depth (e.g. Norwegian Sea), there is little evidence of zonation in the deep-sea fishes. Instead each species has a depth range which can extend over several thousand meters, as in the cut-throat eel (*Synaphobranchus kaupi*) or over a few hundred meters, as in the tripod fish (*Bathypterois dubius*) (both examples from the north-east Atlantic). The 'bigger-deeper' phenomenon is a common feature among the deep-water demersal fishes, although it might be more correctly referred to as 'smaller-shallower'. The juveniles of many of the demersal fishes of the continental slopes live at shallower depths than the adults. While in some regions the horizontal distribution of a species can be well documented there is little information on stock discrimination. With present technology it is difficult to tag, release, and recapture deep-water fishes and therefore there is very little information on the movements of deep-water fishes. Some of the commercial deep-water fisheries exist because they often target spawning aggregations, such as orange roughy in the South Pacific and blue ling (*Molva dypterygia*) in the North Atlantic. Some of the shark species are often found in single sex shoals, and in the exploited leafscale gulper shark (*Centrophorus squamosus*) of the North Atlantic the gravid females have never been found. The juveniles of many demersal species have never been found in trawl surveys, which suggests that there are separate nursery grounds or that they occur higher in the water column and are not sampled by bottom trawls.

See also

Bioluminescence. Deep-sea Fishes. Demersal Species Fisheries. Fish Migration, Vertical. Fish Reproduction. Fish Schooling. Mesopelagic Fishes. Open Ocean Fisheries for Deep-water Species. Upwelling Ecosystems.

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DEEP-SEA RIDGES, MICROBIOLOGY

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Introduction

Microbes are central to deep-sea ridge ecosystems. Here, in the absence of light energy, the geochemical energy is the primary energy source for microbial growth. These microbes gain energy from oxidation of inorganic compounds such as sulfide and are referred to as chemolithotrophs. Chemolithotrophy or chemosynthesis is the basis of the primary productivity at deep-sea hydrothermal vents, and its discovery challenged our traditional view that all ecosystems were driven by light energy and photosynthesis. The chemolithotrophic microbes are found free-living as well as associated as symbionts with the invertebrates. Additionally, heterotrophic microbes are present that utilize the abundant organic carbon available as a result of the high productivity of these ecosystems.

Many of the microbiological discoveries of ocean ridges were gleaned through studying microbial processes or trying to grow novel microbes from these environments. More recently, however, a much more comprehensive picture of the diversity of deep-sea vent microbes is emerging owing to culture-independent diversity assessments. This article will indicate how these different approaches have provided a complementary approach to understanding the dynamics of microbes in deep ocean ridge ecosystems.

Geological Setting

Hydrothermal venting occurs both in the terrestrial and marine environments, primarily as a direct result of plate tectonic movement. Divergent boundaries (spreading centers) and convergent margins that produce island arcs are two areas where heat release occurs from the ocean crust, generating high-temperature water activity. At spreading centers, as the tectonic plates are pulled apart, hot molten rock deep within the earth will rise up and fill the gap. Additionally, fissures develop in the crust, and sea water percolates into the crust, reacts with the surrounding rocks, and is heated. This chemically altered sea water will eventually be forced back convectively to the ocean floor as superheated, highly reduced, hydrothermal fluid rich in gases and minerals (**Figure 1**) – primary energy sources for microbial growth. Back-arc basins form along active plate margins when old ocean crust is subducted beneath the continental plate. Water can move with the sinking oceanic crust and react with the mantle. As the hydrothermal fluid chemistry is a record of its path within the earth's crust, these back-arc spreading centers produce heterogeneous hydrothermal fluid chemistry relative to the more stable mid-ocean ridge chemistries. A third basic type of tectonic activity that results in hydrothermal activity comprises 'hot spots' and seamounts. Hotspots are places where plumes of hot molten rock may begin deep within the mantle and rise up through the entire mantle and crust.

Figure 2 identifies some of the hydrothermal areas that have been studied. Back-arc basins and seamounts are of particular interest for vent biologists as they represent examples of possible island biogeography for vent-related species. The differences in chemistries of these different systems may result in selecting for different physiological types of microbes, but few ecological studies have been addressed to explore such microbial ecological questions in marine vent environments.

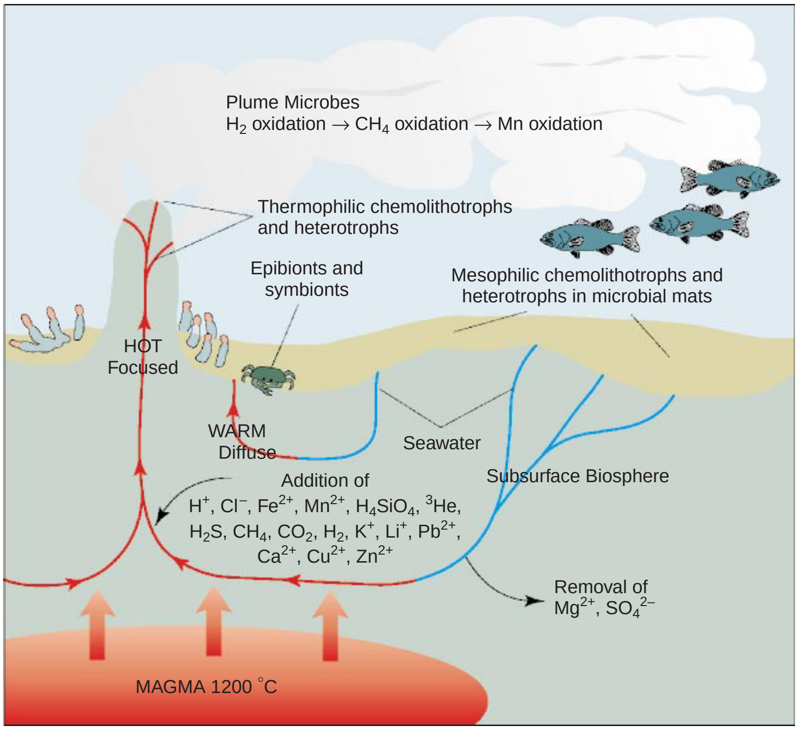

Figure 1 Diagrammatic cross-section of a seafloor spreading center. The vertical is not to scale. The arrows indicate direction of fluid flow.

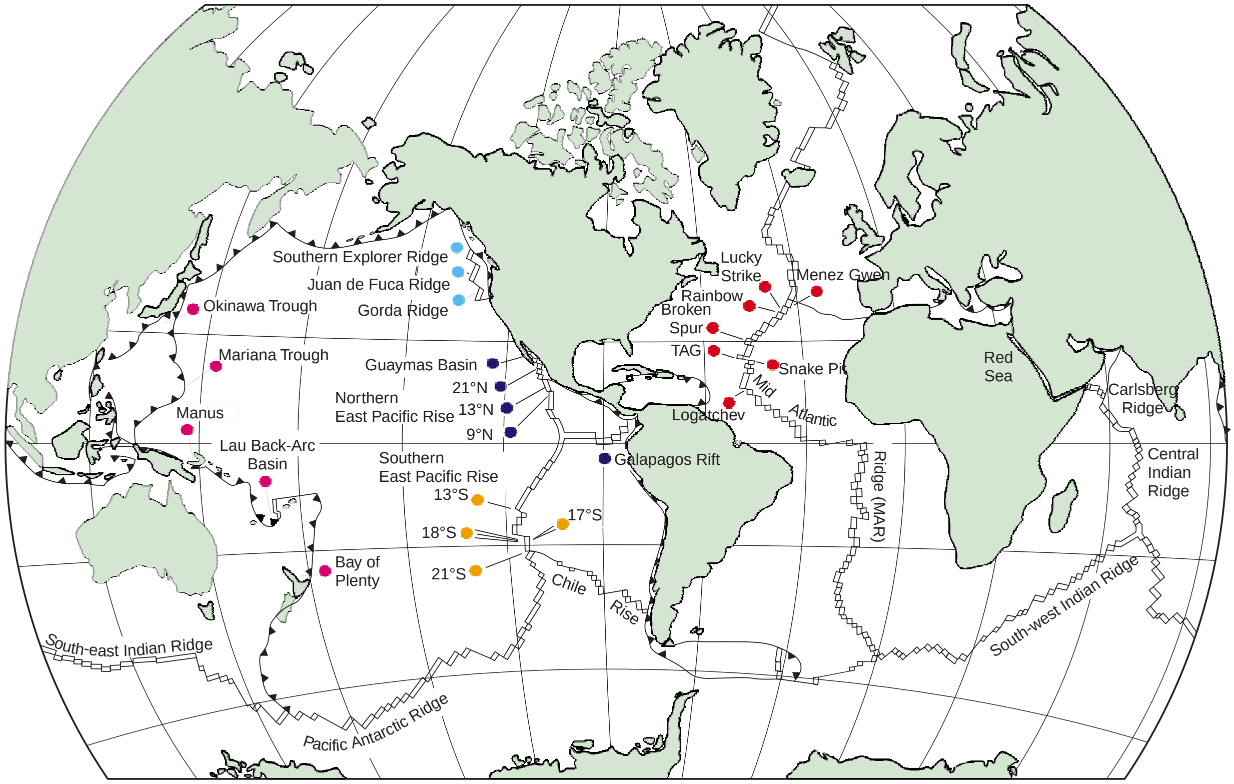

Figure 2 World map depicting some of the known marine hydrothermal vent sites.

Microbial Habitats

Deep-sea hydrothermal vents represent one of the most chemically diverse habitats for microbial growth. The geochemical and thermal gradients provide a wide range of possible niches for microbes, with a continuum from oxic to anoxic, pH 3.5 to 8.0, 4°C to 400°C, and chemical gradients that mirror the physical gradients (**Figure 1**). These gradients provide a geochemical disequilibrium, which in turn provides chemical energy for microbial growth. Therefore, there are a multitude of different combinations of electron donors and acceptors and carbon sources for microbial growth. The microbes can be psychrophilic (able to grow best below 15°C), mesophilic (growing best between 25 and 40°C), or thermophilic (growing best above 45°C). Hyperthermophiles are thermophiles that grow best at temperatures above 80°C. The mesophilic microbes can be free-living, growing in the cold nutrient-rich sea water surrounding deep-sea vents in areas such as the buoyant plume that results as the hydrothermal fluid rises into the water column and disperses laterally or microbial mats covering sediments and rocks. Other mesophilic microbes at vents include epibionts that attach to the invertebrates colonizing the vents, or endosymbionts found in specialized intracellular compartments in the invertebrates. Thermophilic microbes are restricted to areas where there is close contact with the high-temperature hydrothermal fluid. This may be in the porous sulfidic rocks or chimney structures, in the mineral sediments covering diffuse flow areas, or perhaps in the subsurface environment. Consider, for example, a cross-section through a porous hydrothermal chimney (**Figure 3**). From fluid flow and geochemical models one can predict the potential physiological types that can inhabit this thermal environment. However, by far the more abundant niches for microbial growth at deep-sea vents are in the aerobic zone surrounding the high-temperature venting, and it has been estimated that microbial processes other than sulfide oxidation may account for as little as 4% of the total microbial productivity (in terms of energy yield) of the vent ecosystem.

Microbial Diversity at Deep-sea Vents

Measures of Diversity

Traditionally, microbial diversity was measured by what could be grown and identified in the

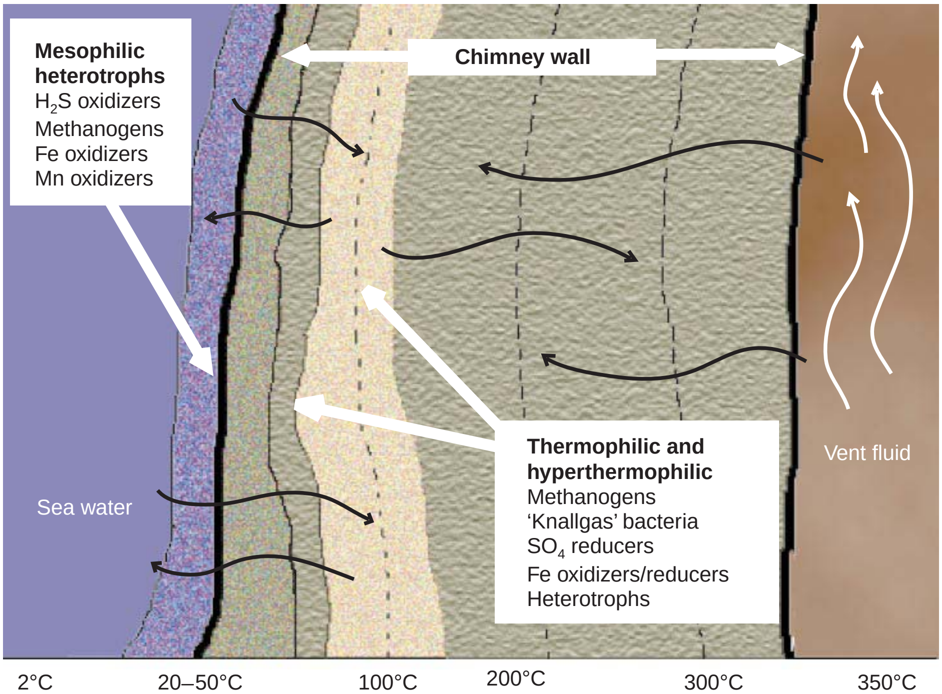

Figure 3 Schematic representation of a hydrothermal vent chimney showing possible microniches for chemolithotrophic thermophiles. (Modified from McCollom and Shock (1997).)

laboratory. This approach is heavily biased toward how successfully we are able to understand the conditions that support growth of deep-sea microbes. However, the use of nucleotide sequence comparisons of the small subunit rRNA (16S rRNA in *Archaea* and *Bacteria*), has provided an evolutionary molecule by which all life can be compared. With this emerged the 'Universal Tree of Life,' in which all life is placed within a phylogenetic framework of three domains, the *Archaea*, the *Bacteria* (both prokaryotic lacking a cell nucleus), and the *Eukarya* (all eukaryotes). Since the 16S rRNA molecule is present in all Bacteria and Archaea, one can extract DNA from an environmental sample, amplify the gene that encodes for the 16S rRNA using the polymerase chain reaction (PCR), sort the different genes from the different microbes by cloning, and sequence the individual genes that represent the 'fingerprints' of each phylogenetically distinct microbe in the environment. These sequences can be placed in the phylogenetic framework of a tree, and the diversity of the microbes in the environment can then be identified without the reliance on trying to grow them in the laboratory. This molecular phylogenetic approach to identifying microbes that have previously resisted cultivation has revolutionized our perception of the microbial world. For example, many symbionts cannot grow without their hosts. All of the endosymbionts of deep-sea hydrothermal invertebrates were identified using these molecular phylogenetic approaches.

Endosymbionts

The initial discovery of deep-sea hydrothermal vents more than 20 years ago was accompanied by the discovery of a deep-sea oasis for invertebrate life. The invertebrates included large bivalves and giant tubeworms (*Riftia pachyptila*), and later it was shown that many of the invertebrates also harbored endosymbionts. The high productivity of these deep-sea oases has been linked to the successful associations between the chemoautotrophic endosymbionts and their macroinvertebrate hosts.

Most of the endosymbionts are chemolithotrophic sulfur-oxidizing gamma *Proteobacteria*. *Riftia pachyptila*, the giant tubeworm, houses its symbionts in a specialized structure called the trophosome. The worm is mouthless and gutless and the densities of the endosymbionts can be up to $\sim 3.7 \times 10^9$ cells per gram of trophosome. The endosymbionts require sulfide, oxygen, and carbon dioxide. Sulfide oxidation provides the energy for carbon dioxide fixation. The host supplies the microbes with these gases, whereas the symbiont provides the host with a continuous supply of organic carbon. The host transports high concentrations of oxygen and hydrogen sulfide, in the less toxic HS^- form, via an unusual hemoglobin. These gases are taken directly via the host's vascular system to the endosymbionts. Carbon dioxide is transported freely as CO_2 or HCO_3^- in the host's blood without the aid of hemoglobin.

The sulfur-oxidizing endosymbionts associated with many of the deep-sea vent invertebrates highlighted the importance of chemoautotrophy in the overall productivity of hydrothermal ecosystems. In areas where methane is prevalent, another endosymbiotic relationship between a microbe and invertebrate also exists, namely between a giant bathymodiolid mussel and methylotrophic (methane-oxidizing) endosymbionts. The symbionts in this methane-based symbiosis are housed in the gill tissues and the symbionts have the stacked internal membrane structures diagnostic of methylotrophs. In some cases where methane and sulfide are in abundance, such as at the Mid-Atlantic Ridge (Snake Pit), the mussels have two different symbionts in their gills, the sulfur-oxidizing symbionts and the methylotrophs. Clearly this provides the mussels with the metabolic versatility to capitalize on the different potential energy sources that may be available any given time at a vent environment.

Using molecular techniques, it has been shown that the symbionts of the bivalves such as the giant clams and mussels are transferred vertically, viz. from adults to offspring via the ovarian tissue and oocytes. In tubeworms, however, there is no evidence to support the transmission of symbionts from the adult through the eggs and larvae. In this case, it is thought that the tubeworm has to acquire its symbionts from the environment, and the larval tubeworms probably do so by ingestion of free-living forms of the symbionts.

So how did the symbiotic relationships evolve in the bivalves? There is evidence from molecular phylogenetic comparisons of host phylogenies and the symbiont phylogenies that in the vesicomyid clam (another symbiotic invertebrate from deep-sea vents) the symbiont and host have coevolved and cospeciated. As additional molecular phylogenetic studies are completed for other host–symbiont relationships, more insight into the population genetics and cospeciation of vent invertebrates will no doubt be gleaned.

Epibionts

Several studies have explored the diversity of epibionts associated with hydrothermal invertebrates. Initial microscopic observations of invertebrates, such as with the polychaete *Alvinella pompejana* and the vent shrimp *Rimicaris exoculata*, revealed dense colonization of microbiota associated with dorsal integuments (**Figure 4**) and mouth parts, respectively. In both cases, the identity of these epibionts was determined using culture-independent approaches and 16S rRNA phylogenetic analysis. These epibionts belong to the epsilon *Proteobacteria*, a group that appears to be prevalent both as epibionts and as free-living microbes in the hydrothermal vent environment. The role these epibionts have in relation to their hosts is unclear; however, they may have some nutritional benefit for their host. The dominant epibiont associated with *Alvinella pompejana* showed some interesting variation between the populations colonizing the anterior and posterior parts of the worm. This small variation in 16S rRNA sequence was not enough to designate the two different population types as different species, but the variation may represent a variation in ecological niche. Recently it was proposed that microbiologists take on a 'natural concept' for microbial species, in which environmental gradients provide different ecological niches and cause environmentally induced genetic variation resulting in different ecotypes or ecospecies.

Figure 4 An *Alvinella pompejana* on a petri plate. Note the white microbial filaments covering the parapodia; these have been identified using 16S rRNA techniques and belong to the epsilon *Proteobacteria.*

Free-living Microbial Diversity

Mesophiles The rising particle- and nutrient-rich hydrothermal fluid forms the hydrothermal plume that can be detected many kilometers away from the actual vent site. This buoyant plume is enriched in reduced compounds and provides ecological niches for a succession of different metabolic types, laterally and further from the site of venting. Initial rapid hydrogen oxidation takes place, then methane oxidation, and finally manganese oxidation. The shifts in the microbial community laterally along the hydrothermal source are being investigated.

Immediately surrounding the deep-sea vents is a very diverse and dense (up to 10^9 cells per ml) community of microbes that range from obligate chemolithotrophs to heterotrophs. Much of the initial research on these communities focused on the sulfur-oxdizers that form visible microbial mats such as those seen at Guaymas Basin (**Figure 5**). These communities are dominated by large filaments belonging to the genera *Beggiatoa* and *Thiothrix*. Like its close relatives *Thiomargarita* and *Thioplaca*, *Beggiatoa*, has very large cells, much of which is devoid of cytoplasm. The vacuolar space is where nitrate can accumulate. These organisms can couple anoxic–oxidation of H_2S with nitrate reduction, so they can occupy the anoxic–oxic water interface.

Several new surprises emerged using a molecular phylogenetic approach to assess the microbial diversity in a mat associated with the active deep-sea hydrothermal system at Pele's vents (Loihi Seamount, Hawaii). Not only did the epsilon proteobacteria (similar to the epibiont described above) predominate in these mats, but also a wide diversity of *Archaea* were detected, closely related to *Archaea* from the marine planktonic environment and coastal sediments. This study further supported the growing evidence that archaea are ubiquitous and not restricted to extreme environments.

Perhaps one of the most significant discoveries made regarding mesophilic microbial activity at deep-sea hydrothermal vents was the discovery of microbes that produce copious amounts of inorganic filaments of sulfur. *Arcobacter*-related isolates are able to produce filamentous sulfur at the sulfide–oxygen interface of a gradient and are probably responsible for the white flocculent material (floc) that covers fresh basalt within weeks following an eruption. These microbes may also proliferate in the shallow subsurface and produce the sulfur filaments in areas where hydrothermal fluid is mixing with oxygenated sea water. If an eruption occurs, this flocculent material is then dispersed onto the ocean floor (**Figure 6**).

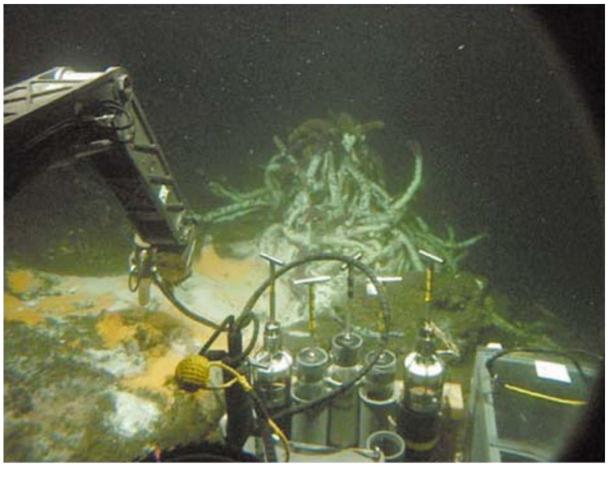

Figure 5 An extensive microbial mat surrounding a clump of *Riftia pachypitila* in Guaymas Basin, Mexico. The sampling basket and arm of submersible *Alvin* are in the foreground. (Photograph by A.-L. Reysenbach, S. Cary, and G.W. Luther.)

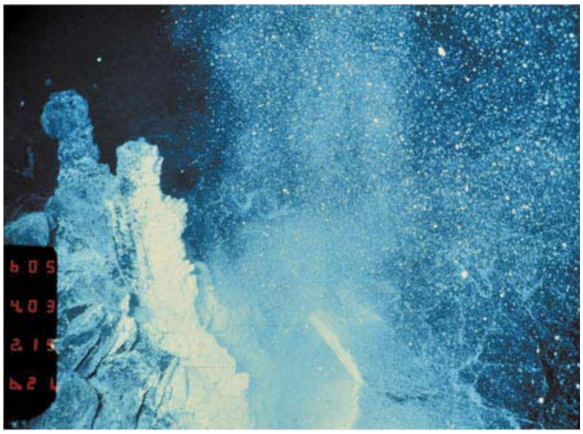

Figure 6 Biogenic flocculent material (floc) in the water column surrounding a newly erupted vent field at 9°N on the East Pacific rise. (Photograph by R. Haymon and D. Fornari, courtesy T. Shank.)

Thermophiles An emerging theme with studies of microbial diversity at deep-sea hydrothermal vents is that the thermophiles that have been obtained in cultures are only a very minor component of the diversity of thermophiles at deep-sea vents. Many of the enrichment cultures have focused on microbes that grow best above 80°C (hyperthermophiles). Most of these organisms fall within the *Archaea*, and include over 20 different reports of new members of the heterotrophic and sulfur-reducing *Thermococcales*. Other archaea that have been isolated include thermophilic methanogens such as *Methanococcus jannaschii* (whose genome was recently fully sequenced) and *Methanopyrus*, and sulfate-reducing archaea of the order *Archaeoglobales*. Other *Archaeal* isolates obtained from deep-sea vents are the facultatively aerobic obligate chemolithoautotroph *Pyrolobus fumarii* that was obtained from a hydrothermal chimney sample and grows up to 113°C, the highest temperature recorded for a microbe growing in laboratory culture.

Surprisingly few thermophilic *Bacteria* have been obtained from deep-sea vents; however, culture-independent approaches may change this perception. Thermophilic *Bacillus* and *Thermus* species have been reported from deep-sea vents, as have members of sheathed thermophilic heterotrophs, the *Thermotogales*. More recently, and perhaps more significantly, representatives of two new lineages never previously reported from vents have been isolated. One, named *Desulfurobacterium*, is the only sulfur-reducing obligate chemolithotrophic thermophile in the domain *Bacteria*. Additional isolates of this group have confirmed that it may represent a new order. A second lineage, relatively closely related to the deeply branching *Aquificales* lineage, has also been isolated and is a microaerophilic hydrogen oxidizer.

Interestingly, this *Aquificales* lineage was first recognized as existing at deep-sea vents by analyzing the diversity associated with the deployment of an *in situ* growth chamber using a culture-independent approach. This chamber is placed on top of a hydrothermal vent for a predetermined time. The fluid flows through the chamber, and microbes can colonize surfaces that are placed in the chamber. Upon retrieval, the chamber is brought back to the surface and the diversity of organisms that are present in the chamber is analyzed using DNA-based techniques. Several interesting surprises emerged from one such study. Not only were there novel bacterial lineages prevalent in this environment, but the epsilon *Proteobacteria* also thrived in this chamber, raising the question whether these prevalent types are perhaps thermophilic inhabitants of deep-sea vents. Additionally, novel archaeal lineages were detected that were related to known iron oxidizers and thermoacidophiles (acid- and heat-loving organisms). In an independent study that explored the archaeal diversity of deep-sea vent chimneys, many novel very deeply diverging lineages were identified. Molecular-based inventories of deep-sea microbial diversity provide the baseline database for rigorous microecological studies at vents. Additionally, these assessments provide guidance for enrichment culturing strategies.

Subsurface Biosphere

It has been estimated that the subsurface is the major biosphere for microbes. Deep-sea hydrothermal vents may represent surface manifestations of this biosphere, and offer 'windows' into the Earth's interior ecosystem. The challenges now are to explore the extent of this biosphere. These include ocean drilling of hydrothermal environments, but also monitoring of microbial, geochemical, and biological changes that occur after new eruptions on the ocean floor. Perhaps one of the most spectacular examples of indirect evidence for an extensive subsurface biosphere at deep-sea vents is the initial biogenic sulfur flocs that are seen being emitted from eruptions (**Figure 6**). As described above, this flocculant material is produced by a mesophilic vibriod microbe that produces strands of filamentous sulfur at the sulfide–oxygen interface.

Deep-sea Hydrothermal Vents and the Origins of Life

As the early Earth accreted more than 4.0 billion years ago, it had a hot volcanic environment and a surface bombarded by asteroids. As the Earth started to cool, hydrothermal activity was extensive, and it is estimated that there was three times more heat flow due to hydrothermal activity in the Archaean Earth, than there is today. Some of the first evidence for life dates back to 3.8 Ga and some of the first microfossils date to about 3.5 Ga when there is no evidence for oxygen in the environment. Additionally, the deepest branching lineages within the tree of life are all represented by thermophilic microbes. These microbes may represent modern day analogues of their thermophilic ancestors. If life did originate in a hot hydrothermal environment, it is likely that the rich CO_2 environment and geochemical disequilibrium associated with the hydrothermal venting was an excellent energy source for the evolution of chemolithotrophs. Prior to the evolution of life, it is also possible that some of the first molecules may have evolved in this environment. A patent attorney and chemist, Gunter Wächterhäuser has proposed an elegant theory of how some of life's precursor molecules could have assembled on positively charged surfaces such as pyrite, an abundant mineral in hydrothermal systems.

Conclusion

Deep-sea hydrothermal ecosystems represent a frontier in science. Microbiologists have only begun to explore this new frontier. With the use of molecular techniques, rapid genomic sequencing, and better methods for sampling microbial niches at ridge ecosystems we will gain a much more comprehensive insight into the roles that microbes play in these ecosystems. Furthermore, understanding how these organisms thrive in this hostile deep environment, how they may influence the precipitation of minerals, and how they may become fossilized into the rock has implications in our search for the evidence of life (past or present) on other planets.

See also

Hydrothermal Vent Biota. Hydrothermal Vent Deposits. Hydrothermal Vent Ecology. Hydrothermal Vent Fauna, Physiology of. Mid-ocean Ridge Seismic Structure.

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DEEP-SEA SEDIMENT DRIFTS

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Introduction

The recognition that sediment flux in the deep ocean basins might be influenced by bottom currents driven by thermohaline circulation was first proposed by the German physical oceanographer George Wust in 1936. His, however, was a lone voice, decried by other physical oceanographers and unheard by most geologists. It was not until the 1960s, following pioneering work by the American team of Bruce Heezen and Charlie Hollister, that the concept once more came before a critical scientific community, but this time with combined geological and oceanographic evidence that was irrefutable.

A seminal paper of 1966 demonstrated the very significant effects of contour-following bottom currents (also known as contour currents) in shaping sedimentation on the deep continental rise off eastern North America. The deposits of these currents soon became known as contourites, and the very large, elongate sediment bodies made up largely of contourites were termed sediment drifts. Both were the result of semipermanent alongslope processes rather than downslope event processes. The ensuing decade saw a profusion of research on contourites and bottom currents in and beneath the present-day oceans, coupled with their inaccurate identification in ancient rocks exposed on land.

By the late 1970s and early 1980s, the present author had helped establish the standard facies models for contourites, and demonstrated the direct link between bottom current strength and nature of the contourite facies, especially grain size. Discrimination was made between contourites and other deep-sea facies, such as turbidites deposited by catastrophic downslope flows and hemipelagites that result from continuous vertical settling in the open ocean. Since then, much progress has been made on the types and distribution of sediment drifts, the nature and variability of bottom currents, and the correct identification of fossil contourites.

Of particular importance has been the work at Cambridge University in decoding the often very subtle signatures captured in contourites in terms of variation in deep-sea paleocirculation. As this is closely linked to climate, the drift successions of ocean basins hold one of the best records of past climate change. This clear environmental significance, together with the recognition that sandy contourites are potential reservoirs for deep-sea oil and gas, has spurred much current research in the field.

Bottom Currents

At the present day, deep-ocean bottom water is formed by the cooling and sinking of surface water