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The fouling serpulids (Polychaeta: Serpulidae) from United States coastal waters: an overview

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Abstract. Serpulids are an important component of fouling communities. This paper provides an overview of the serpulid species found in North America, as part of a broader study of fouling invertebrates focused on NIS (non-indigenous species) in United States coastal ecosystems. Almost 4400 serpulid specimens were examined from selected fouling plates. Fouling plates were deployed in 26 bays and coastal lagoons along the continental coasts of the United States and Hawaiian islands, primarily in bays and lagoons with salinities averaging 20‰ or greater. Twenty-five serpulid species were identified, including four new records for the United States (*Ficopomatus uschakovi*, *Hydroides* cf. *brachyacantha*, *H. longispinosa* and *Protula longiseta*), three known NIS, two presumed NIS, three cryptogenic serpulids, and several range extensions. *Crucigera websteri* extends its northward range from Santa Barbara Island to Humboldt Bay, California; *Ficopomatus enigmaticus*, first recorded in North America from San Francisco, California in 1920, Rockport, Texas in 1952 and Barnegat Bay, New Jersey in 1980, is now recorded at additional localities on the east coast (Chesapeake Bay, Virginia, Charleston, South Carolina and Indian River, Florida) and the northern Gulf of Mexico (Galveston Bay, Texas); *F. miamiensis* extends its westward range from Louisiana to Texas; *F. uschakovi*, an Indo-Pacific and Western African species, was recorded formally for the first time from the northern Gulf of Mexico (Galveston Bay and Corpus Christi, Texas) and the east coast of Florida (Jacksonville). *Hydroides* cf. *brachyacantha* extends its northward range from Curaçao to Pensacola Bay, Florida; *H. dirampha* from Veracruz, Mexico to Corpus Christi, Texas; *H. floridana* extends its westward range from Louisiana to Texas; *H. gracilis* extends its northward range from Pacific Grove to San Francisco, California; *Salmacina huxleyi* from Cape Hatteras, North Carolina to Rhode Island; and *Spirobranchus minutus* from Veracruz, Mexico to Pensacola Bay, Florida. The following additional species range extensions are provisional in that they represent only one record or were not found in the most recent surveys (e.g., *Hydroides elegans* - east coast): *H. longispinosa* from Marshall Islands to Oahu, Hawaii; *Protula balboensis* from Florida to Texas; *P. longiseta* from the Mexican Caribbean to the Indian River, Florida; *H. elegans* from San Francisco to Humboldt Bay, northern California and on the east coast from the Indian River, Florida, to Cape Cod, Massachusetts. Among surveyed bays, Biscayne Bay, Florida and Corpus Christi, Texas (northern Gulf of Mexico) had the greatest number of species (14 and 8, respectively); in contrast, almost all sites in Alaska, Washington, Oregon (northwest Pacific), Rhode Island, Virginia and South Carolina (Atlantic) had only one or two species each. *Hydroides dianthus* was, by far, the most abundant serpulid species on fouling plates in the northern Gulf of Mexico and the east coast, while *Pseudochitinopoma occidentalis* was the most abundant serpulid detected on the west coast. For each species recorded herein, we include the synonyms and some key references, a material studied section, a diagnosis, and updated distributional information. A checklist and identification key to the known shallow-water serpulids *sensu stricto* of the United States are included.

Keywords. *Ficopomatus*, fouling, *Hydroides*, non-indigenous species, tube worms.

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Introduction

The serpulids are a group of tubiculous polychaetes, the only family that builds calcareous tubes, with the exception of a sabellid genus *Glomerula* Nielsen, 1931. The family Serpulidae includes the subfamilies Serpulinae, Filograninae, Ficopomatinae and Spirorbinae. The Serpulidae *sensu lato* include more than 600 described species (Fauchald 1977; Knight-Jones *et al.* 1979; Bastida-Zavala & ten Hove 2002; ten Hove & Kupriyanova 2009). Here, we evaluate the occurrence of shallow-water serpulids in North America, excluding the Spirorbinae which will be addressed in a separate paper.

Serpulids are sessile polychaetes and filter-feeders. Some species are common components of the fouling community globally, and can occur in very high densities (ten Hove 1979; ten Hove & van den Hurk 1993). In the latter case, they can have undesirable effects such as the fouling of ship hulls, clogging of seawater intake pipes and fouling of other man-made structures in coastal waters (Hoagland & Turner 1980; Ben-Eliahu & ten Hove 2011; Çinar 2013). Transport of serpulids, as fouling fauna on vessels and other surfaces, also permits them to invade areas outside of their original geographical distribution. This can alter the composition and function of benthic communities, as occurrs with some species of *Ficopomatus* Southern, 1921. For instance, *Ficopomatus enigmaticus* (Fauvel, 1923), originally described from Caen Canal, northwestern France, and recorded worldwide in temperate and subtropical waters (ten Hove & Kupriyanova 2009), builds large, reef-like colonies that can have strong ecological and economic impacts. In brackish water lagoons, reefs built by *F. enigmaticus* are located in: Long Beach, California (Pernet *et al.* 2016); Tunis Lake (ten Hove & van den Hurk 1993); Menorca Albufera, Spain (Fornós *et al.* 1997); Orbetello Lagoon, Italy (Bianchi & Morri 2001); and Mar Chiquita Lagoon, Argentina (Schwindt *et al.* 2001, 2004). Large reefs were present for many decades in Lake Merritt, Oakland, San Francisco Bay, prior to the lagoon becoming more marine (James T. Carlton, pers. comm.).

Table 1. Number of serpulid specimens per species confirmed from fouling plates along United States coasts. *Hydroides* sp. represents juveniles that were not identifiable to species level. Abundances with an asterisk (*) are new records for the region or state. Key to sites: RI = Narragansett Bay, Rhode Island; CB = Chesapeake Bay, Virginia; CH = Charleston, South Carolina; JX = Jacksonville, Florida; IR = Indian River, Florida; BB = Biscayne Bay, Florida; TB = Tampa Bay, Florida; PB = Pensacola Bay, Florida; GB = Galveston Bay, Texas; CC = Corpus Christi, Texas; DH = Dutch Harbor, Alaska; AK = Kechamak Bay, Alaska; AV = Valdez, Alaska; PW = Prince William Sound, Alaska; KD = Kodiak, Alaska; ST = Sitka, Alaska; KT = Ketchikan, Alaska; WA = Puget Sound, Washington; OR = Coos Bay, Oregon; HB = Humboldt Bay, California; SF = San Francisco, California; MO = Morro Bay, California, LB = Long Beach, California; MI = Mission Bay, California, SD = San Diego, California, HI = Oahu, Hawaii.

Localities	**East Coast**						**Gulf of Mexico**				**West Coast**															**Hawaii**	Speci-mens
Taxa	RI	CB	CH	JX	IR	BB	TB	PB	GB	CC	DH	AK	AV	PW	KD	ST	KT	WA	OR	HB	SF	MO	LB	MI	SD	HI	
Crucigera																											
websteri	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1*	–	–	–	–	–	–	1
zygophora	–	–	–	–	–	–	–	–	–	–	–	61	1	2	26	58	4	11	3	13	–	–	–	–	–	–	179
Ficopomatus																											
enigmaticus	–	64*	17*	–	1*	–	2	–	12*	–	–	–	–	–		–	–	–	–	–	47	–	–	–	–	–	143
miamiensis	–	–	–	4	92	65	10	24	27*	2*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	224
uschakovi	–	–	–	2*	–	26*	–	–	32*	13*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	73
Hydroides																											
bispinosa	–	–	–	–	–	8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8
cf. *brachyacantha*	–	–	–	–	–	1*	–	6*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7
dianthus	108	352	117	99	99	78	38	323	356	217	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1787
dirampha	–	–	–	6	78	5	–	–	–	19*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	41	1	150
elegans	–	–	–	–	123	1	32	–	–	–	–	–	–	–	–	–	–	–	–	1*	–	–	87	5	87	48	384
floridana	–	–	–	–	–	1	–	4	–	5*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	10
gracilis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3*	5*	185	7	32	–	232
longispinosa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2*	2
parva	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
sanctaecrucis	–	–	–	–	–	28	9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	37
sp. (juveniles)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	2	–	2	14	–	22
Pomatostegus																											
stellatus	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Protula																											
balboensis	–	–	–	13	–	2	–	–	–	1*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	16
longiseta	–	–	–	–	1*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Pseudochitinopoma																											
occidentalis	–	–	–	–	–	–	–	–	–	–	24	66	7	4	358	81	8	75	1	18	12	4	–	–	–	–	658
Pseudovermilia																											
occidentalis	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3
Salmacina																											
huxleyi	2*	–	–	–	1	110	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	115
tribranchiata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6	–	–	–	–	–	–	–	1	205	17	229
Serpula																											
columbiana	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1
Spirobranchus																											
kraussii	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
minutus	–	–	–	–	–	–	–	59	3*	46*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	108
no. species by site	**2**	**2**	**2**	**5**	**7**	**14**	**5**	**5**	**5**	**8**	**1**	**2**	**2**	**2**	**2**	**3**	**3**	**2**	**2**	**4**	**3**	**2**	**2**	**3**	**4**	**5**	**–**
no. specimens by site	**110**	**416**	**134**	**124**	**395**	**330**	**91**	**416**	**430**	**305**	**24**	**127**	**8**	**6**	**384**	**145**	**13**	**86**	**4**	**33**	**62**	**9**	**272**	**13**	**365**	**69**	**4371**

We combined field surveys of the fouling community (Table 1) with an analysis of records from the literature to document 62 species of shallow-water serpulids in the waters of the United States. Of these, we identified 42 species on the east coast of the United States and the northern Gulf of Mexico (Salazar-Vallejo 1996; Perkins 1998; Bastida-Zavala & Salazar-Vallejo 2000a, 2000b; Bastida-Zavala & ten Hove 2002) and 26 species from the Hawaiian Islands and from the west coast of the United States, including Alaska (Zibrowius 1969a; Knight-Jones *et al.* 1979; Bastida-Zavala & ten Hove 2003; Bastida-Zavala 2008) (Table 2).

Material and methods

This work is part of a broader study examining patterns of invasion in the fouling community of North America, focused on detection of non-indigenous species (NIS) (Ruiz *et al.* 2001, 2004). Settlement plates were deployed on the east, west and Gulf coasts of North America and in Hawaii for a period of three months. Twenty-six different bays and coastal lagoons were sampled from 1999 to 2013, monitoring many states along each coastline: Alaska (seven sites), California (six sites), Florida (five sites), Hawaii (one site), Oregon (one site), Rhode Island (one site), South Carolina (one site), Texas (two sites), Virginia (one site), and Washington (one site). We examined more than 1400 voucher samples containing almost 4400 specimens of serpulids, from at least five randomly chosen fouling plates per 10 sites within each

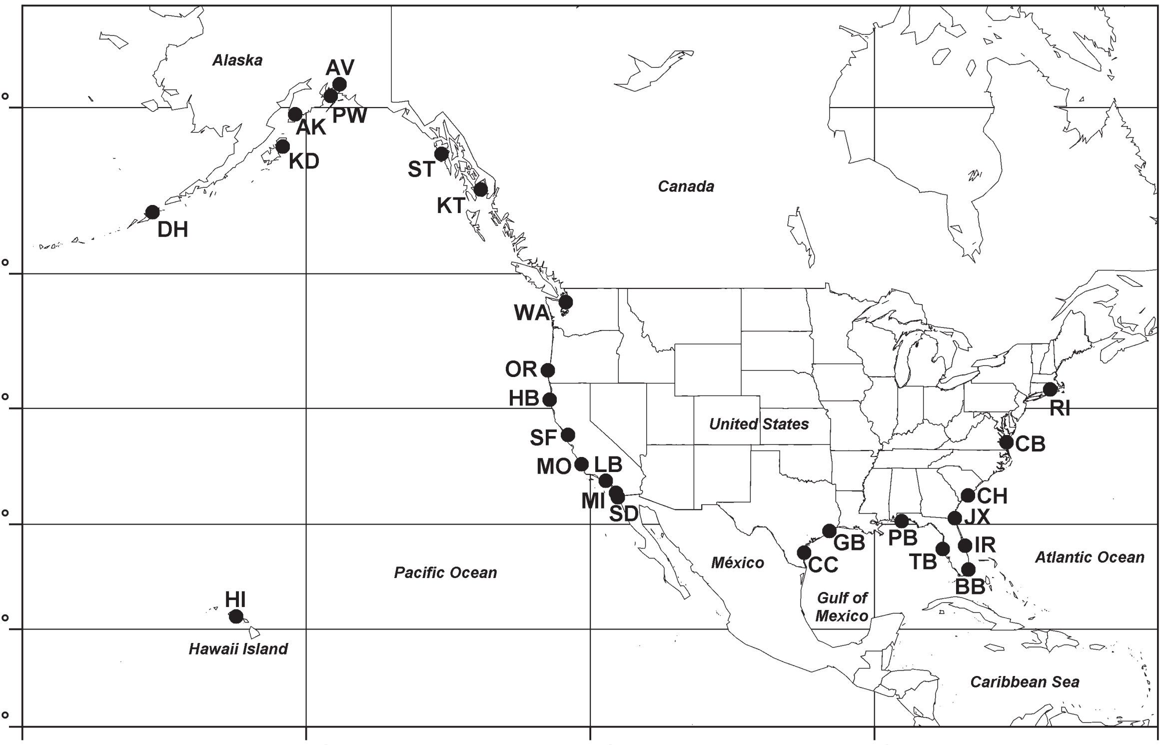

Fig. 1. Study area. Site abbreviations following decreasing latitude from east to west coasts: RI = Narragansett Bay, Rhode Island; CB = Chesapeake Bay, Virginia; CH = Charleston, South Carolina; Florida: JX = Jacksonville, IR = Indian River, BB = Biscayne Bay, TB = Tampa Bay and PB = Pensacola Bay; GB = Galveston Bay and CC = Corpus Christi, Texas; Alaska: DH = Dutch Harbor, KD = Kodiak, AK = Kechamak Bay, AV = Valdez, PW = Prince William Sound, ST = Sitka and KT = Ketchikan; WA = Puget Sound, Washington; OR = Coos Bay, Oregon; California: HB = Humboldt Bay, SF = San Francisco, MO = Morro Bay, LB = Long Beach, MI = Mission Bay and SD = San Diego; HI = Oahu, Hawaii.

bay or coastal lagoon for a total of 1253 plates (Fig. 1). This material is part of the reference collections at the Smithsonian Environmental Research Center (SERC) in Edgewater, Maryland, United States (U.S.). A representative sample of specimens was deposited by the first author in the collection of the Laboratorio de Sistemática de Invertebrados Marinos (LABSIM) in Oaxaca, Mexico.

Each specimen in our surveys was identified to species using key characters. The operculum of serpulids is a structure with particularly useful characters for the identification of the species. The operculum shape, as well as the number and arrangement of chitinous or calcareous ornamentations, are important for the diagnosis of each species. Tube ornamentations and collar chaetae are less specific characters, but used in combination with the operculum are often useful for the determination of the species. However, not all serpulids have an operculum, and the importance of the tube and collar chaetae increases in these cases (ten Hove & Jansen-Jacobs 1984).

For each species in our analysis we included: an exhaustive synonymy section, including key references; a material studied section with abbreviated collection localities and number of specimens (n); a short diagnosis that contains the description of the tube, opercular peduncle, operculum, collar chaetae and thoracic characters; general habitat; updated distributional information; and relevant remarks to assist with identification. A more detailed description of the character terminology can be found in Bastida-Zavala & ten Hove (2002) and ten Hove & Kupriyanova (2009). A species checklist, combining the results of this survey with the current literature (Table 2), and an identification key to shallow-water serpulids (excluding the Spirorbinae) from the United States are also provided.

Collection abbreviations

ECOSUR = El Colegio de la Frontera Sur, reference collection, Chetumal, Quintana Roo, México
LACMNH = Los Angeles County Museum of Natural History, Los Angeles, California, USA
MBL-SD = Marine Biology Laboratory, San Diego, California, USA
SERC = Smithsonian Environmental Research Center, Edgewater, Maryland, USA
UMAR-Poly = Universidad del Mar, scientific collection, polychaete section, Puerto Ángel, Oaxaca, México
USNM = National Museum of Natural History, Washington DC, USA.

Locality abbreviations for United States collection locations in alphabetical order

AK = Kachemak Bay, Alaska
AV = Valdez, Alaska
BB = Biscayne Bay, Florida
CB = Chesapeake Bay, Virginia
CC = Corpus Christi, Texas
CH = Charleston, South Carolina
DH = Dutch Harbor, Alaska
GB = Galveston Bay, Texas
HB = Humboldt Bay, California
HI = Oahu, Hawaii
IR = Indian River, Florida
JX = Jacksonville, Florida
KD = Kodiak, Alaska
KT = Ketchikan, Alaska
LB = Long Beach, California
MI = Mission Bay, California
MO = Morro Bay, California
OR = Coos Bay, Oregon

PB = Pensacola Bay, Florida
PW = Prince William Sound, Alaska
RI = Narragansett Bay, Rhode Island
SD = San Diego, California
SF = San Francisco, California
ST = Sitka, Alaska
TB = Tampa Bay, Florida
WA = Puget Sound, Washington

For clarification purposes, many of our species occur in the West Indies, which encompasses both the Caribbean island chains of the Greater and Lesser Antilles, and the Bahama Archipelago, which includes the Bahamas and Turks and Caicos Islands.

Results

Almost 4400 specimens of serpulids were examined. Twenty-five species of Serpulidae were identified (Table 1). Among the survey sites, the greatest species richness was in Biscayne Bay (FL) with 14 species, followed by Corpus Christi (TX) with eight species, while the lowest was in Dutch Harbor (AK) with only one species. Four species are new records for the United States: *Ficopomatus uschakovi* (Pillai, 1960), *Hydroides* cf. *brachyacantha* Rioja, 1941a, *Hydroides longispinosa* Imajima, 1976b and *Protula longiseta* Schmarda, 1861. The surveys detected range extensions in the coastal waters of the United States for 10 additional species, including *Crucigera websteri* Benedict, 1887, *Ficopomatus enigmaticus* (Fauvel, 1923), *F. miamiensis* (Treadwell, 1934), *Hydroides dirampha* Mörch, 1863, *H. elegans* (Haswell, 1883), *H. floridana* (Bush, 1910), *H. gracilis* (Bush, 1905), *Protula balboensis* Monro, 1933, *Salmacina huxleyi* (Ehlers, 1887) and *Spirobranchus minutus* (Rioja, 1941b).

Key to shallow-water serpulids from the United States

1. With operculum 2
– Without operculum 45

2. Opercular peduncle thin, with pinnules (operculum on one radiole) 3
– Opercular peduncle thick and smooth 4

3. Five thoracic chaetigers; capillary (Fig. 9L) and sharply-limbate collar chaetae (Fig. 9M) .... ***Josephella marenzelleri*** Caullery & Mesnil, 1896
– Six to 12 thoracic chaetigers; collar with fin-and-blade chaetae, with basal denticulate expansion and flattened distal blade (Fig. 9N) .... ***Filogranula calyculata*** (Costa, 1861) [1]

4. Collar with chaetae 5
– Collar without chaetae 43

5. Operculum funnel-shaped, without chitinous plates (Figs 2A–D, 4A–J, 9A–B) 6
– Operculum with chitinous (Fig. 7A) or calcareous plates (Fig. 9C, G), sometimes fused, sometimes with spines like “deer horns”, never funnel-shaped 28
– Operculum otherwise 40

6. Operculum as a simple funnel, calcified .... ***Pyrgopolon ctenactis*** (Mörch, 1863)
– Operculum as a simple funnel, fleshy (Fig. 2A–D) 7
– Operculum as a fleshy basal funnel and a distal chitinous verticil (Fig. 4A–J) .... ***Hydroides*** Gunnerus, 1768 …12

7. Operculum with basal digitate or rounded processes (Fig. 2A–D) ....***Crucigera*** Benedict, 1887 …8
– Operculum with no basal processes (Fig. 9A–B) ....***Serpula*** Linnaeus, 1758 …9 [2]

8. Operculum with one basal rounded process; inner surface of funnel smooth ....***Crucigera irregularis*** Bush, 1905
– Operculum with three basal rounded processes, one dorsal and two laterals (Fig. 2C–D), sometimes the dorsal rounded process split in two; inner surface of funnel smooth ....***C. zygophora*** (Johnson, 1901)
– Operculum peduncle with four basal digitate processes (Fig. 2B); inner surface of funnel with tubercles (Fig. 2B) ....***C. websteri*** Benedict, 1887

9. Opercular funnel with less than 20 radii; shallow constriction between peduncle and operculum ....***Serpula* sp. A** in ten Hove & Wolf 1984 [3]
– Opercular funnel with more than 20 radii; deep constriction between peduncle and operculum .. 10

10. Opercular funnel short, with 46–160 radii (Fig. 9A–B), pointed tips, inner surface with numerous tiny conical tubercles ....***S. columbiana*** Johnson, 1901 [4]
– Opercular funnel elongate; with 21–35 radii, rounded tips, inner surface smooth 11

11. Tube with five longitudinal ridges; collar with bayonet chaetae (similar to Fig. 9H–J) with five teeth ....***S. watsoni*** Willey, 1905
– Tube with 6–8 longitudinal ridges; collar with bayonet chaetae with two teeth ....***S. vossae*** Bastida-Zavala, 2012 [2]

12. Verticil spines without lateral spinules, with expanded tips, without wings (Fig. 4D) 13
– Verticil spines with lateral spinules, without wings (Fig. 4A, 4E, 4H–I) 14
– Verticil spines without lateral spinules (Fig. 4B–C, 4G), without expanded tips, sometimes with wings (Fig. 4F, 4J) 21

13. Verticil spines with rounded tips; bayonet chaetae with two teeth and proximal rasp (Fig. 9K) ....***Hydroides microtis*** Mörch, 1863
– Verticil spines with flat almost T-shaped tips (Fig. 4D); bayonet chaetae with two teeth, without proximal rasp (Fig. 9H–I) ....***H. dirampha*** Mörch, 1863

14. Verticil spines with only one pair of lateral spinules (Fig. 4A, 4I) 15
– Verticil spines with more than one pair of lateral spinules (Fig. 4E, 4H) 18

15. Funnel without radii, with 3–6 blunt processes only; verticil with straight spines ....***H.*** cf. ***mucronatus*** Rioja, 1958
– Funnel formed by radii; verticil spines curving inwards 16

16. Funnel radii with blunt tip (Fig. 4A) ....***H. bispinosa*** Bush, 1910
– Funnel radii with pointed tip (Fig. 4I) 17

17. Verticil spines abruptly curving inwards, with a pronounced distal knob ....***H. parva*** (Treadwell, 1902)
– Verticil spines curving inwards rather smoothly, without distal knob ......***H. crucigera*** Mörch, 1863

18. Verticil spines complex, with many lateral and external spinules; dark-brown basally and hyaline distally; internal spinules enlarged .... ***H. mongeslopezi*** Rioja, 1958
– Verticil spines simple, with few lateral and without external spinules; uniform colour pattern; internal spinules short 19

19. Verticil spines with 2–4 pairs of lateral spinules; central spine short (Fig. 4E) or without this spine 20
– Verticil spines with 5–8 pairs of lateral spinules; central spine long (Fig. 4H) .... ***H. longispinosa*** Imajima, 1976b

20. Verticil spines straight or curving outwards (Fig. 4E) .... ***H. elegans*** (Haswell, 1883)
– Verticil spines curving inwards .... ***Hydroides* sp. A** in ten Hove & Wolf 1984[3]

21. Funnel radii with laterally expanded tips, T-shaped .... ***H. gairacensis*** Augener, 1934
– Funnel radii with pointed tips (Fig. 4B–C, 4F–G, 4J) 22

22. Verticil spines straight or curving outwards; bayonet chaetae with two teeth and proximal rasp (Fig. 9K) .... ***H. protulicola*** Benedict, 1887
– Verticil with at least dorsal –if not all– spines curving inwards; bayonet chaetae with two teeth without proximal rasp (Fig. 9H–I) 23

23. Dorsal spines curving inwards, ventral spines curving outwards (Fig. 4C, 4J) 24
– All spines curving inwards (Fig. 4B, 4F–G) 25

24. Verticil spines without external spinule and wings (Fig. 4C) .... ***H. dianthus*** (Verrill, 1873)
– Verticil spines with external spinule (at least ventral ones) and wings (Fig. 4J) .... ***H. sanctaecrucis*** (Krøyer in Mörch, 1863)

25. Verticil with spines long and slender, gradually curving inwards, without wings, all spines similar in shape and size (Fig. 4G) .... ***H. gracilis*** (Bush, 1905)
– Verticil with spines short and thick, strongly curving inwards, without wings, 1–5 dorsal spines larger than the others (Fig. 4B) 26
– Verticil with spines long and slender, gradually curving inwards, with wings, all spines similar in shape and size (Fig. 4F) 27

26. Only one dorsal spine, remaining verticil spines equally sized, with subdistal knobs .... ***H. brachyacantha*** Rioja, 1941a
– Only one dorsal spine, remaining verticil spines equally sized, without subdistal knobs (Fig. 4B) .... ***H.* cf. *brachyacantha*** Rioja, 1941a
– 3–5 dorsal bigger spines, with external tubercles on smaller spines .... ***H.* cf. *amri*** Sun, Wong, ten Hove, Hutchings, Williamson & Kupriyanova, 2015[5]

27. Branchial crown with more than 29 pairs of radioles; funnel with 45–61 radii .... ***H. spongicola*** Benedict, 1887
– Branchial crown with less than 24 pairs of radioles; funnel with 27–38 radii (Fig. 4F) .... ***H. floridana*** (Bush, 1910)

28. Operculum with 1–7 distal calcareous plates (Fig. 9C, 9G), sometimes with spines like “deer horns” .... ***Spirobranchus*** Blainville, 1818…29
– Operculum with a column of chitinous concentric plates (Fig. 7A), sometimes with a distal stalk stellate .... Pomatostegus stellatus (Abildgaard, 1789)
– Operculum with 1–14 distal chitinous plates fused (Fig. 7G), sometimes with one distal branched spine or a hook 34

29. Operculum with 1–7 successive calcareous plates, distal spines absent .... ***Spirobranchus latiscapus*** (Marenzeller, 1885)
– Operculum with one calcareous plate, with spines similar to deer horns, or when the plate is smooth has an ovoid or conical shape 30

30. Operculum lacks spines (Fig. 9C, 9G); with a few limbate collar chaetae (Fig. 9M), sometimes none 31
– Operculum with spines; collar chaetae always present 33

31. Tube with two longitudinal ridges, with spine or flap projection over entrance, lacks alveoli (holes) (Fig. 9D); collar without chaetae ....***Spirobranchus kraussii*** (Baird, 1865)
– Tube with one or three longitudinal ridges, never two ridges, lacks projection over entrance, with alveoli (Fig. 9F); collar with few chaetae 32

32. Operculum ovoid, with a projection; tube with one longitudinal ridge and one line of small alveoli in older sections ....***S. americanus*** Day, 1973
– Operculum conical (Fig. 9G) or bilobed, with 1–2 small projections; tube with three longitudinal ridges and two lines of large alveoli along tube (Fig. 9F) ....***S. minutus*** Rioja, 1941b

33. Operculum with two very large (equal to or larger than opercular plate) and thin horns and one short horn, with several short spines ....***S. giganteus*** (Pallas, 1766)[6]
– Operculum with two large (smaller than opercular plate) and thick horns, sometimes with a third large horn, with few large spines..***S. corniculatus*** (Grube, 1862)[6, 7]
– Operculum with five short and wide horns, with several large spines ....***S. spinosus*** Moore, 1923

34. Thoracic membrane extends up to 3–6 chaetigers; thoracic uncini with anterior blunt tooth ....***Vermiliopsis*** Saint-Joseph, 1894[8] …35
– Thoracic membrane extends up to second chaetiger; thoracic uncini with anterior bifurcate tooth 36

35. Operculum with 1–7 fused discs ....***Vermiliopsis annulata*** (Schmarda, 1861)[8]
– Operculum with 10–14 fused discs ....***V. multiannulata*** Gravier, 1906[8]

36. Insertion of opercular peduncle is at second radiole; thoracic uncini saw to rasp-shaped ....***Semivermilia pomatostegoides*** (Zibrowius, 1969b)[9]
– Insertion of opercular peduncle just below and between first and second radioles; thoracic uncini saw-shaped ....***Pseudovermilia*** Bush, 1907…37

37. Operculum black or dark brown (Fig. 7G) 38
– Operculum yellow or colorless 39

38. Tube with longitudinal ridges and alveoli rows, lacks peristomes and transverse ridges; operculum with tree-shaped spines ....***Pseudovermilia multispinosa*** (Monro, 1933)
– Tube with longitudinal and transverse ridges, sometimes with peristomes, lacks alveoli; operculum with a simple curved spine, with some minor spines or spines absent (Fig. 7G) ....***P. occidentalis*** (McIntosh, 1885)

39. Tube with several denticulate ridges and alveoli rows, with transverse brown bands ....***P. fuscostriata*** ten Hove, 1975
– Tube smooth, with a longitudinal ridge, without alveoli rows, entirely white ....***P. conchata*** ten Hove, 1975

40. Tube with a longitudinal keel, without peristomes; operculum with a smooth convex to conical chitinous cap (Fig. 7F); collar with fin-and-blade chaetae, with basal denticulate expansion and flattened distal blade (Fig. 9N) ....***Pseudochitinopoma occidentalis*** (Bush, 1905)

– Tube without a longitudinal keel, with peristomes (Fig. 2E, 2I); operculum with spines (Fig. 2G, 2N) or smooth (Fig. 2J–K); collar chaetae coarsely serrated, without basal expansion (Fig. 9O) .... ***Ficopomatus*** Southern, 1921…41

41. Thoracic membranes dorsally fused (Fig. 2M, 2O); opercular spines curved outwards (Fig. 2N); tropical species .... ***Ficopomatus uschakovi*** (Pillai, 1960)
– Thoracic membranes free (Fig. 2F); opercular spines curved inwards (Fig. 2G) or absent (Fig. 2J–K) 42

42. Operculum concave with black incurving spines (Fig. 2G), not black or lacking in juveniles; subtropical species ....***F. enigmaticus*** (Fauvel, 1923)
– Operculum bulbous (Fig. 2J), slightly convex (Fig. 2K), without spines; tropical species ....***F. miamensis*** (Treadwell, 1934)

43. Opaque tube without dorsal ridge, sometimes with brood chambers; thorax with sickle chaetae or "*Apomatus*" chaetae (distally curved) ....***Rhodopsis pusilla*** Bush, 1905 [10]
– Hyaline tube with dorsal ridge, without brood chambers; thorax without sickle chaetae ....***Placostegus*** Philippi, 1844…44

44. Tube without transverse ridges; operculum bulbous proximally, concave and zygomorphic dorsally ....***Placostegus californicus*** Hartman, 1969
– Tube with transverse ridges in posterior half section; operculum unknown ....***P. incomptus*** Ehlers, 1887

45. Collar chaetae limbate (Fig. 9M) or capillaries (Fig. 9L), without basal denticulate expansion; uncini with long main tooth 46
– Collar with fin-and-blade chaetae, with basal denticulate expansion and flattened distal blade (Fig. 9N), or bayonet chaetae with several teeth (Figs 7I, 9J); uncini with short main tooth 49

46. Seven to nine thoracic chaetigers ....***Protula*** Risso, 1826…47
– 11–14 thoracic chaetigers ....***Filogranella* sp.** in Fosså & Nielsen 1996 [11]

47. Nine thoracic chaetigers; radioles with a single row of pinnules ....***Protula setosa*** (Bush, 1910) [12]
– Seven thoracic chaetigers; radioles with a double row of pinnules .... 48 [13]

48. Tube with longitudinal ridges; branchial crown lacks basal round processes; thoracic membrane narrow, reaches fourth chaetiger ....***P. longiseta*** Schmarda, 1861 [14]
– Tube with rough texture, without longitudinal ridges (Fig. 7B); branchial crown with basal round process on each radiole (Fig. 7D); thoracic membrane wide, reaches seventh chaetiger (Fig. 7E) .... ***P. balboensis*** Monro, 1933 [14]
– Tube smooth, sometimes with shallow transverse ridges; branchial crown with 31–51 radioles; thoracic membrane narrow, reaches seventh chaetiger; uncini smooth ....***P. atypha*** Bush, 1905

49. Tube with internal longitudinal ridges ....***Spiraserpula*** Regenhardt, 1961 …50
– Tube without internal longitudinal ridges ....***Salmacina*** Claparède, 1870…51

50. Tube with dorsal internal ridge serrated, ventral ones with Y-shape ....***Spiraserpula ypsilon*** Pillai & ten Hove, 1994 [15]
– Tube with dorsal internal ridge not serrated, ventral ones serrated ....***S. caribensis*** Pillai & ten Hove, 1994 [15]

51. Collar chaetae with many small teeth 52
– Collar chaetae with 4–8 large teeth (Fig. 7I) 53

52. Three, sometimes four, pairs of radioles (Fig. 7J); thoracic uncini with 8–9 rows of teeth and 3–4 teeth per row .... ***Salmacina tribranchiata*** (Moore, 1923) [16, 17]
– Four pairs of radioles; thoracic uncini with seven rows of teeth and 2–3 teeth per row .... ***S. dysteri*** (Huxley, 1855) [16]
– Five pairs of radioles; thoracic uncini with more than 10 rows of teeth .... ***Salmacina* sp. A** in ten Hove & Wolf 1984 [3, 16, 17]

53. Without prostomial eyes; teeth of collar chaetae distally increasing regularly in size (Fig. 7I); 20 or fewer abdominal segments (Fig. 7H) .... ***S. huxleyi*** (Ehlers, 1887) [16]
– With prostomial eyes; collar chaetae with 4–6 large teeth of similar size; up to 40 abdominal segments .... ***S. incrustans*** Claparède, 1870 [16]

Notes for the identification key

1) *Filogranula calyculata* (O.G. Costa, 1861) was described from the Mediterranean.

2) Recently Bastida-Zavala (2012) described two species of *Serpula* from the tropical western Atlantic at sublittoral depths: *S. madrigalae* from Turks and Caicos and *S. vossae* from several sites in the western Caribbean and Bahamas; at least the second species is likely to be found on the U.S. east coast.

3) *Salmacina* sp. A, *Hydroides* sp. A and *Serpula* sp. A were recorded by ten Hove & Wolf (1984) from the northern Gulf of Mexico.

4) Kupriyanova (1999) revised the status of *Serpula* cf. *columbiana* Johnson, 1901 and demonstrated that the apparently cosmopolitan *S. vermicularis* includes three species: *S. vermicularis*, from the North Atlantic and Arctic, *S. columbiana* from the American Pacific and *S. uschakovi* from the Western Boreal Pacific. Bastida-Zavala (2008) synonymized *S. nannoides* Chamberlin, 1919b with *S. columbiana*.

5) Bastida-Zavala & ten Hove (2003) recorded *Hydroides* cf. *brachyacantha* from Hawaii; according to Bastida-Zavala *et al.* (2016: 411–413), these records belong to a species similar to *Hydroides amri*, described by Sun *et al.* (2015) in temperate waters from Australia; however, because Hawaii is in tropical waters Bastida-Zavala *et al.* (2016) tentatively used the name *H.* cf. *amri*.

6) *Spirobranchus giganteus* and *S. corniculatus* were considered part of the *Spirobranchus giganteus*-complex (see Fiege & ten Hove 1999, fig. 4). *Spirobranchus giganteus* has been recorded worldwide in tropical waters, but the use of this name should be restricted to the Caribbean and Gulf of Mexico.

7) Recently, three species of the Indo-West Pacific *Spirobranchus corniculatus* complex, *S. corniculatus*, *S. gaymardi* (Quatrefages, 1866) and *S. cruciger* (Grube, 1862), were genetically analysed using nuclear and mitochondrial DNA markers which revealed a single, monophyletic clade for the *S. corniculatus* complex (Willette *et al.* 2015). The authors found that "the genetic and morphological variation observed is not geographically based, indicating that the former *S. corniculatus* complex of three morphospecies is a single, morphologically variable species across the Central Indo-Pacific".

8) The differences between the species in *Vermiliopsis* are very tiny, and the morphological characters should be reviewed (Zibrowius 1970). *Vermiliopsis multiannulata* belongs to the *V. infundibulum*-complex, and *V. annulata* may include at least two species.

9) *Semivermilia pomatostegoides* was described off Tripoli, Libya, in the Mediterranean, from 140 m (Zibrowius 1969b). Bailey-Brock (1987) recorded the species off Keahole Point, Hawaii Island and Lahaina Harbor, Maui Island, between 15 and 20 m. The species has not, to date, been reported from any locations beyond the Mediterranean and Hawaiian Islands, and we thus suggest that the identity of the Hawaiian material deserves further analysis and confirmation.

10) *Rhodopsis pusilla* was re-described by Ben-Eliahu & ten Hove (1989), and it is a small serpulid recorded worldwide in tropical waters.

11) *Filogranella elatensis* Ben-Eliahu & Dafni, 1979 was described from the Mediterranean; Fosså & Nielsen (1996) recorded *Filogranella* sp. in the Caribbean. However, these records should be confirmed.

12) The type specimens of *Salmacinopsis setosa* Bush, 1910 were revised by ten Hove (pers. comm. 1999), confirming the presence of a narrow thoracic membrane (which reaches the sixth chaetiger) and more than five pairs of radioles. The only diagnostic character is the single row of pinnules on the radioles, a character that should be analyzed with new material. In all serpulids the pinnules are arranged in double rows. Ten Hove & Kupriyanova (2009) invalided the genus *Salmacinopsis* and tentatively transferred this species to *Protula*.

13) One specimen of *Protula* sp. A was recorded by ten Hove & Wolf (1984) from the northern Gulf of Mexico; it lacked a tube, and the authors refrained from identification to species level due to the importance of tube characters.

14) The differences between these two species of *Protula* are very small and need more detailed morphological review. *Protula longiseta* was described by Augener (1925) from a Jamaican coral reef, while *Protula balboensis* was described from both sides of Panama (Monro 1933). All specimens to which we assigned this name consistently have the basal round process on the radioles, as it is typical in *P. balboensis*, except one specimen from the Indian River that does not have them and was identified as *P. longiseta*.

15) Both species of *Spiraserpula* do not have an operculum, only a rudimentary filament.

16) The description of denticulate variation of the collar chaetae of *Salmacina* species should be revised, as ten Hove & Wolf (1984) and Nogueira & ten Hove (2000) recommended. The world-wide distribution of *Salmacina dysteri* and *S. incrustans*, described from Europe, is doubtful.

17) Moore (1923: 250) described *Filograna tribranchiata*, from California, with a "gill… the right dorsal usually bearing a spoon-shaped operculum", and he was likely referring to the swollen appearance of the tip of a radiole. Later Monro (1933) relocated the species to *Salmacina* using non-operculate specimens (Nogueira & ten Hove 2000). Also, *Salmacina* sp. A, a sublittoral species from the northern Gulf of Mexico, has radioles with an enlarged spherical tip (ten Hove & Wolf 1984).

Systematics

The species are treated in alphabetical order.

Class Polychaeta Grube, 1850
Family Serpulidae Rafinesque, 1815
Genus ***Crucigera*** Benedict, 1887

Crucigera websteri Benedict, 1887
Figs 2A–B, 3

Crucigera websteri Benedict, 1887: 550–551, pl. 21, figs 24–25, pl. 22, figs 26–30 (type locality: off Florida, United States, 29°16'30" N, 85°32" W; 43.5 m).

Serpula (Crucigera) websteri – Monro 1933: 1079–1080 (Taboga Island, Panama; 2–4 m; on dead coral).

Crucigera websteri – Berkeley & Berkeley 1941: 57 (Newport Bay, southern California; on "boat bottom"). — Rioja 1961: 311–313, figs 35–39 (Verde Island, Veracruz, eastern Mexico; 9 m, on rocks, corals and mollusk shells). — Hartman 1969: 751–752, figs 1–4 (southern California; the figures are from Benedict 1887). — Nonato & Luna 1970: 99, figs 102–105 (Alagoas coast, Brazil; 51–100 m, on sand and mud). — ten Hove & Wolf 1984: 55–15, figs 55-9, 55-10a–m (western Florida; 43 m, coarse sand). — ten Hove & Jansen-Jacobs 1984: 155–160, figs 3a, 4j–l, 5a, 6a–e, 7a–k, 10e, 12 (revision of the genus; Florida, Surinam, Pacific of Panama and southern California; 2–86 m;

occasionally as fouling). — Laverde-Castillo 1988: 86–87, figs 2a–e (Málaga Bay, Colombian Pacific; shallow water, on rocks). — León-González 1990: 336, fig. 3a–d (west coast of Baja California Peninsula: Punta San Juanico and Cabo San Lázaro, Baja California Sur; 27–30 m). — Perkins 1998: 95 (checklist of shallow-water polychaetes of Florida). — Bastida-Zavala 2008: 16–17, figs 4C–D (California and Mexican Pacific: Baja California Sur, Guerrero and Oaxaca; intertidal to 73 m). — Bastida-Zavala *et al.* 2016: 409–410, figs 3, 10H–I (Oaxaca, southern Mexican Pacific).

Material examined

One specimen: HB (1) Sep. 2003.

Additional material

Three specimens: LACMNH s.n., 1 specimen (33°28–40' N, 119°00–30' W, 1.6 km off eastern side of Santa Barbara Island, California, Velero III, sta. 1409, Blake trawl, sand, sea urchins, 37–73 m, 15 Sep. 1941, as *Serpula* n. sp.); LACMNH s.n., 1 specimen (33°35–36' N, 117°52–53' W, Newport Harbor, Balboa Peninsula, "bay side, floats off Fred Lewi's Landing", California, Velero III, sta. 1449, intertidal, "collected off harbor floats and piles from a skiff", 13 Mar. 1942, as *Serpula* sp.); LACMNH N8819, 1 specimen (approx. 32°42' N, 118°17' W, San Pedro, California).

Diagnosis

Juvenile specimen. Tube white, thin and smooth; without peristomes, transverse ridges, longitudinal ridges or alveoli. Opercular peduncle smooth, white, with a bulbous region below funnel (Fig. 2A). In adult specimens, base of operculum with four digitate processes (Fig. 2B). Operculum with a radially symmetric funnel, with 43–52 radii with rounded tips (Fig. 2A–B); inner surface of funnel with some rounded tubercles (Fig. 2A–B). Collar with bayonet chaetae, with 2–3 blunt and long teeth, smooth distal blade.

Taxonomic remarks

The only specimen of *Crucigera websteri* from fouling plates was a juvenile, which can be distinguished from juveniles of *C. zygophora* (Johnson, 1901), because the former has a deeply concave funnel and its inner surface has rounded tubercles (Fig. 2A), while in the latter the funnel is shallow and smooth, without tubercles (Fig. 2C). In adult forms, *C. websteri* has four digitate processes on the opercular base (Fig. 2B), while *C. zygophora* only has three rounded processes (Bastida-Zavala 2008).

Ecology

Intertidal to 86 m (ten Hove & Jansen-Jacobs 1984; Bastida-Zavala 2008); occasionally as fouling on skiffs, floats and dock pilings (Bastida-Zavala 2008).

Distribution

Amphi-American. Western Atlantic from Florida and Gulf of Mexico to Brazil; eastern Pacific from southern California to Panama (ten Hove & Jansen-Jacobs 1984). The Amphi-American status of *Crucigera websteri* follows the hypothesis of Bastida-Zavala *et al.* (2016: 439), that the eastern Pacific population of this species likely is a Pleistocene relict, because the first Californian record was made by Treadwell (1914), with samples collected at least two years before, and prior to the Panama Canal operation, in addition to the scarce presence of this species in the fouling fauna. Only one specimen was found on a fouling plate from Humboldt Bay, California (Fig. 3), in 2003, suggesting that the species may now be present in northern California. However, additional sampling is necessary to confirm that *C. websteri* is currently established in northern California.

Crucigera zygophora (Johnson, 1901)

Figs 2C–D, 3

Serpula zygophora Johnson, 1901: 433–434, pl. 19, figs 205–208 (type locality: Alki Point, Puget Sound, Washington, United States).

Crucigera formosa Bush, 1905: 233–234, pl. 28, figs 3–4, pl. 33, fig. 4, pl. 39, figs 6–7, 10–11, 14 (type locality: Dutch Harbor, Unalaska Island; also from Wrangell, southern Alaska).

Crucigera hespera Chamberlin, 1919b: 270, pl. 2, fig. 9 (type locality: Mendocino, northern California, United States).

Crucigera zygophora – Bush 1905: 233, pl. 29, fig. 5, pl. 31, fig. 2, pl. 33, fig. 3, pl. 39, figs 8, 12–13, 15, 17, 20 (Sitka, Orca and Virgin Bay, and Prince William Sound, southern Alaska; attached to shell fragments, in twisted masses). — Treadwell 1914: 227 (Alaska and Santa Barbara, Southern California). — Berkeley 1930: 73 (Nanoose Bay, British Columbia; 36–55 m). — ten Hove & Jansen-Jacobs 1984: 165–170, figs 4a–c, 5d, 8d, 9a–j, 10a, c–d, 11a–h, 12 (revision of the genus; Alaska, British Columbia, Washington and California). — Bastida-Zavala 2008: 17–19, figs 4E–F (Alaska and California; 12–64 m).

Crucigera formosa – ten Hove & Jansen-Jacobs 1984: 166 (synonymy).

Material examined

179 specimens: AK (61) Jul. 2000, AV (1) Aug. 2000, PW (2) Aug. 2003, KD (26) Aug. 2001, ST (58) Aug. 2001, KT (4) Sep. 2003, WA (11) Aug. 2000, OR (3) Aug. 2000, HB (13) Sep. 2003.

Additional material

Approximately 13 specimens: LACMNH N2128, 1 specimen (approx. 55°55' N, 161°27' W, Canoe Bay, north shore, Alaska, King Crab Investigation, sta. 12–40, 17 Sep. 1940; see Hartman 1948); LACMNH N2129, several specimens (approx. 55°19' N, 162°57' W, Cold Bay, Alaska, King Crab Investigation, sta. 70–40, 27–64 m, 17 Oct. 1940); LACMNH N2789, 1 specimen (approx. 55°55' N, 161°27' W, Canoe Bay, Alaska, from crab trap, 23 Sep. 1940, coll. N.L. Schmitt); LACMNH N412, 1 specimen (approx. 38°15' N, 122°58' W, Dillon Beach, Perch Rock Pt, California, Jun. 1941, coll. S.F. Light).

Diagnosis

Juvenile specimens. Tube white, thin and smooth; without peristomes, transverse ridges, longitudinal ridges or alveoli. Opercular peduncle smooth, white, with a bulbous region below funnel (Fig. 2C). In adult, base of operculum yoke-shaped, with a rounded dorsal process and two latero-ventral ones (Fig. 2D). Operculum a nearly radially symmetric funnel, shallow and smooth, without tubercles, with 13–34 radii with rounded tips (Fig. 2C–D). Collar with bayonet chaetae, with 1–2 blunt, short teeth and minute accessory teeth, smooth distal blade.

Taxonomic remarks

Juveniles of *Crucigera zygophora* can be mistaken for *Serpula columbiana* Johnson, 1901 (Fig. 9A), since the operculum funnel is symmetrical and the basal processes appear as a bulbous region (Fig. 2C), less prominent than in the adult specimens (Fig. 2D). However, the number of radii of the juveniles of *C. zygophora* is mostly less than 25 radii (Fig. 2C), and in adult between 28 to 34 radii, while *S. columbiana* have more than 100 radii (Fig. 9B). Also, juveniles of *C. zygophora* could be confused with *C. websteri* (see previous remarks on this species).

Ecology

Sublittoral, 12–250 m (ten Hove & Jansen-Jacobs 1984; Bastida-Zavala 2008).

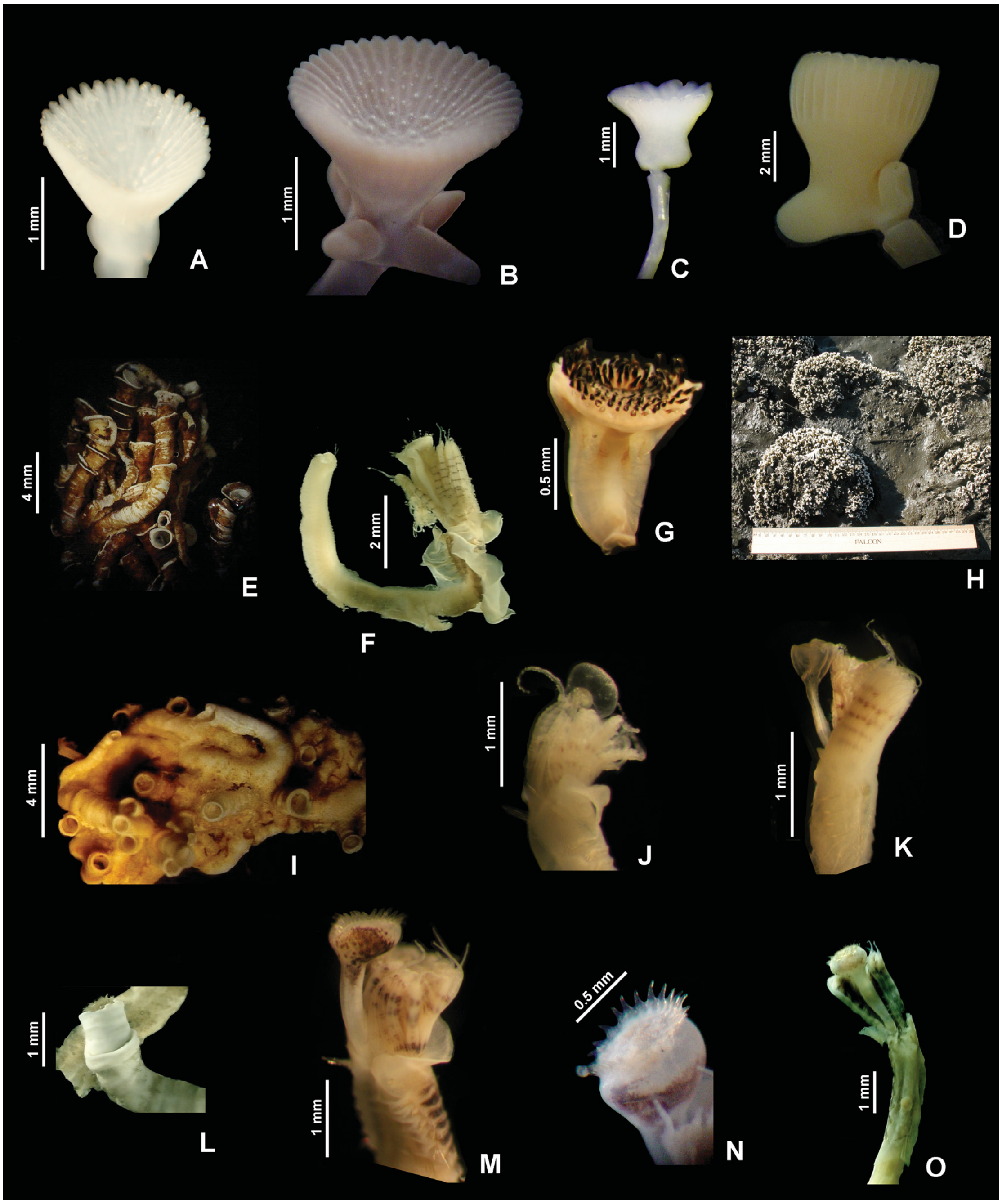

Fig. 2. Serpulids from United States fouling plates. *Crucigera websteri*. **A**. Operculum, juvenile from Humboldt Bay, California. **B**. Operculum, adult from San Pedro, California (LACMNH-N8819). – *C. zygophora*. **C**. Operculum, juvenile from Alaska (SERC). **D**. Operculum, adult from Canoe Bay, Alaska (LACMNH-N2128). – *Ficopomatus enigmaticus*. **E**. Tubes from Lake Merritt, California (LACMNH-N5141). **F**. Body, from Chesapeake Bay, Virginia (SERC-59327). **G**. Operculum, from Chesapeake Bay, Virginia (SERC-60530R). **H**. Colonies in Long Beach, California (photo by Bruno Pernet). – *F. miamiensis*. **I**. Tubes, from Chetumal Bay, Mexican Caribbean (ECOSUR). **J–K**. Operculum, from Galveston Bay, Texas (SERC-88344RF). – *F. uschakovi*. **L**. Tube, from Corpus Christi, Texas (SERC-88883). **M**. Thorax and operculum, from Galveston Bay, Texas (SERC-86995). **N**. Operculum, from La Encrucijada, Chiapas (UMAR-Poly 113). **O**. Thorax and operculum, from Corpus Christi, Texas (SERC-88883).

Distribution

Pacific: Northern Japan, U.S. west coast from Alaska to southern California (Treadwell 1914; ten Hove & Jansen-Jacobs 1984; Bastida-Zavala 2008). In this work, *Crucigera zygophora* juveniles were abundant on fouling plates from Kachemak Bay, Kodiak and Sitka, Alaska; and occasionally found in Valdez, Prince William Sound and Ketchikan, Alaska; Puget Sound, Washington; Coos Bay, Oregon; and Humboldt Bay, northern California (Fig. 3).

Genus ***Ficopomatus*** Southern, 1921

Ficopomatus enigmaticus (Fauvel, 1923)

Figs 2E–H, 3

Mercierella enigmatica Fauvel, 1923: 424–430, figs 1a–o (type locality: Caen Canal, Normandy, France; on stems of *Phragmites* (Poaceae grass), submerged wood, stones and shells in brackish water; associated with the bivalve *Congeria cochleata* (Nyst, 1835), now *Mytilopsis leucophaeata* (Conrad, 1831), the amphipod *Corophium volutator* (Pallas, 1766) and the bryozoan *Membranipora lacroixii* (Audouin, 1826), now *Conopeum reticulum* (Linnaeus, 1767)).

Mercierella enigmatica – Fauvel 1933: 190–192 (Lake Merritt, Oakland, San Francisco Bay; on pilings, piers, docks and boat hull associated with the amphipod *Corophium bonelli* Milne Edwards, 1830 (actually *Monocorophium insidiosum* (Crawford, 1937) sensu James T. Carlton, pers. comm.), the hydrozoan *Syncoryne* Steenstrup, 1842 (actually *Sarsia tubulosa* (M. Sars, 1835) sensu James T. Carlton, pers. comm.), and *Mytilus* Linnaeus, 1758). — Hartman 1952: 64 (Rockport, Texas; fouling). — Rioja 1943: 547—550 (Puerto Quequén, Argentina). — Straughan 1969: 234 (Ala Wai Canal, Kewalo Basin and Pearl Harbor, Oahu, Hawaii). — Bailey-Brock 1976: 73 (Oahu and Maui islands, Hawaii; associated with channels, fish farms and oysters).

Ficopomatus enigmaticus – ten Hove & Weerdenburg 1978: 114–116, figs 2e–i, 3d–e, l–q, 4a–d, s, aa–bb, nn–vv, zz, 5c (revision of the genus; Netherlands, Tunisia, South Africa, Australia, Japan, Uruguay, Argentina and United States: San Francisco, Texas and Hawaii). — Hoagland & Turner 1980: 60 (Oyster Creek Nuclear Generating Station, Barnegat Bay, New Jersey; 0.8–2 m; occurs in low densities on wood plates in the mouth of creeks flowing to the bay). — Zibrowius 1992: 91 (discussion about its origin). — ten Hove & van den Hurk 1993: 42–44, figs 5A–D, 6A–C (Lake Tunis reefs; intertidal to 1.9 m, salinity 28–47‰, temperature 10–30°C). — Perkins 1998: 95 (checklist of shallow-water polychaetes from Florida). — Bianchi & Morri 2001: 216–218 (Orbetello Lagoon, Italy; reef-builders, competition with *Hydroides dianthus* (Verril, 1873) and ecological preferences; salinity 13–48‰, temperature 7–30°C). — Schwindt *et al.* 2001: 139–147 (impacts on Mar Chiquita Lagoon, Argentina). — Schwindt *et al.* 2004: 111–118 (physical effects on the same lagoon). — Bastida-Zavala 2008: 19, fig. 5A (California and Hawaii). — Carlton & Eldredge 2009: 60–61 (Hawaii; invasion history and local economic impacts). — Ben-Eliahu & ten Hove 2011: 14 (Israel, Suez Canal and Egypt; 0.3 m; under rocks, encrustation of tin can). — Cohen 2011: webpage (Los Angeles Harbor, California; small boat marina; four specimens). — Pernet *et al.* 2016: 13–18 (Los Angeles River, California; established populations).

Material examined

143 specimens: CB (64) Sep. 2000, 2001 and Aug. 2012, CH (17) Sep. 2004, IR (1) Aug. 2005, TB (2) Jul. 2002, GB (12) Sep. 2002, SF (47) Sep. 2000, 2011 and 2012.

Additional material

25 specimens: LACMNH N8835 and N1873, many specimens (Lake Merritt, Oakland, California, 27 Jul. 1934 and 24 Jul. 1937); LACMNH N5141, 15 specimens (approx. 21°17' N, 157°50' W, Ala Wai Canal, Honolulu, Hawaii, 18 Apr. 1948, coll. R.W. Hiatt).

Diagnosis

This species is gregarious and can build large colonies. Tube white, often covered by a dark film of microalgae; with large peristomes (collar-like rings); without longitudinal ridges or alveoli (Fig. 2E). Opercular peduncle smooth, white. Operculum fig-shaped, with a brown, horny plate covered with black spines, curving inwards (Fig. 2G), sometimes with accessory spinules. Sometimes, the horny plate is completely covered by these spines. Thoracic membranes well developed, not fused dorsally (Fig. 2F). Special collar chaetae coarsely serrated.

Measurements: Total length = 11.1 mm (n = 14, range (r): 3.1–25.3, SD = 6.9); thorax length = 2.7 mm (n = 15, r: 1.4–3.8, SD = 0.9), thorax width = 0.9 mm (n = 15, r: 0.5–1.6, SD = 0.3); peduncle and operculum length = 1.7 mm (n = 15, r: 0.8–3.0, SD = 0.6); operculum length = 1.1 mm (n = 15, r: 0.6–1.6, SD = 0.3); operculum diameter = 0.7 mm (n = 15, r: 0.5–1.0, SD = 0.2).

Taxonomic remarks

Ficopomatus enigmaticus has a long historical record of invasions (ten Hove & Weerdenburg 1978). Zibrowius (1992: 91) suggested that *F. enigmaticus* was probably introduced to Europe and San

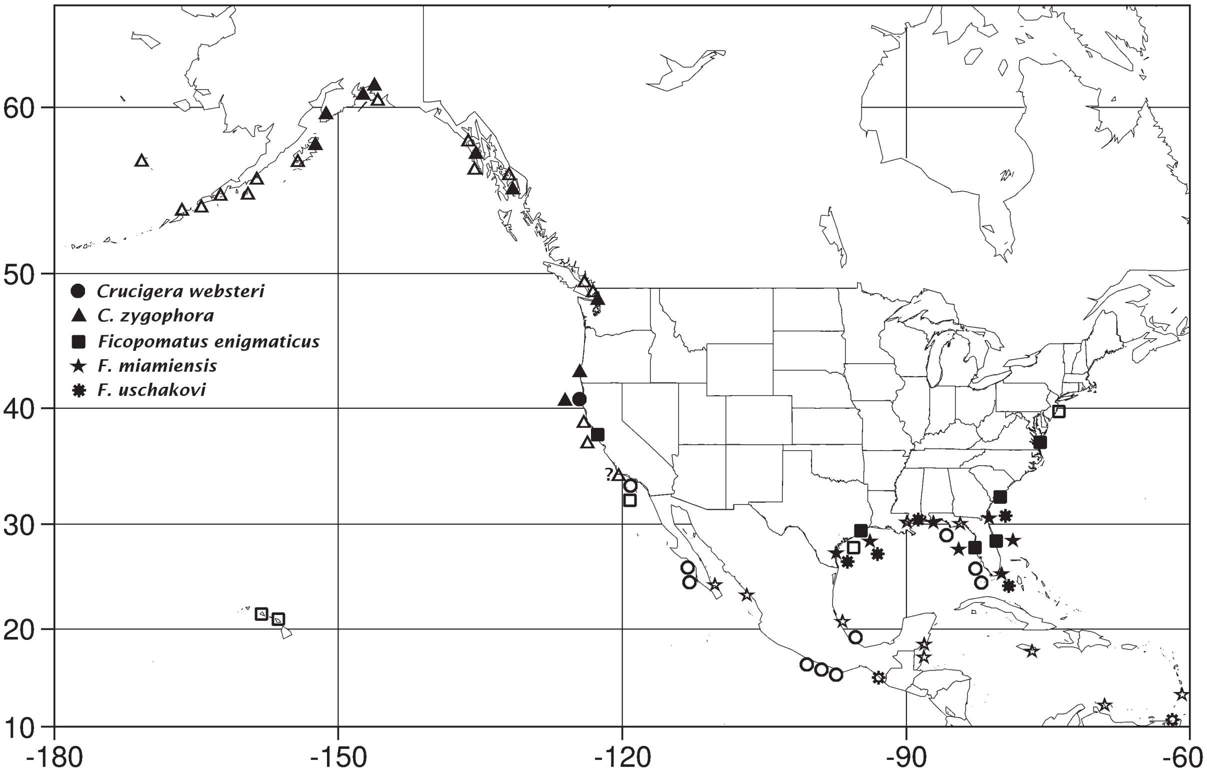

Fig. 3. Distribution of serpulids (*Crucigera* and *Ficopomatus* spp.) from United States fouling plates (closed symbols) and literature records (open symbols).

Francisco during the First World War (1914–1919), because the first records in Europe, including the original description (Fauvel 1923), Rioja (1931) from Spain, and the specimens collected in 1931 from Lake Merrit, Oakland (revised by ten Hove & Weerdenburg 1978), were made a few years after the war. Zibrowius also rejected the hypothesis of Fauvel (1923) of an Indian-Indonesian origin. He thought it more likely that the species originates in a subtropical to temperate region, perhaps southern Australia. Given that five of the six species of *Ficopomatus* are present in Asia, this region seems a likely point of origin. Recently, Styan *et al*. (2017) analyzed several populations of *Ficopomatus enigmaticus* from southern Australia, using mitochondrial (Cyt B) sequencing and nuclear marker (iSSR) profiles, concluding that these populations represents cryptic sympatric species.

This species plays an important ecological role in some localities, because it builds large colonies in some Mediterranean (ten Hove 1974; ten Hove & Weerdenburg 1978; ten Hove & van den Hurk 1993; Fornós *et al.* 1997; Bianchi & Morri 2001) and Patagonian coastal lagoons (Schwindt *et al.* 2001, 2004), where it forms reefs or micro-atolls, 2–3 m in diameter (ten Hove & van den Hurk 1993; Schwindt *et al.* 2001, 2004), and can reach 750 m in length as in Lake Tunis (ten Hove & van den Hurk 1993).

Recently, colonies (Fig. 2H) of this species were collected from Long Beach, California (Pernet *et al.* 2016). Bastida-Zavala (2008) recorded *F. enigmaticus* from fouling plates in San Diego, California; however, this record was a mistake because the samples examined were actually from San Francisco, California.

Ecology

Intertidal to sublittoral (2 m). In lagoons with salinities of 13–48‰, temperature 7–30°C (Bianchi & Morri 2001); on Poaceae grass, submerged wood, stones and shells, bivalves, bryozoans, rocky, sandy and artificial substrates such as tin cans (Fauvel 1923; ten Hove & Weerdenburg 1978; Ben-Eliahu & ten Hove 2011) and settlement plates (this study).

Distribution

World-wide in temperate, brackish-water lagoons. Northern Europe, Mediterranean, Black Sea, Caspian Sea, South Africa, southern Australia, Japan, Hawaii, California, northern Gulf of Mexico, Uruguay and northern Argentina (ten Hove & Weerdenburg 1978). In this work, *Ficopomatus enigmaticus* was found abundantly on fouling plates from Chesapeake Bay, Virginia (first recorded there in 1994 by L. McCann) and San Francisco Bay, California; and occasionally from Charleston, South Carolina, Indian River and Tampa Bay, Florida, and Galveston Bay, Texas (Fig. 3). The material studied extends its eastward range from Rockport, Texas (ten Hove & Weerdenburg 1978), to Pensacola Bay, Florida (750 km); our study also extends its southward range from Barnegat Bay, New Jersey (Hoagland & Turner 1980) to Indian River, Florida (1500 km), though only one specimen was found there.

Ficopomatus miamiensis (Treadwell, 1934)

Figs 2I–K, 3

Sphaeropomatus miamiensis Treadwell, 1934: 339–341; figs 1–5 (type locality: Miami River, Florida, United States).

Mercierellopsis prietoi Rioja, 1945: 413–417, pl. I, figs 1–20, pl. II, figs 21–23 (type locality: Larios Estuary, Tecolutla and Carmen Lagoon, Veracruz, eastern Mexico; also from Barra de Nautla, Veracruz; in brackish water, on mangrove roots, *Ostrea* and other bivalves).

Ficopomatus miamiensis – ten Hove & Weerdenburg 1978: 106–109, figs 1f–i, 3c, 4h–i, q, v–w, ee–ii, xx, 5a–b (revision of the genus and specimens from Florida, Louisiana, Jamaica, Barbados, Curaçao, Belize, and Canal Zone of Pacific Panama; in brackish water, 2.5–31‰, intertidal to 1 m, on the carapace of *Macrobrachium jamaicensis* Gundlach, 1887, now *M. carcinus* (Linnaeus, 1758), shell of *Isognomon alatus* (Gmelin, 1791), pebbles, limestone boulders on sandy mud and *Caulerpa*). — Perkins 1998: 95 (checklist of shallow-water polychaetes from Florida). — Bastida-Zavala & Salazar-Vallejo 2000a: 813, fig. 4i–s (eastern Mexico: Tecolutla, Veracruz and Chetumal Bay, Mexican Caribbean; on oysters and docks). — Bastida-Zavala & ten Hove 2003: 92 (probably from Costa Rica; on mangrove oysters, *Ostrea iridiscens*, now *Striostrea prismatica* (Gray, 1825) and *Crassostrea columbiensis* (Hanley, 1846), with *Hydroides humilis* (Bush, 1905) and *Spirobranchus minutus* (Rioja, 1941b)). — Bastida-Zavala 2008: 19–21, fig. 5B–D (Sinaloa, Mexican Pacific and Canal Zone of Pacific Panama). — Tovar-Hernández *et al.* 2009: 327–328, figs 3g–i, 6a, 7a–c (as an invasive species in Mazatlán, Sinaloa, Mexican Pacific). — Tovar-Hernández *et al.* 2012: 12, figs a–e (Gulf of California: La Paz, Baja California Sur).

Material examined

224 specimens: JX (4) Aug. 2001, IR (92) Aug. 2005, BB (65) Aug. 2004, TB (10) Jul. 2002, PB (24) Aug. 2002, GB (27) Sep. 2002, CC (2) Sep. 2002.

Additional material

More than 160 specimens: ECOSUR s.n., 129+ specimens (Chetumal Bay, pier, 1990–1996, coll. S.I. Salazar-Vallejo *et al.*); UMAR-Poly 51, 10+ specimens (23°09' N, 106°19' W, Urias estuary, Mazatlán, Mexico, 1999, coll. N. Méndez); USNM 58659, 20+ specimens (approx. 8°59'40" N, 79°35'20" W, Miraflores Spillway, Canal Zone, Panama City, Panama, sta. 130–5, “on bottom, standing water”, 2 Apr. 1973, coll. M.L. Jones *et al.*).

Diagnosis

This species is gregarious and can form colonies. Tube white, with small peristomes; without transverse ridges, longitudinal ridges or alveoli (Fig. 2I). Opercular peduncle smooth, white. Operculum spherical or with a flat end-plate, never with spines (Fig. 2J–K). Thoracic membranes not fused dorsally. Special collar chaetae coarsely serrated.

Measurements: Total length = 6.2 mm (n = 10, r: 2.6–11.9, SD = 2.9); thorax length = 1.6 mm (n = 13, r: 0.7–3.2, SD = 0.6), thorax width = 0.6 mm (n = 13, r: 0.4–0.9, SD = 0.2); peduncle and operculum length = 1.3 mm (n = 13, r: 0.6–2.8, SD = 0.6); operculum length = 0.6 mm (n = 13, r: 0.3–0.9, SD = 0.2); operculum diameter = 0.4 mm (n = 13, r: 0.2–0.7, SD = 0.2).

Taxonomic remarks

Ficopomatus miamiensis has a spherical (Fig. 2J), slightly convex (Fig. 2K) or flat operculum that lacks spines, while, the other two species of *Ficopomatus* recorded as NIS in the United States have spines on the operculum (Fig. 2G, M–N).

The native distribution of *F. miamiensis* is assumed to be the Gulf of Mexico and Caribbean Sea. The NIS records from Urías Estuary, Sinaloa, Mexican Pacific (Salgado-Barragán *et al.* 2004; Tovar-Hernández *et al.* 2009), were likely due to the accidental introduction of larvae included in the water with shrimp transported from the Gulf of Mexico for aquaculture, or as adults encrusting bivalves moved from the Gulf of Mexico to Sinaloa, Mexican Pacific, with oysters for oyster culture, while the specimens recorded from Pacific Panama (Bastida-Zavala 2008) and Costa Rica (Bastida-Zavala & ten Hove 2003: 92) presumably invaded following transport by ballast water or by oyster translocation. Recently, *F. miamiensis* was found in La Paz, Baja California Sur, Gulf of California (Tovar-Hernández *et al.* 2012).

Ecology

Intertidal to sublittoral (3 m). On mangrove roots, oysters, shrimp carapace, algae, and rocky and artificial substrates (ten Hove & Weerdenburg 1978).

Distribution

Gulf of Mexico and Caribbean Sea, in tropical brackish water lagoons and the mouth of rivers. Also recorded from the Pacific side of the Canal Zone of Panama (Bastida-Zavala 2008) and Urías Estuary, Sinaloa, Mexican Pacific, as an invasive species (Tovar-Hernández *et al.* 2009). In this work, *Ficopomatus miamiensis* was found abundantly on fouling plates from the Indian River, Biscayne Bay and Pensacola Bay, Florida, and Galveston Bay, Texas; and occasionally from Jacksonville and Tampa Bay, Florida, and Corpus Christi, Texas (Fig. 3). This species extends its westward range from Lake Pontchartrain, Louisiana (ten Hove & Weerdenburg 1978) to Galveston Bay, Texas (500 km).

Ficopomatus uschakovi (Pillai, 1960)

Figs 2L–O, 3

Neopomatus uschakovi Pillai, 1960: 28–32, figs 10, 11A–H, pl. I, figs 1–2 (type locality: Panadura River estuary, Madu Ganga estuary, Balapitiya and Ratgama Lake, Dodanduwa, Sri Lanka).

Ficopomatus enigmaticus (*non* Fauvel 1933) – Lakshmana Rao 1969: 16–17, pl. 13, figs a–g (Visakhapatnam and Cochin, India; harbours).

Ficopomatus uschakovi – ten Hove & Weerdenburg 1978: 109–112, figs 2a–d, 3a, f–k, 4j–n, r, x–z, jj–mm, yy, 5d (revision of the genus and specimens from Sri Lanka, India, Indonesia, Philippines, Solomon Islands, Australia, Nigeria, Ivory Coast, and Netherlands; in freshwater creek and brackish lagoon, on pebble, coconut petiole, and barnacles). — de Assis *et al.* 2008: 51–58, fig. 2A–G (Sossego Creek, eastern Brazil; brackish water). — Bastida-Zavala & García-Madrigal 2012: 48–52, figs 1A–E, 2A–I (La Encrucijada Lagoon, Chiapas, southern Mexican Pacific; brackish water, 20–35‰, intertidal to 1 m; on mangrove root and gastropod shell). — Liñero-Arana & Díaz-Díaz 2012: 234–237, fig. 1a–j (Gulf of Paria, Venezuela; brackish water). — Arteaga-Flórez *et al.* 2014: 1–11, fig. 2A–F (Gulf of Urabá, Colombian Caribbean; brackish water). — Bastida-Zavala *et al.* 2016: 410–411, figs 3, 10G (La Encrucijada Lagoon, Chiapas, southern Mexican Pacific; on wooden trunk, salinity = 19.39‰).

Material examined

73 specimens: JX (2) Aug. 2001, BB (26) Aug. 2004, GB (32) Sep. 2002, CC (13) Sep. 2002.

Additional material

33 specimens: UMAR-Poly 113, 20 specimens (La Encrucijada Biosphere Reserve, Zacapulco, Chiapas, southern Mexican Pacific; brackish water, intertidal to 0.5 m, on mangrove root and gastropod shell, 21 Sep. 2011, col. R. Bastida-Zavala); LACMNH N10947, 11 specimens (Panadara River estuary, Ceylon, brackish water, 9 Oct. 1961, coll. G. Pillai); USNM 186523, 2 specimens (Pascagoula River, Mississippi, 2.5 m, 11 Nov. 1997, coll. J. McLelland).

Diagnosis

This species is gregarious and can form small colonies. Tube white to pinkish, sometimes covered by a dark film of microalgae; with small peristomes and three longitudinal ridges; without transverse ridges or alveoli (Fig. 2L). Opercular peduncle smooth, white or, sometimes, proximal section of operculum with black or brownish spots. Operculum spherical, with a horny plate and 1–4 rows of yellowish or colorless single spines, curving outwards (Fig. 2M–N); sometimes external row of larger spines forms an incomplete circle on operculum. Thoracic membrane fused dorsally (Fig. 2O). Special collar chaetae coarsely serrated.

Measurements: Total length = 5.6 mm (n = 9, r: 3.5–9.1, SD = 2.2); thorax length = 1.6 mm (n = 11, r: 1.1–2.5, SD = 0.4), thorax width = 0.6 mm (n = 11, r: 0.3–0.8, SD = 0.1); peduncle and operculum length = 1.3 mm (n = 10, r: 0.7–2.4, SD = 0.6); operculum length = 0.4 mm (n = 11, r: 0.2–0.6, SD = 0.1); operculum diameter = 0.5 mm (n = 11, r: 0.3–0.6, SD = 0.1).

Taxonomic remarks

J. McLelland, on November 1997, collected the first specimens in the United States (USNM 1866523), from Pascagoula River, Mississippi, on settlement plates suspended near the bottom within the salt wedge (11.8–19.2‰), at 2.5 m depth. Hartmann-Schröder (1971) recorded *Ficopomatus uschakovi* from the Gulf of Guinea, although Rullier (1955) recorded the species earlier, as *F. enigmaticus*, from Abidjan, the Ivory Coast. Ten Hove & Weerdenburg (1978) revised material from Lagos, Nigeria, and Abidjan, Ivory Coast, and concluded that only *F. uschakovi* is established in tropical western Africa; they found many specimens attached to pieces of wood. Moreover, several tubes and dried opercula were collected from wood cast ashore on beaches in the Netherlands in 1974; however, ten Hove & Weerdenburg (1978) do not consider this as real evidence of invasion, due to the brisk local trade in tropical wood. Excluding this last incidental record, there are no additional records in Europe. Being a tropical species, it probably can not survive winter temperatures in western Europe.

Styan *et al*. (2017) recorded a population in Southeast Australia they determined to be *Ficopomatus* cf. *uschakovi*, with an operculum similar to that of the nominal species; however, the thoracic membranes are not fused, one of the distinguishing characteristic of *F. uschakovi sensu stricto*, so it is possible that it is a new or cryptic species.

Juvenile specimens of *F. uschakovi*, *F. miamiensis* and *F. enigmaticus* can easily be confused because the operculum lacks spines (ten Hove & Weerdenburg 1978). In general, the characteristic spines of *F. uschakovi* and *F. enigmaticus* (Fig. 2G, 2M–N) were always observed in specimens examined in this work, decreasing the possibility of incorrect identifications. In some cases, assemblages of *F. uschakovi* with *F. enigmaticus*, or *F. miamiensis*, and even with *Hydroides dianthus*, were observed.

Ecology

Intertidal to sublittoral (2.5 m). In tropical freshwater creeks and brackish water lagoons, on mangrove roots, pebbles, coconut petioles, barnacles, gastropod shells and artificial substrates (ten Hove & Weerdenburg 1978; Bastida-Zavala & García-Madrigal 2012).

Distribution

Indo-Pacific and western Africa (Nigeria and Ivory Coast). Recently recorded from Brazil, Venezuela, Colombian Caribbean and Chiapas, southern Mexican Pacific (de Assis *et al.* 2008; Bastida-Zavala & García-Madrigal 2012; Liñero-Arana & Díaz-Díaz 2012; Arteaga-Flórez *et al.* 2014). In this work, *Ficopomatus uschakovi* was found abundantly on fouling plates from Biscayne Bay, Florida and Galveston Bay, Texas and occasionally from Jacksonville, Florida and Corpus Christi, Texas (Fig. 3). *Ficopomatus uschakovi* is recorded formally for the first time from Texas (Galveston Bay and Corpus Christi), Pascagoula River, Mississippi, and eastern Florida (Biscayne Bay and Jacksonville). The nearest record in the western Atlantic is the Gulf of Urabá, Colombian Caribbean (Arteaga-Flórez *et al.* 2014), 2000 km to the south of Biscayne Bay, Florida.

Genus ***Hydroides*** Gunnerus, 1768

Hydroides bispinosa Bush, 1910

Figs 4A, 5

Hydroides bispinosa Bush, 1910: 496 (type locality: Bermuda, western Atlantic).

Hydroides crucigera (*non* Mörch 1863) – Rioja 1958: 250–251 (Verde Island and Santiaguillo Island, Veracruz, eastern Mexico; on coral and mollusk shells). — Day 1973: 132 (Cape Hatteras and Beaufort, North Carolina; intertidal to 18 m).

Hydroides bispinosus – Díaz 1994: 618 (Barbados; settlement and succession experiments; 10 m; coral plates, on *Montastrea annularis,* now *Orbicella annularis* (Ellis & Solander, 1786)). — Perkins 1998: 95 (checklist of shallow-water polychaetes from Florida). — Bastida-Zavala & Salazar-Vallejo 2000b: 844, fig. 1b–l (La Habana, Cuba, and eastern Mexico: Champotón, Campeche; Ría Lagartos and San Felipe, Yucatán; Contoy Island, Nichupté Lagoon and Cozumel Island, Quintana Roo; intertidal to 4 m, on seagrass, algae, sponges, rocks, wood dock pilings). — Bastida-Zavala & ten Hove 2002: 125–127, figs 11A–I, 15 (Bermuda, Florida, Aruba and eastern Mexico: Campeche and Quintana Roo; 1–15 m, on pagurid carapace, rocks, wooden pier and coral debris).

Hydroides bispinosa – Wells & Gray 1964: 74 (Cape Hatteras, North Carolina; hard substrates). — ten Hove & Wolf 1984: 55-18–55-21, figs 55-13, 55-14a–m (western Florida; 19–43 m, coarse to silty sand).

Hydroides sanctaecrucis (*non* Krøyer in Mörch 1863) – Díaz-Díaz & Liñero-Arana 2001: 11, 13–14, figs 2a–f, 3g–l (Cariaco Gulf, Venezuela; on PVC dock pilings; description and figure).

Material examined

Eight specimens: BB (8) Aug. 2004.

Diagnosis

Tube white; with two longitudinal ridges; without peristomes, transverse ridges or alveoli. Opercular peduncle smooth, white. Operculum funnel with 12–19 radii with blunt tips (Fig. 4A); verticil with 7–10 spines, curving abruptly inwards, almost geniculate, tip of spines pointed; dorsal spines somewhat longer; all spines with basal internal spinule and two lateral spinules in middle position, without external spinules, wings or central tooth (Fig. 4A). Special collar chaetae with two pointed-elongate teeth and distal blade with small teeth.

Taxonomic remarks

Rioja (1958) recorded *Hydroides crucigera* Mörch, 1863 from Veracruz, eastern Mexico, a species similar to *H. bispinosa* because of the presence of two lateral spinules in the verticil spines (Fig. 4A). However, from their brief description it is possible to deduce by the small number of funnel radii (14) that the specimen corresponds to *H. bispinosa* rather than to *H. crucigera*.

Hydroides bispinosa is frequently associated with calcareous substrates and occasionally found on PVC substrates (Díaz-Díaz & Liñero-Arana 2001). Weisbord (1964: 156) collected an empty tube from northern Venezuela, as *H.* aff. *bispinosa*, but identification to species with only the tube, in the genus *Hydroides* is doubtful.

Ecology

Intertidal to sublittoral (43 m, ten Hove & Wolf 1984). In tropical and subtropical marine areas, on coral, mollusk shells, seagrass, algae, sponges, rocks and artificial substrates

(Rioja 1958; Díaz 1994; Díaz-Díaz & Liñero-Arana 2001; Bastida-Zavala & Salazar-Vallejo 2000b; Bastida-Zavala & ten Hove 2002).

Distribution

Gulf of Mexico, Caribbean Sea and eastern United States. In this work, *Hydroides bispinosa* was occasionally found on fouling plates from Biscayne Bay, Florida (Fig. 5).

Hydroides cf. ***brachyacantha*** Rioja, 1941a

Figs 4B, 5

Hydroides cf. *brachyacanthus* – Bastida-Zavala & ten Hove 2002: 154–155, figs 29A–K, 31A–D, 33 (Curaçao, Venezuela and Grenada; intertidal to 20 m, on *Rhizophora* and *Thalassia*, mud and sand, and a destroyer hull).

Hydroides brachyacantha (*non* Rioja 1941a) – Zibrowius 1970: 6 (São Sebastião, Ubatuba, Brazil; 6–15 m, rocks, corals and gorgonians). — Díaz-Díaz & Liñero-Arana 2001: 11–12, fig. 2g–m (Cariaco Gulf, Venezuela; on PVC dock pilings).

Material examined

Seven specimens: BB (1) Aug. 2004, PB (6) Aug. 2002.

Diagnosis

Tube white; without peristomes, transverse ridges, longitudinal ridges or alveoli. Opercular peduncle smooth, white. Opercular funnel with 19–30 radii with pointed tip (Fig. 4B); verticil with 7–8 spines, strongly curving inwards; dorsalmost spine larger; all spines with basal internal spinule, without external and lateral spinules, or wings (Fig. 4B). Special collar chaetae with two blunt, short teeth and smooth distal blade.

Taxonomic remarks

The nominal species, *Hydroides brachyacantha*, has been recorded in various parts of the world including Australia (Dew 1959; Straughan 1967; Kupriyanova *et al.* 2006), Hawaii (Straughan 1969; Bailey-Brock 1976, 1987; Bastida-Zavala & ten Hove 2003; Carlton & Eldredge 2009), Palau and Yap Islands (Imajima 1982), Truk and Ponape Islands, and Majuro Atoll (Imajima & ten Hove 1984), Solomon Islands (Imajima & ten Hove 1986), Israel (Ben-Eliahu 1991; Ben-Eliahu & ten Hove 1992), northeastern Venezuela (Díaz-Díaz & Liñero-Arana 2001) and Turkey (Çinar 2006).

However, most of the records of *H. brachyacantha* from Australia belong to a new species recently described from Australia, *H. amri* Sun, Wong, ten Hove, Hutchings, Williamson & Kupriyanova, 2015. The records from Hawaii also belong to a similar species, recently reported as *H.* cf. *amri* (Bastida-Zavala *et al.* 2016). The specimens recorded from Turkey apparently belong to *H. brachyacantha sensu stricto*, which might have reached the Turkish coast via ship-borne fouling (Çinar 2006, fig. 2). Due to the absence of a holotype, a specimen collected from the type locality (Mazatlán, Mexico) was designated as the neotype (Sun *et al.* 2016b).

While the specimens recorded from the western Atlantic also resemble *H. brachyacantha*, they do not have the characteristic large knobs on the verticil spines of the nominal species (Bastida-Zavala & ten Hove 2003: figs 3A, C, G–K), nor the small "sharp to round knob" of *H. amri* (Sun *et al.* 2015: fig. 3A–B). Apparently, in the Caribbean there are two forms of *H.* cf. *brachyacantha*, one from Grenada with a large dorsal spine and six smaller spines on the rest of the verticil (Bastida-Zavala & ten Hove 2002: fig. 29A–C), and the other from Brazil and Venezuela, with dorsal spines smaller than those in Grenada's specimens

(Bastida-Zavala & ten Hove 2002: fig. 29D–F). The specimens examined in this survey (Fig. 4B) are more similar to the Brazilian and Venezuelan form.

Ecology

Intertidal to sublittoral (20 m). In tropical marine areas, on mangrove, seagrass, rocks, corals and gorgonians, and artificial substrates (Zibrowius 1970; Díaz-Díaz & Liñero-Arana 2001; Bastida-Zavala & ten Hove 2002).

Distribution

Eastern Caribbean to southeastern Brazil (Zibrowius 1970; Bastida-Zavala & ten Hove 2002). In this work, *Hydroides* cf. *brachyacantha* was occasionally found on fouling plates from Biscayne Bay and Pensacola Bay, Florida (Fig. 5). This species extends its northward range from Curaçao, southern Caribbean (Bastida-Zavala & ten Hove 2002) to Pensacola Bay, Florida (2700 km).

Hydroides dianthus (Verrill, 1873)

Figs 4C, 5

Serpula dianthus Verrill, 1873: 620 (type locality: New Jersey to Massachusetts, United States).

Serpula hexagona Bosc, 1801: 205 (type locality: Charleston, South Carolina, United States; on oyster shells). — Zibrowius 1971: 697, 699 (name indeterminable; the tube description does not match *H. dianthus*, but records on the US east coast are misidentified and really belong to *H. dianthus*). — Read *et al*. 2016: 22–23 (name no longer in use and representing a *species inquirenda*).

Hydroides (Eupomatus) dianthoides Augener, 1922: 49–50 (specimens from Veracruz, eastern Mexico; partial synonymy).

Serpula dianthus – Treadwell 1891: 276–280 (Long Island, New York; anatomy and histology). — Wilson 1905: 119 and table (fossil records from Pleistocene of Sankaty Head, Nantucket, Massachusetts; abundant tubes). — Oldale *et al.* 1982: fig. 5 (same).

Eupomatus dianthus – Richards 1933: 198 and table (fossil records from Cape May Formation, an interglacial warm stage from New Jersey). — Hartman 1945: 48, pl. 10, fig. 1 (North Carolina; under stones, shell fragments); 1951: 118–119 (Southwestern Florida, Louisiana, South Texas; intertidal, snail shell, rocks). — Rioja 1958: 260–262 (Sacrificios and Verde Islands, Veracruz, eastern Mexico; on rocks, mollusk shells, corals and ship hulls). — Wells & Wells 1961: 152, 154–155, Beaufort, off Portsmouth Island and Pamlico Sound, North Carolina; 3.5–11 m, salinity 15–25‰; associated with the gastropod *Fargoa dianthophila* (Wells & Wells, 1961) (previously in the genus *Odostomia*). — Wells & Gray 1964: 74 (Cape Hatteras, North Carolina; hard substrates). — Wells & Wells 1969: 109–110 (North Carolina; Buzzard's Bay, Massachusetts; Panama City, Alligator Harbor and Cedar Key, Florida; associated with *F. dianthophila*).

Hydroides dianthus – Webster & Benedict 1884: 737 (Massachusetts; intertidal, on shells). — Benedict 1887: 549, pl. 20, fig. 10 (Chesapeake Bay; on living oysters, shells and stones). — Cushman 1906: 9 (fossil records from Pleistocene of Sankoty Head, Nantucket). — Roberge 1968: 145 (Buzzard's Bay, Massachusetts; subtidal rocks; as host of parasite gastropod *F. dianthophila*). — Zibrowius 1971: 697–705 (east coast of United States, Atlantic France, Mediterranean and Senegal, Western Africa; 1–189 m, salinity 18–50‰, temperature 5–30°C; on sand and the seagrass *Posidonia*, bryozoan nodules and oysters). — Day 1973: 132 (Cape Hatteras to South Carolina; intertidal to 30 m). — Robertson & Mau-Lastovicka 1979: 323 (Woods Hole; "host" of *Fargoa bartschi* (Winkley, 1909)). — Haines & Maurer 1980a: 646–647 (Delaware Bay; 6 m, salinity 23.3–28.3‰, temperature 3–25.4°C, on muddy sand); 1980b: 44–46 (Delaware Bay; invertebrates associated with *H. dianthus*; same data as 1980a). — ten Hove & Wolf 1984: 55-21, figs 55-15, 55-16a–j (western Florida; 22 m, medium sand). — ten Hove & van den Hurk 1993: 41–42, fig. 4B, D (Baffin Bay

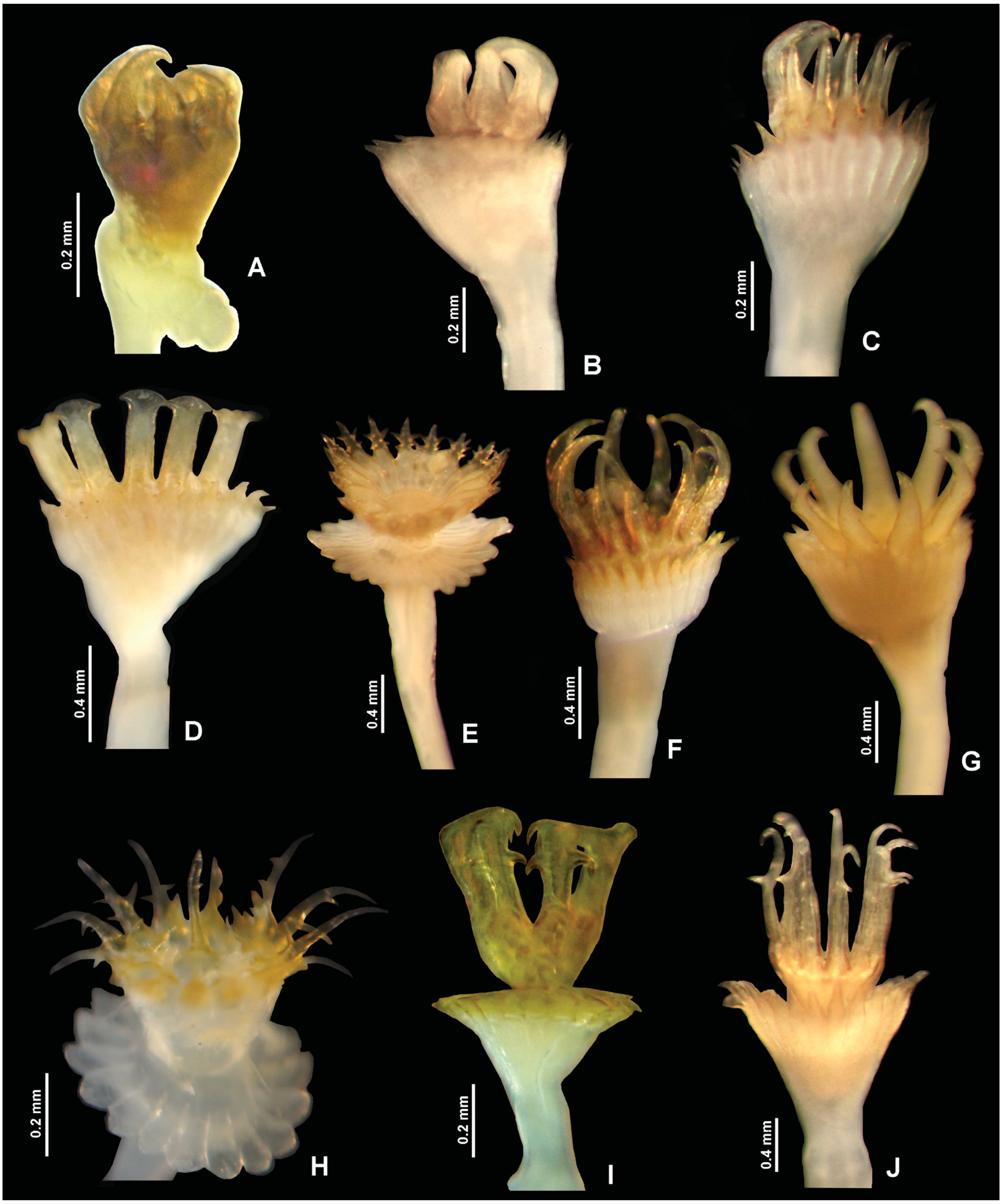

Fig. 4. Serpulids from United States fouling plates. *Hydroides bispinosa*. **A**. Operculum, from Biscayne Bay, Florida (SERC-118756). – *H.* cf. *brachyacantha*. **B**. Operculum, Pensacola Bay, Florida (SERC-92415). – *H. dianthus*. **C**. Operculum, Corpus Christi, Texas (SERC-87878RB). – *H. dirampha*. **D**. Operculum, Biscayne Bay, Florida (SERC-118709). – *H. elegans*. **E**. Operculum, San Diego, California (SERC-04075R). – *H. floridana*. **F**. Operculum, Corpus Christi, Texas (SERC-87968). – *H. gracilis*. **G**. Operculum, San Diego, California (SERC-34585R). – *H. longispinosa*. **H**. Operculum, Oahu, Hawaii (SERC-19654). – *H. parva*. **I**. Operculum, Biscayne Bay, Florida (SERC-118709). – *H. sanctaecrucis*. **J**. Operculum, Tampa Bay, Florida (SERC-66920R).

and Corpus Christi, Texas; 0.6–2.4 m and in concrete tunnels supplying cooling water to a power station; salinity average 51.7‰). — Perkins 1998: 95 (checklist of shallow-water polychaetes of Florida). — Bastida-Zavala & Salazar-Vallejo 2000b: 845, fig. 1m–u (eastern Mexico: San Juan de Ulúa, Veracruz; Champotón, Campeche; Celestún Beach, Ría Lagartos and San Felipe, Yucatán; Contoy Island, Nichupté Lagoon and Yalahau Lagoon, Quintana Roo; 0.5–4 m; on seagrass, algae, sponges, rocks, fort wall covered with vermetids, oysters and ascidians, wood dock pilings). — Sun & Yang 2000: 120–121, fig. 2e–k (China). — Bianchi & Morri 2001: 216–218 (Orbetello Lagoon, Italy; reef-builders, competitor with *Ficopomatus enigmaticus*; salinity 13–48‰, temperature 7–30°C). — Toonen & Pawlik 2001: 104–112 (Wrightsville Beach, North Carolina; gregarious and non-gregarious settlement; intertidal). — Bastida-Zavala & ten Hove 2002: 143–146, figs 23A–M, 24A–K, 28 (Connecticut, Massachusetts, North Carolina, and eastern Mexico: Veracruz, Yucatán and Quintana Roo; 0.6–28 m, salinity 1–34‰, on oysters, rocks and wooden pier). — Link *et al.* 2009: 1–6, figs 1a–g, 2 (Tokyo Bay, Japan, as NIS; 0.8 m, on PVC plates). — Otani & Yamanishi 2010: 63–64, fig. 3a–g (Osaka Bay, Japan, as NIS; seasonal change in densities; intertidal to 4 m, salinity 26.5–32.3‰, temperature 17.7–19.1°C; on concrete blocks). — Ben-Eliahu & ten Hove 2011: 14–16 (Cyprus; 0.3 m, from ship propeller). — Boltachova *et al.* 2011: 34–38 (Crimea, Black Sea). — Sun *et al.* 2016a: poster (discussion as global invader or a complex of species).

Hydroides (Eupomatus) dianthoides – Bastida-Zavala & ten Hove 2002: 143 (partial synonymy).

Material examined

1787 specimens: RI (108) Sep. 2001, CB (352) Sep. 2000 and Aug. 2012, CH (117) Sep. 2004, JX (99) Aug. 2001, IR (99) Aug. 2005, BB (78) Aug. 2004, TB (38) Jun. 2012, PB (323) Aug. 2002, GB (356) Sep. 2002, CC (217) Sep. 2002.

Diagnosis

This species is gregarious and can form small colonies. Tube white, with two longitudinal ridges; lacks peristomes, transverse ridges or alveoli. Opercular peduncle smooth, white. Opercular funnel with 24–37 radii with pointed tips (Fig. 4C); verticil with 8–13 spines, all curving ventrally, with one basal internal spinule, without external and lateral spinules or wings (Fig. 4C). Special collar chaetae with two blunt, short teeth and smooth distal blade.

Taxonomic remarks

Hartman (1945, 1951) mentioned that the distribution of *Hydroides dianthus* includes the West Indies; the only record of this subtropical species, in the Caribbean Sea, is from Weisbord (1964: 158), who collected several empty tubes from northern Venezuela, as *H.* cf. *dianthus*, but species identification with only the tube in the genus *Hydroides*, is doubtful.

Hydroides dianthus was recorded, as *Eupomatus,* by Holguín-Quiñones (1994) from Socorro Island, in the Mexican Pacific; however, the record is indeterminable because it lacks a description and figures, and the specimens were not deposited in a collection (Holguín-Quiñones, pers. comm. 2011; Bastida-Zavala *et al.* 2016: 418).

By far, *Hydroides dianthus* is the most abundant species (1787 specimens) on fouling plates from the 10 localities on the east coast of the United States and northern Gulf of Mexico (Table 1). In one sample from the northern Gulf of Mexico, two of four specimens had an operculum with red verticil spines (see also *H. floridana* (Bush, 1910)), a character never seen before.

In Delaware Bay and Virginia's coastal lagoons (Haines & Maurer 1980a: 647), *H. dianthus* builds tube clusters (10–400 cm^3) and at the former site the clusters harbor up to 54 invertebrate species (Haines & Maurer 1980b). The gregarious settlement of this species was studied in North Carolina

(Toonen & Pawlik 2001) and the Mediterranean, where *H. dianthus* builds large reefs in coastal lagoons (Bianchi & Morri 2001). It competes with other NIS, such as *Ficopomatus enigmaticus*, at several sites in the Mediterranean (Zibrowius 1973; Bianchi & Morri 2001).

Due to its euryhaline (1–51.7‰) and eurythermic (3–30°C) tolerances, *H. dianthus* has successfully invaded many harbors around the world. However, in Osaka Bay Otani & Yamanishi (2010) found that salinities above 30‰, combined with biological interactions with macroalgae or mussels, may be limiting the distribution of *H. dianthus*.

Hydroides dianthus, previously considered native to the US east coast (Bosc 1801; Verrill 1873), should be considered cryptogenic (see the 'Cryptogenic species' section in the Discussion below).

Ecology

Intertidal to sublittoral (189 m). In subtropical and tropical marine and brackish waters; salinities of 1–51.7‰, temperature 3–30°C (Zibrowius 1971; Haines & Maurer 1980a; Bianchi & Morri 2001); on rocks, mollusk shells, corals, seagrass, algae, sponges and artificial substrates (Rioja 1958; Zibrowius 1971; Bastida-Zavala & Salazar-Vallejo 2000b; Bastida-Zavala & ten Hove 2002; Ben-Eliahu & ten Hove 2011); also associated with the gastropods *Fargoa dianthophila* and *F. bartschi* (Robertson & Mau-Lastovicka 1979; Wells & Wells 1969). *Fargoa dianthophila* was considered a parasite of *Hydroides dianthus* by Roberge (1968).

Distribution

East coast of United States, Bermuda, Gulf of Mexico, Mexican Caribbean, Mediterranean, European Atlantic, Senegal (western Africa), Japan (Zibrowius 1971; Bastida-Zavala & ten Hove 2002; Link *et al.* 2009; Otani & Yamanishi 2010), China, Brazil and Black Sea (Sun & Yang 2000; Boltachova *et al.* 2011; Sun *et al.* 2016a). In this work, *Hydroides dianthus* was found abundantly and frequently on fouling plates from Narragansett Bay, Rhode Island; Chesapeake Bay, Virginia; Charleston, South Carolina; Jacksonville, Indian River, Biscayne Bay, Tampa Bay and Pensacola Bay, Florida; and Galveston Bay and Corpus Christi, Texas (Fig. 5).

Hydroides dirampha Mörch, 1863

Figs 4D, 5

Hydroides (Eucarphus) dirampha Mörch, 1863: 379, pl. 11, fig. 10 (type locality: St. Thomas, Lesser Antilles, Caribbean).

Hydroides (Eucarphus) benzoni Mörch, 1863: 380, pl. 11, fig. 11 (type locality: Bahia, Brazil; on the gastropod *Purpura haemastoma*, now *Stramonita haemastoma* (Linnaeus, 1767)).

Hydroides (Eucarphus) cumingii navalis Mörch, 1863: 379 (type locality: New Zealand).

Eupomatus lunulifer Claparède, 1870: 181–182 (type locality: Gulf of Naples, Italy; hull of a vessel in refit).

Eucarphus serratus Bush, 1910: 495–496 (type locality: Bermuda).

Hydroides malleophorus Rioja, 1942: 126–130, figs 7–14 (type locality: Mazatlán, Sinaloa, Mexican Pacific; on rocks).

Hydroides (Eucarphus) cumingii – Ehlers 1905: 70–72 (Oahu, Hawaii; harbor).

Hydroides sp. – Treadwell 1914: 226, pl. 12, fig. 48 (Hawaii; yacht bottom).

Hydroides lunulifera – Monro 1933: 1082 (Colon, Atlantic side of Panama; on pier pilings). — Edmonson & Ingram 1939: 268–271 (Kaneohe Bay and Pearl Harbor, Oahu, Hawaii; pier fouling). — Edmonson 1944: 3–16 (Pearl Harbor, Oahu, Hawaii; fouling experiments; 0–4 m). — Rioja 1961: 310–311 (Antón Lizardo Beach, Veracruz, eastern Mexico; on ascidians). — Straughan 1969: 232 (Oahu, Hawaii, samples from 1929 to 1968; intertidal to 1.5 m). — Nelson-Smith 1967: 31, fig. 16 (Panama Canal). — Lakshmana Rao 1969: 5–6, pl. 3, figs a–g (Visakhapatnam and Madras, now Chennai, India; harbours).

Hydroides dirampha – Zibrowius 1971: 705–707, figs 6–9 (Italy, Bermudas, Florida, Lesser Antilles, Veracruz, eastern Mexico, Panama, Venezuela, Brazil, South Africa, Java, Hawaii and New Zealand; intertidal to 90 m; on scleractinian corals *Cladocora arbuscula* (Le Sueur, 1820) and *Astrangia* sp.; on pier and hull of boat). — Long 1974: 28 (Oahu, Hawaii; 9–36 m; fouling plates). — Bailey-Brock 1976: 77–78 (Oahu Island and Hawaii Island; reef flats, epifauna of mobile substrata (mollusks and crustaceans), boat harbors and lagoons and reef slope). — Imajima 1978: 54–56, fig. 3a–j (Ō-shima Island; intertidal); 1979: 168–169 (Kushimoto Harbour, southern Japan; on rope). — Dueñas 1981: 100, fig. 30A–F (Cartagena Bay, Colombia; on cement wall and plastic tubes related to shrimp culture ponds). — Bailey-Brock 1987: 420 (Hawaii). — Zibrowius 1992: 91 (discussion about its origin in tropical American Atlantic). — Bastida-Zavala 1993: 35 (Gulf of California: Caimancito Beach, La Paz Bay, Baja California Sur; rocks and sand). — Perkins 1998: 95 (checklist of shallow-water polychaetes of Florida). — Dueñas 1999: 14 (Cartagena Bay, Colombia). — Díaz-Díaz & Liñero-Arana 2001: 12–13 (Cariaco Gulf, Venezuela; PVC dock pilings).

Hydroides diramphus – Bastida-Zavala & Salazar-Vallejo 2000b: 845–846, figs 2a–d (San Juan de Ulúa, Veracruz, eastern Mexico; 1–1.5 m; on wall with vermetids, oysters and ascidians). — Bastida-Zavala & ten Hove 2002: 161–164, figs 34A–P, 36 (Bermuda, Veracruz, eastern Mexico, Curaçao, Atlantic Panama, Venezuela and Brazil; intertidal to 23 m; on *Rhizophora*, salinity: 31–37‰); 2003: 83–86, fig. 10A–L (southern California, Hawaii and Baja California Sur, Mexican Pacific; intertidal to 1 m; on pier piling and rocks on sand). — Rodríguez-Valencia 2004: 520 (Petacalco Bay, Guerrero, southern Mexican Pacific; 3–21 m). — Çinar 2006: 226, fig. 3A–C (as NIS from eastern Levantine coast of Turkey). — Bastida-Zavala 2008: 25, fig. 6G (Hawaii, southern California and Sinaloa, Mexican Pacific; intertidal to 2 m). — Carlton & Eldredge 2009: 61–62 (Hawaii; invasion history). — Ben-Eliahu & ten Hove 2011: 17–19, figs 4, 5A–C (Israel, Egypt, Suez Canal and Red Sea; 0.3–10 m; on algae (*Digenea* C. Agardh), sponges, mollusks (*Brachidontes pharaonis* (P. Fischer, 1870), *Crenatula picta* (Gmelin, 1791), and *Pinctada radiata* (Leach, 1814)), rocks, artificial substrates such as a barge, tin can, rubber fenders, iron frames and ship hulls). — Tovar-Hernández *et al.* 2012: 14–15 (Gulf of California: Guaymas, Sonora); 2014: 388, 390, fig. 2g (Gulf of California: Guaymas, Sonora, and La Paz, Baja California Sur). — Sun *et al.* 2015: 20–21, fig. 5a–b (New South Wales, Queensland and Western Australia; 0.5–11.8 m; on sand bottom, rocks, cement and wooden pilings, fouling plates and ship hulls). — Bastida-Zavala *et al.* 2016: 418–419, figs 4, 11E (Mexican Pacific: Baja California Sur and Oaxaca; intertidal to 1 m; in marinas and harbors, fouling).

Material examined

150 specimens: JX (6) Aug. 2001, IR (78) Aug. 2005, BB (5) Aug. 2004, CC (19) Sep. 2002, SD (41) Aug. 2000, HI (1) Aug. 2006.

Additional material

Four specimens: UMAR-Poly 63, 4 specimens (Hawaii inter-island cargo barge, HF-023, hull fouling community roughly two years old; barge only operates in Hawaii, coll. S. Godwin).

Diagnosis

Sometimes this species is gregarious. Tube white, with 2–3 longitudinal ridges, with transverse ridges, with or without peristome rings; but not alveoli. Opercular peduncle smooth, white. Opercular funnel with 25–39 radii with pointed tips (Fig. 4D); verticil with 11–17 spines, straight, with tip T-shaped and flattened, with one basal internal spinule, without external and lateral spinules or wings (Fig. 4D). Special collar chaetae with two pointed-elongate teeth and smooth distal blade.

Taxonomic remarks

While formerly considered to be native to the Caribbean (Zibrowius 1992; Ben-Eliahu & ten Hove 2011), *Hydroides dirampha* may actually be native to the tropical eastern Pacific (Sun *et al.* 2015). Bastida-Zavala & ten Hove (2002) recorded the species from the Caribbean, at both undisturbed and polluted sites, while Rioja (1942) and Bastida-Zavala (1993) recorded the species from the Mexican Pacific, only at undisturbed sites, but close to harbors (Mazatlán and La Paz, respectively). Recent surveys in the Mexican Pacific (Tovar-Hernández *et al.* 2012, 2014; Bastida-Zavala *et al.* 2016), found *H. dirampha* frequently in marinas and harbors. *Hydroides dirampha* has been in Hawaii for at least 120 years (Ehlers 1905), and in southern California for 100 years (Treadwell 1914). Thus, molecular analyses of the different world-wide populations are needed to solve the problem of the origin of this species. In this work, *Hydroides dirampha* is considered a cryptogenic species.

Ecology

Intertidal to sublittoral (36 m). In subtropical and tropical marine and brackish waters; salinities of 31–37‰ (Bastida-Zavala & ten Hove 2002); on reef flats, epifauna of mobile substrata (mollusks and crustaceans), boat harbors and lagoons and reef slope (Bailey-Brock 1976); also on the gastropod *Stramonita haemastoma*, algae *Digenea*, sponges, the bivalves *Brachidontes pharaonis*, *Crenatula picta*, and *Pinctada radiata*, the scleractinian corals *Cladocora arbuscula* and *Astrangia* sp. (Zibrowius 1971), rocks, *Rhizophora*, and artificial substrates such as boat hulls, barges and ships, ropes, wood dock pilings, buoys, PVC plates, tin cans, rubber fenders and iron frames (Claparède 1870; Treadwell 1914; Long 1974; Imajima 1979; Bastida-Zavala & Salazar-Vallejo 2000b; Bastida-Zavala & ten Hove 2002; Ben-Eliahu & ten Hove 2011).

Distribution

Circum(sub)tropical. Caribbean Sea, Bermuda, Gulf of Mexico, Brazil, Hawaii, southern California, Mexican Pacific, Panama, Mediterranean, Suez Canal, South Africa, India, Java, Hong Kong, Philippines, Australia, New Zealand, southern Japan and Marshall Islands (Mörch 1863; Claparède 1870; Treadwell 1914; Fauvel 1932; Day 1967; Zibrowius 1971; Imajima 1978; Bastida-Zavala & ten Hove 2002, 2003; Çinar 2006; Bastida-Zavala 2008; Ben-Eliahu & ten Hove 2011; Bailey-Brock *et al.* 2012; Sun *et al.* 2012, 2015). In this work, *Hydroides dirampha* was found abundantly on fouling plates from the Indian River, Florida, and San Diego, California; and occasionally from Jacksonville and Biscayne Bay, Florida, Corpus Christi, Texas, and Oahu, Hawaii (Fig. 5). This species extends its northward range from Veracruz, eastern Mexico (Bastida-Zavala & ten Hove 2002) to Corpus Christi, Texas (940 km).

Hydroides elegans (Haswell, 1883)

Figs 4E, 5

Eupomatus elegans Haswell, 1883: 633, pl. 12, fig. 1 (type locality: Port Jackson [= Sydney], Australia).
Eupomatus pectinatus Philippi, 1844: 195, pl. 6, fig. R (type locality: Mediterranean).
Hydroides abbreviata Krøyer in Mörch, 1863: 377, pl. 11, figs 6–7 (type locality: Saint Croix Island, Lesser Antilles, Caribbean Sea).
Hydroides pacificus Hartman, 1969: 759–760, figs 1–5 (type locality: Velero IV, sta. 1454–42, from ship hull; central and southern California).

Hydroides norvegica (*non* Gunnerus 1768) – Edmonson & Ingram 1939: 268–271 (Kaneohe Bay and Pearl Harbor, Oahu, Hawaii; pier fouling). — Edmonson 1944: 3–16 (Pearl Harbor, Oahu, Hawaii; fouling experiments; 0–4 m). — Berkeley & Berkeley 1941: 56 (Newport Bay, southern

California; from piling). — Hartman 1952: 63–64, figs 1–2 (Corpus Christi Bay, Texas; bottom of a boat; some specimens with double funnel). — Renaud 1956: 35 (Miami, Florida; bottom of R/V Physalia). — Hartman 1961: 44 (Los Angeles harbor, southern California; fouling on hulls of ships). — Rioja 1961: 311 (Antón Lizardo Beach, Veracruz, eastern Mexico; on ascidians and shells). — Lakshmana Rao 1969: 5, pl. 2, figs a–g (Visakhapatnam and Madras, now Chennai, India; harbours).

Serpula vermicularis (*non* Linnaeus 1767) – Lakshmana Rao 1969: 2–3, pl. 1, figs a–g (Visakhapatnam and Madras, now Chennai, India; harbours).

Hydroides elegans – Zibrowius 1971: 721–725, figs 56–64 (Mediterranean, Western Africa, South Africa, Mozambique, Java, Australia, Hawaii, California, Florida; extensive revision; intertidal to 6 m; on hull of boats). — Long 1974: 28 (Pearl Harbor, Oahu, Hawaii; 9 m; with little coverage on fouling plates). — Bailey-Brock 1976: 77–78 (Oahu Island and Hawaii Island; reef flats, on chlorophyte *Dictyosphaeria cavernosa* (Forsskål) Børgesen, epifauna of mobile substrata (mollusks and crustaceans), boat harbors and lagoons, brackish waters and reef slope). — Imajima 1976b: 237–238, fig. 3a–n (Tokyo Bay, Kanagawa Prefecture, Shizuoka Prefecture, Mie Prefecture, Wakayama Prefecture, Osaka Bay, Hiroshima Bay, Nagasaki Harbour, Amakusa Bay and Kagoshima Bay, Kochi Prefecture, Koniya Island, Japan; on the oysters *Pinctada fucata* (Gould, 1850), *Crassostrea gigas* (Thunberg, 1793) and *Pteria penguin* (Röding, 1798)); 1979: 169 (around Shionomisaki Cape and Kushimoto Harbour, southern Japan; 19–75 m; on shell, gravel and rope). — Dueñas 1981: 100–101, fig. 31A–G (Cartagena Bay, Colombia; on plastic pond related to shrimp culture). — Imajima 1982: 46 (Arumizu Bay, Palau Islands). — Bailey-Brock 1987: 420–421 (Hawaii). — Zibrowius 1992: 91 (discussion about its origin). — Nishi 1995a: 101–102 (southern Japan; on chelae and carapace of the crab *Charybdis riversandersoni* Alcock, 1899). — Ishaq & Mustaquim 1996: 170, fig. 5A–H (Karachi, Pakistan; intertidal, on rocks, buoy and boat hull). — Nishi 1996: 306–308 (Okinawa Island, Southwest Japan; buried in the coral *Montastrea* sp. and attached to dead coral, *Pocillopora damicornis* (Linnaeus, 1758)). — Perkins 1998: 95 (checklist of shallow-water polychaetes from Florida). — Dueñas 1999: 14 (Cartagena Bay, Colombia). — Bastida-Zavala & Salazar-Vallejo 2000b: 846–848, fig. 2e–f (eastern Mexico: San Juan de Ulúa, Veracruz; Champotón, Campeche; Celestún, Yucatán; and Contoy Island, Quintana Roo; 0.3–3.5 m; on calcareous rocks, seagrass and macroalgae, wood dock pilings, and fort wall cover with vermetids, oysters and ascidians). — Díaz-Díaz & Liñero-Arana 2001: 12 (Cariaco Gulf, Venezuela; PVC dock pilings). — Bastida-Zavala & ten Hove 2002: 164–166, figs 35A–J, 36 (Florida, Texas, Puerto Rico, Atlantic Panama, Aruba, Curaçao, and eastern Mexico: Veracruz, Campeche and Quintana Roo; intertidal to 7 m; 31–37‰; on coral debris, fouling of wood pier and boats). — Bastida-Zavala & ten Hove 2003: 86–87, fig. 11A–S (California and Hawaii; intertidal to 1 m; among algae and bryozoans, fouling of marina piers and ship and submarine hulls). — Rodríguez-Valencia 2004: 520 (Petacalco Bay, Guerrero, southern Mexican Pacific; 3–21 m). — Çinar 2006: 226–227, fig. 3D–E (as NIS from eastern Levantine coast of Turkey). — Bastida-Zavala 2008: 25–26, fig. 6H (California and Baja California Sur, Mexican Pacific; intertidal to 1 m, on PVC plates and hull of boats). — Carlton & Eldredge 2009: 62 (Hawaii; invasion history). — Díaz-Castañeda & Valenzuela-Solano 2009: 513 (west coast of Baja California Peninsula: Salsipuedes Bay, Baja California; vicinity of tuna farm sea-cages). — Tovar-Hernández *et al.* 2009: 331, figs 3l, 8a-c (as fouling species in Mazatlán, Sinaloa, Mexican Pacific). — Ben-Eliahu & ten Hove 2011: 19–25, figs 5D–E, 6–7 (Turkey, Cyprus, Israel, Egypt, Suez Canal and Red Sea; 0.2–10 m, on algae (*Cystoseira myrica* C. Agardh now *Polycladia myrica* (S.G. Gmelin) Draima, Ballesteros, F.Rousseau & T. Thibaut, *Digenea*, *Laurensia* and *Sargassum*), sponges, gastropods (*Murex forskoehli* Röding, 1798), bivalves (*Brachidontes pharaonis*, *Chama gryphoides* Linnaeus, 1758, *Chicoreus erythraeus,* now *Murex erythraeus* P. Fischer, 1870, *Crenatula picta*, *Fulvia fragilis* (Forsskål in Niebuhr, 1775), *Fusinus verrucosus* (Gmelin, 1791), *Malvufundus normalis* (Lamarck, 1819), now *Malleus anatinus* (Gmelin, 1791), *M. regulus* (Forsskål in Niebuhr, 1775), *Pinctada* *radiata*, *Spondylus spinosus* Schreibers, 1793 and Pectinidae), bryozoans, barnacles, crabs, tunicates, under rocks, artificial substrates such as canal walls, a tin can submerged in mud, rubber fenders and iron frames). — Tovar-Hernández *et al.* 2012: 16–17 (Gulf of California: Guaymas, Sonora and Topolobampo, Sinaloa); 2014: 388, 390 (Gulf of California: Topolobampo, Sinaloa; Guaymas, Sonora; La Paz, Baja California Sur). — Schwan *et al.* 2015: 3–6, fig. 2A–I (southeastern Brazil; intertidal to 1 m; fouling of harbors, marinas and PVC plates). — Sun *et al.* 2015: 23–29, fig. 6a–b (New South Wales, Northern Territory, Queensland, South and Western Australia; intertidal to 20 m; on scallop and mussel clumps on sandy bottom, fine mud, under rocks, unvegetated sediment, *Zostera*, *Caulerpa filiformis*, brown algae, on barnacles, cement and wooden pilings, floating pontoon, fouling plates, inside air-conditioning cooling pipe, and ship hulls). — Bastida-Zavala *et al.* 2016: 419–420, figs 4, 11F–G (Mexican Pacific: Baja California Sur and Oaxaca; in marinas and harbors, fouling; intertidal to 1 m).

Hydroides pacificus – Díaz-Castañeda 2000: 327 (west coast of Baja California Peninsula: Todos Santos Bay, Baja California; 10 m; terracota plates).

Material examined

384 specimens: IR (123) Aug. 2005, BB (1) Aug. 2004, TB (32) Jun. and Jul. 2012, HB (1) Sep. 2003, LB (87) Sep. 2003, MI (5) Jul. 2013, SD (87) Sep. 2000 and Jul. 2013, HI (48) Aug. 2006.

Additional material

18 specimens: LACMNH s.n., colony (southern California, 33°21'03" N, 118°19'55" W, off Avalon, Santa Catalina Island, Velero III, sta. 1377, grey sand, 110 m, 3 Aug. 1941, as *Serpula* sp.); LACMNH s.n., 1 specimen (southern California, 33°44'02" N, 118°32'03" W, 10 km from Pt Vicente lighthouse, Velero IV, sta. 2475, peel grab, mud, specimen attached to hexactinellid sponge, 740 m, 28 Oct. 1953); LACMNH

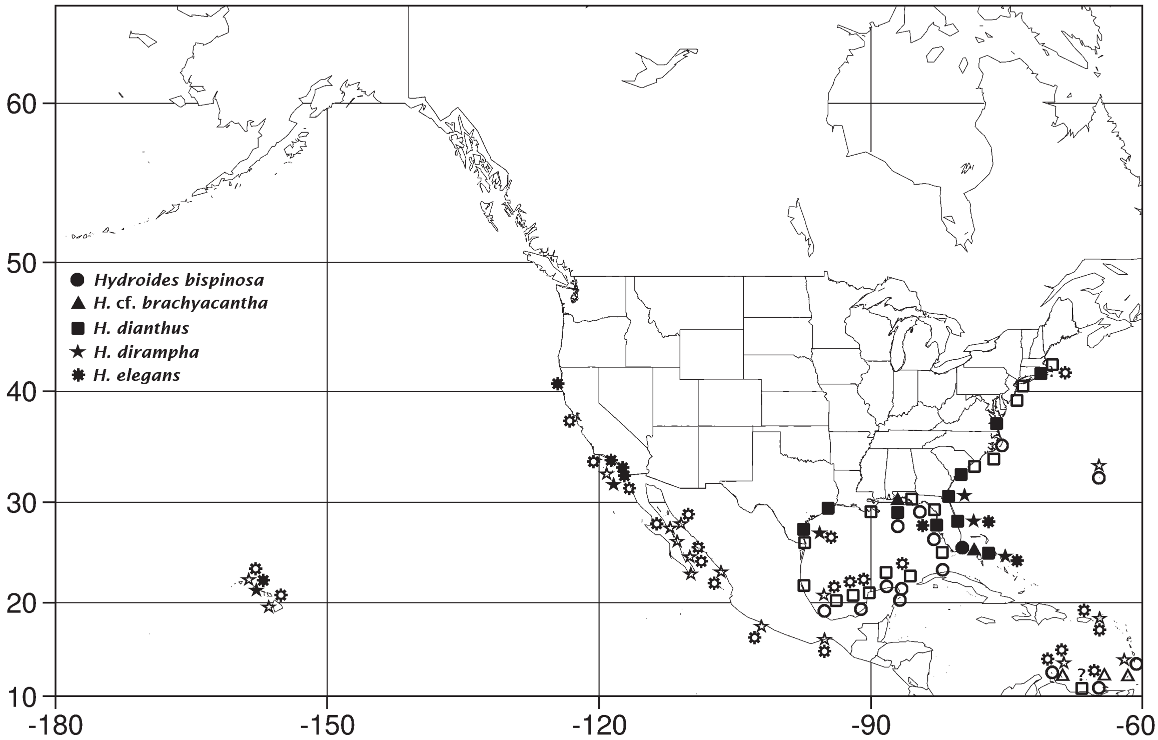

Fig. 5. Distribution of serpulids (*Hydroides* spp.) from United States fouling plates (closed symbols) and literature records (open symbols).

s.n., 1 specimen (southern California, 33°47'59" N, 118°33'59" W, 11.5 km from Palos Verdes Point, Velero IV, sta. 2792, Hayward grab, mud, 600 m, 22 May 1954); LACMNH s.n., 1 specimen (southern California, 33°14' N, 118°18'04" W, 6.9 km from East End Light, Santa Catalina Island, Velero IV, sta. 2850, Campbell grab, 1200 m, 23 Jun. 1954); MBL-SD s.n., 5 specimens (southern California, approx. 32°43' N, 117°13' W, San Diego, CSA P–161, 1 month plate, 7 Oct. to 7 Nov. 1974, as *H. pacificus*).

Diagnosis

This species is gregarious and can form small colonies. Tube white, with or without two longitudinal ridges, with or without peristomes; but not alveoli. Opercular peduncle smooth, white. Opercular funnel with 15–31 radii (21–35 in eastern Pacific specimens) with blunt tips (Fig. 4E); verticil with 11–18 spines, straight, with pointed tips (Fig. 4E); all spines with 0–4 internal spinules and 2–3 pairs of lateral spinules (2–5 in eastern Pacific specimens), without external spinules and/or wings (Fig. 4E). Special collar chaetae with two pointed-elongate teeth and a proximal rasp, distal blade with notch and many denticles.

Taxonomic remarks

Hydroides elegans now exhibits a world-wide distribution in tropical and subtropical ports, marinas and eutrophic lagoons (ten Hove 1974). Due to its rapid colonization and population growth, it is considered an invasive species (Zibrowius 1973, 1992, 1994; Tovar-Hernández *et al.* 2009, 2014). The main means of dispersal of this species is through fouling on boats and ships and/or as larvae in ballast water (Nelson-Smith 1967; Tovar-Hernández *et al.* 2009).

Although *H. elegans* was described from Australia (Haswell 1883), and Zibrowius (1992) and several authors speculate that it is native there (Ben-Eliahu & ten Hove 2011; Sun *et al.* 2015), this is not clear evidence of an Australian origin. Bastida-Zavala *et al.* (2016: 420) draw attention to the fact that both the Hawaiian (Long 1974; Bailey-Brock 1976) and Australian (Sun *et al.* 2015) records of this species were from both natural and man-made substrates, suggesting a broader Indo-West Pacific origin. However, there are also records of this species from both natural and artificial substrates in the Gulf of Mexico and Caribbean Sea (e.g., Hartman 1952; Bastida-Zavala & Salazar-Vallejo 2000b; Bastida-Zavala & ten Hove 2002). In addition, 20 years before *H. elegans* was described, Krøyer (in Mörch 1863) described *H. abbreviata*, a senior synonym of the former species, from Saint Croix, a Caribbean Island, suggesting a possible Caribbean origin as well. Finally, the oldest description of a senior synonym of *H. elegans* is *H. pectinatus*, described by Philippi in 1844, from the Mediterranean. One of these old names could take precedence over the name *H. elegans* (Principle of Priority, ICZN 1999, art. 23); however, nomenclatural stability will not promote the re-introduction of these oldest available names, and therefore the conditions for reversal of precedence are met (ICZN 1999, art. 23.9). To resolve the origin of this species, a molecular analysis of the different world-wide populations will be necessary. In this work, *Hydroides elegans* is considered a cryptogenic species.

Ecology

Intertidal to sublittoral (10 m). Some records off California (additional material from LACMNH) have questionable depth data (110–1200 m). In subtropical and tropical marine and brackish waters; salinities of 31–37‰ (Bastida-Zavala & ten Hove 2002); on reef flats, on chlorophytes, epifauna of mobile substrata (mollusks and crustaceans), boat harbors, lagoons and reef slope (Bailey-Brock 1976); on the oysters *Pinctada fucata*, *Crassostrea gigas* and *Pteria (Magnavicula) penguin* (Imajima 1976b); on the crab *Charybdis riversandersoni*, dead coral (*Pocillopora damicornis*) and buried in the coral *Montastrea* sp. (Nishi 1995a, 1996); also on rocks, seagrass, macroalgae (*Cystoseira myrica*, *Digenea*, *Laurencia* and *Sargassum*), sponges, gastropods (*Murex forskoehli*), bivalves (*Brachidontes pharaonis*, *Chama gryphoides*, *Chicoreus erythraeus*, *Crenatula picta*, *Fulvia fragilis*, *Fusinus verrucosus*, *Malvufundus normalis*, *M. regulus*, *Pinctada radiata*, *Spondylus spinosus* and Pectinidae), bryozoans, barnacles, crabs, tunicates, coral debris, under rocks, and on artificial substrates such as boat and ship hulls, cement and wood dock pilings, buoys, PVC or terracotta plates, canal walls, tin cans, rubber fenders and iron frames (Hartman 1952; Long 1974; Díaz-Castañeda 2000; Bastida-Zavala & Salazar-Vallejo 2000b; Bastida-Zavala & ten Hove 2002, 2003; Ben-Eliahu & ten Hove 2011).

Distribution

Worldwide in tropical to temperate waters. Western Atlantic: Caribbean Sea, Bermuda, Gulf of Mexico, Brazil; eastern Pacific: Hawaii, southern California, Mexican Pacific, Panama; other regions: Mediterranean, Suez Canal, western and South Africa, Mozambique, Pakistan, Java, Hong Kong, Australia, southern and central Japan, Palau Islands (Mörch 1863; Fauvel 1932; Day 1967; Zibrowius 1971; Imajima 1976b, 1979, 1982; Ishaq & Mustaquim 1996; Bastida-Zavala & ten Hove 2002, 2003; Çinar 2006; Bastida-Zavala 2008; Ben-Eliahu & ten Hove 2011; Sun *et al.* 2012, 2015). In this work, *Hydroides elegans* was found abundantly and frequently on fouling plates from the Indian River and Tampa Bay, Florida; Long Beach and San Diego Bay, California; and Oahu, Hawaii; and occasionally from Biscayne Bay, Florida, and Humboldt Bay and Mission Bay, California (Fig. 5). Only one specimen was found on a fouling plate from Humboldt Bay, California, in 2003, suggesting that the species may now be present in northern California. However, additional sampling is necessary to confirm that *H. elegans* is currently established in northern California.

Hydroides elegans was observed at Eel Pond, Cape Cod, Massachusetts, on one occasion in the summer and fall of 2011, surviving the winter 2011–2012, and found again in the spring of 2012 occurring at remarkable abundances. However, after the second winter, no live specimens were found (Fofonoff *et al.* 2003; Jim Carlton, pers. comm., 2011–2013) so it is not clear if the species is still established there. If so, this record extends the northward range of the species on the east coast, from the Indian River, Florida, to Cape Cod, Massachusetts (1750 km). The remarkable abundance observed by Carlton demonstrates the colonization potential of *H. elegans* with warming temperatures, such as those predicted under the climate change scenario. On the east coast, Eel Pond has a latitude of 41°33' N, while on the west coast, Humbolt Bay, northern California, is located at 40°45' N; both localities represent the northernmost records of this species on mainland North America, suggesting that continued monitoring is necessary to evaluate the species spread.

Hydroides floridana (Bush, 1910)

Figs 4F, 6

Eupomatus floridanus Bush, 1910: 498 (type locality: Cape Dear Rio, Florida (probably Cape Fear, North Carolina), United States; *nomen novum* for *E. uncinatus* recorded by Ehlers (1887)).
Eupomatus rostrata Iroso, 1921: 53 (*nomen novum* for *E. uncinatus* recorded by Ehlers (1887)).
Eupomatus decorus Treadwell, 1931: 4–5, fig. 3 (type locality: Grand Isle, Lousiana, United States).

Eupomatus uncinatus (*non* Philippi 1844) – Ehlers 1887: 285–286, pl. 58, figs 6–11 (off Cape Dear Rio, and fishing grounds in Cape Rear, Florida; 13 m). — Day 1973: 132–134, fig. 18h–i (off Beaufort, North Carolina; 6.5–18 m).
Eupomatus floridanus – Wells & Gray 1964: 74 (Cape Hatteras, North Carolina; hard substrates). — Wells & Wells 1969: 109–110 (off St. Augustine, Panama City, near Dog Island, and Cedar Key, Florida; associated with *Fargoa dianthophila*).
Hydroides floridanus – Robertson & Mau-Lastovicka 1979: 323 (northeastern and northwestern Florida; "host" of *Fargoa dianthophila*). — Perkins 1998: 95 (checklist of shallow-water polychaetes of Florida). — Bastida-Zavala & ten Hove 2002: 118–122, figs 6K–P, 7A–F, 9A–F, 10 (North Carolina, Louisiana, Campeche, eastern Mexico; 10–40 m; on shells of *Argopecten gibbus* (Linnaeus, 1758) and a submerged derrick).

Material examined

Ten specimens: BB (1) Aug. 2004, PB (4) Aug. 2002, CC (5) Sep. 2002.

Diagnosis

Tube white; with three longitudinal ridges; without peristomes, transverse ridges or alveoli. Opercular peduncle smooth, white. Opercular funnel with 26–32 radii with pointed tip (Fig. 4F); verticil with 11–12 spines, curving inwards, with one basal internal spinule, without external and lateral spinules (Fig. 4F). Most specimens have spines with lateral wings extending for less than half the length of the spine. Special collar chaetae with two blunt, short teeth and smooth distal blade.

Taxonomic remarks

The type locality of *Hydroides floridana* is unknown, from Florida or somewhere nearby. Ehlers (1887: 286) recorded the localities as “Cape Dear Rio” and “Inside fishing ground Cape Rear”, but these are probably transcription errors, as these placenames were not found in Florida (Read 2016); instead, “Cape Dear” and “Cape Rear” might refer to Cape Fear, in North Carolina.

Some specimens examined here have the verticil spines colored red (see *H. dianthus*). The specimens from Corpus Christi are the first records for the Texas coast. *Hydroides floridana* is rare as a fouling organism.

Ecology

Intertidal to sublittoral (40 m). On hard substrates, shells of *Argopecten gibbus* and on a submerged derrick (Wells & Gray 1964; Bastida-Zavala & ten Hove 2002); also associated with the gastropod *Fargoa dianthophila* (Wells & Wells 1969).

Distribution

Gulf of Mexico and east coast of the United States: From North Carolina to Florida and Louisiana (Bastida-Zavala & ten Hove 2002). In this work, *Hydroides floridana* was found occasionally on fouling plates from Biscayne Bay and Pensacola Bay, Florida, and Corpus Christi, Texas (Fig. 6). This species extends its westward range from Louisiana (Treadwell 1931) to Texas (710 km).

Hydroides gracilis (Bush, 1905)

Figs 4G, 6

Eupomatus gracilis Bush, 1905: 234–235, pl. 27, fig. 9, pl. 34, fig. 25, pl. 37, figs 26–27 (type locality: Pacific Grove, California, United States).
Eupomatus intereans Chamberlin, 1919a: 23 (type locality: Laguna Beach, southern California).

Eupomatus gracilis – Treadwell 1914: 225 (San Pedro and San Diego, southern California).
Hydroides uncinata (*non* Philippi 1844) – Berkeley & Berkeley 1941: 56 (southern California; on seaweed holdfast); 1958: 405 (west coast of Baja California Peninsula: Tortugas Bay, Baja California Sur).
Hydroides gracilis – Zibrowius 1971: 694–695 (synonymization of *E. intereans* and *H. uncinata* recorded by Berkeley & Berkeley 1941, 1958). — Bastida-Zavala & ten Hove 2003: 89–92, fig. 13A–V (California and Baja California, Mexican Pacific; intertidal to 5 m; on colony of vermetid *Aletes* sp., on Trochidae, also from aquaculture tanks and lead filter). — Bastida-Zavala 2008: 27, fig. 6K (California; PVC plates).

Material examined

232 specimens: SF (3) Sep. 2000 and 2001, LB (185) Sep. 2003, MO (5) Sep. 2013, MI (7) Aug. 2013, SD (32) Aug. 2000 and Jul. 2013.

Diagnosis

Tube white; with two longitudinal ridges, with or without peristomes; but no transverse ridges or alveoli. Opercular peduncle smooth, white. Opercular funnel with 16–42 radii with pointed tips (Fig. 4G); verticil with 9–12 smooth spines, curving inwards, without internal, external or lateral spinules or wings (Fig. 4G). Special collar chaetae with two blunt or pointed teeth and smooth distal blade.

Taxonomic remarks

Two tiny specimens have the *Hydroides* "*priscus*" type opercula (ten Hove & Ben-Eliahu 2005), with only a chitinous funnel instead of the normal funnel and verticil. The abundance of *H. gracilis* is variable in the fouling community, sometimes occurring at high abundances. Nonetheless, its distribution is restricted to California and the west coast of the Baja California Peninsula.

Ecology

Intertidal to sublittoral (5 m). On holdfast of seaweeds, shells of gastropods (*Aletes* sp. and Trochidae), and in aquaculture facilities (Berkeley & Berkeley 1941; Bastida-Zavala & ten Hove 2003).

Distribution

California to Bahía Tortugas, west coast of Baja California Peninsula (Bastida-Zavala & ten Hove 2003). In this work, *Hydroides gracilis* was found abundantly on fouling plates from Long Beach and San Diego, California; and occasionally from San Francisco, Morro Bay and Mission Bay, California (Fig. 6). *Hydroides gracilis* extends its range northward from Pacific Grove (Bush 1905) to San Francisco, California (140 km).

Hydroides longispinosa Imajima, 1976b

Figs 4H, 6

Hydroides longispinosa Imajima, 1976b: 240–246, fig. 5a–q (type locality; Koniya, Amami-Oshima, southern Japan; on the pearl oyster *Pteria penguin* (Röding, 1798)).
Hydroides centrospina Wu & Chen, 1981: 354–355 (type locality: South China Sea).

Hydroides longispinosa – Imajima 1977: 95 (Ogasawara Islands, southern Japan; intertidal to sublittoral; on buoy and underside of reef corals). — Imajima 1982: 46 (Palau Islands; intertidal to sublittoral; attached to boat). — Imajima & ten Hove 1984: 48 (Pohnpei Island (formerly known as Ponape), Federated States of Micronesia, and Lizard Island, Australia; outer reef on experimental fouling plates). — Imajima & ten Hove 1986: 3 (Solomon Islands and Gilbert Islands; attached to rope). — Kupriyanova *et al.* 2015: 286–288, fig. 6 (Lizard Island, Great Barrier Reef, Australia; 2–20 m; on coral rubble and fouling plates). — Sun *et al.* 2015: 46–50, fig. 14 (New South Wales and Queensland, Australia; 2–20 m; on shells and dead coral substrate).
Hydroides centrospina – Fiege & Sun 1999: 116 (synonymy).
Hydroides longispinosus – Fiege & Sun 1999: 116–118, figs 6A–D, 7A–B (Hainan Island, South China Sea; 2–14 m; on bivalve shells, seagrass, algae and the barnacle *Solidobalanus socialis* (Hoek, 1883)). — Bailey-Brock *et al.* 2012: 969, 972, fig. 3D (Enewetak, Rongelap, Marshall Islands; 12–18 m; on coral).

Material examined

Two specimens: HI (2) Aug. 2006.

Diagnosis

Tube white, with or without two longitudinal ridges, with or without peristomes; but no alveoli. Opercular peduncle smooth, white. Opercular funnel with 18 radii with blunt tips (Fig. 4H); verticil with 12 spines, straight, with pointed tips (Fig. 4H); all spines with 2–3 internal spinules and 5–6 pairs of lateral spinules, without external spinules or wings (Fig. 4H); with a long, smooth central spine (Fig. 4H). Special collar chaetae with two pointed, elongate teeth and a proximal rasp, distal blade with notch and many denticles.

Taxonomic remarks

The specimens recorded here are slightly different from the original description of *Hydroides longispinosa* (Imajima 1976b): the number of radii (18) is slightly less, as in the original description there are 20 radii; the verticil spines have fewer internal spinules (2–3), versus 15–18, and few lateral spinules (5–6 pairs), versus 7–9 pairs.

Hydroides longispinosa is widely distributed in the western and central Pacific; however, this report represents the first record in the Hawaiian Islands, where it was found on fouling plates. Given the distance between the Polynesian Islands, it is likely that the species was dispersed as fouling on yachts or ships, rather than by natural dispersion. Several records in the western Pacific were from artificial substrates (Imajima 1982; Imajima & ten Hove 1984, 1986).

Ecology

Intertidal to 20 m. On seagrass, algae, the barnacle *Solidobalanus socialis*, the pearl oyster *Pteria (Magnavicula) penguin* and other bivalve shells, underside of reef corals (Imajima 1976b, 1977; Fiege & Sun 1999), and also on artificial substrates such as boats, buoys, ropes and fouling plates (Imajima 1977, 1982; Imajima & ten Hove 1984, 1986).

Distribution

Western and central Pacific: Southern Japan, South China Sea, Australia, Palau, Pohnpei, Solomon and Marshall Islands (Imajima 1976b, 1977; Wu & Chen 1981; Imajima 1982; Imajima & ten Hove 1984, 1986; Fiege & Sun 1999; Bailey-Brock *et al.* 2012; Sun *et al.* 2015). In this work, only two specimens of *Hydroides longispinosa* were found, on a fouling plate from Oahu, Hawaii (Fig. 6). This represents a possible range extension northward from Enewetak, Marshall Islands (Bailey-Brock *et al.* 2012) to Oahu, Hawaii (4300 km).

Hydroides parva (Treadwell, 1902)

Figs 4I, 6

Eupomatus parvus Treadwell, 1902: 210, figs 79–80 (type locality: Boqueron Bay, Puerto Rico; on encrusting bryozoans).

Hydroides dianthus (*non* Verrill 1873) – Webster 1884: 327 (Bermuda). — Zibrowius 1971: 699 (synonymy).

Hydroides (Eupomatus) n. sp. – Augener 1925: 16–17 (Saint Croix, Lesser Antilles, Caribbean). — Bastida-Zavala & ten Hove 2002: 127 (synonymy).

Hydroides (Eupomatus) parvus – Augener 1927: 80, textfig. 8 (Spaanse Water and Schottegat, Curaçao, Caribbean; on mangrove root). — Augener 1934: 116–117 (Gairaca, Santa Marta, Colombian Caribbean; intertidal to 15 m).

Hydroides parvus – Bush 1910: 496–497 (Bermuda). — Treadwell 1939: 305–306 (Puerto Rico). — Rioja 1958: 251–254, figs 1–2 (Veracruz, eastern Mexico). — Wells & Gray 1964: 74 (Cape Hatteras, North Carolina; hard substrates). — Zibrowius 1970: 6–7, pl. 1, figs 5–6 (Recife, Brazil; 30 m; on rocks). — Rullier & Amoreux 1979: 194 (off Ipojuca River and Abrolhos Archipelago, Brazil; intertidal to 27 m; sand, shells and rocks). — Díaz 1994: 618 (Barbados, settlement and succession experiments; 10 m; coral plates, *Orbicella annularis*). — ten Hove & San Martín 1995: 16

(de la Juventud Island, Cuba; 0.5–4 m; on mollusk shells, algae and mangrove roots). — Carrera-Parra & Vargas-Hernández 1997: 314 (Enmedio Island, Veracruz, eastern Mexico; 1–9 m; on the sponge *Ircinia felix* (Duchassaing & Michelotti, 1864)). — Perkins 1998: 95 (checklist of shallow-water polychaetes from Florida). — Dueñas 1999: 14 (Providencia Island, Colombia). — Bastida-Zavala & Salazar-Vallejo 2000b: 851, fig. 2n–p (Puerto Rico and eastern Mexico: Términos Lagoon and Champotón, Campeche; Celestún, Yucatán; Yucatán Canal; Cabo Catoche, Contoy Island, Puerto Morelos, Ascensión Bay and Chinchorro Bank, Quintana Roo; intertidal to 41 m; on mangrove roots, seagrasses and algae, sea urchin spines, gastropods shells, sponges, corals, calcareous rocks and fouling of wood dock pilings). — Bastida-Zavala & ten Hove 2002: 127–129, figs 12A–K, 15 (Florida; eastern Mexico: Veracruz, Campeche, Yucatán and Quintana Roo; Puerto Rico; Montserrat; Atlantic Panama; Curaçao; Atlantic Colombia and Brazil; 0.6–41 m; salinity 31–37‰; on mangrove roots, seagrasses and algae, sea urchin spines, bivalve and gastropods shells, sponges, calcareous rocks, live corals and fouling of wood dock pilings and canal docks).

Hydroides parva – Day 1973: 132 (Cape Hatteras, North Carolina, United States; intertidal). — Díaz-Díaz & Liñero-Arana 2001: 13 (Cariaco Gulf, Venezuela; PVC dock pilings).

Material examined

One specimen: BB (1) Aug. 2004.

Diagnosis

Tube missing. Opercular peduncle smooth, white. Operculum funnel with 23 radii with pointed tips (Fig. 4I); verticil with seven yellowish spines, curving abruptly inwards, forming an external knob (Fig. 4I); all spines similar in shape and size, with pointed tips; with basal internal spinule and two well-developed lateral spinules in middle position, without external spinules, wings or central tooth (Fig. 4I). Special collar chaetae with two pointed, short teeth and smooth distal blade.

Taxonomic remarks

Hydroides parva is frequently confused with *H. bispinosa*, because both species have vertical spines with a pair of lateral spinules; however, the main difference is the shape of the funnel radii: rounded in *H. bispinosa*, sharp in *H. parva*. This species is more often found on natural substrates; however, occasionally it is found on artificial substrates (Bastida-Zavala & Salazar-Vallejo 2000b; Díaz-Díaz & Liñero-Arana 2001; Bastida-Zavala & ten Hove 2002).

Ecology

Intertidal to 41 m. On mangrove roots, bryozoans, seagrasses and algae, sea urchin spines, gastropod shells, sponges, corals (*Orbicella annularis*), calcareous rocks and on artificial substrates such as fouling on wood dock pilings (Díaz 1994; Bastida-Zavala & Salazar-Vallejo 2000b; Bastida-Zavala & ten Hove 2002).

Distribution

Caribbean Sea, Bermuda, Gulf of Mexico, eastern United States (Florida and North Carolina) and Brazil (Bastida-Zavala & ten Hove 2002). In this work, only one specimen of *Hydroides parva* was found on a fouling plate from Biscayne Bay, Florida (Fig. 6).

Hydroides sanctaecrucis Krøyer in Mörch, 1863

Figs 4J, 6

Hydroides (Eucarphus) sanctae crucis Krøyer in Mörch, 1863: 378–379, pl. 11, fig. 12 (type locality: Saint Croix Island, Lesser Antilles, Caribbean Sea).

Hydroides (Eupomatus) dianthoides Augener, 1922: 49–50 (type locality: Haiti; partial synonymy).

Eupomatus sanctae crucis – Fauvel 1919: 478–479, fig. 2e–g (Père Island, Mère Island, Montabo Cove, French Guiana). — Rioja 1958: 262–264, fig. 6A–E (Verde Island and Santiaguillo Island, Veracruz, eastern Mexico; on mollusk shells and corals).

Hydroides sanctaecrucis – Zibrowius 1971: 699–700 (Caribbean: Saint Croix Island, Puerto Rico, Jamaica, Atlantic Panama, Aruba and French Guiana; extensive revision; intertidal to 2 m; on hull of ship). — Day 1973: 132 (North Carolina). — Long 1974: 28 (Oahu, Hawaii; 15 m; asbestos plates). — Perkins 1998: 95 (checklist of shallow-water polychaetes of Florida). — Dueñas 1999: 14 (Cartagena Bay and Cispatá Bay, Colombia). — Bastida-Zavala & ten Hove 2002: 146–149, figs 25A–R, 28 (French Guiana, Florida, Caribbean: Haiti, Puerto Rico, U.S. Virgin Islands, Atlantic Colombia, Atlantic and Pacific side of Panama; intertidal to 5 m, salinity 18–31‰; in tidal creek and in marinas, on floats, docks and fouling plates). — Bastida-Zavala & ten Hove 2003: 101–102, fig. 19P–Q (Oaxaca, southern Mexican Pacific and Pacific Panama; salinity 19–25‰; on rocks and floats). — Lewis *et al.* 2006: 666–669, figs 1–2 (North Queensland, Northern Territory and Tasmania, Australia and Singapore; marina and vessel hulls). — Bastida-Zavala 2008: 29, fig. 6R (Huatulco, Oaxaca, southern Mexican Pacific; intertidal to 1 m; on pier pilings). — Sun *et al.* 2012: 20–21, figs 10A–G (Hong Kong; intertidal to 10 m; on pier pilings and fouling plates at fish farm). — Tovar-Hernández *et al.* 2012: 18–19 (Gulf of California: Topolobampo, Sinaloa; Guaymas, Sonora; La Paz, Baja California Sur); 2014: 386, 388, 390, fig. 2f (Gulf of California: Topolobampo, Sinaloa; Guaymas, Sonora; La Paz, Baja California Sur). — Sun *et al.* 2015: 76–79, fig. 25 (Northern Territory and Queensland, Australia; 0.5 m; on hulls of vessels and settlement plates). — Bastida-Zavala *et al.* 2016: 426, figs 6, 12E (Mexican Pacific: Sonora, Baja California Sur and Oaxaca; in marinas and harbors, fouling; intertidal to 1 m).

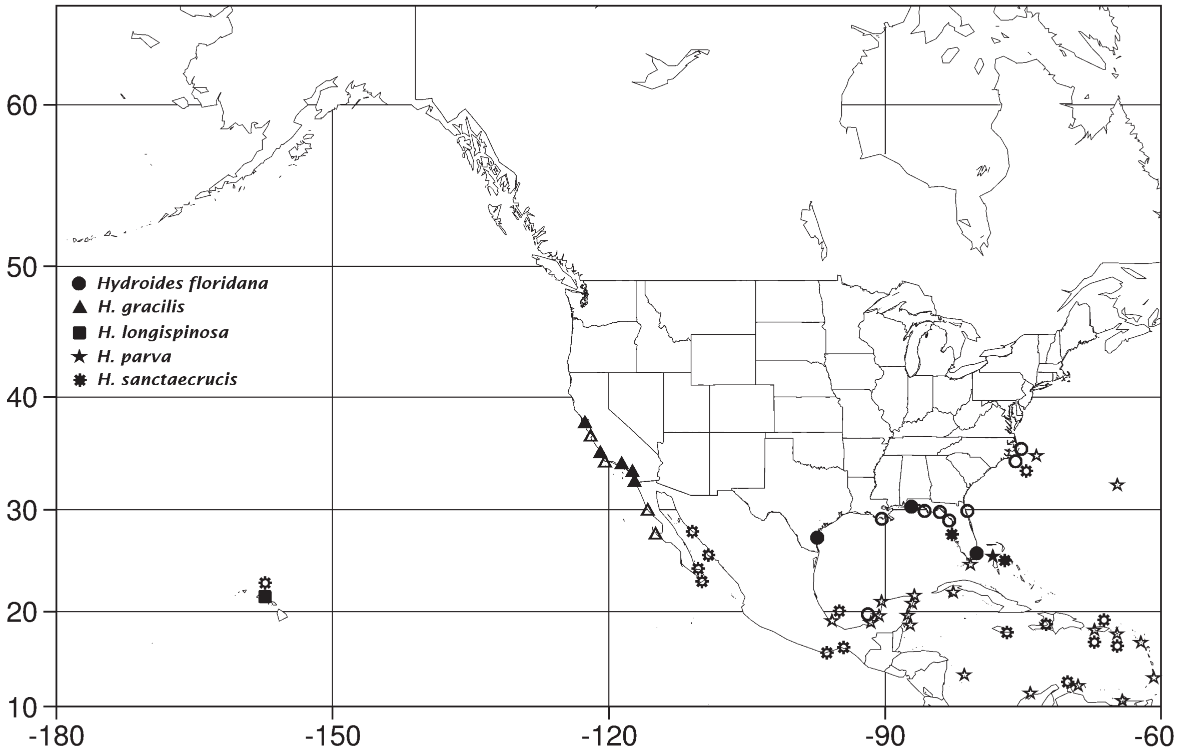

Fig. 6. Distribution of serpulids (*Hydroides* spp.) from United States fouling plates (closed symbols) and literature records (open symbols).

Hydroides santaecrusis – Dueñas 1981: 99–100, fig. 29A–F (Cartagena Bay, Colombia; on mangrove roots; auct. lapsus). — Quirós-Rodríguez *et al.* 2013: 91, Table 3 (Córdoba, Colombian Caribbean; intertidal; on red algae).

Hydroides (Eupomatus) dianthoides – Bastida-Zavala & ten Hove 2002: 147 (partial synonymy).

Material examined

37 specimens: BB (28) Aug. 2004, TB (9) Jul. 2002, Jun. 2012 and Jun. 2014.

Diagnosis

Tube white, with two longitudinal ridges or none; without peristomes or alveoli. Opercular peduncle smooth, white. Opercular funnel with 19–28 radii with pointed tips (Fig. 4J); verticil with 11–14 spines, all curving ventrally, with or without one basal internal spinule, with an external spinule on all or almost all spines, without lateral spinules, with wings extending more than half of spine length (Fig. 4J). Special collar chaetae with two blunt or pointed teeth and smooth distal blade.

Taxonomic remarks

Hydroides sanctaecrucis is an invasive species that has established itself in several localities along the Pacific coast of the Americas (Mexican Pacific: Oaxaca and Gulf of California, and Panama), in Australia and Hong Kong. The species has been found only once in Hawaii (Long 1974), so it is not clear whether it is established there. The main means of dispersal is likely as fouling on vessels; the species was generally limited to polluted harbors in the sites invaded (Bastida-Zavala & ten Hove 2002, 2003; Lewis *et al.* 2006; Tovar-Hernández *et al.* 2014; Sun *et al.* 2012, 2015; Bastida-Zavala *et al.* 2016).

Ecology

Intertidal to 15 m, salinity 18–31‰. On mangrove roots, mollusk shells, corals, rocks and on artificial substrates at marinas and piers, on floats, docks and fouling plates (Rioja 1958; Dueñas 1981; Bastida-Zavala & ten Hove 2002; Lewis *et al.* 2006; Sun *et al.* 2015).

Distribution

Caribbean Sea, French Guiana, Gulf of Mexico, east coast of United States, Pacific side of Panama, Oaxaca (southern Mexico), Gulf of California, Hawaii, Australia, Hong Kong (Zibrowius 1971; Bastida-Zavala & ten Hove 2002, 2003; Lewis *et al.* 2006; Sun *et al.* 2012, 2015; Tovar-Hernández *et al.* 2014; Bastida-Zavala *et al.* 2016). In this work, *Hydroides sanctaecrucis* was found abundantly on fouling plates from Biscayne Bay, Florida, and occasionally from Tampa Bay, Florida (Fig. 6).

Genus ***Pomatostegus*** Schmarda, 1861

Pomatostegus stellatus (Abildgaard, 1789)

Figs 7A, 8

Terebella stellata Abildgaard, 1789: 142–144, pl. A, fig. 5A–B (type locality: West Indies, Caribbean Sea).

Pomatostegus macrosoma Schmarda, 1861: 31–32, pl. 21, fig. 182 (type locality: South of Jamaica). — Mörch 1863: 398–399 (comparison with *P. stellatus*).

Pomatostegus brachysoma Schmarda, 1861: 32, pl. 21, fig. 183 (type locality: Jamaica, on coral reef).

Pomatostegus stellatus tetrapoma Mörch, 1863: 397 (type locality: Saint Thomas, Lesser Antilles, Caribbean Sea).

Pomatostegus stellatus fruticosa Mörch, 1863: 397–398 (type locality: Saint Thomas, Lesser Antilles, Caribbean Sea).

Cymospira quadruplicata Krøyer in Mörch, 1863: 398, pl. 11, fig. 13 (type locality: Saint Croix, Lesser Antilles, Caribbean Sea, probably the first use of the name; according to Mörch 1863: 398 is *P. stellatus pentapoma*).

Pomatostegus stellatus – Mörch 1863: 396–397, pl. 11, fig. 14 (Saint Croix and Saint Thomas, Lesser Antilles, Caribbean Sea). — Benedict 1887: 551, pl. 22, figs 32–35, pl. 23, figs 36–37 (Jamaica and Curaçao, Caribbean Sea; shallow water). — Ehlers 1887: 296–300 (East Key, Florida; 24 m). — Treadwell 1902: 210 (Caballo Blanco Reef, Guanica Bay and Ensenada Honda, Puerto Rico). — Augener 1927: 79, textfig. 7 (Spaanse Water and Caracas Bay, Curaçao; on coral and mangrove roots). — Treadwell 1928: 483 (near Saba Island, Antilles). — Augener 1934: 118 (Los Testigos Archipelago, Venezuela, and Tagduga, now Taganga, Santa Marta, Colombian Caribbean; intertidal to 11 m). — Rioja 1958: 293–296, figs 92–100 (Mexican Caribbean: Chancanab Lagoon, Cozumel). — Zibrowius 1970: 13–14, pl. 3, figs 16–20 (Abrolhos Archipelago, Brazil; 16–48 m; sand and coral debris). — ten Hove & San Martín 1995: 17 (de la Juventud Island, Cuba; 1–6 m; on mollusk shells, mangrove roots, rocks, corals and wood debris). — Perkins 1998: 95 (checklist of shallow-water polychaetes from Florida). — Dueñas 1999: 14 (Santa Marta, Tayrona National Park, Providencia Island, Cartagena Bay and Cispatá Bay, Colombia). — Bastida-Zavala & Salazar-Vallejo 2000a: 815–817, figs 3b, 5g–q, 6a–d (San Juan, Puerto Rico; de la Juventud Island, Cuba; eastern Mexico: Alacranes Key, Ría Lagartos and San Felipe, Yucatán; Contoy Island, Nizuc Point, Nichupté Lagoon, Xcacel, Xcayal, Cozumel Island, Xahuayxol and Chinchorro Bank, Quintana Roo; intertidal to 43 m; under rocks with algae, seagrass and sponges, corals and on cement pier covered by *Millepora* spp.).
Pomatostegus macrosoma – Mörch 1863: 398–399 (comparison with *P. stellatus*). — Bastida-Zavala & Salazar-Vallejo 2000a: 816 (synonymy).
Pomatostegus brachysoma – Mörch 1863: 400 (comparison with *P. stellatus*). — Bush 1910: 498–500 (Dominica Island, Lesser Antilles, Caribbean Sea). — Bastida-Zavala & Salazar-Vallejo 2000a: 816 (synonymy).
Pomatostegus stellatus tetrapoma – Bastida-Zavala & Salazar-Vallejo 2000a: 816 (synonymy).
Pomatostegus stellatus fruticosa – Rullier 1974: 72, fig. 9A–I (Batabanó Bay, Cuba; 2 m; in sponge). — Bastida-Zavala & Salazar-Vallejo 2000a: 816 (synonymy).
Pomatostegus quadruplicatus – Bastida-Zavala & Salazar-Vallejo 2000a: 816 (synonymy).

Material examined

One specimen: BB (1) Aug. 2004.

Diagnosis

Tube missing. Opercular peduncle spotted, with wide wings (Fig. 7A). Operculum chitinous, forming three concentric plates, joined by central hollow column (Fig. 7A); margin of plates with sharp spines. Collar with "*Spirobranchus*" chaetae, coarsely serrated on subapical section.

Taxonomic remarks

Several publications indicate that *Pomatostegus stellatus* is widely distributed (Zibrowius 1970; Imajima 1977, 1982; Imajima & ten Hove 1984, 1986; Nishi 1995b; Bastida-Zavala 2008); however, some authors (Bastida-Zavala & Salazar-Vallejo 2000a; ten Hove & Kupriyanova 2009) suggest that its distribution could be more limited, as the larvae are short lived and there is very little evidence of large scale dispersal through fouling (Kupriyanova *et al.* 2001). Therefore, until further analysis, it is better to distinguish three species geographically: *P. stellatus* is limited to the tropical western Atlantic, while *P. kroyeri* Mörch, 1863 is limited to the tropical eastern Pacific region and *P. actinoceras* Mörch, 1863 is limited to the Indo-West Pacific (ten Hove & Kupriyanova 2009).

Ecology

Intertidal to 48 m. On mangrove roots, mollusk shells, corals, sponges, under rocks, wood debris and on a cement pier covered by the coral *Millepora* spp. (ten Hove & San Martín 1995; Bastida-Zavala & Salazar-Vallejo 2000a).

Distribution

Caribbean Sea, from Florida to southern Brazil; in the Gulf of Mexico, it is only recorded from Alacranes Key (Ehlers 1887; Zibrowius 1970; ten Hove & San Martín 1995; Bastida-Zavala & Salazar-Vallejo 2000a). In this study, only one specimen of *Pomatostegus stellatus* was found on a fouling plate from Biscayne Bay, Florida (Fig. 8).

Genus ***Protula*** Risso, 1826

Protula balboensis Monro, 1933
Figs 7B–E, 8

Protula tubularia var. *balboensis* Monro, 1933: 1088–1090, figs 30A–D (type locality: Balboa and Taboga Island, Pacific Panama; Gorgona Island, Colombia; on rocks, rock-pools, pier pilings and intertidal at low tides).

Protula tubularia (*non* Montagu 1803) – Steinbeck & Ricketts 1941: 367 (Gulf of California: Puerto Refugio, Angel de la Guarda Island, Baja California). — Rioja 1942: 133–134 (from Acapulco, Guerrero, southern Mexican Pacific, according to Rioja 1963: 222). — Rioja 1963: 220–222 (Gulf of California: Carmen Island, Baja California Sur; 111 m). All indeterminable records are presumably *P. balboensis* (see taxonomic remarks).

Portula balboensis – Zibrowius 1970: 17–18, pl. 4, figs 7–8 (Recife de Liza, Bahia, Brazil; 5 m).

Protula tubularia balboensis – Kudenov 1975: 228 (Gulf of California: Cholla Bay, Puerto Peñasco, Sonora; intertidal; on rock).

Protula balbaoensis – Perkins 1998: 95 (checklist of shallow-water polychaetes from Florida).

Protula balboensis – Bastida-Zavala 2008: 37, fig. 8H (Mexican Pacific: Baja California, Baja California Sur, Sonora and Guerrero; incorrectly located in Puerto San Carlos, Baja California Sur; shore; in rocky reef and shingle). — Bastida-Zavala *et al.* 2016: 429–430, figs 7, 13A–B (Baja California and Michoacán, Mexican Pacific, and Atlantic Panama; intertidal to 1 m; in marinas and harbors, fouling).

Protula diomedea (*non* Benedict 1887) – Bastida-Zavala & Salazar-Vallejo 2000a: 817, fig. 7h–o (Jururú Bay, northeastern Cuba).

Material examined

16 specimens: JX (13) Aug. 2001, BB (2) Aug. 2004, CC (1) Sep. 2002.

Additional material

One specimen collected on the pier of the Smithsonian Institution station in Bocas del Toro, Caribbean side of Panama (photographed in vivo by Betel Martínez-Guerrero, 14 Aug. 2008, coll. Leslie Harris).

Diagnosis

Tube white; with shallow transverse ridges; without longitudinal ridges, peristomes or alveoli (Fig. 7B). Branchial crown with 24 radioles per lobe; radioles with rounded process at end of interradiolar membrane (Fig. 7D, detail); two small specimens with 9–12 radioles per lobe. Thoracic membrane wide, reaches seventh chaetiger. Operculum and opercular peduncle absent (Fig. 7C–D). Collar chaetae limbate. Living adult specimens have a reddish thoracic membrane and radioles with numerous red spots (Fig. 7E).

Taxonomic remarks

Large specimens of *Protula balboensis* were found in small assemblages attached to other serpulids (*Hydroides dianthus*). *Protula balboensis* differs from *P. longiseta*, in that the latter species lacks the characteristic rounded processes on the radioles at the end of the interradiolar membrane (Fig. 7D, detail); however, the differences between these species are very small and need a more detailed morphological review (ten Hove & Kupriyanova 2009).

Some records from the Gulf of California and Acapulco, Guerrero, in the southern Mexican Pacific (Steinbeck & Ricketts 1941; Rioja 1942, 1963) are indeterminable because there are no voucher specimens; however, later Bastida-Zavala (2008) confirmed the presence of *P. balboensis* along the Gulf of California (Baja California, Baja California Sur, Sonora) and from Acapulco, southern Mexican Pacific. Recently, Bastida-Zavala *et al.* (2016: 430) confirmed more specimens of *P. balboensis* from the Mexican Pacific and Atlantic Panama.

Ecology

Intertidal to 111 m (Rioja 1963). In rock-pools, on rocks, shingle, and as fouling on pier piling at marinas (Monro 1933; Bastida-Zavala 2008; Bastida-Zavala *et al.* 2016).

Distribution

Tropical eastern Pacific, from Gulf of California to Colombia; possibly as NIS in the western Atlantic from Cuba, Florida (Perkins 1998; Bastida-Zavala & Salazar-Vallejo 2000a) and questionably from Brazil (Zibrowius 1970). However, it is also possible that the origin of this species is the western Atlantic and that it has been introduced in the eastern Pacific. In this study, *Protula balboensis* was found occasionally on fouling plates from Jacksonville, Florida, and it was rare from Biscayne Bay, Florida, and Corpus Christi, Texas (Fig. 8). This species provisionally extends its westward range from western Florida (Perkins 1998) to Corpus Christi, Texas (1400 km).

Protula longiseta Schmarda, 1861

Fig. 8

Protula longiseta Schmarda, 1861: 32–33, pl. 22, fig. 184 (type locality: Jamaica, Caribbean Sea; in coral reef).

Protula longiseta – Augener 1925: 39–42 (type specimen revision and redescription). — Bastida-Zavala & Salazar-Vallejo 2000a: 817, fig. 7h–o (Nizuc Point and Xahuayxhol Beach, Quintana Roo, Mexico; on rocks).

Material examined

One specimen: IR (1) Aug. 2005.

Diagnosis

Tube missing. Branchial crown with 16 radioles per lobe; radioles lack rounded process at end of interradiolar membrane. Thoracic membrane reaches fourth chaetiger. Operculum and opercular peduncle absent. Collar chaetae limbate.

Taxonomic remarks

Augener (1925) synonymized *Protula antennata* Ehlers, 1877 (from Morro Light, Florida) with *P. longiseta*; however, the first species was described from bathyal depths (534 m), while *P. longiseta*

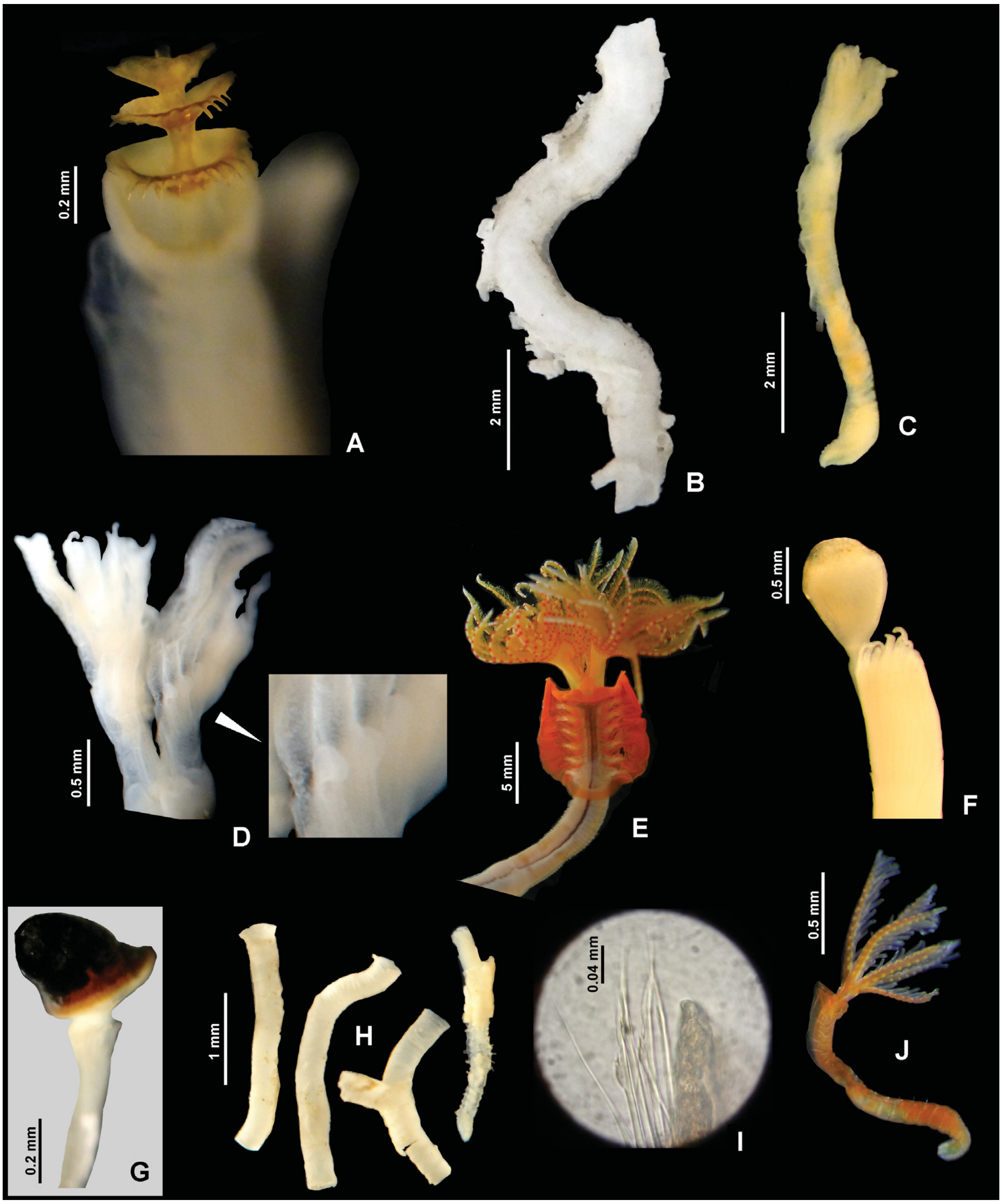

Fig. 7. Serpulids from United States fouling plates. *Pomatostegus stellatus*. **A**. Operculum, from Biscayne Bay, Florida (SERC-118825). – *Protula balboensis*. **B–D**. Tube, body and branchial crown, white arrow shows detail of rounded processes, Biscayne Bay, Florida (SERC-118825). **E**. Body of live adult from Smithsonian Institution station in Bocas del Toro, Panama (photo by Betel Martínez-Guerrero). – *Pseudochitinopoma occidentalis*. **F**. Operculum, Puget Sound, Washington (SERC-33385R). – *Pseudovermilia occidentalis*. **G**. Operculum, Biscayne Bay, Florida (SERC-118450). – *Salmacina huxleyi*. **H–I**. Tubes, body and collar chaetae, Biscayne Bay, Florida (SERC-118449). – *S. tribranchiata*. **J**. Body, Galapagos Island (SERC-233687).

lives in shallow waters associated with coral reefs (Schmarda 1861). A revision of the species of this genus is necessary (ten Hove & Kupriyanova 2009).

Ecology

Shallow waters. On corals (Schmarda 1861), rocks and algae (Bastida-Zavala & Salazar-Vallejo 2000a).

Distribution

Caribbean Sea, from Jamaica to Mexico (Bastida-Zavala & Salazar-Vallejo 2000a). In this study, only one specimen of *Protula longiseta* was found on a fouling plate from the Indian River, Florida (Fig. 8). This species provisionally extends its northward range from the Mexican Caribbean (Bastida-Zavala & Salazar-Vallejo 2000a) to the Indian River, Florida (1000 km).

Genus ***Pseudochitinopoma*** Zibrowius, 1969a

Pseudochitinopoma occidentalis (Bush, 1905)

Figs 7F, 8

Hyalopomatopsis occidentalis Bush, 1905: 229–230, pl. 40, figs 3, 22, pl. 44, figs 2, 4, 8–9 (type locality: Virgin Bay, Prince William Sound, southern Alaska, United States; on tubes of *Serpula splendens* Bush, 1905, now *S. columbiana*).

Chitinopoma occidentalis – Hartman 1948: 50–51, fig. 12a–f (Alaska, Peninsula; intertidal to 229 m).

Chitinopoma groenlandica (*non* Mörch 1863) – Berkeley & Berkeley 1961: 663 (Carmel Canyon, central California; 36–55 m).

Pseudochitinopoma occidentalis – Zibrowius 1969a: 7–9, fig. 2a–g (Canoe Bay, Alaska; Shelton, San Juan Archipelago and Puget Sound, Washington; off Santa Rosa Island and Carmel Canyon in central California; intertidal to 229 m). — Bastida-Zavala 2008: 38–39, fig. 9A–D (Alaska, Washington, Oregon and California; intertidal to 16 m; on rocky bottoms and PVC plates). — Kupriyanova *et al.* 2012: 68–72, figs 7A–E, 8A–E (Canada: British Columbia; United States: Alaska, Washington and California; Mexico: Baja California; intertidal to 157 m; on tubes of *Serpula* sp., *Crucigera zygophora*, *Vermiliopsis infundibulum* (Philippi, 1844), now as *V. multiannulata* (Moore, 1923) for eastern Pacific records, shells of the brachiopod *Laqueus californianus* (Koch, 1848), alcyonarians, solitary corals, tunicates, burrowing clams, rock and fouling plates).

Material examined

658 specimens: DH (24) Aug. 2002, AK (66) Jul. 2000, AV (7) Aug. 2000, PW (4) Aug. 2003, KD (358) Aug. 2001, ST (81) Aug. 2001, KT (8) Sep. 2003, WA (75) Aug. 2000, OR (1) Aug. 2000, HB (18) Sep. 2003, SF (12) Sep. 2001 and 2011, MO (4) Sep. 2013.

Additional material

Five specimens: LACMNH N1908, 1 specimen (California, approx. 36°36' N, 121°53' W, Monterey Shale, dredged off Del Monte, 12–16 m, 3 Jun. 1934, coll. E.F. Ricketts, as *Ditrupa* sp.); LACMNH N1909, 2 specimens (California, approx. 37°12' N, 122°24' W, Moss Beach, Jul. 1933, as ?*Ditrupa*); LACMNH N1910, 2 specimens (California, approx. 37°12' N, 122°24' W, Moss Beach, 1934, as ?*Ditrupa*).

Diagnosis

Tube white, smooth; with a longitudinal ridge; without transverse ridges, peristomes or alveoli. Opercular peduncle smooth, white. Operculum white, spherical or conical (Fig. 7F). Collar with fin-and-blade chaetae (Fig. 9N).

Taxonomic remarks

Pseudochitinopoma occidentalis was the species with the largest distribution in the survey, with 12 localities in the northeastern Pacific, from Dutch Harbor, Alaska, to Morro Bay, California. It was also the second most common species represented on fouling plates; only *Hydroides dianthus*, a species from the U.S. east coast, was encountered more often (Table 1). Despite its frequency on fouling plates, *P. occidentalis* has not been reported as NIS elsewhere.

Ecology

Intertidal to 229 m (Hartman 1948; Zibrowius 1969a). Rocky bottoms, on tubes of *Serpula columbiana*, *Crucigera zygophora*, *Vermiliopsis multiannulata*, shells of the brachiopod *Laqueus californianus*, alcyonarians, solitary corals, tunicates, burrowing clams and PVC fouling plates (Bush 1905; Bastida-Zavala 2008; Kupriyanova *et al.* 2012).

Distribution

Northeastern Pacific, from Alaska to Ensenada, west coast of Baja California Peninsula (Kupriyanova *et al.* 2012). In this survey, *Pseudochitinopoma occidentalis* was abundantly and frequently on fouling plates from Dutch Harbor, Kachemak Bay, Kodiak and Sitka, Alaska, and Puget Sound, Washington; occasionally from Valdez Bay, Prince William Sound and Ketchikan, Alaska, Coos Bay, Oregon, Humboldt Bay, San Francisco Bay and Morro Bay, California (Fig. 8).

Genus ***Pseudovermilia*** Bush, 1907

Pseudovermilia occidentalis (McIntosh, 1885)

Figs 7G, 8

Spirobranchus occidentalis McIntosh, 1885: 529–530, pl. 55, fig. 10, pl. 29a, figs 31–32 (type locality: off the Bermudas, western Atlantic; 795 m, coral mud, on tube of *Placostegus assimilis* McIntosh, 1885).
Pseudovermilia pileum Bush, 1907: 136 (type locality: Bermuda).
Vermiliopsis hawaiiensis Treadwell, 1943: 3, figs 14–15 (type locality: Hawaii).
Vermiliopsis cornuta Rioja, 1947b: 525–526, figs 14–21 (type locality: La Paz, Baja California Sur, Gulf of California).

Vermiliopsis acanthophora (*non* Augener 1914) – Monro 1933: 1085 (James Island, Galápagos; 9–11 m; in clean sand and weed).
Vermiliopsis multiannulata (*non* Moore 1923) – Hartman 1969: 781–782, figs 1–2 (central and southern California).
Pseudovermilia occidentalis – Zibrowius 1970: 9–11, pl. 2, figs 1–11, 15–16 (São Sebastião, Ubatuba, Rios de Janeiro, Fernando de Noronha Island, Pernambuco, Lizxa Reef and Abrolhos Archipelago, Brazil; 1–120 m; in sand with rocky bottoms, shell debris, corals and gorgonians). — ten Hove 1975: 59–72, figs 114–123, 144–145, 155–156, 159, 161–164, 170–172, pls 1, 2a–e, 3, 7 (synonymy; Hawaii, southern California, Georgia, Florida, Gulf of Mexico, Galápagos, Panama, Bermuda, Mexican Caribbean, Honduras, Bahamas, Jamaica, Puerto Rico, Lesser Antilles, Netherlands Antilles, Tobago, Suriname, Brazil, ?Azores, ?Portugal, Senegal, Gulf of Guinea, St. Helena Island and Red Sea; sublittoral to 720 m; on the corals *Astrangia*, *Madracis*, *Phyllangia americana* Milne Edwards & Haime, 1849, on the sponge *Stromatospongia vermicola* Hartman, 1969). — ten Hove & Wolf 1984: 55: 31, figs 55–25, 55–26a–j (western Florida and Alabama; 19–75 m; coarse and silty sand). — Díaz 1994: 618 (Barbados, settlement and succession; 10 m; coral plates, *Obicella annularis*). — ten Hove & San Martín 1995: 17 (de la Juventud Island, Cuba; 1–6 m; on mollusk shells, mangrove roots, rocks, corals and wood debris). — Perkins 1998: 95 (checklist of

shallow-water polychaetes from Florida). — Bastida-Zavala & Salazar-Vallejo 2000a: 820, fig. 8r–u (Diego Pérez Key, Cuba, and eastern Mexico: Champotón Beach and Campeche Bank, Campeche; Alacranes Key, Arenas Key and Ría Lagartos, Yucatán; Nichupté Lagoon, Nizuc Point, Aventuras Beach, Xcacel Beach, Xcayal Beach, Allen Point, Majagual Reef, Contoy Island, Cozumel Island and Chinchorro Bank, Quintana Roo; intertidal to 230 m; on rocks, the coral *Acropora*, the sponges *Clathria calla* (de Laubenfels, 1934) and *Agelas dispar* Duchassaing & Michelotti, 1864, seagrass and algae). — Bastida-Zavala 2008: 40–42, figs 9H–I (Mexican Pacific: Baja California Sur and Oaxaca; intertidal to 7 m; on rocks, mixed beaches, the coral *Pocillopora*, epifauna of the sea urchin *Eucidaris* and the bivalve *Spondylus calcifer* Carpenter, 1857), now *Spondylus limbatus* G.B. Sowerby II, 1847). — Bastida-Zavala *et al.* 2016: 431–432, figs 7, 13C (Mexican Pacific: Baja California Sur, Michoacán and Oaxaca; 2–9 m; on sabellariid colonies and the coral *Pocillopora damicornis*).

Material examined

Three specimens: BB (3) Aug. 2004.

Diagnosis

Tube white; with longitudinal and transverse ridges, sometimes with peristomes; alveoli absent. Opercular peduncle smooth, white. Operculum with fleshy, bulbous part and distal, black horny cap (Fig. 7G); latter with several internal septa. Collar with bundles of few chaetae, chaetae limbate. Thorax with "*Apomatus*" chaetae occurring from third chaetiger onwards. Thoracic uncini with anterior bifurcate tooth.

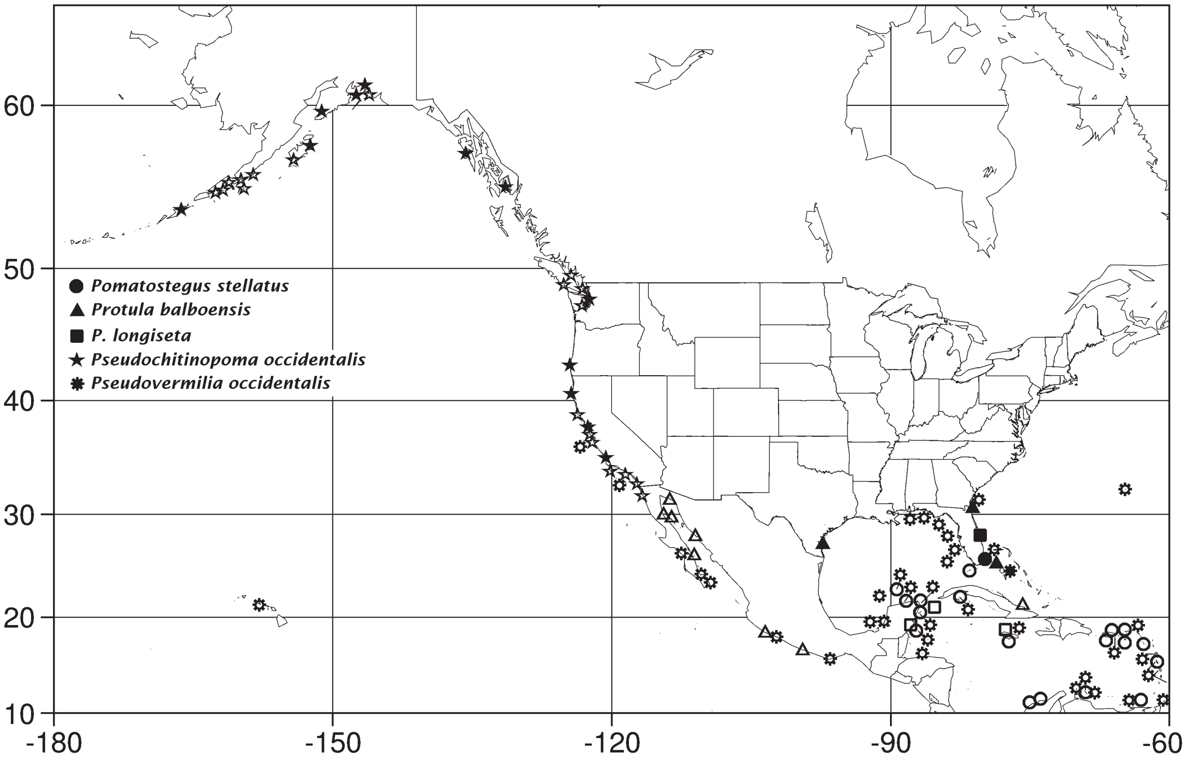

Fig. 8. Distribution of serpulids (*Pomatostegus*, *Protula*, *Pseudochitinopoma* and *Pseudovermilia* spp.) from United States fouling plates (closed symbols) and literature records (open symbols).

Taxonomic remarks

Pseudovermilia occidentalis is very common in the Caribbean Sea (ten Hove 1975) and the tropical eastern Pacific (Bastida-Zavala 2008). The species has a wide distribution; however, ten Hove (1975) noted that the populations from the Atlantic and the Pacific differ subtly in some tube, peduncle and operculum characters. Thus a thorough review of these populations is necessary.

Ecology

Intertidal to 250 m; rare and the deepest records (300–895 m) are considered doubtful (ten Hove 1975). On rocky and mixed bottoms, with seagrass and algae, on tubes of *Placostegus assimilis* (doubtful according to ten Hove 1975), tubes of sabellariid polychaetes, epibionts on spines of the sea urchin *Eucidaris*, shells of the bivalve *Spondylus limbatus*, the corals *Astrangia*, *Madracis*, *Phyllangia americana*, *Acropora*, *Pocillopora damicornis*, the sponges *Stromatospongia vermicola*, *Clathria calla* and *Agelas dispar*, and also on coral plates of *Orbicella annularis* (ten Hove 1975; Díaz 1994; Bastida-Zavala & Salazar-Vallejo 2000a; Bastida-Zavala 2008).

Distribution

Amphi-American and Amphi-Atlantic. Gulf of Mexico, Caribbean Sea, Georgia (United States) to Brazil, Gulf of Guinea, Cabo Verde and Santa Helena Islands; California, Mexican Pacific to Galapagos, Hawaii (ten Hove 1975; Bastida-Zavala 2008). In this study, only three specimens of *Pseudovermilia occidentalis* were found, on fouling plates from Biscayne Bay, Florida (Fig. 8).

Genus ***Salmacina*** Claparède, 1870

Salmacina huxleyi (Ehlers, 1887)

Figs 7H–I, 10

Filigrana huxleyi Ehlers, 1887: 314–320, pl. 56, figs 4–9 (type locality: Dry Tortugas and Loggerhead Key, southern Florida, United States; 26 m).

Salmacina dysteri (*non* Huxley 1855) – Hartman 1945: 48 (Beaufort, North Carolina; under shells and stones, shell fragments). — Rioja 1946: 202 (Veracruz, eastern Mexico; on tubes of the sabellid *Sabellastarte indica* (Savigny, 1822), now *Sabellastarte spectabilis* (Grube, 1878)). — Wells & Gray 1964: 74 (Cape Hatteras, North Carolina; hard substrates).

Salmacina sp. A – ten Hove & Wolf 1984: 55-7, figs 55-1, 55-2a–g (western Florida; 37–88 m; coarse to medium sand).

Filograna huxleyi – Perkins 1998: 95 (checklist of shallow-water polychaetes from Florida).

Salmacina huxleyi – Nogueira & ten Hove 2000: 158–159, Tables 1–2 (discussion).

Salmacina incrustans (*non* Claparède 1870) – Augener 1927: 81–82, textfig. 9 (Spaanse Water, Curaçao, Caribbean Sea; on mangrove roots). — Augener 1934: 121 (Gairaca, Santa Marta, Colombian Caribbean; 30 m). — Bastida-Zavala & Salazar-Vallejo 2000a: 812–813, fig. 4a–h (eastern Mexico: San Juan de Ulúa, Veracruz; San Felipe and Ría Lagartos, Yucatán; Puerto Morelos Beach, Nichupté Lagoon, Nizuc Point, Sam Point, Boca Paila, Contoy Island, Mujeres Island, Cozumel Island and Chinchorro Bank, Quintana Roo; intertidal to 43 m; mixed beaches, on rocks, seagrass, algae, corals, epifauna of the sea urchin *Eucidaris tribuloides* (Lamarck, 1816), the sponge *Agelas dispar*, on vermetids, oysters and ascidians, and wood dock pilings).

Material examined

115 specimens: RI (2) Sep. 2001, IR (1) Aug. 2005, BB (110) Aug. 2004, CC (2) Sep. 2002.

Diagnosis

This species is gregarious and can build colonies. Tube white, thin; with minute transverse ridges; without peristomes, longitudinal ridges or alveoli (Fig. 7H). Branchial crown with four radioles per lobe. Without opercular peduncle or operculum (Fig. 7H). Collar with fin-and-blade chaetae, with 6–7 large teeth (Fig. 7I). Thorax with 7–9 segments; all thoracic chaetigers (except collar segment) with "*Apomatus*" chaetae.

Taxonomic remarks

Salmacina huxleyi is a tiny and non-operculate serpulid, and was the first species of the genus described (as *Filigrana*) from the western Atlantic. Other *Salmacina* species, *S. dysteri* (Huxley, 1855) and *S. incrustans* Claparède, 1870, were described from Europe and recorded in several localities from the Gulf of Mexico, Caribbean Sea and eastern Pacific, among other localities around the world. There are three other species described from the western Atlantic, *S. amphidentata* Jones, 1962, *S. piranga* (Grube, 1872) and *S. ceciliae* Nogueira & ten Hove, 2000. Except for the latter species, which is well characterised, the differences between the other species (*S. amphidentata*, *S. huxleyi* and *S. piranga*) are very subtle and should be studied with scanning electron micrography (Nogueira & ten Hove 2000; Ben-Eliahu & ten Hove 2011). Therefore, we currently prefer to use the name *S. huxleyi*, the first species described from this region.

Ecology

Intertidal to 43 m. Mixed bottoms, on rocks, seagrass, algae, corals, epifauna of the sea urchin *Eucidaris tribuloides*, the sponge *Agelas dispar*, vermetids, oysters and ascidians, and wood dock pilings (Bastida-Zavala & Salazar-Vallejo 2000a).

Distribution

Gulf of Mexico, east coast of the United States and Caribbean Sea (Augener 1927; Hartman 1945; ten Hove & Wolf 1984; Bastida-Zavala & Salazar-Vallejo 2000a). In this study, *Salmacina huxleyi* was abundant on fouling plates from Biscayne Bay, Florida and occasionally from Narragansett Bay, Rhode Island, the Indian River in Florida, and Corpus Christi, Texas (Fig. 10). This species extends its northward range from Cape Hatteras, North Carolina (Wells & Gray 1964) to Rhode Island (750 km).

Salmacina tribranchiata (Moore, 1923)

Figs 7J, 10

Filograna tribranchiata Moore, 1923: 250–251 (type locality: off Santa Rosa Island, California, United States; 69–82 m; small mass of tubes on mixed bottom (mud, sand and rocks)).

Salmacina dysteri (*non* Huxley 1855) – Steinbeck & Ricketts 1941: 367 (Gulf of California: Los Angeles Bay, Baja California, and San Francisquito Island, Baja California Sur; encrusting on rocks).

Salmacina dysteri tribranchiata – Monro 1933: 1090–1091, textfig. 31 (Tagus Cove, Isabela (Albemarle) Island, Galápagos; from a marine garden sheltered from the sun by an overhanging rock). — Berkeley & Berkeley 1941: 56 (Corona del Mar, Monterey Bay and Santa Cruz Island, California; 9–31 m).

Salmacina tribranchiata – Rioja 1941b: 738–739, pl. 9, figs 11–14 (La Aguada Beach, Acapulco, Guerrero, southern Mexican Pacific; on the sabellariid *Idanthyrsus johnstoni* McIntosh, 1885, now *Idanthyrsus luciae* (Rochebrune, 1882), colonies). — Hartman 1969: 771–772, figs 1–6 (central and southern California; intertidal to shelf depths; mixed bottoms). — Nogueira & ten Hove 2000: 158–159, Tables 1–2 (discussion). — Bastida-Zavala 2008: 43, fig. 10H–J (Alaska, California, Hawaii and Mexican Pacific: Sinaloa and Oaxaca; intertidal to 116 m). — Carlton & Eldredge 2009: 62–63 (Hawaii;

invasion history); 2015: 34 (Hawaii; introduction confirmed). — Bastida-Zavala *et al.* 2016: 433–434, figs 8, 12E–F (Mexican Pacific: Baja California, Baja California Sur and Oaxaca; intertidal to 1 m; in marinas and harbors, fouling).

Filograna implexa (*non* Berkeley 1835) – Kudenov 1980: 122 (Sonora coast, Gulf of California). — Kerstitch & Bertsch 2007: 38, fig. 63 (field guide of the Gulf of California; 46 m).

Material examined

212 specimens: ST (6) Aug. 2001, MI (1) Jul. 2013, SD (205) Aug. 2000 and Jul. 2013.

Additional material

More than 12 specimens: MBL-SD s.n., 2 specimens (approx. 32°40' N, 117°25' W, off San Diego, RV, sta. E–9 and E–14, 3 Oct. 1996 and 15 Jul. 2003, 116 m and 98 m); SERC-233687, one specimen (Galapagos, photographed in vivo, by Erica Keppel, 1 May 2016, coll. SERC); UMAR-Poly 94, colony (Hawaii inter-island cargo barge, HF–023, hull fouling community roughly two years old; barge only operates in Hawaii, coll. S. Godwin).

Diagnosis

This species is gregarious and can form colonies. Tube white, thin, with transverse ridges; without peristomes, longitudinal ridges or alveoli. Branchial crown with 3–4 radioles in each lobe (Fig. 7J). Without opercular peduncle or operculum. Collar with fin-and-blade chaetae, with 3–5 big teeth. Thorax with seven segments; all thoracic chaetigers (except collar segment) with "*Apomatus*" chaetae.

Taxonomic remarks

Salmacina tribranchiata was the first species of the genus described from the eastern Pacific and as is the case for *S. huxleyi*, this name is preferred in the region until the status of species in this genus is clarified with SEM and/or molecular studies (Nogueira & ten Hove 2000; Ben-Eliahu & ten Hove 2011).

Ecology

Intertidal to 116 m (Bastida-Zavala 2008). On mixed bottoms, on rocks, on the sabellariid *Idanthyrsus luciae*, and as fouling of pier pilings (Bastida-Zavala *et al.* 2016).

Distribution

Northeastern Pacific, from Alaska to Gulf of California, Hawaii, southern Mexican Pacific and Galápagos Islands (Bastida-Zavala 2008). In this work, *Salmacina tribranchiata* was found abundantly and frequently on fouling plates from San Diego, southern California, and occasionaly from Sitka Bay, Alaska, and Mission Bay, southern California (Fig. 10).

Genus ***Serpula*** Linnaeus, 1758

Serpula columbiana Johnson, 1901

Figs 9A–B, 10

Serpula columbiana Johnson, 1901: 432–433, pl. 19, figs 199–204 (type locality: Alki Point, Puget Sound, Washington, United States).

Serpula splendens Bush, 1905: 230–232, pl. 26, fig. 3, pl. 29, fig. 2, pl. 30, figs 2–3, pl. 33, fig. 31, pl. 35, fig. 18, pl. 37, fig. 31, pl. 39, fig. 33 (type locality: Orca and Virgin Bay, Prince William Sound, southern Alaska).

Serpula nannoides Chamberlin, 1919b: 270, pl. 2, fig. 8 (type locality: off Crescent City, California).

Serpula vermicularis (*non* Linnaeus 1767) – Chamberlin 1919b: 269 (Mendocino, northern California and Gulf of Georgia (Strait of Georgia), Washington). — Berkeley 1930: 73 (Nanaimo Region). — Berkeley & Berkeley 1941: 55 (Santa Cruz Island, southern California). — Hartman 1948: 47 (Seldovia, Alaska). — Kupriyanova 1999: 24 (synonymy).

Serpula columbiana – Pixell 1912: 784–786 (Departure Bay, Canada and Puget Sound, Washington; undersides of stones on rocky shores and in rock pools). — Treadwell 1914: 225 (Puget Sound, Washington, to San Diego, southern California). — Kupriyanova 1999: 24–27, figs 1, 3, 4B, D (Alaska, Washington and California). — Bastida-Zavala 2008: 45–46, figs 11A–E (Washington and California; 30–60 m; on bottoms with coralline sand and kelp, on shells, cobble and boulders).

Serpula splendens – Kupriyanova 1999: 24 (synonymy).

Serpula nannoides – Bastida-Zavala 2008: 45 (synonymy).

Material examined

One specimen: KT (1) Sep. 2003.

Diagnosis

Tube missing. Opercular peduncle smooth, white, with marked constriction. Operculum funnel symmetric, with 46 radii with blunt tips, and concave inner surface, with numerous tiny conical tubercles (Fig. 9A). Collar with bayonet chaetae, with two blunt, short teeth, smooth distal blade. In adult forms, *Serpula columbiana* has an operculum with 55–160 radii (Fig. 9B) and a symmetric funnel (Kupriyanova 1999).

Taxonomic remarks

The status of *Serpula columbiana* was resolved by Kupriyanova (1999). It is mainly a sublittoral species that is extremely unlikely to belong to the fouling fauna.

Ecology

Intertidal to 60 m. Under stones on the shore-line, in rock-pools (Pixell 1912), and on bottoms with coralline sand and kelp, on shells, cobble and boulders (Bastida-Zavala 2008).

Distribution

Northeastern Pacific, from Alaska to southern California (San Diego) (Kupriyanova 1999; Bastida-Zavala 2008). In this work, only one specimen of *Serpula columbiana* was found on a fouling plate from Ketchikan Bay, Alaska (Fig. 10).

Genus ***Spirobranchus*** de Blainville, 1818

Spirobranchus kraussii (Baird, 1865)

Figs 9C–E, 10

Pomatoleios cariniferus var. Kraussii Baird, 1865: 13–15 (type locality: Promontorio Bonae Spei [= Cape of Good Hope], South Africa).

Pomatoleios crosslandi Pixell, 1913: 85–86, pl. 9, fig. 10 (type locality: Ras Shangani and Chwaka, Zanzibar, Tanzania, East Africa).

Pomatoleios kraussii – Day 1967: 800–801, fig. 38.3a–f, Cape and Natal (now KwaZulu-Natal), South Africa and Mozambique). — Straughan 1967: 235 (Queensland, Australia; intertidal; forming colonies). — Straughan 1969: 235–236 (Coconut Island (or Moku o Lo‘e), Hawaii; intertidal to 1.5 m; rocks and coral rubble on reef flat and on fouling plates). — Imajima 1976a: 135–136 (Tanegashima Island, southern Japan). — Bailey-Brock 1976: 77–78 (Oahu Island, Maui Island and Hawaii

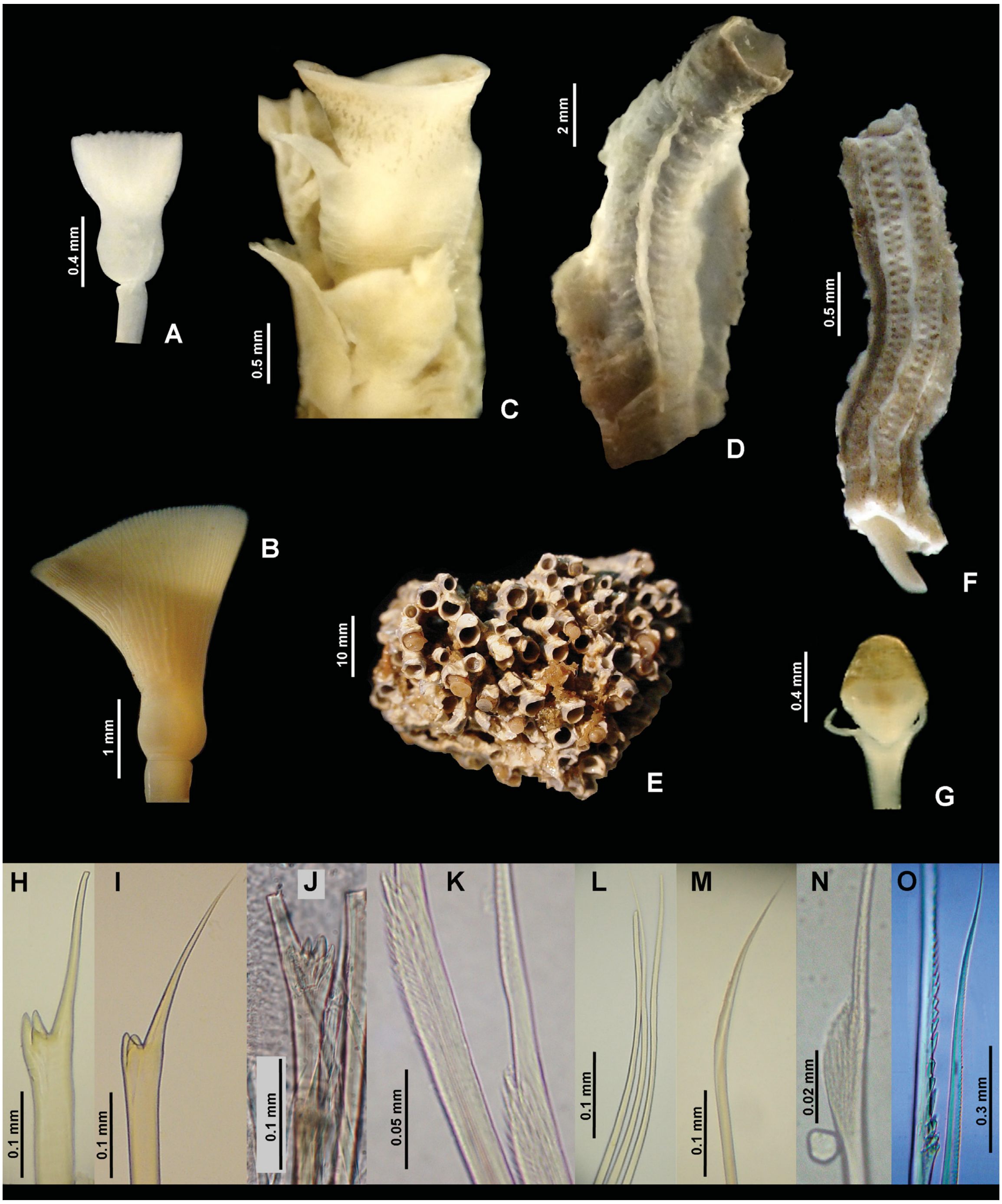

Fig. 9. Serpulids from United States fouling plates. *Serpula columbiana*. **A**. Operculum, from Ketchikan Bay, Alaska (SERC-81981). **B**. Operculum, adult from San Diego, California (LACMNH-Poly4928);. – *Spirobranchus kraussii*. **C-D**. Operculum and tube fragment, from Oahu, Hawaii (SERC-114603). **E**. Colony, from Natal, South Africa (LACMNH-N5217). – *S. minutus*. **F**. Tube, from Santa Catarina, Brazil (USNM-43239). **G**. Operculum, From Tampa Bay, Florida (SERC-93759). Types of collar chaetae. **H–J**. Bayonet. **K**. Bayonet with proximal rasp. **L**. Capillaries. **M**. Limbate. **N**. Fin-and-blade chaetae. **O**. Coarsely serrated. – *Hydroides sanctaecrucis* (**H**, **L**). – *H*. cf. *brachyacantha* (**I**). – *Spiraserpula ypsilon* (**J**). – *H. elegans* (**K**). – *H. ochotereana* (**M**).– *Pseudochitinopoma occidentalis* (**N**).– *Ficopomatus uschakovi* (**O**, modified from Arteaga-Flórez *et al.* 2014).

Island; rocky intertidal, reef flats, epifauna of mobile substrata (mollusks and crustaceans) and boat harbors). — Imajima 1977: 100–101 (Ogasawara Islands, southern Japan; intertidal; on reefs and rocks in sheltered areas). — Imajima 1978: 54–56, fig. 3a–j (Ō-shima Island, southern Japan; intertidal). — Imajima 1979: 178 (Sabiura and near Andonohana, Shionomisaki Cape, southern Japan; intertidal, on rock). — Zibrowius 1979: 133–134 (Toulon, France: on hull of the aircraft carrier "Foch" and the navy ship "Balny" after returning from Indian Ocean missions via the Suez Canal and western Africa, respectively). — Imajima 1982: 50 (Arumizu Bay, Palau Islands). — Bailey-Brock 1987: 421, fig. 3.11.193 (Hawaii; on intertidal reefs flats and in shallow subtidal waters). — Ben-Eliahu & ten Hove 1992: 37–44, 52–53 (Israel, as Lessepsian migrant; intertidal to 6 m; on the gastropod *Thais haemostoma* (Linnaeus, 1758), now *Stramonita haemastoma*, on or under rocks, and on asbestos plates). — ten Hove & van den Hurk 1993: 35, fig. 3A (discussion about serpulids and intertidal zonation). — Nishi 1993: 30–31, figs 1–2 (Okinawa Island, Southwest Japan; fouling on piers and concrete wall). — Ishaq & Mustaquim 1996: 172–174, fig. 7A–F (Karachi, Pakistan; intertidal; on rocks and buoy). — Fiege & Sun 1999: 130–131, fig. 18A–D (Hainan Island, South China Sea). — Çinar 2006: 231, fig. 8 (as NIS from eastern Levantine coast of Turkey). — Bastida-Zavala 2008: 33, fig. 7N–O (brief diagnosis). — Carlton & Eldredge 2009: 62 (Hawaii; invasion history). — Ben-Eliahu & ten Hove 2011: 43–45 (Israel and Suez Canal; 0.5–6 m; on the gastropod *S. haemastoma*, under stones, and on artificial substrates such as a breakwater and asbestos plates). — Sun *et al.* 2012: 28–30, fig. 12A–F (Hong Kong; intertidal to 1 m; rocky bottom). — Carlton & Eldredge 2015: 34 (Hawaii; introduction confirmed).

Pomatoleios crosslandi – Lakshmana Rao 1969: 9–10, pl. 7, figs a–e (Visakhapatnam, Madras, now Chennai, and Bombay, now Mumbai, India; harbours).

Spirobranchus kraussii – Pillai 2009: 146–148, 168, fig. 49E–G, new combination (United Arab Emirates, Persian Gulf).

Material examined

One specimen: HI (1) Sep. 2006.

Additional material

More than 100 specimens: colony, from Umhlali, Natal, South Africa (LACMNH-N5217).

Diagnosis

Tube white, apparently broken, with a longitudinal ridge (Fig. 9D). Opercular peduncle yellowish, with triangular, smooth and thick wings (Fig. 9C). Operculum yellowish, with slightly concave calcareous plate (Fig. 9C). Without collar chaetae. Based on the size, this specimen is an adult (Fig. 9C).

Taxonomic remarks

Specimens from Natal, South Africa (LACMNH-N5217), build colonies; however, material from this locality differed slightly from our specimen (from Hawaii) and from the original description in that the tubes have two longitudinal ridges ending in a flap above the mouth of the tube (Fig. 9E), while our only specimen had a single longitudinal ridge. This was in line with the original description which says "…dorsal keel is perhaps rather flatter and less sharp-pointed at its extremity" (Baird 1865: 15). Comparison of the different populations of *Spirobranchus kraussii* from the Indian Ocean, the western Pacific and Hawaii should be reexamined together to facilitate a genus revision.

Although *Spirobranchus kraussii* is a very common fouling species that attaches to many different types of artificial substrate (Straughan 1969; Bailey-Brock 1976; Zibrowius 1979; Ben-Eliahu & ten Hove 1992; Nishi 1993), it was only recorded once in our surveys.

Ecology

Intertidal to 6 m (Ben-Eliahu & ten Hove 1992). The nominal species is found on or under intertidal rocks, coral rubble on the reef flat, as epifauna of mobile substrata (mollusks and crustaceans), on the gastropod *Stramonita haemastoma*, and artificial substrates such as asbestos plates, fouling plates, piers, concrete wall, breakwaters, buoys, in boat harbours and the hulls of navy ships (Straughan 1967; Bailey-Brock 1976; Zibrowius 1979; Ben-Eliahu & ten Hove 1992; Nishi 1993; Ishaq & Mustaquim 1996; Ben-Eliahu & ten Hove 2011).

Distribution

The nominal species has an Indo-Pacific distribution: South Africa, Mozambique, Tanzania, Red Sea, Persian Gulf, India, Australia, southern Japan, Palau Island, Hawaii (Pixell 1913; Day 1967; Straughan 1967, 1969; Ishaq & Mustaquim 1996; Pillai 2009); and as NIS in the Mediterranean Sea (Zibrowius 1979; Ben-Eliahu & ten Hove 1992). In this survey, only one specimen of *Spirobranchus kraussii* was found, on a fouling plate from Oahu, Hawaii (Fig. 10).

Spirobranchus minutus (Rioja, 1941b)

Figs 9F–G, 10

Pomatoceros minutus Rioja, 1941b: 734–738, pl. 9, figs 15–26 (type locality: Acapulco, Guerrero, Mexican Pacific; on the hydrozoan *Pennaria*).

Serpulorbis catella Weisbord, 1962: 156–157, pl. 13, figs 17–18 (fossil, type locality: Lower Mare and Abisinia formations, Venezuelan Pliocene and Pleistocene; on bivalve shell).

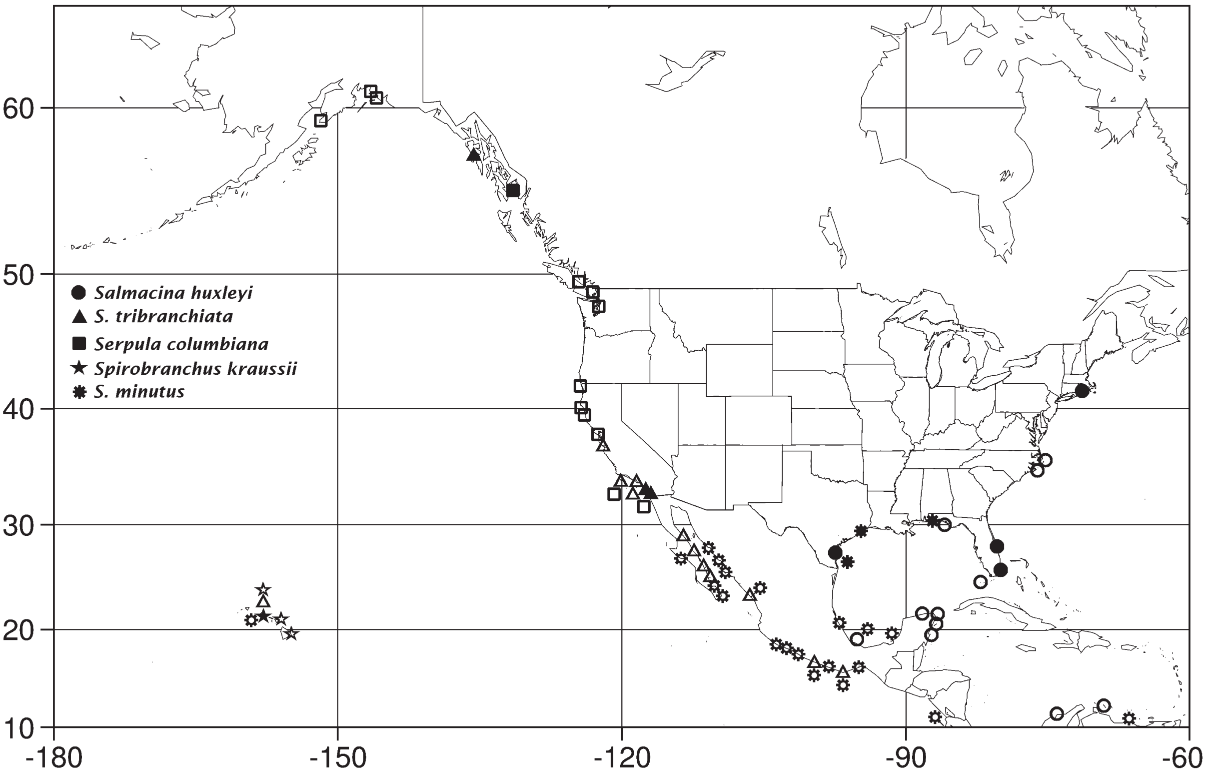

Fig. 10. Distribution of serpulids (*Salmacina*, *Serpula* and *Spirobranchus* spp.) from United States fouling plates (closed symbols) and literature records (open symbols).

Pomatoceros minutus – Rioja 1942: 130–132, figs 15–21 (Mazatlán, Sinaloa, and Río Mayo, Sonora, Mexican Pacific; 15 m; on shell of the bivalve *Avicula* sp., now *Pteria*). — Rioja 1946: 201–202 (Veracruz, eastern Mexico; on algae entangled in fishing nets). — Rioja 1947a: 215 (Gulf of California: Mapahui, Topolobampo and Navachiste, Sinaloa, Mexico). — Berkeley & Berkeley 1958: 405 (west coast of Baja California Peninsula: Abreojos Point, Baja California Sur; floating seaweed). — Weisbord 1964: 161–164, pl. 21, figs 4–5, pl. 22, figs 3–4 (recent, Playa Grande Yachting Club and Higuerote beaches, northern Venezuela; on several mollusk shells; and fossil, same as *Serpulorbis catella*). — Zibrowius 1970: 15–16, pl. 3, figs 11–15 (São Sebastião and Ubatuba, Brazil; 6–15 m; on rocks, madrepores and gorgonians). — Shepherd 1972: 5 (Gulf of California: La Paz Bay, Baja California Sur; epifauna on *Pinctada mazatlanica* (Hanley, 1856)). — Bastida-Zavala 1993: 35 (Gulf of California: Caimancito Beach, Baja California Sur). — Perkins 1998: 95 (checklist of shallow-water polychaetes of Florida). — Lewis *et al.* 2006: 669 (ten Hove collected specimens from the sailing vessel "Gorch Fock" in Sydney, Australia). — Bastida-Zavala 2008: 31–33, fig. 7H–M (Hawaii, Mexican Pacific: Baja California Sur, Guerrero and Oaxaca, Pacific side of Costa Rica and Perú; intertidal to 17 m; on dead coral (*Pocillopora*), the gastropod *Muricanthus*, the oyster *Spondylus*, mangrove roots, sabellariid colony, on a pier piling and a sailboat hull).

Pomatoceros caeruleus (*non* Schmarda 1861) – Rioja 1963: 220 (Mexican Pacific: Mazatlán, Sinaloa, Guaymas, Sonora, and Zihuatanejo, Guerrero; on algae and mollusk shells).

Placostegus sp. – Bastida-Zavala 1995: 25 (Gulf of California: Cabo Pulmo Reef, Baja California Sur, Mexico; 4–17 m; on coral).

Pomatoleios crosslandi (*non* Pixell 1913) – Bastida-Zavala 1995: 25 (Gulf of California: Cabo Pulmo Reef, Baja California Sur, Mexico; 17 m; on coral).

Pomatoceros cf. *minutus* – Bastida-Zavala & Salazar-Vallejo 2000a: 814–815, fig. 5a–f (eastern Mexico: Cazones, Veracruz, and Campeche Bank, Campeche; 42 m).

Spirobranchus minutus – Pillai 2009: 146–148 (new combination). — Bastida-Zavala *et al.* 2016: 435–437, figs 8, 13H (Mexican Pacific: Baja California Sur, Michoacán, Guerrero and Oaxaca; intertidal to 1 m; in marinas and harbors, fouling).

Material examined

108 specimens: PB (59) Aug. 2002, GB (3) Sep. 2002, CC (46) Sep. 2002.

Additional material

Ten specimens: UMAR-Poly 73, several specimens (approx. 21°17' N, 157°50' W, Honolulu, HF-018, on the hull of a sailboat that traveled to Hawaii from San Francisco via Los Angeles, Mexico, Hilo, Hawaii and finally reached Honolulu; the entire travel period was four months, coll. S. Godwin); USNM-43239, three specimens (Santa Catarina, Brazil, sta. 45 and 47, Nov. 1965, coll. Jones-Lowe).

Diagnosis

Tube white, with three longitudinal ridges and rows of alveoli between ridges; without peristomes (Fig. 9F). Opercular peduncle with thin distal wings, white (Fig. 9G). Operculum conical, with calcareous distal plate, with rounded tip (Fig. 9G). With 2–3 limbate collar chaetae, but sometimes lacking collar chaetae altogether; with a glandular spot in the position of the collar chaetae.

Taxonomic remarks

Spirobranchus minutus was recorded for the first time during our survey from the northern Gulf of Mexico (Galveston Bay and Corpus Christi, Texas) and Florida (Pensacola Bay).

In several specimens of *S. minutus*, the opercular peduncle lacks wings or has tiny wings. Another similar species in the northern Gulf of Mexico, *S. americanus* Day, 1973, has a sublittoral (>40 m) distribution. *Spirobranchus americanus* has more collar chaetae (4–6), a fully calcareous operculum, only one longitudinal ridge on the tube and has one line of alveoli on each side of the tube, while *S. minutus* has fewer collar chaetae (2–3) or lacks them completely, an operculum with a calcareous plate on a chitinous base, and the tube has three longitudinal ridges and two lines of alveoli on each side of the tube (Fig. 9F).

Ecology

Intertidal to 42 m (Bastida-Zavala & Salazar-Vallejo 2000a). On rocks, on the hydrozoan *Pennaria*, mollusk shells (*Pteria* sp., *Pinctada mazatlanica*, *Muricanthus*, *Spondylus*), the coral *Pocillopora*, gorgonians, sabellariid colony, algae, mangrove roots, floating seaweed, on a marina pier piling and sailboat hulls (Rioja 1941b, 1942, 1946; Berkeley & Berkeley 1958; Zibrowius 1970; Lewis *et al.* 2006; Bastida-Zavala 2008).

Distribution

Amphi-American. Eastern tropical Pacific, from Gulf of California to Perú; Hawaii; western tropical Atlantic, from Gulf of Mexico to southern Brazil (Zibrowius 1970; Bastida-Zavala & Salazar-Vallejo 2000a; Bastida-Zavala 2008). In this study, *Spirobranchus minutus* was abundant on fouling plates from Pensacola Bay, Florida, and Corpus Christi, Texas, and was found occasionally on plates from Galveston Bay, Texas (Fig. 10). This species extends its northward range from Cazones, Veracruz (Bastida-Zavala & Salazar-Vallejo 2000a) to Pensacola Bay, Florida (1450 km).

Discussion

The greatest species richness of serpulids on fouling plates occurred in Biscayne Bay, Florida (14 species) and Corpus Christi, Texas (eight species) (Table 1). Overall, the faunistic composition of the serpulids (25 species) found on fouling plates represents only 40.3% of the total number of serpulids (62) recorded from shallow waters (intertidal to 50 m deep) of both coasts of the United States, including Alaska and Hawaii (Table 2). This checklist was made with the information updated by ten Hove (1975), ten Hove & Jansen-Jacobs (1984), ten Hove & Wolf (1984), Bailey-Brock (1987), Perkins (1998), Bastida-Zavala & ten Hove (2002, 2003), Bastida-Zavala (2008) and Bastida-Zavala *et al.* (2016).

Considering shallow-water species richness by coast, of the 22 known species of serpulids on the east coast, 16 (72.7%) were found on fouling plates; of the 39 serpulids species from the northern Gulf of Mexico, 12 (30.8%) were found on fouling plates; on the west coast there are 17 known serpulids, of which nine (52.9%) were found on fouling plates; on the Hawaiian coast there are 16 serpulids, of which five (31.3%) were found on the plates in our study (Tables 1 and 2). Thus, the proportion of the known fouling species collected in this study was variable among regions, with the east coast having the highest proportion of fouling species and the northern Gulf of Mexico with the lowest proportion.

The pattern of decreasing diversity as one moves from the equator to the poles, seen in many different marine taxa (Ruiz *et al.* 2000; Ruiz & Hewitt 2009; Ruiz *et al.* 2009) is evident for the fouling serpulids on plates for the east coast, but the pattern is less clear for the west coast (Table 1). In general, the sites in colder waters, for instance Alaska, have fewer species (and NIS records) and a higher proportion of fouling serpulids (2–3 species), than the temperate-subtropical sites in southern California (3–4) (Table 1).

In the panel survey, more species of serpulids were detected in the genus *Hydroides* (10 species, 40% of the total) than in any other genus of serpulid (Table 1). Three of these species are on the west coast, eight on the east coast, six in the northern Gulf of Mexico, and three in Hawaii, reflecting the mostly tropical distribution of this genus. However, *H. dianthus* was, by far, the most abundant species, with

1787 specimens (41%) on fouling plates from the northern Gulf of Mexico and the east coast, including Rhode Island, which is a site with seasonally cold water. *Pseudochitinopoma occidentalis* was the most abundant species along the west coast, with 658 specimens (15%).

Many of the common serpulid species recorded historically in the Gulf of Mexico and on the Pacific coast, such as *Crucigera websteri*, *Hydroides bispinosa*, *H. crucigera*, *H. protulicola* Benedict, 1887, *H.* cf. *mucronatus* Rioja, 1958, *Pseudovermilia occidentalis*, *Serpula columbiana*, *Spirobranchus americanus*, were not recorded in this study or were found very occasionally (Tables 1 and 2). This may reflect substrate specificity of serpulid larvae, but it may also result from the specific sampling strategy used in this study, including the substrate used (PVC plates), season and exposure time, the specific habitat sampled (urban embayments), the relatively high average salinities (>20ppt) and the depth of the plates at the sites. Previous work with fouling plates suggests that this substrate may preferentially attract non-native species (deRivera *et al.* 2005; Ruiz *et al.* 2006) which were the focus of the field survey.

Of the 25 serpulid species found in this survey, three are known NIS (*Ficopomatus enigmaticus*, *F. uschakovi* and *Spirobranchus minutus*), two are presumably NIS (*Protula balboensis* and *Pseudovermilia occidentalis*) pending further research to confirm this status, and three are cryptogenic (*Hydroides dianthus*, *H. dirampha* and *H. elegans*).

In this study, the proportion of NIS (including the two presumed NIS) and cryptogenic species detected was variable among the four major regions, but together always comprised at least 30% of the species present on fouling plates (Table 2). On the east coast, 16 serpulids were found on fouling plates, and of these, six (37.5%) were NIS or cryptogenic. The northern Gulf of Mexico had the highest proportion of NIS and cryptogenic species with seven out of twelve (58.3%). On the west coast, nine species were sampled and three of them (33.3%) were NIS or cryptogenic, while on the fouling plates from Hawaii two of five serpulids (40%) were cryptogenic (Tables 1 and 2). In contrast, considering just Alaskan localities (Table 1), only four serpulids were found on fouling plates, but none were NIS or cryptogenic. Biscayne Bay, Florida, and Corpus Christi, Texas, were the localities with greatest species richness and also with the greatest number of NIS found in this survey. In Biscayne Bay, 14 serpulid species were found, five of which were NIS or cryptogenic (35.7%), while Corpus Christi had a total of eight serpulid species of which five (62.5%) were NIS or cryptogenic (Tables 1 and 2). It is worth noting that two NIS (*F. enigmaticus* and *H. elegans*) historically recorded from Corpus Christi were not detected on fouling plates in this survey.

The three known non-indigenous (*Ficopomatus enigmaticus*, *F. uschakovi*, and *Spirobranchus minutus*) and three cryptogenic serpulids (*Hydroides dianthus*, *H. dirampha*, and *H. elegans*) were present frequently and abundantly on the plates, while the two presumed NIS (*Protula balboensis* and *Pseudovermilia occidentalis*) were present occasionally or rarely (Tables 1 and 2). Two cryptogenic species, *Hydroides dirampha* and *H. elegans*, are present on fouling plates from all four regions of the United States (east and west coast, Gulf Coast and Hawaii). In this study, all historical records of non-indigenous serpulids on the mainland coasts of North America were detected on fouling plates. In contrast, three known NIS (*F. enigmaticus*, *Hydroides crucigera* Mörch, 1863 and *S. minutus*) and three presumed NIS (*Protula atypha*, *Pseudovermilia occidentalis* and *Serpula watsoni* Wiley, 1905) historically recorded from Hawaii were not detected on fouling plates in this survey (Tables 1 and 2), highlighting a different situation for the islands.

First records and range extensions

During this study, three first records were detected for North America *Ficopomatus uschakovi*, *Hydroides* cf. *brachyacantha* and *Protula longiseta.* There are no new records for the mainland west coast, but *H.*

Table 2 (continued next page)**.** Checklist of the 62 serpulids recorded in continental United States and Hawaii shallow waters (< 50 m) with their geographical distribution. Notes: ● = literature record; ★ = found in this survey; ✧ = first record here; CRY = cryptogenic species; NIS = non-indigenous records; presumed NIS records are marked with a "?"; F = observed frequently (n > 20 specimens) on plates; O = observed occasionally (N ≤ 20) on plates; R = observed rarely (n = 1–3) on plates.

–	United States				Relative abundance found here on fouling plates
Serpulids	East Coast	Gulf Coast	West Coast	Hawaii	
Crucigera irregularis Bush, 1905	–	–	●	–	–
C. websteri Benedict, 1887	–	●	★	–	**R**
C. zygophora (Johnson, 1901)	–	–	★	–	**F**
Ficopomatus enigmaticus (Fauvel, 1923)	★ **NIS**	★ **NIS**	★ **NIS**	● **NIS**	**F**
F. miamiensis (Treadwell, 1934)	★	★	–	–	**F**
F. uschakovi (Pillai, 1960)	✧ **NIS**	✧ **NIS**	–	–	**F**
Filogranella sp. in Fosså & Nielsen 1996	–	●	–	–	–
Filogranula calyculata (Costa, 1861)	–	●	–	–	–
Hydroides cf. *amri* Sun *et al.*, 2015	–	–	–	●	–
H. bispinosa Bush, 1910	★	●	–	–	**O**
H. brachyacantha Rioja, 1941a	–	–	●	–	–
H. cf. *brachyacantha* Rioja, 1941a	✧	✧	–	–	**O**
H. crucigera Mörch, 1863	–	–	–	●	–
H. dianthus (Verrill, 1873)	★ **CRY**	★ **CRY**	–	–	**F**
H. dirampha Mörch, 1863	★ **CRY**	✧ **CRY**	★ **CRY**	★ **CRY**	**F**
H. elegans (Haswell, 1883)	★ **CRY**	★ **CRY**	★ **CRY**	★ **CRY**	**F**
H. floridana (Bush, 1910)	★	★	–	–	**O**
H. gairacensis Augener, 1934	●	●	–	–	–
H. gracilis (Bush, 1905)	–	–	★	–	**F**
H. longispinosa Imajima, 1976b	–	–	–	✧	**R**
H. microtis Mörch, 1863	●	●	–	–	–
H. mongeslopezi Rioja, 1958	–	●	–	–	–
H. cf. *mucronatus* Rioja, 1958	–	●	–	–	–
H. parva (Treadwell, 1902)	★	●	–	–	**R**
H. protulicola Benedict, 1887	●	●	–	–	–
H. sanctaecrucis (Krøyer in Mörch, 1863)	★	★	–	–	**F**
H. spongicola Benedict, 1887	●	●	–	–	–
Hydroides sp. A in ten Hove & Wolf 1984	–	●	–	–	–
Josephella marenzelleri Caullery & Mesnil, 1896	–	●	–	–	–
Placostegus californicus Hartman, 1969	–	–	●	–	–
P. incomptus Ehlers, 1887	–	●	–	–	–
Pomatostegus stellatus (Abildgaard, 1789)	★	–	–	–	**R**
Protula atypha Bush, 1905	–	–	●	● **NIS?**	–
P. balboensis Monro, 1933	★ **NIS?**	★ **NIS?**	–	–	**O**
P. longiseta Schmarda, 1861	✧	–	–	–	**R**
P. setosa (Bush, 1910)	–	●	–	–	–
Protula sp. A in ten Hove & Wolf 1984	–	●	–	–	–
Pseudochitinopoma occidentalis (Bush, 1905)	–	–	★	–	**F**
Pseudovermilia conchata ten Hove, 1975	–	–	●	–	–
P. fuscostriata ten Hove, 1975	–	●	–	–	–
P. multispinosa (Monro, 1933)	–	●	–	–	–
P. occidentalis (McIntosh, 1885)	★	●	● **NIS?**	● **NIS?**	**R**
Pyrgopolon ctenactis (Mörch, 1863)	–	●	–	–	–
Rhodopsis pusilla Bush, 1905	●	–	–	–	–
Salmacina huxleyi (Ehlers, 1887)	★	★	–	–	**F**
S. tribranchiata Moore, 1923	–	–	★	★	**F**
Salmacina sp. A in ten Hove & Wolf 1984	–	●	–	–	–
Semivermilia pomatostegoides (Zibrowius, 1969b)	–	–	–	●	–
Serpula columbiana Johnson, 1901	–	–	★	–	**R**
S. watsoni Willey, 1905	–	–	–	●	–
Serpula sp. A in ten Hove & Wolf 1984	–	●	–	–	–

Table 2 (continued)**.**

–	United States				Relative abundance found here on fouling plates
Serpulids	East Coast	Gulf Coast	West Coast	Hawaii	
Spiraserpula caribensis Pillai & ten Hove, 1994	–	●	–	–	–
S. ypsilon Pillai & ten Hove, 1994	–	●	–	–	–
Spirobranchus americanus Day, 1973	●	●	–	–	–
S. corniculatus (Grube, 1862)	–	–	–	●	–
S. giganteus (Pallas, 1766)	–	●	–	–	–
S. kraussii (Baird, 1865)	–	–	–	★	**R**
S. latiscapus (Marenzeller, 1885)	–	–	–	●	–
S. minutus Rioja, 1941b	–	**★ NIS**	–	**● NIS**	**F**
S. spinosus Moore, 1923	–	–	●	–	–
Vermiliopsis annulata (Schmarda, 1861)	–	●	–	–	–
V. multiannulata Gravier, 1906	–	–	●	●	–
Total species: 62 **Number of species**	**22**	**39**	**17**	**16**	**25**
Species found on fouling plates	**16**	**12**	**9**	**5**	–
Non-indigenous records in this survey	**2**	**3**	**1**	**0**	–
Presumed non-indigenous species in this survey	**1**	**1**	**0**	**0**	–
Cryptogenic species records in this survey	**3**	**3**	**2**	**2**	–

longispinosa is a new record for Hawaii. *Ficopomatus uschakovi* and *H.* cf. *brachyacantha* are both new records for the east coast, and northern Gulf of Mexico. *Protula longiseta* is the first record for the east coast, and *H. dirampha* the first for the northern Gulf of Mexico.

New records are noted for 14 species in 14 different localities (including the finding of *Hydroides elegans* in Eel Pond, Cape Cod, Massachusetts), mostly from the east coast and northern Gulf of Mexico (see Table 1). Note that some of these records are based on only one specimen, so further surveys are necessary to confirm their establishment (see individual species distribution sections for details).

On the northern Gulf of Mexico, seven first records were detected, mostly in Texas and one in Pensacola Bay, Florida (*H.* cf. *brachyacantha*). Corpus Christi, Texas, with six species (*F. miamiensis*, *F. uschakovi*, *H. dirampha*, *H. floridana*, *P. balboensis*, and *Spirobranchus minutus*), is the locality with the greatest number of new records, followed by Galveston Bay, Texas, with four new records (*F. enigmaticus*, *F. miamiensis*, *F. uschakovi* and *S. minutus*), the only locality where all three species of *Ficopomatus* were detected together on the fouling plates.

On the east coast, three first records were recognized in this study, along with five new locality records for previously reported species. The new locality records include: Charleston, South Carolina and Chesapeake Bay, Virginia (*F. enigmaticus*), Narragansett Bay, Rhode Island (*Salmacina huxleyi*), and the Indian River, Florida (*F. enigmaticus* and *Protula longiseta*). First records are reported for Biscayne Bay (*F. uschakovi* and *H.* cf. *brachyacantha*), and Jacksonville, Florida (*F. uschakovi*).

From the west coast, for all localities from central and northern California, there are four new locality records, one each for Morro Bay and San Francisco Bay (*H. gracilis*) and two for Humboldt Bay (*Crucigera websteri* and *H. elegans*).

New distributional records of several of these species could reflect natural short range dispersal or human spread, resulting in range extensions. For instance, *H. floridana* was recorded here for the first time from Corpus Christi, Texas, although it is a common species at other sites in the Gulf of Mexico and on the east coast (Bastida-Zavala & ten Hove 2002). *Hydroides* cf. *brachyacantha* extends its northward range from Curaçao to Pensacola Bay, Florida (Bastida-Zavala & ten Hove 2002), a new record for the United States, while *H. longispinosa*, described from southern Japan and recorded in the South China Sea, Micronesia, Melanesia and eastern Australia, extends its range in the Pacific from the Marshall Islands to Hawaii. *Protula balboensis*, originally described from the Pacific side of Panama and recorded previously from Brazil, Florida and Cuba (Zibrowius 1970; Perkins 1998; Bastida-Zavala & Salazar-Vallejo 2000a), is now recorded in Corpus Christi, Texas. Although it is probable that some previous records of shallow-water *Protula* species have been misidentified (ten Hove & Wolf 1984), this distribution is likely the result of human-aided dispersal through shipping or other means.

Non-indigenous species

Three non-indigenous and two presumed non-indigenous species, belonging to the Serpulidae *sensu stricto*, are spreading or have been naturalized along the United States coast.

Ficopomatus enigmaticus, although described from northern France, is thought to be from southern Australia (ten Hove & Weerdenburg 1978; Styan *et al*. 2017), and it is one of the serpulid NIS with the most extensive distribution and oldest records in the United States, presenting the greatest number (five) of new locality records in this survey. This serpulid was recorded almost 100 years ago from Lake Merritt, California (Fauvel 1933; Carlton 1979; Cohen & Carlton 1995). In the northern Gulf of Mexico, it was first recorded more than 60 years ago from Rockport, Texas (Hartman 1952), and recorded in Hawaii about 80 years ago from Ala Wai Canal, Kewalo Basin and Pearl Harbor (Straughan 1969). All of these first records are in harbors visited by both commercial and military vessels. On the east coast, *F. enigmaticus* was recorded almost 40 years ago from Barnegat Bay, New Jersey (Hoagland & Turner 1980) near a power plant effluent. The species has spread in subtropical and temperate waters worldwide introduced by ship transport and/or translocation of oysters for culture.

Ficopomatus uschakovi, an Indo-Pacific species which probably arrived by artificial means, is now recorded in Florida (Jacksonville) and in Texas (Mississippi, Galveston Bay and Corpus Christi), presenting the second greatest number (four) of new locality records in this survey (Fig. 3). The original distribution of this species was India, Sri Lanka, Sonda Archipelago, and eastern Australia (ten Hove & Weerdenburg 1978). Since the 1950's, the species has been recorded in the Gulf of Guinea, Western Africa. Recently, it was recorded from eastern Brazil (de Assis *et al.* 2008), Chiapas, the southern Mexican Pacific (Bastida-Zavala & García-Madrigal 2012), Venezuela (Liñero-Arana & Díaz-Díaz 2012) and the Colombian Caribbean (Arteaga-Flórez *et al.* 2014). In this work, the species is recorded in the northern Gulf of Mexico and the U.S. east coast and, likely, has been present since at least 1997 (USNM and SERC, collection data).

Protula balboensis was described from the Pacific coast of Panama (Monro 1933). Later, it was recorded from the Mexican Pacific (Steinbeck & Ricketts 1941; Rioja 1942, 1963; Bastida-Zavala 2008) and from Bocas del Toro, on the Atlantic coast of Panama (Bastida-Zavala *et al.* 2016). It was also recorded in Brazil (Zibrowius 1970), Florida (Perkins 1998) and from northeastern Cuba (Bastida-Zavala & Salazar-Vallejo 2000a). In this study, the species was recorded from Corpus Christi, Texas, and from Jacksonville and Biscayne Bay, Florida. This species has probably spread across the tropical western Atlantic through ship transport.

Pseudovermilia occidentalis is a tropical western Atlantic species (McIntosh 1885). This species was recorded more than 70 years ago from Hawaii (Treadwell 1943), while on the west coast, it was reported almost 50 years ago from central and southern California (Hartman 1969). The species has a wide distribution (Amphi-American and Amphi-Atlantic) but was rare on the fouling plates, with only three specimens found from Biscayne Bay, Florida. An extensive revision of the species was recommended by ten Hove (1975).

Spirobranchus minutus was described from the Mexican Pacific (Rioja 1941b). Later, Rioja (1946) and Bastida-Zavala & Salazar-Vallejo (2000a) recorded *S. minutus* from Veracuz, in the southern Gulf of Mexico, Zibrowius (1970) recorded it from Brazil and Perkins (1998) from Florida. Recently, it was recorded from Honolulu, Hawaii (Bastida-Zavala 2008). In this survey, *S. minutus* was recorded from Corpus Christi and Galveston Bay, Texas, and from Pensacola Bay, Florida. This species has probably spread across the Gulf of Mexico through ship transport.

Cryptogenic species

Three cryptogenic species, belonging to the Serpulidae *sensu stricto*, were documented along the United States coast.

Hydroides dianthus, the most abundant species on fouling plates in this study, has been considered native to the US east coast (Bosc 1801; Verrill 1873), in part based on a long fossil record of a serpulid species in a region where *H. dianthus* was the only serpulid present (Wilson 1905; Cushman 1906; Richards 1933; Oldale *et al.* 1982). However, recent molecular studies suggest a possible Mediterranean origin (Sun *et al.* 2016a, 2017). If this is the case, this species is the oldest serpulid introduction in the United States, as it has been present along the US east coast at least since the end of the nineteenth century. Further complicating the story, Sun *et al.* (2017) also suggest the presence of a complex of species in the group that are indistinguishable morphologically. Until further evidence and analysis of both the genetic and paleontological data is provided, the species is considered here as cryptogenic.

Hydroides dirampha is considered a cryptogenic species, although Zibrowius (1992) and Ben-Eliahu & ten Hove (2011) suggest that its origin is likely the Caribbean Sea. If this is the case, it throws into question its introduced status along the US east coast and northern Gulf of Mexico. This species has been present in Hawaii for at least 110 years in Oahu (Ehlers 1905). Along the US west coast, *H. dirampha* was recorded almost 20 years ago from San Diego, California (Bastida-Zavala & ten Hove 2003). The species has spread in tropical and subtropical waters worldwide through ship transport.

Hydroides elegans is another species mentioned as cryptogenic, although some authors consider it to be of Australian origin (Ben-Eliahu & ten Hove 2011; Sun *et al.* 2015; Bastida-Zavala *et al.* 2016). This species was recorded at least 80 years ago from Kaneohe Bay and Pearl Harbor, Hawaii (Edmonson & Ingram 1939; Edmonson 1944). It was first reported on the US west coast 75 years ago from Newport Bay, southern California (Berkeley & Berkeley 1941). On the northern Gulf of Mexico, it was recorded more than 60 years ago from Corpus Christi Bay, Texas (Hartman 1952) and Miami, Florida (Renaud 1956). The species has spread in subtropical and temperate waters worldwide through ship transport. Their calcareous tubes and rapid reproduction cause problems for vessels and other maritime structures (Nedved & Hadfield 2008).

Additional analyses are required to evaluate the abundance and effects of these new faunal acquisitions for the coasts of the United States. However, potential impacts of serpulids related to their life history and growth forms can be deduced by looking at their original distributions and by examining the behavior of other invasive species of the group, such as *F. enigmaticus*. Thus, depending on environmental conditions, the species may contribute to increased fouling on ships and maritime structures, and could form large colonies, such as those formerly seen in Lake Merritt, Oakland, California, which may modify the physical and hydrodynamic characteristics of coastal lagoons. Both *F. enigmaticus* and *F. uschakovi* may cause dramatic impacts on benthic communities in the U.S. (e.g., Straughan 1968; Hartmann-Schröder 1971; ten Hove & Weerdenburg 1978; Schwindt *et al.* 2001, 2004). The ecological and economic effects of most serpulids have not been studied and are unknown. However, small invertebrates such as serpulids are often overlooked or ignored until an impact is observed. For this reason, it is important to assess the distribution, expansion, and ecology of these and other invasive serpulid species in the U.S. and throughout the world.

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