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Photosymbiosis on a Mid-Devonian Reef: Evidence from Coral-Bound Nitrogen Isotopes

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Scleractinian corals are believed to owe much of their ecological success in low-nutrient, low-productivity tropical surface waters to a symbiotic network of diverse reef organisms. Most prominently, the endosymbiotic relationship with single-celled photosynthetic dinoflagellates of the family Symbiodiniacea generates an internal cycle of nutrients (in particular, nitrogen and phosphorus) that yields an additional source of organic carbon to the host. While molecular dating indicates that Symbiodiniacea originated during the Eocene cooling period (~50 Ma) and diversified during the mid-Miocene (~15 Ma), geochemical analyses of coral-bound nitrogen isotopes (expressed as: CB-$\delta^{15}N = [(^{15}N/^{14}N)_{sample} / (^{15}N/^{14}N)_{air} - 1]*1000$ in ‰) have traced some form of photosymbiosis in scleractinian corals to the Late Triassic. However, in the case of Palaeozoic reef environments, there is no clear consensus as to whether photosymbiosis was prevalent in extinct coral groups, such as tabulate or rugose corals. Here, we present the first analyses of nitrogen isotopes of coral-bound organic matter of samples from a mid-Devonian reef (Givetian, ca. 385 Ma) in the northern Rhenish Massif (north-western Sauerland), Germany. We analysed tabulate (auloporid) corals, colonial (loosely dendroid to phaceloid morphotypes) and solitary rugose corals, as well as surrounding sediment matrix and sparite. Diagenetic effects were evaluated based on laboratory experiments and independent thermal alteration proxies (e.g., Conodont alteration index). Our analyses reveal that tabulate and loosely colonial rugose corals have relatively low CB-$\delta^{15}N$ (1.85‰ and 1.45‰, respectively). This finding by itself might be interpreted as either evidence of a photosymbiotic association or the result of low baseline $\delta^{15}N$ for the Devonian reef ecosystem. However, we also find that CB-$\delta^{15}N$ of solitary rugose corals was on average >3‰ higher (4.62‰), indicating a trophic offset. Taken together, the CB-$\delta^{15}N$ measurements suggest that the herein studied tabulate and loosely colonial rugose corals had an active photosymbiosis, whereas the solitary rugose corals did not. In accordance with earlier suggestions based on coral morphology, our geochemical data provide evidence that coral photosymbiosis was already prevalent in the Palaeozoic and point to a new strategy for investigating the changing relationship between carbon and nutrient cycles over the Phanerozoic Eon.