

MARINE RECORD

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A new record of *Lamellibrachia columna* (Siboglinidae, Annelida) from cold seeps off New Zealand, and an assessment of its presence in the western Pacific Ocean

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Abstract

Lamellibrachia columna Southward was originally described from hydrothermal vents of the Lau Basin, between Fiji and Tonga. This study utilizes phylogenetic and morphological analyses to confirm the collection of *Lamellibrachia columna* from cold seeps on the Hikurangi Margin off New Zealand, thereby extending its geographic range southward by approximately 1900 km. We also propose, based on molecular evidence, that specimens previously reported from vents in the Nankai Trough, Japan and seeps off southern and eastern Japan are *L. columna*. Furthermore, we suggest that *Lamellibrachia sagami* Kobayashi et al. described from cold seeps off southern and eastern Japan is a junior synonym of *Lamellibrachia columna*. Our work confirms that *L. columna* is found at two types of chemosynthetic habitat over a wide geographic range in the western Pacific Ocean.

Keywords: Vestimentifera, Deep sea, Pacific Ocean, Phylogeny, Synonymy

Background

Members of Vestimentifera (originally introduced by Jones (1985), and now one of four informal lineages within Siboglinidae Caullery, 1914 [Hilário et al. 2011; Pleijel et al. 2009]) live in chemosynthetic environments such as hydrothermal vents (Bright and Lallier 2010; Jones 1980; Shank et al. 1998), cold seeps (Bright and Lallier 2010; Levin et al. 2012; Webb 1969), and whale falls (Bright and Lallier 2010; Feldman et al. 1998), where they subsist off endosymbiotic chemoautotrophic bacteria (Bright and Lallier 2010). *Lamellibrachia* Webb, 1969 is one of the few vestimentiferan genera with a broad geographic and habitat distribution, having been reported from seeps, vents, and whale bones in the Pacific, Atlantic, Caribbean, and Gulf of Mexico (Bright and Lallier 2010; Feldman et al. 1998; Kobayashi et al. 2015; Nishijima et al. 2010; Watanabe et al. 2010). Of the nine *Lamellibrachia* species described to date, *Lamellibrachia columna* Southward, 1991 was the first

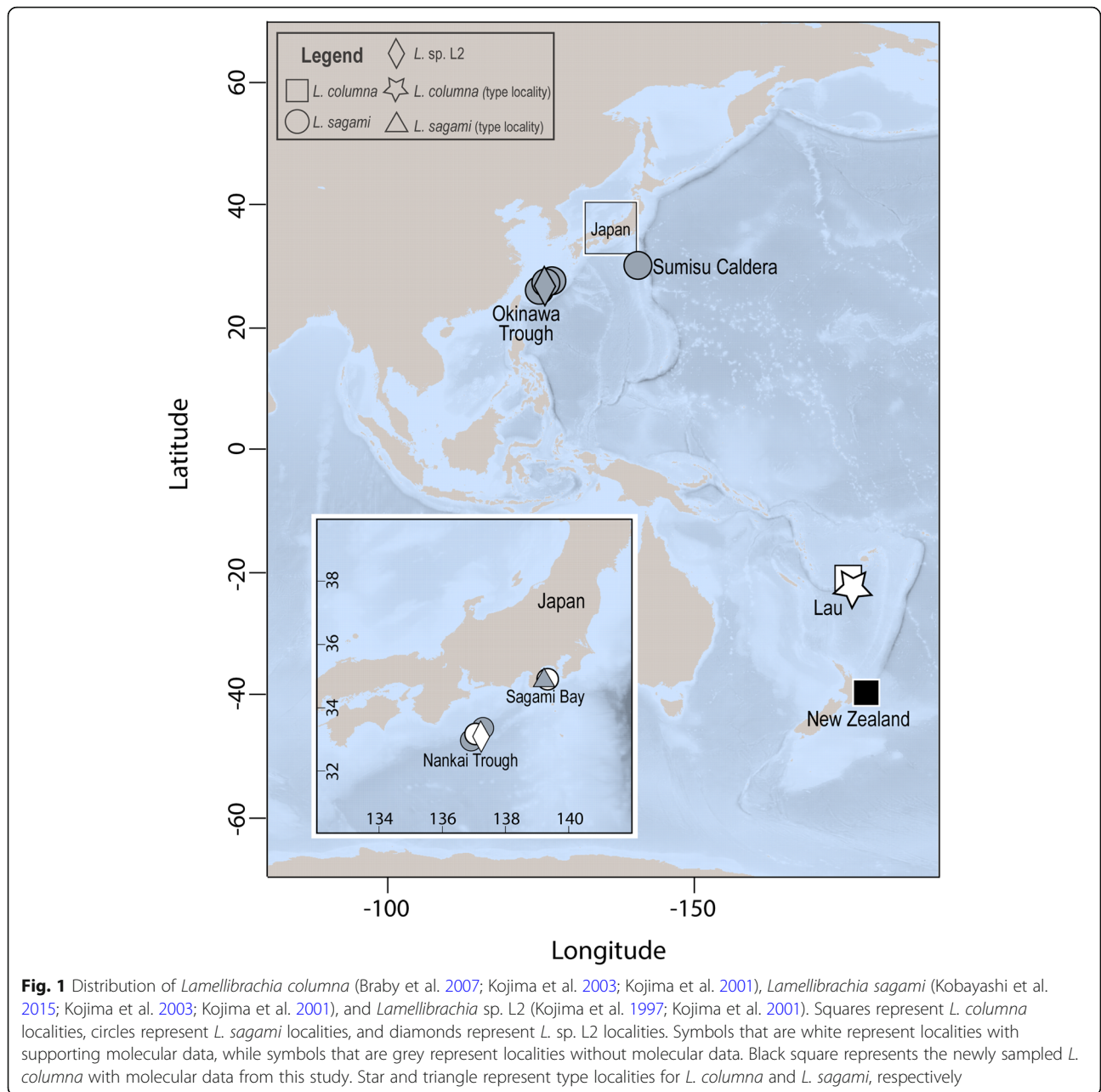
to be described from the southwestern Pacific, at 1870 m in an area of diffuse venting at the Lau Back-arc Basin (Southward 1991). Since its initial discovery, *L. columna* has been reported at diffuse vents from the southwestern Pacific back-arc basin at Lau from 1832 to 1914 m (Black et al. 1997; Kojima et al. 1997, 2001; Southward 1991; Southward et al. 2011) (Fig. 1). To date, *Lamellibrachia columna* is most easily differentiated from other *Lamellibrachia* species by its numbers of sheath and branchial lamellae (Southward 1991). Other diagnostic characteristics such as obturaculum dimensions and plaque size are quite variable and overlap with those of other *Lamellibrachia* species, making DNA data and phylogenetic analyses an important part of the identification process (Kobayashi et al. 2015; McCowin and Rouse 2018; Southward 1991; Southward et al. 2011). The Japanese samples identified as *Lamellibrachia* sp. L1 and *Lamellibrachia* sp. L2 (Kojima et al. 2001) were noted as being very close to a published sequence (Black et al. 1997) of *Lamellibrachia columna* from the type locality, with L2 as the sister taxon to *L. columna*. Kojima et al. (2001) even noted that “L1 and L2 might be conspecific with *L. columna*”.

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The samples identified as *Lamellibrachia* sp. L1 in Kojima et al. 2001 were subsequently described as *Lamellibrachia sagami* Kobayashi et al 2015, with the type locality being a cold seep at 853 m in Sagami Bay, Japan. *Lamellibrachia sagami* was differentiated from other *Lamellibrachia* species by its sheath and branchial lamellae and the sizes of its vestimental and trunk plaques (Kobayashi et al. 2015). It has also been reported from other cold seeps along the eastern coast of Japan (Fig. 1) at depths of 290–2180 m (Kobayashi et al. 2015; Kojima et al. 2015; Kojima et al. 1997; Miura and Fujikura 2008).

Lamellibrachia sagami has been found sympatrically with its close genetic relative *L. sp. L2* (Kojima et al. 2001; Kojima et al. 1997) off the east coast of Japan at the Nankai Trough (Kobayashi et al. 2015; Kojima et al. 2003; Kojima et al. 2001; Kojima et al. 1997).

Here we report a new record of *Lamellibrachia columna* collected from cold seeps of the Hikurangi Margin off New Zealand. Phylogenetic and morphological analyses confirm the identification of specimens collected at this locality as *L. columna*, thereby extending its range southward by approximately 1900 km. We

explore other records of closely-related *Lamellibrachia* species from Japan, and discuss the resulting biogeographical implications for *Lamellibrachia columna*.

Methods

Samples (NIWA 27133) were loaned to Scripps Institution of Oceanography by New Zealand's National Institute of Water and Atmospheric Research (NIWA). These samples were from among other samples of unidentified *Lamellibrachia* specimens originally collected in 2006 from cold seeps off the east coast of the North Island of New Zealand (see Baco et al. 2010 and Bowden et al. 2013 for a full description of the habitat and locations where the tube worms were found, and their densities). The anterior and a portion of the trunk of the specimens examined here for DNA analysis, were originally fixed in 99% ethanol and later frozen (-20°C). These three specimens were collected from the Builder's Pencil seep site, between 810 and 817 m (NIWA 27133A, NIWA 27133B, SIO-BIC A9468). Whole specimens were photographed prior to preservation using a Nikon D70S with 90 mm Nikkor lens mounted on a fixed copy stand column. Ten plaques from the vestimentum and ten plaques from the trunk of each specimen were measured by cutting thin pieces of epidermis from the vestimentum and trunk and placing them on a glass slide with a 5% sodium hydroxide solution prior to observation. Analysis of morphological features of whole specimens was completed post-preservation and compared to morphological records of *L. columna* published by Southward (Southward 1991; Southward et al. 2011).

DNA was extracted from the vestimentum of the New Zealand specimens with the Zymo Research DNA-Tissue Miniprep kit, following the protocol supplied by the manufacturer. Approximately 1275 base pairs (bp) of mitochondrial cytochrome subunit I (COI) were amplified using the vestimentiferan *mtCOI* primer set COI_f and COI_r (Nelson and Fisher 2000) and up to 600 bp of 16S rRNA (16S) were amplified using the primer set 16S_{brH} and 16S_{ArL} (Palumbi 1996). Amplification was carried out in a thermal cycler (Eppendorf) with 12.5 μL Apex 2.0x RED DNA Polymerase Master Mix (Genesee Scientific), 1 μL each of the appropriate forward and reverse primers (10 μM), 8.5 μL water, and 2 μL eluted DNA. The vestimentiferan COI temperature profile was as follows: 95 $^{\circ}\text{C}/300\text{ s}$ – (94 $^{\circ}\text{C}/60\text{ s}$ – 55 $^{\circ}\text{C}/60\text{ s}$ – 72 $^{\circ}\text{C}/120\text{ s}$) * 35 cycles – 72 $^{\circ}\text{C}/420\text{ s}$. The 16S temperature profile was as follows: 95 $^{\circ}\text{C}/180\text{ s}$ – (95 $^{\circ}\text{C}/40\text{ s}$ – 50 $^{\circ}\text{C}/40\text{ s}$ – 72 $^{\circ}\text{C}/50\text{ s}$) * 35 cycles – 72 $^{\circ}\text{C}/300\text{ s}$. The PCR products were purified with the ExoSAP-IT protocol (USB, Affymetrix), and sequencing was performed by Eurofins Genomics (Louisville, KY).

Alignments of the newly generated sequences and available sequence data from GenBank for COI and 16S

(Table 1) published in the most recent siboglinid phylogenies (Black et al. 1997; Braby et al. 2007; Cowart et al. 2014; Kobayashi et al. 2015; Kojima et al. 2001; Li et al. 2017; Li et al. 2015; McCowin and Rouse 2018; McMullin et al. 2003; Miglietta et al. 2010; Sun et al. 2018), including sequences for *Lamellibrachia columna* from the type locality (Lau Back Arc Basin), were performed using MAFFT with default settings (Katoh and Standley 2013) and concatenated with SequenceMatrix v.1.6.7 (Gaurav et al. 2011). For species that showed very little variation in COI (*L. anaximandri*, *L. cf. luymesii*, *L. satsuma*, *L. barhami*), a single individual was chosen to represent each lineage in the phylogenetic analyses. *Lamellibrachia juni* also showed little intra-specific variation in COI, but multiple individuals were chosen to represent the lineage for comparison with the other analyses conducted in this study. This species has also been recorded in the closest geographic proximity to the species of *Lamellibrachia* examined here (i.e., hydrothermal vents of the Kermadec Arc, to the north of New Zealand – 524 km distant) (Miura and Kojima 2006). Maximum likelihood (ML) analyses were conducted on the concatenated dataset using RAxML v.8.2.19 (Stamatakis 2014) with each partition assigned the GTR + G + I model by the Akaike information criterion (AIC) in jModelTest 2 (Darriba et al. 2012; Guindon and Gascuel 2003). Node support was assessed via a thorough bootstrapping (1000 replicates). Bayesian Inference (BI) analyses were also conducted using MrBayes v.3.2.5 (Ronquist et al. 2012) with the same best-fit models assigned to their respective partitions. Maximum parsimony (MP) analyses were conducted using PAUP* v.4.0a (Swofford 2002), using heuristic searches with the tree-bisection-reconnection branch-swapping algorithm and 100 random addition replicates. Support values were determined using 100 bootstrap replicates. Uncorrected pairwise distances were calculated for the COI dataset (~1275 bp) with PAUP* v.4.0a (Swofford 2002). A model-corrected distance analysis for a reduced COI dataset containing the New Zealand specimens (NIWA 27133/SIO-BIC A9468), *L. columna*, *L. sp. L2*, and *L. sagami* (selection supported by all molecular analyses) was also conducted with the best-fit model, HKY (Hasegawa and Kishino 1985), selected via AIC in jModelTest 2. An additional model-corrected distance analysis (best-fit model HKY selected via AIC) was conducted for the *L. juni* COI dataset (all terminals available on GenBank) for comparison with the *L. columna/L. sp. L2/L. sagami* dataset. A haplotype network of the New Zealand specimens, *L. columna*, *L. sp. L2*, and *L. sagami* COI dataset was created with PopART v.1.7 (Bandelt et al. 1999) using the median-joining option and epsilon set at 0.

Table 1 Origin of sequenced terminals, vouchers, and GenBank accession numbers. New sequences are set in bold. *GM* Gulf of Mexico, *CR* Costa Rica, *NZ* New Zealand, *SP* South Pacific

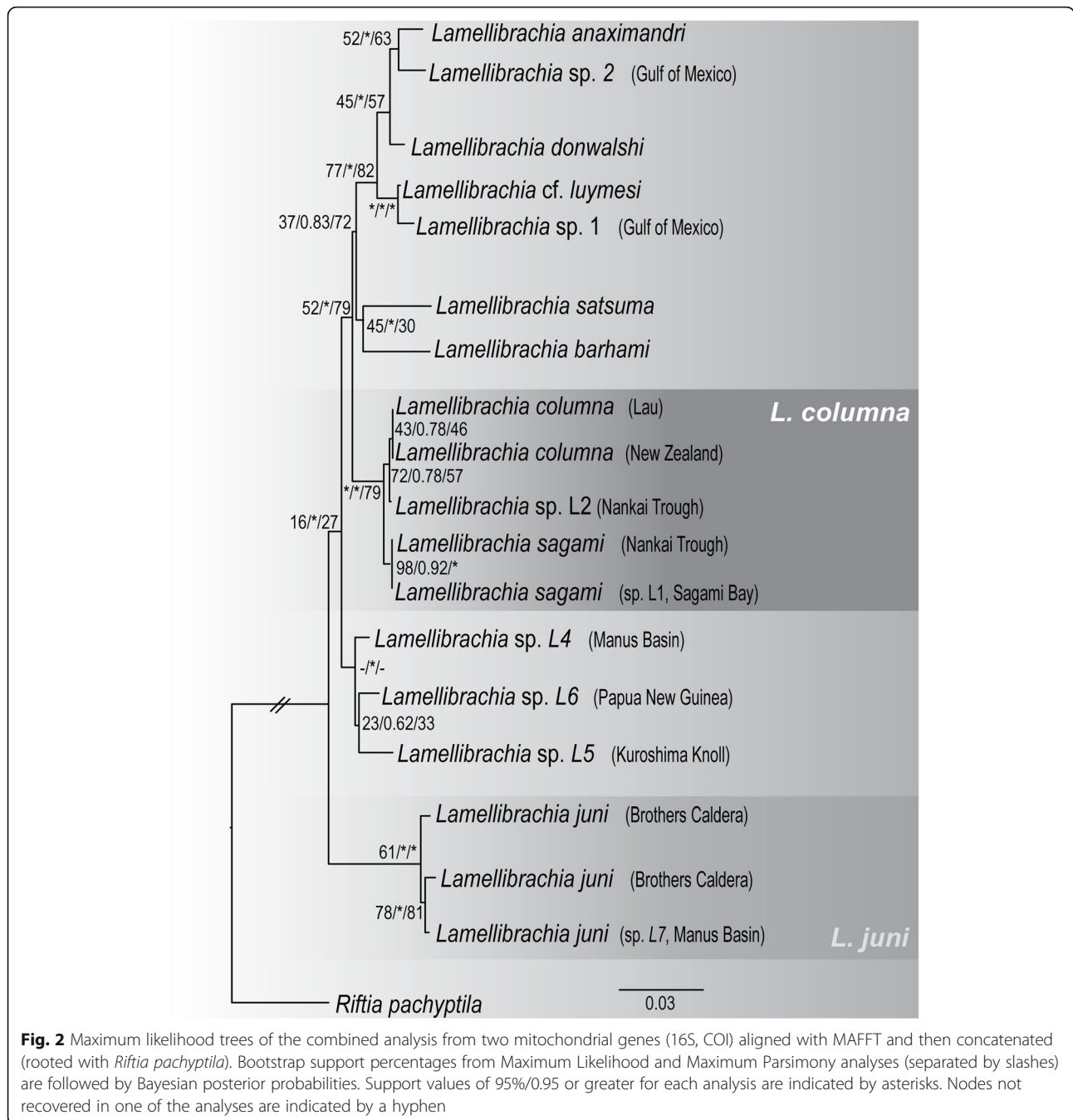
Scientific Name	Origin	COI	16S	Voucher or Reference
<i>Lamellibrachia anaximandri</i>	Eastern Mediterranean	EU046616	HM746782	SMH-2007a
<i>Lamellibrachia barhami</i>	Jaco Scar, CR	MH670766–92	MH660399	SIO-BIC A8343
<i>Lamellibrachia columna</i>	Lau Back Arc Basin	U74061	–	Black et al. 1997
<i>Lamellibrachia columna</i>	Lau Back Arc Basin	DQ996645	FJ347646	Braby et al. 2007, Vrijenhoek et al. 2009
<i>Lamellibrachia columna</i>	Hikurangi Margin, NZ	MK496532-34	MK93453-55	SIO-BIC A9468, NIWA 27133A, NIWA 27133B
<i>Lamellibrachia</i> sp. L2	Nankai Trough, Japan	D50592	–	Kojima et al. 1997
<i>Lamellibrachia donwalshi</i> sp. nov.	Mound 12, CR	MH670827	MH664918	SIO-BIC A8382
<i>Lamellibrachia juni</i> 1	TOTO Caldera, Mariana Arc	AB264601	–	Kojima et al. 2006
<i>Lamellibrachia juni</i> 2	Manus Basin, SP	AB264602	–	Kojima et al. 2003
<i>Lamellibrachia juni</i> 3	Manus Basin, SP	AB264603	–	Kojima et al. 2006
<i>Lamellibrachia juni</i> 4	Brothers Caldera, Kermadec Arc, NZ	AB264604	–	Miura and Kojima 2006
<i>Lamellibrachia juni</i> 7	Manus Basin, SP	AB088675	–	Kojima et al. 2003
<i>Lamellibrachia</i> cf. <i>luymesii</i>	Green Canyon, GM	GU059225	GU068209	Miglietta et al. 2010
<i>Lamellibrachia sagami</i>	Sagami Bay, Japan	LC064365	–	JAMSTEC 1140043315
<i>Lamellibrachia sagami</i> (L. sp. L1)	Nankai Trough, Japan	D38029	–	JAMSTEC 1150054786
<i>Lamellibrachia satsuma</i>	Kagoshima Bay, Japan	KP987801	KP987801	Patra et al. 2016
<i>Lamellibrachia</i> sp. 1	GM	GU059165–66, GU059169, GU059227, GU059237	GU068253–54, GU068257, GU068212, GU068227	Miglietta et al. 2010
<i>Lamellibrachia</i> sp. 2	GM	GU059173, GU059175–77	GU068265, GU068269	Miglietta et al. 2010
<i>Riftia pachyptila</i>	East Pacific Rise	KJ789166	KJ789166	Li et al. 2015

Results

The ML, BI, and MP analyses (Fig. 2) were congruent, with strong support for the inclusion of the *Lamellibrachia* specimens from New Zealand within *L. columna*. An uncorrected pairwise distance analysis and an HKY-corrected distance analysis based on COI sequences showed a maximum distance of 0.50% between the *L. columna* specimens from the type locality and *L. columna* specimens from New Zealand (Table 2). The haplotype network revealed a two-base-pair divergence between the same samples (Fig. 3). Morphological analyses of the *L. columna* specimens from New Zealand revealed (Table 3) that all characteristics except the obturaculum and plaque dimensions fell within or near the expected range for *L. columna* established by Southward 1991. The number of sheath lamellae ranged from 14 to 16 (expected range 8–16 [Southward 1991]), while the number of branchial lamellae ranged from 20 to 22

(expected 21 [Southward 1991]) for each specimen. The obturaculum lengths ranged from 7 to 13 mm (expected range 15–42 mm [Southward 1991]), while obturaculum widths ranged from 5 to 8 mm (expected range 8–13 mm [Southward 1991]). The diameters of the vestimental plaques ranged from 59 to 60 μm (expected range 65–90 μm [Southward et al. 2011]), and the diameters of the trunk plaques ranged from 67 to 75 μm (expected range 70–120 μm [Southward et al. 2011]).

The phylogenetic tree also showed strong support for referring *Lamellibrachia* sp. L2 as *L. columna*. There was a maximum uncorrected distance of 0.33% in COI sequences between the *L. columna* specimens from the type locality and *L. sp.* L2 (Table 2). In addition, an HKY-corrected distance analysis based on COI sequences showed a maximum distance of 0.5% between the *L. sp.* L2 specimens from Japan and the specimens from New Zealand. The haplotype network also revealed



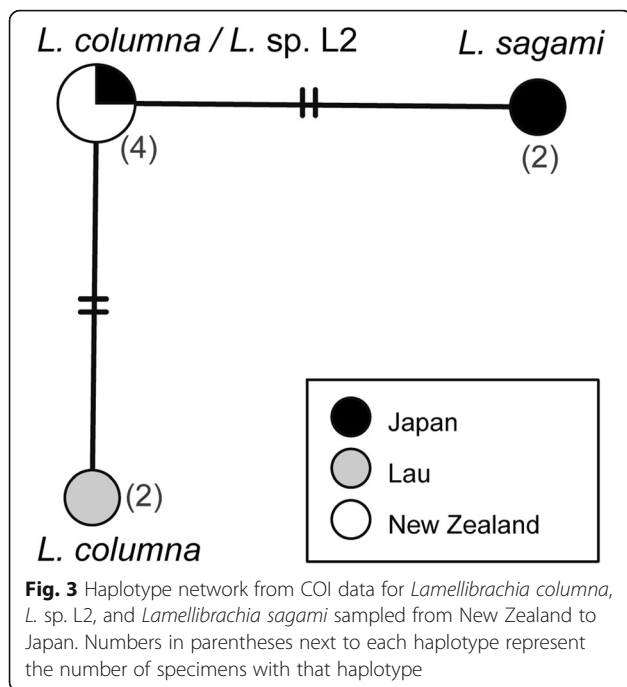
minimal divergence between *L. sp. L2* and *L. columna*. *Lamellibrachia sp. L2* was found to differ by only two base pairs from *L. columna* (from the type locality) and shared a haplotype with the New Zealand specimens (Fig. 3).

The phylogenetic tree and both distance analyses also revealed a close relationship between *Lamellibrachia columna* and *L. sagami* (Fig. 2, Table 2). Both the uncorrected and corrected analyses based on COI sequences revealed a minimum distance of 0.95–0.98% between *L.*

sagami and the *L. columna* from the type locality, 0.67–0.69% between *L. sagami* and the *L. columna* from New Zealand, and 0.64% between *L. sagami* and the *L. sp. L2* from Japan. The HKY-corrected analysis showed a maximum distance of 1.35% between *L. sagami* and *L. columna* from their respective type localities, 0.99% between *L. sagami* and *L. sp. L2*, and 1.24% between *L. sagami* and *L. columna* from New Zealand. An HKY-corrected analysis of *L. juni* Miura and Kojima, 2006 (Miura and Kojima 2006) generated for comparison

Table 2. Uncorrected pairwise distances for COI data (all *L. columnna* and *L. sagami* terminals included, non-identical *L. juni* terminals included, duplicates of other species removed), generated with PAUP*. SB Sagami Bay, NT Nankai Trough, MA Mariana Arc, MB Manus Basin, NZ New Zealand. Terminals comparing *L. columnna*, *L. sagami*, and *L. sp. L2* are set in bold.

	<i>L. juni</i> 1 (MA)	<i>L. juni</i> 2 (MB)	<i>L. juni</i> 3 (MB)	<i>L. juni</i> 4 (NZ)	<i>L. juni</i> 7 (MB)	<i>L. sp. L4</i>	<i>L. sp. L5</i>	<i>L. sp. L6</i>	<i>L. sagami</i> (SB)	<i>L. sagami</i> (NT)	<i>L. columnna</i> (Lau 1)	<i>L. columnna</i> (Lau 2)	<i>L. columnna</i> sp. L2 (NT)	<i>L. columnna</i> (NZ 1)	<i>L. columnna</i> (NZ 2)	<i>L. columnna</i> (NZ 3)	<i>L. satsuma</i>	<i>L. barhami</i>	<i>L. cf. luy-mesi</i>	<i>L. sp. 1</i>	<i>L. sp. 2</i>	<i>L. don-walshi</i>		
<i>L. juni</i> 2 (MB)	1.18																							
<i>L. juni</i> 3 (MB)	1.38	0.39																						
<i>L. juni</i> 4 (NZ)	1.38	0.89	1.08																					
<i>L. juni</i> 7 (MB)	1.09	0.00	0.00	0.79	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>L. sp. L4</i>	6.68	6.48	6.68	6.29	6.33	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>L. sp. L5</i>	6.78	6.97	6.98	6.78	6.73	2.62	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>L. sp. L6</i>	7.10	6.89	6.70	6.98	6.54	1.85	2.83	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>L. sagami</i> (SB)	7.13	6.81	6.81	6.82	6.49	4.13	4.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>L. sagami</i> (NT)	7.60	7.40	7.50	7.20	7.23	4.10	4.49	4.60	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>L. columnna</i> (Lau 1)	7.78	7.57	7.67	7.36	7.45	4.66	4.95	4.75	0.98	1.33	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>L. columnna</i> (Lau 2)	7.15	6.83	6.83	6.84	6.52	4.05	4.37	3.60	0.95	0.78	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>L. sp. L2</i> (NT)	7.49	7.29	7.39	7.09	7.13	4.09	4.29	4.40	0.64	0.98	0.31	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>L. columnna</i> (NZ 1)	7.61	7.41	7.51	7.21	7.31	4.21	4.60	4.51	0.67	1.21	0.33	0.20	-	-	-	-	-	-	-	-	-	-	-	-
<i>L. columnna</i> (NZ 2)	7.65	7.46	7.56	7.25	7.35	4.23	4.62	4.54	0.68	1.22	0.50	0.20	0.00	-	-	-	-	-	-	-	-	-	-	-
<i>L. columnna</i> (NZ 3)	7.68	7.48	7.58	7.28	7.38	4.25	4.64	4.55	0.69	1.22	0.49	0.20	0.00	0.00	-	-	-	-	-	-	-	-	-	-
<i>L. satsuma</i>	8.27	8.18	8.48	8.08	8.10	5.69	5.87	5.69	5.51	6.18	6.15	5.44	5.89	5.80	5.77	5.85	-	-	-	-	-	-	-	-
<i>L. barhami</i>	7.32	7.32	7.54	7.54	7.23	5.09	5.30	5.52	4.99	5.34	5.68	4.87	5.32	5.52	5.53	5.54	6.06	-	-	-	-	-	-	-
<i>L. cf. luy-mesi</i>	7.36	7.36	7.46	7.36	7.19	4.09	4.47	4.28	4.14	4.11	4.28	3.83	3.79	3.66	3.70	3.69	5.12	6.27	-	-	-	-	-	-
<i>L. sp. 1</i> (GoM)	8.16	7.86	7.86	7.87	7.54	5.16	4.71	4.71	4.49	4.43	4.92	4.19	4.29	4.32	4.36	4.38	5.94	5.93	1.01	-	-	-	-	-
<i>L. sp. 2</i> (GoM)	8.26	7.24	7.42	7.59	7.10	5.05	5.21	5.07	4.45	4.43	4.60	4.38	4.60	4.59	4.59	4.59	6.12	4.55	3.36	3.38	-	-	-	
<i>L. don-walshi</i>	7.67	7.04	7.25	7.57	6.95	4.42	4.72	4.53	4.34	4.46	4.68	3.88	4.21	4.19	4.19	4.20	6.25	5.42	2.85	3.59	2.37	-	-	
<i>L. anaxi-mandri</i>	8.24	7.78	7.79	7.64	7.59	5.18	4.28	4.74	4.56	4.60	5.23	4.50	4.77	4.58	4.64	4.65	6.18	5.52	2.87	2.50	2.71	2.49	-	



revealed a maximum distance of 1.39% among *L. juni* specimens from various localities. The minimum uncorrected COI distance between *L. juni* from the Kermadec Arc, New Zealand and the New Zealand *L. columna* specimens was 7.28%. Haplotype networks generated for the COI data from *L. columna* (type locality), the New Zealand specimens, *L. sp. L2*, and *L. sagami* (Fig. 3) showed minimal divergence between specimens (at most two base pairs between haplotypes).

The morphological characteristics of *Lamellibrachia sagami* also fall within or very close to the accepted range for *L. columna* (Kobayashi et al. 2015; Southward 1991; Southward et al. 2011) and exhibited by the New Zealand *L. columna* specimens, including obturaculum length (*L. sagami* measures 5.8–22.5 mm [Kobayashi et al. 2015]), obturaculum width (4.4–10.8 mm [Kobayashi et al. 2015]), number of branchial lamellae (19–26 [Kobayashi et al. 2015]), and vestimental and trunk plaque diameters (59–101 μm and 67–130 μm, respectively [Kobayashi et al. 2015]), Table 3. The number of

sheath lamellae is the only characteristic that is not partially or completely shared by *L. sagami* and *L. columna* (ranges of sheath lamellae reported are 3–6 for *L. sagami* [Kobayashi et al. 2015] and 8–16 for *L. columna* [Southward 1991]).

Discussion

All phylogenetic analyses (Figs. 2 and 3) clearly support the inclusion of the specimens collected off New Zealand within *Lamellibrachia columna*. The minimal base pair differences shown in the haplotype networks (Fig. 3), and the low pairwise distances (corrected and uncorrected) between sequences from *L. columna* and the New Zealand specimens provide strong support for this result. Morphological measurements of the New Zealand specimens fell within or very close to the accepted ranges for diagnostic characters of *L. columna* (Southward 1991; Southward et al. 2011). This morphological similarity can be seen clearly when comparing specimens from New Zealand and Lau in Table 3 and Fig. 4. However, the measurements made of the obturaculum for the New Zealand specimens do show a slight reduction from the previous ranges recorded for this species of 15–42 mm length and 8–13 mm width (Southward 1991; Southward et al. 2011). The New Zealand specimens were below this range (7–13 mm length, 5–8 mm width) and also exhibited some variation in number of branchial lamellae, which has not been previously reported for this species. However, phenotypic plasticity is common in other Vestimentifera, such as *Ridgeia* Jones, 1985 (Southward et al. 1995), and has often been a source of past confusion in differentiation of vestimentiferan species (e.g., *Ridgeia piscescae* Jones, 1985 and its junior synonym *R. phaeophiale* Jones 1985, which exhibited stark morphological differences but no genetic differentiation [Southward et al. 1995]). Furthermore, Southward et al. (1995) suggested that phenotypic plasticity within vestimentiferan species may be a response to physical variation in their environment, and recounted major variation in tubes and various size measurements of *R. piscescae* with environmental differences (Southward et al. 1995).

Table 3 Morphological characters of *Lamellibrachia columna* and *Lamellibrachia sagami*. OL Obturaculum length, OW Obturaculum width, BL Number of branchial lamellae, SL Number of sheath lamellae, VP diameter of vestimental plaques, TP diameter of trunk plaque

Taxon	n	OL (mm)	OW (mm)	BL	SL	VP (μm)	TP (μm)	Reference
<i>Lamellibrachia columna</i>	13	15–42	8–13	21	8–16	65–90	70–120	Southward 1991, Southward et al. 2011
<i>Lamellibrachia columna</i> (New Zealand)	3	7–13	5–8	20–22	14–16	59–60	67–75	This study
<i>Lamellibrachia sagami</i> (holotype, Sagami Bay)	1	15.7	10.5	25	5	67–81	91–102	Kobayashi et al. 2015
<i>Lamellibrachia sagami</i> (paratypes, Sagami Bay)	17	5.8–22.5	4.4–10.8	19–26	3–6	59–101	67–130	Kobayashi et al. 2015
<i>Lamellibrachia sagami</i> (Nankai Trough)	1	10.2	6.8	23	5	58–67	70–104	Kobayashi et al. 2015

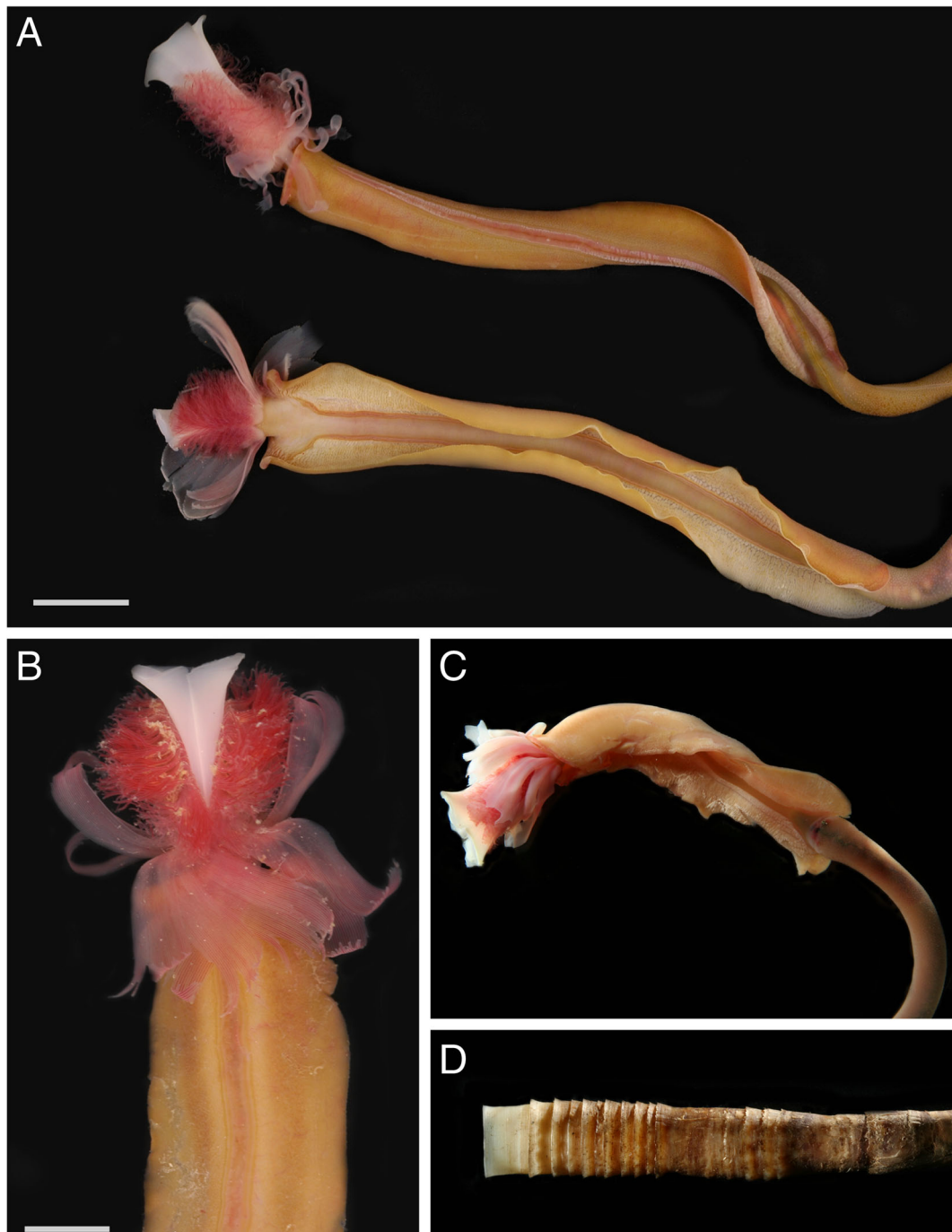


Fig. 4 In situ photographs of *Lamellibrachia columna* (New Zealand NIWA 27133/SIO-BIC A9468 and Lau specimens). **a** Ventral (top) and dorsal (bottom) anterior of two *L. columna* specimens (New Zealand, NIWA 27133/SIO-BIC A9468), scale bar represents 10 mm. **b** Ventral anterior of *L. columna* (New Zealand, NIWA 27133/SIO-BIC A9468), scale bar represents 5 mm. **c** Dorsal anterior of *L. columna* (Lau [Vrijenhoek et al. 2009]). **d** *L. columna* tube anterior (Lau [Vrijenhoek et al. 2009])

Phenotypic plasticity is clearly present within *Lamellibrachia* as well, as is made apparent by the already wide ranges of morphological characters previously established for various *Lamellibrachia* species (Gardiner and Hourdez 2003; Jones 1985; Kobayashi et al.

2015; McCowin and Rouse 2018; Miura et al. 1997; Miura and Kojima 2006; Southward 1991; Webb 1969). Thus, a slight widening of the range for a few morphological traits of *L. columna* is not surprising. We therefore designate the New Zealand *Lamellibrachia* specimens

as *L. columna*, which will extend the geographic range of *L. columna* southward by approximately 1900 km and the depth range of *L. columna* by approximately 1000 m (for a new depth range of 810–1914 m).

All phylogenetic analyses also supported the inclusion of *Lamellibrachia* sp. L2 within *L. columna* (Fig. 2). The phylogenetic tree (Fig. 2) shows a very short branch length between *L. columna* and *L. sp. L2* that is comparable to the branch lengths within *L. juni* (Kojima et al. 2003; Kojima et al. 2001). The haplotype network (Fig. 3) and distance analyses (Table 2) also clearly show that there are few genetic differences between *L. columna* from the type locality and *L. sp. L2*. This similarity has been noted before by Kojima et al. (2001). It was reported in that study that the genetic distance between *L. columna* and *L. sp. L2* was approximately 0.3% (Kojima et al. 2001), which is consistent with the uncorrected distances calculated in this study (Table 2). Based on the previously accepted variation within the *L. juni* clade (Kojima et al. 2003; Kojima et al. 2001) represented numerically by the small corrected and uncorrected pairwise distances of up to 1.39% between *L. juni* specimens from various localities (Table 2), *L. sp. L2* should be considered conspecific with *L. columna*, as it exhibits similarly minute corrected and uncorrected pairwise distances (0.31–0.34%, Table 2) from *L. columna* specimens from the type locality. There is no morphological data published for *L. sp. L2* (Kojima et al. 2003; Kojima 2002; Kojima et al. 2001), but the molecular evidence overwhelmingly supports the referral of *L. sp. L2* sequences to *L. columna*. This will extend the depth range of *L. columna* to 3270 m (Kojima et al. 2001; Kojima et al. 1997) and its geographic range to southeastern Japan. As a result, *L. columna* will represent the most broadly distributed *Lamellibrachia* species to date, with a geographic range spanning approximately 9000 km from the coast of New Zealand to the coast of Japan and a depth range of 810–3270 m. This range extension will also result in the putative geographic sympatry of *L. columna* and *L. sagami*, since both *L. sp. L2* and *L. sagami* have been sampled from the Nankai Trough (Kobayashi et al. 2015; Kojima et al. 2001).

Our results (Fig. 2), and those previously published (Kojima et al. 2001), showed high support for the close sister relationship between *L. sagami* and *L. columna*/*L. sp. L2*. This topology is reminiscent of the level of variation within the *L. juni* clade, which has a similar topology, suggesting that the *L. sagami*/*L. columna*/*L. sp. L2* clade should also represent a single species. The uncorrected and corrected pairwise distances between *L. sagami* and *L. columna* provide additional support for this potential revision. The maximum HKY-corrected distance was 1.35% between *L. columna* and *L. sagami* from their respective type localities, 0.99% between the

sympatric *L. sp. L2* (*L. columna*) and *L. sagami* sequences, and 1.24% between *L. sagami* from Japan and *L. columna* from New Zealand (all uncorrected distances were smaller, Table 2). The small distances between *L. columna* and *L. sagami* and *L. sp. L2* (*L. columna*) recovered in this study have been previously noted, and *L. sagami* (called “*L. sp. L1*” prior to its formal description in 2015) and *L. sp. L2* (now *L. columna*) were reported as potentially “conspecific with *L. columna*” due to their small genetic distances (0.5–1.1%) from *L. columna* (Kojima et al. 2001). Other *Lamellibrachia* species in Japan and New Zealand that are geographically close to or sympatric with *L. columna* and *L. sagami*, such as *L. juni* and *L. satsuma*, are clearly genetically distinct, with uncorrected distances ranging between 5.44 and 8.48% (Table 2). The distance between *L. sagami* and *L. columna* is comparable to distances calculated within the single species *L. juni* (0–1.38% uncorrected, 0–1.39% HKY-corrected). The haplotype network (Fig. 3) of *L. sagami*, *L. columna*, and *L. sp. L2* provides a visual representation of this close relationship (two base-pair distances between haplotypes) which also supports their synonymy. The referral of *L. sp. L2* to *L. columna* in this paper also results in the sympatry of *L. columna* and *L. sagami* off the eastern coast of Japan, with records from each at the Nankai Trough (Kobayashi et al. 2015; Kojima et al. 2001, 2003; Southward 1991; Southward et al. 2011). The morphological data also reveals similarities between *L. sagami* and *L. columna*. Nearly all of the morphological characters of *L. sagami* (obturatorium length and width, plaque diameters, branchial lamellae) closely overlap with the ranges accepted for *L. columna* (Kobayashi et al. 2015; Southward 1991; Southward et al. 2011) (Table 3), except for the number of sheath lamellae, which falls in a smaller range for *L. sagami* (3–6 [Kobayashi et al. 2015]) than for *L. columna* (8–16 [Southward et al. 2011; Southward 1991]). As was made evident by Southward et al. (Southward et al. 1995), phenotypic plasticity is not uncommon in Vestimentifera and has resulted in past confusion regarding species descriptions based heavily on morphology. The molecular analyses, morphological analyses, and geographic sympatry support the synonymy of *L. sagami* with *L. columna*. Past studies have shown low levels of variation in the mitochondrial genes 16S and COI in Vestimentifera (Coward et al. 2014; Coward et al. 2013; McMullin et al. 2003), so further genetic data is required to elucidate more detailed patterns of gene flow in widely distributed species like *L. columna*. However, present evidence, especially the small number of base pair variations and the distance comparison with *L. juni* and other *Lamellibrachia* species, justifies the synonymy of *L. sagami* with *L. columna*. We synonymize the two here and amend the diagnosis of *L. columna* to include the additional

morphological variation represented by its junior synonym *L. sagami* (see below).

Biogeographies of hydrothermal vent fauna indicate that vent fauna of the western Pacific are generally distinct from those of the eastern Pacific (Van Dover et al. 2002; Moalic et al. 2012), but also indicate various levels of latitudinal sub-division among the vent fauna of the western Pacific (Bachraty et al. 2009; Rogers et al. 2012). These sub-divisions presumably represent evolutionary and modern-day processes that influence population connectivity (Mitarai et al. 2016), and while our finding of a high degree of relatedness among *Lamellibrachia columna* from off Japan and New Zealand does not refute the proposed sub-divisions of the overall vent faunal assemblages of the western Pacific, it provides an interesting example of at least one species of chemosynthetic environments that maintains a population across almost the entire latitudinal range of the region. Our study now confirms that *L. columna* is found at both vents and cold seep habitats, and that at the southernmost extent of its range off New Zealand it occurs at seeps, but apparently does not occur at vents off New Zealand. It is possible that environmental conditions at vent sites off New Zealand are not suitable for *L. columna*, where *L. juni* is found (Miura and Kojima 2006), or that the species is yet to be discovered at these sites. Whatever the reason may be for the apparent lack of *L. columna* at vents off New Zealand, our finding of the species at seeps is useful in terms of documenting the extent of the habitat flexibility of *Lamellibrachia*, and for developing a biogeography of cold seep fauna which is much less well-understood than for vent fauna.

Taxonomy

Siboglinidae Caullery, 1914.

Lamellibrachia Webb, 1969.

Lamellibrachia columna Southward, 1991

Lamellibrachia sp. L1 (Sagami Bay, Nankai Trough): Kojima et al. 1997 (*L. sp.* La1-4, Lc1-4, Ld1, Ld2-3, Ld4), p. 509; Kojima et al. 2001, p. 211; Kojima 2002, p. 57; Kojima et al. 2003, p. 625; Kojima et al. 2006, p. 1357; Miura and Kojima 2006, p. 209; Miura and Fujikura 2008, p. 57; Miura and Fujikura 2008, p. 153, Fig. 9.3 A–C.

Lamellibrachia sp. L2 (Nankai Trough): Kojima et al. 1997 (*L. sp.* Le1, Le2), p. 509; Kojima et al. 2001, p. 213; Kojima 2002, p. 346; Kojima et al. 2003, p. 631.

Lamellibrachia sagami new synonym (Sagami Bay): Kobayashi et al. 2015, p. 99. Figs. 2–5.

Material examined: Three specimens were collected from the Builder's Pencil seep site off the east coast of the North Island of New Zealand, between 810 and 817 m, using an epibenthic sled (Station TAN0616/32; 39°

32.4' S, 178° 20.4' W). Two of these specimens are deposited at NIWA (NIWA 27133A, NIWA 27133B), and one specimen is deposited at the Scripps Institution of Oceanography Benthic Invertebrates Collection (SIO-BIC A9468).

Diagnosis (emended): The obturaculum width ranges from 4.4–13 mm (Kobayashi et al. 2015; Southward 1991) and its length ranges from 5.8–42 mm; it is surrounded by the branchial plume (1,8), Fig. 4a–c. There are 19–26 pairs of branchial lamellae surrounding the obturaculum (Kobayashi et al. 2015; Southward 1991). There are 3–16 pairs of sheath lamellae which enclose the crown region and vary in size but are all shorter than the obturaculum, Fig. 4a–c. The smallest lamellae are near the mid-ventral line (Kobayashi et al. 2015; Southward 1991). The anterior edge of the vestimentum forms a collar with a central split (Kobayashi et al. 2015; Southward 1991). Paired dorsal ciliated genital grooves with epidermal folds occur in males (Fig. 4a, c), while females lack epidermal folds and grooves appear less obvious (Kobayashi et al. 2015; Southward 1991). Tubes are fairly straight and smooth, with an anterior diameter ranging from 14 to 20 mm (Southward 1991) (Fig. 4d). Vestimental plaques range in diameter from 58 to 101 µm, while trunk plaques range from 67 to 130 µm in diameter.

Distribution: *Lamellibrachia columna* is known from vents at the Lau Back-arc basin (Black et al. 1997; Braby et al. 2007; Southward 1991), vents and seeps along the middle Honshu coast of Japan (including, but not limited to, the Sagami Bay, Nankai Trough, and Okinawa Trough) (Kobayashi et al. 2015; Kojima et al. 2001; Kojima et al. 1997), and seeps on the Hikurangi margin east of New Zealand, at depths between 270 and 3270 m (Baco et al. 2010; Black et al. 1997; Bowden et al. 2013; Braby et al. 2007; Kobayashi et al. 2015; Kojima et al. 1997, 2001; Southward 1991).

Remarks: Southward's 1991 diagnosis of *Lamellibrachia columna* has been amended to accommodate the inclusion of specimens from New Zealand (NIWA 27133, SIO-BIC A9468), Japan (*L. sp.* L2), and its new junior synonym *L. sagami*. Phylogenetic and morphological evidence suggests that *L. columna* exhibits wider ranges of lamellae counts, plaque diameters, and obturaculum sizes than previously reported.

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Authors' contributions

GWR, AR conceived the paper. AR provided specimens from New Zealand, collection data, and input regarding the manuscript. MM performed DNA extraction and amplification and morphological examination of New Zealand specimens, conducted the molecular and phylogenetic analyses, generated the figures and drafted the manuscript. GWR, AR, and MM then finalized the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

Sequence data generated and/or analyzed during this study are available on GenBank (accession numbers provided in Table 1) (Benson et al. 2005).

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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