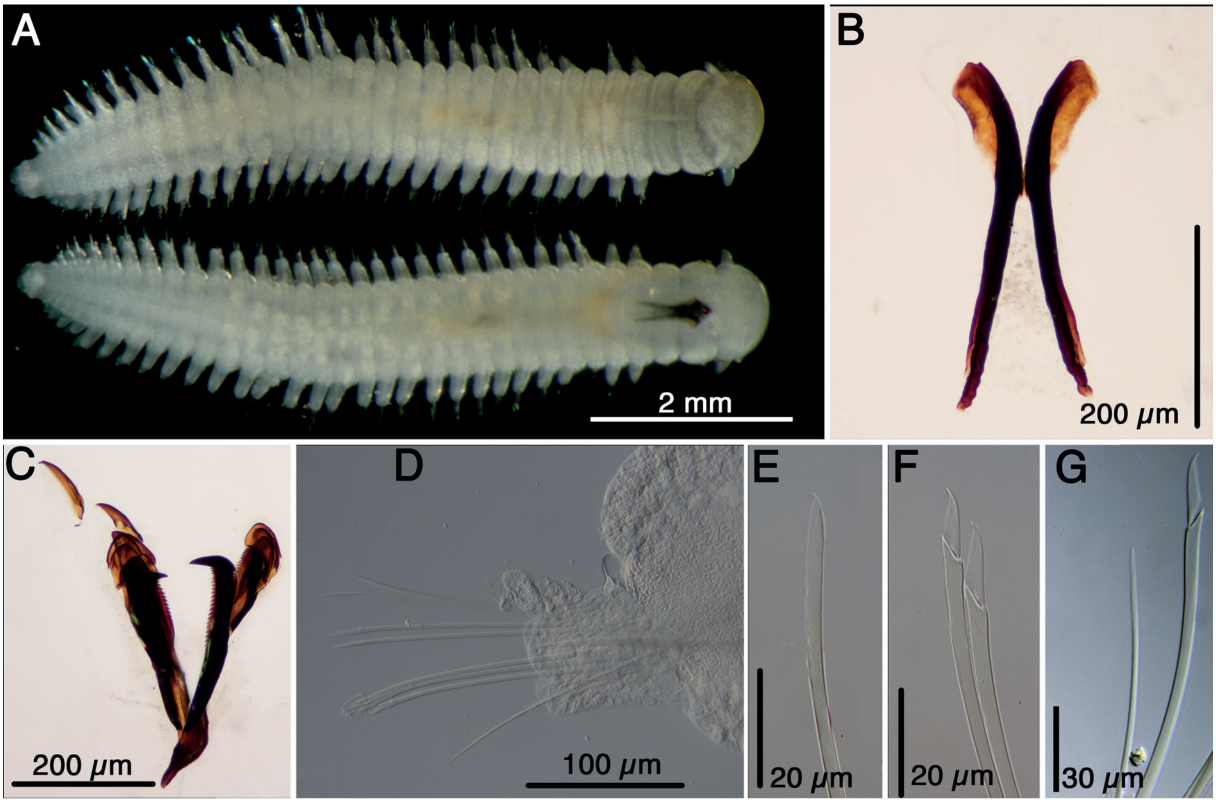

**Fig. 3.** *Ophryotrocha* cf. *akessoni* Blake, 1985. **A**. Dorsal and ventral views of live specimen (SIO-BIC A14105). **B**. Mandibles (SIO-BIC A14107). **C**. Maxillae (SIO-BIC A14107). **D**. Parapodium (SIO-BIC A14105). **E**. Simple supra-acicular chaetae (SIO-BIC A14105 ). **F**. Compound sub-acicular chaetae (SIO-BIC A14105 ). **G**. Simple sub-acicular chaeta (SIO-BIC A14106 ).

**Table 3.** Comparative list of selected characters for the vent-endemic radiation of *Ophryotrocha* Claparède & Mecznikow, 1869 in clade B. * = No further details or drawing are provided in Blake (1985).

| **species** | ***O. akessoni*** Blake, 1985 | ***O.* cf. *akessoni*** Blake, 1985 | ***O. jiaolongi*** Zhang, Zhou, Wang & Rouse, 2017 | ***O. marinae*** sp. nov. | ***O. pruittae*** sp. nov. | ***O. charlottae*** sp. nov. | ***O. kailae*** sp. nov. |
|---|---|---|---|---|---|---|---|
| **locality** | Galapagos Rift | East Pacific Rise (southern) | Three Indian Ocean Ridges | Pescadero Basin, Gulf of California | Alarcon Rise, Gulf of California | East Pacific Rise (southern) | East Pacific Rise (southern) |
| **antennae and palps** | Long digitiform, extend beyond prostomium | Long digitiform, extend beyond prostomium | Short digitiform | Long digitiform, extend beyond prostomium | Long digitiform, extend beyond prostomium | Long digitiform, extend beyond prostomium | Short digitiform |
| **maxillae** | P- to K-type | P-type | P-type | P-type | P-type | P-type | P-type |
| **mandible** | curved cutting plate | curved cutting plate | triangular cutting plate | triangular cutting plate | L-shape cutting plate | sub-triangular cutting plate | curved cutting plate |
| **pygidial cirri** | 2 anal cirri* | 2 anal papillae | 2 anal cirri, one median papilla | 2 anal cirri | 2 conical cirri | 2 anal cirri, one median papilla | 2 anal cirri |
| **dorsal cirri** | long | long | long | long | long | fusiform | short |
| **ventral cirri** | short | short | short | short | short | short | short |
| **data source** | Blake (1985) | This study | Zhang *et al.* (2017), Zhou *et al.* (2022) | This study | This study | This study | This study |

Macnaughton *et al.* (2010) inferred that mandibles of a range of species of *Ophryotrocha* show basically adult size and shape of cutting plates since the larval stage, they only lengthen and enlarge their proximal shafts with maturity. It is possible that the juvenile mandibles in Blake's (1985) original description of *O. akessoni* may belong to another *Ophryotrocha*. Furthermore, *O. akessoni* was described with a P-type tending to K-type maxillae, with lateral teeth on the forceps (Blake 1985). However, the forceps of K-type maxillae are unidentate or bidentate with the lateral dentition completely reduced (Paxton 2004; Macnaughton *et al.* 2010). Thus, according to the original description, it may be that *O. akessoni* has P-type maxillae as seen in our specimens (Fig. 3C). Blake (1985) described the presence of two anal cirri but provided no further details or drawings. Our specimens had two short papillae which could correspond to those of Blake's specimens, but examination of the types is needed. Based on the variation in morphological characters (Table 3) and the lack of any DNA sequences for *O. akessoni* from the type locality, we consider it prudent to report our specimens as *O.* cf. *akessoni*.

### ***Ophryotrocha charlottae*** sp. nov.

urn:lsid:zoobank.org:act:2AC55385-EA0C-41E5-8EAF-4D6F32818D94

Fig. 4

## Etymology

Named in honor of Charlotte Seid, collection manager of the Benthic Invertebrate Collection at Scripps Oceanography, for her dedication to facilitating biodiversity research.

## Material examined

### Holotype

EAST PACIFIC OCEAN • 1 spec. (fixed in ethanol and the posterior end used for DNA extraction); Southern East Pacific Rise, northwest of Easter Island, active hydrothermal vents; 23.823° S, 115.456° W;

depth 2649 m; 2 Apr. 2005; Greg Rouse, Nerida Wilson and Robert Vrijenhoek leg.; collecting event: HOV Alvin dive 4097; GenBank: OP311739 (COI), OP304893 (16S), OP311648 (H3); SIO-BIC A14096.

### Paratypes

EAST PACIFIC OCEAN • 1 spec. (fixed in ethanol and midsection tissue used for DNA extraction); same collection data as for holotype; GenBank: OP311741 (COI); SIO-BIC A14163 • 1 spec. (fixed in ethanol and midsection tissue used for DNA extraction); same collection data as for holotype; GenBank: OP311740 (COI); SIO-BIC A14164.

### Other material

EAST PACIFIC OCEAN • 1 spec. (fixed in ethanol and entirely used for DNA extraction); same collection data as for holotype; GenBank: OP311738 (COI); SIO-BIC A14097 • 7 or more specs (7 fixed in glutaraldehyde, additional material fixed in formalin and entirely used for slides of parapodia, additional tissue fixed in ethanol); same collection data as for holotype; SIO-BIC A14098 • 1 spec. (fixed in ethanol and midsection tissue used for DNA extraction); same collection data as for holotype; SIO-BIC A14187 • 1 spec. (fixed in ethanol); same collection data as for holotype; SIO-BIC A14188.

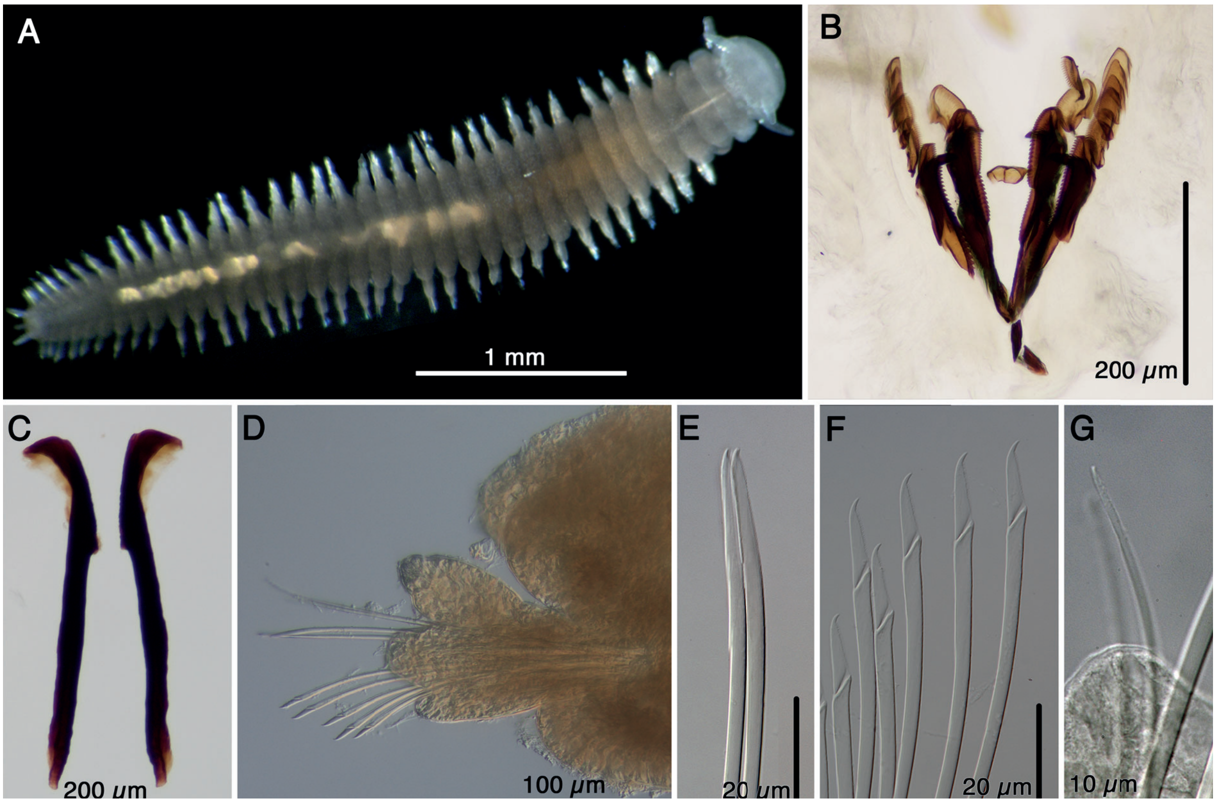

**Fig. 4.** *Ophryotrocha charlottae* sp. nov. **A**. Whole body of living holotype (SIO-BIC A14096). **B**. Maxillae of holotype (SIO-BIC A14096). **C**. Mandibles from holotype (SIO-BIC A14096). **D**. Parapodium of paratype (SIO-BIC A14098). **E**. Simple supra-acicular chaetae of paratype (SIO-BIC A14098). **F**. Compound sub-acicular chaetae of paratype (SIO-BIC A14098). **G**. Simple sub-acicular chaeta of paratype (SIO-BIC A14098).

### Description

In life light brown (Fig. 4A), opaque white after preservation. Body ~3 mm long, with more than 35 segments of similar width, slightly tapering posteriorly (Fig. 4A). Prostomium rounded, wider than long, with paired digitiform antennae inserted dorsally, paired digitiform palps inserted ventral-laterally, similar in length with antennae. Peristomium two equal rings, each similar in size to the following segments (Fig. 4A). Eyes not visible. Maxillae P-type, forceps comb-like, with large main fang, fused together basally. Four rows of seven free denticles, the posterior-most free denticles (D1) comb-like, like the forceps, other free denticles (D2–D7) shovel-shaped with fine teeth (Fig. 4B). Mandibles heavily sclerotized, shafts rod-like, cutting plates sub-triangular, lateral wings weakly sclerotized (Fig. 4C). Parapodia uniramous, acicular lobe with rounded distal margin, dorsal cirri enlarged fusiform, similar in size with acicular lobe, reaching distal margin of acicular lobe, ventral cirri short and stubby (Fig. 4D). Supra-acicular chaetae simple, distally serrated, tapering into a main fang (Fig. 4D–E). Sub-acicular chaetae compound, hooked with serrated blades (Fig. 4D, F). Sub-acicular chaetal lobe also with one or two simple chaetae (Fig. 4D, G). Pygidium with two digitiform cirri inserted laterally, a small median papilla posteriorly placed (Fig. 4A).

### Distribution

Known only from vents at 2649 m depth near Easter Island (Rapa Nui) at the southern end of the East Pacific Rise (Pacific Antarctic Ridge).

### Remarks

*Ophryotrocha charlottae* sp. nov. resembles *O.* cf. *akessoni*, which also occurs on the Southeast Pacific Ridge. They are similar in the shape of the prostomium, peristomium, antennae, palps, jaws, and chaetae. *Ophryotrocha charlottae* has distinctive parapodia with enlarged fusiform dorsal cirri, which easily distinguishes it from *O. akessoni*/*O.* cf. *akessoni*, *O. jiaolongi* and *O. marinae* sp. nov. Also, *O. charlottae* has two long digitiform anal cirri and a media papilla while *O.* cf. *akessoni* only has two short nub-like anal cirri (Fig. 3A). *Ophryotrocha kailae* sp. nov. is another species from southern end of the East Pacific Rise (Pacific Antarctic Ridge). It differs from *O. charlottae* in the form of antennae, palps, mandibles, dorsal cirri and pygidium (Fig. 5). *Ophryotrocha charlottae* can also be easily distinguished from other species of the "*akessoni*" clade, based on mandibles and parapodia (Table 3). The four rows of maxillae found in *O. charlottae* differ from that in close relatives such as *O. akessoni*, *O.* cf. *akessoni* (Fig. 3C) and *O. jiaolongi* that show only two rows (Blake 1985; Zhang *et al.* 2017), but four rows were also observed in *O. marinae* and *O. pruittae* sp. nov. (see below). It is possible that the outermost pair of rows represent molted jaws as has been observed in other *Ophryotrocha* by Paxton (2004), so this should not be interpreted as diagnostic without further study.

## ***Ophryotrocha kailae*** sp. nov.

urn:lsid:zoobank.org:act:FC8AD84C-5C47-49D2-BEC4-55FC04F3DFBC

Fig. 5

### Etymology

Named for Kaila Pearson, an expert on another group of vent and seep-associated polychaetes, phyllodocids belonging to *Galapagomystides* Blake, 1985.

### Material examined

#### Holotype

EAST PACIFIC OCEAN • 1 spec. (anterior fixed in formalin, posterior fixed in ethanol and used for DNA extraction); Southern East Pacific Rise, active hydrothermal vents; 31.151° S, 111.932° W; depth

2237 m; 29 Mar. 2005; Greg Rouse, Nerida Wilson and Robert Vrijenhoek leg.; collecting event: HOV Alvin dive 4094; GenBank: OP311745 (COI); SIO-BIC A14100.

### Paratypes

EAST PACIFIC OCEAN • 1 spec. (fixed in ethanol and the posterior end used for DNA extraction); Southern East Pacific Rise, Saguaro Vent Field, active hydrothermal vents; 31.865° S, 112.044° W; depth 2235 m; 28 Mar. 2005; Greg Rouse, Nerida Wilson and Robert Vrijenhoek leg.; collecting event: HOV Alvin dive 4093; GenBank: OP311748 (COI); SIO-BIC A14099 • 1 spec. (fixed in ethanol and the posterior end used for DNA extraction); Southern East Pacific Rise, German Flats Vent Field, active hydrothermal vents; 37.793° S, 110.916° W; depth 2216 m; 22 Mar. 2005; Greg Rouse, Nerida Wilson, Robert Vrijenhoek leg.; collecting event: HOV Alvin dive 4088; GenBank: OP311746 (COI), OP304894 (16S), OP311650 (H3); SIO-BIC A14101 • 1 spec. (fixed in ethanol and the posterior end used for DNA extraction); same collection data as for holotype; GenBank: OP311747 (COI); SIO-BIC A14102 • 1 spec. (fixed in formalin); same collection data as for holotype; SIO-BIC A14103 • 1 spec. (anterior fixed in formalin, posterior fixed in ethanol); same collection data as for holotype; SIO-BIC A14104.

### Description

In life, translucent with light yellow gut and white eggs mid-body, body opaque white after preservation. Body length ~4.5 mm with more than 30 segments, similar width through the body, slightly tapering posteriorly (Fig. 5A). Eyes not visible. Prostomium rounded, wider than long, with paired short digitiform antennae inserted dorsally, paired digitiform palps inserted ventral-laterally, similar in length with antennae. Peristomium two rings, similar in length to following segments (Fig. 5A). Mandibles heavily sclerotized, shafts rod-like, cutting plates curved, with single blunt peak, lateral wings weakly

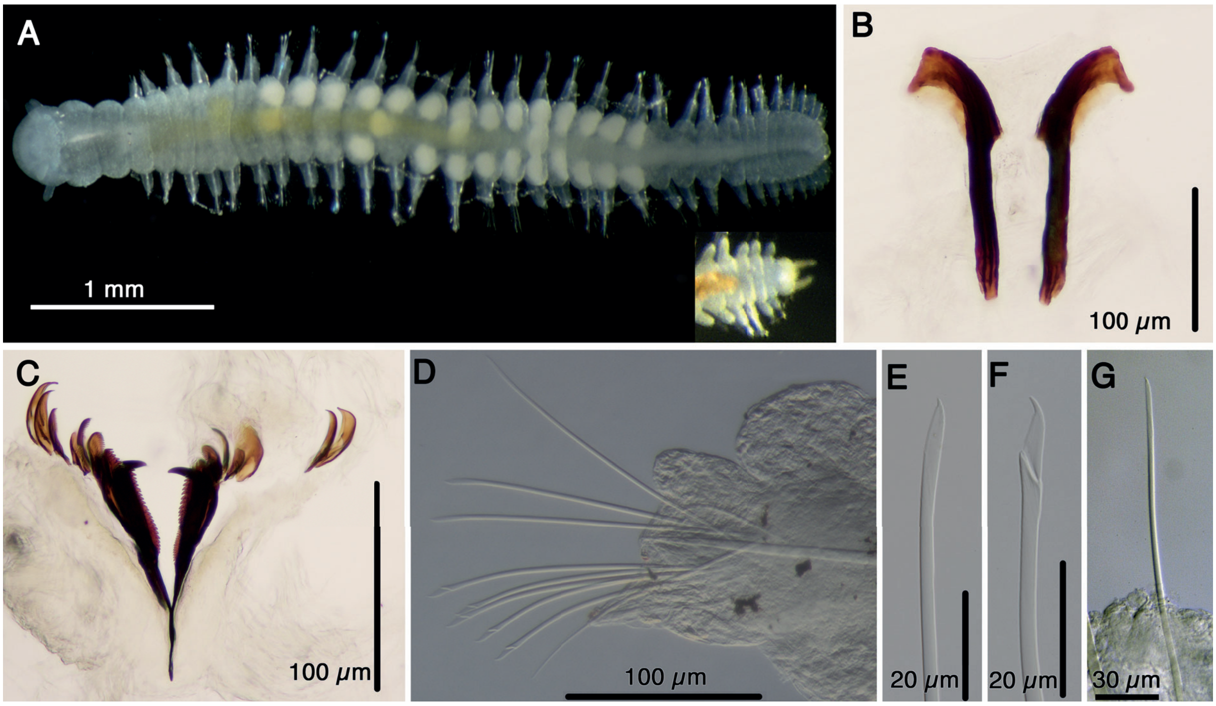

**Fig. 5.** *Ophryotrocha kailae* sp. nov. **A**. Whole body of living holotype (SIO-BIC A14100); inset shows the posterior end of paratype (SIO-BIC A14099) with pygidial cirri. **B**. Mandibles of paratype (SIO-BIC A14099). **C**. Maxillae of paratype (SIO-BIC A14099). **D**. Parapodium of paratype (SIO-BIC A14102). **E**. Simple supra-acicular chaetae of paratype (SIO-BIC A14102). **F**. Compound sub-acicular chaetae of paratype (SIO-BIC A14102). **G.** Simple sub-acicular chaeta of paratype (SIO-BIC A14102).

sclerotized (Fig. 5B). Maxillae P-type, forceps comb-like, with large main large fang. Two rows of 7 free denticles, posterior most free denticles (D1) comb-like, D2–D7 shovel-shaped (Fig. 5C). Parapodia uniramous, acicular lobe with rounded distal margin, dorsal cirri subtriangular, barely extending beyond distal margin of acicular lobe, ventral cirri stubby (Fig. 5C). Supra-acicular chaetae simple, distally serrated, tapering into a fang (Fig. 5D–E). Sub-acicular chaetae compound, with serrated blades (Fig. 5D, F). Sub-acicular chaetal lobe with one simple chaeta (Fig. 5D, G). Pygidium with two anal cirri inserted laterally (Fig. 5A inset).

### Distribution

Known only from vents at 2216–2237 m along the southern East Pacific Rise (Pacific Antarctic Ridge).

### Remarks

While the DNA data suggests *Ophryotrocha kailae* sp. nov. is most closely related to *O. pruittae* sp. nov. (Fig. 1), morphologically it resembles *Ophryotrocha akessoni* in having similar mandibles with curving cutting plates, which are otherwise not seen in the vent clade that also includes *O. charlottae* sp. nov., *O. jiaolongi*, *O. marinae* sp. nov. and *O. pruittae*. *Ophryotrocha kailae* differs from *O. akessoni* in the form of its head appendages and possibly pygidial cirri (Table 3).

## ***Ophryotrocha marinae*** sp. nov.

urn:lsid:zoobank.org:act:5B66661D-DDF9-425D-860F-412872058C27

Figs 6–7

*Ophryotrocha* cf. *akessoni* sp. 1 – Goffredi *et al.* 2017: supplemental, table 1.
*Ophryotrocha* cf. *akessoni* – Salcedo *et al.* 2019: 6, table 1.

### Etymology

Named in honor of Marina McCowin for her dedication in the study of the fauna associated with seeps and vents. Marina has studied Siboglinidae and *Ophryotrocha marinae* sp. nov. was notable for being associated in large numbers with the tubes of *Oasisia alvinae* Jones, 1985 (Fig. 6A).

### Material examined

#### Holotype

MEXICO • 1 spec. (fixed in ethanol and the posterior end used for DNA extraction); Gulf of California, Pescadero Basin, active hydrothermal vents; 23.960° N, 108.863° W; depth 3676–3756 m; 18 Apr. 2015; Greg Rouse leg.; collecting event: ROV Doc Ricketts dive 750 (specimens associated with tubes of *Oasisia alvinae*); GenBank: OP311750 (COI);, ICML-EMU-13289, (ex SIO-BIC A14109).

#### Paratypes

MEXICO • 1 spec. (fixed in ethanol and the posterior end used for DNA extraction); same collection data as for holotype; GenBank: OP311749 (COI), KY701727 (16S), OP311651 (H3); SIO-BIC A6308 • 1 spec. (fixed in ethanol and the posterior end used for DNA extraction); same collection data as for holotype; GenBank: OP311755 (COI); SIO-BIC A14108 • 1 spec. (fixed in ethanol and the posterior end used for DNA extraction); same collection data as for holotype; GenBank: OP311751 (COI); SIO-BIC A14110 • 1 spec. (fixed in ethanol); same collection data as for holotype; SIO-BIC A14111 • ca 35 specs (10 fixed in formalin, ca 25 fixed in ethanol); same collection data as for holotype; SIO-BIC A14112. • 11 specs (5 fixed in paraformaldehyde / glutaraldehyde, 6 fixed in ethanol); Gulf of California, Pescadero Basin, Auka Vent Field, region of P Vent and Z Vent; 23.96° N, 108.86° W; depth 3648–3671 m; 3 Nov. 2021; Greg Rouse leg.; collecting event: ROV SuBastian dive 475; GenBank: OP561817 (COI); SIO-BIC A14031.

### Other material

MEXICO • 7 specs (3 fixed in formalin, 4 fixed in ethanol); Gulf of California, Pescadero Basin, Auka Vent Field, Matterhorn area, active hydrothermal vents; 23.95° N, 108.86° W; depth 3650 m; 14 Nov. 2018; Greg Rouse and Ekin Tilic leg.; collecting event: ROV SuBastian dive 193, sample S0193-S4 (suction sampler chamber 4, specimens associated with tubes of *Oasisia alvinae*); SIO-BIC A9974 • 7 specs (2 fixed in formalin, 5 fixed in ethanol); same collection data as for preceding; SIO-BIC A9975 • 4 specs (fixed in ethanol); same locality as for preceding; 23.95369° N, 108.86231° W; depth 3668 m; 29 Oct. 2021; Greg Rouse leg.; collecting event: ROV SuBastia*n* dive 470, sample S0470-S3 (suction

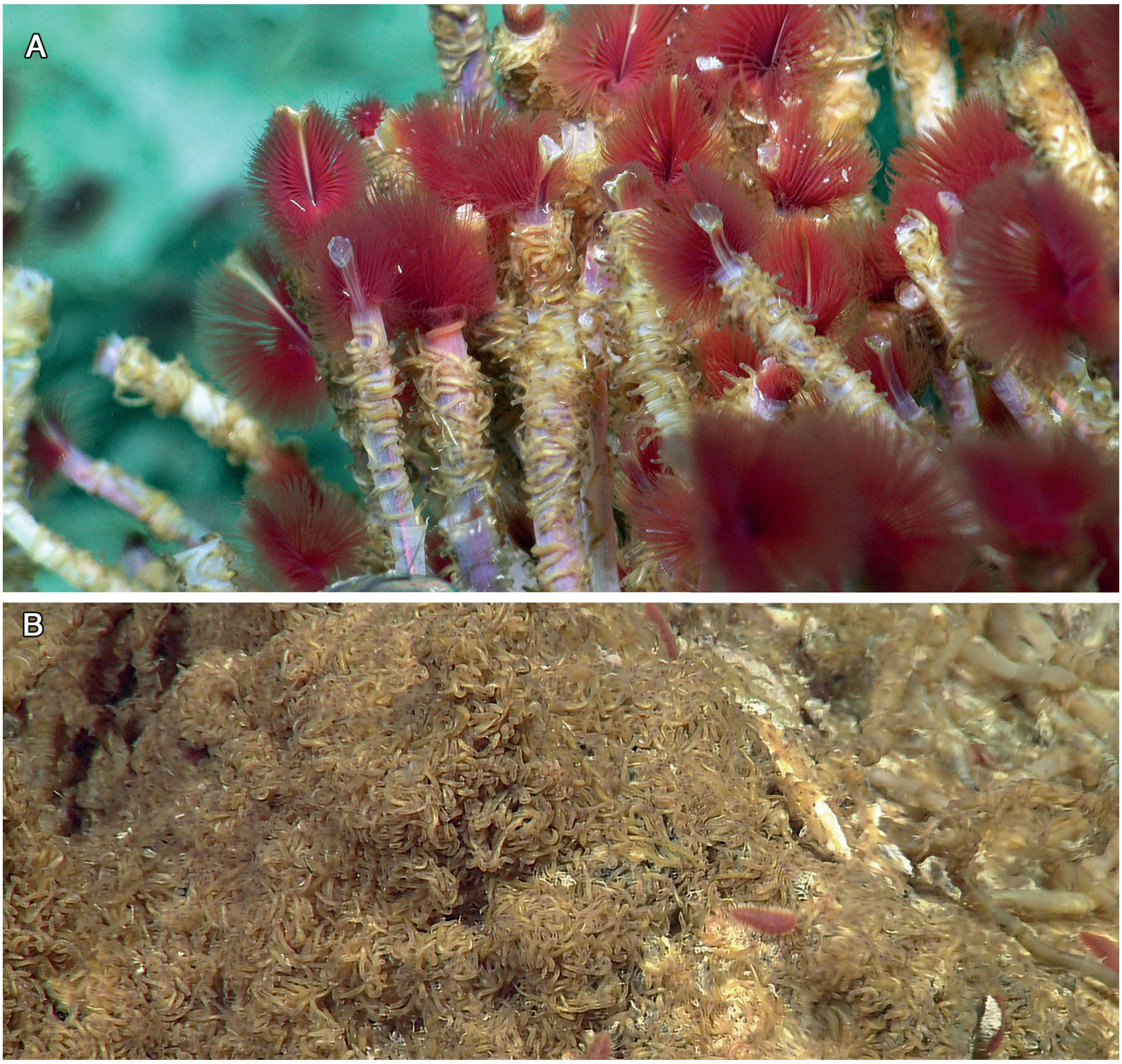

**Fig. 6.** *Ophryotrocha marinae* sp. nov. **A**. Numerous specimens associated with the tubes of *Oasisia alvinae* Jones, 1985 (Vestimentifera) at active hydrothermal vents of the Pescadero Basin (Mexico). Image from ROV SuBastian dive S0495, courtesy of the Schmidt Ocean Institute. **B**. Numerous specimens associated with microbial mat on the seafloor at active hydrothermal vents adjacent to a large mass of *Oasisia alvinae*. Some of these were collected and formed lots (SIO-BIC A6308, A1408–14112). Image from ROV Doc Ricketts dive 750 in the Pescadero Basin, courtesy of the Monterey Bay and Aquarium Research Institute.

sampler chamber 3, among tube worms); SIO-BIC A13987 • 2 specs (1 anterior fragment fixed in ethanol, 1 anterior fixed in formalin and posterior fixed in ethanol and used for DNA extraction); Gulf of California, Pescadero Basin, Auka Vent Field, Z Mound area, active hydrothermal vents; 23.95616° N, 108.86191° W; depth 3688 m; 17 Nov. 2018; Greg Rouse and Ekin Tilic leg.; collecting event: ROV SuBastian dive 196, sample S0196-PC1 (push core 1 at microbial mat with venting); GenBank: OP311752 (COI); SIO-BIC A9987 • at least 15 specs (3 fixed in formalin, 12 fixed in RNAlater, additional material fixed in ethanol); same locality as for preceding; 23.9561° N, 108.8619° W; depth 3688 m; 21 Nov. 2018; Greg Rouse and Ekin Tilic leg.; collecting event: ROV SuBastian dive 200, samples S0200-S1 and S0200-S2 (suction sampler chambers 1 and 2, microbial mat with venting); SIO-BIC A10029 • 1 spec. (fixed in ethanol and the posterior end used for DNA extraction); same collection data as for preceding; GenBank: OP311753 (COI); SIO-BIC A14114 • 4 specs (3 fixed in ethanol, 1 anterior fixed in formalin and posterior fixed in ethanol); Gulf of California, Pescadero Basin, Auka Vent Field, oily mat site southeast of Z Vent; 23.95° N, 108.86° W; depth 3650–3662 m; 5 Nov. 2021; Greg Rouse leg.; collecting event: ROV SuBastian dive 477; SIO-BIC A14045 • 7 specs (6 fixed in paraformaldehyde, 1 fixed in ethanol); Gulf of California, Pescadero Basin, midway between Auka and JaichMaa 'ja'ag Vent Fields; 23.95369° N, 108.86231° W; depth 3663–3687 m; 1 Nov. 2021; Greg Rouse leg.; collecting event: ROV SuBastian dive 473; SIO-BIC A14007 • 11 specs (2 fixed in formalin, 9 fixed in ethanol); Gulf of California, Pescadero Basin, JaichMaa 'ja'ag Vent Field, Cavern Tay Ujaa (Big Cave), active hydrothermal vents; 23.94157° N, 108.85570° W; depth 3675 m; 18 Nov. 2018; Greg Rouse and Ekin Tilic leg.; collecting event: ROV SuBastian dive 197, sample S0197-S6 (suction sampler chamber 6, specimens associated with small tubes of *Oasisia alvinae*); SIO-BIC A10002 • 1 spec. (fixed in ethanol and the posterior end used for DNA extraction); same collection data as for preceding; GenBank: OP311754 (COI); SIO-BIC A14113 • ca 50 specs (fixed in ethanol); Gulf of California, Guaymas Basin, sedimented hydrothermal vents; 27.016° N, 111.410° W; depth 2012 m; 13 Nov. 2009; Anna-Louise Reysenbach leg.; collecting event: HOV Alvin dive 4558; SIO-BIC A14115 • 1 spec. (fixed in ethanol and the posterior end used for DNA extraction); same collection data as for preceding; GenBank: OP311756 (COI); SIO-BIC A14116 • 1 spec. (fixed in ethanol and the posterior end used for DNA extraction); same collection data as for preceding; GenBank: OP311757 (COI); SIO-BIC A14117 • 1 spec. (fixed in ethanol and the posterior end used for DNA extraction); same collection data as for preceding; SIO-BIC A14118 • ca 15 specs (fixed in ethanol); Gulf of California, Guaymas Basin, sedimented hydrothermal vents; 27.015° N, 111.410° W; depth 2010 m; 15 Nov. 2009; Anna-Louise Reysenbach leg.; collecting event: HOV Alvin dive 4560; SIO-BIC A14119 • 1 speci. (fixed in ethanol and the posterior end used for DNA extraction); same collection data as for preceding; GenBank: OP311758 (COI); SIO-BIC A14120 • 1 spec. (fixed in ethanol and the posterior end used for DNA extraction); same collection data as for preceding; GenBank: OP311759 (COI); SIO-BIC A14121 • 1 spec. (fixed in ethanol and the posterior end used for DNA extraction); same collection data as for preceding; GenBank: OP311760 (COI); SIO-BIC A14122.

### Description

In life, golden color with white eggs mid-body (Fig. 7A–B), opaque white after preservation. Body length 10.5 mm, with 50+ segments, slightly dorso-ventrally compressed, widest anteriorly, gradually tapering posteriorly (Fig. 7A–B). Prostomium rounded, wider than long, posterior medial area slightly raised, with paired digitiform antennae, tapering distally, inserted dorsally, paired digitiform palps similar in length with antennae, inserted ventral-laterally (Fig. 7A). Peristomium with two rings, sub-equal in length to the following segments (Fig. 7A). Eyes not visible. Mandibles heavily sclerotized, with rod-like shafts, sub-triangular shape cutting plates, with single blunt peak anteriorly, lateral wings weakly sclerotized (Fig. 7C). Maxillae P-type, forceps comb-like, with large main fang. Four rows of free denticles, the posterior-most free denticles (D1) comb-like, like the forceps, other free denticles shovel-shaped with fine teeth, D2–D4 smaller than D5–D7 (Fig. 7D). Parapodia uniramous, acicular lobe with rounded distal margin, dorsal cirri long digitiform, extending beyond distal margin of acicular

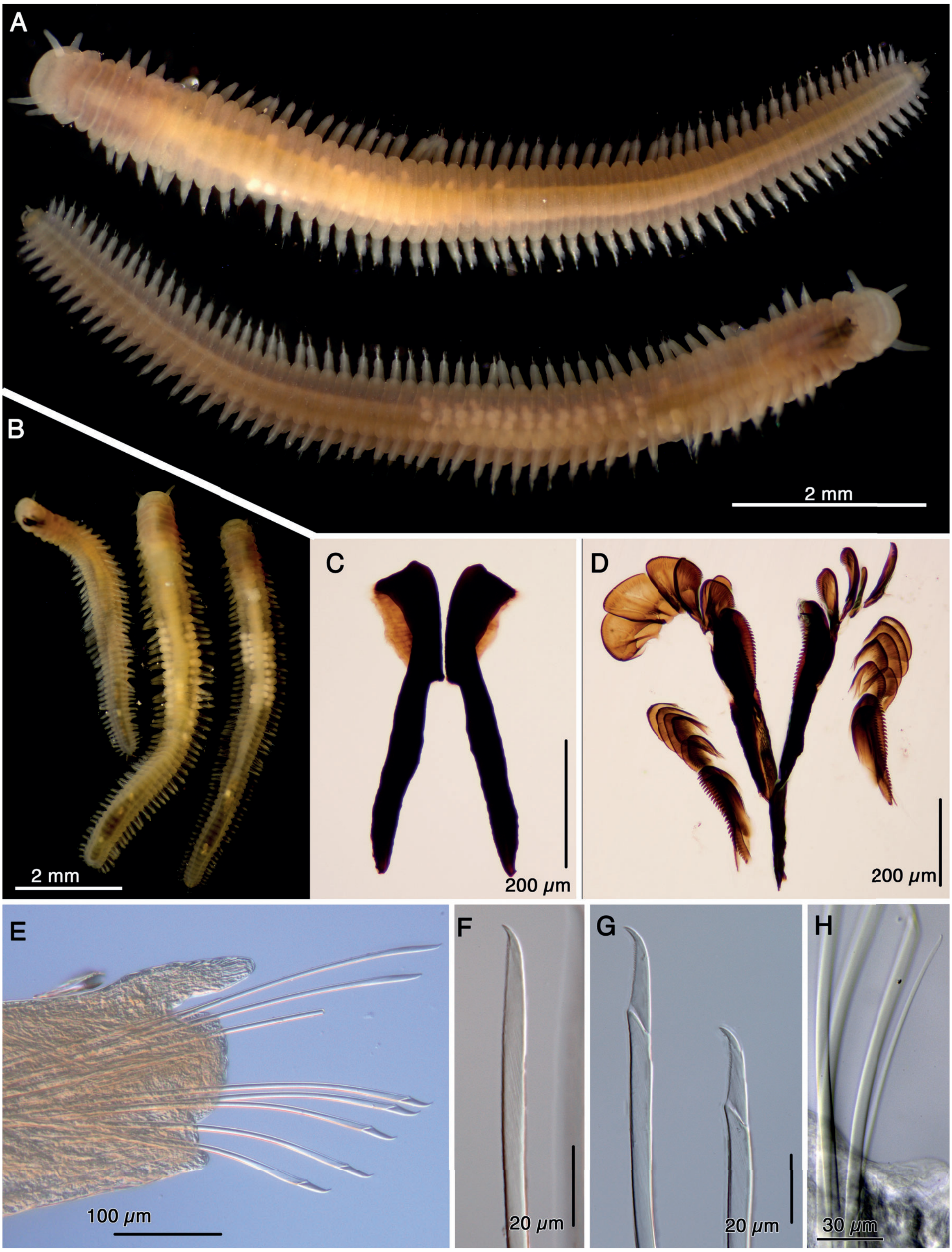

**Fig. 7.** *Ophryotrocha marinae* sp. nov. **A**. Dorsal and ventral views of living paratype (SIO-BIC A14031). **B**. Whole specimens from paratype (SIO-BIC A14112). **C**. Mandibles of specimen from paratype (SIO-BIC A6308). **D**. Maxillae of specimen from paratype (SIO-BIC A6308). **E**. Parapodium of holotype (SIO-BIC A14109). **F**. Simple supra-acicular chaetae of holotype (SIO-BIC A14109). **G**. Compound sub-acicular chaetae of holotype (SIO-BIC A14109). **H**. Simple sub-acicular chaeta of paratype (SIO-BIC A14109).

lobe, ventral cirri short and stubby (Fig. 7E). Supra-acicular chaetae simple, distally serrated, tapering into a main fang (Fig. 7F). Sub-acicular chaetae compound, with serrated blades (Fig. 7G). Sub-acicular chaetal lobe usually with one simple chaeta (Fig. 7H). Pygidium with two digitiform cirri inserted laterally (Fig. 7A).

### Distribution

Known from Gulf of California hydrothermal vents of the Pescadero Basin at over 3500 m and the Guaymas Basin sedimented vents at ~2000 m. Found in huge numbers on tubes of *Oasisia* (Fig. 6A), or on microbial mats near active flow (Fig. 6B).

### Remarks

This species was initially reported in Goffredi *et al.* (2017) as *Ophryotrocha* cf. *akessoni* sp. 1 with a partial DNA sequence for mitochondrial 16S rRNA lodged on GenBank (KY701727). *Ophryotrocha marinae* sp. nov. most closely resembles *Ophryotrocha jiaolongi* described from hydrothermal vents of the Indian Ocean, including sharing distinctive mandibles that distinguish these two taxa from all other *Ophryotrocha*. Morphologically, *O. marinae* differs from *O. jiaolongi* based on body color, the form of antennae and palps, and in lacking a median pygidial papilla (Table 3). In life, *O. marinae* is golden while *O. jiaolongi* is white and translucent. *Ophryotrocha marinae* also has antennae and palps that are distally tapering and longer than the length of prostomium, while in *O. jiaolongi* antennae and palps are shorter than the length of prostomium. The minimum COI uncorrected distance obtained between *O. marinae* and *O. jiaolongi* specimens was relatively small at 3.73% (Table 2). Other relatively small distances that are currently known are up to 4.8% between *O. notoglandulata* Pfannenstiel, 1972 and *O. japonicus* Paxton and Åkesson, 2010 (both Japanese taxa) and 6.1% between *O. flabella* and *O. globopalpata* (both from deep waters of the eastern Pacific). Given the morphological differences between *O. marinae* and *O. jiaolongi,* the reciprocal monophyly based on numerous COI sequences and vast geographic separation, we regard them here as separate species. One notable difference between *O. jiaolongi* and *O. marinae* was that the latter species showed four rows of maxillae compared to the two rows in *O. jiaolongi* found by Zhang *et al.* (2017). As discussed above for *O. charlottae* sp. nov. it is possible that the outermost pair of rows represent molted jaws as has been observed in other *Ophryotrocha* by Paxton (2004).

## ***Ophryotrocha pruittae*** sp. nov.

urn:lsid:zoobank.org:act:BE33115E-1B4C-405A-A425-AF518EE5E093

Fig. 8

*Ophryotrocha* cf. *akessoni* sp. 2 – Goffredi *et al.* 2017: supplemental, table 1.

### Etymology

Named for Jessica Pruitt, an aficionada and expert on deep-sea *Ophryotrocha*.

### Material examined

#### Holotype

MEXICO • 1 spec. (fixed in ethanol and the posterior end used for DNA extraction); Gulf of California, Alarcón Rise, active hydrothermal vents; 23.377° N, 108.531° W; depth 2309 m; 22 Apr. 2015; Greg Rouse leg.; collecting event: ROV Doc Ricketts dive 754; GenBank: OP311761 (COI); ICML-EMU-13288, (ex SIO-BIC A13689).

**Paratypes**

MEXICO • 1 spec. (fixed in ethanol and the posterior end used for DNA extraction); same collection data as for holotype; GenBank: KY701728 (16S), OP311652 (H3); SIO-BIC A6322 • 1 spec. (fixed in ethanol); same collection data as for holotype; SIO-BIC A14123 • 1 spec. (fixed in ethanol); same collection data as for holotype; SIO-BIC A14124 • 1 spec. (fixed in ethanol and most tissue used for DNA extraction); same collection data as for holotype; SIO-BIC A14125 • 1 spec. (fixed in ethanol); same collection data as for holotype; SIO-BIC A14126 • at least 4 specs (1 fixed in formalin, 3 individuals and additional fragments fixed in ethanol); same collection data as for holotype; SIO-BIC A14127 • 1 spec. (fixed in ethanol); same collection data as for holotype; SIO-BIC A14128 • 1 spec. (fixed in ethanol); same collection data as for holotype; SIO-BIC A14129 • 1 spec. (fixed in ethanol); same collection data as for holotype; SIO-BIC A14130 • 1 spec. (fixed in ethanol); same collection data as for holotype; SIO-BIC A14131 • 1 spec. (fixed in ethanol); same collection data as for holotype; SIO-BIC A14132.

## Description

In life, golden color (Fig. 8A), opaque white after preservation. Body 10.5 mm long, 50+ segments of similar width through the body. Eyes not visible. Prostomium rounded, wider than long, with paired digitiform antennae inserted dorsally, paired digitiform palps inserted ventral-laterally, similar in length with antennae. Peristomium two equal rings, similar size to the following segments (Fig. 8A). Maxillae P-type, forceps comb-like, with large main large fang, fused together basally. Four rows of seven free denticles, the posterior most free denticles (D1) comb-like, similar to the forceps, other free denticles shovel-shaped with fine teeth, D2–D4 smaller than D5–D7 (Fig. 8B). Mandibles heavily sclerotized,

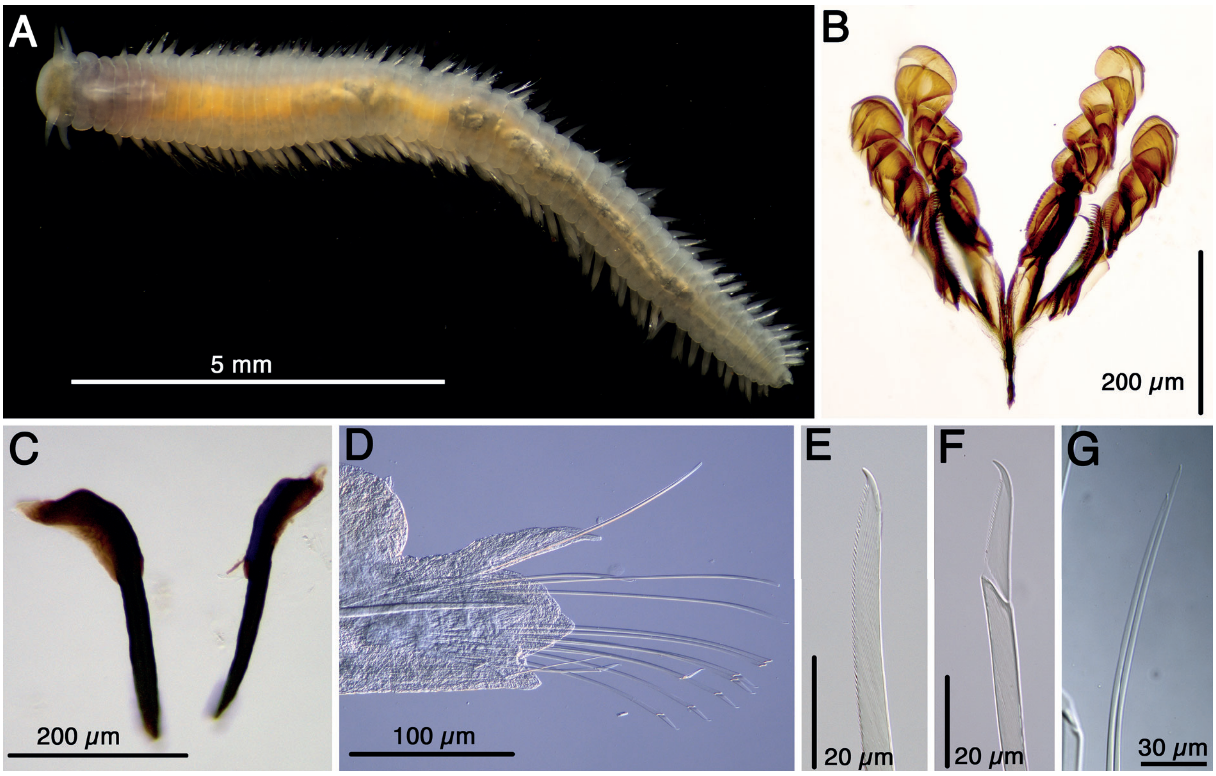

**Fig. 8.** *Ophryotrocha pruittae* sp. nov. **A**. Dorsal view of living holotype (ICML-EMU-13288). **B**. Maxillae from paratype (SIO-BIC A14123). **C**. Mandibles from paratype (SIO-BIC A14123). **D**. Parapodium from paratype (SIO-BIC A6322). **E**. Simple supra-acicular chaetae from paratype (SIO-BIC A6322). **F**. Compound sub-acicular chaetae from paratype (SIO-BIC A6322). **G**. Simple sub-acicular chaetae of paratype (SIO-BIC A6322).

shafts rod-like, cutting plates L-shape, anterior edge flat with pointed lateral peaks weakly sclerotized, lateral wings weakly sclerotized (Fig. 8C).

Parapodia uniramous, acicular lobe triangular with a blunt point distally, dorsal cirri cirriform, long, extend beyond distal margin of acicular lobe, ventral cirri short and stubby (Fig. 8D). Supra-acicular chaetae simple distally serrated, tapering into a large main fang, 2–5 per fascicle (Fig. 8D–E). Five to eight compound sub-acicular chaetae, with serrated blades (Fig. 8D, F). Sub-acicular chaetal lobe holds one or two simple chaetae (Fig. 8D, G). Pygidium with two short conical cirri inserted laterally (Fig. 8A).

### Distribution

Only known from the Alarcón Rise vents in the southern Gulf of California at 2309 m depth.

### Remarks

*Ophryotrocha pruittae* sp. nov. was initially reported in Goffredi *et al.* (2017) as *Ophryotrocha* cf. *akessoni* sp. 2 with a partial DNA sequence for mitochondrial 16S rRNA lodged on GenBank (KY701727). *Ophryotrocha pruittae* has a rounded prostomium, two equal segments of peristomium, digitiform antennae and palps and P-type maxillae, which are all features found in the vent-clade of Clade B. It differs from these species by having the mandibles with the L-shape cutting plates and two conical anal cirri, while *O. marinae* sp. nov. has triangular cutting plates and two digitiform anal cirri, *O. akessoni* / *O.* cf. *akessoni* has curved cutting plates, *O. charlottae* sp. nov. has subtriangular cutting plates and two lateral cirri and one median anal cirrus, *O. kailae* sp. nov. has curved cutting plates and two digitiform anal cirri (Table 3). *Ophryotrocha pruittae* showed four rows of maxillae. As discussed above for *O. charlottae* and *O. marinae* it is possible that the outermost pair of rows represent molted jaws as has been observed in other *Ophryotrocha* by Paxton (2004).

## ***Ophryotrocha bohnorum*** sp. nov.

urn:lsid:zoobank.org:act:181A86F6-7F8D-401C-B252-21FF39F6C5C0

Fig. 9

### Etymology

*Ophryotrocha bohnorum* sp. nov. is named for Jeffrey and Brenda Bohn and their family in recognition of their enduring support of deep-sea research.

### Material examined

#### Holotype

TONGA • 1 spec. (fixed in ethanol and a midbody piece used for DNA extraction); Lau Back-Arc Basin, Southern Valu Fa Ridge, Hine Hina Vent Field, active hydrothermal vents; 22.539° S, 176.718° W; depth 1845–1906 m; 22–23 May 2005; Greg Rouse, Fredrik Pleijel and Robert Vrijenhoek leg.; collecting event: ROV Jason II dive 146; GenBank: OP311742 (COI), OP304895 (16S), OP311649 (H3); SIO-BIC A14092.

#### Paratypes

TONGA • 1 spec. (fixed in ethanol); same collection data as for holotype; SIO-BIC A14094 • 4 specs (fixed in formalin); same collection data as for holotype; SIO-BIC A14095 • 1 spec. (fixed in ethanol and a midbody piece used for DNA extraction); same collection data as for holotype; GenBank: OP311744 (COI); SIO-BIC A14165 • 1 spec. (fixed in ethanol and a midbody piece used for DNA extraction); same collection data as for holotype; GenBank: OP311743 (COI); SIO-BIC A14166 • 1 spec. (fixed in ethanol); same locality as for holotype; 22.532° S, 176.719° W; depth 1818–1907 m; 21–22 May

2005; Greg Rouse, Fredrik Pleijel and Robert Vrijenhoek leg.; collecting event: ROV Jason II dive 145; SIO-BIC A14088 • 1 spec. (fixed in ethanol); same collection data as for preceding; SIO-BIC A14089 • 1 spec. (fixed in ethanol); same collection data as for preceding; SIO-BIC A14090 • 3 specs (fixed in formalin); same collection data as for preceding; SIO-BIC A14091 • 1 spec. (fixed in ethanol); same collection data as for holotype; SIO-BIC A14093.

### Description

In life, white, yellow gut, with white eggs mid-body (Fig. 9A), opaque white after preservation. Body 12 mm long with 60+ segments, tapering slightly along body. Prostomium rounded, wider than long, with a slightly rise posteriorly in the middle. Paired antennae long cirriform, inserted dorsally, tapering distally. Paired palps cirriform, slightly shorter than antennae, inserted dorsal-laterally (Fig. 9A). Peristomium two equal rings, similar in length to first chaetiger, slightly longer than following chaetigers, with two brown spots located dorsal-laterally between the two rings (Fig. 9A–B). Maxillae P-type, maxillary carriers comb-like, with large main fang, 8 pairs of free denticles. Posterior 4 denticles (D1–D4) heavily sclerotized, with large main fang and sharp teeth; anterior 4 denticles (D5–D8) translucent, with a small main fang and tiny teeth, D5–D6 overlap with D3–D4 (Fig. 9C). Mandibles transparent, rod-like shafts, cutting plates triangular, with blunt teeth on the anterior edge (Fig. 9D). Parapodia uniramous, acicular lobe rounded with a small tip in the middle of the distal margin, dorsal cirri short, rounded lobes, ventral cirri long extending from distal margin of acicular lobe (Fig. 9E). Supra-acicular chaetae simple, distally

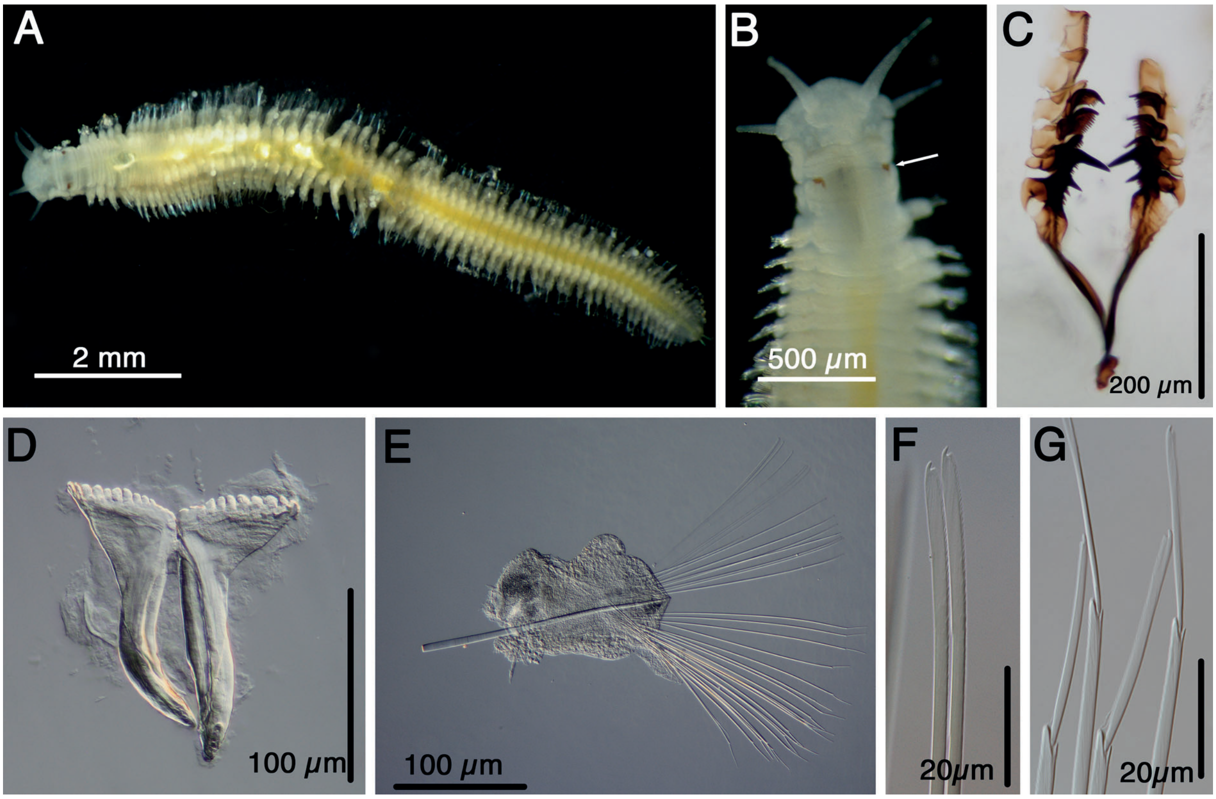

**Fig. 9.** *Ophryotrocha bohnorum* sp. nov. **A**. Whole body of living paratype (SIO-BIC A14095). **B**. Dorsal view of anterior living holotype (SIO-BIC A14092) one of the distinctive brown spots on the peristomium indicated by white arrow. **C**. Mandibles of paratype (SIO-BIC A14093). **D**. Maxillae of paratype (SIO-BIC A14093). **E**. Parapodium of paratype (SIO-BIC A14093). **F**. Simple supra-acicular chaetae of paratype (SIO-BIC A14093). **G**. Compound sub-acicular chaetae of paratype (SIO-BIC A14093).

serrated, with a small hook on the tip (Fig. 9F). Sub-acicular chaetae all compound, shafts bifid on the top, serrated blades with a small hook similar as supra-acicular chaetae on the tip (Fig. 9G). Pygidium with two long digitiform cirri (Fig. 9A).

### Distribution

Only known from vents at the Lau Back-Arc Basin, southwest Pacific Ocean at depths of 1845–1907 m.

### Remarks

The phylogenetic results (Fig. 1) show that *Ophryotrocha bohnorum* sp. nov. is most closely related to an undescribed species complex of *Ophryotrocha* (*O.* Seep4) from eastern Pacific methane seeps (Thornhill *et al.* 2012). There is no morphological information available for these specimens. A clade comprising other eastern Pacific species, *Ophryotrocha globopalpata* from hydrothermal vents, *O. flabella* from a whale fall and *O.* Seep3 (Thornhill *et al.* 2012), is then the well supported sister group to this clade. Based on this topology *Ophryotrocha bohnorum* appears to have independently colonized hydrothermal vents from *O. globopalpata* (Fig. 1). *Ophryotrocha bohnorum* has hooked tips of the supra- and sub-acicular chaetae and red-brown spots located dorsal-laterally between two peristomial segments, features not seen in other species from hydrothermal vents. Only four species of *Ophryotrocha*, *O. atlantica* Hilbig & Blake, 1991, *O. mediterranea* Martin Abello & Cartes, 1991, *O. pachysoma* Hilbig & Blake, 1991, and *O. socialis* Ockelmann & Åkesson, 1990, have been described with chaetae with hooked tips. *Ophryotrocha bohnorum* can be easily distinguished from these species by its transparent mandibles with serrated anterior edge.

## Discussion

*Ophryotrocha* have been reported from a wide variety of marine habitats, including organic falls, seeps, hydrothermal vents, beneath fish farms and shallow-water environments that were possibly rich in organic materials (Wiklund *et al.* 2021; Rouse *et al.* 2022). To date there have been relatively few taxa from chemosynthetic habitats included in phylogenetic analyses, with most being undescribed taxa from methane seeps (Thornhill *et al.* 2012). Two species of *Ophryotrocha* named from hydrothermal vents, *O. globopalpata* and *O. jiaolongi*, and also possibly *Exallopus jumarsi* (though the published sequences are from a whale fall specimen) have been included to date (Wiklund *et al.* 2009, 2012; Zhang *et al.* 2017). With this study data for six species of *Ophryotrocha*, five of them new, has been added to help increase our understanding of the success of Dorvilleidae in extreme environments. The phylogenetic results found here showed a branching pattern similar to the most recent study (Ravara *et al.* 2021) using the same three markers (Fig. 1). In the Ravara *et al.* (2021) and Zhang *et al.* (2017) studies it was apparent that vents had been colonized several times by *Ophryotrocha,* and this study adds one more independent event for *O. bohnorum* sp. nov. from western Pacific vents. We also provide evidence for an evolutionary radiation of six species where there had previously only been data for *O. jiaolongi* from the Indian Ocean.

The close relationship between the Indian *O. jiaolongi* and eastern Pacific species of *Ophryotrocha* is further evidence of a biogeographic link between these two regions. The implication of our phylogenetic results (Fig. 1) is that *O. jiaolongi* represents a colonization of the Indian Ocean by *Ophryotrocha* from the Pacific. Similar results have also been recently recovered in several other vent annelids, such as Alvinellidae Desbruyères & Laubier, 1986, Amphinomidae Lamarck, 1818, *Amphisamytha* Hessle, 1917, and *Hesiolyra* Blake, 1985, through the patterns differ (Borda *et al.* 2013; Zhou *et al.* 2019; Wang *et al.* 2020; Han *et al.* 2021). In the case of the first alvinellid to be described from outside the Pacific, *Paralvinella mira* Han, Zhang, Wang & Zhou, 2021, the closest relatives were western Pacific *Paralvinella* (Han *et al.* 2021). *Archinome jasoni* Borda, Kudenov, Chevaldonné, Blake, Desbruyères, Fabri, Hourdez, Pleijel, Shank, Wilson, Schulze & Rouse, 2013 (Amphinomidae) is a widespread taxon that occurs at vents of the Mid-Atlantic Ridge, Indian Ocean and the southwest and northwest Pacific (Borda *et al.* 2013; Jimi *et al.* 2019), with the Mid-Atlantic Ridge and Indian Ocean lineages forming a clade that is sister group to a Pacific clade. Four species of *Amphisamytha* are known from the Indian Ocean and there appear to have been several separate colonizations of the Indian Ocean from Pacific / Atlantic sources (Zhou *et al.* 2019). *Hesiolyra bergi* Blake 1985, an eastern Pacific vent hesionid, shows a different pattern in being nested among Indian Ocean species of *Hesiolyra* (Wang *et al.* 2020) and so suggesting that *Hesiolyra bergi* has an origin outside the Pacific.

Further sampling of other vent dorvilleid species such as *O. akessoni* and *O. platykephale* from the eastern Pacific, *O. fabriae* from the Mid-Atlantic Ridge, *Ophryotrocha* spp. in the Northwest Pacific and *Exallopus* from the Gulf of California (Blake 1985; Miura 1997; Paxton & Morineaux 2009; Watanabe & Kojima 2015) will be valuable in further elucidating the evolutionary pattern of colonization.

## Acknowledgements

Many thanks to Bob Vrijenhoek and the Monterey Bay Aquarium Research Institute for inviting GWR on cruises that obtained many of the key samples for this study. Other specimens were collected based on cruises funded by the Schmidt Ocean Institute. Many thanks to the captain and crew of the R/V Atlantis, R/V Melville, R/V Western Flyer, and R/V Falkor and the pilots of the HOV Alvin and ROVs Jason II, Doc Ricketts and SuBastian for crucial assistance in specimen collection. The authors are grateful to Chief Scientists Bob Vrijenhoek and Victoria Orphan and the science parties. Anna-Louise Reysenbach kindly collected and preserved samples of annelids from the Guaymas Basin sedimented vents. Thanks also to Charlotte Seid (SIO-BIC) for attention to detail and careful cataloguing, and to the Bohn family for their continued support of deep-sea research. Additional funding to support DZ and YZ came from China Ocean Mineral Resources R&D Association (No. DY135-E2-1-02) and the Scientific Research Fund of the Second Institute of Oceanography, MNR (Grant No. QNYC1902). We are grateful to the two anonymous reviewers for their very useful comments on the initial submission.

## References

Åkesson 1974. Reproduction and larval morphology of five *Ophryotrocha* species (Polychaeta, Dorvilleidae). *Zoologica Scripta* 2: 145–155. https://doi.org/10.1111/j.1463-6409.1974.tb00746.x

Blake J.A. 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.

Blake J.A. & Hilbig B. 1990. Polychaeta from the vicinity of deep-sea hydrothermal vents in the eastern Pacific. II. New species and records from the Juan de Fuca and Explorer Ridge systems. *Pacific Science* 44: 219–253.

Borda E., Kudenov J.D., Chevaldonné P., Blake J.A., Desbruyères D., Fabri M.-C., Hourdez S., Pleijel F., Shank T.M., Wilson N.G., Schulze A. & Rouse G.W. 2013. Cryptic species of *Archinome* (Annelida: Amphinomida) from vents and seeps. *Proceedings. Biological sciences / The Royal Society* 280 (1770): 20131876. https://doi.org/10.1098/rspb.2013.1876

Carr C.M., Hardy S.M., Brown T.M., Macdonald T.A. & Hebert P.D.N. 2011. A tri-oceanic perspective: DNA barcoding reveals geographic structure and cryptic diversity in Canadian polychaetes. *PloS One* 6: e22232. https://doi.org/10.1371/journal.pone.0022232

Clement M., Posada D. & Crandall K.A. 2000. TCS: a computer program to estimate gene genealogies. *Molecular Ecology* 9: 1657–1659. https://doi.org/10.1046/j.1365-294x.2000.01020.x

Colgan D.J., McLauchlan A., Wilson G.D.F., Livingston S.P., Edgecombe G.D., Macaranas J., Cassis G. & Gray M.R. 1998. Histone H3 and U2 snRNA DNA sequences and arthropod molecular evolution. *Australian Journal of Zoology* 46: 419–437. https://doi.org/10.1071/zo98048

Dahlgren T.G., Akesson B., Schander C., Halanych K.M. & Sundberg P. 2001. Molecular phylogeny of the model annelid *Ophryotrocha*. *The Biological Bulletin* 201: 193–203. https://doi.org/10.2307/1543334

Darriba D., Posada D., Kozlov A.M., Stamatakis A., Morel B. & Flouri T. 2020. ModelTest-NG: A new and scalable tool for the selection of DNA and protein evolutionary models. *Molecular Biology and Evolution* 37: 291–294. https://doi.org/10.1093/molbev/msz189

Desbruyères D., Segonzac M. & Bright M. 2006. Handbook of Deep-Sea Hydrothermal Vent Fauna. *Denisia* 2006: 1–565.

Edgar R.C. 2004. MUSCLE: Multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32: 1792–1797. https://doi.org/10.1093/nar/gkh340

Edler D., Klein J., Antonelli A. & Silvestro D. 2021. raxmlGUI 2.0: A graphical interface and toolkit for phylogenetic analyses using RAxML. *Methods in Ecology and Evolution* 12: 373–377. https://doi.org/10.1111/2041-210x.13512

Eibye-Jacobsen D. & Kristensen R. 1994. A new genus and species of Dorvilleidae (Annelida, Polychaeta) from Bermuda, with a phylogenetic analysis of Dorvilleidae, Iphitimidae and Dinophilidae. *Zoologica Scripta* 23: 107–131. https://doi.org/10.1111/j.1463-6409.1994.tb00379.x

Folmer O., Black M., Hoeh W.R., Lutz R.A. & Vrijenhoek R.C. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3: 294–299.

Goffredi S.K., Johnson S., Tunnicliffe V., Caress D., Clague D., Escobar E., Lundsten L., Paduan J.B., Rouse G., Salcedo D.L., Soto L.A., Spelz-Madero R., Zierenberg R. & Vrijenhoek R. 2017. Hydrothermal vent fields discovered in the southern Gulf of California clarify role of habitat in augmenting regional diversity. *Proceedings. Biological Sciences / The Royal Society* 284: 20170817. https://doi.org/10.1098/rspb.2017.0817

Han Y., Zhang D., Wang C. & Zhou Y. 2021. Out of the Pacific: A new alvinellid worm (Annelida: Terebellida) from the northern Indian Oocean hydrothermal vents. *Frontiers in Marine Science* 8: 543. https://doi.org/10.3389/fmars.2021.669918

Heggøy K.K., Schander C. & Åkesson B. 2007. The phylogeny of the annelid genus *Ophryotrocha* (Dorvilleidae). *Marine biology research* 3: 412–420. https://doi.org/10.1080/17451000701695361

Jimi N., Chen C. & Hiroshi K. 2019. New record of the hydrothermal vent-endemic polychaete *Archinome jasoni* Borda *et al.*, 2013 (Annelida, Amphinomidae) from the Northwest Pacific. *Check List* 15 (3): 523–526. https://doi.org/10.15560/15.3.523

Katoh K. & Standley D.M. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* 30: 772–780. https://doi.org/10.1093/molbev/mst010

Kozlov A.M., Darriba D., Flouri T., Morel B. & Stamatakis A. 2019. RAxML-NG: a fast, scalable and user-friendly tool for maximum likelihood phylogenetic inference. *Bioinformatics* 35: 4453–4455. https://doi.org/10.1093/bioinformatics/btz305

Leigh J.W. & Bryant D. 2015. POPART: full-feature software for haplotype network construction. *Methods in Ecology and Evolution / British Ecological Society* 6: 1110–1116. https://doi.org/10.1111/2041-210x.12410

Levin L.A., Ziebis W., Mendoza G.F., Growney V.A., Tryon M.D., Brown K.M., Mahn C., Gieskes J.M. & Rathburn A.E. 2003. Spatial heterogeneity of macrofauna at northern California methane seeps: influence of sulfide concentration and fluid flow. *Marine Ecology Progress Series* 265: 123–139. https://doi.org/10.3354/meps265123

Macnaughton M.O., Worsaae K. & Eibye-Jacobsen D. 2010. Jaw morphology and ontogeny in five species of *Ophryotrocha*. *Journal of Morphology* 271: 324–339. https://doi.org/10.1002/jmor.10800

Miura 1997. Two new species of the genus *Ophryotrocha* (Polychaeta, Iphitimiidae) from Kagoshima Bay. *Bulletin of Marine Science* 60: 300–305.

Orensanz J.M. 1990. The eunicemorph polychaete annelids from Antarctic and Subantarctic Seas. *Antarctic Research Series* 52: 1–183.

Palumbi S.R. 1996. Nucleic acids II: The polymerase chain reaction. *In*: Hillis D.M., Moritz C. & Mable B.K. (eds) *Molecular Systematics. 2nd Edition*: 205–247. Sinauer Associates, Sunderland, Massachusetts.

Paxton H. 2004. Jaw growth and replacement in *Ophryotrocha labronica* (Polychaeta, Dorvilleidae). *Zoomorphology* 123: 147–154. https://doi.org/10.1007/s00435-004-0097-4

Paxton H. & Morineaux M. 2009. Three species of Dorvilleidae (Annelida: Polychaeta) associated with Atlantic deep-sea reducing habitats, with the description of *Ophryotrocha fabriae*, new species. *Proceedings of the Biological Society of Washington* 122: 14–25. https://doi.org/10.2988/08-22.1

Pleijel F. & Eide R. 1996. The phylogeny of *Ophryotrocha* (Dorvilleidae, Eunicida, Polychaeta). *Journal of Natural History* 30: 647–659. https://doi.org/10.1080/00222939600770361

Premoli M.C. & Sella G. 1995. Sex economy in benthic polychaetes. *Ethology Ecology & Evolution* 7: 27–48. https://doi.org/10.1080/08927014.1995.9522968

Rambaut A. & Drummond A.J. 2003. *FigTree 1.1.2*. Available form http://tree.bio.ed.ac.uk/software/figtree/ [accessed 28 Mar. 2023].

Rambaut A., Drummond A.J., Xie D., Baele G. & Suchard M.A. 2018. Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology* 67: 901–904. https://doi.org/10.1093/sysbio/syy032

Ravara A., Wiklund H. & Cunha M.R. 2021. Four new species and further records of Dorvilleidae (Annelida, Polychaeta) from deep-sea organic substrata, NE Atlantic. *European Journal of Taxonomy* 736: 44–81. https://doi.org/10.5852/ejt.2021.736.1251

Read G. & Fauchald K. 2022. World Polychaeta Database. Dorvilleidae Chamberlin, 1919. Available from Accessed through: World Register of Marine Species. Available from https://www.marinespecies.org/aphia.php?p=taxdetails&id=971 [accessed 14 Jun. 2022].

Ronquist F., Teslenko M., van der Mark P., Ayres D.L., Darling A., Höhna S., Larget B., Liu L., Suchard M.A. & Huelsenbeck J.P. 2012. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539–542. https://doi.org/10.1093/sysbio/sys029

Rouse G.W., Pleijel F. & Tilic E. 2022. *Annelida*. Oxford University Press, London / New York. https://doi.org/10.1093/oso/9780199692309.001.000

Salcedo D.L., Soto L.A. & Paduan J.B. 2019. Trophic structure of the macrofauna associated to deep-vents of the southern Gulf of California: Pescadero Basin and Pescadero Transform Fault. *PloS One* 14: e0224698. https://doi.org/10.1371/journal.pone.0224698

Salvo F., Wiklund H., Dufour S.C., Hamoutene D., Pohle G. & Worsaae K. 2014. A new annelid species from whalebones in Greenland and aquaculture sites in Newfoundland: *Ophryotrocha cyclops*, sp. nov. (Eunicida: Dorvilleidae). *Zootaxa* 3887: 555–514. https://doi.org/10.11646/Zootaxa.3887.5.3

Solis Weiss V. & Hilbig B. 1992. Redescription of *Ophryotrocha platykephale* Blake (Polychaeta, Dorvilleidae) from the Guaymas Basin hydrothermal vents. *Bulletin of the Southern California Academy of Sciences* 91: 92–96.

Swofford D.L. 2002. *PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4*. Sinauer Associates, Sunderland, Massachusetts.

Taboada S., Bas M., Leiva C., Garriga M., Sarda R. & Avila C. 2016. Life after death: shallow-water Mediterranean invertebrate communities associated with mammal bones. *Marine Ecology – an Evolutionary Perspective* 37: 164–178. https://doi.org/10.1111/maec.12257

Taboada S., Wiklund H., Glover A.G., Dahlgren T.G., Cristobo J. & Avila C. 2013. Two new Antarctic *Ophryotrocha* (Annelida: Dorvilleidae) described from shallow-water whale bones. *Polar Biology* 36: 1031–1045. https://doi.org/10.1007/s00300-013-1326-4

Templeton A.R., Crandall K.A. & Sing C.F. 1992. A cladistic analysis of phenotypic associations with haplotypes inferred from restriction endonuclease mapping and DNA sequence data. III. Cladogram estimation. *Genetics* 132: 619–633. https://doi.org/10.1093/genetics/132.2.619

Thornhill D.J., Dahlgren T.G. & Halanych K.M. 2009. Evolution and Ecology of *Ophryotrocha* (Dorvilleidae, Eunicida). *In*: Shain D.H. (ed.) *Annelids in Modern Biology*: 242–256. Wiley & Blackwell.

Thornhill D.J., Struck T.H., Ebbe B., Lee R.W., Mendoza G.F., Levin L.A. & Halanych K.M. 2012. Adaptive radiation in extremophilic Dorvilleidae (Annelida): diversification of a single colonizer or multiple independent lineages? *Ecology and Evolution* 2: 1958–1970. https://doi.org/10.1002/ece3.314

Wang Z., Xu T., Zhang Y., Zhou Y., Liu Z., Chen C., Watanabe H.K. & Qiu J.-W. 2020. Molecular phylogenetic and morphological analyses of the ‘monospecific’ *Hesiolyra* (Annelida: Hesionidae) reveal two new species. *Deep Sea Research Part I: Oceanographic Research Papers* 166: 103401. https://doi.org/10.1016/j.dsr.2020.103401

Watanabe H. & Kojima S. 2015. Vent Fauna in the Okinawa Trough. *In*: Ishibashi J.-I., Okino K. & Sunamura M. (eds) *Subseafloor Biosphere Linked to Hydrothermal Systems: TAIGA Concept*: 449–459. Springer Japan, Tokyo.

Wiklund H., Altamira I.V., Glover A.G., Smith C.R., Baco A.R. & Dahlgren T.G. 2012. Systematics and biodiversity of *Ophryotrocha* (Annelida, Dorvilleidae) with descriptions of six new species from deep-sea whale-fall and wood-fall habitats in the north-east Pacific. *Systematics and Biodiversity* 10: 243–259. https://doi.org/10.1080/14772000.2012.693970

Wiklund H., Glover A.G. & Dahlgren T.G. 2009. Three new species of *Ophryotrocha* (Annelida: Dorvilleidae) from a whale-fall in the North-East Atlantic. *Zootaxa* 2228: 43–56. https://doi.org/10.11646/zootaxa.2228.1.3

Wiklund H., Purschke G. & Ravara A. 2021. 7.12.2 Dorvilleidae Chamberlin, 1919. *In*: Purschke G., Böggemann M. & Wilfried W. (eds) *Handbook of Zoology, Annelida Volume 1: Annelida Basal Groups and Pleistoannelida, Sedentaria III and Errantia I.*: 361–382.

Yen N.K. & Rouse G.W. 2020. Phylogeny, biogeography and systematics of Pacific vent, methane seep, and whale-fall *Parougia* (Dorvilleidae : Annelida), with eight new species. *Invertebrate Systematics* 34: 200. https://doi.org/10.1071/is19042

Zhang D., Zhou Y., Wang C. & Rouse G.W. 2017. A new species of *Ophryotrocha* (Annelida, Eunicida, Dorvilleidae) from hydrothermal vents on the Southwest Indian Ridge. *ZooKeys* 686:1–9. https://doi.org/10.3897/zookeys.687.13046

Zhou Y., Chen C., Sun Y., Watanabe H.K., Zhang R. & Wang C. 2019. *Amphisamytha* (Annelida: Ampharetidae) from Indian Ocean hydrothermal vents: Biogeographic implications. *Deep Sea Research Part I: Oceanographic Research Papers* 154: 103148. https://doi.org/10.1016/j.dsr.2019.103148

Zhou Y., Chen C., Zhang D., Wang Y., Watanabe H.K., Sun J., Bissessur D., Zhang R., Han Y., Sun D., Xu P., Lu B., Zhai H., Han X., Tao C., Qiu Z., Sun Y., Liu Z., Qiu J.-W. & Wang C. 2022. Delineating biogeographic regions in Indian Ocean deep-sea vents and implications for conservation. *Diversity & Distributions* 28: 2858–2870. https://doi.org/10.1111/ddi.13535

*Manuscript received: 6 October 2022*
*Manuscript accepted: 22 December 2022*
*Published on: 24 April 2023*
*Topic editor: Tony Robillard*
*Desk editor: Eva-Maria Levermann*

Zeitschrift/Journal: European Journal of Taxonomy

Jahr/Year: 2023

Band/Volume: 0864

Autor(en)/Author(s): Zhang Dongsheng, Zhou Yadong, Yen Nicole, Hiley Avery S., Rouse Greg W.

Artikel/Article: Ophryotrocha (Dorvilleidae, Polychaeta, Annelida) from deep-sea hydrothermal vents, with the description of five new species 167-194