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A new species of scale-worm (Polychaeta: Polynoidae), Levensteiniella iris sp. nov., from the Rainbow and Lucky Strike vent fields (Mid-Atlantic Ridge)

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Abstract: A new species of scale-worm belonging to the sub-family Macellicephalinae, *Levensteiniella iris* sp. nov., is described. It was collected on the Mid-Atlantic Ridge, on the Lucky Strike and Rainbow vent sites, associated to the mussel *Bathymodiolus azoricus* on very low flow hydrothermal vents.

Résumé : Une nouvelle espèce de Polynoidae (Polychaeta), Levensteiniella iris sp. nov. des sites hydrothermaux Rainbow et Lucky Strike (dorsale médio-Atlantique). Une nouvelle espèce de Polynoidae appartenant à la sous-famille des Macellicephalinae, Levensteiniella iris sp. nov., est décrite. Elle a été récoltée sur la dorsale médio-Atlantique, sur les sites hydrothermaux Lucky Strike et Rainbow, associée à des moulières à *Bathymodiolus azoricus* sur des évents tièdes à très faible flux.

Keywords: Hydrothermal vents, Mid-Atlantic Ridge, Polychaeta, Macellicephalinae, new species.

Introduction

The family Polynoidae is very successful at deep-sea hydrothermal vents, with approximately 40 species described to date from the known vent areas around the world (Tunnicliffe et al., 1998). Deep-sea hydrothermal vents on the Mid-Atlantic Ridge occur at a wide range of depths, from 840-865 m for Menez Gwen (37°51'N, 31°31.2'W) to 3050-3875 m for Broken Spur (29°10'N, 43°10.4'W) and 3635-3670 m for TAG (26°08'N, 44°49.6'W) [Desbruyères et al., 2000]. Both distance and depth can be serious barriers to dissemination, and one expects specific variations among sites accordingly. To date,

among the Polynoidae, two species have been reported from the Mid-Atlantic Ridge: the commensal Branchipolynoe aff. seepensis Pettibone 1990, associated to the mussel Bathymodiolus azoricus Von Cosel, Comtet & Krilova, 1999, and the free-living Lepidonotopodium jouinae Desbruyères & Hourdez, 2000. The former has been found in samples from Menez Gwen, Lucky Strike (37°17'N, 32°16.3'W, 1620-1730 m depth), Rainbow (36°13'N, 33°54.1'W, 2260-2350 m depth), Broken Spur, Snake Pit (23°237'N, 44°56.1'W, 3480 m depth), and Logatchev (14°45'N, 44°58.7'W, 2930-3020 m depth) [Desbruyères et al., 2000]. By contrast, the latter polynoid species was found only in samples from Lucky Strike and Menez Gwen (Desbruyères & Hourdez, 2000). Other reports mention a new Opisthotrochopodus and a new Levensteiniella, in the same family of Polychaetes, in samples from Lucky Strike and Rainbow (Desbruyères et al., 2001).

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In this paper we describe *Levensteiniella iris*, a new species of Macellicephalinae (Polychaeta; Polynoidae) from the Rainbow and Lucky Strike vent fields. It was found in washings of the mussel *Bathymodiolus azoricus*.

Materials and methods

Animal collection

The specimens used in this paper were collected from two sites on the Mid-Atlantic Ridge: the Rainbow vent site (36°13'N, 33°54'W, 2260-2350 m depth) and the Lucky Strike vent field (Tour Eiffel) (37°17.16'N, 32°16.29'W, 1690 m) [Fig. 1]. The animals were found in washings of the mussel *Bathymodiolus azoricus*. These collections were made during the cruises LUCKY STRIKE, MARVEL, PICO, and ATOS, with the manned submersibles *Alvin* and *Nautile*, and the remotely operated vehicle *Victor*. Both vent sites have beds of the mussel *Bathymodiolus azoricus* but the Rainbow vent field is deeper and more heavily sedimented that the Lucky Strike field (Desbruyères et al, 2001).

Sample preparation for scanning electron microscope (SEM)

Two specimens, preserved with 7% formalin in sea water and transferred to ethanol 80°, were prepared for SEM. The specimens were critical point dried with carbon dioxide, sputtered with gold and examined with a Philips scanning electron microscope (XL30).

Systematics Subfamily MACELLICEPHALINAE Hartmann-Shröder, 1971, Emended Pettibone, 1976 Genus *Levensteiniella* Pettibone, 1985 Emended

The genus *Levensteiniella* was erected by Pettibone (1985) for the single species *L. kincaidi*. Then, *L. raisae* Pettibone, 1989, *L. intermedia* Pettibone, 1990 and *L. plicata* Hourdez & Desbruyères, 2000, were described. The genus is here emended to include *L. plicata* and the new species, *L. iris*.

Diagnosis

Body short, flattened, fusiform; number of segments from 24 to 28 (the first achaetous). Eleven pairs of elytra and prominent elytrophores on segments 2, 4, 5, 7, and on alternate segments to 21. Elytra either thickened with a large median longitudinal fold (*L. plicata*) or delicate, covered at some degree with micro-tubercles and short extensions on their posterior margin (all other species). Dorsal tubercles well developed and nodular on the non elytra-bearing segments.



Figure 1. Map of the collection sites on the Azores Triple Junction area.

Figure 1. Carte des sites de récolte dans la région du Point Triple des Açores.

Prostomium bilobed; anterior lobes triangular, with frontal filaments. Median antenna inserted on small ceratophore in anterior notch of prostomium, style rather short. Paired palps moderately long; no eyes and no lateral antennae.

Peristomium or tentacular segment (first segment) achaetous, surrounding the mouth ventrally and forming a facial tubercle, slit dorso-ventrally; pair of tentaculophores lateral to prostomium, each bearing one pair of tentacular cirri.

Second segment (first chaetigerous segment) with one pair of ventral cirri, longer than following ones. Parapodia biramous, both rami well developed, conical, with projecting acicular processes. Notopodia shorter than neuropodia; notochaetae numerous, stouter than neurochaetae, smooth (*L. intermedia*) or with spinous rows appearing as scales (all other species). Neurochaetae very numerous, spinous, with slightly hooked and tapered tips (not flattened). Dorsal cirri with bulbous cirrophores and moderately long styles. Ventral cirri short, inserted basally on parapodia.

Males exhibit one (*L. intermedia* and *L. iris* sp. nov.) or two (*L. kincaidi*, *L. raisae*, and *L. plicata*) pairs of elongated ventral papillae on segment 11 or segments 11 and 12. Females without elongated ventral papillae.

Pharynx with seven pairs of papillae at opening and two pairs of jaws that can either be denticulate (*L. plicata*) or bare.

Pygidium small, rectangular, with one pair of anal cirri.

Levensteiniella iris sp. nov. (Figs 2-4)

Type locality

Mid-Atlantic Ridge, Rainbow vent field, 36°13'N, 33°54'W, 2260-2350 m depth.





Figure 2. Levensteiniella iris sp. nov.. All specimens are from the Lucky Strike vent site. **a**, **b** light microscope and **c-f** SEM views. The SEM views are from two specimens (**c-e**. MARVEL 1193; **f**. LUCKY STRIKE Al 2605). **a**. Formalin preserved specimen (PICO 1267) in dorsal view (elytra removed). **b**. Dorsal view of a formalin preserved specimen (ATOS 119) with some elytra retained. **c**. View of the posterior border of an elytron with the iron oxide cover partly removed and a macrotubercule. **d**. View of the elytral surface showing scattered bumps and overall smooth aspect. **e**. Dorsal view of the posterior left-sided parapodia showing the clear offset of the cirrophores (arrows). **f**. Posterior non elytrophore notopodia with a well developed dorsal tubercule (arrow) and rows of cilia.

Figure 2. Levensteiniella iris sp. nov.. Tous les spécimens proviennent du site Lucky Strike. **a**, **b** vues en microscopie optique et **c-f** vues en microscopie électronique à balayage (MEB). Les vues MEB ont été réalisées sur deux individus (**c-e.** MARVEL 1193 ; **f**. LUCKY STRIKE Al 2605), **a**. Animal fixé au formol (PICO 1267) en vue dorsale (élytres enlevées). **b**. Vue dorsale d'un individu fixé au formol avec encore quelques élytres en place (ATOS 119). **c**. Vue de la marge postérieure d'une élytre en vue dorsale, la couverture d'oxyde de fer ayant été partiellement retirée; mise en évidence d'un des macrotubercules postérieurs. **d**. Vue de la surface de l'élytre montrant les bosses dispersées et l'aspect généralement lisse. **e**. Vue dorsale des parapodes postérieurs gauches : remarquer la position postérieure des cirrophores (flèches). **f**. Notopode montrant les rangées de cils et le tubercule dorsal (flèche) présent sur les segments non-élytrophores.

Type material

5 mm

С

Holotype (Muséum National d'Histoire Naturelle, MNHN Paris) from the type locality, Rainbow vent field (36°13.4'N, 33°54.2W, 2280 m). Paratypes (USNM, n° 1009844 and n° 1009845 Washington, D.C.) respectively from Rainbow vent field and from Lucky Strike Vent Field (Tour Eiffel) (37°17.16'N, 32°16.29'W, 1690 m).



Figure 3. *Levensteiniella iris* sp. nov. **a**, **b**, **d-f** SEM views, and **c** light microscopy. All SEM views are from the same specimens as in Fig. 2c-f. **a.** Dorsal view of the left side of a median segment, showing lateral rows of cilia; these rows are missing on the mid-dorsum. **b.** Dorsal view of anterior part: bilobed prostomium, with median antenna and two palps, tentacular segment (first segment) with tentaculophores (arrowheads) visible laterally, and second segment (also first chaetigerous segment) with the elytra removed, well visible dorsally. **c.** Ventral view of the same anterior part as in b. Tentacular segment (arrowheads on the tentaculophores) and slit facial tubercle (arrow) surround the mouth, second segment with ventral parapodial cirri (asterisks). **d.** Parrot beak-like jaw. **e.** Anterior view of the 10th right parapodium.

Figure 3. Levensteiniella iris sp. nov. **a**, **b**, **d**-**f** vues en microscopie électronique à balayage (MEB), **c** vue en microscopie optique. Toutes les vues MEB sont réalisées sur les mêmes individus que ceux des figures 2c-f. **a**. Vue dorsale du côté gauche d'un segment médian montrant les rangées ciliaires latérales interrompues dorsalement. **b**. Vue dorsale de la région antérieure : prostomium bilobé, avec antenne médiane et palpes, segment tentaculaire (premier segment) avec tentaculophores (tête de flèche), visible seulement latéralement, deuxième segment (premier sétigère) avec élytres retirées, bien visible dorsalement. **c**. Vue ventrale de la même région qu'en b. Segment tentaculaire (pointes de flèche sur les tentaculophores) et tubercule facial (flèche), avec sa fente médiane, entourent la bouche. Second segment bien visible ventralement avec cirres parapodiaux ventraux (astérisques). **d**. Mâchoire en forme de bec de perroquet. **e**. Vue antérieure du 10^e parapode droit. **f**. Vue postérieure du 9^e parapode droit. S. HOURDEZ, D. DESBRUYÈRES



Figure 4. Levensteiniella iris sp. nov.. All specimens are from Lucky Strike vent site. a-d & f SEM views. All the SEM views are from one specimen (MARVEL 1193). e light microscopy. a, b. Unidentate notochaetae, details, c, d. Unidentate neurochaetae, details. e. Ventral view of median ventral part of a male specimen (PICO 1267) showing two ventral papillae on the eleventh segment (arrows). f. Ventral view of the posterior part showing the pair of anal cirri.

Figure 4. Levensteiniella iris sp. nov.. Tous les spécimens proviennent du site Lucky Strike. a-d & f vues en microscopie électronique à balayage (MEB). Toutes les observations MEB ont été effectuées sur un seul spécimen (MARVEL 1193). e. vue en microscopie optique. a, b. Vue des soies notopodiales unidentées, détails. c, d. Vue des soies neuropodiales grèles, unidentées, détails. e. Vue ventrale d'un spécimen mâle formolé (PICO 1267) montrant deux papilles ventrales sur le 11^e segment (flèches). f. Vue ventrale de la région postérieure montrant les deux cirres anaux.





Figure 5. World map showing the distribution of the five species of Levensteiniella described to date (data from Pettibone, 1985b, 1988, 1989, 1990, Hourdez & Desbruyères,

2000 and pers. obs.). Figure 5. Carte du monde montrant la répartition des cing espèces de *Levensteiniella* décrites à ce jour (données tirées de Pettibone, 1985, 1988, 1989, 1990, Hourdez & Desbruyères, 2000 et obs. pers.).

Other material examined

LUCKY STRIKE Cruise *Alvin* 2605, Lucky Strike Vent field (1 ind.), MARVEL *Nautile* 1193, Tour Eiffel, Lucky Strike vent field (4 ind.), MARVEL *Nautile* 1205, Lucky Strike vent field (1 ind.), PICO *Nautile* 1267 Lucky Strike vent field (1 ind.), PICO *Nautile* 1269 Lucky Strike vent field (1 ind.), ATOS *Victor* 103 Rainbow vent field (4 ind., including holotype), ATOS *Victor* 105 Rainbow vent field (1 ind.), ATOS *Victor* 107 Rainbow vent field (1 ind.), ATOS *Victor* 119 Lucky Strike vent field (1 ind.).

Description

Holotype: Length 14 mm for 24 segments, width 5 mm including parapodia (excluding chaetae), 3.5 mm without parapodia.

Paratypes: largest 21 mm in length for 25 segments, smallest 8.5 mm in length for 22 segments.

Body short, tapering anteriorly and posteriorly (Fig. 2a). Living specimens translucent or greenish, with goldcoloured chaetae. Elytra and chaetae often covered with mineral deposits (iron oxides). Specimens become either white or deep green after preservation.

Eleven pairs of elytra on segments 2, 4, 5, 7, 9, alternating to 21 (they are deciduous). Elytra attached eccentrically on prominent elytrophores overlap with following pair and cover mid-dorsal line. Short dorsal cirri, not longer than parapodia, on the non-elytra bearing segments. Elytra translucent, smooth, oval, with posterior, raised, irregularly-spaced macrotubercles (Fig. 2b, c). Under scanning electron microscope, when cleaned of oxide deposits (Fig. 2d), elytral surface smooth or slightly covered of small scattered bumps.

Dorsal cirri with short cylindrical cirrophores attached on posterior dorsal side of notopodia, with a clear offset (Fig. 2e). Cirri are as long as parapodia, with tapering tips. Nonelytra bearing segments with strongly developed dorsal tubercles (Fig. 2f). Parapodia covered with transverse rows of cilia (Figs. 2f, 3a) except on ventral side and on middorsum (Fig. 3a).

Prostomium bilobed, with cephalic peaks and frontal filaments as long as 1/3 of prostomium length (Fig. 3b). Median antenna, inserted in anterior notch of prostomium on short ceratophore (Fig. 3b), approximately as long as prostomium, with tapering tip and terminal filament. Lateral antennae absent. Palps short and thick, approximately 1.5 times the length of prostomium, with terminal filaments (Fig. 3b,c). Eyes lacking.

Tentacular segment or peristomium, achaetous, not visible dorsally. Tentaculophores lateral to prostomium (Fig. 3b,c) with tentacular cirri relatively short (approximately the length of prostomium). Peristomium visible ventrally, forming facial tubercle and lips surrounding mouth opening (Fig. 3c).

Second segment with biramous parapodia and first pair of large elytrophores (Fig. 3b). Ventral cirri with terminal filament, attached basally on prominent cirrophores lateral to ventral mouth (Fig. 3c). Ventral cirri of second segment morphologically similar to tentacular cirri, and longer than following ventral cirri.

Pharynx never fully everted in studied specimens, can be seen through body wall in dorsal view, as long as one third of body. Dissected pharynx opening with seven pairs of papillae, all similar in size. Two pairs of jaws at opening of pharynx without any teeth but with tip curved as parrot beak (Fig. 3d).

Parapodia biramous. Notopodia shorter than neuropodia and located on their anterior-dorsal side (Fig. 3e). Notopodia cylindrical, with bundle of notochaetae radiating on dorsal side (Fig. 2e, 3e, f). Acicular lobe as pointed, scoop-like ligule underneath bundle of notochaetae (Fig. 3f). Neuropodia not cleft in upper and lower parts. Neuropodial acicular lobe as a pointed ligule on anterodorsal side (Fig. 3e). Notochaetae (approximately 15-20 per notopodium), stouter than neurochaetae (Fig. 3e, f), short, curved on one side, with rows of scales on curved side (Fig. 4a, b), taper to blunt tips (Fig. 4b). Neurochaetae numerous, thinner than notochaetae, forming fan-shaped bundle oriented dorso-ventrally. Neurochaetae with two lateral rows of spines on one side (Fig. 4c), unidentate, slightly hooked at tip (Fig. 4d). Ventral cirri short, tapered, at base of neuropodia (Fig. 3e,f, 4e, f).

Pygidium small, rounded, with a pair of anal cirri (Fig. 4f), absent on holotype, present on some paratypes. Two ventral papillae developed in males, in segment 11, unconspicuous in other segments, absent in females (Fig. 4e).

Etymology: The species is named after the Latin goddess of the rainbow, Iris, referring to the type locality of the species.

Discussion

Deep-sea polynoids, and more specifically the subfamily Macellicephalinae, are characterized by a reduction of the number of antennae and segments (Levenstein, 1984). Numerous species have since been described from deep-sea hydrothermal vents and all the new subfamilies described from these vents lack lateral antennae, and are short-bodied: typically less than 32 segments and as little as 21. The genus *Levensteiniella* comprises five species: *L. kincaidi*, *L. raisae*, *L. intermedia*, *L. plicata*, and *L. iris* sp. nov. This latter is the shortest species of *Levensteiniella* described to date, with 24 segments compared to 26-28 in the other species (Table 1). *L. raisae* has been reported from the Mariana Back Arc Basin only (Pettibone, 1989), *L. plicata* from 9°50'N on the East Pacific Rise (EPR) only (Hourdez &

	L. kincaidi	L. raisae	L. intermedia	L. plicata	L. iris
Reference	Pettibone, 1985, 1988, 1990	Pettibone, 1989	Pettibone, 1990	Hourdez & Desbruyères, 2000	This paper
Number of segments	25-26	27	Not reported	28	24-25
Number and position of elongated ventral papillae*	2 pairs (segments 11 and 12)	2 pairs (segments 11 and 12)	Single pair on segment 11	2 pairs (segments 11 and 12)	Single pair on segment 11
Elytra	Filiform micropapillae on surface and posterior border (some with enlarged bases)	Micro- and macro- papillae on surface and posterior border	Thickened bulbous projections on posterior border and oval micropapillae on surface	Smooth, with large median longitudinal fold	Smooth, with thickened bulbous projections on posterior border
Notosetae	With spinous rows	Curved on one side, with scales on the curved side	Smooth or with widely spaced spines along one side	Flattened, with series ca. 15 scales on one edge	Curved on one side, with scales on the curved side
Jaws	No teeth	No teeth	Not reported	Ca. 20 teeth	No teeth
Postsetal lobe	No	No	No	Yes	No

 Table 1: Characteristics of the five species of Levensteiniella known to date.

 Tableau 1 : Caractéristiques des cinq espèces de Levensteiniella connues à ce jour.

* not present on all individuals, a character of male specimens

Desbruyères, 2000), *L. kincaidi* from all explored sites along the EPR and North East Pacific (Pettibone, 1990, 1988, 1985, pers. obs.), *L. intermedia* from Gorda Ridge, Juan de Fuca Ridge, and 9°50'N on the EPR (Pettibone 1990, pers. obs.). Finally, *L. iris* was found at two sites of the Azores Triple Junction on the Mid-Atlantic Ridge (this report).

Species belonging to this genus are generally found in low-flow areas at hydrothermal vents, among either mussels or vestimentiferan tube-worms. Although mussels are often found in the same collections, *Levensteiniella* is free-living and has never been found inside the mussels' mantle cavity. This genus has also been reported from cold-seep tubeworm aggregations collected on the Louisiana Slope in the Gulf of Mexico (Bergquist et al., in press).

Only the males possess elongated ventral papillae (as evidenced by the sperm visible through the papillae wall). *Levensteiniella iris* resembles *L. intermedia* in having one pair of elongated ventral papillae on segment 11, instead of two pairs on segments 11 and 12 for the other three species. *L. iris* and *L. intermedia* can be distinguished by the notochaetae, smooth or with widely spaced spines on *L. intermedia* and with scales on one side for *L. iris*. For females (i.e. without ventral papillae), species determination can prove difficult. The first character setting *L. iris* apart from the other species is the number of segments. Another character specific to *L. iris* is the length of the acicular lobe on the notopodia, almost as long as the notochaetae. In *L. plicata*, it also reaches the length of the

notochaetae but these are very short. *L. plicata* can easily be identified by the very unusual elytra (smooth surface, with a large median longitudinal fold) and the presence of teeth on the jaws. A key to the species of *Levensteiniella* follows.

Key to the species of Levensteiniella

Elytra with surface and posterior border ornamentation. Jaws without teeth. Less than 28 segments.

2- Elongated notopodial acicular lobe forming a scoop-like ligule, extending almost as much as the notochaetae, one pair of elongated ventral papillae on segment 11 for males (absent for females). 24-25 segments.

..... L. iris

Notopodial acicular lobe not elongated. At least 25 segments. 3

3- Notochaetae smooth or with widely spaced spines along one side. one pair of elongated ventral papillae on segment 11 for males (absent for females).

..... L. intermedia

Notochaetae with scales or spinous rows on one side. Two pairs of elongated ventral papillae on segments 11 and 12 for males (absent in females). 4 4- Few scales or spinous rows on one side of the notochaetae. Elytra covered with macro- and micro-papillae. 27 segments. *L. raisae*

Numerous scales or spinous rows on one side of the notochaetae. Elytra delicate, with scattered micro-papillae. 25-26 segments. *L. kincaidi*

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References

- Bergquist D.C., Ward T., Cordes E.E., McNelis T., Kosoff R., Hourdez S., Carney R., & Fisher C.R. 2003. Community structure of vestimentiferan-generated habitat islands from upper Louisiana slope cold-seeps. Journal of Experimental Marine Biology and Ecology (In press).
- Desbruyères D., Almeida A., Biscoito M., Comtet T., Khripounoff A., Le Bris N., Sarradin P.M. & Segonzac M. 2000. A review of the distribution of hydrothermal vent communities along the northern Mid-Atlantic Ridge: dispersal vs. environmental controls. *Hydrobiologia*, 440: 201-216.
- Desbruyères D., Biscoito M., Caprais J.-C., Colaço A., Comtet T., Crassous P., Fouquet Y., Khripounoff A., Le Bris N., Olu K., Riso R., Sarradin P.-M., Segonzac M. & Vangriesheim A. 2001. Variations in deep-sea hydrothermal vent communities on the Mid-Atlantic Ridge near the Azores plateau. *Deep-Sea Reearch I*, 48: 1325-1346.
- Desbruyères D. & Hourdez S. 2000. A new species of scaleworm (Polychaeta, Polynoidae), *Lepidonotopodium jouinae* sp.

nov., from the Azores Triple Junction on the Mid-Atlantic Ridge. *Cahiers de Biologie Marine*, **41**: 399-405.

- Hartmann-Shröder G. 1971. Annelida, Borstenwürmer, Polychaeta. Volume 58 in: Die Tierwelt Deutschlands und der angrenzenden Meeresteile. (G. Fischer ed), 594 pp. Neubearbeitete Aufl. Edition: Berlin.
- Hourdez S. & Desbruyères D. 2000. A new species of scaleworm (Polychaeta: Polynoidae), *Levensteiniella plicata* sp. nov., from the East Pacific Rise. *Cahiers de Biologie Marine*, 41: 97-102.
- Levenstein R.Y. 1984. On the ways of formation of the deep-sea polychaete fauna of the family Polynoidae. In: *Proceedings of the first international polychaete conference*. (P.A. Hutchings, ed), pp 72-85. The Linnean Society of New South Wales: Sidney.
- Pettibone M.H. 1976. Revision of the genus Macellicephala Mcintosh and the subfamily Macellicephalinae Hartmann-Shröder (Polychaeta; Polynoidae). Smithsonian Contributions to Zoology, 229: 1-71.
- **Pettibone M.H. 1985.** New genera and species of deep-sea Macellicephalinae and Harmothoinae (Polychaeta: Polynoidae) from the hydrothermal Rift areas off the Galapagos and Western Mexico at 21°N and from the Santa Catalina Channel. *Proceedings of the Biological Society of Washington*, **98**: 740-757.
- Pettibone M.H. 1988. New species and new records of scaled polychaetes (Polychaeta: Polynoidae) from hydrothermal vents of the Northeast Pacific Explorer and Juan de Fuca Ridges. *Proceedings of the Biological Society of Washington*, 101: 192-208.
- Pettibone M.H. 1989. New species of scale-worms (Polychaeta: Polynoidae) from the hydrothermal rift-area of the Mariana back-arc basin in the Western Central Pacfic. *Proceedings of the Biological Society of Washington*, 102: 137-153.
- **Pettibone M.H. 1990.** New species and new records of scales polychaetes (Polychaeta: Polynoidae) from the Axial Seamount caldera of the Juan de Fuca Ridge in the Northeast Pacific and the East Pacific Ocean off Northern California. *Proceedings of the Biological Society of Washington*, **103**: 825-838.
- Tunnicliffe V., McArthur A.G. & McHugh D. 1998. A biogeographical perspective of the deep-sea hydrothermal vent fauna. In: Advances In Marine Biology, (J. H. S. Blaxter, A. J. Southward and P. A. Tyler eds), 34, pp 353-442. Academic Press: London.
- Von Cosel R., Comtet T. & Krylova E.M. (1999). Bathymodiolus (Bivalvia: Mytilidae) from Hydrothermal Vents on the Azores Triple Junction and the Logatchev Hydrothermal Field, Mid-Atlantic Ridge. Veliger, 42: 218-248.