

Species boundaries of Gulf of Mexico vestimentiferans (Polychaeta, Siboglinidae) inferred from mitochondrial genes

Maria Pia Miglietta, Stéphane Hourdez, Dominique A. Cowart, Stephen W. Schaeffer, Charles Fisher

► To cite this version:

Maria Pia Miglietta, Stéphane Hourdez, Dominique A. Cowart, Stephen W. Schaeffer, Charles Fisher. Species boundaries of Gulf of Mexico vestimentiferans (Polychaeta, Siboglinidae) inferred from mitochondrial genes. Deep Sea Research Part II: Topical Studies in Oceanography, 2010, 57 (21-23), pp.1916-1925. 10.1016/j.dsr2.2010.05.007. hal-01250940

HAL Id: hal-01250940 https://hal.science/hal-01250940

Submitted on 5 May 2020 $\,$

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution 4.0 International License

Species boundaries of Gulf of Mexico vestimentiferans (Polychaeta, Siboglinidae) inferred from mitochondrial genes

Maria Pia Miglietta ^{a,*}, Stephane Hourdez ^b, Dominique A. Cowart ^a, Stephen W. Schaeffer ^a, Charles Fisher ^a

^a The Pennsylvania State University, Department of Biology, 208 Mueller Lab, University Park, PA 16802-5301, USA ^b Station Biologique de Roscoff, CNRS-UPMC, BP74, 29680 Roscoff, France

At least six morphospecies of vestimentiferan tubeworms are associated with cold seeps in the Gulf of Mexico (GOM). The physiology and ecology of the two best-studied species from depths above 1000 m in the upper Louisiana slope (Lamellibrachia luymesi and Seepiophila jonesi) are relatively well understood. The biology of one rare species from the upper slope (escarpiid sp. nov.) and three morphospecies found at greater depths in the GOM (Lamellibrachia sp. 1, L. sp. 2, and Escarpia laminata) are not as well understood. Here we address species distributions and boundaries of cold-seep tubeworms using phylogenetic hypotheses based on two mitochondrial genes. Fragments of the mitochondrial large ribosomal subunit rDNA (16S) and cytochrome oxidase subunit I (COI) genes were sequenced for 167 vestimentiferans collected from the GOM and analyzed in the context of other seep vestimentiferans for which sequence data were available. The analysis supported five monophyletic clades of vestimentiferans in the GOM. Intra-clade variation in both genes was very low, and there was no apparent correlation between the within-clade diversity and collection depth or location. Two of the morphospecies of Lamellibrachia from different depths in the GOM could not be distinguished by either mitochondrial gene. Similarly, E. laminata could not be distinguished from other described species of Escarpia from either the west coast of Africa or the eastern Pacific using COI. We suggest that the mitochondrial COI and 16S genes have little utility as barcoding markers for seep vestimentiferan tubeworms.

1. Introduction

For the better part of the last century, marine biologists assumed oceans were largely interconnected by currents that enabled larvae and propagules to reach distant shores and assure gene flow even over great distances. More recently, the use of molecular tools has challenged assumptions regarding population structure and speciation in the ocean and demonstrated that marine animals often have genetically distinct populations despite geographic proximity (Palumbi and Warner, 2003). Although sharp genetic breaks between close populations have been recorded throughout the ocean, most of what is known about speciation patterns and phylogeography has been inferred from shallow-water and coastal systems, which represent only about 15% of the aquatic environment. Thus, our knowledge of processes that lead to population divergence and speciation in the

* Corresponding author.

E-mail address: mp.miglietta@psu.edu (M. Pia Miglietta).

open ocean is relatively limited (Thornhill et al., 2008, and references therein; Zardus et al., 2006).

Vestimentiferan tubeworms, which include 10 genera in the polychaete family Siboglinidae (Halanych et al., 2001; Kojima et al., 2002; McMullin et al., 2003; Rouse, 2001), are abundant at deep-sea hydrothermal vents and cold seeps at depths ranging from 80 to 9345 m (Cordes et al., 2007b; Mironov, 2000; Miura et al., 2002). In the deep Gulf of Mexico, six morphospecies have been reported (Cordes et al., 2009). Two described species, Lamellibrachia luymesi (van der Land and Narrevang, 1975) and Seepiophila ionesi (Gardiner et al., 2001), are relatively well studied, and their ecology and physiology are well understood (Bergquist et al., 2002; Cordes et al., 2007a, b). They occur on the upper Louisiana slope at between \sim 500 and 950 m depth and occasionally co-occur with a rare undescribed species, escarpiid sp. nov. The three other morphological species are found on the lower Louisiana slope at depths greater than about 950 m (Lamellibrachia sp. 1, L. sp. 2, and Escarpia laminata).

In this paper, we present phylogenetic hypotheses based on the mitochondrial large ribosomal subunit rDNA gene (16S) and mitochondrial cytochrome oxidase 1 gene (COI) of over 200 vestimentiferans (sequenced for either or both genes) including 180 individuals from the six morphospecies that occur in the Gulf of Mexico. Phylogenetic trees are used to examine the distribution of vestimentiferans in the Gulf of Mexico and their relations to other vestimentiferans around the world. We examined the concordance between the morphological and phylogenetic data to identify differences between the genealogical and morphological species analyzed. Finally, we compared between- and within-species 16S and COI genetic distances and show that these two mitochondrial genes have little utility as "barcoding molecules" for vestimentiferans.

2. Material and methods

2.1. Collection of material

Vestimentiferans were collected in the deep Gulf of Mexico from 12 sites on two cruises in 2006 and 2007, using the DSV ALVIN and R.V. *Atlantis* in 2006 and ROV JASON II and the NOAA ship *Ronald Brown* in 2007 (see Fig. 1). Vestimentiferans were collected using either the Bushmaster Jr. collection device (for samples destined also for community ecology analyses, see Cordes et al., 2010) or the submersible manipulators and placed directly into a collection box. Aboadship, all vestimentiferans were identified using morphological criteria, and subsamples of vestimentum tissue were frozen for subsequent analyses at the Pennsylvania State University. Additional frozen vestimentiferan tissue samples collected previously from shallower sites on the upper Louisiana slope using the DSV JOHNSON SEA LINK were also analyzed for this study (see Table 1 for a complete list of specimens).

2.2. DNA sequencing

DNA was extracted either by boiling a small amount of frozen tissue in $600 \,\mu$ L of 10% Chelex solution (Bio-Rad) or using a CTAB+PVP method modified from Doyle and Doyle (1987), followed by a standard ethanol precipitation.

A 524 bp fragment of the mitochondrial 16S gene was amplified using primers 16Sar and 16Sbr (Kojima et al., 1995). A 689 bp fragment of the mitochondrial gene COI was amplified using the primers HCO and LCO (Folmer et al., 1994). Amplification was performed under the following PCR conditions: $94 \degree C$ (1 min); $50 \degree C$ (2 min); and 72 $\degree C$ (2.5 min) for 30 cycles. All PCR reactions

were performed using 0.5 μ l of each primer, 2.5 μ l of 10XBuffer, 2 μ l of 10 μ M dNTPs, 0.2 μ l of taq, 16.5 μ l of water, and 3 μ l of template. The PCR product was first purified with the ExoSap-it protocol (USB, Affimetrix) and then run on a 2% agarose gel stained with ethidium bromide to enable us to check the quantity and quality of the product. The purified PCR product was used as a template for double-stranded sequencing that was carried out at the Pennsylvania State University Sequencing Core Facility, University Park, Pennsylvania, using ABI 3730 sequencer machines.

2.3. Phylogenetic analysis

Sequences were first assembled and edited using Geneious Pro 4.0.4 (Biomatters Ltd.), and then aligned using ClustalX (Thompson et al., 2002). All alignments were confirmed and edited visually in MacClade 4.06 OS X (Maddison and Maddison, 2000) to insure that indel variation was aligned consistently among all sequenced genes.

Phylogenetic analyses of the aligned sequences were conducted using the maximum parsimony (MP) optimality criterion and neighbor joining (Saitou and Nei, 1987) (NJ) in PAUP* version 4.0b10 for Macintosh (Wilgenbusch and Swofford, 2003), and the maximum likelihood (ML) optimality criterion in GARLI v0.951.OsX-GUI (Zwickl, 2006) and PhylML (Guindon and Gascuel, 2003). The best-fit model used in PhyML and PAUP* was assessed using the akaike information criterion as implemented in modeltest (Posada, 2003; Posada and Crandall, 1998). The best-fit model was (HKY+I+G) for the COI dataset and (GTR+G) for the 16S dataset. Clade stability was assessed by ML bootstrap analysis (Felsenstein, 1985) in GARLI (100 bootstrap replicates) and NJ (1000 replicates) in PAUP*. The ML analyses in GARLI were performed using random starting trees and default termination conditions. Within- and between-species distances were estimated in MEGA 4 (Tamura et al., 2007).

3. Results

The complete COI dataset includes 146 sequences (Table 1) of the six Gulf of Mexico (GOM) cold-seep morphospecies, the available GenBank sequences of *E. southwardae, E. spicata,* and assorted *Lamellibrachia* species from around the world. Sequences from the hydrothermal vent-dwelling genera *Riftia, Oasisia, Tevnia,* and *Arcovestia* were used as outgroups. We restricted our analyses to



Fig. 1. Map of new deep-water collection sites in the Gulf of Mexico.

Table 1

Genbank accension numbers and genes analyzed.

Sample ^a	Clade	Location ^b	GenBank Accession #	Genes
1 AC818	Escarpia laminate	GOM AC818	16S' GU068165	16S/COI
1110010	256alpia ianinate		COI: GU059163	100/001
2 40918	Escarnia laminata	COM AC818	COI: CU059195	COI
2.6018	Escarpia laminata	COM AC818	165, CU069166	165/001
5.AC010	Escurpia ianinata	GOIM ACOTO	105. GU008100	105/001
4.4.0010		CON4 4 CO10	COI: GU059205	100/001
4.AC818	Escarpia laminata	GOM AC818	16S: GU068167	16S/COI
			COI: GU059214	
5.AC818	Escarpia laminata	GOM AC818	16S: GU068168	16S/COI
			COI: GU059222	
6.AC818	Escarpia laminata	GOM AC818	16S: GU068169	16S/COI
			COI: GU059228	
7.AC818	Escarpia laminata	GOM AC818	16S: GU068170	16S/COI
			COI: GU059234	,
8 AC818	Lamellibrachia hyvmesi/sp. 1	COM AC818	16S: GU068171	165
10 GB697	Escarnia laminata	COM GB697	16S: GU068172	165/001
10.00037	Escurpia laminata	dom dboor	COI: CU059164	105/001
11 CR920	Facarnia laminata	COM CR220	165: CU069172	165/001
11.GD029	Escurpia iaminata	GOIM GD829	105. GU008175	105/001
10 (2000)				100/001
12.GB829	Escarpia laminata	GOM GB829	16S: GU068174	16S/COI
			COI: GU059174	
13.GC600	Escarpia laminata	GOM GC600	16S: GU068175	16S
14.GC852	Escarpia laminata	GOM GC852	16S: GU068176	16S/COI
			COI: GU059185	
17.GC852	Escarpia laminata	GOM GC852	16S: GU068177	16S/COI
	I I I I I I I I I I I I I I I I I I I		COI: GU059192	
18 60852	Escarpia laminata	COM CC852	COI: CU059193	COL
10.00052	Escarpia laminata	COM CC852	165: CU069179	165/001
19.60032	Escurpia iaminata	GOW GC852	COL CU050104	103/001
100 46010	Provide Levels and	COM AC 818	COI: GU059194	601
19B.AC818	Escarpia laminata	GOM AC 818	COI: GU059195	COI
20.WR269	Escarpia laminata	GOM WR269	16S: GU068179	16S/COI
			COI: GU059197	
21.WR269	Escarpia laminata	GOM WR269	16S: GU068180	16S/COI
			COI: GU059198	
22.WR269	Escarpia laminata	GOM WR269	16S: GU068181	16S/COI
			COI: GU059199	,
23 WR269	Escarnia laminata	GOM WR269	COI: GU059200	COL
24 WR269	Escarpia laminata	COM WR269	COI: CU059201	COL
26 AT240	Escarpia laminata	COM AT240	165. CU069192	165
20.A1540	Escarpia laminata	GOM AT240	105. GU008182	105
27.AI340	Escarpia iaminata	GOWI AT340	165: GU068183	165/001
			COI: G0059202	
28.A1340	Escarpia laminata	GOM AT340	16S: GU068184	16S/COI
			COI: GU059203	
29.AT340	Escarpia laminata	GOM AT340	16S: GU068185	16S/COI
			COI: GU059204	
30.AT340	Escarpia laminata	GOM AT340	16S: GU068186	16S/COI
	-		COI: GU059206	
31 AT340	Escarnia laminata	GOM AT340	16S. CU068187	16S/COI
	<i>F</i>		COI: CU059207	,
32 473/0	Escarpia laminata	COM AT340	16S: CU068188	165/001
52.71540	Escurpia iaminata	60W //1540	COL: CU050208	105/001
22 472 40	Provide Levels and	COM 47240	COI. GU059208	100/001
33.A1340	Escarpia iaminata	GOM A1340	165: GU068189	165/001
			COI: GU059209	
34.WR264	Escarpia laminata	GOM WR269	16S: GU068190	16S
35.WR269	Escarpia laminata	GOM WR269	16S: GU068191	16S/COI
			COI: GU059210	
37.AC601	Escarpia laminata	GOM AC601	16S: GU068192	16S/COI
			COI: GU059211	
38 AC601	Escarnia laminata	COM AC601	16S: CU068193	16S/COI
50.7 1000 1	Escurpia laminata	Gommedon	COI: CU059212	105/001
20 40601	Escarpia laminata	COM AC601	16S: CU069104	165/001
39.AC001	Escurpia iaminata	GOM ACOUT	COL CU050212	103/001
10 1 0001		0014 40004	COI: GU059213	100/001
40.AC601	Escarpia laminata	GOM AC601	165: GU068195	165/001
			COI: GU059215	
41.AC601	Escarpia laminata	GOM AC601	16S: GU068196	16S
42.AC601	Escarpia laminata	GOM AC602	16S: GU068197	16S/COI
			COI: GU059216	
43.AC601	Escarpia laminata	GOM AC601	16S: GU068198	16S/COI
	a	· · · · -	COI: GU059217	
44 AC601	Escarnia laminata	GOM AC602	16S: GU068199	16S/COI
	Locarpia ianinata	Gom //C002	COL: CLI050218	105/001
45 40601	Ecornic Invincto		160, 00033210	160/007
4J.ACOU1		GUIVI ACOUI		105/001
10.100.10			COI: GU059219	
46.AT340	Escarpia laminata	GOM AT340	16S: GU068201	16S
47.AC601	Escarpia laminata	GOM AC601	16S: GU068202	16S/COI
			COI: GU059220	

Table 1 (continued)

Sample ^a	Clade	Location ^b	GenBank Accession #	Genes
48 AC601	Escarnia laminata	GOM AC601	16S: CU068203	165
10 AC601	Escarpia laminata	COM AC601	16S: CU068204	165/001
49.//001	Escurpia iuminata	GOW ACOUT	COL: CU050221	103/001
50 40601	Eccamia Iaminata	COM AC601	165: CU068205	165/001
50.AC601	escurpia iuminata	GOW ACOUT	105. G0008205	105/001
E1 AT240	Eccamia Iaminata	COM AT240	165, CU068206	165
51.A1540	Escarpia laminata	GOM AT240	105. GU008200	105
52.A1540	Escarpia laminata	GOM ACCOL	105. GU008207	105
54.AC601	Escarpia iaminata	GOM AC601	165: GU068208	165/001
			COI: G0059224	
55.L. luymesi BH	Lamellibrachia luymesi/sp. 1	GOM GC185	16S: GU068209	16S/COI
501 1 00005		6014 CD 207	COI: GU059225	1.00
56.L. sp. 1 GB697	Lamellibrachia luymesi/sp. 1	GOM GB697	16S: GU068210	165
57.L. luymesi GC234	Lamellibrachia luymesi/sp. 1	GOM GC234	165: GU068211	165/001
50 4 0 00 50		6014 66050	COI: GU059226	100/001
58.L. sp. 1 GC852	Lamellibrachia luymesi/sp. 1	GOM GC852	16S: GU068212	16S/COI
			COI: GU059227	
59.L. sp. 1 AC601	Lamellibrachia luymesi/sp. 1	GOM AC601	16S: GU068213	16S
60.L. luymesi BH	Lamellibrachia luymesi/sp. 1	GOM GC185	16S: GU068214	16S
61.L. luymesi BH	Lamellibrachia luymesi/sp. 1	GOM GC185	16S: GU068215	16S
62.L. luymesi BH	Lamellibrachia luymesi/sp. 1	GOM GC185	16S: GU068216	16S/COI
			COI: GU059229	
63.L. luymesi BH	Lamellibrachia luymesi/sp. 1	GOM GC185	16S: GU068217	16S
64.L. luymesi BH	Lamellibrachia luymesi/sp. 1	GOM GC185	16S: GU068218	16S/COI
			COI: GU059230	
65.L. luymesi BH	Lamellibrachia luymesi/sp. 1	GOM GC185	16S: GU068219	16S
66.L. luymesi BH	Lamellibrachia luymesi/sp. 1	GOM GC185	16S: GU068220	16S/COI
			COI: GU059231	
67.L. luymesi BH	Lamellibrachia luymesi/sp. 1	GOM GC185	16S: GU068221	16S
68.L. luymesi BH	Lamellibrachia luymesi/sp. 1	GOM GC185	16S: GU068222	16S/COI
-			COI: GU059232	
69.L. luymesi BH	Lamellibrachia luymesi/sp. 1	GOM GC185	16S: GU068223	16S/COI
5	5 / I		COI: GU059233	,
70.L. luymesi BH	Lamellibrachia luymesi/sp. 1	GOM GC185	16S: GU068224	16S/COI
·····	5 11		COI: GU059235	
71.L. luvmesi BH	Lamellibrachia luvmesi/sp. 1	GOM GC185	16S: GU068225	165
72.L. luvmesi BP	Lamellibrachia luvmesi/sp. 1	GOM GC233	16S: GU068226	16S/COI
			COI: GU059236	,
73.L. sp. 1 GB697	Lamellibrachia luvmesi/sp. 1	GOM GB697	16S: GU068227	16S/COI
	Zamenisraenia raymeerjopr 1		COI: GU059237	100/201
74 L sp 1 GB697	Lamellibrachia luvmesi/sp 1	GOM GB697	16S: GU068228	165
75 I sp 1 GB697	Lamellibrachia luymesi/sp. 1	COM GB697	16S: GU068229	165
761 sp + 62667	Lamellibrachia hymesi/sp. 1	COM GB829	16S: GU068230	165/001
70.E. Sp. 1 GB025	Eunembrachia laymestisp. 1	Gom GB025	COI: GU059238	105/001
77 L sp 1 GB829	Lamellihrachia luvmesi/sp. 1	COM CB829	16S: GU068231	165
781 sp. 1 GB023	Lamellibrachia hymesi/sp. 1	COM CB829	16S: CU068232	165
70.2. Sp. 7 GB023	Lumenibraema taymesiisp. 1	Gom GD025	COI: CU059239	105
791 sp 1 GB829	Lamellibrachia hyvmesi/sp 1	COM CB829	16S: GU068233	165
801 sp 1 GB829	Lamellibrachia hymesi/sp. 1	COM GB829	16S: GU068234	165
81 L hymesi GC234	Lamellibrachia luymesi/sp. 1	COM CC234	16S: GU068235	165
83 L humasi CC234	Lamellibrachia hymesi/sp. 1	COM CC234	165: CU068235	165/001
85.L. luyinesi GC254	Lumenibrachia iaymesi/sp. 1	GOW 6C254	COL: CU050240	105/001
84 L. humasi CC224	Lamollibrachia humosilan 1	COM CC324	165: CU069227	165
84.L. Iuymesi GC234	Lamellibrachia humaci/sp. 1	COM CC224	165, CU062222	105
86 L humesi CC224	Lamellibrachia hymesilsp. 1	COM CC234	165: CU068230	165/001
80.L. Iuymesi GC254	Lumenibrachia iaymesi/sp. 1	GOW GC234	COL CU050241	103/001
88 J sp 1 CC600	Lamellibrachia humesilen 1	COM CC609	16S. CH068240	165/001
88.L. Sp. 1 GC600	Lamenibrachia iuymesi/sp. 1	GOINI GC600	165: GU068240	165/001
00 L 1 CCC00	I and Hill and in Lange silver 1	COM CCC00	COI: GU059242	166/601
89.L. sp. 1 GC600	Lamellibrachia luymesi/sp. 1	GOM GC600	16S: GU068241	16S/COI
001 1 00050		6014 66050	COI: GU059243	100/001
90.L. sp. 1 GC852	Lamellibrachia luymesi/sp. 1	GOM GC852	16S: GU068242	16S/COI
			COI: GU059244	
91. <i>L</i> . sp. 1 GC852	Lamellibrachia luymesi/sp. 1	GOM GC852	16S: GU068243	16S
92. <i>L</i> . sp. 1 GC852	Lamellibrachia luymesi/sp. 1	GOM GC852	16S: GU068244	16S
			COI: GU059245	
93.L. luymesi BH	Lamellibrachia luymesi/sp. 1	GOM GC185	16S: GU068245	16S/COI
			COI: GU059246	
94.L. luymesi BH	Lamellibrachia luymesi/sp. 1	GOM GC185	16S: GU068246	16S
95.L. luymesi BH	Lamellibrachia luymesi/sp. 1	GOM GC185	16S: GU068247	16S
96.L. luymesi BH	Lamellibrachia luymesi/sp. 1	GOM GC185	16S: GU068248	16S
97.L. luymesi GC234	Lamellibrachia luymesi/sp. 1	GOM GC234	16S: GU068249	16S
98.L. luymesi GC234	Lamellibrachia luymesi/sp. 1	GOM GC234	16S: GU068250	16S
99.L. luymesi GC234	Lamellibrachia luymesi/sp. 1	GOM GC234	16S: GU068251	16S/COI
			COI: GU059247	
100.L. sp. 1. WR269	Lamellibrachia luymesi/sp. 1	GOM WR269	16S: GU068252	16S
102.L. sp. 1 WR269	Lamellibrachia luymesi/sp. 1	GOM WR269	16S: GU068253	16S/COI
			COI: GU059165	

Table 1 (continued)

Sample ^a	Clade	Location ^b	GenBank Accession #	Genes
103.L. sp. 1 AT340	Lamellibrachia luymesi/sp. 1	GOM AT340	16S: GU068254	16S/COI
104.L. sp. 1 WR269	Lamellibrachia luymesi/sp. 1	GOM WR269	16S: GU068255	16S/COI
105.L. sp. 1 WR269	Lamellibrachia luymesi/sp. 1	GOM WR269	16S: GU068256	16S/COI
107.L. sp. 1 AC601	Lamellibrachia luymesi/sp. 1	GOM AC601	16S: GU068257	16S/COI
110.L. sp. 1 AC601	Lamellibrachia luymesi/sp. 1	GOM AC601	COI: GU059169 16S: GU068258	16S/COI
112 CP607	Lamallibrachia cp. 2	COM CP607	COI: GU059171	165
112.GB697 113.GB697	Lamellibrachia sp. 2	GOM GB697 GOM GB697	16S: GU068259	165 16S/COI
	r.		COI: GU059172	
114.GB697	Lamellibrachia sp. 2	GOM GB297	16S: GU068261	16S
115.GB697	Lamellibrachia sp. 2	GOM GB297	16S: GU068262	16S
116.GB829	Lamellibrachia sp. 2	GOM GB829	16S: GU068263	16S
117.GC600	Lamellibrachia sp. 2	GOM GC600	16S: GU068264	165
118.GC852	Lamellibrachia sp. 2	GOM GC852	165: GUU68265 COI: CU059173	165/001
119 6 6 8 5 2	Lamellibrachia sp. 2	GOM GC852	16S: GU068266	165
120 GC852	Lamellibrachia sp. 2	GOM GC852	165: GU068267	165
121.WR269	Lamellibrachia sp. 2	GOM WR269	16S: GU068268	165
122.AT340	Lamellibrachia sp. 2	GOM AT340	16S: GU068269	16S/COI
	F		COI: GU059175	,
123.WR2695	Lamellibrachia sp. 2	GOM WR269	16S: GU068270	16S/COI
	L.		COI: GU059176	,
124.AC601	Lamellibrachia sp. 2	GOM AC601	COI: GU059177	COI
126.AC601	Lamellibrachia sp. 2	GOM AC601	COI: GU059178	COI
128.L. sp. 1 AT340	Lamellibrachia luymesi/sp. 1	GOM AT340	16S: GU068271	16S/COI
			COI: GU059179	
130.GB697	Seepiophila jonesi	GOM GB697	16S: GU068272	16S/COI
121 CDC 47	Considerability in and	COM CDC47	COI: GU059180	166/601
131.GB647	Seepiophila Jonesi	GOIM GB647	165: GU068273	165/001
132 ((234	Seenionhila ionesi	COM CC234	16S: CU068274	165/001
152.66254	Seepiophila Jonesi	GOM GC254	COI: CU059182	103/001
133.GC234	Seepiophila ionesi	GOM GC234	16S: GU068275	16S
134.GC234	Seepiophila jonesi	GOM GC234	16S: GU068276	16S/COI
	1 1 5		COI: GU059183	
134b.GC234	Seepiophila jonesi	GOM GC234	16S: GU068277	16S/COI
			COI: GU059184	
135.GC234	Seepiophila jonesi	GOM GC234	16S: GU068278	16S
136.GC234	Seepiophila jonesi	GOM GC234	16S: GU068279	16S
137.BH	Seepiophila jonesi	GOM GC185	16S: GU068280	16S
138.BH	Seepiophila jonesi	GOM GC185	16S: GU068281	16S
139.GC234	Seepiophila jonesi	GOM GC234	16S: GU068282	16S
140. GC234	Seepiophila jonesi	GOM GC234	16S: GU068283	16S
141.GB647	Seepiophila jonesi	GOM GB647	16S: GU068284	16S/COI
142 CDC 47	Comionhile ionori	COM CDC47		100
142.GB047	Seepiophila jonesi	GOM GB647	165: GU068285	165/001
143.60047	seepiophila jonesi	GOINI GB047	COI: CU059187	165/001
144 CB647	Seenionhila ionesi	COM GB647	16S: GU068287	165/COI
111.00017	Seepiophila Jonesi		COI: GU059188	105/201
145.AC818	Escarpia laminata	GOM AC818	16S: GU068288	16S/COI
	•		COI: GU059189	
146.BH	Seepiophila jonesi	GOM GC185	16S: GU068289	16S
147.GB647	Seepiophila jonesi	GOM GB647	COI: GU059190	COI
148.GB647	Seepiophila jonesi	GOM GB647	COI: GU059191	COI
149.AC601	Escarpia laminata	GOM AC601	COI: GU059248	COI
151.GB697	Lamellibrachia luymesi	GOM GB697	COI: GU059250	COI
152.GC234	Lamellibrachia luymesi/sp. 1	GOM GC234	COI: GU059253	COI
153.GC600	Lamellibrachia luymesi/sp. 1	GOM GC600	COI: GU059254	COI
154.NewEscarpidGB485	Escarpiid sp. nov.	GOM GB425	16S: GU068290	16S/COI
155 November 166224	E	COM (C22)4	COI: GU059255	166/601
155.NewescarpiaGC234	Escarpiiu sp. nov.	GUIVI GC234	105: GUU08291 COI: CU050256	105/001
157 L sp 1 GB697	Lamellibrachia luvmesi/sp 1	GOM GB697	COI: GU059229	COL
159 GB697	Seenionhila ionesi	GOM GB697	COI: GU059251	COL
160.GB697	Seepiophila jonesi	GOM GB697	COI: GU059252	COL
161.GC234	Lamellibrachia luvmesi/sp. 1	GOM GC234	XXX-XXX	COI
162.GC600	Lamellibrachia luymesi/sp. 1	GOM GC600	xxx-xxx	COI
165.GC852	Lamellibrachia sp. 2	GOM GC852	XXX-XXX	COI
166.L.sp1 AT340	Lamellibrachia luymesi/sp. 1	GOM AT340	xxx-xxx	COI
S. jonesi BH	Seepiophila jonesi	GOM GC185	AF317287	COI
S. jonesi GB425	Seepiophila jonesi	GOM GB425	AF317288	COI

Table 1 (continued)

Jandwardi Landblrachia laymesi COM CC234 MY2D135 COI Arcovestia Arcovestia inanciana West Pacific MY2D135 COI Arcovestia Arcovestia inanciana West Pacific MY2D136 COI E sontibroutine 1 Escargia fautimata West Africa MY2B3030 COI E sontibroutine 2 Escargia southwardae West Africa MY2B3030 COI E sontibroutine 2 Escargia southwardae West Africa MY2B3030 COI E sontibroutine 2 Escargia southwardae West Africa MY2B4001 COI CossistiafaploP Cassis drinnee Ess Pacific MY4B4001 COI CossistiafaploP Cassis drinnee Ess Pacific MY4B4001 COI CossistiafaploP CassistiafaploP CossistiafaploP COI ConsistiafaploP Coi Cam.2007Asymptin Lamellibrachia barbami Ess Pacific MY2D137 COI Cam.2007Asymptin Lamellibrachia barbami Ess Pacific MY12D145 COI Cam.2007Asymptin	Sample ^a	Clade	Location ^b	GenBank Accession #	Genes	
Bashbranchia mariana 1 Mestmantia mariana 1 West Pacific M2078 C01 Acrovestia Acrovestia wonovi West Malaric AB073491 C01 E iomihuada Excarpia burinata West Affacia M20303 C01 E iomihuada Excarpia southwordae West Affacia M2320303 C01 E southwordae Escarpia southwordae West Affacia M3220303 C01 E southwordae Est Pacific M464001 C01 Conscientinghof C01 Descisidrapiof Cassia drinae Est Pacific M7464016 C01 Conscientinghof Cassia drinae Est Pacific M7464016 C01 Lam.2000Anaki Lamellibrachia sp. West Pacific M20373 C01 Lam.200Anami10 Lamellibrachia barbarni Est Pacific M7129138 C01 Lam.200Anami31 Lamellibrachia barbarni Est Pacific M7129143 C01 Lam.200Anami31 Lamellibrachia barbarni Est Pacific M7129143 C01 Lam.200Anami30 Lamellibrachia	Lamluymesi GC234	Lamellibrachia luymesi	GOM GC234	AY129136	COI	
Arcosetia Arcosetia isonovi West Pacific Montpace Coll E. lominata Escarpia suthwardae West Africa V7326304 Coll E. southwardae West Africa V7326304 Coll E. southwardae West Africa V7326304 Coll E. southwardae Est Pacific V746610 Coll Oussisid abine Est Pacific V7466001 Coll Oussisid abine Est Pacific V7466001 Coll Oussisid abine Est Pacific V7466001 Coll Lam.2000Anakk Lamellbrachicis p. West Pacific B808674 Coll Lam.30xSagami Lamellbrachicis p. West Pacific AV129137 Coll Lam.30xSagami Lamellbrachicis barhami Est Pacific V7129134 Coll Lam.30xMannibi Lamellbrachicis barhami Est Pacific V7129134 Coll Lam.30xMannibi Lamellbrachicis barhami Est Pacific V7129143 Coll Lam.30xMannibi Lamellbrachicis barhami Est Pacific	Basibranchia mariana 1	Basibranchia mariana	West Pacific	U74078	COI	
E. Immination Example annihumation West Africa U74063 COI E. southwordne 1 Example southwordne West Africa M326303 COI E. southwordne 2 Example southwordne West Africa M326303 COI E. splictat Example southwordne Exat Pacific M34622 COI Dassisti daylop Oosisia daylone Exat Pacific AV64601 COI Oasisid laylop Oosisia daylone Exat Pacific D50592 COI DamazdooNapati Lamelibrachia pap West Pacific D50592 COI Lam.2000Nataki Lamelibrachia partonia Exat Pacific D101317 COI Lam.abrhami11b Lamelibrachia brhami Exat Pacific AV129137 COI Lam.brhami8b Lamelibrachia brhami Exat Pacific AV129145 COI Lam.brhami8b Lamelibrachia brhami Exat Pacific AV129145 COI Lam.brhami8b Lamelibrachia brhami Exat Pacific AV129145 COI Lam.brhami8 Lamelibrachia brhami <t< td=""><td>Arcovestia</td><td>Arcovestia ivanovi</td><td>West Pacific</td><td>AB073491</td><td>COI</td></t<>	Arcovestia	Arcovestia ivanovi	West Pacific	AB073491	COI	
E. southwardae 1 Exarpia southwardae West Africa A*326304 COI E. southwardae Escarpia spicata East Pacific A*326303 COI E. spl.t.b Lamelharachia kuymesiyan GOM AT340 Ur40611 COI Oasisida HaploA Desisia abrinae East Pacific A*6640016 COI Oasisida HaploA Desisia abrinae East Pacific A*664016 COI Lam.3005agami Lamelharachia sp. West Pacific A*8088674 COI Lam.3005agami Lamelharachia sp. West Pacific A*129137 COI Lam.barhami10b Lamelharachia barhami East Pacific A*129147 COI Lam.barhami4 Lamelharachia barhami East Pacific A*129147 COI Lam.barhami4 Lamelharachia barhami East Pacific A*129143 COI Lam.barhami4 Lamelharachia barhami East Pacific A*129144 COI Lam.barhami4 Lamelharachia barhami East Pacific A*129144 COI Lamabarhami4 Lamelharachia barhami	E. laminata	Escarpia laminata	West Atlantic	U74063	COI	
E. soukhwardae 2 Escarpia southwardae West Africa AV326303 COI E. spictat Escarpia southwardae Est Pacific U44061 COI L. sp. 1.b Lamelibrachia laymesişp. 1 GOM AT340 U74061 COI Oasisid alyhae East Pacific AV646016 COI Oasisid alyhae Lamelibrachia sp. West Pacific D300592 COI Lam.300Sagami Lamelibrachia sp. West Pacific D300592 COI Lam.brhami10b Lamelibrachia brhami East Pacific AV129137 COI Lam.brhami10b Lamelibrachia brhami East Pacific AV129147 COI Lam.brhami7 Lamelibrachia brhami East Pacific AV129143 COI Lam.brhami8 Lamelibrachia brhami East Pacific AV12	E. southwardae 1	Escarpia southwardae	West Africa	AY326304	COI	
E. spich Esarpia spicata Esar Pacific 084262 COI Oassida HaploA Oassida divinae Esar Pacific AY646016 COI Oassida HaploA Oassida divinae Esar Pacific AY646016 COI Lama 3005agami Lamelibrachia sp. West Pacific A8088674 COI Lama bottami fulti Lamelibrachia sp. West Pacific A8088674 COI Lam.barbami 10b Lamelibrachia barbami Esar Pacific AY129137 COI Lam.barbami/10b Lamelibrachia barbami Esar Pacific AY129145 COI Lam.barbami/91 Lamelibrachia barbami Esar Pacific AY129145 COI Lam.barbami/91 Lamelibrachia barbami Esar Pacific AY129145 COI Lam.barbami/91 Lamelibrachia barbami Esar Pacific VA1054 COI Lam.barbami/91 Lamelibrachia barbami Esar Pacific VA1054 COI Lam.barbami/91 Lamelibrachia barbami Esar Pacific VA1054 COI Lam.barbami/91 Lamelibrachia barbami	E. southwardae 2	Escarpia southwardae	West Africa	AY326303	COI	
L spl.1.b Lomellibrachia hymesiys.1 GOM AT340 U74061 COI Oasisid aploP Oasis a dvinae East Pacific AY64001 COI Oasisid aploP Oasis a dvinae East Pacific AY64001 COI Consolvanaki Lamellibrachia sp. West Pacific AB088674 COI Lam.3005agami Lamellibrachia sp. West Pacific AY129137 COI Lam.brdnmi10b Lamellibrachia brahami East Pacific AY129138 COI Lam.brdnmi10b Lamellibrachia brahami East Pacific AY129146 COI Lam.brdnmi10b Lamellibrachia brahami East Pacific AY129146 COI Lam.brdnmi37 Lamellibrachia brahami East Pacific AY129146 COI Lam.brdnmi39 Lamellibrachia brahami East Pacific AY129145 COI Lam.brdnmi39 Lamellibrachia brahami East Pacific AY129141 COI Lam.brdnmi39 Lamellibrachia brahami East Pacific U74054 COI Lam.brdnmi30 Lamellibrachia brahami East Pacific U74054 COI Lam.brdnmi30 Lamellibrachia brahami East Pacific U74054 COI Lam.brdnmi30 Lamellibrachia brahami East Pacific U74051 COI Lam.brdnmi30 Lamellibrachia brahami East Pacific U74051 COI Lam.brdnmi30 Lamellibrachia brahami East Pacific BA151645 ISS L brahami3 Lamellibrachia brahami East Pacific BA28388 COI Lam.brdnmi30 Lamellibrachia brahami East Pacific BA28388 COI Lam.brdnmi30 Lamellibrachia brahami East Pacific BA28388 COI Lam.juni Lamellibrachia juni West Pacific BA28388 COI COI Lam.juni taplo3 Lamellibrachia juni West Pacific BA284808 COI Lam.juni taplo3 Lamellibrachia juni West Pacific BA284808 COI Lam.junestRHA Lamellibrachia juni West Pacific BA284808 COI Lam.junestRHA Lamellibrachia juni West Paci	E. spicata	Escarpia spicata	East Pacific	U84262	COI	
OasisidaploAOasis advinaeEast PacificAV64601COIConsisidaploPOasis advinaeEast PacificA964016COILam.2005aganiLamellibrachia sp.West PacificA908874COILam.3005aganiLamellibrachia sp.West PacificA93029COILam.barhami10bLamellibrachia barhamiEast PacificAY129137COILam.barhami11bLamellibrachia barhamiEast PacificAY129147COILam.barhami11bLamellibrachia barhamiEast PacificAY129147COILam.barhami31bLamellibrachia barhamiEast PacificAY129147COILam.barhami31bLamellibrachia barhamiEast PacificAY129143COILam.barhami39Lamellibrachia barhamiEast PacificAY129143COILam.barhami30Lamellibrachia barhamiEast PacificAP15045165Lam.barhami3Lamellibrachia barhamiEast PacificAP515045COILam.barhami3Lamellibrachia barhamiEast PacificAP515045165Lam.columna 1Lamellibrachia columnaWest PacificAB24883COILam.columna 1Lamellibrachia columnaWest PacificAB24801COILam.juritaplo1Lamellibrachia juriWest PacificAB24801COILam.juritaplo3Lamellibrachia juriWest PacificAB24801COILam.juritaplo3Lamellibrachia juriWest PacificAB264003COILam.juritaplo4Lamellibrachia juriWes	<i>L</i> . sp.1_b	Lamellibrachia luymesi/sp. 1	GOM AT340	U74061	COI	
ObsisticalpioP Ossista alvinae East Pacific AV546016 COI Lam.2000Nanaki Lamellibrachia sp. West Pacific AB088674 COI Lam.300Sagami Lamellibrachia sp. West Pacific AB0029 COI Lam.bottomi T0b Lamellibrachia barhami East Pacific AY129137 COI Lam.bottomi T0b Lamellibrachia barhami East Pacific AY129147 COI Lam.barhamiT0b Lamellibrachia barhami East Pacific AY129147 COI Lam.barhamiMb Lamellibrachia barhami East Pacific AY129143 COI Lam.barhamiBb Lamellibrachia barhami East Pacific AY4054 COI Lam.barhamiBb Lamellibrachia barhami East Pacific AY4054 COI Lam.barhamiB Lamellibrachia barhami East Pacific AP20541 COI Lam.barhamiB Lamellibrachia barhami East Pacific AP20541 COI Lam.barhamiB Lamellibrachia parimi East Pacific AP205401 COI Lam.barhamiB Lamellibr	OasisiaHaploA	Oasisia alvinae	East Pacific	AY646001	COI	
Lam.2005apami Lamellbrachia sp. West Pacific D50592 C01 Lam.3005apami Lamellbrachia sp. West Pacific D38029 C01 Lam.borbami110b Lamellbrachia sp. West Pacific D38029 C01 Lam.borbami110b Lamellbrachia barbami East Pacific AV129137 C01 Lam.borbami170b Lamellbrachia barbami East Pacific AV129146 C01 Lam.borbami71 Lamellbrachia barbami East Pacific AV129145 C01 Lam.borbami8b Lamellbrachia barbami East Pacific AV129145 C01 Lam.borbami7 Lamellbrachia barbami East Pacific AV129145 C01 Lam.borbami3 Lamellbrachia barbami East Pacific AV129145 C01 Lam.borbami7 Lamellbrachia barb	OasisiaHaploP	Oasisia alvinae	East Pacific	AY646016	COI	
Lam.3005sgami Lamelibrachia sp. West Pacific AB088674 COI Lam.3005sgami Lamelibrachia barhami Est Pacific AT129137 COI Lam.barhami10b Lamelibrachia barhami Est Pacific AT129136 COI Lam.barhami11b Lamelibrachia barhami Est Pacific AT129146 COI Lam.barhami11b Lamelibrachia barhami Est Pacific AT129146 COI Lam.barhami8b Lamelibrachia barhami Est Pacific AT129146 COI Lam.barhami9i Lamelibrachia barhami Est Pacific AT150455 I685 Lam.barhami8 Lamelibrachia barhami Est Pacific AF315045 I685 Lam.columma Lamelibrachia columna West Pacific AF315045 I685 Lam.columna Lamelibrachia columna West Pacific AF324875 COI Lam.junitaplo1 Lamelibrachia juni West Pacific AF3248601 COI Lam.aufitaplo2 Lamelibrachia juni West Pacific AF324603 COI Lam.junitaplo3 Lamelibrachi	Lam.2000Nanaki	Lamellibrachia sp.	West Pacific	D50592	COI	
Lam.3053gani 1Lamelibrachia sp.West PacificD38029COILam.borhami10bLamelibrachia barhamiEast PacificAY129137COILam.borhami11bLamelibrachia barhamiEast PacificAY129146COILam.borhami71Lamelibrachia barhamiEast PacificAY129146COILam.borhami8bLamelibrachia barhamiEast PacificAY129143COILam.borhami90Lamelibrachia barhamiEast PacificAY129143COILam.borhami90Lamelibrachia barhamiEast PacificAY129143COILam.borhami91Lamelibrachia barhamiEast PacificAY135045165L. barhami3Lamelibrachia barhamiEast PacificA7315045165Lam.columnaLamelibrachia columnaWest PacificA8315045165Lam.columnaLamelibrachia columnaWest PacificA82248001COILam.juni1api01Lamelibrachia juniWest PacificA82248001COILam.juni1api02Lamelibrachia juniWest PacificA8224803COILam.juni1api04Lamelibrachia juniWest PacificA8204602COILam.juni1api04Lamelibrachia juniWest PacificA8204603COILam.juni1api04Lamelibrachia juniWest PacificA805500COILam.juni1api04Lamelibrachia juniWest PacificA805500COILam.juni1api04Lamelibrachia junesiGOM CCI85AY129133COILam.juni1api05Lamelibrachia junesiGOM	Lam.300Sagami	Lamellibrachia sp.	West Pacific	AB088674	COI	
Lam.barhami10bLamellibrachia borhamiEast PacificAY129137COILam.barhami4bLamellibrachia borhamiEast PacificAY129143COILam.barhami4bLamellibrachia borhamiEast PacificAY129146COILam.barhami7bLamellibrachia borhamiEast PacificAY129146COILam.barhami8bLamellibrachia borhamiEast PacificAY129146COILam.barhami8bLamellibrachia borhamiEast PacificU7054COILam.barhami8bLamellibrachia borhamiEast PacificU7054COILam.barhami8Lamellibrachia borhamiEast PacificU7054COILam.columnaLamellibrachia borhamiEast PacificU7061COILam.columnaLamellibrachia columnaWest PacificAB264601COILam.juni1Lamellibrachia juniWest PacificAB264603COILam.juni1aplo1Lamellibrachia juniWest PacificAB264603COILam.juni1aplo3Lamellibrachia juniWest PacificAB264603COILam.juni1aplo4Lamellibrachia juniWest PacificAB264603COILam.juni1aplo5Lamellibrachia juniWest PacificAB264603COILam.juni1aplo5Lamellibrachia juniWest PacificAB264603COILam.juni1aplo5Lamellibrachia juniWest PacificAB264603COILam.juni1aplo5Lamellibrachia juniWest PacificAB264603COILam.juni1aplo5Lamellibrachia juni	Lam.300Sagami 1	Lamellibrachia sp.	West Pacific	D38029	COI	
Lam.barhami 1bLamellibrachia borhamiEast PacificAY129138COILam.barhami7bLamellibrachia borhamiEast PacificAY129147COILam.barhami7bLamellibrachia borhamiEast PacificAY129143COILam.barhami8bLamellibrachia borhamiEast PacificAY129141COILam.barhami8bLamellibrachia borhamiEast PacificAY129141COILam.barhami9Lamellibrachia borhamiEast PacificAY13045IsSL barhami3Lamellibrachia borhamiEast PacificAY315045IsSL barhami3Lamellibrachia borhamiEast PacificAY315045OILam.columnaLamellibrachia columnaWest PacificAB24258COILam.juni1Lamellibrachia juniWest PacificAB246001COILam,juni1Aplo1Lamellibrachia juniWest PacificAB264602COILam,juni1Aplo3Lamellibrachia juniWest PacificAB264603COILam,juni1Aplo4Lamellibrachia juniWest PacificAB264603COILam,juni1Aplo5Lamellibrachia juniWest PacificAB264603COILamJuni1Aplo4Lamellibrachia juniWest PacificAB264603COILamJuni1Aplo5Lamellibrachia p.West PacificAB264603COILamJumi3Palo4Lamellibrachia p.West PacificAB264603COILamJumi3Palo5Lamellibrachia p.West PacificAB264603COILamJumesiBHLamellibrachia pumesiGOM CCIS	Lam.barhami10b	Lamellibrachia barhami	East Pacific	AY129137	COI	
Lam.barhami4bLamellibrachia barhamiEast PacificN129147COILam.barhami8bLamellibrachia barhamiEast PacificN129146COILam.barhami8bLamellibrachia barhamiEast PacificN129141COILam.barhami8bLamellibrachia barhamiEast PacificN129141COILam.barhamibLamellibrachia barhamiEast PacificN130451685L. barhami3Lamellibrachia barhamiEast PacificN7315045165LancolumnaLamellibrachia barhamiEast PacificN4315045001Lam.columna 1Lamellibrachia columnaWest PacificA8242858COILam.juniLamellibrachia juniWest PacificA82426401COILam.juniHaplo1Lamellibrachia juniWest PacificA8264603COILam.juniHaplo3Lamellibrachia juniWest PacificA8264603COILam.juniHaplo4Lamellibrachia juniWest PacificA8264603COILam.juniHaplo5Lamellibrachia juniWest PacificA8264603COILam.juniHaplo5Lamellibrachia juniWest PacificA8264603COILam.juniHaplo5Lamellibrachia piniWest PacificA8055210COILam.juniHaplo5Lamellibrachia piniWest PacificA8058675COILam.juniHaplo5Lamellibrachia hymesiCOM CC185A7129132COILam.juniHaplo5Lamellibrachia hymesiCOM CC185A7129132COILam.junesiBHLamellibrachia hymesiC	Lam.barhami11b	Lamellibrachia barhami	East Pacific	AY129138	COI	
Lam.barhamin7Lamellibrachia barhamiEast PacificAY129145COILam.barhamin8bLamellibrachia barhamiEast PacificAY129145COILam.barhamin9Lamellibrachia barhamiEast PacificU74054COIL. barham3Lamellibrachia barhamiEast PacificN7315045165L. barham3Lamellibrachia barhamiEast PacificN4061COILam.colummaLamellibrachia columnaWest PacificN4061COILam.juniLamellibrachia columnaWest PacificAB224858COILam.juni1Lamellibrachia juniWest PacificAB264602COILam.juni14aplo1Lamellibrachia juniWest PacificAB264602COILam.juni14aplo3Lamellibrachia juniWest PacificAB264602COILam.juni14aplo4Lamellibrachia juniWest PacificAB264603COILam.juni14aplo5Lamellibrachia juniWest PacificAB264603COILam.juni14aplo5Lamellibrachia juniWest PacificAB264604COILam.juni14aplo5Lamellibrachia juniWest PacificAB264603COILam.juni14aplo5Lamellibrachia sp.West PacificAB055210COILamL4Lamellibrachia sp.West PacificAB055210COILamL5Lamellibrachia sp.West PacificAB055210COILamL4Lamellibrachia sp.West PacificAB055210COILamL4Lamellibrachia sp.West PacificAB055210COI <td>Lam.barhami4b</td> <td>Lamellibrachia barhami</td> <td>East Pacific</td> <td>AY129147</td> <td>COI</td>	Lam.barhami4b	Lamellibrachia barhami	East Pacific	AY129147	COI	
Lam.barhami8bLamellibrachia barhamiEast PacificAY129143COILam.barhami9Lamellibrachia barhamiEast PacificAY129141COIL barhami2Lamellibrachia barhamiEast PacificA7315045165L barhami3Lamellibrachia barhamiEast PacificA7315045165Lam.columnaLamellibrachia barhamiEast PacificA7315045165Lam.columnaLamellibrachia columnaWest PacificA8024253COILam.juniLamellibrachia juniWest PacificA8244601COILam.juniLamellibrachia juniWest PacificA824603COILam.juniHaplo1Lamellibrachia juniWest PacificA8264603COILam.juniHaplo3Lamellibrachia juniWest PacificA8264603COILam.juniHaplo4Lamellibrachia juniWest PacificA8264603COILam.JuniHaplo5Lamellibrachia juniWest PacificA8264603COILam.JuniHaplo5Lamellibrachia juniWest PacificA8055209COILam.JuniHaplo5Lamellibrachia sp.West PacificA8088674COILam.JuniHaplo5Lamellibrachia sp.West PacificA8088674COILam.lymesiBH2Lamellibrachia lymesiCOM CC185A7129133COILam.lymesiBH2Lamellibrachia lymesiCOM CC185A712913COILam.lymesiBH2Lamellibrachia lymesiCOM CC233A7129134COILam.lymesiBH2Lamellibrachia lymesiCOM CC234A	Lam.barhami7	Lamellibrachia barhami	East Pacific	AY129146	COI	
Lam.barhami9Lamellibrachia barhamiEast PacificAY129141CO1L.barhami2Lamellibrachia barhamiEast PacificU74064CO1L. barhami3Lamellibrachia barhamiEast PacificAF315045165Lam.columnaLamellibrachia columnaWest PacificU74061CO1Lam.columna 1Lamellibrachia columnaWest PacificAB055210CO1Lam.juni1Lamellibrachia columnaWest PacificAB24858CO1Lam.juni1Lamellibrachia juniWest PacificAB264601CO1Lam.juni1Aplo2Lamellibrachia juniWest PacificAB264603CO1Lam.juni1Aplo3Lamellibrachia juniWest PacificAB264603CO1Lam.juni1Aplo4Lamellibrachia juniWest PacificAB264603CO1Lam.juni1Aplo4Lamellibrachia juniWest PacificAB264604CO1Lam.loLamellibrachia juniWest PacificAB264605CO1Lam.Juni1Aplo5Lamellibrachia sp.West PacificAB264603CO1Lam.JoLamellibrachia sp.West PacificAB08674CO1Lam.LoLamellibrachia sp.West PacificAB08674CO1Lam.LoLamellibrachia sp.West PacificAB08674CO1Lam.LoymesiBH5Lamellibrachia luymesiGOM GC185AY129133CO1Lam.LoymesiBH5Lamellibrachia luymesiGOM GC185AY129130CO1Lam.LoymesiCA525Lamellibrachia luymesiGOM GC33AY129134CO1<	Lam.barhami8b	Lamellibrachia barhami	East Pacific	AY129145	COI	
LambarhamihLamellibrachia barhamiEast PacificU74054C01L. barhami2Lamellibrachia barhamiEast PacificAF315045165L. barhami3Lamellibrachia columnaWest PacificAB055210C01Lam.columna 1Lamellibrachia columnaWest PacificAB055210C01Lam.juniLamellibrachia columnaWest PacificAB242858C01Lam.juniHaplo1Lamellibrachia juniWest PacificAB264601C01Lam.juniHaplo2Lamellibrachia juniWest PacificAB264602C01Lam.juniHaplo3Lamellibrachia juniWest PacificAB264603C01Lam.juniHaplo3Lamellibrachia juniWest PacificAB264603C01Lam.juniHaplo4Lamellibrachia juniWest PacificAB264603C01Lam.luLamellibrachia juniWest PacificAB055209C01Lam.luLamellibrachia sp.West PacificAB055210C01Lam.luLamellibrachia sp.West PacificAB055209C01Lam.luLamellibrachia sp.West PacificAB055209C01Lam.luLamellibrachia sp.West PacificAB055210C01Lam.lumesiBH 2Lamellibrachia luymesiGOM GC185AY129133C01Lam.luymesiBH 2Lamellibrachia luymesiGOM GC185AY129133C01Lam.luymesiBH 2Lamellibrachia luymesiGOM GC233AY129133C01Lam.luymesiBH 2Lamellibrachia luymesiGOM GC185AY129134C01 </td <td>Lam.barhami9</td> <td>Lamellibrachia barhami</td> <td>East Pacific</td> <td>AY129141</td> <td>COI</td>	Lam.barhami9	Lamellibrachia barhami	East Pacific	AY129141	COI	
L barhami2Lamellibrachia barhamiEast PacificAP31504516SL barhami3Lamellibrachia columnaWest PacificAP31504516SLam.columna 1Lamellibrachia columnaWest PacificAB055210COILami,uniLamellibrachia juniWest PacificAB242858COILami,uni 1Lamellibrachia juniWest PacificAB248601COILami,uni Haplo1Lamellibrachia juniWest PacificAB264602COILami,uni Haplo2Lamellibrachia juniWest PacificAB264603COILami,uni Haplo3Lamellibrachia juniWest PacificAB264603COILami,uni Haplo5Lamellibrachia juniWest PacificAB264605COILami,uni Haplo5Lamellibrachia juniWest PacificAB055210COILami,uni Haplo5Lamellibrachia sp.West PacificAB055210COILamL4Lamellibrachia sp.West PacificAB088675COILamL5Lamellibrachia sp.West PacificAB088675COILamLymesiBH 2Lamellibrachia lymesiGOM GC185AY129133COILam.hymesiBPLamellibrachia lymesiGOM GC354AY129139COILam.hymesiBPLamellibrachia lymesiGOM GC354AY129136COILam.hymesiC4252Lamellibrachia satsumaWest PacificAB242671COILam.hymesiG4252Ecarpii d sp. nov.GOM GC354AY129136COILam.hymesiG4254Ecarpii d sp. nov.GOM GC354AY129136	Lam.barhamib	Lamellibrachia barhami	East Pacific	U74054	COI	
L. barhami3Lamellibrachia barhamiEast PacificAP31504516SLam.columnaLamellibrachia columnaWest PacificAB055210COILam.juniLamellibrachia columnaWest PacificAB24801COILam.juniLamellibrachia juniWest PacificAB264601COILam.juniHaplo1Lamellibrachia juniWest PacificAB264603COILam.juniHaplo2Lamellibrachia juniWest PacificAB264603COILam.juniHaplo3Lamellibrachia juniWest PacificAB264603COILam.juniHaplo5Lamellibrachia juniWest PacificAB264604COILam.juniHaplo5Lamellibrachia juniWest PacificAB055209COILamL5Lamellibrachia sp.West PacificAB055210COILamL5Lamellibrachia sp.West PacificAB088674COILamL7Lamellibrachia sp.West PacificAB088674COILamLymesiBH 2Lamellibrachia tymesiCOM CC185AY129132COILam.hymesiBH 5Lamellibrachia lymesiGOM CC185AY129135COILam.hymesiGC354Lamellibrachia lymesiGOM CC344AY12913COILam.hymesiGC452Escarpid sp. nov.GOM CC354AY129134COILam.hymesiGC454Lamellibrachia lymesiGOM CG354AY129134COILam.hymesiGC454Escarpid sp. nov.GOM CG354AY129136COIColsisia fujikuraiOasisa fujikuraiSouth/West PacificAB242857COI <td>L. barhami2</td> <td>Lamellibrachia barhami</td> <td>East Pacific</td> <td>AF315045</td> <td>16S</td>	L. barhami2	Lamellibrachia barhami	East Pacific	AF315045	16S	
Lam.columnaLamellibrachia columnaWest PacificU74061COILam.columna 1Lamellibrachia juniWest PacificAB055210COILam.juniHaplo1Lamellibrachia juniWest PacificAB24858COILam.juniHaplo2Lamellibrachia juniWest PacificAB264601COILam.juniHaplo3Lamellibrachia juniWest PacificAB264602COILam.juniHaplo3Lamellibrachia juniWest PacificAB264603COILam.juniHaplo4Lamellibrachia juniWest PacificAB264604COILam.juniHaplo5Lamellibrachia juniWest PacificAB264605COILam.juniHaplo5Lamellibrachia sp.West PacificAB055210COILamL4Lamellibrachia sp.West PacificAB088674COILamL5Lamellibrachia sp.West PacificAB088675COILamL4Lamellibrachia luymesiGOM GC185AY129133COILamLymesiBH 2Lamellibrachia luymesiGOM GC233AY129132COILam.luymesiBH5Lamellibrachia luymesiGOM GC354AY129126COILam.luymesiBH5Lamellibrachia luymesiGOM GC354AY129132COILam.luymesiBH5Lamellibrachia luymesiGOM GC4825AY129134COILam.luymesiVKLamellibrachia luymesiGOM GC354AY129134COILam.luymesiVKLamellibrachia luymesiGOM GC4825AY129134COILam.luymesiVKLamellibrachia satsumaWest PacificAB34671 <td>L. barhami3</td> <td>Lamellibrachia barhami</td> <td>East Pacific</td> <td>AF315045</td> <td>16S</td>	L. barhami3	Lamellibrachia barhami	East Pacific	AF315045	16S	
Lam.columna 1Lamellibrachia columnaWest PacificAB05210COILam.juniLamellibrachia juniWest PacificAB24858COILam.juniHaplo1Lamellibrachia juniWest PacificAB264601COILam.juniHaplo2Lamellibrachia juniWest PacificAB264603COILam.juniHaplo3Lamellibrachia juniWest PacificAB264603COILam.juniHaplo5Lamellibrachia juniWest PacificAB264603COILam.juniHaplo5Lamellibrachia juniWest PacificAB055209COILam.loLamellibrachia sp.West PacificAB05874COILamL5Lamellibrachia sp.West PacificAB088675COILamL04Lamellibrachia sp.West PacificAB088674COILamLymesiBH 2Lamellibrachia luymesiGOM GC185AY129133COILamLuymesiBH2Lamellibrachia luymesiGOM GC185AY129132COILam.luymesiBH5Lamellibrachia luymesiGOM GC354AY129135COILam.luymesiCG354Lamellibrachia luymesiGOM VK826AY129126COILam.luymesiCG354Lamellibrachia luymesiGOM VK826AY129134COILam.luymesiCG354Lamellibrachia sq. from Med.MediterraneanEU046616COILam.luymesiCG354Lamellibrachia sq. from Med.MediterraneanEU046616COILam.luymesiCG354Lamellibrachia sq. from Med.MediterraneanEU046616COILam.luymesiCG354Lamellibrachia sq. fro	Lam.columna	Lamellibrachia columna	West Pacific	U74061	COI	
Lam.juniLamellibrachia juniWest PacificAB242858COILam.juniHaplo1Lamellibrachia juniWest PacificAB264601COILam.juniHaplo2Lamellibrachia juniWest PacificAB264603COILam.juniHaplo3Lamellibrachia juniWest PacificAB264604COILam.juniHaplo5Lamellibrachia juniWest PacificAB264604COILam.juniHaplo5Lamellibrachia juniWest PacificAB264605COILam.JuniHaplo5Lamellibrachia sp.West PacificAB055209COILamL4Lamellibrachia sp.West PacificAB088675COILamL5Lamellibrachia sp.West PacificAB088675COILamL7Lamellibrachia sp.West PacificAB088675COILamLymesiBH 2Lamellibrachia luymesiGOM GC185AY129133COILam.luymesiBH 4Lamellibrachia luymesiGOM GC185AY129139COILam.luymesiBHLamellibrachia luymesiGOM GC34AY129136COILam.luymesiBCG354Lamellibrachia luymesiGOM VK826AY129124COILam.luymesiVKLamellibrachia sp. from Med.MedteraneanEU046616COILam.stsumabLamellibrachia sp. from Med.MedteraneanEU046616COILam.stsumabLamellibrachia sp. from Med.MedteraneanEU046616COILam.stsumabLamellibrachia sp. nov.GOM GE425AY129134COIDarissi fujikuraiOasisa fujikuraiSotth/West Pacific </td <td>Lam.columna 1</td> <td>Lamellibrachia columna</td> <td>West Pacific</td> <td>AB055210</td> <td>COI</td>	Lam.columna 1	Lamellibrachia columna	West Pacific	AB055210	COI	
Lam.jumiHaplo1Lamellibrachia juniWest PacificAB264601COILam.jumiHaplo2Lamellibrachia juniWest PacificAB264603COILam.jumiHaplo3Lamellibrachia juniWest PacificAB264603COILam.jumiHaplo4Lamellibrachia juniWest PacificAB264605COILam.jumiHaplo5Lamellibrachia juniWest PacificAB264605COILam.jumiHaplo5Lamellibrachia sp.West PacificAB055209COILamL5Lamellibrachia sp.West PacificAB088674COILamL6Lamellibrachia sp.West PacificAB088675COILamL04Lamellibrachia sp.West PacificAB088675COILamLuymesiBH 2Lamellibrachia luymesiGOM GC185AY129133COILam.luymesiBHLamellibrachia luymesiGOM GC233AY129132COILam.luymesiBH2Lamellibrachia luymesiGOM GC34AY129135COILam.luymesiG4252Lamellibrachia luymesiGOM VK826AY129124COILam.luymesiG4252Lamellibrachia luymesiGOM VK826AY129134COILam.luymesiG4252Escarpid sp. nov.GOM K252AY129134COILam.luymesiG4252Escarpid sp. nov.GOM GR425AY129134COILam.luymesiG4252Escarpid sp. nov.GOM GR425AY129134COILam.luymesiG4252Escarpid sp. nov.GOM GR425AY129134COILam.luymesiG4252Escarpid sp. nov.GOM K8425AY129134COI </td <td>Lam.juni</td> <td>Lamellibrachia juni</td> <td>West Pacific</td> <td>AB242858</td> <td>COI</td>	Lam.juni	Lamellibrachia juni	West Pacific	AB242858	COI	
Lam.juniHaplo2Lamellibrachia juniWest PacificAB264602COILam.juniHaplo3Lamellibrachia juniWest PacificAB264603COILam.juniHaplo4Lamellibrachia juniWest PacificAB264605COILam.juniHaplo5Lamellibrachia juniWest PacificAB264605COILam.juniHaplo5Lamellibrachia sp.West PacificAB055210COILamL5Lamellibrachia sp.West PacificAB088675COILamL6Lamellibrachia sp.West PacificAB088675COILamL7Lamellibrachia uymesiGOM GC185AY129133COILam.lymesiBH 2Lamellibrachia luymesiGOM GC185AY129132COILam.lymesiBPLamellibrachia luymesiGOM GC33AY129135COILam.lymesiBHLamellibrachia luymesiGOM GC354AY129126COILam.luymesiGVA252Lamellibrachia luymesiGOM VK826AY129126COILam.luymesiGVA255Escarpiid sy nov.GOM GR425AY129134COILam.luymesiGVA255Escarpiid sy nov.GOM GB425AY129134COIOdisis fujikuraiOasia fujikuraiSout/Nest PacificAB264604COILam.sumabLamellibrachia sy nov.GOM GB425AY129134COINewEscarpiidGB425Escarpiid sy nov.GOM GB425AY129134COIOdisis fujikuraiOasia fujikuraiSout/Nest PacificAB248671COINewEscarpiidGB425Ridgeia piscesaeJuan de Fuca RidgeAF315054 </td <td>Lam.juniHaplo1</td> <td>Lamellibrachia juni</td> <td>West Pacific</td> <td>AB264601</td> <td>COI</td>	Lam.juniHaplo1	Lamellibrachia juni	West Pacific	AB264601	COI	
Lam.juniHaplo3Lamellibrachia juniWest PacificAB264603COILam.juniHaplo4Lamellibrachia juniWest PacificAB264604COILam.juniHaplo5Lamellibrachia juniWest PacificAB264605COILam.JuniHaplo5Lamellibrachia sp.West PacificAB055209COILamL5Lamellibrachia sp.West PacificAB088674COILamL6Lamellibrachia sp.West PacificAB088675COILamL7Lamellibrachia luymesiGOM CC185AY129133COILam.lymesiBH2Lamellibrachia luymesiGOM CC185AY129132COILam.lymesiBH5Lamellibrachia luymesiGOM CC33AY129135COILam.luymesiBPLamellibrachia luymesiGOM CC354AY129135COILam.luymesiG2354Lamellibrachia luymesiGOM CC354AY129135COILam.luymesi VKLamellibrachia luymesiGOM CC354AY129126COILam.luymesi VKLamellibrachia luymesiGOM CM K826AY129124COILam.luymesi VKLamellibrachia sutumesiSouth/West PacificAB242877COILam.luymesi QC354Lamellibrachia sutumesiSouth/West PacificBA242877COILam.luymesi VKLamellibrachia sutumeWest PacificBA242877COILam.luymesi QC354Ridgeia piscesaeJuan de Fuca RidgeAF315054165Ridgeia fujkuraiSouth/West PacificBA242877COICOILam.luymesi QC354Ridgeia piscesaeJuan d	Lam.juniHaplo2	Lamellibrachia juni	West Pacific	AB264602	COI	
Lam.juniHaplo4Lamellibrachia juniWest PacificAB264604COILam.juniHaplo5Lamellibrachia juniWest PacificAB264605COILaml4Lamellibrachia sp.West PacificAB055209COILamL5Lamellibrachia sp.West PacificAB088674COILamL7Lamellibrachia sp.West PacificAB088675COILamL7Lamellibrachia uymesiCOM CC185AY129133COILamLymesiBH 2Lamellibrachia luymesiCOM CC185AY129132COILam.luymesiBH5Lamellibrachia luymesiCOM CC185AY129133COILam.luymesiBH2Lamellibrachia luymesiCOM CC185AY129133COILam.luymesiGA252Lamellibrachia luymesiCOM CC343AY129139COILam.luymesiCQ4252Lamellibrachia luymesiCOM CC34AY129126COILam.luymesiCQ4252Lamellibrachia luymesiCOM CC34AY129126COILam.luymesiCQ4255Escarpiid sp. from Med.MediterraneanEU046616COILam.sumabLamellibrachia sumaWest PacificAF342671COIOaisia fujikuraiSouth/West PacificD50594COICOIRidgeiaRidgeia piscesaeJuan de Fuca RidgeAF315051165RidgeiaRidgeia piscesaeJuan de Fuca RidgeAF315051165RidgeiaRidgeia piscesaeJuan de Fuca RidgeAF315051165RidgeiaRidgeia piscesaeJuan de Fuca RidgeAF315054165 <t< td=""><td>Lam.juniHaplo3</td><td>Lamellibrachia juni</td><td>West Pacific</td><td>AB264603</td><td>COI</td></t<>	Lam.juniHaplo3	Lamellibrachia juni	West Pacific	AB264603	COI	
Lam.lumiHaplo5Lamellibrachia juniWest PacificAB264605COILamL4Lamellibrachia sp.West PacificAB055209COILamL5Lamellibrachia sp.West PacificAB088674COILamL6Lamellibrachia sp.West PacificAB088675COILamL7Lamellibrachia sp.West PacificAB088675COILamLymesiBH 2Lamellibrachia luymesiCOM CC185AY129133COILam.luymesiBH5Lamellibrachia luymesiCOM CC233AY129135COILam.luymesiC64252Lamellibrachia luymesiCOM GC485AY129135COILam.luymesiC64252Lamellibrachia luymesiCOM GC334AY129135COILam.luymesiC64252Lamellibrachia luymesiCOM GC354AY129126COILam.luymesiGC354Lamellibrachia luymesiGOM GC4825AY129124COILam.luymesi VKLamellibrachia satsumaWest PacificAF342671COILam.luymesi GG425Escarpii ds p. nov.COM GB425AY129134COIOatista fujikuraiSouth/West PacificAB242857COIParaescarpiaParaescarpia cf. echinospicaWest PacificAB24257COIRidgeia 2Ridgeia piscesaeJuan de Fuca RidgeAF315054I65Ridgeia 2Ridgeia piscesaeJuan de Fuca RidgeAF315054I65Ridgeia 2Ridgeia piscesaeJuan de Fuca RidgeAF315054I65Ridgeia 3Ridgeia piscesaeJuan de Fuca RidgeAF315054I65	Lam.juniHaplo4	Lamellibrachia juni	West Pacific	AB264604	COI	
LamlALamellibrachia sp.West PacificAB055209COILamLSLamellibrachia sp.West PacificAB055210COILamLGLamellibrachia sp.West PacificAB088674COILamLJLamellibrachia laymesiCOM GC185AY129133COILamLymesiBH 2Lamellibrachia luymesiCOM GC185AY129132COILam.luymesiBHLamellibrachia luymesiGOM GC185AY129132COILam.luymesiBHLamellibrachia luymesiGOM GC233AY129139COILam.luymesiGB4252Lamellibrachia luymesiGOM GC354AY129126COILam.luymesiG4252Lamellibrachia luymesiGOM CG354AY129124COILam.luymesi VKLamellibrachia luymesiGOM VK826AY129124COILam.luymesi VKLamellibrachia suymesiGOM CG455AY129124COILam.luymesi VKLamellibrachia suymesiGOM CM25AY129134COILam.luymesi VKLamellibrachia suymesiCOM VK826AY129134COILam.satsumabLamellibrachia satsumaWest PacificAF342671COINewEscarpidCB425Escarpid Sp. nov.GOM GB425AY129134COIOaisisa fujikuraiSouth/West PacificAB242857COIParaescarpiaParaescarpia (e chinospicaWest PacificAB242857COIParaescarpiaRidgeia piscesaeJuan de Fuca RidgeAF315054I6SRidgeia 2Ridgeia piscesaeJuan de Fuca RidgeAF315054I6S <tr< td=""><td>Lam.juniHaplo5</td><td>Lamellibrachia juni</td><td>West Pacific</td><td>AB264605</td><td>COI</td></tr<>	Lam.juniHaplo5	Lamellibrachia juni	West Pacific	AB264605	COI	
Laml.5Lamellibrachia sp.West PacificAB055210COILaml.6Lamellibrachia sp.West PacificAB088674COILaml.7Lamellibrachia luymesiGOM GC185AY129133COILam.luymesiBH 2Lamellibrachia luymesiGOM GC185AY129132COILam.luymesiBHbLamellibrachia luymesiGOM GC233AY129132COILam.luymesiBH2Lamellibrachia luymesiGOM GC233AY129139COILam.luymesiGB4252Lamellibrachia luymesiGOM GC234AY129135COILam.luymesiGS454Lamellibrachia luymesiGOM GC354AY129124COILam.luymesiGK354Lamellibrachia luymesiGOM VK826AY129124COILam.luymesi VKLamellibrachia sp. from Med.MediterraneanEU046616COILam.satsumabLamellibrachia satsumaWest PacificAF342671COINewEscarpid GB4255StiglikuraiSouth/West PacificAB242857COIOaisia fujikuraiSouth/West PacificAB242857COIRidgeiaRidgeia piscesaeJuan de Fuca RidgeAF315051165RidgeiaRidgeia piscesaeJuan de Fuca RidgeAF315051165Ridgeia 2Ridgeia piscesaeJuan de Fuca RidgeAF315054165Ridgeia 3Ridgeia piscesaeJuan de Fuca RidgeAF315054165Ridgeia 3Ridgeia piscesaeJuan de Fuca RidgeAF315054165Ridgeia 3Ridgeia piscesaeJuan de Fuca RidgeAF31505416	LamL4	Lamellibrachia sp.	West Pacific	AB055209	COI	
Laml6Lamellibrachia sp.West PacificAB088674COILamL7Lamellibrachia uymesiWest PacificAB088675COILamluymesiBH 2Lamellibrachia luymesiGOM GC185AY129133COILam.luymesiBHbLamellibrachia luymesiGOM GC185AY129132COILam.luymesiGB4252Lamellibrachia luymesiGOM GC233AY129135COILam.luymesiGS454Lamellibrachia luymesiGOM GB425AY129126COILam.luymesiGV54Lamellibrachia luymesiGOM CC354AY129124COILam.luymesiVKLamellibrachia luymesiGOM VK826AY129124COILam.luymesi VKLamellibrachia sutsumaWest PacificAF342671COILam.stumabLamellibrachia sutsumaWest PacificAF342671COINewEscarpiidGB425Escarpiid sp. nov.GOM GB425AY129134COIOaisia fujikuraiOasia fujikuraiSouth/West PacificAB242877COIParaescarpiaParaescarpia cf. echinospicaWest PacificD50594COIRidgeia piscesaeJuan de Fuca RidgeAF315054165Ridgeia piscesaeJuan de Fuca RidgeAF315042165Ridgeia SiesaeJuan de Fuca RidgeAF315042 <td>LamL5</td> <td>Lamellibrachia sp.</td> <td>West Pacific</td> <td>AB055210</td> <td>COI</td>	LamL5	Lamellibrachia sp.	West Pacific	AB055210	COI	
Lamellibrachia sp.West PacificAB088675COILamulymesiBH 2Lamellibrachia luymesiGOM GC185AY129133COILam.luymesiBHbLamellibrachia luymesiGOM GC185AY129132COILam.luymesiBPLamellibrachia luymesiGOM GC233AY129139COILam.luymesiGC354Lamellibrachia luymesiGOM GC354AY129126COILam.luymesiGC354Lamellibrachia luymesiGOM CG354AY129124COILam.luymesi VKLamellibrachia luymesiGOM K826AY129124COILam.luymesi VKLamellibrachia sp. from Med.MediterraneanEU046616COILam.satsumabLamellibrachia sp. from Med.MediterraneanEU046616COIOasisai fujikuraiSouth/West PacificAB242857COIParaescarpiidGB425Escarpiid sp. nov.GOM GB425AY129134COIOasisai fujikuraiSouth/West PacificD50594COIRidgeiaRidgeia piscesaeJuan de Fuca RidgeAF315051165Ridgeia 2Ridgeia piscesaeJuan de Fuca RidgeAF315051165Ridgeia 3Ridgeia piscesaeJuan de Fuca RidgeAF315051165Ridgeia 4Rifia pachyptilaEast PacificN645989COITorvia jerichonanaEsc PacificAY645989COIFundaRifia pachyptilaEast PacificAY645989COIFundaSeepiophila jonesiGOM GC185AF317287COIS. jonesi BHSeepiophila jonesiGOM	LamL6	Lamellibrachia sp.	West Pacific	AB088674	COI	
LamluymesiBH 2Lamellibrachia luymesiGOM GC185AY129133COILam.luymesiBHbLamellibrachia luymesiGOM GC185AY129132COILam.luymesiBPLamellibrachia luymesiGOM GC233AY129135COILam.luymesiGB4252Lamellibrachia luymesiGOM GC354AY129135COILam.luymesiGC354Lamellibrachia luymesiGOM GC354AY129126COILam.luymesiGVKLamellibrachia luymesiGOM VK826AY129124COILam.luymesi <vk< td="">Lamellibrachia sp. from Med.MediterraneanEU046616COILam.satsumabLamellibrachia sp. from Med.MediterraneanEU046616COIOaisia fujikuraiSouth/West PacificAF342671COIOaisia fujikuraiSouth/West PacificD50594COIOaisia fujikuraiSouth/West PacificD50594COIRidgeiaRidgeia piscesaeJuan de Fuca RidgeAF31505116SRidgeiaRidgeia piscesaeJuan de Fuca RidgeAF31505416SRidgeia3Ridgeia piscesaeJuan de Fuca RidgeAF31505416SRidgeia3Ridgeia piscesaeJuan de Fuca RidgeAF31505416SRiftiaRifti pachyptilaEast PacificCOIY645995COITorvini jerichonanaTervini jerichonanaEast PacificAF45999516S/COIS. jonesi BHSeepiophila jonesiGOM GC185AF317287COIS. jonesi GB425Seepiophila jonesiGOM GC185AF317287COI<td>LamL7</td><td>Lamellibrachia sp.</td><td>West Pacific</td><td>AB088675</td><td>COI</td></vk<>	LamL7	Lamellibrachia sp.	West Pacific	AB088675	COI	
Lam.luymesiBHbLamellibrachia luymesiGOM GC185AY129132COILam.luymesiBPLamellibrachia luymesiGOM GC233AY129139COILam.luymesiGB4252Lamellibrachia luymesiGOM GB425AY129135COILam.luymesiGC354Lamellibrachia luymesiGOM GC354AY129126COILam.luymesi VKLamellibrachia luymesiGOM VK826AY129124COILam.MedLamellibrachia satsumaWest PacificAF342671COILam.satsumabLamellibrachia satsumaWest PacificAF342671COIOaisia fujikuraiOasisa fujikuraiSouth/West PacificAB242857COIOaisia fujikuraiOasisa fujikuraiSouth/West PacificD50594COIRidgeiaRidgeia piscesaeJuan de Fuca RidgeAF315054IGSRidgeia 2Ridgeia piscesaeJuan de Fuca RidgeAF315054IGSRidgeia 3Ridgeia piscesaeJuan de Fuca RidgeAF315054IGSRidgeia 4Riftia pachyptilaEast PacificCOIAY645985COITevnia jerichonanaFeus PacificAF315054IGSRidgeia3Ridgeia piscesaeJuan de Fuca RidgeAF315054IGSS. jonesi BHSeepiophila jonesiGOM GC185AF317287COISoil- XY645995IGS/COIS. jonesi GB425Seepiophila jonesiGOM GC185AF317288COI	LamluymesiBH 2	Lamellibrachia luymesi	GOM GC185	AY129133	COI	
Lam.luymesiBPLamellibrachia luymesiGOM GC233AY129139COILam.luymesiGB4252Lamellibrachia luymesiGOM GB425AY129135COILam.luymesiGC354Lamellibrachia luymesiGOM GC354AY129126COILam.luymesi VKLamellibrachia luymesiGOM VK826AY129124COILam.NedLamellibrachia sp. from Med.MediterraneanEU046616COILam.satsumabLamellibrachia satsumaWest PacificAF342671COINewEscarpidGB425Escarpiid sp. nov.GOM GB425AY129134COIOaisis fujikuraiOasisa fujikuraiSouth/West PacificAB242857COIParaescarpiaParaescarpia cf. echinospicaWest PacificD50594COIRidgeiaRidgeia piscesaeJuan de Fuca RidgeAF31505416SRidgeia 2Ridgeia piscesaeJuan de Fuca RidgeAF31505416SRidgeia 3Ridgeia piscesaeJuan de Fuca RidgeAF31505416SRidgeia 4Ridgeia piscesaeJuan de Fuca RidgeAF31505416SRidgeia 3Ridgeia piscesaeJuan de Fuca RidgeAF31505416SRidgeia 4Ridgeia piscesaeJuan de Fuca RidgeAF31505416SRidgeia 5Seepiophila jonesiGOM GC185AF317287COIS. jonesi BHSeepiophila jonesiGOM GM255AF317288COIS. jonesi GB425Seepiophila jonesiGOM GM255AF317288COI	Lam.luymesiBHb	Lamellibrachia luymesi	GOM GC185	AY129132	COI	
Lam.luymesiG4252Lamellibrachia luymesiGOM G425AY129135COILam.luymesiGC354Lamellibrachia luymesiGOM GC354AY129126COILam.luymesi VKLamellibrachia luymesiGOM VK826AY129124COILam.luymesi VKLamellibrachia isp. from Med.MediterraneanEU046616COILam.satsumabLamellibrachia satsumaWest PacificAF342671COINewEscarpiidGB425Escarpiid sp. nov.GOM GB425AY129134COIOaisisia fujikuraiOasisia fujikuraiSouth/West PacificAB242857COIParaescarpiaParaescarpia ci. echinospicaWest PacificD50594COIRidgeiaRidgeia piscesaeJuan de Fuca RidgeAF315054165Ridgeia 2Ridgeia piscesaeJuan de Fuca RidgeAF315054165Ridgeia 3Ridgeia piscesaeJuan de Fuca RidgeAF315054165Ridgeia 4Rifdie a piscesaeJuan de Fuca RidgeAF315054165Ridgeia 3Ridgeia piscesaeJuan de Fuca RidgeAF315054165Ridgeia 4Riftia pachyptilaEast PacificY645989COITevnia jerichonanaEast Pacific165: AF315042COIS. jonesi BHSeepiophila jonesiGOM GC185AF317287COIS. jonesi GB425Seepiophila jonesiGOM GB425AF317288COI	Lam.luymesiBP	Lamellibrachia luymesi	GOM GC233	AY129139	COI	
Lam.luymesiGC354Lamellibrachia luymesiGOM GC354AY129126COILam.luymesi VKLamellibrachia luymesiGOM VK826AY129124COILam.MedLamellibrachia sp. from Med.MediterraneanEU046616COILam.satsumabLamellibrachia satsumaWest PacificAF342671COINewEscarpiidGB425Escarpiid sp. nov.GOM GB425AY129134COIOaisia fujikuraiOasisia fujikuraiSouth/West PacificAB242857COIParaescarpiaParaescarpia cf. echinospicaWest PacificD50594COIRidgeiaRidgeia piscesaeJuan de Fuca RidgeAF31505416SRidgeia 2Ridgeia piscesaeJuan de Fuca RidgeAF31505416SRidgeia 2Ridgeia piscesaeJuan de Fuca RidgeAF31505416SRidgeia 3Ridgeia piscesaeJuan de Fuca RidgeAF31505416SRidgeia 4Ridgeia piscesaeJuan de Fuca RidgeAF31505416SRidgeia 3Ridgeia piscesaeJuan de Fuca RidgeAF31505416SRidgeia 4Ridgeia piscesaeJuan de Fuca RidgeAF31505416SRiftiaRiftia pachyptilaEast PacificCOIAY645989COIS. jonesi BHSeepiophila jonesiGOM GC1855AF317287COIS. jonesi GB425Seepiophila jonesiGOM GB425AF317288COI	Lam.luymesiGB4252	Lamellibrachia luymesi	GOM GB425	AY129135	COI	
Lam.luymesi VKLamellibrachia luymesiGOM VK826AY129124COILam.MedLamellibrachia sp, from Med.MediterraneanEU046616COILam.satsumabLamellibrachia satsumaWest PacificAF342671COINewEscarpiidGB425Escarpiid sp, nov.GOM GB425AY129134COIOaissia fujikuraiOasisia fujikuraiSouth/West PacificAB242857COIParaescarpiaParaescarpia cf. echinospicaWest PacificD50594COIRidgeiaRidgeia piscesaeJuan de Fuca RidgeAF31505416SRidgeia 2Ridgeia piscesaeJuan de Fuca RidgeAF31505116SRidgeia 2Ridgeia piscesaeJuan de Fuca RidgeAF31505116SRidgeia 3Ridgeia piscesaeJuan de Fuca RidgeAF31505116SRidgeia 4Ridgeia piscesaeJuan de Fuca RidgeAF31505116SRidgeia 3Ridgeia piscesaeJuan de Fuca RidgeAF31505116SRidgeia 4Riftia pachyptilaEast PacificAY645989COITevnia jerichonanaTevnia jerichonanaEast Pacific16S: AF315042COI: AY64599516S/COIS. jonesi BHSeepiophila jonesiGOM GC1855AF317287COIGOIS. jonesi GB425Seepiophila jonesiGOM GB425AF317288COI	Lam.luymesiGC354	Lamellibrachia luymesi	GOM GC354	AY129126	COI	
Lam.MedLamellibrachia sp. from Med.MediterraneanEU046616COILam.satsumabLamellibrachia satsumaWest PacificAF342671COINewEscarpiidGB425Escarpiid sp. nov.GOM GB425AY129134COIOaisia fujikuraiOasisa fujikuraiSouth/West PacificAB242857COIParaescarpiaParaescarpia cf. echinospicaWest PacificD50594COIRidgeiaRidgeia piscesaeJuan de Fuca RidgeAF022233COIRidgeiaRidgeia piscesaeJuan de Fuca RidgeAF31505416SRidgeia 2Ridgeia piscesaeJuan de Fuca RidgeAF31505116SRidgeia3Ridgeia piscesaeJuan de Fuca RidgeAF31505416SRidgeia4Ridgeia piscesaeJuan de Fuca RidgeAF31505416SRidgeia5Ridgeia piscesaeJuan de Fuca RidgeAF31505416SRidgeia6Ridgeia piscesaeJuan de Fuca RidgeAF31505416SRiftiaRiftia pachyptilaEast PacificAY645989COITevnia jerichonanaTevnia jerichonanaEast Pacific16S: AF315042COI:S. jonesi BHSeepiophila jonesiGOM GC1855AF317287COIS. jonesi GB425Seepiophila jonesiGOM GB425AF317288COI	Lam.luymesi VK	Lamellibrachia luymesi	GOM VK826	AY129124	COI	
Lam.satsumabLamellibrachia satsumaWest PacificAF342671COINewEscarpiidGB425Escarpiid sp. nov.GOM GB425AY129134COIOaisia fujikuraiOasisia fujikuraiSouth/West PacificAB242857COIParaescarpia cf. echinospicaWest PacificD50594COIRidgeiaRidgeia piscesaeJuan de Fuca RidgeAF022233COIRidgeia 2Ridgeia piscesaeJuan de Fuca RidgeAF31505416SRidgeia 3Ridgeia piscesaeJuan de Fuca RidgeAF31505116SRidgeia 4Ridgeia piscesaeJuan de Fuca RidgeAF31505416SRidgeia 3Ridgeia piscesaeJuan de Fuca RidgeAF31505416SRidgeia 4Rifti pachyptilaEast PacificAY645989COITevnia jerichonanaEast Pacific16S: AF315042ToOI:AY645995516S/COIS. jonesi BHSeepiophila jonesiGOM GC1855AF317287COIS. jonesi GB425Seepiophila jonesiGOM GB425AF317288COI	Lam.Med	Lamellibrachia sp. from Med.	Mediterranean	EU046616	COI	
NewEscarpidGB425Escarpid sp. nov.GOM GB425AY129134COIOaisia fujikuraiOasisia fujikuraiSouth/West PacificAB242857COIParaescarpia cf. echinospicaWest PacificD50594COIRidgeiaRidgeia piscesaeJuan de Fuca RidgeAF022233COIRidgeia 2Ridgeia piscesaeJuan de Fuca RidgeAF31505416SRidgeia 3Ridgeia piscesaeJuan de Fuca RidgeAF31505116SRidgeia3Ridgeia piscesaeJuan de Fuca RidgeAF31505416SRifdgeia3Rifti pachyptilaEast PacificAY645989COITevnia jerichonanaEast Pacific16S: AF315042Testica ParaesS. jonesi BHSeepiophila jonesiGOM GC1855AF317287COIS. jonesi GB425Seepiophila jonesiGOM GB425AF317288COI	Lam.satsumab	Lamellibrachia satsuma	West Pacific	AF342671	COI	
Oatsista JujikuralSouth/West PacificAB242857COIParaescarpiaParaescarpia cf. echinospicaWest PacificD50594COIRidgeiaRidgeia piscesaeJuan de Fuca RidgeAF022233COIRidgeia 2Ridgeia piscesaeJuan de Fuca RidgeAF31505416SRidgeia 3Ridgeia piscesaeJuan de Fuca RidgeAF31505416SRidgeia 3Ridgeia piscesaeJuan de Fuca RidgeAF31505416SRidgeia 3Ridgeia piscesaeJuan de Fuca RidgeAF31505416SRiftiaRiftia pachyptilaEast PacificAY645989COITevnia jerichonanaEast Pacific16S: AF315042ToS. jonesi BHSeepiophila jonesiGOM GC1855AF317287COIS. jonesi GB425Seepiophila jonesiGOM GB425AF317288COI	NewEscarpiidGB425	Escarpiid sp. nov.	GOM GB425	AY129134	COI	
ParaescarpiaParaescarpia cf. echinospicaWest PacificD50594COlRidgeiaRidgeia piscesaeJuan de Fuca RidgeAF022233COlRidgeiaRidgeia piscesaeJuan de Fuca RidgeAF31505416SRidgeia 2Ridgeia piscesaeJuan de Fuca RidgeAF31505116SRidgeia 3Ridgeia piscesaeJuan de Fuca RidgeAF31505416SRiftiaRiftia pachyptilaEast PacificAY645989COlTevnia jerichonanaTevnia jerichonanaEast Pacific16S: AF315042S. jonesi BHSeepiophila jonesiGOM GC185AF317287COlS. jonesi GB425Seepiophila jonesiGOM GB425AF317288COl	Oaisisia fujikurai	Oasisia fujikurai	South/West Pacific	AB242857	COI	
RidgeiaRidgeia piscesaeJuan de Fuca RidgeAF022233COIRidgeiaRidgeia piscesaeJuan de Fuca RidgeAF31505416SRidgeia 2Ridgeia piscesaeJuan de Fuca RidgeAF31505116SRidgeia 3Ridgeia piscesaeJuan de Fuca RidgeAF31505416SRiftiaRiftia pachyptilaEast PacificAY645989COITevnia jerichonanaTevnia jerichonanaEast Pacific16S: AF315042S. jonesi BHSeepiophila jonesiGOM GC185AF317287COIS. jonesi GB425Seepiophila jonesiGOM GB425AF317288COI	Paraescarpia	Paraescarpia cf. echinospica	West Pacific	D50594	COI	
RidgeiaRidgeia piscesaeJuan de Fuca RidgeAF315054165Ridgeia 2Ridgeia piscesaeJuan de Fuca RidgeAF315051165Ridgeia 3Ridgeia piscesaeJuan de Fuca RidgeAF315054165RiftiaRiftia pachyptilaEast PacificAY645989COITevnia jerichonanaTevnia jerichonanaEast Pacific165: AF315042S. jonesi BHSeepiophila jonesiGOM GC185AF317287COIS. jonesi GB425Seepiophila jonesiGOM GB425AF317288COI	Ridgeia	Ridgeia piscesae	Juan de Fuca Ridge	AF022233	COI	
Ridgela 2Ridgela piscesaeJuan de Fuca RidgeAF315051165Ridgeia 3Ridgeia piscesaeJuan de Fuca RidgeAF315054165RiftiaRiftia pachyptilaEast PacificAY645989COITevnia jerichonanaTevnia jerichonanaEast Pacific165: AF315042COI: AY645995165/COIS. jonesi BHSeepiophila jonesiGOM GC185AF317287COIS. jonesi GB425Seepiophila jonesiGOM GB425AF317288COI	Ridgeia	Ridgeia piscesae	Juan de Fuca Ridge	AF315054	165	
Ridgela JuscesaeJuan de Fuca RidgeAF315054165RiftiaRiftia pachyptilaEast PacificAY645989COITevnia jerichonanaEast Pacific165: AF315042COI: AY645995165/COIS. jonesi BHSeepiophila jonesiGOM GC185AF317287COIS. jonesi GB425Seepiophila jonesiGOM GB425AF317288COI	Ridgeia 2	Ridgeia piscesae	Juan de Fuca Ridge	AF315051	165	
RiftiaRiftia pachyptilaEast PacificAY645989COITevnia jerichonanaTevnia jerichonanaEast Pacific16S: AF315042COI:S. jonesi BHSeepiophila jonesiGOM GC185AF317287COIS. jonesi GB425Seepiophila jonesiGOM GB425AF317288COI	Ridgeia3	Ridgeia piscesae	Juan de Fuca Ridge	AF315054	165	
Ievnia jerichonanaIevnia jerichonanaEast Pacific165: AF315042COI: AY645995165/COIS. jonesi BHSeepiophila jonesiGOM GC185AF317287COIS. jonesi GB425Seepiophila jonesiGOM GB425AF317288COI	KIJTIA Transis inishanan	Kijtia pachyptila	East Pacific	AY645989	COI	
S. jonesi BHSeepiophila jonesiGOM GC185AF317287COIS. jonesi GB425Seepiophila jonesiGOM GB425AF317288COI	Tevnia jerichonana	Tevnia jerichonana	East Pacific	165: AF315042	100/001	
S. jonesi GB425Seepiophila jonesiGUM GC185AF31/28/COIGOM GB425Seepiophila jonesiGOM GB425AF317288COI		Comionhile innoi	COM CC125	CUI: AY645995	165/001	
5. jonest G6425 Seeptopnita jonest GOW G8425 AF51/288 COI	S. Jonesi BH	Seepiophila jonesi	GOIM GC185	AF31/28/	COL	
	5. junest GD425		GUIVI GD420	AC31/200	COI	

^a Samples analyzed for this study are numbered and labeled as for Figs. 2 and 3. Sequences from Genbank are listed by names assigned in Genbank.

^b Samples from the Gulf of Mexico are indicated by GOM followed by the abbreviation of their collection sites. VK826, GC185, GC233, GB425, GC234, and GC354 are all on the upper Louisiana slope at depths < 800 m. The other GOM sites are at depths > 900 m and are indicated on Fig. 1.

the species' boundaries for *Lamellibrachia*, *Escarpia*, and *Seepiophila*, and we do not infer higher level phylogenetic relationships among genera because neither 16S nor COI offers sufficient resolution at deeper nodes. The complete and aligned COI dataset included 690 bp, of which 460 were invariant sites, 207 were phylogenetically informative sites, and 23 were autapomorphies.

The complete 16S dataset consisted of 133 sequences (see Table 1 for the complete list of samples), 127 of which were from the Gulf of Mexico. Sequences from the vent-dwelling genera *Tevnia* and *Ridgeia* were used as outgroups. The aligned 16S dataset consisted of 524 bp, of which 433 were invariant sites, 72 were phylogenetically informative, and 19 were autapomorphies.

MP, ML, and NJ analyses produced congruent trees, and the GARLI ML phylogeny is presented in Fig. 2 A and B and 3A and B.

Both 16S and COI phylogenies identify five distinct monophyletic clades of vestimentiferans in the Gulf of Mexico. Four of the clades represent single morphospecies, *S. jonesi, E. laminata, Lamellibrachia* sp. 2, and escarpiid sp. nov., from the upper slope. However, the fifth clade includes both *Lamellibrachia* sp. 1 from the collections in the deeper GOM and *L. luymesi* from the upper Louisiana slope sites. They were, therefore, considered a single species when within- and between-species distances for the 16S and COI datasets were estimated. Additionally, COI sequences of *E. laminata* did not differ from those of *E. spicata* and



Fig. 2. COI maximum likelihood (ML) tree. Outgroups are shown in italics, and bootstrap support above 50% (NJ 1000 replicates) is indicated below each node. All new sequences are preceded by a number, followed by the abbreviation for the seep site or lease block from which they were collected. VK=Viosca Knoll, BH=Bush Hill, and BP=Brine Pool. Those sites, together with GB425, GC234, and GC354, are from the upper Louisiana slope of the GOM (< 800 m depth). All other lease blocks are on the lower slope (Fig. 1).

Table	2
-------	---

16 S Between- and within-species (in bold, on diagonal) *p* distances for the 16 S gene of the GOM species.

	[1] (%)	[2] (%)	[3] (%)	[4] (%)	[5] (%)
 [1] E. laminata [2] L. luymesi/ sp. 1 [3] L. sp. 2 [4] S. jonesi [5] Escarpid sp. new 	0.10 9.60 9.00 2.00 3.50	0.00 2.20 8.40 8.30	0.10 8.10 8.90	0.00 3.70	0.00

Table 3

Between- and within-species (in bold, on diagonal) p distances for the COI gene.

	[1] (%)	[2] (%)	[3] (%)	[4] (%)	[5] (%)
 [1] E. laminata/southwardae/spicata [2] L. luymesi/ sp. 1 [3] L. sp. 2 [4] S. jonesi 	0.9 13.7 13.8 9.7	0.4 2.8 14.2	0.3 14.4	0.3	
[5] Escarpid sp. new	7.1	14.8	14.6	7.1	0.0

E. southwardae from the East Pacific and East Atlantic, respectively. We were unable to obtain 16S sequences for *E. spicata* or *E. southwardae*.

Estimates of within- and between-species diversity (p) for both genes are shown in Tables 2 and 3. Within a species, p distances range from 0% to 0.1% for 16S and 0% to 0.9% for the more variable

COI. The very low values for the undescribed escarpiid may reflect the small number of individuals of this species analyzed (n=3 for COI and n=2 for 16S).

4. Discussion

4.1. Distribution of vestimentiferan species in the Gulf of Mexico and relation to other seep species

Vestimentiferans have been collected from both hydrothermal vent and cold-seep sites. The vent and seep species fall into two different clades. However, it should be noted that "seep species" are sometimes found in sedimented hydrothermal vent areas with low levels of diffuse flow, and that "cold-seep" fluids may have temperatures elevated over background (Black et al., 1998; Kojima et al., 1997; MacDonald et al., 2000; Joye et al., 2005); so this separation really reflects more aspects of their habitat than temperature alone. Vestimentiferans found at cold seeps worldwide can be further divided into two clades. One clade includes at least five named and three unnamed species in the genus Lamellibrachia. The other clade includes three named species in the genus Escarpia, S. jonesi, Paraescarpia echinospica, and a rarely collected species (escarpiid sp. nov.) from the shallow GOM. Although Arcovestia seems basal to the Lamellibrachia clade (Fig. 2B), this position is not well supported.

Three species in the escarpiid clade of seep vestimentiferans are found in the GOM: *S. jonesi* has been collected from numerous sites,



Fig. 3. 16S maximum likelihood (ML) tree. Outgroups are shown in italics and bootstrap support above 50% (NJ 1000 replicates) is indicated below each node. Sample identifications and abbreviations are as in Fig. 2.

ranging in depth from 500 to 950 m; escarpiid sp. nov. from two sites ranging in depth from 600 to 640 m, where it co-occurs with S. jonesi (although it has been reported also from GC234 at 525 m; see Cordes et al., 2003); and E. laminata from 950 to 3200 m depth. S. jonesi and E. laminata co-occurred at only one site, GB647, at a depth of 950 m. The undescribed escarpiid differs morphologically from S. jonesi, as it lacks the curl of the ventral vestimental fold that is a defining character of the genus Seepiophila (Gardiner et al., 2001). Additionally, the obturacular process of the undescribed escarpiid forms a spike, whereas it is flat in S. jonesi and barely protrudes from the top of the obturaculum.

Both the COI and 16S phylogenetic trees distinguish these three species and place them within the escarpiid clade of seep vestimentiferans (Figs. 2 and 3). Both the 16S tree and the 16S p distance matrix suggest E. laminata is more closely related to S. jonesi (between-species uncorrected p=2%) than to the undescribed escarpiid (between-species uncorrected p=3.50%). However, the COI tree groups the undescribed escarpiid with the described Escarpia spp. The bootstrap value based on COI data supporting this clade is low (61%), and the grouping observed for the 16S dataset has a bootstrap below 50%. Neither tree allows us to state clearly whether this new escapiid is more closely related to Escarpia, Paraescarpia, or Seepiophila.

As previously noted by other authors, COI does not separate Escarpia southwardae, E. spicata, and E. laminata, respectively, from cold seeps on the west coast of Africa in the eastern Atlantic, Guaymas Basin, off the coast of Mexico, and the GOM (Black et al., 1998). Also, there is very little to no intra-clade diversity within this group (Table 3). This result may indicate that those three nominal species represent a single genealogical species with a surprisingly wide geographic distribution and variable morphology. However, this assumption would require a high level of gene flow between quite distant localities, especially since the closing of the Isthmus of Panama 3.5 million years ago, followed the closing of the deep sea exchange 10 million years ago (Burton et al., 1997). This level of genetic exchange over these distances seems quite unlikely, considering what is known about larval development times for vestimentiferans (Marsh et al. 2001, Young et al., 1996). Although the life span of Escarpia larvae has not been determined, the larval life span of the vent species Riftia pachyptila is estimated at about three weeks (Marsh et al., 2001) and the larval life span of the seep vestimentiferan L. luymesi is estimated to be about one month (Young et al., 1996). Tyler and Young (1999) estimate that the maximal dispersal distances for these species are on the order of 60 km per generation, which is unlikely to support the level of genetic mixing necessary to maintain genetic homogeneity among the three described species of Escarpia from such widely separated geographic locations. It is possible, however, that undiscovered seeps around South America could connect all of these species.

The lack of fixed COI differences within Escarpia spicata, E. laminata, and E. southwardae could also be due to different rates of evolution of the COI gene in different taxa. COI has been used for higher level phylogenetic reconstructions in other groups of annelids (Halanych and Janosik, 2006) and has been adopted as an appropriate gene for the "barcode of life" for animals in general by the barcode of life initiative (BOLI; http://www.dnabarcodes. org/). However, the fact that COI fails to identify morphologically distinct populations of Escarpia from such widely separated areas implies that in this clade the mutation rate may be considerably slower than in other lineages. Slower rates of evolution in the mitochondrial DNA have been recognized in some other groups, such as the cnidarian class Anthozoa, where this phenomenon has been linked to an especially efficient repair system of their mitochondrial DNA (France and Hoover, 2002; Pont-Kingdon et al., 1998); however, no evidence of a similar system has been found in vestimentiferan mitochondrial DNA. Seep vestimentiferans can also be extremely long-lived (Bergquist et al., 2000; Cordes et al., 2007a), which may contribute to a slower rate of change of mitochondrial DNA (see for example Nabholz et al. (2008) for a consideration of longevity effects on mitochondrial rates of evolution in vertebrates).

In the COI dataset, the Lamellibrachia clade is divided into eight distinct groups that represent presumptive species, including five basal species (L. juni, L. barhami, L. satsuma, L. sp. Japan, and L. sp. West Pacific), all of which are from the Pacific Ocean and four of which are from the western Pacific. This observation is consistent with the hypothesis that the genus Lamellibrachia originated in the Pacific, likely the western Pacific, and subsequently radiated to the eastern Pacific, the Atlantic, and the GOM.

Three morphological species of Lamellibrachia were identified in collections from the GOM: L. luymesi, from the upper slope at between about 400 m and 800 m; *L*. sp. 1, from 950 to 2320 m; and *L*. sp. 2, from 1175 to 2320 m. *L*. *luymesi* and *L*. sp. 1 have a similar number of sheath lamellae, but the deep-water *L*. sp. 1 generally has more gill lamellae, ranging between 21 and 27 in the 28 individuals examined, whereas the shallow-water *L*. *luymesi* has between 15 and 22 gill lamellae in the 20 individuals examined for the species description. The morphological character that allowed rapid identification of animals aboardship was the relatively short and fat vestimentum of *L*. sp. 1. The ratio of length to width of the vestimentum of *L*. sp. 1 ranges from 2.4 to 4.7 and from 6.2 to 16.4 in *L*. *luymesi*. *L*. sp. 2 has a similar number of sheath and gill lamellae as *L*. sp. 1, and the vestimentum length to width ratio tends to be shorter (1.9 to 3). The most distinct field character for *L*. sp. 1.

Despite morphological characters that distinguish the three GOM *Lamellibrachia* presumptive species, only either the COI or the 16S phylogenetic trees resolved two of them. Specifically, both genes failed to separate *L luymesi* from the shallow GOM and *L* sp. 1 from the deeper GOM sites. This lack of genetic differences between individuals that span such a wide depth range is unusual (Chase et al., 1998; Zardus et al., 2006) and surprising, given the morphological differences. Both 16S and COI genes consistently identify *Lamellibrachia* sp. 2 as a separate clade, sister to the *L luymesi/L* sp. 1 clade.

There were no apparent geographic distributional patterns that were independent of depth for the seep vestimentiferans in the Gulf of Mexico. The common species present on the upper Louisiana slope (*L. luymesi* and *S. jonesi*) have been found at both the eastern-most and western-most sites where we have collected vestimentiferans. *E. laminata* from the lower slope ranges from the Alaminos Canyon sites, our most westerly collection sites for this study, to the Florida Escarpment in the eastern GOM (Cordes et al., 2009; McMullin et al., 2003). Both of the *Lamellibrachia* spp. found at the deeper sites occurred over the entire E–W range of sites within their depth range (from the Alaminos Canyon sites in the west to AT340 in the east).

4.2. Within-species diversity of the GOM vestimentiferans

Tables 2 and 3 report within- and between-species *p* distance calculated for the GOM genetic species. In most cases, withinspecies diversity for both 16S and in the COI genes is strikingly low, a finding that is in contrast to previous studies on deep-sea mollusks and echinoderms, where large amounts of genetic variation were observed over small distances (Chase et al., 1998; Howell et al., 2004; Quattro et al., 2001). However, largescale studies indicate that low within-species genetic variation may be typical of deep-sea organisms (Bisol et al., 1984) and even suggest that it may decrease with increase in depth (France and Kocher, 1996). Genetic variation has been suggested to be an important feature of the genome of an organism that allows it to adapt to a changing environment (Powers et al., 1991). Organisms that live in the deep sea may experience a long-term stable environment, resulting in low levels of within-species genetic diversity. Alternatively, low within-species genetic diversity may be the result of fewer replication errors, more efficient repair in the germ line, or repeated population bottlenecks.

E. laminata, E. spicata, and *E. southwardae clade* and *L. luymesi* sp. 1 and *L.* sp. 2 have a moderate degree of intra-specific diversity (Figs. 2 and 3). However, as with all of the GOM vestimentiferans analyzed, none of the within-species clades grouped by specific geographic locations or depth. A similar pattern was found in the seep mussel *Bathymodiolus childressi*, which, based on markers ranging from microsatellites to mitochondrial genes, has a panmictic population in the GOM ranging across 550 km east to west and from 540 to 2200 m depth (Carney et al., 2006; Cordes

et al., 2007b). In contrast, genetic breaks and barriers that restrict gene flow were identified in both hydrothermal vent vestimentiferans and mussels along the East Pacific Rise (EPR). Specifically, Won et al. (2003) used COI sequences to identify two highly divergent clades on the EPR on the two sides of the Easter Island Microplate. Similarly, Hurtado et al. (2004) used COI sequences to identify several geographic breaks and barriers that restrict gene flow in three genera of annelids along the EPR, including two species of vestimentiferan (*Riftia pachypitla* and *Tevnia jerichonana*).

5. Summary

In this study, our primary goals were to identify and characterize the distributions of vestimentiferans at seep sites covering a wide geographic and depth range in the Gulf of Mexico and to investigate their relationship to other seep vestimentiferan species, using phylogenetic analysis of mitochondrial gene sequences. Although the genetic analyses confirmed identification of most of the morphological species during collections, we also identified an unexpected discrepancy between the morphospecies identified during the collections and genealogical species identified using the mitochondrial genes COI and 16S. Using morphological characters, we identified two new species of Lamellibrachia (spp. 1 and 2). However, neither COI nor 16S distinguished the deeper occurring morphospecies L. sp. 1 from L. luymesi, the common Lamellibrachia species on the upper Louisiana slope. Our molecular genetic analyses confirm the presence of three vestimentiferan species within the escarpiid clade in the Gulf of Mexico. However, since COI also does not differentiate between E. laminata found in the Gulf of Mexico and the other described Escarpia species off the coast of Africa or in the eastern Pacific Ocean, we suggest that COI or 16S genes may not reliably distinguish closely related species of long-lived seep vestimentiferans. We are currently evaluating the usefulness of several nuclear genes to clarify the relationships among the named species of Escarpia and the Lamellibrachia species in the Gulf of Mexico.

Acknowledgments

This work was funded by a subcontract to Bureau of Ocean Energy Management, Regulation and Enforcement (BOEMRE) contract #1435-01-05-39187, "Investigations of Chemosynthetic Communities on the Lower Continental Slope of the Gulf of Mexico (Chemo III)," with vessel and submergence facilities support provided by National Oceanic and Atmospheric Administration's Office of Ocean Exploration and Research. This study would not have been possible without the support and expertise of the captains, crews, and expedition leaders of the Research Vessel Atlantis, the DSV ALVIN, the NOAA ship Ronald Brown, and the ROV JASON II. The authors are grateful to Erik Cordes and Erin Becker for help at sea, to Stephanie Lessard-Pilon, Erin Becker, and Meredith Cole Patterson for help in the laboratory, to Erin McMullin for sharing DNA and expertise, and to A. Faucci and ChEss Siboglinidae Workshop participants for suggestions and helpful discussion.

References

Bergquist, D.C., Urcuyo, I.A., Fisher, C.R., 2002. Establishment and persistence of seep vestimentiferan aggregations on the upper Louisiana slope of the Gulf of Mexico. Marine Ecology—Progress Series 241, 89–98.

- Bergquist, D.C., Williams, F.M., Fisher, C.R., 2000. Longevity record for deep-sea invertebrate. Nature 403 (6769), 499–500.
- Bisol, P.M., Costa, R., Sibuet, M., 1984. Ecological and genetic survey on two deep-sea holothurians—benthogone-rosea and benthodytes-typica. Marine Ecology—Progress Series 15 (3), 275–281.

- Black, M.B., Trivedi, A., Maas, P.A.Y., Lutz, R.A., Vrijenhoek, R.C., 1998. Population genetics and biogeography of vestimentiferan tube worms. Deep-Sea Research II: Topical Studies in Oceanography 45, 1–3.
- Burton, K.W., Ling, H.F., Onions, R.K., 1997. Closure of the Central American Isthmus and its effect on deep-water formation in the North Atlantic. Nature 386 (6623), 382–385.
- Carney, S.L., Formica, M.I., Divatia, H., Nelson, K., Fisher, C.R., Schaeffer, S.W., 2006. Population structure of the mussel "Bathymodiolus" childressi from Gulf of Mexico hydrocarbon seeps. Deep-Sea Research I: Oceanographic Research Papers 53 (6), 1061–1072.
- Chase, M.R., Etter, R.J., Rex, M.A., Quattro, J.M., 1998. Bathymetric patterns of genetic variation in a deep-sea protobranch bivalve, *Deminucula atacellana*. Marine Biology 131 (2), 301–308.
- Cordes, E.E., Bergquist, D.C., Fisher, C.R., 2009. Macro-ecology of Gulf of Mexico cold seeps. Annual Review of Marine Science 1, 143–168.
- Cordes, E.E., Bergquist, D.C., Redding, M.L., Fisher, C.R., 2007a. Patterns of growth in cold-seep vestimenferans including *Seepiophila jonesi*: a second species of longlived tubeworm. Marine Ecology—An Evolutionary Perspective 28 (1), 160–168.
- Cordes, E.E., Becker, E.L., Hourdez, S., Fisher, C.R., 2010. Influence of foundation species, depth, and location on diversity and community composition at Gulf of Mexico lower-slope cold seeps. Deep-Sea Research II: Topical Studies in Oceanography 57 (21–23), 1870–1881.
- Cordes, E.E., Carney, S.L., Hourdez, S., Carney, R.S., Brooks, J.M., Fisher, C.R., 2007b. Cold seeps of the deep Gulf of Mexico: Community structure and biogeographic comparisons to Atlantic equatorial belt seep communities. Deep-Sea Research 1: Oceanographic Research Papers 54 (4), 637–653.
- Cordes, E.E., Bergquist, D.C., Shea, K., Fisher, C.R., 2003. Hydrogen sulfide demand of long-lived vestimentiferan tube worm aggregations modifies the chemical environment at deep-sea hydrocarbon seeps. Ecology Letters 6 (2003), 212–219.
- Doyle, J.J., Doyle, J.L., 1987. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. Phytochemical Bulletin 19, 11–15.
- Felsenstein, J., 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39 (4), 783–791.
- Folmer, O., Black, M., Hoeh, W., Lutz, R., Vrijenhoek, R., 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology 3 (5), 294–299.
- France, S.C., Hoover, L.L., 2002. DNA sequences of the mitochondrial COI gene have low levels of divergence among deep-sea octocorals (Cnidaria: Anthozoa). Hydrobiologia 471, 149–155.
- France, S.C., Kocher, T.D., 1996. Geographic and bathymetric patterns of mitochondrial 16S rRNA sequence divergence among deepsea amphipods, *Eurythenes gryllus*. Marine Biology 126 (4), 633–643.
- Gardiner, S.L., McMullin, E., Fisher, C.R., 2001. Seepiophila jonesi, a new genus and species of vestimentiferan tube worm (Annelida: Pogonophora) from hydrocarbon seep communities in the Gulf of Mexico. Proceedings of the Biological Society of Washington 114 (3), 694–707.
- Guindon, S., Gascuel, O., 2003. A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. Systematic Biology 52 (5), 696–704.
- Halanych, K.M., Feldman, R.A., Vrijenhoek, R.C., 2001. Molecular evidence that Sclerolinum brattstromi is closely related to vestimentiferans, not to Frenulate pogonophorans (Siboglinidae: Annelida). Biological Bulletin 201 (1), 65–75.
- Halanych, K.M., Janosik, A.M., 2006. A review of molecular markers used for annelid phylogenetics. Integrative and Comparative Biology 46 (4), 533–543.
- Howell, K.L., Rogers, A.D., Tyler, P.A., Billett, D.S.M., 2004. Reproductive isolation among morphotypes of the Atlantic seastar species *Zoroaster fulgens* (Asteroidea : Echinodermata). Marine Biology 144 (5), 977–984.
- Hurtado, L.A., Lutz, R.A., Vrijenhoek, R.C., 2004. Distinct patterns of genetic differentiation among annelids of eastern Pacific hydrothermal vents. Molecular Ecology 13 (9), 2603–2615.
- Joye, S.B., MacDonald, I.R., Montoya, J.P., Peccini, M., 2005. Geophysical and geochemical signatures of Gulf of Mexico seafloor brines. Biogeosciences 2, 1–15.
- Kojima, S., Ohta, S., Yamamoto, T., Miura, T., Fujiwara, Y., Fujikura, K., Hashimoto, J., 2002. Molecular taxonomy of vestimentiferans of the western Pacific and their phylogenetic relationship to species of the eastern Pacific-II—Families Escarpiidae and Arcovestiidae. Marine Biology 141 (1), 57–64.
- Kojima, S., Segawa, R., Hashimoto, J., Ohta, S., 1997. Molecular phylogeny of vestimentiferans collected around Japan, revealed by the nucleotide sequences of mitochondrial DNA. Marine Biology 127 (3), 507–513.
- Kojima, S., Segawa, R., Kobayashi, T., Hashimoto, T., Fujikura, K., Hashimoto, J., Ohta, S., 1995. Phylogenetic relationships among species of *Calyptogena*

(bivalvia, vesicomyidae) collected around Japan revealed by nucleotide sequences of mitochondrial genes. Marine Biology 122 (3), 401–407.

- MacDonald, I.R., Buthman, D., Sager, W.W., Peccini, M.B., Guinasso Jr., N.R., 2000. Pulsed oil discharge from a mud volcano. Geology 28 (10), 907–910.
- Maddison, D.R., Maddison, W.P., 2000. MacClade 4: Analysis of Phylogeny and Character Evolution. Sinauer Associates Inc., Sunderland, MA, USA.
- Marsh, A.G., Mullineaux, L.S., Young, C.M., Manahan, D.T., 2001. Larval dispersal potential of the tubeworm *Riftia pachyptila* at deep-sea hydrothermal vents. Nature 411 (6833), 77–80.
- McMullin, E.R., Hourdez, S., Schaeffer, S.W., Fisher, C.R., 2003. Phylogeny and biogeography of deep sea vestimentiferan tubeworms and their bacterial symbionts. Symbiosis 34 (1), 1–41.
- Mironov, A.N., 2000. New taxa of stalked crinoids from the suborder Bourgueticrinina (Echinodermata, Crinoidea). Zoologichesky Zhurnal 79 (6), 712–728.
- Miura, T., Nedachi, M., Hashimoto, A., 2002. Sulphur sources for chemoautotrophic nutrition of shallow water vestimentiferan tubeworms in Kagoshima Bay. Journal of the Marine Biological Association of the United Kingdom 82 (4), 537–540.
- Nabholz, B., Glemin, S., Galtier, N., 2008. Strong variations of mitochondrial mutation rate across mammals - the longevity hypothesis. Molecular Biology and Evolution 25 (1), 120–130.
- Palumbi, S.R., Warner, R.R., 2003. Ecology. Why gobies are like Hobbits. Science 299 (5603), 51–52.
- Pont-Kingdon, G., Okada, N.A., Macfarlane, J.L., Beagley, C.T., Watkins-Sims, C.D., Cavalier-Smith, T., Clark-Walker, G.D., Wolstenholme, D.R., 1998. Mitochondrial DNA of the coral Sarcophyton glaucum contains a gene for a homologue of bacterial MutS: a possible case of gene transfer from the nucleus to the mitochondrion. Journal of Molecular Evolution 46 (4), 419–431.
- Posada, D., 2003. Using MODELTEST and PAUP* to select a model of nucleotide substitution. Current Protocols for Bioinformatics, Unit 6, 5 Chapter 6.
- Posada, D., Crandall, K.A., 1998. MODELTEST: testing the model of DNA substitution. Bioinformatics 14 (9), 817–818.
- Powers, D.A., Lauerman, T., Crawford, D., DiMichele, L., 1991. Genetic mechanisms for adapting to a changing environment. Annual Review of Genetics 25, 629–659.
- Quattro, J.M., Chase, M.R., Rex, M.A., Greig, T.W., Etter, R.J., 2001. Extreme mitochondrial DNA divergence within populations of the deep-sea gastropod *Frigidoalvania brychia*. Marine Biology 139 (6), 1107–1113.
- Rouse, G., 2001. A cladistic analysis of Siboglinidae caullery, 1914 (Polychaeta, Annelida): formerly the phyla pogonophora and vestimentifera. Zoological Journal of the Linnean Society 132, 55–80.
- Saitou, N., Nei, M., 1987. The neighbor-joining method: a new method for reconstructing phylogenetic trees. Molecular and Biological Evolution 4, 406–425.
- Tamura, K., Dudley, J., Nei, M., Kumar, S., 2007. MEGA4: molecular evolutionary genetics analysis (MEGA) software version 4.0. Molecular Biology and Evolution 24 (8), 1596–1599.
- Thompson, J.D., Gibson, T.J., Higgins, D.G., 2002. Multiple sequence alignment using ClustalW and ClustalX. Current Protocols in Bioinformatics, Chapter 2, Unit 23.
- Thornhill, D.J., Mahon, A.R., Norenburg, J.L., Halanych, K.M., 2008. Open-ocean barriers to dispersal: a test case with the Antarctic Polar Front and the ribbon worm *Parborlasia corrugatus* (Nemertea: Lineidae). Molecular Ecology 17 (23), 5104–5117.
- Tyler, P.A., Young, C.M., 1999. Reproduction and dispersal at vents and cold seeps. Journal of the Marine Biological Association of the United Kingdom 79, 193–208.
- van der Land, J., Narrevang, A., 1975. The systematic position of Lamellibrachia [sic] (annelida, vestimentifera). In: Norrevang, A. (Ed.), The Phylogeny and Systematic Position of Pogonophora, pp. 86–101.
- Wilgenbusch, J.C., Swofford, D., 2003. Inferring evolutionary trees with PAUP*. Current Protocols in Bioinformatics, Chapter 6, Unit 64.
- Won, Y., Young, C.R., Lutz, R.A., Vrijenhoek, R.C., 2003. Dispersal barriers and isolation among deep-sea mussel populations (mytilidae: *Bathymodiolus*) from eastern Pacific hydrothermal vents. Molecular Ecology 12 (1), 169–184.
- Young, C.M., Vazquez, E., Metaxas, A., Tyler, P.A., 1996. Embryology of vestimentiferan tube worms from deep-sea methane/sulphide seeps. Nature 381 (6582), 514–516.
- Zardus, J.D., Etter, R.J., Chase, M.R., Rex, M.A., Boyle, E.E., 2006. Bathymetric and geographic population structure in the pan-Atlantic deep-sea bivalve *Deminucula atacellana* (Schenck, 1939). Molecular Ecology 15 (3), 639–651.
- Zwickl, D.J., 2006. Genetic algorithm approaches for the pylogenetic analysis of large biological sequence datasets under the maximum liklihood criterion. [www.bioutexas.edu/faculty/antisense/garli/Garli/html] Ph.D. dissertation, The University of Texas at Austin, TX, USA.