Phylogenetic radiation of chemosymbiotic vesicomyids: trends, adaptations, timing

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Clams of the subfamily Pliocardiinae (Bivalvia; Vesicomyidae) are noticeable members of chemosynthetic communities distributed worldwide from sublittoral to hadal zones. All studied pliocardiins contain in their gills symbiotic, intracellular, sulphur-oxidizing gammaproteobacteria that provide most of the clams' nutrition. With 20 currently recognizable Recent and fossil genera, pliocardiins are the most diverse group of bivalves occupying deep-sea reducing environments. In contrast to other chemosymbiotic bivalves, the number of pliocardiin genera co-inhabiting the same site can be as great as 5-6. Given the high degree of specialization to bacterial symbiotrophy, questions emerge about factors that might trigger such diversification, including morpho-anatomical adaptations and the evolutionary age of pliocardiin radiations. Our fossil-calibrated molecular phylogeny based on 6 genes supports the hypothesis that pliocardiins may split from deep-dwelling predecessors during the Late Cretaceous to the early Cenozoic. Since the middle Eocene, pliocardiins radiated into a variety of major clades that diversified further mostly during the late Oligocene to mid-Miocene. The youngest radiation in the subfamily was in the late Miocene to early Pleistocene. The main trigger for initial diversification probably resulted from the incorporation of bacteria that allowed the clams to exploit sulphide-rich deep-sea hydrocarbon seeps. Subsequent radiations might have been linked to morpho-physiological adaptations that facilitated the partly infaunal behavior of clams. Adaptations of pliocardiin genera to exploit the narrow and diverse ecological niches associated with the redox-gradients found in seep and vent environments and colonization of different depths are discussed.