The origin of scaly-foot gastropod's scale and iron sulfide nanoparticles inside

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Animals produce hard tissues for skeletal support, protection, and feeding, and inorganic minerals are often utilized as a component. The biologically produced minerals are usually oxygen-containing such as carbonates and phosphates, and other group-16 elements such as sulfur are usually absent in the biominerals. Scaly-foot gastropods (*Chrysomallon squamiferum*), possessing scales on their soft body found in hydrothermal vents on the Cehtral Indian Ridge, Indian Ocean, is a rare exception among animals besides bacteria, and possesses iron sulfide particles such as pyrite ang greigite in their scales only when the vent fluid is rich in iron. The mechanisms of iron sulfide mineralization within the scales of scaly-foot gastropods has been ambiguous for 18 years from their discovery. Here we revealed the mechanisms of iron sulfide mineralization from three viewpoints; origin of sulfur by nanoscale isotopic microanalyses, three-dimensional nanoscopic alignment and elemental distribution by electron microscopy, and pathways of iron incorporation by translocation of dead scaly-foot scales between two vents.
The isotopic analyses revealed that the sulfur isotope ratio ($^{34}S/^{32}S$) in pyrite particles were −9.6 ±0.1‰, which was considerably lower than that of sulfide vent minerals, vent fluids, and soft part of another vent mussel (4.4–7.5‰, 6.8–7.0‰, 3.4–5.6‰, respectively). This clearly shows that the sulfur is of biological origin, and implies several biological processes involved in the sulfur transport to the sulfide minerals in the scales.
Electron microscopic investigation revealed that the sulfide minerals were in columnar alignment along with the longitudinal axis of the scale, and sulfur-rich domains lacking iron were also found. In addition, the cross-sectional lamellar from frozen scales without sulfide minerals revealed the existence of channel-like pores in which fluids can pass through. These results support the sulfur supply to the scales through body fluid.
The iron transport mechanisms is investigated by translocating dead scaly-foot's scales without iron sulfide minerals in the habitat of iron sulfide-bearing scaly foot. The scales collected after 13 days of incubation contained iron only near the surface, indicating the iron diffusion toward inside of the scales.
In conclusion, we have revealed the iron sulfide mineralizaton mechanisms as follows: sulfur-transporting columns are created within scales, and into which sulfur species are supplied through the body fluid. Iron ions are diffused into the scales from the surrounding seawater, and mineralization takes place within the scales. This hybrid mechanism in which only one of the mineral component is spontaneously supplied by an animal is a novel form of biomineralization. In addition, scaly-foot snails may utilize the sulfur transportation mechanisms to discard sulfur waste produced by endosymbionts to adapt to the extreme environment of hydrothermal vent.

Keywords: Chrysomallon squamiferum, Biomineralization, Pyrite nanoparticles, FIB/SEM tomography, Nano-SIMS

