



Fossil clams from a serpentinite-hosted sedimented vent field near the active smoker complex Rainbow, MAR, 36°13'N: Insight into the biogeography of vent fauna

Franck Lartaud

Laboratoire d'Ecogéochimie des Environnements Benthiques, CNRS FRE 3350, UPMC Université Paris 6, Observatoire Océanologique, avenue du Fontaulé, F-66650 Banyuls-sur-Mer, France (franck.lartaud@obs-banyuls.fr)

ISTeP, CNRS UMR 7193, Laboratoire Biominéralisations et Environnements sédimentaires, UPMC Université Paris 6, CNRS, Case Postale 116, 4 place Jussieu, F-75252 Paris CEDEX 05, France

Marc de Rafelis

ISTeP, CNRS UMR 7193, Laboratoire Biominéralisations et Environnements sédimentaires, UPMC Université Paris 6, CNRS, Case Postale 116, 4 place Jussieu, F-75252 Paris CEDEX 05, France

Graham Oliver

Department of Biodiversity and Systematic Biology, National Museum of Wales, Cathays Park, Cardiff CF10 3NP, UK

Elena Krylova

P.P. Shirshov Institute of Oceanology, Nakhimovskii Pr., 36, Moscow, 117997, Russia

Jérôme Dymont

Géosciences Marines, Institut de Physique du Globe de Paris, 4 place Jussieu, F-75252 Paris, France

Benoît Ildefonse

Géosciences Montpellier, CNRS UMR 5243, Université Montpellier 2, CC60, F-34095 Montpellier CEDEX 05, France

Remy Thibaud

Naval Academy Research Institute, Lanveoc-Poulmic, BP 600, F-29240 Brest Naval, France

Pascal Gente

Université Européenne de Bretagne, 3 rue des Archives, F-29238 Brest CEDEX 3, France.

Domaines Océaniques, CNRS UMR 6538, place Nicolas Copernic, F-29280 Plouzané, France

UMR 6538, Université de Brest, OSU-IUEM, rue Dumont d'Urville, F-29280 Plouzané, France

Eva Hoisé

Laboratoire de Géologie de l'Ecole Normale Supérieure, UMR 8538, Ecole Normale Supérieure, 24 Rue Lhomond, F-75231 Paris CEDEX 05, France

Anne-Leïla Meistertzheim

Biologie et Ecologie Tropicale et Méditerranéenne, CNRS UMR 5244, UPVD, 52 Avenue Paul Alduy, F-66860 Perpignan CEDEX, France

Yves Fouquet

Département Géosciences Marines, Centre de Brest, IFREMER, BP 70, F-29280 Plouzané, France

Françoise Gaill

AMEX, CNRS UMR 7138, UPMC, IRD, MNHN, 4 place Jussieu, F-75252 Paris CEDEX 05, France

Nadine Le Bris

Laboratoire d'Ecogéochimie des Environnements Benthiques, CNRS FRE 3350, UPMC Université Paris 6, Observatoire Océanologique, avenue du Fontaulé, F-66650 Banyuls-sur-Mer, France

Laboratoire Environnement Profond, Centre de Brest, IFREMER, BP 70, F-20280 Plouzané, France

[1] Hydrothermal circulation at ultramafic-hosted sites supports a large variety of high- and low-temperature hydrothermal vents and associated ecosystems. The discovery of abundant fossil vesicomid and thyasirid shell accumulations at the ridge crest, approximately 2.5 km east of the active Rainbow vent field on the Mid-Atlantic Ridge (MAR, 36°13'N), increased our knowledge regarding the diversity of vent communities at slow spreading ridges. Bivalve molluscs of the family Vesicomidae were represented by the genus *Phreagena*. Here we present the first record of this genus in the Atlantic Ocean. This second vesicomid species known from the MAR, *Phreagena* sp., was found to be associated with a *Thyasira* species that is affiliated with *T. southwardae* (at the Logatchev vent field on the MAR) and with *T. vulcolutre* (in the Gulf of Cadiz). These two clams have close relationships with seep taxa along the continental margin, and were likely associated with sedimented vent fields. $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ analyses of the shells suggested that the burrowing bivalve *Thyasira* could incorporate isotopically light carbon, derived from the oxidation of methane in the sediment, while the signature of *Phreagena* sp. shells denoted a different carbonate source. ^{14}C dating of the shells denoted that the hydrothermal activity in the Rainbow area began at least ~25.5 kyr BP, which is similar to the model of the hydrothermal vent field distribution that was proposed for the Logatchev hydrothermal site. The results provide new insight regarding the diversity of chemosynthetic fauna on the MAR over geologic time. Ultramafic-hosted, on-axis sedimented vent fields extend the range of habitats for chemosynthetic communities, underlying the need to further explore the geology of these types of environments on slow-spreading ridges and to determine their role in the ecology of deep-sea vent communities.

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Theme: From the Mantle to the Ocean: Life, Energy, and Material Cycles at Slow Spreading Ridges

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1. Introduction

[2] In contrast to the vast majority of deep-sea communities, hydrothermal vent assemblages are exceptional in their biomass, distribution and composition [Hessler and Smithey, 1983; Desbruyères et al., 2000]. The ecological success of fossil and actual hydrothermal vent fauna is attributed to tight associations with chemosynthetic bacteria. Symbiosis with primary producers and specific adaptations to environmental constraints are reflected by a high percentage of obligate taxa [Tunnicliffe, 1991; Van Dover, 2000; Tarasov et al., 2005]. Understanding the processes by which species, associated with deep-sea hydrothermal vents successfully establish and maintain their communities in patchily distributed and ephemeral habitats has been a primary goal of hydrothermal vent ecology but they remain poorly understood [Tunnicliffe, 1991; Mullineaux et al., 2003; Mullineaux et al., 2009].

[3] The diversity of communities associated with hydrothermal vents on the Mid-Atlantic Ridge (MAR) was described by Van Dover [1995], Gebruk et al. [1997] and Desbruyères et al. [2001]. A limited number of dominant symbiotic associations have been documented, including some symbiotic bivalves [Desbruyères et al., 2001; Southward et al., 2001], which rely on diverse chemical energy sources including sulfide, methane and possibly hydrogen and iron (see reviews by Dubilier et al. [2008], Schmidt et al. [2008], and Le Bris and Duperron [2010]). Known hydrothermal activity along the Mid Ocean Ridges (MOR) is dominantly associated with basaltic rocks. However, a growing number of high-temperature (>200°C) hydrothermal systems along the slow-spreading ridges were discovered on an ultramafic basement, and displayed both metal sulfide deposition and methane production associated with the serpentinization of peridotites [e.g., Charlou et al., 2002; Simoneit et al., 2004; Charlou et al., 2010]. Ultramafic-hosted sites are often associated with long-lived detachment faults formed along one flank of the ridge, exposing deep sections of heterogeneous oceanic lithosphere to the seafloor [e.g., Ildefonse et al., 2007; McCaig et al., 2007; Escartin et al., 2008]. On the MAR, only two such sites have been documented for the diversity of dominant taxa: Rainbow (36°N) [Fouquet et al., 1997] and Logatchev (14°N) [Bogdanov et al., 1995]. A third, recently discovered (Ashadze, 13°N), is known to be the deepest hydrothermal vent field, however the diversity of its communities has not been characterized (4000 m [Fouquet et al., 2007]). The two vent fields at the

ridge axis (Logatchev and Rainbow) display slightly different fluid chemistries, but share the same dominant taxa (i.e., *Bathymodiolus* mussels and *Rimicaris* shrimps [Gebruk et al., 2000; Desbruyères et al., 2001]). The main difference lies in the fact that the Logatchev vent field encompasses both, a high temperature smoker complex and diffuse vents through sediments covered with species more classically related to this type of habitat [Gebruk et al., 2000].

[4] Here, we document the occurrence of fossil communities in the vicinity of the Rainbow vent field, and report the presence of a dominant bivalve genus previously unknown on the MAR. The distribution and abundance of fossil shells are described, in combination with the geomorphology and mineralogy of the area. Furthermore, the isotopic fractionation of bivalve shells was analyzed in order to investigate their energy pathways and carbon source(s) (see reviews by Rio et al. [1992], Kiel and Peckmann [2007], McConnaughey and Gillikin, [2008], and Lartaud et al. [2010b]), using data sets established for various vent and seep fauna [Schöne and Giere, 2005; Hein et al., 2006; Naraoka et al., 2008; Lietard and Pierre, 2009]. The results provide new insights regarding the mechanisms governing long-term changes in dominant species diversity, evolution and biogeography of deep-sea chemosynthetic species at slow-spreading ridges.

2. Materials and Methods

2.1. Collection of Fossil Shells and Seafloor Images

[5] As part of the MoMARDREAM cruise program (August–September 2008), numerous fossil shells were collected by dredging approximately 2.5 km east of the Rainbow vent field (36°13.80'N, 33°52.85'W), at a depth of ~1980 m (Figure 1). A ROV Victor 6000 dive was subsequently performed using a more extensive survey of the area (Figure 2). Digital images were acquired using a high-resolution OTUS camera mounted on the ROV for a vertical view at an altitude approximately 10 m above the seafloor. Complete photographic coverage of two boxes (300 × 300 m and 100 × 100 m) was utilized to determine the small-scale distribution of the bivalve community (Figure 3). ROV navigation was estimated using a combination of Ultra Short Baseline (USBL) acoustic data (POSIDONIA system) complemented by the information heading and the loch of the submersible. The precise position of the ROV was

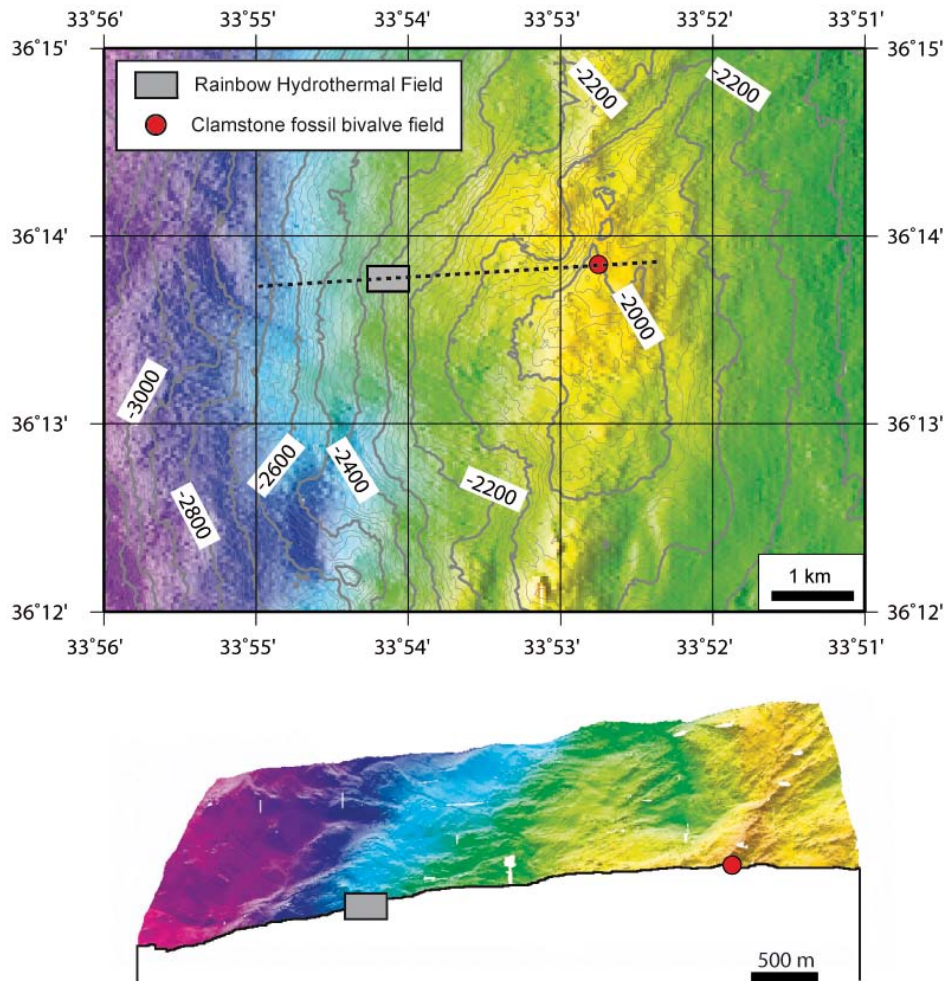


Figure 1. (top) Shipborne multibeam bathymetry on Rainbow Massif (cruise Flores of the R/V *L'Atalante*), and (bottom) the perspective view from high resolution multibeam bathymetry acquired by ROV Victor at an altitude of 50 m (adapted from *Dyment et al.* [2009]), showing the location of the hydrothermal site Rainbow and the “Clamstone” fossil bivalve fields.

further calibrated using an arbitrary reference station in the surveyed box (marker).

2.2. Shell Preparation and Analysis

[6] Immediately upon collection, bivalves were scrubbed in distilled water with a toothbrush to remove loosely attached biogenic and inorganic particles. Before carbon and oxygen isotopic analyses, we conducted an X-ray diffraction analysis (Siemens D501) in order to confirm the preservation of original aragonite in both vesicomid and thyasirid shells. Sample powders of shell calcium carbonate (3–4 mg) were obtained using a rotary drill with a diamond-tipped burr. Samples were drilled to a depth of ~1 mm from the external surface of the outer layer (Figure 4). Two locations

in the shells were drilled close to the umbo (which corresponds to the juvenile phase of the shell) and to the ventral margin (which corresponds to the growth period preceding death) in order to take into account the isotopic range related to ontogenic effects (i.e., the ontogenic-related $\delta^{13}\text{C}$ decrease; see review by *Gillikin et al.* [2009]). Powdered samples were pre-treated with 1.5% NaClO for 30 min to remove organic contaminants, and rinsed three times with distilled water following a protocol modified after *Sponheimer and Lee-Thorp* [1999] and *Ségalen and Lee-Thorp* [2009]. Resulting powders were acidified in 100% H_3PO_4 at 50°C under vacuum. Evolved CO_2 was collected and analyzed using a mass spectrometer (VG Micromass 602). Isotopic data are reported in the conventional delta (δ) notation relative to Vienna Pee Dee

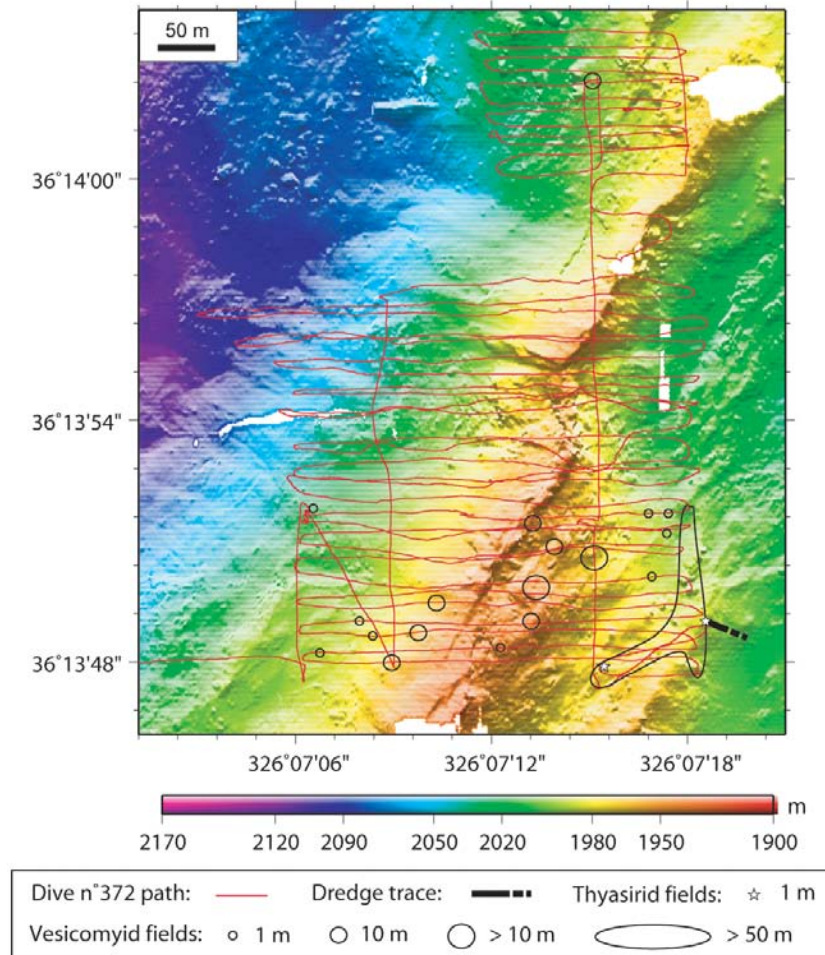


Figure 2. High resolution multibeam bathymetry acquired by ROV Victor at an altitude of 50 m in the “Clamstone” area (background). The red line shows the track of Dive 372, performed at low altitude, in order to ensure full coverage of vertical OTUS photographs (see Figures 1 and 5). The distribution of fossil bivalve fields is shown by ellipses and stars.

Belemnite (VPDB). The standard used for the analyses was an internal standard calibrated using NBS-19. The standard deviation for $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ was $\pm 0.10\%$. Additional thyasirid shells coming from cold seep environments (G. Oliver, National Museum Wales collection) were analyzed for their isotopic composition in order to complement the data set reference for the thyasirid species. The material consisted of 4 shells of *Axinus cascadiensis* obtained from the Baby Bare seamount [Voight and Grehan, 2000; Oliver and Holmes, 2007], associated with hydrothermal seeps with traces of methane and sulfur; 5 shells of *Thyasira sarsi* collected in the North Sea [Oliver and Killeen, 2002], which derived their sulphur or methane source from oil impregnated drilling cuttings; and 3 shells of *T. vulcolutre* obtained from active methane seeps of the Captain Arutyunov

mud volcano located in the Gulf of Cadiz [Rodrigues et al., 2008].

[7] The data were statistically evaluated using the non-parametric Mann and Whitney U-test to assess the difference in $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values between bivalve shells from this study and the reference data set. A stepwise forward canonical discriminant analysis (CDA) was performed on data expressing both $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values in samples (independent variables), in order to classify the different types and nature of fluid-related shells (grouping variables).

[8] Three vesicomyid shells were dated using ^{14}C analyses under a liquid scintillation counter (LSC) at the LOCEAN laboratory (UPMC Univ Paris 06, Pa 2499), using the protocol from Stuiver and Polach [1977]. Beta-counting measurements on

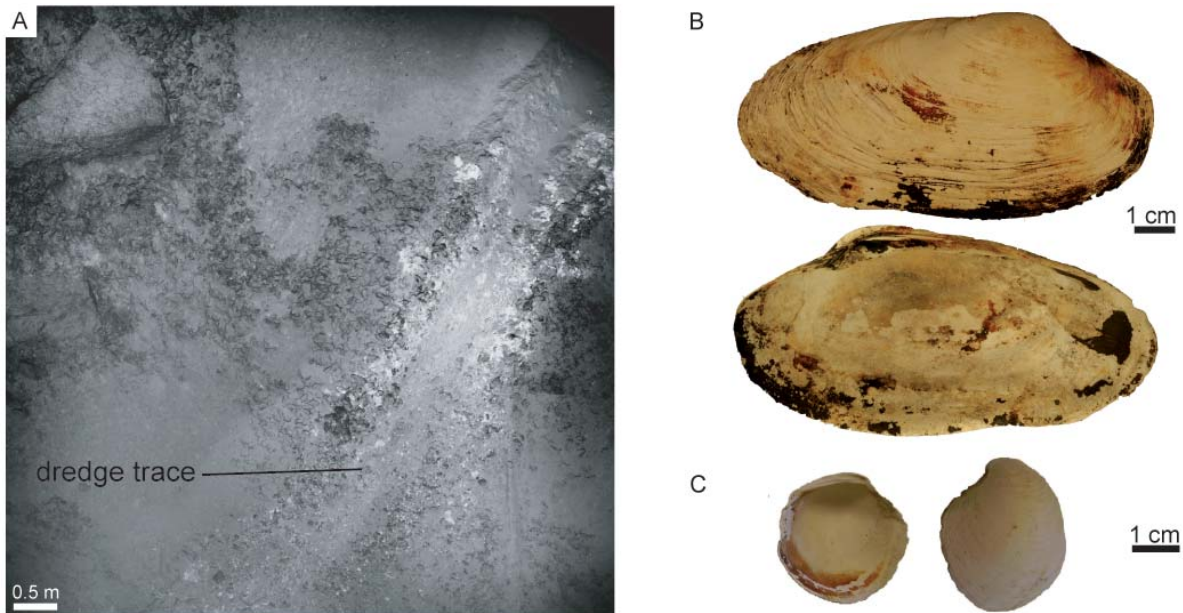


Figure 3. (a) Trace of the dredge in a clam field containing shells of (b) vesicomyid, and (c) thyasirid species. Note the oxidation (in black) inside and outside the vesicomyid shell. (Copyright for the original photo (Figure 3a): IFREMER-MoMARDREAM.)

carbonates were performed after superficial cleaning of the shell fragments (diluted HCl). All of the radiocarbon results are expressed as conventional ages, after normalization of $\delta^{13}\text{C} = -25\text{‰}$. The uncertainty of the age determination and the standard error of the conventional ^{14}C age, is given as \pm one standard deviation, as determined after stabilization of the scintillation over repeated periods of 100 min during 4 to 5 days.

3. Results

3.1. Location of the Bivalve Fields

[9] Dead bivalve shells coated with iron and manganese oxides were observed approximately 2.5 km

east of the Rainbow hydrothermal vent field (Figure 1), and were found at the top of a small, sedimented ultramafic mount, between 1945 and 2005 m depth. The dredge revealed the presence of serpentinized peridotites (including serpentine, magnetite, and brucite), and carbonate veins and clays associated with shells. Shells were sparsely distributed over an area covering $100\text{ m} \times 300\text{ m}$ named “Clamstone,” in reference to the appearance of the shell accumulations. Eighteen fields of dead vesicomyids were identified (Figure 2) with an additional patch further north. On videos the distribution of the shells is very uneven, varying from small groups (dozens of individuals) to aggregations covering several square meters with a density greater than 150 individuals per m^2 . Shells were

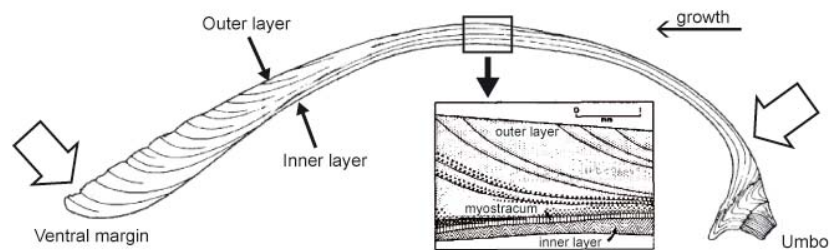


Figure 4. Section of a bivalve shell showing the geochemical micro-sampling strategy for this study (white arrows). Carbonate powders were removed from the outer layer during the juvenile period (close to the umbo), and close to death (ventral margin). Modified after *Fatton and Roux* [1981].

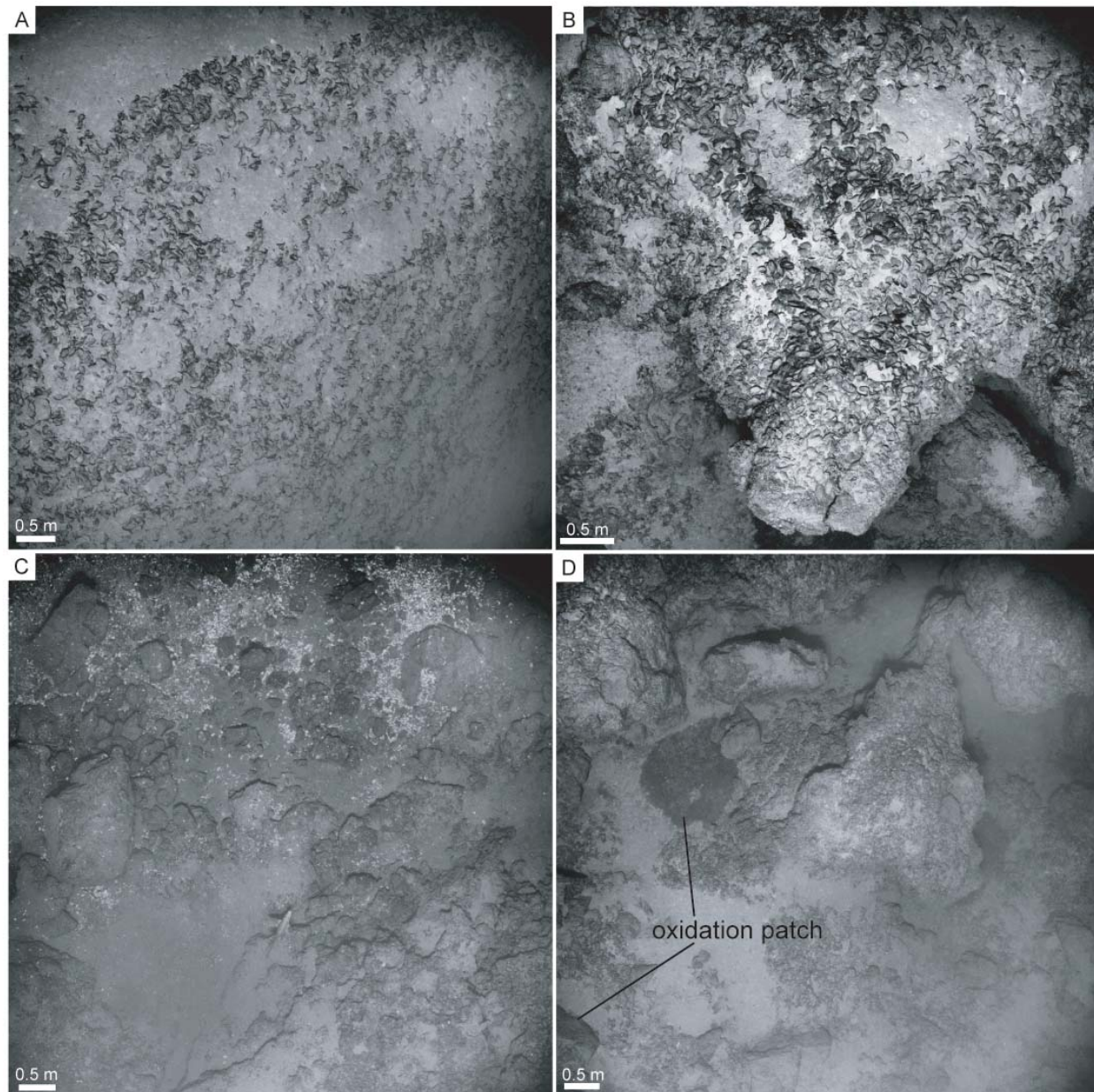


Figure 5. Vertical OTUS photographs taken by ROV Victor at an altitude ≤ 10 m showing the distribution of bivalve populations discovered during Dive 372 at “Clamstone”: (a and b) vesicomyid shells, (c) thyasirid shells (in white on the picture), and (d) the oxidation patch close to the bivalve fields. (Copyright of original photographs: IFREMER-MoMARDREAM.)

dissociated, most of them partly buried in soft sediment (Figure 5a) or formed small banks, presumably following a pattern of past fluid discharge issued from cracks in the underlying rocks (Figure 5b). In addition to the vesicomyids, three intact thyasirid shells >30 mm in diameter were recovered in the dredge. Only one visible patch of the thyasirid was identified on the seafloor on videos (see Figure 4 and Figure 5c). Black surfaces, potentially indicating iron or manganese oxide

deposits were also seen, often in close proximity to bivalve fields (Figure 5d).

3.2. Shell Identification

[10] Vesicomyid clams dominated dead shell assemblages in the “Clamstone” area. Morphologically, the vesicomyid valves from Rainbow were close to the genus *Phreagena*, which was established for the early Pliocene species *P. lasia* from the Los

Table 1. Mean and the Range of Oxygen and Carbon Isotopic Compositions of Shells Collected in the “Clamstone” Area, Compared to Values Measured in Thyasirids From Cold Seeps and Reference Data for Shells of Various Bivalve Species From Hydrothermal Vents and Cold Seeps^a

	Sample Number (n)	$\delta^{18}\text{O}$ (‰ VPDB)	Min-Max	$\delta^{13}\text{C}$ (‰ VPDB)	Min-Max
Hydrothermal vents (1, 3, 4) (HV)	45	3.58 ± 0.17	2.24 — 4.56	3.37 ± 0.25	1.88 — 6.20
Cold seeps (2, 4) (CS)	82	3.18 ± 0.17	1.70 — 4.53	-3.01 ± 1.20	-18.9 — 3.04
Thyasirid - cold seeps (TCS)	12	2.20 ± 0.28	1.53 — 2.81	-3.55 ± 1.22	-7.02 — -1.05
<i>Aximus cascadiensis</i>	1A	2.7		-1.87	
<i>Aximus cascadiensis</i>	1C	2.81		-1.05	
<i>Aximus cascadiensis</i>	1D	2.68		-2.02	
<i>Aximus cascadiensis</i>	1E	2.62		-2.18	
<i>Thyasira vulcolutre</i>	2A	1.6		-6.49	
<i>Thyasira vulcolutre</i>	2B	1.69		-7.02	
<i>Thyasira vulcolutre</i>	2D	1.53		-5.67	
<i>Thyasira sarsi</i>	6A	2.13		-3.19	
<i>Thyasira sarsi</i>	6B	2.05		-3.89	
<i>Thyasira sarsi</i>	6C	2.38		-2.31	
<i>Thyasira sarsi</i>	6D	2.09		-3.73	
<i>Thyasira sarsi</i>	6E	2.11		-3.22	
<i>Phreagena</i> sp. (Clamstone) (PCL)	7	4.62 ± 0.25	4.14 — 4.99	5.16 ± 1.51	2.86 — 8.35
<i>Phreagena</i> sp.	CAL 2	4.42		5.37	
<i>Phreagena</i> sp.	CAL 3-1	4.71		5.15	
<i>Phreagena</i> sp.	CAL 3-2	4.7		8.35	
<i>Phreagena</i> sp.	CAL4	4.99		4.73	
<i>Phreagena</i> sp.	CAL5-1	4.62		4.72	
<i>Phreagena</i> sp.	CAL5-2	4.78		4.91	
<i>Phreagena</i> sp.	CAL 6	4.14		2.86	
<i>Thyasira</i> aff. <i>southwardae</i> (Clamstone) (TCL)	3	3.27 ± 0.59	3.01 — 3.47	-7.69 ± 1.60	-8.10 — -6.95
<i>Thyasira</i> aff. <i>southwardae</i>	3A	3.01		-8.1	
<i>Thyasira</i> aff. <i>southwardae</i>	3B	3.33		-6.95	
<i>Thyasira</i> aff. <i>southwardae</i>	3C	3.47		-8.02	

^aThe mean is shown with the \pm standard deviation. References: 1, *Schöne and Giere* [2005]; 2, *Hein et al.* [2006]; 3, *Naraoka et al.* [2008]; 4, *Lietard and Pierre* [2009].

Angeles Basin [Woodring, 1938]. Some authors have suggested that *Phreagena* should be synonymized with *Calyptogena* [Boss and Turner, 1980], and with *Archivesica* [Amano and Kiel, 2007]. Later it was shown that the genus *Phreagena*, in fact, differs considerably from *Calyptogena* [Krylova and Sahling, 2006]. Although the genera *Phreagena* and *Archivesica* are closely related, a morphological analysis pointed out some differences [Krylova and Janssen, 2006], which were further confirmed by molecular data (A. Audzijonyte, manuscript in preparation, 2010). For these reasons *Phreagena* is considered in the present article a valid genus.

[11] The other bivalve species sampled from the dead shell field was *Thyasira* aff. *southwardae* (Thyasiridae, Figure 1). The species is congeneric with *T. southwardae* [Oliver and Holmes, 2006] from the Logatchev MAR vent field and with *T. vulcolutre* [Rodrigues et al., 2008] from the

Captain Arutyunov mud volcano in the Gulf of Cadiz.

3.3. Isotopic Composition of Bivalve Shells

[12] The ^{14}C analyses of *Phreagena* sp. shells revealed ages range from $24,120 \pm 215$ to $26,799 \pm 55$ yr BP ($n = 3$).

[13] The $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ isotopic values of collected shells are listed in Table 1. For comparison, additional original data obtained for thyasirids from cold seep environments, and published data for bivalve shells of different species (bathymodiolins, lucinids, and vesicomyids) from hydrothermal vents and cold seeps are presented in Table 1 and Figure 6.

[14] The shells of both bivalve species displayed a narrow oxygen isotopic range ($<1\%$). *Phreagena* sp. shells were slightly enriched in ^{18}O ($\delta^{18}\text{O} =$

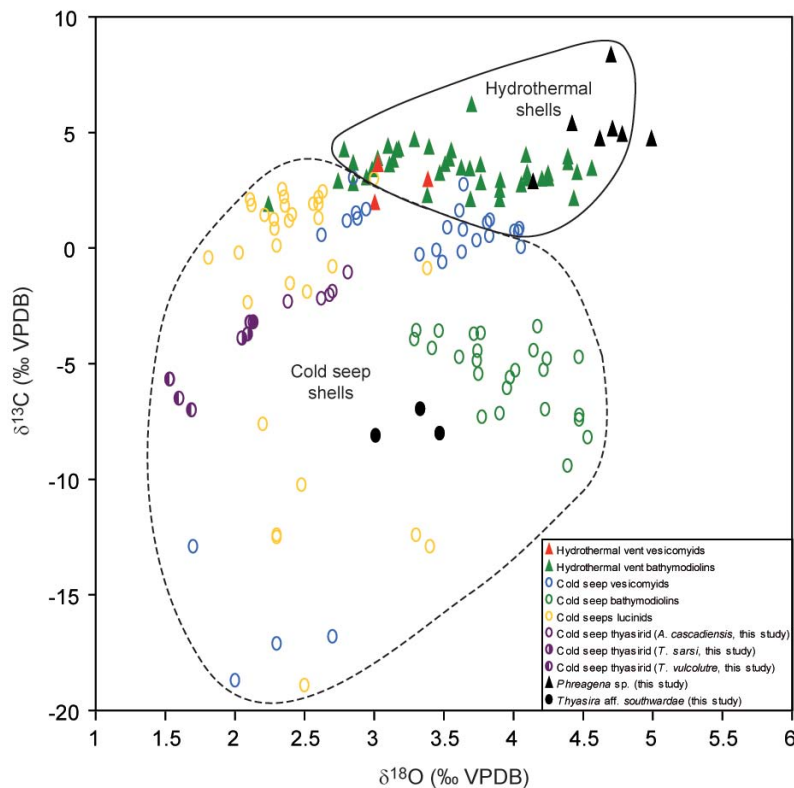


Figure 6. The oxygen and carbon isotopic composition of shells of *Phreagena* sp. (black triangles) and *Thyasira* aff. *southwardae* (black circles) obtained from the “Clamstone” area, compared to additional thyasirids from cold seeps (*A. cascadiensis*, *T. sarsi* and *T. vulcolutre*), as well as reference data of shells from hydrothermal vents and cold seeps [after Schöne and Giere, 2005; Hein et al., 2006; Naraoka et al., 2008; Lietard and Pierre, 2009]. Domains limited by a solid line (resp. dotted line) represent the scatterplot of canonical scores obtained by applying discriminant functions to the data from hydrothermal vents (cold seeps).

4.62 ± 0.25‰) compared to other vent and seep bivalve species. Conversely, with a mean of 3.27 ± 0.59‰, the δ¹⁸O signature of *Thyasira* aff. *southwardae* shells from “Clamstone” were not significantly different than those previously measured for shells from both cold seeps and hydrothermal vents (Mann and Whitney U-test, $p > 0.05$; Table 2). In contrast, the mean δ¹⁸O of additional cold seep thyasirid shells analyzed in this study were significantly lower and found at the lowest end of the reported range (2.20 ± 0.28‰, $p < 0.05$).

[15] The carbon isotopic composition of the shells from each environment covered a wider range. *Phreagena* sp. shells exhibited the highest δ¹³C (5.16 ± 1.51‰), and were significantly different ($p < 0.05$) than the δ¹³C of shells from other environments. *Thyasira* aff. *southwardae* shells displayed much more ¹³C depleted δ¹³C (−7.69 ± 1.60‰), lower but not significantly different ($p > 0.05$) from the δ¹³C of shells from the reference data set for cold seeps (−3.01 ± 1.20‰) and from

the additional thyasirid shells analyzed in this study (−3.55 ± 1.22‰; see Table 2).

[16] An overall analysis, including both the δ¹⁸O and the δ¹³C signature, was performed using Canonical Discriminant Analysis (CDA) in order to classify different groups of shells according to the

Table 2. Statistical Difference of δ¹³C (up) and δ¹⁸O (Above the Diagonal) of Shells Between Our Samples and the Reference Data Collected, Depending on the Nature of the Fluids^a

	HV	CS	TCS	PCL	TCL
HV		8.949*	5.285*	3.15*	2.875*
CS	2.747*		1.314	4.344*	1.929
TCS	5.148*	3.756*		3.55*	2.454*
PCL	3.901*	4.161*	3.55*		2.393*
TCL	1.022	0.095	2.599*	2.393*	

^aThe statistical difference was evaluated with the Mann and Whitney U-test. The asterisk (*) indicates $p < 0.05$. HV, hydrothermal vents; CS, cold seeps; TCS, *Thyasira* from cold seeps; PCL, *Phreagena* sp. from “Clamstone”; TCL, *Thyasira* aff. *southwardae* from “Clamstone.”

nature of related-fluids (grouping variables). A scatterplot (Figure 6) relative to the two discriminant functions ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of the shells) displayed good separation between the shells of actual specimens according to the type of fluid (i.e., hydrothermal vents versus cold seeps). With the exception of one outlier, *Phreagena* sp. shells collected at “Clamstone” exhibited an isotopic signal close to that of shells obtained from living bivalves in hydrothermal vents. In contrast, *Thyasira* aff. *southwardae* shells from “Clamstone” displayed a marked “cold seep” isotopic signature.

[17] The $\delta^{13}\text{C}$ of living thyasirid shells analyzed in this study confirmed that bivalves from this family can be distinguished according to habitat type using this signature. The shells of *Axinus cascadiensis* (Baby Bare sea-mount) and, to a lesser extent, those of *Thyasira sarsi* (North Sea), had the highest $\delta^{13}\text{C}$ values when compared to thyasirids from “Clamstone” ($-1.78 \pm 0.80\text{‰}$ and $-3.27 \pm 0.77\text{‰}$, respectively). Shells of *Thyasira vulcolutre* (mud volcano in the Gulf of Cadiz) had mean $\delta^{13}\text{C}$ values similar ($-6.39 \pm 1.69\text{‰}$) to those of thyasirids from “Clamstone” ($p > 0.05$).

4. Discussion

4.1. Biogeographical Implications

[18] The fossil bivalve *Phreagena* sp., described here, differed from those currently known from hydrothermal environments on the MAR or from other MOR that are more or less dominated by representatives of *Bathymodiolus* and two species of vesicomyids: *Abyssogena southwardae* or “*Calypptogena*” *magnifica* [Boss and Turner, 1980; Krylova et al., 2010].

[19] Vesicomyid bivalves themselves have rarely been described on MAR vent fields. An undetermined vesicomyid has been reported in the Snake Pit area (23°N , 3420–3480 m [Segonzac, 1992]). Juvenile bivalves morphologically similar to vesicomyid specimens were recovered within wood substrate deployed at Rainbow [Gaudron et al., 2010]. Another vesicomyid species, represented only by a broken valve, was recorded at the Logatchev hydrothermal field-2, 2677 m [Cherkashev et al., 2000]. Initially referred to *Vesicomya* sp., the valve is now identified as *Pliocardia atalanta* [von Cosel and Olu, 2009; E. Krylova, personal communication, 2010], a species originally described from the REGAB pockmarks (in the Gulf of Guinea) at depths of 3113–3159 m [von Cosel and Olu, 2009].

Later, this species was also collected in the Gulf of Cadiz at 3060 m (C. F. Rodrigues and M. R. Cunha, personal communication, 2010). The third vesicomyid recorded from the MAR was *A. southwardae*, which dominates the Anya’s Garden community (a slightly off-axis site in the Logatchev area, $14^\circ 45'\text{N}$), in contrast to the Logatchev active high-temperature vents dominated by mytilids [Gebruk et al., 2000; Southward et al., 2001]. The population of *A. southwardae* in Anya’s Garden is now extinct (A. V. Gebruk, personal communication, 2007). *A. southwardae* has also been subsequently recognized in a site north of Logatchev ($15^\circ 07'\text{N}$) where some sparse dead shells were found in an off-axis sedimented fracture-zone [Van Dover, 1995; Krylova et al., 2010]. Live specimens of vesicomyid, most likely *A. southwardae*, were also reported in the Vema fracture zone, at depths of 4500–5000 m, more than 100 km away from the MAR axis [Auzende et al., 1989]. Recently *A. southwardae* was also found at the Widawake Field (MAR, $\sim 5^\circ\text{S}$) at 2985 m [Krylova et al., 2010]. Besides the MAR, *A. southwardae* has also been reported in the eastern Atlantic near the Canary Islands off Henry Seamount (valves only) and in the western Atlantic off Barbados, the West Florida Escarpment, and offshore Virginia at depths of 2985–5100 m [Krylova et al., 2010]. Thus the vesicomyid species identified on the MAR exhibit a broad distribution, including near-continental regions of the Atlantic, and lives in a wide variety of geologic settings.

[20] The genus *Phreagena* needs an entire revision and its composition is not yet completely defined [Krylova and Janssen, 2006]. Recent species, which can be tentatively assigned to *Phreagena*, live in various reducing biotopes including submarine volcanoes (*P. edisonensis*), cold seeps (*P. soyoae*, *P. kilmeri*, *P. ochotensis*, *C. nankaiensis*) and hydrothermal vents (*P. okutanii*, *P. nankaiensis*). Only two species, *P. okutanii* and *P. nankaiensis*, inhabit both hydrothermal vents (the Mid-Okinawa Trough) and seeps (Sagami Bay and the Nankai Trough) [Fujikura et al., 2000; Kojima et al., 2005]. *Phreagena* is distributed in the western and eastern regions of the Pacific Ocean and in the northern region of the Indian Ocean [Krylova and Sahling, 2006]. The present finding of *Phreagena* sp. is the first report of the genus in the Atlantic Ocean. To date, the assemblage of *Phreagena* sp. is the northernmost and shallowest locality of vesicomyids discovered on the MAR. The dispersion of *Phreagena* sp. to the south along the MAR could be limited by its bathymetrical range. The

known vertical range for the genus *Phreagena* is 549–2005 m. For comparison, the vertical range of the genus *Abyssogena* is 2985–6400 m. Previous studies have indicated that some groups of vesicomids have restricted vertical ranges and diverge along with the depth of the habitat [Kojima *et al.*, 2000]. The Central Atlantic is an example of such a divergence, with *Abyssogena* dominating sites at abyssal depths and *Phreagena* dominating low-bathyal sites.

[21] Although commonly encountered in shallow-water vents or other reducing habitats [Gebruk *et al.*, 1997], in cold seep communities [Olu *et al.*, 1996; Rodrigues *et al.*, 2008] and in non-chemosynthetic deep-sea habitats of the Atlantic Ocean [Payne and Allen, 1991], specimens of *Thyasira* have rarely been observed in deep-sea hydrothermal communities. The only thyasirid species ever reported in a MOR hydrothermal environment was found in the sedimented Anya's Garden site, in Logatchev [Gebruk *et al.*, 2000; Southward *et al.*, 2001; Oliver and Holmes, 2006]. Only a fraction of thyasirid species are symbiotic, and the symbionts are mostly extracellular [Dufour, 2005]. Thyasirids are generally considered to be associated with thiotrophic bacteria [Dubilier *et al.*, 2008]. Southward *et al.* [2001] have shown that *Thyasira southwardae* collected from the Anya's Garden site in Logatchev (i.e., the closest species to *Thyasira* from the "Clamstone" site) is dependent on thiotrophic symbionts.

[22] The hydrothermal vent fields Rainbow and Logatchev belong to different biogeographical provinces and are characterized by different depth, topography, and deep circulation [Van Dover *et al.*, 2002]. *Thyasira* aff. *southwardae* seems to be the only bivalve species common to both fields, demonstrating much more eurybathic ability as compared to vesicomids and bathymodiolins at the species-level. The distribution pattern of both identified vesicomid species from the MAR (*A. southwardae* and *P. atalanta*) suggests an ability to disperse over large geographical areas and bathymetrical range. Various groups of bivalves observed on the MAR exhibit different types of distribution patterns and likely have different colonization pathways on slow-spreading ridges. Both species of *Bathymodiolus* observed on the MAR do not have a closely related species in either the western or eastern Atlantic Ocean [Olu-Le Roy *et al.*, 2007] that could suggest dispersion throughout the MOR system. Conversely, *P. atalanta*, which is widely distributed in the eastern Atlantic, may have colonized the MAR

from seep communities of the nearby continental margin of Africa. Similarly, *Thyasira* aff. *southwardae* observed on the MAR also has close relationships with species from the Gulf of Cadiz in the eastern Atlantic. As for *Phreagena* sp., the data are too sparse for conclusions, as the absence of *Phreagena* in the western or eastern Atlantic is likely the result of under-sampling.

[23] The presence of a thyasirid species closely related to the species discovered at Logatchev [Gebruk *et al.*, 2000] suggests the potential for long-distance dispersion over geological time scales, despite the relative isolation of the Azores Plateau area as emphasized by Van Dover *et al.* [2002]. Furthermore, the close relationship of this thyasirid species with *T. vulcolutre* from the Gulf of Cadiz suggests that the ecological plasticity of *Thyasira* has allowed this genus to colonize different types of sedimented reducing environments, as reported for vesicomids by Peek *et al.* [1997, 2000]. The absence of living *Phreagena* on the MAR and the recent extinction of *A. southwardae* at Logatchev suggests that the geographical distribution of each species of vesicomids is a dynamic feature, whereas their bathymetrical range is much more conservative.

4.2. Hydrothermal Signatures in the Habitat of Fossil Bivalves

[24] The diagenetic fingerprint of fossil carbonates results in the decrease of both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ signatures [Brigaud *et al.*, 2008]. The diagenetic transition of aragonite, a metastable form of calcium carbonate, to low-Mg calcite is accompanied by distinct stable isotopic changes that can be used as a criteria to determine shell preservation [Krantz *et al.*, 1996]. Both "Clamstone" species exhibit primary aragonite shell material, which excludes an influence of diagenetic alterations on the shell isotopic signal.

[25] The oxygen isotopic composition of carbonate shells is mainly controlled by ambient temperature and the $\delta^{18}\text{O}$ composition of seawater in which precipitation takes place [Epstein *et al.*, 1953; Chauvaud *et al.*, 2005; Lartaud *et al.*, 2010a]. However, little is known regarding deep-sea bivalve ^{18}O isotopic fractionation. Lietard and Pierre [2008] have shown that isotopic temperature calculated using the $\delta^{18}\text{O}$ of *Myrtea* aff. *amorpha* from the Kazan mud volcano (3000 m depth) is consistent with in situ temperatures measured at the seafloor, which suggests that the shells are close to isotopic equilibrium. Using the

$\delta^{18}\text{O}$ -temperature relationship for aragonite shells [Grossman and Ku, 1986] and an isotopic composition of deep-North Atlantic waters during the Last Glacial Maximum of $+0.75\text{‰}$ [Adkins et al., 2002; Schrag et al., 2002], we estimate that the paleotemperature is $3.8 \pm 1.1^\circ\text{C}$ in the “Clamstone” *Phreagena* habitat. The temperature is slightly lower than those measured in live *Bathymodiolus azoricus* habitats of the Rainbow hydrothermal vent field ($\sim 6 \pm 2^\circ\text{C}$ [Desbruyères et al., 2001; Le Bris and Duperron, 2010]). The temperatures indicates a limited hydrothermal influence in the habitat such as that described for *Calyptogena magnifica*, which thrive at the periphery of EPR vents with no or little temperature anomaly [Grassle, 1987; Childress and Fisher, 1992].

[26] Conversely, the lower $\delta^{18}\text{O}$ signal measured in *Thyasira* aff. *southwardae* shells from the “Clamstone” area denotes a higher habitat temperature of $\sim 9.7 \pm 2.5^\circ\text{C}$. The value is a lower estimate, since the ^{18}O enrichment of water circulating through serpentinite rocks [Mével, 2003; Kelley et al., 2005] could have led to a positive bias. The higher habitat temperature for *Thyasira* as compared to *Phreagena* bivalves is consistent with different habitat conditions. *Thyasirid* bivalves burrow in the sediment to a depth of up to approximately 9 times their shell length. They use their vermiform foot to build a 3-dimensional network of tunnels to a similar depth below their shells [Dando and Southward, 1986; Dubilier et al., 2008]. Owing to the vertical hot fluid gradient in the sediment, a higher temperature of the habitat is expected. As an example, a temperature gradient of 2 to 12°C along a 30 cm depth profile on a sedimented ridge was reported by Grehan and Juniper [1996].

[27] Collected specimens of *Phreagena* sp. are not significantly different from other hydrothermal vent species reported to date in regards to their carbon isotopic signature. More surprising is the observation of a significantly different isotopic signal for *thyasirids* from “Clamstone.” As compared to other hydrothermal vent species, the $\delta^{13}\text{C}$ signature of these shells appears to be more closely related to cold seep species according to previous references [Hein et al., 2006; Lietard and Pierre, 2009] and the original data provided in this study for methane seep-related *T. vulcolutre* shells (Figure 6). Like other vesicomyid species, *Phreagena* are considered to host sulfide-oxidizing symbionts [Childress et al., 1991; Dubilier et al., 2008]. Similarly, symbionts identified to date in *thyasirids* from vents, seeps, or organic falls were inferred as sulfide-oxidizers from their phyloge-

netic affiliation [Southward, 1986; Dufour, 2005; Dubilier et al., 2008]. Although the occurrence of methanotrophic symbionts in these fossil species cannot be ruled out, it is more likely that both species undergo a thiotrophic nutrition style.

[28] The carbon isotopic composition of organic tissues is strongly influenced by the source of metabolic carbon and, thus, by the relative abundance of sulfide-oxidizing and methanotrophic symbiotic bacteria gills [Kennicutt et al., 1992; Southward et al., 2001; Colaço et al., 2002]. However, only a low fraction of metabolic C is transferred to the shells (e.g., $<15\%$ of metabolic C in *Bathymodiolus* shells). Rio et al. [1992], Schmaljohann et al. [1990], McConnaughey et al. [1997] and McConnaughey and Gillikin [2008] argued that cold seeps and hydrothermal bivalves build their shell mainly from ambient dissolved inorganic carbon and that their isotopic signature should reflect environmental conditions rather than metabolic traits. Consistently, Hein et al. [2006] inferred that $\delta^{13}\text{C}$ depleted shells from cold seeps (up to -17.1‰) reflect the depleted signature of dissolved inorganic carbon (DIC) in sediment pore waters resulting from CH_4 oxidation ($\delta^{13}\text{C}_{(\text{CH}_4)} = -75.8\text{‰}$), and argued for a depleted ^{13}C contribution in the pore sediment from the oxidation [Brooks et al., 1984; Charlou et al., 2003]. Dando and Spiro [1993] further supported this assumption by reporting lower $\delta^{13}\text{C}$ in *T. sarsi* shells from a methane seepage area (-12‰) than from non-seep locations ($>-6.16\text{‰}$) of a Norwegian fjord. This is also observed in this study since lower $\delta^{13}\text{C}$ values are found in shells associated with methane seeps (i.e., *T. vulcolutre* from Captain Arutyunov mud volcano in the Gulf of Cadiz, Figure 6).

[29] The highly depleted isotopic composition of *Thyasira* aff. *southwardae* shells has only been described in cold seep methane-rich environments to date. Although mechanisms which produce such low $\delta^{13}\text{C}$ values in shells remain poorly studied, we hypothesize that this signal reflects a methane-rich environment, which could have been partly supported by serpentinitization processes. Despite $\delta^{13}\text{C}_{(\text{CH}_4)}$ values of -18 to -15.8‰ , Rainbow fluids, like other MAR hydrothermal fluids [Charlou et al., 2002], are significantly lower than the $\delta^{13}\text{C}_{(\text{DIC})}$ of deep-Atlantic waters (~ 0 to 1‰ [see Kroopnick, 1985; Zeebe and Wolf-Galdrow, 2001]), but they are much higher than commonly found at cold seeps ($<-40\text{‰}$). The potential role of biogenic methane to contribute to this ^{13}C depleted signature cannot be discarded as described for the Guaymas hydrothermal systems [Welhan, 1988; Seewald

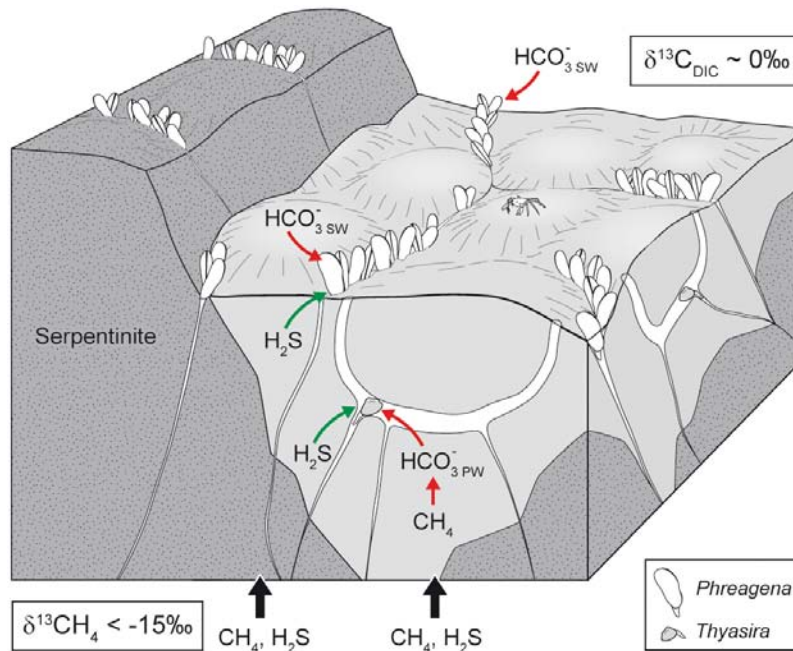


Figure 7. Red arrows represent the model of carbon source uptake in shells originating from Clamstone. Unlike *Phreagena* sp., which has a higher contribution of seawater-derived carbon (enriched in ^{13}C), the burrowing species *Thyasira* aff. *southwardae* has a mix of ^{13}C -enriched seawater (sw) and ^{13}C -depleted pore water (pw)-derived carbon. The value of deep-seawater $\delta^{13}\text{C}_{\text{DIC}}$ was derived from Kroopnick [1985] and the estimation of $\delta^{13}\text{C}_{\text{CH}_4}$ emission from the Rainbow massif was derived from Charlou *et al.* [2002]. Green arrows correspond to the nutrition pathways, assuming both *Phreagena* sp. and *Thyasira* aff. *southwardae* form symbioses with sulfide-oxidizing bacteria.

et al., 1994]. The oxidation of methane-rich sediment pore waters at “Clamstone” may have caused a ^{13}C depleted seawater-brine mixture and the low $\delta^{13}\text{C}$ values in *Thyasira* shells living in burrows. In contrast, *Phreagena* sp., which are able to dig in the sediment to get sulfide from the deeper layer, live at the seafloor and have a higher contribution of seawater-derived DIC in their shell (Figure 7).

4.3. Fossil Evidence of Abundant, Fault-Related, Sedimented, Mid-ocean Ridge Vent Communities

[30] The minimum estimated age of past fluid emissions in the “Clamstone” area, inferred from the ^{14}C age of fossil bivalve communities, is consistent with evidence of Rainbow vent activity initiation (23 ± 1.5 kyr [see Kuznetsov *et al.*, 2006]). Shell distribution at the seafloor combines vesicomimid and thyasirid genera usually known from diffuse fluid areas through soft sediments, and is quite similar to previous descriptions of Anya’s Garden, in Logatchev [Gebruk *et al.*, 2000]. The Logatchev hydrothermal complex lies on heavily sedimented and uplifted ultramafic rocks [Bogdanov *et al.*, 1995]. Anya’s Garden is only a few hundred meters from the active black smokers known as

Irina 2. At Anya’s Garden, vesicomimid and thyasirid bivalves are clearly associated with hydrothermal fluids venting through the sediment. More recently, undetermined empty bivalve shells have been observed at the summit of an elongated WNW-ESE striking ridge, 3 km east of the Logatchev-2 hydrothermal field in an area called Logatchev-4 [Petersen *et al.*, 2009].

[31] Based on slow spreading rates (<2 cm/yr) in this section of the MAR since the last 690 kyr [Le Douaran *et al.*, 1982] and the ^{14}C age of shells (~ 25.5 kyr BP), the present “Clamstone” area has moved by less than 500 m from its estimated past location at the time it was active, whereas the present Rainbow field is 2.5 km away. With respect to the active, focused vent area, localization of the “Clamstone” shell accumulation appears similar to the Logatchev-4 area. In both settings, shells have been found at the summit of the crest that dominates hydrothermal vent field areas (Figure 1). To date, sedimented habitats have mostly been investigated from MOR located close to continental margins, such as from the Guaymas basin in the Gulf of California [Grassle *et al.*, 1985; Grehan and Juniper, 1996]. Therefore, our observations expand the idea that fault-related sedimented low-

temperature hydrothermal sites are more widespread than expected on the MOR.

[32] Figures 3 and 4 show that “Clamstone” is located on a NE–SW trending fault scarp, which may be part of the fault scarps described by *Gràcia et al.* [2000] from side-scan sonar imaging. The geologic setting of serpentinite-hosted hydrothermal systems at Rainbow can be viewed in the framework of the *McCaig et al.* [2007] oceanic detachment fault model. In this model, fluids are transported along the main detachment fault and/or a set of high-angle normal faults are connected to this detachment. In the Logatchev-2 vent area, *Petersen et al.* [2009] inferred that a low-angle detachment fault focuses and transports hydrothermal fluids away from a heat source, located below focused vents, to fuel distant diffuse vents. Such a model may apply at Rainbow. However, a major caveat is that despite many detailed surveys in the area (including ours) no major detachment fault has been unambiguously detected in the Rainbow area. Whatever the exact tectonic setting of this area, the large distribution of hydrothermal communities in the “Clamstone” area (Figure 2) supports the occurrence of a fault network offering numerous fluid pathways through the underlying crust, and vigorous long-lasting venting.

5. Conclusion

[33] Vent species are generally assumed to have evolved with a certain degree of isolation under habitat conditions, leading to a high level of specialization and endemism within biogeographic provinces. Over the geologic time-scale, different species have apparently dominated vent assemblages on the MAR, as previously shown for other ridge systems [*Little et al.*, 1998; *Little and Vrijenhoek*, 2003]. However, our results suggest that dispersal and gene flow over a large geographical area may have also occurred for opportunistic species.

[34] Most deep-sea hydrothermal exploration has focused on ridge axes, since methods used to detect hydrothermal activity require that neutrally buoyant hydrothermal plumes form in the water column from high-temperature vents. This approach has limited the capacity to find off-axis and fault-related diffuse vent fields. The fossils described in this study suggest that sedimented serpentinite-hosted hydrothermal systems and their associated communities may be more widespread than previously thought. Such systems display a variety of suitable habitats for both vent and seep-related

species, and offer great opportunities to better understand the biogeography and temporal dynamics of hydrothermal vent and chemosynthetic communities through geologic time.

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