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An inordinate fondness for *Osedax* (Siboglinidae: Annelida): Fourteen new species of bone worms from California

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Abstract

We incorporate DNA sequences from a comprehensive sampling of taxa to provide an updated phylogeny of *Osedax* and discuss the remarkable diversity of this clade of siboglinids. We formally describe 14 new species of *Osedax* from Monterey Bay, California, USA, raising the total number of properly named *Osedax* species to 25. These new species had formerly been recognized by informal names in various publications, and on GenBank. The descriptions document the occurrence of dwarf males in five of the new species. The distribution for the 19 species of *Osedax* known to occur in Monterey Bay across depths from 385 to 2898 meters and various bone substrates is documented. The exploitation of extant bird and marine turtle bones by *Osedax* is reported for the first time.

Key words: Siboglinidae, Annelida

Introduction

Osedax is a clade of siboglinid annelids that rely on sunken vertebrate bones and symbiotic bacteria for nutrition. The genus is also notable for its members having unusual life histories and was erected with descriptions of two species discovered in the Monterey Canyon, California, USA (Rouse *et al.* 2004). Following these initial descriptions nine new species were described over 10 years from localities worldwide, including the northeast Atlantic, the northwest Pacific, and the Southern Ocean (Tables 1, 3). Evidence also exists for numerous additional species, delineated mostly by unique DNA sequences. For instance, sunken bones recovered from the Monterey Canyon provided evidence for 15 other unnamed species (Braby *et al.* 2007; Jones *et al.* 2008; Rouse *et al.* 2015; Salathé & Vrijenhoek 2012; Vrijenhoek *et al.* 2009). New putative species were also reported from the Mediterranean Sea ('mediterranea', Taboada *et al.* 2015) and south Atlantic near Brazil ('1336_61_2'). Apart from *O. japonicus*, the single described species from Japan, unpublished DNA sequences deposited on GenBank provide evidence for additional *Osedax* species (Tables 1-3). This proliferation of placeholder names and informal epithets for newly discovered species (e.g., 'mediterranea', 'MB16', '1336_61_2', 'Sagami-6') creates a 'nomenclatural housekeeping problem' (Brower 2010) and contributes to the 'dark taxa' problem (Page 2016), which impede unambiguous communication about the remarkable diversity and evolutionary ecology of these unusual worms.

The goals of this study were twofold: (1) to rectify a significant portion of this nomenclatural problem by formally describing 14 new species from Monterey Bay, California, USA; and (2) to use DNA sequences from a comprehensive sampling of taxa to construct a robust molecular phylogeny for *Osedax*. Bringing the total number of named *Osedax* species to 25, these descriptions document the occurrence of dwarf males in five of the new species and report the recovery of *Osedax* from experimentally deployed bird (*Meleagris gallopavo)* and turtle *(Chelonia mydas*) bones. The phylogenetic analysis benefitted from new DNA sequences generated for this study, along with recently published (Sumida *et al.* 2016; Taboada *et al.* 2015) and unpublished GenBank sequences for several undescribed species. A recent phylogenomic analysis of the Siboglinidae (Li *et al.* 2016) helped us identify

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the most appropriate outgroup, Monilifera, for *Osedax*. Though we have attempted to amply illustrate the new *Osedax* species described herein, we generally follow a 'turbotaxonomic' approach (see Summers *et al.* 2014) with short diagnoses and descriptions.

TABLE 1. Named, unnamed and new species of *Osedax*.

Epithet	Authority	Year	Type locality/Locality
Named species			
rubiplumus	Rouse, Goffredi & Vrijenhoek	2004	Monterey Bay, CA, USA
frankpressi	Rouse, Goffredi & Vrijenhoek	2004	Monterey Bay, CA, USA
mucofloris	Glover, Källstrom, Smith & Dahlgren	2005	Northeast Atlantic
japonicus	Fujikura, Fukiwara & Kawato	2006	Cape Nomamisaki, Japan
roseus	Rouse, Worsaae, Johnson, Jones & Vrijenhoek	2008	Monterey Bay, CA, USA
antarcticus	Glover, Wiklund & Dahlgren in Glover *et al.* 2013	2013	Antarctic
deceptionensis	Taboada, Cristobo, Avila, Wiklund & Glover in Glover *et al.* 2013	2013	Antarctic
crouchi	Amon, Wiklund, Dahlgren, Copley, Smith, Jamieson & Glover	2014	Antarctic
nordenskjoeldi	Amon, Wiklund, Dahlgren, Copley, Smith, Jamieson & Glover	2014	Antarctic
rogersi	Amon, Wiklund, Dahlgren, Copley, Smith, Jamieson & Glover	2014	Antarctic
priapus	Rouse, Wilson, Worsaae, & Vrijenhoek	2015	Monterey Bay, CA, USA
New species			
bryani	Rouse, Goffredi, Johnson & Vrijenhoek	this study	Monterey Bay, CA, USA
docricketts	Rouse, Goffredi, Johnson & Vrijenhoek	this study	Monterey Bay, CA, USA
jabba	Rouse, Goffredi, Johnson & Vrijenhoek	this study	Monterey Bay, CA, USA
knutei	Rouse, Goffredi, Johnson & Vrijenhoek	this study	Monterey Bay, CA, USA
lehmani	Rouse, Goffredi, Johnson & Vrijenhoek	this study	Monterey Bay, CA, USA
lonnyi	Rouse, Goffredi, Johnson & Vrijenhoek	this study	Monterey Bay, CA, USA
packardorum	Rouse, Goffredi, Johnson & Vrijenhoek	this study	Monterey Bay, CA, USA
randyi	Rouse, Goffredi, Johnson & Vrijenhoek	this study	Monterey Bay, CA, USA
ryderi	Rouse, Goffredi, Johnson & Vrijenhoek	this study	Monterey Bay, CA, USA
sigridae	Rouse, Goffredi, Johnson & Vrijenhoek	this study	Monterey Bay, CA, USA
talkovici	Rouse, Goffredi, Johnson & Vrijenhoek	this study	Monterey Bay, CA, USA
tiburon	Rouse, Goffredi, Johnson & Vrijenhoek	this study	Monterey Bay, CA, USA
ventana	Rouse, Goffredi, Johnson & Vrijenhoek	this study	Monterey Bay, CA, USA
westernflyer	Rouse, Goffredi, Johnson & Vrijenhoek	this study	Monterey Bay, CA, USA
Unnamed taxa			
'MB16'	Salath & Vrijenhoek 2012	2012	Monterey Bay, CA, USA
'mediterranea'	Taboada *et al.*	2015	Mediterranean
'1336_61_2'	Sumida *et al.*	2016	off S-SE Brazil
'Sagami-3'	Pradillon *et al.* GenBank	unpubl	Sagami Bay, Japan
'Sagami-4'	Pradillon *et al.* GenBank	unpubl	Sagami Bay, Japan
'Sagami-5'	Pradillon *et al.* GenBank	unpubl	Sagami Bay, Japan

TABLE 2. Specimen voucher and GenBank accession numbers for the DNA sequences used in this study. Bold indicates new sequences. COI = cytochrome c oxidase, H3 = Histone H3, other loci are for ribosomal RNA.

			ribosomal RNA			
Taxa	Source/Authority	COI	16S	18S	28S	H3
Outgroup Monilifera						
Lamellibrachia columna	Webb, 1969	DQ996645	FJ347646	FJ347679	**MG264417**	FJ347696
Riftia pachyptila	Jones, 1985	KP119562	KP119573	KP119591	KP119582	KP119555
Sclerolinum brattstromi	Webb, 1964	FJ347644	FJ347645	FJ347680	FJ347677	FJ347697
Osedax						
antarcticus	(Glover *et al*. 2013)	KF444422	KF444418	KF444420	-	-
bryani n. sp.	This study	KP119563	KP119574	KP119597	KP119584	KP119561
crouchi	(Amon *et al*. 2014)	KJ598032	KJ598035	KJ598038	-	-
deceptionensis	(Taboada *et al.* 2015)	KF444428	KF444419	KF444421	**MG264418**	KT860546
docricketts n. sp.	This study	FJ347626	FJ347650	FJ347688	FJ347666	FJ347710
frankpressi	(Rouse *et al.*, 2004)	FJ347607	FJ347658	FJ347682	FJ347674	FJ347705
jabba n. sp.	This study	FJ347638	FJ347647	FJ347693	FJ347676	FJ347703
japonicus	(Fujikura *et al*., 2006)	FM998111	-	FM995535	-	-
knutei n. sp.	This study	FJ347635	FJ347648	FJ347692	FJ347664	FJ347700
lehmani n. sp.	This study	DQ99664	FJ347660	FJ347689	FJ347672	FJ347706
lonnyi n. sp.	This study	FJ347643	FJ347651	FJ347695	FJ347663	FJ347699
mucofloris	(Glover *et al*., 2005)	AY827562	-	AY941263	-	-
nordenskjoeldi	(Amon *et al.* 2014)	KJ598033	KJ598036	KJ598039	-	-
packardorum n. sp.	This study	FJ347629	FJ347661	FJ347690	FJ347673	FJ347707
priapus	(Rouse *et al*. 2015)	KP119564	KP119575	KP119594	KP119585	KP119556
randyi n. sp.	This study	FJ347615	FJ347659	FJ347684	FJ347675	FJ347712
rogersi	Amon *et al*. 2014)	KJ598034	KJ598037	KJ598040	-	-
roseus	(Rouse *et al.*, 2008)	FJ347609	FJ347657	FJ347683	FJ347670	FJ347709
rubiplumus	(Rouse *et al.*, 2004)	EU852488	FJ347656	FJ347681	FJ347671	FJ347704
ryderi n. sp	This study	KP119563	KP119574	KP119597	KP119584	KP119561
sigridae n. sp.	This study	FJ347642	FJ347655	FJ347694	FJ347669	FJ347711
talkovici n. sp.	This study	FJ347621	FJ347654	FJ347685	FJ347668	FJ347698
tiburon n. sp.	This study	FJ347624	FJ347653	FJ347687	FJ347662	FJ347702
ventana n. sp.	This study	EU236218	FJ347652	FJ347686	FJ347665	FJ347701
westernflyer n. sp.	This study	FJ347631	FJ347649	FJ347691	FJ347667	FJ347708
1336_61_2	(Sumida *et al*. 2016)	LC106303	-	-	-	-
MB16	(Salathé & Vrijenhoek 2012)	JX280613	KP119581	KP119592	KP119588	KP119560
'mediterranea'	(Taboada *et al.* 2015)	KT860548	KT860055	KT860550	KT860549	KT860547
Sagami-3	(Pradillon *et al*. unpubl.)	FM998081	-	FM995537	-	-
Sagami-4	(Pradillon *et al*. unpubl.)	FM998082	-	FM995541	-	-
Sagami-5	(Pradillon *et al*. unpubl.)	FM998110	-	FM995539	-	-
Sagami-6	(Pradillon *et al.* unpubl.)	FM998107	-	FM995540	-	-
Sagami-7	(Pradillon *et al.* unpubl.)	FM998109	-	FM995542	-	-
Sagami-8	(Pradillon *et al*. unpubl.)	FM998110	-	FM995534	-	-

Materials and methods

Specimens. Bones from naturally occurring and experimentally-deployed cetacean, pinniped, bovid, and teleost bones were deployed and collected by remotely operated vehicle (ROV) over the course of 15 years (details available in Braby *et al.* 2007; Jones *et al.* 2008; Rouse *et al.* 2011; Rouse *et al.* 2015; Salathé & Vrijenhoek 2012; Vrijenhoek *et al.* 2009). Additional bone samples of turkey (*Meleagris gallopavo)* and green turtle bones *(Chelonia mydas*), not reported in previous studies, were deployed at 1018 m depth on 10/29/2010 and 5/25/2010, respectively and recovered on 6/2/2011. All specimens are lodged at the Scripps Institution of Oceanography Benthic Invertebrate Collection (SIO-BIC) in La Jolla, California.

DNA sequences. Most DNA sequences analyzed here were previously published, though we incorporate the unpublished data of Pradillon *et al.* that is lodged in GenBank (GB) (see Tables 2, 3). A new *28S* rDNA sequence was generated for *Lamellibrachia columna* (GB MG264417) and a longer *28S* rDNA sequence (GB MG264418) was added to GenBank acc. no. KT860544 for *O. deceptionensis.* New mitochondrial cytochrome-*c*-oxidase subunit 1 (*COI*) sequences were included with the descriptions of type specimens for *O. knutei* **n. sp.** (GB MG262305-MG262307), *O. ryderi* **n. sp.** (GB MG262308-MG262309), *O. talkovici* **n. sp.** (GB MG262310-MG262313), and *O. westernflyer* **n. sp.** (GB MG262302-MG262304), and lodged with GenBank (Table 3).

Phylogenetic analysis. A single representative sequence of the following genes (when available) was used to represent each *Osedax* species (Table 2): mitochondrial *COI* (1004 bp) and 16S rDNA (*16S*, 501 bp); and nuclear 18S rDNA (*18S*, 1644 bp), 28S rDNA (*28S,* 1057 bp) and Histone H3 (*H3*, 370 bp). The sequences were aligned with Q-INS-i option of MAFFT 7 (Katoh & Standley 2013), concatenated and analyzed using maximum likelihood (ML) analysis with bootstrapping (x500) conducted via RAxML 8 (Stamatakis 2014) under the GTR+G substitution model. Alignments were also analyzed with MrBayes 3.2 (Ronquist *et al.* 2012) where each locus was coded separately for the appropriate substitution model determined with the Bayesian Information Criterion (BIC) with Modeltest (Posada & Crandall 1998) within Geneious (R10.2.3, ©Biomatters Ltd.). Multiple replicates of MrBayes analyses (BI) were run for 10^8 generations, with sampling every 1000 generations for two separate runs. Mixing and convergence were assessed with Tracer 1.6 (Rambaut *et al.* 2014). Uncorrected pairwise distances for representative *COI* data were calculated (Table 4) using PAUP* (Swofford 2002).

Results

The present phylogenetic analyses for 28 *Osedax* 'species' recovered a topology that was identical for both the ML and BI runs (Fig. 1) and these did not differ fundamentally from the results reported by Taboada *et al.* (2015), despite the exclusion of divergent outgroup sequences. The major clades within *Osedax* (as indicated in Figure 1) followed those delineated in previous studies (Rouse *et al.* 2015; Taboada *et al.* 2015; Vrijenhoek *et al.* 2009). The new results showed that the western Atlantic species, *Osedax* '1335_61_2' (Sumida *et al.* 2016), belongs in clade IV and it constituted a well-supported sister-group to *Osedax frankpressi* from California (Fig. 1).

As with Taboada *et al.* (2015), there was poor support for several nodes, the most notable being the grouping of clades I and II, as well as placing clades I, II and VI together (Fig. 1). Relationships within clade II, which represents most of the *Osedax* species with 'nudepalps', were also generally poorly supported. Despite use of the most appropriate outgroup, Monilifera (Fig.1), as evidenced from the phylogenomic results in Li *et al.* (2016), further sequence data from other loci is clearly needed to resolve the internal phylogeny of *Osedax*. The current placement of *Osedax deceptionensis*, a nudepalp species, outside of clade II, has implications for the evolution of palps, the primary respiratory organ in *Osedax*. *Osedax* taxa with palps and pinnules are found in clades I, IV and V, suggesting that pinnulate palps have either evolved twice or been lost several times. Further, the placement of *Osedax jabba* **n. sp.**, the only species that lacks palps, in its own in clade III (Fig. 1), illustrates this lack is a character loss. Pradillon *et al.* reported evidence for eight *Osedax* species from Japan (unpublished GenBank data, designated as the previously described *O. rubiplumus*, *O. roseus* and Sagami-3 through -8). Five of them (*O. rubiplumus*, *O. roseus*, *O. westernflyer* **n. sp.**, *O. docricketts* **n. sp.**, and *O. randyi* **n. sp.**) also occur off of California.

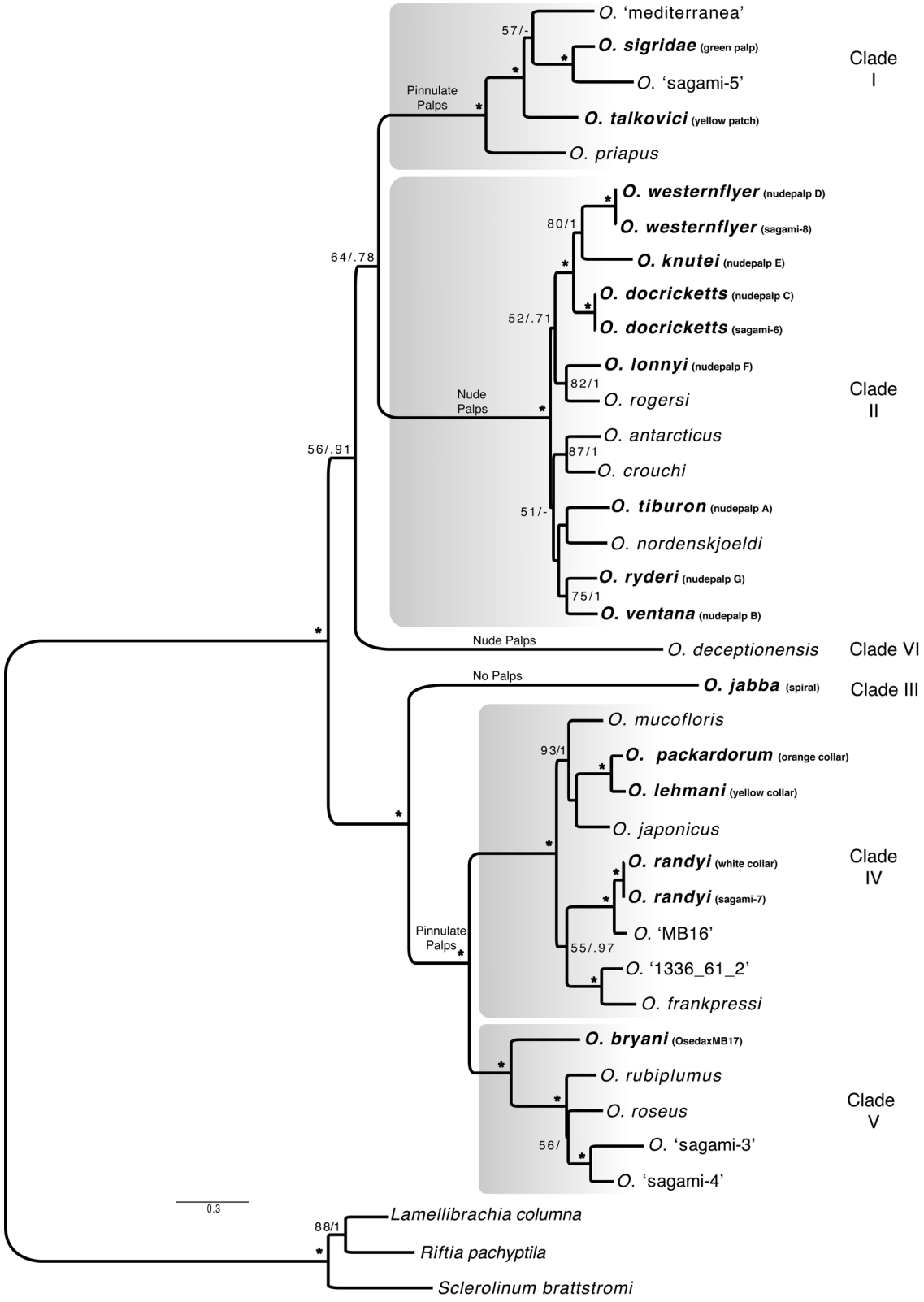

FIGURE 1. *Osedax* phylogenetic analyses. *Osedax* multi-gene phylogeny with Monilifera as outgroup. Maximum likelihood tree topology based on a partitioned dataset of five gene segments (MAFFT-aligned) for data shown in Table 2. The Bayesian analyses gave the same topology. Bootstrap support % (BS) is at each node, followed by posterior probability (PP) from the MrBayes analyses. * indicates values were ≥ 95% (BS) and 0.95 (PP). Missing values indicate BS < 50% and PP < 0.7. Six major *Osedax* clades are distinguished, following Vrijenhoek *et al.* (2009), Rouse *et al.* (2015) and Taboada *et al.* (2015). The various forms of palps (or absence thereof in the case of *O. jabba* **n. sp.**) are indicated for the major clades but these are not intended to indicate apomorphic states.

TABLE 3. Details of *Osedax* species locations, substrates, depth, vouchers, types and GenBank sequences (*COI*). New species are bold.

Species	Substrate	Latitude	Longitude	Depth (m)	Other names	Vouchers or types	COI sequences
antarcticus	Whale	63°10.98'S	61°38.16'W	568-1446		(Glover *et al.* 2013)	e.g. KF444422
***bryani* n. sp.**	**Whale, cow**	**36°42.496'N**	**122°6.316'W**	**1820**	**'MB17'**	**SIO-BIC A4619 (Holotype)**	**JX280609 (Holotype), JX80610**
crouchi	Whale	63°10.98'S	61°38.16'W	1446		(Amon *et al.* 2014)	e.g. KJ598038
deceptionensis	Whale	62°59.33'S	30°33.45'W	10-156		(Taboada *et al.* 2015)	e.g. KF444428
***docricketts* n. sp.**	**Whale**	**36°46.308'N**	**122° 4.981'W**	**1018**	**'nude-palp C'**	**SIO-BIC A1644 (Holotype)**	**FJ347625-6 (Holotype), EU267675-6**
	Whale	**35°05'N**	**139°13'E**		**Sagami-6**	(Pradillon *et al.* unpublished)	**FM998088-107; Some questionable, see text**
frankpressi		36°42.496'N	122°6.316'W	1820			
	Whale	36°36.606'N	122°26.122'W	2898		(Rouse *et al.* 2004)	e.g., AY586486, EU223312-16, FJ347606
***Jabba* n. sp.**	**Whale**	**36°36.606'N**	**122°26.122'W**	**2898**	**'spiral' 'sp.1 SBJ-2006'**	**SIO-BIC A1639, A7832 (Holotype), A7833, A7834, A7835, A7836, A7837, A7838, A7839**	**DQ996622 (A7833), DQ996623, DQ996624 (A1639), FJ347636-7 (A7834, A7835), FJ347638 (Holotype)**
japonicus	Whale	31°23.865'N	129°58.766'E	234		(Fujikura *et al.* 2006)	e.g. AB259569
***knutei* n. sp.**	**Whale, cow, teleost turkey**	**36°46.308'N**	**122° 4.981'W**	**1018**	**'nude-palp E'**	**SIO-BIC A1646, A7812 (Holotype), A7813, A7814, A7815, A7816**	**FJ347632(A7814), J347634, FJ347634 (A1646), FJ347635 (Holotype), JF509952 (A7815), JF509952-55, MG262305, MG262306 (A7816)**
	Teleost	**36°36.606'N**	**122° 26.12'W**	**2898**			**MG262307**
***lehmani* n. sp.**	**Whale, cow**	**36°47.401'N**	**122° 53.235'W**	**389**	**'yellow collar'**	**SIO-BIC A1640, A7804 (Holotype), A7805, A7806, A7807, A7808**	**EU223320-31, EU223332 (A7807), EU223333-36, EU223337 (A7808), EU223338, DQ996629 (Holotype)**
					'sp. 3 SBJ-2006' 'sp. 4 SBJ-2006' 'orange collar' sic		**DQ996630-31 (A1640, A7806), DQ996632-38 As 'sp. 4 SBJ-2006 DQ996640, DQ996643 As orange collar EU267762**
***lonnyi* n. sp.**	**Whale**	**36°36.606'N**	**122° 26.12'W**	**2898**	**'nude-palp F'**	**SIO-BIC A1647**	**FJ347643** (Holotype)
mucofloris	Whale	58°53.1'N	11°06.4'E	125		(Glover *et al.* 2005)	AY827562-AY827568
	Cow	38°16.856'N	09°06.734'W	120		(Schander *et al.* 2010)	HM045512-13
nordenskjoeldi	Whale	63°10.98'S	61°38.16'W	1446		(Amon *et al.* 2014)	e.g. KJ598039
***packardorum* n. sp.**	**Whale**	**36°47.401'N**	**122° 53.235'W**	**389**	**'orange collar' 'sp. 4 SBJ-2006'**		EU267673-4, FJ347627 DQ996639, DQ996641, DQ996642
	Whale, cow	**36°48.178'N**	**121°59.677'W**	**633**		**SIO-BIC A7844**	FJ347628-29, FJ4311989-9, **FJ431200 (A7844),** FJ431202-204
	Whale	**36°46.308'N**	**122° 4.981'W**	**1018**		**SIO-BIC A1641 (Holotype), A7840, A7841, A7842, A7843**	**EU223339 (A7840), EU223340 (A7841), EU223341 (Holotype), EU223342 (A7843), EU223343 (A7842),** EU223344-46, EU223349-55
priapus	Elephant seal	36°48.178'N	121°59.677'W	633	'pinnnules' (some)	(Rouse *et al.* 2015)	FJ431196-7, FJ431201, FJ431205, KP119564-71
	Fur seal	36°36.307'N	122°9.240'W	873	'sp. 16'		GQ504740-1

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TABLE 3. (Continued)

Species	Substrate	Latitude	Longitude	Depth (m)	Other names	Vouchers or types	COI sequences
***randyi* n. sp.**	**Whale**	**36°46.308'N**	**122° 4.981'W**	**1018**	**'white collar'**	**SIO-BIC A1648, A7845 (Holotype), A7846, A7847**	**FJ347610-11, FJ347612-14 (A7845, A7846, A7847), FJ347615 (Holotype)**
	Whale	**35°05'N**	**139°13'E**		**Sagami-7**	(Pradillon *et al.* unpublished)	**FM998108-9**
rogersi	Whale	59°41.671'S	28°21.089'W	1446		(Amon *et al.* 2014)	e.g. KJ598034
roseus	Whale	36°48.178'N	121°59.677'W	633	SBJ-2007a	(Rouse *et al.* 2008)	EU164760-73
	Whale, cow	36°46.308'N	122° 4.981'W	1018	sp.2 SBJ-2006		DQ996625-28, EU032471-84, EU164774,
	Whale	36°42.496'N	122°6.316'W	1820	'rosy'		KJ598034, JF509949, KJ598037, KJ598040 EU032469-70
	Whale	35° 04.897'N	139° 13.987'E		roseus (Japan)	(Paradillon *et al.* unpublished)	FM998064-077
rubiplumus	Whale, cow	36°42.496'N	122°6.316'W	1820		(Rouse *et al.* 2004)	EU852298-305, EU852431-88
	Whale	36°36.606'N	122°26.122'W	2898			EU852306-09, EU852420-30
	Whale	35° 04.897'N	139° 13.987'E		rubiplumus (Japan)	(Pradillon *et al.* unpublished)	FM998060-63
***ryderi* n. sp.**	**Whale, teleost, turtle**	**36°36.606'N**	**122°26.122'W**	**2898**	'nude-palp G', 'nude palp #20'	**SIO-BIC A4617 (Holotype), A4618 (Allotype)**	**KP119563 (Holotype), MG262308-09**
***sigridae* n. sp.**	**Whale, cow**	**36°42.496'N**	**122°6.316'W**	**1820**	**green palp**	**SIO-BIC A1650, A7809 (Holotype), A7810, A7811**	**FJ347639, FJ347640, FJ347641 (Holotype), FJ347642**
***talkovici* n. sp.**	**Whale, Elephant seal**	**36°48.178'N**	**121°59.677'W**	**633**	**'yellow patch' 'pinnules'**	**SIO-BIC A1649, A7822, A7823, A7824, A7825, A7826, A7827, A7828, A7829, A7830**	**FJ347620 (A7822), FJ347620 (A1649), FJ431196-97 (A7823, A7824), FJ431201 (A7825), FJ431205, (A7826), MG262311 (A7829), MG262310 (A7827)**
		36°46.308'N	**122° 4.981'W**	**1018**	**'yellow patch'**		**JF509950-51, FJ347616-18**
	Whale, cow, teleost, turkey, turtle					**No vouchers SIO-BIC A7821 (Holotype), A7831**	**MG262313 (Holotype), MG262312 (A7831)**
***tiburon* n. sp.**	**Whale, cow**	**36°42.496'N**	**122°6.316'W**	**1820**	**'nude-palp-A'**	**SIO-BIC A1642, A7817 (Holotype), A7818, A7819, A7820**	**FJ347622 (Holotype), FJ347623-24 (A7818, A7819), EU223356, EU223357 (A7820) EU223358-59 (A1642)**
***ventana* n. sp.**	**Cow**	**36°36.606'N**	**122°26.122'W**	**2898**	**'nude-palp-B'**	**SIO-BIC A1643 (Holotype)**	**EU236218**
***westernflyer* n. sp.**	**Whale**	**36°46.308'N**	**122° 4.981'W**	**1018**	**'nude-palp-D'**		**FJ347630**
	Whale, cow	**36°42.496'N**	**122°6.316'W**	**1820**		**SIO-BIC A1645 (Holotype), A7802, A7803**	**FJ347631, MG262303 (Holotype), MG262303 (A7802), MG262304 (A7803)**
	Whale	**35°05'N**	**139°13'E**	**925**	**Sagami-8**	(Pradillon *et al.* unpublished)	**FM998110**
1336_61_2	Whale	28° 31.119′ S	41° 39.401′ W	4204		(Sumida *et al.* 2016)	LC106303
MB16	Whale, cow	36°42.496'N	122°6.32'W	1820		(Salathé & Vrijenhoek 2012)	JX280611-13 (No vouchers)
mediterranea	Whale	41°40' 15' N	2°53' 23' E	53		(Taboada *et al.* 2015)	KT860548
Sagami-3	Whale	35°05'N	139°13'E	925		(Pradillon *et al.* unpublished)	FM998078-81
Sagami-4	Whale	35°05'N	139°13'E	925		(Pradillon *et al.* unpublished)	FM998082
Sagami-5	Whale	35°05'N	139°13'E	925		(Pradillon *et al.* unpublished)	FM998083-87

TABLE 4. COI pairwise uncorrected distance table generated with PAUP*. Distances are expressed as % and are rounded off. The sequences are as listed in Table 2, except for the following additional sequences: *O. knutei* **n. sp.** B is GB sequence JF59952, *O. lehmani* **n. sp.** B is GB sequence DQ996629**,** *Osedax lehmani* **n. sp.** C is GB sequence DQ996631. Sagami 6 B is FM998090. *Osedax* Sagami 6 is regarded here as part of *O. docricketts* **n. sp.**, *Osedax* Sagami 7 is regarded here as part of *O. randyi* **n. sp.**, *Osedax* Sagami 8 is regarded here as part of *O. westernflyeri* **n. sp.**, Distances highlighted as bold are discussed in the text.

	Osedax	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**
1	*antarcticus*																																					
2	***bryani* n.sp.**	18																																				
3	*crouchi*	14	18																																			
4	*deceptionensis*	19	19	18																																		
5	***docricketts* n.sp.**	18	17	14	18																																	
6	**Sagami 6**	18	17	14	19	**1**																																
7	Sagami 6 B	19	17	15	19	**3**	**3**																															
8	*frankpressi*	18	18	17	18	17	16	16																														
9	***jabba* n.sp.**	20	19	17	19	17	17	17	18																													
1	*japonicus*	18	17	18	19	18	18	18	16	17																												
11	***knute*i n.sp.**	18	18	16	19	15	15	15	19	17	19																											
12	***knutei* n.sp. B**	18	18	16	20	**15**	15	15	18	17	18	**4**																										
13	***lehmani* n.sp.**	21	18	17	19	18	18	18	17	17	14	17	18																									
14	***lehmani* n.sp. B**	22	17	18	20	18	18	18	17	17	15	18	17	**2**																								
15	***lehmani* n.sp. C**	21	18	19	20	19	19	19	18	18	16	18	18	**3**	**3**																							
16	***lonnyi* n.sp.**	15	16	14	18	**14**	14	15	18	17	17	15	15	18	18	18																						
17	*mucofloris*	21	20	18	21	18	18	18	17	17	15	17	18	15	16	15	20																					
18	*nordenskjoeldi*	16	18	14	19	16	16	17	17	18	17	17	16	20	19	20	16	17																				
19	***packardorum* n.sp.**	21	17	19	20	17	17	17	17	17	13	18	18	7	**8**	**9**	18	16	19																			
20	*priapus*	18	19	17	19	17	16	16	18	16	16	18	18	16	16	17	15	20	16	18																		
21	***randyi* n.sp.**	20	18	18	20	19	19	19	17	18	14	18	18	16	16	17	17	18	19	15	16																	
22	Sagami 7	20	18	18	20	19	20	20	17	18	14	18	18	16	16	17	17	18	18	16	16	**1**																
23	*rogersi*	15	18	15	20	15	15	15	17	18	17	16	16	18	18	19	**12**	18	15	18	16	17	18															
24	*roseus*	17	16	16	19	17	17	18	16	17	15	19	17	16	16	17	16	18	18	16	17	17	17	18														
25	*rubiplumus*	18	**15**	16	19	16	16	17	16	17	15	18	18	16	16	17	15	20	18	16	17	17	16	17	14													
26	***ryderi* n.sp.**	17	18	14	19	**14**	14	15	17	16	16	16	16	17	17	17	13	18	15	17	15	17	17	15	16	15												
27	***sigridae* n.sp.**	18	17	17	17	17	17	17	16	18	17	18	18	17	17	18	16	20	16	17	14	18	18	17	16	16	15											
28	***talkovici* n.sp.**	22	17	17	19	17	17	17	18	17	17	17	17	16	16	17	17	19	17	17	17	19	19	17	18	18	16	**16**										
29	***tiburon* n.sp.**	18	18	15	20	15	15	16	17	17	18	17	17	17	17	18	16	18	**15**	17	16	19	19	15	17	18	**14**	16	18									
30	***ventana* n.sp.**	19	19	15	18	**14**	14	15	16	16	17	16	17	18	18	19	14	19	15	19	16	18	18	15	16	17	**12**	16	18	15								
31	***westernflyer* n.sp.**	18	18	17	20	**15**	**15**	14	18	17	19	**16**	**16**	19	19	19	16	19	16	18	18	19	20	16	17	17	17	17	18	17	16							
32	Sagami 8	17	18	17	19	14	14	14	19	18	19	16	16	19	20	19	16	19	16	18	18	19	20	16	17	17	17	17	18	17	16	**0**						
33	1336_61_2	17	18	17	18	16	16	16	**10**	17	15	17	17	18	17	19	16	17	16	18	17	15	16	17	16	16	17	16	18	18	16	17	17					
34	MB16	20	18	17	20	18	18	18	16	18	13	17	17	15	15	16	16	18	17	17	16	**7**	**6**	17	17	16	15	17	18	20	17	19	19	16				
34	'mediterranea'	21	17	17	18	17	17	17	18	17	17	20	20	17	17	19	18	20	18	17	15	17	17	17	17	18	18	14	**16**	17	18	19	19	16	16			
36	Sagami3	19	17	17	20	18	18	18	16	18	17	18	19	15	16	16	17	19	17	16	18	17	18	18	14	14	16	17	17	18	18	17	17	17	17	19		
37	Sagami4	17	16	15	20	17	17	18	17	18	15	18	18	16	16	16	15	18	18	15	16	15	15	18	13	12	15	16	18	18	17	18	18	16	17	17	14	
38	Sagami5	19	19	17	19	17	17	17	17	18	17	18	18	18	17	18	17	18	17	19	15	18	18	17	17	16	16	**11**	**17**	17	17	17	17	17	19	15	18	16

Siboglinidae Caullery, 1914

***Osedax* Rouse, Goffredi & Vrijenhoek 2004**

Diagnosis. Siboglinids with females having a contractile trunk, bulbous ovisac, and branching 'roots'. A crown of palps usually present, with or without pinnules. Trunk lies within transparent tube emergent from bone surface. Mostly males are dwarfs resembling larvae, exceptionally having a crown, contractile trunk, bulbous testis sac, and branching 'roots', as in *O. priapus*. Crown in females, when present, comprised of cylindrical oviduct plus four palps. *Osedax priapus*, the only species known to produce adult bone-eating males, has crown with only two palps. No mouth or obvious gut. Cylindrical trunk comprised mostly of longitudinal muscles and glands, with large dorsal and ventral blood vessels present. Oviduct or sperm duct runs dorsally along trunk surface into posterior ovisac, or testis sac. Ovisac or testis sac enclosed by epidermis and trophosome with bacteriocytes, which also extends outwards as vascularized 'roots'. No chaetae or segmentation apparent in females or bone-eating males. In most species, paedomorphic dwarf males cluster around oviduct in gelatinous tube surrounding trunk of female. The dwarf males possess anterior prototroch and posterior hooked chaetae arranged on two segments. Hooks, lacking rostrum, comprise capitium with curved teeth over subrostral process. Internally, males contain spermatids and sperm anteriorly.

Remarks. This diagnosis is revised from that in Rouse *et al.* (2004) to accommodate the diversity of *Osedax* forms. These include *Osedax jabba* **n. sp.** where the females lack palps entirely and *Osedax priapus* where the males are not paedomorphic dwarfs, but also consume bone and have similar anatomy to females. Many *Osedax* species have palps that lack obvious pinnules. The dorsal placement of the oviduct reflects the reorientation of *Osedax* as reported in Huusgaard *et al.* (2012) and Worsaae *et al*. (2016).

***Osedax sigridae* n. sp.**
Figure 2

'green palp' (Katz *et al.* 2010; Katz *et al.* 2011; Katz & Rouse 2013; Rouse *et al.* 2015; Vrijenhoek *et al.* 2009)

Material examined. Holotype: SIO-BIC A7809 female (GenBank *COI* sequence FJ347641), collected from an experimentally deployed whale carcass (*Eschrichtius robustus*) deployed at 1820 meters depth in Monterey Submarine Canyon, California (36°42.496'N; 122°6.316'W) ROV *Tiburon* dive number 1163, Dec. 20, 2007. Fixed in formalin preserved in ethanol. **Paratypes**: All females. Fixed in formalin preserved in ethanol; SIO-BIC A7811 same locality and date as holotype (GenBank *COI* sequence FJ347642); SIO-BIC A1650 (GenBank *COI* sequence FJ347639) and SIO-BIC A7810 (GenBank *COI* sequence FJ347640), collected on cow bones deployed at 1820 meters depth in Monterey Submarine Canyon, California (36°42.496'N; 122°6.316'W) ROV *Tiburon* dive number 1119, Aug. 16, 2007.

Diagnosis and description. Holotype female (Fig. 2D); trunk 1 mm long, 0.5 mm wide; crown of pinnulated palps contracted, 2 mm long. Tube gelatinous, up to 10 mm long, 5 mm across. Oviduct shorter than palps (Fig. 2C). In life, palps green-yellow (Figs 2A, C, D). Pinnules of all four palps oriented dorsally (Fig. 2D). No obvious pigmentation on trunk, or clear demarcation into upper and lower trunk. Ovisac spheroidal with roots as simple lobes (Figs 2B, D). Males not found.

Distribution. Known from Monterey Bay, California from 1820 meters depth (Table 2). It has been found in whale and cow bones.

Etymology. This species is named (noun in the genitive case) for Sigrid Katz, whose Ph.D. project involved detailed study of the anatomy of this species (Katz *et al.* 2010; Katz *et al.* 2011).

Remarks. *Osedax sigridae* **n. sp.** is part of *Osedax* clade I and closest relative to the undescribed Japanese taxon *Osedax* 'Sagami-5' (Fig. 1). All four available *COI* sequences for *Osedax sigridae* **n. sp.** (Table 3) show less than 1% uncorrected sequence divergence, while the minimum uncorrected distance to *Osedax* 'Sagami-5' is 11% (Table 4). Careful searching for males in some of the tubes of the *Osedax sigridae* **n. sp.** females shown in Figure 2A failed, though Katz & Rouse (2013) did find sperm in the ovisac of females. The most distinguishing features of the *Osedax sigridae* **n. sp.** specimens collected to date are the distinctive green/yellow palps and the lobate roots (Fig. 2).

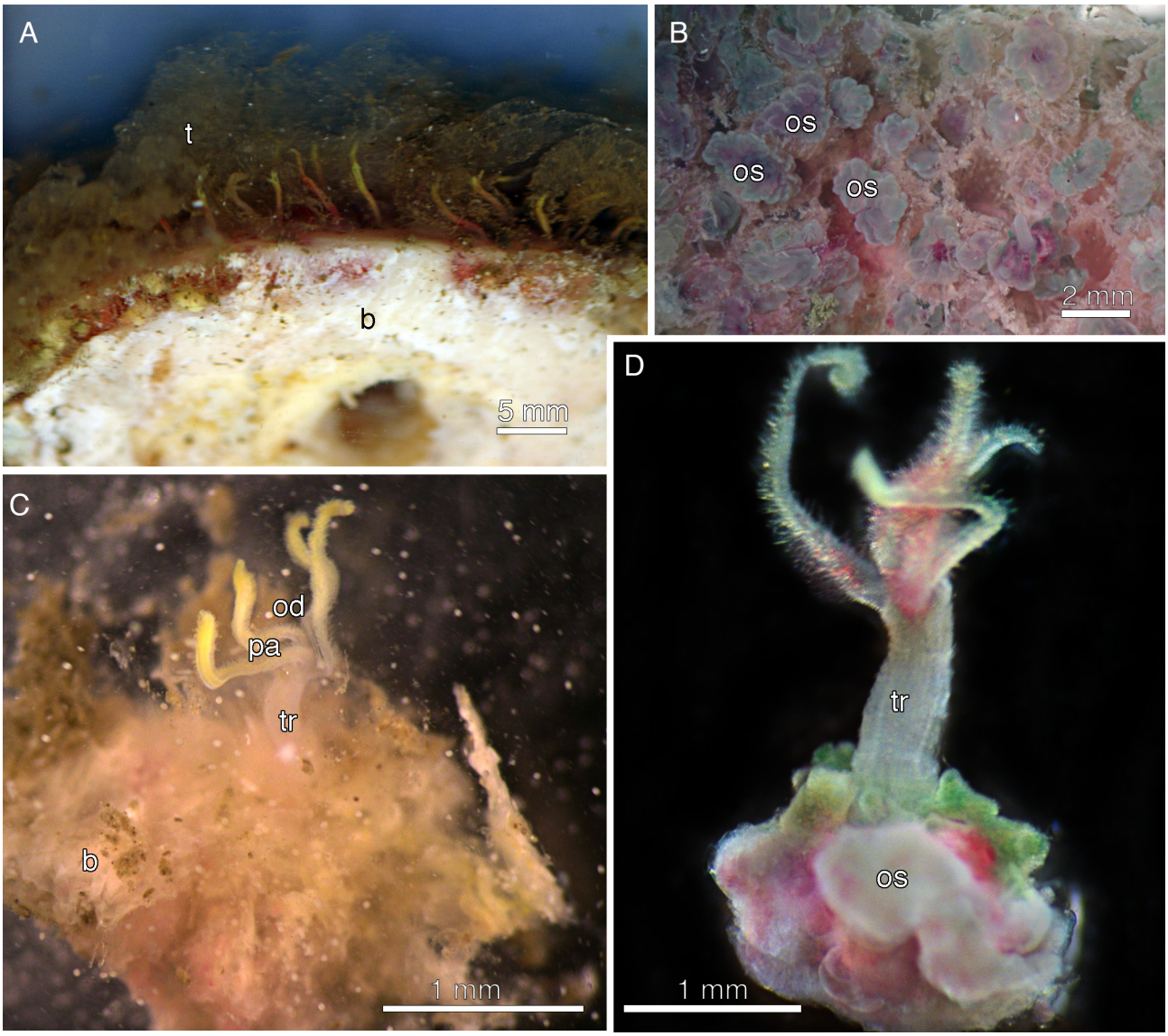


FIGURE 2. ***Osedax sigridae*** **n. sp.**, previously *Osedax* 'green palp'. **A**. View of cut surface of a cow femur deployed at 1820 meters in Monterey Canyon. Uncut surface of the bone has been heavily colonized by *Osedax sigridae* **n. sp.** Note greenish-yellow color of the palps. **B**. *Osedax sigridae* **n. sp.** specimens in A. penetrated through outer surface of the cow bone and then expanded into the area beneath. This allowed for the whole outer layer of outer bone, and the *Osedax*, to be peeled away. Posterior ends (ovisacs) of multiple individuals are shown here. No major root structures extend from the ovisacs. **C**. Paratype of *Osedax sigridae* **n. sp.** (SIO-BIC A7810) with some bone surrounding the trunk. Oviduct is visible and pinnules of all four palps are oriented dorsally. **D.** Dorso-lateral view of holotype of *Osedax sigridae* **n. sp.** (SIO-BIC A7809) dissected from bone. Oviduct is not visible as it lies among the palps, which have pinnules oriented dorsally. Note greenish hue of palps. Green tissue surrounding part of the ovisac.

Osedax talkovici **n. sp.**

Figure 3

'yellow patch' (Rouse *et al.* 2011; Rouse *et al.* 2015; Vrijenhoek *et al.* 2009)

Material examined. Holotype: SIO-BIC A7821 female (GenBank *COI* sequence MG262313), fixed in glutaraldehyde-preserved in ethanol, collected from turkey (*Meleagris gallopavo*) bone deployed at 1018 meters depth in Monterey Submarine Canyon, California (36°46.308'N; 122° 4.981'W) ROV *Doc Ricketts* dive number 233, June 2, 2011. **Paratypes**: Females, all fixed in formalin-preserved in ethanol, SIO-BIC A1649 (GenBank *COI* sequence FJ347621), SIO-BIC A7822, A7823, A7824, A7825, A7826 (GenBank *COI* sequences FJ347620,

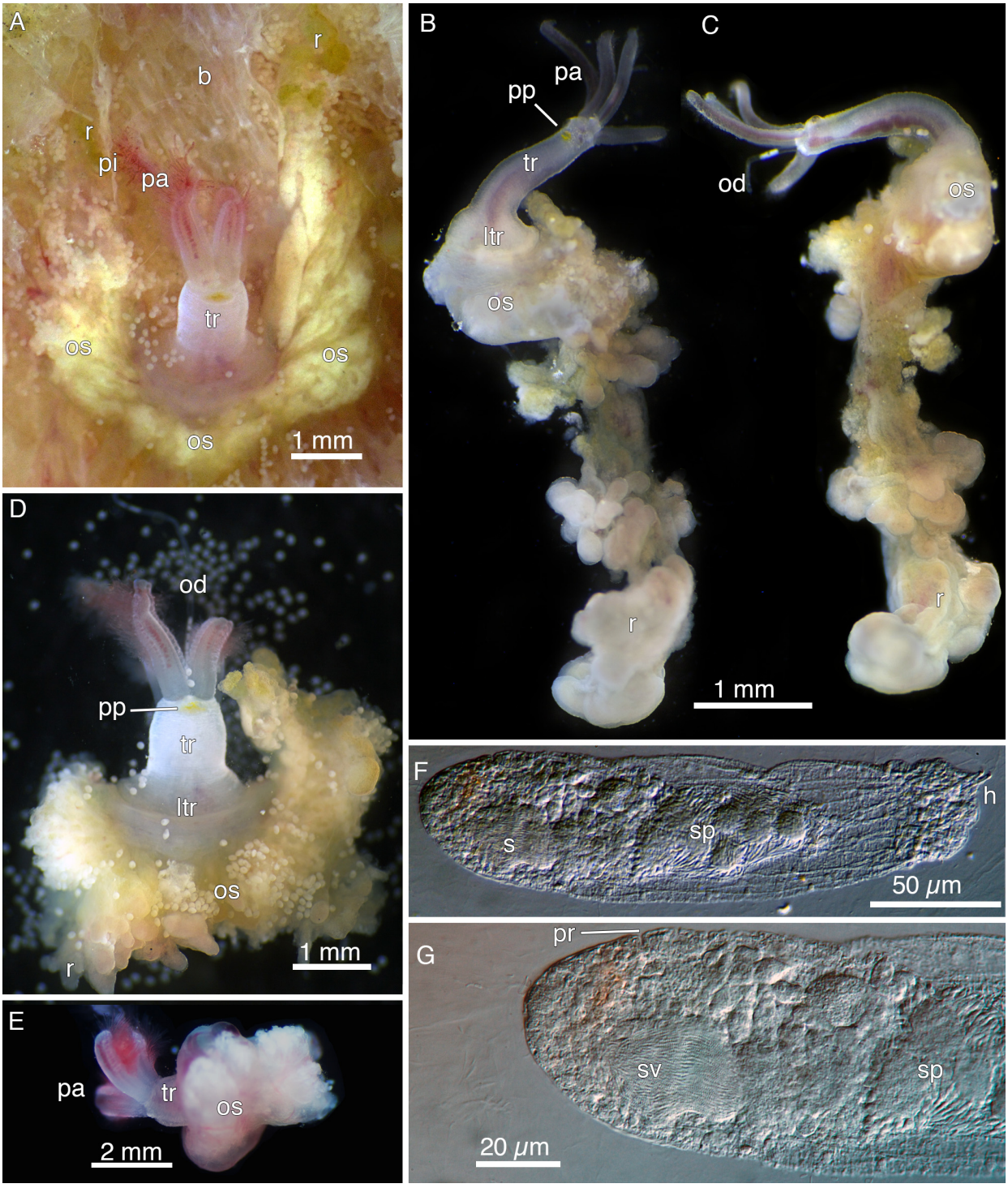


FIGURE 3. ***Osedax talkovici*** **n. sp.**, previously *Osedax* 'yellow patch'. **A.** Paratype (SIO-BIC A7831) in green turtle (*Chelonia mydas*) bone deployed at 1018 meters in Monterey Canyon, with bone partially dissected away from specimen. Note distinctive yellow patch on ventral part of the anterior trunk. Palps have dorsally-oriented pinnules. In this specimen, ovisac and roots extend laterally beneath surface of the bone rather than penetrating deeply into bone. **B.** and **C.** Holotype (SIO-BIC A7821) in ventrolateral (B) and dorsolateral (C) views. Holotype is a female dissected from turkey (*Meleagris gallopavo*) bone deployed at 1018 meters. Root mass extended into the bone in this specimen, away from the ovisac. Oocytes are visible in oviduct in C. **D.** Ventral view of female paratype (SIO-BIC A7831) shown in **A.**, now dissected from green turtle bone. **E.** Lateral view of paratype (SIO-BIC A7829), a female dissected from whale bone deployed at 633 meters. Pinnules of all palps are oriented dorsally. **F.** Dwarf male allotype (SIO-BIC A7828) taken from the tube of female paratype (SIO-BIC A7830). Hooked chaetae visible posteriorly, with spermatids in mid-body region and mass of mature sperm anteriorly. **G.** Anterior end of dwarf male allotype (SIO-BIC A7830) showing sperm mass.

431196, 431197, 431201, 431205), whale (*Eschrichtius robustus*) deployed at 633 meters depth in Monterey Submarine Canyon, California (36°48.178'N; 121°59.677'W) ROV *Tiburon* dive number 1160, Dec. 18, 2007; Female SIO-BIC A7829 (GenBank *COI* sequence MG262311) and dwarf males (allotypes) SIO-BIC A7830 whale fall at 633 meters depth in Monterey Submarine Canyon, California (36°48.178'N; 121°59.677'W) ROV *Doc Ricketts* dive number 205, October 26, 2010; Female SIO-BIC A7827 (GenBank *COI* sequence MG262310) and dwarf males (allotypes) SIO-BIC A7828, whale (*Eschrichtius robustus*) deployed at 633 meters depth in Monterey Submarine Canyon, California (36°48.178'N; 121°59.677'W) ROV *Doc Ricketts* dive number 233, June 2, 2011; Female SIO-BIC A7831 (GenBank *COI* sequence MG262312) on green turtle bone (*Chelonia mydas*), deployed at same locality and date as holotype.

Diagnosis and description. Holotype female (Figs 3B, C); in life trunk 1.8 mm long, 0.3 mm wide; crown of palps contracted, 1.5 mm long. Tube gelatinous. Oviduct 0.75 mm (Figs 3C, D). In life, palps reddish with blood (Figs 3A–E). Pinnules of all four palps oriented dorsally (Figs 3A, D, E). Trunk with bright yellow patch on midventral anterior edge (Figs 3A, B, D). Clear demarcation into upper and lower trunk (Fig. 3D). Ovisac spheroidal in holotype (Figs 3B, C), extending laterally, or as simple lobes in other specimens. Roots of holotype longer that the remaining body, extending posteriorly as a single lobate mass (Figs 3B, C). In other specimens (Figs 3A, D, E), roots as simple lobes or extending laterally in two lobes. Males dwarfs, resembling trochophore larvae, with spermatids and sperm (Figs 3F, G).

Distribution. Known from Monterey Bay, California from 633 to 1018 meters depth (Table 2). It has been found in whale, elephant seal, cow, turkey, turtle and teleost bones.

Etymology. This species is named (noun in the genitive case) for Mark Talkovic, Senior ROV pilot for MBARI, who collected many bones containing *Osedax* over the years.

Remarks. *Osedax talkovici* **n. sp.** is part of *Osedax* Clade I and forms a well-supported clade with the undescribed species *O*. 'mediterranea' and a clade comprised of *Osedax sigridae* **n. sp.** and the undescribed species *O*. Sagami-5 (Fig. 1). It has a minimum uncorrected distance, for *COI*, of at least 16% from each of these (Table 4). The 15 available *COI* sequences for *Osedax talkovici* **n. sp.** (Table 3) show less that 1% sequence divergence. The most distinguishing feature of *Osedax talkovici* **n. sp.** is the bright yellow patch ventrally on the anterior trunk (Fig. 3).

***Osedax tiburon* n. sp.**
Figure 4A, B, C

'nude-palp-A' (Jones *et al.* 2008; Rouse *et al.* 2011; Rouse *et al.* 2009; Rouse *et al.* 2015; Vrijenhoek *et al.* 2009)

Material examined. Holotype: SIO-BIC A7817 female (GenBank *COI* sequence FJ347622), fixed in formalin preserved in ethanol, collected from whale carcass (*Eschrichtius robustus*) deployed at 1820 meters depth in Monterey Submarine Canyon, California (36°42.496'N; 122°6.316'W) ROV *Tiburon* dive number 1163, Dec. 20, 2007. **Paratypes**: All females, fixed in formalin preserved in ethanol, SIO-BIC A1642 (GenBank *COI* sequence EU223359), SIO-BIC A7820 (GenBank *COI* sequence EU223356, EU223357), same locality as holotype, ROV *Tiburon* dive number 1119, Aug. 16, 2007; SIO-BIC A7818, A7819 (GenBank *COI* sequences FJ347623, FJ347624, respectively) same locality and date as holotype.

Diagnosis and description. Holotype female (Fig. 4B); preserved trunk 0.75 mm long, 0.2 mm wide; crown of four palps, 3 mm long. Tube gelatinous 6 mm long (Fig. 4A). Oviduct not discerned. In life, palps reddish with blood (Fig. 4A). Four palps without obvious pinnules (Fig. 4B, C). Trunk with no obvious demarcation into upper and lower trunk (Fig. 4B, C). Ovisac mostly missing in holotype, some traces of roots present (Fig. 4A). In paratype ovisac and root complex extends laterally on either side of trunk and posteriorly (Fig. 4C). Males not seen.

Distribution. Known from Monterey Bay, California from 1820 meters depth (Table 2).

Etymology. This species is named (noun in apposition) for the ROV *Tiburon*, which was used to collect the first *Osedax* specimens.

Remarks. *Osedax tiburon* **n. sp.** is part of *Osedax* Clade II and is closest relative (though with low support) to *Osedax nordenskjoeldi* from which it shows a divergence of 15%, though it shows a smaller pairwise distance

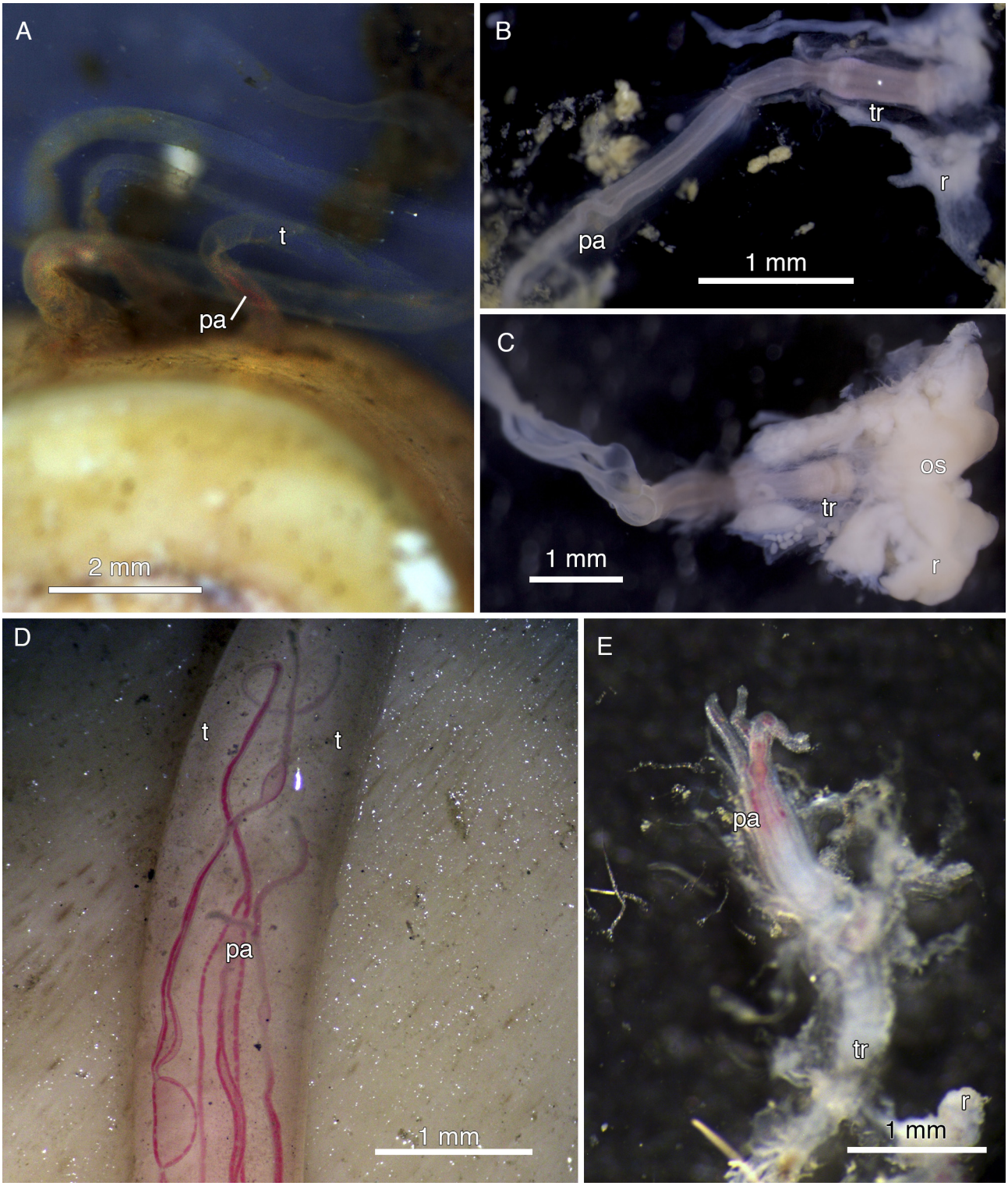


FIGURE 4. ***Osedax tiburon*** **n. sp**., previously *Osedax* 'nude-palp-A'; ***Osedax ventana*** **n. sp**., previously *Osedax* 'nude-palp-B'; ***Osedax docricketts*** **n. sp**., previously *Osedax* 'nude-palp-C'. **A**. Lateral view of *Osedax tiburon* **n. sp.** *in situ* in cow bone before dissection. Elongate apinnulate ('nude') palps are within a gelatinous tube. **B**. *Osedax tiburon* **n. sp.** preserved holotype (SIO-BIC A7817), removed from cow bone, showing elongate palps clustered together, obscuring oviduct. Trunk is relatively short and ovisac and roots were largely removed for DNA sequencing. **C**. *Osedax tiburon* **n. sp.** preserved paratype (SIO-BIC A7818) removed from cow bone, also showing elongate palps clustered together, obscuring oviduct. **D.** Holotype (SIO-BIC A1643) of *Osedax ventana* **n. sp.** before removal from cow bone deployed at 2898 meters depth in Monterey Canyon. Elongate apinnulate ('nude') palps are within gelatinous tube and are all that were retained for this species. **E**. Holotype (SIO-BIC A1644) of *Osedax docricketts* **n. sp.** incomplete after dissection, and before preservation.

(14%) to *O. ryderi* **n. sp.** (Table 4). The seven available *COI* sequences for *Osedax tiburon* **n. sp.** (Table 3) show less than 1% sequence divergence. It has been found in whale bones and experimentally deployed cow bones. There is little to distinguish *Osedax tiburon* **n. sp.** from other 'nude palp' species in Clade II, which share a similar morphology. The species status of *Osedax tiburon* **n. sp.** is supported largely on its *COI* divergence from other *Osedax*.

***Osedax ventana* n. sp.**
Figure 4D

Osedax 'nude-palp-B' (Jones *et al.* 2008; Rouse *et al.* 2011; Rouse *et al.* 2009; Rouse *et al.* 2015; Vrijenhoek *et al.* 2009)

Material examined. Holotype: SIO-BIC A1643 palps only (GenBank *COI* sequence EU235218), fixed in formalin preserved in ethanol, collected from cow bones deployed at 2898 meters depth in Monterey Submarine Canyon, California (36°36.606'N; 122°26.122'W) ROV *Tiburon* dive number 1069, Oct. 1, 2007.

Diagnosis and description. Holotype represented by fragments of four palps (Fig. 4D), still within a gelatinous tube. Oviduct not discerned. In life, palps reddish with two blood vessels in each, lacking obvious pinnules (Fig. 4D).

Distribution. Known from Monterey Bay, California from 2898 meters depth (Table 2). It has only been found in experimentally deployed cow bones.

Etymology. This species is named (noun in apposition) for the ROV *Ventana*, which was used to collect many *Osedax* specimens.

Remarks. *Osedax ventana* **n. sp.** is known from only a single partial specimen, sequenced by Jones *et al.* (2008). It was found on a deployed cow bone and was not discovered during any subsequent sampling at the same site. *Osedax ventana* **n. sp.** is part of *Osedax* Clade II and closest relative (with low support) to *Osedax ryderi* **n.sp**., from which it shows an uncorrected divergence of 12% (Table 4). Given the holotype is a fragment, there is little, except for its unique *COI* sequence, to distinguish *Osedax ventana* **n. sp.** from other Clade II species. Three other *Osedax* species: *O. crouchi*, *O. nordenskjoeldi* and *O. rogersi*, were similarly erected based on fragmented specimens and DNA data (Amon *et al.* 2014).

***Osedax docricketts* n. sp.**
Figure 4E

'nude-palp-C' (Higgs *et al.* 2014; Rouse *et al.* 2011; Rouse *et al.* 2015; Vrijenhoek *et al.* 2009)
'Sagami-6' (GenBank *COI* sequence series FM998088-FM998107; Pradillon et al. unpublished)

Holotype: SIO-BIC A1644, Female (GenBank *COI* sequence FJ347626), fixed in formalin preserved in ethanol, collected from whale fall deployed at 1018 meters depth in Monterey Submarine Canyon, California (36°46.308'N; 122° 4.981'W), ROV *Tiburon* dive number 1049, Oct. 25, 2006.

Diagnosis and description. Holotype incomplete female; preserved trunk 0. 5 mm long, 0.2 mm wide; crown of four palps, 2 mm long (Fig. 4E). Tube gelatinous cylinder around trunk and base of palps. Oviduct not discerned. In life, palps white with some reddish patches. Palps without obvious pinnules (Fig. 4E). Trunk with no obvious demarcation into upper and lower trunk, or any pigmentation. Ovisac mostly missing in holotype, some traces of roots present. Males not seen.

Distribution. Known from Monterey Bay, California from 1820 meters depth, and Sagami Bay, Japan (Table 2). It has been found living on cow and whale bones.

Etymology. This species is named (noun in apposition) for the ROV *Doc Ricketts*, which was used to collect many *Osedax* specimens.

Remarks. *Osedax docricketts* **n. sp.** is part of *Osedax* Clade II, which all show apinnulate palps, and is closest relative to the clade comprised of *Osedax westernflye*r **n. sp.** and *O. knutei* **n. sp.** (minimum divergence of 15%) though it shows smaller distance (14%) to other taxa such as *O. lonnyi* **n. sp.** (Table 4). The four available *COI* sequences for *Osedax docricketts* **n. sp.** from California (Table 3) show less that 1% sequence divergence. The only

retained specimen is the holotype as the others were destroyed for sequencing and the holotype itself is only a partial specimen. Twenty additional *COI* sequences were referred to *Osedax* sp. Sagami-6 (Pradillon et al., GenBank, unpublished). Together, the four California and 11 of the Japanese sequences (FM998088, FM998089, FM998091, FM998093, FM998094, FM998098, FM998099, FM998100, FM998101, FM998103, FM998107) encompass less than 1% sequence divergence; so, we propose that *Osedax docricketts* **n. sp.** is also found in Japan. The nine remaining Japanese specimens with >2.4% uncorrected pairwise distance from the 11 Japanese sequences (GenBank sequences: FM998090, FM998092, FM998095, FM998096, FM998097, FM998102, FM998104, FM998105, FM998106) require further investigation before their assignment to *Osedax docricketts* **n. sp.** can be justified. See Table 4 for comparison of California *Osedax docricketts* **n. sp.** versus Japanese Sagami-6 representative sequences. There is little to distinguish *Osedax docricketts* **n. sp.** from other Clade II species.

***Osedax westernflyer* n. sp.**
Figure 5

'nude-palp-D' (Rouse *et al.* 2011; Rouse *et al.* 2015; Vrijenhoek *et al.* 2009)
'Sagami 8' (GenBank *COI* sequence FM998110; Pradillon *et al*. unpublished)

Material examined. Holotype: SIO-BIC A1645, Female (GenBank *COI* sequence MG262303), fixed in formalin preserved in ethanol, collected from a whale carcass (*Eschrichtius robustus*) deployed at 1820 meters depth in Monterey Submarine Canyon, California (36°42.496'N; 122°6.316'W), ROV *Doc Ricketts* dive number 12, March 13, 2009. **Paratypes**: All females, fixed in formalin preserved in ethanol, SIO-BIC A7802, A7803 (GenBank *COI* sequence MG262302, MG262304), same locality and date as holotype.

Diagnosis and description. Holotype female (Fig. 5C); in life trunk 2.8 mm long, 0.5 mm wide; crown of four palps, 3.5 mm long. Tube gelatinous, thin, fitting about trunk and base of crown, 3 mm long (Fig. 5C). Oviduct among palps 2.3 mm long (Figs 5A-C). In life, palps with white patches with no visible blood vessels, without obvious pinnules (Figs 5A-C). Trunk with demarcation into upper and lower trunk (Fig. 5C), white pigment patch mid-ventrally on anterior tip of trunk (Figs 5B, C). Ovisac 1.5 mm by 1 mm with lobate greenish roots extending outwards (Figs 5B, C). Males not found.

Distribution. Known from Monterey Bay, California from 1820 meters depth and Sagami, Bay Japan (Table 2). It has been found in cow and whale bones.

Etymology. This species is named (noun in apposition) for the Research Vessel *Western Flyer*, which has been critical to *Osedax* studies.

Remarks. *Osedax westernflyer* **n. sp.** is part of *Osedax* Clade II and is closest relative to *O. knutei* **n. sp.**, with a minimum divergence of 16 % for *COI,* though it shows a smaller distance, 14% to *O. docricketts* **n. sp.** (Table 4). The four available *COI* sequences for *Osedax westernflyer* **n. sp.** from California (Table 3) are less that 1% divergent. The holotype and two paratypes all showed distinct white pigment on the palps, though these were all collected from one patch of bone and the color may have been caused by a bacterial coating. A single *COI* sequence on GenBank (FM998110), referred to *Osedax* sp. Sagami-8 (Pradillon et al., unpublished), is less than 1% divergent from the four California *COI* sequences (Table 4), leading us to propose that *Osedax westernflyer* **n. sp.** is also found in Japan. There is little to distinguish *Osedax docricketts* **n. sp.** from other Clade II species, apart from the white pigmentation at the anterior end of the trunk and on the pigmentation on palps.

***Osedax knutei* n. sp.**
Figure 6

'nude-palp-E' (Rouse *et al.* 2011; Rouse *et al.* 2015; Vrijenhoek *et al.* 2009; Worsaae *et al.* 2016)

Material examined. Holotype: SIO-BIC A7812, Female (GenBank *COI* sequence FJ347635), fixed in formalin preserved in ethanol, collected from whale fall (*Balaenoptera musculus*) deployed at 1018 meters depth in Monterey Submarine Canyon, California (36°46.308'N; 122° 4.981'W), ROV *Tiburon* dive number 1049, Oct. 25, 2006; **Allotype**, dwarf male from tube of holotype SIO-BIC A7813. **Paratypes**: All females, fixed in formalin

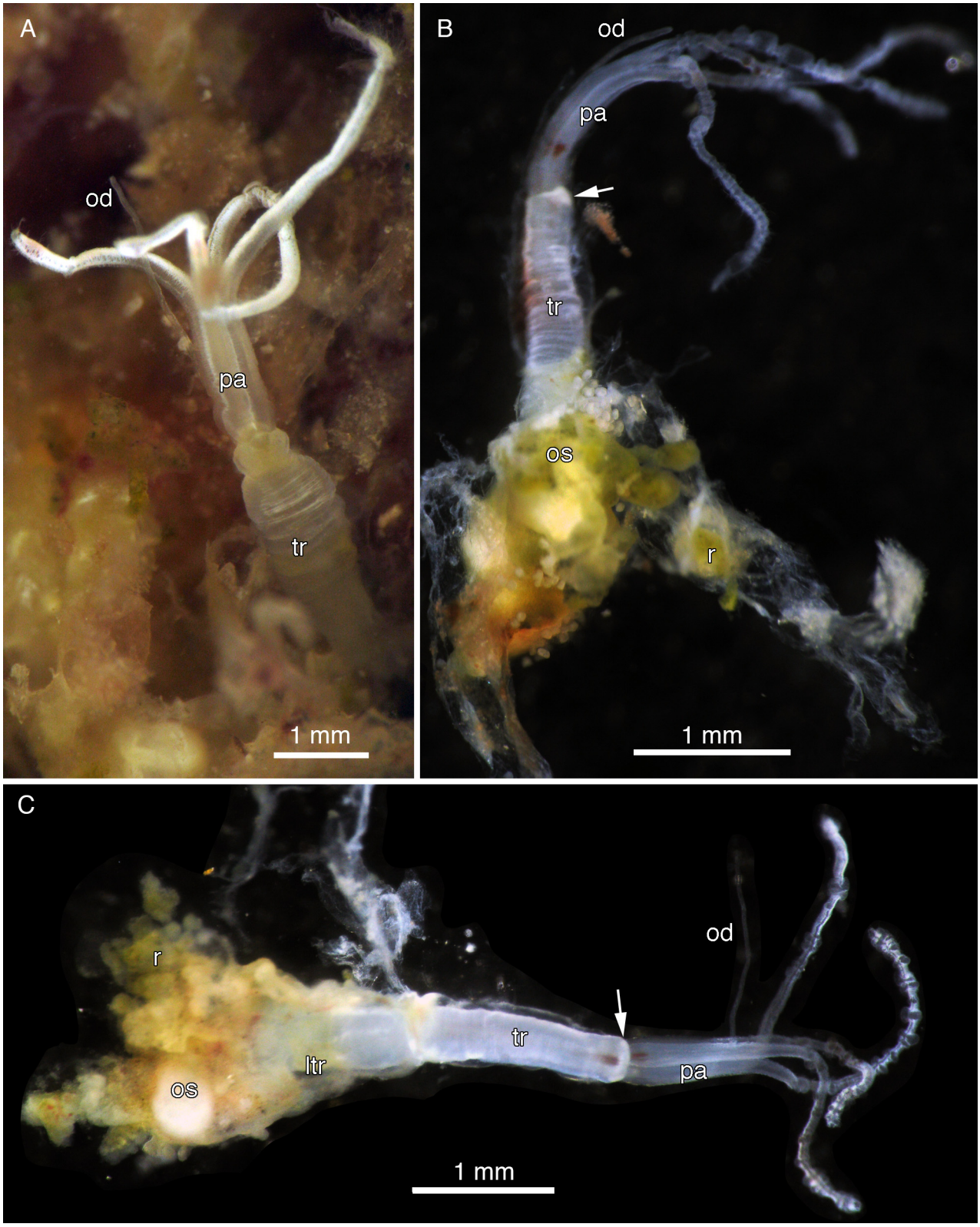


FIGURE 5. ***Osedax westernflyer*** **n. sp.**, previously *Osedax* 'nude-palp-D'. **A**. Lateral view of *Osedax westernflyer* **n. sp.** paratype (SIO-BIC A7802), with distinctive white pigment (or bacteria) on palps, while still living and in degraded bone. **B.** Ventro-lateral view of paratype (SIO-BIC A7803) dissected from bone and still alive. Note ventral lobe-like projection of anterior trunk beneath palps (arrow). Oviduct is about half length of the palps. **C.** Dorsal view of holotype (SIO-BIC A1645) dissected from bone and still alive.

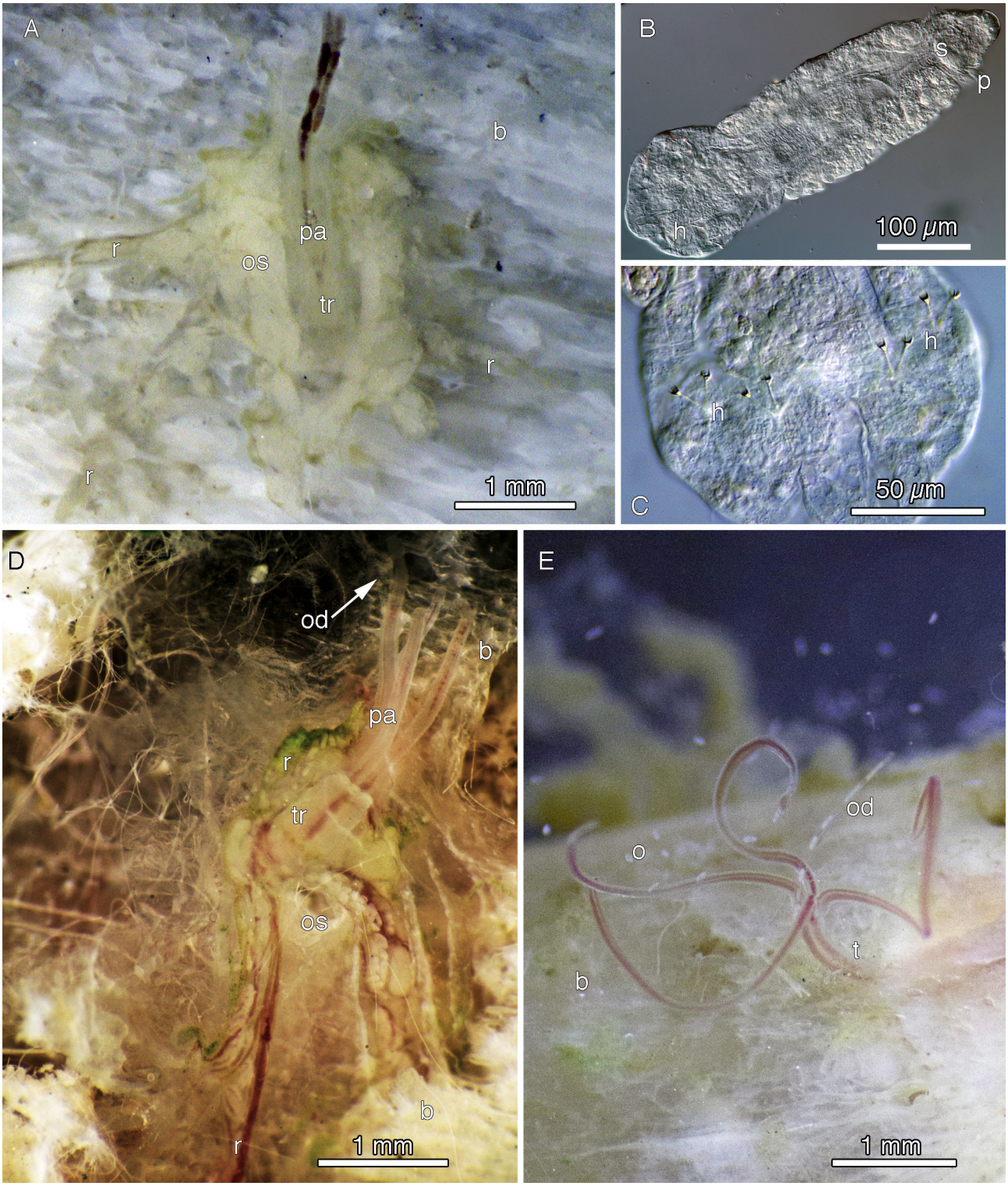


FIGURE 6. ***Osedax knutei*** **n. sp.**, previously *Osedax* 'nude-palp-E'. **A.** Preserved female holotype (SIO-BIC A7812) with bone dissected away, but leaving body in place. Roots have ramified laterally parallel to bone surface. Trunk is short and palps, though contracted, are much longer. **B**. Dwarf male allotype (SIO-BIC A7813) found in tube of holotype. Prominent prototroch and sperm mass anteriorly. Posterior segmented region is slightly swollen with hooked chaetae clearly visible. **C**. Posterior region of allotype (SIO-BIC A7813), showing paired hooks on one side of segments 2 and 3. **D**. Live image of paratype (SIO-BIC A7816) partially dissected from bone. Palps are contracted, but still longer than the trunk. Ovisac is visible with root and blood vessel extending further into the bone. **E**. Live female *Osedax knutei* **n. sp.** in turkey bone and spawning oocytes into water. Trunk and lower palp region retracted into bone. Palps and oviduct extend out of the tube and compressed oocytes are visible in oviduct and freshly deposited in water. Specimen was destroyed for sequencing = GB MG262305.

preserved in ethanol; SIO-BIC A1646 (GenBank *COI* sequence FJ347634), SIO-BIC A7814, (GenBank *COI* sequence FJ347632), same locality and date as holotype; SIO-BIC A7815, (GenBank *COI* sequence JF509952), collected from fish bones deployed at 1018 meters depth in Monterey Submarine Canyon, California (36°46.308'N; 122° 4.981'W), ROV *Doc Ricketts* dive number 209, Oct. 29, 2010; SIO-BIC A7816, (GenBank *COI* sequences MG262306), collected from turkey (*Meleagris gallopavo*) bone deployed at 1018 meters depth in Monterey Submarine Canyon, California (36°46.308'N; 122° 4.981'W), ROV *Doc Ricketts* dive number 233, June 2, 2011.

Diagnosis and description. Holotype female preserved partially dissected from whale bone (Fig. 6A); trunk contracted 1.6 mm long, 0.3 mm wide; crown of apinnulate palps contracted, 2.3 mm long. Tube not kept for holotype, but forms a tight sheath in other specimens, from which palps emerge. Oviduct not visible in holotype (Fig. 6A), but is slightly shorter (1.5 mm) than contracted palps in paratype SIO-BIC A7816, and much shorter than extended palps in live specimen spawning eggs (Fig. 6D). In life, palps reddish with two blood vessels each (Fig. 6E). Trunk with no obvious pigmentation or demarcation into upper and lower trunk (Figs 6A, D). Ovisac represented as lobes on either side of trunk in holotype, extending laterally, or as long lobes in other specimens. Roots of holotype longer that the remaining body, extending in several directions (Fig. 6A). In other specimens, roots also extend in various directions (Fig. 6D). Males dwarfs, 450 µm long by 100 µm wide, with anterior prototroch and sperm, two posterior expanded segments bearing hooked chaetae (Figs 6B, C).

Distribution. Known from Monterey Bay, California from 1018 to 2898 meters depth (Table 2). It has been found in whale, cow, turkey and teleost bones.

Etymology. This species is named (noun in the genitive case) for Knute Brekke, Chief ROV pilot for MBARI, who expertly collected many bones and *Osedax* over the years.

Remarks. *Osedax knutei* **n. sp.** is part of *Osedax* Clade II and closest relative to *Osedax westernflyer* n. sp, (Fig. 1) with a minimum uncorrected distance for *COI* of 16% (Table 4). Twelve *COI* sequences for *Osedax knutei* **n. sp.** (Table 3) generally showed less that 1.2% sequence divergence from each other. An exceptional sequence (JF509952) from paratype SIO-BIC A7815 dissected from fishbone (Rouse *et al.* 2011), diverged by 3.2% to 4.5% from the other *Osedax knutei* **n. sp.** specimens (see example distance in Table 4). The tentative assignment of paratype SIO-BIC A7815 to *Osedax knutei* **n. sp.** requires further investigation. Two new *COI* sequences for *Osedax knutei* **n. sp.** were also deposited on GenBank for which no voucher specimens were retained; MG262305 was recovered from a fishbone deployed at 2898 meters and MG262307 was from a turkey deployed at 1018 meters

***Osedax lonnyi* n. sp.**

Figure 7

'nude-palp-F' (Rouse *et al.* 2015; Vrijenhoek *et al.* 2009)

Material examined. Holotype: Female, SIO-BIC A1647 (GenBank *COI* sequence FJ347643), fixed in glutaraldehyde-preserved in ethanol, collected from natural whale fall (*Eschrichtius robustus*) found at 2898 meters depth in Monterey Submarine Canyon, California (36°36.606'N; 122°26.122'W) ROV *Tiburon* dive number 1162, Dec. 19, 2007.

Diagnosis and description. Holotype female; in life trunk 1 mm long, 0.5 mm wide (Fig. 7A), crown of four palps, 2.5 cm long (Fig. 7A), likely contracted even at this length. Tube gelatinous, thin, fitting about trunk and base of crown, 4 cm long (Fig. 7A). In life, palps with visible blood vessels and greenish tips (Fig. 7A, inset). Palps without obvious pinnules, oviduct extends slightly beyond palps (Fig. 7A inset). Trunk with pigmented ring demarking upper and lower trunk (Fig. 7B). Ovisac 2 mm by 1 mm with damaged lobate greenish roots extending outwards (Fig. 7B). Males not found.

Distribution. Known from Monterey Bay, California from 2898 meters depth (Table 2). It has only been found in a whale bone fragment, adjacent to the main skeleton.

Etymology. This species is named (noun in the genitive case) for Lonny Lundsten, Senior Research Technician at MBARI, for his enthusiasm and assistance on many *Osedax* expeditions.

Remarks. *Osedax lonnyi* **n. sp.** is part of *Osedax* Clade II and is the well-supported sistergroup to *Osedax*

rogersi, an Antarctic species with an uncorrected divergence of 12%. *Osedax lonnyi* **n. sp.** is remarkable for the very long palps (2.5 cm) that it shows relative to the very short trunk (1.5 mm). The species is known from only a single specimen (holotype) collected in 2007 and no further specimens were found during any subsequent sampling at the same site. This is somewhat surprising as it is one of the larger species of Clade II and the whale fall was sampled a number of times.

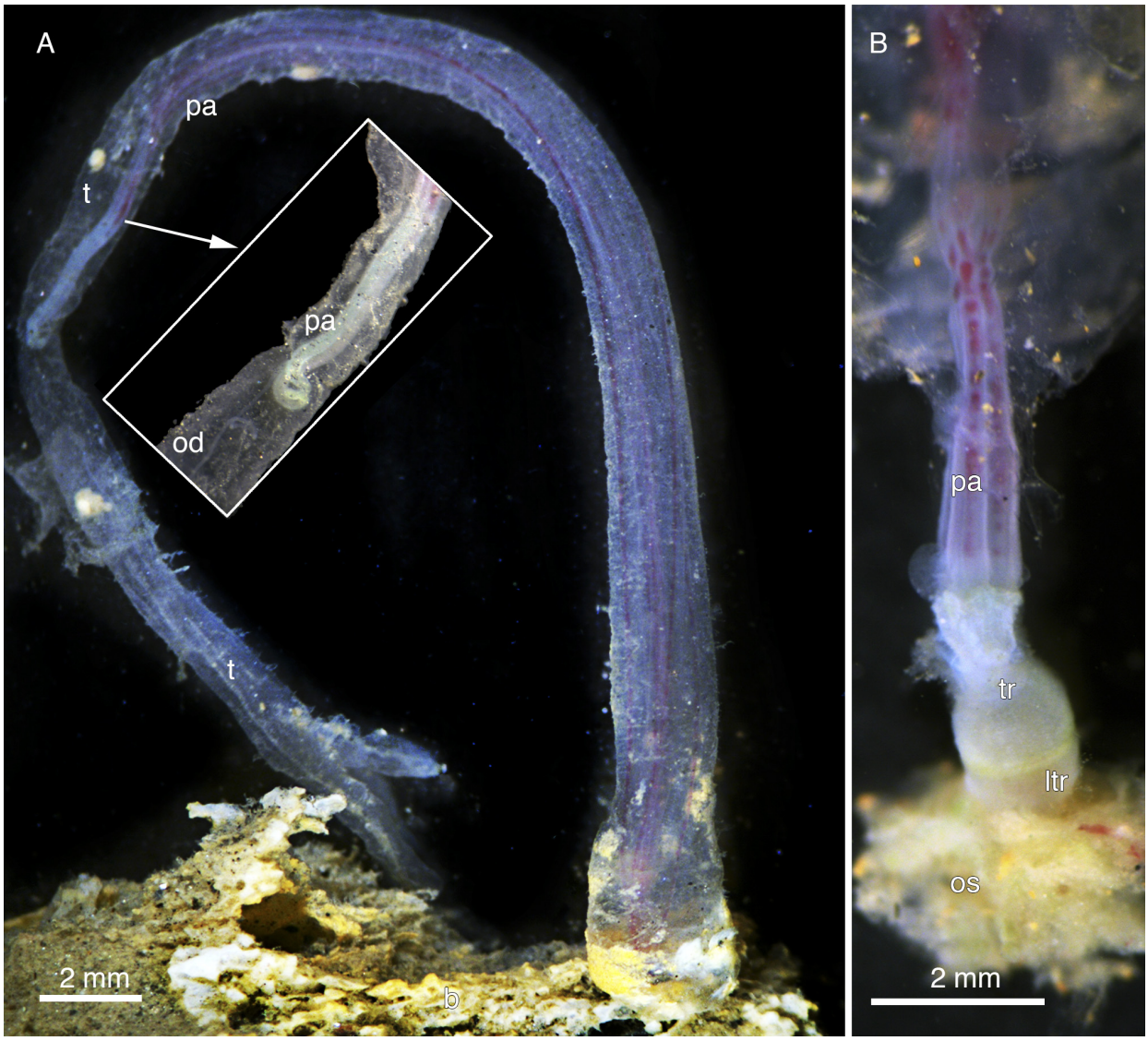


FIGURE 7. ***Osedax lonnyi*** **n. sp.**, previously *Osedax* 'nude-palp-F'. **A**. Image of live holotype (SIO-BIC A1647) still in tube and attached to whale bone lying at 2898 meters. Note very long palps occupying about 2/3 of tube. No part of trunk is apparent. **B**. Live holotype dissected from bone and tube. Note short trunk with pigmented ring separating upper and lower trunk. Little root tissue could be extracted, but there was an ovisac region.

Osedax ryderi **n. sp.**
Fig. 8

'nude-palp-G', 'nude palp #20' (Higgs *et al.* 2014; Rouse *et al.* 2015)

Material examined. Holotype: Female, SIO-BIC 4617 (GenBank *COI* sequence KP119563), fixed in glutaraldehyde-preserved in ethanol, collected from a natural whale fall (*Eschrichtius robustus*) found at 2898 meters depth in Monterey Submarine Canyon, California (36°36.606'N; 122°26.122'W) ROV *Doc Ricketts* dive number 234, June 3, 2011. **Allotype**: Male found in tube of holotype, SIO-BIC A4618.

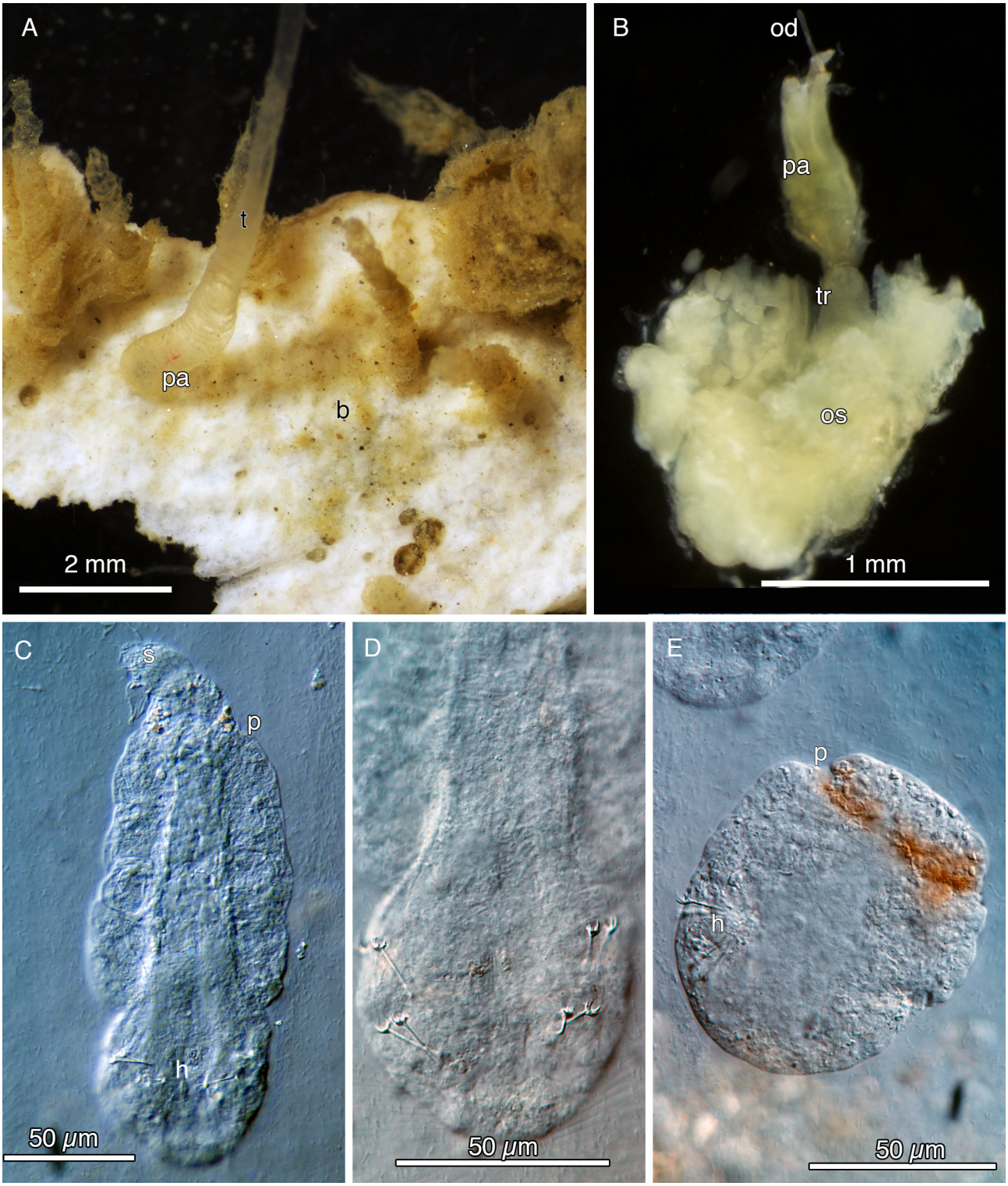


FIGURE 8. ***Osedax ryderi*** **n. sp.**, previously *Osedax* 'nude-palp-G', 'nude palp #20'. **A**. Live holotype (SIO-BIC A4617) female, with dwarf male allotypes (SIO-BIC A4618) in tube (not visible) before dissection from whale bone at 2898 meters. **B**. Preserved holotype, with intact ovisac. Trunk is short and the palps contracted to be shorter than oviduct. **C**. One of two males (SIO-BIC A4618) found in tube of holotype. Male has been squeezed with sperm coming out of head region. Prototroch is visible anteriorly with orange pigmentation. Several hooks are visible in posterior segmented region. **D**. Posterior segmented region showing hooked chaetae in pairs on one side of segments 2 and 3. Other chaetae are not in plane of focus. **E**. Developing dwarf male (SIO-BIC A4618), or larval stage that has yet to become mature. No sperm or spermatids are visible in body. Prototroch is visible with prominent orange pigmentation and hooked chaetae are visible posteriorly.

Diagnosis and description. Holotype female preserved partially dissected from bone; trunk contacted 0.6 mm long, 0.3 mm wide; crown of apinnulate palps contracted, 0.7 mm long (Fig. 8B). Tube not kept for holotype, but forms a tapering sheath in life, from which palps were not seen emerging (Fig. 8A). Oviduct slightly longer than palps visible in holotype (Fig. 8B). In life, palps reddish with two blood vessels each (Fig. 8A). Trunk with no obvious pigmentation or demarcation into upper and lower trunk. Ovisac represented as lobes on either side of trunk in holotype, extending laterally, or as long lobes in other specimens. Roots of holotype longer that the remaining body, extending in several directions as a single lobate mass (Fig. 8B). Male in a tube of holotype a dwarf, 210 µm long by 50 µm wide, with anterior prototroch and sperm squeezed out of head, two posterior expanded segments bearing hooked chaetae (Figs 8C, D). Another possible male, also in tube, resembled newly-recruited *Osedax* larva (Fig. 8E).

Distribution. Known from Monterey Bay, California from 2898 meters depth (Table 2). It has been found in whale and turtle bones.

Etymology. This species is named (noun in the genitive case) for Ryder Williams, for his generosity in sharing his mom for our research efforts.

Remarks. *Osedax ryderi* **n. sp.** is part of *Osedax* Clade II and is the well-supported sistergroup to *Osedax ventana* **n. sp.**, another Monterey Bay species with an uncorrected divergence of 12%. Two other *COI* sequences obtained for specimens from the type locality, for which no voucher material was obtained, differed from the type specimen by less than 1% (MG262308 from whale bone and MG262309 from turtle bone). There is little to distinguish *Osedax ryderi* **n. sp.** from other Clade II species, apart from genetic differences.

***Osedax jabba* n. sp.**
Figures 9-13

'spiral', (Braby *et al.* 2007; Katz & Rouse 2013; Rouse *et al.* 2015; Vrijenhoek *et al.* 2009; Worsaae & Rouse 2010)
'sp.1 SBJ-2006' (GenBank *COI* sequence DQ996622- DQ996624)

Material examined. Holotype: SIO-BIC A7832, Female (GenBank *COI* sequence FJ347638), fixed in glutaraldehyde preserved in formalin, collected from a natural whale fall (*Eschrichtius robustus*) found at 2898 meters depth in Monterey Submarine Canyon, California (36°36.606'N; 122°26.122'N) ROV *Tiburon* dive number 1069, Oct. 1, 2007. Allotypes, male in the tube of holotype, same catalogue number. **Paratypes**: Females, fixed in formalin or glutaraldehyde; preserved in formalin, glutaraldehyde or ethanol: SIO-BIC A7833 (GenBank *COI* sequence DQ996622), same locality as holotype, ROV *Tiburon* dive number 769, Nov. 11, 2004; SIO-BIC A1639 (GenBank *COI* sequence DQ996624), same locality as holotype, ROV *Tiburon* dive number 777, Jan. 6, 2005; SIO-BIC A7834, A7835 (GenBank *COI* sequence FJ347636, FJ347637), same locality as holotype, ROV *Tiburon* dive number 777, Jan. 6, 2005; SIO-BIC A7838 (no GenBank *COI* sequence), same locality as holotype, ROV *Tiburon* dive number 917, Nov. 6, 2005; SIO-BIC A7836, A7837 (no GenBank *COI* sequences), same locality as holotype, ROV *Doc Ricketts* dive number 98, Nov. 19, 2009. Dwarf males (allotypes), fixed in formalin, preserved in formalin: SIO-BIC A7839 (no GenBank *COI* sequence), still in tube of female, same locality as holotype, ROV *Tiburon* dive number 932, Jan. 5, 2006.

Diagnosis and description. Holotype female (Fig. 11E), partially dissected from tightly surrounding tube; trunk demarcated into two regions, main part 5.6 cm long, 3.8 mm wide at base of main trunk, tapering to 2.3 mm at rounded tip of trunk (Fig. 11E). Lower trunk widens, greenish in life, and transitions into ovisac (Figs 10D, 12B). Trunk 'deflated' in width, but not contracted in length (Fig. 11E), when compared to images of living individuals *in situ* and some collected samples (Figs 9A-D, 10A-E 11A, B). Crown absent, no palps or emergent oviduct (Figs 9A-D, 10A-E 11A, B). Trunk and ovisac enclosed in tube in life (Figs 9A-D, 10A, 11A); preserved holotype has trunk occupying entire tube. Other specimens with trunk contracted to varying degrees within tube (Figs 10A, E, 11A, B). Oviduct (Figs 11C-E) runs dorsally along length of trunk from lower trunk/ovisac to trunk tip (Figs 10A-C, 11E). Main trunk color pink in live 'contracted' individuals (Figs 10A-D, 11E). In 'inflated' individuals, trunk is translucent (Figs 10E, 11B). Trunk in cross section shows extensive outer musculature and glands. Prominent dorsal and ventral blood vessels present as well as smaller vessels. Otherwise trunk is largely 'empty' with a few oocytes present and may filled (and inflatable) with coelomic fluid. (Figs 12G, H). A single large ganglion ventrolaterally in the mid-trunk region (Figs 11B, F). Lower trunk, demarcated by emergence of oviduct (Fig.

12B), transitions to white cylindrical ovisac, wider than trunk, encased in the base of tube and extending posteriorly into sediment (Figs 10D, 11A, E, 12B). Ovisac wall translucent with ovaries visible inside (Figs 10D, 12B). Ovisac wall tissue extends posteriorly, becomes sediment encrusted and branches out forming a large root mass extending and branching in all directions (Figs 11A, 12A-F). Ends of the roots are attached to various bone fragments. Roots largely covered in sediment, either light brown or orange. Fine ends of roots branching over and attached to surfaces of bone fragments (Figs 12A-F). Numerous males in tube of holotype and paratypes, lying in tube lumen near oviduct at base of trunk Figs (10E, F). All dwarfs, ~200 µm long by 50 µm, with anterior prototroch and sperm with spiral nuclei in head region, two posteriorly expanded segments bearing hooked chaetae (Figs 13A-F).

Distribution. Known only from Monterey Bay, California from 2898 meters depth (Table 2). *Osedax jabba* **n. sp.** was only found in sediment surrounding the natural whale fall at this depth (Figs 9A-D). Most specimens were at the head end of the whale, near a mass of baleen (Fig. 9A). All had bone fragments attached to the root mass buried in the sediment.

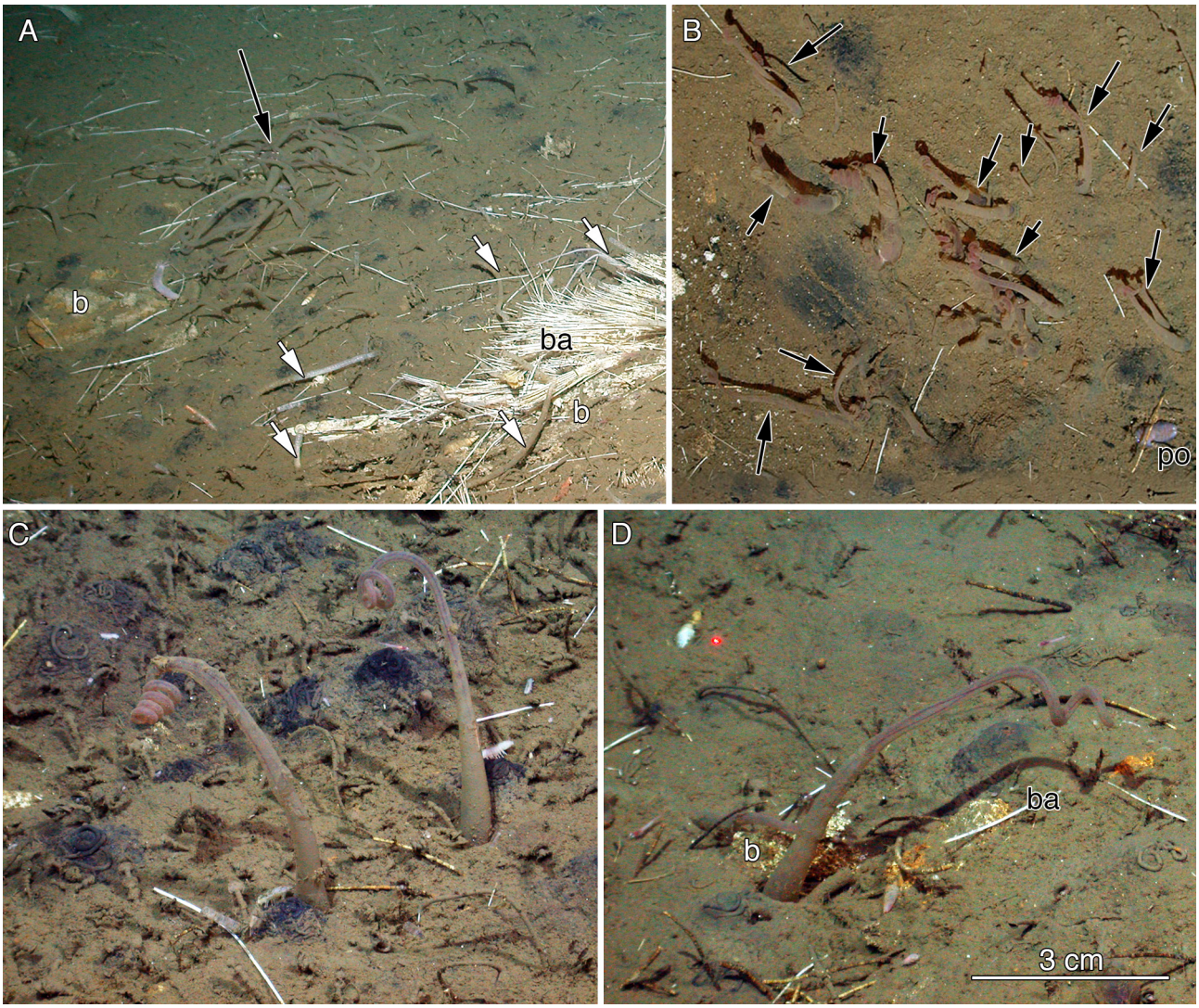


FIGURE 9. ***Osedax jabba*** **n. sp.**, previously *Osedax* 'spiral', sp.1 SBJ-2006. **A**. Anterior end of whale fall 'Ruby' at 2898 meters in September 2004. Baleen is prominent on surface of sediment in foreground with tubes (white arrows) of large chaetopterid annelid *Phyllochaetopterus gigas* (see Nishi & Rouse 2014). Little bone obvious on sediment surface. Background has a cluster of more than 10 *Osedax jabba* **n. sp.** (black arrow) with their tubes coming directly out of the sediment. **B**. Cluster of more the 10 (black arrows) *Osedax jabba* **n. sp.** at 2898 meters in November 2004. No obvious bone on the sediment surface. **C**. Two specimens of *Osedax jabba* **n. sp.** at 2898 meters in November 2005. Two prominent red blood vessels are visible through the tube of each specimen and these indicate the trunk is occupying whole of tube and is coiled anteriorly. Trunk does not appear to emerge from tube. **D**. Lateral view of an *Osedax jabba* **n. sp.** specimen emerging from sediment surface, though adjacent to a piece of bone, at 2898 meters in January 2006. Blood vessels are visible, indicating trunk is filling tube.

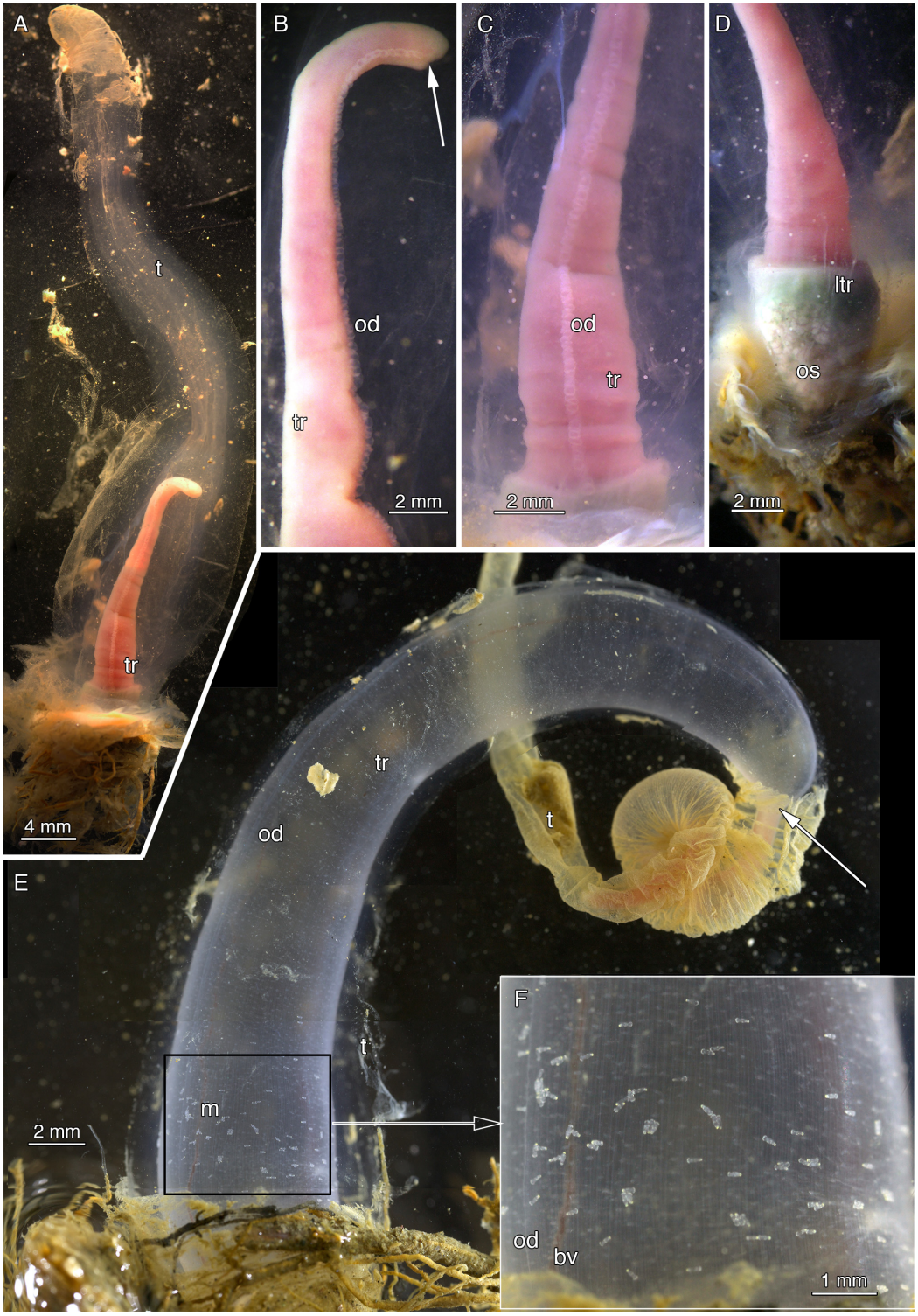


FIGURE 10. ***Osedax jabba*** **n. sp.**, previously *Osedax* 'spiral', sp.1 SBJ-2006. **A**. Preserved paratype (SIO-BIC A1639) female, highly contracted and still in tube collected at 2898 meters, Nov. 2004. Note absence of palps. **B**. Lateral view of trunk of preserved paratype (SIO-BIC A1639), showing oviduct running dorsally along trunk and terminating at anterior end of trunk. **C**. Dorsal view of posterior region of trunk of preserved paratype (SIO-BIC A1639) showing oviduct emerging from lower trunk region. **D**. Lower trunk and ovisac of preserved paratype (SIO-BIC A1639). **E**. Photomontage lateral view of living paratype (SIO-BIC A7836) collected at 2898 meters, November 2009. Tube has been partly peeled away to reveal inflated trunk. Distal (anterior) part of tube is intact and contains anterior part of the trunk that is not inflated (arrow). Oviduct is visible dorsally (left) and does not contain any oocytes. Cluster of more than 20 dwarf males is present at the base of the trunk. **F.** Close up of base of trunk of living paratype (SIO-BIC A7836) in 10E, showing scattered dwarf males lying on its surface. Oviduct is the white line in left of the image. Blood vessel inside transparent trunk is also visible.

FIGURE 11. ***Osedax jabba*** **n. sp.**, previously *Osedax* 'spiral'; sp.1 SBJ-2006. **A.** Image of live paratype (SIO-BIC A7837) female, still in tube, collected at 2898 meters in November 2009. Much of trunk is still relatively expanded, but anterior end is contracted (arrow points to tip of trunk) and trunk has pulled back along the tube. Mass of fine roots is attached to several small pieces of bone. **B**. Ventral view of same specimen (SIO-BIC A7837) with sediment-covered part of the tube peeled away to show the transparent trunk (arrow points to tip of trunk). Large ganglion is visible in ventrolateral region of the trunk. **C**. Close up of dorsal mid-trunk of paratype (SIO-BIC A7837) female, showing oviduct filled with oocytes and an adjacent blood vessel. **D**. Another close-up of oviduct, more posteriorly near base of trunk, showing some dwarf males in vicinity of oviduct. Oocytes ellipsoidal, 150 µm by 120 µm. **E.** Living holotype (SIO-BIC A7832) collected October 2007 at 2898 meters with tube dissected open to show main trunk, which has largely 'deflated'. Oviduct can be seen running along the trunk. Tube also contains lower trunk and ovisac region. Arrow points to position of where 10 dwarf males were found in lumen of tube against body of the female. **F.** Close-up of large ganglion in trunk of paratype (SIO-BIC A7837) female, seen in Figure 11B.

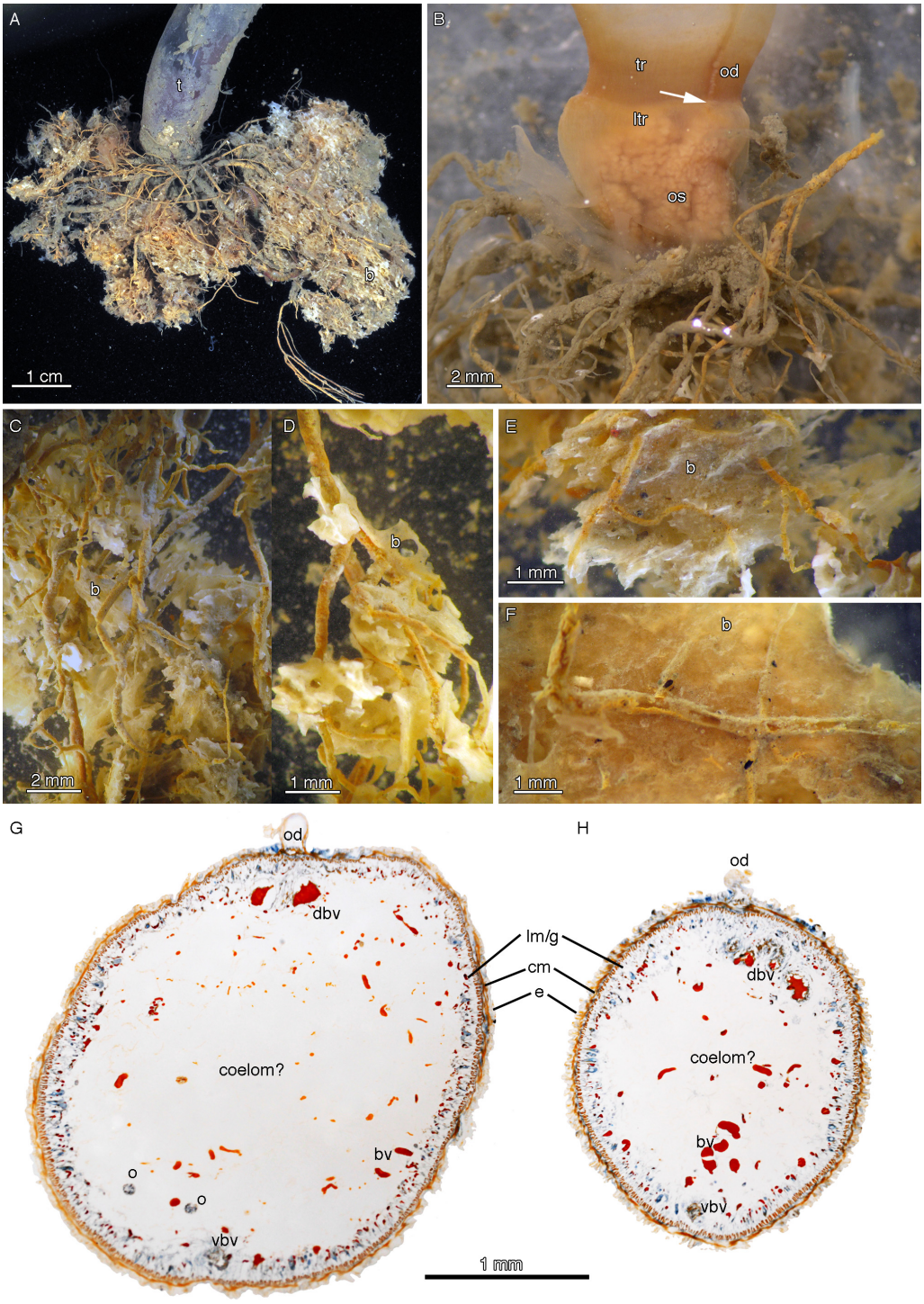


FIGURE 12. ***Osedax jabba*** **n. sp.**, previously *Osedax* 'spiral'; sp.1 SBJ-2006. **A**. Lower trunk and roots and attached bone fragments of live paratype (SIO-BIC A7837) female. Two obvious roots forms; those emerging from ovisac are thick and covered in grey sediment and not directly in contact with bone. These branch into thinner roots that are covered in yellowish sediment. These thinner roots branch as well and cover the pieces of bone. **B**. Lower trunk and roots and attached bone fragments of preserved paratype (SIO-BIC A7838) collected June 2006 at 2898 meters. Large main roots can be seen emerging from posterior end of ovisac. **C–F**. Various view of finer roots of paratype (SIO-BIC A7838), showing how they branch and also are in contact with fragments of bone of various sizes. Root surfaces not in contact with the bone are covered in sediment. **G**. Transverse section (7 µm) of paratype (SIO-BIC A7835), near base of trunk where oviduct has emerged to the outer dorsal surface. As with other *Osedax,* there is an outer epidermis, circular and longitudinal muscles and glands, as well as two major blood vessels. However, the majority of the trunk interior has no obvious tissue, except for some minor blood vessels and a few oocytes. This interior space is interpreted here as the coelom. **H**. Another transverse section (7 µm) of paratype (SIO-BIC A7835) towards the distal (anterior) end of the trunk. The same basic structure as seen in G is also apparent here.

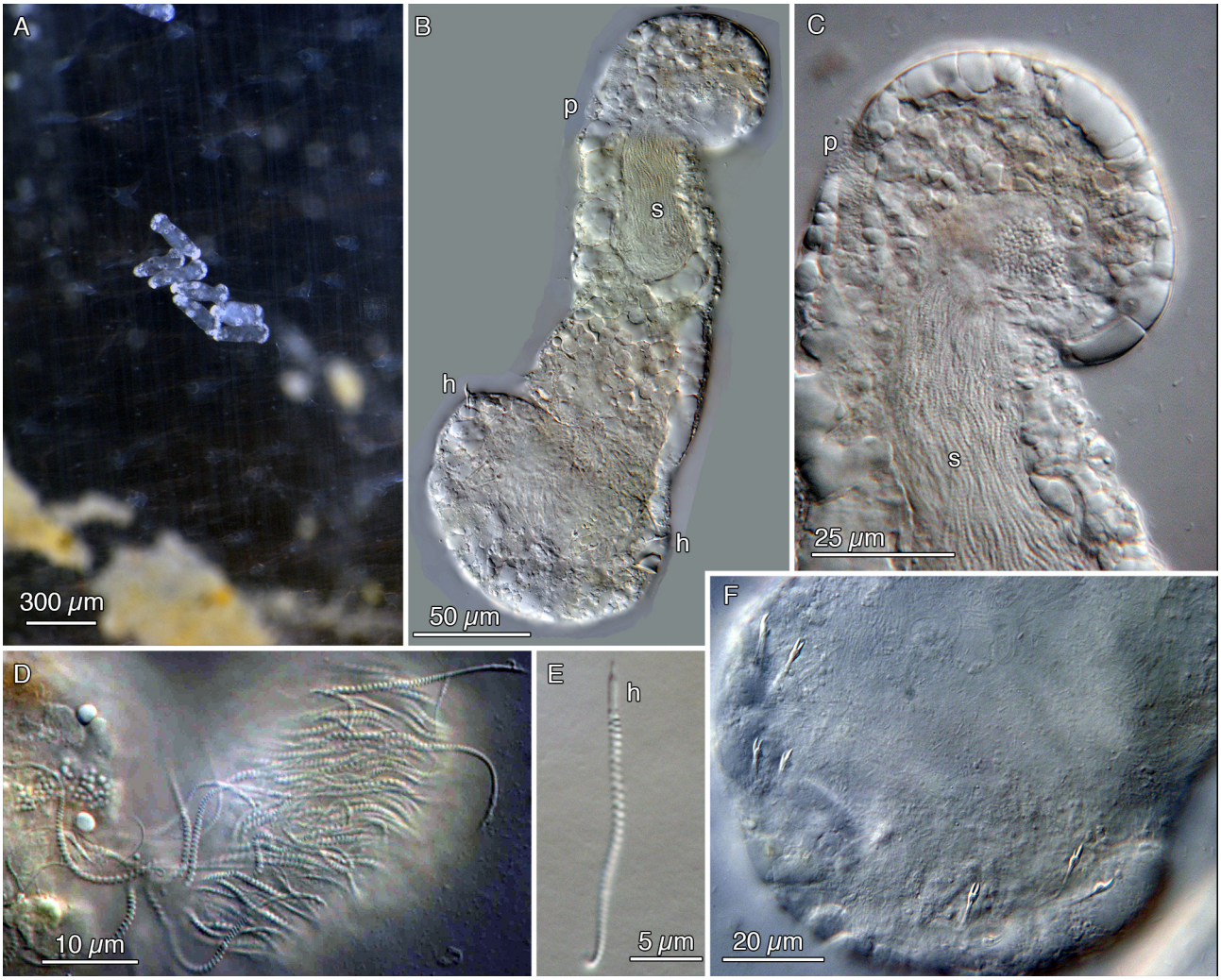


FIGURE 13. ***Osedax jabba*** **n. sp.**, previously *Osedax* 'spiral'; sp.1 SBJ-2006. **A**. Cluster of males lying between in tube lumen, in contact with the trunk of a female paratype 4 (SIO-BIC A7836). **B**. Photomicrograph montage of male allotype (SIO-BIC A7839), from tube of paratype 6 (SIO-BIC A7838). Prototroch is visible anteriorly, as is a mass of mature sperm. Some hooks are visible in expanded posterior region. **C**. Closeup of head showing prototroch and mass of mature sperm. **D**. Mature sperm squeezed out the head of male. **E**. Mature sperm. **F**. Close up of posterior segmented region showing hooked chaetae in pairs on one side of segments 2 and 3. Other chaetae are not in plane of focus.

Etymology. The trunk of the new species is reminiscent of the tail of the mythical creature *Jabba the Hutt* from the Star Wars franchise (Sansweet 1998). We name the new species (noun in apposition) in its honor.

Remarks. *Osedax jabba* **n. sp.** is the only member of *Osedax* Clade III and is the well-supported sistergroup to *Osedax* Clade IV, all of which have females that have four pinnulate palps. While the males of *Osedax jabba* **n. sp.** are similar (Fig. 13) to the dwarfs found in other *Osedax* species (Worsaae & Rouse 2010), the anatomy of the females is unique among *Osedax* species and they show what appear to be striking adaptations to exploit bone fragments that have become buried in the sediment. Further study on the roots of *Osedax jabba* **n. sp.** are underway (Rouse & Goffredi in prep.). The exploitation of buried bone fragments by *Osedax jabba* **n. sp.** does not explain the absence of palps in this species. Based on the phylogeny of *Osedax*, (Fig. 1) this absence would appear to be a character loss. The presence of dwarf males towards the base of the tube is also unusual, as in other species the dwarfs tend to be found in the middle to anterior regions of the female tube (Rouse *et al.* 2004; Rouse *et al.* 2008; Vrijenhoek *et al.* 2008) and it is not clear how larvae would be caught from the plankton and brought into the tube, as is surmised for other *Osedax* species (Vrijenhoek *et al.* 2008).

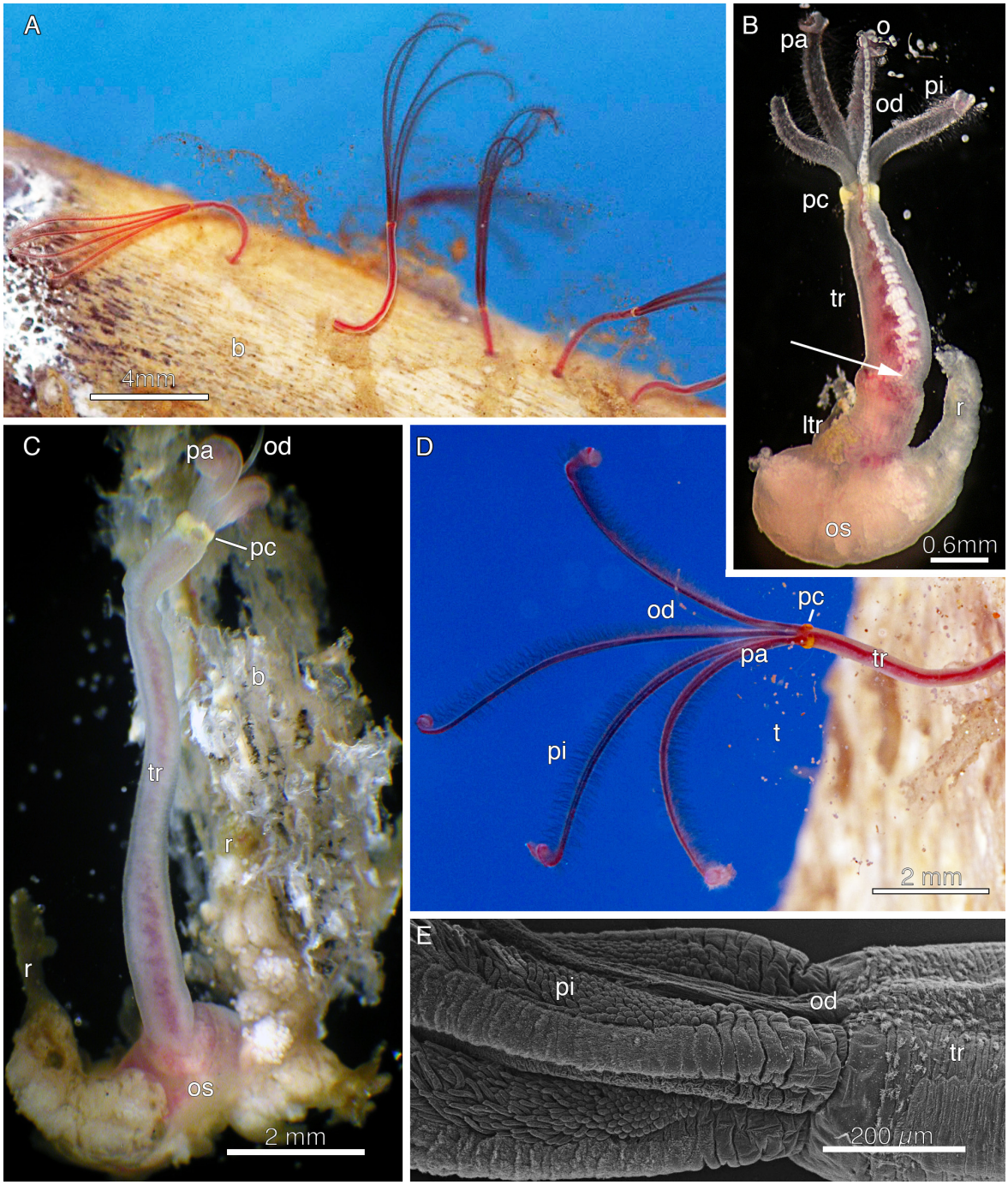


FIGURE 14. ***Osedax lehmani*** **n. sp.**, previously *Osedax* 'yellow collar'. **A**. Several adult females on rib bone of a gray whale calf (*Eschrichtius robustus*) that was deployed at 385 meters in Monterey Canyon. Rib was recovered to study the *Osedax* in an aquarium setting. Note distinctive yellow ring around most of the anterior end of trunk. The massive circulatory system in trunk and palps is evident from red color of worms. **B.** Micrograph of live paratype 4 (SIO-BIC A7808), a female, in dorsal view dissected from gray whale deployed at 385 meters. The 'root' mass is a single lobe extending away to the right of ovisac. Palps are retracted and partly curled, with pinnules all oriented dorsally. Note mid-dorsal gap in yellow pigment ring, through which oviduct runs and extends into crown. Note demarcation of the lower and upper trunk (arrow). Oviduct emerges onto surface of dorsal trunk at this point. Oviduct is full of oocytes and highly contracted nature of the trunk is evident in zigzag shape of the oviduct on trunk. **C.** Live holotype (SIO-BIC A7804), a female, in ventral view. Holotype is partially dissected from the gray whale deployed at 385 meters. Root mass (also containing ovarian tissue) has been dissected out of bone on right side and more extends into the bone, away from ovisac. Palps are retracted and curled. Note midventral gap in yellow pigment ring. **D.** Live adult female in lateral view on same rib bone as in A. There is a gap in yellow pigment ring where oviduct traverses the trunk to become part of the crown. **E**. Scanning electron micrograph of a female dissected from whale bone deployed at 385 meters. Pinnules of all palps are oriented dorsally.

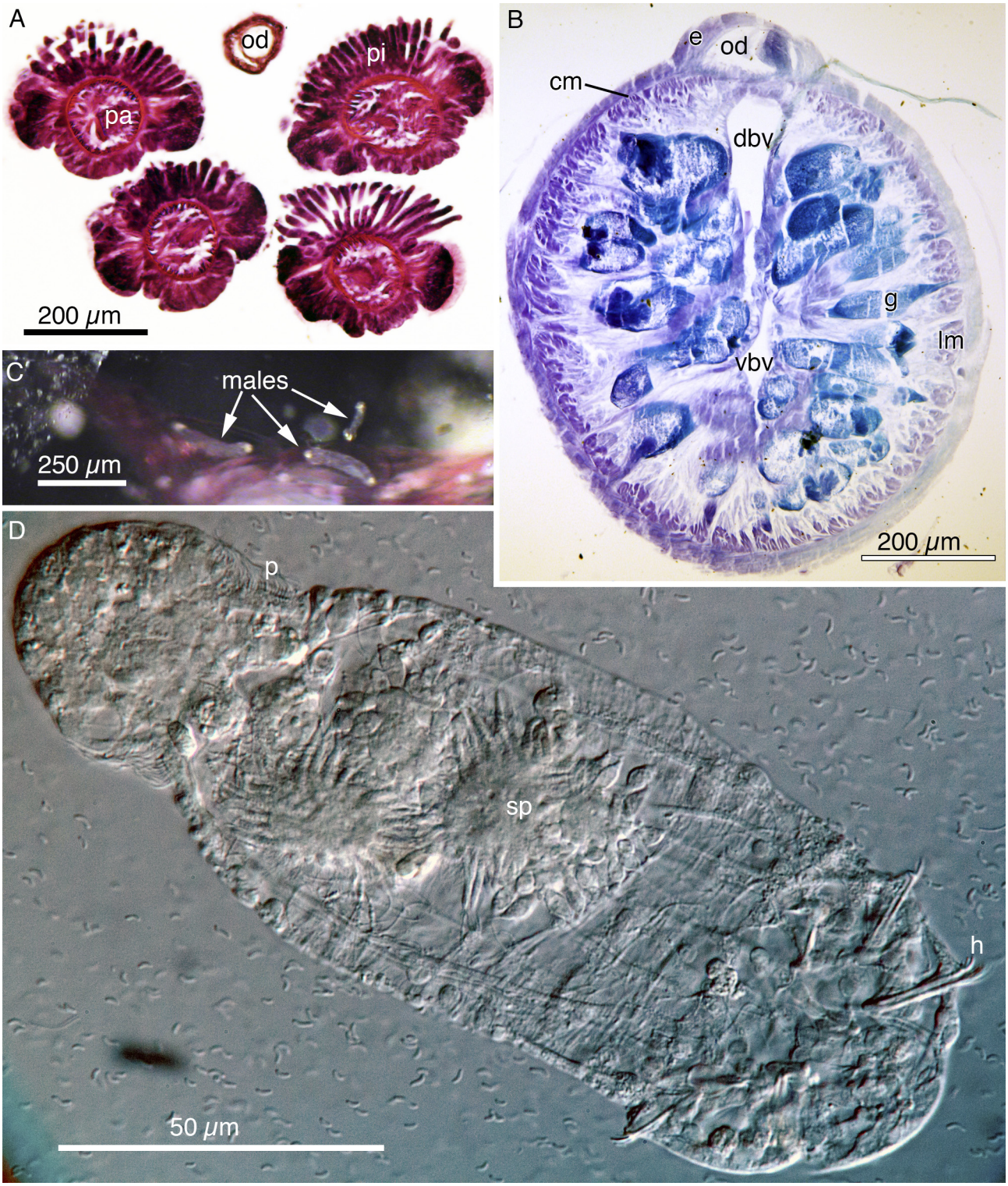


FIGURE 15. ***Osedax lehmani*** **n. sp.**, previously *Osedax* 'yellow collar', 'sp. 3 SBJ-2006'. **A**. Transverse section (7 µm) of paratype 3 (SIO-BIC A7807), through crown showing pinnules of all palps oriented dorsally and oviduct lying between the dorsalmost pair of palps. **B.** Transverse section (7 µm) through trunk of paratype 3 (SIO-BIC A7807) showing extensive musculature and glands. Prominent dorsal and ventral blood vessels are also visible. **C.** Live males, allotypes (SIO-BIC A7805) in tube of their female (her pinnules are visible). Males show small patches of pigment anteriorly and posteriorly. **D**. Differential interference micrograph of a male dissected from tube of paratype 2 (SIO-BIC A7806). Prototroch is visible anteriorly. Some hooks are visible in expanded posterior region. No mature sperm is visible, though there are several bundles of spermatids.

***Osedax lehmani* n. sp.**
Figures 14, 15

'yellow collar', (Braby *et al.* 2007; Huusgaard *et al.* 2012; Katz & Rouse 2013; Rouse *et al.* 2009; Rouse *et al.* 2015; Tresguerres *et al.* 2013; Vrijenhoek *et al.* 2009; Worsaae *et al.* 2016)
'sp.3 SBJ-2006' (GenBank *COI* sequences DQ996629- DQ99638)
'sp.4 SBJ-2006' (GenBank *COI* sequences DQ996640, DQ99643)
'orange collar' (GenBank *COI* sequence EU267672)

Material examined. Holotype: SIO-BIC A7804, Female (GenBank *COI* sequence DQ996629), fixed in glutaraldehyde, preserved in ethanol, collected from a whale carcass (*Eschrichtius robustus*) deployed at 385 meters depth in Monterey Submarine Canyon, California (36°47.401'N; 122° 53.235'W), ROV *Tiburon* dive number 933, Jan. 6, 2006. **Paratypes**: Females, fixed in formalin or glutaraldehyde, preserved in ethanol, same locality and date as holotype, SIO-BIC A1640 (GenBank *COI* sequence DQ996630), same locality and date as holotype, SIO-BIC A7806 (GenBank *COI* sequence DQ996631); SIO-BIC A7807 and A7808 (GenBank *COI* sequence EU223332 and EU223337, respectively), same locality as holotype, ROV *Tiburon* dive number 1070, Jan. 11, 2007; dwarf males (Allotypes) SIO-BIC A7805 (no GenBank *COI* sequence), several in tubes of various females, same locality and date as holotype.

Diagnosis and description. Holotype female, in life trunk 8 mm long, 0.6 mm wide; crown of palps contracted, curled, 1.5 mm long (Fig. 14C). Palps up to 10 mm long when extended in other specimens (Figs 14A, D). Pinnules of all palps oriented dorsally and the oviduct lying between the dorsalmost pair of palps (Figs 14B, D, E, 15A). Oviduct extends from trunk into crown for 1.75 mm (Figs 14B-D). In life, palps reddish with two major blood vessels in each (Figs 14A, D). Tube a gelatinous loose mass around trunk (Fig. 14D). Trunk with pale yellow ring around anterior margin; ring broken mid-dorsally by oviduct (Figs 14B, D). and mid-ventrally by an oval unpigmented patch (Fig. 14C). Clear demarcation of upper and lower trunk with oviduct emerging onto outer surface of upper trunk (Fig. 14B). Internally trunk shows extensive musculature and glands with prominent dorsal and ventral blood vessels (Fig. 15B). Ovisac in holotype extending laterally as two masses; simple lobes in other specimens (Fig. 14C). Roots of holotype extend from ovisac lobes (Fig. 14C); in other specimens, roots as simple lobes or extending laterally in two lobe or lobes (Fig. 14B). Males dwarfs, with spermatids and sperm, chaetal-bearing segments not inflated; found in tube lumen of females (Fig. 15C-D).

Distribution. Known from Monterey Bay, California only from 349 meters depth (Table 2). It has been found in whale and cow bones.

Etymology. This species is named (noun in the genitive case) in memory of Alan George Lehman, father of Ellen Lehman, in recognition of her long and continued support of the Scripps Oceanographic Collections.

Remarks. *Osedax lehmani* **n. sp.** is part of *Osedax* Clade IV and is closest relative to *Osedax packardorum* **n. sp.**, (Fig. 1), with a minimum uncorrected distance for *COI* of 8-9% (Table 4). This is one of the smaller intraspecific distances among *Osedax* species, with others being between *O. frankpressi* and the *O.* '1336_61_2' specimen from the Atlantic at ~10%; and *O. randyi* **n. sp.** and O. 'MB16 at ~ 6-7% (Table 4). The majority of the 31 available *COI* sequences for *Osedax lehmani* **n. sp.** (Table 3) show less than 1% divergence, though a few sequences e.g. DQ996640 are around 2% divergent from the majority and DQ996631 shows the greatest distance, at ~3% (Table 4), so the possibility of there being a cryptic species complex for *O. lehmani* **n. sp.** needs further investigation. The most distinguishing feature of *Osedax lehmani* **n. sp.** is the yellow ring around the anterior part of the trunk. (Fig. 14A-D). This is the only *Osedax* species from Monterey Bay that was not found deeper than 389 meters depth.

***Osedax packardorum* n. sp.**
Figure 16

'orange collar' (Braby *et al.* 2007; Rouse *et al.* 2009; Rouse *et al.* 2015; Tresguerres *et al.* 2013; Vrijenhoek *et al.* 2009)
'sp.4 SBJ-2006' (GenBank *COI* sequence DQ996639, DQ996641-2)

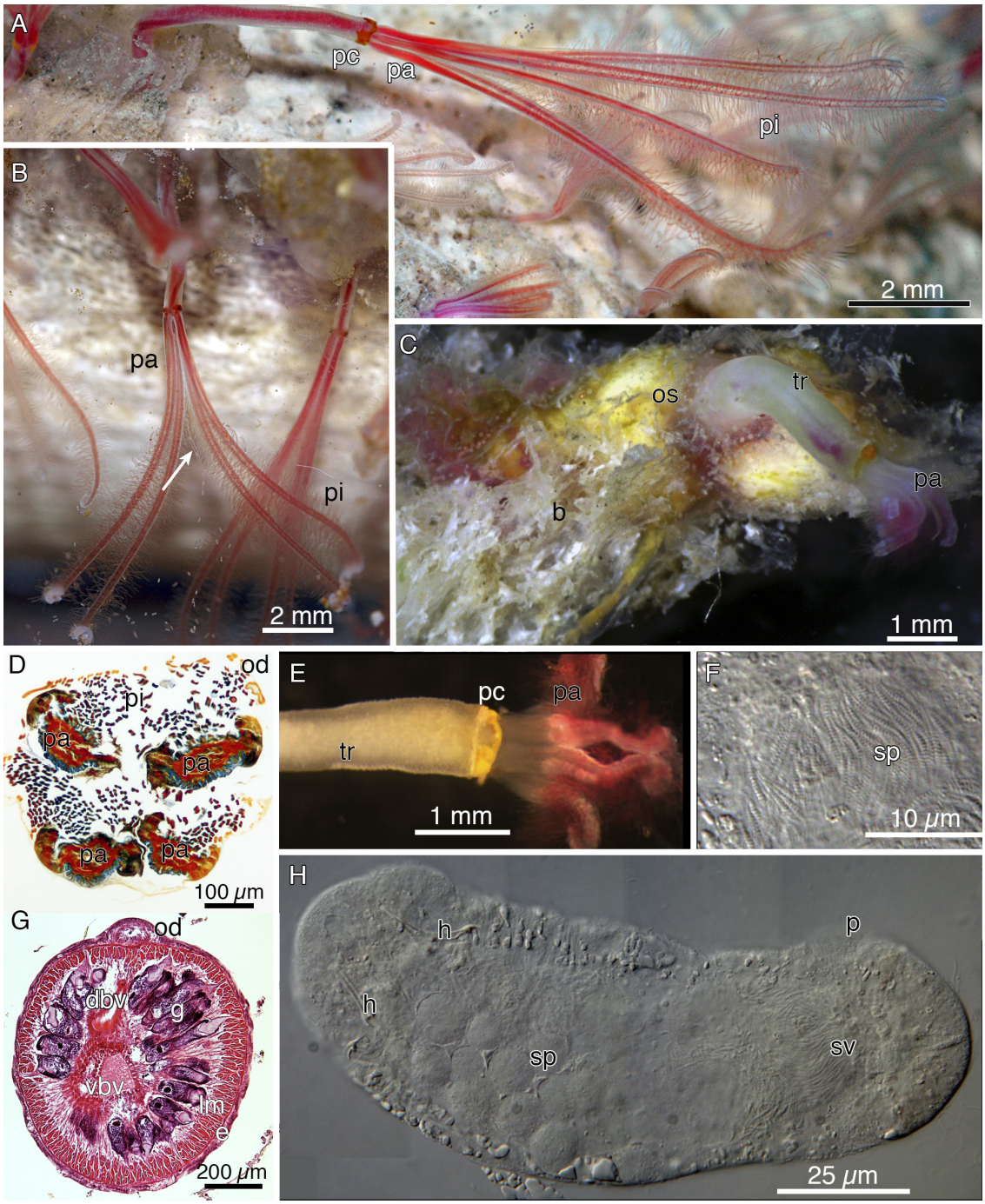


FIGURE 16. ***Osedax packardorum*** **n. sp.**, previously *Osedax* 'orange collar'. **A**. Ventral view of the trunk and crown of adult female on bone of a gray whale calf (*Eschrichtius robustus*) deployed at 385 meters in Monterey Canyon. Bone was recovered and brought to laboratory. Note distinctive dark orange ring around anterior end of trunk two blood vessels in each palp and numerous pinnules. Also note midventral gap in orange pigment ring. **B**. Another female from same bone in an aquarium. Female is spawning oocytes into water via oviduct that extends from trunk into crown of palps. Arrowhead indicates tip of oviduct. **C**. Micrograph of live paratype (SIO-BIC A7843) with ovisac and roots still largely in bone. **D.** Transverse section (7 µm) of paratype (SIO-BIC A7843) through crown showing pinnules of all palps oriented dorsally and oviduct lying slightly to side of the dorsalmost palps. **E**. Ventral view of trunk of paratype (SIO-BIC A7844). Pigmented ring is less orange in this specimen, but shows midventral gap. Pinnules of all palps are oriented dorsally. **F.** Mature sperm in head of a male dissected from the tube of paratype (SIO-BIC A7842). **G.** Transverse section (7 µm) through trunk of paratype (SIO-BIC A7843) showing extensive musculature and glands. Prominent dorsal and ventral blood vessels are also visible. **H**. Differential interference micrograph of male in the tube of paratype (SIO-BIC A7842). Prototroch is visible anteriorly as is a mass of mature sperm. Spermatid bundles (very squeezed) fill majority of body. Hooked chaetae are visible in expanded posterior region.

Material examined. Holotype: Female, fixed in formalin preserved in ethanol, SIO-BIC A1641 (GenBank *COI* sequence EU223341), collected from whale carcass (*Balaenoptera musculus*) deployed at 1018 meters depth in Monterey Submarine Canyon, California (36°46.308'N; 122° 4.981'W), ROV *Tiburon* dive number 1049, Oct. 25, 2006. **Paratypes**: Female and dwarf males (allotypes), fixed in formalin preserved in ethanol SIO-BIC A7840, A7842 (female GenBank *COI* sequences EU223339, EU223343), same locality and date as holotype; Female, fixed in formalin preserved in ethanol, SIO-BIC A7841(GenBank *COI* sequence EU223340), same locality and date as holotype; Female, sectioned for histology, same locality and date as holotype, SIO-BIC A7843 (GenBank *COI* sequence EU223342); Female, fixed in formalin preserved in ethanol, SIO-BIC A7844 (GenBank *COI* sequence FJ431200), collected from whale fall (*Eschrichtius robustus*) at 663 meters depth in Monterey Submarine Canyon, California (36°48.178'N; 121°59.677'W) ROV *Tiburon* dive number 1160, Dec. 18, 2007.

Diagnosis and description. Holotype female, in life trunk 11 mm long, 0.6 mm wide; crown of palps contracted, curled, 2 mm long (image not shown as the trunk is damaged). Palps up to 12 mm long when extended in other specimens (Figs 16A, B). Pinnules of all palps oriented dorsally and the oviduct lying between the dorsalmost pair of palps (Figs 16B, D, E). Oviduct extends from trunk into crown for 3 mm (Fig. 16B). In life, palps reddish with two major blood vessels in each (Figs 16A, B). Tube a gelatinous loose mass around trunk (Figs 16A, B). Trunk with pale to dark orange ring around anterior margin; ring broken mid-dorsally by oviduct and mid-ventrally by and oval unpigmented patch (Figs 16A, B, E). Internally trunk shows extensive musculature and glands with prominent dorsal and ventral blood vessels (Fig. 16G). Ovisac in holotype an ellipsoidal mass (not shown); extending laterally as lobes in other specimens (Fig. 16C). Roots of holotype extend from ovisac on one side as one mass; in other specimens, roots as long branching masses. Males dwarfs, with spermatids and sperm (Figs 16F, G), chaetal-bearing segments not inflated (Fig. 16H); found in tube lumen of females.

Distribution. Known from Monterey Bay, California at 349, 633, and 1018 meters depths (Table 2). Found in whale and cow bones.

Etymology. This species is named (noun in the genitive case) in honor of the Packard family whose foundation supports MBARI and enabled the discovery of all of the *Osedax* species in California.

Remarks. *Osedax packardorum* **n. sp.** is part of *Osedax* Clade IV and closest relative to *Osedax lehmani* **n. sp**., (Fig. 1), from which it has a minimum uncorrected distance for *COI* of 8-9% (Table 4). As pointed out above, this is one of the smaller interspecific distances among *Osedax* species and the two species are morphologically very similar. All 27 available *COI* sequences for *Osedax packardorum* **n. sp.** (Table 3) comprise less than 1% sequence divergence. The most distinguishing feature of *Osedax packardorum* **n. sp.** is the orange ring around the anterior part of the trunk. (Fig. 16A-C, E).

Osedax randyi n. sp.

Figure 17

'white collar' (Rouse *et al.* 2015; Vrijenhoek *et al.* 2009)
'Sagami-7' (GenBank *COI* sequence FM998108-9; Pradillon et al. unpublished)

Material examined. Holotype: Female, fixed in formalin preserved in ethanol, SIO-BIC A7845 (GenBank *COI* sequence FJ347615), collected from a whale carcass (*Balaenoptera musculus*) deployed at 1018 meters depth in Monterey Submarine Canyon, California (36°46.308'N; 122° 4.981'W), ROV *Tiburon* dive number 1049, Oct. 25, 2006. **Paratypes**: Female, fixed in formalin preserved in ethanol SIO-BIC A1648, SIO-BIC A7846 (GenBank *COI* sequence FJ347612, FJ347613), same locality and date as holotype; Female and dwarf males (allotypes), fixed in formalin, female sectioned, males preserved in ethanol SIO-BIC A7847 (female GenBank *COI* sequence FJ347614), same locality and date as holotype.

Diagnosis and description. Holotype female, in life trunk 5 mm long, 0.8 mm wide; crown of palps somewhat contracted, 4.5 mm long (Fig. 17A). Pinnules of all palps oriented dorsally and the oviduct lying between the dorsalmost pair of palps (Figs 17A, B, D). Oviduct extends from trunk into crown for 1-2 mm (Figs 17A, B). In life, palps reddish with pigmented white outer margins (Fig. 17A). Trunk with white ring around anterior margin; ring broken mid-dorsally by oviduct and mid-ventrally by and oval unpigmented patch (Figs 17A, B). Clear demarcation of upper and lower trunk (Fig. 17A). Internally trunk shows extensive musculature and glands with prominent dorsal and ventral blood vessels (Fig. 17E). Ovisac in holotype, damaged, an ellipsoidal mass; similar

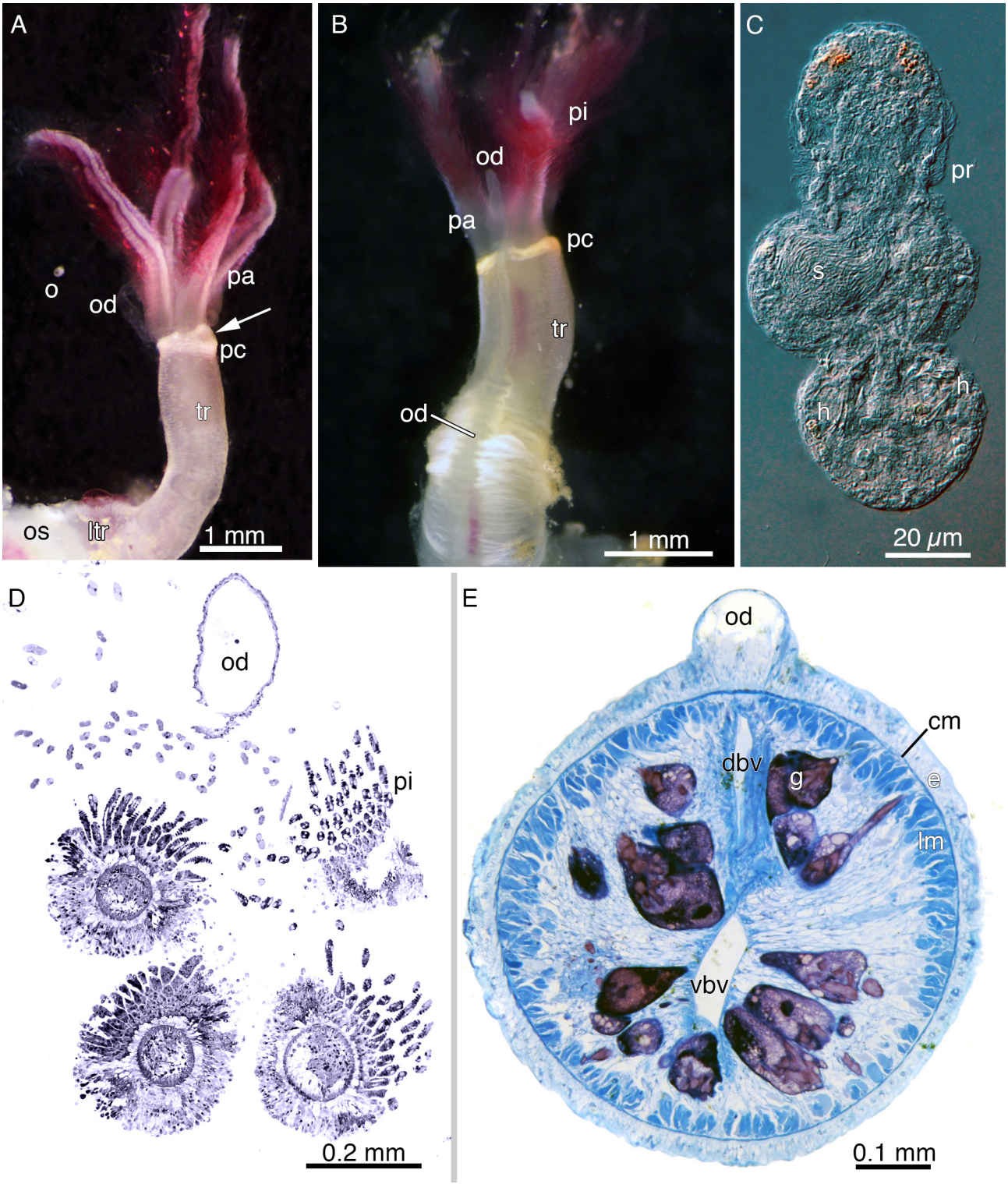


FIGURE 17. ***Osedax randyi*** **n. sp.**, previously *Osedax* 'white collar'. **A**. Micrograph of live holotype (SIO-BIC A7845), female in lateral view, removed from its tube and showing crown, trunk and part of ovisac. Note midventral gap in white pigment ring. **B**. Dorsal view of live specimen (paratype SIO-BIC A7847) showing white pigmented ring anteriorly with a dorsal gap where oviduct runs through it. Note pinnules of all palps oriented dorsally and oviduct lying between dorsalmost pair of palps. **C.** Differential interference micrograph of a solitary male dissected from tube of paratype (SIO-BIC A7847). Some hooks are visible in expanded posterior region. A large mass of mature sperm is visible in mid-body and extending into head, though there are a few obvious spermatids. **D**. Transverse section (7 µm) of paratype (SIO-BIC A7847), through crown showing pinnules of all palps oriented dorsally and oviduct lying between dorsalmost pair of palps. **E.** Transverse section (7 µm) through the trunk of paratype (SIO-BIC A7847) showing extensive musculature and glands. Prominent dorsal and ventral blood vessels are also visible.

shape in paratypes. Roots incomplete, simple lobes where present in all specimens. Males dwarfs, with spermatids and sperm, chaetal-bearing segments inflated (Fig. 17C), found in tube lumen of females.

Distribution. Known from Monterey Bay, California from 1018 meters depth, and from Sagami Bay, Japan (Table 2). It has been found in whale and cow bones.

Etymology. This species is named (noun in the genitive case) in honor of Randy Prickett, Senior ROV pilot for MBARI, who collected many bones and *Osedax* over the years.

Remarks. *Osedax randyi* **n. sp.** is part of *Osedax* Clade IV and closest relative to the undescribed *Osedax* species from California known as *O.* 'MB16' (Fig. 1) with a minimum uncorrected *COI*-distance of ~6-7% (Table 4). As previously noted, this is among the smaller interspecific distances among *Osedax* species. Two *COI* sequences, referred to *Osedax* sp. Sagami-7 (Pradillon *et al*., GenBank unpublished, Table 3) are much less than 1% divergent from the six California *Osedax randyi* **n. sp.** sequences (example distance in Table 4). Thus, it is reasonable to propose that *Osedax randyi* **n. sp.** is also found in Japan. The most distinguishing features of *Osedax randyi* **n. sp.** are the white ring around the anterior part of the trunk and white pigment on the palps of females (Fig. 17A, B), though a similar whitish ring is found on females of *O. bryani* **n. sp.** (Fig. 18A, B) and *O. frankpressi* (Rouse *et al.* 2004), with the latter species also showing white pigmentation on the palps. DNA sequencing is most likely the best way to distinguish *Osedax randyi* **n. sp.** from these species.

***Osedax bryani* n. sp.**

Figure 18

'MB17' (Rouse *et al.* 2015; Salathé & Vrijenhoek 2012)

Material examined. Holotype: SIO-BIC 4619, Female (GenBank *COI* sequence JX280609), fixed in formalin preserved in ethanol, collected from a whale carcass deployed at 1820 meters depth in Monterey Submarine Canyon, California (36°42.496'N; 122°6.316'W), ROV *Doc Ricketts* dive number 12, March 13, 2009.

Diagnosis and description. Holotype and only available specimen female (Figs18A, B); in life trunk 4 mm long, 1.8 mm wide; crown of palps somewhat contracted, curled, 4.5 mm long. Pinnules of all palps oriented dorsally and the oviduct lying between the dorsalmost pair of palps. Oviduct extends from trunk into crown for 5 mm (Figs 18A, B). In life, pinnules of palps reddish, otherwise no obvious pigment. Trunk with white ring around anterior margin; ring broken mid-dorsally by oviduct and mid-ventrally by and oval unpigmented patch. Clear demarcation of upper and lower trunk. Ovisac in holotype, damaged, a large ellipsoidal mass (Figs 18A, B). Green root tissue visible but torn. Possible male found in tube of holotype, with chaetal-bearing segments inflated; found in tube lumen of females, lost following microscope slide preparation (Fig. 18C).

Distribution. Known from Monterey Bay, California from 1820 meters depth in whale bone.

Etymology. This species is named (noun in the genitive case) in honor of Bryan Touryan-Schaefer, ROV Pilot/ Technician for MBARI, who collected many bones with *Osedax* over the years.

Remarks. *Osedax bryani* **n. sp.** is part of *Osedax* Clade V and is sister taxon to the *O. rubiplumus* and *O. roseus* clade (Fig. 1). It shows a minimum uncorrected distance, for *COI*, of ~15% to *O. rubiplumus* (Table 4). *Osedax bryani* **n. sp.** shares distinguishing feature of a white ring around the anterior part of the trunk with *O. randyi* **n. sp.** and *O. frankpressi* and as with Clade II of *Osedax,* these species likely need to be distinguished with DNA data. The documentation of dwarf males in *Osedax bryani* **n. sp.** is the first for this species, which was listed as unknown in Rouse *et al.* (2015).

Discussion

The current study brings the total number of described species *Osedax* collected from the Monterey Submarine Canyon to 18. A nineteenth species from Monterey Bay, *Osedax* 'MB 16' (Salathé & Vrijenhoek 2012) remains unnamed because no voucher specimens were available. Five of the Monterey species appear to have trans-Pacific distributions since sequences listed on GenBank by Pradillon *et al*. (unpublished, Table 3), from Sagami Bay, Japan, arguably belong to *O. roseus, O. rubiplumus, O. docricketts* **n. sp.**, *O. randyi* **n. sp.** and *O. westernflyer* **n. sp.** Because larval duration (Rouse *et al.* 2009) is unlikely to be sufficient for trans-Pacific dispersal in one

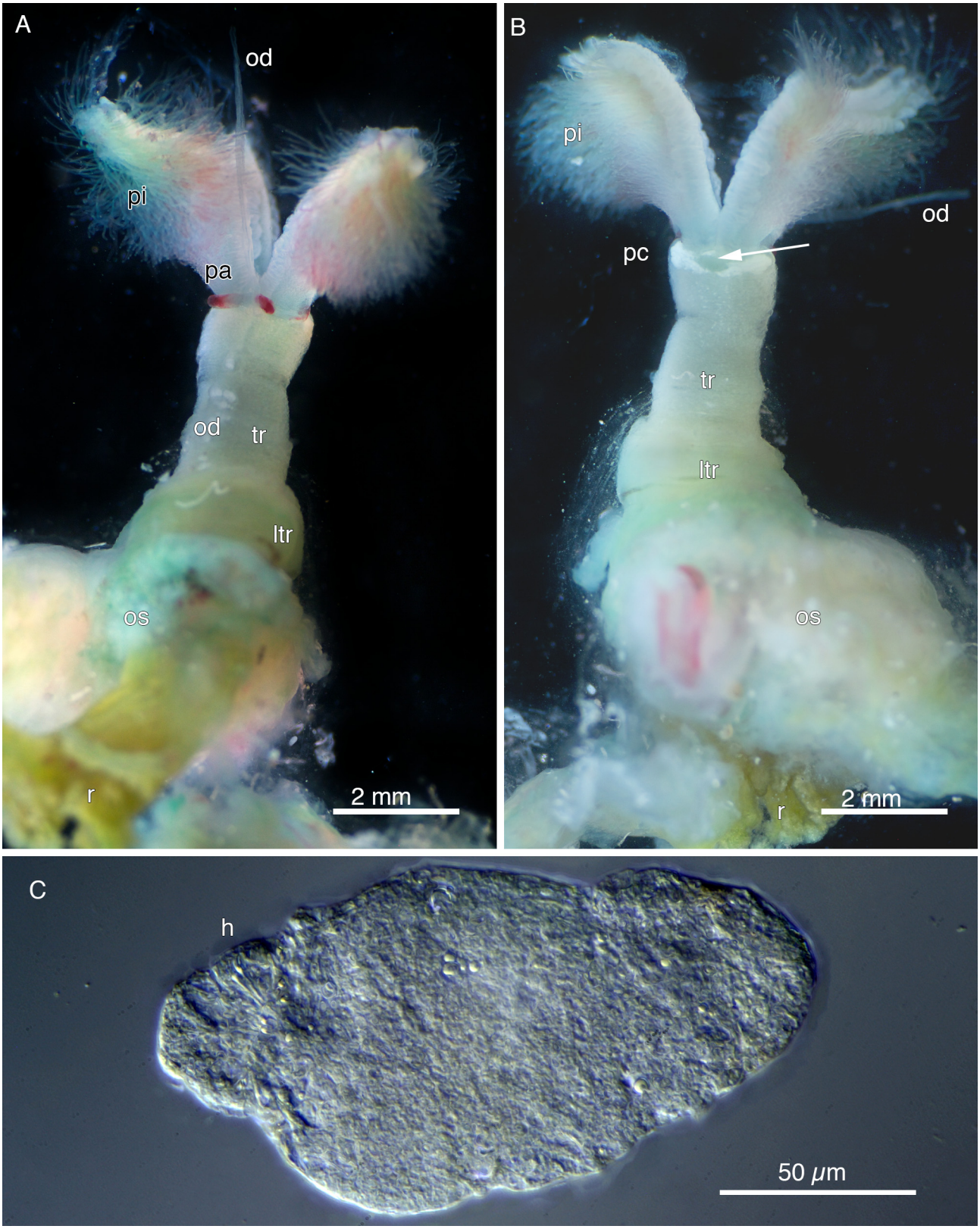
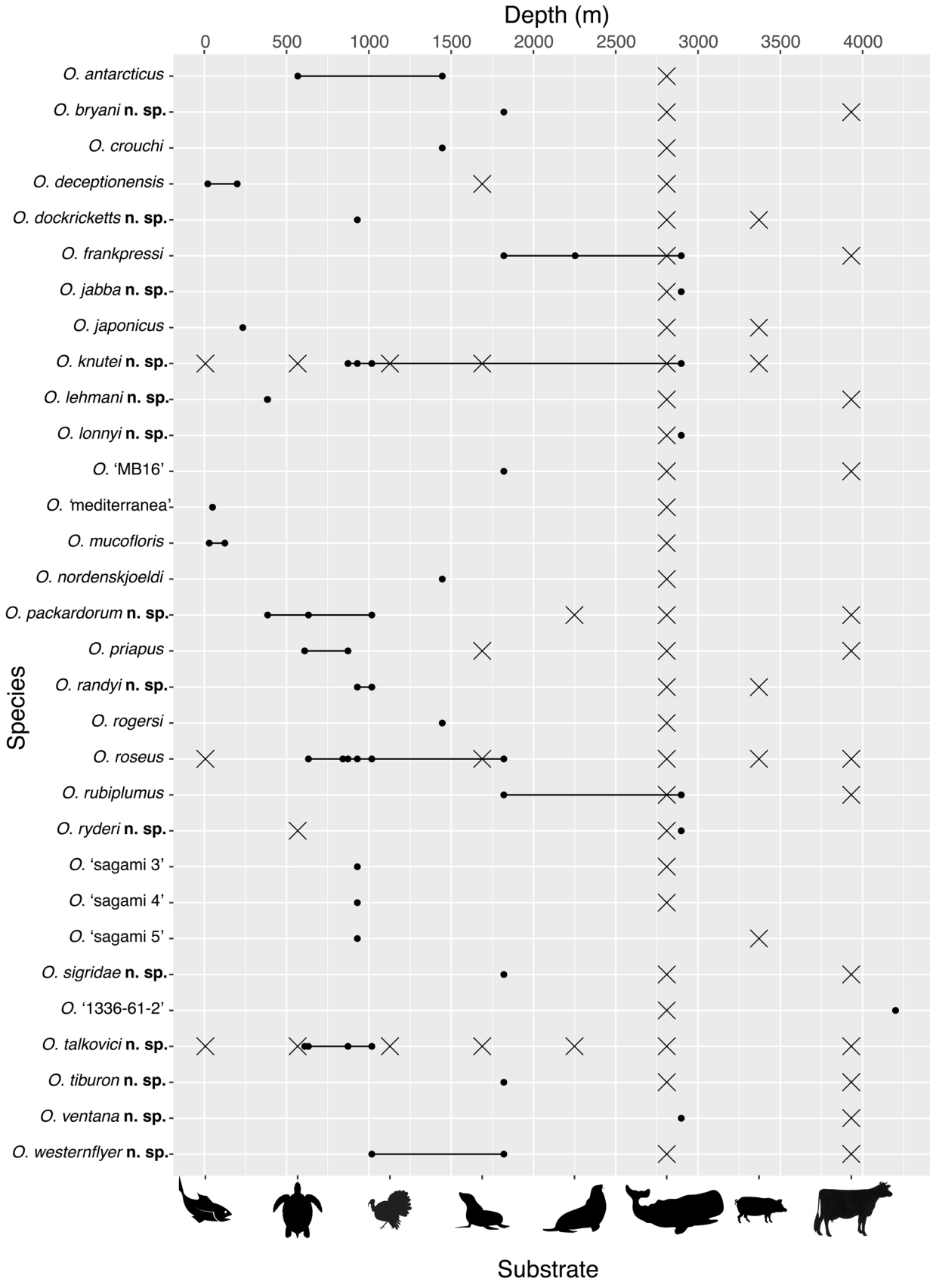


FIGURE 18. ***Osedax bryani*** **n. sp.**, previously *Osedax* 'MB17'. **A**. Micrograph of live holotype (SIO-BIC A4619), female in dorsal view, removed from its tube and showing crown, trunk and part of ovisac. Oviduct lies between dorsalmost pair of palps. Little apparent pigmentation around anterior trunk **B**. Ventral view of live holotype (SIO-BIC A4619) showing white pigmentation anteriorly with midventral gap. Pinnules of all palps oriented dorsally. Arrow indicates oval unpigmented patch. **C.** Differential interference micrograph (from a stack series) of a solitary male (or larval stage?) dissected from tube of holotype (SIO-BIC A4619). Some hooks are visible in expanded posterior region. No mature sperm is visible though there are several bundles of spermatids.

TABLE 5. Colonization (x, axis x_1 lower) of fish, turtle, turkey, fur seal, elephant seal, whale, pig, and cow on lower x axis, with known depth ranges on upper x axis (●, axis x_2 upper) by *Osedax* species.



generation, we hypothesize that an abundant supply of vertebrate bones facilitates stepping-stone dispersal along the entire North Pacific margin. Interestingly, relatively little divergence exists between the Monterey and Sagami samples of most of these respective species. The exception is that, of the 20 available *COI* sequences assigned to *Osedax* 'Sagami-6' by Pradillon *et al.* (unpublished), nine diverge by ~3% (see example in Table 4) from what are accepted here as *O. docricketts* **n. sp.** sequences from Monterey (four sequences) and Japan (11 sequences). To date no *Osedax* species has shown such intraspecific variation, though the smallest interspecific distance known for described species is between *Osedax lehmani* **n. sp.** and *O. packardorum* **n. sp.** at 7.4% (uncorrected). Further assessment from additional Sagami Bay specimens and gene fragments would be useful to resolve the inclusiveness of *O. docricketts* **n. sp.**

Monterey Canyon is remarkably rich in *Osedax* diversity, with 18 named species, plus *Osedax* 'MB 16' (Tables 1, 3, 4, 5). Reasons for this high level of diversity remain obscure, however depth, stage of whale fall decomposition, and substrate flexibility could be influential. No single species of *Osedax* was found to occupy the entire depth range of whale falls and bone deployments studied. Only two species were found at 385 meters, four at 633 meters, seven at 1018 meters, eight at 1820 meters, and seven at 2898 meters (Tables 3, 5). *Osedax knutei* **n. sp.** spans the broadest depth range, almost two km, from 1018 to 2898 meters depth. Three species span about one km: *Osedax frankpressi* (1820–2898 m), *O. rubiplumus* (1820–2898 m), and *O. roseus* (633–1820 m). Other species span narrower ranges: *O. packardorum* **n. sp**. (385–1018 meters), *O. talkovici* **n. sp.** (633–1018 m) and *O. westernflyer* **n. sp**. (1018–1820 m). There is only evidence for two other *Osedax* species occurring across a range of depths (Tables 3, 5). *Osedax antarcticus* has been found from 546-1446 meters (Glover *et al.* 2013; Amon *et al.* 2014), and *O. deceptionensis* is known from 10-156 meters (Taboada *et al.* 2015).

Ten of the Monterey species are only known from single depths (Tables 3, 5). Several species also segregated by timing of colonization. For example, *O. rubiplumus* typically colonized bones first, but was quickly replaced by *O. frankpressi* (Braby *et al.* 2007; Rouse *et al.* 2004). Other species, like *Osedax jabba* **n. sp.**, differed ecologically from the others, by exploiting small bone shards buried in the sediment, as opposed to consuming larger exposed bones. In *O. jabba* **n. sp.**, the 'roots' are long and filamentous and exposed to the sediment (Figs. 12A-F), differing dramatically from those of other species.

Several experiments were conducted testing whether *Osedax* could settle on and consume bones from different vertebrate origins, including fish, turkeys, marine turtles, pigs, and cows (Tables 3, 5). There was no obvious difference among species of *Osedax* for settlement patterns on these experimental substrates versus whale bones (data not shown) although the qualitatively lower densities of worms on experimental substrates often made it much easier to see and collect the 'nude-palp' species. This substrate flexibility was not surprising given that *Osedax* has been shown to successfully exploit teleost bones (Rouse *et al.* 2011), and fossil evidence indicates they exploited plesiosaur, marine turtle (Danise & Higgs 2015) and bird bones (Kiel *et al.* 2012). The one species that produces bone-eating males, *O. priapus*, appears to colonize smaller more ephemeral bones (Rouse et al. 2015). It is possible, therefore, that the ability to exploit variable bone substrates, and in various states of decay, may have even enabled further diversification within the *Osedax.*

Fossil and molecular evidence indicate that the origin of *Osedax* dates into the Cretaceous period (Danise & Higgs 2015; Taboada *et al.* 2015; Vrijenhoek *et al.* 2009). In this sense *Osedax* resembles the radiation of vestimentiferans, but no records exist for such high species diversity among vestimentiferan or frenulate siboglinids in comparably small geographic areas as in Monterey Bay. Given that *Osedax* was first described in 2004, it seems likely that many more species remain to be discovered in the world's oceans.

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Abbreviations used in figures

b bone, **ba** baleen, **bv** blood vessel, **cm** circular muscle, **dbv** dorsal blood vessel, **e** epidermis, **g** glands, **h** hooked chaetae, **lm** longitudinal muscle, **ltr** lower trunk, **m** dwarf males, **n** nerve ganglion, **o** oocytes, **od** oviduct**, os** ovisac**, p** prototroch, **pa** palp, **pc** pigmented collar, **pi** pinnules, **po** polynoid scaleworm, **pp** pigmented patch, **r** roots, **s** sperm, **sp** spermatids, **sv** seminal vesicle, **t** tube, **tr t**runk, **vbv**

References

Amon, D.J., Wiklund, H., Dahlgren, T.G., Copley, J.T., Smith, C.R., Jamieson, A.J. & Glover, A.G. (2014) Molecular taxonomy of *Osedax* (Annelida: Siboglinidae) in the Southern Ocean. *Zoologica Scripta*, 43, 405–417. https://doi.org/10.1111/zsc.12057

Braby, C.E., Rouse, G.W., Johnson, S.B., Jones, W.J. & Vrijenhoek, R.C. (2007) Bathymetric and temporal variation among *Osedax* boneworms and associated megafauna on whale-falls in Monterey Bay, California. *Deep-Sea Research Part I*, 54, 1773–1791. https://doi.org/10.1016/j.dsr.2007.05.014

Brower, A.V.Z. (2010) Alleviating the taxonomic impediment of DNA barcoding and setting a bad precedent: names for ten species of ' *Astraptes fulgerator*' (Lepidoptera: Hesperiidae: Eudaminae) with DNA-based diagnoses. *Systematics and Biodiversity*, 8, 485–491. https://doi.org/10.1080/14772000.2010.534512

Caullery, M. (1914) Sur les Siboglinidae, type nouveau d'invertébrés receuillis par l'expédition du Siboga. *Bulletin de la Société Zoologique de France (Evolution et Zoologie)*, 39, 350—353.

Danise, S. & Higgs, N.D. (2015) Bone-eating *Osedax* worms lived on Mesozoic marine reptile deadfalls. *Biology Letters*, 11, 20150072. https://doi.org/10.1098/rsbl.2015.0072

Fujikura, K., Fujiwara, Y. & Kawato, M. (2006) A new species of *Osedax* (Annelida: Siboglinidae) associated with whale carcasses off Kyushu, Japan. *Zoological Science*, 23, 733–740. https://doi.org/10.2108/zsj.23.733

Glover, A.G., Källstrom, B., Smith, C.R. & Dahlgren, T.G. (2005) World-wide whale worms? A new species of *Osedax* from the shallow north Atlantic *Proceedings of the Royal Society B*, 272, 2587–2592. https://doi.org/10.1098/rspb.2005.3275

Glover, A.G., Wiklund, H., Taboada, S., Avila, C., Cristobo, J., Smith, C.R., Kemp, K.M., Jamieson, A.J. & Dahlgren, T.G. (2013) Bone-eating worms from the Antarctic: the contrasting fate of whale and wood remains on the Southern Ocean seafloor. *Proceedings: Biological Sciences*, 280, 1–10. https://doi.org/10.1098/rspb.2013.1390

Gould, S.J. (1993) A special fondness for beetles. *Natural History*, 102, 4–9.

Higgs, N.D., Glover, A.G., Dahlgren, T.G., Smith, C.R., Fujiwara, Y., Pradillon, F., Johnson, S.B., Vrijenhoek, R.C. & Little, C.T.S. (2014) The morphological diversity of *Osedax* worm borings (Annelida: Siboglinidae). *Journal of the Marine Biological Association of the UK*, 94, 1429–1439. https://doi.org/10.1017/S0025315414000770

Huusgaard, R.S., Vismann, B., Kühl, M., Macnaugton, M., Colmander, V., Rouse, G.W., Glover, A.G., Dahlgren, T. & Worsaae, K. (2012) The potent respiratory system of *Osedax mucofloris* (Siboglinidae, Annelida) - a prerequisite for the origin of bone-eating *Osedax*? *PLoS ONE*, 7, e35975. https://doi.org/10.1371/journal.pone.0035975

Jones, W.J., Johnson, S.B., Rouse, G.W. & Vrijenhoek, R.C. (2008) Marine worms (genus *Osedax*) colonize cow bones. *Proceedings of the Royal Society B*, 275, 387–391. https://doi.org/10.1098/rspb.2007.1437

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

Katz, S., Klepal, W. & Bright, M. (2010) The skin of *Osedax* (Siboglinidae, Annelida): An ultrastructural investigation of its epidermis. *Journal of Morphology*, 271, 1272–1280. https://doi.org/10.1002/jmor.10873

Katz, S., Klepal, W. & Bright, M. (2011) The *Osedax* trophosome: organization and ultrastructure. *Biological Bulletin*, 220, 128–139.
https://doi.org/10.1086/BBLv220n2p128
Katz, S. & Rouse, G.W. (2013) The reproductive system of *Osedax* (Annelida, Siboglinidae): sperm ultrastructure, ovary structure and fertilization. *Invertebrate Biology*, 132, 368–385.
https://doi.org/10.1111/ivb.12037
Kiel, S., Kahl, W.-A. & Goedert, J.L. (2012) Traces of the bone-eating annelid *Osedax* in Oligocene whale teeth and fish bones. *Paläontologische Zeitschrift*, 87, 161–167.
https://doi.org/10.1007/s12542-012-0158-9
Li, Y.N., Kocot, K.M., Whelan, N.V., Santos, S.R., Waits, D.S., Thornhill, D.J. & Halanych, K.M. (2016) Phylogenomics of tubeworms (Siboglinidae, Annelida) and comparative performance of different reconstruction methods. *Zoologica Scripta*, 46, 200–213.
https://doi.org/10.1111/zsc.12201
Nishi, E. & Rouse, G.W. (2014) First whale fall chaetopterid; a gigantic new species of *Phyllochaetopterus* (Chaetopteridae: Annelida) from the deep sea off California. *Proceedings of the Biological Society of Washington*, 126, 287–298.
https://doi.org/10.2988/0006-324X-126.4.287
Page, R.D.M. (2016) DNA barcoding and taxonomy: dark taxa and dark texts. *Philosophical Transactions Of The Royal Society B-Biological Sciences*, 371, 20150334.
https://doi.org/10.1098/rstb.2015.0334
Posada, D. & Crandall, K.A. (1998) Modeltest: Testing the model of DNA substitution. *Bioformatics*, 14, 817–818.
https://doi.org/10.1093/bioinformatics/14.9.817
Rambaut, A., Suchard, M., Xie, D. & Drummond, A. (2014) Tracer v1.6. Available from: http://tree.bio.ed.ac.uk/software/tracer/ (accessed 5 December 2017)
Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61, 539–542.
https://doi.org/10.1093/sysbio/sys029
Rouse, G.W., Goffredi, S.K., Johnson, S.B. & Vrijenhoek, R.C. (2011) Not whale-fall specialists, *Osedax* worms also consume fishbones. *Biology Letters*, 7, 736–739.
https://doi.org/10.1098/rsbl.2011.0202
Rouse, G.W., Goffredi, S.K. & Vrijenhoek, R.C. (2004) *Osedax*: Bone-eating marine worms with dwarf males. *Science*, 305, 668–671.
https://doi.org/10.1126/science.1098650
Rouse, G.W., Wilson, N.G., Goffredi, S.K., Johnson, S.B., Smart, T., Widmer, C., Young, C.M. & Vrijenhoek, R.C. (2009) Spawning and development in *Osedax* boneworms (Siboglinidae, Annelida). *Marine Biology*, 156, 395–405.
https://doi.org/10.1007/s00227-008-1091-z
Rouse, G.W., Wilson, N.G., Worsaae, K. & Vrijenhoek, R.C. (2015) A dwarf male reversal in bone-eating worms. *Current Biology*, 25, 236–241.
https://doi.org/10.1016/j.cub.2014.11.032
Rouse, G.W., Worsaae, K., Johnson, S.B., Jones, W.J. & Vrijenhoek, R.C. (2008) Acquisition of dwarf male 'harems' by recently settled females of *Osedax roseus* n. sp. (Siboglinidae; Annelida). *Biological Bulletin*, 214, 67–82.
https://doi.org/10.2307/25066661
Salathé, R.M. & Vrijenhoek, R.C. (2012) Temporal variation and lack of host specificity among bacterial endosymbionts of *Osedax* bone worms (Polychaeta: Siboglinidae). *BMC Evolutionary Biology*, 12, 189.
https://doi.org/10.1186/1471-2148-12-189
Sansweet, S.J. (1998) Hutt. *In:* Del Rey (Ed.), *Star Wars Encyclopedia*. Ballantine, New York, p. 134.
Schander, C., Rapp, H.T. & Dahlgren, T.G. (2010) *Osedax mucofloris* (Polychaeta, Siboglinidae), a bone-eating marine worm new to Norway. *Fauna Norvegica*, 30, 5–8.
https://doi.org/10.5324/fn.v30i0.632
Stamatakis, A. (2014) RAxML Version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, 30, 1312–1313.
https://doi.org/10.1093/bioinformatics/btu033
Sumida, P.Y.G., Alfaro-Lucas, J.M., Shimabukuro, M., Kitazato, H., Perez, J.A.A., Soares-Gomes, A., Toyofuku, T., Lima, A.O.S., Ara, K. & Fujiwara, Y. (2016) Deep-sea whale fall fauna from the Atlantic resembles that of the Pacific Ocean. *Scientific Reports*, 6, 22139.
Summers, M.M., Al-Hakim, I. & Rouse, G.W. (2014) Turbo-taxonomy: 21 new species of Myzostomida (Annelida). *Zootaxa*, 3873 (4), 301–344.
https://doi.org/10.11646/zootaxa.3873.4.1
Taboada, S., Riesgo, A., Bas, M., Arnedo, M.A., Cristobo, J., Rouse, G.W. & Avila, C. (2015) Bone-eating worms spread: Insights into shallow-water *Osedax* (Annelida, Siboglinidae) from Antarctic, Subantarctic, and Mediterranean waters. *PLoS ONE*, 10, e0140341.

https://doi.org/10.1371/journal.pone.0140341
Tresguerres, M., Katz, S. & Rouse, G.W. (2013) How to get into bones: proton pump and carbonic anhydrase in *Osedax* boneworms. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 280, 20130625. https://doi.org/10.1098/rspb.2013.0625
Vrijenhoek, R.C., Johnson, S. & Rouse, G.W. (2009) A remarkable diversity of bone-eating worms (*Osedax*; Siboglinidae; Annelida). *BMC Biology*, 7, 74. https://doi.org/10.1186/1741-7007-7-74
Vrijenhoek, R.C., Johnson, S.B. & Rouse, G.W. (2008) Bone-eating *Osedax* females and their 'harems' of dwarf males are recruited from a common larval pool. *Molecular Ecology*, 17, 4535–4544. https://doi.org/10.1111/j.1365-294X.2008.03937.x
Worsaae, K., Rimskaya-Korsakova, N.N. & Rouse, G.W. (2016) Neural reconstruction of bone-eating *Osedax* spp. (Annelida) and evolution of the siboglinid nervous system. *BMC Evolutionary Biology*, 16, 83. https://doi.org/10.1186/s12862-016-0639-7
Worsaae, K. & Rouse, G.W. (2010) The simplicity of males: progenetic dwarf males of four species of *Osedax* (Annelida) investigated by confocal laser scanning microscopy. *Journal of Morphology*, 271, 127–142. https://doi.org/10.1002/jmor.10786
Swofford, D.L. (2002) *PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4.* Sinauer Associates, Sunderland, Massachusetts. [software]