
Symbiosis of Thioautotrophic Bacteria with *Riftia pachyptila*

Frank J. Stewart, Colleen M. Cavanaugh

1

Introduction

The symbiosis between the giant vestimentiferan tubeworm *Riftia pachyptila* and an intracellular sulfur-oxidizing bacterium still fascinates researchers over 20 years after its discovery. This association, the first between a marine invertebrate and a chemoautotroph to be described, remains the best studied of the symbioses found at sulfide-rich hydrothermal vents. In the decade following the initial description of this symbiosis in 1981 (Cavanaugh et al. 1981; Felbeck 1981), many important studies have helped to characterize the physiological, biochemical, and anatomical adaptations that sustain this association (for other reviews see Fisher 1995; Nelson and Fisher 1995; van Dover 2000; Minic and Herve 2004; van Dover and Lutz 2004; Cavanaugh et al. 2005). Stable carbon isotope data and the absence of a mouth and gut strongly suggest that the adult *R. pachyptila* relies entirely on its bacterial symbionts for nutrition (see Fisher 1995; Nelson and Fisher 1995). These bacteria, which belong to the gamma subdivision of the Proteobacteria (Distel et al. 1988), oxidize reduced inorganic sulfur compounds to obtain energy and reducing power for autotrophic carbon fixation. Given their ability to synthesize C₃ compounds from a C₁ compound using chemical energy, *Riftia* symbionts are referred to as “chemosynthetic” (Cavanaugh et al. 2005).

Over the past 15 years, increasingly sophisticated experimental techniques (e.g., pressure chambers, vascular catheters) and new molecular technologies have dramatically increased our understanding of chemosynthetic symbioses. Specifically, for the *R. pachyptila* symbiosis, researchers provided new insights into the processes by which metabolites (e.g., carbon, sulfide, nitrogen) and waste products (e.g., protons) cycle among host, symbiont, and environment and identified some of the genes and corresponding enzymes involved in both host and symbiont metabolism. In addition, questions of host-

F.J. Stewart, C.M. Cavanaugh (e-mail: cavanaugh@fas.harvard.edu)
Department of Organismic and Evolutionary Biology, Harvard University,
The Biological Laboratories, 16 Divinity Avenue, Cambridge MA 02138, USA

symbiont co-evolution and symbiont transmission were addressed in a number of studies, including recent work that successfully detected the free-living tubeworm protosymbiont using 16S rRNA probes for in situ hybridization (Harmer et al. 2005).

But many questions remain unanswered, particularly regarding the mechanisms of symbiont acquisition by the tubeworm, the spatio-temporal dynamics and processes of symbiont growth and metabolism, and the genetic structure and dispersal of symbiont populations. Our pursuit of answers to these questions has been hindered by the inability to culture the *Riftia* symbiont apart from its host. Fortunately, given the recent advances in genetic techniques and the substantial progress towards sequencing the *Riftia* symbiont genome (R. Feldman and R. Felbeck, pers. comm.), researchers are poised to reveal many of the genes and genetic interactions that guide the physiological, ecological, and evolutionary processes involved in this important, ecosystem-structuring symbiosis. This chapter presents an overview of the physiological ecology and evolution of the *Riftia* symbiosis, with mention of the genes thus far described for this association and the underlying questions that may guide future research.

1.1

Discovery of the *Riftia pachyptila* Symbiosis

Scientific understanding of chemosynthetic symbioses derives in large part from studies of the unique fauna associated with deep-sea hydrothermal vents. Early explorations revealed that, in contrast to common perceptions, the deep benthos was not a cold, food-limited habitat but instead contained flourishing ecosystems localized at hot springs emanating from mid-ocean spreading centers. First characterized along the Galapagos Rift and the East Pacific Rise in the eastern Pacific Ocean, hydrothermal vents were shown to support high concentrations of free-living microorganisms and dense aggregations of invertebrates, including the vestimentiferan tubeworm *Riftia pachyptila* (Fig. 1; Lonsdale 1977; Grassle 1985; van Dover 2000). Scientists first argued that suspended particulate organic matter and free-living chemoautotrophic bacteria were being filtered from the water column to support the abundant invertebrate populations (Lonsdale 1977; Corliss et al. 1979). But studies soon revealed that the adult *R. pachyptila* lacked a mouth and gut (Jones 1981) and was therefore incapable of suspension feeding. It appeared that tubeworm nutrition, and therefore the flux of energy through the vent food web, instead depended substantially on endosymbiotic chemosynthetic bacteria.