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## Anaerobic sulfur oxidation underlies adaptation of a chemosynthetic symbiont to oxic-anoxic interfaces

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### Abstract:

Chemosynthetic symbioses occur worldwide in marine habitats, but comprehensive physiological studies of chemoautotrophic bacteria thriving on animals are scarce. Stilbonematinae are coated by monocultures of thiotrophic Gammaproteobacteria. As these nematodes migrate through the redox zone, their ectosymbionts experience varying oxygen concentrations. However, nothing is known about how these variations affect their physiology or metabolism. Here, by applying omics, Raman microspectroscopy and stable isotope labelling, we investigated the effect of oxygen on *Candidatus Thiosymbion oneisti*. Unexpectedly, sulfur oxidation genes were upregulated in anoxic relative to oxic conditions, but carbon fixation genes and incorporation of <sup>13</sup>C-labeled bicarbonate were not. Instead, several genes involved in carbon fixation were upregulated in oxic conditions, together with genes involved in organic carbon assimilation, polyhydroxyalkanoate (PHA) biosynthesis, nitrogen fixation and urea utilization. Furthermore, in the presence of oxygen, stress-related genes were upregulated together with vitamin biosynthesis genes likely necessary to withstand its deleterious effects, and the symbiont appeared to proliferate less. Based on its physiological response to oxygen, we propose that *Ca. T. oneisti* may exploit anaerobic sulfur oxidation coupled to denitrification to proliferate in anoxic sand. However, the ectosymbiont would still profit from the oxygen available in superficial sand, as the 69 energy-efficient aerobic respiration would facilitate carbon and nitrogen assimilation by the ectosymbiont.

Keywords: ectosymbionts, oxygen, anaerobic sulfur oxidation, anoxic, carbon fixation genes, *Candidatus Thiosymbion oneisti*