Genetics and Evolution of Deep-Sea Chemosynthetic Microbes and Their Invertebrate Hosts

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The free-living chemosynthetic microbes found in reducing marine environments are faced with the problem of extracting energy from narrow redox zones, absorbing reduced gases from the substrate below and oxygen from the ambient water above. Symbiotic microbes, on the other hand, span broader oxic-anoxic boundaries by exploiting the complex behaviors, physiologies and morphologies of their large eukaryotic hosts. For example, at deep-sea hydrothermal vents and hydrocarbon seeps, large vesicomyid clams and giant siboglinid tubeworms (formerly relegated to the obsolete phylum Vestimentifera) host intracellular gamma-Proteobacteria that oxidize hydrogen sulfide concentrated in vent and seep fluids. Versatile species of bathymodiolin mussels are capable of hosting sulfide or methane oxidizing bacteria, or both types simultaneously. These animals depend on the endosymbionts for most, and in some cases all, of their nutrition.

The modes of symbiont transmission employed by various animal taxa can have profound consequences for genetic, demographic, and evolutionary processes affecting the bacteria and hosts. Vesicomyid clams transmit their endosymbionts vertically through the eggs, a process that leads to clonality of the symbionts and accelerated rates of molecular evolution. Vertical transmission for the past 40 million years has contributed to significant genome reduction in the clam symbiont lineages. These bacteria have lost nearly half their genomic DNA and many of the genes that encode motility components and control of DNA replication, which were required for living in the ambient environment. On the other hand, some genes involved in energy production appear to be enhanced. These vertical endosymbionts and their clam hosts exhibit phylogenetic evidence for cospeciation, but recent evidence suggests that rare "host transfers" may have occurred. In contrast, siboglinid tubeworms acquire their endosymbionts horizontally from the ambient environment. The larval worms are infected when they settle on appropriate substrates that support an infectious stage of the bacterium. The tubeworm symbionts have not undergone genome reduction, and they do not exhibit cospeciation with their hosts. Instead, individual worms may be infected with multiple symbiont strains, and the genetic diversity of these strains is structured geographically according to habitat type, i.e. vents vs. seeps. Nonetheless, present genomic evidence suggests that genes involved in energy production have been enhanced, so co-evolution may be occurring even though cospeciation is not. Various species of bathymodiolin mussels acquire endosymbionts locally from the ambient environment, but a vertical component of transmission cannot be ruled out at this time. No evidence exists for cospeciation and genome sequences have not been obtained for the sulfur-oxidizing or methanotrophic endosymbionts hosted by the mussels.

A challenge facing deep-sea chemosynthetic organisms is finding suitable island-like habitats in the vast ocean basins. Vents and seeps themselves can be relatively ephemeral in time and disconnected in space. Most of the sessile and relatively immobile benthic animals are capable of dispersing by means of a larval stage. Vertical transmission provides invertebrate hosts with "symbiont assurance," because the bacteria "hitchhike" along with host larvae as they disperse and colonize new vent and seep habitats. Nonetheless, this benefit has an associated cost — dispersing larvae might not carry the optimal bacterial strains for habitats in which they might settle. In contrast, host species that acquire symbionts after settlement have the potential to adopt "locally optimal strains" of the symbiont. Major unresolved issues in these studies concern the demographic consequences for the symbionts of the various transmission modes. Strictly vertical symbionts are effectively "enslaved" by the host, eventually losing their ambient phase and control over their own replication. Horizontal symbionts, however, might enhance overall fitness if their numbers are amplified during the symbiont phase and recycle to an ambient phase. Evolutionary trade-offs involved in the transition from horizontal to vertical transmission deserve more study. Future research on deep-sea chemosynthetic symbionts may shed considerable light on these matters.