The paradox of "clam shrimp" paleoecology

Olsen, P. E.[1]

[1]LDEO of Columbia University, Palisades, NY, 10968 USA. polsen@ldeo.columbia.edu

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Clam shrimp are small (~1 – 10 mm) bivalved crustaceans traditionally placed in the paraphyletic Conchostraca [1], now divided into the diverse Spinocaudata, the much less diverse Laevicaudata, and the low diversity and small but widespread Cyclestherida [2]. The have a hinged carapace composed of a multi-laminar chitin composite variously hardened with calcium phosphate [3] and/or calcite. Today, all but the Cyclestherida are apparently restricted to temporary bodies of fresh to low salinity water - basically playas, pans, and puddles - lacking predatory fish [1,4], with the latter generally assumed to be what excludes them from permanent waters. With considerable taxonomic diversity, clam shrimp are by far the most abundant larger fresh water crustaceans found in Late Paleozoic, Mesozoic, and Early Cenozoic lacustrine deposits [5], and nearly all palaeontologists and geologists have used their present adaptive zone as *the* key to their past sedimentary environments. However, fossil clam shrimp commonly co-occur with fossil fish and often in lithologies, such as microlaminated, articulated-fish-bearing mudstones, that otherwise would be interpreted as not just perennial lakes, but giant perennial lakes, such as the Middle Devonian Caithness Flagstones of Scotland [6], the Late Triassic Lockatong Formation of eastern North America [7], the Jehol Group of China [8], and the Eocene Green River Formation [9], to cite several iconic exemplars. In fact, clam shrimp are frequently found in fish coprolites [10], and therefore they *persisted* despite predation. Based on the fossil record, clam shrimp were *the* dominant zooplankton in pre-Neogene lakes, and this glaring conflict with their present adaptive zone presents the paradox of their paleoecology. Very few (e.g., Hethke [11]) have accepted the overwhelming evidence from ancient environments and concluded that some clam shrimp lived in permanent waters. This "paradox of clam shrimp paleoecology" presents the difficult biological question, "why did their adaptive zone change if the clam shrimp did not?". Plausibly, the vast narrowing of the clam shrimp adaptive zone is related to the late Paleogene-Neogene revolutionary rise of diatom dominance [12,13] among lacustrine phytoplankton. There is a tight temporal linkage of the two trends, both of which are independent of the timing of the establishment of clades of modern predators such as diverse teleost fishes, which become common in lakes much earlier. A potentially testable hypothesis is that the filter-feeding clam shrimp might consistently lose under predator-mediated competition with filter-feeding Cladocera (their smaller sister group), given the late Paleogene replacement of previously dominant less refractory phytoplankton by diatoms.Regardless, of the proximal cause of their present exclusion from permanent waters, clam shrimp were major perennial lake zooplankters for two-thirds of the Phanerozoic (at least ~360 M.y.). Their present is not the key to their past.

This is a contribution to UNESCO-IUGS IGCP Project 632.

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