Article

Laminatubus (Serpulidae, Annelida) from eastern Pacific hydrothermal vents and methane seeps, with description of two new species

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Abstract

The bathyal serpulid *Laminatubus alvini* ten Hove & Zibrowius, 1986 was described from the periphery of hydrothermal vents of the Galapagos Rift and has been recorded from other vent communities of the East Pacific Rise (EPR). Here we assessed the biodiversity of serpulids collected from eastern Pacific hydrothermal vents and methane seeps using DNA sequences and morphology. *Laminatubus alvini* showed little genetic variation over a wide geographic range from the Alarcon Rise vents in southern Gulf of California (~23°N), to at least a point at 38°S on the EPR. Specimens from several methane seeps off Costa Rica and the Gulf of California (Mexico) differed markedly from those of *Laminatubus alvini* on DNA sequence data and in having seven thoracic chaetigers and lacking *Spirobranchus*-type special collar chaetae, thus fitting the diagnosis of *Neovermilia*. However, phylogenetic analysis of molecular data showed that *L. alvini* and the seep specimens form a well-supported clade. Moreover, among the seep specimens there was minimally a ~7% distance in mitochondrial cytochrome b sequences between a shallow-water (1000 m) seep clade restricted to Costa Rica and a deep-water clade (1800 m) from Costa Rica to Gulf of California. We describe the seep taxa here as morphologically indistinguishable *L. paulbrooksi* **n. sp.** and *L. joycebrooksae* **n. sp.**

Key words: Cold seeps, Sabellida, *Neovermilia, Hyalopomatus*

Introduction

The biological communities associated with methane (= cold or hydrocarbon) seeps and hydrothermal vents have received considerable attention from deep-sea biologists owing to the unusual habitats involved, their novel biodiversity, and their complex interrelationships (Levin 2005). Many previously unknown species were described from these environments, among the most famous being the giant siboglinid annelid *Riftia pachyptila* Jones, 1981. Many other annelids are known from these habitats, including Ampharetidae, Amphinomidae, Dorvilleidae, and Aphroditiformia (Borda *et al.* 2013; Desbruyères & Segonzac 1997; Eilertsen *et al.* 2017; Hatch *et al.* 2020; McCowin & Rouse 2018a; Stiller *et al.* 2013; Zhang *et al.* 2017).

Two serpulids, *Protis hydrothermica* ten Hove & Zibrowius, 1986 and *Laminatubus alvini* ten Hove & Zibrowius, 1986 have been reported on the periphery of hydrothermal vent communities in the eastern Pacific (Desbruyères & Segonzac 1997; Micheli *et al.* 2002; Mullineaux & Manahan 1998; Mullineaux *et al.* 2009; Mullineaux *et al.* 2003). The latter species was originally described based on material from four hydrothermal vent areas collected via submersible on cruises to the Galapagos Rift (about 1°N at ~2400–2850 m depth) and along the East Pacific Rise (10°N, 13°N and 21°N at depths of 2500–2600 m), with the type locality selected at the Galapagos Rift. There were no genetic studies dedicated to population connectivity in this species and only six DNA sequences have been published under this name (Goffredi *et al.* 2017; Kupriyanova *et al.* 2006).

Even less is known about serpulids associated with methane seeps; to the point that more 'species' have been reported from fossil seeps than contemporary ones (Vinn *et al.* 2012). Juniper & Sibuet (1987) examined methane seep communities in Japan subduction zones and reported numerous serpulids attached to empty clam valves in Tenryu Canyon, the Nankai Trough (33°37'N, 13°032'E, 3830 m). Olu *et al.* (1996) found large and densely dis-

tributed serpulids identified as *Neovermilia* **n. sp.** (Helmut Zibrowius, pers. comm.) covering 200 m² in a methane seep community along the Peruvian active margin. In the Terevaka intra-transform ridge (off Easter Island) an assemblage of 'giant' serpulids covered hundreds of m² of the dyke-complex walls (Segonzac *et al.* 1997). Sibuet & Olu (1998) stated that similar serpulids apparently belonging to *Neovermilia*, have been reported from Nankai prism, Peru Trench, the Mexico Trench and the southern Barbados prism. López-González *et al.* (2003) also mention *Neovermilia* sp. (again *fide* Helmut Zibrowius) from a methane seep community in the eastern Pacific in the Middle American Trench off Manzanillo (Mexico), between 3354 and 3795 m.

Hydrothermal vents and methane seeps were considered separate environments until a hydrothermal vent-seep ecosystem was discovered at a base of a seamount within the Costa Rica subduction zone (Levin *et al.* 2012). While the site had classic vent organisms such as the mussel *Bathymodiolus thermophilus* Kenk & Wilson (McCowin *et al.* 2020), the fauna showed little overall overlap with the East Pacific Rise vents. Vestimentiferan tube worms (*Lamellibrachia barhami* Webb, 1969) and nearby rocks were covered with large serpulids that were preliminarily identified by the present authors (EKK and GWR) as a new species of *Neovermilia* (see Levin *et al.* 2012). Most recently additional *L. alvini* specimens were collected from hydrothermal vent and seep communities in the southern Gulf of California (Goffredi *et al.* 2017). Sequences of the 18S rRNA gene were used to report that *Laminatubus alvini* was present at Alarcon Rise vents at 2500m, while an undescribed *Laminatubus* sp. was present nearby at methane seeps in the Pescadero Basin (~2400 m) (Goffredi *et al.* 2017).

The present paper assesses the status of *Laminatubus* from eastern Pacific hydrothermal vents and methane seeps. We document *Laminatubus alvini* along the East Pacific Rise, describe two new species of *Laminatubus* from methane seeps, and discuss the relationships of the *Laminatubus* and *Neovermilia*.

Material and methods

Collecting and morphological observations

Sampling was conducted from 2005–2019 at multiple localities via the Deep Submergence Vehicle (DSV) *Alvin* (via R/V *Atlantis*) and the Remote Operated Vehicles (ROV) *Doc Ricketts* (via R/V *Western Flyer*) and *SuBastian* (via R/V *Falkor*) (Fig. 1). Specimens of *Laminatubus alvini* were collected along the East Pacific Rise (EPR) from 23°S to 37°S and the southern Gulf of California at northern end of the EPR in the Alarcon Rise vent field (~23°N) (Table 1). Specimens of other serpulids were collected during expeditions to methane seeps off Pacific coast of Costa Rica and the Pescadero and Guaymas Basins in the Gulf of California (Mexico) (Table 2). Serpulids were attached to rocks and siboglinid *Lamellibrachia* tubes. Museum samples of other serpulids were included as outgroups (see Table 2). Vouchers and types of the new species have been deposited in the Scripps Institution of Oceanography Benthic Invertebrate Collection (**SIO**), La Jolla, California, USA, Museo de Zoología (Universidad de Costa Rica), San José, Costa Rica (**MZUCR**), Australian Museum (**AM**), Sydney, and South Australian Museum, Adelaide (**SAM**). One specimen deposited at the Field Museum of Natural History (**FMNH**) was collected at ~9°N of the East Pacific Rise. A specimen from ~12°N deposited at **AM** has been also examined.

Specimens were photographed alive shipboard with a Canon SLR camera mounted on a Leica S8Apo or MZ9.5 stereomicroscopes or a Canon SLR with 100 mm macro lens. Tissue samples were taken from abdomens of freshly collected specimens and fixed in 95% ethanol. Specimens for morphological study were fixed in 10% seawater-formaldehyde and then preserved in 70% ethanol after rinsing, with the abdomen tip usually sampled into 95% ethanol. Preserved specimens were viewed and measured under a dissecting microscope using an ocular micrometer at **AM** or **SIO**. For comparative purposes, we examined the holotype of *Neovermilia globula* (Dew, 1959) from **AM**) and a specimen of *N.* cf. *sphaeropomata* (Benham, 1927) deposited in **AM** and collected from the Great Australian Bight (GAB). To examine the details of chaetae and uncini, specimens were prepared for scanning electron microscopy (SEM) observations. The specimens were dehydrated in ethanol series, critical point dried, coated with 20 nm of gold, and examined under JEOL JSM-6480 at Macquarie University, Sydney. For descriptions we follow the morphological terminology of ten Hove & Kupriyanova (2009).

DNA extraction, amplifications, and sequencing

Molecular analyses were done at **AM** and **SIO**. At **AM**, before the extractions, ethanol was removed by washing tissues preserved in 95% ethanol three times in 0.5 ml of TE buffer. Total DNA extraction was performed using

a Bioline Isolate II genomic DNA kit following the manufacturer's protocols. Stock DNA was diluted 1:10 or 1:100 with deionized water to produce template strength DNA for Polymerase Chain Reactions (PCR). Partial or near complete 18S rRNA gene (18S) sequences were amplified in two overlapping fragments, one of approximately 1100 bp with the primers TimA (AMC TGG TTG ATC CTG CCA G) and 1100R2 (CGGTATCTGATCGTCTTCGA) from Nøren & Jordelius (2002); the other of approximately 1300 bp using 18s2F (GTTGCT GCAGTTAAA) and 18s2R (3' ACCTTGTTAGCTGTTTTACTTCCTC) (Kupriyanova *et al.* 2006). An approximately 350 bp fragment of Histone H3 (H3) gene was amplified with the primers from Brown *et al.* (1999): (1) ATG GCT CGT ACC AAG CAG ACV GC and ATA TCC TTR GGC ATR ATR GTG AC or (2) ATG GCT CGT ACC AAG CAG AC and ATR TCC TTG GGC ATG ATT GTT AC. A part (approximately 350 bp) of the mitochondrial Cytochrome b (CytB) was amplified with the primer pair Cytb424F GGWTAYGTWYTWCCWTGRGGWCARAT and cobr825 AARTAY-CAYTCYGGYTTRATRTG (Burnette *et al.* 2005).
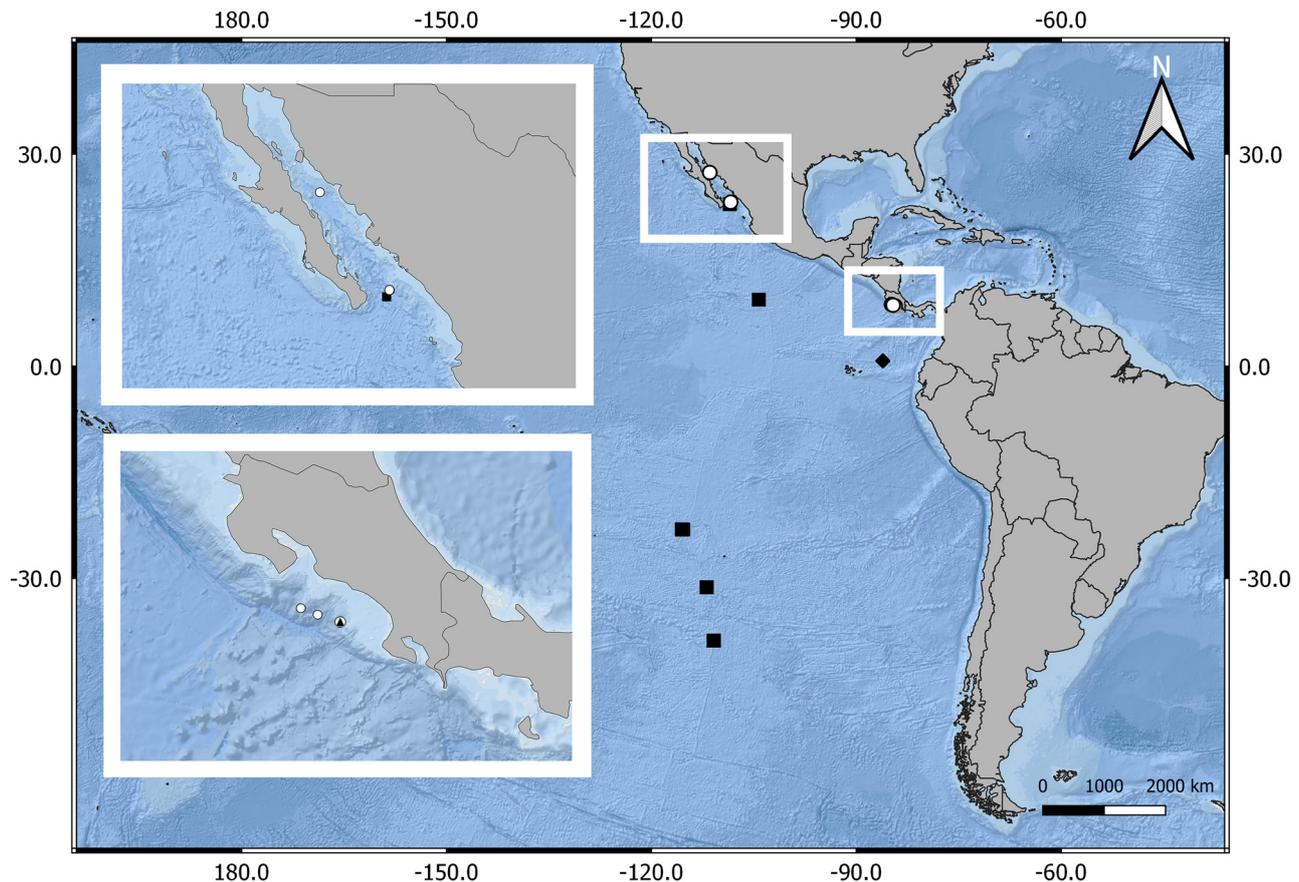

FIGURE 1. Distribution of *Laminatubus* spp. in East Pacific. Black square (*L. alvini*), white circles (*L. paulbrooksi* **n. sp.**) and grey triangle (*L. joycebrooksae* **n. sp.**). A black diamond is the type locality of *L. alvini* on the Galapagos Rift.

Polymerase chain reactions were conducted in a Thermal Cycler GenAmp PCR System 9700 (Applied Biosystems) under the following conditions: an initial denaturation step at 94°C for 3 min (18S and CytB), 40 cycles at 94°C for 30 s (18S) respectively 45 cycles at 94°C for 1 min (CytB), 52°C for 30 s (18S) respectively 50°C for 30 s (CytB), 72°C for 30 s (18 S) respectively 72°C for 1 min (CytB), with a final extension at 72°C for 5 min (18S) respectively 8 min. The reaction mix (total reaction volume 20 μl) included: 13.1 μl water of H_2O, 2 μl Coral Load Qiagen PCR buffer, 1.5 μl dNTPs, 0.4 μl of each primer (forward and reverse), 1.5 μl $MgCl_2$, 0.1 μl MyTaq DNA Polymerase Bioline, and 1 μl of template DNA. PCR products were separated by TBE gel electrophoresis in 1.5% agarose gel and visualized under UV a Bio-Rad XR+ Gel Documentation System. Amplification products were purified and sequenced in both directions using the same primers as in PCR by Macrogen TM, South Korea. Sequences were assembled and edited using Codon Code Aligner.

At **SIO**, total DNA was extracted from organisms fixed in 95% ethanol using the ZR Genomic DNA -Tissue MiniPrep kit following manufacturer's instructions. 18S rRNA was amplified using Lambda Conquest PCR mastermix (Lambda Biotech) following the manufacturer protocol in three overlapping fragments with the primer pairs

(1) 1F (5'-TAC CTG GTT GAT CCT GCC AGT AG-3') and 5R (5'-CTT GCC AAA TGC TTT CGC-3') (950 bp); (2) 3F (5'-GTT CGA TTC CGG AGA GGG A-3') and bi (5'-GAG TCT CGT TCG TTA TCG GA-3') (900 bp); (3) A.20 (5'-ATG GTT GCA AAG CTG AAA C-3') and 9R (5'-GAT CCT TCC GCA GGT TCA CCT AC-3') (850 bp) with the following reaction profile 95ºC for 180s, 40 cycles of 95ºC for 30s, 50ºC for 30s, and 72 ºC for 90s, and finally 72ºC for 480s (Giribet *et al.* 1996). Amplifying CytB and H3 was done with the same parameters as at **AM**. PCR products were purified with ExoSAP-IT (GE Healthcare, Uppsala, Sweden) and sequenced by Eurofins Inc. using Applied Biosystems (ABI) 3730xl DNA analyzers. Overlapping sequence fragments were assembled using Geneious version R8 (Biomatters).

Sequence analyses

The concatenated sequences were aligned with Q-INS-i option of MAFFT 7 (Katoh & Standley 2013). They were analysed using maximum likelihood with 10 iterations and thorough bootstrapping conducted via RAxML 8 (Stamatakis 2014) under the GTR+G substitution model. Node support was assessed via thorough bootstrapping (1000 pseudoreplicates). Sequences of the serpulids *Hyalopomatus mironovi* Kupriyanova, 1993 and *H. biformis* (Hartman, 1960) were included as outgroups based on Kupriyanova & Nishi (2010), Kupriyanova *et al.* (2010), and Kupriyanova *et al.* in prep. We also included new data for *Neovermilia* cf. *sphaeropomata* and *N. globula* as terminals since we had proposed the new methane seep species as *Neovermilia* in Levin *et al.* (2012).

Haplotype networks using the CytB data were generated for *L. alvini* and a combined *L. joycebrooksae* **n. sp.** and *L. paulbrooksi* **n. sp.** with PopART v.1.7 (Leigh & Bryant 2015) using the median-joining option (Bandelt *et al.* 1999) with epsilon set at 0. Uncorrected pairwise distances were calculated for the CytB dataset using PAUP* (Swofford 2002) and CytB was also used to assess species delimitation with Automatic Barcoding Gap Discovery (ABGD) (Puillandre *et al.* 2012) with the following settings: p_{min}=0.001, p_{max}=0.1, Steps=20, X=1.5, Nb bins=20. ABGD analysis was conducted with uncorrected and Kimura (K80) model-corrected distance (with TS/TV= 7.5) following assessment of the combined *L. joycebrooksae* **n. sp.** and *L. paulbrooksi* **n. sp.** with jModelTest2 (Darriba *et al.* 2012).

Molecular results

The maximum likelihood analysis of the combined molecular data (Fig. 2) showed that the EPR hydrothermal vent specimens from 23°N to 38°S formed a well-supported clade with other sequences previously published as *Laminatubus alvini*. There was very little substructure within the *L. alvini* clade, even though the samples were collected from across ~7000 km. An 18S sequence previously published as *Hyalopomatus biformis* by Kupriyanova & Nishi (2010) was also recovered as nested within *L. alvini* rather than with the other included *Hyalopomatus* terminals. *Laminatubus alvini* was the sister group to a clade of most of the seep specimens collected for this study, ranging from Costa Rica to the Gulf of California (Mexico) and we regard these to also be referrable to *Laminatubus* rather than to *Neovermilia,* as previously proposed by us in Levin *et al*. (2012). The outgroups could be used to root the tree in several ways resulting in either *Hyalopomatus* or *Neovermilia* as closer to *Laminatubus*, but we show the third alternative of *Hyalopomatus* and *Neovermilia* as a clade that was sister group to *Laminatubus*, pending more detailed studies across Serpulidae. Two of the specimens from the seeps, one from Jaco Scar (Costa Rica) and the other from the Guaymas Basin (Mexico), did not group with the seep *Laminatubus* specimens but were instead part of the *Hyalopomatus* clade and these require further study. The two terminals of *Hyalopomatus mironovi*, one previously published from vents off Fiji and one newly sequenced from the type locality, did not form a single clade.

The seep-dwelling *Laminatubus* formed two major subclades that sorted on geography and/or depth. One well-supported major clade was restricted to Costa Rica at ~1000 meters and was the sister group to the remaining seep *Laminatubus* that were all from 1400 meters or greater in depth, most of them from 1800 meters or greater. This second major clade from deeper-dwelling specimens ranged from the Guaymas and Pescadero Basins (Mexico) to Costa Rica and did sort into clades based on this geographical distribution, but each with poor support.

We explored the relationships of the seep-dwelling *Laminatubus* further using the most variable gene, mitochondrial CytB, with pairwise distances, haplotype networks and species delimitation plots (ABGD). jModeltest (using BIC) recommended HKY as the appropriate model for the CytB data for the seep-dwelling *Laminatubus* samples, with ti/tv= 7.6. Unlike the CytB haplotype network for *L. alvini*, which showed only two haplotypes from 23°N to

38°S (Fig. 3), the seep *Laminatubus* showed much more variation, with 14 haplotypes (Fig. 4). There was a clear break between the Costa Rica ~1000 m (Mound 12) specimens and the rest, which represented a 6.4%–8.5% uncorrected distance (6.9–9.5% HKY-corrected). The pairwise distance between the Mound 12 Costa specimens and the deep-water ones (Jaco Scar and Parrita Seep) was at least 7.6% (uncorrected; 8.3% HKY-corrected), even though they are physically separated by less than 100 km. Within the deeper clade of seep-dwelling *Laminatubus*, extending from Mexico to Costa Rica, there was a maximum distance of 4.9% (uncorrected; 5.1% HKY-corrected). The plot of the pairwise distances using ABGD (using the Kimura K80 model since HKY is not implemented) showed the break between the 1000 m specimens and the deep-water ones in another way (Fig. 5), with the normally expected peak of small distances followed by several others that represent the pairwise distances among the Guaymas, Pescadero and deep Costa Rica clades. The fourth peak represents the distances between the 1000 m Costa Rica clade and the deeper water specimens. Based on these analyses we apply two species level taxa, *Laminatubus joycebrooksae* **n. sp.** for the clade restricted to Mound 12 at 1000 m (Costa Rica) and *Laminatubus paulbrooksi* **n. sp.** for the more widespread and deeper-dwelling clade. These new taxa are described below.

Discussion

This is the first study examining genetic diversity within *Laminatubus*. The previously proposed range of *L. alvini* over 6000 km along the East Pacific Rise (EPR) from 23°N to 32°S is supported here (e.g. Desbruyères *et al.* 2006; Hey *et al.* 2006), with a further range extension to nearly 38°S. We could not confirm the listing by Tunnicliffe *et al.* (1998) of *L. alvini* at the Guaymas Basin sedimented vents at 27° N, as we had no samples for DNA sequencing from this site. We did have samples from nearby seeps, and these represent *L. paulbrooksi* **n. sp.** Unfortunately, there is no DNA data for *L. alvini* from the type locality of the Galapagos Rift hydrothermal vents (ten Hove & Zibrowius 1986), so we cannot be unequivocally certain that the EPR *Laminatubus* are in fact *L. alvini*. However, DNA studies of other annelids and other animals that occur along the EPR and the Galapagos Rift show that the same species are often found in both places (Borda *et al.* 2013; Hurtado *et al.* 2004; Johnson *et al.* 2013; Stiller *et al.* 2013) and it is a reasonable hypothesis that *L. alvini* is widespread at eastern Pacific vents. Interestingly, *Laminatubus alvini* showed little mitochondrial haplotype variation over the sampled geographic range (Fig. 3), with one of the two haplotypes found from 23°N to 38°S. This low haplotype variability was markedly different to *Laminatubus paulbrooksi* **n. sp.**, which was sampled over a much smaller geographic range (Fig. 4), but is similar to that reported for the vestimentiferan siboglinid *Riftia pachyptila* (Hurtado *et al.* 2004) and suggests larvae that disperse widely. Details on reproduction and dispersal in these species are not known, but the egg size of both *L. alvini* and *L. joycebrooksae* **n. sp.** was measured, and the diameter of 150 μm suggests lecithotrophic development.

The sister group to *L. alvini* was found to be a collection of serpulids from methane seeps off the Pacific coast of Costa Rica and the Gulf of California (Mexico). There were two clear clades of these seep-dwellers that we name here as new species; *L. joycebrooksae* **n. sp.** and *L. paulbrooksi* **n. sp.** *Laminatubus joycebrooksae* **n. sp.** was only found at one site (~1000 m, Mound 12, Costa Rica) and was minimally 6.4% distant to *L. paulbrooksi* **n. sp.** on CytB. This is a relatively small genetic distance compared to recent studies on other serpulids (e.g., Halt *et al.* 2009), but is not unusual relative to other annelids (Nygren 2013). The bathymetric isolation of *L. joycebrooksae* **n. sp.** relative to *L. paulbrooksi* **n. sp.** has also been seen in other taxa at the Costa Rica seeps and the 1000 m site seems to be somewhat unique with regard to endemic taxa. The most famous is the yeti crab *Kiwa puravida* Thurber, Jones & Schnabel, 2011, which is also only known at Mounds 11 and 12 (Thurber *et al.* 2011). There are three species of *Bathymodiolus* mussel at the seeps and one of them is restricted to the ~1000 m sites (McCowin *et al.* 2020). Similarly, there are two species of *Lamellibrachia*, but *Lamellibrachia donwalshi* McCowin & Rouse 2018b is only known from ~1000 m (McCowin & Rouse 2018b). In contrast to *Laminatubus joycebrooksae* **n. sp.**, *L. paulbrooksi* **n. sp.** was always found at deeper sites, but also had a much wider geographic range, from Costa Rica to the Gulf of California (Mexico). It was found at seeps near the vents where *L. alvini* was found, but there appears to have been no overlap between the two taxa.

Two specimens from seeps in Mexico (Guaymas Basin) and Costa Rica (Jaco Scar) recovered with the *Hyalopomatus* terminals (Fig. 2) require further study, as they may represent two new species. A previously published 18S sequence, as *Hyalopomatus biformis,* by Kupriyanova & Nishi (2010), from a seamount off Alaska, was recovered as nested among the *Laminatubus alvini* sequences rather than with the other *Hyalopomatus* sequences.
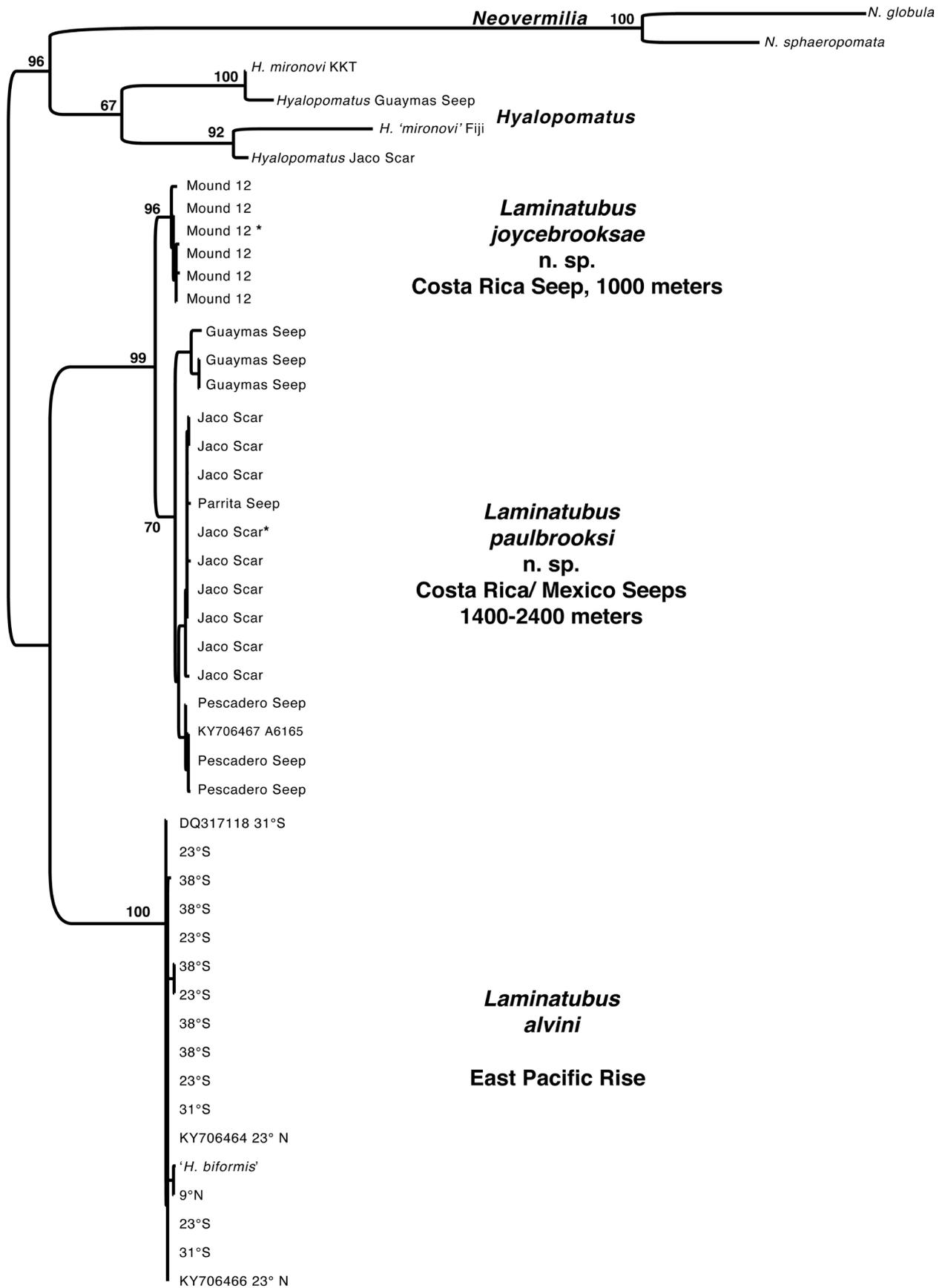
FIGURE 2. Maximum likelihood (ML) tree from the analysis of the combined sequences from CytB, 18S, and Histone H3. Numbers on nodes are those bootstrap scores above 50%. * indicates the holotypes for *L. paulbrooksi* **n. sp.** and *L. joycebrooksae* **n. sp.** respectively.
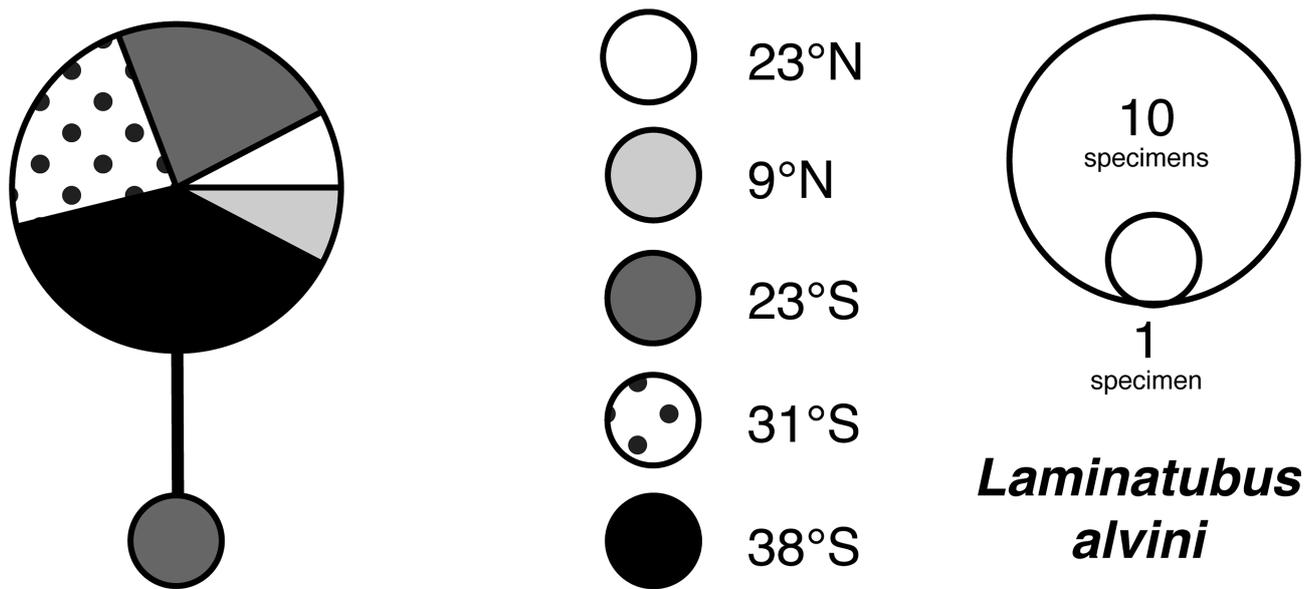
FIGURE 3. Haplotype networks from CytB data for *Laminatubus alvini* from an extensive section of the East Pacific Rise from 23°N to 38°S, over 7000 km. Only two haplotypes were found.
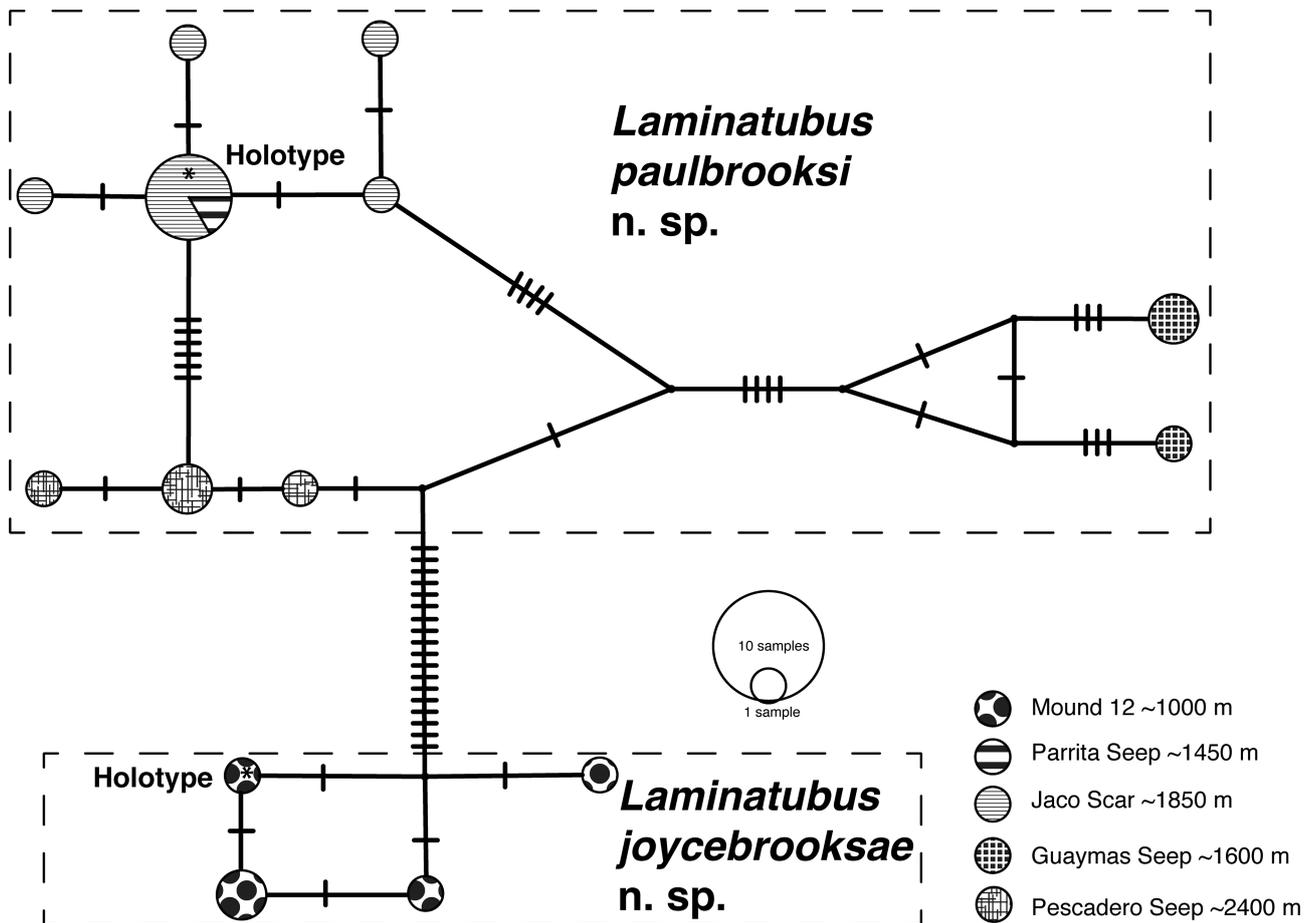

FIGURE 4. Combined haplotype networks from CytB data for *Laminatubus paulbrooksi* **n. sp.** (top) from Pacific Costa Rica margin and Gulf of California (Mexico) localities and *L. joycebrooksae* **n. sp.** (bottom) from Costa Rica. There was little variability among the *L. joycebrooksae* **n. sp.** sequences and a distinct break to *L. paulbrooksi* **n. sp.** This corresponds to a minimum 6.4% uncorrected distance. *Laminatubus paulbrooksi* **n. sp.** showed marked intraspecific variability with distinct breaks among the three main sites; Costa Rica (9°N), Pescadero (23°N) and Guaymas Basin (27°N). * indicates the holotypes for *L. paulbrooksi* **n. sp**. and *L. joycebrooksae* **n. sp.** respectively.

This suggests that this sequence is mislabeled, though further investigation is required. Also, the new 18S sequence included here for *Hyalopomatus mironovi* from the type locality in the Kuril–Kamchatka Trench did not group with the previously published 18S sequence (Kupriyanova *et al.* 2010) of *H. mironovi* from a hydrothermal vent off Fiji. This suggests that the Fiji specimen may be a new species of *Hyalopomatus*.
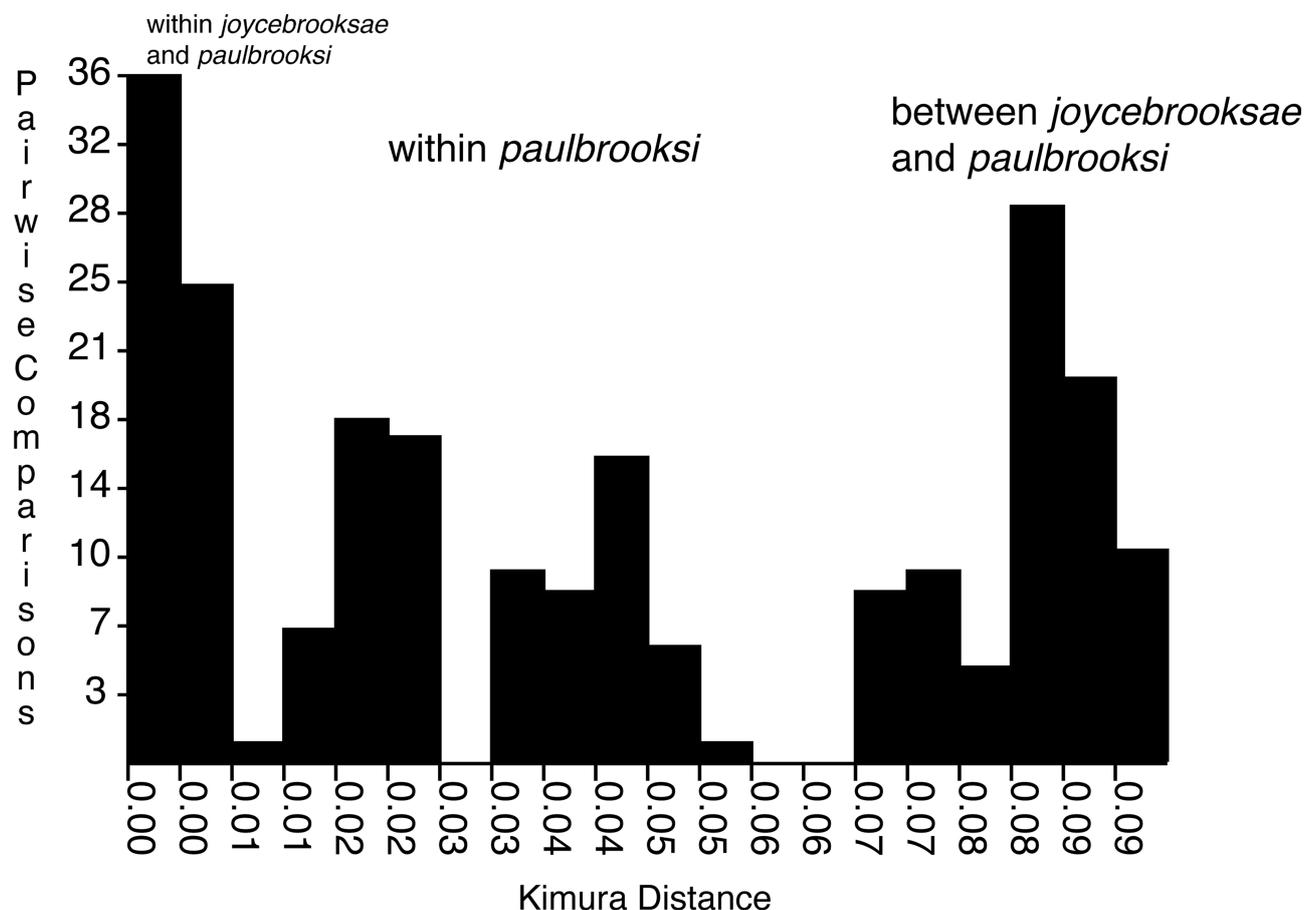

FIGURE 5. Plot using ABGD (Puillandre *et al.* 2012) of pairwise distances across all *Laminatubus joycebrooksae* **n. sp.** and *L. paulbrooksi* **n. sp.** CytB sequences using the Kimura (K80) model. There is a clear 'barcode' gap between *L. joycebrooksae* **n. sp.** and *L. paulbrooksi* **n. sp.** with the latter taxon showing a high level of intraspecific variation. Uncorrected pairwise distances gave a similar distribution.

Taxonomy

Serpulidae Rafinesque, 1915

Laminatubus **ten Hove & Zibrowius, 1986 (emended)**

Type-species: *Laminatubus alvini* ten Hove & Zibrowius, 1986

Diagnosis. Tube white, with keel, granular overlay absent, hyaline outer layers may be present. Operculum globular, semitransparent or divided into proximal ampulla and distinct endplate made of thickened yellowish cuticle. Peduncle cylindrical, gradually merging into opercular ampulla, constriction absent; inserted to left side, proximal from first and second normal radiole. Pseudoperculum absent. Radioles not connected by inter-radiolar membrane, arranged into slightly ascending spiral of up to two whorls. Stylodes and radiolar eyes absent. Mouth palps absent. Six or seven thoracic chaetigerous segments. Collar with medio-ventral and two latero-dorsal lobes, continuous with thoracic membranes, forming apron. Tonguelets absent. Collar chaetae simple limbate or *Spirobranchus*-type and limbate. *Apomatus* chaetae absent. All uncini saw-shaped with 5–7 teeth, anterior fang simple pointed. Thoracic

tori converging posteriorly, forming triangular depression. Abdominal chaetae long, with hollow trumpet-shaped tip. Posterior abdominal chaetae become longer, but posterior capillary chaetae absent. Achaetous anterior abdominal zone absent. Posterior glandular pad absent.

Remarks. Until now *Laminatubus* was monotypic and the diagnosis has been emended here to account for the presence of variable number (six or seven) thoracic chaetigerous segments as well as variability in the presence of *Spirobranchus*-type collar chaetae. This is to allow for features found in the two new species described here. *Laminatubus* was erected by ten Hove & Zibrowius (1986), who did not do any phylogenetic analysis and decided that, based on a unique combination of characters, *L. alvini* did not fit in with any existing genera at the time. A comparative table in ten Hove & Zibrowius (1986) included *Laminatutus* and 11 genera where *L. alvini* potentially belonged. Of these, *Laminatubus alvini* was most similar to *Neovermilia* as the two taxa share a chaetation pattern (including true trumpet-shaped abdominal chaetae, saw-shaped uncini with few teeth and pointed fangs, and lack of 'Apomatus chaetae'), a similar globular operculum, and a long thoracic membrane forming an apron. However, *Neovermilia* is problematic and unlikely to be monophyletic as was suggested by ten Hove & Kupriyanova (2009). It was established by Day (1961) for *N. capensis,* a single specimen without a tube dredged from 18 m off Cape Province, South Africa. According to Day (1961: page 551), the new taxon has "characters intermediate between *Serpula* and *Vermiliopsis*", the operculum "is borne on a slender triangular peduncle without wings, is radially symmetrical, soft and funnel-shaped". Thus, while the table of ten Hove & Zibrowius (1986) listed the presence of peduncular ledges (= winglets) in *Neovermilia* as a character separating it from *Laminatubus,* based on Day (1967: fig. 38.6a), this feature is absent in *N. sphaeropomata*. While presence of seven thoracic chaetigers and lack of *Spirobranchus*-type special collar chaetae indicates the two new *Laminatubus* species belong with *Neovermilia*, these characters are somewhat labile. A broader phylogenetic analysis with denser taxon sampling is required to resolve the relationships and status of *Laminatubus* and *Neovermilia* and we presently regard *Laminatubus* as a valid taxon. It remains unclear whether species reported as *Neovermilia* **n. sp.** as identified by H. Zibrowius from Middle American Trench off Manzanillo in Mexico and cold seeps in Nankai prism of Peru Trench, Peruvian active margin and Terevaka intra-transform ridge off Easter Island, Chile (in Sibuet & Olu 1998) belong to *Laminatubus*.

Laminatubus alvini ten Hove & Zibrowius, 1986
Figures 6–8

Laminatubus alvini ten Hove & Zibrowius, 1986 (description, line drawings, photo of tube, SEM of tube ultrastructure).
Laminatubus alvini.—Tunnicliffe (1992) (distribution Galapagos; East Pacific Rise: 13°N to 21°N); Desbruyères & Segonzac (1997) (diagnosis, figures, distribution Galapagos; East Pacific Rise: 21°N to 23°S); Mullineaux & Manahan (1998) (photo of colony *in situ*); Mullineaux *et al.* (1998) (recruitment at 9°50′N vent localities); Tunnicliffe *et al.* (1998) (biogeography: Guaymas vents 27°N, EPR at 21°N, Galapagos); Michelli *et al.* (2002) (9°50′N vent localities, ecology); Mullineaux *et al.* 2003 (9°50′N vent localities, succession); Desbruyères *et al.* (2006) (diagnosis, figures, distribution Galapagos; East Pacific Rise: 21°N to 23°S); Hey *et al.* (2006) (name and photo, 31°S and 32°S vent localities); Kupriyanova *et al.* (2006) (phylogeny, morphology and DNA; specimen from 31°S); Vinn *et al.* (2008) (tube ultrastructure and mineral composition; specimen from 9°N); ten Hove & Kupriyanova (2009) (diagnosis, SEM of chaetae from Galapagos Rift specimen); Mullineaux *et al.* (2009) (9°50′N vent localities, ecology; Goffredi *et al.* (2017) (DNA; two specimens from 23°N vent).

Material examined. AM: W.38421, 12°50'N, 103°57'W, Jeanie Site, 2010 Mescal cruise; W.49888, W.49956–499562; W.49961 and W.38421 prepared for SEM**; SAM**: E5851–E5879; **SIO-BIC**: A8568–8579 (see Table 1 for localities and measurement). **FMNH**: 7045; **SAM**: 1717, E3531; **SIO-BIC**: A1654, A1658, A1660, A1662, A1668, A1670, A6158, A6327 (see Tables 1 and 2 for localities and GenBank accession numbers).

Description. TUBE: white opaque, semi-circular to circular in cross-section, without wide flaring peristomes, growth rings indistinct, attached to the substrate throughout its length. High, sharp, undulating longitudinal keel and distinct solid flattened attachment flange lacking alveoli present (Fig. 6A, B, 7A). External hyaline layer present.

RADIOLAR CROWN: Radioles not connected by inter-radiolar membrane (Fig. 7C, D, E), arranged into slightly ascending spiral of up to two whorls. Stylodes and radiolar eyes absent.

PEDUNCLE: smooth cylindrical (circular in cross-section), at least twice as thick as normal radioles (Fig. 7C–E), gradually merging into opercular ampulla, constriction absent (Fig. 7B, C). Small distal latero-dorsal "winglets" (flattened distal parts of the peduncle) or pair of lateral wings proximal to opercular ampulla absent. Peduncle inserted on left side of radiolar crown, below line of radioles (Fig. 7C, D, E).
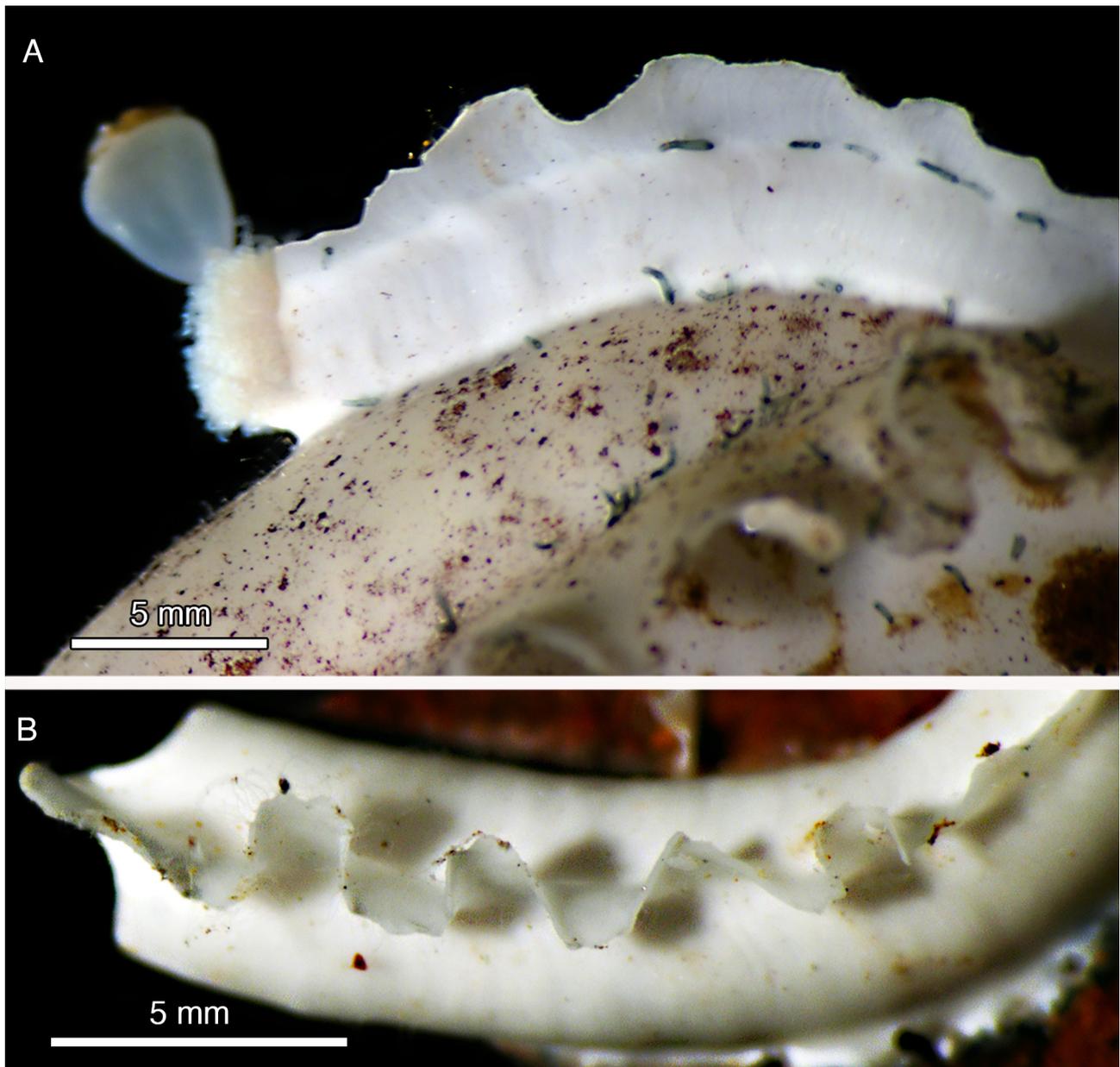
FIGURE 6. Photos of *Laminatubus alvini* tubes, *Alvin* dive 4091. A—lateral view, B—dorsal view.

OPERCULUM: bulbous to inverted conical proximal semi-transparent ampulla with distinct distal flattened to convex or pointed yellowish-brownish endplate covered with thickened cuticle (Fig. 7A–C).

COLLAR AND THORACIC MEMBRANES: collar high, covering bases of radiolar lobes, clearly trilobed, with longer and wider ventral lobe and smaller lateral ones (Fig. 8A) and entire edge (Fig. 7D, E, 8A), continuous with thoracic membranes as wide as thoracic tori, forming apron across anterior abdominal chaetigers (Figs 7E, 8A). Pairs of small, wart-like protuberances of collar chaetiger or elongated tonguelets between ventral and lateral collar parts absent.

THORAX: with collar chaetiger and five uncinigerous chaetigers (Fig. 7E), fascicle of collar chaetae separated from first uncinigerous chaetiger by a wide gap (Fig. 8A). Thoracic tori of approximately same length, gradually converging posteriorly, forming distinct triangular depression (Fig. 8A, C), but not touching each other medio-ventrally (Fig. 8C). Collar chaetae fascicle with limbate and poorly developed *Spirobranchus*-type chaetae or special chaetae absent altogether (Fig. 8B). Subsequent thoracic chaetae simple limbate, of two sizes, *Apomatus* chaetae absent (Fig. 8D). Uncini along entire thorax saw-shaped with 5–6 teeth, anterior fang simple pointed (Fig. 8F). Pair of prostomial eyes absent.
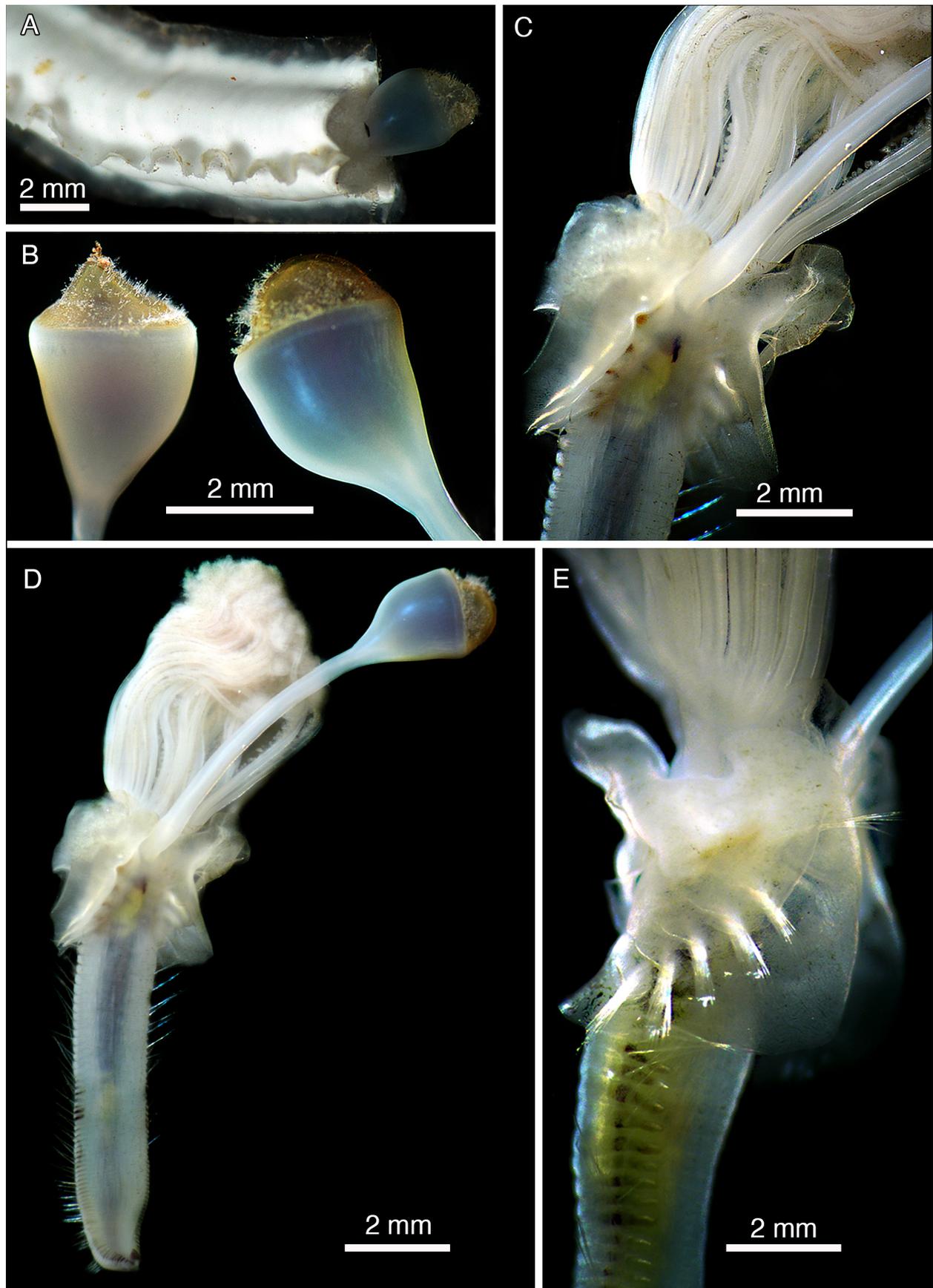
FIGURE 7. Photos of *Laminatubus alvini* specimens, *Alvin* dive 4094. A, B—variability of opercula, C—view of the thorax showing insertion of peduncle, D—dorsal view of an entire specimen removed from tube, E—lateral view of thorax.
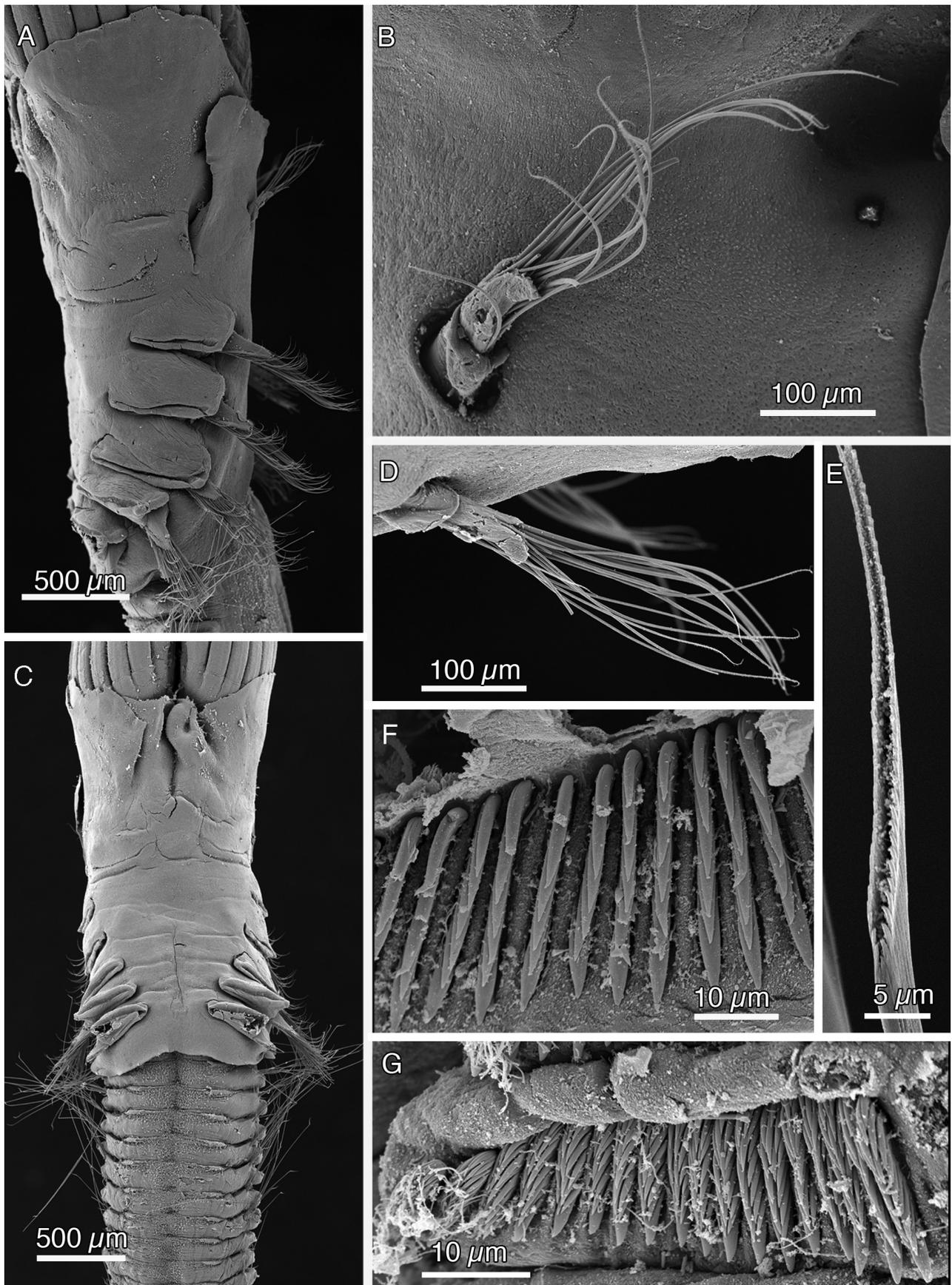
FIGURE 8. SEM of *Laminatubus alvini* AM W.38421 body and chaetae. A—lateral view of thorax, B– collar chaetae, C—ventral view of thorax, D—chaetae of the second thoracic chaetiger, E—anterior abdominal chaetae, details of hollow tip, F—anterior thoracic uncini, G—anterior abdominal uncini.

ABDOMEN: with up to 120 abdominal chaetigers. Achaetous anterior abdominal zone absent, distinct chaetae with long shaft (length similar to that of thoracic tori) starting from first abdominal segment. Tips of chaetae slightly bent and hollow, made of two rows of pointed teeth, thus true trumpet-shaped chaetae (Fig. 8E). Posterior capillary chaetae absent. Uncini saw-shaped anteriorly, with pointed fangs and 5–7 teeth, similar to thoracic ones; posterior-most uncini rasp-shaped with 3–4 rows of teeth, bluntly pointed fang and 7–8 teeth in profile view (Fig. 8G). Posterior glandular pad absent (Fig. 7C).

SIZE: length up to 29 mm (5.2–29 mm, Table 1). Radioles and operculum accounting for 2/5 of entire animal length.

TABLE 1. Specimens of *Laminatubus alvini* examined. Abbreviations: P—peduncle (=radiolar length), Th—thorax, A-abdomen, R—radioles. Length of complete specimens only is reported in the text.

Catalogue number	Length, mm	*Alvin* Dive	Coordinates	Depth, meters
AM W.49888	P7, Th2, A4	A4091	37°40.351S ,110°52.617W	2236
AM W.49956	P5.5, Th1.5, A3	A4091	37°40.351S, 110°52.617W	2236
AM W.49957	P11, Th3.5, A-	A4091	37°40.351S, 110°52.617W	2236
AM W.49958	P12, Th2, A-	A4094	31°0939S, 111°55.919W	2237
AM W.49959	P11, Th3.5, A9.5	A4094	31°0939S, 111°55.919W	2237
AM W.49960	P11, Th2.5, A-	A4096	23°32.780S, 115°34.179W	2595
AM W.49961	P11, TH3.5, A8.5	A4096	23°32.780S, 115°34.179W	2595
AM W.49962	P11, Th2.5, A9	A4096	23°32.780S, 115°34.179W	2595
SAM E5851	P8, Th2.5, A-	A4096	23°32.780S, 115°34.179W	2595
SAM E5852	P8, Th3, A6	A4096	23°32.780S, 115°34.179W	2595
SAM E5853	P11, Th2, A-	A4096	23°32.780S, 115°34.179W	2595
SAM E5854	P7, Th2, A3	A4096	23°32.780S, 115°34.179W	2595
SAM E5855	P6.5, Th1.5, A3	A4091	37°40.351S, 110°52.617W	2236
SAM E5856	P-, Th2, A6.5	A4091	37°40.351S, 110°52.617W	2236
SAM E5857	P3, Th1, A2	A4091	37°40.351S, 110°52.617W	2236
SAM E5858	P3, Th0.7, A1.5	A4091	37°40.351S, 110°52.617W	2236
SAM E5859	P3, Th1.5, A-	A4091	37°40.351S, 110°52.617W	2236
SAM E5860	P6, Th1, A-	A4091	37°40.351S, 110°52.617W	2236
SAM E5861	P3, Th0.6, A-	A4091	37°40.351S, 110°52.617W	2236
SAM E5862	P6, Th-, A-	A4091	37°40.351S, 110°52.617W	2236
SAM E5863	P4, Th1, A2.5	A4091	37°40.351S, 110°52.617W	2236
SAM E5864	P6, Th1, A4	A4094	31°0939S, 111°55.919W	2237
SAM E5865	P6, Th2, A-	A4096	23°32.780S, 115°34.179W	2595
SAM E5866	P4, Th1.5, A2.5	A4096	23°32.780S, 115°34.179W	2595
SAM E5867	P9	A4096	23°32.780S, 115°34.179W	2595
SAM E5868	P -, Th1.5, A2.5	A4096	23°32.780S, 115°34.179W	2595
SAM E5869	P4.5, Th1, A3	A4096	23°32.780S, 115°34.179W	2595
SAM E5870	P11, Th3, A-	A4096	23°32.780S, 115°34.179W	2595
SAM E5871	R6, Th3, A-	A4096	23°32.780S, 115°34.179W	2595
SAM E5872	P6, Th1.5, A3	A4091	37°40.351S, 110°52.617W	2236
SAM E5873	P9, Th4, A-	A4096	23°32.780S, 115°34.179W	2595
SAM E5874	P9, Th2, A7	A4096	23°32.780S, 115°34.179W	2595
SAM E5875	P6.5, Th1.5, A4.5	A4096	23°32.780S, 115°34.179W	2595
SAM E5876	P6, Th1, A3	A4096	23°32.780S, 115°34.179W	2595
SAM E5877	P6.5, Th1, A3	A4096	23°32.780S, 115°34.179W	2595

TABLE 1. (Continued)

Catalogue number	Length, mm	*Alvin* Dive	Coordinates	Depth, meters
SAM E5878	P7, Th3, A5.5	A4096	23°32.780S, 115°34.179W	2595
SAM E5879	P9, Th2.5, A-	A4096	23°32.780S, 115°34.179W	2595
SIO-BIC A8568	P8, Th2, A-	A4091	37°40.351S, 110°52.617W	2236
SIO-BIC A8569	P7, Th2, A5.5	A4091	37°40.351S, 110°52.617W	2236
SIO-BIC A8570	P12, Th4, A13	A4091	37°40.351S, 110°52.617W	2236
SIO-BIC A8571	P1, Th1, A3, A-	A4092	31°51.789S, 112°02.534W	2334
SIO-BIC A8572	P9, Th2.5, A3.5	A4094	31°0939S, 111°55.919W	2237
SIO-BIC A8573	P7, Th2, A5	A4094	31°0939S, 111°55.919W	2237
SIO-BIC A8574	P6, Th2, A7	A4094	31°0939S, 111°55.919W	2237
SIO-BIC A8575	P11, Th3, A-	A4096	23°32.780S, 115°34.179W	2595
SIO-BIC A8576	P4.5, Th1.5, A5	A4096	23°32.780S, 115°34.179W	2595
SIO-BIC A8577	P7, Th2.5, A4.5	A4096	23°32.780S, 115°34.179W	2595
SIO-BIC A8578	P7, Th2.5, A9	A4096	23°32.780S, 115°34.179W	2595
SIO-BIC A8579	P9, Th3, A6.5	A4096	23°32.780S, 115°34.179W	2595

COLOUR: white radiolar crown, white to yellowish body (Fig. 7B–E)

Distribution. Hydrothermal vents fields of East Pacific Rise, from 23°N to 38°S.

Reproduction. Two specimens from *Alvin* Dive 4091 released eggs 150 μm in diameter.

Remarks. Ten Hove and Zibrowius (1986) reported the distribution of *L. alvini* as "four areas with hydrothermal activity on the Galapagos Ridge and on the East Pacific Rise (approx. 1°N, 10°N, 13°N and 21°N), at depths of about 2500–2600 m", with the type locality being the Galapagos vents. Desbruyères & Segonzac (1997) and Desbruyères *et al.* (2006) reported distribution on the Galapagos vents and the East Pacific Rise from 21°N to 23°S. In their review Tunnicliffe *et al.* (1998) extended the distribution with their reporting of *L. alvini* from the sedimented Guaymas Basin vents at 27°N and Hey *et al.* (2006) reported the species further south on the East Pacific Rise from 31°–32°S vent localities. We did not sequence *L. alvini* from the type locality, but did demonstrate that a single *Laminatubus* species, with very little genetic variability extends along the East Pacific Rise from 38°S to 23°N. We lacked specimens from the sedimented Guaymas Basin vents at 27°N, but samples from the nearby seeps in the Guaymas Basin turned out to be one of the new species described below.

Laminatubus paulbrooksi **n. sp.**
Figures 9–11

Neovermilia **n. sp.**—Levin *et al.* (2012)
Laminatubus **n. sp.**—Goffredi *et al.* (2020)

Material examined. Holotype: SIO-BIC A1416A, Jaco Scar, Costa Rica. For locality details see Table 2.

Paratypes: SIO-BIC A1397, Parrita Seep, Costa Rica, 1 spec.; A1416B, Jaco Scar, Costa Rica, 1 spec.; A1586, Jaco Scar, Costa Rica (prepared for SEM); A6165, Pescadero Basin, Mexico, 3 spec.; A8099A, Pescadero Basin, Mexico, 1 spec; A8099B, Pescadero Basin, Mexico, 1 spec.; A8099C, Pescadero Basin, Mexico, 1 spec.; A9602A, Jaco Scar, Costa Rica, 1 spec.; A9602B, Jaco Scar, Costa Rica, 1 spec.; A9603, Jaco Scar, Costa Rica, 1 spec.; A9908, Jaco Scar, Costa Rica, 1 spec.; A10072, Jaco Scar, Costa Rica, 2 spec.; A11567, Guaymas Basin, 1 spec.; A11568, Guaymas Basin, Mexico, 1 spec.; A11569, Guaymas Basin, Mexico, 1 spec.; **MZUCR** 1505-01, ex A8304, Jaco Scar, Costa Rica, 1 spec.; **MZUCR** 1506-01 ex A9589, Jaco Scar, Costa Rica, 1 spec.

Additional material examined: *Neovermilia globula* holotype, **AM** W.3630, Australia, NSW, Cronulla, Port Hacking, 34°4'30"S, 151°8'48"E; W.49842, Australia, NSW, Port Kembla, 34°27.5667'S,150°55.7667'E.

Neovermilia cf. *sphaeropomata* **AM** W.50911, R/V *Investigator*, voyage INV2015-C01, Op. 114-157, Great Australian Bight, 34º42.3333'S,132º31.85'E.

Description. TUBE: white opaque, semi-circular to circular in cross-section, without wide flaring peristomes,

some growth rings distinct, attached to the substrate throughout its length (Fig. 9). Smooth low, sometimes slightly undulating medial keel and flattened attachment flange lacking alveoli present (Fig. 10A, D). External hyaline layer absent.

RADIOLAR CROWN: radioles not connected by inter-radiolar membrane, arranged into semicircles or incomplete spiral of up to two whorls (Fig. 10B, D). Stylodes and radiolar eyes absent.

PEDUNCLE: smooth cylindrical (circular in cross section), about twice as thick as normal radioles (Fig. 10A, C, D), gradually merging into opercular ampulla, constriction absent (Fig. 10A, C, D) Peduncle inserted on left side of radiolar crown, below line of radioles. Small distal latero-dorsal "winglets" (flattened distal parts of the peduncle) or pair of lateral wings proximal to opercular ampulla absent (Fig. 10C, D).
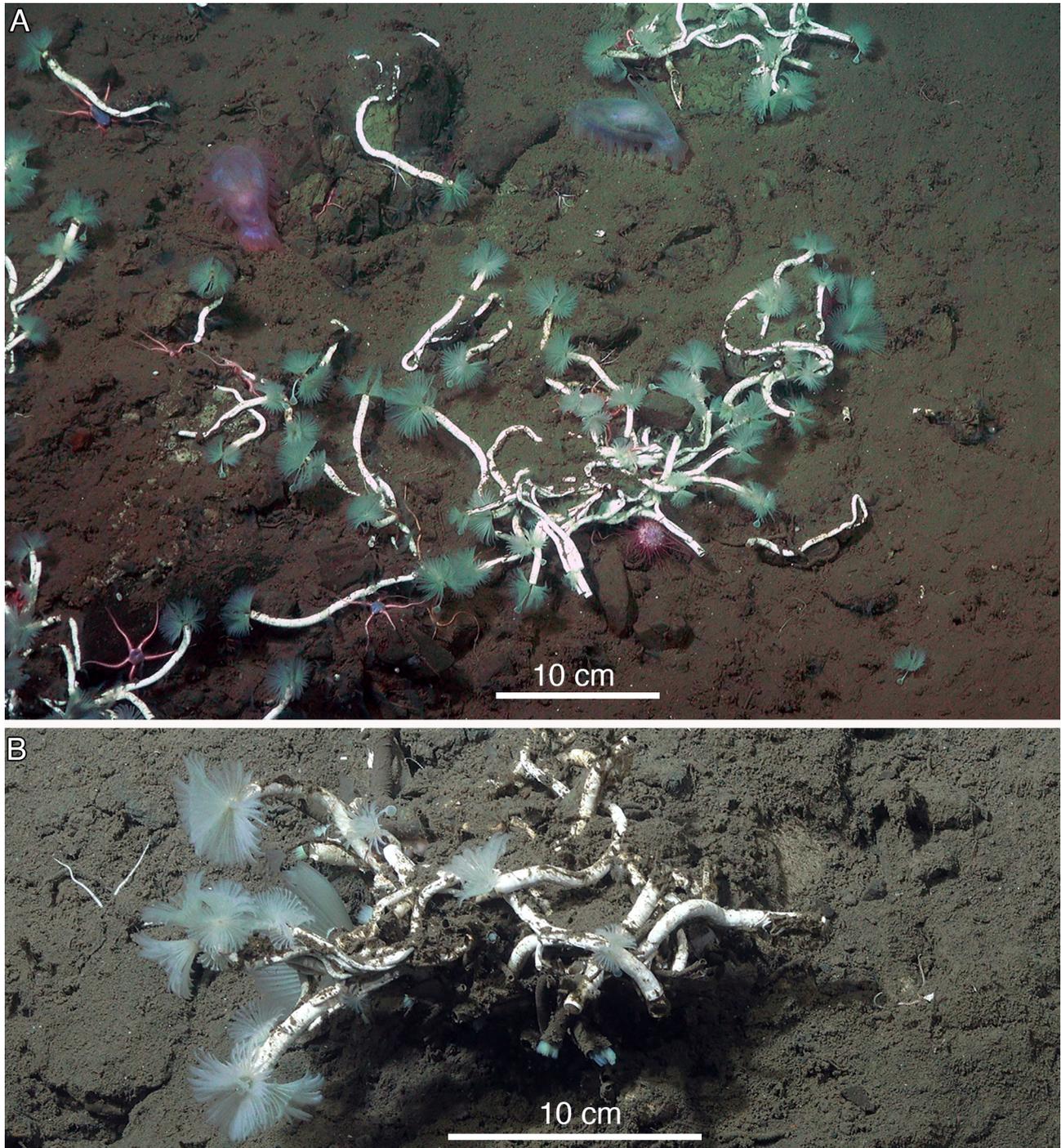

10 cm

10 cm

FIGURE 9. Photos of *Laminatubus paulbrooksi* **n. sp.** *in situ*. At Jaco Scar, Costa Rica. Photo credit: ROV SuBastian, Schmidt Ocean Institute.
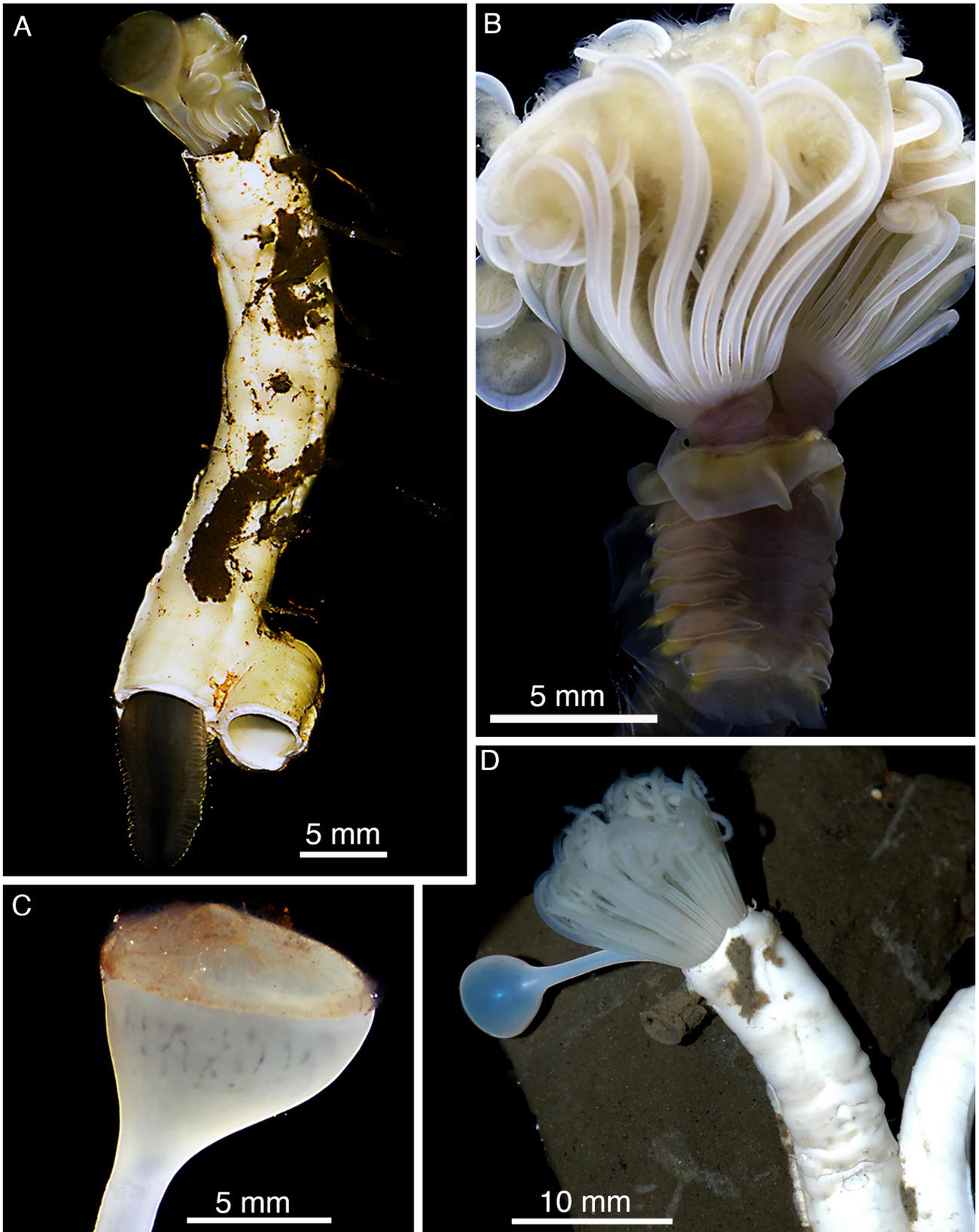
FIGURE 10. Photos of *Laminatubus paulbrooksi* **n. sp.** A–C—SIO-BIC A11567, A11568, A11569, Guaymas Basin, 1565 m; A—specimen in tube; B—ventro-lateral view of the thorax, C—close-up view of the operculum. D—specimen in tube, *Alvin* dive 4509, Jaco Scar, Costa Rica, 1866 m.
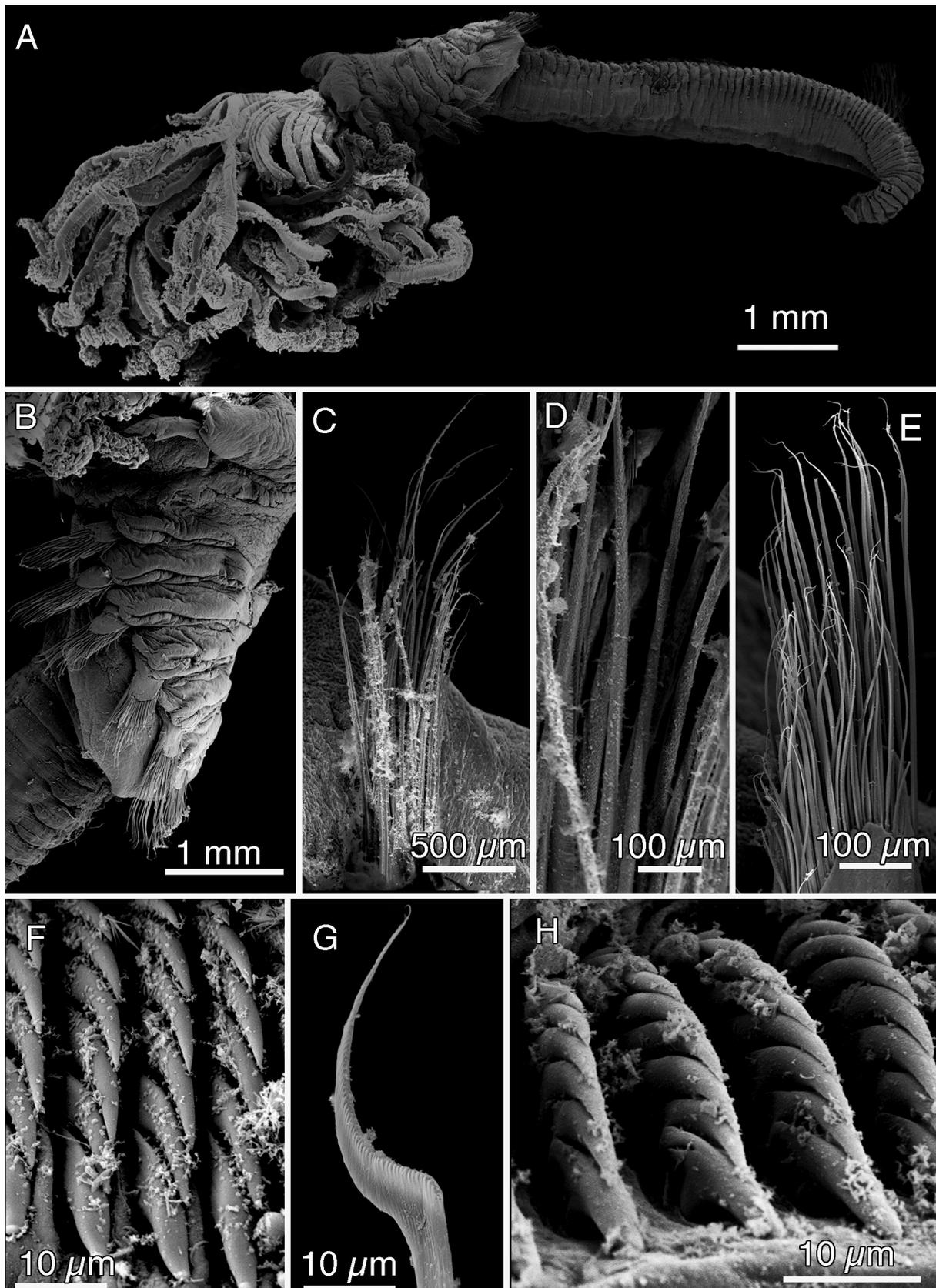
FIGURE 11. SEM of *Laminatubus paulbrooksi* **n. sp.** (SIO-BIC A1586). A—lateral view of a specimen with radiolar crown. B—close-up view of the thorax. C—collar chaetae. D—close-up view of collar chaetae. E—thoracic chaetae. F—thoracic uncini. G—close-up view of anterior abdominal true trumpet-shaped chaeta. H—anterior abdominal uncini.

OPERCULUM: semi-transparent, completely globular or slightly flattened distally, opercular top slightly sclerotized, without distinct yellowish-brownish endplate (Fig. 10A, C, D).

COLLAR AND THORACIC MEMBRANES: collar high, clearly trilobed, with longer and wider ventral lobe and smaller lateral ones (Fig. 10B, 11A) and with entire edge, continuous with thoracic membranes as wide as thoracic tori, forming apron across anterior abdominal chaetigers. Pairs of small, wart-like protuberances of collar chaetiger or elongated tonguelets between ventral and lateral collar parts absent.

THORAX: with collar chaetiger and six uncinigerous chaetigers (specimen from A1586 with six uncinigerous segments on one side and five on the other), fascicle of collar chaetae separated from first uncinigerous chaetiger by a wide gap. Thoracic tori of the same length, gradually converging posteriorly, forming distinct triangular depression, but not touching each other medio-ventrally (Fig. 10B). Collar chaetae limbate only, no *Spirobranchus*-type chaetae present (Fig. 11C, D). Subsequent chaetae limbate, of two sizes, *Apomatus*-chaetae absent (Fig. 11E). Uncini along entire thorax saw-shaped, with 6–7 curved teeth, anterior fang slightly rounded to pointed (Fig. 11F). Pair of prostomial eyes absent.

ABDOMEN: with up to 80 abdominal chaetigers. Achaetous anterior abdominal zone absent, distinct chaetae with long shaft starting from first abdominal segment and continuing throughout entire abdomen. Tips of chaetae distinctly curved and hollow, made of two rows of pointed teeth, thus true trumpet-shaped (Fig. 11G). Distinctly longer capillary chaetae absent in posterior chaetigers. Uncini saw-shaped, with bluntly pointed fang and 6–7 teeth (Fig. 11H); posterior-most uncini rasp-shaped with 3–4 rows of teeth, bluntly pointed fang and 7–8 teeth in profile view posteriorly. Posterior glandular pad absent (Fig. 11A).

SIZE: length up to 45 mm. Radioles and operculum accounting for 2/5 of entire animal length.

COLOUR: white radiolar crown, yellow to reddish body (Fig. 9, 10)

Etymology. This species was named for Paul Brooks in recognition of his long-term commitment and support of the Scripps Oceanographic Collections, particularly the Benthic Invertebrate Collection.

Distribution. Jaco Scar, Parrita Seep, Quepos Seep hydrothermal methane seeps on the Pacific Costa Rica margin (1400–1900 m), and Pescadero and Guaymas Basins (Gulf of California) methane seeps (1700–2400 m).

Remarks. *Laminatubus paulbrooksi* **n. sp.** is what was reported in Levin *et al.* (2012) as a new species of *Neovermilia*. This was based on a personal communication from the present authors and was based on the marked morphological differences from *Laminatubus alvini* that suggested it did not belong in that genus. The new species differs from *L. alvini* by the semi-transparent uniform operculum without a distinct yellowish-brownish endplate, presence of seven thoracic chaetigers and lack of *Spirobranchus*-type special collar chaetae. *Laminatubus paulbrooksi* **n. sp.** was reported in Goffredi *et al.* (2020) as showing a novel animal-bacterial symbiosis, driven by methane with distinct aerobic methane-oxidizing bacteria (*Methylococcales*), localized in the radiolar crown. There was a clear isotope signature showing that the worms were deriving nutrition from the bacteria.

Laminatubus joycebrooksae **n. sp.**
Figures 12–15

Material examined. Holotype: SIO-BIC: A8255, Mound 12, Costa Rica. For locality details see Table 2.

Paratypes: SIO-BIC: A8256A, Mound 12, Costa Rica, 1 spec. prepared for SEM; A8256B, Mound 12, Costa Rica, 1 spec.; **MZUCR** 1507-01 ex A10063, 1 spec.; **MZUCR** 1508-01 ex A11296, 1 spec. Mound 12, Costa Rica (see Table 2 for details).

Additional material. SIO-BIC: A1315A, 1 spec.; A1315B, 1 spec. prepared for SEM; A1330, 6 spec.; A1494, 1 spec. (All from Mound 12, Costa Rica; see Table 2 for details).

Description. TUBE: white opaque, semi-circular to circular in cross-section, without wide flaring peristomes, some growth rings distinct, attached to the substrate throughout its length (Fig. 9). Smooth low, sometimes slightly undulating medial keel and flattened attachment flange lacking alveoli present (Figs 12, 13B). External hyaline layer absent.

RADIOLAR CROWN: radioles not connected by inter-radiolar membrane, arranged into semicircles or incomplete spiral of up to two whorls (Fig. 13A). Stylodes and radiolar eyes absent.

PEDUNCLE: smooth cylindrical (circular in cross section), about twice as thick as normal radioles (Fig. 13A), gradually merging into opercular ampulla, constriction absent (Fig. 13A, C). Peduncle inserted on left side of radiolar crown, below line of radioles. Small distal latero-dorsal winglets proximal to opercular ampulla absent (Fig. 13A, D).

OPERCULUM: semi-transparent, completely globular or slightly flattened distally, opercular top slightly scler-

otized, with more or less distinct endplate in some. May be enhanced by epibiotic growth of unknown nature (Fig. 13C, D). Others lack distinct endplate (Fig. 13A, B).

COLLAR AND THORACIC MEMBRANES: collar high, clearly trilobed, with longer and wider ventral lobe and smaller lateral ones and with entire edge, continuous with thoracic membranes as wide as thoracic tori, forming apron across anterior abdominal chaetigers (Figs 13A, D, 14A, B). Pairs of small, wart-like protuberances of collar chaetiger or elongated tonguelets between ventral and lateral collar parts absent (Fig. 14B).
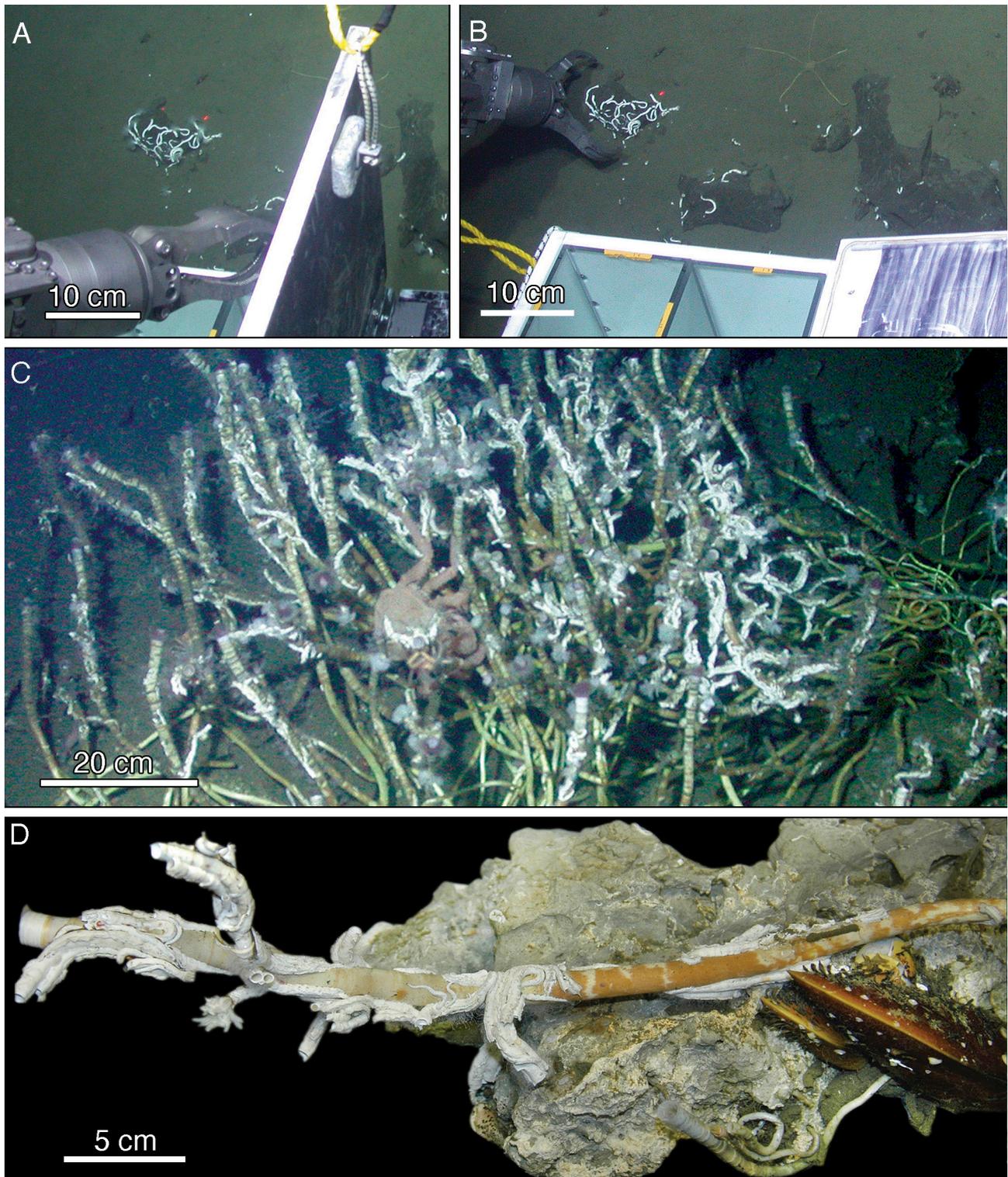

FIGURE 12. Photos of *Laminatubus joycebrooksae* **n. sp.** A–C—animals *in situ*, *Alvin* dive 4501, Mound 12, Costa Rica, 1008 m; D—close-up views of tubes, *Alvin* dive 4502, Mound 12, Costa Rica, 1000 m. Photo credit: HOV Alvin, Woods Hole Oceanographic Institute.
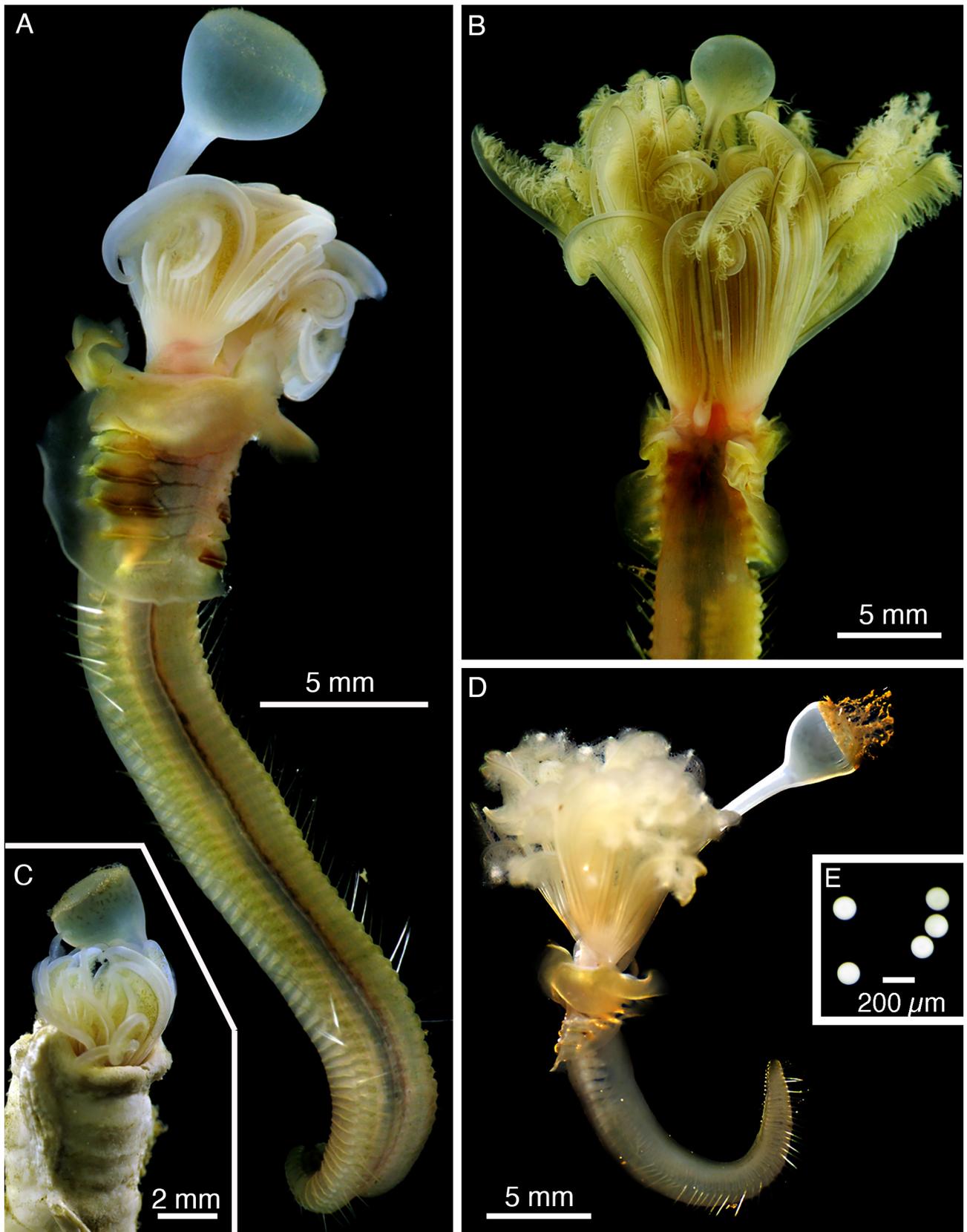
FIGURE 13. Photos of *Laminatubus joycebrooksae* **n. sp.** A, B, C—SIO-BIC A1315, *Alvin* dive 4501, Mound 12, Costa Rica, 1008 m. D—SIO-BIC A8255, Mound 12, Costa Rica, 1001 m. E– eggs released by the animal.
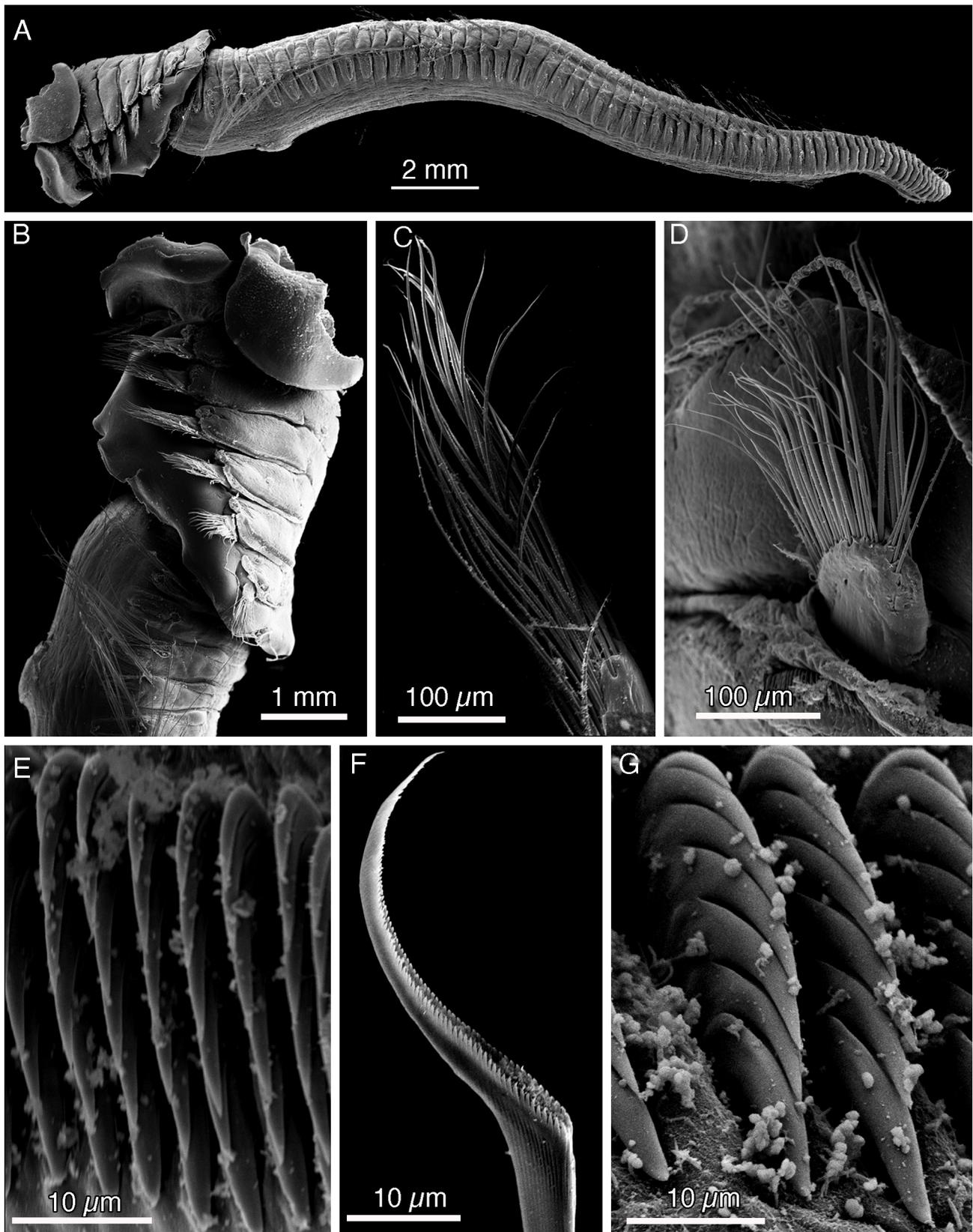
FIGURE 14. SEM of *Laminatubus joycebrooksae* **n. sp.** (SIO-BIC A8256A). A—lateral view of a specimen without radiolar crown. B—close-up view of the thorax. C—collar chaetae. D—thoracic chaetae of the last thoracic chaetigerous segment. E—thoracic uncini. F—anterior abdominal true trumpet-shaped chaeta. G—anterior abdominal uncini.

TABLE 2. Terminal taxa used in the phylogenetic analysis with collection localities, voucher numbers, and GenBank accession numbers. **Bold** are new sequences from this study. * indicates holotype.

Species	Name on tree	Locality	Coordinates, depth (m)	Voucher	Accession number		
					CytB	H3	18S
Hyalopomatus mironovi	H. mironovi KKT	Kuril-Kamchatka Trench	43°2.8333'N,152°59.433'E, 5216 m	AM W.50990	-	-	**MT472383**
H. cf. mironovi	H. 'mironovi' Fiji	Fiji-Lau Back Arc Basin	16°59.48'S,173°54.89'W, 1991 m	SAM E3728	**MT468442**	**MT468421**	GU441862
H. biformis	'H. biformis'	Gulf of Alaska, USA	54°33.967'N,150°25.2167'W, 337 m	FMHN 6202	-	-	GU441858
Hyalopomatus sp.	Hyalopomatus J	Jaco Summit, Costa Rica	9°10.32'N, 84°56.4'W, 745 m	SIO-BIC A1434	-	-	**MT472387**
Hyalopomatus sp.	Hyalopomatus G	Guaymas Basin, Gulf of California	26°21.6'N, 110°44.7'W, 2812 m	SIO-BIC A11566	-	-	**MT472386**
Neovermilia globula	N. globula	Port Kembla, Australia	34°27.5667'S,150°55.7667'E, 10 m	AMW.49842	**MT490636**		**MT472384**
N. cf. sphaeropomata	N. sphaeropomata	Great Australian Bight	34°42.3333'S,132°31.85'E, 3261 m	AM W.50911	**MT468443**	-	**MT472385**
Laminatubus alvini	23°S	East Pacific Rise	23°32.76'S,115°34.2'W, 2595 m	SIO-BIC A1670	**MT468469**	-	**MT472400**
L. alvini	23°S	East Pacific Rise	23°32.04S, 115°34.26W, 2598 m	SIO-BIC A1668	**MT468470**	-	**MT472402**
L. alvini	KY706466 23°N	Alarcon Rise, Mexico	23°22.62'N, 108°31.86'W, 2309 m	SIO-BIC A6158	-	-	KY706466
L. alvini	KY706464 23°N	Alarcon Rise, Mexico	23°22.62'N, 108°31.86'W, 2309 m	SIO-BIC A6327	**MT468477**	**MT468423**	KY706464
L. alvini	23°S	East Pacific Rise	23° 32.78'S, 115° 34.179'W, 2595 m	SIO-BIC A8575	**MT468466**	**MT468431**	**MT472396**
L. alvini	23°S	East Pacific Rise	23° 32.78'S, 115°34.179'W, 2595 m	SAM E5851	**MT468465**	**MT468430**	**MT472397**
L. alvini	23°S	East Pacific Rise	23° 32.78'S, 115°34.179'W, 2595 m	AM W. 49960	**MT468467**	**MT468433**	**MT472398**
L. alvini	31°S	East Pacific Rise	31°09.039'S, 111°55.919'W, 2237 m	AM W. 49958	**MT468468**	**MT468432**	**MT472395**
L. alvini	31°S	East Pacific Rise	31° 09.039'S, 111°55.919'W, 2237 m	SAM E1717	**MT468476**	**MT468438**	**MT472407**
L. alvini	DQ317118 31°S	East Pacific Rise	31°9.0383'S, 111°55.918'W, 2237 m	SAM E3531	-	-	DQ317118
L. alvini	38°S	East Pacific Rise	37°40.35'S, 110°52.62'W, 2236 m	SIO-BIC A1654	**MT468472**	**MT468435**	**MT472403**
L. alvini	38°S	East Pacific Rise	37°40.35'S, 110°52.62'W, 2236 m	SIO-BIC A1658	**MT468473**	**MT468436**	**MT472404**
L. alvini	38°S	East Pacific Rise	37°40.35'S, 110°52.62'W, 2236 m	SIO-BIC A1660	**MT468474**	-	**MT472405**
L. alvini	9°N	East Pacific Rise	9°50.733'N, 104°17.49'W, 2307 m	FMNH 7045	**MT468464**	**MT468439**	**MT472408**
L. alvini	38°S	East Pacific Rise	37°40.35'S, 110°52.62'W, 2236 m	SIO-BIC A1662	**MT468475**	-	**MT472406**
L. alvini	38°S	East Pacific Rise	37° 40.35'S, 110°52.62'W, 2236 m	SIO-BIC A8568	**MT468471**	**MT468434**	**MT472399**
L. joycebrooksae n. sp.	Mound12	Mound 12, Costa Rica	8°55.8'N, 84°18.8'W, 1011 m	MZUCR 1507-01	**MT468458**	-	-
L. joycebrooksae n. sp.	Mound12	Mound 12, Costa Rica	8°55.9'N, 84°18.8'W, 1001 m	MZUCR 1508-01	**MT468446**	**MT468428**	-

TABLE 2. (Continued)

Species	Name on tree	Locality	Coordinates, depth (m)	Voucher	Accession number		
					CytB	H3	18S
L. joycebrooksae **n. sp.**	Mound12	Mound 12, Costa Rica	8°55.9'N, 84° 18.8'W, 1001 m	SIO-BIC A8256A	MT468447	MT468427	-
L. joycebrooksae **n. sp.***	Mound12	Mound 12, Costa Rica	8°55.9'N, 84° 18.8'W, 1001 m	SIO-BIC A8255	MT468444	MT468425	MT472391
L. joycebrooksae **n. sp.**	Mound12	Mound 12, Costa Rica	8°55.9'N, 84° 18.8'W, 1001 m	SIO-BIC A8256B	MT468445	MT468426	-
L. paulbrooksi **n. sp.**	Guaymas Seep	Guaymas Basin, Mexico	27°35.4'N, 111°28.2'W, 1565 m	SIO-BIC A11568	MT468450	-	MT472389
L. paulbrooksi **n. sp.**	Guaymas Seep	Guaymas Basin, Mexico	27°35.4'N, 111°28.2'W, 1565 m	SIO-BIC A11569	MT468449	-	MT472388
L. paulbrooksi **n. sp.**	Guaymas Seep	Guaymas Basin, Mexico	27°35.4'N, 111°28.2'W, 1565 m	SIO-BIC A11567	MT468451	MT468422	MT472390
L. paulbrooksi **n. sp.***	Jaco Scar	Jaco Scar, Costa Rica	9°7.0'N, 84°51'W, 1866 m	SIO-BIC A1416A	MT468478	MT468440	MT472409
L. paulbrooksi **n. sp.**	Jaco Scar	Jaco Scar, Costa Rica	9°7.0'N, 84°51'W, 1866 m	SIO-BIC A1416B	MT468479	MT468441	MT472410
L. paulbrooksi **n. sp.**	A10072_Jaco	Jaco Scar, Costa Rica	9°7.1'N, 84°51'W, 1841 m	SIO-BIC A10072	MT468459	-	-
L. paulbrooksi **n. sp.**	Jaco Scar	Jaco Scar, Costa Rica	9°7.0'N, 84°50'W, 1785 m	SIO-BIC A9908	MT468456	-	-
L. paulbrooksi **n. sp.**	Jaco Scar	Jaco Scar, Costa Rica	9°7.01N, 84°50'W, 1784 m	SIO-BIC A9603	MT468453	-	-
L. paulbrooksi **n. sp.**	Jaco Scar	Jaco Scar, Costa Rica	9°6.9'N, 84°50'W, 1887 m	SIO-BIC A9602B	MT468454	-	-
L. paulbrooksi **n. sp.**	Jaco Scar	Jaco Scar, Costa Rica	9°6.9'N, 84°50'W, 1887 m	SIO-BIC A9602A	MT468455	-	-
L. paulbrooksi **n. sp.**	Jaco Scar	Jaco Scar, Costa Rica	9°7.0'N, 84°51'W, 1824 m	MZUCR 1506-01	MT468457	-	-
L. paulbrooksi **n. sp.**	Jaco Scar	Jaco Scar, Costa Rica	9°6.9'N, 84°50'W, 1859 m	MZUCR 1505-01	MT468448	MT468429	-
L. paulbrooksi **n. sp.**	Parrita Seep	Parrita Seep, Costa Rica	9°1.8' N, 84°37.4'W, 1433 m	SIO-BIC A1397	MT468463	MT468437	MT472401
L. paulbrooksi **n. sp.**	KY706467 A6165	Pescadero Basin, Mexico	23°38.54'N, 108°23.66'W, 2380 m	SIO-BIC A6165	MT468452	MT468424	KY706467
L. paulbrooksi **n. sp.**	Pescadero Seep	Pescadero Basin, Mexico	23°39.0'N, 108°24.3'W, 2478 m	SIO-BIC A8099A	MT468461	-	MT472393
L. paulbrooksi **n. sp.**	Pescadero Seep	Pescadero Basin, Mexico	23°39.0'N, 108°24.3'W, 2478 m	SIO-BIC A8099B	MT468460	-	MT472392
L. paulbrooksi **n. sp.**	Pescadero Seep	Pescadero Basin, Mexico	23°39.0'N, 108°24.3'W, 2478 m	SIO-BIC A8099C	MT468462	-	MT472394

THORAX: with collar chaetiger and six uncinigerous chaetigers (Fig. 14A, B), fascicle of collar chaetae not distinctly separated from first uncinigerous chaetiger by a gap. Thoracic tori of the same length, gradually converging posteriorly, forming distinct triangular depression, but not touching each other medio-ventrally (Fig. 13A). Collar chaetae limbate only, no *Spirobranchus*-type chaetae present (Fig. 14C). Subsequent chaetae limbate, of two sizes, *Apomatus*-chaetae absent (Fig. 14D). Uncini along entire thorax saw-shaped, with 6–7 curved teeth, anterior fang slightly rounded to pointed (Fig. 14E). Prostomial eyes absent.

ABDOMEN: with up to 80 abdominal chaetigers. Achaetous anterior abdominal zone absent, distinct chaetae with long shaft starting from first abdominal segment and continuing throughout entire abdomen (Fig. 14B). Tips of chaetae distinctly curved and hollow, made of two rows of pointed teeth, thus true trumpet-shaped (Fig. 14F). Distinctly longer capillary chaetae absent in posterior chaetigers. Uncini saw-shaped, with pointed fang and 6–7 teeth (Fig. 14G); posterior-most uncini rasp-shaped with 3–4 rows of teeth, bluntly pointed fang and 7–8 teeth in profile view posteriorly. Posterior glandular pad absent (Fig. 14A).

SIZE: length up to 35 mm. Radioles and operculum accounting for 2/5 of entire animal length.

COLOUR: white radiolar crown, yellowish body (Figs 12, 13).

Etymology. The species was named after Joyce Brooks in recognition of her commitment and support of the Scripps Oceanographic Collections, particularly the Benthic Invertebrate Collection.

Distribution. Mound 12 methane seep, Costa Rica margin (~1000 m).

Reproduction. A specimen from *Alvin* Dive 4502 released white spherical eggs ~150 μm in diameter (Fig. 13E).

Remarks. Using the techniques employed here, *L. joycebrooksae* **n. sp.** is morphologically indistinguishable to *L. paulbrooksi* **n. sp.** The two species are reciprocally monophyletic sister groups (Fig. 2) and show a clear divergence in mitochondrial cytochrome b sequences (Fig. 4). They also are found at different depths with *L. joycebrooksae* **n. sp.** only found at ~1000 m at Mound 12 (Costa Rica), while *L. paulbrooksi* **n. sp.** was found from 1400–2400 meters off Costa Rica and Mexico. Assigning species status to *L. joycebrooksae* **n. sp.** is therefore warranted.

Acknowledgements

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