Quick guides

Giant tubeworms

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What is the giant tubeworm? In 1977, a joint French and U.S. expedition to the Galapagos Rift led to the discovery of hydrothermal vents, geothermally heated waters gushing through cracks and crevices of the basalt in the deep sea. Among the unexpected animal communities found down there was an extremely large polychaete worm, *Riftia pachyptila*. Shortly thereafter, the giant tubeworm was described as the first symbiosis between an animal and sulfur-oxidizing chemoautotrophic (thiotrophic) bacteria.

Why tubeworm? *Riftia* lives in a chitinous tube reaching a length of up to two meters. Most of the soft body is protected, but the crimson plume, the bushy gas exchange organ, extends into the seawater. Whereas most other polychaetes have a digestive system, *Riftia* has reduced its mouth and gut. Instead, it harbours an intracellular bacterial endosymbiont, called *Candidatus* Endoriftia persephone, in high densities in a special organ, the trophosome. These tubeworms form huge aggregations of up to several thousand animals per square metre, providing a large three-dimensional structure for about 60 other animal species to live in (Figure 1). This makes them a so-called foundation species. The symbionts consume toxic sulfide and thereby allow the associated animals to survive in this otherwise poisonous environment.

How can they live without a mouth and gut? The plume takes up all the chemicals the symbionts and the host need. Both oxygen and sulfide bind simultaneously and with high affinity to specialized hemoglobin, which is transported in the blood. This way, toxic sulfide can be transported through the worm without inhibiting aerobic respiration. In the trophosome, the symbionts gain energy through sulfide oxidation used in two different carbon fixation pathways, the Calvin-Benson-Bassham cycle and the reductive tricarboxylic acid cycle (rTCA). Large amounts of fixed carbon are released to the host immediately after fixation. Additionally, the host digests some of the symbionts.

Where do these worms live? *Riftia* thrives in craters of deep-sea volcanoes restricted to the eastern Pacific Ocean. They cluster around hydrothermal vent fluid emerging from the earth's crust in about 2500 m depth. *Riftia* does not colonize every vent, but selects a specific physico-chemical environment for colonization. The tubeworm prefers vent flow with considerable amounts of sulfide and temperatures up to 54°C. The tube sticks to the rocky seafloor and is exposed to a highly fluctuating vent fluid, but the worm's plume extends into more moderate fluids already mixed with cold, oxygenated deep-sea water. Once it settles as a larva, the tubeworm is stuck and its life depends mainly on the persistence of its vent, which typically lasts for less than 10 years. Therefore, fast growth and reproduction appear to be vital in this unstable vent environment, with its frequent volcanic eruptions. Indeed, cell proliferation rates matching those of cancer cells result in growth of 85 cm per year, making *Riftia* the fastest growing invertebrate we know of.

How do the worms 'find' the bacteria? Symbiont transmission takes place anew in each host generation (Figure 1). Males release sperm bundles, which travel in the water to females. Internally fertilized, eggs free of symbionts are released from females. Although researchers have searched intensively, early developmental stages have never been detected in the ocean. Small swimming larvae settle to vents and initiate metamorphosis, during which *Endoriftia* infects the host. Only a few symbionts invade the host skin. They cross several cell layers until they reach the mesodermal tissue surrounding the foregut, analogous to pathogen infections. There, they take up residence in specialised cells, called bacteriocytes, and

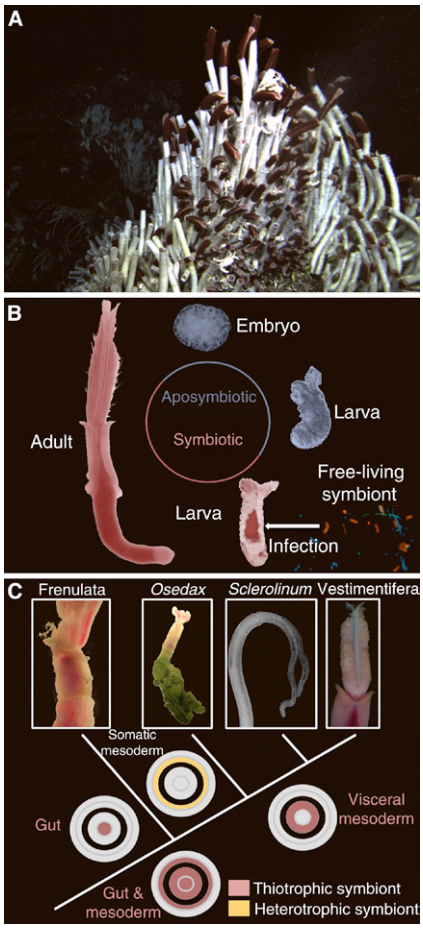

Figure 1. The giant tubeworm *Riftia pachyptila*. (A) Dense aggregation at a hydrothermal vent of the East Pacific Rise. (B) Life cycle with aposymbiotic phase from fertilized egg to settled larva (blue), and symbiotic phase from larva in metamorphosis to adult (red). Infection of *Endoriftia* (red) from a free-living microbial community occurs in the larva. (C) Relationships of siboglinids outlining a hypothetical scenario of evolution of symbiosis in the trophosome originating from several tissues in the last common ancestor with a thiotrophic symbiont (pink) to the gut in frenulates, the visceral mesoderm in vestimentiferans and *Sclerolinum*, and the somatic mesoderm with a heterotrophic symbiont (yellow) in *Osedax*.

proliferation of the trophosome is initiated. Once the individual is infected, apoptosis, a form of programmed cell death, in the host skin prevents further symbiont invasion, so that transmission is only possible during a short time.

How does the worm manage to control the symbiont population? The trophosome is a highly structured, multi-lobed organ. Most of the trophosome consists of bacteriocytes, which follow a cell

cycle with terminal differentiation. A unipotent host cell population acts as stem cells, which proliferate and migrate from the center of each lobule to the periphery, cease division, and die through apoptosis. During this journey they carry along their symbionts, which divide in the center, stop dividing, and subsequently become digested in the periphery. Digestion thus serves both in host nourishment and the control of the symbiont population density.

What do we know about the symbionts? The *Endoriftia* 16S rRNA phylotype was detected in the environment, both on surfaces and in the water. Its metagenome shows the presence of genes for the oxidative TCA cycle indicating the ability to live as heterotrophs outside the host. Genes for chemotaxis suggest that *Endoriftia* actively seeks the prospective host. This points to a highly versatile bacterium capable of surviving in the biofilms of hydrothermal vents and adjacent deep sea as well as thriving under host control as endosymbionts.

How do vent and seep tubeworms differ? Some tubeworms, such as *Riftia*, inhabit hydrothermal vents, while other species live on whale bones or at seeps, deposits of oil and gas leaking through sediments to the sea floor. Vents are highly disturbed, short-lived ecosystems, while seeps may persist for ten thousands of years. Consistent with the temporal dynamics of these contrasting ecosystems, *Riftia* grows fast and is short-lived, whereas *Lamellibrachia luymesi* from the seeps of the Gulf of Mexico grows slowly and is — with estimated ages of up to 300 years — among the longest lived of any of the non-colonial invertebrates. Although carbon fixation rates of *Riftia* exceed those of *Lamellibrachia*, both symbionts are highly active and support similar, high cell proliferation rates. However, apoptosis rates are low in *Riftia*, but in *Lamellibrachia* match those of proliferation. Thus *Riftia* grows fast, whereas *Lamellibrachia* grows slowly and consistently renews its tissue, supporting longevity.

Who are the tubeworms' relatives? Vestimentiferan tubeworms belong to the small polychaete family Siboglinidae (Figure 1). Unlike other polychaetes, siboglinids share an obligate symbiotic life style in chemosynthesis-based ecosystems, such as vents, seeps, and whale bones. The thiotrophic symbiosis probably evolved once rather than several times independently. This is supported by the position of the trophosomes at the exact same location in the first segment of the different worms. The remarkable differences of trophosome origins, however, suggest that the last common ancestor harbored symbionts in several tissues. Consequently, in frenulates, the trophosome became restricted to the gut, in *Osedax* to the somatic mesoderm, and in vestimentiferans and its sister *Sclerolinum* to the visceral mesoderm. Horizontal transmission not only ensures continuation of symbiosis, it also allows for the uptake of appropriate symbionts, which can be selected in each generation anew. Most remarkably, *Osedax*, which colonizes whale bones, must have replaced its thiotrophic symbiont with heterotrophic Oceanospirillales nourished by the host.

Where can I find out more?

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Polo-like kinases

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What is Polo and what are Plks? Plk stands for Polo-like kinase. In the 1980s, genetic screens in budding yeast and *Drosophila* identified several key regulators of mitosis, including the founding member of the Polo kinase family. Since then, a total of five mammalian paralogs of the *Drosophila Polo* gene have been discovered. These exhibit largely non-redundant functions and are differently expressed, localized, and regulated. The *Polo* homolog *Plk1* is common to all eukaryotes, apart from plants and certain protozoan parasites. *Plk4* is also present in most vertebrates and invertebrates and probably arose early on, in a first round of gene duplication. The evolutionarily 'younger' *Plk2* sub-family is only found in some bilaterian animals and comprises two genuine kinases, *Plk2* and *Plk3*, as well as the kinase-deficient *Plk5*.

Is Plk1 the leader of the pack? Plk1 is a wizard of both mitosis and meiosis (M phase of the cell cycle). It is expressed in proliferating cells and regulates many aspects of M-phase progression — notably mitotic entry, spindle architecture and positioning, sister-chromatid separation, and cytokinesis. Hence, inactivation of Plk1 in cultured cells leads to cell-cycle arrest in early mitosis, followed by apoptosis. In addition, Plk1 is also involved in key processes, such as release of amphibian eggs from cell-cycle arrest upon fertilization, recovery of mammalian cells from DNA damage, and RNA polymerase III-dependent transcription. At this point in time, it seems fair to state that Plk1 is top dog of the family. But Plk4, another key regulator of cell division (see below), is increasingly challenging Plk1's leadership position. In contrast, the roles of the younger Plk2 family members still remain sketchy.

How does Plk1 manage all these different functions? The answer lies in the structure. Plk1, like all other family members, has a topology with two conserved domains: an amino-terminal serine/threonine kinase