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## **A review on the phylogeography of potentially chemoautotrophic bacteria from major vent and seep fauna and their contribution to primary production**

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### **Abstract**

Though geochemically and microbially well-defined, the phylogeographic data of microbial symbionts in these highly productive vent and seep systems require a closer examination and synthesis. QIIME analysis of 16S rDNA of bacterial associates of major fauna from 1995 to 2015 was thus undertaken to examine phylogeography of their microbial symbionts along with host specificity. While phylotypes were generally unrelated, bivalve *Calyptogena* exhibited vertical transmission sharing similar symbionts in geographically separated geosystems. Different species of tubeworms possessed identical symbionts through horizontal acquisition at geographically distinct Guaymas basin vent and the Arctic seep. Vents were more versatile with both mobile and sessile fauna hosting ecto- and endo-symbionts. Comparatively, seeps were more specialized with sessile animal hosts with endosymbionts. With C-fixation rate measurements still scanty for sediments, bedrocks and serpentine systems; vent, seep, anoxic and oxic basins were shown to fix up to 22, 325, 96 and 37400 g C m<sup>-3</sup> y<sup>-1</sup> respectively. Estimation of chemosynthetic primary production rates in chemoautotrophic ecosystems could endeavor to improve existing biogeographic models by coupling volcanism and plate-tectonics to global climate and phylogeography.

**Keywords:** phylogeography, chemoautotrophs, primary production, vent, seep

## 1. Introduction

Phylogeny of bacteria associated with vent- and seep- fauna delves into the evolutionary history of a species and their phylogeography revolves around the principles and processes controlling the geographical distribution of related species in these systems (Avisé 2000). Though both vents and seeps are chemically reducing systems, vents are driven geothermally and seeps by either thermogenic or biogenic processes (Krause et al. 2017). Globally, deep-sea hydrothermal vents occur along mid-ocean ridges and back arc basins. The plumes rising from the vents are enriched with reduced chemicals predominantly sulfide, ammonia, methane, iron and manganese (Jannasch and Mottl 1985; Distel et al. 1988; de Angelis et al. 1993; Lam et al. 2004; Dick et al. 2009b; Petersen et al. 2011; Anantharaman et al. 2016). Cold seeps are prominent along the continental margins where fluids enriched in hydrocarbons especially methane are expelled through sedimentary rocks towards seafloor through fissures created via tectonic processes (Greinert et al. 2001; Krause et al. 2017). Thermogenic methane production occurs at depths >1000 m where temperature ranges from 60 to 220 °C (Tissot and Welte 1984; Floodgate and Judd 1992; Stolper et al. 2014). In contrast, biogenic production of methane takes place at the shallower depths where the temperature is <80 °C (Wilhelms et al. 2001; Valentine 2011). Methane production also occurs at low temperature via serpentinization in the presence of carbon dioxide (Abrajano et al. 1990).

There is enough chemical energy in the form of reduced compounds like H<sub>2</sub>S and CH<sub>4</sub> to drive the primary production in these ecosystems. In this process, the inorganic carbon is fixed chemosynthetically to form organic carbon (Fisher 1996; Van Dover et al. 2002; Hourdez and Lallier 2007). Nutrient-rich fluid that oozes out from the vents and seeps stimulates the proliferation of chemosynthetic microbes and also supports the development of diverse invertebrates which rely on these microbes for nutrition (Van Dover et al. 2002; Zbinden et al. 2015).

The vent ecosystems are ephemeral features in the mid-oceanic ridges, arc and back-arc basins with the temperature reaching upto 400°C and pressure between 200-300 atmospheres (Angel 1990; Dable et al. 2006). These conditions are also accompanied by a high concentration of metals and reduced chemicals with very low organic matter especially in the initial stages of venting (Sander and Koschinsky 2011). Prominent vent fauna which harbor chemoautotrophic bacteria include tubeworms *Riftia pachyptila*, *Escarpia spicata* and *Ridgeia piscesae*, polychaete *Alvinella pompejana*, molluscs *Alviniconcha* spp., *Ifremeria* sp., *Calypptogena* spp., *Abyssogena* spp., *Maorithyas hadalis*, *Vesicomys* spp., *Bathymodiolus* spp., and arthropods *Rimicaris exoculata* and *Kiwa hirsuta* (Desbruyères 2006; Stewart et al. 2008; Hügler et al. 2011; Vrijenhoek 2013).

Cold seep ecosystems have conditions like high organic content along with a large amount of reduced chemicals like sulfide, methane, and ammonia (Won 2006). However, temperature and pressure are generally not extreme, except in deep seep areas like the Japan Trench where a temperature of 1.79 °C and pressure of 769.8 atmospheres have been reported (Fujikura et al. 1999; Takai et al. 2014). The cold seeps last much longer and are characteristic of continental margins. In seeps, the important hosts are tubeworms *Lamellibrachia* spp., *Seepiophila jonesi*, *Oligobrachia* spp., *Sclerolinum* sp., *Osedax* sp., and molluscs *Bathymodiolus* spp., *Calymene* spp., *Acharax* spp., *Lucinoma* spp., *Idas* spp., *Isorropodon* spp., *Elenaconcha guiness* and *Pliocardia* sp. (Peek et al. 1998; Barry et al. 2002; Imhoff et al. 2003; Lösekann et al. 2008; Hilário et al. 2011; Oliver et al. 2011; Rodrigues et al. 2012; Duperron et al. 2013; ).

Various bacterial associates reported from vents and seeps include  $\alpha$ -,  $\beta$ -,  $\gamma$ -,  $\delta$ -,  $\epsilon$ -,  $\epsilon$ -*Proteobacteria*, Actinobacteria, Spirochetes, Bacteroidetes, Chloroflexi, Verrucomicrobia and several unaffiliated bacteria (López-García et al. 2002; Kimura et al. 2003; Goffredi et al. 2008). Deep ocean circulation and equatorial and coastal currents help in their distribution and dispersal, though there are certain endemic forms (Galand et al. 2010; Müller et al. 2014).

The mode of transmission of symbionts is either transovarial/vertical (parent to offspring) or horizontal from different hosts or environment (Vrijenhoek 2009). In the case of vertical transmission, co-evolution of host and symbiont leads to a more stable relationship and the symbiont becomes an integral part of host survival. Vesicomylid clams and tubeworms are ideal examples of vertical and horizontal transmission, respectively (Vrijenhoek 2010; Hilário et al. 2011; Roselers and Newton 2012). A recent study by Klose et al. (2015) has revealed that symbionts escape from the tubeworms upon the host's death and decay, perhaps to be taken up by the offsprings, thus providing evidence for host and environment connectivity.

Since the discovery of vents in 1977 (Corliss et al. 1979) and seeps in 1984 (Paull et al. 1984), considerable ground has been covered on the diversity and ecology of the hosts and associated bacteria (Cavanaugh et al. 1981; Felbeck 1981; Rau 1981; Cavanaugh 1983; Fiala-Médioni 1984; Stein et al. 1988; Van Dover et al. 1988; Distel and Cavanaugh 1994). In spite of the appreciable differences in the chemistry and flow rates of fluids in these two systems, studies have proven the evolutionary, physiological and adaptational relatedness in vent and seep fauna (Scott and Fisher 1995). However, similar studies on the bacterial associates have been comparatively limited, especially on chemoautotrophic microbial symbionts/associates (Stewart et al. 2008; Vrijenhoek 2010; Heijden et al. 2012).

In this review, the distribution of major classes of bacterial associates of the representative fauna of these two prominent chemosynthetic systems viz., vent and seep, is contrasted and their phylogeography is discussed. Considering the specificity of some of these associates with their host, we were prompted to understand the phylogeography of these bacteria. This review would help us to appreciate how the host-symbiont specificity spreads over time and space. Phylogeography deals with species formation over time from current to geological time scale and also over space covering different oceans. It also gives an insight into the historical events responsible for geographic variation in genes. Understanding the phylogeography of an organism along with its life style could be important in formulizing its evolutionary mode. The objectives of the present review include 1. To understand the extent of similarities and differences within and between bacterial associates of the vent and seep fauna 2. To elucidate their phylogeography by their common lineage driven by either physical forces like current and tectonics or general biological processes like host mobility and evolution and 3. To review the status of primary production rates measured in vents, seeps and allied systems as this information could be important for understanding their contribution to climate modulation. Published literature and sequences from Genbank database of NCBI (National Centre for Biotechnology Information) were accessed and analyzed to meet the objectives. The approach was based on phylogeny of 16S rDNA of bacterial associates. This marker gene is gaining importance for taxonomy in tracing the evolutionary changes. Further, the class-wise distribution of thiotrophs, methanotrophs, and groups with unknown functions in vents and seeps were plotted on a map using GIS (Geographic Information System) approach.

This review focuses on the phylogenetic analysis of 16S rDNA sequences of >1300 bases in length. Phylogeny of prokaryotes especially associated bacteria would help to elucidate their phylogeography, which in turn would delineate the gene flow that is important for modeling and planning conservatory measures. This review is primarily restricted to Annelida, Arthropoda, Mollusca and their bacterial associates. This approach would cover the more explored major host phyla. Besides, covering newly discovered and other minor phyla would make the data set larger and less practical.. The review essentially probes the intra and intersystem relatedness of the bacterial associates to appreciate their modes of transmission. Further, it also elucidates their phylogeography based on the mechanism of dispersal. Most importantly, interactions with hydrothermal systems may result in bursts of productivity in deep, oligotrophic waters, thus imparting a profound impact on ocean carbon cycling. As studies on chemosynthetic carbon fixation rates have begun to grow, an overview of some of the representative records on primary production from chemosynthetic systems are presented and discussed. Awareness of the relevance and lacunae of phylogeographic study of

chemoautotrophic bacterial associates of the vent and seep fauna prompted us to review this important yet least examined aspect of ecology. Hence an attempt has been made to analyze these two disparate yet comparable systems to understand the similarities and differences.

We have often used the more general term ‘associates’ which is wider and could include the true symbionts as well. Though archaea have been reported, they are fewer in number and therefore this review is mainly restricted to bacteria.

## **2. Materials and Methods**

Mining of 16S rDNA sequences of associated bacteria of vent and seep fauna was done covering the period 1995-2015. Distinct 16S rDNA sequences of length of >1300 bases belonging to prominent hosts, in terms of abundance and frequency of occurrence, in the most explored vents and seeps in world oceans were selected. Sulfur oxidizers, methane oxidizers and also sequences of other bacteria with unknown functions were chosen. To the best of our knowledge, sequences reported for ammonia oxidizers were not of required length (>1300 bases) and hence excluded. We have chosen 84 sequences on the basis of the mentioned criteria which actually represent 2219 sequences, comprising mostly similar (>97.5% similarity) and related clones. The sequences were downloaded in FASTA format from Genbank database of NCBI (National Centre for Biotechnology Information). About 50 bacterial sequences representing vents including East Pacific Rise (EPR), Mid-Atlantic Ridge (MAR), Central Indian Ridge (CIR), Pacific-Antarctic Ridge (PAR) and 34 from seeps including East Pacific (EP), West Pacific (WP), Mediterranean Sea (MS), Atlantic and Arctic counterparts have been analyzed. Phylogenetic analysis was performed using the software QIIME (Quantitative Insights Into Microbial Ecology) (Kuczynski et al. 2011). The sequences were aligned using the software MUSCLE (Multiple Sequence Comparison by Log-Expectation) with a minimum 75% identity (Edgar 2004). These aligned sequences were used to generate the phylogenetic tree using FastTree method (Price et al. 2010). This method infers an approximately Maximum Likelihood Tree (Felsenstein 1981). FastTree computes the local support values by resampling the site likelihood 1000 times and uses the Shimodaira-Hasegawa test to estimate the reliability of each split in the tree (Shimodaira and Hasegawa 1999). The tree file was visualized in a circular mode using iTOL (Interactive Tree Of Life) (Letunic and Bork 2007) with a bootstrap display ranging from 0.129 to 1. Pairwise alignment of sequences was also done using NCBI-BLAST to check the identity score of sequences with reliable bootstrap values. Geographical co-ordinates showing the distribution of bacterial associates from various vent and seep fauna were plotted on a map using DIVA-GIS (a geographical information system) (Hijmans et al. 2005).

### 3. Analyses and Discussion

#### 3.1. Geochemistry, characteristic fauna and associated bacteria in hydrothermal vents of different oceans

##### 3.1.1. Pacific Ocean

In the Pacific Ocean (PO), EPR is the most explored and best-studied ridge on faunal and microbial diversity (Desbruyères 2006; Vrijenhoek 2010; Sylvan et al. 2012). Since this is a fast spreading ridge, with a rate of 9 to 18 cm y<sup>-1</sup>, the spatial frequency of high-temperature venting can be as high as 1/5<sup>th</sup> km of the ridge axis (Mac Donald et al. 1991; Williams et al. 2002; Stewart and Cavanaugh 2009). EPR consists of diverse types of hydrothermal vents including inactive vents, warm springs, white smokers and hot springs. Hot springs are reducing, acidic and sulfidic with a maximum reported temperature of 350 °C. These metal rich habitats form tall chimneys called black smokers with deposition of black metal sulfides (Chester 2000). Concentration of sulfide in the Pacific vents varied from bdl (below detection limit) to 24 mM. Other electron donors for chemoautotrophy such as methane (2.1 nM-0.11 mM), ammonia (10-14700 µM), Fe (14 µM-750 mM) and Mn (<0.01 µM-753 mM) were also present in nM to mM range. Inorganic carbon in the form of CO<sub>2</sub> in these vents amounted to 187-227 mM (Table 1) (Arp et al. 1984; Campbell et al. 1988; Campbell et al. 1994; Ishibashi et al. 1994; Tsunogai et al. 2000; Seyfried et al. 2003; Le Bris et al. 2006; Lutz et al. 2008; Keir 2010; Kawagucci et al. 2011; Teske et al. 2016). The prominent invertebrate phyla in the Pacific vents include Protozoa, Nematoda, Annelida, Mollusca and Arthropoda (Powell and Somero 1986; Katz et al. 2006; Kouris et al. 2007; Goffredi et al. 2008). Tubeworms were abundant in the Pacific vents dominated by *Riftia pachyptila* and *Ridgeia piscesae*. These are mouthless and gutless worms which live in a chitinous tube and possess haemoglobin inside the retractable plume. These fauna are anchored on the rocks, and the base of the tube keeps contact with the sulfide and carbon dioxide rich-water. The anterior end of the red plume extends into the cold (2 °C) oxygen rich bottom water (Zierenberg et al. 2000). The haemoglobin binds to sulfide and oxygen and transports them to the trophosome of the worm where the endosymbionts colonize. These symbionts, mainly  $\gamma$ -*Proteobacteria* produce carbohydrate chemoautotrophically, using energy derived from sulfide oxidation. In return, the host worm offers stable niche to the symbionts (Distel et al. 1988; Childress and Fisher 1992; Polz and Cavanaugh 1996; Di Meo et al. 2000; Van Dover CL 2000; López-García et al. 2002; Pflugfelder et al. 2005; Harmer et al. 2008; Howe 2009; ).

*Riftia* carries 3.7 x 10<sup>9</sup> prokaryotic cells per gram of trophosome (Cavanaugh et al. 1981). A single phylotype of  $\gamma$ -*Proteobacteria* constitutes the characteristic symbiont of *Riftia* (Distel et al. 1988;

Pflugfelder et al. 2005; Harmer et al. 2008). Various other groups including  $\alpha$ -,  $\delta$ -,  $\epsilon$ - *Proteobacteria*, Bacteroidetes, Verrucomicrobia and the candidate division OP8 were also discovered from *Riftia* of the EPR, of which members of  $\epsilon$ -*Proteobacteria* were dominant (López-García et al. 2002). *Ridgeia piscesae* (Siboglinidae), harboring chemoautotrophs was earlier discovered from an active sulfide chimney in Mothra and Main Endeavour vent fields along the JFR, north east Pacific. Activity of intracellular sulfide oxidizing symbionts belonging to  $\gamma$ -*Proteobacteria* was detected in the host tissue (Feldmann et al. 1997; Nyholm et al. 2008). They were also seen as vacuolated attached epibionts on *Ridgeia*. These symbionts, accommodated at the anterior end of the tubeworm, get exposed to low concentrations of sulfide and maintain brief contact with oxic seawater (Kalanetra and Nelson 2010). Vestimentiferan tubeworms harbor two distinct phylotypes (I and II) of thiotrophic bacteria which diverged 200 Ma. The less variable phylotype II is present in *Riftia* and *Ridgeia* (Feldman et al. 1997; Robidart et al. 2008).

*A. pompejana* popularly known as ‘Pompeii worm’ lives in the acidic environment and is highly tolerant to temperature up to 100 °C. They are common inhabitants of the hydrothermal vents of the EPR. They are sessile and form large colonies enclosed in delicate tubes which are thermally and chemically stable. The tubes get attached to chimneys of black smokers (Desbruyeres et al. 1983; Le Bris et al. 2005; Georgieva et al. 2015). They maintain relatively lower temperature of 29-81°C and neutral pH of 7 inside the tube. This is accomplished by the replenishment of the fluid inside the tube through active ventilation or passive convection (Le Bris and Gaill 2007; Georgieva et al. 2015). Mixing of cool oxygenated water and hot vent water carrying reduced electron donor especially sulfide takes place inside the tube (Desbruyeres et al. 1998; Van Dover 2000). The epibionts on the dorsal surface of the worm get exposed to H<sub>2</sub>S, CO<sub>2</sub> and O<sub>2</sub> which they use to synthesize carbohydrate through chemoautotrophy. Most of the bacterial associates from *A. pompejana* were later assigned under  $\epsilon$ -*Proteobacteria* (Haddad et al. 1995; Carry et al. 1997; Arndt et al. 1998; Campbell and Cary 2001; Campbell et al. 2003). Since bacteria belonging to  $\epsilon$  class are characteristically sulfur metabolizers and microaerophiles, they play a prominent role in the sulfur cycle at vents (Desbruyères et al. 1998; Campbell et al. 2001).

The characteristic Yeti crab *Kiwa hirsuta* was discovered from PAR hydrothermal vents. They were spotted towards the base of the chimneys of black smokers along with mussels (MacPherson et al. 2005). The crab harvests epibiotic chemoautotrophic bacteria on the carapace as the main source of nutrition which is taken in by specialized maxilliped ‘comb’ (Zierenberg et al. 2000). Observations also suggest that this species is omnivorous (MacPherson et al. 2005). Studies assumed that radiation

of *Kiwa hirsuta* could be recent on the basis of its ectosymbiotic relationship with the bacteria. This is considered to be an initial step to acquire the bacteria as the most specific endosymbiont (Zierenberg et al. 2000). *K. hirsuta* from PAR harbored  $\gamma$ -,  $\delta$ -,  $\epsilon$ -*Proteobacteria*, Bacteroidetes and Chloroflexi (Goffredi et al. 2008).

In general, bacterial associates from PO included thiotrophs, methanotrophs, ammonia oxidizers, and those with unknown functions belonging to various classes such as  $\alpha$ -,  $\gamma$ -,  $\delta$ -,  $\epsilon$ -*Proteobacteria*, Actinobacteria, Spirochete, Bacteroidetes, Verrucomicrobia and unaffiliated classes (Figure 1, Table 2) (Anthony 1982; de Burgh and Singla 1984; Jannasch et al. 1985; Distel et al. 1988; Stein et al. 1988; Galchenko et al. 1992; Dubilier et al. 1998; Di Meo et al. 2000; Fujiwara et al. 2000; Arndt et al. 2001; Campbell and Cary 2001; López-García et al. 2002; Imhoff et al. 2003; Nakagawa et al. 2005; Urakawa et al. 2005; Katz et al. 2006; Kouris et al. 2007; Won et al. 2008; Harmer et al. 2008; Kalanetra and Nelson 2010).

Diversity of bacteria was higher in the fauna of Galápagos Rift and Juan de Fuca Ridge (JFR) vents than EPR vents (Desbruyères et al. 1983; Burgh and Singla 1984; Jannasch et al. 1985; Distel et al. 1988; Girguis et al. 2000; Arndt et al. 2001; de Campbell and Cary 2001; López-García et al. 2002; Nakagawa et al. 2005; Pflugfelder et al. 2005; Katz et al. 2006; Kouris et al. 2007; Harmer et al. 2008; Nyholm et al. 2008). Our analyses suggest that thiotrophs were abundant in the east Pacific (EP) while methanotrophs were comparatively more in the west Pacific (WP). The following reasons could be attributed to this difference 1. EP is more studied. 2. More vents were dominated by thiotrophs in EP 3. WP is less studied but characterized by more ephemeral back-arc basins and mud volcanoes. 4. WP has also cold seeps in the vicinity accounting for the prominent presence of methanotrophs.

### 3.1.2. Atlantic Ocean

MAR hydrothermal systems are influenced by the slower rate of crustal accretion of 2.5 cm  $y^{-1}$  when compared to the EPR (Stewart and Cavanaugh 2009). Besides, due to slow spreading rates, the number of venting sites encountered here could be as low as one per 100 to 350 km (Murton et al. 1994; German et al. 1996). In the EPR vents, geographical isolation leads to faunal diversification, but in the MAR, vent-wise variations in physico-chemical parameters govern the species differences (Desbruyères et al. 2000). The deeper vents in the MAR such as Logatchev, Snake Pit and TAG are relatively stable. They extrude high temperature fluid up to 350 °C and deposit large piles of sulfide (Van Dover 1995; Gebruk et al. 1997; Desbruyères et al. 2000; Klevenz et al. 2011). Temperature and pH in the MAR vents varied from 2 to >370 °C and 2.5 to 8.02, respectively. Sulfide content in



the Atlantic vents (4  $\mu\text{M}$  – 2.5 mM) was relatively lower than that of the Pacific. On the other hand, a maximum of 4 mM methane was measured in the Atlantic which is considerably higher than that in the Pacific. Concentrations of  $\text{NH}_4^+$ , Fe and Mn in Atlantic vents ranged from 10–14700  $\mu\text{M}$ , 14  $\mu\text{M}$ –750 mM and  $< 0.01$   $\mu\text{M}$ –753 mM, respectively (Table 1) (Renninger et al. 1995; Sarradin et al. 1999; Charlou et al. 2000; Konn et al. 2009; Perner et al. 2009; Keir 2010; Klevenz et al. 2011; Seyfried Jr et al. 2011).

Bathymodiolid mussels are ubiquitous and the dominant fauna in hydrothermal vents especially MAR. Phylogeny suggests that they have colonized the deeper environments quite recently. Their ancestors were considered to be shallow water suspension feeding mussels (Barry et al. 2002; Kimura et al. 2003). *Bathymodiolus* mussels are mixotrophic, retaining a functional gut and filter feeding habit. They shelter bacterial symbionts, especially thiotrophs and methanotrophs, in the gill bacteriocytes (Fiala-Médioni et al. 1986; Arndt et al. 2001; Fujiwara et al. 2001;). The shrimp *Rimicaris exoculata* is another characteristic fauna of the MAR. It is known for its tremendous swimming potential (Jan et al. 2014). Filamentous bacterial cells in the inner surface of shells of *Rimicaris exoculata* were associated with different oxidation states of metal sulfides. The bacterial community was also located on the maxillae appendages, part of the carapace, legs and gills (Van Dover et al. 2001). Most of them were sulfide oxidizing  $\gamma$ - and  $\epsilon$ - *Proteobacteria* (Polz and Cavanaugh 1995). The recently discovered epibiotic  $\alpha$ -*Proteobacteria* from the gill chambers of the shrimp *R. exoculata* possessed genes responsible for iron oxidation (Jan et al. 2014).

In general, the potential chemoautotrophic bacterial associates of the fauna from the Atlantic vents include thiotrophs, methanotrophs, iron oxidizers and those with unknown functions belonging to  $\gamma$ -,  $\epsilon$ - and  $\alpha$ - *Proteobacteria* (Figure 1, Table 2)

### 3.1.3. Indian Ocean

In the Indian Ocean (IO), which is not as ancient as the Pacific or as young as the Atlantic, vent research is still nascent. Maximum temperature measured in the IO vent was 365 °C with pH ranging from 3.4 to 6.6. Concentration of sulfide and methane ranged from 3.93 to 4.07 mmol kg<sup>-1</sup> and 0.17 to 3.5 mmol kg<sup>-1</sup> respectively (Table 1) (Gallant and Damm 2006). Chemical characteristics of fluids from high-temperature vent (Kairie field) in the IO share some common traits of both PO and AO (Gamo et al. 2001).

The records to date from the IO show that the dominant hosts are the molluscs (Goffredi et al. 2004; McKiness and Cavanaugh 2005; Stewart et al. 2008; Won et al. 2008). Gammaproteobacteria are specific to *Bathymodiolus* sp. and to snail *Alviniconcha* sp. (Stewart et al. 2008; Won et al. 2008).

Hydrothermal vents in the CIR support large diverse aggregates of sedentary gastropod species including *Alviniconcha* spp. and characteristic scaly snails. *Alviniconcha* spp. generally inhabits the Indo-Pacific hydrothermal vents. Since this snail lives in highly acidic conditions, it has degraded shells with spikes (Johnson et al. 2014). In the case of scaly snail, the scales are composed of iron sulfides and unlike other snails, it lacks the operculum (Goffredi et al. 2004). Thiotrophic  $\gamma$ -*Proteobacteria* were hosted inside the oesophageal gland of a scaly snail from Rodriguez Triple Junction (RTJ) on the Indian Ocean ridge. This single microbial type seemed to be the source of nutrition for the snail. The sclerite of the scale possessed epibionts such as  $\gamma$ -,  $\delta$ - (sulfate reducing lineage) and  $\varepsilon$ -*Proteobacteria* and the shell consisted of  $\gamma$ -,  $\varepsilon$ -*Proteobacteria* and Bacteroidetes (Suzuki et al. 2005). The participation of sulfate-reducing bacteria could be important especially when the supply of sulfide is low. Generally, in the Indian Ocean,  $\gamma$ - and  $\varepsilon$ -*Proteobacteria* were dominant as observed in the Atlantic, apart from  $\delta$ -*Proteobacteria* and Bacteroidetes (Figure 1, Table 2) (Goffredi et al. 2004; McKiness and Cavanaugh 2005; Stewart et al. 2008; Barton and Fauque 2009).

### **3.2. Geochemistry, characteristic fauna and associated bacteria in cold seeps of different oceans**

#### **3.2.1. Pacific Ocean**

In the Pacific Ocean, most of the cold seeps are distributed on the active subduction zones along the coast of South America, Central America to southern California and Oregon in EP and Japan to New Zealand in the WP. Some of the world's deepest seeps are located in the WP (Lewis and Marshall 1996; Mironov 2000). Most studied seeps include Nankai Trough and Sagami Bay off Japan and Off Oregon and Monterey Bay in northern California (Sibuet and Olu 1998; Sibuet and Olu-LeRoy 2002). The basement of the Pacific seeps are made up of fine-grained sediment with phosphorite pebbles in Peru margin, basaltic in seamounts and carbonate pavements in Monterey Bay (Bohrmann et al. 1998; Stakes et al. 1999). Generally, in seeps, methane rich porewater gets transported towards the sediment surface which further gets oxidized in the anoxic sediment of the methane sulfate transition zone (Valentine 2002). Coupling of sulfate reduction with anaerobic methane oxidation generates a high concentration of sulfide up to 26 mM off Oregon and Monterey Bay, eventually leading to the biomass production of thiotrophs and methanotrophs (Sahling et al. 2002; Levin et al. 2003). Maximum measured concentrations of methane, ammonia, Fe and Mn from the Pacific seeps were 2.5 M, 1.4 mM, 2.2  $\mu$ M and 220 nM, respectively (Table 1) (Tsunogai et al. 1996).

In the Pacific seeps, the major fauna includes vestimentiferan tubeworms, bathymodiolid mussels and vesicomyid clams. Seep tubeworms are long and thin compared to their vent counterparts. Since cold seeps hold sulfide only in the sediment, the tube worms access sulfide via thin extension of their posterior part (Zierenberg et al. 2000). Autotrophic symbionts of worms living in anaerobic conditions inside the trophosome oxidize  $H_2S$  and release chemical energy for carbon fixation (Naganuma 1998). Besides *Lamellibrachia* spp., another tubeworm *Escarpia spicata* from the seeps in the Guaymas Basin also harbored thiotrophic  $\gamma$ -*Proteobacteria* as the endosymbiont (Nelson and Fisher 2000). *Lamellibrachia* spp. harbored  $\alpha$ -,  $\beta$ -,  $\gamma$ - and  $\epsilon$ -*Proteobacteria* (Peek et al. 1998). Phylotypes of  $\epsilon$ -*Proteobacteria* were closely related to *Acrobacter* spp.. They were discovered as intracellular symbionts in the trophosome of *Lamellibrachia* sp. from methane seeps in Sagami Bay, Japan. Coccoid  $\alpha$ -*Proteobacteria* was discernible in the trophosome of *Lamellibrachia* sp. from a methane-rich seep of Sagami Trough (Elsaied et al. 2002). Thiotrophic and methanotrophic bacteria and those with unknown functions belonging to  $\alpha$ -,  $\beta$ -,  $\gamma$ -, and  $\epsilon$ -*Proteobacteria* and unidentified groups were found in the seeps of WP especially from Sagami Trough, Japan (Elsaied and Naganuma 2001; Fujiwara et al. 2001; Imhoff et al. 2003; Kimura et al. 2003; Duperron et al. 2007; Naganuma et al. 2007).

The vesicomyid clams prefer habitats ranging from soft bottom sediments to basaltic rocks in the seeps of PO. They are mixotrophic, burying three fourth of their body in the sediment. They penetrate their feet into the sediment and access  $H_2S$  which further gets transported to endosymbionts present in the gill (Hashimoto et al. 1995). Microbes involved in the production of  $H_2S$  from anaerobic decomposition of  $CH_4$  coupled with  $SO_4^{2-}$  reduction were present in the annelid *Escarpia spicata*, molluscs *Calyptogena* spp. and *Vesicomya lepta* (Peek et al. 1998; McKiness et al. 2005). Several unidentified bacterial associates were also discovered from various hosts (Cary and Giovannoni 1993; Imhoff et al. 2003). Majority of the bacterial associates in the Pacific seeps were recovered from Monterey Canyon, California (Cary and Giovannoni 1993; Peek et al. 1998; McKiness et al. 2005). In general, fauna from the Pacific seeps harbored potential chemoautotrophs comprising thiotrophs, methanotrophs and those with unknown functions belonging to  $\alpha$ -,  $\beta$ -,  $\gamma$ - and  $\delta$ -*Proteobacteria* (Figure 2, Table 2).

### 3.2.2. Atlantic Ocean

In the AO, seeps occur off the coast of Brazil, Gulf of Mexico, near Barbados, the Blake Ridge off the Carolinas, the Laurentian Fan, the Gulf of Cadiz, the Sea of Marmara, and the coasts of Angola and Nigeria (Vogt et al. 1999; Pinheiro et al. 2003; Cordes et al. 2007; Olu-Le Roy et al. 2007; Zitter

et al. 2008). The first cold seep system was discovered 32 years ago in the Florida Escarpment in GoM in the AO where the concentration of methane reaches up to 10 mM (Table 1) (Paull et al. 1984; Chanton et al. 1991). Hydrocarbon cold seeps are prominent along GoM which includes petroleum seeps, gas hydrate seeps and tar balls (Sassen et al. 1993, 1999; MacDonald et al. 2004). Generation of sulfide in the Atlantic seeps is from the anaerobic oxidation of methane, hydrocarbon and organic matter coupled with sulfate reduction (Aharon and Fu 2000; Arvidson et al. 2004; Joye et al. 2004). Methane and ammonia concentrations in the Atlantic seeps varied from 32  $\mu$ M to 10 mM and bdl to 1800  $\mu$ M, respectively. Other electron donors such as Fe and Mn were in nanomolar range (Table 1) (Chanton et al. 1991; Hensen et al. 2007; Lemaitre et al. 2014). The major fauna in the Atlantic seeps include vestimentiferan tubeworms belonging to the family Siboglinidae, bathymodiolid mussels and clams belonging to the families, Vesicomidae, Thyasiridae, Solemyidae and Lucinidae.

Thiotrophic and methanotrophic symbionts belonging to  $\gamma$ -*Proteobacteria* and unidentified groups were recorded from seeps in the Atlantic, mostly from GoM (Cavanaugh et al. 1987; Fisher et al. 1987; Southward 1988; Vacelet and Boury-Esnault 1995; Vacelet et al. 1996; Nelson and Fisher 2000; Raggi et al. 2013). Tubeworms *Lamellibrachia* sp., *Seepiophila jonesi*, molluscs *Calyptogena* sp. and *Bathymodiolus* spp. sustained  $\gamma$ -*Proteobacteria* (Vacelet et al. 1996; Peek et al. 1998; Nelson and Fisher 2000). Several unidentified bacteria exhibiting chemosynthetic and cryptic functions were also present in the sponge *Cladorhiza* sp., molluscs *Calyptogena* sp., *Vesicomya* sp. *Bathymodiolus* sp. and unidentified mytilids (Anthony 1982; Childress et al. 1986; Fisher et al. 1993; Vacelet and Boury-Esnault 1995). In general, chemosynthesis dependent invertebrates in the seeps of AO harbored thiotrophs, methanotrophs, and those with unknown functions belonging to  $\gamma$ -*Proteobacteria*, Bacteroidetes and unidentified bacteria (Figure 2, Table 2).

### 3.2.3. Mediterranean Sea

Adjacent to the AO in the north east, seeps in the Nile deep sea fan (NDF) of the MS harboured thiotrophic and methanotrophic symbionts belonging to  $\gamma$ -*Proteobacteria* and Bacteroidetes (Figure 2, Table 2) (Fisher et al. 1993). The central part of the NDF possessed only thiotrophs and a combination of thio and methanotrophs in the north. Maximum sulfide and methane measured in the Mediterranean seep was 23 and 120 mM, respectively (Table 1) (Haese et al. 2003; Ristova et al. 2015). *Gammaproteobacteria* were sustained by the clam *Lucinoma* aff. *kazani* and mussel *Idas* sp. Bacteroidetes however, was restricted to mussels. Presence of *Lucinoma* aff. *kazani* can be correlated

with local enrichments in sulfide through the activity of symbiotic microbes involved in sulfate reduction coupled to anaerobic oxidation of methane (Duperron et al. 2007).

#### **3.2.4. Indian Ocean**

Though seeps have been discovered in the IO particularly off the coast of Pakistan, Indonesia and the Bay of Bengal, studies on invertebrates and associated microbes are scarce (Cordes et al. 2010).

#### **3.2.5. Arctic Ocean**

In the Arctic, a prominent cold seep system was discovered in the Håkon Mosby Mud Volcano, off the coast of Norway. Several experiments demonstrated and supported the very high concentration of methane up to 266  $\mu\text{M}$  (Table 1) (Ginsburg et al. 1999; Lein et al. 1999; Milkov et al. 2004). Sulfide content up to 0.15 mM was detected in the sediment samples (Table 1) (Milkov et al. 1999; Lösekann et al. 2008). Tubeworms especially Pogonophorans constituted the dominant fauna including genera *Oligobrachia* and *Sclerolinum* (Pimenov et al. 1999). Below siboglinid tubeworm, bacterial mats composed of methylococcales (aerobic methanotrophic bacteria), ANME-2 (anaerobic methanotrophic archaea) and ANME-3 (undescribed archaea) were detected. Different species of sulfur-oxidizing filamentous genera *Beggiatoa* were also present in the microbial mat. The absence of sulfate and oxygen in the mud volcano fluids limit the availability of electron acceptors for methane oxidation (Milkov et al. 1999; de Beer et al. 2006; Niemann et al. 2006).

Additional information on the geochemistry of the vents and seeps are detailed in the Supplementary Table 1. Generally, hydrothermal vents are highly sulfidic and cold seeps are rich in methane. However, a relatively higher concentration of methane (up to 4 mmol kg<sup>-1</sup>) and sulfide (23 mM) have been measured at MAR vents and cold seeps of Eastern Mediterranean, respectively. Higher concentration of ammonia in both vents (max. 14 mM) and seeps (max. 4.5 mM) shows its importance as electron donor in chemoautotrophy in both these systems. Metal concentrations, especially Fe and Mn were also higher in the vents ( $\mu\text{M}$  to mM) than seeps (nM) (supplementary table 1) (Boulègue et al. 1987; Gallant and Damm 2006; Kawagucci et al. 2011; Klevenz et al. 2011; Ristova et al. 2015). Detailed information on the diversity of bacterial associates, host, metabolism and chemical environment are presented in the Supplementary Table 2a and 2b.

### **3.3. Age of chemosynthetic fauna and changing earth**

Appearance of the present prominent fauna in vents and seeps can be correlated with the final stages of breakup of the Pangaea as per molecular clock (Hurtado 2002; Bachraty et al. 2009). These recent groups especially vestimentiferan tubeworms could be the descendants of ancestors from other deeps

sea or shallow water habitats (Black et al. 1997). The relationship between symbionts could be inferred in the light of the origin and evolution of host fauna (Krueger and Cavanagh 1997). Molecular analyses of the major vent and seep fauna including vestimentiferan tubeworms, bathymodiolus mussels, vesicomysid clams, yeti crabs and bresiliid shrimps reflected their Mesozoic (250 Ma) to Cenozoic (65 Ma) origin (Van Dover et al. 2002). Fossils and molecular studies showed that vestimentiferan tubeworms evolved during early Jurassic (200 Ma) and late Cretaceous (100 Ma) periods in vents and seeps (Kauffman et al. 1996; Campbell et al. 2002; Little 2002; Hikida et al. 2003). Phylogenetic studies revealed the diversification of vestimentiferan tubeworms in cold seeps (Van Dover et al. 2002). Evolution of Yeti crab (Kiwidae) was also estimated to have taken place during mid-Cretaceous (92.8 – 121 Ma) (Roterman et al. 2013). Vesicomysid clams originated in seep about 100 Ma. This time period was much more than the molecular estimate of 22- 44 Ma (Little and Vrijenhoek 2003). They originated in cold seeps and further expanded their niche to hydrothermal vents and whale bones (Baco et al. 1999). The vent and seep *Bathymodiolus* mussels evolved during the late Cretaceous period (56 – 94 Ma) (Little and Vrijenhoek 2003) from their shallow water suspension feeding counterparts (Craddock et al. 1995; Distel et al. 2000). Bresiliid shrimps evolved very recently, <20 Ma from vents (Shank et al. 1999). The oldest fossil of chemosynthetic brachiopods belonging to the Jurassic period was found in the hydrocarbon seep deposit off eastern Oregon (Peckmann et al. 2013). Some chronological aspects of plate tectonics since the Jurassic could have influenced the relationships among regional fauna inhabiting the mid-ocean ridges (Tunnicliffe et al. 1996).

More importantly, plate tectonics could have played a central role in the diversification of vent and seep fauna and their bacterial associates. Presence of certain common species such as bivalves *Calyptogena kilmeri*, *C. elongata*, *Idas washingtonia* and vestimentiferan tube worm *Escarpiia spicata* or related ones in different reducing habitats such as seep and whale bones reflect their common origin and later separation due to vicariance (Tunnicliffe et al. 1996; Smith and Baco 2003). Plate tectonic events such as formation of seamounts due to volcanism, closure of oceanic basins, seafloor spreading cessation and ridge jumps affect the continuity of a plate boundary that serves as a biogeographic province. The mid-ocean ridges are classified as fast, intermediate and slow spreading ridges based on the rate of spreading between a pair of associated lithospheric plates. On the fast spreading centres (e.g. EPR), frequent (one eruption in 3-14 years) volcanic eruptions occur, resulting in the formation of large seamounts and plateaus (Sinton et al. 2002; Van Dover et al. 2002). Formation of such large seamounts or plateaus created by volcanism serves as barriers to the dispersal. Thus, it adversely affects the continuity of the biogeographic provinces, resulting in the

geographical isolation of hydrothermal vent fauna. In addition, those frequent volcanisms wipe out all the living organisms present in its vicinity (Howe 2008). Conversely, the slow spreading ridges (e.g. MAR) are not associated with major volcanisms and therefore serve as the biogeographic province with possibly longer dispersal pathways. This information suggests that on slow spreading ridges, the hydrothermal fauna is not frequently disturbed by tectonic activity as in the case of fast spreading ridges (Bachraty et al. 2009). The intermediate to slow spreading rates observed in the CIR suggest that this ridge could act as a passage for simultaneous dispersal of biota from different ocean basins (German et al. 1998; Van Dover 2002). Therefore, the spreading rate of a mid-ocean ridge plays an important role in the capabilities of dispersal and gene flow of hydrothermal vent fauna. The spreading ridge cessation and ridge jumps result in the reorganization and lengthening of the transform faults between two segments of a mid ocean ridge and thereby disconnect the continuity of the ridge axis. These situations also act as barriers for the dispersal of hydrothermal vent fauna of existing biogeographic provinces.

### **3.4. Phylogeography of potential chemoautotrophs associated with vent and seep fauna**

#### **3.4.1. Hydrothermal vent**

Thiotrophic  $\gamma$ -Proteobacterial symbionts of mussels *B. septemdierum* and *Myrina* sp. from Myojin Knoll and Suiyo seamount in the WP shared 99% identity (Figure 3a). Geographically, these two vents are a part of Izu-Bonin-Mariana Arc system. Studies reported that the hydrothermal fluid chemistry of these vents is similar (Lizasa et al. 1998; Desbruyères et al. 2006). These findings suggest that similar chemical conditions prevailing in these two vents support highly related bacterial phylotypes. As explained by the niche theory, the environmental conditions select the species composition through habitat filtering (Dumbrell et al. 2010; Pontarp et al. 2012; Coutinho et al. 2015). Moreover, the local currents along the mid-ocean ridges could also aid in the transportation of microbes between vents (Howe 2008).

The tubeworms *R. pachyptila* and *R. piscesae* from EPR and JFR, north east Pacific respectively, shared 99% identical  $\gamma$ -Proteobacterial thiotrophic symbionts (bootstrap value 0.99) (Figure 3a). These vestimentiferan tubeworms are likely to possess a single or highly similar bacterial phylotypes (Feldman et al. 1997; Laue and Nelson 1997; di Meo et al. 2000; Nelson and Fisher 2000; McMullin et al. 2003; Stewart and Cavanaugh 2006). They have been known to acquire the symbionts from a pool of free-living bacteria. Initially, the above-mentioned vents were a part of a single continuous ridge system (Pacific mid-ocean ridge) which rifted apart 30 Ma due to tectonic fracturing of the Farallon plate (Tunnicliffe et al. 1996; Atwater and Stock 1998). Consequently, the gene flow

between organisms in the two vents ceased. This led to the reproductive isolation of *Riftia*, which was suggested to have the Mesozoic or Cenozoic origin. This tubeworm further evolved into a different species, *Ridgeia piscesae*. This evolution is also supported by molecular clock, which depicts the intrinsic link of vent fauna and the formation and separation of mid-ocean ridges (Halanych et al. 1998; Chevaldonné et al. 2002; Howe 2008). The observed high similarity between the symbionts of *Riftia* and *Ridgeia* shows that the evolution did not weaken the specificity of the previously acquired symbiont to its host i.e., the host evolved without any changes in the symbiont.

Thiotrophic  $\epsilon$ -Proteobacterial epibiont of polychaete *Alvinella pompejana* from the EPR and shrimp *Rimicaris exoculata* from the MAR showed 94% identity (bootstrap value 1) (Figure 3a). Earlier studies also showed the extremely high relatedness of epibiotic  $\epsilon$ -Proteobacteria of Alvinellid polychaete and *Rimicaris* (Madrid et al. 2001). It was also proven that this particular clade of bacteria is abundant and endemic to the Pacific and Atlantic vents (Polz and Cavanaugh 1996; Longnecker and Reysenbach 2001). Though there is no direct ridge connection between Pacific and Atlantic, the past connection between these oceans before the formation of the Central Isthmus of Panama (about 3 Ma), could be the possible reason for finding similar microbes (Miura et al. 2012). Also, the ancient Tethys Sea which existed between Eurasia and Africa about 100 Ma could have been the direct passage of microbes between Pacific and North Atlantic (Gebruk et al. 1997; Jolivet et al. 1998; Van Dover 2000).

Phylogeographically, the symbionts in the MAR vents especially those of Bathymodiolus mussels appear to be less related to those from other vents. Deeper ridge valleys in the MAR retain larvae and prevent their transmission (Van Dover et al. 2002). Thiotrophs and methanotrophs in the MAR mussels belong to two independent lineages of  $\gamma$ -Proteobacteria (Figure 3a). Thiotrophs in the mussel *Bathymodiolus azoricus* from various MAR vents were not identical. Previous studies also showed that *B. azoricus* acquire thiotrophic symbionts from their surroundings (Won et al. 2003). These reasons could be attributed to the observed diversity among thiotrophs in the mussels from different vent sites. Geochemical differences among the MAR vents also support this observation (Desbruyères et al. 2000). Moreover, an earlier study also described that diversification of thiotrophs among host mussels increases with the geographical distance between the sites (Won et al. 2008). Such observations have been made in distantly separated MAR vents (Butterfield et al. 1990; German and Parson 1998). On the contrary, methanotrophs in *B. azoricus* from different vents in the MAR were highly related, sharing 99% identity (bootstrap 1) (Figure 3a). This is because methane-oxidizing symbionts of mussels are generally host specific (Peterson and Dubilier 2009). The degree



of similarity of some symbiont phylotypes between different species of *Bathymodiolus* mussels depends on the mode of acquisition of the symbiont. Certain host specific bacterial phylotypes are maternally transmitted for several generations, but there are bacteria which the hosts acquire directly from the environment (Le Pennec and Beninger 1997; Eckelbarger and Young 1999; Won et al. 2003; DeChaine and Cavanaugh 2005). Moreover, the post-larval stage of *B. azoricus* was found to harbor thiotrophic and methanotrophic symbionts. Dispersal of these larvae could also cause symbiont transport between different locations (Won et al. 2003). Here the inter vent variations in thiotrophs are high due to 1) restriction in the mobility of host *Bathymodiolus*, 2) transforming faults and azores plateau (formed due to tectonic activity) acting as barriers, 3) slower spreading rates in Atlantic than Pacific and most importantly 4) less host specificity (Cannat et al. 1999; Heijden et al. 2012). From these studies, it is obvious that the mobile fauna are content with chemoautotrophs that are epibiotic as evidenced in both the ancient yeti crab and the recently evolved *Rimicaris*. However, the sessile forms prefer to harbor the endosymbiotic forms in sync with their life style.

Ectosymbiotic thiotrophic  $\gamma$ -*Proteobacteria* of shrimp *Rimicaris exoculata* (MAR) showed 94% identity to epibiotic bacteria associated with the yeti crab *Kiwa hirsuta* from the Annie's Anthill Vent field (AAV, PAR), well supported by a bootstrap value of 0.99 in the phylogenetic tree (Figure 3a). The relatedness between the epibiotic bacteria hosted by the shrimp and the crab despite the distance separating them could be attributed to two reasons. Firstly, it is probable that the prevailing currents connecting these oceans enhance the dispersal of host larvae with the symbionts which remain unaltered or undergo genetic differentiation due to geographic isolation (Vrijenhoek 2010; Rogers et al. 2012). Secondly, the existing connection between the mid-oceanic ridge in the Pacific and the Atlantic through PAR could facilitate the dispersal of symbionts via currents along the ridges (Tunnicliffe et al. 1996). Shrimp *Rimicaris* is also known to be a capable swimmer and also has free-living planktotrophic post-larvae which feed on the photosynthetic material (Pond et al. 2000). The juveniles also possess tremendous swimming potential. Moreover, the nutritional strategy allows the larvae to disperse from the vent sites despite the presence of large fracture zones in the MAR vents (Van Dover et al. 2002). The larvae could also be carried away by criss cross currents along the ridges (Howe 2008).

One of the epibiont from the scaly snail in the IO showed high similarity (93%) to a  $\delta$ -Proteobacterial associate of tubeworm *Riftia pachyptila* from EPR and also to that from the Yeti crab *Kiwa hirsuta* from AAV (PAR) which is well supported by a bootstrap value of 0.99 and 1, respectively (Figure 3a). It is thus inferred that dispersal of bacterial associates between entirely

different hosts across the Indian and Pacific oceans is highly possible due to warm water currents which link these two oceans. The major pathway is apparently via the Indonesian Through Flow, which is responsible for the transfer of warm surface water from the tropical north-west Pacific along the Makassar Strait, into the Flores and Banda Sea and the Indian Ocean (Figure 4) (German et al. 1996; Gordon and Fine 1996). Another possible route is the PAR and Macquarie Ridge Complex, which act as an intermediate dispersal pathway of the Pacific and the Indian Ocean species (Desbruyères 2006). Moreover, existing mid-ocean ridge connection between the Pacific and the Atlantic through the Indian Ocean and the PAR facilitate the dispersal and spreading of Pacific biota in these regions (Tunnicliffe and Fowler 1996). These connecting routes with the prevailing currents between different oceans facilitate the dispersal and exchange of free-living bacteria and metazoan larvae harbouring bacterial symbionts (Tunnicliffe and Fowler 1996; Van Dover et al. 2002; Bachraty et al. 2009; Vrijenhoek 2010; Rogers et al. 2012). The probability of the existence of allied vent fauna and bacteria in different parts of the world ocean before the continental drift can also be a remote possibility, which could support the occurrence of related species which hitherto defied evolutionary divergence (Tunnicliffe et al. 1997). Map showing the locations of the vents included in this review is depicted in Figure 3b.

#### **3.4.2. Cold seep**

Different species of *Calymene* clams from the seeps in the east and west Pacific, such as *C. kilmeri* off Oregon (EP), and *C. soyoe* from Sagami Bay (WP) shared 99% identical thiotrophic symbionts (bootstrap value 0.85) (Figure 3a). Earlier studies with COI sequence analysis of *Calymene* clams showed that *C. kilmeri* clustered with *C. soyoe* which revealed their close evolutionary relatedness (Peek et al. 1997; Kojima et al. 2004; Decker et al. 2012). Since vesicomyid clams are known for maternal/vertical transfer of symbionts, these species probably acquired the same symbionts from their common ancestor before divergence due to geographical isolation. *Calymene extenta* from the seeps in the west and east Pacific also hosted identical symbionts. This is a very good example of maternal inheritance of species-specific symbionts. They carry out oxidation of H<sub>2</sub>S produced by the microbial reduction of sulfate using methane in seep sediments. Thus they synthesize organic matter utilizing dissolved inorganic carbon (Masuzawa et al. 1992). It should also be noted that generally different species of vesicomyid clams co-occur together in the Pacific seeps (Barry et al. 1997; Kojima 2002). However, in the Monterey Bay, different *Calymene* clams preferred different sulfide concentrations (Barry et al. 1997).

*Bathymodiolus heckerae* from adjacent seeps such as the Western Florida Escarpment (WFE) and another seep in the GoM shared 99% identical thiotrophic symbionts (boot strap value 0.97) (Figure 3a). According to previous studies, this particular symbiont species belonged to the ‘T2’ phylotype of *B. heckerae* and its closest relative is that of the host *B. septemdirum* from the vents in WP (Duperron et al. 2007). This relatedness is evident in the phylogenetic tree (Figure 3a). Methanotrophic symbiont of *B. childressi* from the GoM in the west Atlantic and *B. hirtus* from Kuroshima Knoll in the west Pacific shared 99% identity (bootstrap value 0.97) (Figure 3a). The latter was identified as  $\gamma$ -*Proteobacteria*. Generally, methanotrophs are host specific but occasionally a single phylotype can be seen in multiple hosts (Won et al. 2003; Duperron et al. 2005; DeChaine et al. 2006). Here, the two hosts *B. childressi* and *B. hirtus* are also phylogenetically placed under ‘group 1’ of subfamily Bathymodiolinae based on their COI sequences (Miyazaki et al. 2010). Hence, in this case, phylogenetically related hosts sustain highly similar symbionts. Two different genera of vestimentiferan tubeworms such as *Escarpi* sp. and *Seepiophila jonesi* from GoM shared 98% identical thiotrophic symbionts (boot strap value 1) (Figure 3a). These symbionts belonged to phylotype 1 of the two phylotypes recovered from vestimentiferan tube worms. This particular phylotype diverged from the second, more than 200 Ma, much before the radiation of their hosts and widely occurred in vestimentiferan genera in the cold seeps of Atlantic (Fieldman et al. 1997; Vrijenhoek 2010).

In a conundrum where one wonders which arrived first in a habitat, the host or the symbiont, the above observation suggests that there could be instances where the host follows the potential symbiont. However, it is known that bacteria were early colonizers. Hence, it could be possible but that the host evolved to match the available symbiont. Thus, it is highly plausible that the symbiont evolved faster than the host. It is widely known that the bacterial inhabitants are atleast as old as the earth itself. Panspermia theory proposes that their age could be much older than the age of the earth itself (Parrilli et al. 2011). Hence, in this case, the symbiotic relationship could be as old as the host, but not the bacterial lineage.

Smaller vesicomyid clams such as *Isorropodon megadesmus* from a seep in the Gulf of Cadiz in north east Atlantic and *I. perplexum* from a seep in the east Mediterranean have 99% identical thiotrophic symbionts (bootstrap value 0.99, Figure 3a). The latter is the only vesicomyid clam reported in the eastern Mediterranean (Oliver et al. 2011). The Gulf of Cadiz is a region where mixing of Mediterranean and Atlantic waters occurs. There is also a possibility of symbiont transfer from Atlantic to Mediterranean waters via the Strait of Gibraltar, since this is the only connection

between them (Figure 5) (Tintore et al. 1988; Darling et al. 2007). Though symbiont transmission is generally vertical in vesicomid clams, this particular case is an example of the horizontal host-host acquisition because it was hypothesized that *I. perplexum* in EM originated from EA ancestors 5.96-5.33 Ma (Heezen and Johnson 1969; Madelain 1970; Cary and Giovannoni 1993; Baraza et al. 2003; Duggen et al. 2003; Dubilier et al. 2008; Stewart et al. 2008). Map showing the locations of seeps included in this review is depicted in Figure 3b.

### 3.4.3. Comparison between bacterial associates of vent and seep fauna

Our analysis shows that bacterial associates from these two ecosystems are generally unrelated. In certain cases like *Calyptogena* clams, the symbiont is host specific rather than environment dependent. *C. fausta* from the Nankai Trough, a seep in WP and *C. pacifica* from JFR vent in EP harbored nearly identical (99%) thiotrophic symbionts (bootstrap value 0.97) (Figure 3a). Similar level of affinity has been observed in the case of siboglinid tubeworms. *Escarpia spicata* from the vent in Guaymas Basin, EP and *Scerolinum contortum* from the seep in the Arctic Ocean shared 99% identical thiotrophic symbionts (bootstrap value 0.99) (Figure 3a). This particular symbiont type is unique in hosts that colonize sediment vent and cold seep (Schulze and Halamyh 2003). In this case, the Guaymas basin is a sediment vent (Campbell et al. 2013). This phylotype of thiotrophic symbiont is a successful chemolithoautotroph common to both sediment vent and cold seep. Hence, they could be environment dependent. They could have been acquired by the tubeworms to meet their nutritional requirements. Maximum numbers of bacterial phylotypes have been reported from the vents and seeps of PO followed by Atlantic.

A summary of prominent hosts and potential chemoautotrophic bacterial associates in the vent and seep ecosystem is presented in Figure 6. The diversity as depicted by the number of host species and the number of bacterial associates were higher in the vents. The high diversity of different bacterial classes encountered in tubeworms could be attributed to its ancient origin. Generally, most of the  $\alpha$ - and  $\epsilon$ -*Proteobacteria* were thiotrophs while  $\gamma$ -*Proteobacteria* comprised of both thio and methanotrophs. Our review shows that  $\gamma$ -*Proteobacteria* are the most successful symbionts harbored by diverse host species residing in the vents and seeps of global Ocean. This is followed by  $\epsilon$ -*Proteobacteria* in vents and  $\alpha$ -*Proteobacteria* in seeps other than a relatively high number of unidentified phylotypes. Percentage of bacterial phylotypes reported from vents and seeps of the world ocean is shown in Figure 7. Among the vents, the maximum numbers of host-associated bacterial phylotypes were from PO, representing 77%. Similarly, the seeps in PO possessed 59% of total bacterial phylotypes. These observations could be attributed to the following reasons: 1)

occurrence of the extensive vent and seep systems, 2) more diverse host phyla, and 3) most importantly, more research in the PO. Among the three major oceans, the IO is the least explored so far, with only 5% of reported phylotypes from the vents. In the AO, the seeps harbor relatively more number of bacterial phylotypes (31.4%) than the vents (18.26%). Relatively low percentage of bacterial phylotypes has also been encountered from the seeps in the Arctic Ocean and the Mediterranean Sea.

#### **3.4.4. Lineages of bacterial associates of different fauna in the two ecosystems**

The present analysis shows that in general, thiotrophic bacterial associates of clams were more divergent with 6 different lineages than mussels and tubeworms (Figure 3a). Thiotrophs from different species of *Bathymodiolus* constitute a single lineage. A similar trend was also observed in their methanotrophic counterparts. Bacterial associates of tubeworms, snails, crabs and shrimps were interrelated and appeared to have diverged more recently than the symbionts of the bivalves. The bivalves show their specificity in harboring particular symbiont by facilitating vertical transmission. However, higher relatedness observed between the bacterial associates of tubeworms, snails, crabs and shrimps suggest horizontal acquisition of symbionts from geochemically similar habitats.

The above scenario described in our review could change, or reiterate established patterns with the discovery of new vents and seeps. Generally, geochemical gradients in the vents and seeps dictate how the free-living and symbiotic bacteria colonize and spread in the intra and inter systems. Physical and tectonic forces in the current and geological ages were either responsible for bringing the distantly separated hosts and their bacterial associates together or scattering them to evolve separately. This review provides some salient aspects on how microbial associates of vent and seep fauna spread over time and space. Though there is enough coverage on the abundance, distribution and diversity of the vent and seep fauna, the study on activity is mostly restricted to functional genes, and not necessarily to their expression in the form of the processes they mediate. These include some attempts on measuring chemosynthetic rates in these and allied systems.

#### **3.5. Rates of chemoautotrophic production in vent, seep, anoxic and oxic basin**

Rates of chemosynthetic carbon fixation in various deep-sea settings have been compared by Karl (1995) and Mandernack and Tebo (1999). A summary of these is presented along with some of our published data (Table 3). Though the data collected by different authors under different environmental conditions have been expressed in different units, we have tried to convert as many as possible to a common unit to be able to appreciate similarities and differences. Values of carbon fixation were converted from their original units of  $\text{nmol C g}^{-1}\text{d}^{-1}$  for sediments and mats and  $\text{nmol C}$

$\text{l}^{-1} \text{d}^{-1}$  for water to a common unit of  $\text{g C m}^{-3} \text{y}^{-1}$ . It is not an ideal comparison because of different environmental parameters including oxygen content, bacterial numbers and incubating conditions. The table thus gives an overview and brings out the importance of chemoautotrophic carbon fixation rates in all the sediments studied and is not restricted to typical vents and seeps.

The carbon fixed in vent waters ranged from  $0.056\text{--}21.9 \text{ g C m}^{-3} \text{y}^{-1}$ . In the cold seep of the Håkon Mosby Mud Volcano, the values for carbon fixed were  $325 \text{ g C m}^{-3} \text{y}^{-1}$  and  $76.8 \text{ g C m}^{-2} \text{y}^{-1}$  (Mandernack and Tebo 1999; Lichtschlag et al. 2010). The oxic sedimentary basin fixed  $19.9$  to  $37400 \text{ g C m}^{-3} \text{y}^{-1}$  (Das et al. 2011). However, still higher values of carbon fixation in symbiotic hosts have been reported where the maximum value per single gram of vent tubeworm tissue is about  $\sim 4 \text{ g C y}^{-1}$  (Childress et al. 1991) (Table 4). These values reveal the enormous potential of the deep-sea bed and vent fauna to fix carbon microbially. The global estimate of carbon production in deep-sea vents is of  $5 \text{ Tg C y}^{-1}$  (Hügler and Sievert 2010).

It would be relevant to compare these estimates with those from other systems. Ammonia-oxidizing archaea may fix approximately  $400 \text{ Tg C y}^{-1}$  in the pelagic realm via 3-HP/4-HB (3-hydroxypropionate/4-hydroxybutyrate) cycle (Schouten et al. 2004; Wuchter et al. 2006). Anammox bacteria in the same ecosystem contribute up to  $3.5 \text{ Tg C y}^{-1}$  through the WL (Wood-Ljungdahl) pathway (Schouten et al. 2004; Strouset al. 2006; Raven 2009). Iron, hydrogen and/or sulfide oxidation produce an estimate of  $\sim 1 \text{ Tg C y}^{-1}$  within the ocean crust (Bach and Edwards 2003). This rate could probably be an underestimate. Sulfide which could exist up to mmolar level in deep-sea reducing habitats is high enough to contribute a significant percentage to total dark carbon fixation.

## Summary and conclusion

Though vents and seeps host distinct bacterial associates, there could be similarities in the symbionts from these two disparate systems in the case of, 1. Closely related species of vesicomyid clams. 2. Geochemical similar systems and 3. Geographical proximity of vent and seep. Phylogeographically, though the Atlantic and Pacific fauna have their uniqueness, the Indian Ocean seems to share the features of hosts from both the oceans besides maintaining its own uniqueness. This mini-review emphasizes that the endosymbionts are specific and more ancient and generally associated with less mobile hosts. On the contrary, ectosymbionts are more varied, recent and mainly associated with mobile hosts. Proteobacteria is the most ecologically successful bacterial phylum as evidenced by its abundance and distribution. Within this phylum, *γ-Proteobacteria* is the most successful. Besides, it is also capable of both sulfur and methane oxidation in the vents and seeps. While *α*- and *ε*-*Proteobacteria* are involved in sulfur oxidation, *δ-Proteobacteria* is predominantly a sulfate reducer.

However, they are sometimes obligate chemoautotrophs that use electron donors other than sulfide for chemoautotrophy. Thiotrophs are more ecologically successful than methanotrophs because they are less specific and have a broader host range. Although concentrations of methane and ammonia were detected up to mmolar levels in the vents and seeps, the rates of chemosynthesis at the expense of these compounds are yet to be estimated. The chemoautotrophic contribution of vents and seeps to the climate could be small for a particular region. However, it could be significant when the vast extent of their habitats is taken into consideration. Estimating chemoautotrophic rates in these ecosystems would help to understand their contribution to carbon fixation linked to other biogeochemical cycles both on local and global scale. Such studies would help to refine and improve the existing climate models and could also be suitably adopted for biogeographic models.

## **Future scope**

We are aware that this review could be affected by sampling as the Pacific is more studied than the Atlantic or the Indian Ocean. The review is limited to the sequences of associated microbes of major fauna from vents and seeps. With the discovery of new vents and seeps and perhaps new hosts in the coming years, the lineage could be re-examined for a refinement/ or newer pattern of origin and distribution. The information would be useful for modeling and conservatory measures when deep-sea mining come into practice in the near future. With the growing database of bacterial associates and the pertinent functional genes, the phylogeographical analysis could give a better perspective. More detailed information on diversity and function of chemoautotrophic bacterial associates could be obtained by metagenomic analysis using next-generation sequencing (NGS). With affordable costs, NGS would elucidate the diversity pattern with ease, pointing out the main groups which are abundant and contributing to different functions. This could be suitably complemented by improved and optimized culturing methods. These complementary approaches would lend direction to the renewed effort in reducing the great plate count anomaly which in turn could update the database of reference cultures. The importance of these symbiotic and free-living chemoautotrophs would be better understood if we know the extent of their contribution to primary productivity, as there is a sparse availability of data on carbon fixation in the sediments and symbiotic fauna worldwide. Such information would help us to contrast chemosynthetic production with photosynthesis. Some uniformity in measurement would be desirable for comparative appreciation as in the case of  $^{14}\text{C}$  method for light-driven photosynthetic production. Inverse modeling with some of the rates that are

currently known could also be a complementary approach. With the advent of new technologies, it would be possible to constrain these chemosynthetic rates and fluxes on a more dynamic scale.

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**Table 1.** Range of basic physico-chemical parameters of vents and seeps of the world oceans.

		T (°C)	O <sub>2</sub> (μM)	pH	HS <sup>-</sup>	SO <sub>4</sub> <sup>2-</sup>	CH <sub>4</sub>	NH <sub>4</sub>	Fe	Mn	DIC/CO <sub>2</sub>
V	PO	2–350	70.5–209.6	3.44–7.5	bdl– 24 mM	≤3 nM– 30 mM	2.1 nM– 0.11 mM	10– 14,700 μM	14 μM– 750 mM	< 0.01 μM–753 mM	187–227 mM (CO <sub>2</sub> )
	AO	2–370	bdl–224	2.5–8.02	4 μM– 2.5 mM	0.27– 17.24 mM	300 nM– 4 mmol kg <sup>-1</sup>	0.15– 6.75 μM	5–2410 μM	338 μM	3.2–31 mM (CO <sub>2</sub> )
	IO	315–365	NA	3.4–6.6	3.93– 4.07 mmol kg <sup>-1</sup>	479– 1560 μmol kg <sup>-1</sup>	0.171–3.5 mmol kg <sup>-1</sup>	17.1– 38.8 μmol kg <sup>-1</sup>	3.5–6 mmol kg <sup>-1</sup>	NA	4.53–5.13 mmol kg <sup>-1</sup> (DIC)
S	PO	1.1–15	13.3–84.7	8.01–8.16	≤0.1 μM– 26 mM	4–30 mM	9.1 nM–2.5 M	<5– 1400 μM	<0.02– 2.2 μM	0.20 – 220 nM	~2.4–23 mM (DIC)
	AO	4.39–7	27–276	6.4–6.8	bdl–10 mM	4–30 mM	32 μM– 10 mM	bdl– 1800 μM	7–34 nmol kg <sup>-1</sup>	3–47 nmol kg <sup>-1</sup>	1–21 mM (DIC)
	MS	13.7–26.3	186.8–222.5	7.99–8.22	bdl–23 mM	bdl–30 mM	<0.01– 2 μM	bdl– 4500 μM	NA	NA	2–30 mM (DIC)
	Ar	–0.77 to –0.85	10–280	7.6–8.0	bdl– 0.15 mM	2–28 mM	0.004– 266 μM	NA	NA	NA	0.02–0.2% (CO <sub>2</sub> )

**Table 1.** Range of basic physico-chemical parameters of vents and seeps of world oceans

NA: Not Available; bdl: below detection limit; V: Vent, S: Seep, PO: Pacific Ocean, AO: Atlantic Ocean, IO: Indian Ocean, MS: Mediterranean Sea, Ar: Arctic Ocean

Vent: Pacific Ocean (Seyfried et al. 2003; Arp et al. 1984; Campbell et al. 1988; Lutz et al. 2008; Keir 2010; Teske et al. 2016; Campbell et al. 1994; Tsunogai et al. 2000; Ishibashi et al. 1994; Le Bris et al. 2006; Kawagucci et al. 2011; Tsunogai et al. 2010); Atlantic Ocean (Perner 2009; Seyfried Jr. et al. 2011; Konn et al. 2009; Sarradin et al. 1999; Keir 2010; Klevenz et al. 2011; Renninger et al. 1995) Indian Ocean (Gallant and Damm 2016).

Seep: Pacific Ocean (Gieske's et al. 2005; Sibuet and Olu 1998; Levin et al. 2012; Boulègue et al. 1987; Levin et al. 2012; Collier and Lilley 2005; Tsunogai et al. 1996; 2010) Atlantic Ocean (Humes 1988; Lemaitre et al. 2014; Hensen et al. 2007; Joye et al. 2004) Mediterranean Sea (Ristova et al. 2015; Fesker et al. 2010; Ritt et al. 2012; Techtman et al. 2015) Arctic Ocean (Lösekann et al. 2008; Milkov et al. 2004; Niemann et al. 2006)

Bacterial associates	Phyla		Genera		Species		Geographical distribution	
	V	S	V	S	V	S	V	S
<i>α-Proteobacteria</i>	2	1	2	1	3	2	P: EP	P: WP
<i>β-Proteobacteria</i>		1		1		1		P: WP
<i>γ-Proteobacteria</i>	3	2	14(+2)*	9	24+5	13(+4)*	P: EP, SP, WP, SWP A: MA, I: SI, CI	P: EP, WP A: WA, SEA M: EM Ar
<i>δ-Proteobacteria</i>	3		2(+1)*		2+1		P: EP, SP I: SI	
<i>ε-Proteobacteria</i>	3	1	6(+2)*	1	6+3	1	P: EP, SP, WP I: CI, SI A: MA	P: WP
<i>z-Proteobacteria</i>	1		1		1		A: MA	
Actinobacteria	1		1		1		P: EP	
Spirochete	1		1		1		P: EP	
Bacteroidetes	3	1	2(+1)*	1	2+1	1	P: EP, SP I: SI	M: EM
Chloroflexi	1		1		1		P: SP	
Verrucomicrobia	1		1		1		P: EP	
Unidentified symbionts	4	3	11(+3)*	7(+7)*	17+9	13(+16)*	P: EP, SWP, WP A: MA	P: WP, NWP A: WA I: NI, EI

**Table 2.** Number of major metazoan phyla, genera and species that host potentially chemoautotrophic bacterial associates in vent and seep ecosystems

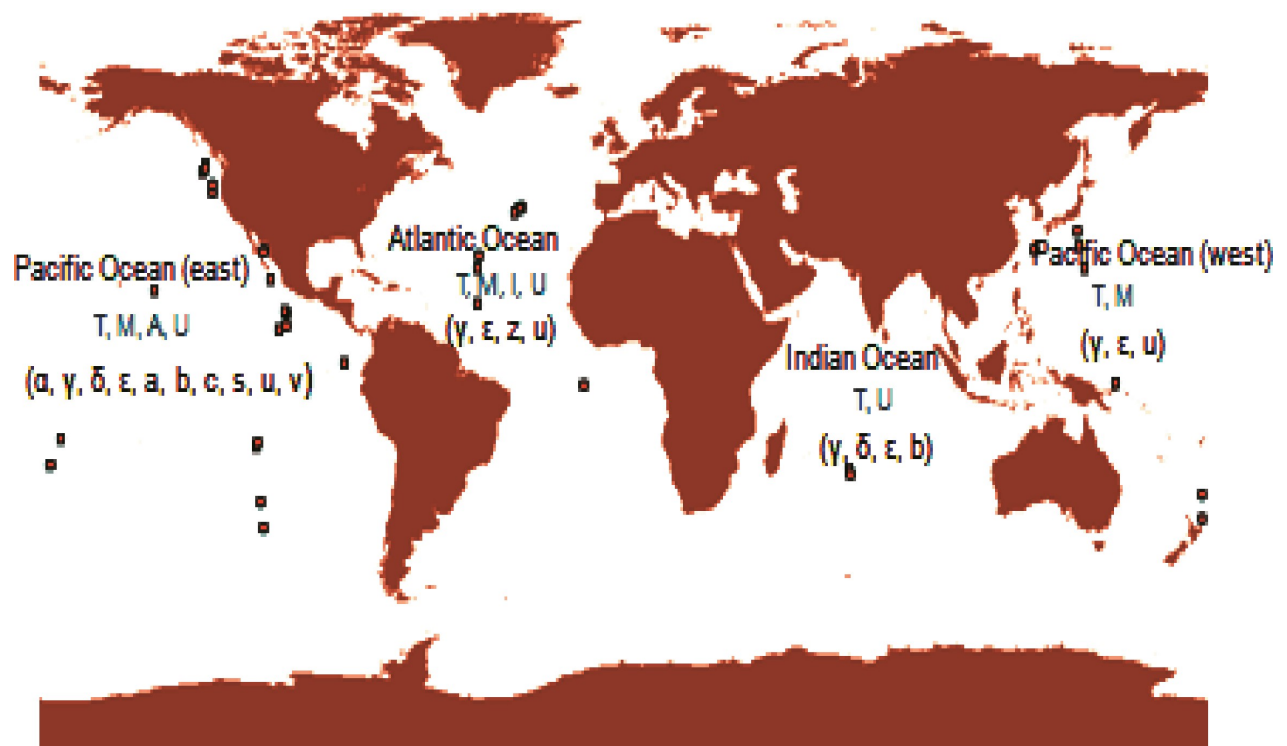
V:Vent, S:Seep, P: Pacific Ocean, A: Atlantic Ocean, Ar: Arctic Ocean, IO: Indian Ocean, MA: Mid Atlantic, SI: South Indian Ocean, CI: Central Indian Ocean, EP: East Pacific, WP: West Pacific, SP: South Pacific, SWP: South West Pacific, WA: West Atlantic, SEA: South East Atlantic, M: Mediterranean, EM: East Mediterranean, EI: East Indian Ocean, NI: North Indian Ocean, NWP: North West Pacific. (+)\* number unidentified

Ecosystem	Location	Type	CO <sub>2</sub> fixation (g C m <sup>-3</sup> y <sup>-1</sup> )
Hydrothermal vents	21°N, EPR	Water (White smoker)	5.56E-02
	JFR	Water	8.83E-01
	Guaymas Basin	Bacterial Mats	3.50E+04
	TAG (MAR)	Water	2.37E-01 to 8.02E-01
	Rose Garden (Galápagos Rift)	Water	6.57E-00 to 2.19E+01
Anoxic basins	Black sea	Water	8.76E-03 to 3.65E-00
	Framvaren fjord	Water	4E+01 to 4.91E+01
	Solar lake	Water	6E+01 to 9.64E+01
Cold seeps	Haakon Mosby mud volcano	Sediment	3.61E-01 to 3.25E+02
Oxic basins	Central Indian Basin	Siliceous ooze sediments	1.99E+01 to 1.79E+02
	Central Indian Basin	Red clay with volcanic signature	9.16E+02 to 3.74E+04
	Central Indian Basin	Red clay with volcanic ashes	3.98E+02 to 1.99E+03
	Central Indian Basin	Red clay with volcanic ashes	3.98E+02 to 1.99E+03
	Central Indian Basin	Manganese nodules	2.31E+02 to 1.78E+03

**Table 3.** Overview of carbon fixation rates in chemosynthetic sites in g C m<sup>-3</sup> y<sup>-1</sup>(modified from Karl (1995), Mandernack and Tebo (1999) and Das et al. (2011)).

Organism	Species	Carbon fixation rate $\mu\text{M C g}^{-1} \text{h}^{-1}$ (g C g tissue <sup>-1</sup> y <sup>-1</sup> )
Tubeworm	<i>Riftia pachyptila</i>	35 (3.68)
Mussel	<i>Bathymodiolus thermophilus</i>	3.4 (3.3)
Clam	<i>Calymene magnifica</i>	0.3 (0.03)

**Table 4.** Carbon fixation rates in tubeworms, mussels and clams of vent ecosystem (Childress et al. 1991a,b; Nelson et al. 1995)

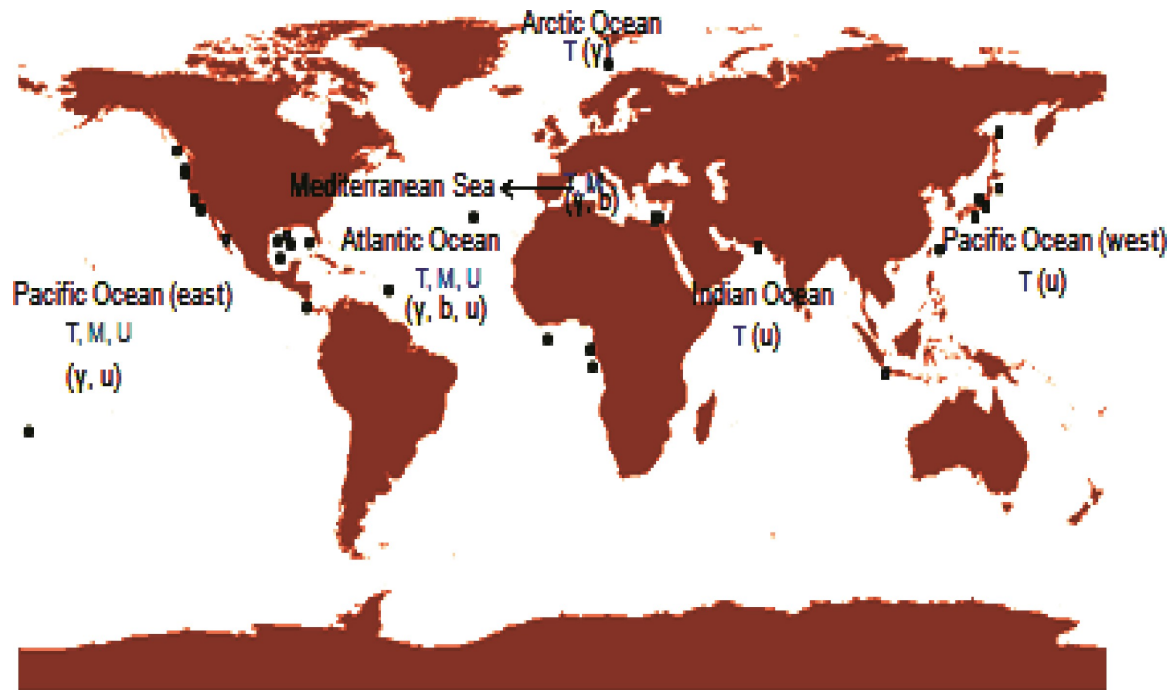


**Figure 1.** Distribution of potential chemoautotrophic bacterial associates of vent fauna.

α, γ, δ, ε, z (Proteobacteria), b. Bacteroidetes, c. Chloroflexi, s. Spirochetes, u. Unaffiliated, v.

Verrucomicrobia, T. Thiotroph, M. Methanotroph, I. Iron oxidizer, A. Ammonia oxidizer, U.

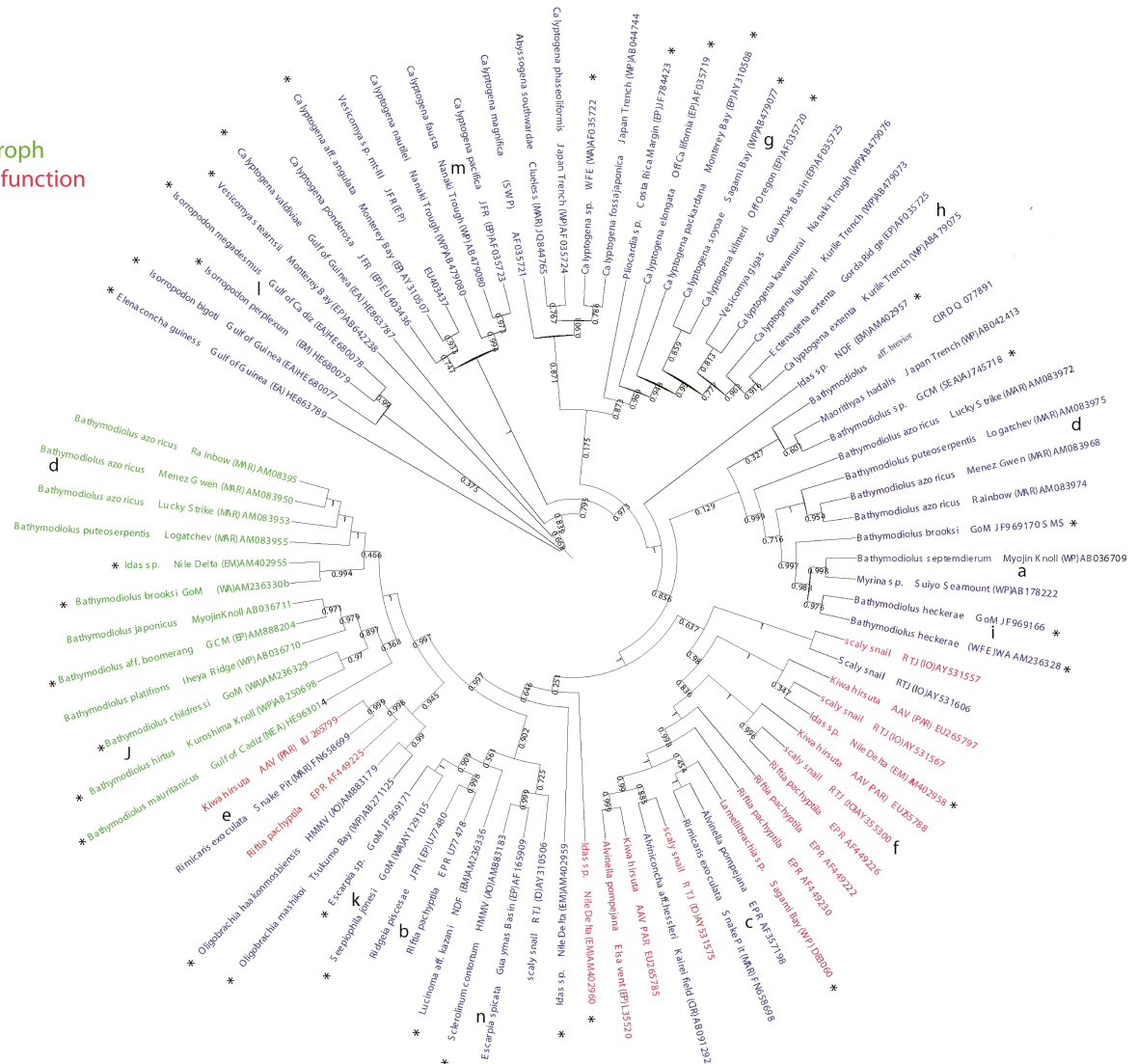
Bacteria with unknown function



**Figure 2.** Distribution of potential chemoautotrophic bacterial associates of seep fauna.

$\alpha$ ,  $\beta$ ,  $\gamma$ ,  $\delta$  (Proteobacteria), b. Bacteroidetes, u. Unaffiliated, EM. Eastern Mediterranean T. Thiotrophs, M. Methanotrophs, U. bacteria with unknown function

Thiotroph  
Methanotroph  
Unknown function



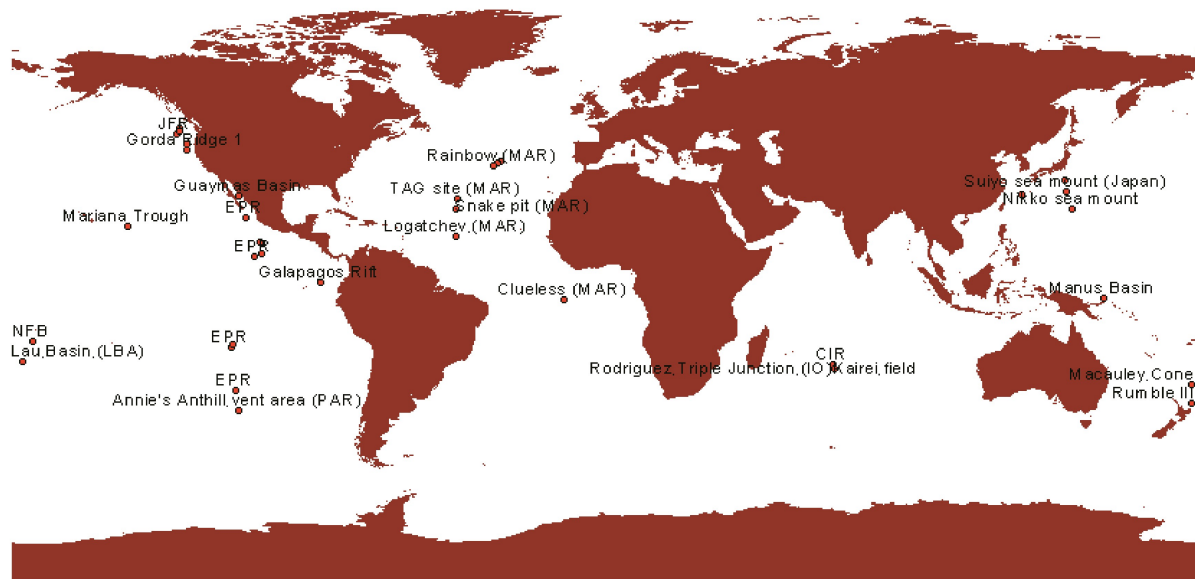
**Figure 3a.** Phylogeny of potential chemoautotrophic bacterial associates of vent and seep fauna

\*bacterial associates from seeps

- Thiotrophic symbionts of *B. septemdiarium* and *Myrina* sp. from two vents in WP possess identical symbionts with bootstrap value 0.998
- R. piscesae* and *R. pachyptila* from vents in EPR harbor identical (99%) thiotrophic symbionts with boot strap value 0.998
- Thiotrophic symbiont of *A. pompejana* and *R. exoculata* shows 94% identity with boot strap value 1.

- d. Thiotrophic and methanotrophic symbionts of *Bathymodiolus* sp. from different vent sites in MAR form distinct clades
- e. Thiotrophic symbiont of *R. exoculata* from MAR showed 94% identity to the associated bacteria of yeti crab *K. hirsuta* of AAV(PAR) with boot strap value 0.99
- f. *R. pachyptila*, scaly snail and *K. hirsuta* harbor bacteria belonging to a common clade
- g. *C. kilmeri* off Oregon(EP) and *C. soyoae* from Sagamy Bay(WP) share identical (99%) thiotrophic symbionts with boot strap value 0.85
- h. Two related species of vesicomid clams *E. extenta* and *C. extenta* from seeps in WP and EP share a common phylotype of thiotrophic symbionts have 100% identity with boot strap value 0.91
- i. *B. heckerae* from adjacent seeps in WA, WFE and GoM share identical (99%) thiotrophic symbionts with boot strap value 0.97
- j. *B. childressi* from seep in WA and *B. hirtus* from seep in WP are identical (99%) with boot strap value 0.97
- k. *Escarpia* sp. and *S. jonesi* from GoM share identical (98%) thiotrophic symbionts with boot strap value 1
- l. *I. megadesmus* from seep in EA and *I. perplexum* from seep in EM have identical (99%) thiotrophic symbionts with boot strap value 0.99
- m. *C. fausta* from Nanaki Trough (seep) in WP and *C. pacifica*, JFR vent from EP harbor 99% identical thiotrophic symbionts with boot strap value 0.97
- n. *E. spicata* from vent in EP and *S. contortum* from seep in Arctic Ocean share identical (99%) thiotrophic symbiont with boot strap value 0.99

## Vent

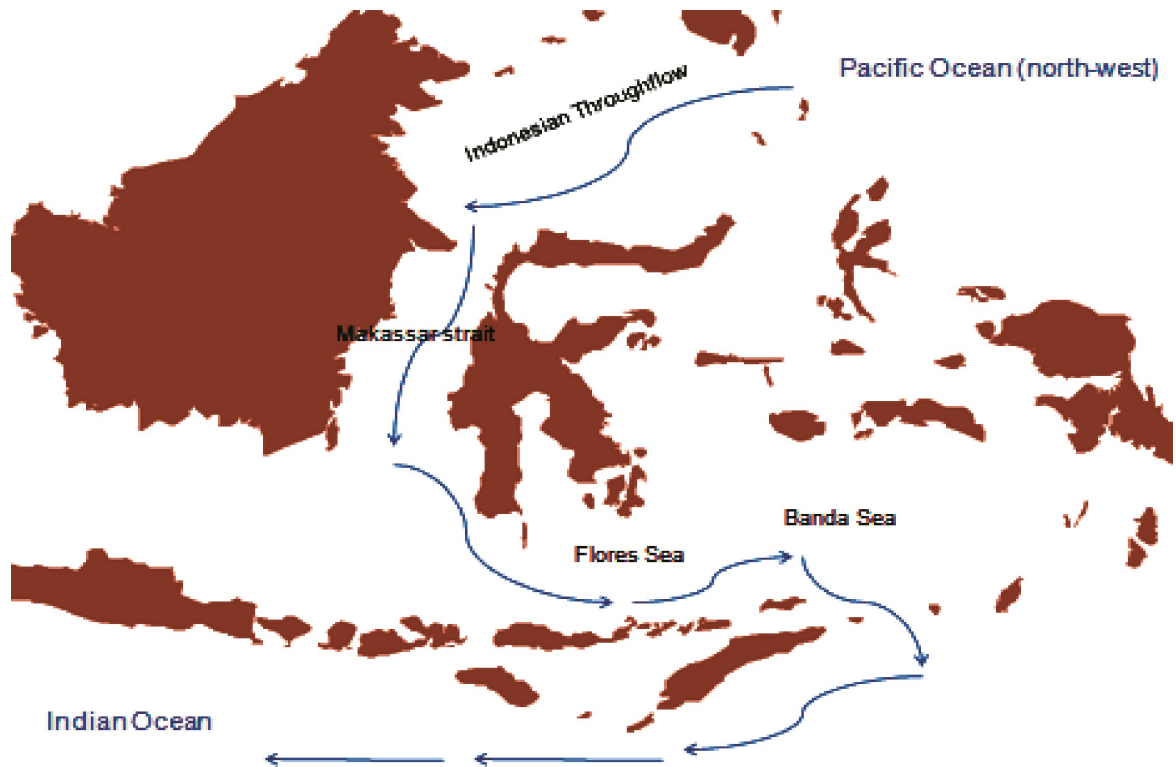


## Seep

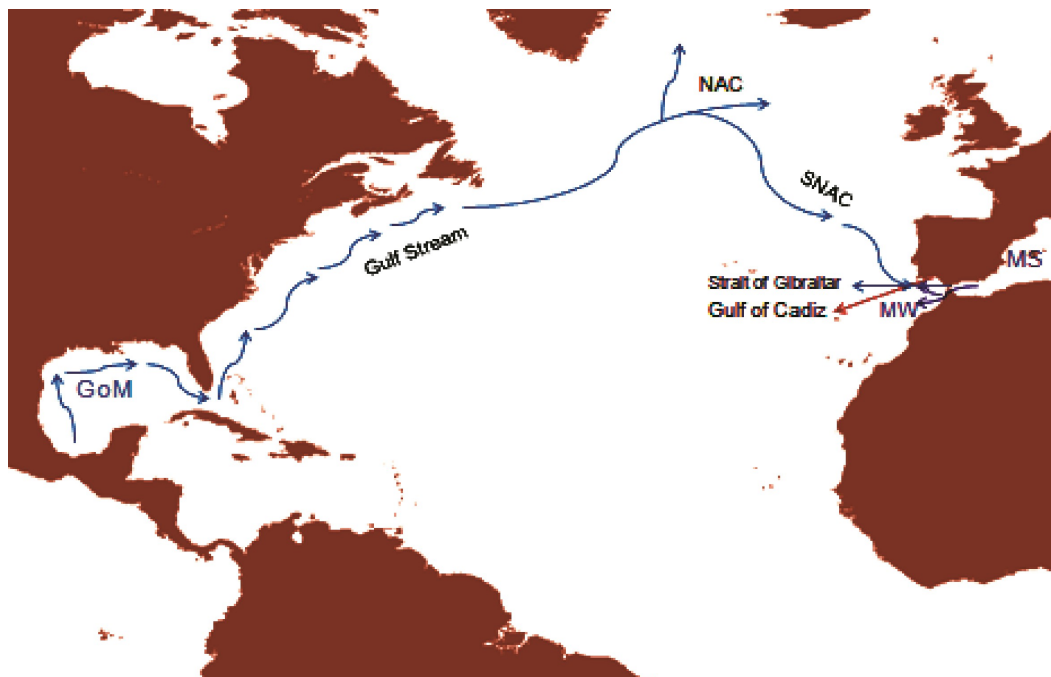


**Figure 3b.** Geographical distribution of potential chemoautotrophic bacterial associates of vent and seep fauna.

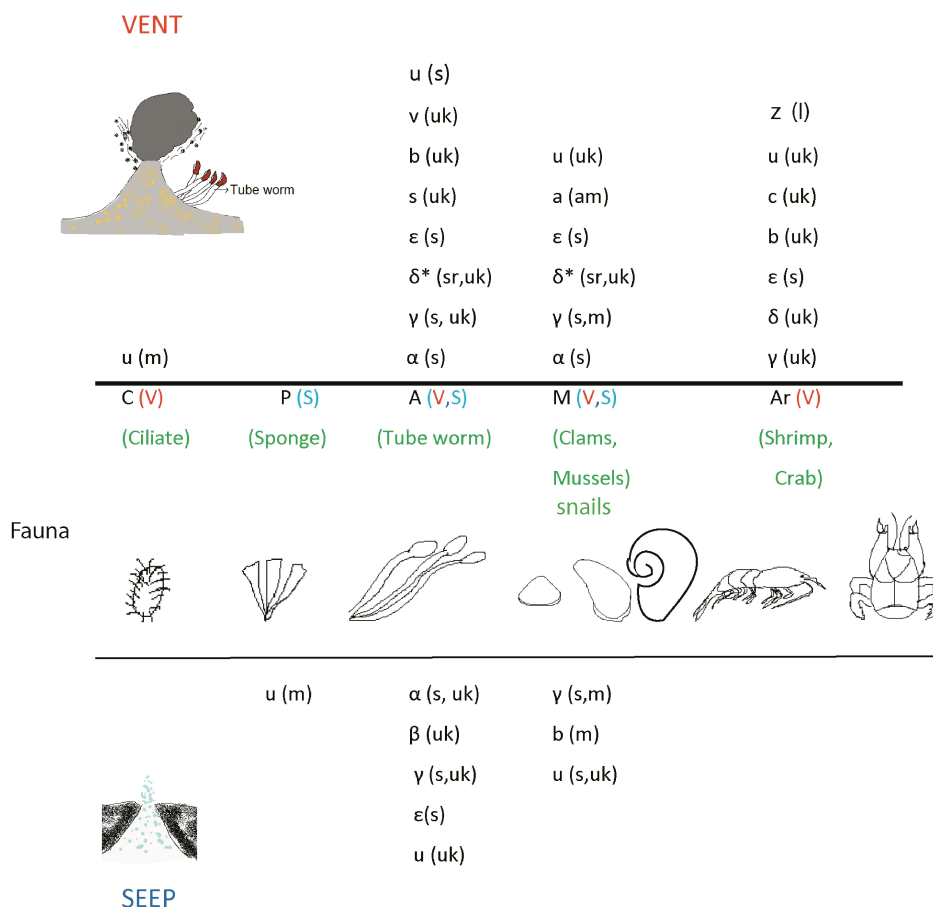




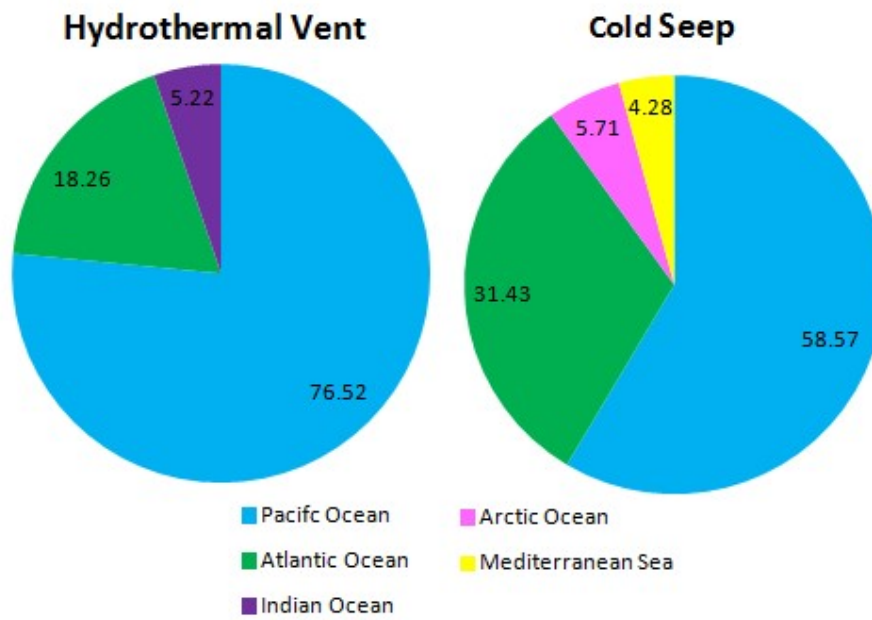
**Figure 4.** Possible path of bacterial dispersal between Pacific Ocean and Indian Ocean (possibly one way).



**Figure. 5.** Possible path of bacterial dispersal between Atlantic Ocean and Mediterranean Sea  
GoM: Gulf of Mexico, NAC: North Atlantic Current, SNAC: South North Atlantic Current, MS: Mediterranean Sea, MW: Mediterranean Water



**Figure. 6** Potential chemoautotrophic bacterial associates of vent and seep fauna and their functions. V-Vent, S-Seep, C-Ciliophora, P-Porifera, A-Annelida, M-Mollusca, Ar-Arthropoda, a, b, g, d, e, z (Proteobacteria), a-Actinobacteria, b-Bacteroidetes, s-Spirochete, v-Verrucomicrobia, u-Unidentified, t-Thiotroph, sr-Sulfate reducer, m-Methanotroph, am-Ammonia oxidizer, uk-unknown function Though d-Proteobacteria are sulfate reducers, some of them are known for anaerobic methane oxidation in consortia. Yet in others, the function is still unknown.



**Figure 7.** Percentages of phylotypes of potential chemoautotrophic bacteria from vent and seep fauna in the global oceans

Sl.No	Scientific name of the host	Ambient geochemical data (Location (habitat))	Genbank accession number of 16S rDNA of bacterial associates	Copy number/ related sequence	Reference
1	<i>Calyptogen fausta</i>	CH <sub>4</sub> : 1.41 to 5.85 µM, Fe: 7 to 34 nmol kg <sup>-1</sup> , Mn: 3 to 47 nmol kg <sup>-1</sup> (Gabon: Gulf of Guinea (seep))	AB479081	1	Duperron et al. 2012 <sup>a</sup> Lemaitre et al. 2014 <sup>b</sup>
2	<i>Calyptogen pacifica</i>	pH: 3.44 to 6.17, H <sub>2</sub> S: 2.8 to 24 mM, Fe: 14 µM to 2.2 mM, Mn: 2 to 372 µM (Endeavour, JFR (vent))	AF035723	1	Peek et al. 1998 <sup>a</sup> Seyfried Jr et al. 2003 <sup>b</sup>
3	<i>Calyptogen nautiliei</i>	CH <sub>4</sub> : 1.41 to 5.85 µM, Fe: 7 to 34 nmol kg <sup>-1</sup> , Mn: 3 to 47 nmol kg <sup>-1</sup> (Gabon: Gulf of Guinea (seep))	AB479080	1	Duperron et al. 2012 <sup>a</sup> Lemaitre et al. 2014 <sup>b</sup>
4	<i>Calyptogen aff. angulata</i>	T: 4.1°C, O <sub>2</sub> : 13.3 µM, H <sub>2</sub> S: 2 to 20 mM, SO <sub>4</sub> <sup>2-</sup> : 4 to 30 mM, CH <sub>4</sub> : 621 µM (Monterey Bay (seep))	AY310507	1	Roeselers and Newton 2012 <sup>a</sup> Gieskes et al. 2005 <sup>b</sup> Sibuet and Olu 1998 <sup>b</sup> Levin et al. 2012 <sup>b</sup>
5	<i>Vesicomya</i> sp. mt-III	pH: 3.44 to 6.17, H <sub>2</sub> S: 2.8 to 24 mM, Fe: 14 µM to 2.2 mM, Mn: 2 to 372 µM (Endeavour, JFR (vent))	EU403437	11	Stewart et al. 2008 <sup>a</sup> Seyfried Jr et al. 2003 <sup>b</sup>
6	<i>Calyptogen valdiviae</i>	CH <sub>4</sub> : 1.41 to 5.85 µM, Fe: 7 to 34 nmol kg <sup>-1</sup> , Mn: 3 to 47 nmol kg <sup>-1</sup> (Gabon: Gulf of Guinea (seep))	HE863787	64	Duperron et al. 2012 <sup>a</sup> Lemaitre et al. 2014 <sup>b</sup>
7	<i>Isorropodon bigoti</i>	CH <sub>4</sub> : 32 to 132 µM, Fe: 7 to 34 nmol kg <sup>-1</sup> , Mn: 3 to 47 nmol kg <sup>-1</sup> (Gabon: Gulf of Guinea (seep))	HE680077	58	Rodrigues et al. 2012 <sup>a</sup> Lemaitre et al. 2014 <sup>b</sup>
8	<i>Vesicomya stearnsii</i>	T: 4.1°C, O <sub>2</sub> : 13.3 µM, H <sub>2</sub> S: 2 to 20 mM, SO <sub>4</sub> <sup>2-</sup> : 4 to 30 mM, CH <sub>4</sub> : 621 µM (Monterey Bay (seep))	AB642238	1	Kuwahara et al. 2011 <sup>a</sup> Gieskes et al. 2005 <sup>b</sup> Sibuet and Olu 1998 <sup>b</sup> Levin et al. 2012 <sup>b</sup>
9	<i>Isorropodon megadesmus</i>	SO <sub>4</sub> <sup>2-</sup> : 4 to 30 mM; NH <sub>4</sub> : bdl to 1.8 mM, CH <sub>4</sub> : 2.9 to 8 mM (Gulf of Cadiz (seep))	HE680078	24	Rodrigues et al. 2012 <sup>a</sup> Hensen et al. 2007 <sup>b</sup>
10	<i>Isorropodon perplexum</i>	H <sub>2</sub> S: bdl to 23 mM, SO <sub>4</sub> <sup>2-</sup> : bdl to 30 mM, DIC: 2 to 30 mM, NH <sub>4</sub> : bdl to 4.5 mM (Eastern Mediterranean (seep))	HE680079	48	Rodrigues et al. 2012 <sup>a</sup> Ristova et al. 2015 <sup>b</sup>
11	<i>Calyptogen ponderosa</i>	NH <sub>4</sub> : bdl to 30 µM, H <sub>2</sub> S: bdl to 4.5 mM, NO <sub>3</sub> <sup>-</sup> : bdl to 3.9 mM; DIC: 1 to 21 mM, DOC: 3 to 11.5 mM, CH <sub>4</sub> : bdl to 2.2 mM; TOC: 2-5%, C/N: 10-40 (Gulf of Mexico(seep))	EU403436	1	Stewart et al. 2008 <sup>a</sup> Joye et al. 2004 <sup>b</sup>

12	<i>Elenaconcha guiness</i>	CH <sub>4</sub> : 1.41 to 5.85 $\mu$ M, Fe: 7 to 34 nmol kg <sup>-1</sup> , Mn: 3 to 47 nmol kg <sup>-1</sup> (Gabon: Gulf of Guinea (seep))	HE863789	1	Duperron et al. 2012 <sup>a</sup> Lemaitre et al. 2014 <sup>b</sup>
13	<i>Calyptogena phaseoliformis</i>	T: 1.2°C, pH: 8.01 to 8.15, SO <sub>4</sub> <sup>2-</sup> : 26 – 27.4 mM, Fe: < 0.02 to 1.47 $\mu$ M, Mn: 40 to 220 nM, CH <sub>4</sub> : 2.66 nM; NH <sub>4</sub> : 0.1 mM, H <sub>2</sub> S: $\leq$ 0.1 $\mu$ M (Japan Trench (seep))	AF035724	1	Peek et al. 1998 <sup>a</sup> Boulègue et al. 1987 <sup>b</sup>
14	<i>Calyptogena</i> sp.	NH <sub>4</sub> : bdl to 30 $\mu$ M, H <sub>2</sub> S: bdl to 4.5 mM, NO <sub>3</sub> <sup>-</sup> : bdl to 3.9 mM; DIC: 1 to 21 mM, DOC: 3 to 11.5 mM, CH <sub>4</sub> : bdl to 2.2 mM; TOC: 2-5%, C/N: 10-40 (Western Florida Escarpment (GoM))	AF035722	1	Peek et al. 1998 <sup>a</sup> Joye et al. 2004 <sup>b</sup>
15	<i>Abyssogena southwardae</i>	O <sub>2</sub> : 145 to 224 $\mu$ M, H <sub>2</sub> S: 4 to 39 $\mu$ M, CH <sub>4</sub> : 355 to 945 nM, H <sub>2</sub> : 5 to 36 nM, Fe: 5 to 15 $\mu$ M (Clueless site, MAR (vent))	JQ844765	96	Heijden et al. 2012 <sup>a</sup> Perner et al. 2009 <sup>b</sup>
16	<i>Calyptogena fossajaponica</i>	T: 1.2°C, pH: 8.01 to 8.15, SO <sub>4</sub> <sup>2-</sup> : 26 – 27.4 mM, Fe: < 0.02 to 1.47 $\mu$ M, Mn: 40 to 220 nM, CH <sub>4</sub> : 2.66 nM, NH <sub>4</sub> : 0.1 mM, H <sub>2</sub> S: $\leq$ 0.1 $\mu$ M (Japan Trench (seep))	AB044744	1	Kuwahara et al. 2011 <sup>a</sup> Boulègue et al. 1987 <sup>b</sup>
17	<i>Calyptogena magnifica</i>	T: 335 to 355 °C (max.), pH: 3.6 to 4.0, H <sub>2</sub> S: 7.4 to 8.1 mM, Fe: 660 to 750 mM, Mn: 699 to 753 mM, (south west Pacific (vent))	AF035721	1	Peek et al. 1998 <sup>a</sup> Arp et al. 1984 <sup>b</sup> Campbell et al. 1988 <sup>b</sup>
18	<i>Pliocardia</i> sp.	T: 3.6 to 5.2 °C, O <sub>2</sub> : 71.4 to 84.7 $\mu$ M, CH <sub>4</sub> : bdl to 800 nM, SO <sub>4</sub> <sup>2-</sup> : 13.8 mM (Jaco Scarp summit, Off Costa Rica (Seep))	JF784423	1	Martin and Goffredi 2012 <sup>a</sup> Levin et al. 2012 <sup>b</sup>
19	<i>Calyptogena elongata</i>	T: 7.9 to 13.9 °C, CH <sub>4</sub> : 60 to 110 mmol kg <sup>-1</sup> , H <sub>2</sub> S: 43.30 to 73.67 $\mu$ M (East Pacific Rise (vent))	AF035719	1	Peek et al. 1998 <sup>a</sup> Lutz et al. 2008 <sup>b</sup> Keir 2010 <sup>b</sup>
20	<i>Calyptogena packardana</i>	T: 4.1°C, O <sub>2</sub> : 13.3 $\mu$ M; H <sub>2</sub> S: 2 to 20 mM, SO <sub>4</sub> <sup>2-</sup> : 4 to 30 mM, CH <sub>4</sub> : 621 $\mu$ M (Monterey Bay (seep))	AY310508	1	Roeselers and Newton 2012 <sup>a</sup> Levin et al. 2012 <sup>b</sup>
21	<i>Calyptogena kilmeri</i>	T: 7.5 to 15 °C, SO <sub>4</sub> <sup>2-</sup> : 6.9 mM, CH <sub>4</sub> : 5 to 167 nM (Cascadia continental margin (Seep))	AF035720	1	Peek et al. 1998 <sup>a</sup> Goffredi and Barry 2002 <sup>b</sup> Collier and Lilley 2005 <sup>b</sup>
22	<i>Calyptogena soyoae</i>	H <sub>2</sub> S: < 0.01 to 0.14 mmol kg <sup>-1</sup> , SO <sub>4</sub> <sup>2-</sup> : 16.2 to 27.7 mmol kg <sup>-1</sup> , NH <sub>4</sub> : < 5 to 1400 $\mu$ mol kg <sup>-1</sup> , CH <sub>4</sub> : 91 nmol kg <sup>-1</sup> to 2.5 mol kg <sup>-1</sup>	AB479077	1	Okutani et al. 2009 <sup>a</sup> Tsunogai et al. 1996 <sup>b</sup>

		(Sagami Trough, Japan (Seep))			
23	<i>Calyptogena kawamurai</i>	T: 7.83 to 8.28 °C, SO <sub>4</sub> <sup>2-</sup> : 27.3 mM, NO <sub>3</sub> <sup>-</sup> : 10.7 µM, Fe: 0.68 to 2.2 µM, Mn: 0.20 to 50 nM, NH <sub>4</sub> : 0.1 mM, H <sub>2</sub> S: ≤ 0.1 µM (Nankai Trough, Japan (Seep))	AB479076	1	Okutani et al. 2009 <sup>a</sup> Boulègue et al. 1987 <sup>b</sup>
24	<i>Vesicomys gigas</i>	T: 4 to 95 °C, pH: 6 to 7.5, Eh: -440 to +50 mV, H <sub>2</sub> S: bdl to 1.2 mM, SO <sub>4</sub> <sup>2-</sup> : 1 to 30 mM (Guaymas basin (vent))	AF035725	1	Peek et al. 1998 <sup>a</sup> Teske et al. 2016 <sup>b</sup>
25	<i>Calyptogena laubieri</i>	T: 1.11 to 1.13 °C, pH: 8.01 to 8.16, SO <sub>4</sub> <sup>2-</sup> : 26.3 to 27.0 mM, Fe: 790 to 800 nM, Mn: 11 to 14 nM, CH <sub>4</sub> : 3.63 to 4.97 nM, NH <sub>4</sub> : 0.1 mM, H <sub>2</sub> S: ≤ 0.1 µM (Kuril Trench (seep))	AB479073	1	Okutani et al. 2009 <sup>a</sup> Boulègue et al. 1987 <sup>b</sup>
26	<i>Calyptogena extenta</i>	T: 1.11 to 1.13 °C, pH: 8.01 to 8.16, SO <sub>4</sub> <sup>2-</sup> : 26.3 to 27.0 mM, Fe: 790 to 800 nM, Mn: 11 to 14 nM, CH <sub>4</sub> : 3.63 to 4.97 nM, NH <sub>4</sub> : 0.1 mM, H <sub>2</sub> S: ≤ 0.1 µM (Kuril Trench (seep))	AB479075	1	Okutani et al. 2009 <sup>a</sup> Boulègue et al. 1987 <sup>b</sup>
27	<i>Calyptogena (Ectenagena) extenta</i>	T: 15 to 220 °C, pH: 5.4, NH <sub>4</sub> : 5.6 mmol kg <sup>-1</sup> , H <sub>2</sub> S: 1.1 to 1.5 mmol kg <sup>-1</sup> , Fe: 0 to 10 µmol kg <sup>-1</sup> , Mn: 10 to 21 µmol kg <sup>-1</sup> (Gorda Ridge (vent))	AF035725	1	Peek et al. 1998 <sup>a</sup> Campbell et al. 1994 <sup>b</sup>
28	<i>Bathymodiolus heckerae</i>	NH <sub>4</sub> : bdl to 30 µM, H <sub>2</sub> S: bdl to 4.5 mM, NO <sub>3</sub> <sup>-</sup> : bdl to 3.9 mM; DIC: 1 to 21 mM, DOC: 3 to 11.5 mM, CH <sub>4</sub> : bdl to 2.2 mM; TOC: 2-5%, C/N: 10-40 (Gulf of Mexico (seep))	AM236328	14	Duperron et al. 2007 <sup>a</sup> Joye et al. 2004 <sup>b</sup>
29	<i>Bathymodiolus heckerae</i>	NH <sub>4</sub> : bdl to 30 µM, H <sub>2</sub> S: bdl to 4.5 mM, NO <sub>3</sub> <sup>-</sup> : bdl to 3.9 mM; DIC: 1 to 21 mM, DOC: 3 to 11.5 mM, CH <sub>4</sub> : bdl to 2.2 mM; TOC: 2-5%, C/N: 10-40 (Gulf of Mexico (seep))	JF969166	58	Raggi et al. 2013 <sup>a</sup> Joye et al. 2004 <sup>b</sup>
30	<i>Bathymodiolus septemdirum</i>	T: 78 to 278 °C (max.), CH <sub>4</sub> : 2.1 to 10.96 nmol kg <sup>-1</sup> , O <sub>2</sub> : 70.5 to 209.7 µM (Myojin Knoll, Izu-Bonin Arc (vent))	AB036709	22	Fujiwara et al. 2000 <sup>a</sup> Tsunogai et al. 2000 <sup>b</sup>
31	<i>Myrina</i> sp.	T: 300 °C (max.), CO <sub>2</sub> : 40.6 mM, H <sub>2</sub> : 100 to 150 µM, CH <sub>4</sub> : 140 µM, NH <sub>4</sub> : 10 to 20 µM, H <sub>2</sub> S: 1.5 mM (Suiyo sea mount, Japan (vent))	AB178222	1	Ikuta et al. 2015 <sup>a</sup> Ishibashi et al. 1994 <sup>b</sup>
32	<i>Idas</i> sp.	H <sub>2</sub> S: bdl to 23 mM, SO <sub>4</sub> <sup>2-</sup> : bdl to 30 mM; DIC: 2 to 30 mM, NH <sub>4</sub> : bdl to 4.5 mM (Eastern Mediterranean (seep))	AM402957	4	Duperron et al. 2008 <sup>a</sup> Ristova et al. 2015 <sup>b</sup>

33	<i>Maorithyas hadalis</i>	T: 1.2°C, pH: 8.01 to 8.15, H <sub>2</sub> S: ≤ 0.1 μM, SO <sub>4</sub> <sup>2-</sup> : 26 to 27.4 mM, Fe: < 0.02 to 1.47 μM, Mn: 40 to 220 nM, CH <sub>4</sub> : 2.66 nM, NH <sub>4</sub> : 0.1 mM (Japan Trench (seep))	AB042413	1	Fujiwara et al. 2001 <sup>a</sup> Boulègue et al. 1987 <sup>b</sup>
34	<i>Bathymodiolus aff. brevior</i>	T: 315 to 365 °C (max.), pH: 3.35 to 3.51, CO <sub>2</sub> : 4.53 to 5.13 mmol kg <sup>-1</sup> , H <sub>2</sub> S: 3.93 to 4.07 mmol kg <sup>-1</sup> , SO <sub>4</sub> <sup>2-</sup> : 0.479 to 1.56 mmol kg <sup>-1</sup> , NH <sub>4</sub> : 17.1 to 38.8 μmol kg <sup>-1</sup> , CH <sub>4</sub> : 171 to 203 μmol kg <sup>-1</sup> , H <sub>2</sub> : 7.89 to 8.19 mmol kg <sup>-1</sup> , Fe: 3.5 to 6 mmol kg <sup>-1</sup> (Kairei field, Central Indian Ridge (vent))	DQ077891	30	McKiness and Cavanaugh 2005 <sup>a</sup> Gallant and Damm 2006 <sup>b</sup>
35	<i>Bathymodiolus</i> sp.	CH <sub>4</sub> : 1.41 to 5.85 μM, Fe: 7 to 34 nmol kg <sup>-1</sup> , Mn: 3 to 47 nmol kg <sup>-1</sup> (Gabon: Regab, Gulf of Guinea (seep))	AJ745718	140	Duperron et al. 2005 <sup>a</sup> Lemaitre et al. 2014 <sup>b</sup>
36	<i>Bathymodiolus brooksi</i>	NH <sub>4</sub> : bdl to 30 μM, H <sub>2</sub> S: bdl to 4.5 mM, NO <sub>3</sub> <sup>-</sup> : bdl to 3.9 mM; DIC: 1 to 21 mM, DOC: 3 to 11.5 mM, CH <sub>4</sub> : bdl to 2.2 mM; TOC: 2-5%, C/N: 10-40 (Gulf of Mexico (seep))	JF969170	267	Raggi et al. 2013 <sup>a</sup> Joye et al. 2004 <sup>b</sup>
37	<i>Bathymodiolus azoricus</i>	T: 2 to 370 °C, pH: 2.99 to 5.05, CO <sub>2</sub> : 3.2 to 31 mM, H <sub>2</sub> : bdl to 15.8 mM, H <sub>2</sub> S: bdl to 3 mM, SO <sub>4</sub> <sup>2-</sup> : 0.27 to 17.24 mM, CH <sub>4</sub> : 2.5 mmol kg <sup>-1</sup> , Fe: < 0.01 to 24.1 mM, Mn: < 0.01 to 1.8 mM (Rainbow, MAR (vent))	AM083974	18	Duperron et al. 2005 <sup>a</sup> Seyfried Jr et al. 2011 <sup>b</sup> Konn et al. 2009 <sup>b</sup>
38	<i>Bathymodiolus azoricus</i>	T: 6 to 323 °C, pH: 4.57 to 8.02, ΣS: < 0.5 to 2360 μM, CH <sub>4</sub> : 0.68 mM, NH <sub>4</sub> : 0.15 to 6.75 μM (Lucky Strike, MAR (vent))	AM083972	“	Duperron et al. 2005 <sup>a</sup> Sarradin et al. 1999 <sup>b</sup> Charlou et al. 2000 <sup>b</sup>
39	<i>Bathymodiolus azoricus</i>	T: 10 to 279 °C (max.), pH: 4.90 to 7.88, ΣS: < 0.5 to 1100 μM, CH <sub>4</sub> : 1.7 mmol kg <sup>-1</sup> , NH <sub>4</sub> : 0.33 to 1.71 μM (Menez Gwen, MAR (vent))	AM083968	“	Duperron et al. 2005 <sup>a</sup> Sarradin et al. 1999 <sup>b</sup> Keir 2010 <sup>b</sup>
40	<i>Bathymodiolus puteoserpentis</i>	T: 350 °C, pH: 3.3, CH <sub>4</sub> : 2.1 to 4 mmol kg <sup>-1</sup> , H <sub>2</sub> S: 2.5 mmol kg <sup>-1</sup> , O <sub>2</sub> : 0, H <sub>2</sub> : 19 mmol kg <sup>-1</sup> , SO <sub>4</sub> <sup>2-</sup> : 0, CO <sub>2</sub> : 10.1 mmol kg <sup>-1</sup> , Fe: 2410 μmol kg <sup>-1</sup> , Mn: 338 μmol kg <sup>-1</sup> (Logatchev, MAR (vent))	AM083975	“	Duperron et al. 2005 <sup>a</sup> Klevenz et al. 2011 <sup>b</sup>
41	<i>Idas</i> sp.	H <sub>2</sub> S: bdl to 23 mM, SO <sub>4</sub> <sup>2-</sup> : bdl to 30 mM; DIC: 2 to 30 mM, NH <sub>4</sub> : bdl to 4.5 mM (Eastern Mediterranean (seep))	AM402959	20	Duperron et al. 2008 <sup>a</sup> Ristova et al. 2015 <sup>b</sup>

42	<i>Escarpiia</i> sp.	NH <sub>4</sub> : bdl to 30 µM, H <sub>2</sub> S: bdl to 4.5 mM, NO <sub>3</sub> <sup>-</sup> : bdl to 3.9 mM, DIC: 1 to 21 mM, DOC: 3 to 11.5 mM, CH <sub>4</sub> : bdl to 2.2 mM, TOC: 2-5%, C/N: 10-40 (Gulf of Mexico (seep))	JF969171	209	Raggi et al. 2013 <sup>a</sup> Joye et al. 2004 <sup>b</sup>
43	<i>Seepiophila jonesi</i>	NH <sub>4</sub> : bdl to 30 µM, H <sub>2</sub> S: bdl to 4.5 mM, NO <sub>3</sub> <sup>-</sup> : bdl to 3.9 mM, DIC: 1 to 21 mM, DOC: 3 to 11.5 mM, CH <sub>4</sub> : bdl to 2.2 mM, TOC: 2-5%, C/N: 10-40 (Gulf of Mexico (seep))	AY129105		Nelson and Fisher 2000 <sup>a</sup> Joye et al. 2004 <sup>b</sup>
44	<i>Ridgeia piscesae</i>	T: 15 to 220 °C (max.), pH: 5.4, NH <sub>4</sub> : 5.6 mmol kg <sup>-1</sup> , H <sub>2</sub> S: 1.1 to 1.5 mmol kg <sup>-1</sup> , Fe: 0 to 10 µmol kg <sup>-1</sup> , Mn: 10 to 21 µmol kg <sup>-1</sup> . (Gorda Ridge (vent))	U77480	1	Feldman et al. 1997 <sup>a</sup> Campbell et al. 1994 <sup>b</sup>
45	<i>Riftia pachyptila</i>	T: 7.9 to 13.9 °C, CH <sub>4</sub> : 60 to 110 mmol kg <sup>-1</sup> , H <sub>2</sub> S: 43.30 to 73.67 µmol kg <sup>-1</sup> (East Pacific Rise (vent))	U77478	1	Feldman et al. 1997 <sup>a</sup> Lutz et al. 2008 <sup>b</sup> Keir 2010 <sup>b</sup>
46	<i>Lucinoma aff. kazani</i>	H <sub>2</sub> S: bdl to 23 mM, SO <sub>4</sub> <sup>2-</sup> : bdl to 30 mM, DIC: 2 to 30 mM, NH <sub>4</sub> : bdl to 4.5 mM (Eastern Mediterranean (seep))	AM236336	92	Duperron et al. 2007 <sup>a</sup> Ristova et al. 2015 <sup>b</sup>
47	scaly snail	T: 315 to 365 °C (max.), pH: 3.35 to 3.51, CO <sub>2</sub> : 4.53 to 5.13 mmol kg <sup>-1</sup> , H <sub>2</sub> S: 3.93 to 4.07 mmol kg <sup>-1</sup> , SO <sub>4</sub> <sup>2-</sup> : 479 to 1560 µmol kg <sup>-1</sup> , NH <sub>4</sub> : 17.1 to 38.8 µmol kg <sup>-1</sup> , CH <sub>4</sub> : 171 to 203 µmol kg <sup>-1</sup> , H <sub>2</sub> : 7.89 to 8.19 mmol kg <sup>-1</sup> , Fe: 3.5 to 6.0 mmol kg <sup>-1</sup> (Kairei field, Central Indian Ridge (vent))	AY310506	75	Goffredi et al. 2004 <sup>a</sup> Gallant and Damm 2006 <sup>b</sup>
48	Scaly snail	T: 315 to 365 °C (max.), pH: 3.35 to 3.51, CO <sub>2</sub> : 4.53 to 5.13 mmol kg <sup>-1</sup> , H <sub>2</sub> S: 3.93 to 4.07 mmol kg <sup>-1</sup> , SO <sub>4</sub> <sup>2-</sup> : 479 to 1560 µmol kg <sup>-1</sup> , NH <sub>4</sub> : 17.1 to 38.8 µmol kg <sup>-1</sup> , CH <sub>4</sub> : 171 to 203 µmol kg <sup>-1</sup> , H <sub>2</sub> : 7.89 to 8.19 mmol kg <sup>-1</sup> , Fe: 3.5 to 6.01 mmol kg <sup>-1</sup> (Kairei field, Central Indian Ridge (vent))	AY531606	65	Goffredi et al. 2004 <sup>a</sup> Gallant and Damm 2006 <sup>b</sup>
49	Scaly snail	T: 315 to 365 °C (max.), pH: 3.35 to 3.51, CO <sub>2</sub> : 4.53 to 5.13 mmol kg <sup>-1</sup> , H <sub>2</sub> S: 3.93 to 4.07 mmol kg <sup>-1</sup> , SO <sub>4</sub> <sup>2-</sup> : 479 to 1560 µmol kg <sup>-1</sup> , NH <sub>4</sub> : 17.1 to 38.8 µmol kg <sup>-1</sup> , CH <sub>4</sub> : 171 to 203 µmol kg <sup>-1</sup> , H <sub>2</sub> : 7.89 to 8.19 mmol kg <sup>-1</sup> , Fe: 3.5 to 6.0 mmol kg <sup>-1</sup> (Kairei field, Central Indian	AY531567	8	Goffredi et al. 2004 <sup>a</sup> Gallant and Damm 2006 <sup>b</sup>



		Ridge (vent))			
50	<i>Escarpia spicata</i>	T: 4 to 95 °C, pH: 6 to 7.5, Eh: -440 to +50 mV, H <sub>2</sub> S: bdl to 1.2 mM, SO <sub>4</sub> <sup>2-</sup> : 1 to 30 mM (Guaymas basin (vent))	AF165909	1	Di Meo et al. 2000 <sup>a</sup> Teske et al. 2016 <sup>b</sup>
51	<i>Idas</i> sp.	H <sub>2</sub> S: bdl to 23 mmol kg <sup>-1</sup> , SO <sub>4</sub> <sup>2-</sup> : bdl to 30 mmol kg <sup>-1</sup> , DIC: 2 to 30 mmol kg <sup>-1</sup> , NH <sub>4</sub> : bdl to 4.5 mmol kg <sup>-1</sup> (Eastern Mediterranean (seep))	AM402958	1	Duperron et al. 2008 <sup>a</sup> Ristova et al. 2015 <sup>b</sup>
52	<i>Sclerolinum contortum</i>	T: -0.77 to -0.85 °C, pH: 7.6 to 8, O <sub>2</sub> : 0.01 to 0.28 mM, H <sub>2</sub> S: bdl to 0.15 mM (Haakon Mosby Mud Volcano, Arctic (seep))	AM883183	224	Lösekann et al. 2008 <sup>a,b</sup>
53	<i>Rimicaris exoculata</i>	T: 366 °C (max.), ΣS: 1 – 6.0 mM, CH <sub>4</sub> : 0.06 mmol kg <sup>-1</sup> (Snake Pit, MAR (vent))	FN658699	8	Hügler et al. 2011 <sup>a</sup> Renninger et al. 1995 <sup>b</sup> Keir 2010 <sup>b</sup>
54	Scaly snail	T: 315 to 365 °C (max.), pH: 3.35 to 3.51, CO <sub>2</sub> : 4.53 to 5.13 mmol kg <sup>-1</sup> , H <sub>2</sub> S: 3.93 to 4.07 mmol kg <sup>-1</sup> , SO <sub>4</sub> <sup>2-</sup> : 479 to 1560 μmol kg <sup>-1</sup> , NH <sub>4</sub> : 17.1 to 38.8 μmol kg <sup>-1</sup> , CH <sub>4</sub> : 171 to 203 μmol kg <sup>-1</sup> , H <sub>2</sub> : 7.89 to 8.19 mmol kg <sup>-1</sup> , Fe: 3.5 to 6.0 mmol kg <sup>-1</sup> (Kairei field, Central Indian Ridge (vent))	AY531557	12	Goffredi et al. 2004 <sup>a</sup> Gallant and Damm 2006 <sup>b</sup>
55	<i>Kiwa hirsuta</i>	T: ~32 °C (Annie's Antill vent, Pacific Antarctic Ridge (vent))	EU265797	7	Goffredi et al. 2004 <sup>a,b</sup>
56	<i>Kiwa hirsuta</i>	T: ~32 °C (Annie's Antill vent, Pacific Antarctic Ridge (vent))	EU265799	18	Goffredi et al. 2008 <sup>a,b</sup>
57	<i>Riftia pachyptila</i>	T: 54 °C pH: 4.4 H <sub>2</sub> S: 95 μmol kg <sup>-1</sup> ; Fe: 65 μmol kg <sup>-1</sup> (East Pacific Rise (vent))	AF449225	1	López-García et al. 2002 <sup>a</sup> Le Bris et al. 2006 <sup>b</sup>
58	<i>Oligobrachia haakonmosbiensis</i>	T: -0.77 to -0.85 °C, pH: 7.6 to 8, O <sub>2</sub> : 0.01 to 0.28 mM, H <sub>2</sub> S: bdl to 0.15 mM (Håkon Mosby Mud Volcano, Arctic (seep))	AM883179	52	Lösekann et al. 2008 <sup>a,b</sup>
59	<i>Oligobrachia mashikoi</i>	T: 9 to 23 °C (Tsukumo Bay, Japan)	AB271125	7	Kubota et al. 2007 <sup>a,b</sup>
60	<i>Bathymodiolus aff. boomerang</i>	CH <sub>4</sub> : 1.41 to 5.85 μM, Fe: 7 to 34 nmol kg <sup>-1</sup> , Mn: 3 to 47 nmol kg <sup>-1</sup> (Gabon: Regab, Gulf of Guinea (seep))	AM888204	2	Cambon-Bonavita et al. 2009 <sup>a</sup> Lemaitre et al. 2014 <sup>b</sup>
61	<i>Bathymodiolus japonicus</i>	T: 70 to 325 °C (max.), pH: 4.7 to 5.3, CO <sub>2</sub> : 187 to 227 mmol kg <sup>-1</sup> , H <sub>2</sub> : 25 to 229 μmol kg <sup>-1</sup> , H <sub>2</sub> S: 0.2 to 4.5 mmol kg <sup>-1</sup> , NH <sub>4</sub> : 1.7 to 14.7 mmol kg <sup>-1</sup> , SO <sub>4</sub> <sup>2-</sup> :	AB036711	7	Fujiwara et al. 2000 <sup>a</sup> Kawagucci et al. 2011 <sup>b</sup>

		3.05 to 12.9 nmol kg <sup>-1</sup> , Mn: < 0.01 to 1.12 mmol kg <sup>-1</sup> , Fe: < 0.13 to 0.15 mmol kg <sup>-1</sup> (North Knoll, Iheya (vent))			
62	<i>Bathymodiolus mauritanicus</i>	SO <sub>4</sub> <sup>2-</sup> : 4 to 30 mM, NH <sub>4</sub> : 1 to 1.8 mM, CH <sub>4</sub> : 2.9 to 8 mM (Gulf of Cadiz (seep))	HE963014	17	Rodrigues et al. 2012 <sup>a</sup> Hensen et al. 2007 <sup>b</sup>
63	<i>Bathymodiolus platifrons</i>	T: 70 to 325 °C, pH: 4.7 to 5.3, CO <sub>2</sub> : 187 to 227 mmol kg <sup>-1</sup> , H <sub>2</sub> : 25 to 229 μmol kg <sup>-1</sup> , H <sub>2</sub> S: 0.2 to 4.5 mmol kg <sup>-1</sup> , NH <sub>4</sub> : 1.7 to 14.7 mmol kg <sup>-1</sup> , SO <sub>4</sub> <sup>2-</sup> : 3.05 to 12.9 nmol kg <sup>-1</sup> , Mn: < 0.01 to 1.12 mmol kg <sup>-1</sup> , Fe: < 0.13 to 0.15 mmol kg <sup>-1</sup> (North Knoll, Iheya (vent))	AB036710	27	Fujiwara et al. 2000 <sup>a</sup> Kawagucci et al. 2011 <sup>b</sup>
64	<i>Bathymodiolus childressi</i>	NH <sub>4</sub> : bdl to 30 μM, H <sub>2</sub> S: bdl to 4.5 mM, NO <sub>3</sub> : bdl to 3.9 mM; DIC: 1 to 21 mM, DOC: 3 to 11.5 mM, CH <sub>4</sub> : bdl to 2.2 mM; TOC: 2 to 5%, C/N: 10 to 40 (Gulf of Mexico (seep))	AM236329	50	Duperron et al. 2007b <sup>a</sup> Joye et al. 2004 <sup>b</sup>
65	<i>Bathymodiolus hirtus</i>	T: 8 °C, CH <sub>4</sub> : 0.9 to 15 mmol kg <sup>-1</sup> (Kuroshima Knoll (seep))	AB250698	1	Li et al. 2014 <sup>a</sup> Tsunogai et al. 2010 <sup>b</sup>
66	<i>Bathymodiolus brooksi</i>	NH <sub>4</sub> : bdl to 30 μM, H <sub>2</sub> S: bdl to 4.5 mM, NO <sub>3</sub> : bdl to 3.9 mM, DIC: 1 to 21 mM, DOC: 3 to 11.5 mM, CH <sub>4</sub> : bdl to 2.2 mM, TOC: 2 to 5%, C/N: 10 to 40 (Gulf of Mexico (seep))	AM236330	44	Duperron et al. 2007b <sup>a</sup> Joye et al. 2004 <sup>b</sup>
67	<i>Idas</i> sp.	H <sub>2</sub> S: bdl to 23 mM, SO <sub>4</sub> <sup>2-</sup> : bdl to 30 mM, DIC: 2 to 30 mM, NH <sub>4</sub> : bdl to 4.5 mM (Eastern Mediterranean (seep))	AM402955	74	Duperron et al. 2008b <sup>a</sup> Ristova et al. 2015 <sup>b</sup>
68	<i>Bathymodiolus azoricus</i>	T: 2 to 370 °C (max.), pH: 2.99 to 5.05, CO <sub>2</sub> : 3.2 to 31 mM, H <sub>2</sub> : bdl to 15.8 mM, H <sub>2</sub> S: bdl to 3 mM, SO <sub>4</sub> <sup>2-</sup> : 0.27 to 17.24 mM, CH <sub>4</sub> : 2.5 mmol kg <sup>-1</sup> , Fe: < 0.01 to 24.1 mM, Mn: < 0.01 to 1.8 mM (Rainbow, MAR (vent))	AM083954	5	Duperron et al. 2005 <sup>a</sup> Seyfried Jr et al. 2011 <sup>b</sup> Konn et al. 2009 <sup>b</sup>
69	<i>Bathymodiolus azoricus</i>	T: 6 to 323 °C(max.), pH: 4.57 to 8.02, ΣS: < 0.5 to 2.36 mM, CH <sub>4</sub> : 0.68 mM, NH <sub>4</sub> : 0.15 to 6.75 μM (Lucky Strike MAR (vent))	AM083950	“	Duperron et al. 2005 <sup>a</sup> Sarradin et al. 1999 <sup>b</sup> Charlou et al. 2000 <sup>b</sup>
70	<i>Bathymodiolus azoricus</i>	T: 10 to 279 °C (max.), pH: 4.90 to 7.88, ΣS: < 0.5 to 1.1 mM, CH <sub>4</sub> : 1.7 mmol kg <sup>-1</sup> , NH <sub>4</sub> : 0.33 to 1.71 μmol kg <sup>-1</sup> (Menez Gwen, MAR (vent))	AM083953	“	Duperron et al. 2005 <sup>a</sup> Sarradin et al. 1999 <sup>b</sup> Keir 2010 <sup>b</sup>
71	<i>Bathymodiolus</i>	T: 350 °C (max.), pH: 3.3, CH <sub>4</sub> :	AM083955	9	Duperron et al. 2005 <sup>a</sup>

	<i>puteoserpentis</i>	2.1 to 4 mmol kg <sup>-1</sup> , H <sub>2</sub> S: 2.5 mmol kg <sup>-1</sup> , O <sub>2</sub> : bdl, H <sub>2</sub> : 19 mmol kg <sup>-1</sup> , SO <sub>4</sub> <sup>2-</sup> : bdl, CO <sub>2</sub> : 10.1 mmol kg <sup>-1</sup> , Fe: 2.4 mmol kg <sup>-1</sup> , Mn: 338 µmol kg <sup>-1</sup> (Logatchev, MAR (vent))			Klevenz et al. 2011 <sup>b</sup>
72	<i>Idas sp</i>	H <sub>2</sub> S: bdl to 23 mmol kg <sup>-1</sup> , SO <sub>4</sub> <sup>2-</sup> : bdl to 30 mmol kg <sup>-1</sup> ; DIC: 2 to 30 mmol kg <sup>-1</sup> , NH <sub>4</sub> : bdl to 4.5 mmol kg <sup>-1</sup> (Eastern Mediterranean (seep))	AM402960	33	Duperron et al. 2008 <sup>a</sup> Ristova et al. 2015 <sup>b</sup>
73	<i>Riftia pachyptila</i>	T: 54 °C, pH: 4.4, H <sub>2</sub> S: 95 µmol kg <sup>-1</sup> , Fe: 65 µmol kg <sup>-1</sup> (East Pacific Rise (vent))	AF449226	1	López-García et al. 2002 <sup>a</sup> Le Bris et al. 2006 <sup>b</sup>
74	Scaly snail	T: 315 to 365 °C (max.), pH: 3.35 to 3.51, CO <sub>2</sub> : 4.53 to 5.13 mmol kg <sup>-1</sup> , H <sub>2</sub> S: 3.93 to 4.07 mmol kg <sup>-1</sup> , SO <sub>4</sub> <sup>2-</sup> : 479 to 1560 µmol kg <sup>-1</sup> , NH <sub>4</sub> : 17.1 to 38.8 µmol kg <sup>-1</sup> , CH <sub>4</sub> : 171 to 203 µmol kg <sup>-1</sup> , H <sub>2</sub> : 7.89 to 8.19 mmol kg <sup>-1</sup> , Fe: 3.5 to 6.0 mmol kg <sup>-1</sup> (Kairei field, Central Indian Ridge (vent))	AY355300	22	Goffredi et al. 2008 <sup>a</sup> Gallant and Damm 2006 <sup>b</sup>
75	<i>Kiwa hirsuta</i>	T: ~32 °C (Annie's Antill vent, Pacific Antarctic Ridge (vent))	EU265788	3	Goffredi et al. 2004 <sup>a,b</sup>
76	<i>Riftia pachyptila</i>	T: 54 °C, pH: 4.4, H <sub>2</sub> S: 95 µmol kg <sup>-1</sup> , Fe: 65 µmol kg <sup>-1</sup> (East Pacific Rise (vent))	AF449222	1	López-García et al. 2002 <sup>a</sup> Le Bris et al. 2006 <sup>b</sup>
77	<i>Riftia pachyptila</i>	T: 54 °C, pH: 4.4, H <sub>2</sub> S: 95 µmol kg <sup>-1</sup> , Fe: 65 µmol kg <sup>-1</sup> (East Pacific Rise (vent))	AF449230	2	López-García et al. 2002 <sup>a</sup> Le Bris et al. 2006 <sup>b</sup>
78	<i>Lamellibrachia sp.</i>	H <sub>2</sub> S: < 0.01 to 0.14 mmol kg <sup>-1</sup> , SO <sub>4</sub> <sup>2-</sup> : 16.2 to 27.7 mmol kg <sup>-1</sup> , NH <sub>4</sub> : < 5 to 1400 µmol kg <sup>-1</sup> , CH <sub>4</sub> : 9.1 nM to 2.5 M (Sagami Trough, Japan (seep))	D83060	1	Naganuma et al. 1997 <sup>a</sup> Tsunogai et al. 1996 <sup>b</sup>
79	<i>Alvinella pompejana</i>	T: 7.9 to 13.9 °C, CH <sub>4</sub> : 60 to 110 mmol kg <sup>-1</sup> , H <sub>2</sub> S: 43.30 to 73.67 µmol kg <sup>-1</sup> (East Pacific Rise (vent))	AF357198	1	Campbell et al. 2001 <sup>a</sup> Lutz et al. 2008 <sup>b</sup> Keir 2010 <sup>b</sup>
80	<i>Rimicaris exoculata</i>	T: 366 °C (max.), ΣS: 1 to 6000µM, CH <sub>4</sub> : 0.06 mmol kg <sup>-1</sup> , (Snake Pit, MAR (vent))	FN658698	19	Hügler et al. 2011 <sup>a</sup> Renninger et al. 1995 <sup>b</sup> Keir et al. 2010 <sup>b</sup>
81	Scaly snail	T: 315 to 365 °C (max.), pH: 3.35 to 3.51, CO <sub>2</sub> : 4.53 to 5.13 mmol kg <sup>-1</sup> , H <sub>2</sub> S: 3.93 to 4.07 mmol kg <sup>-1</sup> , SO <sub>4</sub> <sup>2-</sup> : 479 to 1560 µmol kg <sup>-1</sup> , NH <sub>4</sub> : 17.1 to 38.8 µmol kg <sup>-1</sup> , CH <sub>4</sub> : 171 to 203 µmol kg <sup>-1</sup> , H <sub>2</sub> : 7.89 to 8.19 mmol kg <sup>-1</sup> , Fe: 3.5 to 6.0 mmol kg <sup>-1</sup> (Kairei field, Central Indian	AY531575	56	Goffredi et al. 2008 <sup>a</sup> Gallant and Damm 2006 <sup>b</sup>

		Ridge (vent))			
82	<i>Alviniconcha hessleri</i>	T: 70 to 325 °C (max.), pH: 4.7 to 5.3, CO <sub>2</sub> : 187 to 227 mmol kg <sup>-1</sup> , H <sub>2</sub> : 25 to 229 µmol kg <sup>-1</sup> , H <sub>2</sub> S: 0.2 to 4.5 mmol kg <sup>-1</sup> , NH <sub>4</sub> : 1.7 to 14.7 mmol kg <sup>-1</sup> , SO <sub>4</sub> <sup>2-</sup> : 3.05 to 12.9 nmol kg <sup>-1</sup> , Mn: < 0.01 to 1120 µmol kg <sup>-1</sup> , Fe: < 0.13 to 0.15 mmol kg <sup>-1</sup> (Iheya- Mid-Okinawa Trough (vent))	AB091292	1	Inagaki et al. 2004 <sup>a</sup> Kawagucci et al. 2011 <sup>b</sup>
83	<i>Kiwa hirsuta</i>	T: ~32 °C (Annie's Antill vent, Pacific Antarctic Ridge (vent))	EU265785	24	Goffredi et al. 2004 <sup>a,b</sup>
84	<i>Alvinella pompejana</i>	T: 7.9 to 13.9 °C, CH <sub>4</sub> : 60 to 110 µmol kg <sup>-1</sup> , H <sub>2</sub> S: 43.30 to 73.67 µmol kg <sup>-1</sup> (East Pacific Rise (vent))	L35520	139	Haddad et al. 1995 <sup>b</sup> Lutz et al. 2008 <sup>b</sup> Keir 2010 <sup>b</sup>
				Total = 2219	

**Supplementary Table 1.** Details of host, 16S rDNA accession number and frequency of related sequences of the associated bacteria along with the available geochemical parameters of their habitats.

bdl: below detectable level; temperature could be either of the immediate surroundings of the fauna or the maximum reported temperature (max.) of the vent. '1' denotes the representative sequence in the literature when its copy number is not given. Information of the host and symbiont<sup>a</sup> and geochemistry of the habitat<sup>b</sup> belong to two different references, due to lack of data from the same literature. The geochemical data could be either specific to the local sampling site or generic to a wider area.

Bacterial associate	Host phylum	Host scientific name/mode of nutrition (symbiont type (organ))	Location/ environment	Region	Latitude and longitude used for map to minimize clustering/overlap	Latitude and longitude (as published)
<i>α-Proteobacteria</i>	Annelida	<i>Riftia pachyptila</i> / Thiotrophy (endosymbiont (trophosome))	EPR/ basaltic sulfidic vents	EP	9°00'23.86"N, 106°15'35.04"W	9°00'23.86"N, 106°15'35.04"W
		“	EPR/ basaltic sulfidic vents	EP	13°00'55.12"N, 104°35'03.73"W	13°00'55.12"N, 104°35'03.73"W
	Mollusca	<i>Helicoradomenia cf. acredema</i> / Thiotrophy, Heterotrophy (epibiont, endosymbiont (cuticle))	TICA (EPR)/ basaltic sulfidic vents	EP	9°50'26.82"N, 104°17'29.58"W	9°50'26.82"N, 104°17'29.58"W
		<i>Helicoradomenia</i> sp. 1/ Thiotrophy, Heterotrophy (epibiont, endosymbiont (cuticle))	TICA (EPR)/ basaltic sulfidic vents	EP	9°50'26.82"N, 104°17'29.58"W	9°50'26.82"N, 104°17'29.58"W
<i>γ-Proteobacteria</i>	Annelida	<i>Escarpia spicata</i> / Thiotrophy (endosymbiont (trophosome))	Guaymas Basin/ basaltic sulfidic vents	EP	27°00'00.00"N, 111°00'00.00"W	Not given
		<i>Lamellibrachia</i> sp. 7/ Thiotrophy (endosymbiont (trophosome))	Gorda Ridge/ basaltic sulfidic vents	EP	42°45'00.00"N, 126°42'00.00"W	42°45'00.00"N, 126°42'00.00"W
		<i>Lamellibrachia columna</i> / Thiotrophy (endosymbiont (trophosome))	Lau Basin, Hine Hina (Lau-Fiji)/ back-arc basin rich in sulfide	SWP	22°32'00.00"S, 176°43'00.00"W	22°32'00.00"S, 176°43'00.00"W
		<i>Oasisia alvinae</i> / Thiotrophy (endosymbiont (trophosome))	TICA (EPR)/ basaltic sulfidic vents	EP	9°50'26.82"N, 104°17'29.58"W	9°50'26.82"N, 104°17'29.58"W
		“	EPR/ basaltic sulfidic vents	EP	20°50'00.00"N, 109°00'00.00"W	20°47'00.00"N, 109°08'00.00"W
		<i>Riftia pachyptila</i> / Thiotrophy (endosymbiont (trophosome))	TICA (EPR)/ basaltic sulfidic vents	EP	9°50'26.82"N, 104°17'29.58"W	9°50'26.82"N, 104°17'29.58"W
		“	EPR/ basaltic sulfidic vents	EP	9°00'23.86"N, 106°15'35.04"W	9°00'23.86"N, 106°15'35.04"E
		“	EPR/basaltic sulfidic vents	EP	13°00'55.12"N, 104°35'03.73"W	13°00'55.12"N, 104°35'03.73"W
		“	Galápagos	EP	0°48'14.82"N,	Not given

			vent /sulfidic vents		86°13'28.68"W	
		“	Guaymas Basin/ basaltic sulfidic vents	EP	27°00'00.00"N, 111°00'00.00"W	26°59'00.00"N, 111°24'00.00"W
		<i>Ridgeia piscesae</i> / Thiotrophy (endosymbiont (trophosome))	JFR/basaltic sulfidic vents	EP	45°56'06.00"N, 130°00'48.00"W	Not given
		<i>Tevnia jerichonana</i> / Thiotrophy (endosymbiont (trophosome))	TICA (EPR)/ basaltic sulfidic vents	EP	9°50'26.82"N, 104°17'29.58"W	9°50'26.82"N, 104°17'29.58"W
		Unidentified polychaete/ Thiotrophy (endosymbiont (trophosome))	Nikko seamount/ basaltic sulfidic vents	WP	23°05'00.00"N, 142°20'00.00"E	23°05'00.00"N, 142°20'00.00"E
	Mollusca	<i>Ifremeria nautilei</i> / Thiotrophy, Methanotrophy (endosymbiont (gill))	PACMANUS vent (Manus Basin)/low sulfidic vents	WP	3°44'00.00"S, 151°40'00.00"E	3°43'42.00"S, 151°40'12.00"E
		Unidentified scaly snail/ Thiotrophy (epibiont (sclerite)), (endosymbiont (oesophageal gland))	RTJ (Indian Ocean)/ black smoker chimney rich in sulfide	SI	25°19'13.80"S, 70°02'25.20"E	25°19'13.80"S, 70°02'25.20"E
		<i>Calymene magnifica</i> / Thiotrophy, Heterotrophy (endosymbiont (gill))	Galápagos vent/ sulfidic vents	EP	0°48'14.82"N, 86°13'28.68"W	Not given
		“	Pacific/ basaltic sulfidic vents	SP	18°00'00.00"S, 113°00'00.00"W	18°00'00.00"S, 113°00'00.00"W
		<i>Calymene pacifica</i> / Thiotrophy, Heterotrophy (endosymbiont (gill))	Clam Bed (Endeavour segment, JFR)/sulfidic vents	EP	47°00'00.00"N, 129°00'00.00"W	Not given
		<i>Ectenagena extenta</i> , Thiotrophy, Heterotrophy (endosymbiont (gill))	Gorda Ridge/ basaltic sulfidic vents	EP	41°00'00.00"N, 127°00'00.00"W	41°00'00.00"N, 127°00'00.00"W
		<i>Vesicomys gigas</i> / Thiotrophy (endosymbiont (gill))	Guaymas Basin/ sediment vents rich in sulfide	EP	27°00'00.00"N, 111°00'00.00"W	27°00'00.00"N, 111°00'00.00"W
		<i>Abyssogena southwardae</i> / Thiotrophy (endosymbiont (gill))	Clueless (MAR)/ basaltic sulfidic vents	MA	4°28.8'00"S 12°22.2'00"W	4°28.8'00"S 12°22.2'00"W
		<i>Myrina</i> sp.	Suiyo	WP	28°35'59.99"N	Not given

		Thiotrophy (endosymbiont (gill))	Seamount (Japan)/ sulfidic vents		140°37'59.99"E	
		<i>Bathymodiolus azoricus</i> / Thiotrophy, Methanotrophy, Heterotrophy (endosymbiont (gill))	Menez Gwen (MAR)/active chimneys rich in sulfide and methane	MA	37°50'21.60"N, 31°31'16.80"W	37°50'21.60"N, 31°31'16.80"W
		“	“	“	37°50'21.60"N, 31°31'16.80"W	37°17'00.00"N, 32°15'00.00"W
		“	Lucky Strike (MAR)/ active chimneys rich in sulfide and methane	MA	37°17'15.60"N, 32°16'30.60"W	37°17'15.60"N, 32°16'30.60"W
		“	“	“	37°17'15.60"N, 32°16'30.60"W	37°17'15.60"N, 32°16'28.80"W
		“	“	“	37°17'15.60"N, 32°16'30.60"W	37°17'17.40"N, 32°16'27.60"W
		“	“	“	37°17'15.60"N, 32°16'30.60"W	37°17'37.80"N, 32°16'31.80"W
		“	“	“	37°17'15.60"N, 32°16'30.60"W	Not given
		“	Rainbow (MAR)/ active chimneys rich in sulfide and methane	MA	36°13'26.40"N, 33°53'34.80"W	36°13'26.40"N, 33°53'34.80"W
		“	“	“	36°13'26.40"N, 33°53'34.80"W	36°13'30.00"N, 33°53'54.00"W
		“	“	“	36°13'26.40"N, 33°53'34.80"W	36°14'14.40"N, 33°54'05.40"W
		<i>Bathymodiolus brevior</i> / Thiotrophy, Heterotrophy (endosymbiont (gill))	Lau Basin/ active back- arc basin rich in sulfide	SWP	23°13'00.00"S, 176°38'00.00"W	23°13'00.00"S, 176°38'00.00"W
		<i>Bathymodiolus</i> aff. <i>brevior</i> / Thiotrophy, Heterotrophy (endosymbiont (gill))	CIR/active chimneys rich in sulfide and methane	CI	23°53'00.00"S, 69°36'00.00"E	Not given
		<i>Bathymodiolus japonicus</i> / Methanotrophy, Heterotrophy (endosymbiont (gill))	North Knoll (Iheya Ridge, Okinawa Trough)/ active back- arc basin rich in sulfide	WP	27°47'13.20"N, 126°53'54.36"E	27°47'10.86"N, 126°53'59.10"E
		<i>Bathymodiolus marisindicus</i> / Thiotrophy,	CIR/active chimneys rich in	CI	23°53'00.00"S, 69°36'00.00"E	23°53'00.00"S, 69°36'00.00"E

		Heterotrophy, (endosymbiont (gill))	sulfide and methane			
		<i>Bathymodiolus platifrons</i> / Methanotrophy, Heterotrophy (endosymbiont (gill))	North Knoll (Iheya Ridge, Okinawa Trough)/ active back- arc basin rich in sulfide	WP	27°47'13.20"N, 126°53'54.36"E	27°47'10.86"N, 126°53'59.10"E
		<i>Bathymodiolus puteoserpentis</i> / Thiotrophy, Methanotrophy, Heterotrophy (endosymbiont (gill))	Snake pit (MAR)/active vents rich in sulfide and methane	MA	23°22'12.00"N, 44°57'02.40"W	23°22'12.00"N, 44°57'02.40"W
		“	“	“	23°22'12.00"N, 44°57'02.40"W	23°22'06.00"N, 44°56'54.60"W
		“	“	“	23°22'12.00"N, 44°57'02.40"W	23°22'07.80"N, 44°57'00.00"W
		“	“	“	23°22'12.00"N, 44°57'02.40"W	23°22'00.00"N, 44°56'00.00"W
		“	Logatchev (MAR)/ active vents rich in sulfide	MA	14°45'18.60"N, 44°58'44.40"W	14°45'18.60"N, 44°58'44.40"W
		“	“	“	14°45'18.60"N, 44°58'44.40"W	14°45'16.20"N, 44°58'42.00"W
		“	“	“	14°45'18.60"N, 44°58'44.40"W	14°45'25.20"N, 44°58'47.40"W
		<i>Bathymodiolus septemdiarum</i> / Thiotrophy, Heterotrophy (endosymbiont (gill))	Myojin Knoll (Izu-Bonin Arc)/ active volcanic arc rich in sulfide and methane	WP	32°06'17.52"N, 139°52'11.10"E	32°06'17.52"N, 139°52'11.10"E
		“	Mariana Trough	WP	18°13'00.00"N, 144°42'00.00"W	18°13'00.00"N, 144°42'00.00"W
		<i>Bathymodiolus thermophilus</i> / Thiotrophy, Heterotrophy (endosymbiont (gill))	Galápagos vent/ sulfidic vents	EP	0°48'14.82"N, 86°13'28.68"W	Not given
		“	Galápagos Rift/ sulfidic vent	EP	0°48'14.82"N, 86°13'28.68"W	0°48'00.00"N, 86°13'00.00"W
		<i>Bathymodiolus</i> aff. <i>thermophilus</i> / Thiotrophy, Heterotrophy (endosymbiont (gill))	EPR/ balsaltic sulfidic vents	SP	31°52'00.00"S, 112°03'00.00"W	31°52'00.00"S, 112°03'00.00"W
		<i>Bathymodiolus</i> sp.4/ Thiotrophy, Heterotrophy (endosymbiont (gill))	Manus Basin/ active sulfidic vents	WP	3°44'00.00"S, 151°40'00.00"E	3°44'00.00"S, 151°40'00.00"E



		<i>Bathymodiolus</i> sp. 5/ Thiotrophy (epibiont (scaphognathite, branchiostegite))	JFR/ Black smoker rich in sulfide	NEP	45°56'06.00"N, 130°00'48.00"W	Not given
		<i>Vulcanidas insulatus</i> / Thiotrophy (endosymbiont (gill))	Macauley Cone /sulfidic vents	SWP	30°13'00.00"S, 178°27'00.00"E	30°13'00.00"S, 178°27'00.00"E
		<i>Gigantidas gladius</i> / Thiotrophy (endosymbiont (gill))	Rumble III/active sulfidic volcanic arc	SWP	35°44'00.00"S, 178°30'00.00"E	35°44'00.00"S, 178°30'00.00"E
		<i>Helicoradomenia</i> sp. 1/ Thiotrophy, Heterotrophy (epibiont, endosymbiont (cuticle))	TICA (EPR)/ basaltic sulfidic vents	EP	9°50'26.82"N, 104°17'29.58"W	9°50'26.82"N, 104°17'29.58"W
	Arthropoda	<i>Kiwa hirsuta</i> / Thiotrophy, Heterotrophy (epibiont (setae))	Annie's Anthill vent area (PAR)/ extinct vents, active sulfidic vents, sulfide black smokers	SWP	37°46'29.40"S, 110°54'43.20"W	37°46'29.40"S, 110°54'43.20"W
<i>δ-Proteobacteria</i>	Annelida	<i>Riftia pachyptila</i> / Thiotrophy (endosymbiont (trophosome))	EPR/ basaltic sulfidic vents	EP	9°00'23.86"N, 106°15'35.04"W	9°00'23.86"N, 106°15'35.04"E
		“	EPR/ basaltic sulfidic vents	EP	13°00'55.12"N, 104°35'03.73"W	13°00'55.12"N, 104°35'03.73"W
	Mollusca	Unidentified scaly snail/ Thiotrophy (epibiont (sclerite, shell), endsymbiont (oesophageal gland))	RTJ (Indian Ocean)/ sulfidic vents	SI	25°19'13.80"S, 70°02'25.20"E	25°19'13.80"S, 70°02'25.20"E
	Arthropoda	<i>Kiwa hirsuta</i> / Thiotrophy, Heterotrophy (epibiont (setae))	Annie's Anthill vent area (PAR)/ extinct vents, active sulfidic vents, sulfidic black smokers	SP	37°46'29.40"S, 110°54'43.20"W	37°46'29.40"S, 110°54'43.20"W
<i>ε-Proteobacteria</i>	Annelida	<i>Riftia pachyptila</i> / Thiotrophy (endosymbiont (trophosome))	EPR/ basaltic sulfidic vents	EP	9°00'23.86"N, 106°15'35.04"W	9°00'23.86"N, 106°15'35.04"E
		“	“	EP	13°00'55.12"N, 104°35'03.73"W	13°00'55.12"N, 104°35'03.73"W

		<i>Alvinella pompejana</i> / Thiotrophy (epibiotic (integument, tube))	Elsa vent (EPR)/ White smokers rich in sulfide	EP	12°48'00.00"N, 103°56'00.00"W	12°48'00.00"N, 103°56'00.00"W
		“	EPR/ basaltic sulfidic vents	EP	9°50'00.00"N, 104°18'00.00"W	9°50'00.00"N, 104°17'00.00"W
		“	“	EP	12°48'00.00"N, 103°56'00.00"W	12°48'00.00"N, 103°56'00.00"W
		“	“	EP	12°48'00.00"N, 103°56'00.00"W	12°49'00.00"N, 103°56'00.00"W
		“	Guaymas Basin/ sediment vents rich in sulfide	EP	27°00'00.00"N, 111°00'00.00"W	Not given
		Unidentified polychaete	North Big Chimney (Iheya North hydrothermal field)/ active hydrothermal mound rich in sulfide, methane and ammonia	WP	27°47'13.20"N, 126°53'54.36"E	27°47'30.00"N, 126°53'48.00"E
	Mollusca	<i>Alviniconcha</i> aff. <i>hessleri</i> / Thiotrophy (endosymbiont (gill))	Kairei field (Hakuho Knoll, CIR)/active sulfidic vents rich in hydrogen	CI	25°19'14.40"S, 70°02'24.00"E	25°19'14.40"S, 70°02'24.00"E
		<i>Alviniconcha</i> sp. Thiotrophy (endosymbiont (gill))	PACMANUS vent (Manus Basin)/ active sulfidic vents	WP	3°44'00.00"S, 151°40'00.00"E	3°43'42.00"S, 151°40'12.00"E
		Unidentified scaly snail/ Thiotrophy (epibiont (sclerite, shell))	RTJ (Indian Ocean)/ sulfidic vents	SI	25°19'13.80"S, 70°02'25.20"E	25°19'13.80"S, 70°02'25.20"E
	Arthropoda	<i>Rimicaris exoculata</i> / Thiotrophy, Heterotrophy (epibiont (scaphognathite, branchiostegites))	Snake pit (MAR)/ active vents rich in sulfide and methane	MA	23°22'12.00"N, 44°57'02.40"W	23°23'00.00"N, 44°58'00.00"W
		“	Rainbow (MAR)/ active chimneys rich in sulfide and methane	MA	36°13'26.40"N, 33°53'34.80"W	Not given

		<i>Kiwa hirsuta</i> / Thiotrophy, Heterotrophy (epibiont (setae))	Annie's Anthill vent (PAR)/ extinct vents, active sulfidic vents, sulfidic black smokers	SP	37°46'29.40"S, 110°54'43.20"W	37°46'29.40"S, 110°54'43.20"W
<i>z-Proteobacteria</i>	Arthropoda	<i>Rimicaris exoculata</i> / Thiotrophy, Heterotrophy (epibiont (scaphognathite, branchiostegites))	Rainbow (MAR)/ active chimneys rich in sulfide and methane	MA	36°13'26.40"N, 33°53'34.80"W	36°14'00.00"N, 33°54'00.00"W
Actinobacteria	Mollusca	Unidentified limpet/ (endosymbiont (gills))	Axial Seamount (JFR)/ active submarine volcano rich in sulfide and methane	EP	45°56'06.00"N, 130°00'48.00"W	45°58'54.00"N, 130°02'18.00"W
Spirochete	Annelida	<i>Alvinella pompejana</i> / Thiotrophy (epibiotic (integument, tube)), (endosymbiont (gill))	EPR/ basaltic sulfidic vents	“	9°50'26.82"N, 104°17'29.58"W	Not given
Bacteroidetes	Annelida	<i>Riftia pachyptila</i> / Thiotrophy (endosymbiont (trophosome))	EPR/ basaltic sulfidic vents	EP	9°00'23.86"N, 106°15'35.04"W	9°00'23.86"N, 106°15'35.04"E
		“	“	EP	13°00'55.12"N, 104°35'03.73"W	13°00'55.12"N, 104°35'03.73"W
	Arthropoda	<i>Kiwa hirsuta</i> / Thiotrophy, Heterotrophy (epibiont (setae))	Annie's Anthill vent area (PAR)/ extinct vents, active sulfidic vents, sulfidic black smokers	SP	37°46'29.40"S, 110°54'43.20"W	37°46'29.40"S, 110°54'43.20"W
Chloroflexi	Arthropoda	<i>Kiwa hirsuta</i> / Thiotrophy, Heterotrophy (epibiont (setae))	Annie's Anthill vent area (PAR)/ extinct vents, active sulfidic vents, sulfidic black smokers	SP	37°46'29.40"S, 110°54'43.20"W	37°46'29.40"S, 110°54'43.20"W
Verrucomicrobia	Annelida	<i>Riftia pachyptila</i> / Thiotrophy (endosymbiont (trophosome))	EPR/ basaltic sulfidic vents	EP	9°00'23.86"N, 106°15'35.04"W	9°00'23.86"N, 106°15'35.04"E
		“	“	EP	13°00'55.12"N,	13°00'55.12"N,

					104°35'03.73"W	104°35'03.73"W
Unaffiliated bacteria	Ciliophora	<i>Folliculinopsis</i> sp./ (epibiont (lorica)), (endosymbiont (cytoplasm))	Marker N3 (Axial volcano, JFR)/ active submarine volcano rich in sulfide and methane	EP	45°58'54.00"N, 130°02'18.00"W	45°52'02.87"N, 130°00'55.04"W
	Annelida	<i>Alvinella pompejana</i> / Thiotrophy (epibiont (integument))	EPR/ basaltic sulfidic vents	EP	20°50'00.00"N, 109°00'00.00"W	20°50'00.00"N, 109°00'00.00"W
		<i>Riftia pachyptila</i> Thiotrophy (endosymbiont (trophosome))	Galápagos Rift/ sulfidic vents	EP	0°48'14.82"N, 86°13'28.68"W	Not given
		“	Rose Garden (Galápagos Rift)/ sulfidic vents	EP	0°48'14.82"N, 86°13'28.68"W	0°47'00.00"N, 86°07'00.00"W
		“	“	EP	9°50'00.00"N, 104°18'00.00"W	9°50'00.00"N, 104°18'00.00"W
		<i>Ridgeia piscesae</i> / Thiotrophy epibiont (tube)), (endosymbiont (trophosome))	Mothra Endeavour vent field (JFR)/sulfidic vents	EP	47°55'24.00"N, 129°05'49.20"W	47°55'24.00"N, 129°05'49.20"W
		“	Main Endeavour vent field (JFR)/ sulfidic vents	EP	47°55'24.00"N, 129°05'49.20"W	47°57'00.00"N, 129°05'49.20"W
		“	Clam Bed (Endeavour segment, JFR)/ sulfidic vents	EP	47°00'00.00"N, 129°00'00.00"W	47°57'43.80"N, 129°05'33.00"W
		Unidentified polychaete (epibiont (tube))	EPR/ basaltic sulfidic vents	EP	20°50'00.00"N, 109°00'00.00"W	21°00'00.00"N, 109°00'00.00"W
	Mollusca	<i>Alviniconcha hessleri</i> / Thiotrophy (endosymbiont (gill))	Kayo (North Fiji Back-Arc Basin)/ sulfidic back-arc basin	SWP	16°59'00.00"S, 173°43'00.00"W	16°59'00.00"S, 173°43'00.00"W
		“	Mariana Back-Arc Basin/back-arc basin rich in sulfide and methane	WP	18°13'00.00"N, 144°42'00.00"W	Not given
		<i>Ifremeria nautilei</i> / Thiotrophy, Methanotrophy (endosymbiont (gill))	Kayo (North Fiji Back-Arc Basin)/ active vents rich in sulfide	SWP	16°59'00.00"S, 173°43'00.00"W	16°59'00.00"S, 173°43'00.00"W

			and methane			
		“	LHOS site (North Fiji Back- Arc Basin)/back- arc basin rich in sulfide and methane	SWP	16°59'00.00"S, 173°43'00.00"W	16°59'39.00"S, 173°54'43.80"E
		“	Manus Basin (Bismarck Sea)/ sulfidic vents	WP	3°44'00.00"S, 151°40'00.00"E	Not given
		Unidentified snail	Snail pit (Mariana Back-Arc Basin)/ active vents rich in sulfide and methane	WP	18°13'00.00"N, 144°42'00.00"W	18°11'00.00"N, 144°43'00.00"W
		<i>Calyptogena magnifica</i> / Thiotrophy, Heterotrophy (endosymbiont (gill, ovary))	Galápagos Rift/ sulfidic vents	EP	0°48'14.82"N, 86°13'28.68"W	0°48'14.82"N, 86°13'28.68"W
		“	EPR/ basaltic sulfidic vents	EP	20°50'00.00"N, 109°00'00.00"W	20°51'00.00"N, 109°06'00.00"W
		“	“		20°50'00.00"N, 109°00'00.00"W	20°50'00.00"N, 109°06'00.00"W
		<i>Calyptogena pacifica</i> Thiotrophy, Heterotrophy (endosymbiont (gill, ovary))	JFR/ basaltic sulfidic vents	EP	45°56'06.00"N, 130°00'48.00"W	45°56'06.00"N, 130°00'48.00"W
		<i>Vesicomya</i> sp.mt.II Thiotrophy (endosymbiont (gills))	JFR/ basaltic sulfidic vents	“	47°57'24.00"N, 129°05'54.00"W	47°57'24.00"N, 129°05'54.00"W
		<i>Vesicomya</i> sp. (endosymbiont (gills))	Logatchev (MAR)/ active sulfidic vents	“	14°45'18.60"N, 44°58'44.40"W	14°45'19.20"N, 44°58'47.40"W
		<i>Bathymodiolus azoricus</i> / Thiotrophy, Methanotrophy, Heterotrophy (endosymbiont (gill))	Menez Gwen (MAR)/ active chimneys rich in sulfide and methane	MA	37°50'21.60"N, 31°31'16.80"W	37°50'21.60"N, 31°31'16.80"W
		“	“	“	37°50'21.60"N, 31°31'16.80"W	37°51'00.00"N, 31°31'00.00"W
		“	Lucky Strike (MAR)/ active chimneys rich	MA	37°17'15.60"N, 32°16'30.60"W	37°17'15.60"N, 32°16'30.60"W

			in sulfide and methane			
		“	“	“	37°17'15.60"N, 32°16'30.60"W	37°17'15.60"N, 32°16'28.80"W
		“	“	“	37°17'15.60"N, 32°16'30.60"W	37°17'17.40"N, 32°16'27.60"W
		“	“	“	37°17'15.60"N, 32°16'30.60"W	37°17'37.80"N, 32°16'31.80"W
		“	“	“	37°17'15.60"N, 32°16'30.60"W	37°17'00.00"N, 32°16'00.00"W
		“	“	“	37°17'15.60"N, 32°16'30.60"W	37°17'00.00"N, 32°16'00.00"W
		“	Rainbow (MAR)/ active chimneys rich in sulfide and methane	MA	36°13'26.40"N, 33°53'34.80"W	36°13'26.40"N, 33°53'34.80"W
		“	“	“	36°13'26.40"N, 33°53'34.80"W	36°13'30.00"N, 33°53'54.00"W
		“	“	“	36°13'26.40"N, 33°53'34.80"W	36°14'14.40"N, 33°54'05.40"W
		“	“	“	36°13'26.40"N, 33°53'34.80"W	36°13'00.00"N, 33°54'00.00"W
		<i>Bathymodiolus brevior</i> / Thiotrophy, Heterotrophy (endosymbiont (gill))	North Fiji Back- Arc Basin/ sulfidic vents	SWP	16°59'00.00"S, 173°43'00.00"W	16°59'39.00"S, 173°54'43.80"E
		“	Lau Basin/ active sulfidic back-arc basin	SWP	23°13'00.00"S, 176°38'00.00"W	Not given
		<i>Bathymodiolus</i> aff. <i>brevior</i> / Thiotrophy, Heterotrophy (endosymbiont (gill))	North Fiji Back- Arc Basin/ sulfidic vents	SWP	16°59'00.00"S, 173°43'00.00"W	16°59'39.00"S, 173°54'43.80"E
		<i>Bathymodiolus elongatus</i> / Thiotrophy, Heterotrophy (endosymbiont (gill))	Lau Basin/ active back-arc basin rich in sulfide	SWP	23°13'00.00"S, 176°38'00.00"W	Not given
		“	Fiji Arc Basin/ sulfidic vents	SWP	16°59'00.00"S, 173°43'00.00"W	Not given
		<i>Bathymodiolus thermophilus</i> / Thiotrophy, Heterotrophy (endosymbiont (gill))	Rose Garden (Galápagos Rift)/ sulfidic vents	EP	0°48'14.82"N, 86°13'28.68"W	0°47'00.00"N, 86°07'00.00"W
			Rose Garden	EP	0°48'14.82"N,	0°47'00.00"N,

			(Galápagos Rift)/ sulfidic vents		86°13'28.68"W	86°07'00.00"W
			Galápagos Rift/ sulfidic vents	EP	0°48'14.82"N, 86°13'28.68"W	Not given
		<i>Bathymodiolus</i> sp. 1/ Thiotrophy, Methanotrophy, Heterotrophy (endosymbiont (gill))	Menez Gwen (MAR)/ active chimneys rich in sulfide and methane	MA	37°50'21.60"N, 31°31'16.80"W	37°50'00.00"N, 31°31'00.00"W
		<i>Bathymodiolus</i> sp. 2/ Thiotrophy, Heterotrophy (endosymbiont (gill))	Iheya vent (Okinawa Trough)/ active back- arc basin rich in sulfide	WP	27°47'13.20"N, 126°53'54.36"E	27°47'13.20"N, 126°53'54.36"E
		<i>Bathymodiolus</i> sp. 3/ Thiotrophy, Methanotrophy, Heterotrophy (endosymbiont (gill))	Eiffel Tower, Sintra (Lucky strike, MAR)/ active chimneys rich in sulfide and methane	MA	37°17'30.00"N, 32°16'30.00"W	37°17'30.00"N, 32°16'30.00"W
		<i>Helicoradomenia</i> cf. <i>acredema</i> Thiotrophy, Heterotrophy (epibiont), endosymbiont (cuticle))	TICA (EPR)/ basaltic sulfidic vents	EP	9°50'26.82"N, 104°17'29.58"W	9°50'26.82"N, 104°17'29.58"W
		<i>Helicoradomenia</i> sp. 1 Thiotrophy, Heterotrophy (epibiont), endosymbiont (cuticle))	TICA (EPR)/ basaltic sulfidic vents	EP	9°50'26.82"N, 104°17'29.58"W	9°50'26.82"N, 104°17'29.58"W
		<i>Bathymodiolus</i> <i>puteoserpentis</i> / Thiotrophy, Methanotrophy, Heterotrophy (endosymbiont (gill))	Snake pit (MAR)/ active vents rich in sulfide and methane	MA	23°22'12.00"N, 44°57'02.40"W	23°22'12.00"N, 44°57'02.40"W
		“	“	“	23°22'12.00"N, 44°57'02.40"W	23°22'06.00"N, 44°56'54.60"W
		“	“	“	23°22'12.00"N, 44°57'02.40"W	23°22'07.80"N, 44°57'00.00"W
		“	“	“	23°22'12.00"N, 44°57'02.40"W	23°23'00.00"N, 44°56'00.00"W
		“	Logatchev (MAR)/ active sulfidic vents	MA	14°45'18.60"N, 44°58'44.40"W	14°45'18.60"N, 44°58'44.40"W

		“	“	“	14°45'18.60"N, 44°58'44.40"W	14°45'16.20"N, 44°58'42.00"W
		“	“	“	14°45'18.60"N, 44°58'44.40"W	14°45'25.20"N, 44°58'47.40"W
		“	“	“	14°45'18.60"N, 44°58'44.40"W	14°45'11.40"N, 44°58'44.40"W
		<i>Bathymodiolus</i> aff. <i>puteoserpentis</i> / Thiotrophy, Methanotrophy, Heterotrophy (endosymbiont (gill))	Irina-2 (Logatchev, MAR)/ active sulfidic vents	MA	14°45'18.60"N, 44°58'44.40"W	14°45'12.00"N, 44°58'48.00"W
		Unidentified mytilid (endosymbiont (gill))	Snake pit (MAR)/ active vents rich in sulfide and methane	MA	23°22'12.00"N, 44°57'02.40"W	23°23'00.00"N, 44°58'00.00"W
	Arthropoda	<i>Rimicaris exoculata</i> / Thiotrophy, Heterotrophy (epibiont (cephalothorax, maxillae, carapace, legs))	Snake Pit (MAR)/ active vents rich in sulfide and methane	MA	23°22'12.00"N, 44°57'02.40"W	Not given
		“	TAG (MAR)/ active sulfidic vents	MA	26°08'00.00"N, 44°49'00.00"W	26°08'00.00"N, 44°49'00.00"W

**Supplementary Table 2a.** Potential chemoautotrophic bacterial associates, hosts and dominant geochemistry of their vent habitats

EPR: East Pacific Rise, JFR: Juan de Fuca Ridge, MAR: Mid Atlantic Ridge, CIR: Central Indian Ridge. RTJ: Rodriguez Triple Junction, MA: Mid Atlantic; SI: South Indian Ocean; CI: Central Indian Ocean; EP: East Pacific; WP: West Pacific; SP: South Pacific; SWP: South West Pacific; PAR: Pacific Antarctic Ridge; ‘Mode of nutrition’ of the host is not given where there is ambiguity



Bacterial associate	Host Phylum	Host scientific name/ mode of nutrition (symbiont type (organ))	Location	Region	Latitude and longitude used for map to minimize clustering/ overlap	Latitude and longitude (as published)
<i>α-Proteobacteria</i>	Annelida	<i>Lamellibrachia</i> sp. 1/ Thiotrophy (endosymbiont (trophosome))	Sagami Trough (Japan)/seep rich in sulfide, methane and ammonia	WP	35°00'12.00"N, 139°20'30.00"E	35°00'12.00"N, 139°20'30.00"E
		<i>Lamellibrachia</i> sp. 5/ Thiotrophy (endosymbiont (trophosome))	Off-Hatsushima (Sagami Bay, Japan)/seep rich in sulfide, methane and ammonia	WP	35°00'12.00"N, 139°20'30.00"E	Not given
<i>β-Proteobacteria</i>	Annelida	<i>Lamellibrachia</i> sp. 5/ Thiotrophy (endosymbiont (trophosome))	Off-Hatsushima (Sagami Bay, Japan)/ seep rich in sulfide, methane and ammonia	WP	35°00'12.00"N, 139°20'30.00"E	Not given
<i>γ-Proteobacteria</i>	Annelida	<i>Escarpia spicata</i> / Thiotrophy (endosymbiont (trophosome))	Guaymas Basin/ seep rich in sulfide and methane	EP	26°59'00.00"N, 111°24'00.00"W	26°59'00.00"N, 111°24'00.00"W
		<i>Escarpia</i> sp./ Thiotrophy (endosymbiont (trophosome))	Chapopote (GoM)/ seep rich in sulfide, methane and ammonia	WA	21°53.98'00"N, 93°26.12'00"W	21°53.98'00"N, 93°26.12'00"W
		<i>Lamellibrachia</i> sp. 5/ Thiotrophy (endosymbiont (trophosome))	Off-Hatsushima (Sagami Bay, Japan)/ seep rich in sulfide, methane and ammonia	WP	35°00'12.00"N, 139°20'30.00"E	Not given
		<i>Lamellibrachia</i> sp. 6/ Thiotrophy (endosymbiont (trophosome))	Green Canyon (GoM)/ seep rich in sulfide, methane and ammonia	WA	22°32'00.00"S, 176°43'00.00"W	22°32'00.00"S, 176°43'00.00"W
		<i>Seepiophila jonesi</i> / Thiotrophy (endosymbiont (trophosome))	GoM/ seep rich in sulfide, methane and ammonia	WA	25°18'15.49"N, 90°03'57.31"W	Not given
		<i>Sclerolinum contortum</i> / Thiotrophy (endosymbiont)	HMMV (Barents Sea)/ seep rich in sulfide and	Ar	72°0.15'00"N, 14°44.17'00"E	72°0.15'00"N, 14°44.17'00"E

		(trophosome))	methane			
		<i>Oligobrachia haakonmosbiensis</i> / Thiotrophy (endosymbiont)	HMMV (Barents Sea)/ seep rich in sulfide and methane	Ar	72°0.15'00"N, 14°44.17'00"E	72°0.15'00"N, 14°44.17'00"E
		<i>Oligobrachia mashikoi</i> / Thiotrophy (endosymbiont)	Tsukumo Bay (Japan)/ seep rich in sulfide and methane	WP	37°18'29"N, 137°14'29"E	37°18'29"N 137°14'29"E
	Mollusca	<i>Calymene aff. angulata</i> / Thiotrophy (endosymbiont (gill))	Monterey Bay, California/ seep rich in sulfide, sulfate and methane	EP	36°46'31.80"N, 122°05'12.60"W	36°47'00.00"N, 122°05'00.00"W
		<i>Calymene elongata</i> / Thiotrophy (endosymbiont (gills))	Off California/ methane seep	EP	34°00'00.00"N, 120°00'00.00"W	34°00'00.00"N, 120°00'00.00"W
		<i>Calymene kilmeri</i> / Thiotrophy (endosymbiont (gills))	Off Oregon/ methane seep	EP	44°00'00.00"N, 125°00'00.00"W	44°00'00.00"N, 125°00'00.00"W
		“	Monterey Canyon/ seep rich in sulfide, sulfate and methane	EP	36°46'31.80"N, 122°05'12.60"W	36°46'31.80"N, 122°05'12.60"W
		<i>Calymene packardana</i> Thiotrophy (endosymbiont (gill))	Monterey Bay, California/ seep rich in sulfide, sulfate and methane	EP	36°46'31.80"N, 122°05'12.60"W	36°47'00.00"N, 122°05'00.00"W
		<i>Calymene Phaseoliformis</i> / Thiotrophy (endosymbiont (gill))	Japan Trench/ seep rich in sulfate, methane and ammonia	WP	40°00'00.00"N, 144°00'00.00"E	40°00'00.00"N, 144°00'00.00"E
		<i>Calymene kawamurai</i> / Thiotrophy (endosymbiont (gill))	Nankai Trough, Okinawa Trough (Japan)/ methane seep	WP	32°32'11.5"N, 135°49'56.7"E	Not given
		<i>Calymene laubieri</i> / Thiotrophy (endosymbiont (gill))	Nankai Trough, Okinawa Trough (Japan)/ methane seep	WP	32°32'11.5"N, 135°49'56.7"E	Not given
		<i>Calymene</i> n.sp./ Thiotrophy (endosymbiont (gill))	WFE/ methane seep	WA	26°00'00.00"N, 84°00'00.00"W	26°00'00.00"N, 84°00'00.00"W

		<i>Calypptogena valdiviae</i> / Thiotrophy (endosymbiont (gill))	Gulf of Guinea/ Methane seep	EA	1°34.65'00" S, 8°32.91'00"E	1°34.65'00" S 8°32.91'00"E
		<i>Isorropodon bigoti</i> / Thiotrophy (endosymbiont (gill))	Gulf of Guinea/ Methane seep	EA	1°34.65'00" S, 8°32.91'00"E	1°34.65'00" S 8°32.91'00"E
		<i>Isorropodon megadesmus</i> / Thiotrophy (endosymbiont (gill))	Gulf of Guinea/ Methane seep	EA	1°34.65'00" S, 8°32.91'00"E	1°34.65'00" S 8°32.91'00"E
		<i>Isorropodon perplexum</i> / Thiotrophy (endosymbiont (gill))	Gulf of Guinea/ Methane seep	EA	1°34.65'00" S, 8°32.91'00"E	1°34.65'00" S 8°32.91'00"E
		<i>Elenaconcha guiness</i> /Thiotrophy (endosymbiont (gill))	Gulf of Guinea/ Methane seep	EA	1°34.65'00" S, 8°32.91'00"E	1°34.65'00" S 8°32.91'00"E
		<i>Vesicomys stearnsii</i> / Thiotrophy (endosymbiont (gill))	Monterey Bay, California/ Seep rich in sulfide, sulfate and methane	EP	36°46'31.80"N, 122°05'12.60"W	Not given
		<i>Lucinoma</i> aff. <i>kazani</i> / Thiotrophy (endosymbiont (gill))	North Alex Mud Volcano (Nile deep sea fan, Eastern Mediterranean) / seep rich in sulfide, methane and ammonia	EM	31°58'12.00"N, 30°08'12.00"E	31°58'12.00"N, 30°08'12.00"E
		“	Pockmarks of the central area (Nile deep sea fan, Eastern Mediterranean) / seeps rich in sulfide, methane and ammonia	EM	32°31'36.00"N, 30°20'42.00"E	32°31'36.00"N, 30°20'42.00"E
		“	Isis mud volcano (Nile deep sea fan, Eastern Mediterranean) / seep rich in sulfide, methane and ammonia	EM	32°21'42.00"N, 31°23'24.00"E	32°21'42.00"N, 31°23'24.00"E

		<i>Maorithyas hadalis</i> / Thiotrophy (endosymbiont (gill))	Japan Trench/ seep rich in sulfate, methane and ammonia	WP	40°00'00.00"N, 144°00'00.00"E	Not given
		<i>Vesicomys lepta</i> Thiotrophy, (endosymbiont (gill))	Monterey Bay, California/ seep rich in sulfide, sulfate and methane	EP	36°46'31.80"N, 122°05'12.60"W	36°00'00.00"N, 122°00'00.00"W
		<i>Bathymodiolus mauritanicus</i> / Thiotrophy, Methanotrophy, Heterotrophy (endosymbiont (gill))	Gabon Continental Margin (Gulf of Guinea, Regab) methane seep	SEA	0°53'00.00"N, 5°28'00.00"W	0°53'00.00"N, 5°28'00.00"W
		<i>Bathymodiolus brooksi</i> / Thiotrophy, Heterotrophy (endosymbiont (gill))	Chapopote (GoM)/ seep rich in sulfide, methane and ammonia	WA	21°53.98'00"N, 93°26.12'00"W	21°53.98'00"N, 93°26.12'00"W
		<i>Bathymodiolus childressi</i> / Methanotrophy, Heterotrophy (endosymbiont (gill))	Alaminos Canyon (GoM)/ seep rich in sulfide, methane and ammonia	WA	26°21.32'00"N, 94°30.12'00"W	26°21.32'00"N, 94°30.12'00"W
		<i>Bathymodiolus aff. boomerang</i> / Methanotrophy, Heterotrophy (endosymbiont (gill))	Gabon continental margin/ methane seep	SEA	0°53'00.00"N, 5°28'00.00"W	Not given
		<i>Bathymodiolus hirtus</i> / Methanotrophy, Heterotrophy (endosymbiont (gill))	Kuroshima Knoll (Japan)/ methane seep	WA	24°07.812'00.00"N, 124°11.539'00.00"E	Not given
		<i>Bathymodiolus</i> sp. 6/ Thiotrophy (endosymbiont (gill))	Regab/ methane seep	SEA	5°52'48.80"S, 9°37'56.51"E	5°52'48.80"S, 9°37'56.51"E
		<i>Idas</i> sp./ Thiotrophy, Methanotrophy (endosymbiont (gill))	Central Province (North of the Nile deep sea fan)/ seeps rich in sulfide, methane and ammonia	EP	32°38'24.00"N, 29°55'00.00"W	32°38'24.00"N, 29°55'00.00"W
<i>ε-Proteobacteria</i>	Annelida	<i>Lamellibrachia</i> sp. 2/ Thiotrophy,	Sagami Bay (Japan)/ seep	WP	35°00'12.00"N, 139°20'30.00"E	Not given

		(endosymbiont (trophosome))	rich in sulfide, methane and ammonia			
<b>Bacteroidetes</b>	Mollusca	<i>Idas</i> sp./ Thiotrophy, Methanotrophy (endosymbiont (gill))	Central Province (North of the Nile deep sea fan)/ seeps rich in sulfide, methane and ammonia	EM	32°38'24.00"N, 29°55'00.00"W	32°38'24.00"N, 29°55'00.00"W
<b>Unaffiliated bacteria</b>	Porifera	<i>Cladorhiza</i> sp./ Methanotrophy, Heterotrophy (epibiont (matrix), endosymbiont (mesohyl))	Mud volcanoes (Barbados Trench)/ methane seep	WA	13°49'36.00"N, 57°39'58.00"W	13°49'36.00"N, 57°39'58.00"W
	Annelida	<i>Lamellibrachia</i> sp. 3/ Thiotrophy, (endosymbiont (trophosome))	Off-Hatsushima (Sagami Bay, Japan)/ seep rich in sulfide, methane and ammonia	WP	35°00'12.00"N, 139°20'30.00"E	Not given
		<i>Lamellibrachia</i> sp. 4/ Thiotrophy, (endosymbiont (trophosome))	Sagami Trough (Japan)/ seep rich in sulfide, methane and ammonia	WP	35°00'12.00"N, 139°20'30.00"E	Not given
		Unidentified polychaete (endosymbiont)	Louisiana slope (GoM)/ seep rich in sulfide, methane and ammonia	WA	27°41'00.00"N, 91°32'00.00"W	Not given
	Mollusca	<i>Calymptogena fossajaponica</i> / Thiotrophy (endosymbiont (gill))	Japan Trench/ seep rich in sulfate, methane and ammonia	WP	40°00'00.00"N, 144°00'00.00"E	Not given
		<i>Calymptogena fausta</i> Thiotrophy (endosymbiont)	Nankai Trough, Japan/ methane seep	WP	32°32'11.5"N, 135°49'56.7"E	Not given
		<i>Calymptogena okutani</i> / Thiotrophy (endosymbiont (gill))	Sagami Bay/ methane seep	WP	35°00'12.00"N, 139°20'30.00"E	34°57'00.00"N, 139°12'00.00"E
		<i>Calymptogena phaseoliformis</i> Thiotrophy (endosymbiont (gill))	Monterey Canyon/ seep rich in sulfide, sulfate and methane	EP	36°46'31.80"N, 122°05'12.60"W	36°23'00.00"N, 122°53'00.00"W
		<i>Calymptogena Ponderosa</i> Thiotrophy	GoM/ seep rich in sulfide, methane and	WA	25°18'15.49"N, 90°03'57.31"W	27°40'52.80"N, 91°32'06.00"W

		(endosymbiont (gill))	ammonia			
		<i>Calymene bairdii</i> / Thiotrophy (endosymbiont (gill))	Hatsushima site (Sagami Bay, Japan)/seep rich in sulfide, methane and ammonia	WP	35°00'12.00"N, 139°20'30.00"E	34°59'54.00"N, 139°13'36.00"E
		<i>Calymene</i> sp. 1/ Thiotrophy (endosymbiont (gill))	Makran convergent margin (off Pakistan, northern Indian Ocean)/ methane seep	NI	24°33'00.00"N, 64°15'38.40"E	24°33'00.00"N, 64°15'38.40"E
		<i>Calymene</i> sp. 2/ Thiotrophy (endosymbiont (gill))	Southern summit of hydrate ridge (Cascadia convergent margin (off Oregon))/ methane seep	EP	44°34'12.00"N, 125°08'48.00"W	44°34'12.00"N, 125°08'48.00"W
		<i>Calymene</i> sp. 3/ Thiotrophy (endosymbiont (gill))	Mud Mount East (Cascadia convergent margin (off Oregon))/ methane seep	EP	44°34'12.00"N, 125°08'48.00"W	44°40'12.00"N, 125°03'18.00"W
		<i>Calymene</i> sp. 4/ Thiotrophy (endosymbiont (gill))	NW-Knoll (Cascadia convergent margin (off Oregon))/ methane seep	EP	44°34'12.00"N, 125°08'48.00"W	44°43'54.00"N, 125°13'54.00"W
		<i>Pliocardia</i> sp./ Thiotrophy (symbiont)	Jaco Scarp summit (Off Costa Rica)/ methane seep	EP	9°10.36'00.00"N, 84°47.93'00.00"W	Not given
		<i>Conchocele</i> sp./ Thiotrophy, Heterotrophy (endosymbiont (gill))	Sakhalin continental slope (Sea of Okhotsk)/ methane seep	NWP	54°27'00.00"N, 144°05'00.00"E	54°27'00.00"N, 144°05'00.00"E
		<i>Ectenagena extenta</i> / Thiotrophy (endosymbiont (gill))	Monterey Canyon/ seep rich in sulfide, sulfate and methane	EP	36°46'31.80"N, 122°05'12.60"W	36°40'55.20"N, 122°07'12.60"W
		<i>Vesicomya gigas</i> / Thiotrophy, Heterotrophy	Mendocino Fracture Zone/	EP	49°20'03.60"N, 127°39'41.40"W	49°20'03.60"N, 127°39'41.40"W

		(endosymbiont (gill))	methane seep			
		<i>Vesicomya</i> sp.mt.I/ Thiotrophy (endosymbiont (gill))	Monterey Bay (California)/ seep rich in sulfide, sulfate and methane	EP	36°46'31.80"N, 122°05'12.60"W	36°47'00.00"N, 122°05'00.00"W
		<i>Vesicomya</i> sp.mt.III/ Thiotrophy (endosymbiont (gill))	Monterey Bay (California)/ seep rich in sulfide, sulfate and methane	EP	36°46'31.80"N, 122°05'12.60"W	36°37'47.40"N, 122°19'55.20"W
		<i>Acharax</i> sp. 1/ Thiotrophy (endosymbiont (gill))	Makran convergent margin (off Pakistan, northern Indian Ocean)/ methane seep	NI	24°33'00.00"N, 64°15'38.40"E	24°33'00.00"N, 64°15'38.40"E
		<i>Acharax</i> sp. 2/ Thiotrophy (endosymbiont (gill))	Sunda fore-arc basin (off Java, eastern Indian Ocean)/ methane seep	EI	7°58'13.75"S, 106°16'26.25"E	7°58'13.75"S, 106°16'26.25"E
		<i>Acharax</i> sp. 3/ Thiotrophy (endosymbiont (gill))	Southern summit of hydrate ridge (Cascadia convergent margin (off Oregon, NE Pacific))/ methane seep	EP	44°34'12.00"N, 125°08'48.00"W	44°34'12.00"N, 125°08'48.00"W
		“	Mud Mount East (Cascadia convergent margin (off Oregon, NE Pacific))/ methane seep	EP	44°34'12.00"N, 125°08'48.00"W	44°40'12.00"N, 125°03'18.00"W
		“	NW-Knoll (Cascadia convergent margin (off Oregon, NE Pacific))/ methane seep	EP	44°34'12.00"N, 125°08'48.00"W	44°43'54.00"N, 125°13'54.00"W
		<i>Bathymodiolus heckerae</i> / Thiotrophy, Methanotrophy, Heterotrophy (endosymbiont (gill))	WFE/ seep rich in sulfide and methane	WA	26°00'00.00"N, 84°00'00.00"W	26°02'00.00"N, 84°55'00.00"W
		<i>Bathymodiolus</i>	Hatsushima	WP	35°00'12.00"N,	34°59'54.00"N,

		<i>platifrons</i> / Methanotrophy, Heterotrophy (endosymbiont (gill))	site (Sagami Bay, Japan)/ seep rich in sulfide, ammonia and methane		139°20'30.00"E	139°13'36.00"E
		<i>Bathymodiolus childressi</i> Methanotrophy, Heterotrophy (endosymbiont (gill))	Louisiana Slope (GoM)/ seep rich in sulfide, methane and ammonia	WA	27°41'00.00"N, 91°32'00.00"W	27°41'00.00"N, 91°32'00.00"W
		“	Alaminos Canyon (GoM)/ seep rich in sulfide, methane and ammonia	WA	26°30'00.00"N, 94°35'00.00"W	26°30'00.00"N, 94°35'00.00"W
		“	GoM/ seep rich in sulfide, methane and ammonia	WA	25°18'15.49"N, 90°03'57.31"W	Not given
		“	GoM/seep rich in sulfide, methane and ammonia	WA	25°18'15.49"N, 90°03'57.31"W	Not given

**Supplementary Table 2b.** Potential chemoautotrophic bacterial associates, hosts and dominant geochemistry of their seep habitats

GoM: Gulf of Mexico, WFE: Western Florida Escarpment, WA: West Atlantic; SEA: South East Atlantic; EM: East Mediterranean; EI: East Indian Ocean; NI: North Indian Ocean; EP: East Pacific; WP: West Pacific; NWP: North West Pacific. ‘Mode of nutrition’ is not given wherever there is ambiguity