

The World's First Clam Shrimp Symposium: Drawing Paleontology and Biology Together

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After a symposium and special issue devoted to the study of clam shrimp, it is tempting to ask what is next... where is the study of clam shrimp going? Rather than try to read the tea leaves to predict the future, we will instead offer some closing thoughts on where the study of clam shrimp should go and what areas are ripe for investigation. Many of these ideas integrate both fossil and modern clam shrimp to get at a more complete view of their evolution and ecology.

Phylogeny and Evolutionary History

The holy grail of phylogenetic studies is the integration of fossil and modern taxa so that the timing of divergences and rate of evolutionary radiations can be determined. We are only just beginning this task. However, we are held back by the problems in discerning crown group versus stem group clam shrimp in the fossil record (Hegna and Astrop 2020). Molecular phylogenies only give us the crown group divergences, because fossils cannot provide the DNA to be included in such an analysis. Spinicaudata could be phylogenetically defined as the last common ancestor of *Cyzicus gynecius* (Mattox, 1950) and *Eulimnadia texana* (Packard, 1871) and all of its descendants (following the phylogeny of Schwentner et al. 2020). Certainly, not all fossil clam shrimp with growth lines lie within the phylogenetically-defined Spinicaudata—some must lie outside of that group on its stem (as discussed in Hegna and Astrop 2020). Thus, paleontologists must be careful to not uncritically assign their fossils to the crown group Spinicaudata, lest some data-mining phylogeneticist use it to erroneously date the origin of the Spinicaudata.

Morphological phylogenies remain important, and should be pursued. They remain our only hope for integrating fossils into sound phylogenetic hypotheses.

Thus far, they have not progressed to the same degree as molecular phylogenies (but see Weeks et al. 2009)—more characters are needed (see below). This has become abundantly clear as molecular phylogenetics has upended the validity of traditionally used genera and the characters used to justify them (Schwentner et al. 2020). It may be, particularly for fossils, that we will never pull enough morphological characters from the preserved morphology to develop a fully independent morphological phylogenetic tree.

Likewise, clam shrimp biodiversity through time has been sadly neglected (but see Astrop 2014). The paleobiodiversity of clam shrimp needs to be systematically cataloged into a comprehensive global taxonomic database with a standardized taxonomy (informed by advances in the extant taxa) in order to understand their evolutionary dynamics. This is a monumental task, but one that could be made easier with platforms like the Paleobiology Database (paleobiobd.org). Doing so could help illuminate the apparent radical paucity of clam shrimp from the Cenozoic. But, it must be kept in mind that paleontological clam shrimp taxa may likely be very different entities than modern clam shrimp taxa. Fossil clam shrimp never preserve the same level of detail visible in modern specimens. Furthermore, when differentiating based on carapace

shape and ornamentation patterns, sexual dimorphism can easily be mistaken for species differentiation (see Astrop et al. 2012 2020). This is a part of a more general problem—that the criteria for recognizing taxa has real and frustrating limitations in the fossil forms. Biology has shown us that clam shrimp carapace morphology is not as informative as we would like (Rogers et al. 2012), and that many species are only discernable by egg morphology, telson morphology, or even genetics.

Therefore, it is very likely that within the fossil clam shrimp we have at the same time two opposite, yet equal problems informed by the extant taxa. One is that there is very probably an *overestimation* of taxonomic diversity, in that carapace morphology is extremely variable due to nutrient quality of food, epibiont erosion, water chemistry (Rogers et al. 2012), and gender (Astrop et al. 2012 2020) within extant families, genera and species. The second problem is that there is likely just as great an *underestimation* of taxonomic diversity, in that multiple taxa with identical carapace morphology can co-occur in the same region, area, and even pool. These two equal, yet opposite problems confound our abilities to marry the fossil record with the modern record with real confidence.

Morphology

It is important to note that clam shrimp science is only just emerging from the descriptive phase into a new era where we have sufficient observations to start generating real hypotheses testable by modern methods. However, that does not mean we abandon descriptive and observational treatments in these animals. Instead, we need to increase our standards of illustration. SEM technology should be integrated into every taxonomic paper. The more illustrations there are, the more potential characters they will reveal. Both fossil and modern taxonomic studies should illustrate the carapace ornamentation, to test the validity of the hypothesis that ornamentation can be used to unite fossil and modern taxonomic systems (Konstans et al. 2019, Li and Teng 2019). A basic documentation of carapace ornamentation patterns may eventually allow us to construct a scenario for the evolution and differentiation of carapace ornamentation patterns (*i.e.*, Wang 1989). However, if ornamentation is to become a key characteristic in extant clam shrimp taxonomy, as it already is in fossil taxonomy, we must develop a better understanding of how the carapace grows and how the ornamentation patterns are initiated and how they develop. It is vital that we delve deeper into the morphology, and test which morphological characters are actually useful in describing phylogenetic patterns, especially in concert with molecular studies.

Paleo / Ecology and Population Dynamics

The ecology of fossil clam shrimp has been interpreted in light of what we know of modern clam shrimp (Frank 1988)—with the present illuminating the past. However, there are strong reasons for thinking that may not be the entire story. Work by Hethke (2014) and others strongly suggests that clam shrimp of the Paleozoic and Mesozoic occupied a different niche than those alive today—that of permanent freshwater habitats rather than ephemeral freshwater bodies. The paradox referred to in Olsen's (2016) abstract title is that though the adaptive zone of clam shrimp seems to have changed, their morphology apparently did not change. This idea is a provocative idea and may be a driver behind the dynamics of clam shrimp diversity through time.

Many systematic studies are guilty of using one specimen as an exemplar of an entire population or species. We need to appreciate and document the morphological diversity within populations and species. Doing so in modern situations will help us to better constrain what is a reasonable amount of variation to observe in a fossil species, perhaps correcting some of the radical species splitting that has occurred throughout our history.

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