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## A trend in evolution from extra- to intracellular symbiosis in whale-fall mussels

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Deep-sea mussels harboring chemoautotrophic symbionts from hydrothermal vents and seeps are assumed to have evolved from shallow-water asymbiotic relatives by way of biogenic reducing environments such as wood and whale falls. Such symbioses have been well characterized in mussels from vents, seeps, and sunken wood but in only a few from whale falls.

Here we report symbioses in the gill tissues of two whale-fall mussels, *Adipicola crypta* and *Adipicola pacifica*, collected at shelf depths in the northwestern Pacific. The bacterial symbionts were characterized by molecular, morphological, and stable isotopic analyses. Electron microscopic observations showed that the symbionts were located on the apical surfaces of epithelial cells of the gills intracellularly in *A. crypta* and extracellularly in *A. pacifica*. Stable isotopic analyses of carbon and sulfur indicated the chemoautotrophic nature of *A. crypta* and mixotrophic nature of *A. pacifica*. Molecular phylogenetic analyses of the host mussels showed that *A. crypta* constituted a monophyletic clade with other intracellular symbiotic (endosymbiotic) mussels and that *A. pacifica* was the sister group of all endosymbiotic mussels so far reported. These results strongly suggest that the symbiosis in *A. pacifica* is at a more primordial stage in evolution than that of other endosymbiotic mussels. Whale falls may have been acting as refugia for primal chemoautotrophic symbioses between eukaryotes and prokaryotes since the extinction of ancient large marine vertebrates.

**Keywords:** Whale-fall ecosystem, *Adipicola*, Chemosynthetic symbiosis, Evolution, Extracellular symbiosis, Stable isotopic ratio