Symbioses between Bacteria and Gutless Marine Oligochaetes

Nicole Dubilier, Anna Blazejak, Caroline Rühland

1 Introduction

The first description of a gutless marine oligochaete was published in 1977 (Jamieson 1977), but it was not until 1979 that the reduction of a mouth and gut in this species and several other marine tubificid worms was recognized (Erséus 1979a,b; Giere 1979). At the time, the only other free-living worms known to lack a mouth or gut were pogonophores (now called Frenulata) that were most commonly found buried deep in the reducing sediments of continental slopes. Extensive studies on these very long and thin pogonophore worms indicated that their high surface areas enabled them to gain their nutrition from the uptake of dissolved organic compounds from the environment (Southward and Southward 1980). It was therefore assumed that the gutless oligochaetes that are also quite thin (0.1–0.2 mm) and relatively long (up to 2–3 cm), also gain their nutrition through the diffusive uptake of organic compounds from the sediment pore waters.

The discovery of the giant tube worm, *Riftia pachyptila*, at hydrothermal vents in the late 1970s revolutionized our understanding of the nutrition of gutless marine worms. These worms without a mouth or gut were clearly too thick and the concentration of organic compounds at the vents too low to explain the high biomass of these worms through diffusive uptake of nutrients alone. Indeed, very soon after their discovery Cavanaugh et al. (1981) and Felbeck (1981) showed that *R. pachyptila* lives in symbiosis with chemoautotrophic sulfur-oxidizing bacteria that use reduced sulfur compounds from vent fluids as electron donors to gain energy, and fix CO_2 into organic compounds that are passed on to the worms.

In the wake of the discovery of the *Riftia* symbiosis it became quickly clear that other marine invertebrates with reduced guts could harbor

N. Dubilier (e-mail: ndubilie@mpi-bremen.de), A. Blazejak, C. Rühland
Max-Planck-Institut für Marine Mikrobiologie, Celsiusstr. 1, 28359 Bremen, Germany

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similar symbionts. The reexamination of the morphology of gutless oligochaetes revealed the presence of a thick layer of bacteria just below the cuticle (outer most layer of the body wall) of the worms (Giere 1981; Richards et al. 1982). Enzyme assays and uptake experiments with inorganic carbon indicated that the bacterial symbionts are thiotrophic (i.e., CO_2-fixing sulfur oxidizers) (Felbeck et al. 1983), although we now know that this is only part of the story, as only some of the symbionts in these hosts are sulfur-oxidizing bacteria (see Sect. 12.5 and 12.6).

Since the early 1980s a wealth of morphological and ecophysiological studies by Olav Giere (University of Hamburg, Germany) and taxonomical studies of the hosts by Christer Erséus (University of Göteborg, Sweden) have laid the basis for research on these symbioses with molecular analyses of the symbionts by the authors of this review adding a new dimension since the mid 1990s. In the following, we will describe these molecular investigations in detail but also review earlier studies, to provide a comprehensive understanding of what is known about the symbioses between bacteria and gutless oligochaetes (see also a recent review by Bright and Giere 2005).

2
Biogeography of the Hosts

Gutless oligochaetes are an ideal host group for studying the biogeography and evolution of marine symbioses as they occur throughout the world in a wide range of different habitats with some species widely distributed and others highly endemic (Erséus 1992). They are also one of the few marine groups in which such a large number of host species (>100) are so closely related to each other, forming a monophyletic group with all gutless oligochaetes descendents from a single common ancestor (Nylander et al. 1999).

2.1
Geographic Distribution

The first gutless oligochaetes were found in coral reef sediments in the Pacific (Jamieson 1977), and North Atlantic (Erséus 1979b; Giere 1979), and the highest diversity of oligochaete species is still regularly found in shallow water calcareous sediments (Erséus 1984, 1990). For example, as many as 18 species have been described from sediments around a small island in the Bahamas (Erséus 2003). While tropical and subtropical coral