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Chloroplast harvesting by a miliolid expands the evolutionary range of kleptoplasty in foraminifera

Doron Pinko¹, Sigal Abramovich¹, Eyal Rahav², Belkin Natasha², Maxim Rubin Blum², Maria Holzmann³, and Uri Abdu⁴

¹Department of Earth and Environmental Science, Ben-Gurion University of the Negev, Beer Sheva, Israel

²National Institute of Oceanography, Israel Oceanographic and Limnological Research, Haifa, Israel

³Department of Genetics and Evolution, University of Geneva, Quai Ernest Ansermet 30, 1211 Geneva 4, Switzerland

⁴Department of Life Science, Ben-Gurion University of the Negev, Beer Sheva, Israel

Foraminifera are highly abundant marine unicellular eukaryotes. They are known for their important ecological role in most marine ecosystems, their major contribution to the carbon cycle, and their remarkable physiological plasticity. Many foraminiferal species have mixotrophic metabolism that is often based on partnerships with diverse algae, or in some cases, on harvesting diatom chloroplasts, known as kleptoplasty. To date, kleptoplasty was shown only in rotaliid lineages. Here, we report the first discovery of a diatom kleptoplasty in the *Hauerina diversa*, a tropical shallow-water miliolid that is an unexpected candidate for this life strategy. To elucidate this adaptation, we collected *H. diversa* specimens from the southeastern Mediterranean coast and visualized many intact chloroplasts in clustered structures within the foraminiferal cytoplasm using transmission electron microscopy. Preliminary genetic analyses confirmed that the harvested chloroplasts originated from diatoms. Primary production estimates using isotopically labeled $\text{NaH}^{14}\text{CO}_3$ as a carbon source suggest photosynthetic activity of the 'stolen' chloroplasts inside the host cell. This activity was found to be about two orders lower compared to the diatom-bearing species *Amphistegina lobifera*. We finally provide the first molecular phylogeny of *H. diversa* and its evolutionary relationship to ancient alveolind foraminifera. We thus demonstrate the first case of kleptoplasty in the ancient group of alveolind-miliolids, expanding the evolutionary range of kleptoplasty in foraminifera